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Phylogeny and systematics of mitriform gastropods (Mollusca: Gastropoda: Neogastropoda)

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Abstract

With about 800 Recent species, "miters" are a widely distributed group of tropical and subtropical gastropods that are most diverse in the Indo- West Pacific. They include the two families Mitridae and Costellariidae, similar in shell morphology and traditionally treated as close relatives. Beside, some genera of deep water Ptychatractidae and Volutomitridae are close to miters in shell morphology, and the term "mitriform gastropods" has been introduced to refer to Mitridae, Costellariidae and this assortment of convergent forms. The present study aims at reconstruction of phylogenetic relationships of mitriform gastropods based on representative taxon sampling. Four genetic markers (COI, 16S rRNA, 12S rRNA and H3) were sequenced for over 90 species in 20 genera, and the molecular dataset was supplemented by studies of radula morphology. Our analysis recovered Mitridae as a monophyletic group, while the genus *Mitra* is found polyphyletic. Of 42 mitrid species included in the analysis, 37 formed a well supported "core Mitridae" consisting of four major clades, three of them consistent with the subfamilies Cyndromitriinae, Imbricariinae, and Mitriinae, and *Strigatella paupercula* standing out by itself. Basal to the "core Mitridae" are four minor lineages, with the genus *Charitodoron* recognized as sister group to all other Mitridae. The deep water family Pyramimitridae shows a sister relationship to the Mitridae, with high support for a Pyramimitridae + Mitridae clade. Our results recover the monophyly of the Costellariidae, which form a well supported clade that also includes Ptychatractidae, Columbariinae and Volutomitridae, but not Mitridae. Most derived and diverse among Costellariidae are species of *Vexillum*, characterized by a bow-shaped, multicuspidate rachidian tooth. Several previously unrecognized deep water costellariid lineages are revealed. Their members retain some plesiomorphies - in particular a tricuspidate rachidian tooth - that makes them morphologically intermediate between ptychatractids and *Vexillum*. The taxa of Ptychatractidae included in the analysis are not monophyletic, but form three well supported, unrelated, groupings, corresponding respectively to *Ceratoxancus* + *Latiromitra*, *Exilia*, and *Exiliodea*. None of them shows an affinity to Pseudolividae.

Keywords: Phylogeny, Neogastropoda, Mitriform gastropods, Mitridae, Costellariidae, Ptychatractidae, Volutomitridae, *Mitra*, *Vexillum*, radula, marine molluscs.

Introduction

Almost one-fourth of the diversity of marine molluscs is represented by the order Neogastropoda. With more than 12,000 Recent species classified in 40 families, these predatory and scavenging snails are one of the most evolutionary successful taxa of marine molluscs, playing a key role in marine benthic ecosystems at all latitudes and depths. However, although the superfamilies Conoidea (Puillandre *et al.*, 2008; 2011), Buccinoidea (Hayashi, 2005; Oliverio & Modica, 2010), and the families Muricidae (Barco *et al.*, 2010) and Cancellaridae (Modica *et al.*, 2011) have been specifically targeted by recent molecular phylogenies, a not inconsiderable fraction of the Neogastropoda - including some ancient and diverse lineages - has remained essentially outside the sphere of molecular systematics. One such untouched group is the so called "miters", a name that refers to members of the two families Mitridae and Costellariidae that together encompass some 800 species (WoRMS, 2015). Miters are widely distributed in tropical and subtropical waters and reach their highest diversity in the Indo-West Pacific in 0-100 meters, where they form a characteristic element of soft bottom benthic communities. Miter shells have long been popular among collectors, and many new species continue to be discovered by amateur taxonomists. Miters usually have high, fusiform shells, with an elongated aperture, strong columellar folds, and an adult size mostly in the 10-50 mm range. Based on this superficial resemblance in shell morphology, a number of costellariid species were originally described under mitrid genera and *vice versa*. A similar shell is also found in other neogastropod genera, such as *Latiromitra* (Ptychatractidae) or *Microvoluta* (Volutomitridae), and the term "mitriform gastropods" (Ponder, 1972) informally refers to the miters as well as such miter-resembling forms.

The state-of-the-art of miters systematics still rests to a large extent on the work carried out by Walter Cernohorsky (1966, 1970, 1976, 1991). However, relationships within both these families remain poorly understood, and the monophyly of neither Costellariidae nor Mitridae, and its subfamilies, has ever been tested. Despite Mitridae and Costellariidae have similar shell morphology, their close relationship has been challenged based on radula morphology and anatomy of the digestive tract (Iredale, 1929, Cernohorsky, 1966, 1970; Ponder, 1972; Fedosov & Kantor, 2010). What little is available in terms of molecular data likewise suggests that the two families are not close relatives: the single mitrid species sequenced so far clustered with the Muricidae and Olividae, while the single costellariid species showed a closer affinity to the deep water families Ptychatractidae and Volutomitridae (Oliverio & Modica, 2010; Zou, Lee & Kong, 2011). In fact, the close relationship between Costellariidae and Ptychatractidae was first suggested by Thiele back in 1929. However, a combination of plesiomorphies in morphology of Ptychatractidae (the simple radula with tricuspidate rachidian and sickle-shaped laterals; open

seminal groove) justified the later placement of this group in the family Turbinellidae (Bouchet & Warén, 1985; Bouchet & Kantor, 2000). A recent morphological study, however, revealed a deep water member of the family Costellariidae that showed a remarkable similarity to ptychatractids in foregut anatomy and radula morphology (Fedosov & Kantor, 2010); this discovery supports a close relationship between Costellariidae and Ptychatractidae, and renders morphological differences between the two families quite subtle. With this background of contradictory morphological and molecular data, the relationships of Mitridae, Costellariidae, and other lineages of mitriform gastropods remain quite uncertain and speculative, and require a fresh re-evaluation. The purpose of the present study is precisely to map the phylogeny of mitriform gastropods, with an emphasis on the two families of miters, and to describe their relationships within the Neogastropoda.

Material and Methods

1. *Taxon sampling*

The material used in the present study was collected in a series of shore based expeditions and deep water cruises conducted by Museum National d'Histoire Naturelle (MNHN), Institut de recherche pour le Développement (IRD) and Joined Russian Vietnamese Tropical Center in the tropical Indo-Pacific, West Africa and the Mediterranean (Figure 1, Table 1). In the field, molluscs were either anesthetized using magnesium chloride (MgCl₂), or in some cases shells were drilled, or, in the most recent expeditions, were processed using a microwave oven (Galindo *et al.*, 2014); a tissue clip was then cut and fixed in 95% ethanol. Voucher shells, kept intact for identification, are deposited in MNHN (Table 1). Taxonomy of the family Mitridae follows Cernohorsky (1976, 1991), taxonomy of the families Costellariidae, Ptychatractidae and Volutomitridae is based on several sources as indexed in WoRMS (WoRMS, 2015).

A number of mitriform species in the families Ptychatractidae (genera *Exilia*, *Exilioidea*, *Ceratoxancus* and *Latiromitra*), Volutomitridae (genera *Volutomitra* and *Microvoluta*), Turbinellidae (subfamily Vasinae, genus *Vasum*; subfamily Columbariinae, genera *Coluzea* and *Fustifusus*) were included as putative sister groups of the family Costellariidae. A suite of species from 17 other neogastropod families in the superfamilies Conoidea, Cancellarioidea, Buccinoidea, Muricoidea, Olivoidea and Pseudolivoidea was included in the analysis to ensure adequate representation of major evolutionary lineages of the Neogastropoda and likely inference of mitriform gastropods relationships. *Tonna galea* (Caenogastropoda, Tonnoidea, Tonnidae) was used as non-neogastropod outgroup. Overall classification follows Bouchet & Rocroi (2005).

2.2. *PCR amplification and DNA sequencing*

Total genomic DNA was extracted from muscle tissue using NucleoSpinR 96 Tissues (Macherey–Nagel) and following the manufacturer's instructions. Fragments of the mitochondrial genes Cytochrome Oxidase I (COI), 16S rRNA and 12S rRNA as well as the nuclear gene H3 were sequenced (Table 2). PCR reactions were performed in 20 µl final volume, containing approximately 3 ng template DNA, 1.5 mM MgCl₂, 0.26 mM of each nucleotide, 0.3 µl of each primer, 5% DMSO and 0.75 µl of Taq Polymerase (Qbiogene).

For amplification of each COI, 16S and H3 only one pair of primers has been used (see Table 2). 12S sequences were amplified using two different primer combinations. For most specimens the pair 12SA-12SB was used, producing a fragment of about 370-380 bp. However, due to poor results with these primers in most Mitridae, a primer pair 12SI-12SIII has been used, resulting in a fragment of about 540 bp (Table 2).

The PCR profile for the COI started with 5 min at 95°C followed by 40 cycles with the denaturation at 95°C (35 sec), annealing at 50°C (35 s) and elongation at 72°C (1 min), with final elongation phase at 72°C (10 min). Similar PCR profiles were set for 16S (annealing at 55°C, elongation at 72°C for 50 s), 12S with the primer pair 12SA-12SB (annealing at 57°C, elongation at 72°C for 50 s) and H3 (annealing at 57°C, elongation at 72°C for 45 s). For the primer pair 12SI-12SIII a touch-down PCR protocol with gradual decrease of the annealing temperature from 62 to 56°C has been used. All genes were sequenced for both directions to confirm accuracy of each sequence. The sequencing has been performed by Eurofins. Chromatograms were edited using CodonCode Aligner version 3.7.1.1.

2.3 Sequence alignments

Sequences were aligned for each gene independently using MUSCLE (Edgar, 2004). The accuracy of automatic alignments was confirmed by eye using BioEdit version 7.0.9.0 (Hall, 1999). No indels were detected in protein coding genes COI and H3, the fragments 658 bp and 328 bp in length were sequenced for these two markers respectively. After the alignment of 12S where fragments of different length were amplified, absent positions at 3'-end were treated as missing data.

2.4 Datasets

Six datasets were analyzed. The first three datasets correspond to the three mitochondrial genes, COI, 16S and 12S, analyzed separately. The fourth dataset represents concatenated COI, 16S, and 12S sequences (1875 positions) and is referred to as MCPV-3mit (MCPV – abbreviated Mitridae-Costellariidae-Ptychactridae-Volutomitridae). To evaluate the robustness of the mitochondrial phylogeny, a fifth dataset corresponding to the nuclear H3 gene was analyzed. Finally the concatenated dataset of 2203 positions (referred to as MCPV-4G) was obtained by adding H3 sequences to the MCPV-3mit dataset.

2.5 Phylogenetic analyses

Best-fit substitution models were identified for each gene separately, and for each combined dataset using ModelgeneratorV.85 (Keane *et al.*, 2006) (Table 2). Best-scoring Maximum Likelihood (ML) trees were estimated using RaxML (Stamatakis, 2006) from 100 independent searches each starting from distinct random trees. Robustness of the nodes was assessed using the thorough bootstrapping algorithm (Felsenstein, 1985) with 1000 iterations. RaxML was performed on the Cipres Science Gateway (<http://www.phylo.org/portal2>), using RAXML-HPC2 on XSEDE.

Bayesian Analyses (BAs) were performed running two parallel analyses in MrBayes (Huelsenbeck and Ronquist, 2001). For single gene analyses each run consisted of six Markov chains and 5,000,000 generations with default number of swaps chains. For MCPV-3mit and MCPV-4G datasets each analysis consisted of eight Markov chains of 50,000,000 generations with the number of swaps chains set to five. A sampling frequency was one tree each 10,000 generations, and the chain temperature was set at 0.02 in all analyses. Convergence of each analysis was evaluated using Tracer1.4.1 (Rambaut et al. 2014) to check that all ESS values exceeded 200. Consensus tree were calculated after omitting the first 25% trees as burn-in. The combined MCPV-3mit and MCPV-4G datasets were separated into five and eight unlinked partitions respectively: 16S, 12S, three codon positions of the COI gene (both datasets) plus three codon positions of the H3 gene (MCPV-4G dataset). Analyses were performed on the Cipres Science Gateway (<http://www.phylo.org/portal2>), using tool MrBayes 3.2.2 on XSEDE.

2.6. *Radula morphology*

Foregut anatomy of sequenced specimens was examined or, in some cases, additional specimens conspecific with sequenced material were dissected. During dissection the buccal mass was isolated and cleaned with diluted bleach (1 part of commercially available bleach to 3-4 parts of water) until tissues are completely dissolved. Cleaned radulae were rinsed in several changes of distilled water and mounted on clear glass cover-slips for SEM investigation.

Results

DNA sequences

Of the 106 species studied, the COI gene was successfully amplified for 99 species, 16S and 12S for 87 species, and H3 for 69 species. All sequences were deposited in GenBank and BOLD (Table 1). For the total count of sequences analyzed and details of the substitution models selected, see Table 2.

Phylogenetic analyses of single gene datasets

The trees obtained after the single gene analyses are characterized by the weak support of most nodes; however, no supported conflicting topologies were found. Because of the weak resolution of the single gene analyses, their results are not discussed here.

Phylogenetic analysis: MCPV-3mit dataset

The topologies of the consensus trees obtained from BA and ML are largely congruent, with the exception of unresolved deepest branches, which show slightly different topologies in trees obtained with BA and ML, though without support in either case. We will mainly discuss the topology of the tree obtained with BA (Fig. 2) and will refer to ML bootstrap support values where applicable.

