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Philippe Bouchet
Muséum National d'Histoire Naturelle, 55 rue Buffon, 75005 Paris, France
Email: pbouchet@mnhn.fr

Yuri I. Kantor
A.N. Severtzov Institute of Problems of Evolution of Russian Academy of Sciences, Leninski prosp. 33, Moscow 117071, Russia

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New Caledonia: the major centre of biodiversity for volutomitrid molluscs (Mollusca: Neogastropoda: Volutomitridae)

Abstract Recent deep-sea explorations in the South Pacific have documented around New Caledonia the most diverse fauna of gastropods of the family Volutomitridae anywhere in the world. Fourteen species (nine new, two remaining unnamed) are recorded, all essentially confined to the 250–750 m depth range. The high number of species in the New Caledonia region does not appear to be an effect of sampling intensity, but appears to result from four factors: regional spatial heterogeneity, frequency of hard substrates, syntopy, and a historical heritage shared with Australia and New Zealand, which until now ranked as the major centre of volutomitrid diversity. In the New Caledonia region, volutomitrids show a marked preference for hard bottoms and up to three species may co-occur in the same dredge haul. Many species appear to have extremely narrow geographical distributions within the region (e.g. a single seamount or a single submerged plateau); conversely, *Microvoluta joloensis*, the only non-endemic volutomitrid present in New Caledonia, ranges from the Mozambique Channel to Tonga.

Key words Bathyal, benthos, tropical, Gastropoda, anatomy, new species, Pacific Ocean, New Caledonia

Introduction

The Volutomitridae constitute a small group of neogastropods with maximum diversity in the southern hemisphere, especially in cold waters in the Antarctic, southern Australia and New Zealand. A few species are known from high northern latitudes in the Pacific and Atlantic Oceans. Volutomitrids have lowest diversity at low latitudes, and then only in deeper waters. A couple of species of *Volutomitra* have been described from 200–600 m in the tropical South-West Pacific (Cernohorsky, 1982; Bouchet & Kantor, 2000b), but these represent only the tip of the iceberg of a New Caledonia diversity of 14 species, the most diverse fauna of volutomitrids anywhere in the world. In the present paper, we review the composition of the family and describe the taxa from the tropical South-West Pacific, consisting mostly of undescribed species of *Volutomitra* and *Microvoluta*.

The mitriform shell of the Volutomitridae, with 2–5 columellar plaits, is superficially similar to that of the Mitridae and Costellariidae. The family is characterized anatomically by the wishbone-shaped central tooth of the radula, and needle-like lateral teeth, when present. The anterior part of the digestive tract differs from that of any other neogastropod in the mid-oesophagus being very elongated, convoluted, and broad, its posterior part being extremely muscular; in the valve of Leiblein being well anterior to the nerve ring; and in the gland of Leiblein being very small and tubular. A single accessory salivary gland is present (Ponder, 1998; Kantor & Harasewych, 1992).

The standard monographic reference on the family is Cernohorsky (1970b) who recognized six genera and 88 species (Recent and fossil), with at that time four genera and 24 species in Recent faunas; six genera and 41 Recent species are currently known. The oldest fossil species unambiguously assignable to the Volutomitridae is from the lower Paleocene of Denmark, with one doubtful species in the Upper Cretaceous of North America (Tracey *et al*., 1993). In Europe, the diversity of the family peaks in the Paleogene (essentially in the Eocene) where it lived in shallow to sublittoral depths, and almost faded out from the fossil record in the lower Miocene (Lozouet, 1999). By contrast, the Volutomitridae remain present throughout the fossil record in the Neogene of New Zealand, where they mainly lived in bathyal environments (Beu & Maxwell, 1990).

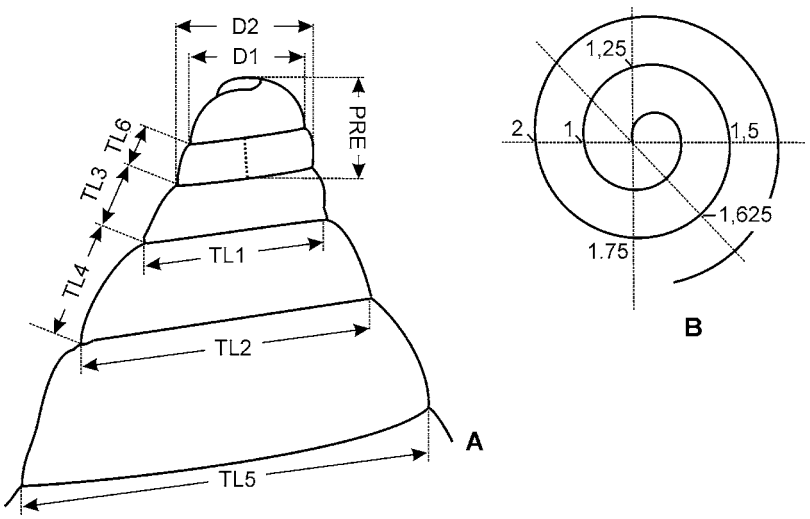

Figure 1 Standard orientation of protoconch and measurements taken. A, Shell in the standard position with protoconch-teleoconch transition (marked by dotted line). Measurements taken on protoconch: D1, D2, PRE. Measurements taken on teleoconch: TL1 to TL6. See Material and Methods for description and references. B, count of whorls numbers.

Material and methods

The present paper is based on the vast material collected recently by expeditions in the New Caledonia area (Richer de Forges, 1990, 1993; Richer de Forges & Chevillon, 1996), Wallis and Futuna (Richer de Forges & Menou, 1993), Vanuatu (Richer de Forges *et al*., 1996) and Fiji (Richer de Forges *et al*., 2000a, b). Unless otherwise stated, this material is stored in the Muséum National d'Histoire Naturelle, Paris (MNHN), and paratypes have been distributed to the Museum of New Zealand *Te Papa Tongarewa*, Wellington (NMNZ) and the Australian Museum, Sydney (AMS). No MNHN museum number is allocated to individual lots, but the material reported in this paper is unambiguously designated (and retrievable) through the combination of expedition acronym, e.g. BATHUS 3, and station number, e.g. DW1435. This information is present on labels accompanying individual lots. In the lists of material examined, lv refers to live-taken specimens and dd to empty shells.

Standard shell measurements were taken: shell length, SL; last whorl length, BWL; aperture length, AL; shell diameter, SD. For the purposes of species discrimination, we used a number of protoconch and teleoconch measurements following those defined and described in detail by Tursch & Germain (1985, 1986), and proven to be operational. Measurements taken from camera lucida drawings being more accurate than those made directly on the shell with the aid of an ocular micrometer, protoconchs were drawn with a camera lucida in standard position, with the protoconch-teleoconch transition facing the observer (Fig. 1); standard measurements taken from the drawings. Instead of protoconch diameter, we used D2, which equals the diameter of the protoconch + 1/4 of the first teleoconch whorl. PRE represents the exposed height of the protoconch and is referred to in the text as protoconch elevation. The number of protoconch and teleoconch whorls was counted with an accuracy of 1/8 whorl, and the number of axial ribs was counted on the first three teleoconch whorls. (It should be noted that the method used for counting number of protoconch whorls, or measuring protoconch diameter, is usually not specified in the literature, making comparisons difficult).

Radulae and jaws were studied with SEM after cleaning in diluted bleach, mounting on glass slides, air drying and coating with gold-palladium. Two species of *Microvoluta* were embedded in paraffin, serially sectioned at 8 μm, and stained with Masson triple stain.

Composition of the family

In his monograph the Volutomitridae, Cernohorsky (1970b) recognized six genera, two of which were known only as fossils. Since then, several changes and additions have taken place in the generic composition of the family. *Latiromitra* Locard, 1897 (treated by Cernohorsky as a subgenus of *Volutomitra*) has been recognized as a genus of Turbinellidae Ptychatractinae (Bouchet & Warén, 1985; Harasewych, 1987; Bouchet & Kantor, 2000a), *Waimatea* Finlay, 1927 has been synonymized with *Volutomitra* (Maxwell, 1992), and Kilburn (1974) described the monotypical genus *Magdalemitra*. Finally, Petuch (1987) described two Recent species of *Conomitra*, a genus previously known only as fossil. As a result, six Recent genera are currently recognized: *Volutomitra* H. and A. Adams, 1853; *Conomitra* Conrad, 1865; *Microvoluta* Angas, 1877; *Paradmete* Strebel, 1908; *Peculator* Iredale, 1924; and *Magdalemitra* Kilburn, 1974.

At species level, Cernohorsky recognized 88 species, of which 24 were Recent. In the last 30 years, the latter total was increased to 41 Recent species, and the present paper adds a further nine (and describes but does not name two more), thus bringing the total number of Recent named species of Volutomitridae to 50 (Appendix).

Generic diagnoses

Generic definitions in the Volutomitridae are based on conchological characters and, in many cases, the allocation of species to genera seems somewhat arbitrary. The review below represents the current state of the art, rather than a full re-evaluation of the validity of the Recent genera; the latter would necessitate examination of fossil material, which is beyond the scope of this paper.

Genus *Volutomitra* H. and A. Adams, 1853

Type species: *Mitra groenlandica* Beck *in* Möller, 1842 (by subsequent designation, Fischer, 1884). Recent, North Atlantic.

Diagnosis: Shell of small to large size for the family (6.6–47 mm), shape from fusiform-ovate to fusiform-elongate, with low to medium-high spire. Protoconch large, attaining at least 1.6 mm in diameter and consisting of 1.75–2.5 smooth whorls. Axial sculpture of weak axial ribs or absent, spiral sculpture indistinct in most species, of very low inconspicuous striae, of narrow distinct cords in a few species (*V. erebus*, *V. bayeri*). Aperture high (from about 60 to 70% of shell length), smooth inside. Columellar plaits well developed and broadly spaced, 3–5 in number, with second adapical strongest in most species. Shell colour from white under olivaceous or brown periostracum to beige and pinkish spotted, with brown zigzag lines in a few species.

Operculum vestigial, present in juveniles, absent in adults.

Chitinous jaw present, in the shape of closed or semi-closed funnel. Lateral radular teeth vestigial.

Distribution: Recent: northern and central-western Atlantic, northern and north-western Pacific, Hawaii, Australia, New Zealand, New Caledonia, 10 to 1570 m. Fossil: Eocene to Miocene, New Zealand (Cernohorsky, 1970b; Beu & Maxwell, 1990).

Genus *Conomitra* Conrad, 1865

Type species: *Mitra fusoides* Lea, 1833 (subsequent designation, Dall, 1889). Eocene, southeastern United States.

Diagnosis: Shell of small to medium size for the family (10–18 mm), shape from biconical to elongate-fusiform, with angulate shoulder in most species, with medium-high to high spire. Protoconch consisting of about 2 smooth whorls. Axial sculpture well developed, consisting of narrow closely spaced axial ribs, spiral sculpture well developed, consisting of distinct cords, forming reticulated structure while crossing axial ribs. Aperture medium-high (about 60% of shell length), narrow, smooth inside. Columellar plaits 4, well developed, second adapical strongest. Colour white to pale tan with dots and zigzag lines, spiral colour bands present in some species.

Animal not known.

Distribution: Recent: Caribbean, 35 to 90 m. Fossil: Paleocene to late Miocene; Europe, USA, Australia, New Zealand.

Remarks: The genus includes only three Recent species, which form the basis for the diagnosis above. None of them has been described anatomically, but their general shell morphology leaves no doubt as to their placement in the Volutomitridae. Cernohorsky (1970b) classified in *Conomitra* about 40 fossil species, ranging from stout and biconical, similar to *Peculator*, to elongate, similar to *Microvoluta*. The generic allocation of a number of them probably requires reconsideration.

Genus *Paradmete* Strebel, 1908

Type species: *Paradmete typica* Strebel, 1908 (by application of ICZN Art. 68.3) [= *Volutomitra fragillima* Watson, 1882]. Recent, Antarctic and sub-Antarctic.

Diagnosis: Shell of small to medium size for the family (7–25 mm), shape from fusiform elongate to stout, nearly turriform, with low to medium-high spire. Protoconch medium-sized to large (0.8–2.7 mm in diameter), consisting of about 2.5 smooth whorls. Axial sculpture ranges from very weak axial ribs, marked only in the subsutural zone, to clearly defined ones, extending towards the shell base; spiral sculpture ranges from very low and inconspicuous striae to rather narrow, but distinct, cords. Aperture high (60–70% of shell length), narrow to broad, smooth inside. Columellar plaits 2–4 in number, from very poorly pronounced to rather distinct.

Operculum present in the adults of most species, but absent in at least one.

Chitinous jaw present, but morphology not described in detail. Lateral radular teeth relatively large and stout.

Distribution: Recent only. Antarctic and sub-Antarctic seas, 30 to 810 m.

Remarks: Although *Paradmete*, and especially its type species *P. fragillima*, is rather similar conchologically to *Volutomitra* (and was treated as a subgenus by Cernohorsky, 1970b), it differs from it by the less pronounced columellar plaits, more developed lateral radular teeth, and different shape of the central tooth (see below).

Genus *Microvoluta* Angas, 1877

Type species: *M. australis* Angas, 1877 (by monotypy). Recent, southeastern Australia.

Diagnosis: Shell of very small to small size for the family (3.8–14.5 mm), shape from biconical to elongate-fusiform, nearly turriform in some species, with medium-high to high spire. Protoconch small (diameter 630–820 μm) in most species and consisting of about 1.5–2.1 smooth whorls. Axial sculpture well developed in most species, consisting of closely spaced axial ribs, often producing knobs on shoulder; spiral sculpture poorly developed, usually of very low inconspicuous striae. Aperture from low to medium high (rarely reaching 60% of shell length), narrow, smooth or lirate inside (within the same population of some species). Columellar plaits 3–5 in number, well developed in most species, second adapical strongest. Shell colour white in most species, banded, blotched and/or streaked with brown in a few species.

Operculum absent in adults.

Chitinous jaw present, in the shape of horse-shoe plate with long lateral flaps. Lateral radular teeth relatively large and stout.

Distribution: Recent: Atlantic: central eastern Atlantic, Caribbean; South Africa; Indo-Pacific: western and southwest Pacific, from Japan and the Philippines to Australia and New Caledonia, Fiji, Wallis and Futuna, and Tonga; New Zealand; 50 to 1900 m (shell only). Fossil: Miocene-Pliocene, Australia and New Zealand (Cernohorsky, 1970b; Beu & Maxwell, 1990).

Remarks: *Microvoluta* is a well defined genus, distinguished from other genera by its small elongated shell with attenuated spire, and different jaw morphology.

Genus *Peculator* Iredale, 1924

Type species: *Peculator verconis* Iredale, 1924 (by monotypy). Recent, southern Australia.

Diagnosis: Shell of small size for the family (6.5–12 mm), stout, shape biconical, with low spire. Protoconch consisting of about 1.5–2 smooth whorls. Axial sculpture poorly developed, consisting of thickened growth lines and, in some species, narrow and low ribs; spiral sculpture poorly developed, of low closely spaced striae. Aperture high (60–70% of shell length), narrow, smooth or lirate inside. Columellar plaits 3–4 in number, well developed and broadly spaced, first or second adapical largest. Shell colour pale brown, with paler spots in some species.

Operculum vestigial, present in adults.

Chitinous jaw may be present, shape unknown. Lateral radular teeth vestigial.

Distribution: Recent: Australia and New Zealand, now New Caledonia, in 6 to 260 m. Fossil: Eocene to Pliocene, Australia and New Zealand (Cernohorsky, 1970b; Beu & Maxwell, 1990).

Remarks: *Peculator* is a well defined genus, distinguished from other genera by its small, stout, biconical shell with low spire and narrow aperture.

Genus *Magdalemitra* Kilburn, 1974

Type species: *Magdalemitra gileosum* Kilburn, 1974 (by original designation).

Diagnosis: Shell of medium size for the family (19 mm), shape cylindrical, pupoid, with a low, blunt and tumid spire. Protoconch unknown. Axial sculpture of riblets on first teleoconch whorl only; spiral sculpture consisting of striae on the first teleoconch whorl and on the shell base. Aperture narrow, columellar plaits 4, adapical largest. Colour brown with darker subsutural band.

Animal not known.

Distribution: Monotypical genus, known only from the Recent of South Africa, from Port Alfred to Embotyi, Pondoland.

Remarks: The single known species presents a unique combination of columbellid shell shape and columellar plaits. Pending an examination of the radula and anatomy, the allocation of *Magdalemitra* to the family Volutomitridae remains unconfirmed. A position in the Costellariidae also is possible (R.N. Kilburn, pers. comm.).

Species descriptions

Class Gastropoda
Unranked group Caenogastropoda
Order Neogastropoda Wenz, 1938
Family Volutomitridae Gray, 1854

Genus *Volutomitra* H. and A. Adams, 1842

Volutomitra glabella Bouchet and Kantor, 2000 (Fig. 2)

Volutomitra glabella Bouchet & Kantor, 2000b: 182–187, figs. 1A–H; 2A, C, D, E; 3; 4.

Type material: Holotype and 3 paratypes in MNHN, 1 paratype each in NMNZ and AMS.

Type locality: South of New Caledonia, Norfolk Ridge, Banc Eponge, 24°57′S, 168°21′E, 517–559 m [SMIB 10, sta. DW205].

Material examined: 33 lots (about 115 specimens) from north of New Caledonia and 2 lots (2 specimens) from south of New Caledonia (list of material in Bouchet & Kantor, 2000). Dimensions of the largest specimen: shell height 25.0 mm, diameter 12.0 mm, last whorl height 19.1 mm, aperture height 16.5 mm.

Distribution: North and South of New Caledonia, on hard bottoms, alive in 258–525 m, shells in 190–613 m.

Remarks: This distinctive species differs from its sympatric congeners by usually reaching a much larger adult size (although the sizes of the largest *V. vaubani* [18.2 mm] and of the smallest adult *V. glabella* [17.0 mm] slightly overlap), and by its broader shell with a lower spire. Even at comparable sizes, young or small *V. glabella* are readily separated from any other *Volutomitra* of the region by their significantly larger and more elevated protoconch (Table 3).

Volutomitra vaubani Cernohorsky, 1982 (Figs 3, 4, 5, 10A)

Volutomitra (Waimatea) vaubani Cernohorsky, 1982: 999, pl. IV, figs 23–28.

Type material: Holotype and 5 paratypes in MNHN.

Type locality: South of New Caledonia, 22°49′S, 167°12′E, 395 m [R/V *Vauban* 1978–79 sta. 15].

Material examined: 22 lots (194 specimens) from north of New Caledonia and 13 lots (88 specimens) from south of New Caledonia.

North of New Caledonia. LAGON, R/V *Alis*: sta. 444, Atoll de Surprise, 18°15′S, 162°59′E, 300–350 m, 1 lv [co-occurring with *V. glabella*].

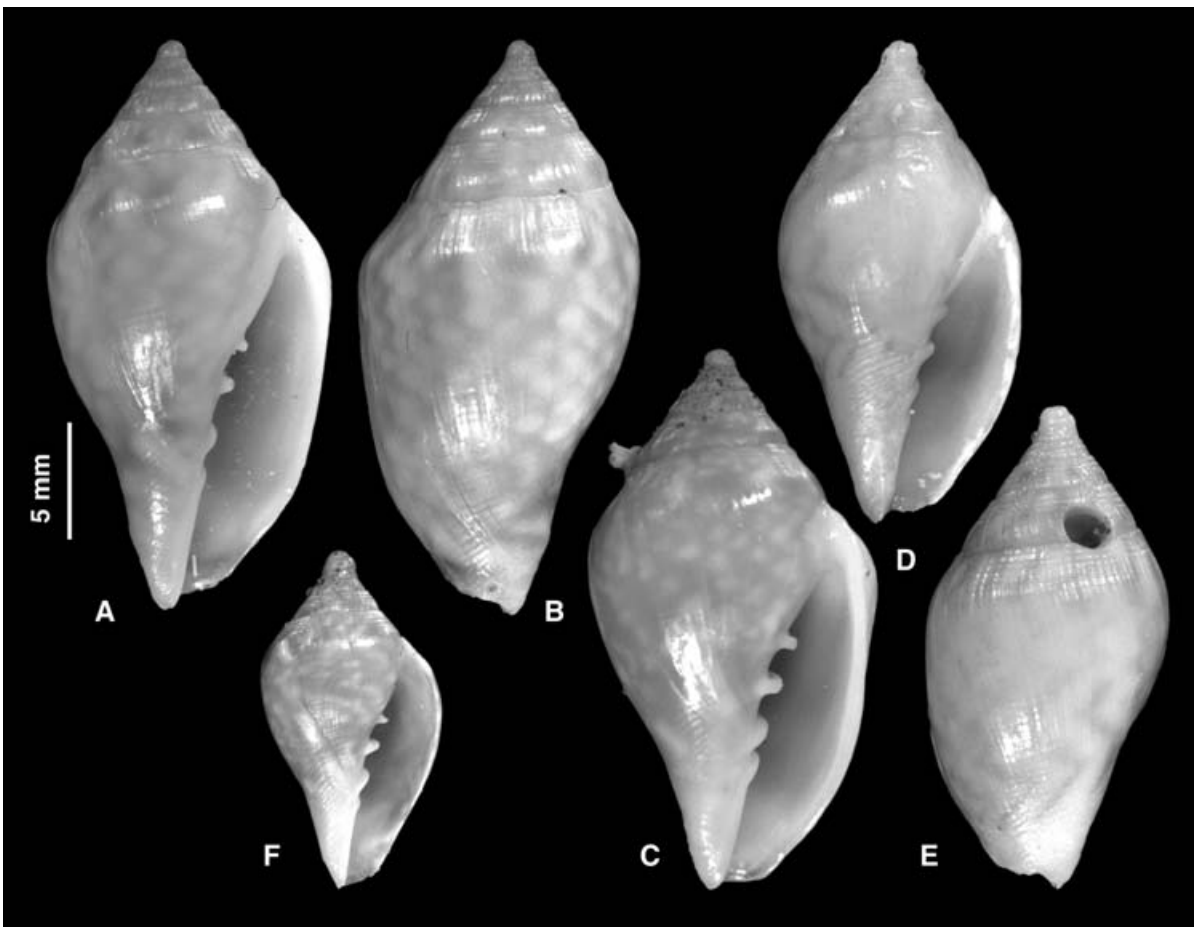

Figure 2 *Volutomitra glabella*. A–B, Holotype, South of New Caledonia, SMIB 10, sta. DW205, SL 24.0 mm; C, Paratype, BATHUS 4, sta. DW941, SL 18.5 mm; D–E, Paratype, BATHUS 4, sta. DW923, SL 19.8 mm; F, Juvenile paratype, BATHUS 4, sta. DW941, SL 14.0 mm.

MUSORSTOM 4, R/V *Vauban*: sta. DW156, 18°54′S, 163°19′E, 525 m, 1 dd [co-occurring with *V. ziczac*, n. sp.]. – Sta. DW164, 18°33′S, 163°13′E, 255 m, 5 dd. – Sta. DW197, 18°51′S, 163°21′E, 550 m, 1 dd [co-occurring with *V. ziczac*, n. sp.].

BATHUS 4, R/V *Alis*: sta. DW914, 18°49′S, 163°15′E, 600–616 m, 40 dd. – Sta. DW923, 18°52′S, 163°24′E, 470–502 m, 6 dd, 1 lv [co-occurring with *V. ziczac*, n. sp.]. – Sta. DW927, 18°56′S, 163°22′E, 444–452 m, 2 lv, 9 dd.

South of New Caledonia. R/V *Vauban* 1978–79: sta. 15, 22°49′S, 167°12′E, 395 m, 2 lv (holotype and paratype). – Sta. 16, 22°46′S, 167°12′E, 390–400 m, 4 lv (paratypes).

