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**Deep-sea wood-eating limpets of the genus *Pectinodonta* Dall, 1882 (Mollusca:
Gastropoda: Patellogastropoda: Pectinodontidae) from the tropical West Pacific**

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Running Title: *Pectinodonta* from the tropical West Pacific

ABSTRACT

Seven species of *Pectinodonta* Dall, 1882 are recorded from the tropical West Pacific, of which the following six are described as new: *P. alpha* n. sp. and *P. alis* n. sp. from the Solomon Islands and Vanuatu; *P. aurora* n. sp. and *P. beta* n. sp. from Papua New Guinea and the Solomon Islands; *P. gamma* n. sp. from Vanuatu and New Caledonia; and *P.*

philippinarum n. sp. from off Luzon, Philippine Islands. *Pectinodonta orientalis* Schepman, 1908, previously known from off Sulawesi and southern Japan, is newly recorded from off Taiwan, the Philippines, Papua New Guinea and the Solomon Islands. Specimens were sorted into morphospecies and tentatively attributed to available species names. Morphospecies were then evaluated using COI, 28S and/or ITS1 gene polymorphism. The description of the six new species includes a molecular diagnosis. The New Zealand species *P. marinovichi* Marshall, 1998 is recovered as close to *P. orientalis*, whereas *P. alis* n. sp. from the Solomon Islands and Vanuatu is recovered as close to the New Zealand species *P. aoupouria* Marshall, 1985 and *P. morioria* Marshall, 1985. Two other named tropical species, *P. alta* Schepman, 1908, from off Timor, and *P. obtusa* (Thiele, 1925), from off Sumatra (holotype illustrated), have not been recollected.

RÉSUMÉ

Patelliformes xylophages du genre *Pectinodonta* Dall, 1882 (Mollusca: Gastropoda: Patellogastropoda: Pectinodontidae) de la zone tropicale profonde du Pacifique-Ouest

Sept espèces de *Pectinodonta* Dall, 1882 sont reportées de la zone tropicale du Pacifique-Ouest. Parmi elles, six nouvelles espèces sont décrites: *P. alpha* n. sp. et *P. alis* n. sp. des Iles Salomon et du Vanuatu, *P. aurora* n. sp. et *P. beta* n. sp. de Papouasie-Nouvelle-Guinée et des Iles Salomon, *P. gamma* n. sp. du Vanuatu et de Nouvelle-Calédonie et *P. philippinarum* n. sp. de la province de Luzon aux Philippines. *Pectinodonta orientalis* Schepman, 1908, précédemment connus du Sulawesi et du sud du Japon, est ici reportée pour la première fois de Taïwan, des Philippines, de Papouasie-Nouvelle-Guinée et des Iles Salomon. Les spécimens collectés ont tout d'abord été triés en morpho-espèces, auxquelles ont été attribués les noms d'espèces. Ces morpho-espèces ont ensuite été comparées aux résultats obtenus par l'analyse du polymorphisme des gènes COI, 28S et/ou ITS1. La description des six nouvelles

espèces inclut une diagnose moléculaire. *P. marinovichi* Marshall, 1998, de Nouvelle-Zélande, est phylogénétiquement proche de *P. orientalis*, alors que *P. alis* n. sp. des Iles Salomon et du Vanuatu est proche de *P. aupouria* Marshall, 1985 and *P. morioria* Marshall, 1985 de Nouvelle-Zélande. Deux autres espèces tropicales déjà décrites, *P. alta* Schepman, 1908, du Timor, et *P. obtusa* (Thiele, 1925), de Sumatra (holotype illustré), n'ont pas été retrouvées.

INTRODUCTION

Pectinodontidae are a family of deep-sea limpets that live in association with sunken wood, hot vents and cold seeps. The group comprises three genera: *Pectinodonta* Dall, 1882 (type species *P. arcuata* Dall, 1882), all species of which live and feed on sunken wood, *Bathyacmaea* Okutani *et al.* 1992 (type species *B. nipponica* Okutani, Tsuchida & Fijikura, 1992) from cold seeps and hot vents (Okutani *et al.* 1992, 1993; Beck 1996; Sasaki *et al.* 2003, 2005, 2006), and *Serradonta* Okutani, Tsuchida & Fijikura, 1992 (type species *S. vestimentifericola* Okutani, Tsuchida & Fijikura, 1992) from cold seeps (Okutani *et al.* 1992; Sasaki *et al.* 2003, 2005). The family is characterised by a distinctive radular morphology, specifically a crossrow comprising a single pair of short (*Pectinodonta* and *Serradonta*) or elongate (*Bathyacmaea*) lateral teeth, each tooth of which shows sutures (*Pectinodonta* and *Serradonta*) or structure (*Bathyacmaea*) suggesting origin through fusion of at least three teeth. The group has long been treated as a subfamily of Acmaeidae (following Pilsbry 1891), but is now firmly established at family level within Lottioidea on anatomical and molecular evidence (Sasaki 1998; Nakano & Ozawa 2007).

Pectinodonta species, the subject of the present contribution, are intimately associated with sunken wood at bathyal to abyssal depths, the shallowest record (150–163 m) being an

undescribed species from off Bohol, Philippine Islands (MNHN, PANGLAO 2005, stn CP2380), the deepest (4200–4400 m) being the type material of *P. maxima* (Dautzenberg, 1925) from off the Azores. Anatomically the genus is characterised by a digestive system that contains dense communities of symbiotic bacteria that are involved in wood digestion (Zbinden *et al.* 2010). Zbinden *et al.* (2010) recorded three species within the digestive mass of a single *Pectinodonta* species (*P. alpha* n. sp. described herein) and intriguingly, a further two species on the gill. Gill-associated bacteria in vent and seep taxa are thought to contribute to host nutrition, though Zbinden *et al.* (2010) found no evidence for a nutritional role in *Pectinodonta* from stable isotope analysis or cellulolytic activity measured in the tissues. Perhaps they protect the host from toxicity of hydrogen sulphide or methane, which is elevated on sunken decaying wood (Leschine 1995). The majority of species have pronounced commarginal and radial shell sculpture, but radial sculpture is weak or lacking in a few species, notably *P. alta* Schepman, 1908, *P. maxima* (Dautzenberg, 1925) and *P. waitemata* Marshall, 1985. Judging from examination of hundreds of pieces of sunken wood supporting various combinations of specialist wood-associated molluscs such as mytilid and boring xylophagaid bivalves, cocculinid and pseudococculinid limpets and skeneimorph gastropods, occurrence on sunken wood tends to be sporadic (B.A.M. and S.S., independent observations). When present, however, they tend to be abundant and to dominate the external biota (Marshall 1985, fig. 1; Pailleret *et al.* 2007: 235, fig. 3; Warén 2011: fig. 496E). The evolutionary history of this abundant fauna, remains largely underexplored, and recent work on mytilid bivalves (Lorion *et al.* 2010, Thubaut *et al.* in press) and buccinid gastropods (Kantor *et al.* unpubl. data) tends to prove that the evolution of sunken-wood organisms is tightly entangled with that of cold-seep and vent lineages (Cosel & Marshall 2010; Samadi *et al.* 2010). Another common feature is the large number of undescribed species from sunken wood. Extensive sampling in the tropical West Pacific has yielded many undescribed species

of mollusc, including the *Pectinodonta* species recorded herein. Thus we contribute to the knowledge of this little-known fauna for a better understanding of the evolutionary processes that led to its diversification.

MATERIAL AND METHODS

Sampling and morphological analyses

The following report is based on study of roughly a thousand specimens of *Pectinodonta* species obtained by French cruises off the Philippine Islands (AURORA 2007), the Solomon Islands (SALOMON 1, SALOMON 2 and SALOMONBOA 3), Papua New Guinea (BIOPAPUA), Vanuatu (BOA 1 and SANTO 2006) and New Caledonia (CONCALIS) (Bouchet *et al.* 2008). All specimens were picked from wood in the field and fixed and stored in 98% ethanol. To enhance sculptural contrast for photographic imaging, dry shells were stained with water-soluble green food colouring and whitened by holding in smoke produced by burning magnesium. Radulae were cleared using the non-destructive method described by Holznagel (1998), mounted on adhesive carbon tape and coated with gold/palladium for scanning electron microscopy.

DNA sequencing

Live-taken specimens were selected in each recognized morphospecies for molecular analyses. Additionally, specimens of three New Zealand *Pectinodonta* species (*P. aupouria* Marshall, 1985, *P. marinovichi* Marshall, 1998 and *P. morioria* Marshall, 1985) were sequenced and added to the analyses for comparison. Tissue clips of approximately 1–2 mm² were taken for extraction, using in most cases the 6100 Nucleic Acid Prepstation system (Applied Biosystems). The universal primers LCO1490 and HCO2198 (Folmer *et al.* 1994), 28S-C1' and 28S-D2 (Dayrat *et al.* 2001; Jovelin & Justine 2001) and ITS1 and ITS2 (White

et al. 1990) were used for the amplification of the mitochondrial COI barcode fragment, and a fragment of ~900 bp of the 28S rRNA and the ITS1 nuclear genes, respectively. All polymerase chain reactions (PCR) were performed in 20 μ L, containing 300–600 ng of DNA, 1 \times reaction buffer, 2.5 mM MgCl₂, 0.26 mM dNTP, 0.25 μ M of each primer, 5% DMSO, 0.01mg of BSA and 1.2 U of Q-Bio Taq (MPBiomedicals) for COI and 1.2 U of Taq Pol (MPBiomedicals) for 28S and ITS1. The reaction program consisted of 5 min at 94°C, followed by 35 cycles of 40 sec at 94°C, 40 sec at 48°C, 56°C and 59°C for COI, 28S and ITS1 respectively, and 1 min at 72°C. Upon completion of the 35 cycles, the thermal program concluded with 10 min at 72 °C, followed by a hold at -12°C. PCR products were purified and sequenced (in both directions) at the Genoscope sequencing facility. A list of material sequenced is provided that includes DNA voucher numbers, holotype and paratype registration numbers (see descriptions below), BOLD (Barcode of Life database) process IDs and GenBank accession numbers (Table 1). All material is at MNHN unless specified.

Phylogenetic analyses

Sequences were automatically aligned using Muscle (Edgar 2004) with default parameters. Phylogenetic analyses were performed on each gene separately, using a Bayesian approach as implemented in MrBayes (Huelsenbeck *et al.* 2001), consisting each of eight Markov chains of 10,000,000 generations each with a sampling frequency of one tree each thousand generations. The number of swaps was set to five, and the chain temperature at 0.02. A substitution model with six substitution categories, a gamma-distributed rate variation across sites approximated in four discrete categories and a proportion of invariable sites, was used; each codon position was considered as an unlinked partition for COI. Convergence of each analysis was evaluated using Tracer v. 1.4.1 (Rambaut & Drummond 2007) by checking if the ESS values were all superior to 200. A consensus tree was then calculated after omitting the

first 25% trees as burn-in. Maximum Likelihood analyses were also performed, using RAxML 7.0.4 (Stamatakis 2006), with a GAMMAI substitution model; similarly to the Bayesian analyses, each codon position was considered as an unlinked partition for COI. RaxML analyses were performed on the Cipres Science Gateway (<http://www.phylo.org/portal2/>) using the RAxML-HPC2 on TG Tool. Accuracy of the results was assessed by bootstrapping (1000 replicates). GenBank sequences of *Lottia digitalis* (Rathke, 1833) (Lottioidea; GU443647.1, DQ248942.1) were used as distant outgroups to artificially root the COI and 28S trees; no alignable outgroup was available in GenBank for the ITS1 gene.

To resolve the phylogenetic relationships among the defined species, we first tested the monophyly of *Pectinodonta* and Pectinodontidae using GenBank sequences. Unfortunately, among the three genes we sequenced, only COI was available for several species in GenBank. All the Lottioidea sequences were downloaded, and COI coding sequences were manually sorted. A sequence of *Patella depressa* was used as outgroup. To reduce the size of the dataset, a maximum of three sequences from three different species for each genus was kept, except for the Pectinodontidae, for which all available sequences were analysed. Since no supported incongruence was revealed between each independent analysis, the three genes were concatenated for one specimen for each recognized species in order to resolve phylogenetic relationships among *Pectinodonta* species. Bayesian and Maximum Likelihood analyses were performed as described for the independent gene analyses, with three different partitions for the Lottioidea dataset (three codon positions of COI) and five different partitions for the *Pectinodonta* dataset (28S, ITS1 and three codon positions of COI).

Text conventions

Measurements of shell height is height minus depth of basal arch (basal plane is concave from side to side). Anterior length is measured at a right angle to the apertural plane. Overall depth ranges are determined by giving the maximum minimum depth and minimum maximum depths in given ranges (Bouchet *et al.* 2008).

New species descriptions include a molecular diagnosis with a list of diagnostic sites for each species and gene. The position of the diagnostic sites is based on COI, 28S and ITS1 alignments performed on our *Pectinodonta* dataset; these alignments are published in TreeBase (<http://purl.org/phylo/treebase/phylows/study/TB2:S14155>).

Abbreviations

Repositories

MNHN	Muséum national d'Histoire naturelle, Paris;
NMNZ	Museum of New Zealand Te Papa Tongarewa, Wellington;
RMNH	Naturalis Biodiversity Center, Leiden;
ZMA	Zoological Museum Amsterdam collections, now in Naturalis Biodiversity Center, Leiden (RMNH);
ZMB	Museum für Naturkunde, Berlin.

Specimens

juv	juvenile;
mm	millimetre;
spm(s)	specimen(s).

Station data

m metre;
stn station.

The prefix to station number denotes:

AT *Alis* trawl (beam trawl or Warén dredge);
CC shrimp trawl;
CP beam trawl;
DW Warén dredge.