Within Neogastropoda, *Plesiotriton silinoensis* Verhecken, 2011 (Cancellariidae) and *Melo melo* (Lightfoot, 1786) (Volutidae) constitute a well supported clade (PP=1, B=68%) that is sister to all other neogastropods. At the next dichotomy, a rather well supported monophyletic clade corresponding to the superfamily Buccinoidea (PP=0.99, B=69%) splits out from the weakly supported main Neogastropoda grouping (PP=0.95). Six supported major clades can be recognized within the main Neogastropoda grouping, the relationships to each other being unresolved. Three of these major clades correspond to (a) the superfamily Conoidea (monophyletic, PP=1, B=73%), (b) the turbinellid subfamily Vasininae (monophyletic, PP=1, B=100%) and (c) the family Muricidae (monophyletic, PP=0.94). Members of the families Olividae, Olivellidae and Pseudolividae together form a fourth major clade (PP=0.99, B=71%), that can be called Olivoidea. The fifth clade, which is referred to as a “Clade A”, comprises species currently assigned to the four neogastropod families Costellariidae, Turbinellidae (Columbariinae), Volutomitridae and Ptychatractidae. Finally the sixth major clade (PP=1, B=95%) combines the families Mitridae (PP=1, B=95%) and Pyramimitridae (PP=1, B=100%), both monophyletic.

Clade A

Within clade A, the species currently assigned to the neogastropod families Costellariidae and Volutomitridae together with the turbinellid subfamily Columbariinae form three well supported clades (PP=1, B=100%), consistent with their accepted taxonomic status. Conversely, the species of Ptychatractidae do not form a single grouping and three distinct clades can be recognized corresponding to (a) the genus *Exilia*, (b) the genus *Exilioidea* and (c) the genera *Ceratoxancus* and *Latiromitra*. Analysis of the three genes dataset recognizes *Exilioidea* as a sister group to the family Volutomitridae, though with no support, while the *Ceratoxancus-Latiromitra* clade clusters with Costellariidae (PP=1, B=100%). The affinities of *Exilia* within clade A remain uncertain.

Within the family Costellariidae, the only species of *Thala* included in the analysis branches out by itself and forms the first offshoot from the costellariid stem, which includes five well supported clades, the branching order of which is not supported, reflecting the weak resolution of the tree based on the mitochondrial genes. The majority of the species of *Vexillum*

clustered in the well supported grouping *Vexillum* s.s. (PP=1, B=100%), forming a long branch on the tree. This clade comprises mostly shallow water species and includes in particular *V. plicarium* (Linnaeus, 1758), the type species of *Vexillum*, as well as *Z. ziervogelii* (Gmelin, 1791), the type species of *Zierliana*. Species of *Vexillum* s.s. tend to form two separate clades, though none of them is supported. The rather well supported clade *Vexillum* II (PP=0.98, B=0.5) includes six species conventionally assigned to *Vexillum*, both from deep water and from subtidal / intertidal depths, in turn forming two separate clades, a well supported one with *Vexillum balutense* Herrmann, 2009 and *V. choslenae* Cernohorsky, 1982 (PP=1, B=100%) and a weakly supported one combining the other four species. The three remaining costellariid clades are labeled C-I (PP=1, B=97), C-II (PP=1, B=99) and C-III (PP=1, B=98) on the molecular tree. These include mostly deep water forms, representing an essentially unrecognized and unnamed diversity of the Costellariidae (of 13 sequenced species, two only can be identified with certainty).

Mitridae

The monophyly of the family Mitridae (PP=1, B=99%) is supported by both BA and ML, as well as its close affinity to the enigmatic deep water family Pyramimitridae (PP=1, B=95%). The first dichotomy of the Mitridae separates the well supported *Charitodoron* clade (PP=1, B=100%) from the rest of the Mitridae (PP=1, B=100%). Subsequently, three species, *Mitra tuberosa* Reeve, 1845, *M. bernhardina* Röding, 1798 and *M. itra peculiaris* Reeve, 1845 split out from the general mitrid stem, forming three independent lineages, though the lack of support in the corresponding nodes leaves the possibility of alternative branching. Later on, we will refer to the combined group including *Charitodoron* species, *Mitra tuberosa*, *M. bernhardina* and *M. peculiaris* as “basal Mitridae”. The remaining 37 mitrid species form a rather well supported core clade (PP=0.97, B=63%), which in turn consists of four major groupings (referred to as clades M-I to M-IV), either well supported (M-I, M-II and M-IV), or consisting of a single species (M-III). Clade M-I (PP=1, B=63%) combines two species of *Pterygia* (monophyletic, PP=1, B=100%), including its type species, *P. dactylus* (Linnaeus, 1767), and two species currently placed in *Mitra*, *M. glabra* Swainson, 1821 and *M. incompta* (Lightfoot, 1786). Clade M-II (PP=1, B=69%) contains an assortment of *Mitra* species that form several well supported clades and a set of single-species lineages with unsupported relationships. One of these well supported clades is formed by *Mitra mitra* (Linnaeus, 1758), the type species of *Mitra*, and the closely related *M. papalis* (Linnaeus, 1758), and it will consequently be referred to as *Mitra* s.s. Another well supported grouping in the M-II clade corresponds to *Nebularia* (monophyletic PP=1, B=96%). Three clades within M-II are solely represented by deep water, mostly

undescribed, forms (on the tree referred to as Mitridae DW-1 to 3), and we did not find any genus-group name to designate them. Clade M-II also encompasses two lineages which correspond to the genera *Domiporta* (monophyletic, PP=1, B=100%) and *Ziba* (only represented by *Z. carinata* (Swainson, 1824), the type species of the genus). As mentioned before, clade M-III includes a single species, *Strigatella paupercula* (Linnaeus, 1758), the type species of *Strigatella*. Clade M-IV (PP=1, B=100%) includes 13 species traditionally classified in the genera *Neocancilla*, *Scabricola*, *Imbricaria*, *Cancilla*, *Ziba*, and *Subcancilla*, which were all allocated to the subfamily Imbricariinae by Cernohorsky (1991). Three well supported lineages can be distinguished within that clade, one comprising the monophyletic *Neocancilla* (PP=1, B=98%), monophyletic *Scabricola* (represented by two species of the subgenus *Swainsonia*) and *Imbricaria olivaeformis* (Swainson, 1821). The second lineage combines two closely related species of the genus *Cancilla* (*Cancilla fibula* Poppe, Tagaro & Salisbury, 2009, and *C. cf. fibula*) and *Mitra schepmani* Salisbury & Guillot de Suduiraut, 2003. Finally the third lineage of clade M-IV combines species traditionally assigned to *Ziba* (*Z. flammigera* (Reeve, 1844), *Z. fulgetrum* (Reeve, 1844) and *Z. insculpta* (A. Adams, 1851)), *Subcancilla* (*S. pugnaxa* Poppe, Tagaro & Salisbury, 2009) and *Imbricaria* (represented by *I. conularis* (Lamarck, 1811), the type species of the genus).

Phylogenetic analysis: MCPV-4G dataset

The tree obtained after the BA of the MCPV-4G dataset (Fig. 3) is similar to the mitochondrial genes based tree discussed above and largely congruent with it, but the branching order differs in some clades. In general the four genes tree has better resolution, and many of the crucial nodes have higher support values. The composition of major neogastropod groupings remains unchanged, while the relationships among them are rather weakly supported. Among the noteworthy changes are increased supports of clade A (PP=1, B=60%) and of the Volutomitridae+*Exilioidea* grouping (PP=0.94, B=68%).

While the topology of the Mitridae segment of the MCPV-4G tree is nearly identical to the MCPV-3mit tree, the arrangement of Costellariidae clades differs. In the four genes tree, the most derived position is occupied by *Vexillum* s.s. (PP=1, B=100%), which in species composition corresponds to the *Vexillum* s.s. clade of the MCPV-3-mit tree and only slightly differs in internal branching. Conversely, the former clade *Vexillum* II is now split into several separate lineages, which cluster with the *Vexillum* s.s. clade. *Vexillum patriarchalis* (Gmelin, 1791), *V. rubrum* (Broderip, 1836) and *V. nodospiculum* (Cernohorsky, 1870) are closest to *Vexillum* s.s., and the highly supported clade formed by *Vexillum* s.s. and these three species (PP=1, B=85) will thus be referred to as *Vexillum* s.l. The single species lineage of *Vexillum*

dekkersi forms a sister group to *Vexillum* s.l.; *V. dekkersi* Herrmann, Stossier & Salisbury, 2014 and a set of similar species were recently placed in a separate subgenus *Protoelongata* Herrmann, Stossier & Salisbury, 2014, and this name can be used for that clade. Finally the well supported clade (referred to as C-IV) of two deep water species, *V. balutense* and *V. cf. choslenae*, form a sister group to the *Vexillum* s.l.-*Protoelongata* clade with high support of the resulting grouping (PP=1, B=83%).

Given the increased resolution of the MCPV-4G tree compared to the mitochondrial genes tree, our results will be discussed in the context of the phylogenetic scheme inferred from the four genes dataset. Of the three nominal genera of Costellariidae studied, *Thala* was represented by a single species, so its monophyly was not tested; *Zierliana* comes out monophyletic, but its inclusion into the *Vexillum* s.s. clade implies a revision of its rank; *Vexillum* is undoubtedly polyphyletic, and the extent of its polyphyly depends on how broad its boundaries are defined (see Discussion).

Among mitrid genera, monophyly is supported for *Charitodoron*, *Pterygia*, *Domiporta*, *Neocancilla*, *Cancilla* and *Scabricola* and for the subgenus *Mitra* (*Nebularia*). Monophyly is not rejected for *Subcancilla*, of which a single species has been studied, and for *Strigatella*. The genera *Imbricaria* and *Ziba* are definitely polyphyletic. It is noteworthy that *Z. carinata*, the type species of *Ziba*, ended up within the clade M-II, separately from three other species traditionally placed in *Ziba*, *Z. fulgetrum*, *Z. flammigera* and *Z. insculpta*, which cluster in clade M-IV. Finally the genus *Mitra* appears highly polyphyletic: species conventionally assigned to *Mitra* are found in all four clades of the core Mitridae and also among the “basal Mitridae”.

Radula morphology

All species in the *Vexillum* s.s. clade are similar in radula morphology: they have triserial radulae with a multicuspidate rachidian and simple, unicuspid laterals (Figs. 4, 5). The shape of rachidian ranges from robust with relatively short cusps, in *Zierliana ziervogeli* and *Vexillum semifasciatum* (Lamarck, 1811) (Fig. 5), to more elaborate, bow-shaped with long pointed cusps in *Vexillum exasperatum* (Gmelin, 1791) or *V. gloriae* Poppe, Tagaro & Salisbury, 2009 (not shown). The number of cusps varies from seven (*Vexillum cancellarioides*, Fig. 5) to more than 20 (*V. exasperatum*). A similar radula is found in the two species of *Vexillum* s.l., *Vexillum rubrum* and *Vexillum nodulospiculum*.

The other costellariid species (clades C-I – C-IV, *Protoelongata* and *Thala*) have monocuspid laterals similar to those found in *Vexillum* s.s., but differ in structure of the rachidian, which bears only three cusps, although it varies in shape, robustness, base width, orientation and length of the cusps (Fig. 4, 5). “*Vexillum*” *balutense* has a rachidian with two

minor intermediate cusps, positioned on both sides of the central cusp (Fig. 5). Lateral teeth vary from slender, sickle-shaped in Costellariidae gen. sp. (IM-2013-40629) to robust, almost triangular, in “*Vexillum*” *isaoi* (Kuroda & Sakurai, 1959).

The same general radula morphology characterizes the Ptychotractid genera *Ceratoxancus*, *Latiromitra* and *Exilia* and, also, the Columbariine *Coluzea* cf. *liriope* Harasewych, 1986, but *Exilioidea* is remarkably different (Figs 4, 5). In *Ceratoxancus* cf. *melichrous* Kantor & Bouchet, 1997 and two species of *Latiromitra*, *L. crosnieri* Bouchet & Kantor, 2000 and *L. barthelowi* (Bartsch, 1942), there is a robust rachidian bearing three short and blunt cusps on a moderately wide base, and rather slender laterals; in *Exilia krigei* (Kilburn, 1971), the rachidian has a proportionally wider base and closely set, long and pointed cusps; in *Coluzea* cf. *liriope*, the only distinguishing feature is the very narrow base of the rachidian. The rachidian of *Exilioidea* is characterized by the massive base and three cusps, situated on the tip of long blade-like projection. This projection of the rachidian apical segment is directed along the longitudinal axis of the radula and forms a distinct longitudinal furrow, so that the apical part of a tooth interlocks in the furrow of the next one.

Mitridae show considerable variation in shell and radular morphology (Figs 6, 7). A triserial radula with a rather small rachidian and broad, multicuspidate laterals characterizes members of clade M-II as well as *Strigatella paupercula* of the clade M-III, and *Mitra peculiaris* and *Charitodoron* in the "basal Mitridae". Typically, the lateral teeth are nearly rectangular, bear 14 to more than 20 cusps that are stronger medially and gradually reduce in size towards the margins. The rachidian is about three times narrower than the laterals and bears 5-7 subequal, rather short and stout cusps. However, in one unidentified species (IM-2013-40651) of clade M-II, the rachidian and laterals are similar, each tooth has a slightly convex margin that bears 12-13 equal cusps.

The three species in clade M-IV also have triserial radulae, but their morphology differs notably from that seen in clade M-II, and also from each other. The number of cusps on the laterals is reduced to six (*Ziba flammigera*), five (*Scabricola fusca* (Swainson, 1824)) or even one (*Imbricaria olivaeformis*), and one cusp is always much longer and stronger than the others, giving the laterals the appearance of a can opener (Figs 6, 7). Remarkably, the position of the enlarged cusp differs between species: in *Ziba flammigera* the second proximal cusp is the largest, while in *Scabricola fusca* it is the most distal one. The morphology of the rachidian also differs between species; *Scabricola fusca* possesses a rachidian resembling a hair comb with long cusps of equal length, but *Imbricaria olivaeformis* and *Ziba flammigera* have rachidians with two central cusps greatly enlarged in comparison to those positioned laterally.

