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## The collapse of Mitra: molecular systematics and morphology of the Mitridae (Gastropoda: Neogastropoda)

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**The collapse of Mitra: Molecular systematics and morphology of the Mitridae (Gastropoda: Neogastropoda)**

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Keywords:	Mollusca < Taxa, new genera < Taxonomy, new species < Taxonomy, new classification < Taxonomy, species diversity < Taxonomy, molecular phylogeny < Genetics, character evolution < Phylogenetics, phylogeography < Geography
Abstract:	In the present study we reconstruct phylogeny and revise systematics of the neogastropod family Mitridae based on the DNA sequence data from four molecular markers (mitochondrial COI, 16S and 12S rRNA, and nuclear H3). Our taxonomic sampling includes 103 species representing 16 of the 19 currently accepted extant genera. In all phylogenetic reconstructions, the genus Charitodoron forms a distantly related sister group to the Mitridae s.s. clade, containing all other studied Mitridae. Based on the profound morphological differences between Charitodoron and Mitridae s.s., we erect the new family Charitodoronidae; the monophyletic lineage comprising families Pyramimitridae, Charitodoronidae and Mitridae is here ascribed to the new superfamily Mitroidea. Three traditional subfamilies of Mitridae correspond to three of the eight inferred major lineages of Mitridae s.s. Two more lineages are here ascribed to the reinstated Strigatellinae Troschel, 1869 and the new subfamily Isarinae. The sixth subfamily Pleioptygmatinae is included in Mitridae based on morphological considerations only. Furthermore, we reinstate the genera <i>Episcomitra</i> Monterosato, 1917, <i>Isara</i> H. & A. Adams, 1853, and <i>Probata</i> Sarasua, 1989, and establish 11 new genera. Species diversity, and biogeography of the 32 genera here assigned to Mitridae are discussed, along with general trends of morphological evolution in the family.

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2 The collapse of *Mitra*: Molecular systematics and morphology of the Mitridae  
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4 (Gastropoda: Neogastropoda)  
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10 Oliverio<sup>5</sup>, Polina Dgebuadze<sup>1</sup>, Maria Vittoria Modica<sup>6</sup> & Philippe Bouchet<sup>4</sup>  
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**Abstract**

Alongside confirmation of the monophyly of the gastropod family Mitridae, a recent molecular phylogenetic analysis disclosed multiple inconsistencies with the existing taxonomic framework. In the present study we expanded the molecular sampling to 103 species, representing 26% of the 398 extant species currently accepted in the family and 16 of the 19 currently accepted extant genera; 83 species were sequenced for four molecular markers [cytochrome c oxidase subunit I (*COI*), *16S* and *12S* rRNA, and *H3* (Histone 3)]. Molecular analyses were supplemented by morphological studies, focused on characters of the radula and, in a more restricted dataset, proboscis anatomy. These data form the basis for a revised classification of the Mitridae. A first dichotomy divides mitrids into two unequal clades, *Charitodoron* and the Mitridae s.s. Species of *Charitodoron* show profound differences to all other Mitridae in foregut anatomy (lacking an epiproboscis) and shell morphology (smooth columella, bulbous protoconch of non-planktotrophic type), which leads to the erection of the separate family Charitodoronidae fam. nov. Three traditional subfamilies (Mitrinae, Cyndromitrinae, Imbricariinae) correspond to three of the inferred phylogenetic lineages of Mitridae s.s.; we redefine their contents, reinstate Strigatellinae Troschel, 1869 as valid, and establish the new subfamily Isarinae. In the absence of molecular material, a sixth subfamily, Pleioptygmatinae, is included in Mitridae based on morphological considerations only. To resolve the polyphyly of *Mitra* and *Cancilla* in their current taxonomic extension, we reinstate the genera *Episcomitra* Monterosato, 1917, *Isara* H. & A. Adams, 1853, and *Probata* Sarasúa, 1989, and establish 11 new genera, *Quasimitra*, *Roseomitra*, *Fusidomiporta*, *Profundimitra*, *Cancillopsis*, *Pseudonebularia*, *Gemmulimitra* and *Neotiara* in Mitrinae, *Imbricariopsis* in Imbricariinae; *Carinomitra* and *Condylomitra* are left unassigned to a subfamily. Altogether 32 genera are recognized within the family. Their diversity and distribution are discussed, along with general trends in morphological evolution of the family.

## Introduction

The neogastropod family Mitridae (miter shells, or miters) is a distinctive and familiar group of benthic gastropods, its key features being a solid, usually fusiform, colorful shell with strong columellar folds, predominant spiral sculpture and a smooth inner side of the labrum. Some iconic *Mitra* species like *Mitra mitra* (Linnaeus, 1758), *Mitra papalis* (Linnaeus, 1758) or *Mitra cardinalis* (Gmelin, 1791) were known since pre-Linnean times; the genus name established by Lamarck in 1798 and various specific epithets were named by early conchologists for their supposed resemblance with Church's ceremonial headwear.

The affinities of the miters were traditionally inferred from shell morphology. Following Reeve (1844-1845), the name "mitres" was used broadly to refer to an array of marine snails that share a 'mitriform' habitus. However, as knowledge on the diversity and morphology of miters progressed, it became evident that "mitres" was in fact a heterogeneous group (Risbec, 1955; Cernohorsky, 1966, 1970; Ponder, 1972) including two large, distinct families, Mitridae and Costellariidae. In our recent study (Fedosov et al. 2015), we revised the composition and relationships of mitriform gastropods, demonstrating that the four mitriform families - Mitridae, Costellariidae, Ptychatractidae and Volutomitridae - do not form a single evolutionary lineage, with Mitridae appearing unrelated to the remaining three families. The distinctiveness of Mitridae is fully supported by morphological data: the organs of the digestive tract, the structure of the renal organ and the female reproductive system are drastically different in Mitridae and the other mitriform families (Ponder, 1972). Moreover, in the anatomy of the foregut and in the structure of the radula, the Mitridae show no apparent similarity to any other neogastropod family (Ponder et al. 1972; Taylor & Morris 1988; Fedosov et al. 2015). Two key features of Mitridae morphology, which set them apart from the rest of the Neogastropoda, are the epiproboscis - a complex muscular organ enclosed within the proboscis - and a radula with wide multicuspidate lateral teeth. Neither of these two features was found in species of the deep water family Pyramimitridae, a group sister to Mitridae in phylogenetic analyses (Fedosov et al. 2015).

The Mitridae as currently restricted are a group flourishing in shallow waters of the Indo-Pacific, with a remarkable diversity of forms and sometimes great abundance. Although, the taxonomic diversity of ~400 Recent species worldwide (398 valid species currently indexed as valid in WoRMS) is not really impressive by neogastropod standards, it is still high, given some peculiarities of mitrid biology. Molluscs of the family Mitridae are predators with probably the most conserved dietary guilds among the Neogastropoda: all published data suggest that they feed exclusively on Sipuncula, however they do not appear to follow a strict species-specific prey specialization, and different, unrelated mitrid species appear to prey on the same sipunculan species within the same habitat (Taylor, 1989; 1993).

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As of May 2017, 180 of the 398 accepted Recent species of Mitridae indexed in WoRMS (WoRMS 2016) are classified in the genus *Mitra*, although the understanding that the genus, as currently circumscribed, is not consistent with a single evolutionary lineage has emerged long ago (Cernohorsky, 1996). Our previous phylogenetic analysis (Fedosov et al. 2015) revealed that the species currently classified in *Mitra* are distributed throughout the mitrid tree, in Mitrinae, Imbricariinae and Cylindromitrinae, as well as in lineages that fell outside these three currently recognized subfamilies. Besides, obvious incongruences between relationships and current placement were uncovered in the genera *Domiporta* and *Ziba*. Thus there is no doubt that a revision of Mitridae systematics in a phylogenetic framework is needed. Several crucial mitrid lineages and type species of nominal genera were missing from the previous study, making the resulting tree insufficient for a thorough taxonomic re-evaluation. In the present study, we present a more robust tree based on an increased taxonomic coverage and revise the classification of the family based on this expanded molecular phylogenetic framework.

## Material and Methods

### *Taxon sampling*

The present study is largely based on material collected during multiple expeditions conducted by MNHN and IRD, University La Sapienza of Roma, the joint Russian-Vietnamese Tropical Center, and other *ad hoc* field work. The specimens studied originate from Panama, the Caribbean (Guadeloupe, French Guiana), Mediterranean (Adriatic, Aegean and Tyrrhenian Seas), the Azores, West Africa (People's Republic of Congo) and numerous Indo-Pacific localities from Madagascar to French Polynesia (see Table 1). To improve the taxon sampling of our previous study (Fedosov et al. 2015), 121 additional mitrid specimens were analyzed, bringing the total number of specimens studied to 163 (Table 1). Before 2012, specimens were treated in the field with an isotonic solution of magnesium chloride until relaxed (showing no response to touch), and then a tissue clip was cut. Starting in 2012, specimens were processed using a microwave oven (Galindo et al. 2014), i.e. in most cases the entire body, or at least the last 1 - 1.5 whorls, were available for study. Tissue samples were preserved in 96% ethanol. Voucher shells are kept in MNHN, University La Sapienza and in the repository of the Laboratory of Ecology and Morphology of Marine Invertebrates of IEE.

The shells of the specimens selected for molecular analysis and morphological studies were first sorted to morphospecies and identified by the authors. Taxonomy follows WoRMS - largely based on Coan (1966), Cernohorsky (1970; 1976; 1991) with later updates (Poppe & Tagaro 2006; Turner 2007; Lussi 2009; Poppe et al. 2009; Huang 2011; Huang & Salisbury 2017, etc.). Subsequently, the barcode fragment of the COI gene was sequenced for as many as possible tissue clipped specimens. Morphospecies were thus used as preliminary hypotheses, to be verified by the analysis of the COI gene. When all specimens of a given morphospecies clustered in a single clade in the phylogenetic tree obtained with the COI gene, and this clade included only specimens of a single morphospecies, then it was considered that our species hypothesis was confirmed for subsequent analyses. When a morphospecies included only one specimen, the COI gene was used to check that it constituted a distinctive lineage of its own. Subsequently, a reduced dataset, with a selection of species best representing the currently recognized supra-specific taxa and the morphological diversity of Mitridae, was built. For these species, one only or a few specimens were sequenced for additional genes (16S rRNA, 12S rRNA and H3) to reconstruct phylogenetic relationships within the family. 12S sequence of one more species, "*Mitra*" *carbonaria*, analyzed by Colgan and coworkers (2007) was accessed from GenBank, and the photo of the voucher shell C.335424 in AMS was examined to confirm its identification and ensure that it is not conspecific with any other specimen sequenced in the present study.

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2 To complete the type series of inferred new species verified by the phylogenetic analysis,  
3 additional dry material from MNHN collections was studied to characterize their shell variation.  
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#### 5 6 7 *DNA extraction and PCR*

8 DNA extraction and PCR were carried out as described in Fedosov et al. (2015). All PCR  
9 fragments were pair-end sequenced by Eurofins and Macrogen (Amsterdam).  
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#### 12 13 *Datasets*

14 To ensure the consistency of phylogenetic analyses with the results obtained earlier, the  
15 entire Mitridae-Costellariidae-Ptychactractidae-Volutomitridae (MCPV) datasets with multiple  
16 outgroups, as analyzed in Fedosov et al. (2015), were used and supplemented with newly  
17 obtained sequences. Six molecular datasets have been analyzed, four of them corresponding to  
18 the individual three mitochondrial (COI, 16S, 12S) and one nuclear (H3) markers. When the  
19 resulting phylogenetic reconstructions were checked for congruency, two concatenated datasets  
20 were assembled, one corresponding to the 3 mitochondrial genes (1,887 positions, 166 taxa, 7 %  
21 of missing data), referred to as "3-mit" and consistent with our earlier analysis, and the second a  
22 four genes dataset (2,215 positions, 166 taxa, 11 % of missing data), referred to as "4G" (Table  
23 2). Finally, a reduced four genes dataset 4G-red was built to minimize the effects of missing  
24 data; only those 139 specimens that had at least three genetic markers sequenced, one of which is  
25 COI, were included in this dataset.  
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#### 36 37 *Phylogenetic analysis*

38 Newly obtained COI and H3 sequences were aligned manually; 16S and 12S sequences  
39 were first aligned automatically with Muscle (Edgar, 2004) and then modified manually where  
40 necessary. In the analysis of multi-gene datasets, multiple neogastropod lineages were included  
41 as outgroups to ensure consistency with our earlier analyses (Fedosov et al. 2015, Fedosov et al.  
42 2016); in the single gene COI analysis - primarily aimed at species delimitation -, three  
43 specimens of the Pyramimitridae genera *Teremitra* and *Vaughanites* were used as outgroups  
44 based on the demonstrated sister relationship between Mitridae and Pyramimitridae (Fedosov et  
45 al. 2015).  
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51 The best-fit substitution models were identified for each gene separately, using  
52 Modelgenerator V.85 (Keane et al., 2006) (Table 2). The single gene datasets of 12S, 16S and  
53 H3 were analyzed as a single partition each; three partitions corresponding to 1st, 2nd and 3rd  
54 codon positions were analyzed independently for COI. The combined MCPV-3mit and MCPV-  
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4G datasets were separated into five and six unlinked partitions respectively: 16S, 12S, three codon positions of the COI gene (both datasets) plus H3 gene (4G and 4G-red datasets).

Best-scoring Maximum Likelihood (ML) trees were estimated using RaxML (Stamatakis, 2006), robustness of the nodes was assessed using the Thorough Bootstrapping algorithm (Felsenstein, 1985) with 1,000 iterations. Bayesian Analyses (BAs) were performed in two parallel runs in MrBayes (Huelsenbeck et al. 2001). For 16S, 12S and H3 single gene analyses, each run consisted of six Markov chains and 10,000,000 generations with default number of chain swaps and sampling frequency of one tree in each 1,000 generations. For the COI, 3-mit, 4G, and 4G-red datasets, BA were performed with the number of chains set to 8, number of generations to 30,000,000, number of chain swaps to 5 and sampling frequency to one tree each 5,000 generations. Chain temperature of 0.02 was used in all analyses. Convergence of each analysis was checked using Tracer1.4.1 (Rambaut and Drummond, 2007); the two runs were considered converged if all ESS values exceeded 200. Consensus trees were calculated after discarding the first 25% trees as burn-in. All analyses were performed on the Cipres Science Gateway (<http://www.phylo.org/portal2>), using tools MrBayes 3.2.3 on XSEDE and RAXML-HPC2 on XSEDE (8.1.11). K2P genetic distances were computed using MEGA version 6.06 (Tamura et al. 2013).

### *Morphological studies*

The specimens used for morphological study were, when possible, selected from among molecular vouchers to ensure an objective linkage of morphological and phylogenetic information. In other cases, conspecificity of the molecular vouchers and of specimens studied for morphology was based on examination of shell characters and preferentially those specimens that were collected from the same general localities were used for morphological studies. The snails were dissected, and the entire proboscis was extracted and transferred to distilled water. For radula preparation, the proboscis was dissected and the buccal mass isolated from the anterior portion of proboscis; the buccal mass was suspended in diluted commercial bleach, where it was kept for 2-10 minutes until soft tissues completely dissolved; the radula was then rinsed in several shifts of distilled water and then transferred on clean 12 mm cover glass, where it was unfolded, air-dried and mounted for SEM study.

Due to the small size of studied specimens, anatomy of the proboscis was studied by serial sectioning, longitudinal in the case of *Charitodoron* and transversal for all other species. The extracted proboscis was dehydrated and embedded in paraplast, subsequently 7  $\mu$ m thin serial sections were prepared and stained with Masson's trichrome (*Charitodoron*) or standard hematoxilin-eosin (all other species).

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5 *Abbreviations of repositories and facilities used in text*  
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7 AMS – Australian Museum, Sydney, Australia;

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12 BAU – Department of Biology and Biotechnology ‘Charles Darwin’, University La Sapienza of  
13 Rome, Italy;

14 IEE – A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Science,  
15 Moscow, Russia;

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18 MNHN – Muséum National d’Histoire Naturelle, Paris, France;

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21 NHMUK – The Natural History Museum, London, UK;

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24 NMW – National Museum of Wales, Cardiff, UK;

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27 SIEE RAS – Laboratory of Molecular Genetics, A.N. Severtsov Institute of Ecology and  
28 Evolution, Russian Academy of Science, Moscow, Russia;

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31 *Anatomical abbreviations*  
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33 aoe – anterior oesophagus; bl – buccal lip; bm – buccal mass; bt – buccal tube; bw – body wall;  
34 bv – blood vessel; cm – columellar muscle; ep – epiproboscis; moe – mid-oesophagus; n –  
35 nerves; nr – nerve ring; od – odontophore; odr – odontophore retractor; oe – oesophagus; poe –  
36 posterior oesophagus; pt – tip of the proboscis; pw – proboscis wall; rd – radular diverticulum;  
37 sd – salivary duct; sg – salivary gland; vl – valve-like structure.  
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43 *Other abbreviations*  
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45 SH – Shell height; w/h – ratio of shell width to shell height; a/h – ratio of aperture height to shell  
46 height; law/h – ratio of last adult whorl height to shell height; lv – live collected specimen(s);  
47 dd – dead collected specimen(s); B – Maximum likelihood bootstrap support value; PP –  
48 Bayesian Posterior Probability support value; BI – Bayesian Inference; ML – Maximum  
49 likelihood; OD – original designation of type species; SD – subsequent designation of type  
50 species; M – type species by monotypy.  
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*Decisions on the generic assignment of individual species are based on:* <sup>1</sup> – molecular evidence and radula morphology, or molecular data only; <sup>2</sup> – shell characters and radula morphology; <sup>3</sup> – solely shell characters.

For Review Only

## Results

### *Single gene datasets*

Transition substitution model with constant proportion of invariable sites and gamma distributed rate variation among sites (TIM+I+G) was selected as a best fit substitution model for the COI and 16S datasets, and Tamura-Nei substitution model with constant proportion of invariable sites and gamma distributed rate variation among sites (TrN+I+G) was found a best fit model for 12S and H3 (Table 2). The trees obtained after analyses of single gene datasets were largely congruent and contained no highly supported conflicting topologies. Whereas many inferred clades were well supported, in particular in the COI tree, the deeper nodes remained unstable and in most cases lacked support, being thus of little use for phylogenetic inference. Thus, we here only discuss the topology of the COI tree, as it was built upon a notably larger dataset compared to other single-gene trees and provides means for species delimitation.

The 149 mitrid specimens sequenced for COI were primarily segregated into 89 morphospecies. In all but four cases, species hypotheses based on shell morphology correspond to clades in the COI tree (or to an independent lineage when represented by a single specimen). For the convenience of the presentation, we subdivided the COI tree in 28 clades, either moderately or well supported, or represented by single specimen; relationships among these 28 clades remained unresolved based on the analysis of COI.

Two morphospecies delineated based on the shell morphology each corresponds to two not closely related phylogenetic lineages in the COI based tree: (a) Specimens initially identified as *Strigatella paupercula* fell into two separate clades 7 and 11 (Figs 1, 2 A), and (b) the deep water specimens MNHN IM-2007-35618, MNHN IM-2007-35711 and IM-2013-40665, initially assigned to one morphospecies, ended up in clades 15 and 19 (Figs 1, 2 B). Conversely, morphologically diverse specimens that were initially treated as putative species complexes and identified as *Cancilla rehderi / fibula* (in subclade 24-7) and *Mitra glaphyria* (in clade 13 - Figs 1, 2 C, D), in fact formed rather homogeneous molecular clades, each of them consistent with a single species: The computed K2P genetic distances varied from 0 to 0.8% among specimens of *Mitra glaphyria*, and from 0 to 3.9% among specimens of *Cancilla rehderi / fibula*. The latter, although demonstrating a rather high genetic variation, showed no bimodal distribution of pairwise distances, and we are inclined to attribute the observed genetic disparity to a consequence of its broad geographic distribution (sequenced specimens originated from localities spanning from the Philippines and Papua New Guinea to the Society Islands).

Fourteen additional species with distinctive morphology were included in the molecular studies, although amplification of the COI was not successful, but they were deemed important for the study and were included in further molecular analyses. All of them, based on genetic

1 markers other than COI, appeared sufficiently divergent from other inferred lineages to exclude  
2 possible conspecificity. Therefore, our dataset includes 103 species as defined by both  
3 morphological and molecular characters.  
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5 Of the 103 species segregated, 94 are attributable to existing species names, including six  
6 that were identified with ambiguity and may (*Cancilla* cf. *fibula*, *Domiporta* cf. *carnicolor*,  
7 *Subcancilla* cf. *leonardhilli*) or may not (*Mitra* aff. *inca*, *Mitra* aff. *labecula*, *Strigatella* aff.  
8 *paupercula*) represent the taxon in question. Eight species were not identified, of which one is a  
9 subadult, and seven are adult and can confidently be recognized as undescribed.  
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11 The sequenced species represent 16 currently accepted genera; of these only two  
12 correspond to a single clade in the COI tree: *Pterygia* (Clade 22-4, 4 species, PP=1), and  
13 *Charitodoron* (Clade 28, 2 species, PP=1).  
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#### 15 Concatenated datasets: "3-mit" based tree

16 The consensus trees obtained from the analyses of multi-gene datasets showed similar topologies  
17 with no supported conflicts. In maximum likelihood (ML) and Bayesian analyses (BA) of all  
18 three concatenated datasets (Figs 3 - 5), the first dichotomy splits a two-species clade,  
19 corresponding to *Charitodoron*, from the rest of the Mitridae (from here onwards referred to as  
20 Mitridae s.s.), both clades forming very long branches, and showing maximum nodal support in  
21 all analyses. The Mitridae s.s. clade is composed of eight major groupings, marked with different  
22 colours in the molecular trees (Figs 3 - 5); their compositions were entirely consistent between  
23 trees, while support values and within-clade branching pattern varied slightly depending on the  
24 dataset analyzed. At the same time, relationships among these lineages remain unresolved;  
25 weakly supported affinities identified in one analysis appear unsupported in others. Here we  
26 describe the topology of the 3-mit tree (Fig. 3) and refer to other reconstructions where  
27 necessary.  
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29 The first major lineage (orange in Fig. 3), moderately supported in BA and weakly  
30 supported in ML (PP=0.97; B=74), comprises an assortment of *Mitra* lineages, along with  
31 species currently assigned to *Nebularia*, *Domiporta* and *Ziba*. This is the largest inferred lineage  
32 of Mitridae, combining 29 of the 82 species included in our 3-mit and 4G analyses. The distinct  
33 clades included in this first major lineage are:  
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35 1.1) a well supported *Mitra mitra* - *Mitra papalis* clade (PP=1; B=100);

36 1.2) a rather supported *Mitra sanguinolenta* - *M. sophiae* - *M. cardinalis* - *M. puncticulata*  
37 clade (PP=1; B=59);  
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39 1.3) a *Domiporta* grouping, moderately supported in BA (PP=0.98), combining (1.3a) a  
40 distinctive four species *Domiporta* s.s. clade (PP=1; B=100); (1.3b) a two species *Mitra*  
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2 *millepunctata* - *M. rosacea* clade (PP=100; B=1); and two clades formed by undescribed deep-  
3 water mitrids: (1.3c) IM-2013-40651 and IM-2013-40654 (PP=1; B=100), and (1.3d) the single-  
4 species clade of IM-2013-40665.  
5

6 1.4) a clade, moderately supported in BA (PP=0.99), combining a two species *Mitra*  
7 *avenacea*-Gen. sp. MNHN IM-2013-40655 clade (PP=1; B=98) with a well-supported grouping  
8 formed by three species currently assigned to *Nebularia*, *Nebularia connectens*, *N. pediculus*, *N.*  
9 *maesta* and *Mitra tornata* (PP=1; B=99).  
10

11 1.5) a clade, well supported in BA (PP=0.99), combining “*Mitra*” *glaphyria* and “*Mitra*”  
12 *invicta* from deep-water of the Indo-Pacific, and a distinct well supported clade including three  
13 New World *Mitra* species (PP=1; B=99).  
14

15 1.6) a clade, moderately supported in BA (PP=0.97), combining the West African *Ziba*  
16 *carinata* and the Mediterranean species pair *Mitra cornicula* and *M. zonata* (PP=1; B=99).  
17

18 Relationships among the six clades of the first major mitrid lineage are not resolved in 3-  
19 mit or any other analysis. From a nomenclatural point of view, the following species should be  
20 noted: *Mitra mitra* (type species of *Mitra*), *Domiporta filaris* (type species of *Domiporta*), *Ziba*  
21 *carinata* (type species of *Ziba*), and *Mitra zonata* (type species of *Episcomitra*) are marked with  
22 asterisks on the phylogenetic tree. From here onwards we will refer to this major lineage as the  
23 *Mitra-Domiporta-Ziba-Episcomitra* lineage.  
24

25 The second major lineage of Mitridae s.s. (yellow in Figs 3 – 5) is weakly supported in the  
26 3-mit analysis (PP=0.96) and forms a sister group to the first major lineage, although their  
27 relationship is also weakly supported by BA (PP=0.96). The second major lineage comprises  
28 multiple species commonly assigned to *Strigatella* from both the Indo-Pacific (*S. paupercula*, *S.*  
29 *litterata*, *S. decurtata* and *S. scutulata*) and the Panamic (*S. tristis*) regions, along with some  
30 Indo-Pacific species traditionally placed in *Mitra*, which form three well supported clades within  
31 the second major lineage: *M. aurantia* plus *M. vexillum* (PP=1; B=99); *M. ambigua* plus *M.*  
32 *fulvescens* (PP=1; B=100); and *M. lugubris* plus *M. coronata* (PP=1; B=100). From a  
33 nomenclatural point of view, the following species should be noted: *Strigatella paupercula* (type  
34 species of *Strigatella*) and *Mitra coronata* (type species of *Chrysame*) are marked with asterisks  
35 on the tree. From here onwards we will refer to this major lineage as the *Strigatella-Chrysame*  
36 lineage.  
37

38 The third major lineage of Mitridae (PP=1, B=100: green in Figs 3 – 5) consists of three  
39 distinct, well supported clades that include 20 Indo-Pacific species commonly classified in the  
40 Imbricariinae:  
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1  
2 3.1a) a first clade (PP=1, B=99) combining *Imbricaria conularis*, two species of  
3 *Subcancilla*, and five species of shallow-water *Ziba* from the Indo-West Pacific, *Z. bantamensis*,  
4 *Z. flammigera*, *Z. fulgetrum*, *Z. insculpta* and *Z. verrucosa*;

5  
6 3.2) a second clade (PP=1, B=100) including the morphologically variable deep-water  
7 species *Cancilla fibula*, represented in our analysis by three specimens, and *Swainsonia*  
8 *schepmani*;

9  
10 3.3) a third, distinctive and well supported, grouping including: (3.3a) a well supported  
11 *Neocancilla* clade, with (3.3b) weakly supported *Scabricola* clade showing supported affinity to  
12 *Neocancilla*, (3.3c) the two-species *Swainsonia* clade and (3.3d) *Imbricaria punctata*, which is  
13 recovered as a sister group to the rest of 3.3.

14  
15 From a nomenclatural point of view, the following species should be noted: *Imbricaria conularis*  
16 (type species of *Imbricaria*), *Neocancilla papilio* (type species of *Neocancilla*) and *Scabricola*  
17 *variegata* (type species of *Scabricola*). From here onwards we will refer to this major lineage as  
18 the *Neocancilla-Imbricaria-Scabricola* lineage.

19  
20 The fourth major Mitridae lineage (grey in Figs 3 – 5) includes two species, *Mitra tuberosa*  
21 and *M. bernhardina*, the affinities of which are moderately supported by BA and weakly  
22 supported in ML (PP=0.98, B=81). From here onwards we will refer to this lineage as the *Mitra*  
23 *tuberosa* lineage.

24  
25 The fifth and sixth major lineages show sister relationships which are well supported at  
26 least by BA (PP=0.99, B=80). The fifth major lineage (PP=1, B=98: blue in Figs 3 – 5) combines  
27 (5.1) a distinct *Pterygia* clade (PP=1, B=100) and (5.2) a well supported four-species clade,  
28 which includes Indo-Pacific species of *Mitra* (*M. incompta* and *M. eremitarum*), *Mutyca* (*M.*  
29 *acuminata*), and *Nebularia* (*N. contracta*) (PP=1, B=94). From a nomenclatural point of view,  
30 the following species should be noted: *Pterygia dactylus* (type species of *Pterygia*) and  
31 *Nebularia contracta* (type species of *Nebularia*), respectively included in the first and second  
32 clades. From here onwards we will refer to this lineage as the *Pterygia-Nebularia* lineage.

33  
34 The sixth major Mitridae lineage (PP=1, B=0.98: lilac in Figs 3 – 5) combines species of  
35 *Mitra* and *Subcancilla*. The lineage includes two clades, one of which comprises three Panamic  
36 *Subcancilla* species (PP=1, B=0.98), and the other combines *Mitra glabra* from Western  
37 Australia, *Mitra nigra* from West Africa, *Mitra cornea* from European seas, and *Subcancilla*  
38 *straminea* from the western Atlantic. The latter clade has a moderate nodal support in BA, and is  
39 not supported in ML (PP=0.96; B=68). From a nomenclatural point of view, it should be noted  
40 that *Mitra glabra* is the type species of *Isara* and *Mitra nigra* is the type species of *Fuscomitra*;  
41 from here onwards we will refer to this lineage as the *Isara-Fuscomitra* lineage.

1  
2 The seventh major Mitridae lineage comprises a single species, the shallow water  
3 Caribbean *Mitra barbadensis*.

4  
5 The eighth lineage (PP=1, B=100; light brown in Figs 3 – 5) is formed by two Indo-Pacific  
6 *Mitra* species, *Mitra peculiaris* and *M. typha*, from here onwards referred to as the *Mitra*  
7 *peculiaris* lineage.  
8  
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#### 10 11 *Other concatenated datasets*

12 Compared to the 3-mit tree, the 4G tree (Fig. 4) shows a slightly decreased support value for the  
13 *Mitra-Domiporta-Ziba* lineage (PP=0.95, B=79), and an insignificant rearrangement in the  
14 internal branching order. However, the support for the *Strigatella* lineage is higher in the 4G  
15 analysis compared to 3-mit, (PP=1, B=71), and nine of 12 species included in this lineage form a  
16 well supported grouping (PP=1, B=81). Neither content, nor support values changed  
17 significantly for the *Neocancilla-Imbricaria-Scabricola*, *Pterygia-Nebularia* or *Isara-*  
18 *Fuscomitra* lineages, as well as for the *Mitra tuberosa* and *Mitra peculiaris* lineages. However,  
19 the support has changed in some internal nodes, in particular the *Swainsonia casta- Swainsonia*  
20 *fusca* lineage shows a higher support compared to the 3-mit analysis (PP=1, B=76). Similarly,  
21 the clade that combines *Neocancilla* and *Scabricola* gains a higher support (PP=1, B=89) and is  
22 now clearly subdivided into two subclades, one corresponding to *Neocancilla* (PP=1, B=99), and  
23 the other combining *Scabricola variegata*, *S. desetangsii* and *S. olivaeformis* (PP=0.87, B=84).  
24  
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26 Conversely, the grouping which unified the *Pterygia-Nebularia* and *Isara-Fuscomitra*  
27 major lineages shows even a lower support compared to the 3-mit analysis (PP=0.93, B=64).  
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34 Not unexpectedly, the phylogenetic tree based on the analysis of the 4G-red dataset (Fig. 5)  
35 shows more significant changes in contents of the inferred groupings, primarily because of the  
36 reduced number of analyzed taxa. Nevertheless, and with the exception of *Mitra barbadensis*  
37 which was not included in 4G-red dataset, the seven major Mitridae lineages defined in the 3-mit  
38 and 4G analyses retained their principal composition, with support values comparable to those  
39 obtained in the 3-mit and 4G analyses. Among others, the *Mitra-Domiporta-Ziba-Episcomitra*  
40 lineage shows the greatest decrease in BA support (PP=0.9; B=0.79), however, the six clades  
41 that compose this major Mitridae s.s. lineage remain distinctive and well supported. Similarly,  
42 the phylogenetic clades corresponding to the large *Neocancilla-Imbricaria-Scabricola*, *Pterygia-*  
43 *Nebularia* and *Isara-Fuscomitra* lineages retained acceptable support values.  
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55 The support values of phylogenetic lineages inferred in analyses of the COI, 3-mit, 4G and  
56 4G-red datasets are summarized in Table 3; the clade names used in the table and on the trees are  
57 discussed in the section below. Only few of the currently recognized mitrid genera emerge  
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1  
2 monophyletic in our analyses: we confirm the monophyly of *Pterygia* and *Charitodoron*, while  
3 the other genera are either found to be poly- or paraphyletic, or their identification on the  
4 molecular tree is not straightforward (see section below).  
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### 8 *Morphological studies*

9  
10 Here we present data on the foregut anatomy of two diverging groups of Mitroidea that have not  
11 been addressed before and are important for understanding evolutionary pathways in Mitroidea  
12 in general (see Discussion).  
13

14  
15 *Charitodoron veneris*. Foregut anatomy based on NMSA D4172 [off Durban, 29°50.4'S,  
16 31°14.0'E, 150 m, sandstone gravel, 14.1 mm], radula based on NMSA E9237 [northern Natal,  
17 off Shellfield Beach, 29°39.8'S, 31°30.16'E, 150 m].  
18  
19

20 Although the specimen had been positioned for obtaining sagittal sections, the proboscis was  
21 diverted and sectioned nearly in frontal plane (Fig. 6 A, D). Proboscis moderately long, broad,  
22 conical, strongly contracted, so that its wall forms several telescopic folds (Figs 6 A, C, D).  
23 Mouth opening into medium long buccal tube, spanning around 1/3 of proboscis length and  
24 leading into broad buccal cavity. Buccal cavity subdivided into two chambers by the large  
25 circular fold of its wall (Fig. 6 D, arrow), both chambers lined with tall, densely ciliated  
26 epithelium, epithelial cells with large basal or central nuclei. Wall of the posterior chamber  
27 bearing very tall longitudinal folds (Figs 6 D - F). Wide anterior oesophagus leaving buccal  
28 cavity dorsally, forming rather long loop within proboscis, leaving proboscis and narrowing  
29 before passing through the nerve ring and then widening before transition to the posterior  
30 oesophagus (Fig. 6 D). Distinct valve-like structure, identifiable as a valve of Leiblein although  
31 lacking a ciliary cone, delimiting an anterior and a posterior oesophagus (Fig. 6G, vl). Anterior  
32 oesophagus empty in sectioned specimen, posterior oesophagus filled with food material (Fig. 6  
33 D, G) in which, however, no detectable remnants were found. After the oesophageal valve, tall  
34 and lightly stained epithelium of anterior oesophagus changing to low epithelium formed by  
35 small cubic cells. Anterior oesophagus lined with thin layer of muscular fibers, which become  
36 notably stronger in posterior oesophagus (Fig. 6 G).  
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48 Thin and strongly convoluted salivary ducts adjoining anterior oesophagus in front of  
49 passage through nerve ring and passing forward being embedded into its muscular wall, leaving  
50 oesophageal wall closer to the proboscis tip and entering buccal mass. Paired odontophore  
51 cartilages well developed, not fusing with strong lateral odontophore protractor muscles attached  
52 to odontophore ventrally (Fig. 6 D). Strong and massive odontophore retractor adjoining the  
53 columellar muscle shortly behind the nerve ring. Radular diverticulum opening into buccal  
54 cavity ventrally in posterior position, behind thick circular fold of the buccal cavity wall,  
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1 forming massive "lip", longer dorsally (buccal lip, bl – Fig. 6 D, E). After entering buccal cavity  
2 wall, distal salivary ducts passing inside that lip laterally on both sides of radular diverticulum  
3 opening (Fig. 6 D, E), and opening in the buccal cavity ventrally, underneath the semi-circular  
4 fold (Fig. 6 F). Epiproboscis absent.  
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8 Salivary gland large, unpaired, situated to the left of posterior oesophagus and dorsally to  
9 the nerve ring, histologically represented by a compactly packed, strongly convoluted tube with  
10 one layer of tall highly vacuolar, obviously glandular, cells and thin outer connective tissue  
11 layer (Fig. 6 A, B).  
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16 *Condylomitra tuberosa* [PANGLAO 2004, Stn B5].  
17

18 Proboscis moderately long, leaf-shaped, anteriorly flattened dorso-ventrally (Figs 7 A – H) and  
19 cylindrical at its base (Fig. 7 I). On transversal sections, proboscis with two lateral lobes at mid-  
20 length and ventral part with rounded axial keel. Proboscis wall with thick cuticle and nearly  
21 cubic epithelium, with large basal nuclei; epithelium underlined by a layer of circular muscle  
22 fibers (Figs 7 C, E, H). Lateral lobes occupied by complex interlacement of dorso-ventral,  
23 oblique, and longitudinal muscular fibers; two blood vessels (7 F, bv) running along margins of  
24 proboscis (Figs 7 B, D, F, G). Central part of proboscis occupied with oesophagus, anterior  
25 buccal mass and epiproboscis complex forming a single stem.  
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32 Mouth opening anteriorly on the dorsal side of the proboscis in short dorsal groove; mouth  
33 surrounded by small peristome rim (Fig. 7 A). Compact buccal mass situated shortly after mouth,  
34 furnished with thick muscular walls and triangular lumen; radular diverticulum opening ventrally  
35 into buccal cavity (Figs 7 B, C). Anterior oesophagus quadrangular on transversal sections, lying  
36 dorsally in the anterior part of the proboscis, attached to proboscis wall by thin muscular fibers  
37 (Figs 7 D – H). Dorsal and ventral walls of oesophagus very thin, lateral walls with two large  
38 longitudinal folds jutting out into the lumen of oesophagus. Lateral folds of oesophagus  
39 disappearing at mid proboscis height and thick layer of muscular fibers evenly covering it (Fig. 7  
40 I). Radular diverticulum rather short; odontophore formed by two small cartilages (Figs 7 D, E),  
41 not fused anteriorly. Odontophore retractor very strong, lying in a muscular sheath in its anterior  
42 portion (Figs 7 F – H), and dividing into two symmetrical branches at mid proboscis length (Fig.  
43 7 I).  
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52 Epiproboscis short, formed by densely packed longitudinal muscle fibers, with no  
53 epithelium. Epiproboscis lying ventrally from radular diverticulum, enclosed inside its own  
54 muscular sheath, which is attached to the radular diverticulum along most of its length (Figs 7 D  
55 – H). Both epiproboscis and its sheath originating from the ventral part of the radular retractor  
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1 sheath (Figs 7 G, H). Epiproboscis sheath opening ventrally on the anterior border of the buccal  
2 mass.  
3

4  
5 Salivary ducts passing forward along the anterior oesophagus, embedded into lateral folds  
6 of oesophagus wall (Figs 7 D – I); salivary gland itself not sectioned. Salivary ducts shifting  
7 ventrally in the walls of the buccal cavity adjoining the epiproboscis sheath. More distally,  
8 salivary ducts running backwards along the epiproboscis sheath to its proximal part, where they  
9 enter the epiproboscis and run through its entire length to open at its tip (Fig. 7 E).  
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## 17 Discussion

### 18 Application of family-group names to the phylogenetic clades

19  
20 The phylogenetic trees obtained in analyses of multiple-gene datasets were largely congruent and  
21 consistent with each other with respect to the nodal support of inferred lineages, thus providing  
22 robustness for the phylogenetic hypotheses of Mitridae. We chose the 4G based tree for further  
23 taxonomic inferences, because of (1) the better taxonomic coverage compared to the 4G-red  
24 based tree, and (2) the fewer polytomies in the 4G tree compared to the 3-mit based tree.  
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26  
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28 Our results agree in general with those obtained in earlier analyses (Fedosov et al. 2015).  
29 The assignment of names to the major lineages of Mitridae s.s. is straightforward in three cases.  
30 (A) Based on the inclusion of *Mitra mitra* (type species of *Mitra*, itself the type genus of  
31 Mitrinae), we designate the *Mitra-Domiporta-Ziba-Episcomitra* lineage as subfamily Mitrinae.  
32 Within it, the *Mitra mitra-Mitra papalis* clade is distinct and well supported, and shows no  
33 supported affinity to any other clade within the Mitrinae; thus we restrict the genus *Mitra* to this  
34 *Mitra mitra-Mitra papalis* clade (with a few other, presumed closely related, species). The genus  
35 *Tiarella* thus becomes a junior synonym of *Mitra*. The numerous species (even including *Mitra*  
36 *cardinalis* !) traditionally classified in *Mitra* that fall outside this clade are assigned below to  
37 other genera. (B) The *Neocancilla-Imbricaria-Scabricola* lineage, well supported in all  
38 phylogenetic analyses, includes the type species of *Imbricaria*, *I. conularis*, thus we designate it  
39 as subfamily Imbricariinae. (C) *Pterygia* (with its subjective synonym *Cylindromitra*) is the only  
40 genus classified in the subfamily Cylindromitridae (Cernohorsky 1970; 1991). The *Pterygia*  
41 clade is unequivocally identified in our phylogenetic trees, including the type species *P.*  
42 *dactylus*. Because the *Pterygia* lineage shows a well supported affinity to the *Nebularia*  
43 *contracta* clade in all analyses, the name Cylindromitridae can be applied to the resulting  
44 *Pterygia-Nebularia* lineage.  
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57 Beyond the names in current use above, another available name is Strigatellidae which,  
58 although little used, can be applied to the *Strigatella* major lineage, so here it is designated as  
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60

1 subfamily Strigatellinae. Conversely, there is no name available for the *Isara-Subcancilla* major  
2 lineage, for which we establish below the new subfamily Isarinae.  
3  
4

5 Finally, the three major lineages "*Mitra*" *peculiaris*, "*Mitra*" *tuberosa* and "*Mitra*"  
6 *barbadensis* are here treated as separate mitrid genera, but their subfamily assignments are  
7 uncertain and we leave them as *incertae sedis*.  
8  
9

10 The Mitridae s.s. clade has a maximum support in all multiple-genes analyses, and is  
11 defined by a very long branch. Moreover, all studied members of the Mitridae s.s. share  
12 morphological features that are not present in *Charitodoron*. We thus restrict the family name  
13 Mitridae to the Mitridae s.s. clade and establish a new family for *Charitodoron*. The obvious  
14 morphological distinctiveness of *Charitodoron*, and its position on the molecular tree as a sister  
15 group to all other Mitridae justify its inclusion in a separate family. The lineage comprising  
16 Mitridae, Charitodoronidae fam. nov. and Pyramimitridae is well supported in all our  
17 phylogenetic analyses, and is consistent with earlier results (Fedosov et al. 2015); therefore we  
18 rank it as superfamily Mitroidea stat. nov.  
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#### 27 *Application of genus-group names to the phylogenetic clades*

28 Our 4G molecular dataset includes the type species of 13 nominal genera: nine (*Domiporta*,  
29 *Imbricaria*, *Mitra*, *Nebularia*, *Neocancilla*, *Pterygia*, *Scabricola*, *Strigatella* and *Ziba*) currently  
30 treated as valid and four (*Chrysame*, *Episcomitra*, *Fuscomitra* and *Isara*) treated as synonyms [of  
31 *Mitra*]. Here we elaborate a new classification of the Mitridae based on genetically defined  
32 monophyletic groups. The inferred lineages including one (or more) of the type species  
33 mentioned above are named with certainty, but for the other clades we have to apply names  
34 based on their common usage and in agreement with shell and radular characters. The clades for  
35 which there is no available name are treated as new genera.  
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42 We unequivocally ascribe the genera *Mitra*, *Domiporta* and *Ziba* to the subfamily Mitrinae,  
43 based on their inclusion in the Mitrinae lineage of the phylogenetic trees. Based on the analysis  
44 of the COI gene, we transfer *Neocancilla circula* to the genus *Domiporta*. As here circumscribed  
45 the genus *Ziba* corresponds to a West African clade, and numerous Indo-Pacific imbricariine  
46 species assigned to *Ziba* after Cernohorsky (1991) are here transferred to *Imbricaria*. Two other  
47 clades within the Mitrinae lineage have available names: *Mitra zonata* is the type species of  
48 *Episcomitra*, subsequently synonymized (Cernohorsky, 1976) with *Mitra*. Based on the  
49 sequenced type species, we reinstate *Episcomitra* at the rank of genus with two Mediterranean  
50 species assigned to it, "*Mitra*" *zonata* and "*Mitra*" *cornicula*. Based on shell and radula  
51 characters we tentatively attribute the Indo-Pacific deep water clade "*Mitra*" *glaphyria* - "*Mitra*"  
52 *invicta* to the genus *Calcimitra*.  
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2 Although the Mitrinae lineage comprises the six distinct clades described above, some of  
3 them show morphological, geographical, bathymetric, and molecular disparities that lead us to  
4 further subdivide them. Thus we delineate on the molecular tree twelve well supported clades  
5 (some being single-species) that we rank as genera (marked light grey on the trees). Five of them  
6 have applicable names, and the remaining seven are here treated as new genera:  
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9  
10 *Quasimitra* n. gen. for the Indo-Pacific clade of "*Mitra*" *sophiae*, "*Mitra*" *puncticulata*,  
11 "*Mitra*" *cardinalis*, and "*Mitra*" *sanguinolenta*;

12  
13 *Roseomitra* n. gen. for the Indo-Pacific clade of "*Mitra*" *rosacea* and "*Mitra*"  
14 *millepunctata*;

15  
16 *Fusidomiporta ponderi* n. gen. and sp. for the single-species clade of MNHN IM-2013-  
17 40665 (Indo-Pacific, deep water);

18  
19 *Profundimitra* n. gen. for the Indo-Pacific deep water clade of MNHN IM-2013-40651 and  
20 MNHN IM-2013-40654;

21  
22 *Pseudonebularia* n. gen. for the Indo-Pacific "lesser" *Nebularia* clade of "*Nebularia*"  
23 *pediculus*, "*N.*" *connectens*, "*N.*" *maesta*, and "*Mitra*" *tornata*, which show no affinity to either  
24 *Mitra* or *Nebularia* as circumscribed here (the latter genus as typified by *N. contracta* is found to  
25 be closely related to *Pterygia* - see below);  
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28  
29 *Gemmulimitra* n. gen. for the Indo-Pacific clade of "*Mitra*" *avenacea* and MNHN IM-  
30 2013-40655;

31  
32 *Neotiara* n. gen. for the clade of New World species "*Mitra*" *lens*, "*Mitra*" *nodulosa* and  
33 "*Mitra*" cf. *inca*.

34  
35 *Cancellopsis* n. gen. for the Indo-Pacific clade 1 of our COI based tree, which shows no  
36 affinity to any other mitrid lineage in the analysis.

37  
38 Five species of *Strigatella*, including the type species, *S. paupercula*, are included in the  
39 Strigatellinae lineage of our trees, along with numerous "*Mitra*" species. As *Strigatella* and  
40 "*Mitra*" species do not form clades but are well intermixed, we recognize within this subfamily  
41 only one genus *Strigatella* and assign to it all the species in the Strigatellinae lineage. However,  
42 the genus name *Chrysame* (the type species *Mitra coronata* is included in our dataset) would  
43 apply to the *Mitra coronata* - *Mitra lugubris* subclade, which forms a very long branch and has a  
44 peculiar monoserial radula (see below) which differs remarkably from the radula of the rest of  
45 the Strigatellinae. From a cladistic point of view, recognition of *Chrysame* would render  
46 *Strigatella* paraphyletic, or many new genera would need to be established. We think the latter  
47 approach would be premature and, despite the unique position of *Chrysame* in the molecular  
48 trees, we treat it as a synonym of *Strigatella*.  
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The first clade of the Imbricariinae includes *Imbricaria conularis* (type species of the genus) and an assortment of "Ziba" and "Subcancilla" species from the Indo-Pacific, which we thus transfer to *Imbricaria*. The second inferred imbricariine clade combines *Cancilla rehderi* / *fibula* and "Mitra" *schepmani*. Based on the similarity in shell and radula morphology between the *Cancilla* species included in this clade and the type species *C. isabella* (as examined recently by Salisbury and Huang 2015), we tentatively attribute the name *Cancilla* to this clade. The third imbricariine molecular clade combines *Neocancilla* with *Scabricola*, *Swainsonia* and two former "Imbricaria" species. As *Neocancilla* species form a well supported clade with *N. papilio* (the type species) included in it, we confidently allocate this clade to *Neocancilla*. In sister position to the *Neocancilla*, the well supported grouping of *Scabricola variegata* (type species of *Scabricola*), *S. desetangsii* and *S. olivaeformis* is recovered; here we allocate it to the genus *Scabricola*. The *Swainsonia fusca* - *Swainsonia casta* clade is recovered as a sister group to the *Neocancilla*-*Scabricola*. As the type species of *Swainsonia*, *Mitra fissurata*, closely resembles *Scabricola fusca* in characters of the shell and radula, we consider that the name *Swainsonia* is available for it. *Neocancilla*, *Scabricola* and *Swainsonia* (as circumscribed here) form a well supported clade that is sister to the single species clade formed by "Imbricaria" *punctata*; for the latter, we establish *Imbricariopsis* n. gen.

Apart from *Pterygia*, the newly circumscribed Cylindromitrinae includes a closely related clade which combines "larger" *Mitra* species, "M." *eremitarum* and "M." *incompta*, with *Mutyca acuminata* and *Nebularia contracta*; the latter is the type species of *Nebularia*, and hence we attribute the name *Nebularia* to this four-species clade.

The names *Isara* and *Fuscomitra*, hitherto considered synonyms of *Mitra*, are available for the well supported "Mitra" *glabra* - "Mitra" *nigra* - "Mitra" *cornea* - *Subcancilla straminea* clade, as the type species of these nominal genera are included in it. Here we allocate the name *Isara* to this clade, and treat *Fuscomitra* as a synonym. The *Isara* clade forms a sister group to another well supported clade formed by three Panamic species of *Subcancilla*. As circumscribed by Cernohorsky (1991), the genus *Subcancilla* combined species from the Panamic and Caribbean regions, as well as from the Indo-Pacific, and the monophyly of the genus remained unconfirmed and doubtful (Thorsson & Salisbury, 2008). The type species *Subcancilla sulcata* is Panamic and, according to Cernohorsky (1991), it differs significantly from the Indo-Pacific species in the morphology and dimensions of radula. Our analysis confirms the non-monophyly of the *Subcancilla* species from the Panamic region with those from the Indo-Pacific. Based on biogeographical grounds and radular morphology, we here attribute the name *Subcancilla* to the clade of Panamic species, which is recovered as the sister group to the newly circumscribed *Isara*.

We tentatively attribute the name *Probata* to the single species clade of "*Mitra*" *barbadensis*, following Cernohorsky (1976), although we question the synonymy of *Mitra espinosai* (type species of *Probata*) with *M. barbadensis*, as suggested by Cernohorsky.

No genus group names are available for the inferred *Mitra tuberosa* clade and *Mitra peculiaris* clade. Thus we establish two new genera, *Condylomitra* n. gen. and *Carinomitra* n. gen., respectively for these distinctive lineages.

Three further lineages showed no supported affinity to any of the inferred major lineages that we rank as subfamilies; at present we abstain from giving them any subfamilial assignment, and treat them as *incertae sedis*. Two genera that are not represented in our dataset, *Atrimitra* Dall, 1918 and *Dibaphimitra* Cernohorsky, 1970, also cannot be attributed to any of the newly identified subfamilies based on the published morphological data (Bayer, 1942; Cernohorsky, 1970), thus at present we also treat them as *incertae sedis*, pending further molecular studies to clarify their affinities.

In conclusion, the combined molecular and morphological data lead to the revised classification below.

### Superfamily Mitroidea\* Swainson, 1831

#### Family Charitodoronidae new family

Genus *Charitodoron* Tomlin, 1932.

#### Family Mitridae Swainson, 1831

##### Subfamily Mitrinae Swainson, 1831

Genera *Mitra* Lamarck 1798, *Ziba* H. Adams & A. Adams, 1853, †*Clifdenia* Laws, 1932, *Eumitra* Tate, 1889, *Episcomitra* Monterosato, 1917, *Domiporta* Cernohorsky, 1970, *Calcimitra* Huang, 2011, *Fusidomiporta* n. gen., *Gemmulimitra* n. gen., *Cancillopsis* n. gen., *Neotiara* n. gen., *Profundimitra* n. gen., *Pseudonebularia* n. gen., *Quasimitra* n. gen., *Roseomitra* n. gen.

##### Subfamily Strigatellinae Troschel, 1869

Genus *Strigatella* Swainson, 1840.

##### Subfamily Imbricariinae Troschel, 1867

Genera *Imbricaria* Schumacher, 1817, *Cancilla* Swainson, 1840, *Scabricola* Swainson, 1840, *Neocancilla* Cernohorsky, 1966, *Swainsonia* H. Adams & A. Adams, 1853, *Imbricariopsis* n. gen.

##### Subfamily Cylindromitrinae Cossmann, 1899

Genera *Pterygia* Röding, 1798, *Nebularia* Swainson, 1840.

##### Subfamily Isarinae subfam. nov.

Genera *Isara* H. Adams & A. Adams, 1853, *Subcancilla* Olsson & Harbison, 1953.

Subfamily **Pleioptygmatinae** Quinn, 1989Genus *Pleioptygma* Conrad, 1863*Incertae sedis*

Genera *Atrimitra* Dall, 1918, *Vicimitra* Iredale, 1929, *Dibaphimitra* Cernohorsky, 1970, *Probata* Sarasúa, 1989, *Magnamitra* Huang & Salisbury, 2017, *Carinomitra* n. gen., *Condylomitra* n. gen.

