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Phylogeny, systematics, and evolution of the family Costellariidae (Gastropoda: Neogastropoda)

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The neogastropod family Costellariidae is a large and successful group of carnivorous marine mollusks that encompasses about 475 living species. Costellariids are most diverse in the tropical Indo-Pacific at a depth interval of 0–200 m, where they are largely represented by numerous species commonly assigned to the genus *Vexillum*. The present work expands the taxon sampling of a previous phylogeny of the mitriform gastropods to resolve earlier problematic relationships, and thus establish a robust framework of the family, revise its taxonomy, and uncover major trends in the evolution of costellariid morphology. A multicuspidate rachidian is shown to have appeared at least twice in the evolutionary history of the family: it is regarded as an apomorphy of the primarily Indo-Pacific *Vexillum*–*Austromitra*–*Atlantilux* lineage, and has evolved independently in the *Nodicostellaria*–*Mitromica* lineage of the western hemisphere. The genera *Ceratoxancus* and *Latiromitra* are transferred from the Ptychactinidae to the Costellariidae. *Tosapusia*, *Protoelongata*, and *Pusia* are ranked as full genera, the latter with the three subgenera *Pusia*, *Ebenomitra*, and *Vexillena*. *Vexillum* (*Costellaria*) and *Zierliana* are treated as synonyms of *Vexillum*. The replacement name *Suluspira* is proposed for *Visaya* Poppe, Guillot de Suduiraut & Tagaro, 2006, non Ahyong, 2004 (Crustacea). We introduce four new genera, *Alisimitra*, *Costapex*, *Turriplificifer*, and *Orphanopusia*, and characterize their anatomy; 14 new species, mostly from deep water in the Indo-Pacific, are described in the genera *Tosapusia*, *Alisimitra*, *Costapex*, and *Pusia*. At least two species of *Costapex* gen. nov. have been collected from sunken wood.

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ADDITIONAL KEYWORDS: Indo-Pacific – morphology – new genus – new species – phylogeny – radula – taxonomy – *Vexillum*.

INTRODUCTION

The family Costellariidae Macdonald, 1860 encompasses about 475 living species of carnivorous gastropods (WoRMS, 2016), and is widely distributed in

tropical and temperate waters from intertidal to bathyal depths. Like many other neogastropod families, Costellariidae are traced back in the fossil record to the Upper Cretaceous, and their greatest diversity in recent faunas is recorded in the Indo-Pacific (Cernohorsky, 1970; Taylor, Morris & Taylor, 1980; Turner, 2001; Robin & Martin, 2004; Poppe, Tagaro & Salisbury, 2009). Numerous costellariid

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species in the genus *Vexillum* commonly occur sympatrically, and even syntopically, in shallow waters of the tropical Indo-Pacific, predominantly on sandy bottoms, mud, or coral rubble (Cernohorsky, 1966; Ponder, 1998; A. Fedosov, pers. observ.). A little over 30 costellariid species are also known from the Western Atlantic, and the genera *Atlantilux*, *Nodicostellaria*, and *Turricostellaria* are known only from American waters.

Our recent phylogenetic study of mitriform gastropods (Fedosov *et al.*, 2015) confirmed the monophyly of the Costellariidae and characterized its relationships within the Neogastropoda. The ptychactrid genera *Latiromitra* and *Ceratoxancus* were recovered as a sister group to the Costellariidae; the family Volutomitridae and the turbinellid subfamilies Columbariinae and Vasiniae were found to be more distantly related. Noteworthy, the family Mitridae, which was long considered most closely related, showed no affinity whatsoever to the Costellariidae.

Although admittedly new species continue to be routinely discovered and described, we have a fair knowledge of the species-level diversity of the ‘mitre’ families Costellariidae and Mitridae, undoubtedly as a consequence of their interest to shell collectors and amateur taxonomists. By contrast, the genus-level taxonomy in current use remains very traditional and has not significantly departed from that used by Walter Cernohorsky in his review published almost 50 years ago (Cernohorsky, 1970). A case in point is the genus *Vexillum*, which Cernohorsky (1966: 102) viewed as ‘famous dumping grounds for an array of unrelated forms’, a situation that has not significantly changed since then. With 370 valid described species (WoRMS, 2016), *Vexillum* currently encloses 80% of costellariid diversity. Although four subgenera are traditionally accepted, their boundaries remain weakly defined. Species traditionally assigned to *Vexillum* (*Pusia*) typically – though not always – possess a radula with a tricuspidate rachidian (Azuma, 1965; Cernohorsky, 1966; Fedosov & Kantor, 2010). Species classified in *Vexillum* (*Vexillum*) and *Vexillum* (*Costellaria*) both have a multi-cuspidate rachidian (Cernohorsky, 1966), and the criteria of their delimitation are rather conventional. *Vexillum* (*Protoelongata*) was recently established (Herrmann, Stossier & Salisbury, 2014) to accommodate a set of shallow-water species with a pointed multi-whorled protoconch, a black head-foot with few yellow streaks, and a tricuspidate rachidian similar to those depicted by Azuma (1965) for *Pusia*.

Our recent phylogenetic analysis demonstrated that the genus *Vexillum* is not monophyletic. In our tree two species of *Zierliana* were nested in the *Vexillum* *s.s.* clade, and conversely a diversity of deep-water forms fell outside this clade. The deep-water

species of Costellariidae formed four distinct clades, which, together with *Thala*, were referred to as ‘basal Costellariidae’ (Fedosov *et al.*, 2015); these were shown to share a radula of plesiomorphic morphology with a tricuspidate rachidian, similar to the radulae found in the ptychactrid genera *Ceratoxancus*, *Latiromitra*, and *Exilia*.

The inferred relationships of the Costellariidae indicated the need for a considerable rearrangement of its taxonomy. Our analysis had limitations that precluded a formal reassessment of costellariid classification: for instance, none of the western hemisphere taxa were represented in our data set; species from the Mediterranean as well as species of *Austromitra* were missing; and several crucial nodes, important for understanding the evolutionary history of the family, were lacking support. The purpose of the present study is thus to carry out a more thorough analysis of costellariid phylogeny based on an extended molecular data set, supplemented by detailed morphological analysis. Based on results of the phylogenetic analysis, we carry out a reconstruction of the evolutionary history of the family, correlating molecular and morphological characters, and we provide formal descriptions of the new genera *Alisimitra*, *Costapex*, *Turriplificifer*, and *Orphanopusia*, and of 14 new species, mostly from deep water in the Indo-Pacific, in the genera *Tosapusia*, *Alisimitra*, *Costapex*, and *Pusia*.

MATERIAL AND METHODS

TAXON SAMPLING

The present study is largely based on material vouchered in Muséum National d’histoire Naturelle (MNHN), collected during multiple expeditions conducted by MNHN and Institut de recherche pour le développement (IRD), the joint Russian–Vietnamese Tropical Centre, and other *ad hoc* fieldwork (see Acknowledgements). To improve taxon sampling compared with our previous study, 89 additional costellariid specimens were analysed, bringing the total number of specimens studied to 123 (see Table 1). Before 2012, specimens were treated with an isotonic solution of magnesium chloride until relaxed (showing no response to touch), and then a tissue clip was cut. Starting from early 2012, specimens were processed using a microwave oven (Galindo *et al.*, 2014), i.e. in most cases the entire body, or at least the last 1–1.5 whorls, were available for study. Tissue samples were preserved in 96% ethanol. Voucher shells are kept in MNHN or in the repository of the Laboratory of Ecology and Morphology of Marine Invertebrates of the A.N. Severtsov Institute of Ecology and Evolution (IPEE).

Table 1. Specimens included in phylogenetic analyses

Family	Genus	Genus revised	Species	Voucher ID	Expedition	Station	Collection data	BOLD ID	COI	16S	12S	H3
Costellariidae	<i>Vexillum</i> (<i>Vexillum</i>)	<i>Vexillum</i>	<i>plicarium</i>	MNHN IM-2013-13646	PAPUA NIUGINI	PM27	04°59.3'S 145°47.6'E, intertidal	MITRI007-15	KR087312	KR088059	-	KR088139
Costellariidae	<i>Vexillum</i> (<i>Vexillum</i>)	<i>Vexillum</i>	<i>plicarium</i>	MNHN IM-2007-30061	PANGLAO 2004	M5	9°35.5'N 123°43.3'-123°44.3'E, 2 m	NEOGA232-10	KU986473	-	-	-
Costellariidae	<i>Vexillum</i> (<i>Vexillum</i>)	<i>Vexillum</i>	<i>plicarium</i>	S2009-03*	Philippines, Olango Is.		10°16.8'N 124°05.4'E, 10-25 m	-	KU727945	-	-	-
Costellariidae	<i>Vexillum</i> (<i>Vexillum</i>)	<i>Vexillum</i>	<i>formosense</i>	MNHN IM-2007-34552	AURORA 2007	CP2762	15°52'N 121°51'E, 66 m	NEOGA770-10	KU986458	-	-	-
Costellariidae	<i>Vexillum</i> (<i>Vexillum</i>)	<i>Vexillum</i>	<i>formosense</i>	S2009-02*	Philippines, Olango Is.		10°16.8'N 124°05.4'E, 10-25 m	-	KU873937	-	-	-
Costellariidae	<i>Vexillum</i> (<i>Vexillum</i>)	<i>Vexillum</i>	<i>gruneri</i>	MNHN IM-2007-30180	SANTO 2006	VM09	15°35.8'S 167°06.1'E, 10-25 m	NEOGA259-10	KU986459	-	-	-
Costellariidae	<i>Vexillum</i> (<i>Vexillum</i>)	<i>Vexillum</i>	<i>lyratum</i>	30111	SANTO 2006	ED05	15°31.7'S 167°09.4'E, 9-13 m	NEOGA245-10	KU986470	-	-	-
Costellariidae	<i>Vexillum</i> (<i>Vexillum</i>)	<i>Vexillum</i>	<i>lyratum</i>	MNHN IM-2007-30057	SANTO 2006	AT53	15°31.8'S 167°13.6'E, 62-71 m	NEOGA230-10	KU986469	-	-	-
Costellariidae	<i>Vexillum</i> (<i>Vexillum</i>)	<i>Vexillum</i>	<i>rugosum</i>	MNHN IM-2007-30203	PANGLAO 2004	D1	9°37.2'N 123°52.2'E, 2 m	NEOGA280-10	KU986477	-	-	-
Costellariidae	<i>Vexillum</i> (<i>Vexillum</i>)	<i>Vexillum</i>	<i>rugosum</i>	S2009-01*	Philippines, Olango Is.		10°16.8'N 124°05.4'E, 10-25 m	-	KU727944	-	-	-
Costellariidae	<i>Vexillum</i> (<i>Vexillum</i>)	<i>Vexillum</i>	<i>subdivisum</i>	S2009-04*	Philippines, Olango Is.		10°16.8'N 124°05.4'E, 10-25 m	-	KU727946	-	-	-
Costellariidae	<i>Vexillum</i> (<i>Vexillum</i>)	<i>Vexillum</i>	<i>vulpecula</i>	S2009-05*	Philippines, Olango Is.		10°16.8'N 124°05.4'E, 10-25 m	-	KU727947	-	-	-
Costellariidae	<i>Vexillum</i> (<i>Costellaria</i>)	<i>Vexillum</i>	<i>semifasciatum</i>	MNHN IM-2013-11594	PAPUA NIUGINI	PM12	05°00.2'S 145°47.6'E, 0-1 m	MITRI003-15	KR087317	KR088062	KR087404	KR088143
Costellariidae	<i>Vexillum</i> (<i>Costellaria</i>)	<i>Vexillum</i>	<i>amandum</i>	MNHN IM-2007-30342	SALOMON 2	CP2286	8°41' S 157°24' E, 248-253 m	NEOGA305-10	KU986444	-	-	-
Costellariidae	<i>Vexillum</i> (<i>Costellaria</i>)	<i>Vexillum</i>	<i>costatum</i>	MNHN IM-2009-11058	SANTO 2006	DR64	15°27.6'S 167°14.3'E, 6-35 m	-	HQ401586.1	HQ401718.1	HQ401655.1	-
Costellariidae	<i>Vexillum</i> (<i>Costellaria</i>)	<i>Vexillum</i>	<i>costatum</i>	MNHN IM-2007-30005	SANTO 2006	DR64	15°27.6'S 167°14.3'E, 6-35 m	NEOGA207-10	KU986450	-	-	-
Costellariidae	<i>Vexillum</i> (<i>Costellaria</i>)	<i>Vexillum</i>	<i>cf. collinsoni</i>	MNHN IM-2007-30206	PANGLAO 2004	S27	9°37.2'N 123°52.2'E, 2 and 12 m	NEOGA261-10	KU986445	-	-	-
Costellariidae	<i>Vexillum</i> (<i>Costellaria</i>)	<i>Vexillum</i>	<i>deshayesii</i>	MNHN IM-2007-30259	SANTO 2006	DS51	15°31.4'S 167°09.7'E, 5 m	NEOGA274-10	KR087304	-	KR087392	KR088132
Costellariidae	<i>Vexillum</i> (<i>Costellaria</i>)	<i>Vexillum</i>	<i>exasperatum</i>	MNHN IM-2013-11680	PAPUA NIUGINI	PR14	05°12'S 145°48.1'E, 2-3 m	MITRI015-15	KR087305	KR088055	KR087393	KR088133
Costellariidae	<i>Vexillum</i> (<i>Costellaria</i>)	<i>Vexillum</i>	<i>exasperatum</i>	MNHN IM-2007-30012	SANTO 2006	LD01	15°29'S 167°14.9'E, 2-4 m	NEOGA210-10	KU986456	-	-	-
Costellariidae	<i>Vexillum</i> (<i>Costellaria</i>)	<i>Vexillum</i>	<i>exasperatum</i>	MNHN IM-2007-30100	PANGLAO 2004	D1	9°37.2'N 123°52.2'E, 2 m	NEOGA242-10	KU986455	-	-	-
Costellariidae	<i>Vexillum</i> (<i>Costellaria</i>)	<i>Vexillum</i>	<i>flexicostatum</i>	MNHN IM-2007-30283	SANTO 2006	DS51	15°31.4'S 167°09.7'E, 5 m	NEOGA281-10	KU986457	-	-	-

Table 1. Continued

Family	Genus	Genus revised	Species	Voucher ID	Expedition	Station	Collection data	BOLD ID	COI	16S	12S	H3
Costellariidae	<i>Vexillum</i> (<i>Costellaria</i>)	<i>Vexillum</i>	<i>humile</i>	MNHN IM-2007-30325 <i>intertaeniatum</i>	PANGLAO 2004	S22	04°59.1'S 145°47.6'E, 11 m	NEOGA300-10	KU986461	-	-	-
Costellariidae	<i>Vexillum</i> (<i>Costellaria</i>)	<i>Vexillum</i>	-	-	MNHN IM-2007-30305	SANTO 2006	LD01 167°14.9'E, 2-4 m	15°29'S	-	-	-	-
NEOGA289-10 Costellariidae	KU986466 <i>Vexillum</i> (<i>Costellaria</i>)	<i>Vexillum</i>	-	-	MNHN IM-2007-30263	SANTO 2006	LD34 15°33.4'S 167°12.4'E, 2-6 m	15°29'S 167°14.9'E, 2-4 m	-	-	-	-
NEOGA275-10 Costellariidae	KU986465 <i>Vexillum</i> (<i>Costellaria</i>)	<i>Vexillum</i>	-	-	MNHN IM-2007-30308	SANTO 2006	LD01	15°29'S 167°14.9'E, 2-4 m	-	-	-	-
NEOGA291-10 Costellariidae	KU986467 <i>Vexillum</i> (<i>Costellaria</i>)	<i>Vexillum</i>	-	-	PANGLAO 2005	DW2500	24°52'S 159°21'E, 310-320 m	NEOGA499-10	KU986468	-	-	-
Costellariidae	<i>Vexillum</i> (<i>Costellaria</i>)	<i>Vexillum</i>	<i>leforti</i>	MNHN IM-2007-32151	-	-	-	-	-	-	-	-
Costellariidae	<i>Vexillum</i> (<i>Costellaria</i>)	<i>Vexillum</i>	<i>micra</i>	MNHN IM-2013-4734	PAPUA NIUGINI	PB28	05°11.9'S 145°49.6'E, 10 m	MITRI001-15	KR087309	KR088057	KR087397	-
Costellariidae	<i>Vexillum</i> (<i>Costellaria</i>)	<i>Vexillum</i>	<i>micra</i>	MNHN IM-2007-30312	PANGLAO 2004	B12	9°35.6'N 123°43.2'E, 24-27 m	NEOGA295-10	KU986471	-	-	-
Costellariidae	<i>Vexillum</i> (<i>Costellaria</i>)	<i>Vexillum</i>	<i>gloriae</i>	MNHN IM-2013-40634	NT2011	ND3	12°10.084'N 109°17.771'E, 6-18 m	MITRI009-15	KR087306	-	KR087394	KR088134
Costellariidae	<i>Vexillum</i> (<i>Costellaria</i>)	<i>Vexillum</i>	<i>noduliferum</i>	S2009-15*	Philippines, Olango Is.	-	10°16.8'N 124°05.4'E, 10-25 m	-	KU727949	-	-	-
Costellariidae	<i>Vexillum</i> (<i>Costellaria</i>)	<i>Vexillum</i>	<i>roseum</i>	MNHN IM-2007-30327	PANGLAO 2004	S5	9°37.1'N 123°46.1'E, 2-4 m	NEOGA301-10	KU986475	-	-	-
Costellariidae	<i>Vexillum</i> (<i>Costellaria</i>)	<i>Vexillum</i>	<i>roseum</i>	MNHN IM-2007-30267	SANTO 2006	DB65	15°25.8'S 167°13.0'E, 13 m	NEOGA277-10	KU986476	-	-	-
Costellariidae	<i>Vexillum</i> (<i>Costellaria</i>)	<i>Vexillum</i>	<i>sanguisuga</i>	MNHN IM-2013-14245	PAPUA NIUGINI	PR68	05°01.6'S 145°48.1'E, 5 m	MITRI013-15	KR087315	KR088061	KR087402	-
Costellariidae	<i>Vexillum</i> (<i>Costellaria</i>)	<i>Vexillum</i>	<i>sanguisuga</i>	MNHN IM-2007-30101	PANGLAO 2004	M51	9°36.8'N 123°52.2'E, intertidal	NEOGA243-10	KU986478	-	-	-
Costellariidae	<i>Vexillum</i> (<i>Costellaria</i>)	<i>Vexillum</i>	<i>pagodula</i>	MNHN IM-2007-30310	SANTO 2006	DB12	15°36.6'S 167°00.1'E, 10-18 m	NEOGA293-10	KR087310	-	KR087399	KR088137
Costellariidae	<i>Vexillum</i> (<i>Costellaria</i>)	<i>Vexillum</i>	<i>pagodula</i>	MNHN IM-2007-30324	PANGLAO 2004	S25	9°41.5'N 123°51.0'E, 21 m	NEOGA299-10	KU986472	-	-	-
Costellariidae	<i>Vexillum</i> (<i>Costellaria</i>)	<i>Vexillum</i>	<i>pagodula</i>	MNHN IM-2007-30303	SANTO 2006	NR21	15°31.4'S 167°09.7'E, 5 m 3-22 m	NEOGA288-10	KU986439	-	-	-
Costellariidae	<i>Vexillum</i> (<i>Costellaria</i>)	<i>Vexillum</i>	<i>scitulum</i>	MNHN IM-2013-40633	EXBODI	CP3824	21°57'S 166°58'E, 280-296 m	MITRI005-15	KR087316	-	KR087403	KR088142
Costellariidae	<i>Vexillum</i> (<i>Costellaria</i>)	<i>Vexillum</i>	cf. <i>subtruncatum</i>	<i>subtruncatum</i> 30318	MNHN IM-2007-30318	EBISCO	DW2632	21°05'S 160°45'E, 297-378 m	-	-	-	-
NEOGA297-10 Costellariidae	KU986449 <i>Vexillum</i> (<i>Costellaria</i>)	<i>Vexillum</i>	-	-	PANGLAO 2004	S27	9°41.5'N 123°51.0'E, 12 m	NEOGA231-10	KU986479	-	-	-
Costellariidae	<i>Vexillum</i> (<i>Costellaria</i>)	<i>Vexillum</i>	<i>vibex</i>	MNHN IM-2007-30055	-	-	-	-	-	-	-	-

Table 1. Continued

Family	Genus	Genus revised	Species	Voucher ID	Expedition	Station	Collection data	BOLD ID	COI	16S	12S	H3
Costellariidae	<i>Vexillum</i> (<i>Costellaria</i>)	<i>Vexillum</i>	<i>virgo</i>	MNHN IM-2013-13079	PAPUA NIUGINI	PD24	05°05.3'S 145°48.6'E, 3–6 m	MITRI014-15	KR087318	KR088063	KR087405	KR088144
Costellariidae	<i>Vexillum</i> (<i>Costellaria</i>)	<i>Vexillum</i>	<i>virgo</i>	MNHN IM-2007-30004	SANTO 2006	LD05	15°29.6'S 167°14.9'E, 2–5 m	NEOGA206-10	KU986480	-	-	-
Costellariidae	<i>Vexillum</i> (<i>Costellaria</i>)	<i>Vexillum</i>	<i>virgo</i>	MNHN IM-2007-30043	SANTO 2006	LD05	15°29.6'S 167°14.9'E, 2–5 m	NEOGA222-10	KU986481	-	-	-
Costellariidae	<i>Vexillum</i> (<i>Pusia</i>)	<i>Vexillum</i>	<i>cancelarioides</i>	MNHN IM-2013-40631	MNHN IM-2013-40631	TUHAA PAE 2013	AT04 23°25.13'S 149°27.0'W, 12 m	23°25.13'S 149°27.0'W, 12 m	MITRI012-15	KR087301	KR088051	KR087388
KR088128	<i>Vexillum</i> (<i>Pusia</i>)	<i>Vexillum</i>	<i>herosae</i>	MNHN IM-2013-40630	MIRIKY	CP3204	12° 37.03'S 48° 30.3' E, 59–60 m	MITRI017-15	KR087307	-	KR087395	KR088135
Costellariidae	<i>Vexillum</i> (<i>Pusia</i>)	<i>Vexillum</i>	<i>herosae</i>	MNHN IM-2007-30258	SANTO 2006	EP36	15°33.1'–33.3'S 167°12.4'–12.7'E, 20–60 m	NEOGA273-10	KU986460	-	-	-
Costellariidae	<i>Vexillum</i> (<i>Pusia</i>)	<i>Vexillum</i>	<i>discolorium</i>	MNHN IM-2007-30013	SANTO 2006	DB53	15°28.8'S 167°15.2'E, 5 m	NEOGA211-10	KU986452	-	-	-
Costellariidae	<i>Vexillum</i> (<i>Pusia</i>)	<i>Vexillum</i>	<i>discolorium</i>	MNHN IM-2007-30257	SANTO 2006	DB12	15°36.6'S 167°10.1'E, 10–18 m	NEOGA272-10	KU986453	-	-	-
Costellariidae	<i>Vexillum</i> (<i>Pusia</i>)	<i>Vexillum</i>	<i>discolorium</i>	MNHN IM-2007-30287	SANTO 2006	DB12	15°36.6'S 167°10.1'E, 10–18 m	NEOGA282-10	KU986451	-	-	-
Costellariidae	<i>Vexillum</i> (<i>Pusia</i>)	<i>Vexillum</i>	<i>discolorium</i>	MNHN IM-2007-30280	SANTO 2006	DB53	15°28.8'S 167°15.2'E, 5 m	NEOGA279-10	KU986454	-	-	-
Costellariidae	<i>Vexillum</i> (<i>Pusia</i>)	<i>Vexillum</i>	<i>infaustum</i>	MNHN IM-2007-30245	PANGLAO 2004	S27	9°41.5'N 123°51.0'E, 12 m	NEOGA266-10	KU986463	-	-	-
Costellariidae	<i>Vexillum</i> (<i>Pusia</i>)	<i>Vexillum</i>	<i>infaustum</i>	MNHN IM-2007-30248	PANGLAO 2004	S18	9°41.5'N 123°51.0'E, 12 m	NEOGA288-10	KU986464	-	-	-
Costellariidae	<i>Vexillum</i> (<i>Pusia</i>)	<i>Vexillum</i>	<i>infaustum</i>	MNHN IM-2007-30249	PANGLAO 2004	S25	9°41.5'N 123°51.0'E, 21 m	NEOGA269-10	KU986462	-	-	-
Costellariidae	<i>Vexillum</i>	<i>Vexillum</i>	sp.	MNHN IM-2007-30239	PANGLAO 2004	D1	9°37.2'N 123°52.2'E, 2 m	NEOGA263-10	KU986436	-	-	-
Costellariidae	<i>Vexillum</i>	<i>Vexillum</i>	sp.	MNHN IM-2007-30255	SANTO 2006	DS31	15°31.4'S 167°09.7'E, 5 m	NEOGA270-10	KU986433	-	-	-
Costellariidae	<i>Vexillum</i>	<i>Vexillum</i>	sp.	MNHN IM-2007-30069	EBISCO	DW2588	19°46'S 158°26'E, 175–200 m	NEOGA236-10	KU986434	-	-	-
Costellariidae	<i>Vexillum</i>	<i>Vexillum</i>	sp.	MNHN IM-2007-30346	BOAI	CP2479	16°44.9S 167°51.8E, 350–358 m	NEOGA306-10	KU986442	-	-	-
Costellariidae	<i>Vexillum</i>	<i>Vexillum</i>	sp.	MNHN IM-2007-30288	SANTO 2006	FS79	15°33.1'S 167°09.6'E, 2 m	NEOGA283-10	KU986437	-	-	-
Costellariidae	<i>Vexillum</i>	<i>Vexillum</i>	sp.	MNHN IM-2007-30296	SANTO 2006	DS31	15°31.4'S 167°09.7'E, 5 m	NEOGA286-10	KU986441	-	-	-
Costellariidae	<i>Vexillum</i>	<i>Vexillum</i>	sp.	MNHN IM-2007-30349	EBISCO	DW2631	21°03'S 160°44'E, 372–404 m	NEOGA308-10	KU986443	-	-	-
Costellariidae	<i>Vexillum</i>	<i>Vexillum</i>	sp.	MNHN IM-2007-33510	SANTO 2006	LD34	15°33.4'S 167°12.4'E, 2–6 m	NEOGA713-10	KU986432	-	-	-
Costellariidae	<i>Vexillum</i>	<i>Vexillum</i>	sp.	MNHN IM-2007-38136	MIRIKY	CP3203	12° 35.92' S 48° 35.22' E, 50–52 m	MITRI105-16	KU986435	-	-	-
Costellariidae	<i>Zierhiana</i>	<i>Vexillum</i>	<i>ziervogelii</i>	MNHN IM-2013-15865	PAPUA NIUGINI	PM41	05°08.1'S 145°49.3'E, 0–1 m	MITRI010-15	KR087326	KR088072	KR087413	KR088151

Table 1. Continued

Family	Genus	Genus revised	Species	Voucher ID	Expedition	Station	Collection data	BOLD ID	COI	16S	12S	H3
Costellariidae	<i>Zieritana</i>	<i>Vexillum</i>	<i>uolademarii</i>	MNHN IM-2013-12694	PAPUA NIUGINI Western	PM8	05°15.3'S 145°46.6'E, 0–1 m	MITRI002-15	KR087325	KR088071	KR087412	–
Costellariidae	<i>Austrornitra</i>	<i>Austrornitra</i>	sp.	MNHN IM-2013-40667*	Australia Tasmania	WE03	33°59.6'S 122°13.33'E, 11 m	MITRI138-16	KU986402	–	KU876533	KU876547
Costellariidae	<i>Austrornitra</i>	<i>Austrornitra</i>	<i>vineta</i>	MNHN IM-2013-40671	Tasmania	TA21	42°59.93'S 147°39.92'E, intertidal	MITRI098-16	KU986405	KU873935	KU876536	KU876550
Costellariidae	<i>Austrornitra</i>	<i>Austrornitra</i>	aff. <i>volucra</i>	MNHN IM-2013-40672	Tasmania	TA62	41°46.05'S 145°17.95'E, intertidal	MITRI099-16	KU986403	–	KU876534	KU876548
Costellariidae	<i>Austrornitra</i>	<i>Austrornitra</i>	<i>scita</i>	MNHN IM-2013-40673	Tasmania	TA58	41°07.55'S 144°40.14'E, 1–4 m	MITRI100-16	KU986404	–	KU876535	KU876549
Costellariidae	<i>Atlantilux</i>	<i>Atlantilux</i>	<i>exigua</i>	MNHN IM-2009-31184			KARUBENTHOS	GS02	–	–	–	–
16°20.942'N, 61°34.392'W, intertidal	MITRI109-16	KU986400	KU873933	KU876531								
Costellariidae	<i>Vexillum</i> (<i>Pusia</i>)	<i>Atlantilux</i>	<i>puella</i>	MNHN IM-2013-20368			KARUBENTHOS	GM06	16°09.0'N 61°33.7'W, intertidal	MITRI130-16	–	KU873934
KU876532	–	–	–	–	–	–	–	–	–	–	–	–
Costellariidae	<i>Vexillum</i> (<i>Costellaria</i>)	<i>Atlantilux</i>	<i>nudospicula</i>	MNHN IM-2013-40632	AURORA 2007	CP2794	15°57'N 121°49'E, 453–460 m	MITRI006-15	–	–	KR087398	KR088136
Costellariidae	<i>Vexillum</i> (<i>Pusia</i>)	<i>Atlantilux</i>	<i>rubra</i>	MNHN IM-2013-1747	PAPUA NIUGINI	PB10	05°17.9'S 145°46.7'E, 10 m	MITRI016-15	KR087314	KR088060	KR087401	KR088141
Costellariidae	<i>Vexillum</i> (<i>Pusia</i>)	<i>Atlantilux</i>	<i>rubra</i>	MNHN IM-2007-30819	PANGLAO 2004	B9	9°37.2'N 123°52.2'E, 2 m 8–9 m	NEOGA298-10	KU986401	–	–	–
Costellariidae	<i>Vexillum</i> (<i>Pusia</i>)	<i>Atlantilux</i>	<i>rubra</i>	S2009-08*	Philippines, Olango Is.		10°16.8'N 124°05.4'E, 10–25 m	–	KU727948	–	–	–
Costellariidae	<i>Vexillum</i> (<i>Pusia</i>)	<i>Pusia</i> (<i>Pusia</i>)	<i>lauta</i>	MNHN IM-2013-47927*	KAVIENG	KR20	02°33.2'S 150°48.2'E, 3–20 m	MITRI091-16	KU986423	–	KU876541	KU876556
Costellariidae	<i>Vexillum</i> (<i>Pusia</i>)	<i>Pusia</i> (<i>Pusia</i>)	<i>vassardi</i> n. sp.	MNHN IM-2013-40682	ATIMO VATAE	TS4	25°02.3'S 47°00.3'E, 22–24 m	MITRI087-16	KU986425	KU873938	KU876543	KU876558
Costellariidae	<i>Vexillum</i> (<i>Ebenomitra</i>)	<i>Pusia</i>	<i>ebenus</i>	MNHN IM-2013-40660*	Sicily, Ciracuse	PS01	37°0.460'N 15°18.62'E, 6–12 m	MITRI134-16	KU986421	–	KU876540	KU876555
Costellariidae	<i>Vexillum</i> (<i>Ebenomitra</i>)	<i>Pusia</i>	<i>saignyvi</i>	MNHN IM-2013-40674	Sicily, Ciracuse	PS01	37°0.460'N 15°18.62'E, 6–12 m	MITRI097-16	KU986424	–	KU876542	KU876557
Costellariidae	<i>Vexillum</i> (<i>Vexillena</i>)	<i>Pusia</i>	<i>balutensis</i>	MNHN IM-2013-40637	BIOPAPUA	CP3747	05°33'S 155°59'E, 458 m	MITRI020-15	KR087300	KR088050	KR087387	KR088127
Costellariidae	<i>Vexillum</i> (<i>Vexillena</i>)	<i>Pusia</i>	<i>johnuolffi</i>	MNHN IM-2007-32140	EBISCO	DW2513	24°06'S 159°42'E, 280–500 m	NEOGA495-10	KU986422	–	–	–
Costellariidae	<i>Vexillum</i> (<i>Vexillena</i>)	<i>Pusia</i>	cf. <i>choslenae</i>	MNHN IM-2007-38378	EXBODI	CP3826	21°52'S 166°51'E, 354–509 m	MITRI060-15	KR087302	KR088052	KR087389	KR088129
Costellariidae	<i>Vexillum</i> (<i>Vexillena</i>)	<i>Pusia</i>	cf. <i>choslenae</i>	MNHN IM-2007-32371	EBISCO	DW2528	22°49'S 159°23'E, 320–345 m	NEOGA524-10	KU986420	–	–	–
Costellariidae	Gen.	<i>Pusia</i> (<i>Vexillena</i>)	<i>jenyai</i> n. sp.	MNHN IM-2007-32136	EBISCO	DW2607	19°33'S 158°40'E, 400–413 m	NEOGA494-10	KU986419	–	–	–

Table 1. Continued

Family	Genus	Genus revised	Species	Voucher ID	Expedition	Station	Collection data	BOLD ID	COI	16S	12S	H3
Costellariidae	<i>Vexillum</i>	<i>Orphanopusia</i>	<i>patriarchalis</i>	MNHN IM-2013-10241	PAPUA NIUGINI	PS04	05°10.0'S 145°50.1'E, 12 m	MITRI008-15	KR087311	KR088058	KR087400	KR088138
Costellariidae	<i>Vexillum</i>	<i>Turriplicifer</i>	<i>australis</i>	MNHN IM-2013-40675	Western Australia	WE08	33°54.95'S 121°54.6'E, 5-30 m	MITRI103-16	KU986408	KU873936	KU876538	KU876552
Costellariidae	<i>"Astromitra"</i>	<i>Turriplicifer</i>	aff. <i>cinnamomea</i>	MNHN IM-2013-40668* (<i>Protoelongata</i>)	Western Australia <i>Protoelongata</i>	WE03	33°59.6'S 122°13.33'E, 11 m	MITRI139-16	KU986407	-	KU876537	KU876551
Costellariidae	<i>Vexillum</i>			KR087391	KR088131	<i>dekkersi</i>	MNHN IM-2007-30242	PANGLAO 2004	B7	09°35.9'N		
123°51.8'E, 4-30 m	<i>Vexillum</i>	KF671189	KR088054	(<i>Protoelongata</i>)	<i>Protoelongata</i>		<i>loyalyensis</i>	MNHN IM-2007-30307	SANTO 2006	NB43	15°35.6'S	
Costellariidae	<i>Vexillum</i>	NEOGA290-10	KU986418	-	-	-	<i>KARUBENTHOS</i>	GR18	16°05.8'N 61°46.3'W, intertidal	MITRI144-16	KU986417	-
Costellariidae	<i>Vexillum</i>	<i>Nodicostellaria</i>	<i>laterculata</i>	MNHN IM-2013-9022*								
-	KU876554											
Costellariidae	<i>Thala</i>	<i>Thala</i>	<i>exilis</i>	MNHN IM-2013-3389	PAPUA NIUGINI	PM25	05°01.1'S 145°47.9'E, intertidal	MITRI011-15	KR087299	KR088048	KR087384	-
Costellariidae	<i>Thala</i>	<i>Thala</i>	<i>jaculanda</i>	MNHN IM-2007-30240	PANGLAO 2004	B9	9°37.2'N 123°52.2'E, 2 m 8-9 m	NEOGA264-10	KU986427	-	-	-
Costellariidae	<i>Thala</i>	<i>Thala</i>	sp.	MNHN IM-2007-30289	SANTO 2006	VM54	15°28.9'S 167°15.5'E, intertidal	NEOGA284-10	KU986426	-	-	-
Costellariidae	<i>Alisimitra</i>	<i>Alisimitra</i>	<i>fuscolineata</i>	MNHN IM-2007-39271	TARASOC	DW3429	16°43'S 150°38'W, 493-540 m	MITRI108-16	KU986415	-	-	-
Costellariidae	Gen.	<i>Alisimitra</i>	<i>samadae</i>	MNHN IM-2013-40638	PAPUA NIUGINI	CP4079	04°34'S 145°52'E, 960 m	MITRI019-15	-	KR088000	KR087344	KR088088
Costellariidae	Gen.	<i>Alisimitra</i>	<i>deprgesi</i>	MNHN IM-2007-38256	EBISCO	DW2606	19°37'S 158°42'E, 442-443 m	MITRI018-15	KR087244	KR087997	KR087339	KR088085
Costellariidae	Gen.	<i>Alisimitra</i>	<i>barazeri</i>	MNHN IM-2007-38639	TARASOC	DW3434	16°42'S 151°03'W, 700-785 m	MITRI106-16	KU986412	-	-	-
Costellariidae	Gen.	<i>Alisimitra</i>	<i>barazeri</i>	MNHN IM-2007-39400	TARASOC	DW3452	16°51'S 151°19'W, 600-705 m	MITRI022-15	KR087248	KR088001	KR087345	KR088089
Costellariidae	Gen.	<i>Alisimitra</i>	<i>barazeri</i>	MNHN IM-2013-40664*	BIOPAPUA	CP3724	05°59'S 147°39'E, 860-880 m	MITRI136-16	KU986406	-	-	-
Costellariidae	<i>Tongsuapusia</i>	<i>Alisimitra</i>	<i>tehuorum</i>	MNHN IM-2007-39258	TARASOC	DW3458	16°46'S 151°23'W, 573-611 m	MITRI107-16	KU986411	-	-	-
Costellariidae	<i>Tongsuapusia</i>	<i>Alisimitra</i>	<i>tehuorum</i>	MNHN IM-2013-19796*	PAPUA NIUGINI	DW3983	05°12'S 146°59'E, 470-508 m	MITRI129-16	KU986416	-	-	-
Costellariidae	<i>Tongsuapusia</i>	<i>Alisimitra</i>	<i>tehuorum</i>	MNHN IM-2013-40663*	TERRASSES	DW3036	22°41'S 168°58'E, 800 m	MITRI135-16	KU986414	-	-	-
Costellariidae	<i>Tongsuapusia</i>	<i>Alisimitra</i>	<i>tehuorum</i>	MNHN IM-2013-44146	NANHAI	CP4102	15°03'N 116°31'E, 339-533 m	MITRI140-16	KU986409	-	-	-
Costellariidae	Gen.	<i>Costapex</i>	<i>joliveti</i>	MNHN IM-2013-40132	PAPUA NIUGINI	CP4055	03°03'S 142°18'E, 370-374 m	MITRI024-15	KR087250	KR088003	KR087347	-
Costellariidae	Gen.	<i>Costapex</i>	<i>joliveti</i>	MNHN IM-2013-40666*	AURORA 2007	CP2720	14°27'N 121°47'E, 300-301 m	MITRI137-16	KU986413	-	-	-

Table 1. *Continued*

Family	Genus	Genus revised	Species	Voucher ID	Expedition	Station	Collection data	BOLD ID	COI	16S	12S	H3
Costellariidae	Gen.	<i>Costapex</i> gen. nov.	<i>sulcatus</i>	MNHN IM-2013-40627	PANGLAO 2005	CP2381	08°43'N 123°19'E, 259–280 m	MITRI075-15	KR087246	–	KR087342	–
Costellariidae	Gen.	<i>Costapex</i> gen. nov.	<i>levis</i> n. sp.	MNHN IM-2013-40628	BIOPAPUA	DW3777	05°01'S 152°00'E, 40–619 m	MITRI076-15	KR087245	–	KR087341	KR088087
Costellariidae	Gen.	<i>Costapex</i> gen. nov.	<i>levis</i> n. sp.	MNHN IM-2009-4609	PANGLAO 2005	CP2358	8°52.1'S 123°37.1'E, 569–583 m	–	FM999162	FM999111	FM999080	–
Costellariidae	Gen.	<i>Costapex</i> gen. nov.	cf. <i>levis</i> n. sp.	MNHN IM-2013-40629	BIOPAPUA	CP3652	05°56'S 147°08'E, 700–740 m	MITRI077-15	–	KR087998	KR087340	KR088086
Costellariidae	Gen.	<i>Costapex</i> gen. nov.	n. sp.	MNHN IM-2013-4814	PAPUA NIUGINI	CP3949	05°12'S 145°51'E, 380–407 m	MITRI023-15	KR087249	KR088002	KR087346	–
Costellariidae	Gen.	<i>Costapex</i> gen. nov.	n. sp.	MNHN IM-2007-31766	SANTO 2006	AT96	15°07'S 166°53'E, 328–354 m	NEOGA382-10	KU986410	–	–	–
Costellariidae	Gen.	<i>Costapex</i> gen. nov.	<i>exbodi</i> n. sp.	MNHN IM-2013-40626	EXBODI	CP3835	22°06'S 167°06'E, 325–346 m	MITRI133-16	–	–	KU876539	KU876553
Costellariidae	<i>Vexillum</i>	<i>Tosapusia</i>	<i>isaoi</i>	MNHN IM-2013-40636	BIOPAPUA	CP3748	05°37'S 154°01'E, 398–399 m	MITRI021-15	KR087308	KR088056	KR087396	–
Costellariidae	<i>Vexillum</i>	<i>Tosapusia</i>	<i>isaoi</i>	MNHN IM-2007-34557	AURORA 2007	CP2709	15°12'N 121°34'E, 244–286 m	NEOGA771-10	KR087303	KR088053	KR087390	KR088130
Costellariidae	<i>Vexillum</i>	<i>Tosapusia</i>	<i>evelynae</i>	MNHN IM-2007-36747	MIRIKY	CP3289	14°29'S 47°26'E, 332–379 m	MITRI104-16	KU986448	–	–	–
Costellariidae	<i>Vexillum</i>	<i>Tosapusia</i>	<i>evelynae</i>	MNHN IM-2013-40669*	MIRIKY	CP3250	15°22'S 46°00'E, 493–750 m	MITRI146-16	KU986447	–	–	–
Costellariidae	<i>Vexillum</i>	<i>Tosapusia</i>	<i>evelynae</i>	MNHN IM-2013-40670*	MIRIKY	CP3283	14°52'S 46°56'E, 228–257 m	MITRI147-16	KU986446	–	–	–
Costellariidae	<i>Vexillum</i>	<i>Tosapusia</i>	<i>duplex</i>	MNHN IM-2013-44575*	NANHAI	CP4118	20°01'N 115°02'E, 700–723 m	MITRI141-16	KU986474	–	–	–
Costellariidae	<i>Vexillum</i>	<i>Tosapusia</i>	aff. <i>duplex</i>	MNHN IM-2007-35967	BIOPAPUA	CP3741	09°14'S 152°18'E, 694–766 m	MITRI069-15	KR087313	–	–	KR088140
Costellariidae	Gen.	<i>Tosapusia</i>	cf. <i>duplex</i>	MNHN IM-2007-35624	CONCALIS	CP3026	20°17'S 163°50'E, 590–809 m	NEOGA839-10	KU986429	–	–	–
Costellariidae	Gen.	<i>Tosapusia</i>	<i>myurella</i> n. sp.	MNHN IM-2007-30847	SALOMON 2	CP2189	08°20' S 160°02' E, 660–854 m	NEOGA307-10	KR087243	–	KR087338	–
Costellariidae	Gen.	<i>Tosapusia</i>	<i>vittaz</i> n. sp.	MNHN IM-2013-40624	BIOPAPUA	CP3719	06°03'S 147°36'E, 410 m	MITRI074-15	KR087247	KR087999	KR087343	–
Costellariidae	Gen.	<i>Tosapusia</i>	<i>longirostris</i> n. sp.	MNHN IM-2007-34550	AURORA 2007	CP2707	15°04'N 121°41'E, 368–442 m	NEOGA769-10	KU986428	–	–	–
Costellariidae	Gen.	<i>Tosapusia</i>	<i>turriiformis</i> n. sp.	MNHN IM-2013-19792*	PAPUA NIUGINI	DW3983	05°12'S 146°59'E, 470–508 m	MITRI128-16	KU986440	–	–	–
Costellariidae	Gen.	<i>Tosapusia</i>	<i>bismarckiana</i> n. sp.	MNHN IM-2013-19695	PAPUA NIUGINI	CP3979	04°44'S 146°11'E, 540–580 m	MITRI127-16	KU986438	–	–	–
Costellariidae	<i>Cerataxancus</i>	<i>Cerataxancus</i>	<i>teramahii</i>	MNHN IM-2007-36797	TERRASSES	DW3077	23°15'S 168°14'E, 420–540 m	MITRI061-15	KR087239	–	–	KR088080
Costellariidae	<i>Cerataxancus</i>	<i>Cerataxancus</i>	<i>leios</i>	MNHN IM-2007-35024	NORFOLK 2	DW2060	24°40'S 168°39'E, 582–600 m	NEOGA820-10	KR087236	–	–	KR088077
Costellariidae	<i>Cerataxancus</i>	<i>Cerataxancus</i>	cf. <i>melichrous</i>	MNHN IM-2013-40623	EXBODI	DW3914	19°45'S 165°45'E, 620–725 m	MITRI068-15	KR087235	KR087992	KR087333	–
Costellariidae	<i>Cerataxancus</i>	<i>Cerataxancus</i>	sp.	MNHN IM-2007-39277	TARASOC	DW3394	15°49'S 148°17'W, 500–510 m	MITRI055-15	KR087237	–	–	KR088078

Table 1. Continued

Family	Genus	Genus revised	Species	Voucher ID	Expedition	Station	Collection data	BOLD ID	COI	16S	12S	H3
Costellariidae	<i>Ceratoxaneus</i>	<i>Ceratoxaneus</i>	sp.	MNHN IM-2007-38552	TARASOC	DW3401	15°51'S 148°18'W, 789–831 m	MITRI081-15	KR087238	KR087993	KR087334	KR088079
Costellariidae	<i>Latiromitra</i>	<i>Latiromitra</i>	<i>barthelouii</i>	MNHN IM-2007-35820	SALOMONBOA ³	CP2800	08°41'S 161°04'E, 556–864 m	NEOGA854-10	KR087265	–	KR087358	KR088100
Costellariidae	<i>Latiromitra</i>	<i>Latiromitra</i>	<i>crossneri</i>	MNHN IM-2007-38178	MIRIKY	no data	no data	MITRI070-15	KR087266	KR088016	KR087359	KR088101
Psychatracidae	<i>Exilia</i>	<i>Exilia</i>	<i>vagrans</i>	MNHN IM-2007-34067	SALOMON 2	CP2251	07°28' S 156°14' E, 1000–1050 m	NEOGA752-10	KR087258	–	–	KR088097
Psychatracidae	<i>Exilia</i>	<i>Exilia</i>	<i>"hilgendorfi"</i>	MNHN IM-2007-34612	AURORA 2007	CP2751	15°36'N 121°56'E, 1456–1471 m	NEOGA773-10	KR087254	–	–	KR088093
Psychatracidae	<i>Exilia</i>	<i>Exilia</i>	<i>"hilgendorfi"</i>	MNHN IM-2007-38603	TARASOC	DW3493	17°28' S 149°27' W, 556–565 m	MITRI073-15	KR087256	KR088008	KR087351	KR088095
Psychatracidae	<i>Exilia</i>	<i>Exilia</i>	<i>"hilgendorfi"</i>	MNHN IM-2007-36877	MIRIKY	CP3187	12°30' S 48°08' E, 691–695 m	MITRI071-15	KR087255	KR088007	KR087350	KR088094
Psychatracidae	<i>Exilia</i>	<i>Exilia</i>	<i>krigei</i>	MNHN IM-2007-38331	MAINBAZA	CC3171	25°59' S 34°42' E, 771–776 m	MITRI072-15	KR087257	KR088009	KR087352	KR088096
Volutomitridae	<i>Exilioidea</i>	<i>Exilioidea</i>	sp.	MNHN IM-2007-34633	AURORA 2007	CP2690	14°58' N 123°03' E, 1071–1147 m	NEOGA777-10	KR087259	KR088010	–	–
Volutomitridae	<i>Exilioidea</i>	<i>Exilioidea</i>	sp.	MNHN IM-2013-40625	PAPUA NIUGINI	CP3963	05°06' S 145°53' E, 960–980 m	MITRI067-15	KR087260	KR088011	KR087353	–
Volutomitridae	<i>Microvolata</i>	<i>Microvolata</i>	<i>joloensis</i>	MNHN IM-2013-40620	BIOPAPUA	DW3720	06°03' S 147°35' E, 520–523 m	MITRI086-15	–	KR088017	KR087360	KR088102
Volutomitridae	<i>Volutomitra</i>	<i>Volutomitra</i>	<i>glabella</i>	MNHN IM-2007-35070	CONCALIS	DW3003	18°34' S 163°08' E, 450–454 m	NEOGA824-10	KR087319	KR088064	KR087406	KR088145
Volutomitridae	<i>Volutomitra</i>	<i>Volutomitra</i>	<i>ziczac</i>	MNHN IM-2007-35073	CONCALIS	DW2944	18°59' S 163°24' E, 320–335 m	NEOGA826-10	KR087321	KR088066	KR087408	KR088147
Volutomitridae	<i>Volutomitra</i>	<i>Volutomitra</i>	sp.	MNHN IM-2007-38357	TERRASSES	DW3123	22°53' S 167°13' E, 420–450 m	MITRI085-15	KR087320	KR088065	KR087407	KR088146
Columbaridae	<i>Fustifusus</i>	<i>Fustifusus</i>	<i>pinicola</i>	MNHN IM-2007-43438	TERRASSES	DW3120	22°44' S 167°15' E, 320–360 m	NEOGA932-10	KR087262	KR088013	KR087355	–
Columbaridae	<i>Coluzea</i>	<i>Coluzea</i>	cf. <i>liriope</i>	MNHN IM-2007-38972	MAINBAZA	CP3139	23°35' S 36°06' E, 1092–1195 m	MITRI082-15	KR087242	KR087995	KR087336	KR088083

Specimens were initially segregated into morphospecies based on shell morphology. Then the barcode fragment of the cytochrome *c* oxidase subunit I (*COI*) gene was sequenced for all specimens with tissue clips available. A phylogenetic analysis was used to check whether the morphospecies corresponded to monophyletic groups or not, each including specimens separated by low genetic distances (compared with between-group genetic distances). The generally low number of sequenced specimens per species hampered the use of automatic species delimitation tools. Finally, one specimen for each species, as defined using shell characters and *COI* sequences, was also sequenced for additional genes, *16S* rRNA, *12S* rRNA, and Histone 3 (*H3*), to reconstruct the phylogenetic relationships between species.

