



Deep-water Rissoidae of the genera
Benthonella Dall, 1889 and *Benthonellania* Lozouet, 1990
(Gastropoda, Caenogastropoda, Rissooidea)
from French Polynesia

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Deep-water Rissoidae of the genera *Benthonella* Dall, 1889 and *Benthonellania* Lozouet, 1990 (Gastropoda, Caenogastropoda, Rissooidea) from French Polynesia

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ABSTRACT

The deep-water extant Rissoidae Gray, 1847 of the genera *Benthonella* Dall, 1889 and *Benthonellania* Lozouet, 1990 collected in French Polynesia are herein revised. Three species of *Benthonella* and eight of *Benthonellania* are described as new (all but one from French Polynesia): *Benthonella boucheti* n. sp., *Benthonella basistriata* n. sp., *Benthonella communis* n. sp., *Benthonellania thielei* n. sp. (from East Africa), *Benthonellania bouteti* n. sp., *Benthonellania alis* n. sp., *Benthonellania tarava* n. sp., *Benthonellania megan* n. sp., *Benthonellania tuamotu* n. sp., *Benthonellania lozoueti* n. sp. and *Benthonellania maestratii* n. sp. Two taxa are transferred to *Benthonella*: *Rissoa olangoensis* Poppe, Tagaro & Stahlschmidt, 2015 and the fossil *Pusillina kazakhstanica* Amitrov, 2010. Seven taxa are transferred to *Benthonellania*: *Rissoa precipitata* Dall, 1889, *Rissoa hertzogi* Thiele, 1925, *Rissoa africana* Thiele, 1925, *Rissoa aequatorialis* Thiele, 1925, *Rissoa profundior* Hedley, 1907, *Rissoa sumatrana* Thiele, 1925 and *Alvania colombiana* Romer & Moore, 1988. A lectotype for *Rissoa africana* Thiele, 1925 is designated, to stabilize the use of the name.

KEY WORDS

Gastropoda,
Rissoidae,
French Polynesia,
Benthonella,
Benthonellania,
lectotypification,
new combinations,
new species.

RÉSUMÉ

Rissoïdæ des genres *Benthonella* Dall, 1889 et *Benthonellania* Lozouet, 1990 (*Gastropoda*, *Caenogastropoda*, *Rissooïdeæ*) des eaux profondes de Polynésie française.

Les Rissoïdæ Gray, 1847 récents d'eaux profondes des genres *Benthonella* Dall, 1889 et *Benthonellania* Lozouet, 1990 collectés en Polynésie française sont ici révisés. Trois espèces de *Benthonella* et huit de *Benthonellania* sont décrites comme nouvelles (toutes sauf une de Polynésie française) : *Benthonella boucheti* n. sp., *Benthonella basistriata* n. sp., *Benthonella communis* n. sp., *Benthonellania thielei* n. sp. (d'Afrique orientale), *Benthonellania bouteti* n. sp., *Benthonellania alis* n. sp., *Benthonellania tarava* n. sp., *Benthonellania megan* n. sp., *Benthonellania tuamotu* n. sp., *Benthonellania lozoueti* n. sp. et *Benthonellania maestratii* n. sp. Deux taxons sont transférés dans *Benthonella*: *Rissoa olangoensis* Poppe, Tagaro & Stahlschmidt, 2015 et le fossile *Pusillina kazakhstanica* Amitrov, 2010. Sept taxons sont transférés dans le genre *Benthonellania*: *Rissoa precipitata* Dall, 1889, *Rissoa hertzogi* Thiele, 1925, *Rissoa africana* Thiele, 1925, *Rissoa aequatorialis* Thiele, 1925, *Rissoa profundior* Hedley, 1907, *Rissoa sumatrana* Thiele, 1925 et *Alvania colombiana* Romer & Moore, 1988. Un lectotype pour *Rissoa africana* Thiele, 1925 est désigné, afin de stabiliser l'utilisation du nom.

MOTS CLÉS

Gastropoda,
Rissoïdæ,
Polynésie française,
Benthonella,
Benthonellania,
lectotypification,
combinaisons nouvelles,
espèces nouvelles.

INTRODUCTION

The Rissoïdæ are a family of caenogastropods classified into 36 Recent and 13 fossil genera (MolluscaBase 2021a), having diversified mostly in shallow waters throughout the world, from tropical to polar waters. However, a few lineages have also colonised deeper waters, on the continental shelves but also on bathyal and abyssal bottoms. The species currently included in the two clearly related genera *Benthonella* Dall, 1889 and *Benthonellania* Lozouet, 1990, represent one such lineage. We have revised here the material referable to these genera, in the samples collected during deep-sea cruises to French Polynesia (Fig. 1) by the Muséum national d'Histoire naturelle (MNHN) and the Institut de Recherche pour le Développement (IRD). Neither *Benthonella* nor *Benthonellania* had been so far reported in works dealing with molluscs from French Polynesia, including Tröndlé & von Cosel (2005), Salvat & Tröndlé (2017), Tröndlé & Boutet (2009) and Boutet *et al.* (2020), which anyway treated almost only shallow water species.

The genus *Benthonella* includes a group of marine species living from the lower continental shelf to bathyal and abyssal depths, down to *c.* 5500 m (Bouchet & Warén 1993: 700). The origin of *Benthonella* seems to be traceable back to the Eocene of France, with subsequent diversification in the Oligocene (Lozouet 1990: 313; 2014: 21; Amitrov 2010: 387). The genus as currently conceived, has a very wide range, occurring in the Atlantic and the Indo-Pacific, with ten accepted species of which six are fossil only (MolluscaBase 2021b). In a phylogenetic analysis of the Rissoïdæ (Criscione *et al.* 2016), two unidentified species of *Benthonella* have been included: they represented a distinct lineage within the Rissoïdæ, one of the two that independently colonised deep waters.

The genus *Benthonellania* was described (Lozouet 1990: 314) to include five Recent and fossil deep-water species. Subsequently, other species have been described or included in *Benthonellania* by several authors (Moolenbeek & Faber 1991; Bouchet & Warén 1993; Bosch *et al.* 1995; Gofas 1999;

Absalão & Santos 2004; Oliver & Rolán 2017) yielding a diversity of 15 currently recognised species of which two are fossil (MolluscaBase 2021c).

Benthonella and *Benthonellania* are similar in their thin shell, devoid of coloration (except, in most of the species, for the coloured protoconch), the sharp outer lip (sometimes only slightly thickened), and the frequent adapical thickening of the axial ribs, yielding a sort of subsutural crown often highlighted by a spiral groove; they have also similar radulae, lack metapodial tentacles and live in deep waters. The two genera are diagnosed by shell and anatomical features: *Benthonella* has a less slender teleoconch and a protoconch with a low spire, with a sculpture of 1-3 spiral cordlets; the protoconch in *Benthonellania* is generally more slender with a more marked and diversified sculpture. *Benthonellania* has pallial tentacles, eyes and a well developed posterior gland (all lacking in *Benthonella*), and the anterior pedal gland is not visible (see Lozouet 1990; Ponder 1985).

However, during the present revision, the study of large samples from an unprecedented series of species of this group, showed that, in the lack of anatomical data, shell features alone are probably inadequate to consistently classify species in the appropriate genus (Bouchet & Warén 1993: 679).

MATERIAL AND METHODS

We have studied a total of *c.* 9000 shells collected at 93 stations during the MUSORSTOM 9 (1997: PI Bertrand Richer de Forges, <https://doi.org/10.17600/97100020>) [4 stations], BENTHAUS (2002: PI Bertrand Richer de Forges, <https://doi.org/10.17600/2100100>) [31 stations] and TARASOC (2009: PI Philippe Bouchet, <https://doi.org/10.17600/9100040>) [58 stations] deep-sea cruises organised by the MNHN and IRD to Marquesas Islands, Tarava Seamounts, Austral Islands, Society Islands and Tuamotu Islands. Further information on the cruises, full lists of stations, participants and published results can be found on the “Basexp” site (<https://expeditions.mnhn.fr/>).

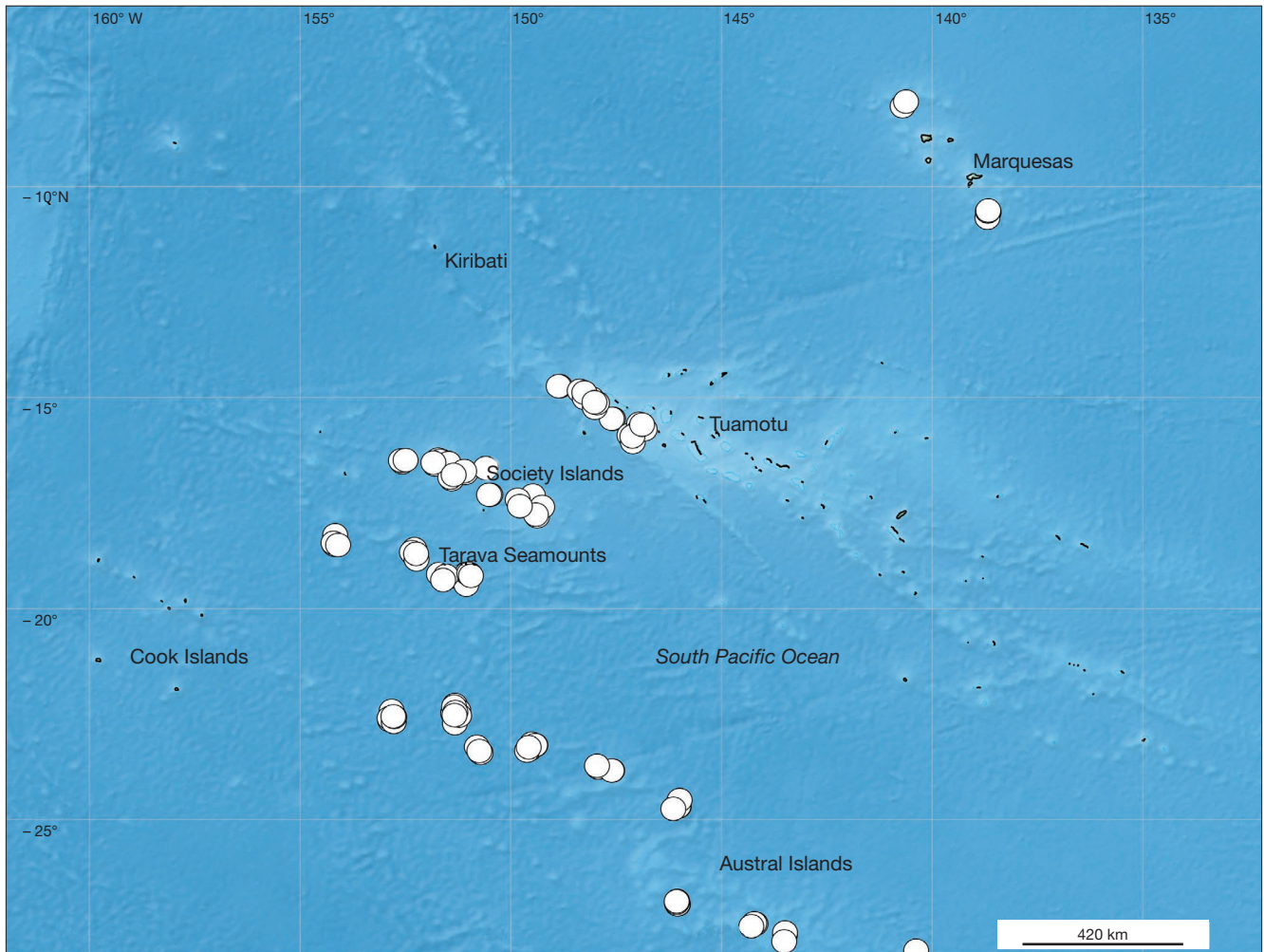


Fig. 1. — Map of French Polynesia with the sampling stations (○) that yielded material examined in this revision.

The list of oceanographic stations in French Polynesia that yielded material examined in this revision follows:

MUSORSTOM 9. DR1244, DR1247, CP1275, CP1278;

BENTHAUS. DW1875, DW1884, DW1885, DW1886, DW1887, DW1889, DW1924, DW1925, DW1932, DW1933, DW1937, DW1941, DW1943, DW1951, DW1955, DW1956, DW 1961, DW1962, DW1973, DW1974, DW1975, DW1979, DW1981, DW1998, DW1999, DW2003, DW2004, DW2010, DW2012, DW2020, DW2021;

TARASOC. CP3329, CP3439, DW3300, DW3302, DW3308, DW3309, DW3310, DW3311, DW3314, DW3316, DW3317, DW3318, DW3319, DW3321, DW3327, DW3328, DW3330, DW3331, DW3332, DW3333, DW3340, DW3349, DW3351, DW3359, DW3373, DW3379, DW3380, DW3387, DW3388, DW3389, DW3407, DW3416, DW3418, DW3420, DW3421, DW3425, DW3426, DW3429, DW3434, DW3435, DW3436, DW3442, DW3447, DW3451, DW3452, DW3457, DW3459, DW3460, DW3461, DW3474, DW3476, DW3481, DW 484, DW3487, DW3491, DW3498, DW3501, DW3559.

We have also studied for comparison, the type material of some taxa described by Thiele (1925) (ZMB) from the Indian Ocean; we have included in the Systematic part the redescription of these taxa.

Photographs have been taken with a Sony Cyber-shot DSC-W110 digital camera mounted on a Kyowa KBS and a Kyowa SDZ-P stereomicroscopes, edited with the software Combine-Z (Hadley 2006). SEM photographs were taken with a Philips XL30 and a FE-SEM ZEISS Sigma Gemini 300 at the interdepartmental laboratory of electron Microscopy (LIME: University “Roma Tre”, Rome).

We have used a standardised format for the citation of specimen data in Type material and Other material examined sections, as described by Chester *et al.* (2019). All the samples studied are housed at MNHN, unless stated otherwise.

ABBREVIATIONS AND ACRONYMS

Institutions

MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts;
MNHN	Muséum national d’Histoire naturelle, Paris;
ZMB	Museum für Naturkunde – Leibniz-Institut für

Evolutions-und Biodiversitätsforschung an der Humboldt-Universität zu Berlin, Berlin.

Others

dd empty shell(s);
 lv live collected specimen(s);
 SEM scanning electron microscope;
 Stn station.

SYSTEMATICS

REMARK

Citation of unpublished names is not intended for taxonomic purposes.

Class GASTROPODA Cuvier, 1795
 Subclass CAENOGASTROPODA Cox, 1960
 Order LITTORINIMORPHA
 Golikov & Starobogatov, 1975
 Superfamily RISSOIDEA Gray, 1847
 Family RISSOIDEA Gray, 1847

Genus *Benthonella* Dall, 1889

Benthonella Dall, 1889: 281.

TYPE SPECIES. — *Benthonella gaza* Dall, 1889: 282, currently *Benthonella tenella* (Jeffreys, 1869), by original designation.

DIAGNOSIS. — Shell of small to medium size for the family, with transparent, colourless teleoconch; axial sculpture present, and spiral sculpture, when present, only on the base; protoconch multispiral with a low spire, finely keeled and coloured.
 Pallial tentacles, eyes and posterior gland lacking.

REMARKS

Most of the species have both axial and spiral sculptures on the teleoconch and a slightly thickened labial varix, followed by a fragile and sharp edge, usually preserved intact only in freshly collected specimens. The umbilicus may be open, broad or narrow, or closed; sometimes the columellar lip may be expanded over the umbilical area, producing a false umbilical chink. For the description of the soft parts see Ponder (1985: 63) based on *B. tenella*, who addressed a very peculiar sperm duct opening to the kidney, and a possible renal copulation. We could not examine material of *Benthonella* =? *loriei* Weisbord, 1962, which is described as paucispiral (Weisbord 1962: 129-130, pl. 46: figs 7-8, pl. 47: 6-7), and if confirmed, would represent the only known species of *Benthonella* with non-planktotrophic development.

Some deep-water taxa, mostly described under the genus *Rissoa* Desmarest, 1814, actually belong to *Benthonella*. For instance, *Rissoa olangoensis* Poppe, Tagaro & Stahlschmidt, 2015 from Philippines, off Olango Island in the Mactan Channel in front of Baring, 130 m depth, clearly belongs to *Benthonella* (see Poppe *et al.* 2015: 24, pl. 8, figs 1-3). It has, like the type species, a blunt, coloured protoconch with two peripheral keels and therefore, we propose *Benthonella olangoensis* (Poppe, Tagaro & Stahlschmidt, 2015) as a new combination.

Pusillina kazakhstanica Amitrov, 2010 from the Oligocene of Kazakhstan, also belongs to *Benthonella*. Very similar to *Benthonella lutetiana* Lozouet, 2014 and to *Benthonella priabonica* Lozouet, 2014, it essentially differs from both species for the presence on the protoconch of a thin median spiral keel vs 2 well spaced (one subsutural, the other suprasutural) in *B. lutetiana* and *B. priabonica*. Furthermore, the subsutural thickening of the axial ribs is stronger in *B. lutetiana* and *B. priabonica*. We propose *Benthonella kazakhstanica* (Amitrov, 2010) as a new combination.

Hasegawa (2005) reported two distinct undescribed species belonging to *Benthonella* (as “*Alvania* sp.” and “*Benthonella* sp.” – Hasegawa 2005: 149, fig. 5I; 149, figs K, L).

We have found three species of *Benthonella* in French Polynesia, all undescribed: *Benthonella boucheti* n. sp., *Benthonella basistriata* n. sp., *Benthonella communis* n. sp.

Benthonella boucheti n. sp.

(Figs 2A-G; 5A-E; 25A; 26A; Tables 1; 2)

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TYPE MATERIAL. — **Holotype**. Tarava Seamounts • dd (height 4.32 mm, width 2.75 mm, Figs 6A; 7A-C); Mont Honu, TARASOC Stn DW3340; 18°24'S, 154°09'W; 787-798 m; MNHN-IM-2000-37666.

Paratypes • 22 dd; same locality data as holotype; MNHN-IM-2000-37667.

TYPE LOCALITY. — Tarava Seamounts, Mont Honu, TARASOC Stn DW3340, 18°24'S, 154°09'W, 787-798 m.

OTHER MATERIAL EXAMINED. — **Tarava Seamounts** • 2 dd; Mont 'Otaha, TARASOC Stn DW3333; 18°45'S, 152°18'W; 795-975 m; 26.IX.2009; MNHN • 3 dd; Mont 'Otaha, TARASOC Stn DW3328; 18°46'S, 152°15'W; 788-836 m; 26.IX.2009; MNHN • 1 dd; Mont 'Otaha, TARASOC Stn DW3331; 18°45'S, 152°17'W; 766 m; 26.IX.2009; MNHN.

Marquesas • 2 dd; Fatu Hiva, MUSORSTOM 9 Stn DR1247; 10°34'S, 138°42'W; 1150-1250 m; 1.IX.1997; MNHN.

Australes • 9 dd; Banc Président Thiers, BENTHAUS Stn DW1933; 24°41'S, 146°01'W; 500-850 m; 14.XI.2002; MNHN • 2 dd; Récif Neilson, BENTHAUS Stn DW1925; 27°00'S, 146°05'W; 560-790 m; 12.XI.2002; MNHN • 15 dd; Récif Neilson, BENTHAUS Stn DW1925; 27°00'S, 146°05'W; 560-790 m; 12.XI.2002; MNHN • 21 dd; South coast of Rurutu, BENTHAUS Stn DW2010; 22°32'S, 151°21'; 520-950 m; 24.XI.2002; MNHN • 1 dd; Tubuai, BENTHAUS Stn DW1961; 23°21'S, 149°34'; 470-800 m; 19.XI.2002; MNHN • 4 dd; Tubuai, BENTHAUS Stn DW1955; 23°19'S, 149°26'W; 750-850 m; 18.XI.2002; MNHN • 6 dd; Tubuai, BENTHAUS Stn DW1956; 23°18'S, 149°27'W; 600-990 m; 18.XI.2002; MNHN • 1 dd; Tubuai, BENTHAUS Stn DW1962; 23°21'S, 149°33'W; 470-800 m; 19.XI.2002; MNHN • 3 dd; North of Raivavae, BENTHAUS Stn DW1943; 23°49'S, 147°39'W; 950 m; 15.XI.2002; MNHN • 3 dd; Marotiri, BENTHAUS Stn DW1886; 27°51'S, 143°32'W; 620-1000 m; 6.XI.2002; MNHN • 2 dd; Marotiri, BENTHAUS Stn DW1887; 27°52'S, 143°33'W; 750-1000 m; 6.XI.2002; MNHN • 9 dd; Banc Arago, BENTHAUS Stn DW1981; 23°21'S, 150°43'W; 650-1150 m; 21.XI.2002; MNHN • 15 dd; Rimatara, BENTHAUS Stn DW2021; 22°37'S, 152°49'W; 1200-1226 m; 25.XI.2002; MNHN • 9 dd; Rimatara, BENTHAUS Stn DW2020; 22°37'S, 152°49'W; 920-930 m; 25.XI.2002; MNHN • 9 dd; East coast of Rurutu, BENTHAUS Stn DW2004; 22°28'S, 151°19'W; 430-850 m; 24.XI.2002.

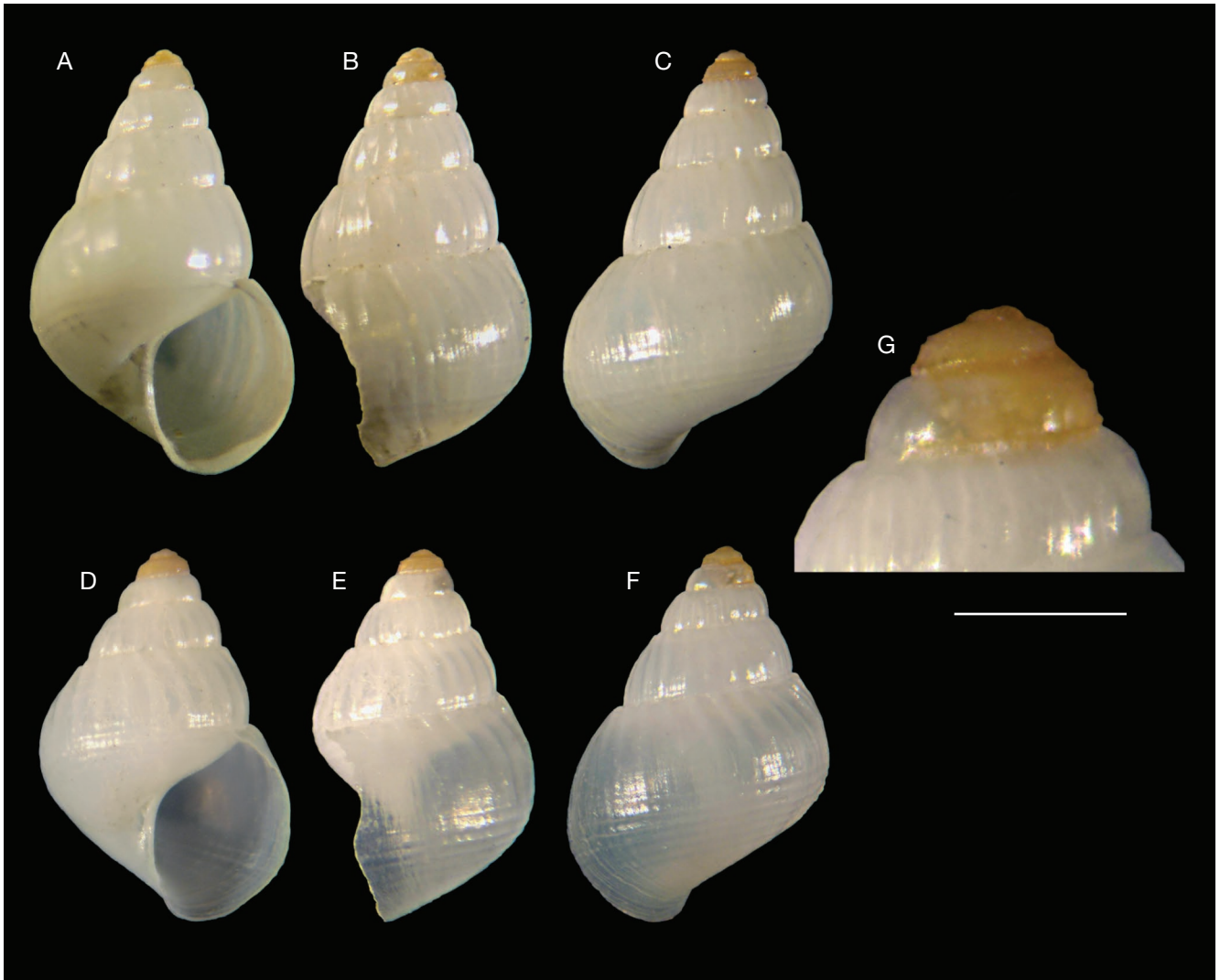


FIG. 2. — *Benthonella boucheti* n. sp.: A-C, holotype, height 4.32 mm, width 2.75 mm, Tarava Seamounts: TARASOC Stn DW3340 787-798 m 18°24'S, 154°09'W (MNHN-IM-2000-37666); D-G, specimen, height 3.75 mm, width 2.6 mm, Australes: BENTHAUS Stn DW1933 500-850 m 24°41'S, 146°01'W, MNHN. Scale bar: G, 0.50 mm.

Tuamotu • 1 dd; between Tikehau and Rangiroa, TARASOC Stn DW3349; 15°05'S, 148°03'W; 976-997 m; 30.IX.2009; MNHN.

DISTRIBUTION AND SYMPATRY. — *Benthonella boucheti* n. sp. is known from the South Pacific Ocean, in the Tarava Seamounts (Mont Honu, Mont 'Otaha), Australes (Banc Président Thiers, Récif Neilson, South Coasts of Rurutu, East coasts of Rurutu, Tubuai, North of Raivavae, Marotiri, Banc Arago, Rimatara), Marquesas (Ile Fatu Hiva), Tuamotu (between Tikehau and Rangiroa), with empty shells collected in 430-1250 m depth (Fig. 25A).

Benthonella boucheti n. sp. is sympatric with *Benthonellania maestratii* n. sp. at the Australes (Récif Neilson, South coast of Rurutu); with *Benthonella communis* n. sp. at the Australes (Banc Président Thiers, Récif Neilson, South Coasts of Rurutu, East coasts of Rurutu, Tubuai, North of Raivavae, Marotiri, Banc Arago, Rimatara), Tuamotu (between Tikehau and Rangiroa); with *Benthonellania bouteti* n. sp. at the Tarava Seamounts (Mont Honu and Mont 'Otaha), Australes (Banc Président Thiers, Récif Neilson, South Coasts of Rurutu, East coasts of Rurutu, Banc Arago, Rimatara, Tubuai), Tuamotu (between Tikehau and Rangiroa); with *Benthonellania tarava* n. sp. at the Tarava Seamounts (Mont Honu and Mont 'Otaha), Australes (Rimatara, South coast of Rurutu, East coast of Rurutu), Tuamotu (between Tikehau and Rangiroa); with *Benthonellania tuamotu* n. sp.

at the Tarava Seamounts (Mont 'Otaha), Australes (Rimatara, South coast of Rurutu, Récif Neilson), Tuamotu (between Tikehau and Rangiroa); with *Benthonellania lozoueti* n. sp. at the Marquesas (Ile Fatu Hiva), Australes (Rimatara); with *Benthonellania alis* n. sp. at the Australes (East coast of Rurutu, South coast of Rurutu, Rimatara, Marotiri, Tubuai, Banc Président Thiers), Tarava Seamounts (Mont 'Otaha, Mont Honu) (Table 2).

ETYMOLOGY. — Named after Philippe Bouchet (MNHN), for his indefatigable work during decades, aimed at improving the knowledge of marine biodiversity.

DESCRIPTION OF HOLOTYPE.

Shell (Figs 2A-C; 5A-E)

Large for the genus, height 4.3 mm, width 2.7 mm, height/width ratio 1.57, ovate-conical, rather fragile, with broad last whorl.

Protoconch (Figs 2G; 5B, C, E)

Multispiral, dome-shaped, of 2.4 whorls, height 0.4125 mm, nucleus diameter 0.075 mm, first half whorl diameter

TABLE 1. — Measurements of teleoconch and protoconch of the studied species in mm, with minimum-maximum range and mean [standard deviation in square parentheses]. Sample size in parentheses with the species name. Symbols: +, present; -, absent; M, multispiral; P, paucispiral.

Teleoconch	<i>Benthonella basistriata</i> n. sp. (10)	<i>Benthonella boucheti</i> n. sp. (2)	<i>Benthonella communis</i> n. sp. (20)	<i>Benthonellania aequatorialis</i> (Thiele, 1925) n. comb. (2)	<i>Benthonellania africana</i> (Thiele, 1925) n. comb. (4)	<i>Benthonellania alis</i> n. sp. (10)	<i>Benthonellania bouteti</i> n. sp. (17)	<i>Benthonellania hertzi</i> (Thiele, 1925) n. comb. (2)	<i>Benthonellania lozoueti</i> n. sp. (10)	<i>Benthonellania maestratii</i> n. sp. (3)	<i>Benthonellania megan</i> n. sp. (6)	<i>Benthonellania tarava</i> n. sp. (20)	<i>Benthonellania thielei</i> n. sp. (4)	<i>Benthonellania tuamotu</i> n. sp. (10)
Height	3.6-4.95 4.21 [0.43]	3.75-4.32 4.03 [0.40]	1.27-2.40 2.04 [0.31]	1.80-1.95 1.87 [0.10]	3.35-4 3.72 [0.27]	3.05-4.0 3.5 [0.27]	2.92-4.15 3.49 [0.35]	2.47-2.85 2.66 [0.27]	2.35-4.45 3.62 [0.57]	2.50-3.12 2.80 [0.31]	2.40-2.70 2.56 [0.10]	2.67-3.75 3.16 [0.29]	2.55-3.20 2.94 [0.27]	2.15-2.77 2.49 [0.19]
Width	2.15-2.77 2.49 [0.19]	2.60-2.75 2.67 [0.10]	0.92-1.60 1.342 [0.17]	1.35-1.37 1.36 [0.01]	2.02-2.35 2.17 [0.13]	1.75-2.20 1.96 [0.14]	1.65-2.20 1.93 [0.15]	1.75-1.95 1.85 [0.14]	1.60-2.75 2.30 [0.34]	1.62-2.07 1.85 [0.23]	1.47-1.60 1.53 [0.06]	1.55-1.92 1.72 [0.12]	1.82-2.05 1.93 [0.09]	2.15-2.77 2.49 [0.19]
Height/Width ratio	1.625-1.787 1.688 [0.064]	1.442-1.572 1.507 [0.058]	1.380-1.606 1.5155 [0.057]	1.333-1.423 1.378 [0.064]	1.574-1.860 1.720 [0.129]	1.725-1.875 1.790 [0.049]	1.660-1.917 1.803 [0.072]	1.411-1.461 1.436 [0.035]	1.468-1.674 1.572 [0.073]	1.507-1.538 1.519 [0.016]	1.594-1.733 1.662 [0.062]	1.706-1.953 1.833 [0.071]	1.401-1.588 1.518 [0.082]	1.625-1.787 1.688 [0.064]
Aperture height	1.5-2.0 1.73 [0.18]	1.90-2.0 2.05 [0.07]	0.57-1.02 0.86 [0.11]	1.0-1.02 1.01 [0.01]	1.25-1.55 1.42 [0.13]	1.10-1.45 1.29 [0.11]	1.10-1.42 1.27 [0.10]	1.25-1.40 1.32 [0.106]	1.17-1.90 1.59 [0.22]	1.10-1.35 1.25 [0.13]	1.0-1.10 1.04 [0.04]	1.0-1.27 1.12 [0.11]	1.20-1.35 1.28 [0.06]	1.5-2.0 1.73 [0.18]
Height/Height aperture ratio	2.250-2.687 2.440 [0.129]	1.983-2.162 2.241-2.600 2.41 [0.101]	2.028-2.633 1.983-2.162 2.067 [0.134]	1.800-1.911 2.028-2.633 2.3472 [0.133]	2.466-2.857 2.621 [0.185]	2.590-2.800 2.716 [0.076]	2.464-3.058 2.760 [0.165]	1.976-2.036 2.006 [0.042]	2.008-2.500 2.267 [0.140]	2.154-2.311 2.246 [0.082]	2.400-2.500 2.451 [0.035]	2.670-3.045 2.822 [0.106]	2.125-2.461 2.296 [0.141]	2.250-2.687 2.440 [0.129]
Height last whorl	2.4-3.15 2.78 [0.26]	2.80-2.90 2.85 [0.07]	0.92-1.70 1.39 [0.19]	1.47-1.50 1.48 [0.02]	2.25-2.55 2.44 [0.13]	1.92-2.40 2.18 [0.14]	1.87-2.32 2.12 [0.14]	1.80-2.07 1.94 [0.191]	1.70-3.0 2.48 [0.37]	1.75-2.15 1.95 [0.2]	1.60-1.75 1.68 [0.051]	1.67-2.20 1.90 [0.16]	2.0-2.2 2.12 [0.09]	2.4-3.15 2.78 [0.26]
Height/Height last whorl ratio	1.456-1.571 1.516 [0.037]	1.351-1.491 1.444-1.562 1.503 [0.033]	1.380-1.552 1.463 [0.049]	1.200-1.326 1.263 [0.089]	1.451-1.632 1.528 [0.078]	1.522-1.666 1.603 [0.046]	1.500-1.773 1.642 [0.093]	1.372-1.377 1.375 [0.004]	1.378-1.541 1.459 [0.051]	1.428-1.451 1.438 [0.012]	1.454-1.562 1.520 [0.039]	1.599-1.718 1.663 [0.036]	1.275-1.454 1.382 [0.077]	1.456-1.571 1.516 [0.037]
No. of whorls	4.0-5.1 4.46 [0.33]	3.4-4.2 3.8 [0.28]	2.2-3.6 3.1 [0.35]	2.65-2.80 2.72 [0.11]	3.50-4.25 3.89 [0.35]	3.8-4.6 4.18 [0.24]	3.5-5.2 4.38 [0.54]	2.75-3.10 2.92 [0.25]	3.2-4.5 3.98 [0.38]	3.2-3.5 3.32 [0.16]	3.2-3.5 3.38 [0.14]	3.6-4.65 4.22 [0.26]	3.35-3.60 3.45 [0.12]	4.0-5.1 4.46 [0.33]
No. axial ribs on last whorl (excluding the varix, when present)	14-20 17.5 [1.8]	20-21 20.5 [0.7]	16-27 20.2 [2.7]	17 17.5 [0.7]	8-10 8.7 [0.9]	19-24 21.1 [1.7]	12-23 16.9 [2.8]	24-26 25 [1.4]	16-27 22.4 [3.7]	35-57 45.7 [11.0]	14-19 16.5 [1.6]	11-16 13.35 [1.3]	13-20 16.2 [3.3]	14-20 17.5 [1.8]

TABLE 2. — List of Recent *Benthonella* Dall, 1889 and *Benthonellania* Lozouet, 1990 from French Polynesia, with their occurrence in the explored archipelagos (grey shaded cells) and the sympatric co-occurrence with other species (black shaded cells).

Species	Archipelagos	<i>B. boucheti</i> n. sp.	<i>B. basistriata</i> n. sp.	<i>B. communis</i> n. sp.	<i>B. bouteti</i> n. sp.	<i>B. alis</i> n. sp.	<i>B. tarava</i> n. sp.	<i>B. megan</i> n. sp.	<i>B. tuamotu</i> n. sp.	<i>B. lozoueti</i> n. sp.	<i>B. maestratii</i> n. sp.
<i>Benthonella boucheti</i> n. sp.	Tarava S. Australes Tuamotu Marquesas Society	Grey	Black	Black	Black	Black	Black	Black	Black	Black	Black
<i>Benthonella basistriata</i> n. sp.	Tarava S. Australes Tuamotu Marquesas Society		Grey	Black	Black	Black	Black	Black	Black		
<i>Benthonella communis</i> n. sp.	Tarava S. Australes Tuamotu Marquesas Society	Black	Black	Grey	Black	Black	Black	Black	Black		Black
<i>Benthonellania bouteti</i> n. sp.	Tarava S. Australes Tuamotu Marquesas Society	Black	Black	Black	Grey	Black	Black	Black	Black		Black
<i>Benthonellania alis</i> n. sp.	Tarava S. Australes Tuamotu Marquesas Society	Black	Black	Black	Black	Grey	Black	Black	Black		Black
<i>Benthonellania tarava</i> n. sp.	Tarava S. Australes Tuamotu Marquesas Society	Black	Black	Black	Black	Black	Grey	Black	Black		Black
<i>Benthonellania megan</i> n. sp.	Tarava S. Australes Tuamotu Marquesas Society	Black						Grey			
<i>Benthonellania tuamotu</i> n. sp.	Tarava S. Australes Tuamotu Marquesas Society	Black	Black	Black	Black	Black	Black	Black	Grey		Black
<i>Benthonellania lozoueti</i> n. sp.	Tarava S. Australes Tuamotu Marquesas Society	Black						Black		Grey	
<i>Benthonellania maestratii</i> n. sp.	Tarava S. Australes Tuamotu Marquesas Society	Black		Black	Black	Black	Black	Black	Black		Grey

0.1375 mm, maximum diameter 0.60 mm; protoconch I with 4 threads, interspaces covered by microtubercles (Fig. 5C); protoconch II with two pairs of spiral cordlets, and closely set axial micro-riblets in the interspace of the abapical pair (Fig. 5B). Protoconch-teleconch, boundary indistinct, sinuous.

