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Monograph

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Pseudolatirus Bellardi, 1884 revisited, with the description of two new genera and five new species (Neogastropoda: Fasciolariidae)

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Abstract. The genus *Pseudolatirus* Bellardi, 1884, with the Miocene type species *Fusus bilineatus* Hörnes, 1853, has been used for 13 Miocene to Early Pleistocene fossil species and eight Recent species and has traditionally been placed in the fasciolariid subfamily Peristerniinae Tryon, 1880. Although the fossil species are apparently peristerniines, the Recent species were in their majority suspected to be most closely related to *Granulifusus* Kuroda & Habe, 1954 in the subfamily Fusininae Wrigley, 1927. Their close affinity was confirmed by the molecular phylogenetic analysis of Couto *et al.* (2016). In the molecular phylogenetic section we present a more detailed analysis of the relationships of 10 Recent *Pseudolatirus*-like species, erect two new fusinine genera, *Okutanius* gen. nov. (type species *Fusolatirus kuroseanus* Okutani, 1975) and *Vermeijius* gen. nov. (type species *Pseudolatirus pallidus* Kuroda & Habe, 1961). Five species are described as new for science, three of them are based on sequenced specimens (*Granulifusus annae* sp. nov., *G. norfolkensis* sp. nov., *Okutanius ellenae* gen. et sp. nov.) and two (*G. tatianae* sp. nov., *G. guidoi* sp. nov.) are attributed to *Granulifusus* on the basis of conchological similarities to sequenced species. New data on radular morphology is presented for examined species.

Keywords. Gastropod, Fasciolariidae, *Pseudolatirus*, molecular phylogeny, new genera, new species, Southwest Pacific.

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Introduction

The species of Fasciolariidae inhabit warm temperate to tropical seas, mostly in intertidal and offshore subtidal depths, with some genera having radiated into deeper water (e.g., *Granulifusus* Kuroda & Habe, 1954 and *Amiantofusus* Fraussen, Kantor & Hadorn, 2007). Most fasciolariids form rather sparse populations and are usually represented in museum collections by lots with one or just a few specimens, making it difficult to assess the value of characters in terms of within-population and between-population variation. The taxonomy of Fasciolariidae up to present has been based mostly on shell and, to a lesser extent, radula characters. In many cases attribution of species to genera and genera to subfamilies is done by tradition, without an explicit discussion of the values of these characters. Only recently the phylogeny of the entire family was addressed from a molecular point of view, with the first multilocus molecular tree of Fasciolariidae (Couto *et al.* 2016), resulting in drastic changes in the composition of the three currently recognized subfamilies. In particular, the subfamily Peristerniinae Tryon, 1880 appeared to be restricted to *Peristernia* Mörch, 1852 (non-monophyletic) and *Fusolatirus* Kuroda & Habe, 1971. Most of the formerly peristerniine genera ended up in Fasciolariinae Gray, 1853, while the Recent species assigned to *Pseudolatirus* Bellardi, 1884 ended up in Fusininae Wrigley, 1927. Six species referrable to *Pseudolatirus* on the basis of shell characters were included in the analysis of Couto *et al.* (2016) and they formed three separate clades, not closely related to each other. This result indicated that further molecular studies were needed to clarify the affinities of *Pseudolatirus*-like species, and consider their proper taxonomic treatment.

As conceived by Bellardi (1884), the genus *Pseudolatirus* comprised the type species (by subsequent designation by Cossmann 1901: 24) *Fusus bilineatus* Hörnes, 1853 (Miocene of central Europe) and seven additional Miocene and Pliocene European species: *Latirus* (*Peristernia*) *cognatus* Bellardi, 1884; *Latirus* (*Pseudolatirus*) *concinnus* Bellardi, 1884; *Fasciolaria costata* (Bellardi & Michelotti, 1840) [renamed *Fasciolaria subcostata* by d'Orbigny (1852)]; *Latirus* (*Pseudolatirus*) *fornicatus* Bellardi, 1884; *Latirus* (*Pseudolatirus*) *ligusticus* Bellardi, 1884; *Latirus* (*Pseudolatirus*) *pinensis* Bellardi, 1884 and *Pseudolathyrus rarocingulata* (Foresti, 1876). *Pseudolathyrus* Cossmann, 1901, is an unjustified emendation and thus an objective synonym of *Pseudolatirus*. Subsequently, five Late Miocene to Pleistocene species from Indonesia and Japan were further included in *Pseudolatirus*: *Pseudolathyrus burcki* Koperberg, 1931; *Pseudolathyrus esi* Koperberg, 1931; *Colus (?) teschi* Finlay, 1927 (new name for *Latirus fusiformis* Tesch, 1915); *Latirus gerthi* Wanner & Hahn, 1935 and *Pseudolatirus yonabaruensis* MacNeil, 1961 (Koperberg 1931; Finlay 1927; Wanner & Hahn 1935; MacNeil 1961). Shutō (1969: 150) reported *P. esi* from the Neogene of Panay, Philippine Islands, and noted its similarity to *P. gerthi*; he also reported *P. teschi* from the same deposits and noted that it was allied to *P. burcki*. Finally, MacNeil (1961: 83) noted that *P. burcki*, *P. esi* and *P. teschi* all resemble *P. yonabaruensis* described from the Late Miocene of Okinawa, a species subsequently reported by Robba *et al.* (1989: 80) from the Early Pleistocene of Timor (Indonesia). A careful examination of these species leads us to conclude that they probably all represent a single widely-distributed and variable species, which we attribute to *Pseudolatirus* and for which the valid name would be *Pseudolatirus teschi* (Finlay, 1927).

Seven Recent species are currently assigned to *Pseudolatirus* of which five were originally described as members of the genus: *Pseudolatirus discrepans* Kuroda & Habe, 1961; *Pseudolatirus pallidus* Kuroda & Habe, 1961; *Pseudolatirus kurodai* Okutani & Sakurai, 1964; *Fusolatirus kuroseanus* Okutani, 1975; *Pseudolatirus leucostriatus* Kosuge, 1979; *Pseudolatirus aikeni* Lussi, 2014 and *Pseudolatirus*

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jeanpierrevezzaroi Cossignani, 2017. In the original descriptions the generic position of these species was neither justified nor discussed and these assignments were based solely on shell characters.

Only a fraction of the available material was used in the molecular phylogeny of Couto *et al.* (2016) and we have material of several additional species attributed or attributable to *'Pseudolatirus'* as currently recognized that is appropriate for molecular studies. The purpose of the present paper, based on a phylogenetic analysis of an extended molecular dataset of the Fusininae, is to critically re-assess the position of the Recent species that were assigned to *Pseudolatirus*. Molecular phylogeny combined with morphological studies lead to the recognition of previously unrecognized lineages of Fusininae; which are formally described herein.

Material and methods

Our study is based on considerably more material than was available to workers before us, and it comes essentially from two sources: material from deep-water oceanographic expeditions in the Indo-West Pacific over the last 40 years or so (MNHN), and material originating from tangle nets and other commercial operations in the Philippines (ex M.A. Snyder' S Collection, now in ANSP). Background information on the expeditions, with narratives of the cruises, station lists, maps, etc. can be found in Richer de Forges (1990, 1991, 1993) and Richer de Forges & Chevillon (1996: New Caledonia cruises), Richer de Forges & Menou (1993: MUSORSTOM 7 cruise to Wallis and Futuna) and Richer de Forges *et al.* (1996: MUSORSTOM 8 cruise to Vanuatu, 1999: MUSORSTOM 9 cruise to the Marquesas, 2000a and 2000b: Fiji cruises). As a result of these expeditions, over 800 new species of molluscs have been described from the deep waters off New Caledonia alone (Héros *et al.* 2016).

Specimens from the general collection of MNHN are mostly uncatalogued. Part of the material was specifically preserved for molecular studies and each of those specimens bears a unique registration number, as do the type specimens. In the text we present registration numbers for every catalogued specimen and mention whether it was sequenced or not.

Taxon sampling

Material for molecular studies was collected in New Caledonia, the Solomon Islands, Papua New Guinea, Madagascar, Taiwan and Vanuatu in a series of deep water cruises (Table 1). Until 2012, live specimens for molecular analysis were anaesthetized with an isotonic solution of $MgCl_2$ and fixed in 96% ethanol. Specimens collected during later expeditions were processed with a microwave oven (Galindo *et al.* 2014): the living molluscs in small volumes of sea water were exposed to microwaves for 7–30 seconds, depending on specimen size. Bodies were immediately removed from shells and placed in 96% ethanol. Specimens were registered in the MNHN collection and sequences were deposited in BOLD (Barcode of Life Datasystem) and GenBank (Table 1). The GenBank accession numbers are provided for corresponding genes in the last three columns in Table 1.

Radulae were prepared by standard methods (Kantor & Puillandre 2012) and examined with scanning electron microscope TeScan TS5130MM at the Institute of Ecology and Evolution of Russian Academy of Sciences (IEE RAS).

DNA extraction and PCR

Total genomic DNA was extracted from foot muscle tissue using either NucleoSpinR 96 Tissues (Macherey–Nagel) reagent kit, or Thermo Scientific GeneJET Genomic DNA Purification 50 Kit following the manufacturer's instructions. Fragments of the mitochondrial gene Cytochrome Oxidase I (COI) as well as of the nuclear genes 28S rRNA and H3 were amplified. Standard pairs of primers: LCO1490 and HCO2198 (Folmer *et al.* 1994) for COI, C1 and D2 (Jovelin & Justine 2001) for 28S

Table 1. List of sequenced specimens analyzed. Original sequences highlighted in bold typeface. The three last columns include the GenBank numbers.

Specimen ID	Family/Sub-family	Genus species	Expedition	Station	Collection data	BOLD	COI	28S	H3
MNHN IM-2007-36620	Buccinidae	*Manaria formosa* Bouchet & Warén, 1986	MIRIKY	CP3290	Madagascar, near Narendry Bay, 14°29′26″ S, 47°26′17″ E, 409–425 m	FASCI008-17	**MG838141**	**MG936635**	**MG838011**
MNHN IM-2007-38241	Buccinidae	Gen. sp.	MIRIKY	CP3250	Madagascar, off Majumga, 15°21′39″ S, 46°0′24″ E, 493–662 m	FASCI022-17	**MG838112**	**MG936627**	**MG838003**
MNHN IM-2013-42515	Buccinoidea	*Dolicholatirus spiceri* (Tenison-Woods, 1876)	WESTERN AUSTRALIA 2011	WE01	Westen Australia, Esperance, 15°16′56″ S, 124°6′18″ E	FASCI042-17	KT753936	KT753703	KT754067
MNHN IM-2013-11873	Fasciolariinae	*Benimakia lanceolata* (Reeve, 1847)	PAPUA NIUGINI	PB10	Papua New Guinea, BilBil I., 5°17′54″ S, 145°46′44″ E	FASCI029-17	KT753959	KT753726	KT754090
MNHN IM-2013-19559	Fasciolariinae	*Fasciolaria tulipa* (Linnaeus, 1758)	KARUBENTHOS 2012	GM11	Guadeloupe, 16°11′58″ N, 61°34′17″ W	FASCI032-17	KT753954	KT753721	KT754085
MNHN IM-2013-42511	Fasciolariinae	*Hemipolygona armata* (A. Adams, 1855)	Dakar′09	4	SenegalL, sector of Dakar, 14°40′12″ N, 17°23′48″ W	FASCI040-17	KT753974	KT753741	KT754104
MNHN IM-2013-56511	Fasciolariinae	*Lamellilatirus* sp.	GUYANE 2014	CP4380	French Guiana, 6°31′6″ N, 52°27′15″ W, 102–104 m	FASCI049-17	KT754007	KT753775	KT754136
MNHN IM-2013-20181	Fasciolariinae	*Leucozonia nassa* (Gmelin, 1791)	KARUBENTHOS 2012	GM27	Guadeloupe, Point of Saline, 16°12′10″ N, 61°26′41″ W	FASCI024-17	KT753902	KT753668	KT754032
MNHN IM-2007-32591	Fasciolariinae	*Pleuroploca trapezium* (Linnaeus, 1758)	SANTO 2006	FR95	Vanuatu	NEOGA045-10	KT753962	KT753729	KT754093
MNHN IM-2013-17100	Fasciolariinae	*Turrilatirus turritus* (Gmelin, 1791)	PAPUA NIUGINI	PR162	Papua New Guinea, Tab I., 5°10′6″ S, 145°50′15″ E, 1–4 m	FASCI028-17	KT753981	KT753748	KT754111
MNHN IM-2007-32913	Fusininae	"*Fusinus*" sp.	PANGLAO 2005	CP2395	Philippines, Bohol Sea, 9°36′12″ N, 123°43′48″ E, 382–434 m	–	KT753952	KT753719	KT754083
MNHN IM-2013-44400	Fusininae	*Amiantofusus pacificus* Fraussen, Kantor & Hadorn, 2007	NanHai 2014	DW4112	China seas, An-Da Chiao, 10°24′52″ N, 114°46′9″ E, 464–1076 m	FASCI039-17	KT753947	KT753714	KT754078
MNHN IM-2013-44196	Fusininae	*Amiantofusus sebalis* Fraussen, Kantor & Hadorn, 2007	NanHai 2014	DW4103	China seas, V bis (seamount), 15°5′22″ N, 116°29′40″ E	FASCI038-17	KT753958	KT753725	KT754089
MNHN IM-2007-32574	Fusininae	*Angulofusus nedae* Fedosov & Kantor, 2012	SANTO 2006	DS99	Vanuatu, N Tutuba I., 15°32′28″ S, 167°16′51″ E, 100–105 m	NEOGA037-10	KT753984	KT753751	KT754114
MNHN IM-2013-44302	Fusininae	*Chryseofusus acherusius* (Hadorn & Fraussen, 2003)	NanHai 2014	CP4108	China seas, off Taiping Island, 10°25′37″ N, 114°14′21″ E, 1707–1799 m	FASCI037-17	KT753956	KT753723	KT754087

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MNHN IM-2013-19938	Fusininae	*Chryseofusus graciliformis* (G.B. Sowerby II, 1880)	PAPUA NIUGINI	CP4012	Solomon Sea, Dampier Strait, 5°36′18″ S, 148°12′38″ E, 500–640 m	FASCI034-17	KT753963	KT753730	KT754094
MNHN IM-2013-42532	Fusininae	*Cyrtulus serotinus* Hinds, 1843	PAKAIHI I TE MOANA	MQ11-II-07BIS	Marquesas Islands, Eiao, 7°58′46″ S, 140°42′42″ W	FASCI031-17	KT753969	KT753736	KT754099
MNHN IM-2013-42512	Fusininae	*Fusinus australis* (Quoy & Gaimard, 1833)	WESTERN AUSTRALIA 2011	WA13	Western Australia, Albany, 35°3′52″ S, 117°56′30″ E	FASCI041-17	KT753923	KT753690	KT754054
MZSP-108889	Fusininae	*Fusinus brasiliensis* (Grabau, 1904)	–	–	Southeast Brazil	–	KT754005	KT753773	KT754134
MNHN IM-2007-32560	Fusininae	*Fusinus colus* (Linnaeus, 1758)	EBISCO	CP2542	New Caledonia, N Banc Nova, 22°16′5″ S, 159°25′53″ E, 335–338 m	FASCI004-17	KT753901	KT753666	KT754030
MNHN IM-2007-34663	Fusininae	*Fusinus crassiplicatus* Kira, 1959	CONCALIS	DW3018	New Caledonia, Grand Passage, 19°7′3″ S, 163°28′26″ E, 199–215 m	NEOGA136-10	KT753917	KT753684	KT754048
ANSP-A21957	Fusininae	*Fusinus excavatus* (G.B. Sowerby II, 1880)	–	–	Barbados	–	KT754000	KT753767	KT754129
MNHN IM-2007-38235	Fusininae	*Fusinus forceps* (Perry, 1811)	MIRIKY	CP3272	Madagascar, between Majunga and Cap Saint-André, 15°29′44″ S, 46°5′31″ E, 22–27 m	FASCI002-17	KT753940	KT753707	KT754071
FMNH-413989	Fusininae	*Fusinus mauiensis* Callomon & Snyder, 2006	–	–	Hawaii	–	KT753987	KT753754	KT754117
MCZ-378473	Fusininae	*Fusinus pulchellus* (Philippi, 1840)	–	–	France, Banyuls sur Mer	–	KT753996	KT753763	KT754125
MNHN IM-2007-32588	Fusininae	*Fusinus salisburyi* Fulton, 1930	EBISCO	DW2519	New Caledonia, Banc Kelso, 24°7′38″ S, 159°40′55″ E, 310–463 m	NEOGA043-10	KT753975	KT753742	KT754105
FMNH-414020	Fusininae	*Fusinus sandvichensis* (G.B. Sowerby II, 1880)	–	–	Hawaii	–	KT754009	KT753777	KT754138
ANSP-A20012-411168	Fusininae	*Fusinus similis* (Baird, 1873)	–	–	Japan, Wakayama Prefecture, Honshu, off Cape Kirime, 70 m	–	KT754016	KT753785	KT754146
MNHN IM-2013-19037	Fusininae	*Granulifusus* aff. *kiranus* Shuto, 1958	PAPUA NIUGINI	CP4058	Bismarck Sea, NE Sissano, 2°54′40″ S, 142°10′46″ E, 535–540 m	FASCI035-17	KT753966	KT753733	KT754096
MNHN IM-2007-32816	Fusininae	*Granulifusus* aff. *niponicus* (E.A.Smith, 1859)	EBISCO	–	Coral Sea	FASCI009-17	KT753932	KT753699	KT754063

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MNHN IM-2007-32823	Fusininae	*Granulifusus* aff. *niponicus* (E.A.Smith, 1859)	EBISCO	CP2614	New Caledonia, Chesterfield Plateau , 19°37′46″ S, 158°45′15″ E, 608–642 m	NEOGA086-10	KT753950	KT753717	KT754081
MNHN IM-2013-19210	Fusininae	*Granulifusus hayashi* Habe, 1961	PAPUA NIUGINI	CP4066	Bismarck Sea, Dogreto Bay, 3°17′42″ S, 143°2′22″ E	FASCI036-17	KT753955	KT753722	KT754086
MNHN IM-2013-19903	Fusininae	*Granulifusus niponicus* (E.A.Smith, 1959)	PAPUA NIUGINI	CP4006	Solomon Sea, SE Tuam Is, 6°3′15″ S, 148°8′23″ E, 440–475 m	FASCI033-17	KT753935	KT753702	KT754066
MNHN IM-2007-32750	Fusininae	*Granulifusus staminatus* (Garrard, 1966)	PANGLAO 2004	T36	Philippines, W Pamilacan I., 9°29′18″ N, 123°51′30″ E, 95–128 m	FASCI046-17	KT753973	KT753740	KT754103
MNHN IM-2007-34487	Fusininae	*Granulifusus annae* sp. nov.	AURORA 2007	CP2716	Philippines, 14°30′25″ N, 121°41′10″ E, 335–356 m	NEOGA101-10	**MG838115**		
MNHN IM-2007-34585	Fusininae	*Granulifusus annae* sp. nov.	AURORA 2007	CP2716	Philippines, 14°30′25″ N, 121°41′10″ E, 335–356 m	NEOGA109-10	**MG838113**		
MNHN IM-2007-34586	Fusininae	*Granulifusus annae* sp. nov.	AURORA 2007	CP2717	Philippines, 14°28′56″N, 121°43′9″ E, 311–361 m	NEOGA110-10	**MG838116**	**MG936628**	**MG838004**
MNHN IM-2007-34609	Fusininae	*Granulifusus annae* sp. nov.	AURORA 2007	CP2716	Philippines, 14°30′25″ N, 121°41′10″ E, 335–356 m	NEOGA131-10	**MG838125**		
MNHN IM-2013-14709	Fusininae	*Granulifusus annae* sp. nov.	PAPUA NIUGINI	PP08	Papua New Guinea, Rempi Area, 05°03′ S, 145°49′ E, 120 m	FASCI030-17	KT753937	KT753704	KT754068
MNHN IM-2013-42520	Fusininae	*Granulifusus annae* sp. nov.	E″BODI	CP3823	New Caledonia, 21°55′24″ S, 166°55′24″ E, 246–255 m	FASCI043-17	KT753899	KT753664	KT754028
MNHN IM-2007-34486	Fusininae	*Granulifusus annae* sp. nov.	AURORA 2007	CP2717	Philippines, 14°28′56″ N, 121°43′8″ E, 311–361 m	NEOGA100-10	**MG838121**		
MNHN IM-2007-34488	Fusininae	*Granulifusus discrepans*	AURORA 2007	CP2673	Philippines, 15°01′ N, 121°45′E, 431–493 m	NEOGA102-10	**MG838123**		
MNHN IM-2007-34580	Fusininae	*Granulifusus discrepans*	AURORA 2007	CP2732	Philippines, 15°27′ N, 121°36′ E, 556 m	NEOGA105-10	**MG838122**		
MNHN IM-2007-34581	Fusininae	*Granulifusus discrepans*	AURORA 2007	CP2732	Philippines, 15°27′ N, 121°36′ E, 556 m	NEOGA106-10	**MG838120**		
MNHN IM-2007-34583	Fusininae	*Granulifusus discrepans*	AURORA 2007	CP2673	Philippines, 15°01′ N, 121°45′ E, 431–493 m	NEOGA107-10	**MG838128**		
MNHN IM-2007-34604	Fusininae	*Granulifusus discrepans*	AURORA 2007	CP2657	Philippines, 16°01′ N, 121°51′ E, 342–358 m	NEOGA127-10	KT753928	KT753695	KT754059
MNHN IM-2013-46327	Fusininae	*Granulifusus discrepans*	MADEEP	CP4337	New Britain, 06°07′ S, 149°17′ E, 287–447 m	FASCI050-17	**MG838146**	**MG936638**	**MG838014**

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MNHN IM-2007-34593	Fusininae	*Granulifusus jeanpierrevezzaroi* comb. nov.	AURORA 2007	CP2748	Phillippines, 15°56′ N, 121°465′ E, 247–249 m	NEOGA117-10	**MG838124**		
MNHN IM-2007-35083	Fusininae	*Granulifusus jeanpierrevezzaroi* comb. nov.	CONCALIS	CP3026	New Caledonia, Grand Passage, 20°17′7″ S, 163°50′8″ E, 590–809 m	NEOGA164-10	**MG838127**	**MG936630**	**MG838006**
MNHN IM-2007-36886	Fusininae	*Granulifusus jeanpierrevezzaroi* comb. nov.	TERRASSES	CP3095	New Caledonia, 22°1′52″ S, 167°6′22″ E, 320–380 m	FASCI001-17	**MG838147**	**MG936639**	**MG838015**
MNHN IM-2007-36921	Fusininae	*Granulifusus norfolkensis* sp. nov.	TERRASSES	DW3063	New Caledonia, Norfolk Ridge, 23°23′2″ S, 168°0′19″ E, 430–480 m	FASCI021-17	**MG838154**		
MNHN IM-2013-68811	Fusininae	*Granulifusus norfolkensis* sp. nov.	KANACONO	DW4685	New Caledonia, N Ile des Pins, 22°28′ S, 167°29′ E, 404–405 m	FASCI054-17	**MG838155**	**MG936643**	**MG838019**
MNHN IM-2007-32612	Fusininae	*Granulifusus williami* comb. nov.	SALOMON 2	DW2169	Solomon Islands, 09°01′ S, 159°06′ E, 100–200 m	NEOGA048-10	**MG838118**		
MNHN IM-2007-34608	Fusininae	*Granulifusus williami* comb. nov.	AURORA 2007	CP2709	Philippines, 15°12′ N, 121°34′ E, 244–296 m	NEOGA130-10	**MG838117**		
MNHN IM-2007-35734	Fusininae	*Granulifusus williami* comb. nov.	CONCALIS	CP2960	New Caledonia, Grand Passage, 19°05′ S, 163°13′ E, 382–387 m	NEOGA176-10	**MG838119**		
MNHN IM-2007-39262	Fusininae	*Granulifusus williami* comb. nov.	TARASOC	DW3491	Society Islands, 17°29′ S, 149°26′ W, 440–500 m	FASCI005-17	**MG838151**	**MG936642**	**MG838018**
MNHN IM-2007-39387	Fusininae	*Granulifusus williami* comb. nov.	TARASOC	DW3441	Society Islands, 16°43′ S, 151°26′ W, 350–360 m	FASCI006-17	**MG838149**		
MNHN IM-2007-39389	Fusininae	*Granulifusus williami* comb. nov.	TARASOC	DW3441	Society Islands, 16°43′ S, 151°26′ W, 350–360 m	FASCI007-17	**MG838150**	**MG936641**	**MG838017**
MNHN IM-2009-15090	Fusininae	*Granulifusus williami* comb. nov.	ATIMO VATAE	DW3515	South Madagascar, 24°53′ S, 47°28′ E, 184–203 m	FASCI018-17	**MG838148**	**MG936640**	**MG838016**
MNHN IM-2007-32522	Fusininae	*Okutanius ellenae* gen. et sp. nov.	EBISCO	DW2520	Coral Sea, Banc Kelso, 24°06′ S, 159°41′ E, 350–400 m	NEOGA020-10	**MG838114**		
MNHN IM-2007-38356	Fusininae	*Okutanius ellenae* gen. et sp. nov.	TERRASSES	DW3082	New Caledonia, 22°29′9″ S, 167°23′14″ E, 290 m	FASCI003-17	**MG838144**		
MNHN IM-2013-68819	Fusininae	*Okutanius ellenae* gen. et sp. nov.	KANAKONO	DW4677	New Caledonia, S Ile des Pins, 22°53′ S, 167°35′ E, 376–390 m	FASCI052-17	**MG838143**	**MG936637**	**MG838013**
MNHN IM-2013-68876	Fusininae	*Okutanius ellenae* gen. et sp. nov.	KANAKONO	DW4677	New Caledonia, S Ile des Pins, 22°53′ S, 167°35′ E, 376–390 m	FASCI053-17	**MG838145**		

