

Returning to the roots: morphology, molecular phylogeny and classification of the Olivoidea (Gastropoda: Neogastropoda)

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The superfamily Olivoidea is broadly distributed in the world's oceans mostly in coastal waters at tropical and subtropical latitudes. It encompasses around 30 Recent genera and 460 species. Two families – Olividae and Olivellidae – are classically recognized within the superfamily. Their shell is very characteristic due to the presence of a modified callused anterior end and a fasciole. Prior to the present work, neither the monophyly of the superfamily nor the relationships among its genera had been tested with molecular phylogenetics. Four genetic markers [cytochrome *c* oxidase subunit I (*COI*), 16S and 12S rRNA mitochondrial genes, and Histone 3 (*H3*) nuclear gene] were sequenced for 42 species in 14 genera. Additionally, 18 species were sequenced for *COI* only. The molecular dataset was supplemented by anatomical and radula data. Our analysis recovered, albeit with weak support, a monophyletic Olivoidea, which in turn includes with 100% support, in addition to traditional olivoideans, representatives of a paraphyletic Pseudolividae. The relationships between the former families and subfamilies are drastically revised and a new classification of the superfamily is here proposed, now including five families: **Bellolividae fam. nov.**, **Benthobiidae fam. nov.**, Olividae, Pseudolividae and Ancillariidae. Within Olividae four subfamilies are recognized, reflecting the high morphological disparity within the family: Olivinae, Olivellinae, Agaroniinae and **Calyptolivinae subfam. nov.** All the recent genera are discussed and reclassified based on molecular phylogeny and/or morphology and anatomy. The homology of different features of the shells is established for the first time throughout the superfamily, and a refined terminology is proposed. Based on a correlation between anatomical characteristics and shell features and observations of live animals, we make hypotheses on which part of the mantle is responsible for depositing which callused feature of the shell. Our results demonstrate that morphological data alone should be used with caution for phylogenetic reconstructions. For instance, the radula – that is otherwise considered to be of fundamental importance in the taxonomy of Neogastropoda – is extremely variable within the single family Olividae, with a range of variation larger than within the rest of the entire superfamily. In the refined classification, Pseudolividae are nested within Olivoidea, which is partially returning to 'the roots', that is to the classification of Thiele (1929).

ADDITIONAL KEYWORDS: Ancillariidae – Bellolividae – Benthobiidae – callus – digestive system – mantle anatomy – Olividae – Pseudolividae – radula

INTRODUCTION

The evolutionary history of the predatory/scavenging Neogastropoda is a classic example of a successful,

post-Cretaceous radiation of marine snails. They are the most prolific group of marine predatory gastropods, including no less than 12 000 species (WoRMS, 2016). At present Neogastropoda are classified in 40 Recent families (most represented in the fossil record) and seven exclusively fossil families (Bouchet & Rocroi, 2005; with updates). Their phylogeny is far from resolved despite several attempts including the use of molecular characters

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(e.g. Cunha *et al.*, 2009; Oliverio & Modica, 2010; Zou, Li & Kong, 2011; Osca *et al.*, 2015). Nevertheless, significant progress has recently been achieved for individual neogastropod groups, and this has allowed the construction of robust, molecular-based phylogenies of selected clades at different ranks, from superfamilies (Conoidea – Puillandre *et al.*, 2011) to families (e.g. Muricidae – Barco *et al.*, 2010; Belomitridae – Kantor *et al.*, 2012) and for non-monophyletic groups ('mitriform' neogastropods – Fedosov *et al.*, 2015). Two new neogastropod families have already been established as a result of molecular studies combined with morphological and anatomical data: the above-mentioned Belomitridae – Kantor, Puillandre, Rivasseau & Bouchet, 2012 and Bouchetispiridae – Kantor, Strong & Puillandre, 2012 (Kantor *et al.*, 2012). The family Pyramitridae (Cossmann, 1901), 'lost' in synonymy, was resurrected as valid and its position clarified (Kantor *et al.*, 2014; Fedosov *et al.*, 2015). It should be stressed that in none of these cases were morphological data sufficient for clarifying taxonomic position and relationships. One of the reasons is that neogastropods are characterized by both high shell character homoplasy and relative 'uniformity' of anatomical characters traditionally used in systematics. Correspondingly, the transfer of genera from one family to another is a frequent occurrence. For instance, the mitriform genera *Latiromitra* Locard, 1897, *Ceratoxancus* Kuroda, 1952, and *Exilioidea* Grant & Gale, 1931, previously classified in the family Ptychactatridae on the basis of morphological characters (Kantor & Bouchet, 1997; Bouchet & Kantor, 2000), were transferred respectively to the families Costellariidae (*Latiromitra*, *Ceratoxancus*) and Volutomitridae (*Exilioidea*) on the basis of a multilocus molecular phylogeny (Fedosov *et al.*, 2015).

By contrast, gastropods of the superfamily Olivoidea Latreille, 1825 (*sensu* Bouchet & Rocroi, 2005) – the 'olive shells', or olivoideans – is one of the most easily recognizable groups of tropical and subtropical Neogastropoda, encompassing around 30 Recent genera and 460 accepted Recent species (WoRMS, 2016). Olivoidea mostly live on soft bottoms from the intertidal to the bathyal, to depths of 1855 m (*'Amalda' sibuetae* Kantor & Bouchet, 1999). Olivoidea are most speciose in the tropical realm, with few species penetrating mid latitude waters. Both planktotrophic and lecithotrophic larval development strategies are known in the superfamily.

The peculiar bullet-shaped glossy and smooth shell, together with the characteristic head-foot morphology (broad crescent-shaped propodium and parapodia, laterally embracing the shell), allow for the unambiguous allocation of most species to Olivoidea. Cases where a species from a different family was mistakenly described as an olive, or vice versa, are rare but exist, for example *Plicoliva* Petuch, 1979, originally

established as a subgenus of *Oliva*, was later reallocated to Volutidae (Petuch & Sargent, 1986; Bouchet, 1990). Remarkably, no olivid has ever been described in another family of Neogastropoda.

Despite their distinctiveness, Olivoidea have had a rather complicated taxonomic history. The contents and taxonomic structure of the superfamily have been subjected to numerous alterations, sometimes rather profound. According to Bouchet & Rocroi (2005) seven available family group names have been proposed within olivoideans (in chronological order): Olividae proper; Ancillariinae Swainson, 1840 (= Ancillinae H. & A. Adams, 1853, raised to family rank by Iredale & McMichael, 1962); Olivellinae Troschel, 1869 (raised to family rank by Golikov & Starobogatov, 1989); Agaroniinae Olsson, 1956; Olivancillariidae Golikov & Starobogatov, 1975; and the exclusively fossil Vanpalmeriidae Agedoke, 1977. [The family name Dactylidae H. & A. Adams, 1853, is invalid albeit available (International code of zoological nomenclature, Art. 10.6) since it was based on the genus *Dactylus* H. & A. Adams, 1853, a junior homonym of *Dactylus* Schumacher, 1817 (Gastropoda: Acteonidae)].

Olivoidea was first ranked as a superfamily by Golikov & Starobogatov (1975), who included Harpidae. The same authors later (Golikov & Starobogatov, 1989) erected a separate suborder Olivelloidei for Olivellidae, but did not discuss neither the taxonomic position and rank, nor the scope of other groups of Olivoidea, and these cannot be deduced from their publication. Neither Olivancillariidae nor Olivelloidei were considered as valid taxa by subsequent authors.

One more taxon sometimes associated with Olividae is Pseudolivinae de Gregorio, 1880 (raised to family by Delpy, 1941; = Zemiridae Iredale, 1916), which has had a complicated taxonomic history. This small group includes 9 Recent genera and slightly more than 20 species (WoRMS, 2016). Pseudolivinae was initially established as a subfamily of Buccinidae following the earlier opinion of Sowerby (1846) who believed that *Pseudoliva* Swainson, 1840 and Buccinidae were closely related. This viewpoint was accepted by a number of authors [for a detailed account of the history of Pseudolividae, see Vermeij (1998)] and it was treated either as a subfamily of Buccinidae (e.g. Cossmann, 1901) or as a separate family, but still closely related to Buccinidae (e.g. Golikov & Starobogatov, 1975). In fact, when establishing *Pseudoliva*, Swainson (1840) had already suggested affinities between his new genus and some olivids. This opinion was followed by many authors, including Thiele (1929), Wenz (1943 [in 1938–1944]), Ponder and Darragh (1975), Ponder and Warén (1988) and Kilburn (1989), and pseudolivids were treated by them as a subfamily of Olividae. The position of Pseudolividae was re-assessed by Kantor (1991), who erected a new monotypical suborder Pseudolivelloidei based on morphological

and anatomical data. Although this was not followed in subsequent publications, Pseudolividae together with Ptychactridae Stimpson, 1865 was placed in the superfamily Pseudolivoidea in the latest working classification of Gastropoda (Bouchet & Rocroi, 2005).

Besides the controversial position of Pseudolivinae (-idae), the placement in Olivoidea of the remaining groups has never been questioned. The state of the art was reflected in Bouchet & Rocroi (2005), who attributed two families to Olivoidea – Olivellidae and Olividae (with the subfamilies Olivinae, Ancillariinae and †Vanpalmeriinae, the latter including the single species *Vanpalmeria africana* Agedoke, 1977 from the Palaeocene of Nigeria).

Olivoidea remain relatively poorly studied anatomically. Leaving aside radula descriptions, publications dealing with their anatomy include descriptions of several species of *Oliva*, two species of *Olivancillaria*, two *Amalda*, two *Olivella* and several *Bellovia* (Küttler, 1913; Marcus & Marcus, 1959, 1968; Kantor, 1991; Kantor & Tursch, 2001a; Kantor & Bouchet, 2007). Even these rather fragmentary anatomical data demonstrate significant morphological and anatomical disparity within the group.

With regard to the anatomy of Pseudolividae, data are available on *Zemira* H. Adams & A. Adams, 1853, two *Pseudoliva*, two *Melapium*, one *Luizia* and several *Benthobia* (Ponder & Darragh, 1975; Kantor, 1991; Simone, 2003, 2007).

The feeding habits of Olivoidea are substantiated by some unique morphological and physiological adaptations and have attracted the attention of biologists. The large species (different species of *Oliva* and *Agaronia*) are predators and scavengers, preying on a wide range of invertebrates: polychaetes, crustaceans, bivalves, gastropods (Tursch & Greifeneder, 2001), sea cucumbers and echinoids (Taylor & Glover, 2000). Prey is located and seized by the large crescent-shaped propodium and rapidly transferred into a pouch formed by the folding of the posterior part of the metapodium (Kantor & Tursch, 2001b). At least partial digestion occurs inside the pouch and proteolytic ferments are produced by the epithelium of the sole (Kantor & Tursch, 2001b). Similar observations have been made for *Agaronia propatula* (Conrad, 1849) (Rupert & Peters, 2011; Cyrus *et al.*, 2012), and several short videos of *Agaronia* hunting its prey *Olivella semistriata* (Gray, 1839) can be accessed online as supplementary data to the above-mentioned publications (doi: 10.1093/mollus/eyr019 and 10.1093/mollus/eyr006 correspondingly). *Agaronia* is able to autotomize the posterior metapodium probably as a defence mechanism, but is not able to feed until the foot is totally regenerated.

For small olivoideans, limited data are available only for *Olivella*, which demonstrate a great disparity of

both feeding behaviour and diet. For example, *Olivella minuta* (Link, 1807) feeds on the bivalve *Donax hanleyanus* Philippi, 1847, foraminiferans, different crustaceans, and even scaphopods (Marcus & Marcus, 1959, as *Olivella verreauxii*). In the subgenus *Olivella* (*Pachyoliva*) – which includes the two species *O. columellaris* (Sowerby, 1825) and *O. semistriata* – the snails use their foot appendages to deploy mucus nets between the large propodial and small metapodial appendages for suspension feeding in the backwash of sandy beaches (Troost *et al.*, 2012). *Olivella biplicata* (Sowerby, 1825) feeds on Foraminifera (Hickman & Lipps, 1983).

Until now there has been no molecular phylogeny of Olivoidea, with sequences for only ten species in GenBank (three *Olivella*, four *Oliva*, one each of *Pseudoliva*, *Amalda* and *Bellovia*) and the taxonomy and relationships within the group are based on morphological data. The aim of the present work is to construct a robust molecular phylogeny of Olivoidea, review published data on the morphology and anatomy of the group and present original data, and revise the current classification on the basis of molecular and morphological data.

MATERIAL AND METHODS

TAXON SAMPLING

Material included in this paper was collected during several biodiversity surveys organized mainly by the Muséum National d'Histoire Naturelle (MNHN), Pro-Natura International, and the Institut de Recherche pour le Développement, as part of the *Our Planet Reviewed* and *Tropical Deep-Sea Benthos* programmes (see Bouchet *et al.*, 2008 and the BasExp database at <http://expeditions.mnhn.fr/>). In the field, living specimens were anaesthetized with MgCl₂ or removed from their shells in a microwave oven (Galindo *et al.*, 2014). A piece of the head-foot was cut and preserved in 96–98% ethanol. Bodies were then separated from the shells, with shells kept dry to prevent deterioration by etching and carrying the same registration number as the corresponding body and tissue-clip in 96–98% ethanol. Most of the material (shell, tissue and DNA) is vouchered in MNHN (<http://science.mnhn.fr/>), unless otherwise stated.

In total 124 specimens of Olividae and Pseudolividae (*sensu* Bouchet & Rocroi, 2005), representing 60 species, were sequenced; additionally, sequences of three species representing unique lineages absent in our material were taken from GenBank. Although we included representatives of as many genus-level taxa as possible, some genera recognized as valid are not covered in our dataset, for example *Eburna* (Lamarck, 1801) and *Anolacia* (Gray, 1857). Their taxonomic position will be discussed in the Taxonomy section.

Several new species were discovered in the course of the project and they are described in a separate paper (Kantor *et al.*, 2016).

A suite of 12 species from 12 other neogastropod families in the superfamilies Conoidea, Cancellarioidea, Buccinoidea and Muricoidea was included in the analysis to ensure adequate representation of major evolutionary lineages of Neogastropoda and likely detection of olivoidean gastropod relationships. *Tonna galea* (Caenogastropoda, Tonnoidea and Tonnidae) was used as a distant outgroup. Specimen data as well as repositories are presented in Table 1, and some shells of sequenced vouchers (or conspecific specimens) are illustrated in the following sections.

PCR AMPLIFICATION AND DNA SEQUENCING

Total genomic DNA was extracted from muscle tissue using NucleoSpinR 96 Tissues (Macherey–Nagel) following the manufacturer's instructions. Fragments of the mitochondrial genes cytochrome oxidase subunit I (*COI*), *16S rRNA* and *12S rRNA*, as well as the nuclear gene histone 3 (*H3*) were sequenced (Table 1). All PCR reactions were performed following protocols described in detail earlier (Fedosov *et al.*, 2015). All genes were sequenced for both directions to confirm accuracy of each sequence. The sequencing was performed by Eurofins. Chromatograms were edited using CodonCode Aligner version 3.7.1.1.

SEQUENCE ALIGNMENTS AND PHYLOGENETIC ANALYSIS

Sequences were aligned for each gene independently using MUSCLE (Edgar, 2004). The accuracy of automatic alignments was confirmed by eye and where necessary edited using BioEdit version 7.0.9.0 (Hall, 1999). No indels were detected in protein coding genes *COI* and *H3*.

To delimit species within the genus *Ancilla*, a first dataset including 36 *COI* sequences was analysed together with five *COI* sequences of other Olivoidea, used as outgroups (MNHN IM-2009–25009 *Entomoliva mirabilis*, MNHN IM-2007–31956 *Ancillina cf. sumatrana*, MNHN IM-2009–11968 *Amalda hilgendorffi richeri*, MNHN IM-2013–18534 *Benthobia* sp. and MNHN IM-2013–9727 *Fusulculus crenatus*). Similarly, a dataset including 56 original *COI* sequences of *Oliva*, together with two sequences from Genbank and the same outgroups, was analysed for species delimitation. The web version (<http://www.wabi.snv.jussieu.fr/public/abgd/abgdweb.html>) of ABGD (Automatic Barcode Gap Discovery) (Puillandre *et al.*, 2012) was used to propose primary

species hypotheses, with default parameters, and the simple-distance substitution model. To reconstruct phylogenetic relationships of the entire Olivoidea, one specimen per species of Olivoidea was analysed (Table 1). Best-fit substitution models were identified for each gene separately using ModelgeneratorV.85 (Keane *et al.*, 2006) (Table 2). Each gene was first analysed separately: they provided mostly unsupported trees, and will not be discussed further in this paper. Because no incongruence between each gene tree was detected, they were combined into a concatenated four-gene dataset. In both maximum likelihood (ML) and Bayesian inference analysis (BI), each codon position of the *COI* gene for *Ancilla*, *Oliva* and Olivoidea datasets and each gene (*16S*, *12S*, *H3*) for the Olivoidea dataset were considered as independent partitions, each following a GTR + G and a GTR + I + G model (for ML and BI, respectively). Best-scoring ML trees were estimated using RAXML-HPC2 (Stamatakis, 2006) on XSEDE, as implemented on the CIPRES Science Gateway v.3.1. Robustness of the nodes was assessed using 1000 bootstraps. BIs were performed running two parallel analyses in MrBayes 3.2.6 (Huelsenbeck, Ronquist & Hall 2001) on XSEDE, as implemented on the CIPRES Science Gateway v.3.1. For the *Ancilla* and *Oliva* datasets, used to test the monophyly of the species hypotheses proposed by ABGD, as well as the single gene analyses of the Olivoidea dataset, each run consisted of six Markov chains and 10 000 000 generations with eight chains, five swaps, a sampling frequency of 1000 and a temperature of 0.02. For the four-gene analyses of the Olivoidea dataset, the parameters were the same, except for the number of generations (50 000 000) and the sampling frequency (5000). Convergence of each analysis was evaluated using Tracer1.4.1 (Rambaut *et al.*, 2014) to ensure that all ESS values exceeded 200. Consensus tree were calculated after omitting the first 25% trees as burn-in.

ANATOMY

The anatomy of representatives of every genus confirmed as valid was examined, whenever possible from the sequenced specimens themselves. For some groups (*Belloлива*, *Oliva* and Pseudolividae) published data were available (Kantor, 1991; Kantor & Bouchet, 2007; Kantor & Tursch, 2001a). Special attention was paid to the mantle morphology, anterior foregut and external stomach morphology. The radula was prepared for most species, following the standard protocol in Kantor & Puillandre (2012), and examined with scanning electron microscopes in MNHN and A.N. Severtzov Institute of Ecology and Evolution, Russian Academy of Sciences.

Table 1. List of specimens analysed

Family (Subfamily)	Genus Species	Inventory number,	Expedition	Station	Locality	BOLD	COI	16S	12S	H3	Source
Ancillariidae	<i>Amalda aureomarginata</i> Kilburn & Bouchet, 1988	IM-2007-43655	TERRASSES	DW3123	New Caledonia, Ile des Pins, 22°53'S, 167°13'E, 420–450 m	NEOGA984-10	KX233276	KX233394	KX233432		Original sequence
Ancillariidae	<i>Amalda bellonara</i> Kilburn & Bouchet, 1988	IM-2007-33273	EBISCO	CP2572	New Caledonia, NorthNEOGA672-10, Bellona, 20°23'S, 158°45'E, 324–330 m	NEOGA672-10	KX233363	KX233418	KX233455	KX233481	
Ancillariidae	<i>Amalda cf. hilgendorffi richeri</i> Kilburn & Bouchet, 1988	IM-2009-11963	NORFOLK 2	DW2147	New Caledonia, Ile des Pins, 22°50'S, 167°16'N, 496 m	OLIV009-16	KX233274	KX233392		KX233464	Original sequence
Ancillariidae	<i>Amalda contusa</i> (Reeve, 1864)	IM-2009-22263	INHACA 2011	MR4	Mozambique, 26°6'18"S, 32°58'E, 17–19 m	MITRI063-15	KR087230	KR087986	KR087327	KR088073	Original sequence
Ancillariidae	<i>Amalda fuscolim-gua</i> Kilburn & Bouchet, 1988	IM-2007-43649	TERRASSES	DW3122	New Caledonia, Ile des Pins, 22°47'S, 167°12'E, 390–410 m	NEOGA979-10	KX233275	KX233393			Original sequence
Ancillariidae	<i>Amalda hilgendorffi richeri</i> Kilburn & Bouchet, 1988	IM-2009-11968	CONCALIS	DW2979	Northern New Caledonia, 18°16'S, 162°54'E, 350 m	OLIV010-16	KX233273		KX233431	KX233463	Original sequence
Ancillariidae	<i>Ancilla adelphe</i> Kilburn, 1981	IM-2009-15475	ATIMO VATAE	BM06	South Madagascar, 25°27'55"S, 44°57'38"E, 0–1 m	OLIV014-16	KX233283				Kantor <i>et al.</i> (2016)
Ancillariidae	<i>Ancilla adelphe</i> Kilburn, 1981	IM-2009-15491	ATIMO VATAE	BM07	South Madagascar, 25°27'55"S, 44°57'38"E, 0–1 m	OLIV021-16	KX233281				Kantor <i>et al.</i> (2016)
Ancillariidae	<i>Ancilla adelphe</i> Kilburn, 1981	IM-2009-15510	ATIMO VATAE	BV16	South Madagascar, 25°25'33"S, 44°55'50.9953"E	OLIV030-16	KX233282				Kantor <i>et al.</i> (2016)
Ancillariidae	<i>Ancilla adelphe</i> Kilburn, 1981	IM-2009-15519	ATIMO VATAE	BP42	South Madagascar, 25°22.8'S, 44°51.1'E, 18–20 m	OLIV037-16	KX233278	KX233395	KX233433	KX233465	Original sequence
Ancillariidae	<i>Ancilla adelphe</i> Kilburn, 1981	IM-2009-15524	ATIMO VATAE	BV16	South Madagascar, 25°25'33"S, 44°55'50"E	OLIV042-16	KX233279				Kantor <i>et al.</i> (2016)
Ancillariidae	<i>Ancilla adelphe</i> Kilburn, 1981	IM-2009-15535	ATIMO VATAE	BP41	South Madagascar, 25°22.9'S, 44°51.0–51.6'E, 19–21 m	OLIV052-16	KX233277				Kantor <i>et al.</i> (2016)

Table 1. *Continued*

Family (Subfamily)	Genus Species	Inventory number,	Expedition	Station	Locality	BOLD	COI	16S	12S	H3	Source
Ancillariidae	<i>Ancilla adelphe</i> Kilburn, 1981	IM-2009– 15538	ATIMO VATAE	BP36	South Madagascar, 25°21'52"S, 44°50'13"E, 10–17 m	OLIV054-16	KX233280				Kantor <i>et al.</i> (2016)
Ancillariidae	<i>Ancilla atimo- vatae</i> Kantor <i>et al.</i> , 2016	IM-2009– 15511	ATIMO VATAE	BS01	South Madagascar, 25°28.2'S, 44°56.4'E, 12–14 m	OLIV031-16		KX233399	KX233437		Original sequence
Ancillariidae	<i>Ancilla aureocol- losa</i> (Kilburn & Jenner, 1977)	IM-2007– 39045	MAINBAZA	CP3143	Mozambique Channel, 23°32'S, 35°46'E, 264–277 m	OLIV007-16	KX233284	KX233396	KX233434	KX233466	Original sequence
Ancillariidae	<i>Ancilla cf. gtaquintoi</i> Bozzetti, 2006	IM-2009– 15526	ATIMO VATAE	BP22	South Madagascar, 25°23'26.5164"S, 44°51'39.42"E, 20–22 m	OLIV044-16	KX233285				Kantor <i>et al.</i> (2016)
Ancillariidae	<i>Ancilla kavi- angiensis</i> Kantor <i>et al.</i> , 2016	IM-2013– 51964	KAVIENG 2014	KR82	Papua-New Guinea, 02°39.6'S, 150°39.9'E, 2–12 m	OLIV072-16	KX233294	KX233397	KX233435	KX233467	Original sequence
Ancillariidae	<i>Ancilla kavi- angiensis</i> Kantor <i>et al.</i> , 2016	IM-2013– 55102	KAVIENG 2014	KS57	Papua-New Guinea, 02°38.9'S, 150°40.1'E, 7–9 m	OLIV075-16	KX233297				Kantor <i>et al.</i> (2016)
Ancillariidae	<i>Ancilla kavi- angiensis</i> Kantor <i>et al.</i> , 2016	IM-2013– 55130	KAVIENG 2014	KB62	Papua-New Guinea, 02°36.4'S, 150°42.4'E, 19 m	OLIV076-16	KX233286				Kantor <i>et al.</i> (2016)
Ancillariidae	<i>Ancilla kavi- angiensis</i> Kantor <i>et al.</i> , 2016	IM-2013– 55138	KAVIENG 2014	KD70	Papua-New Guinea, 02°38.3'S, 150°45.6'E, 10–15 m	OLIV077-16	KX233305				Kantor <i>et al.</i> (2016)
Ancillariidae	<i>Ancilla lhaumeti</i> Kantor <i>et al.</i> , 2016	IM-2009– 15481	ATIMO VATAE	BP21	South Madagascar, 25°23.1'S, 44°51.4'E, 20–23 m	OLIV016-16	KX233303				Kantor <i>et al.</i> (2016)
Ancillariidae	<i>Ancilla lhaumeti</i> Kantor <i>et al.</i> , 2016	IM-2009– 15482	ATIMO VATAE	BV16	South Madagascar, 25°25.6'S, 44°55.9'E, 9 m	OLIV017-16	KX233299				Kantor <i>et al.</i> (2016)
Ancillariidae	<i>Ancilla lhaumeti</i> Kantor <i>et al.</i> , 2016	IM-2009– 15503	ATIMO VATAE	BS11	South Madagascar, 25°28'36"S, 44°56'45"E, 8–11 m	OLIV025-16	KX233296				Kantor <i>et al.</i> (2016)
Ancillariidae	<i>Ancilla lhaumeti</i> Kantor <i>et al.</i> , 2016	IM-2009– 15506	ATIMO VATAE	BP42	South Madagascar, 25°22.8'S, 44°51.1'E, 18–20 m	OLIV027-16	KX233288				Kantor <i>et al.</i> (2016)

