



## Research article

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# *Perotrochus caledonicus* (Gastropoda: Pleurotomariidae) revisited: descriptions of new species from the South-West Pacific

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**Abstract.** Morphological (shell) and molecular examination of a large suite of specimens of pleurotomariids from around New Caledonia and the Coral Sea reveals the existence of four species in the complex of *Perotrochus caledonicus*: *Perotrochus deforgesi* Métivier, 1990 and *P. pseudogranulosus* sp. nov. live allopatrically on the plateaus and guyots of the Coral Sea; *Perotrochus caledonicus* Bouchet & Métivier, 1982 and *Perotrochus wareni* sp. nov. live sympatrically - but essentially not syntopically - on the slopes of New Caledonia, Norfolk Ridge and the Loyalty Ridge. All species live in the 300–500 m interval, and together form a significant component of the mollusc fauna living on hard bottoms in the SW Pacific, with individual dredge hauls containing up to 25 specimens of *Perotrochus*.

**Keywords.** *Perotrochus wareni* sp. nov., *Perotrochus pseudogranulosus* sp. nov., Coral Sea, New Caledonia, COI Barcode gene.

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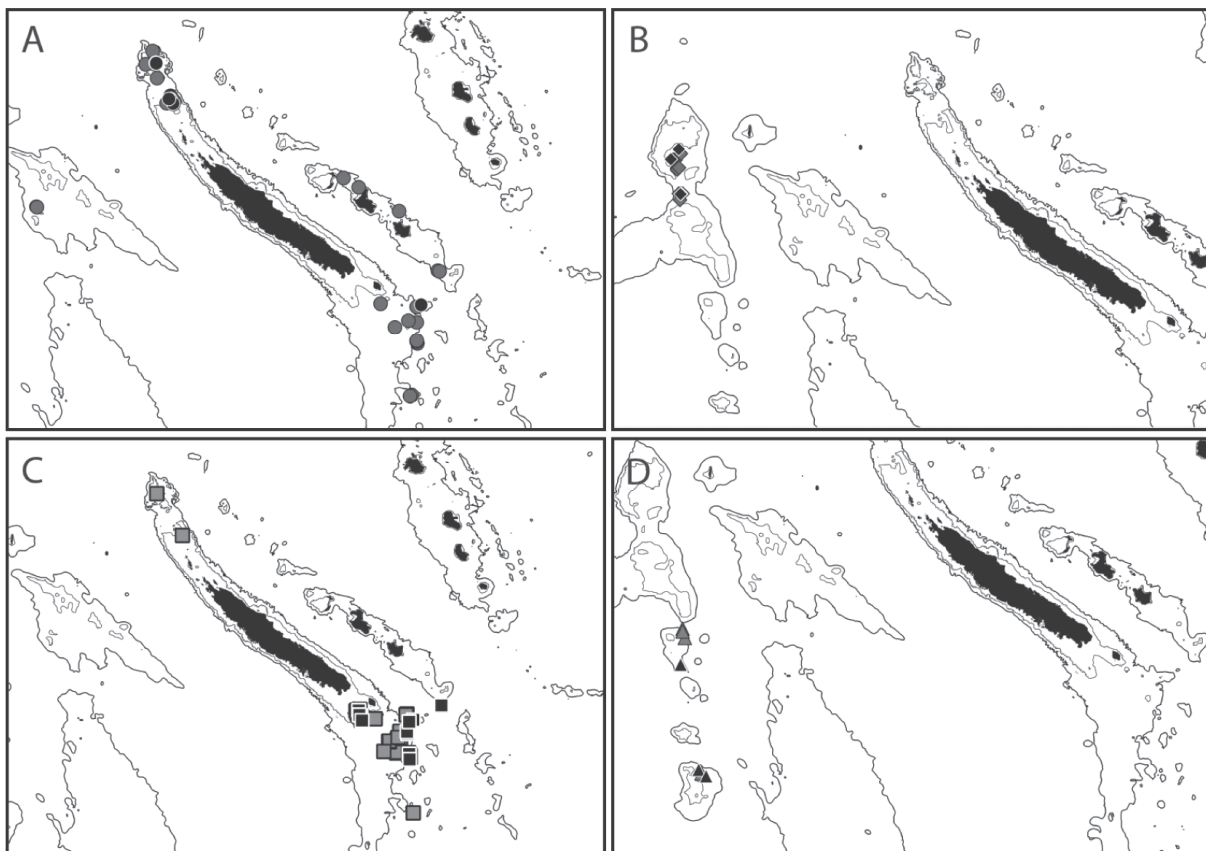
## Introduction

*Perotrochus caledonicus* Bouchet & Métivier, 1982 and *P. tangaroanus* Bouchet & Métivier, 1982 were the first pleurotomariids described from the South Pacific, from New Caledonia and from the Lau Ridge between New Zealand and Fiji (Bouchet & Métivier 1982), respectively. Since then, additional species have been documented from New Caledonia (*Perotrochus deforgesi* Métivier, 1990 and *Bayerotrochus*

*boucheti* (Anseeuw & Poppe, 2001)) and Tonga (*Bayerotrochus poppei* Anseeuw, 2003). Moreover, many populations at first sight referable to *Perotrochus caledonicus* were sampled around New Caledonia and in the Coral Sea.

The type material of *P. caledonicus* from off southern New Caledonia consists of specimens with a macroscopically non-pustulose shell, with rather smooth to weakly beaded spiral cords. Soon after its description, it appeared that a more granulose or pustulose morph also occurred around New Caledonia. However, as such material appeared very similar in terms of size, color and general profile, it was considered to represent just a form of *P. caledonicus*. The two forms were reported in print (Anseeuw 1990; Anseeuw & Goto 1996) and referred to as the “smooth form” and “pustulose form” of *P. caledonicus*, respectively. Since then, dealers and shell collectors have maintained this distinction, using the expression “*caledonicus* pustulose form” or “*caledonicus* granulose form”, with some even suggesting that the latter could warrant full recognition as a species (e.g., [www.conchology.be](http://www.conchology.be)).

New material from New Caledonia and the Coral Sea has now allowed revisiting this issue, using an integrative taxonomic approach combining DNA sequencing and shell characters of both juveniles and adults. DNA sequences provide independent characters to test whether the different forms of *P. caledonicus* correspond to divergent lineages or not. The congruence of the different sets of characters analyzed revealed that three species were hidden under the name *P. caledonicus*, two of which are now described as new. In addition, *Perotrochus deforgesii* was found to be molecularly closely related to this complex - which was not suspected from shell characters alone - and in this paper we will designate these small *Perotrochus* from the SW Pacific together as the “*Perotrochus caledonicus* complex”.



**Fig. 1.** Distribution maps of the four species. **A.** *Perotrochus wareni* sp. nov. **B.** *Perotrochus deforgesii* Métivier, 1990. **C.** *Perotrochus caledonicus* Bouchet & Métivier, 1982. **D.** *Perotrochus pseudogranulosus* sp. nov. Stations with sequenced specimens in black.

## Material and methods

### Material

A total of 284 lots and 879 specimens, including 59 sequenced specimens, attributable to the *Perotrochus caledonicus* complex were collected in the New Caledonia region, including the Coral Sea (Table 1, Fig. 1) during research cruises of the Tropical Deep-Sea Benthos program (Bouchet, Héros, Lozouet & Maestrati 2008). After 2002, live-taken specimens were specifically processed on board for molecular analyses. A piece of the foot was cut and placed in 95° ethanol; the remaining body and the shells were also preserved for further examination. All specimens are preserved at the Muséum National d'Histoire Naturelle (MNHN); each sequenced specimen is linked to a unique MNHN collection number. These specimens are registered in BOLD, the Barcode of Life database, and the corresponding sequences are also registered in GenBank (Table 1, Fig 1).

### DNA sequencing

Total DNA was extracted from the piece of foot using the 6100 Nucleic Acid Prepstation system (Applied Biosystem) or the Epmotion 5075 robot (Eppendorf) following the manufacturer's recommendations. The barcode fragment of the COI gene (658 bp) was tentatively amplified using the universal primers LCO1490 and HCO2198 (Folmer, Black, Hoeh, Lutz & Vrijenhoek 1994). However, the rate of success was very low (less than 10%), and several other protocols and primer pairs were tested. Finally, we were able to amplify most of the specimens, including several for each morphological species hypothesis, using the primers FISHR2 (Steinke & Hanner 2011) and 140F (Ketmaier, Giusti & Caccone 2006), and the following protocol: PCR reactions were performed in 20 µl containing 3 ng of DNA, 10× reaction buffer containing 15 mM MgCl<sub>2</sub>, 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', followed by 38 cycles of denaturation at 95°C for 40", annealing at 50°C for 40", followed by extension at 72°C for 50'. The final extension was at 72°C for 3'. PCR products were purified and sequenced by the Eurofins sequencing facility. Both directions were sequenced to confirm accuracy of each sequence.

### Phylogenetic analyses

In addition to the specimens of *Perotrochus* sequenced by us, COI sequences of Pleurotomariidae from GenBank were included in the dataset, as well as a sequence of *Haliotis tuberculata* (Haliotidae), used as outgroup (Table 1). Phylogenetic analyses were performed using MrBayes (Huelsenbeck, Ronquist & Hall 2001), running two parallel analyses, consisting each of five Markov chains of 20,000,000 generations with a sampling frequency of one tree each 2,500 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 (6 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 5 (Tamura *et al.* 2011).

## Results

### Morphological analyses

With the exception of some juveniles, we could separate all the specimens of the *Perotrochus caledonicus* complex into four different morphotypes (Table 2): one group presents shell characters consistent with the name-bearing holotype of *P. caledonicus* as described by Bouchet & Métivier (1982); the second group corresponds to the "rugose" or "pustulose" form, and is described below as *P. wareni* sp. nov.; a third group, with a geographically limited distribution within the Coral Sea, shows a microgranular

sculpture and is described as *P. pseudogranulosus* sp. nov.; the fourth group is readily assignable to *P. deforgesii*.

### Phylogenetic analyses

The phylogenetic analyses show that the *P. caledonicus* group is a well-supported clade (Posterior Probability PP = 1) within the Pleurotomariidae (Fig. 2). Although based on a single gene, the tree would also suggest that the genus *Perotrochus* is not monophyletic. Furthermore, some GenBank sequences appear to be either misidentified or contaminated; for example, the sequence L78912.1, identified as *Bayerotrochus teramachii* (Kuroda, 1955), is almost identical to three sequences identified as *B. midas* (Bayer, 1965). Within *P. caledonicus* s.l., the analysis of the COI gene diversity revealed the presence of four groups, each corresponding to a well supported clade in the phylogenetic tree (PP = 1 for each of them), and totally congruent with the morphological analysis. *P. deforgesii* is the sister-clade of a group that includes the specimens attributed to *P. caledonicus* and *P. wareni* sp. nov. The mean K2P genetic distance between *P. wareni* sp. nov. and *P. caledonicus* is 3.8%, which is similar to the distance