For Review Only



**Taxonomical part**Superfamily **Mitroidea** Swainson, 1831Family **Charitodoronidae Fedosov, Herrmann, Kantor & Bouchet, new family**

(Fig. 8)

*Diagnosis:* Shell small (13-35 mm), fusiform, white or pale, sometimes with dark bands, or covered with brown periostracum. Protoconch white, bulbous, of about 1.5 smooth glossy whorls and with large initial nucleus. Suture distinct, impressed. Spire tall, orthoconoid; spire whorls evenly convex, smooth or sculptured with weak spiral grooves or cords. Sometimes distinct cancellate sculpture developed. Siphonal canal moderately long, robust or tapering, sometimes slightly recurved at its tip; siphonal notch shallow. Aperture wide, elongate; outer aperture lip smooth, evenly convex. Inner lip with no columellar folds.

Head-foot pale, with sometimes nebulous dark bands. Tentacles moderately long with eyes situated laterally at about mid-length. Siphon long. Osphradium as long as gill, attaining about 2/3 of the length of the latter. Proboscis well developed, without distinct proboscis rim; epiproboscis absent. Radula with narrow rachidian, bearing five subequal cusps, and wide, multicuspidate laterals, with cusps being more dense and stout proximally and becoming more slender towards radula margins; lateral 1/5 portion of teeth smooth. Mid-oesophagus muscular; mid-gut gland absent. Salivary gland single with paired ducts opening in buccal tube ventrally and anterior to radular diverticulum.

*Remarks.* The newly proposed family Charitodoronidae is distinctive in many ways. The shell bears no columellar folds and rather resembles a buccinoid shell; for this reason many *Charitodoron* species were originally erroneously placed in *Columbella*. The bulbous protoconch is unusual for Mitridae and suggests a non-planctotrophic development, consistent with the narrow distribution range. Remarkably, despite in morphology of the radula *Charitodoron* is close to mitrids, it does not possess the key morphological innovation of the Mitridae, the epiproboscis. The obvious morphological distinctiveness of *Charitodoron*, and its position in the molecular tree as a sister group to all other Mitridae justify its recognition as a separate family.

**Genus *Charitodoron* Tomlin, 1932**

*Type species:* *Charitodoron euprosyne* Tomlin, 1932 [junior subjective synonym of *Columbella barbara* Thiele, 1925]; OD.

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*Species included:* *Charitodoron agulhasensis* (Thiele, 1925)<sup>3</sup>, *C. alcyone* Lussi, 2009<sup>3</sup>, *C. barbara* (Thiele, 1925)<sup>3</sup>, *C. bathybius* (Barnard, 1959)<sup>1</sup>; *C. rosadoi* Kilburn, 1995<sup>3</sup>, *C. thalia* Tomlin, 1932<sup>3</sup>, *C. veneris* (Barnard, 1964)<sup>2</sup>.

Family **Mitridae** Swainson, 1831

Subfamily **Mitrinae** Swainson, 1831

(Figs 9-21)

**Genus *Mitra* Lamarck 1798** (Figs 9, 10 A)

*Type species:* *Voluta mitra* Linnaeus, 1758, by tautonymy.

Synonym: *Tiarella* Swainson, 1840. Type species: *Voluta papalis* Linnaeus, 1758; SD (Gray, 1847).

*Diagnosis:* Shell medium-sized to large (50-170 mm), thick-walled, fusiform or elongate-fusiform, with truncated base and colour pattern of multiple rounded or squarish red spots or bands on white background. Protoconch multispiral, of about 3 smooth slightly convex whorls. Suture deeply impressed. Teleoconch whorls gently convex or angulated adapically, bearing a row of short spiny bumps at shoulder. Rest of whorl surface sculptured with weak, evenly spaced, spiral grooves, well pronounced on early spire whorls and often vanishing later. Siphonal canal very short with robust siphonal fasciole delineated from shell base by deep depression. Aperture rather wide, with deep siphonal notch; outer apertural lip nearly straight adapically and strongly convex in its lower portion, bearing numerous fine denticles throughout its length or limited to its abapical margin. Inner lip reflected, with 3-4 subequal oblique columellar folds. Radula with rather narrow rachidian bearing 6 subequal cusps, and very wide laterals bearing cusps throughout their width (Fig 10 A). Cusps rather strong near rachidian and becoming progressively weaker laterally.

*Distribution:* Indo-Pacific, shallow intertidal and subtidal to upper bathyal depths, sand.

*Species included:* ***Mitra mitra* (Linnaeus, 1758)**<sup>1</sup>, *Mitra deprofundis* Turner, 2001<sup>3</sup>, *Mitra papalis* (Linnaeus, 1758)<sup>1</sup>, *Mitra stictica* (Link, 1807)<sup>3</sup>.

*Remarks.* A critical reassessment of the contents of the genus *Mitra* is one of the main outcomes of the present study, and our phylogenetic analysis demonstrates that the name *Mitra* may be confidently applied to a handful of species only. The redefined genus *Mitra* is morphologically

1 distinctive because of the conservative shell shape with rather high spire and low aperture,  
2 presence of denticles on the outer aperture lip and a recognizable colour pattern. At the same  
3 time, its radular morphology is overall the same as in many other mitrid clades and adds little to  
4 the diagnosis of the genus.  
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8 *Quasimitra cardinalis* and *Q. puncticulata* resemble species of *Mitra*. However, *Q.*  
9 *cardinalis* has a notably wider shell with lower spire, and *Q. puncticulata* lacks the characteristic  
10 colour pattern of *Mitra* and bears no denticle on the outer aperture lip. *Nebularia incompta* also  
11 resembles *Mitra* in shell proportions and the presence of denticles on the margin of the outer lip,  
12 but has a stronger sculpture and its siphonal canal is not clearly delineated from the shell base;  
13 besides, it has a typical *Nebularia*-type colour pattern instead of a *Mitra*-type. Some *Strigatella*  
14 species, especially *S. imperialis*, also closely resemble *Mitra* in the morphology of the abapical  
15 part of the shell (aperture and siphonal canal), but they have a notably lower spire and lack the  
16 *Mitra*-type colour pattern as well.  
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#### 24 25 26 27 **Genus *Calcimitra* Huang, 2011** (Figs 10 B-C, 11)

28 *Type species: Calcimitra kingsio* Huang, 2011; OD.

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30 *Diagnosis:* Shell medium-sized to large (35-125 mm), elongate-fusiform, with high orthoconoid  
31 or slightly acuminate spire and slender, tapering siphonal canal. Protoconch narrowly conical,  
32 multispiral, of about 3 smooth convex whorls. Suture deeply impressed or canaliculate. Spire  
33 whorls flattened to evenly convex, smooth, or sculptured with weak and irregular, or distinct,  
34 evenly set cords. Interspaces between spiral cords sometimes ornamented with fine collabral  
35 growth lines or dense riblets sometimes forming fine cancellate sculpture pattern. Siphonal canal  
36 long, tapering, with shallow or indistinct siphonal notch. Aperture elongate, its outer lip smooth,  
37 evenly convex. Inner aperture lip often calloused, sometimes reflected, bearing 3-4 fine  
38 columellar folds. Shell white, pale to orange, sometimes bearing pattern of reddish or brownish  
39 axial bands; fresh specimens often covered with brown periostracum. Radula with rather narrow  
40 rachidian, bearing 6-8 subequal cusps; laterals wide, bearing 12-20 pointed cusps (Figs 10 B, C),  
41 two proximal cusps rather short, weaker than the next five ones that are strongest; marginal 5-8  
42 cusps gradually diminishing.  
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53 *Distribution:* Indo-Pacific, bathyal depths, mud, sometimes on sunken wood.  
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57 *Species included:* *Calcimitra arnoldeyasi* (Poppe, Tagaro & Salisbury, 2010)<sup>3</sup> comb. nov., *C.*  
58 *brinkae* (Salisbury & Kilburn, 1996)<sup>3</sup> comb. nov., *C. brunetta* (Chino & Herrmann, 2015)<sup>3</sup>  
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1 comb. nov., *C. chiangfucius* (Huang & Salisbury, 2017)<sup>2</sup> comb. nov., *C. christinae* (Poppe,  
 2 2008)<sup>1</sup> comb. nov., *C. glaphyria* (Turner, 2001)<sup>1</sup> comb. nov., *C. hilli* (Cernohorsky, 1976)<sup>3</sup>  
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 4 comb. nov., *C. invicta* (Huang & Salisbury, 2017)<sup>1</sup> comb. nov., ***C. kingsio* Huang, 2011**<sup>3</sup>, *C.*  
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 6 *labecula* (Herrmann & Dekkers, 2009)<sup>1</sup> comb. nov., *C. lussii* (Turner & Salisbury, 2007)<sup>3</sup>  
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 8 comb. nov., *C. marrowi* (Turner, 2001)<sup>3</sup> comb. nov., *C. meyeriana* (Salisbury, 1992)<sup>3</sup> comb.  
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 10 nov., *C. morchii* (A. Adams, 1855)<sup>2</sup> comb. nov., *C. philosopha* (Huang & Salisbury, 2017)<sup>2</sup>  
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 12 comb. nov., *C. poppei* (Guillot de Suduiraut, 2000)<sup>3</sup> comb. nov., *C. salva* (Turner, 2001)<sup>3</sup> comb.  
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 14 nov., *C. subflava* (Kuroda & Habe, 1971)<sup>3</sup> comb. nov., *C. taiwanbale* (Huang & Salisbury,  
 15 2017)<sup>3</sup> comb. nov., *C. triplicata* (Martens, 1904)<sup>1</sup> comb. nov., *C. verweyi* (Knudsen, 1970)<sup>3</sup>  
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 17 comb. nov.  
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 20 *Remarks.* The five species included in clade 13 of the COI based tree show considerable  
 21 variation in shell morphology, both intra- and interspecifically. Six sequenced specimens of  
 22 *Calcimitra glaphyria* display a range of sculpture types, from smooth shells resembling  
 23 *Calcimitra kingsio* to distinct, cancellated ones, and differently sculptured specimens can be  
 24 found in the same general locality. While typical *Calcimitra* has a medium-sized, thin-walled  
 25 shells, our phylogenetic analysis placed '*Mitra*' *invicta* in the same phylogenetic clade. The latter  
 26 is a recently described species representative of a group of large deep-water mitrids (here  
 27 referred to as the *C. morchii* complex) that possess heavy, strongly sculptured shells (Huang &  
 28 Salisbury 2017). The close affinity of these conchologically diverse species is consistent with a  
 29 generally conservative radular morphology in *Calcimitra kingsio* (Huang, 2011), *C. morchii*, *C.*  
 30 *chiangfucius*, *C. philosopha* (Huang & Salisbury 2017), *C. glaphyria* and *C. invicta* (herein). The  
 31 intraspecific variation in sculpture pattern demonstrated by *C. glaphyria* challenges the status of  
 32 the species in the *Calcimitra morchii* complex accepted by Huang and Salisbury (2017). The  
 33 distinction of *C. chiangfucius*, *C. taiwanbale* and *C. invicta* is based on subtle differences in shell  
 34 morphology; they may prove to represent variants of a single species, and more comprehensive  
 35 sampling is necessary to clarify species boundaries.  
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47 *Magnamitra sandrogorii* strongly resembles some of the larger species of *Calcimitra*, and  
 48 the distinction of these two genera based on shell characters is problematic. The spiral sculpture  
 49 in *M. sandrogorii* is even stronger than in species of the *Calcimitra morchii* complex, and the  
 50 main distinction between the two genera is in the radula. In *Magnamitra*, the rachidian has a very  
 51 strong unpaired central cusp that notably exceeds lateral cusps, whereas all studied species of  
 52 *Calcimitra* possess a rachidian with equal or subequal cusps. Furthermore, rachidian and laterals  
 53 have comparable width in *Magnamitra sandrogorii*, whereas in species of *Calcimitra* the width  
 54 of the rachidian does not exceed half of the laterals width. Species of *Profundimitra* n. gen.  
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2 superficially resemble *Calcimitra*, but the latter genus can be recognized by the generally larger  
3 shells with proportionally longer siphonal canal and often calloused inner aperture lip. The  
4 radulae of species of *Calcimitra* and *Profundimitra* n. gen. differ greatly, the latter having  
5 rachidian and marginals of about equal width. Species of *Eumitra* are also similar to *Calcimitra*  
6 in shell proportions and sculpture, however *Eumitra* can be distinguished by its columellar folds,  
7 which are reduced to not more than 2 very weak folds, while in *Calcimitra* there are four (very  
8 rarely 3) distinct ones.  
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11 Some species of *Calcimitra*, in particular *C. triplicata*, resemble the Miocene fossil  
12 genus *Clifdenia*, both in whorl outline with evenly rounded inflated shoulders, and in shape and  
13 orientation of columellar plaits (A. Beu, personal communication). Based on this resemblance,  
14 we tentatively allocate *Clifdenia* to the subfamily Mitrinae.  
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### 20 21 22 **Genus *Eumitra* Tate, 1889** (Fig. 12) 23

24 *Type species*: †*Mitra alokiza* Tenison-Woods 1879; SD (Ludbrook, 1958: 71).  
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26 *Diagnosis*: Shell small to medium-sized (15-58 mm), fusiform, thin-walled, with high  
27 orthoconoid spire and slender siphonal canal. Protoconch very low, cyrtoconoid, paucispiral,  
28 with glossy whorls and rather small nucleus in all known species. Suture distinct, impressed.  
29 Early teleoconch whorls subcylindrical, later evenly convex, sometimes resulting in a slightly  
30 acuminate spire profile. Shell smooth, sometimes with very weak axial folds on first teleoconch  
31 whorl or fine grooves on shell base and siphonal canal. Siphonal canal, slender, tapering.  
32 Siphonal notch absent. Aperture elongate, outer lip evenly convex, smooth. Inner aperture lip  
33 either smooth, bearing one very weak or sometimes two distinct, but weak, columellar folds.  
34 Shell uniformly pale to light brown. Radula with very small, narrow rachidian, bearing 5 short  
35 robust cusps, only slightly extending beyond preceding tooth margin, but forming ridges, notably  
36 elevated above surface of rachidian. Laterals wide with 8-10 strong, pointed subequal cusps.  
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46 *Distribution*: New Caledonia, Coral Sea and the Philippines at bathyal depths, and a further  
47 undescribed species referable to *Eumitra* from Indonesia. Fossil species widely distributed in the  
48 Miocene of Europe and in the Australia - New Zealand region.  
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53 *Recent species included*: *Eumitra apheles* Lozouet, 1991<sup>2</sup>, *E. caledonica* Lozouet, 1991<sup>3</sup>, *E.*  
54 *imbricata* Lozouet, 1991<sup>3</sup>, *E. richeri* Lozouet, 1991<sup>3</sup>. '*Eumitra*' *suduirauti* Bozzetti, 1997<sup>3</sup>.  
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*Remarks.* *Eumitra* was not included in our molecular analysis, and our understanding of this genus is largely based on published data (Lozouet 1991), although additional material from the West Pacific has been examined. The placement of *Eumitra* in the newly circumscribed Mitrinae is thus tentative and based on the plesiomorphic radula of *Eumitra* and the presence of a well developed epiproboscis (YK, unpublished). Based on shell characters, *Eumitra* resembles *Calcimitra* and *Profundimitra* n. gen., however in the latter two genera species commonly have 3+ strong columellar folds. Besides, all studied species of *Profundimitra* n. gen. are characterized by a radula with a rachidian as broad as the laterals. Species of *Eumitra* lacking shell sculpture somewhat resemble the costellariid genera *Latiromitra* and *Costapex* (Fedosov et al. 2017), which however can be distinguished by the presence of an operculum, although reduced, and a longer siphonal canal (*Latiromitra*) or 3+ distinct columellar folds (*Costapex*). Moreover, in both *Latiromitra* and *Costapex*, the early teleoconch whorls are sculptured with strong axial ribs that are absent in *Eumitra*.

‘*Eumitra*’ *suduirauti* Bozzetti, 1997 (Fig. 12 E), shows some features (such as a wide aperture, especially wide in its anterior portion, a distinct subsutural ramp, pronounced on late teleoconch whorls, as well, as on early spire whorls) that are uncommon not only in the genus *Eumitra*, but in the family Mitridae in general. However, as no data on radula morphology or DNA of this odd species is available, we maintain it in the genus *Eumitra* pending for better placement to be determined in future.

All known species of *Eumitra* share a paucispiral protoconch that distinguishes them from most other mitrid genera. Nevertheless, given the wide distribution of *Eumitra* in the fossil record, we cannot rule out the possibility of multiple transitions to non-planktotrophic development in the evolutionary history of the genus, and thus some members of *Eumitra* might have retained planktotrophic development, and thus a multispiral protoconch.

**Genus *Neotiara* Fedosov, Herrmann, Kantor & Bouchet, n. gen.** (Figs 10 D, E, 13)

*Type species:* *Mitra lens* W. Wood, 1828; OD, herein.

*Diagnosis:* Shell small to large (20-75 mm), solid, coarsely sculptured, broadly fusiform to about turritiform. Protoconch multispiral, rather wide, cyrtoconoid, of about 3.5 smooth, convex whorls. Spire high; suture deeply impressed. Teleoconch whorls flattened to strongly convex or distinctly shouldered. Sculpture of slightly prosocline, wide and broadly spaced axial folds, or rather dense ribs; axials overridden by spiral cords which are typically wide and flattened, but may be narrow and elevated. Rounded or spirally elongated beads sometimes present at the intersection of spiral and axial sculptural elements. Siphonal canal rather short, stout, with weak or no fasciole. Siphonal notch shallow or indistinct. Outer aperture lip evenly convex, or its adapical half about

1 straight, and abapical half strongly convex. Inner aperture lip with 3-4 strong columellar folds,  
 2 adapicalmost strongest. Shell dull, light to dark brown, sometimes with well developed  
 3 periostracum. Radula with broad laterals, bearing robust, short and blunt cusps on their inner  
 4 portion, turning gradually to fine serration on outer half (Figs 10 D, E). Rachidian with robust,  
 5 very short and deeply rooted cusps, their tips merely reaching anterior margin of adjacent tooth  
 6 base.

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 13 *Species included:* *Neotiara crenata* (Broderip, 1836)<sup>3</sup> comb. nov., *N. fultoni* (E. A. Smith, 1892)  
 14 <sup>3</sup> comb. nov., *N. gausapata* (Reeve, 1845)<sup>3</sup> comb. nov., *N. inca* (d'Orbigny, 1841)<sup>3</sup> comb. nov.,  
 15 *N. lens* (Wood, 1828)<sup>1</sup> comb. nov., *N. muricata* (Broderip, 1836)<sup>3</sup> comb. nov., *N. nodulosa*  
 16 (Gmelin, 1791)<sup>1</sup> comb. nov., *N. pallida* (Nowell-Usticke, 1959)<sup>3</sup> comb. nov., *N. rupicola*  
 17 (Reeve, 1844)<sup>3</sup> comb. nov., *N. sphoni* (Shasky & Campbell, 1964)<sup>3</sup> comb. nov.

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 23 *Etymology:* The name refers to the now disused name *Tiara* Swainson, 1831, one of the genera  
 24 first established in what later became the family Costellariidae.

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 28 *Remarks.* According to Cernohorsky (1976: 454), the type of *Mitra lens*, which used to be in  
 29 Mawe's collection, can no longer be traced. In order to fix the identity of the species and of the  
 30 genus *Neotiara* n. gen., we here designate our sequenced specimen BAU00800 from Panama  
 31 City, Panama, measuring 40.0 x 15.5 mm (Fig. 13 A), as neotype of *Mitra lens*, MNHN IM-  
 32 2000-33145.

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 37 As circumscribed here, the genus *Neotiara* can be recognized among New World Mitridae  
 38 primarily by the well developed, typically coarse sculpture with distinct axial elements. Other  
 39 Caribbean and Panamic Mitridae of the genera *Isara*, *Subcancilla*, *Probata* and *Atrimitra* lack  
 40 axial sculpture, and the spiral elements are either lacking as well, or represented by fine cords.  
 41 As indicated by our phylogenetic analysis, the Panamic *Neotiara lens* and *N. aff. inca*, and the  
 42 Caribbean *N. nodulosa* are closely related and *Neotiara* is at present the only mitrid genus with  
 43 both Pacific and Atlantic species. Although only three species are included in our phylogenetic  
 44 analysis, we classify all heavily sculptured American mitrids in *Neotiara* n. gen.

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 54 **Genus *Ziba* H. Adams & A. Adams, 1853** (Figs 10 F, 14 A – D)

55 *Type species:* *Mitra carinata* Swainson, 1824; SD, Wenz (1943: 1292).

56 *Diagnosis:* Shell small (25-35 mm), elongate to fusiform, usually light brown to olive.

57 Protoconch narrowly conical of about 2.5-3 smooth convex whorls. Suture distinct, impressed.  
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Early teleoconch whorls evenly convex, with weak cancellate sculpture, later whorls typically distinctly carinated. Sculpture of weak grooves on late spire whorls, sometimes missing on last adult whorl. Last adult whorl high, with shell base gradually extended into tapering siphonal canal, typically sculptured with wide and low rounded cords. Siphonal notch weakly or moderately shallow. Aperture elongate, narrow, its outer lip smooth, gently convex or flattened. Inner lip with three fine, oblique columellar folds. Rachidian with five, equally developed, pointed, median cusps, flanked by two notably smaller marginal cusps (Fig. 10 F). Lateral teeth multicuspitate, third proximal cusp strongest, and subsequent cusps gradually diminishing; distal third of tooth smooth, with no cusps.

*Distribution*: West Africa, continental shelf, on mud.

*Species included*: ***Ziba carinata*** (Swainson, 1824)<sup>1</sup>, *Z. gambiana* (Dohrn, 1861)<sup>3</sup>.

*Remarks*. The present study has led to a drastic reconsideration of the position and contents of the genus *Ziba*. Based on the results of our phylogenetic analysis, *Ziba* is now classified in the subfamily Mitrinae and its contents exclude all the Indo-Pacific and West American species hitherto referred to *Ziba* by Cernohorsky (1991). An array of Indo-Pacific *Ziba* species are here transferred to *Imbricaria*, whereas the Panamic *Ziba attenuata* is reclassified in *Subcancilla*, neither of these genera showing an affinity to the true *Ziba*, which ends up being confined to the tropical eastern Atlantic; to our knowledge, there is no Indo-Pacific species referable to this genus. The radula of *Ziba carinata* shows a plesiomorphic morphology which is commonly found in Mitridae and, although supporting placement of *Ziba* in Mitrinae, adds little to understanding its relationships within the subfamily. The moderately supported lineage *Ziba carinata* – *Episcomitra* inferred in the 3-mit tree (though absent in other analyses) may reflect an affinity that makes sense from the biogeographical point of view; however, further studies are needed to determine the relationships of *Ziba*.

**Genus *Episcomitra* Monterosato, 1917** (Figs 10 G, H, 14 E – H)

*Type species*: *Mitra zonata* Marryat, 1818; M.

*Diagnosis*: Shell small to large (15-110 mm), fusiform or elongate fusiform, smooth, with well-developed periostracum. Protoconch large, paucispiral, cyrtoconoid, of about 2 smooth glossy convex whorls. Spire tall or rather low; suture impressed. Spire whorls evenly convex in outline, sculpture represented by fine, dense, collabral lines. Last adult whorl typically evenly convex with rather short siphonal canal bearing a distinct fasciole, separated from shell base by deep



1 groove. Siphonal notch deep or rather shallow. Outer aperture lip evenly convex, or convex in its  
2 adapical portion and straight throughout most of its length. Inner aperture lip with four, fine,  
3 subequal columellar folds. Shell covered with periostracum, light brown to dark brown or olive-  
4 green, uniform or with multiple dark freckles, or (typically) adapical 2/3 of spire whorls slightly  
5 lighter than their abapical portions. Inside of aperture white or orange. Rachidian with 6-8  
6 pointed cusps, increasing in length towards center; laterals wide, bearing rather long and pointed  
7 cusps throughout their length (Figs 10 G, H).

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15 *Species included: Episcomitra cornicula* (Linnaeus, 1758) <sup>1</sup> comb. nov., *E. zonata* (Marryat,  
16 1818) <sup>1</sup>.

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20 *Remarks.* The genus *Episcomitra* includes two of the three mitrid species inhabiting the  
21 Mediterranean, which share a smooth shell with well-developed periostracum. However, the  
22 same uninformative shell morphology characterizes *Isara cornea*, which occurs sympatrically  
23 with *Episcomitra* in the Mediterranean. *Episcomitra* and *Isara* are equally indistinguishable in  
24 radular characters: both share the same general morphology, and the intrageneric variation in  
25 *Isara* by far exceeds the subtle differences between typical *Episcomitra* and *Isara radula*  
26 morphologies. Thus, there are no morphological characters that substantially tell apart the two  
27 genera, as represented by *Episcomitra zonata* and *E. cornicula* and *Isara cornea*. This  
28 remarkable similarity in shell morphology demonstrates the limited use of shell characters for  
29 supraspecific assignments.

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40 **Genus *Quasimitra* Fedosov, Herrmann, Kantor & Bouchet, n. gen.** (Figs 10 I – M, 15)

41 *Type species: Mitra sanguinolenta* Lamarck, 1811; OD, herein.

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43 *Diagnosis:* Shell small to large (20-90 mm), solid, broadly fusiform, vividly coloured.  
44 Protoconch pointed, narrowly-conical, of about 3.5 slightly convex, smooth whorls. Suture  
45 deeply impressed. Shell proportions variable, spire moderately high to rather low, with ortho- or  
46 cyrtoconoid profile. Spire whorls evenly convex to subcylindrical, sometimes distinctly  
47 shouldered. Sculpture of very weak and low, flat or rounded, cords separated by shallow  
48 depressions or fine grooves. Subsutural area smooth or with one row of short spiny warts or  
49 tubercles, giving whorl a somewhat shouldered appearance. Siphonal canal short, with well  
50 developed fasciole usually separated from shell base by narrow concave waist. Siphonal notch  
51 deep. Aperture elongate, wide or moderately wide. Outer lip smooth, inner lip with 4 distinct  
52 columellar folds. Rachidian narrow (1/3 of laterals width) to rather wide (exceeding half of  
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laterals width), with 5-8 subequal cusps (Figs 10 I – M). Laterals rather wide, with 10-14 widely set and triangular, or dense and rather long, pointed cusps distributed throughout tooth width, proximal 1-2 cusps notably smaller than succeeding ones.

*Distribution:* Indo-Pacific, upper subtidal depths, mostly on sand.

*Species included:* *Quasimitra albocarnea* (Bozzetti, 2016)<sup>3</sup> comb. nov., *Q. barbieri* (Poppe & Tagaro, 2006)<sup>3</sup> comb. nov., *Q. bovei* (Keiner, 1838)<sup>3</sup> comb. nov., *Q. bretteinghami* (E.A. Smith, 1906)<sup>3</sup> comb. nov., *Q. cardinalis* (Gmelin, 1791)<sup>1</sup> comb. nov., *Q. floccata* (Reeve, 1844)<sup>3</sup> comb. nov., *Q. fulgurita* (Reeve, 1844)<sup>3</sup> comb. nov., *Q. lacunosa* (Reeve, 1844)<sup>3</sup> comb. nov., *Q. lamarcki* (Deshayes, 1832)<sup>3</sup> comb. nov., *Q. latruncularia* (Reeve, 1844)<sup>3</sup> comb. nov., *Q. leforti* (Turner, 2007)<sup>3</sup> comb. nov., *Q. manuella* (Cossignani & Cossignani, 2006)<sup>3</sup> comb. nov., *Q. marmorea* (Turner, 2007)<sup>3</sup> comb. nov., *Q. nubila* (Gmelin, 1791)<sup>3</sup> comb. nov., *Q. nympa* (Reeve, 1845)<sup>3</sup> comb. nov., *Q. propinqua* (A. Adams, 1853)<sup>3</sup> comb. nov., *Q. pseudobovei* (T. Cossignani & V. Cossignani, 2005)<sup>3</sup> comb. nov., *Q. puncticulata* (Lamarck, 1811)<sup>1</sup> comb. nov., *Q. punctostriata* (A. Adams, 1855)<sup>3</sup> comb. nov., *Q. rinaldii* (Turner, 1993)<sup>3</sup> comb. nov., *Q. roselineae* (Martin & Salisbury, 1987)<sup>3</sup> comb. nov., *Q. rossiae* (Reeve, 1844)<sup>3</sup> comb. nov., *Q. sanguinolenta* (Lamarck, 1811)<sup>1</sup> comb. nov., *Q. sarmiento* (Poppe, 2008)<sup>3</sup> comb. nov., *Q. solida* (Reeve, 1844)<sup>3</sup> comb. nov., *Q. sophiae* (Crosse, 1862)<sup>1</sup> comb. nov., *Q. stossieri* (Herrmann, 2016)<sup>3</sup> comb. nov., *Q. structilis* (Herrmann & Salisbury, 2016)<sup>3</sup> comb. nov., *Q. variabilis* (Reeve, 1844)<sup>3</sup> comb. nov.

*Etymology:* Latin *quasi*, meaning appearing like, which reference to the overall shell resemblance with species of the genus *Mitra*. Gender feminine.

*Remarks.* The genus *Quasimitra* n. gen. is defined primarily based on molecular characters, and there are no apomorphies or clear diagnostic morphological features that support its recognition. Shell proportions and sculpture vary extensively, with two extremes represented by *Q. cardinalis* and *Q. sophiae*, the close affinity of which is evidenced by the molecular data. The radulae of studied species generally retain a plesiomorphic morphology and also do not present any notable feature.

We tentatively assign *Mitra solida* Reeve, 1844 to *Quasimitra*, because of its characteristic sculpture and colour pattern, although varying notably in shell proportions. Cernohorsky treated *Vicimitra prosphora* Iredale, 1929 as a junior synonym of *Mitra solida*, despite *V. prosphora* has a smooth, uniformly pale shell, and only superficially resembles *Mitra solida* and the other

sequenced species here assigned to *Quasimitra*. At present, we treat *Vicimitra prospora* as a separate species in a monotypic genus *Vicimitra*, but the name *Vicimitra* may prove to be a senior synonym of *Quasimitra*.

Some species of *Strigatella*, like *S. luctuosa* or *S. aurantia*, bear a remarkable resemblance to *Quasimitra* in shell outline, and can only be distinguished by the generally more flattened spire whorls; at the same time there is a consistent difference in radular morphology between the two groups: the laterals bear cusps throughout their width in *Quasimitra*, whereas the distal third of laterals is devoid of cusps in the species of *Strigatella* mentioned.

### Genus *Domiporta* Cernohorsky, 1970 (Figs 16 A – E, 17 A – D)

*Type species: Voluta filaris* Linnaeus, 1771; OD.

*Diagnosis:* Shell small to medium-sized (12-65 mm), fusiform to elongate-fusiform, with high spire and rather short aperture. Protoconch pointed, narrowly-conical, of 2.5 – 3.5 smooth, slightly convex whorls to large, cyrtocoid, of nearly 5 smooth whorls. Suture distinct, impressed. Teleoconch whorls evenly convex in outline, with dominating spiral sculpture represented by regular, elevated, widely interspaced cords that are fine or (usually) strong, sometimes slightly gemmate. Interspaces between cords further sculptured by fine spiral grooves intersected by axial grooves of equal strength, resulting in fine, cancellated background pattern. Siphonal canal moderately long, tapering or robust, with well developed fasciole, delimited from shell base by distinct narrow waist, or extended concave stretch of shell base. Aperture rather short, elongate, with distinct siphonal notch. Outer lip gently convex, inner lip with 3-4 fine columellar folds, subequal or adapical strongest. Shell usually white or light with contrasting spiral cords, either uniformly dark brown, or dashed-brown. Rachidian from narrow (about 40% of laterals width) with 11 short, blunt cusps to almost as wide as laterals, arched, with 20+ pointed cusps. Laterals broad, bearing 20-35 equal, pointed cusps set on narrow, straight or arched, plate (Figs 17 A – D).

*Distribution:* Indo-Pacific, perhaps West Africa (*D. hebes*), shallow subtidal to bathyal depths, on sand.

*Species included:* *Domiporta aglais*<sup>3</sup> (Li & Zhang, 2005), *D. carnicolor* (Reeve, 1844)<sup>1</sup>, *D. circula* (Kiener, 1838)<sup>1</sup> comb. nov., *D. daidaleosa* (Li & Li, 2005)<sup>3</sup> comb. nov., *D. filaris* (Linnaeus, 1771)<sup>1</sup>, *D. gloriola* (Cernohorsky, 1970)<sup>3</sup>, *D. granatina* (Lamarck, 1811)<sup>1</sup>, *D. hebes* (Reeve, 1845)<sup>2</sup> comb. nov., *D. latistriata* (Herrmann & Salisbury, 2012)<sup>3</sup> comb. nov., *D.*

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*lichtlei* (Herrmann & Salisbury, 2012)<sup>3</sup> comb. nov., *C. manoui* (Huang, 2011)<sup>3</sup> comb. nov., *D. praestantissima* (Röding, 1798)<sup>1</sup>, *D. shikamai* Habe, 1980<sup>3</sup>, *D. sigillata* (Azuma, 1965)<sup>3</sup>

*Remarks.* The genus *Domiporta* is a rather compact and conchologically moderately variable group, however the colour and sculpture pattern in some species are close to those found in imbricariine genera. For example, *Domiporta circula* and *D. praestantissima* are superficially very much like *Imbricaria* as circumscribed here, while *D. granatina* and *D. carnicolor* resemble species of *Neocancilla*. It was probably this general similarity that led Cernohorsky to assign *Domiporta* to the subfamily Imbricariinae. Nevertheless, the species of *Domiporta* mentioned can be recognized by the higher spire, more convex whorls, and the presence of a concavity which delimits the shell base from the siphonal canal. Among Mitrinae, *Roseomitra* n. gen. is closest to *Domiporta*. The two closely related genera differ, however, in shell proportions: *Domiporta* is characterized by a notably higher spire and lower aperture compared to *Roseomitra* n. gen. Four species of *Domiporta* depart notably in radular morphology, showing a transition from rather typical mitrine radula in *D. filiaris* to the remarkable radulae of *D. granatina* and *D. praestantissima* with arched laterals and rachidian of equal width, bearing 25+ cusps; an intermediate morphology is observed in *D. cf. carnicolor*.

**Genus *Roseomitra* Fedosov, Herrmann, Kantor & Bouchet, n. gen.** (Figs 16 F – I, 17 E, F)

*Type species:* *Mitra millepunctata* G. B. Sowerby III, 1889; OD, herein.

*Diagnosis:* Shell small to medium-sized (10-45 mm) thin-walled, fusiform with rather low spire and high aperture. Protoconch pointed, narrowly conical, of 3+ smooth, glossy, slightly convex whorls. Suture distinct, slightly impressed. Spire rather low, orthoconoid; spire whorls with convex outline, sculptured with narrow, rounded, widely set cords. Interspaces between spiral cords bearing finer and lower secondary cords, or fine, widely interspaced, axial grooves. Last adult whorl very high, evenly convex, with shell base extended without clear distinction into straight, stout siphonal canal. Siphonal fasciole not pronounced, siphonal notch shallow or indistinct. Aperture high and moderately wide, its outer lip evenly convex or strongly convex adapically and nearly straight in its mid-width. Inner lip with five fine folds, adapicalmost strongest and succeeding ones gradually diminishing. Shell white, cream or pink, with brown blotches or with regular brown dots or dashes on spiral cords. Radula with narrow rachidian bearing 5-8 subequal cusps and wide laterals with narrow base and 15-21 moderately long pointed cusps (Figs 17 E, F).

*Distribution:* Indo-Pacific, shallow subtidal to bathyal depths, on sand or mud.

*Species included:* *R. citharoidea* (Dohrn, 1862)<sup>3</sup> comb. nov., *R. earlei* (Cernohorsky, 1977)<sup>3</sup> comb. nov., *R. fluctuosa* (Herrmann & Salisbury, 2013)<sup>3</sup> comb. nov., *R. honkeri* (Poppe, Tagaro & Salisbury, 2009)<sup>3</sup> comb. nov., *R. incarnata* (Reeve, 1845)<sup>3</sup> comb. nov., ***R. millepunctata* (G. B. Sowerby III, 1889)<sup>1</sup>** comb. nov., *R. reticulata* (A. Adams, 1853)<sup>3</sup> comb. nov., *R. rosacea* (Reeve, 1845)<sup>1</sup> comb. nov., *R. roseovitta* (Huang, 2011)<sup>3</sup> comb. nov., *R. strangei* (Angas, 1867)<sup>3</sup> comb. nov., *R. tagaroeae* (Poppe, 2008)<sup>3</sup> comb. nov.

*Etymology:* The genus name refers to the pink(ish) colour that characterizes some species, such as *R. incarnata* or *R. rosacea*. Gender feminine.

*Remarks.* As the type specimen of *Mitra millepunctata* is lost (Cernohorsky 1991 noted that the type specimen cannot be traced, and the first author failed to find it in NHMUK as well), we here designate our sequenced specimen IM-2013-40686, measuring 30.0 x 11.4 mm (Fig. 16 F) as neotype of *M. millepunctata*. This specimen was collected off Nocnocan Is., Central Philippines, at the type locality of *Mitra terryini*, a junior synonym (Herrmann, 2017) of *M. millepunctata*.

Species of the genus *Roseomitra* n. gen. can be recognized by the combination of rather thin walled shell with proportionally low spire and high aperture, distinctly rounded whorls and *Domiporta*-like sculpture. The shell proportions with low spire differentiate *Roseomitra* n. gen. from closely related *Domiporta* and most other mitrid genera. Species of *Pterygia* and *Imbricariopsis* have a proportionally even higher aperture, but in these genera the shell is conical or ovate, whereas it is fusiform in *Roseomitra* n. gen. In turn, *Condylomitra tuberosa*, *C. bernhardina* and *Quasimitra sophia* have a notably stronger sculpture compared to *Roseomitra* spp.

**Genus *Profundimitra* Fedosov, Herrmann, Kantor & Bouchet, n. gen.** (Figs 17 G, H, 18 A – H)

*Type species:* *Profundimitra taylori* n. sp.; OD, herein.

*Diagnosis.* Shell small (20-35 mm), thin-walled, fusiform or elongate-fusiform, with high orthoconoid or slightly acuminate spire. Protoconch pale, semi-translucent, narrowly conical with 3+ smooth whorls [usually strongly eroded]. Suture adpressed, sometimes shallowly canaliculated. Teleoconch whorls gently convex, early teleoconch whorls sometimes subcylindrical. Sculpture variable, from very weak, represented by indistinct spirally aligned

punctures, to deep spiral grooves separating flat, rounded or distinctly gemmate spiral cords. Siphonal canal rather long, straight, tapering, not notched at its tip. Aperture elongate. Outer lip very thin, convex, smooth or slightly undulating. Inner lip with three columellar folds, usually fine but well pronounced, sometimes very weak. Shell white, pale to yellowish, sometimes covered by light brown periostracum. Radula with laterals and rachidian of equal width, with evenly convex anterior margin bearing 12-14 equal pointed cusps (Figs 17 G, H).

*Distribution*: Indo-Pacific, bathyal depths, mostly on mud.

*Species included*: *Profundimitra abyssicola* (Schepman, 1911)<sup>3</sup> comb. nov., *P. planofilum* (Huang, 2011)<sup>1</sup> comb. nov., *P. taylori* n. sp.<sup>1</sup>.

*Etymology*: The name *Profundimitra* refers to the fact that all known species of this new genus inhabit deep water. Gender feminine.

*Remarks*. Whereas all the sequenced species of *Calcimitra* were identifiable to known species, the new deep-water genus *Profundimitra* (as well as the related *Fusidomiporta*) appears to represent a kind of Mitridae *terra incognita*. Of four species recognized in our phylogenetic analysis, only *Profundimitra planofilum* has a name. The latter was initially described in *Cancilla*, and indeed the sculpture pattern and light brown marks on spiral cords of *Profundimitra planofilum* strikingly resemble the pattern seen in species of *Cancilla*. *P. planofilum*, however, differs from *Cancilla* by the shell base outline, which is distinctly concave, and by a slightly higher spire. The immature lectotype of *C. abyssicola* figured by Cernohorsky (1991) is very close to species of the *Profundimitra* clade in shell characteristics, and we tentatively assign this species to *Profundimitra*. It should be noted, though, that *C. abyssicola* as circumscribed by Cernohorsky combined a variety of forms, some of them (like the specimen figured by Cernohorsky 1970: pl. 6 fig. 7, which is undoubtedly conspecific with our specimens IM-2007-35711 and IM-2007-35618) referable to *Profundimitra* n. gen., but most likely not conspecific with the lectotype, while others obviously represent true *Cancilla* or *Imbricaria* as circumscribed here.

The genus *Profundimitra* n. gen. can be recognized by the elongate, typically weakly sculptured shell, either white or pale, sometimes covered with light brown periostacum. The genus *Calcimitra* is closest to *Profundimitra* n. gen. in shell morphology, however species in the latter genus have proportionally higher spire and, correspondingly, lower last adult whorl and siphonal canal. Another genus which seems superficially close to *Profundimitra* n. gen. is

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*Eumitra*, which however is characterized by a smooth columella, typically with no folds or with only one or two distinct folds, while species of *Profundimitra* n. gen. have 3+ columellar folds, albeit sometimes slightly sunken in the aperture. Another notable difference between the two genera is the morphology of protoconch: it is narrow and narrowly-conical in *Profundimitra*, very distinctly demarcated from the much wider first teleoconch whorl, whereas the protoconch of *Eumitra* is very low, cyrtconoid, and not clearly delimited from teleoconch. Moreover, *Profundimitra* n. gen. has a characteristic radula morphology with rachidian and laterals of equal width and similar morphology, as opposed to the very small, narrow rachidian and wide laterals of *Eumitra*.

**Genus *Fusidomiporta* Fedosov, Herrmann, Kantor & Bouchet, n. gen.** (Figs 17 I, 18 I–L)

*Type species: Fusidomiporta ponderi* n. sp.; OD, herein.

*Diagnosis:* As the genus is established primarily based on the molecular data, and its recognition based on the morphology is problematic, we do not provide a formal diagnosis.

*Description* (based on type species): Shell small (about 25 mm), fusiform, heavily sculptured, with rather high spire and stout siphonal canal. Protoconch multispiral, of 3+ whorls usually strongly corroded or missing. Suture canalculated; subsutural shelf well developed, rather narrow, bordered by projecting margin of adapical spiral cord. Sculpture of strong, elevated, gemmate spiral cords separated by deep interspaces; microsculpture of fine growth lines in interspaces between spiral cords. Spiral cords become distinctly beaded on penultimate and last adult whorls, forming rows of closely set, axially expanded, glossy granules. Siphonal rather long and stout, slightly recurved. Aperture elongate, its outer lip gently convex throughout its height, wavy, reflecting arrangement of spiral cords. Inner lip strongly calloused, reflected, with three strong oblique columellar folds at its mid-height. Rachidian and laterals multicuspidate, of about same width.

*Distribution:* Indo-Pacific, bathyal depths in about 400-500 m.

*Species included: F. ponderi* n. sp.<sup>1</sup>

*Etymology:* The name *Fusidomiporta* reflects the close affinity of the new genus to *Domiporta*, and refers to the fusiform shell of the type species. Gender feminine.

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*Remarks.* Morphologically, *Fusidomiporta ponderi* n. sp. falls within the range of variation seen in *Profundimitra* n. gen., both in the shell and radula, and we even initially thought that specimen IM-2013-40665 (now the holotype of *F. ponderi*) was conspecific with IM-2007-35711 (an unknown species of *Profundimitra*). The molecular distinctiveness of *Fusidomiporta ponderi* n. sp. was thus totally unexpected. However, none of the single-gene analyses placed *Fusidomiporta ponderi* n. sp. in the same molecular clade as *Profundimitra*, and a *Fusidomiporta-Profundimitra* grouping is only present in the 3 genes based tree. Thus the genus is largely defined by molecular characters; the morphological basis for the separation between *Fusidomiporta* and *Profundimitra* needs to be more carefully elaborated, for which more specimens need to be examined.

A sculpture pattern close to that present in *Fusidomiporta* n. gen. is also observed in species of *Gemmulimitra* n. gen. (*G. neocaledonica* n. sp. and *G. boucheti*); however, *Gemmulimitra* differs notably from *Fusidomiporta* in radula morphology, showing a classical mitrid radula with a narrow rachidian (Figs 20 F, G).

**Genus *Cancillopsis* Fedosov, Herrmann, Kantor & Bouchet, n. gen.** (Fig. 18 M)

*Type species:* *Cancilla meimiaoae* Huang & Salisbury 2017; OD, herein.

*Diagnosis:* As the genus is established primarily based on the molecular data, and its recognition based on the morphology is problematic, we do not provide a formal diagnosis.

*Description* (based on the type species, adapted from Huang & Salisbury (2017): Shell medium-sized (50-82 mm), fusiform, with high spire and long, stout siphonal canal. Protoconch multispiral, cyrtoconoid, of about 3 glossy whorls. Teleoconch of up to 10 gently convex whorls; suture distinct. Sculpture of rounded spiral cords, intersected by closely set, slightly prosocline axial riblets, forming fine beaded sculpture on early spire whorls. On last adult whorl cords more widely set, and beaded sculpture indistinct, as axial riblets are well pronounced in interspaces between spiral cords only. Siphonal canal stout, deeply notched, slightly recurved at its tip. Aperture elongate, its outer lip evenly convex throughout its length. Inner lip calloused, with four closely set fine columellar folds at its mid-height. Shell white with irregular yellow or brownish blotches.

*Distribution:* Indo-Pacific, bathyal depths.

*Species included:* *Cancillopsis meimiaoae* (Huang & Salisbury 2017)<sup>1</sup> comb. nov., †*C. acuminata* (Shuto, 1969)<sup>3</sup> comb. nov.



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4 *Etymology:* The name *Cancillopsis* refers to the close resemblance between *C. meimiaoae*, the  
5 type species of the new genus, and species of *Cancilla*. Gender feminine.  
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9 *Remarks.* *Cancillopsis meimiaoae* shows a notable resemblance to the species of the imbricariine  
10 genus *Cancilla* as well as to the species of *Profundimitra* n. gen. and *Fusidomiporta* n. gen.,  
11 while showing no phylogenetic affinity to either of them. A visible concavity at the transition of  
12 shell base to the siphonal canal distinguishes the new genus from similarly sculptured *Cancilla*  
13 species. We hypothesize that *Cancillopsis* n. gen. is more closely related to the *Domiporta* group  
14 of Mitrinae, and so we provisionally place it in Mitrinae. However, a more comprehensive taxon  
15 sampling of the deep water Mitridae is obviously needed to delineate these convergent deep  
16 water lineages and to clarify affinities of *Cancillopsis* n. gen.  
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25 **Genus *Pseudonebularia* Fedosov, Herrmann, Kantor & Bouchet, n. gen.** (Figs 19, 20 A – E)

26 *Type species:* *Mitra tornata* Reeve, 1845; OD, herein.

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28 *Diagnosis:* Shell small (9-30 mm), fusiform or broadly fusiform to biconical, vividly coloured.  
29 Protoconch pointed, narrowly conical, of about 3 slightly convex, glossy whorls. Suture slightly  
30 impressed, often indistinct. Teleoconch whorls evenly convex or flattened, sometimes giving the  
31 spire a distinctly stepped profile. Sculpture of strong, rounded spiral cords, regularly interspaced  
32 and covering the entire shell or, rarely, limited to shell base. Interspaces between cords concave,  
33 smooth or bearing fine, dense riblets. Siphonal canal moderately long, stout, siphonal notch  
34 shallow or absent. Aperture rather narrow, elongate, with undulating outer lip, sometimes  
35 bearing rounded denticles on its inside. Inner lip calloused, often reflected, with 3-4 strong  
36 columellar folds, adapicalmost strongest. Radula with broad laterals, bearing equal, rather long,  
37 widely set cusps throughout their width; rachidian not exceeding half the width of the laterals,  
38 multi- or unicuspidate (Figs 20 A – E).  
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48 *Distribution:* Indo-Pacific, intertidal to upper subtidal depths, rocky flats, reef crevices and coral  
49 rubble.  
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53 *Species included:* *P. atjehensis* (Oostingh, 1939)<sup>1</sup> comb. nov., *P. chrysalis* (Reeve, 1844)<sup>3</sup>  
54 comb. nov., *P. cingulata* (A. Adams, 1853)<sup>3</sup> comb. nov., *P. connectens* (Dautzenberg & Bouge,  
55 1923)<sup>1</sup> comb. nov., *P. cucumerina* (Lamarck, 1811)<sup>3</sup> comb. nov., *P. cuyosae* (Poppe, 2008)<sup>3</sup>  
56 comb. nov., *P. doliolum* (Küster, 1839)<sup>3</sup> comb. nov., *P. dovpeledi* (Turner, 1997)<sup>3</sup> comb. nov.,  
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1 *P. fraga* (Quoy & Gaimard, 1833)<sup>2</sup> comb. nov., *P. gracilefragum* (Turner, 2007)<sup>2</sup> comb. nov.,  
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 3 *P. kantori* (Poppe, Tagaro & Salisbury, 2009)<sup>3</sup> comb. nov., *P. kilburni* (Poppe, Tagaro &  
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 5 Salisbury, 2009)<sup>3</sup> comb. nov., *P. lienardi* (G.B. Sowerby II, 1874)<sup>3</sup> comb. nov., *P. maesta*  
 6  
 7 (Reeve, 1845)<sup>1</sup> comb. nov., *P. oliverai* (Poppe, 2008)<sup>3</sup> comb. nov., *P. pediculus* (Lamarck,  
 8  
 9 1811)<sup>1</sup> comb. nov., *P. perdulca* (Poppe, Tagaro & Salisbury, 2009)<sup>3</sup> comb. nov., *P. proscissa*  
 10  
 11 (Reeve, 1844)<sup>3</sup> comb. nov., *P. rubritincta* (Reeve, 1844)<sup>3</sup> comb. nov., *P. ruepellii* (Reeve,  
 12  
 13 1844)<sup>3</sup> comb. nov., *P. semiferruginea* (Reeve, 1845)<sup>3</sup> comb. nov., *P. silviae* (Turner, 2007)<sup>3</sup>  
 14  
 15 comb. nov., *P. tabanula* (Lamarck, 1811)<sup>1</sup> comb. nov., ***P. tornata* (Reeve, 1845)**<sup>1</sup> comb. nov.,  
 16  
 17 *P. wareni* (Poppe, Tagaro & Salisbury, 2009)<sup>3</sup> comb. nov., *P. willani* (Poppe, Tagaro &  
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 19 Salisbury, 2009)<sup>3</sup> comb. nov., *P. yayanae* (Huang, 2011)<sup>3</sup> comb. nov.

20 *Etymology:* *Pseudonebularia* means "false *Nebularia*" and refers to the long accepted, and  
 21  
 22 erroneous, placement of the included species in *Nebularia*, which it resembles superficially.

23 Gender feminine.

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 27 *Remarks.* *Pseudonebularia* n. gen. comprises a group of popular, colourful shallow water or even  
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 29 intertidal miters that are traditionally referred to *Nebularia* but, as demonstrated by our analysis,  
 30  
 31 are not related to it, as *Nebularia* is recovered in a sister position to *Pterygia*. Species of  
 32  
 33 *Pseudonebularia* n. gen. typically have a small, but broad and robust, brightly coloured shell.  
 34  
 35 While red and variegated biconical shells in species of the *P. fraga* group are quite distinctive,  
 36  
 37 more elongated species, for example *P. atjehensis*, resemble species of *Domiporta* or *Imbricaria*  
 38  
 39 as newly circumscribed here. The elongated *Pseudonebularia* species, however, can be  
 40  
 41 distinguished by generally broader, rounded spiral cords that bear no darker lines on their crests.

42 The three species of *Pseudonebularia* studied anatomically show a significant disparity in  
 43  
 44 radular morphology, with rachidian varying considerably from bow-shaped with multiple  
 45  
 46 densely set cusps to very narrow, but robust, bearing a single short, pointed cusps on a bulbous  
 47  
 48 shaft.

49  
 50 **Genus *Gemmulimitra* Fedosov, Herrmann, Kantor & Bouchet, n. gen.** (Figs 20 F, G, 21)

51 *Type species:* *Gemmulimitra neocaledonica* n. sp.; OD, herein.

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 53 *Diagnosis:* As the genus is established primarily based on the molecular data, and its recognition  
 54  
 55 based on the morphology is problematic, we do not provide a formal diagnosis.

56  
 57 *Description* (based on the type species): Shell small (about 20-25 mm), elongate-fusiform to  
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 59 almost biconical. Protoconch multispiral, of 3+ slightly convex, glossy whorls. Suture

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canaliculated. Subsutural ramp forming distinct shelf, giving spire a stepped appearance. Spire whorls sculptured with strong, closely set, spiral cords overriding low indistinct axial ribs to form series of prominent beads. On later teleoconch whorls, interspaces between gemmate spiral cords broadened, with axial ribs becoming more distinct and sculpture rather reticulate. Interspaces between axial ribs and spiral cords forming deep quadrangular depressions with microsculpture of fine axial growth lines. Shell base extended to rather long, tapering, slightly notched siphonal canal. Aperture narrow, elongated. Outer lip wavy, convex in adapical portion and straight below mid-height; inside of outer lip smooth. Inner lip strongly calloused, sometimes reflected, with four closely set fine columellar folds. Rachidian narrow, bearing 8 strong, moderately long, pointed cusps; laterals wide, bearing 16+ strong, pointed, rather widely set cusps.

*Distribution:* Indo-Pacific, subtidal to bathyal depths.

