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Three new species of *Ammonicera* from the Eastern Pacific coast of North America, with redescriptions and comments on other species of Omalogyridae (Gastropoda, Heterobranchia)

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Abstract

The family Omalogyridae comprises some of the smallest known marine snails. Like all micromolluscs, they have been historically neglected and are underrepresented in faunistic surveys. Based on a few focused studies of the family, 15 valid omalogyrid species were previously recognised in the Indian and Pacific Oceans. To these, we add 3 new species based on a morphological analysis of material in the dry collection of the Natural History Museum of Los Angeles County, applying light and scanning electron microscopies. The new species, *Ammonicera mcleani*, *A. mexicana* and *A. sleursi*, are the first omalogyrid species described from the Eastern Pacific coast of North America. Redescriptions of the Australian omalogyrids *Ammonicera sucina* (Laseron, 1954) and *Omalogyra liliputia* (Laseron, 1954) are also presented, detailing for the first time ultrastructural aspects of their shell morphology. Additionally, we present here the first record of *Ammonicera binodosa* Sleurs, 1985b in Sri Lanka, introduce the new combination *Ammonicera vangoethemi* (Sleurs, 1985c) for *Omalogyra vangoethemi*, and formally remove *Transomalogyra* Palazzi & Gaglini, 1979 from Omalogyridae by fixing its type species as *Homalogyra densicostata* Jeffreys, 1884. Finally, we present lists, geographic records and a bibliography of all currently recognised omalogyrid species in the Indian, Pacific and Antarctic Oceans, as well as an update to a previously published compilation of the Atlantic and Mediterranean representatives of the family.

Key words: *Omalogyra*, *Transomalogyra*, *Helisalia*, biodiversity, systematics, micromolluscs

Introduction

Characterised by adult shell diameters well within the size range of protozoans, representatives of the family Omalogyridae G.O. Sars, 1878 are arguably the smallest known gastropods (Bieler & Mikkelsen, 1998; Gofas & Warén, 1998; Habe, 1972). Omalogyrids live in shallow marine environments worldwide, commonly dwelling and grazing on algae (Bieler & Mikkelsen, 1998; Fretter, 1948). Two species of the family are known to be hermaphrodites (Baeumler *et al.*, 2008; Simone, 1997), and the two whose mode of development is known hatch as crawling juveniles from egg capsules (Franc, 1948; Fretter, 1948; Gofas, 2011). The living species are grouped in three genera, *Omalogyra* Jeffreys, 1859b, *Ammonicera* Vayssièrè, 1893, and *Retrotortina* Chaster, 1896.

Omalogyrids are currently placed in a superfamily of their own within the paraphyletic “lower heterobranch” gastropods (e.g. Bouchet *et al.*, 2005; Haszprunar, 1988; Healy, 1993). However, their exact phylogenetic relationships, in particular the supposed closer relationship to the Architectonicoidea, are still unclear (e.g. supported by Dinapoli & Klussmann-Kolb, 2010, but not by Baeumler *et al.*, 2008).

At the species level, the systematics of the family is also poorly understood because, like most micromolluscs, omalogyrids have been historically neglected and are underrepresented in faunistic surveys. Most omalogyrid species have been described only recently in studies specifically focused on the family (e.g. Rolán, 1992a, b; Sleurs, 1985a, b, c). Similarly, distributional information is available only for areas targeted by such studies and it is inexistent even for large regions whose malacofauna is generally well-known, such as the Pacific coast of North America (Fig. 8).

This paper describes three new species of *Ammonicera* from the Pacific coasts of the U.S.A. and Mexico, provides the first record of Omalogyridae in Sri Lanka and redescribes the two known Australian representatives of the family, namely *Ammonicera sucina* (Laseron, 1954) and *Omalogyra liliputia* (Laseron, 1954).

Material and methods

Specimens were received on loan from the dry collection of the Natural History Museum of Los Angeles County. Prior to imaging, they were immersed in distilled water, cleaned with fine brushes or sonicated for 2–10 seconds, and air-dried.

Stacks of photographs were taken using a digital camera attached to a compound microscope (with reflected light). Stacks were then processed in CombineZP (Hadley, 2010) to generate composite images with extended depth of field.

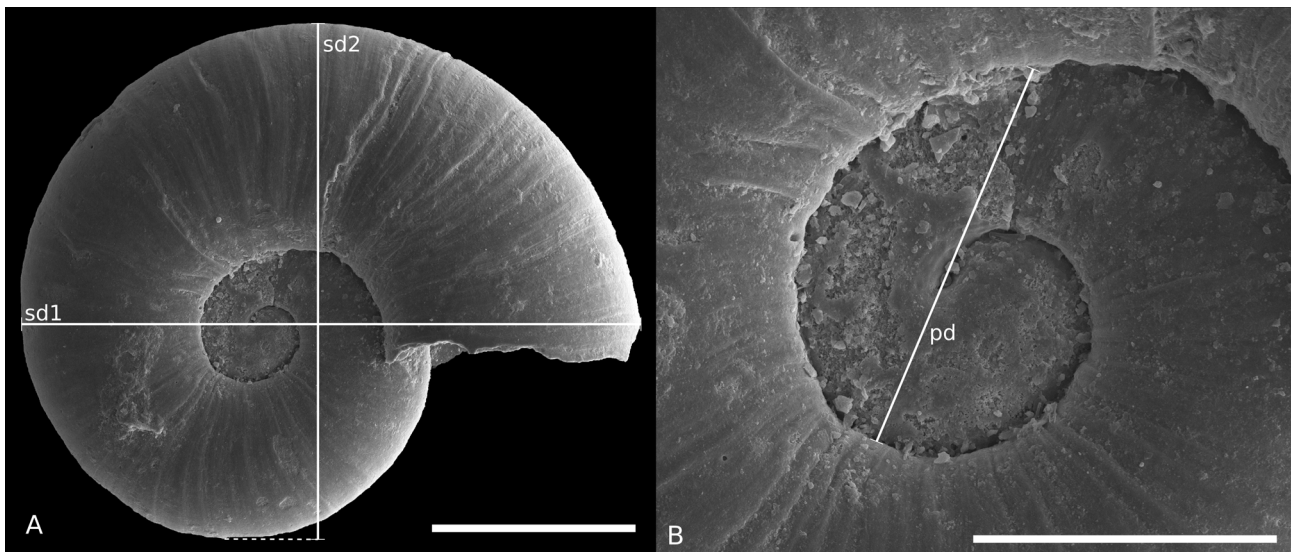


FIGURE 1. Apical views of the shell (A) and protoconch (B) of *Omalogyra liliputia* (Laseron, 1954) (specimen 1), showing the placement of measurements used in this study. Abbreviations: pd, maximum diameter of the protoconch; sd1, maximum diameter of the shell; sd2, maximum diameter of the shell perpendicular to sd1. Scale bars: A = 0.2 mm; B = 0.1 mm.

Scanning electron microscopy (SEM) was conducted on specimens mounted on pin stubs and gold coated. Shell measurements and whorl counts were obtained from the resulting SEM images, using the method of Taylor (as summarized by Jablonski & Lutz, 1980, p. 330, fig. 4) for whorl counts. Figure 1 shows the placement of measurements.

Because of the extremely small shell sizes in this group, type specimens were selected solely from material investigated by SEM and most of the textual descriptions are focused on those specimens. Additional material, usually studied only by stereo light microscopy (Olympus SZH10 at 140x magnification) is listed separately.

Abbreviations used

FMNH	Field Museum of Natural History, Chicago, U.S.A.
LACM	Natural History Museum of Los Angeles County, Los Angeles, U.S.A.
pd	Maximum protoconch diameter
pw	Protoconch whorls
sd1	Maximum shell diameter
sd2	Shell diameter perpendicular to sd1
sw	Shell whorls

Systematic descriptions

Family Omalogyridae G. O. Sars, 1878

Genus *Ammonicera* Vayssière, 1893

Ammonicera Vayssière, 1893, p. 19. Type species by monotypy: *Homalogyra fischeriana* Monterosato, 1869, pp. 274–275, pl. 13, fig. 1.

Diagnosis. Shell extremely minute; protoconch with conspicuous ridges and/or grooves; sculpture of the teleoconch usually prominent, seldom weak; aperture rounded to subquadrate; radular rows composed of two bent, dagger-like teeth, articulating at their outer side with a very small marginal tooth [formula 1-1-0-1-1]; cephalic tentacles cylindrical.

Ammonicera binodosa Sleurs, 1985b

Figure 2

Ammonicera binodosa Sleurs, 1985b, p. 25, figs 4,6,12,16,18.

Examined material (25 specimens). LACM 84-7, 24 specimens (4 under SEM), coral heads and sand, Pigeon Id, off Nilaveli, Sri Lanka, 8°43.5'N, 81°12.2'E, intertidal to 2m, leg. James H. McLean, Edith Abbott, Joan Sherman, 17 March 1984; FMNH 339458, 1 specimen, same collection data as LACM 84-7.

Type locality. Baros Island, North Malé Atoll, Republic of Maldives.

Diagnosis. *Ammonicera* with two spiral rows of nodules on the body whorl; periphery keeled.