BIOCAL, R/V *Jean-Charcot*: sta. DW43, 22°46′S, 167°15′E, 400 m, 4 dd. – Sta. DW44, 22°47′S, 167°14′E, 440–450 m, 39 lv + dd. – Sta. DW46, 22°53′S, 167°17′E, 570–610 m, 4 lv, 27 dd.

MUSORSTOM 4, R/V *Vauban*: sta. DW212, 22°47′S, 167°10′E, 375–380 m, 7 dd. – Sta. DW223, 22°57′S, 167°30′E, 545–560 m, 2 dd. – Sta. DW230, 22°52′S, 167°12′E, 390–420 m, 1 dd.

SMIB 2, R/V *Vauban*: sta. DW1, 22°53′S, 167°13′E, 438–444 m, 7 lv, 1 dd. – Sta. DW4, 22°53′S, 167°13′E, 410–417 m, 1 dd. – Sta. DW5, 22°56′S, 167°14′E, 398–410 m, 2 dd. – Sta. DW8, 22°54′S, 167°13′E, 435–447 m, 3 dd. – Sta. DW9, 22°54′S, 167°15′E, 475–500 m, 3 dd. – Sta. DW12, 22°53′S, 167°14′E, 445–460 m, 1 lv.

SMIB 3, R/V *Vauban*: sta. CP4, 24°54′S, 168°22′E, 530 m, Banc Eponge, 1 dd. – Sta. DW29, 22°47′S, 167°12′E, 405 m, 8 dd.

SMIB 8, R/V *Alis*: sta. DW189, 23°18′S, 168°06′E, 400–402 m, Banc Antigonia, 1 lv. – Sta. DW190, 23°18′S, 168°05′E, 305–310 m, Banc Antigonia, 4 lv. – Sta. DW197–199, 22°51′S, 167°12′E, 408–436 m, Ile des Pins, 5 lv.

BATHUS 2, R/V *Alis*: sta. DW719, 22°48′S, 167°16′E, 444–445 m, 42 lv, 13 dd. – Sta. DW721, 22°54′S, 167°17′E, 525–547 m, 5 lv. – Sta. DW729, 22°52′S, 167°12′E, 400 m, 7 dd.

NORFOLK 1, R/V *Alis*: sta. DW1734, 22°53′S, 167°12′E, 403–429 m, 5 lv. – Sta. DW1735, 22°52′S, 167°12′E, 415–445 m, 4 lv, 1 dd. – Sta. DW1736, 22°51′S, 167°12′E, 383–407 m, 3 dd. – Sta. DW1737, 22°52′S, 167°12′E, 343–400 m, 4 lv, 1 dd. – Sta. DW1738, 22°51′S, 167°10′E, 340–381 m, 1 dd. – Sta. DW1739, 22°51′S, 167°12′E, 404–448 m, 1 lv, 2 dd. Dimensions of the largest specimen (SMIB 8, sta. 197–199) (Fig. 3C): shell height 18.2 mm, diameter 8.0 mm, last whorl height 13.6 mm, aperture height 12.0 mm.

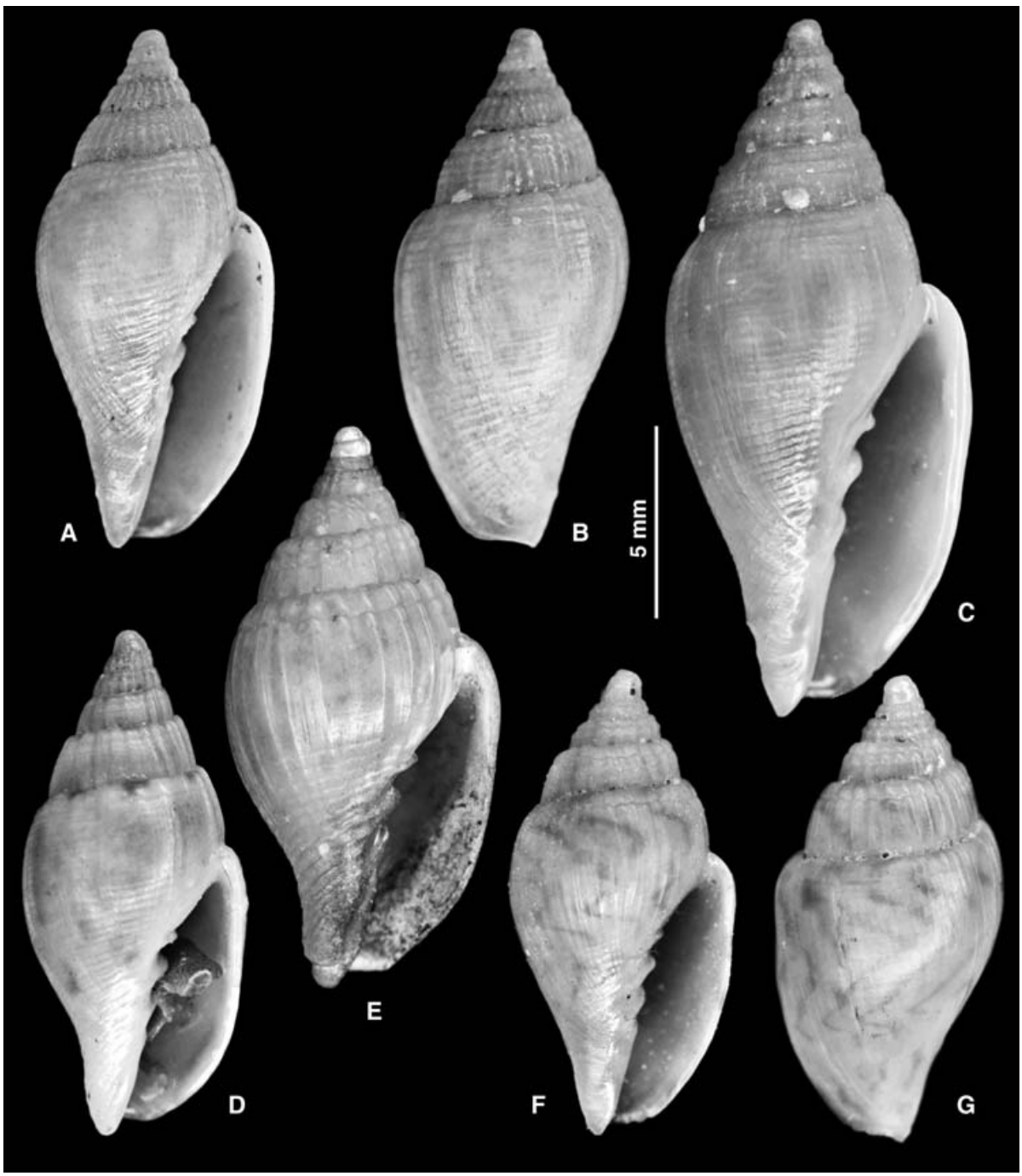

Figure 3 *Volutomitra vaubani*. A–D, South of New Caledonia. A–B, holotype, SL 13.5 mm; C, SMIB 8, sta. 197–199, SL 18.2 mm; D, BIOCAL, sta. DW46, SL 12.2 mm. E–G, North of New Caledonia. E, BATHUS 4, sta. DW914, SL 14.6 mm; F–G, BATHUS 4, sta. DW927, SL 13.2 mm. All shells at the same scale.

Distribution: Off north and south of New Caledonia and Norfolk Ridge, alive in 310–570 m, shells in 255–600 m (Fig. 4).

Remarks: Considerable new material collected since the original description of *V. vaubani* shows that it is a very variable species, with individual as well as geographical variation.

In the north of New Caledonia, *V. vaubani* occurs sympatrically and, occasionally, syntopically (see Discussion at the end of the paper for terminology) with *V. ziczac*, n. sp. (Fig. 4 – arrows indicate stations of co-occurrence) and/or *V. glabella* Bouchet & Kantor, 2000b, and there is no doubt that three species of *Volutomitra* are involved in that region. There, it differs from *V. ziczac*, n. sp. by its less convex and more shouldered whorls, its colour pattern that never forms axial zigzag lines, and by having a strong subsutural groove extending on all whorls including the last adult whorl (Fig. 5). Apart from these constant differences, *V. vaubani* is quite variable in terms of axial sculpture and colour.

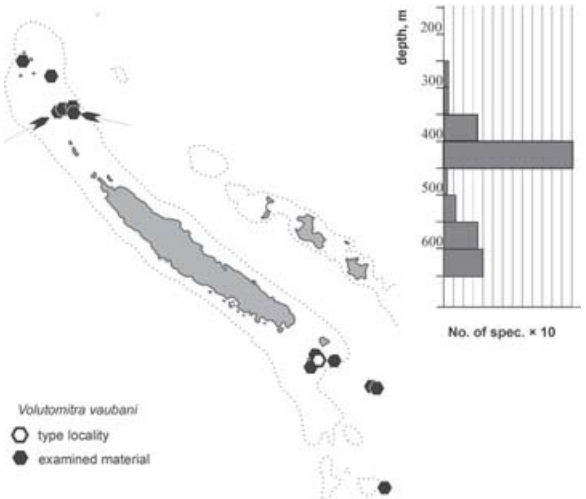

Figure 4 Geographical and bathymetrical distribution of *Volutomitra vaubani*. Arrows indicate stations where the species is syntopic with *V. ziczac*, n. sp. Each column represents 10 specimens (lv or dd). Isobath 1000 m.

Some populations have almost no axial sculpture on the last whorl (Fig. 5E), while others have strong, sharp axial ribs (Fig. 5C). These axially sculptured populations have uniform yellowish-beige shells, while the smooth forms vary from white to yellowish-beige with brown blotches, especially at the shoulder.

In the south of New Caledonia, the populations vary extensively, from specimens with a low spire and convex whorls (resembling *V. ziczac*, n. sp., in outline) to specimens with a higher spire and shouldered whorls (resembling the northern form described above – Fig. 3D); however, they are connected by intermediates. A single species of *Volutomitra* appears to be present in that region, and the name *vaubani* can be applied to it without ambiguity. The question is whether this southern form is conspecific with one of the northern species (and then which one?) or whether it represents a separate species. All southern populations of *vaubani* are uniformly coloured, yellowish-beige, except one population from BIOCAL sta. DW46 where some specimens have a pattern of zigzag brown axial lines and it is tempting to connect these with *V. ziczac*, n. sp. (Fig. 3D). However, this similarity appears to be superficial: in *V. ziczac*, n. sp., the brown axial lines are extremely oblique, with very angular changes of direction, whereas in the specimens from BIOCAL sta. DW46 they are not so oblique, with more obtuse changes of direction. Instead, the strongly sculptured forms of southern *Volutomitra vaubani* share with the northern populations described above the presence of a strong subsutural groove and axial ribs extending over the whole height of the last whorl. We hypothesize that these populations are conspecific.

To summarize, the zigzag pattern that appears to be so characteristic of *Volutomitra ziczac*, n. sp., may occur occasionally in southern populations of *V. vaubani*. In the north of New Caledonia, where the two species co-occur, a zigzag pattern is never observed in *V. vaubani*; this may be interpreted as character displacement.

Volutomitra ziczac, n. sp. (Figs. 5B, D, G, 6, 7, 11A, C)

Type material: Holotype (lv) and 3 paratypes in MNHN.

Type locality: North of New Caledonia, 18°55′S, 163°24′E, 370–405 m [BATHUS 4, sta. DW925].

Material examined: 17 lots (59 specimens) from north of New Caledonia.

North of New Caledonia. MUSORSTOM 4, R/V *Vauban*: sta. DW156, 18°54′S, 163°19′E, 525 m, 3 dd [co-occurring with *V. vaubani*]. – Sta. DW181, 18°57′S, 163°22′E, 350 m, 4 dd, 3 lv. – Sta. DW196, 18°55′S, 163°24′E, 450 m, 3 lv [radula examined, Fig. 11A]. – Sta. DW197, 18°51′S, 163°21′E, 550 m, 1 dd [co-occurring with *V. vaubani*].

HALICAL1, R/V *Alis*: sta. DW01, 18°56′S, 163°24′E, 380–400 m, 2 dd. – Sta. DW04, 18°55′S, 163°24′E, 350–365 m, 1 dd.

BATHUS 4, R/V *Alis*: sta. DW923, 18°52′S, 163°24′E, 470–502 m, 3 dd [co-occurring with *V. vaubani*]. – Sta. DW924, 18°55′S, 163°24′E, 344–360 m, 7 dd. – Sta. DW925, 18°55′S, 163°24′E, 370–405 m, 4 lv (holo- and paratypes), 2 dd. – Sta. DW926, 18°57′S, 163°25′E, 325–330 m, 5 dd. – Sta. DW929, 18°52′S, 163°23′E, 502–516 m, 3 dd. – Sta. DW931, 18°55′S, 163°24′E, 360–377 m, 2 dd. – Sta. DW932, 19°08′S, 163°29′E, 170–190 m, 1 dd. – Sta. DW942, 19°04′S, 163°27′E, 264–270 m, 6 dd.

SMIB 6, R/V *Alis*: sta. DW118, 18°58′S, 163°26′E, 290–300 m, 1 lv. – Sta. DW121, 18°58′S, 163°26′E, 315 m, 1 dd.

LAGON, R/V *Alis*: sta. 1152, 18°58′S, 163°24′E, 335 m, 1 lv, 6 dd [co-occurring with *V. glabella*].

Distribution: Off north of New Caledonia, alive in 300–450 m, shells in 190–550 m.

Description (holotype): Shell solid, glossy, elongate-ovoid, width 48% of height, consisting of *c*. 2.0 protoconch and 5.5 teleoconch whorls. Protoconch slightly eroded in holotype, rather large, bulbous, diameter 1090 μm, exposed height 730 μm, first whorl convex, smooth, second whorl with flat sides, protoconch-teleoconch transition indistinct. Teleoconch whorls convex with tightly impressed suture, ramp slightly concave, nearly flat, exposed part below periphery more convex. Sculpture consisting on early teleoconch whorls of strong straight ribs, crossed by 2 spiral cords on the 2nd and 3rd whorls, intersection forming knobs. On later whorls the sculpture become less distinct, although one cord is visible on all teleoconch whorls. Eighteen axial ribs on first whorl, 17 on second, 17 on third; axial ribs gradually becoming obsolete on last whorl, which has only indistinct undulations at shoulder. Spiral sculpture of very indistinct, closely spaced narrow cords, 14 more distinct on siphonal canal. Last whorl high, 74% of total shell height. Aperture height 68% of shell height, narrowly elongate, smooth inside, outer lip simple. Columella with narrow, thin callus, with 4 widely spaced plaits, abapical one smallest. Siphonal canal short, straight. Colour of shell pinkish brown, with irregularly spaced, brownish, zic-zac chevrons covering entire subadult and adult shell surface.

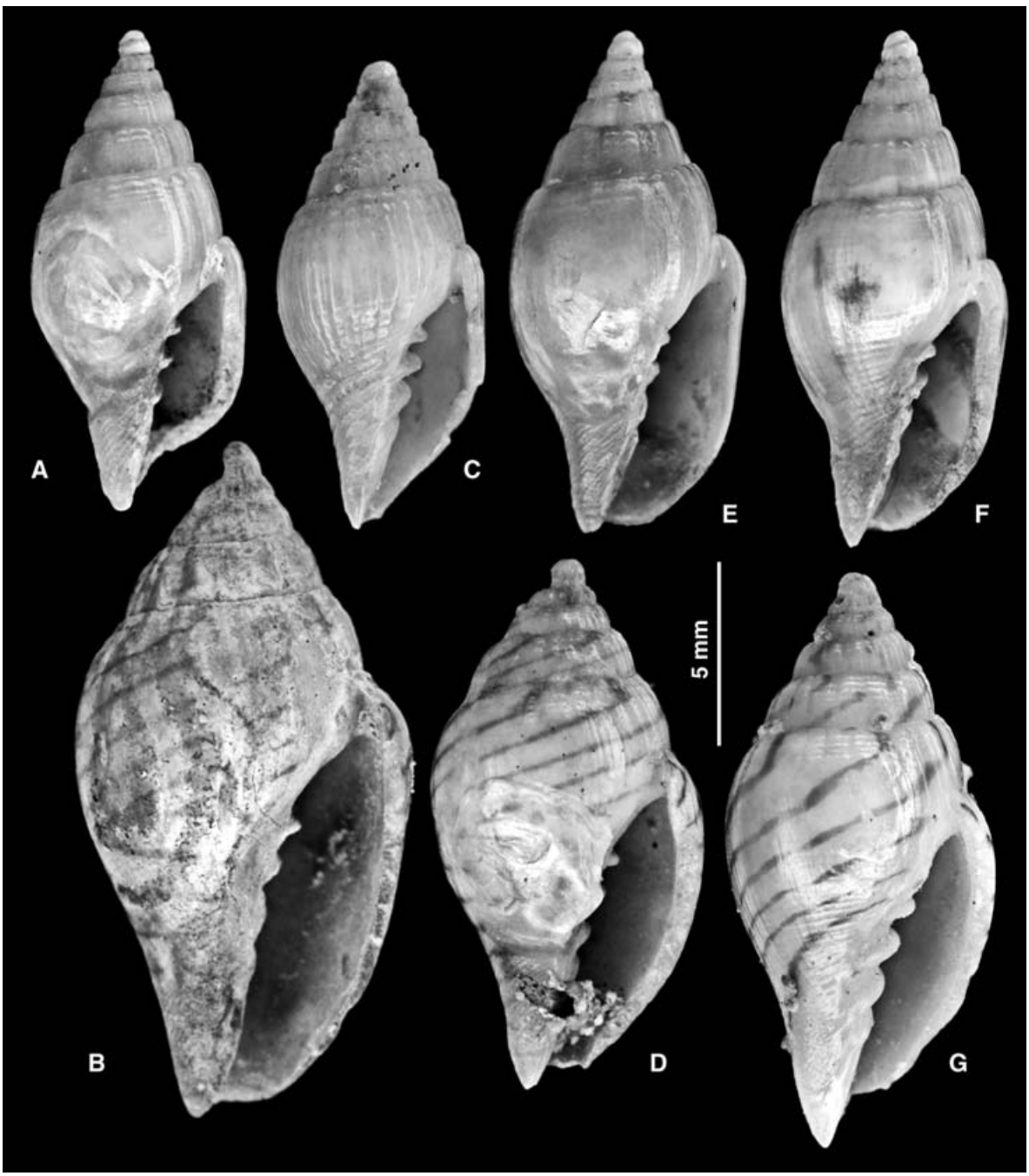

Figure 5 Syntopic specimens of *Volutomitra vaubani* (A, C, E, F) and *V. ziczac* n. sp. (B, D, G). A–B, MUSORSTOM 4, sta. DW156, SL 12.5 mm (A), 17.5 mm (B). C–D, MUSORSTOM 4, sta. DW197, SL 12.2 mm (C), 13.8 mm (D). E–G, BATHUS 4, sta. DW923, SL 12.1 mm (E), 12.5 mm (F), 15 mm (G). All shells at the same scale.

Dimensions (holotype): Shell height 14.2 mm, diameter 6.8 mm, last whorl height 10.5 mm, aperture height 9.7 mm. Largest specimen (paratype): shell height 16.2 mm, diameter 7.8 mm, last whorl height 12.1 mm, aperture height 11.2 mm.

Anatomy: A specimen from MUSORSTOM 4, sta. DW196 has been studied anatomically. It had a shell height of 15.9 mm, diameter 7.8 mm, last whorl height 12.2 mm, aperture height 10.2 mm. Its anatomy is very similar to that described and illustrated for *Volutomitra glabella* (Bouchet & Kantor, 2000b).

External anatomy: Body consists of 5 whorls, mantle spans one whorl, nephridium 0.3 whorl, and digestive gland 3.5 whorls. Body yellowish and lacking specific pigmentation. Operculum absent. Foot with ovate sole, folded lengthwise. Columellar muscle thick anteriorly, consisting of 1.5 whorls, with four deep grooves, corresponding to columellar plaits. In its posterior part, in the place of attachment to columella, muscle is split into separate branches, each inserting between columellar plait. Mantle edge rather thick, while central part of mantle is extremely thin and transparent. Mantle covers head base. Head narrow and small,

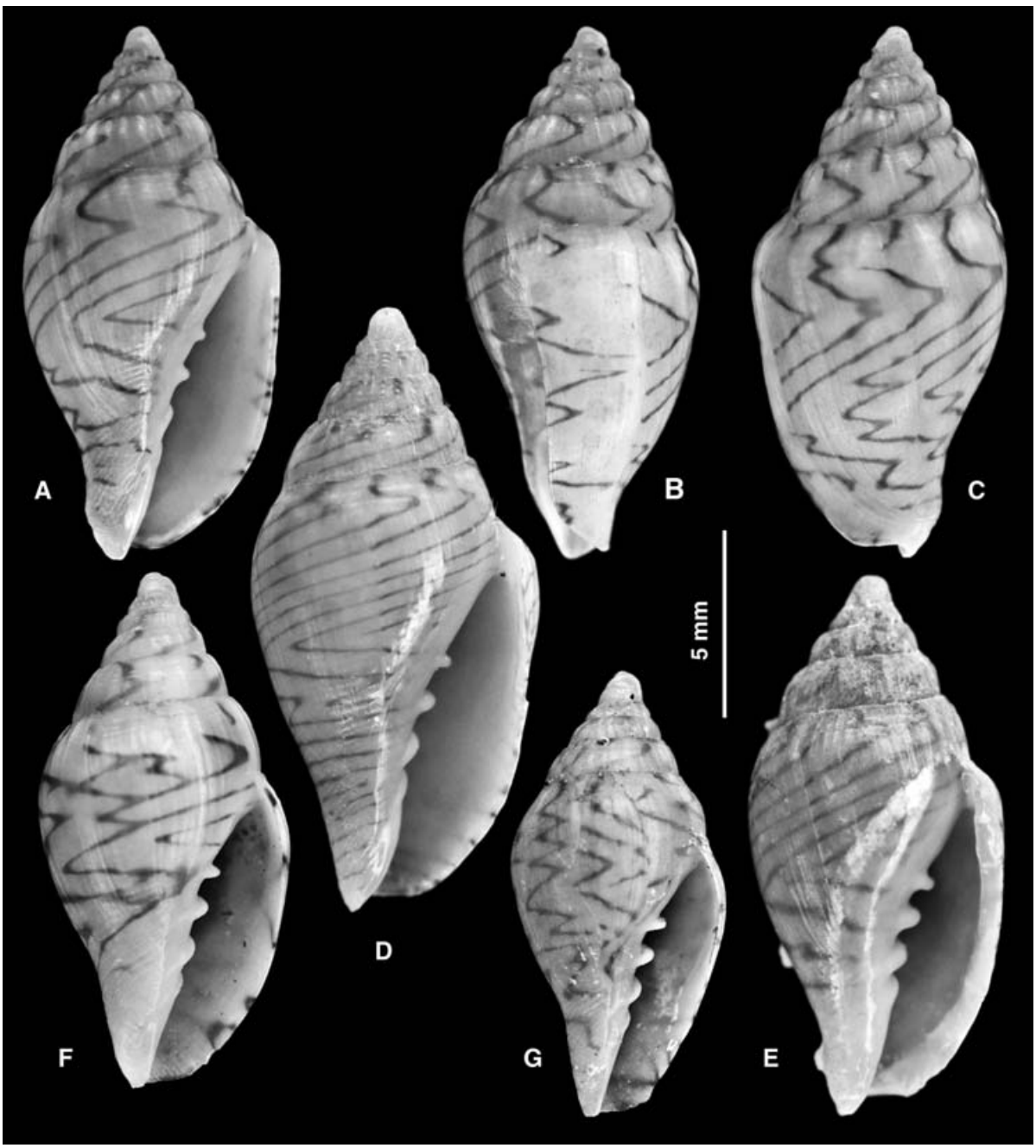

Figure 6 *Volutomitra ziczac*, n. sp. A–C, holotype, SL 14.2 mm. D, paratype, SL 16.2 mm. E, paratype, SL 14.5 mm. F, HALICAL 1, sta. DW01, SL 13.8 mm. G, BATHUS 4, sta. DW 926, SL 12 mm. All shells at the same scale.

with very short conical tentacles and large eyes. The specimen was a mature male and has a penis typical for Volutomitridae, long and flattened with open seminal groove running along inner side of penis to its tip. Seminal papilla absent.

