New species and genera of colloniids from Indo-Pacific coral reefs, with the definition of a new subfamily Liotipomatinae n. subfam. (Turbinoidea, Colloniidae)

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ABSTRACT
The genus *Liotipoma* McLean & Kiel, 2007, was proposed for a remarkable small-shelled gastropod genus from coral reefs of the Indo-Pacific that resemble the family Liotiidae Gray, 1850 in having fine axial lamellae and a thickened terminal lip, but differ in having the solid calcareous operculum of the family Colloniidae Cossmann, 1916. The genus was originally assigned to the otherwise Cretaceous subfamily Petropomatinae Cox, 1960 of the family Colloniidae, because the inner side of the operculum is multispiral, conical and projecting, as in the Mesozoic genera assigned to Petropomatinae. Here the genus *Liotipoma* is assigned to a new colloniid subfamily Liotipomatinae n. subfam., because its axial lamellae are unknown in the Cretaceous genera of Petropomatinae. Four genera are now recognised; all species are known from shell grit samples collected by diving or dredging at coral reefs from recent MNHN expeditions to New Caledonia, the Loyalty Islands, Espiritu Santo (Vanuatu) and Wallis Island, and also from LACM material from Fiji, Papua New Guinea, and the Marshall Islands. The most speciose genus is *Liotipoma*, with eight known species, seven of which are new and described here the largest known species is *L. magna* n. sp. from Santo, Vanuatu. Also described are: *Depressipoma* n. gen. with two new species from the Marshall Islands; *Rhombipoma* n. gen., with one new species from Rowley Shoals, northwestern Australia; and *Paraliotipoma* n. gen., with one new species from Sea Horse Shoal, South China Sea. Although live-collected specimens are still unknown, sexual dimorphism in *Liotipoma* was reported for the type species when the genus was described. Here it is reported from four of the eight known species of that genus, expressed in expansion of the umbilical cavity as a brood chamber in the female shell, as previously reported in the families Liotiidae and Colloniidae. In two species the worn female shell shows an irregular degradation of the umbilical cavity, which is considered the effect of bearing a large egg mass and brood. For reasons unknown, female shells of most species of *Liotipoma* are much less frequent than male shells. Formal validation of Areneidae n. fam. is provided in an addendum to this paper.

KEY WORDS
Gastropoda,
Colloniidae,
Areneidae n. fam.,
Liotipomatinae
n. subfam.,
sexual dimorphism,
Indo-Pacific,
coral reefs,
new subfamily,
new genera,
new species.

RÉSUMÉ

Nouvelles espèces et nouveaux genres de Colloniidae des récifs coralliens de l'Indo-Pacifique, avec la définition d'une nouvelle sous-famille, Liotipomatinae n. subfam. (Turbinoidea).

Le genre *Liotipoma* a été proposé pour un genre remarquable de gastéropodes à petite coquille, originaires des récifs coralliens de la zone indo-pacifique, qui ressemble à la famille des Liotiidae Gray, 1850 par la présence de fines lamelles axiales et d'une lèvre terminale épaissie, mais en diffère par un opercule calcaire solide, comme chez la famille des Colloniidae Cossmann, 1916. Ce genre a d'abord été assigné à la sous-famille des Petropomatinae Cox, 1960 (Colloniidae), connue par ailleurs uniquement du Crétacé, car la face interne de l'opercule est multispiralée, conique et proéminente, comme dans les genres mésozoïques de Petropomatinae. Dans cet article, le genre *Liotipoma* est assigné à une nouvelle sous-famille, les Liotipomatinae n. subfam., car aucun genre de Petropomatinae du Crétacé ne possède de lamelles axiales. Quatre genres y sont reconnus à ce jour; toutes les espèces ont été étudiées à partir d'échantillons de débris de coquillages, récoltés lors de plongées et de dragages dans les récifs coralliens effectués au cours d'expéditions récentes du MNHN en Nouvelle Calédonie, dans les îles Loyauté, autour des îles d'Espiritu Santo (Vanuatu) et de Wallis, mais également à partir du matériel du LACM récolté à Fiji, en Papouasie Nouvelle-Guinée et autour des îles Marchall. Le genre le plus riche en espèces est *Liotipoma*; il comprend huit espèces, dont sept nouvelles et décrites ici; la plus grande connue, *L. magna* n. sp., est originaire de Santo (Vanuatu). Trois autres genres sont également décrits : *Depressipoma* n. gen., avec deux nouvelles espèces des îles Marshall ; *Rhombipoma* n. gen., avec une nouvelle espèce des Rowley Shoals, au nord-ouest de l'Australie; et *Paraliotipoma* n. gen., avec une nouvelle espèce originaire de la mer Horse Shoal, dans la mer de Chine méridionale. Bien qu'aucun spécimen vivant n'a encore été récolté, un dimorphisme sexuel a été constaté chez l'espèce type de *Liotipoma*, quand le genre a été décrit. Ce dimorphisme est attesté ici pour quatre des huit espèces connues du genre : il se caractérise par la formation d'une sorte de chambre d'incubation à partir de l'expansion de la cavité ombilicale, caractère déjà observé chez les Liotiidae et les Colloniidae. Chez les femelles de deux espèces, la coquille usée est dégradée de façon irrégulière au niveau de la cavité ombilicale, dégradation qui pourrait être dûe à la présence d'une grande quantité d'œufs. Pour des raisons inconnues, la coquille des femelles de la plupart des espèces de *Liotipoma* est bien moins fréquente que celle des mâles. Une validation formelle d'Areneidae n. fam. est donnée ici dans un addendum.

MOTS CLÉS
Gastropoda,
Colloniidae,
Areneidae n. fam.,
Liotipomatinae
n. subfam.,
dimorphisme sexuel,
Indo-Pacific,
récifs coralliens,
sous-famille nouvelle,
genres nouveaux,
espèces nouvelles.

INTRODUCTION

The genus *Liotipoma* McLean & Kiel, 2007, first became known to me in the course of studying material for a forthcoming worldwide revision of the family Liotiidae Gray, 1850, a group characterised by calcareous beads arranged in a multispiral pattern on the exterior surface of a conchiolinous operculum. *Liotipoma* is small-shelled (maximum dimension 6.8 mm) and has shell micro-sculpture of fine axial lamellae, similar to that of Liotiidae. Living specimens are yet unknown, but the exterior

surface of the operculum is thickly calcified with a pattern of rugose radial ridges and a deep pit in the center; the inner surface is conical in low relief, with a multispiral pattern of raised volutions. The calcified operculum is indicative of the family Colloniidae Cossmann, 1916, but the shell character are unlike any living or Cenozoic member of Colloniidae.

McLean & Kiel (2007) reviewed Cretaceous members of Petropomatinae Cox, 1960, including the genus *Petropoma* Gabb, 1877, from Peru, and others not assigned to genera; we proposed the genus *Sohlipoma* for three species from Puerto Rico, which were incorrectly assigned by Sohl (1998) to the Jurassic genus *Metriomphalus* Cossmann, 1916. Because the inner side of the operculum of *Liotipoma* agreed with that of *Petropoma*, we assigned it to the Petropomatinae. However, in view of the major distinction in shell characters and the great disparity in geologic age, a new subfamily Liotipomatinae n. subfam. is here proposed for the Neogene genera *Liotipoma*, *Paraliotipoma* n. gen., *Depressipoma* n. gen. and *Rombipoma* n. gen.

Shells of these genera are sufficiently small that they have been collected only from sediment samples from shallow water, which have been screened and picked for small specimens under the dissecting microscope, a process that continues to yield unknown species, particularly from locations in the Indo-Pacific. The sexual dimorphism originally described for the type species of *Liotipoma* has now been confirmed in a total of four known species and further details are now provided for the sexual dimorphism, which is unknown in the three additional new genera.

MATERIAL AND METHODS

Material of the most speciose genus *Liotipoma* has been represented in the collections of the Natural History of Los Angeles County (LACM) for over 25 years. The LACM material was first collected in 1985 from the vicinity of Fiji, extracted from sediment samples collected by the late Antonio Ferreira. Further material was collected by Ken Severin at Papua New Guinea in 1985, and by the late Twila Bratcher at Fiji in 1991.

More recently, *Liotipoma* has been recognised among specimens of Liotiidae in material loaned by the Muséum national d'Histoire naturelle, Paris (MNHN). The MNHN material results from intensive collecting by shore based expeditions, two sites in New Caledonia (MONTROUZIER expedition, 1993, see Bouchet 1994), one site at the Loyalty Islands east of New Caledonia (LIFOU 2000, see Bouchet *et al.* 2001), and another site at Espiritu Santo, Vanuatu (SANTO 2006, see Bouchet *et al.* 2011a), for which Bouchet *et al.* (2011b) provided a general report on the marine molluscs.

The first species of *Depressipoma* n. gen. was collected from Eniwetok Atoll, Marshall Islands, by the U.S. Geological Survey between 1946-1952.

The monotypic *Paraliotipoma* n. gen. was first collected at Sea Horse Shoal, South China Sea, by Boris Sirenko on a Russian expedition in 1974.

The monotypic *Rhombipoma* n. gen. was collected by the late Twila Bratcher at Rowley Shoals, Western Australia, in 1986.

Shells in this group range in size from 2.3-6.8 mm and are best studied by comparison of photos. Three or four standard views are provided: the apertural view perpendicular to the coiling axis, the umbilical view aligned with the coiling axis, the apical view showing how the shell rests on a flat surface, and the tilted apertural view, which shows a direct view of the aperture, provides a more direct view of the basal sculpture, and shows the umbilical cavity of shells here determined to be female.

ABBREVIATIONS

AMS	Australian Museum, Sydney;
LACM	Natural History Museum of Los Angeles County, California;
MNHN	Muséum national d'Histoire naturelle, Paris;
USNM	United States National Museum, Washington;
ZISP	Zoological Institute, St. Petersburg;
H	shell height;
D	maximum diameter.

SYSTEMATICS

Superfamily TURBINOIDEA Rafinesque, 1815

REMARKS

Hickman & McLean (1990) reviewed the classification of trochiform vetigastropods and conservatively

recognised three trochoidean families: Turbinidae Rafinesque, 1815, Trochidae Rafinesque, 1815 and Skeneidae Clark, 1851. They divided Turbinidae into a number of subfamilies, including Angariinae Thiele, 1921, Liotiinae Gray, 1850, Colloniinae Cossmann, 1916, Prisogasterinae Hickman & McLean, 1990, Turbininae Rafinesque, 1815, Gabrieloniinae Hickman & McLean, 1990, Tricoliinae Woodring, 1928, and Phasianellinae Swainson, 1840. Changes to that classification have been made by current authors:

Geiger & Thacker (2005) found the Trochoidea of Hickman & McLean (1990) to be non-monophyletic on molecular evidence. Warén & Bouchet *in* Bouchet & Rocroi (2005: 245) separated the Turbinoidea and the Trochoidea at the superfamily level and raised the rank of many categories. A more extensive molecular study is that of Williams & Ozawa (2006), followed by Williams *et al.* (2008), who found two well-supported clades within the broadly defined Turbinidae, one comprising the Turbininae plus Prisogasterinae and the other including the less derived subfamilies reviewed by Hickman & McLean (1990), except for the anomaly that Liotiidae and Areneidae n. fam. (see Addendum) were not placed in the same superfamily. Moreover, the Colloniidae were assigned to the superfamily Phasianelloidea Swainson, 1840, for which the other included families have shells of high profile and non-nacreous interiors. Acceptance of the assignment of Colloniidae to Phasianelloidea would only be possible in a parallel system of classification in which morphological evidence from the shell and radula as well as the paleontological evidence is ignored. For purposes here, the subfamilies of Hickman & McLean (1990) are treated at the family level, with the assignment to superfamily continuing to be based on all the traditional suites of morphological evidence, as well as paleontological considerations, as further elaborated by McLean & Kiel (2007).

Family Colloniidae Cossmann, 1916

Diagnosis. — Shell with or without interior nacreous layer; aperture nearly radial to oblique; aperture circular with complete peristome, to oval with interrupted peristome. Operculum calcified, circular to oblong; aperture conforming to outline of operculum, which is enveloped on outer side by foot; pattern of outer side varies by genus; inner surface conical or flat, multispiral or multispiral becoming paucispiral.

Remarks

This group was originally intended to apply to non-nacreous genera, in contrast to the nacreous Homalopomatinae Keen, 1960, but Hickman & McLean (1990: 47) included both non-nacreous and nacreous genera in the group. The operculum is known in Cretaceous to Recent groups. Paleontologists concerned with Mesozoic faunas have recognised the family Colloniidae in the Jurassic, for groups with the operculum unknown, as discussed by Monari *et al.* (1966). Such groups are not further mentioned here.

In the typical subfamily Colloniinae, which applies to most living genera, apertures can vary from circular in outline, to elongate; the operculum is flat-surfaced on the inner side, multispiral in early stages and changing to paucispiral in the final whorl.

The Cretaceous subfamily Petropomatinae, as treated by McLean & Kiel (2007), has dominant spiral sculpture and an operculum that is circular in outline, with the inner surface multispiral and conical, and the outer side with fewer whorls and a central pit. Genera include *Petropoma* Gabb, 1877, and *Sohlipoma* McLean & Kiel, 2007, in which spiral sculpture is dominant. The genus *Liotipoma* McLean & Kiel, 2007 was originally assigned to Petropomatinae, but is here assigned to a new subfamily:

Subfamily Liotipomatinae n. subfam.

Type genus. — *Liotipoma* McLean & Kiel, 2007.

Diagnosis. — Aperture round with complete peristome; operculum multispiral, low conical on inner surface, outer surface of operculum with central pit, rugose with central pit, or rugose throughout. Shell with fine axial lamellae and larger cancellate sculpture; expansion of whorl increasing at final stage, final lip broadly expanded, and thickened with layered lamellae that decrease in diameter at terminal stage; umbilicus broadly open, but blocked by extension of inner lip; aperture nearly radial.

DISTRIBUTION. — Indo-Pacific coral reefs. Each of the four genera have limited, non-overlapping distributions: *Liotipoma* is known from island groups south of the equator, including Papua New Guinea, New Caledonia, Lifou, Fiji, Wallis Island, and Espiritu Santo, Vanuatu. *Rhombipoma* n. gen. is known from further east at Rowley Shoals, northwestern Australia. Two of the new genera are known from north of the equator: *Paraliotipoma* n. gen. is known from Seahorse Shoal, South China Sea, and *Depressipoma* n. gen. is known from the Marshall Islands.

FOSSIL RECORD. — Unknown.

LIVING GENERA. — Four living genera are recognised: *Liotipoma* (moderately high profile with peripheral angulation and apertural tongue); *Paraliotipoma* n. gen. (moderately high profile lacking apertural tongue); *Depressipoma* n. gen. (discoidal with angulate periphery); *Rhombipoma* n. gen. (discoidal, with rounded periphery).

REMARKS

The new subfamily is characterised by sculpture of fine axial lamellae, which is unknown in the Cretaceous Petropomatinae. Preserved specimens are yet unknown; all specimens have been recovered from sediment samples, including some in fresh condition with wedged-in opercula.

KEY TO GENERA OF LIOTIPOMATINAE N. SUBFAM.

1. Shell profile moderately high 2
— Shell profile low 3

2. Base of lip with tongue projecting into umbilical area .... *Liotipoma* McLean & Kiel, 2007
— Base of lip lacking tongue ..... *Paraliotipoma* n. gen.

3. Shoulder and base with clathrate sculpture ..... *Depressipoma* n. gen.
— Shoulder devoid of spiral sculpture ..... *Rhombipoma* n. gen.

Genus *Liotipoma* McLean & Kiel, 2007

Liotipoma McLean & Kiel, 2007: 259.

TYPE SPECIES. — *Liotipoma wallisensis* McLean & Kiel, 2007 (by original designation).

