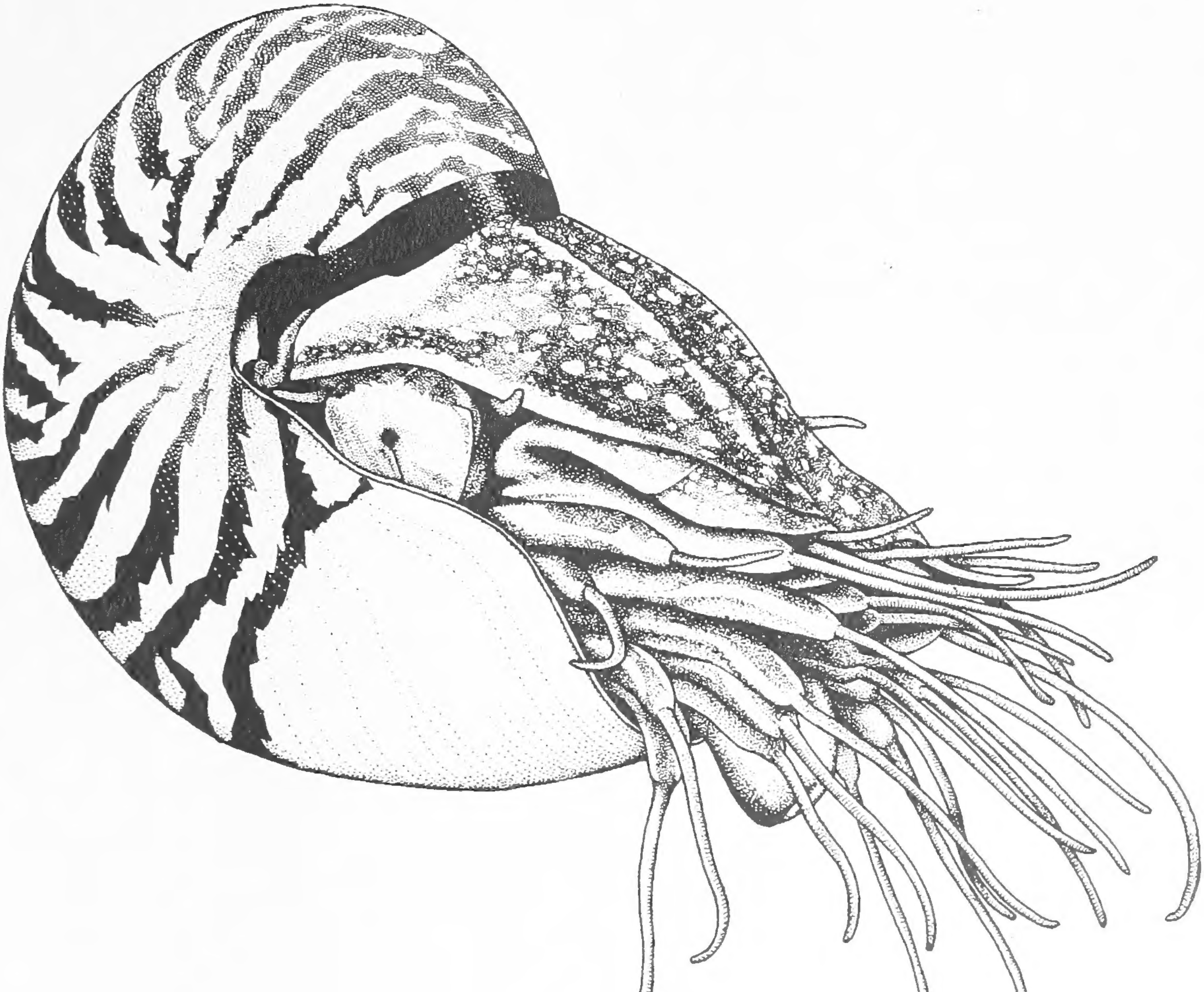
THE NAUTILUS

Volume 122, Number1
March 28, 2008
ISSN 0028-1344

A quarterly devoted
to malacology.



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The subscription rate per volume is US $47.00 for individuals, US $80.00 for institutions. Postage outside the United States is an additional US $10.00 for regular mail and US $25.00 for air delivery. All orders should be accompanied by payment and sent to: THE NAUTILUS, P.O. Box 1580, Sanibel, FL 33957, USA, (239) 395-2233.

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THE NAUTILUS (ISSN 0028-1344) is published quarterly by The Bailey-Matthews Shell Museum, 3075 Sanibel-Captiva Road, Sanibel, FL 33975.

Periodicals postage paid at Sanibel, FL, and additional mailing offices.

POSTMASTER: Send address changes to: THE NAUTILUS
P.O. Box 1580
Sanibel, FL 33957

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New species and new records of southwest Pacific Cancellariidae (Gastropoda)

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ABSTRACT

Fifteen species of Cancellariidae referable to the genera *Zeadmete*, *Admetula*, *Fusiaphera*, *Nipponaphera*, and *Trigonostoma* are reported from depths between 200 and 700 m in New Caledonia and other island groups in the southwest Pacific. Twelve are new species: *Zeadmete bathyomon* new species, *Zeadmete physomon* new species, *Zeadmete bilix* new species, *Admetula affluens* new species, *Admetula marshalli* new species, *Admetula bathynoma* new species, *Admetula lutea* new species, *Admetula emarginata* new species, *Nipponaphera argo* new species, *Nipponaphera agastor* new species, *Nipponaphera tuba* new species, and *Trigonostoma tryblium* new species. All the Recent nominal species of *Fusiaphera* described from localities throughout the Indo-Pacific area are considered to be conspecific, the senior name being *Fusiaphera macrospira* (Adams and Reeve, 1850), now with ten synonyms. The ranges of *Nipponaphera nodosivaricosa* (Petuch, 1979) and *Trigonostoma thysthlon* Petit and Harasewych, 1987, are extended to the South Pacific.

INTRODUCTION

The present paper is a continuation of our study of the deep-water cancellariid fauna of the Southwest Pacific, based on the material originating from recent expeditions in New Caledonia, Vanuatu, Fiji, Tonga, Wallis & Futuna, and the Solomon Islands. In a previous paper (Bouchet and Petit, 2002), we described the new genus *Mirandaphera* and nine new species in the genera *Africotriton*, *Merica*, *Sveltia*, and *Nipponaphera*. We here deal with 15 species (12 new) in the genera *Zeadmete*, *Admetula*, *Fusiaphera*, and *Trigonostoma*, and add further species in *Nipponaphera*. Our review of the deep-water cancellariid fauna so far sampled in the southwest Pacific will be complete after a third paper (in preparation) dealing with the genera *Brocchinia*, *Microcancilla*, and *Gergovia*. In addition, the cancellariid fauna of New Caledonia includes shallow-water to offshore species in the genera *Scalptia* (5 species) *Tritonoharpa* (several species), as well as the rediscovered endemic *Merica semperiana*, which we intend to deal with separately.

Cancellariid radulae are not known to provide discriminating species-level characters, and we thus did not attempt to systematically examine them when we had live-taken specimens available. Much of the material reported in this series was collected in the 1980–1990s and, at the time, fixed in formalin and then rinsed and dried. It is thus not adequate for nucleic-acid sequencing. More recent expeditions generate new material that is specifically put aside for barcoding. Our treatment of the cancellariid fauna is thus currently restricted to a description of the shells, including the protoconch, but we may expect that in the future it will be possible to test some of our species limits through molecular characters.

MATERIALS AND TEXT CONVENTIONS

In the lists of type and other material examined, individual lots in MNHN are unambiguously designated by the combination of cruise acronym (capitalized) and station number. DW (for Drague Warén) refers to dredge hauls, CP (for Chalut à Perche) to beam trawls; lv refers to live-taken specimens, dd to empty shells; spms to individuals that cannot be unambiguously assigned to one of these two categories (essentially commercially obtained specimens). Institutional acronyms are: AMNZ: Auckland Museum, Auckland, New Zealand; BMNH: The Natural History Museum, London, UK; DMNH: Delaware Museum of Natural History, Wilmington, Delaware, USA; MNHN : Museum National d'Histoire Naturelle, Paris, France; NM: Natal Museum, Pietermaritzburg, South Africa; NMW: National Museum of Wales, Cardiff, UK; NSMT: National Science Museum, Tokyo, Japan; USNM: National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; WAM: Western Australian Museum, Perth, Australia.

SYSTEMATICS

Family Cancellariidae Forbes and Hanley, 1851
Genus *Zeadmete* Finlay, 1926

Type Species: *Cancellaria trailli* Hutton, 1873, by original designation. Recent, New Zealand.

Discussion: The genus *Zeadmete* was proposed by Finlay (1926: 429) who later (1930b: 242) considered it to be a subgenus of *Oamaruia* Finlay, 1924 from the Lower Miocene of New Zealand. Powell (1979: 224) also treated *Zeadmete* as a subgenus of *Oamaruia*. However, Garrard (1975: 44) and Wilson (1994: 173) restored *Zeadmete* as a full genus, as did Petit and Harasewych (2000: 151), who gave a brief discussion of its possible relationship to other taxa. Among other differences, the type species of *Oamaruia*, *Admete suteri* Marshall and Murdoch, 1920, has strong columellar folds whereas *Zeadmete* has weak, almost obsolete, folds.

The genus *Zeadmete*, as interpreted here, occurs in the Miocene to Recent faunas of New Zealand and in the Recent faunas of South Africa, Fiji and New Caledonia (*Z. kulanda* Garrard, from Australia, is probably an *Iphinopsis*.) Expedition material in MNHN also contains an undescribed species from the Solomon Islands and another one from New Caledonia, both represented by specimens too imperfect to be named. All live offshore in 300–600 m, with New Zealand records as shallow as 65 meters.

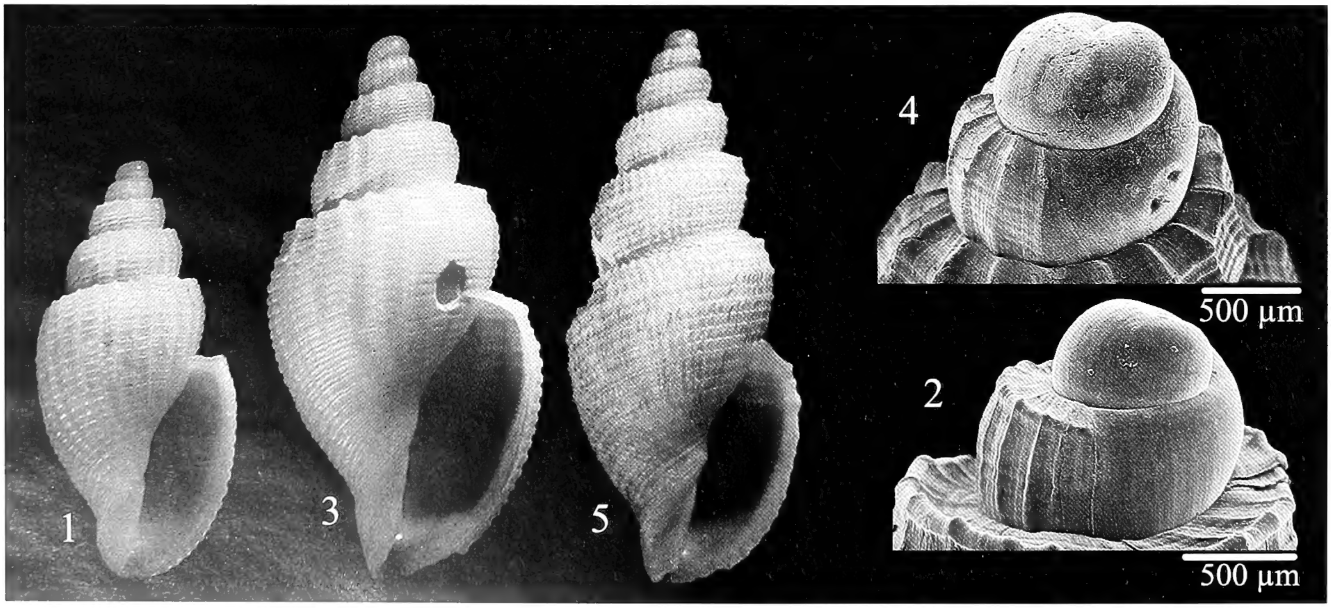
Zeadmete bathyomon new species
(Figures 1–2)

Description: Protoconch glassy, smooth, erect, of about 1.3 whorls, diameter 900 µm. Teleoconch of four whorls. Transition to teleoconch marked by a sharp growth line and a spiral cord forming shoulder angle, shortly followed by onset of weak but sharp axial ribs, forming small nodes at strengthening shoulder angle. Additional spiral cords appear before end of first teleoconch whorl. Shoulder angle prominent, bearing minute coronations formed by intersection of spiral cords and axial ribs. Sutural ramp strongly concave, bearing five to seven fine, low spiral cords. Suture attachment orthogonal. Shoulder raised, bearing three to five closely spaced spiral cords. About 20+ wider, low spiral cords anterior to shoulder angle, extending down onto base. Fine, low, evenly spaced axial ribs extending from shoulder angle to anterior end of shell; about 25 on last whorl; interspaces between axial ribs bearing closely packed fine growth lines. Low, narrow varices, formed only by a slight raising of shell surface, at about 120° increments on final whorls. Outer lip smooth, faintly sinuate adapically, curving back in prosocline direction abapically. Aperture elongate, narrowly elliptical, without lirations inside outer lip. Parietal area with very thin, narrow callus. Columella with three folds, the posterior two weak; anterior fold broad, situated on small siphonal fasciole, forming edge of inductural callus, which then forms edge of distinct siphonal canal. Exterior beige, rims of varices pale straw-yellow.

Type Material: Holotype MNHN 20498, 10.2 × 4.8 mm.

Type Locality: South of New Caledonia, 22°17′ S, 167°12′ E, 390 m [VAUBAN 1978–79: sta. 3].

Material Examined: Norfolk Ridge, south of New Caledonia.—VAUBAN 1978–79: sta. 3, 22°17′ S, 167°12′ E, 390 m, 1 lv (Figure 1).—BIOCAL: sta. DW77, 22°15′ S, 167°15′ E, 440 m, 1 dd.—BATHUS 2: sta. DW719, 22°48′ S, 167°16′ E, 444–445 m, 1 lv.—SMIB 8: sta. DW166, 23°38′ S, 167°43′ E, 433–450 m,



Figures 1–5. *Zeadmete*. **1–2.** *Zeadmete bathyomon* new species. **1.** Holotype, height 10.2 mm; New Caledonia, Norfolk Ridge, 22°17′ S, 167°12′ E, 390 m [*Vauban* 1978–79 sta. 3]. **2.** 23°38′ S, 167°43′ E, 433–450 m [SMIB 8 sta. DW166]. **3, 4.** *Zeadmete physomon* new species, holotype, height 13.1 mm, Fiji, 19°01′ S, 178°25′ E, 500–516 m [BORDAU 1 sta. DW1488]. **5.** *Zeadmete bilix* new species, holotype, height 13.2 mm;, New Caledonia, Norfolk Ridge, 23°02′ S, 168°16′ E, 335 m [SMIB 5 sta. DW98].

1 dd (Figure 2); Sta. DW167, 23°38′ S, 167°43′ E, 430–452 m, 1 dd.—NORFOLK 1: sta. DW1666, 23°42′ S, 167°44′ E, 469–860 m, 2 dd.—NORFOLK 2: sta. DW2024, 23°28′ S, 167°51′ E, 370–371 m, 1 dd.

Etymology: From the Greek *bathus*, deep, combined with *omos*, shoulder, for the deeply concave sutural ramp. To be treated as a noun in apposition.

Distribution: Known only from south of New Caledonia, alive in 390–444 m.

Remarks: In *Zeadmete finlayi* Powell, 1940, the shoulder is also raised but the sutural ramp is not concave. In *Z. bathyomon*, the shoulder is even with, or raised above, the suture. Also, *Z. finlayi* has clathrate sculpture only on the adapical half of the last whorl, whereas the last whorl is entirely clathrate in *Z. bathyomon*. The aperture is two-thirds of the shell height in *Z. finlayi*, but in *Z. bathyomon* the aperture is just over half the shell height.

The only other *Zeadmete* species we are aware of with a sutural ramp that does not slope abapically is an undescribed species represented by two broken, worn specimens from a nearby station on the Norfolk Ridge [BERYX 11: sta. DW35, 23°33′ S, 167°16′ E, 550–570 m], which we leave undescribed because of the poor condition of the specimens. It differs from *Z. bathyomon* in having a shorter spire and a flatter sutural ramp that is devoid of spiral cords. It also has a larger protoconch with a diameter of 1100 μm.

Zeadmete physomon new species
(Figures 3–4)

Description: Protoconch smooth, glossy, of 1.5 whorls, diameter 1250 μm. Transition to teleoconch marked by weak axial rib and faint spiral cords, both of which increase in strength rapidly. Teleoconch of four whorls, shell thin. Spiral cords flat, evenly spaced, with interspaces slightly narrower than cords, about five on sutural ramp and 20+ anterior to shoulder angle. Axial ribs extending from suture to anterior end of teleoconch, interspaces considerably broader than ribs; about 20 ribs on last whorl. Sutural ramp slightly convex, sloping up to impressed suture. Aperture elongate-elliptical, only weakly angulate at shoulder, smooth within. Outer lip sinuous adapically but becoming prosocline anterior to periphery. Parietal wash indistinct on holotype, distinct on one paratype. Columella almost vertical, bearing three folds, posterior fold on top of siphonal fasciole. Anterior folds callused, widely separated, anterior one almost obsolete, forming edge of short siphonal canal. Exterior cream with ill-defined pale brown band on periphery of spire whorls; some ribs on last whorl have brownish tint.

Type Material: Holotype MNHN 20519 (13.1 × 6.5 mm) and 6 paratypes MNHN 20520–20521.

Type Locality: Lau Ridge, Fiji, 19°01′ S, 178°25′ E, 500–516 m [BORDAU 1: sta. DW1488].

Material Examined: Fiji. BORDAU 1: sta. DW1486, 19°01′ S, 178°26′ E, 395–540 m, 1 dd paratype MNHN 20520.— Sta. DW1488, 19°01′ S, 178°25′ E, 500–516 m, 6 dd, holotype MNHN 20519, paratypes MNHN 20521 (Figures 3–4).

Etymology: From the Greek *physao*, inflated, and *omos*, shoulder, for the appearance of the sutural ramp. To be treated as a noun in apposition.

Distribution: Known only from Fiji at the two stations listed above.

Remarks: Protoconch diameter in paratypes ranges from 900 to 1300 μm. *Zeadmete physomon* differs from *Z. bathyomon* in having narrower spiral cords with wider interspaces, fewer, more widely spaced axial ribs, and a slightly convex rather than strongly concave sutural ramp. Also, in *Zeadmete physomon* the axial ribs remain distinct below the periphery.

Zeadmete bilix new species
(Figure 5)

Description: Protoconch prominent, smooth, glassy, of 1.1 whorls, diameter 875 μm. Transition to teleoconch marked by onset of axial ribs and spiral cords. Teleoconch high-spired, of five whorls. Spiral cords narrow, interspaces broader than cords. About three to four fine spiral cords on sutural ramp; eight cords anterior to shoulder angle on penultimate whorl. Last whorl with about 17 narrow spiral cords, one of which forms shoulder angle and another, only slightly more prominent than those adjacent, is just posterior to periphery, giving teleoconch a weakly biconic appearance. Axial ribs fine, spaced almost equal to spacing of spiral cords, rendering teleoconch surface evenly reticulate; about 55 on last whorl. Sutural ramp narrow. Aperture narrowly elliptic. Outer lip orthocline adapically, becoming prosocline only at anterior end. Columella almost straight, bearing three folds; adapical one on siphonal fasciole, other two on a broad heavy callus; anterior one obsolete, forming edge of short siphonal canal. Periostracum pale brown, shell pale straw yellow.

Type Material: Holotype (dd) MNHN 20499 (13.2 × 5.6 mm).

Type Locality: Norfolk Ridge, south of New Caledonia, 23°02′ S, 168°16′ E, 335 m [SMIB 5: sta. DW98].

Material Examined: Only known from the holotype (Figure 5).

Etymology: Latin adjective *bilix*, having a double thread, with reference to the two strong spiral cords around the shoulder angle.

Distribution: Known only from New Caledonia at the type locality.

Remarks: *Zeadmete bilix* is placed in *Zeadmete* based on its columellar structure, which is identical to that of other *Zeadmete* species, but it may be immediately distinguished from its congeners by its elongate shape and relatively short aperture.

Zeadmete bilix superficially resembles the buccinid genus *Iredalula* Finlay, 1926, but species of *Iredalula* have a recurved, notched siphonal canal and lack columellar folds.

Genus *Admetula* Cossmann, 1889

Type Species: *Buccinum evulsum* Solander, 1766, by original designation. Eocene, British Isles.

Discussion: *Admetula* is often placed in the synonymy of *Bonellitia* Jousseaume, 1887 (see discussions in Sacco, 1894: 42; Cossmann, 1899: 33; Davoli, 1982: 62; Verhecken, 1986: 33; but not Verhecken 2007: 286), but we regard *Bonellitia* as distinct, based on the angled whorls and muricated sculpture. We refer to Landau, Petit, and Marquet (2006) for further discussion. The genus *Admetula* is well represented in Paleogene and Neogene Tethyan faunas and in the Recent fauna along continental margins at depths ranging from 75–700 m (Petit and Harasewych, 1991: 181).

Many species of *Admetula* appear superficially very similar, especially based on published illustrations, yet can easily be distinguished when directly compared. Three discrete "subgroups" can be recognized in the genus. One consists of small attenuate species such as *A. cornidei* (Altimira, 1978), *A. epula* Petit and Harasewych, 1991, and *A. afra* Petit and Harasewych, 2000. Larger, wide, rather thin-shelled species such as *A. bayeri* Petit, 1976, and *A. emarginata* (described herein) form a second group, with a third, intermediate group composed of thick shells with an anterior constriction of the last whorl such as *A. vossi* Petit, 1976, and *A. deroyae* (Petit, 1970). Early Tertiary species usually have well-formed varices at irregular intervals, a feature not found on Recent species.

Admetula affluens new species
(Figures 6–8)

Description: Protoconch corroded on holotype, in other specimens consisting of 0.8 whorls, diameter 775 μm, shiny, smooth apically, with six raised threads on abapical part. Transition to teleoconch distinct, marked by onset of teleoconch sculpture. Teleoconch spire high, spire angle 47°; teleoconch consisting of 6.25 whorls, with sculpture of evenly spaced, narrow axial ribs crossed by spiral cords forming small nodes at intersections. About 15 axial ribs on penultimate whorl, about 18 on last whorl. About 12 primary spiral cords on last whorl, with spacing equal to that of axial ribs on shoulder and periphery, more crowded on base; four to seven secondary spiral cords in each interspace. Outer lip sharp, prosocline. Aperture without lirations. Parietal area with very thinly applied callus. Columella sloping, bearing two prominent folds extending to edge of inductural callus, with a third broad siphonal fold. Siphonal canal shallow, well defined. Exterior white with thick, pale olive-brown periostracum.

Type Material: Holotype MNHN 20500 (22.7 × 13.0 mm) and 4 paratypes MNHN 20501–20502.

Type Locality: SW of Malaita, Solomon Islands, 09°46′ S, 160°53′ E, 611–636 m [SALOMON 1: sta. CP1808].

Material Examined: Solomon Islands. SOLOMON 1: sta. CP1749, 09°21′ S, 159°56′ E, 582–594 m, 1 dd.—Sta. CP1750, 09°16′ S, 159°55′ E, 693–696 m, 1 dd.—Sta. CP1751, 09°10′ S, 159°53′ E, 749–799 m, 2 lv (1 paratype MNHN 20501).—Sta. CP1793, 09°13′ S, 160°08′ E, 505–510 m, 1 dd, 1 juv. dd (Figure 8).—Sta. CP1798, 09°21′ S, 160°29′ E, 513–564 m, 2 lv, 1 dd.—Sta. CP1808, 09°46′ S, 160°53′ E, 611–636 m, 1 lv (holotype, Figures 6–7).—Sta. CP1859, 09°33′ S, 160°37′ E, 283–305 m, 1 lv, 2 dd (3 paratypes MNHN 20502). Total of 13 specimens. (Largest specimen: 26.3 x 15.6 mm.)

Distribution: Known only from the Solomon Islands, alive in 305–749 m.

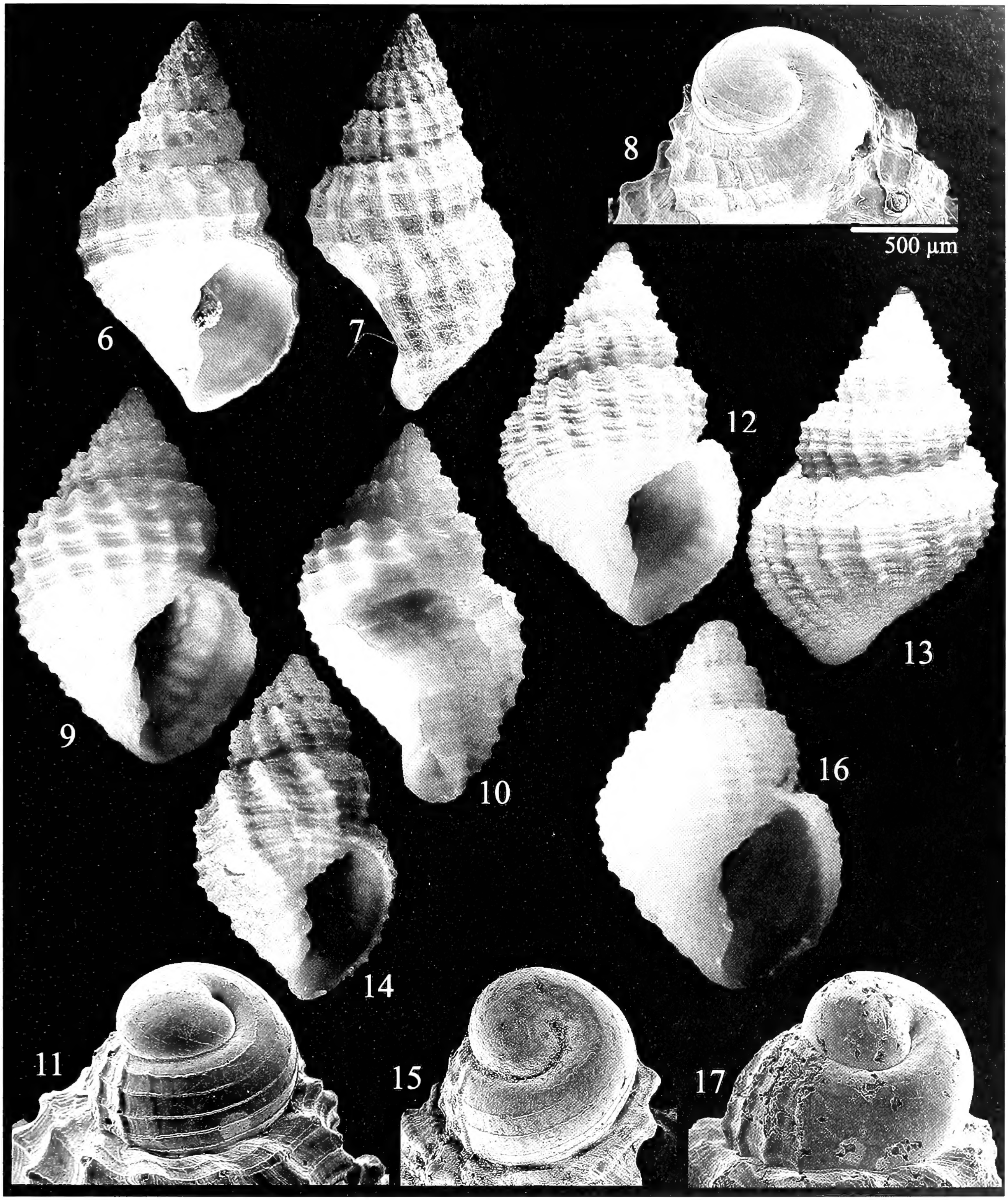
Etymology: From the Latin *affluens*, an adjective meaning abundant or copious, with reference both to its large size and relative abundance in the Solomon Archipelago.

Remarks: *Admetula affluens* superficially resembles the specimen figured as *A. garrardi* (Petit, 1974) by Hasegawa (2000: 585, pl. 291, figure 26) but differs by having narrower axial ribs, a more constricted base and a more twisted columella. It lacks the lirations within the outer lip that are present in *A. garrardi*. It is our opinion that the specimens figured as *A. garrardi* by Hasegawa (2000) and Verhecken (1997: 300, figs. 11–13) are not that species. Verhecken (1986: 34–35, figs. 1–2) examined, redescribed and figured the holotype of *A. garrardi* and explicitly described its multispiral protoconch whereas *A. affluens* has a paucispiral protoconch.

Of the other species of *Admetula* in the tropical southwest Pacific, *A. affluens* is more similar to *A. marshalli*, but differs by its larger adult size, less solid shell, much weaker spiral cords and lack of apertural lirations.

Admetula emarginata new species
(Figures 9–11)

Description: Protoconch glossy, white, of 1.1 whorls, diameter 1000 μm, with five widely spaced spiral cords. Transition to teleoconch indistinct, protoconch cords continuing as teleoconch cords. Teleoconch of five whorls, suture impressed, with sculpture of numerous prominent, well-defined axial ribs crossed by spiral cords forming small nodes at intersections. About 14 widely spaced axial ribs on penultimate whorl and about 12 on last whorl, final one enlarged into terminal varix. About eight primary spiral cords on last whorl, more closely spaced than axial ribs, with one or more secondary spirals in each interspace and about six prominent secondary spiral cords on spire whorls below rounded shoulder angle. Shell thin, axial ribs visible through last whorl.



Figures 6–17. *Admetula* **6–8.** *Admetula affluens* new species. **6–7.** Holotype, height 22.7 mm, Solomon Islands, 09°46S, 160°53′ E, 611–636 m, [SALOMON 1 sta. CP1808]. **8.** Protoconch, Solomon Islands, 09°13′ S, 160°08′ E, 505–510 m, [SALOMON 1 sta. CP1793]. **9–11.** *Admetula emarginata* new species. **9–10.** Holotype, height 16 mm, Coral Sea, 20°03′ S, 158°45′ E, 315 m [MUSORSTOM 5 sta. 335]. **11.** Protoconch, Coral Sea, 19°33.5′ S, 158°30.5′ E, 230 m [CORAIL 2 sta. D31]. **12–13.** *Admetula marshalli* new species, holotype, height 14.7 mm, Fiji, 16°39′ S, 179°57′ W, 591–596 m [BORDAU 1 sta. CP1396]. **14–15.** *Admetula lutea* new species. **14.** holotype, height 13.1 mm, Tonga, 21°19′ S, 175°01′ W, 225–233 m [BORDAU 2 sta. DW1521]. **15.** Protoconch, Fiji, 18°09′ S, 178°39′ W, 290–300 m [BORDAU 1 sta. DW1465]. **16–17.** *Admetula bathynoma* new species. **16.** Holotype, height 7.4 mm, New Caledonia, 22°52′ S, 167°23′ E, 590–600 m [MUSORSTOM 4 sta. DW225]. **17.** Protoconch, New Caledonia, 22°52′ S, 167°16′ E, 530–541 m [BATHUS 2 sta. DW720]. All protoconchs at the same scale, scale bar 500 µm

Outer lip prosocline, sinuous, with everted stromboid notch just anterior to periphery and another everted notch near base. Aperture with nine lirations, visible internally at level of terminal varix, not extending to edge of lip or deeply into aperture. Parietal area with very thinly applied callus. Columella sloping, with two prominent folds extending to edge of inductural callus and a third broad siphonal fold. Siphonal canal shallow, well defined. Shell white, with weakly defined bands of pale brown at shoulder and base, also brown behind outer lip.

Type Material: Holotype MNHN 20503 (16.0 × 10.9 mm) and one paratype MNHN 20504.

Type Locality: Coral Sea, 20°03′ S, 158°45′ E, 315 m [MUSORSTOM 5: sta. 335].

Material Examined: Coral Sea. CHALCAL: sta. D31, 19°33.5′ S, 158°30.5′ E, 230 m, 1 dd (paratype, Figure 11).—MUSORSTOM 5: sta. 335, 20°03′ S, 158°45′ E, 315 m, 1 dd (holotype, Figure 9–10).—EBISCO: sta. CP2571, 20°25′ S, 158°45′ E, 298–309 m, 1 dd.

Etymology: From the Latin *emarginatus* after the sinuous, everted outer lip.

Distribution: Known only from the Coral Sea near the Chesterfield Islands, empty shells in 230–315 m.

Remarks: *Admetula emarginata* differs from other described species of *Admetula* in having diffused coloration. It is much like *A. bayeri* Petit, 1976, from the western Gulf of Mexico in having at the periphery a notch, which is not present in the similar species *A. bathynoma*. *Admetula emarginata* also differs from *A. bathynoma* in having less closely spaced spiral cords and axial ribs. The overall effect of the sculpture on *A. emarginata* is a striking pattern of horizontal rectangles crossed by fine spirals.

Admetula marshalli new species
(Figures 12–13)

Description: Protoconch glossy, brown, of one whorl, diameter 825 μm, with three widely spaced spiral cords. Transition to teleoconch marked by a change in color and onset of axial ribs. Teleoconch of 5.5 whorls. Suture impressed. Spiral cords closely spaced, about 14 primary cords on last whorl with one secondary cord in most interspaces, forming small pointed beads where they cross axial ribs. One spiral cord creates a modest angle between periphery and narrowly rounded shoulder. About 14 rounded axial ribs on last whorl, only final one enlarged into a varix. Fine, densely packed growth lines on entire teleoconch. Outer lip thin, very indistinctly notched just anterior to periphery and with a slight eversion of the siphonal canal. Aperture with nine lirations, visible interior to terminal varix but not extending deeply within aperture or to outer lip. Parietal area with thin but distinct callus. Columella concave, bearing three distinct folds that extend out to edge of inductural callus. Posterior fold largest, separated from central fold by a deep depression; two anterior folds form a shelf bordering short, broad siphonal canal. Shell white, periostracum yellow-brown.

Type Material: Holotype MNHN 20505 (14.7 × 9.0 mm) and 2 paratypes (all dd) MNHN 20506 (largest paratype: 17.0 × 9.7 mm).

Type Locality: Fiji, Lau Ridge, 16°39′ S, 179°57′ W, 591–596 m, [BORDAU 1: sta. CP1396].

Material Examined: Only known from the type material.

Distribution: Known only from the Lau Ridge in Fiji, empty shells in 591–596 m.

Etymology: Named after Bruce Marshall (Museum of New Zealand, Wellington), in appreciation for the standards of his descriptions and illustrations of the molluscan fauna of New Zealand.

Remarks: The New Zealand species *A. superstes* (Finlay, 1930b) is similar in shape and size, but differs in having a translucent white rather than brown protoconch with numerous fine, close spiral threads (versus 3 widely spaced cords), in having weaker axial costae on the teleoconch, in lacking a terminal varix and internal lirations behind the apertural rim at maturity, and in that secondary spiral sculpture is considerably weaker or entirely absent. Additionally, *A. superstes* has a much more strongly developed periostracum, with prominent spines at the summits of the axial lamellae. *Admetula superstes* is endemic to northern New Zealand, living on muddy substrata in 79–550 m off the northeastern (northernmost record at 35°08′ S) and southwestern North Island. A similar species (possibly a local variant) occurs off Three Kings Islands. There is no material of similar species from Norfolk Ridge south of Norfolk Island in NMNZ.

Admetula lutea new species
(Figures 14–15)

Description: Protoconch glassy, of slightly more than one whorl, diameter 975 μm, worn but with traces of spiral cords visible on terminal portion. Transition to teleoconch rather indistinct. Teleoconch of about 4.7 whorls. Whorl profile regularly convex; suture impressed. Sculpture of prominent prosocline axial ribs crossed by weaker spiral cords; about nine to ten axial ribs on last whorl, eleven on penultimate whorl, some forming irregularly placed varices; four primary spiral cords on penultimate whorl and about 12 on last whorl, with one to four secondary spirals in each interspace; spiral cords forming elongate nodes where they cross axial ribs. Outer lip with very indistinct lirations, visible internally at level of terminal varix, not extending either to edge of lip or deeply within aperture. Parietal area with thin callus. Inductura almost vertical. Columella bearing three folds; narrow anterior fold forming edge of short, recurved siphonal canal. Exterior yellow-brown. Periostracum thin, with low incremental lamellae and hairy projections on spiral cords.

Type Material: Holotype MNHN 20507 (13.1 × 7.8 mm) and one paratype MNHN 20508.

Type Locality: Tonga, 21°19′ S, 175°01′ W, 225–233 m [BORDAU 2: sta. DW1521].

Material Examined: Fiji. BORDAU 1: sta. DW1465, 18°09′ S, 178°39′ W, 290–300 m, 2 dd.—Tonga. BORDAU 2: sta. DW 1521, 21°19′ S, 175°01′ W, 225–233 m, 1 dd (holotype, Figure 14).—Sta. CP1576, 19°42′ S, 174°18′ W, 253–263 m, 1 dd (paratype, Figure 15).

Etymology: From the Latin adjective *luteus*, meaning yellow, in reference to the color of the shell.

Distribution: Known only from Fiji and Tonga at localities cited above.

Remarks: This new species differs from its congeners by its strongly prosocline axial ribs forming irregularly placed varices and its spiral sculpture with numerous secondary cords. It is also distinguished from other *Admetula* species by its yellow color.

A specimen of *Admetula lutea* new species in the Petit collection (No. 2872) is said to be from 50–200 m north of Taiwan, but this is a dealer's locality designation that needs to be confirmed.

Admetula bathynoma new species
(Figures 16–17)

Description: Protoconch glassy, white, smooth, of one whorl, diameter 975 μm. Transition to teleoconch marked by onset of axial ribs and spiral cords. Teleoconch of about four whorls. Last whorl bearing about ten to 14 rounded axial ribs, crossed by prominent spiral cords, about five to six cords on spire whorls and about ten on last whorl, with fine secondary spirals in the interspaces. Final axial rib enlarged into a varix. Small nodes formed at intersections where spiral cords cross axial ribs. Sutural ramp narrow, almost flat; suture slightly impressed. Outer lip prosocline, rounded, smooth, without lirations within. Parietal area without wash or callus. Columella slightly inclined, bearing two prominent folds extending out to edge of inductural callus; a third descending fold forming edge of short siphonal canal. No siphonal fasciole. Last whorl well rounded. Shell white.

Type material: Holotype MNHN 20509 (7.4 × 5.0 mm) and one paratype MNHN 20510.

Type locality: Norfolk Ridge, south of New Caledonia, 22°52′ S, 167°23′ E, 590–600 m [MUSORSTOM 4: sta. DW225].

Material examined: Norfolk Ridge. BIOCAL: sta. DW46, 22°53′ S, 167°17′ E, 570–610 m, 1 dd (paratype).—MUSORSTOM 4: sta. DW225, 22°52′ S, 167°23′ E, 590–600 m, 1 lv (holotype, Figure 16).—SMIB 8: sta. DW193-196, 22°59′–23°00′ S, 168°21′–168°23′ E, 491–558 m, 1 juv. dd.—BATHUS 2: sta. DW720, 22°52′ S, 167°16′ E, 530–541 m, 1 juv. dd (Figure 17).

Distribution: Known only from the Norfolk Ridge, in 491–610 m.

Etymology: From the Greek *bathus*, deep, and *nomos*, place of living, treated as an adjective.

Remarks: *Admetula bathynoma* resembles a juvenile *A. marshalli* but differs by being proportionally narrower, with less convex whorls and a larger protoconch (diameter 975–1000 μm versus 825 μm in *A. marshalli*). *Admetula marshalli* also differs in having pointed beads rather than small nodes formed at the intersections of the axial ribs and spiral cords.

Kohn and Arua (1999: pl. 13, fig. 55) illustrated as *C. atopodonta* Petit and Harasewych, 1986 an 8 mm high specimen of *Admetula* from the Early Pleistocene of Viti Levu, Fiji. Their specimen closely resembles the present species except that the Fiji fossil has lirations within the aperture.

Genus *Fusiaphera* Habe, 1961

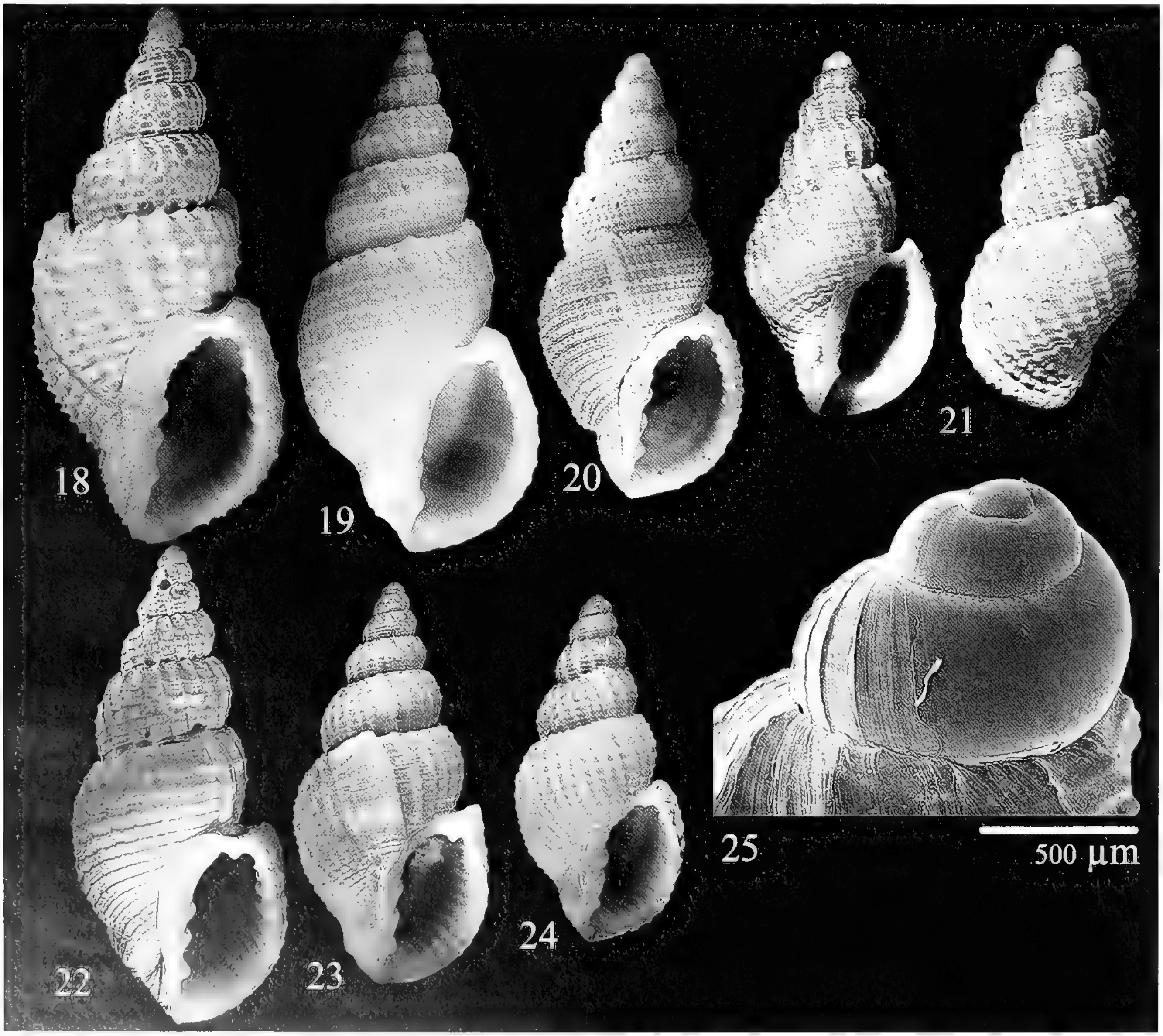
Type Species: *Cancellaria macrospira* Adams and Reeve, 1850, fixed herein to comply with ICZN Article 70.3. Recent, Japan.

Discussion: Habe (1961a) proposed the genus *Fusiaphera* for a species he identified as *Cancellaria macrospira* Adams and Reeve. Later in the same year, he (Habe 1961b) considered the species he had identified as *C. macrospira* to be a different species, which he then named *Fusiaphera macrospiratoides* Habe, 1961. The fact that the type species of *Fusiaphera* was based on a misidentified type species was noted by Verhecken (1986: 35), who stated that there is some confusion in the matter of the type species but did not make a definitive statement about the resolution of the problem. He did list, however, *Fusiaphera macrospira* (Adams and Reeve) as type species, as did Beu and Maxwell (1987: 55), who then stated "but misidentified?, ?really = *Fusiaphera macrospiratoides* Habe, 1961." The confusion is demonstrated by the fact that Matsukuma, Okutani and Habe (1991: 179, pl. 111, fig. 2) figured the type specimen of *F. macrospiratoides* under the name *F. macrospira*. In the absence of a definitive statement by Verhecken and the queries used by Beu and Maxwell, it appears to be necessary to fix a type species to comply with Article 70.3. *Cancellaria macrospira* Adams and Reeve is here selected as the type species of *Fusiaphera* Habe, 1961.

Fusiaphera is distinguished by a slender, nonumbilicate teleoconch with irregular varices and a thick outer lip with a well-defined posterior canal under the shoulder. The aperture is much like that of *Scalptia* but with a straighter columella. The genus *Fusiaphera* ranges from South Africa across the Indian Ocean, north to Japan, to Australia, New Caledonia and Fiji. It thus appears to be restricted to the Indo-Pacific area with the earliest known occurrence in the Miocene of Australia. Darragh (1970: 168) referred the Australian Miocene species *Cancellaria epidromiformis* Tate, 1889 and *C. exaltata* Tate, 1889, to *Fusiaphera*, a placement accepted by Maxwell (1992: 166). However, three New Zealand Eocene species, *Uxia (?) marshalli* Allan, 1926, *Uxia naroniformis* Finlay, 1930, and *Fusiaphera jenkinsi* Maxwell, 1992, placed in *Fusiaphera* by Beu and Maxwell (1990) and Maxwell (1992), are not considered by us to be correctly placed. Also, *Plesiotriton paytensis* Olsson, 1930, from the Eocene of Peru, was tentatively placed in *Fusiaphera* by Beu and Maxwell (1987: 55) but it is here excluded from the genus. It is possible that a new genus will have to be erected to contain these Eocene taxa. Many European Tertiary species of *Unitas* resemble *Fusiaphera* in form but they lack a strongly delineated posterior canal.

Fusiaphera macrospira (Adams and Reeve, 1850)
(Figures 18–25)

Cancellaria macrospira Adams and Reeve, 1850: 41, pl. 10, fig. 2.
Cancellaria wilmeri G. B. Sowerby II, 1881: 637, pl. 56, fig. 2.
Cancellaria pallida E. A. Smith, 1899: 313, text-fig. 4.
Cancellaria producta G. B. Sowerby III, 1903: 220, pl. 4, fig. 5.
Cancellaria (Trigonostoma) luscinia Melvill and Standen, 1903: 319, pl. 23, figs. 14–15.
Cancellaria exquisita Preston, 1905: 3, pl. 1, fig. 9.
Cancellaria tosaensis Habe, 1961a: 72, Appendix 28, pl. 35, fig. 21.



Figures 18–25. *Fusiaphera macrospira* (Adams and Reeve, 1850). **18.** Height 20.2 mm, Philippines, Balicasag I., said to be from 130–230 m. **19.** Height 30.1 mm, Japan, Mikawa. **20.** *macrospiratoides* form, height 16.2 mm, Mikawa Issiki, Japan. **21.** Holotype of *Cancellaria wilmeri* (BMNH 1881.5.20.30), height 11.8 mm. **22.** *tosaensis* form, height 20.4 mm, Minabe, Japan. **23.** Height 15.0 mm, New Caledonia, 19°35′ S, 163°25′ E, 48 m [LAGON sta. 1192]. **24, 25.** Height 11.0 mm, New Caledonia, 19°06′ S, 163°10′ E, 50 m [LAGON sta. 542].

Cancellaria azumai Habe, 1961a: 72, Appendix 28, pl. 35, fig. 20.
Cancellaria macrospiratoides Habe, 1961b: 433, pl. 23, fig. 10; pl. 24, fig. 10.
Fusiaphera dampierensis Garrard, 1975: 17, pl. 2, fig. 8.
Fusiaphera eva Petit, 1980: 215, figs. 5, 6.

Type Data: *F. macrospira*, China Sea, BMNH 1969347, lectotype designated by Verhecken (1986: 36); illustrated by Higo, Callomon and Goto (2001: 99).