Table 1. Continued

Family (Subfamily)	Genus Species	Inventory number,	Expedition	Station	Locality	BOLD	COI	16S	12S	H3	Source
Ancillariidae	<i>Ancilla lhaumeti</i> Kantor <i>et al.</i> , 2016	IM-2009- 15507	ATIMO VATAE	BM06	South Madagascar, 25°27'55"S, 44°57'38"E, 0–1 m	OLIV028-16	KX233300				Kantor <i>et al.</i> (2016)
Ancillariidae	<i>Ancilla lhaumeti</i> Kantor <i>et al.</i> , 2016	IM-2009- 15513	ATIMO VATAE	BP37	South Madagascar, 25°22.4'S, 44°50.2'E, 19–20 m	OLIV033-16	KX233301	KX233398	KX233436		Original sequence
Ancillariidae	<i>Ancilla lhaumeti</i> Kantor <i>et al.</i> , 2016	IM-2009- 15515	ATIMO VATAE	BP37	South Madagascar, 25°22.4'S, 44°50.2'E, 19–20 m	OLIV034-16	KX233302				Kantor <i>et al.</i> (2016)
Ancillariidae	<i>Ancilla lhaumeti</i> Kantor <i>et al.</i> , 2016	IM-2009- 15523	ATIMO VATAE	BV16	South Madagascar, 25°25.6'S, 44°55.9'E, 9 m	OLIV041-16	KX233291				Kantor <i>et al.</i> (2016)
Ancillariidae	<i>Ancilla lhaumeti</i> Kantor <i>et al.</i> , 2016	IM-2009- 15528	ATIMO VATAE	BP42	South Madagascar, 25°22.8'S, 44°51.1'E, 18–20 m	OLIV046-16	KX233293				Kantor <i>et al.</i> (2016)
Ancillariidae	<i>Ancilla lhaumeti</i> Kantor <i>et al.</i> , 2016	IM-2009- 15533	ATIMO VATAE	BP21	South Madagascar, 25°23.1'S, 44°51.4– 51.6'E, 20–23 m	OLIV050-16	KX233298				Kantor <i>et al.</i> (2016)
Ancillariidae	<i>Ancilla lhaumeti</i> Kantor <i>et al.</i> , 2016	IM-2009- 15550	ATIMO VATAE	BV16	South Madagascar, 25°25.6'S, 44°55.9'E, 9 m	OLIV060-16	KX233292				Kantor <i>et al.</i> (2016)
Ancillariidae	<i>Ancilla morrisoni</i> Kantor <i>et al.</i> , 2016	IM-2013- 55401	KAVIENG 2014	KS63	Papua-New Guinea, 02°45.2'S, 150°41.7'E, 10–12 m	OLIV078-16	KX233290				Kantor <i>et al.</i> (2016)
Ancillariidae	<i>Ancilla morrisoni</i> Kantor <i>et al.</i> , 2016	IM-2013- 55403	KAVIENG 2014	KS63	Papua-New Guinea, 02°45.2'S, 150°41.7'E, 10–12 m	OLIV079-16	KX233289				Kantor <i>et al.</i> (2016)
Ancillariidae	<i>Ancilla</i> sp.	IM-2007- 36606	MAINBAZA	CP3133	Mozambique Channel, 25°11'S, 35°10'E, 200–201 m	OLIV005-16	KX233304	KX233400		KX233468	Original sequence
Ancillariidae	<i>Ancilla</i> sp.	IM-2009- 15527	ATIMO VATAE	DW3523	South Madagascar, 24°22'57"S, 47°31'23.4012"E, 200–220 m	OLIV045-16	KX233295				Kantor <i>et al.</i> (2016)
Ancillariidae	<i>Ancilla</i> sp.	IM-2009- 25001	MIRIKY	CP3262	Madagascar, 15°34'9.8" S, 45°43'40.8" E, 227–283 m	OLIV065-16	KX233287				Kantor <i>et al.</i> (2016)
Ancillariidae	<i>Ancilla thom- assini</i> Kilburn, 1981	IM-2009- 15460	ATIMO VATAE	TB13	South Madagascar, 25°01.5'S, 47°00.0'E, 2–4 m	OLIV011-16	KX233307	KX233401	KX233438	KX233469	Original sequence

Table 1. Continued

Family (Subfamily)	Genus Species	Inventory number,	Expedition	Station	Locality	BOLD	COI	16S	12S	H3	Source
Ancillariidae	<i>Ancilla thom-</i> <i>assini</i> Kilburn, 1981	IM-2009– 15534	ATIMO VATAE	T513	South Madagascar, 25°02.3'S, 46°59.6'E, 5–6 m	OLIV051-16	KX233306				Kantor <i>et al.</i> (2016)
Ancillariidae	<i>Ancilla ventricosa</i> (Lamarck, 1811)	IM-2009– 15486	ATIMO VATAE	BP42	South Madagascar, 25°22.8'S, 44°51.1'E, 18–20 m	OLIV020-16	KX233309				Kantor <i>et al.</i> (2016)
Ancillariidae	<i>Ancilla ventricosa</i> (Lamarck, 1811)	IM-2009– 15537	ATIMO VATAE	BP21	South Madagascar, 25°23.1'S, 44°51.4'E, 20–23 m	OLIV053-16	KX233308				Kantor <i>et al.</i> (2016)
Ancillariidae	<i>Ancilla ventricosa</i> (Lamarck, 1811)	IM-2009– 15544	ATIMO VATAE	BP42	South Madagascar, 25°22.8'S, 44°51.1'E, 18–20 m	OLIV057-16	KX233311				Kantor <i>et al.</i> (2016)
Ancillariidae	<i>Ancilla ventricosa</i> (Lamarck, 1811)	IM-2009– 15545	ATIMO VATAE	BV06	South Madagascar, 25°26.9'S, 44°55.9'E, 14–18 m	OLIV058-16	KX233310	KX233402	KX233439	KX233470	Original sequence
Ancillariidae	<i>Ancilla ventricosa</i> (Lamarck, 1811)	IM-2009– 15547	ATIMO VATAE	BP42	South Madagascar, 25°22.8'S, 44°51.1'E, 18–20 m	OLIV059-16	KX233312				Kantor <i>et al.</i> (2016)
Ancillariidae	<i>Ancillina</i> cf. <i>sumatrana</i> (Thiele, 1925)	IM-2007– 31956	PANGLAO 2005	CP2350	Philippines, Bohol Sea, 9°31'24"N; 124°0'36"E, 602–738 m	MITRI064-15	KR087231	KR087987	KR087328	KR088074	Original sequence
Ancillariidae	<i>Ancillina</i> sp.	IM-2007– 38889	TARASOC	DW3349	Tuamotu, 15°05'S, 148°03'W, 976–997 m	OLIV006-16	KX233313	KX233403	KX233440	KX233471	Original sequence
Ancillariidae	<i>Entomoliva mira-</i> <i>bilis</i> Bouchet & Kilburn, 1991	IM-2009– 25009	EXBODI	DW3906	New Caledonia, 19°50'S, 165°33'E, 490–580 m	OLIV066-16	KX233317	KX233407	KX233444	KX233474	Original sequence
Ancillariidae	<i>Turrancilla glans</i> (E. A. Smith, 1899)	IM-2007– 31949	PANGLAO 2005	CP2333	Philippines, Bohol Sea, 9°38'N, 123°44'E, 584–596 m	NEOGA459-10	KX233370	KX233421	KX233458		Original sequence
Ancillariidae	<i>Turrancilla</i> sp.	IM-2013– 19425	PAPUA NIUGINI	CP4078	Bismark Sea, 3°59'36"S, 144°53'44"E, 800–860 m	OLIV069-16	KX233382	KX233423	KX233460		Original sequence
Ancillariidae	<i>Turrancilla</i> sp. 1	IM-2007– 33282	SALOMON 2	CP2186	Solomon Islands, 8°17' S, 160°00' E, 487–541 m	NEOGA676-10	KX233358	KX233416	KX233453	KX233479	Original sequence
Ancillariidae	<i>Turrancilla</i> sp. 2	IM-2007– 31947	PANGLAO 2005	CP2341	Philippines, Bohol Sea, 9°24'N, 123°50'E, 544–712 m	NEOGA457-10	KX233362	KX233417	KX233454	KX233480	Original sequence

Table 1. Continued

Family (Subfamily)	Genus Species	Inventory number,	Expedition	Station	Locality	BOLD	COI	16S	12S	H3	Source
Belloliidae	<i>Bellinia exquisita</i> (Angas, 1871)	IM-2007-34786	CONCALIS	DW2973	Northern New Caledonia, 18°14'S, 163°06'E, 275–288 m	OLIV004-16	KX233314	KX233404	KX233441	KX233472	Original sequence
Belloliidae	<i>Olinellopsis amoni</i> (Sterba & Lorenz, 2005)	IM-2013-47678	KAVIENG 2014	KS11	Papua-New Guinea, 02°33,2'S, 150°48,2'E, 7 m	OLIV070-16	KX233351	KX233413	KX233450	KX233476	Original sequence
Belloliidae	<i>Olinellopsis cf. amoni</i> (Sterba & Lorenz, 2005)	IM-2013-51055	KAVIENG 2014	KB20	Papua-New Guinea, 02°45,2'S, 150°41,7'E, 8 m	OLIV071-16	KX233352	KX233414	KX233451	KX233477	Original sequence
Benthobiidae	<i>Benthobia</i> sp. 1	IM-2009-31002	AURORA 2007	CP2685	Philippines, 14°59'37"N; 123°55'4"E, 1155–1302 m	MITRI065-15	KR087232	KR087988	KR087329		Original sequence
Benthobiidae	<i>Benthobia</i> sp. 2	IM-2013-18534	PAPUA NIUGINI	CP4038	Papua-New Guinea, 04°27'S, 145°34'E, 800–840 m	OLIV068-16	KX233315	KX233405	KX233442	KX233473	Original sequence
Benthobiidae	<i>Fusulculus crenatus</i> Bouchet & Vermeij, 1998	IM-2013-9727	PAPUA NIUGINI	CP4008	Solomon Sea, 06°04'S, 148°10'E, 500–555 m	OLIV080-16	KX233318	KX233408	KX233445	KX233475	Original sequence
Olividae (Agaroniinae)	<i>Agaronia acumi-nata</i> (Lamarck, 1811)	IM-2013-52002	DAKAR'09	I1	Senegal, 14°39'24.0012"N, 17°28'11.9964"W, 7–11 m	OLIV073-16	KX233271		KX233429	KX233461	Original sequence
Olividae (Agaroniinae)	<i>Agaronia anno-tata</i> (Marrat, 1871)	IM-2013-52004	Port ZANAGA	DW515	Congo, 4°43'14"S, 11°49'4"E, 8–9 m	OLIV074-16	KX233272	KX233391	KX233430	KX233462	Original sequence
Olividae (Calyptolivinae)	<i>Calyptoliva bbugaeae</i> Kantor et al., 2016	IM-2007-39266	TARASOC	DW3380	Tuamotu, 15°39'S, 146°56'W, 970–1060 m	OLIV008-16	KX233316	KX233406	KX233443		Original sequence
Olividae (Olivellinae)	<i>Olivella exilis</i> (Marrat, 1871)	IM-2009-24367	KARUBENTHOS 2012	GD41	Guadeloupe, 16°20'54"S; 61°32'13"W, 2 m	MITRI062-15	KR087290	KR088040	KR087378	KR088119	Original sequence
Olividae (Olivellinae)	<i>Olivella minuta</i> (Link, 1807)	IM-2009-24350	KARUBENTHOS 2012	GM19	Guadeloupe, 16°21,3'N, 61°44,92'W, 1 m	OLIV063-16	KX233349	KX233411	KX233448		Original sequence
Olividae (Olivellinae)	<i>Olivella olssonii</i> Van Regteren Altena, 1971	IM-2009-24370	KARUBENTHOS 2012	GD48	Guadeloupe, 16°11,21'N, 61°32,51'W, 27 m	OLIV064-16	KX233350	KX233412	KX233449		Original sequence
Olividae (Olivinae)	<i>Olioa amethystina</i> (Röding, 1798)	IM-2007-31971	PANGLAO 2004	B1	Philippines, 9°33.0'N, 123°46.5'E, 8–14 m	NEOGA471-10	KX233364				Original sequence

Table 1. Continued

Family (Subfamily)	Genus Species	Inventory number,	Expedition	Station	Locality	BOLD	COI	16S	12S	H3	Source
Olividae (Olivinae)	<i>Olioa amethystina</i> (Röding, 1798)	IM-2007–31988	SANTO 2006	DR09	Vanuatu, 15°34'36"S, 167°13'47.98"E, 12 m	NEOGA476-10KR087289	KR088039	KR087377	KR088118		Original sequence
Olividae (Olivinae)	<i>Olioa amethystina</i> (Röding, 1798)	IM-2007–31994	SANTO 2006	NR04	Vanuatu, 15°35'S, 167°15.4'E, 28 m	NEOGA478-10KX233354					Original sequence
Olividae (Olivinae)	<i>Olioa bailevi</i> Petuch, 1979	IM-2007–36138	SALOMONBOA 3	DW2852	Solomon Islands, 9°46'S, 160°51'E, 220 m	NEOGA863-10KX233365	KX233419	KX233456			Original sequence
Olividae (Olivinae)	<i>Olioa carneola</i> (Gmelin, 1791)	IM-2007–33444	PANGLAO 2004	M40	Philippines, Panglao, 9°35.7'N, 123°44.7'E, 3 m	NEOGA700-10KX233381					Original sequence
Olividae (Olivinae)	<i>Olioa carneola</i> (Gmelin, 1791)	IM-2007–33461	SANTO 2006	DR11	Vanuatu, 15°36.6'S, 167°10.1'E, 6–24 m	NEOGA701-10KX233368	KX233420	KX233457			Original sequence
Olividae (Olivinae)	<i>Olioa caroliniana</i> (Duclos, 1840)	IM-2009–15461	ATTIMO VATAE	BP01	South Madagascar, 25°26.6–26.9'S, 44°54.9–55.1'E, 22–23 m	OLIV012-16 KX233320	KX233409	KX233446			Original sequence
Olividae (Olivinae)	<i>Olioa caroliniana</i> (Duclos, 1840)	IM-2009–15462	ATTIMO VATAE	BP20	South Madagascar, 25°24.1'S, 44°51.1'E, 24–26 m	OLIV013-16 KX233333					Original sequence
Olividae (Olivinae)	<i>Olioa caroliniana</i> (Duclos, 1840)	IM-2009–15479	ATTIMO VATAE	BP20	South Madagascar, 25°24.1'S, 44°51.1'E, 24	OLIV015-16 KX233332					Original sequence
Olividae (Olivinae)	<i>Olioa caroliniana</i> (Duclos, 1840)	IM-2009–15492	ATTIMO VATAE	BP20	South Madagascar, 25°24.1'S, 44°51.1'E, 24	OLIV022-16 KX233321					Original sequence
Olividae (Olivinae)	<i>Olioa caroliniana</i> (Duclos, 1840)	IM-2009–15504	ATTIMO VATAE	BP18	South Madagascar, 25°26.1'S, 44°55.2'E, 17–20 m	OLIV026-16 KX233325					Original sequence
Olividae (Olivinae)	<i>Olioa caroliniana</i> (Duclos, 1840)	IM-2009–15508	ATTIMO VATAE	BP06	South Madagascar, 25°25.4'S, 44°54.5'E, 19–20 m	OLIV029-16 KX233331					Original sequence
Olividae (Olivinae)	<i>Olioa caroliniana</i> (Duclos, 1840)	IM-2009–15512	ATTIMO VATAE	BP21	South Madagascar, 25°23.1'S, 44°51.4'E, 20–23 m	OLIV032-16 KX233324					Original sequence
Olividae (Olivinae)	<i>Olioa caroliniana</i> (Duclos, 1840)	IM-2009–15517	ATTIMO VATAE	BP17	South Madagascar, 25°25.9'S, 44°55.1–55.2'E, 18–20 m	OLIV035-16 KX233328					Original sequence
Olividae (Olivinae)	<i>Olioa caroliniana</i> (Duclos, 1840)	IM-2009–15520	ATTIMO VATAE	BP18	South Madagascar, 25°26.1'S, 44°55.2'E, 17–20 m	OLIV038-16 KX233319					Original sequence

Table 1. Continued

Family (Subfamily)	Genus Species	Inventory number,	Expedition	Station	Locality	BOLD	COI	16S	12S	H3	Source
Olividae (Olivinae)	<i>Oliua caroliniana</i> Duclos, 1840	IM-2009-15522	ATIMO VATAE	BP21	South Madagascar, 25°23.1'S, 44°51.4'E, 20–23 m	OLIV040-16	KX233329				Original sequence
Olividae (Olivinae)	<i>Oliua caroliniana</i> Duclos, 1840	IM-2009-15525	ATIMO VATAE	BP18	South Madagascar, 25°26.1'S, 44°55.2'E, 17–20 m	OLIV043-16	KX233327				Original sequence
Olividae (Olivinae)	<i>Oliua caroliniana</i> Duclos, 1840	IM-2009-15530	ATIMO VATAE	BP01	South Madagascar, 25°26.6'S, 44°54.9'E, 22–23 m	OLIV047-16	KX233326				Original sequence
Olividae (Olivinae)	<i>Oliua caroliniana</i> Duclos, 1840	IM-2009-15531	ATIMO VATAE	TP08	South Madagascar, 24°56.5'S, 47°06.7'E, 2–5 m	OLIV048-16	KX233330				Original sequence
Olividae (Olivinae)	<i>Oliua caroliniana</i> Duclos, 1840	IM-2009-15532	ATIMO VATAE	BP06	South Madagascar, 25°25.4'S, 44°54.5'E, 19–20 m	OLIV049-16	KX233322				Original sequence
Olividae (Olivinae)	<i>Oliua caroliniana</i> Duclos, 1840	IM-2009-15540	ATIMO VATAE	BP20	South Madagascar, 25°24.1'S, 44°51.1'E, 24–26 m	OLIV055-16	KX233323				Original sequence
Olividae (Olivinae)	<i>Oliua cf. dubia</i> Schepman, 1904	IM-2007-33432	PANGLAO 2004	T23	Philippines, Bohol, 9°42.2'N, 123°50.6'E, 35–45 m	NEOGA697-10	KX233371				Original sequence
Olividae (Olivinae)	<i>Oliua cf. dubia</i> Schepman, 1904	IM-2009-25391	BIOPAPUA	CP3703	Papua-New Guinea, 3°52'32"S, 144°40'42"E, 361–750 m	OLIV067-16	KX233341				Original sequence
Olividae (Olivinae)	<i>Oliua cf. hirasei</i> Kira, 1959	IM-2007-36213	SALOMONBOA 3	CP2804	Solomon Islands, 09°15'S, 161°21'E, 150–175 m	NEOGA874-10	KX233375				Original sequence
Olividae (Olivinae)	<i>Oliua cf. lacanien-tai</i> Greifeneder & Blöcher, 1985	IM-2007-33275	EBISCO	DW2573	New Caledonia, North Bellona, 20°21'S, 158°46'E, 345–351 m	NEOGA673-10	KX233379	KX233422	KX233459		Original sequence
Olividae (Olivinae)	<i>Oliua cf. lacanien-tai</i> Greifeneder & Blöcher, 1985	IM-2007-33277	EBISCO	DW2547	New Caledonia, West Bellona, 21°06'S, 158°36'E, 356–438 m	NEOGA674-10	KX233374				Original sequence
Olividae (Olivinae)	<i>Oliua cf. lacanien-tai</i> Greifeneder & Blöcher, 1985	IM-2007-33281	EBISCO	DW2573	New Caledonia, North Bellona, 20°21'S, 158°46'E, 345–351 m	OLIV002-16	KX233343				Original sequence
Olividae (Olivinae)	<i>Oliua cf. lacanien-tai</i> Greifeneder & Blöcher, 1985	IM-2007-34783	CONCALIS	DW2956	Northern New Caledonia, 18°58'S, 163°19'E, 400–415 m	NEOGA803-10	KX233369				Original sequence

Table 1. Continued

Family (Subfamily)	Genus Species	Inventory number,	Expedition	Station	Locality	BOLD	COI	16S	12S	H3	Source
Olividae (Olivinae)	<i>Oliva chryso-plecta</i> Tursch & Griefeneder, 1989	IM-2007–31976	PANGLAO 2004	R14	Philippines, Bohol, 9°37.4'N, 123°54.5'E, 6–8 m		NEOGA475-10KX233373				Original sequence
Olividae (Olivinae)	<i>Oliva con-cavospira</i> Sowerby, 1914	IM-2007–34771	AURORA 2007	CP2764	Philippines, 15°49.8'N, 121°36.1'E, 45–47 m		NEOGA802-10KX233376				Original sequence
Olividae (Olivinae)	<i>Oliva con-cavospira</i> Sowerby, 1914	IM-2007–34772	AURORA 2007	CP2764	Philippines, 15°49.8'N, 121°36.1'E, 45–47 m		OLIV003-16 KX233334				Original sequence
Olividae (Olivinae)	<i>Oliva dubia</i> Schepman, 1904	IM-2007–33308	SALOMON 2	CP2282	Solomon Islands, 8°37' S, 157°21' E, 150–160 m		NEOGA688-10KX233367				Original sequence
Olividae (Olivinae)	<i>Oliva dubia</i> Schepman, 1904	IM-2007–33309	SALOMON 2	CP2282	Solomon Islands, 8°37' S, 157°21' E, 150–160 m		NEOGA689-10KX233361				Original sequence
Olividae (Olivinae)	<i>Oliva dubia</i> Schepman, 1904	IM-2007–33324	SALOMON 2	CP2283	Solomon Islands, 8°36' S, 157°23' E, 176 m		NEOGA695-10KX233366				Original sequence
Olividae (Olivinae)	<i>Oliva lacaniantai</i> Griefeneder & Blöcher, 1985	IM-2007–31963	PANGLAO 2005	CP2368	Philippines, Bohol /Sulu Sea sill, 8°56'N, 123°17'E, 318–322 m		NEOGA468-10KX233359				Original sequence
Olividae (Olivinae)	<i>Oliva lacaniantai</i> Griefeneder & Blöcher, 1985	IM-2007–34784	CONCALIS	DW3001	Northern New Caledonia, 18°32'S, 163°09'E, 390–400 m		NEOGA804-10KX233378				Original sequence
Olividae (Olivinae)	<i>Oliva lacaniantai</i> Griefeneder & Blöcher, 1985	IM-2007–34788	CONCALIS	DW2934	Northern New Caledonia, 19°06'S, 163°29'E, 216–226 m		NEOGA806-10KX233372				Original sequence
Olividae (Olivinae)	<i>Oliva leonar-dhilli</i> Petuch & Sargent, 1986	IM-2009–15485	ATIMO VATAE	TP12	South Madagascar, 25°02.6'S, 47°01.0-01.1'E, 39–41 m		OLIV019-16 KX233335				Original sequence
Olividae (Olivinae)	<i>Oliva leonar-dhilli</i> Petuch & Sargent, 1986	IM-2009–15498	ATIMO VATAE	BM07	South Madagascar, 25°21.5'S, 44°50.0'E, 0–1 m		OLIV023-16 KX233337				Original sequence
Olividae (Olivinae)	<i>Oliva leonar-dhilli</i> Petuch & Sargent, 1986	IM-2009–15543	ATIMO VATAE	BP42	South Madagascar, 25°22.8–23.7'S, 44°51.1'E, 18–20 m		OLIV056-16 KX233336				Original sequence
Olividae (Olivinae)	<i>Oliva leonar-dhilli</i> Petuch & Sargent, 1986	IM-2009–18313	ATIMO VATAE	DW3608	South Madagascar, 25°39.4'S, 44°53.0'E, 38–37 m		OLIV062-16 KX233338				Original sequence