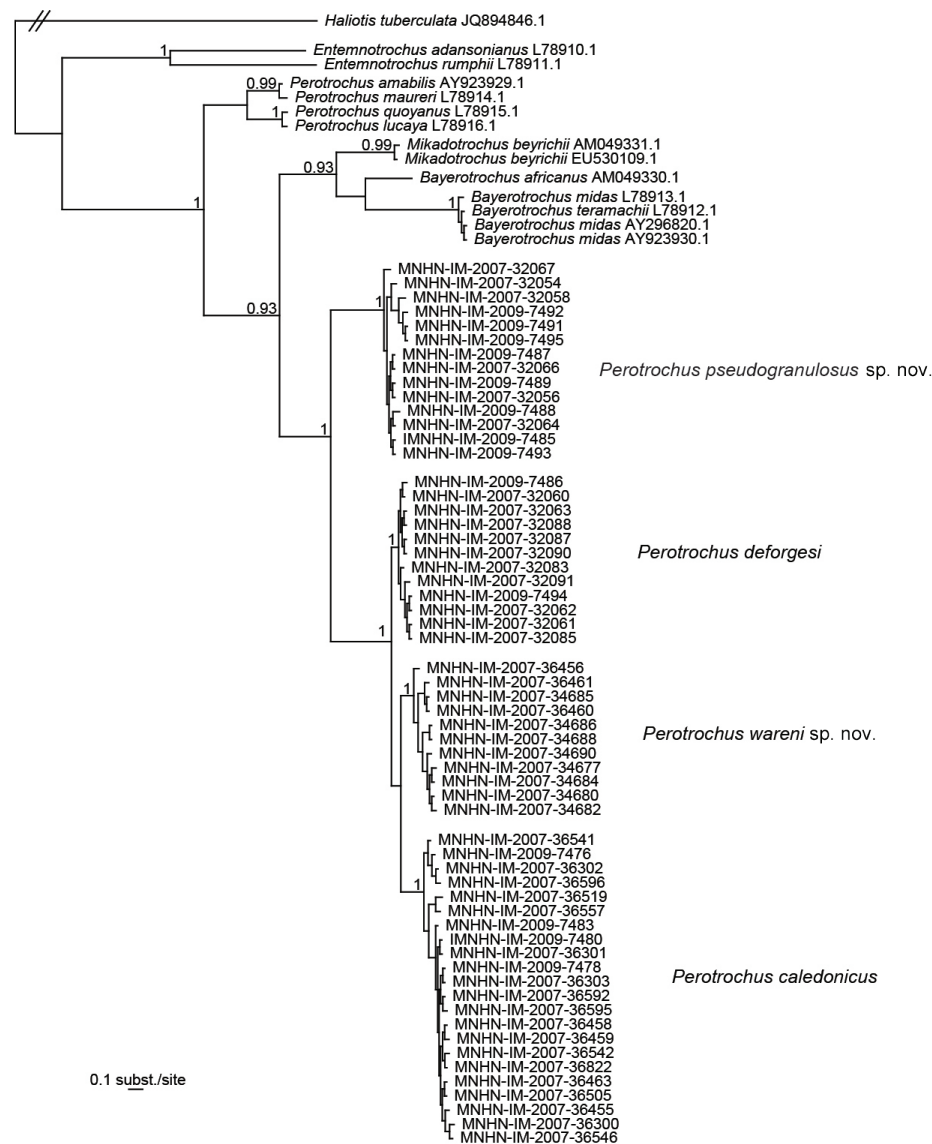


Fig. 2. Bayesian phylogenetic tree. Posterior probabilities (> 0.90) are shown for each node.

between *P. deforgesi* and *P. caledonicus* (3.7%) and greater than the distance between *P. deforgesi* and *P. wareni* sp. nov. (2.1%). This would tend to confirm that if *P. deforgesi* is considered a valid species – which is morphologically indisputable – then the two morphs (*P. caledonicus* s.s. and *P. wareni* sp. nov.), included until now in *P. caledonicus*, should be ranked as species as well. More surprisingly, *P. pseudogranulosus* sp. nov. is the sister-group to a clade that includes the other three species, with a mean genetic distance of 9.9% to the other three species, confirming its validity as a separate species.

### Systematics

Phylum Mollusca Cuvier, 1795  
Class Gastropoda Cuvier, 1795  
Subclass Vetigastropoda Salvini-Plawen, 1980  
Superfamily Pleurotomarioidea Swainson, 1840  
Family Pleurotomariidae Swainson, 1840

Genus *Perotrochus* P. Fischer, 1885

### Comparative material (all in MNHN)

*Perotrochus caledonicus*. 135 lots comprising 560 specimens (Table 1).

*Perotrochus deforgesi*. 36 lots comprising 59 specimens (Table 1).

*Perotrochus wareni* sp. nov.

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Figs 1A, 3A–F, 4A–J

### Etymology

This new species is named in honor of Dr Anders Warén of Naturhistoriska Riksmuseet, Stockholm, in recognition of his lifetime interest in deep-sea exploration and his participation in expeditions around New Caledonia and elsewhere in the South Pacific, many of which yielded specimens used in this paper.

### Material examined

73 lots comprising 176 specimens (Table 1).

### Type material

#### Holotype

NEW CALEDONIA: a sequenced specimen, MNHN-IM-2007-36460.

#### Paratypes

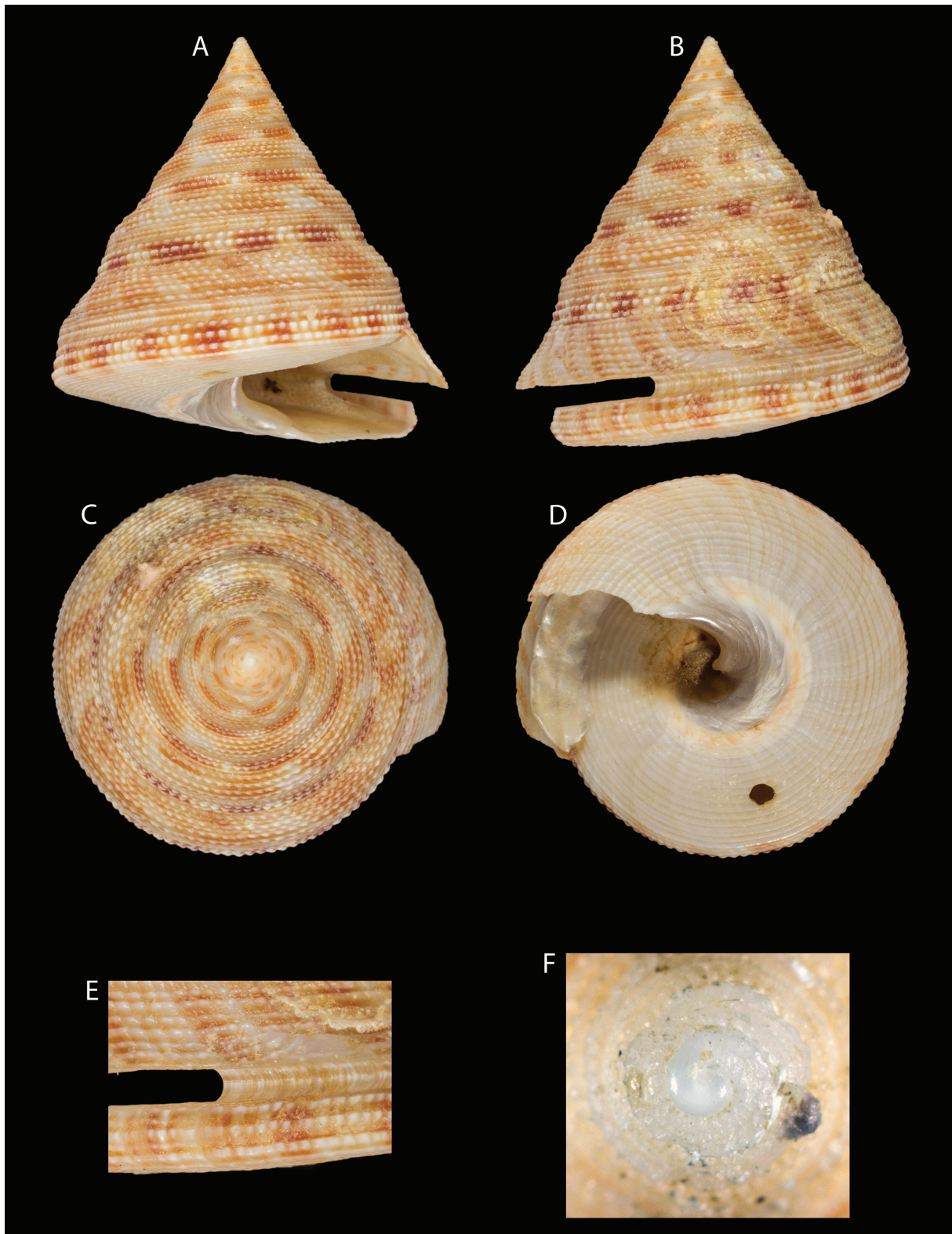
NEW CALEDONIA: MNHN-IM-2007-34680 (Fig. 4A–B); MNHN-IM-2007-34684 (Fig. 4C–D); MNHN-IM-2007-34685 (Fig. 4E–F); MNHN-IM-2007-36456 (Fig. 4G–H); MNHN-IM-2007-36461 (Fig. 4I–J).

### Type locality

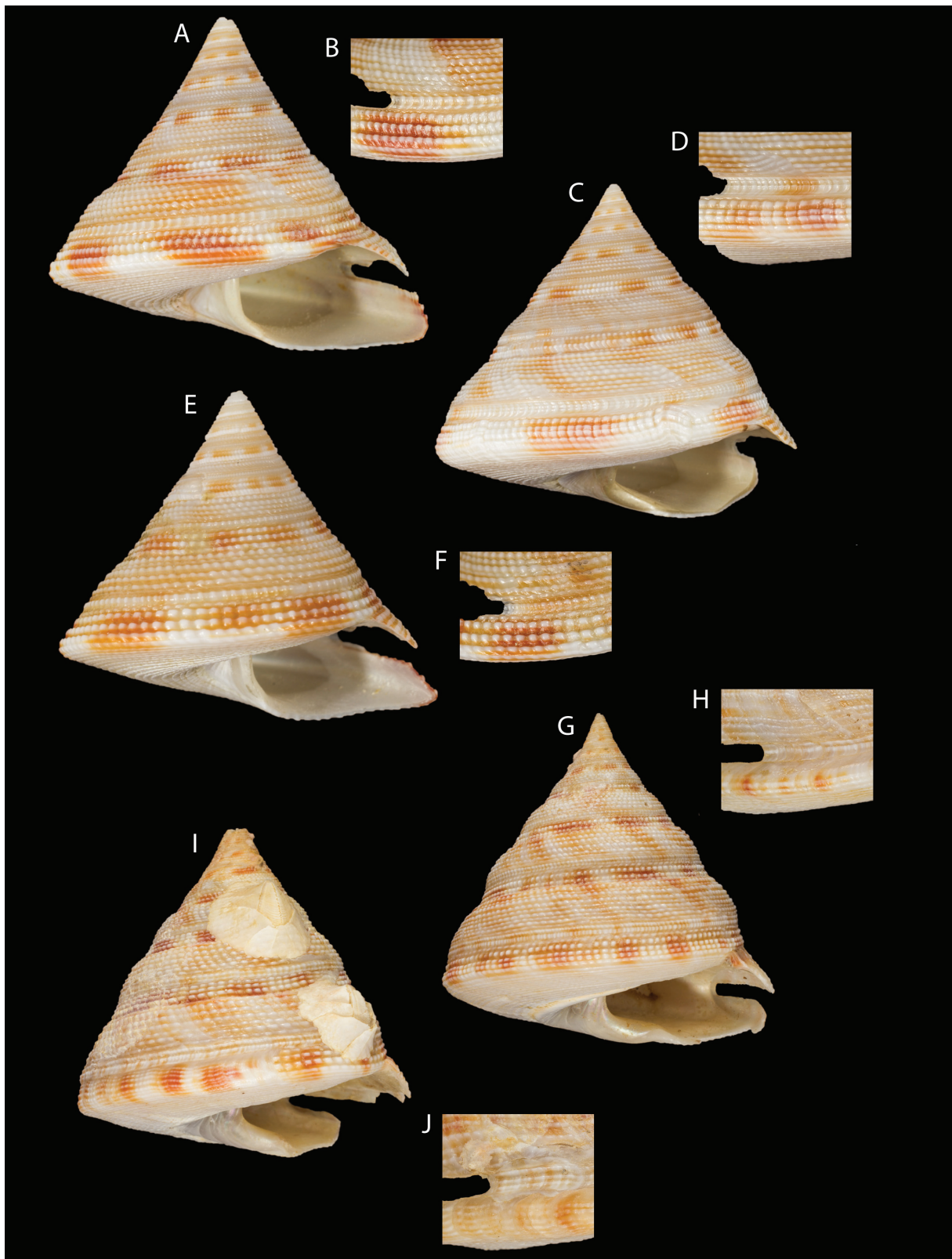
Norfolk Ridge, Munida Bank, 22°59' S, 168°21' E, 320–390 m (TERRASSES sta. DW3101).

### Description (holotype)

Shell of medium size, solid, thick, general profile rather conical, with weakly convex, rather straight-sided whorls, with a diameter a little smaller than its height (H/D ratio = 1.08), numbering 10.5 teleoconch whorls, with a mean spire angle of 65° with weakly impressed suture, whorl surface dull. Protoconch glassy, rather obtusely depressed. Teleoconch with heavily beaded spiral cords very early on. Dominant



**Fig. 3.** *Peretrochus wareni* sp. nov., MNHN-IM-2007-36460, holotype (H = 50.3 mm). **A–D.** Teleoconch. **E.** Slit. **F.** Protoconch.