RESULTS

Among the material gathered from the tropical West Pacific, seven morphospecies were recognized, of which only one could be associated to an available species name (*P. orientalis* Schepman, 1908). These were subjected to molecular analysis together with the three species from New Zealand. Initially the COI and 28S genes were preferentially sequenced. Regrettably, DNA amplifications failed for some specimens (especially for the COI gene). Whereas the COI gene was able to distinguish all species that were morphologically defined (and successfully sequenced for the COI gene), the 28S gene was not able to distinguish two pairs of closely related species: *Pectinodonta beta* n. sp. vs. *P. gamma* n. sp., and *P. aurora* n. sp. vs. *P. alpha* n. sp. (Figs 1A and 1B, respectively). The ITS1 gene, a more variable nuclear marker, was thus sequenced for the members of these two species pairs, plus a few representative specimens of the other species. All species were characterized by unique haplotypes, and the ITS1 was thus able to distinguish *P. beta* n. sp. from *P. gamma* n. sp. and *P. aurora* n. sp. from *P. alpha* n. sp. In each of the two species pairs that were unresolved using 28S, the ITS1 gene allowed diagnoses, but one species in each pair (*P. gamma* n. sp. and *P. aurora* n. sp. – Fig. 1C) was paraphyletic. However, morphological and molecular

analyses failed to fully resolve the identity of 14 specimens for which only the 28S gene was successfully sequenced: ten were identified as *P. alpha* n. sp. or *P. aurora* n. sp., and four as *P. beta* n. sp. or *P. gamma* n. sp. (see Table 1). Morphological identification is thus not fully capable of unambiguously identifying specimens to the species level. Overall, each of the seven newly defined morphospecies, as well as the three New Zealand species, was recognized as a separate entity with at least one marker. We interpret the fact that the 28S gene was not able to discriminate two pairs of species as a lack of variability in this gene; similarly, the non-monophyly of *P. gamma* n. sp. and *P. aurora* n. sp. is probably due to a lack of resolution, and does not contradict the morphospecies hypotheses. The molecular analyses thus support the species boundaries based on morphological characters. Seven morphospecies are supported with at least two independent markers (COI + 28S or COI + ITS1), two are supported with the ITS1 and 28S genes and one was successfully sequenced and supported only with 28S. Most clades that correspond to the morphospecies hypotheses are statistically supported (Posterior Probabilities $PP > 0.90$ and Bootstraps $B > 70$), except *P. aoupouria* ($PP = 0.99$, $B = 49$) for COI, *P. orientalis* ($PP = 0.69$, $B = 93$), *P. morioria* ($PP = 1$, $B = 67$) and *P. philippinarum* n. sp. ($PP = 0.85$, $B = 55$) for the 28S gene and *P. beta* n. sp. ($PP = 0.75$, $B = 78$) and *P. alpha* n. sp. ($PP = 0.88$, $B = 88$) for ITS1.

The COI analysis for our *Pectinodonta* species and for many species of Lottioidea in GenBank revealed that the Pectinodontidae (i.e. *Pectinodonta* and *Bathyacmaea*) are monophyletic (Fig. 2). The other families of Lottioidea are also supported as monophyletic (i.e. Acmaeidae, Lottiidae, Nacellidae, Neolepetopsidae), with the exception of Lepetidae. Within Pectinodontidae, the unique sequence of *Bathyacmaea* is nested within *Pectinodonta* as sister to *P. marinovichi* Marshall, 1998. The dataset thus does not support monophyly of *Pectinodonta*. The unidentified *Pectinodonta* sequences from GenBank (FN421454.1-FN421461.1) all cluster within the *P. alpha* n. sp. clade. To more robustly resolve the

phylogenetic relationships within the genus *Pectinodonta*, the three genes were concatenated (Fig. 3).

SYSTEMATIC ACCOUNT

Superfamily LOTTIOIDEA Gray, 1840

Family PECTINODONTIDAE Pilsbry, 1891

Genus *PECTINODONTA* Dall, 1882

Pectinodonta Dall, 1882: 409.

Type species: *Pectinodonta arcuata* Dall, 1882, by original designation; Recent, Caribbean.

DIAGNOSIS. — Shell 8.00–39.8 mm long at maturity, white, teleoconch I smooth, teleoconch II radially and concentrically sculptured (protoconch unknown: deciduous). Radular formula 0+1+0+1+0, each tooth considerably longer than basal plate, comprising three or perhaps four fused laterals. Digestive system containing symbiotic bacteria that are involved in digestion of decaying wood upon which they feed.

REMARKS. — The highly distinctive *Pectinodonta* radula comprises a single, alternately slightly offset pair of anteriorly converging, elongate, dorso-ventrally short, straight, dorso-ventrally curved, saw-like teeth arranged in a long series. The large anterior cusp in each crossrow seats in the crossrow in front and in the crossrow behind (but does not originate from them), extending about a third of the distance along the crossrow behind that: in other words each tooth is roughly three times longer than the crossrow to which it is attached. Each tooth has been interpreted as a fusion of three laterals (Habe 1949; Hickman 1983; Marshall 1985; Lindberg 1988), the boundaries of which are defined by sutures behind the two (anteriormost) unicuspid teeth. The rest of the tooth has been interpreted as a multicuspid

third lateral, though the presence of a small, blunt subterminal projection (vestigial cusp?) and the deeper separation between the fourth cusp and adjacent ones, suggests that the third and fourth cusps may represent the third tooth and the remainder a multicuspid fourth lateral. Conversely, Okutani *et al.* (1992) considered that the putatively fused teeth in *Pectinodonta* “all come out from the common shaft” and thus comprise only a single pair of lateral teeth, each of which consists of three parts. They also did not accept that the lateral teeth in *Serradonta vestimentifericola* were the result of fusion, though sutures are clearly defined and it seems likely to us that each tooth in this species is indeed the result of fusion of three teeth.

Pectinodonta alpha n. sp.

Figs 4A, B; 5; 6A, B; Table 2

Pectinodonta sp. - Pailleret *et al.* 2007: 235, fig. 3. — Zbinden *et al.* 2010: 451. — Warén 2011: fig. 496E.

TYPE MATERIAL. — Holotype MNHN IM-2009-9314, 15 paratypes MNHN and 2 paratypes NMNZ (as listed Table 1).

TYPE LOCALITY. — Vanuatu, W off Malo, 15°40'S, 167°01'E, alive on sunken wood, 431–445 m, N.O *Alis*, 10 Oct. 2006 [SANTO 2006: stn AT120].

MATERIAL EXAMINED (Table 1). — **Vanuatu.** SANTO 2006: stn AT120, W off Malo, 15°40'S, 167°01'E, alive on sunken wood, 431–445 m, 20 spms. — Stn AT121, off Malo, 15°39'S, 167°01'E, 290 m, 3 spms.). — BOA 1: stn CP2425, 14°54'S, 166°51'E, 777 m, 1 spm

Solomon Islands. SALOMONBOA 3: stn CP2798, E of Malaita, 8°43'S, 161°00'E, 410 m, 4 spms.

DISTRIBUTION. — Solomon Islands and Vanuatu, living at 290–777 m (Fig. 5).

DESCRIPTION. — Shell of moderate size, up to 13.87 mm long, strongly arched (length/height ratio 1.66–2.14, mean 1.85, SD 0.13, n = 14), apex weakly inclined anteriorly. Anterior end occupying 20.7–31.9% (mean 26.9%, SD 3.08, n = 14) of shell length; anterior slope weakly concave in shells 11–12 mm long, then weakly convex, lateral slopes weakly convex, posterior slope broadly convex. Aperture gently arched from side to side. With increasing growth, longitudinal axis gradually twisting up to roughly 5° anticlockwise between teleoconch I and end of teleoconch II in adults. Teleoconch I conical, length 1.60–2.10 mm (mean 1.85 mm, SD 0.13, n = 14), anterior and lateral slopes flat or weakly concave, posterior slope mostly weakly convex, more or less flat in few specimens, glossy, essentially smooth apart from commarginal growth lines and obscure radial lines. Teleoconch II sculptured with radial costae and commarginal ridges, rounded nodules at intersections; fine, crisp, crowded commarginal growth lines throughout. Radial costae rounded, multiplying by intercalation, interspaces narrower than each costa. Radular teeth (adult, paratype NMNZ M.306245 ex MNHN IM-2009-9296) roughly 250 µm long, with 16 cusps, posterior pair small and fused, others sharp.

Holotype length 12.04 mm.

MOLECULAR DIAGNOSIS. — The COI sequence of the holotype is published in GenBank (Table 1). Among available COI sequences, *P. alpha* is reliably and precisely distinguished from other *Pectinodonta* species by possession of a specific combination of nucleotides in the

amplified sequence at sites 85 (C), 95 (C), 181 (G), 220 (C), 242 (C), 250 (C), 274 (C), 407 (C), 494 (C), 496 (G), 583 (G), 628 (C) and 640 (C). There are no diagnostic sites for *P. alpha* in the amplified sequences of the 28S and ITS1 genes.

REMARKS. — *Pectinodonta alpha* n. sp. is distinctive among *Pectinodonta* species in the combination of moderate-sized, acutely conical shell with strongly anterior apex, and relatively weak commarginal ridges. Compared with *P. obtusa* (Thiele, 1925) (Figs 9G, H) from off Sumatra, 750 m, which has similar sculpture, *P. alpha* n. sp. differs in being more elevated, in having the apex closer to the anterior end, and in that teleoconch I is less skewed from the longitudinal axis of the shell.

ETYMOLOGY. — First letter of the Greek alphabet, from our original descriptor for this clade.

Pectinodonta alis n. sp.

Figs 6C, D; 7A, B; 8; Table 3

TYPE MATERIAL. — Holotype MNHN IM-2009-7723, 1 paratype MNHN and 1 paratype NMNZ (as listed Table 1).

TYPE LOCALITY. — Vanuatu, W of Malakula, 15°07'S, 166°51'E, alive on sunken wood, 387 m, 10 Sep. 2005, N.O *Alis* [BOA 1: stn CP2448].

MATERIAL EXAMINED (Table 1). — **Vanuatu**. BOA 1: stn CP2448, W of Malakula, 15°07'S, 166°51'E, alive on sunken wood, 387 m, 3 spms. — SANTO 2006: stn AT96, Big Bay, 15°07'S, 166°53'E, 328-354 m, 1 juv.

Solomon Islands. SALOMON 1: stn CP1860, W of Malaita I., 9°22'S, 160°31'E, 620 m, 1 spm. — SALOMONBOA 3: stn CP2828, off Kirakira, San Cristobal, 10°26'S, 161°58'E, 379 m, 1 spm.

DISTRIBUTION. — Solomon Islands and Vanuatu, living at 354–387 m (Fig. 8).

DESCRIPTION. — Shell of moderate size, up to 9.80 mm long, strongly elevated (length/height ratio 2.10–2.36, mean 2.25, SD 0.13, n = 3), apex distinctly inclined anteriorly. Anterior end occupying 14.2–20.0% (mean 17.8%, SD 3.10, n = 3) of shell length; anterior slope weakly concave, almost flat, lateral slopes weakly convex, posterior slope broadly convex. Aperture gently arched from side to side. With increasing growth, longitudinal axis gradually twisting a few degrees anticlockwise between teleoconch I and end of adult teleoconch. Teleoconch I conical, length 1.50–2.00 mm, anterior and lateral slopes flat or weakly concave, posterior slope weakly convex or more or less flat, glossy, essentially smooth apart from commarginal growth lines and obscure radial lines. Teleoconch II sculptured with radial costae and commarginal ridges, rounded nodules at intersections; fine, crisp, crowded commarginal growth lines throughout. Radial costae rounded, multiplying by intercalation, interspaces much narrower than each costa. Radular teeth (adult, paratype NMNZ M.306246 ex MNHN IM-2009-7722) roughly 170 µm long, with 12 cusps.

Holotype length 9.80 mm

MOLECULAR DIAGNOSIS. — The 28S sequence of the holotype is published in GenBank (Table 1). Among available 28S sequences, *P. alis* is reliably and precisely distinguished from other *Pectinodonta* species by possession of a specific combination of nucleotides in the amplified sequence at sites 217 (G) and 610 (C). *Pectinodonta alis* was not sequenced for the COI and ITS1 genes.

REMARKS. — *Pectinodonta alis* n. sp. resembles the Japanese species *P. rhyssa* (Dall, 1925), the eastern Australian species *P. kapalae* Marshall, 1985, and the New Zealand species *P. aupouria* Marshall, 1985, *P. morioria* Marshall, 1985 and *P. marinovichi* Marshall, 1998 in shell profile, but differs from all of them in much closer radial costae and from the New Zealand species in attaining smaller size. All of these species, including *P. rhyssa* (for which COI sequences were available from GenBank), displayed diagnostic genetic characters for at least one gene. Among the species recorded herein, *P. alis* n. sp. resembles *P. alpha* n. sp. in having a highly arched shell, but differs in that the apex is more strongly inclined anteriorly. Among the species treated here, *P. alis* n. sp. was recovered as being most closely related to the New Zealand species *P. aupouria* and *P. morioria* (Fig. 1B – 28S, but see also Fig. 2 where *P. aupouria* is sister to *P. rhyssa* – COI). It also happens to be the most similar to them in shell shape, though it is more finely sculptured.

ETYMOLOGY. — After N.O *Alis*, with which most of the present material was obtained.

***Pectinodonta aurora* n. sp.**

Figs 4C, D; 5; 6E, F; Table 4.

TYPE MATERIAL. — Holotype MNHN IM-2009-7710, 6 paratypes MNHN and 1 paratype NMNZ (as listed Table 1).

TYPE LOCALITY. — Philippines, Luzon, off Dingalan Bay, 15°27'N, 121°36'E, alive on sunken wood, 556 m,

MATERIAL EXAMINED (Table 1). — **Philippines**. Luzon, off Dingalan Bay, 15°27'N, 121°36'E, 556 m, 8 spms.

Papua New Guinea. BIOPAPUA: stn CP3646, Huon Gulf, off Tami Island, 6°45'S, 147°49'E, 460-485 m, 5 spms. — Stn CP3647, Huon Gulf, off Lae, 6°47'S, 147°12'E, 592-660 m, 3 spms. — Stn CP3655, 02°15'S, 150°16'E, 426-440 m, 2 spms.

DISTRIBUTION. — Philippine Islands and Papua New Guinea, living at 485–592 m (Fig. 5).

DESCRIPTION. — Shell of moderate size, up to 18.13 mm long, moderately arched (length/height ratio 2.15–2.68, mean 2.43, SD 0.18, n = 8), apex weakly inclined anteriorly. Anterior end occupying 29.3–35.1% (mean 31.5%, SD 1.92, n = 8) of shell length; anterior slope weakly concave or more or less flat, lateral slopes weakly convex, posterior slope broadly convex. Aperture gently arched from side to side. With increasing growth, longitudinal axis gradually twisting up to roughly 5° anticlockwise between teleoconch I and end of adult teleoconch II. Teleoconch I conical, length 1.70–1.90 mm, anterior and lateral slopes more or less flat, posterior slope weakly convex or flat, glossy, essentially smooth apart from commarginal growth lines and obscure radial lines. Teleoconch II sculptured with radial costae and commarginal ridges, rounded nodules at intersections; fine, crisp, crowded commarginal growth lines throughout. Radial costae rounded, multiplying by intercalation,

interspaces narrower than each costa. Radular teeth (adult, paratype MNHN IM-2009-5085) roughly 250 µm long, with 16 cusps, posterior pair fused.

Holotype length 13.4 mm

MOLECULAR DIAGNOSIS. — The 28S and ITS1 sequences of the holotype are published in GenBank (Table 1). Among available COI sequences, *P. aurora* is reliably and precisely distinguished from other *Pectinodonta* species by possession of a specific combination of nucleotides in the amplified sequence at sites 37 (G), 40 (C), 95 (A), 163 (G), 421 (C), 436 (A), 454 (G), 502 (G) and 619 (T). There are no diagnostic sites for *P. aurora* in the amplified sequences of the 28S and ITS1 genes.