DESCRIPTION

(REVISED FROM MCLEAN & KIEL, 2007)

Shell small (maximum diameter 6.8 mm), non-nacreous; aperture round; lip massively thickened and projecting, with inward extension, the tongue that partially blocks aperture in male shell; shell profile low, with projecting mid-whorl angulation and projecting subtending cord that forms lowermost projection of base. Sculpture axial and spiral; axial sculpture of raised ridges, overriding spiral sculpture; spiral sculpture of cords that terminate on outer face of final lip. Base with broad low cord in the umbilical area, the emergent cord, separated by narrow groove from prominently projecting subtending cord. Axial micro-sculpture of sharply raised lamellae throughout, strongly expressed as layers across thickened final lip. The calcified periostracum (intriticalyx) of most Liotiidae is also expressed in *Liotipoma*. Most specimens are sufficiently worn to not show the surface layer, but it clearly shows in the SEM view of Figure 12E-G. Whorl diameter in some species expanding in final quarter whorl, mature lip arising abruptly, projecting, strongly thickened; lamellar deposition that forms final lip decreasing in diameter toward final position and showing terminations of spiral sculpture extending across thickened lip. Aperture nearly radial (only slightly oblique); umbilicus open in juvenile shell; umbilical wall with extension of axial sculpture, with inwardly projecting spines corresponding to axial ribs (Fig. 12G). Mature shell of *Liotipoma* species sexually dimorphic; umbilicus of male shell blocked with massive tongue, extending from inner edge of thickened lip. Female shell with open umbilical cavity, reduced tongue, bordered on outside by raised subtending cord, enlarged for brooding of larval stages.

Protoconch (Fig. 1) diameter 320 µm, with fine longitudinal ridges and flared final expansion, positioned at same level as first teleoconch whorl.

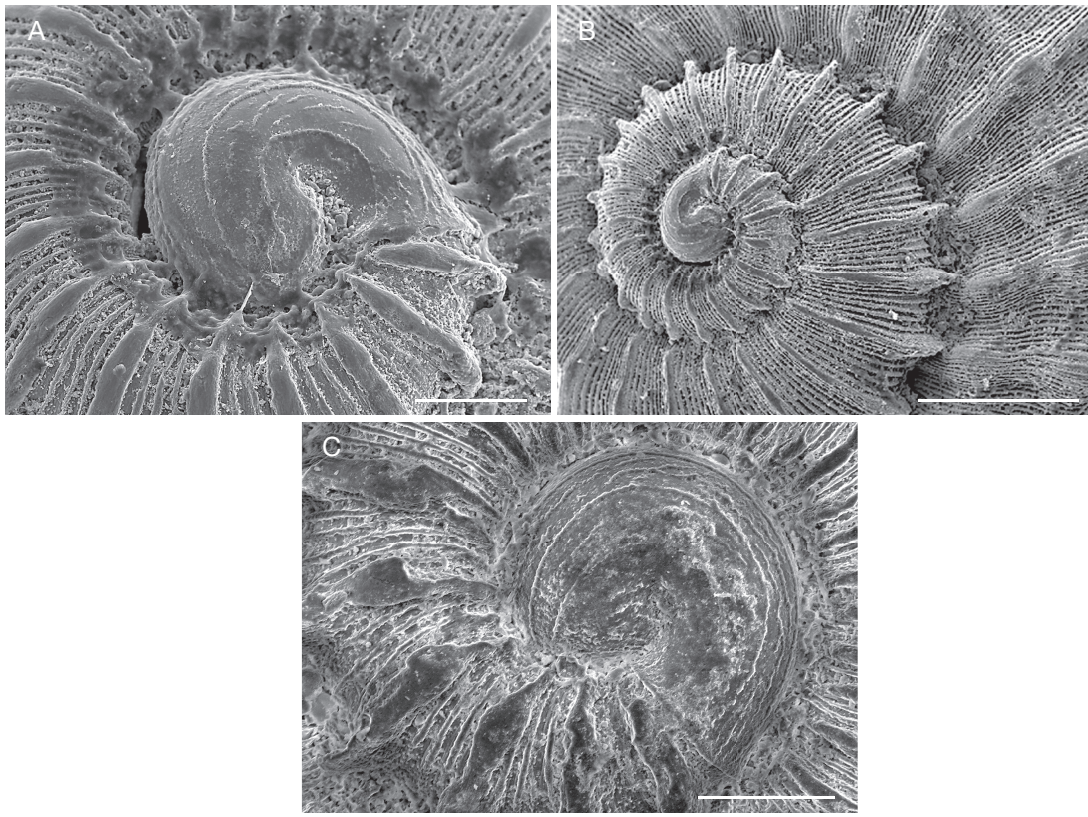

Fig. 1. — Protoconchs of *Liotipoma* McLean & Kiel, 2007 spp.: **A**, **B**, juvenile shell from Santal Bay, Lifou, Loyalty Islands (MNHN, stn 1434), shell diameter 2.4 mm: protoconch (**A**) and early whorls (**B**); **C**, protoconch of *Liotipoma solaris* n. sp., Cape Washington, western end of Kandavu, Fiji (LACM 85-138). Scale bars: A, 0.1 mm; B, 0.5 mm; C, 0.1 mm.

Axial sculpture arising in first teleoconch whorl next to protoconch in first quarter whorl, projecting at periphery (to give a spinose effect in umbilical and apical views) and clumped to project into umbilicus and clumped to form early subtending cord. Most of the figured specimens are sufficiently worn to obscure protoconch sculpture. The assumption is made that protoconchs of all species are like those shown in Figure 1.

Operculum (Fig. 2) calcareous, with deep central pit of ⅓ to ¼ its diameter; outer area raised, with radial, somewhat irregular rugose sculpture separated by deep radial channels; interior surface low conical, with narrow, raised multispiral volutions and long growing edge.

Radula unknown (live-collected specimens unknown).

Distribution. — Central Indo-Pacific, sublittoral, reef-associated. Records for *Liotipoma* include Fiji, Wallis Island, Papua New Guinea, New Caledonia, Loyalty Islands (east of New Caledonia), and Vanuatu at Espiritu Santo. Three sympatric species are known from Lifou, Loyalty Islands (*L. mutabilis* n. sp., *L. dimorpha* n. sp., and *L. lifouensis* n. sp.).

Remarks

Liotipoma is characterised by the operculum with deep, broad central pit, conical inner surface with raised multispiral ridges; and by the shell with fine axial lamellae, the massive final lip produced by the abruptly expanded diameter of final whorl, with incremental lamellar layers decreasing in size; axial ribs are stronger than the spiral cord. The umbilicus in male shells is usually blocked by the massive extension of the inner lip, here called the *tongue*.

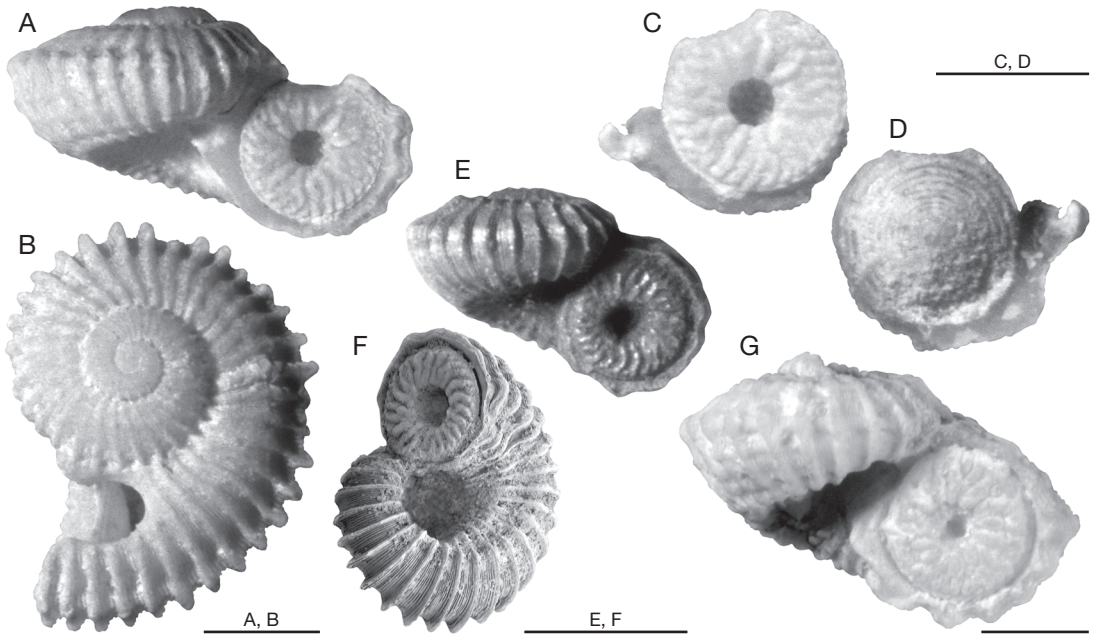

FIG. 2. — Opercula of three immature, sexually indeterminate species of *Liotipoma* McLean & Kiel, 2007; opercula wedged in place in all three specimens; **A**, **B**, *L. wallisensis* McLean & Kiel, 2007, off Wallis Island (MNHN, stn DW523), H 1.9, D 3.5 mm; **C**, **D**, inner and outer views of same operculum from immature specimen from Wallis Island, showing attached portion of columella, after breaking it free in order to show interior view; diameter of operculum 1.2 mm; **E**, **F**, *L. solaris* n. sp., Herald Pass, Great Astrolabe Reef, Fiji (LACM, stn 85-135), H 1.5, D 1.9 mm (SEM views of tilted specimen with operculum; apertural view is photo of coated specimen); **G**, *Liotipoma* sp., off Pointe Lefèvre, Santal Bay, Lifou, Loyalty Islands (MNHN, stn 1435), H 2.4, D 3.7 mm (specimen missing apical whorl). Scale bars: 1 mm.

The surface sculpture of *Liotipoma* has axial lamellae and other sculpture comparable to that of Liotiidae. Without knowledge of the operculum, this genus would surely be placed in the Liotiidae. Most of the available specimens show some wear and encrustation.

Mature shells are large enough that illustration with SEM is not a necessity. An unusually clean, but immature (3.3 mm in diameter) specimen of *L. solaris* n. sp. is presented in Figure 12E-G, showing intricate spines in the umbilical area that represent the termination of axial sculpture, as also expected in Liotiidae.

In most liotiid genera, whorl expansion stalls or retreats at the final stage, still allowing for an expanded lip. The species of *Liotipoma* differ in showing an increase in whorl expansion in addition to the whorl expansion resulting from the final projecting lip.

Shells of this genus are probably represented in other museum and private collections among undetermined micro-gastropods from Indo-Pacific localities, no doubt thought to be small species of Liotiidae. Live-collected specimens are unknown but the operculum is now known from single immature shells of three species, in which it is wedged in place (Fig. 2).

SHELL CHARACTERS

Size

Maximum diameter ranges from 4.0 (*Liotipoma dimorpha* n. sp., Fig. 6E-H) to 6.8 mm (*L. magna* n. sp., female shell, Fig. 9). This is usually a reliable species level character, with about a 1 mm allowance for variation in shell diameter.

Shell height

Most shells thought to represent females are noticeably higher in profile that those of male shells. These distinctions are evident from the dimensions provided in the captions for the illustrations.

Whorl count
Whorl count ranges from 2.6 to 3.3 teleoconch whorls, as determined in apical view. Smaller species generally have fewer whorls.

Count of axial ribs for final whorl
Axial ribs on the final whorl (not including the closely spaced lamellae of the body whorl and the massive final lip) number from 21 to 33. Counts can be made from spire views or from basal views. Some specimens exhibit sudden changes in the spacing of axials (e.g., *L. magna* n. sp., Fig. 8A-D); others may have more closely spaced axials in the pre-terminal condition. This character is considered least reliable as a species level character, in view of the sudden changes observed in some specimens.

Peripheral spines
In most species, the peripheral spines produced by axial sculpture in basal view are directed slightly forward; in some they are pointed straight out, and in one specimen of one species (*L. lifouensis* n. sp., Fig. 10A-D), the spines are directed backward, but this does not apply to the second specimen illustrated here in which the spires are directed straight out (Fig. 10E-H). This is therefore unreliable for species distinctions.

Plane of aperture and plane of tongue
In basal view, it is apparent that the plane of the nearly radial aperture may or may not coincide with the plane of the outer edge of the tongue, the extension of the lip that blocks the umbilicus of the male shells. This is regarded as variable within the species.

Shape of tongue
In basal view the tongue is roughly triangular in outline. This is also regarded as variable within species. In one species (*L. lifouensis* n. sp., Fig. 10), the tongue is longer and narrower than in others, and this is considered a species-level character.

Whorl expansion
In basal or spire views, species differ in the extent of whorl expansion in the final whorl. Some species have very little whorl expansion (e.g., *L. solaris* n. sp., Fig. 11A-D) and others have a more notable whorl expansion (*L. splendida* n. sp., Fig. 13A-D).

Relative strength and positioning of basal cords
Some species have the emergent cord and subtending cord broad (*L. mutabilis* n. sp., Fig. 4), in others the first basal is narrow (*L. dimorpha* n. sp., Fig. 6). These distinctions are regarded as highly consistent for species determination.

Sexual Dimorphism
All species of *Liotipoma* are considered to be sexually dimorphic, although the available material of most species includes a recognisable female shell in only four of the eight species (*L. wallisensis*, *L. mutabilis* n. sp., *L. dimorpha* n. sp., *L. magna* n. sp.). Female shells are unknown for the species *L. lifouensis* n. sp., *L. solaris* n. sp., *L. splendida* n. sp., and *L. clausa* n. sp.

Specimens considered as male shells have the massive tongue extending to block the umbilicus. This is not formed in female shells, which have an open umbilicus with an angular edge for the retention of egg masses and larval stages, with further protection provided by the extended body of the female. The female shell for two species better known from the male shell are shown for *L. wallisensis* n. sp. (Fig. 3E-H), and *L. mutabilis* n. sp. (Fig. 4). In these two species the female shell seems to be worn and resorbed in the umbilical area, which is considered to have been the result of having a large egg mass and brood.

The tongue, a massive lip projection that blocks the umbilical cavity of the male shell of specimens of most species of *Liotipoma* gives it a predation resistant advantage over that of most species of Liotiidae, in which the open umbilical wall is thin-shelled, and often is the site of drill holes made by naticid or muricid gastropods, as is evident in the drilled shells of many species.

The number of mature shells for all species of *Liotipoma* is limited to the material at hand, which in some species consists of very few or single specimens. Male shells are much more common than female shells and some species are known only from male shells. The few known female shells generally have a higher profile than that of male shells, which

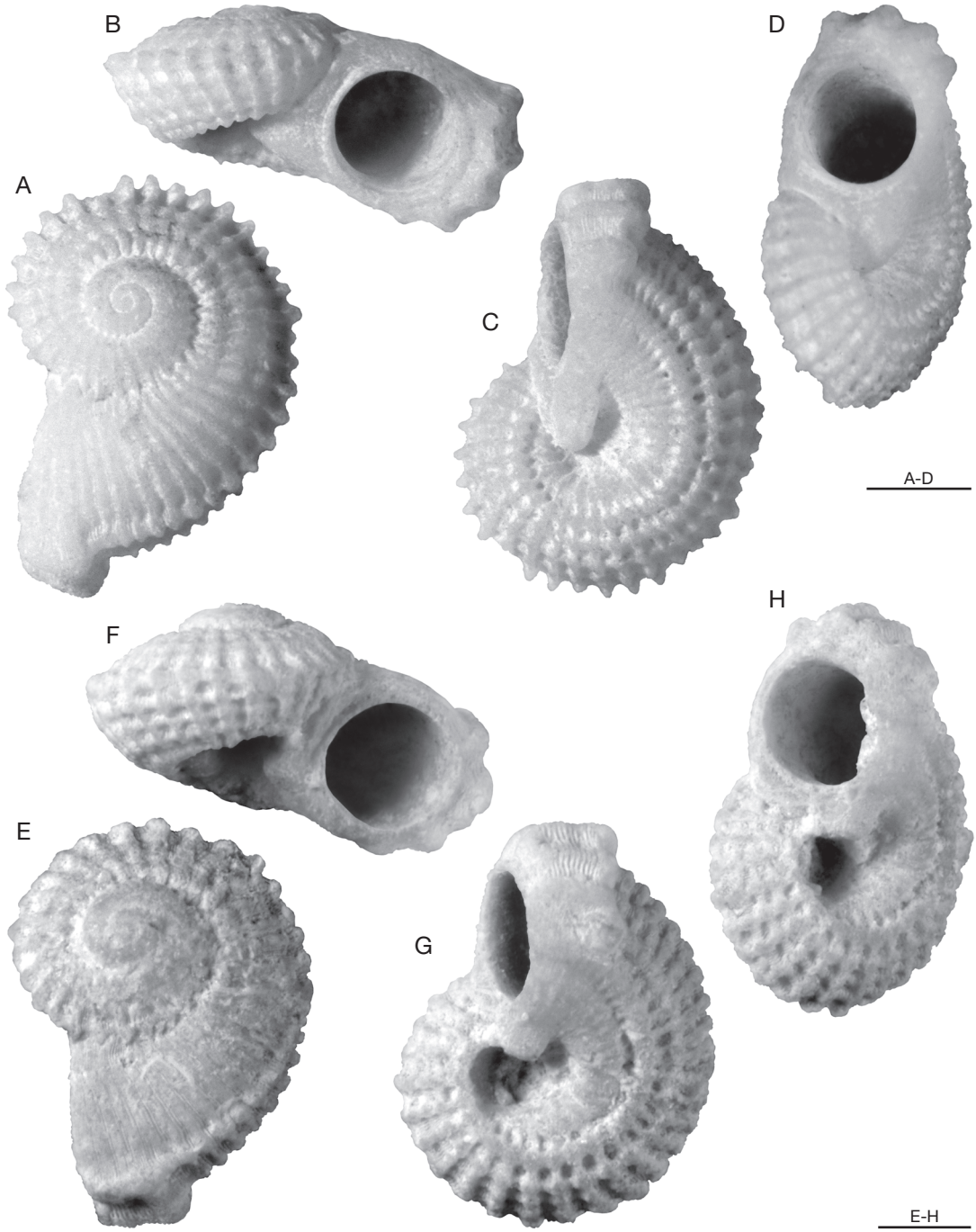

FIG. 3. — Type species of *Liotipoma* McLean & Kiel, 2007, *L. wallisensis* McLean & Kiel, 2007, male and female shells: **A-D**, holotype, male shell (MNHN 24754, stn DW523), off Wallis Island, NE of Fiji, 455-515 m (depth for this and the following specimen probably represents down slope fall from shallow water), H 2.0, D 4.1 mm; **E-H**, paratype, female shell (MNHN 24756, stn DW601), off Wallis Island, 350 m, H 2.6, D 4.4 mm. Scale bars: 1 mm.

serves to expand the umbilical cavity and increase the volume available for brooding. Descriptions of the species are based on male shells, with a supplementary description of the female shells for the species in which it is now recognised.