Mantle: Mantle complex very similar to that of *Volutomitra glabella*. Anal gland seen through mantle as short black strip.

Digestive system: Foregut anatomy is in all details similar to that of *V. glabella* and differs only in its slightly longer valve of Leiblein and significantly (*c.* 2×) longer anterior (i.e. part between the proboscis and the valve) oesophagus. The proboscis, being less contracted, is relatively longer (about 2.0 mm, or 20% of aperture height), conical, and occupies about 2/3 of the rhynchocoel length. Mouth opening circular. The large unpaired ventral proboscis retractor is attached to the anterior part of the rhynchodaeum (proboscis sheath) and to the bottom of the cephalic haemocoel in its posterior part. Small semi-closed funnel-shaped chitinous jaw (Fig. 11C) lines anterior surface of buccal cavity (on the illustration the jaw is partially uncoiled, but in its natural position it is very similar to that of *Volutomitra glabella* – Fig. 11D). Radula (Fig. 11A) long, *c.* 3.0 mm, or

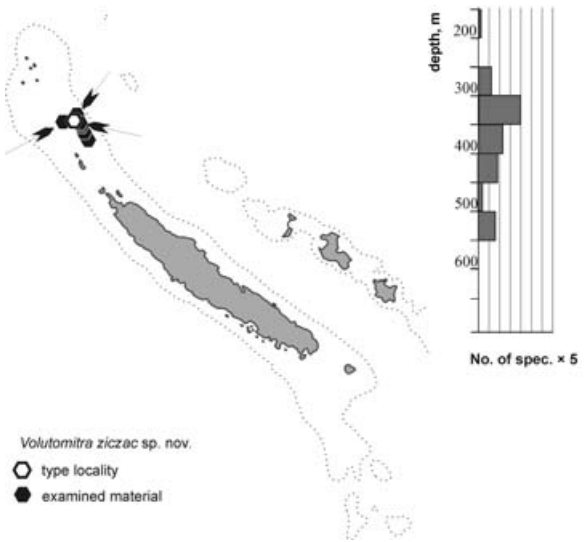

Figure 7 Geographical and bathymetrical distribution of *Volutomitra ziczac*, n. sp. Arrows indicate stations where the species is syntopic with *V. vaubani*. Each column represents five specimens (lv or dd). Isobath 1000 m.

29% of aperture length; forming part long and comprising 20% of the whole radular length. It is of typical morphology for Volutomitridae and consists of wishbone-shaped central teeth with rather long central cusp, having a deep groove on its dorsal surface, into which cusp of the previous row interlocks. Width of central tooth is about 24 μm (0.24% of aperture length). Median cusp/total tooth length ratio 42%. Part of radula in the sublingual pouch is remarkably long and comprises 1/3 of entire membrane length. In its posterior part it is embraced by muscular convoluted rod, which protrudes beyond rear of proboscis. In studied specimen anterior part of the radula was protruding through the jaw. Stomach relatively small and adjoins nephridium. Its shape is very similar to, although more sharply curved, than that of *V. glabella*. Due to the condition of preservation, we were not able to study its inner structure. The digestive gland is bilobate, although less clearly so than in *V. glabella*.

Remarks: The separation between *Volutomitra ziczac* and *V. vaubani* is discussed under the latter species. In the north of New Caledonia, the occurrences of *Volutomitra ziczac* and *V. vaubani* are essentially parapatric, with a narrow zone of overlap, about 6 km broad. Although in allopatric populations, some specimens of *V. ziczac* (BATHUS 4: sta. DW923, sta. DW926, see Fig. 6G) may superficially resemble *V. vaubani* in shell outline (e.g. specimens in Fig. 3F–G), the two species are strikingly different in the zone of co-occurrence (Fig. 5).

Etymology: With reference to the colour pattern of brownish, zic-zac chevrons.

Genus *Microvoluta* Angas, 1877

Microvoluta joloensis Cernohorsky, 1970 (Figs 8, 9, 10E, 11B, 12, 13H, 14, 18)

Microvoluta joloensis Cernohorsky, 1970a: 103–104, figs. 8–10. – Cernohorsky, 1970b: 121–122, pl. 15, figs. 8–10, 12.

Type material: National Museum of Natural History, Smithsonian Institution, holotype (USNM 288396) and 50 paratypes.

Type locality: Philippines, Sulu Sea, off Cagayan Island, 09°38.5′N, 121°11′E, 929 m [U.S. Bureau of Fisheries sta. 5423].

Material examined: A total of 66 lots (507 specimens), of which 37 lots (303 specimens) from the New Caledonia region.

SW Indian Ocean, northern Mozambique channel. BENTHEDI, R/V *Suroit*: sta. DR05, 12°32′S, 47°40.2′E, 150–135 m, 1 dd. – Sta. DR08, 11°29.2′S, 47°18.2′E, 250 m, 1 lv, 2 dd. – Sta. DS10, 11°28.5′S, 47°57.7′E, 440 m, 1 lv, 4 dd. – Sta. DR104, 11°26.4′S, 47°22.3′E, 330–350 m, 2 lv. – Sta. DS120, 11°30′S, 47°24.7′E, 335–390 m, 3 lv, 1 dd. – Sta. DS122, 11°32′S, 47°23.2′E, 615–625 m, 1 dd. – Sta. DS128, 11°32′S, 47°23.2′E, 600 m, 1 dd.

Coral Sea. **Nova Bank**. MUSORSTOM 5, R/V *Coriolis*: sta. 306, 22°08′S, 159°21′E, 375–415 m, 1 dd.

North of New Caledonia. MUSORSTOM 4, R/V *Vauban*: sta. DW159, 18°46′S, 163°16′E, 585 m, 8 dd. – Sta. DW161, 18°39′S, 163°11′E, 550 m, 4 dd. – Sta. DW197, 18°51′S, 163°23′E, 550 m, 3 dd, 1 lv.

BATHUS 4, R/V *Alis*: sta. DW895, 20°15′S, 163°52′E, 315–350 m, 1 dd. – Sta. DW914, 18°49′S, 163°15′E, 600–616 m, 170 dd. – Sta. DW923, 18°52′S, 163°24′E, 470–502 m, 1 lv. – Sta. DW926, 18°57′S, 163°25′E, 325–330 m, 1 dd.

South of New Caledonia. BIOCAL, R/V *Jean-Charcot*: sta. CP26, 22°40′S, 166°27′E, 1618–1740 m, 2 dd. – Sta. CP27, 23°06′S, 166°26′E, 1850–1900 m, 1 dd. – Sta. CP30, 23°09′S, 166°41′E, 1140 m, 1 dd. – Sta. DW56, 23°35′S, 167°12′E, 695–705 m, 2 dd. – Sta. KG73, 22°13′S, 167°29′E, 1285 m, 7 dd. – Sta. CP75, 22°19′S, 167°23′E, 825–860 m, 2 dd [co-occurring with *M. cryptomitra*, n. sp.]. – Sta. DW77, 22°15′S, 167°15′E, 440 m, 4 dd [co-occurring with *M. amphissa*, n. sp.].

SMIB 2, R/V *Vauban*: sta. DW21, 22°40′S, 167°41′E, 460–500 m, 1 dd. – Sta. DW23, 22°31′S, 167°37′E, 410–420 m, 1 dd.

BIOGEOCAL, R/V *Coriolis*: sta. KG210, 22°44′S, 166°31′E, 1190 m, 3 dd. – Sta. DW253, 21°32′S, 166°29′E, 310–315 m, 12 dd.

BATHUS 1, R/V *Alis*: sta. CP651, 21°42′S, 166°40′E, 1080–1180 m, 2 dd.

MUSORSTOM 4, R/V *Vauban*: sta. CC246, 22°08′S, 167°11′W, 410–420 m, 12 dd. – Sta. CC247, 22°09′S, 167°13′W, 435–460 m, 9 lv. – Sta. CC248, 22°09′S, 167°10′W, 380–385 m, 1 dd.

HALIPRO 1, R/V *Alis*: sta. CP866, 21°26′S, 166°17′E, 550–600 m, 2 dd.

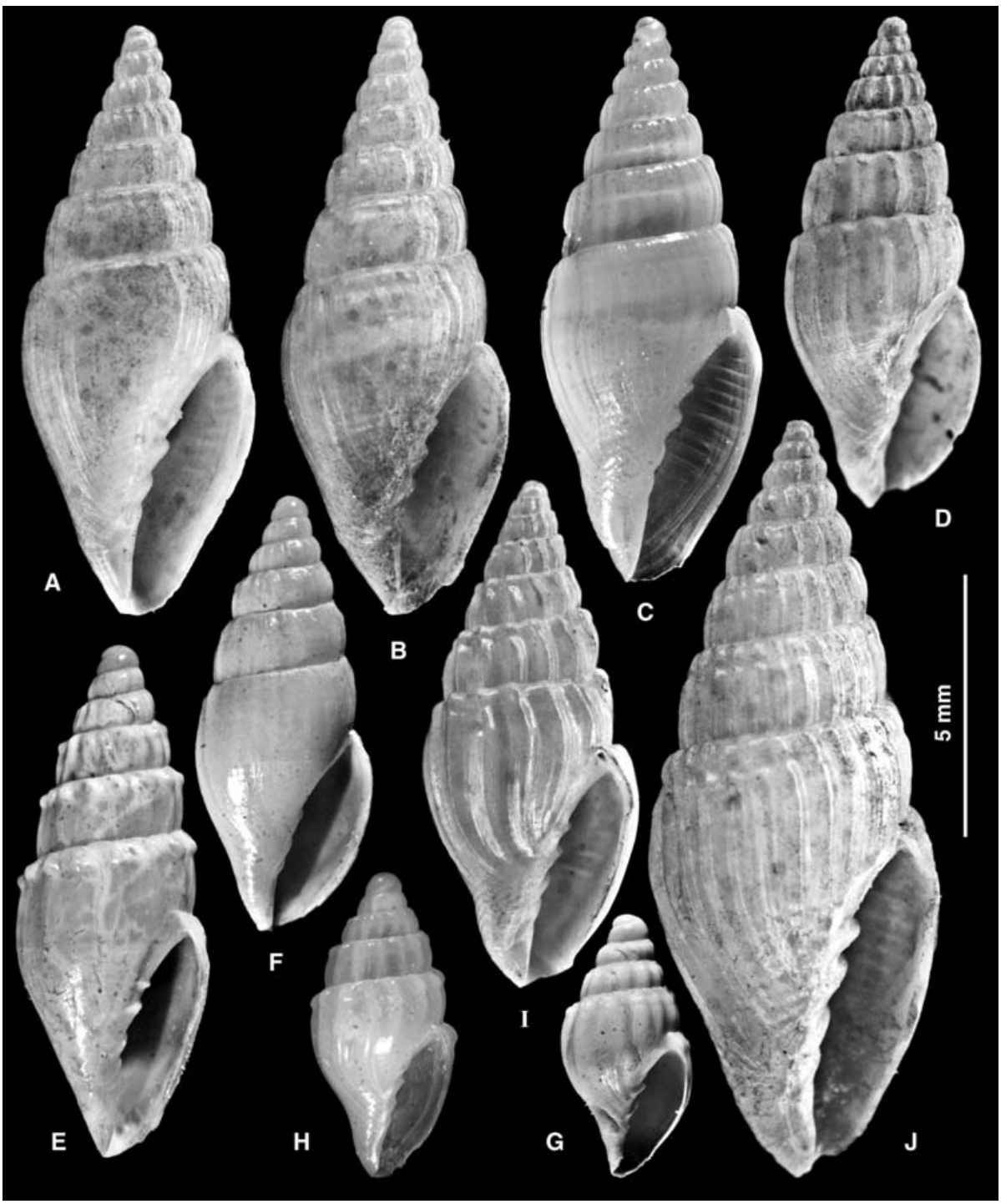

Figure 8 *Microvoluta joloensis*. **North of New Caledonia**. A–B, MUSORSTOM 4, sta. DW161, 550 m, SL of both shells 11.2 mm. C, specimen with lirate aperture, MUSORSTOM 4, sta. DW159, 585 m, SL 11.0 mm. D, specimen with well developed axial ribs, BATHUS 4, sta. DW914, 600–616 m, SL 9.4 mm. **Loyalty Islands**. E–G, BIOCAL, sta. DW79, 1320–1380 m, SL 9.8 mm (E), 8.4 mm (F), 5.0 mm (G). **Southern New Caledonia**. H, BIOCAL, sta. CP30, 1140 m, SL 5.9 mm. **SW Indian Ocean**. I, BENTHEDI, sta. DS120, 335–390 m, SL 9.6 mm. **Norfolk Ridge**. J, BATHUS 3, sta. DW825, 597–605 m, SL 14.2 mm, specimen with spiral grooves and axial ribs on last whorl, extending to shell base. All shells at the same scale.

Norfolk Ridge. BATHUS 3, R/V *Alis*: sta. DW824, 23°19′S, 168°00′E, 601–608 m, 1 dd. – Sta. DW825, 23°22′S, 168°00′E, 597–605 m, 2 dd.

Loyalty Ridge. BIOCAL, R/V *Jean-Charcot*: sta. DW79, 20°40′S, 166°52′E, 1320–1380 m, 4 dd [co-occurring with *M. cryptomitra*, n. sp.]. – Sta. DW80, 20°32′S, 166°48′E, 900–980 m, 2 dd.

BIOGEOCAL, R/V *Coriolis*: sta. CP232, 21°34′S, 166°27′E, 760–790 m, 4 dd. – Sta. CP260, 21°00′S, 166°58′E,

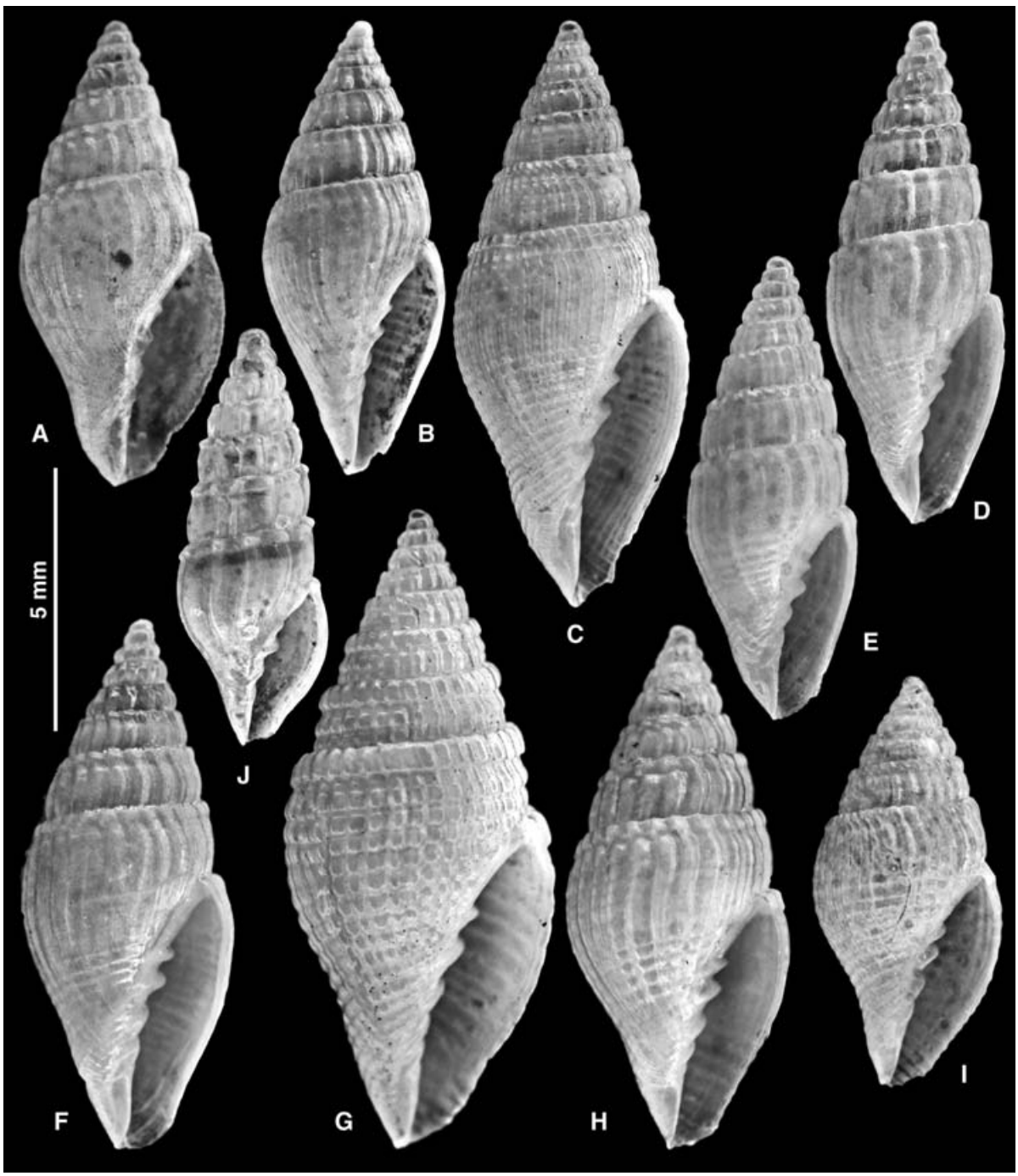

Figure 9 *Microvoluta joloensis*. **North of New Caledonia**. A, specimen intermediate between typical North New Caledonian form and biconical form, BATHUS 4, sta. DW914, 600–616 m, SL 8.9 mm. **Southern New Caledonia**. B, biconical form, HALIPRO 1, sta. CP866, 550–600 m, 8.7 mm. C, specimen with finely reticulated sculpture, MUSORSTOM 4, sta. CC247, 435–460 m, SL 11.2 mm. I, biconical specimen, MUSORSTOM 4, sta. CC246, 410–420 m, SL 7.8 mm. **Fiji**. D–E, elongated specimens, BORDAU 1, sta. DW1485, 700–707 m, SL 9.7 mm (D), 8.8 mm (E). F, biconical specimen, BORDAU 1, st. DW1432, 477–493 m, SL 10.1 mm. G, specimen with strongly reticulated sculpture, BORDAU 1, st. DW1479, 450–460 m, SL 12.2 mm. **SW Pacific, Wallis and Futuna Islands**. H, biconical specimen, MUSORSTOM 7, sta. DW601, 350 m, SL 10.0 mm. **Loyalty Ridge**. J, strongly elongated form, BATHUS 3, sta. DW790, SL 8.0 mm. All shells at the same scale.

1820–1980 m, 1 dd. – Sta. DW313, 20°59′S, 166°59′E, 1600–1640 m, 1 dd.

MUSORSTOM 6, R/V *Alis*: sta. DW410, 20°38′S, 167°07′E, 490 m, 2 dd. – Sta. DW468, 21°06′S, 167°33′E, 600 m, 8 dd [co-occurring with *M. cryptomitra*, n. sp.]. – Sta. DW479, 21°09′S, 167°55′E, 310 m, 11 dd. – Sta. DW485, 21°23′S, 167°59′E, 350 m, 1 dd.

BATHUS 3, R/V *Alis*: sta. DW790, 23°49′S, 169°48′E, 685–715 m, 13 dd [co-occurring with *M. respergens*, n. sp.]. – Sta. DW825, 23°22′S, 168°00′E, 597–605 m, 1 dd.

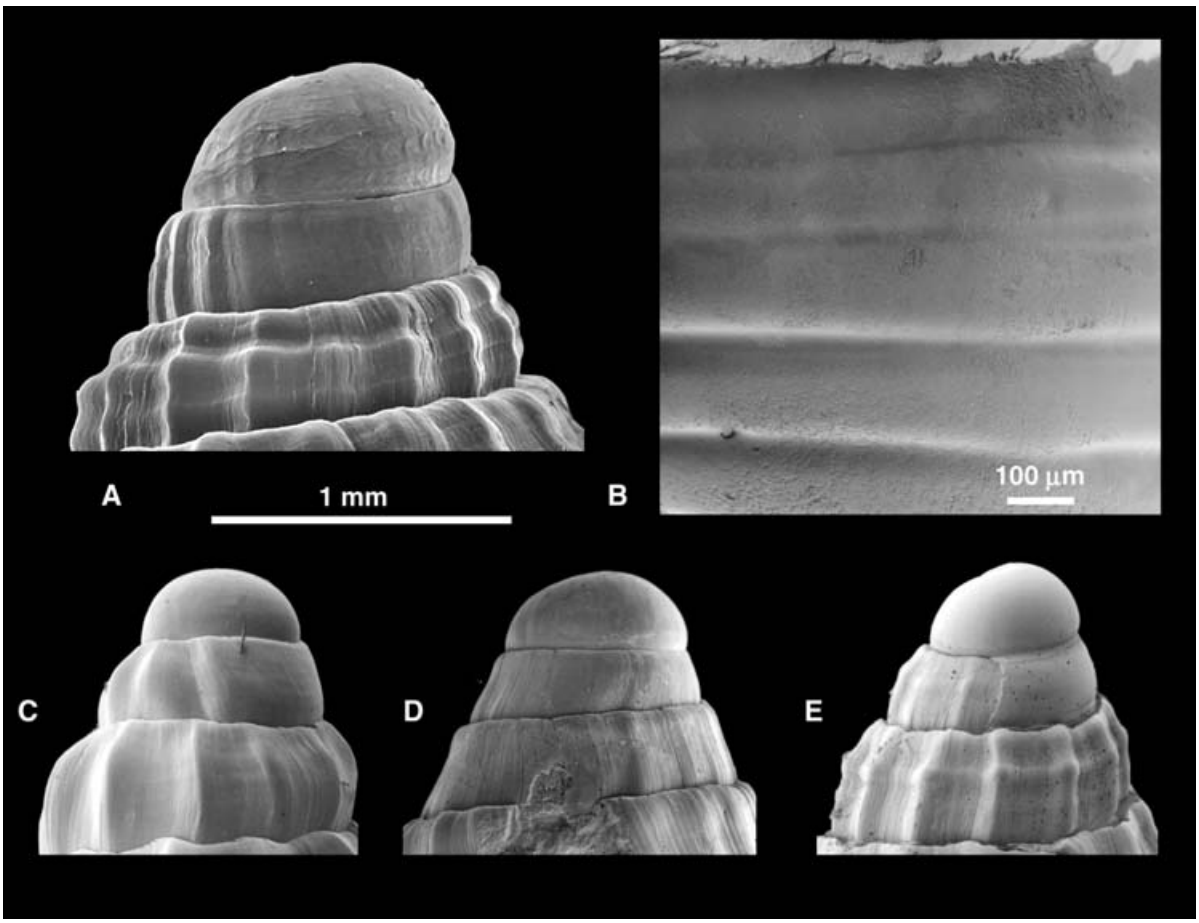

Figure 10 A, *Volutomitra vaubani*, protoconch; southern New Caledonia, BIOCAL, sta. DW46. B, D, *Microvoluta cythara*, n. sp., Chesterfield Plateau, MUSORSTOM 5, sta. 362. B, inner shell surface of the last whorl showing liration. D, protoconch. C, *Microvoluta amphissa*, n. sp., southern New Caledonia, BIOCAL, sta. DW46, protoconch. E, *Microvoluta joloensis*, north of New Caledonia, BATHUS 4, sta. DW914, protoconch.