REMARKS. — *Pectinodonta aurora* n. sp. is closely related to *P. alpha* n. sp. and the two are indistinguishable using the 28S gene but are recovered with COI and ITS1 (Fig. 1). Compared with *P. alpha* n. sp., which has almost identical sculpture, *P. aurora* n. sp. differs primarily in attaining larger size (length up to 18.13 mm vs. 13.87) and in being less elevated (height/length ratio 2.15-2.68, mean 2.43, vs. 1.66–2.14, mean 1.85) and in that the apex is further from the anterior end in most specimens (anterior end occupying 29.3-35.1% vs. 20.7–31.9% of shell length). The two species are allopatric, *P. alpha* n. sp. occurring further south off the Solomon Islands and Vanuatu at similar depths.

ETYMOLOGY. — After Philippine Islands AURORA 2007 expedition.

Pectinodonta beta n. sp.

Figs 6G, H; 7C-F; 11; Table 5

TYPE MATERIAL. — Holotype MNHN IM-2009-7706, 17 paratypes MNHN and 3 paratypes NMNZ (as listed Table 1)

TYPE LOCALITY. — Solomon Islands, W of Vella Lavella Island, 7°43'S, 156°26'E, 582–609 m, N.O *Alis*, 01 Nov. 2005 [SALOMON 2: stn CP2245].

MATERIAL EXAMINED (Table 1). — **Solomon Islands.** SALOMON 2: stn CP2245, W of Vella Lavella Island, 7°43'S, 156°26'E, 582–609 m, 1 spm). — Stn CP2246, W of Vella Lavella Island, 7°43'S, 156°25'E, 664–682 m, 4 spms). — SALOMONBOA 3: stn CP2777, off Savo Island, 9°12'S, 160°55'E, 706–722 m, 1 spm. — Stn CP2787, NW of Malaita Island, 8°31'S, 160°39'E, 570–885 m, 5 spms. — Stn CP2788, NW of Malaita Island, 8°30'S, 160°37'E, 760–1160 m, 1 spm. — Stn CP2821, N of San Cristobal, 10°19'S, 161°54'E, 686–864 m, 2 spms.

Papua New Guinea. BIOPAPUA: stn CP3647, Huon Gulf, off Lae, 6°47'S, 147°12'E, 592–660 m, 6 spms. — Stn CP3681, off Vitu Islands, 4°38'S, 149°27'E, 564–712 m, 7 spms. — Stn CP3708, off Madang, 4°58'S, 145°50'E, 502–529 m, 1 spm. — Stn CP3729, off Mambre Bay, 7°52'S, 148°03'E, 575–655 m, 2 spms. — Stn CP3740, off Woodlark Islands, 9°12'S, 152°16'E, 556–645 m, 2 spms. — Stn CP3780, New Britain, Wide Bay, 5°05'S, 152°02'E, 782–1085 m, 1 spm.

DISTRIBUTION. — Papua New Guinea and Solomon Islands, living at 529–782 m (Fig. 11).

DESCRIPTION. — Shell large, up to 26.20 mm long, moderately arched (length/height ratio 2.27–3.98, mean 3.11, SD 0.53, n = 12), apex weakly inclined anteriorly. Anterior end occupying 25.1–38.2% (mean 35.2, n = 12) of shell length; anterior slope very weakly

convex, lateral and posterior slopes broadly convex. Aperture gently arched from side to side. With increasing growth, longitudinal axis gradually twisting roughly 5° anticlockwise between teleoconch I and end of teleoconch II in adults. Teleoconch I depressed conical, length 1.90–2.20 mm (mean 1.95, SD 0.09, n = 12), anterior and posterior slopes flat to weakly concave, lateral slopes flat, glossy, essentially smooth apart from commarginal growth lines and obscure radial lines. Teleoconch II sculptured with strong radial costae and commarginal ridges, rounded nodules at intersections; fine, crisp, crowded commarginal growth lines throughout. Radial costae rounded, crowded, multiplying by intercalation. Radular teeth (4260, adult) roughly 360 µm long, with 11 cusps.

Holotype length 21.2 mm

MOLECULAR DIAGNOSIS. — The COI, 28S and ITS1 sequences of the holotype are published in GenBank (Table 1). Among available sequences, *P. beta* n. sp. is reliably and precisely distinguished from other *Pectinodonta* species by possession of a specific combination of nucleotides in the amplified sequence of COI at sites 106 (C), 196 (G), 214 (G), 307 (T), 319 (A), 397 (C) and 457 (G), and in the ITS1 gene at site 282 (T). There are no diagnostic sites for *P. beta* n. sp. in the amplified sequence of the 28S gene.

REMARKS. — Compared with *P. orientalis* Schepman, 1908, which is similar in shape and in attaining large size, *P. beta* n. sp. differs in having a smaller teleoconch I (length 1.90–2.20 mm vs. 2.30–2.60 mm), much more closely spaced and more numerous radial costae and commarginal ridges, with interspaces narrower than each costa and ridge. A single specimen of *P. orientalis* Schepman, 1908 was taken within the geographic and bathymetric range of *P. beta* n. sp. (sympatric), and they may well be locally syntopic. A species with extremely similar shell morphology, *P. gamma* n. sp., is described below. Compared with *P. obtusa*

(Thiele, 1925) (holotype and only known specimen 7.00 mm long – adult size unknown: Figs 9G, H) at the same stage of growth, *P. beta* n. sp. differs in having a more elongate PI and stronger, more widely spaced commarginal ridges and more crowded radial costae.

ETYMOLOGY. — Second letter of the Greek alphabet, from our original descriptor for this clade.

Pectinodonta gamma n. sp.

Figs 6I, J; 7G, H; 11; Table 6.

TYPE MATERIAL. — Holotype MNHN IM-2009-5798, 5 paratypes MNHN and 1 paratype NMNZ (as listed Table 1).

TYPE LOCALITY. — Vanuatu, Santo, Big Bay, 15°00'S, 166°55'E, alive on sunken wood, 630–670 m, N.O *Alis*, 6 Sep. 2005 [BOA 1: stn CP2420].

MATERIAL EXAMINED. — **Vanuatu**. BOA 1: stn CP2418, 15°03'S, 166°53'E, 432–532 m, 1 spm. — Stn CP2419, 15°02'S, 166°54'E, 441–568 m, 1 spm. — Stn CP2422, 14°55'S, 166°55'E, 667–750 m, 1 spm. — Stn CP2420, 15°00'S, 166°55'E, 630–670 m, 5 spms. — Stn CP2422, 14°55'S, 166°55'E, 667–750 m, 1 spm. — Stn CP2432, 15°00'S, 166°55'E, 630–705 m, 2 spms. — Stn CP2433, 14°58'S, 166°54'E, 593–630 m, 1 spm. — Stn CP2435, Big Bay, 14°51'S, 166°54'E, 773–900 m, 1 spm. — Stn CP2465, SE of Malakula, 16°43'S, 167°59'E, 770–799 m, 2 spms. — Stn CP2468, SE of Malakula, 16°31'S, 167°56'E, 550–565 m, 2 spms. — Stn CP2470, 16°25'S, 167°52'E, 568–591 m, 3 spms. — Stn CP2471, between Malakula

and Ambrym, 16°23'S, 167°50'E, 627 m, 1 spm. — SANTO 2006: stn AT60, NE of Tutuba Island, 15°33'S, 167°22'E, 880–953 m, 3 spms.

New Caledonia. CONCALIS: stn CP3028, Grand Passage, 20°17'S, 163°49'E, 650–1200 m, 1 spm.

DISTRIBUTION. — Vanuatu and New Caledonia, living at 532–880 m (Fig. 11).

DESCRIPTION. — Shell large, up to 31.74 mm long, moderately arched (length/height ratio 2.55–2.91, mean 2.72, SD 0.12, n = 7), apex weakly inclined anteriorly. Anterior end occupying 31.0–34.0% (mean 32.1%, SD 1.28, n = 7) of shell length; anterior slope very weakly convex, lateral and posterior slopes broadly convex. Aperture gently arched from side to side. With increasing growth, longitudinal axis gradually twisting roughly 5° anticlockwise between teleoconch I and end of teleoconch II in adults. Teleoconch I depressed conical, length 1.70–2.55 mm (mean 2.03 mm, SD 0.26, n = 7), anterior and posterior slopes flat to weakly concave, lateral slopes flat, glossy, essentially smooth apart from commarginal growth lines and obscure radial lines. Teleoconch II sculptured with strong radial costae and commarginal ridges, rounded nodules at intersections; fine, crisp, crowded commarginal growth lines throughout. Radial costae rounded, crowded, multiplying by intercalation.

Radular teeth (adult, holotype MNHN IM-2009-5798) roughly 360 µm long, with 16 cusps, posterior pair fused.

Holotype length 26.5 mm

MOLECULAR DIAGNOSIS. — The COI, 28S and ITS1 sequences of the holotype are published in GenBank (Table 1). Among available COI sequences, *P. gamma* is reliably and precisely distinguished from other *Pectinodonta* species by the possession of a specific

combination of nucleotides in the amplified sequence at sites 43 (T), 46 (C), 67 (G), 133 (C), 280 (G), 328 (A), 343 (G), 478 (A) and 490 (A). There are no diagnostic sites for *P. gamma* in the amplified sequences of the 28S and ITS1 genes.

REMARKS. — *Pectinodonta gamma* n. sp. is closely related to *P. beta* n. sp. and the two are indistinguishable using the 28S gene but are recovered with COI and ITS1 (Fig. 1B). While the genes indicate that they are closely related allopatric species, regrettably we are unable to detect any constant differences in shell morphology by which they may be distinguished. Fortunately, their radulae are very different (Figs 6G–J), *P. gamma* n. sp. having more numerous cusps (16 vs. 11), so by definition they are not sibling species. The two species appear to be allopatric, all specimens sequenced as *P. beta* occurring off the Solomon Islands, while specimens sequenced as *P. gamma* occurred further south off Vanuatu. Compared with *P. obtusa* (Thiele, 1925) at the same stage of growth, like *P. beta* n. sp., *P. gamma* n. sp. differs in having a more elongate PI and stronger, more widely spaced commarginal ridges and more crowded radial costae.

ETYMOLOGY. — Third letter of the Greek alphabet, from our original descriptor for this clade.

Pectinodonta orientalis Schepman, 1908

Figs 6K, L; 9A–F; 11; Table 7

Pectinodonta orientalis Schepman, 1908: 96, pl. 2, fig. 8.

Other references:

Pectinodonta orientalis - Tsuchida & Kitao 1990: 158. — Sasaki 2000: 27, pl. 13, Acmaeidae fig. 2. — Fuchigami & Sasaki 2005: 161, figs 15C, D, 16E.

TYPE MATERIAL. — Holotype ZMA Moll. 135890, RMNH (Figs 9E, F).

TYPE LOCALITY. — Indonesia, Sulawesi, Makassar Strait, 0°32'S, 119°8.5'E, alive, 1300 m, H.M. Siboga, 20 Jun. 1899 [*Siboga* Expedition: stn 88].

OTHER MATERIAL EXAMINED. — **Taiwan**. TAIWAN 2000: stn CP38, Bashi Channel, 21°32'N, 120°48'E, 1314–1317 m, 8 spms (2 NMNZ M.306352).

Philippines. AURORA 2007: stn CP2679, 14°50'N, 123°12'E, 713–741 m, 1 spm. — Stn CP2684, 15°02'N, 123°05'E, 1413–1449 m, 2 spms. — Stn CP2685, 15°00'S, 123°06'E, 1155–1302 m, 1 spm. — Stn CP2686, 14°56'S, 123°09'E, 996–1037 m, 1 spm. — Stn CC2702, off Polillo Is, 14°55'N, 123°12'E, 944–1004, 1 spm. — Stn CP2751, 15°36'N, 121°58'E, 1456–1471 m, 1 spm. — Stn CP2754, 15°37'S, 121°59'E, 1273–1333 m, 2 spms.

Solomon Islands. SALOMONBOA 3: stn CP2801, Malaita, 8°41'S, 161°05'E, 792–1042 m, 1 spm (Table 1).

Papua New Guinea. BIOPAPUA: stn CP3731, off Mambre Bay, 7°50'S, 148°04'E, 895–1150 m, 1 spm. — Stn CP3762, off Feni Islands, 3°57'S, 153°49'E, 995–1050 m, 8 spms. — Stn CP3638, Huon Gulf, S of Lae, 7°23'S, 147°34'E, 890–895 m, 8 spms (Table 1).

DISTRIBUTION. — Japan (Tsuchida & Kitao 1990; Sasaki 2000), Taiwan, Philippines, Sulawesi, Papua New Guinea and Solomon Islands, 741–1456 m, living at 895–1314 m (Fig. 11).

DESCRIPTION. — Shell (holotype) 17.86 mm long, moderately arched, height 7.79 mm (excluding apertural arching), length/height ratio 2.29. Anterior end occupying 34.3% of shell length; anterior slope very weakly convex, lateral and posterior slopes broadly convex. Aperture gently arched from side to side. With increasing growth, longitudinal axis gradually twisting roughly 5° anticlockwise between teleoconch I and end of teleoconch II. Teleoconch I depressed-conical (summit etched away), length 2.40 mm, width 1.70 mm, anterior and lateral slopes weakly convex, posterior slope broadly convex, glossy, essentially smooth apart from commarginal growth lines and obscure radial lines. Teleoconch II sculptured with strong radial costae and commarginal ridges; low, rounded, mostly radially elongate nodules at intersections; fine, crisp, crowded commarginal growth lines throughout. Radial costae rounded, multiplying by intercalation, weaker than commarginals at first (to roughly 8 mm shell length), becoming more sharply defined than commarginals and about as wide as them, most interspaces markedly wider than each costa. Commarginal ridge interspaces wider than each ridge. Although taken alive and the soft parts are still extant, the radula was not illustrated by Schepman (1908). Radular teeth (subadult, MNHN IM-2009-27330) with 13 or 14 sharp cusps.

MOLECULAR DIAGNOSIS. — The holotype of *P. orientalis* Schepman, 1908 was not sequenced, and the following molecular diagnosis may thus not stand for the holotype. Among available sequences, *P. orientalis* is reliably and precisely distinguished from other *Pectinodonta* species by possession of a specific combination of nucleotides in the amplified sequence of the COI gene at sites 35 (A), 70 (A), 130 (G), 166 (G), 169 (T), 232 (T), 241 (A), 334 (T), 355 (T), 382 (G), 401 (T), 403 (A), 493 (G) and 565 (A), in the 28S gene at sites 509 (C), 583 (A) and 612 (G), and in the ITS1 gene at sites 17 (A), 19 (C), 20 (G), 22 (C), 25 (C), 26 (G), 60 (A), 65 (A), 92 (G), 112 (T), 114 (A), 118 (C), 121 (C), 122 (A), 155 (T), 176 (C),

179 (C), 213 (C), 221 (T), 223 (G), 227 (C), 229 (C), 246 (G), 250 (G), 252 (T), 253 (G), 287 (C), 305 (T), 306 (C), 354 (A), 377 (C), 388 (A), 396 (A) and 458 (C).