Teleconch

Of 4.2 slightly convex whorls of slowly increasing height; suture incised, slightly canaliculate and wavy. Height last whorl 2.9 mm, height/height last whorl ratio 1.491. Axial sculpture of weak, flat, curved and prosocline ribs, half as broad as the interspaces, absent on the first half whorl, 20 on

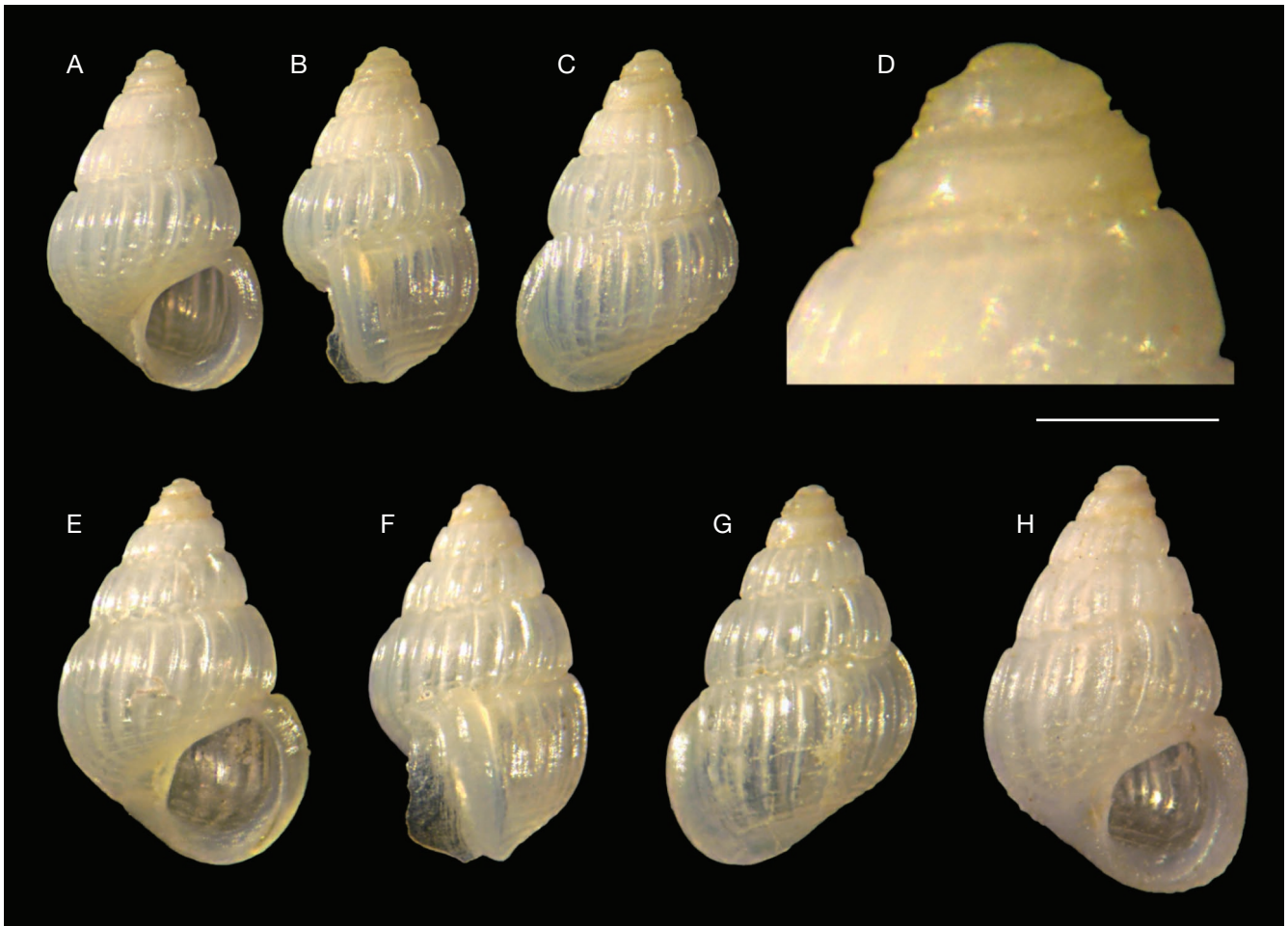


FIG. 3. — *Benthonella basistriata* n. sp.: **A-D**, holotype, height 2.0 mm, width 1.3 mm, Tuamotu: TARASOC Stn DW3389 889 m 14°55'S, 148°15'W (MNHN-IM-2000-37668); **E-G**, specimen, height 2.25 mm, width 1.5 mm, Society Islands: TARASOC Stn DW3481, 610 m, 17°29'S, 149°45'W; **H**, specimen, height 2.52 mm, width 1.55 mm, Society Islands: TARASOC Stn DW3435 500-612 m, 16°41'S, 151°02'W, MNHN. Scale bar: D, 0.50 mm.

the last whorl, gradually vanishing at the base, prominent at suture, giving the whorls a coronated appearance (Fig. 5E). Spiral sculpture of 7 weak, narrow and very low, indistinct spiral cordlets, only on the base. Microsculpture of only growth striae (Fig. 5D). Umbilical chink present. Aperture pyriform, large, height 2.0 mm, height/height aperture ratio 2.162, peristome continuous, outer lip prosocline (broken), internally smooth. Columella arcuate, simple.

Colour

Coloration of teleoconch white, protoconch orange.

Operculum and soft parts

Unknown.

VARIABILITY

Only two full-grown intact specimens available; the variability seems low (see Table 1 and Appendix 1).

REMARKS

Benthonella boucheti n. sp. resembles the northeastern Atlantic and Mediterranean *Benthonella tenella* (Jeffreys 1869:

204, pl. CI, fig. 7) for the conical outline with a broad last whorl, especially in the so-called 'form *fischeri* Dall, 1889' (Ponder 1985: 63, figs 39A, B; Bouchet & Warén 1993: 699, figs 1643-1650; Lozouet 2014: 24, 31, figs 2R, S, and 7A-C), with its axial sculpture on the first teleoconch whorls (absent in the typical form). *Benthonella boucheti* n. sp. differs in its less rounded aperture, spiral sculpture on the base, and different apical sculpture: protoconch II with two pairs of spiral cordlets, in the interspaces of the abapical pair, confused and close axial micro riblets vs protoconch II with two thin spiral cordlets and a subsutural belt of microgranules in *B. tenella*.

Benthonella basistriata n. sp.

(Figs 3A-H; 5F, G; 25B; 26B; Tables 1; 2)

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TYPE MATERIAL. — **Holotype**. Tuamotu. • dd (height 2.0 mm, width 1.3 mm, Figs 8A-D; 10F, G); Tikehau, TARASOC Stn DW3389; 14°55'S, 148°15'W; 889 m depth; MNHN-IM-2000-37668.

Paratypes • 2 dd; same locality data as holotype; MNHN-IM-2000-37669.

TYPE LOCALITY. — Tuamotu, Tikehau, TARASOC Stn DW3389, 14°55'S, 148°15'W, 889 m depth.

OTHER MATERIAL EXAMINED. — **Society Islands** • 1 dd; Huahine, TARASOC Stn DW3425; 16°43'S, 151°03'W; 557 m; 14.X.2009; MNHN • 2 dd; Huahine, TARASOC Stn DW3435; 16°41'S, 151°02'W; 500-612 m; 15.X.2009; MNHN • 1 dd; Moorea, TARASOC Stn DW3459; 17°28'S, 149°48'W; 485-560 m; 19.X.2009 • 3 dd; Moorea, TARASOC Stn DW3481; 17°29'S, 149°45'W; 610 m; 22.X.2009 • 1 dd; Moorea, TARASOC Stn DW3474; 17°28'S, 149°50'W; 720 m; 21.X.2009; MNHN. **Tuamotu** • 15 dd; Kaukura, TARASOC Stn DW3373; 15°41'S, 146°54'W; 507-607 m; 4.X.2009; MNHN.

DISTRIBUTION AND SYMPATRY. — The species is known from the South Pacific Ocean in the Tuamotu (Tikehau, Kaukura) and Society Islands (Huahine, Moorea), with empty shells collected in 485-889 m depth (Fig. 25B).

Benthonella basistriata n. sp. is sympatric with *Benthonella communis* n. sp. at the Society Islands (Huahine, Moorea), Tuamotu (Kaukura); with *Benthonellania bouteti* n. sp. at the Tuamotu (Kaukura, Tikehau), Society Islands (Huahine, Moorea); with *Benthonellania tarava* n. sp. at the Tuamotu (Kaukura, Tikehau), Society Islands (Moorea); with *Benthonellania tuamotu* n. sp. at the Tuamotu (Kaukura, Tikehau) (Table 2).

ETYMOLOGY. — For the particularly marked basal sculpture, from the Latin basis – base, striata – striated.

DESCRIPTION OF HOLOTYPE

Shell (Figs 3A-D; 5F, G)

Small for the genus, height 2.0 mm, width 1.3 mm, height/width ratio 1.538, rather solid, ovate-conical.

Protoconch (Figs 3D; 5G)

Multispiral, dome-shaped, of 2.5 whorls, height 0.3375 mm, nucleus diameter 0.075 mm, first half whorl diameter 0.125 mm, maximum diameter 0.375 mm; protoconch I with 5 spiral threads, interspaces covered by microtubercles (Fig. 5G); protoconch II with 2 fine spiral cordlets, with irregularly set microtubercles on the subsutural area (Fig. 5G). Protoconch-teleoconch boundary indistinct.

Teleoconch

Of 3.25 whorls, the first 2 flat, the others slightly convex, sutures canaliculate, crowned by small tubercles on tip of axial ribs. Height last whorl 1.3 mm, height/height last whorl ratio 1.538. Axial sculpture on the last whorl of 18 curved, opisthocline ribs, almost as broad as the interspaces, gradually vanishing on the base. Spiral sculpture of 6 weak, fine cordlets, only on the base of last whorl (abapical last barely visible); one suprasutural cordlet visible on upper whorls. Microsculpture of only growth striae. Umbilical chink absent. Aperture pyriform, small, height 0.8 mm. height/height aperture ratio 2.424, peristome continuous, varix large; outer lip (broken) prosocline, internally smooth, sharp. Columella angled, simple.

Colour

Coloration of teleoconch white, outer lip orange faded, darker than subsutural zone, protoconch whitish-orange.

Operculum and soft parts

Unknown.

VARIABILITY

Species not very variable (See Table 1 and Appendix 2). Maximum height 2.60 mm, width 1.65 mm (from Tuamotu: Tikehau 889 m). The number of axial ribs on the last whorl can vary from 14 to 20.

REMARKS

Benthonella basistriata n. sp. is similar in the general shape to the fossil *Benthonella lutetiana* Lozouet, 2014 and *Benthonella priabonica* Lozouet, 2014, both from the Eocene of France (see Lozouet 2014: 24-25, 28; 2I-K; 5A-E and 2014: 24-25, 29, figs 2L-N; 6A-H, respectively). They are essentially distinguished by the different sculpture of the protoconch II: *B. lutetiana* and *B. priabonica* have two thin spiral cordlets, one abapical close to the suture, the other adapical closer to the suture in *B. lutetiana*; *B. basistriata* n. sp. has two broader spiral cordlets, the adapical farther from the suture, and microgranules on the subsutural area (apparently lacking in the fossil species).

Benthonella olangoensis (Poppe, Tagaro & Stahlschmidt, 2015) has a similar outline. It differs in the fewer spiral cordlets (2-3 vs 5-6 in *B. basistriata* n. sp.: based on the photos of the type material, since in the original description, this sculpture and the precise number of cordlets are not reported).

B. basistriata n. sp. also resembles *Benthonellania agastachys* Bouchet & Warén, 1993. *Benthonella basistriata* n. sp. has a spiral sculpture of 6 basal cords vs c. 10 basal cords in an adult specimen of *Benthonellania agastachys* figured by Ortega & Gofas (2019: 525, figs 8 A-D; the holotype with 4-5 cords is a juvenile); the umbilical chink absent vs present in *B. agastachys*; the protoconch multispiral, with two fine spiral cordlets and subsutural microtubercles vs paucispiral, lacking spiral cordlets, densely granulated, with granules tending to be spirally arranged in *B. agastachys* (see Bouchet & Warén 1993: 682, figs 1584, 1592-1593).

See under *Benthonellania hertzogi* (Thiele, 1925) n. comb. and *Benthonellania thielei* n. sp. for detailed comparisons.

Benthonella communis n. sp.

(Figs 4A-G; 5H-J; 25C; 26C; Tables 1; 2)

[urn:lsid:zoobank.org:act:C42E14D5-7CED-4B62-BA1A-CAC05282C3E4](https://doi.org/10.21203/rs.3.rs-1234567/v1)

TYPE MATERIAL. — **Holotype**. **Tarava Seamounts** • dd (height 2.2 mm, width 1.45 mm, Figs 9A-C; 10H-J); Mont Ari'i Moana, TARASOC Stn DW3309; 19°12'S, 151°35'W; 614-664 m depth; MNHN-IM-2000-37670.

Paratypes. **Tarava Seamounts** • 13 dd; same locality data as holotype; MNHN-IM-2000-37671 • 11 dd; Mont Ari'i Moana, TARASOC Stn DW3311; 19°12'S, 151°33'W; 24.IX.2009; 571-586 m depth; MNHN-IM-2000-37672 • 50 dd; Mont Ari'i Moana, TARASOC Stn DW3319; 19°14'S, 151°32'W; 25.IX.2009; 480 m depth; MNHN-IM-2000-37673 • 24 dd; Mont Ari'i Moana, TARASOC Stn DW3318; 19°15'S, 151°31'W; 25.IX.2009; 557-569 m depth; MNHN-IM-2000-37674 • 6 dd; Mont Ari'i Moana, TARASOC

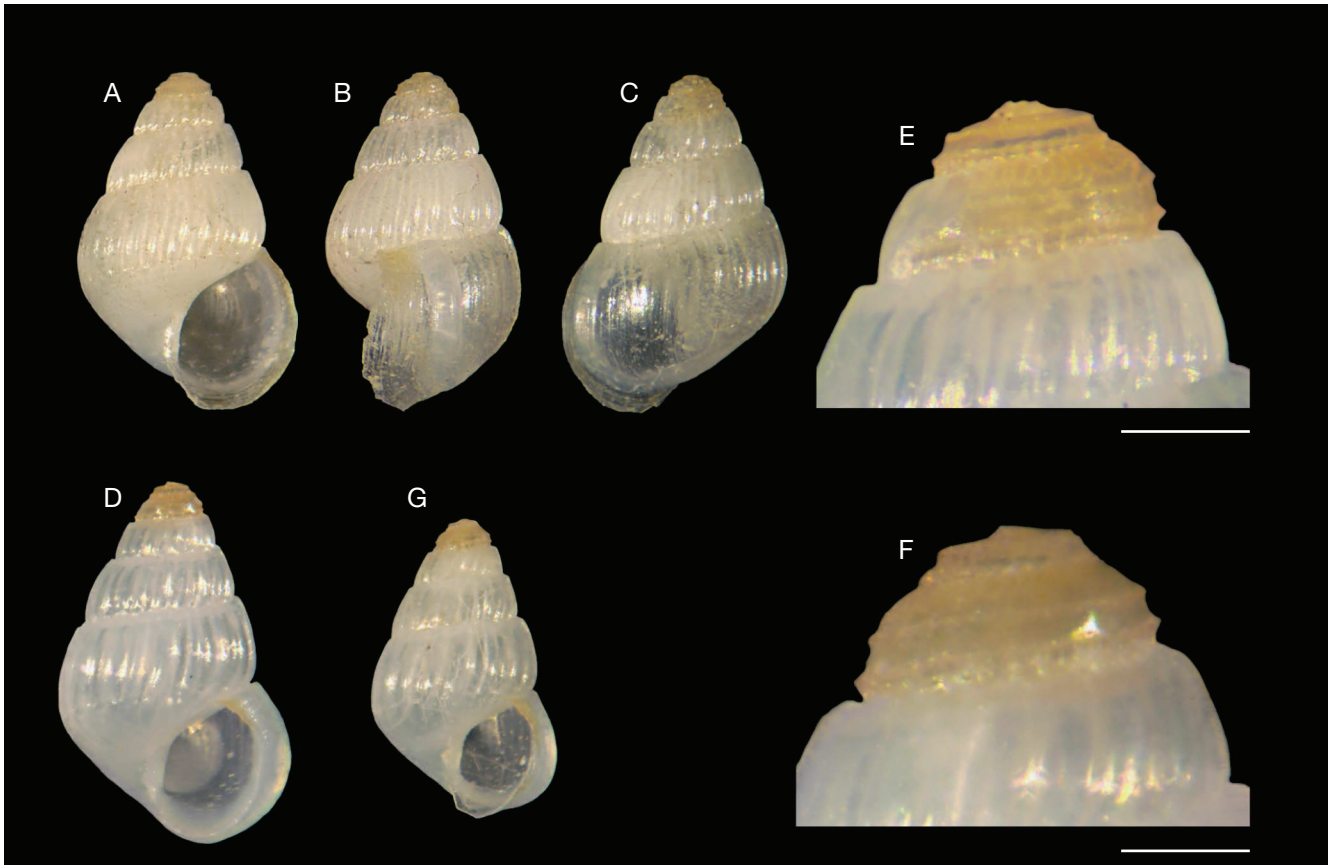


FIG. 4. — *Benthonella communis* n. sp.: **A-C**, holotype, height 2.2 mm, width 1.45 mm, Tarava Seamounts, TARASOC Stn DW3309 614-664 m $19^{\circ}12'S$, $151^{\circ}35'W$ (MNHN-IM-2000-37670); **D-F**, specimen, height 2.35 mm, width 1.5 mm, Australes: BENTHAUS Stn DW1998 250-302 m $22^{\circ}25'S$, $151^{\circ}22'W$, MNHN; **G**, specimen, height 2.01 mm, width 1.35 mm, Australes: BENTHAUS Stn DW1998, 250-302 m, $22^{\circ}25'S$, $151^{\circ}22'W$, MNHN. Scale bars: E, F, 0.25 mm.

Stn DW3321; $19^{\circ}13'S$, $151^{\circ}32'W$; 25.IX.2009; 540-572 m depth; MNHN-IM-2000-37675 • 4 dd; Mont Ari'i Moana, TARASOC Stn DW3310; $19^{\circ}13'S$, $151^{\circ}37'W$; 24.IX.2009; 613-698 m depth; MNHN-IM-2000-37676 • 126 dd; Mont Ari'i Moana, TARASOC Stn DW3316 $19^{\circ}14'S$, $151^{\circ}33'W$; 24.IX.2009; 520 m depth; MNHN-IM-2000-37677.

TYPE LOCALITY. — Tarava Seamounts, Mont Ari'i Moana, TARASOC Stn DW3309; $19^{\circ}12'S$, $151^{\circ}35'W$; 614-664 m depth.

OTHER MATERIAL EXAMINED. — **Society Islands** • 22 dd; Maupiti, TARASOC Stn DW3407; $16^{\circ}32'S$, $152^{\circ}31'W$; 12.X.2009; 445-645 m depth; MNHN • 5 dd; Moorea, TARASOC Stn DW3481; $17^{\circ}29'S$, $149^{\circ}45'W$; 22.X.2009; 610 m depth; MNHN • 20 dd; Tahiti, TARASOC Stn DW3484; $17^{\circ}47'S$, $149^{\circ}23'W$; 23.X.2009; 300-650 m depth; MNHN • 2 dd; Bora Bora, TARASOC Stn DW3416; $16^{\circ}35'S$, $151^{\circ}44'W$; 13.X.2009; 914 m depth; MNHN • 1 dd; Huahine, TARASOC Stn DW3420; $16^{\circ}46'S$, $151^{\circ}04'W$; 14.X.2009; 550 m depth; MNHN • 1 dd; Raiatea, TARASOC Stn DW3451 $16^{\circ}53'S$, $151^{\circ}21'W$; 18.X.2009; 440-490 m depth; MNHN. **Tarava Seamounts** • 33 dd; Mont Punu Taipu, TARASOC Stn DW3302; $19^{\circ}15'S$, $150^{\circ}57'W$; 23.IX.2009; 600-660 m depth; MNHN • 2 dd; Mont Punu Taipu, TARASOC Stn DW3300; $19^{\circ}19'S$, $151^{\circ}00'W$; 22.IX.2009; 670-757 m depth; MNHN. **Tuamotu** • 6 dd; SW Kaukura, TARASOC Stn DW3359; $15^{\circ}57'S$, $147^{\circ}08'W$; 1.X.2009; 462-980 m depth; MNHN • 3 dd; Kaukura, TARASOC Stn DW3373; $15^{\circ}41'S$, $146^{\circ}54'W$; 4.X.2009; 507-607 m depth; MNHN • 4 dd; between Tikehau and Rangiroa, TARASOC Stn DW3349; $15^{\circ}05'S$, $148^{\circ}03'W$; 30.IX.2009; 976-997 m depth; MNHN. **Australes** • 11 dd; Récif Neilson, BENTHAUS Stn DW1924; $27^{\circ}01'S$,

$146^{\circ}05'W$; 12.XI.2002; 340-800 m depth; MNHN • 1 dd; Récif Neilson, BENTHAUS Stn DW1925; $27^{\circ}00'S$, $146^{\circ}05'W$; 12.XI.2002; 560-790 m depth; MNHN • 10 dd; Banc Mac Donald, BENTHAUS Stn DW1875; $28^{\circ}59'S$, $140^{\circ}15'W$; 4.XI.2002; 110-150 m depth; MNHN • 29 dd; Banc Président Thiers, BENTHAUS Stn DW1933; $24^{\circ}41'S$, $146^{\circ}01'W$; 14.XI.2002; 500-850 m depth; MNHN • 54 dd; Banc Président Thiers, BENTHAUS Stn DW1932; $24^{\circ}41'S$, $146^{\circ}02'W$; 14.XI.2002; 500-800 m depth; MNHN • 40 dd; Marotiri, BENTHAUS Stn DW1885; $27^{\circ}52'S$, $143^{\circ}33'W$; 6.XI.2002; 700-800 m depth; MNHN • 3 dd; Rimatara, BENTHAUS Stn DW2012; $22^{\circ}38'S$, $152^{\circ}50'W$; 25.XI.2002; 270-320 m depth; MNHN • 188 dd, 1 lv; Banc Arago, BENTHAUS Stn DW1979; $23^{\circ}21.7'S$, $150^{\circ}43.9'W$; 21.XI.2002; 176-340 m depth; MNHN • 1 dd; Banc Arago, BENTHAUS Stn DW1973; $23^{\circ}23.5'S$, $150^{\circ}43.9'W$; 20.XI.2002; 200-350 m depth; MNHN • 2 dd; Banc Arago, BENTHAUS Stn DW1974; depth $23^{\circ}24'S$, $150^{\circ}44'W$; 20.XI.2002; 450-618 m depth; MNHN • 1 dd; Banc Arago, BENTHAUS Stn DW1975; $23^{\circ}24'S$, $150^{\circ}44'W$; 20.XI.2002; 600-691 m depth; MNHN • 29 dd; South coast of Rurutu, BENTHAUS Stn DW2010; $22^{\circ}32'S$, $151^{\circ}21'W$; 24.XI.2002; 520-950 m depth; MNHN • 1200+ dd; North coast of Rurutu, BENTHAUS Stn DW1998; $22^{\circ}25'S$, $151^{\circ}22'W$; 23.XI.2002; 250-302 m depth; MNHN • 6 dd; Marotiri, BENTHAUS Stn DW1886; depth $27^{\circ}51'S$, $143^{\circ}32'W$; 6.XI.2002; 620-1000 m depth; MNHN • 8 dd; East coast of Rurutu, BENTHAUS Stn DW2003; $22^{\circ}27.6'S$, $151^{\circ}18.9'W$; 24.XI.2002; 250-330 m depth; MNHN • 9 dd; North coast of Raivavae, BENTHAUS Stn DW1943; $23^{\circ}49'S$, $147^{\circ}39'W$; 24.XI.2002; 950 m depth; MNHN • 8 dd; North of Raivavae, BENTHAUS Stn DW1941; $23^{\circ}49'S$, $147^{\circ}42'W$; 15.XI.2002; 290-620 m depth; MNHN • 7 dd; Marotiri, BENTHAUS Stn DW1884; $27^{\circ}54'S$, $143^{\circ}33'W$; 6.XI.2002; 570-620 m depth; MNHN

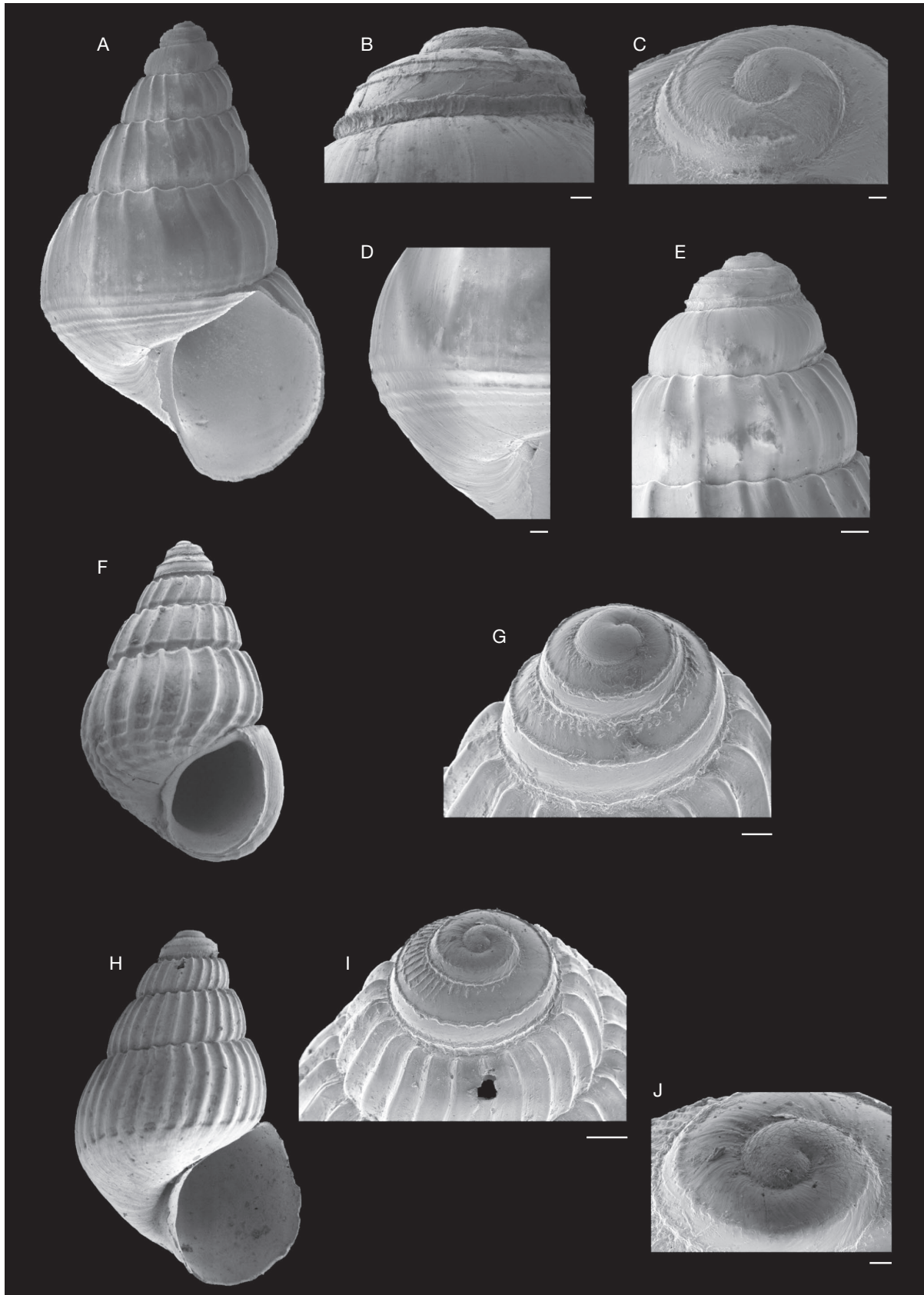


FIG. 5. — *Benthonella* spp. (SEM): **A-E**, *Benthonella boucheti* n. sp. holotype, MNHN-IM-2000-37666, Tarava Seamounts, height 4.32 mm: **A**, shell; **B, C**, detail of the protoconch microsculpture; **D**, detail of the teleoconch sculpture spiral; **E**, detail of the first whorls; **F, G**, *Benthonella basistriata* n. sp. holotype, MNHN-IM-2000-37668, Tuamotu, height 2.0 mm: **F**, shell; **G**, detail of the protoconch microsculpture; **H-J**, *Benthonella communis* n. sp., holotype, MNHN-IM-2000-37670, Tarava Seamounts: height 2.2 mm; **H**, shell; **I, J**, detail of the protoconch microsculpture. Scale bars: B, 40 μ m; C, J, 20 μ m; D, E, I, 100 μ m; G, 50 μ m.

• 50 dd; Tubuai, BENTHAUS Stn DW1962; 23°21'S, 149°33'W; 19.XI.2002; 470-800 m depth; MNHN • 17 dd; Tubuai, BENTHAUS Stn DW1955; 23°19'S, 149°26'W; 18.XI.2002; 750-850 m depth; MNHN • 69 dd; Tubuai, BENTHAUS Stn DW1961; 23°21'S, 149°34'W; 19.XI.2002; 470-800 m depth; MNHN • 1000+ dd; Banc Lotus, BENTHAUS Stn DW1951; 23°49'S, 147°53'W; 17.XI.2002; 206-450 m depth; MNHN • 118 dd; East of Rapa, BENTHAUS Stn DW1889; 27°37'S, 144°16'W; 7.XI.2002; 600-620 m depth; MNHN • 60 dd; Rimatara, BENTHAUS Stn DW2021; 22°37'S, 152°49'W; 25.XI.2002; 1200-1226 m depth; MNHN • 77 dd; Rimatara, BENTHAUS Stn DW2020; 22°37'S, 152°49'W; 25.XI.2002; 920-930 m depth; MNHN.

DISTRIBUTION AND SYMPATRY. — The species is at present known in the South Pacific Ocean from the Tarava Seamounts (Mont Ari'i Moana, Mont Punu Tipu), Society Islands (Maupiti, Moorea, Huahine, Tahiti, Bora Bora, Raiatea), Tuamotu (WS Kaukura, Kaukura, between Tikehau and Rangiroa) and Australes (Récif Neilson, Banc Mac Donald, Banc Président Thiers, Marotiri, Rimatara, Banc Arago, North coast of Rurutu, Tubuai, South coast of Rurutu, East coast of Rurutu, North coast of Raivavae, Banc Lotus, East coast of Rapa), with empty shells collected in 110-1226 m depth, and one live specimen collected at Australes, Banc Arago in 176-340 m depth (Fig. 25C). *Benthonella communis* n. sp. is sympatric with *Benthonella boucheti* n. sp. at the Australes (Récif Neilson, Banc Président Thiers, Marotiri, Rimatara, Banc Arago, Tubuai, South coast of Rurutu, East coast of Rurutu, North coast of Raivavae), Tuamotu (between Tichehau and Rangiroa); with *Benthonella basistriata* n. sp. at the Tuamotu (Kaukura), Society Islands (Huahine, Moorea); with *Benthonellania maestratii* n. sp. at the Australes (Récif Neilson, South coast of Rurutu); with *Benthonellania bouteti* n. sp. at the Tarava Seamounts (Mont Ari'i Moana, Mont Punu Tipu), Society Islands (Maupiti, Moorea, Huahine, Tahiti, Bora Bora, Raiatea), Tuamotu (WS Kaukura, Kaukura, entre Tichehau & Rangiroa), Australes (Récif Neilson, Banc Président Thiers, Rimatara, Banc Arago, North coast of Rurutu, South coast of Rurutu, East coast of Rurutu, Banc Lotus, East of Rapa, Tubuai); with *Benthonellania tarava* n. sp. at the Tarava Seamounts (Mont Ari'i Moana), Society Islands (Moorea), Tuamotu (WS Kaukura, Kaukura, between Tichehau and Rangiroa), Australes (Rimatara, South coast of Rurutu, East coast of Rimatara); with *Benthonellania tuamotu* n. sp. at the Tarava Seamounts (Mont Punu Tipu), Society Islands (Maupiti, Raiatea), Tuamotu (WS Kaukura, Kaukura, between Tikehau and Rangiroa), Australes (Rimatara, South coast of Rurutu, Récif Neilson); with *Benthonellania megan* n. sp. at the Australes (Rimatara); with *Benthonellania alis* n. sp. at the Tarava Seamounts (Mont Punu Taipu), Australes (East coast of Rurutu, South coast of Rurutu, Rimatara, Marotiri, Tubuai, Banc Président Thiers, East of Rapa), Society Islands (Bora Bora) (Table 2).

ETYMOLOGY. — For the large number of specimens found, (Latin) *communis* – common.

DESCRIPTION OF HOLOTYPE.

Shell (Figs 4A-C; 5H-J)

Small for the genus, height 2.2 mm, width 1.45 mm, height/width ratio 1.517, not very solid, ovate-conical.

Protoconch (Figs 4E, F; 5I, J; Table 1)

Multispiral, dome-shaped, of 2.3 whorls, height 0.30 mm, nucleus diameter 0.05 mm, first half whorl diameter 0.112 mm, maximum diameter 0.425 mm; protoconch I with sparse microtubercles and traces of spiral threads (embryonic shell in poor condition) (Fig. 5J), protoconch II with two fine and slightly wavy spiral cordlets, and a series of axial L-shaped subsutural rodlets between abapical cordlet and suture on the

last half protoconch whorl (Fig. 5I). Protoconch-teleoconch boundary indistinct, sinuous.

Teleoconch

Of 3.25 slightly convex whorls, suture canaliculate, crowned by small tubercles on tip of axial ribs. Height last whorl 1.575 mm. height/height last whorl ratio 1.396. Axial sculpture of 27 flexuose, opisthocline ribs on last whorl, as broad as the interspaces, abruptly interrupted before the base. Spiral sculpture absent. Microsculpture of only growth striae (Fig. 5I). Umbilical chink present. Aperture pyriform, small, height 1.0 mm, height/height aperture ratio 2.200, peristome continuous, varix weak; outer lip opisthocline, sharp, internally smooth. Columella arcuate simple.

Colour

Coloration of teleoconch white, outer lip pale orange, slightly darker adapically, protoconch pale whitish-orange.

Operculum and soft parts

Unknown.

VARIABILITY

Species not very variable (see Table 1 and Appendix 3). Minimum height 1.27 (from North coast of Rurutu, 250-302 m); maximum height 2.40 (from Mont Ari'i Moana, 614-664 m). Variable number of axial ribs: 16-27. In about 10% of specimens examined, the external lip presents a more or less conspicuous angulation (Fig. 4G). The axial ribs are thinner when they are more numerous.

REMARKS

The axial ribs abruptly stopping before the base (around the maximum diameter of the whorl), generate a sort of false spiral cord.

Benthonella olangoensis from the Philippines, is very similar to *Benthonella communis* n. sp. in the general shape, but is distinguished by the presence of 2-3 spiral cordlets vs absent in *B. communis* n. sp.

Benthonella brontodes Lozouet, 1990, from the upper Oligocene of the Aquitaine basin (France), is very similar to *B. communis* n. sp., but differs mainly in its different protoconch, narrower and lower (height 151 µm and maximum diameter 379 µm vs height 0.275-0.325 mm and maximum diameter 0.400-0.437 mm in *B. communis* n. sp.), and with different sculpture: with a fine median cordlet, doubled in the first half whorl vs two fine and slightly wavy spiral cordlets, and a series of axial L-shaped subsutural rodlets between abapical cordlet and suture on the last half protoconch whorl (Fig. 10I) in *B. communis* n. sp. (see Lozouet 1990: 325, figs 24-25).

