

The genus *Lophocochlias* Pilsbry, 1921 (Gastropoda, Tornidae) in the Indo-West Pacific

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ABSTRACT. The authors studied the species of the genus *Lophocochlias*, family Tornidae, of the tropical Indo-Pacific, collected during the expeditions of the Tropical deep-sea Benthos, directed by IRD and MNHN, in Madagascar, Reunion Island, New Caledonia, Vanuatu, Fiji, the Solomon Islands, the Philippine Islands, the Society Islands and Papua-New Guinea. New data on geographical distribution and habitat of the species studied are provided, and their morphological variability is discussed. Comparison with some fossil species is done and a new species is described.

RESUMEN. Se estudian las especies de la familia Tornidae, género *Lophocochlias*, del Indo-pacífico tropical, recolectadas durante las expediciones Tropical Deep-Sea Benthos, dirigidas por IRD y MNHN, en Madagascar, Reunión Island, Nueva Caledonia, Vanuatu, Fiyi, Islas Salomón, Islas Filipinas, Islas de la Sociedad y Papua-Nueva Guinea. Se aportan nuevos datos sobre distribución geográfica y hábitat de las especies estudiadas, y se discute su variabilidad morfológica. Se hace comparación con algunas especies fósiles y se describe una nueva especie.

INTRODUCTION

The genus *Lophocochlias* Pilsbry, 1921 comprises a small number of tiny species widely distributed throughout the Indo-Pacific.

Until now it was a monotypic genus whose type species *Haplocochlias* (*Lophocochlias*) *minutissimus* Pilsbry, 1921 was cited from areas as far away as Hawaii (Pilsbry, 1921), Red Sea (Rolán, 2010; Rubio, Fernández-Garcés & Rolán, 2013) and Japan (Fukuda, 1995; Okutani, 2000), which could lead to think that perhaps several distinct species were involved, albeit similar in shape.

Like so many other microgastropods, *L. minutissimus* was known only by the shell, and there are no published data on its anatomy, radula and operculum.

Since initially it was described as a subgenus of the genus *Haplocochlias*, belonging to the family Skeneidae, both in the consulted literature and in some databases *Lophocochlias* is still placed in that family. Lozouet (2011: 50) considered that this genus was not correctly placed in Skeneidae but in Tornidae and more recently, Rubio, Fernández-Garcés & Rolán (2013: 123) agree with this opinion.

After consulting the available literature concerning the Indo-Pacific, we found another older taxon, *Liotia*

parvissima Hedley, 1899, also belonging to *Lophocochlias*, which in one of the databases consulted (WMSD) is included in the genus *Parviturbo* Pilsbry & McGinty, 1945, based on the opinion of Callea *et al.* (2005).

The study of the material deposited in the MNHN in Paris, coming from the different expeditions carried out in the Tropical Indo-Pacific, as well as some material from private collections, has enabled us to confirm the wide distribution of the species of *Lophocochlias*, as well as their bathymetric range, and also to obtain some anatomical, radular and opercular data, which we deem sufficient to place *Lophocochlias* taxonomically in the family Tornidae.

Materials and Methods

In the present work the species of tornids of the genus *Lophocochlias* Pilsbry, 1921 from different oceanographic expeditions undertaken by the MNHN in the Indo-Pacific were studied:

BENTHEDI (1977): Mozambique Channel, Glorieuses Islands.

VAUBAN (1978-1979): South New Caledonia.

MD32 REUNION (1982): Reunion Island.

MUSORSTOM 6 (1989): New Caledonia, Loyalty Ridge.

SMCB (1991): French Polynesia.
 EXPEDITION MONTROUZIER (1993): New Caledonia.
 BATHUS 1-4 (1993-94): New Caledonia proper and the Norfolk Ridge.
 MUSORSTOM 8 (1994): Vanuatu.
 MUSORSTOM 9 (1997): Marquesas Archipelago.
 MUSORSTOM 10 (1998): Fiji.
 LIFOU 2000: Lifou, Loyalty Islands.
 PANGLAO 2004: Central Philippines: Panglao, Dauis, Cortes, Tagbilaran and Baclayon.
 SANTO 2006: Vanuatu.
 ATIMO VATAE (2012): South Madagascar.
 PAPUA NIUGINI 2012: Madang District, Papua New Guinea.

Practically all the material used in this study was obtained in sediments collected by the above mentioned expeditions in shallow and deep water off Reunion Island, Madagascar, New Caledonia, Vanuatu, Fiji, Papua New Guinea and the Philippines Islands. A small part of the material is from the collection of the second author (ER), deposited in MHNS. Finally, a small quantity of material from French Polynesia was obtained from the Letourneux collection.

For most of the *Tropical Deep-Sea Benthos* cruises, station numbers are preceded by a two-letter prefix that refers to the type of gear used: This can be found in Bouchet *et al.*, 2008.

All the studied species are illustrated using Scanning Electron Microscopy (SEM) Quanta 200. As measurements of the teleoconch, the maximum height (H), maximum diameter (D) are based in the scale bar of the SEM photographs. The protoconch was measured by the Verduin (1976) method in which a nucleus is considered at the beginning of the spire. Most of the material is deposited in MNHN, unless otherwise mentioned.

Abbreviations

AMNH: American Museum of Natural History, New York, U.S.A.
 AMS: The Australian Museum, Sydney, Australia.
 ANSP: Academy of Natural Sciences, Philadelphia, U.S.A.
 CACTI: Centro de Apoyo Científico y Tecnológico a la Investigación, University, Vigo, Spain.
 IRD: Institut de recherche pour le développement, Marseille and Nouméa, France.
 MHNS : Museo de Historia Natural of the University, Santiago de Compostela, Spain.
 NHMUK: The Natural History Museum, London, U.K.
 MNHN: Muséum national d'Histoire naturelle, Paris, France.
 CJL: Jean Letourneux collection, Society Islands, French Polynesia.
 stn: stations
 dd: empty shell

lv(s): specimen(s) with rest of soft parts.
 H: total height of the shell
 D: maximum diameter of the shell, measured perpendicular to the axis of coiling

SYSTEMATICS

Superfamily **TRUNCATELLOIDEA** Gray, 1840
 Family **TORNIDAE** Sacco, 1896

Criscione & Ponder (2013) placed Tornidae in Truncatelloidea; after a phylogenetic analysis of 43 species belonging to 14 of the 23 families previously included in Rissooidea and of all the families of Cingulopsoidea, they arrived at the conclusion that Tornidae, represented by two genera (*Circulus* and *Pseudoliotia*), was monophyletic, with *Nozeba* being sister to the Tornidae. More recently, Takano & Kano (2014) published new data on this group: "The Tornidae *sensu* Bouchet & Rocroi (2005) were recovered as non-monophyletic group in our analyses from *Vitrinella* sp. and *Teinostoma lucidum*. The monophyletic nature of the Tornidae (=Vitrinellidae; Bouchet & Rocroi, 2005) is clearly rejected by the sister relationship between *Vitrinella* and *Iravadia*, confirming the previous suspicion that this family comprises heterogeneous groups (Ponder & de Keyser, 1998). Vitrinellidae is not confamilial with *Teinostoma* (Tornidae)".

Subfamily **VITRINELLINAE** Bush, 1897
 Genus *Lophocochlias* Pilsbry, 1921

Lophocochlias Pilsbry, 1921: 377.

Type species by monotypy: *Haplocochlias* (*Lophocochlias*) *minutissimus* Pilsbry, 1921. Recent. Indo-Pacific

Etymology. *Loph-* means crest, ridge, in Greek; *Cochlias*, means marine sea snail.

Diagnosis. Shell minute but solid, tall for the family; protoconch multispiral or paucispiral; teleoconch sculptured with strong acute spiral keels or carinae and axial threads. Aperture with a strong varix. Colour translucent white, protoconch brown or white. Animal with slender cephalic tentacles tipped with immobile cilia and bifid foot ending posteriorly in two lobes. Operculum circular and multispiral. Radula taenioglossate.

Remarks. The species of *Lophocochlias* are distributed from Lower Miocene to Recent. The oldest fossil records are from the Lower Oligocene in the Aquitaine basin (Lozouet, 2011) and from of the Marshall Islands and Fiji, and a Pleistocene fossil from Tonga (Ladd, 1966). The species of *Lophocochlias* have an intertidal down to circalittoral distribution; their bathymetric range is between 0 and 60 m, having been found at greater

depths, but we believe that specimens from deep water may have suffered the dragging effect of surrounding currents.

Their geographical spread is so broad that they have come to colonize all types of substrates, living on both hard and soft bottoms.

The planktotrophic larvae of *Lophocochlias* are free living, and in the adult period apparently they are not commensal with burrowing invertebrates.

Ladd (1966), Sepkoski (2002) and Hendy (2007) list *Lophocochlias* in the family *Skeneidae*, but these are essentially paleontological compilations and we think that without anatomical, radular, and opercular study it is impossible to place *Lophocochlias* in the proper position with any confidence.

Currently, different databases place *Lophocochlias minutissimus* in *Skeneidae*; WoRMS using Kay (1979) as the basis of the record; OBIS placing it in *Haplocochlias* based on their original description. However, museums such as the Australian Museum Sydney (AMS), the National Museum of Natural History in Paris (MNHN) and the Museum of New Zealand Te Papa Tongarewa (Te Papa) among others, placed the samples of *Lophocochlias minutissimus* of their collections in *Tornidae* (= *Vitrinellidae*).

Kay (1971) placed this species in the genus *Lophocochlias* and Kay & Switzer (1974) changed its position to the genus *Parviturbo*. Later, Kay (1979: 56) returned it to *Lophocochlias* and comments: "The veliger larvae exhibit both rissoccean and cerithiacean features, resembling rissoids with respect to the inflated shell and cerithids with respect to sculpture and rounded aperture".