*Species included:* *Gemmulimitra aliciae* (Poppe, Tagaro & Salisbury, 2009)<sup>3</sup> comb. nov., *G. apprimapex* (Poppe, Tagaro & Salisbury, 2009)<sup>3</sup> comb. nov., *G. avenacea* (Reeve, 1845)<sup>1</sup> comb. nov., *G. boucheti* (Cernohorsky, 1988)<sup>2</sup> comb. nov., *G. duplilirata* (Reeve, 1845)<sup>3</sup> comb. nov., *G. edgari* (Poppe, Tagaro & Salisbury, 2009)<sup>3</sup> comb. nov., *G. gonatophora* (Sturany, 1903)<sup>3</sup> comb. nov., *G. hansturneri* (E. Guillot de Suduiraut & E.G. Guillot de Suduiraut, 2009)<sup>3</sup> comb. nov., *G. margaritata* (Poppe, Tagaro & Salisbury, 2009)<sup>3</sup> comb. nov., ***G. neocaledonica*** n. sp.<sup>1</sup>, *G. rubiginosa* (Reeve, 1844)<sup>3</sup> comb. nov., *G. strongae* (Poppe, Tagaro & Salisbury, 2009)<sup>1</sup> comb. nov.

*Etymology:* The genus name refers to the sculpture of gemmate cords that characterizes many species in this newly recognized lineage, including the type species *G. neocaledonica*.

*Remarks.* *Gemmulimitra neocaledonica* n. sp. and *G. avenacea* that together constitute the *Gemmulimitra* clade on multi-gene trees have little in common in shell morphology, and thus this clade is at present defined solely based on the molecular characteristics. The third species confidently included in the genus is *Gemmulimitra strongae* that is close to *G. neocaledonica* n. sp. in the COI based tree. The other species here attributed to *Gemmulimitra* are tentatively classified in this genus based on their general resemblance to the type species or to *Mitra avenacea*, rather than on any specific diagnostic feature. Therefore, the species included in *Gemmulimitra* constitute two conchologically distinctive groups: species in the first group have a typical sculpture of gemmate cords, such as *Gemmulimitra neocaledonica* n. sp., *G. boucheti*

(Fig. 21 C), *G. strongae* (Fig. 21 D), and *G. gonatophora* (holotype figured by Albano et al. 2017), while species in the second group have continuous, smooth spiral cords, such as *G. avenacea* (Fig. 21 E), *G. edgari*, and *G. rubiginosa* (Fig. 21 F). Species of the first group closely resemble *Fusidomiporta ponderi* n. sp., whereas species of the second group resemble species of *Pseudonebularia*, from which, however, they can be distinguished by a more elongated shell with more flattened spire whorls. The radula of *Gemmulimitra* is plesiomorphic and phylogenetically uninformative. More studies are needed to better define the boundaries of *Gemmulimitra* n. gen. and elaborate its diagnosis.

Subfamily **Strigatellinae** Troschel, 1869

(Figs 22, 23)

**Genus *Strigatella* Swainson, 1840**

*Type species: Mitra zebra* Lamarck, 1811 [= *Voluta paupercula* Linnaeus, 1758]; SD, Gray (1847: 141).

*Synonyms: Chrysame* H. Adams & A. Adams, 1853; *Type species: Mitra coronata* Lamarck, 1811; SD, Cox (1927: 91).

*Phaeomitra* Martens, 1880; *Type species: Mitra fulva* Swainson, 1829 [= *Mitra coffea* Schubert & Wagner, 1829]; SD, Coan (1966: 131).

*Diagnosis:* Shell small (12-40 mm), broadly fusiform, solid and stout in appearance, Protoconch pointed, narrowly-conical, of about 2.5-3 smooth, very slightly convex whorls. Suture deeply impressed. Spire whorls gently convex or flattened to subcylindrical, sometimes with narrow subsutural area, giving spire a somewhat telescopic outline. Sculpture typically not developed; sometimes shell sculptured with very faint to strong rounded spiral cords over all the shell surface or limited to shell base. Last adult whorl usually strongly convex, siphonal canal typically short and stout to moderately long, with distinct siphonal fasciole. Siphonal notch shallow or absent. Aperture elongate, narrow; outer lip straight adapically and strongly convex in its abapical portion, often thickened adapically, forming a callous inner varix, constricting aperture. Inner lip with 3-5 fine oblique columellar folds. Shell orange to dark brown, typically with a pattern of white bands and blotches. Radula tri- or monoseriate. In triseriate radulae, rachidian narrow, with 5-7 very short and robust cusps, unpaired central cusp always present (Fig 23); in uniseriate radulae, rachidian bearing 20-25 pointed cusps with unpaired central cusp distinctly exceeding others. Laterals broad, wavy, with their distal halves smooth and 7-10 rather short and robust cusps situated proximally.

*Distribution:* Indo-Pacific and Panamic provinces, intertidal and subtidal depths, mostly on hard substrates (rocky shores, reef crevices or coral rubble).

*Species included:* *Strigatella amaaura* (Hervier, 1897)<sup>3</sup>, *S. assimilis* (Pease, 1868)<sup>3</sup>, *S. aurantia* (Gmelin, 1791)<sup>1</sup> comb. nov., *S. auriculoides* (Reeve, 1845)<sup>3</sup>, *S. aurora* (Dohrn, 1861)<sup>2</sup> comb. nov., *S. colombelliformis* (Kiener, 1838)<sup>2</sup>, *S. coronata* (Lamarck, 1811)<sup>1</sup> comb. nov., *S. crassicosata* (G. B. Sowerby II, 1874)<sup>3</sup> comb. nov., *S. decurtata* (Reeve, 1844)<sup>1</sup>, *S. fasciolaris* (Deshayes, 1834)<sup>3</sup> comb. nov., *S. flavocingulata* (Lamy, 1938)<sup>3</sup>, *S. fulvescens* (Broderip, 1836)<sup>1</sup> comb. nov., *S. holkosa* (Li, Zhang & Li, 2005)<sup>3</sup> comb. nov., *S. imperialis* (Röding, 1798)<sup>1</sup> comb. nov., *S. litterata* (Lamarck, 1811)<sup>1</sup>, *S. luctuosa* (A. Adams, 1853)<sup>1</sup>, *S. lugubris* (Swainson, 1821)<sup>1</sup> comb. nov., *S. nanus* (Reeve, 1844)<sup>3</sup> comb. nov., ***S. paupercula* (Linnaeus, 1758)**<sup>1</sup>, *S. pica* (Dillwyn, 1817)<sup>3</sup>, *S. retusa* (Lamarck, 1811)<sup>3</sup>, *S. scutulata* (Gmelin, 1791)<sup>1</sup> comb. nov., *S. subruppeli* (Finlay, 1927)<sup>3</sup> comb. nov., *S. telescopium* (Reeve, 1844)<sup>3</sup>, *Mitra testacea* Broderip, 1836<sup>3</sup> comb. nov., *S. ticaonica* (Reeve, 1844)<sup>3</sup> comb. nov., *S. tristis* (Broderip, 1836)<sup>1</sup>, *S. vexillum* (Reeve, 1844)<sup>1</sup>, *S. vultuosa* (Reeve, 1845)<sup>3</sup> comb. nov., ?*S. coffea* (Schubert & J. A. Wagner, 1829)<sup>2</sup> comb. nov., ?*S. pudica* (Pease, 1860)<sup>2</sup>, ?*S. tabida* (Herrmann & Salisbury, 2013)<sup>3</sup> comb. nov.

*Remarks.* The sculpture of strong rounded cords of some species of the *Strigatella* clade may lead to a wrong generic allocation; for instance, Cernohorsky (1976) placed *S. vexillum*, *S. aurantia*, *S. lugubris* and even *S. fulvescens* in *Nebularia*, whereas our phylogenetic analysis unequivocally places them in *Strigatella*.

There are three conchologically more or less distinct groups of *Strigatella*, (1) a *S. paupercula* group with typical broadly fusiform *Strigatella* shell, (2) a *S. fulvescens* group with more elongate shell, distinctly recurved siphonal canal and lack of inner callous varix on the outer aperture lip, and (3) a *S. coronata* group with a fusiform shell also lacking a callous varix on the outer aperture lip, and also distinguished by a uniserial radula. *S. coronata* and *S. lugubris* forms a very distinct clade in our phylogenetic tree, and the name *Chrysame* is available for it. Given its distinctive morphology and its long branch on the molecular tree, the *Strigatella coronata* group could be treated as a subgenus of *Strigatella*. However we prefer to abstain from recognizing *Chrysame*, as it would necessitate to also recognize as subgenera the other two *Strigatella* groups - a level of taxonomic splitting that we are not currently prepared to defend.

Subfamily **Imbricariinae** Troschel, 1867

(Figs 24 – 30)

**Genus *Imbricaria* Schumacher, 1817** (Figs 24, 25 A – H)

*Type species: Imbricaria conica* Schumacher, 1817 [unnecessary substitute name for *Mitra conularis* Lamarck, 1811]; M.

*Synonym: Conoelix* Swainson, 1821. *Type species: Conoelix lineatus* Swainson, 1821 [= *Mitra conularis* Lamarck, 1811]; OD.

*Diagnosis:* Shell small to medium-sized (10-55 mm), fusiform, narrowly biconical to nearly conical, uniformly coloured or with variegated pattern. Protoconch narrowly conical, of 3+ slightly convex or flattened, smooth and glossy whorls. Early teleoconch whorls forming narrowly conical apex; later whorls widening at equal rate, resulting in fusiform or biconical shell, or (typically) at increasing rate, resulting in acuminate spire and slightly inflated or conical last adult whorl. Early spire whorls sculptured with rounded spiral cords; late whorls smooth or with spiral cords, the latter wide and rounded or fine and sharp, sometimes bearing regular tubercles. Interspaces between cords smooth or with fine, dense riblets. Siphonal canal tapering, with distinct siphonal notch. Aperture elongate, narrow to slit-like. Outer apertural lip convex in its adapical portion; inner lip with 4-5 fine columellar folds gradually diminishing towards siphonal canal. Rachidian with 4-7 cusps, with 1-2 marginal pairs of cusps notably weaker than the 2 or 3 medial cusps; unpaired central cusp when present equal or weaker than 2 flanking cusps (Fig 25 A – H). Lateral teeth broad, with 7-12 triangular or spindle-like, long and pointed subequal cusps, gradually increasing in size towards rachidian, with one cusp strongest, sometimes very long, greatly exceeding others, resembling a tin opener (Figs 25 D – F).

*Distribution:* Indo-Pacific, intertidal to bathyal depths, mostly on soft bottoms, mud, silty or well washed sand.

*Species included:* *Imbricaria amoena* (A. Adams, 1853)<sup>3</sup> comb. nov., *I. annulata* (Reeve, 1844)<sup>3</sup> comb. nov., *I. armonica* (T. Cossignani & V. Cossignani, 2005)<sup>3</sup> comb. nov., *I. astyagis* (Dohrn, 1860)<sup>3</sup> comb. nov., *I. bacillum* (Lamarck, 1811)<sup>3</sup> comb. nov., *I. baisei* (Poppe, Tagaro & Salisbury, 2009)<sup>3</sup> comb. nov., *I. bantamensis* (Oostingh, 1939)<sup>1</sup> comb. nov., *I. bellulavaria* (Dekkers, Herrmann, Poppe, Tagaro, 2014)<sup>3</sup> comb. nov., *I. cernohorskyi* (Rehder & Wilson, 1975)<sup>3</sup> comb. nov., *I. cloveri* (Cernohorsky, 1971)<sup>3</sup> comb. nov., ***I. conularis* (Lamarck, 1811)**<sup>1</sup>, *I. flammea* (Quoy & Gaimard, 1833)<sup>3</sup> comb. nov., *I. flammigera* (Reeve, 1844)<sup>1</sup> comb. nov., *I. fulgetrum* (Reeve, 1844)<sup>1</sup> comb. nov., *I. hrdlickai* (Salisbury, 1994)<sup>1</sup> comb. nov., *I. insculpta* (A.

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2 Adams, 1851)<sup>1</sup> comb. nov., *I. interlirata* (Reeve, 1844)<sup>2</sup> comb. nov., *I. nadayaoi* (Bozzetti,  
3 1997)<sup>3</sup> comb. nov., *I. philpoppei* (Poppe, Tagaro & Salisbury, 2009)<sup>3</sup> comb. nov., *I. pretiosa*  
4 (Reeve, 1844)<sup>2</sup> comb. nov., *I. pugnaxa* (Poppe, Tagaro & Salisbury, 2009)<sup>1</sup> comb. nov., *I.*  
5 *rufilirata* (Adams & Reeve, 1850)<sup>3</sup> comb. nov., *I. ruberorbis* (Dekkers, Herrmann, Poppe,  
6 Tagaro, 2014)<sup>3</sup> comb. nov., *I. rufogyrata* (Poppe, Tagaro & Salisbury, 2009)<sup>1</sup> comb. nov., *I.*  
7 *salisburyi* (Drivas & Jay, 1990)<sup>2</sup> comb. nov., *I. tahitiensis* (Herrmann & Salisbury, 2012)<sup>3</sup>  
8 comb. nov., *I. verrucosa* (Reeve, 1845)<sup>1</sup> comb. nov., *I. yagurai*, (Kira, 1959)<sup>1</sup> comb. nov., *I.*  
9 *zetema* (Dekkers, Herrmann, Poppe & Tagaro, 2014)<sup>3</sup> comb. nov.

16  
17 *Remarks.* The genus *Imbricaria* is, in the present classification, undergoing a dramatic  
18 rearrangement: whereas species traditionally classified in *Imbricaria*, like *I. punctata* and *I.*  
19 *olivaeformis*, that are conchologically close to *I. conularis*, are excluded from the genus,  
20 numerous Indo-Pacific species earlier assigned to *Ziba* and *Subcancilla* are now transferred to  
21 *Imbricaria*.

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25 As circumscribed here, *Imbricaria* appears rather heterogeneous morphologically, with  
26 shell varying from conical to narrowly-fusiform, most species having a notably higher spire than  
27 *I. conularis*. Shell sculpture may be faint, like in the type species, or represented by strong  
28 elevated cords, and depressions between cords are often sculptured with dense riblets. Moreover,  
29 species of *Imbricaria* display a remarkable disparity in radular morphology, as seen in the degree  
30 of cusp differentiation in both the rachidian and lateral teeth. In this respect, the eight studied  
31 species form a continuous grade from radulae with subequal cusps (presumably a plesiomorphic  
32 state, found in *I. conularis* and *I. pugnaxa* - see Discussion) to more derived ones with one or  
33 two cusps on each tooth greatly exceeding the others.  
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#### 43 **Genus *Cancilla* Swainson, 1840** (Figs 25 I – M, 26)

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45 *Type species:* *Mitra isabella* Swainson, 1831; SD, Herrmannsen (1846: 166).

46  
47 *Diagnosis:* Shell small to rather large (15-110 mm), fusiform, with high aperture and long,  
48 tapering siphonal canal. Protoconch conical, of about 3 very slightly convex smooth whorls.  
49 Spire whorls evenly convex to subcylindrical; suture distinct, impressed. Shell sculptured with  
50 spiral cords that are slightly gemmate or with finely dentate margins, very wide and flat,  
51 separated by narrow grooves, or with strong, narrow and elevated cords separated by broad  
52 depressions bearing regular, very fine riblets. Shell base gradually extended into rather long,  
53 tapering siphonal canal. Siphonal fasciole not pronounced, notch deep or shallow. Aperture  
54 elongate, narrow; outer aperture lip smooth, gently convex apically, and flattened in its lower  
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portion. Inner lip with four oblique columellar folds, adapicalmost strongest. Shell pale or cream, typically with multiple darker spiral strokes on crests of spiral cords. Radula with narrow rachidian, usually bearing four cusps, of which central pair notably stronger (Figs 25 I – M). Lateral teeth with 7-10 pointed triangular cusps, second proximal cusp greatly exceeding others, and subsequently gradually weakening towards margins of radula.

*Distribution:* Indo-Pacific, bathyal depths, mostly on mud.

*Species included:* *Cancilla baeri* (Turner & Cernohorsky, 2003)<sup>1</sup>, *C. fibula* Poppe, Tagaro & Salisbury, 2009<sup>1</sup>, *C. heinickei* (Salisbury & Guillot de Suduiraut, 2003)<sup>3</sup> comb. nov., *C. herrmanni* Dekkers, 2014<sup>3</sup>, *C. isabella* (Swainson, 1831)<sup>2</sup>, *C. liliformis* Huang & Salisbury 2017<sup>3</sup>, *C. rehderi* (Webb, 1958)<sup>1</sup>, *C. schepmani* (Salisbury & Guillot de Suduiraut, 2003)<sup>1</sup> comb. nov., *C. turneri* Poppe, Tagaro & Salisbury, 2009<sup>3</sup>.

*Remarks.* The typification of *Cancilla* renders the identity of the genus a little weak: the specimen of *Mitra isabella* originally illustrated by Swainson (1831) was selected as lectotype by Cernohorsky (1991), but, like many types of Swainson relevant to this study, this specimen is lost (Cernohorsky, 1991). Taking in consideration frequent parallelisms in shell morphology demonstrated in Mitridae, the utility of Swainson's original illustration for taxonomic decisions is limited and it will be desirable in the future to designate a neotype with associated molecular data.

The radula of *C. isabella* was studied by Salisbury and Huang (2015). Although the two specimens dissected by these authors differ notably in shell proportions, their radulae are morphologically close to each other, and rather peculiar. The rachidian bears two pairs of long pointed cusps (the lateral cusps being notably weaker than the central ones), flanked by two pairs of very weak cusps; the laterals bear long pointed cusps that progressively increase in size towards tooth mid-width, whereas the distal halves bear no cusps and show only weak serration (Salisbury & Huang 2015: figs 1.1, 3.2), a pattern comparable to the laterals in *Scabricola*, which are however still more robust.

Of all *Cancilla* species studied by us, *C. baeri* is probably closest to *C. isabella*: the specimen of *C. baeri* MNHN IM-2013-58853 (Fig. 26 A) resembles one of the two specimens of *C. isabella* studied by Salisbury and Huang (2015: fig. 3.2b) in shell proportions, whorl outline and shape of the siphonal canal. The other studied *Cancilla* species - the *C. rehderi* – *C. fibula* complex and *C. schepmani* - are generally smaller, with less convex whorls and stouter siphonal canal, which is not clearly delineated from the shell base. Therefore, the genus *Cancilla*, as we



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2 circumscribe it, is rather heterogeneous, and can be subdivided by shell morphology into two  
3 conventional groups: ‘robust’ *Cancilla* with species, such as *C. isabella*, *C. baeri*, and *C. chuo*,  
4 and ‘slender’ *Cancilla*, with species like *C. fibula*, *C. rehderi*, *C. schepmani* and *C. liliformis*.  
5 The relationships of these two conchological groups is supported by a) inclusion of *C. baeri* in  
6 the *Cancilla* clade (clade 24-7) in the COI based tree, and b) occurrences of very similar radular  
7 morphologies in ‘slender’ species of the *C. fibula* – *C. rehderi* complex (Figs 25 I, K) and in  
8 ‘robust’ *C. baeri* IM-2013-58853 (Fig. 25 L). It should be noted, however, that the radula of *C.*  
9 *schepmani* (Fig. 25 M), with a morphology closest to the radulae of *Strigatella* or of the mitrine  
10 *Neotiara nodulosa* (Fig. 10 E), is thoroughly different from the radulae of other studied *Cancilla*  
11 species. Therefore, *Cancilla* appears to be very heterogeneous in radular morphology as well.  
12 Taking into account this observed radular disparity among sequenced (and thus confirmed  
13 related) *Cancilla* species, we believe that the divergent radular morphology of *Cancilla isabella*  
14 does not contradict its affinity to the other species studied herein.

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16 Species of *Domiporta*, can be distinguished from the ‘robust’ *Cancilla* species by the  
17 sculpture pattern with narrow, elevated, widely interspaced spiral cords, whereas a distinct  
18 concavity at the transition of shell base to siphonal canal distinguishes species of *Domiporta*  
19 from ‘slender’ *Cancilla* species. Moreover, the two genera differ greatly in radular morphology.  
20 Besides, there is a clear resemblance between some species of *Imbricaria* and ‘slender’ *Cancilla*:  
21 *I. fulgetrum* and *C. rehderi / fibula* (especially our immature specimen IM-2013-19073) or the *I.*  
22 *yagurai* group and *C. cf. fibula* (represented by IM-2013-40646). In these pairs, the species of  
23 *Cancilla* can be recognized by the more convex outline of the shell base, which gives the shell a  
24 rather fusiform shape compared to the rather biconical shell of *Imbricaria*. The new genus  
25 *Cancillopsis* can be differentiated from the ‘robust’ *Cancilla* species by the higher spire with  
26 rather subcylindrical whorls, and from the ‘slender’ *Cancilla* species by the presence of a  
27 concavity at the base of the siphonal canal. Finally, the radula with rachidian and lateral teeth of  
28 similar morphology differentiates *Profundimitra* n. gen. and *Fusidomiporta* n. gen. from  
29 *Cancilla*.

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48 **Genus *Imbricariopsis* Fedosov, Herrmann, Kantor & Bouchet, n. gen.** (Figs 27, 28 A)

49 *Type species: Conoelix punctatus* Swainson, 1821; OD, herein.

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51 *Diagnosis:* Shell small (10-20 mm), conical, uniformly pale or with dark tip of siphonal canal.  
52 Protoconch pointed multispiral, narrowly conical, dark. Suture distinct, impressed. Spire very  
53 short, less than 20% of total shell height, conical or distinctly acuminate, starting with several  
54 subcylindrical whorls. Last adult whorl very tall, sculptured with regular, distinctly punctate,  
55 spiral grooves. Siphonal notch shallow or moderately deep. Aperture very tall and narrow, slit-

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2 like. Outer aperture lip thick, flattened, smooth inside; inner lip with five fine oblique folds  
3 situated on abapical portion of columella. Radula triserial; rachidian with six cusps, paired  
4 central cusps greatly exceeding those situated laterally (Fig. 28 A). Lateral teeth with five cusps,  
5 second cusp from rachidian very robust, notably exceeding the others.  
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10 *Distribution*: Indo-Pacific, intertidal and upper subtidal depths, on sand patches and in reef  
11 crevices.  
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15 *Species included*: *Imbricariopsis conovula* (Quoy & Gaimard, 1833)<sup>2</sup> comb. nov., *I. punctata*  
16 (Swainson, 1821)<sup>1</sup> comb. nov., *I. vanikorensis* (Quoy & Gaimard, 1833)<sup>2</sup> comb. nov., ?*I.*  
17 *carbonacea* (Hinds, 1844)<sup>3</sup> comb. nov.  
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22 *Etymology*: The name *Imbricariopsis* reflects the resemblance of the species in this newly  
23 recognized lineage with the type species of *Imbricaria*, *I. conularis*, that has long distracted  
24 mitrid taxonomists. Gender feminine.  
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29 *Remarks*. Few mitrids are characterized by an almost involute conical shell, and these were  
30 formerly allocated to either *Imbricaria* or *Pterygia*. However, we found *Imbricaria* as  
31 traditionally construed to be paraphyletic, with *Imbricaria punctata* forming a lineage of its own,  
32 not closely related to *I. conularis*. Although a single species has been sequenced, we hypothesize  
33 a close relationship between *Imbricaria punctata*, *I. conovula* and *I. vanikorensis*, largely based  
34 on shell characters. *Imbricariopsis* n. gen., as we circumscribe it, constitutes a rather distinctive  
35 group of small shallow water mitrids: species of *Imbricariopsis* can be recognized by conical,  
36 weakly sculptured, or not sculptured at all, pale shells with a minute, pointed apex (that is much  
37 lower than in *Imbricaria conularis*). The radulae of the three species that we assign to  
38 *Imbricariopsis* n. gen. were illustrated by Cernohorsky (1970) and are again figured here; all  
39 three share the same general morphology of lateral radular teeth, with one robust major and  
40 several minor cusps situated on both sides of the major one.  
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49 The enigmatic West African *Mitra carbonacea* Hinds, 1844 resembles species of  
50 *Imbricariopsis* n. gen. in overall shell morphology, and may prove to be related to this genus.  
51 However, given the disparity in geographical distribution, we place this species in *Imbricariopsis*  
52 n. gen. with a question mark, pending future studies. Minor differences in the position of the  
53 columellar folds (situated in the abapical portion of the columella in *Imbricariopsis* and at mid-  
54 height in *M. carbonacea*) may hint at a not-so-close relationship.  
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Cernohorsky (1970) highlighted the notable resemblance of the Upper Cretaceous “*Imbricaria*” *conoidea* (Matheron, 1843) with Recent *Imbricaria* species, in particular, *I. conularis*; based on this resemblance, he placed *conoidea* in *Imbricaria*, although in a separate subgenus *Sohlia*. According to Cernohorsky (1970), “*I.*” *conoidea* is the earliest known fossil *Imbricaria* (as circumscribed by him), although it shows some differences to the Recent members of that genus, in particular the presence of only few columellar folds that are “placed rather low on columellar pillar” (Cernohorsky 1970: 44). Noteworthy, the columellar folds, despite numbering five in *Imbricariopsis* n. gen., are also positioned anteriorly, whereas the species of *Imbricaria* (as circumscribed herein), are characterized by columellar folds set at mid-height of columella. This may indicate that species of *Imbricariopsis* n. gen. are in fact the closest living relatives of the ancient “*Imbricaria*” *conoidea*, which agrees with the rather underived position of *Imbricariopsis* n. gen. in the imbricariine segment of the mitrid tree.

**Genus *Scabricola* Swainson, 1840** (Figs 28 D – F, 29 A – F)

*Type species: Mitra serpentina* Lamarck, 1811 [= *Voluta variegata* Gmelin, 1791]; SD, Gray (1847: 141).

*Diagnosis:* see under Remarks.

*Distribution:* Indo-Pacific, upper subtidal depths, on sand.

*Species included:* *Scabricola bicolor* (Swainson, 1824)<sup>3</sup>, *S. desetangsii* (Kiener, 1838)<sup>1</sup>, *S. olivaeformis* (Swainson, 1821)<sup>1</sup>, *S. padangensis* (Thiele, 1925)<sup>2</sup>, ***S. variegata* (Gmelin, 1791)<sup>1</sup>**, ?*Scabricola barrywilsoni* (J. Cate, 1968)<sup>3</sup>, ?*S. albina* A. Adams, 1853<sup>3</sup>, ?*S. caerulea* (Reeve, 1844)<sup>3</sup>, ?*S. condei* Guillot de Suduiraut, 2001<sup>3</sup>, *S. coriacea* (Reeve, 1845)<sup>2</sup>, ?*S. dampierensis* Salisbury & Heinicke, 1998<sup>3</sup>, *S. dianneae* (Salisbury & Guillot de Suduiraut, 2003)<sup>3</sup> comb. nov., ?*S. eximia* (A. Adams, 1853)<sup>3</sup>, ?*S. geigeri* Poppe, Tagaro & Salisbury, 2009<sup>3</sup>, ?*S. gilbertsoni* (Cate, 1968)<sup>3</sup> comb. nov., ?*S. guttata* (Swainson, 1824)<sup>3</sup> comb. nov., ?*S. hayashii* (Kira, 1959)<sup>3</sup>, ?*S. ivanmorrowi* Marrow, 2016<sup>3</sup>, ?*S. lavoisieri* Guillot de Suduiraut, 2002<sup>3</sup>, ?*S. lorenzi* (Poppe & Tagaro, 2006)<sup>3</sup> comb. nov., ?*S. mariae* (A. Adams, 1853)<sup>3</sup>, ?*S. martini* Poppe & Tagaro, 2006<sup>3</sup>, ?*S. petiti* Poppe & Tagaro, 2006<sup>3</sup>, ?*S. parkinsoni* Salisbury & Wolff, 2005<sup>3</sup>, ?*S. potensis* (Montrouzier, 1858)<sup>3</sup>, ?*S. sowerbyi* d'Orbigny, 1852<sup>3</sup>, ?*S. splendidula* Salisbury & Guillot de Suduiraut, 2003<sup>3</sup>, ?*S. vicdani* Cernohorsky, 1981<sup>3</sup>, ?*S. yaekoae* (Habe & Kosuge, 1966)<sup>3</sup>.

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*Remarks.* The genus *Scabricola* as commonly understood is extremely heterogeneous. It combines such dissimilar forms as *Scabricola yaekoa*, which in shell outline is close to *Mitra mitra*, and *S. potensis* (Montrouzier, 1858), with its ovate shell resembling species of *Pterygia*. The range of sculpture patterns is equally considerable: whereas most species of *Scabricola* are characterized by wide and low cords or punctate grooves, some (e.g., *Scabricola padangensis*) have a "Subcancilla-type" sculpture pattern (Cernohorsky, 1991) of narrow, high cords, and still others, like *S. coriacea*, show a distinctly crenulated sculpture. In the treatment of Cernohorsky, the more slender species of *Scabricola*, with weaker sculpture, were separated in the subgenus *Scabricola (Swainsonia)*. It should be noted, though, that the boundaries of the two subgenera appear blurred, primarily because *S. variegata* (the type species of *Scabricola*) is conchologically closer to *Swainsonia* than to many species of *Scabricola (Scabricola)*. One of the important diagnostic characters of *Scabricola* is the morphology of the radula lateral teeth, unique for the Mitridae, "with 3-5 strong cusps on the inward facing angular plate" (Cernohorsky, 1991: 115) (Figs 28 D – *S. variegata*). This radular morphology is shared by seven species of *Scabricola (Scabricola)* and *Scabricola (Swainsonia)* studied by Cernohorsky (1970), whereas radulae with divergent morphologies are found in *S. desetangsii* (Fig. 28 E) and *S. coriacea* (Cernohorsky, 1970, fig. 120): the former has unicuspidate laterals, the latter lacks the major cusp on laterals which, therefore, have a somewhat intermediate morphology between typical *Scabricola* and *Neocancilla*.

Because the boundaries of the genus remain poorly understood, we are only confident about the placement of those species for which molecular and radular morphology data are available, and the remaining species are placed in *Scabricola* with a question mark. Given this major uncertainty on its contents, we refrain from giving a formal diagnosis of the genus.

**Genus *Swainsonia* H. Adams & A. Adams, 1853** (Figs 28 B, C, 29 G – I)

*Type species:* *Mitra fissurata* Lamarck, 1811; by typification of replaced name [*Mitrella* Swainson, 1831 non Risso, 1826].

*Synonym:* *Mitrella* Swainson, 1831 (not Risso, 1826); *Type species:* *Mitra fissurata* Lamarck, 1811; SD, Cossmann (1899: 152).

*Diagnosis:* Shell small to medium-sized (15-65 mm), fusiform or elongate biconical, weakly sculptured and often polished in appearance. Protoconch narrowly-conical, of about three smooth, weakly convex, whorls. Spire ortho- or cyrtconoid, spire whorls evenly convex to flattened; suture distinct, impressed. Sculpture of regular, shallow, and widely spaced punctate spiral grooves, either covering the entire shell surface, or limited to the adapical whorl portion,

1 or lacking entirely. Axial sculpture usually not developed or, when present, consisting of  
2 numerous, fine, and low, rounded folds, developed on the spire but indistinct on the periphery of  
3 the last adult whorl. Shell base typically with convex outline, continuing into short and stout,  
4 deeply notched, siphonal canal. Siphonal fasciole indistinct or moderately developed. Aperture  
5 elongate, narrow to moderately wide. Outer aperture lip straight or gently evenly convex  
6 adapically; anterior edge of outer lip strongly convex, sometimes slightly drawn abapically.  
7 Inner lip with 4-5 fine or strong, subequal columellar folds. Shell light brown, orange, or white,  
8 typically with intricate scale-like pattern of fine light or white lines. *Scabricola*-type radula with  
9 comb-like rachidian bearing six long, slender cusps, the four central ones notably exceeding the  
10 two marginal ones (Figs 28 B, C). Lateral teeth with very strong, robust cusp, giving tooth the  
11 appearance of a tin-opener, the serrate inner surface of tooth bearing 3-4 weaker cusps. Base of  
12 laterals with curved upper margin, forming a socket interlocking laterals of adjacent rows.  
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23 *Distribution*: Indo-Pacific, upper subtidal depths, on sand.  
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26 *Species included*: *Swainsonia biconica* Bozzetti, 2011<sup>3</sup>, *S. casta* (Gmelin, 1791)<sup>1</sup>, ***S. fissurata***  
27 **(Lamarck, 1811)**<sup>2</sup>, *S. fusca* (Swainson, 1824)<sup>1</sup>, *S. newcombii* (Pease, 1869)<sup>3</sup>, *S. ocellata*  
28 (Swainson, 1831)<sup>3</sup>.  
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33 *Remarks*. Many contemporary authors have treated *Swainsonia* as a subgenus of *Scabricola*  
34 (Cernohorsky 1970; 1991; Pechar, Prior & Parkinson 1980; but see Poppe & Tagaro 2008), but  
35 our results indicate that it should be elevated to full genus. This treatment of *Scabricola* and  
36 *Swainsonia*, however, contradicts the phylogenetic hypothesis implied by radular morphology.  
37 The typical *Scabricola* radula (as described by Cernohorsky 1970) is present in *Scabricola*  
38 *variegata*, *Swainsonia fusca* and *Swainsonia casta*, while the radulae of *Scabricola desetangsii*  
39 and *S. olivaeformis* show a divergent morphology.  
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49 **Genus *Neocancilla* Cernohorsky, 1966** (Figs 28 G – I, 30)

50 *Type species*: *Voluta papilio* Link, 1807; OD.

51 *Diagnosis*: Shell small to medium-sized (10-65 mm), fusiform, with short and stout siphonal  
52 canal. Protoconch pointed, narrowly conical, of about 3 slightly convex glossy whorls. Suture  
53 deeply impressed to canaliculate. Spire orthoconoid, teleoconch whorls evenly convex. Sculpture  
54 of wide spiral cords, low or slightly elevated adapically, or bearing rows of fine beads. Spiral  
55 cords separated by narrow deep groves and intersected by axial riblets of similar strength,  
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1 forming regular cancellate sculpture. Siphonal canal short and robust, gradually merging to shell  
2 base, although separated from it by narrow depression at about the level of the second columellar  
3 fold. Siphonal notch deep. Aperture elongate; outer aperture lip evenly convex along most of its  
4 length. Inner aperture lip with four strong columellar folds, adapicalmost strongest. Shell cream,  
5 pale or orange, usually with contrasting darker bands. Radula with narrow rachidian bearing six  
6 blunt, very robust cusps; paired central cusps greatly exceeding the others (Figs 28 G – I).  
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8 Lateral teeth with four or five very short and blunt cusps situated proximally, distal portions of  
9 teeth without cusp.  
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17 *Distribution:* Indo-Pacific, intertidal and upper subtidal depths, mostly on sand.  
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20 *Species included:* *Neocancilla antoniae* (H. Adams, 1870)<sup>3</sup>, *N. arenacea* (Dunker, 1852)<sup>3</sup>, *N.*  
21 *clathrus* (Gmelin, 1791)<sup>1</sup>, *N. hartorum* Poppe, Salisbury, Tagaro, 2015<sup>3</sup>, *N. hemmenae*  
22 (Salisbury & Heinicke, 1993)<sup>3</sup>, *N. kayae* Cernohorsky, 1978<sup>3</sup>, *N. madagaskarensis* Herrmann,  
23 2017<sup>3</sup>, *N. papilio* (Link, 1807)<sup>1</sup>, *N. rufescens* (A. Adams, 1853)<sup>1</sup>, *N. takiisaoi* (Kuroda, 1959)  
24 <sup>2</sup>, *N. waikikiensis* (Pilsbry, 1921)<sup>2</sup>.  
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30 *Remarks.* The genus *Neocancilla* is one of the few lineages the composition of which is left  
31 rather unchanged after our phylogenetic analysis. The group is well delineated thanks to the  
32 characteristic shell and conservative radular morphology. The radula of the West African  
33 "*Neocancilla*" *hebes* depicted by Cernohorsky (1991) rather resembles the radula of  
34 Strigatellinae, and led Cernohorsky to question the relation of that species to the Indo-Pacific  
35 *Neocancilla*. Here we remove this species from *Neocancilla* and provisionally place it in  
36 *Domiporta*.  
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42 Species of *Domiporta* are closest to *Neocancilla* primarily because of similar shell  
43 proportions and sculpture pattern. Species of *Neocancilla*, however, can be distinguished by the  
44 shell base and siphonal canal, which form a continuous, usually slightly convex, outline with no  
45 concave waist. Besides, there are consistent differences between the two genera in radular  
46 morphology: in *Neocancilla* the radula has few short, blunt and robust cusps on the rachidian and  
47 laterals, while in *Domiporta* the rachidian and laterals bear multiple pointed cusps that are not  
48 differentiated in size or shape. The *Scabricola* – *Swainsonia* grade is closely related to  
49 *Neocancilla*, and the species of these three genera are conchologically similar. However, shells  
50 of *Scabricola* and *Swainsonia* can be differentiated by a notably weaker sculpture, with no or  
51 very weak axial elements; besides, most species of *Scabricola* are wider, with a higher last adult  
52 whorl compared to *Neocancilla*.  
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Subfamily **Cylindromitrinae**

(Figs 31 – 33)

**Genus *Pterygia*** Röding, 1798 (Figs 31, 32 A – C)*Type species: Voluta dactylus* Linnaeus, 1767; SD, Dall (1915: 52).*Synonym: Cylindromitra* P. Fischer, 1884. Type species: *Cylindra coronata* Schumacher, 1817 [objective synonym of *Voluta crenulata* Gmelin, 1791]; by typification of replaced name [*Cylindra* Schumacher, 1817, non Illiger, 1802; itself by M].*Diagnosis:* Shell small to medium-sized (20-70 mm), ovate or ovate-elongate, with very low spire and tall aperture. Protoconch cyrtocoid, with about 3 smooth evenly convex whorls. Spire height attaining only about 10-15% of total shell height, with only 3-4 whorls exposed, and a proportionally very high last adult whorl. Suture adpressed. Last adult whorl convex or strongly convex, smooth or with dominating spiral or cancellate or crenulate sculpture. Spiral elements represented by fine grooves or cords that can be fine or wide, undulating, rounded or resembling scales tiling in posterior direction. Siphonal notch distinct. Aperture elongate, usually narrow. Outer aperture lip convex, smooth or denticulate, inner lip calloused, bearing 6-8 subequal columellar folds. Shell off-white, whitish or brownish, or with a pattern of red or orange bands. Radula very narrow, consisting of rachidian only, bow shaped, bearing multiple cusps, or with a single blunt medial cusp and lateral serration (Figs 32 A – C).*Distribution:* Indo-Pacific, subtidal, mostly on coral rubble, one species occurs on mud.*Species included:* *Pterygia arctata* (G. B. Sowerby II, 1874)<sup>3</sup>, *P. conus* (Gmelin, 1791)<sup>3</sup>, *P. crenulata* (Gmelin, 1791)<sup>2</sup>, *P. dactylus* (Linnaeus, 1767)<sup>1</sup>, *P. fenestrata* (Lamarck, 1811)<sup>1</sup>, *P. gorii* (Turner, 2007)<sup>3</sup>, *P. japonica* Okutani & Matsukuma, 1982<sup>3</sup>, *P. jeanjacquesi* Bozzetti, 2010<sup>3</sup>, *P. nucea* (Gmelin, 1791)<sup>2</sup>, *P. purtymuni* Salisbury, 1998<sup>3</sup>, *P. scabricula* (Linnaeus, 1767)<sup>3</sup>, *P. sinensis* (Reeve, 1844)<sup>1</sup>, *P. undulosa* (Reeve, 1844)<sup>3</sup>.*Remarks.* The genus *Pterygia* is morphologically distinctive thanks to its ovate shell with multiple columellar folds, and monoserial radula. In the present study we leave the contents of the genus unchanged; however, some species currently classified in other genera (for example, *Scabricola potensis*) may actually belong to *Pterygia*. Conical shells resembling those of *Pterygia* are found in *Imbricaria* and *Imbricariopsis* n. gen., which are however phylogenetically very distant from *Pterygia*, and are characterized by a triserial radulae.

**Genus *Nebularia* Swainson, 1840** (Figs 32 D – F, 33)

*Type species: Mitra contracta* Swainson, 1820; SD, Herrmannsen (1847: 110).

*Synonyms: Dibaphus* Philippi, 1847. Type species: *Mitra edentula* Swainson, 1823; M.

*Mutyca* H. Adams & A. Adams, 1853. Type species: *Mitra ancillides* Broderip, 1836; SD, Wenz (1943: 1296).

*Mitroidea* Pease, 1865. Type species: *Mitroidea multiplicata* Pease, 1865; M.

?*Mauritia* H. Adams, 1869. Type species: *Mauritia barclayi* H. Adams, 1869; M.

*Diagnosis:* Shell small to large (15-150 mm), fusiform to elongate fusiform. Protoconch pointed, narrowly-conical, of 3+ slightly convex, smooth and glossy whorls. Teleoconch whorls usually flattened in outline, with orthoconoid or acuminate spire. Sculpture variable, from indistinct to strong and deep grooves separating flattened or rounded, sometimes undulating, cords. Siphonal canal robust, short to moderately long, sometimes with distinct fasciole, giving siphonal canal a recurved appearance. Aperture elongate, its outer lip often thickened in its adapical portion. Margin of outer lip smooth or bearing fine denticles throughout its length. Inner lip with 4-5 delicate folds of subequal strength. Shell pale, usually with a pattern of brown bands and blotches. Radula triserial, with narrow rachidian and laterals of varying width. Rachidian with five cusps of which a central unpaired cusp greatly exceeds the others in strength (Figs 32 D – F). Laterals bearing 6-12 cusps, 2nd-4th from rachidian cusp being strongest, and succeeding ones gradually diminishing.

*Distribution:* Indo-Pacific, intertidal and upper subtidal depths, rocky shores and reef crevices.

*Species included:* *Nebularia acuminata* (Swainson, 1824)<sup>1</sup> comb. nov., *N. aegra* (Reeve, 1845)<sup>3</sup> comb. nov., *N. ancillides* (Broderip, 1836)<sup>3</sup> comb. nov., *N. baerorum* (Poppe & Tagaro, 2010)<sup>3</sup>, *N. bellula* (A. Adams, 1853)<sup>3</sup> comb. nov., *N. chrysostoma* (Broderip, 1836)<sup>3</sup>, *N. coarctata* (Reeve, 1844)<sup>3</sup>, *N. contracta* (Swainson, 1820)<sup>1</sup>, *N. deynzeri* (Cernohorsky, 1980)<sup>3</sup> comb. nov., *N. dondani* (Cernohorsky, 1985)<sup>3</sup> comb. nov., *N. edentula* (Swainson, 1823)<sup>3</sup> comb. nov., *N. eremitarum* (Röding, 1798)<sup>1</sup> comb. nov., *N. fastigium* (Reeve, 1845)<sup>3</sup> comb. nov., *N. ferruginea* (Lamarck, 1811)<sup>2</sup>, *N. gourgueti* (Poppe, Salisbury, Tagaro, 2015) comb. nov., *N. guidopoppei* (Thach, 2016)<sup>3</sup> comb. nov., *N. incompta* (Lightfoot, 1786)<sup>1</sup> comb. nov., *N. inquinata* (Reeve, 1844)<sup>3</sup>, *N. multiplicata* (Pease, 1865)<sup>3</sup> comb. nov., *N. nebulosa* (Broderip, 1836)<sup>3</sup> comb. nov., *N. nivea* (Broderip, 1836)<sup>3</sup> comb. nov., *N. pellisserpentis* (Reeve, 1844)<sup>3</sup> comb. nov., *N.*



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2 *pyramis* (Wood, 1828)<sup>3</sup>, *N. semperi* (Poppe, Tagaro & Salisbury, 2009)<sup>3</sup> comb. nov., *N. thachi*  
3 (Turner, 2007)<sup>3</sup>, *N. ustulata* (Reeve, 1844)<sup>3</sup> comb. nov.  
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7 *Remarks.* Our phylogenetic analysis has led to a considerable rearrangement of the genus  
8 *Nebularia*. The "lesser" *Nebularia* species (*N. fraga* and *N. tornata* groups) appeared unrelated  
9 to the true *Nebularia* typified by *N. contracta*. On the other hand, some large *Mitra* species (*M.*  
10 *incompta*, *M. eremitarum*) showed a close affinity to *N. contracta*, and so did '*Strigatella*'  
11 *acuminata*. The genus *Nebularia*, as circumscribed herein, is supported by several distinctive  
12 morphological shell (colour pattern, a subsuturally thickened outer aperture lip, and an often  
13 recurved tip of the siphonal canal) and radula characters (a very strong unpaired central cusp on  
14 the rachidian). The same features characterize a number of species classically included in *Mitra*  
15 (*M. ancillides*, *M. coarctata*, *M. edentula*, *M. ferruginea*, *M. nebulosa*, *M. nivea*, *M. ustulata*),  
16 which we thus classify in *Nebularia*. As a consequence, we also consider the nominal genera  
17 *Dibaphus*, *Mitroidea* and *Mutyca* to be synonyms of *Nebularia*. Both shell proportions and  
18 development of sculpture vary considerably among the species of *Nebularia*, the two extremes  
19 being *N. incompta* (Fig. 33 D) and *N. ancillides* (Fig. 33 G). An even more cylindrical shell  
20 characterizes *Mauritia barclayi*, which we tentatively place in *Nebularia* as well.  
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### 33 **Subfamily Isarinae Fedosov, Herrmann, Kantor & Bouchet, new subfamily**

34 (Figs 34 – 36)

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37 *Diagnosis:* Shell small to large (15-125 mm) mm, biconical, fusiform to turriiform, pale to dark  
38 brown due to well developed periostracum. smooth, or sculptured with fine to very strong spiral  
39 cords,. Suture distinct, impressed. Spire moderately to very high; teleoconch whorls gently  
40 convex, distinctly shouldered due to pronounced spiral sculpture, or flattened. Sculpture absent,  
41 or represented by regular spiral cords, ranging from wide and flattened to rounded, or narrow,  
42 elevated, separated by wide, concave interspaces. Microsculpture of fine collabral growth lines.  
43 Siphonal canal short and stout with well developed fasciole, to moderately long, strait and  
44 tapering. Siphonal notch rarely deep, commonly shallow or absent. Aperture elongate, varying  
45 from narrow to moderately wide; outer aperture lip evenly convex or straight in its adapical  
46 portion and strongly convex anteriorly. Inner lip with four columellar folds, the anteriormost  
47 notably weaker than succeeding. Rachidian narrow, less than half as wide as the laterals, bearing  
48 5 or 6 cusps of varying shape (Figs 33 A – C). Laterals wide, with 8-40 cusps, of varying  
49 strength.  
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**Genus *Isara* H. Adams & A. Adams, 1853** (Figs 34, 35 A – C)

*Type species: Mitra bulimoides* Reeve, 1845 [= *M. glabra* Swainson, 1821, after Cernohorsky (1976)]; SD, Cossmann (1899: 153).

*Synonym: Fuscomitra* Pallary, 1900. Type species: *Mitra fusca* Pallary, 1900 [= *Mitra cornea* Lamarck, 1811]; SD, Cox (1936: 66). Pallary referred to the type species as "*Mitra (Fuscomitra) fusca* (Swainson) Reeve", i.e. the species identified by Reeve (1844) as *Mitra fusca* Swainson, 1824. Reeve did not establish a new species, and there is no such thing as "*Mitra fusca* Reeve, 1844". Instead, this is a case of a deliberate misidentification of a nominal species used for the fixation of the type species and, under Art. 67.13, Pallary is deemed to have established a new nominal species, *Mitra fusca* Pallary, 1900.

*Diagnosis:* Shell medium-sized to large (30-100 mm), fusiform to turritiform, lightly sculptured, light or dark brown due to well developed periostracum. Suture distinct, impressed. Spire high to very high; teleoconch whorls gently convex to flattened, sculptured by regular or occasional spiral grooves, or smooth, often with a microsculpture of fine collabral growth lines. Siphonal canal short with well developed fasciole to moderately long and tapering. Siphonal notch shallow or absent. Aperture elongate, rather wide; outer aperture lip evenly convex or straight in its adapical portion and strongly convex anteriorly. Inner lip with four columellar folds, the anteriormost notably weaker. Rachidian narrow, less than half as wide as the laterals, bearing 5 or 6 cusps of varying shape (Figs 33 A – C). Laterals wide, with 8-40 cusps, subequal and densely set throughout, or proximal strongest and subsequent ones weakening towards tooth edge.

*Species included:* *Isara aerumnosa* (Melvill, 1888)<sup>3</sup> comb. nov., *I. aikenii* (Lussi, 2009)<sup>3</sup> comb. nov., *I. antillensis* (Dall, 1889)<sup>3</sup> comb. nov., *I. badia* (Reeve, 1844)<sup>3</sup> comb. nov., *I. beui* (Thach, 2016)<sup>3</sup> comb. nov., *I. carbonaria* (Swainson, 1822)<sup>1</sup> comb. nov., *I. chalybeia* (Reeve, 1844)<sup>3</sup> comb. nov., *I. chinensis* (Gray, 1834)<sup>3</sup> comb. nov., *I. cookii* (G. B. Sowerby II, 1874)<sup>3</sup> comb. nov., *I. cornea* (Lamarck, 1811)<sup>1</sup> comb. nov., *I. declivis* (Reeve, 1844)<sup>3</sup> comb. nov., *I. gabonensis* (Biraghi, 1984)<sup>3</sup> comb. nov., ***I. glabra* (Swainson, 1821)**<sup>1</sup> comb. nov., *I. joostei* (Lussi, 2009)<sup>3</sup> comb. nov., *I. lenhilli* (Petuch, 1988)<sup>3</sup> comb. nov., *I. midwayensis* (Kosuge, 1979)<sup>3</sup> comb. nov., *I. nigra* (Gmelin, 1791)<sup>1</sup> comb. nov., *I. pele* (Cernohorsky, 1970)<sup>3</sup> comb. nov., *I. peterclarksoni* (Marrow, 2013)<sup>3</sup> comb. nov., *I. picta* (Reeve, 1844)<sup>3</sup> comb. nov., *I. slacksmithae* (Marrow, 2013)<sup>3</sup> comb. nov., *I. straminea* (A. Adams, 1853)<sup>1</sup> comb. nov. *I. swainsonii* (Broderip, 1836)<sup>3</sup> comb. nov., *I. turtoni* (E. A. Smith, 1890)<sup>3</sup> comb. nov., *I. ulala* (Garcia, 2011)<sup>3</sup> comb. nov.

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*Distribution:* Indo-Pacific, West Africa and Mediterranean, Caribbean, from upper subtidal to upper bathyal depths.

*Remarks.* The type species of *Isara*, *Mitra bulimoides* (Fig. 34 B), was considered by Cernohorsky (1976) a synonym of *M. glabra*, and indeed shows conchological resemblance to it. Cernohorsky (1976) provided no whereabouts of the type specimen of *Mitra glabra* Swainson, 1821, and designated two unnumbered figures on plate 2 of the “*Exotic Conchology*” as the lectotype of *M. glabra*. Although this designation is nomenclaturally valid, ICZN article 74.4 makes it clear that this designation is to be treated as designation of the specimen illustrated. As this specimen cannot currently be traced, we herein designate the holotype of *Mitra bulimoides* NHMUK 1966656 as neotype of *M. glabra*. Thus *Mitra bulimoides* Reeve, 1845 becomes an objective synonym of the *Mitra glabra* Swainson 1821.

The genus *Isara*, as circumscribed herein, is a group largely defined based on molecular characters. Although the included species share a similarity in shell morphology (weak sculpture and, in many cases, well developed periostracum), the shell proportions are drastically different in *I. straminea* and *I. glabra*, and their relatedness would hardly be guessed based on overall shell appearance. The sequenced *Isara* species altogether show an unusually broad distribution: Azores and Mediterranean (*I. cornea*), West Africa (*I. nigra*), Caribbean (*I. straminea*) and Western Australia (*I. glabra* and *I. carbonaria*). Based on the overall shell morphology we tentatively assign *Mitra chinensis* to *Isara*, as well as an array of Australian species (*M. badia*, *M. chalybeia*, *M. peterclarksoni* and *M. slacksmithae*).

The species of *Isara* are commonly large, and their protoconchs are often corroded in (sub)adults; we managed to find an intact protoconch only in juveniles of *I. chalybeia* from southwestern Australia. It is characterized by a shape unusual for Mitridae – paucispiral, cyrtoconoid, broad, with a very small nucleus, and strongly convex whorls. *I. chalybeia* lives in subtropical / warm temperate waters and we doubt that this protoconch morphology also occurs in the tropical species of *Isara*, which are expected to have the plesiomorphic multispiral protoconch present throughout the family.

The pantropical distribution of *Isara* does not include the East Pacific. Whereas no “smooth” *Atrimitra* species from the Panamic province was included in our phylogenetic analysis, the obvious resemblance between the Panamic “*Mitra*” *orientalis*, and “*M.*” *caliginosa*, and the Atlantic *Isara nigra* and *I. cornea*, should be noted. Another species which also remains unstudied, and may prove to be related to *Isara*, is *Atrimitra idae*. At present we treat these New World species as *Atrimitra*, pending availability of molecular data.

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5 **Genus *Subcancilla* Olsson & Harbison, 1953** (Figs 35 D – F, 36)

6 *Type species: Mitra sulcata* Swainson, 1825; OD.