SW Pacific. Wallis and Futuna. MUSORSTOM 7, R/V *Alis*: sta. DW523, 13°12′S, 176°16′W, 455–515 m, 17 lv, 18 dd. – Sta. DW524, 13°12′S, 176°16′W, 300 m, 1 lv. – Sta. DW527, 13°24′S, 176°15′W, 540–560 m, 1 dd. – Sta. DW585, 13°10′S, 176°13′W, 415–475 m, 1 dd. – Sta. DW586, 13°11′S, 176°13′W, 510–600 m, 2 dd. – Sta. DW601, 13°19′S, 176°17′W, 350 m, 31 dd. – Sta. DW604, 13°21′S, 176°08′W, 415–420 m, 6 dd. – Sta. DW608, 13°22′S, 176°08′W, 440–458 m, 2 dd.

SW Pacific, Bank Waterwitch. MUSORSTOM 7, R/V *Alis*: st. DW535, 12°30′S, 176°41′W, 340–470 m, 1 dd. – Sta. DW537, 12°30′S, 176°41′W, 325–400 m, 1 dd. **Bank Combe**: st. DW540, 12°27′S, 177°28′W, 600 m, 1 dd. – Sta. DW541, 12°27′S, 177°26′W, 500–505 m, 2 dd.

Fiji. BORDAU 1, R/V *Alis*: sta. CP1392, 16°49′S, 179°54′W, 545–651 m, 1 dd. – Sta. DW1408, 16°02′S, 179°30′W, 550–561 m, 9 dd. – Sta. DW1432, 17°20′S, 178°44′W, 477–493 m, 8 dd, 4 lv. – Sta. DW1479, 20°58′S, 178°45′W, 450–460 m, 5 dd. – Sta. DW1485, 19°03′S, 178°30′W, 700–707 m, 15 dd. – Sta. DW1486, 19°01′S, 178°26′W, 395–540 m, 19 dd. – Sta. DW1488, 19°01′S, 178°25′W, 500–516 m, 39 dd. – Sta. DW1492, 18°43′S, 178°23′W, 430–450 m, 1 dd.

Tonga. BORDAU 2, R/V *Alis*: st. DW1585, 18°33′S, 173°57′W, 578 m, 1 lv. – Sta. CP1642, 21°05′S, 175°23′W, 532 m, 1 lv.

Distribution: Indian Ocean: NW of Madagascar; Western Pacific: Philippines, New Caledonia region (Coral Sea, New Caledonia proper, Norfolk and Loyalty Ridges), Fiji, Wallis and Futuna, Tonga. Alive in 250–578 m, shells to 1900 m.

Remarks: We interpret *Microvoluta joloensis* as a highly variable species, with variation appearing to reflect environmental conditions more than the very extensive horizontal distribution. Under our taxonomical extension of *M. joloensis*, there is more variation between populations within the New Caledonia region (Table 1) than between any other parts of its geographical range. Another interpretation of the variation observed would be to recognize several species with discrete bathymetrical zonation. However, live-taken samples are too few to adequately document the fine distribution of the different morphs, and we have chosen a conservative approach in terms of number of species. Cernohorsky (1970a) had also interpreted considerable differences in shape, colour and sculpture among Philippines populations as within-species variation.

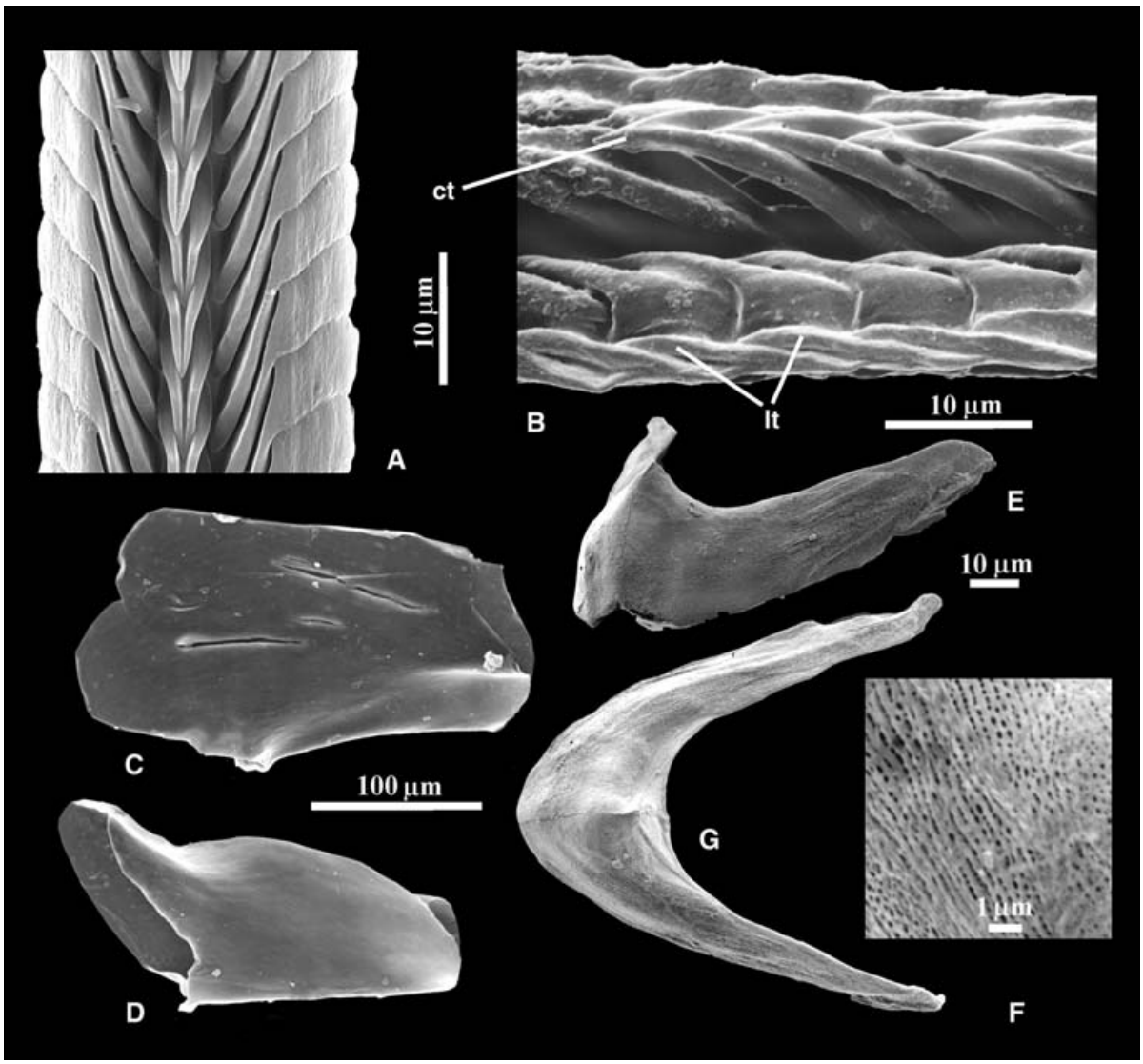

Figure 11 A, C, *Volutomitra ziczac* n. sp., MUSORSTOM 4, sta. DW196. A, dorsal view of radular ribbon. C, jaw (unfolded). D, *Volutomitra glabella*, jaw. B, *Microvoluta joloensis*, MUSORSTOM 7, sta. DW601, lateral view of radular membrane. E–G, *Microvoluta amphissa* n. sp., antero-lateral (E) and dorsal views of the jaw (G). F, microscupture of the jaw surface. Abbreviations: *ct* central tooth, *lt* lateral tooth.

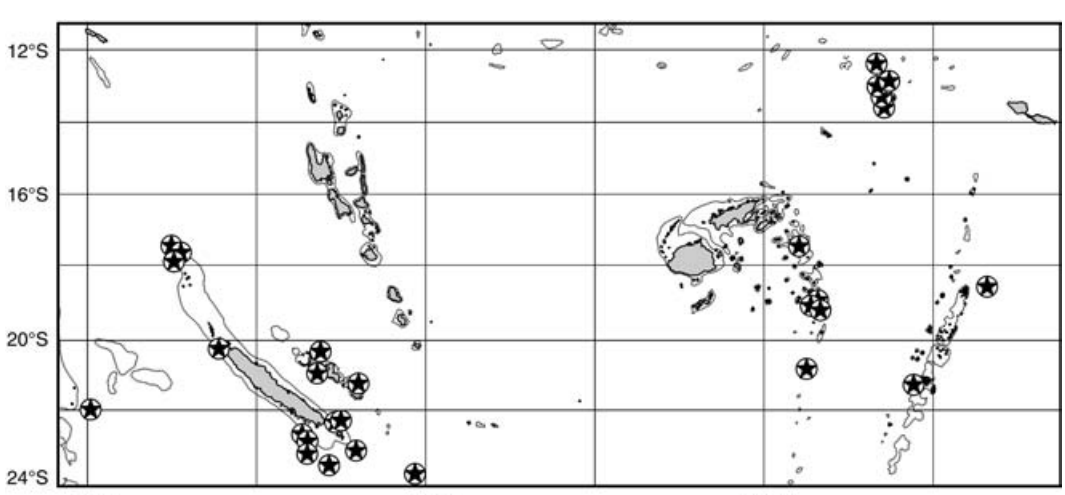

Figure 12 Geographical distribution of *Microvoluta joloensis* in the South-West Pacific. Isobath 500 m.

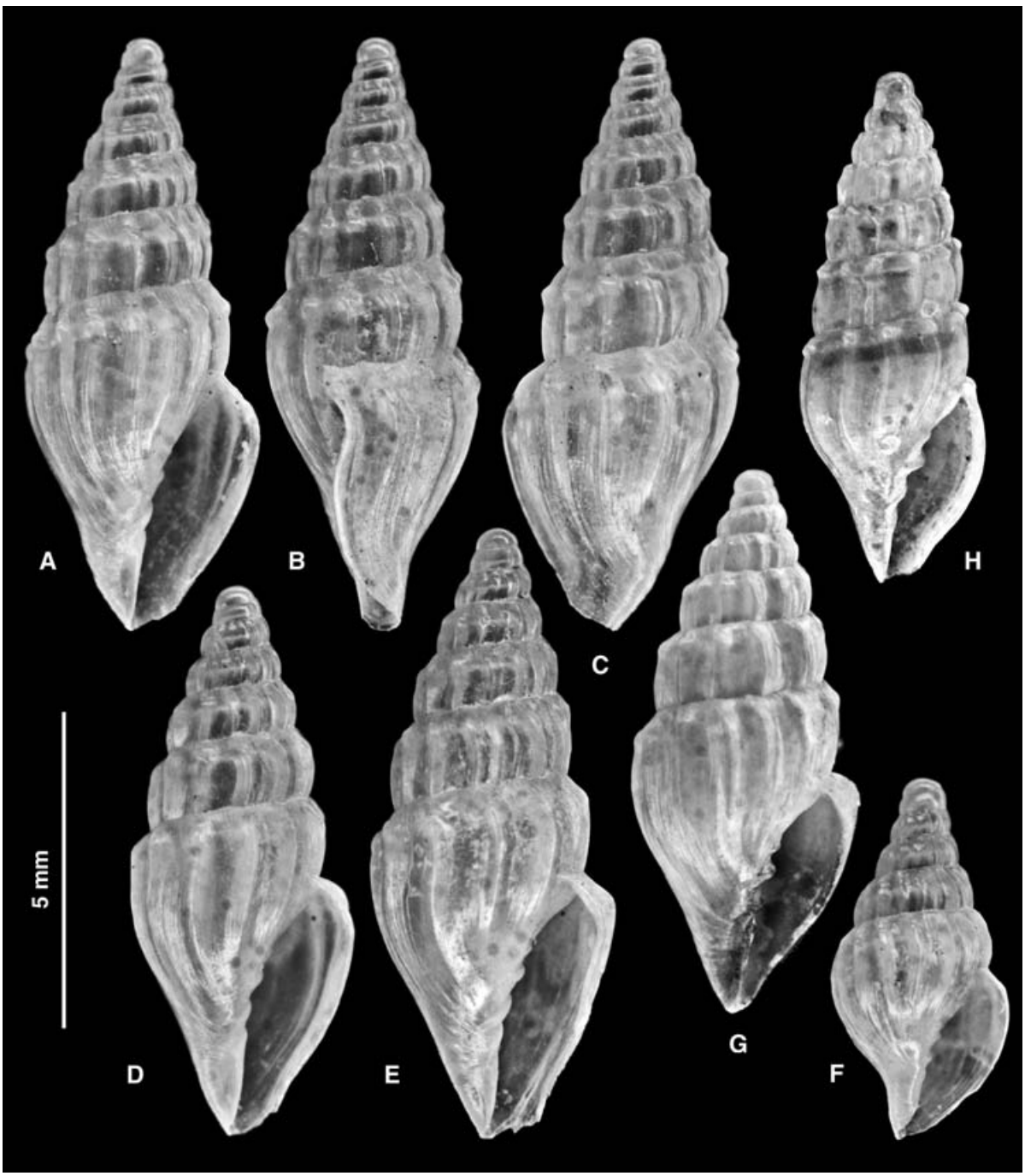

Figure 13 A–G, *Microvoluta respergens*, n. sp. A–F, Loyalty Ridge, BATHUS 3, sta. DW790. A–C, holotype, SL 9.3 mm; D, paratype, 8.6 mm; E, paratype, SL 9.6 mm; F, juvenile, 5.8 mm. G, Southern New Caledonia, BATHUS 2, sta. CP743, SL 8.5 mm. H, *Microvoluta joloensis*, same station as A–F, SL 8.0 mm. All shells at the same scale.

Specimens from the western Indian Ocean are rather uniform (Fig. 8I), and are characterized by oval to slightly biconical shell shape, whorls with adpressed suture, well developed axial ribs with subsutural bulge, extending to the shell base on the last whorl, very poorly developed spiral threads, usually lirate inside aperture of adults (smooth in juveniles). Colour whitish, some specimens with irregular very pale brownish spots under the suture and in some specimens forming irregular spiral bands or broken axial lines.

The variation around New Caledonia (Table 1) appears to be depth-related. In general, specimens collected north of New Caledonia (Fig. 8A–C) and in two samples from the Loyalty Islands in 300–600 m are characterized by elongate-oval shells, with generally smoothened axial ribs on the last and penultimate whorls in adults, as well as poorly developed spiral sculpture. However a large sample (BATHUS 4, sta. DW914), containing about 170 shells, shows all transitions from specimens with a nearly smooth last whorl to specimens with

	Range (μm)	Average (μm)	σ	n	
North of New Caledonia					
protoconch diameter (D2)	780–880	840	36	6	Fig. 9E
protoconch elevation (PRE)	700–830	750	46	6	
last whorl/shell height	0.60–0.67 (adults) up to 0.68 (juv.)	0.63	0.02	10	
diameter/height	0.38–0.47	0.41	0.03	10	
aperture height/shell height	0.49–0.58	0.53	0.03	10	
largest adult	shell height 11.2 mm, diameter 4.2 mm last whorl height 6.8 mm, aperture height 5.7 mm				
South of New Caledonia, 300–400 m					
protoconch diameter (D2)	640–720	690	40	4	
protoconch elevation (PRE)	420–500	470	35	4	
last whorl/shell height	0.68–0.72	0.70	0.02	4	
diameter/height	0.42–0.48	0.45	0.03	4	
aperture height/shell height	0.58–0.62	0.60	0.02	4	
largest adult	shell height 7.4 mm, diameter 3.1 mm last whorl height 5.0 mm, aperture height 4.4 mm				
South and East of New Caledonia, 700–1800 m					
protoconch diameter (D2)	up to 1140	965	80	10	
largest adult	shell height 9.6 mm, diameter 3.8 mm last whorl height 5.4 mm, aperture height 4.5 mm				

Table 1 Biometric characteristics of selected populations of *Microvoluta joloensis* in the New Caledonia region.

strong axial ribs, extending over all the shell surface (Fig. 8D), to specimens with a nearly biconical shell (Fig. 9A). The spiral groove in the subsutural zone is also rather variable, being distinct and rather deep in some specimens, while nearly obsolete in others. On some specimens with better pronounced axial ribs, these tend to form rounded low swellings on the shoulder. All intermediates between a completely smooth aperture and rather strongly lirate were also observed in this sample.

Specimens from south of New Caledonia (Fig. 9B, I) at depths of 300–400 m (shells to 600 m: HALIPRO 1, sta. CP866) are rather constant in shell shape and are characterized by a rather small biconical shell (juveniles in particular have strongly biconical shells) with flat whorls, axial ribs depressed at periphery, and spiral sculpture of indistinct spiral grooves. Shell colour greyish-white with indistinct pale brown colour marks. Number of axial ribs on the first whorl ranges 12–16 (average 13.5, $\sigma = 1.9$, $n = 4$), on second 12–17 (average 14.5, $\sigma = 2.1$, $n = 4$), on third whorl 15–17 (average 16.3, $\sigma = 1.0$, $n = 4$). Protoconch diameter is smaller than in the northern form. Although extreme specimens from the northern and these southern populations may seem strikingly different, all intermediates between them can be found.

In populations from deeper water (400–600 m), the shell is biconical, with high, shouldered whorls, almost canaliculate suture, one strong spiral groove delimiting subsutural node, others grooves more shallow, and the spiral cords are stronger and produce a reticulated shell surface (Figs 8J, 9C). Extreme specimens of these populations may again look very different, but can be connected by intermediates with specimens of populations from shallower water. Shells of this form attain the largest size for *M. joloensis*: shell height 14.2 mm, diameter 5.4 mm, last whorl height 8.8 mm, aperture height 7.1 mm (BATHUS 3, sta. DW825; Fig. 8J). One population from Loyalty Ridge (MUSORSTOM 6, sta. DW479, 310 m) has a rather distinct shell colour, pale brownish irregular spots in the upper part of the whorls and, in some specimens, narrow but distinct, strongly oblique, zigzag lines on the periphery and shell base.

In still deeper water (700–1800 m) in the south and east of New Caledonia, in the Loyalty Basin, and off the Loyalty Islands, a rather distinct form (Figs 8E–H) is characterized by slender, biconical to elongate-oval shell, with fewer axial ribs forming a strong subsutural bulge. Ribs are better developed on adapical teleoconch whorls, but fade on 4th and later whorls, where they are pronounced only at shoulder and periphery. Spiral sculpture is absent from most specimens and the shell is glossy. Subadult shells from these populations look quite different from adults ones due to their shorter last whorl, but the morphology of early teleoconch whorls is identical. This form resembles late Miocene fossils, such as *Microvoluta marwicki* (Vella, 1954) (illustrated by Beu & Maxwell, 1990, pl. 27o) and *M. nodulata* Maxwell, 1988, from deep-water deposits in New Zealand. This deep-water form appears rather distinct, and is only poorly connected by intermediates with forms from more shallow water. However, as we did not find it co-occurring with any other form of *M. joloensis*, and as specimens of *M. joloensis* from intermediate depths, in 500–700 m, show a tendency to larger protoconch diameter with increasing depth, we interpret it as a deep-water morph of *M. joloensis*.

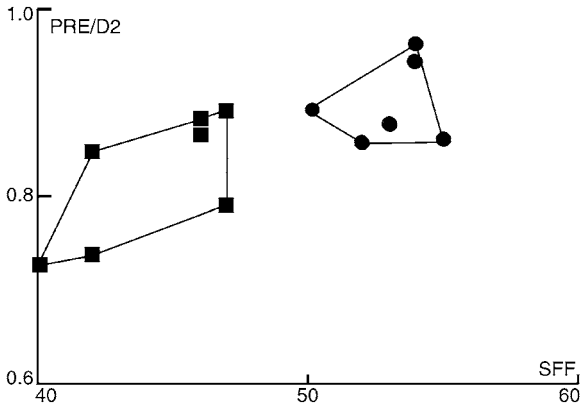

Figure 14 Morphometric comparison of *Microvoluta joloensis* (●, populations from north New Caledonia) and *M. respergens*, n. sp. (■). PRE = exposed height of protoconch; D2 = diameter of protoconch and first 1/4 teleoconch whorl (see Fig. 1); SFF = number of axial folds on first three teleoconch whorls.

An isolated population from a seamount on the Loyalty Ridge (BATHUS 3, sta. DW 790) is characterized by a very slender shell (diameter/shell length ratio 0.36–0.47) with strong knobs on the subsutural rim (Fig. 9J). Because it resembles most some elongated forms of *M. joloensis*, we also interpret it conservatively as a local variation of the latter; molecular data might either prove or disprove this hypothesis.

The numerous lots from Fiji, Wallis and Futuna, and Tonga show a variation most similar to that observed in populations from 400–600 m off southern New Caledonia. Practically all forms, from elongated ones (Fig. 9D, E) to biconical (Fig. 9F, H) and strongly reticulated ones (Fig. 9G), can be found in every archipelago (except Tonga, where the only two shells are of the biconical type).

Radula and jaw of 2 specimens with biconical shell (Wallis and Futuna, MUSORSTOM 7, sta. DW 601; southern New Caledonia, MUSORSTOM 4, sta. CC246) have been examined. The radula is typical for Volutomitridae (Fig. 11B); median cusp/total tooth length ratio 0.56–0.62; lateral teeth rather well developed and long. Jaw is in all details similar to that of *M. amphissa* (Fig. 11E–G – see below).

Microvoluta respergens, n. sp. (Figs 13, 14, 15)

Type material: Holotype (dd) and 6 paratypes (dd) MNHN; 1 paratype (dd) NMNZ, 1 paratype (dd) AMS.

Type locality: Loyalty Ridge, 23°49′S, 169°48′E, 685–715 m [BATHUS 3, sta. DW790].

Material examined: A total of six lots (30 specimens).

Loyalty Ridge. BIOGEOCAL, R/V *Coriolis*: sta. DW289, 20°36′S, 167°00′E, 830–840 m, 1 dd.

BATHUS 3, R/V *Alis*: sta. DW786, 23°54′S, 169°49′E, 699–715 m, 8 dd. – Sta. DW790, 23°49′S, 169° 48′E, 685–715 m, 10 dd (holotype and paratypes) [co-occurring with *M. joloensis*]. – Sta. DW793, 23°47′S, 169°49′E, 731–751 m, 2 lv, 3 dd. – Sta. DW794, 23°48′S, 169°49′E, 751–755 m, 1 lv.

Southern New Caledonia. BATHUS 2, R/V *Alis*: sta. CP743, 22°36′S, 166°26′E, 713–950 m, 5 dd.

Distribution: South of New Caledonia and Loyalty Ridge, alive in 750 m, shells in 715–830 m. Except for one sample from SW of New Caledonia, all other specimens come from a single seamount (unnamed seamount labelled 'J' on ZONECO maps) on the Loyalty Ridge.