REMARKS. — Specimens recorded here from Taiwan, the Philippines, Vanuatu and the Solomon Islands closely resemble the holotype of *P. orientalis* Schepman, 1908 in gross facies. Thus, although molecular data are not available for the holotype, based on morphology the sequenced specimens were attributed to *P. orientalis*. *Pectinodonta orientalis* is distinctive in the combination of low to moderately arched shell that attains very large size (length up to 39.85 mm), size of teleoconch I (length 2.30–2.60 mm), and the widely spaced radial ribs, which appear unusually prominent relative to the commarginal ridges because of the wide spacing of the latter. In the holotype and the sequenced material examined, shell length/height ratio is 2.23–4.32 (mean 3.21, SD 0.65, n = 10), and the anterior end occupies 29.0–41.6% (mean 34.3%, SD 3.14, n = 10) of the shell length. The radula of a specimen from Papua New Guinea is illustrated here (Figs 6K, L). Two superficially similar species, *P. beta* n. sp. and *P. gamma* n. sp. are described above. *Pectinodonta obtusa* (Thiele, 1925) (Figs 9G, H) from off Sumatra, 750 m, differs in having P1 more obliquely skewed and subquadrate rather than oval, and in having stronger, more widely spaced commarginal ridges and more crowded radial costae. Among the species treated here, *P. orientalis* Schepman, 1908 was recovered as being most closely related to the New Zealand species *P. marinovichi* Marshall, 1998 (Fig. 1), the shell of which is similar in shape and sculpture but mostly more elevated (length/height ratio 1.67–2.31 mean 1.98, SD 0.18, n = 9)

Pectinodonta philippinarum n. sp.

Figs 8; 10A–D; Table 8.

TYPE MATERIAL. — Holotype MNHN IM-2009-10788, 1 paratype MNHN and 1 paratype NMNZ (as listed Table 1) .

TYPE LOCALITY. — Philippine Islands, eastern Luzon, off Dingalan Bay, 15°18'N, 121°37'E, 558–587 m.

MATERIAL EXAMINED. — **Philippines**. AURORA 2007: stn CP2663, eastern Luzon, 15°45'N, 121°45'E, 562 m, 2 spms. — Stn DW2728, eastern Luzon, off Dingalan Bay, 15°18'N, 121°37'E, 558–587 m, 1 spm.

DISTRIBUTION. — Philippine Islands, living at ~562 m (Fig. 8).

DESCRIPTION. — Shell small (adult?), up to 9.50 mm long, weakly arched (length/height ratio 3.30–3.55), apex weakly inclined anteriorly. Anterior end occupying 3.20–3.55% of shell length; slopes weakly convex, almost flat. Aperture gently arched from side to side, no indication of twisting with increasing size. Teleoconch I conical, length 2.30–2.40 mm, anterior slope weakly concave, lateral and posterior slopes more or less flat, glossy, essentially smooth apart from commarginal growth lines and obscure radial lines. Teleoconch II sculptured with strong radial costae and commarginal ridges, small rounded nodules at intersections; fine, crisp, crowded commarginal growth lines throughout. Radial costae rounded, multiplying by intercalation, most interspaces narrower than each costa. Radular teeth (holotype MNHN IM-2009-10788) roughly 170 μm long, with 11 cusps, posterior pair fused.

Holotype length 9.50 mm.

MOLECULAR DIAGNOSIS. — The 28S and ITS1 sequences of the holotype are published in GenBank (Table 1). Among available sequences, *P. philippinarum* is reliably and precisely distinguished from the other *Pectinodonta* species by possession of a specific combination of nucleotides in the amplified sequences of the 28S gene at site 502 (T), and in the ITS1 gene at site 455 (T). *Pectinodonta philippinarum* n. sp. was not sequenced for COI.

REMARKS. — In its depressed-conical shape at the same stage of growth, *P. philippinarum* n. sp. resembles *P. beta* n. sp., *P. orientalis* Schepman, 1908 and *P. gamma* n. sp., differing from *P. beta* n. sp. in having a larger PI (length 2.30–2.40 vs. 1.90–2.20 mm) and narrower radial costae, from *P. orientalis* in having a more narrowly oval PI and much more closely spaced commarginal ridges, and from *P. gamma* n. sp. as well as *P. obtusa* (Thiele, 1925) in that PI is not twisted relative to the longitudinal axis of PII.

ETYMOLOGY. — After the type locality, Philippine Islands.

CONCLUSIONS

The seven new species reported here are only a sub-sample of the diversity of *Pectinodonta* from the Western Pacific. Indeed, at least eight additional species from off Taiwan, the Philippine Islands, Indonesia and New Caledonia segregated on shell morphology are not described as either no live material was available or the DNA sequencing was not successful. Most of the well-sampled species display a rather large depth range. In most cases, sister-species pairs displayed an allopatric geographic distribution. The species sampled in a single geographic area (sympatric species) were thus not closely related.

With the seven species reported here, of which six are described as new species, a total of fifteen named *Pectinodonta* species are thus known from the tropical West Pacific (Table 9).

These results are in agreement with those found for other taxonomic groups (Lorion *et al.* 2010; Samadi *et al.* 2010; Sigwart *et al.* 2010; Thubaut *et al.* in press; Fraussen & Stahlschmidt, herein), supporting the hypothesis that, contrary to other chemosynthetic environments in the deep sea such as cold seeps and hydrothermal vents, the diversity on organic falls is still largely underestimated.

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REFERENCES

- BECK L. A. 1996. — Morphology and anatomy of new species of neolepetopsid, acmaeid, fissurellid and pyropeltid limpets from Edison Seamount off Lihir Islands (West Pacific). *Archiv für Molluskenkunde* 125: 87–103.
- BOUCHET P., HEROS 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 : 9–40.
- COSEL R. von & MARSHALL B. A. 2010. — A new genus and species of large mussel (Mollusca: Bivalvia: Mytilidae) from the Kermadec Ridge. *Tuhinga* 21: 59-73.
- DALL W. H. 1882. — On certain limpets and chitons from the deep waters off the eastern coast of the United States. *Proceedings of the United States National Museum* 4: 400–414.
- DALL W. H. 1889. — Report on the Mollusca. Part 2. Gastropoda and Scaphopoda. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877–78) and in the Caribbean Sea (1879–80), by the U.S. Coast Survey Steamer “Blake”, Lieut.-Commander C. D. Sigsbee, U.S.N., and Commander J. R. Bartlett, U.S.N., commanding. 29. *Bulletin of the Museum of Comparative Zoology* 18: 1–492.
- DALL W. H. 1925. — Illustrations of unfigured types of shells in the collection of the United States National Museum. *Proceedings of the United States National Museum* 66: 1–41.
- DAUTZENBERG P. 1925. — Mollusques nouveaux provenant des croisières du Prince Albert Ier de Monaco. *Bulletin de l'Institut Océanographique de Monaco* 457: 1–12.

- DAUTZENBERG P. 1927. — Mollusques provenant des campagnes scientifiques du Prince Albert Ier de Monaco dans l'Océan Atlantique et dans le Golfe de Gascogne. *Résultats des Campagnes Scientifiques Accomplies sur son Yacht par Albert Ier, Prince Souverain de Monaco*, 72
- DAYRAT B., TILLIER A., LECOINTRE G. & TILLIER S. 2001. — New clades of euthyneuran gastropods (Mollusca) from 28S rRNA sequences. *Molecular Phylogenetics and Evolution* 19: 225–235.
- EDGAR R. C. 2004. — MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32: 1792–1797.
- 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.
- FUCHIGAMI T. & SASAKI T. 2005. — The shell structure of the Recent Patellogastropoda (Mollusca: Gastropoda). *Paleontological Research* 9: 143–168.
- HABE T. 1949. — Notes on *Cocculina rhyssa* Dall. *Venus* 15: 67–68
- HASEGAWA K. 1997. — Sunken wood-associated gastropods collected from Suruga Bay, Pacific side of the central Honshu, Japan, with descriptions of 12 new species. *National Science Museum Monographs* 12: 59–123.
- HASEGAWA K. 2009. — Upper bathyal gastropods of the Pacific coast of northern Honshu, Japan, chiefly collected by R/V *Wakataka-maru*. *National Museum of Nature and Science Monographs* 39: 225–383.
- HICKMAN C. S. 1983. — Radular patterns, systematics, diversity, and ecology of deep-sea limpets. *The Veliger* 26: 73–92.
- HOLZNAGEL W. E. — A non-destructive method for cleaning gastropod radulae from frozen, alcohol-fixed, or dried material. *American Malacological Bulletin* 14: 181–183.

- HUELSENBECK J. P. & RONQUIST F. 2001. — MrBayes: bayesian inference of phylogeny. *Bioinformatics* 17: 754–755.
- JOVELIN R. & JUSTINE J.-L. 2001. — Phylogenetic relationships within the polyopisthocotylean monogeneans (Platyhelminthes) inferred from partial 28S rDNA sequences. *International Journal for Parasitology* 31: 393–401.
- LESCHINE S. B. 1995. — Cellulose degradation in anaerobic environments. *Annual Reviews of Microbiology* 49: 399–426.
- LINDBERG D. R. 1988. — The Patellogastropoda. *Malacological Review. Supplement* 4: 35–63.
- LINDBERG D. R. & HEDEGAARD C. 1996. — A deep water patellogastropod from Oligocene water-logged wood of Washington State, USA (Acmaeoidea: *Pectinodonta*). *Journal of Molluscan Studies* 62: 299–314.
- LORION J., BUGÉ B., CRUAUD C. & SAMADI S. 2010. — New insights into diversity and evolution of deep-sea Mytilidae (Mollusca: Bivalvia). *Molecular Phylogenetics and Evolution* 57: 71–83.
- MARSHALL B. A. 1985. — Recent and Tertiary deep-sea limpets of the genus *Pectinodonta* (Mollusca: Gastropoda) from New Zealand and New South Wales. *New Zealand Journal of Zoology* 12: 273–282.
- MARSHALL B. A. 1998. — A new deep-sea limpet of the genus *Pectinodonta* Dall, 1882 from New Zealand, and new distribution records for *P. aupouria* and *P. morioria* Marshall, 1985 (Mollusca: Gastropoda). *The Nautilus* 112: 52–57.
- MARWICK, J. 1931. — The Tertiary Mollusca of the Gisborne district. Wellington. *New Zealand Geological Survey Paleontological Bulletin* 13.
- NAKANO T. & OZAWA T. 2007. — Worldwide phylogeography of limpets of the order Patellogastropoda: molecular, morphological and palaeontological evidence. *Journal of*

- NOLF F. & VERSTRAETEN J. 2003. — Deep-water species of Mollusca in the Mozambique Channel. Part 1. *Neptunea* 2(3): 1–27.
- OKUTANI T. 1964. — Report on the archibenthal and abyssal gastropod Mollusca mainly collected from Sagami Bay and adjacent waters by the R.V. *Sôyô-Marû* during the years 1955–1963. *Journal of the Faculty of Science, University of Tokyo* (2)15: 371–447.
- OKUTANI T., FUJIKURA K. & SASAKI T. 1993. — New taxa and new distribution records of deepsea gastropods collected from or near the chemosynthetic communities in the Japanese waters. *Bulletin of the National Science Museum, Tokyo, Series A* 19: 123–143.
- OKUTANI T., TSUCHIDA E. & FUJIKURA K. 1992. — Five bathyal gastropods living within or near the *Calyptogena*-community of the Hatsushima Islet, Sagami Bay. *Venus* 51: 137–148.
- OLSSON A. A. 1971. — Mollusks from the Gulf of Panama collected by R/V John Elliott Pillsbury, 1967, in BAYER F. M. & VOSS G. L. (eds), *Studies in Tropical American Mollusks. Biological Results of the University of Miami Deep-Sea Expeditions* 77: 35–92.
- PAILLERET M., HAGA T., PETIT P., PRIVÉ-GILL C., SAEDLOU N., GAILL F. & ZBINDEN M. 2007. — Sunken wood from the Vanuatu Islands: identification of wood substrates and preliminary description of associated fauna. *Marine Ecology* 28: 233–341.
- PILSBRY H. A. 1891–92. — Acmaeidae, Lepetidae, Patellidae, Titiscaniidae. *Manual of conchology; structural and systematic, with illustrations of the species, series 1* 13: 1–195.
- RAMBAUT A. & DRUMMOND A. J. 2007. — Tracer v1.4. Available from <http://beast.bio.ed.ac.uk/Tracer>
- SAMADI S., CORBARI L., LORION J., HOURDEZ S., HAGA T., DUPONT J., BOISSELIER M.-C. & RICHER DE FORGES B. 2010. — Biodiversity of deep-sea

- organisms associated with sunken-wood or other organic remains sampled in the tropical Indo-Pacific. *Cahiers de Biologie Marine* 51: 459–466.
- SASAKI T. 1998. — Comparative anatomy and phylogeny of the recent Archaeogastropoda (Mollusca: Gastropoda). *The University Museum, The University of Tokyo, Bulletin*, 38: 1–224.
- SASAKI T. 2000. — Family Acmaeidae. 27, in Okutani T. (ed.), *Marine mollusks in Japan*. Tokai University Press, Tokyo.
- SASAKI T., OKUTANI T. & FUJIKURA K. 2003. — New taxa and new records of patelliform gastropods associated with chemoautosynthesis-based communities in Japanese waters. *The Veliger* 46: 189–210.
- SASAKI T., OKUTANI T. & FUJIKURA K. 2005. — Molluscs from hydrothermal vents and cold seeps in Japan: a review of taxa recorded in twenty recent years (1984–2004). *Venus* 64: 87–133.
- SASAKI T., OKUTANI T. & FUJIKURA K. 2006. — Anatomy of *Bathycyma secunda* Okutani, Fujikura & Sasaki, 1993 (Patellogastropoda: Acmaeidae). *Journal of Molluscan Studies* 72: 295–309
- SCHEPMAN M. 1908. — The Prosobranchia of the *Siboga* Expedition. Part 1. Rhipidoglossa and Docoglossa. *Siboga-Expeditie, Uitkomsten op zoologisch, botanisch, oceanographisch en geologisch gebied verzameld in Nederlandsch Oost-Indië 1899–1900 aan boord H.M. Siboga onder commando van Luitenant ter zee I^e kl. G.F. Tydeman* 49a (39): 1–107.
- SCHOOLEY C., HICKMAN C. S. & LANE W. C. 1982. — Computer graphic analysis of stereo micrographs as a taxonomic tool. *The Veliger* 24: 205–207.
- SIGWART J. D., SCHWABE E., SAITO H., SAMADI S. & GIRIBET G. 2010. — Evolution in the deep sea: a combined analysis of the earliest diverging living chitons (Mollusca: Polyplacophora: Lepidopleurida). *Invertebrate Systematics* 24: 560–572.