Finally, three species, *Pterygia dactylus* (clade M-I), "*Mitra*" *bernhardina* and "*M*". *tuberosa* ("basal Mitridae") have monoserial radulae, lacking lateral teeth and retaining rachidians only (Figs 6, 7); these rachidians vary in shape from species to species, and are all greatly reduced in size, not exceeding 20 µm in width.

Discussion

Radular morphology

Our results on radula morphology essentially fall in line with the published data on Costellariidae (Cernohorsky, 1966, 1970; Bandel, 1984; Fedosov & Kantor, 2010), Ptychatractidae (Bouchet & Warén, 1988; Kantor & Bouchet, 1997; Bouchet & Kantor, 2000; Kantor, Bouchet & Oleinik, 2001), Mitridae (Cernohorsky, 1966, 1970; Ponder, 1972), Volutomitridae (Bouchet & Kantor, 2004) and Columbariinae (Harasewych, 2004). However, some of our results contradict those published earlier, or deserve special attention as novel and important for future discussion.

The radula of *Exilioidea* agrees with the description and illustrations of Bouchet & Warén (1988). Based on the tricuspidate rachidian and triangular unicuspid laterals, Bouchet & Warén suggested the placement of *Exilioidea* in the family Turbinellidae [which, at the time (Bouchet & Warén 1985), included Turbinellinae, Ptychatractinae, Columbariinae and Vasinae]. However, the presence of the strong central projection with its margins half-folded to form a kind of trough recalls the radula of Volutomitridae. The radula of *Exilioidea*, which combines rather plesiomorphic characters of ptychatractid radulae and derived ones of Volutomitridae, supports the relationships of these two groups as suggested by the molecular phylogeny.

All studied species in the *Vexillum* s.l. clade have radulae with multicuspidate rachidian, as those studied by Fedosov & Kantor (2010). Cernohorsky (1970) illustrated the radula of *Vexillum patriarchalis* with a tricuspidate rachidian, matching the radula found by Azuma (1965) in other *Vexillum* species, sometimes classified in the subgenus *Pusia*, such as *V. (Pusia) hizenense* Pilsbry, 1921 [= *Vexillum inerme* (Reeve, 1845)], and *V. (Pusia) australe* (Swainson, 1820) (Ponder, 1998; Robin & Martin, 2004). Corresponding to our results, *Vexillum rubrum* and *V. cancellarioides* (Anton, 1838), which are referable to *Pusia* based on shell morphology, have a multicuspidate rachidian. Furthermore, in our results *Pusia* is not consistent with a single monophyletic grouping, as *V. cancellarioides* is included in the *Vexillum* s.s. clade. Further studies are needed to clarify the position of *V. patriarchalis* in Costellariidae and its relationships to *Vexillum (Pusia) microzonias*, the type of *Vexillum (Pusia)*.

The radula with morphologically identical rachidian and laterals, found in specimen IM-2013-40651, is remarkably close to the one described in *Pleioptygma helenae* (Radwin &

Bibbey, 1972) the only Recent species of the family Pleioptygmatidae (Quinn, 1989). This family was erected largely based on the peculiar foregut anatomy and radular morphology of *Pleioptygma helenae*., and a critical reassessment of the status of Pleioptygmatidae is required. While morphological data can give some hints on its possible relationships, molecular data would be critical. However, it is already clear that a radula with three morphologically identical teeth in a transversal row cannot be regarded as something outstanding in Neogastropoda; a radula of the same morphology is present also in *Colubraria* (Colubrariidae: Buccinoidea) (Oliverio & Modica, 2010).

One of the most interesting results is the finding that several independent mitrid lineages have developed uniserial radulae. To date uniserial radulae have been reported only in *Pterygia* (Ponder, 1998), but they have most likely been overlooked in other mitrids because of their minute size (7-15 µm broad), which complicates preparation.

Relationships among major groups of mitriform gastropods

All our phylogenetic analyses support the monophyly of the families Mitridae, Volutomitridae and Costellariidae, although the boundaries of latter are disputable (see below). In the analyses of both 4G and 3-mit datasets, the four genera of Ptychatractidae do not form a monophyletic grouping, but cluster into three unrelated lineages:

(a) The *Ceratoxancus-Latiromitra* clade shows a close affinity to Costellariidae, a relationship which is highly supported in all analyses (including the analyses of single gene datasets), and a logical conclusion is to expand the boundaries of the family Costellariidae to include these two genera as basal offshoots. The possible distant relationship between *Latiromitra-Ceratoxancus* and other ptychatractids was suggested by Harasewych (1987) based on the cladistic analysis of a morphological dataset. The supposed relationships of *Ceratoxancus* have long remained controversial; Sakurai (1957) suggested an affinity to the Mitridae, and Cernohorsky (1973) to the Volutomitridae. A relationship of *Latiromitra* to *Vexillum* was envisioned by Wenz (1938), who treated *Latiromitra* as a section of *Vexillum*.

(b) The genus *Exilia* is more distantly related to this newly defined costellariid- *Ceratoxancus-Latiromitra* clade.

(c) The close relationship of *Exilioidea* and Volutomitridae is weakly supported by molecular data, but is also suggested by radula morphology.

In conclusion, although the family Ptychatractidae obviously requires revision, it is at present hampered by the lack of material of crucial genera, in particular *Ptychatractus*.

The family Volutomitridae is found to be only distantly related to the Costellariidae, with both Volutomitridae and Costellariidae turning out to be more closely related to genera formerly

classified as Ptychatractids. In our analyses, the branching within Clade A thus contradicts the phylogenetic scheme of Oliverio & Modica (2010), who found the volutomitrid genus *Microvoluta* to be most closely related to *Vexillum*; the same scheme was reproduced later by Zou *et al.*, (2011). In fact, a close relationship between Costellariidae and Volutomitridae is also contradicted by the morphology of the radula and digestive system (Ponder, 1972; Fedosov & Kantor, 2010). We have therefore examined the voucher specimen (MNHN IM-2009-4609) of Oliverio & Modica's (2010) *Microvoluta* sp. It is morphologically close to specimens MNHN IM-2013-40628 and MNHN IM-2013-40627 of our deep water Costellariidae lineage C-II, and its COI sequence even suggests it is conspecific with the former (pairwise distance 0.019). Thus we assign the specimen, studied by Oliverio & Modica's (2010) to Costellariidae, suggesting an initial misidentification that has resulted in a distorted branching in the Ptychatractidae-Volutomitridae-Costellariidae segment of their tree. Admittedly, shell differences between Costellariidae and Volutomitridae are rather subtle, and in day-to-day practice specimens with a bulbous paucispiral protoconch are commonly referred to *Microvoluta*, while those with a multispiral protoconch are referred to *Vexillum*.

One of the crucial hypotheses to be confirmed or rejected is whether the families Costellariidae and Mitridae are closely related. Our results unequivocally demonstrate that these two families are unrelated, as they cluster in two different well supported major groupings of the Neogastropoda. The revealed close affinity between Mitridae and the enigmatic family Pyramimitridae is one of the most unexpected results of our analysis. The family Pyramimitridae was considered extinct until living members of several undoubtedly pyramimitrid genera were discovered in the deep water fauna of the Indo-Pacific (Kantor *et al.*, 2014). The initial molecular phylogenetic analysis failed to attribute Pyramimitridae to any known neogastropod lineage. Despite Mitridae and Pyramimitridae end up closely related in the present molecular phylogeny, they differ overly in radula morphology, with wide and flattened multicuspitate laterals and multicuspitate rachidian in Mitridae, vs triangular laterals and pointed unicuspid rachidian in Pyramimitridae. Although limited anatomical data are available at the moment for Pyramimitridae, we can already point out significant differences between the two families. Thus, the buccal mass occupies a basal position in pyramimitrids, while it is apical in mitrids. Members of the family Pyramimitridae have no epiproboscis (see below), but possess a relatively well developed gland of Leiblein; the latter is lacking in Mitridae. No synapomorphies of the Mitridae-Pyramimitridae clade are known at present.

Published data on the morphology of the monotypic (in the Recent fauna) family Pleioptygmatidae suggest a close relationship to the Mitridae. The anterior alimentary canal of the Mitridae is characterized by the presence of a specific organ - the epiproboscis -, which is not

found in any other family of Neogastropoda, and is often considered an autapomorphy for the family (West, 1991; Ponder, 1998). We suspect that the “proboscis introvert” described by Quinn (1989) for *Pleioptygma helenae* is, in fact, an epiproboscis, as it does not differ in morphology and topology from the mitrid epiproboscis (Ponder, 1972). Unfortunately, the narrow geographic range and rarity of *Pleioptygma* makes it hard to target for molecular studies, which would be essential to clarify unequivocally its position.

Deep relationships within the Neogastropoda

The current empirical classification of the Neogastropoda (Bouchet & Rocroi 2005) places the family Ptychactridae in the superfamily Pseudolivoidea, and Oliverio & Modica's (2010) phylogenetic analysis also suggested an affinity of the Mitridae to Olivoidea and Pseudolividae. However, none of these assignments is supported here, as none of the three evolutionary lineages referable to the Ptychactridae shows a relationship to the two pseudolivids - *Fulmentum sepimentum* (Rang, 1832) and *Benthobia* sp. - included in the present analysis. The latter two taxa fall into a well supported clade with Olivoidea, separated from Clade A, suggesting only a distant relationship between ptychactrids and Pseudolividae.

Ponder & Warén (1988) treated Ptychactrinae as a subfamily of Turbinellidae, together with Columbariinae, Vasinae, Turbinellinae and Tudiculinae. Members of the different turbinellid subfamilies were found to share several anatomical features, e.g. an open seminal groove and a radula with tricuspidate rachidian and simple, unicuspid laterals. These anatomical features were regarded as ancestral for the Neogastropoda, and Turbinellidae *sensu* Ponder & Warén (1988) was often regarded as one of most ancient groups of the Neogastropoda (Ponder, 1998). Our phylogenetic analysis places Columbariinae and various ptychactrids in a well supported clade A, with Vasinae as a sister group (though with no significant support). However, ptychactrids, vasines and columbariines do not form a monophyletic group; instead ptychactrids show closer affinities to Costellariidae and Volutomitridae with their derived anatomy. Therefore, the family Turbinellidae *sensu* Ponder & Warén (1988) and Bouchet & Rocroi (2005) is definitely a non-monophyletic group based essentially on shared plesiomorphies.

With the most basal relationships among Neogastropoda still unresolved, we refrain from a critical revision of the classification at the level of superfamilies. However, some incongruences between the currently accepted systematic arrangement and the present phylogenetic reconstructions (Fig. 8) deserve special mention. Our results confirm the monophyly of the neogastropod superfamilies Buccinoidea and Conoidea, and the monophyly of the Olivoidea and Cancellarioidea is also not rejected. Pseudolivoidea are recovered polyphyletic (see above). The

vast majority of the neogastropod evolutionary lineages, including those specifically targeted in the present study, are currently classified in the superfamily Muricoidea (Bouchet & Rocroi 2005). The families currently classified in Muricoidea (WoRMS, 2015) fall in five inferred major clades: (1) a Muricidae clade, (2) a Vasinae clade, (3) a Mitridae-Pyramimitridae clade, (4) a clade ("clade A") consisting of the families, Costellariidae, Turbinellidae (Columbariinae), Volutomitridae and Ptychactridae, and (5) a Cancellariidae + Volutidae clade (See Fig. 8). Despite the lack of resolution of deep nodes in our trees, at least two points contradict the currently accepted circumscription of the Muricoidea: (i) the inclusion of the ptychactrids into the otherwise muricoid clade A; and (ii) the supported grouping of the volute *Melo melo* with the cancellariid *Plesiotriton silinoensis*. Nevertheless, even the revised position of the Ptychactridae and the exclusion of Volutidae from Muricoidea would not ensure the monophyly of resulting Muricoidea.

Relationships within the Costellariidae: Vexillum versus "basal" lineages

The family Costellariidae is commonly perceived as consisting of the large and extremely diverse genus *Vexillum* and a few, sometimes bizarre, small genera like *Zierliana* or *Visaya*. Our analysis evidences a series of previously unrecognized costellariid lineages, essentially consisting of still unnamed taxa. The four costellariid lineages C-I – C-IV (Fig. 3) correspond to four to-be-established genera with numerous undescribed new species, which will be named elsewhere.