**Fig. 4.** *Perotrochus wareni* sp. nov., paratypes. **A–B.** MNHN-IM-2007-34680 (H = 28.2 mm). **C–D.** MNHN-IM-2007-34684 (H = 43.8 mm). **E–F.** MNHN-IM-2007-34685 (H = 21.5 mm). **G–H.** MNHN-IM-2007-36456 (H = 55.1 mm). **I–J.** MNHN-IM-2007-36461 (H = 48.8 mm).

teleoconch sculpture consisting of finely but strongly beaded spiral cords, intersecting less marked axial riblets. Periphery of basal disc crenulated due to a strongly marked spiral cord running at edge of disc. On last whorl, 13 spiral cords above selenizone, 4 spiral cords below, and 2 major cords in the selenizone itself. Slit short, about  $\frac{1}{7}$ <sup>th</sup> the circumference of last whorl, situated below midwhorl, and very narrow. Aperture rectangularly depressed. Basal disc rather flat, depressed in its center and sharply edged at its periphery, with a very wide (extending over 40% of base diameter) callus pad which is finely ridged radially. Inside aperture, inner slit lips only partially covered by nacre, leaving a V-shaped area uncovered (approximately 25% of surface of inner slit lip extremity in aperture uncovered by nacre, showing only porcellaneous layer). Nacre coverage thick, no surface sculpture showing through it. Background color yellowish beige, with some faint axial orange-red flammulations, not really arranged into a distinct checker-board pattern; basal disc of same colour, with some faint orange axial flammulation reaching only to basal disc edge. Operculum small, multispiral, circular, light yellowish.

### Measurements

Maximum basal diameter (D) 46.75 mm, minimum diameter 43.9 mm. Height (H) 50.27 mm. H/D = 1.08. Length of slit at upper margin 26.7 mm, at lower margin 16.2 mm. Slit width: 1.6 mm; slit length:  $\frac{1}{6.51}$ <sup>th</sup> of circumference of last whorl. Weight of empty shell 26.3 g.

### Discussion

One of the distinctive shell characters separating *Perotrochus wareni* sp. nov. from *P. caledonicus* is the well-marked beading on the teleoconch spiral cords, visible also on the earlier whorls, giving it at first glance its typical pustulose or granular appearance. The intensity of the beading varies between specimens, leading to “heavily beaded”/“very pustulose” specimens and to “weakly beaded” / “light pustulose” specimens, with all different intergrades. This variability may reflect environmental conditions, as the beading intensity is generally stable within one haul / lot and varies between hauls / lots. Leaving aside beading intensity, shell characters are quite stable in *P. wareni* sp. nov. The general profile of the teleoconch, the outline of the aperture, the selenizone and slit width, and the extension of the callus on the basal disc, all show consistent differences between *P. wareni* sp. nov., *P. caledonicus* and *P. pseudogranulosus* sp. nov. (Table 2). *Perotrochus wareni* sp. nov. also bears some resemblance to *P. gotoi* Anseeuw, 1990, and, in fact, a specimen of the granulated *P. “cfr. caledonicus”* ([i.e., *P. wareni* sp. nov.) had been used for comparison at the time of its original description (Anseeuw 1990). *Perotrochus wareni* sp. nov. can be separated from *P. gotoi* by its somewhat shorter slit length ( $\frac{1}{6.51}$ <sup>th</sup> of basal diameter in *wareni* sp. nov. vs  $\frac{1}{6}$ <sup>th</sup> in *gotoi*), the larger number of spiral cords on adult specimens, the more irregularly banded checkerboard colour pattern in the area below the selenizone, the heavier and thicker shell (around 60–70% heavier at comparable shell sizes), the less extensive area uncovered by the nacreous layer inside the apertural inner slit lip extremities, and the umbilical callus occupying a much larger surface on the basal disc (45% in *P. wareni* sp. nov. vs 28% in *P. gotoi*). The two species, however, share (also with *Mikadotrochus salmianus* (Rolle, 1899) the nacreous coverage of the inner slit lips in the aperture, a feature that separates them from *Perotrochus caledonicus* s.s. and *P. pseudogranulosus* sp. nov. (Table 2, Figs 3–4, 7). Other features, like a deeper, more intense colour pattern on the teleoconch and basal disc, fine microgranulosity on the spiral cords, a thin, light shell, and a more lustrous shell surface, further separate *Perotrochus pseudogranulosus* sp. nov. from *P. wareni* sp. nov. (Table 2, Figs 3–6).



*Petrotrochus pseudogranulosus* sp. nov.

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Figs 1D, 5A–F, 6A–J

**Etymology**

The specific epithet emphasizes the beaded spiral sculpture of the species.

**Material examined**

40 lots comprising 84 specimens (Table 1).

**Type material**

**Holotype**

NEW CALEDONIA: a sequenced specimen, MNHN-IM-2009-7495.

**Paratypes**

NEW CALEDONIA: MNHN-IM-2007-32058 (Fig. 6A–B); MNHN-IM-2007-32066 (Fig. 6C–D); MNHN-IM-2009-7485 (Fig. 6E–F); MNHN-IM-2009-7491 (Fig. 6G–H); MNHN-IM-2009-7493 (Fig. 6I–J).

**Type locality**

Coral Sea, Capel Bank, 24°45' S, 159°42' E, 348–354 m (EBISCO sta. CP2494).

**Description** (holotype)

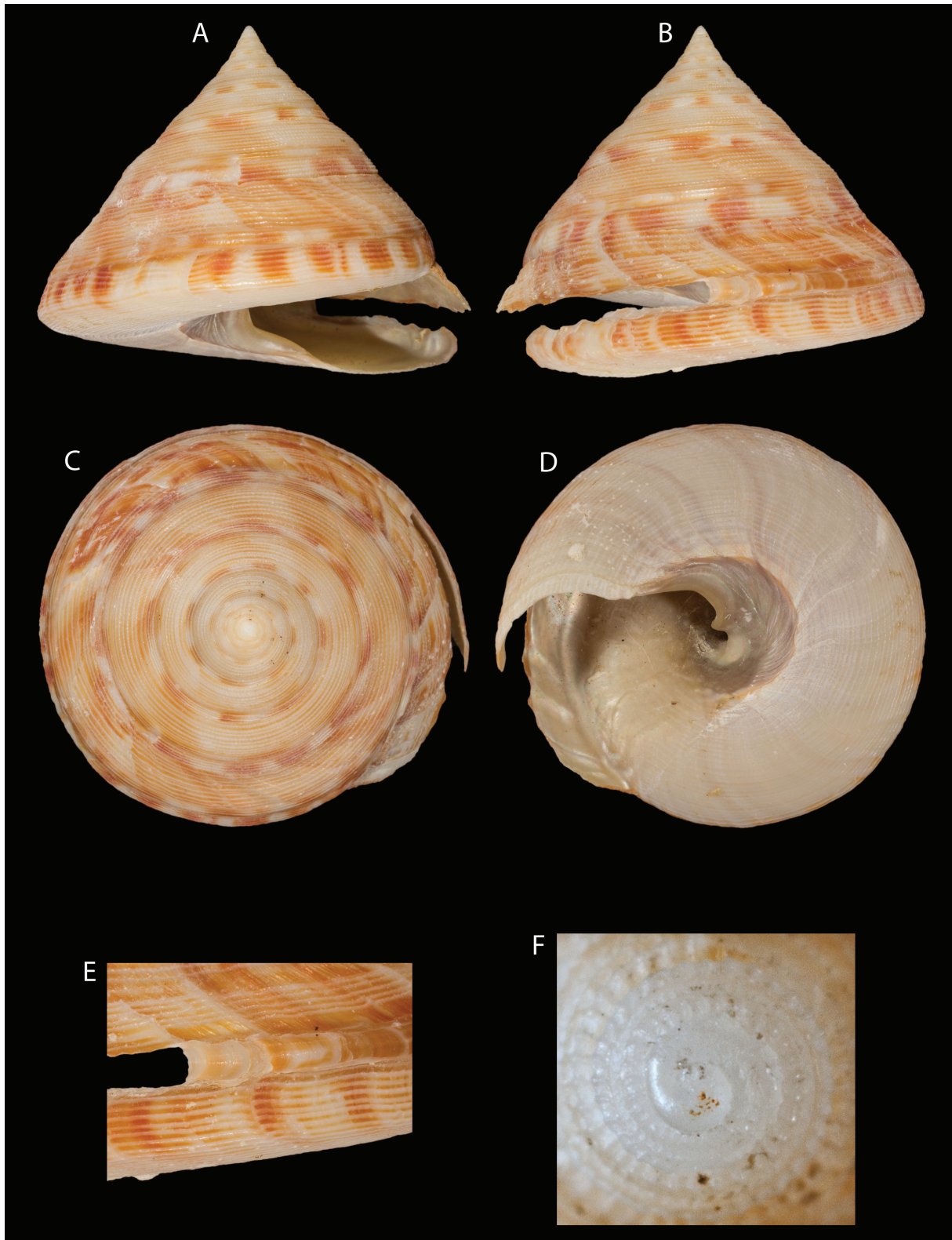
Shell of medium size, light, thin, general profile rather conical, with weakly convex to straight-sided whorls with weakly impressed suture, diameter significantly exceeding height ( $H/D = 0.78$ ), numbering 8 teleoconch whorls, with a mean spire angle of  $80^\circ$ . Protoconch ivory white, depressed. Dominant sculpture of teleoconch consisting of numerous lightly beaded spiral cords, with microsculptural pattern of fine radiating threads, giving the entire whorl surface a shiny metallic luster. On last whorl, 11 spiral cords above selenizone, 7 below and 3 major cords in the selenizone itself. Slit long, about  $\frac{1}{5}$ <sup>th</sup> the circumference of the last whorl, situated below midwhorl, and rather narrow. Aperture depressed. Basal disc rather flattened, with angular edge, with a relatively narrow (extending over 30% of base diameter) light nacreous callus pad which is finely ridged radially and ends in a raised porcellaneous edge. Inside the aperture inner slit lips nearly completely covered by nacre, leaving a narrow area (approximately 15% of the surface) parallel to the inner slit lips uncovered, showing only porcellaneous layer. Background colour yellowish beige, with intense reddish crimson colour markings arranged in very regular checkerboard pattern, overall reinforcing color intensity; basal disc showing some contrasting reddish crimson flammulations, particularly visible at its periphery, and more yellowish tan towards the center. Operculum small, multispiral, circular, light yellowish (fallen off/missing in holotype).

**Measurements**

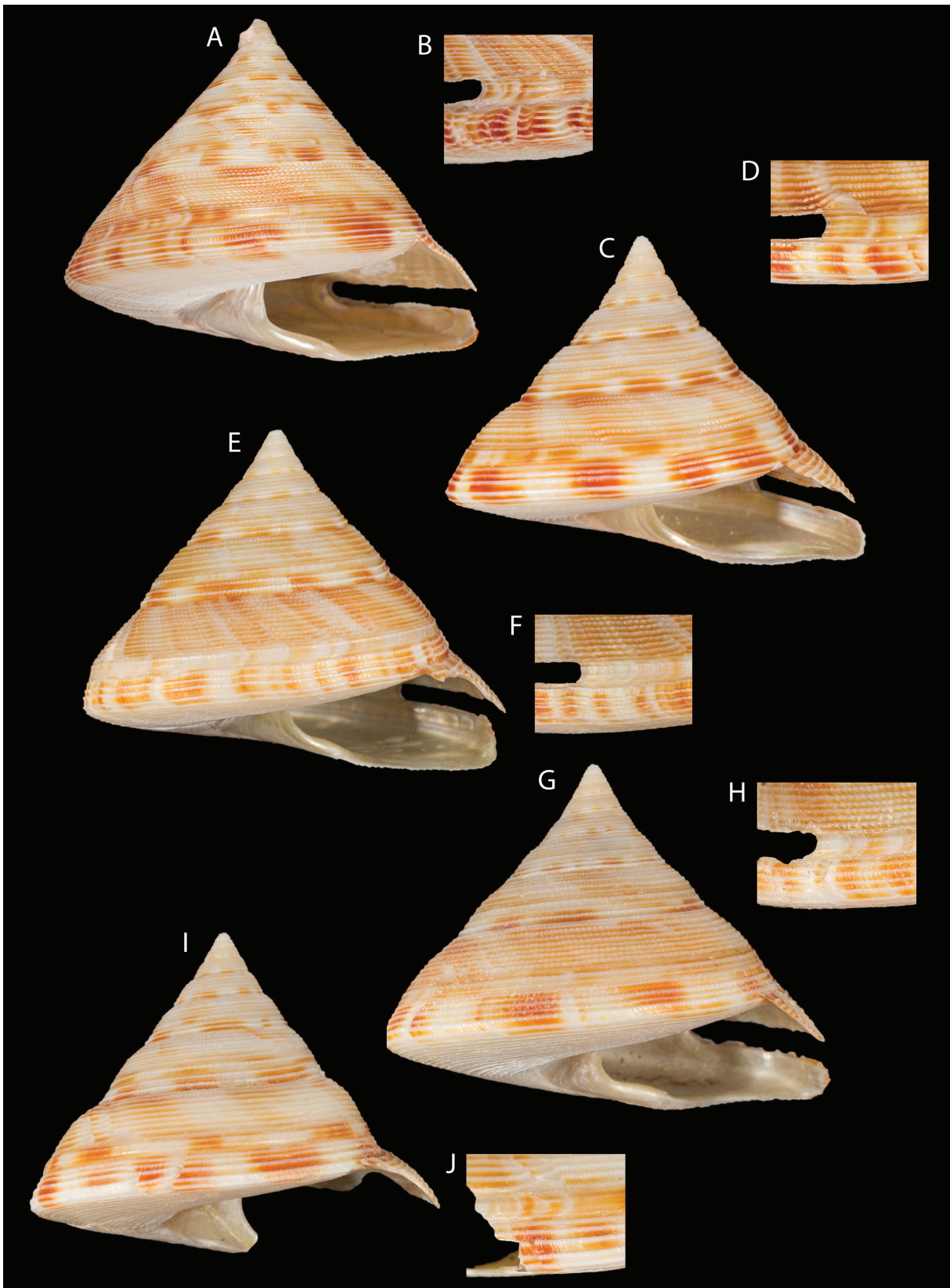
Maximum basal diameter (D) 64.9 mm, minimum diameter 59.1 mm. Height (H) 50.7 mm.  $H/D = 0.78$ . Depth of slit at upper margin 42.1 mm, depth of slit at lower margin 26.9 mm. Slit width 3.1 mm. Slit length:  $\frac{1}{5.64}$ <sup>th</sup> of circumference of last whorl. Weight of empty shell 42.6 g.