Referring to *Discrevitiia balba* Laseron, 1956, species currently located in *Pickworthiidae*, Ponder (1985) makes the following comment: "The family position of this group is questionable." "It is usually placed in the *Archaeogastropoda* but the re-examination of the radula of the similar and probably related *Lophocochlias minutissimus* (Pilsbry) shows it to be typical of the *Vitrinellidae*". We believe that the radula has never been published.

Lophocochlias minutissimus (Pilsbry, 1921)

Figs 1A-I, 2A-H, 3A-I

Haplocochlias (*Lophocochlias*) *minutissimus* Pilsbry, 1921: 377.

Type locality. Mokapu Point, Oahu, Hawaii.

Type material. 4 syntypes in ANSP (107930). Not examined.

Material examined. **RED SEA.** Jordan: 13 dd, Aqaba, 10-20 m (MHNS). Egypt: 5 dd, Hurghada, 15-25 m (MHNS).

INDIAN OCEAN

BENTHEDI: Mozambique, 2 dd, NE Canal du Mozambique, Glorieuses Is., N of Lys I., stn K105, 3730 m; 2 dd, Mayotte, N Passe Sada, stn. 56, 12°53.5'S, 44°57.1'E, 5-3 m.

ATIMO VATAE: South Madagascar, 2 dd, Libanona Beach, stn TB07, 25°02.5'S, 46°59.7'E, 4-5 m, coralline and rocky bottom; 1 dd, off Libanona, stn TB09, 25°02.3'S, 46°59.6'E, 6-7 m, hard bottom; 10 dd, aperture of East Galions Bay, stn TB10, 25°09.3'S, 46°45.3'E, 10 m, brushed stones; 1 dd, Galions Bay, stn TB11, 25°09.2'S, 46°45.4'E, 5-6 m, mudd and rocky bottom; 3 dd, Faux-Cap, stn BM12, 25°34.3'S, 45°31.7'E, 0 m, intertidal; 1 dd, Galions Bay, stn TS16, 25°09.5'S, 46°44.9'E, 9-10 m, slabs of stone with cups.

MD32 REUNION: 2 dd, Reunion Island, stn FA25, 21°21,8'S, 55°45,9'E, 90-95 m.

PACIFIC OCEAN

PANGLAO 2004: Philippines, Panglao Island, 1 dd, BBC Point, stn B4, 9°33.2'N, 123°48.3'E, 24 m, reef slope with overhangs; 1 dd, Biking, stn B5, 9°35.2'N, 123°50.4'E, 4 m, reef slope with overhangs; 1 dd, stn B8, 9°37.1'N, 123°46.1'E, 3 m; 1 dd, Pontod Lagoon 1, stn B39, 9°32.8'N, 123°42.1'E, 17-25 m, reef wall with small caves.

PAPUA NIUGINI: Madang District, 2 dd, Paeowa Island, stn PS07, 05°10,8'S, 145°49,8'E, 13 m, outer slope; 1 dd, N Tadwai Island, stn PB24, 04°59,1'S, 145°47,6'E; 2 dd, Rempi Area, N Tadwai Island, stn PM27, 04°59,3'S, 145°47,6'E, 0 m, night tide, mangrove, sand with abundant soft corals; 1 dd, N Tab Island, Rasch Passage, stn PB31, 05°09,4'S, 145°50'E, 31 m; 1 dd, N Wonad Island, N Mililat Passage, stn PS38, 05°07,1'S, 145°49,4'E, 15 m; 1 dd, S Urembo Island, stn PB40, 05°15,9'S, 145°47,1'E, 9-11 m, outer slope; 1 dd, N Riwo, stn PS46, 05°08,7'S, 145°48,2'E, 2 m, mangrove and seagrass; 1 dd, N Riwo, stn PB48, 05°08,7'S, 145°48,2'E, 2 m, mangrove and seagrass; 5 dd, Wonad Island, stn PD48, 05°08,2'S, 145°49,4'E, 10-20 m; 2 dd, S Sek Island, stn PB49, 05°06,4'S, 145°49,4'E, 6 m.

VAUBAN 1978-1979: S. New Caledonia, 1 dd, stn. DR40, 22°30'S, 166°24'E, 250-350 m.

EXPEDITION MONTROUZIER: New Caledonia, 1 dd, Secteur de Touho, SE off Touho dock, stn 1242, 20°46.2'S, 165°14.5'E, 0 m, tyde, blocks, sand, seagrass; 1 lv + 1 dd, Secteur de Touho, Chenal NE of Banc de Touho, stn 1260, 20°44'S, 165°14'E, 49-59 m, shell grit; 1 dd, Secteur de Touho, Lagon du Grand Rêcif Mengalia, stn 1264, 20°44.5'S, 165°15.9'E, 8 m, muddy sand detritique bottom; 3 dd, Secteur de Touho, Sable Islet, Passe de Touho, stn 1272, 20°49.5'S, 165°19.6'E, 10 m, hard bottom with mudd; 1 dd, Secteur de Touho, external reef, Passe de

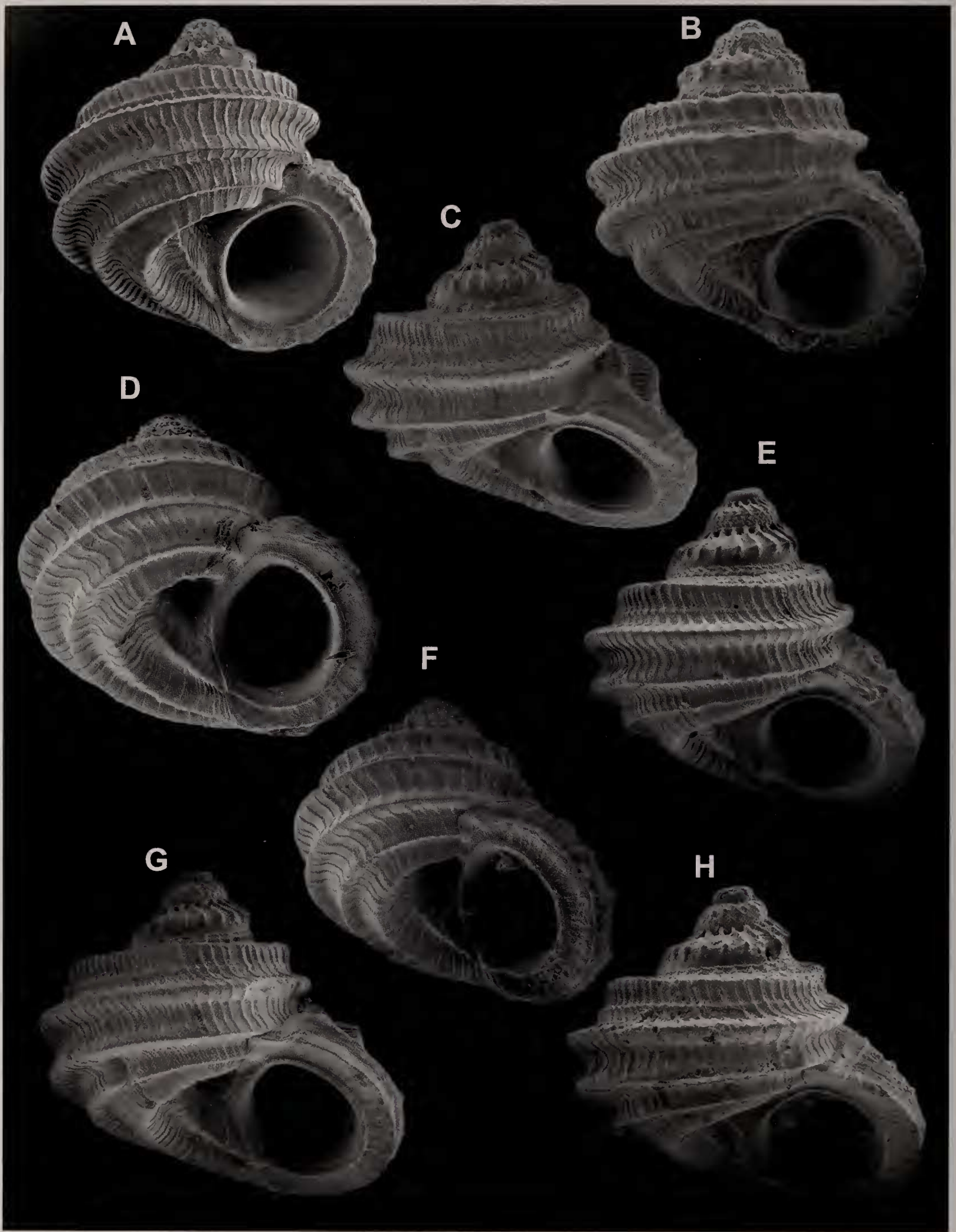


Figure 1A-H. *Lophocochlias minutissimus* (Pilsbry, 1921)

A. Shell, 0.9 mm in diameter, Aqaba, Red Sea, 120 m (MHNS); **B.** Shell, 0.86 mm, South Madagascar (MNHN); **C.** Shell, 1.03 mm, Tuamotu (MNHN); **D.** Shell, 0.94 mm, Loyalty Is. (MNHN); **E-F.** Shells, 0.97, 0.84 mm, Vanuatu (MNHN); **G-H.** Shells, 1.08, 1.05 mm, Tahiti (MNHN). (The dimension of the shell refers to its diameter).