C. wilmeri, Port Blair, Andaman Islands, holotype BMNH 1881.5.20.30, herein Fig. 21.
C. pallida, 25 fms, off Bonaparte Archipelago, NW Australia, holotype BMNH 1891.11.21.96.
C. producta, 40 fms, off mouth of Umhloti River, Natal, syntypes BMNH 1903.7.27.76; SAM–A339 (Giles and Gosliner, 1983: 28).
C. (T.) luscinia, 40 fms, Arabian Sea, 18°58′ N, 71°45′ E, syntypes BMNH 1903.12.15.101–102 (2 syntypes); NMW 1955.158.408.
C. exquisita, Ceylon, holotype BMNH 1905.10.4.75.
C. tosaensis, Kochi Prefecture, Shikoku, Japan, holotype NSMT-Mo 13287; illustrated by Higo, Callomon and Goto (2001: 99).
C. macrospiratoides, Aiki Prefecture, Honshu, Japan, holotype NSMT-Mo 39781; illustrated by Higo, Callomon and Goto (2001: 99).
C. azumai, Aiki Prefecture, Honshu, Japan, NSMT-Mo 13285a (illustrated by Higo, Callomon and Goto 2001: 99) is labeled as type in NSMT but is not the figured specimen and is smaller than dimensions given for holotype.
F. dampierensis, Delambre Island, Dampier Archipelago, northwestern Australia, holotype WAM 550-71.
F. eva, west of central Bazaruto Island, southern Mozambique, holotype NM G4896.

Description: Protoconch smooth, glassy, of two whorls with small initial nucleus, diameter 1000–1125 μm, indicating planktotrophic larval development. Transition to teleoconch marked by sharp axial rib followed by additional ribs and cords. Teleoconch slender, of about 6 whorls. Axial ribs variable in number, 15 to 20 on last whorl of most specimens, extending adapically over slightly channeled sutural ramp to suture. Some ribs forming varices at irregular intervals, others projecting slightly above ramp. Spiral sculpture of fine cords, about 15 on last whorl of most specimens, with weaker secondary cords in most interspaces. Cords form small nodules where they intersect axial ribs. Aperture narrowly ovate. Outer lip thickened into a varix, with about 14–16 strong lirae that do not descend deeply into aperture. Internal liration beneath sutural ramp forms edge of well-defined posterior canal. Parietal shield thin but well developed, with pustules on its outer edge. Columella with three folds, anterior one forming edge of short siphonal canal. Last whorl slightly constricted at base behind weak siphonal fasciole. Exterior brown or white. Many brown specimens with a weak band of white just below periphery and white on the adapical ends of ribs and projections extending above the shoulder.

Material Examined: **Japan**. Off Mikawa, 30 fms, 1 spm (figured by Abbott and Dance, 1982).—Mikawa Isiki, Aichi Pref., 50–70 m, 1 spm (Figure 20).—Off Minabe, Wakayama Pref., 80–100 m, 2 spms (Figure 22).—Off Minabe, 100–200 m, 1 spm.—Off Mikawa, 50 fms, 1 spm (Figure 19).—Off Tosa, 50 fms, 1 spm.—"Japan", 1 spm.—"Japan?", 1 spm (gift from Habe with "*azumai*" in his hand).—Mikawa Bay, 50 m, 1 spm.—Off Mikawa, 40 fms, 1 spm.—Enshu Kei, 2 spms. East China Sea. "180 m", 1 spm. Taiwan. Off Keelung, 50–110 m, 2 spms.—Off Keelung, 100–200 m, 5 spms.—Off SW Taiwan, 1 spm.—Off Keelung, "deep water", 1 spm.—Off SW Taiwan, 60 fms, 1 spm. Philippines. Off Aliguay Island, Mindanao, "240 m", 2 spms.—Off Aliguay Island, "80–120 m", 1 spm.—Off Balicasag Island, "240 m", 1 spm.—Off Balicasag, "130–230 m", 1 spm (Figure 18).—MUSORSTOM 3: sta. DR140, 11°43′ N, 122°34′ E, 93–99 m, 1 dd; Sta. CP 141, 11°45′ N, 122°45′ E, 40–44 m, 1 dd. Vietnam. no locality, "50 m", 1 spm. Indonesia. Masalembo, Java, *ca.* 20 fms, 1 spm. (All above in Petit collection). Solomons. SOLOMON 1: sta. DW1760, 8°47′ S, 160°01′ E, 172–179 m, 1 dd. Coral Sea. CHALCAL sta. D11, 20°31′ S, 161°06′ E, 83 m, 1 dd. New Caledonia. LAGON: sta. 375, 22°32′ S, 167°08′ E, 67–71 m, 1 dd; Sta. 517, 19°09′ S, 163°35′ E, 42 m, 2 dd; Sta. 542, 10°06′ S, 163°10′ E, 50 m, 3 lv (Figures 24–25); Sta. 1129, 19°29′ S, 163°49′ E, 40m, 3 lv, 2 dd; Sta. 1163, 19°11′ S, 163°22′ E, 48m, 2 dd; Sta. 1168, 19°16′ S, 163°09′ E, 50 m, 1 lv; Sta. 1192, 19°35′ S, 163°25′ E, 48m, 1 lv, 1 dd (Figure 23).—MUSORSTOM 4: sta. DW151, 19°07′ S, 163°22′ E, 200 m, 1 dd. Fiji. SUVA2: sta. DW44, Viti Levu, 17°51.7′ S, 177°13′ E, 33 m, 1 dd.

Dimensions: 19.3 × 8.4 mm (Coral Sea, CHALCAL sta. D11), 17.9 × 8.3 mm (New Caledonia, LAGON sta. 1192), 14.8 × 7.3 (New Caledonia, LAGON sta. 1192), 30.2 × 14.0 mm (Japan).

Distribution: Natal, Mozambique, Arabian Sea, Angrias Bank, India, Ceylon, Andaman Islands, northwest Australia, Japan (from Izu Peninsula and Yamaguchi Pref. southwards), Taiwan, the Philippines, Vietnam, Indonesia, Solomon Islands, Queensland, Australia, New Caledonia and Fiji. Offshore from 20 to *ca.* 250 m.

Remarks: Of the eleven nominal species that we include under *Fusiaphera macrospira*, two have type localities in the southwest Indian Ocean, one in the Arabian Sea, two in the Bay of Bengal, two off northwestern Australia, one off Borneo and three off Japan. We have examined representative material from Japan, Taiwan, the Philippines and New Caledonia and fail to recognize more than one species. All specimens have in common a naticoid multispiral protoconch indicating planktotrophic development and we interpret the different names as individual rather than geographical variants, connected by intermediates. Of these, the nominal species *F. macrospiratoides* represents a form where the axial and spiral sculpture are of equal prominence, whereas *F. tosaensis* represents a form with much stronger axial sculpture. Hasegawa (2000: 585) was of the same opinion when he stated that "[*F. macrospiratoides*] and other related species, such as *F. azumai* Habe, 1961 and *F. tosaensis* Habe, 1961 may be intraspecific forms of *F. macrospira* (Adams and Reeve, 1850)." We did not examine extensive material from the Indian Ocean but published descriptions and illustrations suggest that the nominal species from this area also fall within the range of variation of *F. macrospira*. Specimens from northwestern Australia described by Garrard (1975: 17–19) are, however, distinctly smaller with average heights of 10.5 mm to 14 mm.

Genus *Nipponaphera* Habe, 1961

Type species: *Nipponaphera habei* Petit, 1972 by ICZN Opinion 1052; Recent, Japan.

Discussion: Species of *Nipponaphera* have the angled outline of *Trigonostoma* but are less tabulate, have only a small umbilicus if one is present, and have a different columellar morphology. The genus has been utilized primarily to include species having an angled last whorl, a triangular aperture, and three columellar folds. Here we also place in *Nipponaphera* species with a rounded last whorl and rounded aperture, but which are united with those taxa traditionally included in the genus by the peculiar columellar morphology consisting of two anterior columellar folds situated on a slightly raised shelf, much like a widely bifurcate single fold.

The genus *Misteia* Janssen, 1984, from the Miocene of The Netherlands, is similar in outline to the angled species of *Nipponaphera*, but has only two weak folds on the columella.

Axelella Petit, 1988 (a replacement name for the preoccupied *Olssonella* Petit, 1970) has been considered to be confined to the Americas (Petit, 1970: 84; 1972: 104). What appears to be a neat division of genera between the Americas (*Axelella*) and the Indo-Pacific (*Nipponaphera*) is blurred by the enigmatic species *Cancellaria agalma* Melvill and Standen, 1901, from the Gulf of Oman, a species that appears to possess the characters of *Axelella*. Despite that species, which has not been studied in detail, it is our opinion that the similarities between *Axelella* and *Nipponaphera* are superficial and that they can be separated by their columellar morphology.

Recent species of *Nipponaphera* have previously been known from South Africa to the northwestern Indian Ocean, eastward to the Philippines and north to Japan. The range is now extended to New Caledonia. In addition to the species treated by Bouchet and Petit (2002), we now include in *Nipponaphera* the following: *N. semipellucida* (Adams and Reeve, 1850) [described in *Cancellaria*; previously placed in *Cancellaria* by Habe (1961b) and other Japanese authors]; *N. teramachii* (Habe, 1961) [described in *Trigonaphera*, placed in *Scalptia* and *Trigonostoma* by various authors; placed in *Nipponaphera* by Habe (1961a: pl. 36, fig. 4) on the plate caption although in the text it is placed in *Trigonaphera*]; *N. nodosivaricosa* (Petuch, 1979) [described in *Agatrix* (*Olssonella*), placed in *Nipponaphera* by Bouchet and Petit (2002)]; *N. quasilla* (Petit, 1987), new combination [described in *Cancellaria*], *N. kastoroae* (Verhecken, 1997) new combination, and *N. suduirauti* (Verhecken, 1999) new combination [the last two described in *Axelella*].

The fossil record has not been completely searched for *Nipponaphera* but we have recognized *Cancellaria chinenensis* MacNeil, 1961 of the Okinawa Pliocene and *C. yonabaruensis* MacNeil, 1961 of the Okinawa Miocene as belonging here. Also, Oyama, Hirose and Nishimoto (1995) described the new species *Nipponaphera taguchii* from the Miocene of Japan and at the same time transferred *Cancellaria sendoi* Hatai, 1941, to the genus *Nipponaphera*.

Nipponaphera nodosivaricosa (Petuch, 1979)
(Figures 26–29)

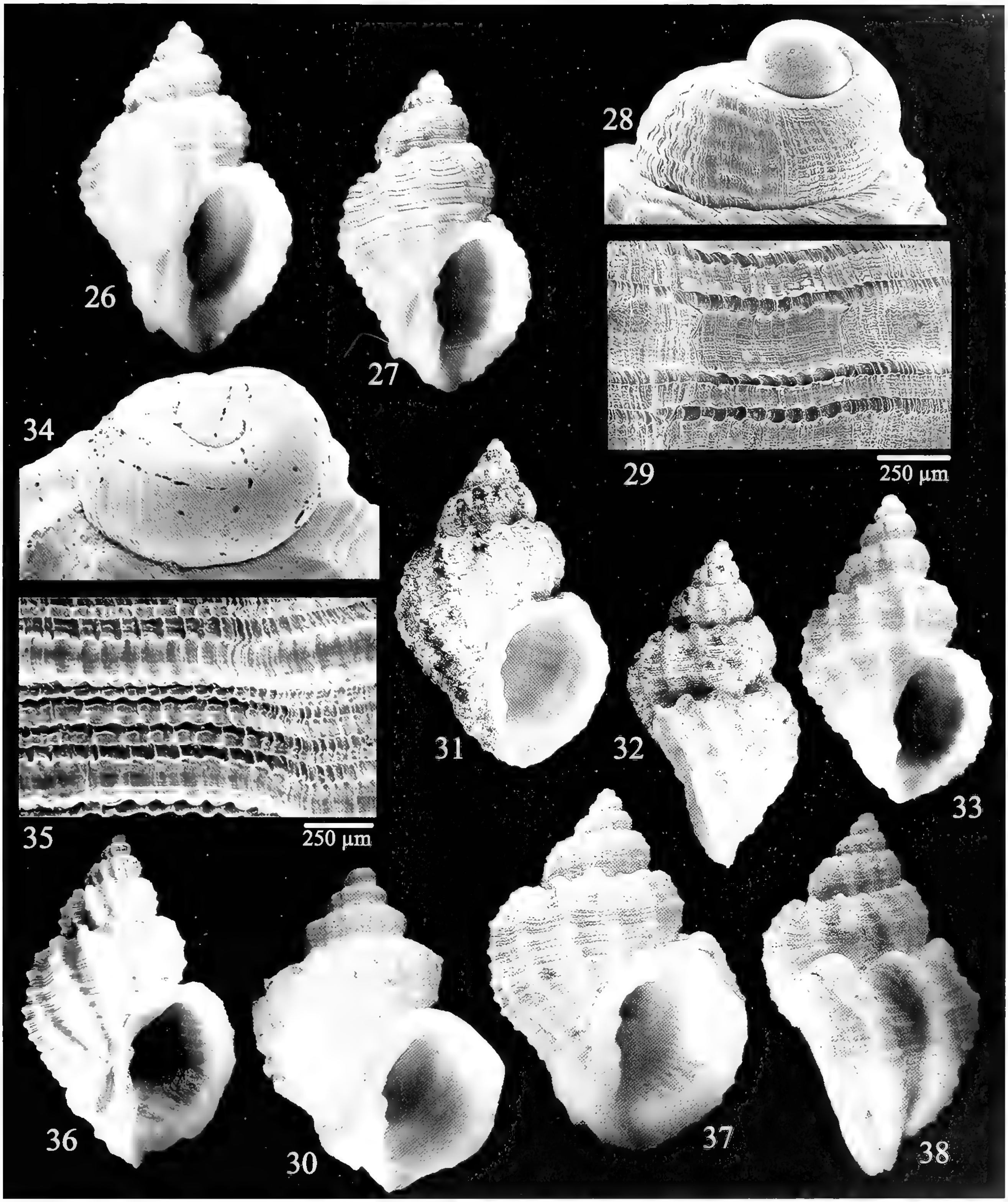
Agatrix (Olssonella) nodosivaricosa Petuch, 1979: 11, figs. 26, 27.

Description: Protoconch pale brown, of about one to 1.2 whorls with fine spiral sculpture on final third. Transition to teleoconch marked by prominent axial rib followed by onset of wide, rounded spiral cords and weak, poorly defined axial ribs. Teleoconch of 3.5 to 4.2 rounded whorls. Spiral sculpture of 12 to 15 rounded primary spiral cords, with weaker secondary cords in each interspace; about six primary cords on penultimate whorl. Primary and secondary cords all bear extremely fine spiral threads. Axial sculpture of eight to 12 prominent, elevated ribs on last whorl, more numerous on earlier whorls; final one or two ribs becoming wider, forming varices. Spiral cords and interspaces crossed by fine, closely spaced growth lines, giving surface a linen-like appearance under low magnification. Suture impressed, sutural ramp convex. Aperture elongate, rounded. Last whorl slightly constricted behind siphonal fasciole. Outer lip only slightly prosocline, edge thin. Interior of outer lip with ten to 14 strong lirations extending deeply into aperture. Stromboid notch manifested by very slight indentation in outer lip. No parietal callus; some specimens with a thin wash on parietal area. Inductural area covered with thin callus, which extends back over chink-like umbilicus. Columella with three folds, posterior one most prominent, almost perpendicular to axis; two anterior folds sharply descending, situated on ends of u-shaped platform, anterior-most one forming edge of short but well-defined siphonal canal. Exterior cream to pale yellow-brown, many specimens with irregular markings; most specimens with two or three white spiral cords at periphery of last whorl, with two or three dark brown cords above and below.

Type Material: Holotype (11 × 9 mm, *fide* Petuch; 12.9 × 8.2 mm, *fide* Verhecken), DMNH 126397.

Type Locality: Off Balicasag Island, Philippines, from 300 m depth.

Material Examined: New Caledonia. BATHUS 1: sta. DW672, 20°48′ S, 165°21′ E, 347–366 m, 1 lv (Fig-



Figures 26–38. *Nipponaphera.* **26–29.** *Nipponaphera nodosivaricosa* (Petuch, 1979). **26.** Height 16.9 mm, New Caledonia 20°17′ S, 163°50′ E, 500–600 m [BATHUS 4 sta. DW898]. **27.** Height 17.0 mm, New Caledonia, 20°48′ S, 165°21′ E, 347–366 m [BATHUS 1 sta. DW672]. **28.** Protoconch, 21°45′ S, 166°37′ E, 250 m [BATHUS 1 sta. CP713]. **29.** Teleoconch microsculpture same specimen as 28, same scale. **30.** *Nipponaphera argo* new species, holotype, height 8.6 mm, Coral Sea, 22°48′ S, 159°24′ E, 450 m [MUSORSTOM 5 sta. 300]. **31–36.** *Nipponaphera agastor* new species 31–32, holotype, height 19.3 mm, Solomon Islands, 9°21′ S, 160°24′ E, 357–359m [SOLOMON 1 sta. CP1800]. **33.** Height 12.4 mm, Fiji, 19°52′ S, 174°40′ W, 383–393 m [BORDAU 1 sta. CP1561]. **34.** protoconch, Vanuatu, 20°20′ S, 169°49′ E, 400–440 m [MUSORSTOM 8 sta. CP963]. **35.** Teleoconch microsculpture same specimen as 34, same scale. **36.** Height 17.9 mm, Philippines, 11°01′ N, 124°04′ E, 214–246 m [MUSORSTOM 3 sta. CP145. **37–38.** *Nipponaphera tuba* new species, holotype, height 20.7 mm, Vanuatu, 15°10′ S, 167°14′ E, 394–421 m [MUSORSTOM 8 sta. CP1087

ure 27), 1 dd.—Sta. CP713, 21°45′ S, 166°37′ E, 250 m, 1 lv (Figures 28–29). BATHUS 2: sta. DW717, 22°44′ S, 167°17′ E, 350–393 m, 1 lv. BATHUS 4: sta. CP897, 20°16′ S, 163°52′ E, 305–350 m, 1 lv.—Sta. DW898, 20°17′ S, 163°50′ E, 500–600 m, 1 dd (Figure. 26).—Sta. DW901, 19°03′S, 163°15′ E, 297 m, 1 dd.—Sta. CP905, 19°02′ S, 163°16′ E, 294–296 m, 1 lv.— Solomon Islands. SOLOMON 1: sta. CP1801, 9°25′ S, 160°26′ E, 264–273m, 1 lv. (Dimensions of largest New Caledonia specimen: 18.5 × 11.6 mm.)

Distribution: At this time *Nipponaphera nodosivaricosa* is known only from New Caledonia, the Solomons and the Philippines (Springsteen and Leobrera, 1986; Verhecken, 1999). The Indonesian specimen figured as *Axelella* cf. *nodosivaricosa* by Verhecken (1997: 299, figs. 5–7) was not attributed by him in his 1999 work to either *N. nodosivaricosa* or *N. suduirauti* (see below). In the New Caledonian dredgings, live specimens were taken from depths of 250–393 m and empty shells from as deep as 600 m.

Remarks: Verhecken (1999) described the species *Axelella suduirauti*, here placed in *Nipponaphera*, distinguished from *N. nodosivaricosa* based on protoconch characteristics. It was stated that *N. suduirauti* has a multispiral protoconch as opposed to the paucispiral protoconch of *N. nodosivaricosa*. Our specimen of *N. nodosivaricosa* from the Solomon Islands has a protoconch that is difficult to attribute to one or the other of the two species and we believe that the separation between *N. nodosivaricosa* and *N. suduirauti* should be reevaluated, perhaps using molecular characters. We refer to Verhecken's (1999) work for his discussion on the question.

Nipponaphera argo new species
(Figure 30)

Description: Protoconch smooth, of 1.1 whorls, diameter 1050 μm. Teleoconch of about 3.1 whorls, high-spired. Whorl profile angulated at shoulder. Sculpture of low, broad axial ribs and much finer spiral cords of rather even strength, except for one on sutural ramp and two at periphery of last whorl, which are more prominent than others; 14 axial ribs on penultimate whorl, seven on last whorl (specimen with severe growth scar and regrowth, distorting sculpture of last whorl); about 15 spiral cords on penultimate whorl and about 35 on last whorl, crossed by thin incremental riblets. Suture shallowly impressed. Last whorl slightly constricted behind siphonal fasciole. Outer lip thin, sharp, smooth within, lacking lirae. Inner lip with well-developed parietal shield, extending slightly over narrow umbilicus. Columella only slightly concave, with three folds; anterior two close together, much like one large bifurcate fold. Siphonal canal short, indistinct. Exterior uniformly very pale yellowish-white.

Type material: Holotype MNHN 20511 (8.6 × 6.5 mm) and one paratype MNHN 20512

Type Locality: Argo Bank, Coral Sea, 22°48′ S, 159°24′ E, 450 m [MUSORSTOM 5, sta. 300].

Material Examined: Coral Sea. MUSORSTOM 5, sta. 299, 22°48′ S, 159°24′ E, 360–390 m, 1 dd (paratype).—Sta. 300, 22°48′ S, 159°24′ E, 450 m, 1 dd (holotype, Figure 30).

Etymology: Named for the Argo Seamount, a prominent topographic feature of the Coral Sea, from which the specimens were collected; to be treated as a noun in apposition.

Distribution: Coral Sea (Argo Seamount), dead in 390–450 m.

Remarks: *Nipponaphera argo* differs from *N. goniata* Bouchet and Petit, 2002 by its sculpture of broad, low, non-lamellar axial ribs. Also, the spiral cords of *N. argo* are of more even strength, except for one on the shoulder and two on the periphery, which imparts a slightly biangular aspect to shells of this species.

Nipponaphera agastor new species
(Figures 31–36)

Description: Protoconch normally smooth, corroded on holotype, of 0.9 whorls, diameter 800 μm. Protoconch/teleoconch boundary indistinct due to corrosion, but distinctly marked by onset of teleoconch sculpture on specimens from Vanuatu. Teleoconch of five rounded whorls; spire angle 64°; suture deeply impressed. Axial sculpture of prominent, regularly spaced ribs, eleven on last whorl, eleven on penultimate whorl. Ribs rounded over steep, narrow sutural ramp. Spiral sculpture of evenly spaced, prominent spiral cords, eight on penultimate whorl, 13 on last whorl, with three to five secondary cords in each interspace; spiral cords rise over axial ribs, forming small nodules on primary cords at intersections. Numerous fine growth lines cross spiral cords, creating small imbrications. Last whorl slightly constricted behind siphonal fasciole. Outer lip prosocline. Inner margin of lip smooth apart from 16 prominent lirae extending into aperture; two indistinct lirae on parietal area. Columellar callus well developed, forming shield over chink-like umbilicus. Columella with three almost equal folds; anterior one sloping sharply down at edge of small but distinct siphonal canal, which recurves abaxially. Exterior chalky white.

Type Material: Holotype 20513 (19.3 x 12.3 mm) and 4 paratypes MNHN 20514.

Type Locality: Between Guadalcanal and Florida Island, Solomon Islands, 9°21′ S, 160°24′ E, 357–359 m [SOLOMON 1: sta. CP1800].

Material Examined: Vanuatu. MUSORSTOM 8: sta. CP963, 20°20′ S, 169°49′ E, 400–440 m, 1 lv (Figures 34–35).—Tonga. BORDAU 2: sta. CP 1561, 19°52′ S, 174°40′ W, 383–393 m, 1 dd (Figure 33).—Solomons. SOLOMON 1: sta. CP1746, 09°23′ S, 159°57′ E, 302–396 m, 1 dd; Sta. CP1800, 9°21′ S, 160°24′ E, 357–

359m, 4 lv, 1 dd (holotype, Figures 31–32, and paratypes).—Philippines. MUSORSTOM 3: sta. CP145, 11°01′ N, 124°04′ E, 214–246 m, 1 dd (Figure 36).—Punta Engaño, tangle nets, approximately 60 fins, 1 spm.

Etymology: From the Greek *agastor*, a noun in apposition, meaning near kinsman or brother, to highlight the similarity to *N. nodosivaricosa*.

Distribution: Only known from the material examined: Philippines, Solomons, Vanuatu and Tonga. Depth range in the southwest Pacific 360–400 m; in the Philippines possibly shallower.

Remarks: Specimens from the Philippines and the Solomons are distinctly larger with adult sizes ranging from 16.8 mm to 19.5 mm, whereas specimens from Vanuatu and Tonga are much smaller with adult sizes at 12.2 mm and 12.3 mm respectively.

Nipponaphera agastor is sympatric with *N. nodosivaricosa* in the Philippines and the Solomon Islands but differs by its spiral sculpture with more numerous (3 to 5) secondary cords, not separated by an incised groove as in *N. nodosivaricosa*. It differs from *N. tuba*, with which it is sympatric in Vanuatu, by being more slender and lacking a stromboid notch.

Nipponaphera tuba new species
(Figures 37–38)

Description: Protoconch smooth, of 0.9 whorls, diameter 800 μm. Protoconch/teleoconch boundary distinctly marked by onset of teleoconch sculpture. Teleoconch of five rounded whorls; spire angle 75°; suture deeply impressed. Axial sculpture of prominent, regularly spaced ribs, ten on last whorl, 14 on penultimate whorl; ribs rounded on steep, narrow sutural ramp. Spiral sculpture of evenly spaced cords of several strengths; primary cords evenly separated by one secondary cord, resulting interspaces filled with two or three tertiary cords; spiral cords rising over axial ribs, forming small nodules on primary spiral cords at intersections. Numerous fine growth lines cross spiral cords, creating small imbrications. Last whorl slightly constricted behind siphonal fasciole. Outer lip prosocline, with distinct stromboid notch adapical to center of lip. Inner margin of lip smooth or slightly crenulate, with 19 prominent lirae extending into aperture, four additional lirae beneath sutural ramp. Columellar callus well developed, forming shield over chink-like umbilicus. Columella with three almost equal folds, anterior one sloping sharply down at edge of small but distinct siphonal canal, which recurves abaxially. Exterior yellow-brown with a band of white below periphery, bordered by indistinct bands of darker brown.

Type Material: Holotype MNHN 20516 (20.7 × 15.0 mm) and one paratype MNHN 20517.

Type Locality: Vanuatu, 15°10′ S, 167°14′ E, 394–421 m [MUSORSTOM 8: sta. CP1087].

Material Examined: Vanuatu. MUSORSTOM 8: sta. CP1087, 15°10′ S, 167°14′ E, 394–421 m, 1 lv, 1 dd (holotype, Figures 37–38, and paratype).— Sta. [no data, mixed lot], 1 dd.

Etymology: From the Latin *tuba*, a war trumpet, which this new species can, with some imagination, be reminiscent of; used as a noun in apposition.

Distribution: Known only from Vanuatu.

Remarks: *Nipponaphera tuba* differs from *N. cyphoma* Bouchet and Petit, 2002 in being more rounded and robust. Also, the spiral sculpture never appears as incised lines as in *N. cyphoma* and *N. nodosivaricosa*. *Nipponaphera tuba* also has a thick outer lip that is not present in *N. cyphoma*.

Genus *Trigonostoma* Blainville, 1827

Trigona Perry, 1811: pl. 51. Type species: *Trigona pellucida* Perry, 1811, by monotypy. Not *Trigona* Jurine, 1807 (Hymenoptera).

Trigonostoma Blainville, 1827: 652. Type species: *Delphinula trigonostoma* Lamarck, 1822 (?= *Buccinum scalare* Gmelin, 1791), by monotypy. Recent, Indo-Pacific.

Remarks: *Trigonostoma* has a different taxonomic composition for various authors. We here use *Trigonostoma sensu lato* to encompass the nominal genera *Ventrilia* Jousseaume, 1887, *Arizelostoma* Iredale, 1936, *Ovilia* Jousseame, 1887, and *Extractrix* Korobkov, 1955. We do not include *Scalptia* Jousseaume, 1887, *Trigonaphera* Iredale, 1936 and *Cancellaphera* Iredale, 1930, which are sometimes treated as subgenera of *Trigonostoma*.

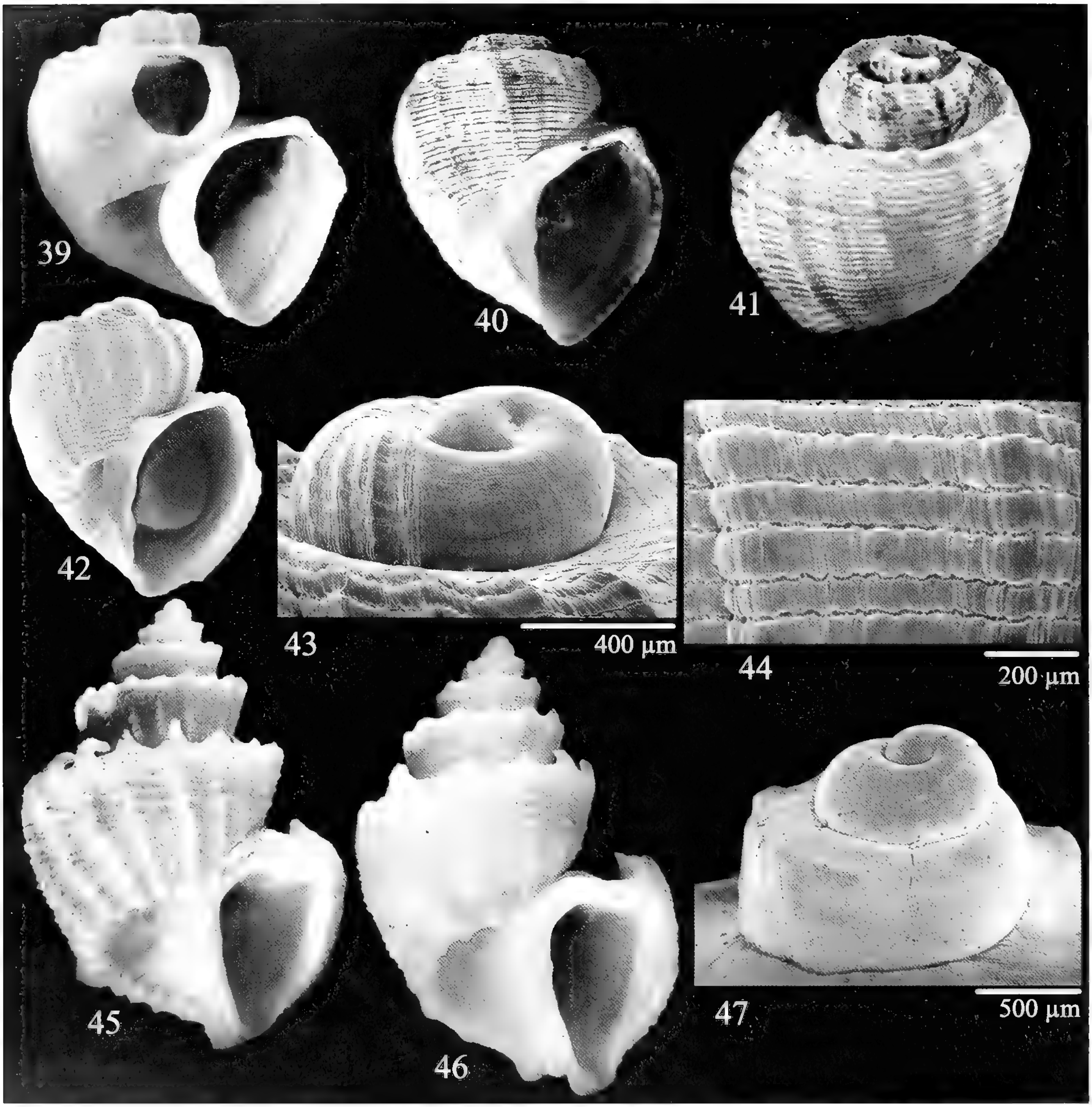
Trigonostoma tryblium new species
(Figures 39–44)

Description: Protoconch smooth, glassy, of one whorl, diameter 1050 μm. Transition from protoconch to teleoconch abrupt, denoted by onset of axial and spiral sculpture. Teleoconch of 2.5 whorls; spire depressed; umbilicus broad. First teleoconch whorl with 16 axial ribs. Second whorl with about 18 axial ribs that have become somewhat obsolete. Spiral sculpture of broad, closely spaced cords with narrow interspaces; about seven to ten spiral cords on sutural ramp and 25 between shoulder angle and umbilical rim. Sutural ramp weakly concave, but forming deeply channeled shoulder between shoulder angle and impressed suture. Aperture narrowly ovate. Outer lip smooth. Inner lip forming parietal shield, partly covering deep, wide umbilicus. Columella with two descending folds. Anterior canal not constricted. Holotype exterior chalky white, with two broad, ill-defined brown bands, best seen through shell.

Type Material: Holotype MNHN 20518 (7.0 × 6.5 mm).

Type Locality: North of Makira Island, Solomon Islands, 10°13′ S, 161°29′ E, 381–383 m [SOLOMON 1: sta. CP1837].

Material Examined: Taiwan. TAIWAN 2000, sta. DW36, 21°54.8 N, 120°36.2 E, 305 m, Bashi Channel, 1



Figures 39–47. *Trigonostoma*. **39–44.** *Trigonostoma tryblium* new species. **39.** Height 8.3 mm, Taiwan, Bashi Channel, 21°54.8′ N, 120°36.2′ E, 305 m [TAIWAN 2000 sta. DW36]. **40–41.** Holotype, height 7.0 mm, Solomon Islands, 10°13′ S, 161°29′ E, 381–383 m [SOLOMON 1 sta. CP1837]. **42.** Height 5.0 mm; New Caledonia, 23°03′ S, 166°58′ E, 397–400 m [BATHUS 2, sta. DW730]. **43–44.** Protoconch and teleoconch microsculpture, same specimen as 42. **45–47.** *Trigonostoma thysthlon* Petit and Harasewych, 1987. **45.** Height 16.9 mm, New Caledonia, 22°47′ S, 167°28′ E, 241–245 m [BATHUS 2 sta. CP728]. **46.** Height 15.0 mm, Fiji, 16°50.1′ S, 178°12.5′ E, 200–215 m [MUSORSTOM 10: sta. DW1333]. **47.** Protoconch, New Caledonia, 22°43′ S, 167°16′ E, 300 m [SMIB 1 sta. DW6].

dd (Figure 39). Solomons. SOLOMON 1: sta. CP1837, 10°13′ S, 161°29′ E, 381–383 m, 1 lv (holotype, Figures 40–41). New Caledonia. BIOCAL Sta. DW77, 22°15′ S, 167°15′ E, 440 m, 1 juv. lv.—BATHUS 2, sta. DW730, 23°03′ S, 166°58′ E, 397–400 m, 1 juv. dd (Figures 42–44).

Etymology: From the Latin *tryblium*, meaning cup, a shape that the new species is somewhat reminiscent of; used as a noun in apposition.

Distribution: Known only from Taiwan, New Caledonia and the Solomons. Alive in 383–440 m; empty shells from 305 m.

Remarks: Of the known Recent species of *Trigonostoma*, *Trigonostoma tryblium* resembles only *T. semidisjuncta* (Sowerby, 1849) in having primarily spiral sculpture. It differs from that species in being more depressed, with a broader umbilicus. In *T. semidusjuncta* there is no spiral sculpture on the sutural ramp. Also, the spiral sculpture of *T. semidisjuncta* is arranged in groups of cords separated by wide furrows.

Trigonostoma thysthlon Petit and Harasewych, 1987 (Figures 45–47)

Trigonostoma thysthlon Petit and Harasewych, 1987: 79, figs. 5, 8–13.

Trigonostoma antiquata—Habe, 1961a: 435, pl. 24, fig. 14; pl. 23, fig. 8; 1961b: 73, pl. 36, fig. 8; Lan, 1979: 95, pl. 41, figs. 93, 93a; Abbott and Dance, 1982: 299 (second figure in bottom row); Habe and Okutani, 1985: 233 (second figure in bottom row); Bosch, et al., 1995: 157, fig. 687. [not *Cancellaria antiquata* Hinds, 1843]

Trigonostoma antiquatum—Oyama and Takemura, 1963: *Trigonaphera* (2) plate, fig. 5. [not *Cancellaria antiquata* Hinds, 1843]

Trigonostama (sic) thysthlon—Hasegawa, 2000: 581, pl. 290, fig. 11.

Type Material: Holotype, USNM 747301 (17.3 × 12.7 mm).

Type Locality: Off west coast of Wasir Island, West Wokam, Aru, Moluccas (5°30′ S, 134°12′ E) in 56–73 m.

Material Examined: New Caledonia. LAGON: sta. 387, 22°39′ S, 167°07′ E, 225 m, 1 dd.—SMIB 1: sta. DW6, 22°43′ S, 167°16′ E, 300 m, 1 dd (Figure 47).—BATHUS 2: sta. CP728, 22°47′ S, 167°28′ E, 241–245 m, 1 lv (Figure 45).—Dredged at "300–400 m", off Belep, north New Caledonia, 1 spm. Fiji. MUSORSTOM 10:sta. DW1333, 16°50.4′ S, 178°12.5′ E, 200–215 m, 1 dd (Figure 46). Solomons. SOLOMON 1: sta. DW1850, 10°28′ S, 161°59′ E, 139–261 m, 1 lv.

Description (of a specimen from New Caledonia): Protoconch smooth, glassy, of 1.8 whorls, diameter 1050 μm. Transition to teleoconch marked by axial rib followed by both axial and spiral sculpture and flattening of the sutural ramp. Teleoconch of up to six tabulate whorls. Sutural ramp flat, bordered by cord-like shoulder angle. Suture impressed. Axial ribs prominent, extending from suture across ramp, over shoulder angle, where they form recurved spines on many specimens, down and over siphonal fasciole, then inside umbilicus. Shoulder spines not formed on all ribs, but many ribs lacking spines form short, sloping buttress against preceding whorl; about 12–15 ribs on last whorl, more numerous on earlier whorls; two thick, closely spaced ribs mark end of growth in adults; a few varix-like rib occurs earlier on some specimens. Fine, closely packed growth lines of varying number in axial interspaces slightly overlap each other, producing a scabrous appearance. Spiral sculpture of very closely spaced cords, rising over ribs to form small nodes. Sutural ramp with about 12–15 spiral cords of uniform prominence; about 15 primary spiral cords on last whorl between shoulder angle and siphonal fasciole; about ten fine secondary cords in each interspace. Spiral cords of equal strength continue inside umbilicus. Outer lip slightly prosocline. Outer lip thickened by varix, slightly serrate on margin, interior with eight to ten short irregular lirae, not extending quite to outer edge of lip and not extending deeply into aperture. Aperture triangular, with small posterior notch under sutural ramp. Posterior portion of inner lip adpressed against siphonal fasciole and anterior quarter of penultimate whorl. Inner lip with two descending folds, posterior one slightly larger than anterior; third incipient fold present in some specimens. Umbilicus extends to protoconch. Siphonal canal short. Exterior white with very faint orange-brown at shoulder. Specimens over 24 mm in height are known.

Distribution: Gulf of Oman to the Moluccas, Japan, the Philippines, Solomon Islands, New Caledonia and Fiji.

Remarks: The imbricate sculpture resulting from the overlap of growth lines, which is so noticeable on the New Caledonian specimens, is absent from *T. antiquatum* and is much less evident on *T. thysthlon* from other areas. However, we do not consider this difference to be of taxonomic significance. This sculpture is a prominent feature of *T. scalare* (Gmelin, 1791), the type of the genus but that species has a more angular shape and its whorls are barely attached.

ACKNOWLEDGMENTS

We thank Bertrand Richer de Forges, the indefatigable companion of the first author on many expeditions, for his skill and determination in exploring the deep-water benthos of the tropical Pacific. Ahmed Abdou did SEM illustrations of protoconchs and microsculpture; Delphine Brabant and Philippe Maestrati did the digital photography and plate assembling. Bruce Marshall helped us interpret our material of *Admetula* from Fiji. Alan Beu helped us improve the manuscript by tracking internal inconsistencies.

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On some Neogene to Recent species related to *Galeodina* Monterosato, 1884, *Galeodinopsis* Sacco, 1895, and *Massotia* Bucquoy, Dautzenberg, and Dollfus, 1884 (Caenogastropoda: Rissoidae) with the description of two new *Alvania* species from the Mediterranean Pleistocene

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ABSTRACT

Six species, related to the subgenera *Galeodina*, *Galeodinopsis*, and *Massotia*, are re-analyzed. *Alvania francescoi* new species (SE Sicily) and *A. rosariae* new species (SE Sicily and NW Peloponnesus) are described from Mediterranean Pleistocene. *Galeodinopsis* is regarded as the appropriate genus for Oligocene-Recent taxa having a quite conical shell close to that of some *Alvania* species and showing *Manzonia*-like combination of two microsculptural characters: the pitted surface on the spiral cords and the arrangement of the roughly prismatic elements forming numerous and very fine spiral threads. Its type species, *Rissoa tiberiana* (previously known from Mediterranean Mio-Pliocene), lives along the tropical W African coasts, where it is known under the name *A. fariai*. As suggested by the oldest record of *Galeodinopsis*, the European Oligocene *Rissoa duboisi*, this genus very likely originated from a pre-Neogene *Alvania* group. The syntype of *Rissoa prusi*, a scarcely known species (Pleistocene of Rhodes), and material (also from type locality) of the almost unknown *R. cingulata* (from Sicily) and of its close relative, *R. tenera* (Mediterranean, Atlantic Morocco and Canary Islands), is shown. These three taxa and the type species of *Galeodina* and *Massotia*, are here tentatively considered as belonging to *Alvania* sensu lato. With the exception of *A. cingulata*, all the discussed species have a multispiral protoconch. Generally, the protoconchs studied exhibit a sculptural pattern known in other rissoid taxa. Protoconch I of the type species of *Massotia*, *A. lactea*, is characterized by a coarser sculpture

Additional Keywords Rissoidae, taxonomy, Mediterranean-W Atlantic, Neogene-Recent, new species

INTRODUCTION

The genus *Alvania* Risso, 1826, comprises one of the most diversified groups in the caenogastropod family Rissoidae, especially when considering the tropical eastern Atlantic and the Mediterranean provinces. They inhabit a large variety of environments, from littoral to bathyal, and their geographical distribution is extensive, including the Mediterranean, Atlantic, Indo-Pacific, and the temperate Australian coasts (Ponder, 1985). Their stratigraphical distribution might extend back to the Late Cretaceous, but the first well-established records date to the early Tertiary (Ponder, 1985). With regard to the rich Mediterranean and European Tertiary *Alvania* assemblages, some of the most informative analyses are those of Sacco (1895), Seguenza (1903), Cossmann (1921), Lozouet (1998), Kowalke and Harzhauser (2004), and Chirli (2006).

Many authorities, e.g. Monterosato (1884), Bucquoy et al. (1884), Weinkauff (1885), Kobelt (1888), Locard (1886), Nordsieck (1968, 1972), Jeffreys (1867, 1869), Pallary (1920), Wenz (1938), Warén (1973, 1974), Gofas and Warén (1982), Van Aartsen (1982a, 1982b), Moolenbeek and Hoenselaar (1989, 1998), Van der Linden and Wagner (1989), Moolenbeek et al. (1991), Van der Linden (1993), Bouchet and Warén (1993), Giannuzzi-Savelli et al. (1996), Palazzi (1997), Gofas (1999), Ávila (2000), and Arduino and Arduino (2001), have contributed to the knowledge of the rich Recent Eastern Atlantic (especially the W Africa and the Macaronesian Province) and Mediterranean fauna. Ponder's rissoid revision (1985), listing five *Alvania* subgenera, provided additional perspective to the taxonomy.

My attention is focused here on a relatively large, informal group of species of *Alvania* sensu lato characterized by shells with wide and ovate aperture, lacking an internal denticulation of the outer lip, and often bearing varices on a well-developed, inflated body whorl. These species have been historically assigned to the subgenera *Galeodina* Monterosato, 1884, *Galeodinopsis* Sacco, 1895, and *Massotia* Bucquoy et al., 1884. This subgeneric settlement was partially rejected by Ponder (1985), who modifying the systematic arrangement of Monterosato (1884) and Bucquoy et al. (1884), stated that grouping of the numerous species of *Alvania* was very difficult at the subgenus level. The same author included *Massotia* (type species: *Rissoa lactea* Michaud, 1830) and *Galeodinopsis* (type species: *R. tiberiana* Coppi, 1876) in the *Alvania* sensu stricto group and doubtfully considered *Galeodina* (type species *Turbo carinatus* Da Costa, 1778) as a valid subgenus on the basis of shell characters. Piani (1979) raised *Galeodina* to generic level and placed *Rissoa cingulata* Philippi, 1836, and *R. tenera* Philippi, 1844, therein.

The principal aim of this work is to provide, for the first time, as complete as possible a taxonomic dataset based on shell features. Species such as *Rissoa cingulata*, [often misidentified as *Alvania carinata* (Da Costa, 1778)], *R. prusi* Fischer, 1877, and *R. tiberiana* Coppi, 1876, are very poorly known or, in the case of the last taxon, the generic attribution to *Alvania* appears incorrect. I also describe two new species from the Pleistocene of the central Mediterranean area.

MATERIALS AND METHODS

Most of the examined material, all consisting of shells, is housed in the Muséum National d'Histoire Naturelle, Paris (Département Systématique et Evolution), in the private collections of Maurizio Forli (Prato, Italy) and of Stefano Palazzi (Modena, Italy). Remaining material is housed in the private collections of medshells.com (made available by Nino Adorni Sbrana, Grosseto, Italy), Stefano Rufini (Anguillara), in the Museum für Naturkunde (Humboldt University, Berlin), the Museo Geologico G.G. Gemmellaro and the Dipartimento di Geologia e Geodesia (both University of Palermo, Italy), in the Goulandris Natural History Museum (Kifissia, Athens), the Dipartimento di Scienze della Terra of the University of Catania, Italy, the Zoologisch Museum of Amsterdam, the Muséum National d'Histoire Naturelle of Paris (Département Histoire de la Terre), and in my personal collection. Many other private collections were visited.

In the parts dedicated to each species, a list of the material is provided with all information given in the original labels. An abbreviated list of essential synonymy and/or citations is provided.

The fossil material (all from the Mediterranean area), from the deposits of Dattilo (NW Sicily), Cartiera Mulino (Vittoria, SE Sicily, type locality of *Alvania francescoi* new species and *Alvania rosariae* new species), and Kyllini (Elea, NW Peloponnesus, Greece), was obtained by washing bulk samples on a serial sieves (0.5, 1, and 2 mm square meshes) and sorted using a stereomicroscope. The same procedure was followed for the Recent bulk samples collected from Magnisi (Siracusa, SE Sicily, the type locality of *Rissoa cingulata* Philippi, 1836) and Mondello (Palermo, NW Sicily) specifically to recover that species. Geological, stratigraphic and paleoecological information on the deposits of Cartiera Mulino, Dattilo and Kyllini are taken from Costa (1989), Garilli (1998; 2004), Garilli et al. (2005a; 2005b) and Garilli and Galletti (2007). The stratigraphic information on the Sicilian deposits of Birgi (Trapani) and Tommaso Natale (Palermo, originally attributed to the upper Pleistocene Thyrrenian by Ruggieri and Milone, 1973) are from Ruggieri and Unti (1988) and Hearty et al. (1986), respectively. For the remaining fossil material (mainly from Coll. Forli *ex*-coll. Palazzi), I followed the stratigraphic attributions reported by the collectors.

For all the discussed species, at least five shells were studied by the scanning electron microscope (SEM) using a Philips XL30 ESEM, except for the (sole) syntype of *Rissoa prusi* and *R. cingulata*, of which there were only three shells available. Specimens examined by SEM were cleaned in a Bransonic 5 ultrasonic machine using distilled water. Particular attention was given to protoconchs and teleoconch microsculptures as potential sources of taxonomic characters at species level. The number of protoconch whorls were counted according to Verduin's method (1977).

Shells were measured using a stereo microscope provided with a cross-line micrometer eyepiece. The position of any varix on the body whorl is indicated in degrees of the angles formed by the plane of the varix and of the outer lip.

Geographic, bathymetric, and stratigraphic distribution of each discussed species is based on the examined material and the literature. Published records were critically evaluated on the basis of good illustrations or satisfactory descriptions. This type of dataset allows for just a rough representation of the geographical distribution, especially for the Adriatic Sea and the easternmost Mediterranean basin, of which I found very little material from the collections studied.