Most species of *Liotipoma* have a similar general appearance, having a subdiscoidal profile with a peripheral angulation, usually two low cords on the shoulder and four cords on the base, crossed by axial ribs that form spinose projections at the periphery and extend across the shoulder and form beaded cords on intersecting the basal cords.

Arrangement of *Liotipoma* species

The type species in which the only known female shell is badly worn is treated first, followed by another species, in which two worn female shells are known. This is followed by two species that have the male and female shells in good condition. Species represented by male shells are treated last.

Key to species of *Liotipoma* McLean & Kiel, 2007

1. Size large, diameter 5.2 mm or larger 7
— Size smaller, diameter usually under 5.2 mm 2

2. Profile very high ..... *L. clausa* n. sp.
— Profile not so high 4

3. Emergent cord broad, subtending cord narrower ... *L. wallisensis* McLean & Kiel, 2007
— Emergent cord of width not differing from that of subtending cord 4

4. Subtending cord narrower than emergent cord ..... *L. dimorpha* n. sp.
— Subtending cord not narrower than emergent cord 5

5. Tongue narrow, extending across umbilicus ..... *L. lifouensis* n. sp.
— Tongue triangular, not extending across umbilicus 6

6. Shell more than 4 mm diameter ..... *L. mutabilis* n. sp.
— Shell less than 4 mm diameter ..... *L. solaris* n. sp.

7. Emergent cord broad, with inner thickening ..... *L. splendida* n. sp.
— Emergent cord broad, no inner thickening ..... *L. magna* n. sp.

Liotipoma wallisensis McLean & Kiel, 2007 (Figs 2A-D; 3)

Liotipoma wallisensis McLean & Kiel, 2007: 259, fig. 4A-G.

Type material. — Holotype: MUSORSTOM 7, R/V *Alis*, stn DW523, Wallis Island, NE of Fiji, 13°12'S, 176°16'W, 455-515 m, 13.V.1993, Bouchet, Metivier, & Richer, ♂ shell, H 2.0, D 4.1 mm (MNHN 24754, Fig. 3A-D). Paratypes: same location as holotype, but stn DW601, 13°19'S, 176°17'W, ♀ shell, H 2.6, D 4.4 mm (MNHN 24756, Fig. 3E-H). — same data as holotype, operculate immature, H 1.9, D 3.5 mm (MNHN 24755, Fig. 2A-D).

Type locality. — Wallis Island. All specimens are considered to be down-slope fall from shallower reef depths (see Remarks, below).

Distribution. — Wallis Island, only. Other MNHN lots from the same expedition, all in very poor condition.

Etymology. — After the type locality, Wallis Island.

Description

Male shell (Fig. 3A-D)

Whorls 3.3; with marked expansion of final half-whorl; profile low for genus, with single projecting peripheral keel slightly above mid-whorl; profile below keel evenly rounded. Axial sculpture of strong ribs, 32 on last whorl; weakly spinose and forward projecting in early whorls, less projecting and more closely spaced in final quarter whorl. Spiral sculpture of three cords on shoulder, fading in intensity on final

quarter; base with strong subtending cord, and two cords of nearly equal strength between peripheral cord and subtending cord; base with pits formed by clathrate sculpture. Umbilicus bordered by broad emergent cord, which becomes broader and lower in final half whorl, emergent cord overridden by narrow axial ribs; umbilicus fully obstructed, also obstructed by massive tongue-like extension of inner lip, extending more than half the diameter of aperture, tongue aligned with projecting lip. Final lip massive, projecting, extending for ⅓ of final quarter whorl, with successively decreasing layers of deposition, with indentations on surface conforming to spiral sculpture. Aperture nearly radial, plane of aperture well outside of coiling axis. H 2.0, D 4.1 mm (holotype); H 1.9, D 3.5 mm (Fig. 2A-D, immature specimen from same station with wedged operculum).

Female shell (Fig. 3E-H)
Profile higher than that of male shell. Tongue-like extension of aperture, very short, not blocking umbilicus; emergent cord exposed, arising deep within umbilicus; subtending cord forming raised edge near aperture, short spinose projections worn down, compared to male shell. H 2.6, D 4.4 mm.

Operculum of immature paratype (Fig. 2A-D)
Wedged in place and visible through the broken upper lip. There is a nick in the operculum, which indicates that the living specimen was drilled on the shoulder, and the animal responded by retracting to the extent possible. This was fortuitous, as it allows a lateral view of the operculum, showing its thickness and that it is conical on its inner side. This operculum was chipped free in order to photograph the interior side (Fig. 2D). This specimen has an open umbilicus and has an umbilical projection, which seems to be a growth phase in the filling of the umbilicus in the male shell.

Remarks
This species is characterised by its broad emergent cord and narrow cords of the base, which produce strong clathrate sculpture where crossed by axial sculpture; earliest lip expansion strongly projecting. The female shell shows dissolution and resorption of the emergent cord near the aperture and narrowing and dissolution of the inward spines on the subtending cord, which is larger than the adjacent basal cords. The female shell is larger and has a higher profile than that of the male shell, as expected in order to increase the size of the brood chamber.

Known from two lots from deep dredging, but all records are considered to be down slope fall because a number of other species from shallow reef depths are represented in the Wallis Island material (P. Bouchet, pers. comm.). No diving on the reefs at Wallis Island was conducted by the MNHN expedition of 1993, so there is no direct evidence that it occurs at reef depths.

Liotipoma mutabilis n. sp.
(Figs 4; 5)

Type material. — Holotype: LIFOU 2000, stn 1435, Loyalty Islands, Lifou Island, Santal Bay, 20°55.2'S, 167°00.7'E, 5-30 m, diving team, 8.XI.2000, ♂ shell, H 3.4, D 5.7 mm (MNHN 24757, Fig. 4A-D).
Paratypes: LIFOU 2000, stn 1436, Loyalty Islands, Lifou Island, Gaatcha Bay, Santal Bay, 20°55.5'N, 167°04.2'E, 10-20 m, diving team, 10.XI.2000, ♂ shell, H 3.0, D 5.1 mm (MNHH 24758, Fig. 4E-H); ♀ shell, H 3.2, D 4.8 mm (MNHN 24759, Fig. 5E-H). — LIFOU 2000, stn 1434, Loyalty Islands, Lifou Island, Huca Hutighé, Santal Bay, 20°52.5'S, 167°08.1'E, 5-20 m, diving team, 6.XI.2000, ♀ shell, H 2.7, D 4.2 mm (MNHN 24760, Fig. 5A-D).

Type locality. — Loyalty Islands, Lifou.

Distribution. — Loyalty Islands, Lifou.

Etymology. — Latin, changeable.

Description
Male shell (Fig. 4A-H)
Whorls 3.0; profile low for genus; peripheral keel at mid-whorl; profile below keel evenly rounded. Whorl expansion more than usual for genus, with strongly projecting peripheral angulation, shoulder ramp nearly flat above. Axial sculpture of strong ribs, 25-28 on last whorl; spinose and projecting in early whorls, spines projecting forward, spinosity and spacing of axial ribs much diminished in final third of last whorl. Spiral sculpture of three strong, low cords on shoulder in early whorls;

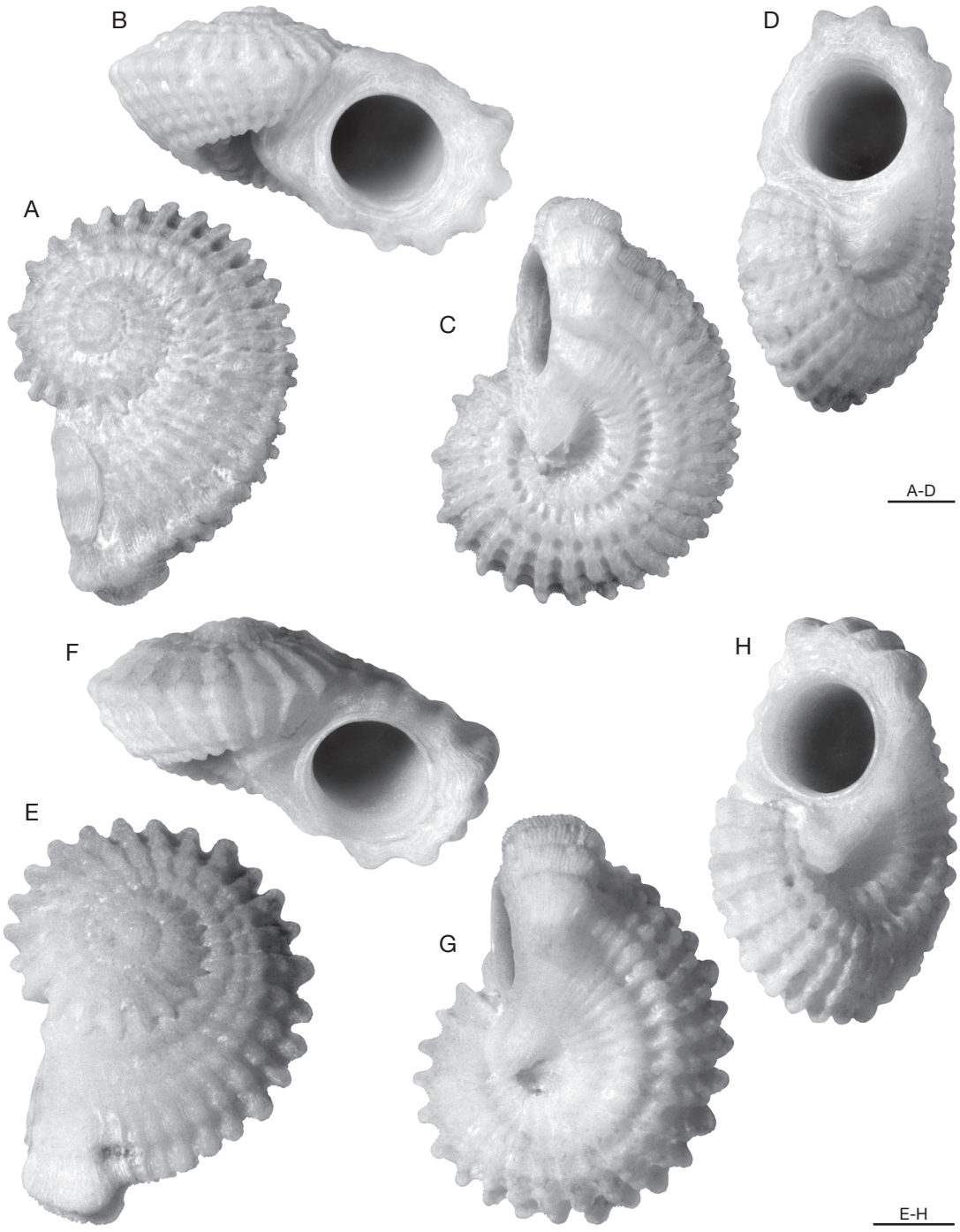

Fig. 4. — *Liotipoma mutabilis* n. sp., male shells: **A**-**D**, holotype (MNHN 24757, stn 1435), Pointe Lefèvre, Santal Bay, Lifou, Loyalty Islands, 5-30 m, H 3.4, D 5.7 mm; **E-H**, paratype (MNHN 24758, stn 1436), Gaatcha Bay, Santal Bay, Lifou, Loyalty Islands, 10-20 m, H 3.0, D 5.1 mm. Scale bars: 1 mm.

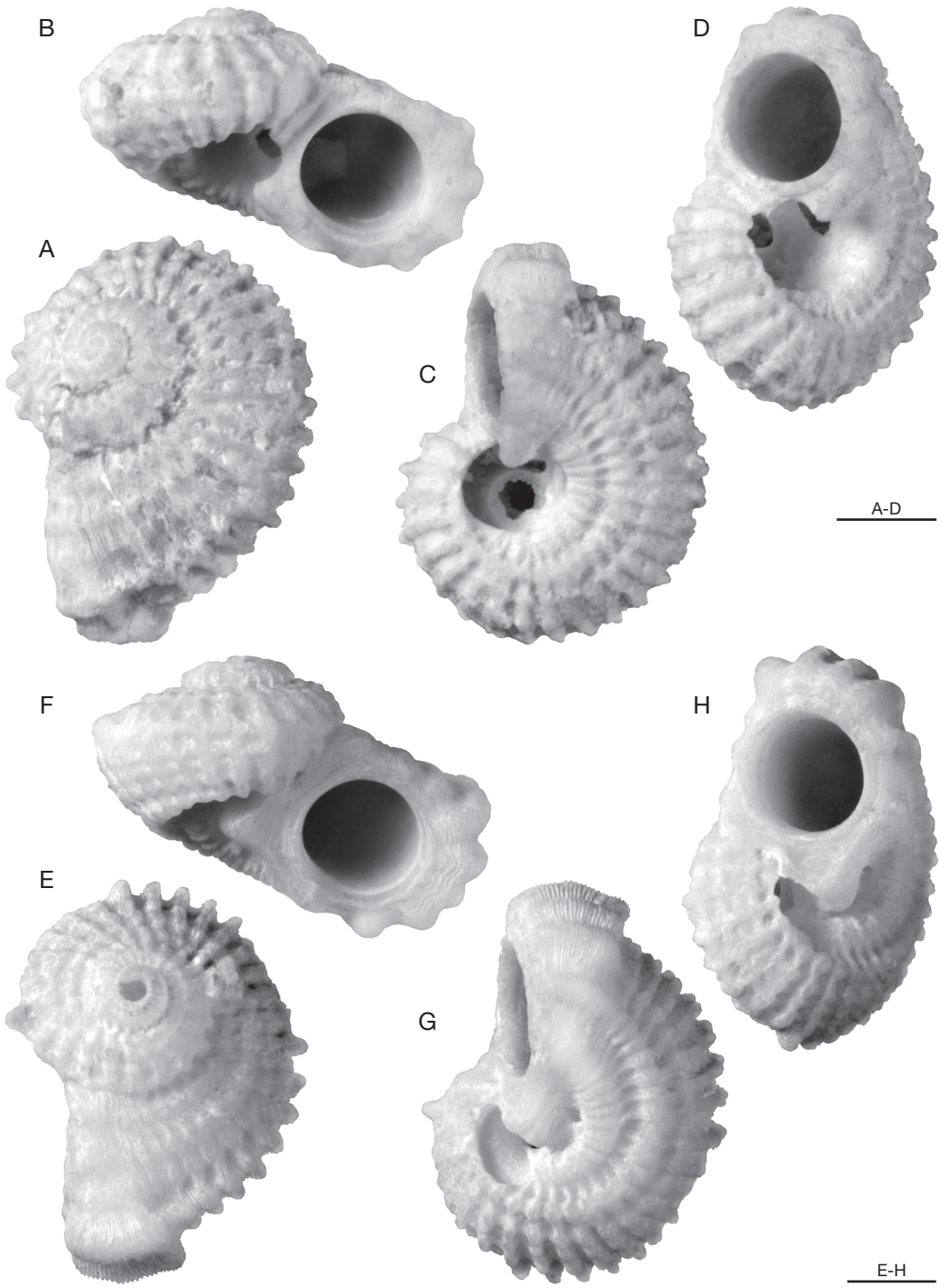

Fig. 5. — *Liotipoma mutabilis* n. sp., female shells: **A-D**, paratype (MNHN 24760, stn 1434), Santal Bay, Lifou, Loyalty Islands, H 2.7, D 4.2 mm; **E-H**, paratype (MNHN 24759, stn 1436), Gaatcha Bay, Santal Bay, Lifou, Loyalty Islands, H 3.2, D 4.8 mm. Scale bars: 1 mm.

changing to three narrow cords in final ⅓ whorl; base with strong subtending cord, and three cords of nearly equal strength between peripheral cord and subtending cord; base with deep pits on outer side of subtending cord and other basal cords. Umbilicus filled by emergent cord, bordered by subtending cord of nearly equal strength, both cords with lamellar extensions of axial sculpture; umbilicus partially open, partially obstructed by short, triangular tongue of inner lip in last half whorl; tongue aligned with aperture or slightly projecting forward, out of alignment with plane of aperture. Final lip massive, extending for ⅓ of final quarter whorl, showing about 20 successively decreasing layers of deposition, lip strongly showing spiral sculpture; tongue extending half the diameter of aperture on previous whorl, showing similar layers of deposition decreasing in extent. Plane of aperture coinciding with umbilical wall, plane of aperture coinciding with edge of tongue. H 3.0, D 5.1 mm (holotype).