Description. Shell planispiral, tightly coiled. Shell wall thick, opaque, glossy, dark amber in coloration. Protoconch 1 (P1) of c. 1.1 whorls (diameter 86 μ m in Figure 2B), sculptured with 1 raised nodule at mid-whorl and reticulate sculpture peripheral to nodule, occupying a broad groove on both the apical and basal surfaces. Boundary to protoconch 2 conspicuous to poorly marked. Protoconch 2 (P2) of c. 0.65 whorls (diameter 151 μ m in Figure 2B, including P1), sculptured with c. 5 nodules at mid-whorl and reticulate sculpture peripheral to nodules on both the apical and basal surfaces; P2 nodules becoming axially elongated and reticulate sculpture fading out towards the boundary with the teleoconch. Boundary between protoconch and teleoconch conspicuous to poorly marked. Teleoconch of c. 1.6 whorls; first 1/4 whorl sculptured by axially elongated nodules extending from mid-whorl to the outer suture on the apical and basal surfaces; subsequently with 2 spiral rows of nodules, 1 adjacent to the inner and 1 to the outer suture on both the apical and basal surfaces. Nodules of the outer row larger than those of the inner row and linked by a spiral cord from the second 1/2 whorl of the teleoconch onwards. Secondary spiral sculpture of the teleoconch composed of numerous very fine lirae, with interspaces approximately matching their width, overlaying the outer rows of nodules and the shell periphery. Body whorl with c. 14–17 nodules on each spiral row; periphery marked by a raised spiral cord; supraperipheral and infraperipheral walls straight to gently concave, with or without an axial sculpture of narrow and low riblets; inner lip broadly concave, flaring slightly. Aperture sub-quadrate.

Shell dimensions (in mm) and whorl counts:

	sd1	sd2	sw	pd	pw
specimen 1	0.64	0.55	3.13	0.15	1.51
specimen 2	0.73	0.61	3.06	?	?

Remarks. This is the first record of this species outside of its type locality in Baros Island, Maldives (Sleurs, 1985b). We based the description above solely on the examined Sri Lankan material, which matches the original description and illustrations of this species very well. A minor but noteworthy difference is the less pronounced secondary spiral ornamentation in our specimens, which appear to lack spiral lirae altogether on the inner row of nodules (compare Figure 2 herein with fig. 4 in Sleurs, 1985b).

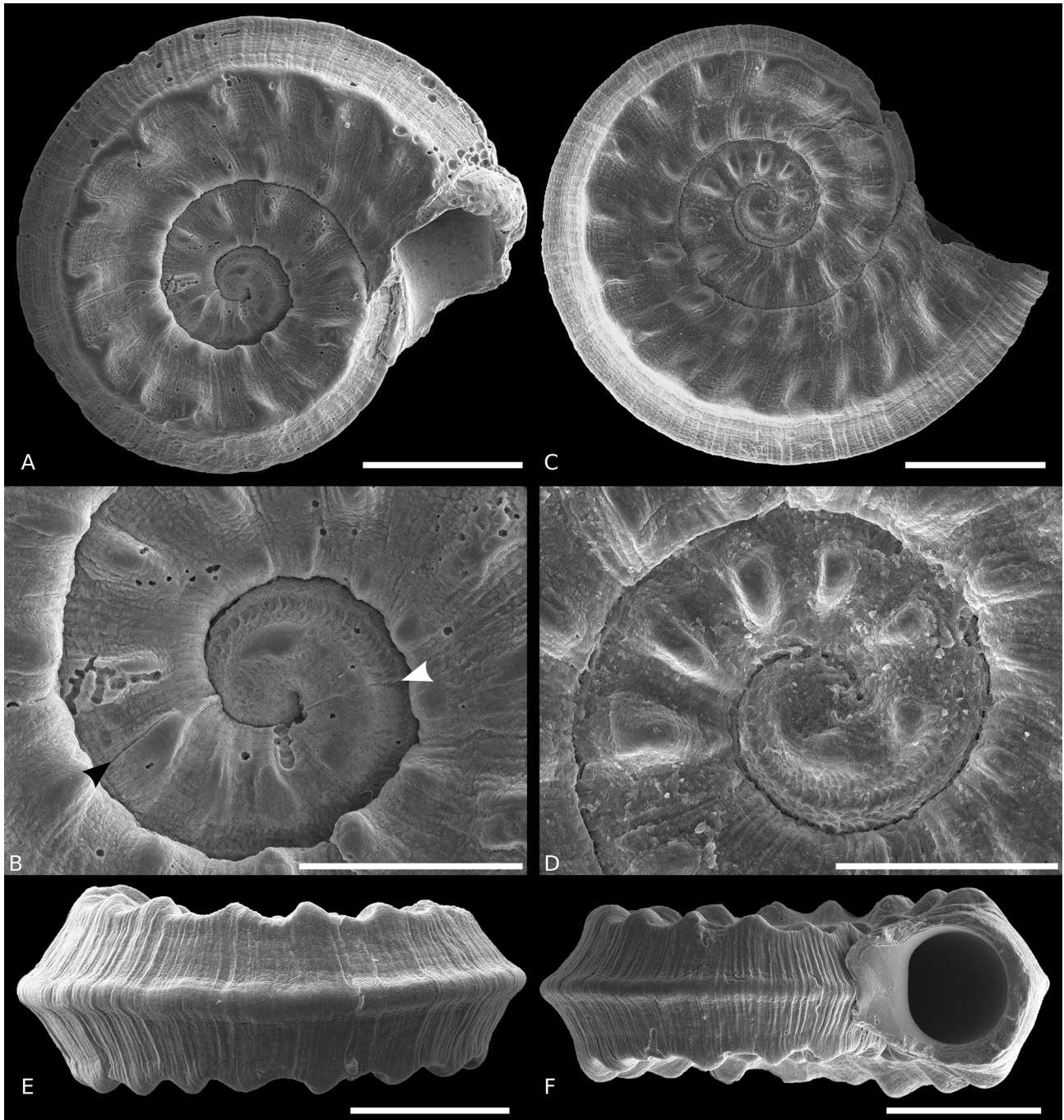


FIGURE 2. *Ammonicera binodosa* Sleurs, 1985b, LACM 84-7. **A–B.** Specimen 1, apical views; **A.** General view; **B.** Detail of the protoconch (interpreted boundaries P1/P2 and P2/teleoconch at white and black arrowheads, respectively); **C–D.** Specimen 2, umbilical views; **C.** General view; **D.** Detail of the protoconch; **E.** Specimen 3, dorsal view; **F.** Specimen 4, apertural view. Scale bars: A, C, E, F = 0.2 mm; B, D = 0.1 mm.

***Ammonicera sucina* (Laseron, 1954)**

Figure 3

Helisalia sucina Laseron, 1954, p. 17, figs 47,47a.

Ammonicera sucina (Laseron, 1954)—Ponder & de Keyzer, 1998, p. 864, fig. 15.185 A, C.

Examined material (12 specimens). LACM 79-58, 11 specimens (4 under SEM, one previously light-photographed), rocky substrate, Long Reef, Sydney, New South Wales, Australia, 33°44.5'S, 151°19.2'E,

intertidal, leg. James H. McLean, 13 May 1979; FMNH 339459, 1 specimen, same collection data as LACM 79-58.

Type locality. North Harbour, New South Wales, Australia.

Diagnosis. *Ammonicera* with a conspicuous spiral groove and a faint spiral cord on the protoconch; teleoconch sculptured by weak axial ribs and by a spiral sculpture of broad, elongated pits interspersed with raised nodules; spiral sculpture fading out on the body whorl.