While *Vexillum* species with multicuspidate rachidians occupy the most derived position in our phylogenetic trees, costellariids other than *Vexillum*, which are characterized by a tricuspidate rachidians, form deep lineages. This radula morphology, which can be regarded as plesiomorphic, is characteristic also for *Ceratoxancus*, *Latiromitra* and *Exilia*, as well for some other lineages of the superfamily Muricoidea (Fedosov & Kantor, 2010). The difference in radula morphology between *Vexillum* and the "basal Costellariidae" parallels differences in the structure of the foregut glands. Earlier studies on the anatomy of the digestive system of costellariids revealed a large, bulky gland of Leiblein in the only studied species referable to "basal Costellariidae" (Fedosov & Kantor, 2010), and a similar gland of Leiblein is present in *Latiromitra* (Bouchet & Kantor, 2000), *Ceratoxancus* (Kantor & Bouchet, 1997) and *Exilia* (Harasewych, 1987; Kantor *et al.*, 2001). By contrast, many species of *Vexillum* are characterized by the reduction of the gland of Leiblein and the presence of a long, highly convoluted, glandular tube, originating from the stripped off folds of the mid-oesophagus, and resembling the venom gland of the Conoidea. An intermediate morphology, with a still noticeable gland of Leiblein and already a rather short tubular duct, was found in *Vexillum* cf.

salisburyi Cernohorsky, 1976 and *V. rubrum* (Fedosov & Kantor, 2010), the latter species falling into the *Vexillum* s.l. group. The origin and evolution of the genus *Vexillum* thus appears to have been linked to the appearance of a multicuspidate rachidian and a rearrangement of the foregut that possibly allowed these snails to develop a new feeding strategy(ies), permitting their explosive radiation. It is however at present unclear whether the multicuspidate rachidian appeared only once in the evolutionary history of the Costellariidae. It could be a synapomorphy of the *Vexillum* s.l. clade (as supported by our 4G dataset), or it could have evolved independently in different Costellariidae lineages. The presence of tricuspidate rachidians in some species of *Vexillum* (*Pusia*) complicates the picture, and the affinities of these species need to be further examined. Moreover the radula of "*Vexillum*" *balutense* of the "basal" clade C-IV, with its rachidian bearing two rudimentary cusps flanking the central cusp, may be considered intermediate between the simple tricuspidate and true multicuspidate.

The discovery of multiple costellariid taxa with tricuspidate rachidians and a well developed, non-tubular gland of Leiblein renders the morphological difference between the Costellariidae and traditional Ptychactidae quite subtle. In fact, the foregut anatomy of "basal Costellariidae" is much closer to the one found in Ptychactidae than it is to the one found in *Vexillum*. Although all costellariids as currently construed lack an operculum, and an operculum is still present in *Ceratoxancus* and *Latiromitra*, we nevertheless suggest the transfer of *Ceratoxancus* and *Latiromitra* from the Ptychactidae to the Costellariidae. Although this rearrangement extends the boundaries of the Costellariidae, it remains a monophyletic group. Altogether, the transfer of *Ceratoxancus* and *Latiromitra* to Costellariidae, the revised status of *Zierliana* and *Protoelongata*, and the future erection of new genera for newly identified deep water lineages will significantly impact the generic composition of the family.

Relationships within the Mitridae: Systematic challenges and morphological diversity

Thiele (1929) recognized three subfamilies in the family Mitridae: Mitrinae, Cylindrinae and Vexillinae [= Costellariinae]. Cernohorsky (1966, 1970) added the subfamily Imbricariinae. Based on a comprehensive analysis of the anatomy of several species of mitriform gastropods, Ponder (1972) pulled Vexillinae outside Mitridae and synonymized Imbricariinae with Mitrinae. However, the validity of Imbricariinae was restored by Ponder & Warén (1988), and the same three mitrid subfamilies were recognized in Bouchet & Rocroi (2005).

Our phylogenetic analysis supports the monophyly of the family Mitridae and recognizes a "core Mitridae" group, which is well supported and encompasses almost 90% of the species studied. Clade M-I includes the monophyletic *Pterygia*, the only genus classified in the subfamily Cylindromitrinae, and therefore the monophyly of *Pterygia* implies the monophyly of

Cylindromitrinae. With some reservations we equate clade M-I to a subfamily Cylindromitrinae, however the clade M-I definitely encloses Cylindromitrinae. The well supported clade M-II includes a diversity of mitrids among which *Mitra* s.s. represented in our dataset by *Mitra mitra*, the type species of the genus, and *M. papalis*; the name Mitrinae is thus applicable to clade M-II. Clade M-III is represented by the single species *Strigatella paupercula*, the type species of *Strigatella* that was treated as a separate genus by Cernohorsky (1976), and subsequently was placed in *Mitra* as a subgenus (Robin & Martin, 2004; WoRMS, 2015). As it is found not immediately related to *Mitra* s.s., and, furthermore, falls outside the Mitrinae clade, the status of *Mitra (Strigatella)* has to be revised and *Strigatella* ranked as a full genus, if not placed in its own subfamily. Finally the well supported clade M-IV includes the genera *Imbricaria*, *Neocancilla*, *Subcancilla* and *Scabricola* and the name Imbricariinae is available for it. However, two genera that are traditionally classified as imbricariine, *Domiporta* and *Ziba*, turn out to be closer to *Mitra* s.s. than to other imbricariines, and their classification must be revised.

Despite the three mitrid subfamilies (with the newly suggested circumscriptions) are supported, there emerge two problems of congruence between the phylogeny of the Mitridae revealed by our analysis and the current classification of the family: 1) the genus *Mitra* turns out to be polyphyletic, comprising multiple unrelated lineages that are spread throughout the mitrid tree, and it requires a thorough revision; and 2) some mitrid lineages (“basal Mitridae” and *Strigatella paupercula* of the M-III clade) are not included in any of the three subfamilies. A separate subfamily for each clade of the “basal Mitridae”, as well as for *Strigatella paupercula* of the “core Mitridae”, would need to be established. Moreover, the assignment of the two mitrid species which cluster with *Pterygia* on our molecular tree, but differ in shell morphology, also remains unclear.

The typical mitrid radula with wide multicuspidate laterals characterizes most members of clade M-II (subfamily Mitrinae), but is also found in two “basal Mitridae”, *Charitodoron* sp. and *Mitra peculiaris*. For this reason, we consider this radula morphology ancestral for the family Mitridae. Whereas this morphology seems to have been conserved in most members of the subfamily Mitrinae, in other mitrid clades the radula has undergone transformations and three different trends can be distinguished:

(i) an increase in the number of cusps of the central tooth, resulting in rachidian and laterals with similar morphology (mitrine species IM-2013-40651 of clade DW2);

(ii) a reduction in the number of cusps of the laterals, with the notable enlargement of one cusp (species of Imbricariinae);

(iii) a complete loss of the laterals, concomitant with a considerable size reduction of the radula; a uniserial radula is found in *Mitra tuberosa*, *M. bernhardina* and *Pterygia* spp., where they are likely to be the result of parallel evolution.

The diversity of radula morphology in the family Mitridae by far exceeds that of Costellariidae, as well as that of many other neogastropod families. Although this might suggest a variety of feeding strategies, the diet of over 30 Indo-Pacific species of *Mitra*, *Imbricaria*, *Nebularia*, and *Strigatella* is known to consist exclusively of sipunculans (Taylor, 1978; 1984; 1986; 1993; Ponder, 1998; Harasewych, 2009), and Mitridae have been regarded as having the most specialized diet among Neogastropoda (Taylor, 1989; Harasewych, 2009). An epiproboscis, which was considered an adaptation for feeding on the soft-bodied sipunculans (West, 1991), is present in all mitrids studied anatomically (Risbec, 1928; Ponder, 1972; West, 1991; Ponder, 1998; Harasewych, 2009; Simone & Turner, 2010). Local sipunculan guilds rarely comprise more than 10 species, i.e. their diversity is notably lower than that of Mitridae, such that an overlap in prey species among syntopic mitrid species is inevitable. A series of studies carried out by Taylor (1978; 1984; 1986, 1989) on Indo-Pacific mitrids showed that most are not species specific predators, and the same prey species may be consumed by taxonomically closely or distantly related species of snails. For example, the sipunculan *Aspidosiphon tenuis* Sluiter, 1886, was shown to contribute significantly to the diet of at least 6 mitrids [*Nebularia fraga* (Quoy & Gaimard, 1833), *N. chryzalis* (Reeve, 1844), *N. cucumerina* (Lamarck, 1811), *Mitra acuminata* Swainson, 1824, *Strigatella litterata* (Lamarck, 1811), and *Imbricaria conovula* (Quoy & Gaimard, 1833)]. In addition, any one species of miter may consume 3-4 different species of sipunculans at any one locality. The broad range of radula types in mitrids, with their feeding specialization on similar prey items, is thus unexpected. It is noteworthy, however, that all the species for which morphological data are available are referable to our "core Mitridae", while none of the "basal Mitridae" lineages has been studied to date.

Conclusion

This study revealed a major incongruence between the currently accepted classification of the Mitridae, Costellariidae and Ptychactridae and the relationships evidenced by molecular phylogenetic trees. Mitriiform gastropods do not form a monophyletic group, with Mitridae standing apart from the rest. The families Pleioptygmatidae and Pyramimitridae are most closely related to the Mitridae, the former based on published data on radula and shell morphology, the latter based on the present phylogenetic analysis. Costellariidae display a close relationship to the ptychactrid genera *Ceratoxancus* and *Latiromitra*, and a more distant affinity to *Exilia*, the

family Volutomitridae and the "turbinellid" subfamilies Columbariinae and possibly Vasinae. Our results also reject an affinity of Ptychatractidae and Pseudolividae, and the superfamily status of Pseudolivoidea is questioned. Finally, our results also show the need for a revised circumscription of the families Ptychatractidae and Turbinellidae, as both are found paraphyletic.

The existing taxonomic framework cannot accommodate the revealed diversity of Costellariidae and Mitridae phylogenetic lineages. A revision of both Costellariidae and Mitridae, with the establishment of multiple new genera for inferred phylogenetic lineages, is needed. In particular the polyphyly of *Mitra* suggests that a number of species currently assigned to *Mitra* should be reassigned elsewhere, in genera still to be established.

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Captions

Figure 1. Map of sampled localities. Black circles mark deep water cruises, grey circles shallow water shore-based expeditions. Diameters of circles proportional to the number of samples used in the present study (see legend in the top left corner).

Figure 2 Phylogenetic tree of mitriform gastropods and outgroup neogastropod taxa obtained after analysis of the MCPV-3mit dataset. The topology corresponds to the tree obtained with BA, support values are indicated for each node as BA PP values (when ≥ 0.8) / ML bootstrap values (when ≥ 50).

Figure 3. Phylogenetic tree of mitriform gastropods and outgroup neogastropod taxa obtained after the analysis of the MCPV-4G dataset. The topology corresponds to the tree obtained with BA, support values are indicated for each node as BA PP values (when ≥ 0.8) / ML bootstrap values (when ≥ 50).

Figure 4. Clade A subtree of the Bayesian tree obtained after analysis of the 4G dataset. Support values are indicated for each node as BA PP values (when ≥ 0.8) / ML bootstrap values (when ≥ 50). Voucher shells for those species studied morphologically are illustrated, numbers in bold correspond to SEM photos of their radulae [shown at the bottom for Volutomitridae (*Microvoluta joloensis* - 1), *Exilioidea* sp. (2) and Columbariinae (*Coluzea cf. liriopae* - 3) and on figure 5 for *Exilia*, *Ceratoxancus*, *Latiromitra* and Costellariidae].

Figure 5. Radular morphology of Costellariidae. Numbers correspond to the vouchers shown on figure 4: 4. *Exilia krigei*; 5. *Ceratoxancus cf. melichrous*; 6. *Latiromitra barthelowi*; 7. *Vexillum cancellarioides*; 8. *Vexillum semifasciatum*; 9. *Zierliana ziervogeli*; 10. *Vexillum plicarium*; 11. *Vexillum exasperatum*; 12. *Vexillum nodospiculum*; 13. *Vexillum rubrum*; 14. *Vexillum (Protoelongata) dekkersi*; 15. "*Vexillum*" *balutense*; 16. *Thala* sp.; 17. Costellariidae Gen. sp.; 18. Costellariidae Gen. sp.; 19. "*Vexillum*" *isaoi*.

Figure 6. Mitridae subtree of the Bayesian tree obtained after analysis of the 4G dataset. Support values are indicated for each node as BA PP values (when ≥ 0.8) / ML bootstrap values (when ≥ 50). Voucher shells for those species studied morphologically are illustrated, numbers in bold correspond to SEM photos of their radulae (shown on figure 7).

Figure 7. Radular morphology of Mitridae. Numbers correspond to the vouchers shown on figure 6. 20. *Charitodoron* sp.; 21. "*Mitra*" *tuberosa*; 22. "*Mitra*" *bernhardina*; 23. "*Mitra*" *peculiaris*; 24. *Pterygia dactylus*; 25. *Strigatella paupercula*; 26. *Mitra mitra*; 27. Mitridae Gen. sp.; 28. *Scabricola fusca*; 29. "*Imbricaria*" *olivaeformis*; 30. "*Ziba*" *fulgetrum*.

Figure 8. BA tree of the MCPV-4G dataset with the current superfamily assignment showed in colour.

Table. 1. List of specimens analyzed. Type species of genera shown in bold.