Table 1. Continued

Family (Subfamily)	Genus Species	Inventory number,	Expedition	Station	Locality	BOLD	COI	16S	12S	H3	Source
Olividae (Olivinae)	<i>Oliva mantichora</i> Duclos, 1840	IM-2007-31964	PANGLAO 2005	CA2366	Philippines, Bohol / Sulu seas sill, 8°33.6'N, 123°16.1'E, 64–65 m	NEOGA469-10KX233355					Original sequence
Olividae (Olivinae)	<i>Oliva mantichora</i> Duclos, 1840	IM-2009-15483	ATIMO VATAE	TR04	South Madagascar, 25°00.2'S, 47°06.2'E, 22–28 m	OLIV018-16	KX233339				Original sequence
Olividae (Olivinae)	<i>Oliva miniacea</i> (Röding, 1798)	IM-2007-31973	SANTO 2006	NR05	Vanuatu, 15°28.7'S, 167°15.2'E, 19 m	NEOGA472-10KX233377					Original sequence
Olividae (Olivinae)	<i>Oliva mustelina</i> Lamarck, 1811						KF186640.1				Original sequence
Olividae (Olivinae)	<i>Oliva nitidula</i> Duclos, 1835	IM-2007-31974	PANGLAO 2004	S15	Philippines, Bohol, 9°41.3'N, 123°49.5'E, 4–6 m	NEOGA473-10KX233357					Original sequence
Olividae (Olivinae)	<i>Oliva oliva</i> (Linnaeus, 1758)	IM-2007-41493	CUMING TOUR 2005	CT24a	Philippines, Luzon, 16°17.41'N, 122°11.44'E, intertidal	NEOGA879-10KX233342					Original sequence
Olividae (Olivinae)	<i>Oliva oliva</i> (Linnaeus, 1758)	IM-2007-41496	CUMING TOUR 2005	CT24a	Philippines, Luzon, 16°17.41'N, 122°11.44'E, intertidal	NEOGA880-10KX233353					Original sequence
Olividae (Olivinae)	<i>Oliva parkinsoni</i> Prior, 1975	IM-2007-31975	SANTO 2006	DR78	Vanuatu, 15°28.4'S, 167°15.2'E, 25 m	NEOGA474-10KX233356		KX233415	KX233452	KX233478	Original sequence
Olividae (Olivinae)	<i>Oliva rufifulgurata</i> Schepman, 1904	IM-2007-31990	SANTO 2006	AT65	Vanuatu, 15°40'S, 167°16'E, 160–167 m	OLIV001-16	KX233340	KX233410	KX233447		Original sequence
Olividae (Olivinae)	<i>Oliva sayana</i> Ravenel, 1834	USNM 888605			Fort Pearce, Florida, USA		U86333.1				Harasewych <i>et al.</i> (1997)
Olividae (Olivinae)	<i>Oliva semmelinki</i> Schepman, 1891	IM-2007-31948	PANGLAO 2005	DW2400	Philippines, Bohol Sea, 9°32'N, 123°42'E, 111–115 m	NEOGA458-10KX233380					Original sequence
Olividae (Olivinae)	<i>Oliva sericea</i> (Röding, 1798)	IM-2007-31968	PANGLAO 2004	R14	Philippines, Bohol, 9°37.4'N, 123°54.5'E, 6–8 m	NEOGA470-10KX233360					Original sequence
Olividae (Olivinae)	<i>Oliva</i> sp.1	IM-2007-41441	CUMING TOUR 2005	CT11a1	Philippines, Mindanao, 6°49.60'N, 125°24.61'E, intertidal	NEOGA877-10KX233344					Original sequence

Table 1. Continued

Family (Subfamily)	Genus Species	Inventory number,	Expedition	Station	Locality	BOLD	COI	16S	12S	H3	Source
Olividae (Olivinae)	<i>Oliva spicata</i> (Röding, 1798)	IM-2009-4616, BAU00278			Las Perlas, (Panama), 8.53 N, 79.09 W, 20–22 m	OLIV081-16	FM999165	FM999114	FM999083		Oliverio & Modica (2010) Original sequence
Olividae (Olivinae)	<i>Oliva todosina</i> Duclos, 1840	IM-2009-15500	ATIMO VATAE	TP05	South Madagascar, 24°59.3-25°00.1'S, 47°00.4-01.4'E, 8–12 m	OLIV024-16	KX233346				Original sequence
Olividae (Olivinae)	<i>Oliva todosina</i> Duclos, 1840	IM-2009-15518	ATIMO VATAE	TP05	South Madagascar, 24°59.3'S, 47°00.4'E, 8–12 m	OLIV036-16	KX233347				Original sequence
Olividae (Olivinae)	<i>Oliva todosina</i> Duclos, 1840	IM-2009-15521	ATIMO VATAE	BP08	South Madagascar, 25°27.3'S, 44°55.2'E, 25–26 m	OLIV039-16	KX233348				Original sequence
Olividae (Olivinae)	<i>Oliva todosina</i> Duclos, 1840	IM-2009-15552	ATIMO VATAE	BP08	South Madagascar, 25°27.3'S, 44°55.2'E, 25–26 m	OLIV061-16	KX233345				Original sequence
Pseudolividae	<i>Pseudoliva ancilla</i> NMSA (Hanley, 1859)	E5279			SW of Mossel Bay, Agulhas Bank, Western Cape (South Africa), 81 m		FM999115.1	FM999084.1			Oliverio & Modica (2010)
Pseudolividae	<i>Pseudoliva septenta</i> (Rang, 1832)	IM-2013-52003	PORT ZANAGA	D502	Congo, 4°42'14"S, 11°47'E	MITRI066-15	KR087261	KR088012	KR087354	KR088098	Original sequence
OUTGROUPS								NC_023080.1	NC_023080.1	NC_023080.1	HQ834157.1 Zou et al. (2011)
Babyloniidae	<i>Babylonia areolata</i> (Link, 1807)		TARASOC	DW3387	Tuamotu, 14°57'S, 148°16'W, 550–600 m	NEOGA1157-11	JQ950224.1	EU870550.1	EU870525.1		Kantor et al. (2012)
Belomitridae	<i>Belomitra bouteti</i> Kantor et al., 2012	IM-2007-38678			Philippines, Bohol / Sulu Sea sill, 8°50'N, 123°35'E, 437–476 m	CANCO28-10	FM999158.1	FM999106.1	FM999075.1		Oliverio & Modica (2010)
Cancellariidae	<i>Plesiotriton vivus</i> Habe & Okutani, 1981	IM-2007-32123	PANGLAO 2005	CP2359	Philippines, Bohol / Sulu Sea sill, 8°50'N, 123°35'E, 437–476 m						Original sequence
Conidae	<i>Conasprella pagoda</i> (Kiener, 1847)	IM-2007-17914	PANGLAO 2005	CP2380	Philippines, Bohol/Sulu seas, 8°41'17"N; 123°17'48"E, 150–163 m	CONO313-08	EU015729	FJ868151	FJ868136	EU015836	Puillandre et al. (2008)
Costellariidae	<i>Vexillum exasperatum</i> (Gmelin, 1791)	IM-2013-11680	PAPUA NIUGINI	PR14	Papua-New Guinea, 05°12'S 145°48.1'E, 2–3 m	MITRI015-15	KR087305	KR088055	KR087393	KR088133	Fedosov et al. (2015)

Table 1. Continued

Family (Subfamily)	Genus Species	Inventory number,	Expedition	Station	Locality	BOLD	COI	16S	12S	H3	Source
Melongenidae	<i>Hemifusus terna-tanus</i> (Gmelin, 1791)	LSGB233031			China, 34°42'N, 119°28'E		JN053014.1	JN052950.1	HQ833889.1	HQ834160.1	Zou <i>et al.</i> (2011)
Mitridae	<i>Charitodoron</i> sp.	IM-2007-38306	MAINBAZA	CC3157	Mozambique Channel, 21°46'S, 36°25'E, 1410–1416 m	MITRI057-15	KR087240	KR087994	KR087335	KR088081	Fedosov <i>et al.</i> (2015)
Muricidae	<i>Drupa ricinus</i> (Linnaeus, 1758)	LSGB23014			China, 18°13'N, 109°29'E		HQ834096	HQ833968	HQ833919	HQ834189	Zou <i>et al.</i> (2011)
Nassariidae	<i>Phos senticosus</i> (Linnaeus, 1758)	LSGB232091			China, 21°26'N, 109°02'E		JN053008.1	JN052944.1	HQ833885.1	HQ834156.1	Zou <i>et al.</i> (2011)
Ptychactractidae	<i>Exilia krigei</i> Kilburn, 1971	IM-2007-38331	MAINBAZA	CC3171	Mozambique Channel, 25°59'S, 34°42'E, 771–776 m	MITRI072-15	KR087257	KR088009	KR087352	KR088096	Original sequence
Tonnidae	<i>Tonna galea</i> (Linnaeus, 1758)	LSGB22802			China, Hainan, 20°02'N, 110°18'E		HQ834116	HQ833984	HQ833862	HQ834135	Zou <i>et al.</i> (2011)
Turbinellidae (Columbarinae)	<i>Coluza cf. liriopae</i> Harasewych, 1986	IM-2007-38972	MAINBAZA	CP3139	Mozambique Channel, 23°35'S, 36°06'E, 1092–1195 m	MITRI082-15	KR087242	KR087995	KR087336	KR088083	Original sequence
Volutidae	<i>Melo melo</i> (Lightfoot, 1786)	LSGB2400102			China, 21°35'N, 108°20'E		HQ834086	HQ833959	HQ833911	HQ834182	Zou <i>et al.</i> (2011)

Table 2. Alignments and substitution models data

Primers	Reference	Annealing temperature	Amplification length bp	Alignment length bp	No. of sequences	Substitution model (hLRTs)	<i>I</i>	gamma
Fw: HCOI-1490 GGTC AACAAAT CATAAAGAYATGYG	Folmer <i>et al.</i> (1994)	48–50	658	658	53	GTR + I + G	0.48	0.39
Rv: LCOI-2198 TAAACTTCAG GGTGACCAARAAYCA	Folmer <i>et al.</i> (1994)							
Fw: 16SH CCGGTCTGAAC TCAGATCAGC	Palumbi (1996)	50	~550	577	52	TVM + I + G	0.16	0.26
Rv: 16LC GTTACC AAAAACATGGCTTC	Palumbi (1996)							
Fw: 12SA AAAC TGGATTAGATACCCACTAT	Palumbi (1996)	55	~380	426	52	GTR + I + G	0.22	0.52
Rv: 12SB GAGGGTGACGGGGGGTGTGT	Palumbi (1996)							
Fw: H3F ATGGCTCGTACCAAGCAGACVGC	Colgan <i>et al.</i> (2000)	57	328	328	37	TrN + I + G	0.47	0.37
Rv: H3R ATATCCTTRGGCATRATRTGAC	Colgan <i>et al.</i> (2000)							

Abbreviations of depositories

NSMK – National Science Museum of Korea, Daejeon, Korea;
BAU – Department of Animal and Human Biology, University of Rome La Sapienza, Rome, Italy;
MNHN – Muséum National d’Histoire Naturelle, Paris, France;
MZUSP – Museu de Zoologia, University of São Paulo, SP, Brasil;
NMSA – Natal Museum, Pietermaritzburg, South Africa.

Conventions

AL – aperture length;
BWL – last whorl length;
D – shell diameter;
M – monotypy;
OD – original designation;
SD – subsequent designation;
SL – shell length.

RESULTS

SPECIES DELIMITATION

ABGD delimited 11 and between 23 and 26 species for the *Ancilla* and *Oliva* datasets respectively. In the phylogenetic tree of *Ancilla* (Fig. 1), 6 of the 11 ABGD groups are represented by several specimens, and they each correspond to a supported monophyletic group. In the *Oliva* datasets, two partition schemes are proposed. In the first partition scheme (with the lowest number of groups), 10 groups out of the 23 are represented by several specimens, and each of them corresponds to a supported monophyletic group in the tree (Fig. 2). In the partition scheme with the highest number of species, *Oliva caroliniana* is divided into two, but one of these groups is paraphyletic. Furthermore, *Oliva lacanientai* is divided into four groups, three of them being represented by a single specimen each, the other corresponding to a non-supported clade (Fig. 2). In all cases, *O. sericea* and *O. miniacea* are grouped together.

PHYLOGENETIC ANALYSIS

The topologies originating from analyses of the concatenated dataset both from ML (Fig. 3) and BI (Fig. 4) are largely congruent and the supported clades were retrieved in both analyses. Here we mainly discuss the topology of the tree obtained with BI (Fig. 4) and refer to ML bootstrap support values where applicable.

The analysed ingroup taxa include the species and genera attributed to the superfamily Olivoidea by Bouchet & Rocroi (2005) – for convenience collectively

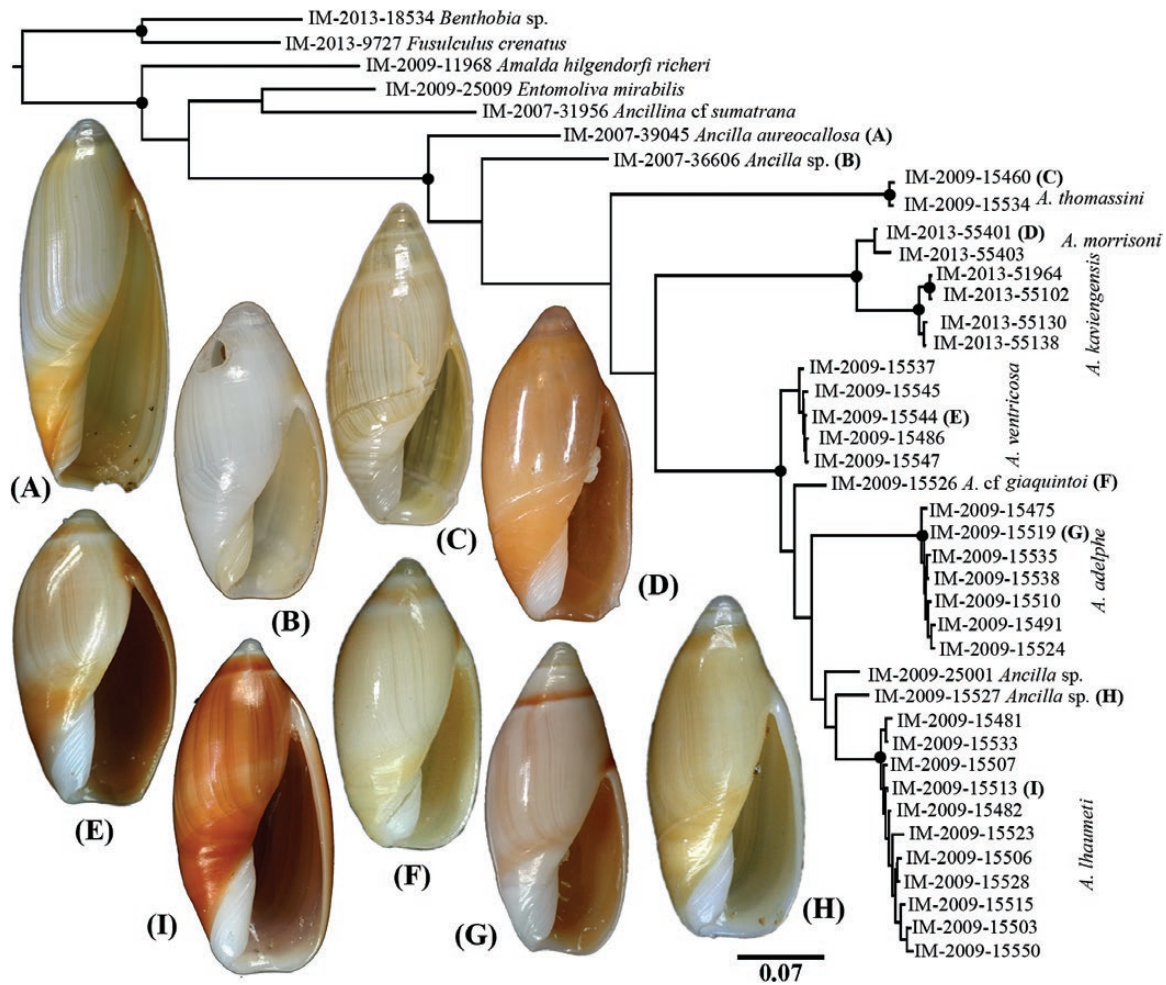


Figure 1. Phylogenetic tree of *Ancilla* and outgroup olivoidean taxa obtained with Bayesian analysis of *COI* gene sequences. Only supported nodes with posterior probability values between 0.98 and 1.00 are marked on the tree with circles. (A) *Ancilla aureocallosa*, MNHN IM-2007–39045, SL 21.7 mm. (B) *Ancilla* sp., MNHN IM-2007–36606, SL 5.6 mm. (C) *A. thomassini*, MNHN IM-2009–15460, SL 6.3 mm. (D) *A. morrisoni*, holotype, MNHN IM-2013–55401, SL 10.0 mm. (E) *A. ventricosa*, MNHN IM-2009–15544, SL 10.7 mm. (F) *A. cf. giaquintoii*, MNHN IM-2009–15526. (G) *A. adelphe*, MNHN IM-2009–15519, SL 11.1 mm. (H) *A.* sp., MNHN IM-2009–15527, SL 12.7 mm. (I) *A. lhaumeti*, holotype, MNHN IM-2009–15513, SL 15.3 mm. MNHN, Muséum National d’Histoire Naturelle, Paris, France; SL, shell length.

referred to in the following as ‘oliviforms’ – as well as those attributed to the family Pseudolividae. Together they form a clade, although only weakly supported (posterior probability 0.81 in the BI tree and bootstrap support only 33 in the ML tree). A clade that includes *Belloлива* Peile, 1922 and *Olivellopsis* Thiele, 1929 [the latter represented by ‘*Olivella (Janaoliva) amoni*’ Sterba & Lorenz, 2005, see below] is strongly supported molecularly (0.96 and 100, respectively for BI and ML analyses) and anatomically, and is a sister-group to the rest of the ingroup.

The rest of the ingroup taxa form a clade supported by ML (84) and strongly supported by BI (0.99). Pseudolividae as currently construed is polyphyletic and includes two distant clades. The first

clade is formed by two species of *Benthobia* Dall, 1889 and *Fusulculus crenatus* Bouchet & Vermeij, 1998. The second includes two species of *Pseudoliva* represented by *P. ancilla* (Hanley, 1859) and ‘*Fulmentum sepimentum*’ (Rang, 1832) (with regard to the generic position of this species, see Taxonomy section). Both clades are strongly supported, but the deeper nodes do not have significant support and their relationships to other ingroup taxa cannot be resolved. The name Pseudolividae can be applied to the second clade, which includes the representatives of the type genus. No name is available for the first clade.

The remaining oliviforms constitute two clades, well supported both in ML and in BI, although relationships between them are not resolved. The first,

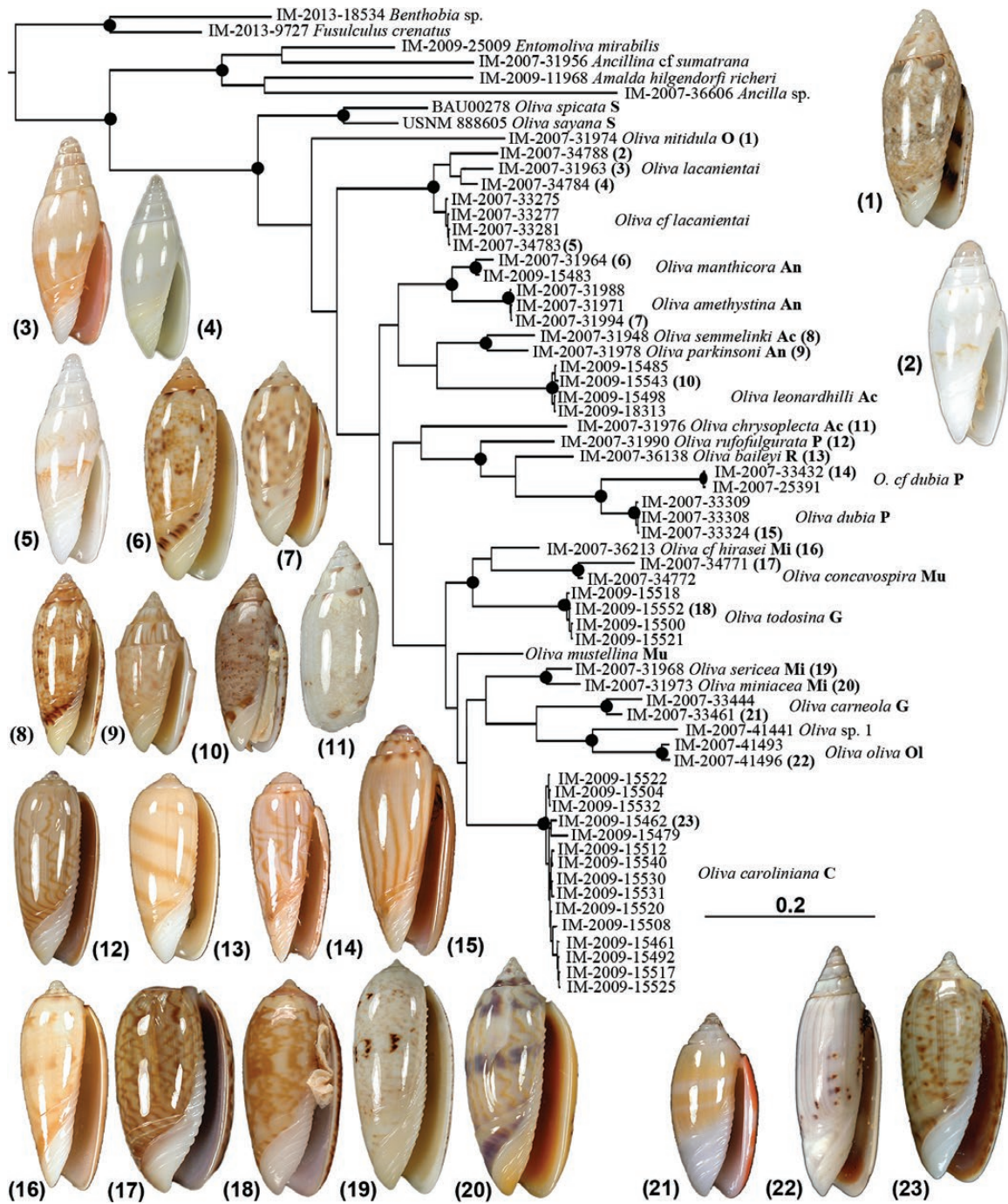


Figure 2. Phylogenetic tree of *Oliva* and outgroup olivoidean taxa obtained with Bayesian analysis of COI gene sequences. Only supported nodes with posterior probability values between 0.98 and 1.00 are marked on the tree with circles. The names of the corresponding subgenera (after Petuch & Sargent, 1986; Hunon et al., 2009) are given after the species names. Ac, *Acutoliva*; An, *Annulatoilva*; C, *Carmione*; G, *Galeola*; Mi, *Miniaceoliva*; Mu, *Musteoliva*; O, *Omogymna*; Ol, *Oliva*; P, *Parvoliva*; R, *Rufoliva*.

referred to as *Olividae* in Figs 3 and 4 and in the following, combines representatives of the genera *Oliva* Bruguière, 1789, *Agaronia* Gray, 1839, *Calyptoliva* Kantor & Bouchet, 2007, and *Olivella* Swainson, 1831.