**Discussion**

*Petrotrochus pseudogranulosus* sp. nov. most closely resembles *P. caledonicus* (Fig. 7) at first glance, but is distinguished by its more conical and higher shell, a more flattened basal disc profile and a more intense and regular checkerboard colour pattern and more lustrous shell surface. It differs from *P. wareni* sp. nov. by its weakly beaded spiral cords with a microsculpture of fine radiating threads, its more intensely



**Fig. 5.** *Peretrochus pseudogranulosus* sp. nov., MNHN-IM-2009-7495, holotype (H = 54.3 mm). A–D. Teleoconch. E. Slit. F. Protoconch.



**Fig. 6.** *Perotrochus pseudogramulosus* sp. nov., paratypes. **A–B.** MNHN-IM-2007-32058 (H = 53 mm). **C–D.** MNHN-IM-2007-32066 (H = 29.8 mm). **E–F.** MNHN-IM-2009-7485 (H = 42.1 mm). **G–H.** MNHN-IM-2009-7491 (H = 36 mm). **I–J.** MNHN-IM-2009-7493 (H = 32.1 mm).

marked checkerboard colour pattern, with metallic luster, a much longer slit and a much smaller callus pad area on the basal disc. Finally, it differs from *P. deforgesii* (Fig. 7), the only other species occurring in the Coral Sea, by its general outline which is distinctly higher conical, its thin shell, its more intense checkerboard colour markings, its less granular spiral cords and smaller callus pad coverage on the basal disc.

Some specimens of *P. pseudogranulosus* sp. nov. have over the years turned up in the shell trade as “*P. cfr. caledonicus*”, supposedly originating from NW Australia or even from the South China Sea (Anseeuw & Goto 1996). However, based on the lack of precise and trustworthy locality data, the lack of more recent confirmation of those alleged findings and, most of all, the general unavailability of such material for study, we reject these localities as intentionally or unintentionally unproven and unverifiable.

## Discussion

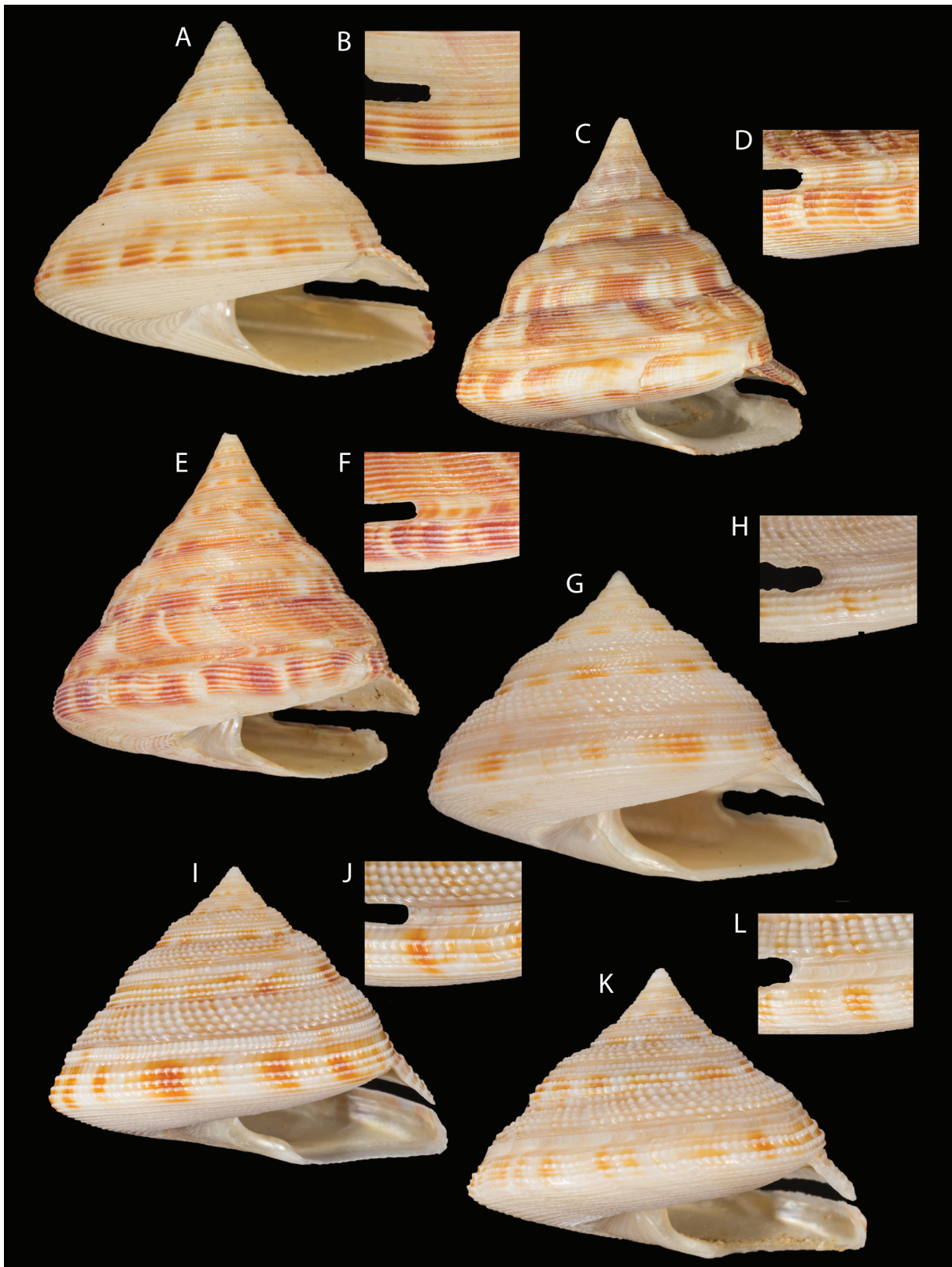
The geographical distribution within the New Caledonia region (Fig. 1) is different for the four species. Many samples of *Perotrochus caledonicus* s.s. originate from the SW off Ile des Pins, southern New Caledonia, with scattered specimens from Norfolk Ridge, the Loyalty Ridge and the Far North of New Caledonia (Grand Passage); the average depth of occurrence, based on 135 lots, is 407 meters. The distribution of *Perotrochus wareni* sp. nov. includes Norfolk Ridge, the Loyalty Ridge, the Far North of New Caledonia (Grand Passage) and the Lansdowne Plateau in the Coral Sea; the average depth of occurrence, based on 73 lots, is 344 meters. *Perotrochus caledonicus* and *P. wareni* sp. nov. thus co-occur locally in the south of New Caledonia, Norfolk Ridge and Grand Passage, where they have different bathymetric preferences, although they were sometimes found at the same stations (LITHIST sta. CP14 and sta. CP16; NORFOLK1 sta. DW1658 and sta. DW1709; MUSORSTOM4 sta. DW222; TERRASSES sta. DW3101 and sta. DW3110). *Perotrochus pseudogranulosus* sp. nov. has a distribution restricted to the Chesterfield Plateau, with a mean depth of 360 meters based on 40 lots. *Perotrochus deforgesii* is also restricted to the Coral Sea, but occurs only on the Bellona Plateau and Capel Bank, thus allopatrically with regard to *P. pseudogranulosus* sp. nov., but at similar depths (mean depth of 380 meters based on 36 lots).

The morphological, molecular and microdistribution data, thus all converge to support the conclusion that there are four small *Perotrochus* in the New Caledonia region, of which two have been described as new in the present paper.

At genus level, although Anseeuw & Poppe (2005) and Aktipis & Giribet (2010) had used the combinations *Mikadotrochus caledonicus* and *M. deforgesii*, the molecular phylogeny shows that *Perotrochus caledonicus* and *P. deforgesii* are not congeneric with *Pleurotomaria beyrichii* Hilgendorf, 1877, the type species of *Mikadotrochus* Lindholm, 1927. However, the tree also shows that the four small New Caledonia *Perotrochus* do not form a monophyletic group with *Pleurotomaria quoyana* P. Fischer & Bernardi, 1856, the type species of *Perotrochus* P. Fischer, 1885. *Perotrochus quoyanus* is a species from the western Atlantic, and the species (*P. amabilis* (Bayer, 1963), *P. maureri* Harasewych & Askew, 1993, *P. lucaya* Bayer, 1965) that cluster with it in the tree are also from the western Atlantic. It thus appears that, although they are traditionally placed in *Perotrochus* (e.g., Anseeuw & Goto 1996; Harasewych 2002), the small pleurotomariids from the Pacific are not congeneric with true *Perotrochus* from the western Atlantic, and a new genus will have to be established to classify them.

## Acknowledgments

The material on which this paper is based has been accumulated during many expeditions of the *Tropical Deep-Sea Benthos* programme in the New Caledonia region. We refer to Bouchet *et al.* (2008) for an



**Fig. 7.** A–F. *Petrotrochus caledonicus* Bouchet & Métivier, 1982. A–B. MNHN-IM-2000-1262, holotype (H = 31.2 mm). C–D. MNHN-IM-2007-36300 (H = 51.2 mm). E–F. MNHN-IM-2007-36301 (H = 47.5 mm). — G–L. *Petrotrochus deforgesii* Métivier, 1990. G–H. MNHN-IM-2000-1391, holotype (H = 33.9 mm). I–J. MNHN-IM-2007-32062 (H = 33.7 mm). K–L. MNHN-IM-2007-32085 (H = 25.1 mm).

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**Table 1.** List of specimens.

