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

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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 402 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 data set, 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, Cylindromitrinae and 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.

ADDITIONAL KEYWORDS: molecular phylogeny – integrative taxonomy – biogeography – species diversity – Indo-Pacific – new family – new genus.

INTRODUCTION

The neogastropod family Mitridae (miter shells or mitres) is a distinctive and familiar group of benthic gastropods, its key features being a solid, usually

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fusiform, colourful 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 was 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 mitres 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 mitres 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 in 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, 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).

Mitridae as currently restricted is 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 (402 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 (Ponder, 1998); 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).

As of August 2017, 184 of the 402 accepted Recent species of Mitridae indexed in WoRMS (WoRMS, 2017) are classified in the genus *Mitra*, although the understanding that the genus, as currently circumscribed, is not consistent with a single evolutionary lineage emerged long ago (Cernohorsky, 1991). 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 incongruence 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, Sapienza University of Rome, 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 (Republic of the 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), that is, 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

Table 1. List of specimens analysed

Genus species	Genus (revised)	Catalog N	Catalog N (old)	Expedition/ Locality	Station	collection data	BOLD	*COI*	16S	12S	*H3*
Charitodoronidae			-								
Charitodoron bathybius	*Charitodoron*	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
Mitridae			-								
Mitra invicta	*Calcimitra*	IM-2013-15373	-	PAPUA NIUGINI	CP3949	05°12'S 145°51'E, 380-407 m	MITRI119-16	MG199473	MG191968	MG192017	MG192062
		IM-2007-32130	-	PANGLAO 2005	CP2383	8°44'42''N 123°18'29.9772''E, 338-351 m	NEOGA490-10	MG199543	-	-	-
Mitra christinae	*Calcimitra*	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	NEOGA493-10	MG199465	-	-	-
Mitra glaphyria	*Calcimitra*	IM-2007-30065	-	PANGLAO 2005	CP2358	8°52'5.988''N 123°37'5.9952''E, 569-583 m	NEOGA234-10	MG199464	-	-	-
		IM-2007-30066	-	PANGLAO 2005	CP2342	9°24'24.012''N 123°52'54.0048''E, 1240-1258 m	NEOGA235-10	MG199501	-	-	-
		IM-2007-30103	-	PANGLAO 2005	CP2354	9°25'59.988''N 124°6'29.988''E, 1769-1773 m	NEOGA244-10	MG199499	-	-	-
		IM-2007-32126	-	PANGLAO 2005	CP2388	9°26'53.988''N 123°34'29.9892''E, 762-786 m	NEOGA488-10	MG199502	-	-	-
		IM-2007-32132	-	PANGLAO 2005	CP2388	9°26'53.988''N 123°34'29.9892''E, 762-786 m	NEOGA492-10	MG199484	-	-	-
		IM-2013-40650	-	BIOPAPUA	CP3728	07°52'S 148°01'E, 498-501 m	MITRI050-15	KR087281	KR088031	KR087373	-
Mitra labecula	*Calcimitra*	IM-2007-30127	-	EBISCO	DW2515	24°4'31.1988''S 159°41'2.4216''E, 330-370 m	NEOGA250-10	MG199466	-	-	-
Mitra triplicata	*Calcimitra*	IM-2007-38186	-	MIRIKI	CP3253	15°24'45''S 45°55'23.988''E, 943-950 m	MITRI150-17	MG199509	-	-	-
Cancilla baeri	*Cancilla*	IM-2013-58853	-	KAVIENG 2014	DW4484	2°25'50.40''S 149°55' 13'' E	MITRI165-17	MG199442	-	-	-
Cancilla rehderi / *fibula*	*Cancilla*	IM-2007-38689	-	TARASOC	DW3441	16°43'S 151°26'W, 350-360 m	MITRI056-15	-	KR087991	KR087332	-

Table 1. *Continued*

Genus species	Genus (revised)	Catalog N	Catalog N (old)	Expedition/ Locality	Station	collection data	BOLD	*COI*	16S	12S	*H3*
		IM-2007-30062	-	PANGLAO 2005	CP2331	9°39'11.988''N 123°47'30.0192''E, 255-268 m	NEOGA233-10	MG199542	-	-	-
		IM-2007-30126	-	PANGLAO 2005	CP2331	9°39'11.988''N 123°47'30.0192''E, 255-268 m	NEOGA249-10	MG199533	-	-	-
		IM-2007-38551	-	TARASOC	DW3459	17°27'47.9988''S 149°49'12.0252''W, 485-560 m	MITRI152-17	MG199549	-	-	-
		IM-2007-38688	-	TARASOC	DW3441	16°41'42''S 151°26'5.9928''W, 350-360 m	MITRI058-15	KR087234	-	-	-
		IM-2007-38801	-	TARASOC	DW3441	16°41'42''S 151°26'5.9928''W, 350-360 m	MITRI153-17	MG199548	-	-	-
		IM-2013-19073	-	PAPUA NIUGINI DW	CP4059	02°38'S 141°18'E, 335 m	MITRI095-16	MG199443	MG191956	MG192006	MG192050
*Cancilla cf. fibula**	*Cancilla*	IM-2013-40646	-	EXBODI	CP3822	21°52'S 166°51'E, 341-506 m	MITRI030-15	-	KR087990	KR087331	KR088076
Mitra schepmani	*Cancilla*	IM-2007-30129	-	EBISCO	DW2514	24°6'25.7976''S 159°41'1.8168''E, 295-310 m	NEOGA251-10	MG199496	-	-	-
		IM-2007-35752	-	CONCALIS	DW2963	18°22'4.8''S 162°58'45.0192''E, 220-240 m	NEOGA848-10	MG199460	-	-	-
		IM-2013-40645	-	EXBODI	DW3926	18°35'S 164°20'E, 364-473 m	MITRI025-15	KR087279	KR088029	KR087371	KR088109
Cancilla meimiaoae	***Cancillopsis***	IM-2007-30011	-	SANTO 2006	AT19	15°40'48''S 167°00'29.99''E, 503-600 m	NEOGA209-10	MG199539	-	-	-
Mitra peculiaris	***Carinimitra***	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	NEOGA271-10	MG199489	-	-	-
Mitra typha	***Carinomitra***	IM-2013-4030	-	PAPUA NIUGINI	PB28	05°11,9'S 145°49,6'E, 10 m	MITRI132-16	MG199510	MG191985	MG192032	MG192074
Mitra bernhardina	***Condylomitra***	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	MITRI157-17	MG199472	-	-	-
Mitra tuberosa	***Condylomitra***	IM-2007-30311	-	PANGLAO 2004	R75	09°32.8'N 123°42.1'E, 3-35 m	NEOGA294-10	KR087283	KR088033	KR087375	KR088112

Table 1. *Continued*

Genus species	Genus (revised)	Catalog N	Catalog N (old)	Expedition/ Locality	Station	collection data	BOLD	*COI*	16S	12S	*H3*
*Domiporta cf. carnicolor**	*Domiporta*	IM-2013-40684	-	PHILIPPINES, off Noc-Nocan Is		10°15.06'N 124°25.07'E, 4-12 m	MITRI159-17	-	MG191958	MG192008	MG192052
Neocancilla circula	*Domiporta*	IM-2007-30018	-	SANTO 2006	LD24	15°31'23.988''S 167°10'0.019''E, 47 m	NEOGA213-10	MG199444	-	-	-
Domiporta filaris	*Domiporta*	IM-2013-12956	-	PAPUA NIUGINI	PD23	05°06'S 145°49.2'E, 3-7 m	MITRI044-15	KR087251	KR088004	KR087348	KR088090
Domiporta granatina	*Domiporta*	IM-2013-15906	-	PAPUA NIUGINI	PM42	05°10,2'S 145°50,4'E, 0-1 m	MITRI121-16	MG199445	MG191957	MG192007	MG192051
		IM-2013-40641	-	INHACA 2011	MR15	26°00.0'S 32°54.4'E, 4 m	MITRI038-15	KR087252	KR088005	KR087349	KR088091
Domiporta praestantissima	*Domiporta*	IM-2007-30081	-	PANGLAO 2004	R36	9°30'11.988''N 123°55'18.0084''E, 3-32 m	NEOGA240-10	MG199447	-	-	-
		IM-2013-40642	-	VIETNAM, Nha-Trang Bay	D3	12°10.084'N 109°17.771'E, 6-18 m	MITRI032-15	KR087253	KR088006	-	KR088092
Mitra cornicula	*Episcomitra*	IM-2013-66184	BAU1578-1	GREECE, Astypalea Is., Agrilidi		36°35’02”N 26°25’24”E, 2-7 m	MITRI172-17	MG199479	MG191971	MG192020	-
		IM-2013-66185	BAU1578-2	GREECE, Astypalea Is., Agrilidi		36°35’02”N 26°25’24”E, 2-7 m	MITRI173-17	MG199480	-	-	-
		IM-2013-40661	-	ITALY, Sicily, Cyracuse		37°0.460'N 15°18.62'E, 6-12 m	MITRI059-15	KR087270	KR088020	KR087363	-
Mitra zonata	*Episcomitra*	IM-2013-66173	BAU2538	ITALY, off Chioggia		45°12’N 12°40’E, 40 m	MITRI175-17	MG199511	MG191987	MG192034	-
Gen. ***ponderi* sp. nov.**	***Fusidomiporta***	IM-2013-40665	-	BIOPAPUA	CP3692	02°10'S 147°19'E, 408-448 m	MITRI156-17	MG199497	MG191981	-	MG192072
***Cancilla* sp. nov.**	***Fusidomiporta***	IM-2007-32153	-	PANGLAO 2005	DW2364	9°0'42.012''N 123°25'30.0108''E, 427 m	NEOGA500-10	MG199462	-	-	-
Mitra avenacea	***Gemmulimitra***	IM-2013-11683	-	PAPUA NIUGINI	PR14	05°12'S 145°48,1'E, 2-3 m	MITRI112-16	MG199471	MG191965	MG192014	MG192059
Gen. ***neocaledonica* sp. nov.**	***Gemmulimitra***	IM-2013-40655	-	EXBODI	CP3821	21°53'S 166°50'E, 211-440 m	MITRI045-15	KR087285	KR088036	-	KR088115
Mitra strongae	***Gemmulimitra***	IM-2007-36727	-	MIRIKI	DW3213	12°30'46.8''S 47°52'19.2''E, 262-289 m	MITRI154-17	MG199504	-	-	-
Ziba bantamensis	*Imbricaria*	IM-2013-16688	-	PAPUA NIUGINI	PD67	05°15,5'S 145°46,8'E, 2-6 m	MITRI123-16	MG199448	MG191959	MG192009	MG192053
Imbricaria conularis	*Imbricaria*	IM-2007-30026	-	SANTO 2006	LD01	15°28'59.988''S 167°14'54.013'E', 24 m	NEOGA216-10	MG199450	-	-	-

Table 1. *Continued*

Genus species	Genus (revised)	Catalog N	Catalog N (old)	Expedition/ Locality	Station	collection data	BOLD	*COI*	16S	12S	*H3*
		IM-2007-30044	-	SANTO 2006	VM09	15°35'48.012"S 167°06'06.0084"E, intertidal	NEOGA223-10	MG199451	-	-	-
		IM-2007-30045	-	SANTO 2006	VM09	15°35'48.012"S 167°06'06.0084"E, intertidal	NEOGA224-10	MG199449	-	-	-
		IM-2007-30046	-	SANTO 2006	VM09	15°35'48.012"S 167°06'06.0084"E, intertidal	NEOGA225-10	MG199452	-	-	-
		IM-2013-18043	-	PAPUA NIUGINI	PR203	05°10.3'S 145°48.5'E, 1-19 m	MITRI053-15	KR087263	KR088014	KR087356	KR088099
Ziba flammigera	*Imbricaria*	IM-2013-40656	-	VIETNAM, Nha-Trang Bay	ND7	12º10.443'N 109º16.298'E, 15-18 m	MITRI028-15	KR087322	KR088068	KR087410	-
Ziba fulgetrum	*Imbricaria*	IM-2007-30016	-	SANTO 2006	LD21	15°31'18.012"S 167°9'53.9748"E, 16 m	NEOGA212-10	MG199545	-	-	-
		IM-2007-30054	-	SANTO 2006	VM32	15°26'35.988"S 167°15'11.9736"E, intertidal	NEOGA227-10	MG199546	-	-	-
		IM-2007-30115	-	SANTO 2006	VM32	15°26'35.988"S 167°15'11.9736"E, intertidal	NEOGA246-10	MG199547	-	-	-
		IM-2013-18112	-	PAPUA NIUGINI	PR240	05°08.2'S 145°48.7'E, 3-20 m	MITRI046-15	KR087323	KR088069	KR087411	KR088149
Subcancilla hrdlickai	*Imbricaria*	IM-2013-18020	-	PAPUA NIUGINI	PD75	05°14,2'S 145°47,8'E, 10-25 m	MITRI125-16	MG199536	MG192001	MG192048	MG192086
Ziba insculpta	*Imbricaria*	IM-2013-40657	-	VIETNAM, Nha-Trang Bay	ND7	12º10.443'N 109º16.298'E, 15-18 m	MITRI048-15	KR087324	KR088070	-	KR088150
Subcancilla yagurai	*Imbricaria*	IM-2007-30340	-	BOA1	CP2442	15°7'26.22"S 166°54'5.418"E, 131-308 m	NEOGA304-10	MG199544	-	-	-
		IM-2007-34547	-	AURORA 2007	CP2716	14°30'N 121°41'E, 335-356 m	NEOGA766-10	KR087295	KR088044	-	-
Subcancilla rufogyrata	*Imbricaria*	IM-2007-36131	-	SALOMONBOA-3	DW2852	9°46'0.012"S 160°51'0.00"E, 220 m	NEOGA861-10	MG199458	-	-	-
Subcancilla pugnaxa	*Imbricaria*	IM-2007-32124	-	PANGLAO 2005	CP2378	8°38'48.012"N 123°20'5.9964"E, 65 m	NEOGA487-10	MG199446	-	-	-
		IM-2007-34548	-	AURORA 2007	CP2763	15°51'2.4012"N 121°51'2.412"E, 42-44 m	NEOGA767-10	MG199456	-	-	-

Table 1. *Continued*

Genus species	Genus (revised)	Catalog N	Catalog N (old)	Expedition/ Locality	Station	collection data	BOLD	*COI*	16S	12S	*H3*
		IM-2007-34549	-	AURORA 2007	CP2763	15°51'2.4012''N 121°51'2.412''E, 42-44 m	NEOGA768-10	MG199457	-	-	-
*Ziba verrucosa**	*Imbricaria*	IM-2013-14284	-	PAPUA NIUGINI	PD39	04°59,3'S 145°47,5'E, 2-4 m	MITRI118-16	-	MG191961	MG192011	MG192055
Imbricaria punctata	***Imbricariopsis***	IM-2013-11604	-	PAPUA NIUGINI	PM12	05°00,2'S 145°47,6'E, 0-1 m	MITRI110-16	MG199453	MG191960	MG192010	MG192054
*Mitra carbonaria**	*Isara*	C.335424	-	AUSTRALIA, Sydney, Collaroy, Long Reef		33°44'42''S , 151°19' E, intertidal		-	-	DQ916435.1	-
Mitra cornea	*Isara*	IM-2013-66179	BAU0709-1	AZORES, Fajal, Ponta dos Capelinhos		38°35'30"N 28°49'43"W, intertidal	MITRI168-17	MG199477	-	-	-
		IM-2013-66181	BAU0709-2	AZORES, Fajal, Ponta dos Capelinhos		38°35'30"N 28°49'43"W, intertidal	MITRI170-17	MG199476	MG191970	MG192019	-
		IM-2013-66183	BAU0709-3	AZORES, Fajal, Ponta dos Capelinhos		38°35'30"N 28°49'43"W, intertidal	MITRI171-17	MG199475	-	-	-
		IM-2013-66175	BAU2537-1	ITALY, Giannutri Is., Punta San Francesco		42°15'06''N, 11°06'59''E, 10-20 m	MITRI167-17	MG199478	-	-	-
		IM-2013-66180	BAU2537-3	ITALY, Giannutri Is., Punta San Francesco		42°15'06''N, 11°06'59''E, 10-20 m	MITRI169-17	MG199474	MG191969	MG192018	-
Mitra glabra	*Isara*	IM-2013-40640	-	W-AUSTRALIA	WE01	15°16.94'S 124° 06.3'E, 11 m	MITRI042-15	KR087272	KR088022	KR087365	KR088105
*Mitra nigra (Gmelin)**	*Isara*	IM-2013-40676	-	ZANAGA	DV08	04°42,93'S 11°47,49'E, 14-15 m	MITRI096-16	-	MG191977	MG192025	MG192068
Subcancilla straminea	*Isara*	IM-2013-56423	-	GUYANE	CP4375	06°39'N 52°30'W, 195-200 m	MITRI088-16	MG199503	MG191983	MG192030	-
Mitra mitra	*Mitra*	IM-2013-40639	-	INHACA 2011	MR15	26°00.0'S 32°54.4'E, 4 m	MITRI052-15	KR087275	KR088025	KR087368	-
Mitra papalis	*Mitra*	IM-2007-30033	-	SANTO 2006	NR07	15°34'23.988''S 167°13'5.9628''E, 9 m	NEOGA219-10	MG199487	-	-	-
		IM-2007-30174	-	SANTO 2006	DR87	15°38.5'S 167°15.1'E, 13 m	NEOGA255-10	KR087276	KR088026	-	-
*Mitra acuminata**	*Nebularia*	IM-2013-13288	-	PAPUA NIUGINI	PM25	05°01,1'S 145°47,9'E, intertidal	MITRI117-16	-	MG191962	MG192012	MG192056
Nebularia contracta	*Nebularia*	IM-2013-10345	-	PAPUA NIUGINI	PR04	05°10,1'S - 145°50,5'E, 30m	MITRI155-17	MG199512	MG191988	MG192035	MG192076

Table 1. *Continued*

Genus species	Genus (revised)	Catalog N	Catalog N (old)	Expedition/ Locality	Station	collection data	BOLD	*COI*	16S	12S	*H3*
*Mitra eremitarum**	*Nebularia*	IM-2013-16323	-	PAPUA NIUGINI	PM51	05°05,5'S 145°48,6'E, 0-1 m	MITRI122-16	-	MG191973	-	MG192064
Mitra incompta	*Nebularia*	IM-2007-30175	-	SANTO 2006	DR78	15°28.4'S 167°15.2'E, 25 m	NEOGA256-10	KR087273	KR088023	KR087366	KR088106
Neocancilla maculosa	*Neocancilla*	IM-2007-30028	-	SANTO 2006	NR05	15°28'41.988''S 167°15'11.9736''E, 19 m	NEOGA218-10	MG199517	-	-	-
		IM-2007-30097	-	PANGLAO 2004	D09	9°30'0.0''N 123°55'18.0084''E, 2-4 m	NEOGA241-10	MG199516	-	-	-
		IM-2007-30177	-	SANTO 2006	FR42	15°28'36.012''S 167°15'5.9868''E, 3-31 m	NEOGA257-10	MG199515	-	-	-
		IM-2007-30178	-	SANTO 2006	DR73	15° 22' 32.22'' S 167° 11' 21.12'' E, 10-25 m	NEOGA258-10	MGXXXXXX	-	-	-
		IM-2007-32368	-	SANTO 2006	FR30	15°27'18''S 167°15'35.982''E, 45 m	NEOGA523-10	MG199513	-	-	-
		IM-2013-18342	-	PAPUA NIUGINI	PS47	05°04,7'S 145°48,9'E, 8 m	MITRI126-16	MG199514	MG191989	MG192036	MG192077
Neocancilla papilio	*Neocancilla*	IM-2007-30210	-	PANGLAO 2004	R14	9°37'23.988''N 123°54'29.9988''E, 6-8 m	NEOGA262-10	MG199518	-	-	-
		IM-2013-12560	-	PAPUA NIUGINI	PR24	05°12.3'S 145°48.8'E, 15 m	MITRI034-15	KR087287	KR088037	KR087376	KR088116
Neocancilla rufescens	*Neocancilla*	IM-2013-40644	-	INHACA 2011	MD22	25°59.7'S 32°46.8'E, 22 m	MITRI033-15	KR087288	KR088038	-	KR088117
*Mitra aff. inca**	***Neotiara***	IM-2013-66186	BAU0279-1	PANAMA, Venado Beach		8°53'35''N, 79°36'25''W, intertidal	MITRI166-17	-	MG191982	MG192029	-
Mitra lens	***Neotiara***	IM-2013-66178	BAU00800	PANAMA, Panama City		08°95'N 79°53'W, intertidal		FM999161	FM999110	FM999079	-
*Mitra nodulosa**	***Neotiara***	IM-2013-9546	-	KARUBENTHOS	GM10	16°12,53'N 61°25,55'W, 1 m	MITRI145-16	-	MG191978	MG192026	MG192069
*Mitra barbadensis**	*Probata*	IM-2013-7772	-	KARUBENTHOS	GR36	16°30,57'N 61°28,45'W, 12 m	MITRI143-16	-	MG191966	MG192015	MG192060
Cancilla planofilum	***Profundimitra***	IM-2007-32149	-	PANGLAO 2005	CP2398	9°32'35.988''N 123°40'30.0108''E, 713-731 m	NEOGA497-10	MG199463	-	-	-
Gen. ***taylori* sp. nov.**	***Profundimitra***	IM-2013-40651	-	BIOPAPUA	CP3671	04°04'S 151°56'E, 585-601 m	MITRI027-15	KR087284	KR088034	-	KR088113

Table 1. *Continued*

Genus species	Genus (revised)	Catalog N	Catalog N (old)	Expedition/ Locality	Station	collection data	BOLD	*COI*	16S	12S	*H3*
Gen. sp. nov.	***Profundimitra***	IM-2007-35618	-	AURORA 2007	CP2658	15°58'1.8012''N 121°49'6.5892''E, 422-431 m	NEOGA836-10	MG199459	-	-	-
Gen. sp. nov.	***Profundimitra***	IM-2007-35711	-	AURORA 2007	CP2658	15°58'1.8012''N 121°49'6.5892''E, 422-431 m	NEOGA841-10	MG199454	-	-	-
Gen. sp. nov.	***Profundimitra***	IM-2007-36757	-	MIRIKI	CP3289	14°29'25.188''S 47°26'21.012''E, 332-379 m	MITRI151-17	MG199498	-	-	-
Gen. sp. nov.	***Profundimitra***	IM-2013-40654	-	EXBODI	CP3829	22°02'S 167°05'E, 350-360 m	MITRI047-15	KR087233	KR087989	KR087330	KR088075
Mitra atjehensis	***Pseudonebularia***	IM-2007-30264	-	SANTO 2006	EP01	15°32'30.012''S 167°8'59.9784''E, 46-47 m	NEOGA276-10	MG199468	-	-	-
Nebularia chrysalis	***Pseudonebularia***	IM-2007-30055	-	SANTO 2006	VM25	15°36'36''S 167°01'36.0192''E, intertidal	NEOGA228-10	MG199482	-	-	-
Nebularia connectens	***Pseudonebularia***	IM-2013-2342	-	PAPUA NIUGINI	PB16	05°10.7'S 145°47.7'E, intertidal	MITRI037-15	KR087271	KR088021	KR087364	-
Nebularia maesta	***Pseudonebularia***	IM-2013-40648	-	MIRIKY	CP3288	14° 31.9' S 47° 26.54' E, 46-54 m	MITRI036-15	KR087274	KR088024	KR087367	KR088107
Nebularia pediculus	***Pseudonebularia***	IM-2007-30330	-	SANTO 2006	FR01	15°32'17.988''S 167°13'5.9628''E, 18-20 m	NEOGA302-10	MG199490	-	-	-
		IM-2013-12705	-	PAPUA NIUGINI	PB15	05°04.7'S 145°48.9'E, 5 m	MITRI035-15	KR087282	KR088032	KR087374	KR088111
Nebularia tabanula	***Pseudonebularia***	IM-2007-30027	-	SANTO 2006	VM37	15°34'29.36''S 167°12'36.025''E, intertidal	NEOGA217-10	MG199505	-	-	-
		IM-2007-30315	-	PANGLAO 2004	M40	9°35'42''N 123°44'42.0108''E, 3 m	NEOGA296-10	MG199506	-	-	-
Mitra tornata	***Pseudonebularia***	IM-2013-12538	-	PAPUA NIUGINI	PB14	05°13,8'S 145°48'E, 15 m	MITRI113-16	MG199508	MG191984	MG192031	MG192073
Pterigia conus	*Pterygia*	IM-2007-30119	-	PANGLAO 2004	M11	9°38'17.988''N 123°49'36.0048''E, 3 m	NEOGA247-10	MG199522	-	-	-
Pterigia dactylus	*Pterygia*	IM-2007-30076	-	PANGLAO 2004	M26	9°40'54.012''N 123°51'6.0084''E, intertidal	NEOGA238-10	MG199519	-	-	-
		IM-2013-14989	-	PAPUA NIUGINI	PM39	05°12.1'S 145°48.4'E, intertidal	MITRI049-15	KR087291	KR088041	KR087379	KR088120

Table 1. *Continued*

Genus species	Genus (revised)	Catalog N	Catalog N (old)	Expedition/ Locality	Station	collection data	BOLD	*COI*	16S	12S	*H3*
Pterigia fenestrata	*Pterygia*	IM-2007-30010	-	SANTO 2006	ZM15	15°38'06''167 °05'53.9808''E, intertidal	NEOGA208-10	MG199521	-	-	-
		IM-2007-30039	-	SANTO 2006	DR09	15°34'36.012''S 167°13'47.9856''E, 12 m	NEOGA221-10	MG199520	-	-	-
		IM-2013-47383	-	KAVIENG	KR12	02°36,3'S 150°46,3'E, 18 m	MITRI093-16	MG199523	MG191990	MG192037	MG192078
Pterigia sinensis	*Pterygia*	IM-2007-34816	-	PANGLAO 2005	CP2378	8°38'48.012''N 123°20'5.9964''E, 65 m	NEOGA808-10	MG199455	-	-	-
		IM-2009-15439	-	ATIMO VATAE	CP3568	25°04.7'S 47°03.4'E, 64-65 m	MITRI054-15	KR087292	KR088042	KR087380	KR088121
*Mitra cardinalis**	***Quasimitra***	IM-2013-40681	-	KAVIENG	KR178	02°45,2'S 150°43,1'E, 2-46 m	MITRI094-16	-	MG191967	MG192016	MG192061
Mitra puncticulata	***Quasimitra***	IM-2013-40685	-	PHILIPPINES, off Noc-Nocan Is		10°15.06'N 124°25.07'E, 4-12 m	MITRI160-17	MG199491	MG191979	MG192027	MG192070
Mitra sanguinolenta	***Quasimitra***	IM-2013-40677	-	INHACA 2011	MS02	26°06.3'S 32°58.0'E, 17-19 m	MITRI089-16	MG199495	MG191980	MG192028	MG192071
Mitra sophiae	***Quasimitra***	IM-2007-30056	-	SANTO 2006	DR09	15°34.6'S 167°13.8'E, 12 m	NEOGA229-10	KR087280	KR088030	KR087372	KR088110
Mitra millepunctata	***Roseomitra***	IM-2013-40686	-	PHILIPPINES, off Noc-Nocan Is		10°15.06'N 124°25.07'E, 4-12 m	MITRI161-17	MG199541	MG192003	-	MG192087
Mitra rosacea	***Roseomitra***	IM-2007-30074	-	PANGLAO 2004	T28	9°34'59.988''N 123°51'24.0012''E, 77-84 m	NEOGA237-10	MG199500	-	-	-
		IM-2007-30309	-	SANTO 2006	AT44	15°36'S 167°03'E, 86-118 m	NEOGA292-10	KR087267	KR088018	KR087361	KR088103
Scabricola desetangsii	*Scabricola*	IM-2013-17614	-	PAPUA NIUGINI	PD66	05°15,5'S 145°47,3'E, 2-6 m	MITRI124-16	MG199526	MG191993	MG192040	MG192081
		IM-2013-50703	-	KAVIENG	KR54	02°42,3'S 150°39,1'E, 7-10 m	MITRI162-17	MG199525	MG191992	MG192039	MG192080
Imbricaria olivaeformis	*Scabricola*	IM-2013-18062	-	PAPUA NIUGINI	PR214	05°10.2'S 145°50.4'E, 1-8 m	MITRI041-15	KR087264	KR088015	KR087357	-
Scabricola variegata	*Scabricola*	IM-2013-40683	-	PHILIPPINES, off Noc-Nocan Is		10°15.06'N 124°25.07'E, 4-12 m	MITRI158-17	MG199527	MG191994	MG192041	MG192082
Mitra ambigua	*Strigatella*	IM-2013-2993	-	PAPUA NIUGINI	PB18	05°06,3'S 145°49,1'E, 26 m	MITRI131-16	MG199467	MG191963	MG192013	MG192057
Mitra aurantia	*Strigatella*	IM-2013-40679	-	INHACA 2011	MB07	25°59.7'S 32°54.2'E, 2-10 m	MITRI090-16	MG199469	MG191964	-	MG192058

Table 1. *Continued*

Genus species	Genus (revised)	Catalog N	Catalog N (old)	Expedition/ Locality	Station	collection data	BOLD	*COI*	16S	12S	*H3*
Mitra coronata	*Strigatella*	IM-2007-30023	-	SANTO 2006	VM36	15°27'29.988"S 167°15'24.0048"E, intertidal	NEOGA215-10	MG199470	-	-	-
		IM-2013-54145	-	KAVIENG	KB40	02°36,6'S 150°32,9'E, 2-7 m	MITRI142-16	MG199481	MG191972	MG192021	MG192063
Strigatella decurtata	*Strigatella*	IM-2013-15843	-	PAPUA NIUGINI	PM41	05°08,1'S 145°49,3'E, 0-1 m	MITRI120-16	MG199528	MG191995	MG192042	MG192083
Mitra fulvescens	*Strigatella*	IM-2013-40680	-	TUHAA PAE	AMA03	21°48,2'S 154°43,2'W, 26 m	MITRI102-16	MG199483	MG191974	MG192022	MG192065
Mitra imperialis	*Strigatella*	IM-2007-30173	-	SANTO 2006	FR01	15°32'17.988"S 167°13'5.9628"E, 18-20 m	NEOGA254-10	MG199492	-	-	-
Strigatella litterata	*Strigatella*	IM-2013-12959	-	PAPUA NIUGINI	PM22	05°04,7'S 145°48,9'E, intertidal	MITRI116-16	MG199529	MG191996	MG192043	MG192084
Mitra luctuosa	*Strigatella*	IM-2013-11682	-	PAPUA NIUGINI	PR14	05°12'S 145°48,1'E, 2-3 m	MITRI111-16	MG199485	MG191975	MG192023	MG192066
Mitra lugubris	*Strigatella*	IM-2013-40678	-	TUHAA PAE	AT07	23°19,7'S 149°29,3'W, 14 m	MITRI101-16	MG199486	MG191976	MG192024	MG192067
Strigatella paupercula	*Strigatella*	IM-2007-30052	-	SANTO 2006	VM02	15°34'54.012"S 167°02'23.9748"E, intertidal	NEOGA226-10	MG199488	-	-	-
Strigatella scutulata	*Strigatella*	IM-2013-12771	-	PAPUA NIUGINI	PM22	05°04,7'S 145°48,9'E, intertidal	MITRI115-16	MG199530	MG191997	MG192044	MG192085
Strigatella tristis	*Strigatella*	IM-2013-66187	BAU0285	PANAMA, Las Perlas, Pedro Gonzalez Is.		8°23'38"N, 79°07'01"W, intertidal	MITRI177-17	MG199532	MG191998	MG192045	-
		IM-2013-66177	BAU2534-2	PANAMA, Rio Mar		8°27'28"N, 79°58'01"W, intertidal	MITRI176-17	MG199531	-	-	-
*Mitra vexillum**	*Strigatella*	IM-2013-12570	-	PAPUA NIUGINI	PR24	05°12,3'S 145°48,8'E, **m	MITRI114-16	-	MG191986	MG192033	MG192075
Strigatella zebra	*Strigatella*	IM-2007-30036	-	SANTO 2006	VM02	15°34'54.012"S 167°02'23.9748"E, intertidal	NEOGA220-10	MG199494	-	-	-
		IM-2007-30122	-	PANGLAO 2004	M26	9°40'54.012N "123°51'6.0084"E, 2 m	NEOGA248-10	MG199493	-	-	-
		IM-2013-15188	-	PAPUA NIUGINI	PM39	05°12.1'S 145°48.4'E, intertidal	MITRI031-15	KR087277	KR088027	KR087369	-
Subcancilla attenuata	*Subcancilla*	IM-2013-66172	BAU0392	PANAMA, Las Perlas, Contadora Is.		08°36'12"N, 079°00'18"W, 22 m	MITRI178-17	MG199535	MG191999	MG192046	-

Table 1. *Continued*

Genus species	Genus (revised)	Catalog N	Catalog N (old)	Expedition/ Locality	Station	collection data	BOLD	*COI*	16S	12S	*H3*
		IM-2013-66182	BAU2535	Panama, Las Perlas		08°36' 21.6"N 079°05'21.6"W, 32.5 m	MITRI179-17	MG199534	-	-	-
*Subcancilla erythrogramma**	*Subcancilla*	IM-2013-66174	BAU0424	PANAMA, Las Perlas, Contadora Is.		08°36'36"N 079°00'12"W, 25 m	MITRI180-17	-	MG192000	MG192047	-
Subcancilla sp.	*Subcancilla*	IM-2013-66176	BAU0421	PANAMA, Las Perlas, San José Is.		08°17'48"N 079°02'36"W, 30.5 m	MITRI181-17	MG199540	MG192002	MG192049	-
Subcancilla leonardhilli	*Subcancilla*	IM-2013-61416	-	KARUBENTHOS 2	DW4637	15°51,50'N 61°20,17'W, 217-225 m	MITRI163-17	MG199538	-	-	-
		IM-2013-61417	-	KARUBENTHOS 2	DW4637	15°51,50'N 61°20,17'W, 217-225 m	MITRI164-17	MG199537	-	-	-
Scabricola casta	*Swainsonia*	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	MITRI092-16	MG199524	MG191991	MG192038	MG192079
Scabricola fusca	*Swainsonia*	IM-2013-40643	-	INHACA 2011	MS8	25°59.5'S 32°52.9'E, 9-17 m	MITRI029-15	KR087294	KR088043	KR087381	KR088122
*Ziba carinata**	*Ziba*	IM-2013-40647	-	ZANAGA	531DW	04°43.0'S 11°47.0'E, 17 m	MITRI026-15	-	KR088067	KR087409	KR088148
Mitra aff. labecula	?	IM-2007-35623	-	CONCALIS	DW3024	18°56'58.1964"S 163°21'45.0108"E, 349-370 m	NEOGA838-10	MG199461	-	-	-
Mitra turgida	?	IM-2007-30270	-	SANTO 2006	LM19	15°38'30.012"S 167°15'5.9868"E, intertidal	NEOGA278-10	MG199507	-	-	-

'?', generic assignment uncertain; '-', no sequence data available.
*Specimens for which *COI* has not been sequenced.

updates (Poppe & Tagaro, 2006; Turner, 2007; Lussi, 2009; Poppe, Tagaro & Salisbury, 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 data set, with a selection of species best representing the currently recognized supraspecific taxa and the morphological diversity of Mitridae, was built. For these species, one 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 *et al*. (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.

To complete the type series of inferred new species verified by the phylogenetic analysis, additional dry material from MNHN collections was studied to characterize their shell variation.

DNA extraction and PCR

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

Data sets

To ensure the consistency of phylogenetic analyses with the results obtained earlier, the entire Mitridae–Costellariidae–Ptychatractidae–Volutomitridae (MCPV) data sets with multiple outgroups, as analyzed in Fedosov *et al*. (2015), were used and supplemented with newly obtained sequences. Six molecular data sets have been analyzed, four of them corresponding to the individual three mitochondrial (*COI*, 16S and 12S) markers and one nuclear (*H3*) marker. When the resulting phylogenetic reconstructions were checked for congruency, two concatenated data sets were assembled, one corresponding to the three mitochondrial genes (1887 positions, 166 taxa, 7% of missing data), referred to as '3-mit' and consistent with our earlier analysis, and the second a four-genes data set (2215 positions, 166 taxa, 11% of missing data), referred to as '4G' (Table 2). Finally, a reduced four-genes data set 4G-red was built to minimize the effects of missing data; only those 139 specimens that had at least three genetic markers sequenced, one of which is *COI*, were included in this data set.