Family	Genus	species	MNHN	Expedition	Station	collection data	COI	16S	12S	H3
COSTELLARIIDAE	<i>Thala</i>	sp.	IM-2013-3389	PAPUA NIUGINI	PM25	05°01.1'S 145°47.9'E, intertidal				
COSTELLARIIDAE	<i>Vexillum</i>	<i>plicarium</i>	IM-2013-13646	PAPUA NIUGINI	PM27	04°59.3'S 145°47.6'E, intertidal				
COSTELLARIIDAE	<i>Vexillum</i>	<i>costatum</i>	IM-2009-11058	SANTO 2006	DR64	15°27.6'S 167°14.3'E, 6-35 m	HQ401586.1	HQ401718.1	HQ401655.1	
COSTELLARIIDAE	<i>Vexillum</i>	<i>pagodula</i>	IM-2007-30310	SANTO 2006	DB12	15°36.6'S 167°10.1'E, 10-18 m				
COSTELLARIIDAE	<i>Vexillum</i>	<i>deshayesi</i>	IM-2007-30259	SANTO 2006	DS31	15°31.4'S 167°09.7'E, 5 m				
COSTELLARIIDAE	<i>Vexillum</i>	<i>micra</i>	IM-2013-4734	PAPUA NIUGINI	PB28	05°11.9'S 145°49.6'E, 10 m				
COSTELLARIIDAE	<i>Vexillum</i>	<i>semifasciatum</i>	IM-2013-11594	PAPUA NIUGINI	PM12	05°00.2'S 145°47.6'E, 0-1 m				
COSTELLARIIDAE	<i>Vexillum</i>	<i>sanguisuga</i>	IM-2013-14245	PAPUA NIUGINI	PR68	05°01.6'S 145°48.1'E, 5 m				
COSTELLARIIDAE	<i>Vexillum</i>	<i>virgo</i>	IM-2013-13079	PAPUA NIUGINI	PD24	05°05.3'S 145°48.6'E, 3-6 m				
COSTELLARIIDAE	<i>Vexillum</i>	<i>exasperatum</i>	IM-2013-11680	PAPUA NIUGINI	PR14	05°12'S 145°48.1'E, 2-3 m				
COSTELLARIIDAE	<i>Vexillum</i>	<i>gloriae</i>	IM-2013-40634	NT2011	ND3	12°10.084'N 109°17.771'E, 6-18 m				
COSTELLARIIDAE	<i>Vexillum</i>	<i>scitulum</i>	IM-2013-40633	EXBODI	CP3824	21°57'S 166°58'E, 280-296 m				
COSTELLARIIDAE	<i>Vexillum</i>	<i>dekkersi</i>	IM-2007-30242	PANGLAO 2004	B7	09°35.9'N 123°51.8'E, 4-30 m				
COSTELLARIIDAE	<i>Vexillum</i>	<i>herosae</i>	IM-2013-40630	MIRIKY TUHAA PAE	CP3204	12°37.03'S 48° 30.3' E, 59-60 m				
COSTELLARIIDAE	<i>Vexillum</i>	<i>cancellarioides</i>	IM-2013-40631	2013	AT04	23°25.13'S 149°27.0'W, 12 m				
COSTELLARIIDAE	<i>Vexillum</i>	<i>rubrum</i>	IM-2013-1747	PAPUA NIUGINI	PB10	05°17.9'S 145°46.7'E, 10 m				
COSTELLARIIDAE	<i>Vexillum</i>	<i>patriarchalis</i>	IM-2013-10241	PAPUA NIUGINI	PS04	05°10.0'S 145°50.1'E, 12 m				
COSTELLARIIDAE	<i>Vexillum</i>	<i>acupictum</i>	IM-2013-40635	NT2011	ND3	12°10.084'N 109°17.771'E, 6-18 m				
COSTELLARIIDAE	<i>Vexillum</i>	<i>nodospiculum</i>	IM-2013-40632	AURORA 2007	CP2734	15°57'N 121°49'E, 453-460 m				
COSTELLARIIDAE	" <i>Vexillum</i> "	<i>balutense</i>	IM-2013-40637	BIOPAPUA	CP3747	05°33'S 153°59'E, 458 m				
COSTELLARIIDAE	" <i>Vexillum</i> "	cf. <i>choslenae</i>	IM-2007-38378	EXBODI	CP3826	21°52'S 166°51'E, 354-509 m				
COSTELLARIIDAE	" <i>Vexillum</i> "	<i>isaoi</i>	IM-2013-40636	BIOPAPUA	CP3748	05°37'S 154°01'E, 398-399 m				
COSTELLARIIDAE	" <i>Vexillum</i> "	cf. <i>isaoi</i>	IM-2007-34557	AURORA 2007	CP2709	15°12'N 121°34'E, 244-296 m				
COSTELLARIIDAE	" <i>Vexillum</i> "	<i>pratasense</i>	IM-2007-35967	BIOPAPUA	CP3741	09°14'S 152°18'E, 694-766 m				
COSTELLARIIDAE	<i>Zierliana</i>	<i>ziervogelii</i>	IM-2013-15865	PAPUA NIUGINI	PM41	05°08.1'S 145°49.3'E, 0-1 m				
COSTELLARIIDAE	<i>Zierliana</i>	<i>woldemari</i>	IM-2013-12694	PAPUA NIUGINI	PM8	05°15.3'S 145°46.6'E, 0-1 m				
COSTELLARIIDAE	Gen.	sp.	IM-2007-30347	SALOMON 2	CP2189	08°20' S 160°02' E, 660-854 m				
COSTELLARIIDAE	Gen.	sp.	IM-2007-38256	EBISCO	DW2606	19°37'S 158°42'E, 442-443 m				
COSTELLARIIDAE	Gen.	sp.	IM-2007-39400	TARASOC	DW3452	16°51'S 151°19'W, 600-705 m				
COSTELLARIIDAE	Gen.	sp.	IM-2013-40624	BIOPAPUA	CP3719	06°03'S 147°36'E, 410 m				
COSTELLARIIDAE	Gen.	sp.	IM-2013-40132	PAPUA NIUGINI	CP4055	03°03'S 142°18'E, 370-374 m				
COSTELLARIIDAE	Gen.	sp.	IM-2013-40627	PANGLAO 2005	CP2381	08°43'N 123°19'E, 259-280 m				
COSTELLARIIDAE	Gen.	sp.	IM-2013-40628	BIOPAPUA	DW3777	05°01'S 152°00'E, 40-619 m				
COSTELLARIIDAE	Gen.	sp.	IM-2013-40629	BIOPAPUA	CP3632	06°56'S 147°08'E, 700-740 m				
COSTELLARIIDAE	Gen.	sp.	IM-2013-40638	PAPUA NIUGINI	CP4079	04°34'S 145°52'E, 960 m				

COSTELLARIIDAE	Gen.	sp.	IM-2013-4814	PAPUA NIUGINI	CP3949	05°12'S 145°51'E, 380-407 m
MITRIDAE	<i>Cancilla</i>	<i>fibula</i>	IM-2007-38689	TARASOC	DW3441	16°43'S 151°26'W, 350-360 m
MITRIDAE	<i>Cancilla</i>	cf. <i>fibula</i>	IM-2013-40646	EXBODI	CP3822	21°52'S 166°51'E, 341-506 m
MITRIDAE	<i>Charitodoron</i>	sp.	IM-2007-38306	MAINBAZA	CC3157	21°46'S 36°25'E, 1410-1416 m
MITRIDAE	<i>Charitodoron</i>	sp.	IM-2013-40658	MAINBAZA	CC3171	25°59'S 34°42'E, 771-776 m
MITRIDAE	<i>Domiporta</i>	<i>granatina</i>	IM-2013-40641	INHACA 2011	MR15	26°00.0'S 32°54.4'E, 4 m 12°10.084'N 109°17.771'E, 6-18 m
MITRIDAE	<i>Domiporta</i>	<i>praestantissima</i>	IM-2013-40642	NT2010	D3	
MITRIDAE	<i>Domiporta</i>	filiaris	IM-2013-12956	PAPUA NIUGINI	PD23	05°06'S 145°49.2'E, 3-7 m
MITRIDAE	<i>Imbricaria</i>	conularis	IM-2013-18043	PAPUA NIUGINI	PR203	05°10.3'S 145°48.5'E, 1-19 m
MITRIDAE	<i>Imbricaria</i>	<i>olivaeformis</i>	IM-2013-18062	PAPUA NIUGINI	PR214	05°10.2'S 145°50.4'E, 1-8 m
MITRIDAE	<i>Mitra</i>	<i>bernhardina</i>	IM-2013-13618	PAPUA NIUGINI	PB19	05°05.1'S 145°48.6'E, 10 m
MITRIDAE	<i>Mitra</i>	<i>incompta</i>	IM-2007-30175	SANTO 2006	DR78	15°28.4'S 167°15.2'E, 25 m
MITRIDAE	<i>Mitra</i>	<i>tuberosa</i>	IM-2007-30311	PANGLAO 2004	R75	09°32.8'N 123°42.1'E, 3-35 m
MITRIDAE	<i>Mitra</i>	<i>papalis</i>	IM-2007-30174	SANTO 2006	DR87	15°38.5'S 167°15.1'E, 13 m
MITRIDAE	<i>Mitra</i>	<i>sophia</i>	IM-2007-30056	SANTO 2006	DR09	15°34.6'S 167°13.8'E, 12 m
MITRIDAE	<i>Mitra</i>	cf. <i>roseacea</i>	IM-2007-30309	SANTO 2006	AT44	15°36'S 167°03'E, 86-118 m
MITRIDAE	<i>Mitra</i>	<i>christinae</i>	IM-2007-32131	PANGLAO 2005	CP2383	08°45'N 123°18'E, 338-351 m
MITRIDAE	<i>Mitra</i>	mitra	IM-2013-40639	INHACA 2011	MR15	26°00.0'S 32°54.4'E, 4 m
MITRIDAE	<i>Mitra</i>	<i>glabra</i>	IM-2013-40640	Western Australia	WE01	15°16.94'S 124°06.3'E, 11 m
MITRIDAE	<i>Mitra</i>	<i>shepmani</i>	IM-2013-40645	EXBODI	DW3926	18°35'S 164°20'E, 364-473 m
MITRIDAE	<i>Mitra</i>	<i>peculiaris</i>	IM-2013-6168	PAPUA NIUGINI	PR218	05°07.3'S 145°49.4'E
MITRIDAE	<i>Mitra</i>	sp.	IM-2013-40650	BIOPAPUA	CP3728	07°52'S 148°01'E, 498-501m
MITRIDAE	<i>Mitra</i>	<i>cornicula</i>	IM-2013-40661	Sicily, Cyracuse		37°0.460'N 15°18.62'E, 6-12 m 14° 31.9' S 47° 26.54' E, 46-54 m
MITRIDAE	<i>Nebularia</i>	<i>maesta</i>	IM-2013-40648	MIRIKY	CP3288	
MITRIDAE	<i>Nebularia</i>	<i>connectens</i>	IM-2013-2342	PAPUA NIUGINI	PB16	05°10.7'S 145°47.7'E, intertidal
MITRIDAE	<i>Nebularia</i>	<i>pediculus</i>	IM-2013-12705	PAPUA NIUGINI	PB15	05°04.7'S 145°48.9'E, 5 m
MITRIDAE	<i>Neocancilla</i>	papilio	IM-2013-12560	PAPUA NIUGINI	PR24	05°12.3'S 145°48.8'E
MITRIDAE	<i>Neocancilla</i>	<i>clathra</i>	IM-2007-30178	SANTO 2006	DR73	15°22.5'S 167°11.4'E, 10-25 m
MITRIDAE	<i>Neocancilla</i>	<i>rufescens</i>	IM-2013-40644	INHACA 2011	MD22	25°59.7'S 32°46.8'E, 22 m
MITRIDAE	<i>Pterygia</i>	dactylus	IM-2013-14989	PAPUA NIUGINI	PM39	05°12.1'S 145°48.4'E, intertidal
MITRIDAE	<i>Pterygia</i>	<i>sinensis</i>	IM-2009-15439	ATIMO VATAE	CP3568	25°04.7'S 47°03.4'E, 64-65 m
MITRIDAE	<i>Strigatella</i>	paupercula	IM-2013-15188	PAPUA NIUGINI	PM39	05°12.1'S 145°48.4'E, intertidal
MITRIDAE	<i>Subcancilla</i>	<i>pugnax</i>	IM-2007-34547	AURORA 2007	CP2716	14°30'N 121°41'E, 335-356 m
MITRIDAE	<i>Scabricola</i>	fusca	IM-2013-40643	INHACA 2011	MS8	25°59.5'S 32°52.9'E, 9-17 m
MITRIDAE	<i>Scabricola</i>	<i>casta</i>	IM-2007-31989	PANGLAO 2004	R38	09°29.4'N 123°56.0'E, 6-37 m
MITRIDAE	<i>Ziba</i>	carinata	IM-2013-40647	ZANAGA	531DW	04°43.0'S 11°47.0'E, 17 m

