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Research Article

Phylogeny and taxonomy of the *Kermia–Pseudodaphnella* (Mollusca: Gastropoda: Raphitomidae) genus complex: a remarkable radiation via diversification of larval development

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Conoidean gastropods of the genera *Kermia*, Oliver, 1915 and *Pseudodaphnella* Boettger, 1895 (Raphitomidae) are common in shallow-water habitats of the tropical Indo-Pacific. They form a distinct morphologically homogeneous complex, easily recognizable by sculpture and colour pattern, encompassing around 80 described species. Examination of a vast material accumulated during recent expeditions in various regions of the Indo-Pacific revealed a number of undescribed species of this complex. Our material included 32 morphospecies available for molecular phylogenetic study; phylogenetic reconstruction based on the COI gene confirmed the species hypotheses based on morphological characters. A total of 18 terminal taxa were attributed to known species and 14 were identified as new species. Of these, 12 species, for which sufficient material was available, are described. Phylogenetic analysis indicated close relationships of the genera *Kermia* and *Pseudodaphnella* with members of some other conoidean genera (specifically *Exomilus* Hedley, 1918, *Paramontana* Laseron, 1954 and *Thetidos* Hedley, 1899) and taxonomic implications of the data obtained are discussed. To test the taxonomic value of protoconch and review its wide use in classification of Conoidea, the evolution of the protoconch morphology was reconstructed using a phylogenetic tree. It has revealed that protoconchs of different types may appear in closely related species, sometimes hardly distinguishable by teleoconch morphology. A switch from planctotrophic to non-planctotrophic mode of development occurred at least four times in the evolutionary history of the *Kermia–Pseudodaphnella* complex, indicating high developmental plasticity of the group. Its role in radiation of the *Kermia–Pseudodaphnella* complex and applications for use of protoconch morphology in the classification of Conoidea are discussed.

Key words: COI gene, Conoidea, Indo-Pacific, integrative taxonomy, new species, planctotrophic development, protoconch, turrid diversity

Introduction

Similar to insects in tropical forests, molluscs are the most diversified animal group in the sea (Bouchet *et al.*, 2011) and the proportion of undescribed species in the phylum Mollusca is very high. Some mollusc taxa remain poorly studied, either because they are difficult to sample (e.g. many deep-water and/or minute species) or analyse (highly variable morphological characters that are difficult to interpret). The turrids, an informal group that brings together all of the conoideans, except the well-defined cone and auger snails (Conidae and Terebridae, respectively), are one of these groups. They belong to the Conoidea, a superfamily remarkable because of the possession of a venom gland and complex feeding mechanisms. To date, *c.* 4000 turrid species have been described (Tucker, 2004; WoRMS – Appeltans *et al.*, 2012), among an estimated total of 10–20 000 species (Bouchet *et al.*, 2009), including rich deep-water fauna and a large proportion of small species, with an adult size less than 10 mm.

As a result of intensive shallow water biodiversity surveys, undertaken by MNHN during recent decades (Bouchet *et al.*, 2008), an unprecedented amount of turrid material has been accumulated, including a number of deep-water species as well as many small to minute species that were never recorded previously. Preliminary sorting revealed an extreme morphological diversity, significantly exceeding the number of described species in most families of turrids. However, because the taxonomy of the turrids based on the shell variability is largely unstable, it

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remained unclear whether some of these forms represented undescribed species or forms of known species.

For more than 10 years, DNA sequencing has been intensively used to tackle this issue in several groups of Conoidea. It proved useful in solving various taxonomic problems, both at the species and phylogenetic levels (Duda & Kohn, 2005; Cunha *et al.*, 2008; Kantor *et al.*, 2008; Puillandre *et al.*, 2010), and for hypotheses on aspects of the biology, ecology and evolution of the group (Williams & Duda, 2008; Duda & Lee, 2009; Castelin *et al.*, 2012). Many groups of turrids, however, remain unstudied at the molecular level, among which Raphitomidae is of particular importance. It is probably the most diverse family of Conoidea, both in terms of species richness and ecological range. Its members occur from shallow waters to abyssal depths from the tropics to the poles. Furthermore, their close phylogenetic relationships with cone snails, a group intensively studied for the therapeutic applications of their toxins, make them an interesting candidate for toxin discovery.

In this study, we focus on the raphitomid genera *Kermia* Oliver, 1915 and *Pseudodaphnella* Boettger, 1895. They constitute both a diverse and easily recognizable group. Characteristic for this group are reticulate shell sculpture with glossy nodules formed on intersections of spiral and axial elements, rounded U-shaped or linguiform anal sinus and an outer lip that is typically varicose and denticulate within at maturity (Powell, 1966; Kilburn, 2009). On the other hand, diagonally cancellate protoconch sculpture, which is generally accepted to be a key feature of the family Raphitomidae, is only present in some members of this generic complex. Shallow-water members of the group are remarkable and distinctive due to contrasting colouration of their shells, usually white with diverse patterns of orange, brown or black bands. The largest species of this generic complex, *Pseudodaphnella philippinensis* (Reeve, 1843) reaches 25 mm in shell height, while the vast majority of its members range from 3 to 9 mm. Presently the group includes around 80 species (WoRMS – Appeltans *et al.*, 2012), widely distributed in the Indo-Pacific from South Africa to Hawaii and from Japan to Southern Australia.

The primary objective of this paper is to propose hypotheses for species delimitation in the *Kermia–Pseudodaphnella* complex and to describe the species identified as new. We applied a two step approach with first the analysis of the morphological variability of the shell to propose primary hypotheses of species delimitation, and second, the analysis of DNA sequences (COI gene) to test the congruence between morphospecies and COI diversity. Thus our study follows an integrative taxonomy approach, where species are considered as hypotheses engaged in a process of modification of validation as new characters are analyzed (De Queiroz, 2007; Barberousse & Samadi, 2010).

In addition to species delimitation, we also inferred the phylogenetic relationships between the delimited species to test several hypotheses regarding the evolution of the group. Relationships within the *Kermia–Pseudodaphnella* complex remain uncertain, and it is yet unclear whether or not the complex corresponds to a monophyletic group (Kilburn, 2009). Traditionally, following Powell's interpretation, supraspecific classification within the *Kermia–Pseudodaphnella* complex was largely based on protoconch morphology: those species with planctotrophic, diagonally cancellate protoconchs assigned to the genus *Kermia*, others, with planctotrophic, but non-diagonally cancellate protoconch forming the genus *Pseudodaphnella*. A few distinct species, characterized by a narrow subcylindrical shell with appressed whorls and a high truncated protoconch devoid of cancellate sculpture, were assigned to the genus *Exomilus* Hedley, 1918 (Powell, 1966; Kilburn, 2009). And finally the genus *Paramontana* Laseron, 1954 was established to accommodate a few species with non-planctotrophic protoconch (Laseron, 1954; Powell, 1966). Since non-planctotrophic protoconchs were deviant and unwelcome in the subfamily Raphitominae, the subfamilial assignment of the latter genus was questioned (Powell, 1966; Taylor *et al.*, 1993; Kilburn, 2009). Laseron (1954), Powell (1966) and Taylor *et al.* (1993) placed it in the subfamily Mangeliinae that implied polyphyly of the *Kermia–Pseudodaphnella* complex. Notwithstanding, the latest classification of Conoidea considers all four mentioned genera to be Raphitomidae (Bouchet *et al.*, 2011).

Mapping of the states of a morphological character on a phylogenetic tree allows tracing the history of its evolutionary transformations and may reveal the mechanisms underlying diversification. Simultaneous correlation of molecular data and morphology allows estimation of the taxonomic value of various morphological character states and their use in phylogenetic reconstructions and taxonomic decisions (Kantor *et al.*, 2008; Fedosov *et al.*, 2011). In the present study we paid special attention to protoconch morphology to challenge its importance in supraspecific taxonomy of the *Kermia–Pseudodaphnella* complex.

Materials and methods

Material

Material for the present study was collected during three expeditions, conducted by Muséum National d'Histoire Naturelle: 'Panglao 2004' (Central Philippines), 'Santo 2006' (Vanuatu) and 'Atimo Vatae 2010' (Southern Madagascar). The total dataset included 77 specimens collected live, segregated in 32 morphospecies. These specimens were anaesthetized with $MgCl_2$, and a piece of tissue was cut from the head–foot of each specimen and fixed in 95% ethanol for molecular analysis. Shells were drilled to remove a piece of tissue, when they were deeply retracted. Additional raphitomid specimens, both from shallow and deep water, were used as closely related outgroups to test the monophyly of the taxa investigated. Three other Conoidea: *Lovellona atramentosa* (Mitromorphidae), *Conus elokismenos* (Conidae) and *Turris babylonia* (Turridae) were used as distant outgroups to artificially root the tree. All these specimens are vouchered in the MNHN collections and published in the Barcode of Life database (BOLD), and their corresponding DNA sequences are registered in GenBank (MNHN IDs, BOLD process IDs and GenBank accession numbers are listed in Table 1).

Additionally, a number of specimens from dry material were used to illustrate the range of morphologic variability and for type series for species recognized as new. To discuss possible relationships of these new species, material of morphologically similar species was used as well. Part of the dry material was collected in earlier expeditions in New Caledonia: Expedition 'Montrouzier' (1993, Koumac, Touho), 'Atelier Lifou' (2000, Loyalty Islands: Lifou), 'Secteur de Noumea' (1992–1993, Noumea).

DNA sequencing

Total DNA was extracted from the piece of foot using the 6100 Nucleic Acid Prepstation system (Applied Biosystem), the Epmotion 5075 robot (Eppendorf) or the Dneasy96 Tissue kit (Qiagen) for smaller specimens, following the manufacturer's recommendations. The barcode fragment of the COI gene (658 bp) was amplified using the universal primers LCO1490 and HCO2198 (Folmer *et al.*, 1994). PCR reactions were performed in 25 μl, containing 3 ng of DNA, 10× reaction buffer containing 15 mM $MgCl_2$, 0.26 mM dNTP, 0.3 μM of each primer, 5% DMSO, 1 mg/ml BSA and 1 unit of QBiotaq (MPBiomedicals). Amplification consisted of an initial denaturation step at 95°C for 5 min, followed by 35 cycles of denaturation at 95°C for 40 s, annealing at 50°C for 30 s, followed by extension at 72°C for 1 min. The final extension was at 72°C for 5 min. PCR products were purified and sequenced by the Eurofins sequencing facility. Both directions were sequenced to confirm accuracy of each sequence.

Phylogenetic analyses

Phylogenetic analyses were performed using MrBayes (Huelsenbeck *et al.*, 2001), running two parallel analyses, consisting each of five Markov chains of 20 000 000 generations with a sampling frequency of one tree each 2500 generations. The number of swaps was set to 3, and the chain temperature at 0.02. Parameters of the substitution model were estimated during the analysis (six substitution categories, a gamma-distributed rate variation across sites approximated in four discrete categories and a proportion of invariable sites). A different model of substitution was applied for each codon position of the COI gene. Convergence of each analysis was evaluated using Tracer 1.4.1 (Rambaut & Drummond, 2007) to check that ESS values were all greater than 200 (default burning). K2P genetic distances were calculated with MEGA 4 (Tamura *et al.*, 2007). A reduced dataset, with only one specimen per species, was used to build a new phylogenetic tree using the method described before. On this tree the evolution of the protoconch was assessed with Mesquite V2.74 (Maddison & Maddison, 2009), using the option 'tracing character history' and the parsimony ancestral reconstruction method. Two states for the protoconch were defined: non-planctotrophic and planctotrophic (Table 2).

Radula preparation

For some species, where additional alcohol-fixed or live-dried material was accessible, radula morphology was studied. During radula preparation bodies were extracted from shells and dissected to isolate buccal complexes. These were treated by 1% solution of sodium hypochlorite until soft tissues were completely dissolved; radulae were cleaned in several changes of distilled water, unfolded and mounted for SEM examination.

Abbreviations of repositories, used in text:

AMS – Australian Museum, Sydney, Australia
NHMUK – The Natural History Museum, London, UK
MNHN – Muséum National d'Histoire Naturelle, Paris, France

Other abbreviations:

SH – shell height
w/h – ratio of shell width to its height

Results

Phylogenetic analysis

The Raphitomidae were found to be monophyletic (posterior probability PP = 0.96 – see Fig. 1). Within the Raphitomidae species of the *Kermia–Pseudodaphnella* group cluster together in a weakly supported group (PP = 0.56), shaded on the tree, except the two species *Kermia* cf. *producta* (probably *K. daedalea* (Garrett, 1873), though precise identification was impossible as the specimen is a juvenile) and *Kermia producta*, forming a separate clade. The 32 *Kermia–Pseudodaphnella* morphospecies, even when they are morphologically highly similar, for example *Pseudodaphnella philippinensis* and *P. crypta* nov. sp. (all formal descriptions are given below in taxonomic account) or *Pseudodaphnella barnardi* (Brazier, 1876) and *P. phaeogranulata* nov. sp., each correspond to a separate lineage. All the morphospecies represented by more than one specimen correspond to a well-supported

Table 1. Specimens of *Kermia–Pseudodaphnella* complex and other conoidean taxa included in phylogenetic analysis.

MNHN Number	BOLD process ID	COI GenBank ID	*Genus*	*species*	Expedition	Country	Latitude, Longitude; depth (m)
IM-2007-17871	CONO251-08	EU015693	*Pseudodaphnella*	*crypta*	PANGLAO 2004	Philippines	9°41.5′N, 123°51.0′E; 21
IM-2007-17878	CONO259-08	EU015700	*Pseudodaphnella*	*aureotincta*	PANGLAO 2004	Philippines	9°29.4′N, 123°56.1′E; 0-16
IM-2007-17880	CONO267-08	EU015702	*Thetidos*	*tridentata*	PANGLAO 2004	Philippines	9°31′N, 123°41′E; 90-110
IM-2007-42335	CONO606-08	KC250721	*Pseudodaphnella*	*variegata*	PANGLAO 2004	Philippines	9°35.9′N, 123°51.8′E; 4-30
IM-2007-42346	CONO617-08	KC250665	*Pseudodaphnella*	*bifasciata*	PANGLAO 2004	Philippines	9°29.4′N, 123°56.0′E; 6-8
IM-2007-42379	CONO650-08	KC250658	*Pseudodaphnella*	*barnardi*	PANGLAO 2004	Philippines	9°36.1′N, 123°45.0′E; 2-4
IM-2007-42381	CONO652-08	KC250674	*Pseudodaphnella*	*crypta*	PANGLAO 2004	Philippines	9°41.5′N, 123°51.0′E; 21
IM-2007-42382	CONO653-08	KC250667	*Pseudodaphnella*	*boholensis*	PANGLAO 2004	Philippines	9°29.4′N, 123°56.0′E; 15-20
IM-2007-42383	CONO654-08	KC250669	*Pseudodaphnella*	*boholensis*	PANGLAO 2004	Philippines	9°29.4′N, 123°56.0′E; 15-20
IM-2007-42384	CONO655-08	KC250668	*Pseudodaphnella*	*boholensis*	PANGLAO 2004	Philippines	9°29.4′N, 123°56.0′E; 15-20
IM-2007-42386	CONO657-08	KC250714	*Pseudodaphnella*	*nsp9*	PANGLAO 2004	Philippines	9°29.4′N, 123°56.1′E; 0-16
IM-2007-42387	CONO658-08	KC250691	*Pseudodaphnella*	*lineata*	PANGLAO 2004	Philippines	9°29.4′N, 123°56.1′E; 0-16
IM-2007-42388	CONO659-08	KC250686	*Pseudodaphnella*	*fallax*	PANGLAO 2004	Philippines	9°29.4′N, 123°56.0′E; 0-38
IM-2007-42392	CONO663-08	KC250725	*Pseudodaphnella*	*philippinensis*	PANGLAO 2004	Philippines	9°38.1′N, 123°51.4′E; 3-4
IM-2007-42393	CONO664-08	KC250727	*Kermia*	*rufolirata*	PANGLAO 2004	Philippines	9°38.1′N, 123°51.4′E; 3-4
IM-2007-42400	CONO671-08	KC250720	*Thetidos*	*tridentata*	PANGLAO 2004	Philippines	9°31′N, 123°41′E; 90-110
IM-2007-42401	CONO672-08	KC250719	*Thetidos*	*tridentata*	PANGLAO 2004	Philippines	9°31′N, 123°41′E; 90-110
IM-2007-42407	CONO678-08	KC250670	*"Kermia"*	*cf. producta*	PANGLAO 2004	Philippines	9°31′N, 123°41′E; 90-110
IM-2007-42410	CONO681-08	KC250718	*Thetidos*	*tridentata*	PANGLAO 2004	Philippines	9°31′N, 123°41′E; 90-110
IM-2007-42414	CONO685-08	KC250728	*Kermia*	*rufolirata*	PANGLAO 2004	Philippines	9°42.9′N, 123°51.6′E; 0-2
IM-2007-42546	CONO863-08	KC250660	*Pseudodaphnella*	*barnardi*	SANTO 2006	Vanuatu	15°36.6′S, 167°10.1′E; 10-18
IM-2007-42595	CONO912-08	KC250672	*Pseudodaphnella*	*crypta*	SANTO 2006	Vanuatu	15°28.9′S, 167°15.5′E; 0-0
IM-2007-42596	CONO913-08	KC250723	*Pseudodaphnella*	*philippinensis*	SANTO 2006	Vanuatu	15°28.9′S, 167°15.5′E; 0-0
IM-2007-42597	CONO914-08	KC250675	*Pseudodaphnella*	*crypta*	SANTO 2006	Vanuatu	15°42.7′S, 167°15.1′E; 0-7
IM-2007-42611	CONO928-08	KC250724	*Pseudodaphnella*	*philippinensis*	SANTO 2006	Vanuatu	15°34′S, 167°16′E; 0-114
IM-2007-42613	CONO930-08	KC250673	*Pseudodaphnella*	*crypta*	SANTO 2006	Vanuatu	15°22.6′S, 167°11.6′E; 0-0
IM-2007-42631	CONO948-08	KC250726	*Pseudodaphnella*	*rubroguttata*	SANTO 2006	Vanuatu	15°33.6′S, 167°16.6′E; 2-4
IM-2009-17247	RAPHI045-12	KC250648	*Kermia*	*reeveana*	ATIMO VATAE	Madagascar	25°02.1-2′S, 46°59.9′E; 0-1
IM-2009-17858	RAPHI023-12	KC250712	*Kermia*	*nsp2*	ATIMO VATAE	Madagascar	24°57.0′S, 47°06.4′E; 5-6
IM-2009-17905	RAPHI051-12	KC250655	*Pseudodaphnella*	*barnardi*	ATIMO VATAE	Madagascar	25°29.0′S, 44°59.6′E; 0-1
IM-2009-17906	RAPHI002-12	KC250659	*Pseudodaphnella*	*barnardi*	ATIMO VATAE	Madagascar	25°29.0′S, 44°59.6′E; 0-1
IM-2009-17946	RAPHI033-12	KC250698	*Pseudodaphnella*	*nympha*	ATIMO VATAE	Madagascar	25°36.0′S, 45°08.7′E; 0-16
IM-2009-17947	RAPHI028-12	KC250702	*Pseudodaphnella*	*nympha*	ATIMO VATAE	Madagascar	25°36.0′S, 45°08.7′E; 0-16
IM-2009-17948	RAPHI049-12	KC250656	*Pseudodaphnella*	*barnardi*	ATIMO VATAE	Madagascar	25°26.3′S, 44°56.5′E; 0-1
IM-2009-17954	RAPHI026-12	KC250717	*Pseudodaphnella*	*sudafricana*	ATIMO VATAE	Madagascar	25°26.4′S, 44°56.1′E; 14-18
IM-2009-17955	RAPHI024-12	KC250706	*"Kermia"*	*producta*	ATIMO VATAE	Madagascar	25°26.4′S, 44°56.1′E; 14-18
IM-2009-17956	RAPHI027-12	KC250707	*Pseudodaphnella*	*punctifera*	ATIMO VATAE	Madagascar	25°26.4′S, 44°56.1′E; 14-18
IM-2009-17965	RAPHI037-12	KC250682	*Pseudodaphnella*	*eugenei*	ATIMO VATAE	Madagascar	25°35.5′S, 45°08.1′E; 0-11
IM-2009-17967	RAPHI038-12	KC250683	*Pseudodaphnella*	*eugenei*	ATIMO VATAE	Madagascar	25°35.5′S, 45°08.1′E; 0-11
IM-2009-17969	RAPHI035-12	KC250678	*Pseudodaphnella*	*eugenei*	ATIMO VATAE	Madagascar	25°35.5′S, 45°08.1′E; 0-11
IM-2009-17970	RAPHI029-12	KC250703	*Pseudodaphnella*	*nympha*	ATIMO VATAE	Madagascar	25°35.5′S, 45°08.1′E; 0-11
IM-2009-17971	RAPHI030-12	KC250699	*Pseudodaphnella*	*nympha*	ATIMO VATAE	Madagascar	25°35.5′S, 45°08.1′E; 0-11
IM-2009-17972	RAPHI031-12	KC250700	*Pseudodaphnella*	*nympha*	ATIMO VATAE	Madagascar	25°35.5′S, 45°08.1′E; 0-11
IM-2009-17973	RAPHI032-12	KC250701	*Pseudodaphnella*	*nympha*	ATIMO VATAE	Madagascar	25°35.5′S, 45°08.1′E; 0-11
IM-2009-17992	RAPHI025-12	KC250705	*"Kermia"*	*producta*	ATIMO VATAE	Madagascar	25°01.3′S, 47° 00.5′E; 0-18