Phylogenetic analysis

Newly obtained *COI* and *H3* sequences were aligned manually; 16S and 12S sequences were first aligned automatically with Muscle (Edgar, 2004) and then modified manually where necessary. In the analysis of multi-gene data sets, multiple neogastropod lineages were included as outgroups to ensure consistency with our earlier analyses (Fedosov *et al*., 2015, 2017); in the single-gene *COI* analysis – primarily aimed at species delimitation – three specimens of the Pyramimitridae genera *Teremitra* and *Vaughanites* were used as outgroups based on the demonstrated sister relationship between Mitridae and Pyramimitridae (Fedosov *et al*., 2015).

The best-fit substitution models were identified for each gene separately, using Modelgenerator v.85 (Keane *et al*., 2006) (Table 2). The single-gene data sets of 12S, 16S and *H3* were analyzed as a single partition each; three partitions corresponding to first, second and third codon positions were analyzed independently for *COI*. The combined MCPV-3mit and MCPV-4G data sets were separated into five and six unlinked partitions, respectively: 16S, 12S, three codon positions of the *COI* gene (both data sets) plus *H3* gene (4G and 4G-red data sets).

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 1000 iterations. Bayesian inference (BI) analyses were performed in two parallel runs in MrBayes (Huelsenbeck, Ronquist & Hall, 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 1000 generations. For the *COI*, 3-mit, 4G and 4G-red data sets, BI was 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 5000 generations. Chain temperature of 0.02 was used in all analyses. Convergence of each analysis was checked using Tracer 1.4.1 (Rambaut *et al*., 2014); the two runs were considered converged if all effective sample size (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

Table 2. Sequence data and parameters of selected substitution models

Gene	Primers	Reference	Annealing temperature	Amplification length (bp)	Alignment length (bp)	Total for Mitridae	Analysed in 4G total (Mitridae)	Substitution model (AIC1)	*I*	Gamma
COI	HCO-1490 GGTCAACAAATCATAAAGAYATGYG	Folmer *et al*. (1994)	48–50	658	658	149	148 (74)	TIM+I+G	0.42	0.48
	LCO-2198 TAAACTTCAGGGTGACCAAARAAYCA	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 AGACGACGGGCGRTTWGTAC	Oliverio, Mariottini, 2002								
H3	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)								

*Touch down PCR was used.

tools MrBayes 3.2.3 on XSEDE and RAXML-HPC2 on XSEDE (8.1.11). K2P genetic distances were computed using MEGA v.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 min until soft tissues completely dissolved; the radula was then rinsed in several rounds of distilled water and then transferred onto clean 12-mm cover glass, where it was unfolded, air-dried and mounted for Scanning Electron Microscope 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, and subsequently 7-µm-thin serial sections were prepared and stained with Masson's trichrome (*Charitodoron*) or standard haematoxylin–eosin (all other species).

ABBREVIATIONS OF REPOSITORIES AND FACILITIES USED IN TEXT

AMS, Australian Museum, Sydney, Australia; BAU, Department of Biology and Biotechnology 'Charles Darwin', University La Sapienza of Rome, Italy; IEE, A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Science, Moscow, Russia; MNHN, Muséum National d'Histoire Naturelle, Paris, France; NHMUK, The Natural History Museum, London, UK; NMW, National Museum of Wales, Cardiff, UK; SIEE RAS, Laboratory of Molecular Genetics, A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Science, Moscow, Russia.

ANATOMICAL ABBREVIATIONS

aoe, anterior oesophagus; bl, buccal lip; bm, buccal mass; bt, buccal tube; bw, body wall; bv, blood vessel; cm, columellar muscle; ep, epiproboscis; moe, mid-oesophagus; n, nerves; nr, nerve ring; od, odontophore; odr, odontophore retractor; oe, oesophagus; poe, posterior oesophagus; pt, tip of the proboscis; pw, proboscis wall; rd, radular diverticulum; sd, salivary duct; sg, salivary gland; vl, valve-like structure.

Other abbreviations

a/h, ratio of aperture height to shell height; BS, ML bootstrap support value; dd, dead collected specimen(s); law/h, ratio of last adult whorl height to shell height; lv, live collected specimen(s); M, type species by monotypy; OD, original designation of type species; PP, Bayesian posterior probability support value; SD, subsequent designation of type species; SH, shell height; w/h, ratio of shell width to shell height.

RESULTS

Single-gene data sets

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 data sets, 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 data sets 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 data set 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 into 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 on the basis of shell morphology, each corresponding to two not closely related phylogenetic lineages in the *COI*-based tree: (1) specimens initially identified as *Strigatella paupercula* fell into two separate clades 7 and 11 (Figs 1, 2A) and (2) 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, 2B). A search in the synonymy of *S. paupercula*, and examination of the relevant type material, retained the name *S. paupercula* for specimen MNHN-IM-2007-30052, and the name *Strigatella zebra* was applied to clade 7 of the *COI*-based tree. 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, 2C, 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 *M. glaphyria*, and from 0 to 3.9% among specimens of *C. 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 molecular studies, although amplification of *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 markers other than *COI*, appeared sufficiently divergent from other inferred lineages to exclude possible conspecificity. Therefore, our data set includes 103 species as defined by both morphological and molecular characters.

Of the 103 species segregated, 95 are attributable to existing species names, including five that were identified with ambiguity and may (*C.* cf. *fibula*, *Domiporta* cf. *carnicolor*, *Subcancilla* cf. *leonardhilli*) or may not (*Mitra* aff. *inca*, *Mitra* aff. *labecula*) represent the taxon in question. Eight species were not identified, of which one is a subadult, and seven are adults and can confidently be recognized as undescribed.

The sequenced species represent 16 currently accepted genera; of these only two correspond to a single clade in the *COI* tree: *Pterygia* (clade 22–4, four species, PP = 1) and *Charitodoron* (clade 28, two species, PP = 1).

Concatenated data sets: ‘3-mit’-based tree

The consensus trees obtained from the analyses of multi-gene data sets showed similar topologies with no supported conflicts. In ML and BI analyses of all three concatenated data sets (Figs 3–5), the first dichotomy splits a two-species clade, corresponding to *Charitodoron*, from the rest of the Mitridae (from here onwards referred to as Mitridae *s.s.*), both clades forming very long branches and showing maximum nodal support in all analyses. The Mitridae *s.s.* clade is composed of eight major groupings, marked with different

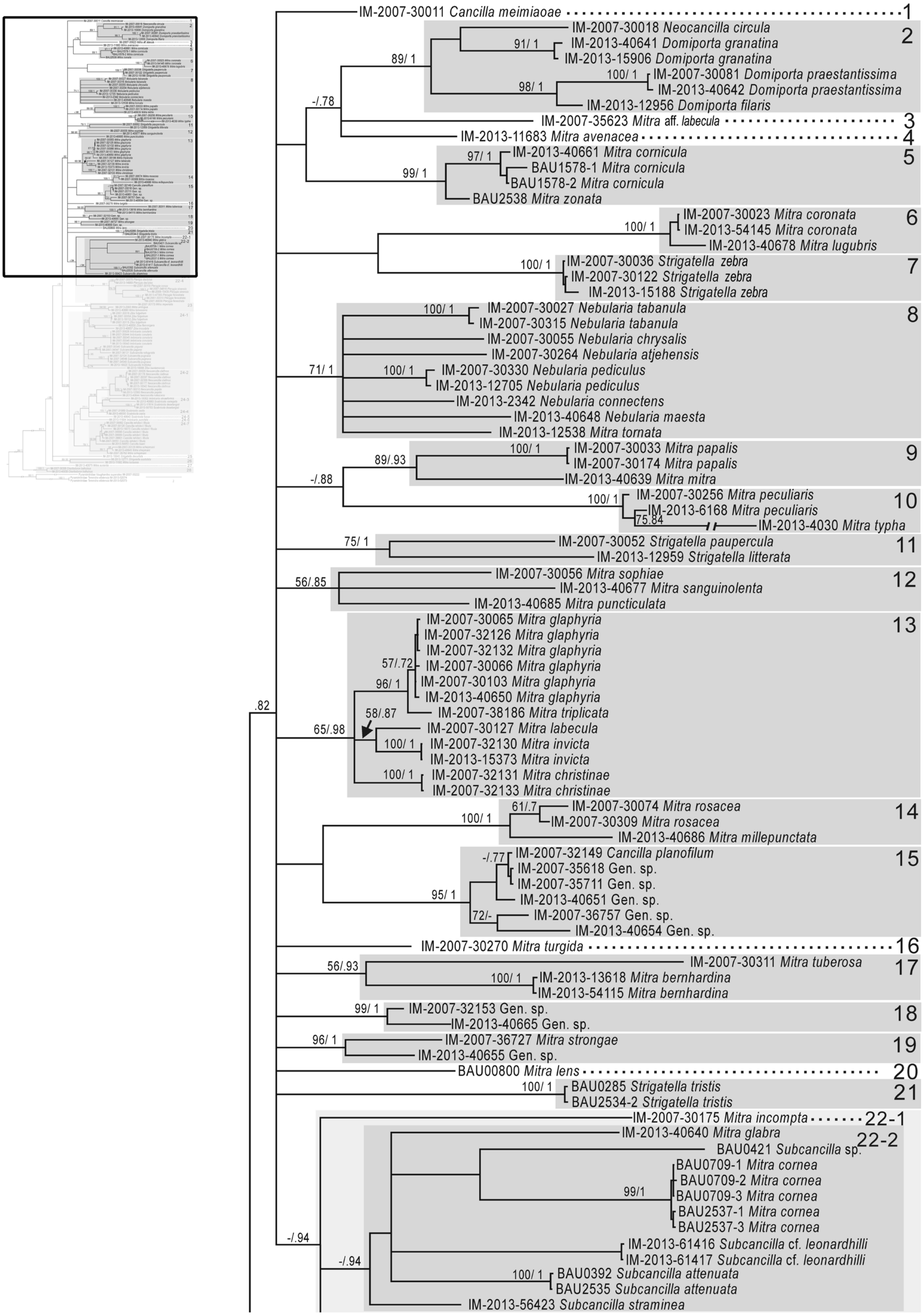

Figure 1. Bayesian phylogenetic tree of Mitroidea based on the analysis of cytochrome oxidase subunit I (*COI*) gene. Branch support as maximum likelihood bootstrap values (when >50)/Bayesian PP (when >0.7).

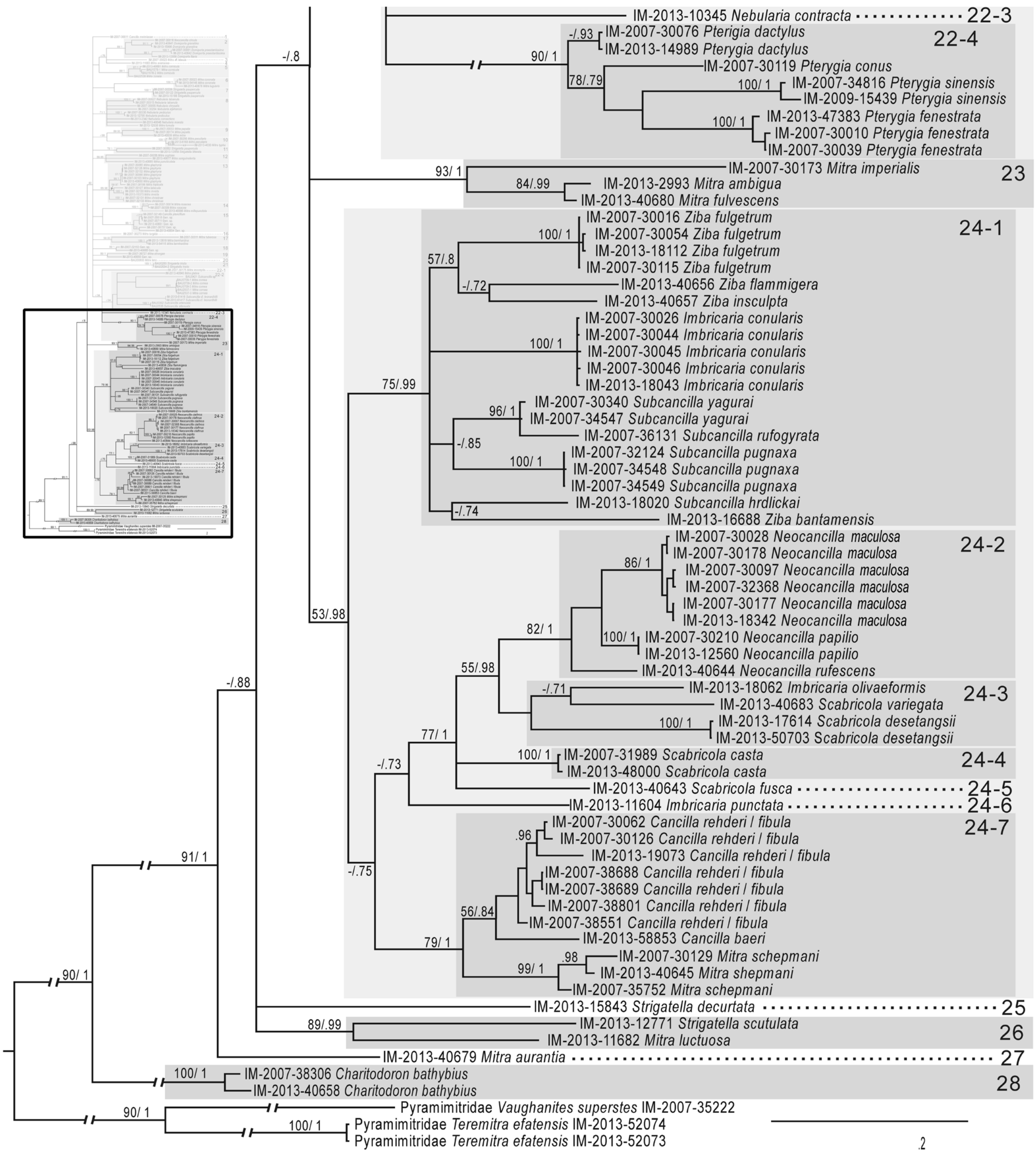

Figure 1. *Continued*

colours in the molecular trees (Figs 3–5); their compositions were entirely consistent between trees, while support values and within-clade branching pattern varied slightly depending on the data set analyzed. At the same time, relationships among these lineages remain unresolved; weakly supported affinities identified in one analysis appear unsupported in others. Here, we describe the topology of the 3-mit tree (Fig. 3) and refer to other reconstructions where necessary.

The first major lineage (orange in Fig. 3) moderately supported by BI and weakly supported in ML (PP = 0.97; BS = 74), comprises an assortment of *Mitra* lineages, along with species currently assigned to *Nebularia*, *Domiporta* and *Ziba*. This is the largest inferred lineage of Mitridae, combining 29 of the 82 species included in our 3-mit and 4G analyses. The distinct clades included in this first major lineage are:

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 paupercula* (in *COI* clade 11); B, C, *Strigatella zebra* (*COI* clade 7); D, E, Mitridae gen. et sp. nov. (in *COI* clade 15); F, Mitridae gen. et sp. nov. (in *COI* clade 18); G–M, '*Mitra*' *glaphyria* (in *COI* clade 13); N–S, *Cancilla fibula*/*rehderi* (in *COI* clade 24–7).

1.1) a well-supported *Mitra mitra*–*Mitra papalis* clade (PP = 1; BS = 100);
1.2) a moderately well-supported *Mitra sanguinolenta*–*M. sophiae*–*M. cardinalis*–*M. puncticulata* clade (PP = 1; BS = 59);
1.3) a *Domiporta* grouping, moderately supported by BI (PP = 0.98), combining (1.3a) a distinctive four-species *Domiporta s.s.* clade (PP = 1; BS = 100); (1.3b) a two-species *Mitra millepunctata*–*M. rosacea* clade (PP = 100; BS = 1); and two clades formed by undescribed deep-water mitrids: (1.3c) IM-2013-40651 and IM-2013-40654 (PP = 1; BS = 100), and (1.3d) the single-species clade of IM-2013-40665.

1.4) a clade, moderately supported by BI (PP = 0.99), combining a two-species *Mitra avenacea*-Gen. et sp. nov. MNHN IM-2013-40655 clade (PP = 1; BS = 98) with a well-supported grouping formed by three species currently assigned to *Nebularia*, *Nebularia connectens*, *N. pediculus*, *N. maesta* and *Mitra tornata* (PP = 1; BS = 99).
1.5) a clade, well supported by BI (PP = 0.99), combining '*Mitra*' *glaphyria* and '*Mitra*' *invicta* from deep water of the Indo-Pacific, and a distinct well-supported clade including three New World *Mitra* species (PP = 1; BS = 99).
1.6) a clade, moderately supported by BI (PP = 0.97), combining the West African *Ziba carinata* and the Mediterranean species pair *Mitra cornicula* and *M. zonata* (PP = 1; BS = 99).

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

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

The third major lineage of Mitridae (PP = 1; BS = 100: green in Figs 3–5) consists of three distinct, well-supported clades that include 20 Indo-Pacific species commonly classified in the Imbricariinae:

3.1a) a first clade (PP = 1; BS = 99) combining *Imbricaria conularis*, two species of *Subcancilla* and five species of shallow-water *Ziba* from the Indo-West Pacific, *Z. bantamensis*, *Z. flammigera*, *Z. fulgetrum*, *Z. insculpta* and *Z. verrucosa*;
3.2) a second clade (PP = 1; BS = 100) including the morphologically variable deep-water species *Cancilla fibula*, represented in our analysis by three specimens, and *Swainsonia schepmani*;
3.3) a third, distinctive and well-supported grouping including: (3.3a) a well-supported *Neocancilla* clade, with (3.3b) weakly supported *Scabricola* clade showing supported affinity to *Neocancilla*, (3.3c) the two-species *Swainsonia* clade and (3.3d) *Imbricaria punctata*, which is recovered as a sister group to the rest of 3.3.

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

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

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

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

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

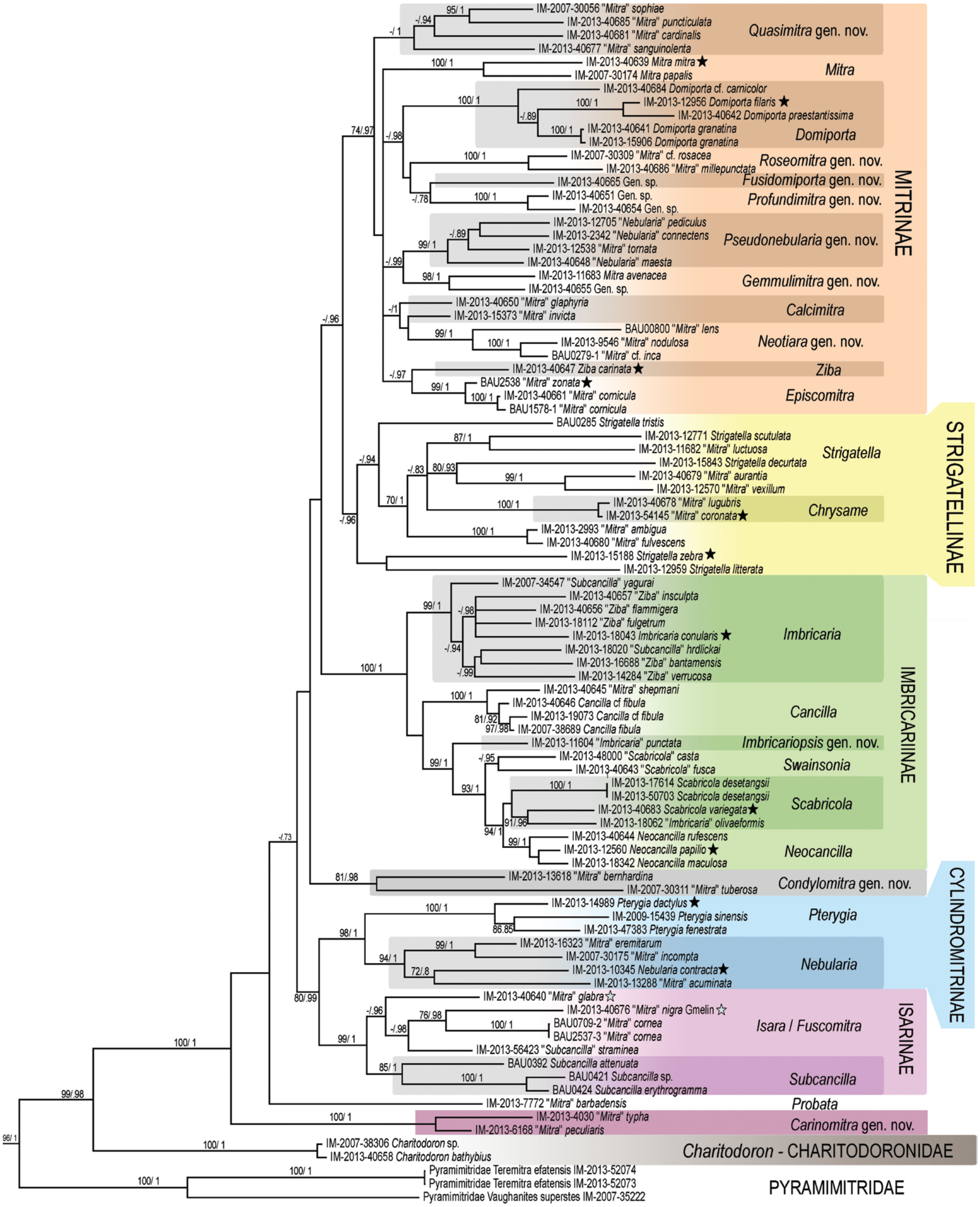

Figure 3. Bayesian phylogenetic tree of Mitridae, **Charitodoronidae fam. nov.** and Pyramimitridae based on the analysis of 3-mit data set. Branch support as maximum likelihood bootstrap values (when >70)/Bayesian PP (when >0.75). Type species of nominal genera marked with asterisks. Inferred phylogenetic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

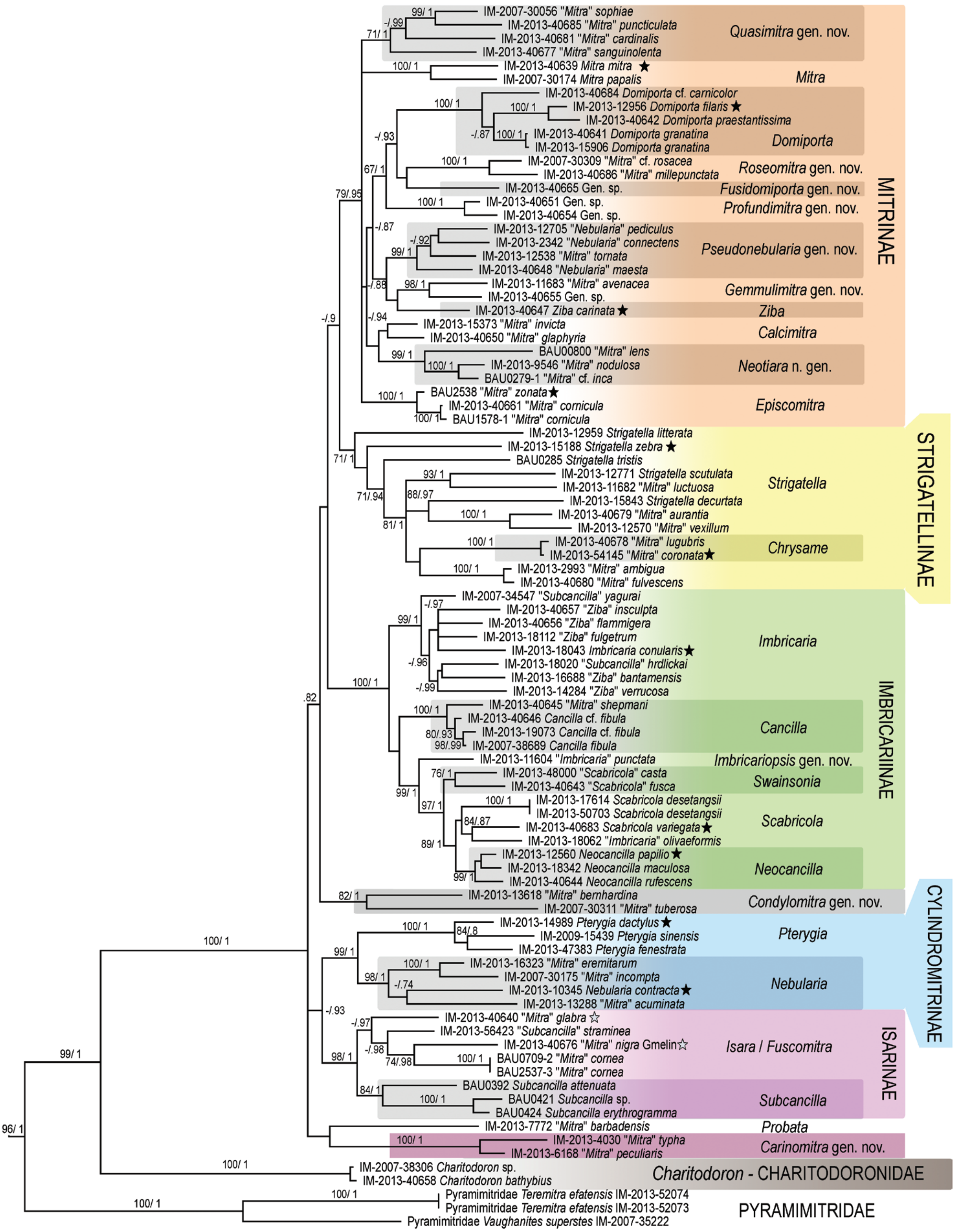

Figure 4. Bayesian phylogenetic tree of Mitridae, **Charitodoronidae fam. nov.** and Pyramimitridae based on the analysis of 4G data set. Support values and labelling as in Figure 3.

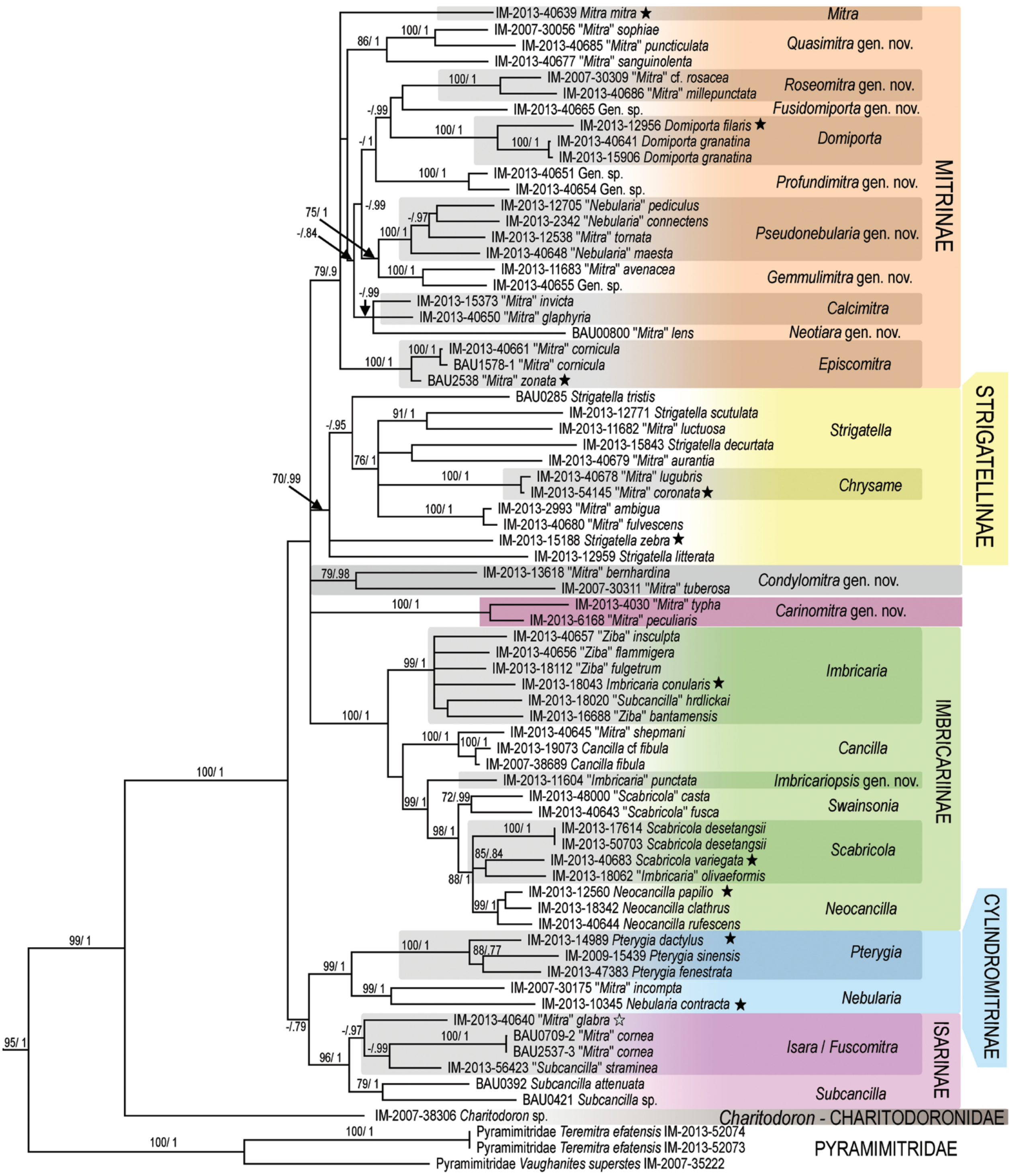

Figure 5. Bayesian phylogenetic tree of Mitridae, **Charitodoronidae fam. nov.** and Pyramimitridae based on the analysis of 4G-red data set. Support values and labelling as in Figures 3 and 4.

The eighth lineage (PP = 1; BS = 100: light brown in Figs 3–5) is formed by two Indo-Pacific *Mitra* species, *Mitra peculiaris* and *M. typha*, from here onwards referred to as the *M. peculiaris* lineage.

OTHER CONCATENATED DATA SETS

Compared to the 3-mit tree, the 4G tree (Fig. 4) shows a slightly decreased support value for the *Mitra–Domiporta–Ziba* lineage (PP = 0.95; BS = 79) and an insignificant rearrangement in the internal branching order. However, the support for the *Strigatella* lineage is higher in the 4G analysis compared to 3-mit (PP = 1; BS = 71), and nine of 12 species included in this lineage form a well-supported grouping (PP = 1; BS = 81). Neither content nor support values changed significantly for the *Neocancilla–Imbricaria–Scabricola*, *Pterygia–Nebularia* or *Isara–Fuscomitra* lineages, as well as for the *M. tuberosa* and *M. peculiaris* lineages. However, the support has changed in some internal nodes, in particular the *Swainsonia casta–Swainsonia fusca* lineage shows a higher support compared to the 3-mit analysis (PP = 1; BS = 76). Similarly, the clade that combines *Neocancilla* and *Scabricola* gains higher support (PP = 1; BS = 89) and is now clearly subdivided into two subclades, one corresponding to *Neocancilla* (PP = 1; BS = 99) and the other combining *Scabricola variegata*, *S. desetangsii* and *S. olivaeformis* (PP = 0.87; BS = 84).

Conversely, the grouping which unified the *Pterygia–Nebularia* and *Isara–Fuscomitra* major lineages shows even a lower support compared to the 3-mit analysis (PP = 0.93, BS = 64).

Not unexpectedly, the phylogenetic tree based on the analysis of the 4G-red data set (Fig. 5) shows more significant changes in contents of the inferred groupings, primarily because of the reduced number of analyzed taxa. Nevertheless, and with the exception of *M. barbadensis* which was not included in 4G-red data set, the seven major Mitridae lineages defined in the 3-mit and 4G analyses retained their principal composition, with support values comparable to those obtained in the 3-mit and 4G analyses. Among others, the *Mitra–Domiporta–Ziba–Episcomitra* lineage shows the greatest decrease in BI support (PP = 0.9; BS = 0.79); however, the six clades that compose this major Mitridae *s.s.* lineage remain distinctive and well supported. Similarly, the phylogenetic clades corresponding to the large *Neocancilla–Imbricaria–Scabricola*, *Pterygia–Nebularia* and *Isara–Fuscomitra* lineages retained acceptable support values.

The support values of phylogenetic lineages inferred in analyses of the *COI*, 3-mit, 4G and 4G-red data sets are summarized in Table 3; the clade names used in the table and on the trees are discussed in the section 'Taxonomical part'. Only a few of the currently recognized mitrid genera emerge monophyletic in our analyses: we confirm the monophyly of *Pterygia* and *Charitodoron*, while the other genera are either found to be poly- or paraphyletic or their identification on the molecular tree is not straightforward (see section 'Morphological studies').

MORPHOLOGICAL STUDIES

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

Charitodoron veneris

Foregut anatomy based on NMSA D4172 (off Durban, 29°50.4′S, 31°14.0′E, 150 m, sandstone gravel, 14.1 mm); radula based on NMSA E9237 (northern Natal, off Shellfield Beach, 29°39.8′S, 31°30.16′E, 150 m).

Although the specimen had been positioned for obtaining sagittal sections, the proboscis was diverted and sectioned nearly in frontal plane (Fig. 6A, D). Proboscis moderately long, broad, conical, strongly contracted, so that its wall forms several telescopic folds (Fig. 6A, C, D). Mouth opening into medium long buccal tube, spanning around 1/3 of proboscis length and leading into broad buccal cavity. Buccal cavity subdivided into two chambers by the large circular fold of its wall (Fig. 6D, arrow); both chambers lined with tall, densely ciliated epithelium, epithelial cells with large basal or central nuclei. Wall of the posterior chamber bearing very tall longitudinal folds (Fig. 6D–F). Wide anterior oesophagus leaving buccal cavity dorsally, forming rather long loop within proboscis, leaving proboscis and narrowing before passing through the nerve ring and then widening before transition to the posterior oesophagus (Fig. 6D). Distinct valve-like structure, identifiable as a valve of Leiblein although lacking a ciliary cone, delimiting an anterior and a posterior oesophagus (Fig. 6G, vl). Anterior oesophagus empty in sectioned specimen, posterior oesophagus filled with food material (Fig. 6D, G) in which, however, no detectable remnants were found. After the oesophageal valve, tall and lightly stained epithelium of anterior oesophagus changing to low epithelium formed by small cubic cells. Anterior oesophagus lined with thin layer of muscular fibres, which become notably stronger in posterior oesophagus (Fig. 6G).

Thin and strongly convoluted salivary ducts adjoining anterior oesophagus in front of passage through nerve ring and passing forward being embedded into its muscular wall, leaving oesophageal wall closer to the proboscis tip and entering buccal mass. Paired odontophore cartilages well developed, not fusing with strong lateral odontophore protractor muscles attached to odontophore ventrally (Fig. 6D). Strong and massive odontophore retractor adjoining the columellar muscle shortly behind the nerve ring. Radular diverticulum opening into buccal cavity ventrally in posterior position, behind thick circular fold of the buccal cavity

Table 3. Support of the inferred lineages of Mitridae and **Charitodoronidae fam. nov.**

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

BI, Bayesian inference; ML, maximum likelihood; n/a, not applicable.
*Taxa represented by single specimen.

wall, forming massive 'lip', longer dorsally (Fig. 6D, E, bl). After entering buccal cavity wall, distal salivary ducts passing inside that lip laterally on both sides of radular diverticulum opening (Fig. 6D, E), and opening in the buccal cavity ventrally, underneath the semi-circular fold (Fig. 6F). Epiproboscis absent.

Salivary gland large, unpaired, situated to the left of posterior oesophagus and dorsally to the nerve ring, histologically represented by a compactly packed, strongly convoluted tube with one layer of tall highly vacuolar, obviously glandular, cells and thin outer connective tissue layer (Fig. 6A, B).