Genus *Benthonellania* Lozouet, 1990

Benthonellania Lozouet, 1990: 314.

TYPE SPECIES. — *Benthonellania gofasi* Lozouet, 1990 by original designation.

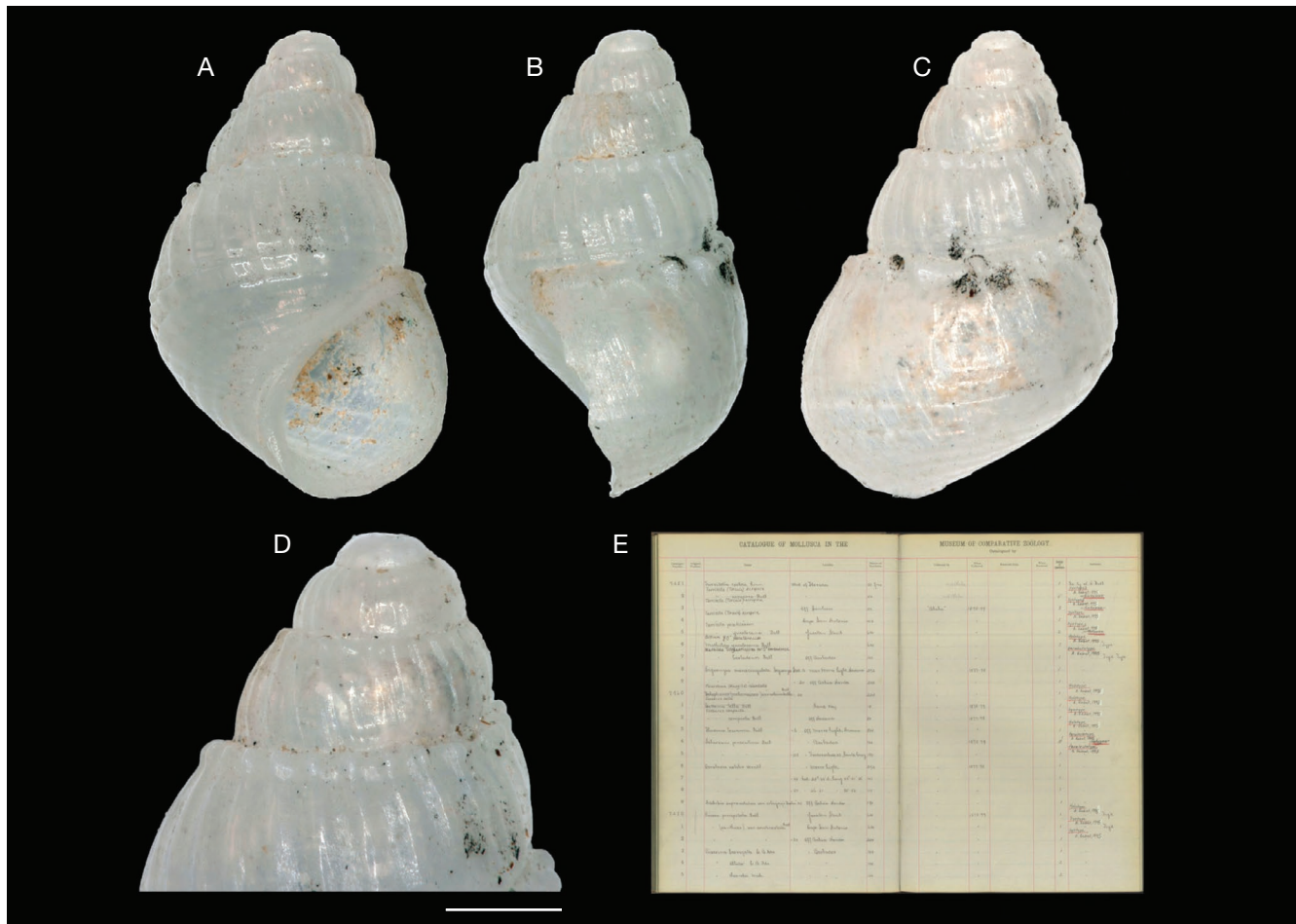


FIG. 6. — *Benthonellania precipitata* (Dall, 1889) n. comb.: A-D, holotype (MCZ-7470), height 3.92 mm; D, detail of the first whorls; E, relevant page of the Catalogue of Mollusca in the Museum of Comparative Zoology (photo by Alana Rivera). Scale bar: D, 0.25 mm.

DIAGNOSIS. — Shell of small to medium size for the family, with transparent, colourless teleoconch; axial sculpture present, spiral cords on the whole teleoconch or only on the base or rarely absent; protoconch slender with spiral cordlets, linear or zig-zag, and usually coloured when multispiral, with a low spire, smooth or with microgranules and colourless when paucispiral. Pallial tentacles and eyes present and posterior gland well developed.

REMARKS

Benthonellania includes species with shell small to medium size, vitreous, colourless and with protoconch generally slender, coloured, with diversified sculpture, or smooth and colourless. For the soft parts see Lozouet (1990: 314); Gofas (1999: 95) (based on *Benthonellania gofasi* Lozouet, 1990). *Benthonellania* includes a group of species living from the lower continental shelf to bathyal depths. The type species is the Recent Eastern Atlantic *B. gofasi*, from Sénégal. Species fitting the shell features of *Benthonellania* are known in the Pleistocene of Nigeria and the Upper Miocene of Angola, and can be traced back to the Upper Oligocene of France (Lozouet 1990: 313; 2014: 21). The genus as currently conceived, has a very wide geographic range, with 15 recognised species occurring in the Atlantic (MolluscaBase 2021c) and one (*Rissoa aequatorialis* Thiele, 1925: 84, pl. 6, fig. 23) from the Indian

Ocean, dubitatively suggested to belong to *Benthonellania* by Lozouet (1990: 326), or to *Pusillina* (*Haurakia*) by Ponder (1985: 30, as synonym of *Rissoa africana* Thiele, 1925).

Furthermore, several deep-water taxa originally introduced under other genera, probably belong to *Benthonellania*. For instance, the drawing of the holotype of *Rissoa precipitata* Dall, 1889, from the Yucatan Strait, 1225 m depth (670 fms; more likely 1170 m [640 fms] as indicated in the MCZ Catalogue, and by Dall himself for other species from the Yucatan Strait), reported by Romer & Moore (1988: 133, fig. 5), does not match Dall's original description and drawing (Dall 1889: 279, pl. XIX, fig. 1) nor the holotype (MCZ-Mala-7470) (Figs 6A-D). It is very similar to e.g. *Benthonellania agastachys* Bouchet & Warén, 1993, and we accordingly propose *Benthonellania precipitata* (Dall, 1889) as a new combination for *Rissoa precipitata* Dall, 1889.

Alvania colombiana Romer & Moore, 1988, from the western Atlantic Ocean (Colombia, Florida, Puerto Rico, Brazil, 45-261 m depth) was originally compared with some species currently in *Benthonellania* (Romer & Moore 1988: 131-133; figs 1, 2). It was kept in *Alvania* by Absalão & Santos (2004: 338) and Da Silva (2012: 48), but a placement in *Benthonellania* was suggested by Moolenbeek & Faber (1991:

51) and Oliver & Rolán (2017: 48), a view on which we agree. Oliver & Rolán (2017: 50) synthetically redescribed the apex as “[...] smooth multispiral protoconch except for the presence of a conspicuous suprasutural spiral cord which tends to be undulating in zig-zag”, and we add that there is also a subsutural series of microgranules. Based on all these features (including also the light brown protoconch and the sculpture of the teleoconch), we, thus, propose *Benthonellania colombiana* (Romer & Moore, 1988) as a new combination for *Alvania colombiana* Romer & Moore, 1988.

Rissoa profundior Hedley, 1907, was described from 33 miles east of Sydney (c. 1458 m depth), and is currently classified in the genus *Haurakia* after Cotton (1944: 294). *Rissoa profundior* is very similar to *Benthonellania charope* (Melvill & Standen, 1901) and *Benthonellania antepelagica* Lozouet, 1990, in its very scalariform profile, robust crown and deep subsutural groove, robust axial sculpture and weaker spiral one more evident on the base (Hedley 1907: 358, pl. LXVII, fig. 15; Lozouet 1990: 319). Thus, we propose *Benthonellania profundior* (Hedley, 1907) as a new combination for *Rissoa profundior* Hedley, 1907.

Rissoa sumatrana Thiele, 1925 (Thiele 1925: 84, pl. 6, fig. 25), from Siberut Island (Indonesia, Indian Ocean) 750 m depth, has the typical slender profile of *Benthonellania* and the crown of small tubercles at tip of axial. Thus, we propose *Benthonellania sumatrana* (Thiele, 1925) as a new combination for *Rissoa sumatrana* Thiele, 1925.

Additionally, we propose to move *Rissoa hertzogi* Thiele, 1925, *Rissoa africana* Thiele, 1925 and *R. aequatorialis* Thiele, 1925 into *Benthonellania* (three new combinations, see below). Within the type material of *Rissoa africana* Thiele, 1925 (see below), 199 shells from East Africa (off Somalia) clearly represented a distinct undescribed species, that we describe here as *Benthonellania thielei* n. sp.

Alvania waisiuensis Beets, 1942 (MolluscaBase 2021d), from the Upper Oligocene of Indonesia, has a paucispiral protoconch (Lozouet 1990: 319), and a teleoconch with ornamentation and profile resembling a typical *Benthonellania*. However, the poor original description and iconography alone (Beets 1942: 269-270; pl. 27, figs 41-42) are not sufficient for a conclusive classification (Lozouet 1990: 319). Therefore, pending examination of the types and/or new material, we refrain from proposing a formal new combination for this species.

Hasegawa (2005) reported an undescribed species of *Benthonellania* (“*Benthonellania* sp.” – Hasegawa 2005: 149, fig. 5J) from Japan.

Nine Recent species (out of 27), *Benthonellania fayalensis* (R. B. Watson, 1886), *B. oligostigma* Bouchet & Warén, 1993, *B. agastachys* Bouchet & Warén, 1993, *B. profundior* n. comb., *B. charope*, *B. hertzogi* Thiele, 1925 n. comb., *B. thielei* n. sp. and *B. africana* n. comb., and the fossil *B. antepelagica* have a paucispiral protoconch with weak or no sculpture. Among the species with multispiral protoconch, several show spiral zig-zag cordlets, a pattern that is not unusual in various – sometimes unrelated – rissoid lineages, as already noted by Oliver & Rolán (2017).

We have found seven undescribed species of *Benthonellania* in French Polynesia: *Benthonellania bouteti* n. sp., *Benthonel-*

lania alis n. sp., *Benthonellania tarava* n. sp., *Benthonellania megan* n. sp., *Benthonellania tuamotu* n. sp., *Benthonellania lozoueti* n. sp. and *Benthonellania maestratii* n. sp. and one in the Western Indian Ocean *Benthonellania thielei* n. sp.

Benthonellania hertzogi (Thiele, 1925) n. comb.
(Figs 7A-J; 9A, B; 13A; 26D; Table 1)

Rissoa hertzogi Thiele, 1925: 82, pl. 6, fig. 15.

TYPE MATERIAL. — Syntypes. South Africa • 2 dd; Agulhas-Bank, Valdivia Stn 109; 35°19'S, 20°12'E; 126 m depth; ZMB/Moll. no. 64981 • 1 dd; Agulhas-Bank, Valdivia Stn 106; 35°26.8'S, 20°56.2'E; ZMB/Moll. no. 64981.

DISTRIBUTION AND SYMPATRY. — *Benthonellania hertzogi* n. comb. is known so far only from south of South Africa (Agulhas-Bank) (Fig. 13A).

DESCRIPTION [BASED ON THE TYPE MATERIAL]

Shell (Figs 7A-F; 9A)

Small for the genus, height 2.47-2.85 mm width 1.75-1.95 mm, height/width ratio 1.411-1.461, rather solid, ovate-conical.

Protoconch (Figs 7I-J; 9B)

Dome-shaped, paucispiral, of 1.25 whorls, height 0.375-0.400 mm, nucleus diameter 0.200-0.212 mm, first half whorl diameter 0.350-0.362 mm, maximum diameter 0.500 mm, glossy, smooth. Protoconch-teleoconch boundary distinct, slightly prosocline and marked by a slight thickening.

Teleoconch

Of 2.75-3.1 very slightly convex whorls, suture subcanaliculate, crowned by weak thickening at tips of axial ribs, enhanced by a slight subsutural depression. Height last whorl 1.8-2.07 mm. height/height last whorl ratio 1.372-1.377. Axial sculpture of 24-26 ribs on last whorl, slightly narrower than the interspaces, continuing partly on the base, prosocline, slightly curved on first whorls, markedly curved on last whorl. Spiral sculpture of 4-5 cordlets on last whorl, well spaced, slightly bulging at intersection with axial ribs, 1 above the aperture, 1 on the suture line and 2-3 on the base. Microsculpture of a very fine subsutural thread on first two teleoconch whorls (Fig. 9B) and weak growth striae on whole surface. Umbilical chink narrow. Aperture pyriform, height 1.25-1.4 mm, height/height aperture ratio 1.976-2.036, peristome continuous, varix absent. Lip thin, orthocline or slightly prosocline, flexuose, smooth on the inside. Columella arcuate, simple.

Colour

Coloration of teleoconch and protoconch translucent white.

Operculum and soft parts

Unknown.

VARIABILITY

The variability of shell morphology is low in the few specimens examined (See Table 1 and Appendix 4).

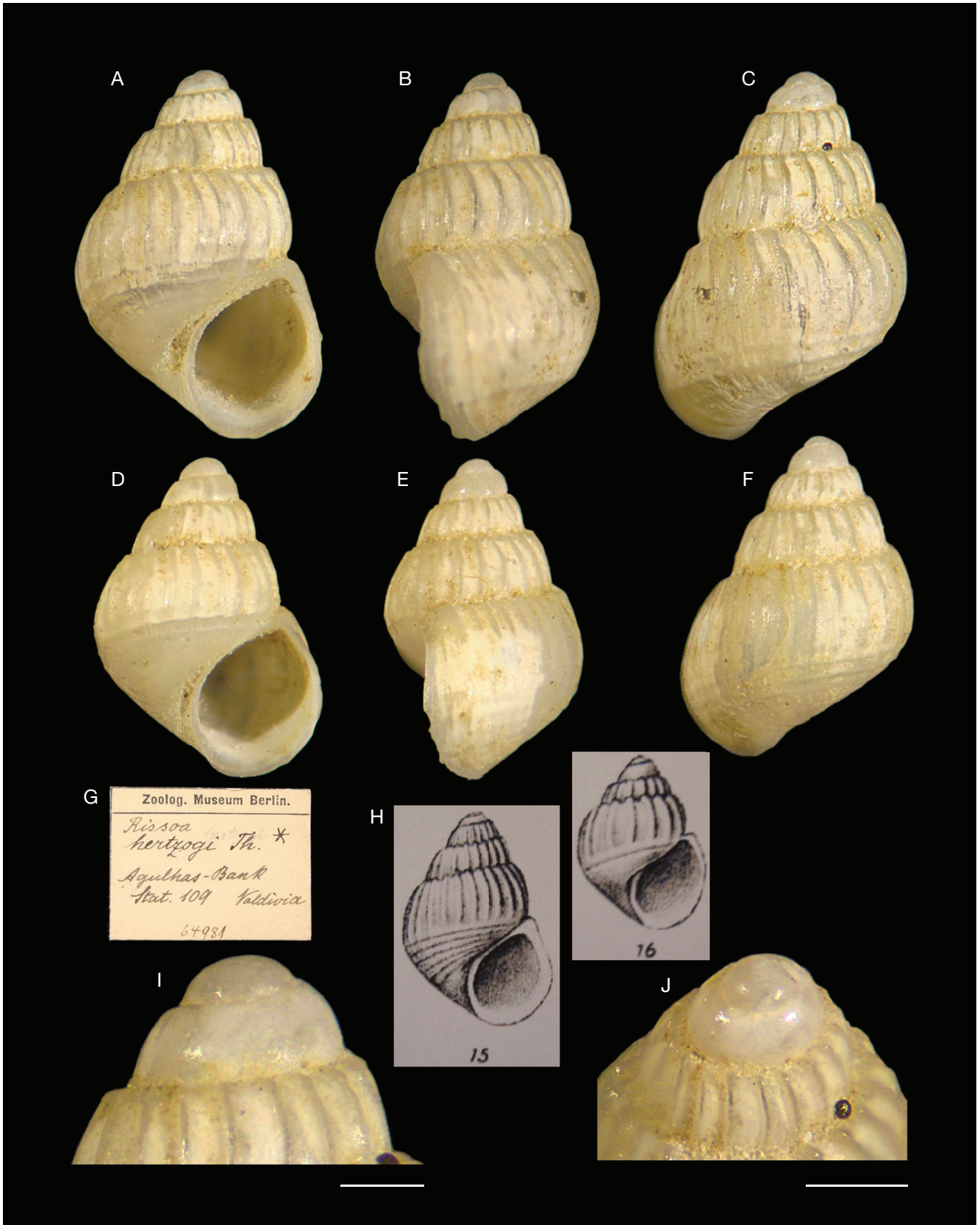


FIG. 7. — *Benthonellania hertzogi* (Thiele, 1925), syntypes, Valdivia Strn 109 (ZMB-64981): **A-C**, syntype, height 2.85 mm (ZMB-64981); **D-F**, syntype, height 2.47 mm (ZMB-64981); **G**, original label; **H**, original drawings (Thiele 1925, 82, pl. 6, fig. 15, 16); **I, J**, syntype (**A-C**), detail of the first whorls. Scale bars: **I, J**: 0.25 mm.

REMARKS

The study of the type material showed that *Rissoa hertzogi* Thiele, 1925 (Figs 7A-J; 9A, B) and *Rissoa africana* Thiele, 1925 (Figs 8A-N; 9C, D) belong to this genus, with their paucispiral protoconchs devoid of spiral sculpture. Both species are very similar to e.g. *B. agastachys*, *B. fayalensis* and *B. oligostigma* with their slender shell and the crown of adapical thickening of axial ribs, enhanced by the subsutural depression. We proposed thus, *Benthonellania hertzogi* (Thiele, 1925) n. comb. and *Benthonellania africana* (Thiele, 1925) n. comb. as new combinations for *Rissoa hertzogi* Thiele, 1925 and *Rissoa africana* Thiele, 1925, respectively.

Benthonellania hertzogi n. comb. differs from *B. basistriata* n. sp. paucispiral vs multispiral protoconch, in its less canalculated sutures, its tight umbilical chink, absent in *B. basistriata*, more numerous axial ribs (24-26 vs 14-20 in *B. basistriata*).

See under *Benthonellania africana* n. comb. and *B. thielei* n. sp. for diagnostic comparison.

Benthonellania africana (Thiele, 1925) n. comb.
(Figs 8A-N; 9C, D; 13A; 26G; Table 1)

Rissoa africana Thiele, 1925: 83, pl. 6, figs 20-22.

TYPE MATERIAL. — **Lectotype**. Somalia • dd (height 3.85 mm, width 2.15 mm, here designated, Figs 11A-C; 13A, B); Valdivia Stn 251; 1°40.6'S, 41°47.1'E; ZMB/Moll. no. 64955a.

Paralectotypes • 223 dd (comprising 34 shells of *Benthonellania africana* n. comb. and 199 shells of *Benthonellania thielei* n. sp.); same locality data as lectotype; ZMB/Moll. no. 64955b.

There might be also material from Valdivia, Stn 245; 5°27.9'S, 39°18.8'E; 463 m depth (Zanzibar) that we have not examined.

DISTRIBUTION AND SYMPATRY. — *Benthonellania africana* n. comb. is known from East Africa (off Somalia and possibly Zanzibar) 693 m depth. *Benthonellania africana* n. comb. is sympatric with *Benthonellania thielei* n. sp. at its type locality, off Somalia, and possibly with *Benthonellania aequistriata* at Zanzibar (fide Thiele) (Fig. 13).

DESCRIPTION OF LECTOTYPE

Shell (Figs 8A-C; 9C, D)

Large for the genus, height 3.85 mm width 2.15 mm, height/width ratio 1.790, rather solid, ovate-conical.

Protoconch (Figs 8J, K; 9D)

Dome-shaped, paucispiral, of 1.4 whorls, height 0.375 mm, nucleus diameter 0.200 mm, first half whorl diameter 0.362 mm, maximum diameter 0.525 mm, glossy, smooth, except for a faint and confused spiral sculpture on the nucleus (Fig. 9D). Protoconch-teleoconch boundary barely visible.

Teleoconch

Of 4.1 very slightly convex whorls, suture canalculated, crowned by small tubercles at tips of axial ribs, highlighted by a slight subsutural depression. Height last whorl 2.50 mm, height/height last whorl ratio 1.540. Axial sculpture of 9 ribs on last whorl, as broad as the interspaces, prosocline and slightly curved, curvature more pronounced on last whorl, gradually vanishing at the base; last half whorl progressively devoid of

axial sculpture. Spiral sculpture of 4 very weak cordlets on last whorl above the aperture and on the suture line, the uppermost suprasutural visible on all whorls, base smooth (Fig. 8N). Microsculpture of only growth striae. Umbilical chink conspicuous. Aperture pyriform, large, height 1.55 mm, height/height aperture ratio 2.483, peristome continuous, varix absent. Thin lip with prosocline inclination. Columella arcuate, simple.

Colour

Coloration of teleoconch and protoconch translucent, white.

Operculum

Thin, light yellow with an eccentric nucleus.

Soft parts

Unknown.

VARIABILITY

Species not very variable (See Table 1 and Appendix 5). It reaches 4 mm in height and 2.35 mm in width; height/width ratio 1.574-1.860; number of axial ribs on the last whorl: 8-10. Maximum diameter of the protoconch 0.575 mm.

REMARKS

Rissoa africana Thiele, 1925 is currently classified in *Haurakia* based on Ponder (1985: 30). Ponder (1985) also considered *Rissoa africana* and *R. aequatorialis* as synonyms (selecting *Pusillina* (*Haurakia*) *africana* as senior one, as first reviser). This is clearly a member of *Benthonellania*, with its shell with canalculated suture, crowned by small tubercles at the tips of axial ribs, enhanced by a slight subsutural depression. We accordingly propose *Benthonellania africana* (Thiele, 1925) n. comb. as a new combination for *Rissoa africana* Thiele, 1925. *Cithna africana* Bartsch, 1915 (taxon inquirendum: MolluscaBase 2021e) from South Africa, has a small shell (height 0.7 mm, width 0.7 mm), devoid of sculpture, and cannot be classified either in *Benthonella* or in *Benthonellania* (see Bartsch 1915: 120, pl. 21, fig. 5).

The examined type material of *Rissoa africana*, comprises two distinct species: one (corresponding to Thiele 1925: fig. 20) has a rather thick shell, more or less slender profile, spiral sculpture of 3-4 very weak cordlets on the last whorl above the aperture and on the suture line and a crown of small tubercles at tip of axial ribs, paucispiral protoconch smooth, except for a faint and confused spiral sculpture on the nucleus; 199 shells (corresponding to Thiele 1925: figs 21, 22) belong to a distinct species that we describe below as *B. thielei* n. sp. To stabilize the use of the name, the lectotype of *Rissoa africana* Thiele, 1925 is herein designated on a specimen of the first form.

Benthonellania africana n. comb. differs from *B. hertzogi* n. comb. by its higher height/width ratio (1.574-1.860 vs 1.250-1.400 in *B. hertzogi* n. comb.), the lower axial ribs in *B. hertzogi* n. comb. and the presence of a very fine subsutural thread on first two teleoconch whorls in *B. hertzogi* n. comb., absent in *B. africana* n. comb.

See under, *Benthonellania thielei* n. sp., *Benthonellania aequatorialis* n. comb. and *Benthonellania alis* n. sp. for diagnostic comparison.

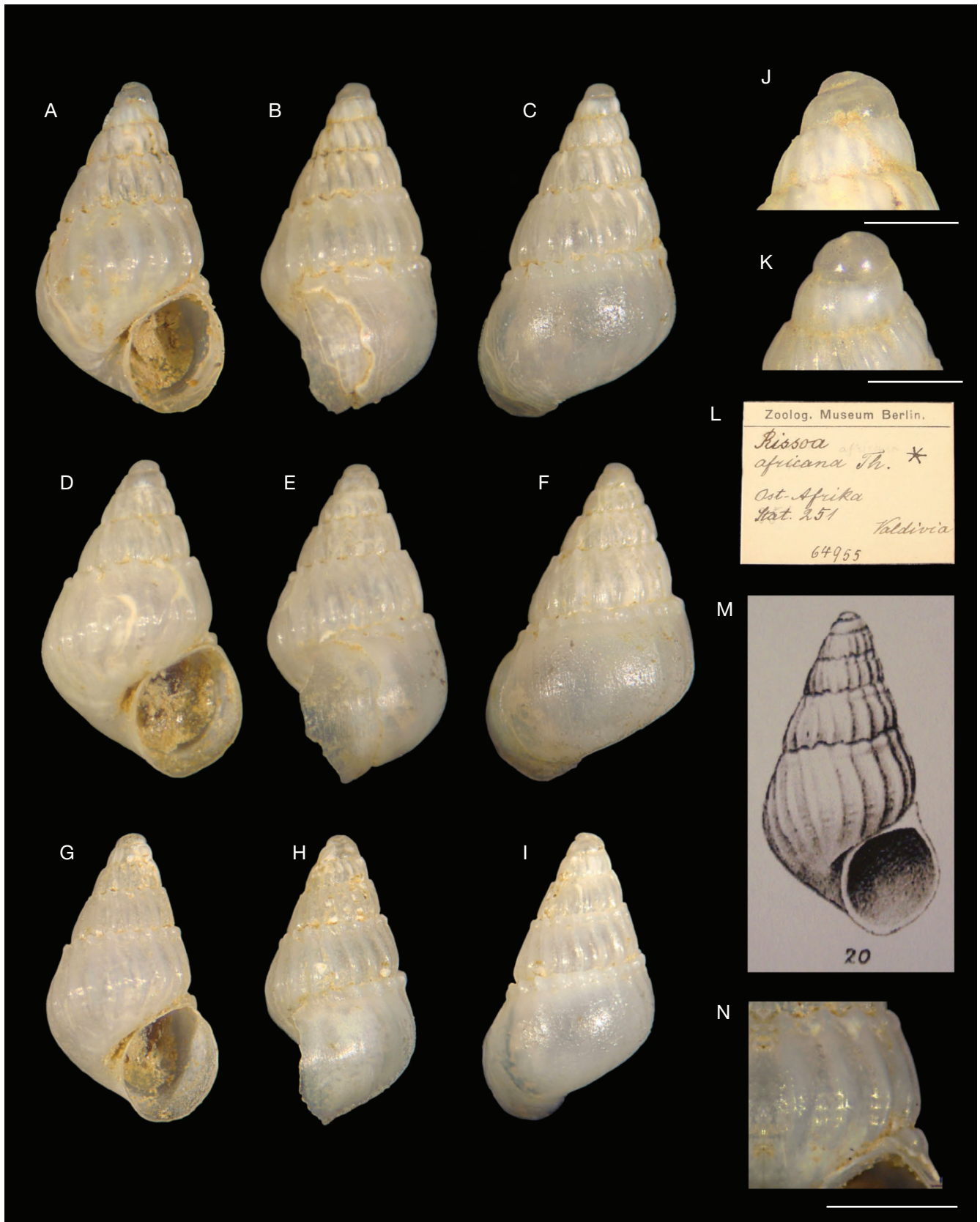


FIG. 8. — *Benthonellania africana* (Thiele, 1925) n. comb.: **A-C**, lectotype, height 3.85 mm; **D-F**, paralectotype height 3.7 mm; **G-I**, paralectotype, height 3.35 mm; Valdivia Stn 251, ZMB-64955; **J, K**, paralectotype, detail of the first whorls; **L**, original label; **M**, original drawing (Thiele 1925, 83, pl. 6, fig. 20); **N**, paralectotype, detail of the teleoconch sculpture spiral on the last whorl. Valdivia Stn 251, ZMB-64955. Scale bars: J, K, N, 0.50 mm.

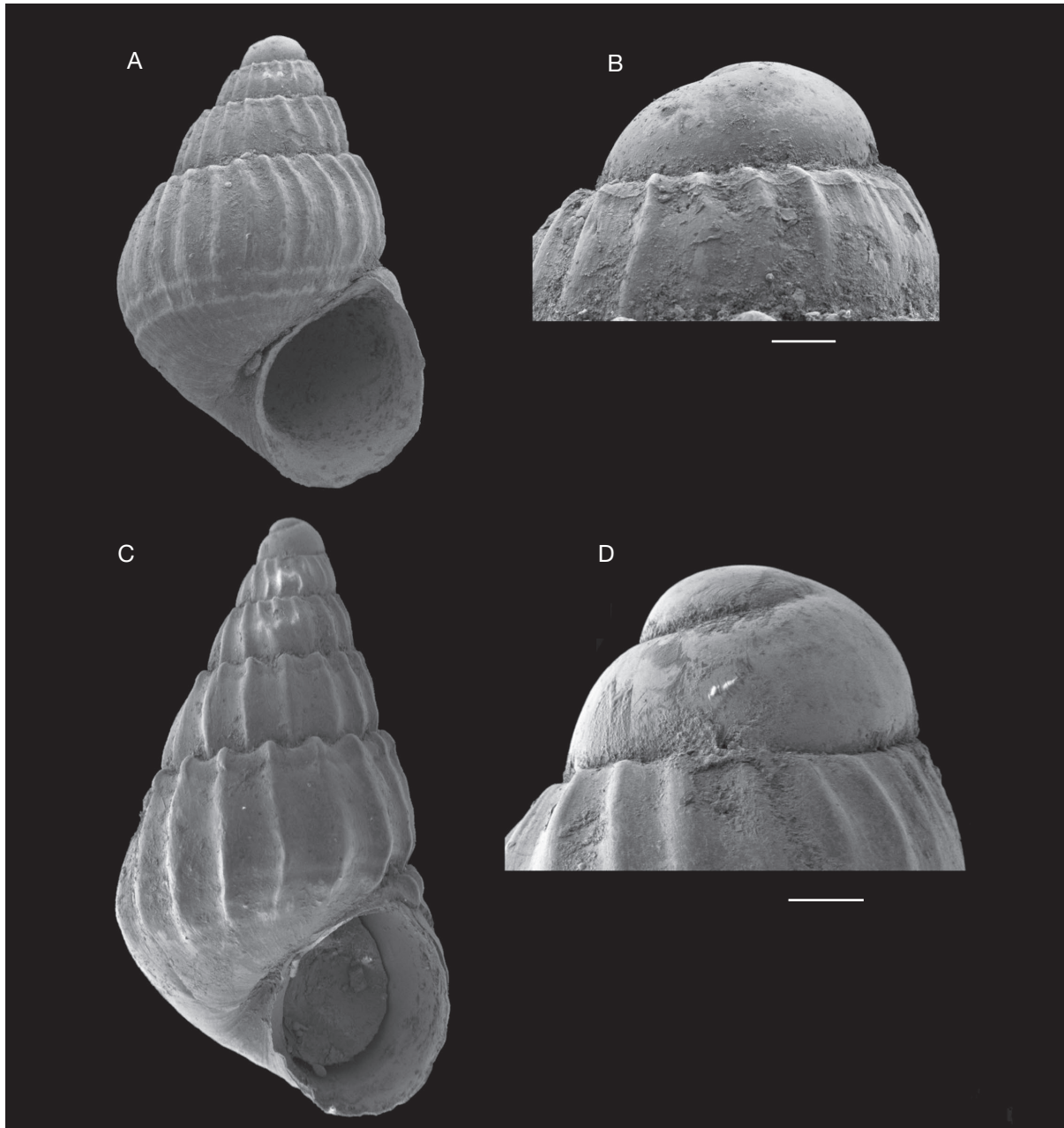


FIG. 9. — *Benthonellania* spp. (SEM): **A, B**, *Benthonellania hertzogi* (Thiele, 1925), syntype, Agulhas-Bank (south of South Africa), height 2.85 mm, ZMB/Moll. no. 64981, shell (**A**), detail of the protoconch (**B**); **C, D**, *Benthonella africana* (Thiele, 1925) n. comb., lectotype, East Africa (off Somalia), height 3.85 mm, ZMB/Moll. No. 64955a, shell (**C**), detail of the protoconch (**D**). Scale bars: B, D, 100 μ m.

Benthonellania thielei n. sp.
(Figs 10A-N; 12A-C; 13A; 26E; Table 1)

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TYPE MATERIAL. — **Holotype.** East Africa • dd (height 3.05 mm, width 1.92 mm, Figs 10A-C, 12A-C); off southern Somalia, Valdivia Stn 251; 1°40.6'S, 41°47.1'E; 693 m depth; ZMB/Moll. no. 64955a. **Paratypes.** East Africa • 198 dd (Fig. 10D-L); same locality data as holotype; ZMB/Moll. no. 64955b.

TYPE LOCALITY. — East Africa, off southern Somalia, Valdivia Stn 251; 1°40.6'S, 41°47.1'E; 693 m depth.

DISTRIBUTION AND SYMPATRY. — *Benthonellania thielei* n. sp. is known from the type locality, off southern Somalia (Indian Ocean), where it is sympatric with *Benthonellania africana* (Thiele, 1925) n. comb. (Fig. 13).

ETYMOLOGY. — Named after Karl Hermann Johannes Thiele, German author of “Gastropoden der Deutschen Tiefsee-Expedition ‘Valdivia’ 1898-1899”.

DESCRIPTION OF HOLOTYPE

Shell (Figs 10A-C; 12A)

Medium for the genus, height 3.05 mm width 1.92 mm, height/width ratio 1588, rather solid, ovate-conical.

Protoconch (Figs 10J-K; 12B)

Dome-shaped, paucispiral, of 1.1 whorls, height 0.337 mm, nucleus diameter 0.187 mm, first half whorl diameter 0.350 mm, maximum diameter 0.475 mm, glossy, smooth, except for a faint and confused spiral sculpture on the nucleus (Fig. 12B). Protoconch-teleoconch boundary distinct, slightly prosocline and marked by a fine thickening.

Teleoconch

Of 3.5 very little convex whorls, suture canaliculate, subscalariform outline, crowned by small tubercles at tips of axial ribs, highlighted by a slight subsutural depression. Height last whorl 2.2 mm, height/height last whorl ratio 1.386. Axial sculpture of 20 ribs on last whorl, slightly narrower than the interspaces, continuing on the base beyond the periphery, prosocline and slightly curved, curvature more pronounced on last whorl. Last 0.25 whorl progressively devoid of axials. Spiral sculpture of 6 cordlets on last whorl, narrower than their interspaces, slightly bulging at intersection with axial ribs, 1 above the aperture, 1 on the suture line and 4 on the base (Fig. 10L). Microsculpture of growth striae (Fig. 12C). Umbilical chink absent. Aperture pyriform, height 1.35 mm, height/height aperture ratio 2.259, peristome continuous, varix absent. Lip thin, orthocline, flexuose, smooth on the inside. Columella arcuate, simple.

Colour

Coloration of teleoconch and protoconch translucent white.

Operculum

Thin, light yellow with an eccentric nucleus.

Soft parts

Unknown.

VARIABILITY

The shell can attain a height of 3.4 mm and a width of 2.05 mm (height/width ratio 1.401-1.700; height/height last whorl ratio 1.275-1.454); with up to 3.6 whorls; number of axial ribs 13-20; spiral striae on the last whorl 4-6; height/height aperture ratio 2.125-2.461. A very narrow umbilical chink may be present. Protoconch: whorls number 1.1-1.25; height 0.300-0.350 mm; nucleus diameter 0.187-0.212 mm; diameter of the first half whorl 0.337-0.350 mm; maximum diameter 0.400-0.475 (See Table 1 and Appendix 6).