Female shell (Fig. 5A-H)

Both specimens retain a portion of the tongue, but it both does not block the umbilical cavity. Two specimens (Fig. 5A-D, E-H) are considered to have been modified by the egg mass and the brooding of larvae to have increased the volume of the umbilical cavity. Both have the emergent cord excavated in a different manner: close to the aperture (tapered in A-D and truncate in E-H), and both have the subtending cord worn to not show the beaded intersection with the axial sculpture; the tongue is short in A-D and less shortened in E-H, but in both specimens the umbilical cavity is enlarged. H 2.7, D 4.2 mm (Fig. 5A-D); H 3.2, D 4.8 mm (Fig. 5E-H).

REMARKS

Liotipoma mutabilis n. sp. resembles *L. splendida* n. sp. (Fig. 9A-D), but has fewer axials (33 compared to 28) and a less expanding final whorl. It differs from *L. dimorpha* n. sp. in the thickness of the subtending cord and the basal cords, those of *L. mutabilis* n. sp. being thicker.

The operculum of *L. mutabilis* n. sp. (Fig. 2G) is known from a wedged-in juvenile specimen from the same station as that of the type material. The diameter of this operculum is 1.4 mm, which is larger than that of the two other known opercula (*L. wallisensis* n. sp. and *L. solaris* n. sp.). It shows a very narrow central pit, which suggests that the pit might disappear altogether in larger specimens of this species.

This species is characterised by its greater expansion of the final whorl than usual for the genus, and its large size (D 5.9 mm), although it is smaller than *L. magna* n. sp. One other large species (*L. splendida* n. sp.) reaches 5.1 mm in diameter.

There is a general resemblance to the species *L. splendida* n. sp. (Fig. 9A-D), but that species has a higher count of axial ribs (33 compared to 28) and has a tongue that extends forward to the plane of the aperture.

Liotipoma dimorpha n. sp.
(Figs 2G; 6; 7)

TYPE MATERIAL. — Holotype: LIFOU, stn 1442, Loyalty Islands, Lifou, Cape Aimé Martin, Santal Bay, 20°46.4'N, 157°02.0'E, 47 m, diving team, 13-14.XI.2000, ♂ shell, H 3.0, D 4.3 mm (MNHN 24761, Fig. 6A-D).
Paratypes: same data as holotype, ♀ shell, H. 3.0, D 5.1 mm (MNHN 24764, Fig. 7A-D). — MONTROUZIER expedition, stn 1331, New Caledonia, Grand Koumac Reef, ♂ shell, H 2.6, D 4.0 mm (MNHN 24763, Fig. 6E-H). — stn 1450, ♀ shell, H 2.5, D 4.5 mm (MNHN 24765, Fig.7E-H).

ADDITIONAL MATERIAL. — **Loyalty Islands**. LIFOU, stn 1435, Loyalty Islands, Lifou, Pointe Lefèvre, Santal Bay, 20°55.2'S, 167°00.7'E, 5-30 m, 8.XI.2000, diving team, 1 immature with operculum (MNHN, Fig. 2G); 1 ♂ shell at 4.6 mm diameter and 2 immature (MNHN). — LIFOU stn 1434, Huca Hutighé, Santal Bay, 20°52.5'S, 167°08.1'E, 5-20 m, 6.XI.2000, diving team, 7 ♂♂ shells, of which the largest is 4.8 mm diameter, plus 3 immature specimens (MNHN). — LIFOU stn 1432, Shelter Reef, Santal Bay, 20°53.5'S, 167°01.7'E, 12-32 m, 21.XI.2000, diving team, 2 mature ♂♂ shells at 4.8 mm diameter, plus 7 immature (MNHN).
New Caledonia. MONTROUZIER expedition, stn 1331, Grand Koumac Reef, Koumac Sector, 20°40'S, 162°12'E, 55-57 m, X.1993, 2 specimens, lip not fully formed on second specimen (MNHN, Fig. 6E-H).

TYPE LOCALITY. — Loyalty Islands, Lifou.

DISTRIBUTION. — Lifou, Loyalty Islands, and Koumac Reef, New Caledonia.

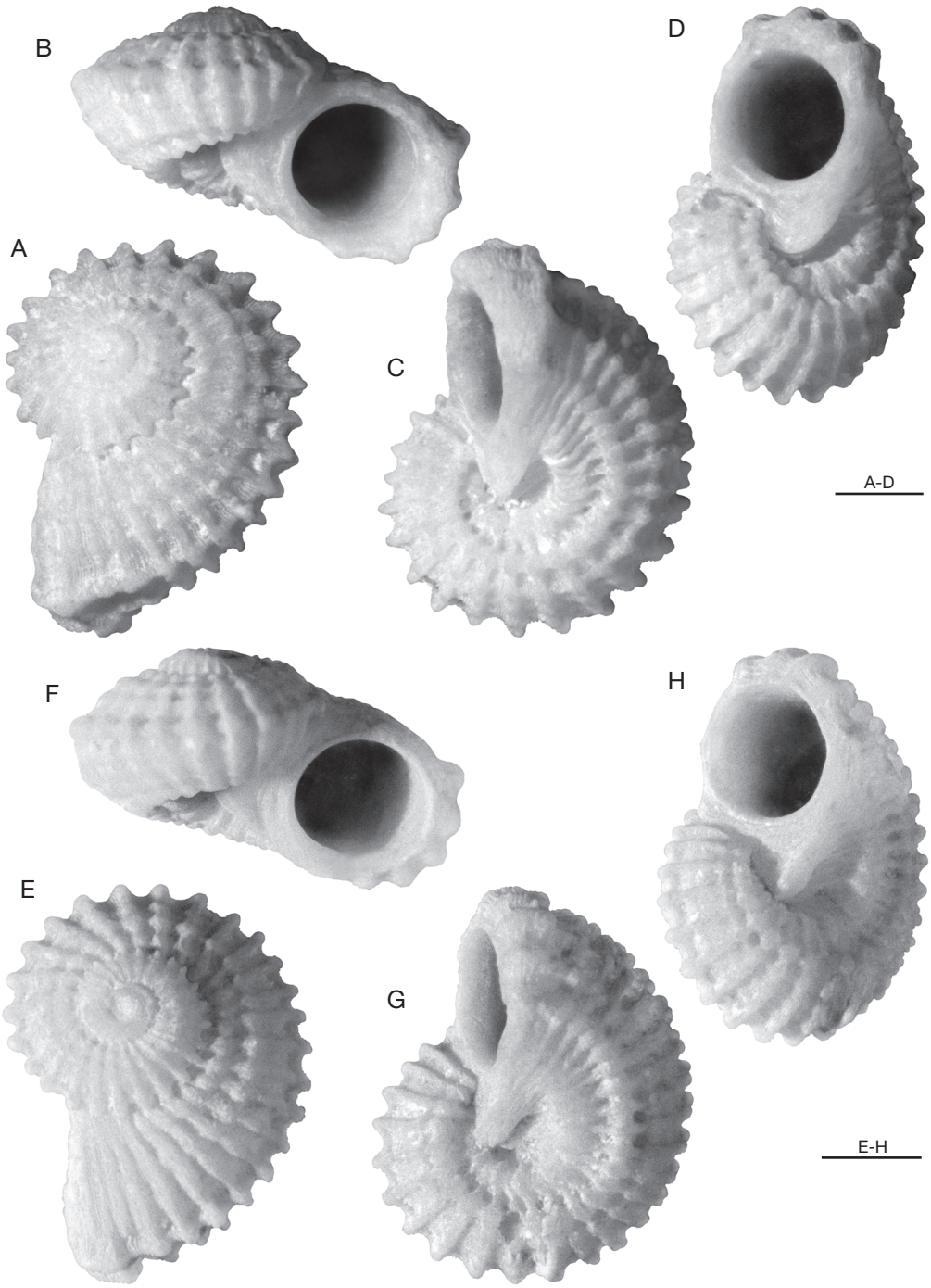

Fig. 6. — *Liotipoma dimorpha* n. sp., male shells: **A-D**, holotype (MNHN 24761, stn 1442), Santal Bay, Lifou, Loyalty Islands, 47 m, H 3.0, D 4.3 mm; **E-H**, paratype (MNHN 24763, stn 1331), Grand Koumac Reef, Koumac Sector, New Caledonia, 55-57 m, H 2.6, D 4.0 mm. Scale bars: 1 mm.

ETYMOLOGY. — The name means two forms, with regard to sexual dimorphism.

DESCRIPTION

Male shell (Fig. 6)

Whorls 3.3; profile moderately high for genus; keel at periphery, slightly higher than mid-whorl; profile below shoulder evenly rounded; subtending cord not strongly projecting. Axial sculpture of strong ribs, 23-25 on last whorl in basal view; strongly spinose in early whorls, more closely spaced in final quarter whorl; spines projecting forward in direction of growth. Spiral sculpture of three cords on shoulder, beaded at intersections with axial ribs. Base with strong subtending cord, and two cords of nearly equal strength between peripheral cord and subtending cord; base with shallow pits on outer side of subtending cord. Umbilicus bordered by broad emergent cord, overridden by narrow axial ribs; umbilicus narrow, obstructed by massive extension of inner lip. Final lip massive, extending for ⅓ of final quarter whorl, with successively decreasing layers of deposition, with indentations conforming to spiral sculpture. Plane of aperture aligned to intersect axis of coiling at umbilicus. Aperture nearly radial, tongue short, triangular, in same plane as plane of aperture. H 3.0, D 4.3 mm (holotype).

Female shell (Fig. 7)

Of higher profile than male shell; emergent cord high on whorl (in basal view), forming protruding carination that enlarges umbilical cavity, subtending cord and first basal cord narrow, interconnected by extensions of axial ribs; tongue not projecting into umbilical cavity for specimen of Figure 7A-D, slightly projecting in specimen of Figure 7E-H. H 3.0, D 5.1 (Fig. 7A-D).

Operculum (Fig. 2G)

Known from immature specimen, with narrow pit in center.

REMARKS

Liotipoma dimorpha n. sp. is characterised by having forward directed spines, a narrow subtending cord and an even narrower first basal cord, by which it differs from *L. mutabilis* n. sp., in which the subtending cord and the first basal cords are significantly broader. By that distinction it also possible to connect the female shell to the male shell and also to separate the separate the female shell from that species. The female shell of this species (Fig. 7) is unlike the female shell of both *L. wallisensis* and *L. mutabilis* n. sp. in having the emergent cord positioned higher (in umbilical view), so that the tongue does not depress it. Female shells are larger than male shells, as expected. The two illustrated male shells differ in the length and direction of the tongue, but these differences are considered intraspecific. In Figure 6A-D it is shorter and in Figure 6E-H it is longer and not in alignment with the plane of the aperture.

Liotipoma magna n. sp.
(Figs 8; 9)

TYPE MATERIAL. — Holotype: SANTO 2006, stn DS103, Vanuatu, SE Santo, off Tutuba Island, 15°34.1'S, 167°16.0'E, 70-80 m, diving team, ♂ shell, H 3.6, D 6.8 mm (MNHN 24766, Fig. 8A-D).
Paratypes: SANTO 2006, stn DS104, W Tutuba Island, 15°34.1'S, 167°16.0'E, ♂ shell, H 3.4, D 5.3 (MNHN 24767, Fig. 8E-H). — SANTO 2006, stn DS105, NW Tutuba Island, 15°33'S, 167°16.7'E, 92 m, 2 ♀♀ shells (MNHN 24768, Fig. 9A-D, H 3.6, D 5.7 mm; MNHN 24769, Fig. 9E-H, H 3.4, D 5.3 mm).

TYPE LOCALITY. — Vanuatu, Espiritu Santo.

ETYMOLOGY. — Latin, "magnus", large, befitting for the largest known species of *Liotipoma*.

DISTRIBUTION. — Known only off Espiritu Santo, Vanuatu.