Specimen ID	Family/Sub-family	Genus species	Expedition	Station	Collection data	BOLD	COI	28S	H3
MNHN IM-2013-59070	Fusininae	*Okutanius kuroseanus* gen. et comb. nov.	KAVIENG 2014	CP4503	Papua New Guinea, New Ireland, 2°30′19″ S, 150°44′2″ E, 191–290 m	FASCI051-17	**MG838142**	**MG936636**	**MG838012**
MNHN IM-2007-32537	Fusininae	*Vermeijius pallidus* gen. et comb. nov.	SALOMON 2	CP2290	Solomon Islands, Tetepare, 8°39′58″ S, 157°31′40″ E , 384–418 m	FASCI045-17	KT753910	KT753677	KT754041
MNHN IM-2007-35093	Fusininae	*Vermeijius pallidus* gen. et comb. nov.	CONCALIS	CP2962	New Caledonia, Grand Passage, 18°58′33″ S, 163°8′7″ E, 580–647 m	NEOGA173-10	**MG838126**	**MG936629**	**MG838005**
MNHN IM-2013-50173	Fusininae	*Vermeijius pallidus* gen. et comb. nov.	DongSha 2014	CP4128	China seas, 20°42′17″ N, 116°8′0″ E, 420–444 m	FASCI047-17	**MG838153**		
MNHN IM-2013-50174	Fusininae	*Vermeijius pallidus* gen. et comb. nov.	DongSha 2014	CP4128	China seas, 20°42′17″ N, 116°8′0″ E, 420–444 m	FASCI048-17	**MG838152**		
MNHN IM-2009-15087	Fusininae	*Vermeijius retiarius* gen. et comb. nov.	ATIMO VATAE	CP3595	South Madagascar, South Point Barrow, 25°35′28″ S, 44°15′25″ E, 821–910 m	FASCI020-17	**MG838129**	**MG936631**	**MG838007**
MNHN IM-2009-15020	Fusininae	*Vermeijius virginiae* gen. et comb. nov.	ATIMO VATAE	CP3585	South Madagascar, South Point Barrow, 25°32′17″ S, 44°15′36″ E, 549–576 m	FASCI015-17	**MG838138**		
MNHN IM-2009-15021	Fusininae	*Vermeijius virginiae* gen. et comb. nov.	ATIMO VATAE	CP3591	South Madagascar, SE Point Barrow, 25°3′9″ S, 43°58′28″ E, 400–402 m	FASCI016-17	**MG838132**		
MNHN IM-2009-15025	Fusininae	*Vermeijius virginiae* gen. et comb. nov.	ATIMO VATAE	CP3585	South Madagascar, South Point Barrow, 25°32′17″ S, 44°15′36″ E, 549–576 m	FASCI017-17	**MG838136**		
MNHN IM-2009-15026	Fusininae	*Vermeijius virginiae* gen. et comb. nov.	ATIMO VATAE	CP3585	South Madagascar, South Point Barrow, 25°32′17″ S, 44°15′36″ E, 549–576 m	FASCI023-17	**MG838131**		
MNHN IM-2009-15030	Fusininae	*Vermeijius virginiae* gen. et comb. nov.	ATIMO VATAE	CP3585	South Madagascar, South Point Barrow, 25°32′17″ S, 44°15′36″ E, 549–576 m	FASCI013-17	**MG838133**		
MNHN IM-2009-15031	Fusininae	*Vermeijius virginiae* gen. et comb. nov.	ATIMO VATAE	CP3585	South Madagascar, South Point Barrow, 25°32′17″ S, 44°15′36″ E, 549–576 m	FASCI025-17	**MG838135**		
MNHN IM-2009-15033	Fusininae	*Vermeijius virginiae* gen. et comb. nov.	ATIMO VATAE	CP3585	South Madagascar, South Point Barrow, 25°32′17″ S, 44°15′36″ E, 549–576 m	FASCI011-17	**MG838130**		

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Specimen ID	Family/Sub-family	Genus species	Expedition	Station	Collection data	BOLD	COI	28S	H3
MNHN IM-2009-15034	Fusininae	*Vermeijius virginiae* gen. et comb. nov.	ATIMO VATAE	CP3585	South Madagascar, South Point Barrow, 25°32′17″ S, 44°15′36″ E, 549–576 m	FASCI014-17	**MG838137**		
MNHN IM-2009-15084	Fusininae	*Vermeijius virginiae* gen. et comb. nov.	ATIMO VATAE	CP3591	South Madagascar, SE Point Barrow, 25°3′9″ S, 43°58′28″ E, 400–402 m	FASCI019-17	**MG838134**	**MG936632**	**MG838008**
MNHN IM-2009-15019	Peristerniinae	*Fusolatirus* sp.	ATIMO VATAE	CP3543	South Madagascar, sector of Fort-Dauphin, 25°27′45″ S, 46°59′25″ E, 148–155 m	FASCI012-17	**MG838140**	**MG936634**	**MG838010**
MNHN IM-2009-15037	Peristerniinae	*Fusolatirus* sp.	ATIMO VATAE	CP3589	South Madagascar, SE Point Barrow, 25°3′8″ S, 43°59′49″ E , 132–153 m	FASCI010-17	**MG838139**	**MG936633**	**MG838009**
MNHN IM-2007-32495	Peristerniinae	*Fusolatirus pearsoni* (Snyder, 2002)	PANGLAO 2004	T39	Philippines, W Pamilacan I., 9°30′6″ N, 123°50′24″ E 100–138 m	NEOGA005-10	KT753921	KT753688	KT754052
MNHN IM-2007-32498	Peristerniinae	*Fusolatirus rikae* (Fraussen, 2003)	SANTO 2006	EP36	Vanuatu, E Aoré I., 15°33′21″ S, 167°12′43″ E	FASCI044-17	KT753976	KT753743	KT754106
MNHN IM-2013-15306	Peristerniinae	*Peristernia marquesana* (A. Adams, 1855)	PAPUA NIUGINI	PR97	Papua New Guinea, Kranket I., 5°12′27″ S, 145°49′1″ E	FASCI026-17	KT753914	KT753681	KT754045
MNHN IM-2013-18061	Peristerniinae	*Peristernia nassatula* (Lamarck, 1822)	PAPUA NIUGINI	PR214	Papua New Guinea, Tab I., 1–8 m	FASCI027-17	KT753957	KT753724	KT754088
MZSP-36166	Peristerniinae	*Hemipolygona mcgintyi* (Pilsbry, 1939)	–	–	USA, Florida	–	KT754023	KT753792	KT754152

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rRNA, and H3F and H3R (Colgan *et al.* 2000) for H3 were used for polymerase chain reactions (PCR). PCRs were performed in 20 µl final volume containing approximately 3 ng template DNA, 1.5 mM MgCl2, 0.26 mM of each nucleotide, 0.3 µl of each primer, 5% DMSO and either 0.75 µl of Taq Polymerase (Qbiogene) or BioHYTaq DNA polymerase (Dialat).

The PCR profile for the COI started with 5 min at 95°C followed by 40 cycles with the denaturation at 95°C (35 sec), annealing at 50°C (35 s) and elongation at 72°C (1 min), with final elongation phase at 72°C (10 min). Similar PCR profiles were set for 28S (annealing at 56°C), and H3 (annealing at 57°C, elongation at 72°C for 45 s). All genes were sequenced in both directions to confirm accuracy of each sequence. The sequencing was performed by Eurofins or in the SIEE RAS molecular facility on an ABI 3500 Genetic analyser.

Phylogenetic analysis

Sequences were aligned for each gene independently using Clustal W, as implemented in BioEdit v. 7.0.9.0 (Hall 1999). The accuracy of automatic alignments was confirmed by eye. No indels were detected in protein coding genes COI and H3, the fragments 658 bp and 328 bp in length were recovered for these two markers respectively; few indels were identified in the 28S fragment leading to the alignment of 700 bp in length.

For phylogenetic inference, four datasets were analyzed. Three of them corresponded to the three individual genes, with the COI dataset including 71 sequencies, and H3 and 28S datasets including 57 sequences each, and were analyzed separately. The resulting single gene trees were then checked for consistency (i.e., absence of strongly supported conflicting topologies), and a concatenated dataset of the three genes and 1687 bp was then constructed.

A combination of a distance based approach ABGD (Puillandre *et al.* 2012), and a tree based approach was used to define molecular taxonomic units (MOTUs) in the analysis of COI, and to compare them with the morphology-based species hypotheses. The maximum intraspecific genetic distance of 3.5% and a gap width of 1.0% were set for the ABGD analysis. We checked whether each of the primary species hypotheses corresponded to a monophyletic lineage on the COI based tree and, where there was disagreement, we re-examined voucher shells to check for possible cross-contamination. In this manner the secondary species hypotheses have been refined.

A total of 71 specimens were included in the COI dataset; two deep water Buccinidae (MNHN IM-2007-36620, *Manaria formosa* Bouchet & Warén, 1986 and MNHN IM-2007-38241, Gen. sp.) were used as outgroups (but are not treated in this paper - see Results). The 40 putative Fusininae specimens were included in the multi-gene dataset, together with 7 species from the '*Fasiolaria tulipa* (Linnaeus, 1758) clade' (subfamily Fasciolariinae) and 7 species from the '*Peristernia nassatula* (Lamarck, 1822) clade' (subfamily Peristerniinae) of Couto *et al.* (2016). The specimen *Dolicholatirus spiceri* (Tenison-Wood, 1876) MNHN IM-2013-42515 as well as above mentioned Buccinidae were used as a non-fasciolariid outgroup based on the relationships inferred by Couto *et al.* (2016).

The phylogenetic relationships among Fusininae lineages were estimated by Bayesian inference (Huelsenbeck & Ronquist 2001). Bayesian Analyses (BAs) were performed running two parallel analyses in MrBayes with parameters of substitution models estimated during the run. Three partitions corresponding to each codon position were analyzed for the COI and H3 datasets, and seven partitions that corresponded to the three codon positions of COI, 28S, together with three codon positions of H3 were analyzed for the concatenated dataset. For primary single-gene analyses, each run consisted of six Markov chains and 5 000 000 generations with default number of swaps and sampling frequency of 1 tree in each 500 generations. 25 000 000 generations of Markov chain, and a sampling frequency of one

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tree in each 2000 generations were used in final analyses of COI and COI-28S-H3 datasets. The chain temperature was set at 0.02 in all analyses. Convergence of each analysis was evaluated using Tracer v. 1.6 (Rambaut *et al.* 2014), where ESS (Effective Sampling Size) values were checked to ensure that they exceeded the threshold value of 200. Consensus trees were calculated after omitting the first 25% trees as burn-in.

The same partitions BA were used in the RaxML analysis (Stamatakis 2006), which was performed for the concatenated dataset only. Robustness of nodes was assessed using the Thorough Bootstrapping algorithm (Felsenstein 1985) with 1000 iterations. All analyses were performed on the Cipres Science Gateway (http://www.phylo.org/portal2), using MrBayes v. 3.2.6 on XSEDE (Miller *et al.* 2010).

To facilitate species identification, COI based molecular diagnoses have been compiled for all *Pseudolatirus*-like species for which 3 or more COI sequences were available. To draw molecular diagnoses, 658 nucleotide positions in the COI alignment that was used for the phylogenetic reconstructions, were numbered from 1 to 658. Then an in-house Python script (Fedosov *et al.* unpublished) was run on this alignment, to identify diagnostic combinations of nucleotides for each predefined species. The diagnostic nucleotide combinations, therefore generally correspond to the compound Character Attributes as implemented in CAOS (Sarkar *et al.* 2008). In order to increase robustness of the diagnosis, for each species we report only independent diagnostic combinations – i.e., a nucleotide position once included in one diagnostic combination will not be involved in any other diagnostic combination.

Abbreviations of repositories:

AMS = Australian Museum, Sydney, NSW, Australia
ANSP = Academy of Natural Sciences of Drexel University, Philadelphia, PA, USA
FMNH = Florida Museum of Natural History, Gainesville, FL, USA
IMT = Institute of Malacology, Tōkyō, Japan
MNHN = Muséum national d'Histoire naturelle, Paris, France
MMM = Malacologia Mostra Mondiale, Cupra Marittima, Italy
MSZ = Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA
MZSP = Museum of Zoology, University of São Paulo, Brazil
NMP = National Museum of the Philippines, Manila
NMSA = Natal Museum, Pietermaritzburg, South Africa
NSMT = National Museum of Nature and Science, Tōkyō, Japan
RGM = Rijksmuseum van Geologie en Mineralogie (now in Naturalis Biodiversity Center), Leiden, the Netherlands
USNM = National Museum of Natural History, Smithsonian Institution, Washington, DC, USA
ZMB = Museum für Naturkunde, Berlin, Germany

Other text abbreviations:

AL = aperture length
dd = empty shell
juv = juvenile
lv = live-collected specimen
MOTU = molecular operational taxonomic unit
SL = shell length
spm = specimen (dd and/or lv)
stn = station
SW = shell width

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Results

Species delimitation and phylogenetic analysis

Shell morphology led to the identification of ten primary species hypotheses among *Pseudolatirus*–like species available for sequencing. The COI tree (Fig. 1) is characterized by high support of the terminal clusters (MOTU 1-10), but deeper nodes often lack support. Nine species hypotheses correspond to nine reciprocally monophyletic clades with high nodal support (Bayesian posterior probabilities 0.99–1). The COI dataset for Fusininae, once analysed with ABGD was split into 29 partitions, of which 10 corresponded to the *Pseudolatirus*-like specimens. The genetically divergent specimen MNHN IM-2007-32612 (MOTU2) was split in the partition of its own. Nevertheless morphologically this specimens falls within the intraspecific variability of the species. At the same time the MOTUs 6 and 7 were placed in one partition by the ABGD. Contrary to previous case, these MOTUs differ markedly in shell morphology precluding uniting them into the single species. Based on the obtained phylogenetic tree, we have critically revisited species hypotheses, and define species consistent with the proposed MOTUs, rather than based on the partitions proposed by the ABGD.

On the basis of comparison with the type material four MOTUs were identified as species previously described in, or assigned to, *Pseudolatirus*: MOTU4 as *Pseudolatirus jeanpierrevezzaroi* Cossignani, 2017; MOTU5 as *Pseudolatirus discrepans* Kuroda & Habe, 1961; MOTU7 as *Fusolatirus kuroseanus* Okutani, 1975; MOTU9 as *Pseudolatirus pallidus* Kuroda & Habe, 1961 (these are labelled in red on Figs 1–2). Additionally MOTU2 was identified as *Fusinus williami* Poppe & Tagaro, 2006; MOTU8 as *Fusinus virginiae* Hadorn & Fraussen, 2002. MOTU10 identified as *Fusus retiarius* von Martens, 1901 was represented in our material by a single specimen (MNHN IM-2009-15087). Three MOTUs (1, 3, and 6) were recognized as new species and are described herein.

The species previously assigned to *Pseudolatirus* do not constitute a monophyletic group, and are scattered across the tree. *Pseudolatirus pallidus* is recovered as a sister species to *Fusinus virginiae*, albeit with low support, and this two-species clade splits off at the basal polytomy of the COI tree. *Fusolatirus kuroseanus* forms a highly supported clade with the new species MOTU6 and the resulting clade shows supported affinity to *Angulofusus nedae* Fedosov & Kantor, 2012. *Pseudolatirus discrepans* is recovered as a sister group to several *Granulifusus* species although without support. *Granulifusus* in a previously accepted volume (Hadorn & Fraussen 2005) does not correspond to a monophyletic clade, since *Granulifusus staminatus* (Garrard, 1966) constitutes a separate phylogenetic lineage.

No supported conflicts were recovered in the single gene analyses, and the analysis of a concatenated dataset returned a tree with notably higher nodal support values (Fig. 2). In this tree, representatives of Fasciolariidae form three distinct lineages. Two of them correspond to the *Fasciolaria tulipa* and *Peristernia nassatula* clades identified by Couto *et al.* (2016) (marked with green and pink respectively). These two clades show a well supported affinity and represent the subfamilies Fasciolariinae and Peristerniinae, respectively. The weakly supported (BI 0.92, bootstrap value 66) Fusininae clade forms a sister group to the Fasciolariinae – Peristerniinae, with high support (BI 1, bootstrap value 94). The minor clade comprising *Manaria formosa* and an undescribed Buccinidae species from deep water off Madagascar (MNHN IM-2007-38241 and MNHN IM-2007-36620) is recovered as a sister group to all other Fasciolariidae; these species are not dealt with in this paper.

The Fusininae itself clearly splits into four clades, all with high support in Bayesian analysis (BI 0.96-0.99) albeit lower support in RaxML analysis (bootstrap values 58–76). The first (marked **A** on the tree) includes *Fusinus* s.s. and *Amiantofusus*; the second (**B**) combines *Chryseofusus* Hadorn & Fraussen, 2003, and three species in a highly supported clade (*Fusinus virginiae*, *Fusus retiarius* and *Pseudolatirus*

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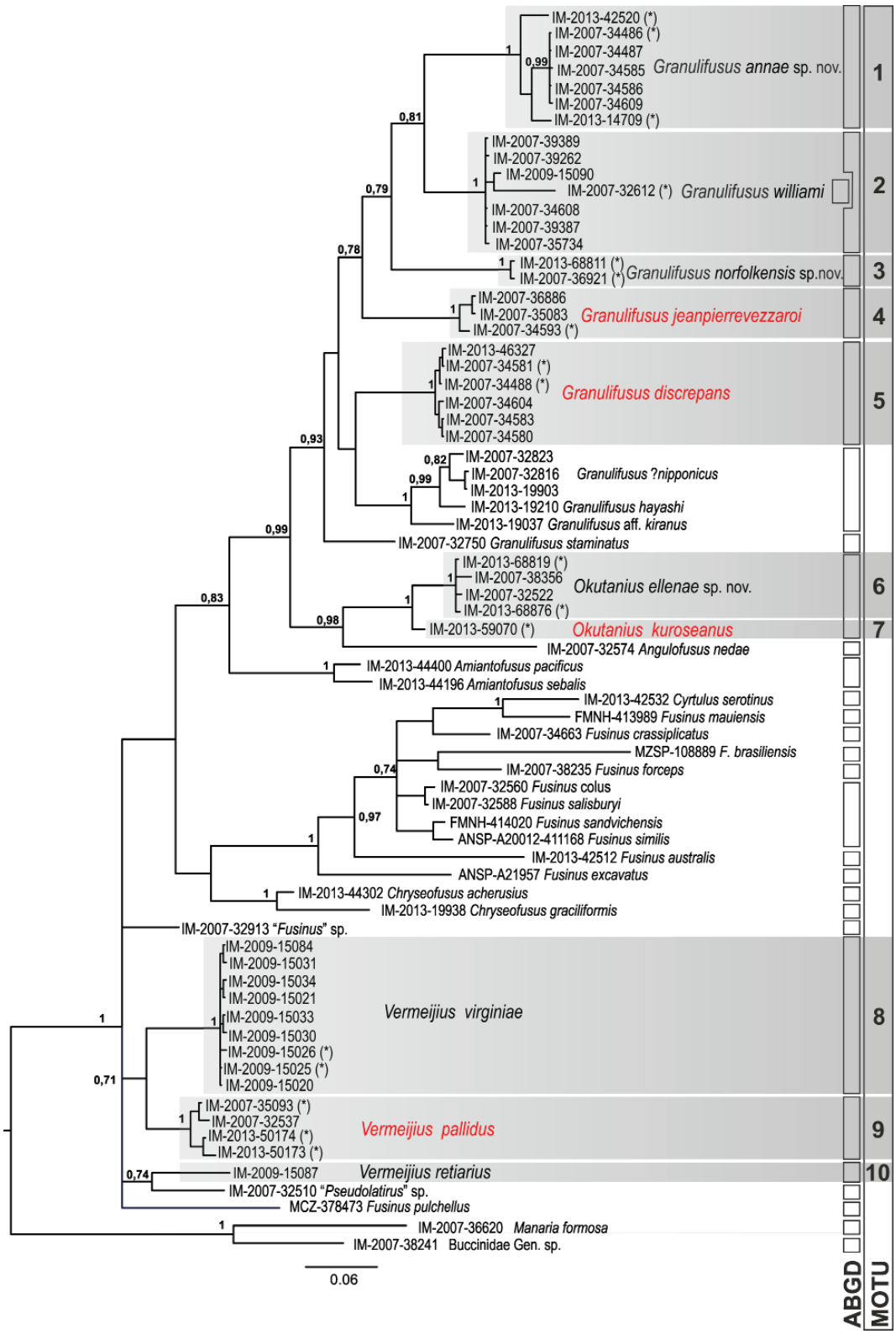

Fig. 1. Bayesian phylogenetic tree of the subfamily Fusininae based on the COI gene. Support values as Bayesian posterior probabilities (PP) indicated when > 0.7. Asterisks mark specimens illustrated on figures. The names of the species previously attributed to *Pseudolatirus* are given in orange. Partitions recovered by ABGD marked as vertical line of rectangles on the right. MOTUs identified in the current study are highlighted in grey.

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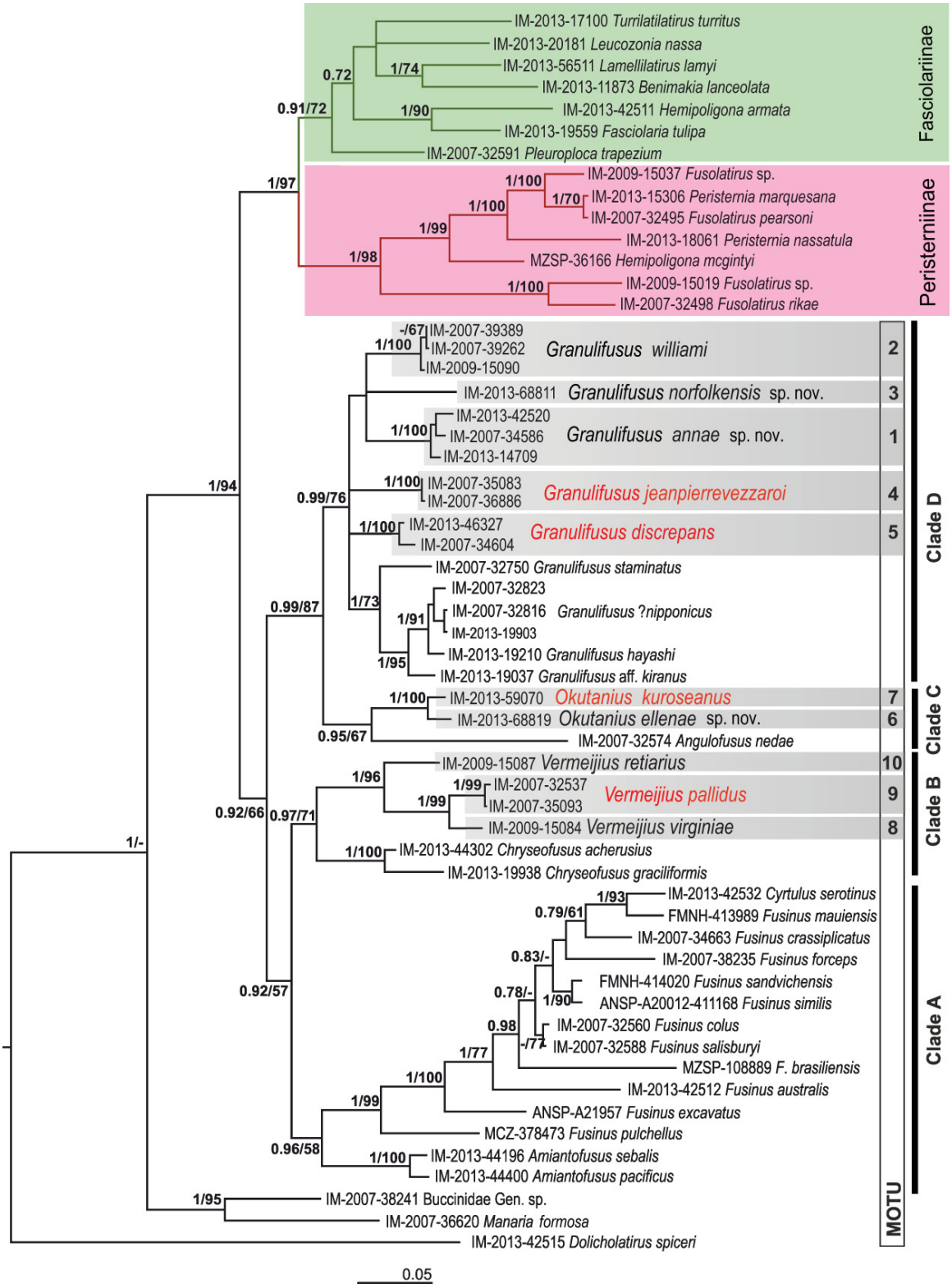

Fig. 2. Bayesian phylogenetic tree of Fasciolariidae based on the combined COI-H3-28S dataset. Subclades corresponding to Couto *et al.*'s (2016) *Fasciolaria tulipa* clade (Fasciolariinae) and *Peristernia nassatula* clade (Peristerniinae) are marked with green and pink, respectively. MOTUs identified in the current study are highlighted in grey. The numbering of MOTU correspond to Fig. 1. Support values as Bayesian posterior probabilities (PP) indicated when > 0.7 / bootstrap values, when > 50.