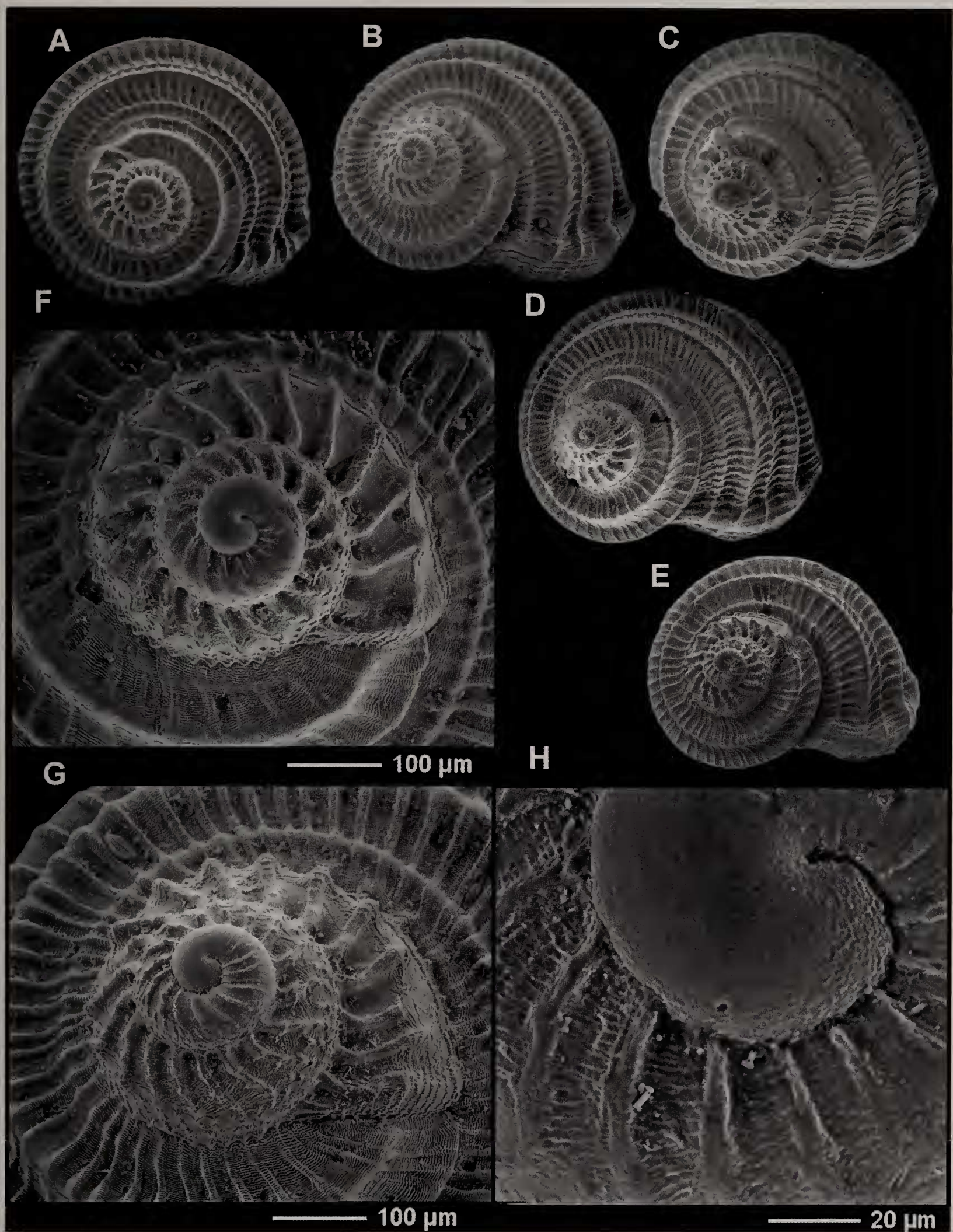


Figure 2A-H. *Lophocochlias minutissimus* (Pilsbry, 1921)

A. Shell, 0.98 mm, Tuamotu (MNHN); B-C. Shell, 0.95 mm, Loyalty Is. (MNHN); C. Shell, 1.08 mm, Tuamotu (MNHN); D. Shell, 1.03 mm, Tahiti (MNHN); E. Shell, 0.85 mm, Aqaba, Red Sea (MHNS); F. Protoconch of the shell (Fig. A); G. Protoconch of the shell (Fig. B); H. Detail of Fig. F. (The dimension of the shell refers to its diameter).

Touho, stn 1273, 20°50.4'S, 165°22.8'E, 20 m, hard bottom, sandy areas; 1 dd, Secteur de Koumac, Lagoon between the land and l'infirmerie, stn 1300, 20°35.6'S, 164°15.2'E, 10-11 m, grey muddy sand; 1 dd, Secteur de Koumac, Lagoon: areas of the Plateau Karembe, stn 1303, 20°37.7'S-20°38.8'S, 164°15.9'E-164°17.1'E, 0-8 m, muddy sand, blocks; 3 dd, Secteur de Koumac, Passe de Koumac, East dropping, stn 1312, 20°40.4'S, 164°14.9'E, 26-40 m, hard bottom; 1 dd, Secteur de Koumac, Chenal de la Passe de Koumac, stn 1313, 20°38.8'S, 164°15.6'E, 33-38 m, bottom of turritelles.

LAGON: New Caledonia, 2 dd, Secteur de Nouméa, Platier Ilot Maître, stn 1351, 22°20.4'S, 166°25.7'E, 0 m, intertidal, detritique elevation; 4 dd, Secteur de Nouméa, Grand Récif Aboré, stn 1352, 22°22.2'S, 166°16.0'E/166°16.1'E, 27-35 m, outer slope; 1 dd, Secteur de Nouméa, Canyon de la Dumbéa, stn 1356, 22°19.7'S, 166°15.4'E, 20-23 m, sand under blocks.

MUSORSTOM 6: 1 dd, Ride des Loyauté, N/O *Alis*, stn DW431, 20°22'S, 166°10'E, 21 m.

LIFOU 2000: Iles Loyauté, Santal Bay, 13 dd, between Cap Wekutr and Cap Wajez, stn 1410, 20°56.7'S, 167°03.1'E, 2-4 m, border of slope; 3 dd, off Peng, stn 1412, 20°54.2'S, 167°07.4'E, 2-5 m, mobile bottoms; 1 dd, off the dock of Drueulu, stn 1413, 20°55.3'S, 167°05.0'E, 3-10 m, mobile bottoms; 8 dd, East of Pointe d'Easo, stn 1418, 20°46.9'S, 167°07.9'E, 1-5 m, sand and herbal around the dock; 1 dd, Gaatcha Bay, stn 1419, 20°55.6'S, 167°04.5'E, 5 m, mud on slabs, photophile algae; 1 dd, Pointe de Chépénéhé, stn 1420, 20°47.7'S, 167°09.35'E, 4-5 m, slab with sediments; 6 lvs + 6dd, between Huca Hutighe islet and the coast, stn 1421, 20°52.4'S, 167°08.5'E, 4 m, thick sand on slab; 1 dd, small bay at west of Pointe d'Easo, stn 1422, 20°47.1'S, 167°07.4'E, 4 m, sand on slabs, coral; 4 dd, off Peng, stn 1423, 20°54.0'S, 167°07.3'E, 12 m, sandy bottom between coral; 4 dd, off Hunete, stn 1426, 20°45.9'S, 167°06.2'E, 4-7 m, slab and small pockets of sediment; 3 dd, W-SW of d'Easo Point, stn 1429, 20°47.5'S, 167°07.1'E, 8-18 m, coralline balls, sediments; 12 dd, W-SW de la Pte d'Easo, stn 1430, 20°47.5'S, 167°07.1'E, 20-25 m, coralline balls, sediments; 1 lv + 10 dd, Récif Shelter, stn 1432, 20°53.5'S, 167°02.7'E, 12-32 m, nodules and coarse coral sand very eroded at the bottom of the slope; 15 dd, off Huca Hutighe Islet, stn 1434, 20°52.5'S, 167°08.1'E, 5-20 m, hard bottom; 2 lvs + 4dd, Pointe Lefevre, stn 1435, 20°55.2'S, 167°00.7'E, 5-30 m, vertical drops; 8 dd, Gaatcha Bay, stn 1436, 20°55.5'S, 167°04.2'E, 10-20 m, coral on slope; 5 dd, Cap Aime Martin, stn 1442, 20°46.4'S, 167°02.0'E, 47 m, base of slope; 17 dd, NE of the Gaatcha Bay, stn 1444, 20°55.0'S, 167°05.2'E, 9-20 m, alternating slopes and coarse sand areas; 21 dd, north of Cap Aimé Martin, stn 1449, 20°45.8'S, 167°01.65'E, 17 m, brushing; 12 lvs + 38 dd, north of Cap Aimé Martin, stn 1450, 20°45.8'S, 167°01.65'E, 27-31 m, brushing; 9 dd, West of d'Easo Point, stn 1451, 20°47.3'S, 167°06.8'E,

10-21 m, second part of coralline balls; 3 dd, between Cap Mandé and Cap Lefevre, stn 1453, 20°54.6'S, 167°02.1'E, 21-30 m, slope with gorgonies; 4 lvs + 6 dd, au South Cap Lefevre, stn 1454, 20°56.65'S, 167°02.0'E, 15-18 m, sciaphile slope; 5 lvs + 6 dd, between Cap Wekutr and Cap Wajez, stn 1455, 20°56.8'S, 167°02.7'E, 15-20 m, dropping area; 29 lvs + 21 dd, off Ngoni, stn 1457, 20°46.8'S, 167°02.75'E, 5-10 m, eaves and blocks.