To complete type series of the inferred new species and characterize their shell variation, additional dry material from MNHN collections was included in the study.

DNA EXTRACTION AND POLYMERASE CHAIN REACTION

For most of the newly added specimens DNA extraction was carried out as described in Fedosov *et al.* (2015). For a set of additional samples (marked with asterisks in Table 1), a Thermo Scientific GeneJET Genomic DNA Purification 50 kit was used; all procedures were performed following the manufacturer's suggested protocol.

About 2 µl of genomic DNA was used for polymerase chain reaction (PCR). The PCR reactions were performed following the temperature profiles described in Fedosov *et al.* (2015), but some *COI* sequences were obtained with a slightly different profile: 3 min of initial denaturation at 95 °C, followed by five cycles with denaturation at 95 °C (15 s), annealing at 45 °C (15 s), and elongation at 72 °C (1 min), and then 35 cycles with the annealing temperature set to 48 °C, and with the final elongation phase at 72 °C (7 min). The sequencing was performed at Genoscope, Eurofins, and the laboratory of molecular genetics, A.N. Severtsov Institute of Ecology and Evolution (SIEE RAS).

DATA SETS

To ensure the consistency of phylogenetic analyses with the results obtained earlier, the entire Mitridae–Costellariidae–Ptychactractidae–Volutomitridae (MCPV) data sets, with multiple out-groups, as analysed in Fedosov *et al.* (2015), were used and supplemented with newly obtained sequences. Seven molecular data sets have been analysed, four of them corresponding to the individual three mitochondrial genes and nuclear marker *H3*. When the resulting phylogenetic

reconstructions were congruent, two concatenated data sets were assembled, one corresponding to the three mitochondrial genes (3mit, consistent with our earlier analysis, 1887 positions), and the second corresponding to a four genes data set (4G, 2215 positions). Finally, a reduced 4G data set was built to reconstruct relationships among species of Costellariidae for which data on anatomy was available.

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. We also checked for consistency with our earlier alignment (Fedosov *et al.*, 2015).

The best-fitting substitution models were identified for each gene separately, using MODELGENERATOR 0.85 (Keane *et al.*, 2006; Table 2). The single-gene data sets of *12S*, *16S*, and *H3* were analysed as a single partition each; three partitions corresponding to first, second, and third codon positions were analysed 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 the *H3* gene (MCPV 4G data set).

Best-scoring maximum likelihood (ML) trees were estimated using RaxML (Stamatakis, 2006), and robustness of the nodes was assessed using the THOROUGH BOOTSTRAPPING algorithm (Felsenstein, 1985) with 1000 iterations.

Bayesian 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 the default number of chain swaps and sampling frequency of one tree in each 1000 generations. For the *COI*, MCPV 3mit, and MCPV 4G data sets, Bayesian analyses with the same parameters used for the single-gene data sets were run first to evaluate the topologies of the resulting trees. Then the final analyses were performed for these data sets with the number of chains set to eight, number of generations set to 30 000 000, number of chain swaps set to five, and sampling frequency set to one tree each 1000 generations. A 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 to have converged if all ESS values exceeded 200. Consensus trees were calculated after discarding the first 25% trees as burn-in. All analyses were performed on the Cipres Science

Table 2. Alignment and substitution model data

Gene	Primers	References	Annealing temperature	Amplification length (bp)	Alignment length (bp)	Substitution model (AIC1)	I	gamma
COI	HCO-1490	GGTCAACAATAATCATAAAGAYATGYG	Folmer <i>et al.</i> (1994)	658	658	GTR+I+G	0.46	0.4
	LCO-2198	TAAACTTCAGGTTGACCAARAAYCA	Folmer <i>et al.</i> (1994)					
16S	16SH	CCGGTCTGAACCTCAGATCAGC	Palumbi (1996)	~550	597	TIM+I+G	0.4	0.51
	16LC	GTTTACCACAAAACATGGCTTC	Palumbi (1996)					
12S	12SA	AAACTGGGATTAGATACCCACTAT	Palumbi (1996)	~380	620	TrN+I+G	0.27	0.58
	12SB	GAGGTTGACGGGGGTGTGT	Palumbi (1996)					
H3	H3F	ATGGCTCGTACCAAGCAGACVGC	Colgan <i>et al.</i> (2000)	328	328	TrN+I+G	0.61	0.72
	H3R	ATATCCTTRGGCATRATRTGAC	Colgan <i>et al.</i> (2000)					

Gateway (<http://www.phylo.org/portal2>) (Miller, Pfeiffer & Schwartz, 2010), using MrBayes 3.2.2 on XSEDE and RAXML-HPC2 on XSEDE (8.1.11).

MORPHOLOGICAL STUDIES

In addition to the 15 species for which the radulae had already been published (Fedosov *et al.*, 2015), 60 additional costellariid species were examined with respect to radular morphology, extracted from the molecular voucher specimens whenever possible to ensure an objective overlay of molecular and morphological data. For specimens with body retracted inside the shell, a hole or a series of holes were drilled to extract the body as completely as possible. For radula preparation, the entire foregut (or the buccal mass only, for larger specimens) was isolated by dissection and treated with a solution of commercially available bleach until the soft tissues were entirely dissolved. Radulae were then rinsed in several changes of distilled water, unfolded, and mounted on a standard 12-mm stub, gold coated, and examined using scanning electron microscopy (SEM; for a detailed description of the procedure, see Kantor & Puillandre, 2012). Each of the major Costellariidae lineages revealed by the molecular analysis was characterized anatomically, and special attention was paid to the anterior alimentary canal and the penis. Where possible, the type species of nominal genera were studied anatomically. For other species, the character states of crucial morphological features (those that display variation throughout the data set) were recorded and entered into the table for subsequent analysis (Table 3). For the out-group and some in-group taxa, anatomical data were retrieved from the literature (Harasewych, 1986; Kantor & Bouchet, 1997; Kantor, Bouchet & Oleinik, 2001; Bouchet & Kantor, 2000a, 2004; Fedosov & Kantor, 2010). Five characters of external morphology and anatomy were examined, their transformation throughout costellariid evolution was traced using the ‘tracing character history’ option, and the parsimony ancestral reconstruction method was implemented in MESQUITE 3.03 (Maddison & Maddison, 2015).

CHARACTERS AND CHARACTER STATES USED IN THE ANALYSIS

1. Operculum: 0, present; 1, vestigial (less than one-quarter of aperture height); 2, absent.
2. Seminal groove: 0, open along entire length of mantle cavity and on the penis; 1, partly closed (a stretch of the seminal canal, but not its entire length, is represented by an open groove); 2, closed.

Table 3. Matrix of morphological characters and their states used in the analysis

Family	Genus	Species	Specimen data	Operculum	Seminal groove	Rachidian	gL	moe
COSTELLARIIDAE	<i>Vexillum</i>	<i>plicarium</i>	IM-2013-13646	2	2	3	3	2
COSTELLARIIDAE	<i>Vexillum</i>	<i>semifasciatum</i>	IM-2013-11594	2	2	3	3	2
COSTELLARIIDAE	<i>Vexillum</i>	<i>costatum</i>	IM-2009-11058	2	2	3	3	2
COSTELLARIIDAE	<i>Vexillum</i>	<i>exasperatum</i>	IM-2013-11680	2	2	3	3	2
COSTELLARIIDAE	<i>Vexillum</i>	<i>virgo</i>	IM-2013-13079	2	2	3	3	2
COSTELLARIIDAE	<i>Vexillum</i>	<i>cancellarioides</i>	IM-2013-40631	2	2	3	3	2
COSTELLARIIDAE	<i>Vexillum</i>	<i>ziervogelii</i>	IM-2013-15865	2	2	3	3	2
COSTELLARIIDAE	<i>Austromitra</i>	sp.	IM-2013-40667	2	2	3	2	1
COSTELLARIIDAE	<i>Austromitra</i>	<i>vincta</i>	IM-2013-40671	2	2	3	2	1
COSTELLARIIDAE	<i>Atlantilux</i>	<i>rubrum</i>	IM-2013-1747	2	2	3	1	1
COSTELLARIIDAE	<i>Atlantilux</i>	<i>exigua</i>	IM-2009-31184	2	2	3	?	?
COSTELLARIIDAE	<i>Pusia (Pusia)</i>	<i>vassardi</i> sp. nov.	IM-2013-40682	2	2	0	?	1
COSTELLARIIDAE	<i>Pusia (Pusia)</i>	<i>lauta</i>	IM-2013-47927	2	2	0	?	?
COSTELLARIIDAE	<i>Pusia (Ebenomitra)</i>	<i>ebenus</i>	see text	2	2	0	2	1
COSTELLARIIDAE	<i>Pusia (Vexillena)</i>	<i>balutensis</i>	IM-2013-40637	2	2	1	1	1
COSTELLARIIDAE	<i>Turriplicifer</i> gen. nov.	<i>australis</i>	IM-2013-40675	2	1	0	2	2
COSTELLARIIDAE	<i>Protoelongata</i>	<i>dekkersi</i>	IM-2007-30242	2	2	0	1	1
COSTELLARIIDAE	<i>Orphanopusia</i> gen. nov.	<i>patriarchalis</i>	IM-2013-10241	2	2	1	1	2
COSTELLARIIDAE	<i>Nodicostellaria</i>	<i>laterculata</i>	IM-2013-9022	2	2	2	2	1
COSTELLARIIDAE	<i>Thala</i>	<i>exilis</i>	IM-2013-3389	2	2	0	0	1
COSTELLARIIDAE	<i>Costapex</i> gen. nov.	<i>sulcatus</i> sp. nov.	Par. 2.	2	1	0	0	0
COSTELLARIIDAE	<i>Costapex</i> gen. nov.	<i>levis</i> sp. nov.	IM-2013-40628	2	1	0	?	?
COSTELLARIIDAE	<i>Alisimitra</i> gen. nov.	<i>deforgesii</i> sp. nov.	IM-2013-9655	2	0	0	0	0
COSTELLARIIDAE	<i>Alisimitra</i> gen. nov.	<i>barazerii</i> sp. nov.	IM-2013-40664	2	0	0	0	0
COSTELLARIIDAE	<i>Tosapusia</i>	<i>isaoi</i>	IM-2013-19926	2	0	0	0	0
COSTELLARIIDAE	<i>Tosapusia</i>	<i>vitiaz</i> sp. nov.	IM-2013-40624	2	0	0	0	0
COSTELLARIIDAE	<i>Ceratoxancus</i>	<i>teramahii</i>	Kantor and Bouchet (1997)	0	0	0	0	0
COSTELLARIIDAE	<i>Ceratoxancus</i>	<i>cf. melichrous</i>	Kantor and Bouchet (1997)	0	0	0	0	0
COSTELLARIIDAE	<i>Latiromitra</i>	<i>barthelowi</i>	IM-2007-35820	0	0	0	0	0
COSTELLARIIDAE	<i>Latiromitra</i>	<i>crosnieri</i>	IM-2007-38178	1	0	0	0	0
PTYCHATRACTIDAE	<i>Exilia</i>	<i>vagrans</i>	Kantor <i>et al.</i> (2001)	0	0	0	0	0
PTYCHATRACTIDAE	<i>Exilia</i>	<i>hilgendorfi</i>	Kantor <i>et al.</i> (2002)	0	0	0	0	0
PTYCHATRACTIDAE	<i>Exilia</i>	<i>krigei</i>	IM-2007-38331	0	0	0	0	0
VOLUTOMITRIDAE	<i>Exilioidea</i>	sp.	IM-2013-40625	0	?	0	?	?
VOLUTOMITRIDAE	<i>Volutomitra</i>	<i>glabella</i>	Bouchet and Kantor (2004)	0	0	4	3	3
VOLUTOMITRIDAE	<i>Volutomitra</i>	<i>ziczac</i>	Bouchet and Kantor (2004)	0	0	4	3	3
VOLUTOMITRIDAE	<i>Volutomitra</i>	sp.	IM-2007-38357	0	?	4	3	3
VOLUTOMITRIDAE	<i>Microvoluta</i>	<i>joloensis</i>	IM-2013-9662	0	0	4	3	3
COLUMBARIIDAE	<i>Coluzea</i>	<i>cf. liriopae</i>	IM-2007-38972	0	0	0	0	?

Type species of nominative taxa of Costellariidae shown in bold

3. Rachidian tooth: 0, tricuspidate; 1, bearing three major and two minor cusps; 2, bearing five equally developed cusps; 3, bearing seven or more equally developed cusps; 4, monocuspidate.
4. Bulky gland of Leiblein: 0, well developed, brown; 1, reduced in size, brown(ish); 2, reduced in size, white (acinous structure of the gland lost and an external layer with muscular and connective tissue fibres developed); 3, vestigial (histology of the gland same as in the previous character state; thickness of gland does not exceed the thickness of the following secondary tubular glandular structure, and its length is about 1.0–1.5 times its thickness).
5. Glandular mid-oesophagus: 0, weakly developed; 1, well developed, widened; 2, well developed, forms a tubular part of gland of Leiblein; 3, muscular.

ABBREVIATIONS OF REPOSITORIES AND FACILITIES USED IN TEXT

AM, Auckland War Memorial Museum, Auckland, New Zealand; AMS, Australian Museum, Sydney, Australia; BPBM, Bishop Museum, Honolulu, Hawaii, USA; IMT, Institute of Malacology, Tokyo, Japan; IPEE, A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Science, Moscow, Russia; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA; MNHG, Muséum d'Histoire Naturelle, Geneva, Switzerland; MNHN, Muséum National d'Histoire Naturelle, Paris, France; NHMUK, The Natural History Museum, London, UK; NMBE, Natural History Museum, Bern, Switzerland; NMNS, National Museum of Natural Science, Taichung, Taiwan; NMP, National Museum of the Philippines, Manila, Philippines; NMST, National Science Museum, Tokyo, Japan; NMNZ, National Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand; NSMN, Nishinomiya Shell Museum, Nishinomiya, Japan; RMNH, Naturalis Biodiversity Centre (formerly Rijksmuseum van Natuurlijke Historie), Leiden, the Netherlands; SIEE RAS, Laboratory of Molecular Genetics, A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Science, Moscow, Russia; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; WAM, Western Australian Museum, Perth, Australia.

ANATOMY ABBREVIATIONS

ag, anal gland; aoe, anterior oesophagus; asg, accessory salivary gland; bm, buccal mass; bt, buccal tube; cm, columellar muscle; ct, ctenidium; dgL, duct of

gland of Leiblein; ft, foot; gL, gland of Leiblein; gmo, glandular mid-oesophagus; me, mantle edge; nr, nerve ring; odr, odontophore retractor; osg, open seminal groove; osp, osphradium; pggL, poorly glandular gland of Leiblein; pe, penis; poe, posterior oesophagus; pr, proboscis; prr, proboscis retractors; prw, proboscis wall; rad, radular membrane; rd, radular diverticulum; rnh, rhynchodaeum; sd, salivary duct; sg, salivary gland; sn, siphon; tn, eye tentacle; vL, valve of Leiblein.

OTHER ABBREVIATIONS AND TEXT CONVENTIONS

a/h, ratio of aperture height to shell height; B, maximum-likelihood bootstrap support value; BI, Bayesian inference; 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; ML, maximum likelihood; OD, original designation of type species; PI, protoconch I; PII, protoconch II; PP, Bayesian posterior probability support value; SD, subsequent designation of type species; SH, shell height; T, type species by tautonymy; *w/h*, ratio of shell width to height.

GENERIC ASSIGNMENT

Decisions on the (sub)generic assignment of the species are based on: (1) molecular evidence and radula morphology, or molecular data only; and (2) shell characters alone.

RESULTS

SPECIES DELIMITATION AND PHYLOGENETIC RELATIONSHIPS

The general time-reversible model GTR+I+G was selected as the best fit for the *COI* data set (for the details of substitution models, see Table 2). Most of the 123 specimens are grouped in the *COI*-based molecular tree in agreement with the identifications based on shell characters (Figs 1, 2): specimens placed in the same morphospecies are grouped in a single clade and, conversely, specimens from different morphospecies are in different lineages. In three cases [*Vexillum evelynae* Guillot de Suduiraut, 2007; *Vexillum isaoi* (Kuroda & Sakurai, 1959), and *Tongsuapusia tehuaorum* Huang, 2015; see below], however, specimens that were initially treated as different putative species based on their divergent shell morphology proved to belong to the same species based on the analysis of *COI*.

Of the 80 species defined using shell characters and congruent with the *COI* tree, 53 were named with certainty, 23 were unnamed, and the four

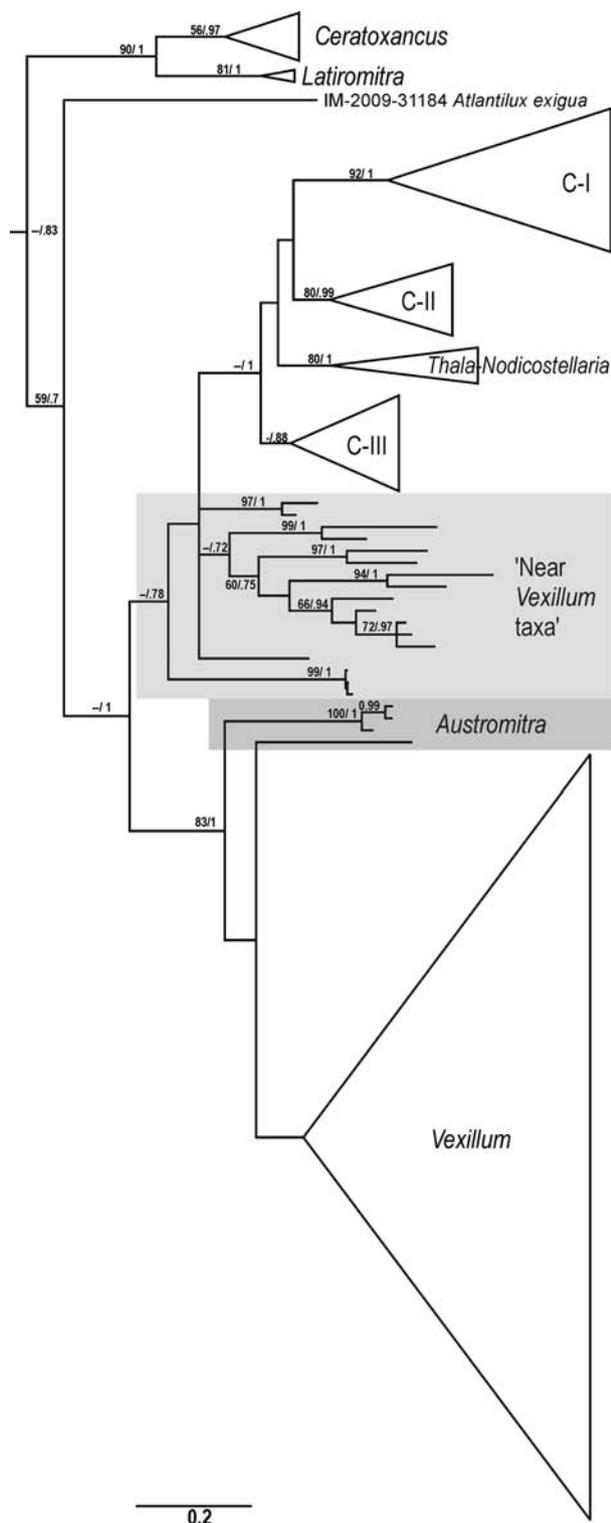


Figure 1. Relationships among major lineages of the Costellariidae based on a Bayesian analysis of cytochrome *c* oxidase subunit I (*COI*); major inferred lineages collapsed, see Fig. 2). Branch support given as Bayesian posterior probability (when >0.8)/maximum-likelihood bootstrap values (when >50).

remaining species were provisionally identified as 'cf.' (*confere*) or 'aff.' (*affinis*), indicating that the specimen was morphologically close to some described species and may (cf.) or may not (aff.) belong to this species. We failed to amplify any *COI* fragment for four more species; however, these were distinctive in shell morphology and fell into already defined clades based on the other genetic markers. Two of them are undescribed species, each represented by a single specimen: MNHN IM-2013-40626 in clade C-II (*Costapex exbodi* sp. nov.) and MNHN IM-2013-40638 in clade C-III (*Alisimitra samadiae* sp. nov.). The other two, represented by specimens MNHN IM-2013-20368 and MNHN IM-2013-40632, were identified as '*Vexillum*' *puella* (Reeve, 1845) and '*Vexillum*' *nodospiculum* Cernohorsky, 1970, respectively, both showing close affinity with '*Vexillum*' *rubrum* (Broderip, 1836).

All the single-gene trees were generally congruent with each other, and contained minimal supported conflicts in topologies (see below). In all single-gene trees, deep nodes were unstable in topology and in most cases weakly supported or not supported at all. In particular, the relationships among 'near-*Vexillum*' taxa (i.e. referred to as '*Vexillum* s.l.' by Fedosov *et al.*, 2015) were not resolved. Thus, we will only refer to the reconstructions derived from the analyses of the concatenated data sets to discuss the phylogenetic relationships between the species that were defined using shell characters and the analysis of *COI*.

The resulting 3mit and 4G phylogenetic trees (Figs 3, 4) were largely congruent with those in Fedosov *et al.* (2015). The pattern of deep nodes in the grouping referred to by Fedosov *et al.* (2015) as 'clade A' (that included Costellariidae with *Ceratoxancus* and *Latiromitra*, Volutomitridae, Columbariinae, and two ptychactrid lineages not related to each other) remained nearly unchanged. Meanwhile, the inclusion of numerous additional costellariid sequences resulted in notable alterations in the topologies of both Bayesian (BI) and maximum-likelihood (ML) trees, as well as in support values. For easier graphic presentation of our results, we collapsed the clades for which the composition remained unchanged from Fedosov *et al.* (2015).

The multiple-gene analyses produced trees with similar topologies; however, some polytomic nodes that were present in the 3mit tree were resolved in the 4G tree. Most of the older nodes on the 4G tree have high support values, indicating the high credibility of the inferred relationships. For the convenience of further discussion we enumerated nodes in the Costellariidae segment of the tree (nodes 1 and 6 on the 3mit tree, and nodes 1 and 9 on the 4G tree; Figs 3, 4). In both trees, the first and second

bifurcations split the well-supported *Ceratoxancus-Latiromitra* and the C–I clades, respectively, from the rest of the Costellariidae. The branching order at nodes 3 and 4 differs between the 3mit and 4G trees: polytomies at these nodes in the 3mit tree reflect unresolved relationships among groupings C–II, C–III, *Thala-Nodicostellaria*, and the rest of the Costellariidae. The high support of node 5 on the 4G tree (PP = 0.99) suggests a close relationship of the *Thala-Nodicostellaria* grouping with the *Vexillum* s.s. clade and ‘near *Vexillum*’ taxa, however. The *Thala-Nodicostellaria* clade deserves special attention, although it does not have significant support. This clade includes the Indo-Pacific *Thala exilis* (Reeve, 1845) as well as the Caribbean ‘*Vexillum*’ *laterculatum* (G.B. Sowerby II, 1874), which from overall shell morphology is referable to *Nodicostellaria* (see below). The well-supported *Austromitra* clade is a sister group to the well-supported *Vexillum* s.s. clade in both multi-gene analyses, and the grouping *Vexillum* s.s.–*Austromitra* is also well supported in both cases. The *Vexillum* s.s.–*Austromitra* clade on the 3mit tree is included in a large polytomic grouping defined by node 4 that also includes: (1) a well-supported grouping of two Australian species ‘*Vexillum*’ *australe* (Swainson, 1820) and ‘*Austromitra*’ aff. *cinnamomea* (A. Adams, 1855) (B = 100; PP = 1); (2) a well-supported grouping of *Atlantilux exigua* (C.B. Adams, 1845), ‘*V.*’ *rubrum*, ‘*V.*’ *nodospiculum*, and ‘*V.*’ *puella* (B = 76; PP = 1); (3) and (4) two single-species clades formed by ‘*Vexillum*’ (*Protoelongata*) *dekkersi* Herrmann, Stossier & Salisbury, 2014 and ‘*Vexillum*’ *patriarchale* (Gmelin, 1791); and (5) a weakly supported grouping that we refer to hereafter as the *Pusia* clade (B = 67; PP = 0.96). The *Pusia* clade combines clade C–IV of Fedosov *et al.* (2015), a closely related ‘*Vexillum*’ sp. (IM-2013-40682)–‘*Vexillum*’ (*Pusia*) *lautum* (Reeve, 1845) clade, and a third clade formed by two Mediterranean species, ‘*Vexillum*’ *ebenus* (Lamarck, 1811) and ‘*Vexillum*’ *savignyi* (Payraudeau, 1826).

The composition of the *Austromitra* clade, *Pusia* clade, *Vexillum* s.s. clade, and clades C–I, C–II, and C–III are consistent in 3mit and 4G trees, with slight differences in support values. However, the ‘*Vexillum*’ *dekkersi* lineage, ‘*Vexillum*’ *australe* – ‘*Austromitra*’ aff. *cinnamomea* clade, and *Pusia* clade are grouped together (although with no support) in the 4G tree, and the clade combining *Atlantilux exigua* and three ‘*Vexillum*’ species clusters with the *Vexillum* s.s. – *Austromitra* clade, whereas the ‘*Vexillum*’ *patriarchale* lineage stands out on its own.

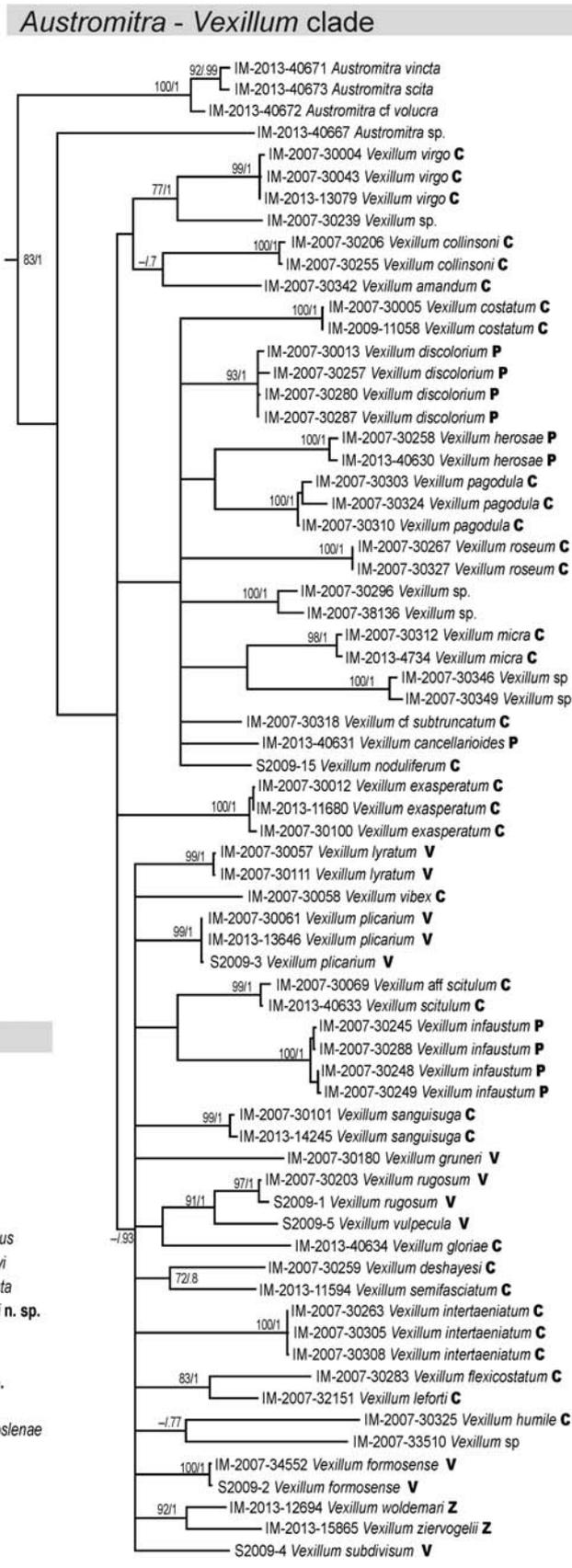
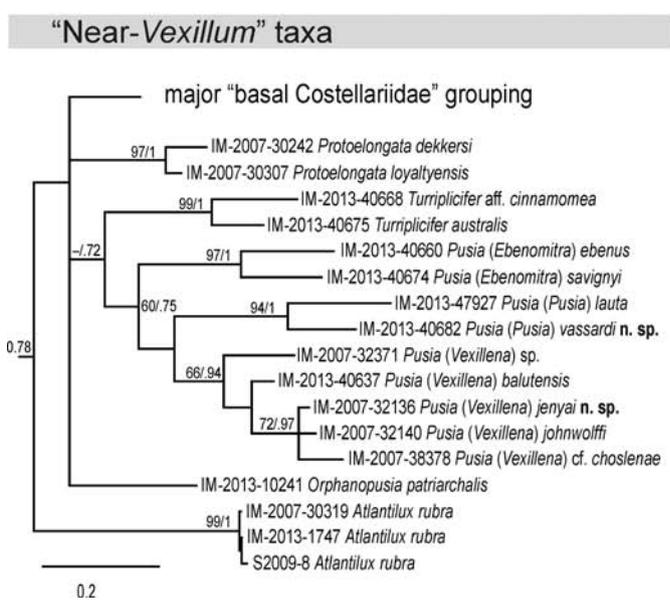
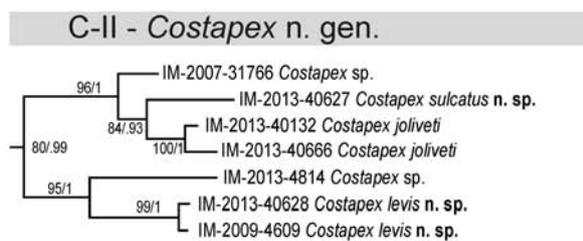
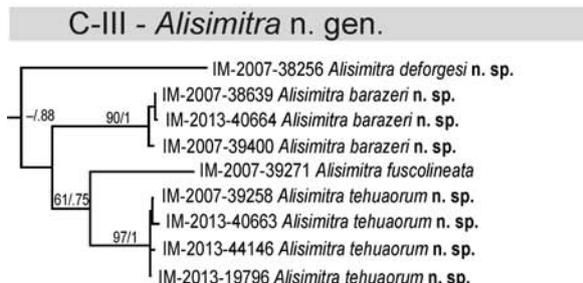
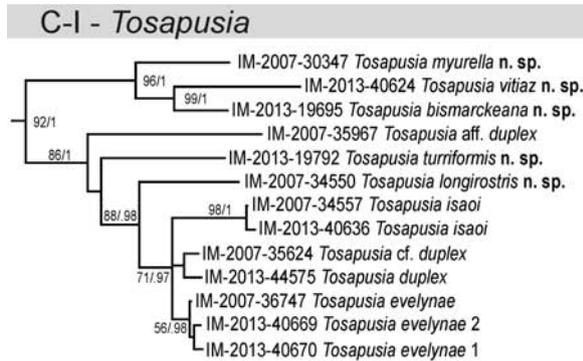
The topology of the *COI*-based tree (Fig. 1) contradicts the topologies of phylogenetic reconstructions based on the multiple-gene analyses. In the first case, *Atlantilux exigua* is sister taxon to

Costellariidae s.s., which in turn is divided into two major clades: one combines the *Vexillum* and *Austromitra* lineages; the other combines all other lineages, and the affinity of the clades C–I, C–II, C–III, and *Thala-Nodicostellaria* is well supported in the Bayesian analysis (PP = 1). In the multiple-gene analyses, the *Vexillum*–*Austromitra* grouping remains unchanged overall, whereas the second major clade is paraphyletic, consistent with the topology obtained in our earlier study (Fedosov *et al.*, 2015). One of the possible reasons for the conflict of topologies is a long branch that defines the *Vexillum* clade: it implies multiple substitutions accumulated in the *COI* fragment, which are shared by the *Vexillum* s.s. species but are absent in the other paraphyletic group. Thus this paraphyletic group shares a plesiomorphic state in multiple positions of the *COI* gene, and is likely to be an artificial group based on these shared plesiomorphies. Similarly, the single-species clade of *Atlantilux exigua*, which is basically excluded from the well-supported Costellariidae s.s. on the *COI*-based tree, forms a well-supported clade with three ‘*Vexillum*’ species in multiple-genes analyses, although retaining its long branch. We are inclined to attribute this conflict to an ambiguity in the placement of the highly divergent *COI* sequence, which was resolved with the addition of three overall more conserved genetic markers.

IMPLICATIONS FOR THE TAXONOMY OF THE COSTELLARIIDAE

In the present section we aim to implement a revised taxonomy of the family Costellariidae derived from the phylogenetic tree. In doing so, and to avoid breaking the logic of the paper, we will also refer to the morphological data that will be presented along with the description of the new taxa. Therefore, some of our rationale will follow below, where the morphological data will be analysed in light of the molecular phylogeny.

The clade corresponding to *Vexillum* s.s. is defined in our 4G tree by node 9 (Fig. 4), and is equally well defined on the *COI*-based tree (Fig. 1). The 65 specimens of *Vexillum* s.s. that were sequenced for *COI* clustered in 37 molecular species (Fig. 2). Consistent with our earlier results, this *Vexillum* s.s. clade combines species of the genus *Zierliana* with members of three subgenera of *Vexillum*, *Vexillum* (*Vexillum*) [indicated by a bold ‘V’ in Fig. 2, including the type species *Vexillum plicarium* (Linnaeus, 1758)], *Vexillum* (*Costellaria*) [indicated by a bold ‘C’, including the type *Vexillum semifasciatum* (Lamarck, 1811)], and species traditionally classified in *Vexillum* (*Pusia*) [indicated by a bold ‘P’, represented by *Vexillum cancellarioides*



(Anton, 1838), *Vexillum herosae* (Herrmann & Salisbury, 2012), and *Vexillum discolorium* (Reeve, 1845), but not including the type species]. Although the two *Zierliana* species are conchologically very distinctive, and they cluster together in the molecular tree, they are just one branch in the *Vexillum* polytomy. Recognition of *Zierliana* as a subgenus or genus would imply dismembering *Vexillum* into numerous (sub)genera, a move that we are not prepared to make. Consequently, we treat *Zierliana* as a synonym of *Vexillum*. The other subgenera are spread throughout the *Vexillum s.s.* clade, without any noticeable pattern. Furthermore, numerous species classically referred to *Vexillum (Pusia)* (marked with black circles on the 4G tree - Fig. 4) are recovered outside the *Vexillum s.s.* clade, and only distantly related to each other. We studied a radula of *Pusia microzonias* (Lamarck, 1811), the type species of *Pusia* (see below), and we sequenced two species, '*Vexillum*' (*Pusia*) *lautum* MNHN IM-2013-47927 and *Pusia vassardi* sp. nov. (MNHN IM-2013-40682) that are close to *Pusia microzonias* in both shell and radula morphology (see below). As a result, we conclude that the name *Pusia* should be restricted to the clade '*Vexillum*' (*Pusia*) *lautum*–*Pusia vassardi* sp. nov., which is only distantly related to *Vexillum*.

Likewise, the five species tentatively assigned to *Austromitra* do not form a clade. '*Austromitra*' aff. *cinnamomea* appears only distantly related to the other four species, which form a well-supported clade, closely related to *Vexillum s.s.* Having compared the morphology of the species studied herein with the morphology of *Austromitra rubiginosa* (Hutton, 1837) as published by Ponder (1972), we conclude that the name *Austromitra* should be attributed to the clade formed by *Austromitra* sp., *Austromitra vineta* (A. Adams, 1855), *Austromitra scita* (Tenison-Woods, 1876), and *Austromitra cf. volucra* (Hedley, 1915).

Our molecular analysis suggests a close relationship between the crown group of Costellariidae, consistent with our *Vexillum s.s.* clade and the *Austromitra* clade (Figs 3, 4); however, because of notable differences in morphology and distribution, we treat these as two separate genera herein. Besides *Zierliana* and *Vexillum (Costellaria)*, the following are also confirmed to be junior synonyms (Turner, 2001) of *Vexillum*: *Arenimitra* Iredale, 1929 (type *Voluta exasperata* Gmelin, 1791), *Pulchritima*

Iredale, 1929 (type *Voluta sanguisuga* Linnaeus, 1758), *Tiara* Swainson, 1831 (type *Voluta rugosa* Gmelin, 1791), and *Vulpecula* Blainville, 1824 (type *Voluta vulpecula* Linnaeus, 1758).

Although the affinity of the *Vexillum s.s.*–*Austromitra* clade with the *Atlantilux exigua*–'*Vexillum*' *rubrum* clade is not supported by molecular data, the phylogenetic grouping composed of these three lineages (defined by node 7 of the 4G tree; Fig. 4) is supported by at least one distinct synapomorphy in morphology (see below). This clade is remarkable as it combines Caribbean (*Atlantilux exigua* and '*Vexillum*' *puella*) and Indo-Pacific ('*Vexillum*' *rubrum* and '*Vexillum*' *nodospiculum*) species that, however, do not form reciprocally monophyletic groups in our phylogenetic reconstructions. We allocate the name *Atlantilux* Huang, 2015 to the entire clade, which we treat as a genus. It should be noted that Atlantic and Indo-Pacific species of *Atlantilux* show consistent differences in protoconch morphology (see below), but the phylogenetic significance of this signal is not known.

There are five names that can potentially apply to the lineages arising from node 6 of our 4G tree, but not included into the *Vexillum*–*Austromitra*–*Atlantilux* grouping: *Pusia* Swainson, 1840; *Ebenomitra* Monterosato, 1917 (type species *Mitra ebenus* Lamarck, 1811); *Pusiolina* Cossmann, 1921 (type species *Mitra tricolor* Gmelin, 1791), *Idiochila* Pilsbry, 1921 (type species *Mitra turben* Reeve, 1845), and *Protoelongata* Herrmann, Stossier & Salisbury, 2014 (type species *Vexillum dekkersi* Herrmann, Stossier & Salisbury, 2014). Specimens of '*Vexillum*' *ebenus* and '*Vexillum*' *dekkersi* were sequenced, which allows us to allocate the names to the inferred phylogenetic clades with certainty. In addition, we sequenced specimens of '*Vexillum*' *savignyi*, a Mediterranean species referable to *Pusiolina*, and undoubtedly close to '*Vexillum*' *tricolor*. The two Mediterranean species '*Vexillum*' *ebenus* and '*Vexillum*' *savignyi* cluster together with high support in all our phylogenetic analyses. Thus we apply the name *Ebenomitra* to this two-species clade (with *Pusiolina* as a junior synonym), and suggest that it applies to all Mediterranean costellariids (see below). Both the 3mit and 4G analyses suggest a close relationship between the *Ebenomitra* clade, the *Pusia* clade (both as newly circumscribed herein), and a deep-water '*Vexillum*' *balutense* Herrmann, 2009–'*Vexillum*' *choslenae* Cernohorsky, 1982 clade,

Figure 2. Major Costellariidae *s.s.* lineages (without *Ceratoxancus* and *Latiromitra*) inferred in the Bayesian analysis of the cytochrome *c* oxidase subunit I gene (*COI*; see Fig. 1A). Branch support as Bayesian posterior probability (when >0.7)/maximum-likelihood bootstrap values (when >50). C, P, V and Z denote species, that in traditional treatment were classified to *Vexillum (Costellaria)*, *Vexillum (Pusia)*, *Vexillum (Vexillum)*, and *Zierliana* respectively.

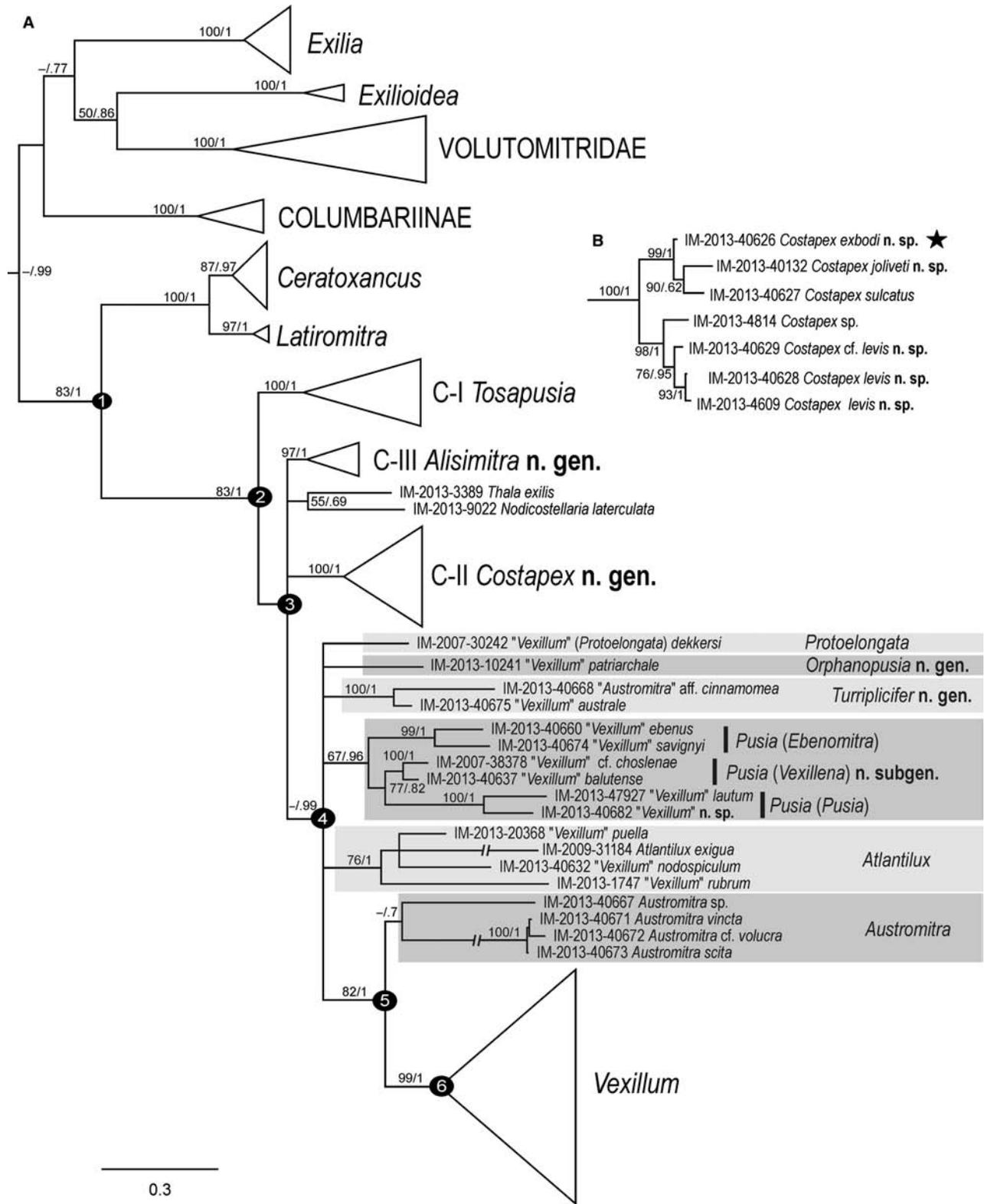


Figure 3. A, phylogenetic tree illustrating relationships between major Costellariidae clades inferred by Fedosov *et al.* (2015) (collapsed), based on a Bayesian analysis of three mitochondrial genes [cytochrome *c* oxidase subunit I (*COI*), *12S* rRNA, and *16S* rRNA: data set 3mit]. Branch support as Bayesian posterior probability (when >0.8)/maximum-likelihood bootstrap values (when >50). B, *Costapex* gen. nov. (C-II) subtree with the position of *Costapex exbodi* sp. nov. indicated by a star.