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pallidus). The third clade (**C**) includes *Angulofusus nedae* and a highly supported clade that includes two species, *Fusolatirus kuroseanus* and MOTU6.

In the fourth clade (**D**), a well-supported in Bayesian analysis crown group combines species attributed presently to *Granulifusus* and five maximal supported single-species clades, of which three correspond to *Pseudolatirus discrepans*, *Pseudolatirus jeanpierrevezzaroi* and *Fusinus williami* and two others, MOTUs 1 and 3. These five species are rather heterogeneous in morphology, although some common characters can be enumerated: a strong shell with a well-attenuated narrow canal, rather strong axial sculpture of few ribs, presence of weak to moderately developed columellar plicae in most specimens, and a radula with narrow central tooth.

Taxonomic account

An important taxonomic question related to the group, is whether the genus name *Pseudolatirus* can be attributed to any of the newly defined clades, which includes the species previously assigned to, or described as, *Pseudolatirus*. In fact, the Recent species of '*Pseudolatirus*' bear little resemblance to the fossil true *Pseudolatirus*. Only the young specimens of '*Pseudolatirus*' *discrepans* have conchological similarities with the type species of *Pseudolatirus*, *Fusus bilineatus*, notably in the spiral and axial sculpture and the presence of a weak columellar fold delimiting the siphonal canal (Fig. 3). There is a significant ontogenic change in the teleoconch sculpture pattern in '*Pseudolatirus*' *discrepans*, with earlier whorls bearing strong axial ribs while later whorls in large shells can be nearly smooth. However, a sculpture pattern similar to that in *F. bilineatus* is found throughout the shells grouped in Peristerniinae (to which we also attribute *Pseudolatirus*), and is insufficient to establish relationships at the generic level. Since *F. bilineatus* is a fossil species from the Miocene, the connections to Recent material have to be especially convincing if the Recent material is to be placed in a genus with a fossil type species, and in the present case the evidence is not sufficiently strong. For this reason we abstain from using the name *Pseudolatirus* for any Recent species, that necessitates to reaccess the generic position of the species formerly assigned to *Pseudolatirus*.

Therefore we erect *Vermeijius* gen. nov. (type species *Pseudolatirus pallidus*) for the subclade in clade B uniting MOTUs 8-10, *Okutanius* gen. nov. (type species *Fusolatirus kuroseanus*) for *F. kuroseanus* and MOTU 6 (described herein as a new species, *O. ellenae* gen. et sp. nov.) forming a subclade in clade C. While erecting these two new genera is straightforward and is undoubtedly supported by the molecular phylogeny, the status of the five species (MOTUs 1–5) in clade D is less obvious. Species traditionally included in *Granulifusus* (and forming a separate, highly supported, branch within the crown clade) differ slightly from the abovementioned five species in having lighter and thinner shells with weaker axial sculpture compared to shells of the abovementioned five species, together with spiral cords forming beads or 'granules' at their intersection with the axial ribs. Protoconchs of *Granulifusus* have up to 1.5 whorls (Hadorn & Fraussen 2005) vs 2.25 (MOTU1) to 4.25 (*Fusinus williami*). Most studied species of *Granulifusus* possess a radula with a shorter and therefore relatively broader central tooth compared to these five species (Hadorn & Fraussen 2005: figs 109–121). An exception is *G. staminatus* which has a narrow central tooth, similar to *Pseudolatirus*-like species of subclade **D** (see Fig. 4 on page 19). In none of the analyses these five species form a clade, while the clade uniting them and *Granulifusus* spp. was always highly supported. The internal relationships within the crown clade are not resolved and it is not impossible however that a more saturated molecular dataset will result in the mentioned species forming a monophyletic clade(s). Nevertheless, we consider it premature to establish a new genus for them and based on the results of molecular analyses have to assign *Pseudolatirus discrepans*, *Pseudolatirus jeanpierrevezzaroi*, *Fusinus williami* and MOTUs 1 and 3, described herein as new species to *Granulifusus* albeit with some reservations.

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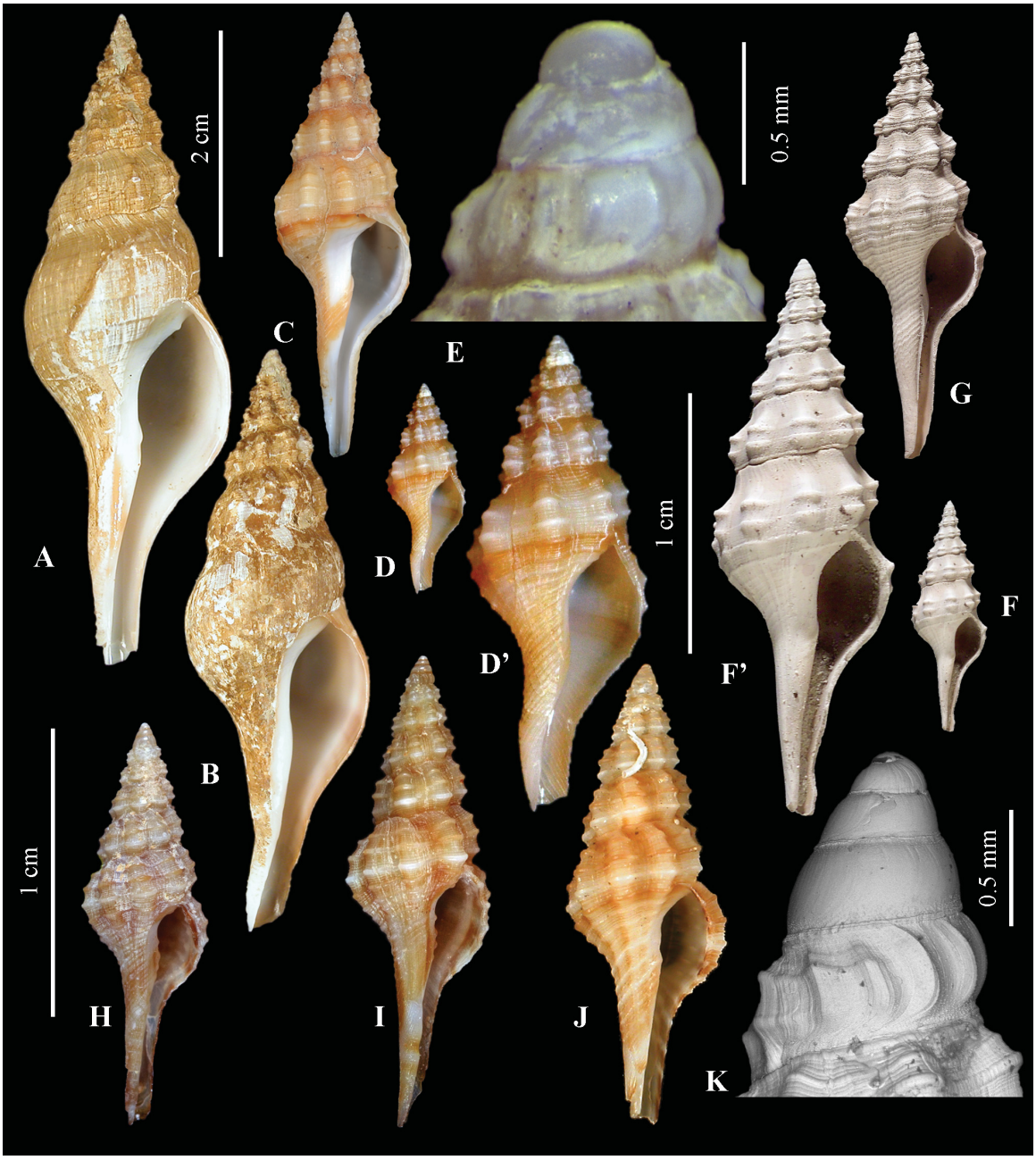

Fig. 3. A–E. *Granulifusus discrepans* (Kuroda & Habe, 1961). **A**. Philippines, SL 58 mm, sequenced specimen (MNHN IM-2007-34581). **B**. Philippines, SL 51.9 mm, sequenced specimen (MNHN IM-2007-34488). **C**. Papua New Guinea, PAPUA NIUGINI, stn CP3949, 05°12′ S, 145°51′ E, 380–407 m (MNHN 2013-15374, not sequenced). **D–E**. Solomon Sea, SL 18.2 mm, sequenced specimen (MNHN IM-2013-46327). **D'**. Same as preceding, enlarged. – **F–G**. *Pseudolatirus bilineatus* (Hörnes, 1853). **F**. Lectotype, SL 20.8 mm (NHMW 1846/0037/0263). **F'**. Same as preceding, enlarged. **G**. Paralectotype, SL 38.7 mm (NHMW 1846/0037/0264). – **H–K**. *Granulifusus williami* (Poppe & Tagaro, 2006) comb. nov. **H**. Papua New Guinea, New Ireland, KAVIENG 2014, stn DW4471, 02°44′ S, 150°38′ E, 126–220 m, SL 14.1 mm (MNHN IM-2013-58726, not sequenced). **I**. Papua New Guinea, New Ireland, KAVIENG 2014, stn DW4484, 02°26′ S, 149°55′ E, SL 16.5 mm (MNHN IM-2013-58866, not sequenced). **J**. Solomon Islands, SL 16.1 mm, sequenced specimen (MNHN IM-2007-32612). **K**. New Caledonia, BERYX 11, stn DW11, 24°43′–24°44′ S, 168°08′–168°10′ E, 270–350 m, protoconch. Scale bars: A–D = 2 cm; F–G = 1 cm; H–J = 1 cm. D' and F' to the same scale.

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Four additional Recent species have been assigned (some tentatively) to *Pseudolatirus* and are not represented in our sequenced material. *Fusus clausicaudatus* Hinds, 1844 was placed in *Pseudolathyrus* [= *Pseudolatirus*] by Kaicher (1986, card no. 4706); it was treated in detail by Stahlschmidt & Fraussen (2012) who erected the new genus *Crassibougia* Stahlschmidt & Fraussen, 2012 to incorporate *F. clausicaudatus* and one more new species. *Pseudolatirus leucostriatus* Kosuge, 1979 is herein placed in synonymy with *Pseudolatirus kuroseanus*. Sabelli *et al.* (1990: 38) placed *Fusus marmoratus* Philippi, 1846 in *Pseudolatirus*, but we consider this species to be a true *Fusinus*. Finally, *Fusus pfeifferi* Philippi, 1846, with an uninformative original description and unknown type locality, was tentatively assigned to *Pseudolatirus* by MacNeil (1961: 83). We hereby treat it as a *nomen dubium*.

Family Fasciolariidae Gray, 1853
Subfamily Fusininae Wrigley, 1927

Granulifusus Kuroda & Habe, 1954

Type species

Fusus niponicus E.A. Smith, 1879, by original designation.

Genus composition

In addition to species previously assigned to the genus (Hadorn & Fraussen 2005), we include sequenced species *Granulifusus discrepans*, *G. williami* comb. nov., *G. jeanpierrevezzaroi* comb. nov., *G. annae* sp. nov. and *G. norfolkensis* sp. nov. In addition to those species we allocate to *Granulifusus*, based on conchological similarities to sequenced species, *G. tatianae* sp. nov., *G. kurodai* comb. nov., and *G. guidoi* sp. nov., known from empty shells only.

Granulifusus discrepans (Kuroda & Habe, 1961)
Figs 3A–E, 4A

Pseudolatirus discrepans Azuma, 1960: 45 (ex Kuroda MS). *nomen nudum*.

Pseudolatirus discrepans – Kuroda & Habe in Habe 1961: 66, pl. 33, fig. 6. — Habe 1962: 102, pl. 33, fig. 6. — Higo, Callomon & Gotō 2001: 87, fig. G3002 (holotype illustrated). — Mallard & Robin 2017: 152.
Granulifusus discrepans – Poppe 2008: pl. 343, fig. 1.

Molecular diagnosis

A molecular diagnosis is given in Table 2.

Type material

Holotype
JAPAN: off Cape Ashizuri, southwestern Shikoku (NSMT Mo 40377) (not seen).

Sequenced material

SOLOMON SEA: 1 lv, MADEEP, stn CP4337, SE Ainto Bay, New Britain, 06°07’ S, 149°17’ E, 287–447 m (MNHN IM-2013-46327).

PHILIPPINES: AURORA 2007, 1 lv, stn CP2657, 16°01′ N, 121°51′ E, 342–358 m (MNHN IM-2007-34604); 2 lv, stn CP2673, 15°01′ N, 121°45′ E, 431–493 m (MNHN IM-2007-34583, MNHN IM-2007-34488); 2 lv, stn CP2732, 15°27′ N, 121°36′ E, 556 m (MNHN IM-2007-34580, MNHN IM-2007-34581).

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Table 2. Molecular diagnostic characters of species of *Vermeijius* gen. nov.

Granulifusus annae sp. nov.	
Sequences analyzed	7
Independent combinations:	[631:'T']
	[31:'A', 641:'C']
	[34:'C', 352:'T']
	[49:'C', 76:'G']
	[55:'T', 266:'C']
	[58:'C', 418:'A']
	[97:'A', 541:'A']
	[100:'A', 121:'G']
	[115:'C', 529:'C']
	[139:'C', 451:'G']
	[205:'G', 385:'C']
	[223:'G', 401:'C']
	[316:'A', 466:'G']
	[337:'G', 649:'G']
	[361:'G', 421:'G']
Granulifusus williami comb. nov.	
Sequences analyzed	7
Independent combinations	[289:'T']
	[304:'C']
	[22:'G', 649:'G']
	[31:'G', 542:'C']
	[34:'T', 49:'C']
	[100:'A', 526:'G']
	[160:'G', 265:'T']
	[184:'A', 607:'C']
	[205:'A', 223:'G']
	[244:'G', 417:'C']
	[286:'A', 287:'C']
Granulifusus jeanpierrevezzaroi comb. nov.	
Sequences analyzed	3
Independent combinations	[25:'G', 328:'G']
	[31:'A', 55:'C']
	[34:'T', 541:'G']
	[79:'T', 400:'G']
	[103:'C', 578:'T']
	[106:'C', 199:'G']
	[205:'A', 634:'C']
	[274:'C', 548:'C']
	[283:'A', 559:'G']
	[298:'T', 640:'C']
	[301:'C', 352:'C']
	[313:'T', 355:'G']
	[322:'G', 607:'C']
	[337:'T', 445:'C']
	[418:'A', 637:'G']
	[481:'A', 568:'C']
Granulifusus discrepans (Kuroda & Habe, 1961)	
Sequences analyzed	6
Independent combinations	[373:'C']
	[34:'T', 85:'G']
	[46:'G', 568:'C']
	[55:'T', 271:'C']
	[67:'G', 91:'C']
	[100:'A', 652:'C']
	[115:'C', 604:'C']
	[205:'A', 478:'G']
	[259:'C', 547:'A']
	[287:'C', 655:'G']
	[316:'G', 355:'G']
	[337:'G', 400:'C']
	[458:'G', 526:'T']
	[475:'G', 607:'C']

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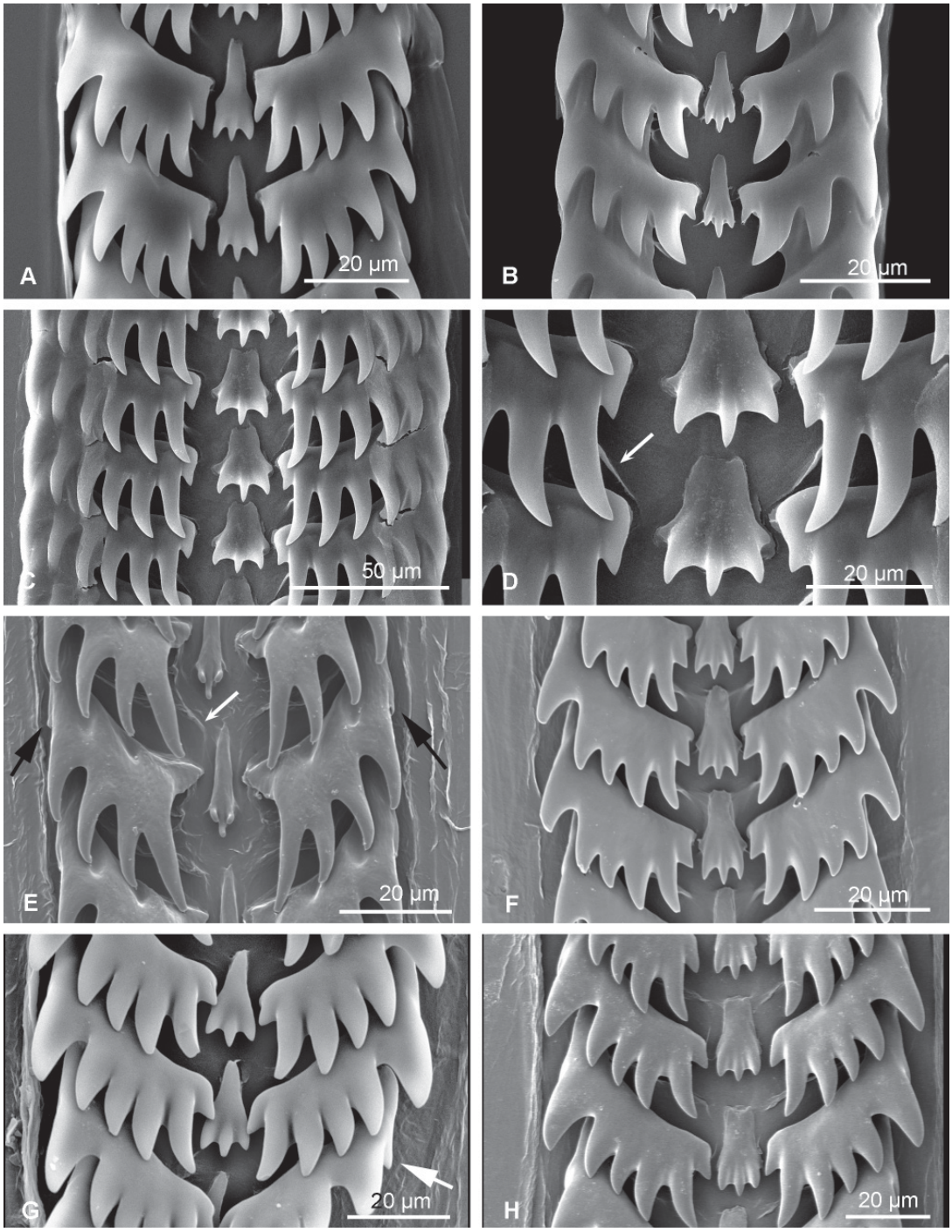

Fig. 4. Radulae of species of *Granulifusus* and *Okutanius* gen. nov. **A**. *Granulifusus discrepans* (Kuroda & Habe, 1961), shell, see Fig. 3D (MNHN IM-2013-46327). **B**. *Granulifusus williami* (Poppe & Tagaro, 2006), comb. nov., shell, see Fig. 3H (MNHN IM-2013-58726). **C–D**. *Granulifusus jeanpierrevezzaroi* (Cossignani, 2017) comb. nov., shell, see Fig. 5B–D, arrow points to regularly spaced folds of the radular membrane (MNHN IM-2007-34593). **E**. *Granulifusus annae* sp. nov., New Caledonia, BATHUS 1, stn CP669, 20°57′ S, 165°35′ E, 255–280 m, shell, see Fig. 6F. **F**. *Granulifusus tatianae* sp. nov., Loyalty Ridge, MUSORSTOM 6, stn DW473, 21°09′ S, 167°55′ E, 236 m. **G**. *Okutanius kuroseanus* (Okutani, 1975) gen. et comb. nov., New Ireland, shell, see Fig. 9A (MNHN IM-2013-59070). **H**. *Okutanius ellenae* gen. et sp. nov., New Caledonia, NORFOLK 1, stn DW1658, 23°26′ S, 167°50′ E, 320–336 m, shell, see Fig. 10H).

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Other examined material

PAPUA NEW GUINEA: 1 lv, PAPUA NIUGINI, stn CP3949, 5°12′ S, 145°51′ E, 380–407 m (MHNH 2013-15374, not sequenced); 1 lv, stn CP4023, 5°22′ S; 145°48′ E, 340–385 m (MNHN IM-2013-9777, not sequenced).

Description

Shell large, with multispiral protoconch of 2.75 conical, smooth, convex, grayish whorls, last ¼ whorl with 6–7 rounded axial riblets progressing in strength, protoconch/teleoconch boundary without varix, defined by appearance of spiral sculpture. Protoconch diameter 960 µm, exposed height 890 µm (Fig. 3E). Teleoconch with regularly convex whorls, upper ones slightly angulated, with long slightly sinuous to nearly straight siphonal canal; aperture in young specimens with 3–4 plicae, in adult with a single columellar plica, delimitating siphonal canal, and sometimes with indistinct parietal tooth. Axial sculpture of distinct axial ribs, 7–8 per whorl on upper whorls, obsolete on posterior whorls in shells over 50 mm. Spiral sculpture of 2–3 raised cords on periphery of upper whorls and numerous thin riblets of even strength. On posterior whorls, cords obsolete and some riblets more pronounced. Background colour tan, with darker brown spiral bands along suture.

Radula (MNHN IM-2013-46327, SL 18.2 mm, Fig. 4A) 1.83 mm in length (32% of AL without canal), of 75 transverse rows of teeth, of which 35 nascent. Radula narrow, distance between outer edges of lateral teeth about 65 µm (1.12% of AL). Lateral teeth medium broad, arcuate, with attenuated outer anterior corner, producing short 'handle'. Lateral teeth with five closely spaced, slightly curved cusps similar in length, small outermost cusp (seen on lower right lateral tooth on Fig. 4A), and much smaller but distinct innermost cusp. Central tooth small, very narrow, trapezoid, with three subequal cusps. Narrow but distinct transverse folds of radular membrane situated serially between rows of lateral teeth. Couto (2016: fig. 58) illustrated the radula of an adult specimen (SL 66 mm). The lateral teeth were relatively much broader, with 6 main cusps nearly identical in size and an additional innermost cusp. The radula had a similar width (1.1% of AL, measurements taken from photo) to the one studied herein; the differences in teeth morphology can possibly be explained by ontogenetic variability.

Distribution

From Japan throughout the East China Sea to the Philippines and the Solomons.

Remarks

This is the largest species of *Granulifusus*, which attains a shell length over 90 mm (http://www.conchology.be, last accessed 6 Mar. 2017). Due to the ontogenic change in sculpture pattern, the shell morphology differs from that in other Recent members of the genus, but the radula is similar. Young specimens bear a superficial resemblance to specimens of the Miocene species *Pseudolatirus bilineatus* of similar size (compare Fig. 3C, G with Fig. 3D', F').

Granulifusus williami (Poppe & Tagaro, 2006) comb. nov.
Figs 3H–K, 4B

Fusinus williami Poppe & Tagaro, 2006: 48, plate 1.

Fusinus williami – Mallard & Robin 2017: 106.

Molecular diagnosis

A molecular diagnosis is given in Table 2.

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Type material

Holotype

PHILIPPINES: off Dipolog, Aliguay Island, from 60 to 150 m, in the National Museum of the Philippines, Manila (not seen).

Paratypes

PHILIPPINES: 4 specimens in the former collection of E. de Suduiraut and Conchology, Inc., Mactan Island (not seen).

Sequenced material

PHILIPPINES: AURORA 2007, 1 lv, stn CP2709, 15°12′ N, 121°34′ E, 244–296 m (MNHN IM-2007-34608).