REMARKS

Thiele mixed in the type material of his *Rissoa africana*, two species: one that we have placed in *Benthonellania* (see above *B. africana* n. comb.), and another that we describe here as *Benthonellania thielei* n. sp. He realised that there was a striking variability within that material but explicitly stated that he believed that “these differences [between his fig. 20 (= *R. africana* s.s.) and fig. 21 (= *B. thielei*)] fall within the limits of a single species” (Thiele 1925: 83). Then, he stated: “Only for one shell that I show in figure 22 [again a *B. thielei*] I have some doubts, and would like to call it a variety,

with the name *pluricostata*”. Eventually, he stated again that “the shells [of *africana*] show variation in the number of axials”. Finally, Thiele did not separate the specimen of his figure 22 (the single specimen upon which he based *Rissoa africana* var. *pluricostata*) and we have been unable to trace it among the 199 ‘*pluricostata*’ shells. We have pondered on the possibility of using the name ‘*pluricostata*’, but this is a paradigmatic case of an Author who introduced explicitly a variety, and “the content of the work unambiguously reveals that the name was proposed for an infrasubspecific entity”: ICZN, 1999: Art. 45.6.1).

Benthonellania thielei n. sp. differs from *B. africana* (Thiele, 1925) n. comb. (among which it was mixed in Thiele’s collection, and which we classify in *Benthonellania*, see below) in its less slender shell, smaller size (height 3.4 mm vs height 4 mm in *B. africana* n. comb.), more numerous axial ribs on the last whorl (13-20 vs 8-10 in *B. africana* n. comb.), spiral cordlets more numerous and arranged differently (*Benthonellania thielei* n. sp.: 4-6 well spaced, slightly bulging at the intersection with the axial ribs, 1 above the aperture, 1 on the suture line and 2-4 on the base; *Benthonellania africana* n. comb.: 3-4 very weak cordlets on the last whorl above the aperture and on the suture line, the uppermost suprasutural visible on all whorls, base smooth); umbilical fissure closed or barely noticeable vs open in *B. africana* n. comb.. Lower protoconch 0.300-0.350 mm vs 0.375-0.450 mm in *B. africana* n. comb., lower maximum diameter 0.400-0.475 mm vs 0.525-0.575 mm in *B. africana* n. comb., fewer whorls 1.10-1.25 vs 1.25-1.40 mm in *B. africana* n. comb.

B. thielei n. sp. differs from *B. hertzogi* (Thiele, 1925) n. comb. in the more numerous whorls (3.5-3.6 vs 2.75-3.1 in *B. hertzogi* n. comb.), fewer axial ribs on the last whorl (13-20 vs 24-26 in *B. hertzogi* n. comb.), more evident subsutural crown of whorls, yielding a more scalariform profile, due to the absence of the fine subsutural cordlet on the first teleoconch whorls, which is present in *B. hertzogi* n. comb., the protoconch lower (height 0.300-0.350 mm vs 0.375-0.400 mm in *B. hertzogi* n. comb.) and smaller (maximum diameter 0.400-0.475 mm vs 0.500 mm in *B. hertzogi* n. comb.).

B. thielei n. sp. is also similar in the general shell outline to the species named ‘*Alvania* sp. 2’ by Hasegawa (2005: 149, fig. 5I), differing for its smaller size (height 3.4 mm vs height 4.5 mm in ‘*Alvania* sp. 2’) and the less slender shell. ‘*Alvania* sp. 2’, as well as the similar ‘*Alvania* sp. (s.s.)’ figured by Hasegawa (2001: 163, pl. 2, fig. F, G), represent quite probably two undescribed species.

Benthonellania thielei n. sp. differs from *Benthonella basistriata* n. sp. in its larger size (height 2.97-4.40 mm, width 1.82-2.05 mm vs height 1.95-2.60 mm, width 1.30-1.62 mm in *B. basistriata* n. sp.); absence of varix vs presence of varix in *B. basistriata* n. sp.; protoconch paucispiral, dome-shaped, glossy, smooth, with fewer whorls 1.10-1.25, vs multispiral, dome-shaped, of 2.3-2.9 whorls, protoconch I with 5 spiral threads, interspaces covered by microtubercles, and protoconch II with 2 fine spiral cordlets, with irregularly set microtubercles on the subsutural area in *B. basistriata* n. sp.

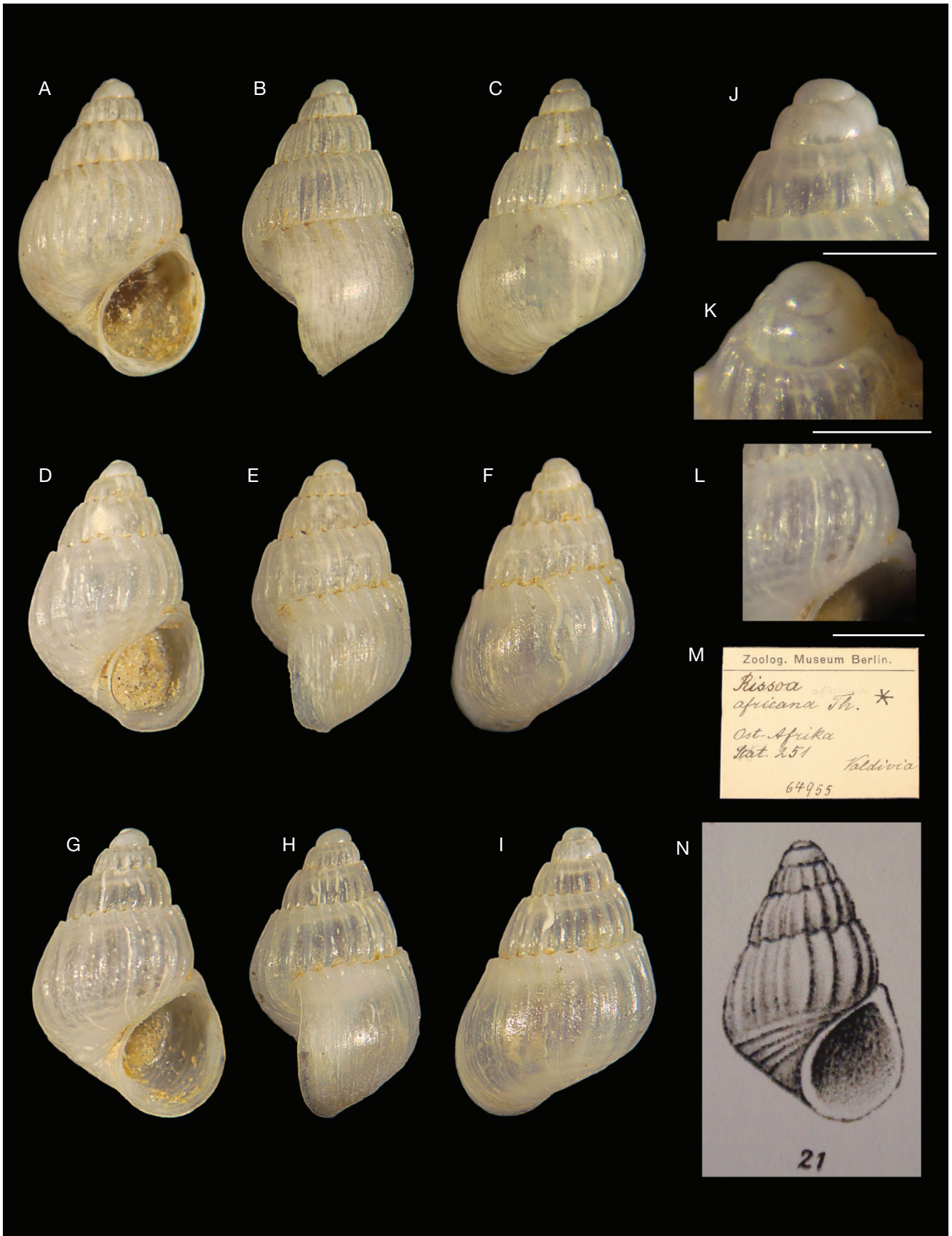


FIG. 10. — *Benthonellania thielei* n. sp., Valdivia Stn 251, East Africa, 693 m depth: **A-C**, holotype, height 3.05 mm width 1.92 mm, ZMB/Moll. No. 64955a; **D-F**, paratype, height 2.8 mm, ZMB/Moll. No. 64955b; **G-L**, paratype, height 2.97 mm, ZMB/Moll. No. 64955b; **J, K**, detail of the first whorls, **L**, detail of the spiral sculpture on the last teleoconch whorl; **M**, original label; **N**, original drawing (Thiele 1925, 83, pl. 6, fig. 21). Scale bars: J, K, L, 0.50 mm.

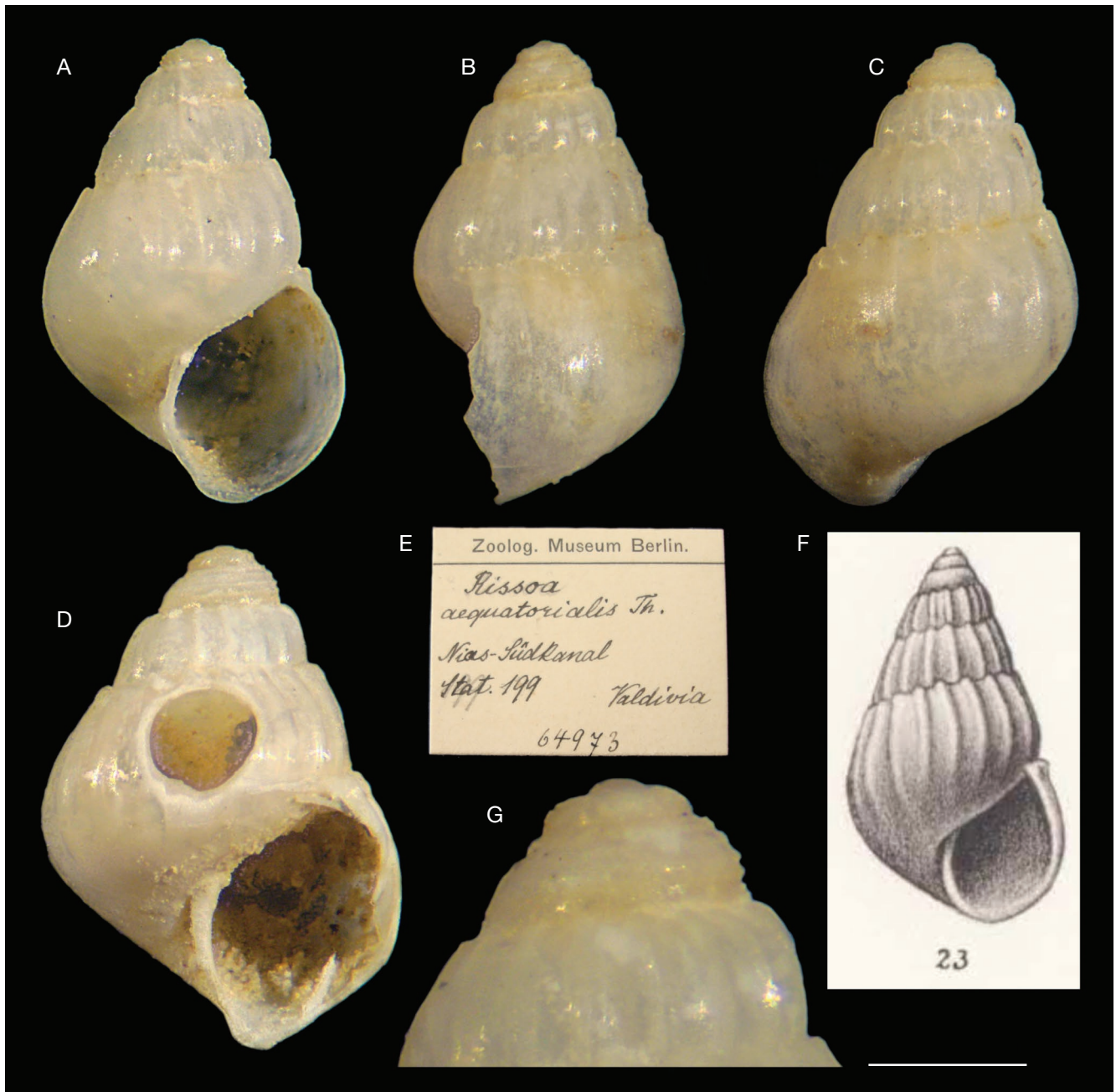


FIG. 11. — *Benthonellania aequatorialis* (Thiele, 1925) n. comb., syntypes: **A-C**, height 1.8 mm; **D**, height 1.95 mm; **E**, original label; **F**, original drawing (Thiele 1925, 84, pl. 6, fig. 23); **G**, syntype, detail of the first whorls; Valdivia Stn 199, ZMB-64973. Scale bar: G, 0.25 mm.

Benthonellania aequatorialis (Thiele, 1925) n. comb.
(Figs 11A-G; 12D, E; 13B; 26H; Table 1)

Rissoa aequatorialis Thiele, 1925: 84, pl. 6, fig. 23.

TYPE MATERIAL. — **Syntypes**. **Indonesia** • 2 dd; Nias-Sudkanal (Sumatra), Valdivia Stn 199; 0°15.5'S, 98°4'E; 470 m depth; ZMB/Moll. no. 64973.

DISTRIBUTION. — The species is known with certainty from Sumatra (Indonesia) (Fig. 13); Thiele (1925) reported it also from the Zanzibar Canal (Tanzania) but we could not examine the relevant material.

DESCRIPTION BASED ON THE EXAMINED TYPES (in parentheses data from the original description)

Shell (Figs 11A-G; 12C, D)

Of medium for the genus, height 1.8-1.95 (3.3) mm width 1.35-1.37 (1.8) mm, height/width ratio 1.333-1.423 (1.833), rather solid, ovate-conical.

Protoconch (Figs 11G; 12E)

Flat, multispiral, of 2-2.2 (2) whorls, height 0.275 mm, nucleus diameter 0.075 mm, first half whorl diameter 0.137-0.150 mm, maximum diameter 0.400-0.450 mm, 5 equi-

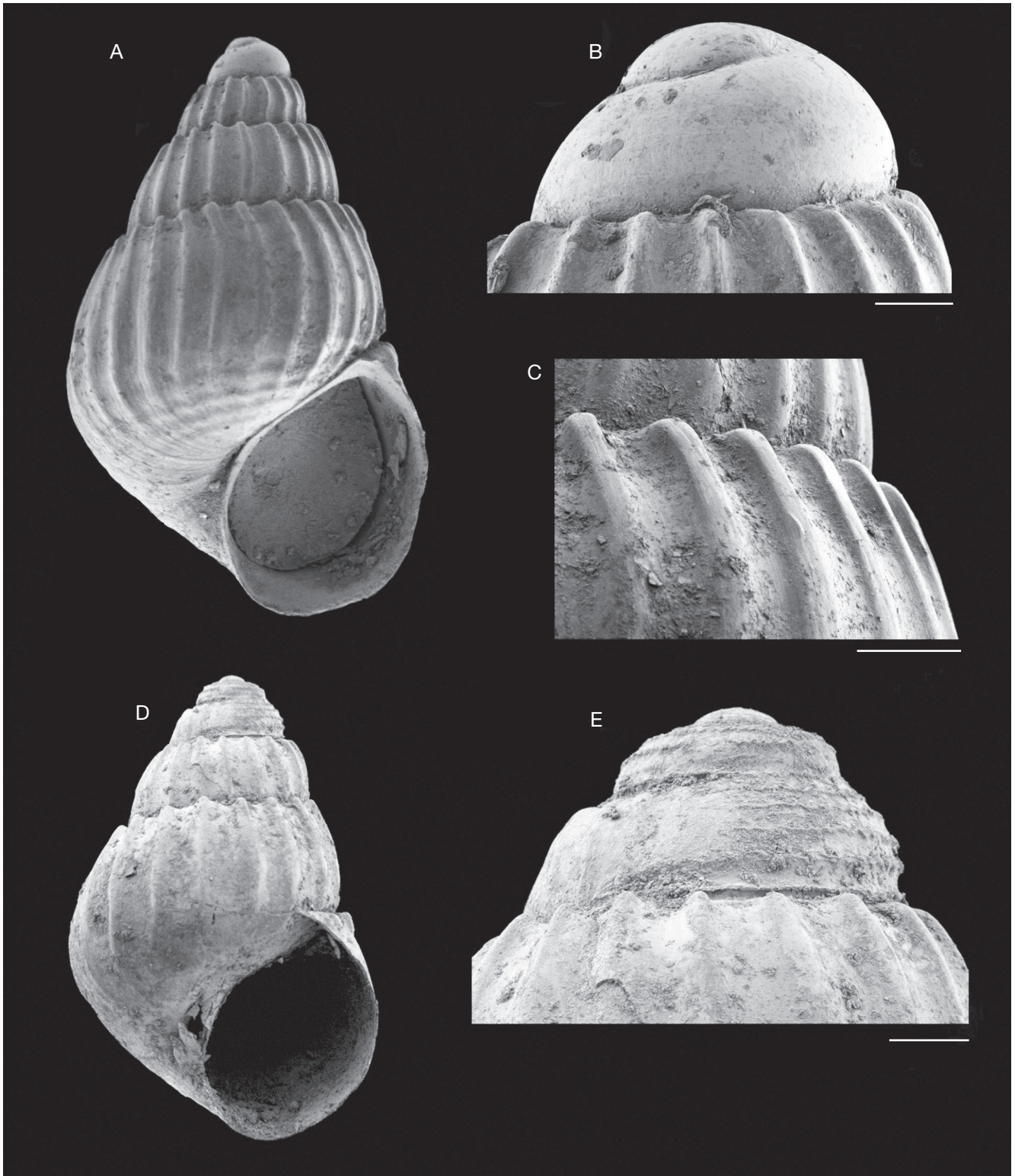


FIG. 12. — *Benthonellania* spp. (SEM): **A-C**, *Benthonellania thielei* n. sp., holotype, East Africa, 693 m depth, height 3.05 mm, ZMB/Moll. No. 64955a: shell (**A**), detail of the protoconch (**B**); detail of the teleoconch axial sculpture (**C**); **D, E**, *Benthonellania aequatorialis* (Thiele, 1925) n. comb., syntype, Sumatra (Indonesia), height 1.8 mm, ZMB/Moll. No. 64973: shell (**D**), detail of the protoconch (**E**). Scale bars: B, C, E, 100 μ m.

distant spiral zigzag cordlets on protoconch II (Fig. 12E) (protoconch I not observable). Protoconch-teleoconch boundary barely visible.

Teleoconch

Of 2.65-2.8 (3.3-4.75), barely convex whorls, suture canaliculate, crowned by small tubercles at tips of axial ribs, high-

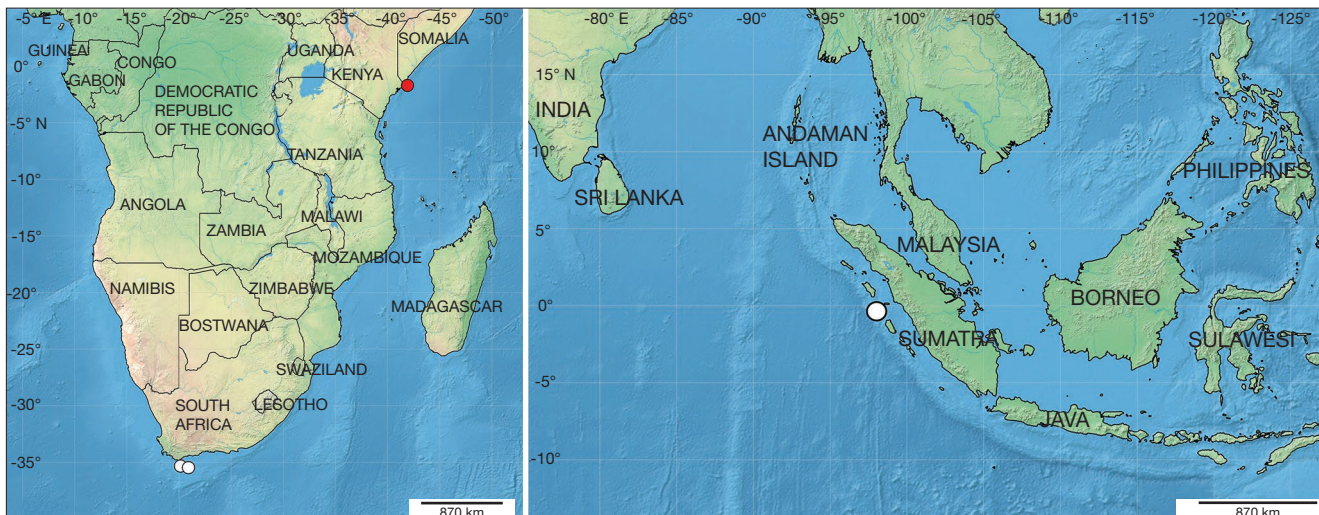


FIG. 13. — Maps of the known distribution of: **A**, *Benthonellania hertzogi* (○), and *Benthonellania thielei* n. sp. and *Benthonellania africana* (Thiele, 1925) n. comb. (both ●); **B**, *Benthonellania aequatorialis* (Thiele, 1925) n. comb.

lighted by a slight subsutural depression. Height last whorl 1.47-1.5 mm, height/height last whorl ratio 1.200-1.326. Axial sculpture of 17-18 ribs on last whorl, narrower than the interspaces, prosocline and slightly curved, gradually vanishing at the base; last half whorl progressively devoid of axial sculpture. Spiral sculpture absent. Microsculpture of only growth striae. Umbilical chink present. Aperture pyriform, small, height 1-1.02 mm height/height aperture ratio 1.800-1.911, peristome continuous, varix absent, outer lip sharp, internally smooth (broken). Columella arcuate, simple.

Colour

Coloration of teleoconch white, protoconch faded orange.

Operculum and soft parts

Unknown.

VARIABILITY

Only two juvenile specimens available (See Table 1 and Appendix 7).

REMARKS

Rissoa aequatorialis Thiele, 1925 was dubitatively suggested by Lozouet (1990) to belong in his new genus *Benthonellania* (see also Hasegawa 2005: 152). Based on the current systematic framework, we agree and propose *Benthonellania aequatorialis* (Thiele, 1925) as new combination for *Rissoa aequatorialis* Thiele, 1925.

Benthonellania aequatorialis n. comb. differs from *B. africana* n. comb. in its multispiral, spirally sculptured protoconch vs paucispiral and smooth in *B. africana* n. comb., and the lack of spiral cordlets on the base, present in *B. africana* n. comb.

As already noticed by Hasegawa (2005) a juvenile specimen of an unidentified *Benthonellania* from southwestern Japan, recalls *Benthonellania aequatorialis* n. comb. (Hasegawa: 152, fig. 5J). However, that specimen quite probably represents a

distinct, undescribed species, differing from *B. aequatorialis* n. comb. by its wider base and more angled periphery, and the faint spiral sculpture on the base (absent in *B. aequatorialis* n. comb.).

See under *Benthonellania bouteti* n. sp. for diagnostic comparison.

***Benthonellania bouteti* n. sp.**

(Figs 14A-H; 16A-E; 25D; 26I; Tables 1; 2)

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TYPE MATERIAL. — **Holotype.** Society Islands • dd (height 3.45 mm, width 1.9 mm, Figs 14A-D; 16A-E); Moorea, TARASOC Stn DW3460; 17°28'S, 149°50'W; 19.X.2009; 660-680 m depth; MNHN-IM-2000-37678.

Paratypes • 34 dd; same data as holotype; MNHN-IM-2000-37679 • 4 dd; Stn DW3481; 17°29'S, 149°45'W; 22.X.2009; 610 m depth; MNHN-IM-2000-37680 • 8 dd; Stn DW3461; 17°27'S, 149°49'W; 19.X.2009; 844-877 m depth; MNHN-IM-2000-37681 • 35 dd; Stn DW 3474; 17°28'S, 149°50'W; 21.X.2009; 720 m depth; MNHN-IM-2000-37682 • 2 dd; Stn DW3476; 17°29'S, 149°45'W; 21.X.2009; 435-490 m depth; MNHN-IM-2000-37683 • 18 dd, 1 lv; Stn DW3459; 17°28'S, 149°48'W; 19.X.2009; 485-560 m depth; MNHN-IM-2000-37684.

TYPE LOCALITY. — Society Islands, Moorea, TARASOC Stn DW3460, 17°28'S, 149°50'W; 660-680 m depth.

OTHER MATERIAL EXAMINED. — **Society Islands** • 36 dd; Huahine, TARASOC Stn DW3425; 16°43'S, 151°03'W; 14.X.2009; 557 m depth; MNHN • 4 dd; Huahine, TARASOC Stn DW3435; 16°41'S, 151°02'W; 15.X.2009; 500-612 m depth; MNHN • 17 dd, 1 lv; Huahine, TARASOC Stn DW3429; 16°43'S, 150°38'W; 15.X.2009; 493-540 m depth; MNHN • 12 dd, 2 lv; Huahine, TARASOC Stn DW3420; 16°46'S, 151°04'W; 14.X.2009; 550 m depth; MNHN • 9 dd; Huahine, TARASOC Stn DW3426; 16°41'S, 151°03'W; 14.X.2009; 801-874 m depth; MNHN • 10 dd, 1 lv; Huahine, TARASOC Stn DW3421; 16°46'S, 151°04'W; 14.X.2009; 782-847 m depth; MNHN • 38 dd; Huahine, TARASOC Stn DW3434;

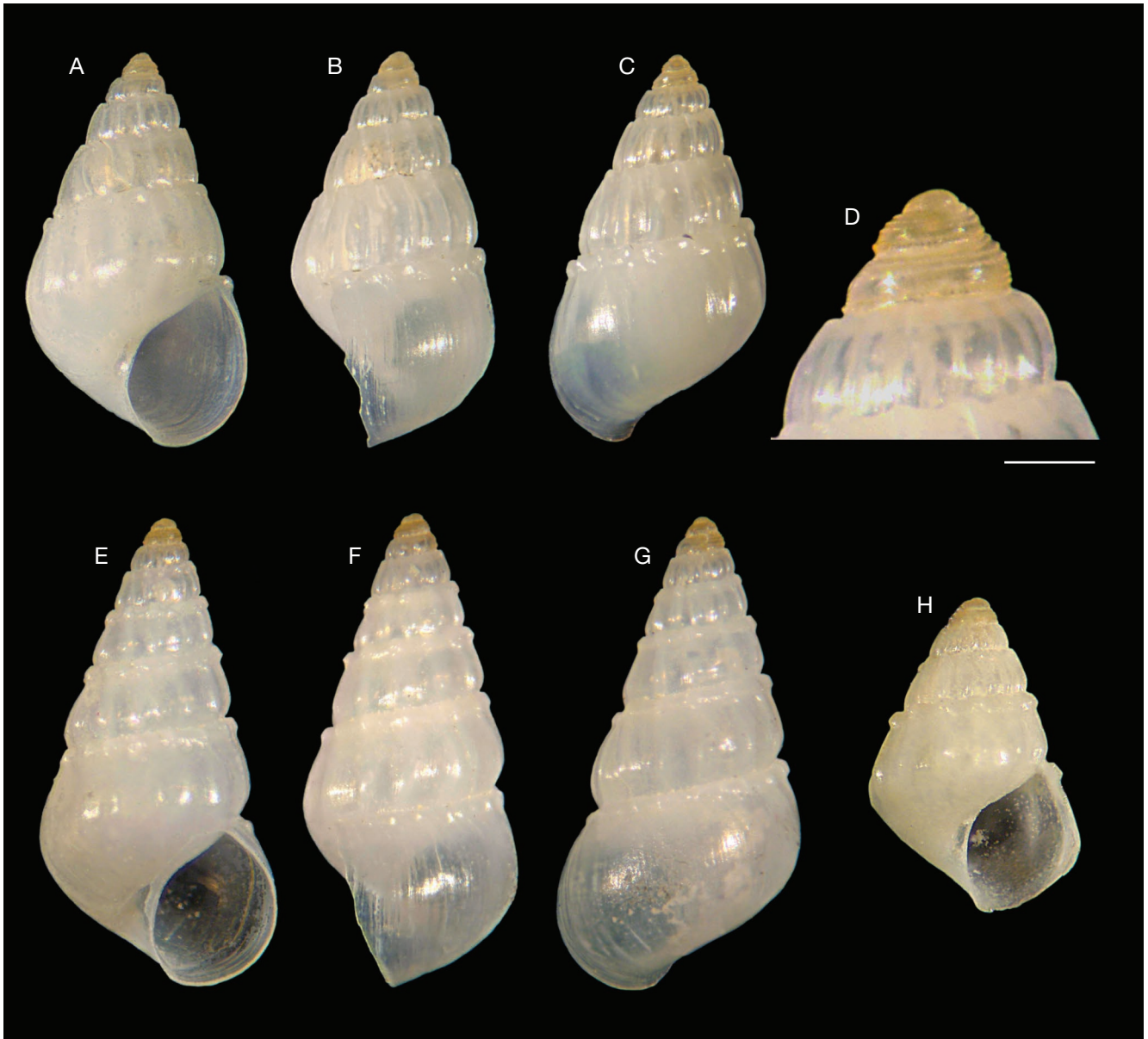


FIG. 14. — *Benthonellania bouteti* n. sp.: **A-D**, holotype, height 3.45 mm, width 1.9 mm, Society Islands: TARASOC Stn DW3460, 660-680 m, $17^{\circ}28'S$, $149^{\circ}50'W$, MNHN-IM-2000-37678; **E-G**, specimen, height 4.15 mm, width 2.2 mm, Marquesas: BENTHAUS Stn DW1889, 600-620 m, $27^{\circ}37'S$, $144^{\circ}16'W$, MNHN; **H**, juvenile specimen, height 2.1 mm, Australes: BENTHAUS Stn DW1962, 470-800 m, $23^{\circ}21'S$, $149^{\circ}33'W$, MNHN. Scale bar: D, 0.25 mm.

$16^{\circ}42'S$, $151^{\circ}03'W$; 15.X.2009; 700-785 m depth; MNHN • 10 dd; Tahiti, TARASOC Stn DW3491; $17^{\circ}29'S$, $149^{\circ}26'W$; 24.X.2009; 440-500 m depth; MNHN • 4 dd; Tahiti, TARASOC Stn DW3501; $17^{\circ}36'S$, $149^{\circ}17'W$; 25 Oct. 2009; 800-820 m depth; MNHN • 48 dd; Tahiti, TARASOC Stn DW3498; $17^{\circ}43'S$, $149^{\circ}17'W$; 25.X.2009; 347-460 m depth; MNHN • 5 dd; Tahiti, TARASOC Stn DW3487; $17^{\circ}47'S$, $149^{\circ}21'W$; 23.X.2009; 400-440 m depth; MNHN • 126 dd; Tahiti, TARASOC Stn DW3484; $17^{\circ}47'S$, $149^{\circ}23'W$; 23.X.2009; 300-650 m depth; MNHN • 4 dd; between Raiatea and Tahaa, TARASOC Stn DW3442; $41^{\circ}S$, $151^{\circ}26'W$; 16.X.2009; 515-550 m depth; MNHN • 6 dd; between Raiatea and Tahaa, TARASOC Stn CP3439; $16^{\circ}43'S$, $151^{\circ}25'W$; 16.X.2009; 800 m depth; MNHN • 10 dd; between Raiatea and Tahaa, TARASOC Stn DW3436; 16.X.2009; 430 m depth; MNHN • 7 dd, 1 lv; Raiatea, TARASOC Stn DW3451; $16^{\circ}53'S$, $151^{\circ}21'W$; 18.X.2009; 440-490 m depth; MNHN • 11 dd; Raiatea, TARASOC Stn DW3452; $16^{\circ}51'S$, $151^{\circ}19'W$; 18.X.2009; 600-705 m depth; MNHN • 5 dd;

Raiatea, TARASOC Stn DW3457; $16^{\circ}45'S$, $151^{\circ}24'W$; 18.X.2009; 520-572 m depth; MNHN • 21 dd; Bora Bora, TARASOC Stn DW3416; $16^{\circ}35'S$, $151^{\circ}44'W$; 13.X.2009; 914 m depth; MNHN • 1 dd; Bora Bora, TARASOC Stn DW3418; 13.X.2009; 580-618 m depth; MNHN • 24 dd; Tahaa, TARASOC Stn DW3447; $16^{\circ}42'S$, $151^{\circ}31'W$; 17.X.2009; 620-700 m depth; MNHN • 12 dd, 1 lv; Maupiti, TARASOC Stn DW3407; $16^{\circ}32'S$, $152^{\circ}31'W$; 12.X.2009; 445-645 m depth.

Tuamotu • 10 dd; SW Kaukura, TARASOC Stn DW3559; $15^{\circ}57'S$, $147^{\circ}08'W$; 1.X.2009; 462-980 m depth; MNHN • 36 dd, 2 lv; Kaukura, TARASOC Stn DW3373; $15^{\circ}41'S$, $146^{\circ}54'W$; 4.X.2009; 507-607 m depth; MNHN • 1 dd; Tikehau, TARASOC Stn DW3387 550-600 m depth; $14^{\circ}57'S$, $148^{\circ}16'W$ 6.X.2009; MNHN • 2 dd; Tikehau, TARASOC Stn DW3389; $14^{\circ}55'S$, $148^{\circ}15'W$; 6.X.2009; 889 m depth; MNHN • 3 dd; between Tikehau and Rangiroa, TARASOC Stn DW3349; $15^{\circ}06'S$, $148^{\circ}03'W$; 30.IX.2009; 976-997 m depth; MNHN • 5 dd; between Tikehau and Rangiroa,

TARASOC Stn DW3351; 15°04'S, 148°01'W; 30.IX.2009; 976-983 m depth; MNHN.

Tarava Seamounts • 10 dd; Mont Ari'i Moana, TARASOC Stn DW3316; 19°14'S, 151°33'W; 24.IX.2009; 519-520 m depth; MNHN • 1 dd; Mont Ari'i Moana, TARASOC Stn DW3317; 19°13'S, 151°29'W; 25.IX.2009; 593-668 m depth; MNHN • 9 dd; Mont Honu, TARASOC Stn DW3340; 18°24'S, 154°09'W; 27.IX.2009; 787-792 m depth; MNHN • 5 dd; Mont Punu Taipu, TARASOC Stn DW3302; 19°15'S, 150°57'W; 23.IX.2009; 600-660 m depth; MNHN • 61 dd; Mont 'Otaha, TARASOC Stn DW3327; 18°45'S, 152°16'W; 26.IX.2009; 747-836 m depth; MNHN • 1 dd; Mont 'Otaha, TARASOC Stn CP3329; 18°45'S, 152°16'W; 26.IX.2009; 755-840 m depth; MNHN • 11 dd; Mont 'Otaha, TARASOC Stn DW3328; 18°46'S, 152°15'W; 26.IX.2009; 788-836 m depth; MNHN.

Australes • 91 dd; Banc Lotus, BENTHAUS Stn DW1951; 23°49'S, 147°53'W; 17.XI.2002; 206-450 m depth • 1200+ dd (many juveniles), 7 lv; East of Rapa, BENTHAUS Stn DW1889; 27°37'S, 144°16'W; 7.XI.2002; 600-620 m depth; MNHN • 53 dd; Tubuai, BENTHAUS Stn DW1962; 23°21'S, 149°33'W; 19.XI.2002; 470-800 m depth; MNHN • 5 dd; Tubuai, BENTHAUS Stn DW1955; 23°19'S, 149°26'W; 18.XI.2002; 750-850 m depth; MNHN • 28 dd; Tubuai, BENTHAUS Stn DW1961; 23°21'S, 149°34'W; 19.XI.2002; 470-800 m depth; MNHN • 19 dd; Rimatara, BENTHAUS Stn DW2020; 22°37'S, 152°49'W; 25.XI.2002; 920-930 m depth; MNHN • 5 dd; Rimatara, BENTHAUS Stn DW2021; 22°37'S, 152°49'W; 25.XI.2002; 1200-1226 m depth; MNHN • 15 dd; Banc Arago, BENTHAUS Stn DW1974; 23°24'S, 150°44'W; 20.XI.2002; 450-618 m depth; MNHN • 2 dd; South coast of Rurutu, BENTHAUS Stn DW2010; 22°32'S, 151°21'W; 24.XI.2002; 520-950 m depth; MNHN • 2 dd; East coast of Rurutu, BENTHAUS Stn DW2004; 22°27.7'S, 151°18.7'W; 24.XI.2002; 430-850 m depth; MNHN • 6 dd; North coast of Rurutu, BENTHAUS Stn DW1999; 22°25'S, 151°22'W; 23.XI.2002; 270-500 m depth; MNHN • 20 dd; Récif Neilson, BENTHAUS Stn DW1925; 27°00'S, 146°05'W; 12.XI.2002; 560-790 m depth; MNHN • 3 dd; Récif Neilson, BENTHAUS Stn DW1924; 27°01'S, 146°03'W; 12.XI.2002; 340-800 m depth; MNHN • 2 dd; Banc Président Thiers, BENTHAUS Stn DW1937; 24°40'S, 145°56'W; 14.XI.2002; 469-500 m depth; MNHN • 1 dd; Banc Président Thiers, BENTHAUS Stn DW1932; 24°41'S, 146°02'W; 14.XI.2002; 500-800 m depth; MNHN.