Description (holotype) (Fig. 13A–C): Shell solid, glossy, semitransparent, slender, fusiform, width 38% of height, consisting of 1.875 protoconch and 6.0 teleoconch whorls. Protoconch large, diameter (D2) 800 μm, high, elevation 710 μm. Whorls convex, first whorl globose, smooth, semitransparent, protoconch-teleoconch transition indistinct, marked by very weak orthocline rib. First half of first teleoconch whorl practically smooth. Teleoconch whorls convex, with impressed suture, slightly angulated at shoulder, without subsutural sulcus. Sculpture consisting of strong, widely spaced, arched but nearly orthocline ribs, forming large rounded knobs on shoulder; ribs equally well developed on all teleoconch whorls, 11 on first, 19 on second, 16 on third, 14 ribs on last whorl, where they extend to shell base. Last whorl short, 58% of total shell height. Aperture low, height 47% of shell height, narrowly elongate, angulated at anterior fifth, where reflected outer lip is flaring; smooth inside, except for a spiral lira corresponding in its position to the row of shoulder knobs. Columella without callus, with 4 rather low columellar plaits, adapical one smallest. Siphonal canal moderately long, slightly curved to right and backward. Colour of the shell uniformly greyish-white.

Dimensions (holotype): Shell height 9.3 mm, diameter 3.5 mm, last whorl height 5.4 mm, aperture height 4.4 mm. Largest adult (paratype): Shell height 9.6 mm, diameter 3.8 mm, last whorl height 5.4 mm, aperture height 4.5 mm.

Remarks: *Microvoluta respergens*, n. sp. is only moderately variable in shell shape, degree of prominence of shoulder knobs and in protoconch elevation. Diameter/height ratio in adults ranges 0.38–0.43 (average 0.41, $\sigma = 0.02$, n = 6), last whorl/shell height ratio 0.57–0.60 (average 0.58, $\sigma = 0.01$, n = 6), aperture height/shell height ratio 0.47–0.50 (average 0.48, $\sigma = 0.01$, n = 6). Number of axial ribs on the first whorl ranges 12–15 (average 12.9, $\sigma = 1.3$, n = 7), on second 15–19 (average 16.9, $\sigma = 1.6$, n = 7), on third whorl 12–16 (average 14.6, $\sigma = 1.8$, n = 7). Protoconch diameter ranges 770–890 μm (average 820, $\sigma = 50$, n = 7), protoconch elevation 620–720 μm (average 670, $\sigma = 40$, n = 7). Subadults are much less slender (diameter/height ratio 0.47) (Fig. 13F) and with proportionately higher last whorl (last whorl/shell height ratio 0.61).

The general shell morphology of *Microvoluta respergens*, n. sp. resembles that of *M. joloensis*, especially specimens from north of New Caledonia. However, *M. respergens*, n. sp. differs in having fewer, stronger axial ribs, in having a distinctly angulated outer aperture lip, as well

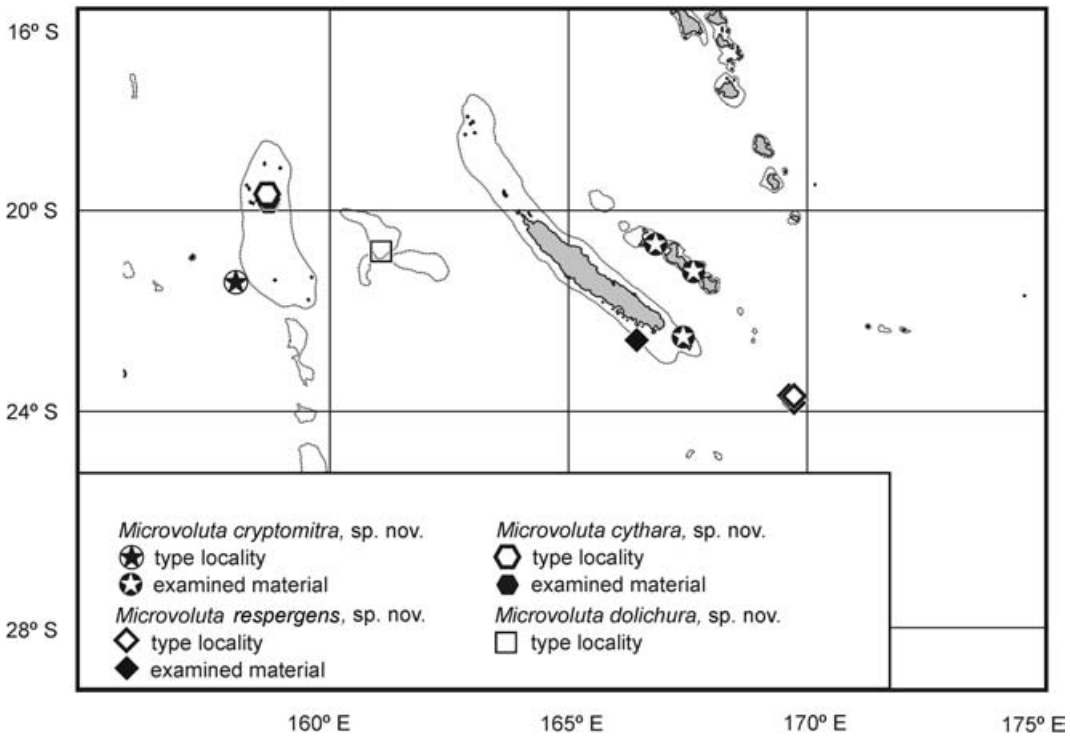

Figure 15 Geographical distribution of *Microvoluta cryptomitra* n. sp., *Microvoluta cythara*, n. sp., *Microvoluta dolichura*, n. sp., and *Microvoluta respergens*, n. sp. Isobath 500 m.

as in having slightly less elevated protoconch (as shown on scatter plot, Fig. 14). *Microvoluta respergens*, n. sp. and *M. joloensis* have been taken together at BATHUS 3 sta. DW 790, where they differ markedly (compare Figs 13A and H).

Etymology: *Respergere* (Latin) – to pour, by reference to the shape of the outer lip of the aperture.

Microvoluta cythara, n. sp. (Figs 10B, D, 15, 16A–G, M, 17, 18)

Type material: holotype (lv) and 11 paratypes (2 lv and 9 dd) MNHN; one paratype (dd) NMNZ, 1 paratype (dd) AMS.

Type locality: Coral Sea, Chesterfield plateau, 19°53′S, 158°40′E, 410 m [MUSORSTOM 5: sta. 362].

Material examined: A total of six lots (40 specimens).

Coral Sea, Chesterfield plateau. MUSORSTOM 5, R/V *Coriolis*: sta. 337, 19°54′S, 158°38′E, 412–430 m, 1 dd. – Sta. 339, 19°53′S, 158°38′E, 380–395 m, 3 dd. – Sta. 361, 19°53′S, 158°38′E, 400 m, 1 lv, 5 dd. – Sta. 362, 19°53′S, 158°40′E, 410 m, 3 lv, 12 dd (holotype and paratypes). – Sta. 378, 19°54′S, 158°38′E, 355 m, 2 dd. – Sta. 379, 19°53′S, 158°40′E, 370–400 m, 5 lv (1 specimen sectioned), 8 dd.

Distribution: Coral Sea, Chesterfield plateau, alive in 400–410 m, shells from 355 m.

Description (holotype) (Fig. 16A–C): Shell solid, glossy, elongate-fusiform, nearly biconical, width 43% of height, consisting of 2.0 protoconch and 5.0 teleoconch whorls. Protoconch diameter (D2) 800 μm, protoconch elevation 605 μm, whorls convex, smooth, protoconch-teleoconch transition indistinct. Teleoconch whorls convex with adpressed suture and strong subsutural sulcus, whorls distinctly concave below subsutural sulcus and becoming convex at periphery. Sculpture consisting of strong sigmoid opisthocline ribs, crossed by very indistinct low spiral striae; 12 ribs on first whorl, 14 on second, 17 on third; axial ribs gradually becoming obsolete on last whorl, last whorl with only indistinct ribs in last half. Rather strong internal spiral lirae visible through semitransparent shell (Fig. 10B), 11 in aperture. Last whorl height 64% of total shell height. Aperture height 54% of shell height, narrowly elongate, with spiral lirae inside, becoming obsolete at the lip, outer lip distinctly deflected in adapical fifth. Columella without a callus, with 4 widely spaced plaits, abapical one smallest. Siphonal canal moderately long, straight. Colour of the shell uniformly glossy white.

Dimensions (holotype): Shell height 10.1 mm, diameter 4.3 mm, last whorl height 6.5 mm, aperture height 5.5 mm. Largest specimen (paratype) (Figs 16F–H): shell height 10.5 mm, diameter 4.5 mm, last whorl height 6.5 mm, aperture height 5.7 mm.

Anatomy: Two specimens have been studied anatomically. One dissected specimen (MUSORSTOM 5, sta. 362) had a shell height of 7.7 mm, diameter 3.7 mm, last whorl height 5.4 mm, aperture height 4.8 mm. One specimen (MUSORSTOM 5, sta. 379; SL 9.6 mm) was sectioned. The description is based mainly on the dissected specimen, with some details added from the sectioned one.

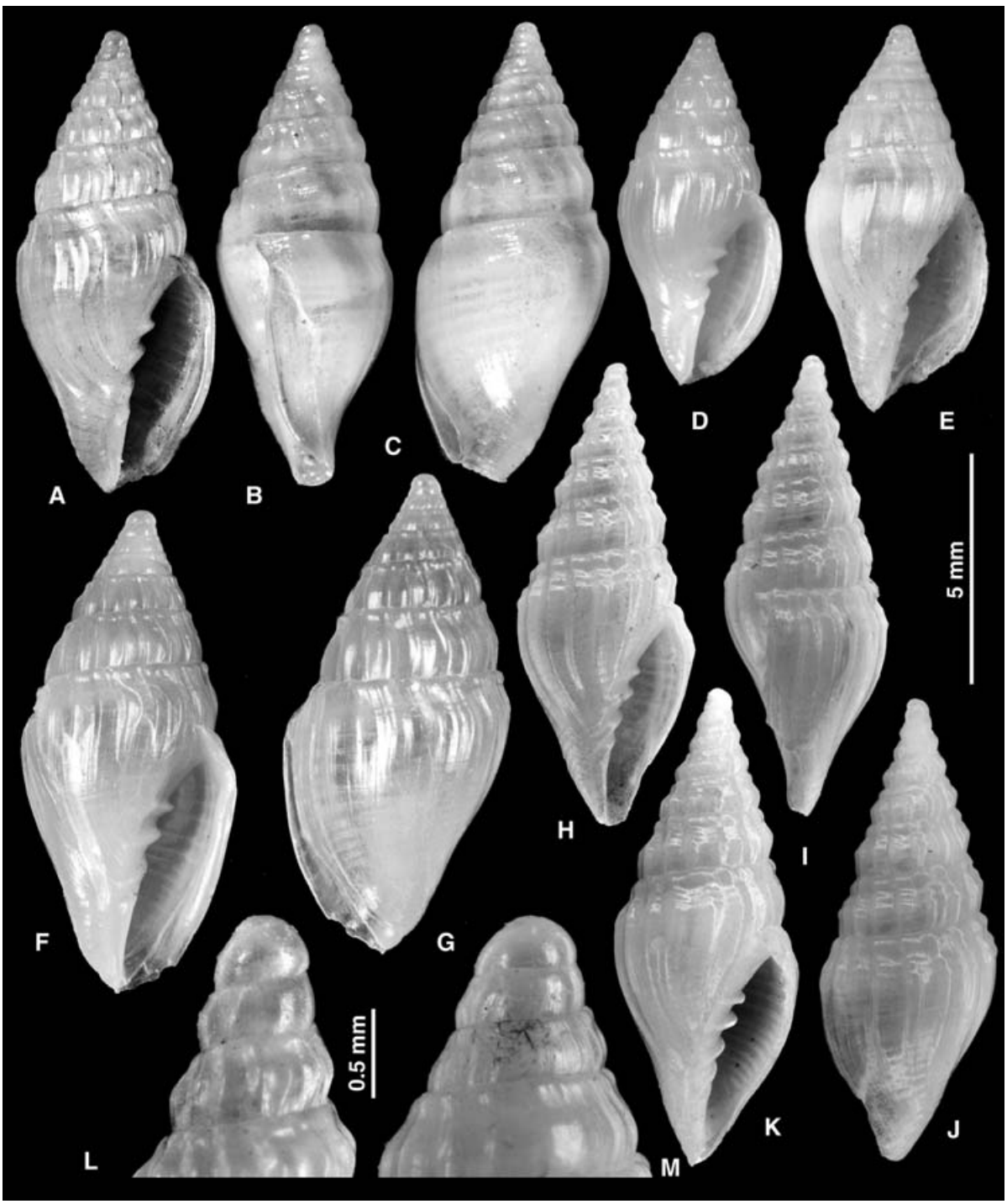

Figure 16 A–G, M, *Microvoluta cythara*, n. sp. A–D, F–G, M, MUSORSTOM 5, sta. 362. A–C, M, holotype, SL 10.1 mm; D, paratype, SL 7.7 mm; F–G, paratype, SL 10.5 mm. E, MUSORSTOM 5, Sta. 379. E, SL 8.5 mm. H–L, *Microvoluta dolichura*, n. sp., CORAIL 2, Sta. DE16. H–J, L, holotype, SL 10.1 mm; K, paratype, SL 10.2 mm. Scale bar 5 mm (A–K) and 0.5 mm (L–M).

External anatomy: The body consists of about 2.5 whorls (1.5 whorls were retrieved from the shell), the mantle spans slightly over 0.5 whorl, the nephridium about 0.3 whorl. The body is yellowish-white and lacks pigmentation; it carries narrow spiral grooves, corresponding to the lirae on the internal shell surface. Operculum absent. The foot has an ovate sole, folded lengthwise. The siphon is short, simple, slightly protruding beyond the mantle edge (Fig. 17A, B – s). The columellar muscle is thick, consisting of 1.75 whorls, with three deep grooves, corresponding to columellar plaits. Abapical muscle branch completely detached from the rest. Mantle very thin and semitransparent, covering head base. Head medium-sized, with short conical tentacles and large eyes.

Mantle: Ctenidium occupying slightly more than half of mantle length, curved and separated into two parts. Anterior part (close to mantle edge) narrow, with lamellae having

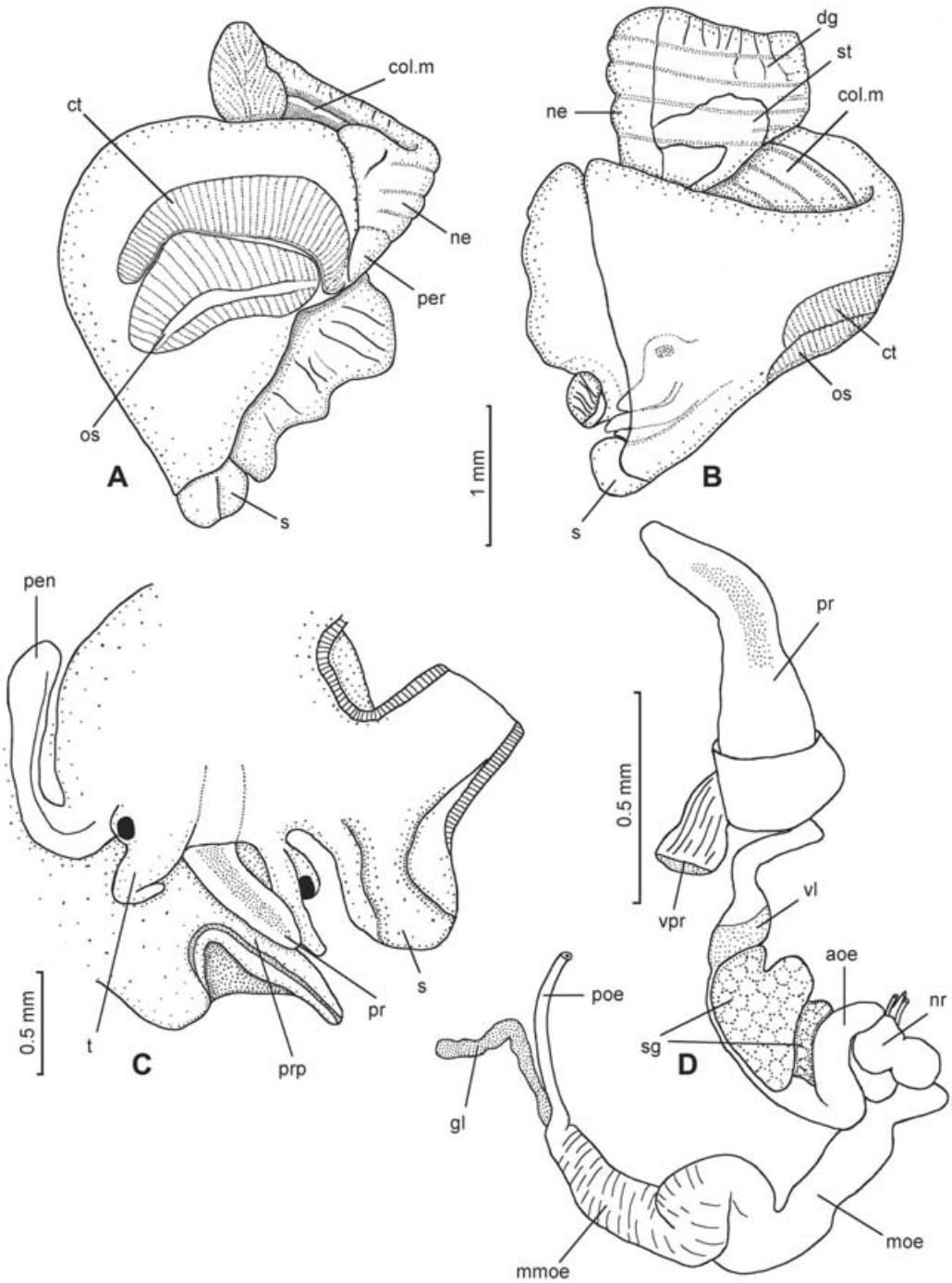

Figure 17 Anatomy of *Microvoluta cythara*, n. sp., male, MUSORSTOM 5, sta. 362. A–B, Body removed from the shell. C, Anterior view of the head-foot, mantle cut along the left side, pulled aside and reflected. D, Anterior digestive system, oesophagus uncoiled, proboscis sheath removed to show the proboscis. Abbreviations: *aoe* anterior oesophagus, *col.m* columellar muscle, *ct* ctenidium, *dg* digestive gland, *gl* gland of Leiblein, *mmoe* muscular posterior part of the mid oesophagus, *moe* mid oesophagus, *ne* nephridium, *nr* nerve ring, *os* osphradium, *pen* penis, *per* pericardium, *poe* posterior oesophagus, *pr* proboscis, *prp* propodium of the foot, *s* siphon, *sg* salivary gland, *st* stomach, *t* cephalic tentacle, *vl* valve of Leiblein, *vpr* ventral proboscis retractor.

narrow base, hanging freely into the cavity. Posteriorly, the ctenidium becomes much wider and consists of triangular lamellae. Osphradium large, slightly wider than ctenidium, asymmetrical, with the right side being at least 1.5× broader than the left. Hypobranchial gland poorly developed, covering partially the rectum and pallial gonoduct. Rectum very narrow, anal gland not seen on dissection.

Digestive system: Proboscis preserved in semi-protracted position, moderately long, about 0.76 mm, or 16% of aperture height, cylindrical and protruded through mouth opening (Fig. 17C – pr). In the sectioned specimen, the proboscis in retracted position occupies most of rhynchocoel length. Proboscis walls thin, lumen between proboscis wall and thick-walled oesophagus broad and filled by large, oval, probably glandular

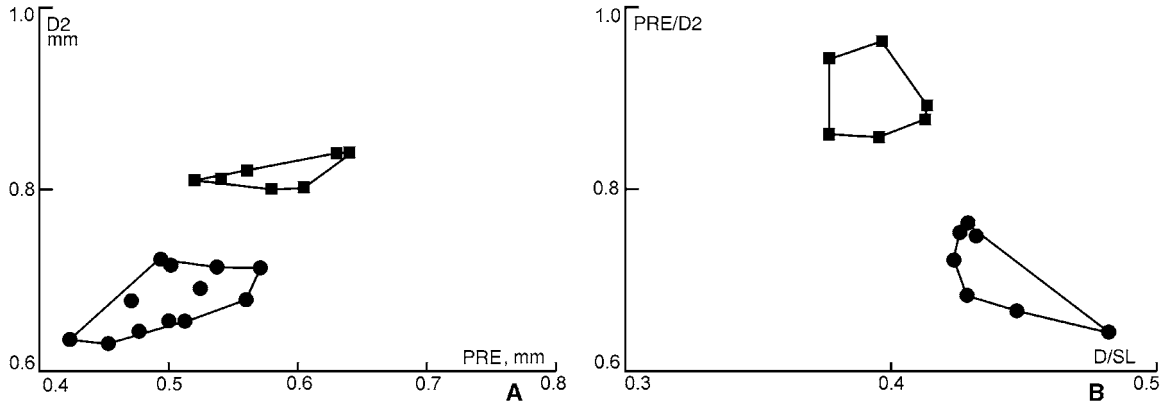

Figure 18 Morphometric comparison of *Microvoluta cythara*, n. sp. (■) and two populations of *Microvoluta joloensis* (●). A, biconical population from south of New Caledonia. B, population from north of New Caledonia. PRE = exposed height of protoconch; D2 = diameter of protoconch and first 1/4 teleoconch whorl (see Fig. 1); D = shell diameter; SL = shell height.

cells. Proboscis and oesophagus walls connected by numerous transverse muscle fibres. Oesophagus wall thick (about twice as thick as proboscis wall) and muscular. Proboscis and oesophagus probably act as muscular pump. Large unpaired ventral proboscis retractor (Fig. 17D – vpr) attached to posterior part of the rhynchodaeum (proboscis sheath) and bottom of cephalic haemocoel. Anteriormost part of proboscis invaginated inside, so that circular fold is situated around narrow mouth opening. The small horse-shoe-shaped chitinous jaw lines the anterior dorsal surface of the buccal cavity and is in all details similar to that of *Microvoluta amphissa* (Fig. 11E–F). Dorsal edge of jaw sharp and serving as cutting edge. Radula about 1.2 mm long, or 25% of aperture length. Lateral teeth simple, needle-shaped. Width of central tooth about 18 μm (0.32% of aperture length). Median cusp/total tooth length ratio 0.47. In its posterior part, the radular sac is embraced by a muscular convoluted rod, which lies completely within the protracted proboscis. Subradular cartilages paired, not fusing in anterior part, but connected with transverse muscle, and running along the entire proboscis length.

Morphology of oesophagus very similar to that described for other Volutomitridae (Ponder, 1972; Arnaud & van Mol, 1979; Kantor & Harasewych, 1992; Bouchet & Kantor, 2000b). Anterior oesophagus (between proboscis and valve of Leiblein) relatively short and thin. Valve of Leiblein (Figure 17D – vl) well demarcated and distinguished by a more whitish colour than rest of oesophagus. Position of torsion is situated at posterior part of the valve of Leiblein. This is expressed in rotation of ventral channel of the valve, which is seen as a dark strip through the wall of the valve. Soon after the valve, the mid-oesophagus widens considerably and forms two loops before passing through the circumoesophageal nerve ring. Posterior part of mid-oesophagus (Fig. 17D – mmoe) becoming extremely thick and convoluted until the entrance of the gland of Leiblein, which is small and tubular (Figure 17D – gL). Posterior oesophagus (after opening of the gland) becoming very narrow and thin-walled. Stomach relatively small, adjoining nephridium (Fig. 17B – st), nearly U-shaped, but with a small caecum, similar in shape to that of *Volutomitra glabella* (Bouchet & Kantor, 2000b) and *Peculator hedleyi* (Ponder, 1972). Salivary glands large, fused, consisting of few acini, very large in diameter. Accessory salivary gland rather long, coiled and protruding beyond the base of the retracted proboscis. Duct very narrow, running along ventral proboscis wall to open near mouth.

The dissected specimen was an immature male with a rather short simple penis with open seminal groove (Fig. 17C – pen).