NEW CALEDONIA: CONCALIS, 1 lv, stn CP2960, North of New Caledonia, Grand Passage, (19°05′ S, 163°13′ E, 382–387 m (MNHN IM-2007-35734).

SOLOMON ISLANDS: SALOMON 2, 1 lv, stn DW2169, 09°01′ S, 159°06′ E, 100–200 m (MNHN IM-2007-32612).

SOCIETY ISLANDS: TARASOC, 2 lv, stn DW3441, 16°43′ S, 151°26′ W, 350–360 m (MNHN IM-2007-39387, MNHN IM-2007-39389); 1 lv, stn DW3491, 17°29′ S, 149°26′ W, 440–500 m (MNHN IM-2007-39262).

MADAGASCAR: ATIMO VATAE, 1 lv, stn DW3515, south Madagascar, 24°53′ S, 47°28′ E, 184–203 m (MNHN IM-2009-15090).

Other material examined (in MNHN if not otherwise mentioned)

TAIWAN: 3 dd, TAIWAN 2000, R/V *Fishery Researcher No. 1*, stn DW34, 22°02′ N, 120°36′ E, 246 m; 1 dd, stn CP35, 22°02′ N, 120°27′ E, 246 m; 1 dd, stn DW36, 21°55′ N, 120°36′ E, 305 m.

PHILIPPINES: 1 spm, Punta Engano, Mactan, in nets at 80–100 m (ANSP 456858); 1 spm, Olango, in lumun lumun nets, 40–100 m (ANSP 456859); 1 spm, Aliguay Island, trawled at 200 m (ANSP 456857); 4 spms, 'by boats from the Philippines' (ANSP 456854); 5 spms, same data as preceding (ANSP 456861); 2 spms, Balicasag Island, in tangle nets, 80–120 m (ANSP 456855); 2 spms, Aliguay Island, in coral rubble, 140 m (ANSP 456856); 2 spms, Aliguay Island, dredged on sandy/rocky mud, 160 m (ANSP 456860). – MUSORSTOM 3: 1 dd, stn CP96, 14°00′ N, 120°18′ E, 190–194 m.

ARAFURA SEA: KARUBAR: 5 dd, stn DW29, 05°36′ S, 132°56′ E, 181–184 m; 1 dd, stn DW32, 05°47′ S, 132°51′ E, 170–206 m.

SOLOMON ISLANDS: SALOMON 1: 6 dd, stn DW1745, 09°23′ S, 159°59′ E, 253–356 m; 1 dd, stn DW1758, 08°49′ S, 159°52′ E, 180–187 m; 1 lv, 8 dd, stn DW1768, 08°21′ S, 160°42′ E, 194–286 m; 3 dd, stn DW1778, 08°19′ S, 160°34′ E, 157–253 m; 1 lv, 6 dd, stn DW1788, 09°19′ S, 160°15′ E, 341–343 m; 1 dd, stn DW1811, 09°46′ S, 160°51′ E, 182–203 m; 1 dd, stn DW1813, 09°47′ S, 160°53′ E, 201–227 m; 3 dd, stn DW1820, 09°52′ S, 160°51′ E, 256–329 m; 1 juv. dd, stn DW1834, 10°12′ S, 161°18′ E, 225–281 m.

PAPUA NEW GUINEA: KAVIENG 2014: 1 lv, stn DW4471, 02°44′ S, 150°38′ E, 126–220 m (MNHN IM-2013-58726, not sequenced); 1 lv, stn DW4484, 02°26′ S, 149°55′ E, 229 m (MNHN IM-2013-58866, not sequenced).

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NEW CALEDONIA: BIOCAL: 1 dd, stn DW43, 22°46′ S, 167°15′ E, 400 m; 1 dd, stn DW82, 20°31′ S, 166°50′ E, 440–460 m; 1 dd, stn DW83, 20°35′ S, 166°54′ E, 460 m. – BIOGEOCAL: 5 dd, stn KG252, 21°31′ S, 166°21′ E, 330 m; 16 juv. dd, stn DW253, 21°32′ S, 166°29′ E, 310–315 m; 1 dd, stn DW292, 20°28′ S, 166°48′ E, 465–470 m; 3 dd, stn DW308, 20°40′ S, 166°58′ E, 510–590 m. – SMIB 2: 2 dd, stn DW23, 22°31′ S, 167°37′ E, 410–420 m. – SMIB 5: 3 dd, stn DW88, 22°19′ S, 166°40′ E, 350 m; 1 dd, stn DW98, 23°02′ S, 168°16′ E, 335 m. –SMIB 6: 1 lv, stn DW126, 18°59′ S, 163°23′ E, 320–330 m. – SMIB 8: 3 dd, stn DW165, 24°47′ S, 168°10′ E, 372–660 m; 1 dd, stn DW187, 23°17′ S, 168°06′ E, 390–540 m; 3 dd, stn DW189, 23°18′ S, 168°06′ E, 400–402 m. – CHALCAL 2: 1 lv, 2 dd, stn DW69, 24°44′ S, 168°08′ E, 260 m. – BATHUS 1: 2 dd, stn DW683, 20°35′ S, 165°07′ E, 380–400 m; 1 dd, stn DW687, 20°35′ S, 165°07′ E, 408–440 m; 1 dd, stn DW688, 20°33′ S, 165°00′ E, 270–282 m; 1 juv. lv, stn CP698, 20°34′ S, 164°57′ E, 491–533 m; 1 dd, stn CP701, 20°58′ S, 165°36′ E, 302–335 m. – BATHUS 2: 1 lv, 3 dd, stn DW724, 22°48′ S, 167°26′ E, 344–358 m; 2 lv, 7 dd, stn DW730, 23°03′ S, 166°58′ E, 397–400 m; 3 lv, stn DW731, 22°49′ S, 166°45′ E, 300–370 m; 1 dd, stn CP759, 22°18′ S, 166°10′ E, 370–420 m. – BATHUS 3: 8 lv+dd, stn DW827, 23°22′ S, 168°01′ E, 381–469 m; 1 lv, stn DW838, 23°01′ S, 166°56′ E, 400–402 m. – BATHUS 4: 2 dd, stn DW885, 22°05′ S, 165°58′ E, 250–300 m; 3 dd, stn DW887, 21°07′ S, 164°28′ E, 320–344 m; 1 lv, stn CP889, 21°01′ S, 164°27′ E, 416–433 m; 6 dd, stn DW902, 19°01′ S, 163°15′ E, 341–351 m; 2 dd, stn CP907, 19°01′ S, 163°13′ E, 370–394 m; 1 dd, stn DW943, 20°12′ S, 164°31′ E, 316–347 m. – BERYX 11: 15 lv+dd, stn DW11/CP23, 24°43′–24°44′ S, 168°08′–168°10′ E, 270–350 m. – MUSORSTOM 5: 2 lv, 3 dd, stn 301, 22°07′ S, 159°25′ E, 487–610 m, Nova Bank. – MUSORSTOM 6: 3 lv, 3 dd, stn DW391, 20°47′ S, 167°06′ E, 390 m; 1 lv, 2 dd, stn DW392, 20°47′ S, 167°05′ E, 340 m; 1 dd, stn DW393, 20°48′ S, 167°10′ E, 420 m; 3 dd, stn DW397, 20°47′ S, 167°05′ E, 380 m; 1 lv, 2 dd, stn DW398, 20°47′ S, 167°06′ E, 370 m; 12 lv+dd, stn DW406, 20°41′ S, 167°07′ E, 373 m; 3 dd, stn DW411, 20°40′ S, 167°03′ E, 424 m; 1 lv, 1 dd, stn DW413, 20°40′ S, 167°03′ E, 463 m; 3 dd, stn DW416, 20°42′ S, 167°00′ E, 343 m; 1 lv, stn DW421, 20°26′ S, 166°40′ E, 245 m; 1 dd, stn DW428, 20°24′ S, 166°13′ E, 420 m; 1 dd, stn DW451, 20°59′ S, 167°25′ E, 330 m; 2 lv, 5 dd, stn DW457, 21°00′ S, 167°29′ E, 353 m; 2 lv, 3 dd, stn DW479, 21°09′ S, 167°55′ E, 310 m; 1 lv, stn DW480, 21°08′ S, 167°56′ E, 380 m; 2 lv, 2 dd, stn DW481, 21°22′ S, 167°50′ E, 300 m. – VOLSMAR: 1 dd, stn DW9, 22°23′ S, 171°41′ E, 275–300 m; 1 dd, stn DW38, 22°22′ S, 168°44′ E, 380–420 m; 1 dd, stn DW51, 20°59′ S, 170°03′ E, 450 m. – NORFOLK 1: 3 lv, stn DW1680, 24°45′ S, 168°10′ E, 385–392 m.

VANUATU: MUSORSTOM 8: 1 lv, stn DW963, 20°20′ S, 169°49′ E, 400–440 m; 1 dd, stn DW964, 20°20′ S, 169°49′ E, 360–408 m; 1 dd, stn DW967, 20°19′ S, 169°53′ E, 295–334 m; 3 dd, stn DW977, 19°25′ S, 169°29′ E, 410–505 m; 8 dd, stn DW978, 19°23′ S, 169°27′ E, 408–413 m; 3 dd, stn DW988, 19°16′ S, 169°24′ E, 372–466 m; 1 dd, stn DW1060, 16°14′ S, 167°21′ E, 375–397 m; 3 dd, stn DW1065, 16°16′ S, 167°21′ E, 360–419 m.

WALLIS AND FUTUNA: MUSORSTOM 7: 3 lv(?), stn DW510, 14°14′ S, 178°11′ W, 280–370 m.

FIJI: MUSORSTOM 10: 9 lv+dd, stn CP1325, 17°16′ S, 177°50′ E, 282–322 m; 2 lv, stn CP1326, 17°14′ S, 177°50′ E, 265–300 m; 7 lv+dd, stn CP1327, 17°13′ S, 177°52′ E, 370–389 m; 1 dd, stn DW1384, 18°19′ S, 178°06′ E, 260–305 m; 7 dd, stn DW1388, 18°19′ S, 178°02′ E, 313–446 m; 2 lv, stn CP1389, 18°19′ S, 178°05′ E, 241–417 m; 1 lv, 2 dd, stn CP1390, 18°19′ S, 178°05′ E, 234–361 m. – BORDAU 1: 1 dd, stn DW1417, 16°27′ S, 178°55′ W, 353 m; 1 lv, 1 dd, stn DW1450, 16°44′ S, 179°58′ E, 327–420 m; 1 lv, stn CP1476, 19°41′ S, 178°11′ W, 310–420 m; 2 lv, 3 dd, stn DW1479, 20°58′ S, 178°45′ W, 450–460 m; 2 lv, stn CP1481, 20°57′ S, 178°45′ W, 441–506 m; 2 lv, stn DW1496, 18°43′ S, 178°23′ W, 392–407 m; 3 dd, stn DW1499, 18°40′ S, 178°27′ W, 389–400 m; 1 lv, stn CP1500, 18°42′ S, 178°26′ W, 366–389 m.

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TONGA: BORDAU 2: 2 dd, stn DW1518, 21°21′ S, 175°07′ W, 336–347 m; 2 dd, stn DW1534, 21°43′ S, 175°19′ W, 302–327 m; 2 dd, stn DW1535, 21°43′ S, 175°18′ W, 268 m; 1 lv, stn DW1536, 21°45′ S, 175°21′ W, 320–323 m; 1 dd, stn DW1567, 21°02′ S, 175°19′ W, 351–356 m; 1 dd, stn DW1583, 18°37′ S, 174°03′ W, 327–360 m; 1 dd, stn DW1585, 18°33′ S, 173°57′ W, 578 m; 1 lv, stn DW1586, 18°34′ S, 173°55′ W, 440–487 m; 1 lv, 3 dd, stn DW1607, 22°15′ S, 175°23′ W, 356–367 m; 4 dd, stn DW1631, 23°23′ S, 176°18′ W, 407–443 m; 2 dd, stn DW1634, 21°45′ S, 175°20′ W, 321–322 m; 2 dd, stn DW1635, 21°44′ S, 175°20′ W, 320–323 m; 2 dd, stn DW1636, 21°44′ S, 175°20′ W, 321–331 m; 1 lv, stn CP1641, 21°09′ S, 175°22′ W, 395 m,.

RÉUNION: MD32: 9 dd, stn DC128, 20°51′ S, 55°36′ E, 280–340 m; 10 dd, stn CP129, 20°51′ S, 55°36′ E, 290–300 m; 1 dd, stn DC136, 20°46′ S, 55°36′ E, 915–922 m.

Description

Shell slender, fusiform, small to medium-sized for genus (attaining 30.8 mm, ANSP 456861). Protoconch multispiral of 4.25 whorls (Fig. 3K), conical, smooth, except scattered microgranules more dense along suture, flesh coloured with reddish thin line along suture. Whorls somewhat convex, last ½ whorl with 11–12 rounded axial riblets progressing in strength, protoconch/teleoconch boundary without varix, defined by appearance of spiral sculpture. Protoconch diameter 1000 µm, exposed height 1240 µm. Teleoconch whorls convex, suture deep, adpressed. Axial sculpture of very prominent ribs, 7–9 per whorl. Spiral sculpture of evenly spaced strong cords, 2 on first whorl, 3–4 on penultimate whorl, 8–9 on last whorl and shell base, becoming much weaker on canal. Weaker but distinct secondary cords between primary cords, one on earliest whorls increasing to 5 on last whorl, primary and secondary cords becoming similar in size on canal. Siphonal canal long, open, straight, about ⅓ of shell length. Aperture with 7–8 smooth teeth periodically appearing and corresponding to interspaces between axial ribs. Inner lip adherent, forming smooth, white columellar callus, 2–3 distinct columellar rounded plicae, adapical two more prominent than abapical one. Teleoconch light brown, usually with lighter spiral band on whorls periphery.

Radula (MNHN IM-2013-58726, SL 14.1, AL 3.1 mm, Fig. 4 B) 2.13 mm in length (69% of AL), of about 125 transverse rows of teeth, of which 30 nascent. Radula narrow, distance between outer edges of lateral teeth about 50 µm (1.6% of AL without canal). Lateral teeth medium broad, arcuate, with attenuated outer anterior corner, producing long ‘handle’. Lateral teeth with three cusps on right side and four on left side, subequal in length, closely spaced, slightly curved and an additional small but distinct innermost cusp. Inner cusp(s) slightly narrower than lateral ones. Central tooth small, long trapezoid with narrower base, with three cusps, central one nearly twice as long as outer ones.

Distribution

Very widely distributed: in Indo-Pacific, from Taiwan and the Philippines, to French Polynesia, Madagascar and off Réunion. Recorded at depths from 170 to 920 m, alive in 225–610 m. Unconfirmed depths from commercial sources in the Philippines from 40 m.

Remarks

The species has a smooth columella and therefore is well differentiated from its congeners with columellar plicae. Besides, *G. williami* comb. nov. has a small, rather slender shell with attenuated straight canal. It is most similar to *Granulifusus norfolkensis* sp. nov., differing in details of colouration and in having a straight siphonal canal rather than inclined to left. Molecular data clearly separate the two species.

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Granulifusus jeanpierrevezzaroi (Cossignani, 2017) comb. nov.
Figs 4C–D, 5

Pseudolathyrus cf. *kurodai* Springsteen & Leobrera, 1986: 177, pl. 48 fig. 1.
Fusolatirus kuroseanus Thach, 2007: 118, pl. 29, no. 518 (not of Okutani 1975).
Pseudolatirus jeanpierrevezzaroi Cossignani, 2017: 14–15.

Pseudolatirus jeanpierrevezzaroi – Mallard & Robin 2017: 152.

Molecular diagnosis

A molecular diagnosis is given in Table 2.

Type material

Holotype
VIETNAM: off Nha Trang, SL 66.3 mm (MMM) (not seen).

Sequenced material

NEW CALEDONIA: TERRASSES: 1 lv, stn CP3095, 22°02′ S, 167°06′ E, 320–380 m (MNHN IM-2007-36886). – CONCALIS: 1 lv, stn CP3026, Grand Passage, 20°17′ S, 163°50′ E, 590–809 m (MNHN IM-2007-35083).

PHILLIPPINES: AURORA 2007: 1 lv, stn CP2748, 15º56′ N, 121º465′ E, 247–249 m (MNHN IM-2007-34593).

Other material examined

SOUTH AFRICA: 2 spms, Agulhas Bank, 160 m (ANSP 425332); 1 spm, Agulhas Bank, 160 m (ANSP 425328); 3 spms, off Durban (ANSP 425336).

TAIWAN: 2 spms, trawled (ANSP 425339); 2 spms, 'by divers under rocks, southeast Sea of Formosa' (ANSP 425338); 2 spms, SW of Taiwan, 140–200 m (ANSP 425335); 2 spms, 200–300 m (ANSP 425333); 1 spm, China Sea, off Taiwan (ANSP 425329); 4 spms, trawled (ANSP 425334).

MOZAMBIQUE: 3 spms (ANSP 425340).

VIETNAM: 1 spm, Nha Trang region, 20–35 m (ANSP 425341).

SOUTH CHINA SEA: 2 spms, on sand bottom (ANSP 422786); 1 spm, 'deep water' (ANSP 422785).

PHILIPPINES: 3 spms, off Bohol, tangle nets (ANSP 425330); 1 spm, Philippine Is (ANSP 425331); 1 dd, off Mindanao (ANSP 425337). – MUSORSTOM 2: 5 lv, stn CP02, 14°01′ N, 120°17′ E, 184–186 m; 37 lv+dd, stn CP26, 13°49′ N, 120°50′ E, 299–320 m; 18 lv+dd, stn CP68, 14°01′ N, 120°18′ E, 195–199 m; 1 lv, stn CP80, 13°45′ N, 120°37′ E, 178–205 m. – MUSORSTOM 3: 1 lv?, stn CP97, 14°00′ N, 120°18′ E, 189–194 m; 5 lv, stn CP112, 14°00′ N, 120°18′ E, 187–199 m.

NEW CALEDONIA: '*Vauban*' 1978–79: 1 dd, stn DR34, 22°32′ S, 166°26′ E, 350–420 m; 1 lv, stn DR40, 22°30′ S, 166°24′ E, 250–350 m. – LAGON: 1 lv, stn 1062, 20°15′ S, 163°53′ E, 300–320 m. – BATHUS 1: 2 lv, 4 dd, stn CP656, 21°13′ S, 165°54′ E, 452–460 m; 2 dd, stn CP657, 21°14′ S, 165°55′ E, 490–530 m; 1 dd, stn CP669, 20°57′ S, 165°35′ E, 255–280 m; 1 lv, 1 dd, stn CP670, 20°54′ S, 165°53′ E, 394–397 m; 1 dd, stn DW683, 20°35′ S, 165°07′ E, 380–400 m; 8 lv, 1 dd, stn CP695, 20°35′ S, 164°58′ E, 410–430 m; 1 dd, stn CP701, 20°58′ S, 165°36′ E, 302–335 m; 1 lv, stn

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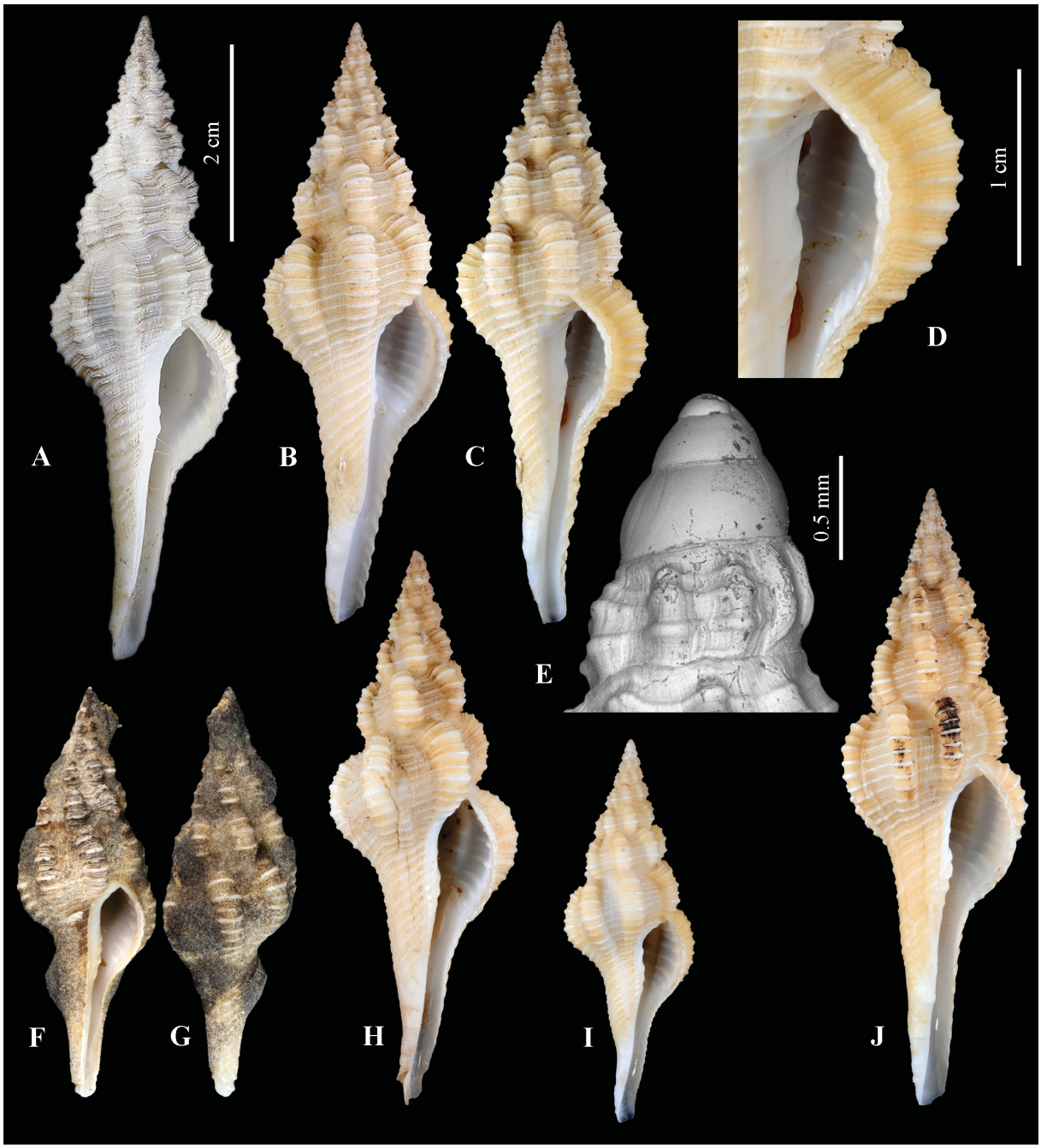

Fig. 5. *Granulifusus jeanpierrevezzaroi* (Cossignani, 2017) comb. nov. **A**. Holotype, SL 66.3 mm (MMM) (photo courtesy of T. Cossignani). **B–D**. Sequenced specimen, SL 62.2 mm (MNHN IM-2007-34593). **D**. Enlarged view of columella to show the plicae. **E**. Protoconch, New Caledonia, BATHUS 1, stn CP713, 21°45′ S, 166°37′ E, 250 m. **F–G**. Philippines, MUSORSTOM 3, stn CP97, 14°00′ N, 120°18′ E, 189–194 m, SL 42.2 mm. **H**. Fiji, MUSORSTOM 10, stn CP1355, 17°50′ S, 178°49′ E, 302–310 m, SL 56.8 mm. **I**. New Caledonia, BATHUS 1, stn CP670, 20°54′ S, 165°53′ E, 394–397 m, SL 39.4 mm. **J**. Philippines, MUSORSTOM 2, stn CP68, 14°01′ N, 120°18′ E, 195–199 m, SL 63.7 mm. All shells to the same scale, except D–E.

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DE705, 21°02′ S, 165°38′ E, 350–400 m; 5 lv, stn CP707, 21°43′ S, 166°36′ E, 347–375 m; 2 dd, stn CP710, 21°43′ S, 166°36′ E, 320–386 m; 1 lv, stn CP711, 21°43′ S, 166°36′ E, 315–327 m; 1 lv, stn CP712, 21°44′ S, 166°35′ E, 210 m; 1 lv, stn CP713, 21°45′ S, 166°37′ E, 250 m. – BATHUS 4: 3 lv, stn CP946, 20°34′ S, 164°58′ E, 386–430 m; 3 lv, stn CP947, 20°34′ S, 164°58′ E, 470–490 m.

FIJI: MUSORSTOM 10: 6 dd, stn CP1320, 17°17′ S, 177°54′ E, 290–300 m; 1 lv, 2 dd, stn CP1325, 17°16′ S, 177°50′ E, 282–322 m; 1 lv, stn CP1326, 17°14′ S, 177°50′ E, 265–300 m; 1 lv, stn DW1347, 17°31′ S, 178°40′ E, 344–349 m; 5 lv, 4 dd, stn CP1348, 17°30′ S, 178°40′ E, 353–390 m; 1 dd, stn CP1351, 17°31′ S, 178°40′ E, 292–311 m; 1 lv, stn CP1355, 17°50′ S, 178°49′ E, 302–310 m; 2 lv, 1 dd, stn CP1360, 18°00′ S, 178°48′ E, 402–444 m; 3 lv, stn CP1368, 18°11′ S, 178°24′ E, 380–469 m; 1 dd, stn CP1369, 18°11′ S, 178°23′ E, 392–433 m.