IM-2009-17993	RAPHI040-12	KC250685	*Pseudodaphnella*	*eugenei*	ATIMO VATAE	Madagascar	25°01.3′S, 47°00.5′E; 0-18
IM-2009-17994	RAPHI044-12	KC250676	*Pseudodaphnella*	*drupelloides*	ATIMO VATAE	Madagascar	25°01.3′S, 47° 00.5′E; 0-18
IM-2009-17999	RAPHI041-12	KC250680	*Pseudodaphnella*	*eugenei*	ATIMO VATAE	Madagascar	25°02.3′S, 47°00.3′E; 22-24
IM-2009-18028	RAPHI034-12	KC250681	*Pseudodaphnella*	*eugenei*	ATIMO VATAE	Madagascar	24°59.8′S, 47°05.7′E; 0-22
IM-2009-18032	RAPHI050-12	KC250657	*Pseudodaphnella*	*barnardi*	ATIMO VATAE	Madagascar	25°01.5′S, 47°00.0′E; 2-4
IM-2009-18038	RAPHI042-12	KC250677	*Exomilus*	*edychroa*	ATIMO VATAE	Madagascar	25°02.3′S, 47°00.3′E; 22-24
IM-2009-18042	RAPHI039-12	KC250684	*Pseudodaphnella*	*eugenei*	ATIMO VATAE	Madagascar	25°01.3′S, 47° 00.5′E; 0-18
IM-2009-18043	RAPHI036-12	KC250679	*Pseudodaphnella*	*eugenei*	ATIMO VATAE	Madagascar	25°09.2′S, 46°45.4′E; 5-6
IM-2009-18054	RAPHI043-12	KC250664	*Pseudodaphnella*	*bifasciata*	ATIMO VATAE	Madagascar	24°59.2′S, 47°05.4′E; 2-7
IM-2009-18058	RAPHI015-12	KC250693	*Pseudodaphnella*	*maculosa*	SANTO 2006	Vanuatu	15°31.4′S, 167°09.8′E; 2-3
IM-2009-18059	RAPHI011-12	KC250694	*Kermia*	*melanoxytum*	SANTO 2006	Vanuatu	15°28.8′S, 167°15.2′E; 2-3
IM-2009-18060	RAPHI012-12	KC250697	*Kermia*	*melanoxytum*	SANTO 2006	Vanuatu	15°24.6′S, 167°14.3′E; 6-43
IM-2009-18099	RAPHI006-12	KC250722	*Pseudodaphnella*	*martensi*	SANTO 2006	Vanuatu	15°34′S, 167°16′E; 0-114
IM-2009-18100	RAPHI020-12	KC250688	*Pseudodaphnella*	*granosa*	SANTO 2006	Vanuatu	15°34′S, 167°16′E; 0-114
IM-2009-18101	RAPHI021-12	KC250687	*Pseudodaphnella*	*granosa*	SANTO 2006	Vanuatu	15°34′S, 167°16′E; 0-114
IM-2009-18104	RAPHI022-12	KC250654	*Pseudodaphnella*	*barnardi*	SANTO 2006	Vanuatu	15°34′S, 167°16′E; 0-114
IM-2009-18105	RAPHI010-12	KC250704	*Pseudodaphnella*	*phaeogranulata*	SANTO 2006	Vanuatu	15°34′S, 167°16′E; 0-114
IM-2009-18108	RAPHI017-12	KC250671	*Exomilus*	*compressa*	SANTO 2006	Vanuatu	15°24.4′S, 167°13.0′E; 0-38
IM-2009-18110	RAPHI009-12	KC250709	*Pseudodaphnella*	*santoa*	SANTO 2006	Vanuatu	15°32.4′S, 167°12.1′E; 0-5
IM-2009-18111	RAPHI007-12	KC250708	*Pseudodaphnella*	*santoa*	SANTO 2006	Vanuatu	15°29.8′S, 167°15.1′E; 0-5
IM-2009-18112	RAPHI008-12	KC250710	*Pseudodaphnella*	*santoa*	SANTO 2006	Vanuatu	15°29.8′S, 167°15.1′E; 0-5
IM-2009-18113	RAPHI013-12	KC250696	*Kermia*	*melanoxytum*	SANTO 2006	Vanuatu	15°24.4′S, 167°13.0′E; 0-38
IM-2009-18114	RAPHI014-12	KC250695	*Kermia*	*melanoxytum*	SANTO 2006	Vanuatu	15°24.4′S, 167°13.0′E; 0-38
IM-2009-18116	RAPHI046-12	KC250661	*Pseudodaphnella*	*barnardi*	ATIMO VATAE	Madagascar	24°56.8′S, 47°06.6′E; 0-7
IM-2009-18117	RAPHI047-12	KC250662	*Pseudodaphnella*	*barnardi*	ATIMO VATAE	Madagascar	24°56.8′S, 47°06.6′E; 0-7
IM-2009-18118	RAPHI048-12	KC250653	*Pseudodaphnella*	*barnardi*	ATIMO VATAE	Madagascar	24°56.8′S, 47°06.6′E; 0-7
IM-2009-18131	RAPHI018-12	KC250666	*Pseudodaphnella*	*bifasciata*	SANTO 2006	Vanuatu	15°31.7′S, 167°09.5′E; 2-3
IM-2009-18132	RAPHI019-12	KC250663	*Pseudodaphnella*	*bifasciata*	SANTO 2006	Vanuatu	15°31.7′S, 167°09.5′E; 2-3
IM-2009-18139	RAPHI005-12	KC250729	*Pseudodaphnella*	*tincta*	SANTO 2006	Vanuatu	15°34′S, 167°16′E; 0-114
IM-2009-18148	RAPHI016-12	KC250692	*Pseudodaphnella*	*maculosa*	SANTO 2006	Vanuatu	15°31.7′S, 167°09.5′E; 2-3
IM-2009-19168	RAPHI004-12	KC250689	*Pseudodaphnella*	*kilburni*	PANGLAO 2004	Philippines	9°32′N, 123°47′E; 83-102
IM-2009-19169	RAPHI003-12	KC250690	*Pseudodaphnella*	*kilburni*	PANGLAO 2004	Philippines	9°32′N, 123°47′E; 83-102
IM-2007-17903	CONO227-08	EU015678	*Eucyclotoma*	*cymathoides*	PANGLAO 2004	Philippines	9°29.4′N, 123°56.0′E; 6-8
IM-2007-42609	CONO926-08	KC250650	*Eucyclotoma*	sp.	SANTO 2006	Vanuatu	15°28.9′S, 167°15.5′E; 0-0
IM-2007-42612	CONO929-08	KC250651	*Eucyclotoma*	sp.	SANTO 2006	Vanuatu	15°34′S, 167°16′E; 0-114
IM-2007-17881	CONO268-08	EU015703	*Daphnella*	sp.	PANGLAO 2004	Philippines	9°31′N, 123°41′E; 90-110
IM-2007-42585	CONO902-08	KC250649	*Daphnella*	sp.	SANTO 2006	Vanuatu	15°22.9′S, 167°11.9′E; 0-20
IM-2007-42402	CONO673-08	KC250716	*Hemilienardia*	sp.	PANGLAO 2004	Philippines	9°31′N, 123°41′E; 90-110
IM-2007-42403	CONO674-08	KC250715	*Hemilienardia*	sp.	PANGLAO 2004	Philippines	9°31′N, 123°41′E; 90-110
IM-2007-42395	CONO666-08	KC250711	*Hemilienardia*	sp.	PANGLAO 2004	Philippines	9°31.3′N, 123°41.2′E; 90-100
IM-2007-42408	CONO679-08	KC250713	*Hemilienardia*	sp.	PANGLAO 2004	Philippines	9°31′N, 123°41′E; 90-110
IM-2007-42404	CONO675-08	KC250732	*Veprecula*	*vepratica*	PANGLAO 2004	Philippines	9°31′N, 123°41′E; 90-110
IM-2007-42405	CONO676-08	KC250731	*Veprecula*	*vepratica*	PANGLAO 2004	Philippines	9°31′N, 123°41′E; 90-110
IM-2009-6039	RAPHI001-12	KC250730	*Thatcheria*	*mirabilis*	SALOMONBOA 3	Solomon islands	9°36′S,160°46′E; 448-523
IM-2007-42425	CONO696-08	KC250652	*Gymnobela*	*mitrodeta*	PANGLAO 2005	Philippines	9°29′N,123°44′E; 271-318
IM-2009-6025	RAPHI052-12	KC250646	*Buccinaria*	*pendula*	SALOMONBOA 3	Solomon islands	09°25′S, 160°31′E; 456-551
IM-2007-42315	CONO583-08	KC250647	*Daphnella*	*mitrellaeformis*	EBISCO	Chestrefield Islands	20°47′S, 161°01′E; 289-294
IM-2007-42552	CONO869-08	HQ401580	*Lovellona*	*atramentosa*	SANTO 2006	Vanuatu	15°35.7′S, 167°07.4′E; 0-11
IM-2007-30848	FRANZ922-09	GU131310	*Conus*	*elokismenos*	SANTO 2006	Vanuatu	15°07′S, 166°53′E; 328-354
IM-2007-17754	CONO226-08	EU015677	*Turris*	*babylonia*	PANGLAO 2004	Philippines	9°37.1′N, 123°52.6′E; 8-22

Table 2. List of specimens used for the protoconch evolution analysis.

MNHN Number	*Genus*	*Species*	*Protoconch morphology**
IM-2007-17754	*Turris*	*babylonia*	
IM-2007-17878	*Pseudodaphnella*	*aureotincta*	1
IM-2007-17881	*Daphnella*	sp.	
IM-2007-17903	*Eucyclotoma*	*cymathoides*	
IM-2007-30848	*Conus*	*elokismenos*	
IM-2007-42315	*Daphnella*	*mitrellaeformis*	
IM-2007-42335	*Pseudodaphnella*	***variegata* nov. sp.**	1
IM-2007-42382	*Pseudodaphnella*	***boholensis* nov. sp.**	0
IM-2007-42386	*Pseudodaphnella*	*nsp9*	1
IM-2007-42387	*Pseudodaphnella*	***lineata* nov. sp.**	1
IM-2007-42388	*Pseudodaphnella*	***fallax* nov. sp.**	0
IM-2007-42392	*Pseudodaphnella*	*philippinensis*	0
IM-2007-42393	*Kermia*	*rufolirata*	1
IM-2007-42400	*Thetidos*	***tridentata* nov. sp.**	1
IM-2007-42402	*Hemilienardia*	sp.	
IM-2007-42407	*Kermia*	*cf. producta*	1
IM-2007-42425	*Gymnobela*	*mitrodeta*	
IM-2007-42552	*Lovellona*	*atramentosa*	
IM-2007-42609	*Eucyclotoma*	sp.	
IM-2007-42613	*Pseudodaphnella*	***crypta* nov. sp.**	1
IM-2007-42631	*Pseudodaphnella*	*rubroguttata*	0
IM-2009-17247	*Kermia*	*reeveana*	1
IM-2009-17858	*Kermia*	*nsp2*	1
IM-2009-17954	*Pseudodaphnella*	***sudafricana* nov. sp.**	1
IM-2009-17955	*Kermia*	*producta*	1
IM-2009-17956	*Pseudodaphnella*	*punctifera*	1
IM-2009-17970	*Pseudodaphnella*	***nympha* nov. sp.**	0
IM-2009-17994	*Pseudodaphnella*	*drupelloides*	1
IM-2009-17999	*Pseudodaphnella*	*eugenei*	1
IM-2009-18038	*Exomilus*	*edychroa*	1
IM-2009-18054	*Pseudodaphnella*	*bifasciata*	1
IM-2009-18059	*Kermia*	*melanoxytum*	1
IM-2009-18099	*Pseudodaphnella*	*?martensi*	1
IM-2009-18100	*Pseudodaphnella*	*granosa*	1
IM-2009-18105	*Pseudodaphnella*	***phaeogranulata* nov. sp.**	1
IM-2009-18108	*Exomilus*	***compressa* nov. sp.**	1
IM-2009-18110	*Pseudodaphnella*	***santoa* nov. sp.**	1
IM-2009-18116	*Pseudodaphnella*	*barnardi*	1
IM-2009-18139	*Pseudodaphnella*	*tincta*	1
IM-2009-18148	*Pseudodaphnella*	*maculosa*	1
IM-2009-19168	*Pseudodaphnella*	***kilburni* nov. sp.**	1
IM-2009-6025	*Buccinaria*	*pendula*	
IM-2009-6039	*Thatcheria*	*mirabilis*	

*0- non-planctotrophic protoconch.
*1- planctotrophic protoconch.

clade (PP = 1), except for *Pseudodaphnella boholensis* nov. sp. and *P. barnardi*, with PP = 0.99 and 0.98 respectively. Maximum within-morphospecies K2P genetic distance (3.9%) is always lower than the minimum between-morphospecies K2P genetic distance (7.8%), a gap corresponding to the so-called 'barcode-gap'. The only exception is a morphospecies identified as *Pseudodaphnella bifasciata*. It includes three groups of specimens collected in three geographic regions (Philippines, Madagascar and Vanuatu) and separated by genetic distances of 12% and 6%. This species may actually comprise a complex of cryptic species, but this result was not confirmed by the morphological analyses and was based on only one gene and a few specimens. It should be confirmed by increasing the size of the dataset and by sequencing at least one independent genetic marker. In other cases, species defined morphologically are compatible with the phylogenetic analyses.

Members of the *Kermia–Pseudodaphnella* complex, with the exception of *K. producta*, form a single clade; but this clade, as well as most of its deepest nodes, is weakly supported. For convenience in description of the tree branching, we divided the *Kermia–Pseudodaphnella* clade into seven subclades (A–G), among these only subclade A has weak support (PP = 0.45), while others are supported with PP > 0.95. Subclades D, F, E and G are clustered together into a larger clade with PP = 0.93.

Among the 30 species falling into the main *Kermia–Pseudodaphnella* clade, 14 were found to be undescribed to date. Among the 16 described species eight are currently assigned to the genus *Kermia* (WoRMS – Appeltans *et al*., 2012) and five to the genus *Pseudodaphnella*, with the type species *P. philippinensis* in clade D. The type species of the genus *Kermia*, *K. benhami* has not been studied molecularly, although one sequenced specimen (IM-2009-17858), is extremely similar in shell morphology to the type material of *Kermia benhami*. To which, if either, of the two genera *Clathurella maculosa*, Pease, 1863 should be assigned remains uncertain (Tucker, 2004). The species originally described as *Pleurotoma reeveana* Deshayes, 1863 is currently assigned to the genus *Daphnella* Hinds, 1844. Finally *Pseudodaphnella tincta aureotincta*, originally described as a variety is shown to be a distinct species, which is not even closely related to *Pseudodaphnella tincta*. It is noteworthy, that species currently assigned to the genera *Kermia* or *Pseudodaphnella* do not tend to cluster together. On the contrary, these are rather randomly spread across the *Kermia–Pseudodaphnella* clade. In at least three major clades (A, B and D), species currently assigned to both genera are mixed, indicating their closer relationships to each other than to their 'traditional congeners' from different clades.

Protoconch morphology

Among 32 morphospecies involved in the present analysis, five are characterized by non-planctotrophic protoconchs (Fig. 2). It is noteworthy that these five species do not constitute a single clade, but on the contrary appear to be spread across the phylogenetic tree – they are found in three major, well-supported clades: B, D and F. The transition from planctotrophic to non-planctotrophic mode of development has occurred independently in three major clades in the *Kermia–Pseudodaphnella* complex, and in clade D it happened twice (Fig. 2). "Planctotrophic" protoconchs in the species examined also vary in shape and sculpture, since some species have a diagonally cancellate protoconch II while in others the adapical area and often periphery of the protoconch whorls are sculptured with axial riblets and cancellate sculpture is only pronounced

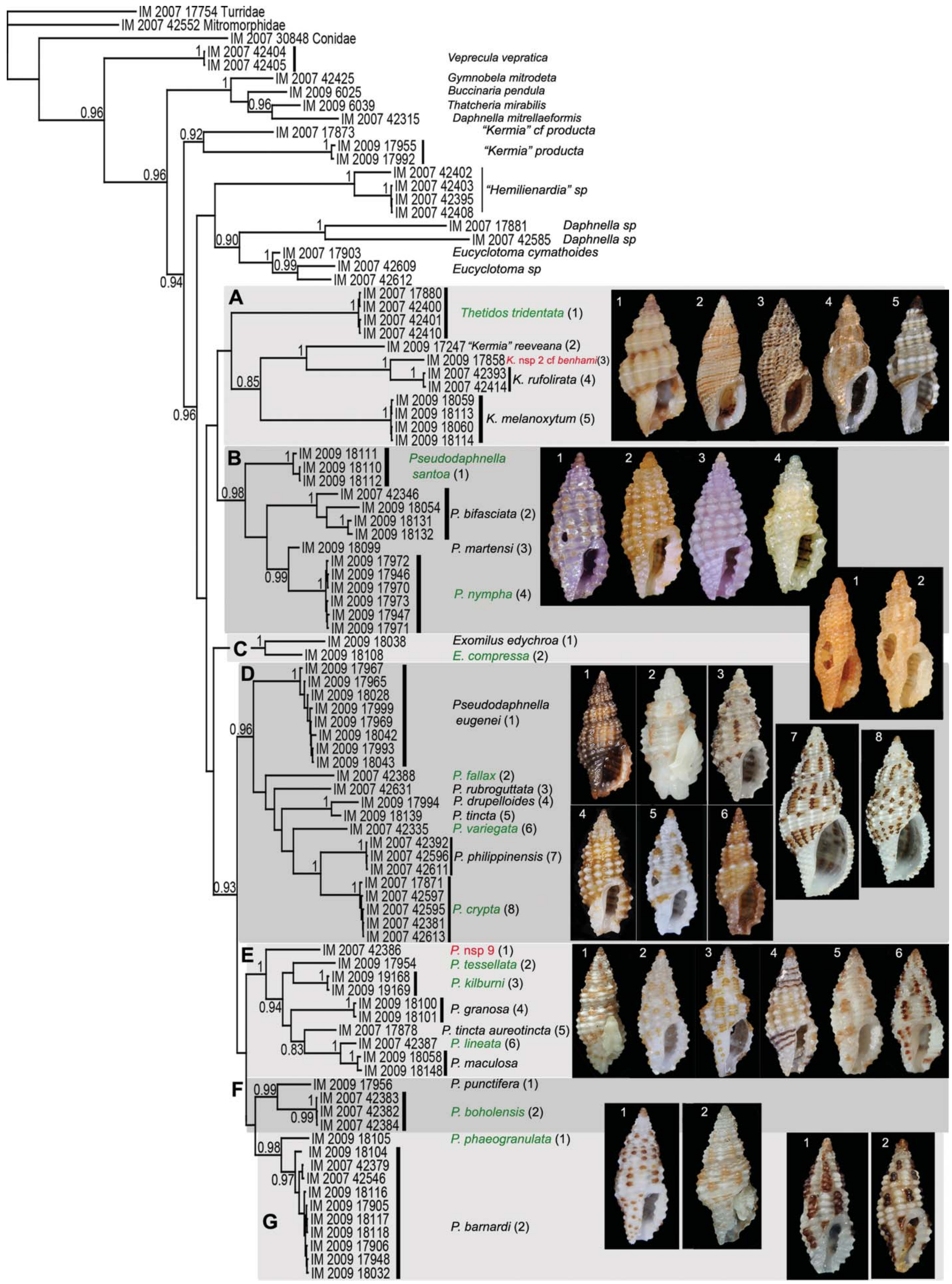


Fig. 1. Bayesian phylogenetic tree obtained with the COI gene. Posterior probabilities (when > to 0.9) are shown above nodes. New species described here are indicated in green; those we do not describe are in red. Photographs of '*Kermia*' *producta*, '*Kermia*' sp. cf. *producta* and *Pseudodaphnella maculosa* are not included.

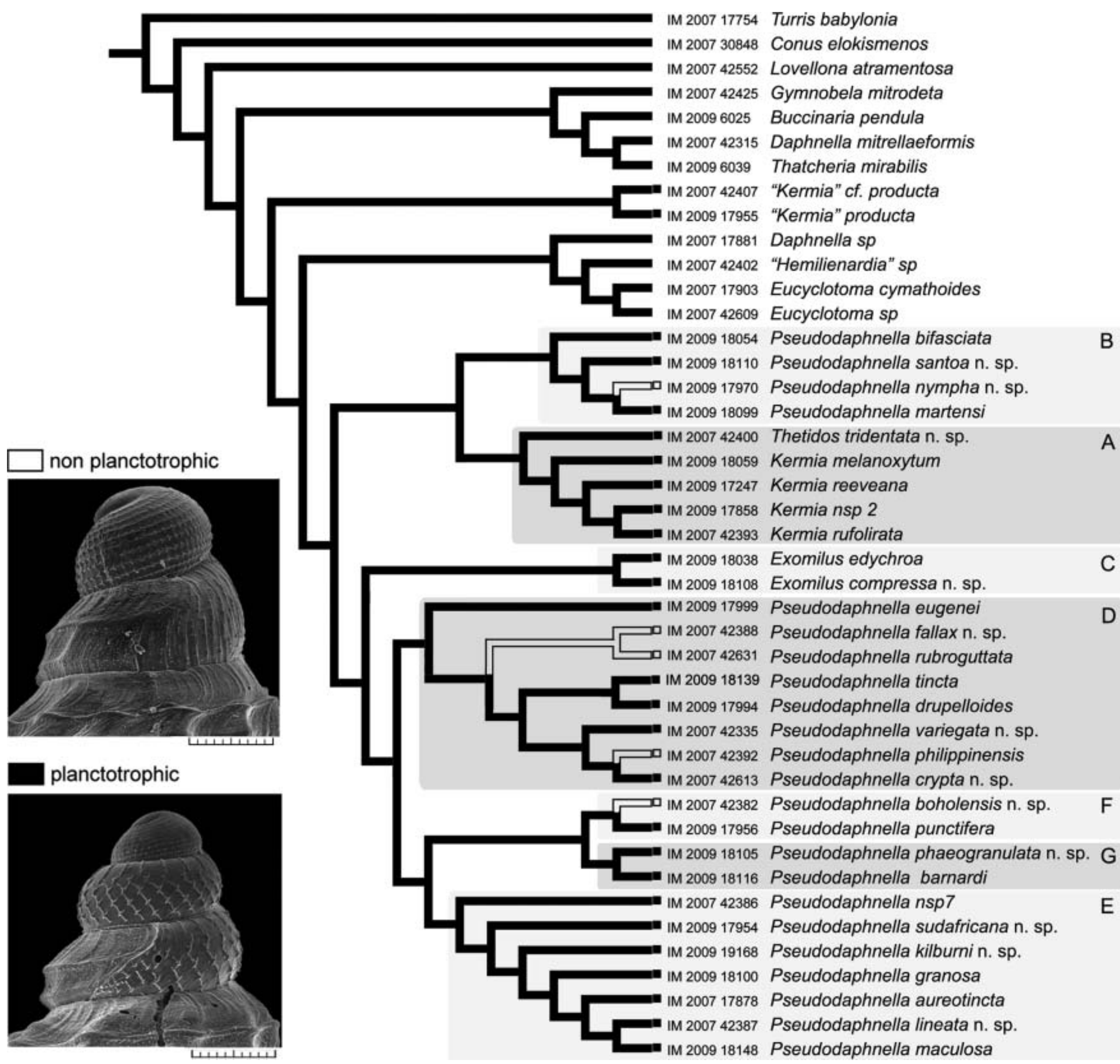


Fig. 2. Character mapping of the diversity of protoconch morphologies based on the phylogenetic tree presented in Fig. 1.

on the abapical part of the whorl. Such protoconch sculpture, considered by Kilburn (2009) as rather atypical, is characteristic of the type species of *Kermia* (Powell, 1966; Kilburn, 2009). Besides that, examination of a vast amount of material revealed a range of intermediate forms between these two patterns of sculpture. Therefore, we consider these two variants of protoconch sculpture to represent variants of the same principal pattern.