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8 *Diagnosis:* Shell small to large (15–125 mm), fusiform, with white or light background colour  
9 and contrasting brown lines on crests of spiral cords. Protoconch smooth, with slightly convex or  
10 flattened whorls, either pointed, narrowly-conical, of about 3 whorls, or bulbous, of about 2  
11 whorls. Suture indistinct. Spire moderately high, spire whorls evenly convex, sometimes  
12 shouldered in appearance due to strong elevated spiral cords that are rather sharp and widely set.  
13 Interspaces between spiral cords sculptured with fine, dense riblets, or smooth with  
14 microsculpture of very fine growth lines. Shell base triangular with straight, tapering siphonal  
15 canal not delineated from shell base. Siphonal notch deep. Aperture high, about half of shell  
16 height, narrow, parallel-sided. Outer aperture lip very gently convex, smooth. Inner lip with three  
17 fine, oblique columellar folds. Thin light-brown periostracum sometimes present. Radula with  
18 narrow rachidian and laterals 2–4 times wider than rachidian (Figs 35 D – F), both  
19 multicuspidate, either with dense pointed cusps of subequal strength or with one cusp on laterals  
20 notably stronger than others and rachidian bearing symmetrical paired cusps also differentiated  
21 in length and strength.  
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33 *Distribution:* Tropical East Pacific, Caribbean, subtidal and bathyal depths.  
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37 *Species included:* *Subcancilla attenuata* (Broderip, 1836)<sup>1</sup>, *S. belcheri* (Hinds, 1843)<sup>3</sup> comb.  
38 nov., *S. calodinota* (S. S. Berry, 1960)<sup>3</sup>, *S. candida* (Reeve, 1845)<sup>3</sup>, *S. directa* (Berry, 1960)<sup>3</sup>,  
39 *S. edithreae* (Sphon, 1976)<sup>3</sup>, *S. erythrogramma* (Tomlin, 1931)<sup>1</sup>, *S. funiculata* (Reeve, 1844)<sup>3</sup>,  
40 *S. gigantea* (Reeve, 1844)<sup>3</sup>, *S. haneti* (Petit, 1852)<sup>3</sup>, *S. hindsii* (Reeve, 1844)<sup>3</sup>, *S. joapyra*  
41 Simone & Cunha, 2012<sup>3</sup>, *S. leonardi* (Petuch, 1990)<sup>1</sup> comb. nov., *S. leonardhilli* Petuch, 1987<sup>2</sup>,  
42 *Subcancilla lindae* Petuch, 1987<sup>3</sup>, *S. lopesi* Matthews & Coelho, 1969<sup>3</sup>, *S. malleti* (Petit de la  
43 Saussaye, 1852)<sup>3</sup>, *S. phorminx* (S. S. Berry, 1969)<sup>3</sup>, ***S. sulcata*** (Swainson, 1825)<sup>2</sup>.  
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50 *Remarks.* Cernohorsky (1991) remarked that the placement of the New World *Subcancilla*  
51 *sulcata* and of Indo-Pacific species in the same genus *Subcancilla* was inconsistent with their  
52 disparate radular morphology, however no alternative was suggested. Thorsson and Salisbury  
53 (2008: 3) stressed that the classification of the Panamic and Caribbean species of *Subcancilla*,  
54 including the type species *S. sulcata*, has not been addressed sufficiently, and that the “exact  
55 placement of *Subcancilla* into the family Mitridae remain[ed] to be absolutely determined”.  
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Based on our phylogenetic analysis we demonstrate a close affinity of three East Pacific and one Caribbean species of *Subcancilla*, and reconsider the contents of the genus, so that only New World species are here assigned to it. The species of *Subcancilla* can be readily distinguished from other American mitrids by their characteristic sculpture of narrow, elevated, usually widely interspaced, spiral cords, often bearing a brown line on their crests; the same sculptural pattern characterizes Indo-Pacific species in the genera *Domiporta* and *Imbricaria*. Members of these three genera are also characterized by similar shell proportions, so that their shells share the same characteristic habitus that has long confused conchologists. Our results demonstrate that the three genera represent three major phylogenetic lineages of Mitridae in the subfamilies Isarinae, Mitrinae and Imbricariinae, and their resemblance is obviously a result of convergence.

The radula differs remarkably in the three studied species, with those of *S. attenuata* and *S. cf. leonardhilli* being overall unremarkable underived mitrid radulae, whereas that of *S. erythrogramma* demonstrates signs of cusp differentiation, resembling imbricariine radulae. The small and unobtrusive radula of *S. sulcata* pictured by Cernohorsky (1991: fig. 79) undoubtedly belongs to the first type.

### Subfamily Pleioptygmatinae Quinn, 1989

#### Genus *Pleioptygma* Conrad, 1863

*Type species*: †*Voluta carolinensis* Conrad 1840: 387; M.

*Diagnosis*: As no material on *Pleioptygma* was available for the present study, we do not provide our own diagnosis to this enigmatic and poorly studied genus, and refer to Quinn (1989).

*Species included*: *Pleioptygma helenae* (Radwin & Bibbey, 1972)<sup>2</sup>.

*Distribution*: Caribbean, subtidal to upper bathyal depths.

*Remarks*. For remarks on the placement of *Pleioptygma*, see section ‘Implications of the morphological studies for the taxonomy of the Mitridae’ below.

#### *Incertae sedis*

**Genus *Carinomitra* Fedosov, Herrmann, Kantor & Bouchet, n. gen.** (Figs 37, 38 A – C)

1  
2 Type species: *Mitra peculiaris* Reeve, 1845; OD, herein.

3  
4 *Diagnosis*: Shell small (7-20 mm), elongate-fusiform, with characteristic pattern formed by light  
5 adapical portions of teleoconch whorls, gradually transiting to yellow or orange peripheries.

6  
7 Protoconch narrowly conical or cyrtoconoid, of 3 to almost 5, evenly convex, smooth and glossy  
8 whorls. Suture distinct, slightly impressed. Early spire whorls with flattened or slightly convex  
9 outlines, later gently convex or distinctly carinated at the suture. Except for subsutural carina,  
10 sculpture limited to very weak spiral grooves on shell base and siphonal canal, thus the shell  
11 appears smooth. Siphonal canal tapering, siphonal notch shallow or indistinct. Aperture elongate,  
12 rather narrow; outer lip smooth, convex. Inner lip with 4-5 fine oblique columellar folds.

13  
14 Rachidian narrow, bearing either six cusps of comparable size, or four cusps with two medial  
15 notably stronger than two laterals. Laterals wide, bearing multiple cusps, of which 2nd and 3rd  
16 from rachidian are strongest.

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24 *Distribution*: Indo-Pacific, upper subtidal depths, reef crevices and coral rubble.

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27 *Species included*: *Carinomitra peculiaris* (Reeve, 1845)<sup>1</sup> comb. nov., *C. saltata* (Peace, 1865)<sup>2</sup>  
28 comb. nov., *C. typha* (Reeve, 1845)<sup>1</sup> comb. nov.

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32 *Etymology*: The name *Carinomitra* refers to the presence of the distinct keel (Latin *carina*) in at  
33 least two species of this newly recognized lineage, including the type species *C. peculiaris*.

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37 *Remarks*. The genus *Carinomitra* is conchologically distinctive due to the carinated or adapically  
38 inflated adult whorls and the characteristic colour pattern. The radulae of the three studied  
39 species exhibit notable disparity. In *M. peculiaris*, the rachidian bears multiple cusps with a  
40 central unpaired cusp; conversely, in *C. saltata* and *C. typha* the unpaired central cusp of the  
41 rachidian is absent, and the paired central cusps greatly exceed the paired lateral cusps. This  
42 variation in radula morphology parallels that observed in *Imbricaria* and *Cancilla* (see  
43 discussion below).

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52 **Genus *Condylomitra* Fedosov, Herrmann, Kantor & Bouchet, n. gen.** (Figs 38 D, E, 39)

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54 *Type species*: *Mitra tuberosa* Reeve, 1845; OD, herein.

55  
56 *Diagnosis*: Shell small (10-25 mm), ovate to almost conical, heavily sculptured, with pointed  
57 conical apex. Protoconch pointed, narrowly-conical, of about 3 very slightly convex, smooth  
58 whorls. Spire whorls convex; last adult whorl proportionally very high, sculptured with densely  
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1 set, gemmate spiral cords, 1 to 3 adapical cords very strong, forming prominent, spirally  
2 elongated rounded tubercles, directed slightly upwards. Siphonal canal very short, with well  
3 developed fasciole, siphonal notch distinct. Aperture elongate, rather narrow, widening  
4 anteriorly. Outer apertural lip gently convex or straight, inner lip with four closely set columellar  
5 folds. Radula very narrow, monoserial, with rachidian bearing strong, unpaired medial cusp,  
6 flanked with 2-8 smaller pointed cusps on each side. Proboscis dorso-ventrally flattened.  
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13 *Distribution*: Indo-Pacific, intertidal and upper subtidal depths, mostly on hard substrates.  
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17 *Species included*: *Condylomitra bernhardina* (Roding, 1798)<sup>1</sup> comb. nov., *C. tuberosa* (Reeve,  
18 **1845**)<sup>1</sup> comb. nov.  
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22 *Etymology*: The name *Condylomitra* combines the Latin word *condylus*, meaning knob, with the  
23 suffix *Mitra*, in reference to the characteristic shell sculpture of tubercles that is shared by the  
24 species in this newly recognized lineage. Gender feminine.  
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29 *Remarks*. Although each on a quite long branch, *Condylomitra bernhardina* and *C. tuberosa*  
30 form a clade in our molecular trees and share features of the shell and radula, and the  
31 characteristic sculpture pattern allows a rather easy recognition of this group. Because of their  
32 superficial similarity, we initially considered *Strigatella lugubris* and "*Mitra*" *pudica* to be  
33 possibly related to *Condylomitra*; however the former is closely related to *Strigatella coronata* in  
34 the *Strigatella* clade, and the latter, although it was not sequenced, is excluded from  
35 *Condylomitra* by its triserial radula.  
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#### 44 ***Magnamitra* Huang & Salisbury, 2017**

45 *Type species*: *Magnamitra sandrogorii* Huang & Salisbury, 2017; OD.

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47 *Diagnosis*: As no material on *Magnamitra sandrogorii* was available for the present study, we do  
48 not provide our own diagnosis to this newly described genus, and refer to Huang and Salisbury  
49 (2017).  
50

51 *Species included*: ***Magnamitra sandrogorii* Huang & Salisbury, 2017<sup>2</sup>**.

52  
53 *Distribution*: Indo-Pacific, bathyal depths.  
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55 *Remarks*. See remarks under *Calcimitra*.  
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#### 58 ***Atrimitra* Dall, 1918** (Figs 40 A – C)

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*Type species: Mitra idae* Melvill, 1893; OD.

*Diagnosis:* As no material on *Atrimitra* was available for the present study, we do not provide a diagnosis to this poorly studied genus.

*Species included: Atrimitra caliginosa* (Reeve, 1844)<sup>3</sup> comb. nov., *A. catalinae* (Dall, 1920)<sup>2</sup> comb. nov., *A. effusa* (Broderip, 1836)<sup>3</sup>, *A. idae* (Melvill, 1893)<sup>3</sup>, *A. orientalis* (Griffith & Pidgeon, 1834)<sup>3</sup> comb. nov., *A. semigranosa* (Martens, 1897)<sup>3</sup> comb. nov.

*Distribution:* Tropical East Pacific, subtidal depths.

*Remarks:* see remarks under *Isara*.

#### ***Vicimitra Iredale, 1929*** (Fig. 40 D)

*Type species: Vicimitra prosthora* Iredale, 1929; M.

*Diagnosis:* As no material on *Vicimitra prosthora* was available for the present study, we do not provide a diagnosis to this genus.

*Species included: Vicimitra prosthora* Iredale, 1929<sup>3</sup> (Fig. 40 D).

*Distribution:* New South Wales, Australia.

*Remarks.* See remarks under *Quasimitra*.

#### **Genus *Probata*** Sarasúa, 1989 (Figs 38 E, 40 E, F)

*Type species: Mitra espinosai* Sarasúa, 1978; OD.

*Diagnosis:* Shell small to medium-sized (15-45 mm), broadly fusiform, light brown, sometimes with occasional white flakes. Protoconch white, pointed, of about 2.5 smooth glossy whorls. Suture distinct, impressed. Teleoconch whorls slightly convex, sculptured with fine, low, evenly interspaced spiral cords. Siphonal canal stout, tapering, siphonal notch shallow. Aperture elongate, outer lip convex, thickened adapically. Inner apertural lip with five fine columellar folds, weakening gradually towards siphonal canal. Radula triserial, rachidian narrow, with eight pointed cusps, two medial longest, those situated laterally becoming gradually weaker. Laterals with 15+ cusps, strong and long compared to length of tooth base.

*Species included: Probata barbadensis* (Gmelin, 1791)<sup>1</sup> comb. nov., ***P. espinosai* (Sarasúa, 1978)<sup>3</sup>**.

*Remarks.* *Mitra espinosai*, the type species of *Probata*, has been considered a junior synonym of *Mitra barbadensis* by Cernohorsky (1991). Indeed, the immature holotype of the former very much resembles *Mitra barbadensis* and, even if not conspecific, they are definitely closely related. Thus we tentatively allocate the name *Probata* to the *Mitra barbadensis* clade. The affinities of *Probata* remain unclear and obviously need further studies. In terms of sculpture pattern, typical *Atrimitra*, as typified by *Mitra idae*, resembles *Probata*; however the latter



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2 differs notably in shell proportions and number of columellar folds. The overall plesiomorphic  
3 radula of *Probata barbadensis* (Fig. 38 F) resembles the radula of many other lineages of  
4 Mitridae and gives no clue as to where the genus should be assigned.  
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8 ***Dibaphimitra* Cernohorsky, 1970** (Fig. 40 G)

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10 *Type species: Mitra florida* Gould, 1856; OD.

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12 *Diagnosis:* As no material on *Dibaphimitra florida* was available for the present study, we do not  
13 provide our own diagnosis to this poorly studied genus, and refer to Cernohorsky (1970).  
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15 *Species included: **Dibaphimitra florida** (Gould, 1856)<sup>2</sup>.*

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17 *Distribution:* Caribbean, subtidal to upper bathyal depths.

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19 *Remarks:* The radula of *D. florida* pictured by Cernohorsky (1970) is overall a typical mitrid  
20 radula, with a narrow rachidian and very wide multicuspidate laterals. Although this morphology  
21 unequivocally places *Dibaphimitra* in Mitridae, it is inconclusive regarding the subfamilial  
22 placement of *D. florida*. More studies are needed to characterize the affinities of this enigmatic  
23 Caribbean lineage.  
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## DESCRIPTION OF NEW SPECIES

***Profundimitra taylori* Fedosov, Herrmann, Kantor & Bouchet, n. sp.***Type data*

*Holotype*. MNHN IM-2013-40651, Papua New Guinea, North of Rabaul, BIOPAPUA Stn CP3671, 04°04'S, 151°56'E, 585-601 m, lv, 24.15 mm (Figs 17G; 18 A, B).

*Paratype*. MNHN IM-2013-58429, KAVIENG 2014 Stn CP4449, 02°10'S, 150°11'E, 623-908 m, lv, 35.5 mm.

*Other material examined*: Papua New Guinea, BIOPAPUA Stn 3736, off Lancasay, 08°14'S 150°32'E, 760-769 m, 1 lv (21.5 mm); PAPUA NUIGINI Stn CP3979, North of Bagabag Is, 04°44'S 146°11'E, 540-580 m, 1lv (MNHN IM-2013-19698, 25.75 mm); Stn CP3994, North from Cape King William, 06°00'S 147°35'E, 648-652 m, 1 lv (MNHN IM-2013-19833, 33.6 mm); MADEEP Stn DW4321 08°39'S 151°47'E, 612 m, 1 lv (MNHN IM-2013-45873). ? NEW CALEDONIA, BATHUS 3 Stn DW790, 23°49'S 169°48'E, 685-715 m, 17.9 mm; Norfolk Ridge, BATHUS 4 Stn DW920 18°45'S 163°17'E, 610-620 m, 15.1 mm (Fig. 18 C).

*Description*

Shell medium sized (holotype 24.15 mm, paratype 35.5 mm), fusiform, with high, cyrtocoid, slightly tilted spire and rather short siphonal canal. Protoconch pointed, subcylindrical, of 2+ whorls (corroded in all specimens studied). Teleoconch of 7.5 gently convex whorls, suture linear, distinctly impressed. First teleoconch whorls with reticulate sculpture formed by four low, very weak, rounded spiral cords, intersected by even weaker rounded spiral folds. Interstices rather deep, forming characteristic pattern of four spirally aligned punctures, well pronounced on two succeeding whorls and rather gentle, widely spaced on later whorls. Penultimate whorl with three distinct spiral rows of punctures on adapical portion, followed by three very weak rows below. Last adult whorl evenly convex, gradually extending to rather short, straight tapering siphonal canal. Adapical portion and periphery of last adult whorl sculptured with ten spiral rows of punctures. On shell base spiral rows of punctures becoming denser, as well as punctures themselves merging to form narrow grooves on abapical part of shell base and strong, oblique grooves on siphonal canal.

Siphonal canal slender, moderately long, tapering, not notched at its tip. Aperture rather low, lanceolate, its outer lip thin, evenly convex. Inner apertural lip evenly concave in its adapical half and straight below, with 3 oblique columellar folds at mid-height, slightly deepened in aperture and weak in appearance.

1 Shell colouration uniformly pale-yellowish; microsculpture of very fine collabral growth  
2 lines.  
3

4 Radula (of holotype) 0.7-0.75 mm long, 0.14 mm wide, consisting of about 85 rows.  
5 Rachidian about 40 µm and laterals 45 µm wide, all three similar, with evenly convex anterior  
6 margin, bearing 12-13 moderately long, pointed subequal cusps, those at teeth margins smaller  
7 than others.  
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13 *Distribution*: Bismarck Sea off mainland New Guinea and New Ireland; East of New Caledonia,  
14 Norfolk Ridge, 580-760m.  
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18 *Etymology*: The species named after our friend and colleague John D. Taylor of the NHMUK in  
19 recognition of his immense contribution to malacology, and in particular to our knowledge of  
20 miter feeding biology.  
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25 *Remarks*: *Profundimitra taylori* n. sp. can be readily distinguished from its congeners by its  
26 almost smooth shell with faint columellar folds; both features are rather characteristic of  
27 *Eumitra*. Members of the latter genus, however, are characterized by more convex whorls, often  
28 with subcylindrical early teleoconch whorls. Smooth species of *Calcimitra*, such as *C. labecula*,  
29 resemble *P. taylori* n. sp. in shell proportions and sculpture; however, *Calcimitra* species can be  
30 recognized by their generally larger shells with strong columellar folds and, typically, by the  
31 presence of a siphonal notch. Finally, the smooth shallow water *Quasimitra sarmientoi*, although  
32 close to *Profundimitra taylori* n. sp. in shell proportions and lack of sculpture, can be  
33 differentiated by the intensely coloured shell and distinct siphonal notch in adult specimens.  
34 Apart from the mentioned shell characters, the characteristic radula with similar laterals and  
35 rachidian differentiates *Profundimitra taylori* n. sp. and its congeners from most other mitrids.  
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47 ***Fusidomiporta ponderi* Fedosov, Herrmann, Kantor & Bouchet, n. sp.**

48 *Type data*

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50 *Holotype*. MNHN IM-2013-40665, Papua New Guinea, BIOPAPUA Stn CP3692, SE of Manus  
51 I., 02°10'S, 147°19'E, 408-448 m, lv, 25.2 mm (Figs 18 I, K).  
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53 *Paratype*. BIOPAPUA Stn CP3629, Gulf of Huon, South of Lae, 06°57'S, 147°08'E, 240-269 m,  
54 dd, 26.15 mm.  
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*Other material examined:* BIOPAPUA Stn DW3735, 08°15'S, 150°34'E, 450-500 m, 21.4 mm; Stn data lost, 28.5 mm; Stn DW3771, 05°34'S, 151°33'E, 295-422 m, 9.2 mm.

*Description*

Shell medium-sized (holotype 25.2 mm), fusiform, heavily sculptured, with rather high spire and elongated aperture. Protoconch pointed, cyrtocoenoid, of 3+ glossy, convex whorls (usually strongly corroded or missing). Teleoconch of 6+ slightly convex whorls, suture distinctly canaliculated. Subsutural shelf well developed, rather narrow, slightly inclined towards axis, bordered by projecting margin of adapical spiral cord. Early teleoconch whorls corroded, third and subsequent teleoconch whorls with five very strong, elevated, gemmate spiral cords separated by deep interspaces. Spiral cords subequal, adapical and abapical cords slightly weaker than intermediate ones, microsculpture of fine growth lines in interspaces between spiral cords; abapical cord of previous whorl partly superposed by adapical cord of succeeding whorl. Gemmules on spiral cords axially aligned, connected by low and weak axial riblets in interspaces between spiral cords. Spiral cords become distinctly beaded on penultimate and last adult whorls, forming rows of closely set, rounded, glossy granules. Five spiral cords on adapical portion of last adult whorl succeeded by six cords on shell base and five cords on siphonal canal, of which last three oblique, weaker than preceding, irregularly gemmate. Siphonal canal delineated from shell base by slightly widened interspace with low wavy spiral thread. Siphonal canal rather long and stout, slightly recurved.

Aperture elongate, its outer lip gently convex throughout its height, wavy, reflecting arrangement of spiral cords. Inside of outer lip with 8 strong lirae. Inner lip strongly calloused, reflected, retaining weak reticulate sculpture adapically, with three strong oblique columellar folds at mid-height.

Shell uniformly white or pale.

Radula of holotype 0.76-0.8 mm long, 0.19-0.20 mm wide, composed of about 65 transverse rows of uniform, delicate, multicuspidate teeth. Rachidian about 60 µm wide, with 17 cusps, of which two marginals very weak, and the others subequal, long and pointed. Laterals about 50 µm wide, with slightly convex anterior margin, bearing 14-15 pointed, rather long cusps.

*Distribution:* Papua New Guinea, North of main island, 269-450 m.

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*Etymology:* The species is named after another giant in malacology, Winston Ponder of the AMS, whose early work, including his studies on mitriform families, set a milestone in our understanding of neogastropod evolution.

*Remarks:* The identification of *Fusidomiporta ponderi* n. sp. is uneasy, mainly because of its striking resemblance to (still undescribed) species of *Profundimitra* n. gen., represented in our analysis by specimens IM-2007-35618 and IM-2007-35711 [both mislaid]. The single live taken specimen of *F. ponderi* n. sp. seems to have a proportionally slightly lower spire and a somewhat stepped appearance of spire whorls, with more elevated spiral cords. At the same time, the distinctive and heavy sculpture pattern makes it quite recognizable from among most Mitridae. Some deep water species of *Gemmulimitra* n. gen. have a somewhat similar, beaded sculpture, which however is nowhere as strong as in *Fusidomiporta ponderi* n. sp. Besides, *Gemmulimitra boucheti* has a proportionally broader shell with more convex whorls compared to *F. ponderi* n. sp. On the contrary, *G. neocaledonica* n. sp. has a rather biconical shell with subcylindrical whorls and a rather reticulate sculpture pattern. However, at this moment, many of the deep water mitrids are still represented in our dataset by too few specimens to assess their intraspecific variation and elaborate robust shell delimitation criteria.

***Gemmulimitra neocaledonica* Fedosov, Herrmann, Kantor & Bouchet, n. sp.**

*Type data*

*Holotype.* MNHN IM-2013-40655, New Caledonia, Kouakoué Canyon, EXBODI Stn 3821, 21°53'S, 166°50'E, 211-440 m, lv, 24.25 mm (Figs 21 A, B).

*Paratypes:* New Caledonia, EXBODI, Stn 3800, East coast off Thio, 21°32'S, 166°22'E, 279-282 m, 1 lv (Paratype 3, 21.5 mm); Stn 3807, East coast off Toupeti, 21°43'S, 166°36'E, 352-372 m, 1 lv (Paratype 2, 26.9 mm); Stn 3810, East coast off Toupeti, 21°44'S, 166°38'E, 384-385 m, 2 lv (Paratype 1, 27.35 mm; Paratype 4, 24.0 mm); Stn 3814, Passe du Solitaire, 21°49'S, 166°44'E, 331-344 m, 1 lv (Paratype 5, 20.4 mm).

*Other material examined*

New Caledonia, EXBODI Stn 3795, 21°32'S, 166°21'E, 240-245m, 1 lv (16.4 mm); Stn 3800, 21°32'S, 166°22'E, 279-282m, 12 lv (16.7 mm, 17.1 mm, 17.3 mm, 15.0 mm, 16.2 mm, 16.2 mm, 16.55 mm, 16.8 mm, 15.05 mm, 23.1 mm, 17.65 mm, 17.8 mm); Stn 3805, 21°42'S, 166°34'E, 302 m, 1 lv (20.9 mm); Stn 3806, 21°42'S, 166°34'E, 307-309 m, 7 lv (22.0 mm, 18.4 mm, 15.9 mm, 16.3 mm, 14.0 mm, 9.15 mm, 9.8 mm); Stn 3807, 21°43'S, 166°36'E, 352-372m,

1 11 lv (22.6 mm, 20.1 mm, 21.05 mm, 20.7 mm, 20.0 mm, 19.2 mm, 17.4 mm, 20.9 mm, 18.1  
2 mm, 18.2 mm, 19.65 mm); Stn 3810, 21°44'S, 166°38'E, 384-385 m, 8 lv (25.5 mm, 25.85 mm,  
3 29.3 mm, 25.5 mm, 27.4 mm, 21.65 mm, 25.5 mm, 23.3 mm); Stn 3814, 21°49'S, 166°44'E, 331-  
4 344 m, 6 lv (22.8 mm, 21.5 mm, 20.6 mm, 21.6 mm, 18.9 mm, 14.1 mm); Stn 3821, 21°53'S,  
5 166°50'E, 211-440 m, 2 lv (25.85 mm, 25.15 mm); Stn 3823, 21°55'S, 166°55'E, 246-255m, 2 lv  
6 (15.5 mm, 14.5 mm); Stn 3825, 21°58'S, 166°59'E, 349-405m, 1 lv (16.2 mm); Stn 3828,  
7 22°00'S, 167°01'E, 300-302m, 1 lv (16.4 mm); Stn 3829, 22°02'S, 167°05'E, 350-360m, 1 lv  
8 (23.0 mm); TERRASSES Stn 3095, 22°02'S, 167°06'E, 320-380 m, 1 lv (21.5 mm).  
9 Papua New Guinea, BIOPAPUA Stn CP3634, 07°29'S, 147°31'E, 279-290 m, 1 dd (21.75 mm).  
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### 17 *Description*

18 Shell small to medium-sized (holotype 24.25 mm), elongate-fusiform to almost biconical,  
19 heavily sculptured, with narrow aperture and stepped appearance of late teleoconch whorls.  
20 Protoconch pointed, cyrtoconoid, translucent, of 3+ slightly convex, glossy whorls. Protoconch /  
21 teleoconch transition distinct. Teleoconch of about 9 whorls; suture canaliculated. Subsutural  
22 ramp forming distinct shelf, flat or even slightly inclined inside, giving teleoconch whorls a  
23 subcylindrical profile. Whorl periphery slightly convex, early spire whorls sculptured with three  
24 strong, closely set, spiral cords overriding low indistinct axial ribs to form series of prominent,  
25 axially aligned, beads. On third teleoconch whorl, adapical spiral cord splits into two, and  
26 succeeding spire whorls sculptured with four gemmate cords, adapical cord bordering subsutural  
27 ramp wavy, slightly narrower than others, delineated from second cord by narrower interspace.  
28 On later teleoconch whorls, interspaces between gemmate spiral cords gradually broadening,  
29 axial ribs becoming more distinct and sculpture rather reticulate. Last adult and penultimate  
30 whorls with 26 axial ribs each. Interspaces between axial ribs and spiral cords forming deep  
31 quadrangular depressions with microsculpture of fine co-axial growth lines, sometimes retaining  
32 fragments of periostracum forming squamiform projections. Shell base extended to moderately  
33 long, tapering, slightly notched siphonal canal. Four gemmate spiral cords on adapical portion of  
34 last adult whorl, and 12 cords on shell base and siphonal canal.  
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47 Aperture narrow, elongated; outer lip wavy, convex in adapical portion and straight below  
48 mid-height. Inside of outer lip smooth. Inner lip strongly calloused, sometimes reflected,  
49 retaining weak reticulate sculpture adapically, with four closely set fine columellar folds at mid  
50 height. Coloration uniformly cream, protoconch white.  
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54 Radula (of paratype 5) 0.62 mm long, 0.13 mm wide, of about 75 rows. Rachidian narrow,  
55 about 20 µm wide, bearing 8 strong, moderately long, pointed cusps. Laterals attaining 47 µm in  
56 width, with straight anterior margin bearing 16+ strong, pointed, rather widely set cusps.  
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*Distribution:* New Caledonia, Papua New Guinea, 255-384 m.

*Etymology:* The species epithet refers to the type locality.

*Remarks:* While the specimens from New Caledonia show a fine reticulate sculpture pattern on the late teleoconch whorls, the specimen from Papua New Guinea is characterized by denser axial ribs and in overall shell morphology is somewhat intermediate between such typical *G. neocaledonica* n. sp. and *Fusidomiporta ponderi* n. sp. The latter species is the one that resembles most *G. neocaledonica* n. sp., but it can be differentiated by its notably stronger spiral cords and rather fusiform shell. The combination of elongate-biconical shell with subcylindrical whorl profile and characteristic reticulate pattern on late whorls allows for easy recognition of *G. neocaledonica* n. sp. Other species of *Gemmulimitra* n. gen. differ either in shell shape or in sculpture pattern, and *G. avenacea*, despite being the closest to *G. neocaledonica* n. sp. in our multi-gene analyses, shows no morphological resemblance to it whatsoever.

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### *Implications of the morphological studies for the taxonomy of the Mitridae*

According to our earlier results (Fedosov et al. 2015), the families Mitridae, Charitodoronidae and Pyramimitridae form a well supported phylogenetic group, which we designate as a superfamily Mitroidea, although they are rather heterogeneous morphologically, as summarized in Table 4.

The morphological distinctiveness of the Mitridae has been appreciated by many authors and, when anatomical descriptions scattered in many papers are brought together, the family ranks among the better studied among neogastropods. Beside multiple illustrations of radulae (Risbec 1928; Cernohorsky, 1970, 1976, 1991), data on the general body morphology and/or foregut anatomy are available, among Mitrinae, for *Mitra mitra* (Ponder 1972), *Ziba carinata* (Simone & Turner, 2010), *Pseudonebularia cucumerina* (Risbec 1928) and *Episcomitra zonata* (Vayssière 1901); among Strigatellinae, for *Strigatella paupercula* (Ponder 1972), *S. retusa* and *S. scutulata* (Risbec 1928); among Imbricariinae, for *Imbricariopsis conovula* (Ponder 1972); among Cyndromitriinae, for *Pterygia crenulata* (Risbec 1928); among Isarinae, for *Isara cornea* (Harasewych 2009); and for *Atrimitra idae* (West 1990), *A. catalinae* (West 1991), and *Condylomitra tuberosa* (herein), that we treat as *incertae sedis*. All the species that were studied with sufficient attention revealed an epiproboscis (referred to as "tube à venin" by Risbec 1928), either in combination with a radula of underived morphology (in most of the species mentioned) or with a uniserial radula (*Pterygia crenulata*, *Condylomitra tuberosa*). Meanwhile, an epiproboscis is not present in the Charitodoronidae, the Neogastropoda clade closest to the Mitridae. There is no doubt that the epiproboscis represents an autapomorphy of the Mitridae and can be used for the anatomical circumscription of the family.

In this connection, the morphology of the Caribbean *Pleioptygma helena*, as addressed by Quinn (1989), deserves special attention. Quinn's description of the foregut anatomy raises many questions; in particular the position of the buccal mass is not described explicitly, as well as the nature of the "proboscis bulb", and we believe that the homologies of these organs may have been misinterpreted by him. This assumption is further reinforced by the fact that the two specimens dissected by Quinn displayed some variation in foregut morphology, which may be an artifact of poor fixation (with the use of rum suggested by the author!). Some parts of the description are of special interest. In particular, the "proboscis bulb attached to the cephalic cavity floor by a broad, rather thick band of muscles originating in the foot" (Quinn 1989: 14) more likely refers to the large buccal mass and a radula / odontophore retractor muscle. Then the peculiar introvert, which "invaginates and runs back through the outer tube / sheath and enters the proboscis bulb [=buccal mass]" may not be anything but an epiproboscis.



Undoubtedly, the anatomy of *Pleioptygma helenae* is peculiar and its homologies need to be clarified based on investigations of additional material. However, given its rarity and the small chance of obtaining live-taken specimens in the near future, we dare reassess the systematics of *Pleioptygma* based on currently available data. Several lines of evidence support a placement of *Pleioptygma* as a separate subfamily within the Mitridae, including 1) the mitriform shell; 2) the radula with rachidian and laterals of about equal morphology - similar to the one in *Domiporta* and 3) the presence of a structure that, based on topology and morphology, is closely comparable to the mitrid epiproboscis, and most likely *is* an epiproboscis.

#### *Evolution of radular morphology in the Mitridae*

Our studies revealed only two major radula types in the family Costellariidae, with a very simple scenario of two independent transitions from plesiomorphic to derived (Fedosov et al. 2017). The situation is incomparably more complex in the Mitridae. Here we recognize six major types of radula; each is referred to a genus that typically represents it (Fig. 41).

- 1 - *Mitra*-type: radula with laterals notably wider than rachidian tooth and bearing multiple equal or subequal cusps. This underived radula morphology is widespread across the Mitridae tree. It characterizes the family Charitodoronidae, most Mitrinae (except the *Domiporta* group and some *Pseudonebularia*), most Isarinae, as well as the *incertae sedis* genera *Probata*, *Carinomitra*, *Atrimitra* (Cernohorsky, 1970; West 1990; 1991) and *Dibaphimitra* (Bayer, 1942).
- 1a - *Strigatella*-type: radula with slightly curved laterals bearing short robust cusps on their medial convex portion and lacking cusps laterally; rachidian always with central unpaired cusp. This type of radula is found in all Strigatellinae (except in the *S. lugubris* – *S. coronata* clade). The *Strigatella*-type of radula represents a modified *Mitra*-type, and intermediate morphologies with *Strigatella*-like laterals but different rachidian are found outside Strigatellinae in *Neotiara nodulosa* (Mitrinae) and *Cancilla schepmani* (Imbricariinae).
- 1b - *Nebularia*-type: is also a slightly modified version of the *Mitra*-type, with a characteristic rachidian bearing only five cusps, the central unpaired cusp being notably enlarged. This type of morphology characterizes the genus *Nebularia* as circumscribed herein.
- 2 - *Profundimitra*-type: very wide rachidian, roughly attaining the width of laterals and bearing equal number of cusps. This type of radula characterizes the mitrine genera *Profundimitra* and *Fusidomiporta*, and is also found in some *Domiporta* (but not in its type species, *D. filaris*), *Pseudonebularia maesta* and, outside Mitrinae, in the genus *Pleioptygma* (Quinn, 1989).
- 3 - *Imbricaria*-type: radula characterized by moderately wide multicuspidate laterals, with one of the medial cusps notably enlarged compared to the others. Cusps of laterals are also differentiated in size, with a central unpaired cusp retained, although often reduced in size. This type of radula is found in all *Imbricaria* species except *I. fulgetrum*.

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- 3a – *Cancilla*-type: resembles the *Imbricaria*-type, but the laterals are more than twice as wide as the rachidian, and the central unpaired cusp of the rachidian is absent. This type of radula is found in *Cancilla isabella* (Salisbury & Huang, 2015) and other species of this genus studied herein, as well as in *Imbricariopsis*, *Subcancilla erythrogramma* and *Imbricaria fulgetrum*.
- 4 – *Scabricola*-type: radula characterized by strongly modified laterals in which the lateralmost cusp is greatly enlarged to form a robust spine. Typically, the rachidian is comb-like (*Scabricola variegata*, *Swainsonia* spp.) but it may also bear a single strong cusp. This type of radula is found in species of *Scabricola* and *Swainsonia*.
- 5 – *Neocancilla*-type: radula characterized by a rachidian with a pair of very robust and blunt central cusps, and laterals bearing few short and robust cusps in their medial portions. This type of radula is known in all species of *Neocancilla*. The radulae of *Scabricola olivaeformis* and *S. coriacea* have morphologies somewhat intermediate between the *Scabricola*-type and the *Neocancilla*-type.
- 6 – *Pterygia*-type: very narrow uniserial radulae remarkable by the complete loss of laterals. Rachidians of varying morphology, but usually flattened, with serrated margins. Radulae of this type are found in all species of the genera *Pterygia* and *Condylomitra*, and in the *Strigatella lugubris* – *Strigatella coronata* clade of *Strigatella*.

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Although the diversity of radular morphologies in the family Mitridae is impressive, the understanding of its evolution is greatly hampered by homoplasies. Radula morphology does not clearly align with the inferred phylogenetic groupings of the Mitridae (Fig. 41) because of an ubiquitous retention, in advanced lineages, of the plesiomorphic state and because of multiple convergences. In fifteen genera of Mitridae, all studied species presented an underived *Mitra*-type radula. Seven genera appeared heterogeneous in radula morphology, combining several general types. Thus specific apomorphies can be identified in only few cases, and in even fewer cases the apomorphic state is shared by all members of the lineage. Only eight genera (*Profundimitra*, *Fusidomiporta*, *Neocancilla*, *Pterygia*, *Nebularia*, *Condylomitra* and, with some reservations, *Imbricariopsis* and *Swainsonia*) are supported by distinct apomorphies in radular morphology. Among them, only *Nebularia* and *Neocancilla* show autapomorphic radula types. Undoubtedly, the subfamily Imbricariinae shows the greatest diversity of radular morphologies, and the pattern of radular evolution is most obvious and consistent in that subfamily. The progressive differentiation of cusps on both the laterals and the rachidian is noteworthy, along with a general tendency to the reduction of the number of cusps. The radulae of *Cancilla* spp. are closest to the underived *Mitra*-type, and alternate courses of radula transformation are observed in the *Imbricaria* and *Scabricola-Neocancilla* clades.

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In addition to a blurred phylogenetic signal of radula characters, our understanding of radula evolution in the Mitridae is impeded by a lack of evidence on the functionality of different

1 types of radula, as there are no data on the possible adaptive value of different morphologies and  
2 selection pressures that have led to the emergence of the observed diversity. Further studies on  
3 the functional morphology and biochemistry of mitrid secretions would in this respect open new  
4 perspectives.  
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#### 8 *Taxonomy of Mitridae: historical considerations and new arrangement*

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10 The current Mitridae species list (as indexed in WORMS consulted on May 30 2017) comprises  
11 398 accepted Recent species, plus the three new species described in the present work. The  
12 baseline of Mitridae systematics is the fundamental revisions by Walter Cernohorsky, who first  
13 dealt with the subfamily Mitrinae (Cernohorsky 1976), and later with the Imbricariinae and  
14 Cylindromitrinae (Cernohorsky 1991). Cernohorsky's monographs had a profound impact on  
15 mitrid taxonomy and systematics, despite the general lumping attitude prevailing in his time,  
16 which resulted in an extensive taxonomic graveyard for many of the species level taxa he  
17 accepted as valid. Several cases of abusive synonymization are demonstrated in the present  
18 study. For instance, *Mitra morchii* A. Adams, 1855, considered by Cernohorsky a synonym of  
19 *Cancilla isabella*, is, based on Huang & Salisbury (2017) and on our data, not related to *Cancilla*  
20 or even to Imbricariinae. Another example is *Mitra millepunctata* G.B. Sowerby III, 1889,  
21 synonymized (Cernohorsky, 1976) with *Domiporta carnicolor* despite notable disparity in shell  
22 proportions, and later described as *Mitra terryi* Poppe, 2008. Altogether the number of valid  
23 species of Mitridae was greatly diminished by Cernohorsky, but the rate of species description  
24 increased notably in the following decades and over 100 species (i.e. almost 30% of the currently  
25 accepted number of species) were described since 1991. This burst of activity in mitrid  
26 taxonomy is also notable for being almost entirely accounted for by the amateur community:  
27 only ten out of 112 species described in the last 25 years were described by academics. Amateurs  
28 perhaps more reluctantly establish new supraspecific taxa, and only two genera *Calcimitra*  
29 Huang, 2011 and *Magnamitra* Huang & Salisbury, 2017 were established in the last 25 years,  
30 whereas 65 species described over this period were originally placed in *Mitra*.  
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47 A concise review of changes in mitrid genus-level taxonomy was presented by Cernohorsky  
48 (1970), in a study that itself contained the description of four new genera and subgenera  
49 (*Domiporta*, *Dibaphimitra*, *Neocancilla* and *Sohlia*). In the present study we have re-assessed the  
50 genus-level systematics of Recent Mitridae based on a combination of molecular and  
51 morphological data. The genus *Charitodoron* is segregated in the newly established family  
52 Charitodoronidae. The 26 genera of the revised Mitridae comprise six subfamilies: Mitrinae  
53 (with 14 genera), Strigatellinae (with the single genus *Strigatella*), Imbricariinae (with six  
54 genera), Cylindromitrinae (with the genera *Pterygia* and *Nebularia*), Isarinae new subfamily  
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1 (with the genera *Isara* and *Subcancilla*) and Pleioptygmatinae (with the single genus  
2 *Pleioptygma*); six genera, *Atrimitra* Dall, 1918, *Carinomitra* gen. nov., *Condylomitra* gen. nov.,  
3 *Dibaphimitra* Cernohorsky, 1970, *Magnamitra* Huang & Salisbury, 2017 and *Probata* Sarasúa,  
4 1989 are treated as *incertae sedis*. Undoubtedly the most revolutionary change in the taxonomy  
5 of the Mitridae is the falling apart of *Mitra* with the genus in its former taxonomic extension now  
6 reassigned to 14 genera, of which 6 are new. Other noteworthy changes are the transfer of the  
7 formerly mitrine *Nebularia* to Cyldromitridinae; of *Strigatella* to its own, newly recognized,  
8 subfamily Strigatellinae; of the formerly imbricariine genera *Ziba* and *Domiporta* to Mitridinae;  
9 and of *Subcancilla* to the newly established subfamily Isarinae. The genera *Mitra* and *Ziba* now  
10 include a much reduced species diversity, as all the Indo-Pacific species earlier placed in *Ziba*  
11 are now transferred to *Imbricaria*. The contents of *Imbricaria* is also expanded as a result of the  
12 transfer of the Indo-Pacific species of *Subcancilla*, which appear unrelated to the New World  
13 species of that genus.  
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15 The 32 genera now recognized in the family Mitridae increase considerably the previously  
16 accepted genus-level diversity (21 genera, including *Charitodoron*, indexed in WORMS as of  
17 May 2017). Still, the placement of several sequenced species remains uncertain. Lineage 3  
18 represented by MNHN IM-2007-35623 and lineage 16 represented by MNHN IM-2007-30270  
19 did not cluster with any other lineage and were not successfully sequenced for genetic markers  
20 other than COI. Thus, they at present remain “hanging” in the list of unallocated Mitridae and  
21 may potentially represent two more new genera.  
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### 23 *Phylogeographic patterns in the Mitridae*

24 It has been widely known that the Indo-West Pacific harbours the greatest diversity of mitrid  
25 species and lineages, and therefore a good representation of IP localities at various depths was a  
26 primary requirement to our work. 88 of the 103 inferred species of Mitridae and  
27 Charitodoronidae in our dataset originate from Indo-Pacific localities. Besides, three species  
28 were sampled from the Mediterranean and NE Atlantic, two from West Africa, four from the  
29 Caribbean, and six from the Panamic province (Fig. 42). 23 mitrid genera were sampled in the  
30 Indo-Pacific, of which 19 do not occur outside the Indo-Pacific according to our data. Moreover,  
31 the subfamilies Imbricariinae and Cyldromitridinae, as circumscribed herein, are represented  
32 solely by Indo-Pacific forms. At least three genera (*Episcomitra*, *Isara* and *Ziba*) are found in  
33 West Africa, with the first two also inhabiting the Mediterranean. The New World fauna of  
34 Mitridae includes at least eight genera in four subfamilies: Mitridinae (*Neotiarra*), Strigatellinae  
35 (*Strigatella*), Isarinae (*Isara*, *Subcancilla*), and Pleioptygmatinae (*Pleioptygma*), plus the genera  
36 *Atrimitra*, *Dibaphimitra* and *Probata* that we treat as *incertae sedis*. The six genera *Atrimitra*,  
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1 *Dibaphimitra*, *Neotiara*, *Pleioptygma*, *Probata*, and *Subcancilla* are currently thought to be  
2 endemic to Panamic and/or the Caribbean, although a close affinity of Panamic and Caribbean  
3 species was herein confirmed only in the genera *Neotiara* and *Subcancilla*.  
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5 Of all studied genera, *Charitodoron* probably demonstrates the narrowest range, being  
6 confined to deep waters in the Mozambique Chanel and off South Africa. According to some  
7 authors (e.g., Obura, 2012), starting in the Eocene, this area served as a main refuge for relict  
8 lineages of Tethyan origin which, for some reason, did not give rise to new radiations. The long  
9 branch that separates *Charitodoron* on the molecular tree, characters such as the underived  
10 morphology (with only the radula indicating its relatedness to Mitridae), and its low diversity in  
11 the Recent fauna, all point to the relict nature of *Charitodoron*. The paucispiral, bulbous  
12 protoconch of *Charitodoron* indicates non-planktotrophic development, which correlates well  
13 with its restricted distribution.  
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15 Conversely, the distribution of *Isara* is the widest among mitrid genera: this is the only  
16 genus recorded in more than two major zoogeographical regions of the shelf (as defined by  
17 Briggs and Bowen 2012) - Indo-West Pacific, East Atlantic and West Atlantic (Fig. 42) -, and it  
18 may be also present in the East Pacific (see Remarks under *Isara*). *Isara* species contribute  
19 significantly to mitrid diversity in the peripheral Indo-Pacific (South Australia, presumably  
20 South Africa) (see Fig. 8), but they are rare and not really diverse in the Central Indo-West  
21 Pacific. In our understanding, *Isara* is undoubtedly an old and underived lineage of Mitridae, and  
22 this pattern may be interpreted in two different ways. According to one possible scenario, it was  
23 once widely distributed in tropical seas and subsequently was replaced by younger and derived  
24 lineages in the Central Indo-West Pacific while maintaining its diversity in peripheral areas. The  
25 other possible scenario suggests that the primarily Indo-Pacific *Isara*, once “forced” into  
26 subtropical waters by growing competition with younger evolutionary lineages of Mitridae, has  
27 adapted to new temperatures and, through this, was capable of spreading beyond the  
28 biogeographical limits of the Indo-Pacific. Although most known species of *Strigatella* occur in  
29 the Indo-Pacific, an amphi-Pacific distribution characterizes this genus, with at least one species  
30 inhabiting shallow water in the Panamic province ending up close to the Indo-Pacific species in  
31 both molecular and morphological characters. Finally, if ‘*Mitra*’ *hebes* is related to the species of  
32 *Domiporta*, as suggested by shell and radular morphology, the range of that genus would also  
33 include West Africa.  
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35 The generally low overlap in regional lists of mitrid genera may be interpreted as a  
36 consequence of the relatively late major diversification of mitrid lineages, dating back to the time  
37 when modern biogeographical barriers were already established, and largely separate  
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2 evolutionary radiations having taken place in i) Late Tethys – Paratethys - Indo-Pacific, ii) West  
3 Africa and iii) the New World.  
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6 We have attempted to circumscribe the bathymetric distribution of the newly delineated  
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8 genera, based primarily on the locality data of sequenced specimens. Given the patchiness of our  
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10 data, we arbitrarily divided the sampled depth range from 0 to about 1800 meters into four depth  
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12 intervals: 1) from 0 to 40 meters, 2) from 41 to 80 meters, 3) from 81 to 300 m and 4) >300 m.

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14 Of the 103 species of Mitridae studied herein based on molecular characters, 72 were  
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16 sampled from the 0-40 meters interval, seven from the 41-80 meters interval, nine from the 81-  
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18 300 meters interval, and 20 from depths in excess of 300 meters. This accounting does not,  
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20 however, strictly reflect changes in species richness with depths, as it is strongly biased by the  
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22 distribution of collecting efforts (Fig. 43). Intertidal and upper subtidal zones (at diveable depths)  
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24 as well as outer slopes from about 200 down to about 1800 meters were sampled incomparably  
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26 better than the mesophotic and abyssal zones. Therefore our data do not necessarily demonstrate a  
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28 drop in species richness in the 41-300 m interval. Nevertheless, despite the sampling bias, there  
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30 is an obvious pattern of greater mitrid diversity in shallow water, decreasing with depth. This  
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32 pattern can be explained by a greater diversity of habitats, often fragmented and intermixed at a  
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34 small scale, in shallow water ecosystems. Another related factor is the multitude of biological  
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36 interactions in these shallow habitats, driven by the complex ecological structure of reefs and  
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38 associated habitats, providing a wealth of niches to be explored by mitrids and their preys.

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40 The bathymetric distribution of the newly delineated mitrid genera, is shown on Figure 43  
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42 based on our results (black vertical bars) and literature (grey vertical bars). Because of the very  
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44 fragmentary data, some of the displayed results are inconsistent, like the disjunct bathymetric  
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46 range of *Gemmulimitra* and *Subcancilla*. We in fact fully expect that many genera, which in our  
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48 results are restricted to the 0-40 meters depth interval, in fact reach deeper, probably down to 80-  
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50 120 meters. Nevertheless, some general conclusions can be drawn from the observed  
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52 bathymetric distribution of the genera. The representation of mitrid genera in shallow water is  
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54 notably higher than at depths in excess of 100 – 150 meters, which mirrors the distribution of  
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56 species diversity discussed above. Whereas *Gemmulimitra*, *Imbricaria*, *Isara*, *Roseomitra*, and  
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58 *Subcancilla* have extensive bathymetric ranges, with congeneric species sampled from the  
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60 intertidal down to 300-400 meters, the mitrid fauna from the greatest depths is essentially  
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62 represented by specialized lineages (treated here as genera), that do not occur in shallower water.  
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64 The genera *Calcimitra*, *Cancilla*, *Cancillopsis*, *Fusidomiporta* and *Profundimitra* represented in  
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66 our dataset by 15 species (plus 2 species of *Charitodoron*) and the genus *Eumitra* (not included  
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68 in our phylogenetic studies) constitute several separate radiations that thrive in the deep sea.

*World diversity of Mitridae*

Of 103 species included in our molecular dataset, 89 were identified with confidence - these constitute 22% of the described diversity of the family Mitridae. Of the remaining 15 species, four were either not identified ("sp.") or were attributed to a described species with an indication of some disparity in morphological or molecular characters (referred to as "cf."); ten proved to be unnamed - although three of them showed some similarity to described species and were allocated to tentative species complexes (referred to as "aff."). Remarkably, of the 60 mitrid species from the Indo-Pacific sampled in the 0-40 meters depth interval only one (*Strigatella* aff. *paupercula*), represented a new species - the notable divergence of our material from the otherwise similar *Strigatella paupercula* was only revealed in the phylogenetic analysis. The proportion of unidentified / undescribed species grows with increasing depth and, of 20 species from depths greater than 300 meters in the analysis, only 11 were identified with confidence, and seven (i.e. 35%) were undoubtedly new, all representing previously undescribed lineages of Mitrinae. Three of these species were here described as *Profundimitra taylori* n. gen. and sp., *Fusidomiporta ponderi* n. gen. and sp., and *Gemmulimitra neocaledonica* n. gen. and sp. Thus, an estimate of 30 to 100 species of Mitridae remaining to be described from the deep waters of the Indo-Pacific seems reasonable to us. Recognition of new deep water mitrid species may be hampered by the high intraspecific variability of shell sculpture and, simultaneously, rampant convergences leading to hardly distinguishable shells in not closely related species. Likewise, the radula appears generally useless for species delimitation, as in most cases it retains plesiomorphic morphology, and the significance of slight variations in the number of cusps is unknown. Thus, molecular data will remain essential for a reliable recognition of new deep water taxa of Mitridae.

Whereas a significant proportion of the deep water mitrids remains undescribed, the overall diversity of the family in deep water pales in comparison with the well documented diversity of the family in shallow water. These contrasting proportions of described Mitridae in shallow *versus* deep water can be viewed as a result of recent efforts by collectors and amateur taxonomists. Since the first half of the 19<sup>th</sup> century and the iconic monograph by Reeve (1844-1845), the comparatively easily accessible species from shallow water are collected steadily throughout many Indo-Pacific locales and then carefully scrutinized by a dedicated community of amateurs, leading to the present day state of mitrid taxonomy, with a pretty well inventoried shallow water fauna. Undoubtedly, there are areas with high local endemism that still hold undescribed species, especially in peripheral locales (e.g., southern Australia, South and East Africa and the Arabian Sea), but this is not the general situation.

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The diversity of mitrids in the Mediterranean is low, and all three species known from that sea were included in the present study. Conversely, we have included only a limited number of species from West Africa and the New World, which makes any judgment on diversity in these regions untimely. Two Panamic species in our dataset were not confidently identified but were represented by subadults, the identification of which is always troublesome, and the uncertainty of our identifications cannot be viewed as an indication of undescribed species. A more thorough sampling in both the Panamic and Caribbean region is definitely required to assess the proportion of undescribed species in these areas and uncover the relationships of their endemic phylogenetic lineages.

For Review Only



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For Review Only

Table 1.