TONGA: BORDAU 2: 3 dd, stn CP1510, 21°05′ S, 175°23′ W, 461–497 m.

Description

Shell slender, fusiform, large for genus (to 90.0 mm, ANSP 425335). Protoconch multispiral, conical, smooth, translucent pale grey, of 3.25 somewhat convex whorls, last ½ whorl with 4–6 rounded axial riblets progressing in strength, protoconch/teleoconch boundary without varix. Protoconch diameter 1100 µm, exposed height 1280 µm (Fig. 5E). Teleoconch whorls convex, suture deep, adpressed. Axial sculpture of very prominent ribs, 7–9 per whorl. Spiral sculpture of evenly spaced strong cords, 2–3 on first whorl, 6–8 on penultimate whorl, about 23–25 on last whorls, becoming evanescent towards tip of canal. Weaker secondary cords between primary strong cord pairs, 1 on earliest whorls increasing to 3 on later whorls. Siphonal canal long, open, straight, about ⅓ of shell length. Aperture with 7–12 interior lirae. Inner lip adherent, forming smooth, white columellar callus, with 3 rounded columellar plicae, adapical two more prominent than abapical one. In side view additional adapicalmost weak plicae can be observed. Teleoconch pale flesh to pale orange-brown with lighter prominent axial cords. Periostracum medium to dark brown.

Radula (MNHN IM-2007-34593, 62.2 mm, Fig. 4C–D) 2.6 mm in length (13% of AL), of more than 105 transverse rows of teeth, of which 37 nascent. Radula narrow, distance between outer edges of lateral teeth about 130 µm (0.67% of AL without canal). Lateral teeth medium broad, arcuate, with attenuated outer anterior corner, producing short 'handle', and with six cusps, subequal in length, closely spaced, slightly curved and one additional small but distinct innermost cusp. Central tooth small, trapezoid with narrower base, with three cusps, central narrowest. Narrow but distinct transverse folds of the membrane situated serially between rows of lateral teeth (arrow). The radula of an additional specimen was examined and it is generally similar, although the left lateral teeth have five cusps, while vs six on the right teeth; also the central teeth are relatively narrower and longer, tricuspid with central cusp longest.

Body morphology and digestive system anatomy are in all details similar to *Angulofusus nedae* Fedosov & Kantor, 2012, the major difference being the longer and thinner proboscis, which attains 20 mm in studied specimen (2.2 AL without canal) and is coiled within rhynchodeum.

Distribution

Throughout the tropical Indo-West Pacific, at depths 140–809 m, one specimen from commercial sources said to have been collected in 20–35 m (Vietnam).

Remarks

Conchologically the species is most similar to *Granulifusus annae* sp. nov. which has a similar size, but *G. jeanpierrevezzaroi* comb. nov. differs in having fewer axial ribs per whorl and being nearly uniformly

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coloured with lighter spiral cords, while in *Granulifusus annae* sp. nov. the spiral cords are darker than the background. These two species also differ in radular morphology.

Granulifusus jeanpierrevezzaroi comb. nov. is a very common species in the Philippines and is found on soft bottoms throughout the tropical Indo-West Pacific. It is remarkable that the species still had to be named, although it had been illustrated several times under incorrect names. Shells of many specimens are covered with zoantharians (e.g., Fig. 5F–G).

Granulifusus annae sp. nov.
urn:lsid:zoobank.org:act:76CA2DC8-A32A-4164-9218-8B50E9AEB780
Figs 4E, 6

Pseudolatirus kurodai Couto *et al.*, 2016: table 1, fig. 6J (not of Okutani & Sakurai 1964).
Pseudolatirus kuroseanus Couto, 2016: 41, fig. 28 (not of Okutani 1975). [The shell depicted under the same name on fig. 27 was accidentally switched in the collection with the shell of sequenced specimen MNHN IM-2013-14709]

Molecular diagnosis

A molecular diagnosis is given in Table 2.

Diagnosis

Shell thin but solid, slender, fusiform, up to 55 mm, protoconch multispiral of 2.25 whorls. Teleoconch whorls convex, axial sculpture of broad, raised axial ribs, spiral sculpture of evenly spaced, strong cords, 35 on last whorl. Aperture lirate inside, columella with several weak plicae. Teleoconch light tan with darker spiral cords.

Etymology

The specific epithet pays homage to Ann Snyder, in fitting tribute for this elegant and beautiful species.

Type material

Holotype

PAPUA NEW GUINEA: Rempi Area, 05°03′ S, 145°49′ E, 120 m, expedition PAPUA NIUGINI, stn PP08, sequenced (Fig. 6A–C) (MNHN IM-2013-14709).

Sequenced material

NEW CALEDONIA: EXBODI: 1 lv, stn CP3823, 21°55′ S, 166°55′ E, 246–255 m (MNHN IM-2013-42520).

PHILIPPINES: AURORA 2007: 3 lv, stn CP2716, 14°30′ N, 121°41′ E, 335–356 m (MNHN IM-2007-34487, MNHN IM-2007-34585, MNHN IM-2007-34609); 2 lv, stn CP2717, 14°29′ N, 121°43′ E, 311–361 m (MNHN IM-2007-34486, MNHN IM-2007-34586).

Other material examined (all in MNHN)

VANUATU: MUSORSTOM 8: 2 dd, stn DW1003, 18°49′ S, 168°59′ E, 200–327 m; 1 lv, stn CP1123, 15°07′ S, 166°55′ E, 262–352 m.

NEW CALEDONIA: HALIPRO 1: 1 dd, stn CP853, 21°45′ S, 166°37′ E, 241–250 m; 2 juv. dd, stn CC855, 21°45′ S, 166°37′ E, 204–220 m; 2 dd, 1 juv. dd, stn CP866, 21°26′ S, 166°17′ E, 550–600 m. – BATHUS 1: 1 lv (radula examined), stn CP669, 20°57′ S, 165°35′ E, 255–280 m; 2 dd, stn CP695,

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20°35′ S, 164°58′ E, 410–430 m; 1 dd, stn CP710, 21°43′ S, 166°36′ E, 320–386 m; 1dd, stn CP713, 21°45′ S, 166°37′ E, 250 m.

LOYALTY RIDGE: MUSORSTOM 6: 1 lv(?), stn DW449, 20°54′ S, 167°18′ E, 300 m.

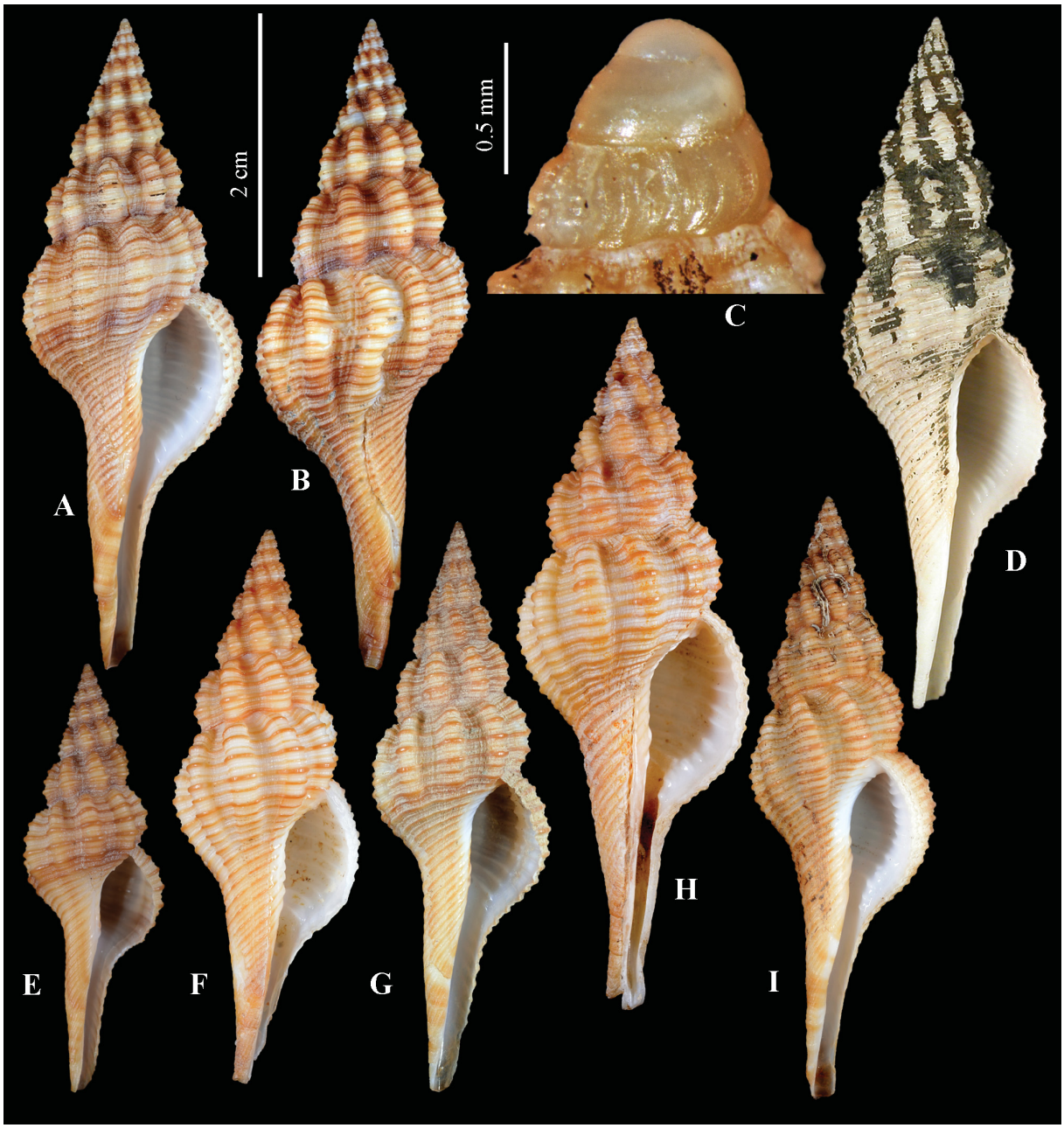

Fig. 6. *Granulifusus annae* sp. nov. **A–C**. Holotype, sequenced, SL 50.3 mm (MNHN IM-2013-14709). **C**. Protoconch. **D**. Philippines, SL 54 mm, sequenced specimen (MNHN IM-2007-34486). **E**. New Caledonia, SL 23.1 mm, sequenced specimen (MNHN IM-2013-42520). **F–G**. New Caledonia, BATHUS 1, stn CP669, 20°57′ S, 165°35′ E, 255–280 m. **F**. SL 42.7 mm (radula, see Fig. 4E). **G**. SL 42.7 mm. **H**. New Caledonia, BATHUS 1, stn CP695, 20°35′ S, 164°58′ E, 410–430 m, SL 53.6 mm. **I**. Vanuatu, MUSORSTOM 8, stn CP1123, 15°07′ S, 166°55′ E, 262–352 m, SL 46.8 mm. All shells to the same scale.

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FIJI: MUSORSTOM 10: 1 dd, stn CP1320, 17°16.8′ S, 177°53.6′ E, 290–300 m; 1dd, stn DW1384, 18°18.5′ S, 178°05.8′ E, 260–305 m. – BORDAU 1: 1 lv(?), 2 dd, stn CP1402, 16°38′ S, 179°36′ E, 260–279 m; 1lv, 1dd, stn CP1403, 16°40′ S, 179°36′ E, 220–224 m.

Description

Shell thin, slender, fusiform, consisting of 2.25 protoconch and 8.5 teleoconch whorls (in holotype). Protoconch bluntly conical (Fig. 6C), with moderately convex whorls, last ½ whorl with 6 axial riblets, protoconch/teleoconch discontinuity distinct. Protoconch diameter 930 µm, exposed height 850 µm. Teleoconch whorls convex, suture deep, impressed. Axial sculpture of broad, raised axial ribs, running from suture to suture, in holotype 9 on first whorl, 8 on 2nd–6th whorls and 9 on last whorl. Spiral sculpture of evenly spaced, strong, raised cords, 3–4 on earlier whorls, abapicalmost strongest, 6 on antepenultimate and penultimate whorls, 35 on last whorl. Between major cords, 1–3 smaller secondary cords, slightly nodulose at intersection with raised growth lines. Siphonal canal open, long, straight. Aperture with 12 weak lirae inside. Inner lip completely adherent to columella, forming very thin, shiny columellar callus with 5 weak columellar plicae. No umbilicus. Protoconch light brown, interior of aperture white. Teleoconch light-tan with still lighter spiral band on shell periphery, spiral cords tan, usually darker than background, upper spiral whorls brownish adapically.

Operculum small, length in holotype 5.3 mm, occupying slightly more than ⅓ of aperture without canal, oval, nucleus supposingly terminal, older part of operculum missing.

Holotype measurements: SL 50.3 mm, AL (with canal) 30.0 mm, SW 15.9 mm.

Radula (Fig. 4E, New Caledonia, BATHUS 1, stn CP669, 20°57′ S, 165°35′ E, 255–280 m, shell on Fig. 6F) narrow, distance between outer edges of lateral teeth about 60 µm (0.48% of AL without canal). Lateral teeth medium broad, arcuate, with attenuated outer anterior corner, producing medium long 'handle'. Lateral teeth with outermost very short small cusp (Fig. 4E, black arrows), four broadly spaced and slightly recurved, long cusps, subequal in length. Inner anterior corner also attenuated, forming a triangular outgrowth, sometimes bearing indistinct an additional innermost small cusp. Central tooth small, very narrow (length to width ratio 5), with three short and blunt cusps, central longest. Narrow but distinct transverse folds of membrane situated serially between rows of lateral teeth, on both sides of central teeth (white arrow).

The radula of the holotype was examined and illustrated by Couto (2016: fig. 28) under the name *Pseudolatirus kuroseanus*. It is in all details similar to the radula figured here, the minor differences are that the outermost small cusp is more distinct, the innermost outgrowth bears a distinct small cusp, and the cusps of the central teeth are sharp rather than blunt.

Distribution

Philippines, New Caledonia, Papua New Guinea, Vanuatu, Fiji, 120–600 m, alive in 120–360 m.

Remarks

This species is moderately variable both in slenderness of the shell and in whorl convexity. Rarely the spiral cords are lighter than the shell background (observed in sequenced juvenile specimen MNHN IM-2007-34609).

This new species is similar to *G. kurodai* comb. nov. and has been confused with it, but can be distinguished by a different protoconch, consisting of 2.25 whorls in *G. annae* sp. nov. rather than only 1.75 whorls in *G. kurodai* comb. nov., as well as by a straight siphonal canal, darker shell coloration, and more pronounced and less numerous primary spiral cords (6 on penultimate whorl in *G. annae*

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sp. nov. and 10 in paratype of *G. kurodai* comb. nov.). The species is also conchologically similar to *G. jeanpierrevezzaroi* comb. nov., differing in the more brownish background shell colour with more contrastingly coloured spiral cords, more dense axial ribs and a smaller protoconch. The molecular analysis clearly differentiates these species.

The radula of the new species is somewhat different from its congeners in having longer and more broadly spaced cusps on the lateral teeth.

Granulifusus norfolkensis sp. nov.
urn:lsid:zoobank.org:act:7483C94B-51FD-44D8-B117-B7140B65F385
Fig. 7A–D

Diagnosis

Shell thin, slender, fusiform, up to 14 mm, protoconch of 4 whorls. Teleoconch whorls weakly convex, axial sculpture of narrow, broadly spaced, axial ribs, spiral sculpture of evenly spaced, strong primary cords, 7 on last whorl and weaker secondary cords between them. Aperture weakly lirate inside, columella with several distinct columellar plicae. Teleoconch light tan with several brown spiral bands present, also on siphonal canal.

Etymology

The specific epithet refers to the collecting locality, the Norfolk Ridge, where the first known specimen of this species was collected.

Type material

Holotype

NEW CALEDONIA: north of Ile des Pins, 22°28′ S, 167°29′ E, 404–405 m, expedition KANACONO, stn DW4685, sequenced (MNHN IM-2013-68811).

Other material examined

NEW CALEDONIA: 1 lv, TERRASSES, stn DW3063, Norfolk Ridge, 23°23′ S, 168°00′ E, 430–480 m, sequenced (MNHN IM-2007-36921).

Description

Shell thin, slender, fusiform, of nearly 4 protoconch and 5 teleoconch whorls (in holotype). Protoconch acutely conical (Fig. 7C), with moderately convex whorls, last ½ whorl with 6 axial, progressively thickening, riblets, protoconch/teleoconch transition abrupt, marked by onset of distinctive sculpture. Protoconch diameter 1130 µm, exposed height 1150 µm. Teleoconch whorls weakly convex, suture deeply impressed. Axial sculpture of broad, prominent ribs extending from suture to suture (7 per whorl in holotype), including on last and penultimate whorls. Spiral sculpture of evenly spaced, strong, raised cords, nodulous at crossings with axial ribs, in holotype 2 on first whorl, 3 on other whorls, 7 on last whorl before transition to canal. Three or four weaker secondary cords situated between primary cords, slightly nodulous at intersections with raised growth lines. Two brown secondary cords situated in each interspace between primary cords on last whorl. Siphonal canal open, long, slightly turned to left and recurved, sculptured by 25 (in holotype) weaker cords of slightly uneven strength. Aperture with 8 weak lirae inside. Inner lip completely adherent to columella, forming very thin, shiny columellar callus with 4 columellar plicae, first very weak. No umbilicus. Protoconch transparent flesh colour, interior of aperture white. Teleoconch light tan with several brown spiral bands also present on canal. Major spiral cords slightly lighter than background, secondary spiral cords mostly brown.

Holotype measurements: SL 13.0 mm, AL (without canal) 3.5 mm, SW 4.7 mm.

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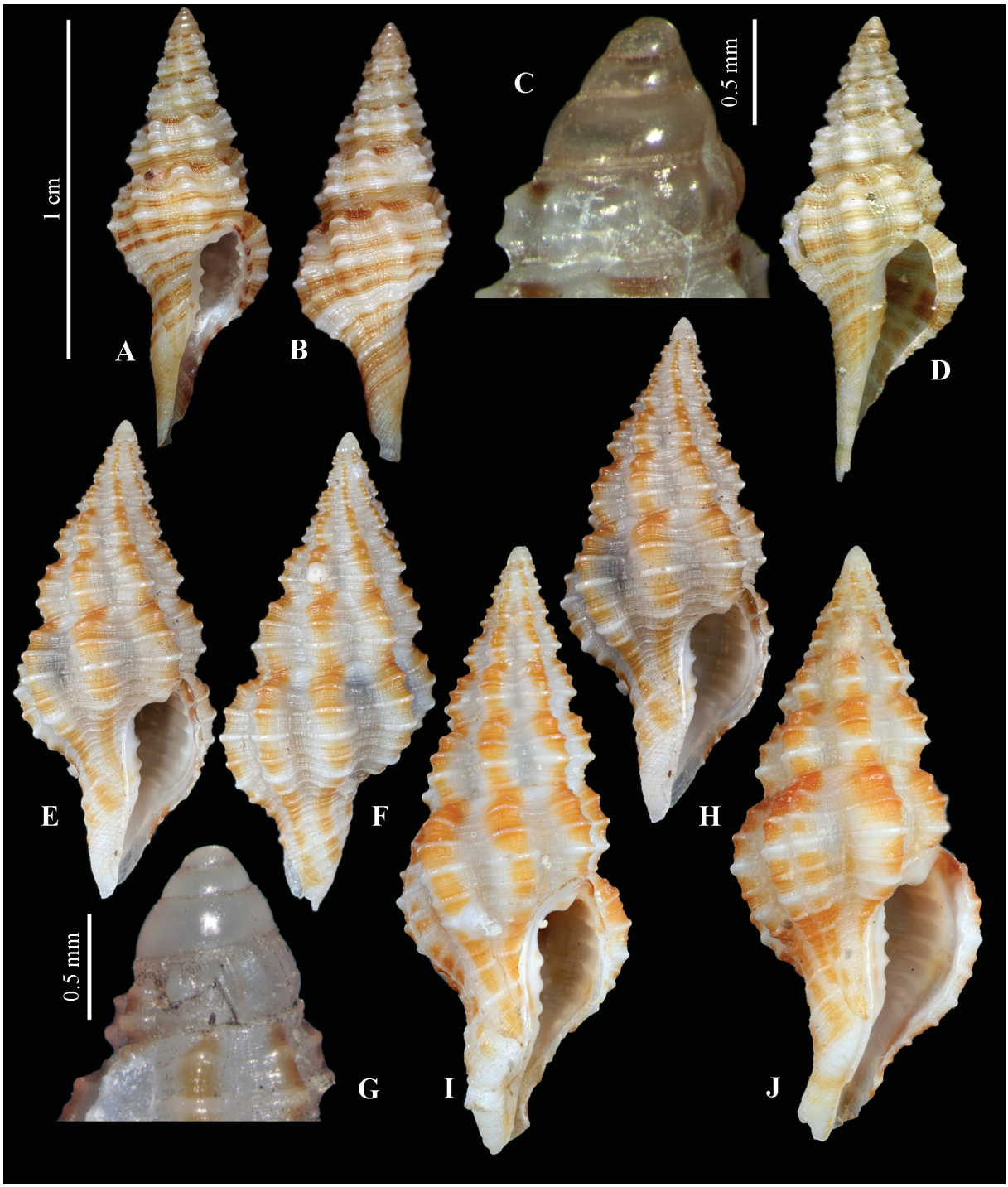

Fig. 7. A–D. *Granulifusus norfolkensis* sp. nov. **A–C**. Holotype, SL 13.0 mm, sequenced (MNHN IM-2013-68811). **D**. New Caledonia, Norfolk Ridge, 23°23′ S, 168°00′ E, 430–480 m, sequenced specimen (MNHN IM-2007-36921). **E–J**. *Granulifusus tatianae* sp. nov. **E–G**. Holotype (MNHN IM-2000-33595). **H**. Paratype, SL 15.0 mm (MNHN IM-2000-33596). **I**. New Caledonia, SMIB 3, stn DW8, 24°45′ S, 168°08′ E, 233 m, SL 18.1mm. **J**. New Caledonia, CHALCAL 2, stn DW84, 23°24′ S, 168°07′ E, 170 m, SL 17.7 mm. All shells to the same scale.

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Distribution

Known only from southern New Caledonia, off Ile des Pins and Norfolk Ridge, in 404–480 m. The multispiral protoconch suggests a planktonic dispersal phase and a possibly broader distribution.

Remarks

The species is known from just two specimens, the holotype and a slightly larger specimen attaining SL 13.8 mm (Fig. 7D). *Granulifusus norfolkensis* sp. nov. can be recognized by its small size, coloration and constricted aperture. Conchologically it is most similar to *Granulifusus tatianae* sp. nov., also from southern New Caledonia, but differs in having a smaller and more slender shell with longer siphonal canal and brown spiral bands.

Granulifusus tatianae sp. nov.
urn:lsid:zoobank.org:act:DBF2EAD7-3434-4F1F-A1A1-6ECE73BE5FC3
Figs 4F, 7E–J

Diagnosis

Shell strong, broadly fusiform, up to 18 mm, protoconch of 3.5 whorls. Teleoconch whorls strongly convex, axial sculpture of broad opisthocline axial ribs, spiral sculpture of strong primary cords and numerous finer secondary cords between them. Aperture lirate inside, columella with several distinct columellar plicae. Teleoconch light tan, axial ribs brown.

Etymology

The specific epithet is named in honour of Tatiana Steyker, wife of Yuri Kantor, patient permanent companion in all travels and many fieldtrips.

Type material

Holotype

NORFOLK RIDGE: south of New Caledonia, 23°17′ S, 168°14′ E, 190–212 m, expedition NORFOLK 1, stn DW1727 (MNHN IM-2000-33595).

Paratype

NORFOLK RIDGE: 1 specimen, same station as for holotype (MNHN IM-2000-33596); 1 specimen (ANSP, ex Snyder collection).

Other material examined (all in MNHN)

NEW CALEDONIA: BIOCAL: 1 dd, stn CP84, 20°43′ S, 167°01′ E, 150–210 m. – SMIB 3: 1 dd, stn DW08, 24°45′ S, 168°08′ E, 233 m. – SMIB 8: 1 dd, stn DW157, 24°46′ S, 168°08′ E, 251–257 m; CHALCAL 2: 3 dd, stn DW84, 23°24′ S, 168°07′ E, 170 m. – NORFOLK 1: 1 lv, 2 dd; stn DW1724, 23°17′ S, 168°14′ E, 200–291 m; 1 lv, 1dd, stn DW1727, 23°17′ S, 168°14′ E, 190–212 m.