SANTO 2006: Vanuatu, 15 dd, W coast of Malo Island, stn ZB09, 15°40.6'S, 167°05.1'E, 5-7 m; 4 dd, NW Malo, stn ZM15, 15°38.1'S, 167°05.9'E, 0 m, intertidal; 4 dd, E Aoré Island, Aisari Bay, stn ZB36, 15°34.3'S, 167°12.4'E, 0 m, intertidal; 1 dd, Palikulo Bay, stn FB43, 15°28.4'S, 167°14.9'E, 19 m; 3 dd, Palikulo Bay, stn DB46, 15°28.8'S, 167°15.2'E, 2-3 m; 3 dd, SE corner of Santo, shallow water; 4 dd, Malokilikili, stn FB52, 15°42.7'S, 167°15.1'E, 7 m; 1 dd, SE Aésé Island, stn DB63, 15°26.9'S, 167°15.8'E, 21 m; 15 dd, stn FB80, 15°33.1'S, 167°09.6'E; 1 dd, SE corner of Santo, shallow water; 2 dd, E Malo Island, stn DB83, 15°43.4'S, 167°15.0'E, 6 m; 2 dd, Tutuba Island, stn FB92, 15°33.6'S, 167°16.6'E, 2-4 m; 1 dd, SE corner of Santo, shallow water.

MUSORSTOM 9: Marquesas Archipelago, 2 dd, Hiva Oa Island, stn. DW1201, 9°51'S, 139°09'W, 275-300 m; 1 dd, Hiva Oa Island, stn. DW1222, 9°44'S, 138°51'W, 340-352 m; 6 dd, Fatu Hiva Island, stn. DR1247, 10°34'S, 138°42'W, 1150-1250 m; 1 dd, Ua Huka Island, stn. DW1288, 8°54'S, 139°38'W, 200-220 m.

MUSORSTOM 10: Fiji, 9 dd, S Viti Levu, stn. DW1381, 18°17.8'S, 177°54.4'E, 275-430 m; 1 dd, SE Viti Levu, stn. CP1353, 879-897 m.

SMCB: French Polynesia, 2 dd, Ile de Fatu-Hiva, stn D86, 10°29'S, 138°40.3'W, 49 m; 50 dd, Tahuata Island, stn. D47, 09°54.5'S, 139°6.8'W, 48 m.

BRYCE & KAYSER 1999: Marquesas Archipelago, 14 dd, Nuku Hiva, Baie Taiohae, W Matauapuna, stn. 2, 8°56.22'S, 140°05.68'W, 10-20 m; 1 dd, Nuku Hiva, Baie Taiohae, W Motu Nui, stn. 3, 8°56.17'S, 140°06.66'W, 10-20 m; 7 dd, Ua Pou, Hakaomaka, stn. 19, 9°20.82'S, 140°05.81'W, 10-20 m; 5 dd, Ua Pou, Motu Mokohe, stn. 20, 9°20.81'S, 140°05.81'W, 10-15 m.

French Polynesia: +100 dd, Society Islands, Tuamotu: Rangiroa, Makemo and Pohue atolls, 0-100 m (CJL); +100 dd, Society Islands: Tahiti, Moorea, Tetiaroa, Mopelia, Motu One, 1-20 m (CJL).

Distribution. Species distributed in almost all the Indo-Pacific. Recorded from Hawaii (Pilsbry, 1921; Kay, 1979); Cocos-Keeling Islands, Indian Ocean (Maes, 1967); Kiribati Republic, Fanning Island, Line Islands, (Kay, 1971; Kay & Switzer, 1974); southwestern Shikoku (Kashiwajima), Amami islands and southwards, Ogasawara islands, Japan (Fukuda, 1995, Okutani, 2000); Tuamotu and Marshall islands (Higo, Calomon & Goto, 1999). From Jordan, Mozambique, Madagascar, Reunion, New Caledonia,

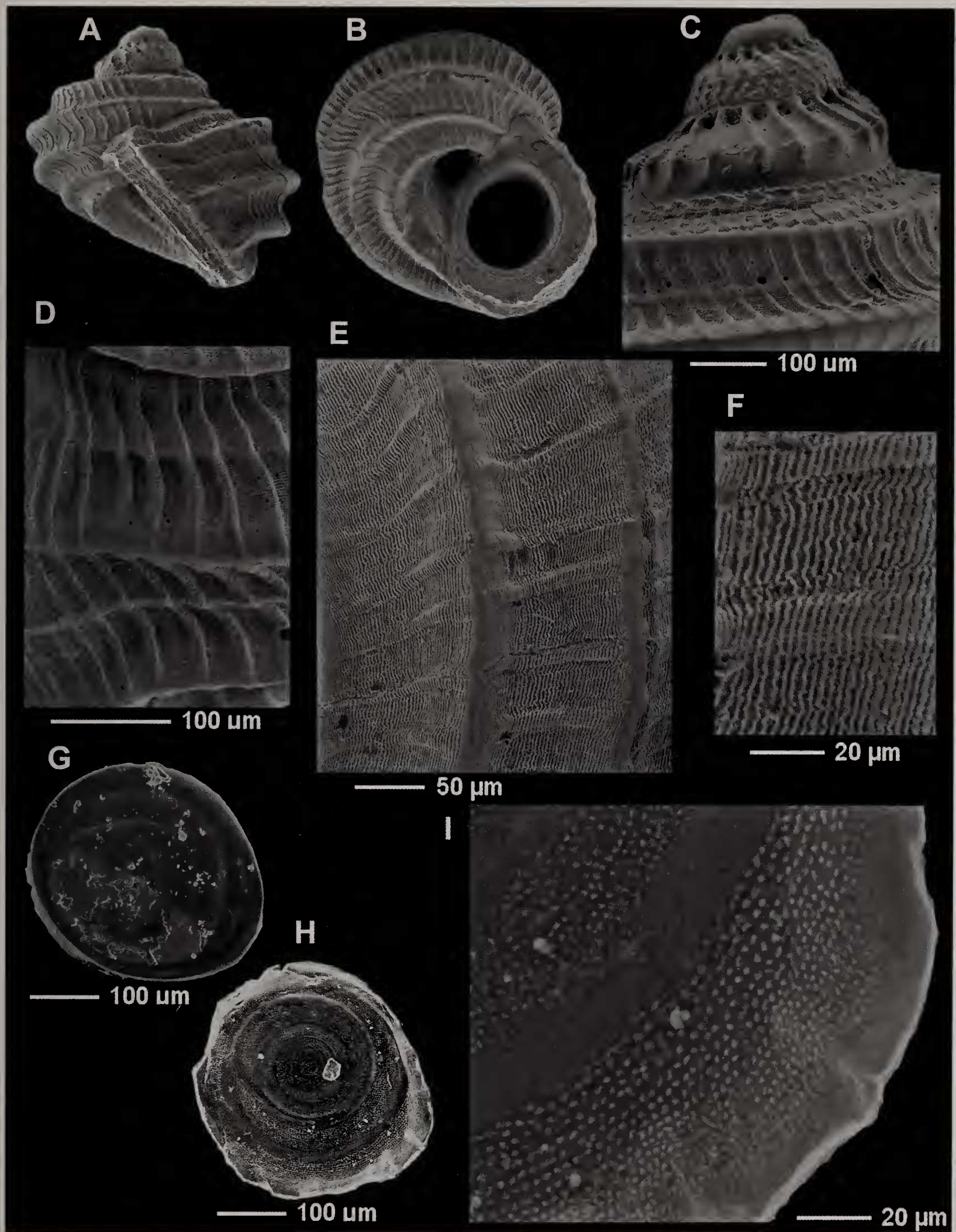


Figure 3A-I. *Lophocochlias minutissimus* (Pilsbry, 1921)

A. Shell, 0.84 mm, Aqaba, Red Sea (MHNS); B. Shell, 1.08 mm, Tahiti (CJL); C. Protoconch in lateral view, from Tuamotu (CJL); D-F. Microsculpture and detail; G-I. Operculum and detail. (The dimension of the shell refers to its diameter).

Loyalty Islands, Vanuatu, Fiji, Papua New Guinea, Philippines, and French Polynesia in the present work.

Description. Pilsbry (1921: 377): Original description of *Haplocochlias* (*Lophocochlias*) *minutissimus*: “The very small shell is umbilicate, turbinate, not nacreous, white with a conic brownish spire. The first whorl appears to be smooth; on the second fine radial folds or puckering appears below the suture, becoming coarser on the following whorl. The last whorl has six strong, smooth spiral keels, narrower than the intervals, which are flat, and crossed by numerous retractively axial threads, which are much narrower than their intervals. Within the umbilicus two rather small spiral cords are seen. The aperture is quite oblique, subcircular. The outer lip is strengthened by a rounded external rib or varix a short distance behind the edge”.

Length 1 mm, diameter 0.9 mm; 4 1/3 whorls.

Kay (1979) extended the original description: “Shell turbiniform; spirally keeled and with fine axial threads; white. Protoconch of two and one-half acute, brown whorls, the apical smooth, the others with oblique axial ribs; teleoconch of three convex whorls, the last the largest. Sculpture: apical whorl with granular axial ribs and spiral threads, the next with two and the last with six spiral keels; interspaces between the spiral keels of greater diameter than the keels, shallow, crossed by numerous axial threads. Aperture: subcircular, oblique; outer lip with an external varix; umbilicus wide and deep; operculum circular, multispiral, horny. Color: white”.

Okutani (2000): “Shell minute but solid, tall for the family, sculptured with acute strong spiral keels and axial threads. Aperture with a strong varix. Color translucent white, protoconch brown”.

Animal with long and slender cephalic tentacles tipped with fine, hairlike, immobile cilia. The bifid foot, ends posteriorly in two lobes.

Operculum circular, multispiral and chitinous; its inner surface is smooth and the area of insertion in the foot can be seen on it; its outer face has micro tubercles spirally aligned, forming a strip that describes a perfect spiral from the centre to the periphery.

Radula taenioglossate, examined by Ponder (pers. com.).