DESCRIPTION

Male shell (Fig. 8)

Whorls 3.0; profile moderately high for genus; peripheral angulation at mid-whorl, shoulder ramp slightly convex above, profile below peripheral angulation evenly rounded. Axial sculpture of strong ribs, 32 on last whorl; spinose and projecting in early whorls, spinosity much diminished in final third whorl and axials more closely spaced in final whorl. Spiral sculpture of three low cords on shoulder; base with strong subtending cord,

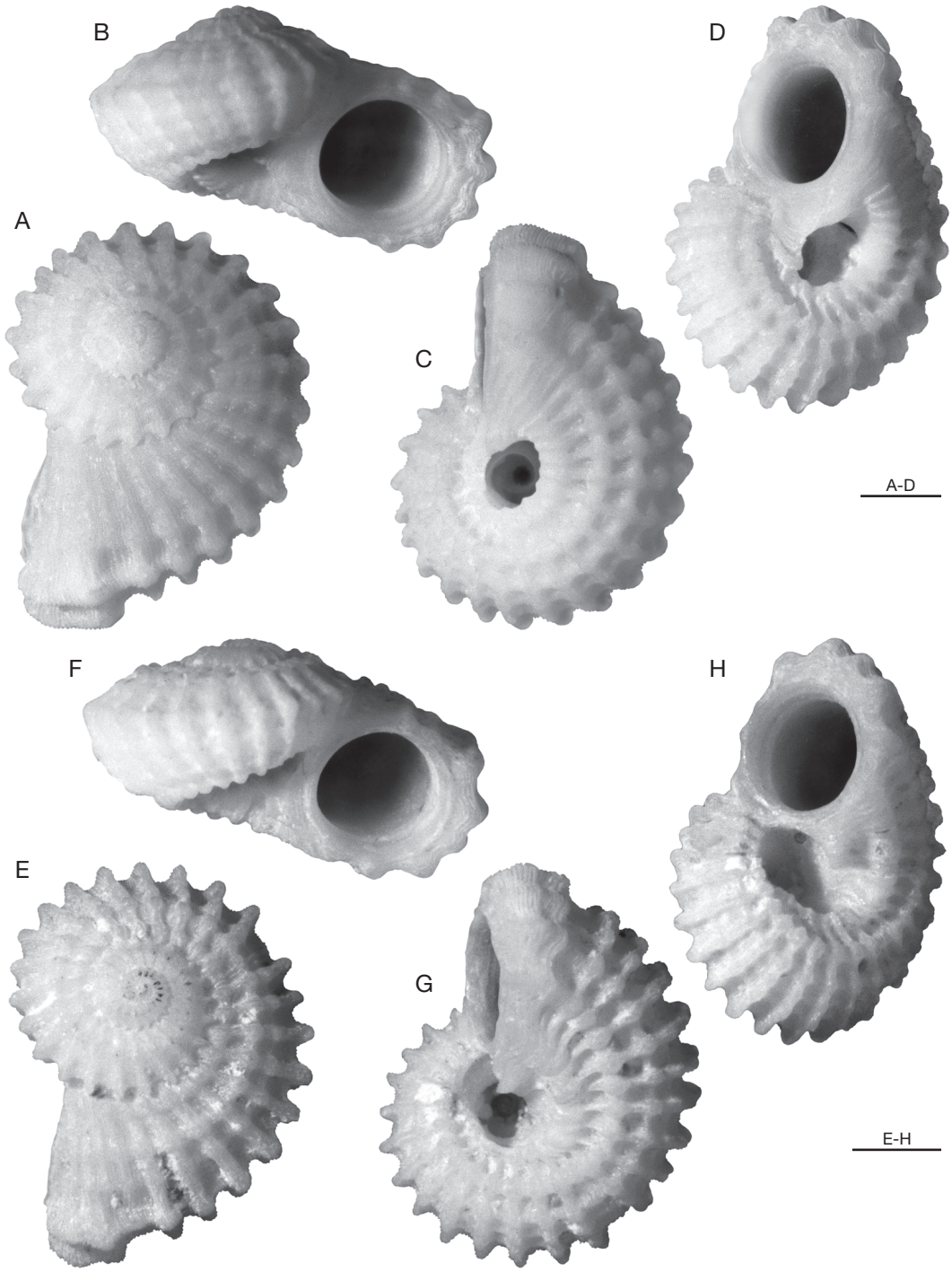

Fig. 7. — *Liotipoma dimorpha* n. sp., female shells: **A-D**, paratype (MNHN 24764, stn 1442), Santal Bay, Lifou, Loyalty Islands, 47 m, H 3.0, D 5.1 mm; **E-H**, paratype (MNHN 24765, stn 1450), Santal Bay, Lifou, Loyalty Islands, 27-31 m, H 2.5, D 4.5 mm. Scale bars: 1 mm.

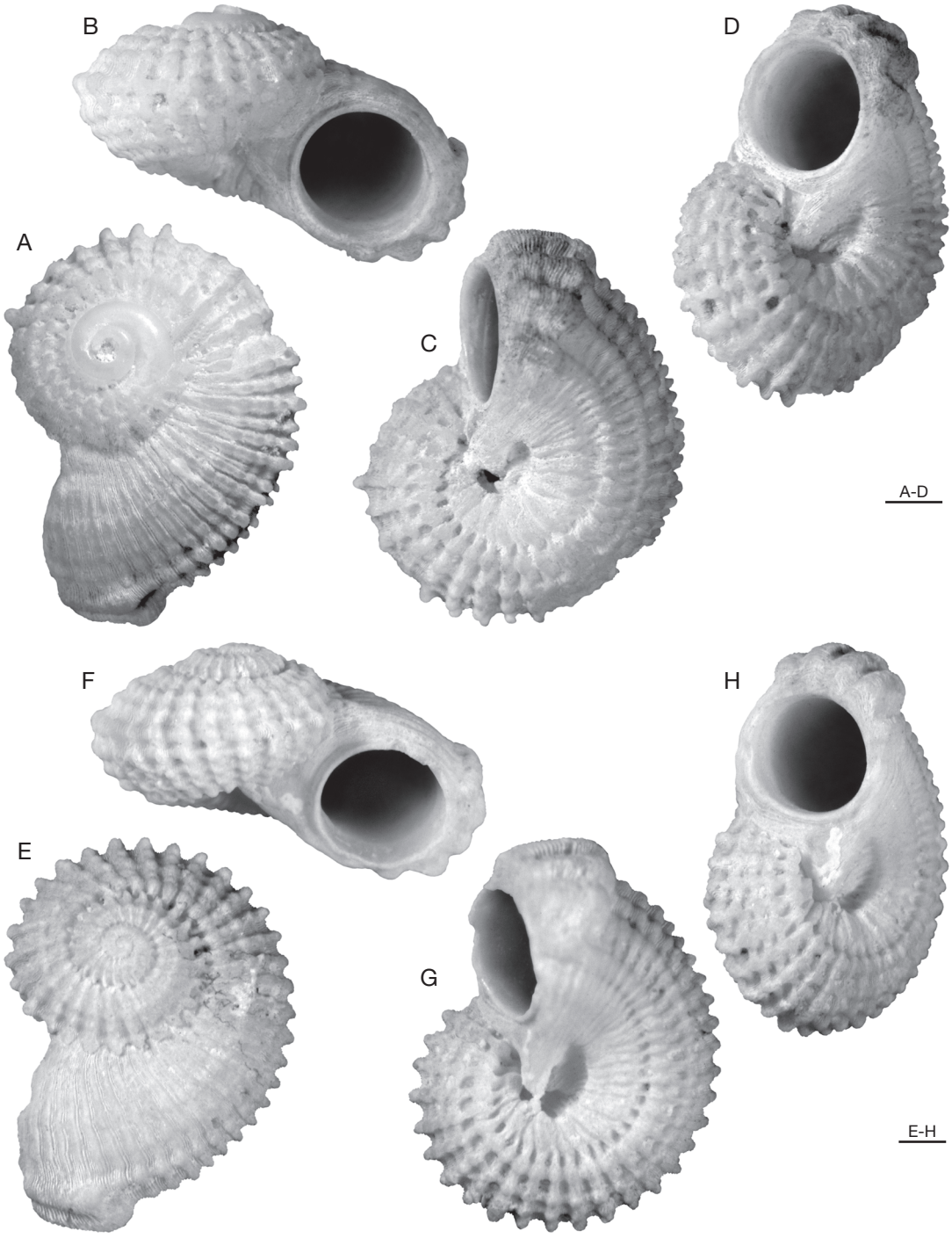

Fig. 8. — *Liotipoma magna* n. sp., male shells: **A-D**, holotype (MNHN 24766, stn DS103), off W side Tutuba Island, Espiritu Santo, Vanuatu, 70-80 m, H 3.6, D 6.8 mm; **E-H**, Paratype (MNHN 24767, stn DS104), 80 m off W side Tutuba Island, Espiritu Santo, Vanuatu, H 3.4, D 5.3 mm. Scale bars: 1 mm.

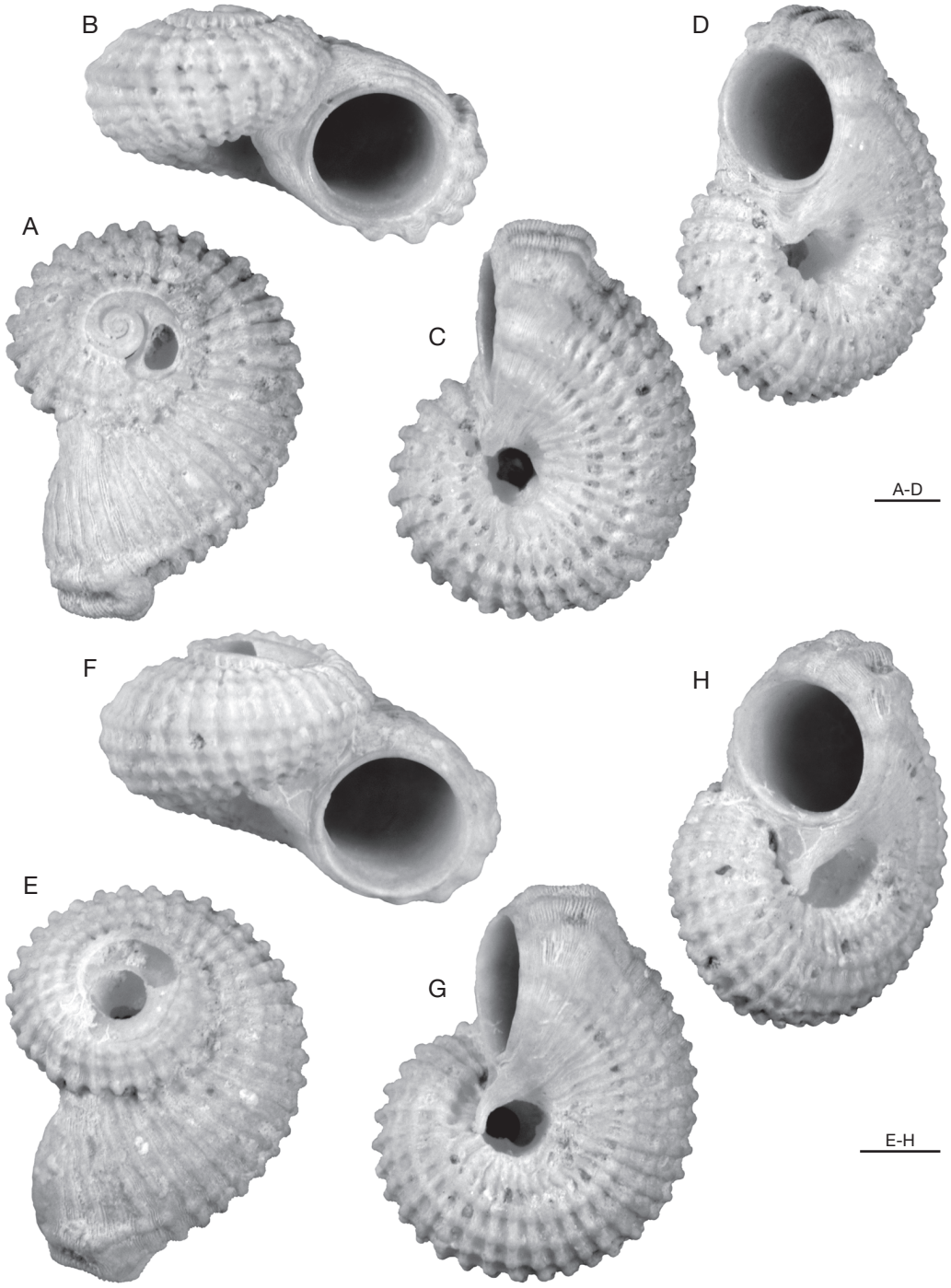

Fig. 9. — *Liotipoma magna* n. sp., female shells: **A-D**, paratype (MNHN 24768, stn DS105), off NW side Tutuba Island, Espiritu Santo, Vanuatu, 92 m, H 3.6, D 5.7 mm; **E-G**, paratype, off W side Tutuba Island (MNHN 24769, stn DS105), off NW side Tutuba Island, Espiritu Santo, Vanuatu, 92 m, H 3.4, D 5.3 mm. Scale bars: 1 mm.

and two cords of nearly equal strength between peripheral cord and subtending cord; umbilicus bordered by broad, angular emergent cord, overridden by narrow axial ribs. Umbilicus partially open, partially obstructed by emergent tongue of lip; tip of tongue directed toward coiling axis. Final lip massive, extending for ⅓ of final quarter whorl, showing about twenty successively decreasing layers of deposition, lip conforming to spiral sculpture; tongue extending half the diameter of aperture on previous whorl, showing similar layers of deposition decreasing in extent. H 3.6, D 6.8 mm (holotype); H 3.4, D 5.3 mm (MNHN 24767, stn DS104).

Female shell (Fig. 9)
Two specimens from Espiritu Santo have holes in the shell in the apical area but are determined as females of this species for their large size and matching sculpture. Both have short tongues that serve to increase the volume of the umbilical cavity. The specimen in Figure 9A-D lacks a projecting tongue; that of Figure 9E-H is higher in profile and has a very narrow extension of the lip that extends to the umbilical edge. Both specimens show a larger volume for the umbilical cavity than the male shells in the tilted views. H 3.4, D 5.3 mm (Fig. 9E-H).

Operculum and radula
Unknown.

Remarks
This is the largest known species of *Liotipoma*. The closest comparison is with *L. splendida* n. sp. (Fig. 13A-D), which is smaller in diameter by 1.5 mm, and has a comparable number of axial ribs. *Liotipoma magna* n. sp. differs in having a short, triangular apertural tongue directed toward the coiling axis, rather than the broad, stubby tongue directed in advance of the aperture of *L. splendida* n. sp. The two male shells differ in detail of the umbilical cavity, as do the female shells. The differences are considered to be intraspecific.

This species is unusual for *Liotipoma* in differing from the general observation that female shells are larger than male shells because the first illustrated male shell (Fig. 8A-D) is greater in diameter by more than 1 mm than both female shells. The female shell of Figure 9E-H has the high profile expected in a female shell.

This is the only species so far known from Vanuatu.

Liotipoma lifouensis n. sp.
(Fig. 10)

Type material. — Holotype: LIFOU, stn 1434, Loyalty Islands, Lifou, Santal Bay, 20°52.5'S, 167°08.1'E, 5-20 m, ♂ shell, H 2.6, D 4.3 mm (MNHN 24770, Fig. 10A-D). Paratype: LIFOU, stn 1432, Shelter Reef, 20°53.5'S, 167°02.7'E, 12-32 m, ♂ shell, H 2.9, D 4.3 mm (MNHN 24771, Fig. 10E-H).

Type locality. — Lifou, Loyalty Islands.

Distribution. — Lifou, Loyalty Islands.

Etymology. — After the type locality, Lifou Island, Loyalty Islands.

Description
Male shell (Fig. 10)
Whorls 3.3; profile of medium height for genus; with single keel at periphery, positioned at mid-whorl; profile below shoulder with weak basal angulation. Axial sculpture of strong ribs, 22 on final whorl, evenly spaced, strongly spinose at periphery, spines projecting backward throughout final whorl. Spiral sculpture of two prominent cords on shoulder, forming coarsely clathrate sculpture. Base with strong subtending cord, and one strong cord between subtending cord and peripheral cord; emergent cord prominent; base with deep pits on both sides of subtending cord; all basal cords broad, with narrow interspaces. Umbilicus bordered by broad periumbilical cord; axial ribs weak across emergent cord. Umbilicus of moderate width, obstructed by narrow, tongue-like extension of inner lip, extending more than half the diameter of aperture, in same plane as aperture. Final lip massive, extending for ¼ of final quarter whorl, with successively decreasing layers of deposition, with indentations conforming to spiral sculpture. Aperture nearly radial, plane of aperture aligned slightly outside of coiling axis. H 2.6, D 4.3 mm (holotype).