Remarks: *Microvoluta cythara*, n. sp. is rather constant in shell shape, with diameter/height ratio 0.43–0.48 (average 0.44, $\sigma = 0.02$, n = 7), last whorl/shell height ratio 0.62–0.71 (average 0.67, $\sigma = 0.04$, n = 7), aperture height/shell height ratio 0.54–0.61 (average 0.58, $\sigma = 0.03$, n = 7). Number of axial ribs on the first whorl 12–15 (average 13.4, $\sigma = 1.3$, n = 7), on second 14–17 (average 15.7, $\sigma = 1.1$, n = 7), on third whorl 16–20 (average 17.6, $\sigma = 1.3$, n = 7). Protoconch diameter (D2) ranges 800–840 μm (average 818, $\sigma = 17$, n = 7), protoconch elevation 520–640 μm (average 580, $\sigma = 46$, n = 7).

M. cythara, n. sp. has some similarities to *M. joloensis*, especially its biconical outline, but is readily distinguished from it by the concave profile of the whorl above the periphery, the larger and more elevated protoconch, and the more numerous axial ribs on the spire whorls (Fig. 18).

Etymology: After the turrid genus *Cythara*, to which it bears a superficial resemblance; used as a noun in apposition.

Microvoluta dolichura, n. sp. (Figs 15, 16H–L)

Type material: holotype (dd) and 4 paratypes (dd) MNHN.

Type locality: Coral Sea, Lansdowne-Fairway Bank, 20°48′S, 160°56′E, 500 m [CORAIL 2: sta. DE16].

Material examined: Only the type lot (five specimens).

Distribution: Known only from the type locality, Coral Sea, Lansdowne-Fairway Bank, dead in 500 m.

Description (holotype) (Fig. 16H–J): Shell solid, glossy, narrow-fusiform, nearly biconical, width 39% of height, consisting of 1.75 protoconch and 6.5 teleoconch whorls. Protoconch diameter (D2) 710 μm, protoconch elevation 710 μm, whorls convex, smooth, first whorl swollen, strongly raised, protoconch-teleoconch transition very indistinct. Teleoconch whorls convex with adpressed suture and strong subsutural sulcus, whorls distinctly concave below subsutural sulcus. Sculpture consisting of strong sigmoid opisthocline ribs, crossed by two strong spiral cords located between the sulcus and periphery, the lower cord forming a prominent shoulder, and very indistinct low spiral striae; 12 ribs on first whorl, 14 on second, 16 on third; axial ribs well pronounced on entire last whorl, 15 in total. Eleven rather strong, closely spaced, spiral cords on the canal. Moderately developed internal spiral lirae visible through semitransparent shell (Fig. 10J), 8 in aperture. Last whorl height 60% of total shell height. Aperture height 49% of shell height, narrowly elongate, with spiral lirae inside, becoming obsolete at the lip, outer lip simple, fragile. Columella without a callus, with 4 widely spaced plaits, abapical one smallest. Siphonal canal moderately long, narrow, straight. Colour of the shell uniformly glossy white.

Dimensions: Shell height 10.1 mm, diameter 3.9 mm, last whorl height 6.1 mm, aperture height 4.9 mm. Largest specimen (paratype) (Fig. 16K): shell height 10.2 mm, diameter 3.9 mm, last whorl height 6.4 mm, aperture height 5.4 mm.

Remarks: *Microvoluta dolichura*, n. sp. is rather constant in shell shape, with diameter/height ratio 0.37–0.39 (n = 3), last whorl/shell height ratio 0.60–0.63 (n = 4), aperture height/shell height ratio 0.49–0.54 (n = 4). Number of axial ribs on the first whorl 11–13 (average 12, $\sigma = 1$, n = 5), on second 13–16 (average 14.4, $\sigma = 1.1$, n = 5), on third whorl 15–16 (average 15.6, $\sigma = 0.5$, n = 5). Protoconch diameter (D2) ranges 700–750 μm (average 730, $\sigma = 20$, n = 5), protoconch elevation 670–780 μm (average 720, $\sigma = 50$, n = 5). The number, strength and position of the spiral cords situated below the subsutural sulcus vary from 1 to 3, and these are better developed in the holotype than in other specimens. In the illustrated paratype, there are three, closely spaced, but less developed.

From *Microvoluta cythara*, n. sp., also found in the Coral Sea but allopatric, *M. dolichura*, n. sp. is readily distinguished by its higher spire, by its narrower shell, by the presence of the spiral cords below the subsutural sulcus, and by the smaller but much more elevated protoconch (Fig. 16L, M).

Etymology: From the Greek words *dolichos* (adjective), meaning long, and *uros*, meaning tail, by reference to the attenuated spire and siphon of the shell.

Microvoluta cryptomitra, n. sp. (Figs 15, 19A–E)

Type material: holotype and 3 paratypes in MNHN.

Type locality: Coral Sea, Chesterfield plateau, 21°19′S, 158°00′E, 975 m [MUSORSTOM 5: sta. 322].

Material examined: A total of four lots (nine specimens).

Coral Sea, Chesterfield plateau. MUSORSTOM 5, R/V *Coriolis*: sta. 322, 21°19′S, 158°00′E, 975 m, 4 dd (holo- and paratypes).

South of New Caledonia. BIOCAL, R/V *Jean-Charcot*: sta. CP75, 22°19′S, 167°23′E, 825–860 m, 3 dd [co-occurring with *M. joloensis*].

Loyalty Islands. BIOCAL, R/V *Jean-Charcot*: sta. DW79, 20°40′S, 166°52′E, 1320–1380 m, 1 dd [co-occurring with *M. joloensis*].

MUSORSTOM 6: sta. DW468, 21°06′S, 167°33′E, 600 m, 1 dd [co-occurring with *M. joloensis*].

Distribution: Coral Sea (Chesterfield plateau), south off New Caledonia, and Loyalty Islands, shells only in 600–1320 m.

Description (holotype) (Fig. 19A–B): Shell fragile, glossy, high-fusiform, width 37% of height, consisting of 1.625 protoconch and 5.5 teleoconch whorls. Protoconch not large, diameter (D2) 840 μm, raised, exposed height 750 μm, whorls convex, smooth, protoconch-teleoconch transition marked by orthocline axial rib. Teleoconch whorls slightly convex with adpressed suture, weak subsutural sulcus, whorl profile concave below sulcus and shoulder. Sculpture consisting of strong, widely spaced, nearly orthocline ribs, equally well developed on all teleoconch whorls, and forming pointed knobs at shoulder, crossed by very indistinct low spiral striae; 11 ribs on first whorl, 9 on second, 8 on third, 8 on last. Shell base and canal with 6 low, but distinct, closely spaced spiral cords. Last whorl height 59% of total shell height. Aperture height 48% of shell height, narrowly elongate, outer lip simple. Columella without callus, with 3 widely spaced plaits, abapicalmost smallest. Siphonal canal moderately long, straight. Colour of the shell uniformly white.

Dimensions: Shell height 9.4 mm, diameter 5.5 mm, last whorl height 4.5 mm, aperture height 3.5 mm. The holotype is the largest and best-preserved specimen, although drilled in the penultimate whorl.

Remarks: *Microvoluta cryptomitra*, n. sp. is rather constant in shell shape, protoconch size, dimensions and axial sculpture. The spiral sculpture is slightly more variable, from nearly obsolete in one paratype, to eight, very distinct, and more widely spaced cords in another.

M. cryptomitra, n. sp. is readily distinguished from its congeners by the narrow shell with a tall spire, and by its axial ribs forming knobs at the shoulder. In general outline it strongly resembles some species of *Belomitra* (Buccinidae), but is separable instantly by the much more developed columellar plaits.

Etymology: After the buccinoid genus *Cryptomitra*, one of the synonyms of *Belomitra* (Buccinidae), to which it bears a superficial resemblance; used as a noun in apposition.

Microvoluta sp. (Figs 19F, 21)

Material examined: North of New Caledonia. MUSORSTOM 4, R/V *Vauban*: sta. DW196, 18°55′S, 163°24′E, 450 m, 1 dd.

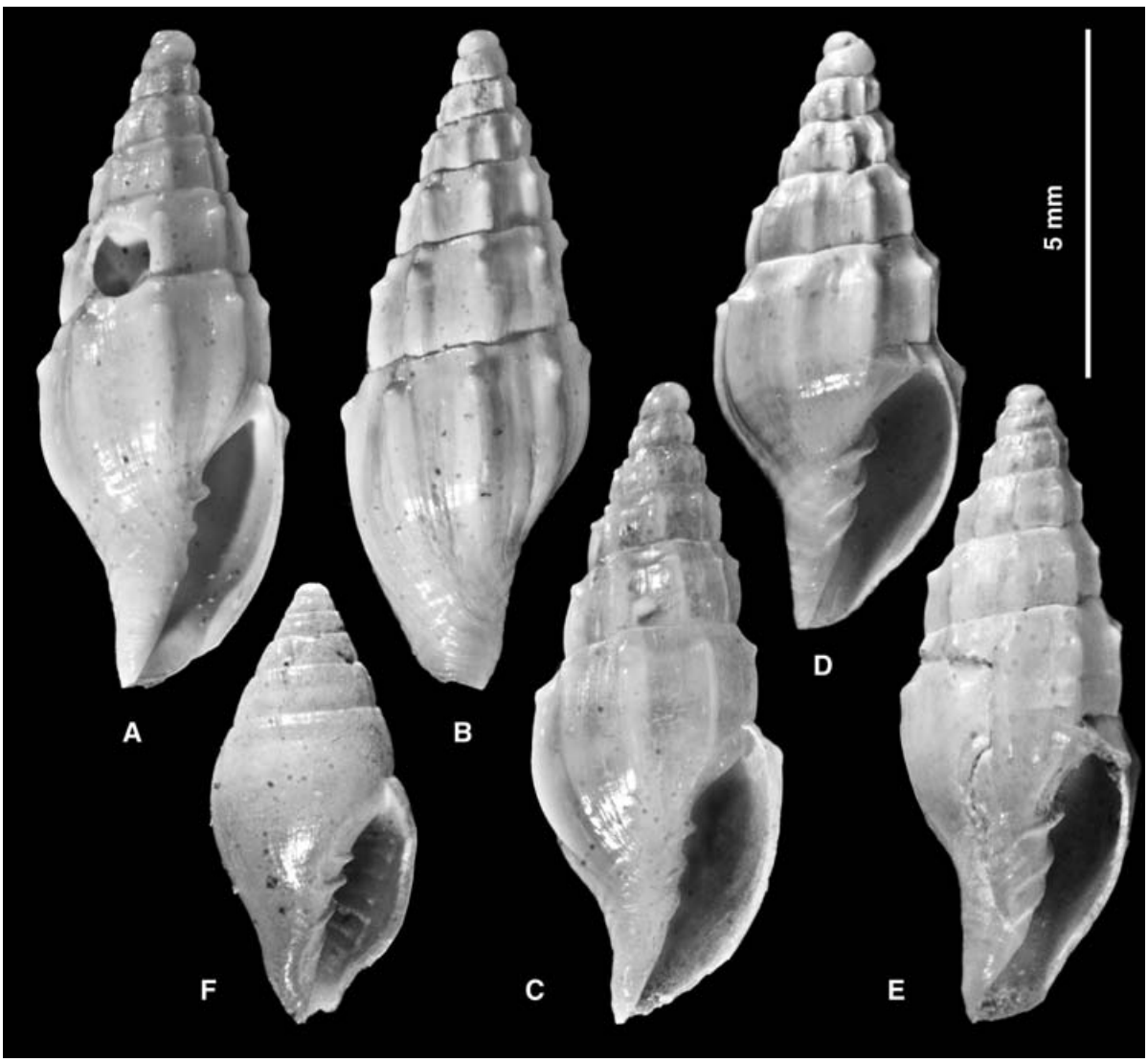

Figure 19 A–E, *Microvoluta cryptomitra*, n. sp. A–C, MUSORSTOM 5, sta. 322. A–B, holotype, SL 9.4 mm; C, paratype, SL 9.2 mm. D, BIOCAL, sta. DW79, SL 8.6 mm. E, BIOCAL, sta. CP75, SL 9.2 mm. F, *Microvoluta* sp., north of New Caledonia, MUSORSTOM 4, sta. DW196, SL 6 mm. Scale bar for Figs A–E, Fig. F not at the same scale.

A single, worn specimen (Fig. 19F) is characterized by a solid, oval shell with a rather high last whorl, nearly flat teleoconch whorls, weak axial ribs, obsolete on the last two whorls, and a very weak subsutural sulcus.

Dimensions: Shell height 6.0 mm, diameter 2.9 mm, last whorl height 4.1 mm, aperture height 3.6 mm.

This specimen represents an unknown species, but the lack of adequate material precludes formal description.

Microvoluta engonia, n. sp. (Figs 20E–G, 21, 22)

Type material: holotype and 2 paratypes in MNHN.

Type locality: West coast of New Caledonia, 21°07′S, 164°28′E, 320–344 m [BATHUS 4, R/V *Alis*: sta. DW887].

Material examined: The type lot (3 specimens) is the only known material.

Description (holotype) (Fig. 20E–F): Shell very small, rather solid, semitransparent, glossy, biconical, width 54% of height, consisting of 1.625 protoconch and 3.75 teleoconch whorls. Protoconch small (although large by comparison with teleoconch), diameter (D2) 620 μm, moderately raised, exposed height 450 μm, whorls convex, smooth, semitransparent. Protoconch-teleoconch transition marked by narrow, weak, orthocline rib. Teleoconch whorls with impressed suture, strongly angulated at periphery, without subsutural sulcus. Whorl profile slightly concave between suture and periphery and slightly convex below periphery. Sculpture consisting of strong, slightly prosocline ribs, producing strong rounded swellings at periphery; 10 ribs on first, 11 on second, 12 on third and last whorl, becoming obsolete on shell base. Last whorl high, height 68% of total shell height. Aperture height 55% of shell height, narrowly elongate, outer lip without internal lirae, simple. Columella without callus, with 4 widely

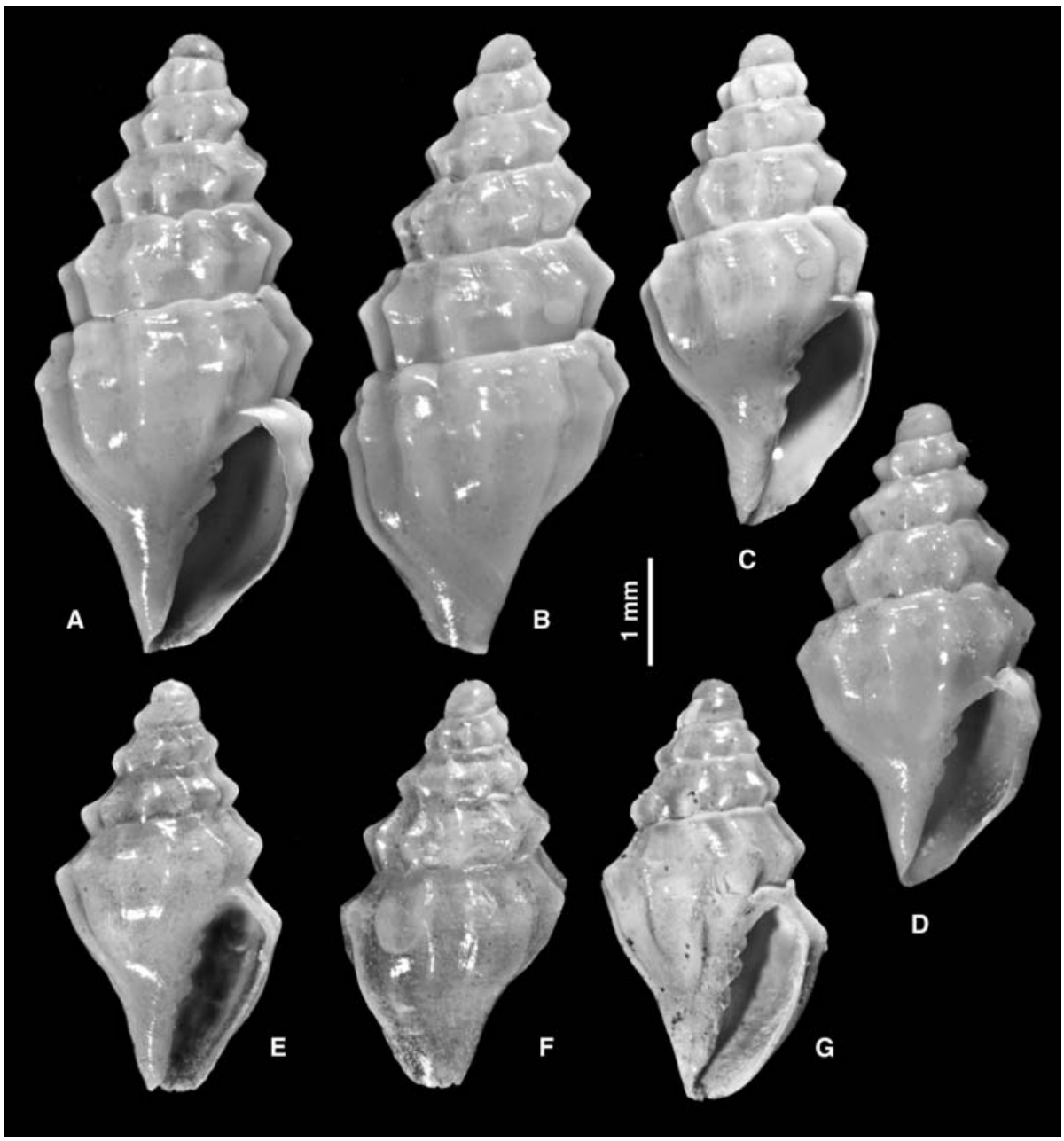

Figure 20 A–D, *Microvoluta echinata*, n. sp., BATHUS 2, sta. DW754. A–B, holotype, SL 5.7 mm; C, paratype, SL 4.5 mm; D, paratype, SL 4.5 mm. E–G, *Microvoluta engonia*, n. sp., BATHUS 4, sta. DW887. E–F, holotype, SL 3.75 mm; G, paratype, SL 3.8 mm. All shells at the same scale.

spaced sharp plaits, abapical one smallest. Siphonal canal moderately long, straight. Colour of the shell uniformly off-white.

Dimensions: shell height 3.75 mm, diameter 2.04 mm, last whorl height 2.54 mm, aperture height 2.06 mm. Largest specimen: shell height 3.80 mm, diameter 2.0 mm, last whorl height 2.62 mm, aperture height 2.12 mm.

Remarks: With only three specimens from a single population at hand, it is difficult to evaluate the variability of *Microvoluta engonia*, n. sp. Diameter/height ratio 0.53–0.54, last whorl/shell height ratio 0.68–0.69, aperture height/shell height ratio 0.55–0.56. Number of axial ribs on the first whorl is constantly 10, on second 10–11, and on third whorl 10–12. Number of protoconch whorls is rather variable from 1.625 to 2.125. Protoconch diameter ranges 610–670 μm, protoconch elevation 440–480 μm.

Microvoluta engonia, n. sp. resembles *M. echinata*, n. sp. in shell outline and sculpture pattern, but differs from it in the absence of a subsutural sulcus, and in having a slightly broader shell (Fig. 22).

Etymology: From the Greek *engonia*, angular, with reference to profile of the whorls; used as a Latin adjective.

Microvoluta echinata, n. sp. (Figs 20A–D, 21, 22)

Type material: holotype (dd) and 5 paratypes (dd) in MNHN.

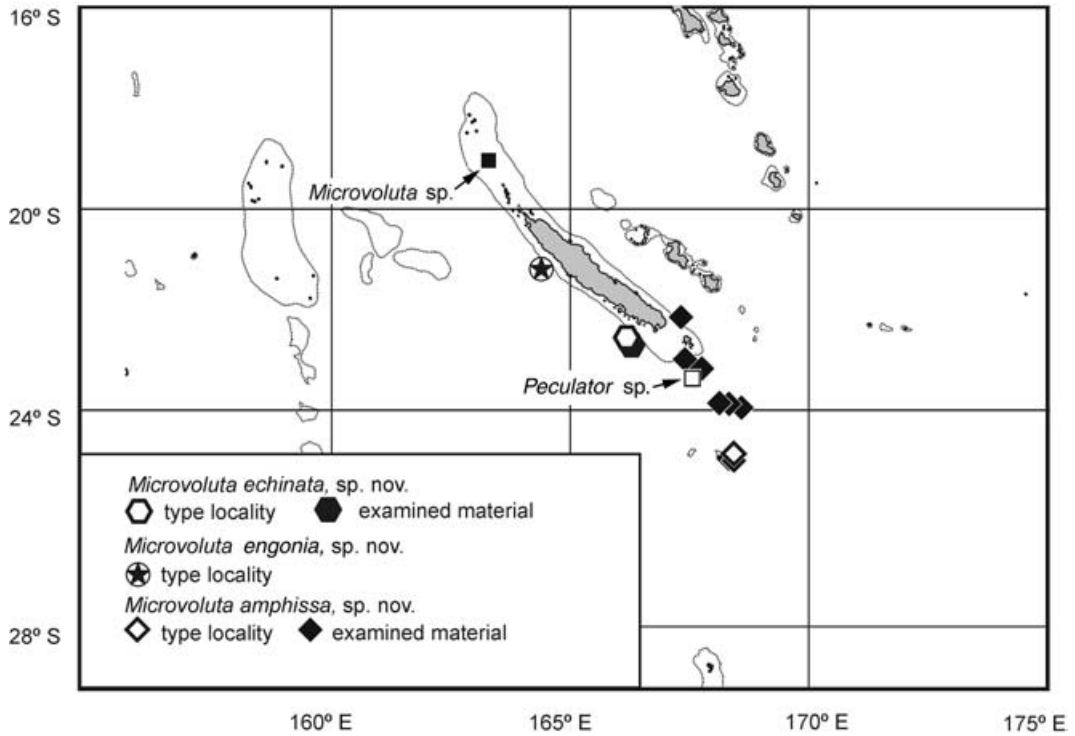

Figure 21 Geographical distributions of *Microvoluta echinata*, n. sp., *M. engonia*, n. sp., *M. amphissa*, n. sp., *Microvoluta* sp., and *Peculator* sp. Isobath 500 m.

Type locality: South of New Caledonia, 22°23′S, 166°13′E, 577–780 m [BATHUS 2: sta. DW754].

Material examined: A total of three lots (24 specimens).

South of New Caledonia. BATHUS 2, R/V *Alis*: sta. DW754, 22°23′S, 166°13′E, 577–780 m, 6 dd (holotype and paratypes). – Sta. DW755, 22°22′S, 166°14′E, 495 m, 2 dd. – Sta. DW761, 22°19′S, 166°11′E, 490–500 m, 15 dd.