Species	Revised Placement	Catalog N	Expedition / Locality	Station	collection data <sup>a</sup>	BOLD	COI	16S	12S	H3	
<b>Charitodoronidae</b>											
<i>Charitodoron bathybius</i>	<i>Charitodoron</i>	IM-2013-40658	MAINBAZA	CC3171	25°59'S 34°42'E, 771-776 m	MITRI040-15	KR087241	-	-	KR088082	
		IM-2007-38306	MAINBAZA	CC3157	21°46'S 36°25'E, 1410-1416 m	MITRI057-15	KR087240	KR087994	KR087335	KR088081	
<b>Mitridae</b>											
<i>Mitra invicta</i>	<i>Calcimitra</i>	IM-2013-15373	PAPUA NIUGINI	CP3949	05°12'S 145°51'E, 380-407 m						
		IM-2007-32130	PANGLAO 2005	CP2383	8°44'42"N 123°18'29.9772"E, 338-351 m			-	-	-	
<i>Mitra christinae</i>	<i>Calcimitra</i>	IM-2007-32131	PANGLAO 2005	CP2383	08°45'N 123°18'E, 338-351 m	NEOGA491-10	KR087269	-	-	-	
		IM-2007-32133	PANGLAO 2005	CP2359	8°49'54.012"N 123°34'54.0228"E, 437-476 m			-	-	-	
<i>Mitra glaphyria</i>	<i>Calcimitra</i>	IM-2007-30065	PANGLAO 2005	CP2358	8°52'5.988"N 123°37'5.9952"E, 569-583 m			-	-	-	
		IM-2007-30066	PANGLAO 2005	CP2342	9°24'24.012"N 123°52'54.0048"E, 1240-1258 m			-	-	-	
		IM-2007-30103	PANGLAO 2005	CP2354	9°25'59.988"N 124°6'29.988"E, 1769-1773 m			-	-	-	
		IM-2007-32126	PANGLAO 2005	CP2388	9°26'53.988"N 123°34'29.9892"E, 762-786 m			-	-	-	
		IM-2007-32132	PANGLAO 2005	CP2388	9°26'53.988"N 123°34'29.9892"E, 762-786 m			-	-	-	
		IM-2013-40650	BIOPAPUA	CP3728	07°52'S 148°01'E, 498-501 m		MITRI050-15	KR087281	KR088031	KR087373	-
		IM-2007-30127	EBISCO	DW2515	24°4'31.1988"S 159°41'2.4216"E, 330-370 m				-	-	-
<i>Mitra labecula</i>	<i>Calcimitra</i>	IM-2007-38186	MIRIKI	CP3253	15°24'45"S 45°55'23.988"E, 943-950 m			-	-	-	
<i>Mitra triplicata</i>	<i>Calcimitra</i>	IM-2007-38186	MIRIKI	CP3253	15°24'45"S 45°55'23.988"E, 943-950 m			-	-	-	
<i>Cancilla baeri</i>	<i>Cancilla</i>	IM-2013-58853	KAVIENG 2014	DW4484	2°25'50.40"S 149°55' 13" E			-	-	-	
<i>Cancilla rehderi / fibula</i>	<i>Cancilla</i>	IM-2007-38689	TARASOC	DW3441	16°43'S 151°26'W, 350-360 m	MITRI056-15	-	KR087991	KR087332	-	
		IM-2007-30062	PANGLAO 2005	CP2331	9°39'11.988"N 123°47'30.0192"E, 255-268 m			-	-	-	
		IM-2007-30126	PANGLAO 2005	CP2331	9°39'11.988"N 123°47'30.0192"E, 255-268 m			-	-	-	
		IM-2007-38551	TARASOC	DW3459	17°27'47.9988"S 149°49'12.0252"W, 485-560 m			-	-	-	
		IM-2007-38688	TARASOC	DW3441	16°41'42"S 151°26'5.9928"W, 350-360 m			-	-	-	
		IM-2007-38801	TARASOC	DW3441	16°41'42"S 151°26'5.9928"W, 350-360 m			-	-	-	
		IM-2013-19073	PAPUA NIUGINI DW	CP4059	02°38'S 141°18'E, 335 m			-	-	-	
<i>Cancilla cf. fibula</i> *	<i>Cancilla</i>	IM-2013-40646	EXBODI	CP3822	21°52'S 166°51'E, 341-506 m	MITRI030-15	-	KR087990	KR087331	KR088076	
<i>Mitra schepmani</i>	<i>Cancilla</i>	IM-2007-30129	EBISCO	DW2514	24°6'25.7976"S 159°41'1.8168"E, 295-310 m			-	-	-	
		IM-2007-35752	CONCALIS	DW2963	18°22'4.8"S 162°58'45.0192"E, 220-240 m			-	-	-	
		IM-2013-40645	EXBODI	DW3926	18°35'S 164°20'E, 364-473 m		MITRI025-15	KR087279	KR088029	KR087371	KR088109
<i>Cancilla meimiaoe</i>	<i>Cancillopsis</i>	IM-2007-30011	SANTO 2006	AT19	15°40'48"S 167°00'29.99"E, 503-600 m			-	-	-	
<i>Mitra peculiaris</i>	<i>Carinomitra</i>	IM-2013-6168	PAPUA NIUGINI	PR218	05°07.3'S 145°49.4'E, 14 m	MITRI051-15	KR087278	KR088028	KR087370	KR088108	
		IM-2007-30256	SANTO 2006	NR21	15°26'48.012"S 167°15'5.9868"E, 3-22 m			-	-	-	
<i>Mitra typha</i>	<i>Carinomitra</i>	IM-2013-4030	PAPUA NIUGINI	PB28	05°11,9'S 145°49,6'E, 10 m						
<i>Mitra bernhardina</i>	<i>Condylomitra</i>	IM-2013-13618	PAPUA NIUGINI	PB19	05°05.1'S 145°48.6'E, 10 m	MITRI043-15	KR087268	KR088019	KR087362	KR088104	
		IM-2013-54115	KAVIENG	KB40	02°36,6'S 150°32,9'E, 2-7 m						
<i>Mitra tuberosa</i>	<i>Condylomitra</i>	IM-2007-30311	PANGLAO 2004	R75	09°32.8'N 123°42.1'E, 3-35 m	NEOGA294-10	KR087283	KR088033	KR087375	KR088112	
<i>Domiporta carnicolor</i> *	<i>Domiporta</i>	IM-2013-40684	PHILIPPINES, off Noc-Nocan Is		10°15.06'N 124°25.07'E, 4-12 m						

<i>Neocancilla circula</i>	<i>Domiporta</i>	IM-2007-30018	SANTO 2006	LD24	15°31'23.988"S 167°10'0.019"E, 47 m	-	-	-	-	-
<i>Domiporta filaris</i>	<i>Domiporta</i>	IM-2013-12956	PAPUA NIUGINI	PD23	05°06'S 145°49.2'E, 3-7 m	MITRI044-15	KR087251	KR088004	KR087348	KR088090
<i>Domiporta granatina</i>	<i>Domiporta</i>	IM-2013-15906	PAPUA NIUGINI	PM42	05°10.2'S 145°50.4'E, 0-1 m	-	-	-	-	-
		IM-2013-40641	INHACA 2011	MR15	26°00.0'S 32°54.4'E, 4 m	MITRI038-15	KR087252	KR088005	KR087349	KR088091
<i>Domiporta praestantissima</i>	<i>Domiporta</i>	IM-2007-30081	PANGLAO 2004	R36	9°30'11.988"N 123°55'18.0084"E, 3-32 m	-	-	-	-	-
		IM-2013-40642	VIETNAM, Nha-Trang Bay	D3	12°10.084'N 109°17.771'E, 6-18 m	MITRI032-15	KR087253	KR088006	-	KR088092
<i>Mitra cornicula</i>	<i>Episcomitra</i>	BAU1578-1	GREECE, Astypalea Is., Agrilidi		36°35'00.0"N 26°25'02.4"E, 2-7 m	-	-	-	-	-
		BAU1578-2	GREECE, Astypalea Is., Agrilidi		36°35'00.0"N 26°25'02.4"E, 2-7 m	-	-	-	-	-
		IM-2013-40661	ITALY, Sicily, Syracuse		37°0.460'N 15°18.62'E, 6-12 m	MITRI059-15	KR087270	KR088020	KR087363	-
<i>Mitra zonata</i>	<i>Episcomitra</i>	BAU2538	ITALY, off Chioggia		45°12'00"N 12°40'00"E, 40 m	-	-	-	-	-
Gen. <i>ponderi</i> sp. nov.	<i>Fusidomiporta</i>	IM-2013-40665	BIOPAPUA	CP3692	02°10'S 147°19'E, 408-448 m	-	-	-	-	-
<i>Cancilla</i> sp. nov.	<i>Fusidomiporta</i>	IM-2007-32153	PANGLAO 2005	DW2364	9°0'42.012"N 123°25'30.0108"E, 427 m	-	-	-	-	-
<i>Mitra avenacea</i>	<i>Gemmulimitra</i>	IM-2013-11683	PAPUA NIUGINI	PR14	05°12'S 145°48.1'E, 2-3 m	-	-	-	-	-
Gen. <i>neocaledonica</i> sp. nov.	<i>Gemmulimitra</i>	IM-2013-40655	EXBODI	CP3821	21°53'S 166°50'E, 211-440 m	MITRI045-15	KR087285	KR088036	-	KR088115
<i>Mitra strongae</i>	<i>Gemmulimitra</i>	IM-2007-36727	MIRIKI	DW3213	12°30'46.8"S 47°52'19.2"E, 262-289 m	-	-	-	-	-
<i>Ziba bantamensis</i>	<i>Imbricaria</i>	IM-2013-16688	PAPUA NIUGINI	PD67	05°15.5'S 145°46.8'E, 2-6 m	-	-	-	-	-
		IM-2007-30026	SANTO 2006	LD01	15°28'59.988"S 167°14'54.013'E, 24 m	-	-	-	-	-
		IM-2007-30044	SANTO 2006	VM09	15°35'48.012"S 167°06'06.0084"E, intertidal	-	-	-	-	-
<i>Imbricaria conularis</i>	<i>Imbricaria</i>	IM-2007-30045	SANTO 2006	VM09	15°35'48.012"S 167°06'06.0084"E, intertidal	-	-	-	-	-
		IM-2007-30046	SANTO 2006	VM09	15°35'48.012"S 167°06'06.0084"E, intertidal	-	-	-	-	-
		IM-2013-18043	PAPUA NIUGINI	PR203	05°10.3'S 145°48.5'E, 1-19 m	MITRI053-15	KR087263	KR088014	KR087356	KR088099
<i>Ziba flammigera</i>	<i>Imbricaria</i>	IM-2013-40656	VIETNAM, Nha-Trang Bay	ND7	12°10.443'N 109°16.298'E, 15-18 m	MITRI028-15	KR087322	KR088068	KR087410	-
		IM-2007-30016	SANTO 2006	LD21	15°31'18.012"S 167°9'53.9748"E, 16 m	-	-	-	-	-
		IM-2007-30054	SANTO 2006	VM32	15°26'35.988"S 167°15'11.9736"E, intertidal	-	-	-	-	-
<i>Ziba fulgetrum</i>	<i>Imbricaria</i>	IM-2007-30115	SANTO 2006	VM32	15°26'35.988"S 167°15'11.9736"E, intertidal	-	-	-	-	-
		IM-2013-18112	PAPUA NIUGINI	PR240	05°08.2'S 145°48.7'E, 3-20 m	MITRI046-15	KR087323	KR088069	KR087411	KR088149
<i>Subcancilla hrdlickai</i>	<i>Imbricaria</i>	IM-2013-18020	PAPUA NIUGINI	PD75	05°14.2'S 145°47.8'E, 10-25 m	-	-	-	-	-
<i>Ziba insculpta</i>	<i>Imbricaria</i>	IM-2013-40657	VIETNAM, Nha-Trang Bay	ND7	12°10.443'N 109°16.298'E, 15-18 m	MITRI048-15	KR087324	KR088070	-	KR088150
		IM-2007-30340	BOA1	CP2442	15°7'26.22"S 166°54'5.418"E, 131-308 m	-	-	-	-	-
		IM-2007-34547	AURORA 2007	CP2716	14°30'N 121°41'E, 335-356 m	NEOGA766-10	KR087295	KR088044	-	-
<i>Subcancilla rufogyrata</i>	<i>Imbricaria</i>	IM-2007-36131	SALOMONBOA-3	DW2852	9°46'0.012"S 160°51'0.00"E, 220 m	-	-	-	-	-
		IM-2007-32124	PANGLAO 2005	CP2378	8°38'48.012"N 123°20'5.9964"E, 65 m	-	-	-	-	-
<i>Subcancilla pugnaxa</i>	<i>Imbricaria</i>	IM-2007-34548	AURORA 2007	CP2763	15°51'2.4012"N 121°51'2.412"E, 42-44 m	-	-	-	-	-
		IM-2007-34549	AURORA 2007	CP2763	15°51'2.4012"N 121°51'2.412"E, 42-44 m	-	-	-	-	-
<i>Ziba verrucosa*</i>	<i>Imbricaria</i>	IM-2013-14284	PAPUA NIUGINI	PD39	04°59.3'S 145°47.5'E, 2-4 m	-	-	-	-	-
<i>Imbricaria punctata</i>	<i>Imbricariopsis</i>	IM-2013-11604	PAPUA NIUGINI	PM12	05°00.2'S 145°47.6'E, 0-1 m	-	-	-	-	-
<i>Mitra carbonaria*</i>	<i>Isara</i>	C.335424	AUSTRALIA, Sydney, Collaroy, Long Reef		33°44'42"S, 151°19' E, intertidal	-	-	-	DQ916435.1	-
<i>Mitra cornea</i>	<i>Isara</i>	BAU0709-1	AZORES, Fajal, Ponta dos Capelinhos		38°35'30"N 28°49'43"W, intertidal	-	-	-	-	-

		BAU0709-2	AZORES, Fajal, Ponta dos Capelinhos		38°35'30"N 28°49'43"W, intertidal					
		BAU0709-3	AZORES, Fajal, Ponta dos Capelinhos		38°35'30"N 28°49'43"W, intertidal					
		BAU2537-1	ITALY, Giannutri Is., Punta San Francesco		42°15'06"N, 11°06'59"E, 10-20 m					
		BAU2537-3	ITALY, Giannutri Is., Punta San Francesco		42°15'06"N, 11°06'59"E, 10-20 m					
<i>Mitra glabra</i>	<i>Isara</i>	IM-2013-40640	W-AUSTRALIA	WE01	15°16.94'S 124°06.3'E, 11 m	MITRIO42-15	KR087272	KR088022	KR087365	KR088105
<i>Mitra nigra</i> (Gmelin)*	<i>Isara</i>	IM-2013-40676	ZANAGA	DV08	04°42,93'S 11°47,49'E, 14-15 m					
<i>Subcancilla straminea</i>	<i>Isara</i>	IM-2013-56423	GUYANE	CP4375	06°39'N 52°30'W, 195-200 m					
<i>Mitra mitra</i>	<i>Mitra</i>	IM-2013-40639	INHACA 2011	MR15	26°00.0'S 32°54.4'E, 4 m	MITRIO52-15	KR087275	KR088025	KR087368	-
<i>Mitra papalis</i>	<i>Mitra</i>	IM-2007-30033	SANTO 2006	NR07	15°34'23.988"S 167°13'5.9628"E, 9 m					
		IM-2007-30174	SANTO 2006	DR87	15°38.5'S 167°15.1'E, 13 m	NEOGA255-10	KR087276	KR088026	-	-
<i>Mitra acuminata</i> *	<i>Nebularia</i>	IM-2013-13288	PAPUA NIUGINI	PM25	05°01,1'S 145°47,9'E, intertidal					
<i>Nebularia contracta</i>	<i>Nebularia</i>	IM-2013-10345	PAPUA NIUGINI	PR04	05°10,1'S - 145°50,5'E, 30m					
<i>Mitra eremitarum</i> *	<i>Nebularia</i>	IM-2013-16323	PAPUA NIUGINI	PM51	05°05,5'S 145°48,6'E, 0-1 m					
<i>Mitra incompta</i>	<i>Nebularia</i>	IM-2007-30175	SANTO 2006	DR78	15°28.4'S 167°15.2'E, 25 m	NEOGA256-10	KR087273	KR088023	KR087366	KR088106
		IM-2007-30028	SANTO 2006	NR05	15°28'41.988"S 167°15'11.9736"E, 19 m					
		IM-2007-30097	PANGLAO 2004	D09	9°30'0.0"N 123°55'18.0084"E, 2-4 m					
<i>Neocancilla clathrus</i>	<i>Neocancilla</i>	IM-2007-30177	SANTO 2006	FR42	15°28'36.012"S 167°15'5.9868"E, 3-31 m					
		IM-2007-30178	SANTO 2006	DR73	15°22' 32.22" S 167°11' 21.12" E, 10-25 m					
		IM-2007-32368	SANTO 2006	FR30	15°27'18"S 167°15'35.982"E, 45 m					
		IM-2013-18342	PAPUA NIUGINI	PS47	05°04,7'S 145°48,9'E, 8 m					
<i>Neocancilla papilio</i>	<i>Neocancilla</i>	IM-2007-30210	PANGLAO 2004	R14	9°37'23.988"N 123°54'29.9988"E, 6-8 m					
		IM-2013-12560	PAPUA NIUGINI	PR24	05°12.3'S 145°48.8'E, 15 m	MITRIO34-15	KR087287	KR088037	KR087376	KR088116
<i>Neocancilla rufescens</i>	<i>Neocancilla</i>	IM-2013-40644	INHACA 2011	MD22	25°59.7'S 32°46.8'E, 22 m	MITRIO33-15	KR087288	KR088038	-	KR088117
<i>Mitra aff. inca</i> *	<i>Neotiarra</i>	BAU0279-1	PANAMA, Venado Beach		8°53'35"N, 79°36'25"W, intertidal					
<i>Mitra lens</i>	<i>Neotiarra</i>	BAU00800	PANAMA, Panama City		08°95'N 79°53'W, intertidal		FM999161	FM999110	FM999079	-
<i>Mitra nodulosa</i> *	<i>Neotiarra</i>	IM-2013-9546	KARUBENTHOS	GM10	16°12,53'N 61°25,55'W, 1 m					
<i>Mitra barbadensis</i> *	<i>Probata</i>	IM-2013-7772	KARUBENTHOS	GR36	16°30,57'N 61°28,45'W, 12 m					
<i>Cancilla planofilum</i>	<i>Profundimitra</i>	IM-2007-32149	PANGLAO 2005	CP2398	9°32'35.988"N 123°40'30.0108"E, 713-731 m					
<i>Gen. taylori</i> sp. nov.	<i>Profundimitra</i>	IM-2013-40651	BIOPAPUA	CP3671	04°04'S 151°56'E, 585-601 m	MITRIO27-15	KR087284	KR088034	-	KR088113
		IM-2007-35618	AURORA 2007	CP2658	15°58'1.8012"N 121°49'6.5892"E, 422-431 m					
		IM-2007-35711	AURORA 2007	CP2658	15°58'1.8012"N 121°49'6.5892"E, 422-431 m					
<i>Gen. n. sp.</i>	<i>Profundimitra</i>	IM-2007-36757	MIRIKI	CP3289	14°29'25.188"S 47°26'21.012"E, 332-379 m					
		IM-2013-40654	EXBODI	CP3829	22°02'S 167°05'E, 350-360 m	MITRIO47-15	KR087233	KR087989	KR087330	KR088075
<i>Mitra atjehensis</i>	<i>Pseudonebularia</i>	IM-2007-30264	SANTO 2006	EP01	15°32'30.012"S 167°8'59.9784"E, 46-47 m					
<i>Nebularia chrysalis</i>	<i>Pseudonebularia</i>	IM-2007-30055	SANTO 2006	VM25	15°36'36"S 167°01'36.0192"E, intertidal					
<i>Nebularia connectens</i>	<i>Pseudonebularia</i>	IM-2013-2342	PAPUA NIUGINI	PB16	05°10.7'S 145°47.7'E, intertidal	MITRIO37-15	KR087271	KR088021	KR087364	-
<i>Nebularia maesta</i>	<i>Pseudonebularia</i>	IM-2013-40648	MIRIKY	CP3288	14°31.9'S 47°26.54' E, 46-54 m	MITRIO36-15	KR087274	KR088024	KR087367	KR088107
<i>Nebularia pediculus</i>	<i>Pseudonebularia</i>	IM-2007-30330	SANTO 2006	FR01	15°32'17.988"S 167°13'5.9628"E, 18-20 m					



		IM-2013-12705	PAPUA NIUGINI	PB15	05°04.7'S 145°48.9'E, 5 m	MITRI035-15	KR087282	KR088032	KR087374	KR088111
<i>Nebularia tabanula</i>	<i>Pseudonebularia</i>	IM-2007-30027	SANTO 2006	VM37	15°34'29.36"S 167°12'36.025"E, intertidal		-	-	-	
		IM-2007-30315	PANGLAO 2004	M40	9°35'42"N 123°44'42.0108"E, 3 m		-	-	-	
<i>Mitra tornata</i>	<i>Pseudonebularia</i>	IM-2013-12538	PAPUA NIUGINI	PB14	05°13,8'S 145°48'E, 15 m					
<i>Pterigia conus</i>	<i>Pterigia</i>	IM-2007-30119	PANGLAO 2004	M11	9°38'17.988"N 123°49'36.0048"E, 3 m		-	-	-	
		IM-2007-30076	PANGLAO 2004	M26	9°40'54.012"N 123°51'6.0084"E, intertidal		-	-	-	
<i>Pterigia dactylus</i>	<i>Pterigia</i>	IM-2013-14989	PAPUA NIUGINI	PM39	05°12.1'S 145°48.4'E, intertidal	MITRI049-15	KR087291	KR088041	KR087379	KR088120
		IM-2007-30010	SANTO 2006	ZM15	15°38'06"167°05'53.9808"E, intertidal		-	-	-	
<i>Pterigia fenestrata</i>	<i>Pterigia</i>	IM-2007-30039	SANTO 2006	DR09	15°34'36.012"S 167°13'47.9856"E, 12 m		-	-	-	
		IM-2013-47383	KAVIENG	KR12	02°36,3'S 150°46,3'E, 18 m					
		IM-2007-34816	PANGLAO 2005	CP2378	8°38'48.012"N 123°20'5.9964"E, 65 m		-	-	-	
<i>Pterigia sinensis</i>	<i>Pterigia</i>	IM-2009-15439	ATIMO VATAE	CP3568	25°04.7'S 47°03.4'E, 64-65 m	MITRI054-15	KR087292	KR088042	KR087380	KR088121
<i>Mitra cardinalis</i> *	<i>Quasimitra</i>	IM-2013-40681	KAVIENG	KR178	02°45,2'S 150°43,1'E, 2-46 m					
<i>Mitra puncticulata</i>	<i>Quasimitra</i>	IM-2013-40685	PHILIPPINES, off Noc-Nocan Is		10°15.06'N 124°25.07'E, 4-12 m					
<i>Mitra sanguinolenta</i>	<i>Quasimitra</i>	IM-2013-40677	INHACA 2011	MS02	26°06.3'S 32°58.0'E, 17-19 m					
<i>Mitra sophiae</i>	<i>Quasimitra</i>	IM-2007-30056	SANTO 2006	DR09	15°34.6'S 167°13.8'E, 12 m	NEOGA229-10	KR087280	KR088030	KR087372	KR088110
<i>Mitra millepunctata</i>	<i>Roseomitra</i>	IM-2013-40686	PHILIPPINES, off Noc-Nocan Is		10°15.06'N 124°25.07'E, 4-12 m					
		IM-2007-30074	PANGLAO 2004	T28	9°34'59.988"N 123°51'24.0012"E, 77-84 m		-	-	-	
<i>Mitra rosacea</i>	<i>Roseomitra</i>	IM-2007-30309	SANTO 2006	AT44	15°36'S 167°03'E, 86-118 m	NEOGA292-10	KR087267	KR088018	KR087361	KR088103
		IM-2013-17614	PAPUA NIUGINI	PD66	05°15,5'S 145°47,3'E, 2-6 m					
<i>Scabricola desetangsii</i>	<i>Scabricola</i>	IM-2013-50703	KAVIENG	KR54	02°42,3'S 150°39,1'E, 7-10 m					
<i>Imbricaria olivaeformis</i>	<i>Scabricola</i>	IM-2013-18062	PAPUA NIUGINI	PR214	05°10.2'S 145°50.4'E, 1-8 m	MITRI041-15	KR087264	KR088015	KR087357	-
<i>Scabricola variegata</i>	<i>Scabricola</i>	IM-2013-40683	PHILIPPINES, off Noc-Nocan Is		10°15.06'N 124°25.07'E, 4-12 m					
<i>Mitra ambigua</i>	<i>Strigatella</i>	IM-2013-2993	PAPUA NIUGINI	PB18	05°06,3'S 145°49,1'E, 26 m					
<i>Mitra aurantia</i>	<i>Strigatella</i>	IM-2013-40679	INHACA 2011	MB07	25°59.7'S 32°54.2'E, 2-10 m					
		IM-2007-30023	SANTO 2006	VM36	15°27'29.988"S 167°15'24.0048"E, intertidal		-	-	-	
<i>Mitra coronata</i>	<i>Strigatella</i>	IM-2013-54145	KAVIENG	KB40	02°36,6'S 150°32,9'E, 2-7 m					
<i>Strigatella decurtata</i>	<i>Strigatella</i>	IM-2013-15843	PAPUA NIUGINI	PM41	05°08,1'S 145°49,3'E, 0-1 m					
<i>Mitra fulvescens</i>	<i>Strigatella</i>	IM-2013-40680	TUHAA PAE	AMA03	21°48,2'S 154°43,2'W, 26 m					
<i>Mitra imperialis</i>	<i>Strigatella</i>	IM-2007-30173	SANTO 2006	FR01	15°32'17.988"S 167°13'5.9628"E, 18-20 m		-	-	-	
<i>Strigatella litterata</i>	<i>Strigatella</i>	IM-2013-12959	PAPUA NIUGINI	PM22	05°04,7'S 145°48,9'E, intertidal					
<i>Mitra luctuosa</i>	<i>Strigatella</i>	IM-2013-11682	PAPUA NIUGINI	PR14	05°12'S 145°48,1'E, 2-3 m					
<i>Mitra lugubris</i>	<i>Strigatella</i>	IM-2013-40678	TUHAA PAE	AT07	23°19,7'S 149°29,3'W, 14 m					
		IM-2007-30036	SANTO 2006	VM02	15°34'54.012"S 167°02'23.9748"E, intertidal		-	-	-	
<i>Strigatella paupercula</i>	<i>Strigatella</i>	IM-2007-30122	PANGLAO 2004	M26	9°40'54.012"N "123°51'6.0084"E, 2 m		-	-	-	
		IM-2013-15188	PAPUA NIUGINI	PM39	05°12.1'S 145°48.4'E, intertidal	MITRI031-15	KR087277	KR088027	KR087369	-
<i>Strigatella aff. paupercula</i>	<i>Strigatella</i>	IM-2007-30052	SANTO 2006	VM02	15°34'54.012"S 167°02'23.9748"E, intertidal		-	-	-	
<i>Strigatella scutulata</i>	<i>Strigatella</i>	IM-2013-12771	PAPUA NIUGINI	PM22	05°04,7'S 145°48,9'E, intertidal					

<i>Strigatella tristis</i>	<i>Strigatella</i>	BAU0285	PANAMA, Las Perlas, Pedro Gonzalez Is.		8°23'38"N, 79°07'01"W, intertidal					
		BAU2534-2	PANAMA, Rio Mar		8°27'28"N, 79°58'01"W, intertidal					
<i>Mitra vexillum*</i>	<i>Strigatella</i>	IM-2013-12570	PAPUA NIUGINI	PR24	05°12,3'S 145°48,8'E, **m					
<i>Subcancilla attenuata</i>	<i>Subcancilla</i>	BAU0392	PANAMA, Las Perlas, Contadora Is.		08°36'12"N, 079°00'18"W, 22 m					
		BAU2535	Panama, Las Perlas		08°36' 21.6"N 079°05'21.6"W, 32.5 m					
<i>Subcancilla erythrogramma*</i>	<i>Subcancilla</i>	BAU0424	PANAMA, Las Perlas, Contadora Is.		08°36'36"N 079°00'12"W, 25 m					
<i>Subcancilla sp.</i>	<i>Subcancilla</i>	BAU0421	PANAMA, Las Perlas, San JosŽ Is.		08°17'48"N 079°02'36"W, 30.5 m					
<i>Subcancilla leonardhilli</i>	<i>Subcancilla</i>	IM-2013-61416	KARUBENTHOS 2	DW4637	15°51,50'N 61°20,17'W, 217-225 m	-	-	-		
		IM-2013-61417	KARUBENTHOS 2	DW4637	15°51,50'N 61°20,17'W, 217-225 m	-	-	-		
<i>Scabricola casta</i>	<i>Swainsonia</i>	IM-2007-31989	PANGLAO 2004	R38	09°29.4'N 123°56.0'E, 6-37 m			NEOGA477-10	KR087293	- - -
		IM-2013-48000	KAVIENG	KS17	02°36,2'S 150°46,3'E, 3 m					
<i>Scabricola fusca</i>	<i>Swainsonia</i>	IM-2013-40643	INHACA 2011	MS8	25°59.5'S 32°52.9'E, 9-17 m			MITRI029-15	KR087294	KR088043 KR087381 KR088122
<i>Ziba carinata*</i>	<i>Ziba</i>	IM-2013-40647	ZANAGA	531DW	04°43.0'S 11°47.0'E, 17 m			MITRI026-15	-	KR088067 KR087409 KR088148
<i>Mitra aff. labecula</i>	?	IM-2007-35623	CONCALIS	DW3024	18°56'58.1964"S 163°21'45.0108"E, 349-370 m					- - -
<i>Mitra turgida</i>	?	IM-2007-30270	SANTO 2006	LM19	15°38'30.012"S 167°15'5.9868"E, intertidal					- - -

Table 2.

Gene	Primers	Reference	annealing temperature	amplification length bp	alignment length bp	total for Mitridae	analysed in 4G total (Mitridae)	substitution model (AIC1)	gamma I	gamma a
<i>COI</i>	HCO-1490 GGTCAACAAATCATAAAGAYATGYG	Folmer et al. (1994)	48-50	658	658	149	148 (74)	TIM+I+G	0.42	0.48
	LCO-2198 TAAACTTCAGGGTGACCAARAAYCA	Folmer et al. (1994)								
16S	16SH CCGGTCTGAACTCAGATCACG	Palumbi (1996)	48-50	605		79	165 (86)	TIM+I+G	0.37	0.48
	16LC GTTTACCAAAAACATGGCTTC	Palumbi (1996)								
12S	12SI TGCCAGCAGCCGCGGTTA	Oliverio, Mariottini, 2001	57*	~540		76	148 (72)	TrN+I+G	0.23	0.54
	12SIII AGACGACGGGCGRTTWTAC	Oliverio, Mariottini, 2002								
<i>H3</i>	H3F ATGGCTCGTACCAAGCAGACVGC	Colgan et al. (2000)	55	328	328	59	126 (67)	TrN+I+G	0.63	0.78
	H3R ATATCCTTRGGCATRATRGTGAC	Colgan et al. (2000)								

Table 3

Taxon	COI		3-mit		4G		4G-red	
	BA	ML	BA	ML	BA	ML	BA	ML
<b>Fam. Charitodoronidae</b>	1	100	1	100	1	100	sp	sp
<b>Fam. Mitridae</b>	1	91	1	100	1	100	1	100
<b>SFam. Mitrinae</b>	-	-	0.97	74	0.95	79	0.9	79
Gen. <i>Mitra</i>	0.93	89	1	100	1	100	sp	sp
Gen. <i>Quasimitra</i> <b>gen. nov.</b>	0.85	56	1	<70	1	71	1	86
Gen. <i>Pseudonebularia</i> <b>gen. nov.</b>	1	71	1	99	1	99	1	100
Gen. <i>Gemmulimitra</i> <b>gen. nov.</b>	1	96	1	98	1	98	1	100
Gen. <i>Calcimitra</i>	0.98	65	-	-	<0.7	<70	-	-
Gen. <i>Neotiara</i> <b>gen. nov.</b>	sp	-	1	99	1	99	sp	sp
Gen. <i>Episcomitra</i>	1	99	1	99	1	100	1	100
Gen. <i>Ziba</i> *	-	-	n/a	n/a	n/a	n/a	n/a	n/a
<i>Domiporta</i> clade	-	-	0.98	-	1	67	1	-
Gen. <i>Domiporta</i>	1	89	1	100	1	100	1	100
Gen. <i>Roseomitra</i> <b>gen. nov.</b>	1	100	1	100	1	100	1	100
Gen. <i>Fusidomiporta</i> <b>gen. nov.*</b>	1	99	n/a	n/a	n/a	n/a	n/a	n/a
Gen. <i>Profundimitra</i> <b>gen. nov.</b>	1	95	1	100	1	100	1	100
<b>SFam. Strigatellinae</b>	-	-	0.96	<70	1	71	99	70
<b>SFam. Imbricariinae</b>	0.98	53	1	100	1	100	1	100
Gen. <i>Imbricaria</i>	0.99	75	1	99	1	99	1	99
Gen. <i>Cancilla</i>	1	79	1	100	1	100	1	100
Gen. <i>Imbricariopsis</i> <b>gen. nov.*</b>	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Gen. <i>Swainsonia</i>	-	-	0.95	<70	1	76	0.99	72
Gen. <i>Scabricola</i>	<0.7	-	<0.7	<70	<0.7	<70	-	-
Gen. <i>Neocancilla</i>	1	82	1	99	1	99	1	99
Gen. <i>Condylomitra</i> <b>gen. nov.</b>	0.93	56	0.98	81	1	82	0.98	79
<b>SFam. Cylindromitrinae</b>	-	-	1	98	1	99	1	99
Gen. <i>Pterygia</i>	1	90	1	100	1	100	1	100
Gen. <i>Nebularia</i>	-	-	1	94	1	98	1	99
<b>SFam. Isarinae</b>	0.94	-	1	99	1	98	1	96
Gen. <i>Isara</i>	-	-	0.96	<70	0.97	<70	0.96	<70
Gen. <i>Subcancilla</i>	-	-	1	85	1	84	1	79
Cylindromitrinae + Isariinae	0.94	-	0.99	80	0.93	<70	0.79	<70
Gen. <i>Probata</i> *	-	-	n/a	n/a	n/a	n/a	n/a	n/a
Gen. <i>Carinomitra</i> <b>gen. nov.</b>	1	100	1	100	1	100	1	100

## Captions

**Figure 1.** Bayesian phylogenetic tree of Mitroidea based on the analysis of cytochrome oxidase subunit I (COI) gene. Branch support as Maximum likelihood bootstrap values (when >50) / Bayesian PP (when >0.7).

**Figure 2.** Examples of conflicting species hypotheses; with morphospecies delineated based on the shell morphology not consistent with the phylogenetic groupings inferred from the analysis of COI. **A.** *Strigatella* aff. *paupercula* (in COI clade 11); **B, C.** *Strigatella paupercula* (COI clade 7); **D, E.** Mitridae gen. sp. (in COI clade 15); **F.** Mitridae gen. sp. (in COI clade 18); **G – L.** “*Mitra*” *glaphyria* (in COI clade 13); **M – R.** *Cancilla fibula* / *rehderi* (in COI clade 24-7).

**Figure 3.** Bayesian phylogenetic tree of Mitridae, Charitodoronidae new family and Pyramimitridae based on the analysis of 3-mit dataset. Branch support as Maximum likelihood bootstrap values (when >70) / Bayesian PP (when >0.75). Type species of nominal genera marked with asterisks. Inferred phylogenetic lineages that are given a taxonomic status labelled correspondingly.

**Figure 4.** Bayesian phylogenetic tree of Mitridae, Charitodoronidae new family and Pyramimitridae based on the analysis of 4G dataset. Support values and labelling as in Figure 3.

**Figure 5.** Bayesian phylogenetic tree of Mitridae, Charitodoronidae new family and Pyramimitridae based on the analysis of 4G-red dataset. Support values and labelling as in Figures 3-4.

**Figure 6.** Histological sections of the foregut of *Charitodoron veneris*. **A.** Section through the tip of the proboscis and salivary gland, general view; **B.** Close up of the salivary gland. **C.** Close up of the proboscis tip; **D.** Section through the buccal mass, mid- and posterior oesophagus, general view. **E.** Close up of the odontophore, radula and salivary ducts; **F.** Same area as previous, few sections further – opening of salivary ducts; **G.** Close up of posterior oesophagus and valve-like structure.

**Figure 7.** Transversal histological sections of the proboscis of *Condylomitra tuberosa*. **A.** Section through the mouth opening; **B.** Section through the buccal cavity; **C.** Close up of the buccal mass and epiproboscis tip; **D.** Section through the buccal mass at the level of the odontophore; **E.** Close up of the buccal mass and epiproboscis complex; **F.** Section through the

1  
2 distal part of radular diverticulum; **G.** Section through the proximal part of the epiproboscis  
3 complex; **H.** Close up of the oesophagus; odontophore retractor and proximal muscles of  
4 epiproboscis; **I.** Section through basal portion of the proboscis.  
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9 **Figure 8.** *Charitodoron* species. **A.** *Charitodoron* sp., MNHN IM-2007-38306, off  
10 Mozambique, MAINBAZA Stn 3157, 21°46'S, 36°25'E, 1410-1416 m; **B.**, **C.** *C. bathybius*,  
11 MNHN IM-2013-40658, off Mozambique, MAINBAZA, Stn 3171, 25°59'S, 34°42'E, 771-776  
12 m, 12.0 mm; **B.** Shell; **C.** Radula; **D.**, **E.** *C. veneris*; **D.** NMSA D4172, off Durban 29°50.4'S,  
13 31°14.0'E, 150 m, 14.1 mm (voucher of sectioned specimen); **E.** NMSA E. 9237, northern Natal,  
14 off Shellfield Beach, 29°39.8'S, 31°30.2'E, 150 m, radula.  
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21 **Figure 9.** *Mitra* species. **A.** *Mitra mitra*, MNHN IM-2013-40639, Mozambique, INHACA 2011  
22 Stn MR15, 26°00.0'S, 32°54.4'E, 4 m, 89.1 mm; **B.** *M. papalis*, MNHN IM-2013-50981, Papua  
23 New Guinea, KAVIENG Stn KR34, 02°34.6'S, 150°46.3'E, 10-22 m, 70.7 mm; **C.** *M. stictica*,  
24 Society Islands, off Moorea, 61.0 mm, MNHN; **D.** *M. deprofundis*, holotype, MNHN IM-2000-  
25 30197, New Caledonia, Antigonina Bank, SMIB 4, Stn DW57, 23°21'S, 168°04'E, 210-260 m,  
26 67.5 mm.  
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33 **Figure 10.** Radulae of Mitrinae species. **A.** *Mitra mitra*, MNHN IM-2013-40639, Mozambique,  
34 INHACA 2011 Stn MR15, 26°00.0'S, 32°54.4'E, 4 m, 89.1 mm; **B.** *Calcimitra glaphyria*,  
35 MNHN IM-2013-40650, Papua New Guinea, BIOPAPUA Stn CP3728, 07°52'S, 148°01'E, 498-  
36 501 m, 31.9 mm; **C.** *C. invicta*, MNHN-IM-2013-15373, PAPUA NIUGINI Stn CP3949,  
37 05°12'S, 145°51'E, 380-407 m, 61.6 mm; **D.** *Neotiarra lens*, Neotype, MNHN IM-2000-33145,  
38 Panama, Panama City, 08°95'N, 79°53'W, intertidal, 40.0 mm; **E.** *N. nodulosa*, MNHN IM-  
39 2013-9552, Guadeloupe, KARUBENTHOS Stn GM10, 16°13'N 61°26'W, 1 m, 29.5 mm; **F.**  
40 *Ziba carinata*, MNHN IM-2013-40647, Congo, Mission ZANAGA, Stn 531DW, 04°43.0'S  
41 11°47.0'E, 17 m, 24.5 mm; **G.** *Episcomitra zonata*, BAU2538, Italy, off Chioggia, 45°12'N,  
42 12°40'E, 40 m, 96.2 mm; **H.** *E. cornicula*, BAU1578.3, Greece, Astypalea Is, Agrilidi,  
43 36°35.0'N, 26°25.4'E, 2-7 m, 12.1 mm; **I.** *Quasimitra puncticulata*, MNHN IM-2013-40685,  
44 Philippines, off Noc-Nocan Is, 10°15.1'N 124°25.1'E, 4-12 m, 40.6 mm; **K.** *Q. sophiae*, IM-  
45 2007-30056, Vanuatu, SANTO 2006 Stn DR09, 15°34.6'S, 167°13.8'E, 12 m, 25.1 mm; **L.** *Q.*  
46 *cardinalis*, MNHN IM-2013-40681, Papua New Guinea, KAVIENG 2014 Stn KR178, 02°45.2'S  
47 150°43.1'E, 2-46 m, 58.8 mm; **M.** *Q. sanguinolenta*, MNHN IM-2013-40677, Mozambique,  
48 INHACA 2011 Stn MS02, 26°06.3'S, 32°58.0'E, 17-19 m, 28.7 mm.  
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**Figure 11.** Genus *Calcimitra*. **A, B.** *C. glaphyria*; **A.** MNHN IM-2007-30066, Philippines, PANGLAO 2005 Stn CP2342, 9°24'N 123°53'E, 1240-1258 m; **B.** MNHN IM-2013-40650, Papua New Guinea, BIOPAPUA Stn CP3728, 07°52'S, 148°01'E, 498-501 m, 31.9 mm; **C.** *C. triplicata*, MNHN IM-2007-38186, Madagascar, MIRIKY Stn CP3253, 15°25'S, 45°55'E, 943-950 m; **D.** *C. labecula*, MNHN IM-2007-30127, Coral Sea, EBISCO Stn DW2515, 24°04'S, 159°41'E, 330-370 m; **E, F.** *C. invicta*; **E.** MNHN IM-2007-32130, Philippines, PANGLAO 2005 Stn CP2383, 08°45'N, 123°18'E, 338-351 m, \*\*\* mm; **F.** MNHN IM-2013-15373, PAPUA NIUGINI Stn CP3949, 05°12'S, 145°51'E, 380-407 m, 61.6 mm; **G, H.** *C. christinae*, **G.** MNHN IM-2007-32131, Philippines, PANGLAO 2005 Stn CP2383, 08°45'N, 123°18'E, 338-351 m; **H.** MNHN IM-2007-32133, Philippines, PANGLAO 2005 Stn CP2359, 8°50'N 123°35'E, 437-476 m.

**Figure 12.** *Eumitra* species. **A.** *Eumitra apheles*, MNHN, New Caledonia, BATHUS 4 Stn 918, 18°49'S, 163°16'E, 613-637 m, 18.6 mm; **B.** *E. caledonica*, holotype, MNHN-IM-2000-30181, Norfolk Ridge, BIOCAL Stn CP61, 24°11'S, 167°32'E, 1070 m, 29.9 mm; **C.** *E. imbricata*, holotype, MNHN-IM-2000-30242, Coral Sea, Lansdowne-Fairway, CORAIL 2 Stn DE14, 21°01'S, 160°57'E, 650-660 m, 15.5 mm; **D, E.** *Eumitra* n. sp.; **D.** Morphology voucher, MNHN, KARUBAR Stn CC56, 08°16'S, 131°59'E, 549-552 m, 48.75mm; **E.** '*Eumitra*' *suduirauti* holotype, MNHN IM-2000-30306, Philippines, Mindanao, off Tanala, 500-600 m, 51.7 mm.

**Figure 13.** *Neotiara* species. **A, B.** *Neotiara lens* **A.** Neotype, MNHN IM-2000-33145, Panama, Panama City, 08°95'N, 79°53'W, intertidal, 40.0 mm; **B.** BAU 2532, same locality as previous, 33.6 mm; **C.** *N. lignaria*, holotype, NHMUK 1967798, Sta Elena, Ecuador, 47.6 mm; **D.** *N. rupicola*, syntype, NHMUK 1964460, Sta Elena, Ecuador, 37.2 mm; **E.** *N. gausapata*, lectotype, NHMUK 1967769/1-2, Galapagos Is, 11.7 mm; **F.** *N. nodulosa*, MNHN IM-2013-9546, Guadeloupe, KARUBENTHOS Stn GM10, 16°12,53'N, 61°25,55'W, 1 m, 27.8 mm; **G.** *N. muricata*, lectotype, NHMUK 1967610/1-3, Galapagos Is, 29 mm; **H.** *N.* sp. cf. *inca*, BAU 0279-1, Panama, Venado Beach, 8°53.5'N, 79°36.4'W, intertidal, 11 mm.

**Figure 14.** *Ziba* and *Episcomitra* species. **A, B.** *Ziba carinata*; **A.** lectotype of *Mitra senegalensis*, NHMUK 1967881, Senegal, 27.9 mm; **B.** MNHN IM-2013-40647, Congo, Mission ZANAGA, Stn 531DW, 04°43.0'S 11°47.0'E, 17 m, 24.5 mm; **C, D.** *Z. gambiana*, syntype, NHMUK 1967768, "Senegambia", 28 mm; **E.** *Episcomitra zonata*, BAU2538, Italy, off Chioggia, 45°12'N, 12°40'E, 40 m, 96.2 mm; **F – H.** *Episcomitra cornicula* **F.** BAU1578.3,

Greece, Astypalea Is, Agrilidi, 36°35.0'N, 26°25.4'E, 2-7 m, 12.1 mm; **G, H.** MNHN IM-2013-40661, Italy, Sicily, Syracuse, 37°00.5'N, 15°18.6'E, 6-12 m, 9.0 mm; **G.** Shell; **H.** Protoconch.

**Figure 15.** *Quasimitra* species. **A.** *Quasimitra sanguinolenta*, MNHN IM-2013-40677, Mozambique, INHACA 2011 Stn MS02, 26°06.3'S, 32°58.0'E, 17-19 m, 28.7 mm; **B.** *Q. cardinalis*, MNHN IM-2013-40681, Papua New Guinea, KAVIENG 2014 Stn KR178, 02°45.2'S 150°43.1'E, 2-46 m, 58.8 mm; **C.** *Q. sophiae*, MNHN IM-2007-30056, Vanuatu, SANTO 2006 Stn DR09, 15°34.6'S, 167°13.8'E, 12 m, 25.1 mm; **M.** *Q. puncticulata*, MNHN IM-2013-40685, Philippines, off Noc-Nocan Is, 10°15.1'N 124°25.1'E, 4-12 m, 40.6 mm.

**Figure 16.** Species of *Domiporta* and *Roseomitra*. **A.** *Domiporta filaris*, MNHN IM-2013-12956, Papua New Guinea, PAPUA NIUGINI Stn PD 23, 05°06'S, 145°49.2'E, 3-7 m, 15.8 mm; **B.** *D. praestantissima*, MNHN IM-2013-40642, Vietnam, Nha-Trang Bay, West of Mun Is, 12°10.1'N, 109°17.8'E, 6-18 m, 25.6 mm; **C.** *D. circula*, MNHN IM-2007-30018, Vanuatu, SANTO 2006 Stn LD24, 15°31.4'S, 167°10.0'E, 47 m; **D.** *D. cf. carnicolor*, MNHN IM-2013-40684, Philippines, off Noc-Nocan Is, 10°15.1'N, 124°25.1'E, 4-12 m, 23.9 mm; **E.** *D. granatina*, MNHN IM-2013-40641, Mozambique, INHACA 2011 Stn MR15, 26°00.0'S, 32°54.4'E, 4 m, 34.2 mm; **F.** *Roseomitra millepunctata*, neotype, MNHN IM-2013-40686, Philippines, off Noc-Nocan Is, 10°15.1'N, 124°25.1'E, 4-12 m, 29.8 mm; **G.** *R. incarnata*, lectotype, NHMUK 196779/1-3, Misamis Is, Mindanao, Philippines, 21.6 mm; **H.** *R. tagaroeae*, Philippines, Olango Channel, dredged from 80 m, 9.5 mm; **I.** *R. rosacea*, Mozambique, INHACA 2011 Stn MD13, 26°03.1'S 33°01.0'E, 50-53 m, 7.9 mm.

**Figure 17.** Radulae in the *Domiporta* clade. **A.** *Domiporta cf. carnicolor*, MNHN IM-2013-40684, Philippines, off Noc-Nocan Is, 10°15.1'N, 124°25.1'E, 4-12 m, 23.9 mm; **B.** *D. granatina*, MNHN IM-2013-40641, Mozambique, INHACA 2011 Stn MR15, 26°00.0'S, 32°54.4'E, 4 m, 34.2 mm; **C.** *D. praestantissima*, MNHN IM-2013-40642, Vietnam, Nha-Trang Bay, West of Mun Is, 12°10.1'N, 109°17.8'E, 6-18 m, 25.6 mm; **D.** *D. filaris*, MNHN, Mozambique, INHACA 2011 Stn MR13, 25°59.7'S, 32°54.5'E, 2-5 m, 17.4 mm; **E.** *Roseomitra rosacea*, MNHN, Mozambique, INHACA 2011 Stn MD13, 26°03.1'S, 33°01.0'E, 50-53 m, 7.9 mm; **F.** *R. millepunctata*, MNHN, IM-2013-40686, Philippines, off Noc-Nocan Is, 10°15.1'N, 124°25.1'E, 4-12 m, 29.8 mm; **G.** *Profundimitra taylori* n. sp., holotype, MNHN, IM-2013-40651, Papua New Guinea, BIOPAPUA Stn CP3671, 04°04'S, 151°56'E, 585-601 m, 24.2 mm; **H.** *Profundimitra* n. sp., MNHN, IM-2013-40654, New Caledonia, EXBODI Stn CP3829, 22°02'S, 167°05'E, 350-360 m, 16.9 mm; **I.** *Fusidomiporta ponderi* n. sp., holotype, MNHN IM-

2013-40665, Papua New Guinea, BIOPAPUA Stn CP3692, 02°10'S, 147°19'E, 408-448 m, 25.2 mm.

**Figure 18.** Species of *Profundimitra* n. gen., *Fusidomiporta* n. gen. and *Cancillopsis* n. sp. **A** – **C.** *Profundimitra taylori* n. sp. **A, B.** Holotype, MNHN IM-2013-40651, Papua New Guinea, BIOPAPUA Stn CP3671, 04°04'S, 151°56'E, 585-601 m, 24.2 mm; **C.** New Caledonia, BATHUS 4 Stn DW920, 18°45'S, 163°17'E, 610-620 m, MNHN, 15.1 mm; **D.** *Profundimitra* n. sp. aff. *taylori*, Papua New Guinea, BIOPAPUA Stn CP3636, 07°27'S, 147°31'E, 462-495 m, 26.8 mm; **E.** *Profundimitra planofilum*, MNHN IM-2007-32149, Philippines, PANGLAO 2005 Stn CP2398, 9°33'N, 123°40'E, 713-731 m; **F.** *Profundimitra* n. sp. aff. *planofilum*, MNHN, IM-2013-40654, New Caledonia, EXBODI Stn CP3829, 22°02'S, 167°05'E, 350-360 m, 16.9 mm; **G.** *Profundimitra* n. sp., MNHN IM-2007-35711, Philippines, AURORA 2007 Stn CP2658, 15°58'N, 121°49'E, 422-431 m; **H.** *Profundimitra* n. sp., MNHN IM-2007-36757, Madagascar, MIRIKY Stn CP3289, 14°29'S, 47°26'E, 332-379 m; **I, K.** *Fusidomiporta ponderi* n. sp., holotype, MNHN, IM-2013-40665, Papua New Guinea, BIOPAPUA Stn CP3692, 02°10'S, 147°19'E, 408-448 m, 25.2 mm; **L.** *Fusidomiporta* n. sp., MNHN IM-2007-32153, Philippines, PANGLAO 2005 Stn DW2364, 09°01'N, 123°25'E, 427 m; **M.** *Cancillopsis meimiaoae* MNHN IM-2007-30011, Vanuatu, SANTO' 2006, Stn AT19, 15°40'48"S 167°00'30"E, 503-600 m.

**Figure 19.** Species of *Pseudonebularia* n. gen. **A, B.** *Pseudonebularia tornata*, **A.** Lectotype of *Mitra tornata*, NHMUK 1967897, Philippines, 18.1 mm; **B.** MNHN IM-2013-12538, PAPUA NIUGINI Stn PB14, 05°13.8'S, 145°48'E, 15 m, 16.5 mm; **C.** *P. atjehensis*, MNHN IM-2007-30264, Vanuatu, SANTO 2006 Stn EP01, 15°32.5'S, 167°09'E, 46-47 m; **D.** *P. maesta*, MNHN IM-2013-40648, Madagascar, MIRIKY Stn CP3288, 14°31.9' S, 47°26.5' E, 46-54 m, 15.6 mm; **E.** *P. connectens*, MNHN IM-2013-2342, PAPUA NIUGINI Stn PB16, 05°10.7'S, 145°47.7'E, intertidal, 10.4 mm; **F.** *P. pediculus*, MNHN IM-2013-12705, PAPUA NIUGINI Stn PB15, 05°04.7'S, 145°48.9'E, 5 m, 11.6 mm; **G.** *P. gracilefragum*, Philippines, Olango I., Caw Oy, 10-25 m, 20.1 mm.