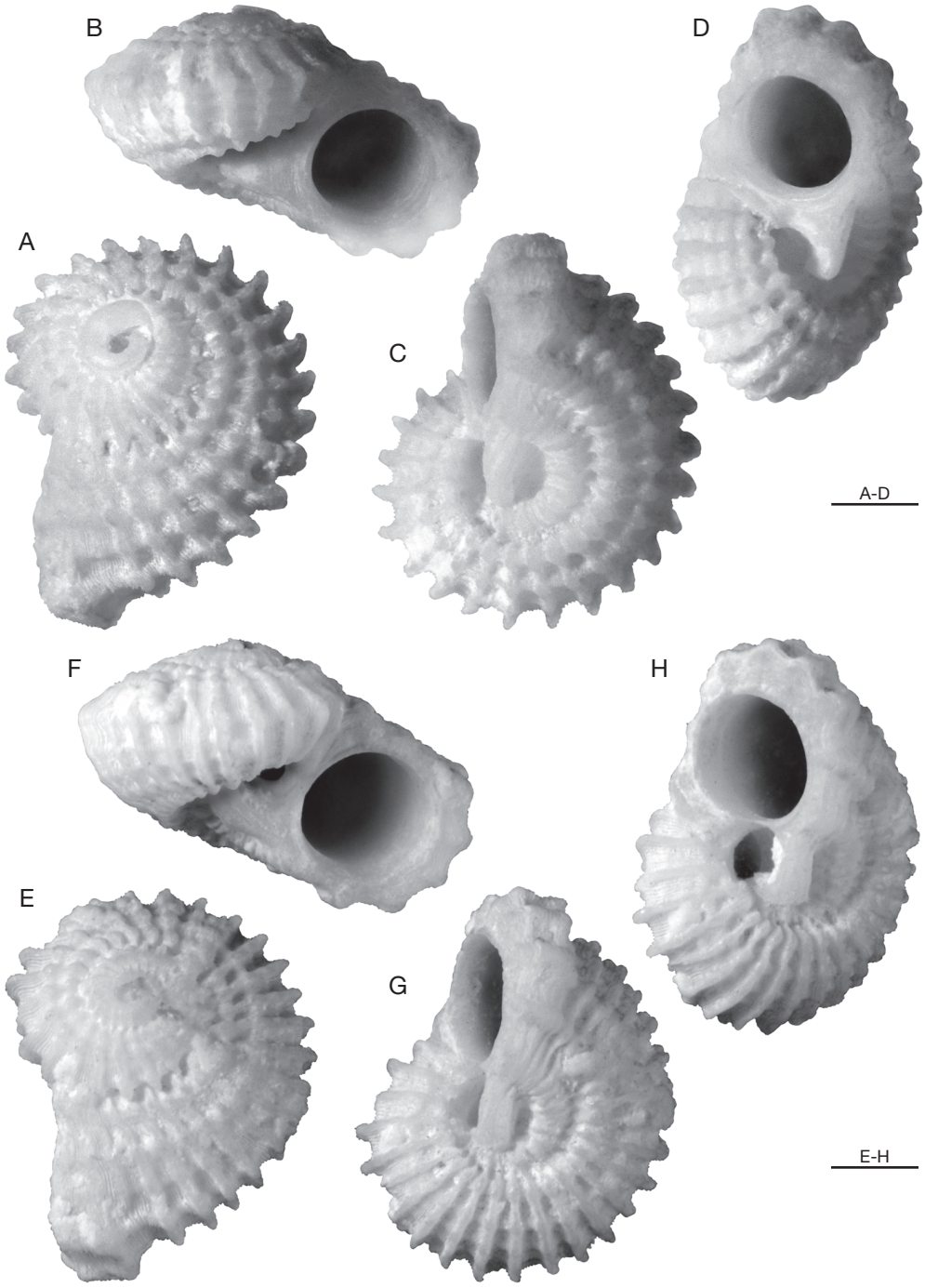

FIG. 10. — *Liotipoma lifouensis* n. sp., male shells: **A**-**D**, holotype (MNHN 24770, stn 1434), male shell, Santal Bay, Lifou, Loyalty Islands, 5-20 m, H 2.6, D 4.3 mm; **E**-**H**, paratype (MNHN 24771, stn 1432), male shell, Shelter Reef, Santal Bay, Lifou, Loyalty Islands, 12-32 m, H 2.9, D 4.3 mm. Scale bars: 1 mm.

Female shell
Unknown.

Operculum
Unknown.

Remarks
The two illustrated male shells have the long narrow tongue that extends across the umbilicus to connect with the emergent cord, which is a condition unlike that of all other species. The holotype shell has backward projecting spines, but this is not seen in the second male shell (Fig. 10E-H). Both specimens have comparable basal sculpture of broad cords with narrow interspaces and coarse clathrate sculpture of the shoulder slope. The specimen shown in Figure 10E-H has an additional basal cord, compared to the holotype specimen, but this is considered to an intra-specific difference. This species cannot be confused with any other species. It is of the same size as the male shell of *L. mutabilis* n. sp. (Fig. 4) from Lifou, but has a longer apertural tongue.

Liotipoma solaris n. sp.
(Figs 2E, F; 11; 12)

Type material. — Holotype: LACM stn 91-188, Fiji, Diamond Seamount, E of Herald Pass, W of Ndravuni Island, inside great Astrolabe Reef, Kandavu Group, 18°45.8'S, 178°28.3'E, 20-25 m, 19.VI.1991, Twila Bratcher, from shell grit sample, ♂ shell, H 2.5, D 4.0 mm (LACM 3107, Fig. 11A-D).
Paratypes: same data as holotype, 2 ♂♂ shells, H 2.1, D 3.5 mm (LACM 3108, Fig. 11E-H). — Papua New Guinea, Horseshoe Reef, Bootless Bay, E of Port Moresby, 8°31'20"S, 147°16'32"E, 25 m, from shell grit sample, Ken Severin, 1985, 1 ♂ shell, H 2.4, D 3.9 mm (LACM 3109, Fig. 12A-D)

Type locality. — Fiji, Diamond Seamount, E of Herald Pass, W of Ndravuni Island, inside great Astrolabe Reef.

Additional material. — LACM stn 85-135, Fiji, Herald Pass, W of Ndravuni Island, NW end of Great Astrolabe Reef, 20 m, in coral rubble, 18.X.1985, Antonio J. Ferreira, 2 immature, including one with wedged operculum (LACM, Fig. 2E, F). — LACM stn 85-138, W end of Kandavu, 19°06.5'N, 177°58'E, 18 m, 27.X.1985, Antonio J. Ferreira, 1 immature (LACM, Fig. 12E-G).

Distribution. — Fiji Islands and Papua New Guinea.

Etymology. — Latin "sol", the sun, suggested by the minimal expansion of the final whorl in this species.

Description
Male shell (Figs 11; 12A-D)
Whorls 3.3; profile of moderate height for genus; with single strongly projecting peripheral keel at mid-whorl; profile below keel evenly rounded. Axial sculpture of strong ribs, 21-25 on final whorl; spinose and projecting in early whorls, becoming weaker and more closely spaced in advance of final lip. Spiral sculpture of single, low cord on shoulder; base with strong subtending cord, and two cords of nearly equal strength between shoulder cord and subtending cord. Base with shallow pits on outer side of subtending cord; umbilicus bordered by broad emergent cord, overridden by narrow axial ribs; umbilicus narrow, obstructed by massive, triangular extension of inner lip; outer edge of tongue directed toward center of umbilicus, in alignment with plane of aperture. Final lip massive, extending for ⅓ of final quarter whorl, with successively decreasing layers of deposition, with strong indentations conforming to spiral sculpture, especially on basal portion. Aperture nearly radial, plane of aperture well outside of coiling axis. H 2.5, D 4.0 mm (holotype).

Female shell
Unknown.

Operculum (Fig. 2E, F)
With deep pit in center, about 20 wavy radial ridges, with some coalescing.

Remarks
Liotipoma solaris n. sp. is known only from male shells with a fully formed tongue. The specimen shown in Figure 12E-G is a male shell that is nearly ready to form the tongue. It is characterised by minimal whorl expansion and a very short, triangular tongue with a pointed tip not in alignment with the plane of the aperture.

Specimens are approximately 1 mm in diameter smaller than *L. mutabilis* n. sp. from Lifou, Loyalty Islands. This has fewer axial ribs than the immature holotype specimen of *L. clausa* n. sp. (Fig. 13E-H), which is also known from Fiji.

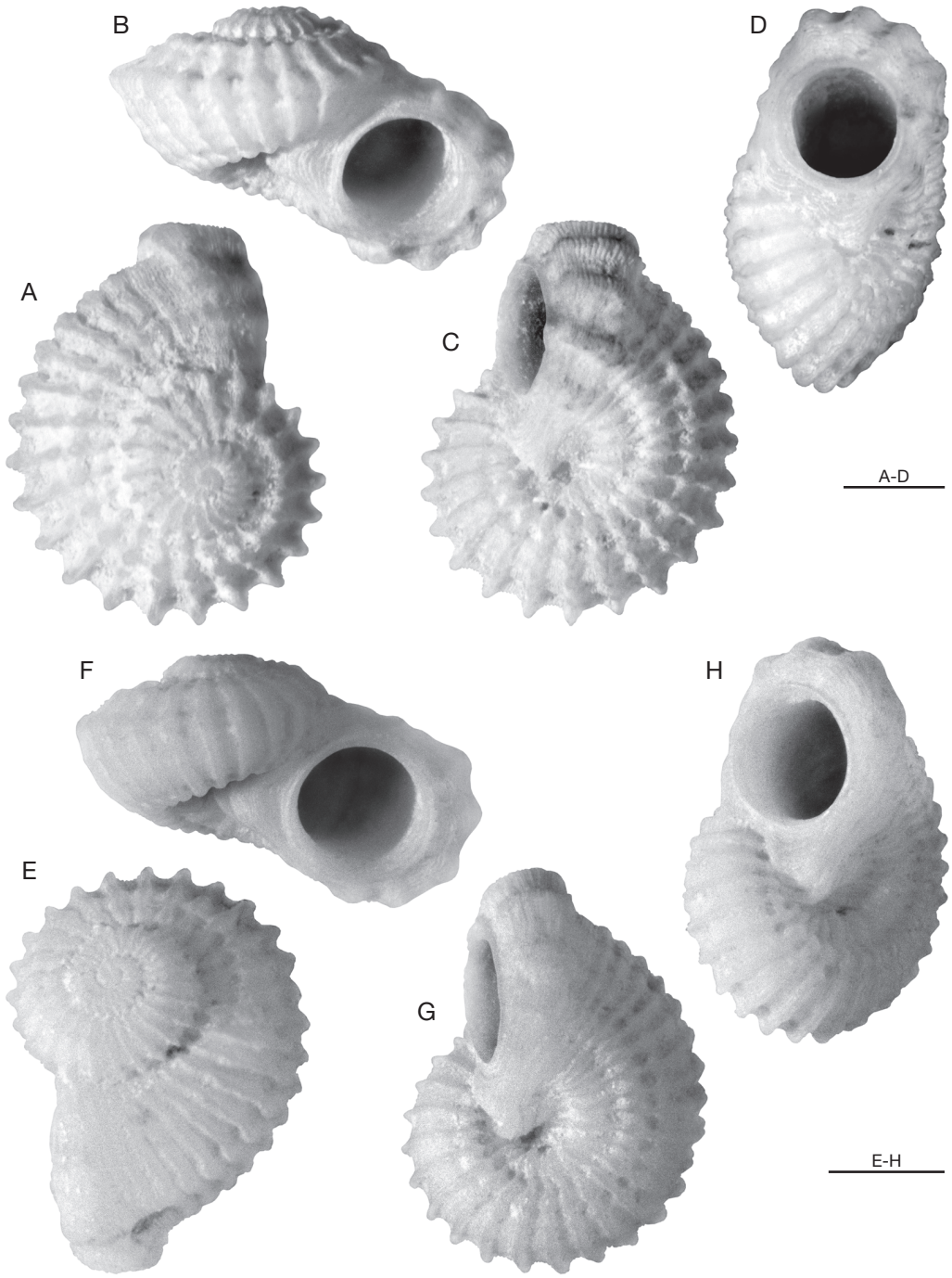

FIG. 11. — *Liotipoma solaris* n. sp., male shells: **A**-**D**, holotype (LACM 3107, stn 91-188), Diamond Seamount, Great Astrolabe Reef, Fiji, 20-25 m, H 2.5, D 4.0 mm; **E**-**H**, paratype (LACM 3108, stn 91-188), Diamond Seamount, Great Astrolabe Reef, Fiji, 20-25 m, H 2.1, D 3.5 mm. Scale bars: 1 mm.

Liotipoma splendida n. sp.
(Fig. 13A-D)

TYPE MATERIAL. — Holotype: MONTROUZIER expedition, stn 1269, New Caledonia, Doiman Reef, Touhou Sector, 20°35.1'S, 165°08.1'E, 15-20 m, diving team, IX.1993, 1 specimen, H 3.2, D 5.1 mm (MNHN 24772, Fig. 13A-D).

TYPE LOCALITY. — New Caledonia, Doiman Reef.

DISTRIBUTION. — Known only from holotype.

ETYMOLOGY. — After the Latin noun, "splendidus".

DESCRIPTION

Male shell (Fig. 13A-D)

Whorls 3.3; profile moderately high for genus; peripheral angulation high on whorl, shoulder ramp nearly flat above, profile below shoulder evenly rounded. Axial sculpture of strong ribs, 33 on last whorl; spinose and projecting in early whorls, spinosity much diminished in final third whorl. Spiral sculpture of single strong, low cord on shoulder in early whorls, changing to three narrow cords in final ⅓ whorl; base with strong subtending cord, and three cords of nearly equal strength between peripheral cord and subtending cord. Base with deep pits on outer side of subtending cord and other basal cords. Umbilicus bordered by broad, angular emergent cord, overridden by narrow axial ribs; umbilicus partially open, partially obstructed by emergent tongue of lip; tongue extending forward of plane of aperture. Final lip massive, extending for ⅓ of final quarter whorl, showing about twenty successively decreasing layers of deposition, lip conforming to spiral sculpture; tongue extending half the diameter of aperture on previous whorl, showing similar layers of deposition decreasing in extent; plane of aperture coinciding with umbilical wall. H 3.2, D 5.1 mm (holotype).

Female shell

Unknown.

Operculum

Unknown.

REMARKS

This species is characterised by the moderately large size, high count of axial ribs, its strongly developed clathrate sculpture, and in having the tongue out of alignment with the plane of the aperture, projecting strongly forward of the aperture so that it does not block the open umbilicus. Although the umbilicus is open, access to the umbilicus is blocked, so this is not a female shell.

The closest comparison is with *L. magna* n. sp. (Figs 8; 9), which is larger and has the apertural tongue pointed along the plane of the aperture and the coiling axis, rather than projecting forward.

Liotipoma clausa n. sp.
(Fig. 13E-H)

TYPE MATERIAL. — Holotype: LACM stn 91-189, Fiji, S side Herald Pass, W side Great Astrolabe Reef, Kandavu Group, 18°46.0'S, 178°27.2'W, 15 m, 20.VI.1991, Twila Bratcher, immature specimen, H 3.0, D 4.2 mm (LACM 3110). Paratype: same data as holotype, immature specimen, H 2.5, D 3.2 mm (LACM).

TYPE LOCALITY. — Fiji, S side Herald Pass, W side Great Astrolabe Reef, Kandavu Group.

DISTRIBUTION. — Known only from type material.

ETYMOLOGY. — Latin, *clausa*, closed, suggested by the massive umbilical plug.

DESCRIPTION

Male shell (Fig. 13E-H).

Whorls 3.2 (but mature lip not formed); profile high for genus; with single keel, periphery with strong carination at mid-whorl; shoulder nearly flat-sided, base below keel evenly rounded. Axial sculpture of strong ribs, 33 on last whorl in spire view; weakly spinose and projecting in early whorls, more closely spaced and less spinose in final half whorl. Spiral sculpture of three strong cords on shoulder; base with strong cords, of which three largest become strongly projecting in last half whorl; emergent cord and adjacent subtending cord prominent. Umbilicus fully obstructed by early formation of tongue that precedes formation of expanded final lip; aperture radial, mature lip unknown. H 3.0, D 4.2 mm (immature male holotype).

Female shell

Unknown.