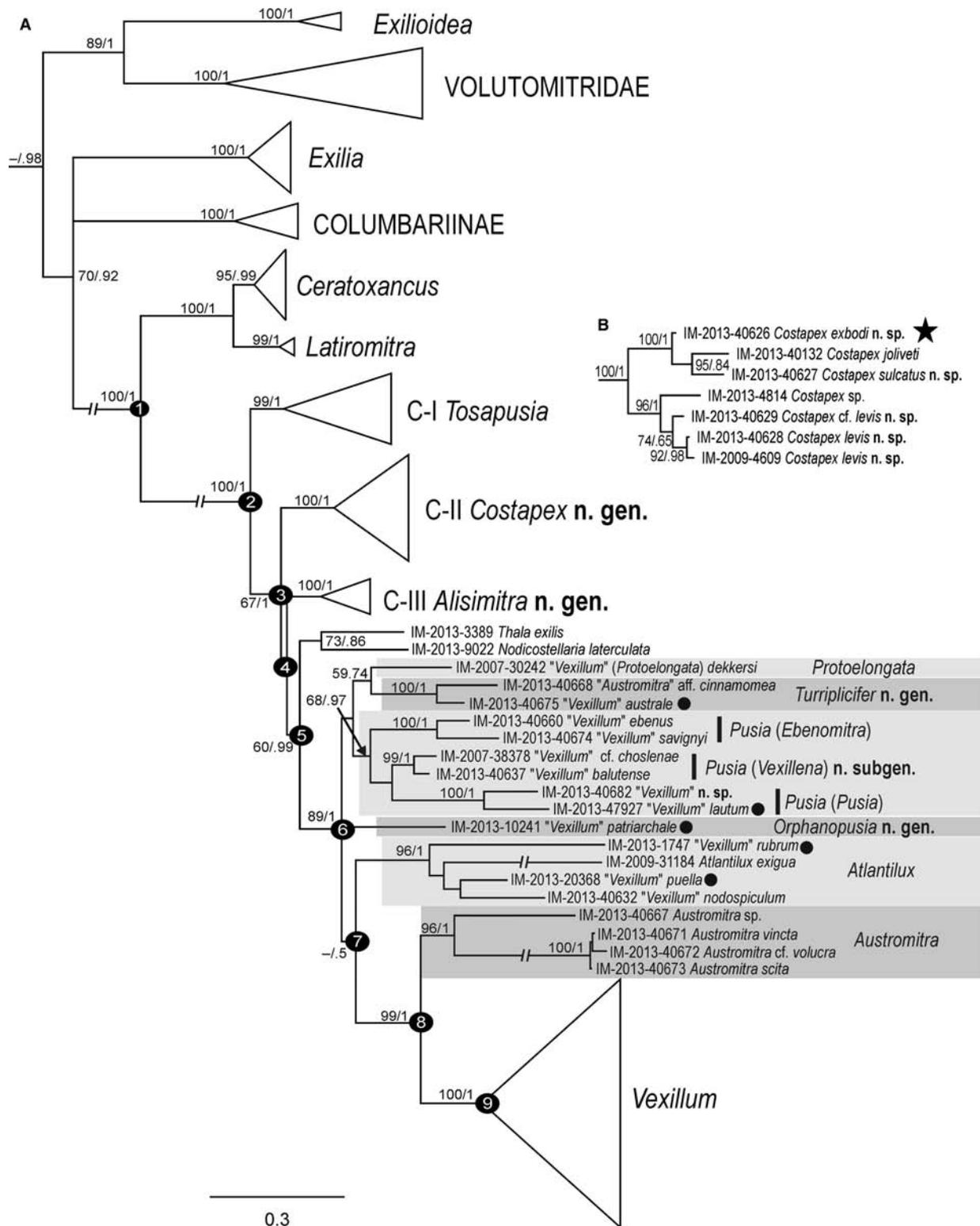


Figure 4. A, phylogenetic tree illustrating relationships between major Costellariidae clades inferred by Fedosov *et al.* (2015) (collapsed) based on a Bayesian analysis of the three mitochondrial genes plus nuclear gene *H3* (data set 4G). Black circles mark the species that are traditionally assigned to *Pusia*. Branch support given as Bayesian posterior probability (when >0.8)/maximum-likelihood bootstrap values (when >50). B, *Costapex* gen. nov. (C-II) subtree with the position of *Costapex exbodi* sp. nov. indicated with a star.

which we here name *Pusia* (*Vexillena*) subgen. nov. Because this clade shows moderate support, we further suggest that these three lineages be ranked as subgenera of *Pusia*: *Pusia* (*Pusia*), *Pusia* (*Ebenomitra*), and *Pusia* (*Vexillena*).

Only one species of *Protoelongata*, *Protoelongata dekkersi*, was included in the 4G analysis, and its affinities to other lineages unified by the node 6 remained poorly resolved. Therefore we retain the circumscription of the taxon as originally defined, but our results suggest ranking it as a full genus rather than a subgenus of *Vexillum*.

Two Western Australian costellariids '*Vexillum*' *australe* and '*Austromitra*' aff. *cinnamomea* form another well-supported clade; albeit with unresolved affinities, this clade is well supported in all our analyses, and as there is no name available for it, we establish the new genus *Turriplicifer* gen. nov. Following the same approach, the single-species lineage formed by '*Vexillum*' *patriarchale* that has long been allocated to *Pusia* is assigned to a genus of its own, *Orphanopusia* gen. nov.

One of the unexpected results of our phylogenetic analysis is the close affinity between Indo-Pacific *Thala* species and the Caribbean '*Vexillum*' *laterculatum*, which we attribute to *Nodicostellaria*. Unfortunately, as our analysis only barely includes American costellariids, and most known Panamic and Caribbean lineages remain essentially untouched by the present study, we refrain from any radical reassessment of their taxonomy besides the transfer of '*Vexillum*' *laterculatum* to *Nodicostellaria*.

The 13 specimens analysed in clade C–I correspond to ten species, and only three of them are named. Two (IM-2007-34557 and IM-2013-40636) were identified as '*Vexillum*' *isaoi* (Kuroda & Sakurai, 1959), the type species of *Tosapusia* Habe, 1964. Although *Tosapusia* was subsequently (Turner, 2001) regarded as a synonym of *Vexillum*, our phylogenetic analysis demonstrates that '*Vexillum*' *isaoi* is only very distantly related to true *Vexillum*, and therefore the name *Tosapusia* is here restored for clade C–I. '*Vexillum*' *duplex*, also included in our clade C–I based on the analysis of *COI*, was designated as the type species of the recently described genus *Tongsuapusia* Huang, 2015, which we thus treat it as a synonym of *Tosapusia*. Of the seven new species recognized in this clade, five are described below. Because the other two species were each represented by a single specimen, we are not able to provide solid morphological delimitation criteria and refrain from formally naming them for the time being.

We did not find names applicable to the clades C–III and C–II. Given their molecular and morphological (see below) distinctiveness, we describe them

as *Alisimitra* gen. nov. and *Costapex* gen. nov., respectively. Of the four species recognized in the *Alisimitra* clade in the *COI* analysis, only two are named (see Fig. 2). A fifth species, also undescribed, is missing from our *COI* data set; however, other sequenced genetic markers clearly place it in *Alisimitra* gen. nov.

Based on the results of the *COI* analysis, five species composed the *Costapex* clade and one more was added based on other genetic markers and overall shell morphology. Only one of the six recognized species is named. Despite the group being rather well represented in our molecular data set, the material available was judged sufficient to constitute appropriate type series for just three new species. A fourth species is described based solely on shell characters; however, we feel confident that it is congeneric with the other species of *Costapex* gen. nov. characterized with molecular data.

EVOLUTION OF MORPHOLOGY

The novel data on the morphology of newly established costellariid taxa *Tosapusia*, *Alisimitra* gen. nov., *Costapex* gen. nov., *Turriplicifer* gen. nov., and *Orphanopusia* gen. nov. were supplemented by data available in the literature for *Austromitra* (Ponder, 1972) and *Vexillum* (Fedosov & Kantor, 2010).

The reconstruction of the evolution of five morphological characters throughout the evolutionary history of the Costellariidae is shown in Figure 5. An operculum – although it may be reduced in size, and at least in juveniles – is present in *Ceratoxancus* and *Latiromitra*, *Exilia*, *Exilioidea*, Columbariidae, and Volutomitridae. Judging from the reconstruction, the loss of operculum takes place at node 1 of the phylogenetic tree, i.e. Costellariidae with the exclusion of the *Latiromitra*–*Ceratoxancus* clade.

The seminal canal is represented by a groove, which is open along its entire length in all non-costellariid groups of 'Clade A' as described by Fedosov *et al.* (2015; Volutomitridae, Columbariidae, *Exilia*, and *Exilioidea*). In Costellariidae, the same morphology of the seminal canal is found in *Ceratoxancus*, *Latiromitra*, *Tosapusia*, and *Alisimitra* gen. nov., whereas in *Costapex* gen. nov. the seminal canal is open only in its proximal part and is closed along the penis length. All but one costellariid unified by node 5 have a closed seminal groove. The exception is *Turriplicifer australis* (Swainson, 1820), which has an open seminal canal before the penis.

All the lineages included in the analysis – with the exception of Volutomitridae – share a radula with three teeth in a row. Among these, all non-costellariid lineages share a tricuspidate rachidian, and so do the five 'basal' costellariid genera

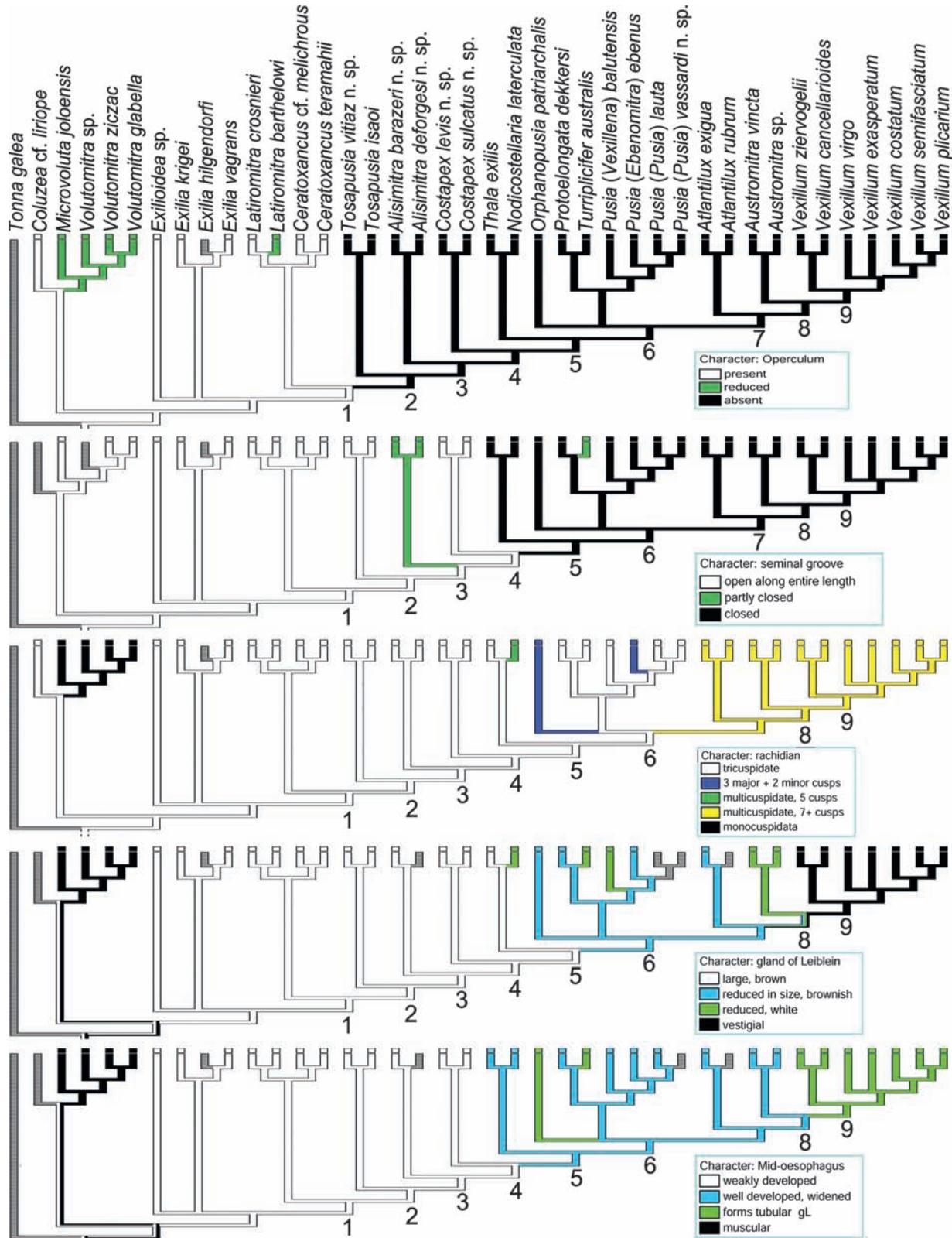


Figure 5. Reconstruction of the ancestral character states for five characters presented in Table 3. Topology derived from the analysis of the 4G data set. Closely related out-group taxa demonstrating no unique morphology and conspecific in-group specimens were removed. Unknown states of selected characters are shown in grey.

Ceratoxancus, *Latiromitra*, *Tosapusia*, *Alisimitra* gen. nov., and *Costapex* gen. nov. Among the more derived Costellariidae, a tricuspidate rachidian is found in *Thala*, *Protoelongata*, *Pusia* (*Pusia*), and *Pusia* (*Ebenomitra*), as well as in the genus *Turriplicifer*. Two accessory cusps flanking the central major cusp are present in two unrelated groups, *Pusia* (*Vexillena*) and *Orphanopusia*, and the rachidian of *Nodicostellaria laterculata* (G.B. Sowerby II, 1874) possesses five equal cusps. All the clades unified by node 7 in our tree have a rachidian with seven or more cusps, which are usually equal. Thus a multicuspidate rachidian (with more than three equal cusps) originated at least twice in the evolutionary history of the Costellariidae: in *Nodicostellaria* and in *Vexillum–Austromitra–Atlantilux* gen. nov. Moreover, some ‘near-*Vexillum*’ species have somewhat intermediate rachidian morphology, with two accessory cusps flanking the central major cusp.

A large, brown, non-tubular (bulky), obviously glandular gland of Leiblein, is present in columbariids and in *Exilia*, as well as in costellariids, in *Ceratoxancus*, *Latiromitra*, *Tosapusia*, *Alisimitra* gen. nov., *Costapex* gen. nov., and *Thala*. A bulky gland of Leiblein, reduced in size but functional (glandular, judging from its histology; see below), is present in *Orphanopusia*, *Protoelongata*, and *Pusia* (*Vexillena*), as well as in *Atlantilux rubra* (Broderip, 1836). In the *Vexillum–Austromitra* lineage, and *Nodicostellaria laterculata*, *Turriplicifer australis*, and *Pusia* (*Ebenomitra ebenus* (Lamarck, 1811), it is further reduced and presumably lacks a secretory function, based on its light colour and altered histology (in these species the non-tubular compartment of the gland of Leiblein shows a well-developed layer of muscular fibres external to the remains of the glandular tissue). Species of *Vexillum s.s.* have a strongly reduced bulky gland of Leiblein that is obviously not glandular and is situated at the distal end of the secondary tubular glandular structure. Thus costellariids demonstrate a tendency to a progressive reduction of the bulky gland of Leiblein; however, as the delineation of states 1 and 2 in this character is rather conventional (largely based on the colour of the gland, which varies continuously), the reconstruction of its evolution lacks precision, and the ancestral state is not defined with certainty for nodes 5–8.

Finally, the situation with the glandular mid-oesophagus is roughly the opposite to that demonstrated by the bulky gland of Leiblein. It is weakly or moderately developed in *Exilia*, *Ceratoxancus*, *Latiromitra*, *Tosapusia*, *Alisimitra* gen. nov., and *Costapex* gen. nov. The glandular compartment of the mid-oesophagus becomes enlarged in the costellariid lineages unified by node 5 of our tree, and in species of

Vexillum s.s. it strips off to form a secondary tubular glandular structure, which retains contact with the reduced bulky gland of Leiblein. Remarkably, two species outside the *Vexillum s.s.* clade, *Turriplicifer australis* and *Orphanopusia patriarchalis*, have independently acquired a secondary tubular glandular structure.

SYSTEMATICS

CLASS GASTROPODA CUVIER, 1795
 SUBCLASS CAENOGASTROPODA COX, 1960
 ORDER NEOGASTROPODA WENZ, 1938
 SUPERFAMILY TURBINELLOIDEA RAFINESQUE, 1815¹
 FAMILY COSTELLARIIDAE MACDONALD, 1860

Diagnosis

Shell small to medium sized, fusiform, elongate-fusiform or turritiform, usually with high spire and well-developed siphonal canal. Suture distinct, impressed or canalculated. Sculpture dominated by axial elements from rounded, widely set folds to dense and sharp ribs. Axials may be lacking or overridden by spiral elements on the adult whorls, but they are always well pronounced on earlier teleoconch whorls. Aperture ranging from very narrow slit-shaped to wide. Inner aperture lip usually with three or four columellar folds, subequal or (in most cases) adapical the strongest. Protoconch glossy, with no sculpture, usually multispiral, narrowly conical, or rarely paucispiral bulbous. Operculum absent (except in *Ceratoxancus* and *Latiromitra*). Eyes always present. Well-developed proboscis, valve of Leiblein, salivary glands, and (usually) accessory salivary gland. Bulky gland of Leiblein well developed or reduced, in latter case secondary tubular secretory structure connected to gland of Leiblein developed. Radula triserial with tri- or multicuspidate rachidian tooth and simple monocuspidate sickle-shaped laterals.

SUPRASPECIFIC TAXA OF RECENT COSTELLARIIDAE (IN ALPHABETIC ORDER)

Genus *Alisimitra* gen. nov. Type species: *Alisimitra barazeri* sp. nov. (OD herein). Composition: see below.

¹The molecular phylogeny of Fedosov *et al.* (2015) recovered several clades in Neogastropoda that are here given superfamily rank: (1) a Muricidae clade; (2) a Mitridae–Pyramimitridae clade; (3) a Cancellariidae + Volutidae clade; and (4) a clade (‘Clade A’) including the families Costellariidae, Turbinellidae (Columbariinae), Turbinellidae (Vasinae), Volutomitridae, and Ptychactridae. Although *Turbinella* was not included in the analysis, we are tentatively using the name Turbinelloidea for the latter clade, because this is the oldest family-group name available, but this requires confirmation.

Genus *Atlantilux* Huang, 2015. Type species: *Mitra exigua* C.B. Adams, 1845 (OD). Composition: see below.

Genus *Austromitra* Finlay, 1926. Type species: *Columbella rubiginosa* Hutton, 1873 (OD). Composition: see below.

Genus *Ceratoxancus* Kuroda, 1952. Type species: *Ceratoxancus teramachii* Kuroda, 1952 (M). Composition: *Ceratoxancus basileus* Kantor & Bouchet, 1997; *Ceratoxancus elongatus* Sakurai, 1958; *Ceratoxancus leios* Kantor & Bouchet, 1997; *Ceratoxancus lorentzi* Poppe, Tagaro & Sarino, 2012; *Ceratoxancus melichrous* Kantor & Bouchet, 1997; *Ceratoxancus niveus* Kantor & Bouchet, 1997; *Ceratoxancus teramachii* Kuroda, 1952.

Genus *Costapex* gen. nov. Type species: *Costapex sulcatus* (OD herein). Composition: see below.

Genus *Latiromitra*, Locard, 1897 (= *Okinawavoluta* Noda, 1980; *Cyomesus* Quinn, 1981). Type species: *Latiromitra specialis* Locard, 1897 (M) (= *Mitra cryptodon* P. Fisher, 1883). Composition: *Latiromitra aratiuncula* (Quinn, 1981); *Latiromitra barthelowi* (Bartsch, 1942); *Latiromitra cacozeliana* Bouchet & Kantor, 2000a,b; *Latiromitra costata* (Dall, 1890); *Latiromitra crosnieri* Bouchet & Kantor, 2000a,b; *Latiromitra cryptodon* (P. Fischer, 1883); *Latiromitra delicatula* (Shikama, 1971); *Latiromitra meekiana* (Dall, 1889); *Latiromitra niveobabelis* Garcia, 2015; *Latiromitra okinavensis* (MacNeil, 1961); *Latiromitra pauciorum* Bouchet & Kantor, 2000a,b; *Latiromitra styliola* (Dall, 1927).

Genus *Mitromica* s.s. Berry, 1958. Type species: *Mitra solitaria* C.B. Adams, 1852 (OD). Composition: *Mitra africana* (Rolán & Fernandes, 1996); *Mitra calliaqua* Rosenberg & Salisbury, 2003; *Mitra christamariae* Salisbury & Schniebs, 2009; *Mitra cosmani* Rosenberg & Salisbury, 2003; *Mitra decaryi* (Dautzenberg, 1932); *Mitra dicksoni* Rosenberg & Salisbury, 2003; *Mitra esperanza* Leal & Moore, 1993; *Mitra foveata* (G.B. Sowerby II, 1874); *Mitra gallegoi* Rolán, Fernández-Garcés & Lee, 2010. *M. gratiosa* (Reeve, 1845); *Mitra jeancateae* (Sphon, 1969); *Mitra omanensis* Herrmann & Gori, 2012; *Mitra oryza* Rosenberg & Salisbury, 2003; *Mitra solitaria* (C.B. Adams, 1852); *Mitra williamsae* Rosenberg & Salisbury, 2003.

Genus *Nodicostellaria* Petuch, 1987. Type species: *Costellaria kaicherae* Petuch, 1979 (OD). Composition: *Nodicostellaria crassa* (Simone, 1995); *Nodicostellaria kaicherae* (Petuch, 1979); *Nodicostellaria kremerae* Petuch, 1987; *Nodicostellaria laterculata* (G.B. Sowerby II, 1874).

Genus *Orphanopusia* gen. nov. Type species: *Voluta patriarchalis* Gmelin, 1791 (OD herein). Composition: see below.

Genus *Protoelongata* Herrmann, Stossier & Salisbury, 2014. Type species: *Vexillum dekkersi* Herrmann, Stossier & Salisbury, 2014 (OD). Composition: *Protoelongata bilineata* (Reeve, 1845) comb. nov.; *Protoelongata corallina* (Reeve, 1845) comb. nov.; *Protoelongata dekkersi* (Herrmann, Stossier & Salisbury, 2014) comb. nov.; *Protoelongata heleneae* (Herrmann, Stossier & Salisbury, 2014) comb. nov.; *Protoelongata loyaltyensis* (Hervier, 1897) comb. nov.; *Protoelongata rubrotaeniata* (Herrmann, Stossier & Salisbury, 2014) comb. nov.; *Protoelongata xerampelina* (Melvill, 1895) comb. nov.

Genus *Pusia* Swainson, 1840.

- Subgenus *Pusia* Swainson, 1840. Type species: *Mitra microzonias* Lamarck, 1811 (M). Composition: see below.
- Subgenus *Ebenomitra* Monterosato, 1917 (= *Pusiolina* Cossmann, 1921). Type species: *Mitra ebenus* Lamarck, 1811 (SD: Coan, 1966: 130). Composition: see below.
- Subgenus *Vexillena* subgen. nov. Type species: *Vexillum balutense* Herrmann, 2009 (OD herein). Composition: see below.

Genus *Suluspira* nom. nov. (= *Visaya* Poppe, Guillot de Suduiraut & Tagaro, 2006, a junior homonym of *Visaya* Ahyong, 2004). Type species: *Visaya rosenbergi* Poppe, Guillot de Suduiraut & Tagaro, 2006 (OD). Composition: *Suluspira rosenbergi* (Poppe, Guillot de Suduiraut & Tagaro, 2006) comb. nov.

Genus *Thala* H. Adams & A. Adams, 1853. Type species: *Mitra mirifica* Reeve 1845 (SD: Cossmann, 1899: 176). Composition: *Thala abelai* Rosenberg & Salisbury, 2014; *Thala adamsi* Rosenberg & Salisbury, 2003; *Thala angiostroma* Pease, 1868; *Thala aubryi* Turner, Gori & Salisbury, 2007; *Thala cernica* (G.B. Sowerby II, 1874); *Thala evelynae* Rosenberg & Salisbury, 2014; *Thala exilis* (Reeve, 1845); *Thala exquisita* Garrett, 1872; *Thala gloriae* Rosenberg & Salisbury, 2003; *Thala gorii* Rosenberg & Salisbury, 2003; *Thala hilli* Rosenberg & Salisbury, 2007; *Thala jaculanda* (Gould, 1860); *Thala kawabei* Herrmann & Chino, 2015; *Thala kilburni* Rosenberg & Salisbury, 2014; *Thala lillicoi* Rosenberg & Salisbury, 2007; *Thala maldivensis* Turner, Gori & Salisbury, 2007; *Thala malvacea* Jousseaume, 1898; *Thala manolae* Turner, Gori & Salisbury, 2007; *Thala merrilli* Rosenberg & Salisbury, 2014; *Thala milium* (Reeve, 1845); *Thala minagaorum* Herrmann

& Chino, 2015; *Thala mirifica* (Reeve, 1845); *Thala ogasawarana* Pilsbry, 1904; *Thala pallida* Rosenberg & Salisbury, 2014; *Thala pemaensis* Herrmann & Gori, 2012; *Thala recurva* (Reeve, 1845); *Thala roseata* (A. Adams, 1855); *Thala ruggeriae* Rosenberg & Salisbury, 2014; *Thala secalina* (Gould, 1860); *Thala simulans* (Martens, 1880); *Thala suduirauti* Rosenberg & Salisbury, 2014; *Thala todilla* (Mighels, 1845); *Thala turneri* Salisbury & Gori, 2013; *Thala violacea* Garrett, 1872.

Genus *Thaluta* Rosenberg & Callomon, 2004.

Type species: *Thala maxmarrowi* Cernohorsky, 1980 (OD). Composition: *Thaluta maxmarrowi* (Cernohorsky, 1980); *Thaluta takenoko* Rosenberg & Callomon, 2004.

Genus *Tosapusia* Habe, 1964 (= *Tongsuapusia* Huang, 2015). Type species: *Mitropifex isaoi* Kuroda & Sakurai, 1959 (M). Composition: see below.

Genus *Turricostellaria* Petuch, 1987. Type species: *Turricostellaria lindae* Petuch, 1987 (OD). Composition: *Turricostellaria amphissa* Simone & Cunha, 2012; *Turricostellaria apyrahi* Simone & Cunha, 2012; *Turricostellaria jukyry* Simone & Cunha, 2012; *Turricostellaria leonardhilli* Petuch, 1987; *Turricostellaria lindae* Petuch, 1987; *Turricostellaria ovir* Simone & Cunha, 2012.

Genus *Turriplificifer* gen. nov. Type species: *Mitra australis* Swainson, 1820 (OD herein). Composition: see below.

Genus *Vexillum* Röding, 1798 (= *Arenimitra* Iredale, 1929; *Costellaria* Swainson, 1840; *Mitropifex* Iredale, 1929; *Pulchritima* Iredale, 1929; *Tiara* Swainson, 1831; *Turricula* H. & A. Adams, 1853; *Zierliana* Gray, 1847). Type species: *Vexillum plicatum* Röding, 1798 (= *Voluta plicarium* Linnaeus, 1758) (SD, Woodring, 1928: 244). Composition: all of the species of Costellariidae not explicitly placed in the other genera.

Status doubtful

Idiochila Pilsbry, 1921. Type species: *Mitra turben* (Reeve, 1845) (OD).

GENUS *TOSAPUSIA* HABE, 1964

Type species: *Mitropifex isaoi* Kuroda & Sakurai, 1959 (M). Habe did not declare *Tosapusia* a new genus, but the name was made available by being monotypic, with the combined description of the genus and species. *Tosapusia* was declared new by Azuma (1965: 56), with the same type species.

Synonym: *Tongsuapusia* Huang, 2015; syn. nov. Type species: *Vexillum duplex* Cernohorsky, 1982: 992; pl. 1, figs 6, 7 (OD).

Diagnosis

Shell elongate fusiform, sometimes widely fusiform or turritiform, typically with high spire and long to very long siphonal canal. Suture typically canaliculated or impressed, often resulting in telescopic appearance of spire. Whorls outline varying from subcylindric to flattened or evenly convex. Axial sculpture of straight ribs strong and widely set to fine and closely set. Spiral sculpture varying from fine grooves, restricted to siphonal canal or pronounced in interspaces between axials only, to strong cords overriding axial ribs to form beads or strong gemmae at intersections. Aperture elongate, its outer lip smooth or bearing fine lirae on its inner surface. Inner lip with between three and five columellar folds, with the upmost fold being the strongest. Shell coloration light, off-white, whitish, or pale, often with darker spiral bands. Head-foot pale, eye tentacles long, with eyes situated laterally at their bases. Radula rachiglossate, with tricuspidate rachidian of varying morphology and unicuspidate widely sickle-shaped or triangular laterals. Jaw present in some species, situated in buccal mass, thin, horse-shoe-shaped. Gland of Leiblein glandular, very large, brown. Males with open seminal groove.

Included species

Tosapusia isaoi (Kuroda & Sakurai, 1959),¹ *Tosapusia bismarckeana* sp. nov.,¹ *Tosapusia duplex* Cernohorsky, 1982,¹ *Tosapusia evelynae* (Guillot de Suduiraut, 2007),¹ †*Tosapusia kalimnanensis* (Cernohorsky, 1970),² *Tosapusia kurodai* (Sakurai & Habe, 1964),² *Tosapusia longirostris* sp. nov.,¹ *Tosapusia myurella* sp. nov.,¹ *Tosapusia sauternesensis* (Guillot de Suduiraut, 1997),² *Tosapusia turritiformis* sp. nov.,¹ *Tosapusia vitiaz* sp. nov.¹

Distribution and habitat

Indo-Pacific, from Madagascar to Japan and French Polynesia, in deep water (300–1000 m) on soft bottoms.

Remarks

Members of *Tosapusia* display high disparity in all key elements of shell morphology – shell shape and proportions, whorl profile, sculpture pattern, and shape of the suture – making it quite difficult to determine shared characters in order to establish the identity of the genus. Conchologically, different *Tosapusia* species may resemble members of other costellariid genera rather than congeners. *Tosapusia isaoi* and *Tosapusia sauternesensis*, with their high spire and relatively short siphonal canal, resemble some deep-water species of *Vexillum*, like *Vexillum tokubeii* (Sakurai & Habe, 1964) or *Vexillum scitulum* (A. Adams, 1853), but can be distinguished by the shape of the axial ribs, which are always straight in *Tosapusia*, but are arcuate and usually slightly

undulating in *Vexillum*. The tip of the siphonal canal is distinctly notched in *Vexillum*, whereas *Tosapusia* species have a relatively longer siphonal canal, never notched at its tip, which easily distinguishes the two genera.

Typical specimens of *Tosapusia duplex*, with their weakly developed spiral sculpture, are superficially close to species of *Latiromitra*; however, the notably stronger columellar plicae and narrower aperture of *Tosapusia duplex* readily differentiate it from *Latiromitra*. The widely fusiform shell of *Tosapusia vitiaz* sp. nov. is close in proportion to *Ceratoxancus*, but can be distinguished by stronger columellar folds and lack of operculum in *Tosapusia vitiaz*, and by the distinctive labral tooth that is characteristic of most *Ceratoxancus* species. For more details, see the Remarks sections in the following species entries.

TOSAPUSIA ISAOI (KURODA & SAKURAI, 1959)
FIGURE 6A, B

Mitropifex isaoi Kuroda & Sakurai, in Kuroda, 1959: 324–326, fig. 1.

Type data

Holotype: NSMN-H323, 50.0 mm, off Tosa, Kochi prefecture, Shikoku, Japan, in Higo, Callomon & Goto (2001).

Paratypes: NSMT-Mo 76260, including one, 50.0 mm, illustrated by Hasegawa & Saito (1995).

Material examined

Papua New Guinea: PAPUA NIUGINI, station CP3985, 05°09'S, 147°02'E, 805–865 m, 2 lv (MNHN IM-2013-40636, 43.4 mm, Fig. 6A; MNHN IM-2013-19746, 30.0 mm); PAPUA NIUGINI, station CP4009,

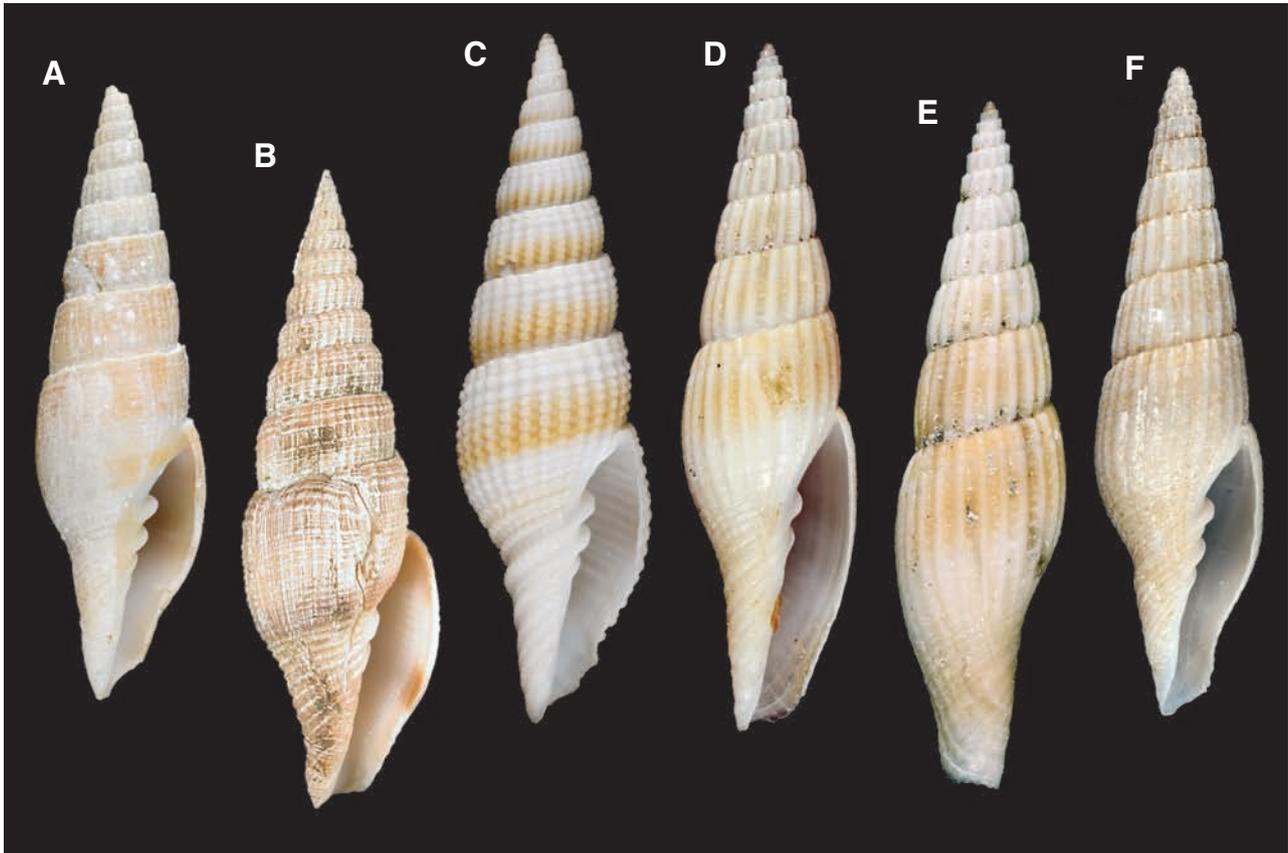


Figure 6. *Tosapusia* species. A, B, *Tosapusia isaoi*: A, MNHN IM-2013-40636, BIOPAPUA, station CP3748, 05°37'S, 154°01'E, 398–399 m, 43.4 mm; B, MNHN IM-2007-34557, Philippines, off Eastern Luzon, AURORA 2007, station CP2709, 15°12'N, 121°34'E, 244–296 m, 57.1 mm; C, *Tosapusia sauternesensis*: holotype of *Vexillum sauternesense*, Philippines, Hilutangan Channel between Mactan and Olango Island, 160 m, 42.2 mm. D–F, *Tosapusia bismarckiana* sp. nov.: D, E, holotype, MNHN IM-2013-19695, Papua New Guinea, off Bagabag Island, PAPUA NIUGINI, station CP3979, 04°44'S, 146°11'E, 540–580 m, 35.1 mm; F, paratype 3, radular voucher MNHN IM-2013-19695, Papua New Guinea, off Bagabag Island, PAPUA NIUGINI, station CP3979, 04°44'S, 146°11'E, 540–580 m, 35.1 mm.

06°04'S, 148°12'E, 550–575 m, 1 lv (MNHN IM-2013-19926, 41.9 mm).

Philippines Sea: AURORA 2007, CP2709, 15°12'N, 121°34'E, 244–296 m, 1 lv (MNHN IM-2007-34557, 57.1 mm, Fig. 6B).

Diagnosis

Shell medium sized, attaining 57.1 mm, elongate fusiform (*w/h* 0.28–0.31; *a/h* 0.44), with stout, moderately long, siphonal canal and high spire. Protoconch unknown because of erosion. Suture distinctly canalculated, giving spire a stepped, telescopic appearance. Teleoconch whorls slightly convex, sub-cylindric in profile, sometimes with indistinct shoulder. Sculpture of dense and low, rounded, axial ribs, intersected by feeble spiral cords. Aperture elongate, with outer lip drawn towards tip of siphonal canal. Inner lip with four strong columellar folds. Shell colour tan, with lighter spiral bands on last adult whorl.

Anatomy

External morphology (Fig. 7A): Body pale yellowish, lacking pigmentation, operculum absent. Siphon simple, moderately long, notably protruding beyond the edge of mantle. Mantle cavity rather long, spanning around one whorl; mantle thin with mantle cavity organs clearly visible. Head bearing rather long eye tentacles with small distinct eyes situated at their bases. Ctenidium very long, narrow, spanning throughout the posterior two-thirds of the mantle cavity. Osphradium large, exceeding half of ctenidium length. Anal gland present, indistinctly seen through the mantle as a narrow dark strip.

Anterior alimentary canal: Proboscis white, in contracted state occupying about two-thirds of rhynchocoel length. Anterior rhynchodaeum thick, pigmented violet. Paired retractors attached ventrolaterally to anterior rhynchodaeum (Fig. 7B). Buccal tube very thin walled, strongly convoluted, connecting mouth with buccal mass. Buccal mass very long, occupying basal two-thirds of proboscis, with odontophore notably retracted backwards inside radular diverticulum (Fig. 7C). Posterior to buccal mass, oesophagus forming broad loop followed by distinct bulbous valve of Leiblein. Salivary glands large, white, bulky, fused together without visible boundary. Salivary ducts adjoining the oesophagus loop anterior to valve of Leiblein. Accessory salivary glands (not shown in figure) distinct, translucent, situated ventrally, anterior to circum-oesophageal nerve ring. Mid-oesophagus just posterior to circum-oesophageal nerve ring, widened to form a glandular compartment. Posterior oesophagus adjoined by very large brown bulky gland of Leiblein that covers oesophagus dorsally.

Radula: MNHN IM-2013-40636 (Fig. 7D) and MNHN IM-2007-34557 (Fig. 7E), about 1.2 mm long and 0.23 mm wide, consisting of about 65 rows. Rachidian tricuspidate with relatively wide base (about one-third of radular width) and short blunt cusps, situated on short and flat projection of the rachidian medial portion. Laterals unicuspidate, triangular, massive in appearance, with drawn pointed cusp.

Male reproductive system: Male with long penis, slightly flattened on the sides (Fig. 7A), without distinct papilla. Open seminal groove running along the inner edge of penis throughout its length, from base to tip.

Distribution and habitat

Japan, Philippines, Papua New Guinea (Bismarck Sea and Solomon Sea), Western Australia (off Port Hedland) (present material; M. Marrow pers. comm.); depth range 296–805 m.

Remarks

Tosapusia isaoi is characterized by a strongly canalculated suture combined with only slightly convex teleoconch whorls that give the spire a distinctive telescopic outline, and a comparatively faint axial sculpture, distinguishing it from congeners.

Our specimens show some variation in shell morphology: the specimen from the Philippines (by far the largest) has notably coarser sculpture, slightly more convex whorls, and liration inside the outer lip. This may represent geographical variation or be attributed to gerontic condition. Molecular data confirm its conspecificity with specimens from Papua New Guinea.

TOSAPUSIA SAUTERNESENSIS

(GUILLOT DE SUDUIRAUT, 1997) COMB. NOV.

FIGURE 6C

Vexillum (Costellaria) sauternesense Guillot de Suduiraut, 1997: 117, 118; figs 3, 4.

Type data

Holotype: MNHN IM-2000-30178, Philippines, Hilutangan channel between Mactan and Olango Island, 160 m, 42.2 mm.

Paratype: Collection Sandro Gori (formerly in collection Guillot de Suduiraut), same locality as holotype, 43.7 mm.

Material examined

Holotype.

Diagnosis

Shell medium sized, attaining 42.2 mm, elongate fusiform, with nine or ten slightly convex teleoconch whorls, high spire with straight spire outline and

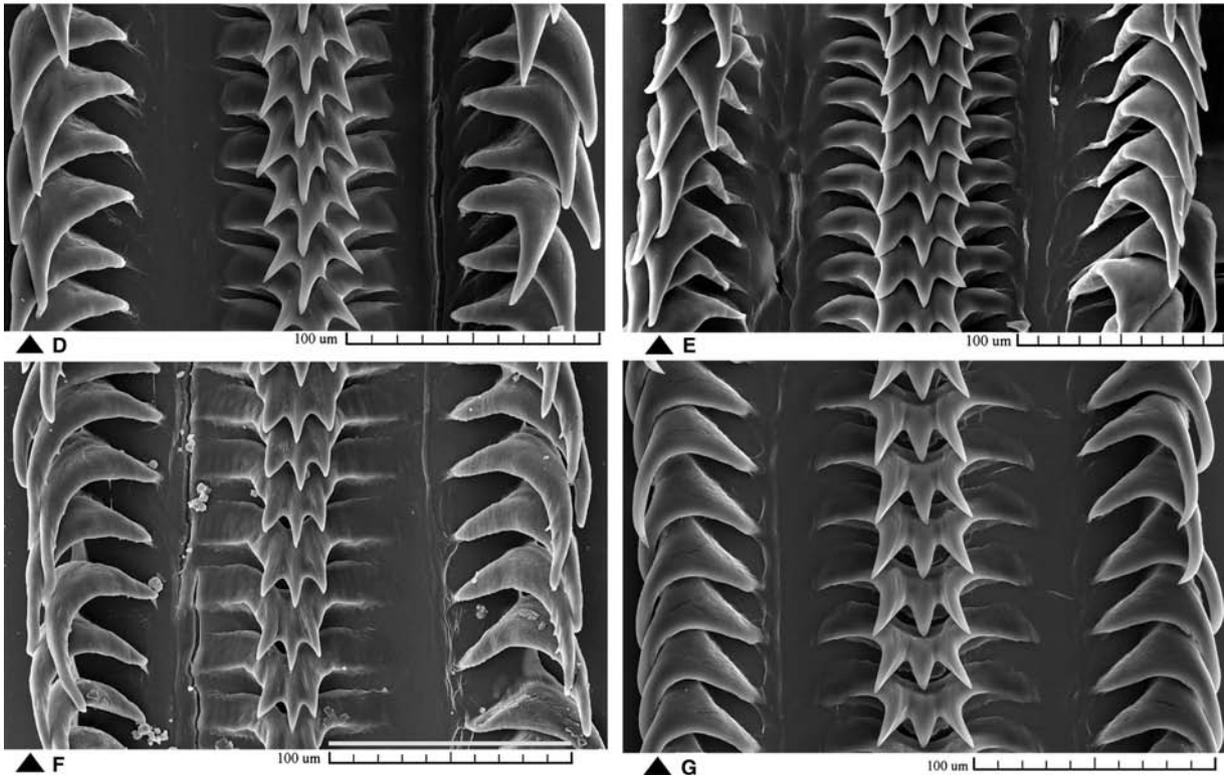
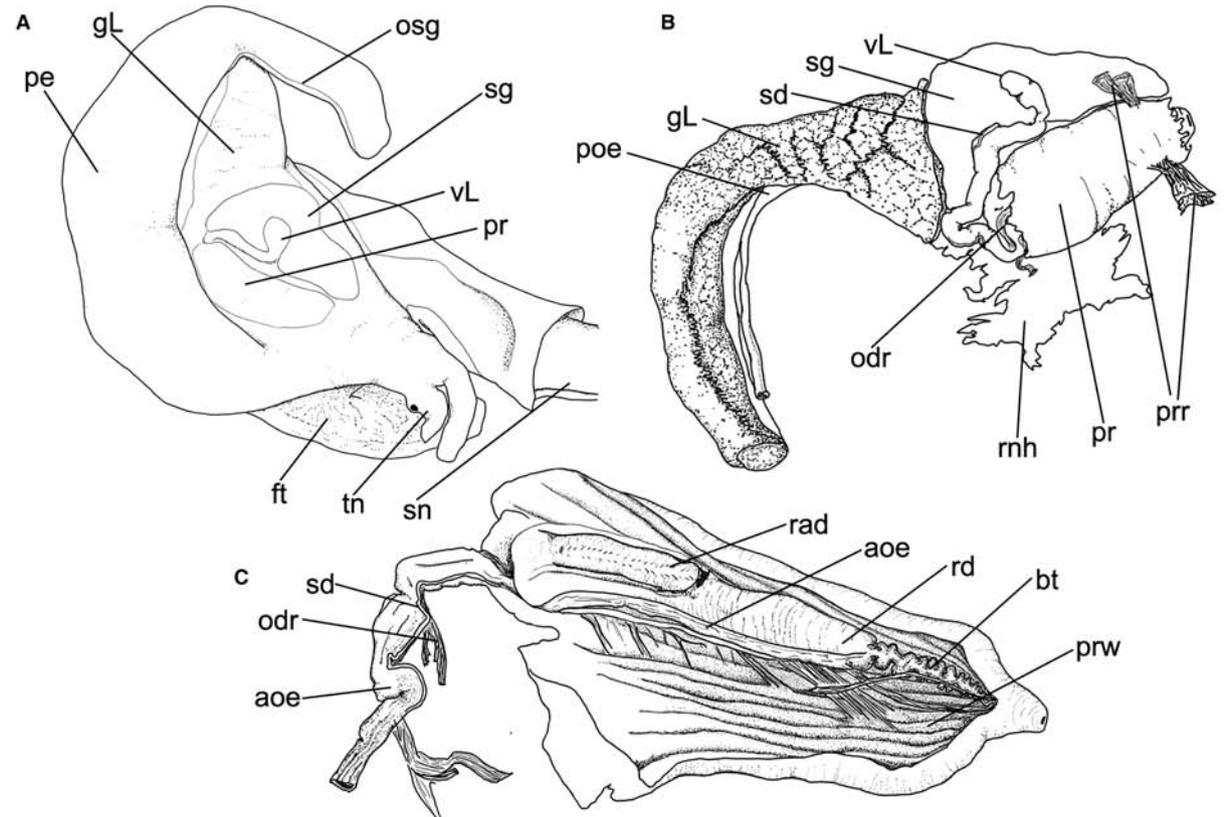


Figure 7. *Tosapusia* morphology. A–E, *Tosapusia isaoi*: A, general morphology of the body with mantle removed; B, anterior alimentary channel; C, dissected proboscis; D, MNHN IM-2013-40636 radula; E, MNHN IM-2007-34557 radula. F, G, radulae of *Tosapusia* species: F, *Tosapusia bismarckiana* sp. nov., holotype; G, *Tosapusia vitiaz* sp. nov., holotype.

distinctly canaliculated suture. Protoconch unknown because of erosion. Penultimate whorl with 25 or 26 axial ribs, and last adult whorl with 30 or 31 strong axial ribs, intersected by, respectively, seven or eight and 13 or 14 spiral grooves, resulting in a slightly beaded appearance. Columella with four or five strong folds weakening towards moderately long, slightly curved siphonal canal. Columellar folds extended outside of aperture to form strong spiral cords with wide interspaces on the siphonal canal. Aperture elongate with crenulated outer lip. Shell colour white with a brown to orange band at abapical half of spire whorls and at periphery of last adult whorl, and a second faded band of same colour above siphonal fasciole; aperture cream white, periostracum transparent.