- STAMATAKIS A. 2006. — RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22: 2688–2690.
- THIELE J. 1925. — Gastropoda der Deutschen Tiefsee-Expedition. II. Teil. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898–1899* 17 (2): 35–382.
- THUBAUT J., PULLANDRE N., FAURE B., CRUAUD C. & SAMADI S. in press. — Are hydrothermal vents evolutionary dead-ends? *Ecology and Evolution*,
- TSUCHIDA E. & ISHIDA F. 1977. — Notes on *Pectinodonta rhyssa* (Dall, 1925) and *Cocculina japonica* Dall, 1907. *Chiribotan* 9: 148.
- TSUCHIDA E. & KITAO K. 1990. — Japanese Pectinodontidae comprises two species. *Venus* 49: 158. [symposium abstract: in Japanese]
- WARÉN A. 2011. — Molluscs on biogenic substrates. 438-448, in BOUCHET P., LE GUYADER H. & PASCAL O. (eds), *The Natural History of Santo*. MNHN, Paris; IRD, Marseille; PNI, Paris. 572 p. (Patrimoines naturels; 70).
- WHITE T. J., BRUNS T., LEE S. & TAYLOR J. 1990. — Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. 315–322, in Innis M. A., Gelfand D. H., Sninsky J. J. & White T. J. (eds), *PCR Protocols: A Guide to Methods and Applications*. Academic Press, Inc., San Diego.
- ZBINDEN M., PAILLERET M., RAVAUX J., GAUDRON S. M., HOYOUX C., LAMBOURDIÈRE J., WARÉN A., LORION J., HALARY S. & DUPERRON S. 2010. — Bacterial communities associated with the wood-feeding gastropod *Pectinodonta* sp. (Patellogastropoda, Mollusca). *FEMS Microbiology Ecology* 74: 450–463

TABLE 1. — List of sequenced *Pectinodonta* specimens.

MNHN number	NMNZ number	species	Status	Coordinates; depth (m)	BOL
IM-2009-7719		alis	paratype MNHN	15°07'S, 166°51'E; 297-387	PECTO0
IM-2009-7722	M.306246	alis	paratype NMNZ	15°07'S, 166°51'E; 297-387	PECTO0
IM-2009-7723		alis	holotype	15°07'S, 166°51'E; 297-387	PECTO0
IM-2009-10766		alis		9°22'S, 160°31'E; 0-620	PECTO0
IM-2009-4314		alis		10°26'S, 161°58'E; 173-379	PECTO0
IM-2009-10771		alis		15°07'S, 166°53'E; 328-354	PECTO0
IM-2009-7708		alpha		14°54'S, 166°51'E; 0-777	PECTO0
IM-2009-4252		alpha		08°43'S, 161°00'E; 314-410	PATEL 10
IM-2009-4253		alpha		08°43'S, 161°00'E; 314-410	PATEL 10
IM-2009-4256		alpha		08°43'S, 161°00'E; 314-410	PATEL 10
IM-2009-4257		alpha		08°43'S, 161°00'E; 314-410	PATEL 10
IM-2009-9259		alpha	paratype MNHN	15°40'S, 167°01'E; 431-445	PATEL 10
IM-2009-9260		alpha	paratype MNHN	15°40'S, 167°01'E; 431-445	PATEL 10
IM-2009-9274		alpha	paratype MNHN	15°40'S, 167°01'E; 431-445	PATEL 10
IM-2009-9275		alpha	paratype MNHN	15°40'S, 167°01'E; 431-445	PATEL 10
IM-2009-9276		alpha	paratype MNHN	15°40'S, 167°01'E; 431-445	PATEL 10
IM-2009-9294		alpha	paratype MNHN	15°40'S, 167°01'E; 431-445	PATEL 10
IM-2009-9296	M.306245	alpha	paratype NMNZ	15°40'S, 167°01'E; 431-445	PATEL 10
IM-2009-9297		alpha	paratype MNHN	15°40'S, 167°01'E; 431-445	PATEL 10
IM-2009-9298		alpha		15°40'S, 167°01'E; 431-445	PATEL 10
IM-2009-9299		alpha	paratype MNHN	15°40'S, 167°01'E; 431-445	PATEL 10
IM-2009-9300		alpha		15°40'S, 167°01'E; 431-445	PATEL 10
IM-2009-9301		alpha	paratype MNHN	15°40'S, 167°01'E; 431-445	PATEL 10
IM-2009-9302		alpha	paratype MNHN	15°40'S, 167°01'E; 431-445	PATEL 10
IM-2009-9311		alpha	paratype MNHN	15°40'S, 167°01'E; 431-445	PATEL 10
IM-2009-9314		alpha	holotype	15°40'S, 167°01'E; 431-445	PATEL 10
IM-2009-9315	M.306245	alpha	paratype NMNZ	15°40'S, 167°01'E; 431-445	PATEL 10
IM-2009-9316		alpha	paratype MNHN	15°40'S, 167°01'E; 431-445	PATEL 10
IM-2009-10768		alpha		15°40'S, 167°01'E; 431-445	PECTO0
IM-2009-10769		alpha		15°40'S, 167°01'E; 431-445	PECTO0
IM-2009-10770		alpha		15°40'S, 167°01'E; 431-445	PECTO0
IM-2009-4217		alpha	paratype MNHN	15°39'S, 167°01'E; 275-290	PATEL 10
IM-2009-4218		alpha	paratype MNHN	15°39'S, 167°01'E; 275-290	PATEL 10

IM-2009-4219		alpha	paratype MNHN	15°39'S, 167°01'E; 275-290	PATEL 10
IM-2009-10786		alpha or aurora		15°18'N, 121°37'E; 558-587	PECT10
IM-2009-27289		alpha or aurora		06°45'S, 147°49'E; 460-485	PECT00
IM-2009-27290		alpha or aurora		06°45'S, 147°49'E; 460-485	PECT00
IM-2009-27293		alpha or aurora		06°45'S, 147°49'E; 460-485	PECT00
IM-2009-27294		alpha or aurora		06°45'S, 147°49'E; 460-485	PECT00
IM-2009-27298		alpha or aurora		06°45'S, 147°49'E; 460-485	PECT00
IM-2009-27300		alpha or aurora		06°47'S, 147°12'E; 592-660	PECT00
IM-2009-27301		alpha or aurora		06°47'S, 147°12'E; 592-660	PECT00
IM-2009-27302		alpha or aurora		06°47'S, 147°12'E; 592-660	PECT00
IM-2009-27323		alpha or aurora		04°58'S, 145°50'E; 502-529	PECT00
	M.284356A	aupouria			
	M.284356B	aupouria			
	M.284356C	aupouria			
IM-2009-5085		aurora	paratype MNHN	15°27'N, 121°36'E; 0-556	PECT03
IM-2009-5087		aurora	paratype MNHN	15°27'N, 121°36'E; 0-556	PECT03
IM-2009-5088	M.306348	aurora	paratype NMNZ	15°27'N, 121°36'E; 0-556	PECT03
IM-2009-5089		aurora	paratype MNHN	15°27'N, 121°36'E; 0-556	PECT03
IM-2009-5090		aurora	paratype MNHN	15°27'N, 121°36'E; 0-556	PECT03
IM-2009-5091		aurora	paratype MNHN	15°27'N, 121°36'E; 0-556	PECT03
IM-2009-7710		aurora	holotype	15°27'N, 121°36'E; 0-556	PECT03
IM-2009-7711		aurora	paratype MNHN	15°27'N, 121°36'E; 0-556	PECT03
IM-2009-27291		aurora		06°45'S, 147°49'E; 460-485	PECT02
IM-2009-27292		aurora		06°45'S, 147°49'E; 460-485	PECT02
IM-2009-27296		aurora		06°45'S, 147°49'E; 460-485	PECT02
IM-2009-27297		aurora		06°45'S, 147°49'E; 460-485	PECT02
IM-2009-27299		aurora		06°45'S, 147°49'E; 460-485	PECT02
IM-2009-27303		aurora		06°47'S, 147°12'E; 592-660	PECT02
IM-2009-27304		aurora		06°47'S, 147°12'E; 592-660	PECT02
IM-2009-27305		aurora		06°47'S, 147°12'E; 592-660	PECT03
IM-2009-27279		aurora		02°15'S, 150°16'E; 402-440	PECT02
IM-2009-27280		aurora		02°15'S, 150°16'E; 402-440	PECT02
IM-2009-27306		beta		06°47'S, 147°12'E; 592-660	PECT03
IM-2009-27307		beta		06°47'S, 147°12'E; 592-660	PECT04
IM-2009-27308		beta		06°47'S, 147°12'E; 592-660	PECT04
IM-2009-27309		beta		06°47'S, 147°12'E; 592-660	PECT04
IM-2009-27310		beta		06°47'S, 147°12'E; 592-660	PECT04
IM-2009-27311		beta		06°47'S, 147°12'E; 592-660	PECT04
IM-2009-27312	M.306349	beta	paratype NMNZ	04°38'S, 149°27'E; 564-712	PECT04
IM-2009-27313		beta	paratype MNHN	04°38'S, 149°27'E; 564-712	PECT04
IM-2009-27314		beta	paratype MNHN	04°38'S, 149°27'E; 564-712	PECT04
IM-2009-27318	M.306349	beta	paratype NMNZ	04°38'S, 149°27'E; 564-712	PECT04
IM-2009-27319		beta	paratype MNHN	04°38'S, 149°27'E; 564-712	PECT04
IM-2009-27320		beta	paratype MNHN	04°38'S, 149°27'E; 564-712	PECT05
IM-2009-27321		beta	paratype MNHN	04°38'S, 149°27'E; 564-712	PECT05
IM-2009-27322		beta		04°58'S, 145°50'E; 502-529	PECT05

IM-2009-27324		beta		07°52'S, 148°03'E; 575-655	PECTO9
IM-2009-27325		beta		07°52'S, 148°03'E; 575-655	PECTO9
IM-2009-27328		beta		09°12'S, 152°16'E; 556-645	PECTO9
IM-2009-27329		beta		09°12'S, 152°16'E; 556-645	PECTO9
IM-2009-27339		beta		05°05'S, 152°02'E; 782-1085	PECTO9
IM-2009-7706		beta	holotype	7°43' S, 156°26' E; 582-609	PECTO6
IM-2009-8328		beta	paratype MNHN	7°43' S, 156°25' E; 664-682	PECTO6
IM-2009-8330		beta	paratype MNHN	7°43' S, 156°25' E; 664-682	PECTO6
IM-2009-8331		beta	paratype MNHN	7°43' S, 156°25' E; 664-682	PECTO6
IM-2009-8333		beta	paratype MNHN	7°43' S, 156°25' E; 664-682	PECTO6
IM-2009-4278		beta	paratype MNHN	09°12'S, 160°55'E; 706-722	PATEL 10
IM-2009-4269		beta	paratype MNHN	08°31'S, 160°39'E; 570-885	PATEL 10
IM-2009-4271		beta	paratype MNHN	08°31'S, 160°39'E; 570-885	PATEL 10
IM-2009-4272		beta	paratype MNHN	08°31'S, 160°39'E; 570-885	PECTO6 PATEL
IM-2009-4273		beta	paratype MNHN	08°31'S, 160°39'E; 570-885	10 PATEL
IM-2009-4285	M.306350	beta	paratype NMNZ	08°31'S, 160°39'E; 570-885	10 PATEL
IM-2009-4284		beta	paratype MNHN	08°30'S, 160°37'E; 160-760	10
IM-2009-4260		beta	paratype MNHN	10°19'S, 161°54'E; 686-864	PECTO9
IM-2009-4261		beta	paratype MNHN	10°19'S, 161°54'E; 686-864	PECTO9
IM-2009-27326		beta or gamma		07°52'S, 148°03'E; 575-655	PECTO9
IM-2009-10763		beta or gamma		15°00'S, 166°55'E; 630-705	PECTO9
IM-2009-10764		beta or gamma		15°00'S, 166°55'E; 630-705	PECTO9
IM-2009-10765		beta or gamma		15°00'S, 166°55'E; 630-705	PECT10 PATEL
IM-2009-4211		gamma		15°03'S, 166°53'E; 432-532	10 PATEL
IM-2009-4195		gamma		15°02'S, 166°54'E; 441-568	10
IM-2009-5787		gamma	paratype MNHN	15°00'S, 166°55'E; 630-670	PECTO6
IM-2009-5788	M.306351	gamma	paratype NMNZ	15°00'S, 166°55'E; 630-670	PECTO7
IM-2009-5789		gamma	paratype MNHN	15°00'S, 166°55'E; 630-670	PECTO7
IM-2009-5797		gamma	paratype MNHN	15°00'S, 166°55'E; 630-670	PECTO7
IM-2009-5798		gamma	holotype	15°00'S, 166°55'E; 630-670	PECTO7 PATEL
IM-2009-4208		gamma		14°55'S, 166°55'E; 667-750	10 PATEL
IM-2009-4198		gamma		15°00'S, 166°55'E; 630-705	10 PATEL
IM-2009-4206		gamma		15°00'S, 166°55'E; 630-705	10 PATEL
IM-2009-4210		gamma		14°58'S, 166°54'E; 593-630	10 PATEL
IM-2009-4202		gamma		14°54'S, 166°56'E; 773-900	10 PATEL
IM-2009-4203		gamma	paratype MNHN	16°43'S, 167°59'E; 770-799	10 PATEL
IM-2009-4205		gamma	paratype MNHN	16°43'S, 167°59'E; 770-799	10 PATEL
IM-2009-4199		gamma		16°31'S, 167°55'E; 550-565	10

IM-2009-4201		gamma		16°31'S, 167°55'E; 550-565	PATEL 10
IM-2009-8354		gamma		16°25'S, 167°52'E; 568-591	PECTO0
IM-2009-8355		gamma		16°25'S, 167°52'E; 568-591	PECTO0
IM-2009-8356		gamma		16°25'S, 167°52'E; 568-591	PECTO0
IM-2009-4216		gamma		16°23'S, 167°50'E; 591-627	PECTO0 PATEL
IM-2007-35459		gamma		20°17'S, 163°49'E; 650-1200	10
IM-2009-10781		gamma		15°33'S, 167°22'E; 880-953	PECTO0
IM-2009-10782		gamma		15°33'S, 167°22'E; 880-953	PECTO0
IM-2009-10783		gamma		15°33'S, 167°22'E; 880-953	PECTO0
	M.298558A	marinovichi			
	M.298558B	marinovichi			
	M.284165A	moria			
	M.284165B	moria			
	M.284165C	moria			
IM-2009-27281		orientalis		07°23'S, 147°34'E; 890-895	PECTO0
IM-2009-27282		orientalis		07°23'S, 147°34'E; 890-895	PECTO0
IM-2009-27283		orientalis		07°23'S, 147°34'E; 890-895	PECTO0
IM-2009-27284		orientalis		07°23'S, 147°34'E; 890-895	PECTO0
IM-2009-27285		orientalis		07°23'S, 147°34'E; 890-895	PECTO0
IM-2009-27286		orientalis		07°23'S, 147°34'E; 890-895	PECTO0
IM-2009-27287		orientalis		07°23'S, 147°34'E; 890-895	PECTO0
IM-2009-27288		orientalis		07°23'S, 147°34'E; 890-895	PECTO0
IM-2009-27327		orientalis		07°50'S, 148°04'E; 895-1150	PECTO0
IM-2009-27330		orientalis		03°57'S, 153°49'E; 995-1050	PECTO0
IM-2009-27331		orientalis		03°57'S, 153°49'E; 995-1050	PECTO0
IM-2009-27332		orientalis		03°57'S, 153°49'E; 995-1050	PECTO0
IM-2009-27333		orientalis		03°57'S, 153°49'E; 995-1050	PECTO0
IM-2009-27335		orientalis		03°57'S, 153°49'E; 995-1050	PECTO0
IM-2009-27336		orientalis		03°57'S, 153°49'E; 995-1050	PECTO0
IM-2009-27337		orientalis		03°57'S, 153°49'E; 995-1050	PECTO0
IM-2009-27338		orientalis		03°57'S, 153°49'E; 995-1050	PECTO0 PATEL
IM-2009-4239		orientalis		08°41'S, 161°05'E; 792-1042	10
IM-2009-10790		philippinarum	paratype MNHN	15°45'N, 121°45'E; 0-562	PECTO0
IM-2009-10792	M.306353	philippinarum	paratype NMNZ	15°45'N, 121°45'E; 0-562	PECTO0
IM-2009-10788		philippinarum	holotype	15°18'N, 121°37'E; 558-587	PECTO0

TABLE 2. — *Pectinodonta alpha* n. sp. Shell measurements (in mm) and ratios of sequenced type specimens from SANTO 2006 stn AT120.