Habitat. Subtidal, common in sediments to depths of 30 m and also in tide pools around bases of seaweeds and on solution benches (KAY, 1979). It is an epifaunal species which feeds on detritus. Under rocks in intertidal and subtidal zones (Okutani, 2000). In rocky, sand and muddy bottom with corals and coarse sand.

Remarks. Reported as Miocene fossils from the Marshall Islands and Fiji, and as a Pleistocene fossil from Tonga (Ladd, 1966).

Pilsbry (1921), in an attempt to place this species in its correct genus, created the subgenus *Lophocochlias*, which was considered different from the nominate subgenus *Haplocochlias* due to its stronger sculpture and an open umbilicus. Actually, these morphological characters (lip thickening, wide umbilicus) are present in many turbinoid species; in spite of this, the protoconch appears to be an exclusive character which distinguishes it from Liotiidae and Skeneidae; it is a spectacular protoconch by its development and complex ornamentation.

We do not have photographs that show in detail the soft parts of *Lophocochlias minutissimus*, but merely a photograph provided by the MNHN (PAPUA NIUGINI expedition) and two others obtained in CalPhotos Photo Database from Moorea (French Polynesia), from which we have been able to differentiate some character of the anatomy of the soft parts.

Moore (1972: 108, figs. 5-6) mention these characters as proper of the vitrinellids, stressing that the bifid foot of *Parviturbo interruptus* is a differential character.

The bifid foot of *Lophocochlias minutissimus* appears to be a different character also present in other species as *Parviturboides interruptus* (C.B. Adams, 1850) (Tornidae) and *Tomura bicaudata* (Pilsbry & McGinty, 1946) (Cornirostridae) with the foot ending posteriorly in two lobes.

Lophocochlias parvissimus (Hedley, 1899)

Fig. 4

Liotia parvissima Hedley, 1899: 554–555, fig. 67.

NOT *Parviturboides parvissimus* (Hedley, 1899) — Kilburn, 1977: 182.

Liotia parvissima Hedley, 1899 — Kay, 1979: 56.

NOT *Lophocochlias parvissimus* (Hedley, 1899) — Tröndle, 1986: 69.

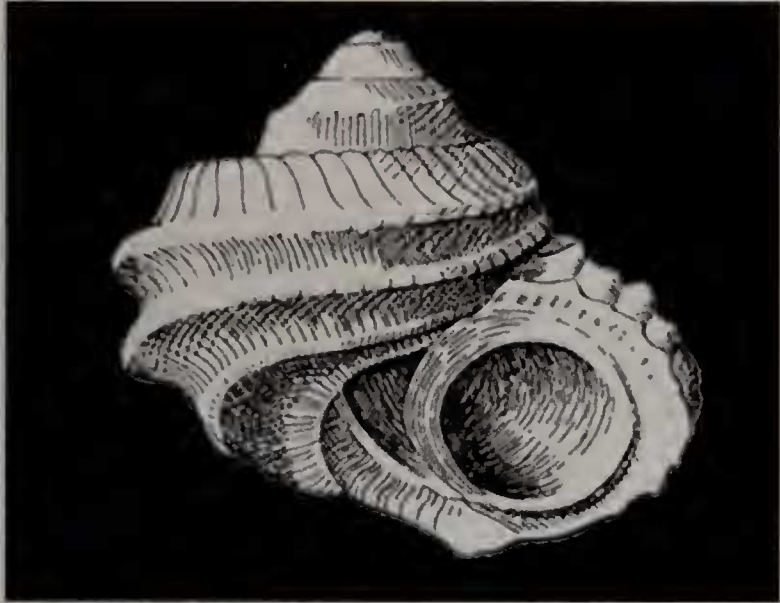
NOT *Parviturbo parvissimus* (Hedley, 1899) — Callea *et al.*, 2005: 85.

Type locality. Off Tutanga Islet, Funafuti Atoll, Tuvalu.

Type material. Not examined: AMS: C.5650 - *Lophocochlias parvissima* (Hedley, 1899) - TUVAlU, Funafuti Atoll, off Tutanga (Tutaga) Is, (8°37'S, 179°5'E), 1898, Holotype. C.5651 - *Lophocochlias parvissima* (Hedley, 1899) - TUVAlU, Funafuti Atoll, off Funamanu (Beacon) Is, (8°34'S, 179°9'E), 1898, paratype.

Other material examined. None.

Distribution. Only known from the type locality.



4. Original figure of *Liotia parvissima* Hedley, 1899. Holotype. *Australian Museum Memoir* 3(9): 554, fig. 67.

Description. Original description by Hedley (1899): "Shell minute, solid, turritate. Colour cream. Whorls four. Sculpture heavy, elevated keel on the shoulder, two equally massive on the periphery, and two smaller on the base. Across keels and interstices run distant, longitudinal, raised threads. Umbilicus small, oblique narrow and deep. Aperture, circular, oblique, with a short but heavy varix, crenulated by the spiral sculpture".

Dimensions: Major diameter '84, minor '66; height '84 mm.

Habitat. Dredged off Tutaga Islet at a depth of 200 fathoms, and off Beacon Islet (Funamanu) at 150 fathoms.

Remarks. Hedley (1899) says: "This, the smallest known *Liotia*, is well distinguished by its simple and massive sculpture."

Since its original description in the genus *Liotia*, this species has been placed in the genera *Parviturbo* by Kilburn (1977), *Lophocochlias* by Tröndle (1986) and *Parviturbo* by Callea *et al.* (2005), but they are probably referring to *L. minutissimus*.

In the Australian Museum, *Pseudoliotia parvissima* is placed in the family Vitrinellidae.

The shell of *L. parvissimus* is very similar to that of *L. minutissimus*, and for this reason it could be thought that both were the same species, but Kay (1979) states the following about *L. minutissimus*: "The shells of *Liotia parvissima* Hedley, 1899, from Funafuti are distinguished by their more prominent spiral keels and different protoconch".

In our opinion, *Lophocochlias parvissimus* is endemic to the Funafuti Atoll. The records of Kilburn (1977), Tröndle (1986) and Callea *et al.* (2005) are of *L. minutissimus*, a species with a vast geographical distribution.

Lophocochlias procerus sp. nov.

Figs 5A-G, 6A-G, 7A-E

Sansonia sp.
(<http://vieocean.free.fr/mollusques/Pickworthiidae.htm>)

Type material. Holotype in MNHN IM-2000-28215; paratypes (in the following collections: MNCN (15.05/60159, 2 s), MHNS (100693, 2 s).

Type locality. Aqaba, Jordan, Red Sea, 10-20 m.

Etymology. The specific name is from the Latin word *procerus*, *a, um*, which means "slender".

Other material studied. RED SEA. Jordan: 8 dd, Aqaba, 10-20 m (MHNS). Egypt: 7 dd, Hurghada, 15-25 m (MHNS).

INDIAN OCEAN

ATIMO VATAE: South Madagascar, 1 dd, Phare Flacourt, stn TB02-TB03, 25°01.3'S, 47°00.5'E, 18 m, rocky bottom with flag-stones; 1 dd, Faux-Cap, stn BM12, 0 m, intertidal.

MD32 REUNION: 1 dd, Reunion Island, stn DR47, 21°23'S, 55°37'E, 205-215 m.

PACIFIC OCEAN

EXPEDITION MONTROUZIER: New Caledonia, 1 dd, Secteur de Touho, Haut-Fond de Tié, stn 1271, 20°52.7'S, 165°19.5'E, 5-25 m, slab drop, sand; 1 dd, Secteur de Koumac, Passe de Koumac, slope East, stn 1311, 20°40.4'S, 164°14.9'E, 10-60 m, hard bottom.

LIFOU 2000: Iles Loyauté, Santal Bay, 1 dd, between Huca Hutighe Islet and the coast, stn 1421, 20°52.4'S, 167°08.5'E, 4 m, thick sand on slab; 2 dd, off Hunete, stn 1426, 20°45.9'S, 167°06.2'E, 4-7 m, slab and small sedimentary pockets; 1 dd, Shelter Reef, stn 1432, 20°53.5'S, 167°02.7'E, 12-32 m, nodules and coralline sandy eroded; 2 dd, NE Gaatcha Bay, stn 1444, 20°55.0'S, 167°05.2'E, 9-20 m, area alternating rocky and sandy bottoms; 1 lv + 4dd, North of Cap Aimé Martin, stn 1450, 20°45.8'S, 167°01.65'E, 27-31 m, brushing; 2 dd, West of d'Easo Point, stn 1451, 20°47.3'S, 167°06.8'E, 10-21 m, coral nodules; 1 lv, between Cap Mandé and Cap Lefevre, stn 1453, 20°54.6'S, 167°02.1'E, 21-30 m, slope area with gorgonians; 1 dd, au Sud du Cap Lefevre, stn 1454, 20°56.65'S, 167°02.0'E, 15-18 m, sciaphile slope; 1 dd, off Ngoni, stn 1457, 20°46.8'S, 167°02.75'E, 5-10 m, sciaphile area and blocks.

SANTO 2006: Vanuatu, 1 dd, Palikulo Bay, stn DB46, 15°28.8'S, 167°15.2'E, 2-3 m.