Distribution and habitat

Known from the Philippines: Bohol and the Mactan–Olango channel, at a depth of 160 m, on sand and coral rubble.

Remarks

Tosapusia sauternesensis has several distinguishing characters, allowing its easy recognition. Among them the presence of a distinct, although narrow, subsutural shelf, wide and strong axial ribs with deep, rather narrow, interspaces, and very widely set spiral cords on the abapical portion of the shell base.

TOSAPUSIA BISMARCKEANA SP. NOV.

FEDOSOV, HERRMANN & BOUCHET
FIGURE 6D–F

Tongsuapusia duplex, Huang, 2015: pl. 1, fig. 2.

Type data

Holotype: Papua New Guinea, Bismarck Sea, off Bagabag Island, PAPUA NIUGINI, station CP3979, 04°44'S, 146°11'E, 540–580 m, lv (MNHN IM-2013-19695, 35.1 mm; Fig. 6D, E).

Paratypes: PAPUA NIUGINI, station CP4008, 06°04'S, 148°10'E, 500–555 m, lv (paratype 1, MNHN IM-2013-19915, 35.2 mm); Papua New Guinea, South-East point of Manus Island, BIOPAPUA, station CP3672, 04°04'S, 151°50'E, 702–724 m, lv (paratype 2, MNHN IM-2000-30201, 25.9 mm); Papua New Guinea, North of Rabaul, BIOPAPUA, station CP3691, 02°11'S, 147°18'E, 499–517 m, lv (paratype 3, MNHN IM-2000-30202, 25.9 mm; Fig. 6F).

Other material examined

Solomon Islands: Guadalcanal, Salomonboa-3, station CP2772, 09°25'S, 160°31'E, 456–551 m, 1 (MNHN IM-2007-36135, 23.2 mm); Salomon-2, station CP2194, 08°25'S, 159°27'E, 440–521 m, 1 (29.9 mm).

Diagnosis

Shell thin walled, medium sized, elongate fusiform, with high spire and long tapering siphonal canal. Early teleoconch whorls cylindrical, later whorls slightly convex with whorl periphery shifted abapically, having slightly compressed outline. Axial sculpture of numerous, distinctly opisthocline, fine axial ribs. Spiral sculpture of regular fine grooves, better seen in interspaces between axials, second uppermost groove widened, overriding axial elements. Siphonal canal straight, long, tapering, aperture elongate, opening of siphonal canal very wide and shallow. Inner aperture lip with three widely interspaced columellar folds, with the adapicalmost fold being strongest. Protoconch light brown, with two or more smooth whorls. Shell whitish, retaining pale background colour in interspaces between axial ribs on late spire whorls.

Description

Shell medium sized, fusiform (w/h 0.26; a/h 0.45–0.46), with high slender spire and elongate aperture. Protoconch light brown, with two or more smooth glossy whorls with clear-cut protoconch/teleoconch transition. Teleoconch of ten and one-quarter whorls, suture distinct, impressed. Early spire whorls cylindrical, with very distinct subsutural shelf, strongly angulated. Later teleoconch whorls with slightly convex outline and less notable subsutural shelf. Axial sculpture of strong but rather narrow and closely set axial ribs, with rather deep intervals, 25 on last adult whorl. Axials distinctly opisthocline on spire whorls and only slightly prosocline on last adult whorl, intersected by a deep groove just below the suture, their adapical portions forming indistinct 'caps' well pronounced on early spire whorls. Adapical area of last adult whorl with two grooves, caps rather indistinct. Below adapical groove spiral sculpture represented by fine, stroke-like, grooves in interspaces between strong axial ribs, seven or eight on penultimate whorl, 15 on last adult whorl, giving way towards siphonal canal to low, rounded, spiral cords, more oblique at the tip of canal. Siphonal canal long and straight. Aperture elongate (AL/SL), narrow, not clearly delineated from siphonal canal. Outer apertural lip gently convex at its adapical part and nearly straight below; inside of outer lip without lirae. Four columellar folds, adapical one strongest, and with succeeding folds gradually reducing in size, with third one rather weak and fourth one indistinct. Shell whitish, retaining pale background colour in interspaces between axial ribs on late spire whorls.

Radula (of holotype; Fig. 7F): Radula ~1 mm long and 0.23 mm wide, with more than 45 rows. Tricuspidate rachidian with relatively wide base (about one-third of radular width) and short blunt

cusps of equal size, set on robust medial projection. Laterals unicuspidate, triangular to widely sickle-shaped, with drawn cusp, sometimes bearing irregular minor cusps on inner edge.

Distribution and habitat

Papua New Guinea (Bismarck Sea and Solomon Sea), Solomon Islands, East China Sea (Huang, 2015), alive in depths of 517–702 m.

Etymology

The species name refers to the Bismarck Sea as the type locality.

Remarks

In shell morphology, *Tosapusia bismarckiana* sp. nov. most resembles *Tosapusia duplex*; however, it can be distinguished from it by being narrower, with more numerous axial ribs, which are distinctly opisthocline (about orthocline in *Tosapusia duplex*). Overall the axial sculpture of numerous rounded opisthocline ribs differentiates *Tosapusia bismarckiana* sp. nov. from other species of *Tosapusia*.

***TOSAPUSIA KURODAI* (SAKURAI & HABE, 1964)**

COMB. NOV.
FIGURE 8A–D

Mitropifex kurodai Sakurai & Habe, 1964: 29–30, 31–32; pl. 2, fig. 6.

Type data

Possible holotype: NMST-Mo 52861, 25.5 mm, off Ashizuri-Misaki, Kochi prefecture, Shikoku, about 200 m deep (Fig. 8A, B).

Paratypes: NMST-Mo 39797, one specimen, 31.9 mm (Fig. 8C); NMST-Mo-70269, four specimens, same locality as holotype.

Material examined

Papua New Guinea: BIOPAPUA, station DW3748, 05°37'S, 154°01'E, 398–399 m, 1 dd (25.7 mm, Fig. 8D); station DW3782, 04°15'S, 152°40'E, 600 m, 1 dd (16.1 mm). *Philippines*: PANGLAO 2005, station CP2343, 9°27'N, 123°49'E, 273–356 m, 1 dd (27.9 mm). *New Caledonia*: EXBODI, station CP3822, 21°52'S, 166°51'E, 341–506 m, 1 dd (22.8 mm).

Diagnosis

Shell medium sized, attaining 31.2 mm; broad, fusiform shell with eight or nine nearly cylindrical teleoconch whorls and straight spire outline. Protoconch unknown because of erosion. Distinct suture with broad subsutural ramp resulting in a stepped appearance. Penultimate and last adult whorl with 20–25 strong axial ribs, vanishing in the lower part of shell base. Fine spiral cords on top of the ribs, not bisecting the ribs, becoming stronger on shell base. Columella with four strong folds. Short, wide, nearly straight to slightly curved siphonal canal, aperture wide. Shell colour yellowish with one white central

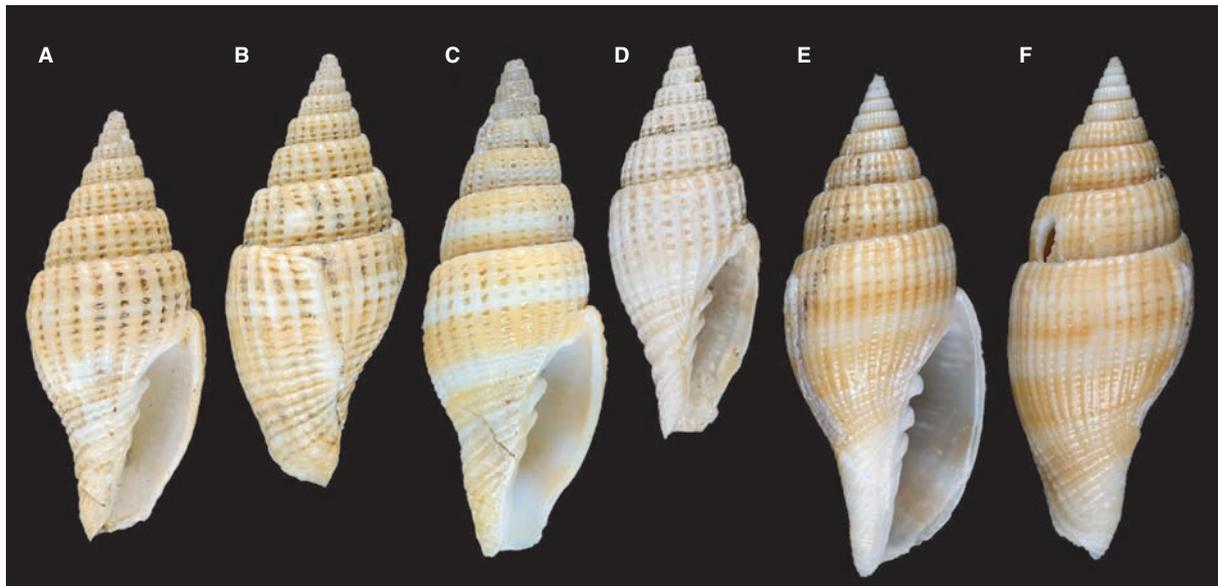


Figure 8. *Tosapusia* species. A–D, *Tosapusia kurodai*: A, B, holotype of *Mitropifex kurodai*, NMST-Mo 52861, 25.5 mm, Japan, Shikoku, Kochi prefecture, off Ashizuri-Misaki, depth ~200 m; C, paratype, NMST-Mo 39797, 31.2 mm, from type locality; D, BIOPAPUA, station DW3748, 05°37'S, 154°01'E, 398–399 m, 25.7 mm. E, F, *Tosapusia vitiaz* sp. nov., holotype, MNHN IM-2013-40624, Papua New Guinea, Vitiaz Strait, BIOPAPUA, station DW3719, 06°03'S, 147°36'E, 410 m, 34.3 mm.

band on the spire whorls and three white bands on the last adult whorl.

Distribution and habitat

Southern Japan, the Philippines, Papua New Guinea, New Caledonia, depth range 356–600 m.

Remarks

The validity of *Tosapusia kurodai* has been repeatedly in doubt. Cernohorsky (1970), Hasegawa & Saito (1995), and Higo, Callomon & Goto (1999) synonymized it with *Vexillum sculptile* (Reeve, 1845), and Tsuchiya (2000: 561; pl. 279, fig. 31) treated it as a synonym of *Vexillum rubellum* (A. Adams & Reeve, 1850). We examined the two syntypes of *Mitra rubella* in NHMUK. The smaller one, apparently a juvenile, indeed shows an extreme resemblance to the holotype of *Tosapusia kurodai*; the only difference is a distinct notch at the tip of the siphonal canal, which is present in both syntypes of *Vexillum rubella*, but is absent in our specimens of *Tosapusia kurodai*. With its higher spire and slightly undulating ribs on the last adult whorl, the larger syntype of *Vexillum rubella* is nearly identical to specimens of *Vexillum scitulum*. In our analysis the latter was placed in *Vexillum* and we therefore allocate *Vexillum rubella* to *Vexillum s.s.* as well. We believe that *Vexillum sculptile* is also a *Vexillum s.s.* The examined syntype of *Vexillum sculptile* has a notched siphonal canal, distinctly arcuate axial ribs on spire whorls and undulating ribs on last adult whorl; these character states are shared by many *Vexillum* species, but not by *Tosapusia kurodai* or other *Tosapusia* species. We thus treat *Tosapusia kurodai* as a valid species of *Tosapusia*.

Tosapusia kurodai differs from most species of *Tosapusia* in shell proportions: it is characterized by a broadly fusiform shell with rather tall last adult whorl and low spire. *Tosapusia vitiaz* sp. nov. resembles *Tosapusia kurodai* in both shell proportions and sculpture pattern; however, *Tosapusia kurodai* differs from *Tosapusia vitiaz* sp. nov. by its much stronger and less numerous axial ribs and rather adpressed whorl profile (*Tosapusia vitiaz* sp. nov. is characterized by gently rounded whorls).

TOSAPUSIA VITIAZ SP. NOV.

FEDOSOV, HERRMANN & BOUCHET

FIGURE 8E, F

Type data

Holotype: Papua New Guinea, Vitiaz Strait, BIOPAPUA, station DW3719, 06°03'S, 147°36'E, 410 m, 1 lv (MNHN IM-2013-40624, 34.3 mm).

Diagnosis

Shell medium sized, widely fusiform, stout, with tall last adult whorl and aperture, and rather low spire. Protoconch unknown because of erosion. Teleoconch whorls evenly convex, whorl periphery shifted abapically. Spire outline slightly telescopic because of canaliculated suture. Sculpture of numerous, thin axial ribs and lower, but about equally wide, spiral cords, well pronounced in interspaces between ribs. Siphonal canal moderately long, stout. Aperture wide, outer lip evenly convex throughout its length. Inner surface of outer lip with irregular lirae. Five columellar folds, adapicalmost very strong, subsequent folds becoming weaker towards siphonal canal. Shell pale with indistinct darker spiral bands, siphonal canal and apex white.

Description

Shell medium sized, widely fusiform, stout, with tall last adult whorl and rather low spire (w/h 0.4, a/h 0.58, and law/h 0.68). Protoconch missing. Teleoconch of between nine and nine and a half slightly convex whorls. Suture strongly impressed, forming deep groove, giving spire whorls a distinctly stepped outline. Sculpture cancellate, with dense axial ribs (38 on last adult whorl, where ribs are slightly prosocline) and almost equally wide and dense, although lower spiral cords pronounced on late whorls. Adapical third of spire whorl with no distinct spiral cords, succeeding portion with three or four cords on late spire whorls, and about 15 on last adult whorl. Spiral cords evenly spaced with rather shallow quadrate interstices of equal width.

Outline of last adult whorl evenly convex with gradual transition to moderately long, stout siphonal canal. Aperture elongate, outer lip evenly convex, inside with irregular lirae. Five distinct columellar folds, adapicalmost three folds strongest, with slightly flattened profile, and fourth and fifth folds weaker and rounded. Adapical angle of aperture with weak convex callous pad.

Background colour pale with orange spiral bands just below suture, on whorl periphery, and wider band on shell base, early spire whorls and siphonal canal pale.

Radula (Fig. 7G): Radula rachiglossate, about 1.4 mm long and 0.25 mm wide, consisting of about 71 rows. Rachidian tricuspidate with rather wide base (about 40% of radula width), medial projection not pronounced, cusps strong, rather short, pointed, central cusp slightly shorter than lateral cusps, which are directed slightly sideways. Lateral teeth unicuspidate, sickle-shaped, with long cusp slightly bent inwards near the tip.

Morphology of the body: The holotype is a male, exhibiting a penis with an open seminal groove

similar to that in *Ceratoxancus*. The animal does not have an operculum.

Distribution and habitat

Known only from Vitiaz Strait, North Papua New Guinea, at a depth of 410 m.

Etymology

The species name comes from the name of the type locality (Vitiaz Strait, between New Britain and the Huon Peninsula on the north coast of New Guinea), itself so named by Nicholai Mikluho-Maklai after the Russian corvette *Vitiaz* that brought him to Astrolabe Bay in September 1871. Used as a noun in apposition.

Remarks

The unusually high aperture and last adult whorl easily distinguish *Tosapusia vitiaz* sp. nov. from all other congeners. In overall shell morphology and in particular in sculpture, *Tosapusia vitiaz* sp. nov. most resembles *Tosapusia kurodai*, but differs in shell proportions, having a comparably even higher last whorl and aperture. The sculpture in *Tosapusia vitiaz* sp. nov. is notably finer than that in *Tosapusia kurodai*, and the latter has a narrower subsutural band, a more elongate siphonal canal, and less convex outer lip. *Tosapusia vitiaz* sp. nov. resembles some species of *Ceratoxancus*, like *Ceratoxancus teramachii* Kuroda, 1952, (Fig. 26A) or *Ceratoxancus elongatus* Sakurai, 1958; however, *Ceratoxancus teramachii* and *Ceratoxancus elongatus* have an even broader shell, with very low spire, and tall aperture, in addition to the characteristic labral tooth. *Ceratoxancus melichrous* Kantor & Bouchet, 1997 (Fig. 26E) has distinctly prosocline axial ribs and a deflected siphonal canal.

Some species of *Pusia* (*Vexillina*) subgen. nov. – for example, its type species *Pusia balutensis* Herrmann, 2009 – have broadly fusiform shells with high last adult whorl, and superficially resemble *Tosapusia vitiaz* sp. nov. This subgenus has weaker spiral sculpture, however, and specimens commonly have a variegated colour pattern and a closed siphonal groove.

TOSAPUSIA EVELYNAE

(GUILLOT DE SUDUIRAUT, 2007) **COMB. NOV.**

FIGURE 9A–E

Vexillum (*Costellaria*) *evelynae* Guillot de Suduiraut, 2007: 96–97; pl. 3, figs 1–3.

Vexillum sp.: Fedosov & Kantor, 2010.

Type data

Holotype: MNHN IM-2000-20641, Philippines, Bohol, Off Balicasag Island, 300–340 m (Fig. 8A), 31.7 mm.

Paratypes: Collection Sandro Gori (ex. collection Guillot de Suduiraut), from type locality, 39.2 mm; collection Conchology Inc., from type locality, 30.1 mm.

Material examined

Typical form (Figs 9A–C).

Philippines: AURORA 2007, station CP2762, 15°52'N, 121°51'E, 66 m, 1 lv (MNHN IM-2007-34552, 28.5 mm); PANGLAO 2005, station CP2393, 9°30'N, 123°42'E, 356–396 m, 1 lv (MNHN IM-2007-32145, 27.4 mm).

Vanuatu: Boa 1, station CP2430, 15°03'S, 166°54'E, 377–492 m, 1 lv (MNHN IM-2007-30345, 28.3 mm); station CP2462, 16°38'S, 167°57'E, 618–641 m, 3 lv (MNHN IM-2007-30217, 38.7 mm; 42.6 mm, 34.2 mm); SANTO 2006, station AT70, 15°41'S, 167°00'E, 517–614 m, 1 lv (MNHN IM-2007-30110, 29.0 mm).

New Caledonia: EXBODI, station CP3826, 21°52'S, 166°51'E, 354–509 m, 2 dd (20.4 mm, Fig. 7B; 17.55 mm).

Madagascar: MIRIKY, station CP3289, 14°29'S, 47°26'E, 332–379 m, 2 lv (MNHN IM-2007-36671, 30.8 mm; MNHN IM-2007-36747, 25.4 mm).

Madagascar form 1 [= *Vexillum* sp. of Fedosov & Kantor (2010)] (Fig. 9D)

Madagascar: MIRIKY, station CP3250, 15°22'S, 46°00'E, 493–750 m, 2 (27.5 mm, 26.9 mm); station CP3283, 14°52'S, 46°56'E, 228–257 m (MNHN IM-2013-40669, 28.1 mm).

Madagascar form 2 (Fig. 9E).

Madagascar: MIRIKY, station CP3283, 14°52'S, 46°56'E, 228–257 m, 2 (MNHN IM-2013-40670, 18.8 mm; 19.3 mm).

Diagnosis

Shell slender, medium sized, elongate fusiform (w/h 0.25–0.27; a/h 0.44–0.46) with high spire and long to very long siphonal canal. Protoconch bulbous, with one and a half white and glossy whorls. Suture canaliculated, teleoconch whorls evenly convex to indistinctly shouldered, subcylindrical. Sculpture of fine, slightly opisthoclinal axial ribs, overridden by rounded spiral cords to form spirally elongate beads in intersections. Axial ribs closely set to widely interspaced. Siphonal canal usually very long, tapering, widely opened and shallow. Aperture elongate, nearly parallel sided. Outer lip thin, evenly convex in its adapical portion, drawn towards siphonal canal. Inner surface of outer lip lirate. Columella with three fine, widely spaced, columellar folds, weakening towards siphonal canal. Background colour white, last adult whorl with three spiral tan bands, one adapical, second on the adapical portion of shell base, and third on siphonal canal, penultimate whorl with one adapical tan band, early spire whorls off white.



Radula (MNHN IM-2007-36671; Fig. 10A): *Radula* rachiglossate, about 1 mm long and 0.18 mm wide, consisting of 60+ rows. Rachidian with very wide

bow-shaped base reaching half of total radular length, bearing three strong pointed cusps; central cusp slightly weaker than lateral cusps, separated

Figure 9. *Tosapusia* species. A–E, *Tosapusia evelynae*: A, holotype of *Vexillum evelynae*, MNHN IM-2000-20641, Philippines, Bohol, off Balicasag Island, 31.7 mm; B, New Caledonia, EXBODI, station CP3826, 21°52'S, 166°51'E, 354–509 m, 20.4 mm; C, Madagascar, Molecular vouchers MNHN IM-2007-36671, MIRIKY station CP3289, 14°29'S, 47°26'E, 332–379 m, 30.8 mm; D, 'Form 1', Madagascar, MIRIKY, station CP3283, 14°52'S, 46°56'E, 228–257 m, 28.1 mm; E, 'Form 2', Madagascar, MIRIKY, station CP3283, 14°52'S, 46°56'E, 228–257 m, 19.3 mm. F–K, *Tosapusia longirostris* sp. nov.: F, G, holotype, MNHN IM-2000-30203, Solomon Islands, North of Guadalcanal, Salomon 1, station CP1800, 9°21'S, 160°24'E, 357–359 m, 25.6 mm; H, paratype 1, MNHN IM-2000-30204, same locality as previous, 25.0 mm; I, Philippines, East of Luzon Island, AURORA 2007, station CP2708, 15°08'N, 121°37'E, 307–309 m, 22.3 mm; K, MNHN IM-2007-34550, Philippines, East of Luzon Island, AURORA 2007, station CP2707, 15°04'N, 121°41'E, 368–442 m, 17.2 mm.

from them by shallow depressions. Lateral teeth elongate-triangular, with robust base and long strong cusp.

Distribution and habitat

Widely distributed in the tropical Indo-Pacific, from Madagascar to the Philippines, New Caledonia, and Vanuatu, depth range 66–618 m.

Remarks

In shell sculpture and colour pattern, *Tosapusia evelynae* is closest to *Tosapusia longirostris* sp. nov. The two species can be distinguished by the outline of the shell base: it is elongate, gradually extending towards the siphonal canal in *Tosapusia evelynae*, but rather shortly constricted in *Tosapusia longirostris* sp. nov. Moreover, *Tosapusia longirostris* sp. nov. is stouter, with a lower spire, and has a coarser sculpture with gemmate spiral cords.

As we interpret it, *Tosapusia evelynae* displays a wide morphologic variability and encompasses several forms that differ in details of sculpture and whorl profile; however, all forms share the same general outline and sculpture pattern of straight, slightly opisthocline axial ribs, overridden by spiral cords and a colour pattern of light-brown spiral bands, and intermediates connect the extreme morphotypes, at least in the West Pacific. The typical form is characterized by subcylindrical, indistinctly shouldered, whorls. The interspaces between axial ribs deep and only slightly exceed axials in width; spiral cords are interspaced by equally wide gaps. The specimens of *Tosapusia evelynae* from New Caledonia are characterized by wide and flattened spiral cords, separated by spiral grooves (Fig. 9B). The whorl profile in these specimens is more evenly convex than in typical form.

The pattern of variation is more complex in North-West Madagascar, where the typical form (Fig. 9C) is encountered along with two local morphotypes (Fig. 9D, E), and with two different morphs occasionally co-occurring at one station (forms 1 and 2 at MIRIKY, station CP3283). 'Form 1' is characterized by stronger and more widely spaced axial ribs,

whereas the spiral cords are wide, flattened, and separated by narrow grooves (Fig. 9D). The second local morphotype ('form 2') is characterized by a smaller shell with a delicate sculpture of fine dense axial ribs and multiple rounded spiral cords (Fig. 9E). Barcode sequences were obtained for all three forms ('typical form' and forms 1 and 2) from Madagascar, and these show only slight variation (see Results of the phylogenetic analysis), consistent with their conspecificity; however, as no specimen of *Tosapusia evelynae* from the type locality in the Philippines was sequenced, we assign the specimens from off Madagascar to *Tosapusia evelynae* based solely on shell morphology. It is noteworthy, that the protoconch, observed intact in a single specimen of form 2 from Madagascar, suggests a non-planctotrophic development of *Tosapusia evelynae*, which questions the suggested wide distribution range of the species.

TOSAPUSIA LONGIROSTRIS SP. NOV. FEDOSOV, HERRMANN & BOUCHET FIGURE 9F–K

Type data

Holotype: MNHN IM-2000-30203, lv, Solomon Islands, North of Guadalcanal, Salomon 1, station CP1800, 9°21'S, 160°24'E, 357–359 m, 25.6 mm (Fig. 9F, G).

Paratypes: Same locality as holotype; paratypes 1–5, MNHN IM-2000-30204, lv [25.9 mm, 25.0 mm (Fig. 9H), 24.6, 20.3 and 17.5 mm]; paratype 6, collection Manfred Herrmann, lv, 24.5 mm.

Other material examined

Philippines, East of Luzon Island: AURORA 2007 station CP2656 16°02'N, 121°54'E, 262–278 m, 1 lv (MNHN IM-2007-34553, 28.2 mm); station CP2658, 15°58'N, 121°49'E, 422–431 m, four (MNHN IM-2007-34564, lv, 17.6, 17.7, 15.0, and 14.9 mm); station CP2672, 14°58'N, 121°41'E, 276–346 m, five (20.85, 20.8, 17.5, 20.3, and 25.9 mm); station CP2708, 15°08'N, 121°37'E, 307–309 m, 2 lv (22.3 mm, Fig. 9I; 17.75 mm); station CP2707, 15°04'N, 121°41'E, 368–442 m, 1 lv (NHN IM-2007-34550, 17.2 mm, Fig. 9K).

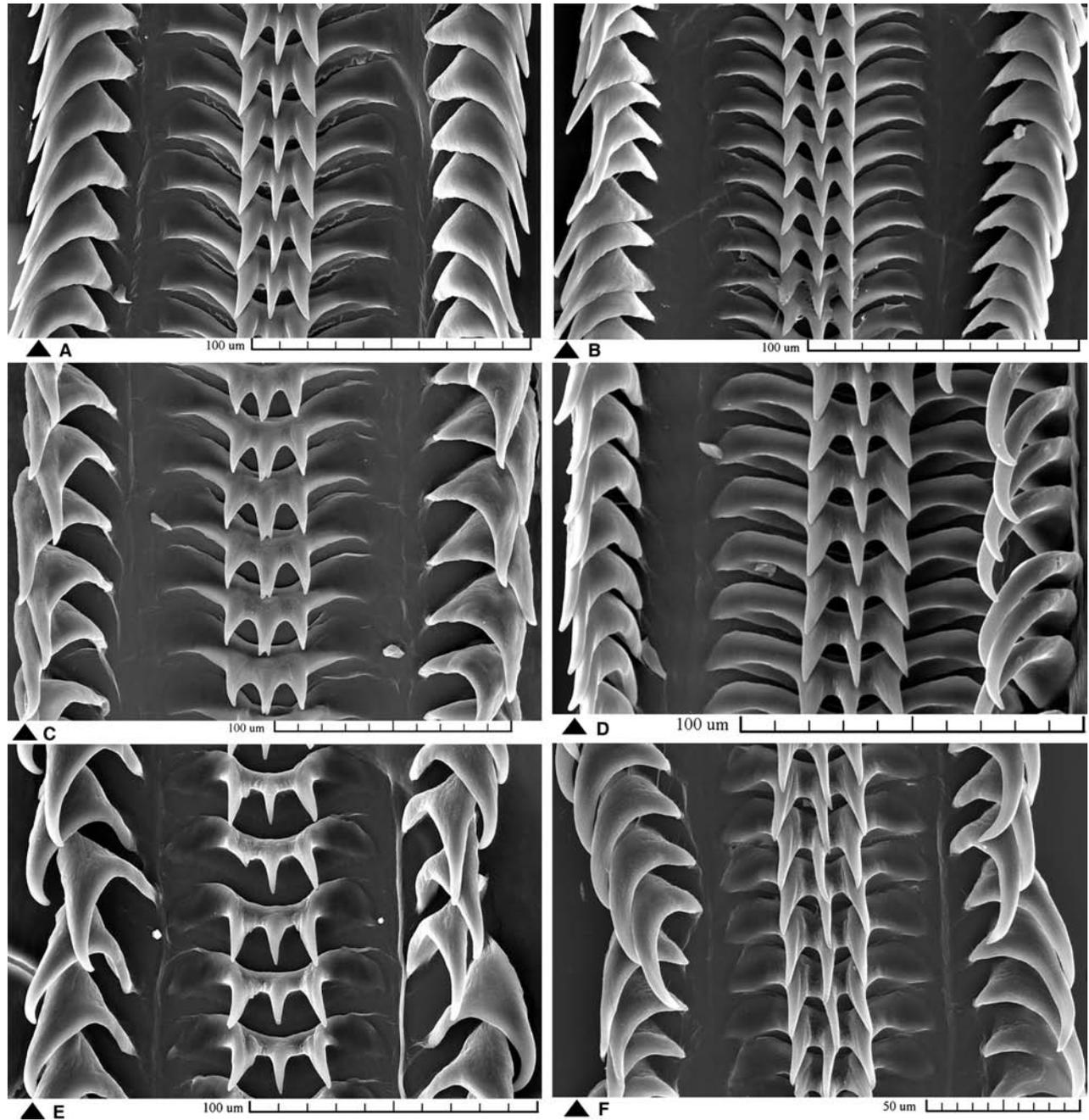


Figure 10. *Tosapusia radulae*: A, *Tosapusia evelynae*, MNHN IM-2007-36671; B, *Tosapusia longirostris* sp. nov., holotype; C, D, *Tosapusia duplex*; C, MNHN IM-2013-44577; D, BIOPAPUA, station CP3741, 29.2 mm; E, *Tosapusia myurella* sp. nov., paratype 1; F, *Tosapusia turiformis* sp. nov., holotype.

Diagnosis

Shell small, stout, fusiform, heavily sculptured, with very long siphonal canal. Protoconch conical, with ~2.7 light gently convex, glossy whorls. Teleoconch whorls convex to almost subcylindrical, with well-developed, though narrow, subsutural shelf. Sculpture consisting of axial ribs overridden by wide, flattened, spiral cords separated by deep grooves,

together forming spiral rows of axially aligned gemules. Shell base shortly constricted to very long, sometimes recurved, siphonal canal. Aperture narrow, elongate, almost parallel-sided. Inner surface of outer lip lirate. Columella with four strong, widely spaced folds, adapicalmost the strongest. Last adult whorl with pattern of white and light-brown spiral bands, earlier spire whorls pale.

Description

Shell small, fusiform, with very long siphonal canal (w/h 0.33–0.35; a/h 0.51–0.52) and pointed apex (although almost always corroded). Protoconch conical, of ~2.7 pale to orange gently convex, glossy whorls. Teleoconch of about nine whorls, suture distinct, slightly impressed. Spire whorls of nearly cylindrical profile, with distinct, though narrow, subsutural shelf and almost flat main portion of whorl. Axial sculpture of dense, closely set, axial ribs, about 28 on last adult whorl, and fine growth lines in interspaces between axials. Axial ribs overridden by wide and rounded spiral cords forming beads at intersection with axials. Early spire whorls with three, penultimate whorl with five, and last adult whorl with 12 spiral cords, separated at transition to siphonal canal by a slightly widened interspace from eight additional, low, rounded, spiral cords, rather oblique towards the tip of canal. Siphonal canal robust and very long, recurved. Aperture narrow, strongly elongate as it extends into wide siphonal canal. Outer lip slightly convex at mid-height and straight abapically, inside of outer lip with ten distinct lirae. Columella with four distinct, rather widely spaced, columellar folds, adapicalmost strongest; two adapical folds bearing shallow spiral groove on their crest, giving them a somewhat bifid profile. Background shell colour cream, last adult whorl with three distinct brown bands, one in subsutural area, second just below periphery, and third at base of siphonal canal. Early spire whorls and tip of siphonal canal white. Protoconch light translucent.

Radula (of holotype; Fig. 10B): Radula rachiglossate, ~0.9 mm long and 0.17 mm wide, consisting of about 72 rows. Rachidian with very wide bow shaped base, exceeding 40% of total radula width, tricuspidate, medial projection not pronounced, cusps equally pronounced, strong, pointed, rather short. Lateral teeth triangular, with robust base and strong, curved cusp.

Distribution and habitat

Solomon Islands, Philippines, depth range 278–422 m.

Etymology

The species name refers to the long, drawn siphonal canal, which distinguishes *Tosapusia longirostris* from other species of *Tosapusia*.

Remarks

Our specimens display slight variations in the orientation of the siphonal canal, sculpture, and shell colour. The holotype has a distinctly recurved siphonal canal, whereas in the larger paratype the canal is coaxial. The juvenile paratype lacks coloration and seems to have more widely spaced axial ribs (19 on

last adult whorl), which do not form beads at intersection with spiral cords; however, as this specimen is strongly damaged by boring *Hydractinia* cnidarians, which entirely covered the shell, we are inclined to attribute the observed differences to individual variation and the destructive activity of commensal *Hydractinia*.

Tosapusia evelynae most resembles *Tosapusia longirostris* sp. nov. The two occur sympatrically in deep water on the Pacific side of Luzon, and can be readily distinguished by shell proportions and sculpture. *Tosapusia longirostris* sp. nov. has a stouter shell with coarser sculpture and more cylindrical whorl profile, whereas *Tosapusia evelynae* is more slender, with evenly convex spire whorls and more delicate sculpture.

TOSAPUSIA DUPLEX (CERNOHORSKY, 1982)

COMB. NOV.

FIGURE 11A–E

Mitra simplicissima Schepman, 1911: 270; pl. 18, figs 11a, b (junior homonym of *Mitra simplicissima* Cooper, 1894);

Mitra simplicissima var. *glabra* Schepman, 1911: 270; pl. 18, fig. 11c (junior homonym of *Mitra glabra* Swainson, 1821, and *Mitra glabra* Pease, 1868);

Vexillum (*Costellaria*) *duplex* Cernohorsky, 1982a: 992; pl. 1, figs 6, 7. nom. nov. pro *Mitra simplicissima* Schepman, 1911;

Vexillum pratasense T.C. Lan, 2004: 5–9, figs 1, 2.

Tongsuapusia duplex, Huang, 2015: 45;

?†*Benthovolva ovalatita* Hu & Li, 1991. (Synonymy after Huang, 2015: 45).

Type data

Holotype by monotypy (type of *Mitra simplicissima* Schepman, 1911): ZMA.MOLL.137842 (RMNH), 21.6 × 6.3 mm, channel between Makjan and Halmahera (Indonesia), 472 m (Fig. 11A). *Holotype* of *Mitra simplicissima* var. *glabra* Schepman, 1911: ZMA.MOLL. 136808 (RMNH), 16.4 × 5.5 mm, Ceram Sea (Indonesia), 835 m (Fig. 11B).

Material examined

South China Sea: NANHAI, station CP4118, 20°01'N, 115°02'E, 700–723 m, 2 lv (MNHN IM-2013-44575, 30.7 mm; MNHN IM-2013-44577, 33.1 mm; Fig. 11C).

Solomon Islands: SALOMON 2, station CP2213, 7°39'S, 157°43'E, 495–650 m, four (MNHN IM-2007-30218, lv 21.7, 20.9, and 17.3 mm; MNHN IM-2007-30344, lv 21.7 mm); station CP2214, 7°42'S, 157°44'E, 550–682 m, five (MNHN IM-2007-30220, lv 25.4, 21.35, 19.6, 19.25, and 16.35 mm); station CP2276, 8°42'S, 157°38'E, 814–980 m, 1 lv (MNHN IM-2007-



30343, broken). SALOMONBOA 3, station CP2768, 09°25'S, 160°31'E, 447–503 m, 1 lv (MNHN IM-2007-35927, 27.4 mm, Fig. 11D); station CP2772, 09°25'S, 160°31'E, 456–551 m, 2 dd (MNHN, 28.8 mm, 23.6 mm); station CP2773, 09°25'S, 160°32'E, 537–619 m, 1 lv (MNHN IM-2007-36139, 22.65 mm);

station CP2777, 09°12'S, 160°55'E, 706–722 m, 1 lv (MNHN IM-2007-36256, 30.3 mm); station CP2833 10°42'S, 162°19'E, 565–585 m, 1 lv (MNHN IM-2007-35987, 23.15 mm); station CP2850, 9°37'S, 160°47'E, 502–621 m, 1 lv (MNHN IM-2007-35969, 26.6 mm); station CP2857, 9°44'S, 160°49'E, 473–505 m, 1 lv

Figure 11. *Tosapusia* species. A–E, *Tosapusia duplex*: A, *Mitra simplicissima*, holotype, ZMA.MOLL.137842 (RMNH), channel between Makjan and Halmahera (Indonesia), 472 m, 21.6 × 6.3 mm; B, *Mitra simplicissima* var. *glabra* Schepman, 1911, holotype, ZMA.MOLL.136808 (RMNH), Ceram Sea (Indonesia), 835 m, 16.4 × 5.5 mm; C, Taiwan, MNHN IM-2013-44575, NANHAI, station CP4118, 20°01'N, 115°02'E, 700–723 m, 30.7 mm; D, Solomon Islands, MNHN IM-2007-35927, SALOMONBOA 3, station CP2768, 09°25'S, 160°31'E, 447–503 m, 27.4 mm; E, elongate form, Papua New Guinea, BIOPAPUA, station CP3741, 09°14'S, 152°18'E, 694–766 m, 29.2 mm; F, *Tosapusia* sp. nov. aff. *duplex* (not described in the present paper), Solomon Islands MNHN IM-2007-35967, SALOMONBOA 3, station CP2850, 9°37'S, 160°47'E, 502–621 m, 27.25 mm. G–I, *Tosapusia myurella* sp. nov.: G, H, holotype, MNHN IM-2000-30205, Papua New Guinea, Woodlark Island, BIOPAPUA, station CP3741, 09°14'S, 152°18'E, 694–766 m, 29.15 mm; I, paratype 1, MNHN IM-2007-30347, Solomon Islands, south-east Isabel Island, SALOMON 2, station CP2189, 8°20'S, 160°02'E, 660–854 m. K, L, *Tosapusia turriiformis* sp. nov. holotype, MNHN IM-2013-19792, Papua New Guinea, Bismark Sea, North of Long Island, PAPUA NIUGINI, station CP3985, 05°09'S, 147°02'E, 805–865 m, 27.15 mm.

(MNHN IM-2007-35924, 28.05 mm); station CP2858, 9°40'S, 160°45'E, 650–725 m, 1 lv (MNHN IM-2007-35876, 20.8 mm).

Papua New Guinea: BIOPAPUA, station CP3672, 04°04'S, 151°50'E, 702–724 m, 1 dd (MNHN, 31.2 mm); station CP3741, 09°14'S, 152°18'E, 694–766 m, 1 dd (MNHN, 29.2 mm; Fig. 11E). PAPUA NIUGINI, station CP3981, 05°11'S, 147°03'E, 688 m, 1 lv (MNHN IM-2013-19727, 23.5 mm).

Diagnosis

Shell small, fusiform to turriiform, with tall spire and elongate aperture (w/h 0.24–0.30; a/h 0.39–0.45). Protoconch pointed, very high, with three or more adpressed whorls (almost always broken or eroded). Teleoconch whorls evenly convex to slightly adpressed in outline, sculptured with very strong, widely set, orthocline ribs, in their adapical third intersected by one or two faint spiral grooves succeeded by a weak rounded cord. Spiral sculpture usually absent on the periphery of the last adult whorl, but regular grooves present on shell base and siphonal canal. Siphonal canal moderately long, tapering, widely and shallowly open. Aperture elongate, its inner lip with three strong, widely set, oblique, columellar folds. Shell colour off-white, often with remains of brown periostracum. Apex usually strongly corroded.

Radula (MNHN IM-2013-44577, Fig. 10C; BIOPAPUA, station CP3741, 29.2 mm, Fig. 10D): *Radula* rachiglossate, about 1 mm long and 0.25 mm wide, consisting of 45+ rows. Rachidian rather narrow but base robust and strong, cusps short and blunt (in the specimen from Taiwan, the central cusp was bifurcated at its tip – a feature we consider to be individual), medial projection not pronounced. Lateral teeth unicuspidate, widely sickle-shaped, robust in appearance.

Distribution and habitat

Indonesia, South China Sea, Papua New Guinea, Solomon Islands. Soft bottoms, depth range 503–814 m.

Remarks

Our material displays considerable variation in shell proportions and details of shell sculpture. The specimens collected in the South China Sea are morphologically very close to the typical form, as well as to the holotype of *Vexillum pratense*, as illustrated by Lan (2004). Their shells are wide, fusiform, with spiral sculpture limited to the adapical portion of the whorls and to the siphonal canal (Fig. 11C).

Specimens from the Solomon Sea here assigned to *Tongsuapusia duplex* vary in proportions from wide and fusiform – similar to those from the South China Sea (Fig. 11D) – to usually more slender, with a taller spire and more widely set axial ribs (Fig. 11E). Examination of 25+ specimens from the Solomon Sea shows that shell proportions, strength of axial ribs, and extent of spiral sculpture vary continuously, and are not strictly correlated: wide fusiform specimens may have fine ribs and well-pronounced spiral sculpture (Fig. 11D), and elongate turriiform specimens may have strong, widely spaced axials with very weak spiral elements (Fig. 11E). We are inclined, therefore, to consider all these forms to represent a single variable species.

Nevertheless, one of the sequenced specimens (Salomonboa-3, station CP2850, 9°37'S, 160°47'E, 502–621 m, MNHN IM-2007-35967; Fig. 11F), initially identified as *Tongsuapusia duplex*, in fact turned out to be not conspecific with a typical *Tongsuapusia duplex* (represented by specimen MNHN IM-2013-44577), and even not closely related to it. We refrain from describing a new species based on this specimen, as the lack of clear diagnostic morphological characters would inevitably hamper its recognition. Obviously more molecular data are needed for accurate species delimitation in the *Tongsuapusia duplex* species complex.

Among *Tosapusia* species, typical *Tongsuapusia duplex* is most similar to *Tongsuapusia bismarckiana* sp. nov., *Tongsuapusia myurella* sp. nov., and *Tongsuapusia turriiformis* sp. nov.; however, it can be readily distinguished from all of them by the shell proportions (even taking into account the observed

intraspecific variation in *Tongsuapusia duplex*), shape of the last adult whorl and sculpture details. *Tongsuapusia bismarckiana* sp. nov. has a longer siphonal canal and finer and narrower opisthocline ribs than in *Tongsuapusia duplex*. By contrast, *Tongsuapusia myurella* sp. nov. and *Tongsuapusia turriiformis* sp. nov. have turriiform shells with a higher spire and flattened whorls profile; the shell base in both of these species is notably shorter than in *Tongsuapusia duplex*, so the last adult whorl is constricted to the siphonal canal and looks somewhat inflated. Finally, shell proportions, a strong axial sculpture, and weakly developed spiral elements in *Tongsuapusia duplex* resemble the genus *Latiromitra*; however, unlike *Tosapusia*, species of *Latiromitra* have very weak columellar folds and possess an operculum, even though it is often reduced.

TOSAPUSIA MYURELLA SP. NOV. FEDOSOV,
HERRMANN & BOUCHET
FIGURE 11G–I

Type data

Holotype: MNHN IM-2000-30205, lv, Papua New Guinea, Woodlark Islands, BIOPAPUA, station CP3741, 09°14'S, 152°18'E, 694–766 m, 29.15 mm (Fig. 11G, H).

Paratypes: Paratype 1, MNHN IM-2007-30347, lv, Solomon Islands, SE Isabel Island, SALOMON 2, station CP2189, 8°20'S, 160°02'E, 660–854 m (Fig. 11I). Paratype 2, MNHN IM-2013-18540, dd, PAPUA NIUGINI, station CP4038, 04°27'S, 145°34'E, 800–840 m, 33.6 mm.

Diagnosis

Shell medium-sized, turriiform with high, slightly acuminate spire and wide last adult whorl, shortly constricted to moderately long tapering siphonal canal. Protoconch unknown because of erosion. Early spire whorls shouldered, subcylindrical, subsequent whorls with flattened outline, gradually widening abapically. Sculpture of evenly spaced, rounded, slightly opisthocline ribs, with regular, short, stroke-like grooves in interspaces between axials. Axial ribs forming low, but distinct 'cap' (see below) in their adapical third. On last adult whorl axial ribs becoming obsolete on shell base, which is shortly constricted to the slender and straight, widely open, siphonal canal. Aperture rather wide, with thin outer lip drawn towards tip of siphonal canal. Adapical aperture angle with callous pad, inner lip with four columellar folds, gradually weakening towards siphonal canal. Shell off-white.

Description

Shell medium sized, thin walled, turriiform, with tall, slightly acuminate spire and wide, slightly inflated,

last adult whorl (w/h 0.35; a/h 0.41; law/h 0.56). Protoconch always eroded, but with light-brown remains. Teleoconch of 9.5 whorls. Early spire whorl subcylindrical to slightly convex, with distinct subsutural shelf, giving them a stepped profile. Subsequent whorls with flattened outline, suture distinct, impressed. Last adult whorl with strongly convex base, shortly constricted to long and slender siphonal canal. Sculpture of arcuate, slightly prosocline, axial folds (19 on last adult whorl; 18 on penultimate whorl) and fine growth lines. Spiral sculpture of evenly spaced, interrupted spiral grooves, sharp in the interspaces between axial folds but obsolete on their crests. Adapical quarter of spire whorls devoid of spiral sculpture, forming indistinct 'cap' (we use this term to refer to a sculpture element, formed by spiral groove intersecting axial ribs near the suture to form a row of subsutural beads rounded adapically and straight cut basally), separated by rather wide and shallow groove from the peripheral portion of the whorl that bears six stroke-like grooves between axial folds. Periphery of last adult whorl strongly convex with fine elements of sculpture polished off. Shell base with no axial elements, only sculptured by continuous grooves, very fine below whorl periphery and widening towards siphonal canal.