Abbreviations are used as following: DGUP: Dipartimento di Geologia e Geodesia, Università di Palermo, Italy; DSTC: Dipartimento di Scienze della Terra, Università di Catania, Italy; GNHM: Goulandris Natural History Museum, Kifissia, Athens, Greece; MGUP: Museo Geologico G.G. Gemmellaro, Università di Palermo, Italy; MNHN-DHT: Muséum National d'Histoire Naturelle, Département Histoire de la Terre, Paris, France; MNHN-DSE: Muséum National d'Histoire Naturelle, Département Systématique et Evolution, Paris, France; MPOB: Dipartimento del Museo di Paleobiologia e dell'Orto Botanico, Università di Modena e Reggio Emilia, Modena, Italy; MSNCS: Museo Regionale di Storia Naturale e Mostra Permanente del Carretto Siciliano, Terrasini, Italy; ZMA: Zoologisch Museum Amsterdam, Holland; ZMB: Museum für Naturkunde, Humboldt Universität, Berlin, Germany; Coll.: collection; Coll. MF: Maurizio Forli collection, Prato, Italy; Coll. PAL: Stefano Palazzi collection, Modena, Italy; Sh(s): shell(s), used in the Material Examined sections only.

SYSTEMATICS

Family Rissoidae Gray, 1847
Subfamily Rissoinae Gray, 1847
Genus *Alvania* Risso, 1826

Type Species: *Alvania europea* Risso, 1826 [synonym of *A. cimex* (Linnaeus, 1758)], subsequent designation by Nevill, 1885

Alvania carinata (Da Costa, 1778)
(Figures 1–14)

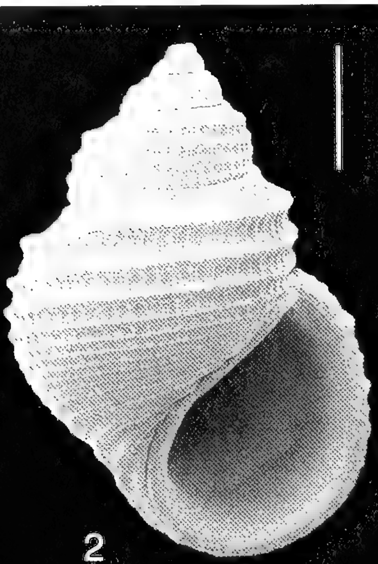
Turbo carinatus Da Costa, 1778: 102–103, pl. 8, fig. 10
Rissoa trochlea Michaud, 1830: 16, fig. 4
Galeodina cingulata (Philippi, 1836).—Piani, 1979: 70–71, figs. 2–3

Description: Shell small, sturdy, conical and keeled to slender and turrited, reaching about 5 mm (rarely 6 mm) in height; 3.9–4.1 mm in width. Protoconch multispiral, conical, consisting of about 2.2 convex whorls. Protoconch I with 0.8 whorls, sculptured with six very fine spiral lirae and microscopic granules between them. Protoconch/teleoconch transition well-marked and sinuous. Protoconch II sculptured with sparse, spirally arranged microscopic pimples, stronger in adapical direction, and one to two spiral ridges, one of them always very close to lower suture. In the largest shells, teleoconch formed by 4–4.5 moderately convex whorls. Common morph (Figures 2, 6–7) with teleoconch whorls markedly dominated by spiral sculpture, which consists of very strong cords (numbering 2–3, 3–6, 6–12, and 12–17 on first, second, third, and last teleoconch whorl, respectively). Secondary, less conspicuous cords may occurr on last whorl. More marked spiral cords on adapical portion of whorls, at a certain distance from suture, give a characteristic keeled shape. Cords progressively less strong on basal area. Unkeeled morph (Figures 1, 4–5) characterized by a slender shell shape, usually bears more spiral cords (18–20) on last whorl. Axial sculpture always formed by numerous (32–50 on penultimate whorl), occasionally very narrow and lamella-like ribs, becoming obsolete toward base. Intersection of ribs with spiral cords gives an almost general clathrate pattern in unkeeled morph. Intersection of spiral and axial sculptures nodular, usually forming squares (Figure 14), with exception of last whorl where a rectangular pattern occurs (Figure 13). Microsculpture consists of very fine spiral threads (Figures 13–14), covering all teleoconch surface, with exception of main spiral pattern. On early teleoconch whorls, spiral lirae often alternate with spiral alignments of microscopic pimples. Sutures slightly inclined. Last whorl well expanded, comprising 3/5 to 3/4 (rarely more than 3/4, Figure 3) of shell height, often bearing one or two varices (mainly in keeled morph) with angles of 10°–340°. Aperture wide, ovate, slightly rounded to angled in the posterior part, comprising 3/5 to 3/4 of last whorl height. Outer lip slightly prosocline, internally smooth, externally markedly thickened by a strong rim very close to lip edge, and covered by spiral cords. Inner lip moderately arcuate and rather thickened, with a very narrow to discretely expanded (Figure 3) callus delimiting a very small umbilical chink.

Type Locality: Cornwall, southwestern England.

Material Examined: Great Britain: Cornwall, Falmouth, 1 sh., coll. MF, 1974, E55A; Channel Islands, Herm, 11 shs, coll. MF, 09.1974, E54A. Atlantic France: Normandy, Carteret, 3 shs, coll. MF, Jul. 1973, E28A; lower Normandy, St. Pair, 7 shs, MNHN coll. Denis, 1945; Brittany, Finistère Anse de Bertheaume, 20–30 m, industrial dredging, 4 shs, MNHN coll. S. Gofas, 1978; Brittany, Cote-du-Nord Plomanac'h, fissures of infralittoral rocks, 1 sh., MNHN coll. S. Gofas, 1973–78; Brittany, Finistère Roscoff, "les Cochons Noirs", sand and conchiferous gravel, 20 m, 27 shs, MNHN coll. Gofas, Jul. 1994; Brittany, St. Lunaire, 20 shs, MNHN Coll. Fischer, 1898; Brittany, St. Servan, 10 shs, MNHN coll. Staadt, 1969; Brittany, St. Lunaire, 2 shs, MNHN coll. Ph. Dautzenberg (figured in Bucquoy et al., 1884, pl. 35, figs. 1, 2); St. Lunaire, 5 shs, MSNCS, 7173 and 7174, 20 Jun. 1970, on the beach at low tide; Brittany, Morlaix, Saint Michel en Grève, 2 shs, coll. MF, 1976, E25A; Brittany, Saint Jacut, 3 shs, coll. MF, 06.1975, E12A; Brittany, Saint Jacut, 14 m, 6 shs, coll. MF, 04.1974, E12B; Brittany, Carnac, Quiberon, 4 shs, coll. MF, 1970, E16B; Brittany, Carnac, Quiberon, Pointe de Couquel, 2 shs, coll. MF, 1970, E11A; Brittany, Saint Malo, 7 shs, coll. MF, 07.1973, E13A; Brittany, St. Malo, Lizardrieux, 1 sh., coll. MF, Aug. 1982, E69A. Atlantic Pyrenees, Aquitaine, St. Jean de Luz, Cote Basque, infralittoral rocks, 1 sh., MNHN coll. S. Gofas, 1980–81; Atlantic Pyrenees, Aquitaine, St. Jean de Luz, 73 shs, MNHN coll. H. Fischer, 1898; Aquitaine, Soulac, 1 sh., MNHN coll. A. Dolfus; Aquitaine, Hendaye, 2 shs, coll. MF, Jul. 1976, E57A. Portugal: Algarve Sagres, Baie de Baleeira, (37°00.7′ N, 08°55.0′ W), tide zone, 1 sh., MNHN, Mission Algarve, May 1988; Algarve Sagres, Ponta da Baleeira, (37°00.3′ N, 08°55.5′ W), 17–23 m, 5 shs, MNHN, Mission Algarve, May 1988; Algarve Sagres, Pontal dos Corvos, (37°01.3′ N, 08°58.3′ W), at the foot of falaise, 17–22 m, 5 shs, MNHN Mission Algarve, May 1988; Albufeira (southern coast), Ponta de Castelo, 3–6 m, 2 shs, coll. MF, 08 Aug. 1985, E50B. Atlantic Morocco: Asilah, mouth of Oued el Helou, conchiferous deposits, beach, 6 shs, MNHN coll. S. Gofas, 1971–72. Strait of Gibraltar: Tanger, Grande Plage, conchiferous deposits, beach, 3 shs, MNHN coll. S. Gofas, 1970–81; Cadiz, Getares, beach, 3 shs, coll. MF, *ex* coll. C. Bogi, legit Hanselaar, 2230 GET; Cadiz, Barbate, conchiferous deposits, beach, 6 shs, MNHN coll. S. Gofas, 1976–81; south Ceuta, Punta del Desnarigado, (35°53.6′ N, 05°16.8′ W), 16–20 m, 1 sh., MNHN coll. Bouchet, Gofas and Lozouet, May 1996. Mediterranean Spain: Castellon, Columbretes Islands, Espinosa Island, 5 m, 1 sh., coll. MF, 26 Jul. 1974, M273A; Malaga, 15 m, 7 shs, coll. MF, *ex* coll. Cesare Bogi, 2127IMA(V002G); Malaga, Algeciras, Torre del Almirante, 3–5 m, 1 sh., coll. MF, 28


1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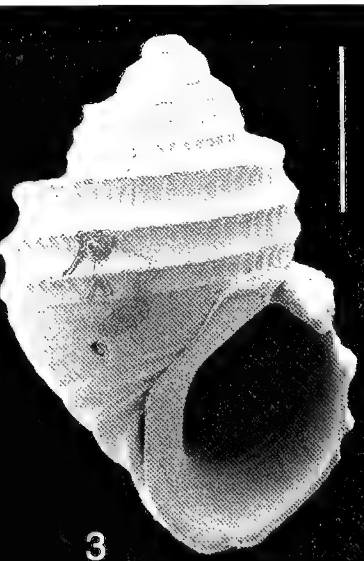
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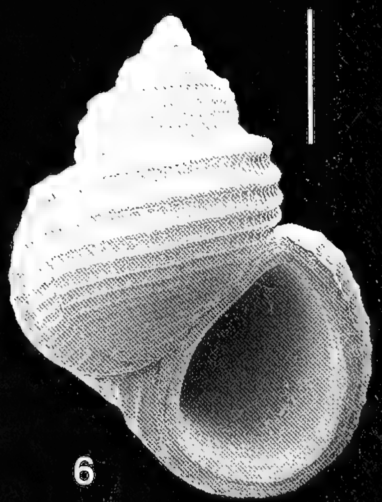
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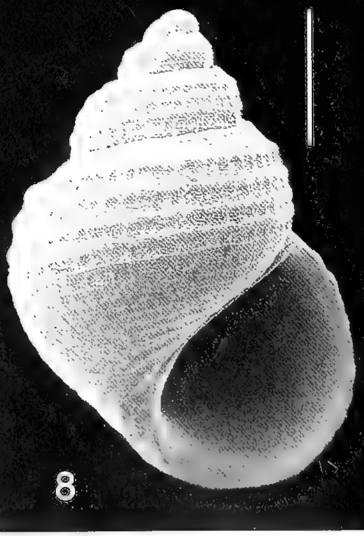
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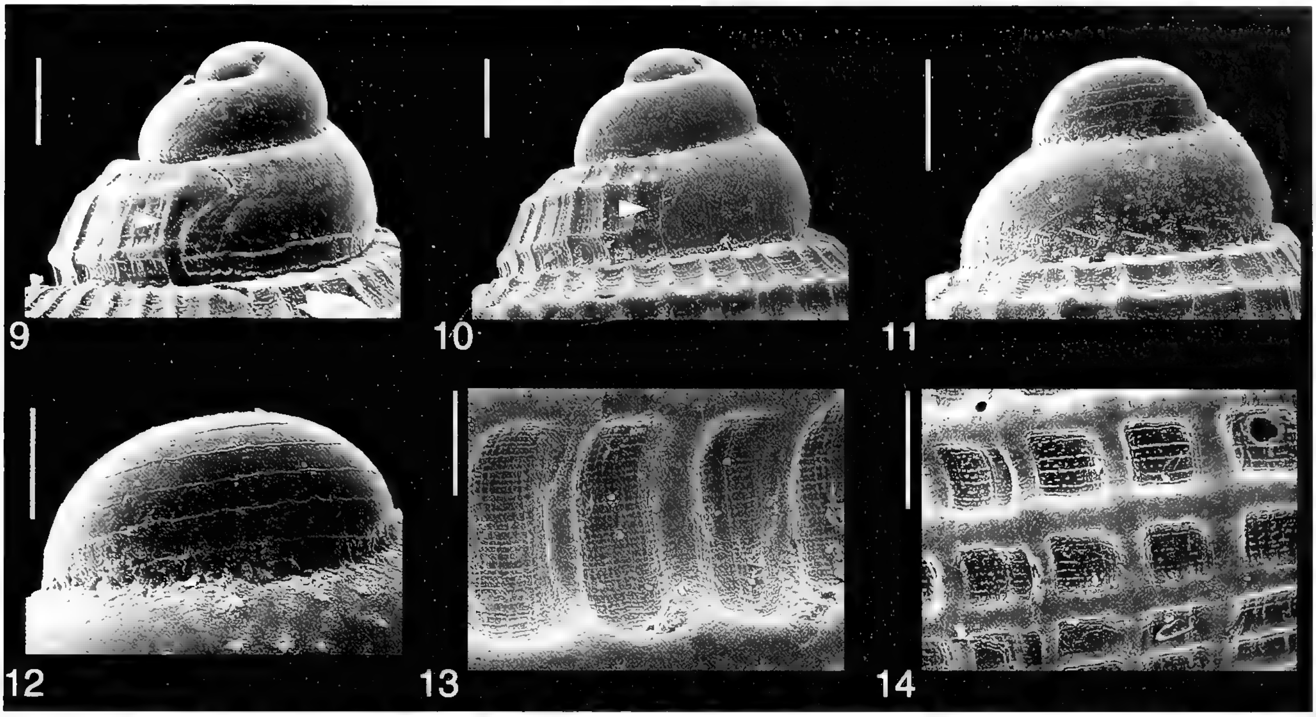

Figures 9–14. *Alvania carinata* (Da Costa, 1778), protoconch and details of sculpture. **9.** Sicily, Palermo, Terrasini, "Magaggiare-Ciucca di Cinisi" beach, coll. PAL, (146E), protoconch. **10.** Provence, Marseille, La Baule, small beach at 25 km west from Marseille, coll. PAL (2128BAU-V008C), protoconch. **11–12.** Shell from the same locality and collection, sculpture of protoconch I and II (11) and a detail of protoconch I (12). **13.** Same shell as Figure 2, detail of teleoconch sculpture on the penultimate whorl, coll. PAL (307B). **14.** Detail of teleoconch sculpture on the last whorl, NW Sicily, Palermo, Terrasini, "Magaggiare-Ciucca di Cinisi" beach, detritus of *Miniacina*, coll. PAL (146E). Scale bars: 100 μm in Figures 9–11 and 13–14; 50 μm in Figure 12. White arrows indicate the protoconch/teleoconch boundary, respectively.

Sep. 1976, M207B; Malaga, Algeciras, 3 shs, coll. MF, 23 Sep. 1976, M207A; Malaga, Fuengirola, 0.5–1 m, 1 sh., coll. MF, 20 Aug. 1973, M68B; Malaga, Algeciras, Playa Getares, 6 m, 1 sh., coll. MF, Aug. 1983, M207E; Malaga, Cabo Pino, detritus, 10 m, 2 shs, coll. S. Rufini, (41.80g). Mediterranean Morocco: M'diq "(anc. Rincón)" conchiferous deposits, beach, 1 sh., MNHN coll. S. Gofas, 1971. Algeria: Alger, 1 sh., MNHN coll. Locard. Mediterranean France: Languedoc, Carnon, conchiferous deposits, beach, 1 sh., MNHN coll. S. Gofas, Aug. 1976; Languedoc, Roussilion, 3 shs, MNHN Coll. Dolfus, 1903; Languedoc, Roussilion, 1 sh., MNHN coll. Ph. Dautzenberg (Moll. du Roussillon); Provence, Marseille, La Baule, small beach at 25 km west from Marseille, 3 shs, coll. MF, *ex* coll. C. Bogi, Oct. 1986, 2128BAU (V008C); Provence, Marseille, Cape Couronne, 4 shs, coll. MF, *ex* coll. C. Bogi, Oct. 1987, 2129COU (V008E); Provence, Marseille, Grand Congloue, (43°10.6′ N, 05°24.2′ E), 33 m, 31 shs, MNHN rec. H. Zibrowius Jun. 1996; Provence, Iles Embiez, conchiferous deposits, beach, 10 shs, MNHN coll. S. Gofas, 1968–70; Provence, Iles Embiez, Petit Rouveau, dredging of sandy conchiferous bottom, 3–5 m, 5 shs, MNHN coll. S. Gofas, 1968–70; Provence, St. Clair, infralittoral rocks, (43°08.2′ N, 6°23.2′ E), 0–1 m, 1 sh., MNHN rec. S. Gofas, Sep. 1992; Provence, St. Raphael, 2 shs, MNHN coll. Locard; Provence, 9 shs, MNHN coll. Petit, 1873; Provence, Sanary, 1 sh., MNHN coll. Locard; Corsica, Ajaccio, 3 shs, MNHN coll. Jousseaume, 1921; Corsica, Galeria, Punta Stollo, 6 m, 1 sh., coll. MF, 07 Aug. 1984, M52D; Corsica, Pianottoli, Anse de Chevanu, 2 shs, coll. MF, Jun. 1988, M77A. Tunisia: Djerba, Aghir, 5 m, *Posidonia* bed, 1 sh., coll. MF, S. Palazzi legit 06 Aug. 1993, M79A; Djerba, Al Jazirah, 1–2.5 m, 1 sh., coll. MF, Aug. 1974, M9B. Italy: Friuli Venizia Giulia, Trieste, beach, 7 shs, coll. MF, D. Di Massa legit 1976,

Figures 1–8. *Alvania carinata* (Da Costa, 1778), variation in shell shape and sculpture. **1.** "Form" *ecarinata* Bucquoy et al., 1884, shell from coll. Ph. Dautzenberg (Moll. du Roussillon), MNHN-DSE. **2.** Typical, keeled morph, Liguria, Genova, Camogli, 42 m, coll. PAL (307B). **3.** Markedly keeled morph, corresponding to *Rissoa trochlea* Michaud, 1830, Strait of Gibraltar, Cadiz, Getares beach, coll. PAL (2230 GET). **4–5.** Small, unkeeled morph, La Spezia, Monterosso, 15–30 m, coll. PAL (70A). **6.** Typical morph with varice, Sardinia, Sassari, Capo Caccia, Cala della Calcina, 6 m, coll. PAL, (112A). **7.** Profile view of the same shell as Figure 2. **8.** Juvenile shell fitting well with the concept of *Alvania cingulata* (Philippi, 1836) *sensu* Piani (1979, figs. 2–3). Scale bars: 1 mm in Figures 1–7; 0.5 mm in Figure 8.

307B; Liguria, Genova, Camogli, 42 m, 1 sh., coll. MF, 06.1981, 271B; La Spezia, Monterosso, 15–30 m, detritus, 1 sh., coll. MF, A. Lugli legit Oct. 1978, 70A; La Spezia, Portovenere, 5–25 m, 3 shs, coll. MF, Oct. 1978, 329A; La Spezia, Riomaggiore, 30 m, 1 sh., coll. MF, Aug. 1978, 312A; Liguria, La Spezia, Punta Mesco, 35 m, 1 sh., coll. MF, Jul. 1987, 176C; Tuscany, Livorno, San Vincenzo, Borraccia, 12 m, 1 sh., coll. MF, 12 Jul. 1987, 190A; Tuscany, Livorno, Secche della Meloria, 6–17 m, 2 shs, coll. MF, 1974, 34E; Tuscany, Livorno, Castiglioncello, 4 shs, coll. MF, 1972, 21A; Tuscany, Livorno, Romito, off mouth of the torrent Chiona, 30–35 m, 2 shs, coll. MF, *ex* coll. C. Bogi, 36A; Tuscany, Livorno, Bagni Fiume, 20 shs, coll. MF, 1977, 34B; Tuscan Archipelago, Island of Capraia, 100/400 m, 2 shs, coll. MF, *ex* coll. C. Bogi, 2126CAP(V005G); Island of Capraia, Punta della Fica, 29 m, 1 sh., coll. MF, 15 Sep. 1985, 28R; Island of Capraia, Punta Civitata, 40 m, 1 sh., coll. MF, 19 Sep. 1985, 28T; Tuscan Archipelago, Gorgona Island, 35–40 m, 11 shs, coll. MF, Aug. 1978, 69A; Gorgona Island, 40 m, 18 shs, coll. MF, legit C. Bogi, 194; Tuscany, Siena, 1 sh., yellow sands from unknown layer, lower Pliocene, coll. MF *ex* coll. PAL, F22A; Tuscany, Grosseto, Punta Ala, Baia Verde, 5 m, 1 sh., coll. MF, G. Terzer legit 08 Sep. 1974, 27A; Tuscany, Grosseto, Punta Ala, Punta Hidalgo, 2 shs, coll. MF, Jun. 1975, 27B; Tuscany, Grosseto, Follonica, Cala Felice, 7 m, 1 sh., coll. MF, 25 Aug. 1987, 55B; Tuscany, Grosseto, Island of Palmaiola, 28 m, 2 shs, coll. MF, 14 Sep. 1986, 172A; Grosseto, Island of Elba, Capo Calamita, Scogli Corbelli, 46 m, 1 sh., coll. MF, Sep. 1972, 5E; Island of Elba, Scoglio Remaiolo, 35 m, 1 sh., coll. MF, May 1980, 5K; Island of Elba, Formiche della Zanca, 20 m, 1 sh., coll. MF, Apr. 1984, 5P; Lazio, Rome, Civitavecchia, 2 shs, coll. MF, 1975, 137B; Sardinia, Sassari, Capo Caccia, Cala della Calcina, 6 m, conchiferous detritus at upper limit of *Posidonia* bed, 10 shs, coll. MF, S. Palazzi legit 19 Aug. 1983, 112A; Sardinia, Sassari, bay at E of Faro di Capo Testa, 7–19 m, 1 sh., coll. MF, 22 Aug. 1983, 125B; Nuoro, Capo Comino, Ruia Island, 0–2 m, 1 sh., coll. MF, 1974, 75A; Sardinia, Cagliari, Island of San Pietro, channel of San Pietro, 2–4 m, *Posidonia* bed, 2 shs, coll. MF, G. Liuzzi legit 10 Oct.1976, 264A; Sardinia, Cagliari, Island of Sant'Antioco, Cala de Saboni, 1 sh., coll. MF, 07 Aug. 1983, 115B; Sardinia, Cagliari, Island of Sant'Antioco, Cala de Saboni, 14 m, 1 sh., coll. MF, 10 Aug. 1983, 115E; Campania, Napoli, Island of Capri, Punta Vivara, 6 m, 1 sh., coll. MF, 08 Sep. 1978, 254B; Campania, Napoli, Island of Procida, Marina Grande, 2.5–9 m, 2 shs, coll. MF, 1974, 105A; Puglia, Bari, off Palese, 12–13 m, 1 sh., coll. MF, 11 Sep. 1979, 77A; Puglia, Taranto, 2 shs, coll. MF, 1973, 84B; Puglia: Taranto. Campomarino, 2 shs., coll. MF, 12 Feb. 1977, 309A; Puglia, Taranto, Maruggio, 1 sh., coll. MF, 1977, 280A; Puglia, Brindisi, "Batteria Brin" beach, 14 shs, coll. MF, G. Oriolo legit 08.1970, 193D; Puglia, Brindisi, Punta Croce, 15 m, 19 shs, coll. MF, G. Oriolo legit Aug. 1974, 262A; Puglia, Brindisi, Torre Guaceto, 5 m, 1 sh., coll. MF, 1976, 42A; Brindisi, Lendinoso, 10–20 m, 1 sh., coll. MF, 1977, 279A; Puglia, Lecce, Gallipoli, Costa Brada, 2 shs, coll. MF, Apr. 1978, 91B; Lecce, Porto Cesareo, 2 shs, coll. MF, Oct. 1977, 46B; Lecce, Porto Cesareo, Torre Lapillo, 1 sh., coll. MF, 06 Jun. 1978, 46C; Lecce, Marina di Ugento, 30 m, 1 sh., coll. MF, 1977, 68C; Lecce, Gallipoli, La Vecchia Torre, 2–6 m, 2 shs, coll. MF, 1976, 91D; Lecce, San Cataldo, 1 sh., coll. MF, Apr. 1973, 260C; Lecce, Specchiulla, 1 sh., coll. MF, Oct. 1974, 281A; Calabria, Reggio Calabria, Pentimele, from fisherman nets, 8 m, 1 sh., coll. MF *ex* coll. Sciano, V060A 194; Reggio Calabria, Laureana di Borrello, Pecoraio, 2 shs, (layer 2), lower Pleistocene, coll. MF *ex* coll. PAL, F24A; Sicily, Trapani, San Giuliano, 10 shs, coll. MF, 25 Jul. 1978, 297A; Trapani, Scopello, Tonnara, 12–20 m, 1 sh., coll. MF, 06 Apr. 1986, 333F; Sicily, Trapani, Egadi Islands, Favignana, Secca del Toro, 30 m, 20 shs, coll. MF, A. Lugli legit 02 Jun. 1983, 272H; Egadi Islands, Favignana, 4 m, 17 shs, coll. MF; Egadi Islands, Favignana, Cala Rotonda, 20–30 m, 3 shs, 04 Jun. 1983, coll. MF, 272G; Egadi Islands, Favignana, Scoglio Corrente, 30 m, 3 shs, coll. MF, 01 Jun. 1983, 272F; Egadi Islands, Favignana, Punta Sottile, 30–40 m, 4 shs, coll. MF, 30 May 1983, 272E; Egadi Islands, Marettimo, Punta Bassana, 41 m, 2 shs, coll. MF, 04 Jun. 1983, 140A; Egadi Islands, Levanzo, Faraglione, 7–12 m, 3 shs, coll. MF, 03 May 1979, 325B; Sicily, Pantelleria Island, Baia dei Fichi d'India, 22 m, 1 sh., coll. MF, Jul. 1983, 154M; Pantelleria Island, Punta Capace, 31 m, 1 sh., coll. MF, Jul. 1983, 154N; Sicily, Palermo, 1 sh., coll. MF *ex* coll. C. Bogi, (V056A) 194; Palermo, Bagheria, Aspra, 18.5 m, 2 shs, coll. MF, Apr. 1973, 124C; Palermo, Punta Raisi, Marina Longa, 1 sh., coll. MF, 28 Feb. 1979, 320A; Palermo, Terrasini, "Magaggiare-Ciucca di Cinisi" beach, detritus of *Miniacina*, 14 shs, coll. MF, S. Palazzi legit 23 Sep. 1977, 146E; Palermo, Island of Ustica, Scoglio del Medico, 25 m, 1 sh., coll. MF, Aug. 1980, 286K; Sicily, Messina, Milazzo, Capo Milazzo, Cala Sant'Antonio, 2 shs, upper yellow sands, upper Pleistocene, coll. MF *ex* coll. PAL, F5A; Messina, Eolie Islands, Lipari, Secca del Bagno, 38–40 m, 3 shs, coll. MF, 05 Sep. 1979, 338A; Sicily, Catania, Acitrezza, 3–25 m, 2 shs, coll. MF, Sep. 1975, 22A; Sicily, Siracusa, Vendicari, bay, 2 shs, coll. MF, 13 Sep. 1977, 20A; Siracusa, Portopalo di Capo Passero, 2–3 m, 1 sh., coll. MF, Jun. 1976, 63A; Siracusa, Peninsula of Magnisi, southern side, 1 sh., coll. V. Garilli, Jun. 2006; Sicily, Palermo, Tommaso Natale, 1 sh., late middle Pleistocene, MGUP 166/2/49; Sicily, Trapani, Birgi, 3 shs, upper Pleistocene, Tyrrhenian Stage, MGUP 1765/36/14; Sicily, Trapani, 12 shs, upper Pleistocene, Tyrrhenian Stage, MGUP 358/3/42. Isle of Malta: Malte, 8 shs, MNHN coll. Jousseaume, 1921. Croatia: Istria, Rovinij, between Rt. Muntrav, Hr. Muntrav and Hr. Azino, 8–15 m, detritus from bottom, 11 shs, coll. MF, S. Palazzi legit 19 Jun. 1978, M188B; Istria, Savudrija, beach, 8 shs, coll. MF, S. Palazzi legit Oct. 1975, M364A; Istria, Rovinij, 6–18 m, 19 shs, coll. MF, 20 Jun. 1978, M188A; Istria, Vrsar, 1 sh., coll. MF, 03

Apr. 1988, M76A; Istria, Umag, 1 sh., coll. MF, 1978, M109A; Istria, Umag, Taverna Lero, 0.3 m, 1 sh., 17 Jun. 1978, coll. MF, M109B; Kaciack, dam of Cigale, 4 m, 1 sh., 29 Jul. 1983, coll. MF, M14A. Greece (Aegean Sea): NW Aegean, Island of Limnos, near Moudros, 3–5 m, 48 shs, coll. MF, A. Lugli legit Aug. 1991, M80A; Sithonia, Ormos Panagias, 2–3 m, 1 sh., Aug. 1982, coll. MF, M31B; Sithonia, Nesis Dhiaporos, 33–34 m, 2 shs, coll. MF, 01 Aug. 1986, M31D. Unknown locality from Mediterranean Sea: 120 shs, MNHN coll. Vayssière.

Habitat: The species is usually found at depths compatible with the upper part of the shelf, the infralitoral stage of Pérès and Picard (1964). Rarely, I found material collected from the tidal zone. According to Gofas and Ponder (1991), *Alvania carinata* lives deeply buried under stones. It seems also to be linked (in the Mediterranean) to phanerogam beds. The finding of two shells from the Island of Capraia (Tuscan Archipelago), collected at a depth of 100–400 m, is much probably due to lower shelf-slope transport.

Distribution: Occurs probably throughout the Mediterranean, but its presence in the easternmost coasts, from which I did not see any material, needs to be confirmed. In the Atlantic it is recorded from the coasts of Great Britain south to Morocco. As fossil, it is rare in the Mediterranean Neogene where it is recorded from the lower Pliocene yellow sands near Siena. It becomes more frequent during the Mediterranean Quaternary, where I found it from the lower Pleistocene of Reggio Calabria, and the middle-upper Pleistocene of Sicily (Tommaso Natale, Capo Milazzo and Trapani).

Remarks: A complete synonymy list was provided by Piani (1979) and Van Aartsen (1982). In various collections, I found different lots of this species containing juvenile shells (not higher than 3 mm, see Figure 8) identified as *Alvania cingulata* (Philippi, 1836), species hereafter re-described and discussed. This wrong determination very likely follows the misidentification of Piani (1979, figs. 2–3) and Giannuzzi-Savelli et al. (1996, figure 499).

Typically, the shell of this species has a characteristic keeled shape due to the presence of well marked spiral cords that become very strong on the well-developed last whorl. The number of cords on adult whorls is slightly variable, 3–4 in the penultimate whorl. The not-keeled morph, characterized by having a slender and turrited shape and more numerous cords (5–6 in the penultimate whorl), is the "form" *ecarinata* Bucquoy et al., 1884 (Figures 1, 4–5), also known as *minor-ecarinata* Monterosato, 1884 (probably corresponding to *Rissoa lucullana* var. *cancellata* Scacchi, 1836, as indicated by Piani, 1979). It has been considered a Mediterranean subspecies of *A. carinata* by Van Aartsen (1982). I found no shells clearly belonging to this morph in the Atlantic material studied (mainly from the MNHN-DSE collections). However, in some Mediterranean areas (e.g. along the French coast in the MNHN-DSE collections), I found the typical morph together with unkeeled shells. Thus I am more inclined to consider it just a case of intraspecific variation, which appears well represented in Mediterranean populations. The keeled morph, characterized by having three spiral cords on subadult whorls and a very expanded body whorl (more than 3/4 of the shell height, see Figure 3) fits well within the concept of *Rissoa trochlea* Michaud, 1830, which is certainly a synonym of *A. carinata*.

Alvania carinata is the type species of *Galeodina* Monterosato, 1884, a genus created for cingulated, keeled, varicose rissoid shells with a wide aperture (Monterosato, 1884a, p. 163). This generic division can appear quite artificial, not being supported by appropriate and constant taxonomic features. Also, the consideration of *Galeodina* as a well-established subgenus of *Alvania*, as indicated by Wenz (1938) and Van Aartsen (1982), appears doubtful. Ponder (1985), who synonymized most of the available subgenera with *Alvania* sensu stricto, expressed some uncertainty when considering *Galeodina* as a valid taxon. He recognized the ignorance of anatomical features as the main gap in solving this systematic question. In any event, the shell characters alone do not provide enough support for *Galeodina* to stand as a subgenus. For example, the unkeeled morph, which usually lacks the main features of *Galeodina*, including the characteristic varices of the keeled morph, might be compared to the *Alvinia* Monterosato, 1884, species group, with which it shares a slender, turreted shell shape. It is noteworthy that Cossmann (1921) cited *Galeodina* as a synonym of *Alvinia*.

Alvania *cingulata* (Philippi, 1836)
(Figures 15–26)

Rissoa cingulata Philippi, 1836: 152–153.
Acinus cingulatus (Philippi).—Monterosato, 1884b: 62.
Cingula (*Onoba*) *cingulata* (Philippi, 1836).—Nordsieck, 1968: 46, pl. VII, fig. 26.35
Alvinia (*Galeodina*) *cingulata* (Philippi, 1836).—Nordsieck, 1972: 181, pl. RVI, fig. 20.

Description: Small, sturdy, conical-ovate shell reaching 3.5 mm in height, 2.2 mm in width. Protoconch paucispiral, consisting of little more than 1.5 convex and very rounded whorls, sculptured by 5–6 very fine spiral lirae. Several prosocirte growth scars precede protoconch/teleoconch transition (Figure 20). Teleoconch consists of about 4 cingulated convex whorls separated by slightly inclined sutures. Very early teleoconch whorls bear two main spiral cords crossed by numerous axial ridges. Sculpture of adult whorls consisting of spiral cords more conspicuous than axials, which are 5–6 and 10–11 on the penultimate and body whorls respectively. Axial sculpture formed by narrower (half the breadth of a spiral cord) ribs, numbering about 40 on penultimate whorl, and which become obsolete toward shell base. Microsculpture consists of spiral rows of small tubercles that do not seem to appear on main sculpture (Figure 26). A few irregular scars cross these spiral rows. Last whorl rather

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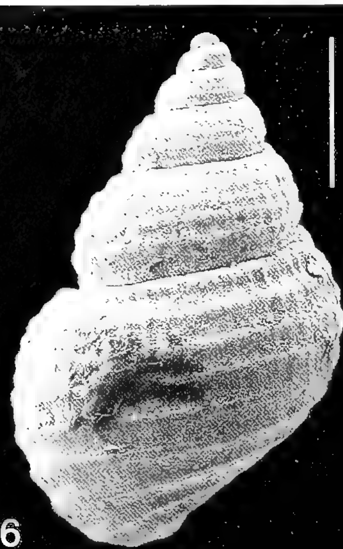

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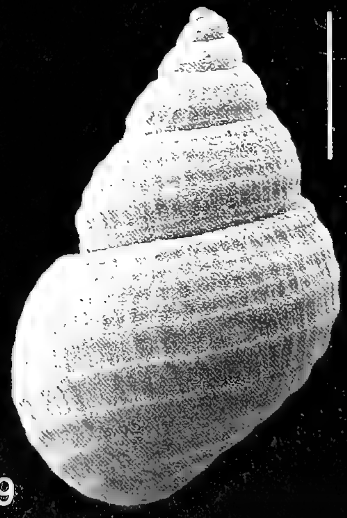

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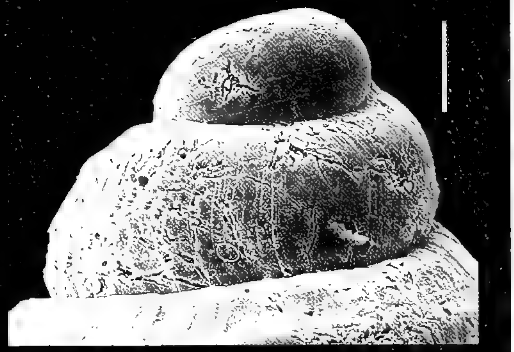

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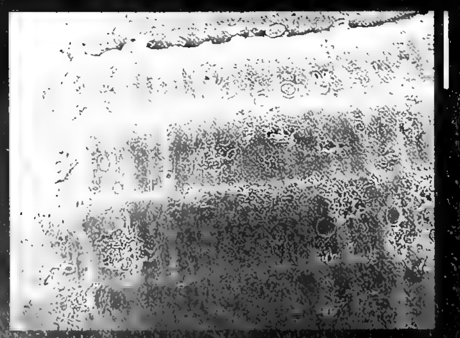

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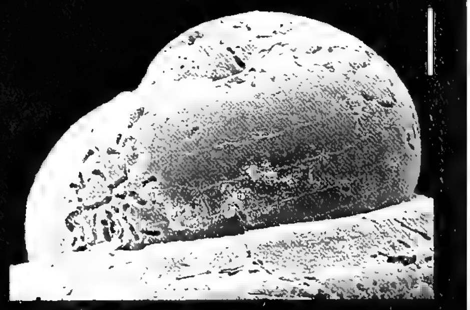

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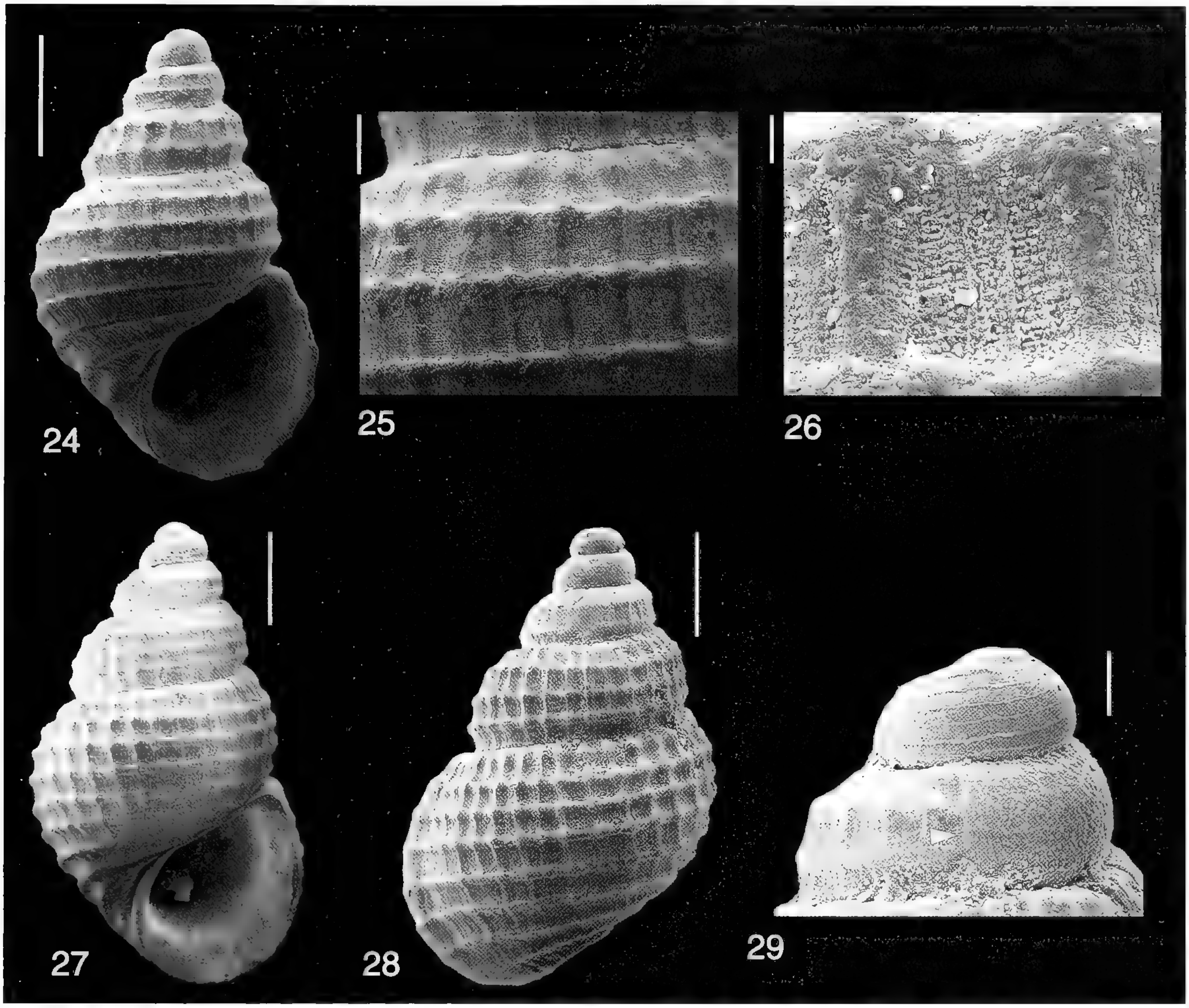

Figures 24–29. *Alvania cingulata* (Philippi, 1836) from type locality (Peninsula of Magnisi, Siracusa, SE Sicily, coll. Garilli), and a slightly resembling *Alvania* sp., from the lower Pleistocene of Musalà (Italy, Reggio Calabria, coll. MF *ex* coll. Pal, F95A), fitting well with the concept of *A. cingulata* stated by Monterosato (1884b). **24–26.** *Alvania cingulata*. Apertural view of a subadult shell (24), sculpture on last whorl (25) and microsculpture (26). **27–29.** *Alvania* sp. Apertural (27), dorsal (28) views and protoconch. Scale bars: 500 μm in figures 24, 27–28; 100 μm in figures 25, 29; 20 μm in Figure 26. The white arrow in Figure 29 indicates the protoconch/teleoconch boundary.

inflated and well-developed, comprising little less than 3/4 total height. Aperture wide and ovate, comprising about 4/9 and 2/3 of total height and last whorl respectively. Outer lip slightly prosocline, internally smooth, externally slightly thickened near edge. Columellar side arcuate, with a thin callus forming a very narrow umbilical chink. Coloration consisting of quite large, reddish-brown bands on a whitish-cream background.

Type Locality: Peninsula of Magnisi, Siracusa, south-eastern Sicily.

Type Material: One possible syntype, ZMB (2326) *ex* coll. Philippi was destroyed by Byne's reaction (M. Glaubrecht, pers. comm., 2006)

Material Examined: Italy: NE Sicily, Messina, 2 shs. ZMB *ex* coll. Monterosato, 80914 (original label by

Figures 15–23. *Alvania cingulata* (Philippi, 1836). **15–17.** Apertural (15), dorsal (16), profile (17) view of one shell from ZMB *ex* coll. Monterosato (80914), Messina, NE Sicily. **20, 23.** Protoconch of the same shell. **18–19** and **21–22.** Another shell from the same lot, apertural (18), dorsal (19), profile (21) view, and a detail of sculpture on the last whorl (22). Scale bars: 1 mm in figures 15–19 and 21; 200 μm in Figure 22; 100 μm in Figure 20; 50 μm in Figure 23. The white arrows indicate the approximate protoconch/teleoconch boundary.

Monterosato: *Acinus cingulatus*, 2, Messina, 1014); SE Sicily, Siracusa, Peninsula of Magnisi, south side, detritus from the beach, 1 sh., coll Garilli, 6/2006

Habitat: Unknown. It is noteworthy that sandy and *Posidonia* bottoms prevail in the south side of the Magnisi Peninsula (from where I collected the beached shell in Figure 24), while an almost paralic (pre-lagoon) environment (with *Cerastoderma*, *Cerithium*, and *Gibbula* spp., on a finely sandy bottom) and a rocky bottom with algae characterize the north and east sides.

Distribution: Its distribution appears to be limited to Sicily, with particular regard to the eastern coast, from Messina to Magnisi. It was recorded from Palermo by Monterosato (1872; 1875; 1878; 1884a; 1884b), who very likely followed the citations of Philippi (1844) and Weinkauff (1885). The latter author, who indicated Mondello (the beach near Palermo), also cited Ognina (Catania) in eastern Sicily. To my knowledge, no fossil record of this species exists.

Remarks: This is a very rare, practically unknown species (see Van Aartsen, 1982a). Its identification has traditionally been quite problematic, above all after the misidentification by Piani (1979, figs.2–3), who illustrated a juvenile shell of *Alvania carinata* (Da Costa, 1778) under the name *Galeodina cingulata* (Philippi, 1836). The shell figured by Giannuzzi-Savelli et al. (1996, fig. 499), under the name *Alvania* (*Alvania*) *cingulata* (Philippi, 1836), is a subadult of *A. carinata*.

My identification is based on three shells (one from the type locality, two from ZMB *ex* Monterosato coll., labelled as *Acinus cingulatus*), which agree well with the original description by Philippi (1836; see also 1844: 128). A few diagnostic characters allow for its correct identification: the primary cingulated sculpture with raised cords, numbering 10–11 on the last whorl; the secondary axial pattern formed by very narrow ribs crossing the cords; the large ovate aperture; and the internally smooth outer lip, slightly thickened near its edge.

As Philippi (1844) noted, *Alvania cingulata* may be compared with *A. tenera*, especially with the slender morph of the latter species (see Figure 78). *Alvania tenera* has a smaller shell (usually not over 2.2 mm in height) with more raised cords (numbering 12–14 on the last whorl), and almost lamella-like ribs, which occur just on the interspaces between the cords (see discussion of *A. tenera*). Furthermore, *A. cingulata* has a paucispiral protoconch.

In addition, Nordsieck (1972) and Van Aartsen (1982) considered this species as belonging to *Galeodina*. However, the similarity between *Alvania cingulata* and *A. carinata* (type species of *Galeodina*) is superficial. Several differences separate the two: *A. cingulata* has a less inflated last whorl bearing less numerous cords and lacking varices, its outer lip lacks a varicose thickness, and its spiral sculpture does not markedly dominate over axial as in the typical *A. carinata*. The latter species also has a multispiral protoconch.

Monterosato (1884a and 1884b) included this species in his genus *Acinus* (synonym of *Alvania* according to Ponder, 1985), creating a link with the type species *Alvania cimex* (Linnaeus, 1758) (which is also the type species of *Alvania*, see Ponder, 1985: 36), mainly based on coloration. In reality, the similarity between the two species is limited to the color pattern of the shell and the nodular sculpture. Strong differences indicate that *A. cingulata* and *A. cimex* could be distant relatives, the latter having a more sturdy shell with a coarser sculpture (with subequal axial and spiral), and a proportionally smaller aperture provided with an internally denticulate outer lip. The concept of *A. cingulata* as expressed by Monterosato (1884b: p. 62) seems to be applicable to an interesting *Alvania* sp. (from the lower Pleistocene of southern Italy, Reggio Calabria, Musalà, 19 shs, F95A, coll., Figures 27–29) rather than to the original description by Philippi. The non-planktotrophic (see the paucispiral protoconch in Figure 29) *Alvania* sp., illustrated here, showing only a moderate similarity with the teleoconch sculpture of *A. cingulata*, has the characteristic general shape of *A. cimex*, with which it shares the apertural features, including the denticulations on the inner part of the outer lip. Furthermore Monterosato himself determined the shells I have illustrated in Figures 15–23 as *A. cingulata*.

In 1968, Nordsieck cited *A. cingulata* as *Cingula* (*Onoba*) *cingulata*. In reality, a vague similarity with some *Cingula* Fleming, 1828 or (more specifically) *Onoba* H. and A. Adams, 1852, species exists; e.g. *Onoba* (*O.*) *carpenteri* (Weinkauff) (see Ponder, 1985: fig. 114a), bears a similar spiral sculpture. Anyway, the genus *Onoba* is characterized by usually elongate shell with a proportionally smaller and more rounded aperture. Its included species, usually lacking the axial sculpture, may have a much weaker axial pattern or this may consist of delicate ribs, which become obsolete towards the sutures (see Bouchet and Warén, 1993: figs. 1508–1509, 1514–1515). In addition, the protoconch sculpture apparent on some non-planktotrophic *Onoba* species resembles that of *A. cingulata*, in having few, very fine spiral widely spaced threads. This kind of sculpture is also seen in *Alvania* (e.g. *A. subsoluta* (Aradas, 1847), see Bouchet and Warén, 1993, fig. 1458). *Cingula* species appear to be less similar to *A. cingulata* in having a thick outer lip and lacking any axial sculptural pattern.

A certain similarity exists with *Alvania watsoni* (Watson, 1873) from Madeira (see Ponder, 1985: fig. 102c–d), with which *A. cingulata* shares the general shell shape, characterized by an inflated last whorl provided with a large, ovate aperture.