Taxonomic implications of phylogenetic analysis

Our results suggest that neither protoconch morphology nor classical hypotheses of generic assignments in *Kermia–Pseudodaphnella* complex are consistent with the phylogenetic relationships inferred from molecular data (Fig. 1). Here we revise generic assignments of the sequenced species based on results of the phylogenetic analysis. Interpreting molecular results, we refer to two major criteria: (i) if any well-supported clade on a molecular tree includes a type species of a relevant genus, we consider this clade to correspond to this genus, and (ii) when we do not have a type species in a well-supported clade, we recognize it as a genus if its members are distinct morphologically from the rest of the *Kermia–Pseudodaphnella* complex and their morphology agrees well with any described genus. As the coverage of the diversity of the *Kermia–Pseudodaphnella* complex in the present study is incomplete, the new genus-level classification we propose should be considered as a primary hypothesis to be proved or falsified in future studies.

The Clade D contains the type species of the genus *Pseudodaphnella*, *P. philippinensis*; here we consider all species of clades D, E, F and G to belong to this genus.

Taking into consideration morphological similarities between members of clades D–G and clade B, and low support of basal nodes in our tree, we tentatively attribute clade B to the genus *Pseudodaphnella* as well. Clade C includes two species with compressed whorls and subcylindrical shells that fit well in the diagnosis of the genus *Exomilus* Hedley, 1918, except for protoconch morphology, which was shown to be taxonomically inconsistent. Consequently, we assign both species of this clade to the genus *Exomilus*. The species we provisionally referred to as *Kermia tridentata* nov. sp. in the clade A with globose whorls and strong dentition of the inside of the outer lip strikingly resembles the type species of *Thetidos*, *T. morsura* Hedley, 1899 (see description below), and we assign the species correspondingly. Generic assignment of the rest of clade A remains problematic. With some reservation we assign species of this clade to the genus *Kermia* taking into consideration similarity of voucher specimen IM-2009-17858, to the type material of *K. benhami*. Provisional generic assignments for *Kermia–Pseudodaphnella* complex are summarized in a checklist (Appendix 1, see supplementary material, which is available on the Supplementary tab of the article's Taylor & Francis Online page at http://dx.doi/10.1080/14772000.2012.753137).

Taxonomic account

In this section, we describe species morphologically identified as new and confirmed by molecular data. We had proper material for designation of type series and compiling description for 12 out of 14 new species (shown in green in Fig. 1); species indicated on molecular tree as *K.* nsp 2 and *P.* nsp 9 in red are not described here, since we did not have sufficient as material.

Class Gastropoda
Order Caenogastropoda
Infraorder Neogastropoda
Superfamily Conoidea
Family Raphitomidae A. Bellardi, 1875

Thetidos Hedley, 1899

Type species by original designation *Thetidos morsura* Hedley, 1899.

Thetidos tridentata nov. sp.
(Figs 3–9)

TYPE MATERIAL. Holotype: MNHN–25603, molecular voucher IM–2007–42400, 6.1 mm, Balicasag Is., Philippines, Expedition Panglao 2004 stn L46, 9°30.89′N 123°41.16′E, 90–110 m. *Paratypes*: Par 1 – MNHN–25604, molecular voucher IM–2009–19199, 5.7 mm, same locality as holotype; Par 2 – MNHN–25605, molecular voucher IM–2007–42410, 4.5 mm, same locality as holotype; Par 3 – MNHN–25606, 6.3 mm, Balicasag Is., Philippines, Expedition 'Panglao 2004' stn. L69–73, 9°30.7′N 123°41.0′E, 90–98 m; Par 4 – MNHN–25607, 7.4 mm, Balicasag Is., Philippines, Expedition 'Panglao 2004' stn. B41, 9°30.9′N 123°40.8′E, 17–19 m; Par 5 – MNHN–25608, 6.2 mm, Panglao Is., Philippines, Expedition 'Panglao 2004' stn. S28, 9°37.2′N 123°46.4′E, 28–32 m.

OTHER MATERIAL EXAMINED. **Philippines**: molecular voucher IM–2007–42401, juv, same locality as holotype; 5.6 mm, 5.4 mm, 5.0 mm, Expedition 'Panglao 2004' stn. L76, 9°36.5′N 123°45.3′E, ∼80 m; 4.8 mm, off Napaling, Expedition 'Panglao 2004' stn. S28, 9°37.13′N 123°46.51′E, 28–32 m; **Vanuatu**: Expedition 'Santo 2006', stn. DS 102, 15°34′04′′S 167°16′00′′E, 98–100 m, 7.0 mm.

ETYMOLOGY. The species name refers to three denticles on the inside of outer opertural lip, characteristic for the species.

DESCRIPTION. Shell small, widely fusiform (SH 4.5–6.25 mm; w/h 0.48–0.50 mm) with well-defined moderately long siphon. Teleoconch of 5 strongly convex to globose whorls. Suture distinct, slightly impressed; subsutural region with 2–3 indistinct wavy spiral lines. Axial sculpture of strong rounded folds (9–10 per whorl). Axial folds intersected by distinct rounded evenly interspaced slightly undulating spiral cords; interstices rather shallow. Spire whorls sculptured by 4 spiral cords, with the third situated on whorls periphery. Last adult whorl with 7 major spiral cords, interstice between 3rd and 4th rather wide with intermediate minor cordlet. Two lower cords on last adult whorl situated on shell base slightly gemmate.

Siphon slightly bent backward, shallowly notched. Fasciole well pronounced, slightly convex, with 5 oblique cords. Aperture elongate; siphonal canal rather broad and shallow. Outer lip strongly convex, bent inward, rapidly constricted to siphon, the inner side with 3 strong denticles. Inner lip slightly convex with labral callus and 2–3 indistinct plicae. Anal sinus rounded, rather wide and shallow.

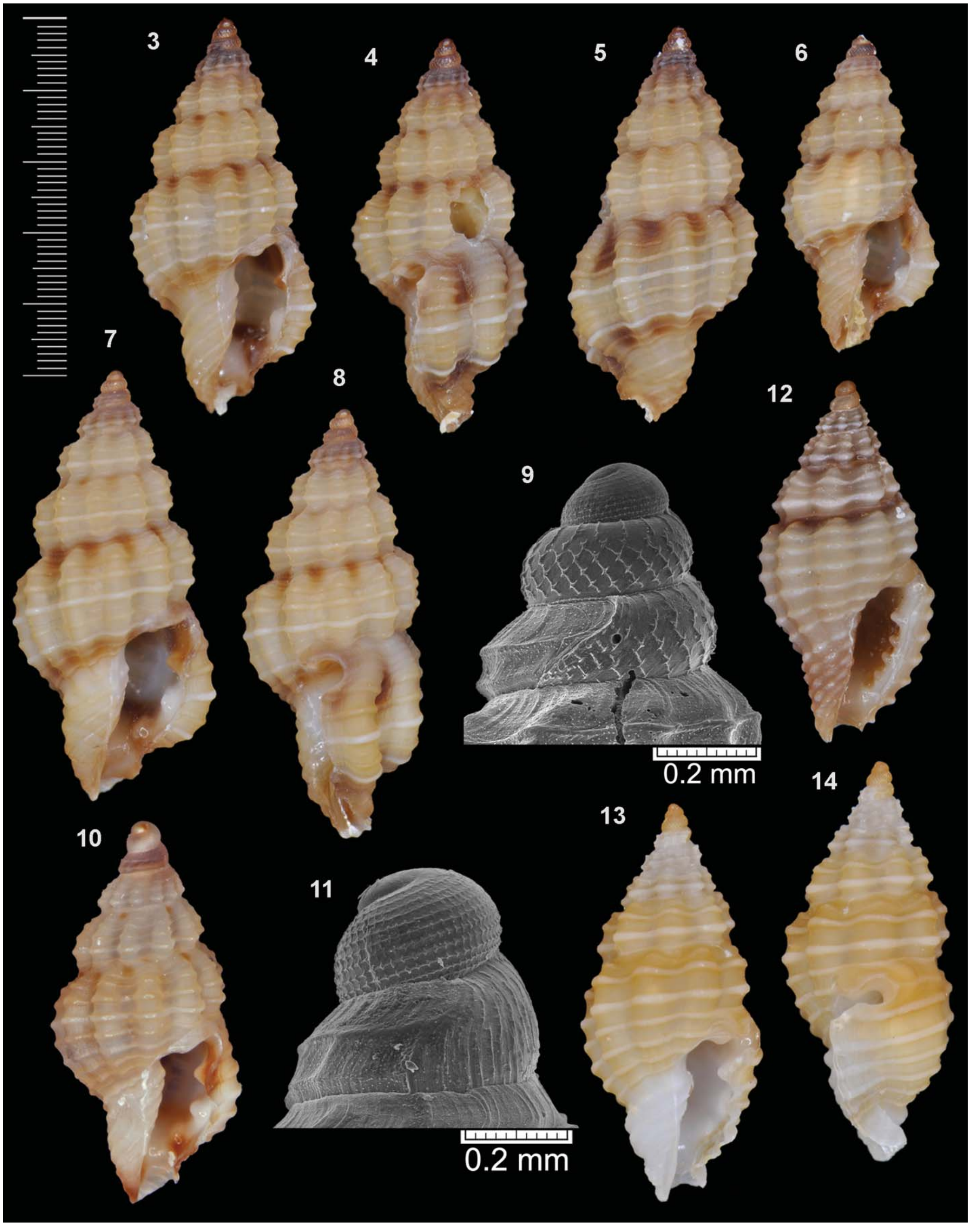
Colour pattern striped – early teleoconch whorls and subsutural regions of latter whorls brown, their peripheries cream to tan. Base with brown band, siphon cream to tan. Third spiral cord on whorl periphery much lighter than others, white or whitish.

Protoconch cyrtoconoid, brown, of *c*. 2.7 evenly convex whorls (Fig. 9). First 1.5 whorls finely granulated; later protoconch whorls with diagonally cancellate sculpture. Last whorl of protoconch deeply adapically notched at transition to teleoconch.

Radula: description of radula morphology given in the end of the Results section.

DISTRIBUTION. Central Philippines and Vanuatu, depth range, living at 20–120 m.

REMARKS. The species can be easily distinguished from the rest of the *Kermia–Pseudodaphnella* complex by its more globose whorls, rather wide aperture and very strong denticles on the inside of the outer lip. *T. tridentata* nov. sp. is extremely similar to the type species of the genus *Thetidos*, *T. morsura* (Figs 10, 11), described by Hedley



Figs 3–14. *Thetidos tridentata* nov. sp. and similar species. Scale 50 mm. **3**–**5**. Paratype 1; **6**. Paratype 2; **7**, **8**. Holotype; **9**. Protoconch morphology, voucher specimen 4.3 mm, Philippines, Expedition 'Panglao 2004', stn. L51–60, 9°37.7′N 123°47.9/48.1′E, 43–62 m; **10**, **11**. *Thetidos morsura*; **10** 5.4 mm, Vanuatu, Tutuba Is., Expedition 'Santo 2006', stn. DS103, 15°34′04″S 167°16′00″E, 10–80 m; **11**. Protoconch morphology, voucher specimen 4.2 mm, Vanuatu, Expedition 'Santo 2006', stn. ZS22, 15°33′03″S 167°09′37″E, 27–29 m; **12**. *Thetidos* nov. sp. aff *tridentata*, 5.1 mm, Vanuatu, Expedition 'Santo 2006', stn. DS91, 15°36′40″S 167°08′26″E, 7 m; **13**, **14**. *Thetidos globulosus* (Hervier, 1897) 5.6 mm, New Caledonia, Noumea, stn. 1341, 22°19.9′S, 166°13.2′E, 35 m.

(1899) from Funafuti (Tuvalu), and later mistakenly assigned to *Lienardia* Jousseaume, 1884 (Hedley, 1922). The two species are nearly indistinguishable from each other in teleoconch morphology, but differ in structure of the protoconch, in *Thetidos morsura* it is 'two whorled, spirally grooved' (Hedley, 1899: p. 473, fig. 42) (Fig. 11). Specimens of at least two other very similar and most likely, closely related species, were collected in the East Pacific. One of them, undescribed to date (Fig. 12), co-occurs with *T. tridentata* nov. sp. in Vanuatu, and appears to be more common there; the other, from New Caledonia, was originally described as *Glyphostoma globulosum* Hervier, 1897 (Figs 13, 14). Both these species, however, differ markedly from *T. tridentata* nov. sp. The species from Vanuatu has a rather biconical shell with less convex whorls, a protoconch with at least 0.5 protoconch whorls fewer than in *T. tridentata* nov. sp. and the outer lip of the aperture with at least five subequal denticles. *Glyphostoma globulosum*, which we re-assign to the genus *Thetidos*, has fewer spiral elements on the last adult whorl, a much deeper anal sinus, constricted at its opening, a straight siphon and a higher protoconch. In addition, the early teleoconch whorls in *T. tridentata* nov. sp. are darker than the rest of the shell, while in *Thetidos globulosus* these are white.

Exomilus Hedley, 1918

Type species by original designation *Mangelia lutraria* Hedley, 1907.

Exomilus compressa nov. sp.
(Figs 15–23)

TYPE MATERIAL. Holotype: MNHN–25617, molecular voucher IM–2009–18108, 3.2 mm, Palikulo Bay, Vanuatu, Expedition 'Santo 2006' stn. DB69, 15°24′22″S 167°13′02″E, 38 m. *Paratypes*: Par 1 – MNHN–25618, 3.5 mm, Touho, New Caledonia, Expedition 'Montrouzier', stn. 1270, 20°45.0′S, 165°16.5′E, 10–35 m; Par 2 – MNHN–25618, 3.2 mm, same locality as Par 1; Par 3 – MNHN–25619, 3.35 mm, Lifou, Loyality Is., Expedition 'Atelier Lifou' stn. 1435, 20°55.2′S, 167°00.7′E; 5–30 m; Par 4 – MNHN–25620, 3.75 mm, Touho, New Caledonia, Expedition 'Montrouzier', stn. 1271, 20°52.7′S, 165°19.5′E; 5–25 m.
OTHER MATERIAL EXAMINED. **Vanuatu**: 3.2 mm; Tanoa Bay, Santo Is., Expedition 'Santo 2006', stn. ZB20 15°36′07″S 167°05′21″E, 15–20 m; 3.1 mm, Santo Canal, Expedition 'Santo 2006' stn. FB90, 15°35′00″S 167°07′42″E, 36–39 m; **New Caledonia**: 3.2 mm, same locality as Par 1.
ETYMOLOGY. Italian feminine adjective *compressa* (compressed) refers to whorl shape, characteristic for the species.
DESCRIPTION. Shell small (SH 3.1–3.75 mm) narrow (w/h 0.38–0.4) subcylindrical in shape, teleoconch of 3.5–4 strongly shouldered compressed whorls. Last adult whorl high, rapidly constricted to siphonal canal, which is weakly defined and bent backward. Suture indistinct. Sculptured by strong slightly prosocline axial ribs (8 on last adult whorl), crossed by low spiral cords. Axial elements well pronounced on flattened whorl periphery, fading on shoulder slope. Sculpture of shoulder slope of 3 closely spaced undulated spiral cords. Spiral cords on whorl periphery evenly and rather widely spaced, rounded and slightly widened at intersections with axial ribs and flattened in interstices. Periphery of body whorl with 5 spiral cords succeeded by 3 slightly crenulated cords on base. Fasciole moderate with oblique cords of which upper two strong and crenulated.

Aperture narrow, outer lip clearly angulated at its lower third, thickened and incurved, with 6 equal denticles on its inside. Inner lip without dentition, bent backward at its lower part, forming edge of siphonal canal. Anal sinus moderately deep, rounded, its opening constricted; labral varix bent backward at its upper part and widened behind anal sinus.

Protoconch conical of about 3.5 evenly convex whorls, early 1.5 whorls sculptured with micro-granules arranged in spiral rows, later 2 whorls diagonally cancellate (Fig. 22). Last whorl deeply adapically notched at its transition to teleoconch.

Colouration pale to light brown with lighter axial elements and darker interstices, protoconch brown.

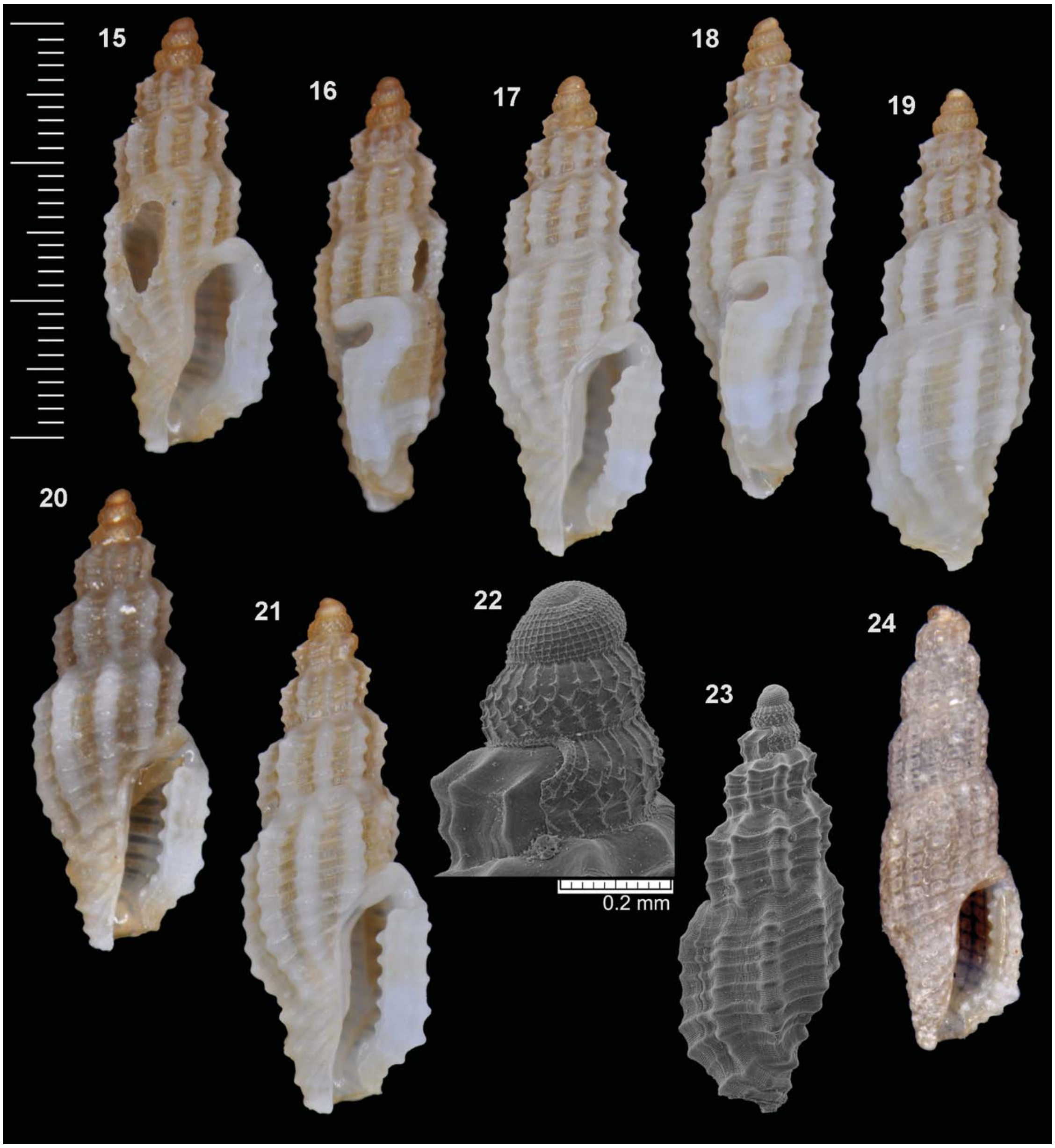
Radula: description of radula morphology given in the end of the Results section.
DISTRIBUTION. Western Pacific: Vanuatu and New Caledonia, depth range, living at 5–40 m.
REMARKS. *E. compressa* nov. sp. is quite distinctive and can be easily recognized from other species, described to date, thanks to its strongly shouldered compressed whorls. The species is closest probably to *Exomilus edychroa* (Hervier, 1897) (Fig. 24), from which, however, it can be easily distinguished by its strong axial sculpture and strongly incurved outer lip. In teleoconch morphology *E. compressa* nov. sp. resembles members of the genus *Exomilus* Hedley, 1918. However, *Exomilus* species are characterized by a 'cap shaped' smooth protoconch (Powell, 1966) that differs markedly from the conical diagonally cancellate protoconch of *E. compressa* nov. sp.