MITRIDAE	<i>Ziba</i>	<i>cf. abyssicola</i>	IM-2013-40654	EXBODI	CP3829	22°02'S 167°05'E, 350-360 m				
MITRIDAE	<i>Ziba</i>	<i>fulgetrum</i>	IM-2013-18112	PAPUA NIUGINI	PR240	05°08.2'S 145°48.7'E, 3-20 m				
MITRIDAE	<i>Ziba</i>	<i>flammigera</i>	IM-2013-40656	NT2011	ND7	12°10.443'N 109°16.298'E, 15-18 m				
MITRIDAE	<i>Ziba</i>	<i>in sculpta</i>	IM-2013-40657	NT2011	ND7	12°10.443'N 109°16.298'E, 15-18 m				
MITRIDAE	Gen.	sp.	IM-2013-40651	BIOPAPUA	CP3671	04°04'S 151°56'E, 585-601 m				
MITRIDAE	Gen.	sp.	IM-2013-40655	EXBODI	CP3821	21°53'S 166°50'E, 211-440 m				
MITRIDAE	Gen.	sp.	IM-2013-40133	PAPUA NIUGINI	CP4035	04°31'S 145°31'E, 380-382 m				
PTYCHATRACTIDAE	<i>Ceratoxancus</i>	sp.	IM-2007-39277	TARASOC	DW3394	15°49'S 148°17'W, 500-510 m				
PTYCHATRACTIDAE	<i>Ceratoxancus</i>	<i>teramachii</i>	IM-2007-36797	TERRASSES	DW3077	23°15'S 168°14'E, 420-540 m				
PTYCHATRACTIDAE	<i>Ceratoxancus</i>	<i>leios</i>	IM-2007-35024	NORFOLK 2	DW2060	24°40'S 168°39'E, 582-600 m				
PTYCHATRACTIDAE	<i>Ceratoxancus</i>	sp.	IM-2007-38552	TARASOC	DW3401	15°51'S 148°18'W, 789-831 m				
PTYCHATRACTIDAE	<i>Ceratoxancus</i>	<i>cf. melichrous</i>	IM-2013-40623	EXBODI	DW3914	19°45'S 165°45'E, 620-725 m				
PTYCHATRACTIDAE	<i>Exilia</i>	<i>vagrans</i>	IM-2007-34067	SALOMON 2	CP2251	07°28' S 156°14' E, 1000-1050 m				
PTYCHATRACTIDAE	<i>Exilia</i>	<i>hilgendorfi</i> s.l.	IM-2007-34612	AURORA 2007	CP2751	15°36'N 121°56'E, 1456-1471 m				
PTYCHATRACTIDAE	<i>Exilia</i>	<i>hilgendorfi</i> s.l.	IM-2007-38603	TARASOC	DW3493	17°28'S 149°27'W, 556-565 m				
PTYCHATRACTIDAE	<i>Exilia</i>	<i>hilgendorfi</i> s.l.	IM-2007-36877	MIRIKY	CP3187	12°30'S 48°08'E, 691-695 m				
PTYCHATRACTIDAE	<i>Exilia</i>	<i>krigei</i>	IM-2007-38331	MAINBAZA	CC3171	25°59'S 34°42'E, 771-776 m				
PTYCHATRACTIDAE	<i>Exilioidea</i>	sp.	IM-2007-34633	AURORA 2007	CP2690	14°58'N 123°03'E, 1071-1147 m				
PTYCHATRACTIDAE	<i>Exilioidea</i>	sp.	IM-2013-40625	PAPUA NIUGINI	CP3963	05°06'S 145°53'E, 960-980 m				
PTYCHATRACTIDAE	<i>Latiromitra</i>	<i>barthelowi</i>	IM-2007-35820	SALOMONBOA 3	CP2800	08°41'S 161°04'E, 556-864 m				
PTYCHATRACTIDAE	<i>Latiromitra</i>	<i>crosnieri</i>	IM-2007-38178	MIRIKY	no data					
TURBINELLIDAE (COLUMBARIINAE)	<i>Fustifusus</i>	<i>pinicola</i>	IM-2007-43438	TERRASSES	DW3120	22°44'S 167°15'E, 320-360 m				
TURBINELLIDAE (COLUMBARIINAE)	<i>Coluzea</i>	<i>cf. liriopae</i>	IM-2007-38972	MAINBAZA	CP3139	23°35'S 36°06'E, 1092-1195 m				
TURBINELLIDAE (COLUMBARIINAE)	<i>Coluzea</i>	<i>groschi</i>	IM-2007-38280	MAINBAZA	CP3143	23°32'S 35°46'E, 264-277 m				
TURBINELLIDAE (VASINAE)	<i>Vasum</i>	sp.	IM-2009-14647	ATIMO VATAE	TA24	25°23.4'S 44°14.0'E, 15-17 m				
TURBINELLIDAE (VASINAE)	<i>Vasum</i>	<i>turbinellus</i>	LSGB23801				HQ834084	HQ833957	HQ833909	HQ834180
VOLUTOMITRIDAE	<i>Microvoluta</i>	<i>joloensis</i>	IM-2013-40620	BIOPAPUA	DW3720	06°03'S 147°35'E, 520-523 m				
VOLUTOMITRIDAE	<i>Volutomitra</i>	<i>glabella</i>	IM-2007-35070	CONCALIS	DW3003	18°34'S 163°08'E, 450-454 m				
VOLUTOMITRIDAE	<i>Volutomitra</i>	<i>zigzag</i>	IM-2007-35073	CONCALIS	DW2944	18°59'S 163°24'E, 320-335 m				
VOLUTOMITRIDAE	<i>Volutomitra</i>	sp.	IM-2007-38357	TERRASSES	DW3123	22°53'S 167°13'E, 420-450 m				

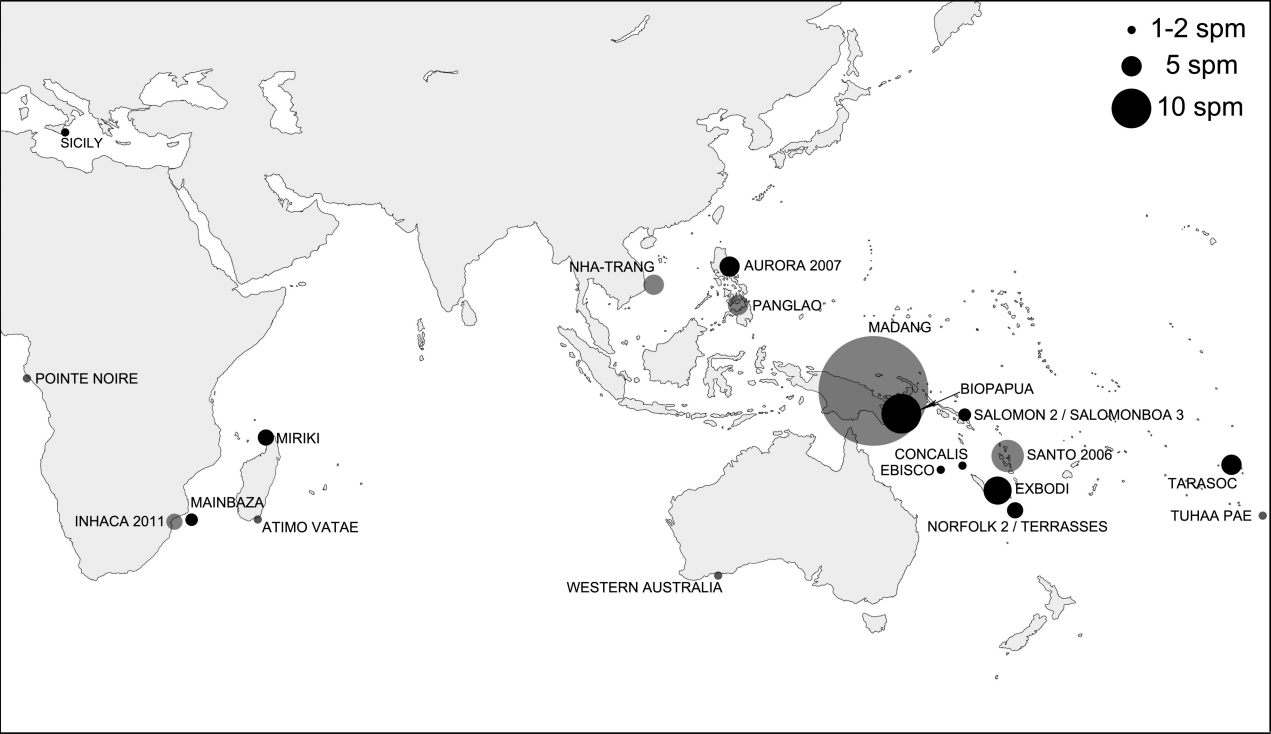
OUTGROUPS

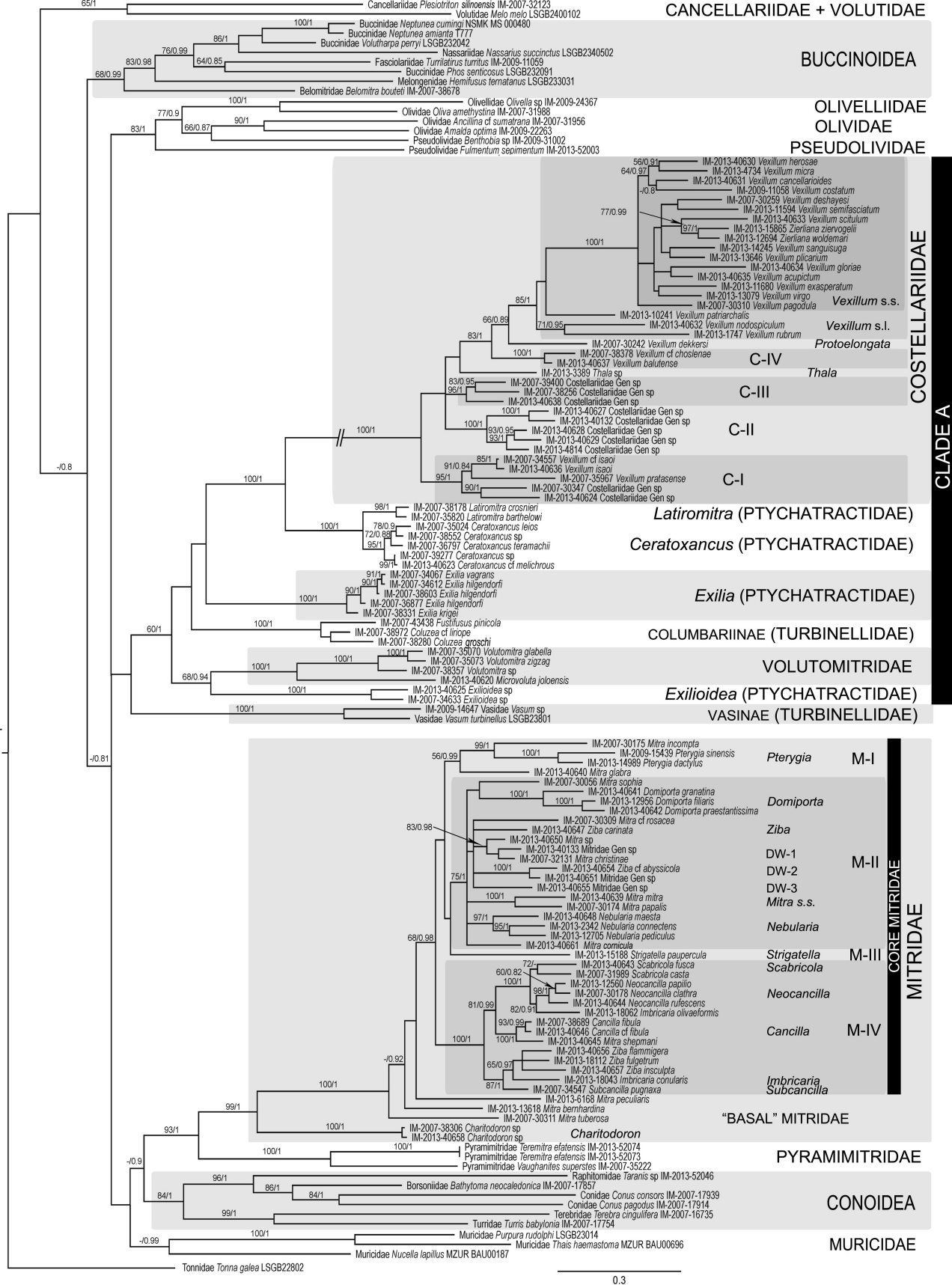
BELOMITRIDAE	<i>Belomitra</i>	<i>bouteti</i>	IM-2007-38678				JQ950224.1	EU870550.1	EU870525.1	
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BORSONIIDAE	<i>Bathytoma</i>	<i>neocaledonica</i>	IM-2007-17857					EU015653	HQ401661	HQ401591	EU015761
BUCCINIDAE	<i>Neptunea</i>	<i>cumingi</i>	NSMK_MS_000480					HM180715.1	JN052941.1	HQ833870.1	HQ834142.1
BUCCINIDAE	<i>Neptunea</i>	<i>amianta</i>	T777					GQ290613.1	GQ290613.1	GQ290613.1	GQ290634.1
BUCCINIDAE	<i>Volutharpa</i>	<i>perryi</i>	LSGB232042					JN053003.1	HQ833930.1	HQ833869.1	HQ834141.1
BUCCINIDAE	<i>Phos</i>	<i>senticosus</i>	LSGB232091					JN053008.1	JN052944.1	HQ833885.1	HQ834156.1
CANCELLARIIDAE	<i>Plesiotriton</i>	<i>silinoensis</i>	IM-2007-32123					FM999158.1	FM999106.1	FM999075.1	
CONIDAE	<i>Conus</i>	<i>consors</i>	IM-2007-17939					EU015751	HQ401672	HQ401605	EU015858
CONIDAE	<i>Conus</i>	<i>pagodus</i>	IM-2007-17914					EU015729	FJ868151	FJ868136	EU015836
FASCIOLARIIDAE	<i>Turriturris</i>	<i>turritus</i>	IM-2009-11059					HQ401585.1	HQ401714.1	HQ401651.1	
MELONGENIDAE	<i>Hemifusus</i>	<i>ternatanus</i>	LSGB233031					JN053014.1	JN052950.1	HQ833889.1	HQ834160.1
MURICIDAE	<i>Purpura</i>	<i>rudolphi</i>	LSGB23014					HQ834096	HQ833968	HQ833919	HQ834189
MURICIDAE	<i>Nucella</i>	<i>lapillus</i>	MZUR_BAU00187					FM999169.1	FM999119.1	FM999088.1	
MURICIDAE	<i>Thais</i>	<i>haemastoma</i>	MZUR_BAU00696					FM999171.1	FM999121.1	FM999090.1	
NASSARIIDAE	<i>Nassarius</i>	<i>succinctus</i>	LSGB2340502					HQ834079.1	HQ833949.1	HQ833901.1	HQ834172.1
OLIVELLIDAE	<i>Olivella</i>	sp.	IM-2009-24367	KARUBENTHOS	GD41	16°20.900'S 61°32.217'W, 2 m					
OLIVIDAE	<i>Oliva</i>	<i>amethystina</i>	IM-2007-31988	SANTO 2006	DR09	15°34.600'S 167°13.800'E, 12 m					
OLIVIDAE	<i>Ancillina</i>	cf. <i>sumatrana</i>	IM-2007-31956	PANGLAO 2005	CP2350	9°31.400'N 124°00.600'E, 602-738 m					
OLIVIDAE	<i>Amalda</i>	<i>optima</i>	IM-2009-22263	INHACA 2011	MR4	26°6.300'S 32°58.00'E, 17-19 m					
PSEUDOLIVIDAE	<i>Benthobia</i>	sp.	IM-2009-31002	AURORA 2007	CP2685	14°59.617'N 123°5.900'E, 1155-1302 m					
PSEUDOLIVIDAE	<i>Fulmentum</i>	<i>sepimentum</i>	IM-2013-52003	ZANAGA	D502	4°42.25'S E 11°47.0'E, 20 m					
PYRAMIMITRIDAE	<i>Teremitra</i>	<i>efatensis</i>	IM-2013-52073	PAPUA NIUGINI	CP4058	2°54.669'S 142°10.772'E, 535-540 m					
PYRAMIMITRIDAE	<i>Teremitra</i>	<i>efatensis</i>	IM-2013-52074	PAPUA NIUGINI	CP4058	2°54.669'S 142°10.772'E, 535-540 m					
PYRAMIMITRIDAE	<i>Vaughanites</i>	<i>superstes</i>	IM-2007-35222					KF840066	KF840067		
RAPHITOMIDAE	<i>Taranis</i>	sp.	IM-2013-52046	PAPUA NIUGINI	CP4049	3°19.413'S 143°27.239'E, 422-425 m					
TEREBRIDAE	<i>Terebra</i>	<i>cingulifera</i>	IM-2007-16735					EU015735	EU685670	EU685379	EU015842.1
TONNIDAE	<i>Tonna</i>	<i>galea</i>	LSGB22802					HQ834116	HQ833984	HQ833862	HQ834135
TURRIDAE	<i>Turris</i>	<i>babylonia</i>	IM-2007-17754					EU015677	HQ401715	HQ401652	EU015786
VOLUTIDAE	<i>Melo</i>	<i>melo</i>	LSGB2400102					HQ834086	HQ833959	HQ833911	HQ834182