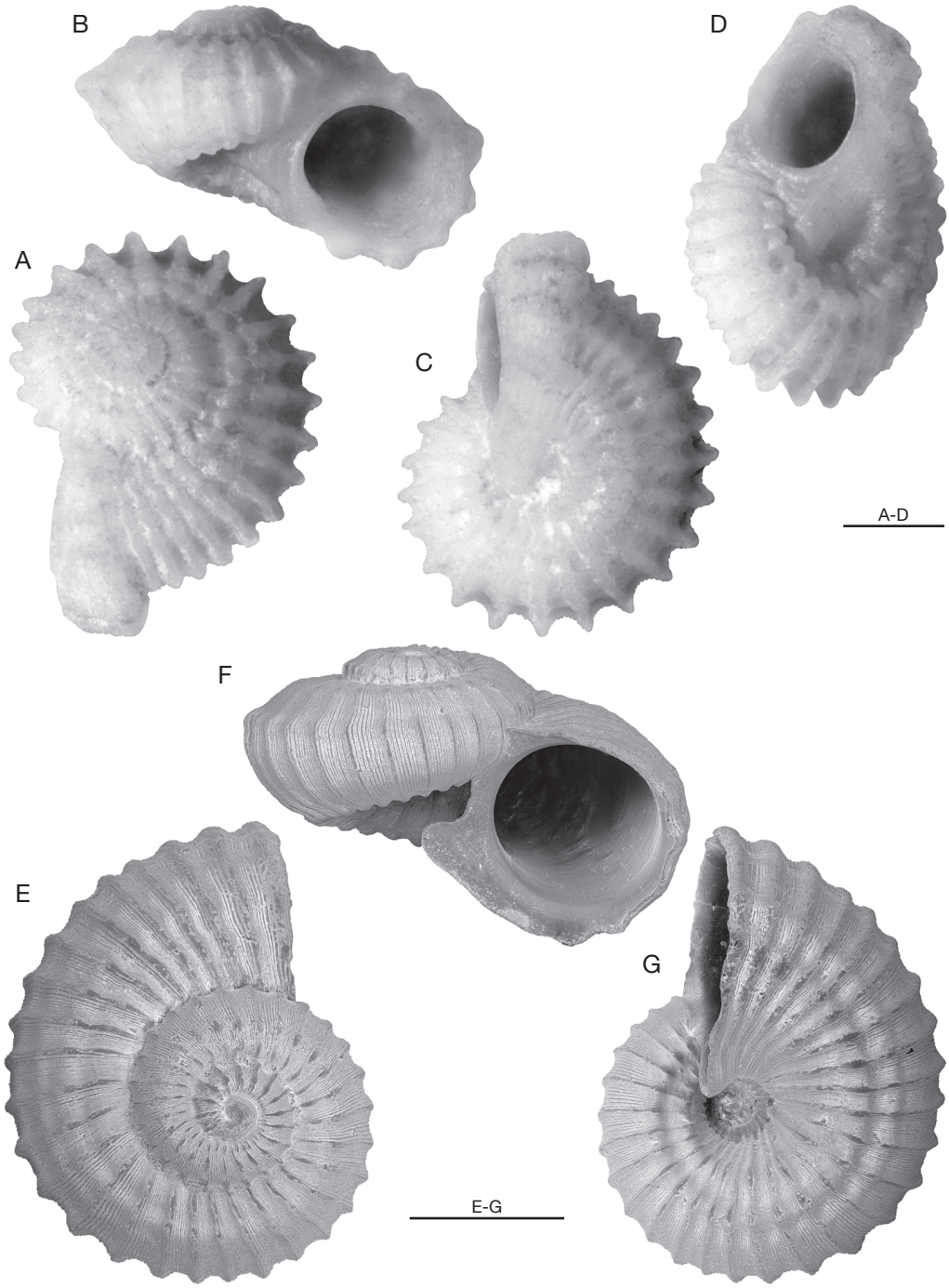

FIG. 12. — *Liotipoma solaris* n. sp., male shells: **A-D**, paratype (LACM 3109), Horseshoe Reef, Bootless Bay, Port Moresby, Papua New Guinea, 25 m, H 2.4, D 3.9 mm; **E-G**, SEM of immature male shell (LACM stn 85-138), Cape Washington, westernmost end of Kandavu, Fiji, 18 m, H 1.5, D 3.3 mm. Scale bars: 1 mm.

Operculum
Unknown.

REMARKS
The holotype specimen seems sufficiently large and mature to suggest that it reached the stage to commence forming the mature lip. This species is characterised by it high number of axial ribs, short spines, and minor whorl expansion. There are many more axial ribs than in *L. solaris* n. sp., which also occurs at Fiji. This species, along with *L. splendida* n. sp. (Fig. 9A-D), has 33 axial ribs, the highest count for the genus. This differs from the other species treated here in its massive development of the basal cords. Although lacking the mature lip, mature shells should be readily recognised in the future.

Genus *Depressipoma* n. gen.

TYPE SPECIES. — *Depressipoma laddi* n. sp.

DIAGNOSIS. — Profile low with strong peripheral angulation midway on whorl, maximum diameter 3.3 mm; whorls rounded above and below peripheral carination, shoulder and base with narrow spiral cords, axial sculpture of narrow, projecting ribs; umbilical area broad, with deposition of callus to strengthen shell; final lip broad and projecting, composed of successive layers of fine lamellae; base of lip with short triangular tongue.

DISTRIBUTION. — Marshall Islands, Micronesia, west of the international date line and just north of the Equator.

REMARKS
Two species resemble *Liotipoma* in sculpture, have a similar aperture and lip with the projecting tongue, but have such a low profile that there would be no possibility to form a brood chamber within the umbilical cavity. The specimen of *D. laddi* n. sp. shows a lumpy deposition of callus across the umbilical area, which serves to strengthen the shell in the position at which its weak early stage would need fortification. The specimen of *D. kwajaleina* n. sp. is in poor condition with agglutinated sand obscuring what is probably the same feature in the umbilical cavity.

KEY TO SPECIES OF *DEPRESSIPOMA* N. GEN.

1. Angulation strong, strong axials ..... *D. kwajaleina* n. sp.
— Angulation weak, with weak axials forming clathrate sculpture ..... *D. laddi* n. sp.

Depressipoma kwajaleina n. sp.
(Fig. 14A-C)

TYPE MATERIAL. — Holotype: Kwajalein Atoll, Marshall Islands, 9°15'N, 167°30'E, ocean side of reef, sediment sample at 20 m, VII.2007, Wes Blackater for Bret Raines, H 1.7, D 3.2 mm (LACM 3213).

TYPE LOCALITY. — Kwajalein Atoll, Marshall Islands.

DISTRIBUTION. — Known only from the holotype.

ETYMOLOGY. — After the type locality, Kwajalein Atoll, Marshall Islands.

DESCRIPTION
Shell (Fig. 14A-C)
Of 2.7 whorls; profile very low, whorls with strong peripheral angulation nearly midway on whorl; whorls rounded and inflated above and below angulation. Axial sculpture of 27 projecting ribs, weakly spinose and projecting in early whorls, becoming less spinose in final whorl. Spiral sculpture of narrow cords, forming radially elongate cancellations; upper half of whorl with three weak cords, lower with three cords; emergent cord obscured. Umbilical slope broad, obscured by agglutinated deposition, partially obstructed by short extension of inner lip, forming short tongue. Final lip massive, extending for ¼ of final quarter whorl, with successively decreasing layers of deposition, with indentations conforming to spiral sculpture. Aperture slightly oblique, plane of aperture aligned with coiling axis. H 1.7, D 3.2 mm (holotype).

Operculum
Unknown.

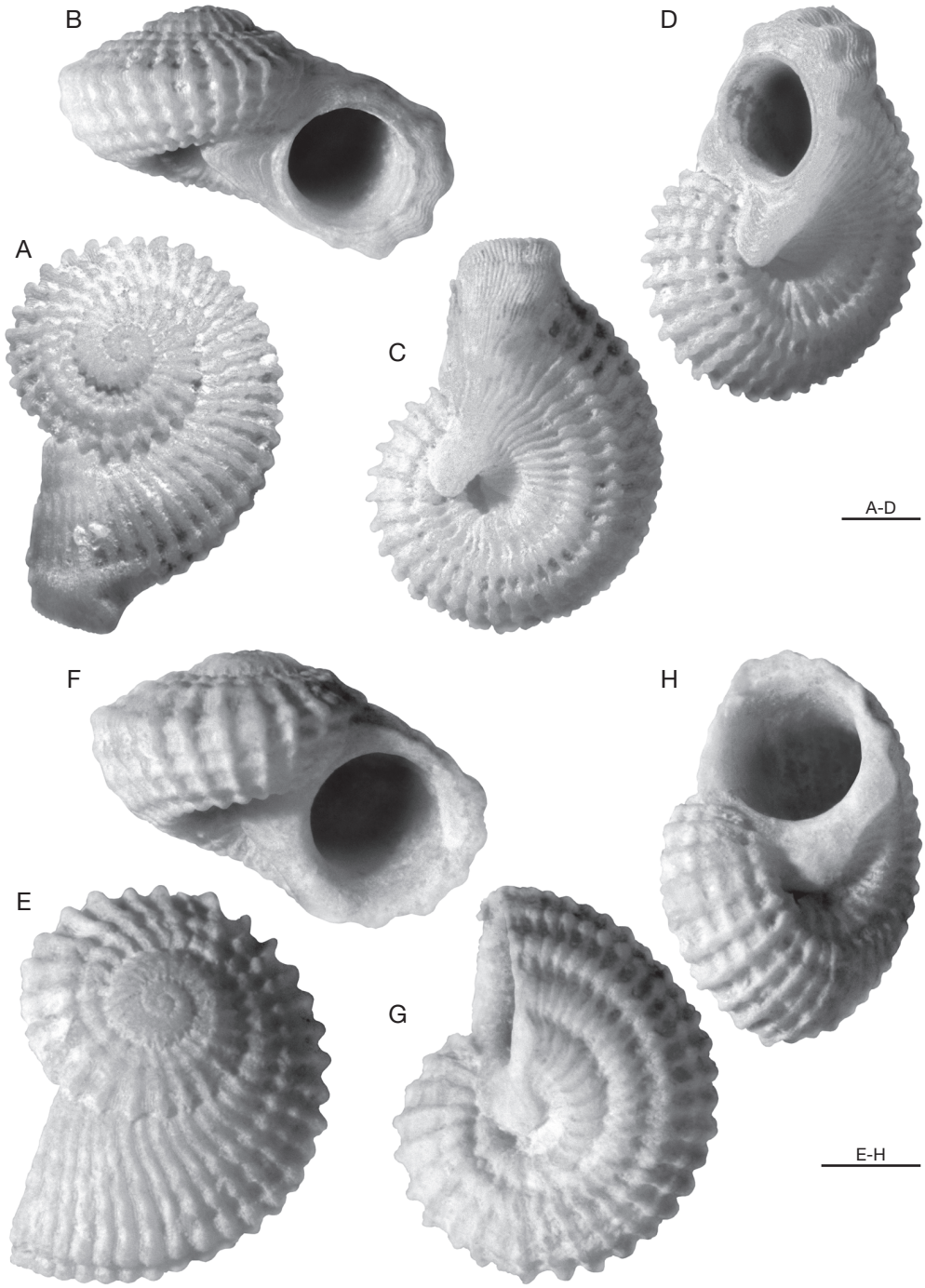

FIG. 13. — **A-D**, *Liotipoma splendida* n. sp. holotype, male shell (MNHN 24772, stn 1269), Doiman Reef, Touhou Sector, New Caledonia, 15-20 m, H 3.2, D 5.1 mm; **E-H**, *Liotipoma clausa* n. sp. Holotype, immature male shell (LACM 3110, stn 91-189), Herald Pass, Great Astrolabe Reef, Fiji, 15 m, H 3.0, D 4.2 mm. Scale bars: 1 mm.

Remarks

The single holotype specimen is poorly preserved and has a hole in the base on the last quarter whorl. It is clearly not the same as *Liotipoma laddi* n. sp., from Eniwetok, Marshall Islands, which has a more rounded profile and narrower spiral cords on the base.

Depressipoma laddi n. sp.
(Fig. 14D-F)

"*Liotina* (*Austroliotia*) cf. *L. botanica* (Hedley)" – Ladd 1966: 46, pl. 7, figs 9-11.

Type material. — Holotype: U.S. Geological Survey, 1946-1952, Eniwetok Atoll, Marshall Islands, Elugelab Islet, sub-Recent from shallow drill hole, 11°40'N, 162°13'E, specimen slightly beach-worn at time of deposition, H 1.4, D 3.3 mm (USNM 648301).

Type locality. — Eniwetok Atoll, Marshall Islands.

Distribution. — Known only from holotype.

Etymology. — Named after the late Dr. Harry S. Ladd, Department of Paleobiology, USNM, who first illustrated this species.

Description

Shell (Fig. 14D-F)

Of 2.7 whorls; profile very low for genus; whorls with weak peripheral angulation high on whorl; whorls rounded and inflated above and below angulation. Axial sculpture of 27 weak, narrow ribs, weakly spinose and projecting in early whorls, but losing all spination in final whorl. Spiral sculpture of narrow ribs, forming square cancellations and pits; upper half of whorl with four weak cords, lower with three cords; emergent cord not strongly defined. Umbilical slope broad, with raised, narrow extensions of axial sculpture; umbilicus fully occluded by callus, partially obstructed by massive extension of inner lip, forming tongue that slightly projects forward but not extending near coiling axis. Final lip massive, extending for ¼ of final quarter whorl, with successively decreasing layers of deposition, with indentations conforming to spiral sculpture. Aperture slightly oblique, plane of aperture aligned with coiling axis. H 1.4, D 3.3 mm (holotype).

Operculum

Unknown.

Remarks

This species is unlike the other species of *Depressipoma* n. gen. and all species of *Liotipoma* in having axial ribs that are not strongly projecting at the periphery, in either apical or basal view, except in the early stages. The sculpture of the base is more clathrate than that of other species.

This species is unlikely to be sexually dimorphic because its low profile would not allow room for a brooding cavity in the umbilicus.

Genus *Rhombipoma* n. gen.

Type species. — *Rhombipoma rowleyana* n. sp.

Diagnosis. — Whorl profile low, rounded; with whorl expansion to make final quarter whorl more projecting, sculpture of about 22 axial ribs; axial ribs absent in on final ⅙ whorl, replaced by more prominent lamellae (lamellae not evident on earlier whorls); the final prominent lamellae continue to form the final lip; spiral sculpture of two beaded cords at periphery; lip very strongly projecting, of eight projecting axial lamellae.

Distribution. — Known only from type species, from shallow sublittoral depths, Rowley Shoals, off northwestern Western Australia.

Remarks

This genus is comparable to *Depressipoma* n. gen. in its small size and low profile, differing in having a rounded, rather than carinate periphery, and in having reduced spiral sculpture on the shoulder and base, compared to that of *Depressipoma* n. gen. and *Liotipoma*. Whorl expansion is most extreme for all members of the subfamily. The final lip is more projecting than in species of *Liotipoma* and *Depressipoma* n. gen., and the lamellae of the projecting lip are larger and fewer, matched in prominence by the lamellae that precede the final lip.

Rhombipoma rowleyana n. sp.
(Fig. 15A-C)

Type material. — Holotype: stn 86-250, Rowley Shoals, N end Mermaid Reef, off northern Western Australia, 17°03'S, 119°36'E, 18-20 m, 20.VIII.1986, Twila Bratcher, in shell grit sample, 1 damaged shell with first whorl eroded and with agglutinated sand filling

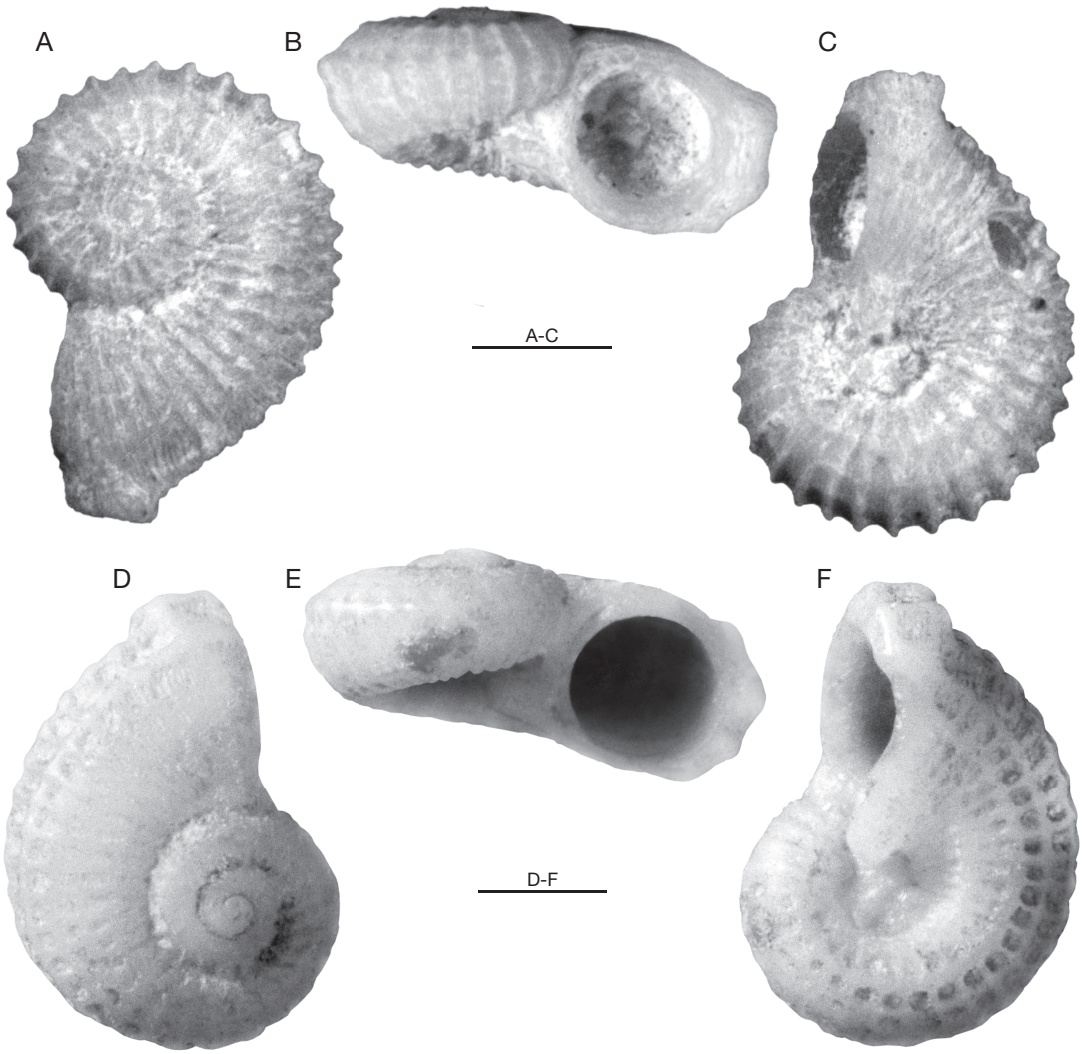

FIG. 14. — **A-C**, *Depressipoma kwajaleina* n. gen., n. sp. holotype (LACM 3213), Kwajalein Atoll, Marshall Islands, 20 m, H 1.7, D 3.2 mm; **D-F**, *Depressipoma laddi* n. gen., n. sp. holotype (USNM 648301), Elugelab Islet, Eniwetok Atoll, Marshall Islands, H 1.4, D 3.3 mm. Scale bars: 1 mm.

aperture and exposed final quarter whorl, in which base of shell is missing, H 1.5, D 3.2 mm (AMS C.212474, ex LACM).