Condylomitra tuberosa (PANGLAO 2004, Stn B5)

Proboscis moderately long, leaf-shaped, anteriorly flattened dorso-ventrally (Fig. 7A–H) and cylindrical at its base (Fig. 7I). On transversal sections, proboscis with two lateral lobes at mid-length and ventral part with rounded axial keel. Proboscis wall with thick cuticle and nearly cubic epithelium, with large basal nuclei; epithelium underlined by a layer of circular muscle fibres (Fig. 7C, E, H). Lateral lobes occupied by complex interlacement of dorso-ventral, oblique and longitudinal muscular fibres; two blood vessels (Fig. 7F, bv) running along margins of proboscis (Fig. 7B, D, F, G). Central part

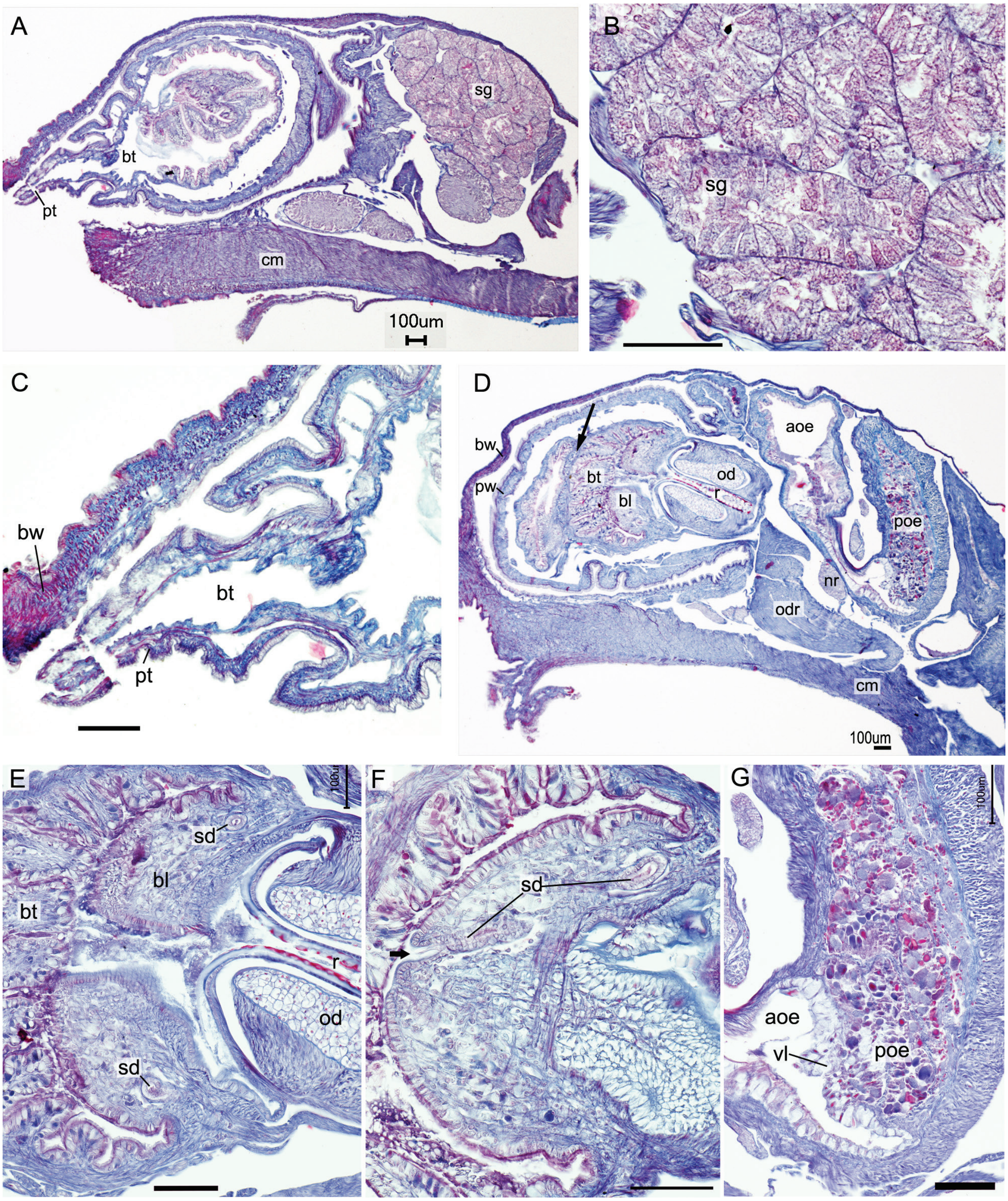

Figure 6. Histological sections of the foregut of *Charitodoron veneris*. A, section through the tip of the proboscis and salivary gland, general view. B, close up of the salivary gland. C, close up of the proboscis tip. D, section through the buccal mass, mid- and posterior oesophagus, general view. 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.

of proboscis occupied with oesophagus, anterior buccal mass and epiproboscis complex forming a single stem.

Mouth opening anteriorly on the dorsal side of the proboscis in short dorsal groove; mouth surrounded by small peristome rim (Fig. 7A). Compact buccal mass situated shortly after mouth, furnished with thick muscular walls and triangular lumen; radular diverticulum opening ventrally into buccal cavity (Fig. 7B, C). Anterior oesophagus quadrangular on transversal sections, lying dorsally in the anterior part of the proboscis, attached to proboscis wall by thin muscular fibres (Fig. 7D–H). Dorsal and ventral walls of oesophagus very thin, lateral walls with two large longitudinal folds jutting out into the lumen of oesophagus. Lateral folds of oesophagus disappearing at mid-proboscis height and thick layer of muscular fibres evenly covering it (Fig. 7I). Radular diverticulum rather short; odontophore formed by two small cartilages (Fig. 7D, E), not fused anteriorly. Odontophore retractor very strong, lying in a muscular sheath in its anterior portion (Fig. 7F–H), and dividing into two symmetrical branches at mid-proboscis length (Fig. 7I).

Epiproboscis short, formed by densely packed longitudinal muscle fibres, with no epithelium. Epiproboscis lying ventrally from radular diverticulum, enclosed inside its own muscular sheath, which is attached to the radular diverticulum along most of its length (Fig. 7D–H). Both epiproboscis and its sheath originating from the ventral part of the radular retractor sheath (Fig. 7G, H). Epiproboscis sheath opening ventrally on the anterior border of the buccal mass.

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

DISCUSSION

Application of family-group names to the phylogenetic clades

The phylogenetic trees obtained in analyses of multiple-gene data sets were largely congruent and consistent with each other with respect to the nodal support of inferred lineages, thus providing robustness for the phylogenetic hypotheses of Mitridae. We chose the 4G-based tree for further taxonomic inferences, because of (1) the better taxonomic coverage compared to the 4G-red-based tree and (2) the fewer polytomies in the 4G tree compared to the 3-mit-based tree.

Our results agree in general with those obtained in earlier analyses (Fedosov *et al.*, 2015). The assignment of names to the major lineages of Mitridae *s.s.* is straightforward in three cases:

1. Based on the inclusion of *M. mitra* (type species of *Mitra*, itself the type genus of Mitrinae), we designate the *Mitra–Domiporta–Ziba–Episcomitra* lineage as subfamily Mitrinae. Within it, the *M. mitra–M. papalis* clade is distinct and well supported and shows no supported affinity to any other clade within the Mitrinae; thus, we restrict the genus *Mitra* to this *M. mitra–M. papalis* clade (with a few other, presumed closely related, species). The genus *Tiarella* (type species *M. papalis*) thus becomes a junior synonym of *Mitra*. The numerous species (even including *M. cardinalis*!) traditionally classified in *Mitra* that fall outside this clade are assigned below to other genera.
2. The *Neocancilla–Imbricaria–Scabricola* lineage, well supported in all phylogenetic analyses, includes the type species of *Imbricaria*, *I. conularis*, thus we designate it as subfamily Imbricariinae.
3. *Pterygia* (with its subjective synonym *Cylindromitra*) is the only genus classified in the subfamily Cylindromitrinae (Cernohorsky 1970, 1991). The *Pterygia* clade is unequivocally identified in our phylogenetic trees, including the type species *P. dactylus*. Because the *Pterygia* lineage shows a well-supported affinity to the *Nebularia contracta* clade in all analyses, the name Cylindromitrinae can be applied to the resulting *Pterygia–Nebularia* lineage.

Beyond the names in current use above, another available name is Strigatellidae, which, although little used, can be applied to the *Strigatella* major lineage, so here it is designated as subfamily Strigatellinae. Conversely, there is no name available for the *Isara–Subcancilla* major lineage, for which we establish below the new subfamily Isarinae.

Finally, the three major lineages ‘*M.*’ *peculiaris*, ‘*M.*’ *tuberosa* and ‘*M.*’ *barbadensis* are here treated as separate mitrid genera, but their subfamily assignments are uncertain and we leave them as *incertae sedis*.

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

Application of genus-group names to the phylogenetic clades

Our 4G molecular data set includes the type species of 13 nominal genera: nine (*Domiporta*, *Imbricaria*,

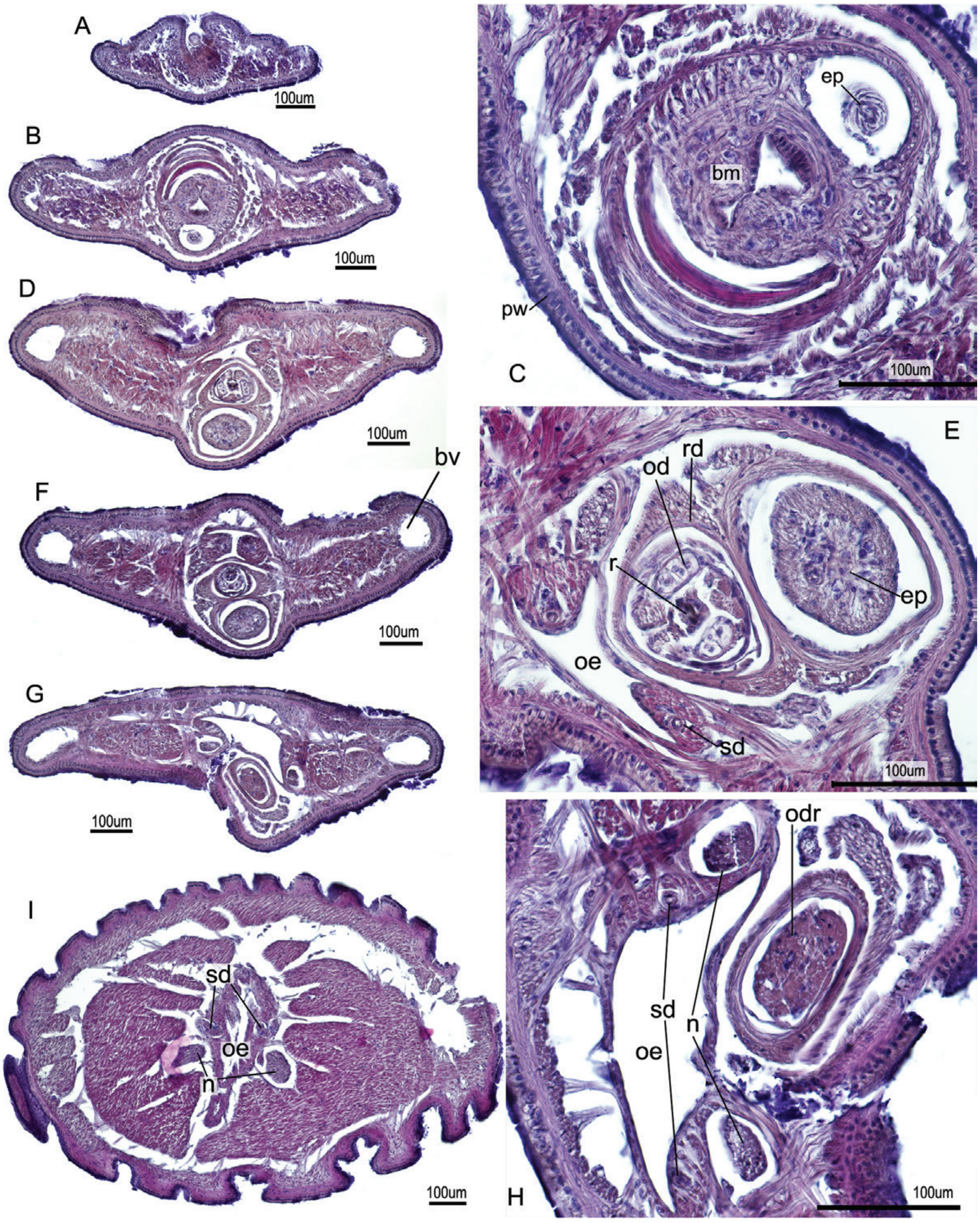

Figure 7. Transversal histological sections of the proboscis of ***Condylomitra tuberosa* comb. nov.** A, section through the mouth opening. B, section through the buccal cavity. C, close up of the buccal mass and epiproboscis tip. D, section through the buccal mass at the level of the odontophore. E, 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.

Mitra, *Nebularia*, *Neocancilla*, *Pterygia*, *Scabricola*, *Strigatella* and *Ziba*) currently treated as valid and four (*Chrysame*, *Episcomitra*, *Fuscomitra* and *Isara*) treated as synonyms (of *Mitra*). Here, we elaborate a new classification of the Mitridae based on genetically defined monophyletic groups. The inferred lineages including one (or more) of the type species mentioned above are named with certainty, but for the other clades, we have to apply names based on their common usage and in agreement with shell and radular characters. The clades for which there is no available name are treated as new genera.

We unequivocally ascribe the genera *Mitra*, *Domiporta* and *Ziba* to the subfamily Mitrinae, based on their inclusion in the Mitrinae lineage of the phylogenetic trees. Based on the analysis of the *COI* gene, we transfer *Neocancilla circula* to the genus *Domiporta*. As here circumscribed, the genus *Ziba* corresponds to a West African clade, and numerous Indo-Pacific imbricariine species assigned to *Ziba* after Cernohorsky (1991) are here transferred to *Imbricaria*. Two other clades within the Mitrinae lineage have available names: *M. zonata* is the type species of *Episcomitra*, subsequently synonymized (Cernohorsky, 1976) with *Mitra*. Based on the sequenced type species, we reinstate *Episcomitra* at the rank of genus with two Mediterranean species assigned to it, '*M.*' *zonata* and '*M.*' *cornicula*. Based on shell and radula characters, we tentatively attribute the Indo-Pacific deep-water clade '*M.*' *glaphyria*–'*M.*' *invicta* to the genus *Calcimitra*.

Although the Mitrinae lineage comprises the six distinct clades described above, some of them show morphological, geographical, bathymetric and molecular disparities that lead us to further subdivide them. Thus, we delineate on the molecular tree 12 well-supported clades (some being single species) that we rank as genera (marked light grey on the trees). Five of them have applicable names, and the remaining eight are here treated as new genera:

Quasimitra gen. nov. for the Indo-Pacific clade of '*Mitra*' *sophiae*, '*Mitra*' *puncticulata*, '*Mitra*' *cardinalis* and '*Mitra*' *sanguinolenta*.

Roseomitra gen. nov. for the Indo-Pacific clade of '*Mitra*' *rosacea* and '*Mitra*' *millepunctata*.

Fusidomiporta ponderi gen. et sp. nov. for the single-species clade of MNHN IM-2013-40665 (Indo-Pacific, deep water).

Profundimitra gen. nov. for the Indo-Pacific deep-water clade of MNHN IM-2013-40651 and MNHN IM-2013-40654.

Pseudonebularia gen. nov. for the Indo-Pacific 'lesser' *Nebularia* clade of '*Nebularia*' *pediculus*, '*N.*' *connectens*, '*N.*' *maesta* and '*Mitra*' *tornata*, which show no affinity to either *Mitra* or *Nebularia* as circumscribed here (the latter genus as typified by *N. contracta* is found to be closely related to *Pterygia* – see below).

Gemmulimitra gen. nov. for the Indo-Pacific clade of '*Mitra*' *avenacea* and MNHN IM-2013-40655.

Neotiara gen. nov. for the clade of New World species '*Mitra*' *lens*, '*Mitra*' *nodulosa* and '*Mitra*' aff. *inca*.

Cancillopsis gen. nov. for the Indo-Pacific clade 1 of our *COI*-based tree, which shows no affinity to any other mitrid lineage in the analysis.

Five species of *Strigatella*, including the type species, *S. zebra*, are included in the Strigatellinae lineage of our trees, along with numerous '*Mitra*' species. As *Strigatella* and '*Mitra*' species do not form clades but are well intermixed, we recognize within this subfamily only one genus *Strigatella* and assign to it all the species in the Strigatellinae lineage. However, the genus name *Chrysame* (the type species *M. coronata* is included in our data set) would apply to the *M. coronata*–*M. lugubris* subclade, which forms a very long branch and has a peculiar monoserial radula (see below), which differs remarkably from the radula of the rest of the Strigatellinae. From a cladistic point of view, recognition of *Chrysame* would render *Strigatella* paraphyletic, or many new genera would need to be established. We think the latter approach would be premature and, despite the unique position of *Chrysame* in the molecular trees, we treat it as a synonym of *Strigatella*.

The first clade of the Imbricariinae includes *I. 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 & 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* gen. nov.

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* gen. nov. and *Carinomitra* gen. nov., 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*. Four genera that are not represented in our data set, *Atrimitra* Dall, 1918, *Vicimitra* Iredale, 1929, *Magnamitra* Huang & Salisbury, 2017 and *Dibaphimitra* Cernohorsky, 1970, also cannot be attributed to any of the newly identified subfamilies based on 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** FEDOSOV, HERRMANN, KANTOR & BOUCHET **FAM. NOV.**

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* gen. nov., *Gemmulimitra* gen. nov., *Cancillopsis* gen. nov., *Neotiara* gen. nov., *Profundimitra* gen. nov., *Pseudonebularia* gen. nov., *Quasimitra* gen. nov., *Roseomitra* gen. nov.

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* gen. nov.

SUBFAMILY CYLINDROMITRINAE COSSMANN, 1899

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

SUBFAMILY **ISARINAE** FEDOSOV, HERRMANN, KANTOR & BOUCHET **SUBFAM. NOV.**

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

SUBFAMILY PLEIOPTYGMATINAE QUINN, 1989

Genus *Pleioptygma* Conrad, 1863.

INCERTAE SEDIS

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

TAXONOMICAL PART

Decisions on the generic assignment of individual species are based on: [1]molecular evidence and radula morphology or molecular data only, [2]shell characters and radula morphology and [3]solely shell characters. In 'Species included' sections, type species of recognized genera are shown in bold.

Superfamily Mitroidea Swainson, 1831

Family **Charitodoronidae** Fedosov, Herrmann, Kantor & Bouchet **fam. nov.**

(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 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 nebulose 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-planktotrophic development, consistent with the narrow distribution range. Despite *Charitodoron* being close to mitrids in radula morphology, 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 in a separate family.

Genus *Charitodoron* Tomlin, 1932

Type species: *Charitodoron euphrosyne* Tomlin, 1932 (junior subjective synonym of *Columbella barbara* Thiele, 1925); OD.

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

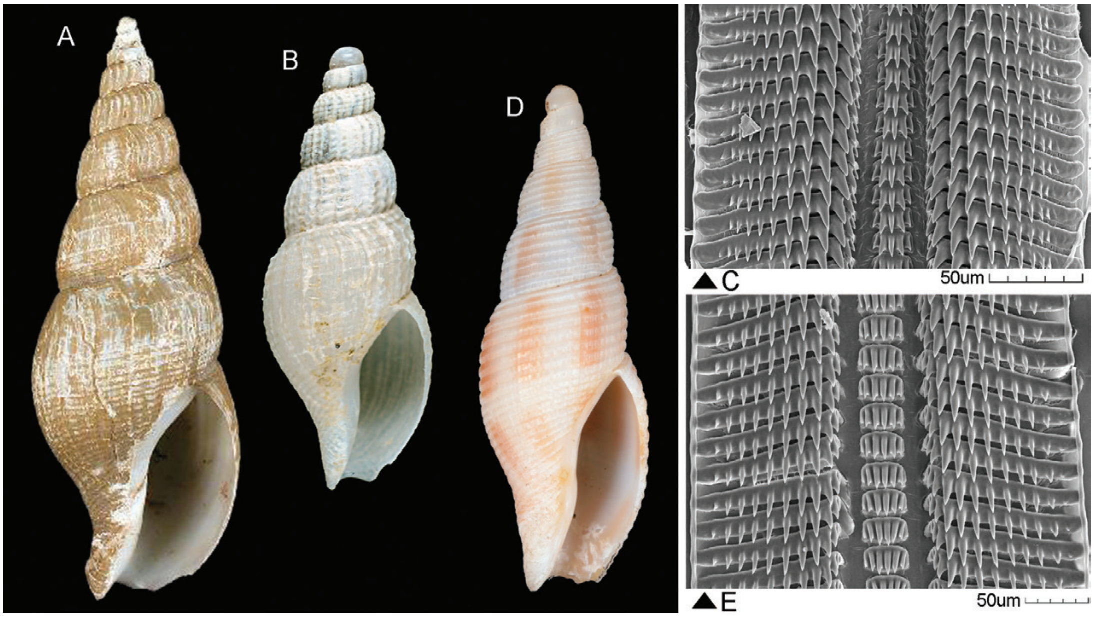

Figure 8. *Charitodoron* species. A, *Charitodoron* sp., MNHN IM-2007-38306, off Mozambique, MAINBAZA Stn 3157, 21°46′S, 36°25′E, 1410–1416 m. B, C, *Charitodoron bathybius*, MNHN IM-2013-40658, off Mozambique, MAINBAZA, Stn 3171, 25°59′S, 34°42′E, 771–776 m, 12.0 mm. B, shell; C, radula. D, E, *Charitodoron 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.

FAMILY MITRIDAE SWAINSON, 1831
SUBFAMILY MITRINAE SWAINSON, 1831
(FIGS 9–21)

GENUS *MITRA* LAMARCK, 1798
(FIGS 9, 10A)

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

Synonym: *Tiarella* Swainson, 1840. Type species: *Voluta papalis* Linnaeus, 1758; SD (Gray, 1847) *Papalaria Dall*, 1915. Type species: *Voluta episcopalis* Linnaeus, 1758 [= *Mitra mitra* (Linnaeus, 1758)]; SD, Coan (1966: 131).

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 three 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 three to four subequal oblique columellar folds. Radula with rather narrow rachidian bearing six subequal cusps, and very wide laterals bearing cusps throughout their width (Fig. 10A). Cusps rather strong near rachidian and becoming progressively weaker laterally.

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

Species included: *Mitra mitra* (Linnaeus, 1758)[1], *Mitra deprofundis* Turner, 2001[3], *Mitra papalis* (Linnaeus, 1758)[1], *Mitra stictica* (Link, 1807)[3].

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 distinctive because of the conservative shell shape with rather high spire and low aperture, presence of denticles on the outer aperture lip and a recognizable colour pattern. At the same time, its radular morphology is overall the same as in many other mitrid clades and adds little to the diagnosis of the genus.

Quasimitra cardinalis and *Q. puncticulata* resemble species of Mitra. However, *Q. cardinalis* has a notably wider shell with lower spire, and *Q. puncticulata* lacks the characteristic colour pattern of *Mitra* and bears no denticle on the outer aperture lip. *Nebularia incompta* also resembles *Mitra* in shell proportions and the presence of denticles on the margin of the outer lip, but has a stronger sculpture and its siphonal canal is not clearly delineated from the shell base; besides, it has a typical *Nebularia*-type colour pattern instead of a *Mitra*-type. Some *Strigatella* species, especially *S. imperialis*, also closely resemble *Mitra* in the morphology of the abapical part of the shell (aperture and siphonal canal), but they have a notably lower spire and lack the *Mitra*-type colour pattern as well.

GENUS *CALCIMITRA* HUANG, 2011
(FIGS 10B, C, 11)

Type species: *Calcimitra kingtsio* Huang, 2011; OD.

Diagnosis: Shell medium sized to large (35–125 mm), elongate-fusiform, with high orthoconoid or slightly acuminate spire and slender, tapering siphonal canal. Protoconch narrowly conical, multispiral, of about three smooth convex whorls. Suture deeply impressed or canaliculate. Spire whorls flattened to evenly convex, smooth or sculptured with weak and irregular, or distinct, evenly set cords. Interspaces between spiral cords sometimes ornamented with fine collabral growth lines or dense riblets sometimes forming fine cancellate sculpture pattern. Siphonal canal long, tapering, with shallow or indistinct siphonal notch. Aperture elongate, its outer lip smooth, evenly convex. Inner aperture lip often calloused, sometimes reflected, bearing three to four fine columellar folds. Shell white, pale to orange, sometimes bearing pattern of reddish or brownish axial bands; fresh specimens often covered with brown periostracum. Radula with rather narrow rachidian, bearing six to eight subequal cusps; laterals wide, bearing 12–20 pointed cusps (Fig. 10B, C), two proximal cusps rather short, weaker than the next five ones that are strongest; marginal five to eight cusps gradually diminishing.

Distribution: Indo-Pacific, bathyal depths, mud, sometimes on sunken wood.

Species included: *Calcimitra arnoldeyasi* (Poppe, Tagaro & Salisbury, 2010)[3] comb. nov., *C. brinkae* (Salisbury & Kilburn, 1996)[3] comb. nov., *C. brunetta* (Chino & Herrmann, 2015)[3] comb. nov., *C. chiangfucius* (Huang & Salisbury, 2017)[2] comb. nov., *C. christinae* (Poppe, 2008)[1] comb. nov., *C. chuoi* (Huang & Salisbury, 2017)[3] comb. nov., *C. glaphyria* (Turner, 2001)[1] comb. nov., *C. hilli* (Cernohorsky, 1976)[3] comb. nov., *C. invicta*

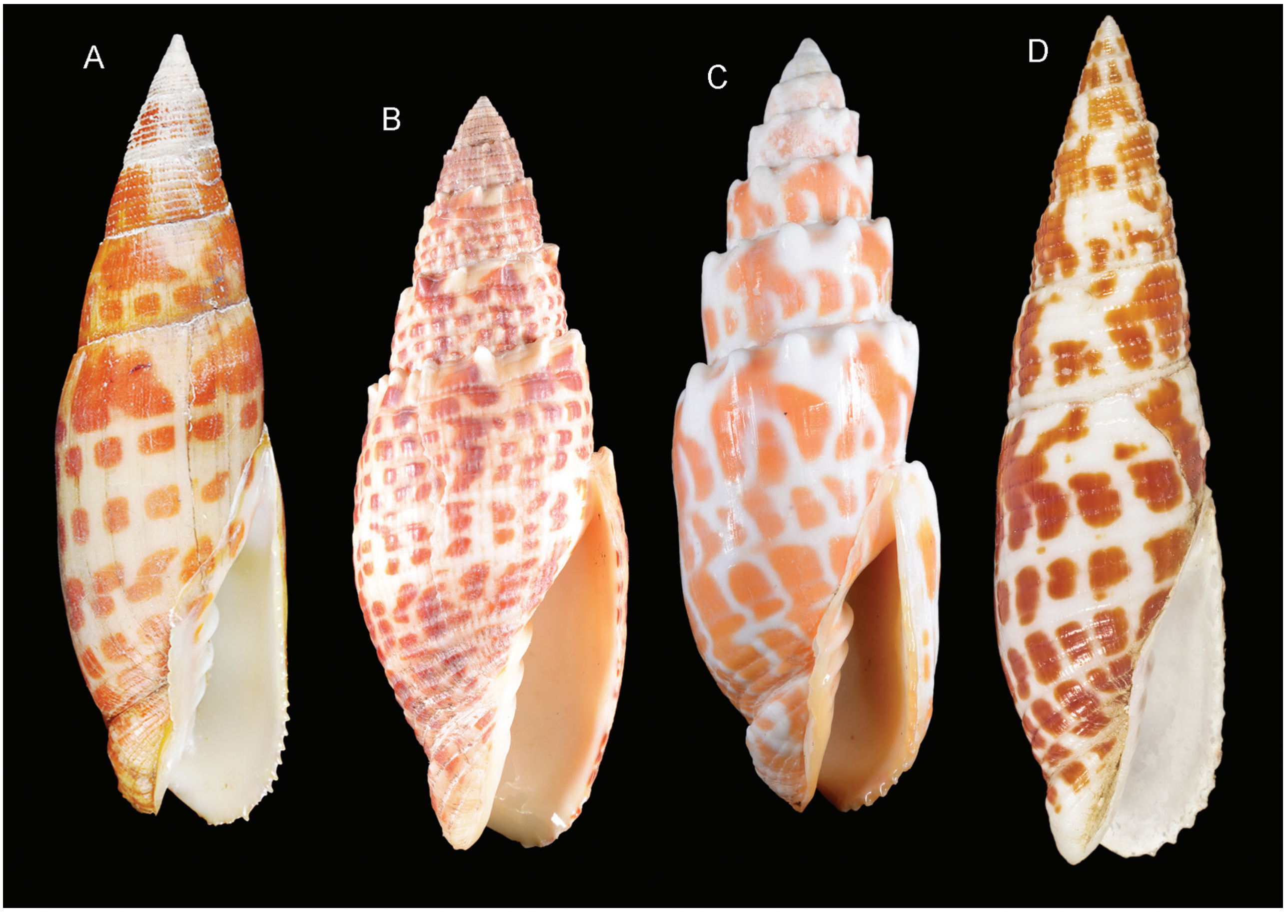

Figure 9. *Mitra* species. A, *Mitra mitra*, MNHN IM-2013-40639, Mozambique, INHACA 2011 Stn MR15, 26°00.0′S, 32°54.4′E, 4 m, 89.1 mm. B, *Mitra papalis*, MNHN IM-2013-50981, Papua New Guinea, KAVIENG Stn KR34, 02°34,6′S, 150°46,3′E, 10–22 m, 70.7 mm. C, *Mitra stictica*, Society Islands, off Moorea,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

(Huang & Salisbury, 2017)[1] comb. nov., *C. kingtsio* Huang, 2011[3], *C. labecula* (Herrmann & Dekkers, 2009)[1] comb. nov., *C. lussii* (Turner & Salisbury, 2007)[3] comb. nov., *C. marrowi* (Turner, 2001)[3] comb. nov., *C. meyeriana* (Salisbury, 1992)[3] comb. nov., *C. morchii* (A. Adams, 1855)[2] comb. nov., *C. philosopha* (Huang & Salisbury, 2017)[2] comb. nov., *C. poppei* (Guillot de Suduiraut, 2000)[3] comb. nov., *C. salva* (Turner, 2001)[3] comb. nov., *C. subflava* (Kuroda & Habe, 1971)[3] comb. nov., *C. taiwanbale* (Huang & Salisbury, 2017)[3] comb. nov., *C. triplicata* (Martens, 1904)[1] comb. nov., *C. verweyi* (Knudsen, 1970)[3] comb. nov.

Remarks: The five species included in clade 13 of the *COI*-based tree show considerable variation in shell morphology, both intra- and interspecifically. Six sequenced specimens of *C. glaphyria* display a range of sculpture types, from smooth shells resembling *C. kingtsio* to distinct, cancellated ones, and differently sculptured specimens can be found in the same general locality. While typical *Calcimitra* are medium-sized, thin-walled shells, our phylogenetic analysis placed '*Mitra*' *invicta* in the same phylogenetic clade. The latter is a recently described species representative of a group of large deep-water mitrids (here referred to as the *C. morchii* complex) that possess heavy, strongly sculptured shells (Huang & Salisbury, 2017). The close affinity of these conchologically diverse species is consistent with a generally conservative radular morphology in *C. kingtsio* (Huang, 2011), *C. morchii*, *C. chiangfucius*, *C. philosopha* (Huang & Salisbury, 2017), *C. glaphyria* and *C. invicta* (herein). The intraspecific variation in sculpture pattern demonstrated by *C. glaphyria* challenges the status of the species in the *C. morchii* complex accepted by Huang & Salisbury (2017). The distinction of *C. chiangfucius*, C. *taiwanbale* and *C. invicta* is based on subtle differences in shell morphology; they may prove to represent variants of a single species, and more comprehensive sampling is necessary to clarify species boundaries.

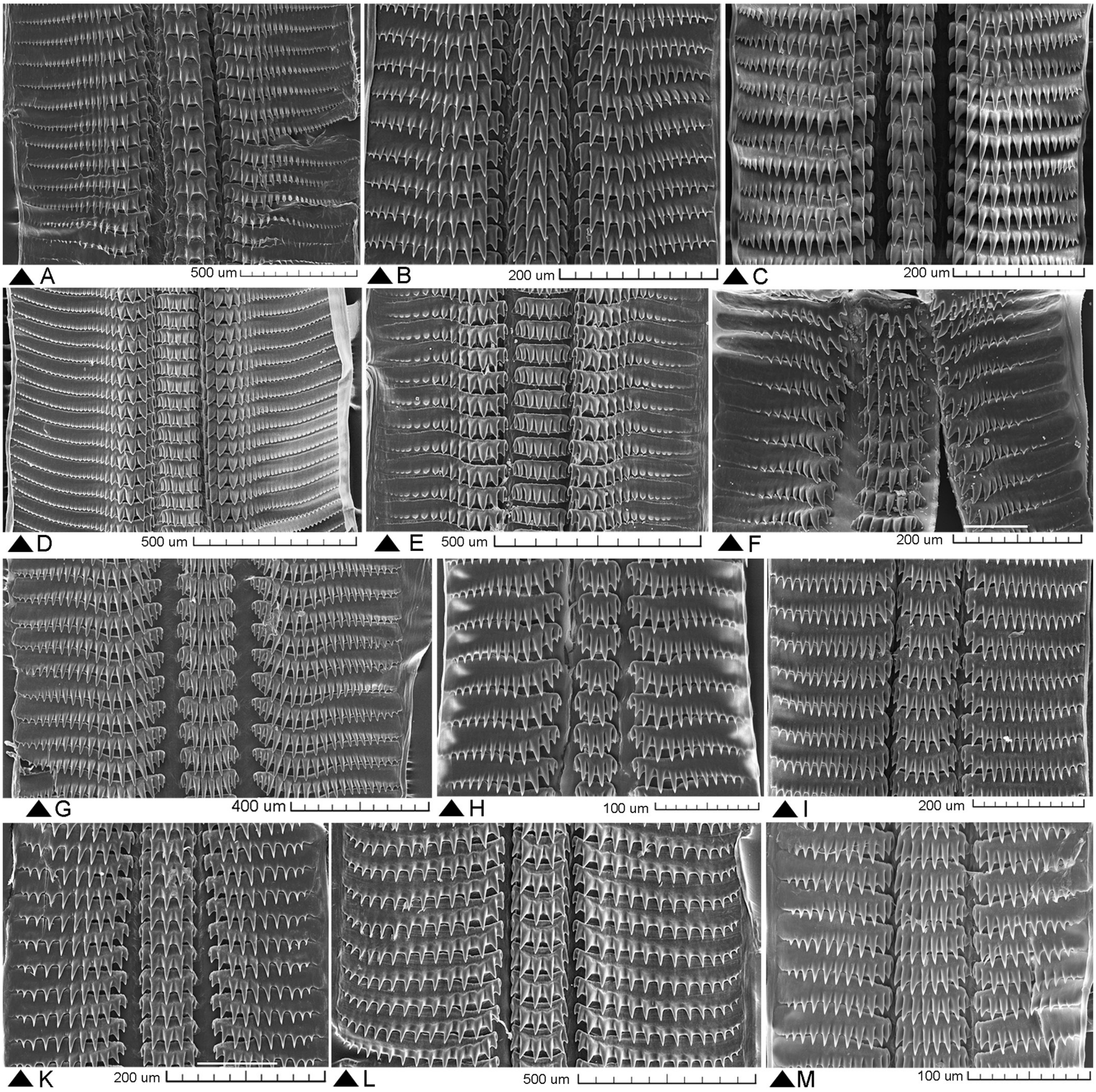

Figure 10. Radulae of Mitrinae species. A, *Mitra mitra*, MNHN IM-2013-40639, Mozambique, INHACA 2011 Stn MR15, 26°00.0′S, 32°54.4′E, 4 m, 89.1 mm. B, ***Calcimitra glaphyria*** **comb. nov.**, MNHN IM-2013-40650, Papua New Guinea, BIOPAPUA Stn CP3728, 07°52′S, 148°01′E, 498–501 m, 31.9 mm. C, ***Calcimitra invicta*** **comb. nov.**, MNHN-IM-2013-15373, PAPUA NIUGINI Stn CP3949, 05°12′S, 145°51′E, 380–407 m, 61.6 mm. D, ***Neotiara lens*** **comb. nov.**, neotype, MNHN IM-2000-33145, Panama, Panama City, 08°95′N, 79°53′W, intertidal, 40.0 mm. E, ***Neotiara nodulosa*** **comb. nov.**, 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, ***Episcomitra cornicula*** **comb. nov.**, BAU1578.3, Greece, Astypalea Is., Agrilidi, 36°35.0′N, 26°25.4′E, 2–7 m, 12.1 mm. I, ***Quasimitra puncticulata*** **comb. nov.**, MNHN IM-2013-40685, Philippines, off Noc-Nocan Is., 10°15.1′N 124°25.1′E, 4–12 m, 40.6 mm. K, ***Quasimitra sophiae*** **comb. nov.**, IM-2007-30056, Vanuatu, SANTO 2006 Stn DR09, 15°34.6′S, 167°13.8′E, 12 m, 25.1 mm. L, ***Quasimitra cardinalis*** **comb. nov.**, 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, ***Quasimitra sanguinolenta*** **comb. nov.**, MNHN IM-2013-40677, Mozambique, INHACA 2011 Stn MS02, 26°06.3′S, 32°58.0′E, 17–19 m, 28.7 mm.