PANGLAO 2004: Philippines, 2 dd, Panglao Island, Biking, stn S1, 9°35.3'N, 123°50.5'E, 5 m, reef slope with overhangs; 1 dd, Bohol Island, Baclayon, stn S2, 9°37.4'N, 123°54.5'E, hard bottom with small pockets of sediment; 2 dd, Panglao Island, Arco Point, stn B3, 9°33.5'N, 123°48.6'E, 8 m, base of reef slope; 1 dd,

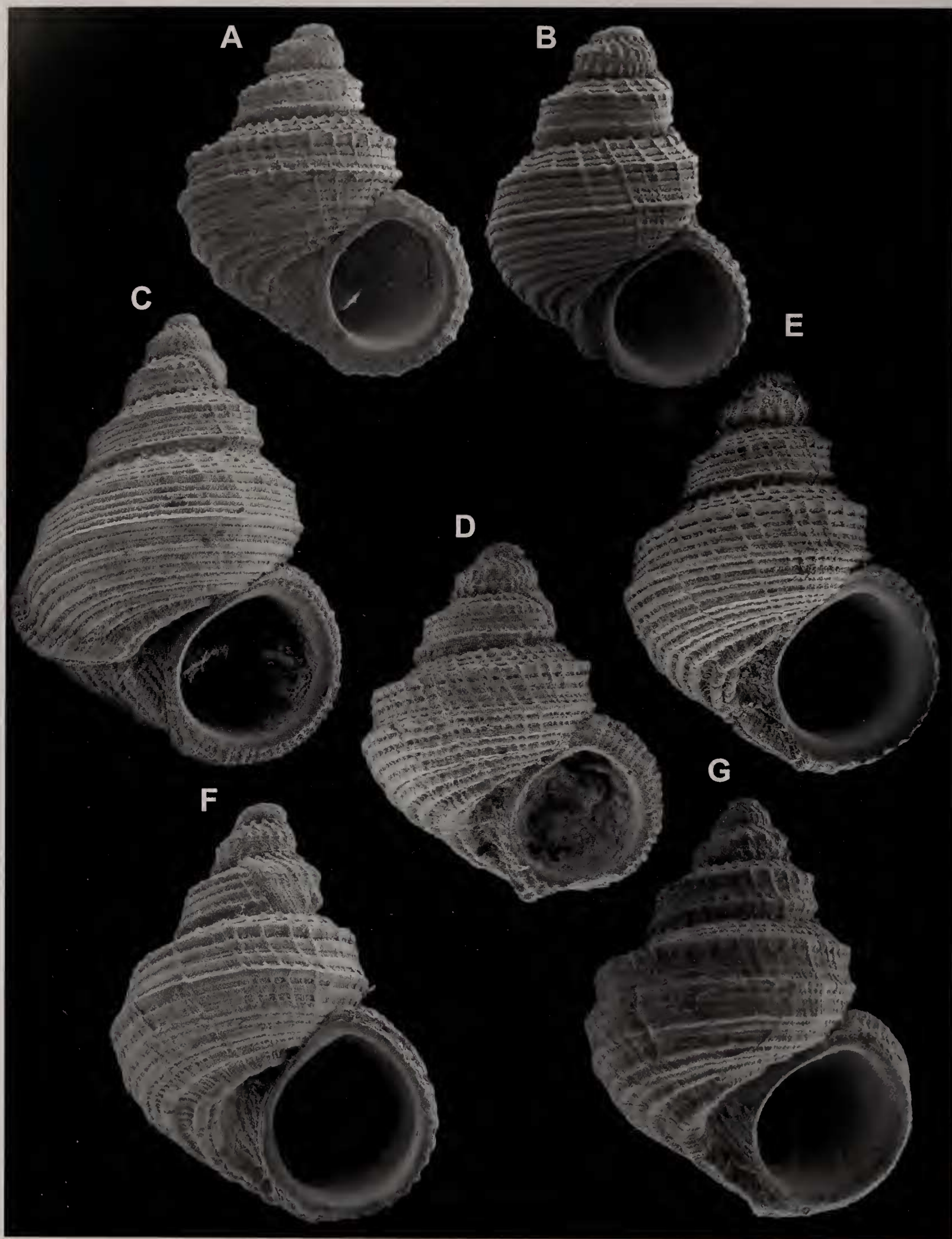


Figure 5A-G. *Lophocochlias procerus* sp. nov.

A. Holotype, 1.1 mm, Aqaba, Jordania, Red Sea (MNHN IM-2000-28215); B. Paratype, 1.1 mm, same locality (MNCN); C. Shell, 1.6 mm, Loyalty Is., stn 1453 (MNHN); D. Shell, 1.1 mm, stn B6, Balicasag, Philippines (MNHN); E. Shell, 1.3 mm, stn 1426, Loyalty Is. (MNHN); F. Shell, 1.2 mm, stn D86, Fatu Hiva Island, French Polynesia (MNHN); G. Shell, 1.6 mm, stn 1311, New Caledonia (MNHN). (The dimension of the shell refers to its diameter).

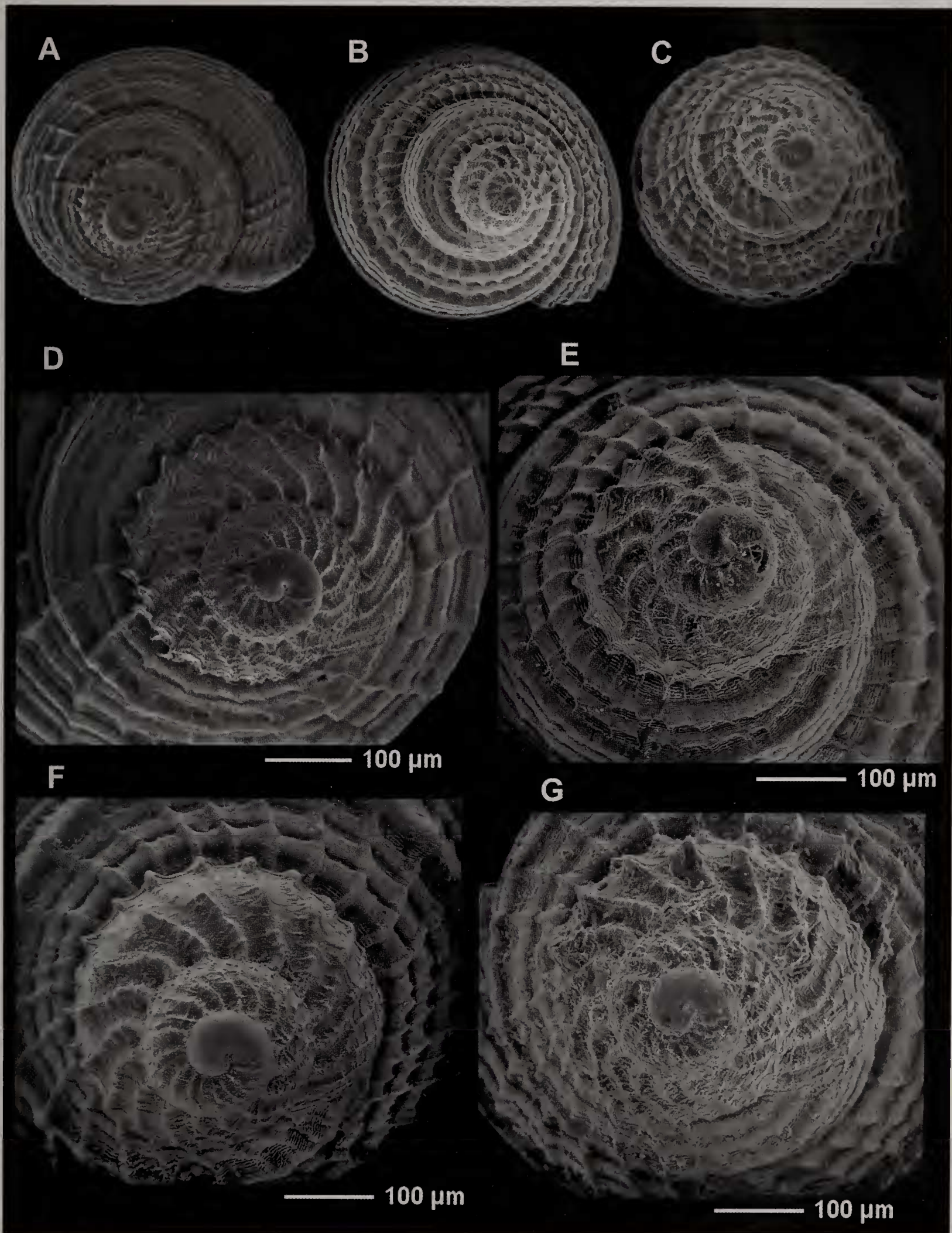


Figure 6A-G. *Lophocochlias procerus* sp. nov.

A. Shell, 0.82 mm in diameter, Aqaba, Jordan (MHNS); B. Shell, 0.87 mm, stn D86, Fatu Hiva, French Polynesia (MNHN); C. 0.77 mm, stn BM12, South of Madagascar (MNHN); D-G. Protoconchs, from stn BM12, South of Madagascar (MNHN), stn D86, Fatu Hiva Island, French Polynesia (MNHN), Aqaba, Jordan (MHNS), and stn K105, Glorieuses Islands, Mozambique Channel (MNHN). (The dimension of the shell refers to its diameter).