MNHN ID	N	SPECIES	MNHN EXPEDITION	STATION	GENERAL AREA	COORDINATES; DEPTH (m)	BOLD ID	GENBANK #
IM-2000-1262	1	<i>P. caledonicus</i>	VAUBAN	DR15		22°49'S, 167°12'E; 390-395		
IM-2000-1324	2	<i>P. deforgesii</i>	CHALCAL 1	DC32	Chesterfield	19°43'S, 158°33'E; 350		
IM-2000-1361	1	<i>P. deforgesii</i>	MUSORSTOM 5	DW337	Chesterfield	19°54'S, 158°38'E; 412-430		
IM-2000-1387	2	<i>P. caledonicus</i>	VAUBAN	DR15		22°49'S, 167°12'E; 390-395		
IM-2000-1389	1	<i>P. deforgesii</i>	MUSORSTOM 5	DC361	Chesterfield	19°52'S, 158°38'E; 400		
IM-2007-32054	1	<i>P. pseudogranulosus</i>	EBISCO	DW2530	S Nova Bank	22°48'S, 159°23'E; 338-343	PLERO010-15	KR087206
IM-2007-32055	1	<i>P. pseudogranulosus</i>	EBISCO	DW2530	S Nova Bank	22°48'S, 159°23'E; 338-343		
IM-2007-32056	1	<i>P. pseudogranulosus</i>	EBISCO	DW2530	S Nova Bank	22°48'S, 159°23'E; 338-343	PLERO011-15	KR087205
IM-2007-32057	1	<i>P. pseudogranulosus</i>	EBISCO	DW2530	S Nova Bank	22°48'S, 159°23'E; 338-343		
IM-2007-32058	1	<i>P. pseudogranulosus</i>	EBISCO	DW2501	Capel Bank	24°50'S, 159°51'E; 325-520	PLERO058-15	KR087194
IM-2007-32059	1	<i>P. wareni</i>	EBISCO	DW2631	S Lansdowne	21°03'S, 160°44'E; 372-404		
IM-2007-32060	1	<i>P. deforgesii</i>	EBISCO	DW2577	N Bellona	20°20'S, 158°39'E; 399-602	PLERO012-15	KR087218
IM-2007-32061	1	<i>P. deforgesii</i>	EBISCO	DW2577	N Bellona	20°20'S, 158°39'E; 399-602	PLERO002-15	KR087208
IM-2007-32062	1	<i>P. deforgesii</i>	EBISCO	CP2567	NW Bellona	20°20'S, 158°42'E; 395-400	PLERO013-15	KR087217
IM-2007-32063	1	<i>P. deforgesii</i>	EBISCO	CP2593	Chesterfield	19°43'S, 158°32'E; 300-323	PLERO014-15	KR087216
IM-2007-32064	1	<i>P. pseudogranulosus</i>	EBISCO	DW2526	S Nova Bank	22°46'S, 159°23'E; 330-340	PLERO015-15	KR087193
IM-2007-32065	1	<i>P. pseudogranulosus</i>	EBISCO	DW2526	S Nova Bank	22°46'S, 159°23'E; 330-340		
IM-2007-32066	1	<i>P. pseudogranulosus</i>	EBISCO	DW2526	S Nova Bank	22°46'S, 159°23'E; 330-340	PLERO016-15	KR087204
IM-2007-32067	1	<i>P. pseudogranulosus</i>	EBISCO	DW2525	S Nova Bank	22°48'S, 159°23'E; 408-410	PLERO017-15	KR087203
IM-2007-32068	1	<i>P. wareni</i>	EBISCO	DW2634	S Lansdowne	21°05'S, 160°46'E; 342-347		
IM-2007-32069	1	<i>P. wareni</i>	EBISCO	DW2634	S Lansdowne	21°05'S, 160°46'E; 342-347		
IM-2007-32070	1	<i>P. pseudogranulosus</i>	EBISCO	DW2525	S Nova Bank	22°48'S, 159°23'E; 408-410		
IM-2007-32071	1	<i>P. pseudogranulosus</i>	EBISCO	DW2525	S Nova Bank	22°48'S, 159°23'E; 408-410		
IM-2007-32072	1	<i>P. pseudogranulosus</i>	EBISCO	DW2528	S Nova Bank	22°49'S, 159°23'E; 320-345		
IM-2007-32073	1	<i>P. pseudogranulosus</i>	EBISCO	DW2528	S Nova Bank	22°49'S, 159°23'E; 320-345		
IM-2007-32074	1	<i>P. pseudogranulosus</i>	EBISCO	DW2528	S Nova Bank	22°49'S, 159°23'E; 320-345		
IM-2007-32075	1	<i>P. pseudogranulosus</i>	EBISCO	DW2528	S Nova Bank	22°49'S, 159°23'E; 320-345		
IM-2007-32076	1	<i>P. pseudogranulosus</i>	EBISCO	CP2529	S Nova Bank	22°47'S, 159°23'E; 330-340		
IM-2007-32077	1	<i>P. pseudogranulosus</i>	EBISCO	CP2529	S Nova Bank	22°47'S, 159°23'E; 330-340		
IM-2007-32078	1	<i>P. pseudogranulosus</i>	EBISCO	CP2529	S Nova Bank	22°47'S, 159°23'E; 330-340		
IM-2007-32079	1	<i>P. pseudogranulosus</i>	EBISCO	CP2529	S Nova Bank	22°47'S, 159°23'E; 330-340		
IM-2007-32080	1	<i>P. pseudogranulosus</i>	EBISCO	CP2529	S Nova Bank	22°47'S, 159°23'E; 330-340		
IM-2007-32081	1	<i>P. pseudogranulosus</i>	EBISCO	CP2529	S Nova Bank	22°47'S, 159°23'E; 330-340		
IM-2007-32082	1	<i>P. pseudogranulosus</i>	EBISCO	CP2529	S Nova Bank	22°47'S, 159°23'E; 330-340		
IM-2007-32083	1	<i>P. deforgesii</i>	EBISCO	CP2593	Chesterfield	19°43'S, 158°32'E; 300-323	PLERO004-15	KR087207
IM-2007-32084	1	<i>P. deforgesii</i>	EBISCO	CP2593	Chesterfield	19°43'S, 158°32'E; 300-323		
IM-2007-32085	1	<i>P. deforgesii</i>	EBISCO	CP2593	Chesterfield	19°43'S, 158°32'E; 300-323	PLERO005-15	KR087215
IM-2007-32086	1	<i>P. deforgesii</i>	EBISCO	CP2593	Chesterfield	19°43'S, 158°32'E; 300-323		
IM-2007-32087	1	<i>P. deforgesii</i>	EBISCO	CP2593	Chesterfield	19°43'S, 158°32'E; 300-323	PLERO006-15	KR087214
IM-2007-32088	1	<i>P. deforgesii</i>	EBISCO	CP2593	Chesterfield	19°43'S, 158°32'E; 300-323	PLERO007-15	KR087213
IM-2007-32089	1	<i>P. deforgesii</i>	EBISCO	CP2593	Chesterfield	19°43'S, 158°32'E; 300-323		
IM-2007-32090	1	<i>P. deforgesii</i>	EBISCO	CP2593	Chesterfield	19°43'S, 158°32'E; 300-323	PLERO008-15	KR087212
IM-2007-32091	1	<i>P. deforgesii</i>	EBISCO	CP2593	Chesterfield	19°43'S, 158°32'E; 300-323	PLERO009-15	KR087211



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MNHN ID	N	SPECIES	MNHN EXPEDITION	STATION	GENERAL AREA	COORDINATES; DEPTH (m)	BOLD ID	GENBANK #
IM-2007-34677	1	<i>P. wareni</i>	CONCALIS	DW2946	Grand Passage	19°02'S, 163°27'E; 276-277	PLERO024-15	KR087219
IM-2007-34678	1	<i>P. wareni</i>	CONCALIS	DW2946	Grand Passage	19°02'S, 163°27'E; 276-277		
IM-2007-34679	1	<i>P. wareni</i>	CONCALIS	DW3025	Grand Passage	18°57'S, 163°23'E; 396-400		
IM-2007-34680	1	<i>P. wareni</i>	CONCALIS	DW2944	Grand Passage	18°59'S, 163°24'E; 320-335	PLERO025-15	KR087228
IM-2007-34681	1	<i>P. wareni</i>	CONCALIS	DW2949	Grand Passage	19°00'S, 163°28'E; 261-272		
IM-2007-34682	1	<i>P. wareni</i>	CONCALIS	DW3024	Grand Passage	18°57'S, 163°22'E; 349-370	PLERO018-15	KR087224
IM-2007-34683	1	<i>P. wareni</i>	CONCALIS	DW2941	Grand Passage	19°3'S, 163°27'E; 271-272		
IM-2007-34684	1	<i>P. wareni</i>	CONCALIS	DW2973	Grand Passage	18°14'S, 163°06'E; 275-288	PLERO019-15	KR087223
IM-2007-34685	1	<i>P. wareni</i>	CONCALIS	DW2943	Grand Passage	18°57'S, 163°23'E; 380-430	PLERO020-15	KR087222
IM-2007-34686	1	<i>P. wareni</i>	CONCALIS	DW2973	Grand Passage	18°14'S, 163°06'E; 275-288	PLERO021-15	KR087221
IM-2007-34687	1	<i>P. wareni</i>	CONCALIS	DW2974	Grand Passage	18°15'S, 163°06'E; 283-326		
IM-2007-34688	1	<i>P. wareni</i>	CONCALIS	CP2975	Grand Passage	18°15'S, 163°06'E; 297-316	PLERO022-15	KR087220
IM-2007-34689	1	<i>P. wareni</i>	CONCALIS	DW2977	Grand Passage	18°15'S, 163°07'E; 326-368		
IM-2007-34690	1	<i>P. wareni</i>	CONCALIS	DW2977	Grand Passage	18°15'S, 163°07'E; 326-368	PLERO023-15	KR087229
IM-2007-34691	1	<i>P. wareni</i>	CONCALIS	DW2977	Grand Passage	18°15'S, 163°07'E; 326-368		
IM-2007-36300	1	<i>P. caledonicus</i>	TERRASSES	DW3101	Norfolk Ridge	22°59'S, 168°21'E; 320-390	PLERO044-15	KR087186
IM-2007-36301	1	<i>P. caledonicus</i>	TERRASSES	DW3075	Norfolk Ridge	23°17'S, 168°14'E; 270	PLERO040-15	KR087190
IM-2007-36302	1	<i>P. caledonicus</i>	TERRASSES	DW3075	Norfolk Ridge	23°17'S, 168°14'E; 270	PLERO041-15	KR087189
IM-2007-36303	1	<i>P. caledonicus</i>	TERRASSES	DW3035	Loyalty Ridge	22°41'S, 168°56'E; 790-800	PLERO038-15	KR087192
IM-2007-36304	1	<i>P. caledonicus</i>	TERRASSES	DW3035	Loyalty Ridge	22°41'S, 168°56'E; 790-800		
IM-2007-36455	1	<i>P. caledonicus</i>	TERRASSES	DW3075	Norfolk Ridge	23°17'S, 168°14'E; 270	PLERO042-15	KR087188
IM-2007-36456	1	<i>P. wareni</i>	TERRASSES	DW3101	Norfolk Ridge	22°59'S, 168°21'E; 320-390	PLERO045-15	KR087227
IM-2007-36457	1	<i>P. caledonicus</i>	TERRASSES	DW3075	Norfolk Ridge	23°17'S, 168°14'E; 270		
IM-2007-36458	1	<i>P. caledonicus</i>	TERRASSES	DW3073	Norfolk Ridge	23°17'S, 168°14'E; 250-270	PLERO039-15	KR087191
IM-2007-36459	1	<i>P. caledonicus</i>	TERRASSES	DW3076	Norfolk Ridge	23°14'S, 168°13'E; 390-570	PLERO043-15	KR087187
IM-2007-36460	1	<i>P. wareni</i>	TERRASSES	DW3101	Norfolk Ridge	22°59'S, 168°21'E; 320-390	PLERO046-15	KR087226
IM-2007-36461	1	<i>P. wareni</i>	TERRASSES	DW3101	Norfolk Ridge	22°59'S, 168°21'E; 320-390	PLERO047-15	KR087225
IM-2007-36462	1	<i>P. wareni</i>	TERRASSES	DW3101	Norfolk Ridge	22°59'S, 168°21'E; 320-390		
IM-2007-36463	1	<i>P. caledonicus</i>	TERRASSES	DW3110	Norfolk Ridge	23°02'S, 168°16'E; 270-310	PLERO048-15	KR087182
IM-2007-36505	1	<i>P. caledonicus</i>	TERRASSES	DW3127	Ile des Pins	23°00'S, 167°16'E; 400-420	PLERO052-15	KR087178
IM-2007-36519	1	<i>P. caledonicus</i>	TERRASSES	DW3127	Ile des Pins	23°00'S, 167°16'E; 400-420	PLERO053-15	KR087177
IM-2007-36525	1	<i>P. caledonicus</i>	TERRASSES	DW3123	Ile des Pins	22°53'S, 167°13'E; 420-450		
IM-2007-36541	1	<i>P. caledonicus</i>	TERRASSES	DW3122	Ile des Pins	22°47'S, 167°12'E; 390-410	PLERO034-15	KR087185
IM-2007-36542	1	<i>P. caledonicus</i>	TERRASSES	DW3122	Ile des Pins	22°47'S, 167°12'E; 390-410	PLERO049-15	KR087181
IM-2007-36545	1	<i>P. caledonicus</i>	TERRASSES	DW3124	Ile des Pins	22°54'S, 167°15'E; 460		
IM-2007-36546	1	<i>P. caledonicus</i>	TERRASSES	DW3123	Ile des Pins	22°53'S, 167°13'E; 420-450	PLERO051-15	KR087179
IM-2007-36557	1	<i>P. caledonicus</i>	TERRASSES	DW3122	Ile des Pins	22°47'S, 167°12'E; 390-410	PLERO050-15	KR087180
IM-2007-36577	1	<i>P. caledonicus</i>	TERRASSES	DW3127	Ile des Pins	23°00'S, 167°16'E; 400-420		
IM-2007-36592	1	<i>P. caledonicus</i>	TERRASSES	CP3048	Norfolk Ridge	23°44'S, 168°16'E; 380-400	PLERO035-15	KR087173
IM-2007-36595	1	<i>P. caledonicus</i>	TERRASSES	DW3127	Ile des Pins	23°00'S, 167°16'E; 400-420	PLERO054-15	KR087176
IM-2007-36596	1	<i>P. caledonicus</i>	TERRASSES	CP3052	Norfolk Ridge	23°49'S, 168°16'E; 500-800	PLERO037-15	KR087171
IM-2007-36822	1	<i>P. caledonicus</i>	TERRASSES	CP3049	Norfolk Ridge	23°42'S, 168°16'E; 380-410	PLERO036-15	KR087172
IM-2009-7476	1	<i>P. caledonicus</i>	NORFOLK 2	DW2156	Ile des Pins	22°54'S, 167°15'E; 468-500	PLERO003-15	KR087183
IM-2009-7477	1	<i>P. caledonicus</i>	NORFOLK 2	DW2156	Ile des Pins	22°54'S, 167°15'E; 468-500		
IM-2009-7478	1	<i>P. caledonicus</i>	NORFOLK 2	DW2156	Ile des Pins	22°54'S, 167°15'E; 468-500	PLERO001-15	KR087174