Alvania francescoi new species
(Figures 30–43)

Description: Shell small, sturdy, conical-ovate, reaching 4.8 mm in height (4.3 mm in holotype) and 3.1 mm in width (2.8 mm in holotype). Protoconch conical, multispiral with partially immersed nucleus and convex whorls. Protoconch I consisting of about 0.8 whorls sculptured by 5–6 fine spiral lirae interspersed spirally and irregularly with microscopic granules. Protoconch II consisting of about 1.2 whorls sculptured by pimples, which are irregular in size and arrangement. They are larger and less numerous in the adapical position; fused into very short prosocline tracts in central part. In the abapical part of late protoconch, groups of pimples are irregularly fused into fine, discontinuous spiral ridges. Protoconch/teleoconch transition well-marked and sinuous. Teleoconch consisting of 3.8–4.6 (4.2 in holotype) rather convex whorls, with strong cancellate sculpture formed by intersection of equally developed spiral cords and axial ribs. Cords are narrow and well raised, numbering 2, 6–7 (6 in holotype) and 13–15 (14 in holotype) in early, penultimate and body whorl, respectively. Two adapical cords are usually more pronounced in penultimate and last whorl. Cords are markedly stronger and more widely spaced on base. Secondary cords may commence on late body whorl, at a certain distance from outer lip. Axial sculpture consists of narrow raised ribs numbering 24–32 (26 in holotype) on the penultimate whorl. On base, ribs progressively become very narrow to obsolete toward columellar area. Intersection of spiral and axial sculpture, producing nodular small knobs, forms a rectangular pattern (with major side of rectangles perpendicular to shell axis) except on last whorl, where a quadrangular to rhomboidal pattern occurs (Figure 43). Microsculpture of very early teleoconch whorls consists of micropustules, sometimes fused, forming spirally, discontinuous and irregular rows, mainly occurring between spiral cords (Figure 42); weak growth lines are present. Fine sculpture of the rest of teleoconch limited to weak growth lines (Figure 43). Suture slightly inclined. Last whorl well-developed, comprising about three fourths of shell height. It may bear single (paratype 6) or double (paratype 4, Figure 37) varices, at angles of about 50° and 70° respectively. Aperture wide, ovate, and with a rounded profile in the posterior part, comprising about two thirds to three fourths of last whorl height. Outer lip orthocline, internally smooth, externally markedly thickened by a strong, sometimes doubled (Figure 31), rim, occurring very close to its edge and covered by spiral cords. Inner lip moderately arcuate and rather thickened, with thin callus delimitating very narrow umbilical chink.

Type Locality: Lower Pleistocene of Cartiera Mulino (36°56′57″ N, 14°34′03″ E), Vittoria, Ragusa, SE Sicily. The stratotype is the phanerogams-rich 3D1 layer of Costa (1989). This deposit crops out at about one hundred meters from the abandoned paper-mill known as Cartiera Mulino. Paleoenvironmental and stratigraphic information about this site are given by Costa (1989).

Type Material: Holotype (4.3 × 2.8 mm), DGUP CMRG 005/488, coll. V. Garilli. Paratype 1 (4.1 × 2.7 mm), DGUP CMRG 006/489, coll. V. Garilli; paratype 2 (4.8 × 3 mm), ZMA Moll. 4.07.007 (*ex* CM GR 007/490, coll. Garilli); paratype 3 (4 × 2.7 mm), ZMB MB.Ga.2479 (*ex* CMGR 008/49, coll. V. Garilli); paratype 4 (4.2 × 2.9 mm), MNHN A25950 (*ex* CMGR 009/492, coll. V. Garilli); paratype 5 (4.6 × 3.1 mm), DGUP CMGR 010/493, coll. V. Garilli; paratype 6 (4.5 × 3.1 mm), DGUP CM GR 011/494, coll. V. Garilli. All type material is from the type locality, 3D1 layer. DATE?

Etymology: The species honors the name of both Francesco Garilli senior, my father and first mentor in my life, and of Francesco Garilli junior, my son.

Habitat: All the shells came from the 3D1 layer of Costa (1989). The paleoenviromental reconstruction for this layer was characterized by Costa (1989) as comparable with the Mediterranean marine-marginal modern ecotone HP (*Posidonia* beds)-SVMC (*sensu* Pérès and Picard, 1964). It is interesting that the 3D1 layer is quite rich in *Posidonia* remains mainly consisting of leaves.

Distribution: This species is known from type locality only, lower Pleistocene of Cartiera Mulino, Vittoria, Ragusa, SE Sicily.

Remarks: This quite characteristic species shows a galeodiniform shape, having a quite inflated and well-developed (also with double varix) last whorl and a large aperture provided with an internally smooth outer lip. However, its spiral sculpture does not markedly prevail over the axial, as in the typical *Alvania carinata*. Its microsculpture, limited to the early teleoconch whorls, is similar to that observed in the analogous whorls of *A. carinata*, but in the latter this microsculpture is distributed over the entire teleoconch.

The strongly cancellated sculptural pattern of *A. francescoi* new species, consisting of well-raised, subequal spiral and axial elements forming marked nodular intersections, resembles that shown by *A. cimicoides* (Forbes, 1844). The latter species, showing a more typical *Alvania* shape, has a more slender shell, a less inflated and much less developed last whorl, and a proportionally smaller aperture with denticulations on the inner part of the outer lip.

Alvania francescoi new species can also be compared with *A. rosariae* new species described later in this report. Remarks on their similarities and differences will be dealt with in the section dedicated to the latter species.

Alvania lactea (Michaud, 1830)
(Figures 44–49 and 53–61)

Rissoa lactea Michaud, 1830: 9–10, figs. 11–12

Rissoa (*Massotia*) *lactea* Michaud.—Bucquoy et al., 1884: 298, pl. 25, figs. 7–13

Massotia Dajerleini Monterosato *ex*-Schwartz ms, 1889: 33.

Massotia lactea (Michaud) forma *Dajerleini* Monterosato, 1917: 12.

Description: Shell sturdy, conical-ovate to cylindrical-ovate, occasionally almost pupoid, reaching 5.2 mm in


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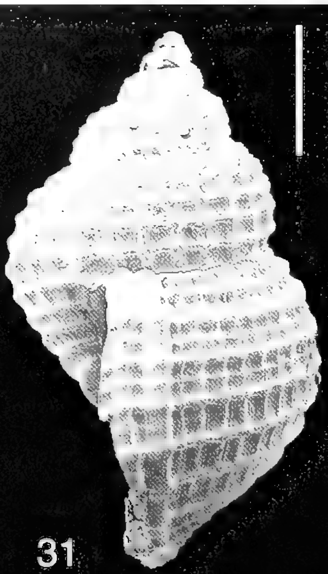
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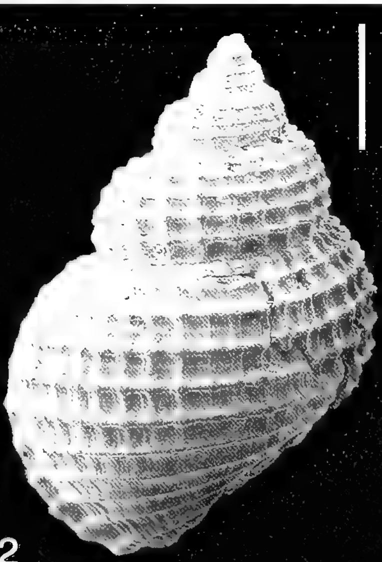
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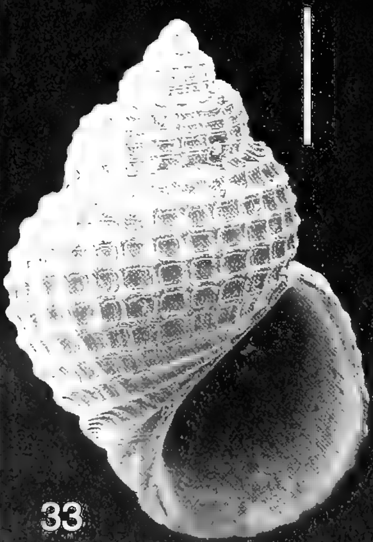
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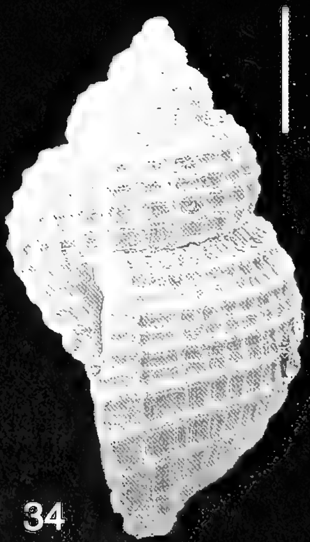

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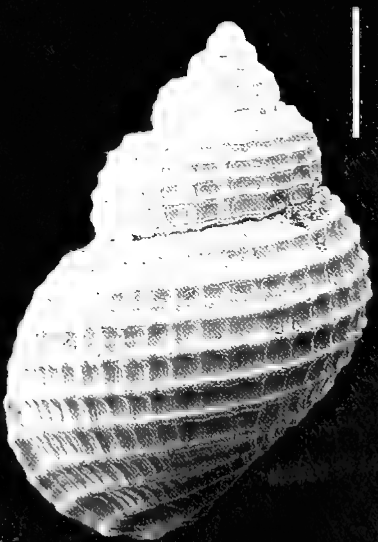
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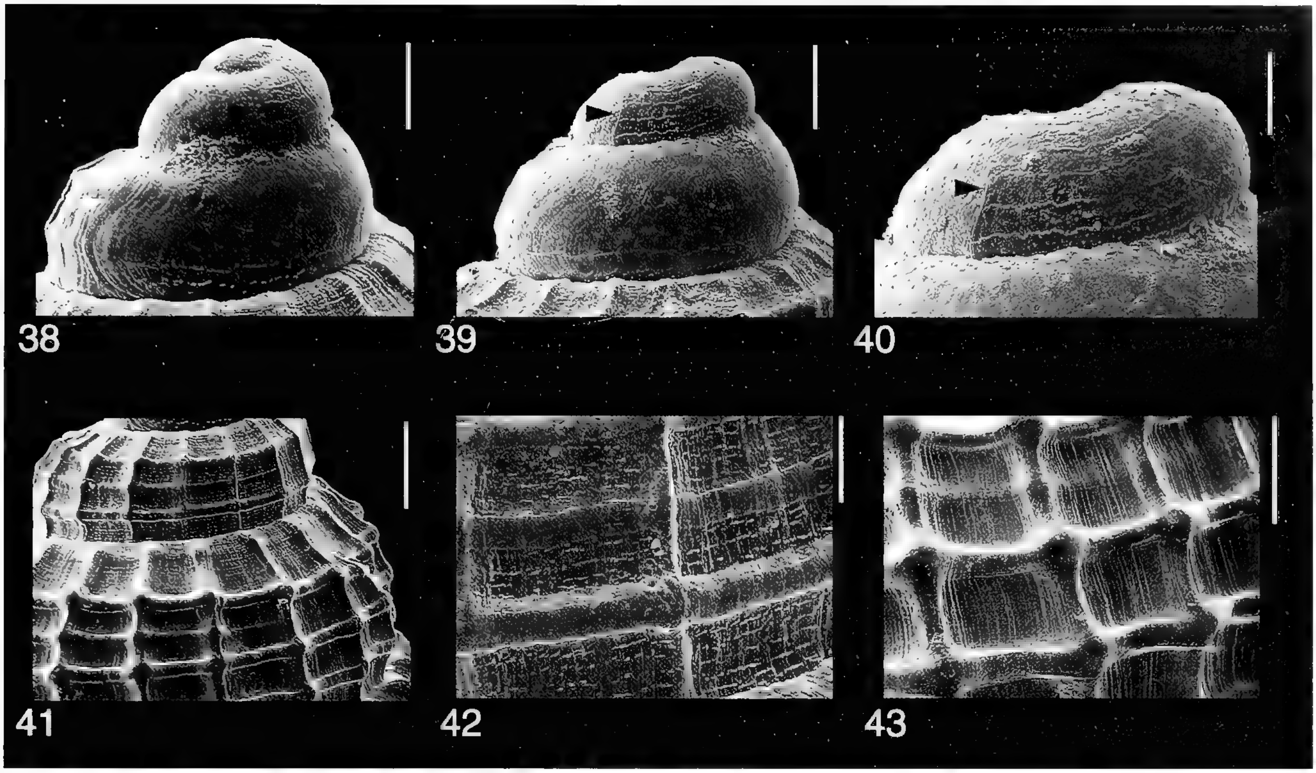
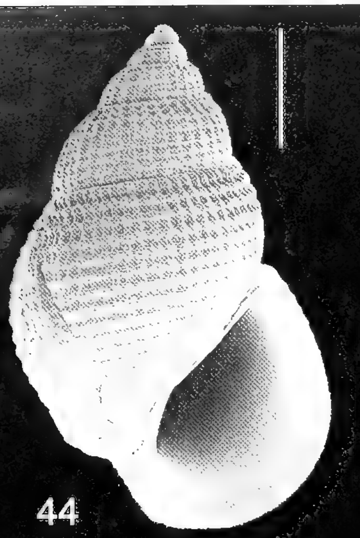


Figures 38–43. *Alvania francescoi* new species, protoconch, teleoconch sculpture and microsculpture, lower Pleistocene of Cartiera Mulino, SE Sicily, Ragusa, Vittoria. **38.** Protoconch, paratype 2. **39.** Protoconch, transition between protoconch I and II, holotype. **40.** protoconch I, holotype. **41.** Sculpture of early teleoconch whorls, note how the spiral microsculpture becomes lacking, paratype 2. **42.** Microsculpture on the first whorl, paratype 2. **43.** Detail of sculpture on the last whorl, note the numerous growth lines, paratype 4. Scale bars: 200 μm in figures 41 and 43; 100 μm in figures 38–39; 50 μm in figures 40 and 42. Black and white arrows indicate the protoconch I/protoconch II and protoconch/teleoconch boundaries, respectively.

height and 3.3 mm in width. Protoconch conical, consisting of about two convex whorls. Nucleus partially immersed. Protoconch I consisting of about 0.8 whorls, sculptured by 5–7 spiral lirae and interspersed with numerous closely packed granules, which are spirally and irregularly arranged. Protoconch II consisting of about 1.2 whorls sculptured by pimples irregular in size and arrangement. Pimples are fused into short inclined lines (opisthocline and prosocline, Figures 53–54) or form one to three discontinuous spiral ridges in abapical aspect of whorl. Protoconch/teleoconch transition well-marked and sinuous. Large shells consist of 4.2–5 weakly to rather convex whorls. These may be sculptured by a finely cancellate pattern formed by the intersection of spiral cords and numerous delicate, narrow axial ribs, or by opisthocline, pronounced ribs. Ribs often start from early whorls and are crossed by finer spiral threads. In cancellate shells, cords and ribs are equal to subequal and numbering up to nine and 40 respectively on penultimate whorl. In ribbed shells, cords and ribs are less numerous, numbering up to eight and 16 respectively on penultimate whorl. In early teleoconch whorls microsculpture consists of fine, irregular, and discontinuous spiral threads formed by groups of small granules, not covering main spiral sculpture; remaining teleoconch with a finely reticulate ultrastructure covering all primary sculpture, formed by intersection of very narrow and raised lamella-like axial ridges and very thin spiral threads. Suture slightly inclined and deeply impressed. Body whorl well-expanded, comprising ¾ of shell height. It may bear a varix, usually with angle of 180°; rarely a double varix may occur, especially in slender and cancellate shells. Aperture wide, ovate to almost pyriforme, rounded on its posterior aspect, narrowed anteriorly, comprising two thirds of last whorl height. Outer lip orthocline, internally smooth, externally thickened, mainly somewhat behind its edge, and covered by primary spiral sculpture. Sometime, in ribbed morphs, the outer lip descends vertically, so that last whorl appears rather cylindrical. Inner lip weakly arcuate, with a thin to rather

Figures 30–37. *Alvania francescoi* new species, holotype and two paratypes, lower Pleistocene of Cartiera Mulino, SE Sicily, Ragusa, Vittoria. **30–32.** Holotype, shell in apertural (30), profile (31) and dorsal (32) view. **33–35.** Paratype 3, shell in apertural (33), profile (34) and dorsal (35) view; **36–37.** Paratype 4, apertural (36) and dorsal (37) view, the last showing a double varix on the last whorl. Scale bars: 1 mm.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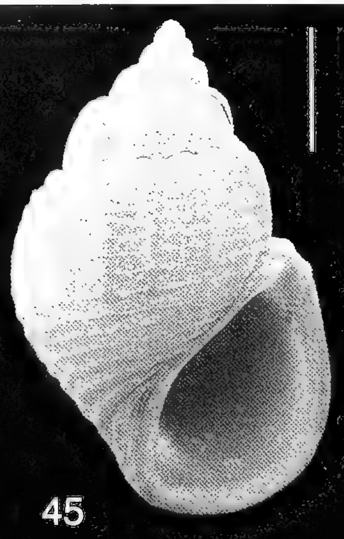
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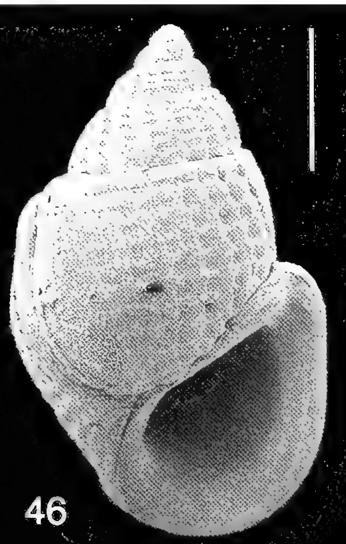
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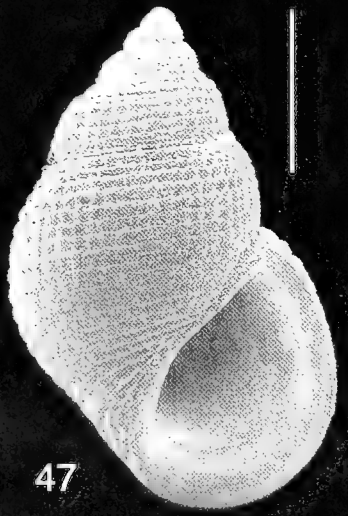
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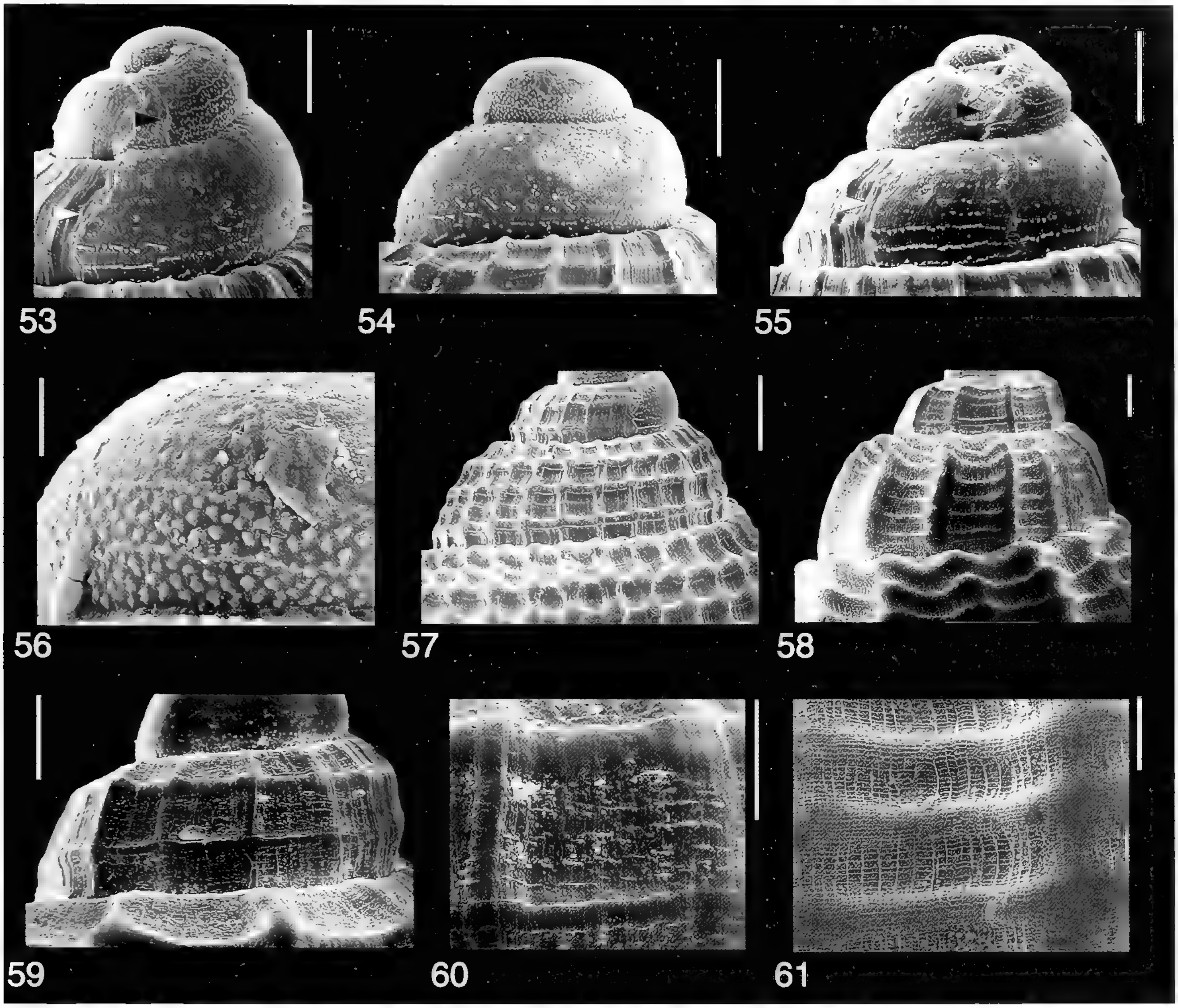

Figures 53–61. *Alvania lactea* (Michaud, 1830), protoconch and teleoconch sculpture and microsculpture. **53–54.** Profile and dorsal views of protoconch from the same shell as Figure 44, Italy, Tuscany, Siena, Poggibonsi, Villa Pietrafitta, podere Melograni, lower Pliocene, coll. MF *ex* coll. PAL (F55E). **52.** Protoconch illustrating variation of the abapical spiral ridges, Italy, Tuscany, Siena, Poggibonsi, Villa Pietrafitta, podere Sant'Uliviere, lower Pliocene, coll. MF *ex* coll. PAL (F55C). **56–57.** Sculpture of protoconch I (56) and early teleoconch whorls (57) of the same shell as figures 44 and 53–54. **58–61.** Early (58) and very early (59) teleoconch sculpture, and microsculpture of first (60) and last whorls (61), from the same shell as Figure 42, Monastir-Khenis, coll. Garilli. Scale bars: 200 μm in figures 57–58 and; 100 μm in figures 53–55, 58, 61; 50 μm in Figure 60; 20 μm in Figure 56. Black and white arrows indicate the protoconch I/protoconch II and protoconch/teleoconch boundaries, respectively

thick narrow callus, leaving a very small umbilical chink. Very fresh shells show a ferruginous periostracum. Shell color white.

Type Locality: Michaud (1831) cited the following localities, all belonging to the French Mediterranean coast: "Agde, Cette (Hérault) [now Sète], Callioure, Port-Vendre (Pyrénées orientales)". (With this citation I consider the second edition, consulted in the MNHN-DSE

Figures 44–52. Shells of *Alvania lactea* (Michaud, 1830) and *Alvania prusi* (Fischer, 1877). **44–49.** *Alvania lactea.* **44.** Italy, Tuscany, Siena, Poggibonsi, Villa Pietrafitta, Podere Melograni, lower Pliocene, coll. MF *ex* coll. PAL (F55E), cancellated morph **45.** Tunisia, Monastir-Khenis, coll. Garilli, ribbed morh (var. *dajerleini* Monterosato). **46.** Italy, Piemonte, Asti province, Pliocene MGUP coll. Doderlein (113B) shell close to the original description by Michaud (1830). **47.** Italy, Piemonte, Alessandria, Tortona, Miocene (Tortonian), MGUP coll. Doderlein (476B). **48.** Profile view of the same shell as Figure 41. **49.** Juvenile shell, Mediterranean France, Provence, Marseille, La Baule, coll. PAL, (2128BAU-V008C). **50–52.** Syntype of *Rissoa prusi* Fischer, 1877 Quaternary of Rhodes, MNHN (DHT) coll. D'Orbigny (R07495), apertural (50), profile (51) and dorsal (52) views. Scale bars 1 mm library, of Michaud's work "Descriptions de plusieurs . . ." published for the first time in 1830. The date 1831 may be doubtful, 1832 being the most commonly cited date; I prefer to follow Palazzi (2003), who provided helpful reasons to choose the former date.)

Material Examined: 37 shs, coll. H. Fischer, with no locality. Atlantic France: Normandy, St Aubin Calvados, 2 shs, MNHN; Normandy, St.Vaast, 1 sh., MNHN; Brittany, Finistère, Anse de Dionan, under stones covered with sand, 75 shs, MNHN legit. S. Gofas, 1973–78; Brittany, St. Lunaire, 40 shs, coll. MNHN coll. Dollfus, 1903; St. Lunaire, 15 shs, MNHN coll. Fischer; Brittany, Penthièrre, 4 shs, MNHN, P. Bouchet legit; Penthièrre (Morbihan), under stones covered with sand, low tide, 10 shs, MNHN coll. P. Bouchet; Penthièrre, 10 shs, MNHN, 27 Apr.1975; Aquitaine, Côte Basque, Hendaye, conchiferous detritus, beach, 5 shs, MNHN coll. S. Gofas, 1981; Côte Basque, Hendaye, infralittoral rocks, 3 shs, MNHN coll. S. Gofas, 1980–81; Côte Basque, Ondarroa, infralittoral rocks, 1 sh., MNHN coll. S. Gofas, 1980–81; Côte Basque, St. Sebastian, infralittoral rocks, 1 sh., MNHN coll. S. Gofas, 1980–81; Côte Basque, St Jean de Luz, infralittoral rocks, 57 shs, MNHN coll. S. Gofas, 1980–81; St Jean de Luz, outside Cape Ste Barbe, tide zone, stones covered with sand, 4 shs, MNHN coll. S. Gofas, Dec. 1988; St Jean de Luz, outside cape Ste Barbe, tide zone, stones covered with sand, 49 shs, MNHN coll. S. Gofas, 1989; St Jean de Luz, 54 shs, MNHN coll. H. Fischer, 1898; Aquitaine, Guéthary, 7 shs, MNHN coll. H. Fischer, 1898. Portugal: Algarve Sagres, Pontal dos Corvos, (37°01.3′ N, 08°58.3′ W), foot of falaise, 17–22 m, 1 sh., MNHN Missione Algarve, 05. 1988; Algarve Sagres, Baie de Baleeira, (37°00.7′ N, 08°55.0′ W), tide zone, 1 sh., MNHN Mission Algarve, May 1988. Atlantic Spain: Cantabria, Oriñon prov. Santander, Punta de Sonabia, infralittoral rocks, 1 sh., MNHN coll. S. Gofas, May 1989; Asturias, Muros prov. Oviedo, playa de la Liana, infralittoral rocks, 2 shs, MNHN coll. J. Ortea-S. Gofas 08.89; Cádiz, Barbate, (36°10.9′ N, 05°56.9′ W), tide zone, infralittoral rocks, 4 shs, MNHN réc. S. Gofas Apr. 1994; Cádiz, Chiclana, (36°22.5′ N, 06°12.5′ W), tide zone, infralittoral rocks and sands, 12 shs, MNHN réc. S. Gofas, Apr. 1994; Cádiz, Barbate, conchiferous detritus, beach, 3 shs, MNHN coll. S. Gofas, 1976–81; Mediterranean Spain: Malaga, Calahonda, conchiferous detritus, beach, 9 shs MNHN coll. S. Gofas, 1976–81; Malaga, Port de Marbella, conchiferous detritus, beach, 3 shs, MNHN coll. S. Gofas, 1978–81; Malaga, Benálmadena-Costa, conchiferous detritus, beach, 3 shs, MNHN réc. S. Gofas, 1991–93. Atlantic Morocco: El Jadida, (33°16′ N, 08°29′ W), large beach, rocky platform, tide zone, 16 shs, MNHN réc. S. Gofas, 26 Sep. 1991; Fedala, Mannesmann beach, conchiferous detritus, beach, 20 shs, MNHN coll. S. Gofas, 1970–72; Asilah, mouth of Oued el Helou, conchiferous detritus, beach, 21 shs, MNHN coll. S. Gofas, 1971–72; Asilah, mouth of Oued el Helou, conchiferous detritus, beach, 30 shs MNHN coll. S. Gofas, 1972–80; Temara, (33°55′ N, 07°00′ W), Sables d'Or beach, rocks and mud, 0–2 m, 24 shs, MNHN, MA48, réc. S. Gofas, 17 Sep.1991; Essaouira (formerly Mogador), (31°31′ N, 09°47′ W), rocky platform, tide zone, 1 sh., MNHN, MA48, réc. S. Gofas, 23 Sep.1991; Rabat, Lahlou, (34°02′ N, 06°51′ W), conchiferous detritus, beach, 2 shs, MNHN réc. S. Gofas, 28 Sep. 1991; Essaouira (formerly Mogador), 4 shs, MNHN; Strait of Gibraltar, Morocco: Tanger, Grande Plage, conchiferous detritus, beach, 8 shs, MNHN coll. S. Gofas, 1970–81. Strait of Gibraltar, Spain: Ceuta Nord, Benzu, infralittoral rocks, 2 shs, MNHN coll. S. Gofas 1976–1981. Algeria: Oran, 6 shs, MNHN coll. Locard. Mediterranean France: Languedoc, Roussilion, Banyuls sur Mer, near the beach de Paulilles, infralittoral rocks, 1 sh., MNHN coll. Bouchet and Gofas, Sep. 1980; Languedoc, Roussilion, 7 shs, MNHN coll. Ph. Dautzenberg, (figured in Moll. Rouss. T. I pl. 35, figs.7–13); Languedoc, Roussilion, Sète, 6 shs, MNHN coll. Locard; Provence, Toulon, 8 shs, MNHN coll. Petit; Provence, Cannes, 21 shs, MNHN coll. Dollfus, 1903; Provence, east coast, Iles Embiez, passe du Gaou, under stones covered with sand, 0–1 m, 5 shs, MNHN réc. S. Gofas, Aug. 1988; Provence, east coast, Iles Embiez, (43°04.3′ N, 5°47.4′ E), passe du Gaou, under stones covered with sand, 0–3 m, 2 shs, MNHN réc. S. Gofas, Aug. 1988; Provence, Iles Embiez, (43°04.3′ N, 5°47.4′ E) passe du Gaou, rocks, photophile algae under stones covered with sand, 0–3 m, 1 sh., MNHN réc. S. Gofas, Jun. 1995; Iles Embiez, côte Nord et Petit Rouveau, infralittoral rocks, 3 shs, MNHN coll. S. Gofas, 1968–70; Provence, Les Embiez, cote Nord et Petit Rouveau, (43°05′ N, 5°47′ E), rocks, photophile algae, 0–1 m, 3 shs, MNHN réc. S. Gofas, Jun. 1995; Iles Embiez, conchiferous detritus, beach, 15 shs, MNHN coll. S. Gofas, 1968–70; Provence, St Clair, (43°08.2′ N, 6°23.2′ E), infralittoral rocks, 0–1 m, 2 shs, MNHN réc. S. Gofas, Sep. 1992; Provence, Porquerolles plage Notre Dame, (43°00.6′ N, 6°13.8′ E), rocks, 0–1 m, 1 sh., MNHN réc. S. Gofas, Sep. 1992; Provence, Le Dramont, conchiferous sand, beach, 3 shs, MNHN réc. J. Pelorce, 1992; Provence, Marseille (Endoume, 43°16.9′ N, 05°21.0′ W), littoral rocks, 1 sh., MNHN réc. S. Gofas Apr. 1995; Provence, St. Raphael, 5 shs, MNHN; Provence, Bandol, 16 shs, MNHN coll. Locard; St. Raphael, 2 shs, MNHN coll. Locard; Corsica, Ajaccio, 17 shs, MNHN coll. Jousseaume; Corsica, Algajole, 35 shs, coll. MF, 2123. Tunisia: Monastir-Khenis, beach, 1 sh., coll. Garilli, legit Garilli and Galletti 4/2000; Djerba, beach, 1 sh., coll. MF *ex* coll. C. Bogi, Jun. 1981, 2163JER. Italy: Piemonte, Asti, Baldichieri, "Grottino Monale", 20 shs, yellow sands, middle-upper Pliocene, coll. MF *ex* coll. PAL, F104A; Piemonte, Asti, 24 shs, Pliocene, MGUP coll. Doderlein, 113B; Piemonte, Alessandria, Tortona, 1 sh., Miocene, MGUP coll. Doderlein, 476B; Alessandria, Villalvernia, at the Cemetery, 1 sh., Astian yellow sands, middle-upper Pliocene, coll. MF *ex* coll. PAL, F118A; Emilia Romagna, Modena, Maranello, Fogliano, Gagliardella, Rio Grizzaga sands, 1 sh., middle Pliocene, coll. MF *ex* coll. PAL, F39A; Tuscany, Siena, Poggibonsi, Villa Pietrafitta, Podere "La Vigna", (SP 36, 4.9 km E side), 7 shs, lower Pliocene, coll. MF *ex* coll. PAL, F55B; Siena, Poggibonsi, Villa Pietrafitta, "Sbarra", (SP 36, 5.2 km), 2 shs, sands, lower Pliocene, coll. MF *ex* coll. PAL, F55D; Siena, Castelnuovo Berardenga, Terre Rosse, (SS 73, 104 km), 1 sh., sands, lower Pliocene, coll. MF *ex* coll. PAL, F36A; Siena, Poggibonsi, Villa Pietrafitta, Podere Sant'Uliviere, 27 shs, lower Pliocene, coll. MF *ex* coll. PAL, F55C; Siena, Poggibonsi, Villa Pietrafitta, Podere Melograni, 6 shs, sands, lower Pliocene, coll. MF *ex* coll. PAL, F55E; Siena, Colle Val d'Elsa, Bibbiano, 2 shs, yellow sands, lower Pliocene, coll. MF *ex* coll. PAL, F108A; Tuscany, Livorno, Tuscan Archipelago, Island of Elba, Procchio, 12 m, *Posidonia* bed, 2 shs, coll. MF *ex* coll. C. Bogi, 2120PROC; Umbria, Terni, Ficulle, quarry near Chiani river, (SS71), 1 sh., *Cidaris* marly sands, lower Pliocene, coll. MF *ex* coll. PAL, F68A; Sardinia, Nuoro, San Teodoro, 6 shs coll. PAL; Puglia, Taranto, MSNCS 44744 (*ex* 1505), 1974, BDA legit and det.; Sicily, Messina, Milazzo, Capo Milazzo, Cala S. Antonio, 12 shs, upper yellow sands, upper Pleistocene, coll. MF *ex* coll. PAL, F5A; Sicily, Catania, Grammichele, C.da Catallarga, 2 shs, coarse sands, lower Pleistocene, coll. MF *ex* coll. PAL, F27A; Sicily, Palermo, 1 sh., MNHN coll. Petit; Sicily, Palermo, 2 shs, MNHN coll. Dollfus, 1903; Palermo, Tommaso Natale, 13 shs, upper Pleistocene, MGUP 167/2/50; Palermo, Addaura, 1 sh., upper Pleistocene, MGUP 587/5/15; Sicily, Catania, 2 shs, MSNCS 44743 (*ex* 1448), 4/1974, G. Gentile legit and det.; Sicily, Siracusa, Vendicari, 1 sh., coll. PAL, 2124. Adriatic Sea: 128 shs, MNHN. Croatia: Zara, 8 shs, MNHN coll. Petit, 1873. Greece: Evvia Island (Euboea), Loukissia, 4–5 m, 1 sh., coll. PAL *ex* coll. Bogi Cesare, 2121LUC. Israel: Haifa, 9 m, 1 sh., coll. PAL *ex* coll. C. Bogi, 1994, 2164HA.

Habitat: As indicated by Jeffreys (1867), Gofas and Ponder (1991), and Bouchet (1978; 1992), this species typically lives buried under stones covered with sand at very shallow waters. I found very fresh shells collected from along all the upper part of the infralittoral stage.

Distribution: All the Mediterranean, probably decreasing abundance in eastward direction. In the eastern Atlantic it lives from the British Islands (see also Jeffreys, 1867; 1869) to Morocco. *Alvania lactea* has also been recorded from the Black Sea (Anistratenko and Starobogatov, 1994). This species probably originated in the Mediterranean Neogene, from where it is recorded from the Miocene of north Italy. It becomes more common in the western and central Mediterranean Pliocene deposits, where it is recorded from several localities of north, central, and south Italy (material herein studied; see also Sacco, 1895, and Chirli, 2006) and Spain (Estepona, Landau et al., 2004). In the Atlantic Pleistocene, as reported by Landau et al. (2004), it is recorded from the postglacial of Iceland, the North Sea Basin and the British Isles. As subfossil, it is recorded from Sweden (Hubendick and Warén, 1969). In Mediterranean, it is common from the lower-upper Pleistocene of Sicily and is also recorded from the lower Pleistocene of Tuscany (Chirli, 2006).

Remarks: This is a very variable species especially with respect to sculpture and shell shape. The typical morph, as described and figured by Michaud (1831: fig. 12), has a clathrate sculpture with the axial pattern dominating over the spiral one. The finely cancellated type, usually characterized by an elongate general shape and more convex whorls, corresponds to the forma *minortenuisculpta* Monterosato, 1917. Two varieties, *semiacostata* and *fusulatovaricosa* (the latter often bearing varices), were described by Sacco (1895) on similar material from the Pliocene of north Italy. This cancellate morph (Figures 44 and 47–48), which seems to be the only representation of the discussed species in the Miocene, is the most common in the Pliocene collections studied (see also Sacco, 1895: p. 28; Chirli, 2006: figs. 9–11 and 15–16) and becomes less common in Quaternary material. The markedly ribbed morph, described by Sacco (1895) as var. *laticostata* (from the Pliocene of Italy), and better known as forma *dajerleini* Monterosato, 1889, bears strong ribs, starting from the early teleoconch whorls. According to Monterosato (1917), this represents the Atlantic morph of *Alvania lactea*. I agree with Van Aatsen et al., considering it not exclusively an Atlantic morph, being present in some Mediterranean localities (see Figure 45). It is noteworthy to remember that in a extensive lot (128 shells, MNHN-DSE) from the Adriatic Sea, all the above mentioned morphs coexist.

Especially when its typical morphs are considered, *Alvania lactea* has a very characteristic ribbed, cylindrical-ovate shell and can not be confused with its congeners. Some problem might occur when considering the cancellate morph, which can be compared to the recently described Pliocene species *A. fredianii* Della Bella and Scarponi, 2000 (see this article for the main differences between the two species). The same morph of *A. lactea* shows strong similarities with the new species described herein, *A. rosariae* (see discussion below for differential diagnosis).

Alvania lactea is the type species of *Massotia* Bucquoy et al., 1884, which is considered a synonym of *Alvania* sensu stricto by Ponder (1985) on the basis of the number of the metapodial tentacles, shown by this species, based on a description by Jeffreys (1867). In my opinion, a more exhaustive anatomical dataset could be provided. Nevertheless, even on the basis of its shell features and intraspecific variation, there is no reason to consider *Massotia* as a well-supported group.

Alvania lactea has a very complicated teleoconch microsculpture, which could certainly be considered as a suite of distinctive characters, not observed in the closely-related taxa discussed in the present report. Early teleoconch whorls show a pattern similar to that observed in *A. carinata*, *A. francescoi* new species, and *A. rosariae* new species (detailed comparisons are provided below), but the remainder of the shell is covered by very narrow, raised lamella-like axial ridges and very thin spiral threads. Also its protoconch I sculpture is rather distinctive, showing a pattern similar to that observed in *A. carinata*, *A. francescoi*, *A. rosariae,* and *A. tenera* (as well as in many other rissoids), but having a coarser ornamentation.

Alvania prusi (P. Fischer, 1877)
(Figures 50–52)

Rissoa (*Alvania*) *Prusi* P. Fischer, 1877: 80.

Description: Shell small, sturdy, conical, partially worn off, 4.7 mm in height, 3.2 mm in width. Protoconch multispiral, conical, consisting of about little more than two convex whorls. Teleoconch is formed by about four convex whorls, provided with a very delicate, cancellated sculpture almost giving a pitted shape to shell surface. This sculpture consists of moderately pronounced spiral cords crossed by apparently flat axial ribs. Spiral cords number 7–8 on penultimate whorl and 16 on body whorl; they are flatter and wider on shell base. Ribs, numbering about 40 on penultimate whorl, are lacking in basal part of last whorl. Sutures slightly inclined and deeply impressed. Last whorl well-expanded, rather angulated at the base and inflated, comprising ¾ of shell height. Aperture wide, ovate to almost pyriforme, pointed adapically, comprising ½ of the total height, ⅔ of last whorl height. Outer lip prosocline, internally smooth, externally with an almost flat, wide thickening, apparently smooth. Inner lip moderately arcuate, with a modest and narrow reflection on columellar area, leaving a very small and narrow umbilical chink (filled up with sediment).

Type Locality: Isle of Rhodes

Type Material: One syntype, R07495 in MNHN-DHT, from type locality.

Material Examined: Eastern Mediterranean Sea, Quaternary of Rhodes, type locality, MNHN-DHT (R07495), 1 sh.

Habitat: It is very difficult to characterize the paleoecological significance of this extinct species since no data about its paleoenvironment are directly available or deducible. Furthermore, Fischer (1877) provided no precise indication about the site, stratotype, and its sedimentological and paleontological nature. Considering all the other molluscan species described from Rhodes by the same author, a shallow water depositional environment (linked to the modern phanerogam infralittoral bottom) can be inferred.

Distribution: The species is known only from the type locality, and its distribution appears to be limited to the Quaternary of Rhodes.

Remarks: This taxon is practically unknown. To my knowledge, the most recent treatment is that of Monterosato (1917), who considered it as a separate species belonging to the *Massotia* group.

Alvania prusi could be confused with juvenile shells of *Alvania lactea* (the form with cancellate sculpture, see Figure 49), which exhibit a very similar body whorl profile. *Alvania prusi* is quite close to *A. fredianii* Della Bella and Scarponi (2000) from the Pliocene of Tuscany. Both species share the general shell shape and the finely reticulated sculpture, but the latter is of smaller size, has a paucispiral protoconch, deeper sutures, and a weakly denticulated outer lip (see Della Bella and Scarponi, 2000: pls. 1 and 2).

Alvania rosariae new species
(Figures 62–79)

Description: Shell small, sturdy, conical-ovate to turriform, moderately to markedly inflated, reaching about 5 mm in height, 3.5 mm in width (holotype 4 mm in height and 2.7 mm in width). Protoconch multispiral, conical, consisting of about 2–2.1 convex whorls. Protoconch I of about 0.8 whorls sculptured by 5–6 very fine spiral lirae irregularly interspersed with microscopic granules. Protoconch/teleoconch transition well marked and sinuous adapically. Protoconch II sculptured by spirally arranged microscopic pimples (stronger in adapical portion) forming one to two spiral threads, the lower very close to the suture, occurring on last whorl. Teleoconch formed by about 4.2 usually very convex whorls, sculptured by numerous axial ribs and slightly stronger spiral cords. The latter, rapidly increasing in count, number 2–6, 6–10 (rarely 11), and 26–34 (in specimens higher than 3.5 mm) on the first, penultimate, and last whorl of the teleoconch, respectively. Some secondary, less marked cords may occur on last whorl, usually close to the outer lip. The adapical one, two, and three spiral cords on first, penultimate and body whorl, respectively are more pronounced. In specimens higher than 3.5 mm, axial sculpture consists of 44–60 narrow ribs (52 in holotype) on the penultimate whorl. Ribs become narrower and lamella-like to obsolete or lacking on shell base, particularly close to columella. The same may occur on the terminal portion of the body whorl (Figure 66). The intersection of spiral cords with axial ribs gives a characteristic cancellate and gently nodular shape, forming a rectangular (almost equilateral in the central portion of the body whorl) pattern. The long axis of these rectangles is perpendicular to the shell axis on the central and abapical portion of whorls and parallel on upper part. Microsculpture consists of very fine, sometime irregularly interspersed, spiral lirae (Figure 77). These become obsolete on the penultimate and body whorls, where numerous, very fine and narrow ribs (possible growth lines) occur. Lirae are continuous only on adapical portion of early teleoconch whorls and never cover primary spiral sculpture. Sutures slightly inclined and rather deeply impressed. Last whorl well-developed, comprising about ⅔ to ⅘ of the shell height, usually with a very convex profile. It sometime bears one or two close varices which may form angles of 10° to 210°. Aperture wide, ovate, comprising ½ to ⅗ of the total height; ⅔ to ¾ of last whorl height. Outer lip orthocline (slightly curved), internally smooth, externally markedly thickened close to lip edge and covered by spiral cords. Inner lip moderately arcuated and rather thickened in the columellar area, where a very narrow umbilical chink occurs.

Type Locality: Lower Pleistocene of Cartiera Mulino (36°56′57″ N, 14°34′03″ E), Vittoria, Ragusa, southeastern Sicily. The stratotype is the 3D1 layer of Costa (1989).

Type Material: Holotype (4.0 × 2.7 mm), DGUP CMRG 12/496, coll. Garilli; Paratype 1 (4.6 × 3.2 mm), ZMA Moll. 4.07.014 (*ex* CMRG 13/497 coll. Garilli); paratype 2 (not-complete shell, 3 mm width), ZMA Moll. 4.07.08 (*ex* CMRG 014/498 coll. Garilli); paratype 3 (3.6 × 2.55 mm), DGUP CMRG 15/499, coll. V. Garilli; paratype 4 (4.5 × 3.3 mm), DGUP CMRG 16/500, coll. Garilli; paratype 5 (3.8 × 2.5 mm), MNHN A25951 (*ex* CMRG 17/501, coll. Garilli); paratype 6 (3.85 × 2.75 mm), ZMB MB.Ga.2480 (*ex* CMRG 18/502, coll. Garilli); paratype 7 (3.6 × 2.4 mm), ZMB MB.Ga.2481 (*ex* CMRG 19/503, coll. Garilli); paratype 8 (3.8 × 2.6 mm), DGUP CMRG 20/504, coll. Garilli; paratype 9 (3.6 × 2.6 mm), DGUP CMRG 21/505, coll. Garilli; paratype 10 (3.95 x 2.6 mm), DGUP CMRG 22/506, coll. Garilli; paratype 11 (4.2 × 2.75 mm), DGUP CMRG 23/507, coll. Garilli; paratype 12 (3.7 × 2.55 mm), DGUP CMRG 24/508, coll. Garilli; paratype 13 (3.9 × 2.5 mm), DGUP CMRG 25/509, coll. Garilli; paratype 14 (3.7 × 2.55 mm), DGUP CMRG 26/510, coll. Garilli; paratype 15 (3.5 × 2.6 mm), DGUP CMRG 27/511, coll. Garilli; paratype 16 (4 × 2.6 mm), DGUP CMRG 28/512, coll. Garilli; paratype 17 (3.9 × 2.7 mm), DGUP CMRG 29/513, coll. Garilli; paratype 18 (3.6 × 2.45 mm), GNHM ID 30.706 (*ex* KIGR 3/514 coll. Garilli); paratype 19 (4 × 2.7 mm), GNHM ID 30.707 (*ex* KIGR 4/515 coll. Garilli); paratype 20 (4.5 × 2.7 mm), GNHM ID 30.708 (*ex* KIGR 5/516 coll. Garilli); paratype 21 (4.7 × 3.4 mm), GNHM ID 30.709 (*ex* KIGR 6/517 coll. Garilli); paratype 22 (4.4 × 2.9 mm), GNHM ID 30.710 (*ex* KIGR 7/518 coll. Garilli); paratype 23 (4 × 2.55 mm), GNHM ID 30.711 (*ex* KIGR 8/519 coll. Garilli); paratype 24 (3.35 × 2.5 mm), GNHM ID 30.712, (*ex* KIGR 9/520 coll. Garilli); paratype 25 (2.9 × 1.95 mm), GNHM ID 30.713 (*ex* KIGR 10/521 coll. Garilli); paratype 26 (not-complete shell), GNHM ID 30.714 (*ex* KIGR 11/522 coll. Garilli); paratype 27 (4.15 × 2.65 mm), GNHM ID 30.715 (*ex* KIGR 12/523 coll. Garilli); paratype 28 (4.0 × 2.6 mm), GNHM ID 30.716 (*ex* KIGR 13/524 coll. Garilli); paratype 29 (not-complete shell, 3.85 mm), GNHM ID 30.717 (*ex* KIGR 14/525 coll. Garilli); paratype 30 (2.7 × 1.9 mm), GNHM ID 30.718 (*ex* KIGR 15/526 coll. Garilli); paratype 31 (3 × 2.05 mm), GNHM ID 30.719 *ex* KIGR 16/527 coll. Garilli); paratype 32 (3.8 × 2.5 mm), GNHM ID 30.720 (*ex* KIGR 17/528 coll. Garilli); paratype 33 (3.55 × 2.5 mm), GNHM ID 30.721 (*ex* KIGR 18/529 coll. Garilli); paratype 34 (4.05 × 2.8 mm), GNHM ID 30.722 (*ex* KIGR 19/530 coll. Garilli); paratype 35 (4.95 × 3.25 mm), GNHM ID 30.723 (*ex* KIGR 20/531 coll. Garilli); paratype 36 (not measured), GNHM ID 30.724 (*ex* KIGR 21/532, coll. Garilli); paratype 37 (not measured), GNHM ID 30.725 (*ex* KIGR 22/533, coll. Garilli). Holotype and Paratypes 4–17, from the lower Pleistocene of Cartiera Mulino, 3D1 bed of Costa (1989), Vittoria, Ragusa, southeastern Sicily. Paratypes 1–3 from the same locality, 3D2 bed of Costa (1989). Paratypes 18–22 and 24–35 from the middle to upper Pleistocene of Kyllini, northwestern Peloponnesus, N2 and H6 beds of Garilli et al. (2005a), respectively. Paratypes 36 and 37, same locality, from the lower to early middle Pleistocene P3 layer of Garilli (2005b) and from a late lower Pleistocene yellowish to reddish sandy layer about 50 m underlying the F14 bed of Garilli and Galletti (2007), respectively.