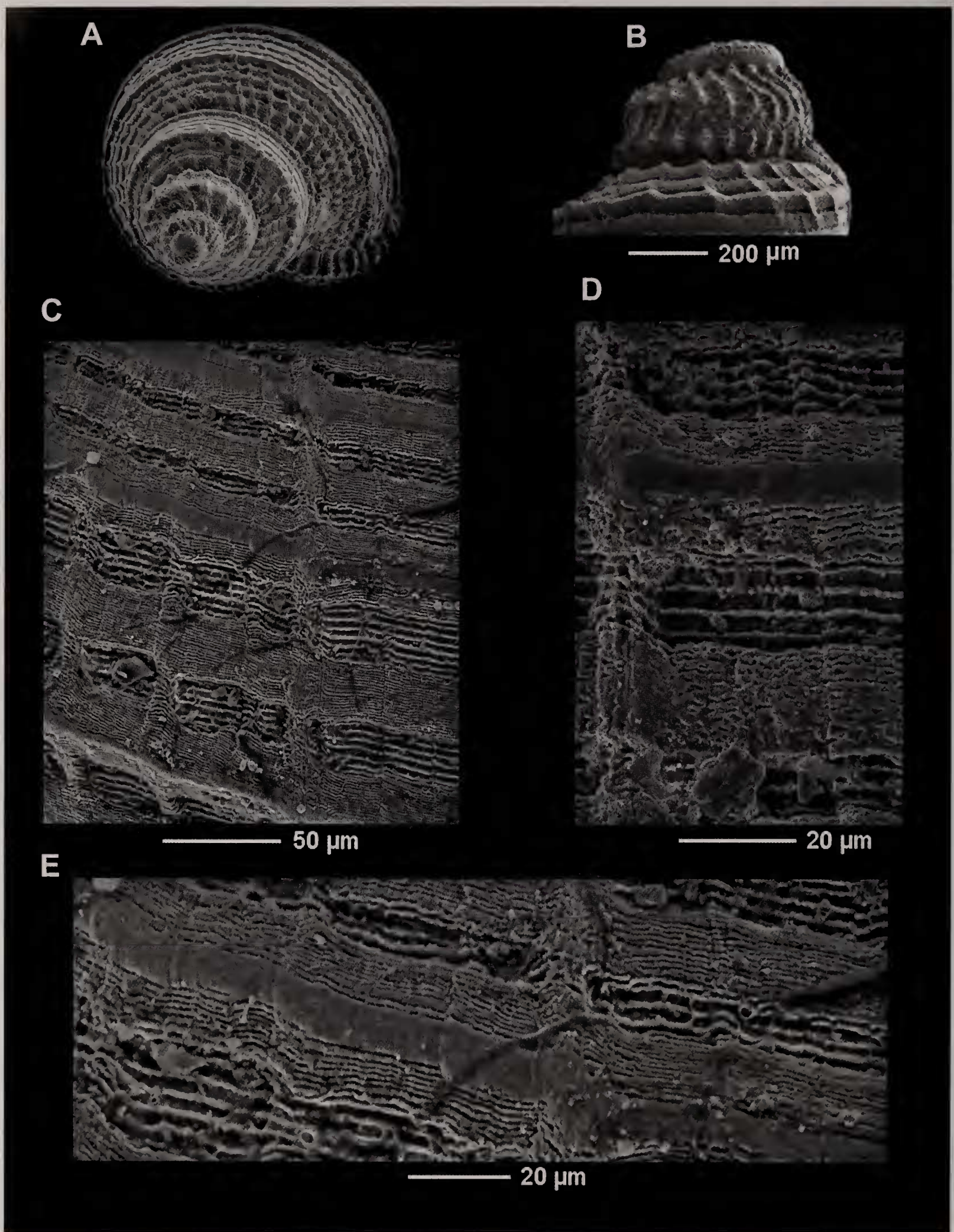


Figure 7A-E. *Lophocochlias procerus* sp. nov.

A. Shell, 0.99 mm, Marquesas Islands, French Polynesia (MNHN); **B.** Lateral view of the protoconch, Aqaba, Jordan (MHNS); **C-E.** Microsculpture: C and E, from a shell of Marquesas Islands, French Polynesia; D. From Aqaba. (The dimension of the shell refers to its diameter).

Balicasag Island, Black Forest, stn B6, 9°31.1'N, 123°41.3'E, 12-14 m, coral patches; 1 dd, Bohol Island, Baclayon Takot, stn B13, 9°37.1'N, 123°52.6'E, 3-5 m, coral rubble;

PAPUA NIUGINI: Madang District, 1 dd, Paeowa Island, stn PS07, 05°10,8'S, 145°49,8'E, 13 m, outer slope; 1 dd, N Sek Island, South coast, stn PS11, 05°04,7'S, 145°48,9'E, 5 m; 1 dd, Rempi Area, N Tadwai Island, stn PM27, 04°59,3'S, 145°47,6'E, 0 m, night tide, mangrove, sand with abundant soft corals.

French Polynesia: 5dd, Marquesas Archipelago, Ua Pou Is., Haakuti Bay, Punahukua, 68 m (CJL); 1dd, Society Archipelago, Tahiti Island, Tiarei, 1 m (CJL).

Description. Species of small size, rissoiform, with 4 $\frac{3}{4}$ spiral whorls, bicarinate and umbilicated. The protoconch has 2 $\frac{3}{4}$ whorls and two distinct phases; the first one is apparently smooth and has $\frac{3}{4}$ whorls, the second has approximately two whorls and it is profusely ornamented with thick, sometimes nodulous, axial ribs, and spiral threads that can be observed in the interspaces and on the top of the ribs; its diameter varies between 320 and 380 μ m. The teleoconch is formed by 2 whorls separated by a deep suture in which there are 2 marked peripheral carinae, which angle the shell, and a thick cord that delimits the umbilicus.

The ornamentation consists of spiral cords, wider than their interspaces and axial ribs in variable numbers crossing the cords and forming nodules at the point of intersection. All the teleoconch is ornamented with fine spiral threads that cover both the spiral cords and the interspaces; on the spiral cords the filets are very numerous and very tight; in the spaces between the cords the filets are more distant and therefore fewer in number.

The umbilicus is delimited by one or two thick spiral cords, and inside there are fine spiral cordlets whose number varies from some localities to others. The aperture is oval and the peristome continuous; the margin of the outer lip is modified by the spiral cords; the parietal area is thick and the columella is curved and is thickened and slightly reflected towards the umbilicus at its base.

The holotype measures 1.1 x 0.93 mm.

Habitat. Infra-circalittoral species, living both on hard as soft bottoms, predominantly at depths ranging between 0 and 60 m, except for the shell from Reunion, which was dredged to 200-215 m, undoubtedly empty shell carried down slope.

Distribution. Indo-West Pacific. Previously recorded on a web side as *Sansonia* sp. from Reunion. Found in Jordan, Madagascar, Reunion, New Caledonia, Loyalty Islands, Vanuatu, Papua New Guinea, the Philippines, and French Polynesia, as mentioned in the present work.

Remarks. The only figure that we know of showing the new species here described appears, as *Sansonia* sp., on the web page <http://vieocean.free.fr/mollusques/Pickworthiidae.htm> and it is from Reunion, taken from sandy bottom between depths of 30 and 50 m.

Lophocochlias procerus sp. nov. differs from *L. parvissimus* mainly by its elongate form, its ornamentation, its smaller umbilicus and the shape of the aperture.

The new species shows some variation in the morphology of the shells from some localities to others; basically they vary in the number of the axial ribs and the aperture of the umbilicus, also varying in the number of the spiral cordlets observed in the inner part of the umbilicus and the dimensions of the protoconch; in this latter case we consider that the variation is due to its decoration being more or less pointed. It would be relatively easy to describe the specimens with major morphological differences as new species, but if we carefully observe them all together (Fig. 5), we see a series of characters which repeated in all of them: type of protoconch, elongated form of the spire, peripheral carinae which angle the shell, ornamentation, shape of the umbilicus and aperture.

The fossil species *L. oblongus* Lozouet, 2011 shows a slight similarity with *L. procerus* but it is somewhat more elongated, with numerous and very thin spiral cordlets, and lacks of any axial sculpture.

FOSSIL SPECIES

Lophocochlias paucicarinatus Ladd, 1966

Fig. 8A

Lophocochlias paucicarinatus Ladd, 1966: 77, pl. 15, figs. 6-8.

Type locality. Lower Miocene, Eniwetok Atoll.

Type material. Holotype USNM 648434.

Remarks. Ladd (1966) comments: "*L. paucicarinatus* has fewer primary keels and a narrower umbilicus than *L. minutissimus* and lacks the axial sculpture of that species".

Lophocochlias oblongus Lozouet, 2011

Fig. 8B

Lophocochlias oblongus Lozouet, 2011: 50, pl. 1, figs. 5-8.

Type locality. Lower Miocene (Upper Aquitanian); upper sand level with *Littorinopsis*.

Type material. Holotype MNHN F A33730.

Remarks. Lozouet (2011) comments: “*Lophocochlias oblougus* more elongate than *L. staupineusis*, and its sculpture is formed by more numerous and less stronger cords and low but more regular and numerous axial striae. These two species can be separated from the Recent species *L. minutissima* (pl. 1 fig. 9-12) by their larger size, a less prosocline aperture and a spiral sculpture of more numerous and less strong cords”.

Lophocochlias stampinensis Lozouet, 2011

Fig. 8C

Lophocochlias staupineusis Lozouet, 2011: 50, pl. 1, figs. 1-4.

Type locality. Lower Oligocene (Rupelian/Stampian); marls with *Oostroubus*.

Type material. Holotype deposited in MNHN F A33729.

Remarks. Lozouet (2011) comments: “*Lophocochlias paucicarinatus* Ladd, 1966 of the lower Miocene from the atoll of Eniwetok has an aperture with a more prosocline labrum and much better marked spiral cords”.