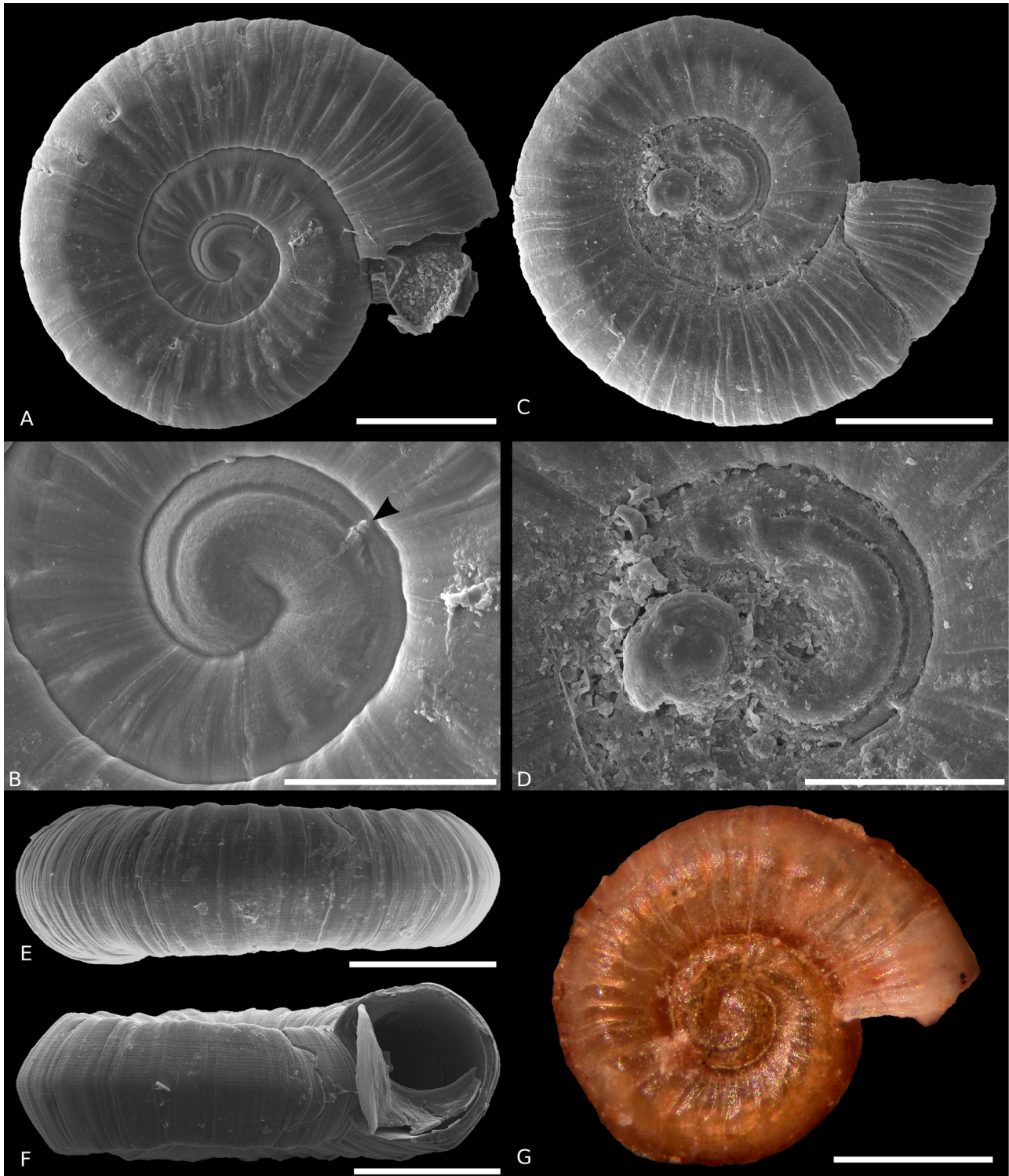


FIGURE 3. *Ammonicera sucina* (Laseron, 1954) A–B. Specimen 1, apical views; A. General view; B. Detail of the protoconch (interpreted boundary between protoconch and teleoconch at arrowhead); C–D. Specimen 2, umbilical views; C. General view; D. Detail of the protoconch; E. Specimen 4, dorsal view; F. Specimen 5, apertural view; G. Specimen 3, apical view. Scale bars: A, C, E–G = 0.2 mm; B, D = 0.1 mm.

Description. Shell planispiral, tightly coiled. Shell wall very thin, pellucid, glossy, amber in coloration. Protoconch of c. 1.2 whorls, finely pitted, sculptured on its apical and basal surfaces by a faint spiral cord mid-whorl and a broad spiral groove positioned equidistantly between the cord and the outer suture. Boundary between P1 and P2 poorly marked to indistinct; boundary between protoconch and teleoconch marked by interruption of the spiral grooves and onset of the axial sculpture of the teleoconch. Teleoconch of c. 2 whorls, with an axial sculpture of weak ribs; spiral groove of the protoconch replaced on the first 1.5 whorls of the teleoconch by a primary spiral sculpture of broad, elongated pits interspersed with raised nodules, the latter positioned at intersections with the axial ribs; primary spiral sculpture fading out on the last 1/2 whorl of the teleoconch. Secondary spiral sculpture of the teleoconch composed of numerous very fine lirae, with interspaces approximately matching their width, occurring on both apical and basal surfaces from mid-whorl to the shell periphery. Shell periphery transitioning from obtusely angled along the first 1.5 whorls of the teleoconch to uniformly rounded subsequently. Apical and umbilical sutures impressed; outer lip sharply convex in the vicinity of the sutures, straight to broadly convex along apical and basal walls, uniformly rounded along periphery; inner lip concave, flaring slightly. Aperture sub-crescent.

Shell dimensions (in mm) and whorl counts:

	sd1	sd2	sw	pd	pw
specimen 1	0.69	0.58	3.19	0.12	1.18
specimen 2	0.61	0.52	3.10	0.15	1.33
specimen 3	0.52	0.43	2.78	0.11	1.12

Remarks. The original description and illustrations of *Helisalia sucina* by Laseron (1954), who tentatively assigned this species to the family Liotiidae Gray, 1850, were based on light microscopy alone and are insufficiently detailed. Ponder & de Keyzer (1998) recognised this species as a member of *Ammonicera* and published the first SEM image of the shell in apical view, as well as a sketch of the live animal. The redescription presented herein is based on SEM micrographs of shells collected c. 10 km north of the type locality.

A. sucina shares with *A. plicata* Sleurs, 1985b, which is only known from its type locality in the Maldives, a similar sculptural pattern, but differs from the latter species in several aspects: (1) the shell periphery is obtusely angled in *A. sucina*, rather than uniformly rounded (compare Figure 3E–F herein with fig. 7 in Sleurs, 1985b); (2) apical and basal walls are flattened in *A. sucina*, whereas they are uniformly rounded in *A. plicata*; (3) *A. sucina* has a shallower apical suture; and (4) the spiral sculpture of the teleoconch fades out sooner in *A. plicata* (approximately from the beginning of the third shell whorl) than it does in *A. sucina* (from the second half of the third shell whorl).

A further related look-alike is the Atlantic *A. lineofuscata* Rolán, 1992b, which is readily distinguished from *A. sucina* by a more pronounced sculpture (see Rolán, 1992b, figs 22, 24, 25), and a colour pattern of three spiral brown bands (see Tunnell *et al.*, 2010, p. 258).

Ammonicera sleursi sp. nov.

Figure 4

Examined material (92 specimens). **Holotype:** LACM 3288 (SEM), flood control channel, Mission Bay, San Diego Co., U.S.A., 32°45.5'N, 117°15.0'W, 5–8 ft [1.5–2.4 m], leg. James H. McLean & Patrick LaFollette, 15 August and 11 October 1971. **Paratypes (3):** LACM 3289 (Paratypes 1, 3; SEM, Paratype 3 previously light-photographed), from the holotype lot; FMNH 339460 (Paratype 2; SEM), from the holotype lot. **Additional material:** LACM 71-101, 9 specimens from the type locality. LACM 71-83, 6 specimens (SEM), Los Arcos, Banderas Bay, Jalisco, West coast of Mexico, 20°32'N, 105°19'W, intertidal to 15 ft [4.6 m], leg. James H. McLean & Jeff Margetts, 30 May to 1 June 1971; LACM 68-41, 1 specimen (SEM), south side of Bahía Cuastocamate (3 air miles NW of Barra de Navidad), Jalisco, Mexico, 19°13'45"N, 104°44'53"W, 15–65 ft [4.6–19.8 m], leg. James H. McLean & Peter Oringer, 13–21 October 1968; LACM 71-14, 66 specimens, east side of Punta Entrada at Sail Rock (north entrance to Magdalena Bay), Baja California, Mexico (24°32.4'N, 112°04'W, 10–50 ft [3–15.2 m]), leg. James H. McLean, 30–31 January 1971; LACM 66-12, 1 specimen, Cape San Lucas, Baja California, Mexico

(22°8'N, 110°W, 25–100 ft [7.6–30.5m], leg. James H. McLean & Peter Oringer, 3–4 April 1966; LACM 71-183, 5 specimens, Man of War Cove, Magdalena Bay, Baja California, Mexico (24°37.5'N, 112°7.5'W, intertidal to 35 ft [10.7 m], leg. James H. McLean & Patrick LaFollette, 31 October 1971.