Another four, uncatalogued paratypes are housed in DSTC (1 sh. from 3D1, 1 sh from 3D2 and 2 shells from 3C bed of Costa, 1989, all from the lot n° 18, as *Galeodina carinata* (Da Costa). One more uncatalogued paratype (*ex* CMRG 030/534 coll. Garilli), from the type locality, 3D1 layer, is in coll. MF (Prato).

Etymology: The species is dedicated to my wife Rosaria.

Material Examined: The type material from the lower Pleistocene of Cartiera Mulino, Vittoria, Ragusa, SE Sicily, 18 shs, and from the late lower (1 sh., from a reddish to yellowish sandy bed about 50 m underlying the F14 bed of Garilli and Galletti, 2007), lower to middle (2 shs, layer P3 of Garilli et al, 2005b), and middle to upper Pleistocene (13 shs, layer H6; 4 shs, layer N2) of Kyllini, Elea, NW Peloponnesus, Greece.

Habitat: In the type locality, the species was mainly recovered from the layers 3D1 and 3D2 which were linked to the ecotone SVMC-HP (sensu Pérès and Picard, 1964) by Costa (1989). In the Kyllini sites, this species was found in cerithids-trochids-rissoids assemblage linked to the present biocenosis HP, characterized by the phanerogam *Posidonia oceanica* (Linnaeus) Delile, 1813 (See Garilli et al. (2005a); Garilli et al. (2005b), and Garilli and Galletti (2007) for more detailed information about the paleoecological characteristics of the cited Kyllini strata.)

Distribution: The species has a lower to middle-upper Pleistocene stratigraphic range, presently limited to SE Sicily and NW Peloponnesus, being recorded from the lower Pleistocene of Sicily (type locality) and from the lower to upper Pleistocene deposits of Kyllini, Greece (NW Peloponnesus).

Remarks: *Alvania rosariae* represents a sort of intermediate form between *A. carinata* and *A. lactea* (cancellate form). Compared with the former taxon, it shows some similarities in the type of intraspecific variation, showing very inflated to quite elongate shells (compare


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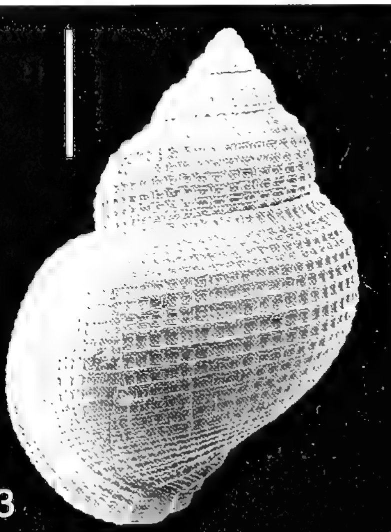
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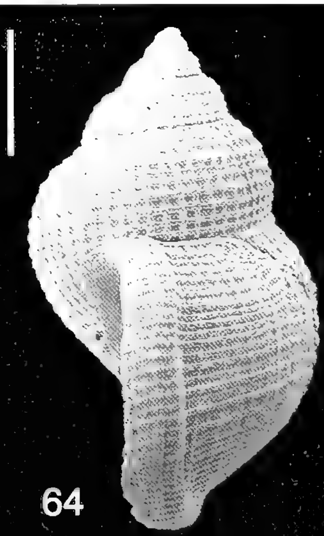
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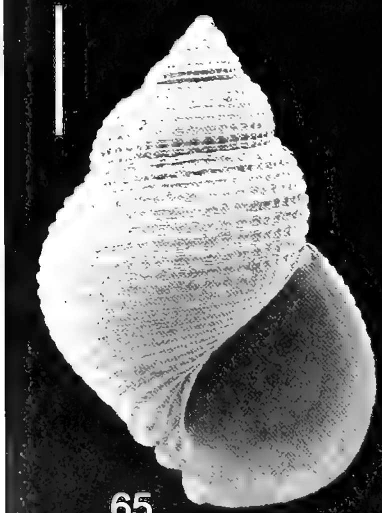
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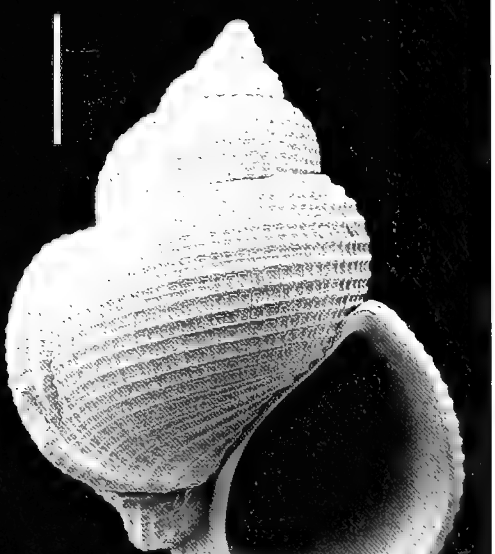
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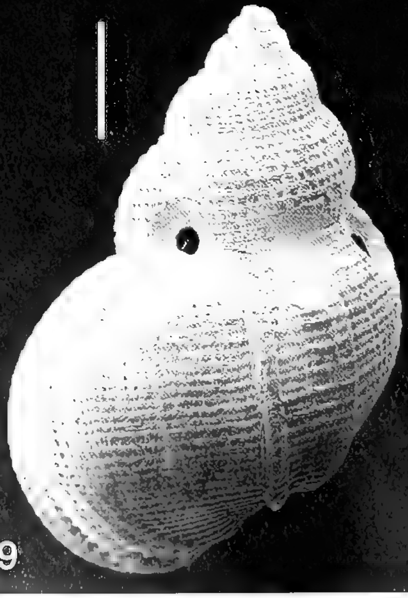
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Figures 68–69 with the "form" *ecarinata* of *A. carinata*, Figures 1, 4, 5), in usually bearing varices, and in the microsculpture of the early teleoconch. In addition, their respective larval shells do not show relevant differences. *Alvania rosariae* new species can be distinguished by absence of a keeled shape, having subequal and more numerous spiral and axial sculptural elements. The cancellate form of *A. lactea* is comparable with *A. rosariae* new species, having a very similar sculpture and occasionally a similar shell shape (only in the very ovate morph, e.g. Figures 44, 47 and 65–66). However, *A. rosariae* new species differs by having more convex whorls and a very different microsculptural pattern, with only irregular, fine, often interrupted spiral threads covering the early teleoconch whorls. Furthermore, the protoconch I of *A. lactea* bears a coarser sculpture, consisting of more numeorus and larger pimples and much more elevated spiral lirae.

Alvania rosariae new species can also be compared with *A. francescoi* new species: both species have a galeodiniform shape, a similar microsculpture, and share a very similar sculptural pattern on the protoconch. Differences between the two species are mainly found in the teleoconch sculpture, which is strongly nodular and coarser in *A. francescoi* new species; furthermore the latter has fewer spiral cords and axial ribs.

Alvania rosariae new species may resemble *A. magistra* Chirli, 2006, an interesting galeodiniform species from the Pliocene of N Italy and S Spain (Chirli, 2006: pl. 11, figs.13–16 and pl. 12, figs.1–8; Landau et al., 2004: pl. 10, figs.3a–e, as *Alvania* sp.), showing a quite similar finely cancellate sculpture, especially in the arrangement of the adapical cords, and a quite wide, ovate aperture. However, the latter species shows an unusual outer lip profile, having a wide sinus at the upper aspect, its protoconch I shows a netted *Manzonia*-like sculpture, while protoconch II appears less sculptured than in *A. rosariae* new species

Alvania tenera (Philippi, 1844)
(Figures 80–89)

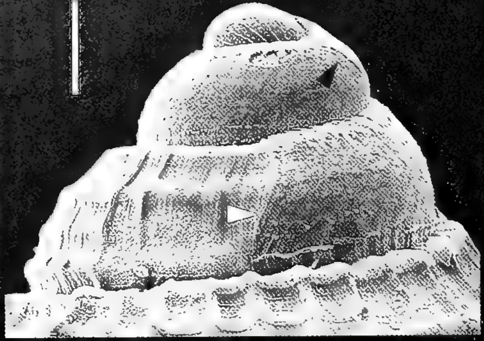
Rissoa tenera Philippi, 1844: 128–129, pl. 23, fig. 15.
Galeodina tenera (Philippi, 1844).—Piani, 1979: 71, fig. 4

Description: Shell minute, conical, and subcarinate, to conical-ovate or elongate, moderately to markedly sturdy, reaching 2.2 mm in height and 1.4 mm in width. Protoconch multispiral, conical, with 2–2.3 convex whorls. Protoconch I consists of about 0.8 whorl, sculptured by six very thin spiral lirae and a few microscopic granules between them. Protoconch II is sculptured by a few to abundant very small granules. These are more numerous on last half whorl, where they are spirally arranged, forming very discontinuous and irregular ridges. Protoconch/ teleoconch transition distinct, with a slight (to very slight) sinuosity. Teleoconch consists of 3–3.5 weakly to discretely convex whorls, quite variable in width. These are sculptured by well-raised, narrow, spiral, occasionally almost keel-like cords (in quite conical shells), which overide the axial sculpture. They number 3–4, 4–5, and 12–13 on first, penultimate, and body whorl, respectively. Usually, weaker cords are present on shell base or close to upper suture. Axial sculpture formed by very narrow, prosocline, rows of short segments, forming discontinous ribs, occurring between spiral cords and becoming very thin to lacking toward shell base. Ribs number 40–60 on last whorl. At the intersections with axial elements, spiral cords generally appear very finely nodular (Figure 86). Last whorl well-expanded, with a rather rounded profile, sometimes inflated, comprising about ⅔ to ¾ (in subcarinate and conical shells) of total shell height. Aperture ovate, anteriorly rounded, posteriorly angulated, comprising about ½ and ⅔ of total shell and last whorl height, respectively. Outer lip rounded, markedly prosocline, thin, internally smooth, externally with no thickening. Inner lip weakly arcuate, with a thin and narrow (Figure 82) to stronger and wider (Figure 80) callus, leaving a very narrow umbilical chink. Coloration usually consists of reddish to brown spots on a cream-whitish or (rarely) brownish background.

Type Locality: Peninsula of Magnisi (originally indicated as "Peninsula Thapsum" from the old Greek name of Magnisi), Siracusa, southeastern Sicily.

Material Examined: Atlantic: Canary Islands, Tenerife, Pal-Mar, 6–8 m, 1 sh., MNHN coll. P. Bouchet, 15 Jul. 1980; Morocco: Asilah, mouth of Oued el Helou, conchiferous detritus, beach, 9 shs, MNHN coll. S. Gofas, 1971–72; El Jadida, (33°16′ N, 08°29′ W), large beach, conchiferous detritus, beach, 5 shs, MNHN réc S. Gofas, 26 Sep. 1991; El Jadida, (33°16′ N, 08°29′ W), large beach, tide zone, 4 shs, MNHN réc S. Gofas, 26 Sep.1991. Strait of Gibraltar: Spain, Cadiz, conchiferous detritus, beach, 2 shs, MNHN coll. S. Gofas, 1976–81; Cadiz, Tarifa, beach, 4 shs, coll. PAL *ex* coll. C. Bogi, Jun. 1986, 2030TAR; Cadiz, Tarifa, Torre de la Peña, conchiferous detritus, beach, 3 shs, MNHN coll. S. Gofas, Aug. 1981; Morocco, Tanger, Grande Plage, conchiferous detritus, beach, 1 sh., MNHN coll. S. Gofas, 1970–81. Mediterranean: Spain, Andalusia, Punta della Mona, 43 m, 5 shs, coll. PAL *ex* coll. C. Bogi, 2032PMO; Spain, Málaga, industrial dredging, 20–40 m, 1 sh., MNHN réc.

Figures 62–69. *Alvania rosariae* new species, holotype and paratypes 16, 21, and 35. **62–63.** Apertural (62), dorsal (63) and profile 64) views of holotype, lower Pleistocene of Cartiera Mulino, bed 3D1 of Costa (1989), SE Sicily, Ragusa, Vittoria. **65–66.** Paratype 16, dorsal (65), illustrating varices on the last whorl, and apertural (66) view, same site and locality. **67.** Paratype 21, a very inflated last whorl and a strong varix opposite the outer lip, middle to upper Pleistocene of Kyllini, NW Peloponnesus, N2 bed of Garilli et al. (2005a). **68–69.** Apertural (68) and dorsal (69) view of paratype 35, showing a quite slender shell, middle to upper Pleistocene of Kyllini, northwestern Peloponnesus, H6 bed of Garilli et al. (2005a). Scale bars 100 μm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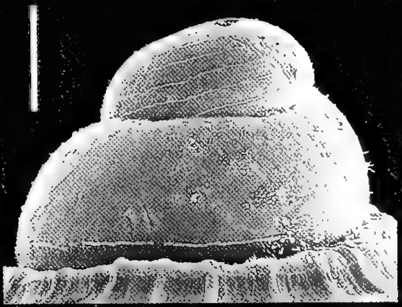
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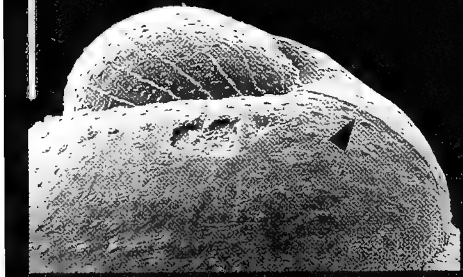
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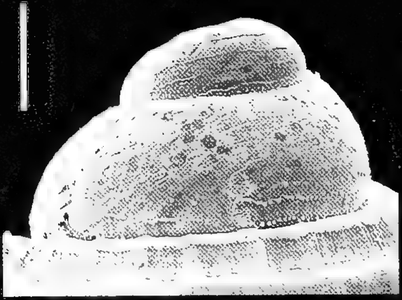
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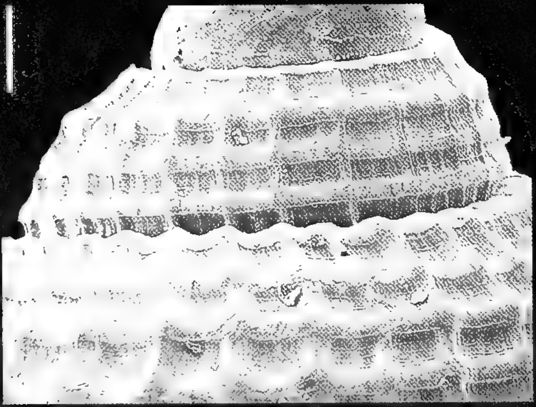
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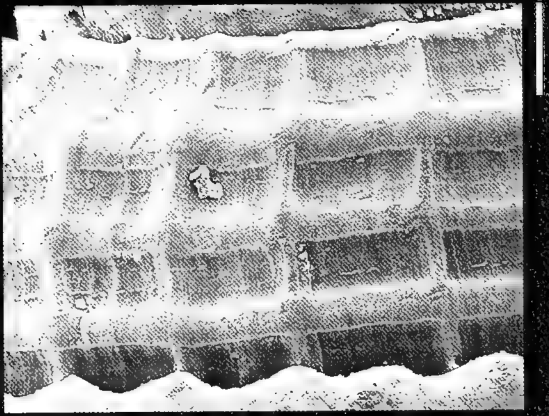
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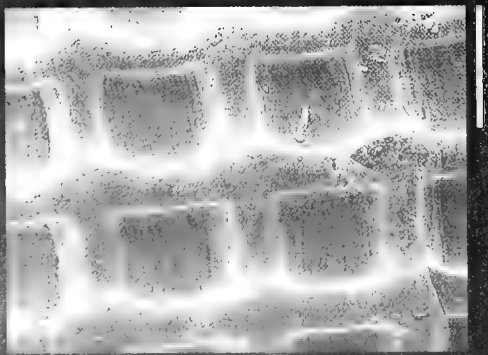
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S. et C. Gofas, May 1991; Malaga, Calahonda, conchiferous detritus, beach, 1 sh., MNHN coll.S. Gofas, 1976–81; Malaga, Benalmádena, conchiferous detritus, beach, 6 shs, MNHN réc S. Gofas, 1991–93; Malaga, Mijas, detritus, 10 m, 4 shs, coll. Stefano Rufini; Malaga, Cabo Pino, detritus, 10 m, 2 shs, coll. SR, (41.80g); Morocco, Cabo Negro, beach, 1 sh., MNHN coll. S. Gofas, det. W. Ponder, 1986; France, Provence, Marseille, Curry, beach, 3 m, 2 shs, coll. PAL *ex* coll. C. Bogi, Jun. 1986, 2037MAR; Provence, Marseille, La Baule, small beach at 25 km west from Marseille, 9 shs, coll. PAL *ex* coll. C. Bogi, Oct. 1986, 2035BAU; Provence, Le Dramont, (43°24.7′ N, 6°51.7 E), 22–30 m, 26 shs, MNHN réc. J. Pelorce, 1992; Provence, Les Embiez, cote Nord et Petit Rouveau, (43°05′ N, 5°47′ E), rocks, algae, 0–1 m, 11 shs, MNHN réc S. Gofas, Jun. 1995; Provence, Marseille, Cap Morgiou, "calque de la Triperie," (43°12.2′ N, 05°26.9′ E), muddy sand , inside cavity, 22 m, 4 shs, MNHN réc H. Zibrowius, Jun. 1996; Provence, Marseille, Grand Congloue, (43°10.6′ N, 05°24.2′ E), 33 m, 50 shs, MNHN réc. H. Zibrowius, Jun. 1996; Provence, Les Embiez, passe du Gaou, rocks, photophile algae, (43°04.3′ N 5°47.4′ E), 0–3 m, 1 sh., MNHN réc S. Gofas, Jun. 1995; Provence, St. Clair, infralittoral rocks, (43°08.2′ N 6°23.2′ E), 0–1 m, 1 sh., MNHN réc. S. Gofas, Sep. 1992; Tunisia, Sfax, 4 shs, MNHN coll. Staadt, 1969; Italy, Liguria, Portofino, 1 sh., coll. PAL, 2038; Italy, Tuscany, Livorno, Antignano, 0.5 m, brown algae on rocks, 1 sh., coll. PAL legit Bogi, Apr. 1999, 2029; Livorno, under littoral rocks, 0.5–1.0 m, 5 shs, coll. PAL *ex* coll. C. Bogi, 2039LIV; Livorno, Meloria, 10–30 m, 3 shs, coll. PAL *ex* coll. C. Bogi, 1995, 2031MEL; Livorno, Tuscan Archipelago, Island of Elba, Capoliveri, 32 m, 2 shs, coll. PAL *ex* coll. C. Bogi, Aug. 1994, 2036CAPOL; Tuscan Archipelago, Gemini Island, (southern side of Island of Elba), 11 m, 3 shs, coll. PAL, 2034; Tuscan Archipelago, Isola del Giglio, Punta Fenaia, 32 m, 1sh., coll. medshells.com *ex* coll. G. Ruggieri; Tuscany, Grosseto, Argentario, 25 m, 1 sh., coll. medshells.com *ex* coll. G. Ruggieri, Jul. 1988; Italy, Lazio, Ostia, Tor Paterno, 33 m, 5 shs, coll. medshells.com *ex* coll. G. Ruggieri; Lazio, Roma, Santa Marinella, *ex* reti, 2 shs, coll. medshells.com *ex* coll. G. Ruggieri; Italy, Sardinia, Oristano, Santa Caterina di Pittinurri, 5 m, 3 shs, coll. PAL *ex* coll. C. Bogi, 30 Aug. 1986, 2040SCP; Sardinia, Sassari, Island of Maddalena, beach, 3 shs coll. PAL *ex* coll. C. Bogi, 2028IMA; Sardinia, Nuoro, Sant'Antioco, Cala Lunga, 20 shs, coll. medshells.com *ex* coll. G. Ruggieri, 03.1989; Italy, Campania, Peninsula of Sorrento, Punta Penna, 2 shs, coll. medshells.com *ex* coll. G. Ruggieri, 1988; Italy, Sicily, Palermo, 2 shs, MNHN coll. Locard; Sicily, 1 sh., MNHN coll. Petit, 1873; Palermo, 3 shs, ZMB *ex* coll. Monterosato, 81013 (originally labelled by Monterosato as *Cingula tenera*, 3, 1125, Palermo); Palermo, Arenella, 2 shs, ZMB *ex* coll. Monterosato, 81014, (originally labelled by Monterosato as "*Cingula tenera* var . . . , 2, Arenella, Palermo"); Sicily, Siracusa, Capo Passero, 16 m, 3 shs, coll. medshells.com *ex* coll. G. Ruggieri, 05 Sep. 1987.

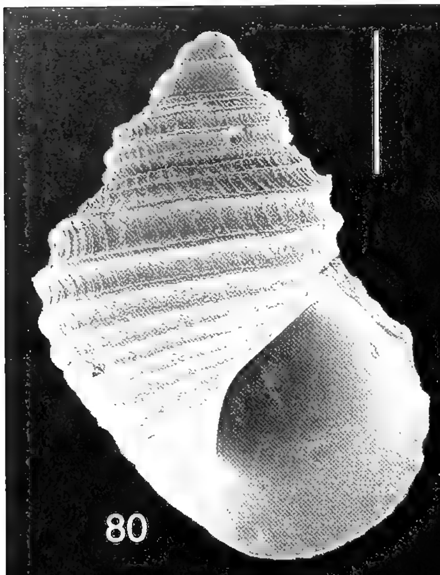
Habitat: This species is clearly limited to infralittoral depths. In the upper part of its distribution, it seems to live in very shallow waters, on algae. It likely lives also in the cavities occurring in infralittoral muddy sandy bottoms.

Distribution: In the western and central Mediterranean the species seems to be well distributed; Adriatic and eastern Mediterranean occurrences should be verified. In the Atlantic it lives along the Moroccan coasts and in the Canary Islands. To my knowledge, there is no fossil record of this species.

Remarks: This small species is characterized by having a variable shell shape and sculpture. The conical shells, bearing a strongly cingulated sculpture, which markedly prevails over the axial, are comparable with typical keeled morph of *Alvania carinata*. In addition, *Cingula* species provided with a strong spiral sculpture are comparable to *A. tenera*. The ovate, slender shells of this last species, with a finely cingulated sculptural pattern, might vaguely resemble some species of *Setia* H. and A. Adams, 1854. As a consequence, Piani (1979) and Van Aartsen (1982) included *A. tenera* in *Galeodina*, whereas Nordsieck (1968; 1972) placed the same species in *Setia* and *Cingula* respectively. The last two views should not be accepted. In fact, the species of *Setia* have a smooth or very slightly sculptured shell with more convex whorls than *A. tenera*, and *Cingula* species are characterized by shells usually lacking axial sculpture and having a very thick outer lip.

The shells from eastern Atlantic (Canary Islands and Morocco) do not show meaningful differences from the Mediterranean ones studied. With regard to the resemblance between *A. tenera* and *A. carinata*, it is manifest in the keeled, conical-inflated shell shape shown by their typical respective morphs, and in having a quite wide and developed aperture. However *A. tenera* never shows va-

Figures 70–79. *Alvania rosariae* new species **70.** Protoconch of the holotype, lower Pleistocene of Cartiera Mulino, bed 3D1 of Costa (1989), SE Sicily, Ragusa, Vittoria. **71.** Protoconch of paratype 16, showing variation of the abapical ridges on protoconch II, same locality and bed. **72.** Dorsal view of protoconch of paratype 21, showing protoconch I sculpture and the abapical ridges on protoconch II, middle to upper Pleistocene of Kyllini, NW Peloponnesus, N2 bed of Garilli et al. (2005a). **73–74.** Holotype, detail of early protoconch (73) showing sculpture of protoconch I and protoconch I/protoconch II boundary, and dorsal view of protoconch (74). **75.** Sculpture of protoconch I, paratype 21. **76–79.** Holotype, detail of teleoconch sculpture: early whorls (76), first to second whorl (77), showing microsculpture, penultimate to last whorl (78), showing the microscopic incremental scars, and last whorl (79). Scale bars: 100 µm in Figures 70–72, 74, 76 and 78–79, 50 µm in Figure 77; 20 µm in Figure 75. Black and white arrows indicate the protoconch I/protoconch II and protoconch/teleoconch boundaries, respectively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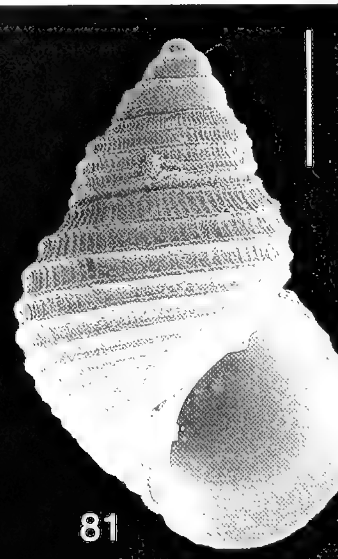
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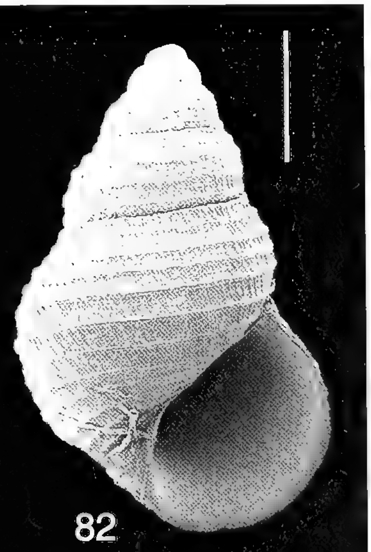
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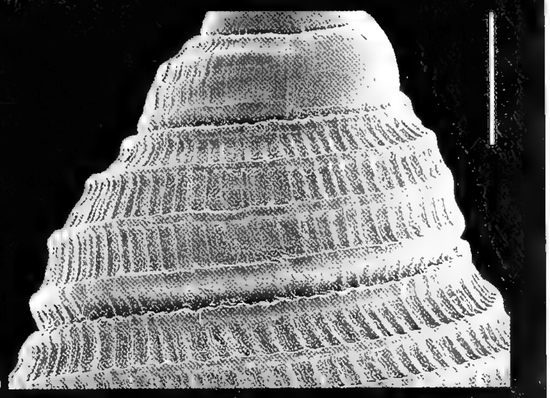
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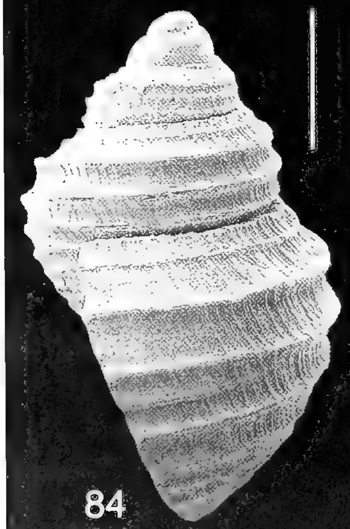
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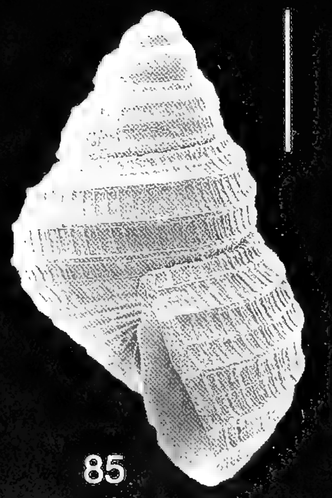
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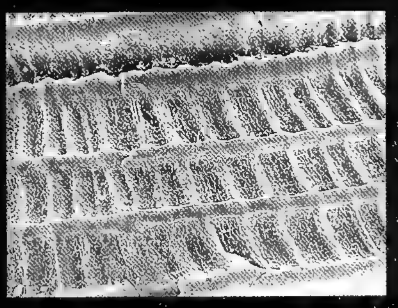
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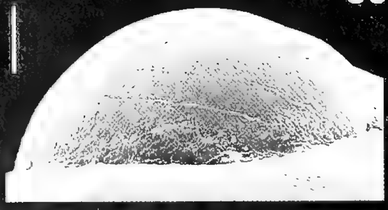
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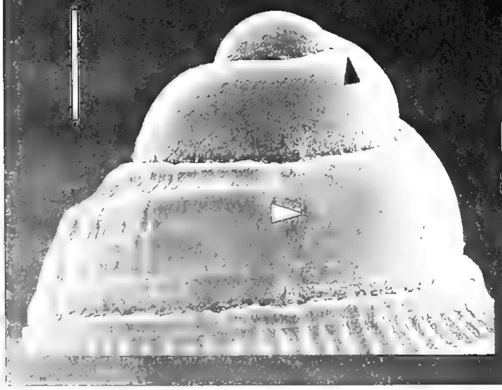
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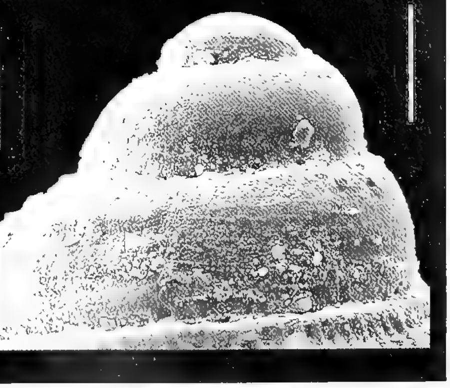
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rices, bears a very delicate axial sculpture, its outer lip is always very thin, and usually has more colored shells.

Genus *Galeodinopsis* Sacco, 1895

Type Species: *Rissoa tiberiana* Coppi, 1876 by original designation.

Galeodinopsis tiberiana (Coppi, 1876)
(Figures 81–99)

1862 *Rissoa tuba* Doderlein, 1862: 17 (*nomen nudum*)
1876 *Rissoa Tiberiana* Coppi, 1876: 201–202.
Manzonia fariai Rolán and Fernandes, 1990: 64–65, pl. 1, figs. 4–6.
Alvania fariai (Rolán and Fernandes, 1990).—Gofas, 1999: 88–89, figs. 39–42.
Alvania fariae (Rolán and Fernandes, 1990).—Landau et al., 2004: 41, pl. 7, figs. 3–4.

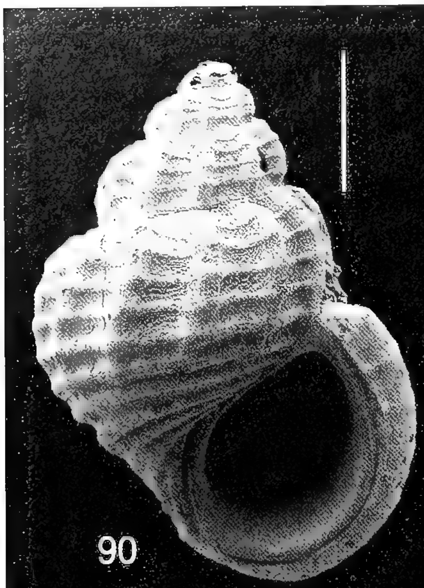
Description: Shell conical, sturdy, reaching 3.75 mm in height and 2.75 mm in width. Protoconch multispiral, conical, with 2–2.2 convex whorls and a rather immersed nucleus. Protoconch I consists of about 0.7–0.8 whorls, with a netted sculpture, consisting of 7–8 very thin spiral lirae and numerous, irregular, short and very narrow axial segments occurring in interspaces between lirae. Protoconch II is sculptured by very small, sparse granules, fused into 2–4 discontinuous ridges on central and abapical portions of latter part of last whorl. Groups of granules form very short, prosocline segments on central area, mainly close to protoconch/teleoconch transition, which is marked by a quite sinous and thin lip. Teleoconch formed by 3–3.5 convex whorls, sculptured by a primary pattern of strong, slightly sinuous and opisthocline ribs, numbering 12–14 on penultimate whorl, becoming very weak to lacking toward shell base. Ribs are covered by a secondary spiral sculpture, formed by flat narrower cords, numbering 4–5 on penultimate whorl, becoming more marked on shell base. Each cord bears a pitted microsculpture, consisting of microscopic subcircular pores forming 8–10 spiral alignments (Figures 99). Between cords, numerous, closely spaced, very fine spiral ridges appear. They are formed by rough prismatic, tooth-like elements, extending perpendicularly from shell surface. At their base, ridges have a lamella-like expansion which covers the interspaces occurring between them. Last whorl inflated, well-expanded, comprising about ¾ of total shell height, often bearing 1–2 strong varices, most frequently just before the outer lip. Aperture ovate, very rounded anteriorly, weakly angulated posteriorly, comprising about little less than ½ and ⅔ of total shell and last whorl height, respectively. Outer lip sinuous, weakly opisthocline; internally smooth, with a thin rim on its edge; externally with a very marked varicose swelling, covered by spiral sculpture, and having a narrow ridge on its base, toward aperture, so that it appears double-rimmed. Inner lip weakly curved, with a very narrow columellar thicknening, forming an obsolete umbilical chink. Shell color white in Recent material.

Type Locality: Coppi (1876) cited "La Tagliata", an unknown name in toponymy (very likely referring to a recently deforested woodland) corresponding to the locality Gagliardella (Maranello, Modena, Emilia Romagna, North Italy) (S. Palazzi personal comm., 2006).

Type Material: A lot (IPUM 13721), from Coppi coll, type locality, with more than 100 possible syntypes (not seen), is housed in the MPOB, Modena.

Material Examined: Senegal: Region de Dakar, 250 m S.W. Cap Manuel, 12 shs, MNHN coll. Marche-Marchad, dét. S. Gofas [The Nautilus 113: 88–89, figs. 40, 42]; Region de Dakar, S.W. Gorée large Cap Vert, 250–150 m, 1 sh., MNHN coll. Marche-Marchad, det. S. Gofas [The Nautilus 113: 88–89, figs. 40, 42]; Region de Dakar, St. 56-1-10A Gorée 150–200 m, 1 sh., MNHN coll. Marche-Marchad, det. S. Gofas [The Nautilus 113: 88–89, figs. 40, 42]; Angola: Luanda, Ilha de Luanda, Circalittoral, 120 m, 3 shs, MNHN coll. S. Gofas, det. S. Gofas [The Nautilus 113(3): 88–89, figs. 40, 42]; Luanda, Ilha de Luanda, circalittoral, 40–60 m, 1 sh., MNHN coll. S. Gofas 1981–82, det. S. Gofas [The Nautilus 113: 88–89, figs. 40, 42]; Luanda, Au large de Mussulo (Mocôco), dredging 50–70 m, 2 shs, MNHN coll. S. Gofas 1981–1987, det. S. Gofas [The Nautilus 113: 88–89, figs. 40, 42]; Au large de Mussulo, circalittoral, 90–100 m, 2 shs, MNHN coll. S. Gofas, det. S. Gofas [The Nautilus 113: 88–89, figs. 40, 42]; Ambrizete, dredging, 80 m, 5 shs, MNHN coll. S. Gofas, det. S. Gofas [The Nautilus 113: 88–89, figs. 40, 42]; Ambrizete, (07°00′ S, 12°20′ E) sediment, 60 m, 3 shs, MNHN coll. S. Gofas, 1983, det. S. Gofas [The Nautilus 113: 88–89, figs. 40, 42); Ambrizete, (06°57′ S, 12°23′ E), sediment, 45 m, 1 sh., MNHN coll.S. Gofas, 1983, det. S. Gofas [The Nautilus 113: 88–89, figs. 40, 42]. Italy: Piemonte, Asti, Baldichieri, "Grottino Monale", 2 shs, yellow sands, middle-upper Pliocene, coll. MF *ex* coll. PAL, F104A; Asti province, 9 shs, Pliocene, MGUP coll. Doderlein, 111A; Liguria, Savona, Rio Torsero, between Ceriale and Peagna, 5 shs, clays, lower Pliocene, coll. MF *ex* coll. PAL, F58A;

Figures 80–89. *Alvania tenera* (Philippi, 1844). **80.** Shell of a keeled and conical morph, Strait of Gibraltar, Spain, Cadiz, Tarifa, coll. PAL (2030TAR). **81–82.** Conical-ovate, not-keeled morphs, illustrating the variable sculpture, France, Provence, Marseille, Curry, coll. PAL (2037MAR). **83.** Profile view of the same shell as Figure 80. **84.** Profile view of an unkeeled morph, France, Provence, Marseille, La Baule, small beach at 25 km west from Marseille, coll. PAL (2035BAU). **85–86.** Sculpture of early teleoconch whorls (85) and detail of sculpture (86), Italy, Tuscany, Livorno, Antignano, coll. PAL (2029). **87–88.** Protoconch (87) and detail of protoconch I (88) of the same shell. **89.** Protoconch of the same shell as Figure 84, showing sculpture variation. Scale bars: 0.5 mm in Figures 80–84; 200 μm in Figure 85; 100 μm in Figures 86–87 and 89; 20 μm in Figure 88. Black and white arrows indicate the protoconch I/protoconch II and protoconch/teleoconch boundaries, respectively.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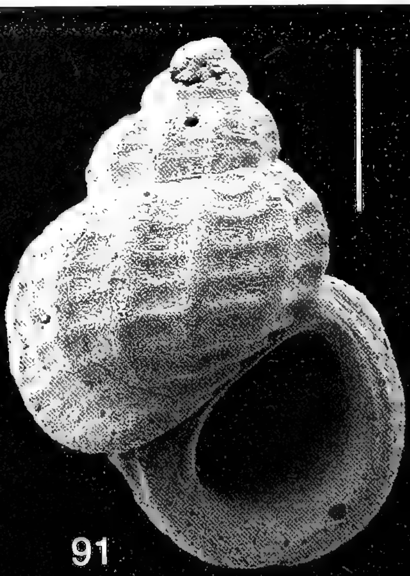
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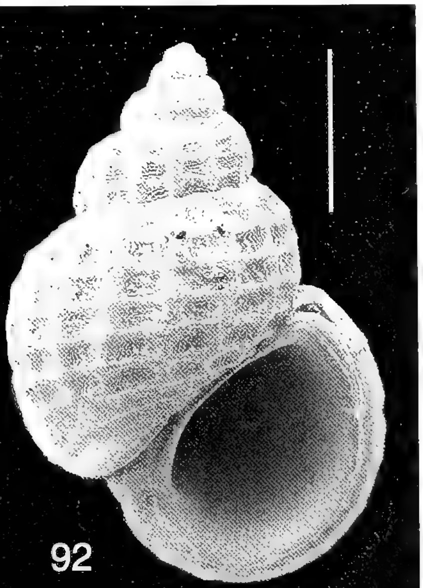
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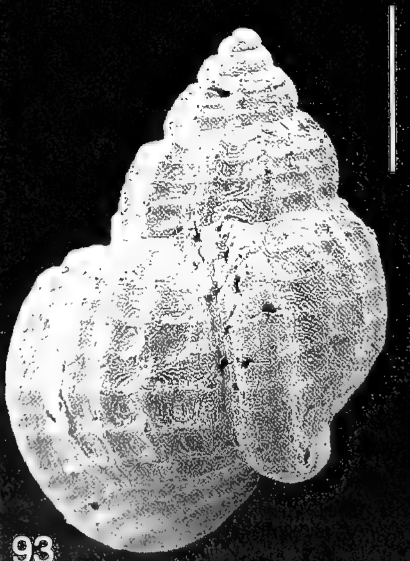
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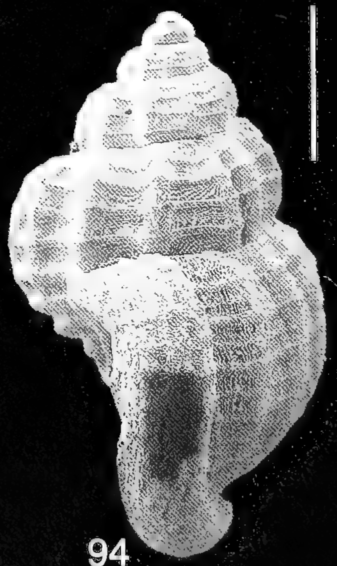
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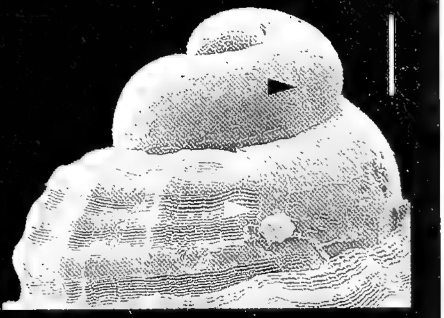
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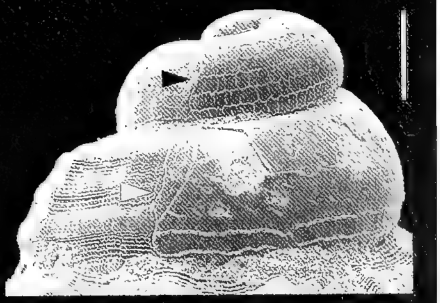
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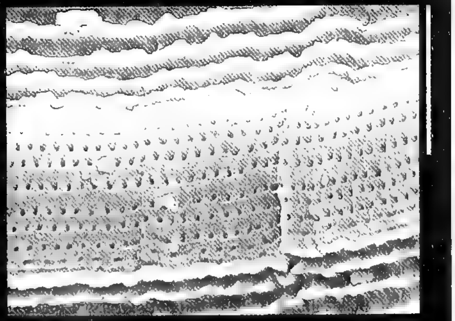
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Emilia Romagna, Modena province, 35 shs, Pliocene, coll. Doderlein, 111B; Emilia Romagna, Modena province, 1 sh., Miocene, MGUP coll. Doderlein, 474; Emilia Romagna, Piacenza, Lugagnano Val d'Arda, 2 shs, "calanchi di valle" (marls), middle-upper Pliocene, coll. MF *ex* coll. PAL, F13A; Piacenza, Castell'Arquato, Monte Padova, 1 sh., blue clays, middle Pliocene, coll. MF *ex* coll. PAL, F16A; Emilia Romagna, Parma, San Nicomede, Stirone river, 50 shs and fragments, lower clays middle-upper Pliocene, coll. MF *ex* coll. PAL, F14B; Emilia Romagna, Modena, Marano on the Panaro, Panaro river, 1 sh., clays stormy layers, middle-upper Pliocene, coll. MF *ex* coll. PAL, F80A; Emilia Romagna, Modena, Maranello, Fogliano, Gagliardella (type locality), Rio Grizzaga, 60 shs, sands, middle Pliocene, coll. MF *ex* coll. PAL, F39A; Tuscany, Siena, San Donato, Ciuciano, Prison, 1 sh., clays and sands, lower Pliocene, coll. MF *ex* coll. PAL, F112A; Siena, Castiglioncello del Trinoro, Poggio Rotondo, 3 shs, marls, lower Pliocene, coll. MF *ex* coll. PAL, F54A; Lazio, Rome, Magliano Sabina, Cladocora yellow sands, 23 shs, lower Pliocene, coll. MF *ex* coll. PAL, F15A; Sicily, Palermo, Altavilla Milicia, rigth side of Milicia river, 12 shs, sands, lower-middle Pliocene, coll. MF *ex* coll. PAL, F2A; Palermo, Partitico, Trappeto, Lido Ciammarito to Nocella river mouth, 11 shs, clays, lower Pliocene, coll. MF *ex* coll. PAL, F72A.

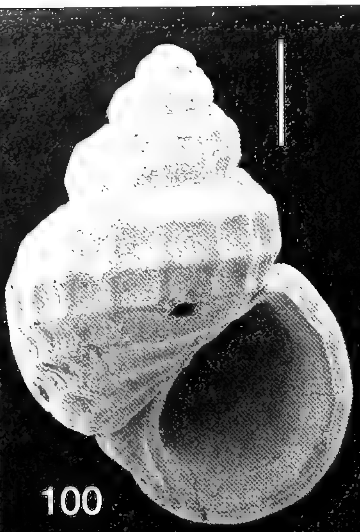
Habitat: In the Atlantic Ocean, the species has a lower shelf-upper slope distribution (see Gofas, 1999), is indicated by the fossil Mediterranean occurrences. A shallower and more restricted distribution, limited to shelf paleoenvironments, with sandy to muddy bottoms.

Distribution: The species lives in the eastern Atlantic, from Senegal to northern Angola (see also Gofas, 1999). It was also collected from the coasts of Mauritania (S. Palazzi, pers. comm., 2006). The species has a Mediterranean Miocene to Pliocene paleoditribution, being recorded from the Miocene of northern Apennines (Modena), the Pliocene of northern (Piemonte, Liguria, Toscana, Emilia Romagna), central (Lazio) and insular (northwestern Sicily) Italy, south Spain (Estepona) Landau et al. (2004, as *Alvania fariae*), and Algeria (Cossmann, 1921). In Atlantic, it is recorded from the Portuguese middle Pliocene of Mondego Basin (Landau et al., 2004). The citation of Wenz (1938: 616), according to which the species lived in the Oligocene (up to Pliocene of Europe, North Africa and North America), should be verified. The species was not found in the very rich molluscan assemblages from the Oligo-Miocene of southwestern France (Lozouet, 1998; 1999).

Remarks: Gofas (1999) and Landau et al. (2004), discussing and re-describing this species, originally described as *Manzonia fariai* by Rolán and Fernandes (1990) from West Africa, did not recognize its identity as *Rissoa tiberiana* Coppi, 1876, the latter being a common species from the Mediterranean Neogene, particularly from the Pliocene. This species, originally not illustrated by Coppi (1876), was figured by Sacco (1895: figs. 67, a-bis and 68, a–b), who designated it as the type species of the subgenus *Galeodinopsis* Sacco, 1895. More recently, this species was illustrated by Cossmann (1921: pl. 1, figs. 55–56) and Wenz (1938: fig. 1715). Comparison between fossil material of *R. tiberiana* (Figures 90–94, also from topotype material; see also Landau et al., (2004: pl. 7, figs. 3–4), to that of Rolán and Fernandes (1990: pl. 1, figs. 4–6), and of Gofas (1999: figs. 39–42) strongly confirms the above mentioned synonymy. The rather conical, ribbed shell with an inflated last whorl, the frequent presence of varices on the last whorl, and the double-rimmed outer lip are the most characteristic features of this species, which shows a modest variability in the number and strength of ribs and in the spire elevation (see Figures 90–92).