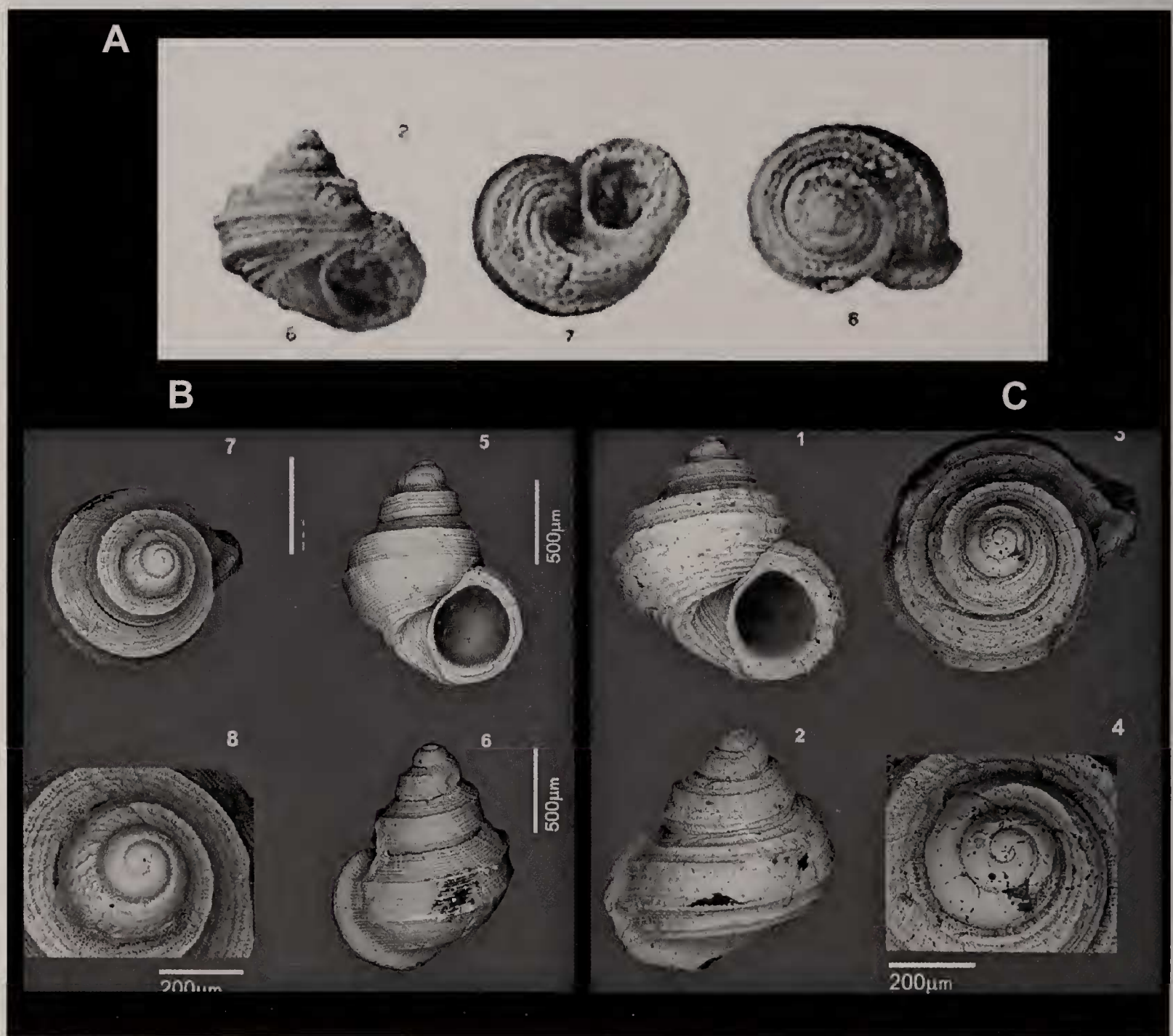


Figure 8A-C

A. *Lophocochlias paucicarinatus* Ladd, 1966. Holotype (USNM 648434) (from Ladd, 1966); **B.** *Lophocochlias oblougus* Lozouet, 2011. Aquitaine Basin, Meilhan SW France (Holotype MNHN.F.A33730) (from Lozouet, 2011); **C.** *Lophocochlias staupineusis* Lozouet, 2011. Stampian, Gaas “Gazoduc” (Holotype MNHN.F.A 33729) (from Lozouet, 2011).

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REFERENCES

- Bouchet, P., Héros, V., Lozouet, P. & Maestrati, P. 2008. A quarter-century of deep-sea malacological exploration of the South and West Pacific: where do we stand? How far to go. Tropical Deep-Sea Benthos, Volume 25. *Mémoires du Muséum National d'Histoire Naturelle*, 196: 9-40.
- Bouchet P. & Rocroi J.P. (Ed.); Frýda J., Hausdorf B., Ponder W., Valdés Á. & Warén A. 2005. Classification and nomenclator of gastropod families. *Malacologia*, 47(1-2): 397 pp. ConchBooks, Hackenheim, Germany.
- Callea, A., Borri, M., Cianfanelli, S., Martignoni, R. & Volpi, C. 2005. Taxonomic and ecological remarks on the marine molluscs of the Mida Creek area (Kenya, Western Indian Ocean). *Atti Soc. it. Sci. nat. Museo civ. Stor. nat. Milano*, 146 (1): 79-94. CalPhotos Photo Database http://calphotos.berkeley.edu/cgi/img_query?where-lifeform=any&rel-taxon=contains&where-taxon=Lophocochlias+minutissimus&rel-namesoup=matchphrase&where-namesoup=&rel-location=matchphrase&where-location=&rel-county=eq&where-county=any&rel-state=eq&where-state=any&rel-country=eq&where-country=any&where-kwid=&max_rows=24. Accessed 01/10/2015.
- Criscione, F. & Ponder, W. 2013. A phylogenetic analysis of rissooidean and cingulopsoidean families (Gastropoda: Caenogastropoda). *Molecular Phylogenetics and Evolution*, 66: 1075-1082.
- Fukuda, H. 1995. Marine gastropoda (Mollusca) of the Ogasawara (Bonin) Islands. Part 3: Additional records. *Ogasawara Research*, 21: 1-142. (pp 67) 1-28(97), 72
- Hedley, Ch. 1899. The Mollusca of Funafuti. (Supplement). *Australian Museum Memoir*, 3(9): 547-565.
- Hendy, A.J.W. 2007. Circum-Pacific Late Cenozoic Paleobiogeography: Consideration of latitudinal gradients, provincialism and beta diversity (Unpublished taxonomic opinions).
- Higo, S., Callomon, P. & Goto, Y. 1999. Catalogue and bibliography of the marine shell-bearing Mollusca of Japan. Elle Scientific Publications, Osaka, pp. 749.
- Kay, E.A. 1971. The littoral marine molluscs of Fanning Island. *Pacific Science*, 25: 260-281.
- Kay, E.A. 1979. Hawaiian marine shells. Reef and shore fauna of Hawaii. Section 4: Mollusca. *Bernice P. Bishop Museum Special Publications*, 64, xviii + 1-653
- Kay, E.A. & Switzer, M.F. 1974. Molluscan Distribution Patterns in Fanning Island Lagoon and a Comparison of the Mollusks of the Lagoon and the Seaward Reefs. *Pacific Science* (1974), Vol. 28, No.3, p. 275-295.
- Kilburn, R.N. 1977. Taxonomic studies on the marine Mollusca of southern Africa and Mozambique. Part 1. *Annals of the Natal Museum*, 23, 173-214.
- Ladd, H.S. 1966. Chitons and Gastropods (Haliotidae through Adeorbidae) from Western Pacific Islands. *United States Geological Survey. Professional Paper*, 531: 1-98.
- Lozouet, P. 2011. Nouvelles espèces de gastéropodes (Mollusca: Gastropoda) de l'Oligocène et du Miocène inférieur d'Aquitaine (Sud-Ouest de la France). Partie 4. *Cossmanniana*, 13: 49-58.
- Maes, V.O. 1967. The Littoral Marine Mollusks of Cocos-Keeling Islands (Indian Ocean). *Proceedings of the Academy of Natural Sciences of Philadelphia*, Vol. 119 (1967), pp. 93-217.
- Moore, D.R. 1972. *Cochliolepis parasitica*, a non parasitic marine gastropod, and its place in the Vitrinellidae. *Bulletin of Marine Science*, 22(1): 100-112.
- Obis Indo-Pacific molluscan database. http://clade.ansp.org/obis/find_mollusk.html. Accessed 4-05-2015.
- Okutani, T. 2000. *Marine Mollusks in Japan*. Tokai University Press, Tokyo. 1173 pp.
- Pilsbry, H.A. 1921. Marine mollusks of Hawaii, XIV-XV. *Proceedings of the Academy of Natural Sciences*, 72: 360-383.
- Ponder, W.F. 1985. A review of the genera of the Rissoidae (Mollusca: Mesogastropoda: Rissoacea). *Records of the Australian Museum supplement* 4: 1-221.
- Ponder, W.F. & de Keyzer, R.G., 1998. Superfamily Rissooidea. In: Beesley, P.L., Ross, G.J.B., Wells, A. (Eds.), Fauna of Australia, Mollusca: The Southern Synthesis, vol.5. CSIRO Publishing, Melbourne, pp. 745-766.
- Rolán, E. 2010. Las mejores fotos de nuestros socios: Protoconcha espectacular. *Noticiario SEM*, 53: 51.

- Rubio, F., Fernández-Garcés, R. & Rolán, E. 2013. The genus *Haplocochlias* (Gastropoda, Skeneidae). *Iberus*, 31(2): 41-126.
- Sepkoski, J.J. 2002. A compendium of fossil marine animal genera. *Bulletins of American Paleontology*, 363: 1-560.
- Takano, T. & Kano, Y. 2014. Molecular phylogenetic investigations of the relationships of the echinoderm-parasite family Eulimidae within Hypsogastropoda (Mollusca). *Molecular Phylogenetics and Evolution*, 79: 258-269.
- Tröndlé, J. 1986. Premières données en écologie et faunistique sur la microfaune malacologique de Tahiti (Société - Polynésie française). *Haliotis* 15: 61-72.
- WMSD
<http://www.bagniliggia.it/WMSD/PDFFamily/SKENEIDAE.pdf>. Accessed 01/10/2015.
- WoRMS Editorial Board, 2013. World Register of Marine Species. Available from <http://www.marinespecies.org> at VLIZ.
<http://www.marinespecies.org/aphia.php?p=taxlist>. Accessed 2013-October-26.