Pseudodaphnella Boettger, 1895

Type species by original designation *Pleurotoma philippinensis* Reeve, 1843.

Pseudodaphnella santoa nov. sp.
(Figs 25–32)

TYPE MATERIAL. Holotype: MNHN–25609, molecular voucher IM–2009–18110, 3.9 mm, Aoré Is., N Side of Ambuei Bay, Vanuatu, Expedition 'Santo 2006', stn. ZB16, 15°32′23″S 167°12′08″E. *Paratypes*: Par 1 – MNHN–25610, 5.6 mm, Malo Kili Kili, Vanuatu, Expedition 'Santo 2006' stn. FB52 15°42′42″S 167°15′05″E, 7 m; Par 2 – MNHN–25611, 4.5 mm, same locality as Par 1; Par 3 – MNHN–25612, 3.8 mm, Segond Channel, NW



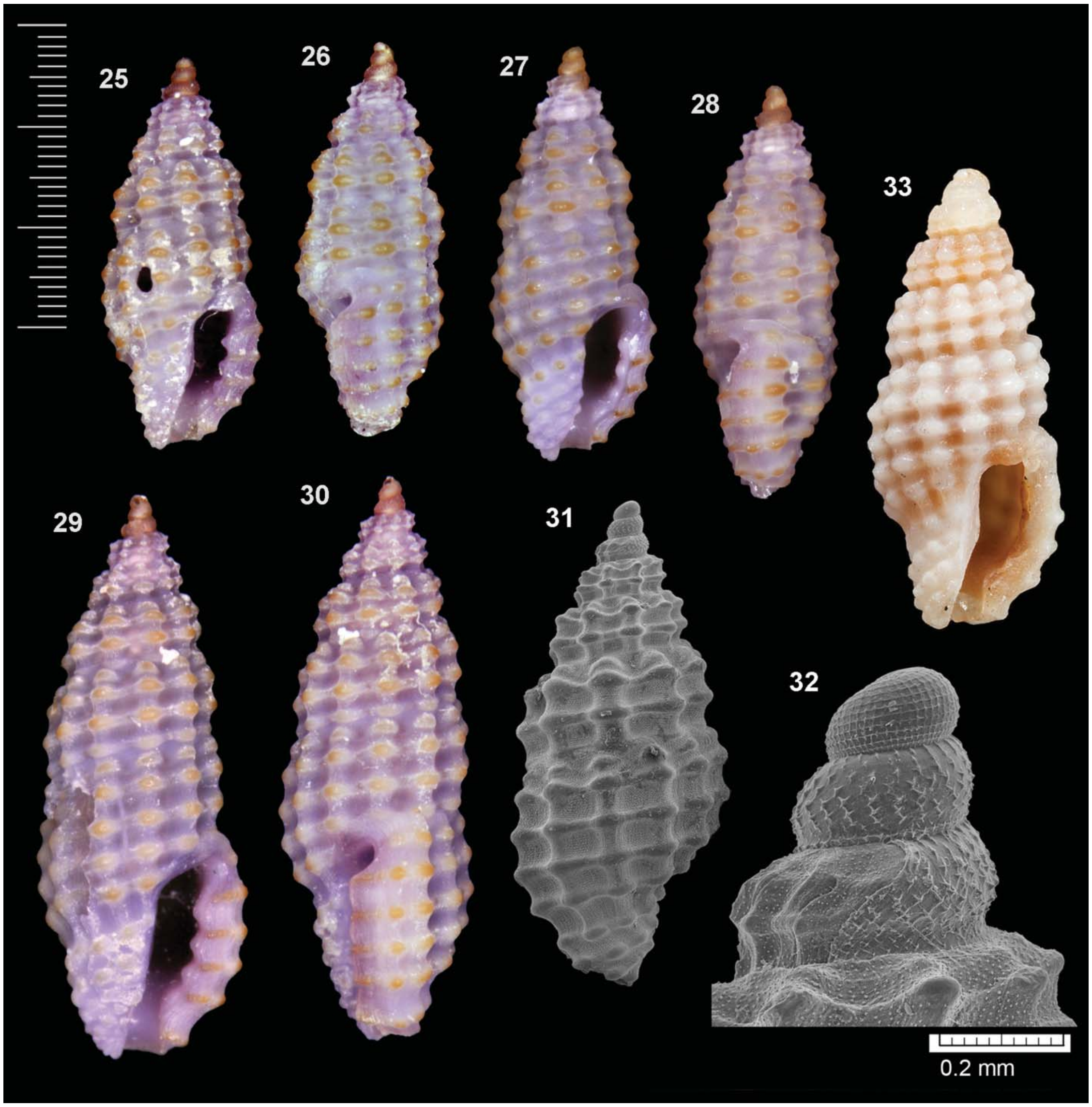
Figs 15–24. *Exomilus compressa* nov. sp. and similar species. Scale 30 mm. **15**, **16**. Holotype; **17**–**19**. Paratype 1, 3.5 mm, New Caledonia, Touho, Expedition 'Montrouzier' stn. 1270, 20°45.0′S, 165°16.5′E, 10–35 m; **20**. Paratype 2, 3.35 mm, Loyality Is., Lifou, Expedition 'Atelier Lifou' stn. 1435, 22′55.2′S 167′00.7′E, 5–30 m; **21**. Paratype 3, 3.75 mm, New Caledonia, Touho, Expedition 'Montrouzier' stn. 1271, 20°52.7′S, 165°19.5′E; 5–25 m; **22**, **23**. 3.0 mm, same locality as Paratype 2; **22**. Protoconch morphology; **23**. Shell structure; **24**. *Clathurella edychroa* Hervier, 1897, holotype, MNHN–2913, 3.7 mm, Loyalty Is., Lifou.

from Aoré Is., Vanuatu, Expedition 'Santo 2006' stn. FS77, 15°33′03″S 167°09′37″E, 29 m; Par 4 – MNHN–25613, 4.1 mm, Segond Channel East from Luganville, Vanuatu, Expedition 'Santo 2006' stn. DS04, 15°31′26″S 167°14′06″E.

OTHER MATERIAL EXAMINED. **Vanuatu**: 3.9 and 3.4 mm, South from Aoré Is., Expedition 'Santo 06' stn. DB12, 15°36′38″S 167°10′03″E, 10–18 m; 4.2 mm, Expedition 'Santo 06', Stn LD25, 15°32′29″S 167°10′31″E, 3–4 m; juveniles: molecular voucher IM–2009–18111 and IM–2009–18112, Palikulo Bay, Expedition 'Santo 06' stn. DB40, 15°28′48″S 167°15′09″E.

ETYMOLOGY. Named after MNHN expedition 'Santo 2006', on which the studied specimens were collected.

DESCRIPTION. Shell small, fusiform (SH 3.5–3.9 mm; w/h), truncated with rather short and thick siphon. Teleoconch of 4.5 evenly convex whorls, suture indistinct. Sculpture of rounded axial folds and strongly undulating spiral cords, notably thickened on intersections with axial folds to form strong spirally extended glossy nodules. Interstices



Figs 25–33. *Pseudodaphnella santoa* nov. sp. and similar species. Scale 30 mm. **25, 26**. Holotype; **27**, **28**. Paratype 4; **29**, **30**. Paratype 1; **31**, **32**. 4.0 mm, Vanuatu, Expedition 'Santo 2006', stn. DB12, 15°36′38″S 167°10′03″E, 10–18 m; **31**. Shell structure; **32**. Protoconch morphology; **33**. Syntype of *Clathurella martensi* BMNH 1904.9.26.10–11, 4.8 mm, Sri Lanka, Balapiti.

rather deep, only slightly wider than width of spiral elements themselves. Spire whorls with 4 spiral cords, uppermost and lowest notably weaker than 2 intermediate cords, which are peripheral. Last adult whorl with 5 evenly spaced spiral cords, adapical cord weaker than succeeding one, forming rounded nodules in intersections with axial elements, and vanishing in interstices. Fasciole strong, convex, separated from base of last adult whorl by distinct waist. Fasciole sculptured with minute rounded nodules.

Aperture narrow, elongated, slightly contorted. Outer lip, thickened and slightly incurved with moderate varix situated behind it. Inside of outer lip with 4 subequal denticles. Inner apertural lip smooth, bent backward where it forms siphonal canal. Anal sinus rounded and rather shallow, directed upward.

Protoconch narrowly conical of *c*. 3.3 evenly convex whorls (Fig. 32). Protoconch 1 bulbous, lirate. Protoconch 2 finely diagonally cancellate, deeply adapically notched at transition to teleoconch.

Protoconch orange. Teleoconch lilac with nodules on intersections of spiral and axial elements bright orange.

DISTRIBUTION. Western Pacific: Vanuatu and New Caledonia, depth range, living at 3–30 m.

REMARKS. The species is close to *P. martensi* (G. Nevill & H. Nevill, 1875) (Fig. 33), judging from the molecular tree, and is also similar in shell morphology. However, *P. santoa* nov. sp. can be distinguished by the characteristic orange spots on the intersections of the spiral and axial elements, and the weaker teleoconch sculpture and higher protoconch.

Pseudodaphnella nympha nov. sp.
(Figs 34–40)

TYPE MATERIAL. Holotype: MNHN–25614, Molecular voucher IM–2009–17970, 3.9 mm, Southern Madagascar, Expedition 'Atimo Vatae', stn. BS2, 25°35.5′S 45°08.1′E, 11 m. *Paratypes*: Par 1 – MNHN–25615, 3.25 mm, Southern Madagascar Expedition 'Atimo Vatae' stn. BS14, 25°36.0′S 45°08.7′E, 16 m; Par 2 – MNHN–25616, 3.9 mm, Southern Madagascar, Expedition 'Atimo Vatae' stn. BS16, 25°34.9′S 45°07.6′E, 15 m; Par 3 – MNHN–25616, 3.2 mm, same locality as Par 2; Par 4 – MNHN–25616, 3.0 mm, same locality as Par 2.
OTHER MATERIAL EXAMINED. **Madagascar**: Molecular vouchers IM–2009–17971 (3.3 mm), IM–2009–17972 (2.9 mm) IM–2009–17973, (3.0 mm), same locality as holotype; molecular voucher IM–2009–17947, 3.1 mm, same locality as Paratype 1.
ETYMOLOGY. Latin *nympha* – a larval stage in some invertebrates. Refers to small size and uniform pale colouration of the shell.
DESCRIPTION. Shell small (2.9–3.9 mm), fusiform or elongate–fusiform. Teleoconch of 3.5–4 evenly convex whorls; suture distinct, slightly wavy. Sculpture of strong wide prosocline axial folds (10 on the last adult whorl), overridden by rounded spiral cords, only slightly thickened on intersections with axial folds on last adult whorl. Interstices quadrate, rather shallow. First two teleoconch whorls with 3 spiral cords, of which adapical notably weaker than succeeding, vanishing in interspaces between axials. Penultimate whorl with 4 spiral cords, abapically partly overlapped by last adult whorl. Last adult whorl with 5 spiral cords, adapical cord rather weak, others similar and evenly interspaced. Fasciole indistinct in juveniles and rather robust in adults, with 5 oblique gemmate cords. Fasciole demarcated from the shell base by the interspace only slightly wider than regular space between spiral cords.

Aperture rather wide, mature outer lip with a varix, bent inward; its inside with 4 fine subequal denticles. Inner lip smooth, recurved adaxially at its midheight. Anal sinus rounded, moderately deep, slightly constricted, directed upward. Siphonal canal moderately wide and deep.

Protoconch bulbous, white, of 1.75 evenly convex whorls, last half whorl sculptured by distinct slightly opisthocyrt riblets (Fig. 39), its morphology indicates non-planctotrophic development of the species.

Shell surface matt with micro-sculpture of dense micro-granules, colouration uniformly cream white.
DISTRIBUTION. All studied specimens collected off southern Madagascar, depth range, living at 10–20 m.

REMARKS. In shell morphology this species is extremely close to *Paramontana punicea* (Hedley, 1922) (Fig. 41), but the latter is notably larger: the holotype *P. punicea* has a shell height of 5.4 mm, while none of studied specimens of *P. nympha* exceed 4 mm. Moreover, *P. punicea* was described from northern Australia (Palm Is., Queensland) and has a protoconch, indicating non-planctotrophic development, so is not likely to be widely distributed throughout the Indo-Pacific as far as southern Madagascar.

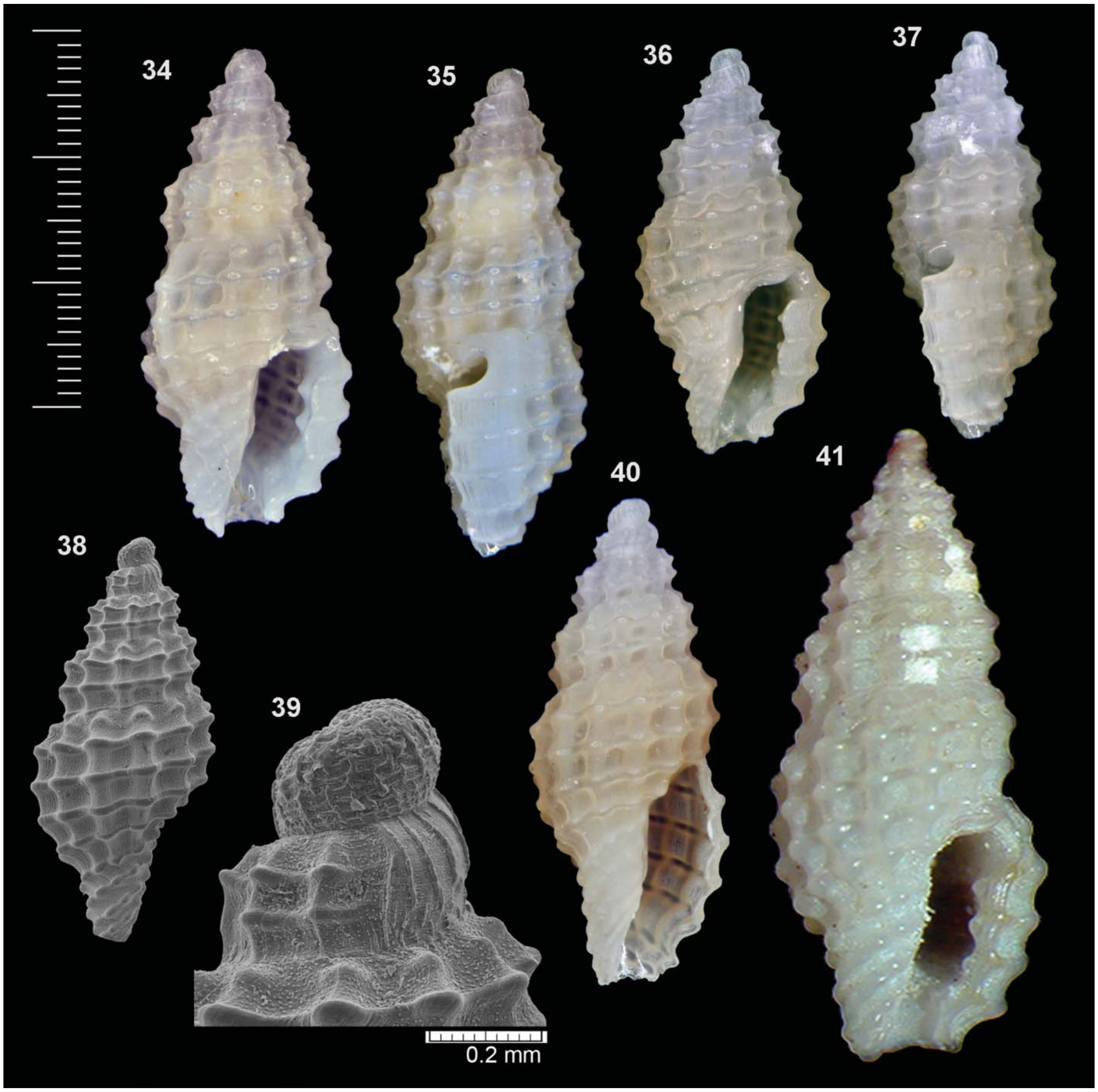
Pseudodaphnella fallax nov. sp.
(Figs 42–48)

TYPE MATERIAL. Holotype: MNHN–25621, 4.9 mm, Philippines, Pamilacan Is., Expedition 'Panglao 2004' stn. B19 9°29.4′N, 123°56.0′E, 17 m. *Paratypes*: Par 1 – MNHN–25622, molecular voucher IM–2007–42387, Philippines, Pamilacan Is., Expedition 'Panglao 2004', stn. B24 9°29.4′N, 123°56.0′E, 38 m; Par 2 and 3 – MNHN–25623, 4.5 mm and 4.5 mm, same locality as holotype.
OTHER MATERIAL EXAMINED. **Vanuatu**: 6.3 mm, Malo Is., Expedition 'Santo 2006' stn. DS 49 15°38.7′S, 167°05.2′E, 10–17 m.
ETYMOLOGY. Latin adjective *fallax* (deceptive) refers to a number of morphologically similar species, which makes recognition of this species difficult, especially if protoconch is missing.
DESCRIPTION. Shell small, fusiform (SH 4.2–6.2 mm; w/h 0.41–0.46), with truncated base and rather short, wide siphonal canal. Teleoconch of 4.5 evenly convex whorls, suture slightly indented, wavy. Sculpture of wide, rounded axial folds (9 on last whorl), overridden by strong undulating spiral cords, thickening on intersections with axial folds to form spirally extended glossy nodules. Interstices between spiral elements quadrate, rather deep. Early teleoconch whorls with 3 spiral cords, adapical cord weaker than others, peripheral. On penultimate whorl suture adjoins 4th abapical spiral cord. Last adult whorl with 6 subequal and evenly distanced spiral cords, succeeded by very wide and distinct 'waist', separating short and thick fasciole, sculptured by 3 oblique, gemmate cords.

Aperture rather wide, ovate; siphonal canal moderately deep, widening at its tip. Outer lip rounded, thickened and slightly incurved with strong varix behind it. Inner side of outer lip with 4 subequal denticles. Inner lip smooth, without dentition. Anal sinus rounded, rather shallow, constricted adapically but distinct callous denticle situated on upper side of aperture.

Protoconch white, of *c*. 2.3 whorls (Fig. 47). First whorl bulbous, strongly convex, spirally lirate. Last half whorl with fine, dense axial or slightly arcuate riblets on adapical surface.

Teleoconch white with light orange bands on alternate axial folds (in molecular voucher), or irregular yellow spots



Figs 34–41. *Pseudodaphnella nympha* nov. sp. and similar species. Scale 30 mm. **34**, **35**. Holotype; **36**, **37**. Paratype 1; **38**, **39**. juvenile 3.2 mm, South Madagascar, Expedition 'Atimo Vatae' stn. BS14, 25°36.0′S, 45°08.7′E, 16 m; **38**. Shell structure; **39**. Protoconch morphology; **40**. Juvenile 3.9 mm, same locality as previous; **41**. *Pseudodaphnella punicea*, holotype, AMS C.9520, 5.5 mm, Australia, Queensland, Palm Is.

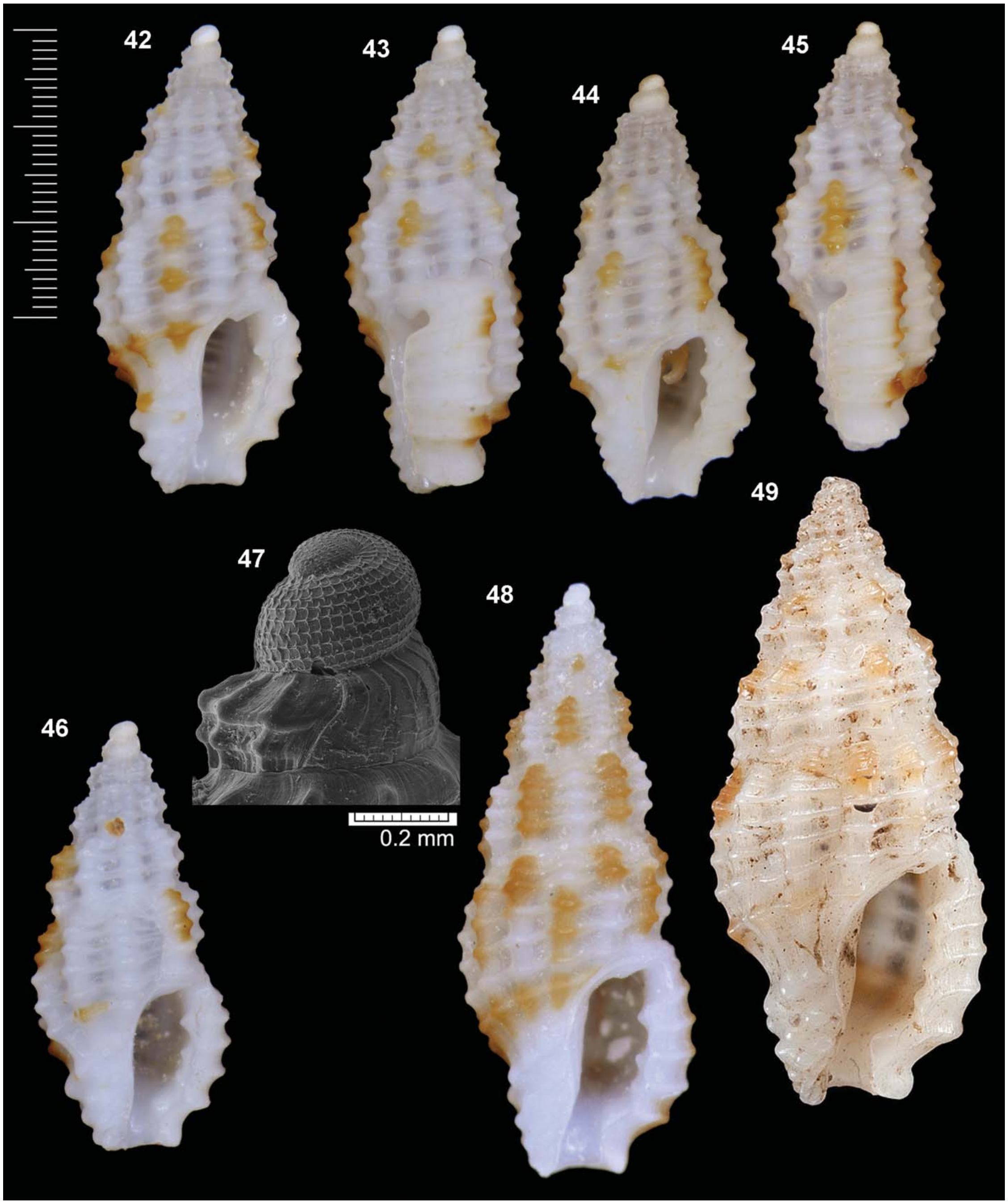
in other specimens. Nodules of fifth spiral cord on last adult whorl orange in most specimens.