Length (L)	Height (H)	Anterior length (AL)	LH ratio	AL%L	Specimen
12.04	5.61	3.70	2.14	30.7	MNHN-IM-2009-9314 (holotype)
12.93	7.77	3.05	1.66	23.5	MNHN-IM-2009-9315
13.23	7.80	2.75	1.69	20.7	MNHN-IM-2009-9316
13.71	7.77	4.00	1.76	29.1	MNHN-IM-2009-9294
13.21	7.92	3.20	1.66	24.2	MNHN-IM-2009-9299
12.60	6.36	3.55	1.98	28.1	MNHN-IM-2009-9274
13.87	7.31	3.30	1.89	23.7	MNHN-IM-2009-9297
13.08	6.94	3.70	1.88	28.2	MNHN-IM-2009-9275
13.06	6.99	3.60	1.86	27.5	MNHN-IM-2009-9296
12.72	6.67	3.45	1.90	27.1	MNHN-IM-2009-9301
13.20	6.86	3.80	1.92	28.7	MNHN-IM-2009-9311
12.68	6.79	4.05	1.86	31.9	MNHN-IM-2009-9260

10.96	6.01	3.15	1.82	28.7	MNHN-IM-2009-9276
11.75	5.91	3.00	1.99	25.5	MNHN-IM-2009-9259
			mean 1.85 (SD 0.13)	mean 26.9 (SD 3.08)	

TABLE 3. — *Pectinodonta alis* n. sp. Shell measurements (in mm) and ratios of sequenced type specimens from BOA 1 stn CP2448.

Length (L)	Height (H)	Anterior length (AL)	LH ratio	AL%L	Specimen
9.80	4.15	1.90	2.36	19.3	MNHN-IM-2009-7723 (holotype)
9.00	3.90	1.80	2.30	20.0	MNHN-IM-2009-7719
8.80	4.10	1.25	2.10	14.2	MNHN-IM-2009-7722
			mean 2.25 (SD 0.13)	mean 17.8 (SD 3.10)	

TABLE 4. — *Pectinodonta aurora* n. sp. Shell measurements (in mm) and ratios of sequenced type specimens from.

Length (L)	Height (H)	Anterior length (AL)	LH ratio	AL%L	Specimen
13.04	5.54	4.00	2.35	30.6	MNHN-IM-2009-7710 (holotype)
11.08	4.16	3.90	2.66	35.1	MNHN-IM-2009-7711
14.41	5.61	4.30	2.56	29.8	M.306348/ MNHN-IM-2009-5088
14.77	6.24	4.90	2.36	33.1	MNHN-IM-2009-5089
14.70	5.48	4.75	2.68	32.3	MNHN-IM-2009-5087
16.71	7.11	4.90	2.35	29.3	MNHN-IM-2009-5085
17.40	8.08	5.30	2.15	30.4	MNHN-IM-2009-5090
18.13	7.67	5.70	2.36	31.4	MNHN-IM-2009-5091
			mean 2.43 (SD 0.18)	mean 31.5 (SD 1.92)	

TABLE 5. — *Pectinodonta beta* n. sp. Shell measurements (in mm) and ratios of sequenced type specimens from SALOMON 2: stns CP2245 and CP2246, and SALOMONBOA 3: stns CP2787, CP2788, CP2777 and CP2821.

Length (L)	Height (H)	Anterior length (AL)	LH ratio	AL%L	Specimen
21.27	6.43	8.14	3.33	38.2	MNHN-IM-2009-7706 (holotype)
25.40	9.27	6.38	3.98	25.1	MNHN-IM-2009-4260
26.20	9.82	7.68	2.66	29.3	MNHN-IM-2009-4261
21.53	5.93	7.92	3.63	36.7	MNHN-IM-2009-8331
20.96	5.79	7.84	3.62	37.4	MNHN-IM-2009-8330
17.28	4.85	6.32	3.56	36.5	MNHN-IM-2009-8333
18.54	6.98	6.72	2.65	36.2	MNHN-IM-2009-4284
18.82	8.27	6.37	2.27	33.8	MNHN-IM-2009-4278

22.59	9.39	8.40	2.40	37.1	MNHN-IM-2009-4269
12.70	4.05	4.75	3.13	37.4	MNHN-IM-2009-4272
13.52	4.31	5.15	3.13	38.0	MNHN-IM-2009-4271
11.37	3.74	4.20	3.04	36.9	MNHN-IM-2009-4273
			mean 3.11 (SD 0.53)	mean 35.2 (SD 4.01)	

TABLE 6. — *Pectinodonta gamma* n. sp. Shell measurements (in mm) and ratios of sequenced type specimens from BOA 1: stns CP2420 and CP2465.

Length (L)	Height (H)	Anterior length (AL)	LH ratio	AL%L	Specimen
26.52	9.59	8.90	2.76	33.5	MNHN-IM-2009-5798 (holotype)
31.74	11.37	10.04	2.79	31.6	MNHN-IM-2009-5797
28.56	10.37	8.87	2.75	31.0	MNHN-IM-2009-5789
25.23	9.23	7.77	2.73	30.7	MNHN-IM-2009-5788
18.83	6.46	5.91	2.91	31.3	MNHN-IM-2009-5787
26.98	10.52	8.80	2.56	32.6	MNHN-IM-2009-4203
21.04	8.25	7.17	2.55	34.0	MNHN-IM-2009-4205
			Mean 2.72 (SD 0.12)	mean 32.1 (SD 1.28)	

TABLE 7. — *Pectinodonta orientalis* Schepman, 1908. Shell measurements (in mm) and ratios for holotype and sequenced specimens from Papua New Guinea (BIOPAPUA: stns CP3731 and CP3638)

Length (L)	Height (H)	Anterior length (AL)	LH ratio	AL%L	Specimen
17.86	7.79	6.12	2.29	34.3	ZMA Moll. 135890 (holotype)
39.85	17.86	13.55	2.23	34.0	MNHN-IM- 2009-27327
30.11	9.76	8.74	3.08	29.0	MNHN-IM- 2009-27281
24.13	7.16	7.78	3.37	32.2	MNHN-IM- 2009-27282
23.00	7.56	7.68	3.04	33.3	MNHN-IM- 2009-27283
23.22	7.89	8.19	2.94	35.2	MNHN-IM- 2009-27284
16.85	4.89	5.80	3.44	34.4	MNHN-IM- 2009-27285
12.66	2.93	4.35	4.32	34.3	MNHN-IM- 2009-27286
11.84	2.99	4.20	3.95	35.4	MNHN-IM- 2009-27287
10.69	3.09	4.45	3.45	41.6	MNHN-IM- 2009-27288
			mean 3.21 (SD 0.65)	mean 34.3 (SD 3.14)	

TABLE 8. — *Pectinodonta philippinarum* n. sp. Shell measurements (in mm) and ratios of sequenced specimens from.

Length (L)	Height (H)	Anterior length (AL)	LH ratio	AL%L	Specimen
9.50	2.99	3.55	3.17	37.3	MNHN-IM-2009-10788 (holotype)
9.30	2.33	3.40	3.99	36.5	MNHN-IM-2009-10792

8.85	2.00	3.20	4.42	36.1	MNHN-IM-2009-10790 (paratype)

TABLE 9. — Living and fossil *Pectinodonta* species

Species	Distribution	Depth	References
<i>P. alpha</i> n. sp.	Solomon Islands and Vanuatu	290–522 m	Figs 4A-B, 6A-B herein
<i>P. alis</i> n. sp.	Solomon Islands and Vanuatu	354–387 m	Figs 6C-D, 7A-B herein
<i>P. alta</i> Schepman, 1908	Timor	390 m	Schepman 1908: 97, p. 2, fig. 9
<i>P. arcuata</i> Dall, 1882	Caribbean	413–1067 m	Dall 1882: 409; Dall 1889: 411, figs 3, 3ab
<i>P. aupouria</i> Marshall, 1985	New Zealand	818–1280 m	Marshall 1985: 277, figs 1, 3F-I, 4A-D; Marshall 1998: 55
<i>P. aurora</i> n. sp.	Papua New Guinea and Solomon Islands	485–592 m	Figs 4C-D, 6E-F herein
<i>P. beta</i> n. sp.	Papua New Guinea and Solomon Islands	529–782 m	Figs 6G-H, 7C-F herein
<i>P. coniformis</i> (Marwick, 1931)	Early–Middle Miocene, New Zealand	-	Marwick 1931: 85, figs 112, 113; Marshall 1985: 274, fig. 2
<i>P. gamma</i> n. sp.	Vanuatu and New Caledonia	532–880 m	Figs 6I-J, 7G-H herein
<i>P. gilbertvossi</i> Olsson, 1971	Gulf of Panama	3193–3200 m	Olsson 1971: 88, figs 71–74
<i>P. kapalae</i> Marshall, 1985	New South Wales, Australia	941–978 m	Marshall 1985: 280, figs 3L, M, 4C, F
<i>P. komitica</i> Marshall, 1985	Early Miocene, New Zealand	-	Marshall 1985: 275, figs 3A, B
<i>P. marinovichi</i> Marshall, 1998	New Zealand	736–1364 m	Marshall 1998: 52, figs 1–6
<i>P. maxima</i> (Dautzenberg, 1925)	Eastern Atlantic	4200–4450 m	Dautzenberg 1925: 11, fig; 13; Dautzenberg 1927: 211, pl. 7, figs 5–7
<i>P. morioria</i> Marshall, 1985	New Zealand	366–1342 m	Marshall 1985: 279, figs 3J, K, 4B, E; Marshall 1998: 57
<i>P. obtusa</i> (Thiele, 1925)	Sumatra	750 m	Thiele 1925: 69, pl. 3, figs 5, 6; Fig. 9G-H herein
<i>P. orientalis</i> Schepman, 1908	Japan, Taiwan, Philippines, Sulawesi, Papua New Guinea and Solomon Islands	741–1456 m	Schepman 1908: 96, pl. 2, fig. 8; Tsuchida & Kitao 1990: 158; Sasaki 2000: 27, pl. 13, Acmaeidae fig. 2; Figs 6K-L, 9A-F herein
<i>P. palaeoxylodia</i> Lindberg & Hedegaard, 1996	Late Oligocene, Washington State, U.S.A.	-	Lindberg & Hedegaard 1996: 312, fig. 17
<i>P. philippinarum</i> n. sp.	Philippines	558–562 m	Fig. 10C-D herein
<i>P. rhyssa</i> (Dall, 1925)	Japan	200–1640 m	Dall 1925: 11, pl. 32, figs 10, 11; Habe 1949, text fig. 1; Okutani 1964: 379, pl. 1, fig. 12; Tsuchida & Ishida 1977, fig. 1; Hasegawa 1977: 63, fig. 2A–C; Sasaki 2000: 27, pl. 13, Acmaeidae fig. 1; Hasegawa 2009: 235, fig. 3
<i>P. waitemata</i> Marshall, 1985	Early Miocene, New Zealand	-	Marshall 1985: 275, fig. 3D, E.
<i>Pectinodonta</i> n. sp. Schooley <i>et al.</i> 1982	Caribbean Panama	776 m	Schooley <i>et al.</i> 1982, fig14; Hickman 1983:77, fig. 6
<i>Pectinodonta</i> n. sp. aff. <i>coniformis</i> (Marwick, 1931) Marshall 1985	Early–Middle Miocene, New Zealand	-	Marshall 1985: 275, fig. 3C
<i>Pectinodonta</i> sp. Nolf & Verstraeten 2003	Madagascar	700 m	Nolf & Verstraeten 2003: 10, text fig

FIGURE CAPTIONS

FIGURE 1. — Bayesian phylogenetic trees obtained with the COI (A), 28S (B) and ITS1 (C) genes. Posterior probabilities (> 0.90) and bootstraps values (> 70) are shown above and below nodes.

FIGURE 2. — Bayesian phylogenetic trees obtained with COI sequences representative of *Pectinodonta* species from our own dataset and Lottioidea species from GenBank. Posterior probabilities (> 0.90) and bootstrap values (> 70) are shown above and below nodes.

FIGURE 3. — Bayesian phylogenetic trees obtained with the COI, 28S and ITS1 genes concatenated for one representative of each species. Posterior probabilities (> 0.90) and bootstrap values (> 70) are shown above and below nodes. Geographic and bathymetric ranges (as described in the text) are provided for each species. PNG = Papua New Guinea.

FIGURE 4. — Shells of *Pectinodonta* species. — **A, B**, *Pectinodonta alpha* n. sp., holotype MNHN-IM-2009-9314 (length 12.04 mm), Vanuatu, 431–445 m, SANTO 2006 stn AT120. — **C, D**, *Pectinodonta aurora* n. sp., holotype MNHN IM-2009-7710 (length 13.04 mm), off Luzon, Philippines, 556 m,.

FIGURE 5. — Distributions of sequenced specimens of *Pectinodonta alpha* n. sp. (●) and *P. aurora* n. sp. (■).