**Figure 20.** Radulae of *Pseudonebularia* n. gen. and *Gemmulimitra* n. gen. **A, B.** *Pseudonebularia pediculus*, MNHN IM-2013-12705, PAPUA NIUGINI Stn PB15, 05°04.7'S, 145°48.9'E, 5 m, 11.6 mm; **C.** *P. connectens*, MNHN IM-2013-2342, PAPUA NIUGINI Stn PB16, 05°10.7'S, 145°47.7'E, intertidal, 10.4 mm; **D, E.** *P. maesta*, MNHN IM-2013-40648, Madagascar, MIRIKY Stn CP3288, 14°31.9' S, 47°26.5' E, 46-54 m, 15.6 mm; **F.** *Gemmulimitra neocaledonica*, MNHN, Paratype 5, New Caledonia, EXBODI Stn CP3814, 21°49'S, 166°44'E,



331-344m, 20.4 mm; **G. *G. boucheti***, MNHN IM-2013-40649, Papua New Guinea, BIOPAPUA Stn DW3641, 06°45'S, 148°01'E, 380-476 m, 11.6 mm.

**Figure 21.** Species of *Gemmulimitra* n. gen. **A, B.** *Gemmulimitra neocaledonica*, holotype, MNHN IM-2013-40655, New Caledonia, EXBODI Stn CP3821, 21°53'S, 166°50'E, 211-440 m, 24.25 mm; **C.** *G. boucheti*, holotype, MNHN IM-2000-30172, Réunion, MD32, Stn DC41, 21°21'S, 55°27'E, 75 m, 9.0 mm; **D.** *G. strongae*, MNHN IM-2007-36727, Madagascar, MIRIKY Stn DW3213, 12°31'S, 47°52'E, 262-289 m; **E.** *G. avenacea*, MNHN IM-2013-11683, PAPUA NIUGINI Stn PB14, 05°13.8'S 145°48'E, 15 m, 14.0 mm; **F.** *G. rubiginosa*, syntype of *Mitra rubiginosa*, NHMUK 1967866, Is of Ticao, Philippines, 37.8 mm.

**Figure 22.** *Strigatella* species. **A.** *Strigatella paupercula*, MNHN IM-2013-15188, PAPUA NIUGINI Stn PM39, 05°12.1'S, 145°48.4'E, intertidal, 22.2 mm; **B.** *S. litterata*, MNHN IM-2013-12959, PAPUA NIUGINI Stn PM22, 05°04.7'S, 145°48.9'E, intertidal, 16.0 mm; **C.** *S. decurtata*, MNHN IM-2013-15843, PAPUA NIUGINI Stn PM41, 05°08.1'S, 145°49.3'E, 0-1 m, 22.1 mm; **D.** *S. scutulata*, MNHN IM-2013-12771, PAPUA NIUGINI Stn PM22, 05°04.7'S, 145°48.9'E, intertidal, 24.7 mm; **E.** *S. aurantia*, MNHN IM-2013-40679, Mozambique, INHACA 2011 Stn MB07, 25°59.7'S, 32°54.2'E, 2-10 m, 21.3 mm; **F.** *Strigatella tristis*, BAU 2534-2, Panama, Rio Mar, 8°27.5'N, 79°58.0'W, intertidal, 20.3 mm; **G.** *S. luctuosa*, MNHN IM-2013-11682, PAPUA NIUGINI Stn PR14, 05°12'S, 145°48.1'E, 2-3 m, 20.9 mm; **H.** *S. vexillum*, MNHN IM-2013-12570, PAPUA NIUGINI Stn PR24, 05°12.3'S 145°48.8'E, 24.0 mm; **I.** *S. imperialis*, MNHN IM-2007-30173, Vanuatu, SANTO 2006 Stn FR01, 15°32.3'S, 167°13.1'E, 18-20 m; **K.** *S. fulvescens*, MNHN IM-2013-40680, TUHAA PAE Stn AMA03, 21°48.2'S, 154°43.2'W, 26 m, 25.5 mm; **L.** *S. lugubris*, MNHN IM-2013-40678, Austral Is, TUHAA PAE Stn AT07, 23°19.7'S 149°29.3'W, 14 m, 13.7 mm; **M.** *S. coronata*, MNHN IM-2013-30023, Vanuatu, SANTO 2006 Stn VM36, 15°27.5'S, 167°15.4'E, intertidal.

**Figure 23.** Radulae in species of *Strigatella*. **A.** *Strigatella paupercula*, MNHN IM-2013-15188, PAPUA NIUGINI Stn PM39, 05°12.1'S, 145°48.4'E, intertidal, 22.2 mm; **B.** *S. luctuosa*, MNHN IM-2013-11682, PAPUA NIUGINI Stn PR14, 05°12'S, 145°48.1'E, 2-3 m, 20.9 mm; **C.** *S. decurtata*, MNHN IM-2013-15843, PAPUA NIUGINI Stn PM41, 05°08.1'S, 145°49.3'E, 0-1 m, 22.1 mm; **D.** *S. vexillum*, MNHN IM-2013-12570, PAPUA NIUGINI Stn PR24, 05°12.3'S 145°48.8'E, 24.0 mm; **E.** *S. coronata*, MNHN, Society Is, off Moorea, 9.0 mm; **F.** *S. lugubris*, MNHN IM-2013-40678, Austral Is, TUHAA PAE Stn AT07, 23°19.7'S 149°29.3'W, 14 m, 13.7 mm; **G.** *S. tristis*, BAU 2534-2, Panama, Rio Mar, 8°27.5'N, 79°58.0'W, intertidal, 20.3 mm.

**Figure 24.** *Imbricaria* species. **A.** *Imbricaria conularis*, MNHN IM-2013-18043, PAPUA NIUGINI Stn PR203, 05°10.3'S 145°48.5'E, 1-19 m, 16.8 mm; **B.** *I. bantamensis*, MNHN IM-2013-16688, PAPUA NIUGINI Stn PD67, 05°15.5'S, 145°46.8'E, 2-6 m, 21.8 mm; **C.** *I. insculpta*, MNHN IM-2013-40657, Vietnam, Nha-Trang Bay, South Mot Is, 12°10.4'N 109°16.3'E, 15-18 m, 18.3 mm; **D.** *I. flammigera*, MNHN IM-2013-40656, Vietnam, Nha-Trang Bay, South Mot I., 12°10.4'N 109°16.3'E, 15-18 m, 14.8 mm; **E.** *I. fulgetrum*, MNHN IM-2013-18112, PAPUA NIUGINI Stn PR240, 05°08.2'S, 145°48.7'E, 3-20 m, 16.8 mm; **F.** *I. verrucosa*, MNHN IM-2013-14284, PAPUA NIUGINI Stn PD39, 04°59.3'S, 145°47.5'E, 2-4 m, 11.6 mm; **G.** *I. salisburyi*, Papua New Guinea, Hansa Bay, 8-18 m, 15.3 mm; **H.** *I. hrdlickae*, MNHN IM-2013-18020, PAPUA NIUGINI Stn PD75, 05°14.2'S, 145°47.8'E, 10-25 m, 16.5 mm; **I.** *I. rufogyrata*, MNHN IM-2007-36131, Solomon Is, SALOMONBOA 3 Stn DW2852, 09°46'S, 160°51'E, 220 m; **K.** *I. pugnaxa*, MNHN IM-2007-32124, Philippines, PANGLAO 2005 Stn CP2378, 08°38.7'N, 123°20.1'E, 65 m.

**Figure 25.** Radulae in the genera *Imbricaria* and *Cancilla*. **A.** *I. pugnaxa*, MNHN, New Caledonia, EXBODI Stn CP3795, 21°32'S, 166°21'E, 240-245 m, 31.9 mm; **B.** *I. conularis*, MNHN, Society Is, Moorea, 13.3 mm; **C.** *I. fulgetrum*, MNHN IM-2013-18112, PAPUA NIUGINI Stn PR240, 05°08.2'S, 145°48.7'E, 3-20 m, 16.8 mm; **D.** *I. flammigera*, MNHN IM-2013-40656, Vietnam, Nha-Trang Bay, South Mot I., 12°10.4'N 109°16.3'E, 15-18 m, 14.8 mm; **E.** *I. insculpta*, MNHN IM-2013-40657, Vietnam, Nha-Trang Bay, South Mot Is, 12°10.4'N 109°16.3'E, 15-18 m, 18.3 mm; **F.** *I. verrucosa*, MNHN, Papua New Guinea, KAVIENG 2014 Stn KR54, 02°42.3'S, 150°39.1'E, 7-10 m, 12.3 mm; **G.** *I. salisburyi*, Papua New Guinea, Hansa Bay, 8-18 m, 15.3 mm; **H.** *I. interlirata*, Vietnam, Nha-Trang Bay, Murray Beach, 12°10.1'N, 109°17.8'E, 6-18 m, 28.6 mm; **I.** *Cancilla fibula / rehderi*, MNHN, Papua New Guinea, BIOPAPUA Stn DW3641, 06°45'S, 148°01'E, 380-476 m, 20.8 mm; **K.** *C. cf. fibula*, MNHN IM-2013-40646, New Caledonia, EXBODI Stn CP3822, 21°52'S, 166°51'E, 341-506 m, 37.6 mm; **L.** *C. baueri*, MNHN IM-2013-58853, Papua New Guinea, KAVIENG 2014 Stn DW4484, 02°26'S, 149°55'E, 229 m, 34.2 mm; **M.** *C. schepmani*, MNHN IM-2013-40645, New Caledonia, EXBODI Stn DW3926, 18°35'S, 164°20'E, 364-473 m, 15.6 mm.

**Figure 26.** *Cancilla* species. **A.** *Cancilla baeri*, IM-2013-58853, Papua New Guinea, KAVIENG 2014 Stn DW4484, 02°26'S, 149°55'E, 229 m, 34.2 mm; **B – D.** *Cancilla fibula / rehderi*; **B.** MNHN, Papua New Guinea, BIOPAPUA Stn DW3641, 06°45'S, 148°01'E, 380-476 m, 20.8 mm; **C.** MNHN IM-2013-19073, PAPUA NIUGINI Stn CP4059, 02°38'S, 141°18'E, 335 m,

23.75 mm; **D.** MNHN IM-2007-38688, Society Is, TARASOC Stn DW3441, 16°41.7'S, 151°26.1'W, 350-360 m; **E.** *Cancilla* cf. *fibula*, MNHN IM-2013-40646, New Caledonia, EXBODI Stn CP3822, 21°52'S, 166°51'E, 341-506 m, 37.6 mm; **F.** *C. schepmani*, MNHN IM-2013-40645, New Caledonia, EXBODI Stn DW3926, 18°35'S, 164°20'E, 364-473 m, 15.6 mm.

**Figure 27.** Species of *Imbricariopsis* n. gen. **A.** *Imbricariopsis punctata*, MNHN IM-2013-11604, PAPUA NIUGINI Stn PM12, 05°00.2'S, 145°47.6'E, 0-1 m, 17.2 mm; **B.** *I. conovula*, lectotype of *Mitra virgo*, NHMUK 1967912, Society Is, 14 mm; **C.** *I. vanikorensis*, lectotype, MNHN IM-2000-30312, Vanikoro, Solomon Is, 22.5 mm; **D.** *Mitra carbonacea*, Senegal, off Gorée I., 10-15 m, 20.5 mm.

**Figure 28.** Radulae in the genera *Imbricariopsis*, *Swainsonia*, *Scabricola* and *Neocancilla*. **A.** *Imbricariopsis punctata*, Mozambique, INHACA 2011 Stn MM3, 26°03.9'S, 32°57.3'E, 0-1 m, 14.7 mm; **B.** *Swainsonia fusca*, MNHN IM-2013-40643; **C.** *Swainsonia casta*, Papua New Guinea, Hansa Bay, 8-18 m, 25.6 mm; **D.** *Scabricola desetangsii*, MNHN IM-2013-50703, Papua New Guinea, KAVIENG 2014 Stn KR14, 02°42.3'S 150°39.1'E, 7-10 m, 24.6 mm; **E.** *Scabricola variegata*, MNHN IM-2013-40683, Philippines, off Noc-Nocan Is, 10°15.1'N, 124°25.1'E, 4-12 m, 45.5 mm; **F.** *Scabricola olivaeformis*, Vietnam, Nha-Trang Bay, Murray Beach, 12°10.1'N, 109°17.8'E, 6-18 m, 13.2 mm; **G.** *Neocancilla papilio*, Society Is, off Moorea, 36.6 mm; **H.** *N. clathrus*, Mozambique, INHACA 2011 Stn MR13, 25°59.7'S, 32°54.5'E, 2-5 m, 14.9 mm; **I.** *N. rufescens*, MNHN IM-2013-40644, Mozambique, INHACA 2011 Stn MD22, 25°59.7'S, 32°46.8'E, 22 m, 16.4 mm.

**Figure 29.** Genera *Scabricola* and *Swainsonia*. **A.** *Scabricola variegata*, MNHN IM-2013-40683, Philippines, off Noc-Nocan Is, 10°15.1'N, 124°25.1'E, 4-12 m, 45.5 mm; **B.** *Scabricola desetangsii*, MNHN IM-2013-50703, Papua New Guinea, KAVIENG 2014 Stn KR14, 02°42.3'S 150°39.1'E, 7-10 m, 24.6 mm; **C.** *Scabricola olivaeformis*, MNHN IM-2013-18062, PAPUA NIUGINI Stn PR214, 05°10.2'S, 145°50.4'E, 1-8 m, 13 mm; **D.** *Scabricola coriacea*, syntype, NHMUK 1967728, Corrigidor I., Philippines, 11.1 mm; **E.** *Scabricola albina*, holotype, NHMUK 1966663, Batangas, Luzon I., Philippines, 26.7 mm; **F.** *Scabricola potensis*, lectotype, MNHN IM-2000-30283, New Caledonia, Belep Is, 24.5 mm; **G.** *Swainsonia fissurata*, Israel, off Eilat, 2-4 m, 63.1 mm.; **H.** *Swainsonia fusca*, MNHN IM-2013-40643, Mozambique, INHACA 2011 Stn MS08, 25°59.5'S, 32°52.9'E, 9-17 m, 18.2 mm; **I.** *Swainsonia casta*, MNHN IM-2013-48000, Papua New Guinea, KAVIENG 2014 Stn KS17, 02°36.2'S, 150°46.3'E, 3 m, 30.5 mm.

**Figure 30.** *Neocancilla* species. **A.** *Neocancilla papilio*, MNHN IM-2013-12560, PAPUA NIUGINI Stn PR24, 05°12.3'S, 145°48.8'E, 28.2 mm; **B.** *N. clathrus*, MNHN IM-2007-30178, Vanuatu, SANTO 2006 Stn DR73, 15°22.5'S, 167°11.3'E, 10-25 m; **C.** *N. rufescens*, MNHN IM-2013-40644, Mozambique, INHACA 2011 Stn MD22, 25°59.7'S, 32°46.8'E, 22 m, 16.4 mm; **D.** *N. hemmenae*, holotype, NHMUK 1992088, off Somalia, 40.8 mm.

**Figure 31.** *Pterygia* species. **A.** *Pterygia dactylus*, MNHN IM-2013-14989, PAPUA NIUGINI Stn PM39, 05°12.1'S, 145°48.4'E, intertidal, 25.1 mm; **B.** *P. sinensis*, MNHN IM-2009-15439, Madagascar, ATIMO VATAE Stn CP3568, 25°04.7'S, 47°03.4'E, 64-65 m; **C.** *P. fenestrata*, MNHN IM-2007-30039, Vanuatu, SANTO 2006 Stn DR09, 15°34.5'S, 167°13.5'E, 12 m; **D.** *P. nucea*, MNHN IM-2013-50702, Papua New Guinea, KAVIENG 2014 Stn KM04, 02°42'S, 150°44'E, 0-1 m, 42 mm.

**Figure 32.** Radulae in the subfamily Cyndromitriinae. **A.** *Pterygia dactylus*, MNHN IM-2013-14989, PAPUA NIUGINI Stn PM39, 05°12.1'S, 145°48.4'E, intertidal, 25.1 mm; **B.** *P. fenestrata*, Society Is, off Moorea, 11.5 mm; **C.** *P. nucea*, MNHN IM-2013-50702, Papua New Guinea, KAVIENG 2014 Stn KM04, 02°42'S, 150°44'E, 0-1 m, 42 mm; **D.** *Nebularia incompta*, Philippines, Olango I. Cow-Oy, 10-25 m, 48.0 mm; **E.** *N. contracta*, Mozambique, INHACA 2011 Stn MR24, 25°54.5'S, 33°02.8'E, 23-26 m, 29.9 mm; **F.** *N. acuminata*, MNHN IM-2013-13288, PAPUA NIUGINI Stn PM25, 05°01.1'S, 145°47.9'E, intertidal, 23 mm.

**Figure 33.** *Nebularia* species. **A.** *Nebularia contracta*, MNHN IM-2013-10345, PAPUA NIUGINI Stn PR04, 05°10.1'S, 145°50.5'E, 30m, 19.7 mm; **B.** *N. chrysostoma*, syntype, NHMUK 1967715, "Isle of Annaa, South Seas" [Anaa, Tuamotu Is], 51.3 mm; **C.** *N. eremitarum*, MNHN IN-2013-16323, PAPUA NIUGINI Stn PM51, 05°05.5'S, 145°48.6'E, 0-1 m, 48.4 mm; **D.** *N. incompta*, Philippines, Olango I., Cow-Oy, 10-25 m, 48.0 mm; **E.** *N. edentula*, 26.7 mm, Mozambique, Matibane Bay, Choca, 2-4 m; **F.** *N. ustulata*, Syntype of *Mitra ustulata*, NHMUK 1967918, ?Viti Is [Fiji], 34.2 mm; **G.** *N. ancillides*, holotype, NHMUK 1967712, "I. of Annaa" [Anaa, Tuamotu Is], 23.6 mm; **H.** *N. acuminata*, MNHN IM-2013-13288, PAPUA NIUGINI Stn PM25, 05°01.1'S, 145°47.9'E, intertidal, 23 mm; **I.** *N. coarctata*, syntype, NHMUK 1967722, locality unknown, 17.5 mm.

**Figure 34.** *Isara* species. **A.** *Isara glabra*, MNHN IM-2013-40640, Esperance, WESTERN AUSTRALIA Stn WE01, 15°16.94'S, 124°06.3'E, 11 m, 62.7 mm; **B.** Holotype of *Mitra bulimoides*, NHMUK 1966656, locality not known, 33.2 mm; **C.** *I. chalybeia*, syntype, NHMUK

1 1967709, locality not known, 51.5 mm; **D.** *I. carbonaria*, molecular voucher, AMS C.335424,  
 2 Australia, North Sydney, Collaroy, Long Reef, 33°44.7'S , 151°19' E, intertidal; **E.** *I. chinensis*,  
 3 lectotype, NHMUK 1967708, "China", 58.6 mm; **F.** *I. nigra*, MNHN IM-2013-40676, Congo,  
 4 Mission ZANAGA Stn DV08, 04°42.9'S, 11°47.5'E, 14-15 m, 45.2 mm; **G.** *I. cornea*,  
 5 BAU2537.1, Italy, Giannutri Is., Punta San Francesco, 42°15.1'N, 11°07'E, 10-20 m, 36.75 mm;  
 6 **H.** *Isara turtoni*, lectotype of *Mitra turtoni*, NHMUK 1889.1.10.-97, St. Helena Is., 26.2 mm; **I.**  
 7 *I. straminea*, MNHN IM-2013-56423, French Guiana, GUYANE Stn CP4375, 06°39'N,  
 8 52°30'W, 195-200 m, 33.5 mm.

16 **Figure 35.** Radulae in the subfamily Isarinae. **A.** *Isara glabra*, MNHN IM-2013-40640,  
 17 Esperance, WESTERN AUSTRALIA Stn WE01, 15°16.94'S, 124°06.3'E, 11 m, 62.7 mm; **B.** *I.*  
 18 *nigra*, MNHN IM-2013-40676, Congo, Mission ZANAGA Stn DV08, 04°42.9'S, 11°47.5'E, 14-  
 19 15 m, 45.2 mm; **C.** *I. straminea*, MNHN IM-2013-56423, French Guiana, GUYANE Stn  
 20 CP4375, 06°39'N, 52°30'W, 195-200 m, 33.5 mm; **D.** *Subcancilla attenuata*, BAU392, Panama,  
 21 Las Perlas, Contadora I., 08°36.2'N, 79°00.2'W, 22 m, 24 mm; **E.** *Subcancilla* cf. *leonardhilli*,  
 22 MNHN IM-2013-61266, Guadeloupe, KARUBENTHOS 2 Stn DW4637, 15°52'N, 61°20'W,  
 23 217-225 m; **F.** *Subcancilla erythrogramma*, BAU424, Panama, Las Perlas, Contadora I.,  
 24 08°36.6'N, 79°00.2'W, 25 m, 24.1 mm.

33 **Figure 36.** *Subcancilla* species. **A.** *Subcancilla erythrogramma*, BAU 0424, Panama, Las Perlas,  
 34 Contadora I., 08°36.6'N, 79°00.2'W, 25 m, 24.1 mm; **B.** *Subcancilla funiculata*, lectotype,  
 35 NHMUK 1967767, Plata I., Pacific coast of Columbia, 27.2 mm; **C.** *Subcancilla* cf. *leonardhilli*,  
 36 MNHN IM-2013-61266, Guadeloupe, KARUBENTHOS 2 Stn DW4626, 15°57'N, 61°37'W,  
 37 210-233 m, 23 mm; **D.** *Subcancilla attenuata*, BAU 0392, Panama, Las Perlas, Contadora I.,  
 38 08°36.2'N, 79°00.2'W, 22 m, 24 mm; **E.** *Subcancilla gigantea*, syntype, NHMUK 1964463,  
 39 Xipixapi, Pacific coast of Columbia, 69.7 mm.

46 **Figure 37.** Species of *Carinomitra* n. gen. **A, B.** *Carinomitra peculiaris*; **A.** syntype, NHMUK  
 47 1967833, Puerto Galera, Mindanao, Philippines, 10 mm; **B.** MNHN IM-2013-6168, PAPUA  
 48 NIUGINI Stn PR218, 05°07.3'S, 145°49.4'E, 11.1 mm; **C – E.** *C. typha*; **C.** syntype, NHMUK  
 49 1967904, Philippines, 9.5 mm; **D.** *C. typha* var. *micans*, MNHN, New Caledonia, Noumea area,  
 50 LAGON Stn 1359, 22°19.9'S, 166°13.2'E, 25-30 m, 9.5 mm; **E.** MNHN IM-2013-4030,  
 51 PAPUA NIUGINI, Stn PB28, 05°11.9'S, 145°49.6'E, 10 m, 8.6 mm.

**Figure 38.** Radulae in the genera *Carinomitra* n. gen., *Condylomitra* n. gen. and *Probata*. **A.** *Carinomitra peculiaris*, MNHN IM-2013-6168, PAPUA NIUGINI Stn PR218, 05°07.3'S, 145°49.4'E, 11.1 mm; **B.** *Carinomitra typha* var. *micans*, MNHN, New Caledonia, Noumea area, LAGON Stn 1359, 22°19.9'S, 166°13.2'E, 25-30 m, 9.5 mm; **C.** *Carinomitra saltata*, MNHN, Society Is, off Moorea, 5.4 mm; **D.** *Condylomitra tuberosa*, MNHN, Philippines, PANGLAO 2004 Stn S12, 9°29.4'N, 123°56.0'E, 6-8 m, 14.4 mm; **E.** *Condylomitra bernhardina* New Caledonia, Noumea area, LAGON Stn 1343, 22°17.8'S, 166°19.9'E, 7 m, 16.1 mm; **F.** *Probata barbadensis*, MNHN IM-2013-7772, Guadeloupe, KARUBENTHOS Stn GR36, 16°30.6'N, 61°28.4'W, 12 m, 20.6 mm.

**Figure 39.** Species of *Condylomitra* n. gen. **A, B.** *Condylomitra tuberosa*; **A.** Syntype, NHMUK 1967899, Philippines, 14.4 mm; **B.** MNHN IM-2007-30311, Philippines, PANGLAO 2004 Stn R75, 09°32.8'N, 123°42.1'E, 3-35 m; **C, D.** *C. bernhardina*; **C.** MNHN IM-2013-54115, Papua New Guinea, KAVIENG 2014 Stn KB40, 02°36.6'S, 150°32.9'E, 2-7 m; **D.** MNHN, New Caledonia, Noumea area, LAGON Stn 1343, 22°17.8'S, 166°19.9'E, 7 m, 16.1 mm.

**Figure 40.** Genera *Atrimitra*, *Vicimitra*, *Probata*, and *Dibaphimitra*. **A.** *Atrimitra idae*, holotype, NMW.1955.158.00066, Point Loma, Lower California, Mexico, 60.0 mm; **B.** *Atrimitra effusa*, lectotype, NHMUK 1966415, Guacomayo, Central America, 31.6 mm; **C.** *Atrimitra caliginosa*, holotype, NHMUK 1966718, locality unknown, 34.9 mm; **D.** *Probata espinosai*, paratype, MNHN-IM-2012-37719, in front of Marianao, Havana, Cuba, 10 mm; **E.** *Probata barbadensis*, MNHN IM-2013-7772, Guadeloupe, KARUBENTHOS Stn GR36, 16°30.6'N, 61°28.4'W, 12 m, 20.6 mm; **F.** *Dibaphimitra florida*, holotype of *Mitra fergusonii* G.B. Sowerby II, 1874, NHMUK 1879.2.26.133, Panama, 42.7 mm.

**Figure 41.** Distribution of different radula types throughout the Mitridae tree. Dark grey – *Mitra* type; yellow – *Strigatella* type; brown – *Nebularia* type; red – *Profundimitra* type; dark-green – *Imbricaria* type; light-green – *Cancilla* type; light-blue – *Scabricola* type; dark blue – *Neocancilla* type; purple – *Pterygia* type; light-grey – no data. The topology corresponds to the 4G tree on Figure 4.

**Figure 42.** Taxonomic composition (subfamilies) and geographical coverage of our molecular sampling. Diameter of the circles proportional to the number of species in each principal location, which is indicated for each circle with more than one species sampled.

1 Charitodoronidae – brown; Cylindromitrinae – blue; Imbricariinae – green; Isarinae – purple;  
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3 Mitrinae – orange; Strigatellinae – yellow; *Incertae sedis* – grey.  
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7 **Figure 43.** Bathymetric distribution of the genera of Mitridae. Black bars – based on our  
8 sampling; grey bars – based on published data (Lozouet, 1991; Cernohorsky 1976; 1991; Huang  
9 & Salisbury, 2017). Numbers next to each bar indicate number of species involved. Blue  
10 horizontal bars show the proportion of stations in each depth interval.  
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For Review Only



Figure 1. Bayesian phylogenetic tree of Mitroidea based on the analysis of cytochrome oxidase subunit I (COI) gene. Branch support as Maximum likelihood bootstrap values (when >50) / Bayesian PP (when >0.7).

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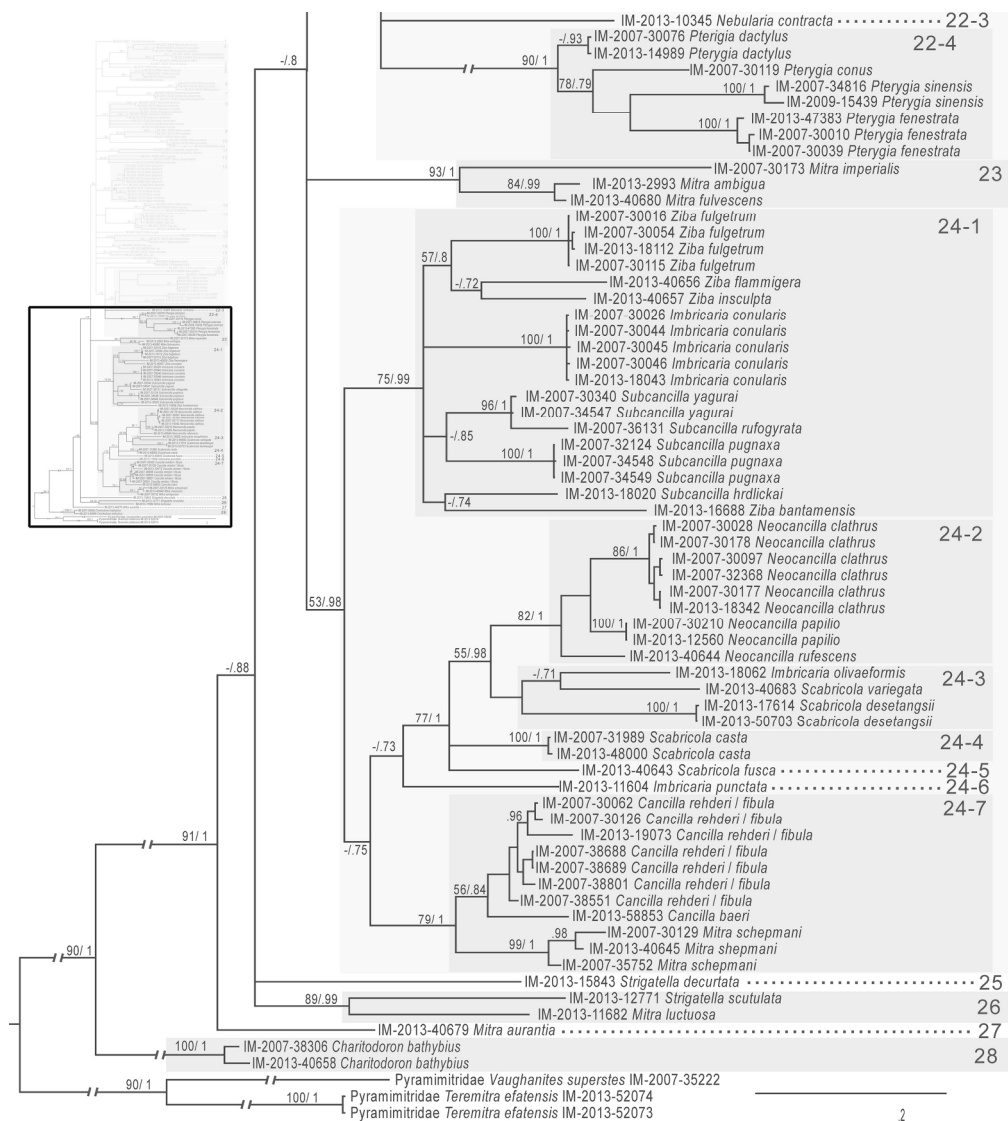


Figure 1. (continued) Bayesian phylogenetic tree of Mitroidea based on the analysis of cytochrome oxidase subunit I (COI) gene. Branch support as Maximum likelihood bootstrap values (when >50) / Bayesian PP (when >0.7).

186x206mm (300 x 300 DPI)



Figure 2. Examples of conflicting species hypotheses; with morphospecies delineated based on the shell morphology not consistent with the phylogenetic groupings inferred from the analysis of COI. A. *Strigatella* aff. *paupercula* (in COI clade 11); B, C. *Strigatella paupercula* (COI clade 7); D, E. *Mitridae* gen. sp. (in COI clade 15); F. *Mitridae* gen. sp. (in COI clade 18); G – L. “*Mitra*” *glaphyria* (in COI clade 13); M – R. *Cancilla fibula* / *rehderi* (in COI clade 24-7).

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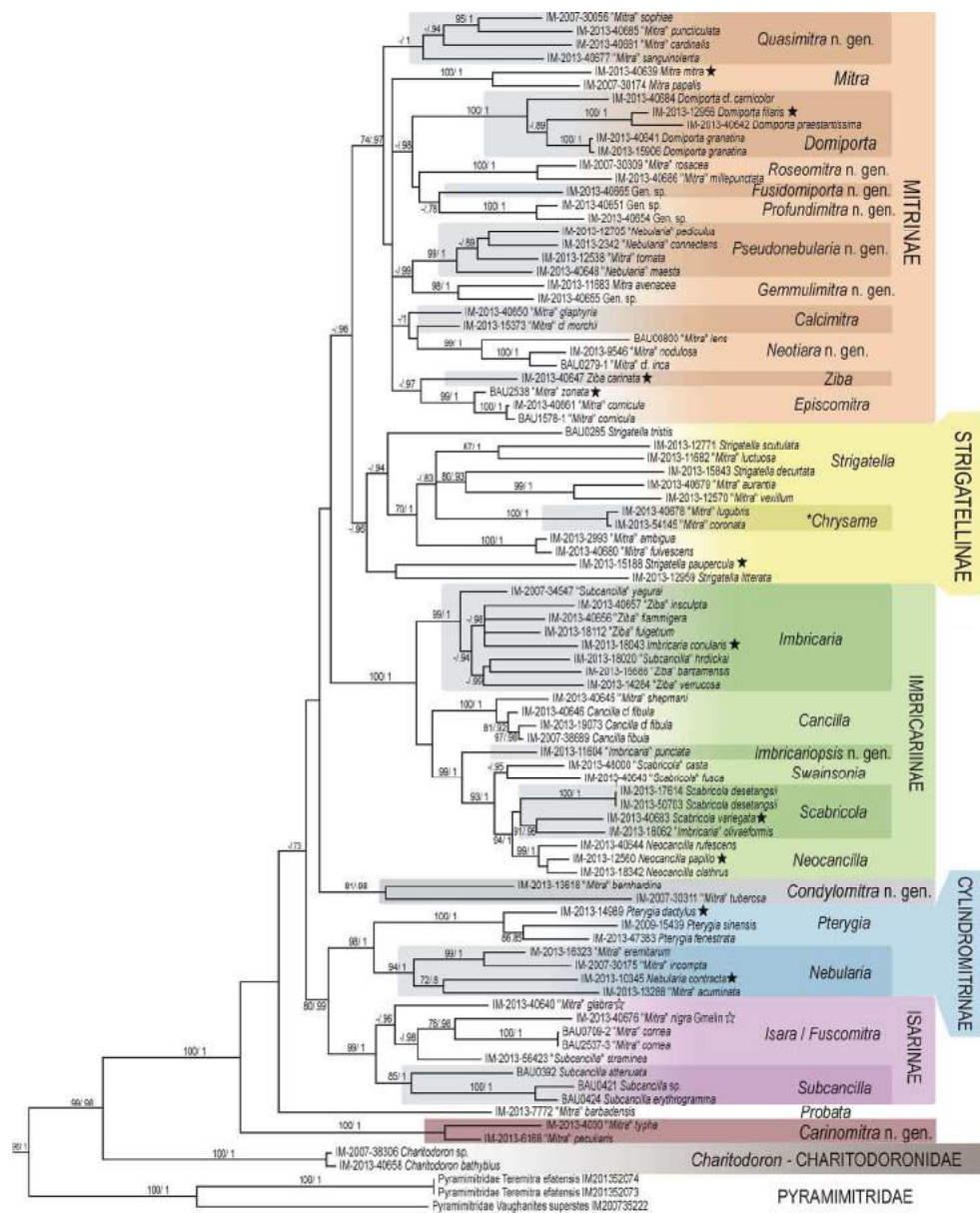


Figure 3. Bayesian phylogenetic tree of Mitridae, Charitodoronidae new family and Pyramimitridae based on the analysis of 3-mit dataset. Branch support as Maximum likelihood bootstrap values (when >70) / Bayesian PP (when >0.75). Type species of nominal genera marked with asterisks. Inferred phylogenetic lineages that are given a taxonomic status labelled correspondingly.

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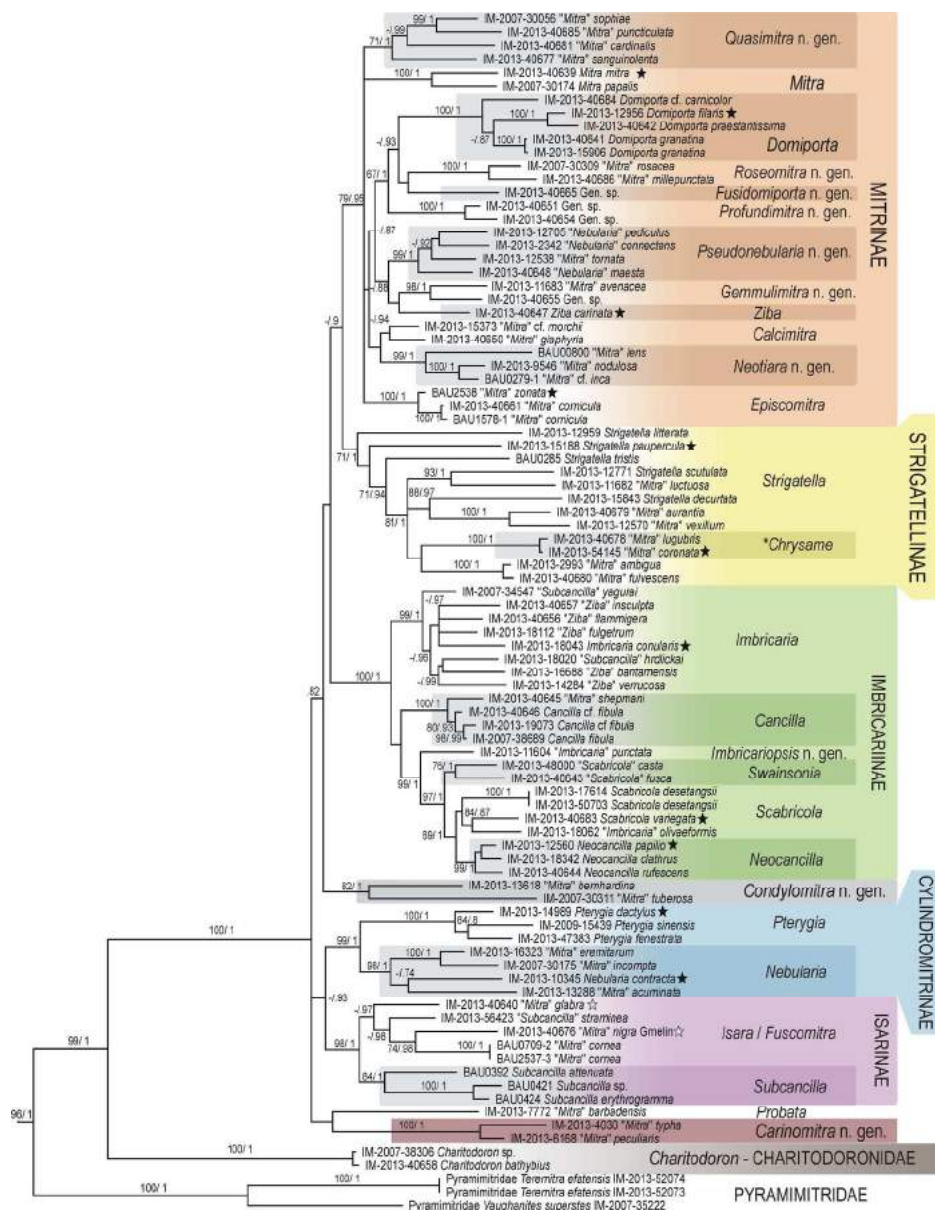


Figure 4. Bayesian phylogenetic tree of Mitridae, Charitodoronidae new family and Pyramimitridae based on the analysis of 4G dataset. Support values and labelling as in Figure 3.

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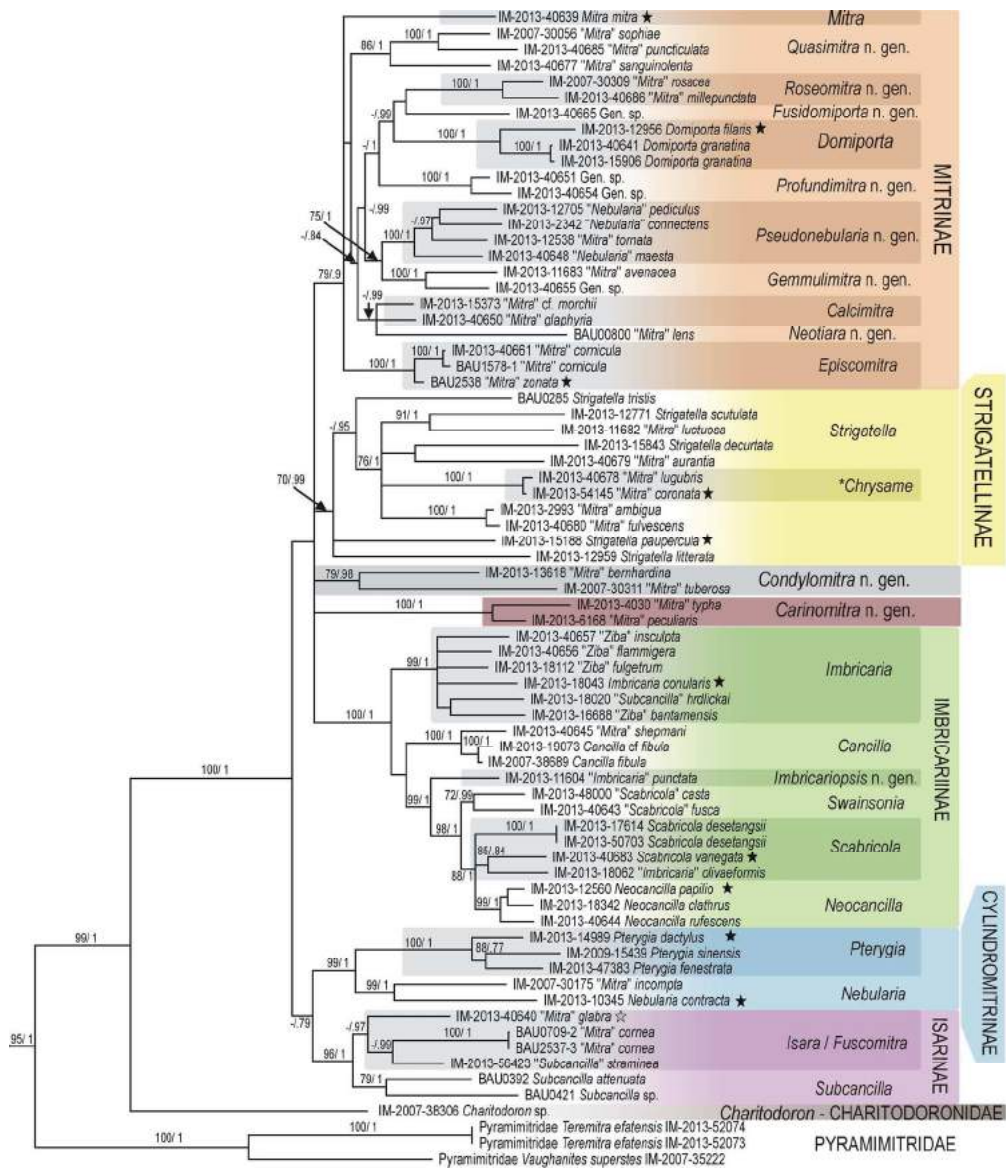


Figure 5. Bayesian phylogenetic tree of Mitridae, Charitodoronidae new family and Pyramimitridae based on the analysis of 4G-red dataset. Support values and labelling as in Figures 3-4.

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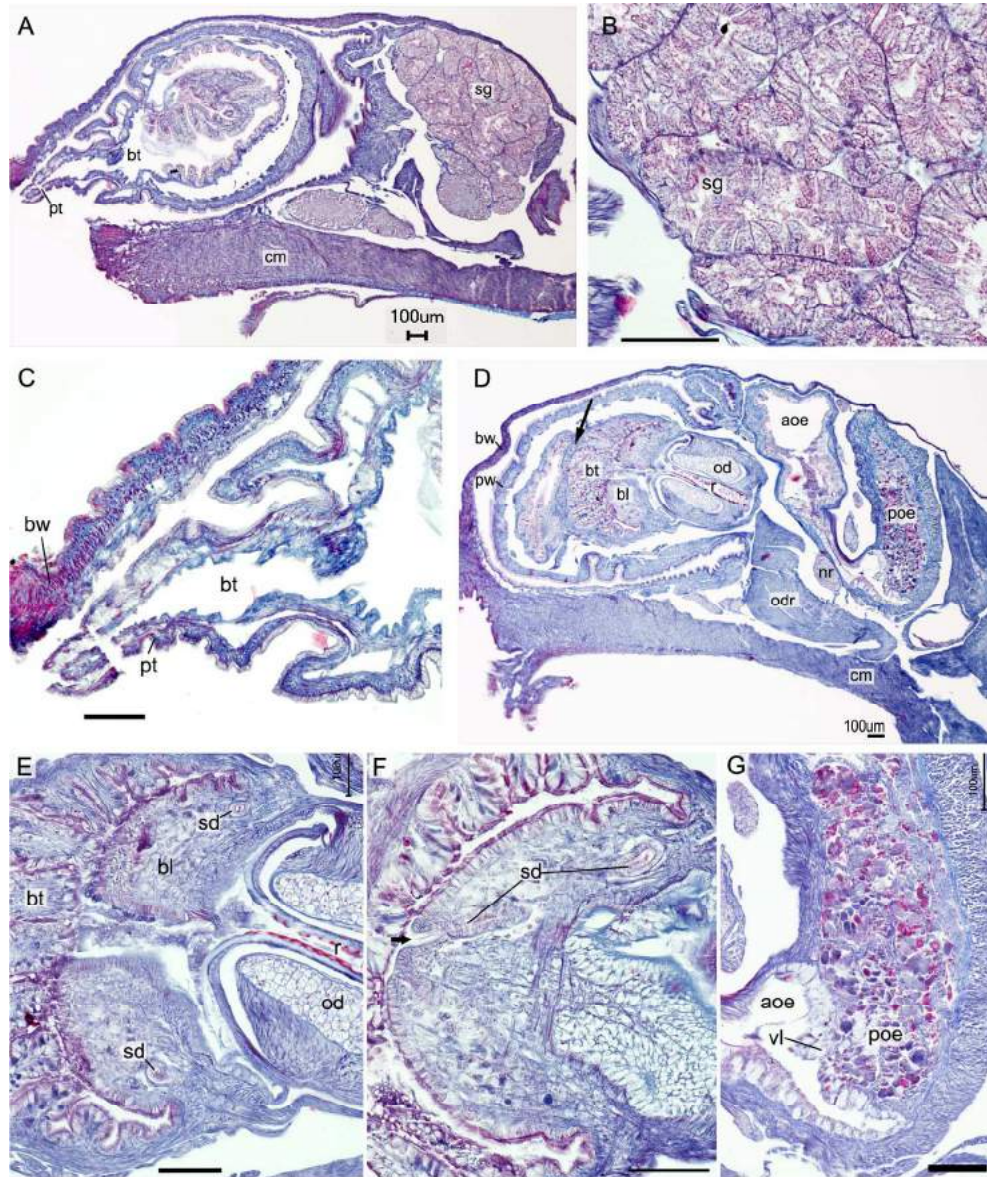


Figure 6. Histological sections of the foregut of *Charitodoron veneris*. A. Section through the tip of the proboscis and salivary gland, general view; B. Close up of the salivary gland. C. Close up of the proboscis tip; D. Section through the buccal mass, mid- and posterior oesophagus, general view. E. Close up of the odontophore, radula and salivary ducts; F. Same area as previous, few sections further – opening of salivary ducts; G. Close up of posterior oesophagus and valve-like structure.

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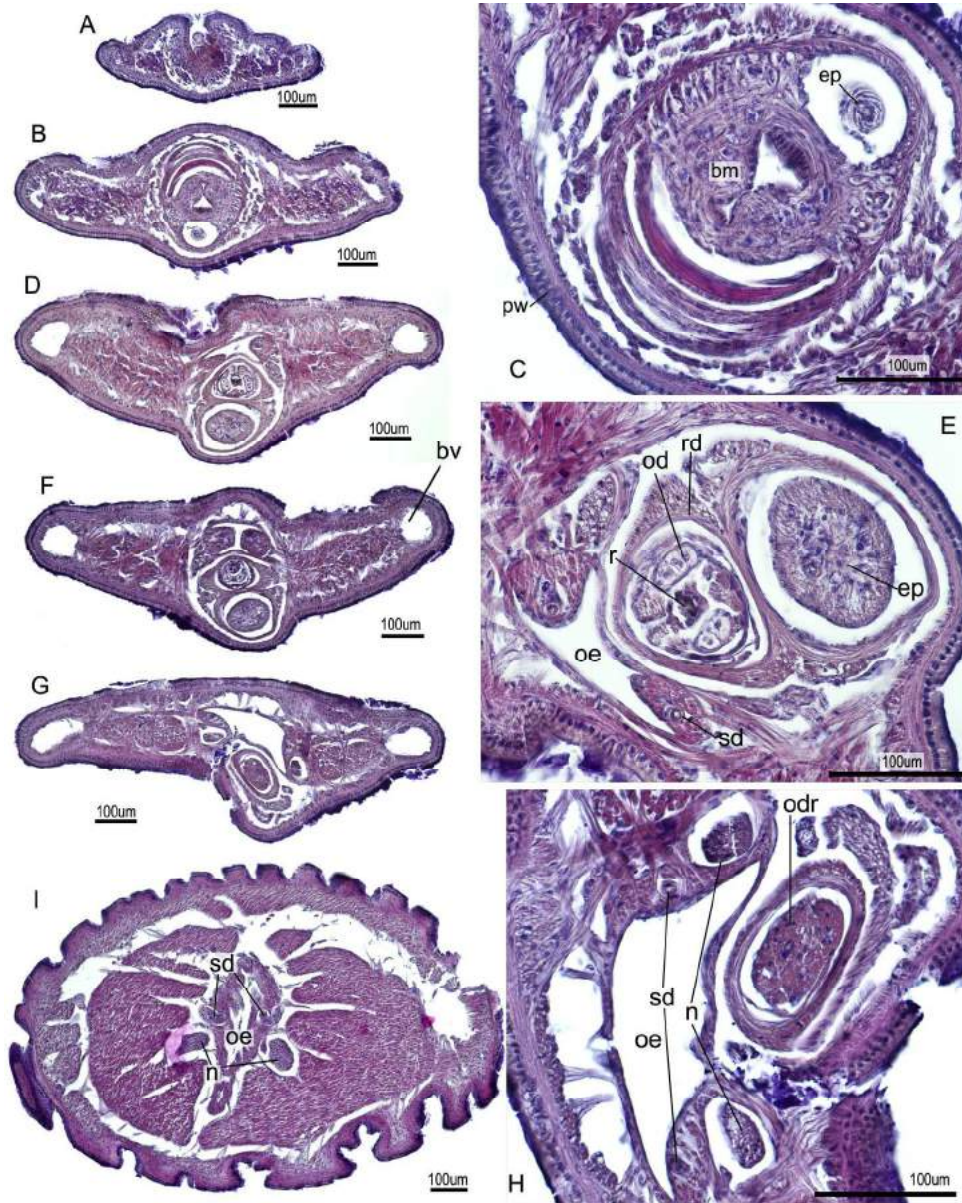


Figure 7. Transversal histological sections of the proboscis of *Condylomitra tuberosa*. A. Section through the mouth opening; B. Section through the buccal cavity; C. Close up of the buccal mass and epiproboscis tip; D. Section through the buccal mass at the level of the odontophore; E. Close up of the buccal mass and epiproboscis complex; F. Section through the distal part of radular diverticulum; G. Section through the proximal part of the epiproboscis complex; H. Close up of the oesophagus; odontophore retractor and proximal muscles of epiproboscis; I. Section through basal portion of the proboscis.

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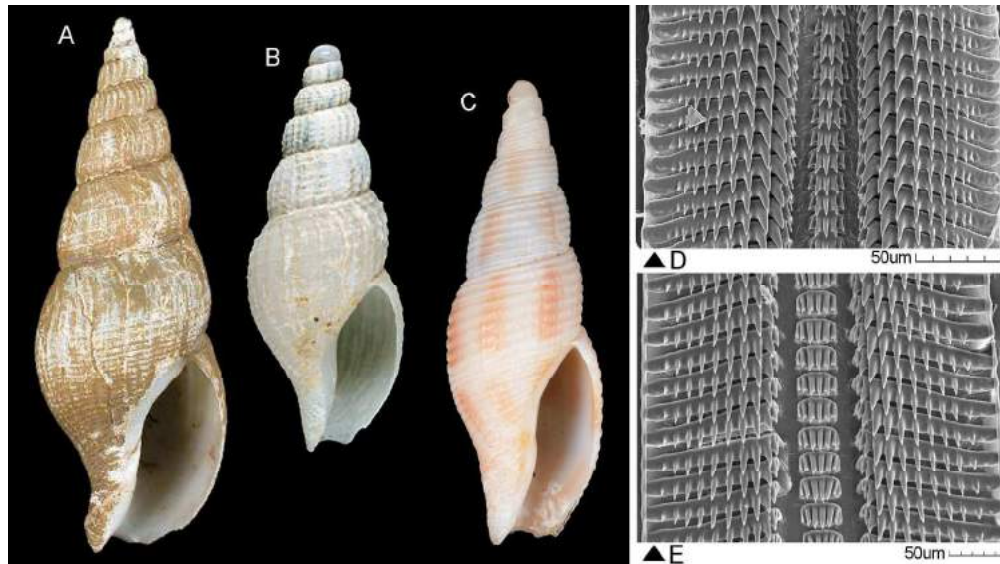


Figure 8. *Charitodoron* species. A. *Charitodoron* sp., MNHN IM-2007-38306, off Mozambique, MAINBAZA Stn 3157, 21°46'S, 36°25'E, 1410-1416 m; B, C. *C. bathybius*, MNHN IM-2013-40658, off Mozambique, MAINBAZA, Stn 3171, 25°59'S, 34°42'E, 771-776 m, 12.0 mm; B. Shell; C. Radula; D, E. *C. veneris*; D. NMSA D4172, off Durban 29°50.4'S, 31°14.0'E, 150 m, 14.1 mm (voucher of sectioned specimen); E. NMSA E. 9237, northern Natal, off Shellfield Beach, 29°39.8'S, 31°30.2'E, 150 m, radula.