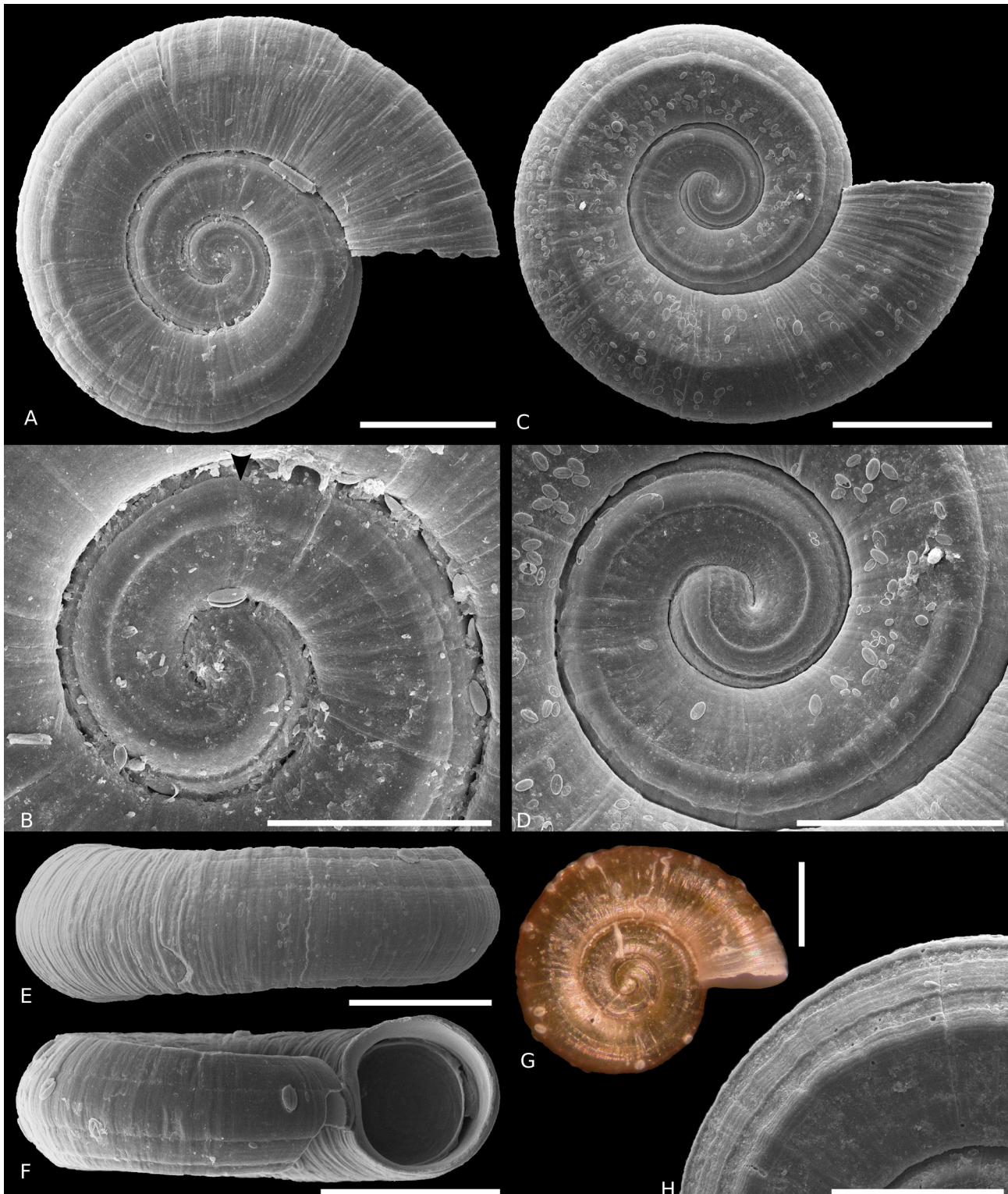


FIGURE 4. *Ammonicera sleursi* sp. nov. **A–B.** Holotype, apical views; **A.** General view; **B.** Detail of the protoconch (interpreted boundary between protoconch and teleconch at arrowhead); **C–D.** Paratype 1, umbilical views; **C.** General view; **D.** Detail of the protoconch; **E** and **G.** Paratype 3; **E.** Dorsal view; **G.** Apical view, showing coloration; **F.** Paratype 2, apertural view; **H.** Specimen from Los Arcos (LACM 71-83), apical view showing wide grooves between spiral cords. Scale bars: A, C, E–G = 0.2 mm; B, D, H = 0.1 mm.

Diagnosis. *Ammonicera* with a broad spiral cord ornamenting the protoconch and teleoconch, gradually fading out on the body whorl; shell diameter c. 0.6–0.7 mm at 3 whorls.

Description. Shell planispiral, tightly coiled. Shell wall very thin, pellucid, glossy, fawn in coloration. Protoconch of c. 1.4 whorls, sculptured with 1 broad spiral cord on its apical and 1 broad spiral cord on its basal surface; spiral cords closer to the outer than to the inner suture. Basal surface of the protoconch finely pitted. Protoconch 2 stage absent; boundary between protoconch and teleoconch conspicuous to poorly marked. Teleoconch of c. 1.8 whorls, with a primary spiral sculpture composed of 5 broad cords separated by 4 marked grooves; the 2 most central cords (1 apical and 1 basal) continuous with those of the protoconch; 1 additional cord positioned at the shell periphery and 2 cords (1 apical and 1 basal) subperipherally; grooves between cords c. 0.1–0.75 the width of the central cords. Secondary spiral sculpture of the teleoconch composed of numerous very fine lirae, with interspaces approximately matching their width, overlaying the primary spiral sculpture. Spiral sculpture gradually fading out in the last 1/2 whorl of the teleoconch. Axial sculpture of the teleoconch composed of growth lines only, which become crowded in the last 1/4 whorl of the teleoconch. Apical and umbilical sutures impressed; outer lip sharply convex in the vicinity of the sutures, uniformly rounded along the apical, peripheral and basal walls; inner lip broadly concave, flaring slightly. Aperture and operculum rounded.

Shell dimensions (in mm) and whorl counts:

	sd1	sd2	sw	pd	pw
holotype	0.70	0.60	3.21	0.15	1.39
paratype 1	0.60	0.50	3.07	0.15	1.47
paratype 2	0.64	0.53	3.23	0.14	1.47
LACM 71–83, spec. 1	0.42	0.29	2.75	0.14	1.46
LACM 71–83, spec. 2	0.33	0.27	2.28	0.16	1.47
LACM 71–83, spec. 3	0.42	0.35	2.70	0.12	1.38
LACM 68–41	0.35	0.29	2.51	0.15	1.54

Remarks. *A. sleursi* is remarkably similar to *A. lignea* Palazzi, 1988, an Eastern Atlantic species endemic to the Madeira Archipelago. They share weak axial sculpture and broad spiral ribs that fade out towards the aperture. However, the shell of *A. sleursi* is considerably smaller than that of *A. lignea* at the same whorl count. The holotype and paratype of *A. lignea* illustrated by Palazzi (1988, figs 8,18) measure c. 0.92 mm at 3.24 whorls, and 0.82 mm at 3.13 whorls, respectively [our measurements], and Segers *et al.* (2009, p. 488) illustrated a specimen of *A. lignea* measuring 0.8 mm at c. 2.94 whorls. In contrast, the largest known shell of *A. sleursi* is the holotype, which measures 0.70 mm at 3.21 whorls. Obviously, the geographic separation of *A. sleursi* and *A. lignea* is also relevant in recognising them as separate species.

A. sleursi is also similar to the Western Atlantic *A. circumcirra* Rolán, 1992b, recorded from Cuba (the type locality; see Rolán, 1992b) and from the Saint Peter and Saint Paul Archipelago, Brazil (Lima *et al.*, 2011). However, the sculpture of *A. circumcirra* is more prominent than that of *A. sleursi*, particularly in the presence of weak elevations formed by the intersection of axial ribs with spiral cords. Additionally, the sculpture of *A. circumcirra* appears to be persistent, rather than fading along the teleoconch (Rolán, 1992b, fig. 23; Lima *et al.*, 2011, fig. 5).

Mediterranean *A. fischeriana* Monterosato, 1869 differs from *A. sleursi* in displaying a colour pattern of three spiral brown bands and in having a more pronounced axial sculpture.

Etymology. This species is dedicated to Dr. Willy J. M. Sleurs, Research Associate of the Royal Belgian Institute of Natural Sciences, in recognition of his contribution to our knowledge of Indo-Pacific omalogyrids.

Ammonicera mcleani sp. nov.

Figure 5

Examined material (19 specimens). **Holotype:** LACM 3284 (SEM, color photograph before SEM), W side of Cerralvo Is., Baja California, Mexico, 24°10'N, 109°52'W, 30–50 ft [9.1–15.2m], leg. James H. McLean, 3 February 1971. **Paratypes (3):** LACM 3285 (Paratypes 1, 2; SEM), from the holotype lot; FMNH 339461