DISTRIBUTION. Central Philippines and Vanuatu, depth range, living at 10–20 m.

REMARKS. In teleoconch morphology *Pseudodaphnella fallax* nov. sp. is closest to *P. tincta* (Reeve, 1843) (Fig. 49), from which it differs in having a white protoconch of non-planctotrophic morphology and a rounded whorl profile with no distinct shoulder. Another morphologically similar species is *P. rubroguttata* (H. Adams, 1872), which is closely related judging from the molecular tree and has similar protoconch, but differs in the colour of the bands on the teleoconch, which in *P. rubroguttata* are dark brown to almost black.

Pseudodaphnella variegata nov. sp.
(Figs 50–57)

TYPE MATERIAL. Holotype: MNHN–25624, molecular voucher IM–2009–19170, 6.45 mm, Philippines, Expedition 'Panglao 2004' stn. B7, 9°35.9′N; 123°51.8′E, 4–30 m. *Paratypes*: Par 1 – MNHN–25625, molecular voucher IM–2009–18144, 6.95 mm, Philippines, Expedition 'Panglao 2004' stn. B4 9°33.2′N 123°48.3′E, 24 m; Par 2 – MNHN–25626, 5.5 mm, Philippines, Expedition 'Panglao 2004' stn. S21 9°41.7′N 123°50.9′E, 4–12 m; Par 3 – MNHN–25627, 5.4 mm Philippines, Expedition 'Panglao 2004' stn. S1 9°35.3′N 123°50.5′E, 5 m; Par 4 – MNHN–25628, 6.7 mm, Second Channel, Vanuatu,

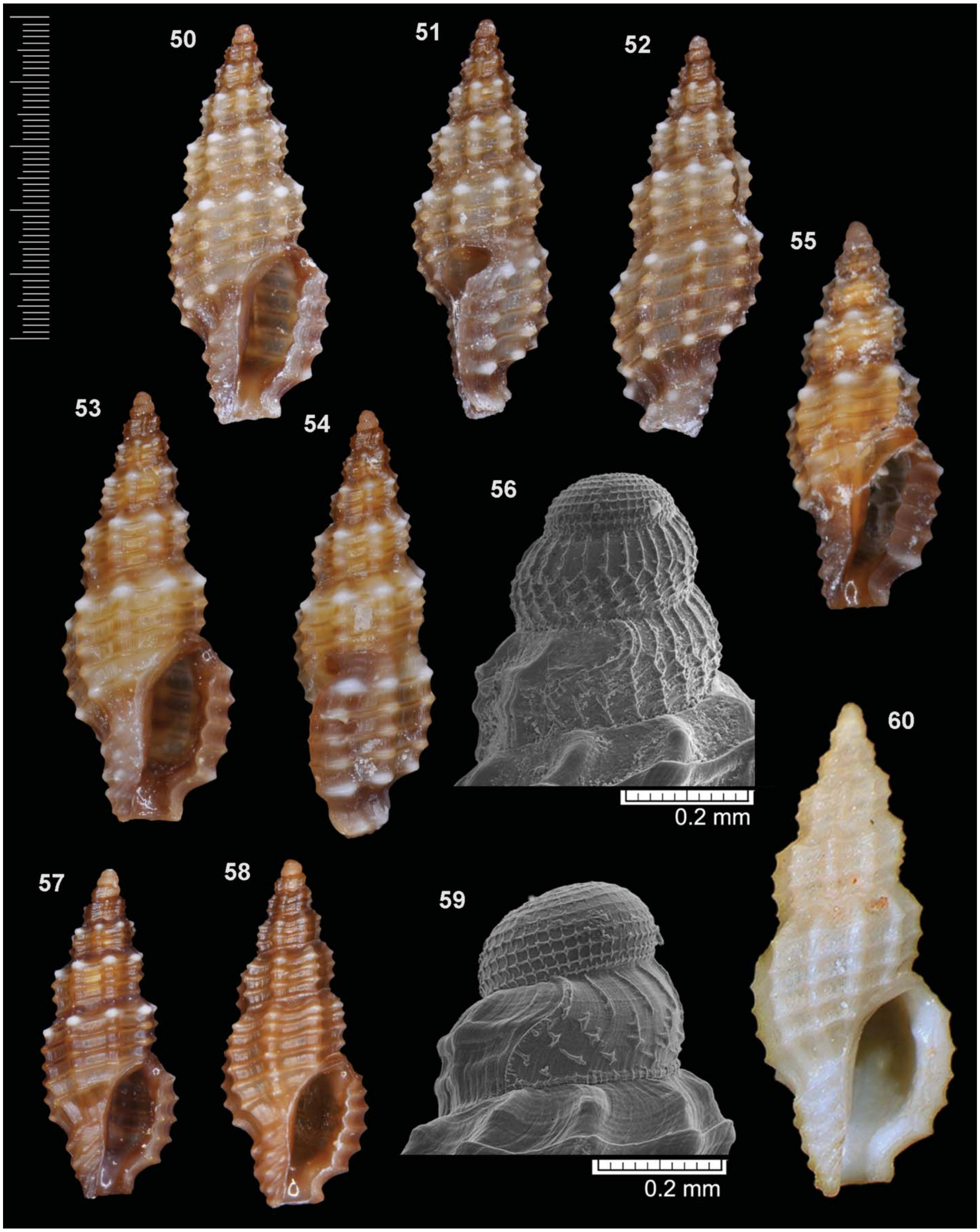


Figs 42–49. *Pseudodaphnella fallax* nov. sp. and similar species. Scale 30 mm. **42**, **43**. Holotype; **44**, **45**. Paratype 2; **46**. Paratype 3; **47**. Protoconch morphology, voucher specimen 3.4 mm; Philippines, Pamilacan Is., Expedition ‘Panglao 2004’, stn. B19, 9°29.4′N, 123°56.0′E, 17 m; **48**. 6.3 mm, Malo Is., Vanuatu, Expedition ‘Santo 2006’ stn. DS49, 15°38.7′S, 167°05.2′E, 10–17 m; **49**. Syntype of *Pseudodaphnella tincta* (Reeve) NHMUK 1900.3.9.37, 9.5 mm, locality unknown.

Expedition ‘Santo 2006’ Stn LS17, 15°31′04′′S 167°10′30′′E, 7 m.

OTHER MATERIAL EXAMINED. **Philippines**: molecular voucher IM–2007–42335 (broken), radula voucher (6.05 mm – broken), both same locality as holotype; 5.6 mm, Expedition ‘Panglao 2004’ stn. B12 9°35.6′N 123°43.2′E, 24–27 m; 6.3 mm, same locality as Par 1; 5.7 and 5.1 mm, Expedition ‘Panglao 2004’ stn. L51–60, 9°37.7′N 123°47.9/48.1′E, 43–62 m; **Vanuatu**: 5.1 mm, Segond Channel, Expedition ‘Santo 2006’, stn. DS04, 15°31′26′′S 167°14′06′′E.

ETYMOLOGY. Latin feminine adjective *variegata* (spotted, colourful) refers to the remarkable colour pattern of the shell of this species.



Figs 50–60. *Pseudodaphnella variegata* nov. sp. and similar species. Scale 50 mm. **50**–**52**. Holotype; **53**, **54**. Paratype 1; **55**, **56**. 6.05 mm (broken), same locality as holotype; **55**. Shell; **56**. Protoconch morphology; **57**. 5.1 mm, Vanuatu, Segond Channel, Expedition 'Santo 2006', stn. DS04, 15°31′26″S 167°14′06″E; **58**, **59**. *P*. nov. sp. cf *variegata*, Vanuatu, Expedition 'Santo 2006', stn. DS91, 15°36′40″S 167°08′26″E, 7 m; **58**. Shell; **59**. Protoconch morphology; **60**. *Pseudodaphnella oligoina*, holotype, AMS C.43688, 7.1 mm, Australia, Queensland, Albany Passage.

DESCRIPTION. Shell small (SH 6–7 mm), fusiform (w/h 0.40–0.41) with high spire and well-defined straight siphon. Teleoconch of 5.0–5.5 distinctly shouldered whorls. Suture slightly impressed. Sculpture cancellate, axial elements evenly spaced, axial ribs well developed on whorl peripheries, but vanishing toward sutures. Axial ribs on last adult whorl slightly prosocline. Spiral sculpture of thin cords, elevated and slightly thickened on intersections with axial ribs to form spirally extended nodules; interstices rather deep. Micro-sculpture of very fine growth lines. Shoulder slope with 1 weak spiral cord bearing small nodules at intersections with axial ribs. Spire whorls with 3–4 spiral cords on peripheries, of these adapical cord surmounts shoulder; abapical cord close to suture, separated from intermediate cords by wider interstice and without nodules. Last adult whorl with 5 equal and evenly interspaced spiral cords.

Last adult whorl constricted toward siphon to form a distinct waist – wide interstice, separating shell base from fasciole, which is weakly convex with 5 oblique gemmate cords.

Aperture rather wide elongate, slightly tapered to wide rather shallow siphonal canal. Outer lip slightly thickened and incurved with 4 obtuse nodules on its inner surface. Inner lip with rather weak callus, straight, indistinctly reflected against waist. Anal sinus rounded, rather wide and shallow.

Protoconch orthoconoid, brown, of *c*. 2.7 evenly convex whorls (Fig. 56). First 1.5 whorls finely granulated; last whorl with a fine sculpture of axial riblets on upper part of whorl and diagonally cancellate below its mid-height. Last whorl of protoconch deeply adapically notched at its transition to teleoconch.

Teleoconch background colour light brown. Early whorls, waist, spiral cords and apertural lips dark brown. Nodules on shoulder white.

Radula: description of radula morphology given in the end of the Results section.

DISTRIBUTION. Central Philippines and Vanuatu, depth range, living at 4–30 m.

REMARKS. There is a currently undescribed species that occurs sympatrically with *P. variegata* nov. sp. in Vanuatu that is remarkably similar (Fig. 58), which we will refer to as *Pseudodaphnella* nov. sp. aff. *variegata*. This differs from *P. variegata* in having more rounded whorl profile, stronger spiral elements, uniform brown colour and a protoconch of 1.5 whorls with no signs of cancellate sculpture (Fig. 59). Another similar species is *P. oligoina* Hedley, 1922 (Fig. 60), which, however, has a protoconch of two whorls and is a uniform pale.

Pseudodaphnella crypta nov. sp.
(Figs 61–67)

TYPE MATERIAL. Holotype: MNHN–25629, Molecular voucher IM–2007–42613, 8.0 mm, Vanuatu, Malparavu Is., Expedition 'Santo 2006' stn. VM59, 15°22′35″S 167°11′37″E, intertidal. *Paratypes*: Par 1 – MNHN–25630, Molecular voucher IM–2007–42597, 8.15 mm, Vanuatu, Santo Is., Off Malo Kili Kili, Expedition 'Santo 2006' stn. FB52, 15°42′42″S 167°15′05″E, 7 m; Par 2 – MNHN–25631, 9.1 mm, same locality as Par 1; Par 3 – MNHN–25632, 11.5 mm, Vanuatu, Expedition 'Santo 2006', stn. NS37 15°31.4′S 167°09.8′E, 2–3 m.

OTHER MATERIAL EXAMINED. **New Caledonia**: 8.5 mm, Koumac, Expedition 'Montrouzier' stn. 1298, 20°35.2′S 164°16.6′E, 2–4 m; 11.3 mm, Koumac Expedition 'Montrouzier' stn. 1303 20°38.8′S 164°16.5′E, 0–8 m; **Loyality Is.**: 7.6 mm, Lifou, Expedition 'Atelie Lifou' stn. 1419, 20°55.6′S 167°04.5′E, 5 m; 7.5 mm, Lifou, Expedition 'Atelie Lifou' stn. 1429, 20°47.5′S 167°07.1′E, 8–18 m.

ETYMOLOGY. Latin feminine adjective *crypta* (hidden). The species name emphasizes the remarkable similarity to *Pseudodaphnella philippinensis* (see Remarks).

DESCRIPTION. Shell small elongate fusiform (SH 6–8.5 mm; w/h 0.425–0.445) with straight rather long siphon, wide aperture and pointed apex. Teleoconch of 5.0–5.5 evenly convex whorls; suture slightly indented. Sculpture reticulate, formed by narrow sharp, widely interspaced, slightly prosocline axial ribs, crossed by fine densely crowded spiral cords. Intersections of spiral and axial elements with distinct rounded tubercles, closely arranged along axial ribs. Interstices rather deep, rectangular. Penultimate whorl with total of 7 spiral cords; last adult whorl with 11 spiral cords followed by 4 indistinct oblique rows of tubercles on fasciolar region.

Aperture ovate, elongate, slightly constricted before wide moderately deep siphonal canal. Outer lip slightly thickened, with moderately developed varix; its inside with 2 distinct denticles, 1 on border between aperture and anal sinus, other between aperture and siphonal canal, and fine dentition between them. Inner lip smooth with moderately developed callus, slightly recurved before siphonal canal. Anal sinus rather shallow, rounded, directed upward. Its upper edge extended towards inner lip to form obtuse oblique ridge on top of aperture.

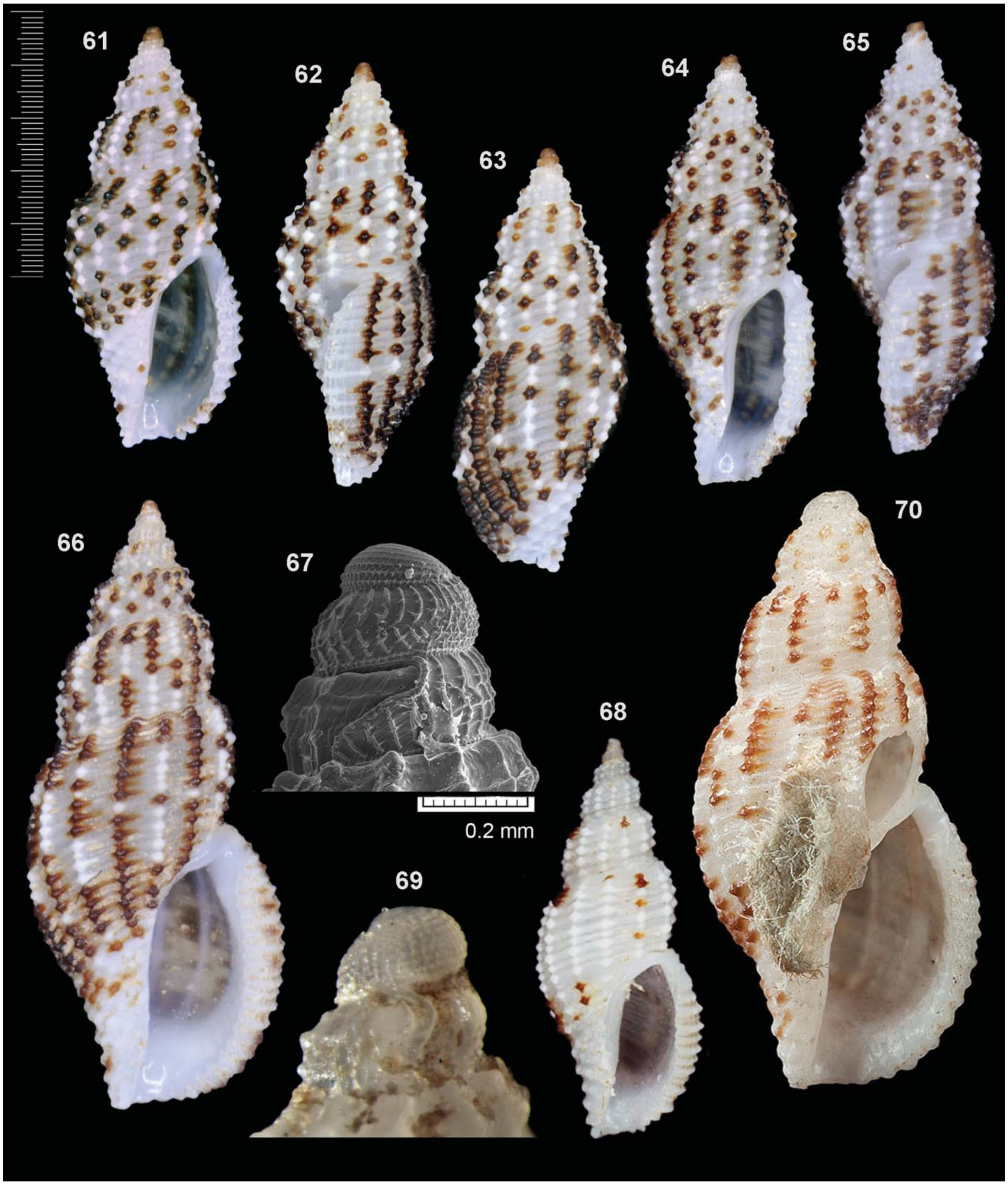
Protoconch narrowly conical of *c*. 2.8 whorls (Fig. 67). Early whorls spirally lirate, later whorls sculptured by orthocline lines, adapically with diagonally cancellate sculpture below mid-height of the whorl. Protoconch deeply adapically notched at transition to teleoconch.

Protoconch brown. Teleoconch white with some tubercles situated on intersections of spiral and axial elements, irregularly coloured brown. Tubercles formed by 3 spiral cords on shell base usually all brown. Fasciole white.

Radula: description of radula morphology given in the end of the Results section.

DISTRIBUTION: Western Pacific: Vanuatu, New Caledonia and probably Philippines (see Remarks), depth range, living at intertidal zone down to the depth of 30 m.

REMARKS. *Pseudodaphnella crypta* nov. sp. is closely related to *P. philippinensis* (Figs 68–70) and these species



Figs 61–70. *Pseudodaphnella crypta* nov. sp. and similar species. Scale 50 mm. **61**–**63**. Holotype; **64**, **65**. Paratype 1; **66**. Paratype 3; **67**. Protoconch morphology, voucher specimen 7.8 mm, Vanuatu, Expedition 'Santo 2006', stn. VM69, 15°33′23″S 167°16′44″E, 7 m; **68**, **69**. *Pseudodaphnella philippinensis*, molecular voucher IM–2007–42392, Philippines, Panglao Is., Expedition 'Panglao 2004' stn. S39, 9°38.1′N 123°51.4′E, 3–4 m; **68**. Shell; **69**. Protoconch morphology; **70**. Syntype of *Pseudodaphnella philippinensis* (not to scale) NHMUK 1963921, 13.7 mm, Philippines, Masbate or Luzon Is.

are hardly distinguishable in teleoconch morphology. Although mature shells of *P. philippinensis* seem to be wider in proportions with rather globose whorls, immature shells of the same size have very similar proportions. The protoconch of *P. philippinensis* differs markedly being white, and of *c*. 2.3 whorls (Fig. 69), with the early whorls finely granulated and later whorls axially ribbed. Unfortunately, most mature specimens of *P. philippinensis* have worn apex and lack the protoconch; among more than 20 examined specimens, including types in NHMUK and MNHN only one specimen (IM–2007–42392) had intact protoconch.

Pseudodaphnella sudafricana nov. sp.

(Figs 71–74)

TYPE MATERIAL. Holotype: MNHN–25633, Molecular voucher IM–2009–17954, 5.1 mm, Southern Madagascar, Expedition 'Atimo Vatae' stn. BS03, 25°26.4′S 44°56.1′E, 14–18 m.

ETYMOLOGY. The species name refers to the region, from where the only known specimen originates.

DESCRIPTION. Shell small, elongate–fusiform (SH 5.1 mm; w/h 0.42), with moderately long siphon. Teleoconch of 5.0–5.5 rather high evenly convex whorls, suture slightly indented. Sculpture of rounded axial folds overridden by undulating spiral cords, thickening on intersections with axial folds to form rather rounded glossy nodules that are only slightly extended spirally. Interstices between spiral elements rather deep. Early teleoconch whorls with 4 spiral cords, adapical weaker than 2 succeeding, situated on whorl periphery. Lowest spiral cord separated from preceding by slightly wider interstice, largely overlapped by succeeding whorl. Penultimate whorl with 3 spiral cords on periphery. Last adult whorl with 7 spiral cords, adapical first and seventh notably weaker than others. Last adult whorl demarcated from fasciole by concave waist, devoid of sculpture. Fasciole convex with rounded nodules arranged in oblique rows.