DISTRIBUTION AND SYMPATRY. — The species is known from the South Pacific Ocean, at the Tarava Seamounts (Mont Ari'i Moana, Mont Punu Taipu, Mont Honu, Mont 'Otaha), Society Islands (Maupiti, Moorea, Huahine, Tahiti, Bora Bora, Raiatea, Btw Raiatea & Tahaa, Tahaa), Tuamotu (SW Kaukura, Kaukura, Tikehau, between Tikehau and Rangiroa) and Australes (Récif Neilson, Banc Président Thiers, Rimatara, Banc Arago, North coast of Rurutu, Tubuai, South coast of Rurutu, East coast of Rurutu, Banc Lotus, East of Rapa), with empty shells collected at 206-1250 m depth, and 16 specimens collected with the soft parts at 440-847 m depth in various locality (see Material examined) (Fig. 25D).

Benthonellania bouteti n. sp. is sympatric with *Benthonella boucheti* n. sp. at the Tarava Seamounts (Mont Honu and Mont 'Otaha), Australes (Récif Neilson, Banc Président Thiers, Rimatara, Banc Arago, South coast of Rurutu, East coast of Rurutu, Tubuai), Tuamotu (between Tikehau and Rangiroa); with *Benthonella basistriata* n. sp. at the Tuamotu (Tikehau, Kaukura), Society Islands (Huahine, Moorea); with *Benthonellania maestratii* n. sp. at the Australes (Récif Neilson, South coast of Rurutu); with *Benthonella communis* n. sp. at the Tarava Seamounts (Mont Ari'i Moana, Mont Punu Tipu), Society Islands (Maupiti, Moorea, Huahine, Tahiti, Bora Bora, Raiatea), Tuamotu (WS Kaukura, Kaukura, between Tikehau and Rangiroa, Tikehau), Australes (Récif Neilson, Banc Président Thiers, Rimatara, Banc Arago, North coast of Rurutu, South coast of Rurutu, East coast of Rurutu, Banc Lotus, East of Rapa, Tubuai);

with *Benthonellania tarava* n. sp. at the Tarava Seamounts (Mont Ari'i Moana, Mont 'Otaha, Mont Honu), Society Islands (Moorea), Tuamotu (SW Kaukura, Kaukura, Tikehau, between Tikehau and Rangiroa), Australes (Rimatara, East coast of Rurutu, South coast of Rurutu); with *Benthonellania tuamotu* n. sp. at the Tarava Seamounts (Mont 'Otaha, Mont Panu Taipu), Tuamotu (SW Kaukura, Kaukura, between Tikehau and Rangiroa, Tikehau), Society Islands (Maupiti, Raiatea), Australes (Rimatara, South coast of Rurutu, Récif Neilson); with *Benthonellania megan* n. sp. from the Australes (Rimatara); with *Benthonellania alis* n. sp. at the Tarava Seamounts (Mont 'Otaha, Mont Punu Taipu, Mont Honu), Australes (East coast of Rurutu, South coast of Rurutu, Rimatara; Banc Président Thiers, East of Rapa, Tubuai) (Table 2).

ETYMOLOGY. — Named after Michel Boutet (Paparua, Tahiti) for his indefatigable work of sorting the fine fractions of the material collected during the TARASOC cruise.

DESCRIPTION OF HOLOTYPE.

Shell (Figs 14A-D; 16A-E)

Large for the genus, height 3.45 mm, width 1.9 mm, height/width ratio 1.816, rather solid, ovate-conical.

Protoconch (Figs 14D; 16B-D)

Conical, multispiral, of 2.5 whorls, height 0.325 mm, nucleus diameter 0.075 mm, first half whorl diameter 0.15 mm, maximum diameter 0.40 mm; protoconch I with six threads with microtubercles in the interspaces (Fig. 16D); protoconch II with 5 spiral cordlets (the three adapical starting as zig-zag for 0.5 whorls) consisting of series of concatenated dart-like microtubercles (Fig. 16B, C). Protoconch-teleoconch boundary weak, flexuose, opisthocline.

Teleoconch

Of 4 slightly convex whorls, suture canaliculate, crowned by small tubercles at tip of axial ribs, highlighted by a spiral subsutural groove. Height last whorl 2.3 mm, height/height last whorl ratio 1.500. Axial sculpture of 15 slightly curved ribs, almost as broad as the interspaces, on the last whorl, gradually vanishing at the base. Last half whorl progressively devoid of axial ribs. Spiral sculpture absent. Microsculpture of growth striae, and subsutural spiral threadlets on interspaces between axial ribs (Fig. 16E). Umbilical chink present. Aperture pyriform, small, height 1.4 mm height/height aperture ratio 2.464, peristome continuous, varix absent, outer lip sharp, internally smooth (broken). Columella arcuate, simple.

Colour

Coloration of teleoconch very light pinkish-orange in fresh, live collected specimens, white in empty shells, protoconch orange.

Operculum and soft parts

Unknown.

VARIABILITY

Species not very variable (See Table 1 and Appendix 8). Less than a dozen specimens from Tahiti (DW3484 300-650 m), have the last whorl smooth or with very thin ribs. Maximum

height 4.15 mm (from Rapa, 600–620 m). In some specimens, the tubercles at the tip of axial ribs of the last 0.25 whorl are smaller and progressively evanescent towards the aperture.

REMARKS

B. bouteti n. sp. differs from *B. aequatorialis* (Thiele, 1925) n. comb. in its more robust tubercles at the subsutural crown; non-angled base (cfr juvenile shell of *B. bouteti* n. sp. in Fig. 14H with *B. aequatorialis* n. comb. in Fig. 11A–D); higher protoconch 0.325–0.375 mm and with five not equidistant spiral cordlets vs 0.275 with five equidistant cordlets in *B. aequatorialis* n. comb.

The juvenile specimen of an unidentified *Benthonellania* from southwestern Japan (Hasegawa: 152, fig. 5J) differs from juveniles of *B. bouteti* n. sp. in its more angled periphery, the weaker tubercled at the tips of axial ribs, and the faint spiral sculpture on the base (absent in *Benthonellania bouteti* n. sp.).

See under *Benthonellania alis* n. sp. for differences with this species.

Benthonellania alis n. sp.

(Figs 15A–H; 16F–H; 25E; 26J; Tables 1; 2)

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TYPE MATERIAL. — **Holotype.** Australes • 1 dd (height 3.35, width 1.87 mm, Figs 15D–G; 16F–H); South coast of Rurutu, BENTHAUS Stn DW2010; 22°32'S, 151°21'W; 24.XI.2002; 520–950 m depth; MNHN-IM-2000-37685.

Paratypes. Australes • 87 dd; same data as holotype; MNHN-IM-2000-37686.

TYPE LOCALITY. — Australes, South coast of Rurutu, BENTHAUS Stn DW2010; 22°32'S, 151°21'W; 520–950 m depth.

OTHER MATERIAL EXAMINED. — **Australes** • 23 dd; East coast of Rurutu, BENTHAUS Stn DW 2004; 22°27.7'S, 151°18.7'W; 24.XI.2002; 430–850 m depth; MNHN • 12 dd; Rimatara, BENTHAUS Stn 2020; 22°37'S, 152°49'W; 25.XI.2002; 920–930 m depth; MNHN • 8 dd; Rimatara, BENTHAUS Stn DW2021 22°37'S, 152°49'W; 25.XI.2002; 1200–1226 m depth; MNHN • 2 dd; Marotiri, BENTHAUS Stn DW1886; 27°51'S, 143°32'W; 6.XI.2002; 620–1000 m depth; MNHN • 3 dd; Tubuai, BENTHAUS Stn DW1955; 23°19'S, 149°26'W; 18.XI.2002; 750–850 m depth; MNHN • 12 dd; Banc Président Thiers, BENTHAUS Stn DW1932; 24°41'S, 146°02'W; 14.XI.2002; 500–800 m depth; MNHN • 11 dd; East coast of Rapa, BENTHAUS Stn DW1889; 27°37'S, 144°16'W; 7.XI.2002; 600–620 m depth; MNHN.

Tarava Seamounts • 5 dd; Mont 'Otaha, TARASOC Stn DW3328; 18°46'S, 152°15'W; 26.IX.2009; 788–836 m depth; MNHN • 1 dd; Mont Punu Taïpu, TARASOC Stn DW3300; 19°19'S, 151°00'W; 22.IX.2009; 670–757 m depth; MNHN • 3 dd; Mont 'Otaha, TARASOC Stn DW3329; 18°45'S, 152°16'W; 20.IX.2009; 755–840 m depth; MNHN • 15 dd; Mont 'Otaha, TARASOC Stn DW3327; 18°45'S, 152°16'W; 26.IX.2009; 747–836 m depth; MNHN • 3 dd; Mont Honu, TARASOC Stn DW3340; 18°24'S, 154°09'W; 27.IX.2009; 787–792 m depth; MNHN.

Society Islands • 2 dd; Bora Bora, TARASOC Stn DW3416; 16°36'S, 151°44'W; 13.X.2009; 914 m depth; MNHN.

DISTRIBUTION AND SYMPATRY. — The species is at present known from the South Pacific Ocean, at Australes (East coast of Rurutu, South coast of Rurutu, Rimatara, Marotiri, Tubuai, Banc Président

Thiers, East of Rapa), Tarava Seamounts (Mont 'Otaha, Mont Punu Taïpu, Mont Honu), Society Islands (Bora Bora), with only empty shells collected in 430–1226 m depth (Fig. 25E).

Benthonellania alis n. sp. is sympatric with *Benthonella boucheti* n. sp. at the Australes (East coast of Rurutu, South coast of Rurutu, Rimatara, Marotiri, Tubuai, Banc Président Thiers), Tarava Seamounts (Mont 'Otaha); with *Benthonellania maestratii* n. sp. at the Australes (South coast of Rurutu); with *Benthonella communis* n. sp. at the Tarava Seamounts (Mont Punu Taïpu), Australes (East coast of Rurutu, South coast of Rurutu, Rimatara, Marotiri, Tubuai, Banc Président Thiers, East of Rapa), Society Islands (Bora Bora); with *Benthonellania bouteti* n. sp. at the Tarava Seamounts (Mont 'Otaha, Mont Punu Taïpu, Mont Honu), Australes (East coast of Rurutu, South coast of Rurutu, Rimatara; Banc Président Thiers, East of Rapa, Tubuai); with *Benthonellania tarava* n. sp. at the Tarava Seamounts (Mont 'Otaha, Mont Honu), Australes (Rimatara, South coast of Rurutu, East coast of Rurutu); with *Benthonellania tuamotu* n. sp. at the Tarava Seamounts (Mont 'Otaha, Mont Punu Taïpu), Australes (Rimatara, South coast of Rurutu); with *Benthonellania megan* n. sp. at the Australes (Rimatara) (Table 2).

ETYMOLOGY. — Dedicated to the research vessel 'Alis' and its crew, which during decades so greatly contributed to the increase of knowledge of the Pacific deep-water fauna.

DESCRIPTION OF HOLOTYPE

Shell (Figs 15D–G; 16G–H)

Large for the genus, height 3.35 mm width 1.79 mm, height/width ratio 1.875, rather solid, ovate-conical.

Protoconch (Figs 15D; 16G, H)

Slender, acute, multispiral, of 2.3 whorls, height 0.337 mm, nucleus diameter 0.075 mm, first half whorl diameter 0.175 mm, maximum diameter 0.412 mm; protoconch I with 4 spiral cordlets of concatenated microtubercles (Fig. 16H), protoconch II with 3 zig-zag spiral cordlets on upper part, and a fourth irregular cordlet on lower part (Fig. 16G). Protoconch-teleoconch boundary barely visible, opisthocline, sinuous.

Teleoconch

Of 4 slightly convex whorls, suture canaliculate, crowned by small tubercles at tips of axial ribs, highlighted by a subsutural spiral groove. Height last whorl 2.2 mm, height/height last whorl ratio 1.522. Axial sculpture of 20 ribs on last whorl, as broad as the interspaces, opisthocline on first whorls, then orthocline, and slightly prosocline on last whorl, gradually vanishing at the base; last half whorl progressively devoid of axial sculpture. Spiral sculpture of 3 very weak cordlets on the suture line, the uppermost suprasutural visible on all whorls, base smooth (Fig. 15H). Microsculpture of only growth striae. Umbilical chink absent. Aperture pyriform, large, height 1.23 mm, height/height aperture ratio 2.723, peristome continuous, varix absent (outer lip broken). Columella arcuate, simple.

Colour

Coloration of teleoconch white, protoconch orange.

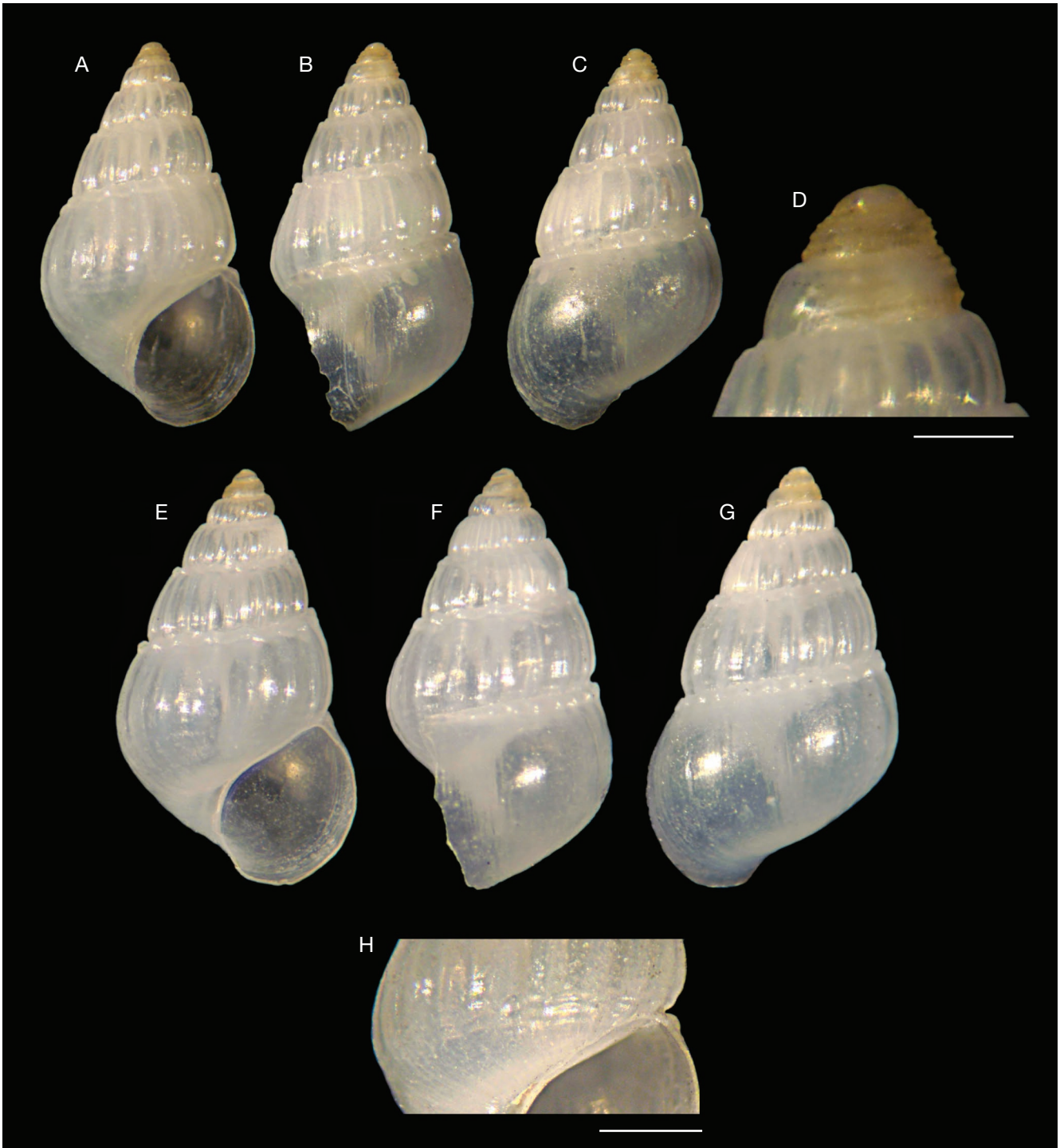


FIG. 15. — *Benthonellania alis* n. sp.: **A-C**, specimen, height 3.7 mm, width 2.15 mm, Australes: BENTHAUS Stn DW2020, 920-930 m, 22°37'S, 152°49'W, MNHN; **D-G**, holotype, height 3.35, width 1.87 mm, Australes: BENTHAUS Stn DW2010 520-950 m, 22°32'S, 151°21'W, MNHN-IM-2000-37685; **H**, paratype, Australes: BENTHAUS Stn DW2010, 520-950 m, 22°32'S, 151°21'W, MNHN-IM-2000-37686, detail of the teleoconch sculpture spiral on the last whorl. Scale bars: D, 0.25 mm; H, 0.50 mm.

Operculum and soft parts
Unknown.

VARIABILITY

Species not very variable (See Table 1 and Appendix 9).

REMARKS

Most of the examined specimens have the outer lip broken; where the peristome is intact, no thickening was observed.

B. alis n. sp. is very similar to *B. bouteti* n. sp. but can be distinguished by the presence of 3-4 fine spiral cords on the last whorl vs absence of spiral sculpture in *B. bouteti* n. sp.;

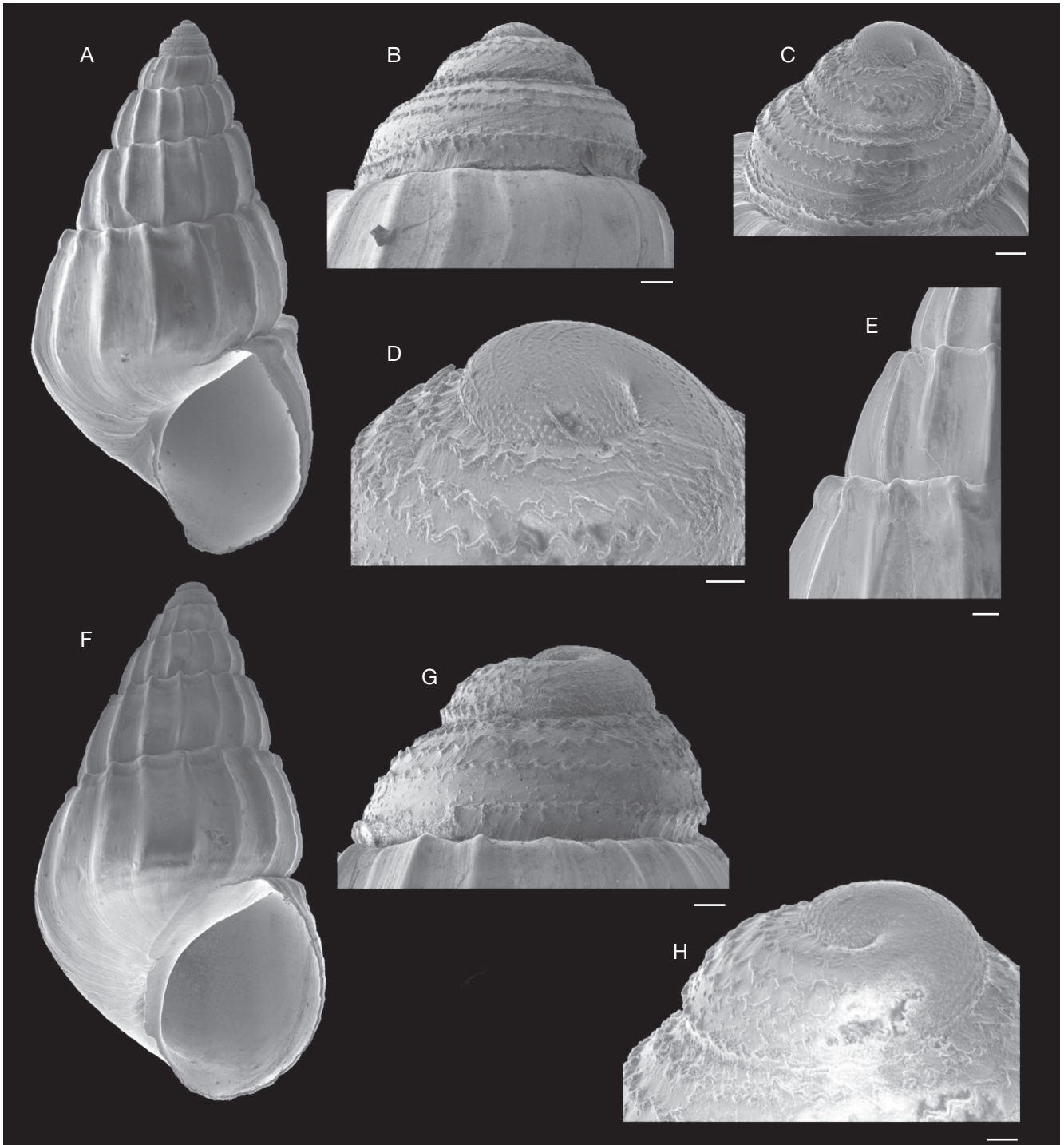


FIG. 16. — *Benthonellania* spp. (SEM): **A-E**, *Benthonellania bouteti* n. sp. holotype, Society Islands, height 3.45 mm, MNHN-IM-2000-37678, shell (**A**), detail of the protoconch microsculpture (**B-D**), detail of the teleoconch axial sculpture (**E**); **F-H**, *Benthonellania alis* n. sp. holotype, Australes, height. 3.35 mm, MNHN-IM-2000-37685; shell (**F**); detail of the protoconch microsculpture (**G, H**). Scale bars: B, C, 40 μ m; D, H, 20 μ m; E, 100 μ m; G, 30 μ m.

the protoconch with 4 spiral cordlets of concatenated microtubercles on protoconch I, and 3 zig-zag spiral cordlets on upper part, and a fourth irregular cordlet on lower part vs protoconch with six threads and microtubercles on protoconch I and 5 spiral cordlets (the three adapical with a zig-zag pattern) of concatenated dart-like microtubercles on protoconch II in *B. bouteti* n. sp.

B. alis n. sp. is also similar to *Benthonellania africana* (Thiele, 1925) n. comb. (Figs 11A-N; 13A, B) from which it differs mostly in its multispiral protoconch with marked spiral sculpture vs paucispiral and smooth, except for a faint and confused spiral sculpture on the nucleus in *B. africana* n. comb.

See under *Benthonellania aequatorialis* (Thiele, 1925) n. comb. for differences with this species.

Benthonellania tarava n. sp.

(Figs 17A-K; 19A-E; 25F; 26K; Tables 1; 2)

[urn:lsid:zoobank.org:act:DCA27C86-C251-4615-B4D9-811FA5EAF87A](https://doi.org/10.21203/rs.3.rs-22514615/v1)

TYPE MATERIAL. — **Holotype**. Tarava Seamounts • 1 dd (height 3.5 mm, width 1.85 mm, Figs 17I-K; 19A-E); Mont ‘Otaha, TARASOC Stn DW3333; 18°45’S, 152°18’W; 26.IX.2009; 795-975 m depth; MNHN-IM-2000-37687.

Paratypes. Tarava Seamounts • 30 dd; same locality data as holotype; MNHN-IM-2000-37688 • 3 dd; Mont ‘Otaha, Stn DW3331; 18°45’S, 152°17’W; 26.IX.2009; 766 m depth; MNHN-IM-2000-37689 • 29 dd; Mont ‘Otaha, Stn DW3328; 18°46’S, 152°15’W; 26.IX.2009; 788-836 m depth; MNHN-IM-2000-37690 • 46 sh; Mont ‘Otaha, Stn DW3327; 747-18°45’S, 152°16’W; 26.IX.2009; 836 m depth; MNHN-IM-2000-37691 • 3 dd; Mont ‘Otaha, Stn CP3329; 18°45’S, 152°16’W; 26.IX.2009; 755-840 m depth; MNHN-IM-2000-37692 • 10 dd; Mont ‘Otaha, Stn DW3332; 18°45’S, 152°18’W; 26.IX.2009; 790-880 m depth; MNHN-IM-2000-37693 • 2 dd; Mont ‘Otaha, Stn DW3330; 18°45’S, 152°16’W; 26.IX.2009; 717-794 m depth; MNHN-IM-2000-37694.

TYPE LOCALITY. — Tarava Seamounts, Mont ‘Otaha, TARASOC Stn DW3333; 18°45’S, 152°18’W; 795-975 m depth.

OTHER MATERIAL EXAMINED. — **Society Islands** • 1 dd, 1 lv; Moorea, TARASOC Stn DW3461; 17°27’S, 149°49’W; 19.X.2009; 844-877 m depth; MNHN.

Australes • 1 dd; Rimatara, BENTHAUS Stn DW2020; 22°37’S, 152°49’W; 25.XI.2002; 920-930 m depth; MNHN • 51 dd; South coast of Rurutu, BENTHAUS Stn DW2010; 22°32’S, 151°21’W 24.XI.2002; 520-950 m depth; MNHN • 2 dd; East coast of Rurutu, BENTHAUS Stn 2004; 22°28’S, 151°19’W; 24.XI.2002; 430-850 m depth; MNHN.

Tuamotu • 13 dd; SW Kaukura, TARASOC Stn DW3359; 15°57’S, 147°08’W; 1.X.2009; 462-980 m depth; MNHN • 1 dd; Kaukura, TARASOC Stn DW3379; 15°38’S, 146°51’W; 5.X.2009; 800 m depth; MNHN • 1 dd; Kaukura, TARASOC Stn DW3380; 15°39’S, 146°56’W; 5.X.2009; 970-1060 m depth; MNHN • 154 dd; between Tikehau and Rangiroa, TARASOC Stn DW3349; 15°05’S, 148°03’W; 30.IX.2009; 976-997 m depth; MNHN • 6 dd; between Tikehau and Rangiroa, TARASOC Stn DW3351; 15°04’S, 148°01’W; 30.IX.2009; 976-983 m depth; MNHN • 4 dd; Tikehau, TARASOC Stn DW3389; 14°55’S, 148°15’W; 6.X.2009; 889 m depth; MNHN. **Tarava Seamounts** • 10 dd; Mont Honu, TARASOC Stn DW3340; 18°24’S, 154°09’W; 27.IX.2009; 787-792 m depth; MNHN • 3 dd; Mont Ari’i Moana, TARASOC Stn DW3314; 19°14’S, 151°39’W; 24.IX.2009; 803-815 m depth; MNHN.

DISTRIBUTION AND SYMPATRY. — The species is at present known from the South Pacific Ocean, at Tarava Seamounts (Mont Ari’i Moana, Mont ‘Otaha, Mont Honu), Society Islands (Moorea), Tuamotu (SW Kaukura, Kaukura, between Tikehau and Rangiroa, Tikehau), and Australes (Rimatara, South coast of Rurutu, East coast of Rurutu), with empty shells collected in 430-1250 m depth, and a single live collected specimen, from the Society Islands (Moorea), 844-877 m depth 17°27’S, 149°49’W (Fig. 25F).

Benthonellania tarava n. sp. is sympatric with *Benthonella boucheti* n. sp. at the Tarava Seamounts (Mont Honu and Mont ‘Otaha), Australes (Rimatara, South coast of Rurutu, East coast of Rurutu); with *Benthonella basistriata* n. sp. at the Tuamotu (Tikehau, Kaukura), Society Islands (Moorea); with *Benthonellania maestratii* n. sp. at the Australes (South coast of Rurutu); with *Benthonella communis* n. sp. at the Tarava Seamounts (Mont Ari’i Moana), Society Islands (Moorea), Tuamotu (SW Kaukura, Kaukura, between Tikehau and Rangiroa), Australes (Rimatara, South coast of Rurutu, East coast of Rurutu); with *Benthonellania bouteti* n. sp. at the Tarava Seamounts (Mont Ari’i Moana, Mont ‘Otaha, Mont Honu), Society Islands

(Moorea), Tuamotu (SW Kaukura, Kaukura, Tikehau, between Tikehau and Rangiroa), Australes (Rimatara, South coast of Rurutu, East coast of Rurutu); with *Benthonellania tuamotu* n. sp. at the Tarava Seamounts (Mont ‘Otaha), Tuamotu (SW Kaukura, Kaukura, between Tikehau and Rangiroa, Tikehau), Australes (Rimatara, South coast of Rurutu); with *Benthonellania megan* n. sp. at the Australes (Rimatara); with *Benthonellania alis* n. sp. at the Tarava Seamounts (Mont ‘Otaha, Mont Honu), Australes (Rimatara, South coast of Rurutu, East coast of Rurutu) (Table 2).

ETYMOLOGY. — The name is after the area of the type locality, the Tarava Seamounts, used as a noun in apposition.

DESCRIPTION OF HOLOTYPE

Shell (Figs 17I-K; 19A-E)

Medium for the genus, height 3.5 mm, width 1.85 mm, height/width ratio 1.891, not very solid, ovate-conical, rather slender.

Protoconch (Fig. 19B-D)

Multispiral, of 2.75 whorls, height 0.425 mm, nucleus diameter 0.0625 mm, first half whorl diameter 0.200 mm, maximum diameter 0.4625 mm; protoconch I seemingly with only microtubercles spirally arranged (embryonic shell in poor condition) (Fig. 19C), protoconch II with two fine spiral cordlets, interspaced by a large smooth median area (Fig. 19B, D). Protoconch-teleoconch boundary marked, opisthocline, sinuous.

Teleoconch

Of *c.* 3.45 slightly convex whorls, suture canaliculate, crowned by small tubercles at tip of axial ribs, highlighted by a sub-sutural spiral groove. Height of last whorl 2.1 mm, height/height last whorl ratio 1.666. Axial sculpture of 9 flexuose, acute and opisthocline ribs on last whorl, almost orthocline on first whorls, narrower than interspaces, abruptly interrupted before the base. Last half whorl progressively devoid of axial ribs. Spiral sculpture of 3 fine cordlets visible only on the base on last whorl, the third upper cordlets is also visible on the upper whorls. Microsculpture of only growth striae (Fig. 19E). Umbilical chink present. Aperture pyriform, small, height 1.27 mm, height/height aperture ratio 2.745, peristome continuous, varix absent; outer lip slightly opisthocline, internally smooth (broken). Columella arcuate, simple.

Colour

Coloration of teleoconch white, protoconch orange.

Operculum and soft parts

Unknown.

VARIABILITY

Species not very variable (See Table 1 and Appendix 10). Generally, on the last quarter of a whorl, the axial ribs flatten and the subsutural nodules become smaller. A probably teratological subadult specimen from Mont ‘Otaha (Tarava Seamounts: TARASOC Stn DW3327 747-836 m 18°45’S, 152°16’W), showed an obsolete axial sculpture, absent on the last whorl. The spiral cordlets (2-3) are almost imperceptible,

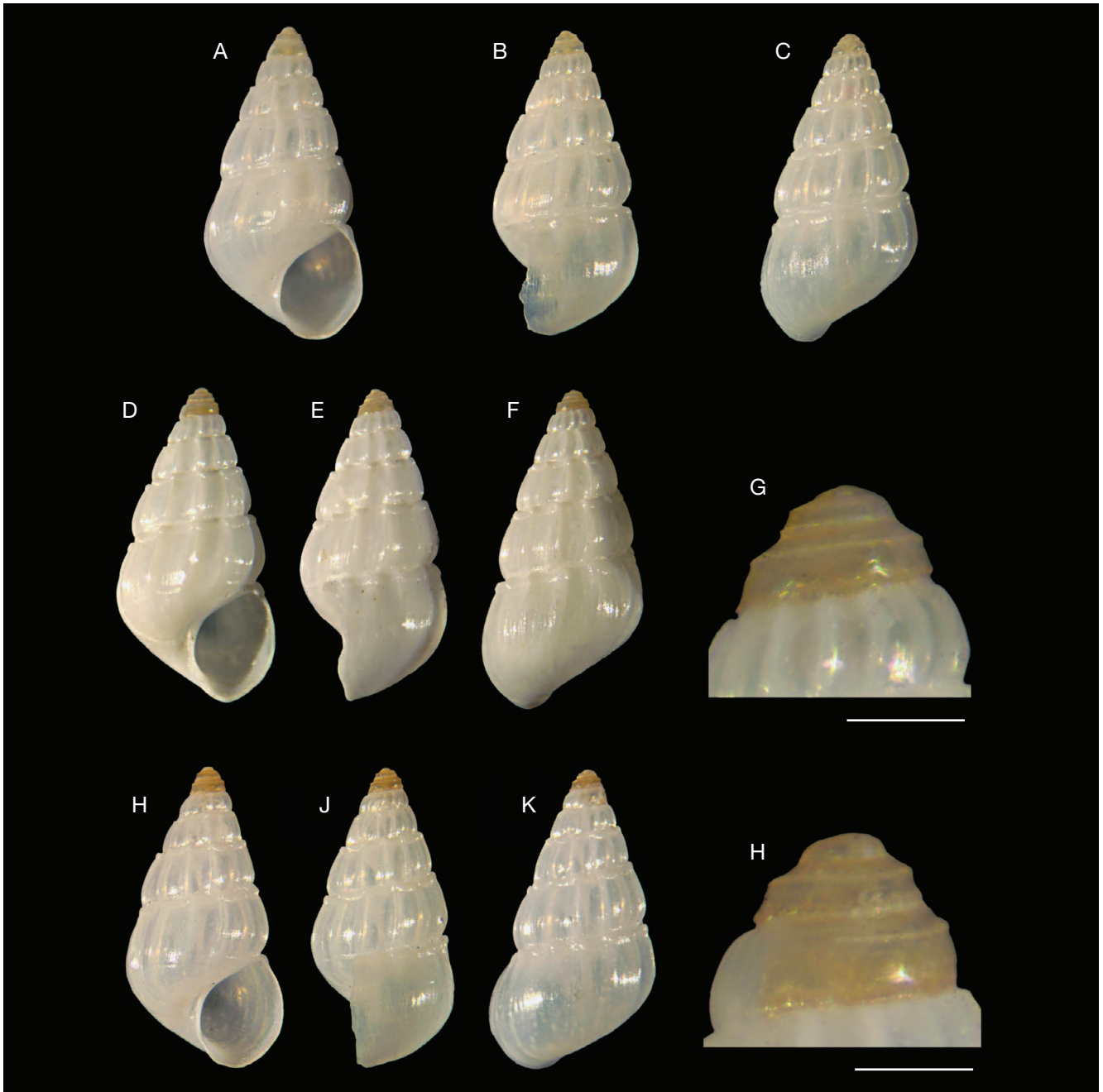


FIG. 17. — *Benthonellania tarava* n. sp.: **A-C**, paratype, height 3.6 mm, width 1.85 mm, Tarava Seamounts: TARASOC Stn DW3333, 795-975 m, 18°45'S, 152°18'W, MNHN-IM-2000-37688; **D-H**, paratype, height 3.75 mm, width 1.92 mm, Tarava Seamounts: TARASOC Stn DW3333, 795-975 m, 18°45'S, 152°18'W, MNHN-IM-2000-37688; **I-K**, holotype, height 3.5 mm, width 1.85 mm, Tarava Seamounts: TARASOC Stn DW3333, 795-975 m, 18°45'S, 152°18'W, MNHN-IM-2000-37687. Scale bars: G, H, 0.25 mm.

making a correct count possible only under raking light. Rare specimens (from South coast of Rurutu, 520-950 m) have up to four very weak spiral cordlets on the base.

REMARKS

Benthonellania tarava n. sp. is similar to *Benthonellania gofasi* Lozouet, 1990, *Benthonellania acuticostata* (Dall, 1889) and *Benthonellania xanthias* (R. B. Watson, 1886), all species with slender shells, which however differ in their more numerous spiral cordlets on the last whorl, and for the different sculp-

tures of the respective protoconchs: with 4 irregular spiral cords; with a series of very jagged spiral cordlets intersecting each other to form a cobweb; with 2 spiral cordlets with short vertical pustules on the lower half of the whorls vs with two fine spiral cordlets, interspaced by a large smooth median area in *B. tarava* n. sp. (see (Lozouet 1990: 322, fig. 23; Dall 1889: 280, pl. XIX, fig. 10; R. B. Watson 1886: 588, pl. XLIV, fig. 5).

See under *Benthonellania megan* n. sp. for diagnostic comparison.