Gofas (1999) moved this species from *Manzonia* Brusina, 1870 [type species *Manzonia crassa* (Kanmacher, 1798), see Figures 104–107] to *Alvania* based on the lack of the characteristic punctate spiral sculpture of the former taxon. This does not appear appropriate. In fact, in reasonably well-preserved shells, the primary spiral cords clearly bears a microsculpture consisting of regular, spirally arranged pits, quite like *M. crassa* (compare Figure 99 with Figure 106). This spiral pitted microsculpture, considered a typical *Manzonia* character by Moolenbeek and Faber (1987), was indicated by Bouchet and Warén (1993) as not restricted to this genus (occurring in *Alvania*, *Gofasia* Bouchet and Warén, 1993, and with a rough similarity, in Rissoininae species, see Gofas, 1999, figs. 79–80, 85, and 89]). The same authors interpreted it as a symplesiomorphy retained in *Manzonia* and in other rissoid genera. However, the particular structure of the secondary, very fine spiral threads, formed by roughly prismatic elements growing perpendicularly to the shell surface, is a character shared by the *Manzonia* species, never observed in *Alvania*, and retained only in the recently described genus *Gofasia* (see Bouchet and Warén, 1993, fig. 1557). The combi-

Figures 90–99. *Galeodinopsis tiberiana* (Coppi, 1876). **90–93.** Shells from the type locality, showing variability and varices, middle Pliocene of Italy, Emilia Romagna, Modena, Maranello, Fogliano, Gagliardella, Rio Grizzaga sands, coll. MF *ex* coll. PAL (F39A). **94.** Profile view of a shell from the middle-upper Pliocene of Italy, Emilia Romagna, Parma, San Nicomede, Stirone River, coll. MF *ex* coll. PAL (F14B). **95–96.** Protoconchs from the same locality, note variation of the abapical sculpture just behind the transiction to teleoconch. **97.** Detail of protoconch I, showing the netted microsculpture and the partially immersed nucleus, same shell as Figure 95. **98.** Detail of teleoconch sculpture from the shell as Figure 90. **99.** Detail of teleoconch microsculpture from the shell as Figures 95–96: note the pitted pattern on the spiral cord and the structure of the fine spiral ridges. Scale bars: 1 mm in Figures 90–94; 100 μm in Figures 95–96; 50 μm in Figure 98; 20 μm in Figures 97, 99. Black and white arrows indicate the protoconch I/protoconch II and protoconch/teleoconch boundaries, respectively.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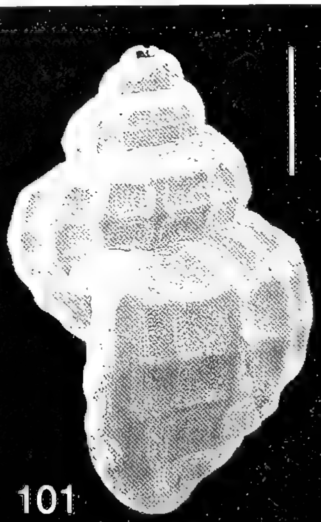
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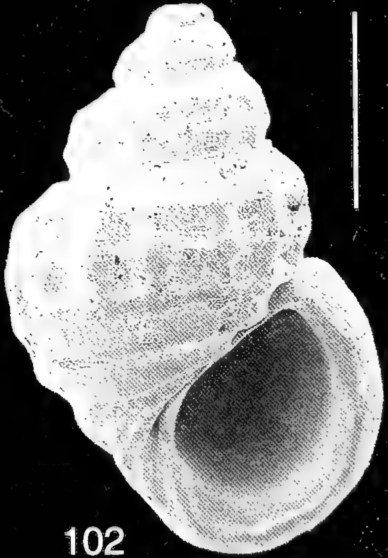
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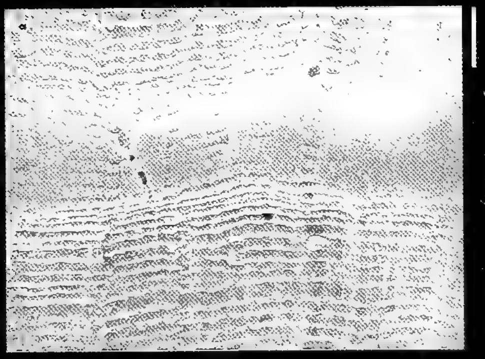
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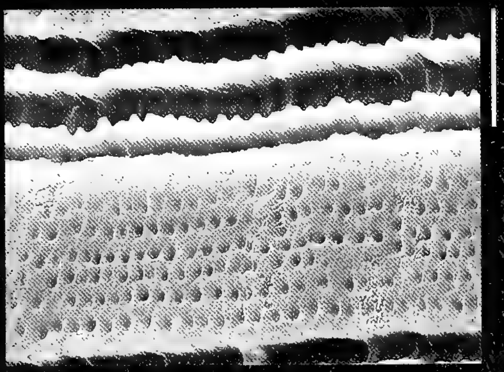
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nation of these characters (pitted sculpture and structure of fine spiral threads) represents a quite singular and original feature, which should be regarded as limited to *Manzonia*-related species.: e.g. *M. darwini* Moolenbeek and Faber, 1987 (pl. 1, fig. 18), *M. crispa* (Watson,1873) (see Moolenbeek and Faber, 1987, pl. 3, fig. 54), *M. boogi lanzarottii* Moolenbeek and Faber, 1987 (pl. 2, fig. 39), *M. spreta* (Watson, 1873) (see Moolenbeek and Faber, 1987, pl. 3, fig. 57), *M. vigoensis* (Rolán, 1983) (see Bouchet and Warén, 1993, p. 656, fig. 1499) and several others. The double rimmed outer lip and the netted sculpture of protoconch I are also characters shared by *Manzonia* species. However, it must be considered that these two features, considered by Ponder (1985: 46) as typical of *Manzonia* sensu stricto, should be regarded with suspicion, being as they are shared by well-recognized *Alvania* species. In regard to the protoconch, species such as *A. testae* (Aradas and Maggiore, 1844), *A. zetlandica* (Montagu, 1815) (see Bouchet and Warén, 1993, figs. 1386–1387 and 1502; Landau *et al.*, 2004, pl. 9, figs. 1b–1d), the Pliocene *Alvania magistra* Chirli, 2006 (pl. 11, fig. 16 and pl. 12, figs. 1–3), have the same sculptural pattern on protoconch I. *A. tomentosa* (Pallary, 1920), which has a paucispiral protoconch, also exhibits this sculpture (see Bouchet and Warén, 1993, fig. 1388).

Rissoa tiberiana could be regarded as one (probably the sole) of the few survivors of a group of species close to *Manzonia* sensu lato, which very likely originated in the upper Paleogene. The European Oligocene *Rissoa duboisi* Nyst, 1843 (Figures 100–103) certainly belongs to this group. Both these species share several intersting characters: a quite conical *Alvania*-like shell shape, often provided with varices on the last whorl, the arrangement of the basal cords (not so strong as in *Manzonia* sensu stricto, where keels occur on the shell base), the above mentioned combination of the microsculptural pattern, and the kind of axial sculpture (with slightly sinuous, less pronounced ribs than those shown by *Manzonia*), and a double, weakly opisthocline outer lip. All this leads me to revalue *Galeodinopsis* as the useful generic placement for such *Manzonia*-related species.

In overall appearance, *G. duboisi* (Nyst, 1843) strongly resambles *G. tiberiana,* from which it differs principally in having less numerous cords and ribs and less convex whorls (see also Ponder, 1985, fig. 100c). Another comparable species is the Recent Macaronesian *M. spreta* (Watson, 1873), which has a similar shell shape but differs from *G. tiberiana* in having a more delicate axial sculpture (the spiral cords being large and almost flat) a more rounded and smaller aperture, and a paucispiral protoconch (see Moolenbeek and Faber, 1987, figs. 47a–b and 55–57). With some significant reservations, it could be regarded as belonging to *Galeodinopsis*. The species *M. foraminata* (Lozouet, 1998), originally described as *Alvania* (from the upper Oligocene of south-western France, see Lozouet, 1998, fig. 9f–h), *M. moulinsi* (d'Orbigny, 1852) (see Lozouet, 1998, fig. 9i–j, from the French upper Oligocene), *M. scalaris* (Dubois, 1831) (Kowalke and Harzhauser, 2004, fig. 8d, from the middle Miocene, Badenian, of Austria, Hungary, Poland and Romania and the Miocene of Russia) and the Recent *Manzonia crispa* (Watson, 1875) (of which I studied 3 shells from Madeira, ZMA Moll. 101.0, *ex* coll. R.G. Moolenbeek; see also Ponder, 1985, fig. 100A and Moolenbeek and Faber, 1987, text-fig. 46, and pl. 3, fig. 52–54) show less affinities, having a more slender shell with more curved ribs (protruding over the suture in *M. scalaris*), which become stronger on the base of the shell. All these four species appear more related to *Manzonia* than to *Galeodinopsis*.

Sacco (1895) and Cossmann (1921) indicated *Rissoa multicostata* Speyer 1864 (pl. 41, figs. 3–5, from the Oligocene of Germany) as a possible *Galeodinopsis* species. I did not see any shells of this *Alvinia* sensu lato-like species, which more closely resembles the group of *Alvania zetlandica* (Montagu, 1815) and *A. weinkauffi* (Weinkauff, 1868 *ex* Schwartz ms.). The original illustrations show a turreted shell with a more finely cancellate (not-ribbed) sculpture, bearing almost orthocline axial ribs, characters which militate against placement in *Galeodinopsis*.

The material of *Rissoa tuba* Doderlein, 1862, housed in the MGUP Doderlein's collection (from the Miocene and Pliocene of North Italy), belongs to this species. Anyway, Doderlein (1862: 17) just listed this taxon without providing a description or a valid reference, so that *R. tuba* must be considered a *nomen nudum*.

CONCLUDING REMARKS

As indicated by Ponder (1985), the systematic grouping of *Alvania* species at the subgeneric level is quite difficult and putative groups usually fold into synonymy with *Alvania* sensu stricto. This viewpoint appears be applicable to the species studied in this report (except for *Rissoa tiberiana* Coppi, 1876). The subgeneric division into *Galeodina* and *Massotia* lacks any valid and convincing basis in shell features (especially on consideration of

Figures 100–107. *Galeodinopsis duboisi* (Nyst, 1843) (100–103), from the upper Oligocene of Hessen (Germany, SE of Kassel, Hessisch-Lichten, Glimmerode, coll. MF *ex* coll. Pal. FE15A) and *Manzonia crassa* (Kanmacher, 1798) (104–107), type species of *Manzonia* Brusina, 1870, from the middle-upper Pleistocene of Kyllini (NW Peloponnesus, Greece, N2 bed of Garilli et al., 2005a). **100–102.** Apertural (100 and 102) and profile (101) views. **103–104.** Microsculptures, showing the typical pitted surface on the flat cords and the microstructure of the narrow spiral threads in *G. duboisi* (103, same shell as Figure 101) and *M. crassa* (104, same shell as Figure 105). **105–106.** Apertural (105) and profile (106) view of shell. **107.** Detail of protoconch I, showing the netted sculpture Scale bars: 1 mm in Figures 97–98; 20 μm in Figure 100; 10 μm in Figure 99. The black arrow indicates the protoconch I/protoconch II boundary.

the often extensive intraspecific variation). In effect, a link between the markedly keeled and inflated shells (e.g. *A. carinata*), and the more typical *Alvania*-shape taxa could be hypothesized. It could be articulated and summarized in the transition *A. carinata*-*A. lactea* (via *A. francescoi* new species-*A. rosariae* new species) to more typical *Alvania* species. A parallel trend could be constructed: *A. tenera* and *A. cingulata*, showing a progressive weakening of the spiral sculpture, the proportional reduction in the expansion of the body whorl and the formation of the outer lip thickening. Furthermore, other interspecific trends, involving various nominal groups of *Alvania*, could be constructed when considering the widely variable shells of most of the species discussed here. Nowstanding this, I cannot deny that all these hypothetical links appears tenuous and that these taxa, sharing a quite inflated and well-expanded body whorls, a wide, internally smooth aperture, seem somewhat distant from *Alvania* sensu stricto This point of view could lead to regard them as belonging to an inclusive taxonomic group (preferably at subgeneric level). *Galeodina* could serve as the appropriate taxonomic unit. Nevertheless, since I believe that appropriate anatomical studies (of which there is no exhaustive data-set) should be used to solve this question, I have preferred a more open-ended option, placing the discussed species here, from *carinata* to *tenera*, in *Alvania* sensu lato

The re-analysis of the Neogene-Recent *R. tiberiana*, type species of *Galeodinopsis*, has lead me to reevaluate the latter taxon as the appropriate genus for grouping species characterized by a particular teleoconch microsculpture (consisting of very fine spiral threads, formed by roughly prismatic elements, extending perpendicularly respect from the shell surface, plus the pitted surface on the primary spiral cords, as seen in *Manzonia*) and by having a conical *Alvania*-like shell shape. The oldest representative of this genus is the European upper Oligocene *R. duboisi*. The upper Oligocene *M. foraminata* and *M. moulinsi* are probably more linked to *Manzonia* sensu lato than to *Galeodinopsis* while the Recent Macaronesian *M. spreta* could be doubtfully regarded as belonging to *Galeodinopsis*.

Because of its affinity with *Alvania*, *Galeodinopsis* probably derived from some Oligocene group of that taxon and could be regarded as a transitional link to *Manzonia*. It is interesting that, as indicated by Lozouet (1998), the genus *Alvania* had a surprising radiation in the upper Oligocene, creating a strong diversification. Furthermore, the *Manzonia* sensu stricto species, characterized by the quite slender shell with strongly opisthocline ribs and very marked spiral cords on the shell base, seem to be well-established from the European Neogene, where they are represented by the following species: *M. crassa*, *M. falunica*, *M. pontileviensis*, and *M. scalaris*.

All the discussed species have a multispiral protoconch, indicating a planktotrophic larval development, with the exception of *A. cingulata*, which is the most geographically restricted species, limited to Sicilian waters. The reason for its very limited geographical distribution is not certainly solely attributable to its non-planktotrophic larval development. Our knowledge about this species is not encouraging: I just know that:

- There is no known fossil record . . . is it a very recent Mediterranean acquisition?
- From a large amount of bulk samples (about 50 liters from Magnisi and 20 liters from Mondello), I picked only a single eroded shell! . . . Is it still a living species?

Among species with planktotrophic development discussed in this report, three show an eastern Atlantic-Mediterranean distribution: *A. carinata*, *A. lactea*, and *A. tenera*. Among these, the first two species have a Neogene to Recent distribution, being known from the Pliocene and the Miocene of Mediterranean basin, respectively, and show a quite extensive east Atlantic distribution, being commonly recorded from the English Channel to Morocco. Regarding the third species, living in Mediterranean and along the Atlantic Morocco and the Canary Islands coasts, I did not find any Mediterranean or Atlantic fossil records. The extinct species *A. francescoi*, *A. prusi*, and *A. rosariae* are limited to the Mediterranean Pleistocene, while *Galeodinopsis tiberiana* has a Miocene-Pliocene Mediterranean distribution and lives along the W African coasts from Mauritania to northern Angola.

In general, the protoconchs of the species reported here do not indicate any distinguishing taxonomical characters at the supraspecific, and, in most cases, at the species level, being characterized by sculptural patterns shown by several rissoid species. Among the planktotrophic species, the commonest sculptural pattern on protoconch I (observed in *A. carinata*, *A. francescoi*, *A. lactea*, *A. rosariae*, and *A. tenera*), consisting of fine spiral lirae and scarce to abundant pimples between them, is shown by *A. cancellata* (Da Costa, 1778) (see Giannuzzi-Savelli et al., 1996, fig. 408b), *A. beani* (Hanley in Thorpe, 1844) (see Giannuzzi-Savelli et al., 1996, fig. 412), *A. cimex* (Linneus, 1758) (see Ponder, 1985, figs.86C–B), *A. cimicoides* (Forbes, 1844) (see Bouchet and Warén, 1993, fig. 1385 and Giannuzzi-Savelli et al., 1996, fig. 408d), *A. dingdensis* (Janssen, 1967) (see Ponder, 1985, figs. 88F–G), *A. geryonia* (Nardo, 1847) (see Giannuzzi-Savelli et al., 1996, fig. 395c), *A. hispidula*, Monterosato, 1884 (see Gofas, 1999, fig. 26), *A. punctura* (Montagu, 1803) (see Giannuzzi-Savelli et al., 1996, fig. 436), *A. stephanensis* Lozouet, 1998 (fig. 9D), *Crisilla semistriata* (Bouchet and Warén, 1993, fig. 1535), *Rissoa parva* (Da Costa, 1778) (see Ponder, 1985, figs. 79B), and several other species. The sculptural pattern on protoconch II (also observed in *G. tiberiana*), consisting of 1–3 more or less discontinuous, abapical to central, spiral threads (also formed by short, fused, prosocline segments close to the beginning of the teleoconch) and tubercles on the remaining surface, is also shown by most of the above mentioned species and several others. *Al-*

vania lactea could represent a slight exception, having a quite characteristic, easily distinguishable protoconch I with a coarser sculpture than that shown by the other studied species. *A. tenera* shows a similar protoconch II sculptural pattern, with few to abundant very small granules spirally arranged, which may form very discontinuous and irregular ridges. Likewise this kind of sculpture is shared by other rissoids (e.g. *A. tarsodes* (Watson, 1886) (see Bouchet and Warén, 1993, fig. 1450) and *Crisilla semistriata*). The sculpture of the paucispiral protoconch of *A. cingulata*, which is almost a replica of protoconch I of the first group discussed above, represents a quite common pattern shown by several nonplanktotrophic rissoids: e.g. *A. argillensis* Lozouet, 1998, *A. macandrewi* (Manzoni, 1868), *Lironoba multilirata* (T. Woods, 1878), *Onoba gianninii* (Nordsieck, 1974) and, with a moderate similarity, by *A. subsoluta* (Aradas, 1847), *Onoba semicostata* (Montagu, 1803), and *A. virodunensis* Lozouet, 1998 (see Ponder, 1985, fis 89A, 109E and 126C; Bouchet and Warén, 1993, figs. 1458, 1525; Lozouet, 1998, figs. 10F and 10K).

There is similarity between the West African rissoid assemblages, including the Macaronesian province, and the European ones, with particular regard to those from the Mediterranean Neogene. This similarity is perhaps more marked than it has been indicated by Gofas (1999). The case of *G. tiberiana* is a further (see Monegatti and Raffi, 2001, and Garilli and Galletti, 2007) interesting case of a molluscan species that lived in the Mediterranean Neogene and today occurrs along the West African coasts. In this view, it is noteworthy to remark that, as a whole, most of the species here included in *Galeodinopsis* lived in the European Oligo-Pliocene while its living representings occurs along the West Africa and Macaronesian Provinces. In addition, *A. tenera*, living in the Mediterranean, Atlantic Morocco, and in the Canary Islands (Tenerife), should be regarded as a new record, further supporting the discussed similarity. The rissoid *Rissoina* d'Orbigny, 1840, species from the Mediterranean Plio-Pleistocene (see the good illustrations of Greco, 1974, figs. 11, 13, 15, 17 and Chirli, 2006, pl. 23, figs. 7–12), usually cited as *R. decussata* (Montagu, 1803), is very likely the same taxon as living along the W African coasts, São Tomé and Cape Verde Islands [see Gofas, 1999: 97, figs. 69–73, and treated as *R. punctostriata* (Talavera, 1975)].

The rather common presence of varices on the last whorl (a rare character in rissoids) of *A. carinata*, *A. francescoi* new species, *A. lactea*, *A. rosariae* new species, and *G. tiberiana* should not be regarded as a salient taxonomic character at the supraspecific level, being present in quite unrelated species (e.g. *A. carinata* and *G. tiberiana*).

ACKNOWLEDGMENTS

This article would not have been possible without the generous support of friends, private collectors, and researchers. I particularly thank Maurizio Forli (Prato), Stefano Palazzi (Modena), Nino Adorna Sbrana (Grosseto), Stefano Rufini (Anguillara) for lending a large amount of precious and indispensable material. Many other people kindly made their collections available. R.G. Moolenbeek (ZMA, Amsterdam) donated three shells of *Manzonia crispa* from ZMA Moll. collection. Rossana Messina (Palermo) provided a special support, measuring most of the investigated shells and assisted me during the bibliographical research in the DGUP library. Luca Galletti (Monreale), a companion for all the fieldworks in Kyllini and Cartiera Mulino, also help me in providing SEM images. My special thanks to M. Glaubrecht (ZMB, Berlin), who very kindly lent precious material (with particular regard to the two *Alvania cingulata* shells from Monterosato collection), to D. Merle, J. M. Pacaud (MNHN-DHT, Paris), V. Héros, and P. Lozouet (MNHN-DSE, Paris), who provided helpful and kind assistance during my visits in MNHN. A. Rosso and I. Di Geronimo (DSTC, Catania) kindly allowed the visit to the malacological collections of the DSTC. Kathie Way (British Museum of Natural History, London), H. J. Niederhöfer (Staatliches Museum fur Naturkunde, Stuttgart) and P. Serventi (MPOB, Modena) provided information on type material. Thanks to M. Fiore, P. Iacopelli, V. P. Li Vigni (MSNCS, Terrasini), who allowed the visit to the conchological collections of the MSNCS. C. D'Arpa (MGUP, Palermo) lent some fossil material housed in the MGUP. Even when the library was moving, G. Barranca (DGUP, Palermo) very kindly allowed me the access to some papers. Riccardo Giannuzzi-Savelli (Palermo) and R. G. Moolenbeek helped me in some bibliographic researches. R. G. Moolenbeek and S. Palazzi also provided very useful and constructive comments on an early manuscript.

I am grateful to D. Merle, R. G. Moolenbeek, H. Scholz (ZMB) and E. Theodorou-Vardala (GNHM, Kifissia), who quickly provided the catalog numbers for type material of *A. francescoi* new species and *A. rosariae* new species. I am also grateful to H. G. Lee (Jacksonville, Florida) and P. Lozouet (MNHN, Paris) who reviewed the manuscript and provided valuable comments. H. G. Lee also kindly helped improve my shaky English. This work also benefited from critical readings by S. Gofas (Departamento de Biologia Animal, Universidad de Málaga) and José H. Leal (The Bailey-Matthews Shell Museum, Sanibel, Florida).

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Reallocation of *Cyamiocardium crassilabrum* Dell, 1964, into *Perrierina* Bernard, 1897 (Bivalvia: Cyamiidae)

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ABSTRACT

Re-examination of the holotype of *Cyamiocardium crassilabrum* Dell, 1964, allowed confirmation that the species was wrongly allocated to the genus *Cyamiocardium*. This material, together with additional specimens from the western Malvinas (Falklands) Islands allowed for a re-description of that species. The species is also properly illustrated through scanning electron microscopy, and its updated generic placement discussed. The presence of a "taxodont" hinge plate is the main morphological character supporting the re-allocation of this species in the genus *Perrierina* Bernard, 1897. Information on the brooding condition of the species is provided.

Additional Keywords: Perrierina, Cyamiidae, Magellanic Region

INTRODUCTION

Study of the mollusks collected by the R/V William Scoresby in the Magellan Region and adjacent Antarctic waters resulted in the discovery of several species new to this region, among them, a small bivalve described by Dell (1964) as *Cyamiocardium crassilabrum*. The only subsequent record of this species was reported by Castellanos (1980) from the western Malvinas (Falkland) Islands.

The genus *Cyamiocardium* was introduced by Soot-Ryen (1951) to allocate *Cyamium denticulatum* E. A. Smith, 1907 (the type species by original designation), a species widely distributed throughout the Antarctic Region (Lamy, 1910, 1911; Powell, 1958; Dell, 1990). Other Antarctic species assigned to this genus by Soot-Ryen (1951) were *Cyamiocardium rotundatum* (Thiele, 1912), *C. dahli* Soot-Ryen, 1957, and *Cyamiocardium crassilabrum* Dell, 1964, from the Magellan Region. In the context of a systematic revision of these species (currently in progress), the type material and additional specimens of "*Cyamiocardium*" *crassilabrum* were examined. As a result, I have concluded in that the placement of this species in *Cyamiocardium* is incorrect. In the present paper the generic placement of this species is revised, and the taxon is re-described and properly illustrated by first time.

MATERIALS AND METHODS

This study is based on dried preserved specimens collected during the R/V Shinkai Maru expedition (1978–79). Voucher specimens have been deposited in the collections of the Museo de La Plata (MLP). Photographs of the holotype of *Cyamiocardium crassilabrum* were received from The Natural History Museum (NHM), London. For comparative purposes, specimens of *Cyamiocardium denticulatum*, *C. rotundatum*, and *C. dahli* were also examined.

The specimens reported by Castellanos (1980) as *Cyamiocardium crassilabrum* could not be located either at the MLP or the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN). The material here studied, originally at the Instituto Nacional de Investigaciones y Desarrollo Pesquero (INIDEP), comes from the same Shinkai Maru sampling station than the material previously reported by Castellanos (1980).

Shell measurements were made under a stereoscopic microscope, according to the following criteria: L: maximum antero-posterior distance; H: maximum dorsoventral distance, perpendicular to L; W: maximum distance across valves, perpendicular to H. Shell morphology was studied under scanning electron microscope; for this, Philips XL30 TMP and JEOL JSN-6360 LV scanning electron microscopes were used.

SYSTEMATICS

Cyamiidae G. O. Sars, 1878
Perrierina Bernard, 1897

Perrierina crassilabrum (Dell, 1964) **new combination**
(Figures 1–12)
Cyamiocardium crassilabrum Dell, 1964: 204, fig. 4, numbers 1, 2, and pl. 6, figs. 1, 2; Castellanos, 1980: 135.

Type Locality: 50°17′ S, 60°06′ W, station 211, R/V William Scoresby, 161–174 m

Material Examined: Photographs of the holotype (NHM 1962863); 7 dried specimens and 1 valve, 51° 29′ S, 61° 50′ W, Malvinas (Falkland) Islands, 192 m (MLP 12606).

Literature Records: 50°17′ S, 60°06′ W, station 210, R/V William Scoresby, 161 m; 50°35′ S, 57°20′ W, station 229, R/V William Scoresby, 210–271 m (Dell, 1964); 51°29′ S, 61°50′ W, 192 m (Castellanos, 1980).

Distribution: Only known from the Atlantic sector of the Magellan Region, in the vicinity of the Malvinas (Falkland) Islands, 161–271 m.

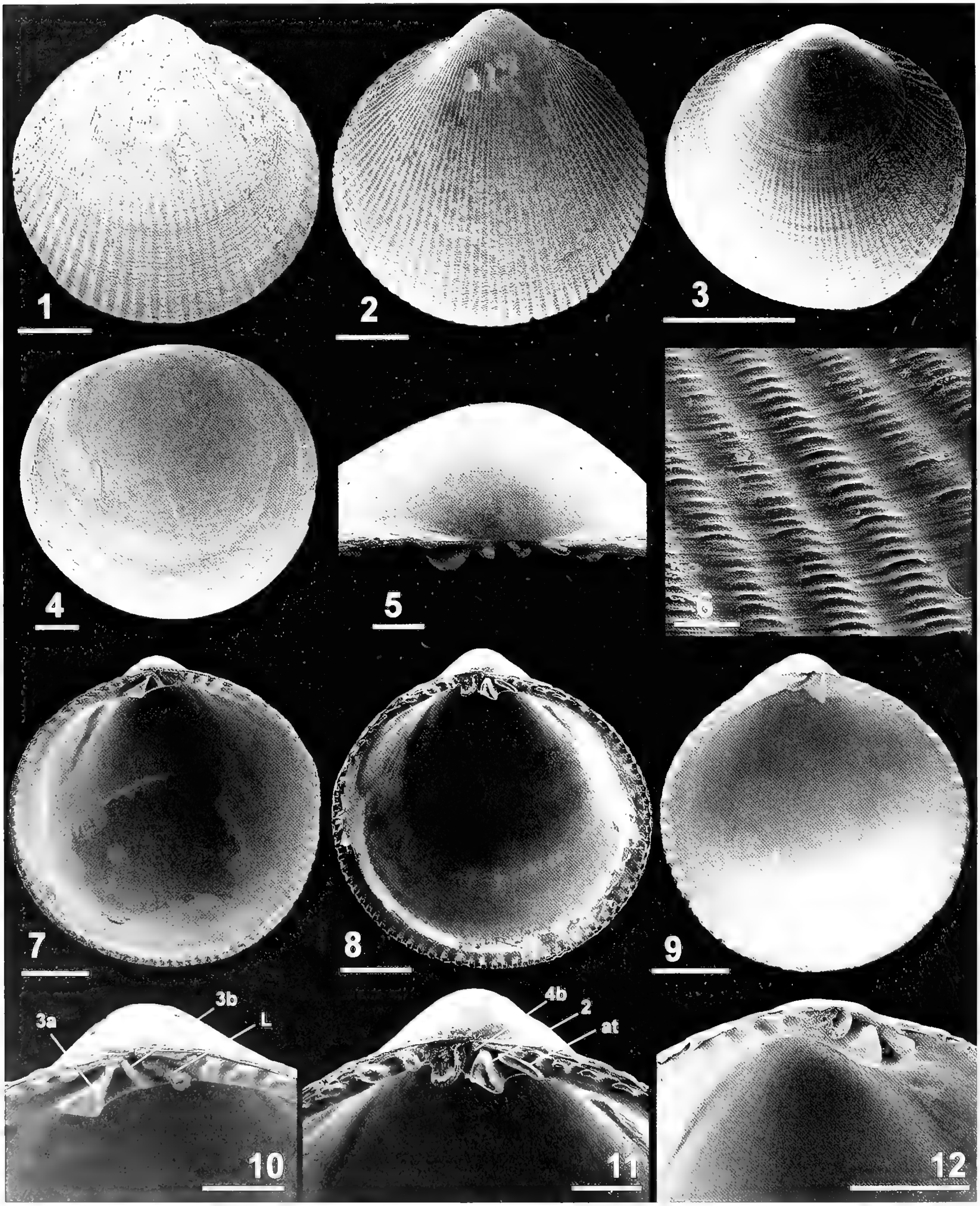
Description: Shell solid, small (maximum L: 6.3 mm), outline nearly circular (H/L = 0.99 ± 0.01, n = 6), slightly inequilateral, not inflated (W/H = 0.65 ± 0.01, n = 5), whitish, glossy. Anterior margin short, curved, continuous with ventral margin, which is evenly arcuate; posterior end rounded, slightly expanded (Figures 1, 2). Juvenile shell slightly ovate in outline, elongated anteroposteriorly (Figure 3). Beaks full, subcentral, directed slightly anteriorly. Protoconch ovate, smooth, about 590 µm in diameter (Figure 5). Shell surface sculptured with rounded, strongly marked, and regularly spaced radial cords, 50–60 in larger specimens (Figure 6); cords separated by interspaces wider than ribs. Regularly separated, microscopic commarginal threads also present. Radial sculpture also evident on inner margins, where they produce prominent crenulations (Figures 7–9). Hinge plate narrow, somewhat broader anterior to beaks, where the cardinal teeth are inserted. Right valve with large, hooked cardinal 3: 3a high, solid, triangular, enlarged at base, which is frequently bifid; 3b delicate, narrow, nearly straight, one-third of size of 3a (Figures 7, 10). Left valve with prominent triangular cardinal 2, thin and styliform cardinal 4b behind resilifer, and slender but solid, nearly straight anterior tooth (referred to as "cardinal 4a" by Bernard (1897) and as "anterior lateral II" by Lamy (1917)) (Figures 8, 9, 11). Both valves with two series of tubercles anterior and posterior to beaks, producing the appearance of a taxodont hinge plate (Figures 10, 11); each series composed of four tubercles; posterior series stronger than anterior in juveniles (Figure 12). In both series, tubercles diminish in size and degree of development from beaks to anterior and posterior ends, where they are followed by marginal crenulations. Internal ligament somewhat solid, located in short, oblique resilifer posterior to cardinal teeth. External ligament short.

Biological Observations: One of the specimens examined contained numerous embryos between the ascending and descending lamellae of inner demibranchs. Embryos were in different stages of development, ranging from incipient (unshelled) to well-developed specimens, the latter numbering 32, and reaching 700 µm in diameter (Figure 4). These observations are consistent with that by Dell (1964), who reported 44 "developing young" contained in one of the specimens he studied.

Remarks: *Perrierina* was proposed by Bernard (1897) for *P. taxodonta* (type species by monotypy; illustrated by Bernard, 1897: fig. 3) a species he described from Île Stewart (New Zealand). The description of the genus was merged with that of the type species, in which Bernard (1897) described the presence of several "lamellae" anterior and posterior to the cardinal teeth, resembling a taxodont hinge. This character, infrequent among Cyamioidea, is also present in *Legrandina* Tate and May, 1901 (type species: *L. bernardi* Tate and May, 1901, by original designation), an Australian genus regarded by Ponder (1971) and Powell (1979) as a subgenus of *Perrierina*.

Perrierina and *Cyamiocardium* have as common characters the number, morphology, and arrangement of hinge teeth, i.e., the presence of a hooked anterior cardinal 3 in the right valve and two prominent cardinal teeth (cardinals 2 and 4) in the left valve. The specimens studied here generally agree with these characteristics, but, additionally, the hinge examined showed several anterior and posterior tubercles, which, as a group produce the appearance of a taxodont hinge, a diagnostic character for *Perrierina* that is absent in *Cyamiocardium*. Furthermore, the studied specimens lack the posterior "pseudo-lateral tooth" described by Smith (1907) for the type species of *Cyamiocardium*. Another character that is useful in separating the genera *Cyamiocardium* and *Perrierina* is the presence in the former of mantle margin papillae (Soot-Ryen, 1951). According to Ponder (1971), mantle margin papillae are absent in *Perrierina*. Unfortunately, the poor preservation of the specimens on which this paper is based made it impossible to confirm the state of this character. Nevertheless, the differences in hinge morphology call for the reallocation of "*Cyamiocardium*" *crassicostatum* into *Perrierina*.

Perrierina crassilabrum shows some characteristics intermediate between the subgenera *Perrierina* and *Legrandina*. The presence of prominent beaks is a characteristic shared with *Perrierina*, whereas a hinge plate broader at the base of the cardinals is characteristic of *Legrandina*. Furthermore, there are some other features of *P. crassilabrum* not previously known for other species of *Perrierina* or *Legrandina*, such as the relatively large adult size, the nearly circular shell outline of adults, and the strong radial ornamentation.



Figures 1–12. *Perrierina crassilabrum* **1, 9.** Holotype (NHM 1962863). **1.** External view of left valve. **9.** Internal view of left valve. **2–8, 10–12.** Specimens from 51° 29′ S, 61° 50′ W, SEM micrographs. **2.** External view of an adult specimen, right valve. **3.** External view of a juvenile. **4.** External views of larvae removed from an adult. **5.** Dorsal view, showing protoconch and hinge plate. **6.** Detail of shell microsculpture. **7.** Inner view of right valve. **8.** Internal view of left valve. **10, 11.** Detail of adult hinge plates. **10.** Right valve. 3a, 3b = cardinal teeth, L = ligament. **11.** Left valve. 2, 4b = cardinal teeth, at = anterior tooth. **12.** Detail of hinge plate of a juvenile of 2–3 mm length. Scale bars: 1–3, 7–9 = 1 mm; 4 = 100 µm; 5 = 200 µm; 6 = 50 µm; 10–12 = 500 µm.

The familial placement of *Perrierina* is somewhat confusing; the genus was successively placed within the Mactridae (Bernard, 1897), Leptonidae (Dall, 1899), and Crassatellidae (Suter, 1913; Lamy, 1917). Later, Marwick (1928) regarded the "taxodont" lamellae of the hinge as a character sufficient to warrant proposition of the family Perrierinidae, but this family was subsequently regarded as a synonym of Cyamiidae (e.g. Chavan (1969), Thiele, (1934), Fleming (1948), Ponder (1971), and Powell (1979)). The Cyamiidae is a family relatively well-diversified in the Magellanic Region, where a total of 12 species belonging to *Cyamium*, *Cyamiocardium*, *Gaimardia*, and *Kidderia* have been reported and recognized as valid by Zelaya (2005). The present paper represents the first record in Magellanic waters of a species of *Perrierina*, a genus thus far known only from Australia, Tasmania, and New Zealand.

ACKNOWLEDGMENTS

The author is grateful to A. Roux (INIDEP) who kindly made available the material collected during the R/V SHINKAI MARU cruise; K. Way and A. MacLellan (NHM) kindly sent photographs of the holotype of *Cyamiocardium crassilabrum*; C. Digiani (MLP) helped with older literature; and C. Ituarte provided valuable criticism and suggestions on an early version of the manuscript.

The author is member of the National Research Council for Science and Technology (CONICET), Argentina. This study was partially supported by a grant from the Western Society of Malacologists, made possible by the Santa Barbara Malacological Society, the Southwestern Malacological Society, the San Diego Shell Club, and the Northern California Malacological Club, and by grant PICT 282 from "Agencia Nacional de Promoción Científica y Tecnológica," Argentina.

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Volume 122, Number 2
June 23, 2008
ISSN 0028-1344

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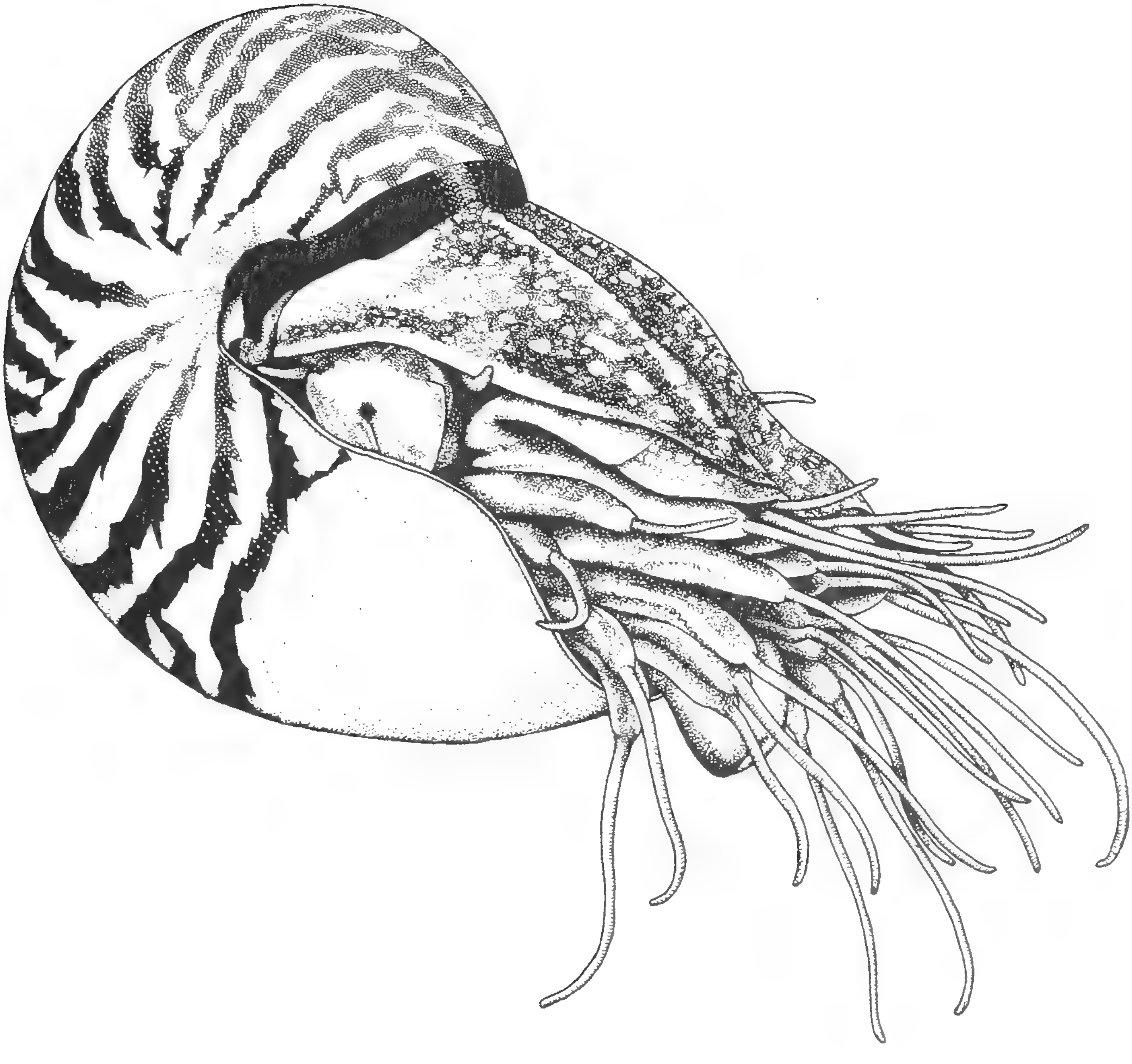

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THE NAUTILUS (ISSN 0028-1344) is published quarterly by The Bailey-Matthews Shell Museum, 3075 Sanibel-Captiva Road, Sanibel, FL 33975.

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THE NAUTILUS

Volume 122, Number 2
June 23, 2008
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Revision of the genus *Spinosipella* (Bivalvia: Verticordiidae), with descriptions of two new species from Brazil

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ABSTRACT

A revision of the deep-water verticordiid genus *Spinosipella* is provided, based on conchological and anatomical characters. The genus is considered distinct from *Verticordia* (of which it was considered a subgenus) based on the strong ribs, prickly surface, reduction of lunula, relative large size, weakly spiral valve shape, and other characters. The following species are considered in the genus: (1) *Spinosipella agnes* new species, ranging from Florida, USA, to Rio de Janeiro, Brazil, and also including the Porcupine Abyssal Plain in the North Atlantic; (2) *S. tinga* new species, occurring from Rio de Janeiro to Rio Grande do Sul, Brazil; (3) *S. acuticostata* (Philippi, 1844), a Pliocene fossil from southern Italy; (4) *S. deshayesiana* (Fischer, 1862), from south and central Indo-Pacific (*S. ericia* Hedley, 1911, the type species of the genus, was revealed to be a new synonym of *S. deshayesiana*); and (5) *S. costeminens* (Poutiers, 1981), from the tropical west Pacific. The five species differ mainly in conchological details of the number and size of ribs, of the prickly sculpture, shape of the shell, of the hinge and the degree of convexity. Anatomical description is also provided for the two Pacific species, which differ among themselves mainly by the size of the pair of renal folds. From the standpoint of anatomical characters, the more significant are: the wide lithodesma; the elongation of the auricles, crossing the roof of pallial cavity; a tall digital fold in posterior region of supraseptal chamber; the low but wide palps; the muscular, gizzard-like stomach; the complete separation of both constituents of the hermaphroditic gonad (a ventro-posterior testicle and a centro-dorsal ovary), and a complete fusion of the visceral ganglia.

Additional Keywords: Mollusca, Anomalodesmata, Septibranchia

INTRODUCTION

The Verticordiidae is a family of septibranch bivalves comprised of carnivorous and mostly deep-water species. They are typically small (less than 10 mm) but some species reach 30–40 mm. They are mostly radially sculptured and usually have nacreous inner surface.

The genus *Spinosipella* Iredale, 1930 (type *Verticordia ericia* Hedley, 1911, by original designation) is usually considered a subgenus of *Verticordia* Sowerby, 1844 (e.g., Thiele, 1934; Moore, 1969; Abbott and Dance, 1983). The genus encompasses species with shell having prickly outer surface, lunule very reduced, thick walls, and generally larger size (up to 30 mm). In addition to the type species, *S. ericia*, three other species are currently included in this genus, *S. acuticostata* (Philippi, 1844), from Atlantic and Mediterranean (middle Tertiary to Recent); *S. deshayesiana* (P. Fischer, 1862a) and *S. costeminens* (Poutiers, 1981), from Indo-Pacific. Some authors have considered *S. deshayesiana* as an Indo-Pacific occurrence of *S. acuticostata* (e.g., Nobre, 1936; Crozier, 1966; Rosenberg, 2005).

Examination of worldwide samples, with an emphasis on the Western Atlantic, showed that two species actually exist in the Atlantic. Both are separate from the fossil S. acuticostata. In addition, it was possible to reorganize the Indo-Pacific species, mainly because of the abundant material deposited at the Muséum national d'Histoire naturelle, Paris (MNHN), which results from several expeditions. A revision of the taxonomy and a necessary re-definition of taxa are provided in this paper, as part of a larger project revising Western Atlantic mollusk taxonomy, based on morphology.

MATERIALS AND METHODS

A detailed list of the material examined follows each species description. Specimens generally belong to museum collections. Most material consists of shells examined under a stereomicroscope. Some few Pacific samples have preserved soft parts in 70% ETOH. They were dissected by standard techniques, under stereomicroscope, with specimen immerse in alcohol. All dissecting steps were digitally photographed; all drawings were made with the aid of a camera lucida. In the case of the material examined of *Spinosipella deshayesiana* and

S. costeminens, as the quantity of examined lots is very large, mainly thorugh courtesy of staff at MNHN (Paris), the list only contains the country and the quantity of specimens. The full list of examined lots of these specimens is being published elsewhere, in a complementary paper (Simone and Cunha, in press).

Abbreviations used in figures are: am, anterior adductor muscle; **an,** anus; **au,** auricle; **bs,** byssus; **by,** byssal gland or furrow; **cc,** cerebral commissure; **ce,** cerebral ganglion; **cj,** connective tissue; **cm,** circular muscle layer; **co,** cerebro-visceral connective; **cr,** crustacean inside stomach; **cv,** ctenidial (efferent) vein; **dd,** ducts to digestive diverticulae; **dg,** digestive diverticula; **es,** esophagus; **fa,** foot aperture of mantle; **fm,** posterior foot retractor muscle; **fr,** anterior foot retractor muscle; **ft,** foot; **ga,** genital aperture; **ge,** gastric epithelium; **gi,** gill; **he,** hemocoel; **ic,** infra-septal chamber; **in,** intestine; **ki,** kidney; **lm,** lateral muscle; **lo,** longitudinal muscle layer; **lt,** lithodesma; **mb,** mantle border; **mf,** fused mantle edge; **mg,** radial mantle gland; **mo,** mouth; **mp,** mantle tentacle; **ms,** mantle muscles of incurrent siphon; **mt,** mantle; **mu,** muscular tissue; **ne,** nephropore; **nv,** nerve; **oy,** ovary; **pa,** posterior adductor muscle; **pc,** pericardium; **pg,** pedal ganglia; **pi,** papilla of excurrent chamber roof; **pm,** pallial muscles; **pp,** palp; **rs,** renal fold; **rt,** rectum; **se,** excurrent siphon; **sh,** shell; **si,** incurrent siphon; **sm,** septum muscle; **sp,** septum; **ss,** style sac; **st,** stomach; **su,** supra-septal chamber; **sy,** crystalline style; **ts,** testis; **um,** shell umbo; **ve,** ventricle; **vg,** visceral ganglia; **vm,** visceral mass.

Abbreviations of institutions: AMS, Australian Museum at Sydney, Australia; EGC, Emilio Garcia collection; FMNH, Florida Museum of Natural History, Florida, USA; HGLC, Harry G. Lee collection; INVEMAR-MHNMC, project of Museo de Historia Natural Marina de Colombia; MHNMC, Museo de Historia Natural Marina de Colombia (Programa de Biodiversidad y Ecosistemas Marinos); MNHN, Muséum national d'Histoire naturelle, Paris, France; MZSP, Museu de Zoologia da Universidade de São Paulo, Brazil; RLPC, Rafael La Perna collection (Universitá di Bali, Italy).

Specimens from other verticordiid species were also examined for comparative purposes. This material includes:

Haliris fischeriana Dall, 1881:

UNITED STATES OF AMERICA. Florida, Fowey Light, 130 m depth, MZSP 19934, 2 valves (R.V. EOLIS sta. 184). BRAZIL. Rio de Janeiro; 22°34′ S, 40°29′ W, 213 m depth, MZSP 18751, 1 valve (on Laminarias, W. Besnard col, est. IX). Rio Grande do Sul; 30°42′ S, 49°03′ W, 182–186 m depth, MZSP 18750, 5 valves (21 Aug. 1972); 32°55′ S, 50°34′ W, 99 m depth, UFRG 1688, 1 shell and 10 valves (sta. 45, 6839 dredge, 04/iv/1998)

Euciroa sp.

BRAZIL. Rio Grande do Sul, off Tramandaí, 30°42′ S, 49°03′ W, 182–186 m, MZSP 18750, 5 valves (R/V W. Besnard, GEDIP sta. 1856, 21 Aug. 1972). MADAGASCAR. 600 m depth, EGC 23588, 1 shell. MOZAMBIQUE. off Morondava, Channel Madagascar, 600–800 m depth, MZSP 61816, 3 shells (Trawled by local fisherman, May 2002).

Euciroa elegantissima (Dall, 1881).

UNITED STATES OF AMERICA. Florida, 27°16′ N, 84°58.99′ W, 457 m depth, EGC 13005, 6 valves (dredged, R/V PELICAN), 24°09′ N, 82°31′ W, about 64.3 km off Southwest of Key West, 549 m depth, EGC 23688, 1 shell (R/V OREGON II col, cruise #45, sta. 13362); Monroe Co. Straits of Florida, 549 m depth, FMNH 209892, 1 shell (Frank Lyman col.), 24°15.1′ N, 82°11.71′ W, 525 m depth, FMNH 164794, 1 valve (G.H. Burgess, et. al. GHB-90-8, 23 Apr. 1990). COLOMBIA. Santa Marta, Cerro de Punta Betin, A.A. 1016, (MHNMC INVEMAR), MHNMC 2782, 3 valves, MHNMC 2781, 1 valve.

SYSTEMATICS

Genus *Spinosipella* Iredale, 1930

Iphigenia Costa, 1850: 398 (type species by original designation *Hippagus acuticostatus* Philippi. 1844) (pre-occupied) (non Schumacher, 1817).

Spinosipella Iredale, 1930: 388 (type species by original designation *Verticordia ericia* Hedley. 1911); Poutier and Bernard, 1995: 142.

Verticordia (Spinosipella): Thiele, 1934: 1428; Moore, 1969: 855.