Aperture rather narrow and elongate; siphonal canal moderately deep. Outer lip rounded, thickened, incurved, with strong varix behind rim. Inner side of outer lip with 6 subequal denticles. Inner lip straight and smooth, without dentition. Anal sinus rounded, rather shallow.

Protoconch conical of *c*. 2.3 convex elaborately sculptured whorls (Fig. 74). Early whorls finely spirally lirate. Later whorls with axial riblets on adapical surface and diagonally cancellate sculpture on periphery.

Teleoconch white with occasional nodules coloured tan on spire whorls; on last adult whorl these form a checkered pattern. All nodules on 6th and 7th spiral cords on last adult whorl tan, forming an indistinct spiral band. Few axial folds behind labral varix tan entirely. Some fasciolar nodules also tan.

DISTRIBUTION. The only known specimen of this species was collected off southern Madagascar at depth of 14–18 metres.

REMARKS. In shell morphology *Pseudodaphnella sudafricana* nov. sp. is closest to *P. tincta*, but the former species is a little narrower and differs in colour pattern. Another similar species is *Pseudodaphnella* nov. sp. 9, which we do not describe in the present paper, because of a lack of good quality material. The latter, however has stronger spiral sculpture and differs in protoconch morphology, which has more than two whorls with diagonally cancellate sculpture. Two other superficially similar species are *P. hadfieldi* (Melvill & Standen, 1895) and *P. boholensis* nov. sp. (see below) both of which, however, have white protoconchs of non-planctotrophic morphology.

Pseudodaphnella kilburni nov. sp.

(Figs 75–83)

TYPE MATERIAL. Holotype: MNHN–25634, Molecular voucher IM–2009–19168, 8.3 mm, Philippines, off Bolod, Expedition 'Panglao 2004' stn. T1, 9°32.38′N 123°47.26′E, 83–102 m. *Paratypes*: Par 1 – MNHN–25635, 8.6 mm, Philippines, Expedition 'Panglao 2004' stn. L74–75, 9°30.7′N 123°40.9/41.0′E, 120–140 m; Par 2 – MNHN–25635, 13.5 mm, same locality as Par 1; Par 3 – MNHN–25635, 9.2 mm, same locality as Par 1; Par 4 – MNHN–25636, 8.3 mm, Philippines, Expedition 'Panglao 2004' stn. T38, 9°32.3′N 123°42.3′E, 80–140 m.

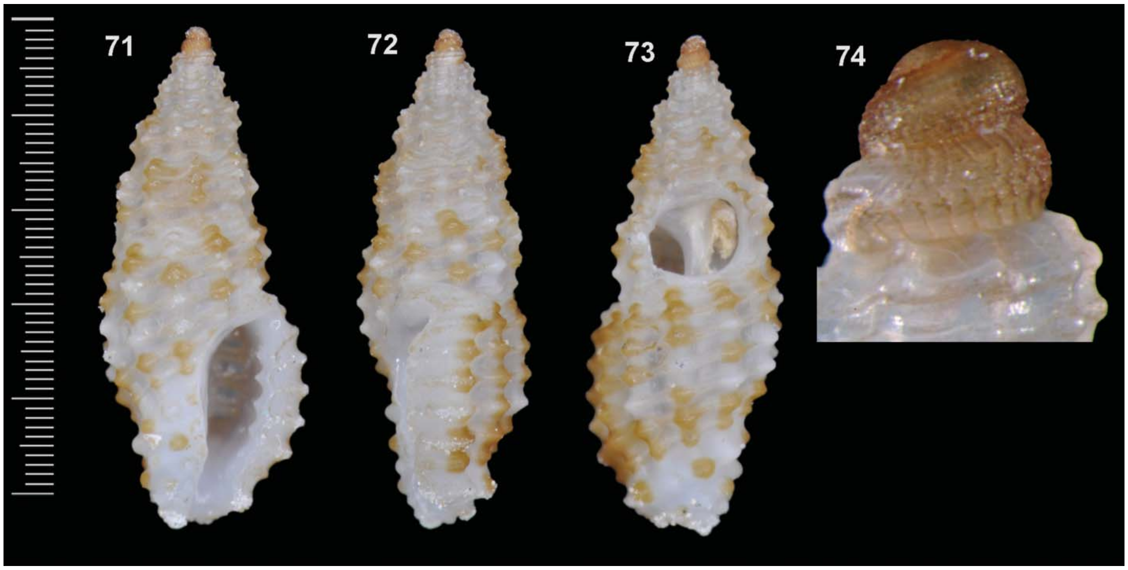
OTHER MATERIAL EXAMINED. **Philippines**: molecular voucher IM–2009–19169, juvenile 5 mm, same locality as holotype; juvenile, protoconch voucher, 7.4 mm, same locality as Par 1 (Fig. 82); 8.1 and 8.9 mm, Expedition 'Panglao 2004' stn. L65–68, 9°29.9′N 123°55.1′E, 55–81 m; ?**Vanuatu**: 9.0 mm, Aoré Is., Expedition 'Santo 2006' stn. ZS22, 15°33′03″S 167°09′37″E, 27–29 m; 5.0 mm, Segond Channel, Expedition 'Santo 2006' stn. FS77, 15°33′03″S 167°09′37″E, 29 m.

ETYMOLOGY. This species is named after Dr Richard Neil Kilburn, outstanding malacologist, whose work contributed a lot into taxonomy of gastropoda in general and of the genera *Kermia* and *Pseudodaphnella* in particular.

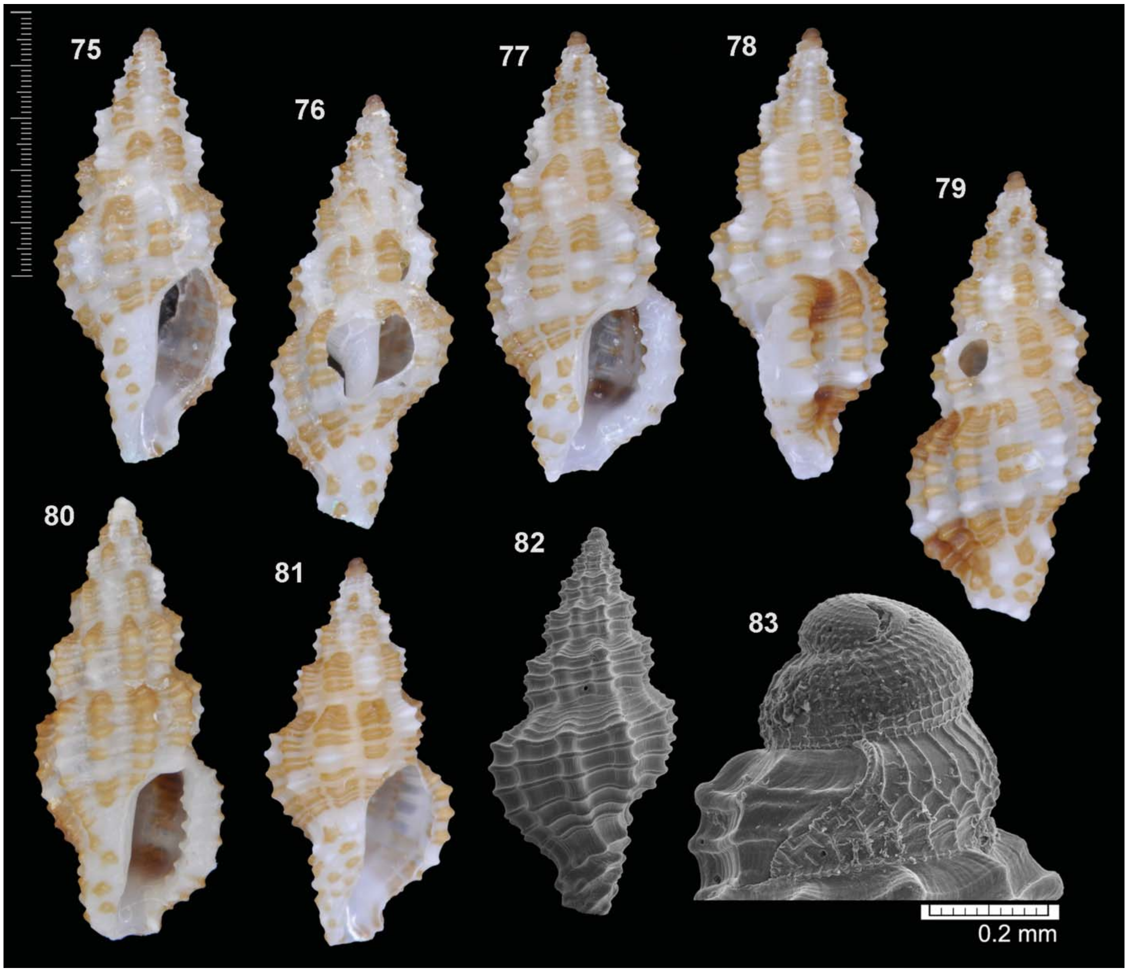
DESCRIPTION. Shell small, fusiform (w/h 0.43–0.45) with high spire and well-defined rather long tapering siphon. Teleoconch of 6 distinctly shouldered whorls. Suture slightly undulating. Sculpture cancellate, axial elements strong, evenly spaced rounded folds (11 on last adult whorl), well developed on periphery, but vanishing adapically and abapically toward suture. Spiral sculpture of dense, rather weak, undulating spiral cords on shoulder slope and stronger, more widely spaced cords on periphery. Spiral cords on whorl periphery elevated and thickened at intersections with axial ribs to form glossy, spirally extended nodules. Penultimate whorl with 3 subequal spiral cords on shoulder slope, succeeded abapically by 4 spiral cords on periphery; third and fourth cords widely spaced. Last adult whorl with 4 spiral cords on shoulder slope, becoming gradually stronger towards shoulder angulation. Periphery of last adult whorl with 4 prominent spiral cords and 2 weaker cords on base.

Fasciole rather weak, sculptured by oblique crenulate cords, separated from base by distinct wide and concave waist.

Aperture rather wide, ovate, tapered to moderately wide rather shallow siphonal canal. Outer lip strongly convex, thickened and slightly incurved, its inside with 7 (paratype 1) distinct denticles, stretched from anal sinus to siphonal



Figs 71–74. *Pseudodaphnella sudafricana* nov. sp. Scale 50 mm. **71–74**. *Holotype*: Molecular voucher IM–2009–17954, 5.1 mm, southern Madagascar, Expedition 'Atimo Vatae' stn. BS03, 25°26.4′S, 44°56.1′E, 14–18 m; **71–73**. Shell; **74**. Protoconch.



Figs 75–83. *Pseudodaphnella kilburni* nov. sp. **75**, **76**. Scale 50 mm. Holotype; **77–79**. Paratype 1; **80**. 9.0 mm; Vanuatu, Expedition 'Santo 2006', stn. ZS22, 15°33′03″S 167°09′37″E, 27–29 m; **81** – **83**. 7.4 mm, same locality as Paratype 1; **81**, **82**. Shell; **83**. Protoconch morphology.

canal. Anal sinus wide and rather shallow, rounded, directed upward. Inner lip straight and smooth, notably recurved at border of siphonal canal.

Protoconch orthoconoid, brown, of *c*. 2.7 evenly convex whorls (Fig. 83). First 1.7 whorls sculptured by fine, weakly crenulated spiral lirae, last whorl diagonally cancellate, deeply adapically notched at transition to teleoconch.

Teleoconch white, some axial folds light brown; Colour pattern on early spire whorls regular with alternate axial folds brown, more chaotic on penultimate and last adult whorls.

Radula: Description of radula morphology given at the end of the Results section.

DISTRIBUTION. Central Philippines and Vanuatu, depth range, living at 80–140 m.

REMARKS. In shell outline *Pseudodaphnella kilburni* nov. sp. resembles *P. excellens* (Sowerby III, 1913) (holotype depicted by Higo *et al.*, 2001; Kilburn, 2009). The latter species, however, has a much more pronounced shoulder than in *P. kilburni* nov. sp. and these species differ markedly in colour pattern as well. In colour pattern *P. kilburni* nov. sp. is similar to *P. hadfieldi*, *P.* nov. sp. 9 and P. *boholensis* nov. sp.; however, the former species could be readily recognized by its distinctly shouldered whorls and rather wide shell.

Pseudodaphnella lineata nov. sp.
(Figs 84–91)

TYPE MATERIAL. Holotype: MNHN–25637, molecular voucher IM–2007–42387, 4.8 mm, Philippines, Expedition 'Panglao 2004' stn. B25, 9°29.4′N 123°56.1′E, 16 m. *Paratypes*: Par 1 – MNHN–25638, 5.05 mm, same locality as holotype; Par 2 – MNHN–25639, 4.2 mm, Philippines, Expedition 'Panglao 2004' stn. B11, 9°29.4′N 123°56.0′E, 2–4 m; Par 3 – MNHN–25640, 4.2 mm, Philippines, Panglao 2004 stn. B13, 9°37.1′N 123°52.6′E 3–5 m.

OTHER MATERIAL EXAMINED. **Vanuatu**: 5.5 mm, Segond Channel, Expedition 'Santo 2006' stn. FS79, 15°33.1′S 167°09.6′E, 2 m; **New Caledonia**: 5.7 mm, Channel Ilot Maitre, stn. 1335, 22°19.7′S 166°25.8′E 20–24 m.

ETYMOLOGY. Latin feminine adjective *lineata* (lined) refers to the colour pattern of fine axial lines, characteristic for this species.

DESCRIPTION. Shell small, fusiform (SH 4.75–5.75 mm; w/h 0.43–0.45), truncated with rather short, wide siphon. Teleoconch of 5 evenly convex whorls, suture slightly indented. Sculpture of rounded axial folds overridden by strong undulating spiral cords, thickening at intersections with axial folds to form strong, spirally extended, glossy nodules, and rather sharp between axial folds. Interspaces between spiral elements rather deep and only slightly wider than spiral cords. Early teleoconch whorls with 3 spiral cords, adapical cord weaker than 2 succeeding ones. Last adult whorl with 6 subequal, evenly spaced spiral cords, succeeded by weak seventh. Last adult whorl demarcated from fasciole by concave smooth waist. Fasciole convex with rounded nodules arranged in oblique rows.

Aperture elongate, gently tapered to moderately deep siphonal canal. Outer lip rounded, thickened and slightly incurved with strong varix behind rim. Inner side of outer lip with 4–6 subequal denticles. Inner lip straight and smooth, without dentition. Anal sinus rounded and rather shallow.

Protoconch conical, of *c*. 2.7 strongly convex, elaborately sculptured whorls (Fig. 91). Early whorls spirally lirate. Later protoconch whorls with distinct axial riblets extending abapically from suture to whorl mid-height, diagonally cancellate below.

Protoconch orange. Teleoconch white with rather regular brown bands marking alternate axial folds. On last adult whorl brown bands extend abapically from suture to 4th spiral cord, 5th spiral cord with no brown markings. In contrast all nodules on 6th and 7th spiral cords brown, forming an indistinct spiral band. Some fasciolar nodules also coloured brown.

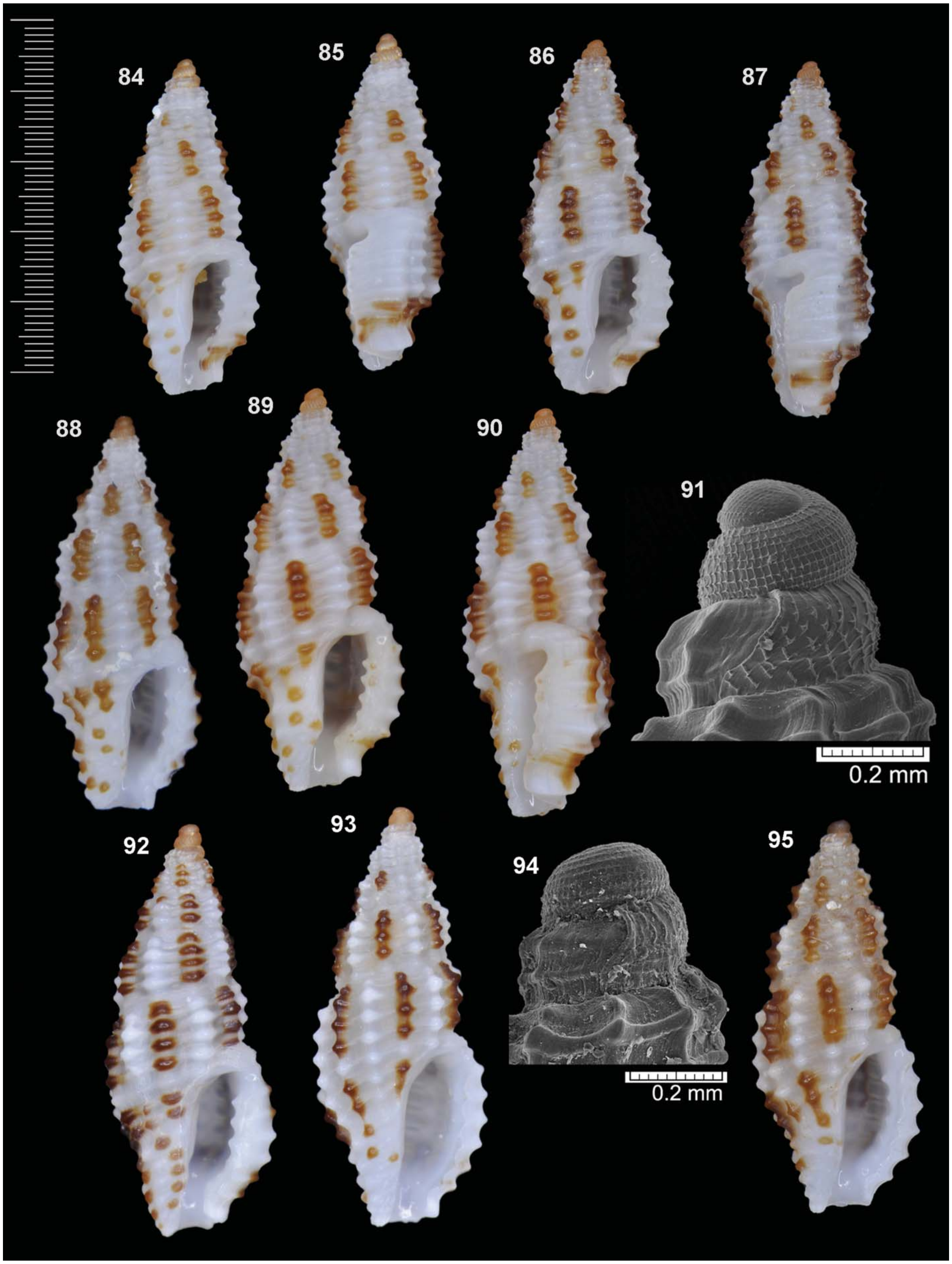
DISTRIBUTION. Western Pacific, from Philippines to New Caledonia, depth range, living at shallow waters from 2 down to 30 metres.

REMARKS. Many species in the *Kermia–Pseudodaphnella* complex are similar to *P. lineata* nov. sp. The species is closest to *Clathurella maculosa* Pease, 1863 (Fig. 92), but differs in colour pattern. The brown bands in *P. lineata* nov. sp. are continuous and mark nodules and interspaces between them as well, while in *P. maculosa* the brown spiral folds are dotted as the interstices between nodules are white. Another extremely similar species (Figs 93–95), still undescribed, occurs sympatrically with *P. lineata* in Vanuatu and New Caledonia. It is practically indistinguishable from *P. lineata* in the Teleoconch morphology, but has a protoconch of at least 0.7 whorls fewer, spirally grooved with no cancellate sculpture. The third species to mention, *P. phaeogranulata* nov. sp. (see description below) is also similar to *P. lineata* in shell proportions and colouration, but differs in having indistinct waist and a thicker siphonal canal.

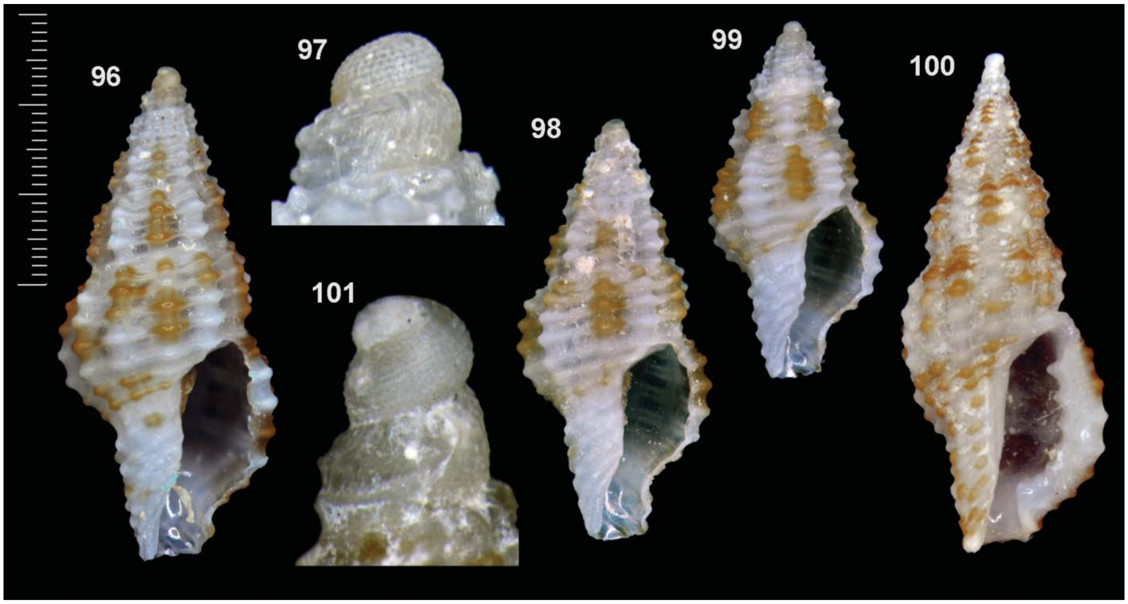
Pseudodaphnella boholensis nov. sp.
(Figs 96–99)

TYPE MATERIAL. Holotype: MNHN–25641, Molecular voucher IM–2009–42382, 5.5 mm, Philippines, Expedition 'Panglao 2004' stn. B22, 9°29.42′N 123°56.00′E, 15 m. *Paratypes*: Par 1 – MNHN–25642, Molecular voucher IM–2009–42383, 5.0 mm, same locality as holotype; Par 2 – MNHN–25643, Molecular voucher IM–2009–42384, 4.3 mm, same locality as holotype.