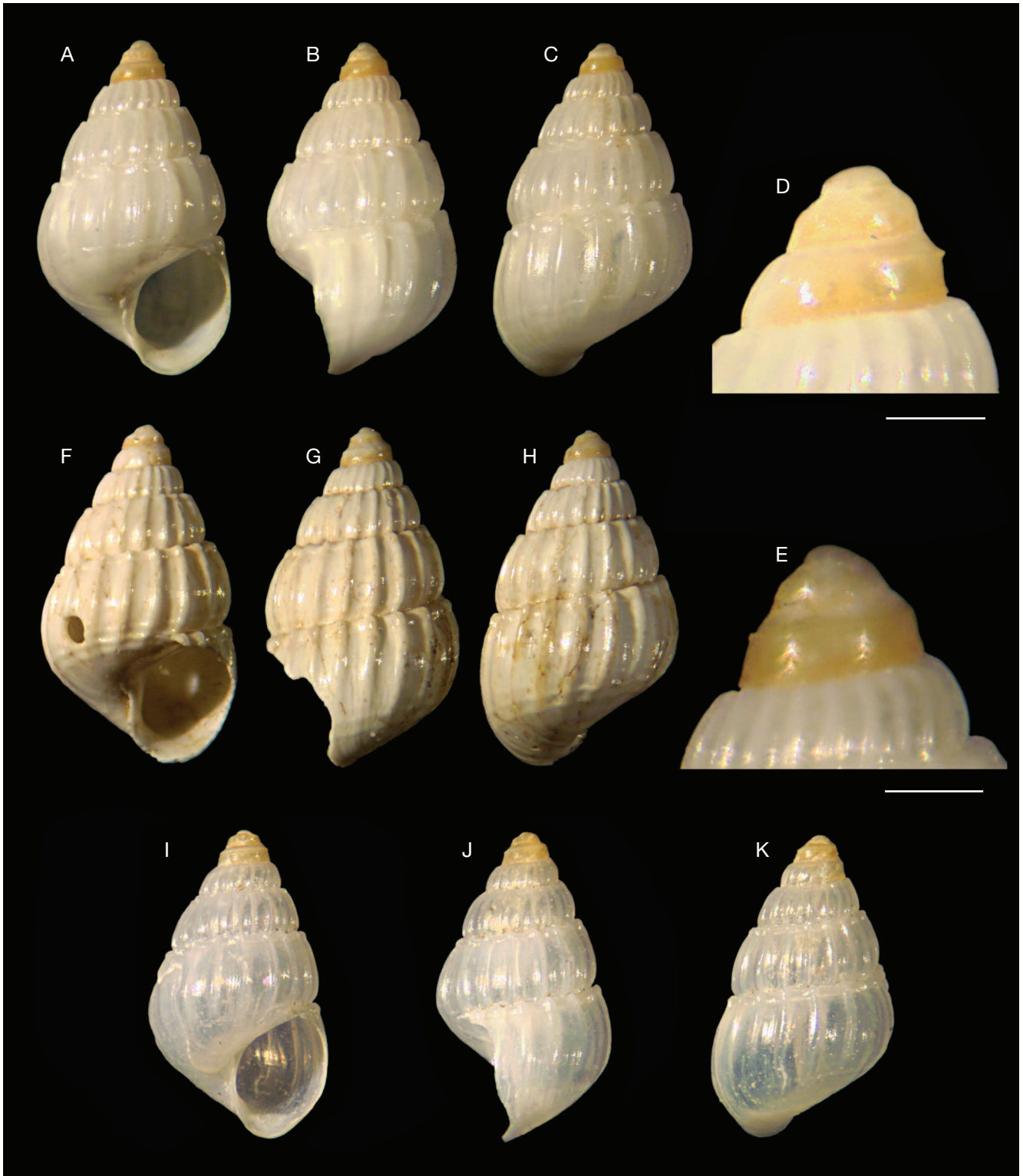


FIG. 18. — *Benthonellania megan* n. sp.: **A-E**, holotype, height 2.7 mm, width 1.6 mm Marquesas: MUSORSTOM 9 Stn DR1247 1150-1250 m $10^{\circ}34'S$, $138^{\circ}42'W$, type locality, [MNHN-IM-2000-37695](#); **F-H**, paratype, height 2.7 mm, width 1.6 mm, type locality, [MNHN-IM-2000-37696](#); **I-K**, paratype, height 2.5 mm, width 1.475 mm, type locality, [MNHN-IM-2000-37696](#). Scale bar: D, E, 0.25 mm.

Benthonellania megan n. sp.
(Figs 18A-K; 19F-H; 25G; 26L; Tables 1; 2)

[urn:lsid:zoobank.org:act:9B36A331-6E3D-48ED-8B90-31C7D64BB919](https://doi.org/10.3896/BI.2022.9B36A331-6E3D-48ED-8B90-31C7D64BB919)

TYPE MATERIAL. — **Holotype**. Marquesas • 1 dd (height 2.7 mm, width 1.6 mm, Figs 18A-E; 19F-H); Fatu Hiva, MUSORSTOM 9 Stn DR1247; $10^{\circ}34'S$, $138^{\circ}42'W$; 1.IX.1997; 1150-1250 m depth; [MNHN-IM-2000-37695](#).

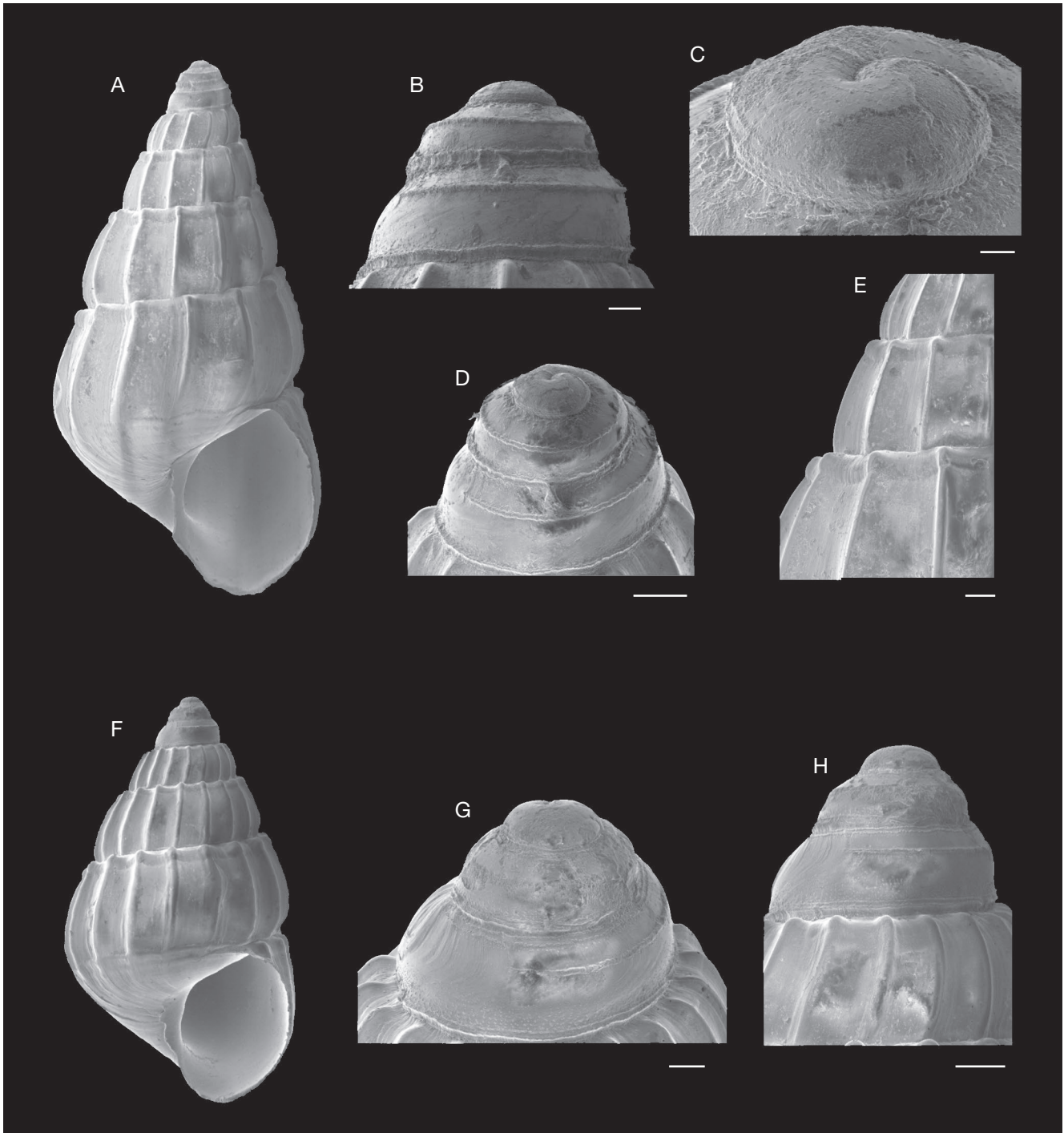


FIG. 19. — *Benthonellania* spp. (SEM): **A-E**, *Benthonellania tarava* n. sp., holotype, Tarava Seamounts, height 3.5 mm, MNHN-IM-2000-37687: shell (**A**); detail of the protoconch microstructure (**B-D**); detail of the teleoconch axial sculpture (**E**); **F-H**, *Benthonellania megan* n. sp., holotype, Marquesas, height 2.7 mm, MNHN-IM-2000-37695: shell (**F**); detail of the protoconch microstructure (**G, H**). Scale bars: B, E, G, H, 100 µm; C, 20 µm; D, 50 µm.

Paratypes. Marquesas • 5 dd; same locality data as holotype; MNHN-IM-2000-37696.

TYPE LOCALITY. — Marquesas, Fatu Hiva, MUSORSTOM 9 Stn DR1247; 10°34'S, 138°42'W; 1150-1250 m depth.

OTHER MATERIAL EXAMINED. — **Australes** • 1 dd; Rimatara, BENTHAUS Stn DW2021; 22°37'S, 152°49'W; 25.XI.2002; 1200-1226 m depth.

DISTRIBUTION AND SYMPATRY. — The species is at present known from the South Pacific Ocean, at Marquesas (Fatu Hiva Island) and Australes (Rimatara), with only empty shells collected in 1150-1250 m depth (Fig. 25G).

Benthonellania megan n. sp. is sympatric with *Benthonella boucbeti* n. sp. at the Marquesas (Fatu Hiva Island) and Australes (Rimatara); with *Benthonella communis* n. sp. at the Australes (Rimatara); with *Benthonellania bouteti* n. sp. at the Australes (Rimatara); with *Benthonellania tarava* n. sp. at the Australes

(Rimatara); with *Benthonellania lozoueti* n. sp. at the Marquesas (Fatu Hiva Island); with *Benthonellania alis* n. sp. at the Australes (Rimatara) (Table 2).

ETYMOLOGY. — Dedicated to Megan Zampa, granddaughter of one of the authors (B. Amati).

DESCRIPTION OF HOLOTYPE

Shell (Figs 18A-C; 19F-H)

Small for the genus, height 2.7 mm, width 1.6 mm, height/width ratio 1.687, pretty solid, ovate-conical.

Protoconch (Figs 18D, E; 19G, H)

Multispiral, acute of 2.5 whorls, height 0.40 mm, nucleus diameter 0.095 mm, first half whorl diameter 0.162 mm, maximum diameter 0.437 mm; (protoconch I in poor condition), protoconch II with two fine spiral keels, the lower larger, a fine cordlet of microtubercles in the subsutural area. Microtubercles spread over the entire surface (Fig. 19G, H). Protoconch-teleoconch boundary barely visible, sinuous.

Teleoconch

Of *c.* 3.5 convex whorls, suture canaliculate, crowned by small tubercles at tips of axial ribs. Height last whorl 1.75 mm, height/height last whorl ratio 1.542. Axial sculpture of 16 curved, slightly opisthocline ribs on last whorl, slightly narrower than interspaces, abruptly interrupted on the suture line. Spiral sculpture of 3 very weak fine cordlets on the base. Microsculpture of only growth striae (Fig. 19H). Umbilical chink absent. Aperture pyriform, large, height 1.1 mm, height/height aperture ratio 2.454, peristome continuous, varix absent (outer lip broken). Columella arcuate, simple.

Colour

Coloration of teleoconch translucent white, protoconch orange.

Operculum and soft parts

Unknown.

VARIABILITY

Species not very variable (See Table 1 and Appendix 11).

REMARKS

All the examined specimens have a broken peristome (presence/absence of lip thickening not observable).

B. tarava n. sp. differs from *B. megan* n. sp. in its larger size height 2.92-3.75 mm vs height 2.40-2.70 mm in *B. megan* n. sp., higher height/width ratio 1.859-1.807 vs 1.662 in *B. megan*; more whorls 4-4.65 vs 3.20-3.50 in *B. megan* n. sp., less numerous axial ribs on the last whorl 11-14 (mean 12.6) vs 14-19 (mean 16.5) in *B. megan* n. sp., and its more slender protoconch with two fine spiral cordlets, with a large smooth median area, and a fine spiral cordlet below the abapical cordlets vs two fine spiral cordlets, the lower larger, a fine cordlet of microtubercles in the subsutural area and microtubercles over the entire surface in *B. megan* n. sp.

Benthonellania tuamotu n. sp.

(Figs 20A-K; 22A-D; 25H; 26M; Tables 1; 2)

[urn:lsid:zoobank.org:act:49FA642C-D59A-49E5-9B73-0A544D048F6A](https://doi.org/10.21203/rs.3.rs-2120312/v1)

TYPE MATERIAL. — **Holotype.** Tuamotu • 1 dd (height 4.42 mm, width 2.5 mm, Figs 20A-C; 22A-D); Tikehau, TARASOC Stn DW3388; 14°56'S, 148°14'W; 6.X.2009; 820-835 m depth; MNHN-IM-2000-37697.

Paratypes • 3 dd; same locality data as holotype • 2 dd; MNHN-IM-2000-37699; Tikehau, Stn DW3389; 14°55'S, 148°15'W; 6.X.2009; 889 m depth; MNHN-IM-2000-37698 • 1 dd; Tikehau, Stn DW3387; 14°57'S, 148°16'W; 6.X.2009; 550-600 m depth; MNHN-IM-2000-37700.

TYPE LOCALITY. — Tuamotu, Tikehau, TARASOC Stn DW3388; 14°56'S, 148°14'W; 820-835 m depth.

OTHER MATERIAL EXAMINED. — **Tuamotu** • 3 dd; SW Kaukura, TARASOC Stn DW3359; 15°57'S, 147°08'W; 1.X.2009; 462-980 m depth; MNHN • 5 dd, 1 lv; Kaukura, TARASOC Stn DW3373; 15°41'S, 146°54'W; 4.X.2009; 507-607 m depth; MNHN • 8 dd; between Tikehau and Rangiroa, TARASOC Stn DW3349; 15°05'S, 148°03'W; 30.IX.2009; 976-997 m depth; MNHN.

Society Islands • 1 dd; Maupiti, TARASOC Stn DW3407; 16°32'S, 152°31'W; 12.X.2009; 445-645 m depth; MNHN • 1 dd; Raiatea, TARASOC Stn DW3451; 16°53'S, 151°21'W; 18.X.2009; 440-490 m depth; MNHN.

Tarava Seamounts • 1 dd; Mont Punu Taipu, TARASOC Stn DW3308; 19°16'S, 151°01'W; 23.IX.2009; 592-632 m depth; MNHN • 1 dd; Mont 'Otaha, TARASOC Stn DW3327; 18°45'S, 152°16'W; 26.IX.2009; 747-836 m depth; MNHN • 2 dd; Mont 'Otaha, TARASOC Stn DW3333; 18°45'S, 152°18'W; 26.IX.2009; 795-975 m depth; MNHN.

Australes • 1 dd; Rimatara, BENTHAUS Stn DW2021; 22°37'S, 152°49'W; 25.XI.2002; 1200-1226 m depth; MNHN • 2 dd; Rimatara, BENTHAUS Stn DW2020; 22°37'S, 152°49'W; 25.XI.2002; 920-930 m depth; MNHN • 3 dd; South coast of Rurutu, BENTHAUS Stn DW2010; 22°32'S, 151°21'W; 25.XI.2002; 520-950 m depth; MNHN • 1 dd; Récif Neilson, BENTHAUS Stn DW1925; 27°00'S, 146°05'W; 12.XI.2002; 560-790 m depth; MNHN.

DISTRIBUTION AND SYMPATRY. — The species is at present known from the South Pacific Ocean, at Tarava Seamounts (Mont 'Otaha, Mont Punu Taipu), Society Islands (Maupiti, Raiatea), Tuamotu (SW Kaukura, between Tikehau and Rangiroa, Tikehau, Kaukura) and Australes (Rimatara, South coast of Rurutu, Récif Neilson), with empty shells collected in 440-997 m depth, and a single live collected specimen, from Tuamotu, Kaukura, TARASOC Stn DW3373 507-607 m 15°41'S, 146°54'W (Fig. 25H).

Benthonellania tuamotu n. sp. is sympatric with *Benthonella boucheti* n. sp. at the Tarava Seamounts (Mont 'Otaha), Australes (Rimatara, South coast of Rurutu, Récif Neilson); with *Benthonella basistriata* n. sp. at the Tuamotu (Tikehau, Kaukura); with *Benthonellania maestratii* n. sp. at the Australes (Récif Neilson, South coast of Rurutu); with *Benthonella communis* n. sp. at the Tarava Seamounts (Mont Punu Taipu), Society Islands (Maupiti, Raiatea), Tuamotu (SW Kaukura, Kaukura between Tikehau and Rangiroa, Tikeha), Australes (Rimatara, South coast of Rurutu, Récif Neilson); with *Benthonellania bouteti* n. sp. at the Tarava Seamounts (Mont 'Otaha, Mont Punu Taipu), Tuamotu (SW Kaukura, Kaukura, between Tikehau and Rangiroa, Tikehau), Society Islands (Maupiti, Raiatea), Australes (Rimatara, South coast of Rurutu, Récif Neilson); with *Benthonellania tarava* n. sp. at the Tarava Seamounts (Mont 'Otaha), Tuamotu (SW Kaukura, Kaukura, between Tikehau and Rangiroa, Tikehau), Australes (Rimatara, South coast of Rurutu); with *Benthonellania alis* n. sp. at the Tarava Seamounts (Mont 'Otaha, Mont Punu Taipu), Australes (Rimatara, South coast of Rurutu) (Table 2).

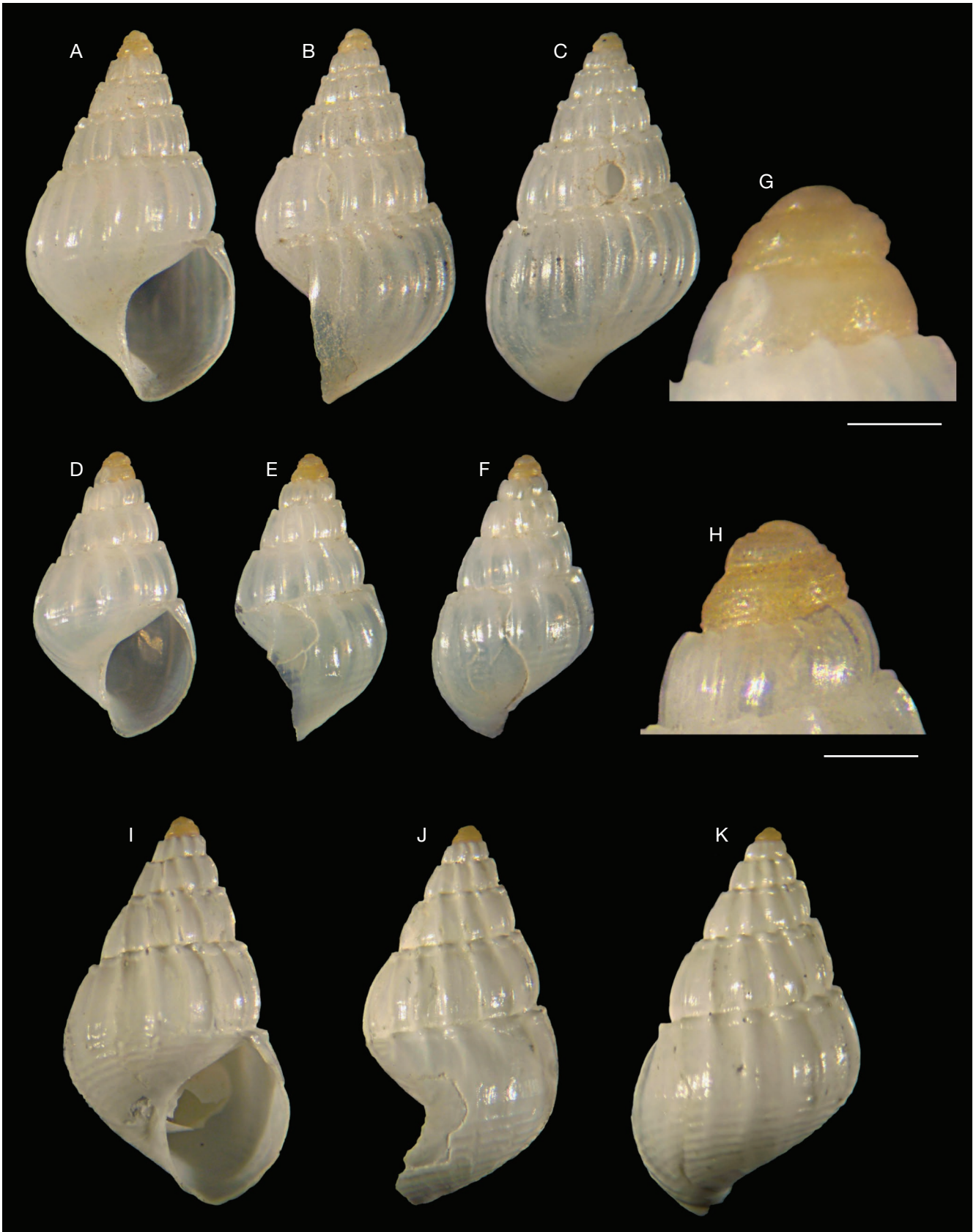


FIG. 20. — *Benthonellania tuamotu* n. sp.: **A-C**, holotype, height 4.42 mm, width 2.5 mm, Tuamotu, TARASOC Stn DW3388, 820-835 m, 14°56'S, 148°14'W, MNHN-IM-2000-37697; **D-H**, paratype, height 3.4 mm, width 1.95 mm, type locality, MNHN-IM-2000-37698; **I-K**, specimen, height 4.70 mm, width 2.75 mm, Tuamotu: TARASOC Stn DW3349, 976-997 m, 15°06'S, 148°03'W. Scale bars: G, H, 0.25 mm.

ETYMOLOGY. — After the name of the area of the type locality (Tuamotu Islands), used as a noun in apposition.

DESCRIPTION OF HOLOTYPE

Shell (Figs 20; 22A–D)

Large for the genus, height 4.42 mm, width 2.5 mm, height/width ratio 1.77, not very solid, ovate-conical, rather slender, with slightly stepped outline, broad base and large aperture.

Protoconch (Fig. 22B, D)

Multispiral, acute of 2.30 whorls, height 0.40 mm, nucleus diameter 0.10 mm, first half whorl diameter 0.187 mm, maximum diameter 0.475 mm; (protoconch I in poor condition) protoconch II with two spiral cordlets with a wavy-zigzag pattern in the upper area, two fine spiral keels in the lower half; in the interspaces oblique microstructures (Fig. 22B). Protoconch-teleoconch boundary marked, prosocline, sinuous.

Teleoconch

Of 4.5 whorls, almost flat apically, the last ones convex, suture canaliculate, crowned by large tubercles at tips of axial ribs, highlighted by a subsutural spiral groove. Height last whorl 2.9 mm, height/height last whorl ratio 1.524. Axial sculpture of 20 slightly curved, barely acute and prosocline ribs on last whorl, almost orthocline on first whorls, slightly narrower than interspaces, abruptly interrupted before the base. Spiral sculpture of 4 fine cordlets only on the base on last whorl. Microsculpture only growth striae (Fig. 22C). Umbilical chink absent. Aperture pyriform, small, height 1.85 mm, height/height aperture ratio 2.391, peristome continuous, outer lip (broken) internally smooth. Columella arcuate, slightly angular, simple.

Colour

Coloration of teleoconch translucent white, protoconch orange.

Operculum and soft parts

Unknown.

VARIABILITY

Species not very variable (See Table 1 and Appendix 12). The only adult specimen (Tuamotu, Kaukura 507–607 m depth) with soft parts and operculum inside the shell, has the intact outer lip without varix.

REMARKS

Benthonellania charope (Melvill & Standen, 1901) from the Gulf of Oman (c. 374 m depth), and *Benthonellania profundior* (Hedley, 1907) n. comb. from 33 miles east of Sydney (c. 1458 m depth), are very similar to each other, and to *Benthonella tuamotu* n. sp. for their outline with stepped whorls. However, both have paucispiral vs multispiral protoconch in *B. tuamotu* n. sp., are smaller (height 1.75 mm *B. charope* and 2.95 mm *B. profundior* n. comb. mm vs 3.60–4.95 mm in *B. tuamotu* n. sp.), have lower height/width ratios (1.476–1.596

in *B. charope* and 1.478–1.609 in *B. profundior* vs 1.625–1.787 in *B. tuamotu* n. sp.) and more pronounced spiral sculptures (see Melvill & Standen 1901: 365, pl. XXII, fig. 8; Hedley 1907: 358, pl. LXVII, fig. 15).

See under *Benthonellania lozoueti* n. sp. for diagnostic comparison.

Benthonellania lozoueti n. sp.

(Figs 21; 22E–I; 25F; 26N; Tables 1; 2)

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TYPE MATERIAL. — **Holotype**. Marquesas • 1 dd (height 4.33 mm, width 2.66 mm, Figs 21A–C, 22E–I); Fatu Hiva, MUSORSTOM 9 Stn DR1244; 10°28'S, 138°42'W; 1.IX.1997; 1015–1020 m depth; MNHN-IM-2000-37701

Paratypes • 10 dd; same locality data as holotype • 6 dd; MNHN-IM-2000-37703; Fatu Hiva, Stn DR1247; 10°34'S, 138°42'W; 1.IX.1997; 1150–1250 m depth; MNHN-IM-2000-37702.

OTHER MATERIAL EXAMINED. — **Marquesas** • 3 dd; Eiao, MUSORSTOM 9 Stn CP1278; 7°52'S, 140°39'W; 5.IX.1997; 1000 m depth; MNHN • 1 dd; Eiao, MUSORSTOM 9 Stn DW1275; 7°53'S, 140°38'W; 5.IX.1997; 627 m depth; MNHN.

TYPE LOCALITY. — Marquesas, Fatu Hiva, MUSORSTOM 9 Stn DR1244; 10°28'S, 138°42'W; 1.IX.1997; 1015–1020 m depth.

DISTRIBUTION AND SYMPATRY. — The species is at present known from the South Pacific Ocean, at Marquesas (Eiao Island and Fatu Hiva Island), with only empty shells collected in 627–1250 m depth (Fig. 25F).

Benthonellania lozoueti n. sp. is sympatric with *Benthonella bouchei* n. sp. at the Marquesas (Fatu Hiva Island); with *Benthonellania megan* n. sp. at the Marquesas (Fatu Hiva Island) (Table 2).

ETYMOLOGY. — This species is named after Pierre Lozouet (MNHN, Paris) for his contribution to Malacology, including his work on *Benthonella* and *Benthonellania*.

DESCRIPTION OF HOLOTYPE

Shell (Figs 21A–C; 22E–I)

Large for the genus, height 3.86 mm, width 2.6 mm, height/width ratio 1.484, pretty solid, ovate-conical.

Protoconch (Fig. 22F–H)

Multispiral, of 2 whorls, height 0.35 mm, nucleus diameter 0.10 mm, first half whorl diameter 0.175 mm, maximum diameter 0.412 mm; protoconch I with only microtubercles, some spirally arranged (Fig. 22G), protoconch II with three zig-zag spiral cordlets on upper part; inferiorly a fourth spiral cord. In the second half of the whorl, numerous microstructures often welded between them (Fig. 22F, H). Protoconch-teleoconch boundary barely visible.

Teleoconch

Of 4 convex whorls, suture canaliculate, crowned by small tubercles at tips of axial ribs, highlighted by a subsutural spiral groove. Height last whorl 2.8 mm, height/height last whorl ratio 1.378. Axial sculpture of 26 curved and opisthocline ribs



FIG. 21. — *Benthonellania lozoueti* n. sp.: A-C, holotype, height 3.86 mm, width 2.6 mm, Marquesas: MUSORSTOM 9 Stn DR1244, 1015-1020 m, 10°28'S, 138°42'W, MNHN-IM-2000-37701; D-G, paratype, height 4.33 mm, width 2.66 mm, type locality, MNHN-IM-2000-37702; H-J, specimen, height 3.55 mm, width 2.3 mm, Marquesas: MUSORSTOM 9 Stn CP1278, 1000 m, 7°52'S, 140°39'W. Scale bar: G, 0.50 mm.

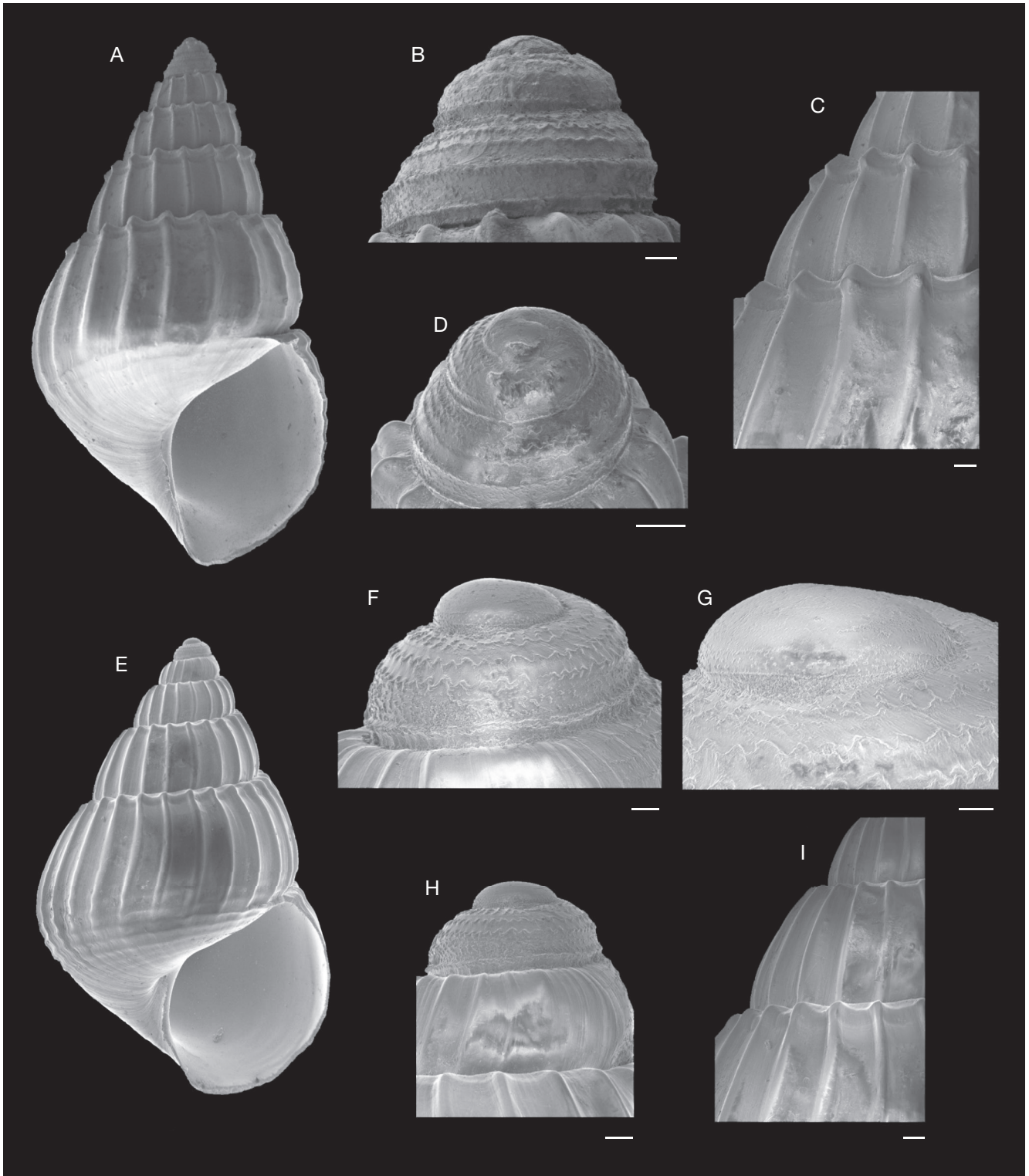


FIG. 22. — *Benthonellania* spp. (SEM): **A-D**, *Benthonellania tuamotu* n. sp., holotype, [MNHN-IM-2000-37697](#), Tuamotu: height 4.42 mm: shell (**A**), detail of the protoconch microsculpture (**B**, **D**); detail of the teleoconch axial sculpture (**C**); **E-I**, *Benthonellania lozoueti* n. sp., holotype, [MNHN-IM-2000-3770](#), Marquesas: height 3.86 mm: shell (**E**), detail of the protoconch microsculpture (**F-H**), detail of the teleoconch axial sculpture (**I**). Scale bars: B, H, 50 µm; C, D, I, 100 µm; F, 30 µm; G, 20 µm.

on last whorl, narrower than interspaces, gradually vanishing towards the base. Spiral sculpture of 7 (last one barely visible) weak fine cordlets on the base, uppermost one, suprasutural, visible on all whorls. Weak bulges at intersections with axial

ribs. Microsculpture of only growth striae (Fig. 22I). Umbilical chink present. Aperture pyriform, large, height 1.75 mm, height/height aperture ratio 2.205, peristome continuous, outer lip broken. Columella arcuate, simple.

Colour

Coloration of teleoconch translucent white, protoconch whitish.

Operculum and soft parts

Unknown.

VARIABILITY

Species not very variable (See Table 1 and Appendix 13).

REMARKS

All the examined specimens have a broken peristome (presence/absence of lip thickening not observable).

B. lozoueti n. sp. differs from *B. tuamotu* n. sp. by the presence of weak thickenings at the intersections of the spiral cordlets with the axial ribs, absent in *B. tuamotu* n. sp.; *B. lozoueti* n. sp. has a slightly convex base vs slightly concave in *B. tuamotu* n. sp. and on average has more numerous and finer axial ribs (22.4 vs 17.5 in *B. tuamotu* n. sp.).

***Benthonellania maestratii* n. sp.**

(Figs 23; 24A-C; 25G; 26O; Tables 1; 2)

[urn:lsid:zoobank.org:act:B89A1D9D-C9AE-42A4-9F2E-B76C317DF351](https://doi.org/10.21203/rs.3.rs-17317351)

TYPE MATERIAL. — **Holotype.** Australes • 1 dd (height 2.50 mm, width 1.62 mm, Figs 23A-E, 24A-C); Récif Neilson, BENTHAUS Stn DW1925; 27°00'S, 146°05'W; 12.XI.2002; 560-790 m depth; MNHN-IM-2000-37704.

TYPE LOCALITY. — Australes, Récif Neilson, BENTHAUS Stn DW1925; 27°00'S, 146°05'W; 560-790 m depth.

OTHER MATERIAL EXAMINED. — Australes • 3 dd; South coast of Rurutu, BENTHAUS Stn DW2010; 22°32'S, 151°21'W; 24.XI.2002; 520-950 m depth; MNHN.

DISTRIBUTION AND SYMPATRY. — The species is known in the South Pacific Ocean from the Australes (Récif Neilson, South coast of Rurutu), with only empty shells collected in 520-950 m depth (Fig. 25G).

Benthonellania maestratii n. sp. is sympatric with *Benthonella boucheti* n. sp., *Benthonella communis* n. sp., *Benthonellania bouteti* n. sp. and *Benthonellania tuamotu* n. sp. at the Australes (Récif Neilson, South coast of Rurutu); with *Benthonellania tarava* n. sp. and *Benthonellania alis* n. sp. at the Australes (South coast of Rurutu) (Table 2).

ETYMOLOGY. — Named after Philippe Maestrati (MNHN), for his friendship and his long lasting, precious contribution to sample treating in the field and at the Muséum.

DESCRIPTION OF HOLOTYPE**Shell (Figs 23A-E; 24A-C)**

Of medium size for the genus, height 2.50 mm width 1.625 mm, height/width ratio 1.538, not very solid, ovate-globose.