This clade encompasses two currently recognized families – *Olividae* and *Olivellidae*, and we retain for it the senior name *Olividae* Latreille, 1825. The species of *Olivella* and *Agaronia* (both monophyletic

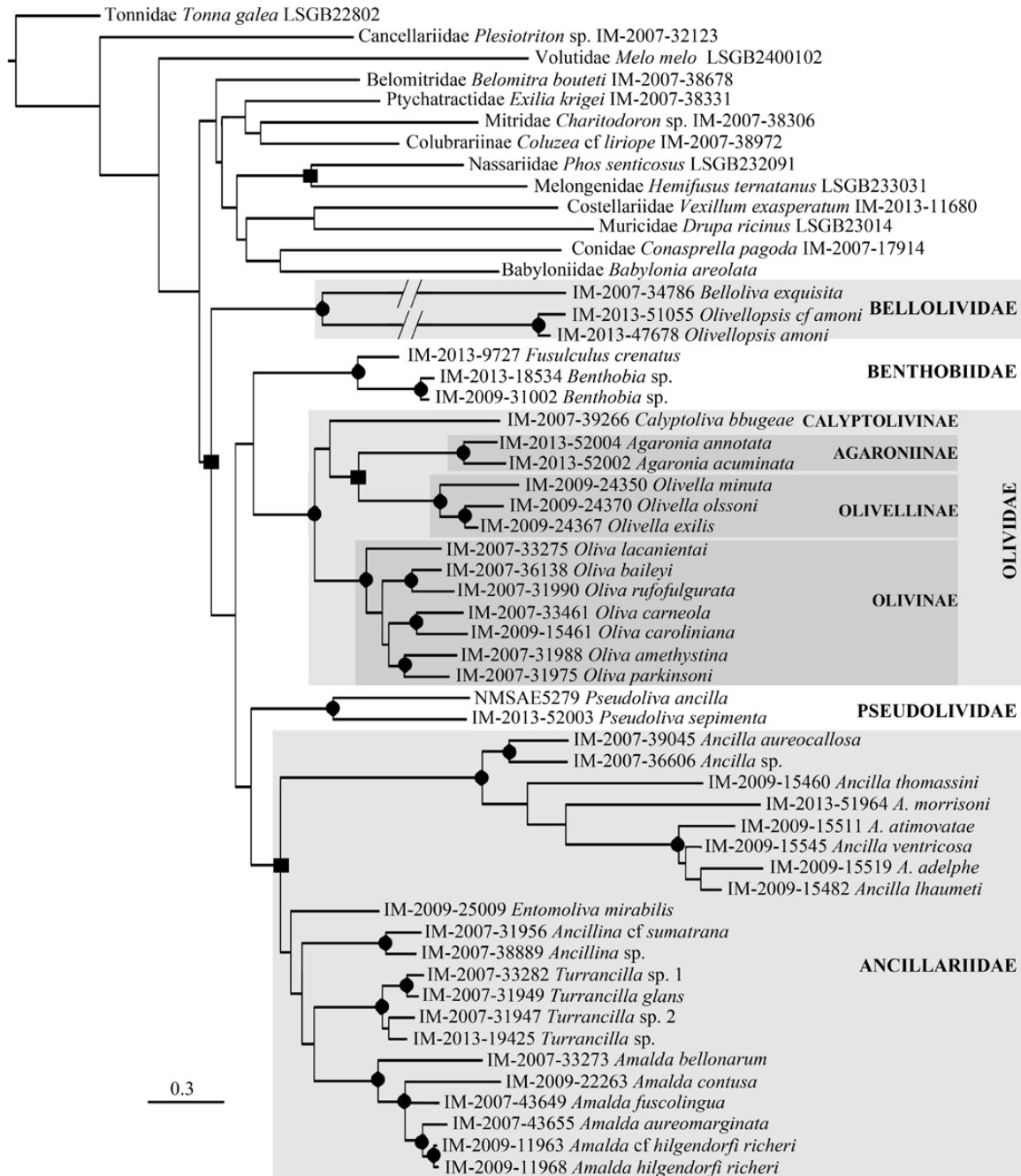


Figure 3. Phylogenetic tree of olivoidean gastropods and outgroup neogastropod taxa obtained with maximal likelihood analysis of *COI*, *16S rRNA*, *12S rRNA* and *H3* genes. Only supported nodes are marked on the tree: squares – bootstrap values between 80 and 89 (supported node), circles – bootstrap values between 90 and 100 (highly supported node).

and well supported) cluster together in ML and BI, although this grouping is not well supported (only by ML analysis bootstrap support = 81). The single species of *Calyptoliva* included in the analysis is sister to *Olivella* + *Agaronia*, albeit again without support. The remaining species in Olividae are representatives of *Oliva* and also form a highly supported clade.

The second large, well-supported, clade corresponds to the generally accepted subfamily Ancillariinae (formerly included in Olividae), and representatives of the five genera are included in the analysis. *Entomoliva* Bouchet & Kilburn, 1991 is represented by a single species, but each of the four remaining genera *Ancilla*, *Turrancilla*, *Ancillina* and *Amalda* corresponds to a

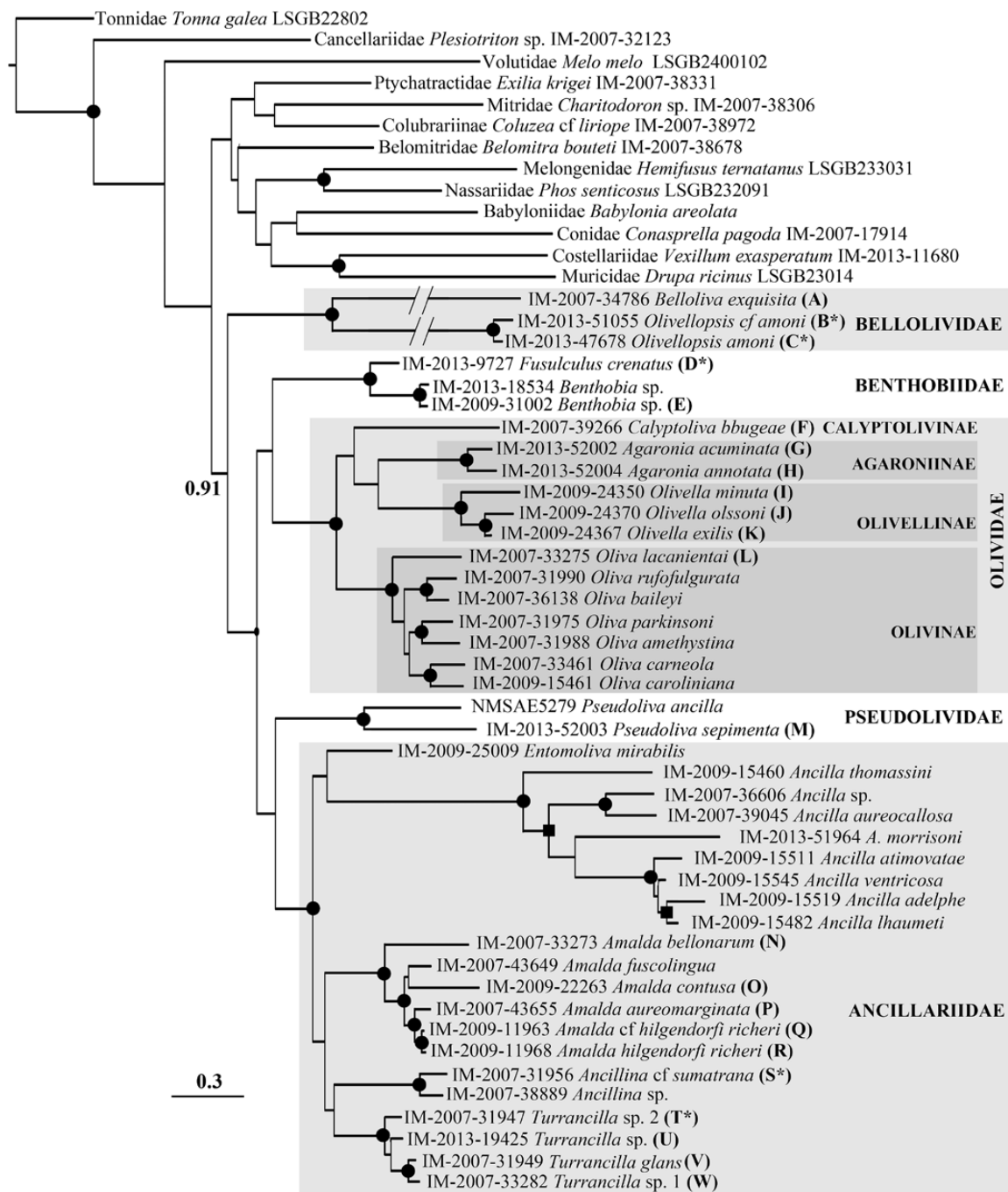


Figure 4. Phylogenetic tree of olivoidean gastropods and outgroup neogastropod taxa obtained with Bayesian analysis of *COI*, *16S rRNA*, *12S rRNA* and *H3* genes. Only supported nodes are marked on the tree (squares – posterior probability values between 0.95 and 0.97, circles – posterior probability values between 0.98 and 1.00). The letters in brackets after the species names refer to photographs of vouchers in Figs 5 and 6.

highly supported clade in both analyses. On the contrary, relationships between genera remain unresolved.

Conversion of the molecular tree into a classification is straightforward, taking into account the anatomical data, which are described and discussed in

the following sections. All the terminal suprageneric taxa are highly supported both in Bayesian and ML analyses (the posterior probabilities are 1, while the bootstrap supports range from 81 for Ancillariinae to 96–100 for all the others).

Conchologically and anatomically, *Belloлива* and *Olivellopsis* are rather similar to Olividae, sharing a number of common characters, including the mantle morphology (which has a mantle filament, and correspondingly a filament channel is present on the shell), similar radular morphology, and presence of the anterior shell band (the characters that are seemingly apomorphic for Olivoidea). Conversely, members of Pseudolividae and Benthobiidae are notably different in shell morphology and anatomy, lacking the above-mentioned characters. Thus, the topology of our molecular trees contradicts the parsimonious scheme of relationships that could be suggested based on morphology.

The ranks of suprageneric taxa are always subjective, even if all the data are taken into consideration. Olivoidea is a remarkable example of this. *Olivella* is morphologically very distinct from other oliviforms, having a very unusual radula with five teeth per transverse row (while all other ingroup genera have only three), and lacking a gland and valve of Leiblein. Nevertheless, the molecular analysis confidently places *Olivella* in the same clade as *Agaronia* and *Oliva*, whereas the morphologically more similar *Belloлива* forms a totally separate branch. Correspondingly, we rank as family the clade combining *Olivella*, *Agaronia*, *Oliva* and *Calyptoliva* and to accentuate the high morphological disparity, we recognize within Olividae the four subfamilies Olivinae, Agaroniinae Olsson, 1956, Olivellinae Olsson, 1956, and Calyptolivinae subfam. nov.

No family group name being available for the clade uniting *Belloлива* and *Olivellopsis*, we propose for it the new family name Bellolividae fam. nov. (see Taxonomy section). Similarly, no name being available for the clade including representatives of *Benthobia* and *Fusulculus*, previously (e.g. Vermeij, 1998) included in Pseudolividae, we propose for it the new family Benthobiidae fam. nov. (see Taxonomy section).

For consistency, we rank Ancillariidae Swainson, 1840, as a family.

MORPHOLOGY

Shell and anatomy are rather variable in Olivoidea and have previously – and in the current paper – been used for classification at different taxonomic levels. After giving consideration to the subject for many years, we offer hypotheses of homologies of the different shell structures and correlate them with the morphology of the mantle. A bold typeface is used for the terms accepted by us, and italics are used for terms proposed earlier that we regard as synonyms (see Table 3 for shell characters).

Shell

The shells of Olivoidea as defined in the current paper can be divided into two types. The first is found in Olividae, Ancillariidae and Bellolividae and is characterized by a glossy surface without periostracum and the presence of the so-called anterior band and fasciole on the anterior part of the last whorl (Fig. 5A–C, F–L, 6). In Benthobiidae and Pseudolividae, the shell is normally covered with a thin-to-thick periostracum, and the anterior band is not pronounced (Fig. 5D–E, M). While refraining from implying any taxonomic value to these terms, we will for convenience refer to these two shell types as the ‘oliviform’ and ‘pseudoliviform’ respectively, and describe them in the following section.

The most complex shell morphology is probably found in species of *Oliva* (Olivinae). It was treated in detail by Tursch and Greifeneder (2001), who suggested homologies with other groups of the superfamily (Tursch and Greifeneder 2001: Fig. 7.21). By giving closer attention to other representatives of the superfamily, we have had to reconsider Tursch & Greifeneder’s scheme (which was focused on *Oliva*) and this leads us to a revised terminology based on revised suggested homologies. Because shell characters have commonly been used in olivoidean taxonomy, many terms have been proposed, usually based on a particular taxon.

The oliviform shell

The oliviform shell is glossy, with the spire, columella, and parietal wall of aperture callused to a different degree; the modified anterior part of the last whorl and fasciole are also callused. The last whorl is separated into three main regions: the **last whorl cloak**, the **anterior band** and the **plication plate**. The **last whorl cloak** is the surface of the adapical part of the last whorl (Fig. 7, CL), it is glossy, enamelled and, except for a few Ancillariidae (e.g. *Entomoliva*), devoid of sculpture. Abapically from the cloak (or from the olivoid band, when present) there is a sharp border (Fig. 7, ②) that delimits the callused band, which is called here the **anterior band** following Tursch & Greifeneder (2001) (Fig. 7, AB). As was pointed out by these authors, this border is represented by a sharp step (which can be easily felt by the finger), although it is often referred to as a groove. In some oliviforms, there is also a spiral groove (Fig. 7, ①) situated at some distance adapically from the **rear edge** (Fig. 7, ②) of the anterior band. In most cases, it is a narrow and deep groove (rarely it looks like a very low ridge) that delimits one more band, the surface of which is similar to the rest of the cloak, although it can differ in color – sometimes rather contrasted, as in, for example *Amalda contusa* (Reeve, 1864). The groove

Table 3. Homology of different structures of the anterior oliviform shell in Olivioidea and correlation of terminology used for its description in different genera

Major and secondary areas (accepted here)	Grooves and borders (accepted here)	<i>Olivia</i> (Tursch, Greifeneder, 2001)	<i>Olivella</i> (Olsson, 1956)	<i>Amalda</i> (Kilburn, 1977)	<i>Ancilla</i> (Kilburn, 1981)	<i>Eburna</i> (Voskuil, 1991)
Body whorl cloak (CL)		Body whorl cloak	General surface	Not specified	Not specified	Not specified
	Olivoid band	absent	absent	Ancillid band	Ancillid band (when present)	Ancillid band
Anterior band (AB)	Upper anterior band (uab)	Upper anterior band	Fasciolar band	Posterior fasciolar band	Fasciolar band	Posterior fasciolar band
	Lower anterior band (lab)	Lower anterior band		Anterior fasciolar band		Anterior fasciolar band
Plication plate (PP)		Parietal plate	Columella pilar + parietal callus	Columella pilar	Columella pilar	Columella pilar
		belt				
		shoe				
	Olivoid groove ①	Absent	Absent	Ancillid groove	Ancillid groove (when present)	Ancillid groove
	Rear edge of anterior band ②	Rear edge of anterior band	Not specified	Not specified	Posterior fasciolar groove	Not specified
	Fasciolar ridge ③	Absent	Submedian line	Posterior fasciolar groove	Absent	Posterior fasciolar groove
	Rear edge of plication plate ④	Rear edge of belt	Not specified	Anterior fasciolar groove	Anterior fasciolar groove	Anterior fasciolar groove

Note: Abbreviations and conventions correspond to Figure 7.



Figure 5. Shells of sequenced species. Conspecific specimens of sequenced vouchers (in cases of poor preservation of the voucher) are marked with asterisk. Shells not to scale. For collection data of registered specimens, see Table 1. (A) *Belloлива exquisita*, MNHN IM-2007–34786, SL 7.2 mm. (B*) *Olivellopsis* cf. *amoni*, Papua-New Guinea, Kavieng Lagoon, South coast of Baudison Island, KAVIENG 2014, st. KB20 02°45,2'S, 150°41,7'E, 8 m, SL 3.4 mm. (C*) *Olivellopsis amoni*, Papua-New Guinea, Kavieng Lagoon, NE corner of Nusa Island, KAVIENG 2014, st. KS19, 02°34'S, 150°47,1'E, 10 m SL 3.9 mm. (D*) *Fusulculus crenatus*, MNHN IM-2007–34041, Solomon Islands, SALOMON 2, st. CP2213, 7°38'42"S; 157°42'53.9856"E, 495–650 m, SL 20.6 mm. (E) *Benthobia* sp., MNHN IM-2009–31002, SL 10.3 mm. (F) *Calyptriliva bbugae*, MNHN IM-2007–39266, SL 8.2 mm. (G) *Agaronia acuminata*, MNHN IM-2013–52002, SL 25.3 mm; (H) *Agaronia annotata*, MNHN IM-2013–52004, SL 18.0 mm. (I) *Olivella minuta*, MNHN IM-2009–24350, SL 9.1 mm. (J) *Olivella olssoni*, MNHN IM-2009–24370, SL 5.4 mm. (K) *Olivella exilis*, MNHN IM-2009–24367, SL 6.6 mm. (L) *Oliva lacanientai*, MNHN IM-2007–33275, SL 16.4 mm. (M) *Pseudoliva sepimenta*, MNHN IM-2013–52005, SL 8.5 mm. MNHN, Muséum National d'Histoire Naturelle, Paris, France; SL, shell length.

is often referred to as *ancillid groove* and the band delimited by it as *ancillid band* (Kilburn, 1977, 1981). To avoid reference to a particular taxon (in this case, the genus *Ancilla*), we suggest here the terms **olivoid groove** and **olivoid band** for the band of the cloak that is delimited by the groove. It is important to note that the surface of the olivoid band is not callused and is similar to the rest of the **last whorl cloak**.

An olivoid groove is found in a number of unrelated olivoideans. It is present in Ancillariidae (in some *Ancilla* spp. and *Turrancilla* spp., and always present in *Ancillina*, *Amalda* and *Eburna*) and Agaroniinae. In species with a well-pronounced olivoid groove, there is usually a more or less developed **labral denticle** (Fig. 7, *Ancilla* – Id), terminating the groove on the lip.

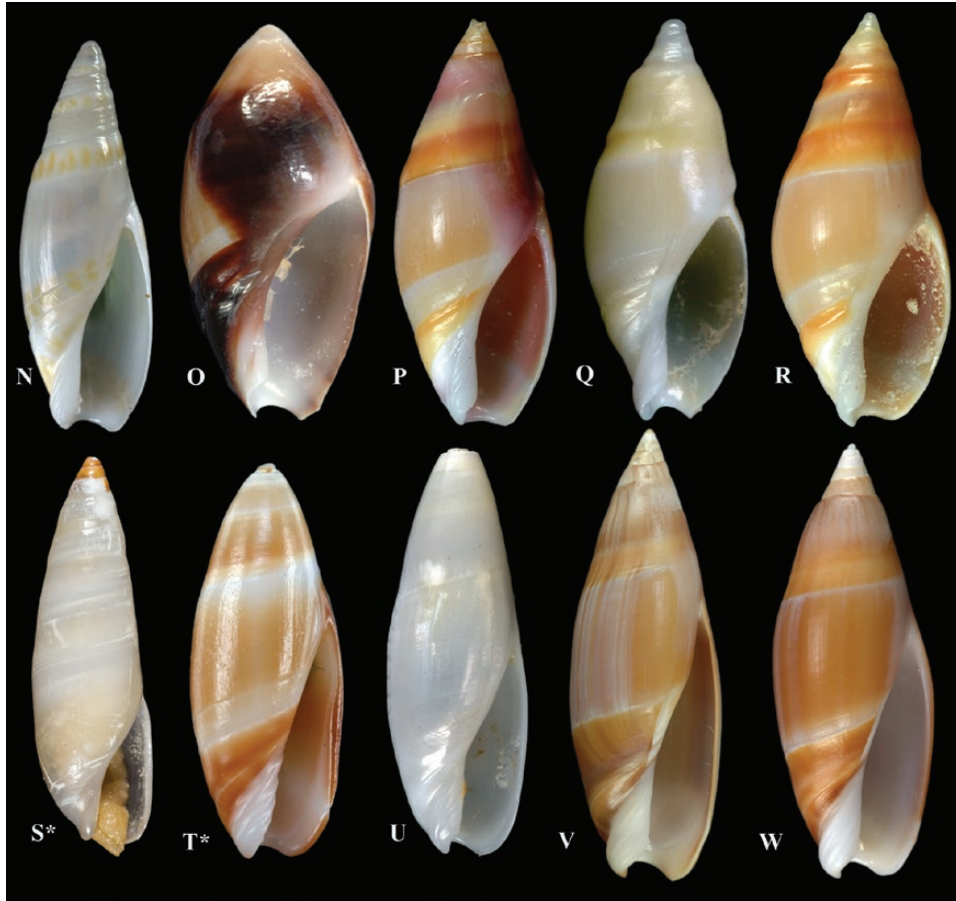


Figure 6. Shell of sequenced species. Conspecific specimens of sequenced vouchers (in cases of poor preservation of the voucher) are marked with asterisk. Shells not to scale. For collection data of registered specimens, see Table 1. (N) *Amalda bellonarum*, MNHN IM-2007–33273, SL 16.6 mm. (O) *Amalda contusa*, MNHN IM-2009–22263, SL 24.9 mm. (P) *Amalda aureomarginata*, MNHN IM-2007–43655, SL 31.5 mm. (Q) *Amalda* cf. *hilgendorfi richeri*, MNHN IM-2009–11968, SL 32.5 mm. (R) *Amalda hilgendorfi richeri*, MNHN IM-2009–11963, SL 14.9 mm. (S*) *Ancillina* cf. *sumatrana*, BIOPAPUA, st. CP3731, 07°50'S, 148°04'E, 895–1150 m, SL 7.3 mm. (T*) *Turrancilla* sp. 2., MNHN IM-2007–31954, PANGLAO 2005, st. CP2360, 8°48'54"N; 123°37'36.0156"E, 357–372 m, SL 12.3 mm. (U) *Turrancilla* sp., MNHN IM-2013–19425, SL 20.5 mm. (V) *Turrancilla glans*, MNHN IM-2007–31949, SL 36.4 mm. (W) *Turrancilla* sp. 1, MNHN IM-2007–33282, SL 34.1 mm. MNHN, Muséum National d'Histoire Naturelle, Paris, France; SL, shell length.

The anterior band of the Ancillariidae has been called the *fasciolar band* by Kilburn (1977, 1981). However, we avoid using this term, since the band extends adapically beyond the limit of the fasciole. This anterior band is callused, usually shagreened to some extent. It can be uniform and rather thin (e.g. in some *Olivella* and *Belloлива*), or it can be very thick, distinctly subdivided into an **upper** (Fig. 7, **uab**) and a **lower** anterior band (Fig. 7, **lab**), sometimes distinguished by a slight difference in color (in some *Oliva* and *Olivella*), sometimes separated by an obtuse or very sharp step (in most Ancillariidae, except *Ancilla*). For the border between the upper and lower parts of the anterior band, we introduce here the term **fasciolar ridge** (Fig. 7, ③). It was referred to as the

posterior fasciolar groove in *Amalda* and *Eburna* (Kilburn, 1977; Voskuil, 1991) and as the *submedian line* for some *Olivella* (Olsson, 1956), although it is not a groove. An important observation in recognizing the homology of the anterior band is that it abuts to the rest of the last whorl, that is the **cloak**.

The rear edge of the anterior band sometimes reaches the outer apertural lip (in, e.g. *Turrancilla*, *Eburna* and *Entomoliva* – Fig. 8C, D), or comes in very close proximity to the lip in *Amalda* (Fig. 8B) but, in *Oliva* and *Ancilla*, this sharp step is smoothed and merged with the anterior notch callus and disappears at some distance from the lip (Fig. 8A).