Siphonal canal moderately long, straight, and slender, sculptured by rounded oblique cords. Aperture elongate, slightly constricted at transition to siphonal canal. Outer lip convex at mid-height, drawn apically towards tip of siphonal canal. Inner lip with four distinct folds, of which the adapicalmost fold is strongest. Adapical angle of aperture with distinct callous pad.

Shell off-white.

Radula (of paratype 1; Fig. 10E): *Radula* rachiglossate, about 1 mm long and 0.17 mm wide, consisting of about 52 rows. Rachidian with wide bow-shaped base, attaining 45% of total radula length, bearing three equally pronounced pointed cusps, which are widely set apart. Two lateral cusps slightly elevated, whereas central cusp seems to be situated in wide depression between them. Medial projection not developed. Lateral teeth robust, triangular, with wide base and pointed cusp, curved at its tip.

Distribution and habitat

Papua New Guinea (Solomon Sea), Solomon Islands, depth range 766–800 m.

Etymology

The species name reflects the resemblance in shell sculpture between this new species of *Tosapusia* and members of the terebrid genus *Myurella*, for example *Myurella undulata* (Gray, 1834).

Remarks

Tosapusia myurella sp. nov. is conchologically closest to *Tosapusia turriiformis* sp. nov. and *Tosapusia duplex*; however, it can be easily differentiated from the former by narrower and more numerous axial ribs, and the presence of spiral grooves throughout the entire height of the whorl, and from the latter by the shell outline with relatively flattened whorl profile, strongly convex last adult whorl, and wider aperture. In general, shell proportions and characteristic sculpture pattern with adapical 'cap' allow for an easy recognition of this species among its congeners.

TOSAPUSIA TURRIIFORMIS SP. NOV. FEDOSOV,
HERRMANN & BOUCHET
FIGURE 11K, L

Type data

Holotype: MNHN IM-2013-19792, lv, Papua New Guinea, Bismark Sea, North of Long Island, PAPUA NIUGINI, station CP3985, 05°09'S, 147°02'E, 805–865 m, 27.15 mm (Fig. 11K, L).

Diagnosis

Shell turriiform, with very high spire and strongly convex last adult whorl, constricted to rather short and widely opened siphonal canal. Protoconch with smooth, light-brown last whorl. Suture distinct, canaliculated; teleoconch whorls slightly convex in abapical portion, with flattened overall outline. Sculpture of very wide and rather low, widely spaced, axial ribs, and fine growth lines; spiral sculpture absent. Last adult whorl strongly convex, shell base forming distinct 'waist' at its transition to siphonal canal, which is rather short, slightly recurved, and thickened at its base because of developed fasciole. Aperture elongate, its outer lip thin, evenly convex, slightly drawn towards wide opening of siphonal canal. Inner aperture lip with three fine oblique folds, with the adapicalmost fold strongest. Shell off-white.

Description

Shell medium-sized, narrowly turriiform (w/h 0.29; a/h 0.39; law/h 0.52). Protoconch pointed, light brown, with smooth, convex last whorl. Teleoconch of 11 whorls, suture wavy, distinctly canaliculated on early spire whorls, and deeply impressed on later whorls. Early spire whorls subcylindrical, later whorls flattened adapically, with convex periphery shifted abapically. Sculpture of strong and very wide opisthocline axial folds (11 on last adult whorl), becoming indistinct on latest portion of last adult whorl. Spiral sculpture of one or two very weak

threads on whorls 6–8 and indistinct on subsequent whorls. Microsculpture of numerous, fine, collabral growth lines. Last adult whorl evenly convex, separated from siphonal canal by slightly concave 'waist'. Siphonal canal rather short and stout, widely opened, with weakly developed fasciole, sculptured by wide oblique cords.

Aperture rather wide, its outer lip thin, evenly convex adapically and drawn towards siphonal canal in its lower portion. Inner aperture lip with three oblique columellar folds, adapicalmost being strongest, and consequent ones progressively fainter.

Shell off-white.

Radula (of *holotype*; Fig. 10F): *Radula* rachiglossate, about 0.75 mm long and 0.16 mm wide, of about 52 rows. Rachidians with moderately wide base bearing three elevated, long, and pointed cusps, separated by notable depressions. Anterior edge of rachidian forming distinct blade-like angulation, medial projection not pronounced. Laterals unicuspidate, sickle-shaped, with long pointed cusp.

Distribution and habitat

North of Long Island, Bismark Sea, Papua New Guinea, 805–865 m.

Etymology

The species name refers to the distinctly turriiform shell.

Remarks

In overall shell morphology, the fossil *Tosapusia kalimnanensis* is undoubtedly closest to *Tosapusia turriiformis* sp. nov. Both have a turriiform shell with rather short siphonal canal; however, *Tosapusia turriiformis* sp. nov. can be distinguished by the wider axial elements and the whorl periphery shifted abapically. Among recent species, *Tosapusia myurella* sp. nov. is most similar to *Tosapusia turriiformis* sp. nov. in shell proportions; however, the two species differ notably in shell sculpture. Overall, a turriiform shell in combination with very wide axial elements and completely lacking spiral sculpture allow an easy recognition of *Tosapusia turriiformis* sp. nov. among other recent species of *Tosapusia*.

The turriiform shell of *Tosapusia turriiformis* resembles some species of *Alisimitra* gen. nov., like *Alisimitra samadiae* sp. nov. or *Alisimitra fuscolineata* (Herrmann & Salisbury, 2012), but the former has much stronger axial elements and a more elongate shell, with longer siphonal canal, and *Alisimitra fuscolineata* has a wider shell with denser axials, intersected by faint grooves that are lacking in *Tosapusia turriiformis* sp. nov. Finally, the strong columellar folds and lack of periostracum differentiate the new species from species of *Latiromitra*, of which

Latiromitra paiciorum Bouchet & Kantor, 2000a,b is most similar to *Tosapusia turrimiformis* sp. nov.

GENUS **ALISIMITRA** GEN. NOV. FEDOSOV,
HERRMANN & BOUCHET

Type species: Alisimitra barazeri sp. nov.

Diagnosis

Shell rather small, under 30 mm in length, fusiform or turritiform, with high, sometimes slightly acuminate spire. Protoconch high, conical with four or more evenly convex, brown, glossy, whorls. Early spire whorls subcylindrical, later weakly convex or flattened. Sculpture of straight, widely spaced, usually orthocone axial ribs; spiral sculpture usually limited to a single or very rarely two or three spiral cords situated at adapical one-quarter to one-third of whorl height, overriding axials, and sometimes forming adapical 'cap', and few strong, rounded, oblique cords on siphonal canal. Siphonal canal usually moderately long, tapering. Aperture elongate with thin outer lip lacking lirae on its inside. Columella with three strong folds, adapicalmost strongest, and subsequent ones gradually weakening. Shell off-white, pale or bearing one or several light-brown spiral bands. Radula rachiglossate with tricuspidate rachidian and unicuspidate sickle-shaped laterals; the anterior margin of rachidians base elevated, with sharp blade-like edges. Buccal mass encloses soft horseshoe-shaped jaw. Medium-sized accessory salivary gland present; gland of Leiblein glandular, large, brown. Seminal groove open.

Included species

Alisimitra barazeri sp. nov.,¹ *Alisimitra deforgesii* sp. nov.,¹ *Alisimitra fuscolineata* (Herrmann & Salisbury, 2012) comb. nov.,¹ *Alisimitra samadiae* sp. nov.,¹ *Alisimitra tehuaorum* (Huang, 2015) comb. nov.¹

Distribution and habitat

Alisimitra is distributed in the Indo-Pacific from Taiwan to New Caledonia and French Polynesia, with the highest species diversity recorded in Papua New Guinea. The multispiral protoconch suggests a long planktonic dispersal phase that correlates with the broad distribution of several species, e.g. *Alisimitra tehuaorum*, which extends from Taiwan to New Caledonia and French Polynesia, and *Alisimitra barazeri* sp. nov., which extends from Papua New Guinea to French Polynesia.

Etymology

The genus is named in honour of the IRD research vessel *Alis*, which served to conduct numerous

biodiversity surveys in the South Pacific. For many new species of marine molluscs the deck of *Alis* was the first station in their journey from ocean depths to museum research collections.

Remarks

The relatively small, thin-walled, lightly coloured, and sculptured shells of *Alisimitra* gen. nov., with their tall spire and orthocone ribs, can in most cases be easily recognized; however, some species deviate from this general outline in sculpture (*Alisimitra deforgesii* sp. nov.) or proportions (*Alisimitra samadiae* sp. nov.). Conchologically similar forms are found in *Pusia* (*Vexillum*) subgen. nov.; however, they display complex, variegated colour patterns, have a lower spire, and an outer aperture lip that is characteristically lirate within (whereas it is smooth in all studied species of *Alisimitra* gen. nov.). The same feature distinguishes *Alisimitra* gen. nov. from some deep-water species of *Vexillum*, like *Vexillum leforti* Turner & Salisbury, 1999, *Vexillum fuscovirgatum* Herrmann & Salisbury, 2012; or *Vexillum troendlei* Herrmann & Salisbury, 2012. Besides, species of *Alisimitra* gen. nov. have finer axial ribs that are always orthocone, and a wider aperture with longer siphonal canal that is not notched at its tip. Species of *Alisimitra* gen. nov. can also be distinguished from *Tosapusia* by their generally smaller shells with only one or two spiral cords, and shorter, tapering siphonal canal. Finally, some species of the ptychactrid genus *Latiromitra* resemble *Alisimitra* gen. nov.; however, *Alisimitra* gen. nov. has very distinct columellar folds, which are rather faint in *Latiromitra*.

ALISIMITRA BARAZERI SP. NOV. FEDOSOV,
HERRMANN & BOUCHET
FIGURES 12A–C AND 13A

Type data

Holotype: MNHN IM-2013-40664, Papua New Guinea, Vitiaz Strait, BIOPAPUA, station CP3724, 05°59'S, 147°39'E, 860–880 m, lv, 14.4 mm (Fig. 12A, B).

Other material examined

Society Islands: TARASOC, station DW3434, 16°42'S, 151°03'W, 700–785 m, Huahine, 1 lv (MNHN IM-2007-38639, Fig. 12C); station DW3452, 16°51'S, 151°19'W, 600–705 m, Raiatea, 1 lv (MNHN IM-2007-39400).

Diagnosis

Shell small, thin-walled, turritiform, with high spire and truncated base. Protoconch cyrtocoid, brown, with four or more convex glossy whorls. Early spire

whorls indistinctly shouldered, later teleoconch whorls with flattened outline. Sculpture of strong, widely set orthocone axial ribs intersected by single adapical spiral cord of even strength where it crosses the ribs and between them. Last adult whorl with strongly convex base, shortly constricted to widely open, tapering siphonal canal. Aperture rather wide, outer lip thin, evenly convex, lacking lirae on its inside. Inner lip with three narrow columellar folds, adapicalmost strongest. Shell off-white.

Description

Shell small, thin walled, turriform, with high spire shortly constricted to short tapering siphonal canal (w/h 0.38–0.39; a/h 0.43–0.45), which gives it a truncated appearance. Protoconch conical, with more than four convex polished whorls, with very fine arcuate growth lines on last one-third of whorl. Protoconch/teleoconch transition distinct. Teleoconch of seven adpressed whorls, their periphery shifted abapically. Suture wavy, impressed. Shell sculptured with strong, widely spaced, orthocone axial ribs (13 on last adult whorl), overridden by one distinct, rounded, spiral cord in adapical quarter, equally well pronounced on early and late teleoconch whorls; other elements of spiral sculpture absent. Microsculpture of very faint growth lines. Last adult whorl shortly constricted to siphonal canal, shell base strongly convex, almost globose. Siphonal canal short, widely opened, tapering, bearing three very wide, rounded spiral cords aligned with the columellar folds. Aperture ovate, shortly constricted towards opening of siphonal canal, rather low. Outer lip thin, strongly convex, slightly drawn at siphonal canal opening, lacking lirae. Inner lip with three distinct but rather thin columellar folds, adapicalmost strongest.

Shell uniformly cream.

Radula (of *holotype*; Fig. 13A): Radula attaining 0.6 mm in length and about 0.1 mm in width, formed by 51+ rows. Rachidian tricuspidate, with rather long pointed cusps and robust, moderately wide base. Anterior margins of rachidians base forming sharp blade-like edges laterally. Laterals monocuspidate, sickle-shaped.

Distribution and habitat

Papua New Guinea (Solomon Sea), French Polynesia (Society Islands), depth range 705–860 m.

Etymology

The species is named after Jean-Francois ('Jeff') Barazer, long-time second captain, then captain, of R.V. *Alis*, and a companion on many research cruises.

Remarks

Alisimitra barazeri sp. nov. is closest to *Alisimitra tehuaorum* in shell morphology, but differs from the latter species in shell outline and details of axial sculpture (for details, see Remarks section of *Alisimitra tehuaorum*). *Alisimitra barazeri* sp. nov. differs from both *Alisimitra deforgesi* sp. nov. and *Alisimitra fuscolineata* in the presence of only one spiral cord in adapical part of whorls, and uniform pale coloration of the shell. The broad shell of *Alisimitra barazeri* sp. nov., with its strongly convex base, differs drastically from the elongate *Alisimitra samadiae* sp. nov., preventing any confusion between the two.

ALISIMITRA DEFORGESI SP. NOV. FEDOSOV, HERRMANN & BOUCHET FIGURE 12D–F

Type data

Holotype: MNHN IM-2007-32137, Coral Sea, Chesterfield plateau, EBISCO, station DW2606, 19°37'S, 158°42'E, 442–443 m, lv, 14.5 mm (Fig. 12H, I).

Paratype: MNHN IM-2007-38256, TERRASSES, station CP3063, 23°23'S, 168°00'E, 430–480 m, lv (Fig. 12K).

Other material examined

Papua New Guinea: BIOPAPUA, station DW3687, 03°04'S, 147°32'E, 305–579 m, south of Manus Island, 1 dd (12.3 mm); station CP3707, 04°59'S, 145°50'E, 460–466 m, off Madang, 2 dd (15.75 mm, 15.7 mm); station DW3734, 08°16'S, 150°30'E, 389 m, off Lancasay, 1 dd (12.4 mm); station CP3740, 09°12'S, 152°16'E, 556–645 m, off Woodlark Island, 1 lv (MNHN IM-2013-9728, 15.8 mm); Papua Niugini, station CP3984, 05°12'S, 146°59'E, 500 m, north-west of Long Island, 1 lv (13.8 mm); station DW4010, 06°02'S, 148°08'E, 400–440 m, south-east of Tuam Island, 1 lv (MNHN IM-2013-9655, 12.2 mm).

Solomon Islands: Salomon 3, station CP2837, 10°26'S, 161°22'E, 381–422 m, West of San Cristobal, 1 dd (15.6 mm).

New Caledonia: EXBODI, station DW3906, 19°50'S, 165°33'E, 490–580 m, north-west of Astrolabe Reef, 1 dd (12.7 mm); station DW3930, 18°37'S, 164°26'E, 448–464 m, Petrie Reef, 1 dd (12.3 mm).

Diagnosis

Shell small, elongate-fusiform, with high orthoconoid spire and strong, tapering siphonal canal. Protoconch cyrtoconoid, brown, with four or more convex, glossy whorls. Spire whorls with flattened outline, sculptured by strong, orthocone axial ribs, forming characteristic adapical 'cap'. Spiral sculpture of regular



Figure 12. *Alisimitra* gen. nov. species. A–C, *Alisimitra barazeri* sp. nov.: A, B, holotype, MNHN IM-2013-40664, Papua New Guinea, Vitiaz Strait, BIOPAPUA, station CP3724, 05°59'S, 147°39'E, 860–880 m, 14.4 mm; C, MNHN IM-2007-38639, Society Islands, TARASOC, station DW3434, 16°42'S, 151°03'W, 700–785 m. D–F, *Alisimitra deforgesi* sp. nov.: D, E, holotype, MNHN IM-2007-32137, Coral Sea, Chesterfield plateau, EBISCO, station DW2606, 19°37'S, 158°42'E, 442–443 m, 14.5 mm; F, paratype 1, MNHN IM-2007-38256, TERRASSES, station CP3063, 23°23'S, 168°00'E, 430–480 m. G–N, *Alisimitra tehuaorum*: G, MNHN IM-2013-44099, Taiwan, NANHAI, station CP4100, 15°05'N, 116°32'E, 534–552 m, 20.7 mm; H, I, MNHN IM-2013-44146, Taiwan, NANHAI station, CP4102, 15°03'N, 116°31'E, 339–533 m, 18.0 mm; K, MNHN IM-2013-19796, Papua New Guinea, North-West of Long Island, PAPUA NIUGINI, station DW3983, 05°12'S, 146°59'E, 470–508 m, 22.7 mm; L, MNHN IM-2013-40663, New Caledonia, Loyalty ridge, TERRASSES, station DW3036, 22°41'S, 168°58'E, 800 m, 15.5 mm; M, New Caledonia, Norfolk ridge, Norfolk 2, station DW2081, 25°54'S, 168°22'E, 500–505 m, 23.7 mm; N, Society Islands, TARASOC, station CP3458, 16°46'S, 151°23'W, 573–611 m.

stroke-like grooves, well pronounced in interspaces between axial ribs. Shell base strongly convex, rather short, siphonal canal moderately long, with very wide opening, sculptured by several strong oblique cords. Aperture elongate, outer lip smooth inside, with flattened adapical part; inner lip with four narrow, oblique columellar folds. Shell off-white, with contrasted pattern of fine orange to light-brown spiral bands on late teleoconch whorls, spire whorls with two bands, one adapical and one on periphery, just above suture, last adult whorl with third spiral band on shell base.

Description

Shell small, elongate-fusiform (w/h 0.35; a/h 0.46), with rather high conical spire and long, tapering siphonal canal. Protoconch conical, with 4.5–4.7 very slightly convex whorls, devoid of any sculpture. PI and PII not distinguished, protoconch/teleoconch transition distinct. Teleoconch of 7.0–7.5 adpressed whorls, almost cylindrical in early whorls. Suture wavy, distinctly impressed. Axial sculpture of fine orthocline ribs (17 on last adult whorl), with adapical part forming a distinct subsutural 'cap', giving the spire a slightly stepped appearance. Spiral sculpture of fine, evenly spaced, dashed grooves, pronounced in interspaces between axials below subsutural caps. Last adult whorl adpressed in its adapical portion and strongly convex below periphery, rather shortly constricted towards siphonal canal. Axial ribs reaching down to distinct waist delineating siphonal canal from shell base. Siphonal canal long and straight, tapering, sculptured by three very strong, rounded, oblique cords. Aperture elongate, outer lip thin, almost coaxial in its adapical third, convex at mid-height and slightly drawn abapically towards tip of siphonal canal; lacking lirae. Inner lip straight, bearing four columellar folds, adapicalmost strongest, apicalmost rather weak. Background colour white, four last teleoconch whorls with distinct, light-brown spiral bands formed by regular blotches in interspaces between axial ribs. Spire whorls with two such bands: one adapical and one just above suture.

Last adult whorl with additional third band on shell base right above waist. Protoconch brown.

Radula (of holotype; Fig. 13B): Radula about 0.35 mm long and 0.08 mm wide, formed by about 47 rows. Rachidians tricuspidate with moderately wide base reaching about 40% of radula width. Anterior margin of rachidian base forming sharp blade-like edges on both sides of cusps. Three cusps of rachidian of about equal length, strong, pointed. Lateral cusps slightly elevated in relation to central cusp and directed slightly sideways. Laterals sickle-shaped, unicuspidate.

Distribution and habitat

Papua New Guinea (Bismarck and Solomon Seas), Solomon Islands, New Caledonia (Loyalty Ridge), mostly on hard bottoms, depth range 389–556 m.

Etymology

The species is named after Bertrand Richer de Forges, in recognition for his immense contribution to the exploration of the South Pacific.

Remarks

Alisimitra deforgesi sp. nov. differs from other species of the genus by the presence of spiral sculpture of dashed grooves throughout whorl height, whereas in most other *Alisimitra* species the spiral sculpture is confined to a single spiral cord on the adapical portion of the whorl. The other exception is *Alisimitra fuscolineata* in which the spiral sculpture elements are still more numerous than in *Alisimitra deforgesi* sp. nov., and the shell base is notably more elongate. The other characteristic feature distinguishing *Alisimitra deforgesi* sp. nov. is its variegated colour pattern with distinct and contrasting colour bands.

Some deep-water *Vexillum* species, in particular *Vexillum fuscovirgatum* Herrmann & Salisbury, 2012 and *Vexillum troendlei* Herrmann & Salisbury, 2012 resemble *Alisimitra deforgesi* sp. nov. in shell proportions and colour pattern; however, both have undulating, arcuate axial ribs, notched siphonal canal, and outer aperture lp liriate within, whereas

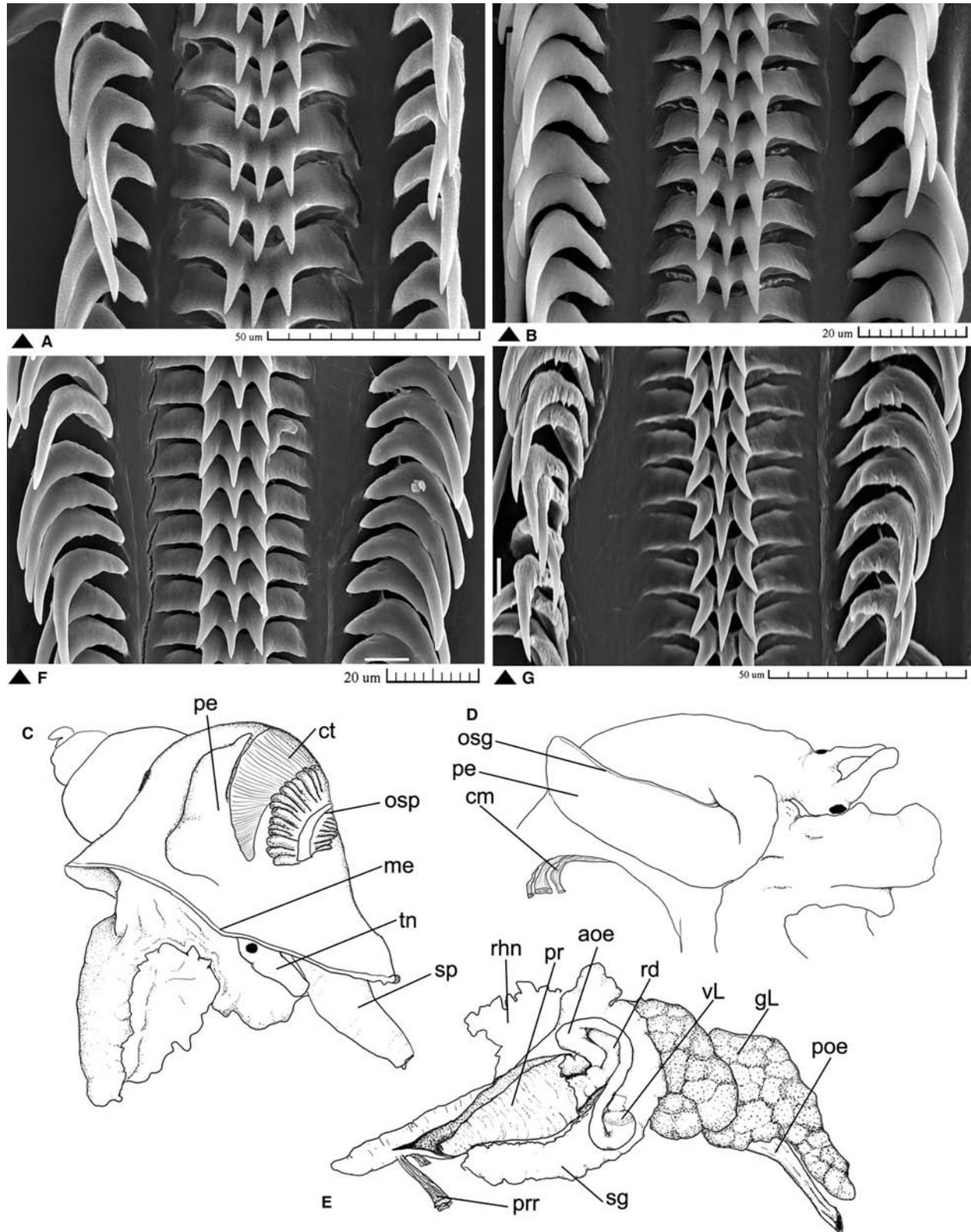


Figure 13. *Alisimitra* gen. nov. morphology: A, *Alisimitra barazeri* sp. nov. radula of holotype; B, *Alisimitra deforgesi* sp. nov. radula of holotype; C–F, *Alisimitra tehuaorum*; C, general morphology of the body, MNHN IM-2013-44099; D, mantle removed; E, anterior alimentary canal; F, radula; G, *Alisimitra samadiae* sp. nov. radula of holotype.

in *Alisimitra deforgesi* sp. nov. the axial ribs are straight, there is no notch at the tip of the siphonal canal, and the inside of the outer lip is smooth.

ALISIMITRA TEHUAORUM (HUANG, 2015)

COMB. NOV.

FIGURES 12G–N AND 13C–F

Tongsuapusia tehuaorum Huang, 2015: 46; pl. 1, fig. 7.

Type data

Holotype: NMNS 7523-001, South China Sea, Pratas Islands, 600 m, 28.24 × 10.05 mm.

Material examined

Taiwan: South China Sea, Expedition NANHAI, station CP4100, 15°05'N, 116°32'E, 534–552 m, 2 lv (MNHN IM-2013-44099, 20.7 mm, Fig. 12G; MNHN IM-2013-44103, 1v, 19.0 mm); station CP4102, 15°03'N, 116°31'E, 339–533 m, 3 lv (MNHN IM-2013-44146, 18.0 mm, Fig. 12H, I; MNHN IM-2013-44156, 18.85 mm, and MNHN IM-2013-44158, 19.4 mm); station CP4103, 15°05'N, 116°30'E, 633 m, 2 lv (MNHN IM-2013-44191, 15.85 mm, and MNHN IM-2013-44200, 16.6 mm).

Papua New Guinea: PAPUA NIUGINI, station DW3983, 05°12'S, 146°59'E, 470–508 m, Bismarck Sea, North-West of Long Island, 1 lv (MNHN IM-2013-19796, 22.7 mm, Fig. 12K).

New Caledonia: TERRASSES, station DW3036, 22°41'S, 168°58'E, 800 m, Loyalty ridge, 1 lv (MNHN IM-2013-40663, 15.5 mm, Fig. 12L); Norfolk 2, station DW2081, 25°54'S, 168°22'E, 500–505 m, Norfolk ridge, 1 lv (23.7 mm, Fig. 12M); station DW2087, 24°56'S, 168°22'E, 518–586 m, Norfolk ridge, 1 lv (25.9 mm).

Society Islands: TARASOC, station CP3458, 16°46'S, 151°23'W, 573–611 m, Raiatea, 1 lv (MNHN IM-2007-39258, Fig. 12N).

Diagnosis

Shell fusiform to elongate fusiform with high, typically acuminate spire and wide last adult whorl. Protoconch cyrtoconoid, brown, with 4.5 convex glossy whorls. Early spire whorls distinctly shouldered, rarely flattened, subsequent teleoconch whorls with convex outline. Sculpture of strong orthocline axial ribs intersected by a single adapical spiral cord, which is faint between axials and forms distinct beads at intersections. Last adult whorl evenly convex; siphonal canal moderately long, tapering, widely open. Aperture elongate, outer lip thin, notably drawn towards tip of siphonal canal, lacking lirae. Inner lip with four columellar folds, the adapicalmost strongest, and subsequent folds gradually diminishing. Background colour teleoconch with white apex and indistinct tan spiral bands on late teleoconch whorls.

Anatomy (MNHN IM-2013-44099)

External morphology: Body pale, lacking pigmentation, with massive head-foot, operculum absent. Siphon simple, rather long. Head with a pair of long eye tentacles (Fig. 13C, D). Eyes large, situated laterally at base of tentacles. Mantle thin, transparent; mantle cavity spanning over two-thirds of last whorl. Ctenidium moderately long, occupying about half the length of mantle cavity, osphradium large, only slightly smaller than ctenidium. No distinct anal gland present.

Anterior alimentary canal: Proboscis conical, in contracted state rather short, occupying about half of the rhynchocoel length. Rhynchodaeum thin, with two retractors attached ventrally to its anterior part (Fig. 13E). Buccal mass situated at mid-length of proboscis, with distal part of radular sac reaching proboscis base. Buccal mass enclosing thin horseshoe-shaped jaw, connected to odontophore by very feeble fibres of connective tissue. Anterior oesophagus forming a loop that lies dorsally above large bulky salivary glands and terminates at distinct pyriform valve of Leiblein. Very thin salivary ducts adjoining mid-oesophagus for a short distance before the valve of Leiblein. Accessory salivary gland bulbous, translucent, situated laterally, partly embedded into salivary gland. Mid-oesophagus situated right behind the circum-oesophageal nerve ring, forming a very short widened glandular compartment. Posterior oesophagus thin, covered dorsally by very long, brown, bulky, gland of Leiblein.

Radula (of *holotype*; Fig. 13F): Radula about 0.4 mm long and 0.1 mm wide, consisting of about 54 rows. Rachidians tricuspidate with moderately wide base attaining about 37% of radula width. Three cusps of rachidian of about equal length, strong, pointed. Lateral cusps directed slightly sideways. Anterior margin of rachidian forming sharp blade-like edge. Laterals sickle-shaped, unicuspidate.

Male reproductive system: The specimen is a male, with a large, flattened, folded penis with no distinct papilla (Fig. 13D). Seminal groove open, spanning the entire length of the penis along its inner edge.

Distribution and habitat

South China Sea, Papua New Guinea, New Caledonia (Loyalty and Norfolk ridges), French Polynesia, hard bottoms, depth range 505–800 m.

Remarks

Alisimitra tehuaorum was described based on a single dead collected shell lacking the protoconch (Huang, 2015: pl. 1, fig. 7a–c), which exceeds in size the specimens studied herein; however, we are confident about the identity of this species. In general, specimens of *Alisimitra tehuaorum* from different

localities show significant variation in shell shape, whorl outline, and number of axial ribs. The form from the South China Sea (Fig. 12G–I) has convex whorls that are somewhat shouldered in appearance because of the distinct beads at the intersection of spiral and axial sculpture. By contrast, specimen MNHN IM-2013-19676 from Papua New Guinea (Fig. 12K) has flattened late spire whorls and weaker spiral sculpture. All specimens of *Alisimitra tehuorum*, from the South Pacific [including MNHN IM-2013-19676 from Papua New Guinea, MNHN IM-2013-40663 from New Caledonia (Fig. 12L), and MNHN IM-2007-39258 (Fig. 12N) from the Society Islands] have notably finer and denser axial ribs, numbering 23–25 on last adult whorl. The conspecificity of the South China Sea and South Pacific populations is confirmed by molecular data, however.

Alisimitra tehuorum is most similar to *Alisimitra barazeri* sp. nov. (see above), but *Alisimitra tehuorum* has a more fusiform shell outline whereas *Alisimitra barazeri* sp. nov. is more turritiform, with a strongly convex base. Besides, specimens of *Alisimitra tehuorum* and *Alisimitra barazeri* sp. nov. from the South Pacific can be distinguished by the axial sculpture: finer and denser ribs in *Alisimitra tehuorum*; stronger and more widely spaced in *Alisimitra barazeri* sp. nov. The lack of spiral grooves segregates *Alisimitra tehuorum* from *Alisimitra deforgesii* sp. nov. and *Alisimitra fuscolineata*, with the latter two remarkable for contrasting spiral bands or lines, which are lacking in *Alisimitra tehuorum*. Finally, the denser axial ribs and comparatively much wider last adult whorl immediately distinguish *Alisimitra tehuorum* from *Alisimitra samadiae* sp. nov.

ALISIMITRA SAMADIAE SP. NOV. FEDOSOV,
HERRMANN & BOUCHET
FIGURE 14A–C

Type data

Holotype: MNHN IM-2013-40638, PAPUA NIUGINI, station CP4079, 04°34'S, 145°52'E, 960 m, Papua New Guinea, Bismarck Sea, West of Karkar Island, lv, 20.3 mm (Fig. 14A, B).

Other material examined

New Caledonia: EXBODI, station CP3842, 22°23'S, 167°22'E, 756–769 m, off Passe de la Sarcelle, 1 dd (14.75 mm; Fig. 14C).

Diagnosis

Shell elongate, with strong axial sculpture and very high orthoconoid spire. Protoconch cyrtoconoid, brown, with about four convex, glossy whorls. Early teleoconch whorls shouldered, later whorls flattened.

Sculpture of very strong and widely spaced axial ribs overridden by a single spiral cord, situated slightly above whorls mid-height, more pronounced on earlier whorls, very faint in interspaces between ribs. Siphonal canal moderately long, tapering, slightly recurved. Aperture narrow, outer lip very thin, smooth inside. Inner lip with three strong columellar folds, adapicalmost strongest. Shell off-white.

Description

Shell elongate-turritiform, with high spire and rather low aperture (w/h 0.28; a/h 0.4–0.42). Protoconch cyrtoconoid, brown, with about four convex, glossy whorls. Teleoconch of about 7.5 adpressed whorls; suture deeply impressed, canaliculate. Axial sculpture of very strong, straight, widely spaced ribs (12 on penultimate whorl) and fine growth lines. Last adult whorl with 13 ribs, of which the last few are wider and weaker, sculpture behind outer lip represented essentially by distinct growth lines. Spiral sculpture of a single spiral cord, situated at adapical third of whorl height, forming rounded beads at intersection with axial ribs, rather feeble in interspaces between them. Axial beads on axial ribs well pronounced on early teleoconch whorls, vanishing on penultimate and last adult whorls. Shell base smooth, convex, with gradual transition to rather short, slightly recurved siphonal canal, sculptured only by growth lines. Aperture elongate, evenly convex, reaching tip of siphonal canal. Outer lip thin, smooth inside. Inner lip slightly bent abaxially, with three strong, subequal columellar folds. Shell off-white.

Radula (of holotype; Fig. 13G): Radula about 0.6 mm long and 0.12 mm wide, consisting of 55 rows. Rachidians tricuspidate, with rather wide, bow-shaped base, its anterior margin forming distinct blade-like edges laterally; three rachidian cusps rather long and pointed, very closely set, lateral cusps directed notably sideways. Laterals unicuspidate, sickle-shaped, bearing irregular plicae at base of cusp.

Distribution and habitat

Papua New Guinea (Bismarck Sea), New Caledonia, depth range 769–960 m.

Etymology

The species is named in honour of Sarah Samadi, the cruise leader of the deep-water expeditions to Papua New Guinea, including the PAPUA NIUGINI cruise of 2012 during which the holotype was collected.

Remarks

The specimen of *Alisimitra samadiae* sp. nov. from New Caledonia retains a protoconch with the same morphology as protoconchs in other *Alisimitra* species. *Alisimitra samadiae* sp. nov. differs markedly

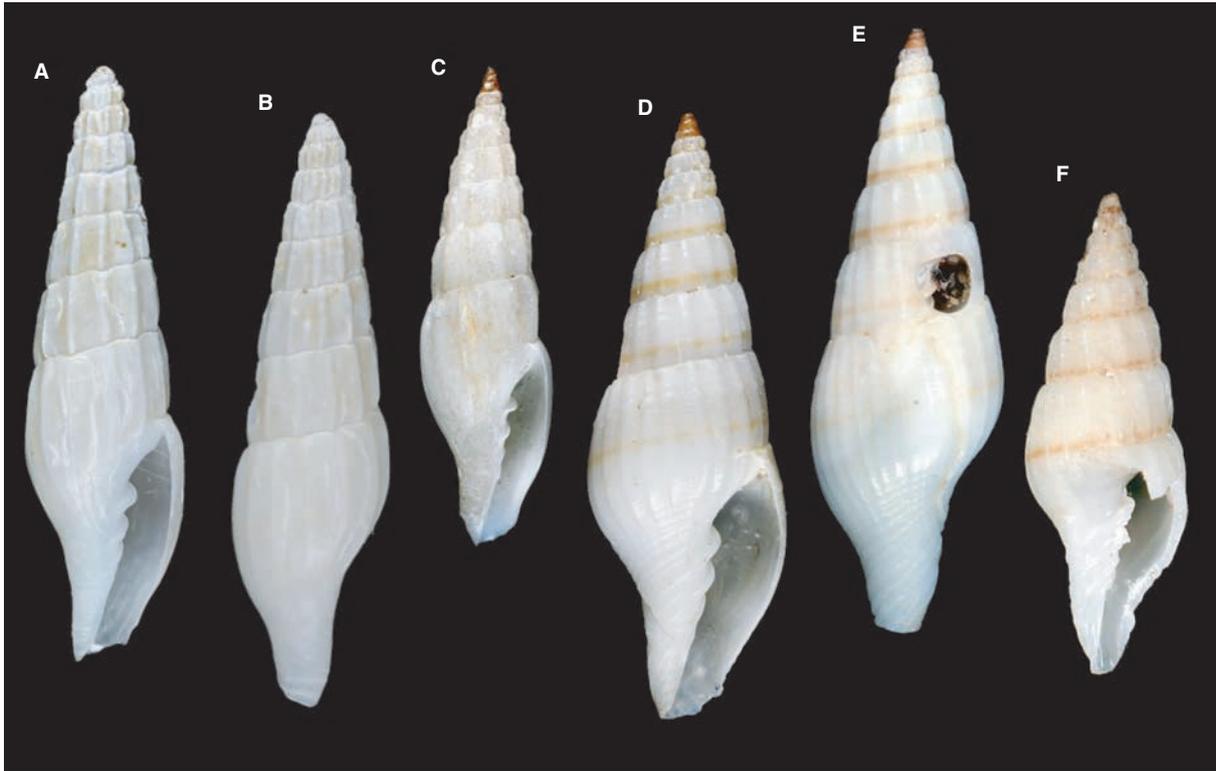


Figure 14. *Alisimitra* species. A–C, *Alisimitra samadiae* sp. nov.: A, B, holotype, MNHN IM-2013-40638, Papua New Guinea, West of Karkar Island, PAPUA NIUGINI, station CP4079, 04°34'S, 145°52'E, 960 m, 20.3 mm; C, New Caledonia, EXBODI station, CP3842, 22°23'S, 167°22'E, 756–769 m, 14.75 mm. D–F, *Alisimitra fuscolineata*: holotype of *Vexillum fuscolineatum*, MNHN IM-2000-25190, French Polynesia, Society Islands, Huahine, TARASOC, station DW3425, 16°43'S 151°03'W, 557 m, 17.3 mm; F, MNHN IM-2007-39271, French Polynesia, Society Islands, Huahine, TARASOC, station DW3429, 16°43'S, 150°38'W, 493–540 m.

from other *Alisimitra* species by its, by far, more elongate shell, with very strong axial sculpture and rather smooth siphonal canal. In shell proportions and morphology of the suture, it rather resembles some species of *Tosapusia*, but can be readily distinguished from them by its adpressed whorls and lack of spiral sculpture other than the single spiral cord, and by the protoconch morphology, which is shared with other *Alisimitra* species.

ALISIMITRA FUSCOLINEATA
(HERRMANN & SALISBURY, 2012) COMB. NOV.
FIGURE 14D–F

Vexillum (*Costellaria*) *fuscolineatum* Herrmann & Salisbury, 2012: 133–138; figs 36–39.

Type data

Holotype: MNHN IM-2000-25190, TARASOC, station DW3425, 16°43'S, 151°03'W, 557 m, French Polynesia, Society Islands, Huahine, dd, 17.3 mm (Fig. 14D, E).

Paratypes: Paratypes 1–5 listed by Herrmann & Salisbury (2012).

Material examined

Type material from French Polynesia; TARASOC, station DW3429, 16°43'S, 150°38'W, 493–540 m, French Polynesia, Society Islands, Huahine, 1 lv (MNHN IM-2007-39271, Fig. 14F).

Diagnosis

Shell fusiform, of medium size, measuring up to 22 mm in height. Protoconch conical, with about three brown glossy whorls. Teleoconch of seven or eight whorls. Spire orthoconoid, elongate, with gently convex whorls. Sculpture of narrow, orthocone axial ribs intersected by low, rounded spiral cords. Number of axial ribs increases from 9–11 on the first whorl to 15–18 on the penultimate whorl, and 24–34 on the last adult whorl; ribs becoming flatter towards last adult whorl. Two or three stronger and widely spaced spiral cords adapically, and finer and more closely set cords on rest of whorl surface. Spiral

cords on shell base sometimes very weak or obsolete. Siphonal fasciole with between four and seven distinct oblique cords. Siphonal canal long, nearly straight in adult specimens. Aperture moderately wide, elongate, with thin outer lip smooth inside; inner lip with four columellar folds, adapicalmost strongest, succeeding folds progressively weaker. Protoconch brown, teleoconch white with narrow brown band slightly above periphery of spire and last adult whorls. Second, faint brown band may be present in lower part of last adult whorl.

Distribution and habitat

French Polynesia (Society Islands, 490–560 m, Tuamotu Archipelago, 500–800 m) and Hawaii (Oahu, about 370 m).

Remarks

In shell proportions and sculpture, *Alisimitra fuscolineata* is close to *Alisimitra deforgesi* sp. nov.; however, *Alisimitra deforgesi* sp. nov. is generally smaller and can be distinguished by the characteristic adapical ‘cap’ and variegated colour pattern. *Alisimitra tehuaorum* and *Alisimitra barazeri* sp. nov., although they have a proportionally shorter siphonal canal, are also close to *Alisimitra fuscolineata*; both are uniformly pale or tan, whereas *Alisimitra fuscolineata* has a characteristic narrow brown band. *Alisimitra fuscolineata* also bears fine spiral cords throughout the shell surface, whereas in both *Alisimitra tehuaorum* and *Alisimitra barazeri* sp. nov. typically only an adapical cord is present.

GENUS *COSTAPEX* GEN. NOV. FEDOSOV, HERRMANN & BOUCHET

Type species: Costapex sulcatus sp. nov.

Diagnosis

Shell small, fusiform or widely fusiform. Protoconch cyrtoconoid with three or more evenly convex glossy whorls. Teleoconch with 4.5–7.0 evenly convex whorls. Sculpture on late teleoconch whorls dominated by spiral elements, some species may lack sculpture and single adapical spiral groove may be present. In contrast, earlier teleoconch whorls sculptured by coarse axial ribs. Siphonal canal rather long, straight, and tapering, or slightly recurved at its tip. Aperture rather wide, with evenly convex, sometimes slightly undulating, outer lip; inside of outer lip smooth or lirate within. Inner lip with three or four narrow columellar folds of equal or subequal strength. Head-foot massive, with light-brown or black bands on dorsal surface of foot. Eye tentacles moderately long, with large eyes situated at bases. Radula with rather broad tricuspidate

rachidian and narrow unicuspidate sickle-shaped laterals. Gland of Leiblein large, glandular, brown. Males with seminal canal represented by open groove within mantle cavity, and closed along entire length of penis.

Included species

Costapex sulcatus sp. nov.,¹ † *Costapex elatior* (Finlay, 1924),² *Costapex exbodi* sp. nov.,¹ *Costapex jolivetii* (Poppe & Tagaro, 2006),² *Costapex levis* sp. nov.,¹ *Costapex margaritatus* sp. nov.,² *Costapex martinorum* (Cernohorsky, 1984).²

Distribution and habitat

Species of *Costapex* gen. nov. are recorded from the tropical western Pacific: Philippines, Papua New Guinea (Bismarck and Solomon Seas), New Caledonia. At least two species of *Costapex* gen. nov. have been collected from sunken wood.

Etymology

From the Latin *costa* (rib) and *apex* (top). The name *Costapex* refers to the characteristic sculpture of early teleoconch whorls.

Remarks

Because of the lack of axial sculpture on late teleoconch whorls or prevailing spiral sculpture, the overall appearance of *Costapex* species recalls deep-water Mitridae, rather than costellariids. The species of *Costapex* gen. nov. can be readily distinguished from mitrids by the presence of strong axial ribs on early teleoconch whorls. In all species of the *Costapex* gen. nov. the columellar folds are thin, of equal or subequal strength; this allows their easy recognition among other deep-water costellariids, which usually have the adapicalmost columellar folds notably stronger. The fine columellar folds and often small shells of some *Costapex* gen. nov. species also render them extremely close to the volutomitrid genus *Microvoluta*. The two genera, however, can be distinguished by the details of columellar folds: these are always rounded in *Costapex* gen. nov. and sharp in *Microvoluta*. In addition, the presence of a translucent, bulbous protoconch readily reveals the species of Volutomitridae.

Six living species, which we assign to the newly established genus *Costapex* sp. nov., can be separated into three morphologically distinct groups. The ‘lesser’ *Costapex* gen. nov. species, *Costapex sulcatus* sp. nov., *Costapex Jolivetii*, and *Costapex margaritatus* sp. nov. (Fig. 15), are characterized by small shells, which do not usually exceed 15 mm in height, and late teleoconch whorls dominated by spiral sculpture, whereas earlier whorls bear strong axial ribs. The ‘larger’ *Costapex* gen. nov. species, *Costapex*

martinorum and *Costapex exbodi* sp. nov. (Fig. 17F–I) are similar to the ‘lesser’ species in sculpture pattern, but are characterized by solid, notably larger shells that are intensely coloured brown. The third group, which can be referred to as ‘smooth’ *Costapex* is represented by the single species *Costapex levis* sp. nov. (Fig. 17A–E), which is distinctive because of its smooth late teleoconch whorls.

COSTAPEX SULCATUS SP. NOV. FEDOSOV,
HERRMANN & BOUCHET
FIGURE 15A–D

Type data

Holotype: MNHN IM-2013-40627, 08°43'N, 123°19'E, 259–280 m, Philippines, East of Aliguay Island, lv, 7.4 mm; Figure 15A, B.

Paratype: MNHN IM-2000-31646, same locality as holotype, lv, 6.5 mm; Figure 15C.

Other material examined

Philippines: PANGLAO 2005, station CP2390, 9°27'N, 123°43'E, 627–645 m, Bohol Sea, 1 dd (3.9 mm); station CP2407, 9°41'N, 123°48'E, 256–268 m, Bohol Sea, Maribojoc Bay, 1 lv (MNHN IM-2007-30321, 9.4 mm).

Solomon Islands: SALOMON 2, station CP2272, 8°56' S, 157°44' E, 380–537 m, New Georgia Island, 1 dd (6.7 mm).

Vanuatu: SANTO 2006, station AT99, 15°06'S, 166°51'E, 351–395 m, Big Bay, 2 lv (MNHN IM-2007-30254, 8.0 mm; MNHN IM-2007-30260, 9.3 mm, Fig. 15D).