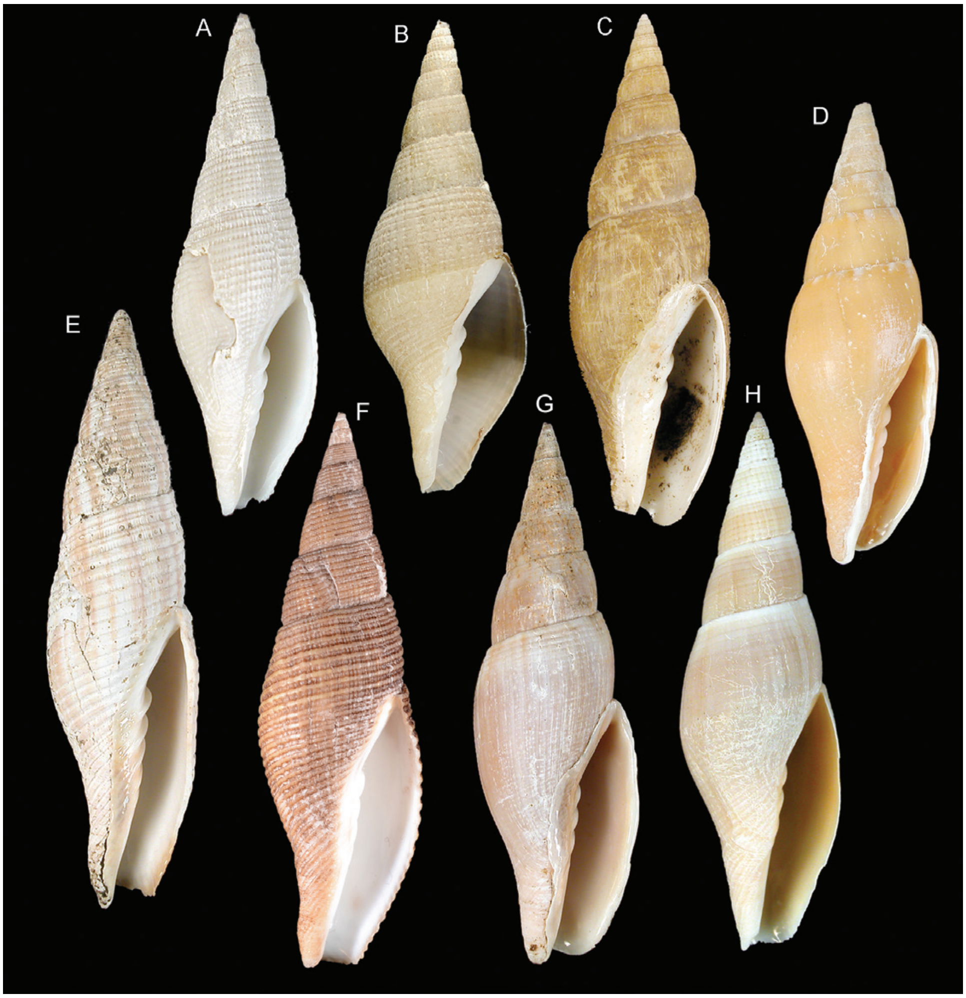

Figure 11. Genus *Calcimitra*. A, B, ***Calcimitra glaphyria* comb. nov.**; A, MNHN IM-2007-30066, Philippines, PANGLAO 2005 Stn CP2342, 9°24′N 123°53′E, 1240–1258 m; B, MNHN IM-2013-40650, Papua New Guinea, BIOPAPUA Stn CP3728, 07°52′S, 148°01′E, 498–501 m, 31.9 mm. C, ***Calcimitra triplicata* comb.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

Magnamitra sandrogorii strongly resembles some of the larger species of *Calcimitra*, and the distinction of these two genera based on shell characters is problematic. The spiral sculpture in *M. sandrogorii* is even stronger than in species of the *C. morchii* complex, and the main distinction between the two genera is in the radula. In *Magnamitra*, the rachidian has a very strong unpaired central cusp that notably exceeds lateral cusps, whereas all studied species of *Calcimitra* possess a rachidian with equal or subequal cusps. Furthermore, rachidian and laterals have comparable width in *M. sandrogorii*, whereas in species of *Calcimitra* the width of the rachidian does not exceed half of the laterals width. Species of *Profundimitra* gen. nov. superficially resemble *Calcimitra*, but the latter genus can be recognized by the generally larger shells with proportionally longer siphonal canal and often calloused inner aperture lip. The radulae of species of *Calcimitra* and *Profundimitra* gen. nov. differ greatly, the latter having rachidian and marginals of about equal width. Species of *Eumitra* are also similar to *Calcimitra* in shell proportions and sculpture; however, *Eumitra* can be distinguished by its columellar folds, which are reduced to not more than two very weak folds, while in *Calcimitra* there are four (very rarely three) distinct ones.

Some species of *Calcimitra*, in particular *C. triplicata*, resemblance the Miocene fossil genus *Clifdenia*, both in whorl outline with evenly rounded inflated shoulders, and in shape and orientation of columellar plaits (A. Beu, personal communication). Based on this resemblance, we tentatively allocate *Clifdenia* to the subfamily Mitrinae.

GENUS *EUMITRA* TATE, 1889

(FIG. 12)

Type species: †*Mitra alokiza* Tenison-Woods 1879; SD (Ludbrook, 1958: 71).

Diagnosis: Shell small to medium sized (15–58 mm), fusiform, thin walled, with high orthoconoid spire and slender siphonal canal. Protoconch very low, cyrtoconoid, paucispiral, with glossy whorls and rather small nucleus in all known species. Suture distinct, impressed. Early teleoconch whorls subcylindrical, later evenly convex, sometimes resulting in a slightly acuminate spire profile. Shell smooth, sometimes with very weak axial folds on first teleoconch whorl or fine grooves on shell base and siphonal canal. Siphonal canal, slender, tapering. Siphonal notch absent. Aperture elongate, outer lip evenly convex, smooth. Inner aperture lip either smooth, bearing one very weak or sometimes two distinct, but weak, columellar folds. Shell uniformly pale to light brown. Radula with very small, narrow rachidian, bearing five short robust cusps, only slightly extending beyond preceding tooth margin, but forming ridges, notably elevated above surface of rachidian. Laterals wide with eight to ten strong, pointed subequal cusps.

Distribution: New Caledonia, Coral Sea and the Philippines at bathyal depths, and a further undescribed species referable to *Eumitra* from Indonesia. Fossil species widely distributed in the Miocene of Europe and in the Australia–New Zealand region.

Recent species included: *Eumitra apheles* Lozouet, 1991[2], *E. caledonica* Lozouet, 1991[3], *E. imbricata* Lozouet, 1991[3], *E. richeri* Lozouet, 1991[3]. '*Eumitra*' *suduirauti* Bozzetti, 1997[3].

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 data). Based on shell characters, *Eumitra* resembles *Calcimitra* and *Profundimitra* gen. nov.; however, in the latter two genera species commonly have three or more strong columellar folds. Besides,

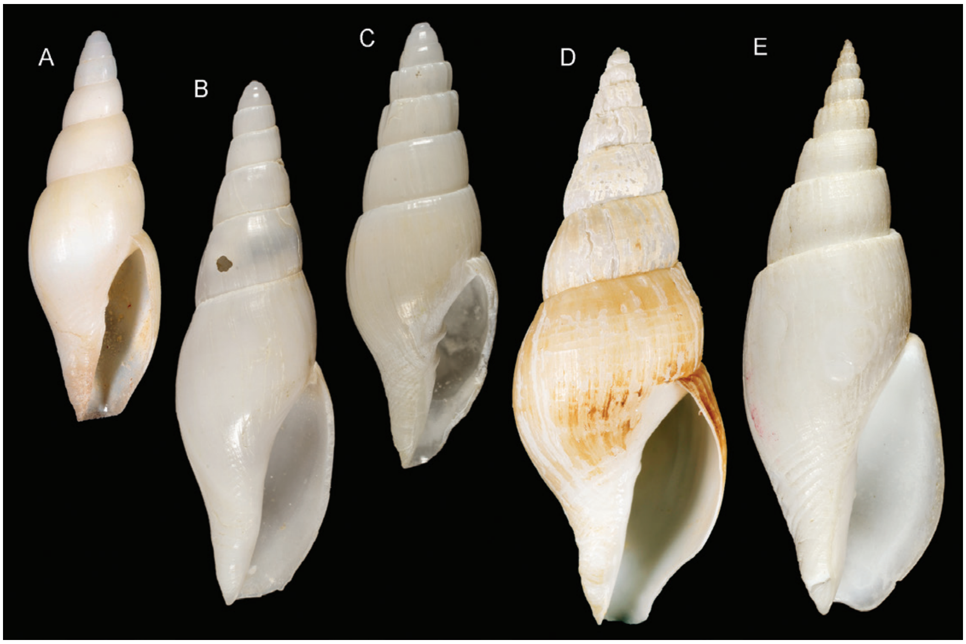

Figure 12. *Eumitra* species. A, *Eumitra apheles*, MNHN, New Caledonia, BATHUS 4 Stn 918, 18°49′S, 163°16′E, 613–637 m, 18.6 mm. B, *Eumitra caledonica*, holotype, MNHN-IM-2000-30181, Norfolk Ridge, BIOCAL Stn CP61, 24°11′S, 167°32′E, 1070 m, 29.9 mm, C, *Eumitra imbricata*, holotype, MNHN-IM-2000-30242,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

all studied species of *Profundimitra* gen. nov. 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 three or more 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. 12E) 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 are available, we maintain it in the genus *Eumitra* pending a 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 **GEN. NOV.**

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

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

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

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

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

GENUS *ZIBA* H. ADAMS & A. ADAMS, 1853

(FIGS 10F, 14A–D)

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

Diagnosis: Shell small (25–35 mm), elongate to fusiform, usually light brown to olive. Protoconch narrowly conical of about 2.5–3 smooth convex whorls. Suture distinct, impressed. 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

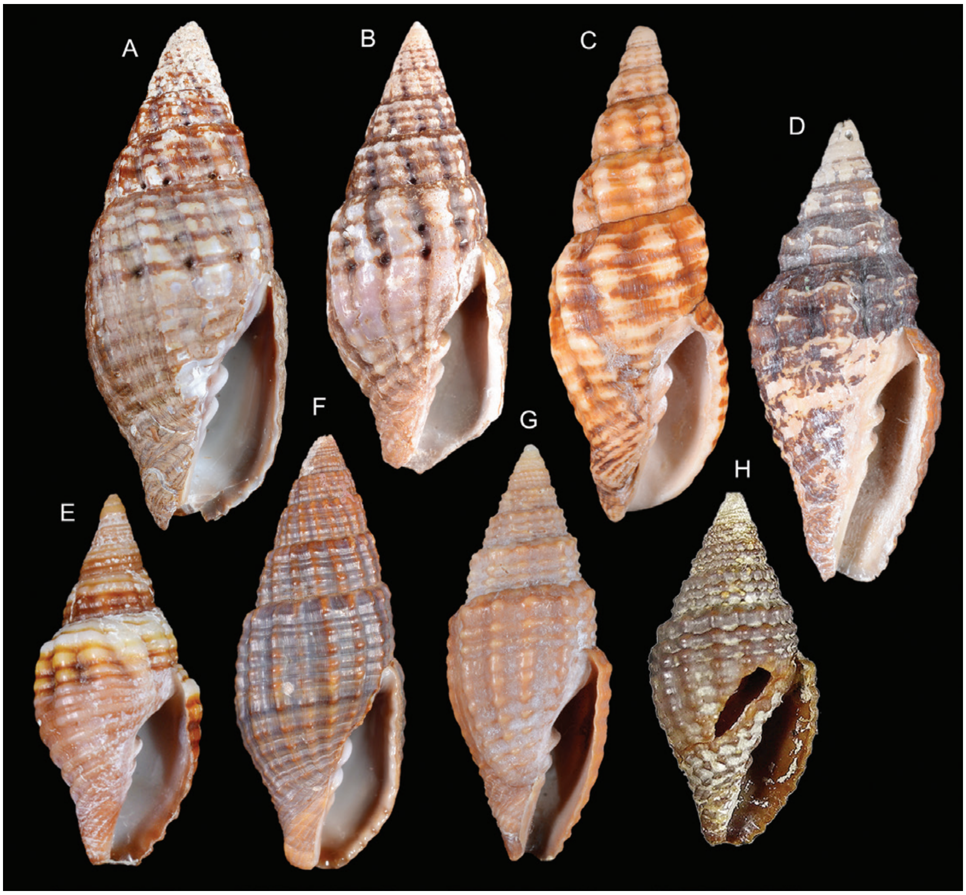

Figure 13. ***Neotiara* gen. nov.** species. A, B, ***Neotiara lens* comb. nov.**; A, neotype, MNHN IM-2000-33145, Panama, Panama City, 08°95′N, 79°53′W, intertidal, 40.0 mm; B, BAU 2532, same locality as previous, 33.6 mm. C, ***Neotiara lignaria* comb. nov.**, holotype, NHMUK 1967798, Sta Elena, Ecuador, 47.6 mm. D, ***Neotiara rupicola* comb. nov.**, syntype, NHMUK 1964460, Sta Elena, Ecuador, 37.2 mm. E, ***Neotiara gausapata* comb. nov.**, lectotype, NHMUK 1967769/1-2, Galapagos Is., 11.7 mm. F, ***Neotiara nodulosa* comb. nov.**, MNHN IM-2013-9546, Guadeloupe, KARUBENTHOS Stn GM10, 16°12.53′N, 61°25.55′W, 1 m, 27.8 mm. G, ***Neotiara muricata* comb. nov.**, lectotype, NHMUK 1967610/1-3, Galapagos Is., 29 mm. H, *Neotiara* aff. *inca*, BAU 0279-1, Panama, Venado Beach, 8°53.5′N, 79°36.4′W, intertidal, 11 mm.

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. 10F). Lateral teeth multicuspidate, 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)[1], *Z. gambiana* (Dohrn, 1861)[3], *Z. ogoouensis* Biraghi, 1984[3].

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 *Z. 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 *Z. carinata*–*Episcomitra* inferred in the 3-mit tree (though absent

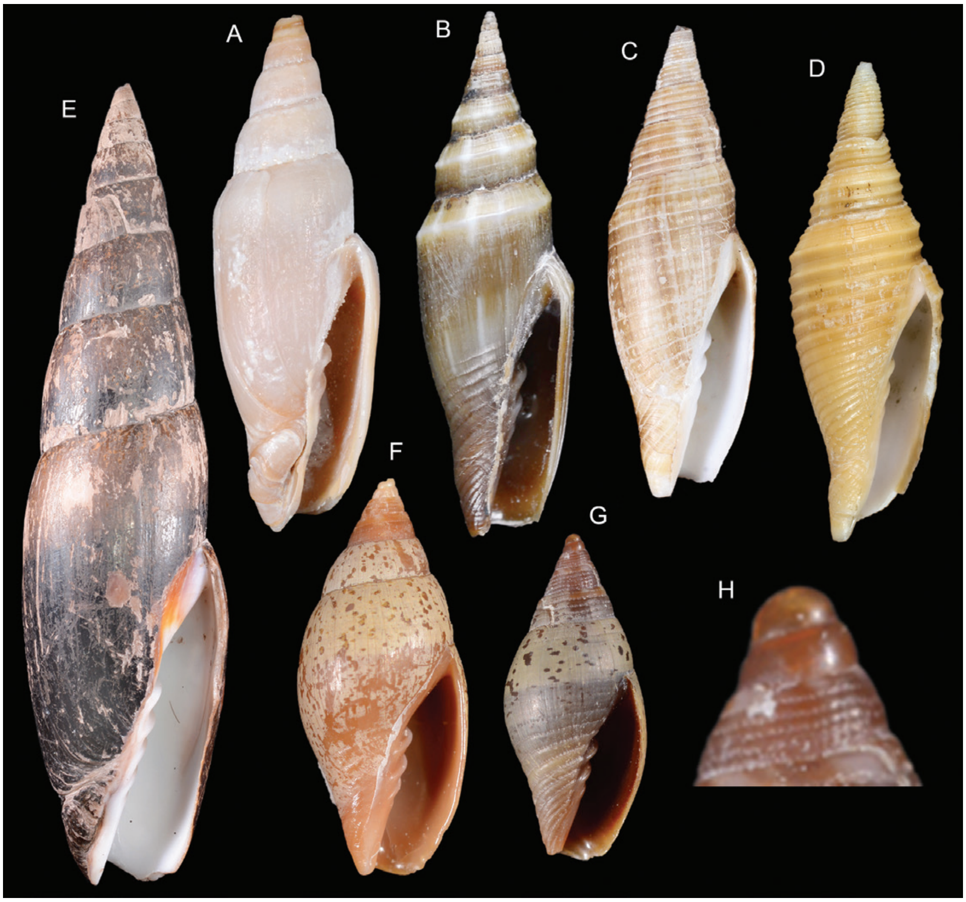

Figure 14. *Ziba* and *Episcomitra* species. A, B, *Ziba carinata*; A, lectotype of *Mitra senegalensis*, NHMUK 1967881, Senegal, 27.9 mm; B, MNHN IM-2013-40647, Congo, Mission ZANAGA, Stn 531DW, 04°43.0′S 11°47.0′E, 17 m, 24.5 mm. C, *Ziba gambiana*, syntype, NHMUK 1967768, 'Senegambia', 28 mm. D, *Ziba ogoouensis*, holotype, MNHN-IM-2000-30269, off Gabon, 20–50 m, 28.8 mm. E, *Episcomitra zonata,* BAU2538, Italy, off Chioggia, 45°12′N, 12°40′E, 40 m, 96.2 mm. F–H, ***Episcomitra cornicula* comb. nov.**; 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.

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 10G, H, 14E–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 two 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 groove. Siphonal notch deep or rather shallow. Outer aperture lip evenly convex, or convex in its adapical portion and straight throughout most of its length. Inner aperture lip with four, fine, subequal columellar folds. Shell covered with periostracum, light brown to dark brown or olive-green, uniform or with multiple dark freckles, or (typically) adapical 2/3 of spire whorls slightly lighter than their abapical portions. Inside of aperture white or orange. Rachidian with six to eight pointed cusps, increasing in length towards centre; laterals wide, bearing rather long and pointed cusps throughout their length (Fig. 10G, H).

Species included: *Episcomitra cornicula* (Linnaeus, 1758)[1] comb. nov., *E. zonata* (Marryat, 1818)[1].

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

GENUS ***QUASIMITRA*** FEDOSOV, HERRMANN, KANTOR & BOUCHET **GEN. NOV.**

(FIGS 10I–M, 15)

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

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

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

Species included: *Quasimitra albocarnea* (Bozzetti, 2016)[3] comb. nov., *Q. barbieri* (Poppe & Tagaro, 2006)[3] comb. nov., *Q. bovei* (Kiener, 1838)[3] comb. nov., *Q. brettinghami* (E.A. Smith, 1906)[3] comb. nov., *Q. cardinalis* (Gmelin, 1791)[1] comb. nov., *Q. floccata* (Reeve, 1844)[3] comb. nov., *Q. fulgurita* (Reeve, 1844)[3] comb. nov., *Q. lacunosa* (Reeve, 1844)[3] comb. nov., *Q. lamarckii* (Deshayes, 1832)[3] comb. nov., *Q. latruncularia* (Reeve, 1844)[3] comb. nov., *Q. leforti* (Turner, 2007)[3] comb. nov., *Q. manuellae* (Cossignani & Cossignani, 2006)[3] comb. nov., *Q. marmorea* (Turner, 2007)[3] comb. nov., *Q. nubila* (Gmelin, 1791)[3] comb. nov., *Q. nympha* (Reeve, 1845)[3] comb. nov., *Q. propinqua* (A. Adams, 1853)[3] comb. nov., *Q. pseudobovei* (T. Cossignani & V. Cossignani, 2005)[3] comb. nov., *Q. puncticulata* (Lamarck, 1811)[1] comb. nov., *Q. punctostriata* (A. Adams, 1855)[3] comb. nov., *Q. raphaeli* (Drivas & Jay, 1990)[3] comb. nov., *Q. rinaldii* (Turner, 1993)[3] comb. nov., *Q. roselineae* (Martin & Salisbury, 2013)[3] comb. nov., *Q. rossiae* (Reeve, 1844)[3] comb. nov., *Q. sanguinolenta* (Lamarck, 1811)[1] comb. nov., *Q. sarmientoi* (Poppe, 2008)[3] comb. nov., *Q. solida* (Reeve, 1844)[3] comb. nov., *Q. sophiae* (Crosse, 1862)[1] comb. nov., *Q. stossieri* (Herrmann, 2016)[3] comb. nov., *Q. structilis* (Herrmann & Salisbury, 2016)[3] comb. nov., *Q. variabilis* (Reeve, 1844)[3] comb. nov.

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

Remarks: The genus *Quasimitra* gen. nov. 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 *M. solida*, despite *V. prosphora* has a smooth, uniformly pale shell, and only superficially resembles *M. solida* and the other sequenced species here assigned to *Quasimitra*. At present, we treat *V. prosphora* 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.

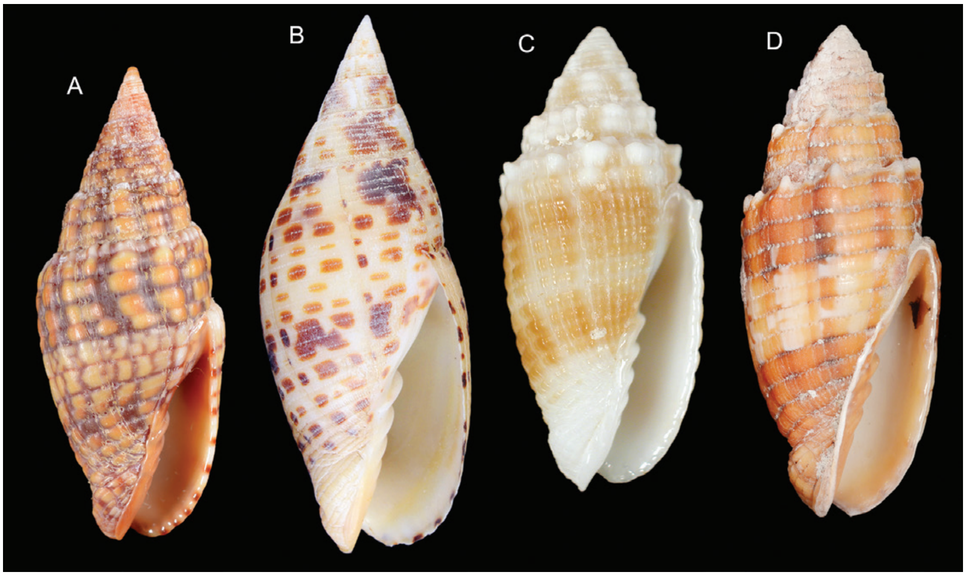

Figure 15. ***Quasimitra*** species. A, ***Quasimitra sanguinolenta* comb. nov.**, MNHN IM-2013-40677, Mozambique, INHACA 2011 Stn MS02, 26°06.3′S, 32°58.0′E, 17–19 m, 28.7 mm. B, ***Quasimitra cardinalis* comb. nov.**, MNHN IM-2013-40681, Papua New Guinea, KAVIENG 2014 Stn KR178, 02°45.2′S 150°43.1′E,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

GENUS *DOMIPORTA* CERNOHORSKY, 1970

(FIGS 16A–E, 17A–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, cyrtoconoid, of nearly five 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 three to four 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 (Fig. 17A–D).

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

Species included: *Domiporta aglais*[3] (Li & Zhang, 2005), *D. carnicolor* (Reeve, 1844)[1], *D. circula* (Kiener, 1838)[1] comb. nov., *D. daidaleosa* (Li & Li, 2005)[3] comb. nov., *D. filaris* (Linnaeus, 1771)[1], *D. gloriola* (Cernohorsky, 1970)[3], *D. granatina* (Lamarck, 1811)[1], *D. hebes* (Reeve, 1845)[2] comb. nov., *D. latistriata* (Herrmann & Salisbury, 2012)[3] comb. nov., *D. lichtlei* (Herrmann & Salisbury, 2012)[3] comb. nov., *C. manoui* (Huang, 2011)[3] comb. nov., *D. praestantissima* (Röding, 1798)[1], *D. shikamai* Habe, 1980[3], *D. sigillata* (Azuma, 1965)[3], *D. valdacantamessae* Maxwell, Dekkers, Berschauer & Congdon, 2017[3].

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, *D. 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* gen. nov.

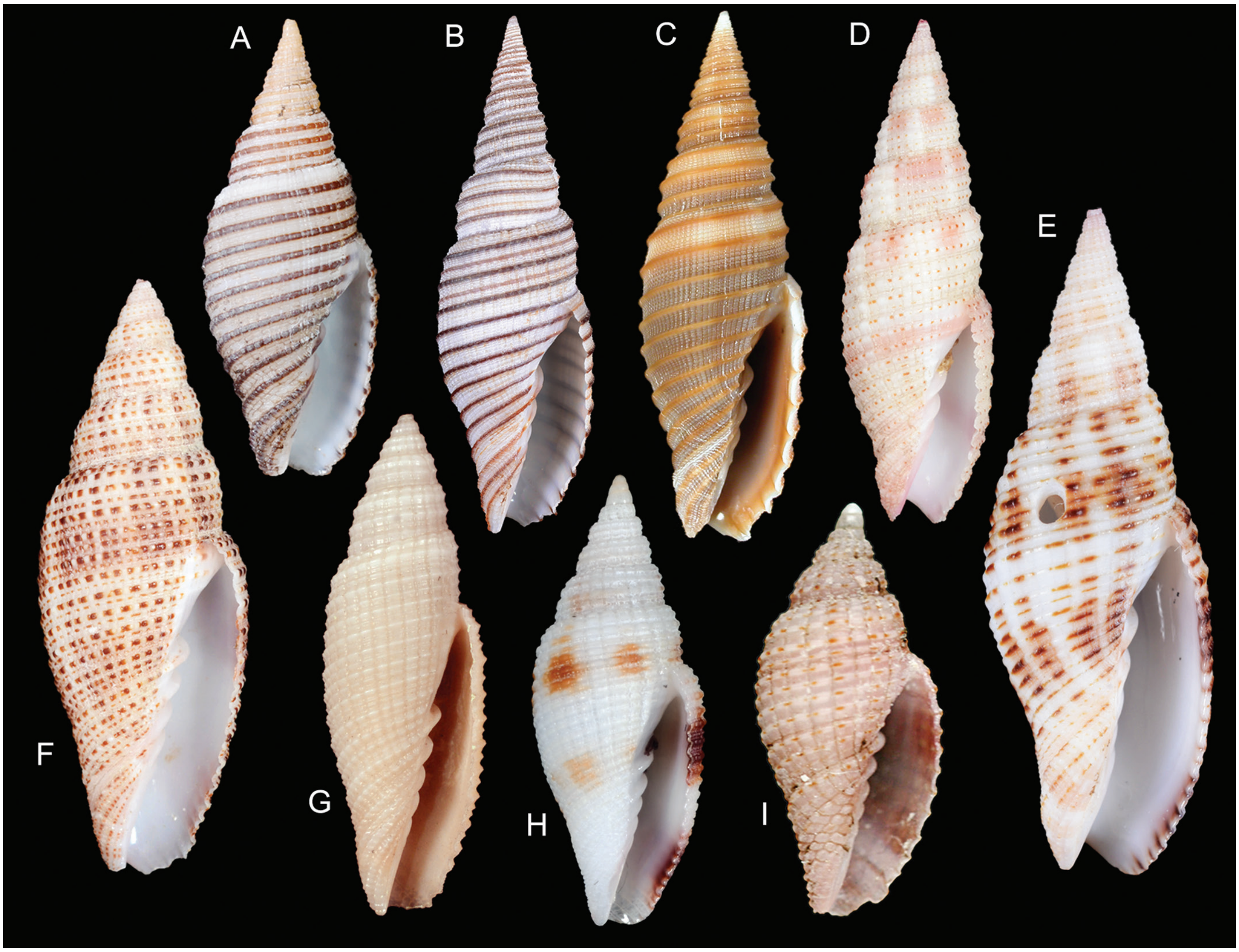

Figure 16. Species of *Domiporta* and ***Roseomitra* gen. nov.**. A, *Domiporta filaris*, MNHN IM-2013-12956, Papua New Guinea, PAPUA NIUGINI Stn PD 23, 05°06′S, 145°49.2′E, 3–7 m, 15.8 mm. B, ***Domiporta praestantissima* comb. nov.**, MNHN IM-2013-40642, Vietnam, Nha-Trang Bay, West of Mun Is., 12°10.1′N, 109°17.8′E, 6–18 m, 25.6 mm. C, *Domiporta circula*, MNHN IM-2007-30018, Vanuatu, SANTO 2006 Stn LD24, 15°31.4′S, 167°10.0′E, 47 m. D, *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. E, *Domiporta 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* comb. nov.**, 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, ***Roseomitra incarnata* comb. nov.**, lectotype, NHMUK 196779/1-3, Misamis Is., Mindanao, Philippines, 21.6 mm. H, ***Roseomitra tagaroae* comb. nov.**, Philippines, Olango Channel, dredged from 80 m, 9.5 mm. I, ***Roseomitra rosacea* comb. nov.**, Mozambique, INHACA 2011 Stn MD13, 26°03.1′S 33°01.0′E, 50–53 m, 7.9 mm.

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* gen. nov. Four species of *Domiporta* depart notably in radular morphology, showing a transition from rather typical mitrine radula in *D. filaris* 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 **GEN. NOV.**

(FIGS 16F–I, 17E, 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 three or more smooth, glossy, slightly convex whorls. Suture distinct, slightly impressed. Spire rather

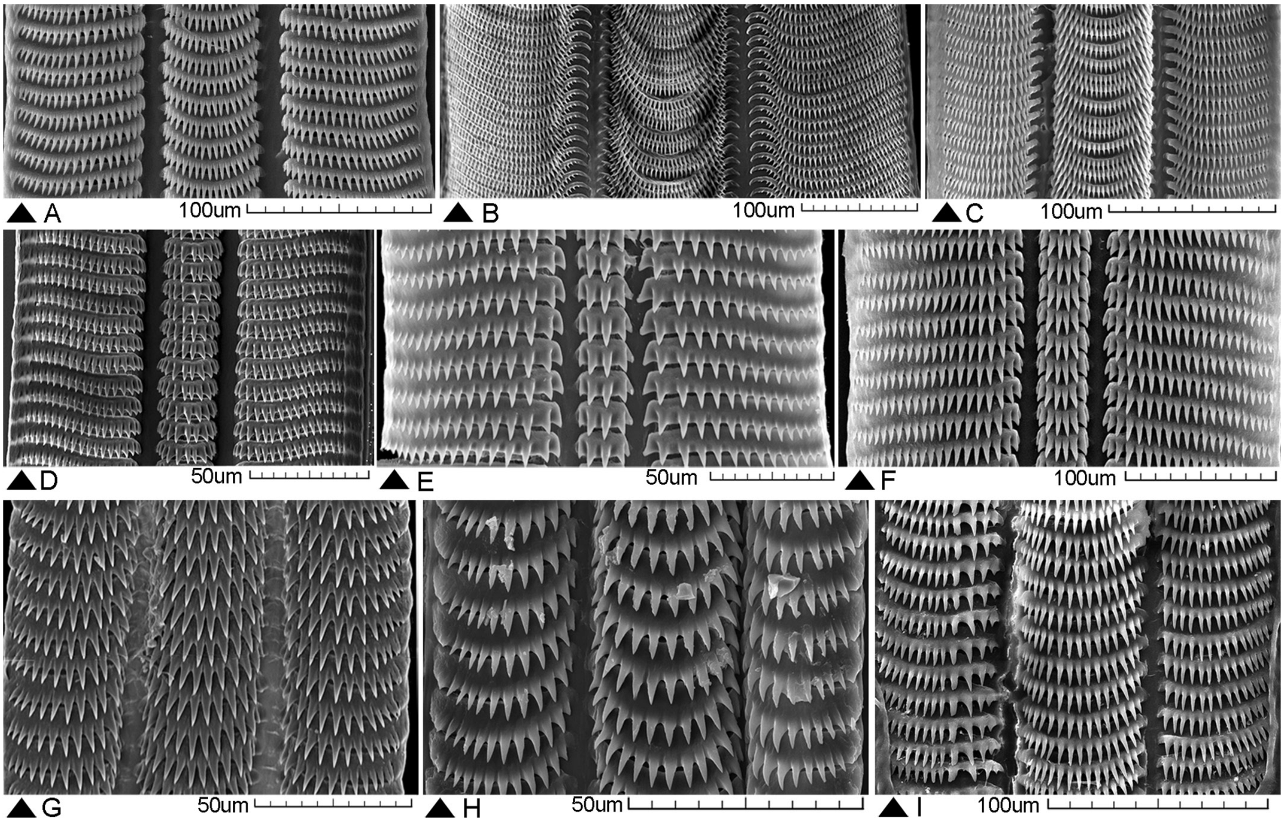

Figure 17. Radulae in the *Domiporta* clade. A, *Domiporta* cf. *carnicolor*, MNHN IM-2013-40684, Philippines, off Noc-Nocan Is., 10°15.1′N, 124°25.1′E, 4–12 m, 23.9 mm. B, *Domiporta granatina*, MNHN IM-2013-40641, Mozambique, INHACA 2011 Stn MR15, 26°00.0′S, 32°54.4′E, 4 m, 34.2 mm. C, *Domiporta praestantissima*, 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, *Domiporta filaris*, MNHN, Mozambique, INHACA 2011 Stn MR13, 25°59.7′S, 32°54.5′E, 2–5 m, 17.4 mm. E, ***Roseomitra rosacea* comb. nov.**, MNHN, Mozambique, INHACA 2011 Stn MD13, 26°03.1′S, 33°01.0′E, 50–53 m, 7.9 mm. F, ***Roseomitra millepunctata* comb. nov.**, 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* sp. nov.**, 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* sp. nov., MNHN, IM-2013-40654, New Caledonia, EXBODI Stn CP3829, 22°02′S, 167°05′E, 350–360 m, 16.9 mm. I, ***Fusidomiporta ponderi* sp. nov.**, holotype, MNHN IM-2013-40665, Papua New Guinea, BIOPAPUA Stn CP3692, 02°10′S, 147°19′E, 408–448 m, 25.2 mm.

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 five to eight subequal cusps and wide laterals with narrow base and 15–21 moderately long pointed cusps (Fig. 17E, F).