The anteriormost part of the shell is most highly raised above the surface of the other part of the posterior

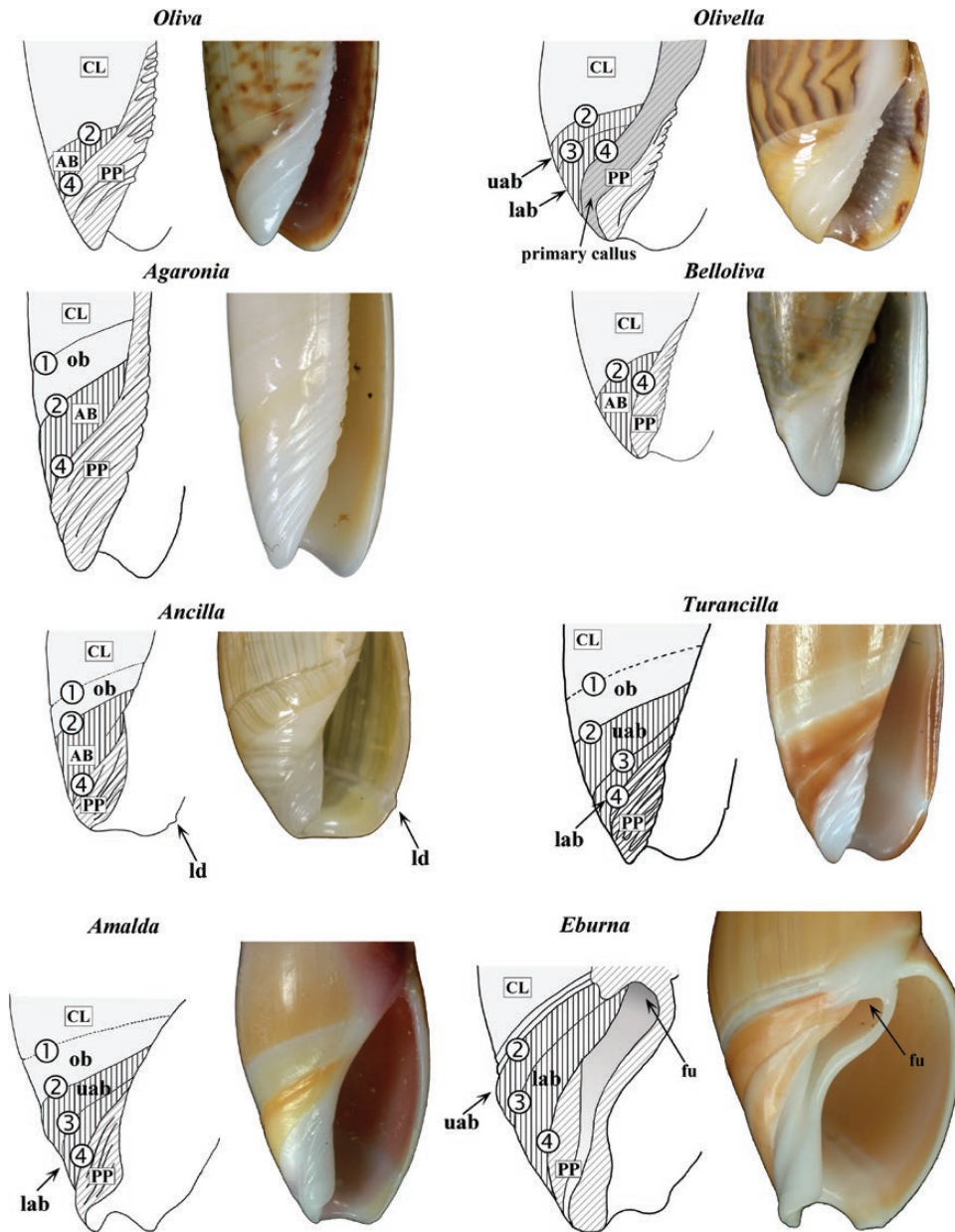


Figure 7. Interpretative drawings and photos of the anterior end of the shell of actual specimens in different Olivoidea, showing terminology and proposed homologies. Homologous areas are similarly tiled. *Oliva* – drawing after Tursch & Greifeneder (2001), shell of *Oliva caroliniana*, MNHN IM-2009–15462. *Olivella* – drawing of *O. (Niteoliva) nitidula* (after Olsson, 1956), shell of *Olivella minuta*, MNHN IM-2009–24350. *Agaronia* – *A. acuminata*, MNHN IM-2013–52002. *Belloliva* – drawing after Kantor & Bouchet (2007), shell – *B. exquisita*, MNHN IM-2007–34786. *Ancilla* – drawing redrawn after Kilburn (1981), shell – *Ancilla thomassini*, MNHN IM-2000–15460. *Turancilla* – *Turancilla* sp. 2, MNHN IM-2007–31954, Philippines, the olivoid groove (depicted by dashed line) is present in this species, but absent in other studied ones. *Amalda* – drawing modified from Kilburn (1977), shell – *Amalda aureomarginata*, MNHN IM-2007–43655. *Eburna* – *E. glabrata* (Linnaeus, 1758), Venezuela, YK collection. ①, olivoid groove; ②, rear edge of anterior band; ③, fasciolar ridge; ④, rear edge of plication plate; AB, anterior band; CL, last whorl cloak; fu, false umbilicus; lab, lower anterior band; ld, labral denticle; ob, olivoid band; PP, plication plate; uab, upper anterior band. MNHN, Muséum National d’Histoire Naturelle, Paris, France; SL, shell length.

whorl and in most cases is off-white and enamelled. It is referred to here as the **plication plate** (Fig. 7, PP – following Tursch & Greifeneder, 2001 = *columella pillar*

of Kilburn, 1977, 1981). We do not follow Kilburn’s terminology, since this structure is not really a columella (this is very convincingly demonstrated by the

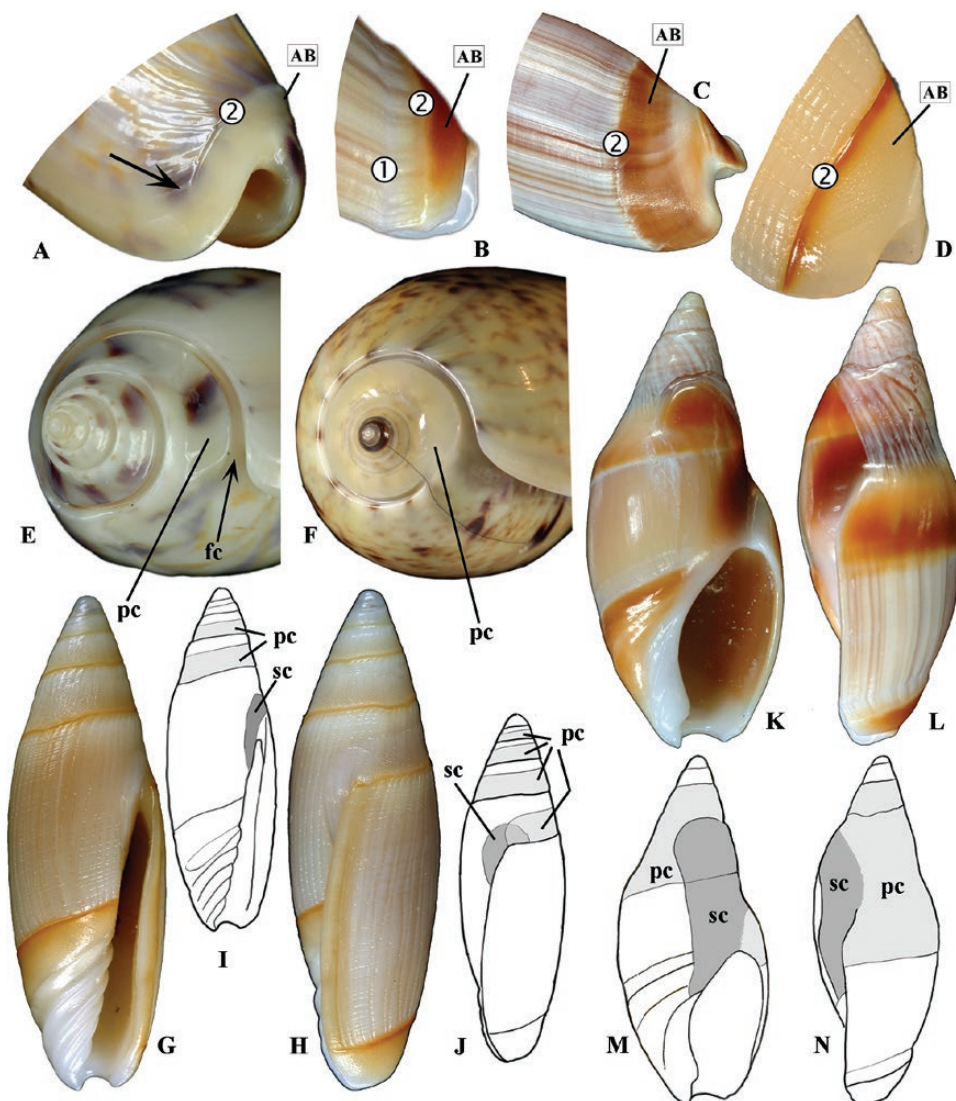


Figure 8. Details of the shell morphology of Olivoidea. (A–D) Dorso-anterior views of the anterior band. (A) *Oliva miniacea*, MNHN IM-2007–31973. An arrow indicated the place, where the anterior band is merging with the siphonal notch callus. (B) *Amalda fuscolingua*, MNHN IM-2007-43649. Rear edge of the anterior band nearly reaches the lip. (C) *Turrancilla* sp. 1, Solomon Islands, SW Choiseul Island, SALOMON 2, st. CP2212, 7°38'S, 157°42'E, 400–475 m. Anterior band is strongly shagreened and its rear edge reaches the lip. (D) *Entomoliva mirabilis*, east coast of New Caledonia, BATHUS1, st. CP713, 21°45'S, 166°37'E, 250 m. Anterior band is strongly shagreened and its rear edge reaches the lip. (E–F) lateral views of the tip and upper part of aperture of *Oliva* spp. (E) *Oliva miniacea*, MNHN IM-2007-31973. The primary spire callus is not overlaying the filament channel. (F) *Oliva bulbiformis* Duclos, 1835, MNHN IM-2007-31996. The primary callus overlaying the filament channel, which remains free along last whorl. The anterior border of the callus is marked by a grey line. (G–N) Photographs of shells and interpretative drawings of the same specimens to show the position of the calluses. (G–J) *Entomoliva mirabilis*, east coast of New Caledonia, BATHUS 1, st. CP713, 21°45'S, 166°37'E, 250 m. (K–N) *Amalda fuscolingua* MNHN IM-2007–43649. For collection data of registered specimens, see Table 1. ①, olivoid groove; ②, rear edge of anterior band; AB, anterior band; fc, filament channel; pc, primary spire callus; sc, secondary spire callus.

illustration of the partial section of the shell of *Oliva* (Tursch & Greifeneder, 2001: Fig. 7.20) and it also extends significantly on the side of the shell, as well as to the parietal wall of aperture. In most cases it bears variously pronounced spiral grooves, defining several

differently pronounced spiral ridges, but can also be completely smooth. The ridges are especially well pronounced in *Oliva*, *Agaronia* and *Entomoliva*. Further subdivision of the plication plate in the former genus is described in detail by Tursch & Greifeneder's (2001:

Fig. 7.15). The border between the plication plate and anterior band is also represented by a step or ridge, which is referred to here as the **rear edge of the plication plate** (Fig. 7, ④). The plication plate can be pronounced on the anterior part of the shell only, or it can extend significantly along the inner lip and parietal part of the aperture. It is adjoining or sometimes fused with the primary spire callus.

In some *Olivella* (e.g. in the subgenus *Niteoliva* Olsson, 1956), the primary spire callus extends anteriorly nearly along the entire plication plate, in fact becoming part of it, although Olsson (1956: Figs 1, 5) gave it a separate name (*parietal callus*).

The shell of *Eburna*, being generally rather typically ancillariid, has two unique characters, the homology of which is not obvious. First, it has two closely spaced olivoid grooves and therefore it is not clear which one is homologous with the olivoid groove of other Olivioidea. Second, the plication plate is separated in its upper part from the parietal wall of the last whorl and forms a false umbilicus (Fig. 7, *Eburna* – fu).

The shell of Olivioidea is callused to different degrees, functional significance of which remains unclear. Sometimes (*Belloliva*, *Calyptoliva*) the callus is limited to a thin glaze on the parietal wall of the aperture, but more often it extends adapically, sometimes nearly reaching the upper spire whorls and effectively covering the entire spire, only leaving exposed the protoconch and a part of the cloak of the last whorl. In Ancillariidae, the callus nearly always overlays the suture, which cannot be seen externally. The callus can be colored contrastingly to the shell cloak, or can be of the same color. In some cases the callus seems to be uniform, but in others it obviously consists of two different layers, the **primary** (Fig. 8I, M, pc) and the **secondary spire callus** (Fig. 8I, M, sc) (following the terminology of Kilburn, 1977). The primary spire callus extends spirally, while the secondary callus rather extends axially, covering the parietal part of the last whorl, sometimes also the columella. When both calluses are present, sometimes they fuse without distinct border in the upper part of the aperture but, at least in *Entomoliva*, it is obvious that the primary spire callus, developed as a band over the suture (and practically leaving the suture free), is slightly overlaid by the secondary callus above the aperture in side view of the shell (Fig. 8H, J). It also should be mentioned that the secondary callus is in many cases positioned on top of the primary callus, deposited on the previous whorl and thus forming a complex multilayered structure.

A different pattern is observed in Olividae and Bellolividae. In Olivinae, the primary callus extends to the penultimate and upper spire whorls, but not to the last whorl. On the penultimate whorl, it does not reach the suture, leaving it open (for the definition of suture see the following paragraph) (Fig. 8E, F), but

on the upper spire whorls it can overlay the suture. For the primary callus of *Oliva*, Tursch & Greifeneder (2001) used the term *posterior callus*. In Agaroniinae, the callus does not overlay the suture on spire whorls, but is otherwise similar to that in *Oliva*. In Olivellinae, the callus extends abapically on the parietal wall and fuses with the plication plate, sometimes extending as far as the anterior end of the shell. On the spire it can cover all whorls, but the callus is situated above the suture, which therefore remains open.

The suture on the shells of Olividae is unique and requires special attention. Sterba (1996) was the first to point out that the narrow channel seen between the whorls of *Oliva* does not correspond to the true suture. The whorls in *Oliva* do not come into direct contact with each other, but the subsequent whorl is connected to the spire callus of the previous one and, in addition, the thin layer is embedded between the whorl and spire callus of the previous whorl. Tursch & Greifeneder (2001: Figs 7.04, 7.09) described the suture area of the shell in detail and came to the conclusion that the narrow channel does not correspond to a canaliculate suture and therefore proposed the term **filament channel**. This terminology is followed herein. A filament channel, which opens into the posterior edge of the aperture (Fig. 8E, F, fc), is present in Olividae (except *Calyptoliva*) and Bellolividae, but is absent in other members of the superfamily.

The pseudoliviform shell

In the pseudoliviform shell, which is much more 'typical' of standard Neogastropoda (Fig. 5D*, E, M), the callus is restricted to the columella and extends slightly onto the parietal wall of the aperture, but never onto the spire. The anterior band is absent. The shell is normally covered by periostracum, which can be very thick (e.g. in *Pseudoliva*). An olivoid groove is always present, usually terminating with a weakly pronounced labral denticle.

Soft body morphology and its correlation with shell

The external morphology of most Olivioidea (except Benthobiidae and Pseudolividae) is rather characteristic. The foot is broad, usually thin and clearly subdivided by a transversal furrow into the anterior propodium and posterior metapodium. The propodium is crescent-shaped and, on the dorsal side, separated into symmetrical halves by a longitudinal furrow (Figs 9; 10A, B, E, F). In some Olivellinae [subgenus *Olivella* (*Pachyoliva*)], the lateral tips of the propodium are thickened and elongated (Fig. 9F, arrow), and play an important role in feeding, producing the mucus nets in which the snails collect suspended detritus in



Figure 9. Live animals of different Olivoidea. (A) *Oliva tessellata* Lamarck, 1811; Papua-New Guinea, Kavieng Lagoon, Nago Island, KAVIENG 2014, st. KR06, 02°36,3'S, 150°46,2'E, 3–12 m, MNHN IM-2013–46528 (photo by L. Charles). (B–C). *Oliva miniacea*, Papua-New Guinea, Kavieng Lagoon, Nago Island, KAVIENG 2014, st. KD01, 02°37,5'S, 150°46,5'E, MNHN IM-2013–47178 (Photo by L. Charles); (B) enlarged anterior end of crawling snail to show anterior mantle tentacle and anterior mantle lobe, forming the anterior band. (D) *Oliva sericea*, Philippines, Panglao Island (photo by S. Tagaro), crawling animal, ventral view of the foot to show the foot pouch. (E) *Olivella biplicata* (Sowerby, 1825), Bodega Bay, California, USA (after Troost *et al.*, 2012, photo courtesy W. S. Peters). (F) *Olivella semistriata* (Gray, 1839), Playa Grande, Costa Rica (after Troost *et al.*, 2012, photo by W.S. Peters). The species possesses very long free propodial tips (marked by an arrow) that form the mucus net during feeding. (G) *Agaronia acuminata*, Senegal, Dakar, DAKAR'09, st. 18, 7–12 m (photo by P. Maestrati). (H) *Amalda contusa*, Mozambique, Inhaca Island, MNHN IM-2009–22263. (I) *Ancillina* sp., Philippines, AURORA 2007, st. CP2730, 358–378 m, 15°21'N, 121°34'E (photo by B. Buge). (J) *Olivellopsis amoni*, Papua-New Guinea, Kavieng, MNHN IM-2013–51055 (photo by L. Charles). (K) *Ancilla ventricosa*, MNHN IM-2009–15537 (photo by P. Maestrati). aml, anterior mantle lobe; amt, anterior mantle tentacle; cept, cephalic tentacle; fp, foot pouch; mf, mantle filament; par, parapodia; prp, propodium; s, siphon.

the backwash (Troost *et al.*, 2012). The metapodium has large paired lateral lobes, the parapodia, which laterally embrace the shell of the crawling snail. In

Ancilla, they nearly completely cover the shell (Fig. 8K), leaving free only the apical part of the spire. In *Oliva* (Kantor & Tursch, 2001a) and *Agaronia* (Rupert

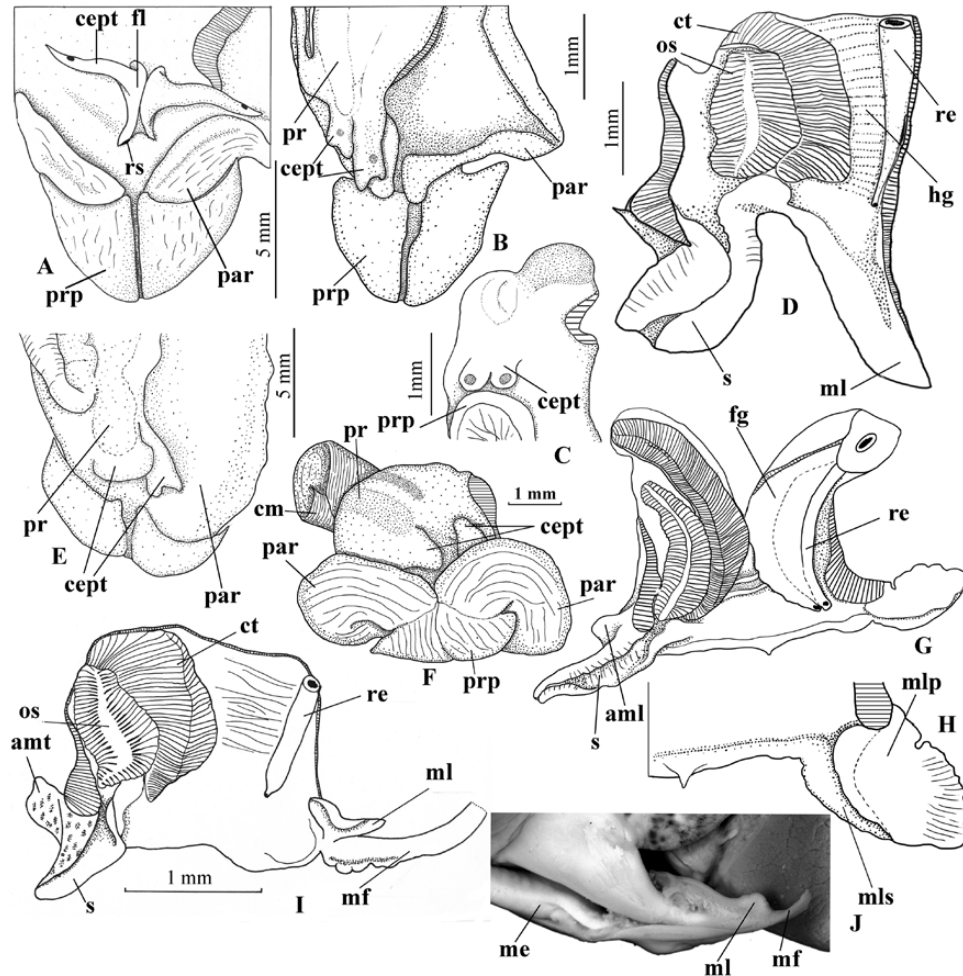


Figure 10. Morphology of head-foot and mantle of different Olivoidea. (A) *Oliva bulbosa* (Röding, 1798) anterior view of the head and propodium, mantle removed (after Kantor, 1991). (B) *Entomoliva mirabilis*, New Caledonia, EXBODI, st. DW3787, 22°13'S, 167°06'E, 223–249 m. Anterior view of the head-foot, mantle removed. (C–D) *Pseudoliva sepimenta*, Congo, MNHN IM-2013–52003. (C) Anterior view of the head-foot, mantle removed; (D) mantle, internal view. (E) *Agaronia acuminata*, Senegal, Casamance, MNHN. Anterior view of the head-foot, mantle removed. (F) *Belloliva alaos* Kantor & Bouchet, 2007, North of New Caledonia, MUSORSTOM 4, st. DW160, 18°42'S, 163°13'E, 668 m (after Kantor & Bouchet, 2007). Head-foot, dorsal view, mantle and visceral mass removed. (G–H) *Amalda aureomarginata*, New Caledonia, Ile des Pins, st. CP3115, 22°48'S, 167°15'E, 440–470 m; (G) mantle complex, (H) enlarged bipartitioned mantle lobe, dashed line shows the border of upper, flexible and reflectable partition (lobe). (I) *Olivella borealis* Golikov, 1967, Japan Sea, Vostok Bay, 5–6 m. Mantle complex, mantle filament partly removed (after Kantor, 1991). (J) *Oliva mantichora*, Mozambique, Inhaca Island, INHACA 2011, st. MB5, 26°01.0'S, 32°54.1'E, 6 m. Photograph of the mantle filament and mantle lobe. aml, anterior mantle lobe; amt, anterior mantle tentacle; cept, cephalic tentacle; cm, columellar muscle; ct, ctenidium; fg, female gonoduct; fl, cephalic flap; hg, hypobranchial gland; mf, mantle filament; ml, mantle lobe; mlp, part of mantle lobe, producing primary callus; mls, part of mantle lobe, producing secondary callus; os, osphradium; par, parapodia; pr, proboscis seen through the body walls; prp, propodium; re, rectum; rs, rhynchostome; s, siphon.

& Peters, 2011), the posterior part of the foot can be folded transversely to form a tightly sealed ventral pouch, in which the prey is kept after capture and during feeding (see details in Kantor & Tursch, 2001b). The epithelium of this portion of the foot is different in color and structure from the rest of the sole (Fig. 9D, fp).

The head of Olivoidea is very variable, with a clear tendency to asymmetry. In Benthobiidae, the head morphology is rather typical of Neogastropoda, with more or less long cylindrical tentacles with closely spaced bases, with (*Fusulculus*) or without (*Benthobia*) eyes (Kantor, 1991: Fig. 14D; Simone, 2003: Figs 7A, 9A). In Pseudolividae, the cephalic tentacles are rather

short, but with broad to very broad basal flaps bearing eyes. In *Pseudoliva sepimenta* (formerly *Fulmentum*), the head bears very short tentacles without basal flaps and large eyes (Fig. 10C), it is slightly asymmetrical, with the rhynchostome, that is the opening through which the proboscis is everting, shifted to the base of the right tentacle.

In Olivinae, the head is externally symmetrical and is formed by paired, vertical, closely spaced flaps, which bear tentacles with eyes (Fig. 10A, fl, cept); however, a closer examination shows that the rhynchostome lies under the right tentacle. In all other groups (except Benthobiidae and Pseudolividae), the head is strongly asymmetrical and formed by dorso-ventrally flattened cephalic flaps (Fig. 10B, E, F). Sometimes the flaps are very broadly spaced and the left one is shifted to the base of the siphon.