170x95mm (300 x 300 DPI)

View Only





Figure 9. Mitra species. A. *Mitra mitra*, MNHN IM-2013-40639, Mozambique, INHACA 2011 Stn MR15, 26°00.0'S, 32°54.4'E, 4 m, 89.1 mm; B. *M. papalis*, MNHN IM-2013-50981, Papua New Guinea, KAVIENG Stn KR34, 02°34,6'S, 150°46,3'E, 10-22 m, 70.7 mm; C. *M. stictica*, Society Islands, off Moorea, 61.0 mm, MNHN; D. *M. deprofundis*, holotype, MNHN IM-2000-30197, New Caledonia, Antigonina Bank, SMIB 4, Stn DW57, 23°21'S, 168°04'E, 210-260 m, 67.5 mm.

170x119mm (300 x 300 DPI)

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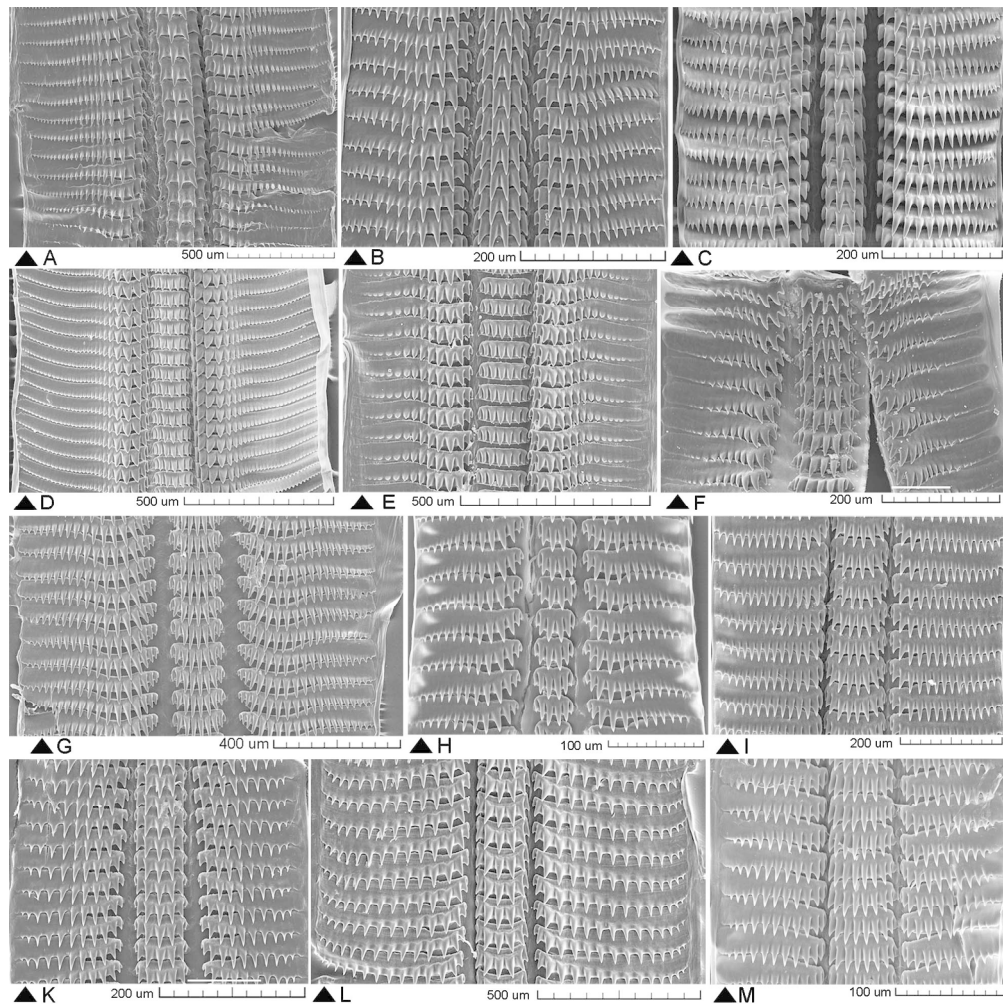


Figure 10. Radulae of Mitrinae species. A. *Mitra mitra*, MNHN IM-2013-40639, Mozambique, INHACA 2011 Stn MR15, 26°00.0'S, 32°54.4'E, 4 m, 89.1 mm; B. *Calcimitra glaphyria*, MNHN IM-2013-40650, Papua New Guinea, BIOPAPUA Stn CP3728, 07°52'S, 148°01'E, 498-501 m, 31.9 mm; C. *C. invicta*, MNHN-IM-2013-15373, PAPUA NIUGINI Stn CP3949, 05°12'S, 145°51'E, 380-407 m, 61.6 mm; D. *Neotiarra lens*, Neotype, MNHN IM-2000-33145, Panama, Panama City, 08°95'N, 79°53'W, intertidal, 40.0 mm; E. *N. nodulosa*, MNHN IM-2013-9552, Guadeloupe, KARUBENTHOS Stn GM10, 16°13'N 61°26'W, 1 m, 29.5 mm; F. *Ziba carinata*, MNHN IM-2013-40647, Congo, Mission ZANAGA, Stn 531DW, 04°43.0'S 11°47.0'E, 17 m, 24.5 mm; G. *Episcomitra zonata*, BAU2538, Italy, off Chioggia, 45°12'N, 12°40'E, 40 m, 96.2 mm; H. *E. cornicula*, BAU1578.3, Greece, Astypalea Is, Agrilidi, 36°35.0'N, 26°25.4'E, 2-7 m, 12.1 mm; I. *Quasimitra puncticulata*, MNHN IM-2013-40685, Philippines, off Noc-Nocan Is, 10°15.1'N 124°25.1'E, 4-12 m, 40.6 mm; K. *Q. sophiaae*, IM-2007-30056, Vanuatu, SANTO 2006 Stn DR09, 15°34.6'S, 167°13.8'E, 12 m, 25.1 mm; L. *Q. cardinalis*, MNHN IM-2013-40681, Papua New Guinea, KAVIENG 2014 Stn KR178, 02°45.2'S 150°43.1'E, 2-46 m, 58.8 mm; M. *Q. sanguinolenta*, MNHN IM-2013-40677, Mozambique, INHACA 2011 Stn MS02, 26°06.3'S, 32°58.0'E, 17-19 m, 28.7 mm

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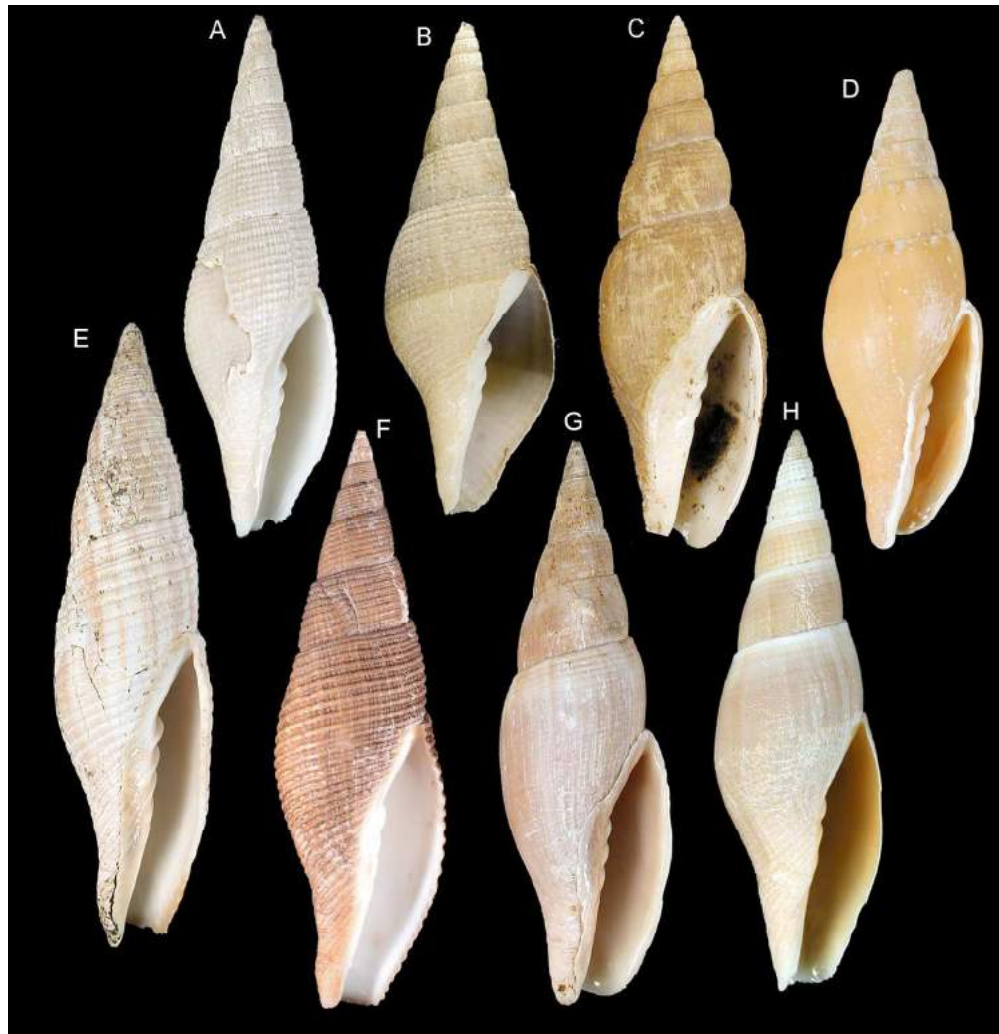


Figure 11. Genus *Calcimitra*. A, B, C. *glaphyria*; A. MNHN IM-2007-30066, Philippines, PANGLAO 2005 Stn CP2342, 9°24'N 123°53'E, 1240-1258 m; B. MNHN IM-2013-40650, Papua New Guinea, BIOPAPUA Stn CP3728, 07°52'S, 148°01'E, 498-501 m, 31.9 mm; C. *C. triplicata*, MNHN IM-2007-38186, Madagascar, MIRIKY Stn CP3253, 15°25'S, 45°55'E, 943-950 m,; D. *C. labecula*, MNHN IM-2007-30127, Coral Sea, EBISCO Stn DW2515, 24°04'S, 159°41'E, 330-370 m; E, F. *C. invicta*; E. MNHN IM-2007-32130, Philippines, PANGLAO 2005 Stn CP2383, 08°45'N, 123°18'E, 338-351 m, \*\*\* mm; F. MNHN IM-2013-15373, PAPUA NIUGINI Stn CP3949, 05°12'S, 145°51'E, 380-407 m, 61.6 mm; G, H. *C. christinae*, G. MNHN IM-2007-32131, Philippines, PANGLAO 2005 Stn CP2383, 08°45'N, 123°18'E, 338-351 m; H. MNHN IM-2007-32133, Philippines, PANGLAO 2005 Stn CP2359, 8°50'N 123°35'E, 437-476 m.

167x173mm (300 x 300 DPI)

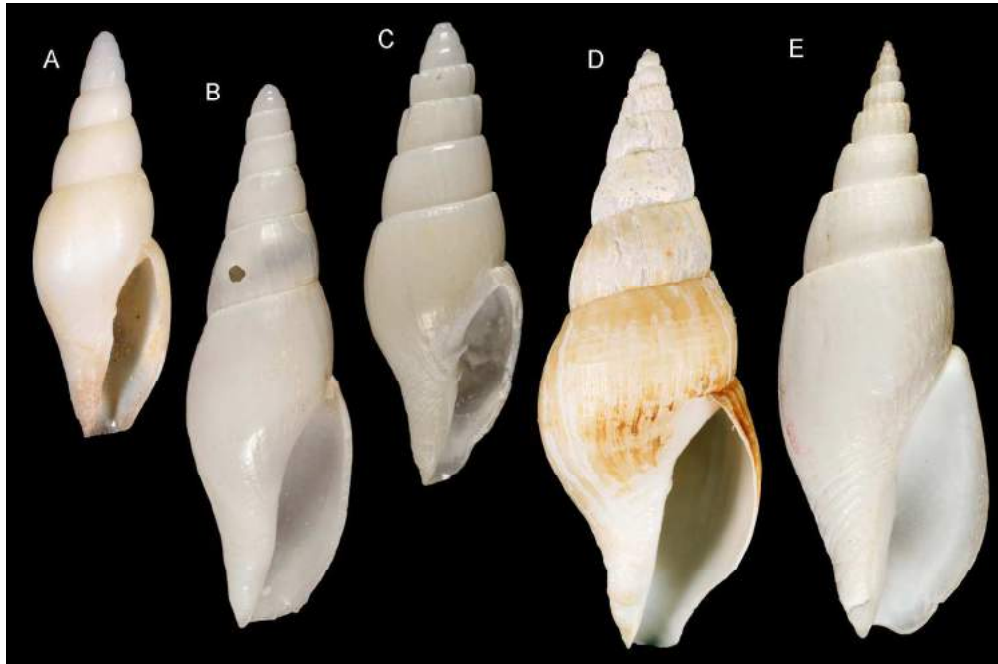


Figure 12. *Eumitra* species. A. *Eumitra apheles*, MNHN, New Caledonia, BATHUS 4 Stn 918, 18°49'S, 163°16'E, 613-637 m, 18.6 mm; B. *E. caledonica*, holotype, MNHN-IM-2000-30181, Norfolk Ridge, BIOCAL Stn CP61, 24°11'S, 167°32'E, 1070 m, 29.9 mm; C. *E. imbricata*, holotype, MNHN-IM-2000-30242, Coral Sea, Lansdowne-Fairway, CORAIL 2 Stn DE14, 21°01'S, 160°57'E, 650-660 m, 15.5 mm; D. *E. Eumitra* n. sp.; D. Morphology voucher, MNHN, KARUBAR Stn CC56, 08°16'S, 131°59'E, 549-552 m, 48.75mm; E. '*Eumitra*' *sudirauti* holotype, MNHN IM-2000-30306, Philippines, Mindanao, off Tanala, 500-600 m, 51.7 mm.

170x112mm (300 x 300 DPI)

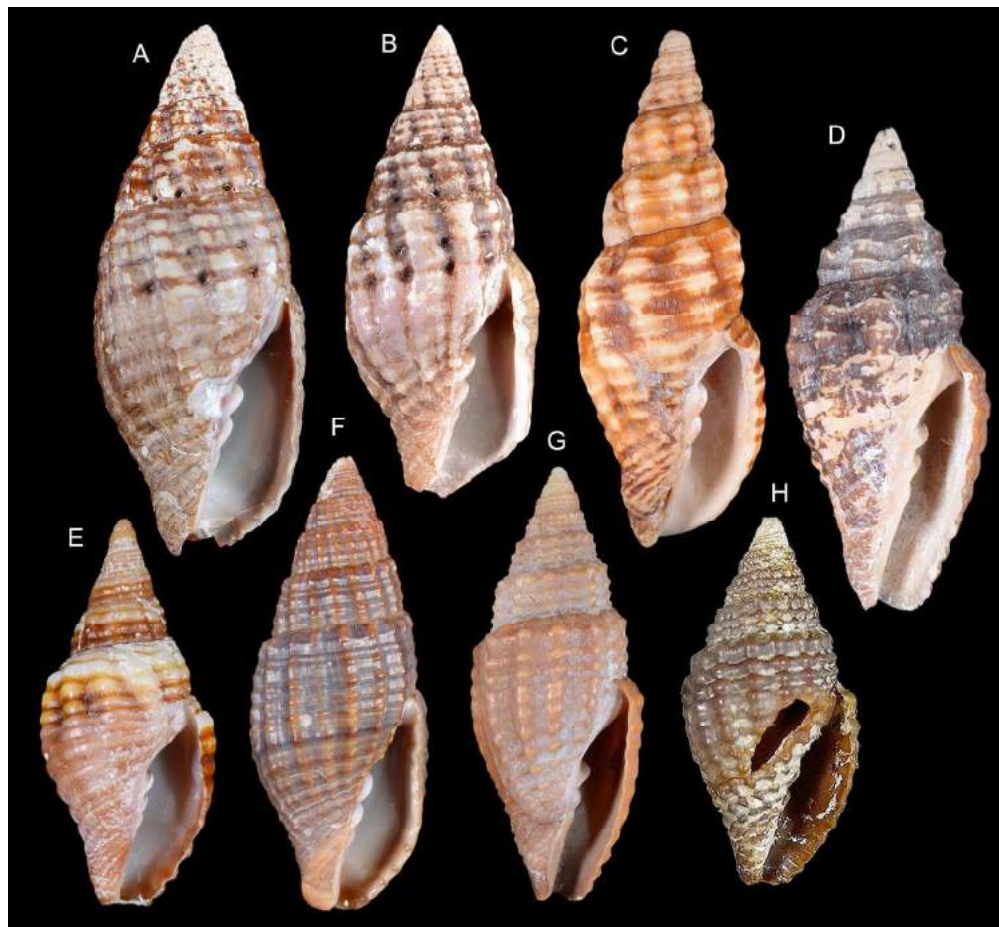


Figure 13. *Neotiarra* species. A, B. *Neotiarra lens* A. Neotype, MNHN IM-2000-33145, Panama, Panama City, 08°95'N, 79°53'W, intertidal, 40.0 mm; B. BAU 2532, same locality as previous, 33.6 mm; C. *N. lignaria*, holotype, NHMUK 1967798, Sta Elena, Ecuador, 47.6 mm; D. *N. rupicola*, syntype, NHMUK 1964460, Sta Elena, Ecuador, 37.2 mm; E. *N. gausapata*, lectotype, NHMUK 1967769/1-2, Galapagos Is, 11.7 mm; F. *N. nodulosa*, MNHN IM-2013-9546, Guadeloupe, KARUBENTHOS Stn GM10, 16°12,53'N, 61°25,55'W, 1 m, 27.8 mm; G. *N. muricata*, lectotype, NHMUK 1967610/1-3, Galapagos Is, 29 mm; H. *N. sp. cf. inca*, BAU 0279-1, Panama, Venado Beach, 8°53.5'N, 79°36.4'W, intertidal, 11 mm.

167x155mm (300 x 300 DPI)

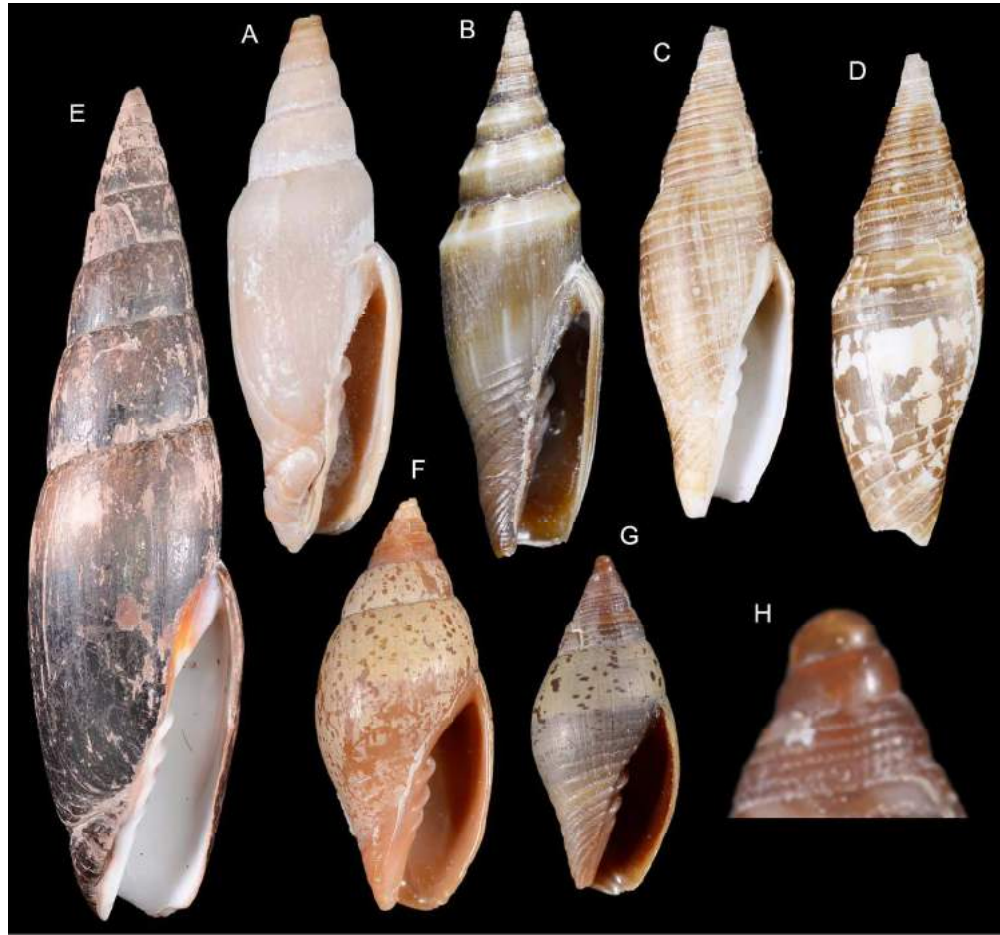


Figure 14. *Ziba* and *Episcomitra* species. A, B. *Ziba carinata*; A. lectotype of *Mitra senegalensis*, NHMUK 1967881, Senegal, 27.9 mm; B. MNHN IM-2013-40647, Congo, Mission ZANAGA, Stn 531DW, 04°43.0'S 11°47.0'E, 17 m, 24.5 mm; C, D. *Z. gambiana*, syntype, NHMUK 1967768, "Senegambia", 28 mm; E. *Episcomitra zonata*, BAU2538, Italy, off Chioggia, 45°12'N, 12°40'E, 40 m, 96.2 mm; F – H. *Episcomitra cornicula* F. BAU1578.3, Greece, Astypalea Is, Agrilidi, 36°35.0'N, 26°25.4'E, 2-7 m, 12.1 mm; G, H. MNHN IM-2013-40661, Italy, Sicily, Syracuse, 37°00.5'N, 15°18.6'E, 6-12 m, 9.0 mm; G. Shell; H. Protoconch.

167x156mm (300 x 300 DPI)

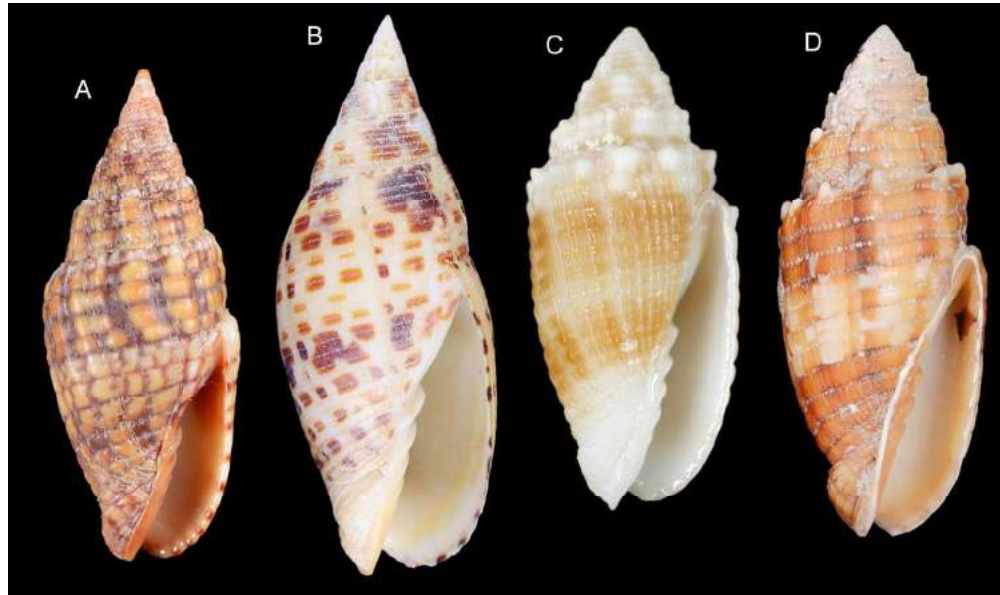


Figure 15. *Quasimitra* species. A. *Quasimitra sanguinolenta*, MNHN IM-2013-40677, Mozambique, INHACA 2011 Stn MS02, 26°06.3'S, 32°58.0'E, 17-19 m, 28.7 mm; B. *Q. cardinalis*, MNHN IM-2013-40681, Papua New Guinea, KAVIENG 2014 Stn KR178, 02°45.2'S 150°43.1'E, 2-46 m, 58.8 mm; C. *Q. sophiae*, MNHN IM-2007-30056, Vanuatu, SANTO 2006 Stn DR09, 15°34.6'S, 167°13.8'E, 12 m, 25.1 mm; D. *Q. puncticulata*, MNHN IM-2013-40685, Philippines, off Noc-Nocan Is, 10°15.1'N 124°25.1'E, 4-12 m, 40.6 mm.

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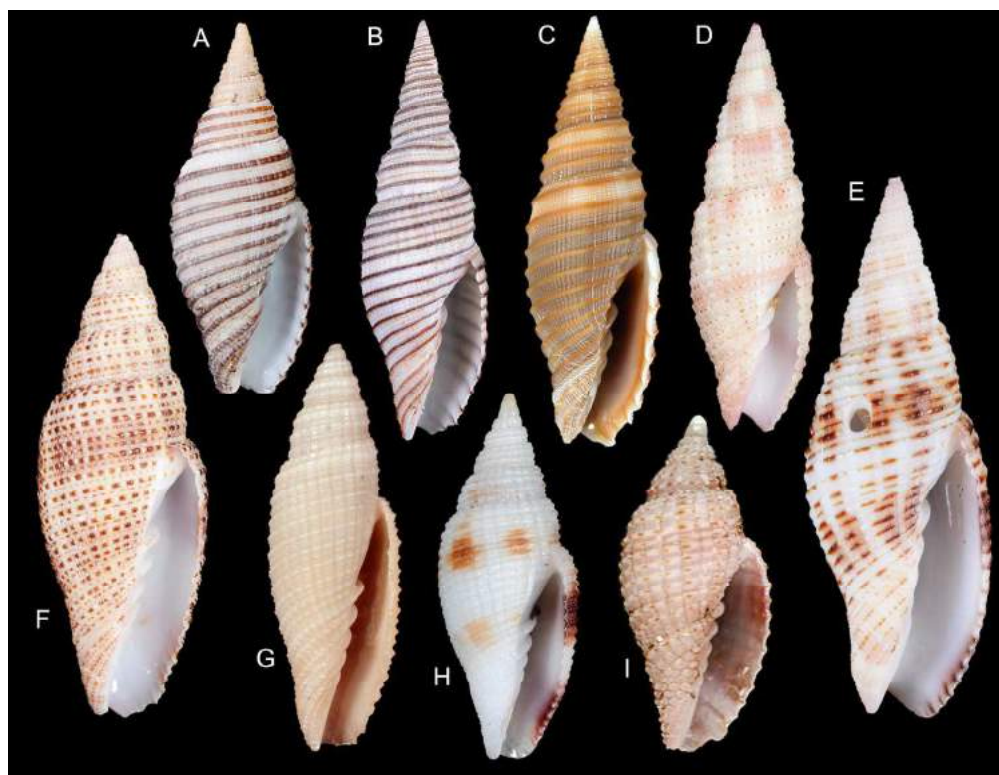


Figure 16. Species of *Domiporta* and *Roseomitra*. A. *Domiporta filaris*, MNHN IM-2013-12956, Papua New Guinea, PAPUA NIUGINI Stn PD 23, 05°06'S, 145°49.2'E, 3-7 m, 15.8 mm; B. *D. praestantissima*, MNHN IM-2013-40642, Vietnam, Nha-Trang Bay, West of Mun Is, 12°10.1'N, 109°17.8'E, 6-18 m, 25.6 mm; C. *D. circula*, MNHN IM-2007-30018, Vanuatu, SANTO 2006 Stn LD24, 15°31.4'S, 167°10.0'E, 47 m; D. *D. cf. carnicolor*, MNHN IM-2013-40684, Philippines, off Noc-Nocan Is, 10°15.1'N, 124°25.1'E, 4-12 m, 23.9 mm; E. *D. granatina*, MNHN IM-2013-40641, Mozambique, INHACA 2011 Stn MR15, 26°00.0'S, 32°54.4'E, 4 m, 34.2 mm; F. *Roseomitra millepunctata*, neotype, MNHN IM-2013-40686, Philippines, off Noc-Nocan Is, 10°15.1'N, 124°25.1'E, 4-12 m, 29.8 mm; G. *R. incarnata*, lectotype, NHMUK 196779/1-3, Misamis Is, Mindanao, Philippines, 21.6 mm; H. *R. tagaruae*, Philippines, Olango Channel, dredged from 80 m, 9.5 mm; I. *R. rosacea*, Mozambique, INHACA 2011 Stn MD13, 26°03.1'S 33°01.0'E, 50-53 m, 7.9 mm.

167x128mm (300 x 300 DPI)



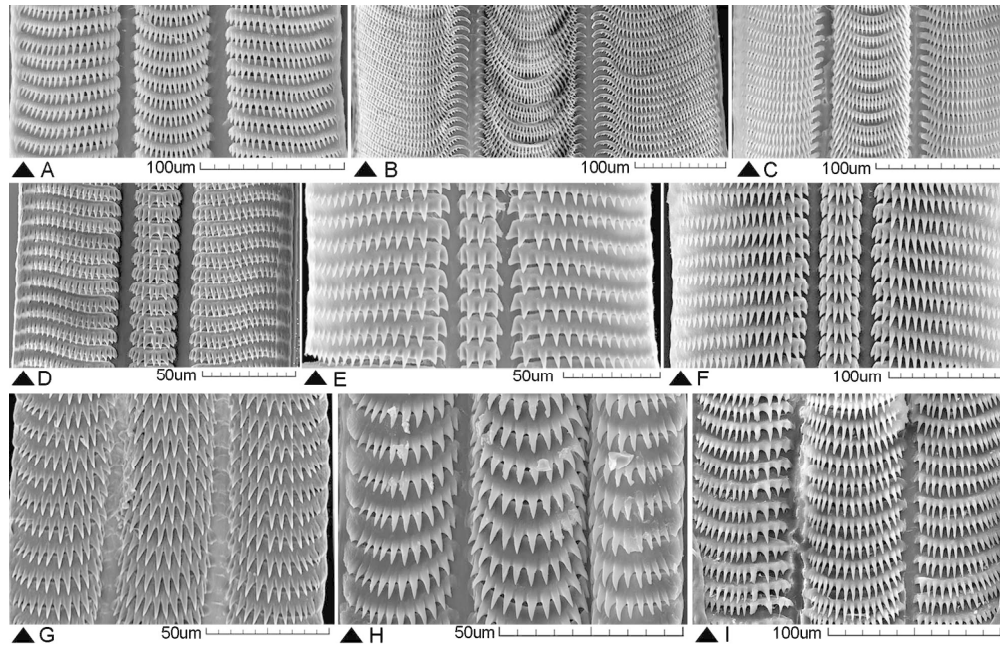


Figure 17. Radulae in the Domiporta clade. A. *Domiporta* cf. *carnicolor*, MNHN IM-2013-40684, Philippines, off Noc-Nocan Is, 10°15.1'N, 124°25.1'E, 4-12 m, 23.9 mm; B. *D. granatina*, MNHN IM-2013-40641, Mozambique, INHACA 2011 Stn MR15, 26°00.0'S, 32°54.4'E, 4 m, 34.2 mm; C. *D. praestantissima*, MNHN IM-2013-40642, Vietnam, Nha-Trang Bay, West of Mun Is, 12°10.1'N, 109°17.8'E, 6-18 m, 25.6 mm; D. *D. filaris*, MNHN, Mozambique, INHACA 2011 Stn MR13, 25°59.7'S, 32°54.5'E, 2-5 m, 17.4 mm; E. *Roseomitra rosacea*, MNHN, Mozambique, INHACA 2011 Stn MD13, 26°03.1'S, 33°01.0'E, 50-53 m, 7.9 mm; F. *R. millepunctata*, MNHN, IM-2013-40686, Philippines, off Noc-Nocan Is, 10°15.1'N, 124°25.1'E, 4-12 m, 29.8 mm; G. *Profundimitra taylori* n. sp., holotype, MNHN, IM-2013-40651, Papua New Guinea, BIOPAPUA Stn CP3671, 04°04'S, 151°56'E, 585-601 m, 24.2 mm; H. *Profundimitra* n. sp., MNHN, IM-2013-40654, New Caledonia, EXBODI Stn CP3829, 22°02'S, 167°05'E, 350-360 m, 16.9 mm; I. *Fusidomiporta ponderi* n. sp., holotype, MNHN IM-2013-40665, Papua New Guinea, BIOPAPUA Stn CP3692, 02°10'S, 147°19'E, 408-448 m, 25.2 mm.

167x108mm (300 x 300 DPI)



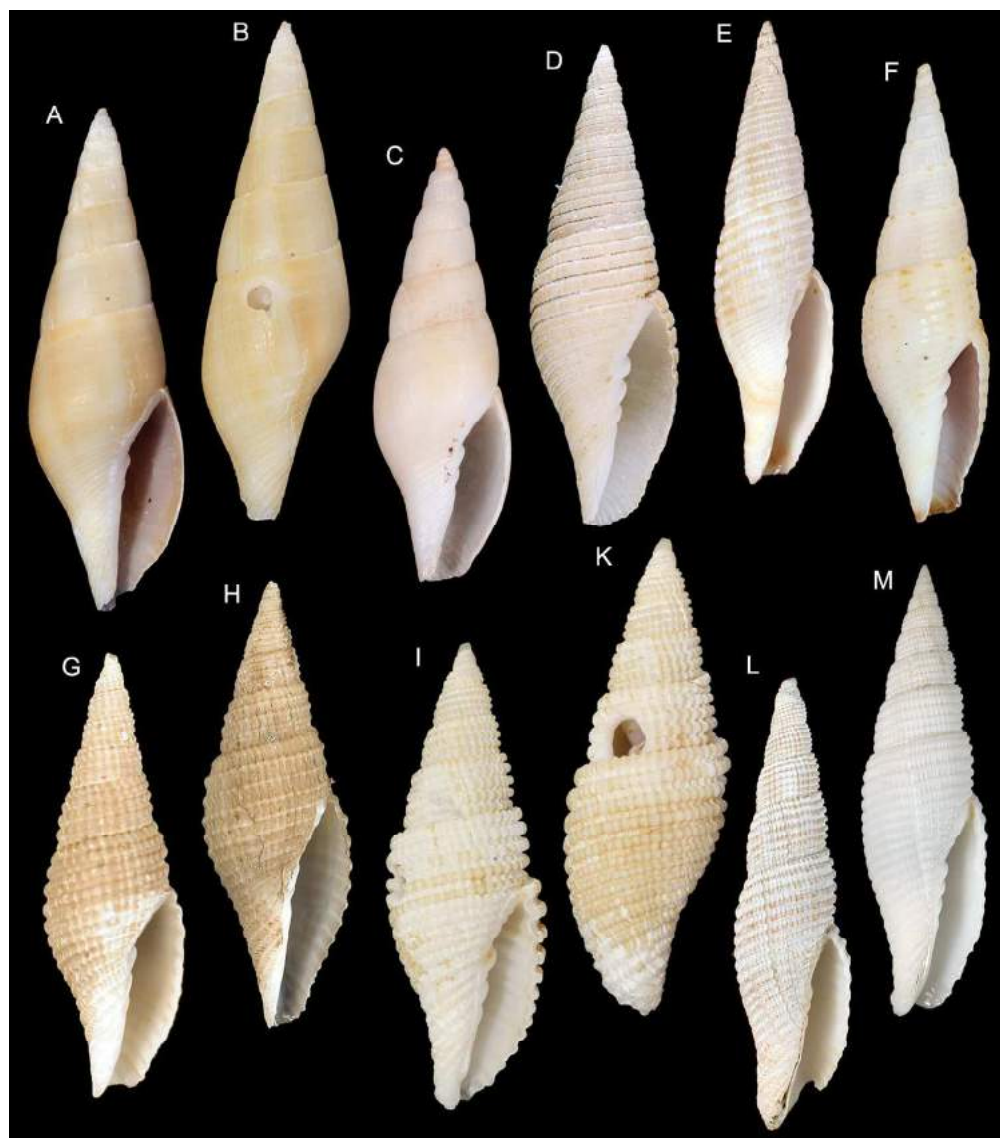


Figure 18. Species of *Profundimitra* n. gen., *Fusidomiporta* n. gen. and *Cancillopsis* n. sp. A – C. *Profundimitra taylori* n. sp. A, B. Holotype, MNHN IM-2013-40651, Papua New Guinea, BIOPAPUA Stn CP3671, 04°04'S, 151°56'E, 585–601 m, 24.2 mm; C. New Caledonia, BATHUS 4 Stn DW920, 18°45'S, 163°17'E, 610–620 m, MNHN, 15.1 mm; D. *Profundimitra* n. sp. aff. *taylori*, Papua New Guinea, BIOPAPUA Stn CP3636, 07°27'S, 147°31'E, 462–495 m, 26.8 mm; E. *Profundimitra planofilum*, MNHN IM-2007-32149, Philippines, PANGLAO 2005 Stn CP2398, 9°33'N, 123°40'E, 713–731 m; F. *Profundimitra* n. sp. aff. *planofilum*, MNHN, IM-2013-40654, New Caledonia, EXBODI Stn CP3829, 22°02'S, 167°05'E, 350–360 m, 16.9 mm; G. *Profundimitra* n. sp., MNHN IM-2007-35711, Philippines, AURORA 2007 Stn CP2658, 15°58'N, 121°49'E, 422–431 m; H. *Profundimitra* n. sp., MNHN IM-2007-36757, Madagascar, MIRIKY Stn CP3289, 14°29'S, 47°26'E, 332–379 m; I, K. *Fusidomiporta ponderi* n. sp., holotype, MNHN, IM-2013-40665, Papua New Guinea, BIOPAPUA Stn CP3692, 02°10'S, 147°19'E, 408–448 m, 25.2 mm; L. *Fusidomiporta* n. sp., MNHN IM-2007-32153, Philippines, PANGLAO 2005 Stn DW2364, 09°01'N, 123°25'E, 427 m; M. *Cancillopsis meimiaoae* MNHN IM-2007-30011, Vanuatu, SANTO' 2006, Stn AT19, 15°40'48''S 167°00'30''E, 503–600 m.

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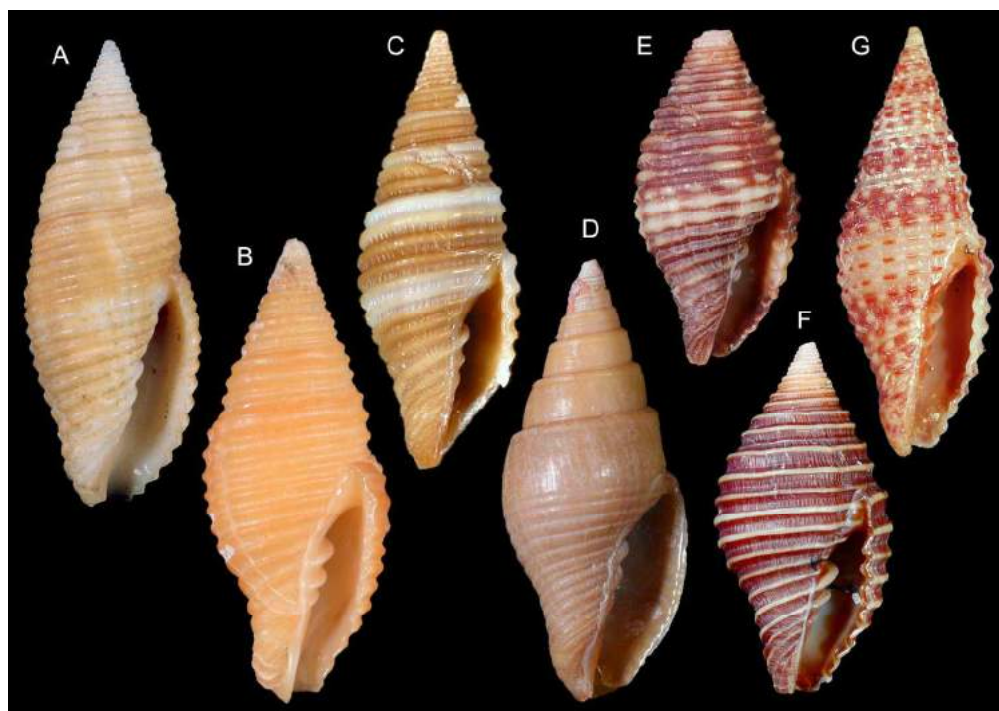


Figure 19. Species of *Pseudonebularia* n. gen. A, B. *Pseudonebularia tornata*, A. Lectotype of *Mitra tornata*, NHMUK 1967897, Philippines, 18.1 mm; B. MNHN IM-2013-12538, PAPUA NIUGINI Stn PB14, 05°13.8'S, 145°48'E, 15 m, 16.5 mm; C. *P. atjehensis*, MNHN IM-2007-30264, Vanuatu, SANTO 2006 Stn EP01, 15°32.5'S, 167°09'E, 46-47 m; D. *P. maesta*, MNHN IM-2013-40648, Madagascar, MIRIKY Stn CP3288, 14°31.9' S, 47°26.5' E, 46-54 m, 15.6 mm; E. *P. connectens*, MNHN IM-2013-2342, PAPUA NIUGINI Stn PB16, 05°10.7'S, 145°47.7'E, intertidal, 10.4 mm; F. *P. pediculus*, MNHN IM-2013-12705, PAPUA NIUGINI Stn PB15, 05°04.7'S, 145°48.9'E, 5 m, 11.6 mm; G. *P. gracilefragum*, Philippines, Olango I., Caw Oy, 10-25 m, 20.1 mm.

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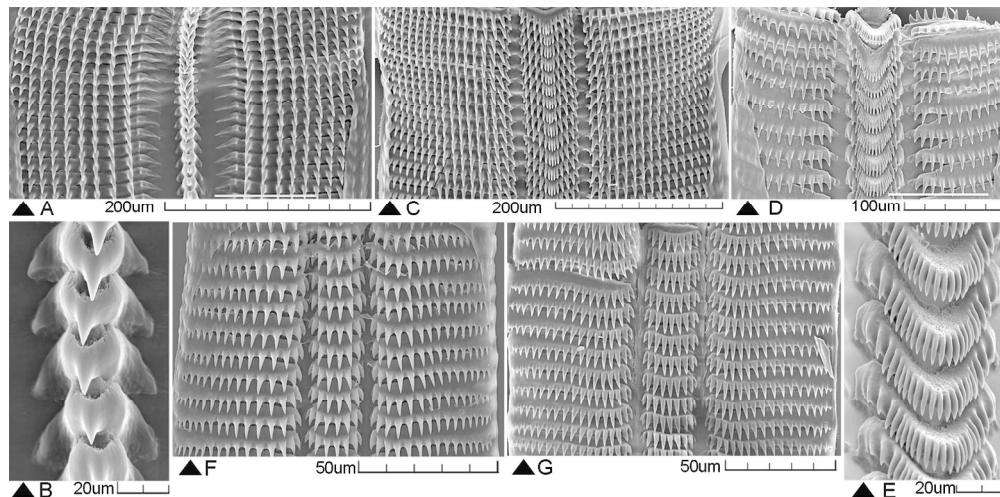


Figure 20. Radulae of *Pseudonebularia* n. gen. and *Gemmulimitra* n. gen. A, B. *Pseudonebularia pediculus*, MNHN IM-2013-12705, PAPUA NIUGINI Stn PB15, 05°04.7'S, 145°48.9'E, 5 m, 11.6 mm; C. *P. connectens*, MNHN IM-2013-2342, PAPUA NIUGINI Stn PB16, 05°10.7'S, 145°47.7'E, intertidal, 10.4 mm; D, E. *P. maesta*, MNHN IM-2013-40648, Madagascar, MIRIKY Stn CP3288, 14°31.9' S, 47°26.5' E, 46-54 m, 15.6 mm; F. *Gemmulimitra neocaledonica*, MNHN, Paratype 5, New Caledonia, EXBODI Stn CP3814, 21°49'S, 166°44'E, 331-344m, 20.4 mm; G. *G. boucheti*, MNHN IM-2013-40649, Papua New Guinea, BIOPAPUA Stn DW3641, 06°45'S, 148°01'E, 380-476 m, 11.6 mm.

167x82mm (300 x 300 DPI)

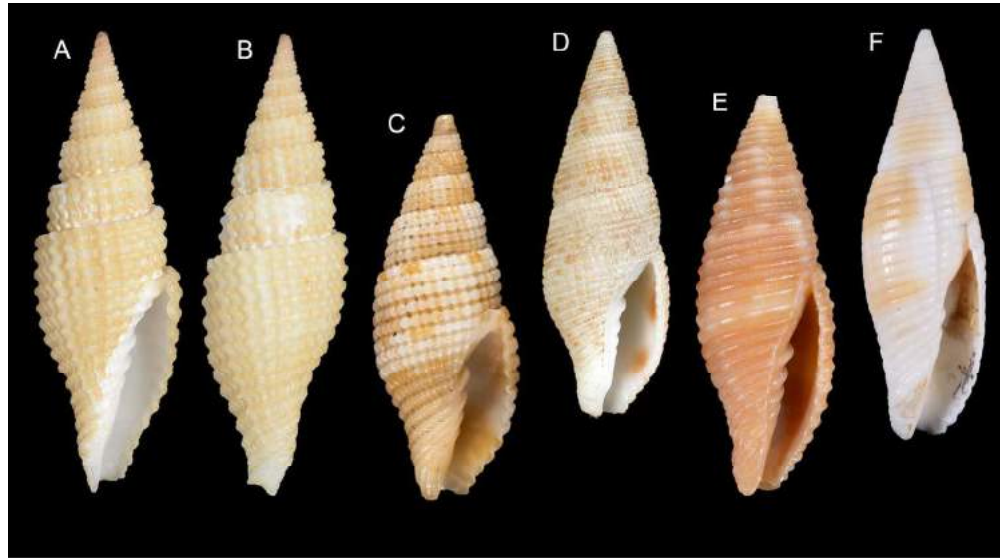


Figure 21. Species of *Gemmulimitra* n. gen. A, B. *Gemmulimitra neocaledonica*, holotype, MNHN IM-2013-40655, New Caledonia, EXBODI Stn CP3821, 21°53'S, 166°50'E, 211-440 m, 24.25 mm; C. *G. boucheti*, holotype, MNHN IM-2000-30172, Réunion, MD32, Stn DC41, 21°21'S, 55°27'E, 75 m, 9.0 mm; D. *G. strongae*, MNHN IM-2007-36727, Madagascar, MIRIKY Stn DW3213, 12°31'S, 47°52'E, 262-289 m; E. *G. avenacea*, MNHN IM-2013-11683, PAPUA NIUGINI Stn PB14, 05°13.8'S 145°48'E, 15 m, 14.0 mm; F. *G. rubiginosa*, syntype of *Mitra rubiginosa*, NHMUK 1967866, Is of Ticao, Philippines, 37.8 mm.

167x93mm (300 x 300 DPI)

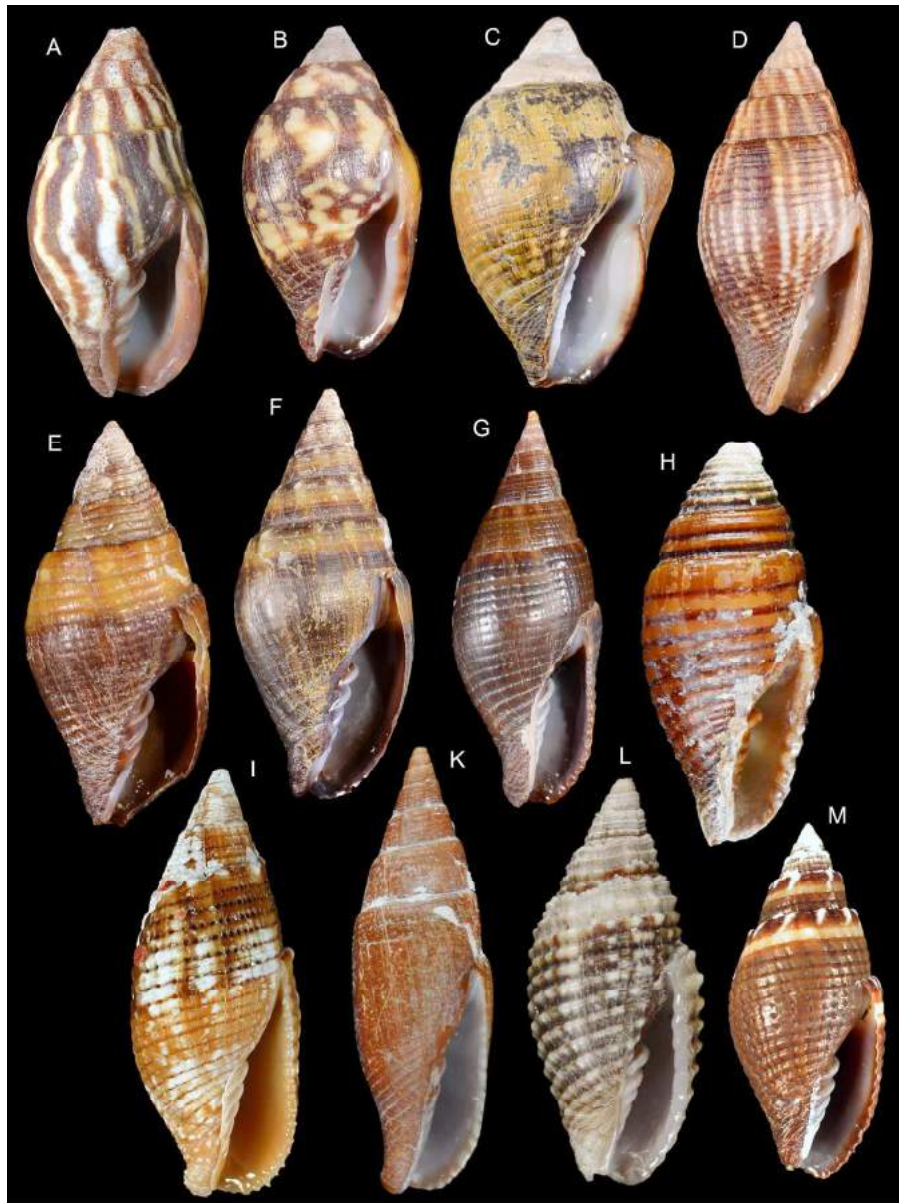


Figure 22. *Strigatella* species. A. *Strigatella paupercula*, MNHN IM-2013-15188, PAPUA NIUGINI Stn PM39, 05°12.1'S, 145°48.4'E, intertidal, 22.2 mm; B. *S. litterata*, MNHN IM-2013-12959, PAPUA NIUGINI Stn PM22, 05°04.7'S, 145°48.9'E, intertidal, 16.0 mm; C. *S. decurtata*, MNHN IM-2013-15843, PAPUA NIUGINI Stn PM41, 05°08.1'S, 145°49.3'E, 0-1 m, 22.1 mm; D. *S. scutulata*, MNHN IM-2013-12771, PAPUA NIUGINI Stn PM22, 05°04.7'S, 145°48.9'E, intertidal, 24.7 mm; E. *S. aurantia*, MNHN IM-2013-40679, Mozambique, INHACA 2011 Stn MB07, 25°59.7'S, 32°54.2'E, 2-10 m, 21.3 mm; F. *Strigatella tristis*, BAU 2534-2, Panama, Rio Mar, 8°27.5'N, 79°58.0'W, intertidal, 20.3 mm; G. *S. luctuosa*, MNHN IM-2013-11682, PAPUA NIUGINI Stn PR14, 05°12'S, 145°48.1'E, 2-3 m, 20.9 mm; H. *S. vexillum*, MNHN IM-2013-12570, PAPUA NIUGINI Stn PR24, 05°12.3'S 145°48.8'E, 24.0 mm; I. *S. imperialis*, MNHN IM-2007-30173, Vanuatu, SANTO 2006 Stn FR01, 15°32.3'S, 167°13.1'E, 18-20 m; K. *S. fulvescens*, MNHN IM-2013-40680, TUHAA PAE Stn AMA03, 21°48.2'S, 154°43.2'W, 26 m, 25.5 mm; L. *S. lugubris*, MNHN IM-2013-40678, Austral Is, TUHAA PAE Stn AT07, 23°19.7'S 149°29.3'W, 14 m, 13.7 mm; M. *S. coronata*, MNHN IM-2013-30023, Vanuatu, SANTO 2006 Stn VM36, 15°27.5'S, 167°15.4'E, intertidal.