TYPE LOCALITY. —Rowley Shoals, N end Mermaid Reef, off northern Western Australia.

DISTRIBUTION. — Known only from the holotype.

ETYMOLOGY. — After the type locality, Rowley Shoals.

DESCRIPTION

Shell (Fig. 15A-C)

Of about three whorls, profile very low, whorls rounded. Axial ribs 22 in basal view, plus seven more closely spaced axials of lesser strength in advance of final lip. Spiral sculpture of two broad peripheral cords arising at final stage and extending over varix of final lip; spiral sculpture lacking on

upper part of whorl; spiral sculpture on base of broad, low subtending cord; last half whorl rapidly expanding in diameter. Final lip comprised of about eight closely spaced axials of similar strength to those that precede the lip; final lip filling about ⅓ of final quarter whorl; base of final lip broken in holotype, but tip of tongue intact, club-like, extending forward of aperture. H 1.5, D 3.2 mm (holotype).

Operculum
Unknown.

Remarks
Rhombipoma rowleyana n. gen., n. sp. is comparable to *L. laddi* n. sp. (Fig. 14D-F) in its extremely low profile, and even more rounded final whorl, but differs in lacking the prominent spiral cords that produce the clathrate sculpture of that species. The full morphology of the umbilical area is not clear because the base of the shell is broken, but if this species is sexually dimorphic, it is unlikely that the holotype is a female shell because there seems not to be an umbilical cavity bordered by a raised rib. It is likely that the extreme lenticular profile precludes sexual dimorphism in this species.

Genus *Paraliotipoma* n. gen.

Type species. — *Paraliotipoma sirenkoi* n. sp.

Diagnosis. — Profile moderately high, with projecting peripheral carination, with weaker cords on shoulder and base, axial sculpture of about 20 primary ribs extending across shoulder and base; axial sculpture extending to partially obstruct umbilicus in final quarter whorl; umbilicus narrow; final whorl expanding, projecting; lip not angular, thickened by repeating lamellae.

Distribution. — Known only from type species, from Chimetan Bank, South China Sea (west of Palawan, Philippine Islands).

Remarks
This genus is clearly a member of Liotipomatinae n. subfam., for its fine axial lamellae, similar size to *Liotipoma*, shell profile with a peripheral angulation and projecting final lip. It differs from *Liotipoma* in having the lip profile in basal view more rounded, rather than angulate as in *Liotipoma*, and it does not have the tongue that extends from the base of the inner lip and projects across the umbilicus as in *Liotipoma*. The basal cords are narrower than is usual in the species of *Liotipoma*.

The fine lamellae between the primary axial ribs that approach the final lip are enlarged, as in *Rhombipoma* n. gen.

Paraliotipoma sirenkoi n. sp.
(Fig. 15D-F)

Type Material. — Holotype: First Tropical Expedition of the Institute of Marine Biology 1974-1975, R/V *Kallisto*, dredge stn 3, Bank Chiametan, also known as Sea Horse Shoal, South China Sea, 10°48'N, 117°45'E, 10-320 m, 17.II.1974, Boris Sirenko, H 2.7, D 4.2 mm (ZISP 61624/1), slightly worn specimen.

Type Locality. — Bank Chiametan (Sea Horse Shoal), South China Sea.

Distribution. — Known only from type locality, Chiametan Bank (Sea Horse Shoal), South China Sea, west of Palawan, Philippines.

Etymology. — After the collector, Boris Sirenko, of Zoological Institute, St. Petersburg, Russiathe (ZISP).

Description
Shell (Fig. 15D-F)
Of about three whorls, height moderate, angulate at periphery; periphery slightly higher than mid-whorl; profile below angulation evenly rounded; axial sculpture of strong primary ribs, 20 on final whorl in either spire or basal view; spinose and projecting in early whorls, less spinose in final quarter whorl; short stage preceding final lip lacking axial rib, but with imbricate sculpture of rest of shell. Axial sculpture of strong imbrications, about three lamellae between each major axial rib. Spiral sculpture of single low cord on shoulder; base with moderately strong subtending cord, and one cord of nearly equal strength between peripheral cord and subtending cord, and one cord serving as weakly indicated periumbilical cord. Umbilicus bordered by broad periumbilical cored, umbilical slope overridden by narrow axial ribs; umbilicus

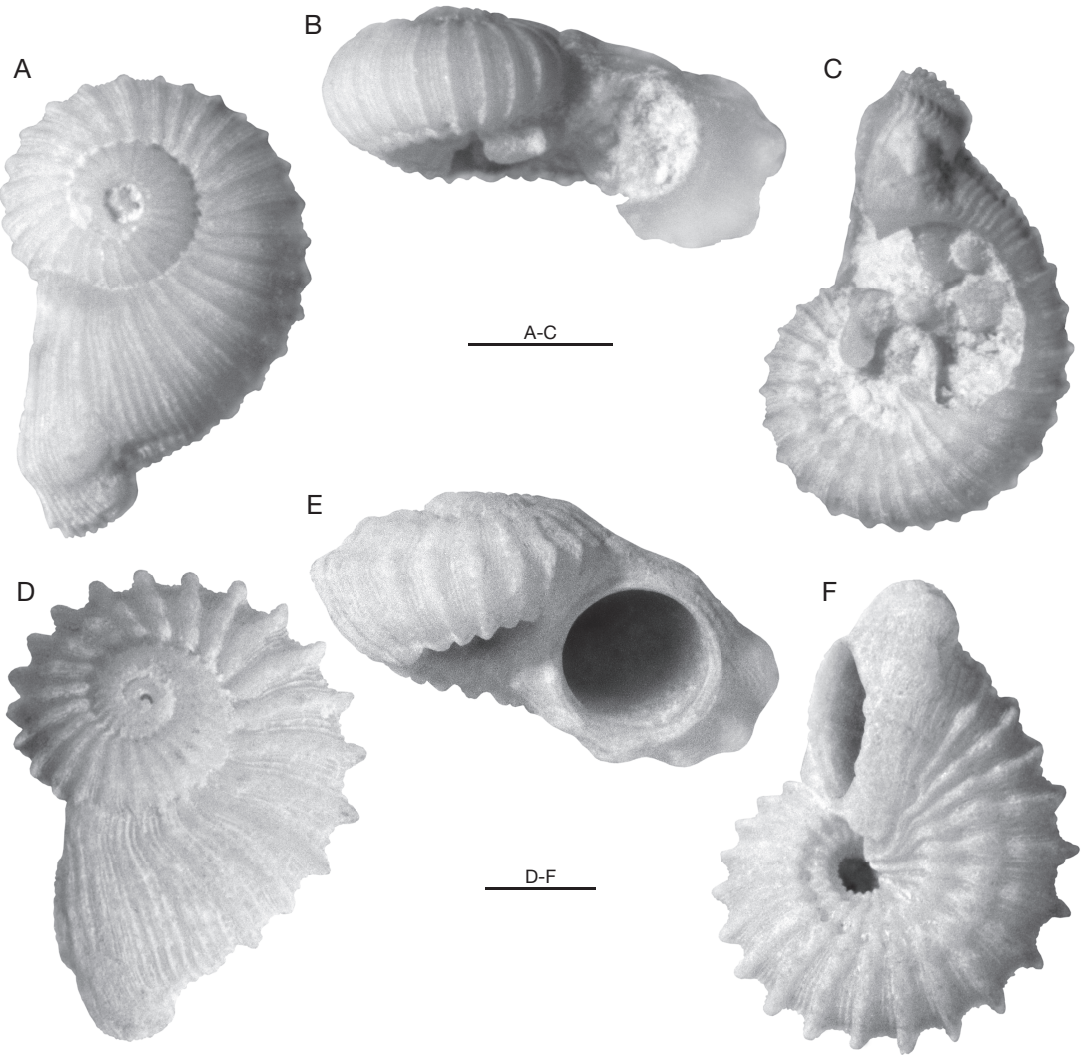

FIG. 15. — **A-C**, *Rhombipoma rowleyana* n. gen, n. sp. holotype (AMS C.212474, ex LACM stn 86-250), N end of Mermaid Reef, Rowley Shoals, off northern Western Australia, 18-20 m, H 1.5, D 3.2 mm (base of shell broken and filled with agglutinated sand); **D-F**, *Paraliotipoma sirenkoi* n. gen., n. sp. holotype (ZISP 61624/1), Sea Horse Shoal, South China Sea, 10-320 m, H. 2.7, D 4.2 mm. Scale bars: 1 mm.

open, of moderate width, only partially obstructed by projecting extension of axial ribs across base of final half-whorl; umbilical wall with finely spinose angulation, becoming thickened and connecting to final lip. Final lip massive, extending for ⅓ of final quarter whorl, with successively decreasing layers of deposition, with only weak indentations conforming to spiral sculpture. Aperture nearly radial, plan of aperture only slightly outside of coiling axis.

DISCUSSION

The speciose genus *Liotipoma, Depressipoma* n. gen. of two species, and the two monotypic genera *Rhombipoma* n. gen. and *Paraliotipoma* n. gen. are significant additions to the Indo-Pacific micro-gastropod fauna. The imbricate sculpture and calcified periostracum of *Liotipoma* is very similar to that of Liotiidae, in which the operculum is not enveloped by the foot.

The calcified operculum places these genera in the Colloniidae, in which the calcareous operculum is enveloped by the foot. The new colloniid subfamily Liotipomatinae n. subfam. is here proposed because its micro-sculpture and calcified periostracum is not represented in other known colloniids. Once living specimens become known, it will be a matter of high interest to compare the affinity by means of molecular genetics, to see if *Liotipoma* is closer to the Colloniidae or to the Liotiidae.

It is remarkable that so many new species of *Liotipoma* and the other less speciose genera have remained undetected until now. This suggests that our knowledge of the entire Indo-Pacific microfauna is still very much incomplete and that many other new species of this and other groups remain to be discovered. If shell grit sampling methods had not been employed by the MNHN workshops and volunteer collectors for the LACM, the entire group would have remained undetected.

Where *Liotipoma* has been found, it is so uncommon that living specimens have not been collected. Possibly it lives within burrows or subsurface tubes of another invertebrate group, like some species of vitrinellids? If so, it would be the first known vetigastropod to have a commensal relationship with other invertebrates.

Four species of *Liotipoma* express sexual dimorphism in which female shells have broader umbilical cavities like those liotiid and areneid species that are known to brood the larval stages in the umbilical cavity. Brooding in the umbilical cavity has previously been demonstrated in the Liotiidae, for which there are published accounts, both for the family Liotiidae by Burn (1976) and Areneidae n. fam. by Shasky (1968) and by Hertz (1998). It is also inferred for *Anadema* H. & A. Adams, 1854, a large-shelled colloniid genus (McLean & Gofas 2008).

All specimens of *Liotipoma* considered to be female have a higher profile than the male shells of their species, allowing for a deeper umbilical cavity. Only one female specimen of *L. wallisensis* and only two for *L. mutabilis* n. sp. are known, but for all three specimens of these two species it seems that the umbilical cavity of the female was further enlarged by the presence of the egg mass and the brooding larvae, causing the shell to resorb part of the umbilical wall to enlarge the umbilical cavity to function as a brood pouch. The reproductive status of *Paraliotipoma* n. gen. is unknown because it is known only from a single specimen. The genus differs from the other three genera in lacking the layered "tongue" that is such a prominent feature that is of the other three genera.

Species of low profile in *Depressipoma* n. gen. and *Rhombipoma* n. gen. are not likely to be brooders, because there would not be the volume available, as in species of higher profile.

ADDENDUM: PROPOSAL OF NEW FAMILY, ARENEIDAE N. FAM.

This paper is preliminary to publication of a full revision of the family Liotiidae, and the family Areneidae n. fam. The Areneidae n. fam. were first recognised by me at the supra-generic level (McLean 2001: 401), in a program abstract for the 2001 World Congress of Malacology in Vienna. However, as noted by Bouchet & Rocroi (2005: 30), I neglected to make an explicit statement that "Areneidae" was being proposed as new, with the designation of a type genus. Meanwhile other authors (e.g., Williams *et. al.* 2008) have used "Areneidae" at the family level without mention of authorship. In order to cite it with authorship in the present paper, I here provide the following formal validation:

Family ARENEIDAE n. fam.

"Areneidae" McLean, 2001: 418 (*nomen nudum*, not validated).

TYPE GENUS. — *Arene* H. & A. Adams, 1854 (here designated).

DIAGNOSIS. — Shell with colour pattern; spiral sculpture stronger than axial sculpture, aperture usually tangential; base of aperture usually with denticles, final lip usually preceded by short phase of whorl expansion.

COMPARISONS. — The family Liotiidae differs in lacking a colour pattern, having stronger axial sculpture, having an aperture that is more radial than tangential, having a complete lack of apertural denticles, and usually having a thicker final lip.

Acknowledgments
This contribution owes much to the malacology staffs of both the MNHN and the LACM for their diligence in the collecting and processing of the shell grit samples that yielded the specimens of *Liotipoma* here described. At the MNHN this resulted from the extended collecting workshops that have taken place at New Caledonia, Lifou, and Vanuatu, organised by Philippe Bouchet, with the assistance of Philippe Maestrati and other members of the MNHN staff, and with the sorting and distribution of the material arranged by Virginie Héros of the MNHN staff. The expeditions to Lifou and Santo were made possible by generous grants from the Total Foundation to Philippe Bouchet. I thank Philippe Bouchet, Virginie Héros and Philippe Maestrati for numerous courtesies with the loan of MNHN material and assistance with the manuscript.

At the LACM the *Liotipoma* material of unusual interest resulted from collecting efforts by our field associates during the 1980s and early 1990s, who collected the shell grit sample, including the late Twila Bratcher, who collected at Fiji and Rowley Shoals, the late Tony Ferreira, from Fiji, and Ken Severin, for Papua New Guinea. Our crew of volunteers from that period, including the late Liz Veal, the late Edith Abbott and the late Jo-Carol Ramsaran picked and sorted the samples.

I thank my previous imaging assistant Michelle Schwengel and my current imaging assistant Brian Koehler for the plate preparation. I thank Lindsey Groves for cataloging of type material and reading the manuscript. An earlier version of this manuscript was reviewed by Bruce Marshall and by Anders Warén, whose suggestions have greatly improved the manuscript. I thank Annemarie Ohler (MNHN) for advice on nomenclataural matters.

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