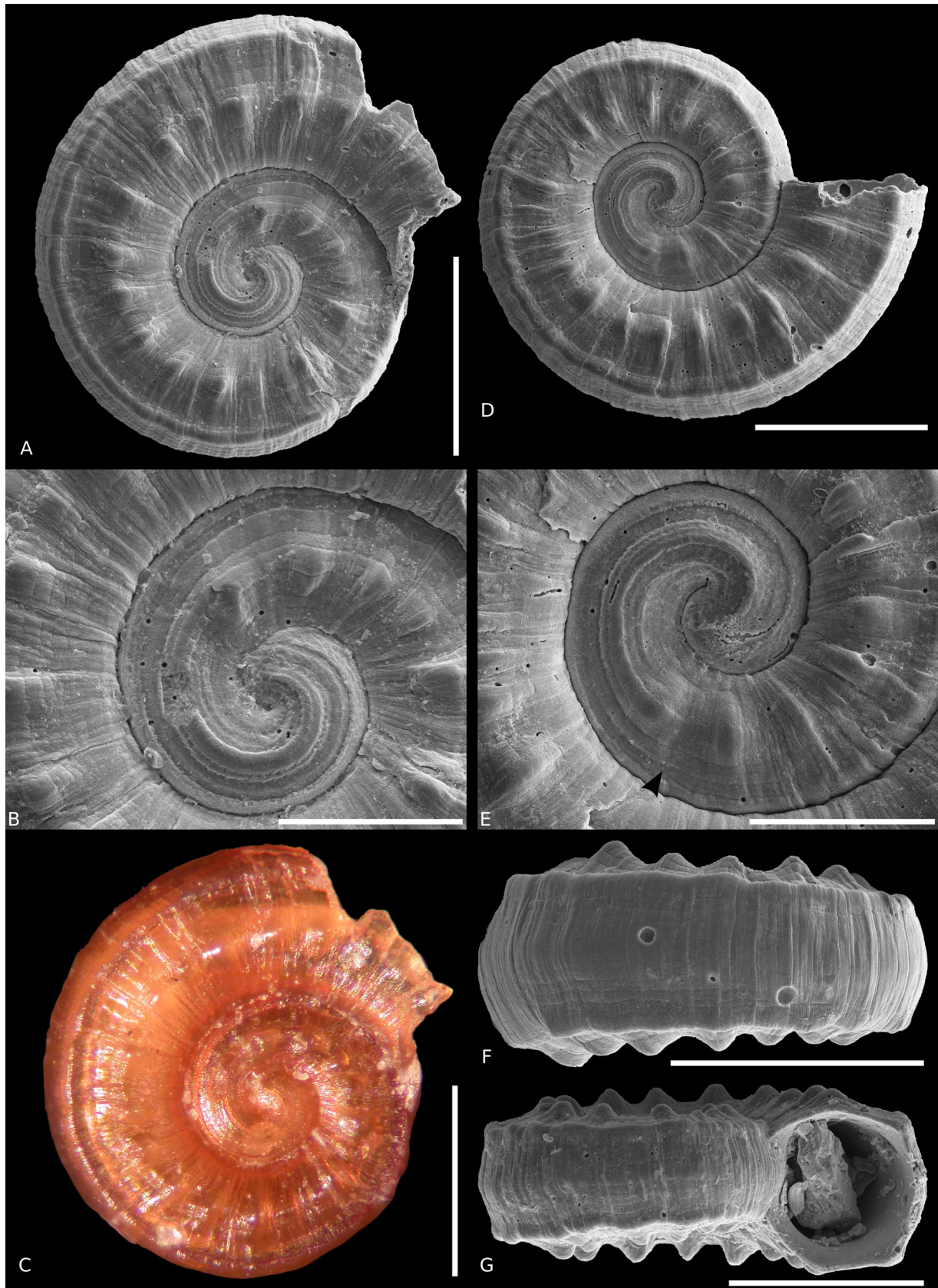


FIGURE 5. *Ammonicera mcleani* sp. nov. **A–C.** Holotype, apical views; **A.** General view; **B.** Detail of the protoconch; **C.** Coloration; **D–E.** Paratype 1, umbilical views; **D.** General view; **E.** Detail of the protoconch (interpreted boundary between protoconch and teleconch at arrowhead); **F.** Paratype 2, dorsal view; **G.** Paratype 3, apertural view. Scale bars: **A, C, D, F, G** = 0.2 mm; **B, E** = 0.1 mm.

(Paratype 3, SEM), from the holotype lot. **Additional material:** LACM 71-24, 11 specimens from the type locality; LACM 71-14, 3 specimens, east side of Punta Entrada at Sail Rock (north entrance to Magdalena Bay), Baja California, Mexico (24°32.4'N, 112°04'W, 10–50 ft [3–15.2m]), leg. James H. McLean, 30–31 January 1971; LACM 71–177, 1 specimen, Punta San Pablo anchorage, outer coast of Baja California, Mexico (27°12'55"N, 114°27'30"W, 70–80 ft [21.3–24.4m]), leg. Swift & Huddleston, 24 October 1971.

Diagnosis. *Ammonicera* with spiral cords delimiting a broadly convex peripheral wall; additionally sculptured by a single row of 19–21 nodules each on the apical and basal walls of the body whorl.

Description. Shell planispiral, tightly coiled. Shell wall very thin, pellucid, glossy, amber in coloration (faded specimens with major cords darkest). Protoconch of c. 1.3 whorls, sculptured on its apical and basal surfaces by 3 spiral cords; central spiral cord positioned mid-whorl, broad, prominent, with a reticulate sculpture on its outer face; inner and outer spiral cords positioned approximately equidistantly between the central cord and the inner and outer sutures, respectively, c. 1/4 the width and height of the central cord. Protoconch 2 stage absent; boundary between protoconch and teleoconch poorly marked. Teleoconch of c. 1.4 whorls, sculptured by 1 broad spiral cord each at the junction of the peripheral wall with the apical and basal walls, and by 1 spiral row of axially elongated nodules, positioned mid-whorl, with interspaces c. 1–2 times their width, gradually increasing in height throughout the teleoconch; body whorl with 19–21 nodules on each row; secondary sculpture of the teleoconch composed of very fine and somewhat wavy spiral grooves. Shell periphery broadly convex. Apical and umbilical sutures shallowly impressed; outer lip straight to broadly convex from the sutures to the middle of the apical and basal walls, and from these points to the junctions with the peripheral wall, broadly convex along the shell periphery; outer lip forming 4 similar, obtuse vertices in the middle of the apical and basal walls, and at the junctions of these walls with the peripheral wall; inner lip concave, not flaring. Aperture almost hexagonal.

Shell dimensions (in mm) and whorl counts:

	sd1	sd2	sw	pd	pw
holotype	0.45	0.38	2.68	0.15	1.33
paratype 1	0.52	0.44	2.68	0.16	1.37

Remarks. The shells of *Ammonicera mcleani* and *A. mexicana* **sp. nov.** (described below) resemble those of Atlantic *A. sculpturata* Rolán, 1992b and Papua New Guinean *A. nodicarinata* (Sleurs, 1985c) in the presence of two spiral cords delimiting the peripheral wall and a single row of nodules on the apical and basal surfaces of the shell. They differ from both of these previously described species in bearing smaller and more numerous nodules on the body whorl (10–15 in *A. nodicarinata*; c. 12 in *A. sculpturata*). They additionally differ from *A. sculpturata* in having a less rounded aperture, and from *A. nodicarinata* in the later ontogenetic onset of their nodules (see Rolán, 1992b; Sleurs, 1985c).

The shape of the periphery is the most obvious criterion to distinguish *A. mcleani* and *A. mexicana*. It is broadly convex in the former species, whereas in the latter a prominent spiral cord divides the peripheral wall in two concave sectors. Additional distinguishing features are the more discoidal shape of *A. mexicana* and the slightly more prominent nodules of *A. mcleani*.

Etymology. This species is dedicated to Dr. James McLean, Curator Emeritus at LACM and renowned specialist of the eastern Pacific gastropod fauna, who personally collected and encouraged us to study the material reported upon in this paper.

Ammonicera mexicana **sp. nov.**

Figure 6

Examined material (24 specimens). **Holotype:** LACM 3286 (SEM, color photograph before SEM), south side of Bahía Cuastocomate (3 air miles NW of Barra de Navidad), Jalisco, Mexico, 19°13'45"N, 104°44'53"W, 15–65 ft [4.6–19.8 m], leg. James H. McLean & Peter Oringer, 13–21 October 1968. **Paratypes (3):** LACM 3287 (Paratypes 1, 2; SEM), from the holotype lot; FMNH 339462 (Paratype 3; SEM), from the holotype lot. **Additional material:** LACM 68-41, 7 specimens from type locality; LACM 71-83, 9 specimens, Los Arcos, Banderas Bay, Jalisco, West coast of Mexico, 20°32'N, 105°19'W, intertidal to 15ft [4.6m], leg. James H. McLean & Jeff Margetts, 30 May to

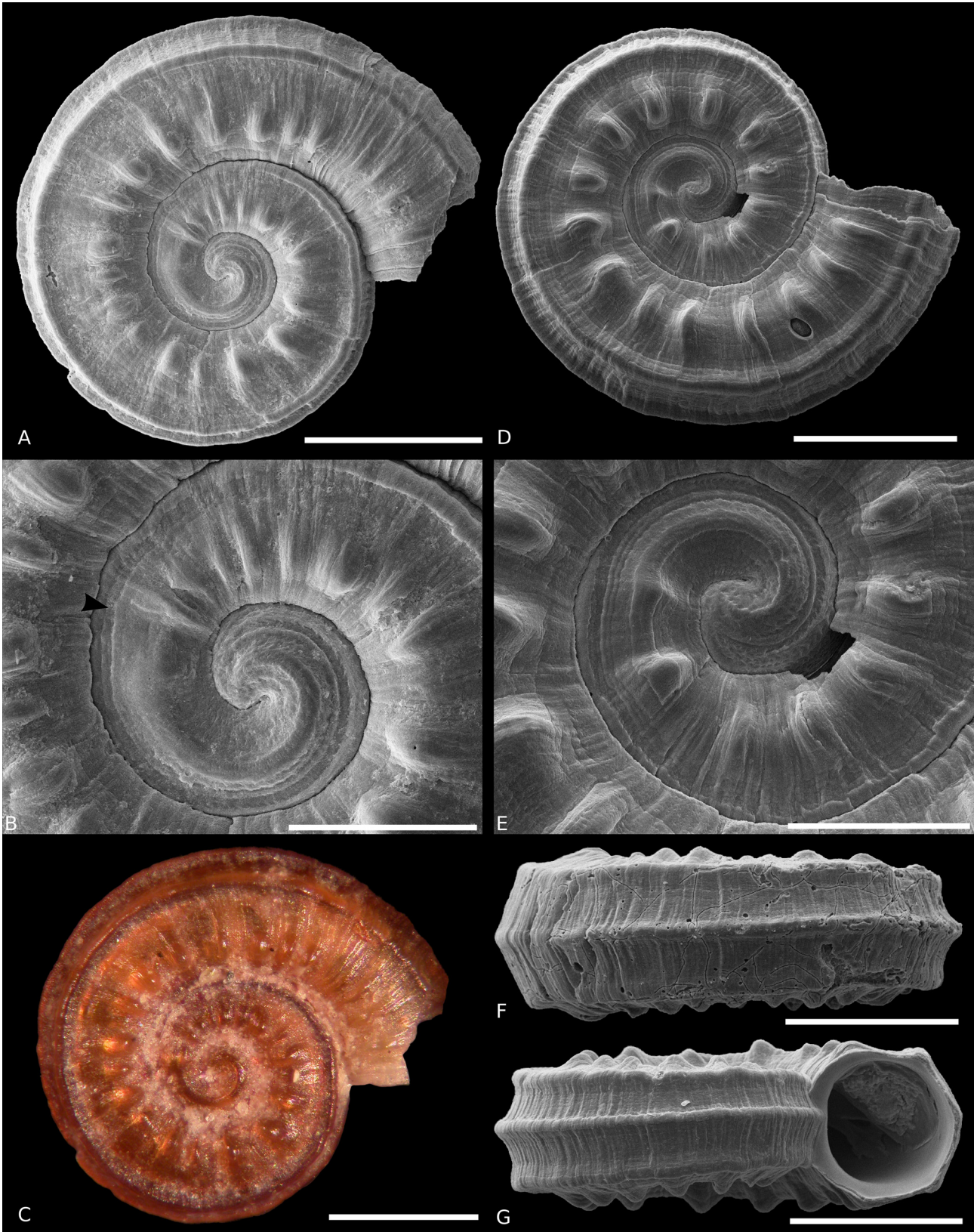


FIGURE 6. *Ammonicera mexicana* sp. nov. **A–C.** Holotype, apical views; **A.** General view; **B.** Detail of the protoconch (interpreted boundary between protoconch and teleconch at arrowhead); **C.** Coloration; **D–E.** Paratype 1, umbilical views; **D.** General view; **E.** Detail of the protoconch; **F.** Paratype 2, dorsal view; **G.** Paratype 3, apertural view. Scale bars: A, C, D, F, G = 0.2 mm; B, E = 0.1 mm.