Table 2. Primers used for amplification and sequences data

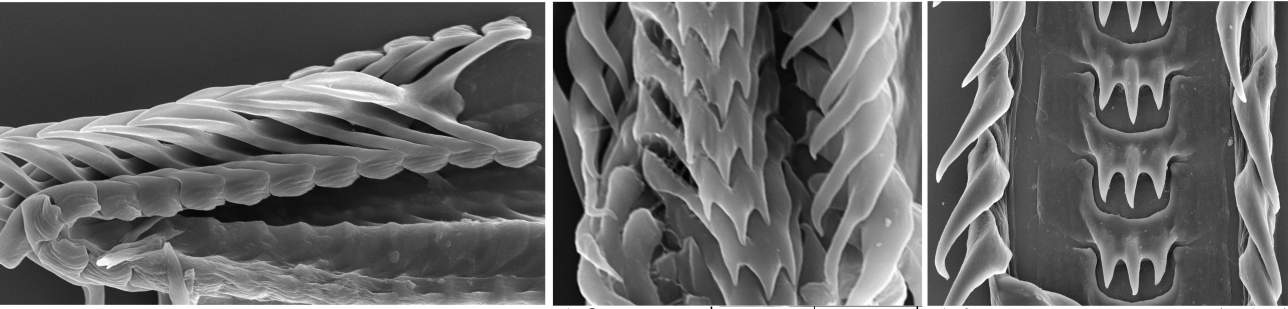
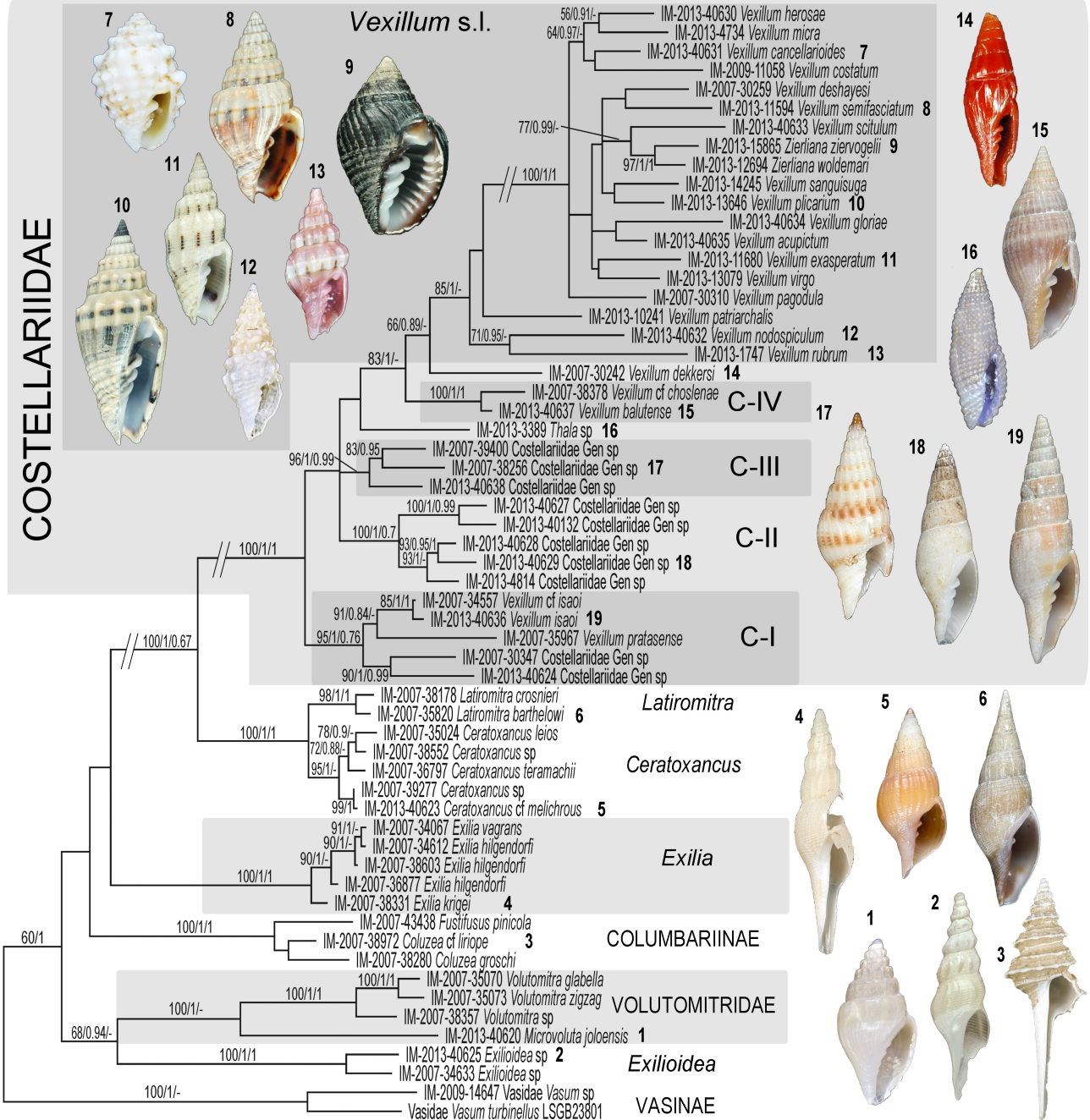
Gene	Primers	annealing temperature C°	amplification length bp	alignment length bp	Number of sequences	substitution model (hLRTs)	I	gamma
COI	HCOI - LCOI	48-50	658	658	120	GTR+I+G	0,44	0,35
16S	16SA - 16SB	55	~550	597	108	TVM+I+G	0,41	0,51
12S	12SA - 12SB	57	~380	620	107	GTR+I+G	0,27	0,62
12S	12SI - 12SIII	57*	~540	620				
H3	H3A - H3B	55	328	328	84	TrN+I+G	0,59	0,64



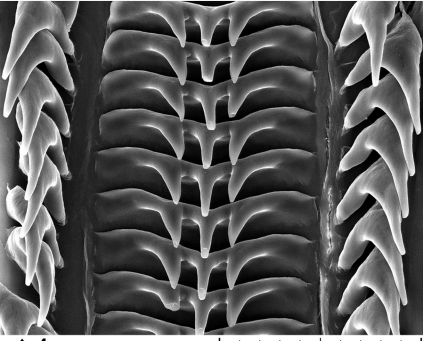


COSTELLARIIDAE

Vexillum s.l.

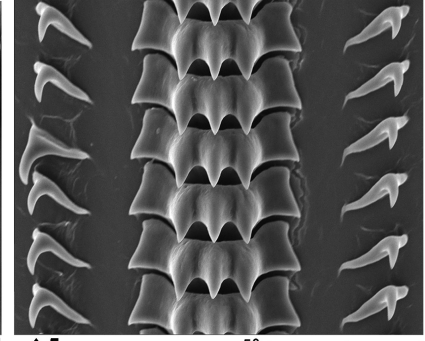


▲ 1 20 2 20 3



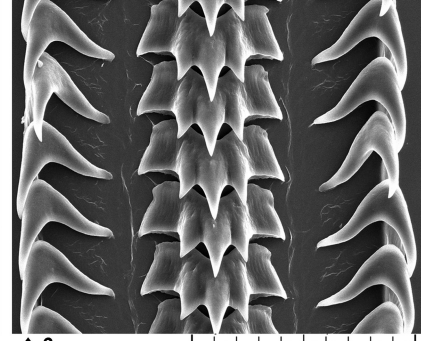
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100 μm



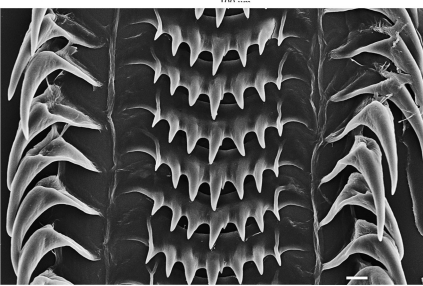
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50



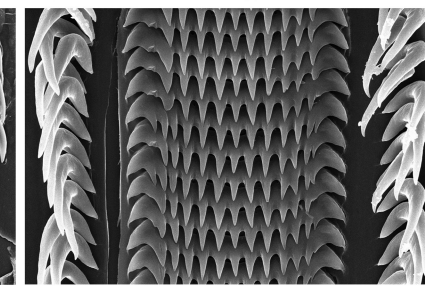
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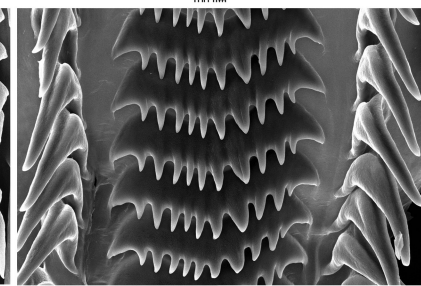
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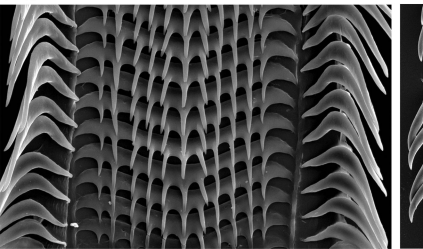
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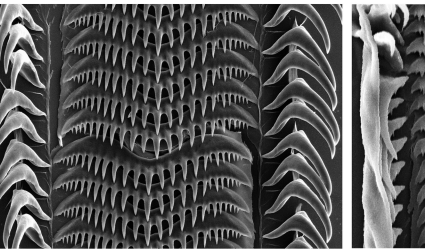
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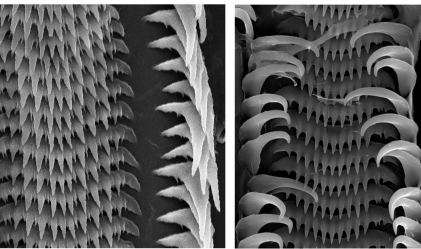
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100 μm



▲ 11

100 μm

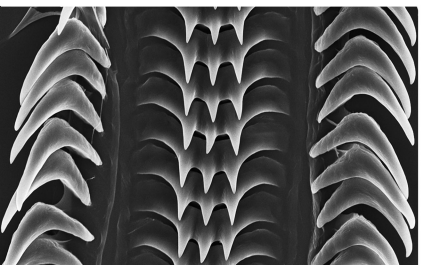


▲ 12

25 μm

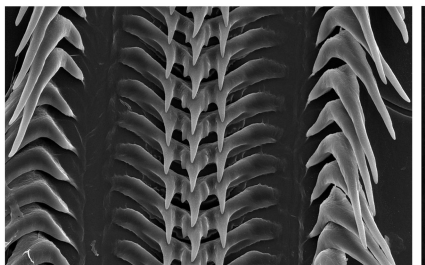
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20 μm



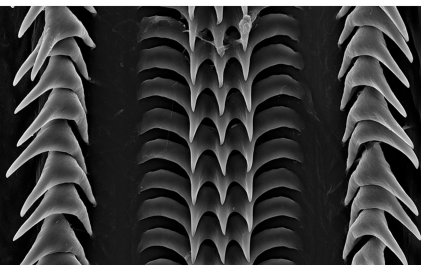
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20 μm



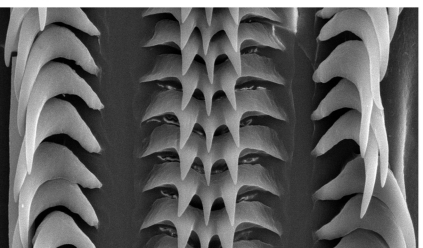
▲ 15

100 μm



▲ 16

50 μm



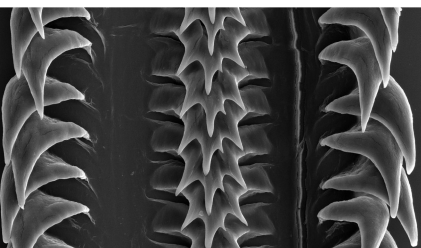
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20 μm