FIGURE 6. — Radulae of *Pectinodonta* species. Full width with some teeth removed to show base plates (**A, C, E, G**) and isolated teeth from left side (**B, D, H**) showing inner face and from right side (**F**) showing outer face. — **A, B**, *Pectinodonta alpha* n. sp., paratype MNHN IM-2009-9296, Vanuatu, SANTO 2006 stn AT120. — **C, D**, *Pectinodonta alis* n. sp., paratype MNHN IM-2009-7722, Vanuatu, BOA 1 stn CP2448. — **E, F**, *Pectinodonta aurora* n. sp. paratype MNHN IM-2009-5085, Philippines, AURORA 2007 stn CP2732. — **G, H**, *Pectinodonta beta* n. sp., paratype MNHN IM-2009-4260, Solomon Islands, SALOMONBOA 3 stn CP2821. — **I, J**, *Pectinodonta gamma* n. sp., holotype MNHN IM-2009-5798, Vanuatu, BOA 1 stn CP2420. — **K, L**, *Pectinodonta orientalis* (Schepman, 1908), MNHN IM-2009-27330, Papua New Guinea, BIOPAPUA stn CP3762, 1. Scale bar = 100 µm, except **F**, scale = 50 µm.

FIGURE 7. — Shells of *Pectinodonta* species. — **A, B**, *Pectinodonta alis* n. sp., holotype MNHN IM-2009-7723 (length 9.80 mm), Vanuatu, 387 m, BOA 1 stn CP2448. — **C, D**, *Pectinodonta beta* n. sp., holotype MNHN IM-2009-7706 (length 21.2 mm), Solomon Islands, 582–609 m, SALOMON 2 stn CP2245. — **E, F**, *Pectinodonta beta* n. sp., paratype MNHN IM-2009-4260 (length 25.4 mm), Solomon Islands, 686–864 m, SALOMONBOA 3 stn CP2821. — **G, H**, *Pectinodonta gamma* n. sp., holotype MNHN IM-2009-5798 (length 26.5 mm), Vanuatu, 630–670 m, BOA 1 stn CP2420.

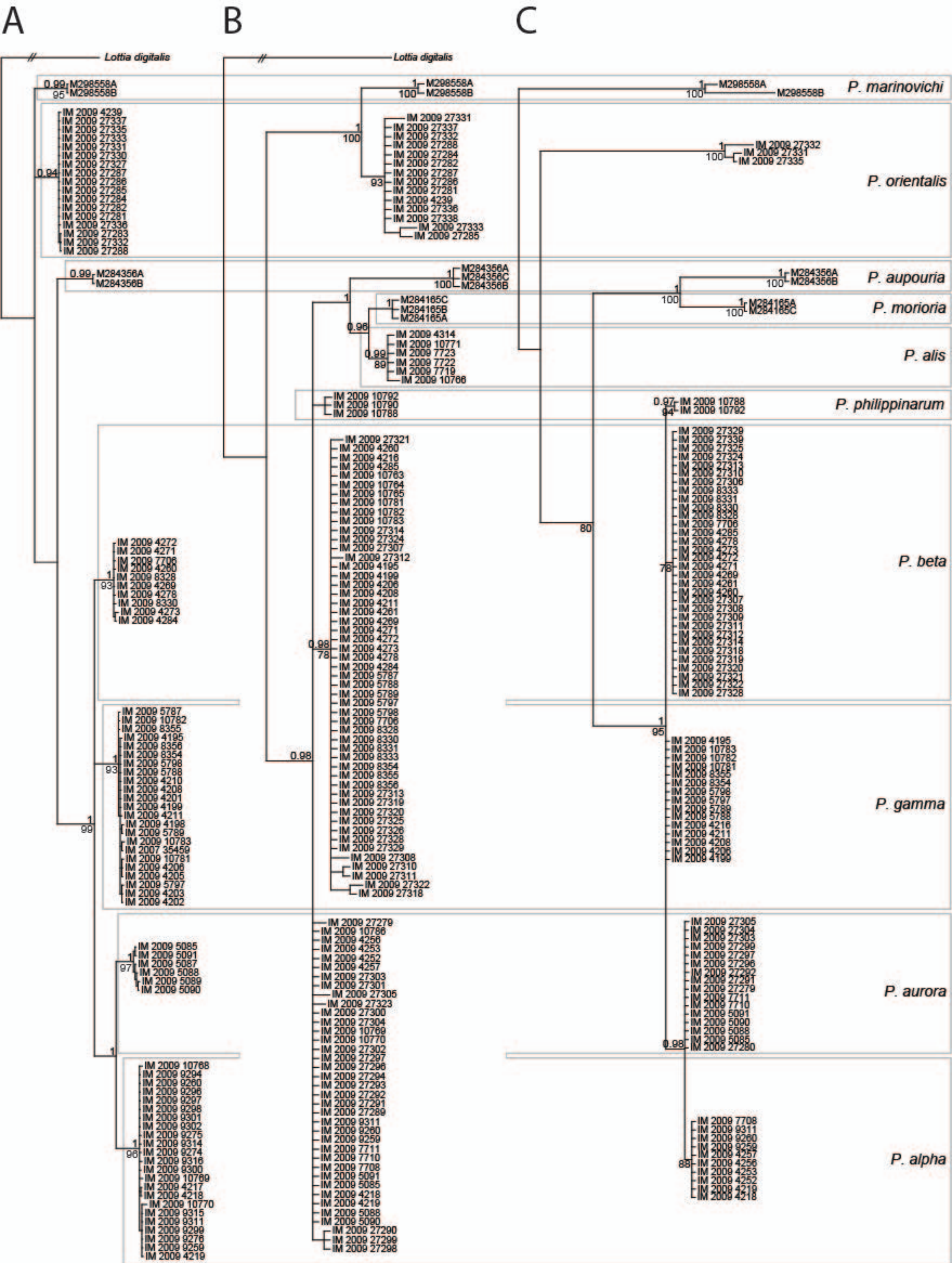
FIGURE 8. — Distributions of sequenced specimens of *Pectinodonta alis* n. sp. (●) and *P. philippinarum* n. sp. (■).

FIGURE 9. — Shells of *Pectinodonta* species. — **A-F**, *Pectinodonta orientalis* (Schepman, 1908). **A, B**, MNHN IM-2009-4239 (length 20.85 mm), Solomon Islands, 792–1042 m, SALOMONBOA 3 stn CP2801; **C, D**, MNHN (length 30.79 mm), Taiwan, 1314–1317 m, TAIWAN 2000 stn CP38; **E, F**, holotype ZMA Moll. 135890, RMNH (length 17.86 mm),

Indonesia, 1300 m. — **G, H**, *Pectinodonta obtusa* (Thiele, 1925), holotype ZMB 109199 (length 7.10 mm), Sumatra, 750 m (H image reversed).

FIGURE 10. — *Pectinodonta philippinarum* n. sp. — **A, B**, shell (length 9.50 mm). — **C, D**, radula, showing full width (**C**) and inner face of isolated left tooth (**D**) holotype MNHN IM-2009-10788, off Philippine Islands, 558–587 m., Scale bar **C** = 100 μ m, **D** = 50 μ m.

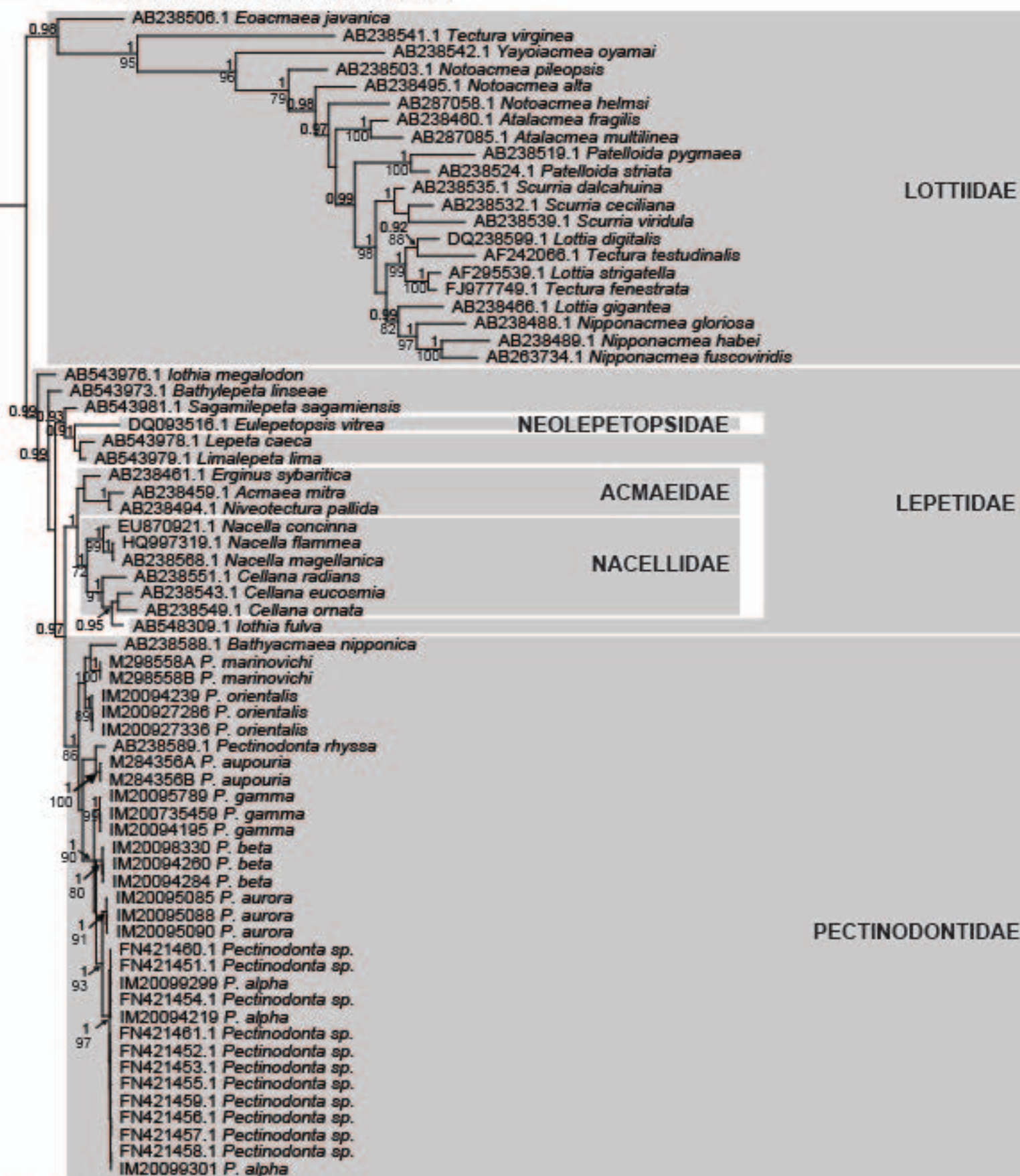
FIGURE 11. — Distributions of sequenced specimens of *Pectinodonta beta* n. sp. (●), *P. gamma* n. sp. (■) and *P. orientalis* (Schepman, 1908) (▲)