Protoconch (Figs 23D, E; 24B, C)

Multispiral, dome-shaped, of 2.3 whorls, height 0.325 mm, nucleus diameter 0.062 mm, first half whorl diameter 0.150 mm, maximum diameter 0.450 mm; protoconch I with 4 spiral threads interspaced by microtubercles more or less welded

together (Fig. 24C), protoconch II with one abapical cordlet, the rest of surface covered with delicate lace-shaped structures, and two median with wavy spiral cordlets (Fig. 24B). Protoconch-teleoconch boundary marked.

Teleoconch

Of 3.2 convex whorls, suture non impressed, with clathrate sculpture. Height last whorl 1.75 mm, height/height last whorl ratio 1.428. Axial sculpture of 35 curved and opisthocline ribs on last whorl, well spaced *c.* 4 times narrower than interspaces, continuing through the columellar fissure. Varix broad, not thickened. Spiral sculpture on the last whorl of 22 cordlets not equidistant, narrower than axial ribs: 15 very fine adapical, 7 basal more spaced; others very fine spiral cordlets in the periumbilical area. Microsculpture of only growth striae. Umbilical chink present. Aperture subpyriform, simple, rounded, height 1.10 mm, height/height aperture ratio 2.272, peristome continuous, outer lip weakly prosocline and slightly varicose, internally smooth. Columella arcuate, simple.

Colour

Coloration of teleoconch translucent white, protoconch orange.

Operculum and soft parts

Unknown.

VARIABILITY

Species not very variable (See Table 1 and Appendix 14), only four specimens examined, two adults, one sub-adult and one juvenile. Maximum dimensions: height 3.13 mm, width 2.05 mm (from South coast of Rurutu). The number of axial ribs and spiral cordlets on the last whorl, are respectively 35-57 and 22-35.

REMARKS

Benthonellania maestratii n. sp. resembles some European species of *Alvania*: *A. stenolopha* Bouchet & Warén, 1993, *A. adiphoros* Bouchet & Warén, 1993, *A. microstriata* Hoenselaar & Goud, 1998 and *A. seinensis* Gofas, 2007. It is easily distinguished from all those species, in its more convex whorls and the multispiral protoconch of 2.25-2.3 whorls vs paucispiral protoconch of 1.4, 1.5, 0.9-1.0 and 1.25 whorls respectively (see Bouchet & Warén 1993: 652-653, figs 1447, 1482-1487, 1516; Hoenselaar & Goud 1998: 91, figs 44-47; Gofas 2007: 795, figs 7E-H).

Alvania nicobarica (Thiele, 1925) [described as *Rissoa (Alvania) nicobarica* by Thiele (1925: 86, pl. 6, fig. 30) (MolluscaBase 2021f)] differs from *B. maestratii* n. sp. for the smaller size (0.95 mm in height and 0.7 mm in width vs 2.5-3.12 mm and 1.62-2.07 in width in *B. maestratii* n. sp.), the lower height/width ratio (1.357 vs 1.507-1.538 in *B. maestratii* n. sp.) and for the protoconch described without sculpture vs protoconch with abapical cordlets and microsculpture in *B. maestratii* n. sp.

Benthonellania listera (Dall, 1927) [*Rissoa listera* Dall, 1927: 117], from the Atlantic Ocean differs from *B. maestratii* n. sp.

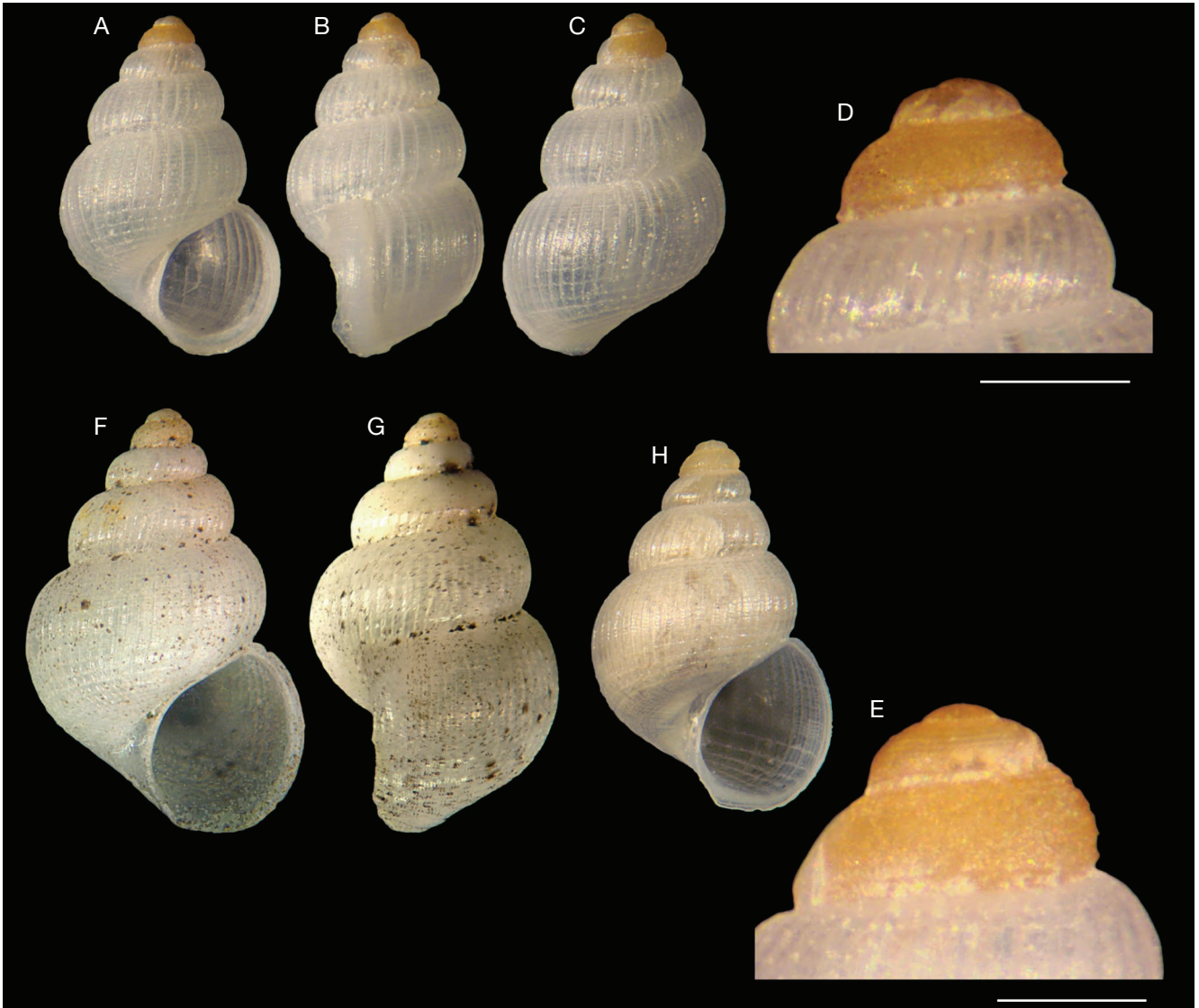


FIG. 23. — *Benthonellania maestratii* n. sp.: **A-E**, holotype, height 2.50 mm width 1.62 mm, Australes: BENTHAUS Stn DW1925, 560-790 m, type locality, [MNHN-IM-2000-37704](#); **F, G**, height 3.12 mm, width 2.07 mm, Australes: BENTHAUS Stn DW2010, 520-950 m depth, [22°32'S, 151°21'W](#); **H**, height 2.8 mm, width 1.85 mm, Australes: BENTHAUS Stn DW2010, 520-950 m depth, [22°32'S, 151°21'W](#). Scale bars: D, E, 0.25 mm.

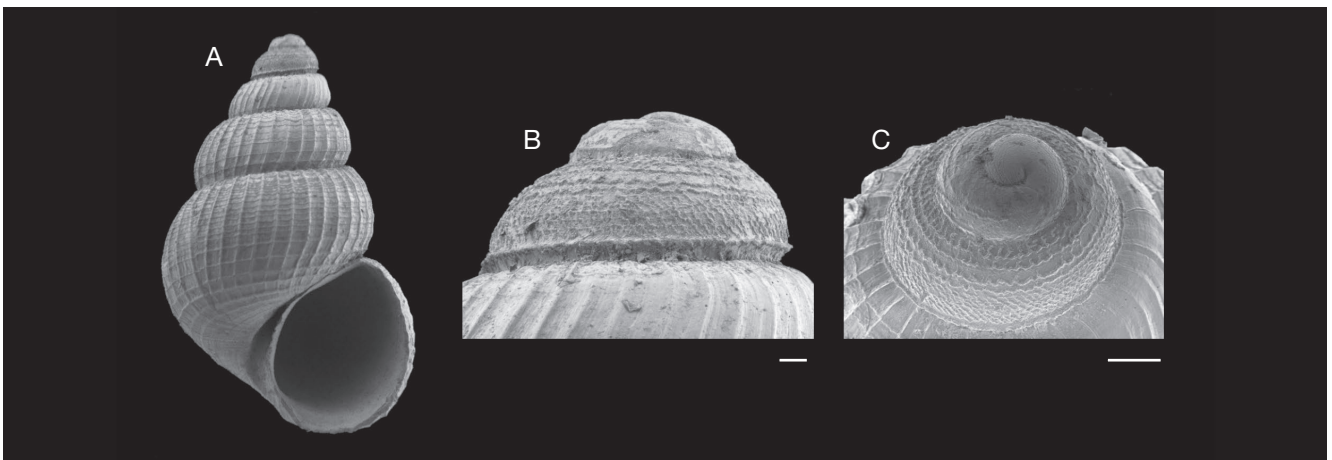


FIG. 24. — *Benthonellania maestratii* n. sp. (SEM): **A-C**, holotype, height 2.50 mm, Australes, [MNHN-IM-2000-37704](#): shell (**A**); detail of the protoconch microstructure (**B, C**). Scale bars: B, 40 μ m; C, 100 μ m.

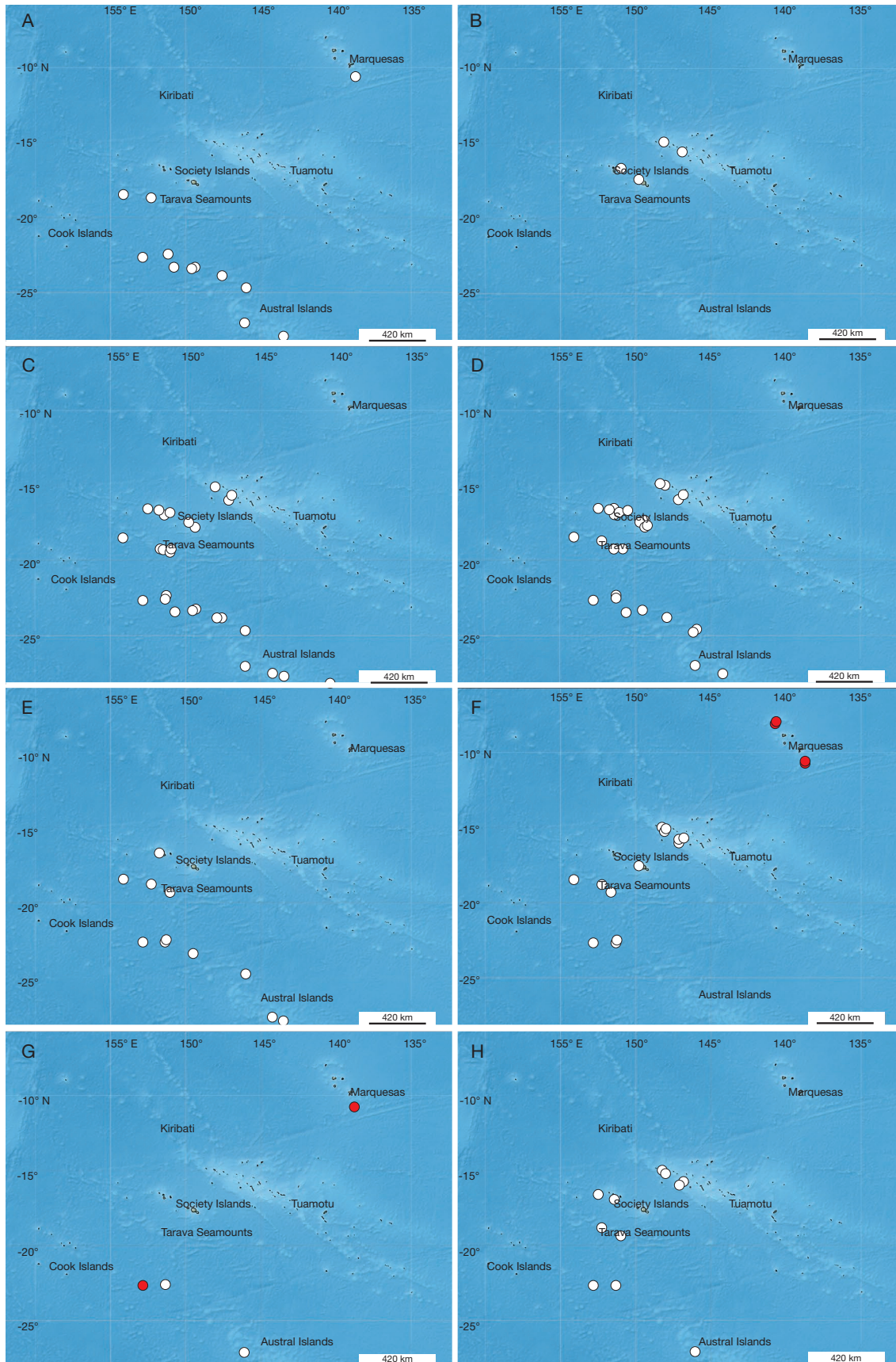


FIG. 25. — Distribution maps of the Polynesian species of *Benthonella* Dall, 1889 and *Benthonellania* Lozouet, 1990: **A**, *Benthonella boucheti* n. sp.; **B**, *Benthonella basistriata* n. sp.; **C**, *Benthonella communis* n. sp.; **D**, *Benthonellania bouteti* n. sp.; **E**, *Benthonellania alis* n. sp.; **F**, *Benthonellania tarava* n. sp. (○) and *Benthonellania lozoueti* n. sp. (●); **G**, *Benthonellania megan* n. sp. (○) and *Benthonellania maestratii* n. sp. (●); **H**, *Benthonellania tuamotu* n. sp.

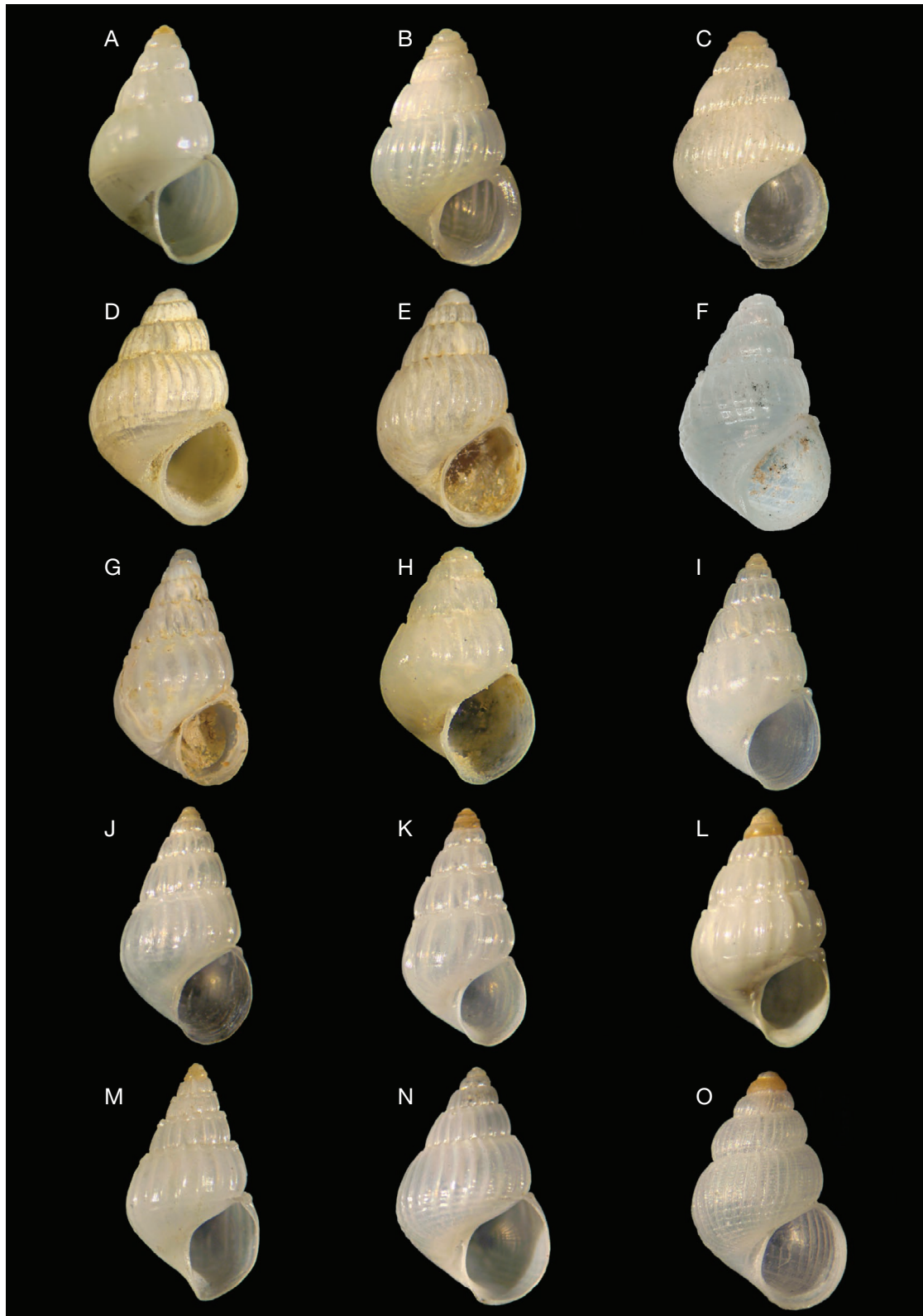


FIG. 26. — *Benthonella* and *Benthonellania* sp.: **A**, *Benthonella boucheti* n. sp., holotype, [MNHN-IM-2000-37666](#), height 4.32 mm; **B**, *Benthonella basistriata* n. sp., holotype, [MNHN-IM-2000-37668](#), height 2.0 mm; **C**, *Benthonella communis* n. sp., holotype, [MNHN-IM-2000-37670](#), height 2.2 mm; **D**, *Benthonellania hertzogi* (Thiele, 1925) n. comb., syntype, ZMB/Moll 64981, height 2.85 mm; **E**, *Benthonellania thielei* n. sp., holotype, ZMB/Moll 64955a, height 3.05 mm; **F**, *Benthonellania precipitata* (Dall, 1889) n. comb., holotype, MCZ-7470, height 3.92; **G**, *Benthonellania africana* (Thiele, 1925) n. comb., lectotype, ZMB-64955, height 3.85 mm; **H**, *Benthonellania aequatorialis* (Thiele, 1925) n. comb., syntype, ZMB-64973, height 1.8 mm; **I**, *Benthonellania bouteti* n. sp., holotype, [MNHN-IM-2000-37678](#), height 3.45 mm; **J**, *Benthonellania alis* n. sp., holotype, [MNHN-IM-2000-37685](#), height 3.35; **K**, *Benthonellania tarava* n. sp., holotype, [MNHN-IM-2000-37687](#), height 3.5 mm; **L**, *Benthonellania megan* n. sp., holotype, [MNHN-IM-2000-37695](#), height 2.7 mm; **M**, *Benthonellania tuamotu* n. sp., holotype, [MNHN-IM-2000-37697](#), height 4.42 mm; **N**, *Benthonellania lozoueti* n. sp., holotype, [MNHN-IM-2000-37701](#), height 3.86 mm; **O**, *Benthonellania maestratii* n. sp., holotype, [MNHN-IM-2000-37704](#), height 2.50 mm.

in its more slender outline with less convex whorls; the crown formed by the subsutural thickening of the axial ribs vs absent in *B. maestratii* n. sp.; the umbilical chink absent vs present in *B. maestratii* n. sp. (see also the drawing of one syntype by Moolenbeek & Faber 1991: 53).

Benthonellania maestratii n. sp. is also similar to *Benthonellania colombiana* (Romer & Moore, 1988) n. comb., but the latter differs in its smaller size (height 1-1.3 mm vs height 2.5-3.13 mm in *B. maestratii* n. sp.), fewer axial ribs (26 vs 35-57 in *B. maestratii* n. sp.), different spiral sculpture (subsutural groove and 7-9 cords vs 22-35 fine cords in *B. maestratii* n. sp.); protoconch with two spiral cordlets, one finer and median, the other suprasutural with a zigzagging pattern, and with tubercles scattered over the entire surface vs protoconch II with abapical cordlet, the rest of surface covered with delicate lace-shaped structures with wavy and oblique spirals in *B. maestratii* n. sp.

DISCUSSION

The extant diversity of deep-water species of rissoids of the *Benthonella-Benthonellania* lineage was estimated to consist of seventeen species before this revision: four species of *Benthonella*, and thirteen species of *Benthonellania*.

We have transferred two species to *Benthonella* (*Benthonella olangoensis* n. comb. and *B. kazakhstanica* n. comb.) and seven to *Benthonellania* (*B. precipitata* n. comb., *B. hertzogi* n. comb., *B. africana* n. comb., *B. aequatorialis* n. comb., *B. profundior* n. comb., *B. sumatrana* n. comb., *B. colombiana* n. comb.), and described eleven new species (three *Benthonella* and eight *Benthonellania*), for a total of twenty species added, with an increase of the formally recognised diversity of 118%.

The known extant diversity was previously centred in the Indo-West Pacific province for *Benthonella*, with three IWP species vs one Atlantic-Mediterranean, but largely in the Atlantic for *Benthonellania*, with only one species from the Indo-West Pacific, and 12 from the Atlantic. After this revision, *Benthonella* comprises nine recognised Indo-West Pacific species and two Atlantic-Mediterranean; *Benthonellania* has 16 recognised Indo-West Pacific species and 14 Atlantic. The total repartition of the species of the *Benthonella-Benthonellania* lineage changed from a 13 vs four Atlantic vs Indo-West Pacific (76% vs 24%), to 16 vs 25 (39% vs 61%). However, we suggest that these figures are still not stabilized, the patterns being biased by a differential taxonomic efforts, and that with more deep-water samples studied, the Indo-West Pacific diversity may even further increase (as e.g. suggested by the undescribed species reported from Japan by Hasegawa 2005).

According to the systematic framework herein adopted, and including all species that we know, named and unnamed (Table 3), all eight extant species of *Benthonella* have a multispiral protoconch indicating a planktotrophic development, as also have six of the seven fossils (with the potential, unchecked exception of *B. loriei*). Of the 30 extant species of *Benthonellania*, 20 have a multispiral protoconch (nine species in the Indo-West Pacific, 11 in the Atlantic), and 10 paucispiral (six in the Indo-West Pacific, four in the Atlantic); one fossil with multispiral protoconch, and one paucispiral.

As is frequent with deep water molluscs, the rate of live collected specimens is very low and this hampers a correct definition of the actual bathymetric range of the species. However, the few live collected specimens in this revision, were sampled between 440 and 877 m depth. Empty shells were collected in the conservative range of 110-1250 m depth. The species with the shallowest range were *Benthonella communis* n. sp. (with the shallowest record from 110 m) and *Benthonellania*

TABLE 3. — List of the extant and fossil (†) known species of the genera *Benthonella* Dall, 1889 and *Benthonellania* Lozouet, 1990 with geographic area, iconographic references and protoconch type.

No.	Species	Geographic area	Iconographic reference	Protoconch type
	<i>Benthonella</i> Dall, 1889			
1	<i>Benthonella alvaniformis</i> Lozouet, 2014 †	Upper Eocene (Priabonian) of France	Lozouet 2014: 24, 26, figs 2C-E, 3A-H	multispiral
2	<i>Benthonella basistriata</i> n. sp.	Pacific	Figs 8A-I; 10F, G; 26B	multispiral
3	<i>Benthonella bearnensis</i> Lozouet, 2014 †	Lower Eocene (Late Ypresian) of France	Lozouet 2014: 24, 27, figs 2A, B, 4A-D	multispiral
4	<i>Benthonella boucheti</i> n. sp.	Pacific	Figs 7A-G; 10A-E; 26A	multispiral
5	<i>Benthonella brontodes</i> Lozouet, 1990 †	Upper Oligocene (Chattian) of France	Lozouet 1990: 24, 30, figs 2O-Q, 7F-I	multispiral
6	<i>Benthonella communis</i> n. sp.	Pacific	Figs 9A-F; 10H-J; 26C	multispiral
7	<i>Benthonella decorata</i> (Thiele, 1925)	Western Indian	Thiele 1925: pl. XIV, fig. 28	multispiral
8	<i>Benthonella kazakhstanica</i> (Amitrov, 2010) n. comb.	Eocene of Kazakhstan	Amitrov 2010: 386, pl. 3, figs 3a-c	multispiral
9	<i>Benthonella loriei</i> Weisbord, 1962 †	Pliocene (Lower Mare formation) of Venezuela	Weisbord 1962 pl. 46, figs 7, 8, 47 figs 6, 7	paucispiral
10	<i>Benthonella lutetiana</i> Lozouet, 2014 †	Middle Eocene (Lutetian) of France	Lozouet 2014: 24, 28, figs 2I-K, 5A-E	multispiral
11	<i>Benthonella margaritifera</i> (R. B. Watson, 1886)	Pacific	Watson 1886: pl. XLIII, fig. 3	multispiral?
12	<i>Benthonella olangoensis</i> (Poppe, Tagaro & Stahlschmidt, 2015) n. comb.	Western Pacific	Poppe et al. 2015: 24, 49, pl. 8, figs 1-3	multispiral
13	<i>Benthonella priabonica</i> Lozouet, 2014 †	Upper Eocene (Priabonian) of France	Lozouet 2014: 25, 29, figs 2L-N, 6E-H	multispiral

Table 3. — Continuation.

No.	Species	Geographic area	Iconographic reference	Protoconch type
14	<i>Benthonella sculpta</i> (Thiele, 1925)	Indian	Thiele 1925: pl. XIV, fig. 27	multispiral
15	<i>Benthonella tenella</i> (Jeffreys, 1869)	Eastern Atlantic – Mediterranean	Jeffreys 1869: pl. C7, fig. 7	multispiral
16	<i>Benthonella</i> sp. cf. <i>tenella</i>	Western Pacific	Hasegawa 2005: 149, fig. 5K	paucispiral?
17	<i>Benthonella</i> sp.	Western Pacific	Hasegawa 2005: 149, figs 5L	multispiral
<i>Benthonellania</i> Lozouet, 1990				
1	<i>Benthonellania acuticostata</i> (Dall, 1889)	Western Atlantic	Dall 1889: pl. XIX, fig. 10	multispiral
2	<i>Benthonellania aequatorialis</i> (Thiele, 1925) n. comb.	Eastern Indian	Figs 12A-G; 13C, D; 26H	multispiral
3	<i>Benthonellania africana</i> (Thiele, 1925) n. comb.	Western Indian	Figs 11A-N; 13A, B; 26G	paucispiral
4	<i>Benthonellania agastachys</i> Bouchet & Warén, 1993	Eastern Atlantic	Bouchet & Warén 1993: 698, 683, figs 1584, 1592, 1593	paucispiral
5	<i>Benthonellania alis</i> n. sp.	Pacific	Figs 15A-H; 16G-H; 26J	multispiral
6	<i>Benthonellania alvanioides</i> J. D. Oliver & Rolán, 2017	Eastern Atlantic	Oliver & Rolán 2017: 49, 51, 53, figs 1A-E, 2A-H, 3A-F	multispiral
7	<i>Benthonellania antepelagica</i> Lozouet, 1990 †	Upper Oligocene of France	Lozouet 1990: 320, figs 10-11	paucispiral
8	<i>Benthonellania bouteti</i> n. sp.	Pacific	Figs 14A-H; 16A-E; 26I	multispiral
9	<i>Benthonellania charope</i> (Melvill & Standen, 1901)	Indian	Melvill & Standen 1901: pl. XXII, fig. 8	paucispiral
10	<i>Benthonellania colombiana</i> (Romer & Moore, 1988) n. comb.	Western Atlantic	Romer & Moore 1988: 132, figs 1, 2	multispiral
11	<i>Benthonellania coronata</i> Absalão & Santos, 2004	Western Atlantic,	Absalão & Santos 2004: 335, figs 5, 10	multispiral
12	<i>Benthonellania donmoorei</i> Moolenbeek & Faber, 1991	Western Atlantic	Moolenbeek & Faber 1991: 52, figs 1-3	multispiral
13	<i>Benthonellania fayalensis</i> (R. B. Watson, 1886)	Eastern Atlantic	Watson 1886: pl. XLIV, fig. 7	paucispiral
14	<i>Benthonellania gofasi</i> Lozouet, 1990	Eastern Atlantic	Lozouet 1990: 315, 323, 326, figs 1-3, 4, 8-9, 20-23	multispiral
15	<i>Benthonellania hertzogi</i> (Thiele, 1925) n. comb.	Western Indian	Figs 3A-J; 6A, B; 26D	paucispiral
16	<i>Benthonellania listera</i> (Dall, 1927)	Western Atlantic	No figure in Dall 1927. Moolenbeek & Faber 1991: 53.	multispiral
17	<i>Benthonellania lozoueti</i> n. sp.	Pacific	Figs 21A-J; 22E-I; 26N	multispiral
18	<i>Benthonellania maestratii</i> n. sp.	Pacific	Figs 23A-H; 24A-C; 26O	multispiral
19	<i>Benthonellania megan</i> n. sp.	Pacific	Figs 18A-K; 19F-H; 26L	multispiral
20	<i>Benthonellania multicostata</i> Absalão & Santos, 2004	Western Atlantic	Absalão & Santos 2004: 335, figs 4, 9	multispiral
21	<i>Benthonellania oligostigma</i> Bouchet & Warén, 1993	Eastern Atlantic	Bouchet & Warén 1993: 680, 693, figs 1581, 1582, 1594	paucispiral
22	<i>Benthonellania praexanthias</i> Lozouet, 1990 †	Upper Miocene of Angola	Lozouet 1990: 320, figs 12-13	multispiral
23	<i>Benthonellania precipitata</i> (Dall, 1889) n. comb.	Western Atlantic	Figs 2A-E; 26F	paucispiral
24	<i>Benthonellania profundior</i> (Hedley, 1907) n. comb.	Pacific	Hedley 1907: pl. LXVII, fig. 15	paucispiral
25	<i>Benthonellania pyrrias</i> (R. B. Watson, 1886)	Western Atlantic	Watson 1886: pl. XLIV, fig. 4	multispiral
26	<i>Benthonellania sumatrana</i> (Thiele, 1925) n. comb.	Eastern Indian	Thiele 1925: pl. XVIII, fig. 25	paucispiral
27	<i>Benthonellania tarava</i> n. sp.	Pacific	Figs 17A-K; 19A-E; 26K	multispiral
28	<i>Benthonellania thielei</i> n. sp.	Western Indian	Figs 5A-N; 6C-E; 26E	paucispiral
29	<i>Benthonellania tuamotu</i> n. sp.	Pacific	Figs 20A-K; 22A-D; 26M	multispiral
30	<i>Benthonellania xanthias</i> (R. B. Watson, 1886)	Western Atlantic	Watson 1886: pl. XLIV, fig. 5	multispiral
31	<i>Benthonellania</i> sp.	Western Pacific	Hasegawa 2005: 149, fig. 5J	multispiral
32	<i>Benthonellania</i> sp. (' <i>B. gofasi</i> ' <i>sensu</i> Bouchet & Warén, 1993)	Eastern Atlantic	Bouchet & Warén 1993: 1583, 1589-1590). See also Absalão & Santos 2004 and Oliver & Rolán 2017	multispiral
32	' <i>Alvania</i> ' sp. 2	Western Pacific	Hasegawa 2005: 149, fig. 5I	paucispiral?

bouteti n. sp. (206 m). The species with the deepest range were *B. boucheti* n. sp., *B. bouteti* n. sp., *B. tarava* n. sp., *B. lozoueti* n. sp., and *B. megan* n. sp. (all with the deepest record from 1250 m), *B. communis* n. sp., and *B. alis* n. sp. (both with 1226 m); it should be noted that these figures correspond to the lower operational limit on board of R/V Alis, which means that they do not necessarily represent the deepest limits of these species ranges.

Benthonella has been proven to represent an independent lineage within the Rissooidea in a molecular phylogenetic analysis (Criscione *et al.* 2016) confirming the similar sug-

gestion derived from its somehow peculiar anatomy (Ponder 1985). *Benthonella* and *Benthonellania* should in principle be diagnosed by shell and anatomical features. *Benthonella* has a less slender shell and a protoconch with a low spire, with a delicate sculpture of 1-3 spiral cordlets; the protoconch in *Benthonellania* is defined as more slender with a more marked and diversified sculpture. Anatomically, *Benthonellania* has pallial tentacles, eyes and a well developed posterior gland (all lacking in *Benthonella*), and the anterior pedal gland not visible (see Ponder 1985; Lozouet 1990). Bouchet & Warén (1993: 679) already addressed the problems of using shell features alone

to distinguish the two genera. We confirm these difficulties. For instance, *Benthonellania tarava* n. sp. has a slender shell (typical of *Benthonellania*) but a low-spired protoconch with two spiral cords (typical of *Benthonella*); *Benthonellania megan* n. sp. has a low height/width ratio (typical of *Benthonella*), a protoconch with two spiral cords (still as in *Benthonella*) but the larval shell has a higher spire, more similar to *Benthonellania*. Morphology clearly suggests that the species currently included in *Benthonella* and *Benthonellania* represent altogether a single lineage of deep-water gastropods. Whether they also represent two actually distinct sublineages should be tested by enlarging the study of the anatomy to more species and by adding molecular phylogenetic analyses: both approaches require the availability of more numerous live collected samples.

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APPENDICES

APPENDIX 1. — Measurements of teleoconch and protoconch of *Benthonella boucheti* n. sp. in mm, with range, mean and standard deviation: **1**, holotype, Tarava Seamounts, Mont Honu, 787-798 m depth; **2**, Australes, Banc Président Thiers, 500-850 m depth.

Teleoconch	1	2	Min-max	Mean	Std
Height	4.32	3.75	3.75-4.32	4.03	0.403051
Width	2.75	2.60	2.60-2.75	2.67	0.106066
Height/Width ratio	1.572	1.442	1.442-1.572	1.507	0.091924
Aperture height	2.0	1.90	1.90-2.0	2.05	0.070711
Height/Height aperture ratio	2.162	1.973	1.973-2.162	2.067	0.133643
Height last whorl	2.90	2.80	2.80-2.90	2.85	0.070711
Height/Height last whorl ratio	1.491	1.351	1.351-1.491	1.421	0.098995
No. of whorls	4.2	3.4	3.4-4.2	3.8	0.565685
No. axial ribs on last whorl	20	21	20-21	20.5	0.707107
No. spiral cords on last whorl	7	6	6-7	6.5	0.707107
Varix	no	no	no	no	–
Umbilical false chink	yes	yes	yes	yes	–
Protoconch	1	2	Min-max	Mean	Std
Height	0.412	0.425	0.412-0.425	0.418	0.009192
Diameter of nucleus	0.075	0.087	0.075-0.087	0.081	0.008485
Diameter of first half whorl	0.137	0.125	0.125-0.137	0.131	0.008485
Maximum diameter	0.600	0.570	0.570-0.600	0.580	0.021213
No. of whorls	2.4	2.5	2.4-2.5	2.45	0.070711
Multispiral	yes	yes	yes	yes	–
Paucispiral	no	no	no	no	–

APPENDIX 2. — Measurements of teleoconch and protoconch of *Benthonella basistriata* n. sp. in mm, with range, mean and standard deviation: **1**, holotype Tuamotu, Tikehau, 889 m depth; **2**, Society Islands, Huahine, 500-612 m depth; **3**, Society Islands, Moorea, 485-560 m depth; **4**, Moorea, 610 m depth; **5**, Society Islands, Huahine, 557 m depth; **6-10**, Tuamotu, Kaukura, 507-607 m depth.