Description (holotype): Shell small, fragile, semitransparent, glossy, biconical, width 46% of height, consisting of 1.75 protoconch and 4.8 teleoconch whorls. Protoconch medium-sized, diameter (D2) 680 μm, moderately raised, exposed height 550 μm, whorls semitransparent, convex, smooth. Protoconch-teleoconch transition marked by strong orthocline rib and change in shell transparency. Teleoconch whorls with impressed suture, strongly angulated at periphery, subsutural sulcus better pronounced on last and penultimate whorls. Whorl profile slightly concave above periphery, slightly convex below periphery on adapical teleoconch whorls, and nearly flat between shoulder and periphery on penultimate and last whorls. Sculpture consisting of strong, slightly prosocline ribs, producing strong rounded swellings at periphery and on shoulder of last and penultimate whorls, and extending towards shell base of last whorl; 9 ribs on first whorl, 8 on second, 10 on third. Last whorl height 55% of total shell height. Aperture height 47% of shell height, narrowly elongate, outer lip thin, simple, without internal lirae. Columella without

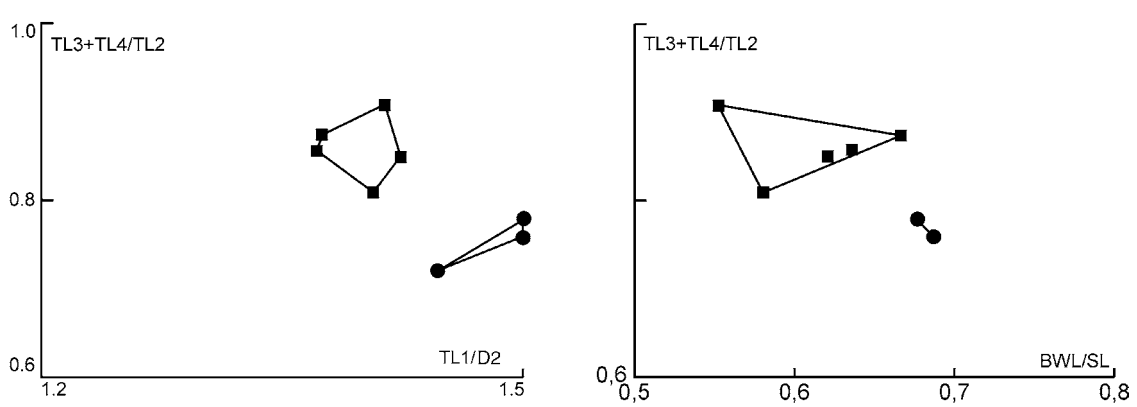

Figure 22 Morphometric comparisons of *Microvoluta echinata*, n. sp. (■) and *Microvoluta engonia*, n. sp. (●). TL1 = diameter of first teleoconch whorl; TL2 = diameter of second teleoconch whorl; TL3 = height of first teleoconch whorl; TL4 = height of second teleoconch whorl (see Fig. 1); BWL = height of last whorl; SL = shell height ratio.

callus, with 3 sharp plaits, central one strongest. Siphonal canal short, straight. Colour of the shell uniformly off-white.

Dimensions: Shell height 5.70 mm, diameter 2.60 mm, last whorl height 3.15 mm, aperture height 2.70 mm. Largest specimen (paratype): shell height 5.90 mm, diameter 2.58 mm, last whorl height 3.42 mm, aperture height 2.76 mm.

Remarks: *Microvoluta echinata*, n. sp. is rather constant in shell shape. Diameter/height ratio 0.46–0.55 (average 0.49, $\sigma = 0.04$, n = 5), last whorl/shell height ratio 0.58–0.67 (average 0.62, $\sigma = 0.04$, n = 5), aperture height/shell height ratio 0.47–0.56 (average 0.50, $\sigma = 0.03$, n = 5). Number of axial ribs on the first whorl 7–10 (average 8.4, $\sigma = 1.0$, n = 5), on second 8–10 (average 9.4, $\sigma = 0.8$, n = 5), and on third whorl constantly 10. Protoconch diameter (D2) 670–730 μm (average 700 μm, $\sigma = 20$, n = 5), protoconch elevation 520–565 μm (average 540 μm, $\sigma = 20$, n = 5). One of the specimens has a lirate aperture.

For a comparison with *M. engonia*, n. sp., see under that species.

Etymology: The Latin adjective *echinatus*, *-a*, *-um*, meaning spiny, with reference to the sculpture.

Microvoluta amphissa, n. sp. (Figs 10C, 11E–G, 21, 23)

Type material: Holotype and 15 paratypes MNHN, 4 paratypes NMNZ, 4 paratypes AMS.

Type locality: Norfolk Ridge, Bank Eponge, 24°55′S, 168°22′E, 508–532 m [SMIB 8: sta. DW146–147].

Material examined: A total of 21 lots (454 specimens).

South of New Caledonia and Norfolk Ridge. SMIB 8, R/V *Alis*: sta. DW146–147, 24°55′S, 168°22′E, 508–532 m, about 170 dd and lv (from which the type material has been selected). – Sta. DW148, 24°56′S, 168°21′E, 510 m, 11 dd. – Sta. DW169, 23°37′S, 167°42′E, 447–450 m, 1 dd.

BIOCAL, R/V *Jean-Charcot*: sta. DW33, 23°10′S, 167°10′E, 675–680 m, 12 dd. – Sta. DW46, 22°53′S, 167°17′E, 570–610 m, about 50 dd, 12 lv. – Sta. DW48, 23°00′S, 167°29′E, 775 m, 2 dd [co-occurring with *M. mitrella*]. – Sta. DW49, 23°03′S, 167°32′E, 825–830 m, 1 dd. – Sta. DW51, 23°05′S, 167°45′E, 680–700 m, 118 dd and lv. – Sta. DW66, 24°55′S, 168°22′E, 505–515 m, about 50 dd, 12 lv. – Sta. DW77, 22°15′S, 167°15′E, 440 m, 1 dd [co-occurring with *M. joloensis*].

BATHUS 2, R/V *Alis*: sta. DW720, 22°52′S, 167°16′E, 530–541 m, 29 dd and lv. – Sta. DW721, 22°54′S, 167°17′E, 525–547 m, 27 dd and lv.

BATHUS 3, R/V *Alis*: sta. DW809, 23°39′S, 167°59′E, 650–730 m, 2 dd and 2 lv. – Sta. DW810, 23°40′S, 167°59′E, 850–900 m, 3 dd.

CHALCAL 2, R/V *Alis*: sta. DW72, 24°55′S, 168°22′E, 527 m, 2 dd. – Sta. DW76, 23°40′S, 167°45′E, 470 m, 7 lv, 3 dd.

BERYX 11, R/V *Alis*: sta. DW09, 24°52′S, 168°22′E, 635–680 m, 4 dd. – Sta. DW10, 24°53′S, 168°21′E, 565–600 m, 5 lv.

NORFOLK 1, R/V *Alis*: sta. DW1692, 24°56′S, 168°21′E, 24°56′S, 168°21′E, 507–967 m, 3 lv, 10 dd. – Sta. DW1697, 24°39′S, 168°38′E, 569–616 m, 2 lv, 14 dd. – Sta. DW1704, 23°45′S, 168°16′E, 400–420 m, 1 lv.

Distribution: South of New Caledonia and Norfolk Ridge, alive in 420–680 m, shells to 850 m.

Description (holotype) (Fig. 23A–C): Shell small, fragile, semitransparent, glossy, fusiform, width 39% of height, consisting of 2.0 protoconch and 4.25 teleoconch whorls. Protoconch medium-sized, diameter (D2) 570 μm, moderately raised, exposed height 530 μm, whorls convex, smooth, semitransparent (Fig. 10C). Protoconch-teleoconch transition marked by strong opisthocline rib. Teleoconch whorls convex, evenly rounded, with impressed suture, and without subsutural sulcus. Sculpture consisting of strong, narrow, widely spaced, arcuate, nearly orthocline ribs, equally well developed on all teleoconch whorls and on last whorl extending nearly to canal; 14 ribs on first whorl, 12 on second, 11 on third and last whorls. Last whorl 62% of total shell height. Aperture height 52% of shell height, narrowly elongate, outer lip thin, simple. Columella without callus, with 4 sharp, closely spaced plaits, middle ones strongest. Siphonal canal short, curved backwards. Colour of the shell uniformly off-white.

Dimensions: Shell height 6.16 mm, diameter 2.37 mm, last whorl height 3.84 mm, aperture height 3.21 mm. Largest specimen (BATHUS 3, sta. 809): shell height 7.47 mm, diameter 3.47 mm, last whorl height 5.20 mm, aperture height 4.47 mm.

Radula and jaw of two specimens were examined. Radula is in all respects similar to that of other *Microvoluta* species, differing from *M. joloensis* in having less developed, shorter lateral teeth. Median cusp /total tooth length 0.57–0.63. Jaw (Fig. 11E–G) chitinous, with porous surface (Fig. 11G) (this may be an artefact of bleaching), rather thin, its ventral edge on transverse sections sharp and acting as a cutting edge.

Remarks: Diameter/height ratio ranges 0.38–0.50 (average 0.46, $\sigma = 0.03$, n = 22), last whorl/shell height ratio 0.57–0.72 (average 0.67, $\sigma = 0.03$, n = 22), aperture height/shell height ratio 0.47–0.66 (average 0.57, $\sigma = 0.04$, n = 22). Number of axial ribs on the first whorl 11–15 (average 12.8, $\sigma = 1.2$, n = 11), on second 10–14 (average 12.0, $\sigma = 1.5$, n = 11), and on third whorl 10–15 (average 12.3, $\sigma = 1.3$, n = 11). Protoconch diameter ranges 710–790 μm (average 770 μm, $\sigma = 20$, n = 11), protoconch elevation 480–580 μm (average 540 μm, $\sigma = 30$, n = 11).

Microvoluta amphissa forms rather distinct morphs, that are never syntopic. One morph (to which the holotype belongs) is characterized by a slightly more slender shell, by its evenly rounded whorls, by its slightly wider and more arcuate axial ribs and by the absence of a shoulder angulation.

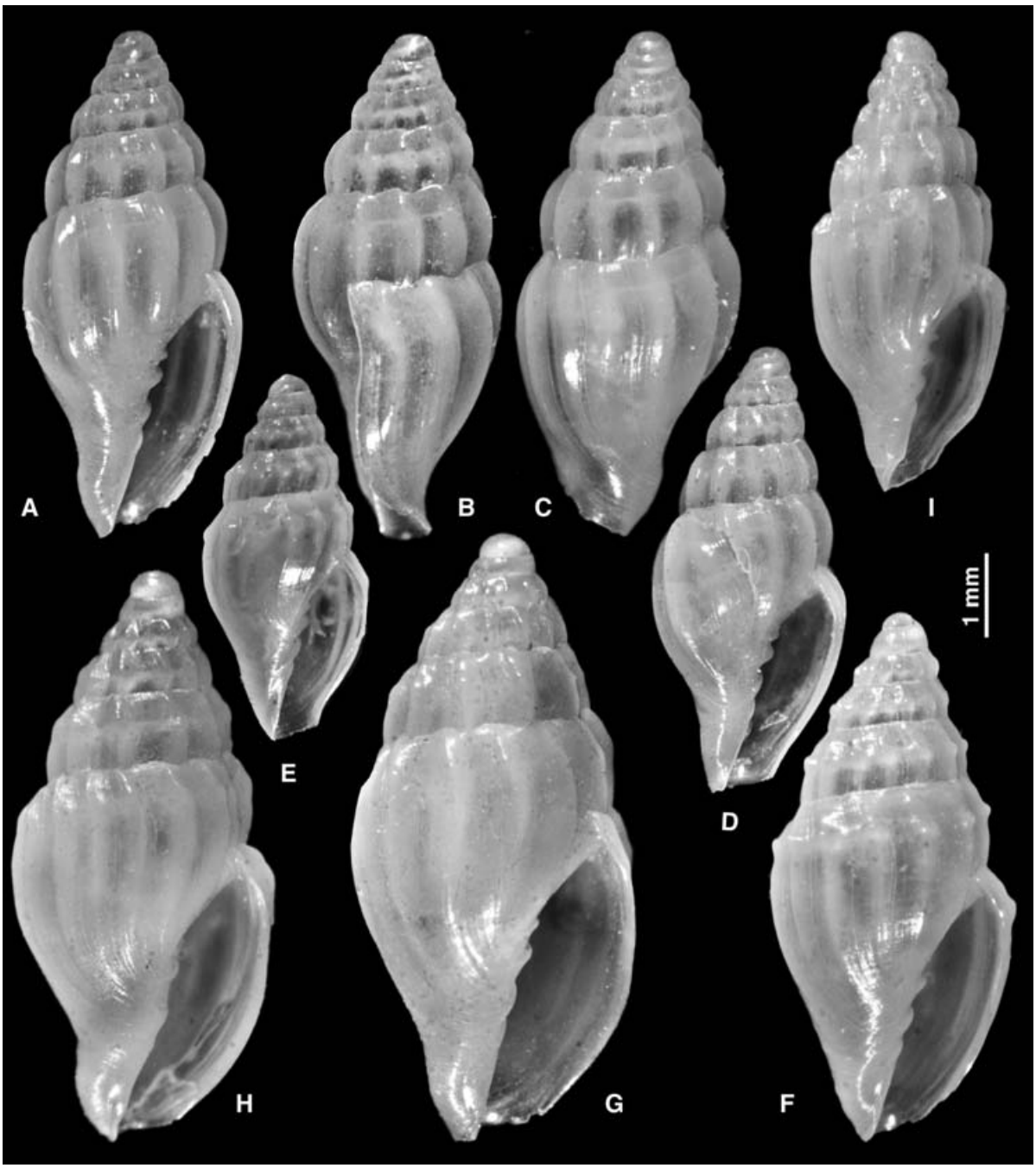

Figure 23 *Microvoluta amphissa*, n. sp. A–D, SMIB 8, sta. DW146–147. A–C, holotype, SL 6.2 mm; D, paratype, SL 5.5 mm. E–F, morphotype with pronounced subsutural sulcus. E, BIOCAL, sta. DW46, SL 4.5 mm; F, BIOCAL, sta. DW51, SL 6.5 mm. G, deep-water morphotype, BATHUS 3, sta. DW809, SL 7.4 mm. H, specimen transitional between deep-water morphotype and morphotype with pronounced sulcus, BATHUS 3, sta. DW809, SL 7.0 mm. I, specimen transitional between morphotype of type locality and morphotype with pronounced sulcus, CHALCAL 2, sta. DW76, SL 5.7 mm. All shells at the same scale.

This morph was found in abundance at depths of 440–532 m. Another morph has a stouter shell with less well developed axial ribs, which form rounded swellings at the shoulder (Fig. 23E–F). These swellings are connected by a single spiral cord, best seen in the rib interspaces. This morph was abundant at stations in slightly deeper water, in 547–680 m. Few intermediate specimens have been found, and then only at stations with a small number of specimens (CHALCAL2, sta. DW76 – Fig. 23I). At even greater depth (730–850 m), the shell may be even stouter and slightly larger (Fig. 23G), with less pronounced, even obsolete, shoulder swellings, but intermediate specimens co-exist in the same station (Fig. 23H). Attempts to distinguish these three morphotypes morphometrically with the use of all shell parameters failed. This, in addition with the occasional occurrence of shells with intermediate characters, leads us to consider them conspecific.

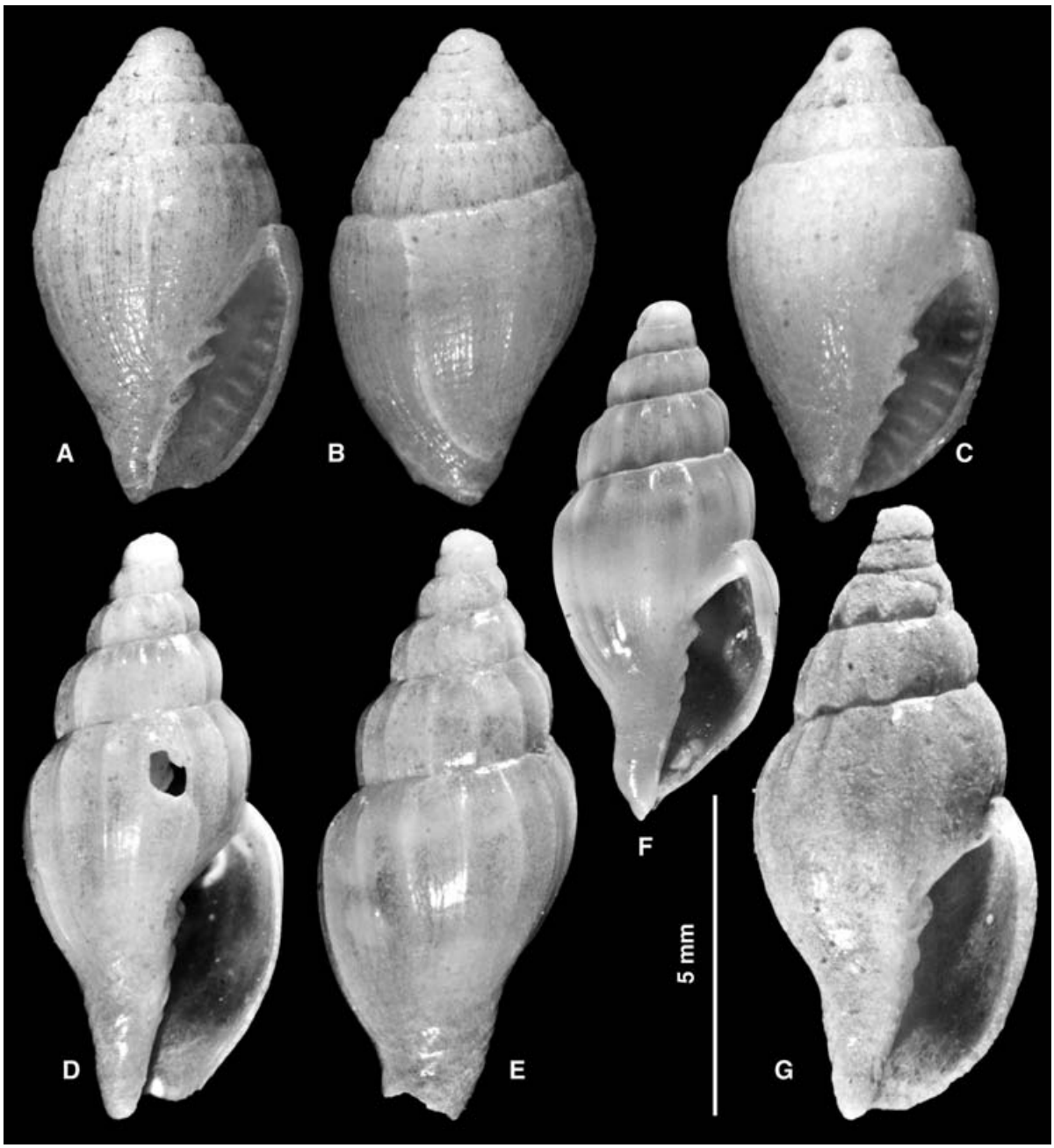

Figure 24 A–C, *Peculator* sp., BIOCAL, sta. DW38. A–B, SL 4.6 mm; C, SL 4.8 mm. D–G, *Microvoluta mitrella*, n. sp., BIOCAL, sta. DW48. D–E, holotype, SL 10.0 mm; F, paratype, SL 8.9 mm; G, paratype, 10.5 mm. Scale bar for *Microvoluta mitrella* only.

Microvoluta amphissa, n. sp. is well distinguished from its congeners by the combination of small adult size, well developed axial ribs, and absence of a pronounced subsutural sulcus.

Etymology: After the columbellid genus *Amphissa*, to which it bears a superficial resemblance; used as a noun in apposition.

Microvoluta mitrella, n. sp. (Fig. 24D–G)

Type material: Holotype and three paratypes in MNHN.

Type locality: South of New Caledonia, 23°00′S, 167°29′E, 775 m [BIOCAL: sta. DW48].

Material examined: Only the type material [co-occurring with *M. amphissa*, n. sp.].

Description (holotype): Shell large, glossy, elongate-oval, width 43% of height, consisting of 1.75 protoconch and 4.125 teleoconch whorls. Protoconch very large, diameter (D2) 1250 μm, raised, exposed height 940 μm, whorls evenly convex, smooth. Protoconch-teleoconch transition indistinct. Teleoconch whorls convex with impressed suture, rounded shoulder and without subsutural sulcus. Sculpture consisting of strong, straight, slightly prosocline ribs, equally developed on all teleoconch whorls, on last whorl extending towards shell base; 12 ribs on first whorl, 11 on second, 13 on third and last

whorls, crossed by spiral cords, 11 low and rounded cords on shell base and canal, 4 abapicalmost strongest. Last whorl high, height 70% of total shell height. Aperture smooth inside, height 60% of shell height, narrowly elongate, outer lip thin, simple. Columella without a callus, with 4 plaits, abapical one indistinct. Siphonal canal moderately long, curved backward. Colour of the shell uniformly off-white.

Dimensions: shell height 10.0 mm, diameter 4.3 mm, last whorl height 7.0 mm, aperture height 5.9 mm. Largest specimen (Fig. 24G): shell height 10.5 mm, diameter 5.0 mm, last whorl height 6.6 mm, aperture height 5.6 mm.

Remarks: The small number of specimens of *Microvoluta mitrella* at hand is rather constant in shell shape and outline. Diameter/height ratio 0.43–0.47, last whorl/shell height ratio 0.63–0.70, aperture height/shell height ratio 0.54–0.59. The number of axial ribs on one paratype (Fig. 24F) 13 on first whorl, 14 on second and third whorls. The protoconch is intact in only one of the three paratypes and its size, diameter 1280 μm, elevation 880 μm, is very similar to that of the holotype.

Microvoluta mitrella is readily distinguished from its congeners by its very large protoconch.

Etymology: After the columbellid genus *Mitrella*, to which it bears a superficial resemblance; used as a noun in apposition.

Genus *Peculator* Iredale, 1924

Peculator sp. (Figs 21, 24A–C)

Material examined: South of New Caledonia. BIOCAL, R/V *Jean-Charcot*: sta. DW38, 23°00′S, 167°29′E, 360 m, 3 dd.

Three worn, but very distinctive, shells strongly resemble in general shell shape and sculpture pattern the Recent species of *Peculator*. Shell height up to 4.8 mm, rounded with very low spire, indistinct subsutural sulcus, closely set axial ribs and rather distinct spiral striation. Diameter/height ratio 0.55–0.57, last whorl/shell height ratio 0.72–0.74 shell height, aperture height/shell height ratio 0.63–0.65.

This finding represents the first occurrence of the genus outside Australia and New Zealand, but we prefer to leave the species unnamed in view of the rather poor state of the specimens.

Discussion

An overview of the volutomitrid fauna of the world known before the present paper, totaling 41 species (Appendix), reveals two major, and two minor, centres of species richness. One major centre is the Australia–New Zealand region, with a total of 13 species (belonging to *Volutomitra*, *Peculator* and *Microvoluta*) and maximum diversity off the southern and eastern coasts of Australia (nine species) and off the North Island of New Zealand (seven species). Another major centre is central eastern America, in fact essentially the Caribbean, where nine species (belonging to *Volutomitra, Conomitra* and *Microvoluta*) have been recorded so far. The Antarctic is characterized by its own radiation in the genus *Paradmete* (five species), with two species penetrating the Magellanic province (Fig. 25). Four species are known from South Africa (assuming that *Magdalemitra* does belong to Volutomitridae), but several species remain to be described (Kilburn, pers. comm.). The fauna of middle and high latitudes in the northern hemisphere is poor, with no more than two species sympatric at a global scale. The scarcity, or even complete absence, of volutomitrids in most parts of the Indo-Pacific is remarkable: a single species is known from the Philippines and Hawaii, two in Japan, and none at all from e.g. Indonesia. The fauna of Japan is well inventoried and the paucity of volutomitrids there cannot be explained by undercollecting. Thus placed in perspective, the discovery of 14 species of Volutomitridae in the New Caledonia region places this part of the world as a major centre of diversity for the family. It brings the total number of Recent Volutomitridae known worldwide to 50 named (and two still unnamed) species or, in other words, the New Caledonia region is home to 25% of the world volutomitrid fauna.