MNHN ID	N	SPECIES	MNHN EXPEDITION	STATION	GENERAL AREA	COORDINATES; DEPTH (m)	BOLD ID	GENBANK #
IM-2009-7479	1	<i>P. caledonicus</i>	NORFOLK 2	DW2156	Ile des Pins	22°54'S, 167°15'E; 468-500		
IM-2009-7480	1	<i>P. caledonicus</i>	NORFOLK 2	DW2156	Ile des Pins	22°54'S, 167°15'E; 468-500	PLERO059-15	KR087184
IM-2009-7481	1	<i>P. caledonicus</i>	NORFOLK 2	DW2156	Ile des Pins	22°54'S, 167°15'E; 468-500		
IM-2009-7482	1	<i>P. caledonicus</i>	NORFOLK 2	DW2156	Ile des Pins	22°54'S, 167°15'E; 468-500		
IM-2009-7483	1	<i>P. caledonicus</i>	NORFOLK 2	DW2156	Ile des Pins	22°54'S, 167°15'E; 468-500	PLERO055-15	KR087175
IM-2009-7485	1	<i>P. pseudogranulosus</i>	EBISCO	DW2528	S Nova Bank	22°49'S, 159°23'E; 320-345	PLERO026-15	KR087202
IM-2009-7486	2	<i>P. deforgesii</i>	EBISCO	CP2593	Chesterfield	19°43'S, 158°32'E; 300-323	PLERO056-15	KR087210
IM-2009-7487	1	<i>P. pseudogranulosus</i>	EBISCO	CP2529	S Nova Bank	22°47'S, 159°23'E; 330-340	PLERO027-15	KR087201
IM-2009-7488	1	<i>P. pseudogranulosus</i>	EBISCO	CP2529	S Nova Bank	22°47'S, 159°23'E; 330-340	PLERO028-15	KR087200
IM-2009-7489	1	<i>P. pseudogranulosus</i>	EBISCO	DW2526	S Nova Bank	22°46'S, 159°23'E; 330-340	PLERO029-15	KR087199
IM-2009-7490	1	<i>P. deforgesii</i>	EBISCO	CP2567	NW Bellona	20°20'S, 158°42'E; 395-400		
IM-2009-7491	1	<i>P. pseudogranulosus</i>	EBISCO	DW2525	S Nova Bank	22°48'S, 159°23'E; 408-410	PLERO030-15	KR087198
IM-2009-7492	1	<i>P. pseudogranulosus</i>	EBISCO	DW2526	S Nova Bank	22°46'S, 159°23'E; 330-340	PLERO031-15	KR087197
IM-2009-7493	1	<i>P. pseudogranulosus</i>	EBISCO	DW2530	S Nova Bank	22°48'S, 159°23'E; 338-343	PLERO057-15	KR087195
IM-2009-7494	1	<i>P. deforgesii</i>	EBISCO	DW2608	Chesterfield	19°33'S, 158°40'E; 393-396	PLERO032-15	KR087209
IM-2009-7495	1	<i>P. pseudogranulosus</i>	EBISCO	CP2494	Capel Bank	24°45'S, 159°42'E; 348-354	PLERO033-15	KR087196
IM-2009-7496	1	<i>P. pseudogranulosus</i>	EBISCO	DW2501	Capel Bank	24°50'S, 159°51'E; 325-520		
IM-2009-7497	1	<i>P. caledonicus</i>	NORFOLK 2	DW2031	Stylaster Bank	23°39'S, 167°44'E; 440		
IM-2010-11117	7	<i>P. caledonicus</i>	SMIB 8	DW197-199	Ile des Pins	22°51'–22°52'S, 168°12'–168°13'E; 408-436		
IM-2010-11118	1	<i>P. caledonicus</i>	SMIB 8	DW185	Antigonia Bank	23°15'S, 168°04'E; 311-355		
IM-2010-11119	27	<i>P. caledonicus</i>	LITHIST	CP16	Jumeau Ouest Bank	23°43'S, 168°16'E; 379-391		
IM-2010-11120	1	<i>P. caledonicus</i>	LITHIST	DW13	Jumeau Est Bank	23°45'S, 168°17'E; 400		
IM-2010-11121	1	<i>P. pseudogranulosus</i>	EBISCO	DW2528	S Nova Bank	22°49'S, 159°23'E; 320-345		
IM-2010-11122	1	<i>P. caledonicus</i>	SMIB 2	DW05	S Ile des Pins	22°56'S, 167°15'E; 398-410		
IM-2010-11123	1	<i>P. caledonicus</i>	BIOCAL	DW38	S Ile des Pins	23°00'S, 167°15'E; 360		
IM-2010-11124	2	<i>P. caledonicus</i>	BATHUS 3	DW829	Norfolk Ridge	23°21'S, 168°02'E; 386-390		
IM-2010-11125	13	<i>P. caledonicus</i>	BATHUS 3	CP811	Norfolk Ridge	23°41'S, 168°16'E; 383-408		
IM-2010-11126	9	<i>P. caledonicus</i>	BATHUS 3	DW817	Norfolk Ridge	23°42'S, 168°16'E; 405-410		
IM-2010-11127	3	<i>P. caledonicus</i>	BATHUS 3	DW818	Norfolk Ridge	23°44'S, 168°16'E; 394-401		
IM-2010-11128	1	<i>P. caledonicus</i>	BATHUS 3	DW829	Norfolk Ridge	23°21'S, 168°02'E; 386-390		
IM-2010-11129	5	<i>P. caledonicus</i>	NORFOLK 2	CP2048	Jumeau Est Bank	23°44'S, 168°16'E; 380-389		
IM-2010-11130	4	<i>P. caledonicus</i>	NORFOLK 2	DW2049	Jumeau Est Bank	23°43'S, 168°15'E; 470-621		
IM-2010-11131	7	<i>P. caledonicus</i>	NORFOLK 2	CP2050	Jumeau Est Bank	23°42'S, 168°16'E; 377		
IM-2010-11132	2	<i>P. caledonicus</i>	NORFOLK 2	DW2052	Jumeau Est Bank	23°42'S, 168°15'E; 473-525		
IM-2010-11133	1	<i>P. caledonicus</i>	NORFOLK 2	DW2108	Jumeau Est Bank	23°47'S, 168°17'E; 403-440		
IM-2010-11134	1	<i>P. caledonicus</i>	NORFOLK 2	CP2114	Jumeau Est Bank	23°45'S, 168°17'E; 390-398		
IM-2010-11135	8	<i>P. caledonicus</i>	NORFOLK 2	CH2115	Jumeau Est Bank	23°45'S, 168°17'E; 377-401		
IM-2010-11136	2	<i>P. caledonicus</i>	NORFOLK 2	CP2118	Antigonia Bank	23°23'S, 168°01'E; 383-393		
IM-2010-11137	3	<i>P. caledonicus</i>	NORFOLK 2	DW2126	Cryphelia Bank	23°16'S, 168°14'E; 398-550		
IM-2010-11138	6	<i>P. caledonicus</i>	NORFOLK 2	DW2155	Ile des Pins	22°52'S, 167°13'E; 453-455		
IM-2010-11139	4	<i>P. caledonicus</i>	NORFOLK 2	CP2153	Ile des Pins	22°47'S, 167°12'E; 395-400		
IM-2010-11140	4	<i>P. caledonicus</i>	NORFOLK 2	DW2156	Ile des Pins	22°54'S, 167°15'E; 468-500		
IM-2010-11141	1	<i>P. caledonicus</i>	NORFOLK 2	DW2023	Brachiopode Bank	23°27'S, 167°51'E; 282-297		
IM-2010-11142	1	<i>P. caledonicus</i>	NORFOLK 2	DW2027	Brachiopode Bank	23°26'S, 167°51'E; 465-650		
IM-2010-11143	2	<i>P. wareni</i>	BATHUS 4	DW926	Grand Passage	18°57'S, 163°25'E; 325-330		