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

Species included: *Roseomitra citharoidea* (Dohrn, 1862)[3] comb. nov., *R. earlei* (Cernohorsky, 1977)[3] comb. nov., *R. fluctuosa* (Herrmann & Salisbury, 2013)[3] comb. nov., *R. honkeri* (Poppe, Tagaro & Salisbury, 2009)[3] comb. nov., *R. incarnata* (Reeve, 1845)[3] comb. nov., *R. millepunctata* (G. B. Sowerby III, 1889)[1] comb. nov., *R. reticulata* (A. Adams, 1853)[3] comb. nov., *R. rosacea* (Reeve, 1845)[1] comb. nov., *R. roseovitta* (Huang, 2011)[3] comb. nov., *R. strangei* (Angas, 1867)[3] comb. nov., *R. tagaroae* (Poppe, 2008)[3] 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 *M. 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 × 11.4 mm (Fig. 16F) as neotype of *M. millepunctata*. This specimen was collected off Noc-nocan Is., Central Philippines, at the type locality of *Mitra terryni*, a junior synonym (Herrmann, 2017) of *M. millepunctata*.

Species of the genus *Roseomitra* gen. nov. 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* gen. nov. 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* gen. nov. In turn, *Condylomitra tuberosa, C. bernhardina* and *Quasimitra sophiae* have a notably stronger sculpture compared to *Roseomitra* spp.

GENUS ***PROFUNDIMITRA*** FEDOSOV, HERRMANN, KANTOR & BOUCHET **GEN. NOV.**

(FIGS 17G, H, 18A–H)

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

Diagnosis: Small shell (20–35 mm), thin walled, fusiform or elongate-fusiform, with high orthoconoid or slightly acuminate spire. Protoconch pale, semi-translucent, narrowly conical with three or more 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 (Fig. 17G, H).

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

Species included: *Profundimitra abyssicola* (Schepman, 1911)[3] comb. nov., *Profundimitra planofilum* (Huang, 2011)[1] comb. nov., *P. taylori* sp. nov.[1].

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 *P. planofilum* has a name. The latter was initially described in *Cancilla*, and indeed the sculpture pattern and light brown marks on spiral cords of *P. planofilum* strikingly resemble the pattern seen in species of *Cancilla*. *Profundimitra 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* gen. nov., but most likely not conspecific with the lectotype, while others obviously represent true *Cancilla* or *Imbricaria* as circumscribed here.

The genus *Profundimitra* gen. nov. can be recognized by the elongate, typically weakly sculptured shell, either white or pale, sometimes covered with light brown periostracum. The genus *Calcimitra* is closest to *Profundimitra* gen. nov. 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* gen. nov. is *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* gen. nov. have three or more 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

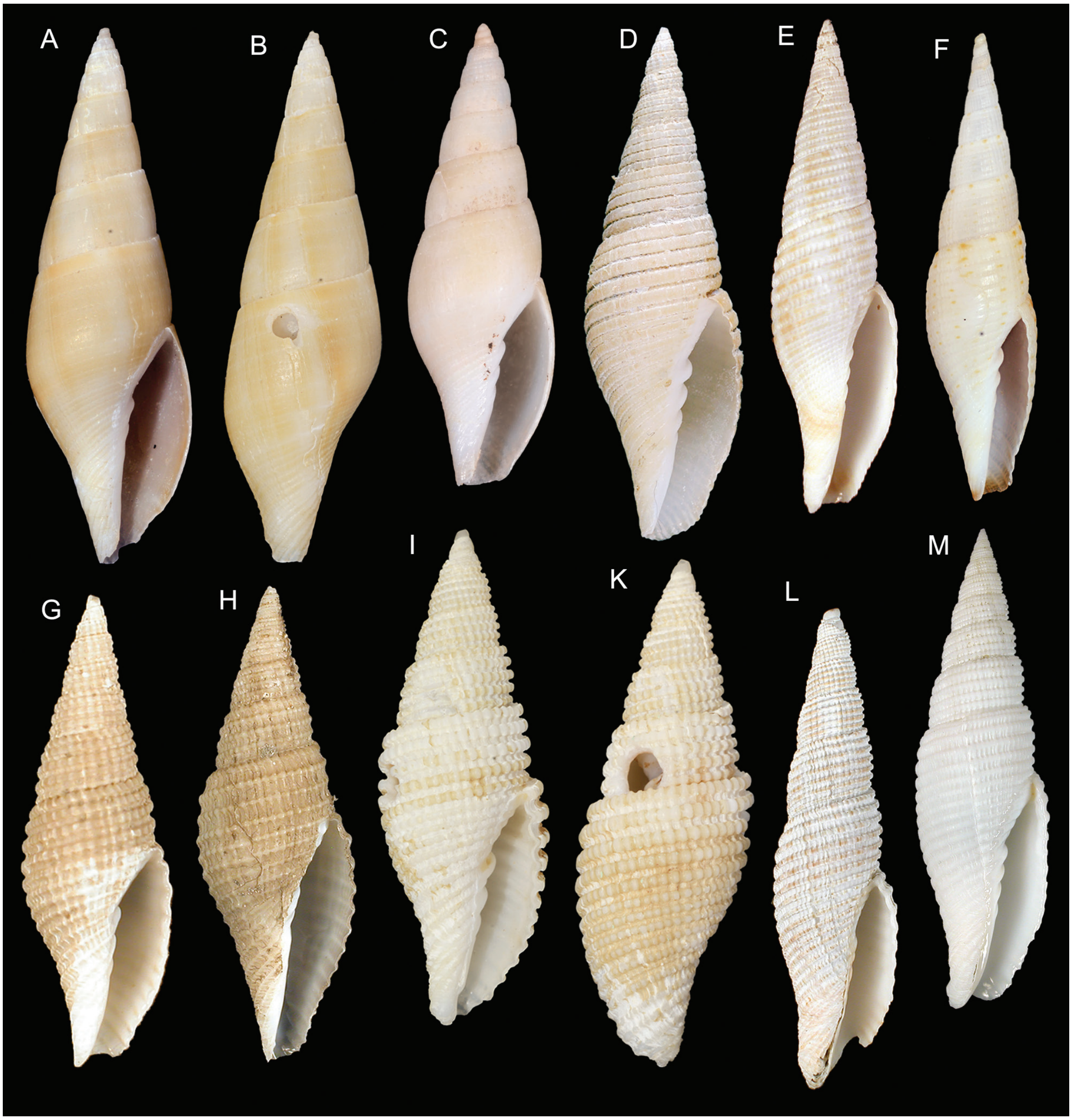

Figure 18. Species of ***Profundimitra*** **gen. nov.**, ***Fusidomiporta*** **gen. nov.** and ***Cancillopsis*** **gen. nov.** A–C, ***Profundimitra taylori*** **sp. nov.**; A, B, holotype, MNHN IM-2013-40651, Papua New Guinea, BIOPAPUA Stn CP3671, 04°04′S, 151°56′E, 585–601 m, 24.2 mm; C, New Caledonia,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

very low, cyrtoconoid, and not clearly delimited from teleoconch. Moreover, *Profundimitra* gen. nov. 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 **GEN. NOV.**

(FIGS 17I, 18I–L)

Type species: *Fusidomiporta ponderi* sp. nov.; 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 three or more whorls usually strongly corroded or missing. Suture canaliculated; 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: *Fusidomiporta ponderi* sp. nov.[1], ?*F. suturata* (Reeve, 1845)[3] comb. nov.

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.

Remarks: Morphologically, *F. ponderi* sp. nov. falls within the range of variation seen in *Profundimitra* gen. nov., 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 *F. ponderi* sp. nov. was thus totally unexpected. However, none of the single-gene analyses placed *F. ponderi* sp. nov. in the same molecular clade as *Profundimitra*, and a *Fusidomiporta–Profundimitra* grouping is only present in the three gene-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* gen. nov. is also observed in species of *Gemmulimitra* gen. nov. (*G. neocaledonica* sp. nov. and *G. boucheti*); however, *Gemmulimitra* differs notably from *Fusidomiporta* in radula morphology, showing a classical mitrid radula with a narrow rachidian (Fig. 20F, G).

GENUS ***CANCILLOPSIS*** FEDOSOV, HERRMANN, KANTOR & BOUCHET **GEN. NOV.**

(FIG. 18M)

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 three glossy whorls. Teleoconch of up to ten 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)[1] comb. nov., †*C. acuminata* (Shuto, 1969)[3] comb. nov.

Etymology: The name *Cancillopsis* refers to the close resemblance between *C. meimiaoae*, the type species of the new genus, and species of *Cancilla*. Gender feminine.

Remarks: *Cancillopsis meimiaoae* shows a notable resemblance to the species of the imbricariine genus *Cancilla* as well as to the species of *Profundimitra* gen. nov. and *Fusidomiporta* gen. nov., while showing no phylogenetic affinity to either of them. A visible concavity at the transition of shell base to the siphonal canal distinguishes the new genus from similarly sculptured *Cancilla* species. We hypothesize that *Cancillopsis* gen. nov. is more closely related to the *Domiporta* group of Mitrinae, and so we provisionally place it in Mitrinae. However, a more comprehensive taxon sampling of the deep-water Mitridae is obviously needed to delineate these convergent deep-water lineages and to clarify affinities of *Cancillopsis* gen. nov.

GENUS ***PSEUDONEBULARIA*** FEDOSOV, HERRMANN, KANTOR & BOUCHET **GEN. NOV.**

(FIGS 19, 20A–E)

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

Diagnosis: Shell small (9–30 mm), fusiform or broadly fusiform to biconical, vividly coloured. Protoconch pointed, narrowly conical, of about three slightly convex, glossy whorls. Suture slightly impressed, often indistinct. Teleoconch whorls evenly convex or flattened, sometimes giving the spire a distinctly stepped profile. Sculpture of strong, rounded spiral cords, regularly interspaced and covering the entire shell or, rarely, limited to shell base. Interspaces between cords concave, smooth or bearing fine, dense riblets. Siphonal canal moderately long, stout, siphonal notch shallow or absent. Aperture rather narrow, elongate, with undulating outer lip, sometimes bearing rounded denticles on its inside. Inner lip calloused, often reflected, with three to four strong columellar folds, adapicalmost strongest. Radula with broad laterals, bearing equal, rather long, widely set cusps throughout their width; rachidian not exceeding half the width of the laterals, multi- or unicuspidate (Fig. 20A–E).

Distribution: Indo-Pacific, intertidal to upper subtidal depths, rocky flats, reef crevices and coral rubble.

Species included: *Pseudonebularia atjehensis* (Oostingh, 1939)[1] comb. nov., *P. chrysalis* (Reeve, 1844)[3] comb. nov., *P. cingulata* (A. Adams, 1853)[3] comb. nov., *P. connectens* (Dautzenberg & Bouge, 1923)[1] comb. nov., *P. cucumerina* (Lamarck, 1811)[3] comb. nov., *P. cuyosae* (Poppe, 2008)[3] comb. nov., *P. damasomonteiroi* (Cossignani & Cossignani, 2007)[3] comb. nov., *P. doliolum* (Küster, 1839)[3] comb. nov., *P. dovpeledi* (Turner, 1997)[3] comb. nov., *P. fraga* (Quoy & Gaimard, 1833)[2] comb. nov., *P. gracilefragum* (Turner, 2007)[2] comb. nov., *P. indentata* (G. B. Sowerby II, 1874)[3] comb. nov., *P. kantori* (Poppe, Tagaro & Salisbury, 2009)[3] comb. nov., *P. kilburni* (Poppe, Tagaro & Salisbury, 2009)[3] comb. nov., *P. lienardi* (G. B. Sowerby II, 1874)[3] comb. nov., *P. maesta* (Reeve, 1845)[1] comb. nov., *P. oliverai* (Poppe, 2008)[3] comb. nov., *P. pediculus* (Lamarck, 1811)[1] comb. nov., *P. perdulca* (Poppe, Tagaro & Salisbury, 2009)[3] comb. nov., *P. proscissa* (Reeve, 1844)[3] comb. nov., *P. rotundilirata* (Reeve, 1844)[3] comb. nov., *P. rubiginea* (A. Adams, 1855)[3] comb. nov., *P. rubritincta* (Reeve, 1844)[3] comb. nov., *P. rueppellii* (Reeve, 1844)[3] comb. nov., *P. rutila* (A. Adams, 1853)[3] comb. nov., *P. sarinoae* (Poppe, 2008)[3] comb. nov., *P. semiferruginea* (Reeve, 1845)[3] comb. nov., *P. silviae* (Turner, 2007)[3] comb. nov., *P. tabanula* (Lamarck, 1811)[1] comb. nov., *P. tornata* (Reeve, 1845)[1] comb. nov., *P. wareni* (Poppe, Tagaro & Salisbury, 2009)[3] comb. nov., *P. willani* (Poppe, Tagaro & Salisbury, 2009)[3] comb. nov., *P. yayanae* (Huang, 2011)[3] comb. nov.

Etymology: *Pseudonebularia* means 'false *Nebularia*' and refers to the long accepted, and erroneous, placement of the included species in *Nebularia*, which it resembles superficially. Gender feminine.

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

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

GENUS ***GEMMULIMITRA*** FEDOSOV, HERRMANN, KANTOR & BOUCHET **GEN. NOV.**

(FIGS 20F, G, 21)

Type species: *Gemmulimitra neocaledonica* sp. nov.; 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): Shell small (about 20–25 mm), elongate-fusiform to almost biconical. Protoconch multispiral, of three or more slightly convex, glossy whorls. Suture canaliculated.

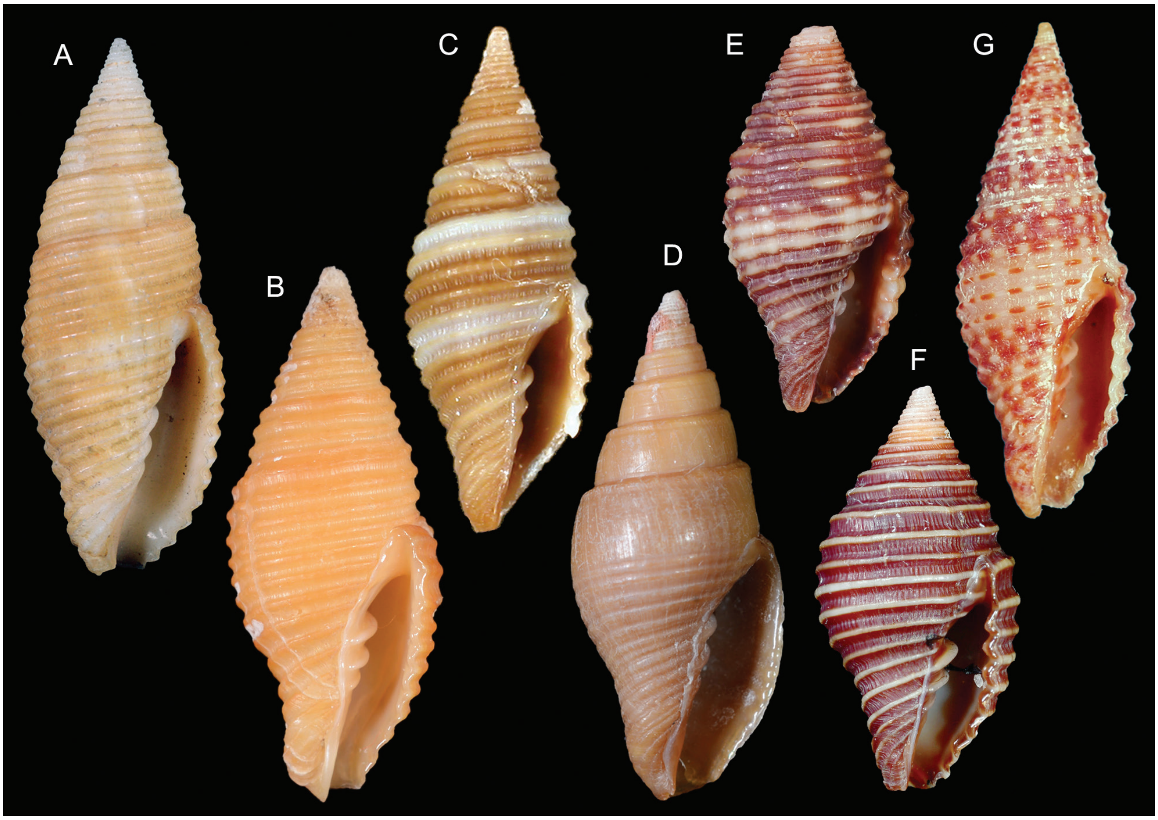

Figure 19. Species of ***Pseudonebularia* gen. nov**. A, B, ***Pseudonebularia tornata* comb. nov.**; A, lectotype of *Mitra tornata*, NHMUK 1967897, Philippines, 18.1 mm; **B**, MNHN IM-2013-12538, PAPUA NIUGINI Stn PB14, 05°13.8′S, 145°48′E, 15 m, 16.5 mm. C, ***Pseudonebularia atjehensis* comb. nov.**,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

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 eight 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)^{3} comb. nov., *G. apprimapex* (Poppe, Tagaro & Salisbury, 2009)^{3} comb. nov., *G. avenacea* (Reeve, 1845)^{1} comb. nov., *G. boucheti* (Cernohorsky, 1988)^{2} comb. nov., *G. duplilirata* (Reeve, 1845)^{3} comb. nov., *G. edgari* (Poppe, Tagaro & Salisbury, 2009)^{3} comb. nov., *G. gonatophora* (Sturany, 1903)^{3} comb. nov., *G. hansturneri* (E. Guillot de Suduiraut & E.G. Guillot de Suduiraut, 2009)^{3} comb. nov., *G. margaritata* (Poppe, Tagaro & Salisbury, 2009)^{3} comb. nov., *G. neocaledonica* sp. nov.^{1}, *G. rubiginosa* (Reeve, 1844)^{3} comb. nov., *G. solanderi* (Reeve, 1844)^{3} comb. nov., *G. strongae* (Poppe, Tagaro & Salisbury, 2009)^{1} comb. nov.

Etymology: The genus name refers to the sculpture of gemmate cords that characterizes many species in this

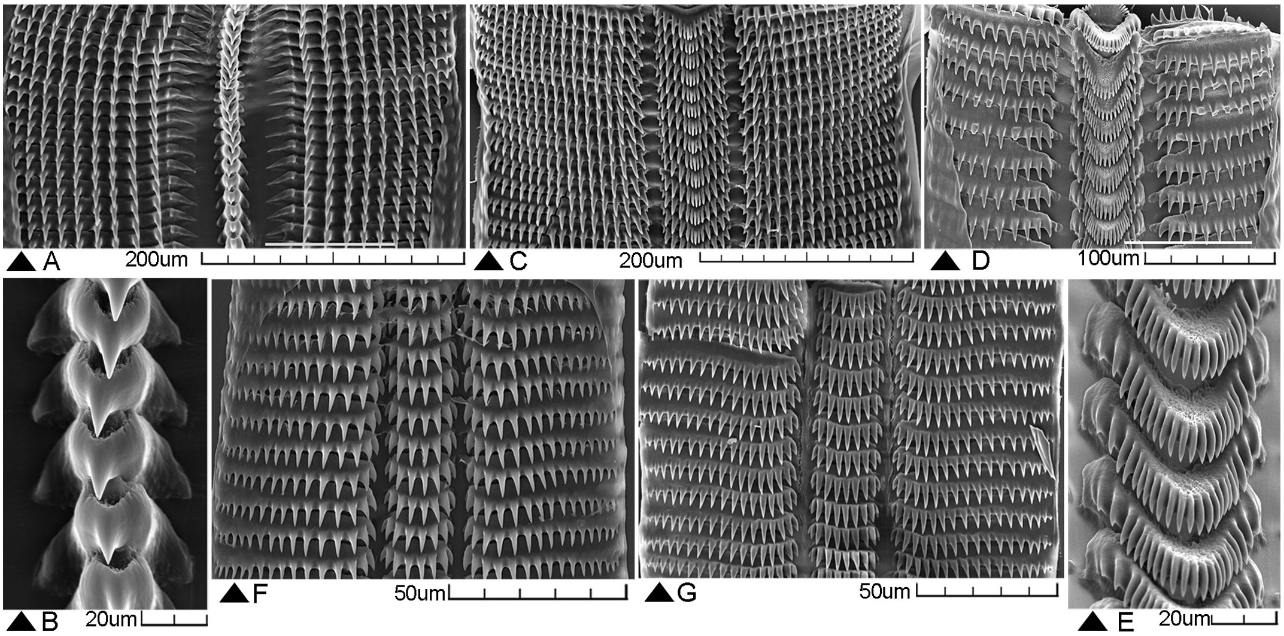

Figure 20. Radulae of ***Pseudonebularia* gen. nov.** and ***Gemmulimitra* gen. nov.** A, B, ***Pseudonebularia pediculus* comb. nov.**, MNHN IM-2013-12705, PAPUA NIUGINI Stn PB15, 05°04.7′S, 145°48.9′E, 5 m, 11.6 mm. C, ***Pseudonebularia connectens* comb. nov.**, MNHN IM-2013-2342, PAPUA NIUGINI Stn PB16, 05°10.7′S, 145°47.7′E, intertidal, 10.4 mm. D, E, ***Pseudonebularia maesta* comb. nov.**, 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* sp. nov.**, MNHN, Paratype 5, New Caledonia, EXBODI Stn CP3814, 21°49′S, 166°44′E, 331–344 m, 20.4 mm. G, ***Gemmulimitra boucheti* comb. nov.**, MNHN IM-2013-40649, Papua New Guinea, BIOPAPUA Stn DW3641, 06°45′S, 148°01′E, 380–476 m, 11.6 mm.

newly recognized lineage, including the type species *G. neocaledonica*.

Remarks: *Gemmulimitra neocaledonica* sp. nov. 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 *G. strongae* that is close to *G. neocaledonica* sp. nov. 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 *G. neocaledonica* sp. nov., *G. boucheti* (Fig. 21C), *G. strongae* (Fig. 21D) 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. 21E), *G. edgari* and *G. rubiginosa* (Fig. 21F). Species of the first group closely resemble *Fusidomiporta ponderi* sp. nov., 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* gen. nov. and elaborate its diagnosis.

Subfamily Strigatellinae Troschel, 1869

(Figs 22, 23)

Genus *Strigatella* Swainson, 1840

Type species: *Mitra zebra* Lamarck, 1811; 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 to three smooth, very slightly convex whorls. Suture deeply impressed. Spire whorls

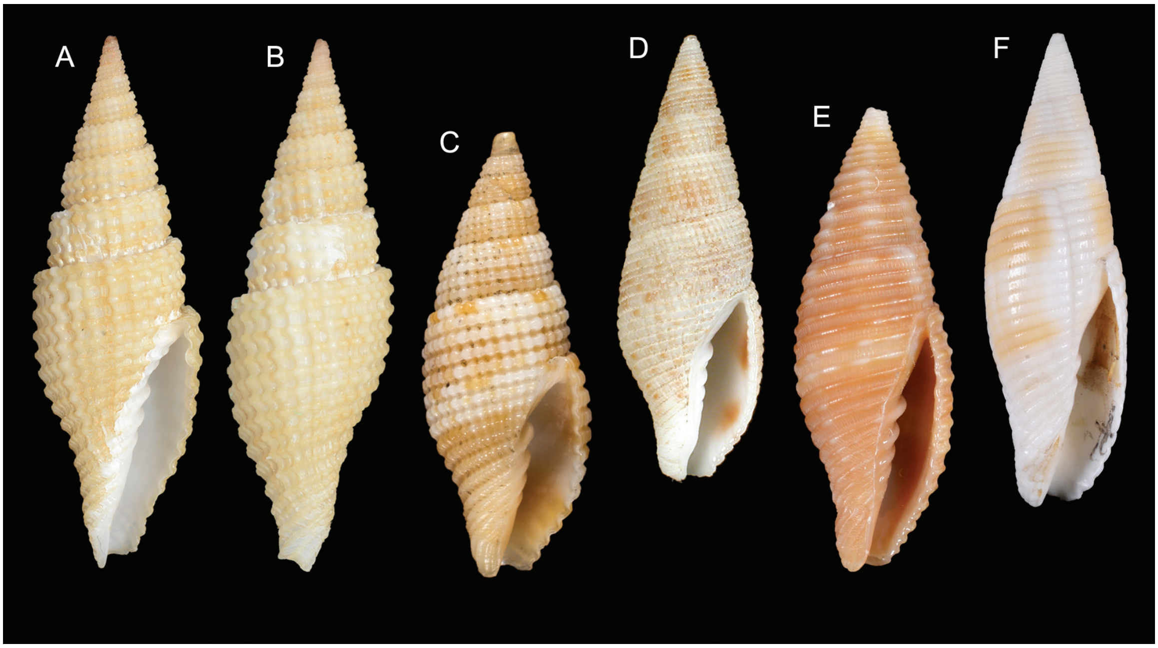

Figure 21. Species of ***Gemmulimitra* gen. nov.** A, B, ***Gemmulimitra neocaledonica* sp. nov.**, holotype, MNHN IM-2013-40655, New Caledonia, EXBODI Stn CP3821, 21°53′S, 166°50′E, 211–440 m, 24.25 mm. C, ***Gemmulimitra boucheti* comb. nov.**, holotype, MNHN IM-2000–30172, Réunion, MD32, Stn DC41,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

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 three to five 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 five to seven 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 seven to ten 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 abacophora* (Melvill, 1888)[3] comb. nov., *S. amaura* (Hervier, 1897)[3], *S. ambigua* (Swainson, 1829)[3] comb. nov., *S. assimilis* (Pease, 1868)[3], *S. aurantia* (Gmelin, 1791)[1] comb. nov., *S. auriculoides* (Reeve, 1845)[3], *S. aurora* (Dohrn, 1861)[2] comb. nov., *S. colombelliformis* (Kiener, 1838)[2], *S. coronata* (Lamarck, 1811)[1] comb. nov., *S. crassicostata* (G. B. Sowerby II, 1874)[3] comb. nov., *S. decurtata* (Reeve, 1844)[1], *S. fasciolaris* (Deshayes, 1834)[3] comb. nov., *S. flavocingulata* (Lamy, 1938)[3], *S. fulvescens* (Broderip, 1836)[1] comb. nov., *S. holkosa* (B.Q. Li, 2005)[3] comb. nov., *S. imperialis* (Röding, 1798)[1] comb. nov., *S. litterata* (Lamarck, 1811)[1], *S. luctuosa* (A. Adams, 1853)[1], *S. lugubris* (Swainson, 1821)[1] comb. nov., *S. nana* (Reeve, 1844)[3] comb. nov., *S. paupercula* (Linnaeus, 1758)[1], *S. pica* (Dillwyn, 1817)[3], *S. retusa* (Lamarck, 1811)[3], *S. scutulata* (Gmelin, 1791)[1] comb. nov., *S. subruppeli* (Finlay, 1927)[3] comb. nov., *S. telescopium* (Reeve, 1844)[3], *S. testacea* (Broderip, 1836)[3] comb. nov., *S. ticaonica* (Reeve, 1844)[3] comb. nov., *S. tristis* (Broderip, 1836)[1], *S. vexillum* (Reeve, 1844)[1], *S. vultuosa* (Reeve, 1845)[3] comb. nov., ?*S. coffea* (Schubert & J. A. Wagner, 1829)[2] comb. nov., ?*S. pudica* (Pease, 1860)[2], ?*S. tabida* (Herrmann & Salisbury, 2013)[3] comb. nov., *S. zebra* (Lamarck, 1811)[1].

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, *Strigatella litterata*, MNHN IM-2013-12959, PAPUA NIUGINI Stn PM22, 05°04.7′S, 145°48.9′E, intertidal, 16.0 mm. C, *Strigatella decurtata*, MNHN IM-2013-15843, PAPUA NIUGINI Stn PM41, 05°08.1′S, 145°49.3′E, 0–1 m, 22.1 mm. D, ***Strigatella scutulata* comb. nov.**, MNHN IM-2013-12771, PAPUA NIUGINI Stn PM22, 05°04.7′S, 145°48.9′E, intertidal, 24.7 mm. E, ***Strigatella aurantia* comb. nov.**, 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, *Strigatella luctuosa*, MNHN IM-2013-11682, PAPUA NIUGINI Stn PR14, 05°12′S, 145°48.1′E, 2–3 m, 20.9 mm. H, *Strigatella vexillum*, MNHN IM-2013-12570, PAPUA NIUGINI Stn PR24, 05°12.3′S 145°48.8′E, 24.0 mm. I, ***Strigatella imperialis* comb. nov.**, MNHN IM-2007-30173, Vanuatu, SANTO 2006 Stn FR01, 15°32.3′S, 167°13.1′E, 18–20 m. K, ***Strigatella fulvescens* comb. nov.**, MNHN IM-2013-40680, TUHAA PAE Stn AMA03, 21°48.2′S, 154°43.2′W, 26 m, 25.5 mm. L, ***Strigatella lugubris* comb. nov.**, MNHN IM-2013-40678, Austral Is., TUHAA PAE Stn AT07, 23°19.7′S 149°29.3′W, 14 m, 13.7 mm. M, ***Strigatella coronata* comb. nov.**, MNHN IM-2013-30023, Vanuatu, SANTO 2006 Stn VM36, 15°27.5′S, 167°15.4′E, intertidal.

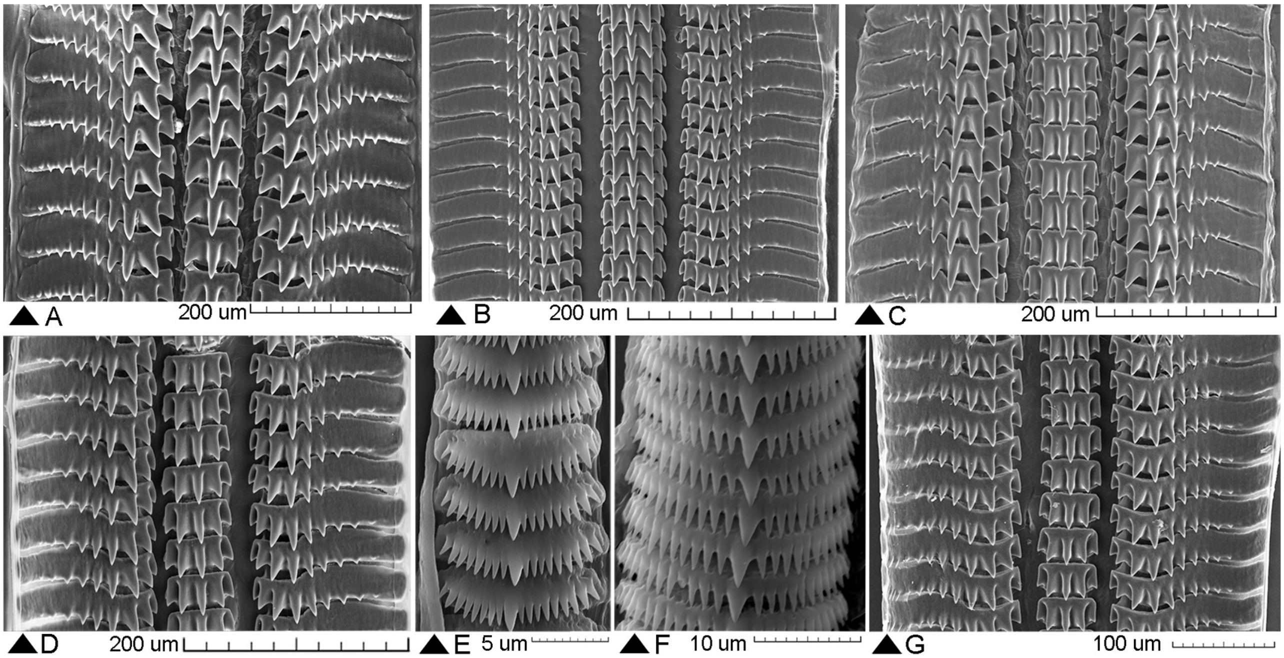

Figure 23. Radulae in species of *Strigatella*. A, *Strigatella paupercula*, MNHN IM-2013-15188, PAPUA NIUGINI Stn PM39, 05°12.1′S, 145°48.4′E, intertidal, 22.2 mm. B, *Strigatella luctuosa*, MNHN IM-2013-11682, PAPUA NIUGINI Stn PR14, 05°12′S, 145°48.1′E, 2–3 m, 20.9 mm. C, *Strigatella decurtata*,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

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. *Strigatella coronata* and *S. lugubris* form 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 *S. 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, 1867

(FIGS 24, 25A–H)

Type species: *Imbricaria conica* Schumacher, 1817 (=*Mitra conularis* Lamarck, 1811); M.

Synonym: *Conoelix* Swainson, 1821. Type species: *Conoelix lineatus* Swainson, 1821 (=*M. 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 three or more 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 acuminated 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 four to five fine columellar folds gradually diminishing towards siphonal canal. Rachidian with four to seven cusps, with one to two marginal pairs of cusps notably weaker than the two or three medial cusps; unpaired central cusp when present equal or weaker than two flanking cusps (Fig. 25A–H). Lateral teeth broad, with seven to 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 (Fig. 25D–F).