LOYALTY RIDGE: MUSORSTOM 6: 1 dd, stn DW442, 20°54′ S, 167°17′ E, 200 m; 1 lv, 1 dd, stn DW473, 21°09′ S, 167°55′ E, 236 m. – LIFOU 2000: 2 dd, stn DW1650, 20°54.2′ S, 167°01.7′ E, 120–250 m.

WALLIS AND FUTUNA: MUSORSTOM 7: 1 dd, stn CP517, 14°13′ S, 178°10′ W, 233–235 m.

Description

Shell fusiform, solid, of 3.5 protoconch and 7 weakly convex teleoconch whorls in holotype. Protoconch bluntly conical (Fig. 7G), last ¾ whorl with axial riblets, protoconch/teleoconch discontinuity distinct,

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marked by appearance of teleoconch sculpture. Protoconch smooth except scattered microgranules, more dense along suture, where they are arranged in oblique lines. Protoconch diameter 820–910 µm (latter in holotype), exposed height 860–920 µm (former in holotype).Teleoconch whorls convex with impressed suture. Axial sculpture of broad, prominent axial ribs, aligned axially on spire from one whorl to the next, 7 ribs per whorl, and of very weak incremental lines. Spiral sculpture of evenly spaced, strong, raised primary cords, in holotype 3 on spire whorls, 13 on last whorl, and numerous, much weaker secondary threads, about 5–7 between two adjacent primary cords. Intersection of secondary spiral threads and incremental lines forming finely reticulate microsculpture. Siphonal canal open, short, recurved. Aperture with 8 strong lirae inside, adapicalmost stronger, forming spirally elongated tooth constricting base of siphonal canal. Inner lip partially detached, with three prominent columellar plicae and one strong parietal tooth, forming well-defined posterior canal. No umbilicus. Colour of protoconch and interior of aperture white. Teleoconch background colour creamy white, axial ribs light brown, spiral cords lighter than ribs.

Holotype measurements: SL 14.3 mm, AL (without canal) 4.5 mm, SW 6.1 mm.

Radula (MUSORSTOM 6, stn DW473, 21°09′ S, 167°55′ E, 236 m, Fig. 4F) narrow, distance between outer edges of lateral teeth about 55 µm, with slender central tooth, about twice as long as broad, bearing three strong cusps. Lateral tooth medium broad, with long basal 'handle' on outer edge, with five strong, subequal cusps, the outermost more clearly separated from the rest, and one smaller inner cusp. Narrow but distinct transverse folds of the membrane situated serially between rows of lateral teeth.

Distribution

Southwest Pacific, known only from Futuna and the New Caledonia region, alive in 200–236 m, empty shells in 170–251 m.

Remarks

Granulifusus tatianae sp. nov. is superficially similar to *Okutanius kuroseanus* gen. et comb. nov. Both species have brown axial ribs aligned along the spire against a lighter, creamy background, and both have a multispiral protoconch indicating planktotrophic larval development. *Okutanius kuroseanus* gen. et comb. nov., however, reaches a much larger adult size and is proportionally broader at comparable size; it has a longer siphonal canal, weaker columellar plicae, and spiral cords of uneven strength, without the very regular pattern of evenly spaced primary cords separated by 5–7 very fine, even, spiral threads of *G. tatianae* sp. nov.

The species also resembles *G. norfolkensis* sp. nov. in sculpture and particularly in apertural armature. Nevertheless, the shell shape in *Granulifusus tatianae* sp. nov. is rather different, and the species can be easily distinguished by size at maturity: *G. tatianae* sp. nov. attains a significantly larger size, up to 18.1 mm, versus 13.6 mm in *G. norfolkensis* sp. nov.

The new species was not examined molecularly and we tentatively assign it to *Granulifusus* based on the similarities of shell sculpture and apertural ornamentation to *G. norfolkensis* sp. nov. and *G. williami* comb. nov.

Granulifusus kurodai (Okutani & Sakurai, 1964) comb. nov.
Fig. 8A–B

Pseudolatirus kurodai Okutani & Sakurai, 1964: 58, pl. 2, fig. 4.

Pseudolatirus kurodai – Hasegawa & Saito 1995: pl. 4, fig. 8 (paratype illustrated).

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Fusolatirus kurodai – Okutani 1975: 193, pl. 10, fig. 22; 2000: 507, pl. 252, fig. 12. — Higo, Callomon & Gotō 2001: 87, fig. G3001 (holotype illustrated).

Type material

Holotype

JAPAN: off Gotō Islands, Nagasaki Prefecture, Western Kyūshū (NSMT Mo 38547), type locality corrected (Okutani & Sakurai 1966) [not seen].

Paratypes

JAPAN: paratype 1, Hyotanse Bank (NSMT-Mo58524) (examined); paratype 2, off Gotō Islands (whereabouts unknown) (not seen); paratype 3, Kashiwajima (NSMT-Mo70270) (examined).

Description

Shell medium-sized, fusiform, with long, slightly sinuous siphonal canal. Protoconch paucispiral, dome-shaped (Fig. 8B), of 1.75 whorls, with strongly convex first whorl and much flatter last ¾ of whorl, with two closely spaced and rather indistinct axial riblets at transition to teleoconch, protoconch/teleoconch discontinuity distinct. Protoconch diameter 900 µm, exposed height 750 µm. Teleoconch with regularly convex whorls, aperture with two very weak columellar plicae, and indistinct parietal tooth; spiral sculpture of unevenly spaced narrow cords of similar strength; axial ribs not aligned along the spire. Background colour cream to yellowish, primary spiral cords light tan.

Distribution

Known from Japan, in 100–200 m, records from other localities may refer to *G. annae* sp. nov. and *G. guidoi* sp. nov.

Remarks

We were able to study two paratypes NSMT-Mo58524 (paratype 1) and NSMT-Mo70270 (paratype 3). They are clearly not conspecific, paratype 3 differing in its much larger protoconch and general shell shape and sculpture; it represents a juvenile *Fusolatirus*, resembling *F. luteus* Snyder & Bouchet, 2006 (see Snyder & Bouchet 2006: fig. 2 D–E). Conchologically, paratype 1 is very similar to the holotype and is the largest known specimen (SL 35.1 mm).

Conchologically *Granulifusus kurodai* comb. nov. is similar to *G. annae* sp. nov.; for differences see the description of the latter. In the absence of data on radula and molecular phylogeny, the assignment of this species to *Granulifusus* is tentative, based on its shell resemblance to sequenced species such as *G. annae* sp. nov.

Granulifusus guidoi sp. nov.

urn:lsid:zoobank.org:act:8630D56D-6613-46EA-BE2D-3F0F4020FC1C

Fig. 8E–H

Latirus kurodai – Mallard & Robin 2005: pl. 45, lower left image (not of Okutani & Sakurai 1964). — Poppe 2008: pl. 348, figs 1–2 (not of Okutani & Sakurai 1964).

Pseudolatirus kurodai – Mallard & Robin 2017: 153 (not of Okutani & Sakurai 1964).

Diagnosis

Shell strong, slender, fusiform, height up to 31 mm, protoconch of 2.5 whorls. Teleoconch whorls strongly convex, axial sculpture of medium broad opisthocline axial ribs, spiral sculpture of thin,

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distinct, primary cords, varying slightly in size. Aperture lirate inside, columella with distinct to weak columellar plicae. Teleoconch light tan with light orange-brown canal and caramel-colored spiral cords.

Etymology

Named for Guido Poppe, the author of the landmark *Philippine Marine Molluscs* and discoverer of many new molluscs in the Philippines and elsewhere, who generously provided some of the type material.

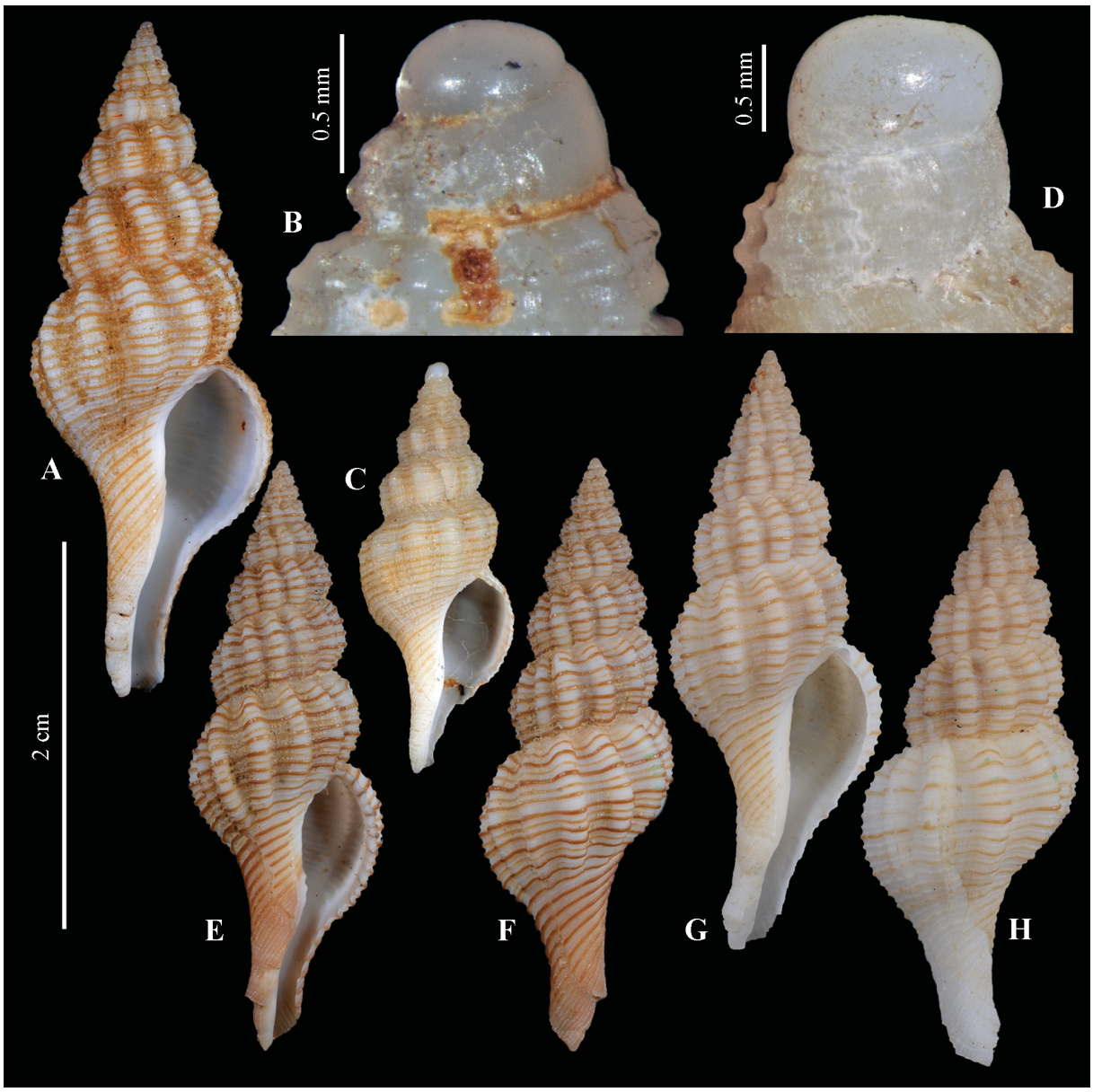

Fig. 8. A–B. *Granulifusus kurodai* (Okutani & Sakurai, 1964) comb. nov., paratype 1, SL 35.1 mm (NSMT-Mo58524). **C–D**. *Fusolatirus* sp. aff. *luteus* Snyder & Bouchet, 2006 (paratype 3 of *Pseudolatirus kurodai*, see the text), SL 21.5 mm (NSMT-Mo70270). **E–H**. *Granulifusus guidoi* sp. nov. **E–F**. Holotype, SL 30.2 mm (MNHN IM-2000-33597). **G–H**. Paratype, SL 30.7 mm (MNHN IM-2000-33598). All shells at the same scale.

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Type material

Holotype

PHILIPPINES: off Aliguay Island, northeast of Mindanao, in 50–150 m (MNHN IM-2000-33597, ex Snyder collection).

Paratypes

PHILIPPINES: 1 specimen, same data as for holotype, SL 30.7 mm (MNHN-2000-33598); 1 specimen, trawled off Aliguay Island, 80–150 m, SL 30.7 mm (ANSP 456853); 1 specimen, trawled off Aliguay Island, 100–150 m, 25.5 mm (NMP).

Description

Shell slender, fusiform, of average size for genus. Protoconch multispiral, of 2.5 smooth whorls in holotype, with 4 axial riblets on last whorl, pale grey-orange. Transition to teleoconch marked by groove between last riblet and first teleoconch axial rib. Teleoconch of 8–9 convex whorls, suture deep, adpressed. Axial sculpture of distinct ribs, closely spaced, 10 on earlier whorls, increasing to 12 on later whorls. Spiral sculpture of dark cords, often with less prominent and paler secondary cords between them. First whorl with single dark cord, adding roughly one cord per whorl, with 7 cords on penultimate whorl. Cords continue to anterior end of canal, crowding closer together at tip; in holotype, last whorl with about 25 cords. Siphonal canal recurved back from aperture, moderately long, open. Dark spiral cords matched on inner lip by low, light brown lirae. Columellar callus white, with a few spiral lines continuing inward at adapical end of shield. Two stronger rounded columellar plicae situated towards aperture and one much weaker towards canal. Teleoconch white to light tan with light orange-brown neck; caramel-colored spiral cords on entire shell.

Holotype measurements: SL 30.2 mm, AL (without canal) 8.1 mm, SW 10.1 mm.

Distribution

Known only from the type locality.

Remarks

Granulifusus guidoi sp. nov. is most similar to *G. kurodai* comb. nov., with which it is often confused. It differs by a multispiral protoconch with more whorls, and a narrower shell with narrower aperture. It is also similar to *Okutanius ellenae* gen. et sp. nov., which has white cords with dark interspaces on the teleoconch whereas *G. guidoi* sp. nov. has dark, caramel-colored cords with light tan interspaces.

In the absence of data on radula and molecular phylogeny, we tentatively assign this species to *Granulifusus* based on shell similarities to such sequenced species as *G. annae* sp. nov.

Okutanius gen. nov.

urn:lsid:zoobank.org:act:FAE994AB-DCBE-4436-BBAD-2D1283674F12

Type species

Fusolatirus kuroseanus Okutani, 1975, here designated.

Diagnosis

Shell medium-size, reaching 30 mm, fusiform to broad fusiform, strong, with spiral colour bands. Teleoconch whorls evenly strongly convex, shell base sharply narrowing towards long, weakly sinuous siphonal canal. Protoconch multispiral, of 3–3.75 whorls. Axial sculpture of distinct broad, weakly

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opisthocline, closely spaced ribs. Spiral sculpture of distinct primary cords, subequal in size, and much thinner cordlets between them. Aperture narrow, oval, relatively small, columella with several weak plicae. No distinct parietal knob.

Operculum spans entire aperture, with terminal nucleus.

Lateral teeth with five closely spaced, slightly curved cusps and much smaller, but distinct, innermost cusp. Outermost very short small cusp present, but usually overlaid by large next cusp and not seen in dorsal view. Central tooth small, narrow, trapezoid, with three cusps. Narrow but distinct transverse folds of membrane situated serially between rows of lateral teeth.

Etymology

The genus is named after Takashi Okutani in recognition of his lifelong contribution to malacology, including the description of the type species of the genus. The gender is masculine.

Differential diagnosis

Okutanius gen. nov. is very similar to *Granulifusus* and conchological and morphological characters overlap at least in some species. Species of *Okutanius* gen. nov. do not reach as large size as in *Granulifusus*. Nevertheless, without molecular data, it would be difficult to suggest the existence of two clearly separate genera.

Genus composition

In addition to two sequenced species, *O. kuroseanus* and *O. ellenae* sp. nov., we allocate *Pseudolatirus aikeni* Lussi, 2014, known from empty shell only, to *Okutanius* gen. nov. based on shell similarity to sequenced *O. kuroseanus*.

Okutanius kuroseanus (Okutani, 1975) gen. et comb. nov.
Figs 4G, 9A–G

Fusolatirus kuroseanus Okutani, 1975: 193, pl. 10, fig 21.
Pseudolatirus leucostriatus Kosuge, 1979: 31, pl. 5, fig. 5, syn. nov.

Fusolatirus kuroseanus – Okutani 2000: 507, pl. 252, fig. 11. — Marais & Kilburn 2010: 127.
Latirus kuroseanus – Mallard & Robin 2005: caption on pl. 45.
Pseudolatirus kuroseanus – Mallard & Robin 2017: 153.

Type material

JAPAN: holotype of of *F. kuroseanus*, Kurose Bank, off Izu islands, south of Honshū, 33°23.5′ N, 139°36.2′ E, 260 m (NSMT Mo 69575) (illustrated by Higo *et al.* 2001: 87); holotype of *P. leucostriatus* (said to be off Midway Island, 32°02′ N, 173°06′ W, 365 m, but label of holotype says 29°46.4′ N, 179°02.9′ E, 265 m) in the Institute of Malacology, Tokyo (IMT 79-18) [examined]; paratype, same location as holotype, said to be donated to USNM.

Sequenced material

PAPUA NEW GUINEA, NEW IRELAND: KAVIENG 2014: 1 lv, stn CP4503, 02°30′ S, 150°44′ E, 191–200 m (MNHN IM-2013-59070).

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Other material examined

TAIWAN: TAIWAN 2000: 2 dd, stn DW05, 23°41′ N, 119°56′ E, 213–236 m; 2 dd, stn DW34, 22°01′ N, 120°36′ E, 240–246 m; 25 dd, stn DW36, 21°54′ N, 120°36′ E, 300–331 m.

PHILIPPINES: 2 spms, Panglao, Bohol, tangle nets, 160 m, (ANSP 425326); 2 spms, off Aliguay I., Mindanao, 150 m (ANSP 425322); 1 spm, Bohol, Balicasag, 240 m (ANSP 425324); 1 spm, Philippine Is, tangle nets (ANSP 425325); 1 spm, Balicasag I., Bohol, tangle nets, 240 m (ANSP 425327); 1 spm, Siquijor I., tangle nets, 150 m (ANSP 425323).

ARAFURA SEA: KARUBAR: 1 lv, 13 dd, stn DW15, 05°17′ S, 132°41′ E, 212–221 m.

SOLOMON ISLANDS: SALOMON 1: 1 dd, stn DW1765, 08°43′ S, 160°07′ E, 325–380 m; 1 dd, stn DW1812, 09°46′ S, 160°52′ E, 222–246 m.

NEW CALEDONIA: "*Vauban*" 1978–79: 1 dd, stn DR37, 22°32′ S, 166°26′ E, 175–250 m. – BIOCAL: 1 dd, stn DW81, 20°29′ S, 166°47′ E, 430–470 m; 1 juv. Lv, stn CP105, 21°31′ S, 166°22′ E, 330–335 m. – BIOGEOCAL: 3 dd, stn DW253, 21°32′ S, 166°29′ E, 310–315 m. – MUSORSTOM 4: 1 dd, stn DW181, 18°57′ S, 163°22′ E, 350 m. – BATHUS 1: 1 dd, stn DW655, 21°17′ S, 165°57′ E, 375 m; 4 dd, stn DW688, 20°33′ S, 165°00′ E, 270–282 m; 2 dd, stn DW689, 20°33′ S, 165°00′ E, 260–265 m. – BATHUS 4: 1 dd, stn DW886, 21°01′ S, 164°28′ E, 250–300 m; 1 dd, stn DW887, 21°07′ S, 164°28′ E, 320–344 m. – SMIB 4: 1 dd, stn DW44, 24°46′ S, 168°08′ E, 270–300 m. – SMIB 5: 1 dd, stn DW90, 22°19′ S, 168°42′ E, 340 m. – SMIB 8: 1 dd, stn DW160, 24°47′ S, 168°08′ E, 280–282 m.

LOYALTY RIDGE: MUSORSTOM 6: 2 lv, 3 dd, stn DW391, 20°47′ S, 167°06′ E, 390 m; 1 dd, stn DW397, 20°47′ S, 167°05′ E, 380 m; 1 lv, 1 dd, stn DW398, 20°47′ S, 167°06′ E, 370 m; 1 dd, stn DW418, 20°42′ S, 167°03′ E, 283 m; 3 dd, stn DW459, 21°01′ S, 167°31′ E, 425 m; 3 dd, stn DW480, 21°08′ S, 167°56′ E, 380 m; 1 dd, stn DW481, 21°22′ S, 167°50′ E, 300 m; 1 dd, stn DW482, 21°21′ S, 167°47′ E, 375 m; 2 dd, stn DW487, 21°23′ S, 167°46′ E, 500 m.

VANUATU: MUSORSTOM 8: 1 dd, stn DW1059, 16°13′ S, 167°21′ E, 408–430 m; 1 dd, stn DW1065, 16°16′ S, 167°21′ E, 360–419 m.

WALLIS AND FUTUNA: MUSORSTOM 7: 1 dd, stn DW496, 14°20′ S, 178°04′ W, 250–330 m (Futuna I.); 1 dd, stn DW509, 14°15′ S, 178°11′ W, 200–240 m (Futuna I.); 1 dd, stn DW523, 13°12′ S, 176°16′ W, 455–515 m (Wallis I.); 1 dd, stn DW569, 12°30′ S, 176°51′ W, 300–305 m (Waterwitch Bank); 1 dd, stn DW571, 12°31′ S, 176°52′ W, 502–508 m (Waterwitch Bank); 1 dd, stn DW610, 13°21′ S, 176°09′ W, 286 m (Wallis I.); 1 dd, stn DW626, 11°54′ S, 179°32′ W, 597–600 m (Bayonnaise Bank).

FIJI: BORDAU 1: 1 lv, 2 dd, stn DW1469, 19°40′ S, 178°10′ W, 314–377 m; 1 lv; stn DW1497, 18°44′ S, 178°25′ W, 335–350 m.

TONGA: BORDAU 2: 2 dd, stn DW1535, 21°43′ S, 175°18′ W, 268 m; 3 dd, stn DW1567, 21°02′ S, 175°19′ W, 351–356 m; 1 dd, stn DW1583, 18°37′ S, 174°03′ W, 327–360 m; 1 lv(?), 1 dd, stn DW1587, 18°37′ S, 173°54′ W, 309–400 m; 1 dd, stn DW1589, 18°39′ S, 173°54′ W, 281 m; 1 lv(?), stn DW1595, 19°03′ S, 174°19′ W, 523–806 m; 1 dd, stn DW1602, 20°49′ S, 174°57′ W, 263–320 m; 1 dd, stn DW1605, 22°17′ S, 175°16′ W, 441 m; 1 lv, stn DW1607, 22°15′ S, 175°23′ W, 356–367 m; 1 lv(?), stn DW1630, 23°23′ S, 176°18′ W, 360 m; 1 lv(?), stn DW1636, 21°44′ S, 175°20′ W, 321–331 m.

CHRISTMAS ISLAND: 2 dd, off NE point, 10°25′ S, 105°42′ E, 183 m, coll. R. Kirkpatrick 1916 (AMS C324273).