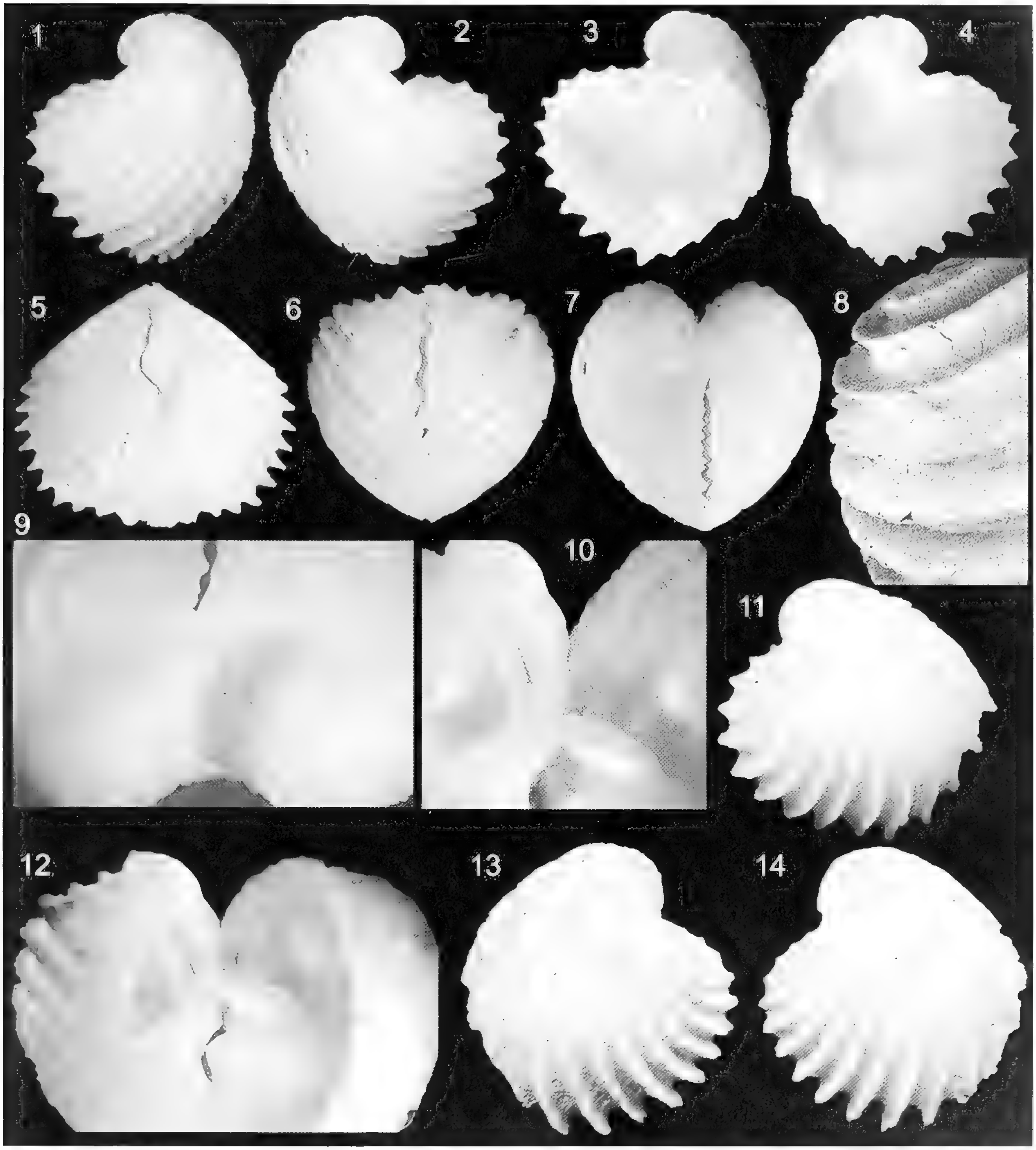
Diagnosis: Shell relatively large, obese, with spiral valves. Surface prickly including on radial ribs. Radial ribs tall, extending beyond shell margin. Lunula very reduced.

Description: SHELL: From small to medium size (up to 30 mm). Width/length ratio usually about 1. Color opaque-whitish. Sculptured by strong and tall radial, weakly curved ribs, triangular in section, bulging weakly beyond shell edge, alternating in both valves. Surface spiny, constituted by uniform sized, very small bulbs, covering almost entire outer surface. Lunula very reduced. Umbo projected, weakly spiral. Right valve with single tall, pointed and broad cardinal tooth. Left valve with low, broad tooth (posterior to tooth of right valve), and plane cardinal concavity as socket of tooth of right valve. Ligament just anterior to anterior hinge tooth, inserted at some distance from median line, in approximately middle way between hinge medial edge and umbonal cavity (Figures 10, 12). Lithodesma wide, curve, occupying about 0.25 of hinge length, possessing a pair of lateral ligamental articulations (Figures 93, 96–105).

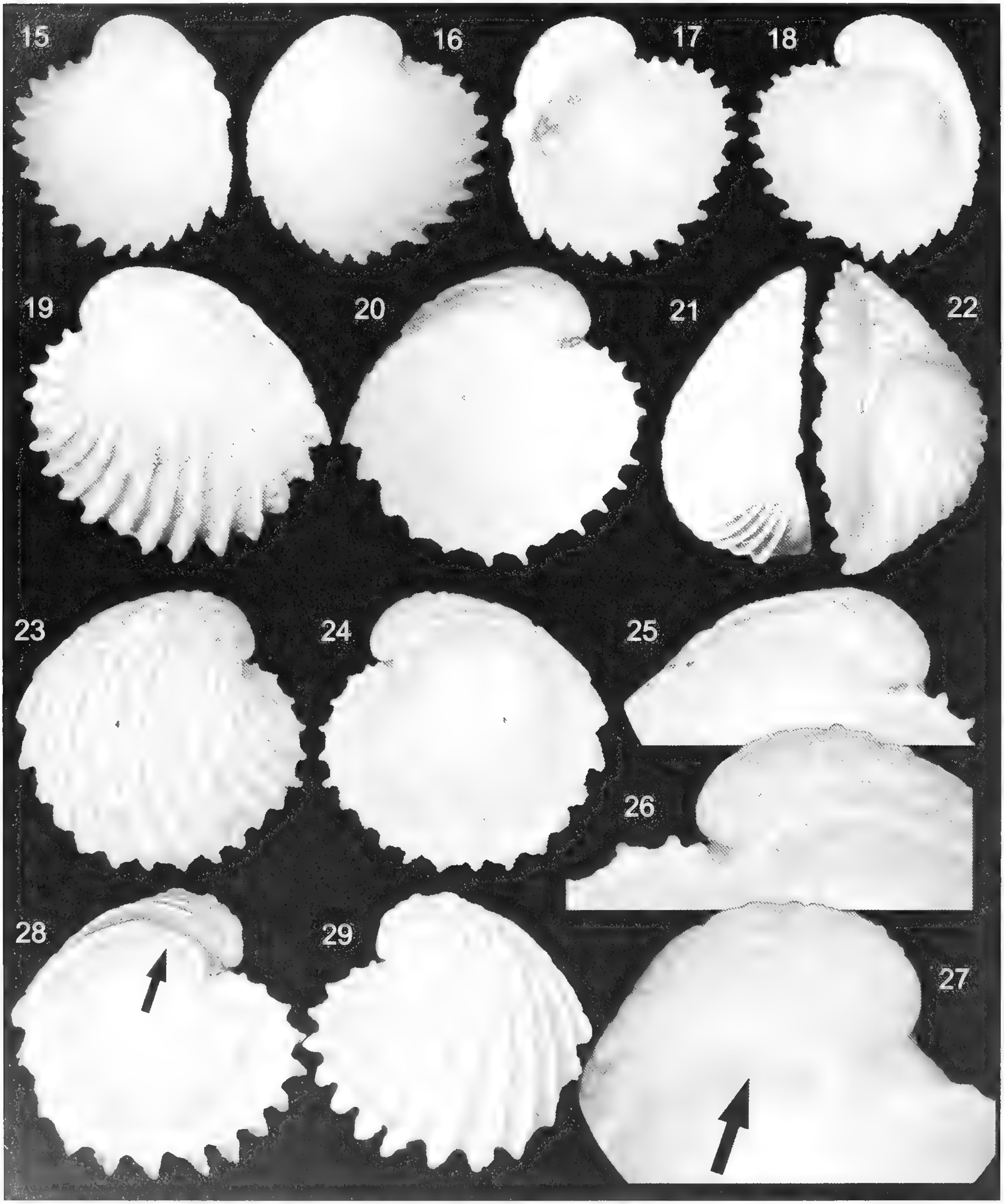
List of Included Taxa: *S. acuticostata* (Philippi, 1844); *S. agnes* new species; *S. costeminens* (Poutiers, 1981); *S. deshayesiana* (P. Fischer, 1862a) [=*S. ericia* (Henley, 1911)]; *S. tinga* new species.

Spinosipella agnes new species
(Figures 1–18, 27–29, 31, 55)

Verticordia acuticostata.—Nobre, 1936: 303–304; 1938: 769–770; Abbott, 1974: 563; Abbott and Dance, 1983: 375



Figures 1–14. *Spinosipella agnes* new species. Shells. **1–10.** Holotype (length 23.2 mm) shell. **1.** Left valve, outer view. **2.** Right valve. **3.** Right valve, inner view; **4.** Left valve, inner view. **5.** Dorsal view. **6.** Posterior view. **7.** Anterior view. **8.** Detail of shell surface in SEM, middle region of right valve. **9.** Detail of inter-umbonal region, dorsal view. **10.** Hinge, ventral-inner view. **11–14.** Paratypes. **11.** HGLC, from Florida, left valve, outer view; 11 mm. **12.** Same, ventral view, valves opened for showing whole view of hinge **13–14.** EGC 17419, from Colombia, outer view of right and left valves; 18 mm.



Figures 15–29. *Spinosipella* new species. Shells. **15–18.** *S. agnes* paratype AMNH 162803, Florida, specimen with remains of soft parts; 14.8 mm. **19–26.** *S. tinga* type specimens. **19–21.** Holotype, left valve, outer, inner and dorsal views; 16.9 mm. **22–24.** Paratype MORG 18085, right valve, dorsal, outer and inner views; 10.1 mm. **25.** Holotype, detail of hinge, left valve. **26.** Paratype MORG 18085, right valve, detail of hinge. **27–29.** *S. agnes.* **27.** Holotype, left valve, detail of hinge; arrow indicating well-developed posterior cardinal tooth. **28–29.** Paratype INV-MOL 2943, from Colombia, a specimen of equivalent size of main types of *S. tinga* (or showing major differences; compare with Figures 19–20); inner and outer views; 17.0 mm; note developed posterior cardinal toot of hinge (arrow), fewer, taller and more spaced ribs and more projected ribs at edges

(fig.); van Aartsen, 1992: 45; Poppe and Goto, 1993: 139; ?McLean and Geiger, 1998: 27, 109 (fig.); Salas, 1996: 46; Rosenberg, 2005 (part) (non Philippi, 1844).
Verticordia deshayesiana.—Rosenberg, 2005 (part) (in synonymy) (non Fischer, 1862a).

Type Material: HOLOTYPE, MZSP 36917; BRAZIL. Rio de Janeiro, off Cabo Frio, 23°41′ S, 41°03′ W, 750–800 m depth (o.t.). PARATYPES. UNITED STATES OF AMERICA. Florida; Off Cape Canaveral, 903 m depth, USNM 64039, 1 right valve; SE of Sand Key, AMNH 248458, 4 shells (Jan. 1970, J. M. Bijur Collection), AMNH 248459, 2 shells (Jun. 1970, J. M. Bijur Collection); Monroe County, S.E. Sand Key, 270 m depth, HGLC, 2 shells, FMNH 154594, 1 specimen (dredged, Jerry Phelps col., Jun. 1970); 120.6 km east of Daytona, 29°17′ N, 79°27′ W, 878 m depth, USNM 810590, 1 shell and 1 left valve (R/V. Oregon, sta. 6690, 9 May 1967); Marquesas Key, 24°15′ N, 82°13′ W, 278–419 m depth, 1 left, USNM 810889, 1 right valve (R/V. Blake, A. Agassiz 1877–1878). COLOMBIA. off Cartagena, 10°28′ N, 75°42′ W, 280 m, MHNMC 2203, 1 valve (E-47), 10°31′ N, 75°37′ W, 309 m, MHNMC 2775, 1 valve (E-141), Palomino, Dibulla, 11°29′ N, 73°27′ W, 476 m, MHNMC 3104, 4 valves, (E-21), Guajira, Bahía Honda, 12°31′ N, 72°8′ W, 452 m, MHNMC 2943, 1 shell (E-12), Guajira Peninsula, 12°30′ N, 72°08′ W, 470 m depth, EGC 17419, 1 shell; Cabo de la Vela, 12°19′ N, 72°42′ W, 464 m, MHNMC 3087, 2 valves (E-19), Islas del Rosario, 10°10′ N, 76°01′ W, 510 m, MHNMC 2208, 2 valves (E-78). BRAZIL. Rio Grande do Norte; 206 m depth, MZSP 84627, 1 shell (Sta. D-22, 10 Nov. 2001); Pernambuco; 690 m depth, MZSP 84628, 1 shell (Sta. D-11).

Diagnosis: Shell with 15–17 radial ribs; smooth pre-umbonal region wide (about 0.25 of shell length); prickly sculpture chaotically organized. Width/length ratio in each valve approximately 0.57. Posterior cardinal tooth of left valve hinge well developed; main cardinal tooth of left valve relatively low and cylindrical; main cardinal tooth of right valve tall (about 0.2 of valve width) and pointed.

Description: Shell: Up to 22 mm, equivalve, inflated, each valve symmetrically and weakly spiral (1 whorl) (Figures 7, 9). Color white. Degree of convexity (width/length) in each valve approximately 0.57. Outer surface spiny, opaque forming an irregular mosaic (Figures 8, 9). Umbones located in middle region of dorsal surface, spiral, high, divergent, separated from each other at about ⅓ of shell width (Figures 1–4, 13–18, 55). Sculptured by strong, uniform, arched, radial ribs, from 15 to 17 in each valve. Posterior edge about twice as wide as anterior edge. Between umbo and anterior edge a concavity bearing transversal ribs, slightly wider than ribs of remaining region (Figures 5, 7, 9). Pre-umbonal region smooth, narrow, 0.2 of shell length (Figures 5, 7, 9). Anterior, ventral and posterior edges forming zigzag (Figures 3, 4); tips of this zigzag coinciding with tips of each rib, tips encasing in concavity of opposite valve (Figures 1, 2, 11, 13–16). Inner surface iridescent, whitish, glossy; including hinge (Figures 3, 4, 10, 12, 17, 18). Hinge with a large cardinal tooth in right valve, stubby, tall (about 20% of valve width), broadly pointed, weakly curved forwards (Figures 3, 10, 12, 18), circular in section; correspondent socket in left valve shallow, restrict to dorsal surface; this socket flanked by small tooth in each side, anterior smaller and lower than posterior (Figures 4, 10, 12, 17, 27–28 [arrow]). Ligament just anterior to anterior hinge tooth, inserted at some distance from median line (Figures 10, 12), approximately midway between hinge medial edge and umbonal cavity. Scars of adductor muscles shallow (Figures 3, 4, 17, 18, 28); anterior scar elliptical (longer dorso-ventrally), located close to anterior edge, area about 1/15 of inner surface of valve; posterior scar circular, about 0.33 larger than anterior scar, located close to posterior shell edge. Pallial line continuous, located at wide distance from shell edge, about 0.33 of distance between ventral and umbonal height.

Measurements (Length, height, width, in mm): Holotype: 20.1 by 23.2 by 22.2; EGC 17419: 15.6 by 15.5 by 15.5.

Geographic Distribution: Florida, USA, to Rio de Janeiro, Brazil.

Habitat: Muddy bottoms, 270–900 m.

Material Examined: Types. BARBADOS. USNM 63200, 3 valves (Blake Coll., sta. 100). CUBA. Havana; Gulf of Mexico, 419 m depth, USNM 63201, 3 right, 4 left valves (Blake Coll., sta. 5). PORTUGAL. Porcupine Bank; USNM 63204, 2 right valves (Jeffreys Coll., Porcupine Exp. 1870). UNITED STATES OF AMERICA. Florida; Gulf of Mexico, off Cape San Blas, 309 m depth, USNM 323871, 1 left, 1 right valve (sta. 2400); 120.6 km east of Daytona, 29°17′ N, 79°27′ W, 878 m depth, USNM 810590, 1 shell and 1 left valve. BRAZIL. Espírito Santo (R/V Marion-Dufresne MD55, May 1987); off Conceição da Barra, 18°59′ S, 37°50′ W, 637 m depth, MNHN, 10 valves (sta. CB76); off Pontal da Regência, 19°34′ S, 38°55′ W, 340–360 m depth, MNHN 1 valve (sta. CB92).

Etymology: The specific epithet refers from the Greek *agnes*, meaning pure, an allusion to the whitish color of the shell.

Remarks: The above listed examined material that was not designed as types are normally lots with eroded specimens, or sometimes they have aberrant characters. This is the case of the MNHN material collected off north coast of Espírito Santo, Brazil. They actually are free valves that resemble the Pacific species *Spinisopella costeminens*, in having a weakly larger radial thread between middle and posterior thirds, and in lacking anterior tooth in hinge. As they can represent another species, they are not designed as types; on the other hand, the material is not sufficiently well-preserved for further analysis. Because of they can only represent an extreme of variation of the *S. agnes*, they are listed as additional examined material of this species.

Spinosipella tinga new species
(Figures 19–26, 30, 32)

Verticordia acuticostata: Marini, 1974: 242, figs. 5, 6 (non Philippi, 1844).
Verticordia (Haliris) acuticostata: Rios, 1975: 262, pl. 85., fig. 1261; 1985: 282, pl. 99, fig. 1391; 1994: 304, pl. 104, figs. 1489 (non Philippi, 1844).
Verticordia deshayesiana: Marini, 1974: 242 (in synonymy); Rios, 1975: 262; 1985: 282; 1994: 304 (in synonymy); Rosenberg, 2005 (part) (in synonymy) (non Fischer, 1862a).

Diagnosis: Shell with 17–18 radial ribs; smooth pre-umbonal region very narrow (less that ⅕ of shell length). Width/length ratio in each valve approximately 0.47. Posterior cardinal tooth of left valve hinge absent; main cardinal tooth of left valve low and cylindrical; main cardinal tooth of right valve lower (about 10% of valve width) and rounded.

Description: SHELL: Up to 11 mm, equivalve, inflated, both valves weakly spiral (1 whorl) (Figures 21, 22). Color white. Degree of convexity (width/length) in each valve approximately 0.47. Umbones located in middle region of dorsal surface (Figures 19, 20, 23, 24); umbones weakly spiraled, somewhat high, divergent, separated from each other. Sculpture of strong, uniform, arched, radial ribs, 17–18 in each valve. Outer surface opaque, covered by a mosaic of small, blunt, loosely aligned spines parallel to radial ribs (Figure 32). Anterior edge almost same size as posterior edge. A concavity bearing transversal ribs of same width as remaining ribs between umbo and posterior edge (Figures 21, 22, 30). Anterior, ventral, and posterior edges rounded, tips of ribs prominent (Figures 19, 20, 23, 24), fitting with concavity in opposite valve. Inner surface iridescent, whitish, glossy, including hinge. Hinge with a somewhat large cardinal tooth in right valve (Figures 20, 25); cardinal tooth stubby, tip rounded, flat in cross-section, tooth length about 10% of valve width; correspondent socket in left valve shallow, restricted to dorsal surface; this socket flanked by small, low, posterior tooth (no anterior tooth) (Figures 24, 26). Ligament just anterior to anterior hinge tooth, inserted at some distance from midline, approximately midway between hinge medial edge and umbonal cavity. Scars of adductor muscles shallow (Figures 20, 24); anterior scar elliptical (longer dorso-ventrally), located close to anterior edge, area about $\frac{1}{15}$ of inner surface of valve; posterior scar circular, about ⅓ larger than anterior scar, located close to posterior shell edge. Pallial line with a very weak pallial sinus, located at wide distance from shell edge, about ⅓ of distance between ventral and umbonal height.

Measurements (respectively length, height, width, in mm): Holotype: 16.9 × 15.3 × 9.6 (single valve); MZSP 18752: Paratype #1, 8.6 × 8.6 × 4.1 (1 valve); Paratype #2, 11.9 × 11.4 × 5.4 (1 valve); MZSP 18753: 9.5 × 9.6 × 4.8 (1 valve).

Type Material: Holotype, MZSP 19345, 1 valve, from type locality (R/V W. BESNARD, GEPID Est. 458, 9 Dec. 1968. Paratypes, Rio de Janeiro, Cabo de São Tomé, 31°08′ S, 49°31′ W, 182–253 m, 1 valve, MZSP 18752 (R/V W. BESNARD, GEDIP st. 1858, 6 Aug. 1972); 22°34′ S, 40°29′ W, 213 m, 1 valve, MZSP 18753; (R/V W. BESNARD, st. IX, 11 Feb.1969), 100 m, 2 valves, MORG 18085 (R/V ALMIRANTE SALDANHA, Mar. 1972), off Solidão, 240 m, 2 valves, MORG 31888 (R/V ATLÂNTICO SUL, Exp. Coltro, 14 Oct.1993).

Type Locality: BRAZIL. Rio Grande do Sul, off Albardão, 33°29′ S, 50°44′ W, 200 m, muddy bottom.

Geographic Distribution: Brazil, from Rio de Janeiro to Rio Grande do Sul.

Etymology: The specific epithet refers to the color white of the shell, from the Tupy language: *tinga*.

Spinosipella acuticostata (Philippi, 1844)
(Figures 33–40)

Hippagus acuticostatus Philippi, 1844: 42 (pl. 14, fig. 19) [fossil in Lamati valley, Calabria, Italy].
Verticordia acuticostata: Micali and Villari, 1991: 353.
Spinosipella acuticostata: Poutiers and Bernard, 1995: 143, 155.

Diagnosis: Shell with 12–13 radial ribs; pre-umbonal region narrow, smooth; posterior cardinal tooth of left valve hinge shallow or absent; main cardinal tooth of left valve longer and flat (Figures 35, 40); main cardinal tooth of right valve shallower (Figures 34, 37) (about 10% of valve width).

Description: SHELL: Up to 24 mm; width/length ratio approximately 1 (Figures 36–38) to 1.5 (Figures 39, 40). Degree of convexity (width/length) in each valve approximately 0.55. Outer surface spiny, opaque, spines forming radially aligned mosaic parallel to ribs (Figures 36, 38, 39). Sculpture of strong, uniform, arched, radial ribs, 12–13 in each valve. Posterior edge about twice as broad as anterior edge. A concavity bearing transversal ribs weakly broader than ribs of remaining region between umbo and anterior edge (Figures 35, 39); pre-umbonal region narrow, smoooth (Figure 33), about 10% of shell length. Anterior, ventral, and posterior edges forming zigzag (Figures 35, 37, 40). Hinge with a large cardinal tooth in right valve, stubby, tall (about 10% of valve width), broadly pointed, weakly curved anteriorly (Figures 34, 37), circular in section; correspondent socket in left valve shallow, restricted to dorsal surface; this socket sometimes flanked by small tooth in each side, anterior absent or very weak (Figures 35, 40).

Measurements (respectively length, height, width, in mm): RLPC #1: 11.4 × 14.5 × 6.6 (valve); #2: 10.0 × 9.8 × 4.7 (valve).

Geographic Distribution: Mediterranean. Pliocene fossil from south Italy (Calabria and Sicily).

Figures 30–47. *Spinosipella* species. Shells. **30.** *S. tinga*, Holotype, left valve, dorsal view. **31.** *S. agnes*, Paratype INV-MOL 2943, from Colombia, a specimen of equivalent size of Holotype of *S. tinga* for showing major differences (compare with Figure 30); dorsal view; 17.0 mm; note higher convexity, fewer, taller and more spaced ribs. **32.** *S. tinga*, left valve, SEM of Holotype, showing prickly sculpture. **33–40.** *S. acuticostata*. **33–38.** Pliocene fossil from Messina, Italy, USNM 63202. **33**, Specimen 2, dorsal-slightly anterior view. **34.** Specimen 3, right valve, detail of hinge. **35–36.** Specimen 1, left valve, inner and outer views; 13.5 mm. **37–38.** Specimen 2, right valve, inner and outer views, hinge broken; 12.2 mm. **39–40.** RLPC, from Rometta, Italy, left valve, specimen with long shape; 19.0 mm. **41–47.** *S. deshayesiana*. **41–43.** Paratype 1 of *S. ericia* AMS 032068, left valve, inner, outer and dorsal views; 3.5 mm. **44.** Paratype 2, right valve, inner view; 2.6 mm. **45**, Type specimen of *S. japonica* ANSP 49639, right valve; 5.2 mm. **46–47.** ANSP 292986 (from India), right valve, outer and inner views; 10.5 mm.

Paleohabitat: Middle and upper Pliocene beds of bathyal environments.

Material Examined: ITALY. Sicily, Messina, 38°11′ N, 15°34′ E, Seguenza, USNM 63202, 2 left, 2 right valves. Middle Pliocene outcrops at Rometta, 4 valves, RLPC.

Spinosipella deshayesiana (Fischer, 1862)
(Figures 41–54, 66, 67, 72–82, 93–102)

Verticordia Deshayesiana Fischer, 1862a: 35–36 (pl. 5, fig. 10–11) [China Sea].
Verticordia japonica A. Adams, 1862: 224.
Verticordia ericia Hedley, 1911: 96; Prezant, 1998: 421 (fig. 9.16A).
Spinosipella deshayesiana.—Poutiers and Bernard, 1995: 110–112, 143, 159, 161 (figs. 7–9).
Spinisopella ericia.—Poutiers and Bernard, 1995: 143, 159.
Verticordia acuticostata.—McLean and Geiger, 1998: 109 (non Philippi, 1844).

Diagnosis: Shell with 16–19 radial ribs uniformly distributed, closely packed; pre-umbonal region narrow, smooth. Each rib bearing well-developed crests with small, prickly granules. Posterior cardinal tooth of left valve hinge absent; main cardinal tooth of left valve low and flat, with insertion of anterior valve edge approximately in middle region of this tooth; main cardinal tooth of right valve high (about 10% of valve width) and pointed.

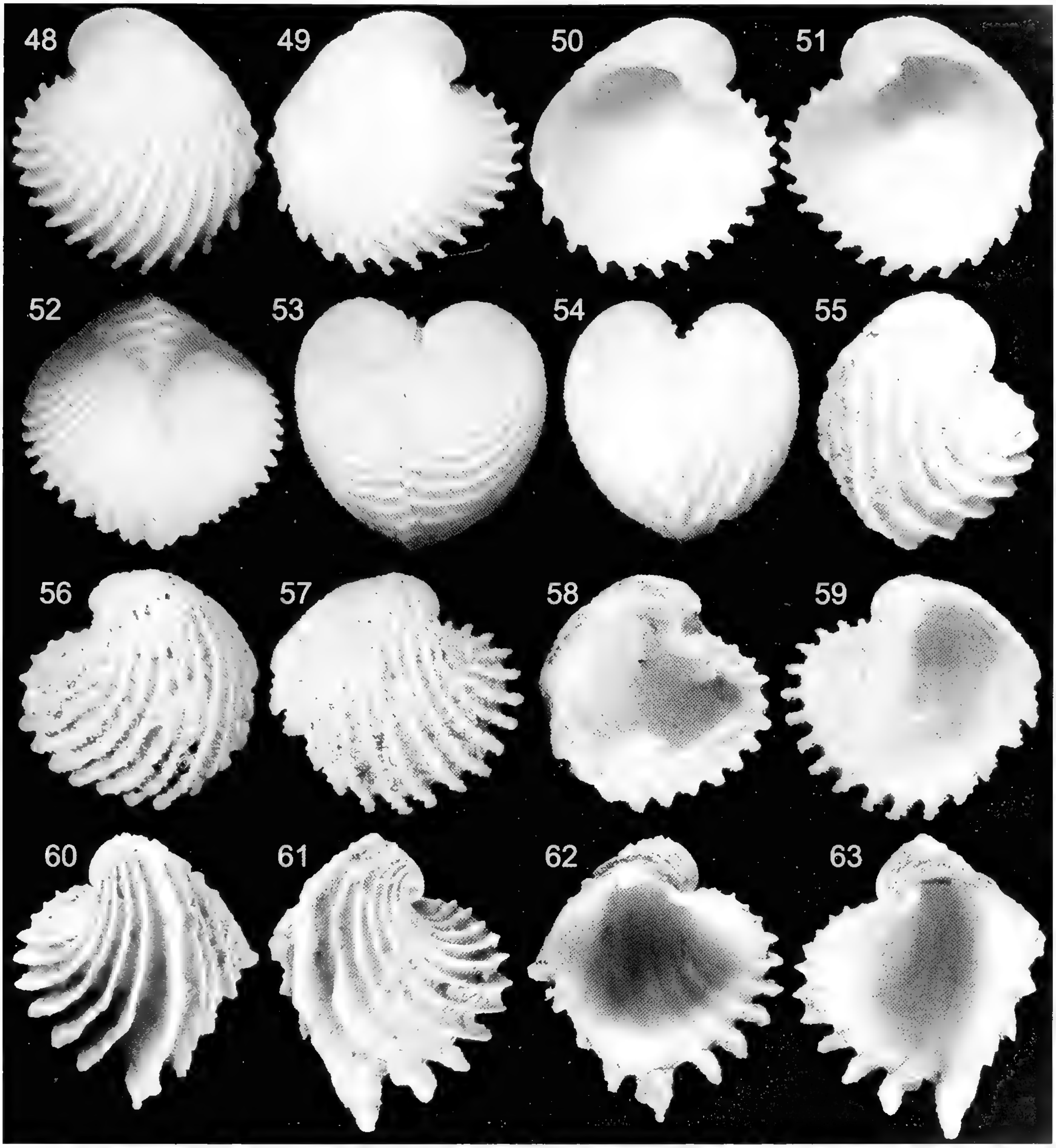
Description: SHELL: Up to 18 mm. Color white. Degree of convexity (width/length) in each valve approximately 0.57. Outer surface spiny, spines organized somewhat radially, parallel to ribs; each rib with well-developed crests with small, prickly granules (Figures 42, 45, 46, 48–54). Sculpture of strong, uniform, arched, radial ribs, 16–19 in each valve (Figures 42, 45, 46, 50), somewhat closely packed. Posterior edge about twice broader than anterior edge. A concavity bearing transversal ribs similar to ribs of remaining region present between umbo and anterior edge (Figures 43, 53); pre-umbonal region narrow, smooth, about 10% of shell length (Figures 43, 53). Anterior, ventral, and posterior edges forming zigzag (Figures 42, 44, 47, 50, 51, 59, 67, 100), with tips projected, longer, and narrower. Hinge with a large cardinal tooth in right valve, stubby, tall (about 10% of valve width), broadly pointed, somewhat flat (Figures 44, 47, 51, 59, 67); correspondent socket in left valve shallow, restrict to dorsal surface; this socket flanked by small posterior tooth, with insertion of anterior valve edge approximately in middle region of this tooth (Figures 41, 50), anterior tooth absent (Figures 41, 50).

LITHODESMA (Figures 93, 96–99): Saddle-shaped, hemi-cylindrical. Dorsal surface concave (Figures 97–98), flanking ventral surface of hinge, along ¼ of hinge length; located just posterior to teeth. Left and right edges straight, turned upwards and medially, connected with valves by dark-brown ligament inside umbonal cavity closer to hinge inner edge (Figures 100–102). Outer surface convex, covering dorsal-middle, inter-umbonal region of visceral mass (Figure 75). Anterior and posterior edges concave; anterior edge slightly deeper and with tenuous slope. Both edges covered by opaque, yellowish periostracum (Figures 96, 101, 102). Lithodesma thickness equivalent to that of shell.

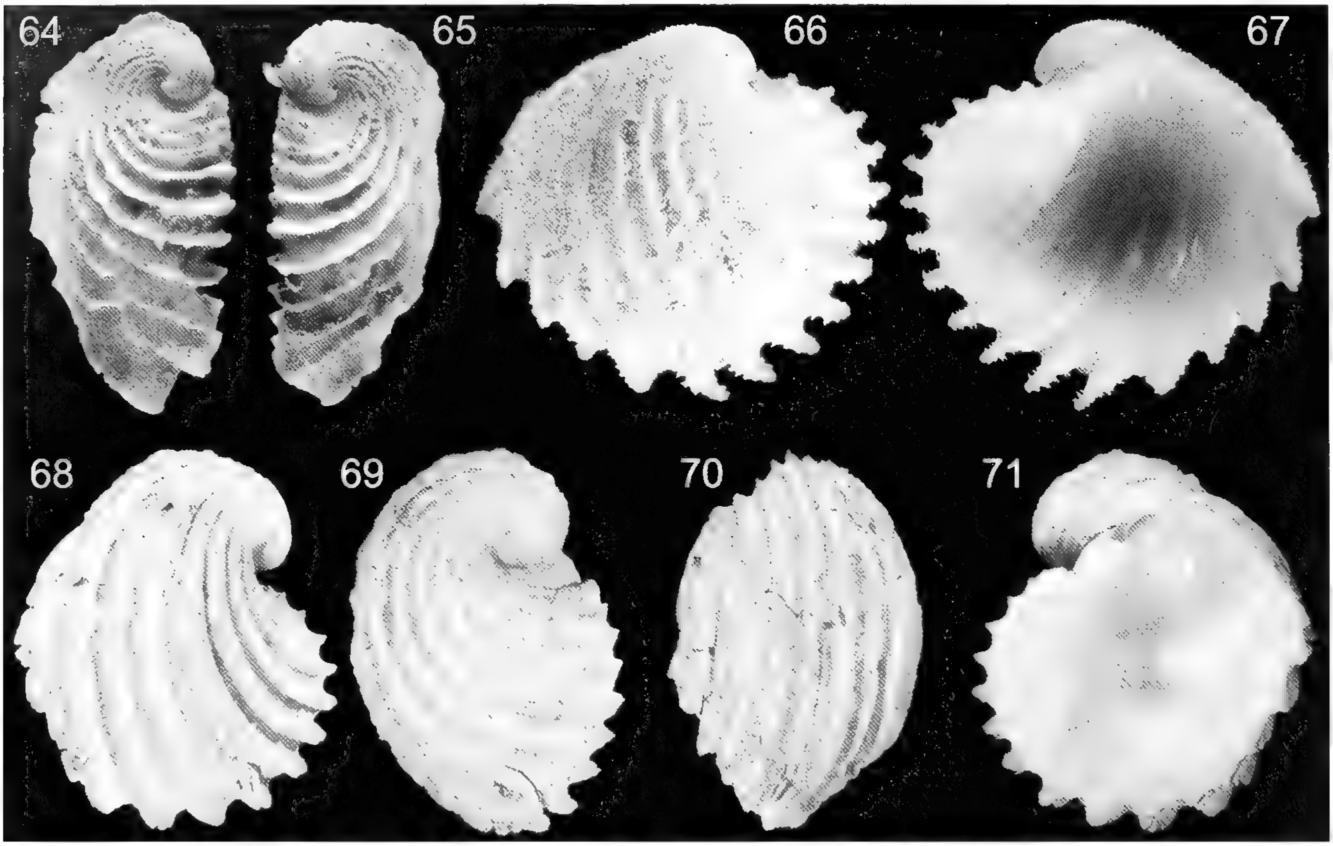
MAJOR MUSCLES (FIGURES 72–75, 77, 78, 80, 91, 92): Both adductor muscles similar in size and position (Figures 72–75), near valve edges; insertion size equivalent to 1/20 of valves inner surface each; approximately two times taller than wide; outer length about half of inner length, with insertion in valves greatly oblique (Figures 75, 91, 92). Anterior adductor muscle with anterior region about 3 times narrower than posterior region, divided transversally (dorsoventral) in two similar halves (quick and slow components). Posterior adductor muscle similar to, but inverted arrangement in comparison to anterior adductor muscle; components different, however, one of them horseshoe-shaped, occupying ventral and posterior sides (Figure 77); another component filling internal region of muscle, only exposed in posterior and dorsal sides (Figure 77). Pair of anterior foot retractor muscles long and narrow (Figure 80); originating just dorsal to anterior adductor muscle in area equivalent to 1/10 of adductor (Figures 75, 80); running ventrally and posteriorly; spreading after insertion in anterior and lateral regions of foot base. Pair of posterior foot retractor muscles similar to anterior pair, but about half narrower (Figures 75, 78, 80); originating just dorsal to posterior adductor muscle in area equivalent to 1/20 of that adductor; running ventral and anteriorly; inserting in posterior and lateral regions of foot base. Pair of palp muscles, septal and pallial muscles described below. Pair of foot protractor muscles absent.

FOOT AND BYSSUS (FIGURES 73, 74, 80): Foot conical, pointed; estimated volume equivalent to 1/6 of that of chamber of valves; base located in middle region of ventral surface of visceral sac. Byssal furrow shallow and very narrow, length about half of that of foot, offset ventrally and distally, lying along posterior surface and midline, ending at short distance from foot apex. Byssus found in a single specimen, brown, with single filament, narrow; proximal end attached to distal region of byssal furrow.

MANTLE (FIGURES 72–74): Dorsal fusion of mantle lobes about ⅓ of their edges, along entire hinge length and about ⅙ of valves height toward ventral, in both sides. Edges of mantle lobes with two folds. Inner fold fused between two lobes along entire posterior half (except for siphonal apertures) (Figure 74). Both lobes free from each other along anterior half, up to dorsal level of anterior adductor muscle; in this region both folds are of similar size, with height equivalent to 1⁄25 of valves height. Mantle edges thick, muscular, insertion relatively thick in pallial line (Figure 72, pm). Pallial muscles originating in pallial line in location about ⅓ from ventro-dorsal distance; no clear pallial sinus. Incurrent siphon as aperture of a septum formed by fusion of inner mantle edge folds; aperture about ⅕ of posterior fused region of mantle,



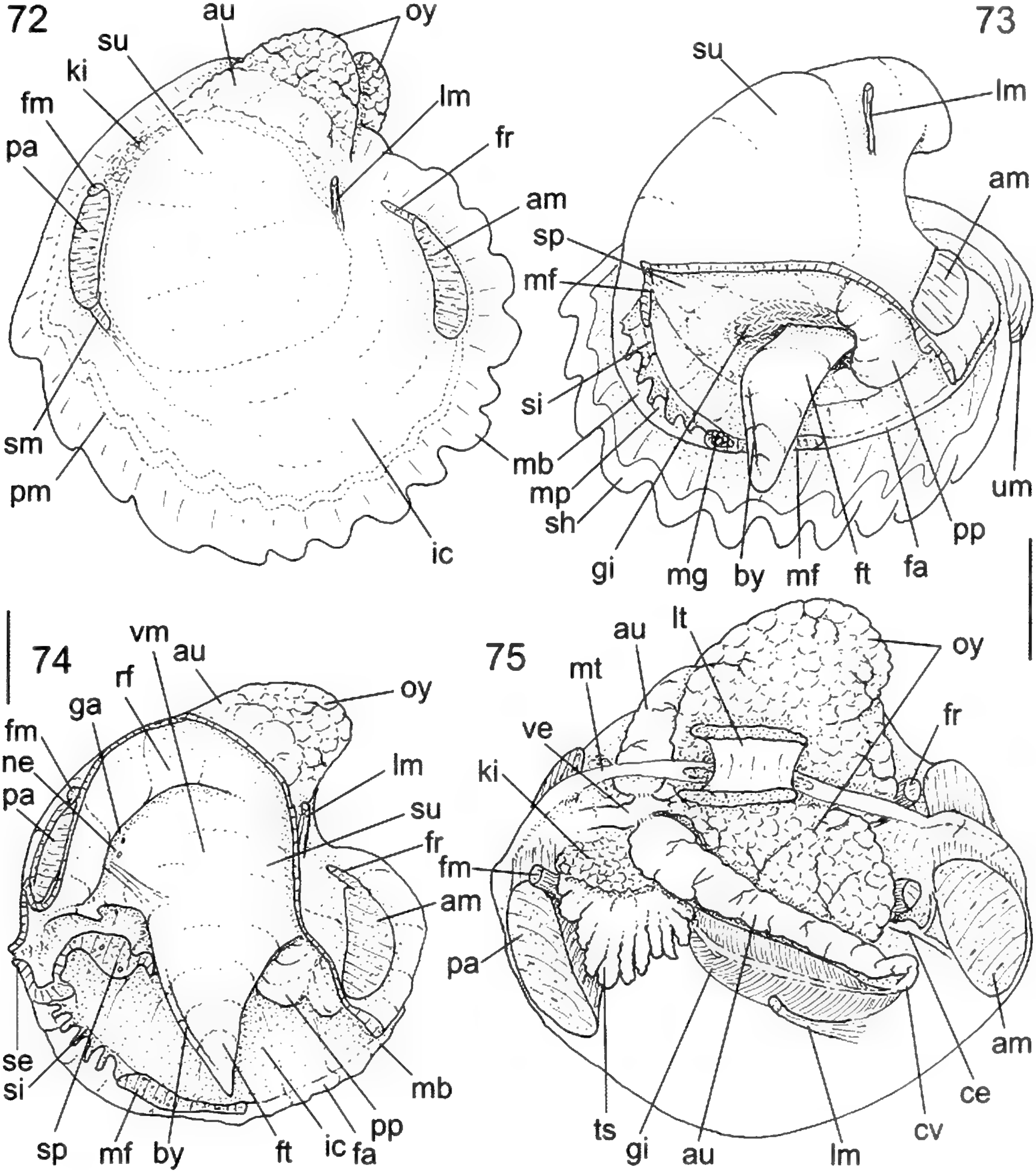
Figures 48–63. *Spinosipella* species. Shells. **48–54, 56–59.** *S. deshayesiana*, adult specimens. **48–53.** MNHN (Sta. CP1475, Fiji); 12.5 mm. **48.** Left valve, outer view. **49.** Right valve, outer view. **50.** Left valve, inner view. **51.** Right valve, inner view. **52.** Posterior view. **53.** Anterior view. **54.** Dorsal view, HGLC, from Philippines; 11.8 mm. **55.** *S. agnes* paratype, BMNH, 18.2 mm. **56–59.** Syntypes of *S. deshayesiana* MNHN. **56.** Outer view, specimen 1, left valve. **57.** Outer view, specimen 2 (possibly figured by Fischer, 1862a), right valve. **58.** Inner view, specimen 1. **59.** Inner view, specimen 2; length = 8 mm. **60–63.** *S. costeminens* Holotype MNHN **60.** Outer view, left valve. **61.** Outer view, right valve. **62.** Inner view, left valve. **63.** Inner view, right valve; 17 mm



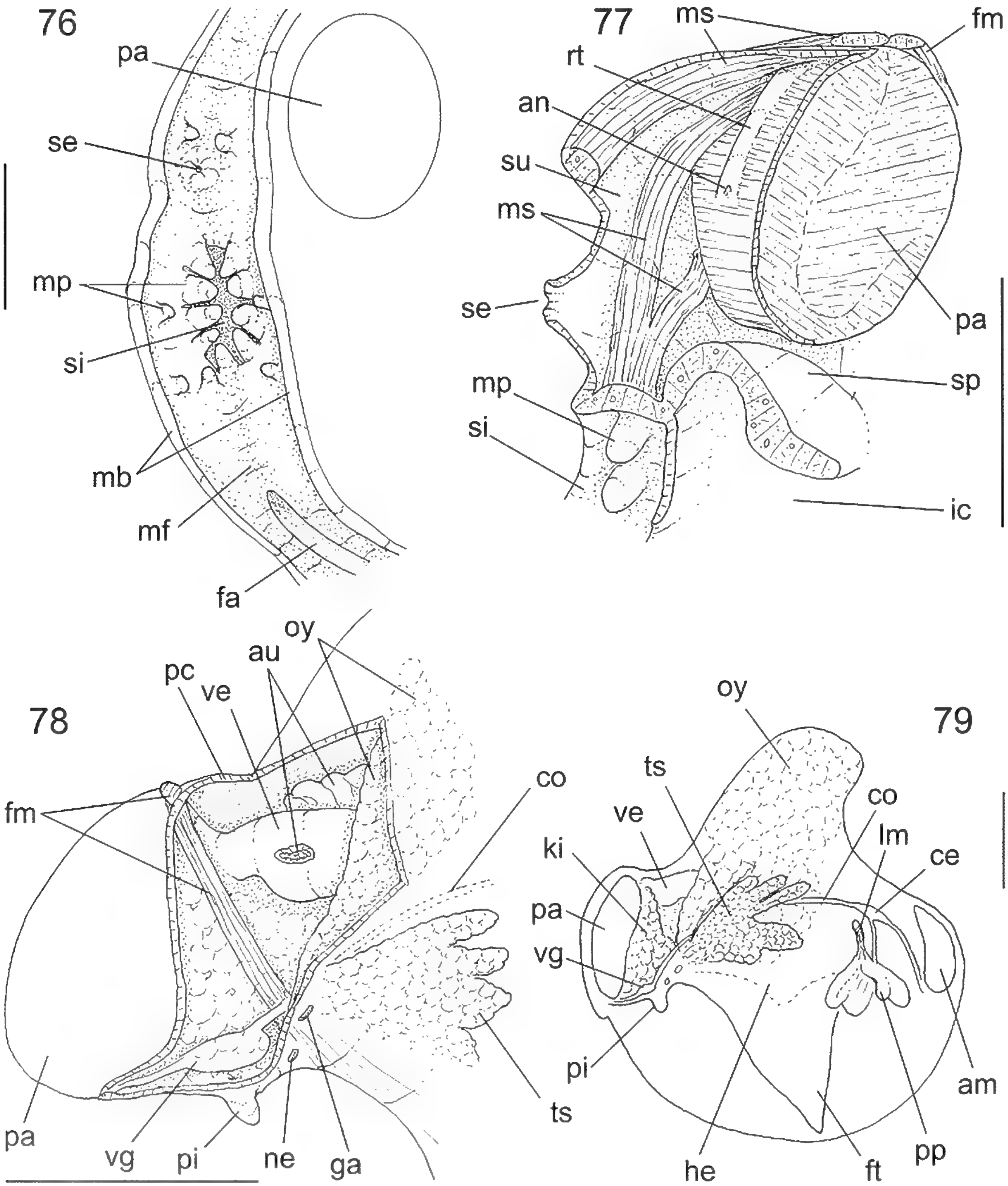
Figures 64–71. *Spinosipella* species. Shells. **64–65.** *S. costeminens* Holotype MNHN. **64.** Right valve, anterior view. **65.** Left valve, anterior view; 17.0 mm. **66–67.** *S. ericia* Holotype AMS, right valve. **66.** Outer view. **67.** Inner view; 5.8 mm. **68–71.** *S. costeminens* lacking projections on ribs, MNHN (Sta. CP 992, Vanuatu), right valve. **68.** Outer-right view. **69.** Anterior view. **70.** Posterior view. **71.** Inner view; 29.0 mm.

longer dorso-ventrally (Figure 76); walls thick, muscular; outer surface flanked by 9 tentacles surrounding siphonal aperture; all tentacles of similar size, turned inwards, somewhat conical, tip blunt and rounded, length equivalent to that of siphonal aperture; single unpaired tentacle located ventrally; five secondary smaller tentacles located externally, midway between siphonal aperture and mantle edge, of similar size, about ⅓ of size of major tentacles, well separated from each other, one of them located in ventral region of siphonal aperture, other four located laterally, in ventral half of siphon (Figure 76). Incurrent siphon a small pore located in small elevation, approximately midway between excurrent siphon and hinge; a pair of small tentacles similar to secondary tentacles of incurrent siphons, located laterally, in dorsal region of siphon base (Figures 74, 76, 77). Radial mantle gland present along mantle edges outer fold (Figures 73, 92, mg), occupying about half of outer fold volume, situated closer to inner surface of this fold.