Diagnosis

Shell small, fusiform, with orthoconoid spire and rather wide aperture. Protoconch pointed, with three or more convex, glossy whorls. Teleoconch whorls flattened in profile, sculptured with evenly spaced deep spiral grooves that have a dashed appearance; an adapical groove usually deeper and stronger than succeeding ones. Axial sculpture of strong, coarse axial ribs on early spire whorls and indistinct low folds on later whorls. Microsculpture of very fine, dense, collabral growth lines. Last adult whorl evenly convex, siphonal canal rather long, straight, tapering. Aperture wide, its outer lip thin, evenly convex throughout its length, smooth inside. Inner lip with five, fine, equal, oblique columellar folds. Seminal canal represented by an open groove on side of body, closed on penis. Radula with tricuspidate rachidian and narrow, sickle-shaped, unicuspidate laterals. Mid-oesophagus widened; gland of Leiblein well developed, large and brown.

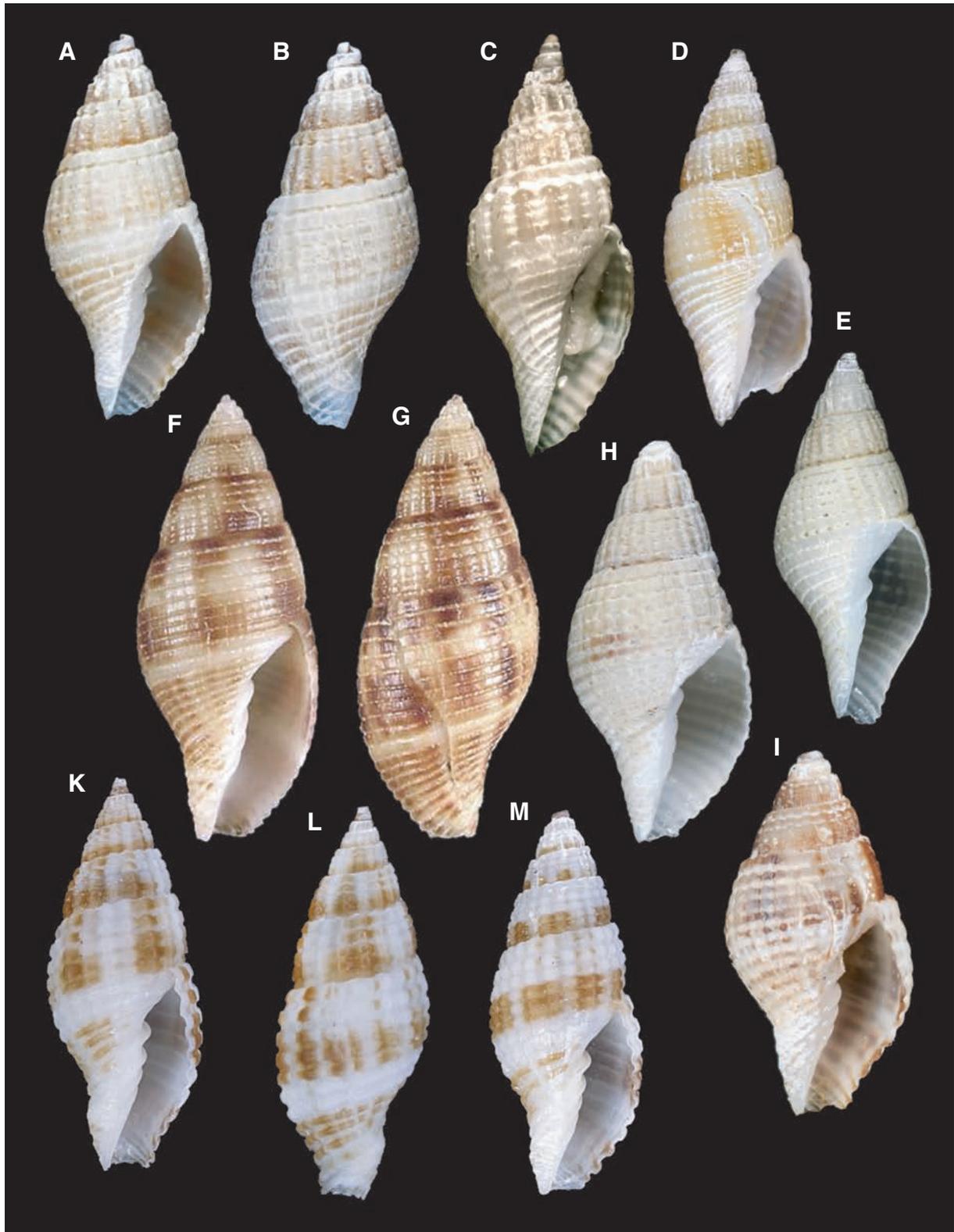
Description

Shell small, thin-walled, fusiform (w/h 0.4; a/h 0.55). Protoconch (intact only in paratype 1; apex strongly corroded and protoconch missing in all other specimens) high, pointed, with about four smooth, convex whorls. Teleoconch with about 4.5 whorls, first two with rather addressed profile; penultimate and last whorls slightly evenly convex. Suture deeply impressed. Sculpture of orthocone rounded axial ribs, more pronounced on first two whorls and becoming flat and indistinct on last adult whorl, and microsculpture of fine growth lines. Axial folds overridden by broad, flattened, slightly undulating spiral cords separated by widely spaced narrow grooves of somewhat ‘perforated’ appearance. Adapical spiral groove strongest, succeeding spiral grooves (four on each spire whorls) weak on second teleoconch whorl, distinct on penultimate whorl, and almost equal to adapical groove on last adult whorl. Six wide and flattened spiral cords on adapical portion of last adult whorl and periphery succeeded on shell base by six narrower and more rounded in profile cords, and six even narrower oblique cords, on siphonal canal. Siphonal canal rather long, straight, tapering. Aperture rather wide; outer lip thin, undulating, evenly convex; smooth inside. Inner lip with five distinct columellar folds of equal strength. Background colour pale, with very faint lighter spiral band on whorl periphery.

Anatomy (paratype)

External morphology: Body pale yellowish, with light-brown bands on foot. Operculum absent. Siphon simple, moderately long, slightly protruding beyond the mantle edge. Head bearing moderately long eye tentacles with large black eyes situated laterally at base (Fig. 16A, B). Mantle cavity spanning ~0.7 whorl; mantle thin with mantle cavity organs clearly visible. Ctenidium very long, narrow, spanning throughout the posterior two-thirds of the mantle cavity. Osphradium large, exceeding one-half of ctenidium length. No distinct anal gland.

Anterior alimentary canal: Proboscis white, in contracted state occupying about two-thirds of the rhynchocoel length. Anterior rhynchodaeum thin, whitish, semi-translucent. Two distinct muscular bundles (retractors) attached laterally to anterior rhynchodaeum (Fig. 16C). Buccal mass moderately long, situated in basal portion of proboscis. Oesophagus forming a loop after leaving the proboscis, lying dorsally, and entering medium-sized bulbous valve of Leiblein. Salivary gland large, white, unpaired, situated posterior to proboscis. Accessory salivary gland(s) not observed, possibly because of the minute size of dissected animal. Posterior oesophagus adjoined by brown bulky gland



of Leiblein, which is massive in its anterior portion and notably extended backwards along the oesophagus.

Radula (of holotype; Fig. 16D): Radula 0.2 mm in length and about 0.04 mm in width, consisting of 58 rows. Rachidian tricuspidate with moderately wide

Figure 15. *Costapex* species. A–D, *Costapex sulcatus* sp. nov.: A, B, holotype, MNHN IM-2013-40627, Philippines, Bohol/Sulu Seas, 8°43'N, 123°19'E, 259–280 m, 7.4 mm; C, paratype 1, same locality as holotype, 6.5 mm; D, MNHN IM-2007-30254, Vanuatu, SANTO 2006, station AT99, 15°06'S, 166°51'E, 351–395 m, 9.3 mm. E, *Costapex* sp. aff. *sulcatus*, MNHN IM-2013-4814, Papua New Guinea, PAPUA NIUGINI, station CP3949, 05°12'S, 145°51'E, 380–407 m, 9.8 mm. F–I, *Costapex joliveti*: F, G, holotype, NMP, East China Sea, 140–180 m, 14.2 mm; H, MNHN IM-2013-40132, Papua New Guinea, Bismarck Sea, off Aitape, PAPUA NIUGINI, station CP4055, 03°03'S, 142°18'E, 370–374 m, 9.9 mm; I, MNHN IM-2013-40666, Philippines, off Eastern Luzon, AURORA 2007, station CP2720, 14°27'N, 121°47'E, 300–301 m, 6.2 mm. K–M, *Costapex margaritatus* sp. nov.: K, L, holotype, Philippines, Balicasag Island, tangle nets, 50–150 m, 10.3 mm; M, paratype 1, same locality as holotype, 11.0 mm.

base and long pointed cusps, which are set notably apart. Lateral teeth narrow, sickle-shaped, curved, with single pointed cusp.

Reproductive system: The paratype studied is male, with a moderately sized penis of subcylindrical (very slightly flattened) shape, without distinct papilla. Seminal canal indistinct on penis, and certainly not forming an open groove. The seminal canal is very distinct on the body of the animal, however: it is wide and represented proximally by an open groove.

Distribution and habitat

Philippines, Solomon Islands, Vanuatu. Alive in depths of 268–351 m. Holotype collected from sunken wood.

Etymology

The species name refers to the characteristic sculpture pattern of multiple spiral grooves (Latin *sulcatus* = grooved).

Remarks

Among known costellariids, *Costapex joliveti* (Poppe & Tagaro, 2006) is closest to *Costapex sulcatus* sp. nov.: both have similar sculpture pattern and coloration, and are closely related based on our phylogenetic analysis; however, *Costapex sulcatus* sp. nov., being generally smaller and more elongate, is characterized by a smooth outer lip of the aperture, whereas it is lirate within in adult specimens of *Costapex joliveti*. Another 'lesser' *Costapex* species, *Costapex margaritatus* sp. nov., although close to *Costapex sulcatus* sp. nov. in proportions, has a notably stronger spiral sculpture, with subsutural and subsequent grooves developed equally. Overall, the dominating spiral sculpture elements of *Costapex sulcatus* sp. nov. make it look rather like a mitrid. A similar sculpture pattern of dashed spiral grooves is characteristic for some deep-water Mitridae: for example, the genus *Calcimitra* Huang, 2011. *Costapex sulcatus* sp. nov., however, can be distinguished by the presence of strong axial ribs on early spire whorls.

Specimen MNHN IM-2013-4814 (Fig. 15 E), despite sharing the same sculpture pattern, is characterized by rather biconical shell with much longer siphonal canal. This specimen comes out separately on the COI-based molecular tree, suggesting that it

represents a separate species; however, with a single specimen at hand we are uncertain about the value of these morphological characters and we refrain from formally naming it here.

COSTAPEX JOLIVETI (POPPE & TAGARO, 2006)

COMB. NOV.

FIGURE 15F–I

Vexillum (*Pusia*) *joliveti* Poppe & Tagaro, 2006: 81–82; pl. 6, figs 1, 2, 4.

Type data

Holotype: East China Sea, 140–180 m, 14.2 × 5.9 mm (Fig. 15F, G). Contrary to the statement in the original publication, the holotype has not been deposited in MNHN, but is in NMP.

Paratypes: Paratypes 1–12, 14.3–18.0 mm, in NMP and private collections.

Other material examined: MNHN IM-2013-40132, PAPUA NIUGINI, station CP4055, 03°03'S, 142°18'E, 370–374 m, Papua New Guinea, Bismarck Sea, off Aitape, lv, 9.9 mm (Fig. 15H); AURORA 2007, station CP2720, 14°27'N, 121°47'E, 300–301 m, lv (MNHN IM-2013-40666, 6.2 mm; Fig. 15I).

Diagnosis

Shell small, broadly fusiform, with orthoconoid spire and long tapering siphonal canal. Protoconch unknown. Teleoconch of about 5.5 evenly convex whorls; suture distinct, deeply impressed. Early spire whorls sculptured with low, rounded axial ribs overridden by broad, also rounded, cords and distinct subsutural groove. Late spire whorls sculptured with broad flattened spiral cords separated by rather deep and narrow grooves. Spiral cords becoming notably narrower below shell periphery and on siphonal canal. Aperture elongate with evenly convex outer lip with about ten lirae inside. Inner lip with four narrow subequal folds. Colour white with bands of irregular brown flecks.

Distribution and habitat

East China Sea, depth range 140–180 m; Philippines, Papua New Guinea, 301–370 m.

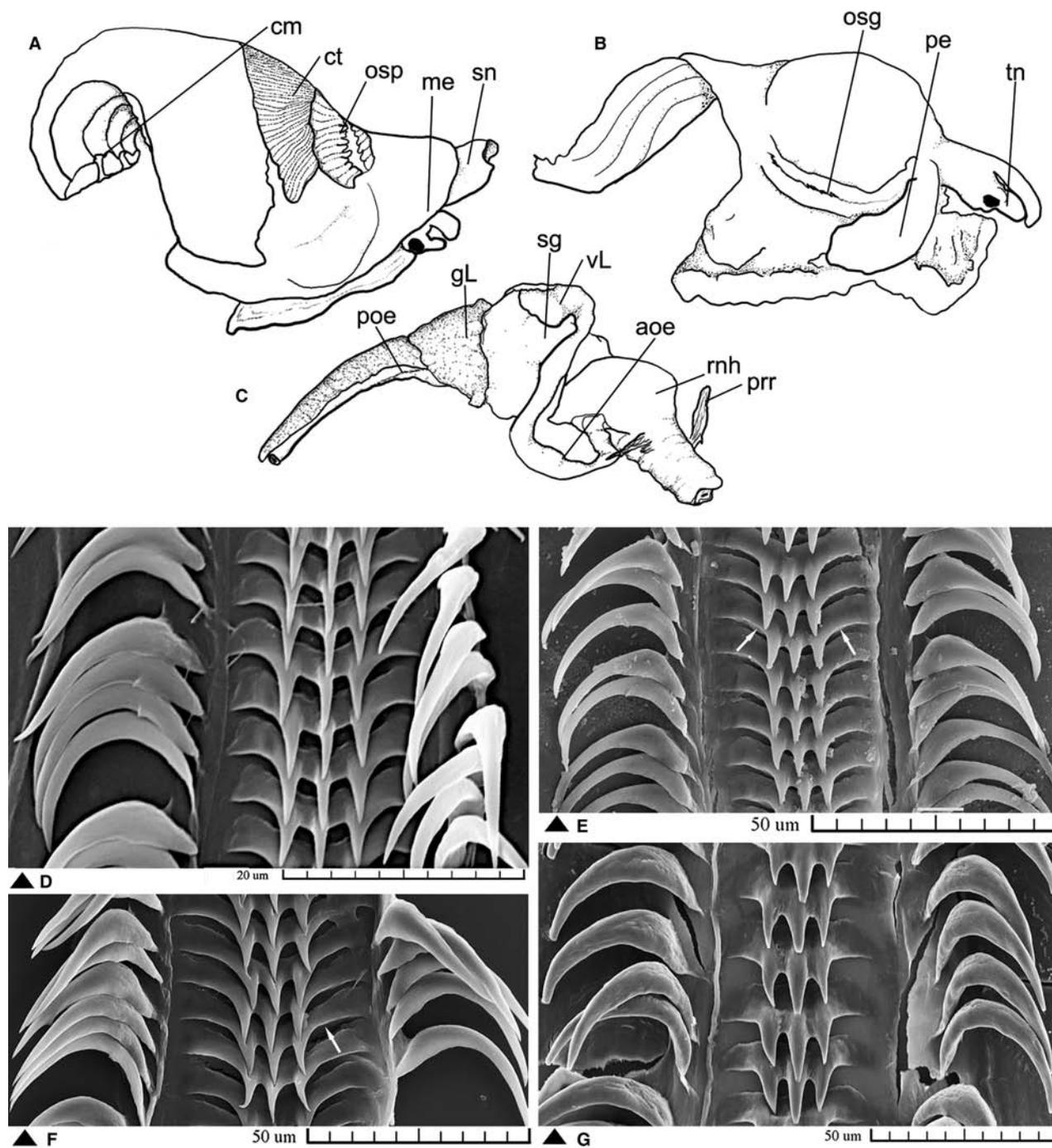


Figure 16. *Costapex* morphology. A–D, *Costapex sulcatus* sp. nov., paratype 1: A, general morphology of the body; B, mantle removed; C, anterior alimentary canal; D, radula. E–G, *Costapex* radulae: E, *Costapex levis* sp. nov., holotype; F, *Costapex levis* sp. nov., MNHN IM-2013-40629; G, *Costapex exbodi* sp. nov.

Remarks

In overall shell morphology, *Costapex sulcatus* sp. nov. is most similar to *Costapex joliveti*, although *Costapex joliveti* has a very weak axial sculpture on the spire whorls, outer aperture lip lirate within, and a generally larger and wider adult shell. *Costapex*

joliveti can be distinguished from *Costapex margaritatus* sp. nov. by the shape of the spiral cords, which are flattened and elevated in *Costapex joliveti*, but have a characteristic beaded structure in *Costapex margaritatus* sp. nov. Conversely, *Costapex levis* sp. nov. can be readily distinguished from *Costapex joliveti* by the

smooth last adult whorl, bearing a single groove just below the suture, whereas *Costapex joliveti* is characterized by multiple spiral grooves on the last adult whorl; moreover, *Costapex joliveti* bears occasional brown bands, which are lacking in *Costapex levis* sp. nov. *Costapex exbodi* sp. nov. is somewhat close to *Costapex joliveti* in shell outline and sculpture pattern; however, both *Costapex martinorum* and *Costapex exbodi* sp. nov. are notably larger, with more solid shells, compared with *Costapex joliveti*.

COSTAPEX MARGARITATUS SP. NOV. HERRMANN,
FEDOSOV & BOUCHET
FIGURE 15K–M

Type data

Holotype: MNHN 2000-30206, Philippines, Balicasag Island, tangle nets, 50–150 m, collected 2011, 10.3 mm (Fig. 15K, L).

Paratypes: Same locality as holotype, paratypes 1–5, collection Manfred Herrmann, 11.0, 10.2, 10.1, 9.4, and 8.6 mm respectively; paratypes 6–8, collection Mitsuo Chino, 16.4, 11.1, and 10.8 mm respectively; paratypes 9–10, collection Günter Stossier, 10.4 and 9.9 mm, respectively.

Diagnosis

Shell small, broadly fusiform. Protoconch pointed, conical, with three or more glossy whorls. Teleoconch whorls with flattened or slightly convex outline. Sculpture of strong axial ribs and spiral cords, forming characteristic beaded sculpture. Shell base separated from siphonal canal by wide waist, both with dominating spiral sculpture elements. Outer lip thin, undulating, with six widely spaced lirae inside. Inner lip with four subequal columellar folds. Shell colour white, with brown band in abapical half of spire whorls and irregular brown blotches throughout shell surface.

Description

Shell small, thin-walled, widely fusiform (w/h 0.38–0.42; a/h 0.49–0.52). Protoconch (missing in almost all specimens) light brown, pointed, with three or more evenly convex glossy whorls. Teleoconch of six whorls: first three subcylindrical, succeeding three evenly convex. Suture deeply impressed. First teleoconch whorl sculptured with 12–14 strong, rounded axial ribs, on succeeding whorls axials overridden by strong, slightly flattened spiral cords of about equal size, resulting in a characteristic beaded sculpture. Penultimate whorl with 17–20 axial ribs and 4 or 5 spiral cords, last adult whorl with 22–28 ribs and 13 or 14 cords; interspaces separating the three adapical cords slightly wider. Shell base and

siphonal canal devoid of axial elements, sculptured with pustulated cords and nearly smooth rounded spiral cords on siphonal fasciole. Siphonal canal moderately long, widely open, separated from the shell base by wide, concave waist. Aperture elongate, moderately wide, outer lip thin, undulating, evenly convex, bearing six widely spaced lirae inside. Inner lip with four distinct columellar folds, adapicalmost fold slightly exceeding the three others in strength. Background colour white with brown spiral band in the abapical half of spire whorls and at the periphery of the last adult whorl, and irregular brown blotches throughout shell surface.

Radula: No data.

Distribution and habitat

Balicasag Island, Philippines, 50–150 m.

Etymology

The species name refers to the characteristic beaded sculpture pattern (*margarita* = pearl).

Remarks

In shell proportions, *Costapex margaritatus* sp. nov. is most similar to *Costapex sulcatus* sp. nov., but can be differentiated from the latter by stronger sculpture elements resulting in the characteristic beaded sculpture, and by lacking growth lines. The characteristic strong beaded sculpture of *Costapex margaritatus* sp. nov. also differentiates it from *Costapex joliveti*. Another feature that separates *Costapex margaritatus* sp. nov. from other 'lesser' *Costapex* species is a distinct siphonal fasciole, which is absent in both *Costapex sulcatus* sp. nov. and *Costapex joliveti*, which have a tapering siphonal canal. *Costapex margaritatus* sp. nov. is also similar to *Costapex martinorum*, mainly because of the sculpture pattern, but *Costapex martinorum* is notably larger, more slender, with spiral interspaces exceeding axial interspaces in width. Moreover, the two differ in colour pattern: *Costapex martinorum* is reddish brown with cream blotches, whereas *Costapex margaritatus* is white with brown bands.

COSTAPEX LEVIS SP. NOV. FEDOSOV,
HERRMANN & BOUCHET
FIGURE 17A–E

Type data

Holotype: MNHN IM-2013-40628, 05°01'S, 152°00'E, 400–619 m (BIOPAPUA, station DW3777), Papua New Guinea, New Britain, Wide Bay, lv, 15.2 mm (Fig. 17A, B).



Figure 17. *Costapex* species. A–E: *Costapex levis* sp. nov. A, B, holotype, MNHN IM-2013-40628, Papua New Guinea, New Britain, Wide Bay, BIOPAPUA, station DW3777, 05°01'S, 152°00'E, 400–619 m, 15.2 mm; C, Papua New Guinea, Solomon Sea, BIOPAPUA, station CP3737, 08°15'S, 150°45'E, 587 m, 12.4 mm; D, E, MNHN IM-2013-40629, Papua New Guinea, Gulf of Huon, BIOPAPUA, station CP3632, 06°56'S, 147°08'E, 700–740 m, 19 mm; F, G, *Costapex martinorum*, holotype of *Vexillum martinorum*, AM-71372, Philippines, Bohol, Coamen, 22.7 mm. H, I, *Costapex exbodi* sp. nov., holotype, MNHN IM-2013-40626, New Caledonia, off Yaté, EXBODI, station CP3835, 22°06'S, 167°06'E, 325–346 m, 22.05 mm.

Paratype: PANGLAO 2005, station CP2358, 8°52.10'N, 123°37.10'E, 569–583 m, Bohol/Sulu Seas, lv (MNHN IM-2009-4609, 11.0 mm).

Other material examined

Philippines: Panglao, 2005 station CP2381 08°43'N, 123°19'E, 259–280 m, Dipolog Bay, 1 dd, 7.4 mm.

Papua New Guinea, Solomon Sea: BIOPAPUA, station CP3632, 06°56'S, 147°08'E, 700–740 m, Solomon Sea, Huon Gulf, 1 lv (MNHN IM-2013-40629, 19 mm; Fig. 17D, E); station CP3737, 08°15'S, 150°45'E, 587 m, off Lancasay, 1 lv, 12.4 mm (Fig. 17C); station DW3748, 05°37'S, 154°01'E, 398–399 m, seamount off Bougainville, 1 dd, 15 mm.

Solomon Islands: Salomon 1, station CP1807, 9°42.2'S 160°52.8'E 1077–1135 m, 1 dd, 24.8 mm; SALOMON 2, station CP2227, 6°37'S, 156°13'E, 508–522 m, Choiseul, 2 dd, 15.25 and 16.5 mm.

Diagnosis

Shell fusiform to broadly fusiform, smooth, with orthoconoid spire and rather long siphonal canal. Protoconch pointed, dark brown, with large nucleus, consisting of three or more smooth whorls. Suture distinct, impressed, whorls slightly convex in outline. Early spire whorls sculptured with widely spaced coarse axial ribs, intersected apically by single groove. Axial ribs disappear on fourth teleoconch whorl, subsequent whorls lacking sculpture, sometimes retaining adapical groove only. Microsculpture of very fine collabral growth lines. Last adult whorl evenly convex with elongate shell base and rather long, tapering, widely open siphonal canal. Aperture elongate with thin, evenly convex outer lip bearing faint lirae on its inner surface. Inner lip with four strong columellar folds, adapicalmost fold slightly exceeding others in strength. Shell colour whitish to pale or tan.

Description

Shell small, elongate-fusiform (w/h 0.31–0.39; a/h 0.45–0.51), with rather tall spire and long, tapering siphonal canal. Protoconch pointed, dark brown, with large nucleus, consisting of three or more smooth whorls. Teleoconch of about seven slightly convex whorls, first three with strong orthocone axial ribs (14 on third teleoconch whorl), giving an indistinctly shouldered profile. Axial ribs intersected by strong spiral groove forming subsutural 'caps', noticeable on early teleoconch whorls. Axial ribs becoming broader and indistinct on fourth teleoconch whorl, and vanishing entirely on succeeding whorls. Last three whorls smooth, sculptured only by very fine growth lines, slightly convex in outline. Suture distinct, very slightly impressed. Last adult whorl evenly convex, forming concave waist with five strong spiral grooves

at its transition to siphonal canal. Siphonal canal long and slender, tapering, with rather deep and narrow opening. Aperture elongate, outer lip thin, evenly convex, with very faint lirae on its inner surface. Inner lip with four strong but rather narrow columellar folds, adapicalmost strongest, then gradually reducing in size. Colour uniformly white, with interspaces between spiral ribs on early teleoconch whorls retaining light-brown periostracum (or possibly stained so by mud).

Radula (holotype, Fig. 16E; MNHN IM-2013-40629, Fig. 16F): Radula about 0.4 mm long and 0.1 mm wide, consisting of about 60 rows. Rachidian with rather wide bow-shaped base and three moderately long pointed cusps; anterior part of rachidian base with sharp, blade-like edge (marked with white arrows). Laterals unicuspidate, sickle-shaped with slightly widened base.

Morphology of the body: The holotype, a male, has well-developed eyes situated at the base of the tentacles. Penis rather small, seminal groove closed.

Distribution and habitat

Philippines, Papua New Guinea (Solomon Sea), Solomon Islands, depth range 280–1077 m. One of the specimens studied was collected from sunken wood.

Etymology

The name of this species emphasizes the lack of the sculpture on late teleoconch whorls (Latin *levis* = smooth, plain, free from coarse hair), which distinguishes *Costapex levis* sp. nov. from congeners.

Remarks

The material examined shows significant variation in shell proportions, from the fusiform holotype to elongate with high spire and relatively shorter aperture (MNHN IM-2007-40629). At present, we are inclined to attribute this variation to bathymetry, as MNHN IM-2013-40629 and an even more elongate specimen from the Solomon Islands were sampled from depths greater (700–740 and 1077–1135 m, respectively) than the others (398–619 m); however, it cannot be excluded that we are dealing with two separate species that do not overlap in bathymetric distribution.

Because of their smooth adult teleoconch whorls, both the typical and elongate forms stand apart from other costellariids. At the same time, the coarse axial ribs on early teleoconch whorls readily distinguish *Costapex levis* sp. nov. from species of mitrids. In overall shell shape, *Costapex levis* sp. nov. shows a certain resemblance to the boreal *Volutomitra groenlandica* (Möller, 1842) (Volutomitridae); however, it can be distinguished by the presence of axial elements on early spire whorls and by the comparative strength of columellar

folds. In *Costapex levis* sp. nov. the adapicalmost fold is the strongest, whereas in *Volutomitra groenlandica* it is notably fainter than the succeeding ones.

***COSTAPEX MARTINORUM* (CERNOHORSKY, 1986)
COMB. NOV.
FIGURE 17F, G**

Vexillum martinorum Cernohorsky, 1986: 50–52; figs 15–20.

Type data

Holotype: AM 71372, Philippines, Bohol, Coamen, 22.7 mm (Fig. 17F, G).

Paratypes: Philippines, Bohol, Coamen, SL 20.1, 20.7, and 19.0 mm.

Diagnosis

Shell fusiform, elongate, with adpressed early spire whorls, late teleoconch whorls evenly convex. Suture deeply impressed. Sculpture of prosocline axial ribs and broad, flattened spiral cords, bisected by axial lirae, producing compressed nodules at their intersection with axials. Microsculpture of fine dense growth lines. First subsutural cord delimited from succeeding cords by widened interspace. Shell base very high, gradually extending to siphonal canal. Aperture elongate, outer lip undulating, lirate inside. Inner lip with four fine columellar folds, adapicalmost fold strongest. Colour reddish brown with cream axial streaks.

Distribution and habitat

Philippines (off Bohol, Cebu, Mindanao), depth range 180–240 m.

Remarks

The fossil *Costapex elatior* (Finlay, 1924) (*Mitra elatior* Finlay, 1924; middle Miocene of New Zealand) most resembles *Costapex martinorum*, but the latter is sculptured by beaded spiral cords, whereas these are flattened in *Costapex elatior*. Apart from that, the dominating sculpture of early spire whorls is opisthocline ribs in *Costapex martinorum*, whereas in *Costapex elatior* the axial sculpture is weak or absent on early spire whorls. Among recent species, *Costapex exbodi* sp. nov. is probably closest to *Costapex martinorum* in overall shell morphology and sculpture pattern; however, *Costapex martinorum* has a more elongate shell with narrower aperture. In sculpture pattern, *Costapex martinorum* is also close to *Costapex sulcatus* sp. nov. and *Costapex margaritatus* sp. nov., but the latter two are notably smaller, never exceeding 11 mm in length, and are thin shelled. Moreover, *Costapex sulcatus* sp. nov.

possesses a characteristic subsutural groove that is missing in *Costapex martinorum*.

***COSTAPEX EXBODI* SP. NOV. FEDOSOV,
HERRMANN & BOUCHET
FIGURE 17H, I**

Type data

Holotype: MNHN IM-2013-40626, New Caledonia, off Yaté, 22°06'S, 167°06'E, 325–346 m (EXBODI, station CP3835), lv, 22.05 mm (Fig. 17H, I).

Diagnosis

Shell medium sized, widely fusiform, with straight tapering siphonal canal and very wide aperture. Early spire whorls sculptured with dense prosocline rounded axial ribs, overridden by low, broad, and flattened cords that together form beaded sculpture with moderately deep square interspaces. Adapical portion of last adult whorl with seven continuous spiral cords, axial sculpture of fine very dense collabral riblets, pronounced in interspaces between spiral cords. Shell base extended towards siphonal canal, without distinct waist. Outer lip evenly convex, finely lirate inside, inner lip with four oblique columellar folds, adapicalmost strongest. Coloration of nebulous brown bands on tan background.

Description

Shell medium sized, widely fusiform (w/h 0.39; a/h 0.52), with orthoconoid spire and wide aperture. Protoconch missing in the single specimen examined. Teleoconch of 6.5 whorls, separated by deeply impressed suture. First two spire whorls with flattened profile, succeeding whorls evenly convex. Shell base long, gradually extending to straight, tapering siphonal canal. Early spire whorls sculptured with dense prosocline rounded axial ribs, overridden by low, broad, flattened cords (five on second and third spire whorls), together forming beaded sculpture with moderately deep square interspaces. First adapical cord followed by slightly widened interspace. Adapical portion of last adult whorl with seven continuous, only slightly undulating, spiral cords, axial sculpture of fine, very dense, collabral riblets, pronounced in interspaces between spiral cords. Interspaces between spiral cords becoming gradually wider on shell base towards siphonal canal. Aperture wide, with evenly convex outer lip, with 20 + very fine lirae inside. Inner lip with four oblique columellar folds, adapicalmost fold strongest. Background colour tan with large nebulous brown bands throughout shell surface. Inside of aperture white.

Radula (of holotype, Fig. 16G): Radula exceeding 0.4 mm in length and about 0.14 mm wide; unfolded fragment consisting of 26 rows. Rachidian with narrow base and three rather closely set cusps, of which the central cusp is strongest. Basal parts of cusps partly fused together to form short medial projection. Lateral teeth sickle-shaped, unicuspidate.

Distribution and habitat

Off Yaté, New Caledonia, 325–346 m.

Etymology

The species is named after the fruitful 2011 expedition EXBODI in deep water off New Caledonia, in the course of which a single specimen was taken. Used as a noun in apposition.

Remarks

Two species, the recent *Costapex martinorum* and the fossil *Costapex elatior*, are closest to *Costapex exbodi* sp. nov.; however, *Costapex exbodi* sp. nov. can be differentiated by its broader shell with notably wider aperture. Moreover, all known specimens of *Costapex elatior* do not exceed 19 mm in length (Cernohorsky, 1980). *Costapex joliveti* is also close to *Costapex exbodi* sp. nov., although the former species is smaller, with more delicate sculpture, and with narrower aperture. All other species classified here in *Costapex* are notably smaller and more fragile, and therefore cannot be confused with *Costapex exbodi* sp. nov. With its colour pattern and spiral elements dominating the last adult whorl, *Costapex exbodi* sp. nov. shows a certain resemblance to species of the mitrid genus *Nebularia*, *Nebularia chrysostoma* (Broderip, 1836) and *Nebularia ferruginea* (Lamarck, 1811), but the wider aperture, weaker, oblique columellar folds, and distinct lirae on the inner surface of the outer aperture lip distinguish *Costapex exbodi* sp. nov. from the aforementioned mitrids.

GENUS *PUSIA* SWAINSON, 1840

Type species: Mitra microzonias Lamarck, 1811 (M).

SUBGENUS *PUSIA (PUSIA)* SWAINSON, 1840
FIGURES 18A–G AND 19A–C

Diagnosis

Shell small, fusiform to broadly fusiform or ovate, last adult whorl 64–74% of shell height. Protoconch multispiral, narrowly conical, with three or more glossy whorls. Suture distinct, impressed. Sculpture of dense, rounded, axial ribs on early spire whorls (sometimes absent), turning into broad and low folds on last teleoconch whorls; spiral sculpture of fine regular grooves, pronounced in interstices between

axials. Shell base sculptured with several broad and flattened, somewhat gemmate, spiral cords. Siphonal canal short or very short, stout, bearing several strong oblique cords. Aperture narrow, elongate, its outer lip lirate within. Inner apertural lip with three or four strong columellar folds, adapicalmost fold strongest. Shell intensely coloured, either orange or dark brown, with spiral row of lighter blotches on periphery of last adult whorl. Head-foot intensely pigmented, dark brown or black. Radula with three teeth in each row; rachidian tricuspidate with width of base and length of cusps of variable proportions. Laterals sickle-shaped, unicuspidate. Seminal canal closed.

Included species

Pusia (Pusia) microzonias (Lamarck, 1811) (Fig. 18A–D), *Pusia (Pusia) lauta* (Reeve, 1845) (Fig. 18E),¹ *Pusia (Pusia) vassardi* sp. nov. (Fig. 18F–H).¹

Distribution and habitat

All over the Indo-Pacific from Madagascar to French Polynesia, in shallow water.

Remarks

The subgenus *Pusia (Pusia)* as defined herein contains only a handful of species, the affinities of which are convincingly demonstrated by the molecular data for *Pusia lauta* (Reeve, 1845) and *Pusia vassardi* sp. nov. We suggest close relationships of these two with *Pusia microzonias* (Fig. 18A–D), based on an unmistakable similarity in shell morphology and coloration, as well as in radula structure: the radula of *Pusia microzonias* was studied by Risbec (1928: fig. 35) and herein (Fig. 19A). As a matter of fact, the identity of *Pusia microzonias* has been questioned by Poppe *et al.* (2009), who suggested that the lectotype selected by Cernohorsky (1969) from among ten syntypes (Fig. 18A, B) with an Indian Ocean type locality in fact belongs to an Atlantic species, an opinion based on consistent conchological differences between the lectotype of *Pusia microzonias* and specimens routinely collected from the Indo-Pacific, and the presence of a conchologically very similar species in the Caribbean. Having made this conclusion, the authors described the Indo-Pacific *Pusia microzonias*-like species as *Vexillum geronimae* Poppe *et al.*, 2009 (Fig. 18I), to which they attributed many specimens from the Indo-Pacific illustrated by earlier authors as *Pusia microzonias*. Instead, we advocate for an Indo-Pacific origin of the lectotype, as the probable holotype of *Tiara semiplicata* Broderip, 1836 (Fig. 18C), the origin of which is more precisely documented (Society Islands), and is undoubtedly conspecific with the lectotype of *Pusia microzonias*.

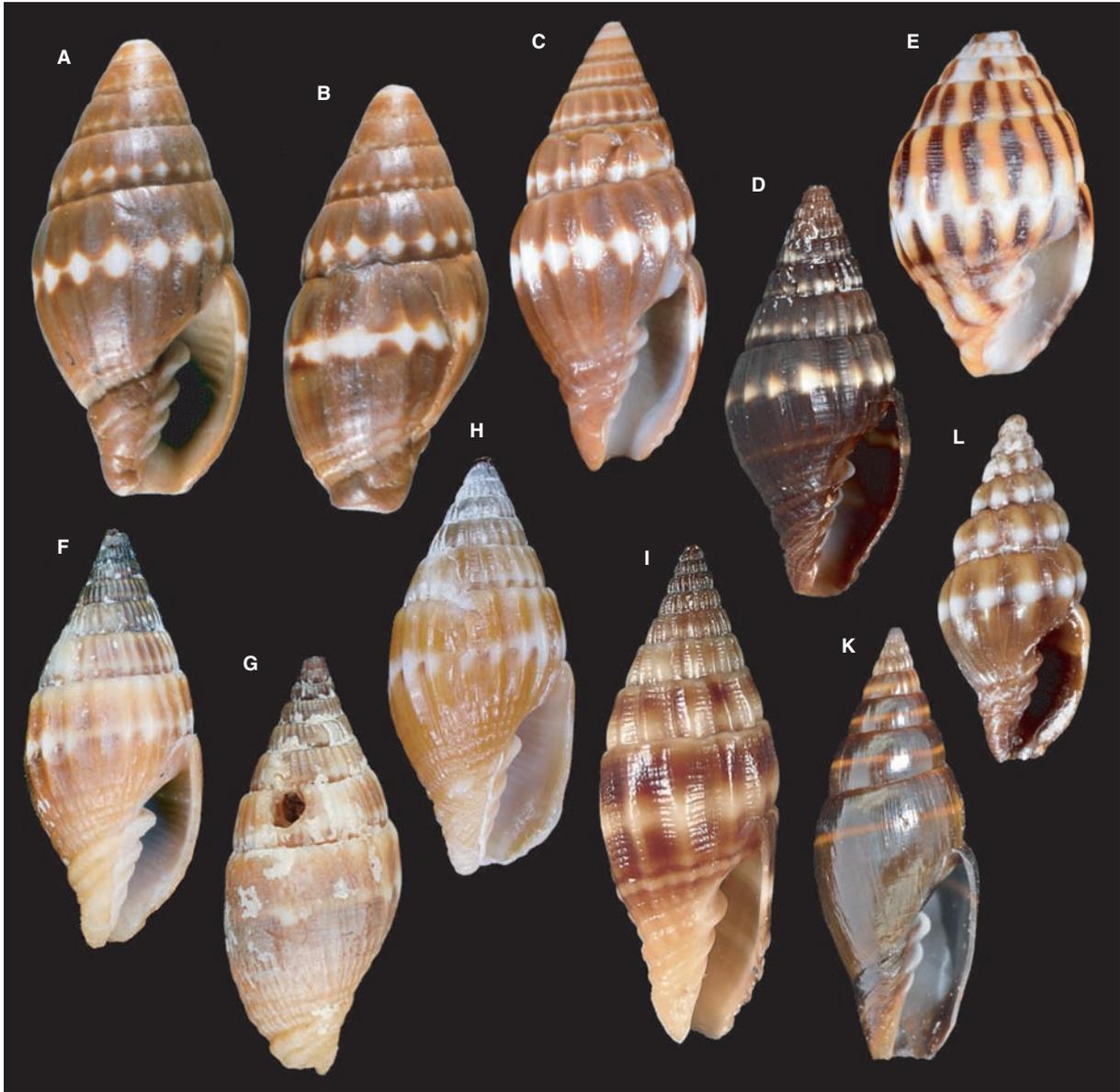


Figure 18. *Pusia (Pusia)* and *Pusia (Ebenomitra)* species. A–D, *Pusia (Pusia) microzonias*: A, B, *Mitra microzonias*, lectotype MNHG 1108/12/1, 18.2 mm ‘L’Océan indien’; C, *Tiara semiplicata* Broderip, 1836, probable holotype, NHMUK 1996421, 19.3 mm, Society Islands; D, New Caledonia, Nouméa area, Lagon 1992, station 1334, 22°20.1’S, 166°23.2’E, 16 m, 12.1 mm. E, *Pusia (Pusia) lauta*, syntype, NHMUK 1967794, ‘Isle of Masbate, Philippines’, 13.8 mm. F–H, *Pusia (Pusia) vassardi* sp. nov.: F, G, holotype, MNHN IM-2013-40682, South Madagascar, ATIMO VATAE, station TS04 25°02.3’S, 47°00.3’E, 22–24 m, 13.0 mm; H, paratype 2, South Madagascar, ATIMO VATAE, station TR02, 25°01.3’S, 47°00.5’E, 17 m, 14.6 mm. I, *Pusia geronimae*, holotype, NMP, Palawan, Balabac Island, 17.4 mm. K, *Pusia (Ebenomitra) ebenus*, MNHN IM-2013-40660, off Siracusa, Sicily, 37°00.5’N, 15°18.6’E, 6–12 m, 18.2 mm. L, *Pusia (Ebenomitra) savignyi*, MNHN IM-2013-40674, off Siracusa, Sicily, 37°00.5’N, 15°18.6’E, 6–12 m, 7.7 mm.

Admittedly, a *Pusia*-like general appearance is widespread in shallow-water Costellariidae, in particular in species allocated here to *Vexillum s.s.*, and often shell morphology alone is not sufficient to tell whether a species belongs to *Pusia (Pusia)* or not. The three species here assigned to *Pusia (Pusia)* are overall characterized by the same colour pattern

(which is shared with other subgenera of *Pusia*) and the siphonal canal, not notched at its tip, which distinguishes them from *Vexillum s.s.*

The species of *Pusia (Ebenomitra)* – see below – are easily distinguishable by their large paucispiral protoconch and lack of spiral sculpture. The species of *Pusia (Vexillena)* are generally larger than *Pusia*

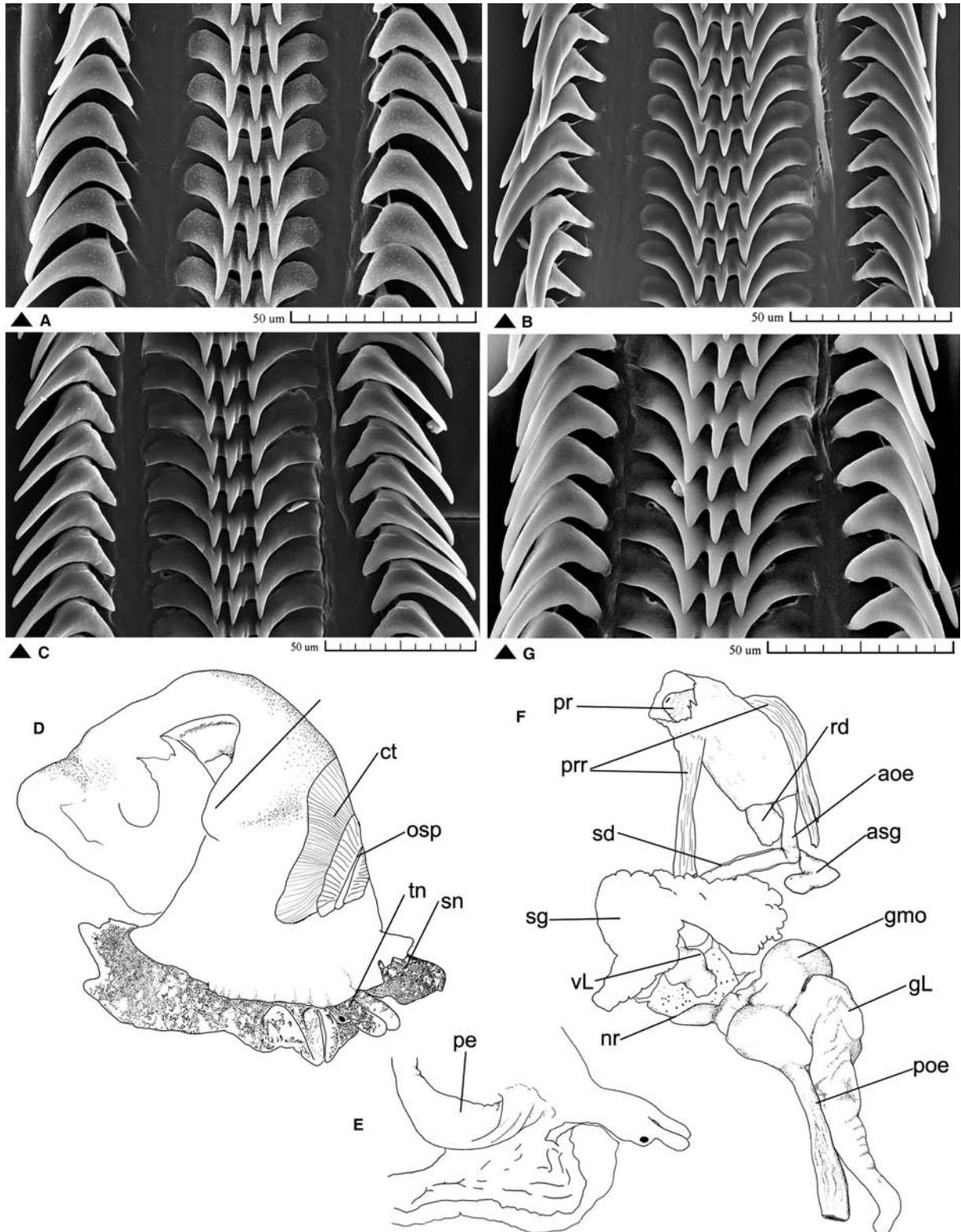


Figure 19. *Pusia* morphology. A–C, *Pusia (Pusia) radulae*: A, *Pusia (Pusia) microzonias*, Lagon 1992, station 1334, 12.1 mm; B, *Pusia (Pusia) vassardi* sp. nov., holotype; C, *Pusia (Pusia) lauta*, MNHN IM-2013-47927. D–G, *Pusia (Ebenomitra) ebenus*, off Calahanda, province of Malaga, Spain, 36°29.4'N, 04°41.8'W, 18 m, 14.35 mm: D, general morphology of the body; E, mantle removed; F, anterior alimentary canal; G, radula.

(*Pusia*), and are characterized by a higher spire, although some species in these two subgenera may be strikingly similar. *Pusia (Pusia)* and *Pusia (Vexillena)* do not overlap in bathymetry: *Pusia (Pusia)* inhabits shallow waters and is commonly found intertidally, whereas *Pusia (Vexillena)* occurs in depths of several hundred metres and, as far as we know, is not found at shallower depths.