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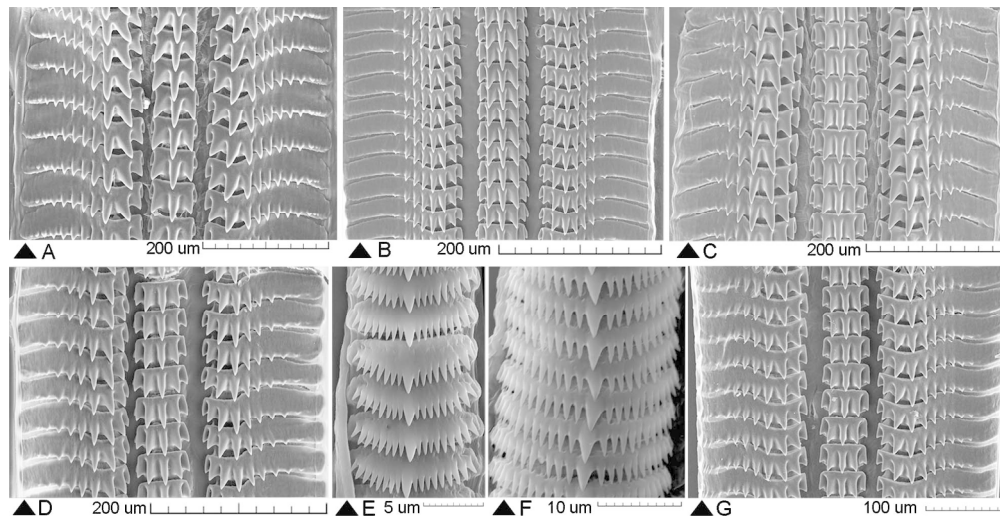


Figure 23. Radulae in species of *Strigatella*. A. *Strigatella paupercula*, MNHN IM-2013-15188, PAPUA NIUGINI Stn PM39, 05°12.1'S, 145°48.4'E, intertidal, 22.2 mm; B. *S. luctuosa*, MNHN IM-2013-11682, PAPUA NIUGINI Stn PR14, 05°12'S, 145°48.1'E, 2-3 m, 20.9 mm; C. *S. decurtata*, MNHN IM-2013-15843, PAPUA NIUGINI Stn PM41, 05°08.1'S, 145°49.3'E, 0-1 m, 22.1 mm; D. *S. vexillum*, MNHN IM-2013-12570, PAPUA NIUGINI Stn PR24, 05°12.3'S 145°48.8'E, 24.0 mm; E. *S. coronata*, MNHN, Society Is, off Moorea, 9.0 mm; F. *S. lugubris*, MNHN IM-2013-40678, Austral Is, TUHAA PAE Stn AT07, 23°19.7'S 149°29.3'W, 14 m, 13.7 mm; G. *S. tristis*, BAU 2534-2, Panama, Rio Mar, 8°27.5'N, 79°58.0'W, intertidal, 20.3 mm.

167x86mm (300 x 300 DPI)

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Figure 24. *Imbricaria* species. A. *Imbricaria conularis*, MNHN IM-2013-18043, PAPUA NIUGINI Stn PR203, 05°10.3'S 145°48.5'E, 1-19 m, 16.8 mm; B. *I. bantamensis*, MNHN IM-2013-16688, PAPUA NIUGINI Stn PD67, 05°15.5'S, 145°46.8'E, 2-6 m, 21.8 mm; C. *I. insculpta*, MNHN IM-2013-40657, Vietnam, Nha-Trang Bay, South Mot Is, 12°10.4'N 109°16.3'E, 15-18 m, 18.3 mm; D. *I. flammigera*, MNHN IM-2013-40656, Vietnam, Nha-Trang Bay, South Mot I., 12°10.4'N 109°16.3'E, 15-18 m, 14.8 mm; E. *I. fulgetrum*, MNHN IM-2013-18112, PAPUA NIUGINI Stn PR240, 05°08.2'S, 145°48.7'E, 3-20 m, 16.8 mm; F. *I. verrucosa*, MNHN IM-2013-14284, PAPUA NIUGINI Stn PD39, 04°59.3'S, 145°47.5'E, 2-4 m, 11.6 mm; G. *I. salisburyi*, Papua New Guinea, Hansa Bay, 8-18 m, 15.3 mm; H. *I. hrdlickae*, MNHN IM-2013-18020, PAPUA NIUGINI Stn PD75, 05°14.2'S, 145°47.8'E, 10-25 m, 16.5 mm; I. *I. rufogyrata*, MNHN IM-2007-36131, Solomon Is, SALOMONBOA 3 Stn DW2852, 09°46'S, 160°51'E, 220 m; K. *I. pugnax*, MNHN IM-2007-32124, Philippines, PANGLAO 2005 Stn CP2378, 08°38.7'N, 123°20.1'E, 65 m.

167x162mm (300 x 300 DPI)

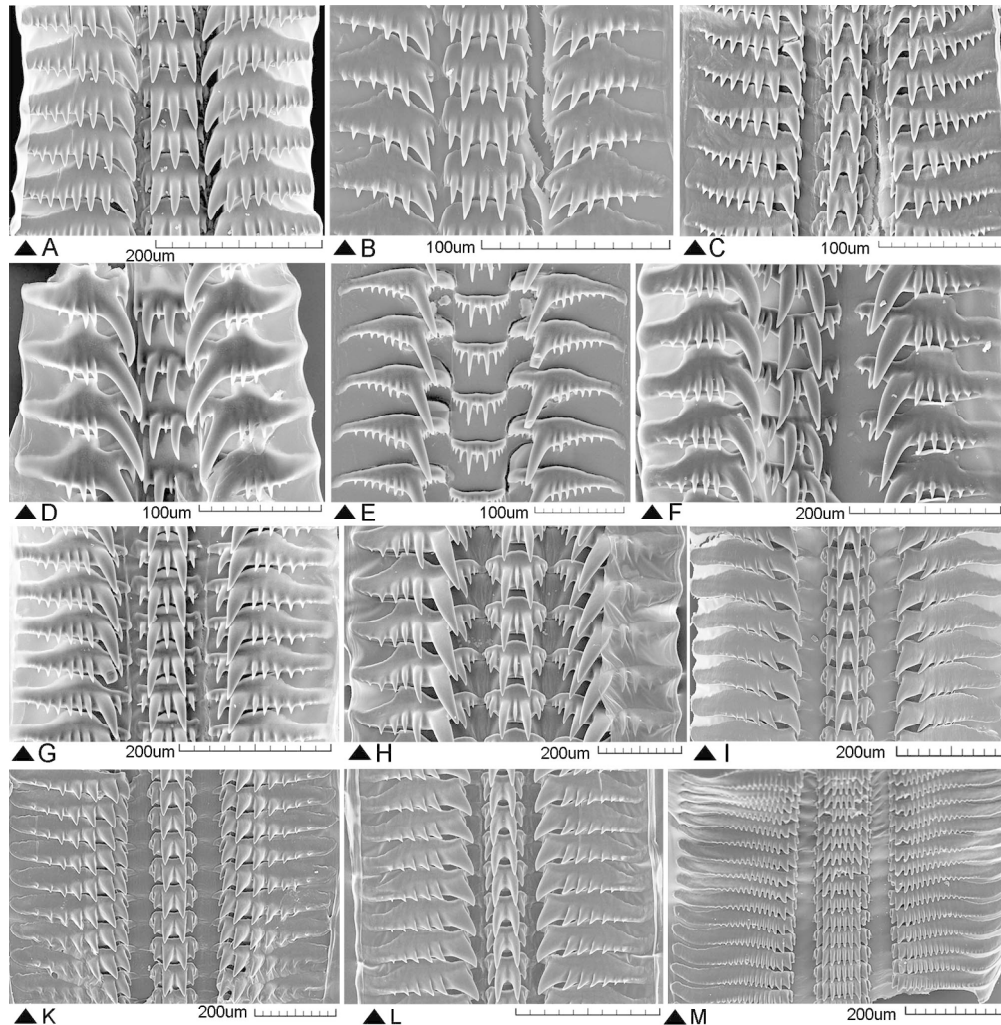


Figure 25. Radulae in the genera *Imbricaria* and *Cancilla*. A. *I. pugnaxa*, MNHN, New Caledonia, EXBODI Stn CP3795, 21°32'S, 166°21'E, 240-245 m, 31.9 mm; B. *I. conularis*, MNHN, Society Is, Moorea, 13.3 mm; C. *I. fulgetrum*, MNHN IM-2013-18112, PAPUA NIUGINI Stn PR240, 05°08.2'S, 145°48.7'E, 3-20 m, 16.8 mm; D. *I. flammigera*, MNHN IM-2013-40656, Vietnam, Nha-Trang Bay, South Mot I., 12°10.4'N 109°16.3'E, 15-18 m, 14.8 mm; E. *I. insculpta*, MNHN IM-2013-40657, Vietnam, Nha-Trang Bay, South Mot Is, 12°10.4'N 109°16.3'E, 15-18 m, 18.3 mm; F. *I. verrucosa*, MNHN, Papua New Guinea, KAVIENG 2014 Stn KR54, 02°42.3'S, 150°39.1'E, 7-10 m, 12.3 mm; G. *I. salisburyi*, Papua New Guinea, Hansa Bay, 8-18 m, 15.3 mm; H. *I. interilirata*, Vietnam, Nha-Trang Bay, Murray Beach, 12°10.1'N, 109°17.8'E, 6-18 m, 28.6 mm; I. *Cancilla fibula* / *rehderi*, MNHN, Papua New Guinea, BIOPAPUA Stn DW3641, 06°45'S, 148°01'E, 380-476 m, 20.8 mm; K. *C. cf. fibula*, MNHN IM-2013-40646, New Caledonia, EXBODI Stn CP3822, 21°52'S, 166°51'E, 341-506 m, 37.6 mm; L. *C. baueri*, MNHN IM-2013-58853, Papua New Guinea, KAVIENG 2014 Stn DW4484, 02°26'S, 149°55'E, 229 m, 34.2 mm; M. *C. schepmani*, MNHN IM-2013-40645, New Caledonia, EXBODI Stn DW3926, 18°35'S, 164°20'E, 364-473 m, 15.6 mm.

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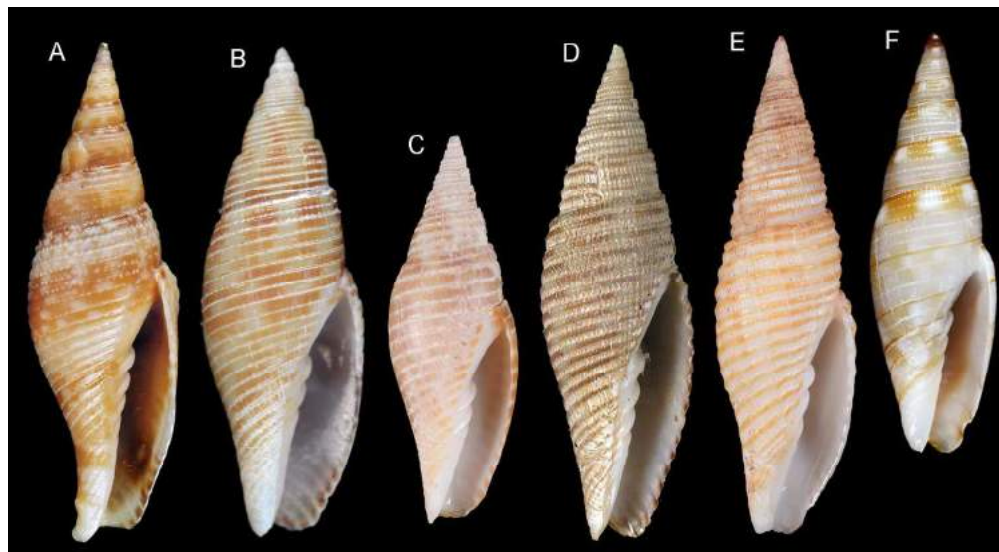


Figure 26. *Cancilla* species. A. *Cancilla baeri*, IM-2013-58853, Papua New Guinea, KAVIENG 2014 Stn DW4484, 02°26'S, 149°55'E, 229 m, 34.2 mm; B – D. *Cancilla fibula* / *rehderi*; B. MNHN, Papua New Guinea, BIOPAPUA Stn DW3641, 06°45'S, 148°01'E, 380–476 m, 20.8 mm; C. MNHN IM-2013-19073, PAPUA NIUGINI Stn CP4059, 02°38'S, 141°18'E, 335 m, 23.75 mm; D. MNHN IM-2007-38688, Society Is, TARASOC Stn DW3441, 16°41.7'S, 151°26.1'W, 350–360 m; E. *Cancilla* cf. *fibula*, MNHN IM-2013-40646, New Caledonia, EXBODI Stn CP3822, 21°52'S, 166°51'E, 341–506 m, 37.6 mm; F. *C. schepmani*, MNHN IM-2013-40645, New Caledonia, EXBODI Stn DW3926, 18°35'S, 164°20'E, 364–473 m, 15.6 mm.

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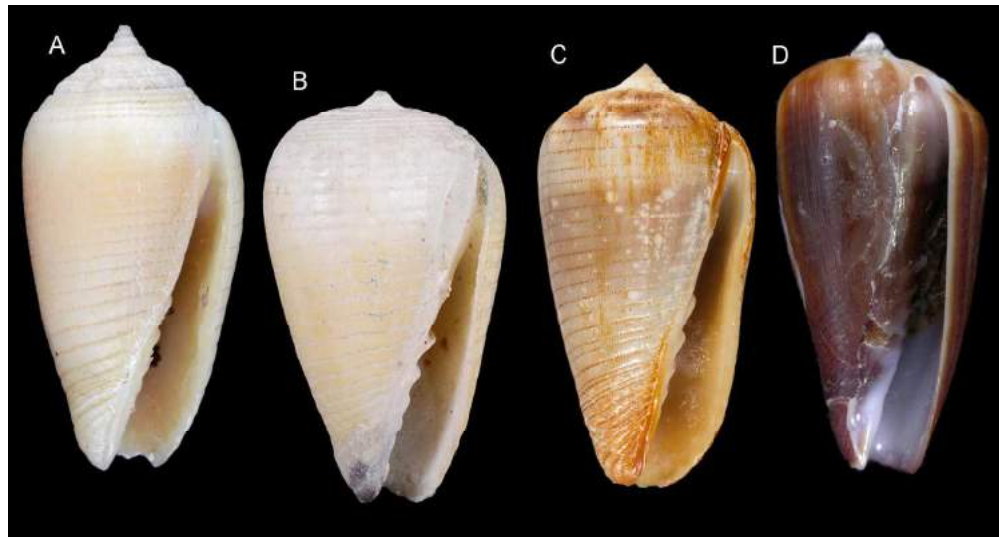


Figure 27. Species of *Imbricariopsis* n. gen. A. *Imbricariopsis punctata*, MNHN IM-2013-11604, PAPUA NIUGINI Stn PM12, 05°00.2'S, 145°47.6'E, 0-1 m, 17.2 mm; B. *I. conovula*, lectotype of *Mitra virgo*, NHMUK 1967912, Society Is, 14 mm; C. *I. vanikorensis*, lectotype, MNHN IM-2000-30312, Vanikoro, Solomon Is, 22.5 mm; D. *Mitra carbonacea*, Senegal, off Gorée I., 10-15 m, 20.5 mm.

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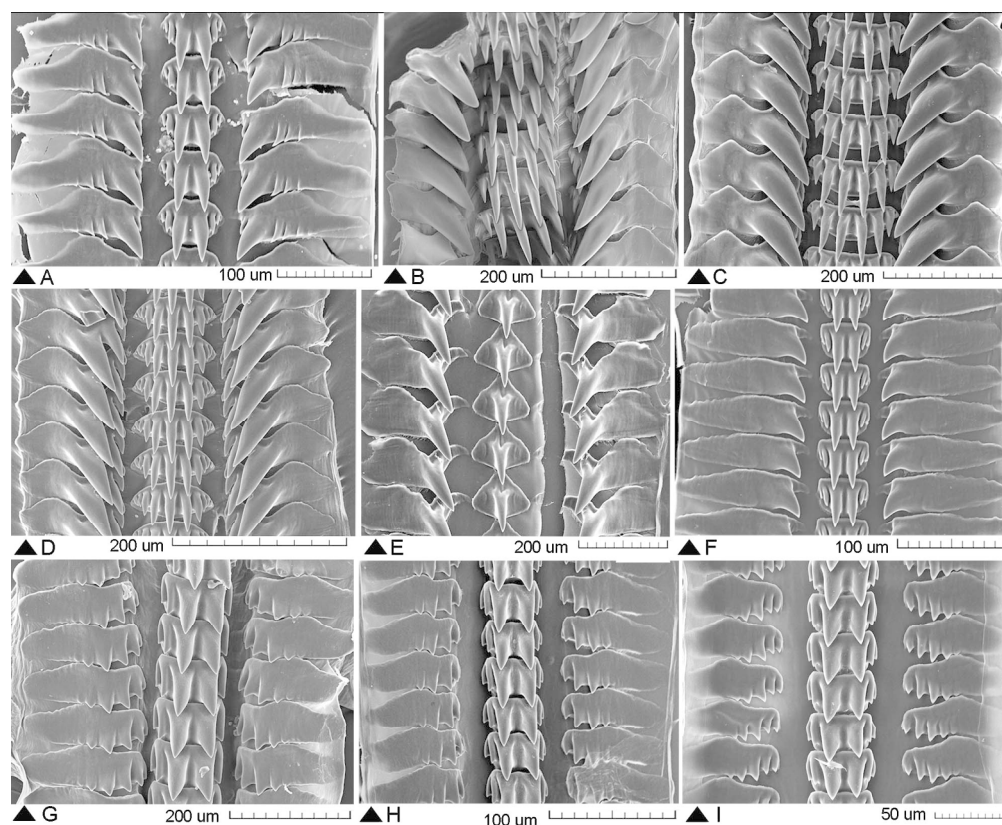


Figure 28. Radulae in the genera *Imbricariopsis*, *Swainsonia*, *Scabricola* and *Neocancilla*. A. *Imbricariopsis punctata*, Mozambique, INHACA 2011 Stn MM3, 26°03.9'S, 32°57.3'E, 0-1 m, 14.7 mm; B. *Swainsonia fusca*, MNHN IM-2013-40643; C. *Swainsonia casta*, Papua New Guinea, Hansa Bay, 8-18 m, 25.6 mm; D. *Scabricola desetangii*, MNHN IM-2013-50703, Papua New Guinea, KAVIENG 2014 Stn KR14, 02°42.3'S 150°39.1'E, 7-10 m, 24.6 mm; E. *Scabricola variegata*, MNHN IM-2013-40683, Philippines, off Noc-Nocan Is, 10°15.1'N, 124°25.1'E, 4-12 m, 45.5 mm; F. *Scabricola olivaeformis*, Vietnam, Nha-Trang Bay, Murray Beach, 12°10.1'N, 109°17.8'E, 6-18 m, 13.2 mm; G. *Neocancilla papilio*, Society Is, off Moorea, 36.6 mm; H. *N. clathrus*, Mozambique, INHACA 2011 Stn MR13, 25°59.7'S, 32°54.5'E, 2-5 m, 14.9 mm; I. *N. rufescens*, MNHN IM-2013-40644, Mozambique, INHACA 2011 Stn MD22, 25°59.7'S, 32°46.8'E, 22 m, 16.4 mm.

167x137mm (300 x 300 DPI)



Figure 29. Genera *Scabricola* and *Swainsonia*. A. *Scabricola variegata*, MNHN IM-2013-40683, Philippines, off Noc-Nocan Is, 10°15.1'N, 124°25.1'E, 4-12 m, 45.5 mm; B. *Scabricola desetangsi*, MNHN IM-2013-50703, Papua New Guinea, KAVIENG 2014 Stn KR14, 02°42.3'S 150°39.1'E, 7-10 m, 24.6 mm; C. *Scabricola olivaeformis*, MNHN IM-2013-18062, PAPUA NIUGINI Stn PR214, 05°10.2'S, 145°50.4'E, 1-8 m, 13 mm; D. *Scabricola coriacea*, syntype, NHMUK 1967728, Corrigidor I., Philippines, 11.1 mm; E. *Scabricola albina*, holotype, NHMUK 1966663, Batangas, Luzon I., Philippines, 26.7 mm; F. *Scabricola potensis*, lectotype, MNHN IM-2000-30283, New Caledonia, Belep Is, 24.5 mm; G. *Swainsonia fissurata*, Israel, off Eilat, 2-4 m, 63.1 mm; H. *Swainsonia fusca*, MNHN IM-2013-40643, Mozambique, INHACA 2011 Stn MS08, 25°59.5'S, 32°52.9'E, 9-17 m, 18.2 mm; I. *Swainsonia casta*, MNHN IM-2013-48000, Papua New Guinea, KAVIENG 2014 Stn KS17, 02°36.2'S, 150°46.3'E, 3 m, 30.5 mm.

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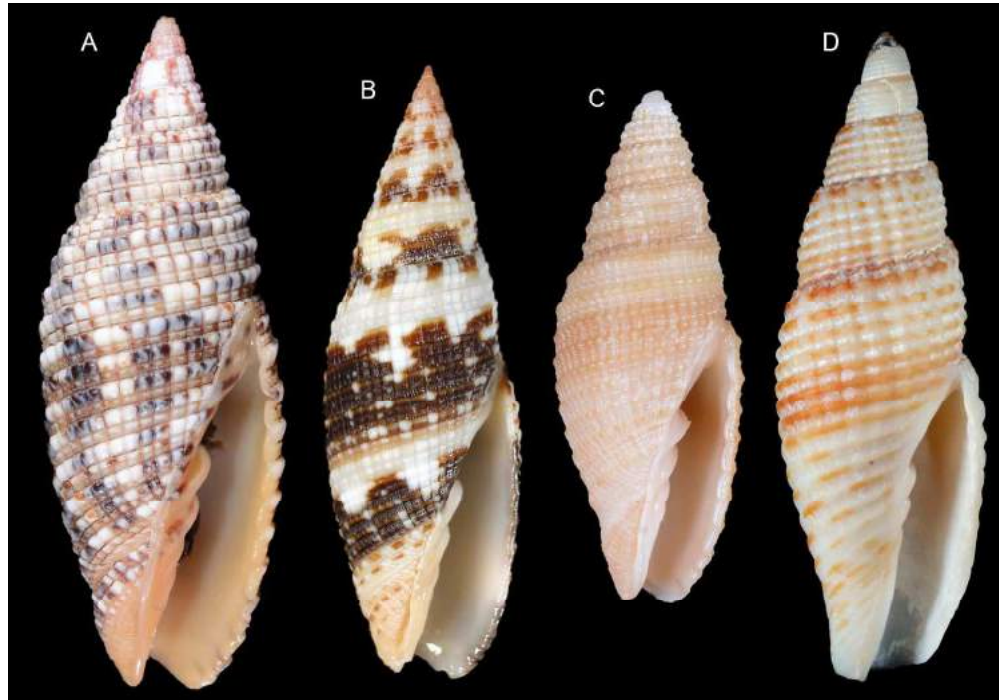


Figure 30. *Neocancilla* species. A. *Neocancilla papilio*, MNHN IM-2013-12560, PAPUA NIUGINI Stn PR24, 05°12.3'S, 145°48.8'E, 28.2 mm; B. *N. clathrus*, MNHN IM-2007-30178, Vanuatu, SANTO 2006 Stn DR73, 15°22.5'S, 167°11.3'E, 10-25 m; C. *N. rufescens*, MNHN IM-2013-40644, Mozambique, INHACA 2011 Stn MD22, 25°59.7'S, 32°46.8'E, 22 m, 16.4 mm; D. *N. hemmenae*, holotype, NHMUK 1992088, off Somalia, 40.8 mm.

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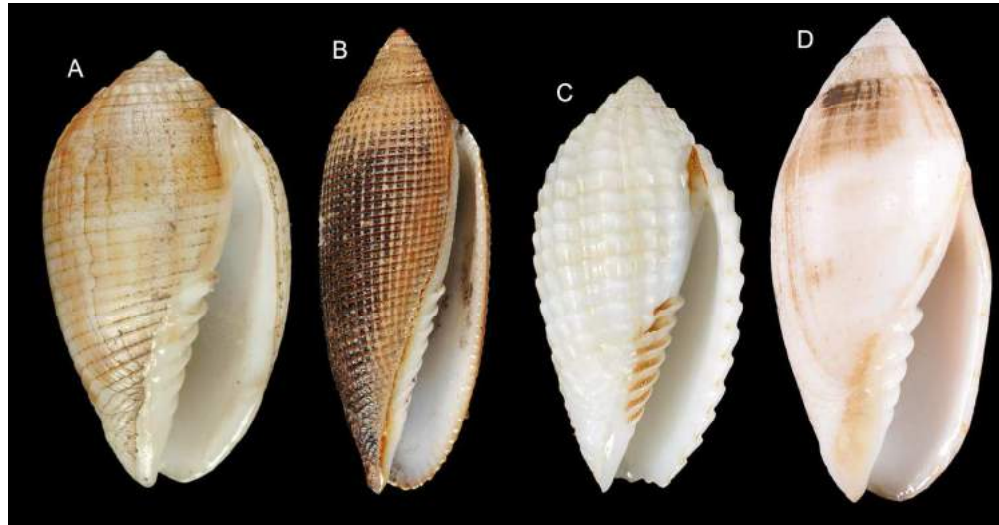


Figure 31. *Pterygia* species. A. *Pterygia dactylus*, MNHN IM-2013-14989, PAPUA NIUGINI Stn PM39, 05°12.1'S, 145°48.4'E, intertidal, 25.1 mm; B. *P. sinensis*, MNHN IM-2009-15439, Madagascar, ATIMO VATAE Stn CP3568, 25°04.7'S, 47°03.4'E, 64-65 m; C. *P. fenestrata*, MNHN IM-2007-30039, Vanuatu, SANTO 2006 Stn DR09, 15°34.5'S, 167°13.5'E, 12 m; D. *P. nucea*, MNHN IM-2013-50702, Papua New Guinea, KAVIENG 2014 Stn KM04, 02°42'S, 150°44'E, 0-1 m, 42 mm.

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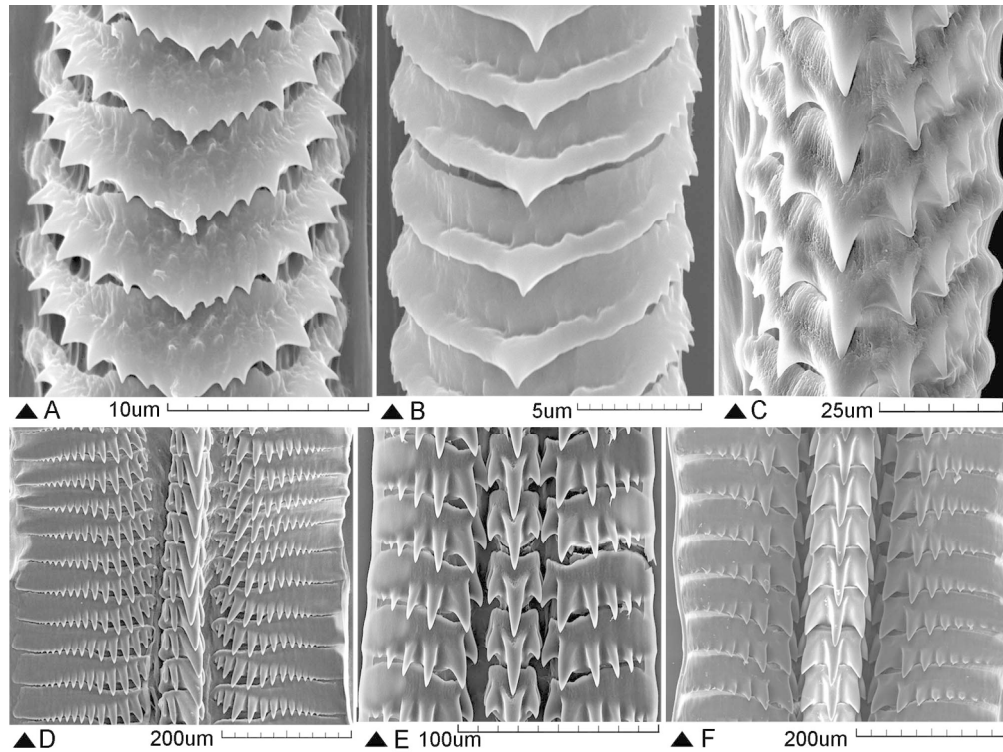


Figure 32. Radulae in the subfamily Cylindromitridae. A. *Pterygia dactylus*, MNHN IM-2013-14989, PAPUA NIUGINI Stn PM39, 05°12.1'S, 145°48.4'E, intertidal, 25.1 mm; B. *P. fenestrata*, Society Is, off Moorea, 11.5 mm; C. *P. nucea*, MNHN IM-2013-50702, Papua New Guinea, KAVIENG 2014 Stn KM04, 02°42'S, 150°44'E, 0-1 m, 42 mm; D. *Nebularia incompta*, Philippines, Olango I. Cow-Oy, 10-25 m, 48.0 mm; E. *N. contracta*, Mozambique, INHACA 2011 Stn MR24, 25°54.5'S, 33°02.8'E, 23-26 m, 29.9 mm; F. *N. acuminata*, MNHN IM-2013-13288, PAPUA NIUGINI Stn PM25, 05°01.1'S, 145°47.9'E, intertidal, 23 mm.

170x127mm (300 x 300 DPI)



Figure 33. *Nebularia* species. A. *Nebularia contracta*, MNHN IM-2013-10345, PAPUA NIUGINI Stn PR04, 05°10.1'S, 145°50.5'E, 30m, 19.7 mm; B. *N. chrysostoma*, syntype, NHMUK 1967715, "Isle of Annaa, South Seas" [Anaa, Tuamotu Is], 51.3 mm; C. *N. eremitarum*, MNHN IN-2013-16323, PAPUA NIUGINI Stn PM51, 05°05.5'S, 145°48.6'E, 0-1 m, 48.4 mm; D. *N. incompta*, Philippines, Olango I., Cow-Oy, 10-25 m, 48.0 mm; E. *N. edentula*, 26.7 mm, Mozambique, Matibane Bay, Choca, 2-4 m; F. *N. ustulata*, Syntype of *Mitra ustulata*, NHMUK 1967918, ?Viti Is [Fiji], 34.2 mm; G. *N. ancillides*, holotype, NHMUK 1967712, "I. of Annaa" [Anaa, Tuamotu Is], 23.6 mm; H. *N. acuminata*, MNHN IM-2013-13288, PAPUA NIUGINI Stn PM25, 05°01.1'S, 145°47.9'E, intertidal, 23 mm; I. *N. coarctata*, syntype, NHMUK 1967722, locality unknown, 17.5 mm.

167x171mm (300 x 300 DPI)



Figure 34. *Isara* species. A. *Isara glabra*, MNHN IM-2013-40640, Esperance, WESTERN AUSTRALIA Stn WE01, 15°16.94'S, 124°06.3'E, 11 m, 62.7 mm; B. Holotype of *Mitra bulimoides*, NHMUK 1966656, locality not known, 33.2 mm; C. *I. chalybeia*, syntype, NHMUK 1967709, locality not known, 51.5 mm; D. *I. carbonaria*, molecular voucher, AMS C.335424, Australia, North Sydney, Collaroy, Long Reef, 33°44.7'S, 151°19' E, intertidal; E. *I. chinensis*, lectotype, NHMUK 1967708, "China", 58.6 mm; F. *I. nigra*, MNHN IM-2013-40676, Congo, Mission ZANAGA Stn DV08, 04°42.9'S, 11°47.5'E, 14-15 m, 45.2 mm; G. *I. cornea*, BAU2537.1, Italy, Giannutri Is., Punta San Francesco, 42°15.1'N, 11°07'E, 10-20 m, 36.75 mm; H. *Isara turtoni*, lectotype of *Mitra turtoni*, NHMUK 1889.1.10.-97, St. Helena Is., 26.2 mm; I. *I. straminea*, MNHN IM-2013-56423, French Guiana, GUYANE Stn CP4375, 06°39'N, 52°30'W, 195-200 m, 33.5 mm.

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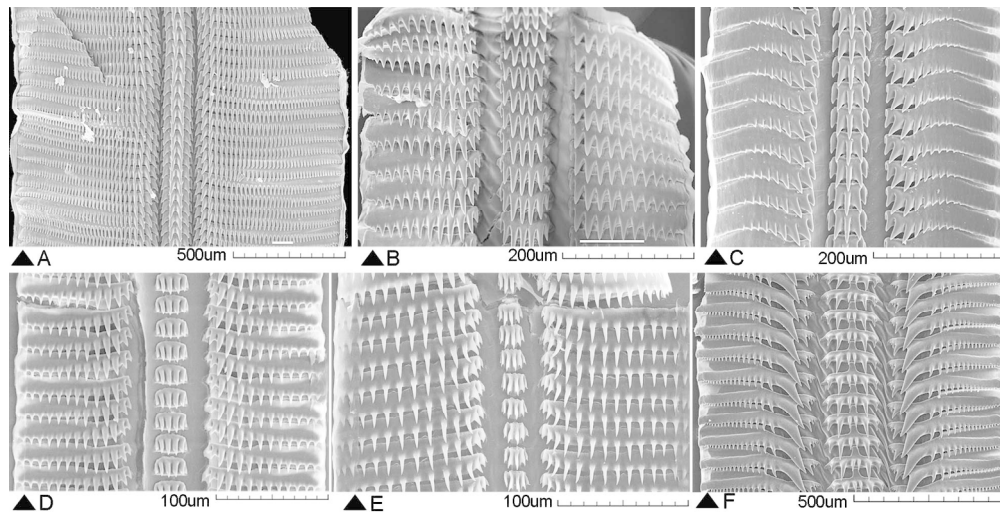


Figure 35. Radulae in the subfamily Isarinae. A. *Isara glabra*, MNHN IM-2013-40640, Esperance, WESTERN AUSTRALIA Stn WE01, 15°16.94'S, 124°06.3'E, 11 m, 62.7 mm; B. *I. nigra*, MNHN IM-2013-40676, Congo, Mission ZANAGA Stn DV08, 04°42.9'S, 11°47.5'E, 14-15 m, 45.2 mm; C. *I. straminea*, MNHN IM-2013-56423, French Guiana, GUYANE Stn CP4375, 06°39'N, 52°30'W, 195-200 m, 33.5 mm; D. *Subcancilla attenuata*, BAU392, Panama, Las Perlas, Contadora I., 08°36.2'N, 79°00.2'W, 22 m, 24 mm; E. *Subcancilla cf. leonardhilli*, MNHN IM-2013-61266, Guadeloupe, KARUBENTHOS 2 Stn DW4637, 15°52'N, 61°20'W, 217-225 m; F. *Subcancilla erythrogramma*, BAU424, Panama, Las Perlas, Contadora I., 08°36.6'N, 79°00.2'W, 25 m, 24.1 mm.

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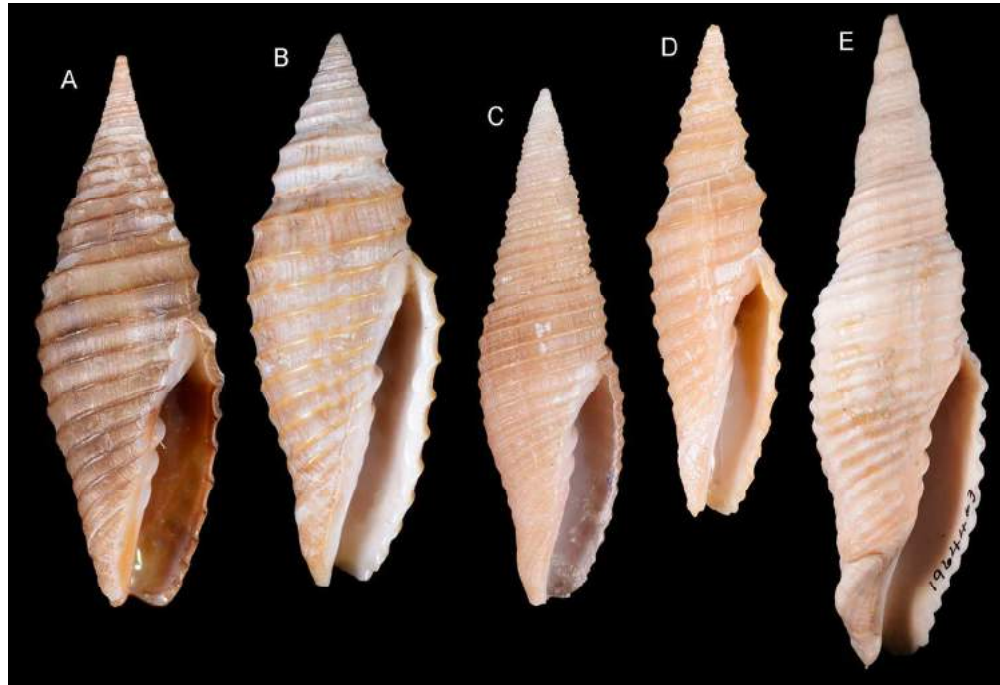


Figure 36. *Subcancilla* species. A. *Subcancilla erythrogramma*, BAU 0424, Panama, Las Perlas, Contadora I., 08°36.6'N, 79°00.2'W, 25 m, 24.1 mm; B. *Subcancilla funiculata*, lectotype, NHMUK 1967767, Plata I., Pacific coast of Columbia, 27.2 mm; C. *Subcancilla* cf. *leonardhilli*, MNHN IM-2013-61266, Guadeloupe, KARUBENTHOS 2 Stn DW4626, 15°57'N, 61°37'W, 210-233 m, 23 mm; D. *Subcancilla attenuata*, BAU 0392, Panama, Las Perlas, Contadora I., 08°36.2'N, 79°00.2'W, 22 m, 24 mm; E. *Subcancilla gigantea*, syntype, NHMUK 1964463, Xipixapi, Pacific coast of Columbia, 69.7 mm.

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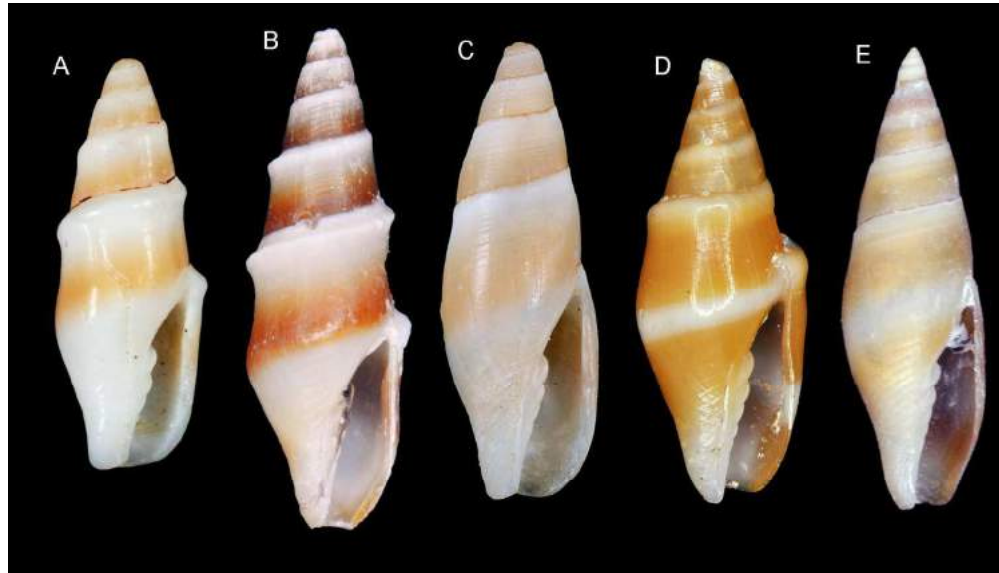


Figure 37. Species of *Carinomitra* n. gen. A, B. *Carinomitra peculiaris*; A. syntype, NHMUK 1967833, Puerto Galera, Mindanao, Philippines, 10 mm; B. MNHN IM-2013-6168, PAPUA NIUGINI Stn PR218, 05°07.3'S, 145°49.4'E, 11.1 mm; C – E. *C. typha*; C. syntype, NHMUK 1967904, Philippines, 9.5 mm; D. *C. typha* var. *micans*, MNHN, New Caledonia, Noumea area, LAGON Stn 1359, 22°19.9'S, 166°13.2'E, 25-30 m, 9.5 mm; E. MNHN IM-2013-4030, PAPUA NIUGINI, Stn PB28, 05°11.9'S, 145°49.6'E, 10 m, 8.6 mm.

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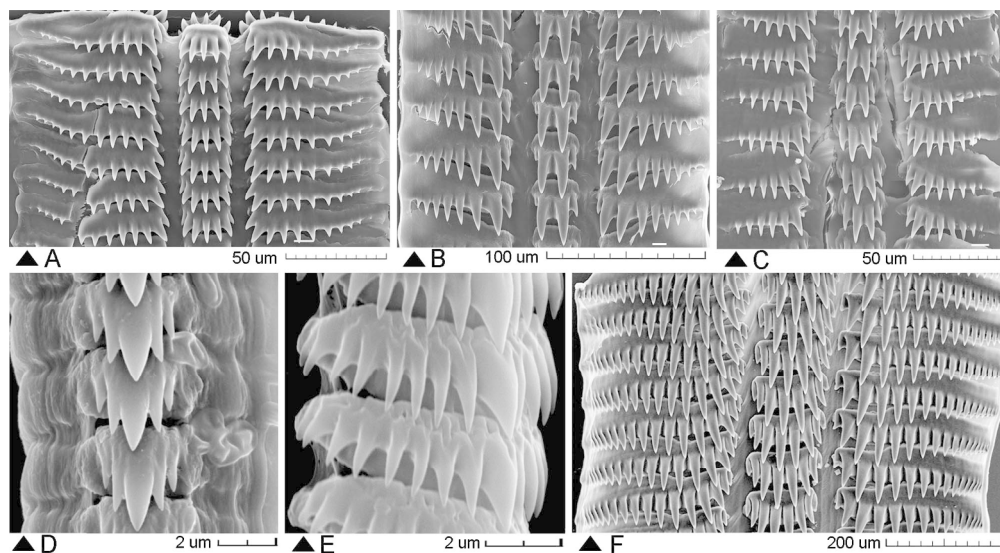


Figure 38. Radulae in the genera *Carinomitra* n. gen., *Condylomitra* n. gen. and *Probata*. A. *Carinomitra peculiaris*, MNHN IM-2013-6168, PAPUA NIUGINI Stn PR218, 05°07.3'S, 145°49.4'E, 11.1 mm; B. *Carinomitra typha* var. *micans*, MNHN, New Caledonia, Noumea area, LAGON Stn 1359, 22°19.9'S, 166°13.2'E, 25-30 m, 9.5 mm; C. *Carinomitra saltata*, MNHN, Society Is, off Moorea, 5.4 mm; D. *Condylomitra tuberosa*, MNHN, Philippines, PANGLAO 2004 Stn S12, 9°29.4'N, 123°56.0'E, 6-8 m, 14.4 mm; E. *Condylomitra bernhardina* New Caledonia, Noumea area, LAGON Stn 1343, 22°17.8'S, 166°19.9'E, 7 m, 16.1 mm; F. *Probata barbadensis*, MNHN IM-2013-7772, Guadeloupe, KARUBENTHOS Stn GR36, 16°30.6'N, 61°28.4'W, 12 m, 20.6 mm.

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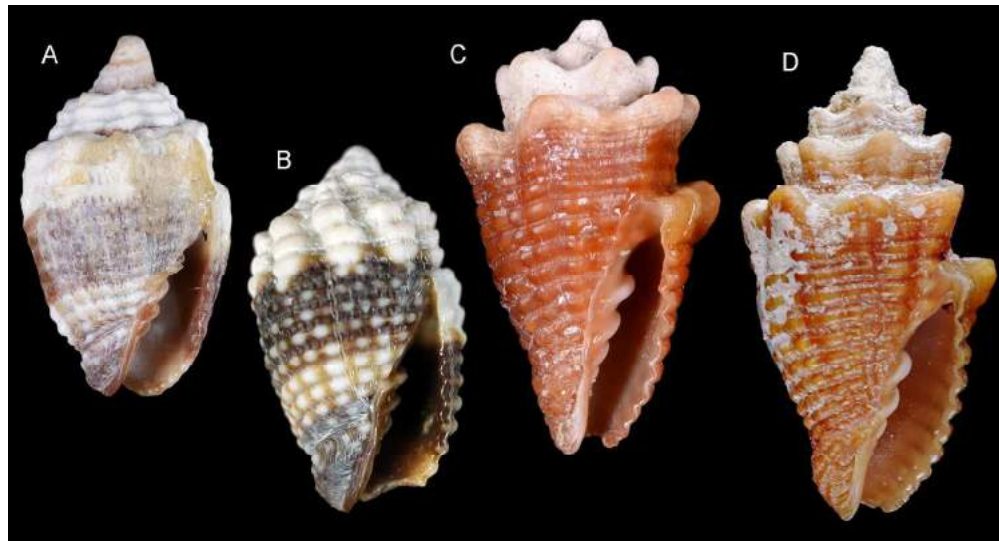


Figure 39. Species of *Condylomitra* n. gen. A, B. *Condylomitra tuberosa*; A. Syntype, NHMUK 1967899, Philippines, 14.4 mm; B. MNHN IM-2007-30311, Philippines, PANGLAO 2004 Stn R75, 09°32.8'N, 123°42.1'E, 3-35 m; C, D. *C. bernhardina*; C. MNHN IM-2013-54115, Papua New Guinea, KAVIENG 2014 Stn KB40, 02°36.6'S, 150°32.9'E, 2-7 m; D. MNHN, New Caledonia, Noumea area, LAGON Stn 1343, 22°17.8'S, 166°19.9'E, 7 m, 16.1 mm.

170x91mm (300 x 300 DPI)

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Figure 40. Genera *Atrimitra*, *Vicimitra*, *Probata*, and *Dibaphimitra*. A. *Atrimitra idae*, holotype, NMW.1955.158.00066, Point Loma, Lower California, Mexico, 60.0 mm; B. *Atrimitra effusa*, lectotype, NHMUK 1966415, Guacomayo, Central America, 31.6 mm; C. *Atrimitra caliginosa*, holotype, NHMUK 1966718, locality unknown, 34.9 mm; D. *Probata espinosai*, paratype, MNHN-IM-2012-37719, in front of Marianao, Havana, Cuba, 10 mm; E. *Probata barbadensis*, MNHN IM-2013-7772, Guadeloupe, KARUBENTHOS Stn GR36, 16°30.6'N, 61°28.4'W, 12 m, 20.6 mm; F. *Dibaphimitra florida*, holotype of *Mitra fergusonii* G.B. Sowerby II, 1874, NHMUK 1879.2.26.133, Panama, 42.7 mm.

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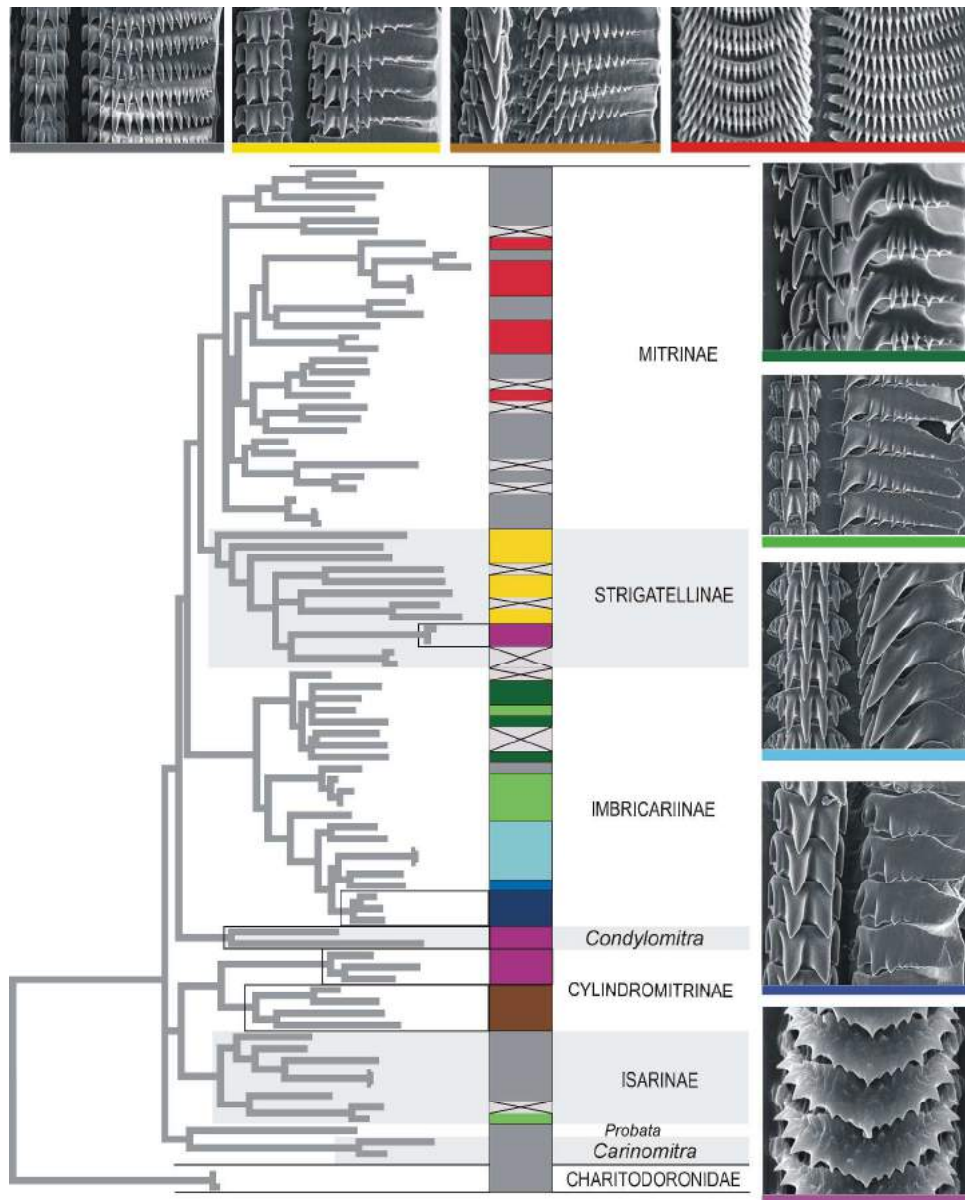


Figure 41. Distribution of different radula types throughout the Mitridae tree. Dark grey – Mitra type; yellow – Strigatella type; brown – Nebularia type; red – Profundimitra type; dark-green – Imbricaria type; light-green – Cancilla type; light-blue – Scabricola type; dark blue – Neocancilla type; purple – Pterygia type; light-grey – no data. The topology corresponds to the 4G tree on Figure 4.

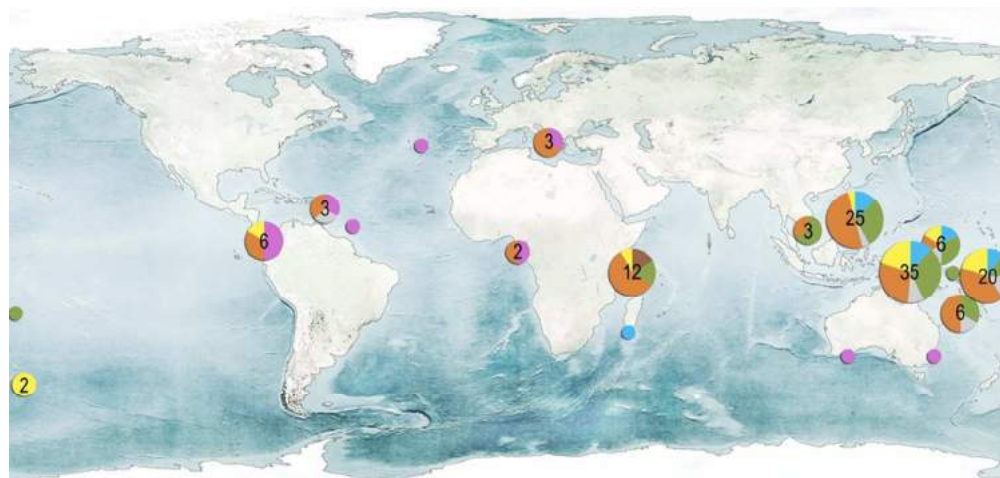


Figure 42. Taxonomic composition (subfamilies) and geographical coverage of our molecular sampling. Diameter of the circles proportional to the number of species in each principal location, which is indicated for each circle with more than one species sampled. Charitodoronidae – brown; Cylindromitrinae – blue; Imbricariinae – green; Isarinae – purple; Mitrinae – orange; Strigatellinae – yellow; Incertae sedis – grey.

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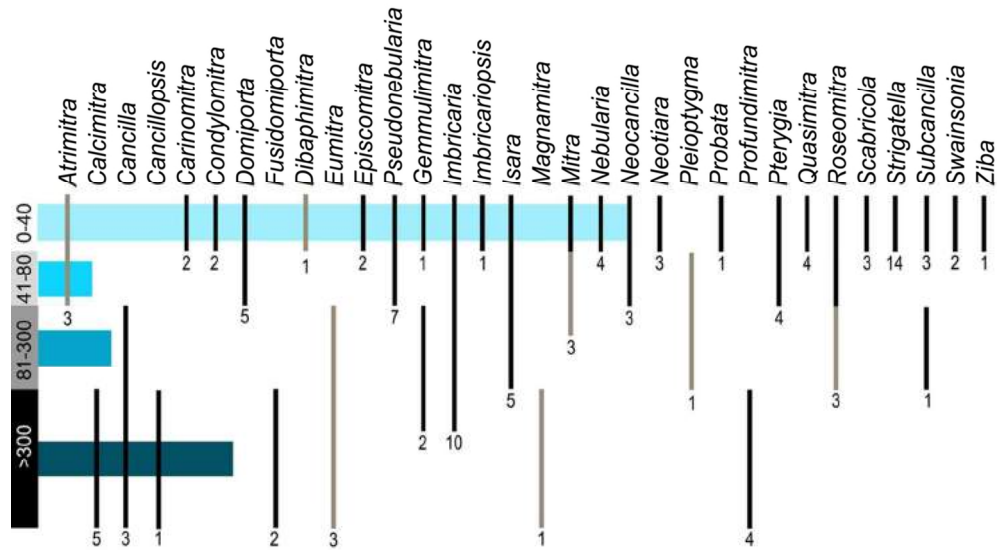


Figure 43. Bathymetric distribution of the genera of Mitridae. Black bars – based on our sampling; grey bars – based on published data (Lozouet, 1991; Cernohorsky 1976; 1991; Huang & Salisbury, 2017). Numbers next to each bar indicate number of species involved. Blue horizontal bars show the proportion of stations in each depth interval.

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