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MNHN ID	N	SPECIES	MNHN EXPEDITION	STATION	GENERAL AREA	COORDINATES; DEPTH (m)	BOLD ID	GENBANK #
IM-2010-11144	1	<i>P. wareni</i>	BATHUS 4	DW925	Grand Passage	18°55'S, 163°24'E; 370-405		
IM-2010-11145	2	<i>P. caledonicus</i>	SMIB 8	DW185	Antigonia Bank	23°15'S, 168°04'E; 311-355		
IM-2010-11146	2	<i>P. caledonicus</i>	SMIB 8	DW179	Jumeau Est Bank	23°46'S, 168°17'E; 400-405		
IM-2010-11147	14	<i>P. caledonicus</i>	SMIB 8	DW199	Ile des Pins	22°52'S, 167°12'E; 408-410		
IM-2010-11148	8	<i>P. caledonicus</i>	SMIB 8	DW197	Ile des Pins	22°52'S, 167°13'E; 414-436		
IM-2010-11149	2	<i>P. caledonicus</i>	SMIB 8	DW198	Ile des Pins	22°52'S, 167°13'E; 414-430		
IM-2010-11150	8	<i>P. caledonicus</i>	NORFOLK 1	DW1704	Norfolk Ridge	23°47'S, 168°17'E; 400-420		
IM-2010-11151	10	<i>P. caledonicus</i>	NORFOLK 1	DW1657	Norfolk Ridge	23°26'S, 167°50'E; 305-332		
IM-2010-11152	36	<i>P. caledonicus</i>	NORFOLK 1	DW1658	Norfolk Ridge	23°27'S, 167°50'E; 320-336		
IM-2010-11153	8	<i>P. caledonicus</i>	NORFOLK 1	CP1705	Norfolk Ridge	23°45'S, 168°16'E; 400-463		
IM-2010-11154	13	<i>P. caledonicus</i>	NORFOLK 1	DW1733	Norfolk Ridge	22°57'S, 167°16'E; 427-433		
IM-2010-11155	5	<i>P. caledonicus</i>	NORFOLK 1	CP1708	Norfolk Ridge	23°41'S, 168°15'E; 381-384		
IM-2010-11156	9	<i>P. caledonicus</i>	NORFOLK 1	DW1709	Norfolk Ridge	23°43'S, 168°16'E; 380-389		
IM-2010-11157	4	<i>P. caledonicus</i>	NORFOLK 1	DW1710	Norfolk Ridge	23°45'S, 168°17'E; 386-426		
IM-2010-11158	13	<i>P. caledonicus</i>	NORFOLK 1	DW1707	Norfolk Ridge	23°41'S, 168°15'E; 381-493		
IM-2010-11159	11	<i>P. caledonicus</i>	NORFOLK 1	DW1738	Norfolk Ridge	22°51'S, 167°12'E; 340-381		
IM-2010-11160	6	<i>P. caledonicus</i>	NORFOLK 1	DW1734	Norfolk Ridge	22°54'S, 167°13'E; 403-429		
IM-2010-11161	23	<i>P. caledonicus</i>	NORFOLK 1	DW1737	Norfolk Ridge	22°51'S, 167°10'E; 400		
IM-2010-11162	14	<i>P. caledonicus</i>	NORFOLK 1	DW1736	Norfolk Ridge	22°52'S, 167°12'E; 383-407		
IM-2010-11163	3	<i>P. caledonicus</i>	NORFOLK 1	DW1735	Norfolk Ridge	22°53'S, 167°13'E; 415-445		
IM-2010-11164	5	<i>P. caledonicus</i>	NORFOLK 1	DW1739	Norfolk Ridge	22°51'S, 167°14'E; 404-448		
IM-2010-11165	1	<i>P. caledonicus</i>	NORFOLK 1	CP1669	Norfolk Ridge	23°41'S, 168°01'E; 302-325		
IM-2010-11166	1	<i>P. caledonicus</i>	NORFOLK 1	CP1715	Norfolk Ridge	23°22'S, 168°03'E; 270-312		
IM-2010-11167	1	<i>P. caledonicus</i>	NORFOLK 1	DW1653	Norfolk Ridge	23°26'S, 167°51'E; 328-340		
IM-2010-11168	1	<i>P. caledonicus</i>	NORFOLK 1	CP1711	Norfolk Ridge	23°48'S, 168°17'E; 409-439		
IM-2010-11169	1	<i>P. caledonicus</i>	NORFOLK 1	DW1712	Norfolk Ridge	23°22'S, 168°03'E; 180-250		
IM-2010-11170	1	<i>P. caledonicus</i>	NORFOLK 1	CP1671	Norfolk Ridge	23°42'S, 168°01'E; 320-397		
IM-2010-11171	1	<i>P. caledonicus</i>	NORFOLK 1	DW1652	Norfolk Ridge	23°27'S, 167°51'E; 290-378		
IM-2010-11172	1	<i>P. caledonicus</i>	LITHIST	CP17	Jumeau Ouest Bank	23°41'S, 168°01'E; 247-281		
IM-2010-11173	15	<i>P. caledonicus</i>	LITHIST	CP15	Jumeau Ouest Bank	23°40'S, 168°15'E; 389-404		
IM-2010-11174	15	<i>P. caledonicus</i>	LITHIST	DW13	Jumeau Est Bank	23°45'S, 168°17'E; 400		
IM-2010-11175	21	<i>P. caledonicus</i>	LITHIST	CP14	Jumeau Ouest Bank	23°42'S, 168°16'E; 378-402		
IM-2010-11176	1	<i>P. wareni</i>	LITHIST	CP16	Jumeau Ouest Bank	23°43'S, 168°16'E; 379-391		
IM-2010-11177	1	<i>P. caledonicus</i>	TERRASSES	DW3127	Ile des Pins	23°00'S, 167°16'E; 400-420		
IM-2010-11178	1	<i>P. caledonicus</i>	TERRASSES	DW3053	Norfolk Ridge	23°45'S, 168°16'E; 410-440		
IM-2010-11179	2	<i>P. caledonicus</i>	TERRASSES	CP3049	Norfolk Ridge	23°42'S, 168°16'E; 380-410		
IM-2010-11180	2	<i>P. caledonicus</i>	TERRASSES	DW3122	Ile des Pins	22°47'S, 167°12'E; 390-410		
IM-2010-11181	2	<i>P. caledonicus</i>	TERRASSES	DW3123	Ile des Pins	22°53'S, 167°13'E; 420-450		
IM-2010-11182	4	<i>P. caledonicus</i>	TERRASSES	DW3124	Ile des Pins	22°54'S, 167°15'E; 460		
IM-2010-11183	3	<i>P. caledonicus</i>	TERRASSES	CP3048	Norfolk Ridge	23°44'S, 168°16'E; 380-400		
IM-2010-11184	2	<i>P. caledonicus</i>	MUSORSTOM 4	DW222	S Grande-Terre	22°58'S, 167°33'E; 410-440		
IM-2010-11185	17	<i>P. caledonicus</i>		ACC. 386350				
IM-2010-11186	6	<i>P. caledonicus</i>	SMIB 2	DW05	S Ile des Pins	22°56'S, 167°15'E; 398-410		
IM-2010-11187	1	<i>P. caledonicus</i>	BATHUS 3	DW817	Norfolk Ridge	23°42'S, 168°16'E; 405-410		
IM-2010-11188	13	<i>P. caledonicus</i>	BATHUS 2	DW729	SW Passe de Dumbéa	22°52'S, 167°12'E; 400		
IM-2010-11189	7	<i>P. caledonicus</i>	SMIB 1	DW02	S Ile des Pins	22°52'S, 167°13'E; 415		

MNHN ID	N	SPECIES	MNHN EXPEDITION	STATION	GENERAL AREA	COORDINATES; DEPTH (m)	BOLD ID	GENBANK #
IM-2010-11190	3	<i>P. caledonicus</i>	SMIB 1	DW07	S Ile des Pins	22°55'S, 167°16'E; 500		
IM-2010-11191	6	<i>P. caledonicus</i>	SMIB 1	DW09	S Ile des Pins	22°55'S, 167°15'E; 450		
IM-2010-11192	1	<i>P. caledonicus</i>	BIOCAL	CP42	S Ile des Pins	22°46'S, 167°14'E; 380		
IM-2010-11193	1	<i>P. caledonicus</i>	LAGON	DW1147	Belep	19°08'S, 163°30'E; 210		
IM-2010-11194	1	<i>P. caledonicus</i>	VAUBAN	DR15		22°49'S, 167°12'E; 390-395		
IM-2010-11195	24	<i>P. caledonicus</i>	SMIB 2	DW03	S Ile des Pins	22°54'S, 167°14'E; 412-428		
IM-2010-11196	3	<i>P. caledonicus</i>	SMIB 2	DW01	S Ile des Pins	22°53'S, 167°13'E; 438-444		
IM-2010-11197	3	<i>P. caledonicus</i>	SMIB 2	DW17	S Ile des Pins	22°56'S, 167°16'E; 428-448		
IM-2010-11198	6	<i>P. caledonicus</i>	SMIB 2	DW14	S Ile des Pins	22°53'S, 167°13'E; 405-444		
IM-2010-11199	4	<i>P. caledonicus</i>	SMIB 2	DW08	S Ile des Pins	22°53'S, 167°14'E; 435-447		
IM-2010-11200	3	<i>P. caledonicus</i>	SMIB 2	DW16	S Ile des Pins	22°52'S, 167°12'E; 390		
IM-2010-11201	2	<i>P. caledonicus</i>	SMIB 2	DW07	S Ile des Pins	22°56'S, 167°14'E; 428		
IM-2010-11202	2	<i>P. caledonicus</i>	SMIB 2	DW04	S Ile des Pins	22°53'S, 167°14'E; 410-417		
IM-2010-11203	1	<i>P. caledonicus</i>	SMIB 2	DW15	S Ile des Pins	22°53'S, 167°12'E; 375-402		
IM-2010-11204	1	<i>P. caledonicus</i>	SMIB 2	DW12	S Ile des Pins	22°51'S, 167°13'E; 445-460		
IM-2010-11205	1	<i>P. caledonicus</i>	SMIB 2	DW09	S Ile des Pins	22°55'S, 167°16'E; 475-500		
IM-2010-11206	1	<i>P. caledonicus</i>	SMIB 3	DW26	SW Ile des Pins	22°55'S, 167°16'E; 450		
IM-2010-11207	1	<i>P. caledonicus</i>	SMIB 3	DW20	Jumeau Ouest Bank	23°40'S, 168°00'E; 280		
IM-2010-11208	1	<i>P. caledonicus</i>	SMIB 3	DW27	SW Ile des Pins	22°55'S, 167°18'E; 457		
IM-2010-11209	1	<i>P. caledonicus</i>	SMIB 3	DW28	SW Ile des Pins	22°46'S, 167°11'E; 394		
IM-2010-11210	1	<i>P. caledonicus</i>	SMIB 3	DW06	Éponge Bank	24°55'S, 168°21'E; 505		
IM-2010-11211	1	<i>P. caledonicus</i>	SMIB 3	DW25	SW Ile des Pins	22°56'S, 167°15'E; 437		
IM-2010-11212	2	<i>P. caledonicus</i>	CHALCAL 2	DW82	Norfolk Ridge	23°14'S, 168°04'E; 304		
IM-2010-11213	1	<i>P. caledonicus</i>	MUSORSTOM 4	CP213	S Grande-Terre	22°51'S, 167°12'E; 405-430		
IM-2010-11214	1	<i>P. caledonicus</i>	MUSORSTOM 4	DW212	S Grande-Terre	22°47'S, 167°10'E; 375-380		
IM-2010-11215	1	<i>P. caledonicus</i>	MUSORSTOM 4	DW229	S Grande-Terre	22°52'S, 167°13'E; 445-460		
IM-2010-11216	5	<i>P. caledonicus</i>	MUSORSTOM 4	CP214	S Grande-Terre	22°54'S, 167°14'E; 425-440		
IM-2010-11217	6	<i>P. caledonicus</i>	SMIB 4	DW65	Ile des Pins	22°56'S, 167°14'E; 400-420		
IM-2010-11218	1	<i>P. caledonicus</i>	SMIB 4	DW57	Antigonia Bank	23°21'S, 168°04'E; 210-260		
IM-2010-11219	1	<i>P. caledonicus</i>	VAUBAN	DR24		22°48'S, 167°09'E; 355-360		
IM-2010-11220	6	<i>P. caledonicus</i>	VAUBAN	DR15		22°49'S, 167°12'E; 390-395		
IM-2010-11221	2	<i>P. caledonicus</i>		444		18°15'S, 162°59'E; 300-350		
IM-2010-11222	1	<i>P. deforgesii</i>	MUSORSTOM 5	DC361	Chesterfield	19°52'S, 158°38'E; 400		
IM-2010-11223	3	<i>P. deforgesii</i>	CHALCAL 1	DC32	Chesterfield	19°43'S, 158°33'E; 350		
IM-2010-11224	1	<i>P. deforgesii</i>	CHALCAL 1	CP08	Chesterfield	19°44'S, 158°35'E; 348		
IM-2010-11225	1	<i>P. deforgesii</i>	MUSORSTOM 5	DW338	Chesterfield	19°52'S, 158°40'E; 540-580		
IM-2010-11226	3	<i>P. deforgesii</i>	MUSORSTOM 5	DC379	Chesterfield	19°53'S, 158°39'E; 370-400		
IM-2010-11227	5	<i>P. deforgesii</i>	MUSORSTOM 5	DC361	Chesterfield	19°52'S, 158°38'E; 400		
IM-2010-11228	1	<i>P. deforgesii</i>	MUSORSTOM 5	DC361	Chesterfield	19°52'S, 158°38'E; 400		
IM-2010-11229	1	<i>P. deforgesii</i>	MUSORSTOM 5	DW337	Chesterfield	19°54'S, 158°38'E; 412-430		
IM-2010-11230	1	<i>P. deforgesii</i>	MUSORSTOM 5	DC361	Chesterfield	19°52'S, 158°38'E; 400		
IM-2010-11231	1	<i>P. deforgesii</i>	MUSORSTOM 5	DC378	Chesterfield	19°54'S, 158°38'E; 355		
IM-2010-11232	1	<i>P. deforgesii</i>	EBISCO	CP2579	N Bellona	20°21'S, 158°40'E; 440-455		
IM-2010-11233	2	<i>P. deforgesii</i>	EBISCO	CP2596	Chesterfield	19°43'S, 158°37'E; 382-386		
IM-2010-11234	1	<i>P. deforgesii</i>	EBISCO	DW2606	Chesterfield	19°37'S, 158°42'E; 442-443		
IM-2010-11235	3	<i>P. deforgesii</i>	EBISCO	DW2564	NW Bellona	20°25'S, 158°41'E; 333-386		