PUSIA (PUSIA) VASSARDI SP. NOV. FEDOSOV,
HERRMANN & BOUCHET
FIGURE 18F–H

Type data

Holotype: MNHN IM-2013-40682, 25°02.3'S, 47°00.3'E, 22–24 m, South Madagascar, Fort-Dauphin area (ATIMO VATAE, station TS04), lv, 13.0 mm (Fig. 18F, G).

Paratypes: Paratype 1, MNHN IM-2000-30207, ATIMO VATAE, station TA50, 24°59.5'S, 47°06.0'E, 10 m, South Madagascar, lv, 16.8 mm; paratype 2, MNHN IM-2000-30208, ATIMO VATAE, station TR02, 25°01.3'S, 47°00.5'E, 17 m, South Madagascar, lv, 14.6 mm (Fig. 18H).

Diagnosis

Shell small to medium sized (13–14 mm), broadly fusiform. Suture deeply impressed, spire slightly acuminate, with spire whorls flattened in outline. Axial sculpture of dense rounded ribs with narrow interspaces, well pronounced on spire whorls; ribs widened on last adult whorl, vanishing below periphery and on latest half of whorl. Interspaces between axial ribs sculptured with low rounded cords on early spire whorls, the pattern changes later to multiple fine grooves, very weak on last adult whorl. Siphonal canal short, tapering. Aperture elongate, its outer lip lirate within, inner lip with strong callosity, bearing four strong columellar folds, adapicalmost fold strongest. Shell orange to light brown, with darker spire and lighter spiral band along periphery of penultimate and last adult whorls.

Description

Shell small to medium sized, broadly fusiform (*w/h* 0.43; *a/h* 0.51), with slightly acuminate spire. Protoconch missing or worn in all specimens studied. Suture distinct, deeply impressed. Teleoconch of about 7.5 whorls, spire whorls with flattened profile, sculptured with multiple, rounded orthocline ribs (30 on fourth adult whorl) with narrow interspaces. Axial ribs forming weak subsutural 'caps' on early spire whorls, interspaces between axials with five or six closely set, broad, rounded cords that are

more pronounced on early spire whorls, and become indistinct, with only shallow grooves remaining, on later whorls. Axial ribs broadened on penultimate and last adult whorls, not pronounced below periphery and on latest half of last adult whorl. Spiral grooves also very weak on adapical portion and periphery of last adult whorl. Shell base gradually extending towards short, tapering siphonal canal, sculptured with three very weak, vaguely gemmate, spiral cords. Siphonal fasciole with three strong rounded cords. Aperture elongate, with evenly convex outer lip, slightly extended towards tip of siphonal canal, lirate within. Inner lip with strong callosity, bearing four strong columellar folds, adapicalmost fold strongest, subsequent folds gradually weakening. Shell orange to light brown, with darker spire and lighter spiral band, widened on crests of axial ribs, at periphery of penultimate and last adult whorls.

Radula (of holotype, Fig. 19B): Radula about 0.12 mm wide. Rachidian with wide base and three closely set cusps, rather short and stout. Laterals strong, sickle shaped, unicuspid.

Distribution and habitat

Known only from Southern Madagascar, in shallow water, depth range 15–24 m.

Etymology

The new species is named after Emmanuel Vassard, who has used his diving skills on multiple MNHN expeditions, among others the ATIMO VATAE expedition to the 'Deep South' of Madagascar.

Remarks

Pusia vassardi sp. nov. resembles the type species *Pusia microzonias*, as well some *Pusia (Vexillena)* species, like *Pusia balutensis*, *Pusia jenyai* sp. nov., and *Pusia dautzenbergi*, primarily in shell proportions and colour pattern; however, *Pusia vassardi* sp. nov. can be easily distinguished from *Pusia microzonias* by its lighter and stouter shell with proportionally higher last adult whorl. *Pusia vassardi* sp. nov. is easily separated from species of *Pusia (Vexillena)* by the characteristic dark spire and weakly sculptured last adult whorl. Apart from that, *Pusia vassardi* sp. nov. can be readily distinguished from *Pusia balutensis* by the smaller shell, flattened outline of spire whorl, and notably widened axials on last adult whorl, and also by the dark color of the spire. Similarly, *Pusia jenyai* sp. nov. is recognized by its distinct, though very wide and flattened, axials that extend to shell base. *Pusia dautzenbergi* has a higher spire and stronger axials; however, paratype 5 of the latter species from the Philippines shows an extraordinary resemblance to *Pusia vassardi* sp. nov.

Finally, *Vexillum geronimae* resembles *Pusia vassardi* sp. nov. in proportions and colour pattern, but the robust base and deeply notched siphonal canal, commonly found in true *Vexillum* species, are distinctive.

SUBGENUS *PUSIA* (*EBENOMITRA*) MONTEROSATO,
1917

FIGURES 18H, I AND 19D–G

Type species: Mitra ebenus Lamarck, 1811 (SD, Coan, 1966: 130).

Synonyms

Pusiola Monterosato, 1912 (invalid: junior homonym of *Pusiola* Wallengren, 1863 [Lepidoptera]; *Pusiolina* Cossmann, 1821 is a replacement name); type species *Voluta tricolor* Gmelin, 1791 (SD: Lamy, 1920: 316). *Pusiolina* Cossmann, 1921; type species *Voluta tricolor* Gmelin, 1791 (type by typification by replaced name).

Diagnosis

Shell small, turritiform or fusiform to widely fusiform, polished and glossy. Protoconch bulbous, paucispiral, with about two glossy whorls. Teleoconch of up to 7.5 moderately or strongly convex whorls. Early spire whorls with strong ribs or very strong and wide folds; later whorls with strong wide folds vanishing below periphery of last adult whorl, or smooth; spiral sculpture not pronounced. Microsculpture of fine dense collabral growth lines. Siphonal canal short to moderately long, sculptured with between two and four strong oblique cords. Aperture ovate to elongate, sometimes constricted towards siphonal canal; outer aperture lip lirate within. Inner apertural lip with three strong oblique columellar folds, adapicalmost fold strongest. Shell light brown to almost black, with lighter spiral band on shell periphery.

Anatomy

Pusia (Ebenomitra) ebenus, off Calahonda, prov. Malaga, Spain, 36°29.4'N, 04°41.8'W, 18 m, 14.35 mm (Fig. 19D–G).

Head-foot with intense black pigmentation, head with eyes situated laterally at the base of tentacles (Fig. 19D). Seminal groove closed along its entire length (Fig. 19E). Proboscis moderately long, occupying about two-thirds of rhynchocoel length; proboscis retractors represented by two strong muscular bundles attached laterally to rhynchodaeum (Fig. 19F). Radular sac situated within the proboscis, occupying about half of its length. Radula triserial with wide tricuspidate rachidian, and strong unicuspidate laterals (Fig. 19G). Salivary gland white, with two

ducts adjoining oesophagus anterior to valve of Leiblein. Bulky gland of Leiblein rather small, pale, translucent. Mid-oesophagus notably widened, obviously glandular.

Included species

Pusia (Ebenomitra) ebenus (Lamarck, 1811),¹ *Pusia (Ebenomitra) granum* (Forbes, 1844),² *Pusia (Ebenomitra) savignyi* (Payraudeau, 1826),¹ *Pusia (Ebenomitra) tricolor* (Gmelin, 1791).²

Distribution and habitat

Mediterranean at subtidal depths.

Remarks

The species of *Ebenomitra* (as defined here) are characterized by a paucispiral protoconch that is indicative of non-planktotrophic larval development – a character unique among species of *Pusia*. *Ebenomitra* species are the only costellariid species recorded in the Mediterranean, and their range does not overlap with the ranges of the other two subgenera of *Pusia*, or of other costellariid lineages. Overall, *Ebenomitra* shells, with their bulbous protoconch and axial sculpture alone (if any), superficially resemble *Austromitra*; however, these two groups are apparently not related, and occur far apart in different hemispheres.

SUBGENUS *PUSIA* (*VEXILLENA*) SUBGEN. NOV.

Type species: Vexillum balutense Herrmann, 2009.

Diagnosis

Shell small to medium sized, fusiform. Protoconch conical, with 3.5 or more glossy, weakly convex whorls, orange or light brown, translucent. Early spire whorls usually slightly flattened, later evenly convex, suture distinct, impressed. Axial sculpture of fine and dense, sometimes strong and evenly spaced ribs, or sometimes absent on late teleoconch whorls. Spiral sculpture of dense fine grooves, pronounced in interspaces between axials, and irregular grooves on shell base, or sometimes absent. Siphonal canal rather long, straight, aperture with three or four distinct columellar folds, adapicalmost fold strongest. Shell intensely coloured with sometimes intricate pattern of light brown or orange blotches. Head-foot pale, with occasional dark blotches and bands on the dorsal surface of foot. Eye tentacles rather long, thin, with basal eyes. Radula rachiglossate with tricuspidate rachidian often bearing small accessory cusps flanking the central major cusp; laterals simple, sickle-shaped unicuspidate. Buccal mass encloses delicate horse-shoe-shaped jaw.

Included species

Pusia (Vexillena) balutensis (Herrmann, 2009) comb. nov.,¹ *Pusia (Vexillena) choslenae* (Cernohorsky, 1982) comb. nov.,¹ *Pusia (Vexillena) dautzenbergi* (Poppe et al., 2006) comb. nov.,² *Pusia (Vexillena) eliscrossi* (Rosenberg & Salisbury, 1991) comb. nov.,² *Pusia (Vexillena) jenyai* sp. nov.,¹ *Pusia (Vexillena) johnwolffi* (Herrmann & Salisbury, 2012) comb. nov.,¹ ?*Pusia (Vexillena) vicmanoui* (Turner & Marrow, 2001) comb. nov.²

Distribution and habitat

West Pacific, from Japan and the Philippines to New Caledonia and the Coral Sea; at depths greater than 200 m.

Etymology

The name *Vexillena* is selected to convey the general similarity of this subgenus to *Vexillum*.

Remarks

Species of *Pusia (Vexillena)* subgen. nov. share a characteristic colour pattern of spirally and axially aligned brown blotches delineated by narrow lighter bands, or the entire shell is coloured brown, bearing spiral line or series of lighter blotches slightly above the periphery of the whorls. The larger size and relatively higher spire normally allow the distinction of *Pusia (Vexillena)* from *Pusia (Pusia)*; however, the delineation of the subgenera *Pusia (Vexillena)* and *Pusia (Pusia)* is somewhat hazy, as some species of the two subgenera are very close in shell proportions, sculpture, and coloration. All studied species of *Pusia (Vexillena)* are characterized by the rachidian with two minor cusps flanking the central major cusp; in *Pusia (Pusia)* and *Pusia (Ebenomitra)*, these minor cusps are absent. Therefore, these cusps may be considered an apomorphy of the *Vexillena* clade. It is also noteworthy that all known species of *Pusia (Vexillena)* inhabit depths greater than 200 m (usually 300–500 m), and thus do not overlap with *Pusia (Pusia)* species in bathymetry.

Equally difficult to distinguish are *Pusia (Vexillena)* subgen. nov. and *Tosapusia*. Although in most

cases the well-developed colour pattern of the shell distinguishes *Pusia (Vexillena)* subgen. nov., in other characteristics the two groups are close, with shells varying from elongate [*Tosapusia isaoi* vs. *Pusia (Vexillena) vicmanoui*] to rather broad [*Tosapusia vityaz* sp. nov. vs. *Pusia (Vexillena) balutensis*], and with remarkably similar sculpture patterns. Consistent differences between the two groups are found in radular morphology, as rachidians of *Pusia (Vexillena)* subgen. nov. species have characteristic minor cusps. Shells in *Vexillena* subgen. nov. also have a longer siphonal canal, resulting in a more fusiform and typically more solid shell, compared with species of *Alisimitra* gen. nov.; moreover, live or fresh specimens of *Vexillena* subgen. nov. have a distinctive shell colour pattern, not observed in *Alisimitra* gen. nov. Finally, *Costapex* gen. nov. differs from *Vexillena* subgen. nov. in having generally smaller shells, with overall dominating spiral sculpture. Moreover, the adapicalmost columellar fold is notably stronger than the succeeding folds in all species of *Vexillena*, whereas in species of *Costapex* gen. nov. the columellar folds are subequal. Finally, species of *Vexillena* spp. can be easily distinguished from *Vexillum* by the shape of the siphonal canal, which is usually deeply notched in *Vexillum* and straight or very shallowly notched in *Vexillena*.

***PUSIA (VEXILLENA) BALUTENSIS* (HERRMANN, 2009) COMB. NOV.**
FIGURE 20A–C

Vexillum (Costellaria) balutensis Herrmann, 2009: 36, figs 1, 2.

Type data

Holotype: SMNS, Philippines, Mindanao, off Balut, deep water, crabbed, 39.8 mm (Fig. 20A, B).

Paratype: Collection Manfred Herrmann, type locality, 43.5 mm.

Material examined

Type material: Papua New Guinea, BIOPAPUA, station CP3747, 05°33'S, 153°59'E, 458 m, 1 lv (MNHN IM-2013-40637, 34.8 mm, Fig. 20C).

Figure 20. *Pusia (Vexillena)* species. A–C, *Pusia (Vexillena) balutensis*: A, B, holotype, SMNS, Philippines, Mindanao, off Balut Island, deep water, 39.8 mm; C, MNHN IM-2013-40637, Papua New Guinea, BIOPAPUA, station CP3747, 05°33'S, 153°59'E, 458 m, 34.8 mm; D–F, *Pusia (Vexillena) jenyai* sp. nov.: D, E, holotype, MNHN IM-2007-32136, New Caledonia, Chesterfield Plateau, EBISCO, station DW2607, 19°33'S, 158°40'E, 400–413 m, 23.6 mm; F, paratype, MNHN IM-2007-30128, Coral Sea, Banc Nova, EBISCO, station DW2528, 22°49'S, 159°23'E, 320–345 m, 18.25 mm. G–K, *Pusia (Vexillena) choslenae*: G, H, paratype 2, AMS C.133281, New Caledonia, off Isle of Pines, 370 m, 32.7 mm; I, New Caledonia, EXBODI, station DW3859, 22°20'S, 169°01'E, 350–388 m, Banc de l'Orne/Walpole, 15.25 mm; K, MNHN IM-2007-38378, New Caledonia, EXBODI, station CP3826, 21°52'S, 166°51'E, 354–509 m. L–N, *Pusia (Vexillena)* radulae: L, *Pusia balutensis*, MNHN IM-2013-40637; M, N, *Pusia choslenae*, New Caledonia, EXBODI, station 3826, 21°52'S, 166°51'E, 354–509 m, 13 mm; M, radula; N, jaw.

Diagnosis

Shell fusiform, reaching about 44 mm in length, with moderately long, tapering siphonal canal. Protoconch

of 1.5–2.0 smooth yellowish whorls. Teleoconch of eight or nine convex, axially ribbed whorls, with orthoconoid or slightly concave spire. Suture distinctly



canaliculated, giving the spire a somewhat stepped appearance. Penultimate whorl with up to 40 thin, rounded, axial ribs with very narrow interspaces. Axial ribs broader and slightly flattened on last adult whorl. Adapical portion of late teleoconch whorls with between two and five fine, rather shallow, grooves intersecting axial ribs. Shell base nearly smooth. Siphonal fasciole with seven or eight widely spaced rounded spiral cords. Aperture rather wide, about half the shell length. Inside of outer lip with between ten and 13 lirations. Columella with four strong folds. Siphonal canal slightly curved upwards.

Radula (MNHN IM-2013-40637, Fig. 20L): Radula about 1.2 mm long and 0.17 mm wide, consisting of about 80 rows. Rachidian with rather wide, bow-shaped base, bearing three widely spaced, major cusps, also separated by depression on rachidian base. Central cusp fringed by two minor projections that are slightly elevated over the tooth surface. Laterals sickle-shaped, unicuspidate.

Distribution and habitat

Philippines and Papua New Guinea (Solomon Sea) in deep water.

Remarks

Pusia balutensis can be easily recognized by the spiral sculpture of fine cords limited to the adapical quarter of teleoconch whorls. *Pusia vassardi* sp. nov., which is close to *Pusia balutensis* in shell proportions and coloration, is notably smaller and has much weaker sculpture on the last adult whorl. Two other similar species from the West Pacific, *Pusia johnwolffi* (Herrmann & Salisbury, 2012) and *Pusia vicmanoui* (Turner & Marrow, 2001), have both more slender shells and stronger spiral elements throughout the whorl height that are only pronounced in interspaces between axial ribs.

PUSIA (VEXILLENA) JENYAI SP. NOV. FEDOSOV,
HERRMANN & BOUCHET
FIGURE 20D–F

Type data

Holotype: MNHN IM-2007-32136, Coral Sea, Chesterfield Plateau, 19°33'S, 158°40'E, 400–413 m (EBISCO, station DW2607), lv, 23.6 mm (Fig. 20D, E).

Paratype: MNHN IM-2007-30128, Coral Sea, EBISCO, station DW2528, 22°49'S, 159°23'E, 320–345 m, Banc Nova, lv, 18.25 mm (Fig. 20F).

Diagnosis

Shell medium sized, fusiform, with acuminate spire and rather short, tapering siphonal canal. Protoconch pale, pointed, with two or more smooth whorls.

Teleoconch of between six and eight whorls, early spire whorls with flattened periphery, later whorls gently convex. Suture distinct. Sculpture of very closely set, broad, and flattened axial ribs, separated by narrow interspaces with fine spiral cords. Shell base evenly convex, with stronger and somewhat irregular spiral cords. Siphonal canal short and robust. Outer lip straight adapically and convex below its mid-height; inside of outer lip with fine lirae. Inner lip with four strong columellar folds. Shell brown with darker spiral band on whorl periphery, bearing series of irregular white blotches. Early spire whorls with pale spiral ribs and brown interspaces between them.

Description

Shell medium sized, fusiform (w/h 0.39–0.49; a/h 0.48–0.56), with acuminate apex and rather broad aperture. Protoconch pale, pointed, with two or more adpressed smooth whorls. Teleoconch of eight evenly convex whorls, suture distinct, impressed, with narrow subsutural shelf giving the spire a slightly stepped outline. First three spire whorls with steeper outline, sculptured by distinct rounded ribs (17 on third teleoconch whorl), interspaced by depressions of equal width. Later whorls with rather wide and low, slightly prosocline folds (36 on last adult whorl). Interspaces between axial folds rather narrow, dashed in appearance, reminiscent of fine, evenly distanced spiral cords. Axial folds wide and flattened on adapical portion of last adult whorl, gradually narrowing below its periphery and fading entirely on shell base. Ten, rather widely interspaced, spiral cords on adapical portion and periphery of last adult whorl, succeeded by 14, more densely set, cords on shell base. Lower five spiral cords of shell base stronger than preceding cords, slightly wavy, followed by notably coarser and more spaced cords on siphonal canal. Siphonal canal stout, moderately long, with distinct fasciole. Aperture rather wide, elongate, its outer lip thin, with distinct subsutural sinus. In apertural view, orientation of outer lip coaxial adapically and convex below its mid-height. Inner lip with well-developed secondary callus, bearing four strong columellar folds, adapicalmost fold strongest. Background colour light brown with darker spiral band on whorl periphery, decorated by spirally aligned white blotches of irregular size. Early spire whorls with pale spiral ribs and brown interspaces between them.

Distribution and habitat

Coral Sea: Banc Nova and Chesterfield Plateau, 345–400 m.

Remarks

Pusia (Vexillena) dautzenbergi is closest to *Pusia jenyai* sp. nov. in overall shell morphology, but the

latter can be easily distinguished by its very dense, wide, and flattened axial ribs, and distinctively acuminate spire outline. Some species referable to *Pusia*, like *Pusia lauta* and *Vexillum consanguineum* (Reeve, 1845), superficially resemble *Pusia jenyai* sp. nov.; however, they both have rather ovate shells with lower spire and proportionally higher last adult whorl.

Etymology

The species is named after Jenya Fedosov, the 6-year-old nephew of the first author.

PUSIA (VEXILLENA) CHOSLENAE
(CERNOHORSKY, 1982) COMB. NOV.
FIGURE 20G–K

Vexillum choslenae Cernohorsky, 1982b: 109–111; figs 1–6.

Type data

Holotype: AM 71368, Japan, Tosa, 128 m, 30.8 mm, probably lost.

Paratypes: Paratype 1, formerly in collection A. Choslen, current whereabouts unknown, type locality, 30.9 mm; paratype 2, AMS C-133281 (formerly in AMS, at present housed in AM), New Caledonia, Isle of Pines, 22°52'S, 167°35.5'E, 370 m, bottom of large slabs of beach rock, 32.7 mm (Fig. 20G, H).

Material examined

New Caledonia: Typical form: EXBODI, station DW3850, 22°18'S, 168°44'E, 450–500 m, Banc Sud Durand, 1 lv (17.1 mm); EXBODI, station CP3826, 21°52'S, 166°51'E, 354–509 m, off Ounia, 1 lv, (15.85 mm); EXBODI, station DW3859, 22°20'S, 169°01'E, 350–388 m, Banc de l'Orne/Walpole, 1 lv (15.25 mm; Fig. 20I). Smooth form: EXBODI, station CP3826, 21°52'S, 166°51'E, 354–509 m, off Ounia, 2 lv (MNHN IM-2007-38378, 13.0 mm; Fig. 20K).

Diagnosis

Shell medium sized, elongate-fusiform (w/h 0.33–0.38; a/h 0.48–0.5), with orthoconoid spire and rather long, stout siphonal canal. Protoconch orange, conical, with four or more glossy gently convex whorls. Teleoconch of up to ten evenly convex whorls. Suture distinct, narrowly canaliculated. Sculpture of dense, rounded, orthocone ribs, well pronounced on spire whorls and usually vanishing later, with last adult whorl nearly smooth. Interspaces between axial ribs typically with distinct rounded cords; squarish deep interstices between cords clearly seen on spire whorls and becoming very faint on last adult whorl. Last adult whorl evenly convex in its upper portion; shortly constricted to straight, rather long and stout, widely open

siphonal canal. Siphonal fasciole with six or seven flattened cords. Aperture elongate, its outer lip lirate within, notably drawn towards tip of siphonal canal, forming slight concavity in its abapical portion. Inner lip with four columellar folds, uppermost strongest, subsequently gradually weakening. Shell colour orange brown with a white peripheral band on the spire whorls and a second white band on the last adult whorl, white and dark brown axial streaks.

Radula (EXBODI, station CP3826, 13.0 mm Fig. 20M): Radula exceeding 0.4 mm in length, 0.08 mm wide, formed by about 43 + rows. Rachidian tricuspidate, with rather narrow base and robust pointed cusps. Some rachidians bear a pair of very feeble intermediate cusps, situated in interspaces between the major cusps. Laterals sickle-shaped, unicuspidate. Buccal mass encloses a soft hitinous horseshoe-shaped jaw (Fig. 20N).

Distribution and habitat

Japan and New Caledonia, in deep water.

Remarks

Pusia (Vexillena) choslenae shows notable variations in sculpture and also in shell proportions. The typical form, distributed from Japan to New Caledonia, is characterized by a well-developed cancellate sculpture, which becomes indistinct only on late teleoconch whorls of adult specimens; a specimen studied herein (Fig. 20I) is closest in morphology to the holotype and paratype 1. A smooth form, represented by paratype 2 (Fig. 20G, H) and a sequenced specimen (MNHN IM-2007-38378), is found off New Caledonia. In addition to a weakly developed sculpture with indistinct spiral elements, this form has a slightly acuminate spire and is overall slightly wider than the typical form; however, specimens of intermediate morphology, with well-developed sculpture, rather wide last adult whorl, and acuminate spire, are present in our material. Having at present sequenced only one specimen, we assume that the observed morphological disparity only represents within-species variation.

Typical *Pusia choslenae* resemble *Pusia vicmanoui* in shell proportions, sculpture, and colour pattern, but can be distinguished from *Pusia vicmanoui* by a rather weak sculpture on the last adult whorl and the morphology of the subsutural area, smooth in *Pusia choslenae*, but undulating in *Pusia vicmanoui* because of axial ribs slightly projecting adapically. Adult *Pusia (Vexillena) choslenae* can be easily distinguished from other *Vexillena* species by the smooth or weakly sculptured late adult whorls. Specimens of *Pusia (Vexillena) choslenae* from New Caledonia (Fig. 20K) often show a more pronounced



Figure 21. *Pusia (Vexillena)* species. A, B, *Pusia (Vexillena) elliscrossi*, holotype, BPBM 219991, Hawaii, Oahu, off Waikiki, 180 m, sand bottom, 18.5 mm. C, D, *Pusia (Vexillena) dautzenbergi*, holotype NMP, Philippines, Bohol Sea, off Ali-guai Island, 60–150 m, 27.7 mm. E–H, *Pusia (Vexillena) johnwolffi*: E, F, holotype, NMBE 28751/1, Philippines, Balicasag Island, 180 m, 30.1 mm; G, MNHN IM-2007-32140, Coral Sea, Banc Kelso, EBISCO station DW2513, 24°06'S, 159°42'E, 280–500 m, 21.0 mm; H, MNHN IM-2007-30072, Coral Sea, south Lansdowne, EBISCO, station 2632, 21°05'S, 160°45'E, 297–378 m, 21.2 mm. I, K, *Pusia (Vexillena) vicmanoui*, topotype, collection Manfred Herrmann, Philippines, Mindanao, Davao Bay, off Talikud Island, sandy mud at 210 m, 53.6 mm.

sculpture; however, this tends to vanish on late teleoconch whorls.

***PUSIA (VEXILLENA) ELLISCROSSI* (ROSENBERG & SALISBURY, 1991) COMB. NOV.**
FIGURE 21A, B

Vexillum elliscrossi Rosenberg & Salisbury, 1991: 149–151; figs 6–9.

Type data

Holotype: BPBM 219991, Pele 1965, Hawaii, Oahu, off Waikiki, 180 m, sandy bottom, 18.5 mm (Fig. 21A, B).

Paratypes: Paratypes 1–5 as listed by Rosenberg & Salisbury (1991).

Material examined

Holotype.

Diagnosis

Shell small, solid, broadly fusiform, of up to eight subcylindrical spire whorls. Suture deep incised, channelled. Sculpture of strong, slightly prosocline axial ribs, crossed by much finer spiral grooves, which are well pronounced in the depressions between axials. Last adult whorl evenly convex, siphonal canal moderately long, stout, and tapering. Aperture rather narrow; outer lip lirate inside, inner lip with four strong columellar folds. Shell colour white with wide brown band on whorl periphery and narrower weaker bands adapically and on shell base.

Distribution and habitat

Hawaiian Islands, depth range 90–180 m.

Remarks

Among *Pusia (Vexillena)* species, *Pusia johnwolffi* most resembles *Pusia elliscrossi* in both shell proportions and colour pattern; however, shells of *Pusia elliscrossi* are notably stouter, and not as elongate as *Pusia johnwolffi*. The other notable difference between the two species is in colour pattern: whereas *Pusia johnwolffi* bears three equally wide bands on its last adult whorl, the major band on the shell periphery of *Pusia elliscrossi* notably exceeds the others in width. Two other *Pusia (Vexillena)* species, *Pusia balutensis* and *Pusia choslenae*, are close to *Pusia elliscrossi* in overall shell shape; however, both can be distinguished by the sculpture pattern: *Pusia balutensis* is sculptured with axial elements only, and they are denser than those in *Pusia elliscrossi*; whereas *Pusia choslenae* lacks any sculpture on late teleoconch whorls whatsoever.

***PUSIA (VEXILLENA) DAUTZENBERGI* (POPPE, GUILLOT DE SUDUIRAUT & TAGARO, 2006) COMB. NOV.**

FIGURE 21C, D

Vexillum (Costellaria) dautzenbergi Poppe, Guillot de Suduiraut & Tagaro, 2006: 107; pl. 3, figs 2–4.

Type data

Holotype: NMP, Philippines, Mindanao, Dipolog, Aliguay Island, 27.7 mm (Fig. 21C, D).

Paratypes: All from type locality; paratype 1, collection Sandro Gori (formerly collection Guillot de Suduiraut), 25.0 mm; paratypes 2–5, collection Conchology Inc., 24.1, 23.2, 22.1, and 24.3 mm, respectively (illustrated in Poppe, Tagaro & Martin, 2008).

Material examined

Topotype, collection Manfred Herrmann, Philippines, Mindanao, Dipolog, Aliguay Island, 240–280 m, 26.7 mm; further material from Balicasag Island and Mactan Island (26–28 mm).

Diagnosis

Shell small to medium-sized, solid, broadly fusiform. Spire orthoconoid or slightly acuminate, with five to six whorls, suture distinct, impressed. Early spire whorls with flattened outline, penultimate and last adult whorls slightly evenly convex. Sculpture of strong, rounded axial ribs, closely set on spire whorls, and more widely spaced on last adult whorl. Interspaces between axial ribs sculptured with fine regular spiral grooves. Siphonal canal moderately long, tapering, sculptured with between five and seven strong rounded cords, the adapical two cords sometimes gemmate. Aperture elongate, inside of outer lip with fine lirae, inner lip with five strong folds, adapicalmost fold strongest. Early three or four spire whorls and tip of siphonal canal white, later whorls brown with narrow white peripheral band, which is widened on crest of axial ribs.

Distribution and habitat

Known from the Philippines (Bohol Sea), depth range 150–240 m.

Remarks

Among *Vexillena* species, *Pusia dautzenbergi* most resembles *Pusia johnwolffi*. Although they can be distinguished by shell proportions and some minor features (see Herrmann & Salisbury, 2012), robust criteria allowing their sure delimitation throughout their ranges are yet to be established (see below). Another species resembling *Pusia dautzenbergi* is *Pusia vicmanoui*, but the latter has a larger and much more slender shell with stronger spiral sculpture formed by evenly spaced spiral cords rather

than grooves. *Pusia jenyai* sp. nov. also resembles *Pusia dautzenbergi*; however, it has characteristic, very closely set, distinctly flattened axial ribs and spiral sculpture of fine cords.

***PUSIA (VEXILLENA) JOHNWOLFFI* (HERRMANN & SALISBURY, 2012) COMB. NOV.**
FIGURE 21E–H

Vexillum (Costellaria) johnwolffi Herrmann & Salisbury, 2012: 138; figs 43–48.

Type data

Holotype: NMBE 28751/1, Philippines, Balicasag Island, 180 m, 30.1 mm (Fig. 21E, F).

Paratypes: Paratypes 2–5, in private collections, Balicasag Island, 24.8–29.7 mm; paratypes 6–12, in private collections, other Philippine locations, 11.7–29.3 mm; paratype 13, MNHN IM-2012-8, Wallis & Futuna, 20.1 mm; paratypes 14–16, MNHN IM-2012-9–11, French Polynesia, 11.1–13.7 mm; paratypes 17–19, MNHN IM-2012-12–14, Solomon Islands, 9.0–13.3 mm.

Other material examined

New Caledonia, Coral Sea: MNHN IM-2007-32140, Banc Kelso, EBISCO, station DW2513, 24°06'S, 159°42'E, 280–500 m, lv, 21.0 mm (Fig. 21G); MNHN IM-2007-30072, South Lansdowne, EBISCO, station DW2632, 21°05'S, 160°45'E, 297–378 m, lv, 21.2 mm (Fig. 21H); MNHN IM-2007-30117, Banc Nova, EBISCO, station DW2528, 22°49'S, 159°23'E, 320–345 m, lv, 17.2 mm.

Diagnosis

Shell medium-sized, elongate-fusiform, suture distinct and undulate, shoulder rounded. Up to nine slightly convex to subcylindrical spire whorls sculptured with strong axial ribs, crossed by fine spiral lirae. Axial ribs becoming obsolete on siphonal fasciole, which is sculptured by strong spiral cords that are a continuation of columellar folds. Aperture strongly lirate inside, small parietal tooth near anal sulcus, four or five columellar folds. Shell colour warm brown with two or three white bands on the last adult whorl, the first and largest band on whorl periphery, often bordered by two dark chocolate lines.

Distribution and habitat

West and South Pacific from the Philippines, Solomon Islands, Coral Sea, Wallis & Futuna to French Polynesia, depth range 180–320 m.

Remarks

There seems to be some geographical variation between specimens from the Philippines and those from the South Pacific, as well as among specimens

from the same area. For example, specimen MNHN IM-2007-32140 (Banc Kelso) is notably narrower than MNHN IM-2007-30072 (South Lansdowne), with a higher aperture and less convex last adult whorl. Both specimens are from the Coral Sea and differ from the holotype in spire height and colour pattern. At the same time, they resemble the specimens from the Solomon Islands and French Polynesia, as depicted by Herrmann & Salisbury (2012). Finally, paratype 1 is somewhat intermediate in morphology between the holotype and the specimens from South Pacific localities. *Pusia (Vexillena) dautzenbergi* is undoubtedly most similar to *Pusia johnwolffi*, and essentially falls in the range of variation illustrated for *Pusia johnwolffi*. In particular, the specimens of *Pusia johnwolffi* examined here are in some features closer to the holotype of *Pusia dautzenbergi*. Molecular data are needed to ensure an accurate delimitation of the two species and to confirm their status. *Pusia johnwolffi* also resembles *Pusia elliscrossi*, but it is more elongate and thin-shelled; the two species also show consistent differences in colour pattern (see above). *Pusia johnwolffi* can be readily differentiated from *Pusia (Vexillena) balutensis* and *Pusia (Vexillena) vicmanoui* by the rather flattened profile of the spire whorls and the more widely spaced axial ribs.

***PUSIA (VEXILLENA) VICMANOUI* (TURNER & MARROW, 2001) COMB. NOV.**
FIGURE 21I, K

Vexillum (Costellaria) vicmanoui Turner & Marrow, 2001: 49, figs 12, 13.

Type data

Holotype: MHNG 29816, Philippines, Mindanao, off Talikud Island, 130–150 m, 50.3 mm.

Paratypes: Three adult paratypes from the Philippines in private collections, 46.6–48.6 mm; a further 17 paratypes (<30 mm) from the Philippines and Japan belong to *Pusia dautzenbergi*, see below.

Material examined

Topotype, collection Manfred Herrmann, Philippines, Mindanao, Davao Bay, off Talikud Island, sandy mud at 210 m, 53.6 mm (Fig. 21I, K). French Polynesia, Austral Islands, Rimatara, Benthaus, station DW2020, 22°37'S 152°49'W, 920–930 m, 1 dd (26.2 mm); station DW2021 22°37'S, 152°49'W, 1200–1226 m, 1 dd (20.1 mm).

Diagnosis

Shell large, elongate-fusiform, with high and straight-sided spire, and long and sharp-edged

siphonal canal. Up to 11 slightly convex spire whorls, sculptured with slender axial ribs, crossed by fine spiral and elevated cords. Axial ribs becoming obsolete on anterior half of the last adult whorl. Siphonal fasciole with seven to eight flat oblique cords. Aperture narrow, strongly lirated within, anal notch sharp and narrow, parietal callus on the parietal side, four columellar folds. First three to four spire whorls white, later whorls medium brown with a lighter anterior half of the last adult whorl; white peripheral band on all whorls with two more white bands on the anterior half of the last adult whorl, one of them often nearly invisible; irregular white streaks present on the top of the ribs.

Distribution and habitat

Philippines (Mindanao, off Talikud) and French Polynesia (Austral Islands), 150–210 m.

Remarks

Pusia vicmanoui can be readily recognized among other *Pusia* (*Vexillena*) species by its large slender shell with long siphonal canal and strong spiral cords that sometimes override the axial ribs. In shell proportions, fine axial elements, and distinctly canaliculated suture, *Pusia vicmanoui* rather resembles species of *Tosapusia*, such as *Tosapusia sauternesensis* or *Tosapusia evelynae*. Unfortunately, no specimens of *Pusia vicmanoui* were available for molecular studies, and its relationships within Costellariidae are still to be determined. At present we provisionally place it in *Pusia* (*Vexillena*) based on its overall appearance and colour pattern.

GENUS **TURRIPLICIFER** GEN. NOV. FEDOSOV,
MALLOW, HERRMANN & BOUCHET
FIGURE 22A–G

Type species: Mitra australis Swainson, 1820.

Diagnosis

Shell medium-sized, solid, fusiform to turritiform, with rather short aperture and weakly developed sculpture. Protoconch bulbous, paucispiral. Teleoconch of up to 7.5–8.0 whorls, spire whorls with flattened or gently convex outline; suture distinct, deeply impressed. Axial sculpture represented by irregular collabral growth lines or numerous low axial ribs; spiral sculpture of irregular spiral cords that are denser on adapical part of whorls and on shell base. Periphery of last adult whorl smooth or sculptured by indistinct ribs only. Siphonal canal stout, very short, sometimes notched at its tip. Aperture elongate, inside of outer lip smooth. Inner lip with four distinct columellar folds, adapicalmost strongest. Radula about 0.12–0.16 mm in width, triserial.

Rachidian tooth tricuspidate, with wide base; laterals unicuspidate, with robust base and pointed cusp.

Anatomy

Turriplicifer australis, Western Australia, Esperance station WE03, 33°59.6'S, 122°13.33'E, 11 m, 30.0 mm (Fig. 22C–F).

General morphology: Head-foot intensely pigmented velvet black (Fig. 22C); tentacles bearing eyes laterally at their base; apical portion of tentacles coloured pale. Body wall transparent with body haemocoel organs clearly visible.

Anterior alimentary system: Proboscis long, cylindrical, occupying almost the entire length of the proboscis sheath (Fig. 22D). Rhynchodaeum thick, with multiple longitudinal muscular bundles embedded into its wall. Two massive proboscis retractors attached laterally to the anterior part of the rhynchodaeum, and adjoining the columellar muscle posteriorly. Numerous muscular fibers connecting rhynchodaeum to the body wall and other foregut structures. Radular sac situated at proboscis base and sticking out to the body haemocoel. Radula about 1.1–1.2 mm long and 0.15 mm wide, bearing about 60 transversal rows with three teeth in each row. Rachidian tooth rather wide and robust, bearing three closely set, short and blunt cusps in its medial part. Laterals sickle-shaped with robust base and one pointed cusp (Fig. 22E). Anterior oesophagus forming a wide loop and opening into the small, inconspicuous valve of Leiblein, which is situated right in front of the nerve ring. Posterior to the nerve ring, oesophagus narrowing considerably, posterior oesophagus very thin. Salivary gland rather small, white, situated anteriorly above the nerve ring. Bulky gland of Leiblein positioned dorsally from post-oesophagus, rather small, pale, covered with a layer of connective tissue fibres. Anterior to the bulky gland of Leiblein lies a long and strongly convoluted secondary glandular structure.

Male reproductive system: Studied specimen a male, with very large translucent prostatic gland (Fig. 22C), occupying half of the whorl on the left side of mantle cavity behind the hypobranchial gland. Open seminal groove running from the prostatic gland to anterior. Penis rather small, curved, with no papilla and with closed seminal canal.

Included species

Turriplicifer apicitinctus (Verco, 1896) comb. nov.,²
Turriplicifer australis (Swainson, 1820) comb. nov.,¹ *Turriplicifer* sp. nov. (aff. *cinnamomea*, to be named by M. Marrow; Fig. 22H, I),¹ *Turriplicifer esperancensis* (Marrow, 2013) comb. nov. (Fig. 22K).²

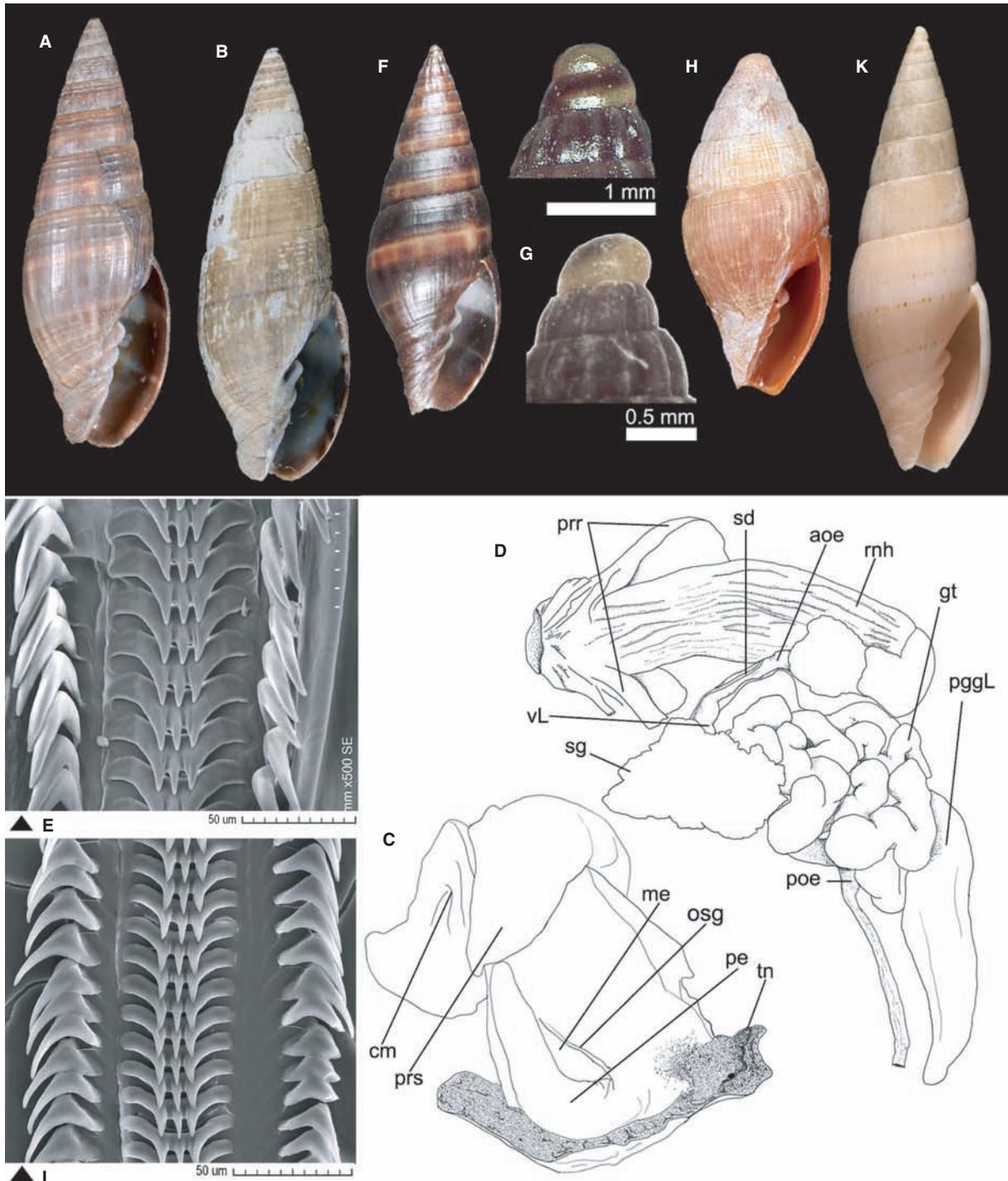


Figure 22. *Turrilicifer* gen. nov. A–G, *Turrilicifer australis*: A, *Mitra kieneri* G.B. Sowerby II, 1874, holotype, NHMUK 1879.2.26.128, locality unknown, 32.4 mm; B, MNHN IM-2013-40675, Western Australia, station WE08, 33°54.95'S, 121°54.6'E, 5–30 m, 33.0 mm; C, D, Western Australia, Esperance, station WE03, 33°59.6'S, 122°13.33'E, 11 m, 30.0 mm; C, general morphology of the body (mantle removed); D, foregut anatomy; E, radula, IM-2013-40675; F, G, southern Australia, Port Fairy, Green Island, intertidal, 20.9 mm; F, shell; G, apex morphology. H, I, *Turrilicifer* sp. aff. *cinnamomea*, MNHN IM-2013-40668, Western Australia, station WE03, 33°59.6'S, 122°13.33'E, 11 m, 15.9 mm; H, shell; I, radula; K, *Mitra esperancensis* Marrow, 2013, holotype, WAM S80373, Cape Le Grande, East of Esperance, South-Western Australia, 24.26 mm.

Distribution and habitat

The three species assigned to this genus occur in near-shore habitats in Western and Southern Australia and Tasmania, in upper subtidal depths.

Etymology

The genus name combines *turris*, referring to the shell with high spire, and *plicifer* = bearing plicae, in reference to the well-developed columellar folds. Gender masculine.

Remarks

The morphology of *Turriplicifer* gen. nov. shows some characteristic features: a weakly developed axial sculpture, a proportionally high spire and short aperture, and, most importantly, smooth inside of the outer lip. Combined together these characters allow an easy recognition of *Turriplicifer* species from among other costellariids. The rather large, weakly sculptured shells in combination with the outer lip

lacking lirations resemble species of Mitridae, for example *Mitra glabra* Swainson, 1821, or *Mitra badia* Reeve, 1844; however, *Turriplicifer* stands apart by the prevalence of axial elements, although weak, in sculpture, and the characteristic intense coloration of the head-foot. One more attribute (found in *Turriplicifer australis* and *Turriplicifer esperancensis*, but usually absent or strongly corroded in adult specimens) of *Turriplicifer* gen. nov. is the bulbous paucispiral protoconch (Fig. 22F, G), which indicates non-planktotrophic larval development, a character state shared with co-occurring *Austromitra* species; however, the latter can be recognized by their smaller and proportionally broader shells.

GENUS **ORPHANOPUSIA** GEN. NOV. FEDOSOV,
HERRMANN & BOUCHET
FIGURE 23A–G

Type species: Voluta patriarchalis Gmelin, 1791.