The New Caledonia region as a centre of volutomitrid diversity

The material studied in the present paper totals 178 lots and 1472 specimens, of which 149 lots and 1268 specimens are from the New Caledonia region alone. Admittedly, this reflects in part the intensity of the collecting effort there, compared with other parts of the Indo-Pacific, but we believe that it does reflect also the reality of a centre of volutomitrid diversity in that part of the South-West Pacific. The 29 samples and 204 specimens collected outside the New Caledonia region (SW Indian Ocean, Fiji, Wallis and Futuna, Tonga) amount to respectively 16% and 14% of the total, but these represent a single species, *Microvoluta joloensis*, or 7.1% of the total number of species. Furthermore, the fact that four species (*Microvoluta engonia*, *M. mitrella*, *M.* sp., and *Peculator* sp.) are all still known from single lots suggests that more species may be awaiting to be discovered in the New Caledonia region.

Bathymetrically, the highest species diversity in New Caledonia is essentially confined to the 250–750 m depth range and, in that respect, differs from the Caribbean and Australia–New Zealand regions, in which the highest richness starts in the shallow offshore. Three of the New Caledonia species have records deeper than 750 m (at 1980 m, a record of *M. joloensis* which could be the deepest record for the family), but these refer to empty shells and may have little or no biological significance.

The high number of species in the New Caledonia region appears to result from four factors: regional spatial heterogeneity; frequency of hard substrates; syntopy; and a historical heritage shared with Australia and New Zealand.

(a) Regional spatial heterogeneity. Not only are all but one (*Microvoluta joloensis*) of the species of Volutomitridae present in the New Caledonia region endemic to that region, but also species are often restricted to one area within the region (Table 2): the distribution of as many as 10 out of 14 species is restricted in this way; the Coral Sea plateaus and the Loyalty Ridge (same latitude, but 900 km longitude apart)

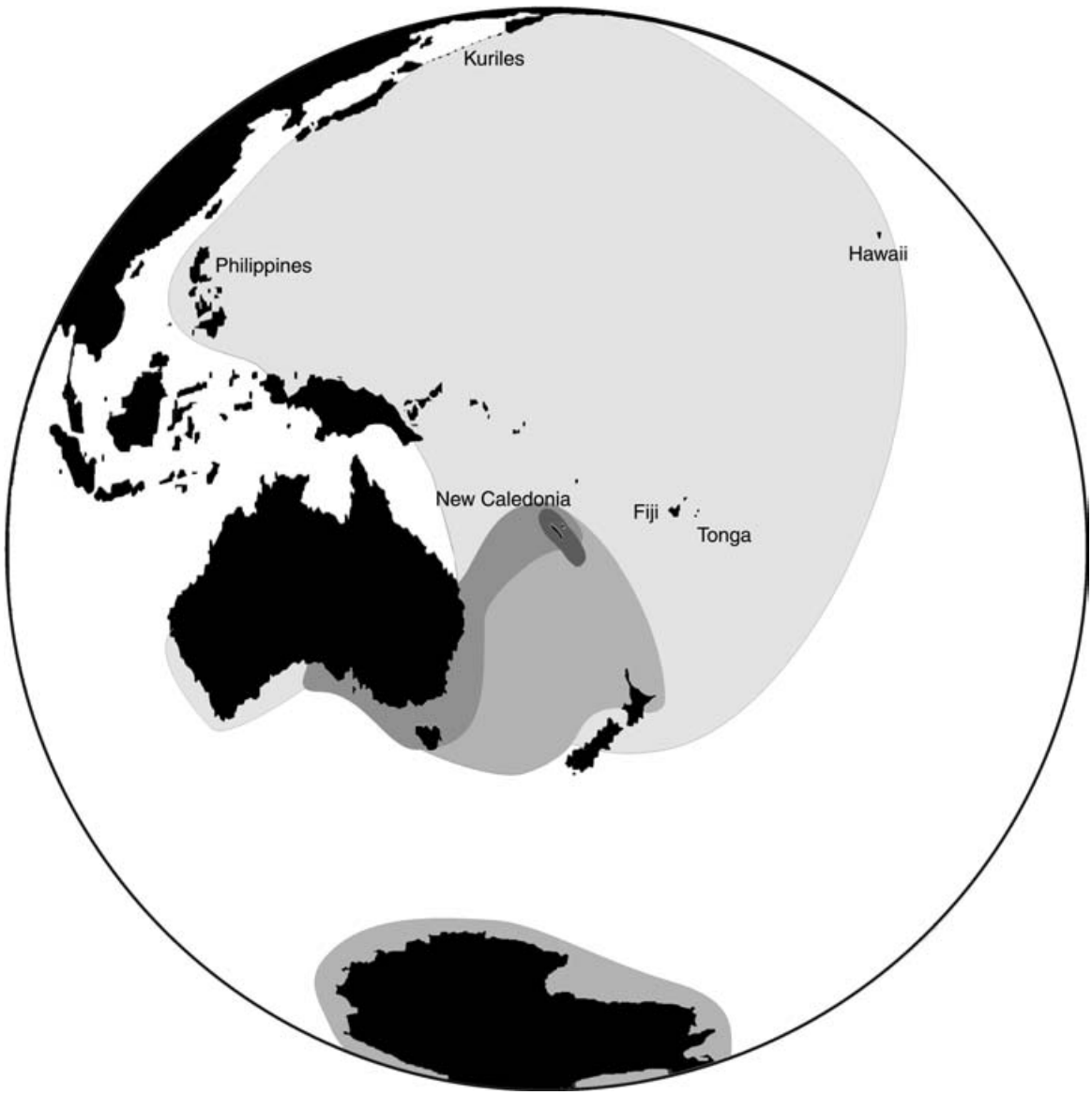

Figure 25 Geographic representation of the diversity of Volutomitridae in Pacific and Antarctic regions. The intensity of the tones of grey is proportional to the number of species: respectively 1–2, 4–5, 6–7 and 14 species.

share only one of their cumulated six species; the areas just north and south of New Caledonia (750 km apart) have together 10 species, but only three species are shared. Such restricted distributions do not appear to be the result of sampling artefact, and even species represented by many lots may have surprisingly narrow ranges. Thus *Volutomitra ziczac* is found in an area of 35 km of maximal extension north of New Caledonia, and this restricted distribution is confirmed by dredgings on the boat *Tui II* operated by M. Creyssac. North of New Caledonia, *V. glabella* was recorded in 30 stations, clustering in an area of 80 km of maximal extension, while in the south of New Caledonia it is confined to an area less than 15 km in maximal extension (Bouchet & Kantor, 2000b).

(b) One environmental parameter that segregates the deep-sea substrates of the New Caledonia area apart from those of many western Pacific archipelagoes and continental areas is the frequency of hard substrates. In fact, most substrates of the Coral Sea plateaus, of the slopes north (Grand Passage) and south (Norfolk Ridge) of New Caledonia, and of the Loyalty Ridge are hard substrates. The only exceptions are off the coasts of New Caledonia itself, where there is a succession of soft substrates on the sediment cone at the outlet of the barrier reef passes. A single sample of *Microvoluta joloensis* (BATHUS 1, sta. CP651) and the type lot of *M. engonia*, n. sp. appear to originate from such soft substrates. This suggests that, at least in that part of the tropical Indo-Pacific, volutomitrids prefer hard substrates, which in turn explains their local relative abundance.

(c) Syntopy. Contrasting with the regional spatial heterogeneity discussed above, the present material also documents several instances of co-occurrence in the same station (= syntopy; as opposed to sympatry = co-occurrence of species in the same geographical area, but not necessarily with the same ecological/bathymetric co-occurrence) of two or more species of Volutomitridae. The three species of

Species	Coral Sea	North of New Caledonia	New Caledonia proper	South of New Caledonia/Norfolk Ridge	Loyalty Ridge
Volutomitra glabella		+		+	
V. vaubani		+		+	
V. ziczac, n. sp.		+			
Microvoluta amphissa, n. sp.				+	
M. cryptomitra, n. sp.	+			+	+
M. cythara, n. sp.	+				
M. dolichura, n. sp.	+				
M. echinata, n. sp.				+	
M. engonia, n. sp.			+		
M. joloensis		+		+	+
M. mitrella, n. sp.				+	
M. respergens, n. sp.					+
M .sp.		+			
Peculator sp.				+	
Total number of species	3	5	1	8	3

Table 2 Regional distribution of the species of Volutomitridae in the New Caledonia area.

Volutomitra (*V. glabella, V. ziczac* and *V. vaubani*) may, although exceptionally, co-occur in the north of New Caledonia, and instances of co-occurrence of two of them are not rare. There are also instances of co-occurrence of *Microvoluta joloensis* with *M. cryptomitra* (three cases), *M. amphissa*, *M. respergens* and *M. mitrella*, and of *M. amphissa* with *M. mitrella* (one case each) on the Norfolk and Loyalty Ridges, but we have no evidence of more than two species of *Microvoluta* co-occurring.

(d) Historical heritage. Although now situated in tropical latitudes, New Caledonia has shared a long tectonic history with New Zealand, stretching back to the Mesozoic, and this is reflected in numerous, well documented, cases of vicariance in the terrestrial biota of the two land masses. The geologically instant dispersal of invertebrate larvae over large distances tends to obscure this historical heritage when shallow water biotas are compared, but this heritage remains apparent when cold, deep-water taxa are considered. For instance, the occurrence in New Caledonia of bathyal species of, e.g. *Alcithoe* (Gastropoda Volutidae; Bouchet & Poppe, 1988) or *Ataxocerithium* (Gastropoda Cerithiopsidae; unpublished observations), is best explained by the historically continuous distribution of these taxa on Norfolk Ridge connecting the North Island of New Zealand and New Caledonia. In other words, the New Caledonia volutomitrid richness deserves separate recognition because it is situated at tropical latitudes, but is otherwise essentially part of the Australia–New Zealand radiation, with which it shares the same genera but not the same species.

Applicability of paucispiral protoconch morphometry to volutomitrid taxonomy

All known Recent species of Volutomitridae have paucispiral protoconchs indicating non-planktotrophic larval development, and all are smooth, without any sculpture. However, it would be erroneous to conclude that the protoconch is useless in volutomitrid taxonomy. In fact, even rather similar paucispiral protoconchs of closely allied species, when accurately measured, provide important information, allowing species discrimination.

The number of protoconch whorls depends greatly on the method of counting; in the present study, we have applied the method described under "Material and Methods" and illustrated in Fig. 1. Cernohorsky (1970b, p. 93, figs. 190–212) illustrated rather variable protoconch morphologies for a number of Recent and fossil species of Volutomitridae. Unfortunately, the protoconchs were not drawn in standard positions and therefore their comparison is hardly possible, and the same is true for several SEM photographs of protoconchs of *Paradmete* illustrated by Numanami (1996).

When placed in a similar, standard position, the protoconchs of all species of *Volutomitra* and *Microvoluta* studied by us seem to be very similar to each other in shape, and differ essentially in size (Fig. 10 – all protoconchs at the same scale). Thus, the average protoconch diameter (D2) ranges 1100–1440 μm in species of *Volutomitra*, and 630–820 μm in most species of *Microvoluta* (Table 3). However, the protoconch of *Microvoluta mitrella*, n. sp. is exceptionally large for the genus, and is comparable in size with those of species of *Volutomitra*. (Nevertheless, the general shell shape suggest a placement in *Microvoluta* rather than *Volutomitra*, though this remains to be confirmed anatomically.) Number of protoconch whorls ranges 1.75–2.5 in *Volutomitra* and 1.5–2.1 in *Microvoluta*. At a finer resolution, when protoconch dimensions are plotted against each other, or against other shell parameters, on a scatter plot, the different forms of *Microvoluta joloensis* are not separable, while *M. cythara*, n. sp. stands clearly apart from *M. joloensis* (Fig. 18).

Species	D2, range (μm)	D2, average (μm)	σ	PRE, range (μm)	PRE, average (μm)	σ	Number of specimens
Volutomitra glabella	1350–1650	1440	10	na	1240	80	8
V. vaubani	1030–1210	1100	40	630–1030	820	90	37
V. ziczac, n. sp.	1010–1300	1210	70	720–900	820	70	15
Microvoluta amphissa, n. sp.	710–790	770	20	480–580	540	20	12
M. cryptomitra, n. sp.	800–840			750–780			2
M. cythara, n. sp.	800–840	820	20	520–640	580	50	7
M. dolichura, n. sp.	700–750	730	20	670–780	720	50	5
M. echinata, n. sp.	670–730	700	20	520–570	540	20	5
M. engonia, n. sp.	610–670	630	30	440–480	460	20	3
M. mitrella, n. sp.	1246–1277			880–940			2
M. respergens, n. sp.	770–900	820	50	620–720	670	40	7

Table 3 Some standard protoconch measurements for studied species of Volutomitridae. D2 = diameter of protoconch and first 1/4 teleoconch whorl; PRE = exposed height of protoconch (see Fig. 1).

Anatomy

The anatomy of *Peculator hedleyi* and *Microvoluta marginata* has been examined by Ponder (1972); of *Paradmete fragillima* and *P. curta* by Arnaud & van Mol (1979); of *Volutomitra groenlandica alaskana* by Kantor & Harasewych (1992); and of *V. glabella* by Bouchet & Kantor (2000b). The present paper describes the gross anatomy of *Volutomitra ziczac*, n. sp., and *Microvoluta cythara*, n. sp., and provides more superficial information on *M. amphissa*, n. sp. and *M. joloensis*.

The morphology of the digestive system of the species studied herein is rather uniform, and minor differences concern the relative length of different parts of the oesophagus, as well as the degree of fusion of the salivary glands. Conversely, we found significant differences in the morphology of the jaw. The volutomitrid jaw was first isolated and illustrated by Kantor & Harasewych (1992) in *Volutomitra groenlandica alaskana*, although Ponder (1972) and Arnaud & van Mol (1979) had already reported a strong cuticular lining of the buccal cavity. The jaw of species of *Volutomitra* forms a thin cuticular shield, folded lengthwise to form an enclosed (*V. groenlandica alaskana*) or semi-enclosed funnel (*V. glabella*, *V. ziczac*, n. sp.), the narrow end of which protrudes through the mouth opening. The jaw of the three species of *Microvoluta* forms a thin horse-shoe-shaped plate, with long and narrow lateral flaps; the ventral edge of its anterior part is sharp and probably acts as a cutting edge. Kantor & Harasewych (1992) speculated on the possible use of the jaw and radula in *Volutomitra*, and hypothesized that *Volutomitra* feeds on fluids, the jaw being used to 'seal' minor incisions made by the radula in the prey's integuments. If correct, this hypothesis cannot be extended to *Microvoluta*, since the jaw is not closed ventrally and cannot be operating in the same way. The diet of *Microvoluta* is not known; Ponder (1972) had recorded fine mineral particles, diatom cases and spicule-like fragments in the faecal material of *M. marginata*.

Radular morphology is basically similar in all taxa examined, and generic and specific differences are small. In *Volutomitra*, the lateral teeth are very small and thin, while in *Microvoluta* they are relatively much larger and more stout

Taxon	Median cusp/total tooth length	Reference
Volutomitra erebus	0.50	Bayer, 1971
V. glabella	0.37	Bouchet and Kantor, 2002b
V. groenlandica groenlandica	0.52	Sars, 1878
V. groenlandica alaskana	0.32	Kantor and Harasewych, 1992
V. persephone	0.43	Bayer, 1971
V. ziczac, n. sp.	0.42	this study
Microvoluta amphissa, n. sp.	0.57–0.63	this paper
M. cythara, n. sp.	0.47	this paper
M. joloensis	0.56–0.62	this paper
Paradmete arnaudi	0.72	Numanami, 1996
P. brevidensis	0.67	Numanami, 1996
P. curta	0.49	Numanami, 1996
P. fragillima	0.72	Numanami, 1996
Peculator hedleyi	0.70	Ponder, 1972

Table 4 Comparison of the shape of central radular tooth in different species of Volutomitridae.

(Fig. 11 – lt); they are also strongly developed in three of four species of *Paradmete* (Numanami, 1996). The central tooth generally has a long median cusp with a transversely concave anterior surface, and the base of the tooth has a pair of anteriorly bent, long, plates, the lower portion of which are curved laterally. Further details of its morphology depend significantly on the angle of observation, but strictly dorsal views allow comparison of the relative length of the median cusp; the ratio between cusp length and total tooth length differs significantly between species (Table 4). Although there is overlap between genera, species of *Volutomitra* tend to have the shortest cusp, those of *Paradmete* and *Peculator* the longest one, with *Microvoluta* having a cusp of intermediate relative length.

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Appendix

Taxa	Maximum size	Depth range	Distribution	Reference
Volutomitra				
V. groenlandica alaskana Dall, 1902	47 mm	73–1504 m	N Pacific north of 32°N	Cernohorsky, 1970b
V. banksi (Dall, 1951)	43 mm	146–586 m	New Zealand from Banks Peninsula to Chatham Islands	Cernohorsky, 1970b
V. erebus Bayer, 1971	36 mm	567–597 m	Colombia	Bayer, 1971
V. bayeri Okutani, 1982[1]	26 mm	334–379 m	Surinam	Okutani, 1982
V. glabella Bouchet & Kantor, 2000	25 mm	(190) 258–525 (613) m	New Caledonia	Bouchet & Kantor, 2000b
V. groenlandica (Beck *in* Möller, 1842)	30 mm	7–770 m	N Atlantic north of 40°N	Cernohorsky, 1970b Bouchet & Warén, 1985
V. hottentotta (Thiele, 1925)	8 mm	155 m	S Africa	Cernohorsky, 1970b; 1983
V. obscura (Hutton, 1873)	22 mm	9–64 m	Southern Australia, Tasmania, North Island of New Zealand	Cernohorsky, 1970b
V. pailoloana (J. Cate, 1963)	30 mm	468–518 m	Hawaiian Islands	Cernohorsky, 1970b
V. persephone Bayer, 1971	41 mm	664–1574 m	Panama [Atlantic]	Bayer, 1971
?V. tenella Golikov & Sirenko, 1998	6.6 mm	1320 m	Central Kurile Islands	Golikov & Sirenko, 1998
V. vaubani Cernohorsky, 1982	18 mm	(255) 310–570 (600) m	New Caledonia	this paper
V. ziczac, n. sp.	16 mm	(190) 300–450 (550) m	New Caledonia	this paper

Appendix Checklist of the Recent species of Volutomitridae, with their geographical and bathymetrical distribution. Depth ranges in New Caledonia refer to live-taken samples or, in parentheses, to empty shells. The status of depth records elsewhere in the world is generally not known and may refer to empty shells.

Taxa	Maximum size	Depth range	Distribution	Reference
Paradmete Strebel, 1908				
P. arnaudi Numanami, 1996	10.5 mm	300 m	Antarctic	Numanami, 1996
P. breidensis Numanami, 1996	7 mm	337–441 m	Antarctic	Numanami, 1996
P. cryptomara (Rochebrune & Mabille, 1885)	22 mm	55–220 m	Magellanic	Cernohorsky, 1970b
P. curta Strebel, 1908	25 mm	95–650 m	Kerguelen Is, Antarctic shelf	Cernohorsky, 1970b; Numanami, 1996
P. fragillima (Watson, 1882)	24 mm	30–603 m	Falkland Islands to Antarctic continental shelf	Cernohorsky, 1970b; Numanami, 1996
P. percarinata Powell, 1951	17 mm	300–810 m	Antarctic	Cernohorsky, 1970b
Peculator Iredale, 1924				
P. baccatus Cernohorsky, 1980	6.5 mm	75–158 m	Southern Australia	Cernohorsky, 1980
P. hedleyi (Murdoch, 1905)	9.5 mm	5–64 m	North Island of New Zealand	Cernohorsky, 1970b
P. obconicus (Powell, 1952)	7 mm	55–260 m	North Island of New Zealand	Cernohorsky, 1970b
P. verconis Iredale, 1924	12 mm	18–46 m	New South Wales, Australia	Wilson, 1994
P. porphyria (Verco, 1896)	11 mm	27–95 m	Southern Australia, North Island of New Zealand	Cernohorsky, 1970b
Microvoluta Angas, 1877				
M. amphissa, n. sp.	7.5 mm	470–680 (850) m	New Caledonia	the present paper
M. australis Angas, 1877	11 mm	9–183 m	Australia, New South Wales	Cernohorsky, 1970b
M. blakeana (Dall, 1889)	10 mm	146–1171 m	Caribbean	Cernohorsky, 1970b
M. cryptomitra, n. sp.	9.5 mm	(600–1320) m	New Caledonia	this paper
M. cythara, n. sp.	10.5 mm	(355) 400–410 m	New Caledonia	this paper
M. dolichura, n. sp.	10 mm	(500) m	New Caledonia	this paper
M. echinata, n. sp.	5.9 mm	(500–577) m	New Caledonia	this paper
M. engonia, n. sp.	3.8 mm	(320–344) m	New Caledonia	this paper
M. euzonata (Sowerby, 1900)[2]	9 mm	sublittoral	S. Africa	Kaicher, 1976, Turner, 2001; Kilburn, pers. comm.
M. garrardi Cernohorsky, 1975	7 mm	100–120 m	Australia, south Queensland	Cernohorsky, 1975; Wilson, 1994
M. hondoana (Yokoyama, 1922)	10.5 mm	50–200 m	Central Honshu, Japan	Kuroda *et al.* 1971; Higo *et al.*, 1999
M. intermedia Dall, 1890	15 mm	750–908 m	Caribbean	Cernohorsky, 1970b
M. joloensis Cernohorsky, 1970	14.5 mm	250–578 (1980) m	SW Indian Ocean, Philippines, New Caledonia, Fiji, Tonga, Wallis and Futuna	the present paper
M. marginata (Hutton, 1885)	8 mm	20–260 m	North Island of New Zealand	Cernohorsky, 1970b
M. miranda (E.A. Smith, 1891) [= *Microvoluta ponderi* Cernohorsky, 1975]	11 mm	120–750 m	Australia, New South Wales	Cernohorsky, 1983
M. mitrella, n. sp.	10.5 mm	(775) m	New Caledonia	this paper
M. respergens, n. sp.	9.5 mm	(715) 751 m	New Caledonia	this paper
M. royana Iredale, 1924	11 mm	27–402 m	Eastern Australia, Kermadec Is.	Cernohorsky, 1970b; 1978

Appendix *continued.*

Taxa	Maximum size	Depth range	Distribution	Reference
M. stadialis (Hedley, 1911)	6 mm	90 m	Southern Australia	Cernohorsky, 1975; Wilson, 1994
M. superstes Bouchet & Warén, 1985	5.6 mm	208–330 m	NE Atlantic	Bouchet & Warén, 1985
M. teretiuscula (Thiele, 1925)	8 mm	155 m	S. Africa	Cernohorsky, 1970b
?M. veldhoveni de Jong & Coomans, 1988	9 mm	?	Curacao, Aruba	de Jong & Coomans, 1988
Conomitra Conrad, 1865				
C. carribeana Weisbord, 1929	14 mm	91 m	Colombia	Petuch, 1987; MALACOLOG
C. leonardhilli Petuch, 1987	18 mm	35 m	Venezuela	Petuch, 1987
C. lindae Petuch, 1987	10 mm	35 m	Colombia	Petuch, 1987
Magdalemitra Kilburn, 1974				
M. gilesorum Kilburn, 1974	20 mm	sublittoral	South Africa	Kilburn, 1974

[1] *Volutomitra bayeri* Okutani, 1982 is hardly distinguishable from *V. erebus* Bayer, 1971, but a revision of the Atlantic species is beyond the scope of this paper, and we treat these two nominal species as valid.

[2] *Microvoluta euzonata* is attributed to Volutomitridae with doubts, as it shares conchological characters of both Costellariidae and Volutomitridae; the radula has never been examined. The only adequate illustration is provided by Kaicher (1976).

Appendix *continued.*