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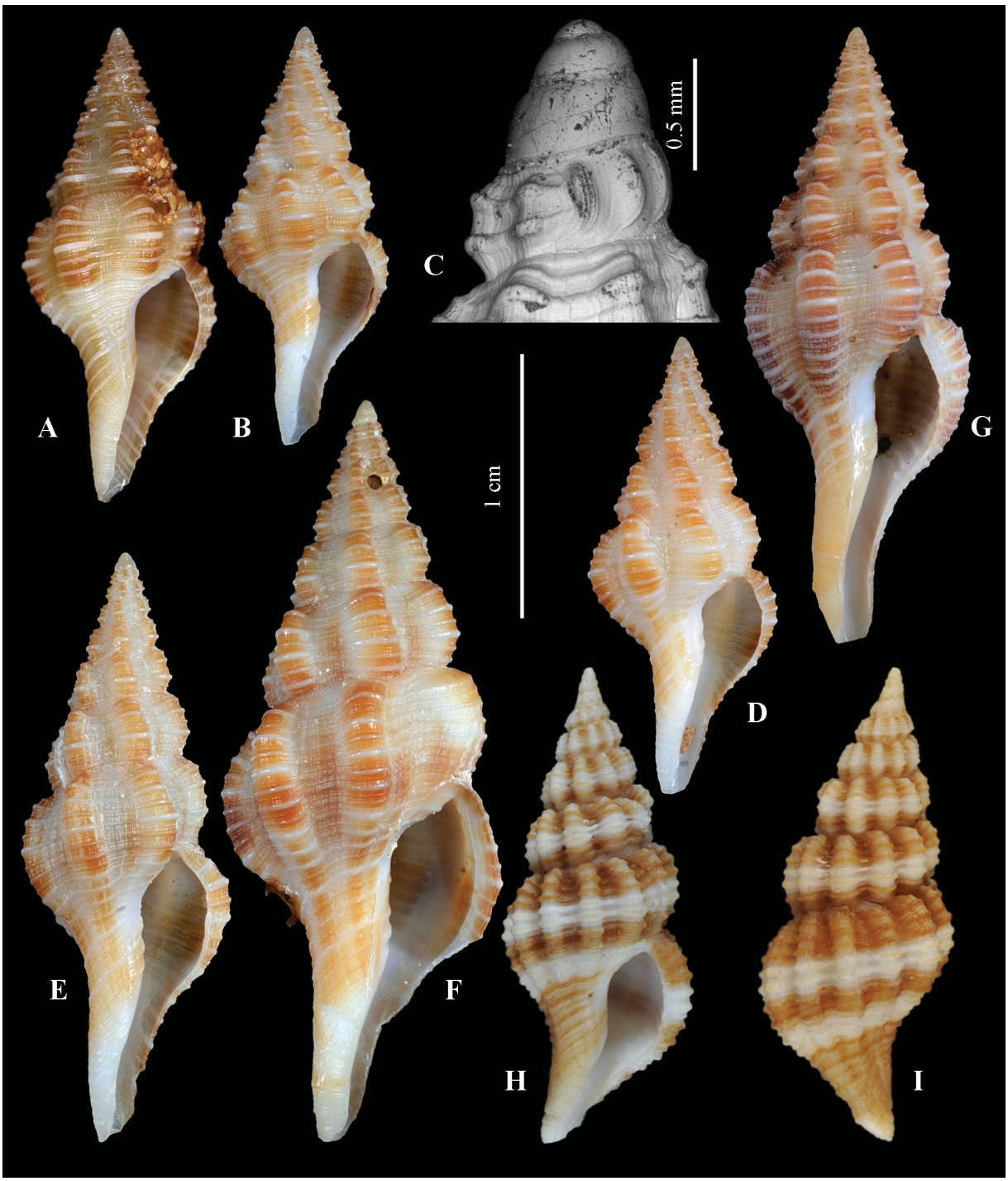

Fig. 9. A–G. *Okutanius kuroseanus* (Okutani, 1975) gen. et comb. nov. **A**. New Ireland, KAVIENG 2014, stn CP4503, 02°30′ S, 150°44′ E, 191–200 m, SL 18.1 mm, sequenced specimen; for radula, see Fig. 4G (MNHN IM-2013-59070). **B**. BORDAU 1, stn DW1469, 19°40′ S, 178°10′ W, 314–377 m, SL 15.9 mm. **C**. Protoconch, New Caledonia, BIOCAL, stn CP105, 21°31′ S, 166°22′ E, 330–335 m. **D–E**. Loyalty Ridge, MUSORSTOM 6, stn DW391, 20°47′ S, 167°06′ E, 390 m. **D**. SL 17.3 mm. **E**. SL 22.3 mm. **F**. Loyalty Ridge, MUSORSTOM 6, stn DW398, 20°47′ S, 167°06′ E, 370 m, SL 28.1 mm. **G**. Taiwan. TAIWAN 2000, stn DW34, 22°02′ N, 120°36′ E, 246 m, SL 23.4 mm. **H–I**. *Okutanius aikeni* (Lussi, 2014) gen. et comb. nov., holotype, SL 25.6 mm. A–B, D–G at the same scale, H–I not to scale.

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RÉUNION: MD32: 1 dd, stn CP129, 20°51′ S, 55°36′ E, 290–300 m; 1 dd worn, stn DC136, 20°46′ S, 55°36′ E, 915–922 m.

SOUTH AFRICA: 1 dd, former Transkei, off Port Grosvenor, 29°57.4′ S, 31°26.4′ E, 105 m (NM C636); 1 lv(?), former Transkei, off Mtamvuna River, 31°08.4′ S, 30°16.6′ E, 160 m (NM C9652); 2 dd, Zululand, SE of Port Durnford, 29°05.8′ S, 32°09.4′ E, 165 m (NM S903); 1 dd, Zululand, SE of Port Durnford, 29°04.6′ S, 32°09.0′ E, 142 m (NM D7822).

Description

Shell fusiform, up to 28 mm in length. Protoconch acutely conical, multispiral, of 3 smooth, weakly convex whorls, with several slightly arcuate axial riblets on last ½ whorl (Fig. 9C). Protoconch diameter 870 µm, exposed height 1000 µm. Teleoconch with regularly convex whorls, without imbricated subsutural spiral ridge, with long siphonal canal; aperture with weak columellar plication, and indistinct parietal tooth; spiral sculpture of unevenly arranged cords of uneven strength; axial ribs aligned along the spire. Background colour from creamy light to yellowish brown, axial ribs brown, primary spiral cords white.

Radula (Fig. 4G) examined in two specimens, from Fiji (BORDAU 1, stn DW1497) and from the New Ireland (MNHN IM-2013-59070, 18.1 mm) (shell: Fig. 9A). They are very similar and that from the New Ireland specimen is illustrated and described. Radula narrow, distance between outer edges of lateral teeth about 70 µm (1.34% of AL). Lateral teeth broad, slightly arcuate, with strongly attenuated outer anterior corner, producing long 'handle'. Lateral teeth with outermost small cusp, on most rows overlaid by following major cusp and not seen on ventral view (marked by white arrow), five almost equal, closely spaced, cusps, outer one more clearly separated from the rest, and one smaller inner cusp. Central tooth trapezoid, with three short blunt cusps, central slightly longer. Distinct transverse folds of the membrane situated serially between rows of lateral teeth, reaching anterior margin of central tooth.

Distribution

Southwest Pacific Ocean, Indian Ocean to KwaZulu-Natal, in 150–620 m, alive in 150–400 m.

Remarks

This distinct, medium-sized species is similar to *Granulifusus tatianae* sp. nov.; for differences, see the description of the latter. It also resembles *Okutanius ellenae* gen. et sp. nov., but can be easily differentiated from the latter species by the colour pattern.

Okutanius ellenae gen. et sp. nov.
urn:lsid:zoobank.org:act:BF7E85A5-AC8A-4A6C-A7BA-671948DB2EE1
Figs 4H, 10

Diagnosis

Shell strong, slender, narrowly fusiform, up to 30 mm, protoconch of 3.75 whorls. Teleoconch whorls strongly convex, axial sculpture of broad, nearly orthocline, axial ribs, spiral sculpture of dense, evenly spaced, strong, raised cords. Aperture lirate inside, columella with weak columellar plicae to nearly smooth. Teleoconch with alternating white spiral cords and orange brown interspaces, and three white bands, one subsutural, one just below periphery of last whorl and one at tip of siphonal canal.

Molecular diagnosis

See Table 3.

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Table 3. Molecular diagnosis of the *Okutanius ellenae* gen. et sp. nov.

Sequences analyzed	4
Independent combinations	[586:'C']
	[1:'G',580:'G']
	[22:'G',223:'T']
	[46:'C',556:'A']
	[55:'C',319:'T']
	[79:'C',469:'G']
	[97:'C',475:'G']
	[112:'C',313:'T']
	[172:'G',526:'G']
	[206:'C',292:'C']
	[250:'C',653:'C']
	[274:'C',401:'C']
	[277:'A',284:'C']
	[280:'G',613:'C']
	[283:'A',622:'C']
	[322:'G',544:'G']
	[454:'A',578:'T']

Etymology

The specific epithet pays homage to Ellen Strong, in fitting tribute for this elegant and handsome species.

Type material

Holotype

NEW CALEDONIA: South of Ile des Pins, 22°53′ S, 167°35′ E, 376–390 m, expedition KANACONO, stn DW4677, sequenced (MNHN IM-2013-68819).

Paratypes

NEW CALEDONIA: 1 sequenced specimen from the type locality (MNHN IM-2013-68876); 2 specimens, 24°44′ S, 168°10′ E, 270–350 m, expedition BERYX 11, stn DW11 (AMS C.572407 and NSMT-Mo 79000); 1 specimen, 22°58′ S, 167°33′ E, 410-440 m, expedition MUSORSTOM 4, stn DW222 (ANSP 476089).

Sequenced material

NEW CALEDONIA: holotype and paratype, TERRASSES: 1 lv, stn DW3082, 22°29′ S; 167°23′ E, 290 m (MNHN IM-2007-38356).

CORAL SEA: EBISCO: 1 lv, stn DW2520, Banc Kelso, 24°06′ S, 159°41′ E, 350–400 m (MNHN IM-2007-32522).

Other material examined

CORAL SEA: MUSORSTOM 5: 2 dd, stn DW299, 22°48′ S, 159°24′ E, 360–390 m; 5 lv, 10 dd, stn DW300, 22°48′ S, 159°24′ E, 450 m; 18 dd, stn DW301, 22°07′ S, 159°25′ E, 487–610 m; 1 dd, stn DW304, 22°10′ S, 159°26′ E, 385–420 m; 2 dd, stn DW306, 22°08′ S, 159°21′ E, 375–415 m; 1 lv, 3 dd, stn DC362, 19°53′ S, 158°40′ E, 410 m.

NEW CALEDONIA: LAGON: 1 lv, stn 444, 18°15′ S, 162°59′ E, 300–350 m. – BIOCAL: 1 dd, stn DW38, 23°00′ S, 167°15′ E, 360 m; 8 lv+dd, stn DW64, 24°48′ S, 168°09′ E, 250 m; 1 lv, 3 dd stn DW65, 24°48′ S, 168°09′ E, 245–275 m. – BIOGEOCAL: 2 dd, stn KG252, 21°31′ S, 166°21′ E, 330 m; 5 dd, stn DW253, 21°32′ S, 166°29′ E, 310–315 m. – SMIB 5: 1 lv, stn DW98, 23°02′ S, 168°16′ E, 335 m. – 1 dd, S. of Ile des Pins, 22°52′ S, 167°35.5′ E, 370 m (AMS C324274). – BATHUS 2: 1 dd, stn DW731, 22°49′ S, 166°45′ E, 300–370 m. – BATHUS 3: 1 dd, stn CP804, 23°41′ S, 168°00′ E, 244–

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278 m. – MUSORSTOM 4: 1 lv, stn DW222, 22°58′ S, 167°33′ E, 410-440 m (paratype ANSP); 2 dd, stn DW234, 22°15′ S, 167°08′ E, 350–365 m. – CHALCAL 2: 14 dd, stn DW69, 24°44′ S, 168°08′ E, 260 m; 1 lv, 3 dd, stn DW70, 24°46′ S, 168°09′ E, 232 m; 2 dd, stn DW71, 24°42′ S, 168°10′ E, 230 m; 1 dd, stn DW78, 23°41′ S, 168°00′ E, 233 m; 3 dd, stn DW79, 23°41′ S, 168°00′ E, 243 m, 3 dd. – BERYX 11: 30 lv+dd, stn DW11, 24°44′ S, 168°10′ E, 270–350 m; 5 spms, stn DW18, 24°48′ S, 168°09′ E, 250–270 m. – HALICAL 1: 1 dd, stn 1–4, 18°53′–18°56′ S, 163°24′ E, 350–400 m. – LITHIST: 1 dd, stn CP10, 24°48′ S, 168°09′ E, 245–261 m; 3 dd, stn DW11, 24°47′ S, 168°08′ E, 254–283 m; 4dd, stn DW12, 24°46′ S, 168°08′ E, 235–280 m; 1 dd, stn DW13, 23°45′ S, 168°17′ E, 400 m. – NORFOLK 1: 15 lv + dd, stn DW1651, 23°27′ S, 167°50′ E, 276–350 m; 1 dd, stn DW1652, 23°26′ S, 167°50′ E, 290–378 m; 3 dd, stn DW1653, 23°28′ S, 167°51′ E, 328–340 m; 1 dd, stn DW1654, 23°28′ S, 167°52′ E, 366–560 m; 1 lv, 2 dd, stn DW1658, 23°26′ S, 167°50′ E, 320–336 m; 1 dd, stn DW1672, 23°43′ S, 168°01′ E, 267–324 m; 2 dd, stn DW1673, 23°39′ S, 168°00′ E, 278 m; 1 dd, stn DW1674, 23°40′ S, 168°00′ E, 245–253 m; 3 dd, stn DW1675, 24°45′ S, 168°09′ E, 231–233 m; 27 lv + dd, stn DW1679, 24°43′ S, 168°10′ E, 298–324 m; 1 dd, stn DW1680, 24°45′ S, 168°10′ E, 385–392 m; 4 dd, stn DW1704, 23°45′ S, 168°16′ E, 400–420 m; 6 dd, stn DW1707, 23°43′ S, 168°16′ E, 381–493 m; 3 dd, stn DW1709, 23°42′ S, 168°16′ E, 380–389 m; 1 dd, stn DW1710, 23°44′ S, 168°17′ E, 386–426 m; 1 dd, stn DW1722, 23°18′ S, 168°01′ E, 540 m; 8 lv + dd, stn DW1723, 23°18′ S, 168°15′ E, 266–267 m; 6 dd, stn DW1729, 23°20′ S, 168°16′ E, 340–619 m; 2 dd, stn DW1732, 23°20′ S, 168°16′ E, 347–1063 m.

VANUATU: VOLSMAR: 2 dd, stn DW07, 22°26′ S, 171°44′ E, 325–400 m; 1 dd, stn DW16, 22°25′ S, 171°41′ E, 420–500 m; 1 dd, stn DW39, 22°20′ S, 168°44′ E, 280–305 m; 1 dd, stn DW49, 21°00′ S, 170°04′ E, 285 m; 1 dd, stn DW50, 20°59′ S, 170°04′ E, 425 m. – MUSORSTOM 8: 1 dd, stn DW967, 20°19′ S, 169°53′ E, 295–334 m.

TONGA: BORDAU 2: 2 dd, stn DW1607, 22°15′ S, 175°23′ W, 356–367 m.

Description

Shell thin, slender, fusiform, consisting in holotype of 3.75 protoconch and 7 teleoconch whorls. Protoconch conical (Fig. 10C), with weakly convex whorls, last ½ whorl with 6 axial riblets, protoconch/teleoconch discontinuity distinct. Protoconch diameter 1070 µm, exposed height 1110 µm. Teleoconch whorls convex, suture deep, adpressed. Axial sculpture of broad, prominent ribs, aligned axially on spire from one whorl to the next, 6 ribs per whorl. Spiral sculpture of evenly spaced, strong, raised cords, in holotype 2 on first whorl, 3 on subsequent whorls, abapicalmost stronger, 5 on antepenultimate and penultimate whorls, 22 on last whorl. No second order axial or spiral sculpture. Siphonal canal open, long, slightly recurved. Aperture with 11 weak lirae inside, base of siphonal canal not clearly demarcated. Inner lip completely adherent to columella, forming smooth, white, shiny columellar shield, with three weak columellar plicae. No umbilicus. Colour of protoconch and interior of aperture white or flesh-coloured. Teleoconch with alternating white spiral cords and orange brown interspaces, and three white bands, one subsutural, one just below periphery of last whorl and one at tip of siphonal canal.

Holotype measurements: SL 22.7, LWL 15.4 mm, AL (without canal) 5.7 mm, SW 7.8 mm.

Live animal has orange body (Fig. 10D) with irregular white spots, more numerous on body than on foot. Operculum transparent, yellow, with terminal nucleus shifted leftwards, closing aperture completely.

Radula (Fig. 4H) examined in two specimens from Norfolk Ridge (NORFOLK 1, stn DW1658, and stn DW1679), very similar in both specimens. Radula narrow, distance between outer edges of lateral teeth about 80 µm (1.6% of AL). Lateral teeth medium broad, arcuate, with attenuated outer anterior corner, producing medium long ‘handle’. Lateral teeth with outermost small cusp, on most rows overlaid by following major cusp and not seen on ventral view (marked by white arrow), five slightly recurved, short cusps, subequal in length, outer more distant from others, and one additional innermost short, but

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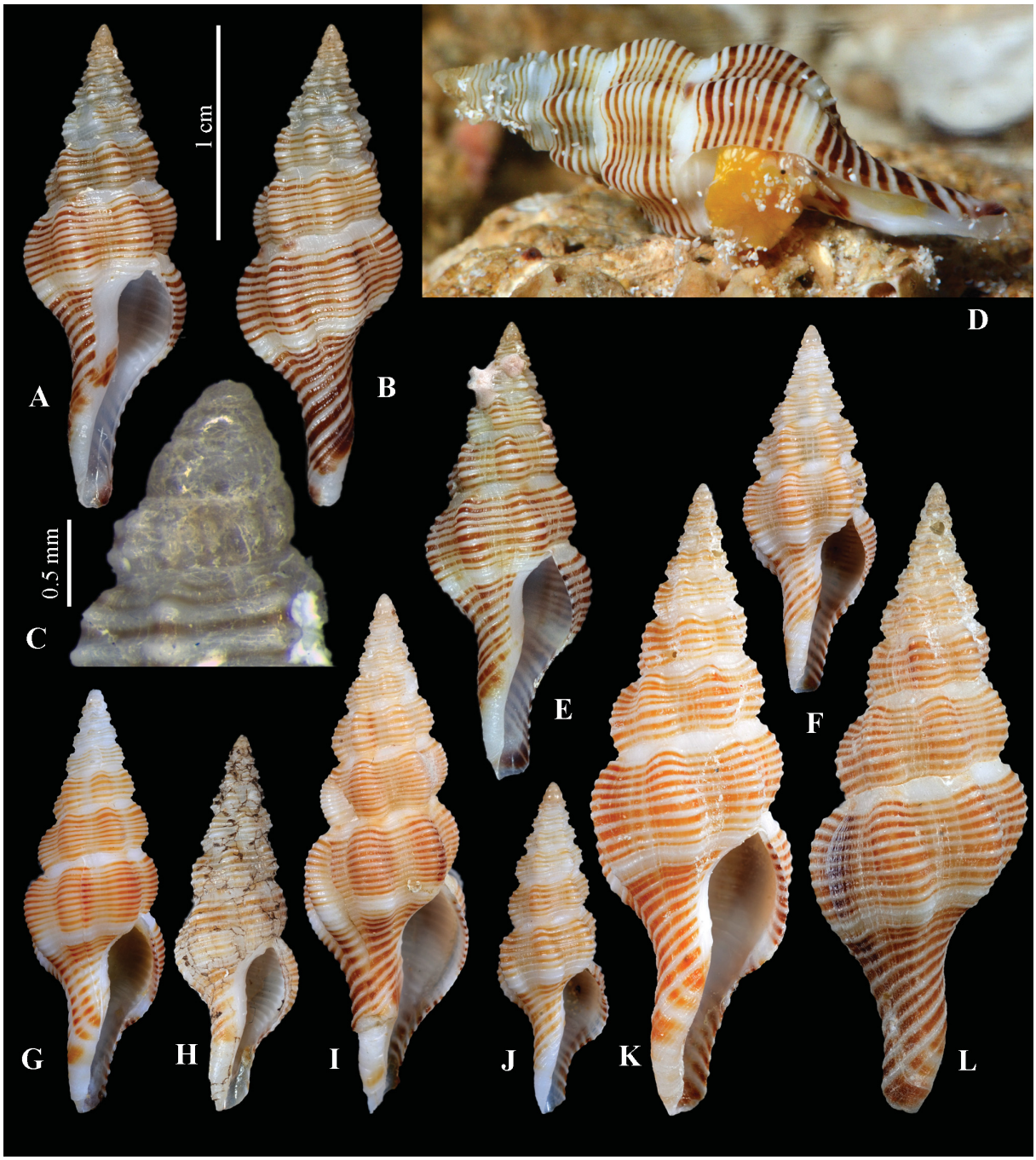

Fig. 10. *Okutanius ellenae* gen. et sp. nov. **A–D**. Holotype, New Caledonia, South of Ile des Pins, 22°53′ S, 167°35′ E, 376–390 m, SL 22.7 mm, sequenced specimen (MNHN IM-2013-68819). **E**. Paratype from the type locality, SL 21.4 mm, sequenced specimen (MNHN IM-2013-68876). **F**. New Caledonia, SMIB 5, stn DW98, 23°02′ S, 168°16′ E, 335 m, SL 17.3 mm. **G**. New Caledonia, BATHUS 3: stn CP804, 23°41′ S, 168°00′ E, 244–278 m, SL 20 mm. **H**. New Caledonia, NORFOLK 1, stn DW1658, 23°26′ S, 167°50′ E, 320–336 m, SL 17.8 mm, radula, see Fig. 4H. **I**. New Caledonia, CHALCAL 2, stn DW79, 23°41′ S, 168°00′ E, 243 m, SL 24.4 mm. **J**. New Caledonia, SMIB 5, stn DW98, 23°02′ S, 168°16′ E, 335 m, SL 15.5 mm. **K–L**. New Caledonia, BATHUS 2, stn DW731, 22°49′ S, 166°45′ E, 300–370 m, SL 29.6 mm. All shells at the same scale.

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distinct, cusp. Central tooth small, trapezoid, with three short cusps, central longest. Narrow but distinct transverse folds of the membrane situated serially between rows of lateral teeth, reaching upper corners of central teeth.

Distribution

Coral Sea, New Caledonia to Tonga, in 245–610 m, alive in 245–450 m.

Remarks

Okutanius ellenae gen. et sp. nov. reaches 29.6 mm in length, showing little variation in shell shape and colouration. It resembles *O. kuroseanus* gen. et comb. nov., but is easily separated by its sculpture of even spiral cords and distinct colour pattern of alternating white cords and dark interspaces. *O. kuroseanus* gen. et comb. nov. reaches a much larger adult size, and is also broader at comparable size. *O. ellenae* gen. et sp. nov. also superficially resembles *Granulifusus tatianae* gen. et sp. nov., which differs by its short siphonal canal, strong apertural barriers, and the presence of second order spiral and axial sculpture.

Okutanius aikeni (Lussi, 2014) gen. et comb. nov.
Fig. 9H–I

Pseudolatirus aikeni Lussi, 2014: 10–11, color images of holotype.

Pseudolatirus aikeni – Mallard & Robin 2017: 151.

Type material

Holotype

South Africa: off Park Rynie, southern KwaZulu – Natal, 110 m, SL 25.6 mm, SW 10.3 mm (NMSA W9698/T3896).

Description

Shell strong, fusiform, up to 25.6 mm. Protoconch and uppermost teleoconch whorls eroded, protoconch conical, multispiral, of 3+ whorls (protoconch tip broken off). Teleoconch with regularly strongly convex whorls, with medium long siphonal canal. Aperture broad, oval, with nearly smooth columella with very weak ridges in the lower part, corresponding to spiral cords not completely overlaid by callus. Spiral sculpture of unevenly spaced distinct cords of varying strength; axial ribs strong, weakly opisthocline, and closely spaced, not aligned along the spire. Background colour creamy, with two darker brown spiral bands and more dark shell base. Primary spiral cords white.

Distribution

Only known from the type locality.

Remarks

The dead collected and partially distorted holotype is the only known specimen. In ventral view it is clearly seen that the shell axis is not straight, and the strongly recurved leftwards siphon is the result of abnormal shell growth. Pending knowledge on the body and radula, we tentatively allocate this species to *Okutanius* gen. nov., based on shell resemblance to sequenced species of the genus.

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Vermeijius gen. nov.
urn:lsid:zoobank.org:act:F4D92EAC-3741-4B91-ACF0-61C1A8E2A116

Type species

Pseudolatirus pallidus Kuroda & Habe, 1961, here designated.

Diagnosis

Shell medium-sized, adult size from 27 mm (*V. wallacei* gen. et comb. nov.) to 60 mm (*V. pallidus* gen. et comb. nov.), fusiform, strong but light, usually offwhite, with evenly convex to inflated teleoconch whorls, constricted shell base and long, straight or weakly sinuous canal. Protoconch paucispiral or multispiral (1.5–3.25 whorls). Axial sculpture of distinct narrow ribs, nearly coaxial, separated by broader (1–2 times) interspaces. Spiral sculpture of distinct cords, unequal in size, covering entire shell surface, major cords nodulose at intersection with axial ribs. Aperture broad, oval, relatively small, with smooth or weakly plaited columella (plaits correspond to spiral cords covered by columellar callus). Parietal knob present in some specimens.

Operculum spans entire aperture, with terminal nucleus.

Lateral teeth with 5–7 closely spaced, slightly curved cusps and much smaller, but distinct, innermost cusp. Outer anterior corner forms long distinct 'handle', tooth outline convex at transition from cusp side to 'handle'. Central tooth small, rectangular, with three cusps. Narrow but distinct transverse folds of membrane situated serially between rows of lateral teeth.

Differential diagnosis

Vermeijius gen. nov. differs from *Granulifusus* and *Okutanius* gen. nov. in its uniformly coloured light shell with smooth or nearly smooth columella, more abruptly constricted shell base, producing a relatively narrow canal. The radula differs in having a proportionally broader central tooth. The molecular phylogenetic analysis clearly demonstrates the isolated position of the new genus as sister taxon to *Chryseofusus*.