ETYMOLOGY. Name '*boholensis*' refers to type locality of the species, widely attributed to the area of Bohol Island, Philippines.



Figs 84–95. *Pseudodaphnella lineata* nov. sp. and similar species. Scale 50 mm. **84**, **85**. Holotype; **86**, **87**. Paratype 1; **88**. 5.5 mm, Vanuatu, Segond Channel, Expedition 'Santo 2006' stn. FS79, 15°33.1′S 167°09.6′E, 2 m; **89**, **90**. 5.7 mm, New Caledonia, Channel Ilot Maitre, Expedition 'Lagon 3' stn. 1335, 22°19.7′S 166°25.8′E 20–24 m; **91**. Protoconch morphology, voucher specimen 4.65 mm, Vanuatu, Santo Is., Palikulo Bay, Expedition 'Santo 2006' stn. DS38, 15°29′40″S 167°14′40″E, 7 m; **92**. *Pseudodaphnella maculosa*, 5.3 mm, Vanuatu, Asuléka Is., Expedition 'Santo 2006' stn. DB25, 15°37′18″S 167°10′31″E, 10 m; **93**–**95**. *Pseudodaphnella* nov.sp. *cf lineata*; **93**, **94**. 5.5 mm, Vanuatu, Luganville Tidal flat, Expedition 'Santo 2006' stn. VM53, 15°33.63′S 167°16.51′E, intertidal; **93**. Shell; **94**. Protoconch morphology; **95**. 5.45 mm, New Caledonia, Channel Ilot Maitre, Expedition 'Lagon 3' stn. 1335, 22°19.7′S 166°25.8′E 20–24 m.



Figs 96–101. *Pseudodaphnella boholensis* nov. sp. and similar species. Scale 50 mm. **96**, **97**. Holotype; **98**. Paratype 1; **99**. Paratype 2; **100**, **101**. *Pseudodaphnella hadfieldi*, 9.1 mm, Loyality Is., Lifou, Expedition 'Atelier Lifou' stn. 1431, 20°47.5′ S, 167°07.1′ E; 18–35 m; **100**. Shell, **101**. Protoconch.

DESCRIPTION. Shell small, fusiform (SH 4.3–5.5 mm; w/h 0.45–0.49), with wide aperture and straight, rather long siphon. Teleoconch of 4.5 – 5.5 whorls, suture wavy slightly indented. Spire whorls weakly convex, with periphery progressively shifting abapically, to form somehow flattened whorl profile and pyramidal outline of spire. Last adult whorl strongly and evenly convex, constricted to distinct waist demarcating base from siphon.

Sculpture of wide, rounded axial folds overridden by strong, dense, undulating spiral cords, slightly thickened at intersections with axial folds to form spirally extended glossy nodules. Spiral interspaces rather deep. Early teleoconch whorls with 3 spiral cords; penultimate with 4 cords, adapical cord weaker than 2 succeeding, abapical 4th cord separated from the suture by distinct grove. Last adult whorl with 7 evenly spaced spiral cords; adapical cord and two cords on shell base weaker than others.

Aperture elongate, gently tapered to moderately wide siphonal canal. Outer lip rounded, thickened and slightly incurved within. Inner side of outer and anal sinus not seen as all studied specimens are subadult.

Protoconch yellowish, bulbous, non-planctotrophic morphology, of *c*. 1.8 whorls (Fig. 97). Early whorls sculptured with dense microgranules arranged in more or less spiral rows, last 2/3 whorl with closely set orthocline threads.

Teleoconch white with yellow bands, marking alternate axial folds on first 4 whorls, pattern rather irregular on later whorls. Two spiral cords on base yellow.

DISTRIBUTION. Central Philippines, shallow water at around 15 metres.

REMARKS. In shell proportions and colour pattern, *P. boholensis* nov. sp. is rather similar to *P. tincta*, *P. aureotincta*, *P. sudafricana* nov. sp. and *P.* nov. sp. 9, but the white, protoconch of non-planctotrophic morphology and slightly flattened whorl outline distinguish *P. boholensis* nov. sp. from all of these species. Another superficially similar *Pseudodaphnella* species with non-planctotrophic protoconch morphology is *P. hadfieldi* (Figs 100, 101), which differs notably in details of protoconch morphology and has evenly convex whorls.

Pseudodaphnella phaeogranulata nov. sp.
(Figs 102–110)

TYPE MATERIAL. Holotype: MNHN–25644, Molecular voucher IM–2007–18105, 4.0 mm, Tutuba Is., Vanuatu, Expedition 'Santo 2006', stn. DS96, 15°33.63′S 167°16.51′E, 114 m. *Paratypes:* Par 1 – MNHN–25645, 3.75 mm, Vanuatu, Santo 2006, stn. VM53, 15°33.63′S 167°16.51′E, intertidal; Par 2 – MNHN–25646, 3.75 mm, Tutuba Is., Vanuatu, Expedition 'Santo 2006', stn. VM69, 15°33.4′S 167°16.7′E, intertidal; Par 3 – MNHN–25646, 3.65 mm, same locality as Par 2; Par 4 – MNHN–25645, 3.45 mm, same locality as Par 1.

OTHER MATERIAL EXAMINED. **Vanuatu**: 3.0 mm, 3.1 mm, 3.4 mm, same locality as Par 1; 3.35 mm, same locality as Par 2; Mounparap Is. Expedition 'Santo 2006', stn.VM39, 15°22.35′S 167°11.61′E, intertidal (3 specimens); Malo Kili Kili, Expedition 'Santo 2006', stn. DB83 15°33′34′′S 167°16.15′02′′E, 6 m (2 specimens).

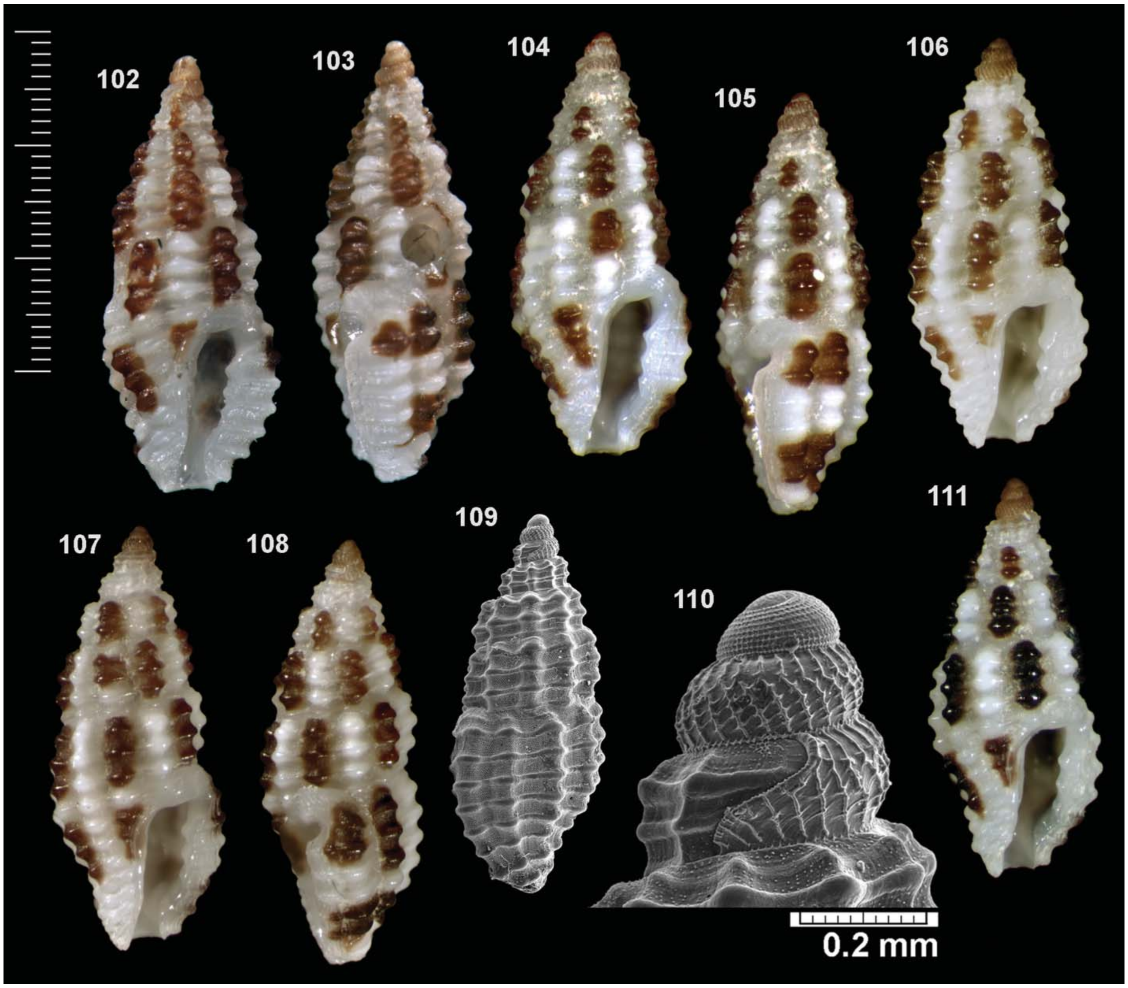
ETYMOLOGY. Greek adjective *phaeo-* (dusky, brown) and Latin feminine adjective *granulata* (granulated), refers to colour and sculptural pattern, characteristic for the species.

DESCRIPTION. Shell small, fusiform (SH 3.2–4.0 mm; w/h 0.42–0.45), with truncated base. Teleoconch of 4–4.5 evenly convex whorls, suture wavy, slightly indented. Sculpture of rounded axial folds (10 on last adult whorl) overridden by undulating spiral cords, thickened at intersections with axial folds to form strong spirally extended glossy nodules, and vanishing between axial elements. Interspaces quadrate, rather deep. First teleoconch whorl with 3 subequal spiral cords; on second whorl 2 abapical cords, peripheral, similar and strong, adapical becoming very weak. Adult penultimate whorl with indistinct adapical spiral cord, and 3 strong spiral cords on periphery. Last adult whorl also with weak adapical cord, succeeded by 6 strong spiral cords .across whorl surface and 2 cords on siphonal canal. All spiral cords on shell base and siphonal canal equally interspaced, with no distinct waist. Fasciole indistinct.

Aperture elongate, gently tapered to moderately deep siphonal canal. Outer lip rounded, thickened and slightly incurved with strong varix behind rim. Inner side of outer lip with 3 subequal denticles. Inner lip straight and smooth, without dentition, slightly recurved adaxially. Anal sinus rounded, rather shallow.

Protoconch conical of *c*. 3 strongly convex, elaborately sculptured whorls. First 1.5 whorls spirally lirate, succeeding whorls distinctively diagonally cancellated. Protoconch deeply adaxially notched at transition to teleoconch.

Teleoconch white with rather regular brown bands marking alternate axial folds. On last adult whorl brown axial bands interrupted by fourth spiral cord, which is white throughout whorl. Protoconch light brown.



Figs 102–111. *Pseudodaphnella phaeogranulata* nov. sp. and similar species. Scale 30 mm. **102, 103**. Holotype; **104**, **105**. Paratype 1; **106**. Paratype 4; **107**, **108**. Paratype 2; **109**, **110**. 3.4 mm, Vanuatu, Luganville Tidal flat, Expedition ‘Santo 2006’ stn. VM53, 15°33.63′S 167°16.51′E, intertidal; **109**. Shell, **110**. Protoconch morphology; **111**. *Kermia barnardi* 3.55 mm, Vanuatu, Luganville Tidal flat, Expedition ‘Santo 2006’ stn. VM53, 15°33.63′S 167°16.51′E, intertidal.

DISTRIBUTION. All examined specimens were collected from Vanuatu, but judging from the planctotrophic morphology of the protoconch characteristic for the species, its distribution may well be wider.
REMARKS. *Pseudodaphnella phaeogranulata* nov. sp. strongly resembles *P. barnardi*, its closest molecular relative. The only difference seems to be in the colour of the axial bands, which are black in *P. barnardi* and brown in *P. phaeogranulata*. Another similar species is *P. geraldsmithi* Kilburn, 2009, which, however, is characterized by the presence of an 'angular sloping shoulder' and a 'slight, but distinct waist' (Kilburn, 2009), both absent in *P. phaeogranulata*. *Pseudodaphnella lineata* nov. sp., also somewhat resembles *P. phaeogranulata*, but the former has a distinct waist and a pronounced fasciole, which are absent in *P. phaeogranulata*.

Radula morphology

Pseudodaphnella philippinensis nov. sp. (Fig. 112). Radula of 15–20 rows of hypodermic teeth. Each tooth 45–50 μm long with long body and subapical pore of moderate size, tip of tooth above pore forming pointed projection, slightly flattened laterally. No barbs or blades.

Thetidos tridentata nov. sp. (Fig. 113). Radula of few rows of awl-shaped hypodermic teeth. Each tooth *c*. 70 μm long, robust, with moderately wide base (Fig. 113). Tooth tip simple, with no barbs or blades. Pore opening subapical slit-shaped, very long (approximately 1/4 of tooth length) and narrow. One margin of pore with 5 equal blunt projections forming distinct serration.

Exomilus compressa nov. sp. (Fig. 114). Radula of few rows of hypodermic teeth. Each tooth *c*. 30 μm long, syringe-needle shape with moderately wide base (Fig. 114). Pore opening subapical, ovate, moderately wide. Tooth tip with pointed projection above pore opening, no barbs or blades.

Pseudodaphnella variegata nov. sp. (Fig. 115). Radula of few rows of hypodermic teeth. Each tooth *c*. 35 μm long, of syringe-needle shape, base rather wide (Fig. 115). Pore opening subapical, elongated. Tooth tip with pointed projection above pore opening; no barbs or blades.

Pseudodaphnella crypta nov. sp. (Fig. 116). Radula of few rows of hypodermic teeth. Each tooth *c*. 45 μm long, of syringe-needle shape; base narrow with long projection (Fig. 116). Pore opening subapical, elongate, very short and narrow. Tooth tip with pointed projection above pore opening; no barbs or blades.

Pseudodaphnella kilburni nov. sp. (Fig. 117). Radula of about 20 rows of hypodermic teeth. Each radular tooth 40–45 μm long, rather wide in shape of syringe needle (Fig. 117). Base, very wide with long flat projection of about half of tooth length. Basal and apical pore openings very wide; tooth tip simple with no barbs or blades, rather short-pointed.
REMARKS. Generally the family Raphitomidae is characterized by a diversity of radular morphologies. Some members of the family, especially those from deep waters (for instance species of the genus *Gymnobela*) possess radulae with fully developed, remarkably large hypodermic teeth with barbs at their tips, resembling teeth of *Conus* species (Bouchet & Waren, 1980; Kantor & Taylor, 2002). Some other deep-water and a majority of studied shallow-water species have radulae with simplified teeth, bearing neither barbs nor blades at their tips. Finally a number of Raphitomidae from different lineages of the family have been shown to lack radula completely (Powell, 1966; Kantor & Taylor, 2002, Kantor, pers. comm., unpubl. data). All species investigated of the *Kermia–Pseudodaphnella* complex have generally unremarkable, rather short radular teeth of hypodermic type with no barbs or blades, in agreement with published data on shallow-water species. Despite the fact that there are some rather minor variations in the structure of radular teeth in the studied species, the data are too incomplete to discuss the significance of observed differences in radular morphology between the members of the different *Kermia–Pseudodaphnella* clades. The only one that is peculiar in radular morphology is *Thetidos tridentata* nov. sp., with its rather long (for shallow-water Raphitomidae) teeth and unusual structure of apical pore with distinct serration. If this radular structure is found to be characteristic of species similar to *Thetidos tridentata* nov. sp. in shell structure, such as *Thetidos morsura* and *Thetidos globulosus*, it may prove to be an apomorphy of the genus *Thetidos*.

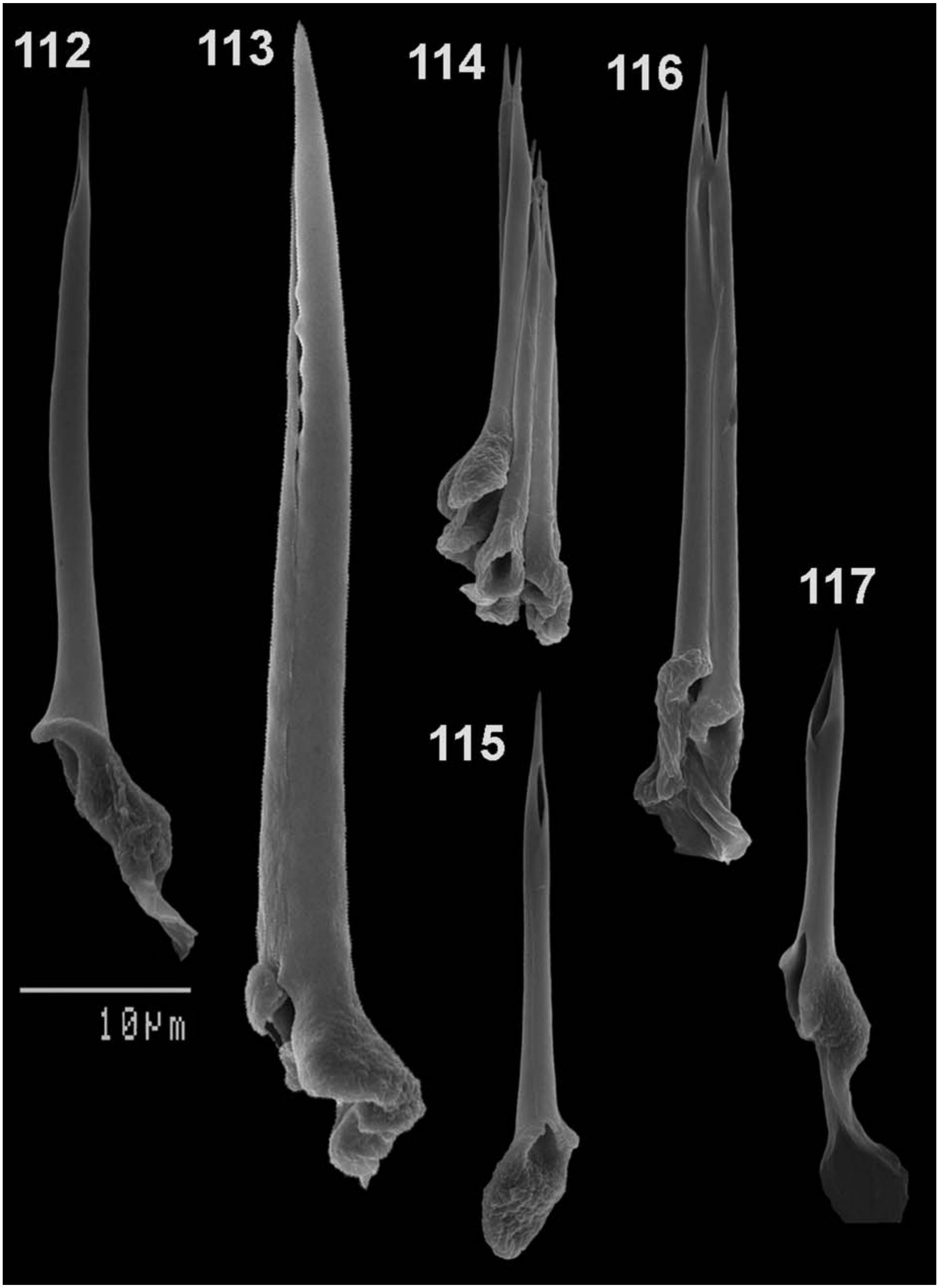
Discussion

Magnitude of species richness in the *Kermia–Pseudodaphnella* complex

In addition to a number of new species, which we have described in the present paper, a dozen other undescribed species of *Kermia–Pseudodaphnella* complex, with distinctive combinations of protoconch and teleoconch characters were recognized. It was found that there exist complexes of presumably closely related species that demonstrate extreme similarity in the structure of teleoconchs, but that differ from each other in protoconch morphology. The best examples are the pairs: *Thetidos morsura* vs. *T. tridentata*; *Pseudodaphnella oligoina* vs. *P. variegata*; *P. philippinensis* vs. *P. crypta*; and *Pseudodaphnella lineata* vs. *P*. sp. aff. *lineata*. The species that remained undescribed to date (some are described herein) and were never mentioned in literature are obviously only a few of the existing examples, demonstrating that diversity of *Kermia–Pseudodaphnella* species is highly underestimated.