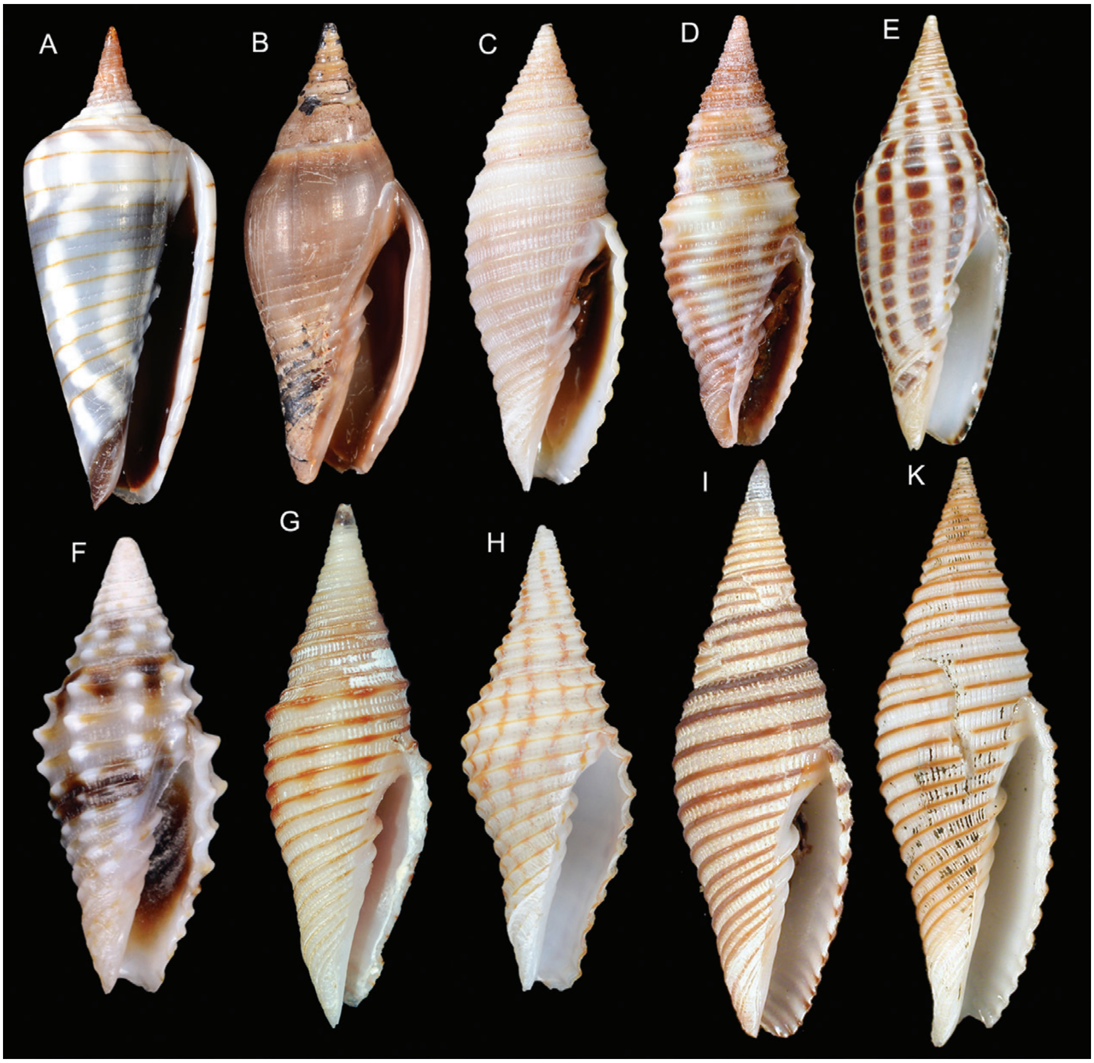

Figure 24. *Imbricaria* species. A, *Imbricaria conularis*, MNHN IM-2013-18043, PAPUA NIUGINI Stn PR203, 05°10.3′S 145°48.5′E, 1–19 m, 16.8 mm. B, ***Imbricaria bantamensis* comb. nov.**, MNHN IM-2013-16688, PAPUA NIUGINI Stn PD67, 05°15.5′S, 145°46.8′E, 2–6 m, 21.8 mm. C, ***Imbricaria insculpta* comb.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

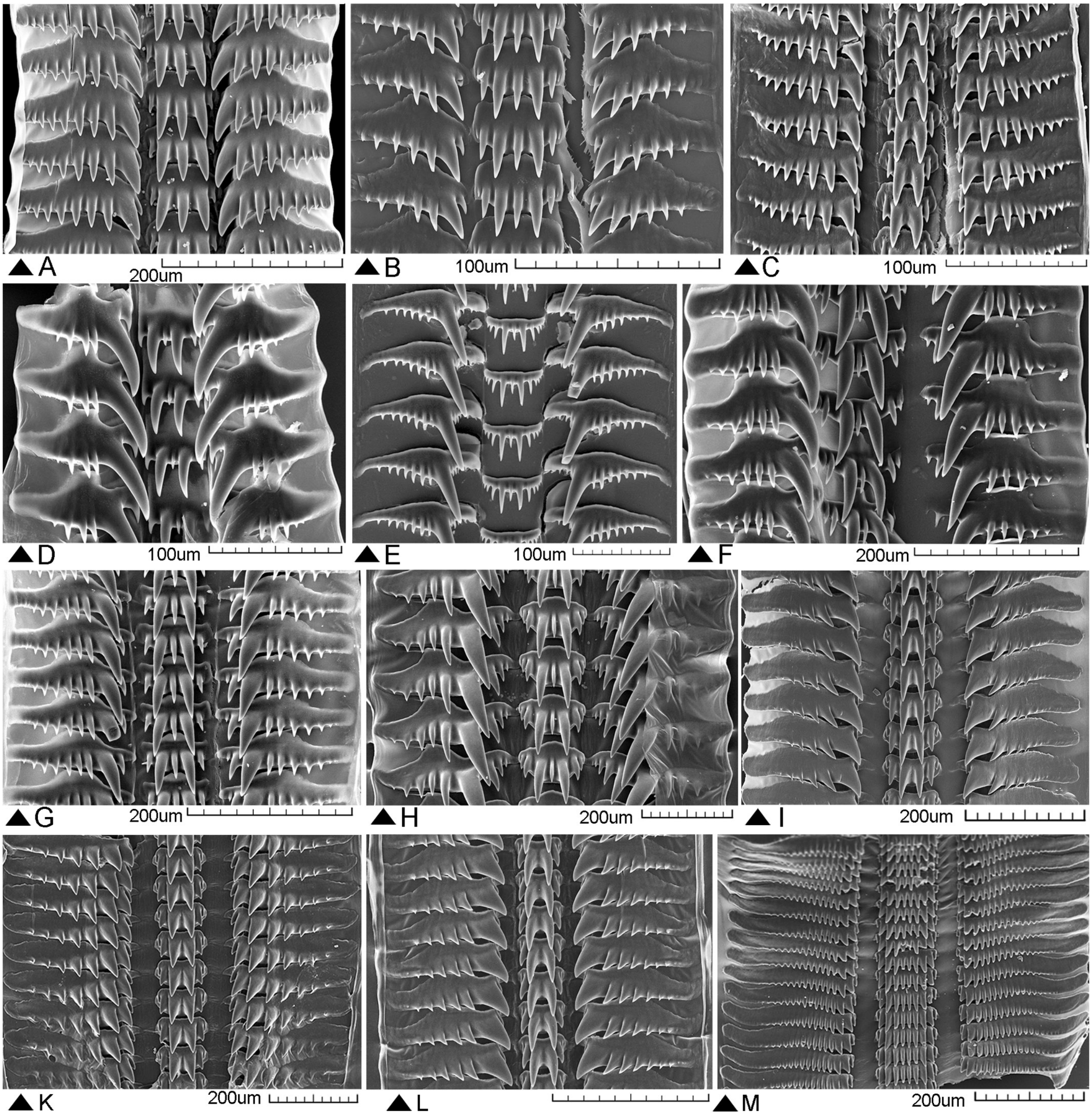

Figure 25. Radulae in the genera *Imbricaria* and *Cancilla*. A, ***Imbricaria pugnaxa* comb. nov.**, MNHN, New Caledonia, EXBODI Stn CP3795, 21°32′S, 166°21′E, 240–245 m, 31.9 mm. B, *Imbricaria conularis*, MNHN, Society Is., Moorea, 13.3 mm. C, ***Imbricaria fulgetrum* comb. nov.**, MNHN IM-2013-18112, PAPUA NIUGINI Stn PR240, 05°08.2′S, 145°48.7′E, 3–20 m, 16.8 mm. D, ***Imbricaria flammigera* comb. nov.**, 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, ***Imbricaria insculpta* comb. nov.**, 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, ***Imbricaria verrucosa* comb. nov.**, MNHN, Papua New Guinea, KAVIENG 2014 Stn KR54, 02°42.3′S, 150°39.1′E, 7–10 m, 12.3 mm. G, ***Imbricaria salisburyi* comb. nov.**, Papua New Guinea, Hansa Bay, 8–18 m, 15.3 mm. H, ***Imbricaria interlirata* comb. nov.**, 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, *Cancilla* cf. *fibula*, MNHN IM-2013-40646, New Caledonia, EXBODI Stn CP3822, 21°52′S, 166°51′E, 341–506 m, 37.6 mm. L, *Cancilla baeri*, MNHN IM-2013-58853, Papua New Guinea, KAVIENG 2014 Stn DW4484, 02°26′S, 149°55′E, 229 m, 34.2 mm. M, ***Cancilla schepmani* comb. nov.**, MNHN IM-2013-40645, New Caledonia, EXBODI Stn DW3926, 18°35′S, 164°20′E, 364–473 m, 15.6 mm.

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

Species included: *Imbricaria amoena* (A. Adams, 1853)[3] comb. nov., *I. annulata* (Reeve, 1844)[3] comb. nov., *I. armonica* (T. Cossignani & V. Cossignani, 2005)[3] comb. nov., *I. astyagis* (Dohrn, 1860)[3] comb. nov., *I. bacillum* (Lamarck, 1811)[3] comb. nov., *I. baisei* (Poppe, Tagaro & Salisbury, 2009)[3] comb. nov., *I. bantamensis* (Oostingh, 1939)[1] comb. nov., *I. bellulavaria* (Dekkers, Herrmann, Poppe & Tagaro, 2014)[3] comb. nov., *I. cernohorskyi* (Rehder & Wilson, 1975)[3] comb. nov., *I. cloveri* (Cernohorsky, 1971)[3] comb. nov., *I. conularis* (Lamarck, 1811)[1], *I. flammea* (Quoy & Gaimard, 1833)[3] comb. nov., *I. flammigera* (Reeve, 1844)[1] comb. nov., *I. fulgetrum* (Reeve, 1844)[1] comb. nov., *I. hidalgoi* (G. B. Sowerby III, 1903)[3] comb. nov., *I. hrdlickai* (Salisbury, 1994)[1] comb. nov., *I. insculpta* (A. Adams, 1851)[1] comb. nov., *I. interlirata* (Reeve, 1844)[2] comb. nov., *I. intersculpta* (G. B. Sowerby II, 1870)[3] comb. nov., *I. kermadecensis* (Cernohorsky, 1978)[3] comb. nov., *I. maui* (Kay, 1979)[3] comb. nov., *I. nadayaoi* (Bozzetti, 1997)[3] comb. nov., *I. philpoppei* (Poppe, Tagaro & Salisbury, 2009)[3] comb. nov., *I. polycincta* (Turner, 2007)[3] comb. nov., *I. pretiosa* (Reeve, 1844)[2] comb. nov., *I. pugnaxa* (Poppe, Tagaro & Salisbury, 2009)[1] comb. nov., *I. rufilirata* (A. Adams & Reeve, 1850)[3] comb. nov., *I. ruberorbis* (Dekkers, Herrmann, Poppe & Tagaro, 2014)[3] comb. nov., *I. rufogyrata* (Poppe, Tagaro & Salisbury, 2009)[1] comb. nov., *I. salisburyi* (Drivas & Jay, 1990)[2] comb. nov., *I. tahitiensis* (Herrmann & Salisbury, 2012)[3] comb. nov., *I. verrucosa* (Reeve, 1845)[1] comb. nov., *I. yagurai*, (Kira, 1959)[1] comb. nov., *I. zetema* (Dekkers, Herrmann, Poppe & Tagaro, 2014)[3] comb. nov.

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

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

GENUS *CANCILLA* SWAINSON, 1840
(FIGS 25I–M, 26)

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

Diagnosis: Shell small to rather large (15–110 mm), fusiform, with high aperture and long, tapering siphonal canal. Protoconch conical, of about three very slightly convex smooth whorls. Spire whorls evenly convex to subcylindrical; suture distinct, impressed. Shell sculptured with spiral cords that are slightly gemmate or with finely dentate margins, very wide and flat, separated by narrow grooves, or with strong, narrow and elevated cords separated by broad depressions bearing regular, very fine riblets. Shell base gradually extended into rather long, tapering siphonal canal. Siphonal fasciole not pronounced, notch deep or shallow. Aperture elongate, narrow; outer aperture lip smooth, gently convex adapically, and flattened in its lower 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 (Fig. 25I–M). Lateral teeth with seven to ten 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)[1], *C. fibula* Poppe, Tagaro & Salisbury, 2009[1], *C. heinickei* (Salisbury & Guillot de Suduiraut, 2003)[3] comb. nov., *C. herrmanni* Dekkers, 2014[3], *C. isabella* (Swainson, 1831)[2], *C. liliformis* Huang & Salisbury 2017[3], *C. rehderi* (Webb, 1958)[1], *C. rikae* Guillot de Suduiraut, 2004[3], *C. schepmani* (Salisbury & Guillot de Suduiraut, 2003)[1] comb. nov., *C. turneri* Poppe, Tagaro & Salisbury, 2009[3].

Remarks: The typification of *Cancilla* renders the identity of the genus a little weak: the specimen of *M. 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

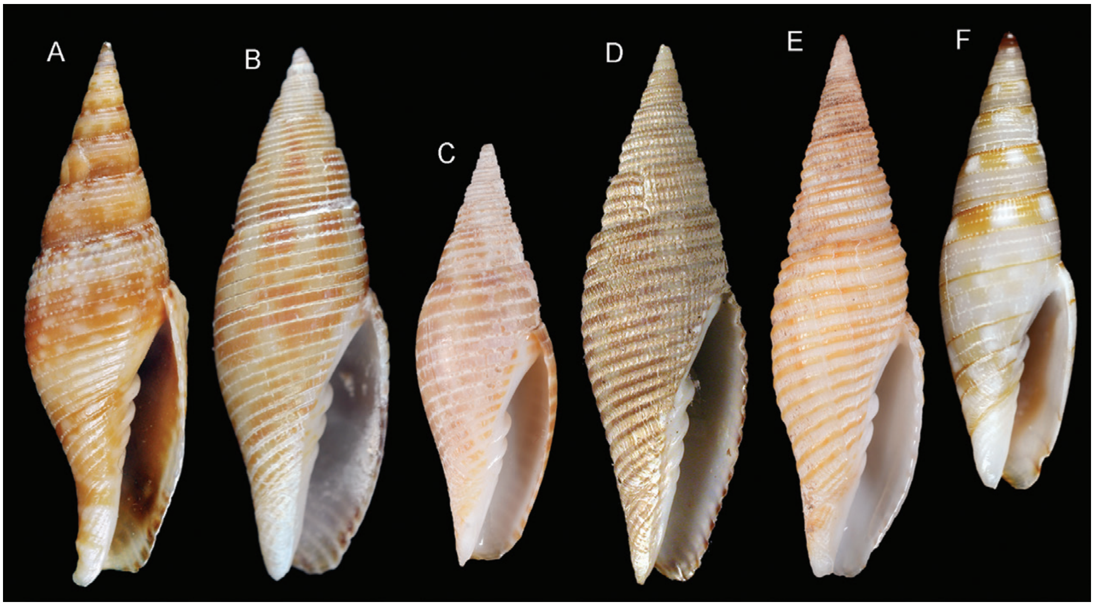

Figure 26. *Cancilla* species. A, *Cancilla baeri*, IM-2013-58853, Papua New Guinea, KAVIENG 2014 Stn DW4484, 02°26′S, 149°55′E, 229 m, 34.2 mm. B–D, *Cancilla fibula/rehderi*; B, MNHN, Papua New Guinea, BIOPAPUA Stn DW3641, 06°45′S, 148°01′E, 380–476 m, 20.8 mm; C, MNHN IM-2013-19073, PAPUA NIUGINI 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, ***Cancilla schepmani* comb. nov.**, MNHN IM-2013-40645, New Caledonia, EXBODI Stn DW3926, 18°35′S, 164°20′E, 364–473 m, 15.6 mm.

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 & 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 midwidth, 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. 26A) resembles one of the two specimens of *C. isabella* studied by Salisbury & 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 circumscribe it, is rather heterogeneous and can be subdivided by shell morphology into two conventional groups: 'robust' *Cancilla* with species such as *C. isabella*, *C. baeri* and *C. chuoi*, and 'slender' *Cancilla* with species like *C. fibula*, *C. rehderi*, *C. schepmani* and *C. liliformis*. The relationships of these two conchological groups is supported by (1) inclusion of *C. baeri* in the *Cancilla* clade (clade 24–7) in the *COI*-based tree and (2) occurrences of very similar radular morphologies in 'slender' species of the *C. fibula*–*C. rehderi* complex (Fig. 25I, K) and in 'robust' *C. baeri* IM-2013-58853 (Fig. 25L). It should be noted, however, that the radula of *C. schepmani* (Fig. 25M), with a morphology closest to the radulae of *Strigatella* or of the mitrine *Neotiara nodulosa* (Fig. 10E), is thoroughly different from the radulae of other studied *Cancilla* species. Therefore, *Cancilla* appears to be very heterogeneous in radular morphology as well. Taking into account this observed radular disparity among sequenced (and thus confirmed related) *Cancilla* species, we believe that the divergent radular morphology of *C. isabella* does not contradict its affinity to the other species studied herein.

Species of *Domiporta* can be distinguished from the 'robust' *Cancilla* species by the sculpture pattern with narrow, elevated, widely interspaced spiral cords, whereas a distinct concavity at the transition of shell base to siphonal canal distinguishes species of *Domiporta* from 'slender' *Cancilla* species. Moreover, the two genera differ greatly in radular morphology.

Besides, there is a clear resemblance between some species of *Imbricaria* and 'slender' *Cancilla*: *I. fulgetrum* and C. *rehderi/fibula* (especially our immature specimen IM-2013-19073) or the *I. yagurai* group and *C.* cf. *fibula* (represented by IM-2013-40646). In these pairs, the species of *Cancilla* can be recognized by the more convex outline of the shell base, which gives the shell a rather fusiform shape compared to the rather biconical shell of *Imbricaria*. The new genus *Cancillopsis* can be differentiated from the 'robust' *Cancilla* species by the higher spire with rather subcylindrical whorls, and from the 'slender' *Cancilla* species by the presence of a concavity at the base of the siphonal canal. Finally, the radula with rachidian and lateral teeth of similar morphology differentiates *Profundimitra* gen. nov. and *Fusidomiporta* gen. nov. from *Cancilla*.

GENUS ***IMBRICARIOPSIS*** FEDOSOV, HERRMANN, KANTOR & BOUCHET **GEN. NOV.**

(FIGS 27, 28A)

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

Diagnosis: Shell small (10–20 mm), conical, uniformly pale or with dark tip of siphonal canal. Protoconch pointed multispiral, narrowly conical, dark. Suture distinct, impressed. Spire very short, less than 20% of total shell height, conical or distinctly acuminate, starting with several subcylindrical whorls. Last adult whorl very tall, sculptured with regular, distinctly punctate, spiral grooves. Siphonal notch shallow or moderately deep. Aperture very tall and narrow, slit-like. Outer aperture lip thick, flattened, smooth inside; inner lip with five fine oblique folds situated on abapical portion of columella. Radula triserial; rachidian with six cusps, paired central cusps greatly exceeding those situated laterally (Fig. 28A). Lateral teeth with five cusps, second cusp from rachidian very robust, notably exceeding the others.

Distribution: Indo-Pacific, intertidal and upper subtidal depths, on sand patches and in reef crevices.

Species included: *Imbricariopsis conovula* (Quoy & Gaimard, 1833)[2] comb. nov., *I. punctata* (Swainson, 1821)[1] comb. nov., *I. vanikorensis* (Quoy & Gaimard, 1833)[2] comb. nov., ?*I. carbonacea* (Hinds, 1844)[3] comb. nov.

Etymology: The name *Imbricariopsis* reflects the resemblance of the species in this newly recognized lineage with the type species of *Imbricaria*, *I. conularis*, that has long distracted mitrid taxonomists. Gender feminine.

Remarks: Few mitrids are characterized by an almost involute conical shell, and these were formerly allocated to either *Imbricaria* or *Pterygia*. However, we found *Imbricaria* as traditionally construed to be paraphyletic, with *I. punctata* forming a lineage of its own, not closely related to *I. conularis*. Although a single species

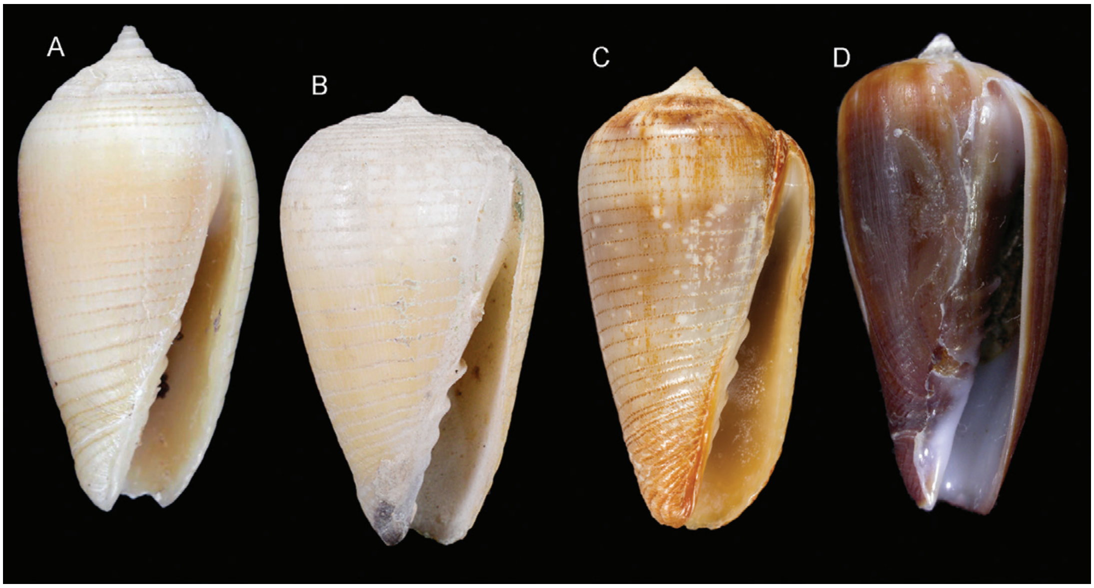

Figure 27. Species of ***Imbricariopsis* gen. nov.** A, ***Imbricariopsis punctata* comb. nov.**, MNHN IM-2013-11604, PAPUA NIUGINI Stn PM12, 05°00.2′S, 145°47.6′E, 0–1 m, 17.2 mm. B, ***Imbricariopsis conovula* comb. nov.**, lectotype of *Mitra virgo*, NHMUK 1967912, Society Is., 14 mm. C, ***Imbricariopsis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

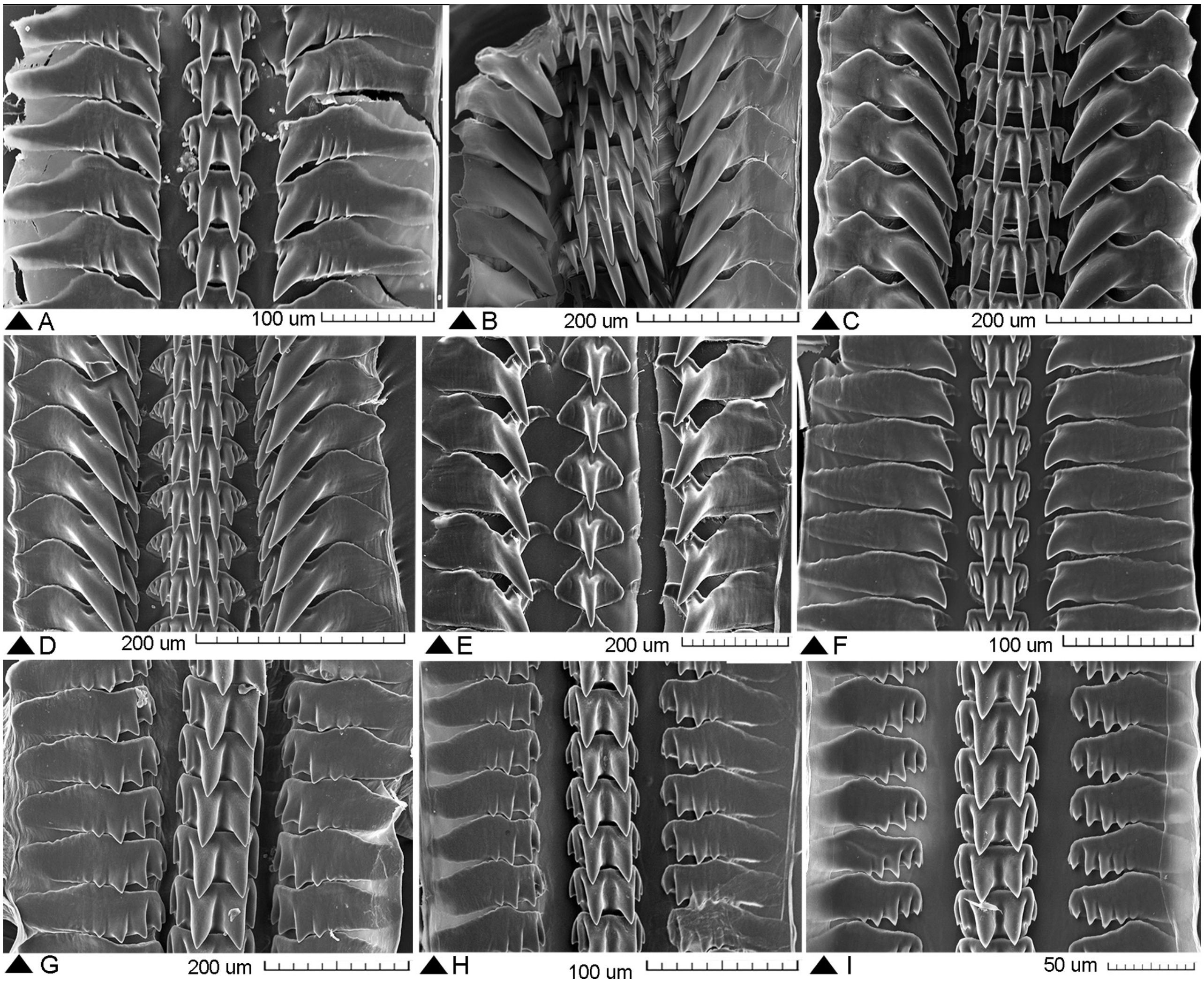

Figure 28. Radulae in the genera *Imbricariopsis* **gen. nov.**, *Swainsonia*, *Scabricola* and *Neocancilla*. A, ***Imbricariopsis punctata*** **comb. nov.**, Mozambique, INHACA 2011 Stn MM3, 26°03.9′S, 32°57.3′E, 0–1 m, 14.7 mm. B, *Swainsonia fusca*, MNHN IM-2013-40643. C, *Swainsonia casta*, Papua 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, *Neocancilla maculosa*, Mozambique, INHACA 2011 Stn MR13, 25°59.7′S, 32°54.5′E, 2–5 m, 14.9 mm. I, *Neocancilla rufescens*, MNHN IM-2013-40644, Mozambique, INHACA 2011 Stn MD22, 25°59.7′S, 32°46.8′E, 22 m, 16.4 mm.

has been sequenced, we hypothesize a close relationship between *I. punctata*, *I. conovula* and *I. vanikorensis*, largely based on shell characters. *Imbricariopsis* gen. nov., as we circumscribe it, constitutes a rather distinctive group of small shallow-water mitrids: species of *Imbricariopsis* can be recognized by conical, weakly sculptured, or not sculptured at all, pale shells with a minute, pointed apex (that is much lower than in *I. conularis*). The radulae of the three species that we assign to *Imbricariopsis* gen. nov. were illustrated by Cernohorsky (1970) and are again figured here; all three share the same general morphology of lateral radular teeth, with one robust major and several minor cusps situated on both sides of the major one.

The enigmatic West African *Mitra carbonacea* Hinds, 1844 resembles species of *Imbricariopsis* gen. nov. in overall shell morphology and may prove to be related to this genus. However, given the disparity in geographical distribution, we place this species in *Imbricariopsis* gen. nov. with a question mark, pending future studies. Minor differences in the position of the columellar folds (situated in the abapical portion of the columella in *Imbricariopsis* and at mid-height in *M. carbonacea*) may hint at a not-so-close relationship.

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* gen. nov., 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* gen. nov. are in fact the closest living relatives of the ancient '*I.*' *conoidea*, which agrees with the rather underived position of *Imbricariopsis* gen. nov. in the imbricariine segment of the mitrid tree.

Genus *Scabricola* Swainson, 1840

(Figs 28D–F, 29A–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)[3], *S. desetangsii* (Kiener, 1838)[1], *S. olivaeformis* (Swainson, 1821)[1], *S. padangensis* (Thiele, 1925)[2], *S. variegata* (Gmelin, 1791)[1], ?*Scabricola barrywilsoni* (J. Cate, 1968)[3], ?*S. albina* A. Adams, 1853[3], ?*S. caerulea* (Reeve, 1844)[3], ?*S. condei* Guillot de Suduiraut, 2001[3], *S. coriacea* (Reeve, 1845)[2], ?*S. backae* (Cernohorsky, 1973)[3], ?*S. dampierensis* Salisbury & Heinicke, 1998[3], ?*S. dianneae* (Salisbury & Guillot de Suduiraut, 2003)[3] comb. nov., ?*S. eximia* (A. Adams, 1853)[3], ?*S. geigeri* Poppe, Tagaro & Salisbury, 2009[3], ?*S. gilbertsoni* (Cate, 1968)[3] comb. nov., ?*S. guttata* (Swainson, 1824)[3] comb. nov., ?*S. hayashii* (Kira, 1959)[3], ?*S. incisa* (A. Adams & Reeve, 1850)[3], ?*S. ivanmarrowi* Marrow, 2016[3], ?*S. lavoisieri* Guillot de Suduiraut, 2002[3], ? *S. lorenzi* (Poppe & Tagaro, 2006)[3] comb. nov., ?*S. mariae* (A. Adams, 1853)[3], ?*S. martini* Poppe & Tagaro, 2006 [3], ?*S. petiti* Poppe & Tagaro, 2006[3], ?*S. parkinsoni* Salisbury & Wolff, 2005 [3], ?*S. potensis* (Montrouzier, 1858)[3], ?*S. sowerbyi* d'Orbigny, 1852[3], ?*S. splendidula* Salisbury & Guillot de Suduiraut, 2003[3], ?*S. vicdani* Cernohorsky, 1981[3], ?*S. yaekoae* (Habe & Kosuge, 1966)[3].

Remarks: The genus *Scabricola* as commonly understood is extremely heterogeneous. It combines such dissimilar forms as *S. yaekoae*, 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. *S. 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) (Fig. 28D – *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. 28E) 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 28B, C, 29G–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).

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.

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 cyrtoconoid, 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, or lacking entirely. Axial sculpture usually not developed or, when present, consisting of numerous, fine and low, rounded folds, developed on the spire but indistinct on the periphery of the last adult whorl. Shell base typically with convex outline, continuing into short and stout, deeply notched, siphonal canal. Siphonal fasciole indistinct or moderately developed. Aperture elongate, narrow to moderately wide. Outer aperture lip straight or gently evenly convex adapically; anterior edge of outer lip strongly convex, sometimes slightly drawn abapically. Inner lip with four to five fine or strong, subequal columellar folds. Shell light brown, orange or white, typically with intricate scale-like pattern of fine light or white lines. *Scabricola*-type radula with comb-like rachidian bearing six long, slender cusps, the four central ones notably exceeding the two marginal ones (Fig. 28B, C). Lateral teeth with very strong, robust cusp, giving tooth the appearance of a tin-opener, the serrate inner surface of tooth bearing three to four weaker cusps. Base of laterals with curved upper margin, forming a socket interlocking laterals of adjacent rows.

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

Species included: *Swainsonia biconica* Bozzetti, 2011[3], *S. casta* (Gmelin, 1791)[1], *S. ekerae* Cernohorsky, 1973[3], *S. fissurata* (Lamarck, 1811)[2], *S. fusca* (Swainson, 1824)[1], *S. limata* (Reeve, 1845)[3], *S. newcombii* (Pease, 1869)[3], *S. ocellata* (Swainson, 1831)[3].

Remarks: Many contemporary authors have treated *Swainsonia* as a subgenus of *Scabricola* (Cernohorsky, 1970, 1991; Pechar, Prior & Parkinson, 1980; but see Poppe & Tagaro, 2008), but our results indicate that it should be elevated to full genus. This treatment of *Scabricola* and *Swainsonia*, however, contradicts the phylogenetic hypothesis implied by radular morphology. The typical *Scabricola* radula (as described by Cernohorsky, 1970) is present in *Scabricola variegata*, *Swainsonia fusca* and *Swainsonia casta*, while the radulae of *Scabricola desetangsii* and *S. olivaeformis* show a divergent morphology.

GENUS *NEOCANCILLA* CERNOHORSKY, 1966

(FIGS 28G–I, 30)

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

Diagnosis: Shell small to medium sized (10–65 mm), fusiform, with short and stout siphonal canal. Protoconch pointed, narrowly conical, of about three slightly convex glossy whorls. Suture deeply impressed to canaliculate. Spire orthoconoid, teleoconch whorls evenly convex. Sculpture of wide spiral cords, low or slightly elevated adapically, or bearing rows of fine beads. Spiral cords separated by narrow deep groves and intersected by axial riblets of similar strength, forming regular cancellate sculpture. Siphonal canal short and robust, gradually merging to shell base, although separated from it by narrow depression at about the level of the second columellar fold. Siphonal notch deep. Aperture elongate; outer aperture lip evenly convex along most of its length. Inner aperture lip with four strong columellar folds, adapicalmost strongest. Shell cream, pale or orange, usually with contrasting darker bands. Radula with narrow rachidian bearing six blunt, very robust cusps; paired central cusps greatly exceeding the others (Fig. 28G–I). Lateral teeth with four or five very short and blunt cusps situated proximally, distal portions of teeth without cusp.

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

Species included: *Neocancilla antoniae* (H. Adams, 1870)[3], *N. arenacea* (Dunker, 1852)[3], *N. clathrus* (Gmelin, 1791)[2], *N. hartorum* Poppe, Salisbury & Tagaro, 2015[3], *N. hemmenae* (Salisbury & Heinicke, 1993)[3], *N. kayae* Cernohorsky, 1978[3], *N. maculosa* (Gmelin, 1791)[1], *N. madagascariensis* Herrmann, 2017[3], *N. papilio* (Link, 1807)[1], *N. rufescens* (A. Adams, 1853)[1], *N. takiisaoi* (Kuroda, 1959)[2], *N. waikikiensis* (Pilsbry, 1921)[2].

Remarks: The genus *Neocancilla* is one of the few lineages the composition of which is left rather unchanged after our phylogenetic analysis. The group is well delineated, thanks to the characteristic shell and conservative radular morphology. The radula of the West African '*Neocancilla*' *hebes* depicted by Cernohorsky (1991) rather resembles the radula of Strigatellinae and led Cernohorsky to question the relation of that species to the Indo-Pacific *Neocancilla*. Here, we remove this species from *Neocancilla* and provisionally place it in *Domiporta*.

Species of *Domiporta* are closest to *Neocancilla* primarily because of similar shell proportions and sculpture pattern. Species of *Neocancilla*, however, can be distinguished by the shell base and siphonal canal, which form a continuous, usually slightly convex, outline with no concave waist. Besides, there are consistent differences between the two genera in radular morphology: in *Neocancilla*, the radula has few short, blunt and robust cusps on the rachidian and laterals, while in *Domiporta* the rachidian and laterals

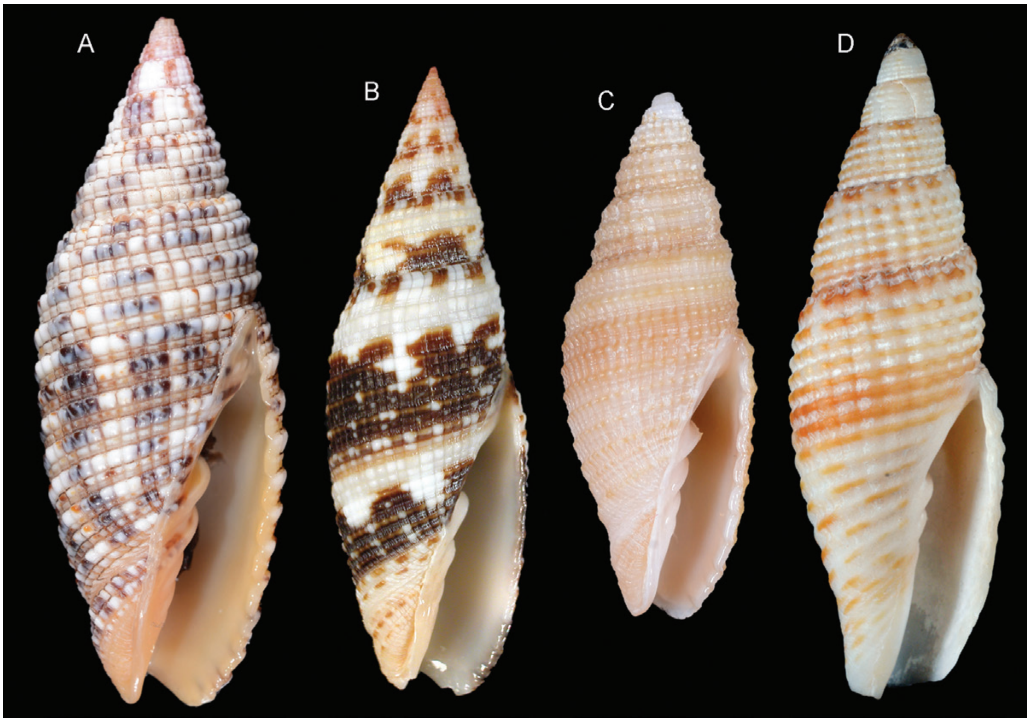

Figure 30. *Neocancilla* species. A, *Neocancilla papilio*, MNHN IM-2013-12560, PAPUA NIUGINI Stn PR24, 05°12.3′S, 145°48.8′E, 28.2 mm. B, *Neocancilla maculosa*, MNHN IM-2007-30178, Vanuatu, SANTO 2006 Stn DR73, 15°22.5′S, 167°11.3′E, 10–25 m. C, *Neocancilla rufescens*, MNHN IM-2013-40644, Mozambique,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

bear multiple pointed cusps that are not differentiated in size or shape. The *Scabricola*–*Swainsonia* grade is closely related to *Neocancilla*, and the species of these three genera are conchologically similar. However, shells of *Scabricola* and *Swainsonia* can be differentiated by a notably weaker sculpture, with no or very weak axial elements; besides, most species of *Scabricola* are wider, with a higher last adult whorl compared to *Neocancilla*.