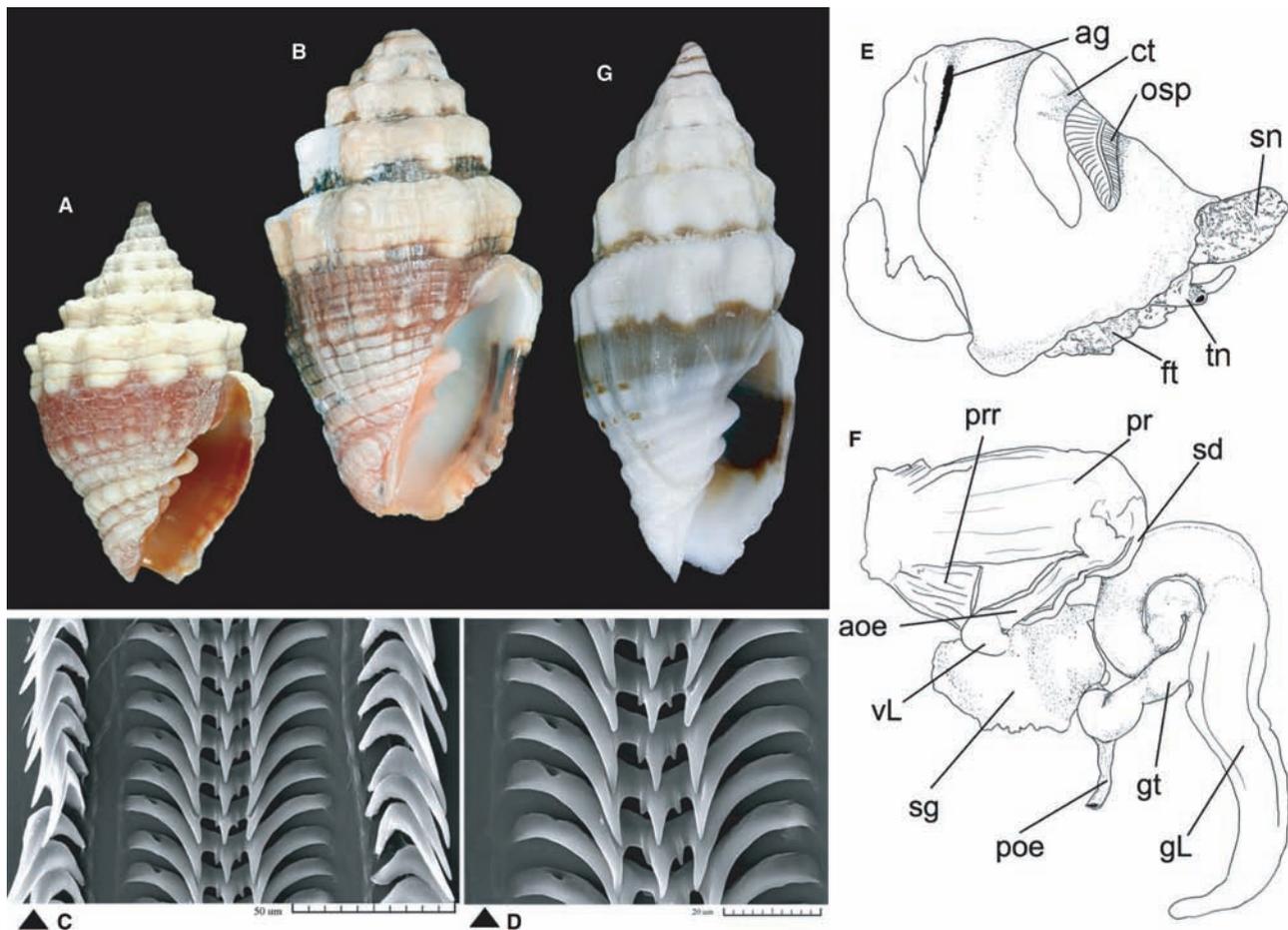


Figure 23. *Orphanopusia* gen. nov. A–F, *Orphanopusia patriarchalis*: A, MNHN IM-2013-10241, Papua Nuigini, station PS04, 05°10.0'S, 145°50.1'E, 12 m, 12.3 mm; B, Philippines, Bohol, off Noc-Nocan Island, 4–7 m, 20.9 mm; C–F, MNHN IM-2013-46644, KAVIENG 2014, station KS 03, 02°33,9'S, 150°46,7'E, 8–10 m; C, D, radula; E, general morphology of the body; F, foregut anatomy; G, *Orphanopusia osiridis* Egypt, Sinai peninsula, 23.5 mm, collection Manfred Herrmann.

Diagnosis

Shell small (about 20 mm, up to 35 mm), solid, broadly biconical, with strongly angulated whorls and robust base. Protoconch dark brown, pointed, with two or more smooth whorls. Teleoconch of between five and seven strongly shouldered whorls of about cylindrical outline. Sculpture of strong, widely spaced axial ribs, well pronounced at whorl periphery and vanishing below. Adapical portions of axial ribs form strong sharp tubercles, giving whorls a shouldered appearance. Spiral sculpture of fine deep grooves that are denser on shoulder slope and more widely spaced on shell base. Shell base very stout, with a row of gemmules about its mid-height. Siphonal canal short and very stout, deeply notched at its tip, sculptured with wide flattened cords somewhat tabulated in appearance. Aperture rather low and narrow. Outer lip thick, lirate within. Inner lip with three columellar folds, adapicalmost fold notably exceeding succeeding fold in strength.

Anatomy

Orphanopusia patriarchalis, MNHN IM-2013-46644, KAVIENG 2014, station KS03, 02°33.9'S, 150°46.7'E, 8–10 m (Fig. 23E, F).

Head-foot pale with multiple black freckles. Eyes situated laterally at base of long eye tentacles, distal portions of which are pale. Operculum absent. Proboscis cylindrical, rather long, occupying almost all the length of proboscis sheath. Proboscis retractors as in other costellariid species, i.e. two strong muscular bands attached laterally to anterior portion of rhynchodaeum. Radular sac occupying basal part of the proboscis. Oesophagus loop well pronounced, terminating at rather small, translucent valve of Leiglein. Salivary gland medium-sized, white, situated dorsally from mid-oesophagus and nerve ring. Paired salivary glands easily traceable, joining the oesophageal loop right in front of the valve of Leiblein and continuing inside the proboscis. Accessory salivary gland paired, compact, white, situated ventrally from salivary gland. Bulky gland of Leiblein reduced in size, light brown inside, covered by thick, semi-transparent layer of muscular fibres. Proximal part of the bulky gland of Leiblein opening into thick tubular secondary glandular structure, which forms several loops and opens in mid-oesophagus.

Radula (Fig. 23C, D): Rachidian tricuspidate, with bow-shaped, wide base and stout, moderately long, pointed cusps. Central cusp flanked by a pair of little accessory cusps. Laterals sickle shaped, unicuspid.

Included species

Orphanopusia patriarchalis (Gmelin, 1791) comb. nov. (Fig. 23A–F),¹ *Orphanopusia osiridis* (Issel, 1869) comb. nov. (Fig. 23G).²

Distribution and habitat

Tropical Indo-West Pacific, Red Sea down to Pennington, Natal, South Africa, (M. Marrow, pers. commun.), in shallow subtidal depths.

Etymology

The genus name refers to a solitary position of *Orphanopusia patriarchalis* in the phylogenetic tree, suggesting only a remote relationship to *Pusia*. Gender feminine.

Remarks

As the genus *Orphanopusia* is segregated primarily because of the molecular distinctiveness of '*Vexillum*' *patriarchale*, the definition of its contents is somewhat speculative as it is based solely on the shell. As *Pusia*-like shells were shown to have evolved convergently in several unrelated lineages of Costellariidae, we refrain from premature assignments; despite some species showing a resemblance to *Orphanopusia patriarchalis* – among them *Vexillum osiridis*, *Vexillum speciosum* (Reeve, 1844), and *Vexillum cavea* (Reeve, 1844) – only the former can be confidently assigned to *Orphanopusia*.

Orphanopusia gen. nov. combines the shell proportions of classical *Pusia* with some characteristics of the true *Vexillum*: principally, the deeply notched siphonal canal. At the same time, the robust shell with characteristic sculptural elements (tubercles on the axial ribs, row of gemmules on shell base, and 'tabulated' sculpture of cords on siphonal canal) allows for an easy recognition of *Orphanopusia patriarchalis* amongst other Costellariidae. Two mitre species, *Mitra bernhardina* Röding, 1798 and *Mitra tuberosa* Reeve, 1845, share a similar sculpture pattern and superficially resemble *Orphanopusia patriarchale*; however, in both species the spiral grooves are wider (comparable in width with spiral cords), and override the axial elements, and the axials either bear multiple weak tubercles (*Mitra tuberosa*) or bear a single strong tubercle, which is blunt and directed 'upwards' (*Mitra bernhardina*). Moreover, both mitrids have a narrower aperture.

GENUS *ATLANTILUX* HUANG, 2015
FIGURE 24A–H

Type species: Mitra exigua C.B. Adams, 1845 (OD).

Diagnosis: Shell small, not exceeding 12 mm, turritiform, elongate-fusiform to biconical, with rather wide aperture and stout siphonal canal. Protoconch wide, bulbous, of about 1.5 glossy, convex whorls, or papilliform, with three or more weakly convex whorls. Suture distinct, impressed. Teleoconch whorls typically with wide, slightly concave, subsutural area sculptured with dense, rounded axial riblets; riblets of similar morphology developed on shell base. Periphery strongly convex, typically situated below whorl mid-height, sculptured with strong and wide rounded ribs. Rarely, whorl outline flattened, and sculpture of two rows of nodules developed, one adapical, other situated at whorl periphery. Spiral sculpture absent or represented by regular fine threads throughout whorl height. Last adult whorl strongly convex, siphonal canal typically constricted to stout, sculptured with several strong oblique cords, formed by the continuation of the columellar folds. Siphonal notch shallow or indistinct. Aperture rather wide, outer lip lirate within. Inner lip bearing four narrow, subequal, oblique folds. Shell typically light- to dark-brown or olive green, or pink, with spiral white band on whorl periphery, often intersected by one or two fine brown threads; shell rarely uniform white. Head-foot and siphon dark grey or black, with multiple white and light-yellow spots. Tentacles rather long with eyes situated laterally at their bases. Radula with robust multicuspidate rachidian and sickle-shaped unicuspidate laterals.

Included species: Caribbean: *Atlantilux exigua* (C.B. Adams, 1845) (Fig. 24A, B);¹ *Atlantilux ampla* Huang, 2015;² *Atlantilux gemmata* (G.B. Sowerby II, 1874);² *Atlantilux narcisselli* Huang, 2015;² *Atlantilux puella* (Reeve, 1845) comb. nov. (Fig. 24C, D).¹

Indo-Pacific: *Atlantilux nodospicula* (Cernohorsky, 1970) comb. nov. (Fig. 24E);¹ *Atlantilux rubra* (Broderip, 1836) comb. nov. (Fig. 24F–H).¹

Distribution and habitat: Caribbean, intertidal and shallow subtidal depths; Indo-Pacific, shallow subtidal and bathyal depths.

Remarks: Typically *Atlantilux* can easily be recognized by its large bulbous protoconch in combination with a characteristic whorl profile, with wide, slightly concave subsutural ramp and whorl periphery shifted towards lower suture. A distinctive sculpture pattern, of dense riblets in subsutural area and notably wider folds on whorl periphery, is developed in *Atlantilux exigua*, *Atlantilux ampla*, and *Atlantilux narcisselli*, and is faint in *Atlantilux gemmata* (Redfern, 2013). These four species form a rather distinctive group that we consider to be 'typical' *Atlantilux* (as it includes the type species). One more Caribbean species, *Vexillum sykesi* (Melvill, 1925), has stronger spiral elements, but is

close overall to typical *Atlantilux* in shell proportions and whorl outline, and is likely to be closely related to the other four species mentioned.

A bulbous protoconch suggestive of non-planktonic development is also present in *Austromitra* and *Pusia* (*Ebenomitra*). *Austromitra* species can usually be distinguished from *Atlantilux* spp. by a weaker sculpture lacking spiral elements, and typically evenly convex whorls. Members of *Ebenomitra*, in addition to their weaker sculpture compared with *Atlantilux*, possess a tricuspidate rachidian, whereas it is multicuspidate in *Atlantilux*.

The Caribbean *Atlantilux puella*, and Indo-Pacific *Atlantilux nodospicula* and *Atlantilux rubra*, are conchologically very divergent from typical *Atlantilux*, and are placed here in *Atlantilux* based on currently available molecular data, and pending a more thorough phylogenetic analysis. The Indo-Pacific species assigned here to *Atlantilux* all have pointed, multi-whorled protoconchs, which readily differentiate them from the Caribbean species. (However, more Indo-Pacific species with paucispiral protoconchs currently placed in *Vexillum* may turn out to belong to *Atlantilux*.) The two species of *Atlantilux* recognized in our phylogenetic analysis differ notably from each other in sculpture and whorl profile, and some minute species of *Vexillum* (for example *Vexillum herosae* Herrmann & Salisbury, 2012; *Vexillum salisburyi* Cernohorsky, 1976, or *Vexillum altisuturatum* Chino & Herrmann 2014), fall well within the range of conchological variation for *Atlantilux*; however, *Vexillum herosae*, at least, is a true *Vexillum* based on our phylogenetic analysis. Further studies are needed to understand the extension and boundaries of *Atlantilux*.

GENUS AUSTROMITRA FINLAY, 1926

FIGURE 24I–M

Type species: *Columbella rubiginosa* Hutton, 1873 (OD).

Diagnosis

Shell small, usually not exceeding 10 mm, fusiform with rather wide aperture. Protoconch large and bulbous, paucispiral, of fewer than two glossy whorls. Suture distinct, impressed. Whorl outline evenly convex (usually) to distinctly angulated (rarely). Sculpture often represented by fine collabral growth lines only, in some species broad and sometimes strong axial folds developed on teleoconch whorls. Siphonal canal usually short and stout, sometimes moderately long, tapering, sculptured with between three and five oblique cords. Aperture rather wide, with three or four subequal oblique folds on inner lip. Dorsal



surface of foot with black patches; eye tentacles long. Radula with wide multicuspidate rachidian, bearing more than ten cusps of varying length, and

unicuspidate sickle-shaped laterals. Accessory salivary glands paired, rather large; mid-oesophagus notably widened, glandular. Gland of Leiblein rather

Figure 24. *Atlantilux* and *Austromitra* species. A, B, *Atlantilux exigua*, MNHN IM-2009-31184, Guadeloupe, KARUBENTHOS, station GS02, 16°20.942'N, 61°34.392'W, intertidal, 7.0 mm: A, shell; B, radula. C, D, *Atlantilux puella*, MNHN IM-2013-20368, KARUBENTHOS, station GM06, 16°09.0'N, 61°33.7'W, intertidal, 9.8 mm; C, shell; D, radula. E, *Atlantilux nodospicula*, MNHN IM-2013-40632, AURORA 2007, station CP2734, 15°57'N, 121°49'E, 453–460 m, 6.0 mm. F–H, *Atlantilux rubra*: F, *Tiara rubra*, syntype, NHMUK 1967867, 'Lord Hood's Is', 7.3 mm; G, MNHN IM-2013-1747, Papua Nuigini, station PB10, 05°17.9'S, 145°46.7'E, 10 m, 6.7 mm; H, radula (after Fedosov & Kantor, 2010). I, *Austromitra rubiginosa*, NMNZ M.052011, 36°16.00'S, 174°48.00'E, Goat Island Bay, Leigh, intertidal, 7.9 mm. K, *Austromitra* sp., MNHN IM-2013-40667, Western Australia, station WE03, 33°59.6'S, 122°13.33'E, 11 m, 6.2 mm. L, *Austromitra scita*, MNHN IM-2013-40673, Tasmania, station TA58, 41°07.55'S, 144°40.14'E, 1–4 m, 7.9 mm. M, N, *Austromitra vincta*, MNHN IM-2013-40671, Tasmania, station TA21, 42°59.93'S, 147°39.92'E, intertidal, 10.6 mm. M, shell; N, radula.

large, glandular, greenish brown (for a detailed anatomical description, see Ponder, 1972).

Included species

Austromitra rubiginosa (Hutton, 1873) (Fig. 24I),² *Austromitra aikenii* Lussi, 2015,² *Austromitra analogica* (Reeve, 1845),² *Austromitra angulata* (Suter, 1908),² *Austromitra arnoldi* (Verco, 1909),² *Austromitra bathyraphe* (G.B. Sowerby III, 1900),² *Austromitra bellapicta* (Verco, 1909),² *Austromitra canaliculata* (G.B. Sowerby III, 1900),² *Austromitra capensis* (Reeve, 1845),² *Austromitra cernohorskyi* Turner, 2008, *Austromitra cinnamomea* (A. Adams, 1855),² *Austromitra decresca* Simone & Cunha, 2012,² *Austromitra distincta* (Thiele, 1925),² *Austromitra euzonata* (G.B. Sowerby III, 1900),² *Austromitra graduspira* Lussi, 2015,² *Austromitra hayesi* Turner, 1999,² *Austromitra ima* (Bartsch, 1915),² *Austromitra kowieensis* (G.B. Sowerby III, 1901),² *Austromitra lausi* Finlay, 1930,² *Austromitra legrandi* (Tenison-Woods, 1876),² *Austromitra maculosa* Turner & Simone, 1998,² *Austromitra minutenodosa* Cernohorsky, 1980;² *Austromitra planata* (Hutton, 1885),² *Austromitra retrocurvata* (Verco, 1909),² *Austromitra rhodarion* Kilburn, 1972,² *Austromitra rosenbergi* Salisbury, 2015,² *Austromitra sansibarica* (Thiele, 1925),² *Austromitra schomburgki* (Angas, 1878),² *Austromitra scita* (Tenison-Woods, 1876) (Fig. 24L),¹ *Austromitra tasmanica* (Tenison-Woods, 1876),² *Austromitra valarieae* Lussi, 2015,² *Austromitra vincta* (A. Adams, 1855) (Fig. 24M, N),¹ *Austromitra volucra* (Hedley, 1915),¹ *Austromitra zafra* Powell, 1952.²

Distribution and habitat

Southern Australia, Tasmania, New Caledonia, New Zealand, and South Africa, up to Tanzania, in shallow water down to 450 m (M. Marrow, pers. commun.).

Remarks

The genus *Austromitra* is primarily distributed in the subtropical and warm temperate waters of the

Southern Hemisphere, where it co-occurs with *Turriplicifer* gen. nov. Both genera are characterized by a weakly developed spiral sculpture and a bulbous protoconch, indicating non-planktotrophic development. Their members can be distinguished by shell size (*Austromitra* being notably smaller than adult *Turriplicifer* gen. nov. species) and proportions (species of *Turriplicifer* gen. nov. have a rather turritiform shell with proportionally taller spire compared with *Austromitra*). Species of *Austromitra* are usually notably smaller than *Vexillum*, and can be readily distinguished from most costellariid taxa of the tropical Indo-Pacific by their weak sculpture with no spiral elements except those on the siphonal fasciole, and a characteristic paucispiral protoconch. In the detail of the shell sculpture and protoconch, *Austromitra* is close to species of *Atlantilux* from the Caribbean and *Pusia* (*Ebenomitra*) from the north-eastern Atlantic and Mediterranean. In common with *Austromitra*, both *Pusia* (*Ebenomitra*) and the Caribbean species of *Atlantilux* have a weakly developed spiral sculpture and possess a large paucispiral protoconch. Telling these three groups apart based on shell morphology is thus somewhat problematic. The radula with tricuspidate rachidian segregates *Pusia* (*Ebenomitra*) from both *Austromitra* and *Atlantilux*, which possess multicuspidate rachidians. In turn, *Atlantilux* demonstrates a characteristic sculpture pattern with dense and fine axial ribs in the adapical part of the whorls and on the shell base, whereas the whorl periphery is sculptured with notably stronger and wider elements. This pattern, in combination with whorl periphery shifted abapically, allows for a more or less straightforward recognition of Caribbean *Atlantilux* species and differentiates them from *Austromitra*.

GENUS VEXILLUM RÖDING, 1798

FIGURE 25

Type species: Vexillum plicatum Röding, 1798 (= *Voluta plicarium* Linnaeus, 1758) (SD, Woodring, 1928) (Fig. 25A).



Figure 25. Studied species of *Vexillum*: A, *Vexillum plicarium*, MNHN IM-2013-13646; B, *Vexillum gruneri*, MNHN IM-2007-30180; C, *Vexillum acupictum*, MNHN IM-2013-40635; D, *Vexillum lyratum*, MNHN IM-2007-30111; E, *Vexillum semifasciatum*, MNHN IM-2013-11594; F, *Vexillum costatum*, MNHN IM-2007-30005; G, *Vexillum exasperatum*, MNHN IM-2013-11680; H, *Vexillum radius*, Papua New Guinea, Hansa Bay, 8–12 m, 17.8 mm; I, *Vexillum* cf. *alvinobalani*, radula voucher R77, New Caledonia, EXBODI, station DW3860, 22°17'S, 169°01'E, 412–436 m, 24.6 mm; K, *Vexillum micra*, MNHN IM-2013-4734; L, *Vexillum infaustum*, MNHN IM-2007-30248; M, *Vexillum gloriae*, MNHN IM-2013-40634; N, *Vexillum pagodula*, MNHN IM-2007-30310; O, *Vexillum cancellarioides*, MNHN IM-2013-40631; P, *Vexillum ziervogelii*, MNHN IM-2013-15865; Q, *Vexillum woldemarii*, MNHN IM-2013-12694.

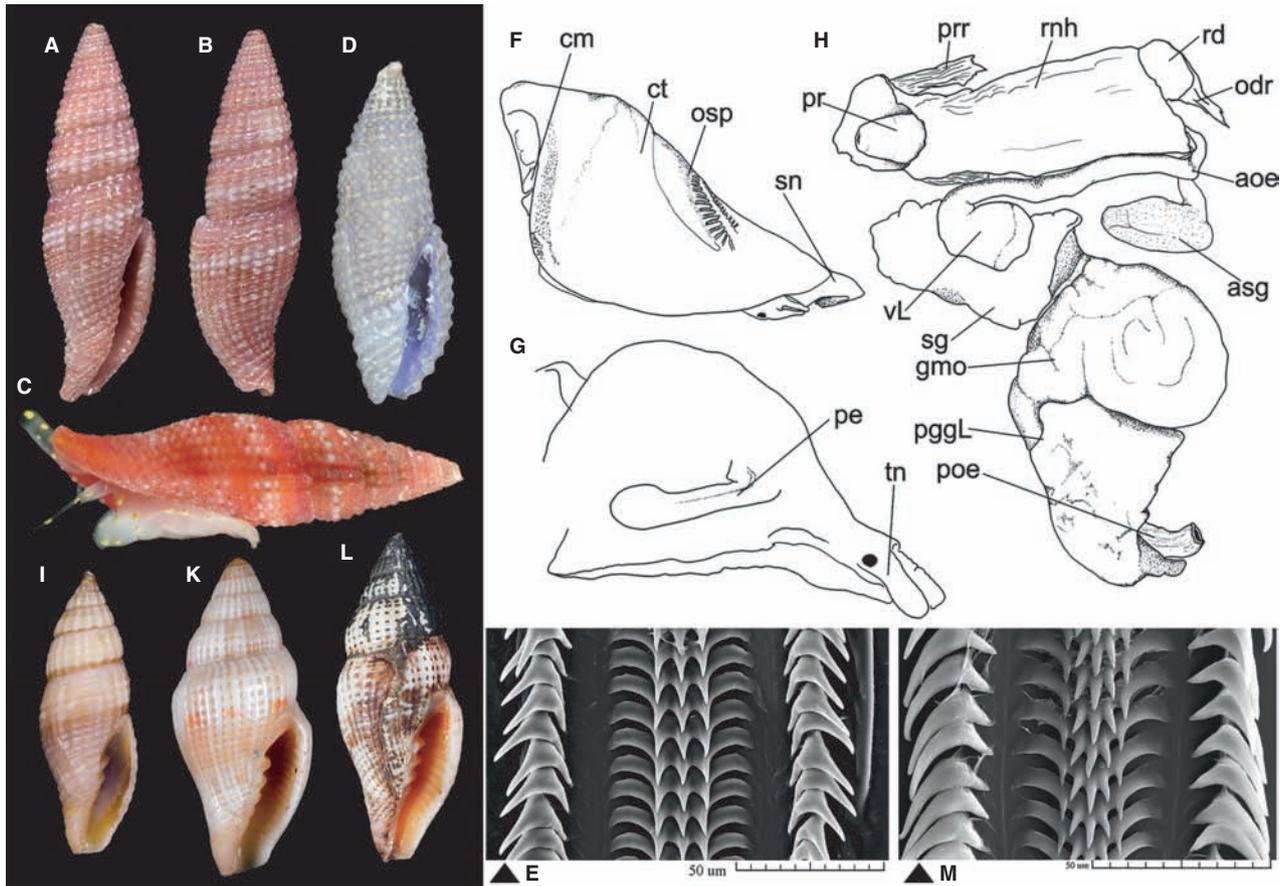


Figure 26. Morphology of the *Thala*–*Nodicostellaria* clade. A–C, *Thala mirifica*: A, B, *Mitra mirifica* Reeve, 1845, lectotype, NHMUK 1966655/1, ‘Isle of Capul, Philippines’, 10.8 mm; C, Vanuatu, Aore Island, SANTO 2006, station ZB16, 15°32.4’S, 167°12.1’E, 5 m, 10 mm. D–E, *Thala exilis*, MNHN IM-2013-3389: D, shell; E, radula. F–H, *Thala exilis*, MNHN IM-2013-55084: F, general morphology of the body; G, mantle removed; H, foregut anatomy; I, *Nodicostellaria kaicherae* holotype, USNM 780657, 17°25’S, 39°07’W, intertidal, 8.3 mm. K–M, *Nodicostellaria laterculata*: K, *Mitra laterculata* G.B. Sowerby II, 1874, syntype, NHMUK 1875.4.19.5, locality unknown, 13.9 mm. L, M, MNHN IM-2013-9022, Guadeloupe, KARUBENTHOS, station GR18, 16°05.8’N, 61°46.3’W, intertidal, 12.5 mm: L, shell; M, radula.

Synonyms

Arenimitra Iredale, 1929; type species *Mitra arenosa* Lamarck, 1811 (= *Voluta exasperata* Gmelin, 1791) (OD) (Fig. 25G);

Callithea Swainson, 1840 [invalid: junior homonym of *Callithea* Feisthamel, 1835 (Lepidoptera)]; *Pulchritima* Iredale, 1929 is a replacement name; type species *Mitra sanguisuga* Linnaeus, 1758 (SD: Herrmannsen, 1846: 155);

Costellaria Swainson, 1840; type species *Mitra rigida* Swainson, 1821 (= *Mitra semifasciata* Lamarck, 1811) (M) (Fig. 25E);

Mitropifex Iredale, 1929; type species *Mitropifex quasillus* Iredale, 1929 (= *Mitra obeliscus* Reeve, 1844) (M);

Pulchritima Iredale, 1929; type species *Mitra sanguisuga* Linnaeus, 1758 (by typification of replaced name);

Tiara Swainson, 1831; type species *Mitra corrugata* Lamarck, 1811 (= *Voluta rugosa* Gmelin, 1791) (SD: Gray, 1847: 142);

Turricula H. & A. Adams, 1853; (invalid: junior homonym of *Turricula* Schumacher, 1817); type species *Voluta vulpecula* Linnaeus, 1758 (SD: Cossmann, 1899: 162);

Vulpecula Blainville, 1824; type species *Voluta vulpecula* Linnaeus, 1758 (T);

Zierliana Gray, 1847; type species *Voluta ziervogelii* Gmelin, 1791 (OD) (Fig. 25H).

Diagnosis

Shell small to medium-sized, fusiform or broadly fusiform to turritiform, ovate or biconical; spire very tall to low. Protoconch tall, conical, whitish or brown, translucent, with three or more evenly convex glossy whorls. Teleoconch whorls evenly convex to



subcylindrical or with flattened outline, typically distinctly shouldered. Sculpture dominated by axial elements, represented by ribs of varying strength, sharp or rounded, usually slightly undulating. Spiral sculpture variable, absent in some species, in others

represented by fine, evenly spaced grooves, pronounced between axial ribs, or throughout shell surface, overriding axial ribs. Siphonal canal short to very long, straight and tapering or recurved at its tip, notched at its end. Aperture elongate, narrow;

Figure 27. *Ceratoxancus* and *Latiromitra* species. A, *Ceratoxancus teramachii*, MNHN IM-2007-33280, New Caledonia, Chesterfield Plateau, EBISCO, station DW2610, 19°33.15'S, 158°40.6'E, 486–494 m. B, *Ceratoxancus basileus* Kantor & Bouchet, 1997, holotype, MNHN IM-2000-22945, SMIB 2, station DW18b, 22°58'S, 167°20'E, 530–535 m, 56.1 mm. C, *Ceratoxancus leios* Kantor & Bouchet, 1997, holotype, MNHN IM-2000-30254, New Caledonia, Norfolk Ridge, SMIB 4, station DW39, 24°56'S, 168°22'E, 525–560 m, 21.0 mm. D, *Ceratoxancus lorenzi* Poppe, Tagaro & Sarino, 2012, holotype, MNHN IM-2000-26953, Philippines, off Balut Island, 250–300 m, 30.8 mm. E, *Ceratoxancus melichrous* Kantor & Bouchet, 1997, holotype, MNHN IM-2000-22946, New Caledonia, Norfolk Ridge, SMIB 4, station DW39, 24°56'S, 168°22'E, 525–560 m, 20.4 mm. F, *Ceratoxancus niveus* Kantor & Bouchet, 1997, holotype, MNHN IM-2000-22948, New Caledonia, Norfolk ridge, Biocal, station DW51, 23°05'S, 167°45'E, 680–700 m, 8.8 mm. G, H, syntypes of *Mitra cryptodon*, off Morocco, 33°09'N, 09°38'W, 1900 m, 30.0 mm. I, *Latiromitra crosnieri* Bouchet & Kantor, 2000a,b; holotype, off north-west Madagascar, station 118, 12°49'S, 48°27'E, 925–975 m, 41.2 mm. K, *Latiromitra paiciorum* Bouchet & Kantor, 2000a,b, holotype, New Caledonia, off Cape Bayes, Bathus 1, station CP661, 21°05'S, 165°50'E, 960–1100 m, 25.1 mm.

outer aperture lip lirate within, sometimes with strong denticles formed by lirae at outer lip's edge. Inner aperture lip with three or four distinct, sometimes very strong columellar folds, uppermost fold strongest. Radula with wide bow-shaped rachidian, typically bearing multiple pointed cusps and unicuspidate sickle-shaped or subtriangular laterals. Accessory salivary gland usually present, very small. Bulky gland of Leiblein strongly reduced, whitish, non-glandular, situated at distal part of long and strongly convoluted secondary glandular structure. Seminal groove closed along its entire length.

Distribution and habitat

Common throughout the Indo-Pacific from Madagascar to French Polynesia. From intertidal to bathyal depths, on sand, mud, coral rubble, or reefs.

Remarks

The remarkable diversity of shell sizes, shapes, and sculpture patterns in *Vexillum* make the circumscription of the genus a not trivial task. The slender, narrowly fusiform shell of *Vexillum radius* (Fig. 25H) has little in common with the robust and heavily sculptured *Vexillum cancellarioides* (Fig. 25O), or the species traditionally included in *Zierliana* (Fig. 25P, Q), with their peculiar dentition of aperture. This diversity of shell forms, however, reflects the diversity of ecological conditions where species of *Vexillum* live. Whereas typical *Vexillum* species can be encountered in numbers on sand or muddy bottoms, a broad and robust 'Pusia-like' shell is commonly observed in species that inhabit rocky shores and intertidal pockets in the reef. The heavily armoured aperture of the species traditionally placed in *Zierliana* most likely evolved in response to intense predation pressure. A similar aperture characterizes *Atlantilux puella*, which is unrelated to the *Zierliana* lineage, and also inhabits intertidal rocky flats. We also presume that the distinct siphonal notch, shared by the vast majority of *Vexillum* species, appeared as an adaptation to burrowing in sediment, as in many other neogastropod sand dwellers,

among them mitrids, olivids, terebrids, etc. On the contrary, the radula of numerous *Vexillum* species remains strikingly conservative, and the variations in foregut anatomy are also rather moderate, compared with the extensive conchological disparity; the function of apomorphic costellariid foregut structures is discussed below.

DISCUSSION

MORPHOLOGICAL EVOLUTION

In general, the evolutionary history of the Costellariidae appears to be unidirectional, from the early diverging *Ceratoxancus* and *Latiromitra* to the most recent *Vexillum*. Based on morphological characters presented earlier (Fedosov & Kantor, 2010; Fedosov *et al.*, 2015), the ancestral and derived character states of the radula, gland of Leiblein, and male reproductive system had been proposed intuitively: those found in *Ceratoxancus* and *Latiromitra* were considered ancestral, and those in *Vexillum* were derived. Our initial hypothesis suggested that transformation would mostly follow the same general scenario, with a one-time switch from ancestral to derived condition that could be easily mapped on the inferred nodes of the molecular tree. We thus expected that the Costellariidae groups would show a row with progressively more derived morphologies aligned along a (*Ceratoxancus*–*Latiromitra*)–*Vexillum* axis; however, as the analysis of a larger morphological data set was performed, it turned out that strictly speaking not one character evolved consistently with the expected scenario.

Thus, despite general trends in the evolution of costellariid morphology being apparent, only a few of the revealed apomorphic character states can be unequivocally attributed to the inferred phylogenetic groupings of the Costellariidae. One prominent costellariid innovation is the multicuspidate rachidian, which is an apomorphy of the *Vexillum*–*Austromitra*–*Atlantilux* clade (although this clade lacks support), and may also prove to be an apomorphy of



Figure 28. Type species of other Costellariidae genera not covered by our phylogenetic studies: A, *Mitromica solitaria*, holotype of *Mitra solitaria*, MCZ 186351, Panama, 17 mm; B, *Protoelongata dekkersi*, holotype, MNHN 27068, Philippines, Panglao Island, off Catarman, 9°36'N, 123°52'E, reef slope with caves, 4–30 m, 12.4 mm; C, *Suluspira rosenbergi*, holotype of *Visaya rosenbergi* (NMP), Philippines, off Aliguai Island, 60–120 m, 18 mm; D, *Thaluta maxmarrowi* Collection Conchology Inc. Philippines, Silijor Island, off Tubod, 52 m, 7.1 mm; E, *Turricostellaria lindae*, holotype, USNM 859870, Colombia, Guajira Peninsula, off Cabo La Vela, 35 m, 18.3 mm.

the New World genus *Nodicostellaria*. A key apomorphy, which characterizes the genus *Vexillum*, is a tubular secondary gland of Leiblein. The extremely rich evolutionary radiation of the genus *Vexillum* might be a result of these two morphological innovations that characterize the genus and appear to have been independently acquired in other costellariids (the tubular compartment of the gland of Leiblein in *Turriplificifer australis* and *Orphanopusia patriarchalis*; and the multicuspidate rachidian in *Nodicostellaria laterculata*). The secretory function of the tubular secondary gland of Leiblein in *Vexillum* seems very likely. Although the nature of the secretion remains unknown, its role in feeding may be substantial, given the impressive size of the gland in some species (see Fedosov & Kantor, 2010).

The development of a complex chemical weaponry by unrelated neogastropod lineages is becoming increasingly well documented (Olivera, 2002; Imperial *et al.*, 2007; Modica *et al.*, 2015), and most likely the evolution of a novel secretory structure by *Vexillum* species was a prerequisite for the development of their own complement of bioactive compounds. Little is known about the feeding biology of *Vexillum*, although the available data suggest that they are active predators, feeding on other molluscs (Taylor

et al., 1980). The first author recently observed (unpublished) a specimen of *Vexillum gloriae* Poppe, Tagaro & Salisbury, 2009 devouring a venerid bivalve, and an earlier study reported *Vexillum* species feeding on other gastropods (Fedosov & Kantor, 2010). Thus, it is likely that *Vexillum* species use a secretion of their mid-oesophageal gland in a predator–prey interaction in a similar manner to conoideans and *Colubraria*.

Fedosov & Kantor (2010) pointed at some anatomical features in the foregut of *Vexillum* that may preclude the use of the tubular gland of Leiblein secretion to penetrate the prey body. The gland of Leiblein opens in the oesophagus behind the valve of Leiblein, which is well developed in all costellariids studied. This latter structure indeed resembles a valve both morphologically (Kantor & Fedosov, 2009) and functionally. It is thought to facilitate a unidirectional movement of food particles and to prevent regurgitation as the proboscis extends and contracts during feeding. As a result of its morphology, the valve of Leiblein may preclude the transportation of the gland of Leiblein's secretion into the anterior oesophagus, especially if the quick release of a considerable volume of the secretion is required to subdue the prey (Fedosov & Kantor, 2010).

The conoidean venom gland, which is also believed to originate from the mid-gut gland (Ponder, 1973; Kantor, 2002), underwent a progressive transformation, and it opens in the posterior part of the buccal mass in all Conoidea studied (Kantor, 2002). Furthermore, almost all conoideans studied morphologically have no valve of Leiblein, which can be considered a result of the shortening and reduction of the anterior oesophagus, enabling an efficient envenomation. Resulting from this rearrangement of the mid-oesophagus, the venom gland of all Conoidea (with the exception of the Cochlespiridae; Yu. Kantor, pers. commun.) passes through the nerve ring before it opens into the buccal mass (Taylor, Kantor & Sysoev, 1993), unlike the tubular gland of Leiblein in *Vexillum*.

Recent studies on the fine morphology of the valve of Leiblein and the following stretch of the mid-oesophagus in some neogastropods described certain morphological features that may provide a mechanism to bypass the valve, thus allowing for the passage of secretion from the gland of Leiblein to the anterior oesophagus. A so-called 'siphon', which connects the gland of Leiblein and the valve of Leiblein, has been found in some muricoidean species, *Nucella* sp. (Andrews & Thorogood, 2005) and *Tenguella marginalba* (Blainville, 1832) (= *Morula marginalba*) (Muricidae), as well as in *Columbarium pagodoides* (Watson, 1882) (Columbariidae) (Golding & Ponder, 2010). Essentially, the siphon comprises a narrow ventral groove, bordered by tall glandular dorsal folds on the inner surface of the mid-oesophagus. Remarkably, the circular fold of the valve is interrupted ventrally, matching the position of the siphon (Golding & Ponder, 2010), thus forming a continuous canal from the opening of the gland of Leiblein to the anterior oesophagus.

Although the suggested functions of the tubular secondary gland of Leiblein seem likely, the adaptive value of the multicuspidate rachidian is rather disputable. On one hand, the repeated appearance of a multicuspidate rachidian within Costellariidae – a notably similar radula is found in the pseudolivid genus *Benthobia* (Simone, 2003) – seems to point to its adaptive value. On the other hand, we lack data on how the radula performs during feeding. The radula in most species of *Vexillum* is situated at mid-length of the proboscis, or even shifted towards its base, and it is not apparent if the mollusc everts its radular apparatus while feeding. Although the adaptive value of the multicuspidate rachidian tooth is not established, some alternative explanations are possible. It cannot be excluded, for example, that the multiple cusps of the rachidian do not have their own adaptive significance, but are a 'side effect' of the widening of the rachidian, as is

observed in *Vexillum*. Whereas the absolute width of the rachidian varies notably, depending on the size of the species, the rachidian width/radula width ratio is more consistent, and is different in *Vexillum* (0.49–0.59) and in costellariids with a tricuspidate rachidian (0.30–0.45), which may infer differences in the mechanisms of tooth secretion. Further studies on the functional morphology of *Vexillum* are needed in order to characterize its feeding mechanism, and in particular to establish the role of radula.

The reduction of the operculum in the evolution of the Costellariidae is paralleled by similar trends observed in Olividae, Mitridae, Cancellariidae, and Marginellidae: other major neogastropod lineages that developed strong columellar folds. Strong operculum or columellar folds can be seen as two different strategies to reduce the risk of predation by crabs. Some neogastropod groups possess both: a distinct operculum, although reduced in size; and weak columellar folds (for example in species of Volutidae, *Ceratoxancus*, and *Latiromitra*).

Finally, the closure of the seminal canal can be observed in most neogastropod taxa, and for this reason cannot be regarded an apomorphy of the Costellariidae.

NEW TAXONOMIC COMPOSITION OF THE COSTELLARIIDAE

Based on the analysis of an unprecedented molecular data set and the examination of vast – dry and wet – collections, we revise relationships within the Costellariidae and establish a new taxonomy of the family, which is consistent with the phylogenetic relationships revealed. There are still gaps in the proposed taxonomy, as the costellariid genera of the New World remain essentially unrevised; nevertheless the Indo-Pacific and Atlantic groups that comprise over 90% of costellariid species diversity are well covered. In the present section we give a short summary of the noteworthy innovations in costellariid taxonomy.

We erect four new genera (*Alisimitra* gen. nov., *Costapex* gen. nov., *Turriplificifer* gen. nov., and *Orphanopusia* gen. nov.) and two genera (*Ceratoxancus* and *Latiromitra*) are transferred from the Ptychatractidae to the Costellariidae (Fig. 26). *Tosapusia* is restored from synonymy and treated as a full genus. We dismiss the traditional subgenus *Vexillum* (*Costellaria*) merely as a junior synonym of *Vexillum*. Two former subgenera of *Vexillum*, *Protoelongata* and *Pusia*, are elevated to full generic rank, the latter with three subgenera. We restore *Ebenomitra*, which we treat as a subgenus of *Pusia*, and describe the new subgenus *Pusia* (*Vexillena*). The replacement name *Suluspira* is suggested for

Visaya Poppe, Guillot de Suduiraut & Tagaro, 2006 to resolve homonymy.

Thus we recognize 18 genera (and three subgenera) within the family Costellariidae, which adds seven genera to the current classification (WoRMS). The six genera *Ceratoxancus*, *Latiromitra*, *Tosapusia*, *Alisimitra*, *Costapex*, and *Turricostellaria*, and the subgenus *Pusia* (*Vexillena*), comprise exclusively deep-water forms. With 14 new species described and four genus-level groups established for the deep-water costellariids, our study showcases the contribution of the deep-water members to the diversity of the family. Whereas deep-water Costellariidae in most cases form distinctive phylogenetic lineages, both deep- and shallow-water members are found in *Vexillum*.

EVOLUTIONARY HISTORY AND DISTRIBUTION OF THE COSTELLARIDAE

One of the important results of our work is that all the early-diverging costellariid lineages, as well as the neogastropod groups that are found closest to Costellariidae, are exclusively deep-water groups. This result suggests two explanations: either the Costellariidae originated in deep water, and the colonization of shallow water, which could have been connected with the major radiation of Costellariidae, and in particular of *Vexillum*, took place later during geological time; or, alternatively, the multiple deep-water lineages are relictual descendants of extinct, primarily shallow-water, taxa. Our results are consistent with a single shallow-water invasion event, which seems more parsimonious to us, as all the shallow-water Costellariidae form a single clade, with *Thala*-*Nodicostellaria* being the first offshoot of the shallow-water costellariid radiation; however, the lack of support at node 4 indicates that other scenarios cannot be excluded.

There are no studies on the morphology of the Indo-Pacific *Thala* and, in fact, of the whole *Thala*-*Nodicostellaria* clade; thus, a specimen of *Thala exilis* (MNHN IM-2013-55084), conspecific with the sequenced specimen (MNHN IM-2013-3389; Fig. 26D, E), was dissected (Fig. 25F-H), and the radulae of *Thala exilis* (MNHN IM-2013-3389; Fig. 26E) and *Nodicostellaria laterculata* (MNHN IM-2013-9022; Fig. 26L, M) were examined.

Interestingly, all Caribbean costellariids studied in respect of radular morphology share a multicuspitate rachidian. In addition to *Nodicostellaria laterculata* and *Vexillum puella* (molecular data for which are presented here), we dissected *Vexillum sykesi*, *Atlantilux exigua*, and an undescribed species referable to *Turricostellaria* from deep water of the Gulf of Mexico; the radular morphology of *Mitromica floridana* was published by [Maes & Raeihle \(1975\)](#).

Vexillum sykesi, *Atlantilux exigua*, and *Atlantilux puella* possess a true multicuspitate rachidian bearing more than ten equal cusps (Fig. 24B, D), whereas the rachidian in the other three species bear between five and seven cusps only. In this connection, it should be noted that the two Caribbean species included in our analysis did not form a single clade, but appeared not closely related to each other. Hence the Western Atlantic Costellariidae represent at least three unrelated lineages, of which one is referable to *Atlantilux*, the second shows an affinity to the Indo-Pacific *Thala* (both sharing a rachidian of advanced morphology), and the third lineage represents the genus *Latiromitra* (Fig. 27G, H).

The second lineage deserves a specific comment. The genus *Thala* is widely distributed across the Pacific, and reaches West America, with at least three species recorded from the coast of California, in the north, to the Galapagos Islands, in the south ([Sphon, 1969](#)). Despite West American species being close to 'classical' *Thala* in shell morphology, [Berry \(1958\)](#) introduced the genus *Mitromica* for them, justified by minor conchological peculiarities ([McLean, 1967](#); [Sphon, 1969](#)). The differences between the two genera as summarized by [Rosenberg & Salisbury \(2003\)](#) seem subtle and unconvincing, and the status of *Mitromica* should be validated by molecular studies, but a close affinity between Indo-Pacific species of *Thala* and New World *Mitromica* is nevertheless most probable. The examination of radular structure in *Mitromica solitaria* (C.B. Adams, 1852) (Fig. 28) from the Galapagos ([McLean, 1967](#)) revealed a rachidian with seven equal cusps, similar to what we found in *Nodicostellaria laterculata*. Thus, having a snapshot of the radular morphologies across New World costellariid lineages, we would not be surprised if future studies uncover a close relationship between *Mitromica*, *Nodicostellaria*, and possibly *Turricostellaria*, with *Thala* being the closest Indo-Pacific relative of this American lineage. One of the interesting implications of this relationship would be that the main New World costellariid radiation is not related to *Vexillum*, which literally dominates the Indo-Pacific. Obviously, further studies based on broader sampling in West Atlantic and East Pacific waters are needed to determine the affinities of the New World lineages.

Whereas the tropical Indo-Pacific is apparently the centre of costellariid species diversity, and also the Central Indo-West Pacific has the highest genus diversity, three groups have successfully adapted to temperate waters. *Austromitra* and *Turriplificifer* gen. nov. of the southern hemisphere, and *Pusia* (*Ebenomitra*) of the northern hemisphere, include a total of ~40 currently accepted species that are distributed primarily in subtropical/warm temperate

waters. As is the case with many temperate-water gastropod taxa with presumed tropical ancestry (Thorson, 1950; Pappalardo, Rodríguez-Serrano & Fernández, 2014), all three costellariid radiations have lost planktotrophic larval development. As a consequence of the loss of the dispersal phase, one would expect restricted distribution ranges (Jablonski & Lutz, 1983; Castelin *et al.*, 2011). If the delimitation among the four species of the Mediterranean and Eastern Atlantic *Ebenomitra* seems rather straightforward, the taxonomic extension of *Austromitra* may be greatly misunderstood. The species conventionally assigned to *Austromitra* occur in the Recent faunas of southern Australia, New Caledonia, and New Zealand, as well as in South Africa (Cernohorsky, 1970, 1980; Lussi, 2015). In the present study we examined four *Austromitra* species from southern Australia and Tasmania, and found that although all four form a clade, *Austromitra* sp. collected off Esperance (Western Australia) is notably divergent from the three Tasmanian species. Even if we assume that the *Austromitra* species from Australia and New Zealand are the descendants of a single radiation, their relationship to species from South Africa is still to be confirmed.

It is noteworthy that a switch to non-planktotrophic development can also be recorded in some costellariid genera from tropical waters. Similar to three subtropical costellariid genera, all Caribbean species of *Atlantilux* possess protoconchs indicating non-planktotrophic development. The two bathyal genera *Ceratoxancus* and *Latiromitra* (Kantor & Bouchet, 1997; Bouchet & Kantor 2000a), as well as shallow-water *Thala* (Rosenberg & Salisbury, 2007, 2014), include both representatives with planktotrophic and with non-planktotrophic development, as inferred from the morphology of their protoconchs. Rosenberg & Salisbury (2014) found a general correlation between the mode of development and the extent of the distribution range in *Thala*, and suggested a high proportion of local endemics in the genus. Such variation in the mode of development was demonstrated in our earlier studies on Conoidea (Puillandre *et al.*, 2010; Fedosov & Puillandre, 2012).

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