Teleoconch	1	2	3	4	5	6	7	8	9	10	Min-max	Mean	Std
Height	2.0	2.47	2.05	2.25	2.25	2.50	2.50	2.50	2.60	1.95	1.95-2.60	2.30,7	0.240002
Width	1.30	1.55	1.30	1.50	1.40	1.55	1.62	1.60	1.55	1.32	1.30-1.62	1.46,9	0.126794
Height/Width ratio	1.538	1.596	1.577	1.500	1.607	1.613	1.543	1.562	1.677	1.477	1.477-1.677	1.56,9	0.05845
Aperture height	0.82	1.0	0.85	0.97	0.95	1.07	1.02	1.0	1.0	0.87	0.82-1.07	0.95,5	0.08182
Height/Height aperture ratio	2.424	2.450	2.412	2.319	2.368	2.336	2.451	2.500	2.600	2.241	2.241-2.600	2.41	0.100975
Height last whorl	1.30	1.65	1.37	1.50	1.50	1.70	1.65	1.06	1.72	1.35	1.30-1.72	1.53,4	0.21145
Height/Height last whorl ratio	1.538	1.500	1.491	1.500	1.500	1.470	1.515	1.562	1.512	1.444	1.444-1.562	1.503	0.032781
No. of whorls	3.25	3.45	3	3.25	3.25	3.75	3.5	3.65	3.75	3	3-3.75	3.38,5	0.279931
No. axial ribs on last whorl	18	15	17	17	20	16	15	14	14	17	14-20	16.3	1.888562
No. spiral cords on last whorl	6	6	6	5	5	6	5	6	6	6	5-6	5.7	0.483046
Varix	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	–
Umbilical chink	no	no	no	no	no	no	no	no	no	no	no	no	–
Protoconch	1	2	3	4	5	6	7	8	9	10	Min-max	Mean	Std
Height	0.34	0.31	0.41	0.40	0.35	0.30	0.32	0.32	0.31	0.32	0.30-0.41	0.338	3.02765
Diameter of nucleus	0.075	0.087	0.075	0.075	0.075	0.062	0.087	0.075	0.070	0.070	0.062-0.087	0.075	0.038239
Diameter of first half whorl	0.125	0.145	0.137	0.145	0.137	0.112	0.145	0.145	0.145	0.120	0.112-0.145	0.135	0.007505
Maximum diameter	0.375	0.400	0.462	0.450	0.425	0.400	0.425	0.412	0.412	0.387	0.375-0.462	0.415	0.012285
No. of whorls	2.5	2.5	2.9	2.75	2.4	2.5	2.3	2.45	2.35	2.5	2.3-2.9	2.51,5	0.026844
Multispiral	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	–
Paucispiral	no	no	no	no	no	no	no	no	no	no	no	no	–

APPENDIX 3. — Measurements of teleoconch and protoconch of *Bertholletia communis* n. sp. in mm, with range, mean and standard deviation: 1, holotype, Tarava Seamounts; Mont. Ari'i Moana 614-664 m depth; 2-10, para-types, Tarava Seamounts, Mont. Ari'i Moana 614-664 m depth; 11-20, Australes, Côte Nord de Rurutu, 250-302 m depth.

Teleoconch	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	Min-max	Mean	Std
Height	2.20	1.92	2.40	2.27	2.37	2.22	2.20	2.10	2.20	1.90	2.22	1.27	1.85	2.35	2.02	2.25	1.85	2.10	1.70	1.42	1.27-2.40	2.0405	0.30607
Width	1.45	1.25	1.60	1.47	1.50	1.42	1.37	1.40	1.45	1.30	1.45	0.92	1.25	1.52	1.35	1.42	1.25	1.32	1.15	1.0	0.92-1.60	1.342	0.17022
Height/Width ratio	1.517	1.536	1.500	1.544	1.580	1.563	1.606	1.500	1.517	1.461	1.531	1.380	1.480	1.546	1.496	1.584	1.480	1.591	1.478	1.420	1.380-1.606	1.5155	0.05742
Aperture height	1.0	0.82	1.02	0.97	0.90	0.97	0.85	0.92	0.82	0.92	0.82	0.57	0.82	1.0	0.87	0.90	0.75	0.85	0.77	0.70	0.57-1.02	0.8675	0.112244
Height/Height aperture ratio	2.200	2.341	2.353	2.340	2.633	2.466	2.268	2.470	2.391	2.317	2.337	2.228	2.256	2.350	2.322	2.500	2.466	2.470	2.208	2.028	2.028-2.633	2.3472	0.133545
Height last whorl	1.57	1.32	1.70	1.55	1.50	1.52	1.50	1.42	1.50	1.30	1.50	0.92	1.30	1.57	1.37	1.45	1.25	1.40	1.17	1.02	0.92-1.70	1.3915	0.192443
Height/Height last whorl ratio	1.396	1.454	1.412	1.464	1.580	1.460	1.466	1.479	1.466	1.461	1.480	1.380	1.423	1.497	1.474	1.552	1.480	1.500	1.453	1.392	1.380-1.552	1.46345	0.049161
No. of whorls	3.25	3.1	3.5	3.3	3.6	3.25	3.2	3.15	3.2	3	3.2	2.2	3.0	3.5	3.1	3.45	3.0	3.2	2.7	2.35	2.2-3.6	3.1125	0.353879
No. axial ribs on last whorl	27	19	22	23	21	19	21	22	23	19	18	24	16	18	18	18	21	18	20	17	16-27	20.2	2.726092
No. spiral cords on last whorl *	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	-
Varix	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes
Umbilical false chink	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes
Protoconch	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	Min-max	Mean	Std
Height	0.300	0.275	0.290	0.287	0.300	0.300	0.300	0.325	0.325	0.325	0.325	0.325	0.315	0.325	0.310	0.325	0.325	0.340	0.325	0.325	0.275-0.340	0.31335	0.017021
Diameter of nucleus	0.050	0.075	0.062	0.062	0.062	0.062	0.062	0.062	0.062	0.062	0.062	0.062	0.062	0.062	0.055	0.057	0.062	0.070	0.075	0.075	0.050-0.075	0.06315	0.006335
Diameter of first half whorl	0.112	0.125	0.125	0.125	0.125	0.125	0.125	0.125	0.125	0.125	0.125	0.112	0.125	0.137	0.120	0.125	0.120	0.137	0.150	0.130	0.112-0.150	0.1259	0.008303
Maximum diameter	0.425	0.412	0.425	0.437	0.437	0.437	0.437	0.400	0.437	0.425	0.450	0.400	0.437	0.450	0.450	0.462	0.450	0.450	0.450	0.437	0.400-0.462	0.4354	0.016832
No. of whorls	2.30	2.35	2.35	2.35	2.35	2.30	2.30	2.30	2.35	2.35	2.35	2.25	2.25	2.30	2.35	2.35	2.40	2.30	2.25	2.30	2.25-2.40	2.32	0.041039
Multispiral	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes
Paucispiral	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	-

APPENDIX 4. — Measurements of teleoconch and protoconch of *Benthonellania hertzogi* (Thiele, 1925) n. comb. in mm, with range, mean and standard deviation: 1, 2, south of South Africa, 126 m depth. Symbol: *, last rib thicker, similar to a varix.

Teleoconch	1	2	Min-max	Mean	Std
Height	2.85	2.47	2-47-2-85	2.66	0.27
Width	1.95	1.75	1.75-1.95	1.85	0.14
Height/Width ratio	1.461	1.411	1.411-1.461	1.436	0.035
Aperture height	1.40	1.25	1.25-1.40	1.325	0.106
Height/Height aperture ratio	2.036	1.976	1.976-2-036	2.006	0.042
Height last whorl	2.07	1.80	1.80-2.07	1.935	0.191
Height/Height last whorl ratio	1.377	1.372	1.372-1.377	1.3745	0.004
No. of whorls	3.10	2.75	2.75-3.10	2.925	0.247
No. axial ribs on last whorl	26	24	24-26	25	1.4
No. spiral cords on last whorl	5	4	4-5	4.5	0.7
Varix (yes-no)	no	no*	no	no	–
Umbilical chink (yes-no)	yes	yes	yes	yes	–
Protoconch	1	2	Min-max	Mean	Std
Height	0.375	0.400	0.375-0.400	0.388	0.018
Diameter of nucleus	0.212	0.200	0.200-0.212	0.206	0.008
Diameter of first half whorl	0.362	0.350	0.350-0.362	0.356	0.008
Maximum diameter	0.500	0.500	0.500	0.5	0
No. of whorls	1.25	1.25	1.25	1.25	0
Multispiral	no	no	no	no	–
Paucispiral	yes	yes	yes	yes	–

APPENDIX 5. — Measurements of teleoconch and protoconch of *Benthonellania africana* (Thiele, 1925) n. comb. in mm, with range, mean and standard deviation: 1-4, off Somalia, 693 m depth.

Teleoconch	1	2	3	4	Min-max	Mean	Std
Height	3.85	3.7	3.35	4	3.35-4	3.725	0.278388
Width	2.15	2.35	2.02	2.15	2.02-2.35	2.1675	0.136229
Height/Width ratio	1.790	1.574	1.658	1.860	1.574-1.860	1.7205	0.128658
Aperture height	1.55	1.50	1.25	1.40	1.25-1.55	1.425	0.132288
Height/Height aperture ratio	2.483	2.466	2.680	2.857	2.466-2.857	2.6215	0.184612
Height last whorl	2.50	2.55	2.25	2.45	2.25-2.55	2.4375	0.131498
Height/Height last whorl ratio	1.540	1.451	1.488	1.632	1.451-1.632	1.52775	0.078504
No. of whorls	4.10	3.50	3.70	4.25	3.50-4.25	3.8875	0.347311
No. axial ribs on last whorl	9	10	8	8	8-10	8.75	0.957427
No. spiral cords on last whorl	4	4	3	4	3-4	3.75	0.5
Varix (yes-no)	no	no	no	no	no	no	–
Umbilical chink (yes-no)	yes	yes	yes	yes	yes	yes	–
Protoconch	1	2	3	4	Min-max	Mean	Std
Height	0.375	0.450	0.412	0.437	0.375-0.450	0.4185	0.03301
Diameter of nucleus	0.200	0.250	0.275	0.225	0.200-0.275	0.2375	0.032275
Diameter of first half whorl	0.362	0.387	0.425	0.387	0.362-0.425	0.39025	0.025992
Maximum diameter	0.525	0.575	0.575	0.525	0.525-0.575	0.55	0.028868
No. of whorls	1.40	1.40	1.25	1.30	1.25-1.40	1.3375	0.075
Multispiral	no	no	no	no	no	no	–
Paucispiral	yes	yes	yes	yes	yes	yes	–

APPENDIX 6. — Measurements of teleoconch and protoconch of *Benthonellania thielei* n. sp. in mm, with range, mean and standard deviation: 1, holotype, off southern Somalia, 693 m depth; 2-4, paratypes off southern Somalia, 693 m depth.

Teleoconch	1	2	3	4	Min-max	Mean	Std
Height	3.05	3.20	2.55	2.97	2.55-3.20	2.9425	0.278493
Width	1.92	2.05	1.82	1.95	1.82-2.05	1.935	0.094692
Height/Width ratio	1.588	1.561	1.401	1.523	1.401-1.588	1.51825	0.082589
Aperture height	1.35	1.30	1.20	1.27	1.20-1.35	1.28	0.062716
Height/Height aperture ratio	2.259	2.461	2.125	2.338	2.125-2.461	2.29575	0.140948
Height last whorl	2.2	2.2	2.0	2.1	2.0-2.2	2.125	0.095743
Height/Height last whorl ratio	1.386	1.454	1.275	1.414	1.275-1.454	1.38225	0.076752
No. of whorls	3.50	3.60	3.35	3.35	3.35-3.60	3.45	0.122474
No. axial ribs on last whorl	20	14	13	18	13-20	16.25	3.304038
No. spiral cords on last whorl	6	4	5	6	4-6	5.25	0.957427
Varix (yes-no)	no	no	no	no	no	no	–
Umbilical chink (yes-no)	no	yes	no	yes	no-yes	no-yes	–
Protoconch	1	2	3	4	Min-max	Mean	
Height	0.337	0.350	0.312	0.300	0.300-0.350	0.32475	0.022824
Diameter of nucleus	0.187	0.212	0.212	0.187	0.187-0.212	0.1995	0.014434
Diameter of first half whorl	0.350	0.337	0.350	0.350	0.337-0.350	0.34675	0.0065
Maximum diameter	0.475	0.425	0.400	0.425	0.400-0.475	0.43125	0.031458
No. of whorls	1.10	1.15	1.10	1.25	1.10-1.25	1.15	0.070711
Multispiral	no	no	no	no	no	no	–
Paucispiral	si	si	si	si	yes	yes	–

APPENDIX 7. — Measurements of teleoconch and protoconch of *Benthonellania aequatorialis* (Thiele, 1925) n. comb. in mm, with range, mean and standard deviation: 1, 2, Nias-Sudkanal 470 m depth ('subadult').

Teleoconch	1	2	Min-max	Mean	Std
Height	1.80	1.95	1.80-1.95	1.875	0.106066
Width	1.35	1.37	1.35-1.37	1.36	0.014142
Height/Width ratio	1.333	1.423	1.333-1.423	1.378	0.06364
Aperture height	1.0	1.02	1.0-1.02	1.01	0.014142
Height/Height aperture ratio	1.800	1.911	1.800-1.911	1.8555	0.078489
Height last whorl	1.50	1.47	1.47-1.50	1.485	0.021213
Height/Height last whorl ratio	1.200	1.326	1.200-1.326	1.263	0.089095
No. of whorls	2.80	2.65	2.65-2.80	2.725	0.106066
No. axial ribs on last whorl	17	18	17	17.5	0.707107
No. spiral cords on last whorl	no	no	no	no	–
Varix (yes-no)	no	no	no	no	–
Umbilical chink (yes-no)	yes	yes	yes	yes	–
Protoconch	1	2	Min-max	Mean	Std
Height	0.275	0.275	0.275	0.275	0
Diameter of nucleus	0.075	0.075	0.075	0.075	0
Diameter of first half whorl	0.150	0.137	0.137-0.150	0.1435	0.009192
Maximum diameter	0.400	0.450	0.400-0.450	0.425	0.035355
No. of whorls	2.0	2.2	2.0-2.2	2.1	0.141421
Multispiral	yes	yes	yes	yes	–
Paucispiral	no	no	no	no	–

APPENDIX 8. — Measurements of teleoconch and protoconch of *Benthonellania boutefi* n. sp. in mm, with range, mean and standard deviation: **1**, holotype, Society Islands, Moorea, 660–680 m depth; **2–7**, paratypes, Society Islands, Moorea, 660–680 m depth; **8–17**, Australes: East of Rapa, 600–620 m depth.

Teleoconch	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	Min-max	Mean	Std
Height	3.45	3.40	3.25	2.92	3.10	3.07	2.95	4.15	3.75	3.65	3.90	3.80	3.40	3.45	3.67	3.67	3.82	2.92–4.15	3.494118	0.352528
Width	1.90	1.90	1.85	1.65	1.80	1.85	1.75	2.20	2.07	2.0	2.17	2.10	1.80	1.80	2.05	2.02	2.0	1.65–2.20	1.935882	0.155485
Height/Width ratio	1.816	1.789	1.757	1.770	1.722	1.660	1.686	1.886	1.811	1.825	1.797	1.809	1.888	1.917	1.790	1.817	1.910	1.660–1.917	1.802941	0.072376
Aperture height	1.40	1.30	1.25	1.15	1.10	1.15	1.15	1.42	1.30	1.30	1.40	1.32	1.20	1.20	1.20	1.37	1.32	1.10–1.42	1.266471	0.100308
Height/Height aperture ratio	2.464	2.615	2.600	2.539	2.818	2.670	2.565	2.955	2.884	2.808	2.786	2.879	2.833	2.875	3.058	2.679	2.894	2.464–3.058	2.760118	0.164884
Height last whorl	2.30	2.20	2.10	1.87	1.95	2.0	1.92	2.32	2.15	2.15	2.32	2.20	2.02	2.05	2.07	2.25	2.25	1.87–2.32	2.124706	0.142308
Height/Height last whorl ratio	1.500	1.545	1.547	1.561	1.590	1.535	1.536	1.789	1.744	1.698	1.681	1.727	1.683	1.683	1.773	1.631	1.698	1.500–1.773	1.642412	0.092945
No. of whorls	4	4	3.8	3.75	3.9	3.7	3.5	5.2	4.9	4.7	4.75	4.75	4.5	4.5	5	4.5	5	3.5–5.2	4.379412	0.537372
No. axial ribs on last whorl	15	15	15	12	14	16	14	23	20	19	17	16	16	17	18	20	20	12–23	16.88235	2.803622
No. spiral cords on last whorl	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	–	–
Varix	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	–	–
Umbilical false chink	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	–	–
Protoconch	1	2	3	4	5	6	7	1	2	3	4	5	6	7	8	9	10	Min-max	Mean	Std
Height	0.325	0.325	0.375	0.375	0.350	0.345	0.375	0.325	0.325	0.375	0.370	0.375	0.325	0.340	0.325	0.375	0.325	0.325–0.375	0.348824	0.02322
Diameter of nucleus	0.075	0.095	0.100	0.087	0.087	0.075	0.077	0.100	0.070	0.087	0.095	0.082	0.070	0.095	0.095	0.087	0.087	0.070–0.100	0.086118	0.009911
Diameter of first half whorl	0.150	0.152	0.160	0.150	0.162	0.145	0.150	0.170	0.170	0.170	0.170	0.135	0.145	0.162	0.162	0.175	0.162	0.135–0.175	0.158235	0.011256
Maximum diameter	0.400	0.400	0.437	0.400	0.400	0.420	0.425	0.375	0.370	0.400	0.387	0.400	0.375	0.387	0.350	0.387	0.387	0.350–0.437	0.394118	0.021112
No. of whorls	2.5	2.35	2.5	2.45	2.35	2.6	2.6	2.25	2.25	2.2	2.3	2.25	2.3	2.3	2.25	2.3	2.25	2.2–2.6	2.352941	0.128051
Multispiral	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	–	–
Paucispiral	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	–	–

APPENDIX 9. — Measurements of teleoconch and protoconch of *Benthonellania alis* n. sp. in mm, with range, mean and standard deviation: **1**, holotype, Australes, Côte Sud de Rurutu, 520-950 m depth; **2-10** paratypes, Australes, Côte Sud de Rurutu, 520-950 m depth.

Teleoconch	1	2	3	4	5	6	7	8	9	10	Min-max	Mean	Std
Height	3.35	4.0	3.5	3.75	3.70	3.45	3.65	3.30	3.25	3.05	3.05-4.0	3.5	0.279881
Width	1.79	2.20	2.0	2.05	2.05	2.0	2.0	1.85	1.87	1.75	1.75-2.20	1.956	0.138098
Height/Width ratio	1.875	1.818	1.750	1.830	1.805	1.725	1.825	1.784	1.738	1.743	1.725-1.875	1.7893	0.049248
Aperture height	1.23	1.45	1.25	1.45	1.40	1.25	1.32	1.20	1.25	1.10	1.10-1.45	1.29	0.11392
Height/Height aperture ratio	2.723	2.758	2.800	2.590	2.643	2.760	2.765	2.750	2.600	2.773	2.590-2.800	2.7162	0.07621
Height last whorl	2.20	2.40	2.15	2.30	2.30	2.20	2.25	2.0	2.10	1.92	1.92-2.40	2.182	0.145358
Height/Height last whorl ratio	1.522	1.666	1.628	1.630	1.608	1.568	1.622	1.650	1.548	1.588	1.522-1.666	1.603	0.045891
No. of whorls	4	4.6	4.2	4.25	4.5	4	4.2	4.2	4.1	3.8	3.8-4.6	4.185	0.235761
No. axial ribs on last whorl	20	24	21	20	21	23	22	22	19	19	19-24	21.1	1.66333
No. spiral cords on last whorl	3	3	3	3	3	3	3	3	3	3	3	3	0
Varix	no	no	no	no	no	no	no	no	no	no	no	no	–
Umbilical false chink	yes	yes	no	yes	yes	yes	no	no	no	no	no-yes	no-yes	–
Protoconch	1	2	3	4	5	6	7	8	9	10	Min-max	Mean	Std
Height	0.337	0.375	0.325	0.350	0.350	0.350	0.375	0.375	0.325	0.325	0.325-0.375	0.3487	0.020822
Diameter of nucleus	0.075	0.075	0.075	0.075	0.087	0.087	0.082	0.087	0.075	0.075	0.075-0.087	0.0793	0.005736
Diameter of first half whorl	0.175	0.125	0.150	0.150	0.157	0.170	0.157	0.162	0.137	0.162	0.125-0.175	0.1545	0.014916
Maximum diameter	0.412	0.400	0.387	0.437	0.420	0.437	0.425	0.450	0.400	0.425	0.387-0.450	0.4193	0.019653
No. of whorls	2.3	2.7	2.3	2.5	2.4	2.25	2.4	2.35	2.4	2.4	2.25-2.7	2.4	0.12693
Multispiral	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	–
Paucispiral	no	no	no	no	no	no	no	no	no	no	no	no	–

APPENDIX 10. — Measurements of teleoconch and protoconch of *Benthonellania tarava* n. sp. in mm, with range, mean and standard deviation: **1**, holotype, Tarava Seamounts, Mont 'Otaha, 795-975 m depth; **2**, paratype, Tarava Seamounts, Mont 'Otaha, 795-975 m depth; **3**, paratype, Tarava Seamounts, Mont 'Otaha, 795-975 m depth; **4**, Tarava Seamounts, Mont Horu, 787-792 m depth; **5-7**, Australes, Côte Sud de Rurutu, 920-950 m depth; **8**, Society Islands, Moorea, 844-877 m depth; **9**, Australes, Rimatara, 920-930 m depth; **10**, Australes, Côte Est de Rurutu, 430-850 m depth; **11-20**, Tuamotu, entre Tikehau & Rangiroa, 976-997 m depth.

Teleoconch	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	Min-max	Mean	Std	
Height	3.5	3.6	3.75	3.5	3.35	3.32	3.35	3.25	3.05	2.92	2.97	2.95	2.8	2.87	2.67	3.07	2.9	3.35	3.1	2.97	2.67-3.75	3.162	0.29325	
Width	1.85	1.90	1.92	1.82	1.80	1.75	1.82	1.85	1.67	1.67	1.60	1.60	1.55	1.62	1.52	1.60	1.70	1.80	1.80	1.62	1.55-1.92	1.723	0.122178	
Height/Width ratio	1.892	1.895	1.953	1.923	1.861	1.897	1.841	1.757	1.826	1.748	1.856	1.844	1.806	1.772	1.756	1.919	1.706	1.861	1.722	1.833	1.706-1.953	1.8334	0.070887	
Aperture height	1.27	1.3	1.35	1.3	1.1	1.15	1.1	1.12	1.1	1.05	1.02	1.07	1.02	1.05	1.0	1.05	1.0	1.22	1.1	1.05	1.0-1.27	1.121	0.108478	
Height/Height aperture ratio	2.745	2.769	2.777	2.692	3.045	2.887	3.045	2.902	2.772	2.781	2.912	2.757	2.745	2.733	2.670	2.924	2.900	2.746	2.818	2.828	2.670-3.045	2.8224	0.106009	
Height last whorl	2.1	2.1	2.2	2.1	1.95	2.0	1.95	1.97	1.87	1.77	1.75	1.77	1.70	1.75	1.67	1.80	1.77	2.05	1.90	1.80	1.67-2.20	1.8985	0.155911	
Height/Height last whorl ratio	1.666	1.714	1.704	1.666	1.718	1.660	1.718	1.650	1.631	1.650	1.697	1.666	1.647	1.612	1.599	1.705	1.638	1.634	1.631	1.650	1.599-1.718	1.6628	0.035734	
No. of whorls	4.45	4.5	4.65	4.5	4.5	4.3	4.5	4.35	4.0	4.2	4.1	4.0	3.9	4.1	3.6	4.1	4.0	4.4	4.1	4.2	3.6-4.65	4.2225	0.26131	
No. axial ribs on last whorl	12	11	13	13	11	13	13	14	13	13	13	15	14	15	12	13	14	15	16	14	11-16	13.35	1.308877	
No. spiral cords on last whorl	3	3	3	3	2	2	2	2	2	2	3	3	2	2	3	3	2	3	3	2	2-3	2.55	0.510418	
Varix	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	—	—	
Umbilical false chink	yes	yes	yes	yes	no	no	yes	yes	no	no	no	no	yes	yes	yes	no	no	no	no	no	no	no	—	—
Protoconch	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10	Min-max	Mean	Std	
Height	0.405	0.400	0.390	0.420	0.410	0.370	0.380	0.340	0.400	0.370	0.390	0.400	0.400	0.410	0.400	0.400	0.400	0.400	0.390	0.340	0.340-0.420	0.39075	0.021292	
Diameter of nucleus	0.087	0.087	0.087	0.087	0.100	0.087	0.087	0.095	0.087	0.100	0.087	0.075	0.087	0.095	0.087	0.095	0.087	0.082	0.080	0.087	0.075-0.100	0.0883	0.006131	
Diameter of first half whorl	0.175	0.175	0.145	0.170	0.150	0.157	0.162	0.150	0.170	0.175	0.170	0.150	0.160	0.175	0.170	0.160	0.175	0.162	0.170	0.162	0.145-0.175	0.16415	0.009805	
Maximum diameter	0.462	0.462	0.475	0.475	0.450	0.437	0.455	0.445	0.475	0.470	0.475	0.475	0.462	0.450	0.450	0.462	0.450	0.450	0.450	0.425	0.425-0.475	0.45775	0.014037	
No. of whorls	2.75	2.5	2.6	2.65	2.75	2.5	2.5	2.25	2.6	2.35	2.75	2.5	2.6	2.6	2.65	2.6	2.5	2.5	2.5	2.35	2.25-2.75	2.55	0.133771	
Multispiral	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	—	—
Paucispiral	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	—	—

APPENDIX 11. — Measurements of teleoconch and protoconch of *Benthonellania megan* n. sp. in mm, with range, mean and standard deviation: **1**, holotype, Marquesas, Fatu Hiva, 1150-1250 m depth; **2**, paratype, Marquesas: Fatu Hiva, 1150-1250 m depth; **3-5**, paratypes Marquesas, Fatu Hiva, 1150-1250 m depth; **6**, Australes, Rimatara, 1200-1226 m depth.

Teleoconch	1	2	3	4	5	6	Min-max	Mean	Std
Height	2.70	2.50	2.60	2.55	2.40	2.62	2.40-2.70	2.561667	0.104003
Width	1.60	1.47	1.50	1.60	1.50	?	1.47-1.60	1.534	0.061482
Height/Width ratio	1.687	1.695	1.733	1.594	1.600	?	1.594-1.733	1.6618	0.06169
Aperture height	1.10	1.0	1.05	1.05	1.0	1.07	1.0-1.10	1.045	0.03937
Height/Height aperture ratio	2.454	2.500	2.476	2.428	2.400	2.448	2.400-2.500	2.451	0.03514
Height last whorl	1.75	1.60	1.70	1.70	1.65	1.70	1.60-1.75	1.683333	0.05164
Height/Height last whorl ratio	1.542	1.562	1.523	1.500	1.454	1.541	1.454-1.562	1.520333	0.038609
No. of whorls	3.5	3.35	3.5	3.25	3.2	3.5	3.2-3.5	3.383333	0.136626
No. axial ribs on last whorl	16	16	17	19	17	14	14-19	16.5	1.643168
No. spiral cords on last whorl	3	4	3	3	3	3	3-4	3.166667	0.408248
Varix	no	no	no	no	no	no	no	no	–
Umbilical false chink	yes	yes	yes	yes	yes	yes	yes	yes	–
Protoconch	1	2	3	4	5	6	Min-max	Mean	Std
Height	0.400	0.375	0.387	0.375	0.375	0.412	0.375-0.412	0.387333	0.015655
Diameter of nucleus	0.095	0.062	0.075	0.087	0.087	0.087	0.062-0.095	0.082167	0.011771
Diameter of first half whorl	0.162	0.175	0.150	0.150	0.150	0.162	0.150-0.175	0.158167	0.010128
Maximum diameter	0.437	0.450	0.437	0.425	0.437	0.437	0.425-0.450	0.437167	0.00791
No. of whorls	2.5	2.3	2.4	2.4	2.3	2.5	2.3-2.5	2.4	0.089443
Multispiral	yes	yes	yes	yes	yes	yes	yes	yes	–
Paucispiral	no	no	no	no	no	no	no	no	–

APPENDIX 12. — Measurements of teleoconch and protoconch of *Benthonellania tuamotu* n. sp. in mm, with range, mean and standard deviation: **1**, holotype, Tuamotu, Tikehau 820-835 m depth; **2**, Australes, Rimatara 920-930 m depth; **3**, Tuamotu, entre Tikehau & Rangiroa, 976-997 m depth; **4-7**, Tuamotu, Kaukura, 507-607 m depth; **8**, Society Islands, Maupiti, 445-645 m depth; **9, 10**, Tuamotu, Tikehau, 889 m depth.

Teleoconch	1	2	3	4	5	6	7	8	9	10	Min-max	Mean	Std
Height	4.42	3.6	4.95	3.9	4.3	4.25	3.6	4.15	4.3	4.7	3.6-4.95	4.217	0.433719
Width	2.50	2.15	2.77	2.4	2.5	2.6	2.28	2.45	2.55	2.75	2.15-2.77	2.495	0.19179
Height/Width ratio	1.770	1.674	1.787	1.625	1.720	1.635	1.579	1.694	1.686	1.709	1.625-1.787	1.6879	0.064018
Aperture height	1.85	1.55	2.0	1.5	1.75	1.75	1.60	1.70	1.60	2.0	1.5-2.0	1.73	0.176698
Height/Height aperture ratio	2.391	2.322	2.475	2.600	2.457	2.428	2.250	2.441	2.687	2.350	2.250-2.687	2.4401	0.128579
Height last whorl	2.9	2.4	3.15	2.55	2.8	2.8	2.45	2.85	2.75	3.15	2.4-3.15	2.78	0.258414
Height/Height last whorl ratio	1.524	1.500	1.571	1.529	1.536	1.518	1.469	1.456	1.564	1.492	1.456-1.571	1.5159	0.037427
No. of whorls	4.5	4.0	5.1	4.2	4.5	4.5	4.0	4.5	4.6	4.7	4.0-5.1	4.46	0.330656
No. axial ribs on last whorl	20	17	18	20	18	18	16	18	14	16	14-20	17.5	1.840894
No. spiral cords on last whorl	4	4	4	4	4	4	4	4	5	8	4-8	4.5	1.269296
Varix	no	no	no	no	no	yes	yes	yes	no	no	yes-no	yes-no	–
Umbilical chink	no	no	no	no	no	no	no	no	no	no	no	no	–
Protoconch	1	2	3	4	5	6	7	8	9	10	Min-max	Mean	Std
Height	0.400	0.375	0.390	0.375	0.375	0.380	0.390	0.350	0.375	0.350	0.350-0.400	0.376	0.016125
Diameter of nucleus	0.100	0.117	0.087	0.100	0.087	0.100	0.112	0.087	0.087	0.087	0.087-0.117	0.0964	0.011296
Diameter of first half whorl	0.187	0.185	0.170	0.190	0.175	0.160	0.187	0.155	0.175	0.175	0.155-0.190	0.1759	0.011808
Maximum diameter	0.475	0.450	0.450	0.437	0.425	0.462	0.412	0.425	0.430	0.455	0.412-0.475	0.4421	0.01953
No. of whorls	2.3	2.25	2.35	2.25	2.3	2.3	2.25	2.3	2.3	2.2	2.2-2.35	2.28	0.042164
Multispiral	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	–
Paucispiral	no	no	no	no	no	no	no	no	no	no	no	no	–

APPENDIX 13. — Measurements of teleoconch and protoconch of *Benthonellania lozoueti* n. sp. in mm, with range, mean and standard deviation: **1**, holotype, Marquesas, Fatu Hiva, 1015-1020 m depth; **2-5**, paratypes, Marquesas, Fatu Hiva, 1015-1020 m depth; **6, 7**, Marquesas: Eiao CP1278, 1000 m depth; **8, 9**, Marquesas, Fatu Hiva DR1247, 1150-1250 m depth; **10**, subadult, Marquesas, Eiao DW1275, 627 m depth.

Teleoconch	1	2	3	4	5	6	7	8	9	10	Min-max	Mean	Std
Height	3.86	4.45	3.60	4.30	3.40	3.30	3.50	3.70	3.75	2.35	2.35-4.45	3.621	0.578378
Width	2.60	2.75	2.15	2.65	2.12	2.17	2.20	2.25	2.5	1.60	1.60-2.75	2.299	0.33818
Height/Width ratio	1.484	1.618	1.674	1.622	1.603	1.520	1.590	1.644	1.500	1.468	1.468-1.674	1.5723	0.072981
Aperture height	1.75	1.90	1.50	1.90	1.50	1.55	1.40	1.67	1.60	1.17	1.17-1.90	1.594	0.224707
Height/Height aperture ratio	2.205	2.342	2.400	2.263	2.266	2.129	2.500	2.215	2.343	2.008	2.008-2.500	2.2671	0.139869
Height last whorl	2.80	3.0	2.45	2.85	2.30	2.30	2.27	2.55	2.55	1.70	1.70-3.0	2.477	0.370826
Height/Height last whorl ratio	1.378	1.483	1.469	1.508	1.478	1.434	1.541	1.450	1.470	1.382	1.378-1.541	1.4593	0.051075
No. of whorls	4	4.5	3.8	4.3	?	3.75	4.2	3.9	4.2	3.2	3.2-4.5	3.983333	0.382426
No. axial ribs on last whorl	26	27	23	27	22	20	24	20	19	16	16-27	22.4	3.687818
No. spiral cords on last whorl	7	6	4	7	7	7	5	6	9	3	3-9	6.1	1.72884
Varix	no	no	no	no	no	no	no	no	no	no	no	no	–
Umbilical false chink	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	–
Protoconch	1	2	3	4	5	6	7	8	9	10	Min-max	Mean	Std
Height	0.350	0.337	0.312	?	?	0.350	0.325	?	0.350	0.325	0.312–0.350	0.335571	0.015306
Diameter of nucleus	0.100	0.087	0.100	?	?	0.100	0.100	0.120	0.100	0.100	0.087–0.120	0.100875	0.008967
Diameter of first half whorl	0.175	0.150	0.162	?	?	0.162	0.187	0.212	0.187	0.187	0.150–0.212	0.17775	0.019652
Maximum diameter	0.412	0.437	0.425	?	?	0.412	0.375	?	0.412	0.387	0.375–0.437	0.408571	0.021236
No. of whorls	2	2.25	2.6	?	?	2.2	1.8	?	1.8	1.8	1.8–2.6	2.064286	0.303746
Multispiral	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	–
Paucispiral	no	no	no	no	no	no	no	no	no	no	no	no	–

APPENDIX 14. — Measurements of teleoconch and protoconch of *Benthonellania maestratii* n. sp. in mm, with range, mean and standard deviation: **1**, holotype, Australes, Recif Neilson, 560-790 m depth; **2**, Australes, Côte Sud de Rurutu, 520-950 m depth; **3**, Australes, Côte Sud de Rurutu, 520-950 m depth.

Teleoconch	1	2	3	Min-max	Mean	Std
Height	2.50	3.12	2.80	2.50-3.12	2.806667	0.310054
Width	1.62	2.07	1.85	1.62-2.07	1.846667	0.225019
Height/Width ratio	1.538	1.507	1.513	1.507-1.538	1.519333	0.016442
Aperture height	1.10	1.35	1.30	1.10-1.35	1.25	0.132288
Height/Height aperture ratio	2.272	2.311	2.154	2.154-2.311	2.245667	0.081746
Height last whorl	1.75	2.15	1.95	1.75-2.15	1.95	0.2
Height/Height last whorl ratio	1.428	1.451	1.436	1.428-1.451	1.438333	0.011676
No. of whorls	3.2	3.5	3.25	3.2-3.5	3.316667	0.160728
No. axial ribs on last whorl	35	57	45	35-57	45.66667	11.01514
No. spiral cords on last whorl	22	32	35	22-35	29.66667	6.806859
Varix	yes	yes	yes	yes	yes	–
Umbilical chink	yes	yes	yes	yes	yes	–
Protoconch	1	2	3	Min-max	Mean	Std
Height	0.325	0.400	0.362	0.325-0.400	0.362333	0.037501
Diameter of nucleus	0.062	0.075	0.087	0.062-0.087	0.074667	0.012503
Diameter of first half whorl	0.150	0.150	0.150	0.150	0.15	0
Maximum diameter	0.450	0.475	0.487	0.450-0.487	0.470667	0.018877
No. of whorls	2.3	2.25	2.3	2.25-2.3	2.283333	0.028868
Multispiral	yes	yes	yes	yes	yes	–
Paucispiral	no	no	no	no	no	–