The shell morphology of Olivoidea is correlated with mantle morphology, particularly with the presence of several appendages that are found in different combinations in different families. It should be noted that in many cases it is impossible to examine the mantle in living crawling snails, since the parapodia completely cover the shell and, when disturbed, the animal withdraws immediately. Nevertheless, in Olividae – especially in *Oliva*, *Agaronia* and *Olivella* – the parapodia are less developed and cover the shell only laterally, thus allowing direct observations of the mantle appendages.

The presence of a filament channel on the shell is correlated with the presence of a **posterior mantle filament** (or *posterior mantle tentacle*) (Figs 9A, 10I, mf). This is an agile muscular rod, originating at the right anterior corner of the mantle, passing through the upper part of the aperture and positioned in the filament channel of the shell. The filament can move in the channel and can be completely withdrawn into the shell when the snail is disturbed. Its histology appears similar in the several studied species, *Olivancillaria auricularia*, *Oliva sayana*, *Olivella verreauxii* (Marcus & Marcus, 1959) and *Olivella borealis* (Kantor, 1991). The filament consists of a layer of separate bundles of longitudinal muscles and contains numerous secretory cells and, at least in some species, a well-developed nerve. The filament extends along all the length of the open part of the channel, which in *Oliva* is usually covered in its upper part by the callus, but can be free in *Olivella* and *Agaronia*, although often occluded with debris in upper whorls, thus indicating that the filament does not extend to the tip of the shell.

In all Olivoidea except Belloliviidae, the right anterior corner of the mantle is transformed into a more or less extended **posterior mantle lobe**. In live *Oliva* animals, this very thin lobe is nearly transparent and highly extensible and covers the area of the primary callus, extending adapically beyond the limits of the

aperture and posterior to the outer lip. In preserved specimens, the lobe is strongly contracted, even when the snails were relaxed in magnesium chloride prior to fixation (Fig. 10J, ml). As in Belloliviidae neither the primary nor the secondary callus is pronounced and a mantle lobe is not visible (Kantor & Bouchet, 2007), we hypothesize that the primary spire callus is deposited by the posterior mantle lobe. In Pseudolividae and Benthobiidae a posterior mantle lobe is also present (Fig. 10D, ml), but there is no primary spire callus and the mantle lobe probably is responsible for depositing the thick parietal callus. In Pseudolividae it forms the plate-like parietal ridge that separates a narrow adapical extension from the rest of the aperture (Fig. 5M, arrow).

In Ancillariidae, in addition to the primary, there can be a pronounced **secondary spire callus**. The distinction between the two is sometimes conventional, because in, for example, *Ancilla* the seemingly uniform callus is covering the entire shell surface and it is not clear whether it can be considered a primary or a secondary one (Kilburn, 1981 considered it primary). Nevertheless in *Amalda* the distinction is rather clear on the ventral shell surface, where both calluses are adjoining each other and sometimes differ markedly in color. In this case the posterior mantle lobe is hypertrophied and clearly subdivided in two partitions or lobes (Fig. 10G, H, ml). Therefore, we hypothesize that both calluses are deposited by the mantle lobe, the primary callus is deposited by a smaller lobe, that is more ventral (Fig. 10H, mlp) while the secondary callus is deposited by a broader lobe, situated more dorsally (Fig. 10H, mls).

The columella of Olivoidea can be smooth and callused or, as in *Oliva* and *Agaronia*, it can bear strong oblique plicae. Judging from their position, callus and plicae should be deposited by the ventral side of the mantle adjoining the columellar muscle. This part of the mantle edge is relatively broad in *Oliva*, although very thin and, in preserved specimens, smooth, without any fold corresponding to the plicae. It is impossible to observe the ventral mantle side in crawling animals.

The left outer corner of the mantle edge surrounding the base of the siphon is free. In living snails, it is reflected outwards and forms an additional structure for which we herein suggest the term **anterior mantle lobe** (Fig. 9B, aml). From observations of live *Oliva*, *Agaronia* and *Olivella*, it extends through the siphonal notch as well as around the anteriormost part of the lip and covers the anterior (closest to the lip) region of the anterior band. When touched, it briefly retracts, but then extends again to the same position. Based on its exact correspondence with the position of the anterior band, there is little doubt that this is the structure responsible for it. The anterior band is present in most

olivoideans (except Pseudolividae and Benthobiidae), although it can be very weak (e.g. in Bellolividae). In Olivinae, Olivellinae and Agaroniinae the lobe ends in a narrowed mobile part – the **anterior mantle tentacle** (Fig. 9A, B, E, G, **amt**). It appears to be an autapomorphy of Olividae.

Digestive system

Anterior foregut. In general, the anterior foregut is typically neogastropod. The proboscis is rather variable in morphology, from medium-long, cylindrical to short or very short and conical in the contracted state. In *Oliva* the proboscis is medium-long, with the buccal mass situated anteriorly (Kantor, 1991; Kantor & Tursch, 2001a). As observed during feeding observations on several species of *Oliva*, the proboscis is very extensible and mobile, and can reach the posterior foot poach, where the prey is kept (Kantor & Tursch, 2001). An anterior position of the odontophore in the retracted proboscis has also been recorded in *Agaronia*. In other Olivoidea, the proboscis is relatively shorter and the buccal mass is shifted away from the proboscis tip and often protrudes beyond the rear end of the retracted proboscis. The proboscis is particularly short in Benthobiidae and Pseudolividae where the major part of the odontophore protrudes backwards (Kantor, 1991; Simone, 2007). In Olivellidae, the proboscis is very short and the odontophore lies nearly completely outside the proboscis, but when the proboscis is protracted the odontophore comes close to the mouth opening (Kantor, unpublished observations on *Olivella olssoni* van Regteren Altena, 1971). It should be noted that it is nearly impossible to estimate the length of the extended proboscis in live specimens based on its contracted state in preserved specimens, since it is capable of extreme contraction. The arrangement of the odontophoral retractor(s) differs between taxa. In Benthobiidae and Pseudolividae, they are paired and pass through the nerve ring to fuse with the bottom of the body haemocoel (Kantor, 1991; Simone, 2007). In Bellolividae, Olivinae and some Ancillariidae the odontophoral retractor bypasses the nerve ring and is attached to the bottom of the haemocoel. In Olivellidae, it is branched with some branches passing through the nerve ring, and others bypassing it (unpublished observations). The proboscis retractors are thin, few and attached laterally to the middle or posterior part of the rhynchodaeum.

In Benthobiidae and Pseudolividae, the salivary glands are compact and acinous, while in Bellolividae and Olividae they are rather loose, composed of narrow branching tubes (ramified-tubular). In Ancillariidae, three types of salivary glands are present, ramified tubular in *Amalda*, *Eburna* and *Turrancilla*, acinous in some *Ancilla*, or broad and tubular in other *Ancilla*, *Ancillina* and *Entomoliva*. Accessory salivary glands

were observed in most Olivoidea. In most cases they are tubular, which is standard in Neogastropoda, but in Benthobiidae the single accessory salivary gland ends in a very large muscular sac (Kantor, 1991; Simone, 2003).

The radula of Olivoidea is rather variable and is generally genus specific (although considerable within-genus disparity can be found in *Ancilla* – Fig. 13, see also Kantor *et al.*, 2016). In most cases a radula row consists of three teeth, but in Olivellinae it contains five (Fig. 11G, H). Judging from the tree topology, the unique radular morphology is an autapomorphy of the subfamily. In addition to the multicuspid rachidian with convex base, there are simple, short, curved lateral teeth. In dorsal view these seem cylindrical, but in some projections it is obvious that they are flat plates, convex on the dorsal side and concave ventrally. Interestingly, and contrary to what is seen in other olivoideans, they are directed outwards, not towards the centre of the membrane. Laterally, there are additional flat rectangular cusplless plates with slightly thickened edges that are very slightly lifted above the membrane. Only in *Pseudoliva* are the laterals bicuspid (Fig. 12A, B); in other genera of Olivoidea the lateral teeth are unicuspid, rather uniformly hook-shaped with a more or less broad base. In many cases the teeth are convex on the anterior (dorsal) side and concave on the posterior side. In Olivinae, Agaroniinae, *Calypsoliva* and Bellolividae the tip of the lateral tooth is characteristically attenuated and is additionally bent (Fig. 11A, C, D, F). The teeth can be bifurcated on the tip (e.g. in *Amalda* cf. *hilgendorfi richeri* – Fig. 12E, F, and particularly in *Ancilla atimovatae* – Kantor *et al.*, 2016: Fig. 9B–C). The central tooth displays more disparity, from tricuspid (e.g. Figs 11F, 12A, B, H), often with additional smaller denticles or serration between the major cusps (Fig. 13D, E), to truly multicuspid (Figs 11G, 12G). The shape of the teeth can be very conservative within the genus; thus, in all *Belloлива*, there are two small additional denticles situated at the outer edge of the lateral cusps of the central tooth (Fig. 11B); similarly, very distinct cusps are present in *Agaronia* (Fig. 11E) and *Olivancillaria* (Teso & Pastorino, 2011). All Olivinae have tricuspid central teeth with a shallowly notched anterior edge and more or less extended lateral flaps of the central tooth (Fig. 11F; Kantor & Tursch, 2001a: Figs 6.20–6.27). In *Turrancilla* (Ancillariidae), all species have very similar central tooth with three large pointed cusps and a very deeply notched anterior profile (Fig. 12H). The posterior edge of the base of the central tooth forms a distinct, long and posteriorly rounded projection which corresponds in shape to the notch of the adjoining row. Rather similar central teeth are found in the two known species of *Entomoliva* (Fig. 12C).

Most Olivoidea have a well-developed pyri-form valve of Leiblein situated just in front of the

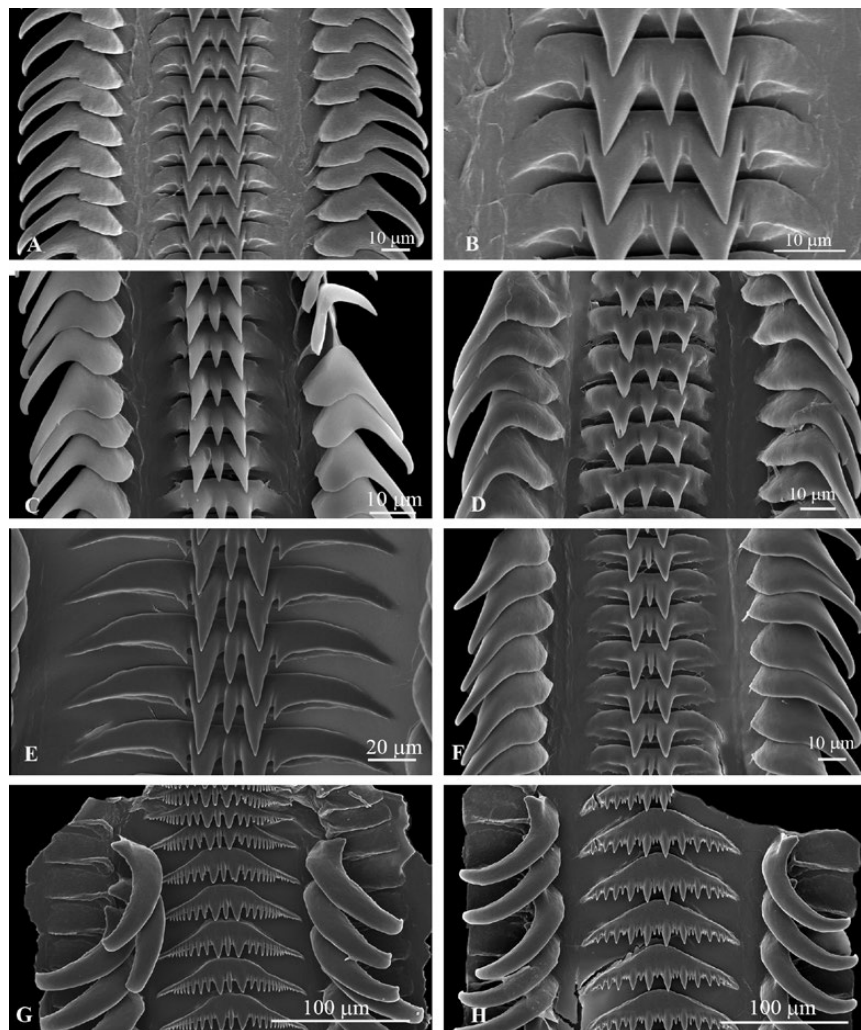


Figure 11. Radulae of Bellolividae (A–C) and Olividae (E–H). (A, B) *Belloлива exquisita*, Northern New Caledonia, MUSORSTOM 4, st. DW 184, 19°04'S, 163°27'E, 260 m (after Kantor & Bouchet, 2007). (C) *Olivellopsis amoni*, Papua-New Guinea, Kavieng Lagoon NE corner of Nusa I., KAVIENG 2014, st. KS19, 02°34'S, 150°47,1'E, 10 m. (D) *Calyptoliva bbugeae*, holotype, MNHN IM-2007–38919. (E) *Agaronia acuminata*, MNHN IM-2013–52002, central tooth. (F) *Oliva rufofulgurata* Schepman, 1904, MNHN IM-2007–36132. (G) *Olivella minuta*, MNHN IM-2009–24350. (H) *Olivella exilis*, MNHN IM-2009–24367.

circumoesophageal nerve ring. The gland of Leiblein is bulky or tubular; in *Ancilla* it is very tightly coiled and its posterior part can have muscular walls; the duct of the gland is always markedly constricted. The mid-oesophagus (between the valve of Leiblein and the duct of the gland) is lined with a glandular epithelium. A remarkable exception is *Olivella* which altogether lacks a gland of Leiblein, a valve of Leiblein, as well as a glandular mid-oesophagus.

In all olivoideans, the stomach is usually sac-like, with a long to very long and narrow posterior mixing area. In *Olivella* the entrance of the posterior oesophagus and the intestine opening are very close together and the stomach has a thick muscular ring in the middle of the posterior mixing area (Kantor, 1991:

Fig. 6A–F). In *Amalda* the very different stomach is tubular, U-shaped, without any posterior mixing area (original data).

TAXONOMY

In the following section we provide brief diagnoses for all recognized suprageneric taxa of Olivoidea and list the valid genera attributed to the recognized families. Genera are marked in the following way: (1) genera placed in the family on the basis of molecular and morphological data; (2) genera placed on the basis of shell and anatomical data; and (3) genera tentatively attributed to the family based on shell characters alone.

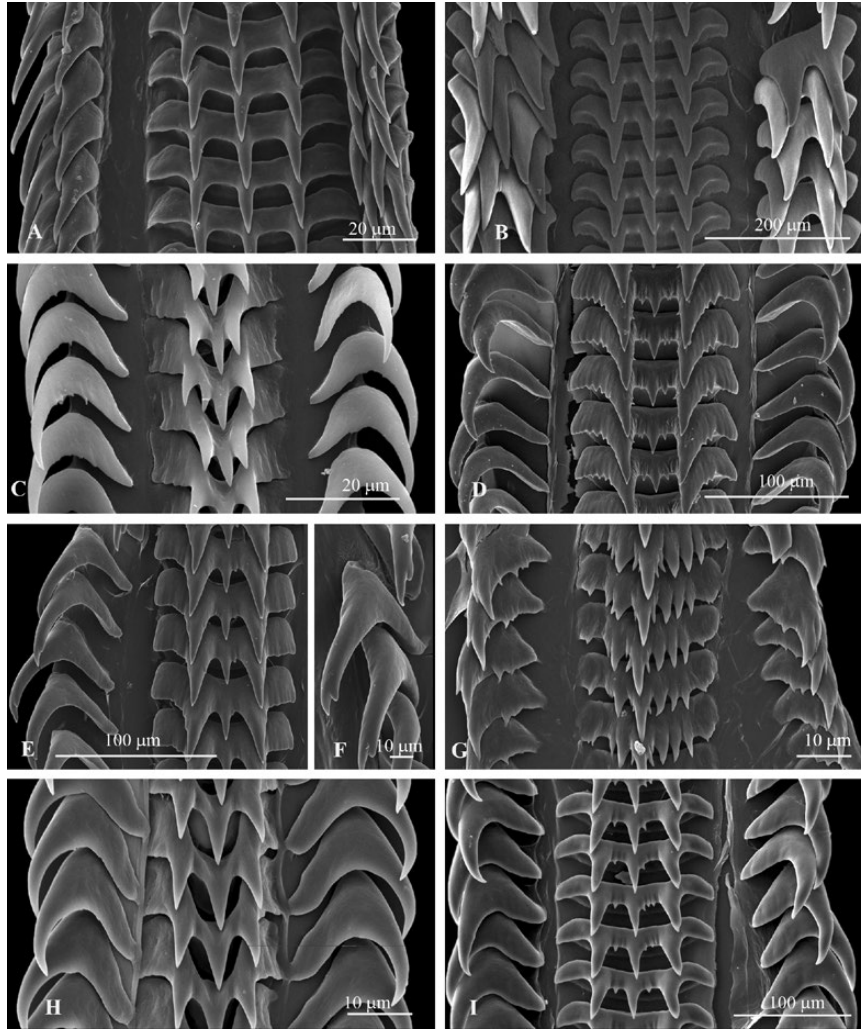


Figure 12. Radulae of Pseudolividae (A–B) and Ancillariidae (C–I). (A) *Pseudoliva sepimenta*, MNHN IM-2013-52005. (B) *Pseudoliva crassa* (Gmelin, 1791), Baia do Baba, Moçâmedes, Angola, 6–20 m, coll. S. Gofas, SL 39.5 mm, AL 31.5 mm. (C) *Entomoliva mirabilis* New Caledonia: Canal de la Havannah, EXBODI, st. DW3787, 22°13'S, 167°06'E, 223–249 m, SL 11.2 mm. (D) *Amalda contusa*, MNHN IM-2009-22264. (E, F) *Amalda* cf. *hilgendorfi richeri*, MNHN IM-2007-43661. (F) enlarged lateral tooth to show bifurcation on the tip. (G) *Ancillina* cf. *sumatrana*, Madagascar, between Majunga and Cap Saint-André, MIRIKY, st. CP3278, 15°24'S, 45°56'E, 750–780 m. (H) *Turrancilla* sp. 2, MNHN IM-2007-31947. (I) *Eburna lienardi* (Bernardi, 1859), MZSP 40140, Proc. Areia Branca, RN, Brazil, 04°45'S, 36°58'W, 9 m.

CLASS GASTROPODA CUVIER, 1795

SUBCLASS CAENOGASTROPODA COX, 1960

ORDER NEOGASTROPODA WENZ, 1938

SUPERFAMILY OLIVOIDEA LATREILLE, 1825

Diagnosis: Shell variable, from broadly oval to narrowly fusiform, with high last whorl and diameter of the spire whorls expanding slowly or rapidly. Siphonal canal either absent (in which case the shell is strongly notched) or very short, unnotched. Shell sometimes covered with thick periostracum, but in most cases not and then shell surface glossy. Protoconch multispiral

or paucispiral. In all families except Pseudolividae and Benthobiidae, anterior end of the shell strongly callused and bearing an anterior band. Callus differently pronounced, sometimes limited to inner apertural lip, but at other times extending on significant part of the last whorl and spire, or even completely covering the shell (some Ancillidae). Radula with five to three teeth per transverse row.

FAMILY OLIVIDAE LATREILLE, 1825

Type genus: *Oliva* Bruguière, 1789

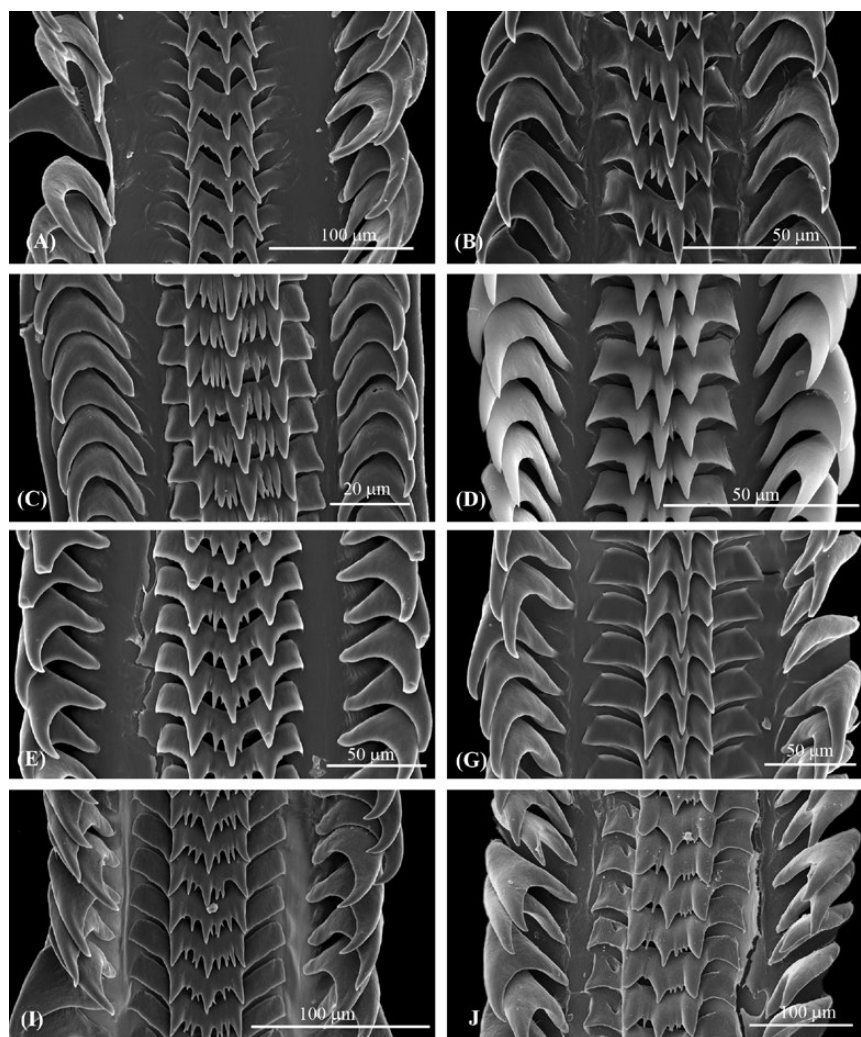


Figure 13. Radulae of species of *Ancilla*. The shells of the specimens are depicted on Fig. 1 (except *Ancilla cinamomea*). (A) *Ancilla aureocallosa*, MNHN IM-2007–39045, SL 21.7 mm. (B) *Ancilla* sp., MNHN IM-2007–36606, SL 5.6 mm. (C) *A. thomassini*, MNHN IM-2009–15460, SL 6.3 mm. (D) *A. morrisoni*, holotype, MNHN IM-2013–55401, SL 10.0 mm. (E) *A. ventricosa*, MNHN IM-2009–15544, SL 10.7 mm. (G) *A. adelphe*, MNHN IM-2009–15519, SL 11.1 mm. (I) *A. lhaumeti*, holotype, MNHN IM-2009–15513, SL 15.3 mm. (J) *A. cinamomea* Lamarck, 1801, Southern India, Rameshwaram (after Kantor & Bouchet, 2007: fig. 30B).

Diagnosis: Shell glossy, lacking periostracum, broadly to narrowly fusiform, with high to very high last whorl and narrow aperture tapering adapically. Siphonal canal absent, anterior end of shell distinctly notched. Anterior part of the shell forming a well-defined anterior band, raised above the shell cloak. Plication plate nearly always with more or less defined spiral plicae. Primary spire callus present, covering at least partially the spire whorls. Narrow filament channel present, but in *Calyptoliva* overlaid by narrow primary callus.

Foot with well-developed crescent-shaped propodium, with median longitudinal cleft on dorsal side and parapodia, partially embracing the shell. Radula with three

or five (*Olivella*) teeth per transverse row. Mantle with mantle filament (except in *Calyptoliva*), with posterior and anterior mantle lobes, and with anterior mantle tentacle (except in *Calyptoliva* and *Olivancillaria*).

SUBFAMILY OLIVINAE LATREILLE, 1825

Type genus: *Oliva* Bruguière, 1789

Diagnosis: Plication plate subdivided into parietal plate, shoe and belt. Filament channel well defined, eventually overlaid by primary spire callus on upper spire whorls, but free at least on last whorl. Operculum absent. Anterior mantle tentacle well defined. Head

with two vertical flaps with narrow tentacles bearing eyes. Radula with three teeth per row, central tooth with short or long lateral flaps, and three large cusps. Stomach with narrow and rather long posterior mixing area.