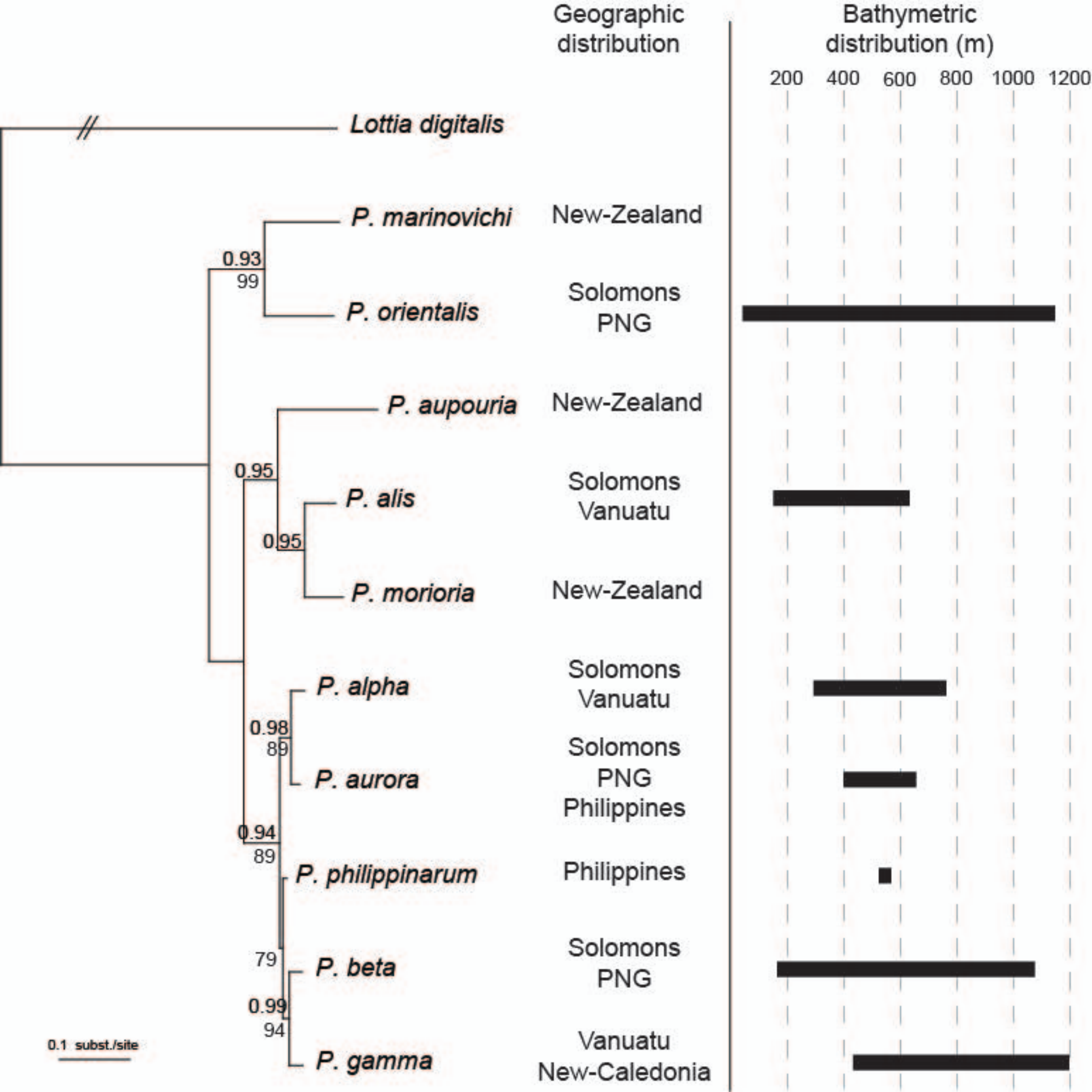


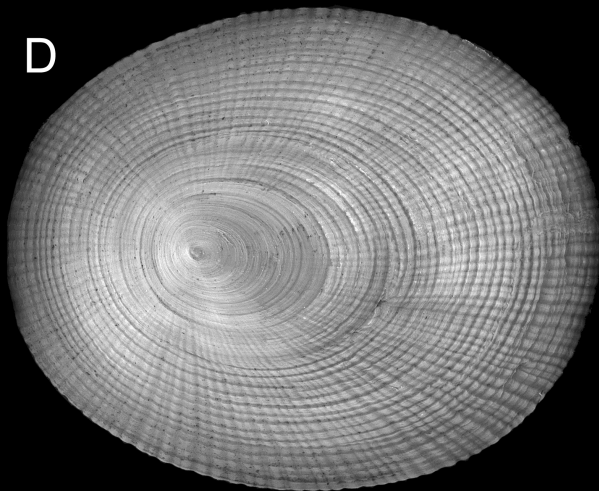
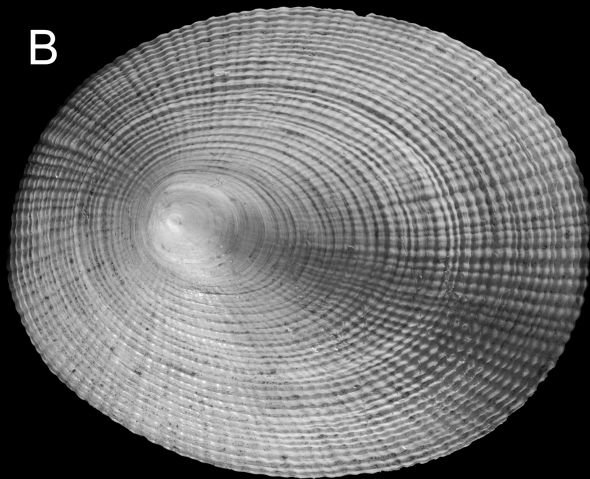
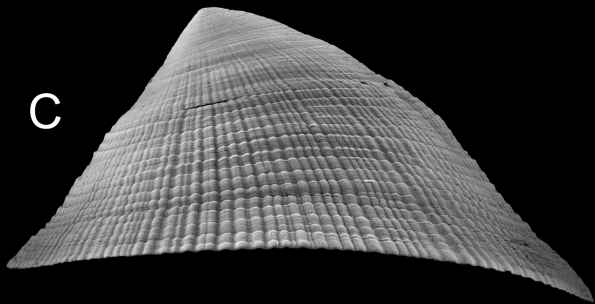
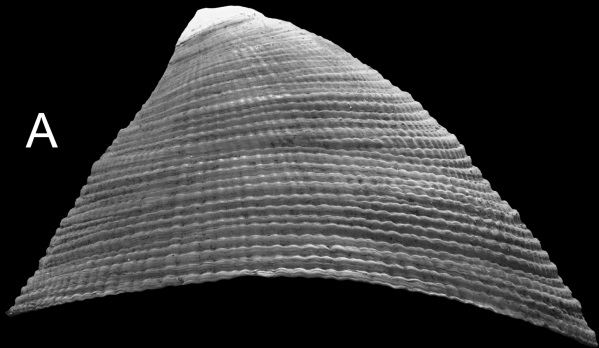
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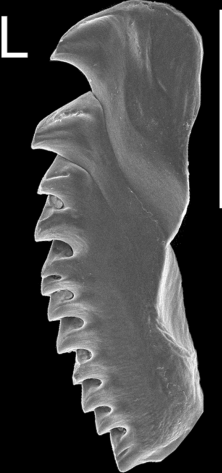
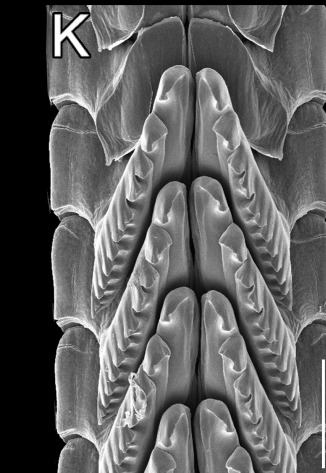
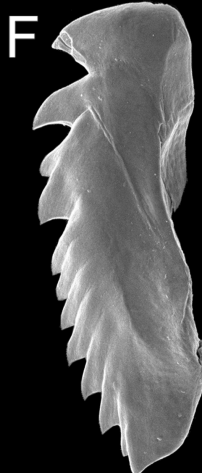
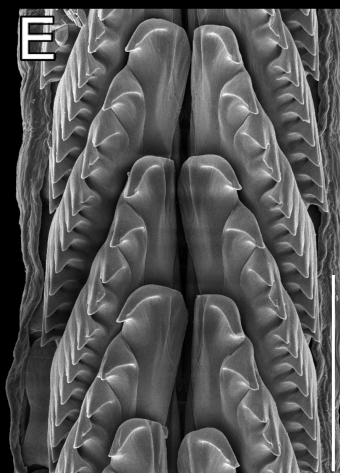
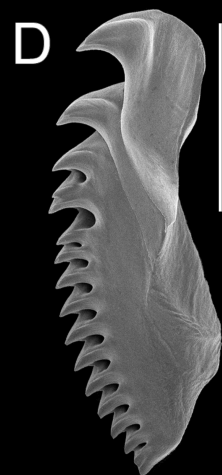
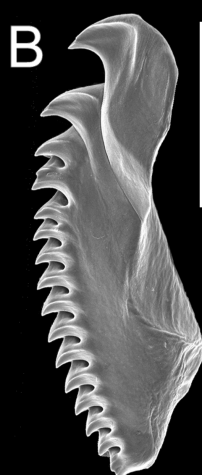
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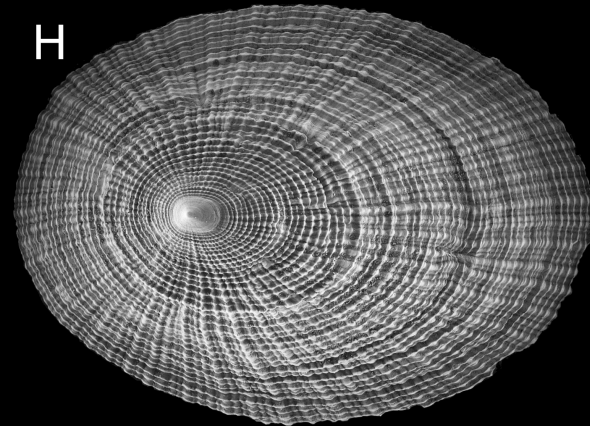
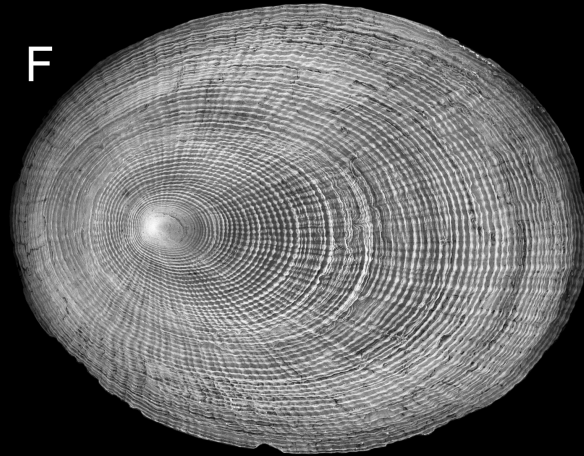
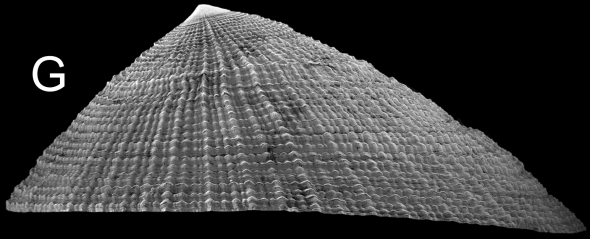
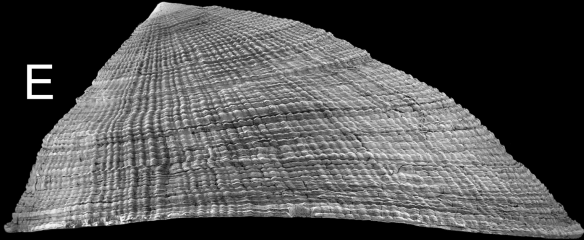
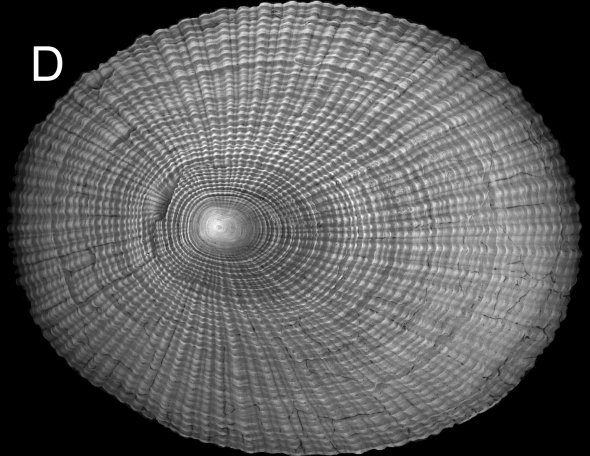
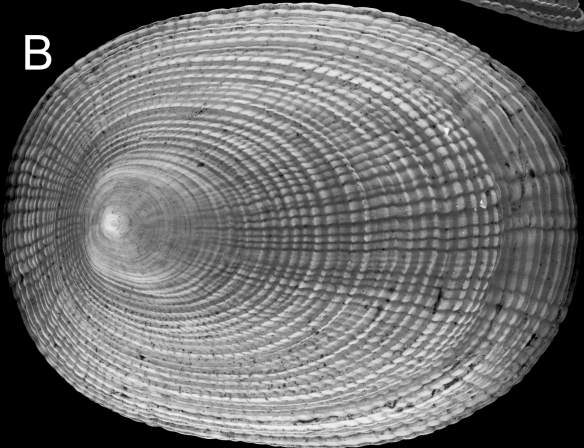
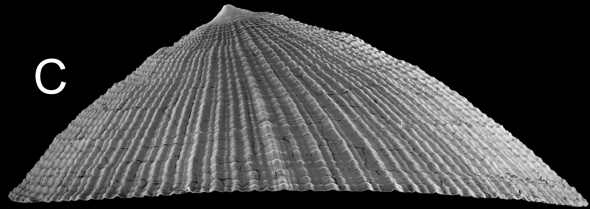
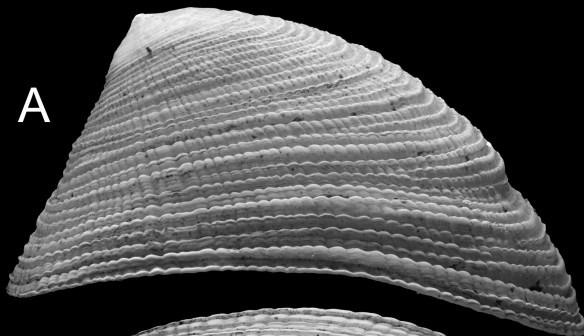
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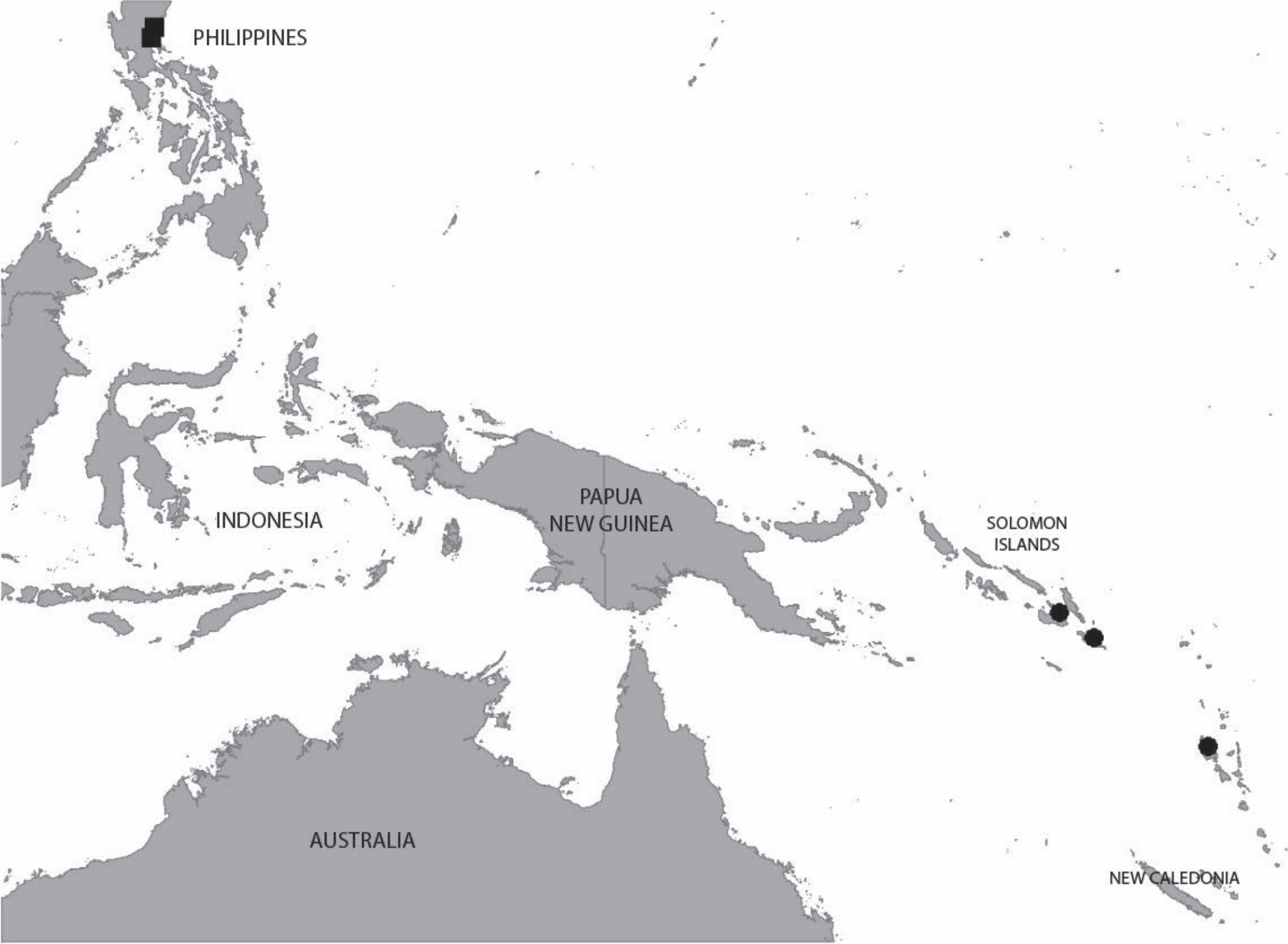
AUSTRALIA

SOLOMON
ISLANDS

NEW CALEDONIA







PHILIPPINES

INDONESIA

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