Role of protoconch morphology in genus and species level taxonomy

The use of protoconch morphology in the classification of Conoidea has been a subject of argument for many years (Powell, 1942; Laseron, 1954; Kilburn, 1983;



Figs 112–117. Radulae of some species of the genera *Thetidos*, *Exomilus* and *Pseudodaphnella* (to scale). **112**. *Pseudodaphnella philippinensis*, Philippines, Expedition "Panglao 2004", stn. S39, 9°38.1'N 123°51.4'E, 3–4 m; **113**. *Thetidos tridentata* nov. sp., Philippines, Expedition "Panglao 2004", stn. L46, 9°31'N 123°41'E, 90–110 m; **114**. *Exomilus compressa* nov. sp., New-Caledonia, Loyalty Island, Expedition "Atelier Lifou", stn. 1435, 22°55.2'S 167°00.7'E, 5–30m; **115**. *P. variegata* nov. sp., Philippines, Expedition "Panglao 2004", stn. B7, 9°35.9'N; 123°51.8'E, 4–30 m; **116**. *P. crypta* nov. sp., Philippines, Expedition "Panglao 2004", stn. S25, 9°41.5'N 123°51.0'E, 21 m; **117**. *P. kilburni* nov. sp., Philippines, Expedition "Panglao 2004", stn. L74–75, 9°30.7'N 123°40.9/41.0'E, 120–140 m

Bouchet, 1990; Bouchet *et al.*, 2011). In Powell's (1942) interpretation 'paucispiral' and 'polygyrate' protoconchs found in species with similar adult shell would suggest their assignment to different genera (the so-called 'turrid pairs' – Bouchet, 1990). Following this approach one could definitely consider *P. philippinensis* and *P. crypta*, as well as species of other pairs listed above, to belong to different genera. Our phylogenetic analysis, even if including only one of these pairs (*P. philippinensis* and *P. crypta* n. sp.), here shown to be sister species, disproves the concept that turrid pairs are referable to different genera. Therefore the universal importance of protoconch in the classification of Conoidea seems to have been largely overestimated. The role of protoconch characters in fixation of species identity, however, is certainly not less than that of the teleoconch. The case of the *Kermia–Pseudodaphnella* complex gives multiple examples of species with very similar teleoconchs but different protoconchs. Undoubtedly, identification of the specimens with missing protoconch may turn into quite challengeable issues. The most troublesome situations may occur if primary type specimens have missing or corroded protoconchs, which may lead to uncertainty in species identity (Bouchet & Strong, 2010). As a conclusion, special attention has to be paid to the selection of qualitative type series for descriptions of any new species to ensure unequivocal subsequent recognition.

On the status of the genera *Kermia, Pseudodaphnella, Paramontana, Exomilus and Thetidos*

In our analysis, key morphological characters (primarily the morphology of protoconch), originally defining generic assignment of studied species were shown to be taxonomically inconsistent. Species traditionally assigned to *Kermia* or *Pseudodaphnella*, or, judging from the morphology of protoconch, to *Paramontana*, do not segregate into separate clades on the phylogenetic tree, but are instead intermixed. Therefore, these generic names refer to artificial groupings within the *Kermia–Pseudodaphnella* complex, and the current taxonomy of the group does not reflect relationships of its members. Major revisions of diagnoses and reconsideration of a number of traditional generic assignments are clearly required.

The lack of morphologic criteria makes delimitation of the genera *Kermia* and *Pseudodaphnella* problematic and uncertain. Taking into consideration the weak support of basal nodes and absence of the type species of the genus *Kermia* (*K. benhami*) from our phylogenetic analysis, any decisions on the status of these genera would be untimely. Involvement of additional phylogenetic markers and inclusion of *Kermia benhami*, is required to fully resolve relationships and set criteria for delimitation of *Kermia* and *Pseudodaphnella*. The genus *Paramontana* was originally defined solely by the non-planctotrophic protoconch morphology of its members and should be considered as a synonym of either *Kermia* or *Pseudodaphnella*.

Exomilus and *Thetidos* species are distinctive in overall shell morphology and the only studied species of *Thetidos* shows some unique features in the structure of radula. Both genera are closely related to *Pseudodaphnella*, but additional phylogenetic studies are needed to specify their relationships. Additional molecular studies are also needed to clarify relationships and the generic assignment of '*Kermia*' *producta* and '*Kermia*' sp. cf. *producta*.

On the biology and developmental plasticity of Raphitomidae

Loss of planctotrophy was documented in different families of the superfamily Conoidea and is believed to be irreversible (Bouchet, 1990). Planctotrophic development with long-living planctonic larvae are advantageous in dispersal as larvae may travel considerable distances with oceanic currents (Jablonski & Lutz, 1983; Leal & Bouchet, 1991). Moreover, it has been demonstrated for some conoidean taxa that the switch from planctotrophic to non-planctotrophic development can give rise to adaptive radiation, especially in polar or insular regions, or in groups with narrow bathymetric distribution (Bouchet, 1990; Leal & Bouchet, 1991). Loss of planctotrophy for example, preceded radiation in the polar genus *Oenopota* (Bogdanov, 1989) or bathyal Indo-Pacific genus *Bathytoma* (Puillandre *et al.*, 2010).

At the species level, the appearance of forms with non-planctotrophic development in groups generally characterized by long-living planctotrophic larvae usually indicates appearance of narrow endemics (Leal & Bouchet, 1991). In some cases, however, species with direct development may have distribution ranges comparable to their congeners with long-living pelagic larvae (Johannesson, 1988; Martel & Chia, 1991); some studies demonstrate capability for efficient post-larval dispersal in some minute bivalves and gastropods (Martel & Chia, 1991).

It is generally accepted that the morphology of the protoconch in gastropods allows determination of the mode of development and estimation of the duration of larval stage in ontogenesis of the species (Jablonski & Lutz, 1983; Bouchet, 1990; Castelin *et al.*, 2010). Multiple switches in mode of development are shown to have occurred in the evolutionary history of the *Kermia–Pseudodaphnella* complex and the diversity of protoconch morphologies found in this group suggests a high developmental and evolutionary plasticity. This plasticity may allow members of the *Kermia–Pseudodaphnella* complex to develop and explore a variety of dispersal strategies, providing, therefore, an evolutionary mechanism for radiation of the group.

A number of pairs of similar, presumably closely related species, of which one has planctotrophic development and the other non-planctotrophic, often sampled in the same localities, implies recent and ongoing speciation linked to the diversification of the mode of development. Species in such pairs employ different dispersal strategies that may reduce competition between members of closely related species. Long-living planctotrophic larvae allow maintenance of a wide geographic range of a species and high genetic integrity between distanced populations (Castelin *et al.*, 2010). On the other hand, larvae released from egg capsules at later stages with a shortened pelagic period may be more efficient in short-distance dispersal, as they have higher survivability, in remote island populations for example. It is believed that the loss of planctotrophic development and formation of local endemic species is associated with fragmentation of a suitable environment on a large scale with the formation of isolated spots, when the distance between neighbouring spots exceeds the distance of larval reach. In this situation larvae with short pelagic periods would have more chances to settle on the 'parent' spot than larvae with long dispersal periods. At the same time neither long living in plankton, nor short living would be able to reach neighbouring spots in significant quantities. Therefore short living in plankton larvae would have higher survivability and finally would be favoured by selection. Some geographically isolated spots, like seamounts, are easy to interpret and discuss, as the fragmentation is obvious. However, in our case identification of the factor restricting the distribution of one or another species is rather problematic.

In Raphitomidae speciation, linked to the loss of planctotrophic larvae, may constitute an alternative to the canonical allopatric model for marine organisms (Coyne & Orr, 2004), as suggested for other gastropods, including conoideans (Duda & Palumbi, 1999; Cunha *et al.*, 2005).

The family Raphitomidae is also remarkable due to the well-documented tendency to repeated loss of crucial conoidean foregut structures (radula, proboscis and venom gland – Kantor & Sysoev, 1989; Taylor *et al.*, 1993; Kantor & Taylor, 2002; Fedosov, 2007) that evidently occurred in different lineages of the family independently (unpubl. data). Many raphitomids, especially small shallow water species that retain the radula, have it notably reduced in size and morphologically simplified. This fact together with the tubular structure of the salivary glands, characteristic for Raphitomidae, but unusual in Conoidea, led Kantor & Taylor (2002) to the conclusion that origin and radiation in the family might had something to do with paedomorphosis.

Paedomorphosis generally implies conservation of some larval or premature characters in adult morphology. It can usually be observed in groups of minute animals where miniaturization is usually accompanied by simplification of morphology or complete loss of definitive structures (Bleidorn, 2007). Loss of the final stages of ontogenesis, usually responsible for the formation of morphologically complex specialized structures, like radula in conoideans, implies decrease of determination in late development which therefore becomes more flexible. This may thus explain the developmental plasticity observed in members of the *Kermia–Pseudodaphnella* complex.

It is noteworthy that the loss of planctotrophy in minute turrids is not necessarily related to simplification of morphology. Some members of the genus *Lienardia* (Clathurellidae), for example the type species *L. rubida* (Hinds, 1843), are characterized by smooth pausispiral protoconch of non-planctotrophic morphology (Hedley, 1922), while most *Lienardia* species have characteristically multispiral protoconchs with a distinct keel on late whorls. At the same time members of the genus *Lienardia*, despite showing certain morphological similarities to the *Kermia–Pseudodaphnella* complex and similar distributions, have highly conservative foregut structure and proportionally large, often morphologically complex radular teeth (Fedosov, 2011).

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References

Adams, H. 1872. Descriptions of fourteen new species of land and marine shells. *Proceedings of the Zoological Society of London* **1872**, 12–15.

Appeltans, W., Bouchet, P., Boxshall, G.A., De Broyer, C., De Voogd, N.J., Gordon, D.P., Hoeksema, B.W., Horton, T., Kennedy, M., Mees, J., Poore, G.C.B., Read, G., Stöhr, S., Walter, T.C. & Costello, M.J. 2012. *World Register of Marine Species* [http://www.marinespecies.org, accessed 21 November 2012].

Barberousse, A. & Samadi, S. 2010. Species from Darwin onward. *Integrative Zoology* **5**, 187–197.

Bleidorn, C. 2007. The role of character loss in phylogenetic reconstruction as exemplified for the Annelida. *Journal of Zoological Systematics and Evolutionary Research* **45**, 299–307.

Bogdanov, J. P. 1989. Morphological transformations of radula and protoconch of Oenopotinae Bogdanov, 1987. *La Conchiglia* **233/236**, 35–47.

Boettger, O. 1895. Die marinen Mollusken der Philippinen (IV) nach den Sammlungen des Herrn José Florencio Quadra in Manila. IV. Die Pleurotomiden. (Schluss.). *Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft* **27**, 41–63.

Bouchet, P. 1990. Turrid genera and mode of development: the use and abuse of protoconch morphology. *Malacologia* **32**, 69–77.

Bouchet, P. & Strong E. 2010. Historical name–bearing types in marine molluscs: an impediment to biodiversity studies. In: Polaszek, A., Ed., *Systema Naturae 250 – The Linnaean Ark.* CRC Press, Boca Raton, FL, pp. 61–72.

Bouchet, P. & Waren, A. 1980. Revision of the north-east atlantic bathyal and abyssal Turridae (Mollusca, Gastropoda). *Journal of Molluscan Studies*, Suppl. **8**, 1–120.

Bouchet, P., Héros, V., Lozouet, P. & Maestrati, P. 2008. A quarter-century of deep-sea malacological exploration in the South and West Pacific: Where do we stand? How far to go? In: Héros, V., Cowie, R.H. & Bouchet, P., Eds., *Tropical Deep–Sea Benthos* ***25****. Mémoires du Muséum national d'Histoire naturelle* **196**. Paris, pp. 9–40.

Bouchet, P., Lozouet, P. & Sysoev, A.V. 2009. An inordinate fondness for turrids. *Deep–Sea Research* **56**, 1724–1731.

Bouchet, P., Héros, V., Lozouet, P., Maestrati, P. & Von Cosel, R. 2011. The marine molluscs of Santo. In: Bouchet, P., Le Guyader, H. & Pascal, O., Eds., *Natural History of Santo. Museum national d'Histoire naturelle*, Paris; IRD, Marseille; ProNatura International, Paris, pp. 421–431.

Bouchet, P., Kantor, Y.I., Sysoev, A.V. & Puillandre, N. 2011. A new operational classification of the Conoidea (Gastropoda). *Journal of Molluscan Studies* **77**, 273–308.

Brazier, J. 1876. A list of the Pleurotomidae collected during the Chevert Expedition, with the description of the new species. *Proceedings of the Linnean Society of New South Wales* **1**, 151–162.

Castelin, M., Lambourdiere, J., Boisselier, M.-C., Lozouet, P., Couloux, A., Cruaud, C. & Samadi, S. 2010. Hidden diversity and endemism on seamounts: focus on poorly dispersive neogastropods. *Biological Journal of the Linnean Society* **100**, 420–438.

Castelin, M., Puillandre, N., Kantor, Y.I., Terryn, Y., Cruaud, C., Bouchet, P. & Holford, M. 2012. Macroevolution of venom apparatus innovations in auger snails (Gastropoda; Conoidea; Terebridae). *Molecular Phylogenetics and Evolution* **64**, 21–24.

Coyne, J.A. & Orr, H.A. (2004) *Speciation*. Sinauer Associates, Sunderland, MA.

Cunha, R.L., Castilho, R., Ruber, L. & Zardoya, R. 2005. Patterns of cladogenesis in the venomous marine gastropod genus *Conus* from the Cape Verde Islands. *Systematic Biology* **54**, 634–650.

Cunha, R.L., Tenorio, M.J., Afonso, C., Castilho, R. & Zardoya, R. 2008. Replaying the tape: recurring biogeographical patterns in Cape Verde *Conus* after 12 million years. *Molecular Ecology* **17**, 885–901.

De Queiroz, K. 2007. Species concepts and species delimitation. *Systematic Biology* **56**, 879–886.

Deshayes, G.P. 1863. Catalogue des mollusques de l'Ile de la Réunion (Bourbon). In: Maillard, L., Ed., *Notes sur l'Ile de la Réunion (*Bourbon*). Mollusques*. Dentu, Paris, pp. 1–144.

Duda, T.F. & Kohn, A.J. 2005. Species-level phylogeography and evolutionary history of the hyperdiverse marine gastropod genus *Conus*. *Molecular Phylogenetics and Evolution* **34**, 257–272.

Duda, T.F. & Lee, T. 2009. Ecological release and venom evolution of a predatory marine Snail at Easter Island. *PLoS One* **4**, e5558.

Duda, T.F. & Palumbi, S. 1999. Developmental shifts and species selection in gastropods. *Proceedings of the National Academy of Sciences USA* **96**, 10272–10277.

Fedosov, A.E. 2007. Anatomy of accessory rhynchodeal organs of *Veprecula vepratica* and *Tritonoturris subrissoides*: new types of foregut morphology in Raphitominae (Conoidea). *Ruthenica* **17**, 33–41.

Fedosov, A.E. 2011. Five new species of the genus *Lienardia* (Conidae: Gastropoda) from the shallow waters of central Philippines. *Ruthenica* **21**, 123–135.

Fedosov, A.E., Watkins, M., Showers Corneli, P., Heralde, F.M., Concepcion, G.P. & Olivera, B.M. 2011. Phylogeny of the Genus *Turris*: correlating molecular markers with radular anatomy and shell morphology. *Molecular Phylogenetics and Evolution* **59**, 263–270.

Folmer, O., Black, M., Hoeh, W., Lutz, R. & Vrijenhoek, R. 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* **3**, 294–299.

Garrett, A. 1873. Descriptions of new species of marine shells inhabiting the South Sea Islands. *Proceedings of the Academy of Natural Science of Philadelphia* **25**, 209–231.

Hedley, C. 1899. The Mollusca of Funafuti. Part I – Gasteropoda. *Memoirs of the Australian Museum* **3**, 395–488.

Hedley, C. 1918. A checklist of the marine fauna of New South Wales. Part 1. Mollusca. *Journal and Proceedings of the Royal Society of New South Wales* **51**, Supplement **1**, M1–M120.

Hedley, C. 1922. A revision of the Australian Turridae. *Records of the Australian Museum* **13**, 213–359.

Hervier, J. 1897. Descriptions d'espèces nouvelles de l'Archipel de la Nouvelle–Calédonie. *Journal de Conchyliologie* **44**, 138–151.

Higo, S., Callomon, P. & Goto, Y. 2001. *Catalogue and Bibliography of the Marine Shell–Bearing Mollusca of Japan. Gastropoda Bivalvia Polyplacophora Scaphopoda Type Figures*. Elle Scientific Publications, Yao.

Hinds, R.B. 1843. On new species of *Pleurotoma, Clavatula,* and *Mangelia. Proceedings of the Zoological Society of London* **1843**, 36–46.

Huelsenbeck, J.P., Ronquist, F. & Hall, B. 2001. MrBayes: Bayesian inference of phylogeny. *Bioinformatics* **17**, 754–755.

Jablonski, D. & Lutz, R.A. 1983. Larval ecology of marine benthic invertebrates: paleobiological implications. *Biological Reviews* **58**, 21–89.

JOHANNESSON, K. 1988. The paradox of Rockall: why is a brooding gastropod (*Littorina saxatilis*) more widespread than one having a planktonic larval dispersal stage (*L. littorea*)? *Marine Biology* **99**, 507–513.

KANTOR, Y.I. & SYSOEV, A.S. 1989. The morphology of toxoglossan gastropods lacking a radula, with a description of a new species and genus of Turridae. *Journal of Molluscan Studies* **55**, 537–550.

KANTOR, Y.I. & TAYLOR, J.D. 2002. Foregut anatomy and relationships of raphitomine gastropods (Gastropoda: Conoidea: Raphitominae). *Bollettino Malacologico* Supplement **4**, 161–174.

KANTOR, Y.I., PUILLANDRE, N., OLIVERA, B.M. & BOUCHET, P. 2008. Morphological proxies for taxonomic decision in turrids (Mollusca, Neogastropoda): a test of the value of shell and radula characters using molecular data. *Zoological Science* **25**, 1156–1170.

KILBURN, R.N. 1983. Turridae (Mollusca: Gastropoda) of southern Africa and Mozambique. Part 1. Subfamily Turrinae. *Annals of the Natal Museum* **25**, 549–585.

KILBURN, R.N. 2009. Genus *Kermia* (Mollusca: Gastropoda: Conoidea: Conidae: Raphitominae) in South African waters, with observations on the identities of related extralimital species. *African Invertebrates* **50**, 217–236.

LASERON, C. 1954. *Revision of the New South Wales Turridae* (*Mollusca*). Australian Zoological Handbook. Royal Zoological Society of New South Wales, Sydney.

LEAL, J.H. & BOUCHET, P. 1991. Distribution patterns and dispersal of prosobranch gastropods along a seamount chain in the Atlantic Ocean. *Journal of the Marine Biological Association of the United Kingdom* **71**, 11–25.

MADDISON, W.P. & MADDISON, D. 2009. *Mesquite: a modular system for evolutionary analysis*. Version 2.01 [http://mesquiteproject.org, accessed 21 November 2012].

MARTEL, A. & CHIA, F.-S. 1991. Drifting and dispersal of small bivalves and gastropods with direct development. *Journal of Experimental Marine Biology and Ecology* **150**, 131–147.

MELVILL, J.C. & STANDEN, R. 1895. Notes on a collection of shells from Lifu and Uvea, Loyalty Islands, formed by the Rev. James and Mrs. Hadfield, with list of species. *Journal of Conchology* **8**, 84–132.

NEVILL, G. & NEVILL, H. 1875. Descriptions of new marine Mollusca from the Indian Ocean. *Journal of the Asiatic Society of Bengal* **44**, 83–104.

OLIVER, W.R.B. 1915. The Mollusca of the Kermadec Islands. *Transactions and Proceedings of the New Zealand Institute* **47**, 509–568.

PEASE, W.H. 1863. Description of new species of marine shells from the Pacific Islands. *Proceedings of the Zoological Society of London* **1862**, 240–243.

POWELL, A.W.B. 1942. The New Zealand recent and fossil Mollusca of the family Turridae. *Bulletin of the Auckland Institute and Museum* **2**, 1–188.

POWELL, A.W.B. 1966. The molluscan families Speightiidae and Turridae: an evaluation of the valid taxa, both Recent and fossil, with lists of characteristic species. *Bulletin of the Auckland Institute and Museum* **5**, 1–184.

PUILLANDRE, N., SYSOEV, A.V., OLIVERA, B.M., COULOUX, A. & BOUCHET, P. 2010. Loss of planktotrophy and speciation: geographical fragmentation in the deep-water gastropod genus *Bathytoma* (Gastropoda, Conoidea) in the western Pacific. *Systematics and Biodiversity* **8**, 371–394.

RAMBAUT, A. & DRUMMOND, A.J. 2007. *Tracer* v1.4 [http://beast.bio.ed.ac.uk, accessed 21 November 2012].

REEVE, L.A. 1843–46. Monograph of the Genus *Pleurotoma*. *Conchologia Iconica, or Illustrations of the shells of molluscous animals*. Reeve Brothers, London, Vol. 1: pls 1–18, species 1–155 (1843.); pl. 19, species 156–165 (1844); pls 20–33, species 166–305 (1845.); pls 34–40, species 306–369 + index and errata (1846).

SOWERBY, G.B. III 1913. Description of new species of Mollusca. *Annals and Magazine of Natural History, series* **8**, 12, 233–239.

TAMURA, K., DUDLEY, J., NEI, M. & KUMAR, S. 2007. MEGA4: Molecular Evolutionary Genetics Analysis (MEGA) software version 4.0. *Molecular Biology and Evolution* **24**, 1596–1599.

TAYLOR, J.D., KANTOR, Y.I. & SYSOEV, A.V. 1993. Foregut anatomy, feeding mechanisms and classification of the Conoidea (=Toxoglossa) (Gastropoda). *Bulletin of the Natural History Museum of London (Zoology)* **59**, 125–170.

TUCKER, J.K. 2004. Catalog of recent and fossil turrids (Mollusca: Gastropoda). *Zootaxa* **682**, 1–1295.

WILLIAMS, S.T. & DUDA, T.F. 2008. Did tectonic activity stimulate oligo-miocene speciation in the Indo–West Pacific? *Evolution* **62**, 1618–1634.

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