GENUS *OLIVA* BRUGUIÈRE, 1789 (1)

Type species: Voluta oliva Linnaeus, 1758; subsequent monotypy by [Lamarck, 1799](#).

Remarks: The genus *Oliva* is rather heterogeneous and a number of subgenera have been proposed, some of them even raised to full genus ([Petuch & Myers, 2014](#)). [Petuch & Sargent \(1986\)](#) recognized 19 subgenera, of which five were monotypic. [Tursch & Greifeneder \(2001\)](#) discussed briefly their status but abstained from the use of subgenera, since in many cases they did not find clear conchological distinctions between them. On the contrary, [Hunon et al. \(2009\)](#) used as valid most of the subgenera that had been proposed earlier, while still leaving some species in *Oliva* (e.g. *O. lacanientai* Greifeneder & Blöcher, 1985). Our COI molecular analysis demonstrates that at least some of the subgenera in their current usage are paraphyletic ([Fig. 2](#) – abbreviated subgenera indicated in bold after species names). Nevertheless, we foresee that, with increased taxon sampling in molecular phylogenies, a number of (sub)genera will be found to be justified. However, with the molecular data currently available, we simply list in the following the accepted subgenera, but abstain from using them.

The species delimitation approach would suggest that *O. sericea* and *O. miniacea* would be a single species. However, because they are represented by a single specimen each in our analysis and because the two species are distinct conchologically, we remained conservative and did not change the status of the species. Furthermore, *Oliva 'lacanientai'* shows great intraspecific variability and probably represents the species complex. We abstained from description of new species, since the species level taxonomy was beyond the scope of the current paper.

List of nominal subgenera (in alphabetic order)

Acutoliva Petuch & Sargent, 1986. Type species: *Oliva panniculata* Duclos, 1835; OD.

Americoliva Petuch, 2013. Type species: *Oliva sayana* Ravenel, 1834; OD.

Annulatoliva Petuch & Sargent, 1986. Type species: *Oliva annulata* Gmelin, 1791; OD.

Arctoliva Petuch & Sargent, 1986. Type species: *Oliva arctata* Marrat, 1871; OD.

Cariboliva Petuch & Sargent, 1986. Type species: *Oliva scripta* Lamarck, 1811; OD.

Carmione Gray, 1858. Type species: *Voluta ventricosa* Dillwyn, 1817 [= *O. bulbosa* Lamarck, 1811]; M.

Galeola Gray, 1858. Type species: *Oliva galeola* Duclos, 1835; by tautonymy. [The identity of the type species is unclear. [Gray \(1858\)](#) placed it in the synonymy of *Galeola avellana* (Lamarck, 1811), a *nomen dubium* according to [Tursch & Greifeneder \(2001\)](#), who treated *O. galeola* as a subjective synonym of *O. sericea* (Röding, 1798), a species attributed to *Miniaceoliva*].

Miniaceoliva Petuch & Sargent, 1986. Type species: *Oliva miniacea* Röding, 1798; OD.

Multiplicoliva Petuch & Sargent, 1986. Type species: *Oliva multiplicata* Reeve, 1850; OD.

Musteloliva Petuch & Sargent, 1986. Type species: *Oliva mustelina* Lamarck, 1811; OD.

Neocylindrus P. Fischer, 1883. Type species: *Oliva tessellata* Lamarck, 1811; M.

Omogymna Martens, 1897. Type species: *Oliva paxillus* Reeve, 1850 [= *O. nitidula* Duclos, 1835]; M.

Parvoliva Thiele, 1929. Type species: *Oliva dubia* Schepman, 1904; M.

Porphyria Röding, 1798. Type species: *Voluta porphyria* Linnaeus, 1758; by tautonymy. Note: The name *Strephona* requires special mention, as it is broadly used in the literature (e.g. by [Petuch & Sargent, 1986](#)) where it is attributed to [Mörch \(1852\)](#). However, earlier than Mörch, [Gray \(1847: 140\)](#) had already made the name available ([Petit, 2012](#)), selecting *Voluta porphyria* Linnaeus, 1758 as type species. *Strephona* Gray, 1847, is thus a junior objective synonym of *Porphyria*.

Proxoliva Petuch & Sargent, 1986. Type species: *Oliva caldania* Duclos, 1835; OD [a *nomen dubium* formerly applied to *O. bretingbami* Bridgman, 1909, according to [Tursch & Greifeneder, 2001](#)].

Rufoliva Petuch & Sargent, 1986. Type species: *Oliva rufula* Duclos, 1835; OD.

Strephonella Dall, 1909. Type species: *Oliva undatella* Lamarck, 1810; OD.

Viduoliva Petuch & Sargent, 1986. Type species: *Oliva vidua* Röding, 1798; OD.

SUBFAMILY AGARONIINAE OLSSON, 1956

Type genus: Agaronia Gray, 1839

Diagnosis: Plication plate not distinctly subdivided, with distinct spiral plicae. Olivoid groove present, shallow. Olivoid band differing or not in color from cloak of last whorl. Filament channel well defined, free on most spire whorls. Operculum absent. Anterior mantle tentacle well defined. Head with dorso-ventrally compressed flaps,

eyes absent in all studied species. Radula with three teeth per transverse row, central tooth with very long lateral flaps, and three large major cusps. Short but very distinct small denticles situated externally from lateral cusps, separated from them by deep, narrow grooves.

GENUS *AGARONIA* GRAY, 1839 (1)

Type species: Voluta hiatula Gmelin, 1791; M.

Synonyms

Hiatula Swainson, 1831 (Invalid: junior homonym of *Hiatula* Modeer, 1793 [Bivalvia]).

Anazola Gray, 1858. *Type species: Oliva acuminata* Lamarck; SD, [Cossmann \(1899\)](#).

Utriculina Gray, 1847. *Type species: Voluta utriculus* Gmelin, 1791 [= *Voluta gibbosa* Born, 1778]; OD.

SUBFAMILY OLIVELLINAE TROSCHER, 1869

Type genus: Olivella Swainson, 1831

Diagnosis: Plication plate not distinctly subdivided, with defined spiral plicae that can extend to columella. Internal shell walls partially resorbed. Primary callus extending up to anterior end of plication plate. Filament channel well defined, free on most spire whorls. Anterior mantle tentacle well defined. Head with small, broadly spaced, dorso-ventrally compressed flaps; eyes absent. Operculum present or absent. Radula with five teeth per transverse row; central tooth broad, with numerous short cusps and convex anterior edge. Lateral teeth hook-shaped; additional rectangular weak plates exterior to lateral teeth.

GENUS *OLIVELLA* SWAINSON, 1831 (1)

Type species: Olivella purpurata Swainson, 1831 [= *Voluta dama* Mawe, 1828]; SD, [Dall \(1909\)](#).

Remarks: *Olivella* is conchologically rather variable, and a number of (sub)genera have been proposed. Only three species were included in our molecular analysis and, based on this limited dataset, we cannot make any conclusion on the possible subgeneric division of the genus. In the following, we list the classification proposed by [Olsson \(1956\)](#) with some additions and corrections.

List of nominal subgenera (in alphabetic order)

Anasser Absalão & Pimenta, 2003. *Type species: Olivella ambli* Watson, 1882; OD.

Callianax H. Adams & A. Adams, 1853. *Type species: Oliva biplicata* G.B. Sowerby I, 1825; SD, [Cossmann \(1899\)](#).

Cupidoliva Iredale, 1924. *Type species: Olivella nymp* Adams & Angas; 1864; OD; [treated by [Olsson \(1956\)](#) as genus of uncertain status, pending data on radular morphology, although [Peile \(1922: Fig. 6\)](#) had previously illustrated the radula of the type species, which proved its placement in Olivellidae].

Dactylidia H. Adams & A. Adams, 1853. *Type species: Oliva nana* Lamarck, 1811; SD, [Weinkauff \(1878: 124, as Dactyliola, an incorrect subsequent spelling\)](#). This type designation was overlooked and later [Cossmann \(1899: 54\)](#) designated *Olivella mutica* (Say, 1822) [an originally included species] as the type species. Olsson followed Cossmann, but did not include *Oliva nana* in his monograph. Therefore, the subgeneric position of *O. nana* as well as the composition of the subgenus remain unclear. *Micana* Gray, 1858. *Type species: Oliva nana* Lamarck, 1811; M. A junior objective synonym of *Dactylidia*.

Dactylidella Woodring, 1928. *Type species: Oliva anazora* Duclos, 1835; OD.

Lamprodoma Swainson, 1840. *Type species: Oliva volutella* Lamarck, 1811; M [= *Ramola* Gray, 1858, *Type species: Oliva volutella* Lamarck, 1811; M].

Macgintiella Olsson, 1956. *Type species: Olivella watermani* McGinty, 1940; OD.

Minioliva Olsson, 1956. *Type species: Olivella perplexa* Olsson, 1956; OD.

Niteoliva Olsson, 1956. *Type species: Porphyria minuta* Link, 1807; OD.

Olivina d'Orbigny, 1841 (in 1834–1847). *Type species: Oliva tehuelchana* d'Orbigny, 1839; SD, [Weinkauff, 1878](#).

Orbignytesta Klappenbach, 1962. *Type species: Olivella formicacorsii* Klappenbach, 1962; OD.

Pachyoliva Olsson, 1956. *Type species: Oliva columellaris* G.B. Sowerby I, 1825; OD.

Parolivella Paulmier, 2007. *Type species: Olivella marginelloides* Paulmier, 2007; OD.

Zanoetella Olsson, 1956. *Type species: Oliva zanoeta* Duclos, 1835; OD.

SUBFAMILY CALYPTOLIVINAE SUBFAM. NOV.

Type genus: Calyptoliva Kantor & Bouchet, 2007

Diagnosis: Plication plate either smooth or with weak spiral plicae that extend to columella. Primary callus very thin, overlaying suture. Anterior band very thin, hardly discernible, very slightly raised above the shell cloak, uniform. Filament channel absent. Anterior mantle tentacle absent. Posterior mantle lobe

moderately or well developed and without anterior mantle tentacle. Head with small, broadly spaced, dorso-ventrally compressed flaps; eyes present or absent. Operculum present. Radula with three teeth per transverse row; central tooth medium broad, tricuspid. Lateral teeth hook-shaped. Stomach with narrow and long posterior mixing area.

GENUS *CALYPTOLIVA* KANTOR & BOUCHET, 2007 (1)

Type species: Calyptoliva bolis Kantor & Bouchet, 2007; OD.

Remarks: *C. bbugae* Kantor *et al.*, 2016 is the only sequenced species and forms a long branch and the sister group cannot be recognized in our analysis. However, the genus is confidently placed in Olividae and differs from all other representatives of the family by the absence of a channelled suture and, correspondingly, by the absence of the mantle filament. The suture is overlaid by a very narrow primary spire callus.

Insertae sedis

GENUS *OLIVANCILLARIA* D'ORBIGNY, 1841
(IN 1834–1847) (2).

Type species: Oliva auricularia Lamarck, 1811; M.

Synonyms

Scaphula Swainson, 1840 [preoccupied by *Scaphula* Benson, 1834 (Bivalvia)]. *Type species: Oliva patula* G.B. Sowerby I, 1825; M.

Olivancillaria (Lintrricula) H. Adams & A. Adams, 1853 (nov. pro *Scaphula* Swainson, 1840, non Benson, 1834). *Type species: Oliva patula* G.B. Sowerby I, 1825; by typification of replaced name.

Claneophila Gray, 1858. *Type species: † Oliva claneophila* Duclos, 1835; by tautonymy. [Gray (1858: 48) listed *Oliva claneophila* in the synonymy of *Claneophila gibbosa*. Although it is not clear which species he meant under the name *gibbosa*, since no authorship or date was provided, the remaining species attributed by Gray to *Claneophila*, beside *O. claneophila* itself, are species of *Olivancillaria*].

Remarks: The position of *Olivancillaria* remains unclear. We did not have access to molecular material and therefore the genus is not included in our analysis. In their revision of *Olivancillaria* in the south-western Atlantic, Teso & Pastorino (2011) briefly considered similarities and differences with other genera of Olivioidea and suggested affinities to *Agaronia*. Marcus

& Marcus (1959) described the anatomy of two species, *O. vesica* (as *Lintrricula auricularia*) and *O. urceus* (as *O. brasiliensis*). The radular characters of all examined species are similar to that of *Agaronia* in having rachidian teeth with three large cusps and smaller additional cusp exterior to the main lateral cusp on each side of the tooth (Fig. 11E), a character not found in Olivinae. Besides, the head has flaps without eyes and tentacles, similar to the situation in *Agaronia*. Based on the description of Marcus & Marcus (1959), Golikov & Starobogatov (1975) erected the new family Olivancillariidae, remarking the differences in shell and radulae as well as in some details of the female reproductive system, which however are not very clearly described by Marcus & Marcus. Despite a radula similar to that in *Agaronia*, *Olivancillaria* lacks the olivoid groove and anterior mantle tentacle. Molecular data will be crucial to clarify the position of *Olivancillaria* and, although morphologically and conchologically it is close to Olivinae, it may prove to form a distinct lineage, consistent with the recognition of a separate subfamily.

FAMILY BELLOLIVIDAE FAM. NOV.

Type genus: Belloliva Peile, 1922

Diagnosis: Shell glossy, lacking periostracum, narrowly fusiform, with high to very high last whorl and narrow aperture tapering adapically. Siphonal canal absent, anterior end of shell distinctly notched. Anterior shell end with poorly defined anterior band, very slightly raised above the shell cloak. Plication plate limited to columella, with spiral plicae (*Belloliva*) or not (*Olivellopsis*). Primary spire callus absent. Narrow filament channel present, opened on all spire whorls.

Foot with well-developed crescent-shaped propodium, subdivided by a longitudinal cleft on the dorsal side, and parapodia partially embracing the shell. Operculum present. Radula with three teeth per transverse row. Central tooth with three large, closely spaced cusps and, in *Belloliva*, with distinct small cusps adjoining the major lateral cusps (Fig. 11B), that are indistinct or absent in *Olivellopsis* (Fig. 11C). Mantle with mantle filament, a small anterior mantle lobe, and without anterior mantle tentacle. Head formed by dorso-ventrally compressed flaps with or without eyes, at least in *Olivellopsis* on very short and narrow tentacle.

GENUS *BELLOLIVA* PEILE, 1922 (1)

Type species: Olivella brazieri Angus, 1877; OD.

Synonym: Belloliva (Gemmoliva) Iredale, 1924. *Type species: Oliva triticea* Duclos, 1835; OD.

GENUS *OLIVELLOPSIS* THIELE, 1929 (1)

Type species: Olivella (Callianax) simplex Pease 1868; M.

Synonym: *Olivella (Janaoliva)* Sterba & Lorenz, 2005, **syn. nov.** Type species: *Olivella amoni* Sterba & Lorenz, 2005; OD.

Remarks: When describing *Janaoliva*, Sterba & Lorenz (2005) compared it with *Olivella*, correctly pointing out the very simplified structure of the plication plate, which differs from other subgenera of *Olivella*. Kantor & Bouchet (2007) overlooked the description of *Janaoliva* and thus did not compare *Olivella amoni* with the very similar species *Olivellopsis simplex*, which they included in *Belloлива*. The very long branches of both *Belloлива* and *Olivellopsis* suggest that they are two separate genera. In the vicinity of Kavieng (New Ireland), the type locality of *O. amoni*, another similar, although molecularly different species was recently found. Their radulae are similar (Fig. 11C) and are close to the radulae of *O. simplex* from New Caledonia (Kantor & Bouchet, 2007; Fig. 12A–D). In the light of the new data indicating the presence of a species complex, *O. simplex* from New Caledonia may be specifically different from *O. simplex*, the type locality of which is the ‘Paumotu Islands’ (Tuamotu Archipelago), French Polynesia. We also found very similar shells off Madagascar. It is possible that a whole radiation of *Olivellopsis* will be uncovered by molecular phylogenetics.

GENUS *JASPIDELLA* OLSSON, 1956 (2)

Type species: Voluta jaspidea Gmelin, 1791; OD.

Remarks: The genus was established in the subfamily Olivinae on the basis of the tricuspidate rachidian tooth. The type species from the Caribbean has a shell similar to that of *Belloлива*, as well as the operculum, also characteristic for this family. No material was available to us and we attribute *Jaspidella* conditionally to Bellolividae on the basis of shell and radula similarities.

FAMILY ANCILLARIIDAE SWAINSON, 1840

Synonym: Ancillinae H. Adams & A. Adams, 1853

Possible synonym: Vanpalmeriidae Adegoké, 1977. Type genus: *Vanpalmeria* Adegoké, 1977. Monotypical family based on *Vanpalmeria africana* Adegoké, 1977, from the Paleocene of Nigeria.

Type genus: *Ancillaria* Lamarck, 1811 [= *Ancilla* Lamarck, 1799]

Diagnosis: Shell glossy or mat, lacking periostracum, fusiform to narrowly fusiform, with high last whorl, and medium broad-to-narrow aperture tapering adapically. Siphonal canal absent, anterior end of shell distinctly notched. Anterior shell end with well-defined anterior band, raised above the shell cloak and often strongly shagreened. Olivoid groove present (at least in some species) in all genera. Plication plate limited to columella, usually with spiral plicae. Primary spire callus well defined, covering most of, or even completely, the shell. Secondary spire callus from poorly defined to very strong. Suture always overlaid by the callus.

Foot with well-developed crescent-shaped propodium, subdivided by longitudinal cleft on dorsal side, and with parapodia partially or completely embracing the shell. Operculum usually present (rarely absent). Radula with three teeth per transverse row. Central tooth tricuspid or multicuspid, lateral teeth mostly simple hook-shaped, sometimes with additional serration along the inner edge (*Ancillina*, Fig. 12G) or bifurcated on the top (*Ancilla atimovatae* – Kantor et al., 2016; Fig. 9A–C). Mantle without mantle filament, with weak anterior mantle lobe, without anterior mantle tentacle, with very well developed posterior mantle lobe, sometimes subdivided into two lobes. Head formed by dorso-ventrally compressed flaps with or without eyes.

Remarks: The monotypic family Vanpalmeriidae is characterized by a heavily callused spire and few weak plications on the columella. It was originally classified in Volutacea and was reduced to a subfamily of Olividae by Bouchet & Rocroi (2005) together with Olivinae and Ancillariinae. Although the position of this enigmatic species remains unclear, it is transferred here conditionally to Ancillariidae based on the presence of the strong primary spire callus that is overlaying the suture.

GENUS *ANCILLA* LAMARCK, 1799 (1)

Type species: Ancilla cinnamomea Lamarck, 1801; by subsequent monotypy.

Synonyms

Anaulax Roissy, 1805. Unnecessary substitute name for *Ancilla* Lamarck, 1799, by Roissy believed to be preoccupied by the genus ‘ancille’ used by Geoffroy for freshwater limpets [= *Ancylus*].

Ancillaria Lamarck, 1811. Substitute name for *Ancilla* Lamarck, 1799, treated by Lamarck as a junior homonym of ‘*Ancylus* Geoffroy’ [*Ancylus* O.F. Müller, 1773].

Ancillus Montfort, 1810. Unjustified emendation of *Ancilla* Lamarck, 1799. Under ICZN Art. 33.2, *Ancillus* is an objective synonym of *Ancilla*, and Montfort's designation of *Ancilla buccinoides* Lamarck, 1803, as type species of *Ancillus* is invalid.

Sparella Gray, 1857. Type species: *Ancillaria ventricosa* Lamarck, 1811; SD, [Cossmann \(1899\)](#).

Sparellina P. Fischer, 1883. Type species: *Ancilla candida* Lamarck, 1811 [= *Voluta ampla* Gmelin, 1791]; M.

Ancillista Iredale, 1936. Type species: *Ancillista velesiana* Iredale, 1936; OD.

Possibly valid (sub)genera

Chilotygya H. Adams & A. Adams, 1853. Type species: *Ancilla exigua* G.B. Sowerby I, 1830; M.

Hesperancilla Kilburn, 1981. Type species: *Ancilla matthewsi* J.Q. Burch & R.L. Burch, 1967; OD.

Remarks: [Kilburn \(1981\)](#) tentatively used *Sparella*, *Sparellina*, *Chilotygya* and *Hesperancilla* as subgenera of *Ancilla*. The obtained sequences show considerable genetic distances between the 11 groups of *Ancilla* delimited with ABGD ([Fig. 1](#)), and the radulae also show considerable disparity ([Fig. 13](#)). Therefore the presence of discrete (sub)genera is possible, although the currently accepted system is hardly plausible. Kilburn's recognition of *Sparella* and *Sparellina* was based mainly on radular characters, *Sparella* generally having a tricuspid rachidian teeth, often with intermediate denticles between main cusps, while *Sparellina* has multicuspid rachidian teeth. We examined the radula of the type species *Ancilla cinamomea* ([Fig. 13J](#)), and it proved to have a tricuspid rachidian. Thus *Sparella* in the definition of Kilburn becomes a synonym of *Ancilla* (*Ancilla*), and most studied species should be attributed to the nominative subgenus. The topology of the COI-based tree of *Ancilla* ([Fig. 1](#)) is nearly identical to that of the reduced dataset based on four genes ([Figs 3, 4](#)). A COI sequence was not available for *Ancilla atimovatae* Kantor *et al.*, 2016, but in the four-gene tree it is sister to the clade including *A. ventricosa* (Lamarck, 1811), *A. adelphe* Kilburn, 1982 and *A. lhaumeti* Kantor *et al.*, 2016. The radula of *A. atimovatae* is very distinctive (especially in the shape of the bifurcating lateral teeth – [Kantor *et al.*, 2016: Fig. 9A–C](#)), but is more similar to the radula of *Sparellina* (as defined by [Kilburn, 1981](#)). Thus *Ancilla* s.s. (= *Sparella*) becomes paraphyletic. Moreover, *Ancillista aureocallosa* Kilburn & Jenner, 1977, the only species of *Ancillista* that was available to us, was confidently placed in *Ancilla*. Its radula ([Fig. 13A](#)) is similar to some other *Ancilla* spp. (e.g. *Ancilla boschi* Kilburn, 1980 – [Kilburn 1981: Fig. 83](#)). In the four-gene analysis, *Ancillista aureocallosa*

is sister to *Ancilla* sp. (MNHN IM-2007–36606), while in the COI analysis it is basal to all other *Ancilla*. The radula of the type species of *Ancillista* remains unknown, but that of *Ancillista muscae* (unpublished) is different from *A. aureocallosa* in the shape of the central tooth, although it is also tricuspid. Therefore, we conditionally synonymize *Ancillista* with *Ancilla*, pending molecular data on the type species.

We did not have specimens of the type species of *Chilotygya*, and *Hesperancilla* and cannot draw any conclusions on them. Both were established based on the shell characters, and we conditionally treat them as separate entities.

GENUS ANCILLINA BELLARDI, 1882 (1)

Type species: † *Ancillaria pusilla* Fuchs, 1877; M (Austria, Miocene)

Synonym: *Ancilla* (*Gracilancilla*) Thiele, 1925. Type species: *Ancilla sumatrana* Thiele, 1925; OD.

GENUS ANOLACIA GRAY, 1857 (3)

Type species: *Ancilla mauritiana* G.B. Sowerby I, 1830; M.

Remarks: Anatomy and radular characters remain unknown; therefore, the validity of the genus is uncertain.

GENUS AMALDA H. ADAMS & A. ADAMS, 1853 (1)

Type species: *Ancillaria tankervillii* Swainson, 1825; SD, [Cossmann \(1899\)](#).

Remarks: The species of *Amalda* together present a wide range of shell forms and it is not surprising that several genus group names have been proposed. Our analysis covers very little of the general diversity of the group, but at least three subgenera are present in our dataset: *Amalda* s.s., *Baryspira* [represented in our analysis by *Amalda contusa* (Reeve, 1864)] and *Alocospira* (represented by *Amalda bellonarum* Kilburn & Bouchet, 1988). Although the support of the genus itself is significant (1 in BA), the genetic distances within its constituents are rather small, compared to, for example, the genus *Ancilla*. Nevertheless, at least *Alocospira* constitutes a rather long branch, and it is possible that future molecular studies will reveal a more complex and robust structuring necessitating the recognition of (sub)genera. At present we abstain from using any subgenera and provide a list of names with Recent type species for future reference.