SUBFAMILY CYLINDROMITRINAE COSSMANN, 1899
(FIGS 31–33)

GENUS *PTERYGIA* RÖDING, 1798
(FIGS 31, 32A–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) *Acuticylindra* Iredale, 1929. Type species: *Voluta nucea* Gmelin, 1791; OD.

Diagnosis: Shell small to medium sized (20–70 mm), ovate or ovate-elongate, with very low spire and tall aperture. Protoconch cyrtoconoid, with about three smooth evenly convex whorls. Spire height attaining only about 10–15% of total shell height, with only three to four 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 six to eight 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 (Fig. 32A–C).

Distribution: Indo-Pacific, subtidal, mostly on coral rubble, one species occurs on mud.

Species included: *Pterygia arctata* (G. B. Sowerby II, 1874)^3, *P. conus* (Gmelin, 1791)^3, *P. crenulata* (Gmelin, 1791)^2, *P. dactylus* (Linnaeus, 1767)^1, *P. fenestrata*

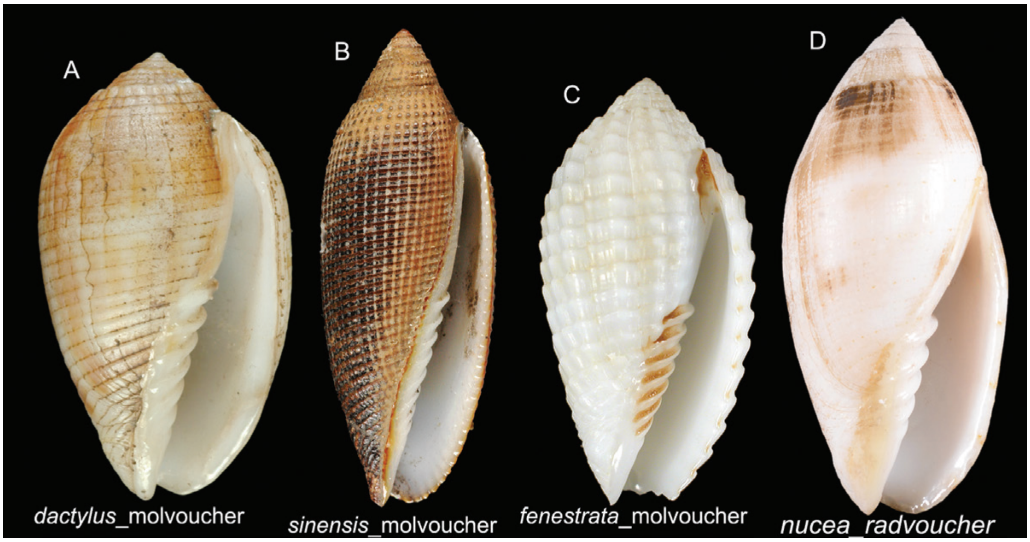

Figure 31. *Pterygia* species. A, *Pterygia dactylus*, MNHN IM-2013-14989, PAPUA NIUGINI Stn PM39, 05°12.1′S, 145°48.4′E, intertidal, 25.1 mm. B, *Pterygia sinensis*, MNHN IM-2009-15439, Madagascar, ATIMO VATAE Stn CP3568, 25°04.7′S, 47°03.4′E, 64–65 m. C, *Pterygia fenestrata*, MNHN IM-2007-30039, Vanuatu,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

(Lamarck, 1811)[1], *P. gorii* (Turner, 2007)[3], *P. japonica* Okutani & Matsukuma, 1982[3], *P. jeanjacquesi* Bozzetti, 2010[3], *P. morrisoni* Marrow, 2016[3], *P. nucea* (Gmelin, 1791)[2], *P. purtymuni* Salisbury, 1998[3], *P. scabricula* (Linnaeus, 1767)[3], *P. sinensis* (Reeve, 1844)[1], *P. undulosa* (Reeve, 1844)[3].

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 (e.g. *Scabricola potensis*) may actually belong to *Pterygia*. Conical shells resembling those of *Pterygia* are found in *Imbricaria* and *Imbricariopsis* gen. nov., which are, however, phylogenetically very distant from *Pterygia* and are characterized by a triserial radulae.

Genus *Nebularia* Swainson, 1840
(Figs 32D–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 three or more 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 groves 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 four to five 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 (Fig. 32D–F). Laterals bearing six to 12 cusps, second to fourth 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)[1] comb. nov., *N. aegra* (Reeve, 1845)[3] comb. nov., *N. ancillides* (Broderip, 1836)[3] comb. nov., *N. baerorum*

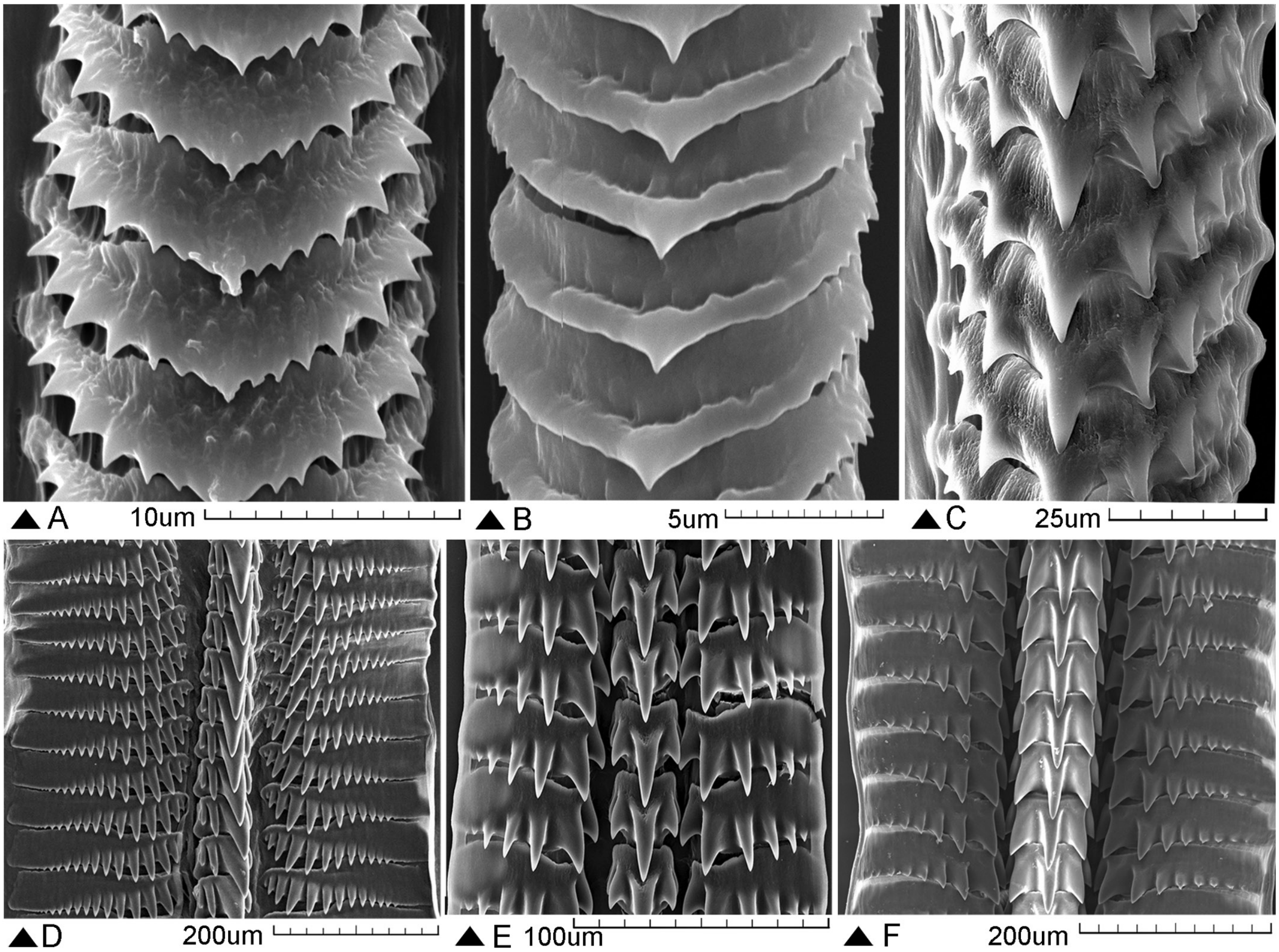

Figure 32. Radulae in the subfamily Cylindromitrinae. A, *Pterygia dactylus*, MNHN IM-2013-14989, PAPUA NIUGINI Stn PM39, 05°12.1′S, 145°48.4′E, intertidal, 25.1 mm. B, *Pterygia fenestrata*, Society Is., off Moorea, 11.5 mm. C, *Pterygia nucea*, MNHN IM-2013-50702, Papua New Guinea, KAVIENG 2014 Stn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

(Poppe & Tagaro, 2010)[3], *N. bellula* (A. Adams, 1853)[3] comb. nov., *N. chrysostoma* (Broderip, 1836)[3], *N. coarctata* (Reeve, 1844)[3], *N. contracta* (Swainson, 1820)[1], *N. deynzeri* (Cernohorsky, 1980)[3] comb. nov., *N. dondani* (Cernohorsky, 1985)[3] comb. nov., *N. edentula* (Swainson, 1823)[3] comb. nov., *N. eremitarum* (Röding, 1798)[1] comb. nov., *N. fastigium* (Reeve, 1845)[3] comb. nov., *N. ferruginea* (Lamarck, 1811)[2], *N. gourgueti* (Poppe, Salisbury & Tagaro, 2015) comb. nov., *N. guidopoppei* (Thach, 2016)[3] comb. nov., *N. incompta* (Lightfoot, 1786)[1] comb. nov., *N. inquinata* (Reeve, 1844)[3], *N. kamehameha* (Pilsbry, 1921)[3] comb. nov., *N. multiplicata* (Pease, 1865)[3] comb. nov., *N. nebulosa* (Broderip, 1836)[3] comb. nov., *N. nivea* (Broderip, 1836)[3] comb. nov., *N. pellisserpentis* (Reeve, 1844)[3] comb. nov., *N. petrosa* (G. B. Sowerby II, 1874)[3] comb. nov., *N. pyramis* (Wood, 1828)[3], *N. semperi* (Poppe, Tagaro & Salisbury, 2009)[3] comb. nov., *N. thachi* (Turner, 2007)[3], *N. ustulata* (Reeve, 1844)[3] comb. nov.

Remarks: Our phylogenetic analysis has led to a considerable rearrangement of the genus *Nebularia*. The 'lesser' *Nebularia* species (*N. fraga* and *N. tornata* groups) appeared unrelated to the true *Nebularia* typified by *N. contracta*. On the other hand, some large *Mitra* species (*M. incompta*, *M. eremitarum*) showed a close affinity to *N. contracta*, and so did '*Strigatella*' *acuminata*. The genus *Nebularia*, as circumscribed herein, is supported by several distinctive morphological shell (colour pattern, a thickened outer aperture lip and an often recurved tip of the siphonal canal) and radula characters (a very strong unpaired central cusp on the rachidian). The same features characterize

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

a number of species classically included in *Mitra* (*M. ancillides*, *M. coarctata*, *M. edentula*, *M. ferruginea*, *M. nebulosa*, *M. nivea*, *M. ustulata*), which we thus classify in *Nebularia*. As a consequence, we also consider the nominal genera *Dibaphus*, *Mitroidea* and *Mutyca* to be synonyms of *Nebularia*. Both shell proportions and development of sculpture vary considerably among the species of *Nebularia*, the two extremes being *N. incompta* (Fig. 33D) and *N. ancillides* (Fig. 33G). An even more cylindrical shell characterizes *Mauritia barclayi*, which we tentatively place in *Nebularia* as well.

SUBFAMILY **ISARINAE** FEDOSOV, HERRMANN, KANTOR & BOUCHET **SUBFAM. NOV.**

(FIGS 34–36)

Diagnosis: Shell small to large (15–125 mm) mm, biconical, fusiform to turriform, pale to dark brown due to well-developed periostracum. Shell smooth, or sculptured with fine to very strong spiral cords. Suture distinct, impressed. Spire moderately to very high; teleoconch whorls gently convex, distinctly shouldered due to pronounced spiral sculpture, or flattened. Sculpture absent, or represented by regular spiral cords, ranging from wide and flattened to rounded, or narrow, elevated, separated by wide, concave interspaces. Microsculpture of fine collabral growth lines. Siphonal canal short and stout with well-developed fasciole, to moderately long, strait and tapering. Siphonal notch rarely deep, commonly shallow or absent. Aperture elongate, varying from narrow to moderately 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 than succeeding. Rachidian narrow, less than half as wide as the laterals, bearing five or six cusps of varying shape (Figs 33A–C). Laterals wide, with eight to 40 cusps, of varying strength.

GENUS *ISARA* H. ADAMS & A. ADAMS, 1853 (FIGS 34, 35A–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', that is, the species identified by Reeve (1844) as *M. fusca* Swainson, 1824. Reeve did not establish a new species, and there is no such thing as '*M. 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, *M. fusca* Pallary, 1900.

Diagnosis: Shell medium sized to large (30–100 mm), fusiform to turriform, 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 five or six cusps of varying shape (Fig. 33A–C). Laterals wide, with eight to 40 cusps, subequal and densely set throughout, or proximal strongest and subsequent ones weakening towards tooth edge.

Species included: *Isara aerumnosa* (Melvill, 1888)[3] comb. nov., *I. aikeni* (Lussi, 2009)[3] comb. nov., *I. antillensis* (Dall, 1889)[3] comb. nov., *I. badia* (Reeve, 1844)[3] comb. nov., *I. beui* (Thach, 2016)[3] comb. nov., *I. carbonaria* (Swainson, 1822)[1] comb. nov., *I. chalybeia* (Reeve, 1844)[3] comb. nov., *I. chinensis* (Gray, 1834)[3] comb. nov., *I. cookii* (G. B. Sowerby II, 1874)[3] comb. nov., *I. cornea* (Lamarck, 1811)[1] comb. nov., *I. declivis* (Reeve, 1844)[3] comb. nov., *I. gabonensis* (Biraghi, 1984)[3] comb. nov., *I. glabra* (Swainson, 1821)[1] comb. nov., *I. goreensis* (Melvill, 1925)[3] comb. nov., *I. joostei* (Lussi, 2009)[3] comb. nov., *I. lenhilli* (Petuch, 1988)[3] comb. nov., *I. midwayensis* (Kosuge, 1979)[3] comb. nov., *I. nigra* (Gmelin, 1791)[1] comb. nov., *I. pele* (Cernohorsky, 1970)[3] comb. nov., *I. peterclarksoni* (Marrow, 2013)[3] comb. nov., *I. picta* (Reeve, 1844)[3] comb. nov., *I. slacksmithae* (Marrow, 2013)[3] comb. nov., *I. straminea* (A. Adams, 1853)[1] comb. nov., *I. swainsonii* (Broderip, 1836)[3] comb. nov., *I. turtoni* (E. A. Smith, 1890)[3] comb. nov., *I. ulala* (Garcia, 2011)[3] comb. nov.

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

Remarks: The type species of *Isara*, *M. bulimoides* (Fig. 34B), 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 *M. 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 Art. 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 *M. bulimoides* NHMUK 1966656 as neotype of *M. glabra*. Thus, *M. bulimoides* Reeve, 1845 becomes an objective synonym of the *M. 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

Figure 34. *Isara* species. A, ***Isara glabra* comb. nov.**, 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, ***Isara chalybeia* comb. nov.**, syntype, NHMUK 1967709, locality not known, 51.5 mm. D, ***Isara carbonaria* comb. nov.**, molecular voucher, AMS C.335424, Australia, North Sydney, Collaroy, Long Reef, 33°44.7′S, 151°19′ E, intertidal. E, ***Isara chinensis* comb. nov.**, lectotype, NHMUK 1967708, 'China', 58.6 mm. F, ***Isara nigra* comb. nov.**, MNHN IM-2013-40676, Congo, Mission ZANAGA Stn DV08, 04°42.9′S, 11°47.5′E, 14–15 m, 45.2 mm. G, ***Isara cornea* comb. nov.**, BAU2537.1, Italy, Giannutri Is., Punta San Francesco, 42°15.1′N, 11°07′E, 10–20 m, 36.75 mm. H, ***Isara turtoni* comb. nov.**, lectotype of *Mitra turtoni*, NHMUK 1889.1.10.97, St. Helena Is., 26.2 mm. I, ***Isara straminea* comb. nov.**, MNHN IM-2013-56423, French Guiana, GUYANE Stn CP4375, 06°39′N, 52°30′W, 195–200 m, 33.5 mm.

Africa (*I. nigra*), Caribbean (*I. straminea*) and Western Australia (*I. glabra* and *I. carbonaria*). Based on the overall shell morphology, we tentatively assign *M. chinensis* to *Isara*, as well as an array of Australian species (*M. badia*, *M. chalybeia*, *M. peterclarcksoni* and *M. slacksmithae*).

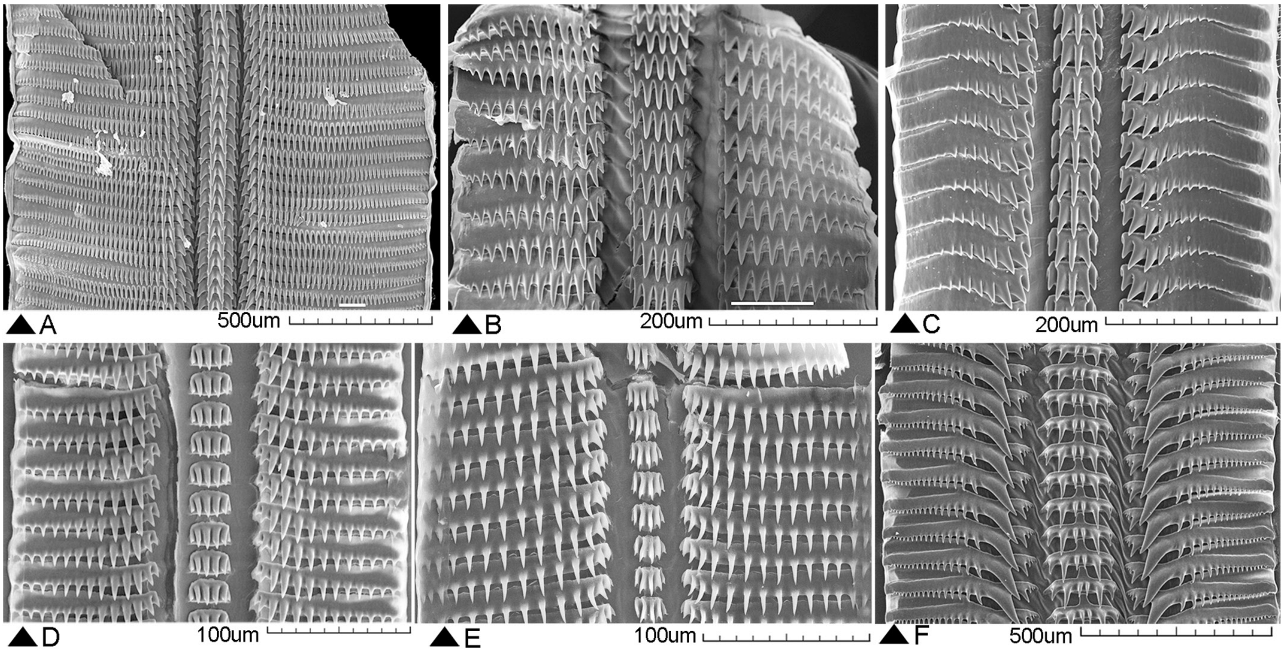

Figure 35. Radulae in **Isarinae subfam. nov.** A, ***Isara glabra* comb. nov.**, MNHN IM-2013-40640, Esperance, WESTERN AUSTRALIA Stn WE01, 15°16.94′S, 124°06.3′E, 11 m, 62.7 mm. B, ***Isara nigra* comb. nov.**, MNHN IM-2013-40676, Congo, Mission ZANAGA Stn DV08, 04°42.9′S, 11°47.5′E, 14–15 m, 45.2 mm. C, ***Isara straminea* comb. nov.**, 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.

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. *Isara 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.

Although we assign to *Isara* the Eastern Pacific *Mitra swainsonii*, the distribution of *Isara* as inferred from the phylogenetic analysis 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 *I. nigra* and *I. cornea*, should also 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.

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

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

Diagnosis: Shell small to large (15–125 mm), fusiform, with white or light background colour and contrasting brown lines on crests of spiral cords. Protoconch smooth, with slightly convex or flattened whorls, either pointed, narrowly conical, of about three whorls, or bulbous, of about two whorls. Suture indistinct. Spire moderately high, spire whorls evenly convex, sometimes shouldered in appearance due to strong elevated spiral cords that are rather sharp and widely set. Interspaces between spiral cords sculptured with fine, dense riblets, or smooth with microsculpture of very fine growth lines. Shell base triangular with straight, tapering siphonal canal not delineated from shell base. Siphonal notch deep. Aperture high, about half of shell height, narrow, parallel-sided. Outer aperture lip very gently convex, smooth. Inner lip with three fine, oblique columellar folds. Thin light brown periostracum sometimes present. Radula with narrow rachidian and laterals two to four times wider than rachidian (Fig. 35D–F), both multicuspidate, either with dense pointed cusps

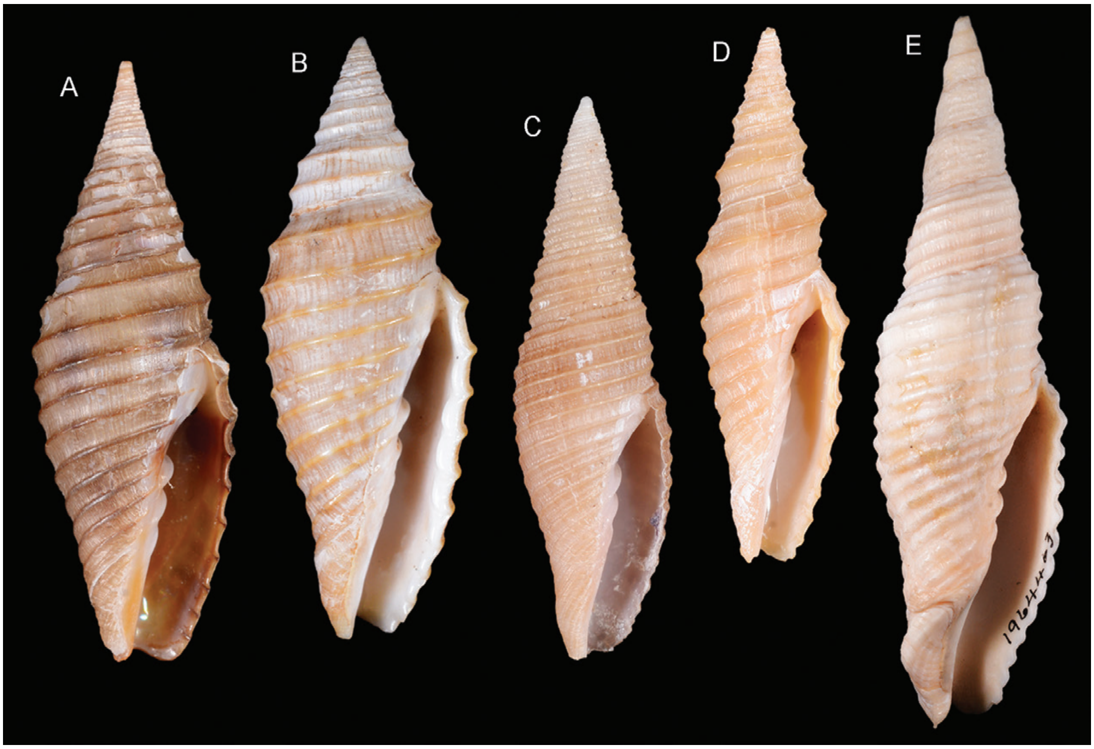

Figure 36. *Subcancilla* species. A, *Subcancilla erythrogramma*, BAU 0424, Panama, Las Perlas, Contadora I., 08°36.6′N, 79°00.2′W, 25 m, 24.1 mm. B, *Subcancilla funiculata*, lectotype, NHMUK 1967767, Plata I., Pacific coast of Columbia, 27.2 mm. C, *Subcancilla* cf. *leonardhilli*, MNHN IM-2013-61266, 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.

of subequal strength or with one cusp on laterals notably stronger than others and rachidian bearing symmetrical paired cusps also differentiated in length and strength.

Distribution: Tropical East Pacific, Caribbean, subtidal and bathyal depths.

Species included: *Subcancilla attenuata* (Broderip, 1836)[1], *S. belcheri* (Hinds, 1843)[3] comb. nov., *S. calodinota* (S. S. Berry, 1960)[3], *S. candida* (Reeve, 1845)[3], *S. directa* (Berry, 1960)[3], *S. edithrexae* (Sphon, 1976)[3], *S. erythrogramma* (Tomlin, 1931)[1], *S. funiculata* (Reeve, 1844)[3], *S. gigantea* (Reeve, 1844)[3], *S. haneti* (Petit de la Saussaye, 1852)[3], *S. hindsii* (Reeve, 1844)[3], *S. joapyra* Simone & Cunha, 2012[3], *S. larranagai* (Carcelles, 1947)[3], *S. leonardi* (Petuch, 1990)[1] comb. nov., *S. leonardhilli* Petuch, 1987[2], *Subcancilla lindae* Petuch, 1987[3], *S. lopesi* Matthews & Coelho, 1969[3], *S. malleti* (Petit de la Saussaye, 1852)[3], *S. phorminx* (S. S. Berry, 1969)[3], †*S. scrobiculata* (Brocchi, 1814)[3], *S. sulcata* (Swainson, 1825)[2].

Remarks: Cernohorsky (1991) remarked that the placement of the New World *S. sulcata* and of Indo-Pacific species in the same genus *Subcancilla* was inconsistent with their disparate radular morphology; however, no alternative was suggested. Thorsson & Salisbury (2008: 3) stressed that the classification of the Panamic and Caribbean species of *Subcancilla*, including the type species *S. sulcata*, has not been addressed sufficiently, and that the 'exact placement of *Subcancilla* into the family Mitridae remain[ed] to be absolutely determined'.

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 unconspicious 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 of *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)[2].

Distribution: Caribbean, subtidal to upper bathyal depths.

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

INCERTAE SEDIS

GENUS ***CARINOMITRA*** FEDOSOV, HERRMANN, KANTOR & BOUCHET **GEN. NOV.**

(FIGS 37, 38A–C)

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

Diagnosis: Shell small (7–20 mm), elongate-fusiform, with characteristic pattern formed by light adapical portions of teleoconch whorls, gradually transiting to yellow or orange peripheries. Protoconch narrowly conical or cyrtoconoid, of three to almost five, evenly convex, smooth and glossy whorls. Suture distinct, slightly impressed. Early spire whorls with flattened or slightly convex outlines, later gently convex or distinctly carinated at the suture. Except for subsutural carina, sculpture limited to very weak spiral grooves on shell base and siphonal canal, thus the shell appears smooth. Siphonal canal tapering, siphonal notch shallow or indistinct. Aperture elongate, rather narrow;

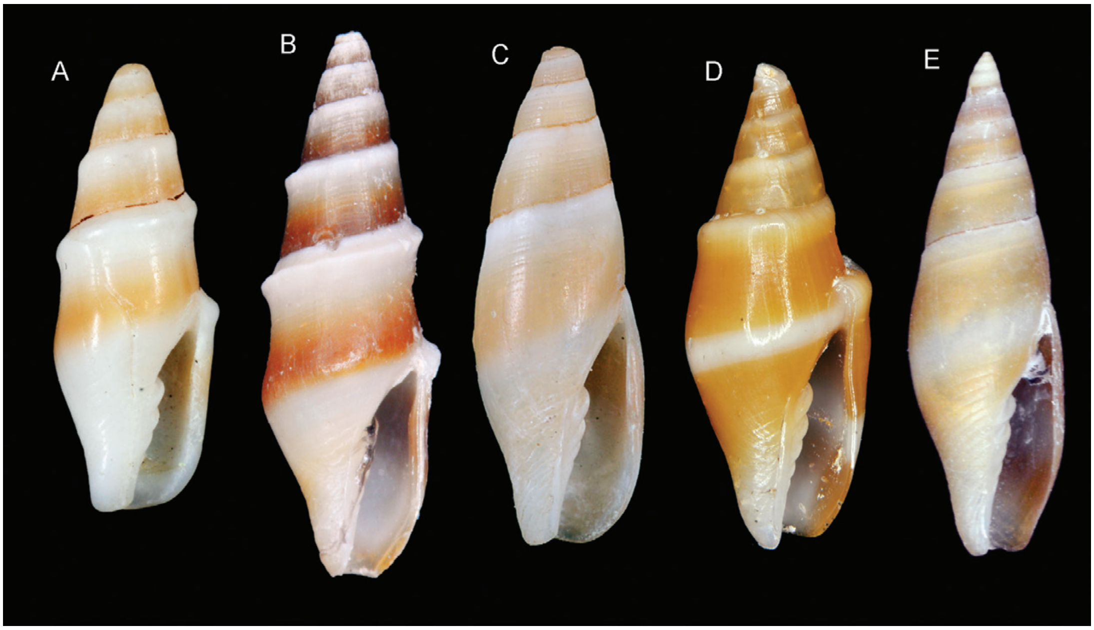

Figure 37. Species of ***Carinomitra* gen. nov.** A, B, ***Carinomitra peculiaris* comb. nov.**; A, syntype, NHMUK 1967833, Puerto Galera, Mindanao, Philippines, 10 mm; B, MNHN IM-2013-6168, PAPUA NIUGINI Stn PR218, 05°07.3′S, 145°49.4′E, 11.1 mm. C–E, ***Carinomitra typha* comb. nov.**; C, syntype, NHMUK 1967904, Philippines, 9.5 mm; D, ***Carinomitra typha* comb. nov.** 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.

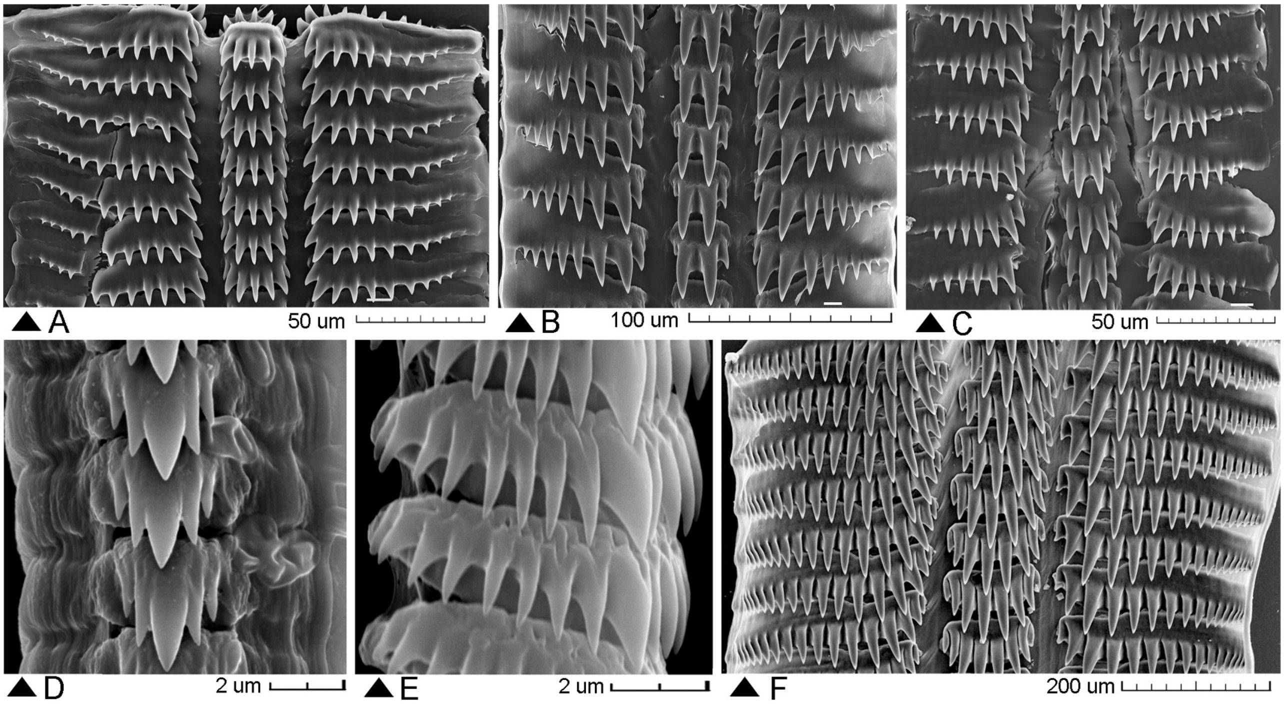

Figure 38. Radulae in the genera ***Carinomitra* gen. nov.**, ***Condylomitra* gen. nov.** and *Probata*. A, ***Carinomitra peculiaris* comb. nov.**, MNHN IM-2013-6168, PAPUA NIUGINI Stn PR218, 05°07.3′S, 145°49.4′E, 11.1 mm. B, ***Carinomitra typha* comb. nov.** var. *micans*, MNHN, New Caledonia, Noumea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

outer lip smooth, convex. Inner lip with four to five fine oblique columellar folds. Rachidian narrow, bearing either six cusps of comparable size, or four cusps with two medial notably stronger than two laterals. Laterals wide, bearing multiple cusps, of which second and third from rachidian are strongest.

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

Species included: *Carinomitra peculiaris* (Reeve, 1845)[1] comb. nov., *C. saltata* (Pease, 1865)[2] comb. nov., *C. typha* (Reeve, 1845)[1] comb. nov.

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

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

GENUS ***CONDYLOMITRA*** FEDOSOV, HERRMANN, KANTOR & BOUCHET **GEN. NOV.**

(FIGS 38D, E, 39)

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

Diagnosis: Shell small (10–25 mm), ovate to almost conical, heavily sculptured, with pointed conical apex. Protoconch pointed, narrowly conical, of about three very slightly convex, smooth whorls. Spire whorls convex; last adult whorl proportionally very high, sculptured with densely set, gemmate spiral cords, one to three adapical cords very strong, forming prominent, spirally elongated rounded tubercles, directed slightly upwards. Siphonal canal very short,

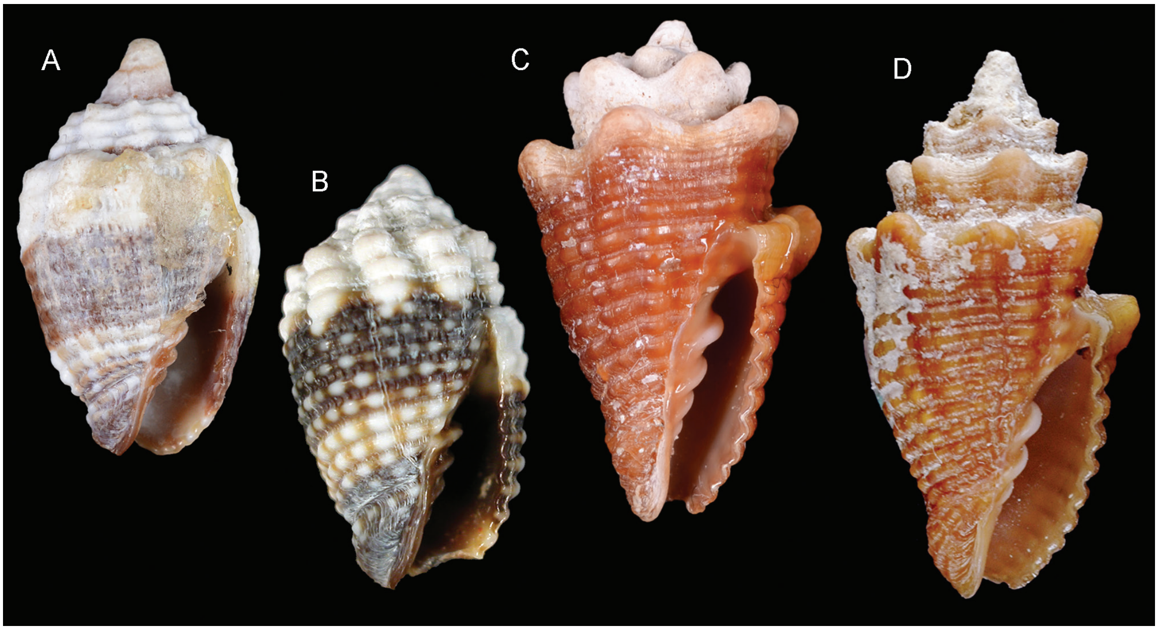

Figure 39. Species of ***Condylomitra* gen. nov.** A, B, ***Condylomitra tuberosa* comb. nov.**; A, syntype, NHMUK 1967899, Philippines, 14.4 mm; B, MNHN IM-2007-30311, Philippines, PANGLAO 2004 Stn R75, 09°32.8′N, 123°42.1′E, 3–35 m. C, D, ***Condylomitra bernhardina* comb. nov.**; C, MNHN IM-2013-54115, 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.

with well-developed fasciole, siphonal notch distinct. Aperture elongate, rather narrow, widening anteriorly. Outer apertural lip gently convex or straight, inner lip with four closely set columellar folds. Radula very narrow, monoserial, with rachidian bearing strong, unpaired medial cusp, flanked with two to eight smaller pointed cusps on each side. Proboscis dorsoventrally flattened.