1 June 1971; LACM 65–28, 1 specimen, Barra de Navidad, Jalisco, West coast of Mexico, 19°20'N, 105°W, 5–20ft [1.5–6.1m], leg. Nick Furjanick, 26 June 1965; LACM 67-9, 1 specimen, Isla Isabela, 45 miles northwest of San Blas, Nayarit, West coast of Mexico, 21°51'N, 105°55'W, 30ft [9.1m], leg. Chuck Snell & Bob McMillen, 11 February 1967; LACM 67-155, 2 specimens, Isla Roqueta, Acapulco de Juaréz, Guerrero, West coast of Mexico, 16°49'N, 99°56'W, 15–20 ft [4.5–6.1m], leg. Twila Bratcher, 10 May 1967.

Diagnosis. *Ammonicera* with spiral cords delimiting a keeled peripheral wall; additionally sculptured by a single row of 14–20 nodules each on the apical and basal walls of the body whorl.

Description. Shell planispiral, tightly coiled. Shell wall very thin, pellucid, glossy, amber in coloration. Protoconch of c. 1.4 whorls, with the first whorl sculptured on its apical and basal surfaces by 3 spiral cords; inner spiral cord positioned approximately mid-whorl, broad, prominent; central and outer spiral cords approximately equidistantly distributed between the inner cord and the outer suture; central cord c. 1/4 the width and height of the inner cord; outer cord c. 1/2 the width and equivalent in height to the central cord; surface of the protoconch finely pitted between inner suture and inner spiral cord, and with a reticulate sculpture between inner spiral cord and outer suture; sculpture of the protoconch transitioning to large nodules positioned mid-whorl along approximately the last 1/2 whorl. Protoconch 2 stage absent; boundary between protoconch and teleoconch poorly marked. Teleoconch of c. 1.4 whorls, sculptured by 1 broad and prominent spiral cord at the shell periphery and on both the apical and basal surfaces by 1 similar spiral cord each at the junction with the peripheral wall; apical and basal surfaces additionally sculptured by 1 spiral row of axially elongated nodules, positioned in the inner half of each whorl, with interspaces c. 1–3 times their width, gradually increasing in height throughout the teleoconch; body whorl with 14–20 nodules; secondary sculpture of the teleoconch composed of very fine and somewhat wavy spiral grooves. Apical and umbilical sutures shallowly impressed; outer lip convex in the vicinity of the sutures, straight along each of 4 segments between obtuse vertices corresponding to the 3 continuous spiral cords and 2 nodulose spiral cords of the teleoconch; inner lip concave, not flaring. Aperture almost hexagonal.

Shell dimensions (in mm) and whorl counts:

	sd1	sd2	sw	pd	pw
holotype	0.53	0.47	2.82	0.16	1.42
paratype 1	0.57	0.48	2.70	0.17	1.38

Remarks. *Ammonicera mexicana* appears to be closely related to *A. mcleani*, from which it differs in having a keeled periphery, a more discoidal shape and slightly less prominent nodules. Criteria to distinguish *Ammonicera mexicana* from seemingly more distantly related look-alikes were discussed under the remarks for *A. mcleani*.

Etymology. Mexicanus-a-um, adjective; from Mexico.

Genus *Omalogyra* Jeffreys, 1859b

Omalogyra Jeffreys, 1859b, p. 498. Type species by subsequent designation of Bucquoy *et al.* (1884, p. 78): *Truncatella atomus* Philippi, 1841, p. 54, pl. 5, figs 4a–d.

Ammonicerina O. G. Costa, 1861, p. 67. Type species by subsequent designation of Dall (1927, p. 134, as “Ammonocerina”):

Ammonicerina simplex O. G. Costa, 1861, p. 72, pl. 11, figs 3a, b.

Homalogyra Jeffreys, 1867, p. 67 (unjustified emendation).

Helisalia Laseron, 1954, p. 16. Type species by original designation: *Helisalia liliputia* Laseron, 1954, pp. 16–17, figs 45,45a.

Diagnosis. Shell extremely minute; protoconch smooth or finely nodulose, devoid of conspicuous axial or spiral sculpture; sculpture of the teleoconch weak or absent; aperture rounded; each radular row composed of a single dagger-like tooth, flanked by one lateral plate on each side [formula 0-(1)-1-(1)-0]; cephalic tentacles forming rounded lobes.

Omalogyra liliputia (Laseron, 1954)

Figures 1,7

Helisalia liliputia Laseron, 1954, pp. 16–17, figs 45,45a.

Omalogyra liliputia (Laseron, 1954)—Ponder & de Keyzer, 1998, p. 864, fig. 15.185 B, D.

Examined material (10 specimens). LACM 79-58, 9 specimens (5 SEM, 1 previously light-photographed), rocky substrate, Long Reef, Sydney, New South Wales, Australia, 33°44.5'S, 151°19.2'E, intertidal; leg. James H. McLean, 13 May 1979; FMNH 339463, 1 specimen, same collection data as LACM 79-58.

Type locality. Castle Rock, Middle Harbour, Port Jackson, New South Wales

Diagnosis. *Omalogyra* of uniform coloration, sculptured by faint axial ribs and fine growth lines; inner lip concave, aperture sub-crescent; shell diameter c. 0.6 mm at 2 1/2 whorls.

Description. Shell planispiral, tightly coiled. Shell wall very thin, pellucid, glossy, amber in coloration. Protoconch of c. 1.2 whorls, much lighter than the teleoconch in coloration, sculptured only by microscopic, irregular nodules on the nuclear shell, gradually fading out toward the boundary with the teleoconch. Protoconch 2 poorly marked or absent; boundary between protoconch and teleoconch very well marked. Teleoconch of c. 1.2 whorls, sculptured by faint, irregularly spaced axial ribs, and by fine growth lines; shell devoid of spiral ornamentation. Apical and umbilical sutures deeply impressed; outer lip uniformly rounded; inner lip concave, flaring slightly. Aperture sub-crescent.

Shell dimensions (in mm) and whorl counts:

	sd1	sd2	sw	pd	pw
specimen 1	0.61	0.50	2.45	0.13	1.23
specimen 2	0.55	0.44	2.41	0.15	1.27

Remarks. This is the type species of the genus *Helisalia* Laseron, 1954, by original designation. The original description and illustrations by Laseron (1954), who tentatively assigned *Helisalia* to the family Liotiidae, were based on light microscopy alone and are insufficiently detailed. Marshall (1988) regarded *Helisalia liliputia* as possibly belonging to Orbitestellidae Iredale, 1917, whereas Healy (1993) and Ponder & de Keyzer (1998) relocated this species to *Omalogyra*. Healy (1993) described the sperm ultrastructure of *O. liliputia*, noting that it shares with *O. atomus* Philippi, 1841 a glycogen helix and paracrystalline material in the midpiece. Ponder & de Keyzer (1998) published the first SEM image of the shell of *O. liliputia* in apical view, as well as a diagram of the live animal. Here, we provide a re-description based on SEM micrographs of shells collected c. 10 km north of the type locality.

O. liliputia shares a morphologically simple shell, devoid of pronounced sculpture, with several other *Omalogyra* species, namely *O. antarctica* Egorova, 1991, *O. atomus*, *O. disculus* Palazzi, 1988, *O. fuscopardalis* Rolán, 1992b, *O. simplex* (O. G. Costa, 1861) and *O. zebrina* Rolán, 1992b.

The uniform coloration of the teleoconch of *O. liliputia* immediately separates this species from the Atlantic *O. zebrina*, *O. fuscopardalis* and Atlantic/Mediterranean *O. simplex*, all of which display coloration patterns on their teleoconch. *O. liliputia* differs from Atlantic *O. disculus* in having a higher, less discoidal shell (compare Figure 7G herein with fig. 3 in Rolán, 1992a [reproduced by Rolán, 2005, fig. 842]) and from the northern hemisphere *O. atomus* in displaying a larger degree of overlap of the body whorl over the previous whorl, which results in a more curved inner lip and less rounded aperture (compare Figure 7G herein with illustrations of *O. atomus* in apertural view by Palazzi, 1988, fig. 26, Gaglini, 1993, p. 928-04 and Gofas, 2011, p. 357).