Etymology

The genus is named after Geerat J. Vermeij from University of California at Davis in recognition of his immense contribution to malacology, including the taxonomy and biogeography of the Fasciolariidae. Gender masculine.

Genus composition

We include in the genus *Pseudolatirus pallidus*, *Fusinus virginiae* and *Fusus? retiarius*; additionally, *Fusinus* (*Simplicifusus*) *guidonis* Delsaerdt, 1995 from Somalia, *Fusinus palmarium* Hadorn & Fraussen, 2006 from eastern Australia and *Fusinus wallacei* Hadorn & Fraussen, 2006 were not sequenced, but are attributed to *Vermeijius* gen. nov. based on conchological similarities.

Vermeijius pallidus (Kuroda & Habe, 1961) gen. et comb. nov.
Figs 11A–E, 12A–B

Pseudolatirus pallidus Kuroda & Habe in Habe, 1961: 66, pl. 33, fig. 9.

Pseudolatirus pallidus – Callomon & Snyder 2009: 167, fig. 20. — Mallard & Robin 2017: 154.

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Table 4. Molecular diagnoses of the species of *Vermeijius* gen. nov.

Vermeijius virginiae comb. nov.	
Sequences analyzed	9
Independent combinations	[283:'C']
	[592:'G']
	[4:'G', 370:'C']
	[25:'G', 451:'T']
	[31:'T', 40:'A']
	[34:'G', 499:'C']
	[55:'G', 235:'C']
	[94:'G', 142:'C']
	[103:'C', 232:'C']
	[212:'C', 508:'G']
	[268:'G', 610:'C']
	[281:'C', 385:'C']
	[287:'C', 541:'T']
	[307:'A', 475:'G']
	[343:'T', 628:'C']
	[511:'G', 533:'C']
	[547:'C', 637:'A']
Vermeijius pallidus comb. nov.	
Sequences analyzed	4
Independent combinations	[316:'C']
	[163:'C']
	[475:'T']
	[31:'T', 196:'G']
	[40:'G', 283:'T']
	[49:'C', 508:'G']
	[55:'G', 214:'G']
	[74:'C', 118:'C']
	[127:'G', 313:'T']
	[142:'C', 463:'C']
	[223:'G', 634:'C']
	[232:'C', 331:'G']
	[265:'A', 562:'C']
	[364:'C', 526:'G']
	[382:'G', 547:'C']
	[499:'G', 610:'C']

Molecular diagnosis

A molecular diagnosis is given in Table 4.

Type material

Holotype

JAPAN: off Cape Ashizuri, Kochi Prefecture (NSMT Mo 40378) [not seen].

Sequenced material

SOLOMON ISLANDS: SALOMON 2: 1 lv, stn CP2290, Tetepare, 8°40′ S, 157°32′ E, 384–418 m (MNHN IM-2007-32537).

NEW CALEDONIA: CONCALIS: 1 lv, stn CP2962, Grand Passage, 18°59′ S, 163°08′ E, 580–647 m (MNHN IM-2007-35093).

SOUTH CHINA SEA: DongSha 2014, 2 lv, stn CP4128, 20°42′ N, 116°08′ E, 420–444 m (MNHN IM-2013-50173, MNHN IM-2013-50174).

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Fig. 11. Species of *Vermeijius* gen. nov. **A–E**. *Vermeijius pallidus* (Kuroda & Habe, 1961) gen. et comb. nov. **A–B**. South China Sea, DongSha 2014, stn CP4128, 20°42′ N, 116°08′ E, 420–444 m. **A**. SL 50.6 mm (MNHN IM-2013-50173). **B**. SL 56.6 mm (MNHN IM-2013-50174). **C**. Solomon Islands, SALOMON 2, stn CP2290, 08°40′ S, 157°32′ E, 384–418 m, SL 59.9 mm (MNHN IM-2007-32537). **D–E**. New Caledonia, CONCALIS, stn CP2962, Grand Passage, 18°59′ S, 163°08′ E, 580–647 m, SL 45.2 mm (MNHN IM-2007-35093). **F–J**. *Vermeijius virginiae* (Hadorn & Fraussen, 2002) gen. et comb. nov. **F**. Holotype, SL 58.9 mm (MNHN IM-2000-9626). **G–H**. South Madagascar, ATIMO VATAE, stn CP3585, 25°32′ S; 44°16′ E, 549–576 m. **G**. SL 53.8 mm (MNHN IM-2009-15025). **H**. SL 52.6 mm (MNHN IM-2009-15026). **I–J**. South Madagascar, ATIMO VATAE, stn CP3591, 25°03′ S, 43°58′ E, 400–402 m, SL 56 mm (MNHN IM-2009-15021). **K**. *Vermeijius retiarius* (Martens, 1901) gen. et comb. nov., South Madagascar, ATIMO VATAE, stn CP3595, 25°35′ S, 44°15′ E, 821–910 m, SL 47.5 mm (MNHN IM-2009-15087). All specimens sequenced, except F. Figures A–D, F–I, K to the same scale.

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Description

Shell up to 60 mm in length, solid, fusiform, with strongly constricted base with long, nearly straight, siphonal canal, slightly inclined to left. Protoconch obtusely conical (Fig. 11E) of 3.25 whorls, with evenly convex, brown, smooth whorls, last half whorl with seven distinct, arcuate, axial ribs, protoconch/teleoconch discontinuity distinct, marked by appearance of spiral sculpture of teleoconch. Protoconch diameter 1160 µm, exposed height 1100 µm. Teleoconch with strongly convex whorls. Aperture wide, oval, with weak columellar plicae, corresponding to primary spiral cords overlaid by callus, from nearly absent to 4–5 on lower half of columella. Spiral sculpture of unevenly arranged cords, alternating in strength, strongly nodulous at intersection with axial ribs. Axial ribs broadly spaced, narrow, not aligned along spire, 10–12 on last whorl. Growth lines usually thickened, forming reticulated structure at intersection with spiral cords. Background colour pale flesh to nearly white.

Operculum elongate, leaf-shaped, nearly spanning the entire aperture. Nucleus terminal, often abraded.

Radula (Fig. 12A–B, MNHN IM-2007-35093, SL 42.5 mm) long, of about 105 rows of teeth, 30 nascent, 4.3 mm long (0.41 of AL without canal); narrow, distance between outer edges of lateral teeth about 140 µm wide (1.33% of AL without canal). Lateral teeth broad, slightly arcuate, with strongly attenuated outer anterior corner, producing long 'handle'. Lateral teeth with six, almost equal, recurved, closely

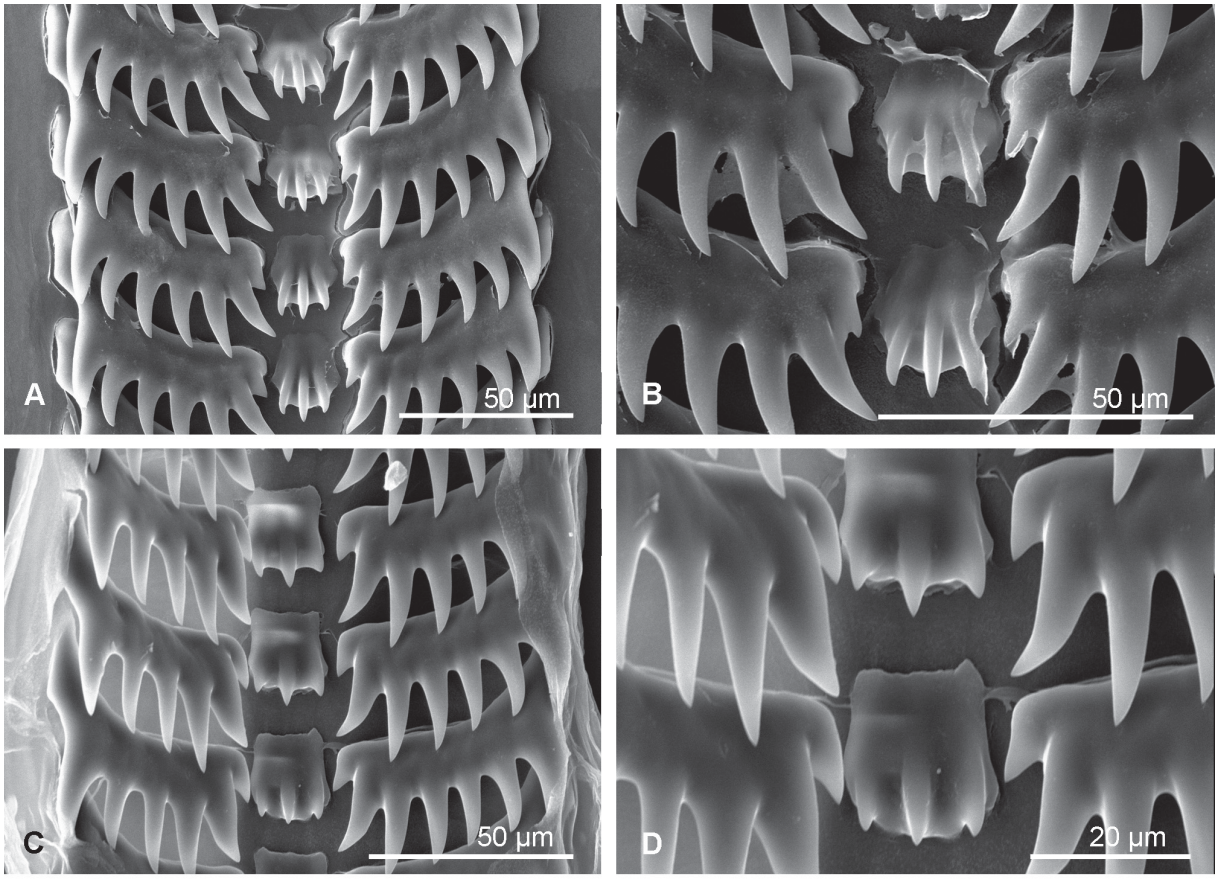

Fig. 12. Radulae of species of *Vermeijius* gen. nov. **A–B**. *Vermeijius pallidus* (Kuroda & Habe, 1961) gen. et comb. nov., New Caledonia, CONCALIS, stn CP2962, Grand Passage, 18°59′ S, 163°08′ E, 580–647 m, shell, see Fig. 11D (MNHN IM-2007-35093). **C–D**. *Vermeijius virginiae* (Hadorn & Fraussen, 2002) gen. et comb. nov., South Madagascar, ATIMO VATAE, stn CP3585, 25°32′ S, 44°16′ E, 549–576 m (MNHN IM-2009-15030).

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spaced, major cusps and one smaller inner cusp. Teeth outline convex at transition of outer cusp side into 'handle'. Central tooth subrectangular, with three short, sharp cusps, central slightly longer. Distinct transverse folds of the membrane situated serially between rows of lateral teeth.

The radula illustrated by line drawing by Hadorn & Fraussen (2002: fig. 22) is very similar, differing in the presence of 7 major cusps on lateral teeth *versus* 6 in our specimen.

Distribution

Japan to New Caledonia, in 384–647 m.

Remarks

Callomon & Snyder (2009) discussed and illustrated the type of the species stored in NSMT (Mo 40378) and concluded that it does not match the dimensions of the holotype (52.2 vs 56.8 mm for the latter according to the original description); the specimen may be a figured paratype.

Vermeijius pallidus gen. et comb. nov. is somewhat similar to *V. virginiae* gen. et comb. nov.; for differences, see the description of the latter.

Vermeijius virginiae (Hadorn & Fraussen, 2002) gen. et comb. nov.
Figs 11F–J; 12C–D

Fusinus virginiae Hadorn & Fraussen, 2002: 70, 72, figs 15–19.

Fusinus virginiae – Mallard & Robin 2017: 104.

Molecular diagnosis

A molecular diagnosis is given in Table 4.

Type material

Holotype

MOZAMBIQUE CHANNEL: off Southwest Madagascar, 22°10′ S, 43°05′ E, 525 m, Campagne Crevettière 1986, stn CH79 (MNHN IM-2000-9626).

Sequenced material

SOUTH MADAGASCAR: ATIMO VATAE: 7 lv, stn CP3585, 25°32′ S, 44°16′ E, 549–576 m (MNHN IM-2009-15020, MNHN IM-2009-15025, MNHN IM-2009-15026, MNHN IM-2009-15030, MNHN IM-2009-15031, MNHN IM-2009-15033, MNHN IM-2009-15034); 2 lv, stn CP3591, 25°03′ S; 43°58′ E, 400–402 m (MNHN IM-2009-15021, MNHN IM-2009-15084).

Description

Shell large for genus, up to 56 mm, strong, fusiform, with strongly constricted base with long, nearly straight, siphonal canal, slightly inclined to left. Protoconch (Fig. 11J) conical of 2.25 moderately convex, smooth, greyish and semitransparent whorls, with elevated first whorl, and 2–5 indistinct axial ribs at transition to teleoconch. Protoconch/teleoconch discontinuity distinct, marked by appearance of teleoconch spiral sculpture. Protoconch diameter 960 µm, exposed height 800 µm. Teleoconch with regularly strongly convex whorls. Aperture broad, oval, columella smooth, or with 1 or 2 weak, inconspicuous plicae, corresponding to underlying spiral sculpture of preceding whorl. Spiral sculpture of unevenly spaced cords, alternating in strength, slightly nodulous at intersection with axial ribs. Growth lines usually thickened, forming reticulated structure at intersection with spiral cords. Axial ribs

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not aligned along spire, 9–11 on last whorl. Background colour pale flesh to nearly white. Operculum elongate, leaf-shaped, spanning nearly the entire aperture. Nucleus terminal.

Radula (Fig. 12C–D, MNHN IM-2009-15030, SL 51.5 mm) long, of about 150 rows of teeth, 40 nascent, 4.5 mm long (0.37 of AL without canal), narrow, distance between outer edges of lateral teeth about 130 µm (1.06% of AL without canal). Lateral teeth broad, slightly arcuate, with strongly attenuated outer anterior corner, producing long 'handle'. Lateral teeth with six, almost equal, recurved, closely spaced, major cusps and one smaller inner cusp. Teeth outline convex at transition of outer cusp side into 'handle'. Central tooth subrectangular, with three very short, sharp cusps, central slightly longer. The radula illustrated by line drawing by Hadorn & Fraussen (2002: fig. 19) is very similar to that of our specimen, but has 7 major cusps on lateral teeth versus 6 in our specimen.

Distribution

Southern Madagascar, in 400–576 m.

Remarks

The species is rather similar conchologically and is a sister to *V. pallidus* gen. et comb. nov. It differs in having fewer protoconch whorls, thinner spiral cords, forming less defined beads at intersection with axial ribs.

Vermeijius retiarius (Martens, 1901) gen. et comb. nov.
Fig. 11K

Fusus? retiarius Martens, 1901: 22.

Fusus? retiarius – Martens 1904: 104–105, pl. 2, fig. 4.
Fusinus retiarius – Hadorn & Fraussen 2002: 64, 66, 68, figs 3–8, 21. — Mallard & Robin 2017: 81.

Type material

Lectotype

SOMALIA: dd, 38.5 × 15.7 mm, off southern Somalia, 01º49′ N, 45°29′ E, 1134 m, *Valdivia*, stn 256, designated by Hadorn & Fraussen (2002) (ZMB 61012).

Sequenced material

SOUTH MADAGASCAR: ATIMO VATAE: 1 lv, stn CP3595, South of Pointe Barrow, 25°35′ S, 44°15′ E, 821–910 m (MNHN IM-2009-15087).

Description

Shell large for genus, up to 57 mm in length, strong, broadly fusiform, gradually constricting to medium long, sinuous, coaxial siphonal canal. Protoconch dome-shaped, paucispiral, of 1.5 convex smooth whorls, greyish, semitransparent, with 3 weak arcuate axial ribs at transition to teleoconch. Protoconch/teleoconch discontinuity distinct, marked by appearance of teleoconch spiral sculpture. Protoconch diameter 1000 µm, exposed height 700 µm. Teleoconch with strongly convex whorls. Aperture broad, oval, columella smooth. Spiral sculpture of moderately strong cords, beaded at intersection with axial ribs and much thinner, although distinct, secondary cords, covering interspaces between primary cords; 4–5 primary spiral cords on spire whorls, including penultimate. Axial ribs not aligned along spire, 11–12 per whorl. Background colour pale flesh to nearly white. Operculum elongate, leaf-shaped, spanning nearly entire aperture. Nucleus terminal.

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Radula (Hadorn & Fraussen 2002: fig. 21) with medium broad, arcuate, lateral teeth, with attenuated outer anterior corner, producing medium long 'handle'. Lateral teeth with five slightly recurved cusps, outermost longest, more distant from others. Additional innermost short, but distinct, cusp present. Central tooth small, subrectangular, with three very short cusps, medium longest.

Distribution

East Africa, from Somalia to South Madagascar, in 500–1134 m.

Remarks

In the COI-based tree *Vermeijius retiarius* gen. et comb. nov. did not cluster with *V. pallidus* gen. et comb. nov. and *V. virginiae* gen. et comb. nov., but in the three genes tree it was recovered as a sister group to the clade combining these two species. The relationships are highly supported in the Bayesian analysis, therefore we include it in *Vermeijius* gen. nov. It differs from the two sequenced species by a more stout shell with paucispiral protoconch.

Discussion

The current taxonomy of Fasciolariidae as well as the division of the family in three subfamilies (Fasciolariinae Gray, 1853, Fusininae Wrigley, 1927 and Peristerniinae Tryon, 1880) was suggested by Snyder (2003) based mostly on shell characters and to lesser degree on radula and anatomy, and accepted in most subsequent studies (e.g., Bouchet & Rocroi 2005; Mallard & Robin 2005). Nevertheless, the difficulties in allocating genera to subfamilies based on shell characters were often emphasized (e.g., Vermeij & Snyder 2006). The situation was dramatically changed with the publication of the first molecular phylogeny of the family (Couto *et al.* 2016). The multigene molecular phylogeny confirmed the monophyly of the family (with the exclusion of the genera *Dolicholatirus* Bellardi, 1884 and *Teralatirus* Coomans, 1965) and its subdivision into three well supported subfamily clades, but the subfamilial allocation of many genera was changed, demonstrating the weaknesses of a conchological approach to the taxonomy of the family. Many genera of Peristerniinae, in particular, were reassigned to other subfamilies. The present analysis of a notably extended molecular dataset of Fusininae allowed the re-evaluation of the generic position of species formerly placed in *Pseudolatirus*, here assigned to two new genera *Vermeijius* gen. nov. and *Okutanius* gen. nov., as well as relocated to *Granulifusus*. The genus *Vermeijius* gen. nov., sister to *Chryseofusus* in our analysis, was recovered with high support in the three genes trees. Conchologically it differs from other '*Pseudolatirus*'-like taxa, having a light coloured '*Fusinus*'-type shell. Not surprisingly, all three sequenced species of *Vermeijius* gen. nov. were earlier described in, or attributed to, *Fusinus*. It should be noted that the specimen MNHN IM-2007-36654, erroneously identified as *Fusinus virginiae* in Couto *et al.* (2016) ends up within the genus *Fusinus* and represents a different, apparently still unnamed species.

Conversely, species that we re-assigned to *Granulifusus* and *Okutanius* gen. nov. demonstrate a significant overlap both in shell and anatomical characters (radula), such that the intrageneric variability exceeds the intergeneric one. The molecular data are therefore crucial for a correct generic assignment. Based on shell characters alone, it would be impossible to recognize two separate genera that appear not even closely related to each other. Similarly, the relationships revealed between the new genera (*Vermeijius* gen. nov. sister to *Chryseofusus* and *Okutanius* gen. nov. sister to *Angulofusus*) could hardly be deduced from shell characters, since these pairs of sister genera have rather different shells. At the same time, the radula of *Vermeijius* gen. nov. (herein) is similar to that of *Chryseofusus* (Couto 2016: fig. 38) in having similarly shaped laterals and trapezoid, relatively broad and short, central teeth. Similarly, the radula of *Okutanius* gen. nov. is rather similar to that in *Angulofusus* (Fedosov & Kantor 2012: fig. 2C–D). Thus, in at least these two cases, the radular morphology is a better proxy for taxonomic decision than shell characters.

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The radulae of the species that we include in *Granulifusus* is variable in the shape of both the lateral and central teeth. The number of cusps on the lateral teeth varies from four to six, the innermost additional small cusp being distinct in all studied species except *G. annae* sp. nov. (Fig. 4E), while the shape of the central tooth varies from very narrow and long in *G. annae* sp. nov. to trapezoid and relatively broad in *G. jeanpierrevezzaroi* comb. nov. (Fig. 4C–D). The radulae of a number of species previously placed in *Granulifusus* illustrated by line drawings by Hadorn & Fraussen (2005) demonstrate a similar degree of disparity. We should stress again that the relationships within the clade that corresponds to newly circumscribed *Granulifusus* are not fully resolved, although the clade itself is highly supported (BI 0.99). Beside, a relatively small number of species of 'traditional' *Granulifusus* were sequenced and included in the analysis, thus not excluding that with a more saturated dataset the polytomies will be fully resolved some new genera can be erected within *Granulifusus*.

One of the peculiarities of the radulae of Fasciolariidae that was never specifically discussed previously is the presence of serially arranged straight or arcuate oblique folds of the membrane that are directed from the base or middle of central teeth backwards, and extend more or less parallel to the anterior margin of the lateral teeth in interspaces between adjacent lateral teeth (marked by white arrows in Fig. 4D–E). These folds were found not only in the species of *Granulifusus*, *Okutanius* gen. nov. and *Vermeijius pallidus* gen. et comb. nov. studied herein but in other fasciolariids as well, particularly in *Crassibougia clausicaudata* (Hinds, 1844) (Stahlschmidt & Fraussen 2012: figs 17–18), in several *Fusolatirus* (Snyder & Bouchet 2006: figs 1L–M, 3K), in *Angulofusus* (Fedosov & Kantor 2012: fig. 2C–D), in *Fusinus* (Couto 2016) and at least in some members of Fasciolariinae, e.g., *Polygona angulata* (Röding, 1798) (Couto 2016: fig. 85). Thus these structures are found in all recognized subfamilies of Fasciolariidae. Their function or homology remain unknown, but one can speculate that they increase the rigidity of the membrane. Another insufficiently studied feature of the fasciolariid radula is that, unlike the radulae of other Buccinoidea, it is not folded longitudinally along the two axes between the central and lateral teeth. The presence of the aforementioned folds may be connected with the radular membrane being permanently unfolded. Another possibility is that the central tooth in Fasciolariidae is actually much broader than is commonly perceived, and the folds represent reduced lateral flaps of the tooth – a morphology of the rachidians found in many other neogastropods. In this case what is considered here the central tooth Fasciolariidae would, in fact, be only the central cuspate part of the tooth.

An additional unusual radular character is that the subradular membrane extends laterally well beyond the outer edges of the lateral teeth. This part of the membrane is thin, and in natural position it covers at least the lateral teeth of the radula. It is very difficult to unfold these lateral parts of the membrane during preparation of the radula for scanning electron microscopy, and it often remains overlaying the teeth as a thin film. This is seen on some of the photos (e.g. on Fig. 4B, where it covers most of the lateral teeth). This peculiarity was found in the three genera examined here in detail, as well in *Angulofusus* (see Fedosov & Kantor 2012: fig. 2C–D) and may be present in other fasciolariids as well. We have not seen such subradular membrane morphology in other Buccinoidea, although many dozens of species were examined by the first author with SEM. On the contrary, usually these are the outermost edges of lateral teeth that expand beyond the limits of the membrane when it is extended.

Presently, we are witnessing an explosion of new taxa descriptions in Fasciolariidae. Out of 55 valid Recent genera accepted in WoRMS, 14 (25%) were described before the 20th century, 9 (16.5%) were described between 1901 and 1950, 9 (16.5%) between 1951 and 2000 and 23 (42%) since 2001. This is the first work where new genera are established based on a molecular phylogenetic analysis. Many of the recently described genera have not yet been analyzed molecularly and their validity is still unconfirmed. Among genera described after 2001, *Chryseofusus* Hadorn & Fraussen, 2003, *Turrilatirus* Vermeij & Snyder, 2006, *Pustulatirus* Vermeij & Snyder, 2006, *Amiantofusus* Fraussen, Kantor & Hadorn, 2007 and

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Angulofusus Fedosov & Kantor, 2012, proved to be monophyletic in the analysis of Couto *et al.* (2016). Other genera (e.g., *Fusolatirus* Kuroda & Habe, 1971) proved to be paraphyletic in their accepted scope; the conchologically distinctive *Cyrtulus* Hinds, 1843 was unequivocally demonstrated to be merely a species of *Fusinus* and *Pseudolatirus*, as demonstrated here, is to be restricted to fossil species only. This suggests that establishing new genera solely on conchological characters is risky and should be avoided unless necessary. The use of morphological characters (radula), although strongly recommended, does not necessarily provide solid evidence for phylogenetic distinctiveness of a lineage in question.

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