Distribution: Indo-Pacific, intertidal and upper subtidal depths, mostly on hard substrates.

Species included: *Condylomitra bernhardina* (Röding, 1798)[1] comb. nov., *C. tuberosa* (Reeve, 1845)[1] comb. nov.

Etymology: The name *Condylomitra* combines the Latin word *condylus*, meaning knob, with the suffix *Mitra*, in reference to the characteristic shell sculpture of tubercles that is shared by the species in this newly recognized lineage. Gender feminine.

Remarks: Although each on a quite long branch, *C. bernhardina* and *C. tuberosa* form a clade in our molecular trees and share features of the shell and radula, and the characteristic sculpture pattern allows a rather easy recognition of this group. Because of their superficial similarity, we initially considered *Strigatella lugubris* and '*Mitra*' *pudica* to be possibly related to *Condylomitra*; however, the former is closely related to *Strigatella coronata* in the *Strigatella* clade, and the latter, although it was not sequenced, is excluded from *Condylomitra* by its triserial radula.

GENUS *MAGNAMITRA* HUANG & SALISBURY, 2017

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

Diagnosis: As no material on *M. sandrogorii* was available for the present study, we do not provide our own diagnosis for this recently described genus, and refer to Huang & Salisbury (2017).

Species included: *Magnamitra sandrogorii* Huang & Salisbury, 2017[2].

Distribution: Indo-Pacific, bathyal depths.

Remarks: See remarks under *Calcimitra*.

GENUS *ATRIMITRA* DALL, 1918
(FIG. 40A–C)

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 for this poorly studied genus.

Species included: *Atrimitra caliginosa* (Reeve, 1844)[3] comb. nov., *A. catalinae* (Dall, 1919)[2] comb. nov., *A. effusa* (Broderip, 1836)[3], *A. idae* (Melvill, 1893)[3], *A. orientalis* (Griffith & Pidgeon, 1834)[3] comb. nov., *A. semigranosa* (Martens, 1897)[3] comb. nov.

Distribution: Tropical East Pacific, subtidal depths.

Remarks: see remarks under *Isara*.

Genus *Vicimitra* Iredale, 1929

(Fig. 40D)

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

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

Species included: *Vicimitra prosphora* Iredale, 1929[3] (Fig. 40D).

Distribution: New South Wales, Australia.

Remarks: See remarks under *Quasimitra*.

Genus *Probata* Sarasúa, 1989

(Figs 38E, 40E, F)

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

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* comb. nov.**, holotype, NHMUK 1966718, locality unknown, 34.9 mm. D, *Vicimitra prosphora*, holotype, AMS C.57846, Sydney Harbour, Australia, 45.4 mm. E, *Probata espinosai*, paratype, MNHN-IM-2012-37719, in front of Marianao, Havana, Cuba, 10 mm. F, ***Probata barbadensis* comb. nov.**, MNHN IM-2013-7772, Guadeloupe, KARUBENTHOS Stn GR36, 16°30.6′N, 61°28.4′W, 12 m, 20.6 mm. G, *Dibaphimitra florida*, holotype of *Mitra fergusoni* G. B. Sowerby II, 1874, NHMUK 1879.2.26.133, Panama, 42.7 mm.

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)[1] comb. nov., *P. espinosai* (Sarasúa, 1978)[3].

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 *M. barbadensis* and, even if not conspecific, they are definitely closely related. Thus, we tentatively allocate the name *Probata* to the *M. 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 differs notably in shell proportions and number of columellar folds. The overall plesiomorphic radula of *P. barbadensis* (Fig. 38F) resembles the radula of many other lineages of Mitridae and gives no clue as to where the genus should be assigned.

GENUS DIBAPHIMITRA CERNOHORSKY, 1970

(FIG. 40G)

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

Diagnosis: As no material on *Dibaphimitra florida* was available for the present study, we do not provide our own diagnosis to this poorly studied genus, and refer to Cernohorsky (1970).

Species included: *Dibaphimitra florida* (Gould, 1856)[2].

Distribution: Caribbean, subtidal to upper bathyal depths.

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

DESCRIPTION OF NEW SPECIES

PROFUNDIMITRA TAYLORI FEDOSOV, HERRMANN, KANTOR & BOUCHET **SP. NOV.**

(FIGS 17G, 18A–C)

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, 18A, 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, 1 lv (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. 18C).

Description: Shell medium sized (holotype 24.15 mm, paratype 35.5 mm), fusiform, with high, cyrtoconoid, slightly tilted spire and rather short siphonal canal. Protoconch pointed, subcylindrical, of two or more 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 three oblique columellar folds at mid-height, slightly deepened in aperture and weak in appearance.

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

Radula (of holotype) 0.7–0.75 mm long, 0.14 mm wide, consisting of about 85 rows. Rachidian about 40 µm and laterals 45 µm wide, all three similar, with evenly convex anterior margin, bearing 12–13 moderately long, pointed subequal cusps, those at teeth margins smaller than others.

Distribution: Bismarck Sea off mainland New Guinea and New Ireland; East of New Caledonia, Norfolk Ridge, 580–760 m.

Etymology: The species named after our friend and colleague John D. Taylor of the NHMUK in recognition of his immense contribution to malacology, and in particular to our knowledge of mitrid feeding biology.

Remarks: *Profundimitra taylori* sp. nov. can be readily distinguished from its congeners by its almost smooth shell with faint columellar folds; both features are rather characteristic of *Eumitra*. Members of the latter genus, however, are characterized by more convex whorls, often with subcylindrical early teleoconch whorls. Smooth species of *Calcimitra*, such as *C. labecula*, resemble *P. taylori* sp. nov. in shell proportions and sculpture; however, *Calcimitra* species can be recognized by their generally larger shells with strong columellar folds and, typically, by the presence of a siphonal notch. Finally, the smooth shallow-water *Quasimitra sarmientoi*, although close to *P. taylori* sp. nov. in shell proportions and lack of sculpture, can be differentiated by the intensely coloured shell and distinct siphonal notch in adult specimens. Apart from the mentioned shell characters, the characteristic radula with similar laterals and rachidian differentiates *P. taylori* sp. nov. and its congeners from most other mitrids.

FUSIDOMIPORTA PONDERI FEDOSOV, HERRMANN, KANTOR & BOUCHET **SP. NOV.**

(FIGS 17I, 18I, K)

Type data: *Holotype*: MNHN IM-2013-40665, Papua New Guinea, BIOPAPUA Stn CP3692, SE of Manus I., 02°10′S, 147°19′E, 408–448 m, lv, 25.2 mm (Fig. 18I, K). *Paratype*: BIOPAPUA Stn CP3629, Gulf of Huon, South of Lae, 06°57′S, 147°08′E, 240–269 m, dd, 26.15 mm.

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, cyrtoconoid, of three or more glossy, convex whorls (usually strongly corroded or missing). Teleoconch of six or more 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 eight 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.

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* sp. nov. is uneasy, mainly because of its striking resemblance to (still undescribed) species of *Profundimitra* gen. nov., represented in our analysis by specimens IM-2007-35618 and IM-2007-35711 (both mislaid). The single live-taken specimen of *F. ponderi* sp. nov. 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. In shell proportions and whorl outline, *F. ponderi* sp. nov. is very close to *F. suturata*; however, the latter has lower and wider spiral cords with narrower grooves between them. Some deep-water species of *Gemmulimitra* gen. nov. have a somewhat similar, beaded sculpture, which however is nowhere as strong as in *F. ponderi* sp. nov. Besides, *Gemmulimitra boucheti* has a proportionally broader shell with more convex whorls compared to *F. ponderi* sp. nov. On the contrary, *G. neocaledonica* sp. nov. 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 data set by too few specimens to assess their intraspecific variation and elaborate robust species delimitation criteria.

GEMMULIMITRA NEOCALEDONICA FEDOSOV, HERRMANN, KANTOR & BOUCHET **SP. NOV.**

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 (Fig. 21A, 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, 17.1, 17.3, 15.0, 16.2, 16.2, 16.55, 16.8, 15.05, 23.1, 17.65, 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, 18.4, 15.9, 16.3, 14.0, 9.15, 9.8 mm); Stn 3807, 21°43′S, 166°36′E, 352–372 m, 11 lv (22.6, 20.1, 21.05, 20.7, 20.0, 19.2, 17.4, 20.9, 18.1, 18.2, 19.65 mm); Stn 3810, 21°44′S, 166°38′E, 384–385 m, 8 lv (25.5, 25.85, 29.3, 25.5, 27.4, 21.65, 25.5, 23.3 mm); Stn 3814, 21°49′S, 166°44′E, 331–344 m, 6 lv (22.8, 21.5, 20.6, 21.6, 18.9, 14.1 mm); Stn 3821, 21°53′S, 166°50′E, 211–440 m, 2 lv (25.85 and 25.15 mm); Stn 3823, 21°55′S, 166°55′E, 246–255 m, 2 lv (15.5 and 14.5 mm); Stn 3825, 21°58′S, 166°59′E, 349–405 m, 1 lv (16.2 mm); Stn 3828, 22°00′S, 167°01′E, 300–302 m, 1 lv (16.4 mm); Stn 3829, 22°02′S, 167°05′E, 350–360 m, 1 lv (23.0 mm); TERRASSES Stn 3095, 22°02′S, 167°06′E, 320–380 m, 1 lv (21.5 mm).

Papua New Guinea, BIOPAPUA Stn CP3634, 07°29′S, 147°31′E, 279–290 m, 1 dd (21.75 mm).

Description: Shell small to medium sized (holotype 24.25 mm), elongate-fusiform to almost biconical, heavily sculptured, with narrow aperture and stepped appearance of late teleoconch whorls. Protoconch pointed, cyrtoconoid, translucent, of three or more slightly convex, glossy whorls. Protoconch/teleoconch transition distinct. Teleoconch of about nine whorls; suture canaliculated. Subsutural ramp forming distinct shelf, flat or even slightly inclined inside, giving teleoconch whorls a subcylindrical profile. Whorl periphery slightly convex, early spire whorls sculptured with three strong, closely set, spiral cords overriding low indistinct axial ribs to form series of prominent, axially aligned, beads. On third teleoconch whorl, adapical spiral cord splits into two, and succeeding spire whorls sculptured with four gemmate cords, adapical cord bordering subsutural ramp wavy, slightly narrower than others, delineated from second cord by narrower interspace. On later teleoconch whorls, interspaces between gemmate spiral cords gradually broadening, axial ribs becoming more distinct and sculpture rather reticulate. Last adult and penultimate whorls with 26 axial ribs each. Interspaces between axial ribs and spiral cords forming deep quadrangular depressions with microsculpture of fine co-axial growth lines, sometimes retaining fragments of periostracum forming squamiform projections. Shell base extended to moderately long, tapering, slightly notched siphonal canal. Four gemmate spiral cords on adapical portion of last adult whorl, and 12 cords on shell base and 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, retaining weak reticulate sculpture adapically, with four closely set fine columellar folds at mid-height. Coloration uniformly cream, protoconch white.

Radula (of Paratype 5) 0.62 mm long, 0.13 mm wide, of about 75 rows. Rachidian narrow, about 20 µm wide, bearing eight strong, moderately long, pointed cusps. Laterals attaining 47 µm in width, with straight anterior margin bearing 16+ strong, pointed, rather widely set cusps.

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* sp. nov. and *Fusidomiporta ponderi* sp. nov. The latter species is the one that resembles most *G. neocaledonica* sp. nov., 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* sp. nov. Other species of *Gemmulimitra* gen. nov. differ either in shell shape or in sculpture pattern, and *G. avenacea*, despite being the closest to *G. neocaledonica* sp. nov. in our multi-gene analyses, shows no morphological resemblance to it whatsoever.

IMPLICATIONS OF 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 relationships between the three mitroidean families are clearly established, but the affinities of Mitroidea remain uncertain. The phylogenetic analysis of Fedosov *et al.* (2015) suggested that Mitroidea may be a sister group to Conoidea; this affinity, however, is not supported by any shared morphological features and needs to be further investigated.

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 Cylindromitrinae, 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 helenae*, as addressed by Quinn (1989), deserves special attention. Quinn's description of the

Table 4. Morphology and anatomy of the Mitroidea families

Character	Pyramimitridae	**Charitodoronidae fam. nov.**	Mitridae
Shell	Turriform	Fusiform	Elongate-fusiform to conical or ovate
Columellar folds	1–2 weak or absent	Absent	Absent or 2 (*Eumitra*), otherwise 3–10
Eyes	Absent	Present	Present
Rachidian tooth	Monocuspid	With 5–7 cusps	Mono- to multicuspidate
Lateral teeth	Narrow, monocuspid	Wide, multicuspidate	Absent or wide, multicuspidate
Peristomal rim	Absent	Absent	Present
Buccal mass	Posterior	At anterior or mid-proboscis	Anterior
Epiproboscis	Absent	Absent	Present
Muscular posterior oesophagus	Absent	Present	Absent
Mid-gut gland	Small, tubular	Absent	Absent

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 artefact of poor fixation (with the use of rhum 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: 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*.

3a – *Cancilla* type: it 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

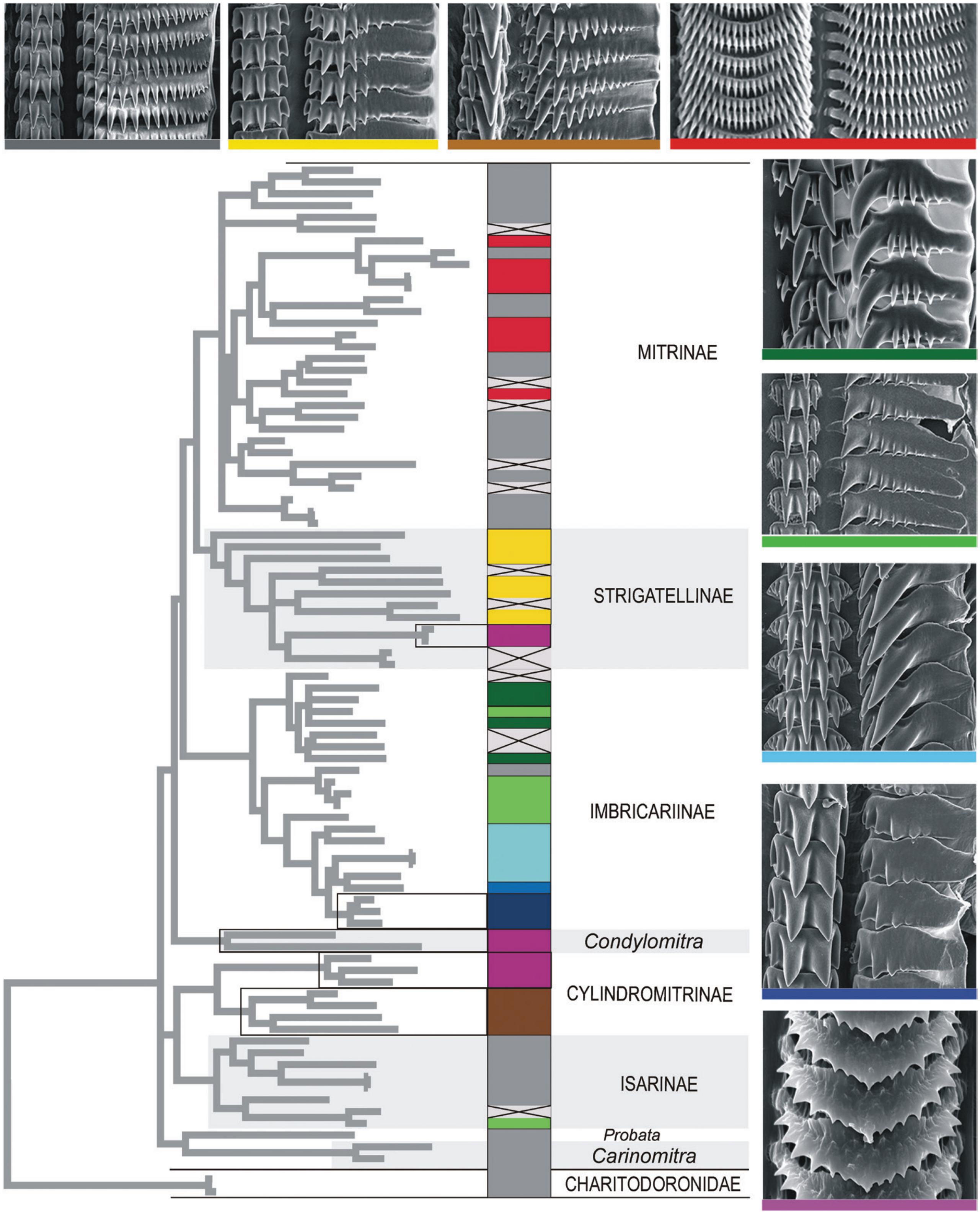

Figure 41. Distribution of different radula types throughout the Mitridae tree. Dark grey – *Mitra* type; yellow – *Strigatella* type; brown – *Nebularia* type; red – *Profundimitra* type; dark green – *Imbricaria* type; light green – *Cancilla* type; light blue – *Scabricola* type; dark blue – *Neocancilla*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

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*.

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 15 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.

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 types of radula, as there are no data on the possible adaptive value of different morphologies and selection pressures that have led to the emergence of the observed diversity. Further studies on the functional morphology and biochemistry of mitrid secretions would in this respect open new perspectives.

TAXONOMY OF MITRIDAE: HISTORICAL CONSIDERATIONS AND NEW ARRANGEMENT

The current Mitridae species list (as indexed in World Register of Marine Species. consulted on 19 August 2017) comprises 402 accepted Recent species, plus the three new species described in the present work. The baseline of Mitridae systematics is the fundamental revisions by Walter Cernohorsky, who first dealt with the subfamily Mitrinae (Cernohorsky, 1976), and later with the Imbricariinae and Cylindromitrinae (Cernohorsky, 1991). Cernohorsky's monographs had a profound impact on mitrid taxonomy and systematics, despite the general lumping attitude prevailing in his time, which resulted in an extensive taxonomic graveyard for many of the species-level taxa he accepted as valid. Several cases of abusive synonymization are demonstrated in the present study. For instance, *Mitra morchii* A. Adams, 1855, considered by Cernohorsky a synonym of *Cancilla isabella*, is, based on Huang & Salisbury (2017) and on our data, not related to *Cancilla* or even to Imbricariinae. Another example is *Mitra millepunctata* G. B. Sowerby III, 1889 synonymized (Cernohorsky, 1976) with *Domiporta carnicolor* despite notable disparity in shell proportions, and later described as *Mitra terryni* Poppe, 2008 (Herrmann, 2017). Altogether the number of valid species of Mitridae was greatly diminished by Cernohorsky, but the rate of species description increased notably in the following decades and over 100 species (i.e. almost 30% of the currently accepted number of species) were described since 1991. This burst of activity in mitrid taxonomy is also notable for being almost entirely accounted for by the amateur community: only ten out of 112 species described in the last 25 years were described by academics. Amateurs perhaps more reluctantly establish new supraspecific taxa, and only two genera *Calcimitra* Huang, 2011 and *Magnamitra* Huang & Salisbury, 2017 were established in the last 25 years, whereas 65 species described over this period were originally placed in *Mitra*.

A concise review of changes in mitrid genus-level taxonomy was presented by Cernohorsky (1970), in a study that itself contained the description of four new genera and subgenera (*Domiporta*, *Dibaphimitra*, *Neocancilla* and *Sohlia*). In the present study, we have re-assessed the genus-level systematics of Recent Mitridae based on a combination of molecular and morphological data. The genus *Charitodoron* is segregated in the newly established family Charitodoronidae. The 26 genera of the revised Mitridae comprise six subfamilies: Mitrinae (with 14 genera), Strigatellinae (with the single genus *Strigatella*), Imbricariinae (with six genera), Cylindromitrinae (with the genera *Pterygia* and *Nebularia*), Isarinae new subfamily (with the genera *Isara* and *Subcancilla*) and Pleioptygmatinae (with the single genus *Pleioptygma*); seven genera, *Atrimitra* Dall, 1918, *Carinomitra* gen. nov., *Condylomitra* gen. nov., *Dibaphimitra* Cernohorsky, 1970, *Magnamitra*

Huang & Salisbury, 2017, *Vicimitra* Iredale, 1929 and *Probata* Sarasúa, 1989 are treated as *incertae sedis*. Undoubtedly the most revolutionary change in the taxonomy of the Mitridae is the falling apart of *Mitra* with the genus in its former taxonomic extension now reassigned to 14 genera, of which six are new. Other noteworthy changes are the transfer of the formerly mitrine *Nebularia* to Cylindromitrinae; of *Strigatella* to its own, newly recognized, subfamily Strigatellinae; of the formerly imbricariine genera *Ziba* and *Domiporta* to Mitrinae; and of *Subcancilla* to the newly established subfamily Isarinae. The genera *Mitra* and *Ziba* now include a much reduced species diversity, as all the Indo-Pacific species earlier placed in *Ziba* are now transferred to *Imbricaria*. The contents of *Imbricaria* is also expanded as a result of the transfer of the Indo-Pacific species of *Subcancilla*, which appear unrelated to the New World species of that genus.

The 32 genera now recognized in the family Mitridae increase considerably the previously accepted genus-level diversity (19 genera, including *Charitodoron*, indexed in WoRMS as of August 2017). Still, the placement of several sequenced species remains uncertain. Lineage 3 represented by MNHN IM-2007-35623 and lineage 16 represented by MNHN IM-2007-30270 did not cluster with any other lineage and were not successfully sequenced for genetic markers other than *COI*. Thus, they at present remain 'hanging' in the list of unallocated Mitridae and may potentially represent two more new genera.

PHYLOGEOGRAPHIC PATTERNS IN THE MITRIDAE

It has been widely known that the Indo-West Pacific harbours the greatest diversity of mitrid species and lineages, and therefore a good representation of IP localities at various depths was a primary requirement to our sampling. Eighty eight of the 103 inferred species of Mitridae and Charitodoronidae in our data set originate from Indo-Pacific localities. Besides, three species were sampled from the Mediterranean and NE Atlantic, two from West Africa, four from the Caribbean and six from the Panamic province (Fig. 42). Twenty-three mitrid genera were sampled in the Indo-Pacific, of which 19 do not occur outside the Indo-Pacific according to our data. Moreover, the subfamilies Imbricariinae and Cylindromitrinae, as circumscribed herein, are represented solely by Indo-Pacific forms. At least three genera (*Episcomitra*, *Isara* and *Ziba*) are found in West Africa, with the first two also inhabiting the Mediterranean. The New World fauna of Mitridae includes at least eight genera in four subfamilies: Mitrinae (*Neotiara*), Strigatellinae (*Strigatella*), Isarinae (*Isara*, *Subcancilla*) and Pleioptygmatinae (*Pleioptygma*), plus the genera *Atrimitra*, *Dibaphimitra* and *Probata* that we treat as *incertae sedis*. The six genera *Atrimitra*, *Dibaphimitra*,

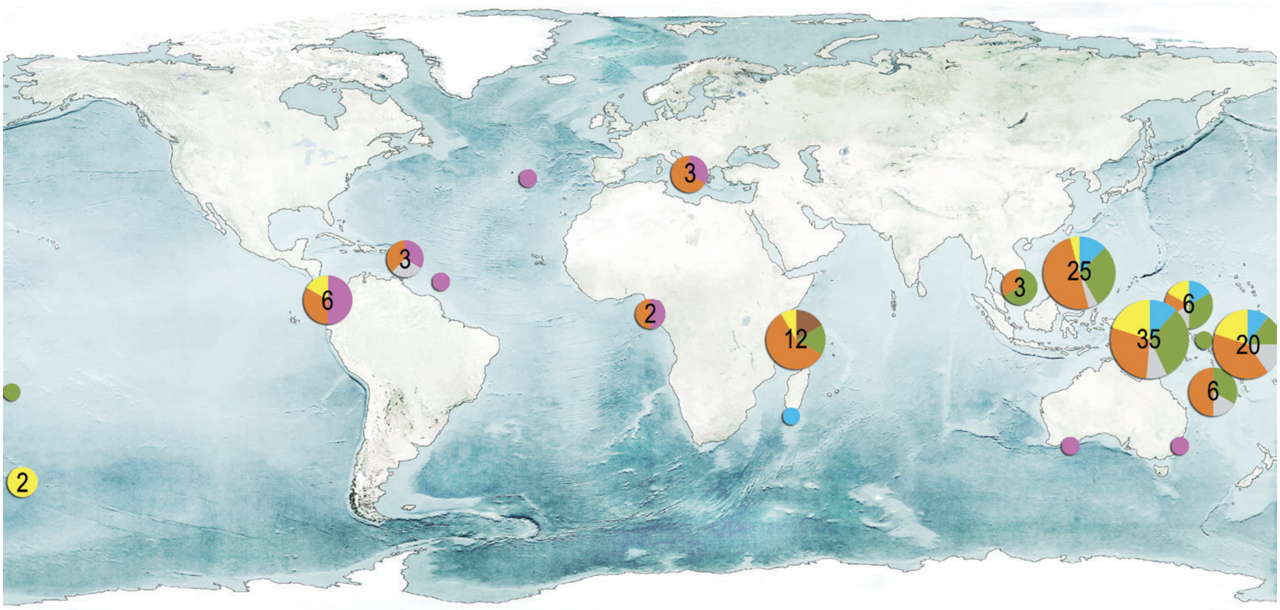

Figure 42. Taxonomic composition (subfamilies) and geographical coverage of our molecular sampling. Diameter of the circles proportional to the number of species in each principal location, which is indicated for each circle with more than one species sampled. **Charitodoronidae fam. nov.** – brown;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

Neotiara, *Pleioptygma*, *Probata* and *Subcancilla* are currently thought to be endemic to Panamic and/or the Caribbean, although a close affinity of Panamic and Caribbean species was herein confirmed only in the genera *Neotiara* and *Subcancilla*.

Of all studied genera, *Charitodoron* probably demonstrates the narrowest range, being confined to deep waters in the Mozambique Chanel and off South Africa. According to some authors (e.g. Obura, 2012), starting in the Eocene, this area served as a main refuge for relict lineages of Tethyan origin which, for some reason, did not give rise to new radiations. The long branch that separates *Charitodoron* on the molecular tree, some characters such as the underived morphology (with only the radula indicating its relatedness to Mitridae), and its low diversity in the Recent fauna, all point to the relict nature of *Charitodoron*. The paucispiral, bulbous protoconch of *Charitodoron* indicates non-planktotrophic development, which correlates well with its restricted distribution.

Conversely, the distribution of *Isara* is the widest among mitrid genera: this is the only genus recorded in more than two major zoogeographical regions of the shelf (as defined by Briggs & Bowen, 2012) – Indo-West Pacific, East Atlantic and West Atlantic (Fig. 42) – and it may be also present in the East Pacific (see remarks under *Isara*). *Isara* species contribute significantly to mitrid diversity in the peripheral Indo-Pacific (South Australia, presumably South Africa) (see Fig. 8), but they are rare and not really diverse in the Central Indo-West Pacific. In our understanding, *Isara* is undoubtedly an old and underived lineage of Mitridae, and this pattern may be interpreted in two different ways. According to one possible scenario, it was once widely distributed in tropical seas and subsequently was replaced by younger and derived lineages in the Central Indo-West Pacific while maintaining its diversity in peripheral areas. The other possible scenario suggests that the primarily Indo-Pacific *Isara*, once 'forced' into subtropical waters by growing competition with younger evolutionary lineages of Mitridae, has adapted to new temperatures and, through this, was capable of spreading beyond the biogeographical limits of the Indo-Pacific. Although most known species of *Strigatella* occur in the Indo-Pacific, an amphi-Pacific distribution characterizes this genus, with at least one species inhabiting shallow water in the Panamic province ending up close to the Indo-Pacific species in both molecular and morphological characters. Finally, if '*Mitra*' *hebes* is related to the species of *Domiporta*, as suggested by shell and radular morphology, the range of that genus would also include West Africa.

The generally low overlap in regional lists of mitrid genera may be interpreted as a consequence of the relatively late major diversification of mitrid lineages, dating back to the time when modern biogeographical barriers were already established, and largely separate evolutionary radiations having taken place in (1) Late Tethys – Paratethys – Indo-Pacific, (2) West Africa and (3) the New World.

We have attempted to circumscribe the bathymetric distribution of the newly delineated genera, based primarily on the locality data of sequenced specimens. Given the patchiness of our data, we arbitrarily divided the sampled depth range from 0 to about 1800 m into four depth intervals: (1) from 0 to 40 m, (2) from 41 to 80 m, (3) from 81 to 300 m and (4) >300 m.

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

The bathymetric distribution of the newly delineated mitrid genera is shown in Figure 43 based on our results (black vertical bars) and literature (grey vertical bars). Because of the very fragmentary data, some of the displayed results are inconsistent, like the disjunct bathymetric range of *Gemmulimitra* and *Subcancilla*. We in fact fully expect that many genera, which in our results are restricted to the 0- to 40-m-depth interval, in fact reach deeper, probably down to 80–120 m. Nevertheless, some general conclusions can be drawn from the observed bathymetric distribution of the genera. The representation of mitrid genera in shallow water is notably higher than at depths in excess of 100–150 m, which mirrors the distribution of species diversity discussed above. Whereas *Gemmulimitra*, *Imbricaria*, *Isara*, *Roseomitra* and *Subcancilla* have

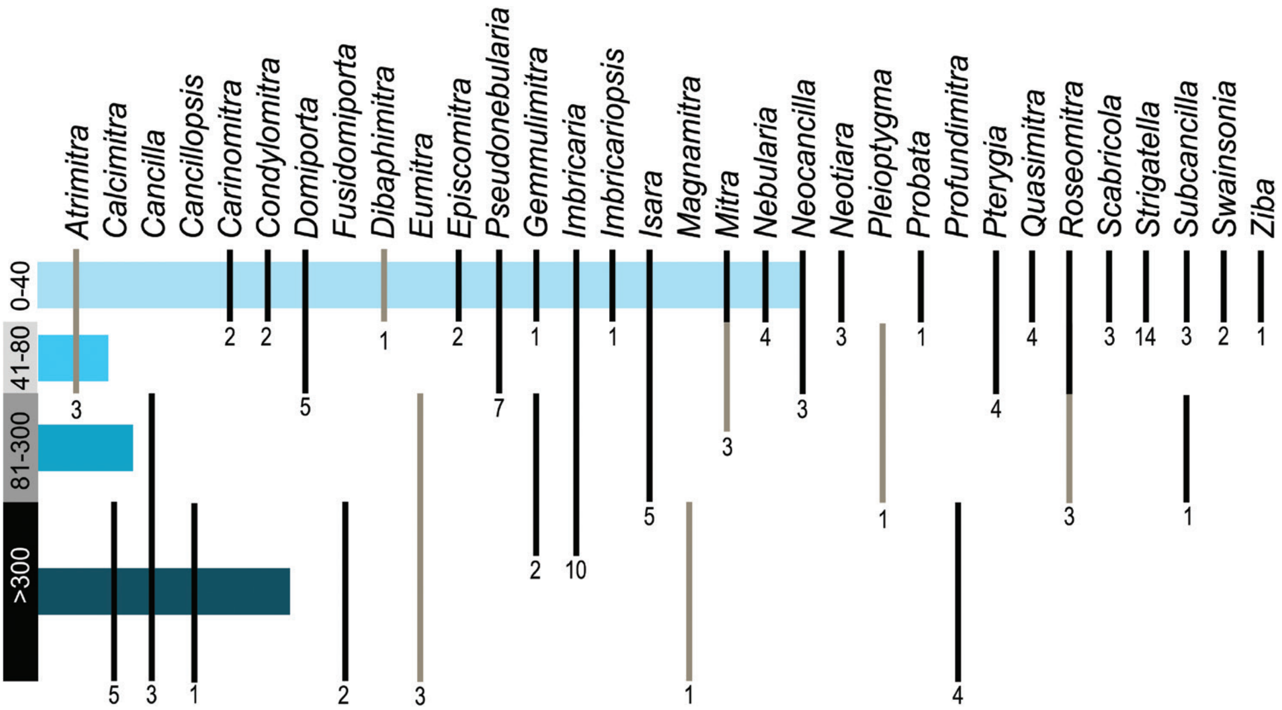

Figure 43. Bathymetric distribution of the genera of Mitridae. Black bars – based on our sampling; grey bars – based on published data (Cernohorsky 1976, 1991; Lozouet, 1991; Huang & Salisbury, 2017). Numbers next to each bar indicate number of species involved. Blue horizontal bars show the proportion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

extensive bathymetric ranges, with congeneric species sampled from the intertidal down to 300–400 m, the mitrid fauna from the greatest depths is essentially represented by specialized lineages (treated here as genera), that do not occur in shallower water. The genera *Calcimitra*, *Cancilla*, *Cancillopsis, Fusidomiporta* and *Profundimitra* represented in our data set by 15 species (plus two species of *Charitodoron*) and the genus *Eumitra* (not included in our phylogenetic studies) constitute several separate radiations that thrive in the deep sea.

Interpretation of the fossil mitrid taxa is difficult, primarily due to the fact that similar shell features, such as shell shape or sculpture pattern, were demonstrated to have evolved convergently in unrelated Recent lineages of the family. The inferred topology of the Mitridae tree, with unresolved early polytomy, further complicates tracing the evolution of shell features and the placement of fossil forms. Cernohorsky (1970, 1976) suggested that the most Recent genera can be traced back to Miocene; however, given the drastic rearrangement of the genus-level taxonomy of the family herein, the validity of Cernohorsky's statement needs to be revisited. Whereas the Oligocene *Clifdenia* is here considered a possible relative of the Recent *Calcimitra*, relationships of the genera *Dentimitra* Koenen, 1890, *Fusimitra* Conrad, 1855 and *Pseudocancilla* Staadt, 1913 are highly speculative. The early Miocene *Austroimbricaria gracilior* (Ihering, 1897), with a low spire and strong columellar folds, is clearly a mitrid; however, it is unclear to which of the conchologically similar *Pterygia* or *Imbricariopsis* it may be close.

WORLD DIVERSITY OF MITRIDAE

Of 103 species included in our molecular data set, 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- to 40-m-depth interval, no new species were identified with confidence. The proportion of unidentified/undescribed species grows with increasing depth and, of 20 species from depths greater than 300 m 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* gen. et sp. nov., *Fusidomiporta ponderi* gen. et sp. nov**.** and *Gemmulimitra neocaledonica* gen. et sp. nov. Thus, an estimate of 30–100 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 vs. deep water can be viewed as a result of recent efforts by collectors and amateur taxonomists. Since the first half of the 19th 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.

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 data set 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.

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