The circum-antarctic *O. antarctica* is the only southern hemisphere species of *Omalogyra* that resembles *O. liliputia*. However, they differ in a number of aspects (Egorova, 1991; Engl, 2012): (1) *O. antarctica* reaches 1.4 mm in diameter and is much larger than *O. liliputia* at the same whorl count; (2) *O. antarctica* has a proportionally lower aperture, with an outer lip that is flattened apically and basally, whereas in *O. liliputia* the outer lip is uniformly rounded; and (3) *O. antarctica* is ornamented only by growth lines, whereas *O. liliputia* has weak axial ribs.

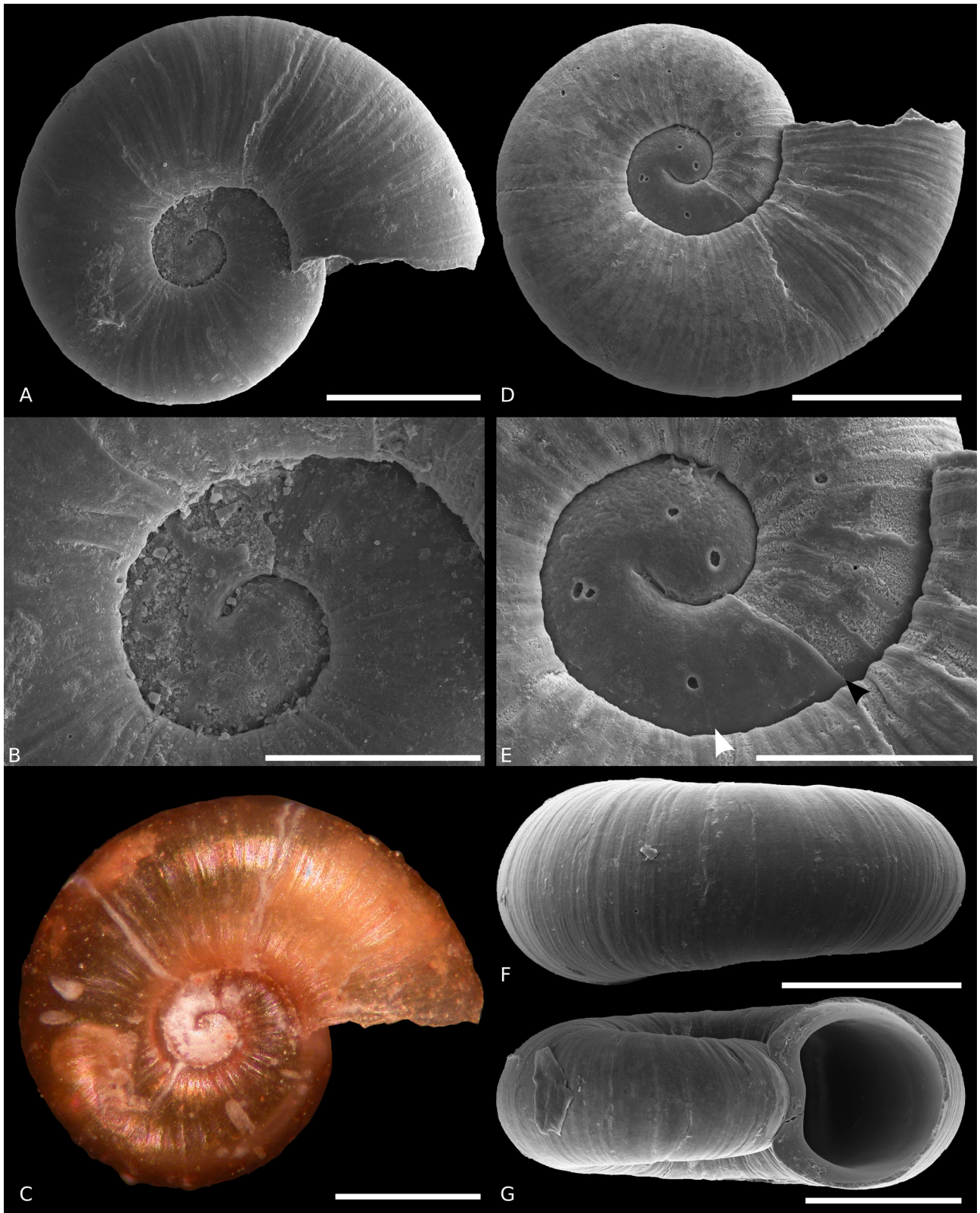


FIGURE 7. *Omalogyra liliputia* (Laseron, 1954) **A–C.** Specimen 1, apical views; **A.** General view; **B.** Detail of the protoconch; **C.** Coloration; **D–E.** Specimen 2, umbilical views; **D.** General view; **E.** Detail of the protoconch (interpreted boundaries P1/P2 and P2/teleoconch at white and black arrowheads, respectively); **F.** Specimen 3, dorsal view; **G.** Specimen 4, apertural view. Scale bars: A, C, D, F, G = 0.2 mm; B, E = 0.1 mm.

Discussion

Genus-level identification. Bieler & Mikkelsen (1998) provided a historical discussion of the taxonomy of omalogyrid genera. The family is composed of three valid genera, *Omalogyra* Jeffreys, 1859b, *Ammonicera* Vayssière, 1893, and *Retrotortina* Chaster, 1896. The last (with type species by monotypy: *Retrotortina fuscata* Chaster, 1896) has a hyperstrophic (i.e. pseudosinistral) shell that distinguishes it from *Omalogyra* and *Ammonicera*.

A close relationship between *Omalogyra* and *Retrotortina* is supported by a number of shared characters, including a protoconch that is smooth or sculptured only by small nodules, a weakly sculptured teleoconch, a radula with one central tooth, and a similar external morphology of the soft parts (with small flap-like tentacles, a small eye in the centre of the base of each tentacle, no snout, no propodial elaboration, and no pedal nor pallial appendages; see Baeumler *et al.*, 2008; Gofas & Warén, 1998). *Ammonicera* is readily distinguished from these genera by the strong sculpture of its protoconch and usually teleoconch, a radula with four teeth per row, and conspicuous cephalic tentacles. The generic placement of the species treated in this paper is thus confidently established.

Sleurs (1985c) described two omalogyrid species from Papua New Guinea in the genus *Omalogyra* (*O. nodicarinata* and *O. vangoethemi*), noting that they form with *A. japonica* Habe, 1972 a very homogeneous group characterised by the presence of at least one strong groove on the protoconch and of at least one axial sculpture on the teleoconch. Recognising that these are diagnostic features of *Ammonicera*, Rolán (1992b) relocated *O. nodicarinata* to *Ammonicera* and we introduce here the new combination *Ammonicera vangoethemi* (Sleurs, 1985c) for *O. vangoethemi*.

Type species of *Transomalogyra* Palazzi & Gaglini, 1979. Palazzi & Gaglini (1979, p. 33) introduced the genus-group name *Transomalogyra* as a subgenus of *Omalogyra*, designating *Ammonicerina simplex* O. G. Costa, 1861 as the type species. This would make *Transomalogyra* an objective synonym of *Ammonicerina* and a subjective synonym of *Omalogyra* (Bieler & Mikkelsen, 1998). However, Palazzi (1988, p. 103) pointed out that he had misidentified *Omalogyra simplex* in his earlier article with Gaglini and argued that the specimen they had figured (Palazzi & Gaglini, 1979, pl. 2, fig. 1) actually represents *Omalogyra densicostata* (Jeffreys, 1884). This opinion was echoed by subsequent workers, including Warén (1991, p. 74), Bieler & Mikkelsen (1998, p. 7) and Kano *et al.* (2009, p. 401). The species introduced as *Homalogyra densicostata* is now generally regarded as a member of *Adeuomphalus* (Vetigastropoda: Seguenzioidea), and *Transomalogyra* as a subjective synonym of that genus (e.g. by Kano *et al.*, 2009; Warén, 1991).

However, the nomenclatural problem involving the type species of *Transomalogyra* has remained, partly because previous editions of the ICZN Code dictated that such cases should be referred to the Commission, which is no longer the case (ICZN, 1999). Hence, to formally solve this issue, we hereby fix the type species of *Transomalogyra* (under Article 70.3 of the 1999 Code) as *Homalogyra densicostata* Jeffreys, 1884, misidentified as *Ammonicerina simplex* O. G. Costa, 1861 in the original designation by Palazzi & Gaglini (1979, p. 33).

Current composition of Omalogyridae. The three new taxa described herein bring the number of known omalogyrid species to 47. Bieler & Mikkelsen (1998) listed the composition of the family in the Atlantic Ocean and Mediterranean Sea, including type localities and a bibliography of 26 species. Since that list was prepared, three omalogyrid species were added to the Atlantic fauna [regions of type localities in brackets]:

Ammonicera plana Simone, 1997, pp. 44–47, figs 1–14 [São Paulo, Brazil]

Ammonicera san Rolán, Luque & Peñas, 2009, p. 136, figs 10–14 [Namibia]

Retrotortina damara Rolán, Luque & Peñas, 2009, pp. 134–135, figs 1–9 [Namibia]

Omalogyra burdwoodiana Strebler, 1908 has its type locality far south in the western Atlantic (Burdwood Bank, 53°45'S, 61°10'W), but it has also been recorded in the Antarctic Ocean (Engl, 2012; Zelaya, 2005). Only one species of the family has its type locality in Antarctic waters:

Omalogyra antarctica Egorova, 1991, pp. 66–67, table 1, figs 1,4,5,6,8 [Cosmonauts Sea]

Very few studies have explored the diversity of omalogyrids in the Indian and Pacific Oceans. Except for the seemingly widely distributed *A. japonica*, with records in Japan (Habe, 1972), Hawaii, Fanning Island (Kay &

Switzer, 1974), Papua New Guinea (Sleurs, 1985c), and the United Arab Emirates (Bosch *et al.*, 1995), most Indo-Pacific omalogyrids have not been treated subsequently to their original description and are thus only known from their type locality and immediate vicinities. Our treatment of *A. binodosa* Sleurs, 1985b, for example, comprises both the first published account of this species after the original description and the first record outside the Maldives.