List of nominal subgenera (in alphabetic order)

- Alocospira* Cossmann, 1899. Type species: *Ancillaria papillata* Tate, 1889; OD.
Austrancilla Habe, 1959. Type species: *Ancilla edithae* Pritchard & Gatliff, 1899; OD.
Baryspira P. Fischer, 1883. Type species: *Ancillaria australis* G.B. Sowerby I, 1830; SD, **Cossmann (1899)**.
Exiquaspira Ninomiya, 1988. Type species: *Amalda ornata* Ninomiya, 1988; OD.
Gracilispira Olsson, 1956. Type species: *Ancillaria novaezelandiae* G.B. Sowerby II, 1859; OD.
Mundaspira Ninomiya, 1990. Type species: *Amalda concinna* Ninomiya, 1990; OD.
Pinguispira Finlay, 1926. Type species: *Ancilla opima* Marwick, 1924; OD.

GENUS *EBURNA* LAMARCK, 1801 (2)

Type species: *Eburna flavida* Lamarck, 1801 [= *Buccinum glabratum* Linnaeus, 1758]; M.

Remarks: We examined the anatomy of *Eburna lienardi* (unpublished data). It is rather typical ancillariid and the genus is attributed to the family on the basis of morphology and radula (Fig. 12I).

GENUS *ENTOMOLIVA* BOUCHET & KILBURN, 1991 (1)

Type species: *Entomoliva incisa* Bouchet & Kilburn, 1991; OD.

GENUS *MICRANCILLA* MAXWELL, 1992 (3)

Type species: † *Amalda granum* Maxwell, 1992 (New Zealand, Eocene); OD.

Remarks: In addition to several fossil species from New Zealand and recently described ones from the Paris and Aquitanian basins, the Recent species *Ancillaria longispira* Strebel, 1908, from the Falkland Islands, was attributed to *Micrancilla* by Pacaud, Merle & Pons (2013). Neither the anatomy nor the radula of *M. longispira* has been examined so far.

GENUS *TURRANCILLA* MARTENS, 1904 (1)

Type species: *Ancillaria lanceolata* Martens, 1901 [a primary homonym of *Ancillaria lanceolata* Tate, 1889, has been renamed *Ancillus (Turrancilla) akontistes* Kilburn, 1980]; SD, Wenz (1943).

FAMILY **BENTHOBIIDAE** FAM. NOV.

Type genus: *Benthobia* Dall, 1889

Diagnosis: Shell covered by periostracum, ovoid to biconical, with high or very high last whorl and medium-broad to broadly ovate aperture. Siphonal canal very short and broad, not notched. Anterior band not pronounced. Olivoid groove present, terminating by a short denticle on the lip. Plication plate either weakly pronounced, limited to columella, smooth (*Benthobia*) or absent (*Fusulculus*). Primary spire callus limited to inner lip, extending up to parietal wall. Spiral sculpture either absent (*Benthobia*) or consisting of rather distinct spiral cords (*Fusulculus*). Suture simple, adpressed.

Foot with narrow propodium, lacking parapodia. Operculum large, with terminal nucleus. Radula with three teeth per transverse row. Central tooth either tricuspid (*Fusulculus*; Bouchet & Vermeij, 1998) or multicuspid (*Benthobia*; Kantor, 1991; Simone, 2003). Lateral teeth unicuspid. Mantle without mantle filament, with weak to moderately pronounced posterior mantle lobe. Head with long cylindrical tentacles, with (*Fusulculus*) or without eyes (*Benthobia*). Rhynchostome shifted to the base of right tentacle. Proboscis very short when retracted, with basal buccal mass and radular odontophoral retractor passing through the nerve ring. Salivary glands acinous. Accessory salivary gland terminating with very large muscular bulb.

GENUS *BENTHOBIA* DALL, 1889 (1)

Type species: *Benthobia tryonii* Dall, 1889; OD.

Synonym: *Nux* Barnard, 1960. Type species: *Nux alabaster* Barnard, 1960; OD.

Remarks: In the absence of anatomical data, Simone (2003) considered *Nux* a separate genus, pointing out its close affinity to *Benthobia*. The radula of *N. alabaster* is nearly identical to that of *Benthobia* (Barnard, 1960) and there are no good reasons to consider it a separate genus. The mantle lobe (called *anal siphon* by Simone 2003) is moderately pronounced and simple.

GENUS *FUSULCULUS* BOUCHET & VERMEIJ, 1998 (1)

Type species: *Fusulculus crenatus* Bouchet & Vermeij, 1998; OD.

Remarks: The anatomy of *Fusulculus crenatus* (own observations) is similar to that of *Benthobia* spp., especially the anterior foregut. The mid-oesophagus

is glandular, as in *Benthobia*, although the glandular epithelium is more pronounced in the former. The synapomorphy is the presence of a single accessory salivary gland, terminating in a very large muscular bulb. Similarly, in both genera, the anteriormost part of the osphradium lacks lamellae on the left side.

FAMILY PSEUDOLIVIDAE DE GREGORIO, 1880

Synonym: Zemiridae Iredale, 1924

Type genus: *Pseudoliva* Swainson, 1840

Diagnosis: Shell covered by periostracum, ovoid to fusiform, with high or very high last whorl, and medium broad to broad ovate aperture. Siphonal canal short to very short, moderately broad, shallowly to deeply notched. Anterior band not pronounced. Olivoid groove present, terminating by short denticle on outer aperture lip, sometimes denticle poorly pronounced. Plication plate not pronounced. Primary spire callus limited to inner lip, at most slightly extending to parietal wall. Parietal wall sometimes forming well-defined fold, partially separating the upper part of aperture (*Pseudoliva*). Spiral sculpture absent (*Pseudoliva*) or present. Suture simple, adpressed, eventually broadly channelled (*Zemira*).

Foot with narrow propodium, lacking parapodia. Operculum large, with terminal nucleus. Radula with three teeth per transverse row. Central tooth tricuspid. Lateral teeth unicuspid or bicuspid (*Pseudoliva*, Fig. 12A, B). Mantle without mantle filament, with weak to moderately pronounced posterior mantle lobe. Head with short flaps with eyes, sometimes flaps producing short tentacles. Rhynchostome slightly shifted to the base of right tentacle. Proboscis very short when retracted, with basal buccal mass and radular odontophoral retractor passing through the nerve ring. Salivary glands acinous. Accessory salivary gland tubular.

Remarks: The anatomy of various Pseudolividae has been reasonably well studied, for some species in detail (Ponder & Darragh, 1975; Kantor, 1991; Simone, 2007).

The genera *Macron* H. Adams & A. Adams, 1853 (type species: *Buccinum aethiops* Reeve, 1847; M) and *Triumphis* Gray, 1856 (type species: *Buccinum distortum* W. Wood, 1828; M) were attributed to Pseudolividae by Vermeij (1998). Thiele (1929) illustrated the radula of the former and described that of the latter. The tricuspid lateral teeth (not found in any other Pseudolividae) and multicuspid central ones are more similar to Buccinoidea. Landau *et al.* (2013) suggested a placement of *Macron* in Nassariidae, a position that was not rejected by Galindo *et al.* (2016) but requires molecular confirmation. The position of

Triumphis is even more uncertain, but it may be tentatively assigned to the Nassariidae as well.

GENUS *PSEUDOLIVA* SWAINSON, 1840 (1)

Type species: *Buccinum plumbeum* Dillwyn, 1817 (= *Buccinum crassum* Gmelin, 1791); OD.

Synonyms

Mariona G.B. Sowerby III, 1890. Type species: *Pseudoliva ancilla* Hanley, 1859; M.

Sylvanocochlis Melvill, 1903. Type species: *Pseudoliva ancilla* Hanley, 1859; OD; Invalid: junior objective synonym of *Mariona*.

Fulmentum P. Fischer, 1884. Type species: *Buccinum sepimentum* Rang, 1832; M.

Remarks: Besides size, the distinction between *Pseudoliva* and *Fulmentum* is in the better development of the plate-like parietal ridge (Fig. 5M), which divides the aperture of *Fulmentum* into two compartments; however, a similar, although weaker, plate is also present in the type species of *Pseudoliva*. *Pseudoliva sepimenta* and *P. crassa* have rather similar and characteristic bicuspid lateral teeth, differing in this from all other pseudolivids that have unicuspid lateral teeth. We consider the conchological differences insufficient for separation of two genera.

GENUS *NAUDOLIVA* KILBURN, 1989 (2).

Type species: *Naudoliva caitlinae* Kilburn, 1989; OD.

GENUS *ZEMIRA* H. ADAMS & A. ADAMS, 1853 (2).

Type species: *Eburna australis* G.B. Sowerby I, 1833; M.

GENUS *LUIZIA* DOUVILLÉ, 1933 (2).

Type species: *Buccinum costae* Douvillé, 1933; M.

Remarks: The only Recent species, *L. zebrina* (A. Adams, 1855) was examined anatomically by Kantor (1991) and proved to be similar to *Pseudoliva ancilla*.

Doubtful taxonomic position

GENUS *RAMOLIVA* COTTON & GODFREY, 1932.

Type species: *Olivella adiorygma* Verco, 1909; OD.

Remarks: The position of this monotypical genus is unclear. Overall, it has an olivoid shell with non-channelled sutures, a very simplified plication plate

and, according to the original illustration of the type species (Verco, 1909: pl. 25, figs 3, 4), it lacks an anterior band. The last whorl is lifting towards the aperture, a character not known in any other Olivoidea. The species is known only from empty shells. Lee (2004) has suggested that this may be a columbellid, a hypothesis that we find convincing.

DISCUSSION

PHYLOGENY OF OLIVOIDEA

One of the most unexpected – based on anatomical characters – results of the phylogenetic analysis is the close relationship between Pseudolividae (in their previously accepted taxonomic extension, for example by Vermeij, 1998) and the remaining Olivoidea. Based on their anatomy Kantor (1991) had rejected the similarity between two groups and even suggested the new suborder Pseudolivoidei. This view was partially accepted later and, in the latest working classification of Gastropoda (Bouchet & Rocroi, 2005), Pseudolividae was attributed together with Ptychotractidae to the superfamily Pseudolivoidea. However, recent phylogenetic analyses of ‘mitriform’ gastropods (Fedosov *et al.*, 2015) have already demonstrated Ptychotractidae as previously recognized is paraphyletic, with some genera (*Latiromitra* Locard, 1897 and *Ceratoxancus* Kuroda, 1952) included in the family Costellariidae, and others representing independent lineages, none of them showing close affinity to Pseudolividae, and there is currently no support for classifying them in the same superfamily. It should be remembered that Thiele (1929) classified Pseudolivinae as a subfamily of Olividae, a position followed by Wenz (1938[in 1938–1944]), with all other olivoideans united in the subfamily Olivinae. Thus, in some respects, the new classification proposed herein is a return to the roots.

Another unexpected result is the non-monophyly of Pseudolividae, which is split here into two families, Pseudolividae and Benthobiidae fam. nov. The former inhabit shallow water (subtidal to 150 m) off western and southern Africa (*Pseudoliva*, *Luizia* and *Naudoliva*) and Australia (*Zemira*). The new family Benthobiidae currently includes only the two genera *Benthobia* and *Fusulculus*, both from bathyal and abyssal depths of the Atlantic and Indo-Pacific regions. The paraphyly of Pseudolividae has already been discussed by Simone (2007) on the basis of a cladistic analysis of morphological characters. His analysis however failed to recognize Pseudolividae as a distinct family, which was recovered as a grade, with *Nassodonta* H. Adams, 1867 (Nassariidae) emerging as a sister group. Thus, although Simone’s paraphyly of Pseudolividae

is congruent with our own results, its relationship to other Neogastropoda as hypothesized here is very different from that suggested by Simone (2007).

Conchologically and anatomically, Pseudolividae and Benthobiidae are different from other Olivoidea, although there are not many autapomorphies that can characterize them. Conchologically, the two families differ from all other olivoideans in the absence of the characteristic anterior band, the presence of periostracum, and the very limited development of the primary callus that does not cover the spire. Pseudolividae and Benthobiidae share the presence of the olivoid groove, which is present in at least some Olividae (Agaroniinae) and many Ancillariidae. A very similar groove can however also be found in other unrelated neogastropods, for example *Ceratoxancus* (currently a basal Costellariidae). Perhaps the only autapomorphy of Benthobiidae is the very unusual accessory salivary gland terminating in a large muscular bulb, described for the first time in detail by Kantor (1991), reconfirmed by Simone (2003), and herein also found in *Fusulculus*.

Olivoidea as a clade is not significantly supported in our analyses, while the node uniting all olivoideans except Bellolividae is highly supported (Figs 3, 4). Although Bellolividae shares a number of characters with Olividae (filament channel of the shell and correspondingly the presence of a mantle filament) and other oliviforms (anterior band of the shell, propodium morphology, parapodia), its relationships to other Olivoidea is not resolved. To check whether the ambiguous position of Bellolividae could be an artefact of the analysis induced by the inclusion of the very different Pseudolividae and Benthobiidae, we reran an analysis of the dataset after removing the two latter families. The resulting tree did not differ significantly in topology and the support of the basal node did not change much, still remaining rather low.

The trees obtained leave the deeper relationships between the major groups of Olivoidea unresolved. Therefore, they do not rule out the possibility that Benthobiidae and Pseudolividae may appear to be sister groups in future analyses with a dataset that includes more taxa. All major terminal clades are well supported and the taxonomic conclusions at the family/subfamily levels are well grounded. However, attempts to reconstruct ancestral states and transformation of the characters with Mesquite software (Maddison & Maddison, 2007–2010) were unsuccessful (results not shown), as the analyses suggested multiple independent origins of obviously homologous characters. Thus, according to that analysis, the anterior band of the shell originated independently in Bellolividae, Olividae and Ancillariidae; similarly, multiple origins were suggested for the crescent-shaped propodium, parapodia and so on. We view this as an artefact of

the tree due to unresolved nodes and we abstain from attempts to reconstruct the evolutionary transformations of these characters until a more resolved tree is available. The poor resolution of basal and intermediate nodes may be a result of either insufficient taxon sampling, or insufficient resolution of the genes used in the analysis.

The close relationship of Olivellinae with Olivinae and Agaroniinae is also an unexpected result of this research. Kantor (1991) pointed out characters that distinguish *Olivella* from *Oliva*, among them are a very distinctive radular morphology, the resorption of the inner shell walls in the upper whorls, the seeming ‘absence’ of the head, valve and gland of Leiblein, and the position of the odontophore at the base of the retracted proboscis. The present study nevertheless demonstrated that at least some of these characters are not autapomorphies of Olivellinae. Thus, Marcus & Marcus (1959) and Kantor (1991) had considered that *Olivella* lacks a differentiated head, since the triangular, dorso-ventrally compressed flaps are very asymmetrical and the rhynchostome opens below the right flap. However, examination of different olivoideans shows that the head is asymmetrical in nearly all of them and, even in *Oliva*, which has a normally symmetrical head formed by vertical flaps with tentacles and eyes, the rhynchostome opens under the right flap. A similar position of the rhynchostome has been observed in Benthobiidae (but we lacked adequate material to check it in Pseudolividae). A ‘head’ with dorso-ventrally compressed flaps is found in a number of olivoideans, including *Agaronia* and Ancillariidae, and thus cannot be considered a unique character of Olivellinae. However, the peculiar radula really sets *Olivella* apart from all other members of the superfamily. The homology of the outermost plates is not clear; although the lateral teeth in *Olivella* look different from other olivoideans (e.g. they are curved outwards, not inwards) (Fig. 11G, H) they are most probably homologous with the lateral teeth of other olivoideans, since they adjoin the rachidian tooth. Thus the outermost plates are either the remains of the marginal teeth, or *de novo* structures. Nothing similar was found in either the outgroup neogastropod taxa or other members of Olividae. Given that the majority of basal caenogastropods have a taenioglossate radula with seven teeth per row, and that in Neogastropoda the number of teeth per row is usually three, two or even one, it is generally assumed that the evolutionary tendency in Neogastropoda is a reduction in number of teeth per row. However, there are five teeth per row in different conoidean taxa (e.g. Taylor, Kantor & Sysoev, 1993; Bouchet *et al.*, 2011), and we hypothesize that the appearance of the marginal plate-like teeth is an autapomorphy of Olivellinae.

By contrast to our findings on the position of Olivellinae, confirmation that Ancillariidae represent its own well-supported clade of family rank is not unexpected. There are several conchological and morphological characters that clearly define the family. Already in the morphology-based cladistic analysis performed by Kantor (1991) *Olivella* and *Oliva* were closer to each other than to *Amalda*. In Ancillariidae the shell is more strongly callused than in any other Olivoidea. The suture is always overlaid with the primary callus, which can be rather narrow, but sometimes (in some *Ancilla*) is extremely broad and covers the entire shell surface. This is reflected in the mantle morphology – the mantle filament is absent, while the posterior mantle lobe responsible for depositing the primary callus is very large and can be hypertrophied. The anterior foregut, on the contrary, does not differ markedly from other olivoideans. We are still missing three valid genera in our analysis – *Ancillista* (the species included in our analysis, *A. aureocallosa*, is rather distinct from the type species, *A. velesiana*), *Eburna* and *Micrancilla* – and their inclusion may change the relationships between genera. At this moment, all recognized genera are however highly supported. The genetic heterogeneity observed in *Ancilla* is also paralleled by the high disparity of radula characters in that genus (Fig. 13). The remaining Ancillariidae for which the radulae are known are characterized by a rather conservative within-genus radular morphology. The current knowledge on the radula of Ancillariidae and the range of its within-genus variability now allows clarification of the position of the deepest water olivoidean species, namely *Amalda sibuetae* Kantor & Bouchet, 1999, described from a depth of 1733–1885 m from off Mauritania. It possesses a radula typical of *Turrancilla* and should be reclassified in that genus. Kantor & Bouchet (1999) pointed out the similarities of the radula of *Amalda sibuetae* to the type species of *Turrancilla*, *Ancillaria lanceolata* Martens, 1901, but due to the then insufficient data on the radular morphology in *Turrancilla*, they did not attribute the new species to that genus.

MORPHOLOGY

One of the remarkable (although not unique) characters of oliviform shells is the great development of the different callused structures: anterior band, columellar callus (= plication plate), primary and secondary spire calluses. Correlation of the soft body anatomy with these shell characters and observations of live animals has allowed us to suggest for the first time which part of the mantle is responsible for depositing which callused feature.

As was stated above, both primary and secondary spire calluses in oliviform shells (as well as the

parietal callus in pseudoliviforms) are deposited by the same mantle outgrowth, the posterior mantle lobe. Characteristic and distinctive between different groups of Olivoidea, the shell morphology is determined by the degree of extension of the posterior mantle lobe in live animals. In *Oliva* the lobe is extending above the aperture on the parietal part of the last whorl towards the apex, but does not extend backwards, in the direction opposite to the shell growth above the aperture. Thus, the primary callus is not overlaying the suture on the last whorl. In Ancillariidae, it is obvious that the posterior lobe is extending above but also backwards to the posterior aperture corner, and is producing both primary and secondary spire calluses. This results in the suture overlaid with a layer of primary spire callus, producing the very characteristic ancillariid appearance of the shell. In some genera (*Ancilla*), the primary callus covers most of the shell surface and on upper whorls it is overlaying the callus deposited during the growth of the previous whorl, producing a multi-layered callused structure. The presence of a reduced posterior mantle lobe in Pseudolividae and Benthobiidae, which deposits the callus that extends only to the parietal part of the last whorl, may represent an initial stage of development of the primary callus.

We do not have at this moment a clue to the functional significance of such prominent character as the spire callus. An obvious hypothesis – that the spire callus renders the shell more smooth to facilitate burrowing and movements in the sediment – is rejected by the fact that in Olivoidea (except Pseudolividae and Benthobiidae) the shell is nearly completely covered by the foot parapodia and is not directly in contact with the sediment.

While the callus is deposited by a subtle, but rather distinct, lobe that can be seen in preserved specimens, the anterior band is deposited by the mantle reflected at the fasciole over the shell edge. This part of the mantle (anterior mantle lobe) does not differ morphologically from the adjoining parts of the mantle. Its role can be deduced only by observations of living animals. In some preserved specimens the anterior mantle lobe forms minor folds, probably corresponding to the plicae on the anterior band, but usually it is smooth.

It should be noted that a significant or even hypertrophied development of the callus is not unique to Olivoidea, but is known in other, not closely related, neogastropods. In some Nassariidae [e.g. *Nassarius arcularia* (Linnaeus, 1758)] at the termination of growth, the parietal callus produces a very thick shield that extends over all the apertural side of the shell. In the fossil *Cyllenina lucinensis* (Landau & Marquet, 1999) from the Pliocene of Spain, the callus completely covers the shell, including the protoconch (Lozouet & Galindo, 2015). Although nothing is known about the

mantle anatomy of such species, it is logical to suggest that the callus should be deposited by some equivalent of the posterior mantle lobe of Olivoidea, sometimes only at growth termination (*N. arcularia*) but sometimes during the entire life (*C. lucinensis*). In most Marginellidae the suture is overlaid by a thin callus, producing an appearance similar to Ancillariidae. Again there are no data on the mantle morphology of marginellids. In Marginellidae the mantle edge is, as in olivoideans, reflected over the siphonal notch and a thickened shell edge is present in most species along the lip and around the fasciole. Obviously, the extra callus layer here is deposited in a similar way as in olivoideans, although it is not as intricate.

Sterba (1996) and, later, Tursch & Greifeneder (2001) mentioned one more unusual character of oliviform shells: they considered the morphology of the suture in *Oliva* to be unique in Gastropoda since the whorls of the shell do not come into direct contact with each other, but are connected by a spiral ribbon which is a part of the primary callus on the parietal whorl of the aperture. Such a peculiarity is in fact present in all oliviform shells (except Belloliviidae, which do not have a spire callus and, correspondingly, no posterior mantle lobe). The mantle filament, housed in the filament channel, is indeed a unique morphological character, present in most Olividae and all Belloliviidae. Several possible functions of the filament have been suggested: a sensory organ, indicating the depths of burial in the sediment (B. Tursch, personal communication to Y. Kantor); a defensive weapon (Zeigler & Porreca, 1969); a 'sense organ that detects danger from behind while the animal is buried in the sand' (Vermeij, 1993); and others. None of these have been evaluated and remain conjectural.

Olivoidea (except Pseudolividae and Benthobiidae) have a very characteristic foot morphology. In crawling animals, the foot is large, very agile, and with a large crescent-shaped propodium, often free on external corners, and a metapodium with two large symmetrical lateral flaps, the parapodia. The propodium is subdivided by a longitudinal furrow. A similar shape of the propodium is also seen in Harpidae; however, it is not subdivided by a longitudinal cleft.

The unique propodial and metapodial morphology of olivoideans can be explained from a functional point of view. Thus the propodium is actively used for collecting food and acts like a pair of pincers, firmly seizing the prey when both halves of the propodium fold along the longitudinal furrow. The broad, thin and agile metapodium of *Oliva* and *Agaronia* serves to form the pouch in which the prey (sometimes several items according to our observations) is kept and digested. The disappearance of the operculum may be related with this ability to form a pouch by facilitating the bending of the metapodium. In Ancillariidae and Olivellidae the

foot is truncated and relatively thicker, and seems to be unable to form a pouch. Correspondingly, an operculum usually persists in these taxa.

Some olivids can swim – probably as an escape response – using either the propodium [as observed by Wilson (1969) in *Ancillista cingulata* (Sowerby, 1830)], or more often the parapodia (in *Olivella* – see Olsson, 1956, Marcus & Marcus, 1959). During fieldwork at King Leopold Station in Laing Island (Papua-New Guinea), the senior author has observed swimming in many species of *Oliva* kept in aquaria in response to food. The propodium is also definitely used as a wedge during burrowing.

Parapodia embrace the shell in crawling snails, sometimes nearly completely. Observations were reported by Kantor (1991) on living *Olivella borealis* in a narrow aquarium that allowed the snail to be seen burrowed in the sediment. In the completely burrowed animal, the parapodia are even more expanded than when the snail crawls on the surface of the sediment. We suggest that the lateral embrace of the shell prevents sand particles from entering the mantle cavity and thus is an adaptation to the burrowing mode of life.

Our results demonstrate that morphological data alone should be used with caution for phylogenetic reconstructions. The morphology-based phylogeny of Olivoidea (Kantor, 1991) was fundamentally different (and correspondingly wrong) in regard to both taxa ranks and their relationships. For example, the radula that is otherwise considered to be of high importance in the taxonomy of Neogastropoda is extremely variable within the one family Olividae, with a range of variation larger than within the entire superfamily. Similarly, the superfamily includes representatives with ‘normal’ foot (narrow propodium, metapodium without parapodia in two families, Pseudolividae and Benthobiidae) and others with the characteristic ‘olivoidean’ foot (crescent-shaped propodium, metapodium with broad parapodia), which was hitherto considered one of the key autapomorphies for the group.

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