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IM-2010-11236	9	<i>P. deforgesii</i>	EBISCO	CP2595	Chesterfield	19°44'S, 158°35'E; 345-377		
IM-2010-11237	3	<i>P. deforgesii</i>	EBISCO	DW2577	N Bellona	20°20'S, 158°39'E; 399-602		
IM-2010-11238	1	<i>P. deforgesii</i>	EBISCO	DW2576	N Bellona	20°20'S, 158°43'E; 390-394		
IM-2010-11239	17	<i>P. pseudogranulosus</i>	EBISCO	DW2530	S Nova Bank	22°48'S, 159°23'E; 338-343		
IM-2010-11240	21	<i>P. pseudogranulosus</i>	EBISCO	CP2531	S Nova Bank	22°47'S, 159°23'E; 330-340		
IM-2010-11241	2	<i>P. pseudogranulosus</i>	EBISCO	CP2503	Capel Bank	24°48'S, 159°46'E; 366-380		
IM-2010-11242	3	<i>P. pseudogranulosus</i>	EBISCO	DW2533	N Nova Bank	22°18'S, 159°28'E; 360-370		
IM-2010-11243	1	<i>P. pseudogranulosus</i>	MUSORSTOM 5	DW304	Nova Bank	22°10'S, 159°25'E; 385-420		
IM-2010-11244	1	<i>P. pseudogranulosus</i>	MUSORSTOM 5	DW300	Nova Bank	22°48'S, 159°24'E; 450		
IM-2010-11245	4	<i>P. pseudogranulosus</i>	MUSORSTOM 5	DW301	Nova Bank	22°07'S, 159°25'E; 487-610		
IM-2010-11246	3	<i>P. pseudogranulosus</i>	MUSORSTOM 5	DW299	Nova Bank	22°48'S, 159°24'E; 360-390		
IM-2010-11301	1	<i>P. wareni</i>	MUSORSTOM 6	DW407	Loyalty Ridge	20°41'S, 167°07'E; 360		
IM-2010-11302	3	<i>P. wareni</i>	HALICAL 1	DW01	Grand Passage	18°56'S, 163°24'E; 380-400		
IM-2010-11303	4	<i>P. wareni</i>	HALICAL 1	DW04	Grand Passage	18°55'S, 163°24'E; 350-365		
IM-2010-11304	3	<i>P. wareni</i>	HALICAL 1	DW03	Grand Passage	18°53'S, 163°24'E; 350-380		
IM-2010-11305	1	<i>P. wareni</i>	MUSORSTOM 4	CC173	Grand Passage	19°02'S, 163°19'E; 250-290		
IM-2010-11306	1	<i>P. wareni</i>	MUSORSTOM 6	DC402	Loyalty Ridge	20°30'S, 166°49'E; 520		
IM-2010-11307	1	<i>P. wareni</i>	BERYX 11	CP51	Norfolk Ridge	23°45'S, 168°17'E; 390-400		
IM-2010-11308	1	<i>P. wareni</i>	TERRASSES	DW3101	Norfolk Ridge	22°59'S, 168°21'E; 320-390		
IM-2010-11309	1	<i>P. wareni</i>	TERRASSES	DW3110	Norfolk Ridge	23°02'S, 168°16'E; 270-310		
IM-2010-11310	1	<i>P. wareni</i>	NORFOLK 2	CP2095	Kaimon Maru Bank	24°46'S, 168°10'E; 283-310		
IM-2010-11311	2	<i>P. wareni</i>	SMIB 5	DW85	NW Walpole	22°20'S, 168°42'E; 240-260		
IM-2010-11312	5	<i>P. wareni</i>	LITHIST	CP14	Jumeau Ouest Bank	23°42'S, 168°16'E; 378-402		
IM-2010-11313	2	<i>P. wareni</i>	SMIB 8	DW160	Kaimon Maru Bank	24°47'S, 168°08'E; 280-282		
IM-2010-11314	2	<i>P. wareni</i>	CONCALIS	DW2968	Grand Passage	18°14'S, 163°02'E; 247-256		
IM-2010-11315	1	<i>P. wareni</i>	CONCALIS	CP3006	Grand Passage	18°32'S, 163°08'E; 400		
IM-2010-11316	2	<i>P. wareni</i>	CONCALIS	CP2975	Grand Passage	18°15'S, 163°06'E; 297-316		
IM-2010-11317	2	<i>P. wareni</i>	CONCALIS	DW2946	Grand Passage	19°02'S, 163°27'E; 276-277		
IM-2010-11318	4	<i>P. wareni</i>	BATHUS 4	DW924	Grand Passage	18°55'S, 163°24'E; 344-360		
IM-2010-11319	3	<i>P. wareni</i>	BATHUS 4	CP938	Grand Passage	19°00'S, 163°26'E; 280-288		
IM-2010-11320	5	<i>P. wareni</i>	BATHUS 4	DW925	Grand Passage	18°55'S, 163°24'E; 370-405		
IM-2010-11321	1	<i>P. wareni</i>	BATHUS 4	DW926	Grand Passage	18°57'S, 163°25'E; 325-330		
IM-2010-11322	8	<i>P. wareni</i>	BATHUS 4	DW931	Grand Passage	18°55'S, 163°24'E; 360-377		
IM-2010-11323	1	<i>P. wareni</i>	NORFOLK 1	DW1709	Norfolk Ridge	23°43'S, 168°16'E; 380-389		
IM-2010-11324	1	<i>P. wareni</i>	NORFOLK 1	DW1658	Norfolk Ridge	23°27'S, 167°50'E; 320-336		
IM-2010-11325	1	<i>P. wareni</i>	NORFOLK 1	DW1729	Norfolk Ridge	23°21'S, 168°16'E; 340-619		
IM-2010-11326	1	<i>P. wareni</i>	SMIB 8	DW189	Antigonia Bank	23°18'S, 168°06'E; 400-402		
IM-2010-11327	1	<i>P. wareni</i>	BATHUS 4	DW924	Grand Passage	18°55'S, 163°24'E; 344-360		
IM-2010-11328	4	<i>P. wareni</i>	MUSORSTOM 4	CP193	Grand Passage	18°56'S, 163°23'E; 430		
IM-2010-11329	1	<i>P. wareni</i>	MUSORSTOM 4	DW196	Grand Passage	18°55'S, 163°24'E; 460		
IM-2010-11330	1	<i>P. wareni</i>	MUSORSTOM 4	DW222	S Grande-Terre	22°58'S, 167°33'E; 410-440		
IM-2010-11331	1	<i>P. wareni</i>	MUSORSTOM 6	DW407	Loyalty Ridge	20°41'S, 167°07'E; 360		
IM-2010-11332	1	<i>P. wareni</i>	MUSORSTOM 6	DW473	Loyalty Ridge	21°09'S, 167°55'E; 236		
IM-2010-11334	2	<i>P. wareni</i>	MUSORSTOM 4			250		
IM-2010-11335	1	<i>P. wareni</i>	SMIB 6	DW121	Grand Passage	18°58'S, 163°26'E; 315		
IM-2010-11336	1	<i>P. wareni</i>	BATHUS 3	CP812	Norfolk Ridge	23°43'S, 168°16'E; 391-440		

MNHN ID	N	SPECIES	MNHN EXPEDITION	STATION	GENERAL AREA	COORDINATES; DEPTH (m)	BOLD ID	GENBANK #
IM-2010-11337	1	<i>P. wareni</i>	VOLSMAR	DW40	Loyalty Ridge	22°19'S, 168°41'E; 275-295		
IM-2010-11340	6	<i>P. wareni</i>	CONCALIS	DW2977	Grand Passage	18°15'S, 163°07'E; 326-368		
IM-2010-11341	6	<i>P. wareni</i>	CONCALIS	DW3025	Grand Passage	18°57'S, 163°23'E; 396-400		
IM-2010-11342	6	<i>P. wareni</i>	CONCALIS	DW2978	Grand Passage	18°16'S, 163°04'E; 360-400		
IM-2010-11343	4	<i>P. wareni</i>	CONCALIS	DW3024	Grand Passage	18°57'S, 163°22'E; 349-370		
IM-2010-11344	2	<i>P. wareni</i>	CONCALIS	DW2943	Grand Passage	18°57'S, 163°23'E; 380-430		
IM-2010-11345	1	<i>P. wareni</i>	CONCALIS	DW2983	Grand Passage	18°01'S, 163°02'E; 367-430		
IM-2010-11346	1	<i>P. wareni</i>	CONCALIS	DW2951	Grand Passage	18°58'S, 163°25'E; 300		
IM-2010-11347	1	<i>P. wareni</i>	CONCALIS	DW2945	Grand Passage	19°00'S, 163°26'E; 297-310		
IM-2010-11348	1	<i>P. wareni</i>	CONCALIS	DW2944	Grand Passage	18°59'S, 163°24'E; 320-335		
IM-2010-11349	11	<i>P. wareni</i>	CONCALIS	DW2947	Grand Passage	19°02'S, 163°26'E; 272-284		
IM-2010-11350	14	<i>P. wareni</i>	CONCALIS	DW2974	Grand Passage	18°15'S, 163°06'E; 283-326		
IM-2010-11351	25	<i>P. wareni</i>	CONCALIS	DW2979	Grand Passage	18°16'S, 162°54'E; 350		
		<i>Bayerotrochus africanus</i>						AM049330.1
		<i>Mikadotrochus beyrichii</i>						AM049331.1
		<i>Bayerotrochus midas</i>						AY296820.1
		<i>P. amabilis</i>						AY923929.1
		<i>Bayerotrochus midas</i>						AY923930.1
		<i>Mikadotrochus beyrichii</i>						EU530109.1
		<i>Entemnotrochus adansonianus</i>						L78910.1
OUTGROUPS		<i>Entemnotrochus rumphii</i>						L78911.1
		<i>Bayerotrochus teramachii</i>						L78912.1
		<i>Bayerotrochus midas</i>						L78913.1
		<i>P. maureri</i>						L78914.1
		<i>P. quoyanus</i>						L78915.1
		<i>P. lucaya</i>						L78916.1
		<i>Haliotis tuberculata</i>						JQ894846.1

**Table 2.** Shell characters in the *Perotrochus caledonicus* species complex. Measurements correspond to mean values (with ranges) calculated on N specimens. Values for *P. deforgesi* are taken from Métivier (1990).

Character	<i>Perotrochus caledonicus</i>	<i>Perotrochus wareni</i> sp. nov.	<i>Perotrochus pseudogranulosus</i> sp. nov.	<i>Perotrochus deforgesi</i>
General appearance	trochoid with regularly increasing weakly convex whorls	conical, with weakly convex to rather straight-sided whorls	rather conical, with weakly convex to straight-sided whorls	depressed turbiniform
H/D ratio	1.00 (0.92-1.00, N = 7)	1.05 (1.01-1.09, N = 6)	0.87 (0.84-0.92, N = 9)	0.76 (N = 20)
Shell weight / thickness	light, thin shell	very heavy, thick shell	light, thin shell	thick, heavy shell
Apical whorls, profile	acute sharp / straight conical (with no whitish cord protruding on surface)	more depressed, with whitish cord protruding near suture of apical whorls	straight conical	depressed
Dominant teleoconch sculpture	macroscopically generally unbeaded to slightly beaded, straight spiral cords	macroscopically finely but distinctly beaded spiral cords, variable strength with crenulated periphery	distinct finely light beaded spiral cords, with angled periphery	strongly beaded spiral ribs above and under selenizone, with angled periphery
Teleoconch microsculpture	fine diverging radiating threads	no diverging radiating microsculpture	fine microsculpture radiating threads	microsculpture radiating threads
Nacreous coverage of inner slit lips at aperture edge	nearly completely covered by nacre (90%), small area with porcellaneous layer parallel to slit margins	partially covered by nacre (75%), leaving V-shaped area with porcellaneous layer uncovered (25%)	nearly completely covered by nacre (85%), small area with porcellaneous layer parallel to slit margins	partially covered by nacre (80%), porcellaneous layer parallel to slit uncovered
Slit width	wide	very narrow	rather wide	rather wide
Slit length	long, 1/6 <sup>th</sup> basal diameter (1/5.7–1/6.6, N = 7)	shorter, 1/7 <sup>th</sup> basal diameter (1/6.5-1/7.6, N = 6)	long, about 1/5 <sup>th</sup> basal diameter (1/5.4-1/5.8, N = 8)	long, 1/5 <sup>th</sup> basal diameter (N = 7)
Whorl surface	dull	dull	metallic lustre	slightly lustrous
Checker-board colour pattern in areas below selenizone	not always clearly marked; rather weak colour intensity, not limited to the area below selenizone	more irregularly sized and spaced colour blocks of less contrasting intensity	very regularly spaced checkerboard color markings of deeper colour intensity; overall deeper colour of teleoconch	orange blotches of variable intensity in areas above selenizone, not below
Surface of umbilical callus pad on basal disc	medium large (34% - 29.1–35.2, N = 6), generally smooth or weakly ridged radially in large adults	very large (45% - 38.0-48.9, N = 6), ridged radially, sharply edged at margin	small (29% - 19.6-40.5, N = 9), finely ridged radially, with clearly raised edge	large (36% - N = 7), clearly ridged radially and with raised edge
Basal disc profile	generally rather convex	flattened	rather flattened	rather flattened