Eighteen species of Omalogyridae have been recorded from the Indian and Pacific Oceans [regions of type localities in brackets]:

- Ammonicera angulata* Sleurs, 1985a, pp. 178–180, pl. 1, figs A–F [Papua New Guinea]
Ammonicera binodosa Sleurs, 1985b, pp. 25–26, figs 4,6,12,16,18 [Maldives]
Ammonicera chosenica Chernyshev, 2003, pp. 110–112, pl. 3, figs A–G [Sea of Japan]
Ammonicera extracarinaricostata Sleurs, 1985b, p. 20, figs 3,8,11 [Maldives]
Ammonicera japonica Habe, 1972, pp. 115–116, figs 1–4 [Japan]
Ammonicera mcleani **sp. nov.** [Baja California, Mexico]
Ammonicera mexicana **sp. nov.** [Jalisco, Mexico]
Ammonicera nodicarinata (Sleurs, 1985c), pp. 5–7, pl. 1, figs 4,5,7,10 [Papua New Guinea]
Ammonicera plicata Sleurs, 1985b, pp. 20–23, figs 2,7,10,13,14 [Maldives]
Ammonicera shornikovi Chernychev, 2003, pp. 109–110, pl. 2, figs A–D [Sea of Japan]
Ammonicera sleursi **sp. nov.** [California, U.S.A.]
Ammonicera sucina (Laseron, 1954), p. 17, figs 47,47a [Australia]
Ammonicera tenuicostata Sleurs, 1985b, pp. 23–25, figs 1,5,9,15,17 [Maldives]
Ammonicera vangoethemi (Sleurs, 1985c), pp. 7–8, pl. 1, figs 2,3,8 comb. nov. [Papua New Guinea]
Ammonicera vladivostokensis Chernyshev, 2003, pp. 107–109, pl. 1, figs C–F [Sea of Japan]
Omalogyra ammonitoides (Powell, 1940), pp. 236–237, pl. 29, figs 1,2 [New Zealand]
Omalogyra fusca Suter, 1908, p. 33, pl. 3, fig. 36 [New Zealand]
Omalogyra liliputia (Laseron, 1954), pp. 16–17, figs 45,45a [Australia]

According to Ponder & de Keyzer (1998), several species of Omalogyridae occur in Australia but only the two species redescribed herein, *A. sucina* and *O. liliputia*, have been named to date. Although Brazier in Henn & Brazier (1894) announced the first Australian record of the family at Green Point, Watson's Bay, Sydney, their *Homalogyra pulcherrima* Brazier in Henn & Brazier, 1894 proved to be a representative of the skeneid genus *Liotella* (see Laseron, 1958). Reported sperm data of "*Omalogyra* sp." from Australian waters by Healy (1988) were reinterpreted by that author as possibly belonging to a member of Architectonicoidea instead (Healy, 1993, p. 273).

Ammonicera mcleani **sp. nov.**, *A. mexicana* **sp. nov.**, and *A. sleursi* **sp. nov.** are the first omalogyrid species named for the Eastern Pacific coast of North America. In a book on intertidal invertebrates from Central California to Oregon, McLean (2007, p. 748, pl. 372, fig. B) provided a description and illustration of "*Omalogyra* sp.", which somewhat resembles *A. japonica*. Specimens of *Omalogyra* have been collected in the Eastern Pacific (e.g., LACM 77-29, Redondo Beach, Los Angeles County, California), and are in need of additional investigation.

Figure 8 summarises our knowledge of the distribution of omalogyrid species. The northern hemisphere sector of the Eastern Atlantic, including the North Sea, Madeira, Cape Verde and the Mediterranean, is by far the best known area, concentrating 216 of the 365 plotted records. Everywhere else, records are quite sparse and it seems obvious that future studies, particularly those focusing in large unexplored areas such as the Eastern Pacific coast of South America, Western Australia, and the East Coast of Africa are likely to reveal the presence of many omalogyrid species new to science.

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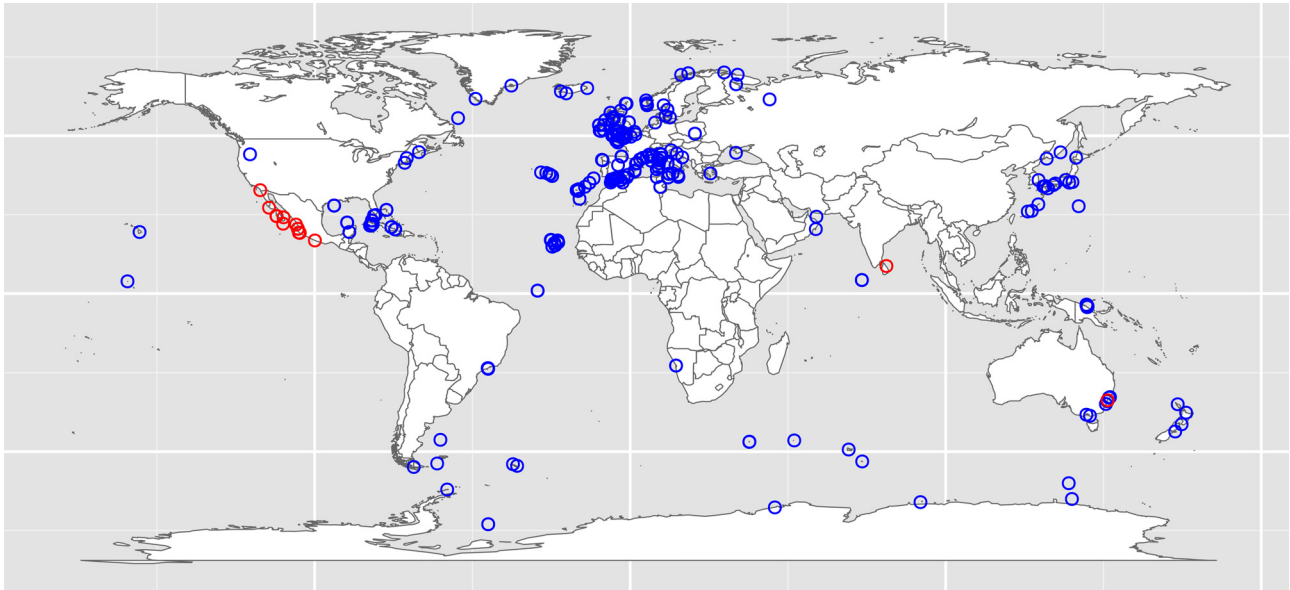


FIGURE 8. Records of specimens of the family Omalogyridae. Blue and red circles represent literature data and records presented in this paper, respectively. Coordinates were taken from literature sources whenever available, or translated from geographic names using the online services by Claus *et al.* (2014) and GeoNames (2014). Sources of records: Ávila (2003), Ávila & Azevedo (1997), Ávila, Cardigos, *et al.* (2004), Ávila, Santos, *et al.* (2005), Babio & Thiriôt-Quévieux (1974), Backeljau *et al.* (1984), Baeumler *et al.* (2008), Ballesteros *et al.* (1986), Baluk (1975), Beck *et al.* (2006), Bieler & Mikkelsen (1998), Borja (1987), Bosch *et al.* (1995), Bucquoy *et al.* (1882–1886), Bullock (1969), Buzzurro *et al.* (1999), Casellato & Stefanon (2008), Castellanos (1989), Chambers (2008), Chaster (1896), Chernyshev (2003), Cornet & Marche-Marchad (1951), Costa (1861), Dantart *et al.* (1990), Demir (2003), Egorova (1991), Engl (2012), Forbes & Hanley (1850–1853), Fretter (1948), Fretter & Graham (1978), Gaglini (1993), Giribet & Peñas (1997), Gofas (2011), Gofas & Warén (1998), Gordillo *et al.* (2005), Habe (1972), Habe & Tuchiya (1998), Harms (1993), Hasegawa (2000), Healy (1993), Jeffreys (1859a, 1867), Kay & Switzer (1974), Keats *et al.* (1999), Laseron (1954), Lima *et al.* (2011), Luque (1986), Marin & Ros (1987), Martins *et al.* (2009), McLean (2007), Monterosato (1869, 1884), Nordsieck (1972), Olabarria & Chapman (2001), Palazzi (1988), Peñas *et al.* (2006), Philippi (1841), Powell (1940, 1979), Redfern (2001), Revkov & Nikolaenko (2002), Rolán (1992a, b, 2005), Rolán *et al.* (2009), Sars (1878), Sasaki (2008), Segers *et al.* (2009), Simone (1997), Sleurs (1985a, b, c), Strebel (1908), Suter (1908), Thorsen (1941, 1944), Trigo Trigo & Otero Schmitt (1987), Tunnell *et al.* (2010), Vafiadis (2010, 2013), Vayssiére (1895), Warén (1991), and Zelaya (2005).

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