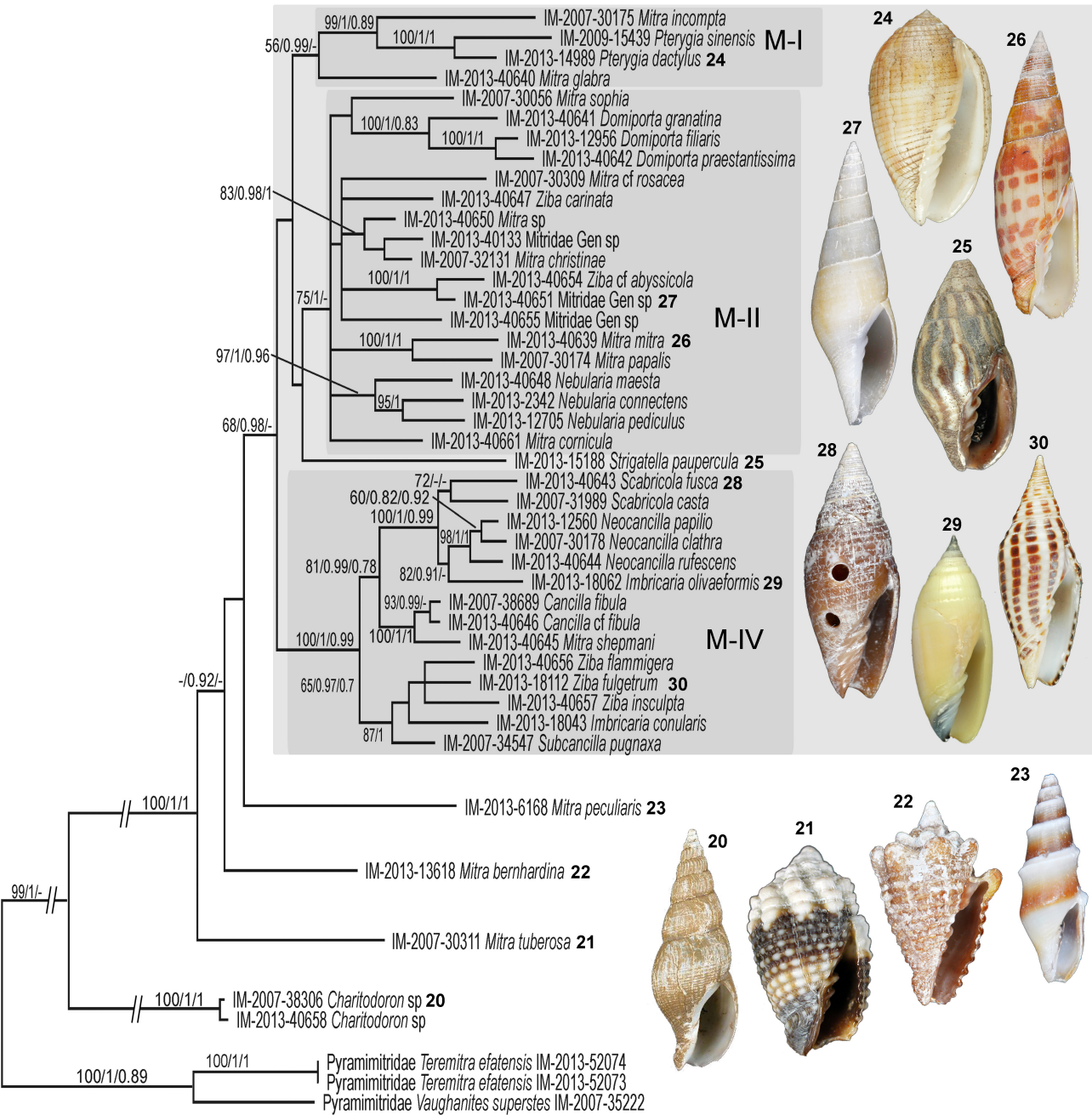
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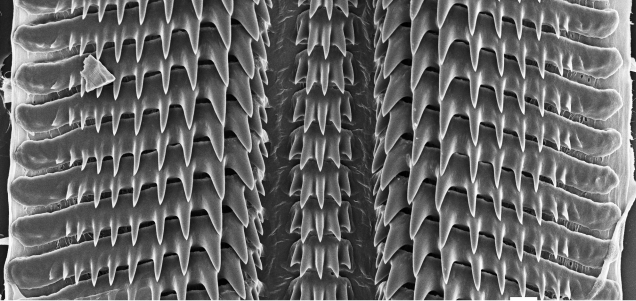
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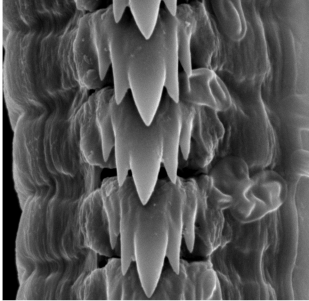
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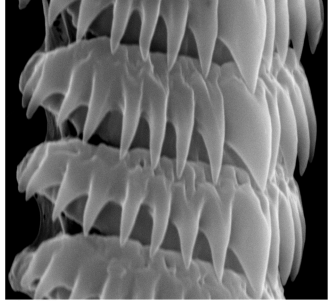
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50 μm



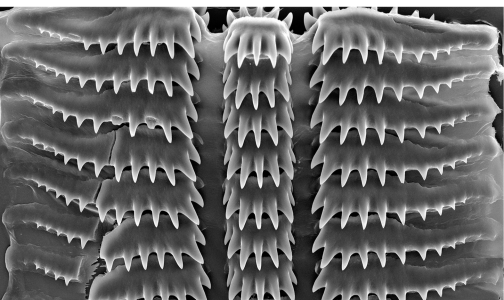
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5 μm



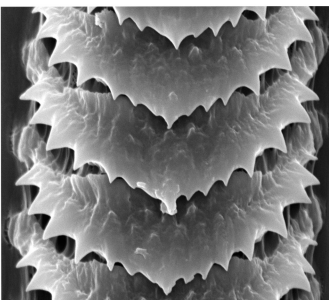
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5 μm



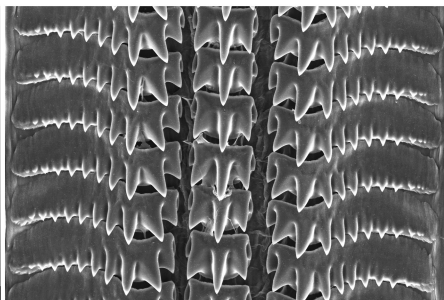
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50 μm



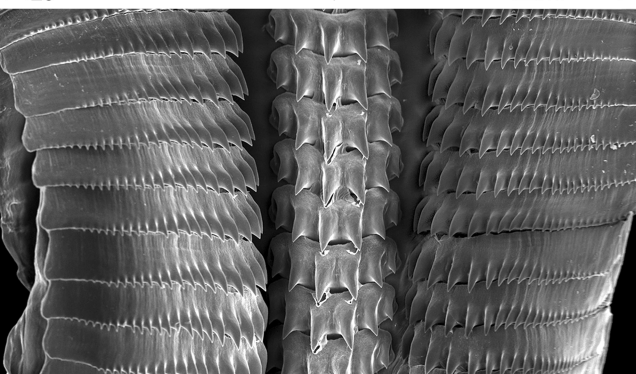
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10 μm



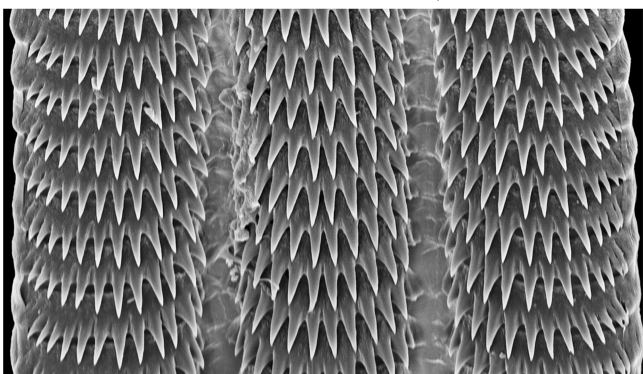
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200 μm



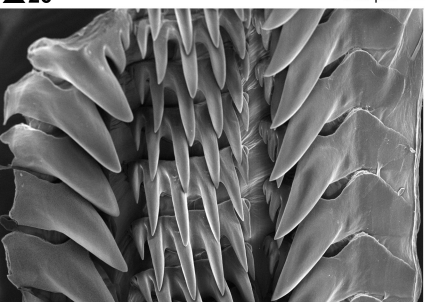
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500 μm



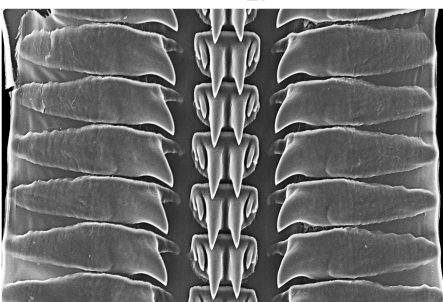
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50 μm



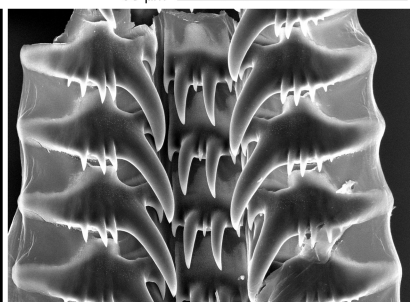
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200 μm



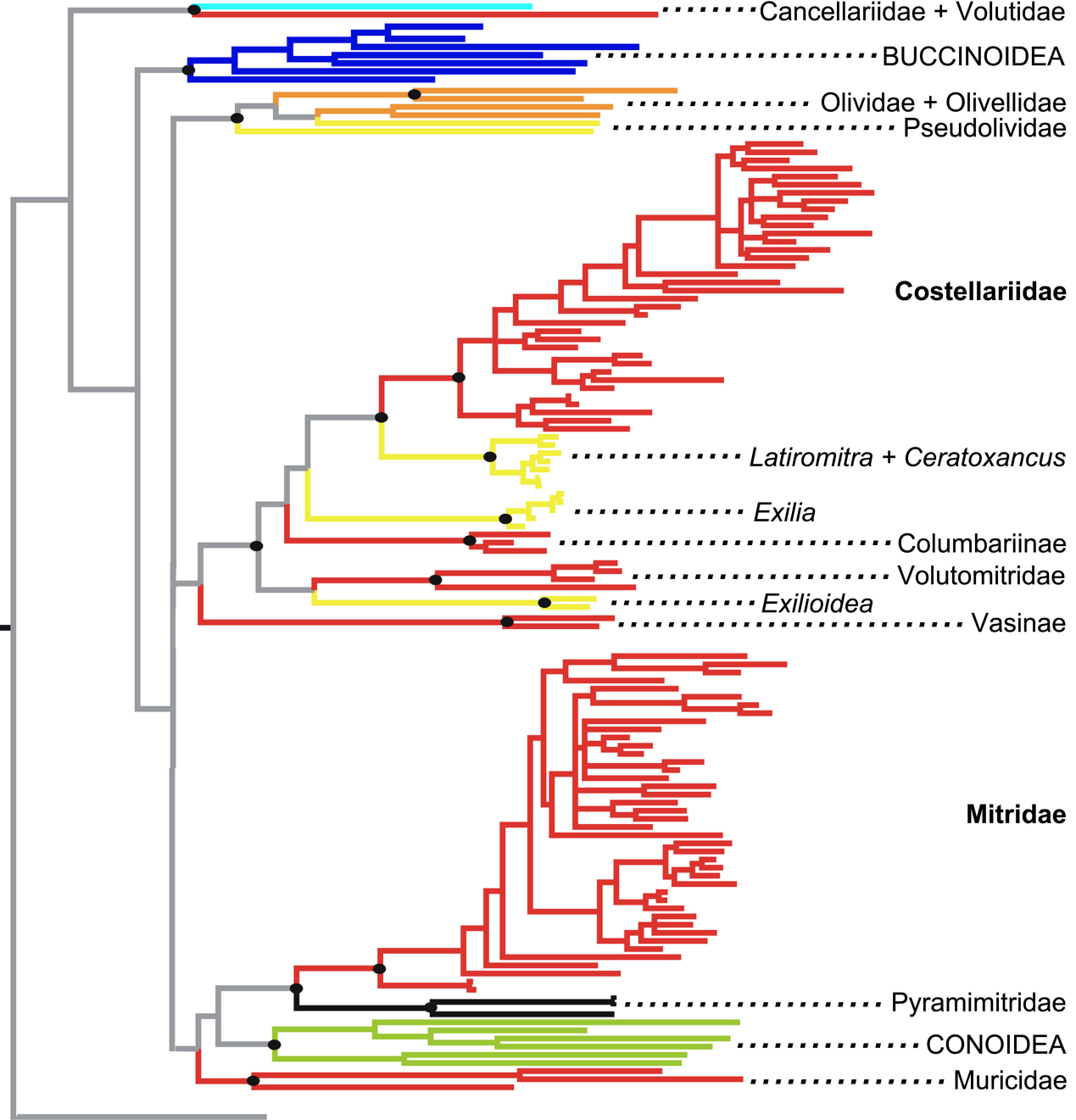
▲ 29

100 μm



▲ 30

100 μm



Cancellarioidea

Oливоidea

Conoidea

Buccinoidea

Pseudolivoidea

Muricoidea

Unassigned