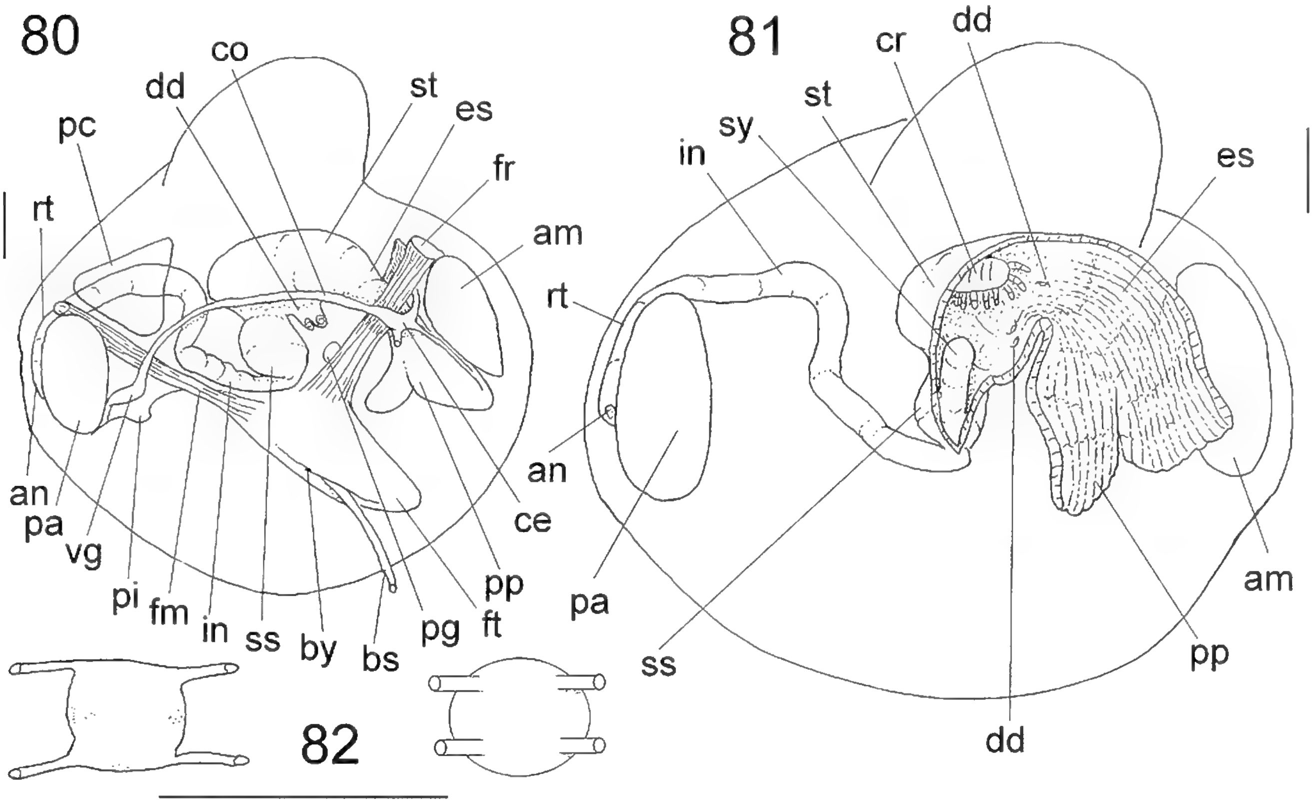
PALLIAL CAVITY (FIGURES 73–75, 94, 95): Occupying about 70% of volume of valves. Transversal, horizontal septum located approximately midway in animal, i.e., supra- and infra-septal chambers of equivalent length (Figure 72). Paired palps low, wide, bilobed folds (Figures 73, 81, 95, pp) that occupy anterior third of dorsal surface of infra-septal chamber, permanently open as a funnel. Pair of palp muscles (Figures 72, 74, 79, lm) located laterally; originating in anterior region of umbonal cavity, in a distance from origin of anterior foot retractor equivalent to ⅓ of anterior adductor muscle height; located in same horizontal level of origin of anterior foot retractor; size equivalent to ¼ of that of anterior foot retractor; running ventrally attached to mantle for a distance equivalent to ⅙ of valve height; spreading after insertion in lateral region between inner and outer hemipalps. Palp muscles also connect anterior end of septum. Septum with two constituents: external one produced by a fold of mantle (about ⅔ of septum area); internal produced by gill (Figures 73, 95). External septum element thick, muscular; posterior muscles originating as a pair, just dorsal to posterior adductor muscle (Figure 77, ms); running ventrally immersed in mantle, at some distance from each other (equivalent to half of their width) and from midline, gradually becoming wider and thicker, in anterior surrounding posterior surface of posterior adductor muscle and lateral edges of excurrent siphon; some secondary muscular bundles originating from centroposterior region of posterior adductor muscle uniting with main, vertical bundles (Figure 77); muscles spreading within septum in region between incurrent and ex-



Figures 72–75. *Spinosipella deshayesiana*. Anatomy. **72.** Whole specimen just extracted from shell, right view. **73.** Same, right mantle lobe in its infra-septal region removed, right-slightly ventral view, left shell valve also shown. **74.** Same, right mantle lobe almost completely removed, right portion of septum also removed. **75.** whole specimen, dorsal-slightly right view, most of mantle and dorsal integument artificially shown as transparent, lithodesma (**lt**) shown in its *in situ* topology. Scale bars = 2 mm



Figures 76–79. *Spinosipella deshayesiana.* Anatomy. **76.** Detail of region of siphons, posterior-slightly right view. **77.** Peri-anal chamber, right view, adjacent region of right mantle lobe sectioned and deflected to show inner surface and muscles, inferior region or right mantle lobe removed along median line. **78.** Reno-pericardial region and adjacent structures, right view, right wall of pericardium removed. **79.** Whole right view, showing topology of genital system, reno-pericardial structures, palps, main ganglia and muscles, most structures artificially shown as transparent. Scale bars = 2 mm.



Figures 80–82. *Spinosipella deshayesiana*. Anatomy. **80.** Whole right view, emphasizing digestive structures, main musculature and main nervous ganglia; topology of some adjacent structures also shown, everything else represented by transparency. **81.** Same, anterior region of digestive structures opened longitudinally, some objects inside stomach preserved, topology of some adjacent structures also shown. **82.** Visceral ganglia (left), ventral view, and pedal ganglia (right), postero-dorsal view. Scale bars = 1 mm.

current siphons. Outer component of septal muscles inserted in shell just ventral to posterior adductor muscle (Figure 72, sm), in area equivalent to ⅒ of that of adductor muscle insertion. Internal element of septum constituted by gills. Gill with both demibranchs narrow, of similar size, flattened, in same plane of remaining septum; both gills surrounding posterior and lateral regions of foot base (Figures 73, 75, 95). Gill attached to remaining septum via tissue; gill attachment to foot by cilia. Connection between gill filaments of 6–7 longitudinal, equidistant bridges of similar width of filaments. Papilla situated in posterior region of roof of supraseptal chamber (Figures 78–80, 94, pi), positioned just ventral to visceral ganglia, internally solid; length about ⅒ of posterior adductor muscle length and about ⅓ of it in width; tip broadly pointed, normally turned to anterior.

Visceral Mass (Figures 72, 75, 79): Strongly bilobed, as internal mould of well-separated umbos (Figures 72, 75). Most dorsal structures, just inside valve apexes, formed by sponge-like connective tissue. Pair of ovaries cream in color, occupying central and dorsal regions surrounding stomach and digestive diverticula, reaching dorsal areas up to dorsal sponge-like connective when fully developed. Testes brown, consistence harder, located ventrally and laterally, totally separated from ovaries; anterior region irregularly digitiform (Figures 75, 79, ts). Digestive diverticula situated compressed between stomach and gonads, color greenish-beige; occupying about ⅕ of visceral volume. Stomach and intestine lying in central region, occupying about ¼ of visceral volume (Figures 80). Reno-pericardial structures located just anterior to posterior adductor muscle and posterior foot retractor muscles, with volume approximately ⅙ of visceral volume (Figures 75, 79).

Circulatory and Excretory Systems (Figures 75, 78): Pericardium located at short distance anterior to posterior adductor muscle; with about half of reno-pericardial volume, and with a pair of expansions toward anterior, surrounding roof of pallial cavity where lies pair of auricles. Auricles connecting to anterior end of gills, in short isolated ctenidial vein (Figure 75, cv); abruptly curving towards posterior and dorsal; after this curve, auricles increasing gradually, surrounding obliquely periphery of visceral mass in roof of pallial cavity (Figures 72, 75), walls thin, translucent; close to midline auricles abruptly narrowing and connecting to ventricle (Figures 75, 78); posterior region relatively lobed. Ventricle located in center of pericardium, surrounding intestine; relatively narrow. Kidney mostly solid, color dark purple-almost black; most of renal gland located just anterior to posterior adductor muscle, ventral to pericardium (Figures 75, ki); a pair of folds originating from this region.

running long roof of pallial, supraseptal cavity, just ventral and external to auricles (Figures 74, rf), this pair of folds with about 1/5 of supraseptal chamber height, running posteriorly in middle region of roof of this chamber, gradually approaching visceral mass towards anterior, fusing to visceral mass after running about 1/6 of chamber length (Figure 74). Pair of nephropores as small slits located in posterior region of supraseptal chamber, covered by posterior end of renal fold, just dorsal to pair of posterior retractor muscles of foot (Figure 74, ne).

DIGESTIVE SYSTEM (FIGURES 80, 81): Palps partially described above (pallial cavity), widely fused as pair of folds along midline (Figures 95, pp). Mouth central (Figure 95, mo), with sphincter relatively well developed. Esophagus with about 1/5 of visceral mass length, not attached to anterior adductor muscle, width about 1/3 of that of anterior adductor muscles; wall relatively thick, muscular; inner surface with about 20 longitudinal, narrow, low folds as continuation from those of palps (Figure 81). Stomach main chamber with about 1/4 of visceral mass volume, elliptical, anteroposteriorly longer; walls thick, muscular (Figure 91, st). Gastric inner surface smooth; two pairs of ducts to digestive diverticula present, each one located in ventro-lateral region just posterior to esophageal insertion. Stomach normally containing 3–4 isopod crustaceans (Figure 81, cr). Style sac with about 1/3 of gastric main chamber volume, located in middle of gastric ventral wall, somewhat elliptical (longer dorso-ventrally); crystalline style occupying entire style sac (Figure 81, sy); inner surface of style sac smooth, lacking any fold separating it from intestine; gastric shield lacking. Intestine a single sigmoid loop with about half of style sac width. Inner surface simple, smooth. Intestinal portion crossing through pericardium in somewhat anteroposterior direction. Rectum attached to dorsal and posterior surface of posterior adductor muscle, with about 2/3 of remaining intestinal width. Anus simple, sessile, located in ventral third of posterior surface of posterior adductor muscle (Figure 77).

GENITAL SYSTEM (Partially described above under VISCERAL MASS): Pair of testes and ovaries converging to a single common, short duct, of about 1/15 of visceral mass length. Genital pores small slits located at short distance from nephropores (Figures 74, 78, 94, ga).

CENTRAL NERVOUS SYSTEM (FIGURES 80, 82): Cerebral ganglia somewhat triangular, each ganglion with volume equivalent to 1/15 of that of anterior adductor muscle; anterior end narrow, possessing thick pair of nerves running to pallial region dorsal to palps; pair of ventral nerves also thick, originated in middle region of ganglia, running ventrally to palps; Posterior end originating cerebro-visceral connective (Figures 80, 106); cerebral commissure length about 1/3 of posterior surface of anterior adductor muscle. Pair of cerebro-visceral commissures relatively thick, running though visceral mass between stomach and testes. Pair of pedal ganglia located in ventral third of anterior pair of pedal retractor muscles, touching these muscles, both totally fused with each other along midline, almost forming a sphere, volume of both equivalent to that of each cerebral ganglion; pedal nerves and cerebropedal connectives originating subterminally in posterior surface of ganglia. Pair of visceral ganglia located anterior to ventral surface of posterior adductor muscle; both also totally fused with each other along median line, being somewhat squared in ventral view; size equivalent to that of pedal pair of ganglia; cerebrovisceral connectives and siphonal nerves located in vertices.

Measurements (respectively length, height, width, in mm): HGLC: 11.5 by 12.2 by 12.0; MNHN (Sta. DW11): 15.7 by 17.7 by 9.2 (valve); MNHN (Sta. CP889): 19.7 by 17.0 by 9.1 (valve).

Geographic Distribution: South and Central Indo-Pacific in 146–805 m depth.

Material Examined: Paratypes of *S. ericia*: AUSTRALIA; South Cape Wiles, 174–183 m, 35°39′ S, 136°40′ E, AMS 032068, 1 left, 1 right valves (Zoological Results of the F.I.S. ENDEAVOUR, 28 Aug. 1909).

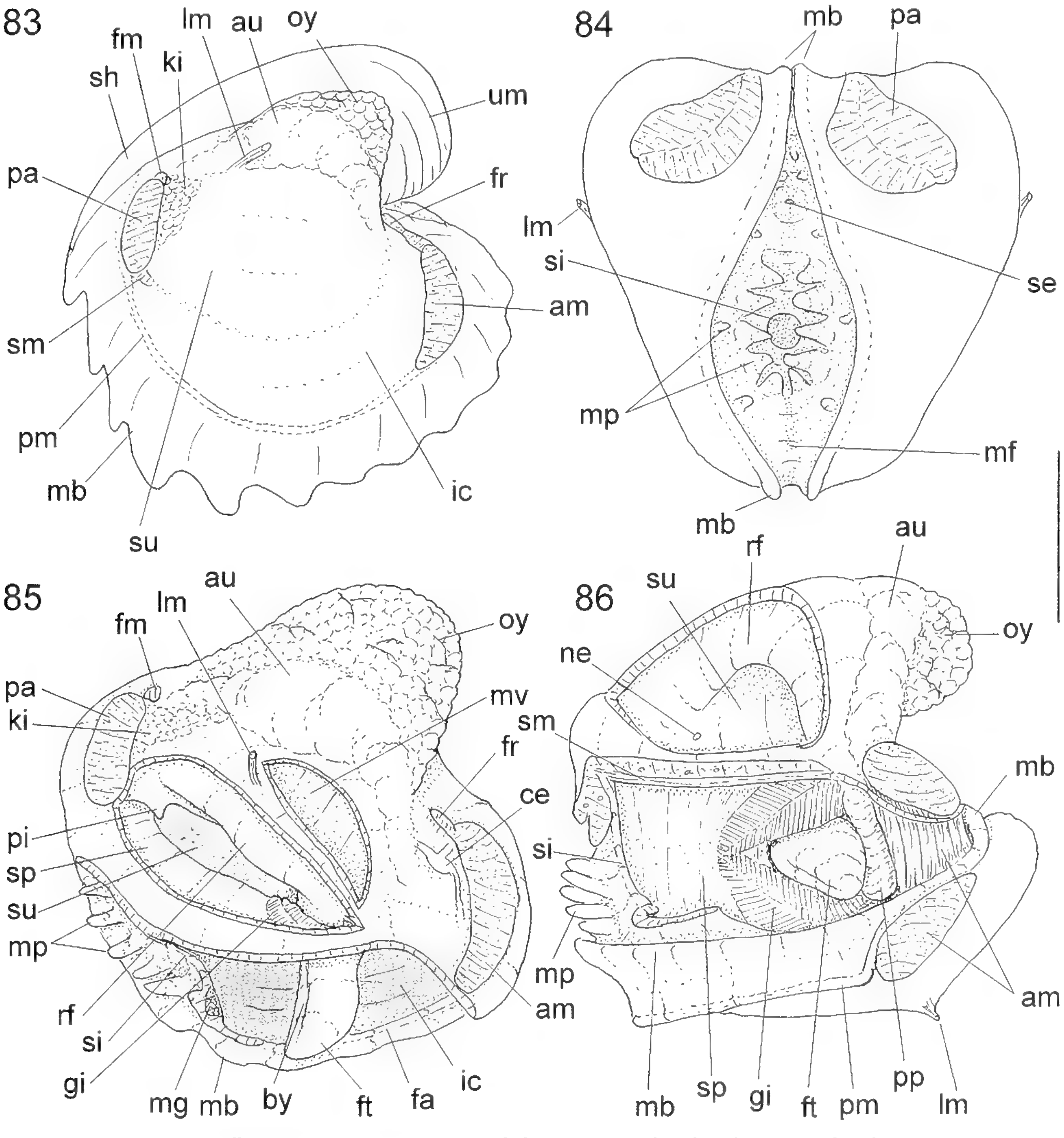
Other Material Examined: Holotype of *S. japonica*: JAPAN. ANSP 49639, 1 shell. MNHN. SW PACIFIC. Loyaute Islands, 16 lots [122 v]. TONGA IS. 12 lots [59 v]. GUAM. Marianas Islands, 3 lots [15 v]. AUSTRALIA. South Cape Wiles, 1 lot [6 v]. NEW CALEDONIA. South, 3 lots [7 specimens]; Banc Esponge, 2 lots [3 specimens]; Chesterfield Plateau, 1 specimen. PHILIPPINES. Aliguri Is. 2 lots [1 specimen and 3 v]; Bohol Sea, Off Balicasag Island, 1 lot [1 v]. FIJI. 1 specimen. MYANMAR (BURMA). 1 lot [5 v] Preparis North Channel, 1 lot [4 v]; N.W. of Tavoy I., 1 lot [11 v]. ANDAMANS SEA. 1 lot [1 v]. THAILAND. Phuket I., 1 lot [11 v]; Andaman Sea, 1 lot [1 v] (Details in Simone and Cunha, in press.)

Spinosipella costeminens (Poutiers, 1981)
(Figures 60–65, 68–71, 83–92, 103–108)

Verticordia (Spinosipella) costeminens Poutiers, 1981: 351 (pl. 4, figs 1–4, text fig 5).
Spinosipella costeminens.—Poutiers and Bernard, 1995: 110, 143, 158 (figs. 1–2).

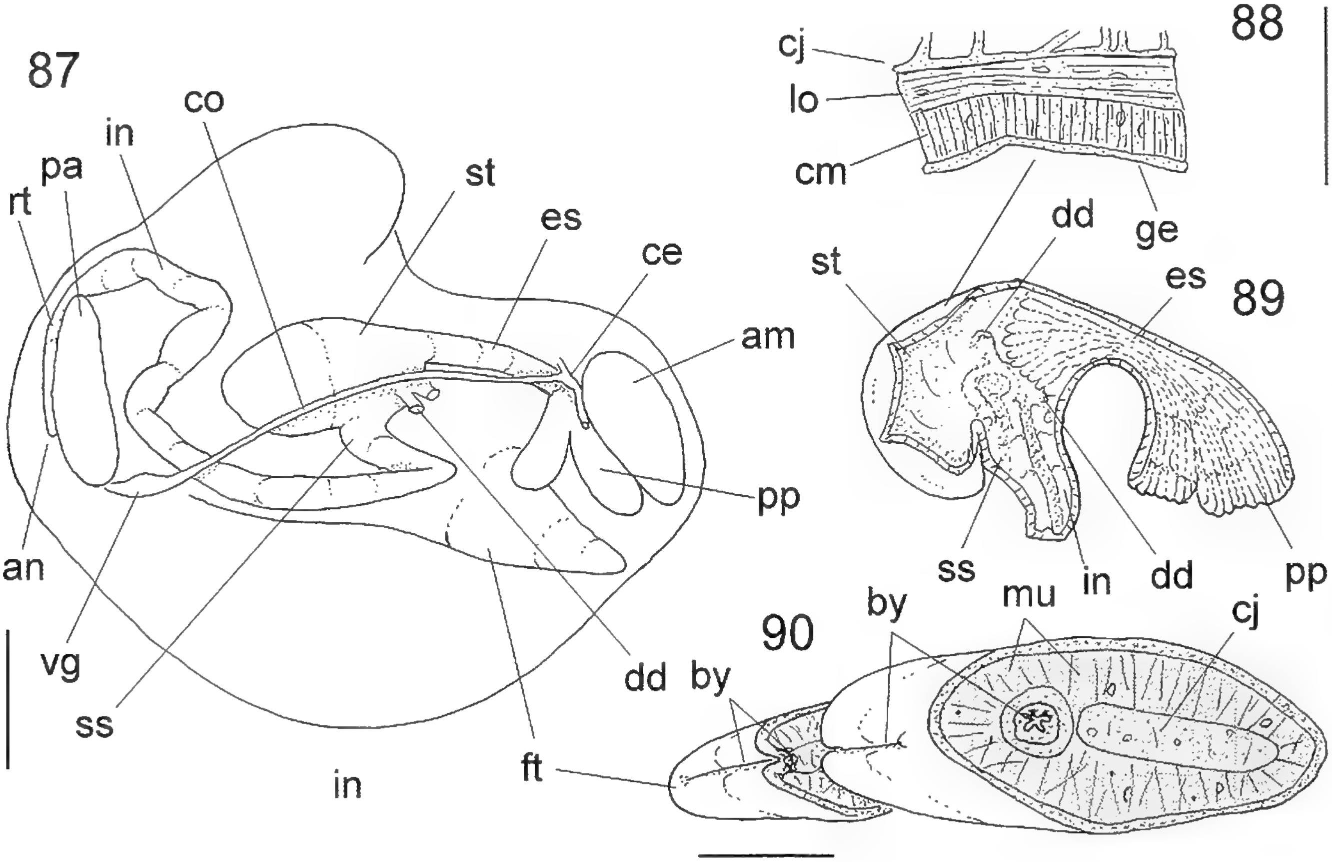
Diagnosis: Shell with 16–17 tall radial ribs, those more posterior to middle surface very taller, normally possessing blade-like projections along tip; 3–4 more posterior abruptly lower, preceded by a very tall, carina-like rib.

Description: SHELL: Up to 30 mm. Color white. Degree of convexity (width/length) in each valve approximately 0.50. Outer surface prickly, with somewhat chaotic organization (Figures 60, 61, 68–70). Sculptured by strong, uniform, arched, radial ribs, from 16 to 17 in each valve (Figures 60, 61); ribs increasing from region anterior to umbo to region between middle and posterior thirds, last ribs in this region taller and more separated from each other, last one on a weak carina (Figure 70); larger ribs normally possessing blade-like, projection



Figures 83–86. *Spinosipella costeminens.* Anatomy. **83.** Whole specimen with right valve extracted, right view. **84.** Specimen extracted from shell, posterior view, showing siphonal area. **85.** Whole right view, some portions of right mantle lobe extracted, particularly regions ventral to septum, and ventral and dorsal to renal fold (**rf**) to expose inner surface; cerebral ganglion (ce) seen by transparency. **86.** Same, ventral-slightly right view. Scale bar = 5 mm.

along tip; posterior third as a slope, having 3–4 ribs similar to those of anterior region; blade like projection absent in some specimens (Figures 68–71). Posterior edge about twice broader than anterior edge. Between umbos and anterior edge a concavity bearing transversal ribs similar to ribs of remaining region (Figures 64, 65); preumbonal region narrow, smooth about 10% of shell length (Figures 64, 65, 69). Anterior, ventral, and posterior edges forming zigzag (Figures 62, 63, 71, 103), with tips longer and narrower projected in those middle and larger ribs. Hinge with a large cardinal tooth in right valve, stubby, tall (about 10% of valve width), broadly



Figures 87–90. *Spinosipella costeminens.* Anatomy. **87.** Whole right view, mainly showing digestive tubes and main ganglia, topology of some structures also shown. Scale bar = 5 mm. **88.** Scheme of layers of tissue in indicated region of stomach. Scale bar = 0.5 mm. **89.** Fore- and midgut opened longitudinally for exposing inner surface (same scale of Figure 87). **90.** Foot, ventral-slightly posterior view, sectioned transversally in two levels to show inner layer of tissues. Scale bar = 1 mm.

pointed, somewhat flat (Figures 63, 71, 103); correspondent socket in left valve shallow, restrict to dorsal surface; this socket flanked by small posterior tooth, with insertion of anterior valve edge approximately in middle region of this tooth (Figure 62), anterior tooth absent (Figure 62).

Additional details for this species see Poutiers (1981), Poutiers and Bernard (1995).

Lithodesma (Figures 103–105): Characters similar to those in preceding species, differing in being proportionally shorter and wider (Figures 104–105). Length about $1/5$ to $1/6$ of hinge length, and about 1.5 times wider and long.

Main Muscle System (Figures 83–87): Characters similar to those in preceding species. Anterior adductor muscle about 20% dorso-ventrally longer (Figures 83, 85).

Foot and Byssus (Figures 85, 84, 90, 107): Shape and disposition similar to those in *S. deshayesiana*. Byssal gland relatively deep, running immersed in ventral region of pedal musculature at about half of byssal furrow

Figures 91–108. *Spinosipella* species. Anatomy. **91.** *S. costeminens*, middle horizontal, longitudinal section through visceral mass at same level as pericardium (MNHN sta. CP767, Mallory, 5 μm). Scale bar = 2 mm. **92.** Same, detail of posterior region of mantle border. Scale bar = 1 mm. **93–102.** *S. deshayesiana*. **93.** Detail of hinge region of left valve with lithodesma (**lt**) still attached, right view. Scale bar = 2 mm. **94.** Detail of posterior region of supraseptal chamber, right view, right mantle lobe removed (MNHN sta. DW1499). Scale bar = 1mm. **95.** Infraseptal chamber roof, ventral view, right mantle lobe removed (MNHN sta. CP767). Scale bar = 2 mm. **96–99.** Lithodesma (MNHN sta. DW739). Scale bar = 1 mm. **96.** Ventral view. **97.** Dorsal view. **98.** Posterior-slightly dorsal view. **99.** Posterior view. **100.** Same specimen, empty shell, ventral view, valves slightly open, lithodesma still in situ. Scale bar = 2 mm. **101.** Same, detail of hinge and lithodesma. **102.** Same, ventral-slightly anterior view. **103–108.** *S. costeminens*. **103.** Shell, ventral view, valves open, lithodesma still attached to left valve (MNHN sta. CP1460). Scale bar = 2 mm. **104–105.** Lithodesma, same lot (other specimen), dorsal and ventral views respectively. Scale bar = 1 mm. **106.** Detail of anterior region, right view, integument removed, mainly showing right cerebral ganglion (**ce**) (same lot). Scale bar = 1 mm. **107.** Infraseptal chamber roof, ventral view, right mantle lobe removed (MNHN CP767). Scale bar = 1 mm. **108.** Detail of posterior (siphonal) region, posterior view (MNHN CP1460). Scale bar = 2 mm

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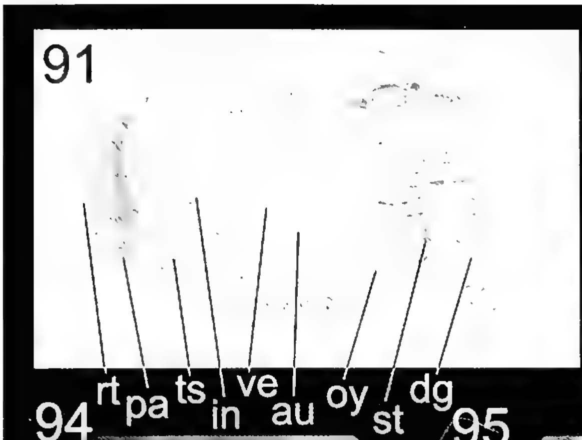

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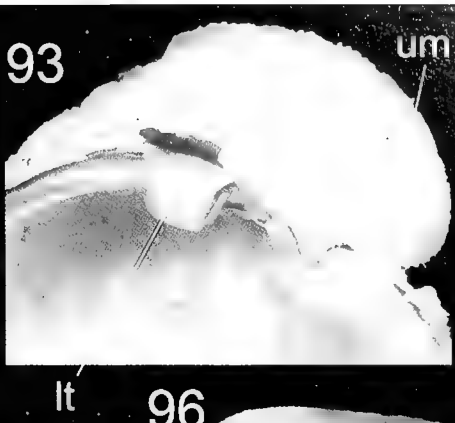

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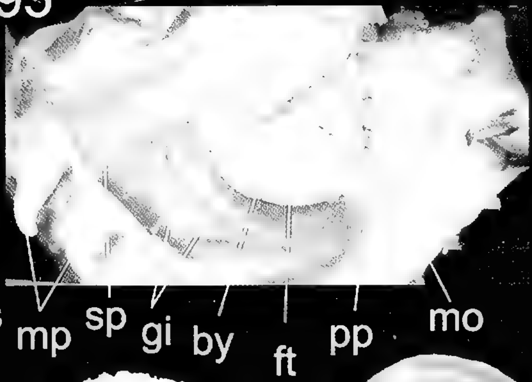

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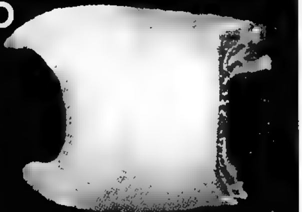

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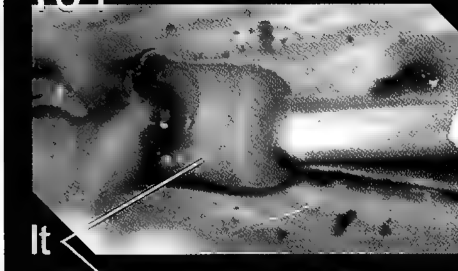

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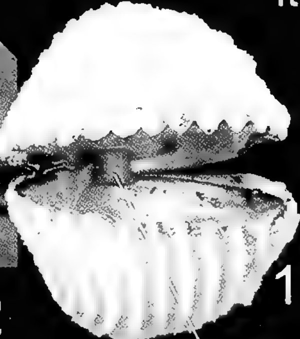

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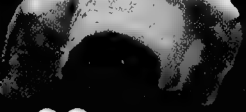

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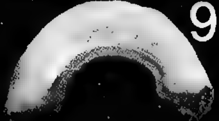

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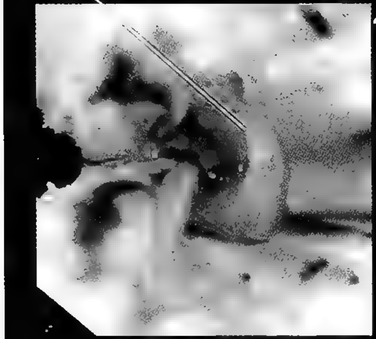

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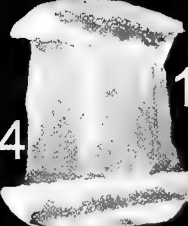

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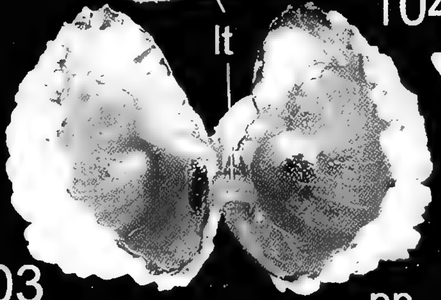

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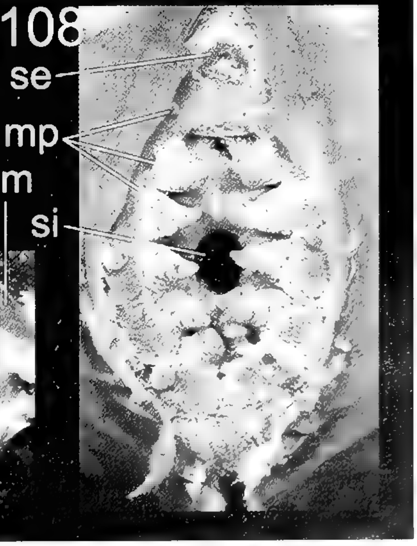

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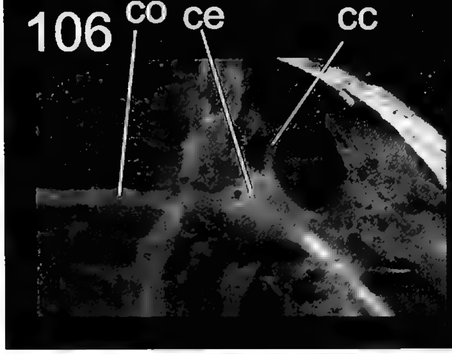

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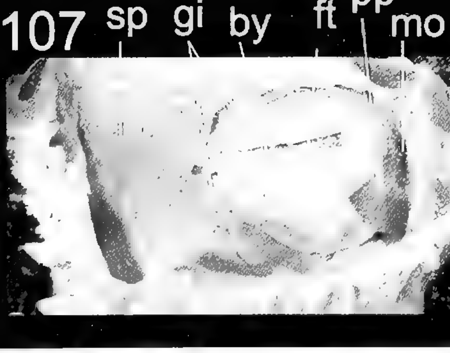

length towards dorsal (Figure 90, by). Thick muscular layer surrounding a nucleus of conective tissue (Figure 90, cj).

MANTLE (FIGURES 84–86, 92, 108): Characters similar to those in preceding species, with following distinctive characters. Pair of secondary tentacles positioned between incurrent and excurrent siphons (Figures 84, 108); remaining tentacles similar in size and position. Ventral pair of tentacles of incurrent siphon generally symmetrical. Zigzag formed by mantle edge having secondary folds positioned in more distal tips, possibly elated to taller radial shell ribs (Figure 108). Radial mantle gland (Figure 92) similar to *S. deshayesiana*.

PALLIAL CAVITY (FIGURES 85–86, 107): Characters similar to those in preceding species, except for wider platform between posterior region of gills as part of septum (Figure 107).

VISCERAL MASS (FIGURES 85–87): Characters similar to those in preceding species, differing mainly by wider region separating pair of renal folds in supraseptal chamber (Figure 85).

CIRCULATORY AND EXCRETORY SYSTEMS (FIGURES 85, 91): Pericardium and heart with characters similar to those in *S. deshayesiana* (Figure 91). Kidneys of similar features, differing mainly by enlargement of pair of renal folds (Figures 85–86, rf), taller and wider, almost dividing supraseptal chamber in two—internal and external—halves. Height of renal fold about 80% of that of supraseptal chamber height. In addition to an enlargement, both renal folds still have posterior end in more anterior position and wider separation between folds and visceral mass (Figure 85).

DIGESTIVE SYSTEM (FIGURES 87–89): Characters similar to those in preceding species. Esophagus with about ⅓ of visceral mass length, running horizontally, perpendicular to posterior surface of anterior adductor muscle (Figure 87, es). Stomach main chamber with longer region as a blind-sac projected posteriorly. Gastric wall constituted by external layer of weak connective tissue (Figure 88, cj), two thick muscular layers of similar size, with outer layer of longitudinal muscle and inner layer of circular muscle (Figure 88, lo and cm). Inner surface of stomach (Figure 89) with posterior end of esophageal folds clearly more evident that together form a flat fold. Another ventral fold surrounding apertures to digestive diverticula. Gastric style narrower (about ⅙ of gastric width); internally a pair of tall folds separating intestinal from style sac components (Figure 88, ss, in).

GENITAL SYSTEM: Characters similar to those in preceding species. Separated masculine and feminine components of gonad shown through histological sections in Figures 91(ts, ov).

CENTRAL NERVOUS SYSTEM (FIGURES 87, 106): Three ganglia with similar localization and size to those of preceding species.

Measurements (respectively length, height, width in mm): MNHN (Sta. 1361): 22.0 by 28.1 by 12.5 (valve); MNHN (Sta. CC996): 20.0 by 24.3 by 14.3 (valve); MNHN (Sta. CP992): 19.6 by 23.3 by 12.6 (valve).

Geographic Distribution: Tropical West Pacific.

Depth Range: 750–925 m.

Material Examined: Holotype; Additional material (MNHN): SW PACIFIC. 4 lots [32 v, 11 specimens]; Wallis Is., 6 lots [15 v]; Banc Combe, 5 Lots [28 v]; Fortuna Is., 5 lots [18 v]; Banc Waterwitch, 2 lots [3 v]; Banc Tuscarora, 29 lots [63 v]; South Vanuatu - Monts Gemini, 4 lots [4 v, 1 specimen]; TONGA IS. 8 lots [52 v]; Eua Is. 6 lots [12 v]; Seamount, 6 lots [29 v]; South of Nomuka group, 1 lot [25 v]; Ha'apai Group, 2 lots [4 v]; N Ha'apai group, 3 lots [6 v]; NW Tongatapu, 3 lots [16 v]; SW Tongatapu, 5 lots [22 v]; Tongatapu, 6 lots [8 v]; S. Nomuka group, 2 lots [6 v]; Vava' group, 1 lot [2 v]; NEW CALEDONIA. 5 lots [5 v, 5 specimens]; Lord Howe, 1 lot [1 v]; Banc Nova, 2 lot [8 v, 1 specimen]; North New Caledonia, 10 lots [tota 20 v]; South New

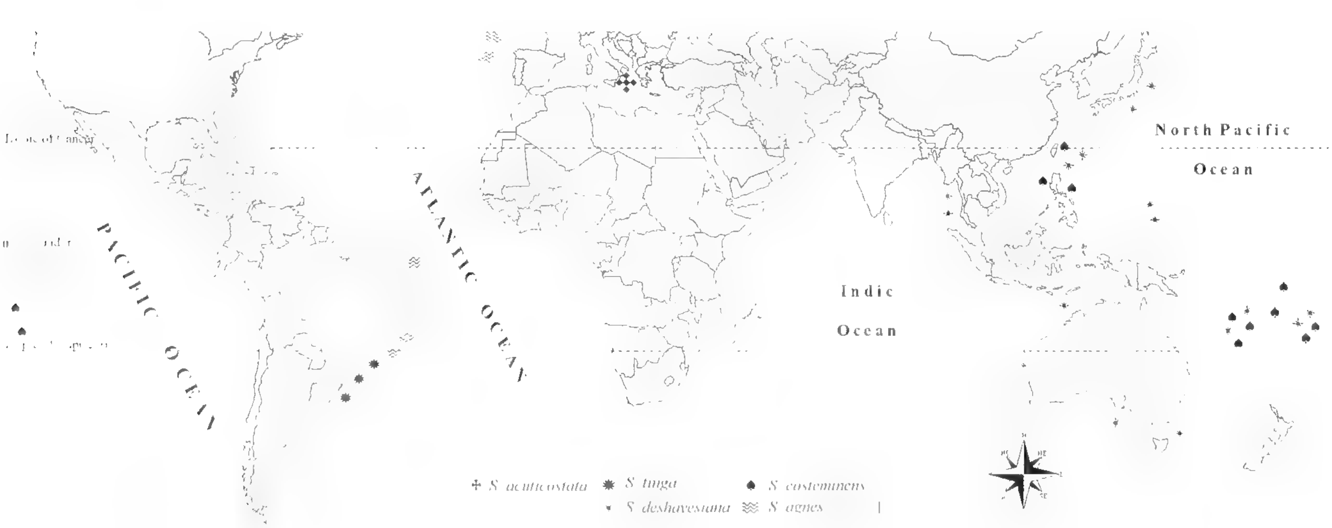

Figure 109. Geographic distribution of *Spinosipella* spp

Caledonia, 13 lots [46 v, 1 specimen]; off Norfolk, 18 lots [98 v]; Banc Esponge, 11 lots [144 v]; Banc Kaimon-Maru, 9 lots [38 v]; Banc Antigonia, 1 lot [1 v]; Banc Jumeau-West, 4 lots [17 v]; Banc Introuvable, 7 lots [16 v]; Banc Stylaster, 1 lot [1 v] ; Volcans Hunter and Matthew, 2 lots [2 v]; S.E. New Caledonia, 2 lots [2 v]; East New Caledonia, 6 lots [30 v] Banc Capel, 1 lot [lota 12 v]; Banc Kelso, 1 lot [6 v]; I. Loyaute, 22 lots [44 v]. FIJI. South of Viti Levu, 42 lots [328 v]; Southeast of Viti Levu, 17 lots [57 v]; Bohol/Sulu Seas, 2 lots [5 v]; Bohol Sea - Balicasag Island, 3 lots [5 v]; Bordau, 1 specimen; TAIWAN. Bashi channel, 2 lots [3 v]; South China Sea, 1 lot [2 v]; East Taiwan, 2 lots [5 v]. (Details in Simone and Cunha, in press.)

DISCUSSION

THE GENUS *SPINOSIPELLA* WITHIN THE VERTICORDIIDAE. Despite their larger size, the prickly outer surface of the shell, and the reduction of the lunule, which differentiates *Spinosipella* from the remaining verticordiids, this taxon has traditionally been considered a subgenus of the genus *Verticordia*. This set of characters is sufficient in my opinion to allocate *Spinosipella* as a separate genus. This view was previously defended by the author of the genus (Iredale, 1930) and by Poutiers and Bernard (1995). Other distinctive characters are the spiral umbones (Figures 5, 7, 21, 22, 33, 54, 53), the tall, somewhat uniform radial sculpture, triangular in section; and the obesity of the valves. The spiral umbones and the obesity of *Spinosipella* are quite similar to those in the fossil genus *Pecchiolia* Savi and Meneghini in Murchison, 1850 [type-species (by monotypy): *Pecchiolia argentea* Savi and Meneghini in Murchison, 1850 (= *Chama arietina* Brocchi, 1814) middle Tertiary, Europe] (Keen, 1969: 857), from which *Spinosipella* differs in having well-developed ribs and zigzag edges.

The full genus status of *Spinosipella* is based on the differences with the typical *Verticordia* sensu stricto [type species (by monotypy) *Verticordia cardiiformis* Sowerby, 1844], such as the higher size and obesity of the valves; the additional development of the prickly surface (which also covers the radial ribs, whereas in *Verticordia*, when a prickly surface is present, it does not cover the radial ribs), the absence of lunule; the spiral fashion of both valves; and the similarity among the radial ribs (representatives of *Verticordia* usually have an unusually larger rib or space between ribs). The same set of characters also differentiates *Spinosipella* from *Trigonulina* d'Orbigny, 1842 [type species (by monotypy) *T. ornata* d'Orbigny, 1842] in the sense of Jung (1996: 46–47).

Representatives of *Spinosipella* also resemble those of the genera *Haliris* Dall, 1886, and *Euciroa* Dall, 1881, by their larger size, convexity, and prickly shell surface. *Spinosipella* differs from those two genera, however, in the higher degree of convexity, reflected in more obese shells in its species; in the much more developed and taller radial ribs; higher degree of spiralization of the valves; and in the expansion of the ribs beyond the shell margin.

Further analysis on the verticordiid systematics and phylogeny can be found in the literature (e.g., Pelseneer, 1888; Salvini-Plawén and Haszprunar, 1982; Bieler and Mikkelsen, 1992).

COMPARISON BETWEEN THE *SPINOSIPELLA* SPECIES

The differentiation between the five species of *Spinosipella* is summarized in the respective diagnoses and in Table 1. The degree of differentiation in the samples of each species examined allows for specific separations. The number of radial ribs is the most notable feature; despite certain a small amount of intraspecific variation, the number of radial ribs is somewhat constant in each species, at least in specimens of larger size. The fossil *S. acuticostata* is the species with fewest ribs, 12–13 (Figures 36, 38, 39), while *S. deshayesiana* has the largest number of ribs, 16–19 (Figures 46, 48, 49, 54, 53). The other species possess an intermediary number of ribs. The species of *Spinosipella* usually have radial ribs of relatively uniform size; the single exception is *S. costeminens*, which has ribs clearly increasing posteriorly; in the posterior shell slope, however, the ribs abruptly reduce in size, although in some specimens, particularly in the young ones, this character is not so clear, i.e., the ribs are somewhat uniform-sized. The shell inflation is well developed in most *Spinosipella* species, but this is clearer in

Table 1. Comparison of characters between the five studied species of *Spinosipella*.

Character	*Spinosipella acuticostata*	*Spinosipella agnes*	*Spinosipella tinga*	*Spinosipella deshayesiana*	*Spinosipella costeminens*
Distribution	Mediterranean	Tropical W. Atlantic; Caribbean; to SE Brazil	S-SE Brazil	South and Central Indo-Pacific	Tropical West Pacific
Shell Inflated	Strongly	Highly	Weakly	Strongly	Highly
Sculptured between radial ribs	Radial	Disorganized	Radial	Radial	Disorganized
Prickly ribs outer surface	Rough	Rough	Weakly prickly	Strongly prickly	Rough
Number of Ribs	12–13	15–17	17–18	18–19	16–17
Size (mm)	20.0	20.2	10.4	11.5	20.0

the larger specimens; while the young specimens are considerably flatter (Figures 41–45). The prickly outer shell surface is an outstanding character of the *Spinosipella* species; however, this character is conservative among the five species; the single exception is the relatively chaotic arrangement in *S. agnes* (Figure 8) and *S. costeminens*, while in the remaining species a radial arrangement is apparent (parallel to the radial ribs) (Figure 32). The Pacific species *S. deshayesiana* has much larger, crispy prickles along the tip of the ribs (Figures 42, 45, 46, 48, 49). This is lacking in the remaining species, except in some very young specimens (e.g., USNM 810889, *S. agnes*, 6 mm), where the prickles, however, are not fully developed. The prickly surface is strongly damaged in eroded specimens (Figure 55), becoming almost completely smooth. *Spinosipella deshayesiana*, perhaps because of this character, has the distal tips of the zigzag edges of the shell even longer and more projected (Figures 41, 44, 47, 50, 51, 59, 67). The series of radial ribs is interrupted in the region between the umbos, where a triangular smooth area appears. This area is particularly large in *S. agnes* (Figures 7, 9), but is practically absent in *S. tinga* (Figures 21, 22); it is narrow in the remaining three species. The size of the specimens appears to be another distinctive feature, as *S. tinga* is small (around 10 mm), whereas the remaining species are larger (20–30 mm). The hinge does not vary much between the *Spinosipella* species; however, some particularities exist. The posterior tooth of the left valve is well developed in *S. agnes* [Figures 4, 10, 12, 27, 28 (arrow)], very low in *S. acuticostata* (Figures 35, 39), and practically absent in remaining species (Figures 20, 25, 50). The tall and pointed cardinal tooth of the right valve is more developed in *S. agnes*, in such it is also sharply pointed and curved (Figures 3, 10, 12). In the remaining species this tooth is weakly shorter and more rounded (Figures 26, 34, 47, 51).

The geographic and stratigraphic distribution are somewhat mutually exclusive for most of the species (Fig. 72); *Spinosipella acuticostata* is the only Mediterranean species, *S. agnes* occurs from Florida to Rio de Janeiro, *S. tinga* is found from Rio de Janeiro to Rio Grande do Sul, along the Brazilian coast. The fine-resolution distribution of the Indo-Pacific species is still unclear, but *S. deshayesiana* and *S. costeminens*, appear to be sympatric. *Spinosipella acuticostata* is a fossil species, occurring in Pliocene strata, while the remaining species are found in the Recent. Apparently no Recent *Spinosipella* occur in the Mediterranean.

All samples of *Spinosipella* from the Atlantic and Mediterranean have previously been accepted as belonging to the single species *S. acuticostata* (e.g., Abbott, 1974; Abbott and Dance, 1983; Rios, 1994). However, analyses of the conchological, geographic, and stratigraphic differences, show that the separation into three species is warranted. As the shape changes considerably during ontogeny, a specimen of *S. agnes* at same size as the holotype of *S. tinga* was chosen to show the differences between those species. Figures 28–31 illustrate these differences. *Spinosipella agnes* has fewer, taller, and more widely spaced ribs than *S. tinga* (Figures 19, 29). The shape of the shell edge is much more uniform in *S. tinga* than in *S. agnes*, in that the tips of the ribs are more expanded, extending longer beyond the shell margin (Figures 20, 24, 28). The posterior cardinal tooth in the hinge of the left valve is present in *S. agnes*, in animals larger than 5–6 mm, while this tooth is never present in *S. tinga* (Figures 20, 25, 27–28, arrow). The degree of convexity is higher in *S. agnes* and in *S. tinga* (Figures 30, 31); *S. agnes* has a degree of convexity (width/length) in each valve of about 0.57, while *S. tinga* it is 0.47.

The comparison of the previously valid species *Spinosipella ericia*, including paratypes (Figures 41–44), and *S. deshayesiana*, does not reveal any distinction between them. Normally, specimens of smaller size were identified as *S. ericia*, and the large ones as *S. deshayesiana*. But examination of shell features along a growth series show a complete gradient linking the two taxa. The same lack of distinction is found in the literature for both species, including the original descriptions. For these reasons, despite the fact that *S. ericia* is the type species of the genus, the older name *S. deshayesiana* should be used. Furthermore, a type specimen of *S. japonica* was also examined (Figure 45), confirming the synonymy of this species with *S. deshayesiana*.

The distinction between the Pacific species *Spinosipella deshayesiana* and *S. costeminens* is not always easy. With the large quantity of specimens kindly provided by the MNHN (Paris), it was possible to analyze the degree of variation of both species. *Spinosipella costeminens* mostly has samples with shell possessing the outstandingly large, carina-like spiral ridge between the middle and posterior thirds of the shell, but sometimes this ridge is not so different from the others, and the animal become more rounded, similar to *S. deshayesiana*. The distinction is based mainly on the presence of at least a weak carina in the region between middle and posterior thirds, and also by the more robust ridges of *S. costeminens* specimens (Figures 60, 61), while those of *S. deshayesiana* lack any clear radial carina and the ridges are more delicate, uniform and apparently close from each other (Figures 46, 48).

The lot USNM 63200 includes 3 valves (2 left and 1 right), collected in Barbados, the known geographic distribution of *Spinosipella agnes*. However, the right valve has the characters of *S. deshayesiana*, instead of those of *S. agnes*. In addition, is looks different in the state of conservation, color and associated sediment, from the other 2 valves of the same sample.

DISCUSSION ON ANATOMY

More in-depth anatomical descriptions and discussions on verticordiids are provided by Allen and Turner

(1974), who studied 19 species of several genera. However, no information on the anatomy of the genus *Spinosipella* is found in the literature. Although anatomical information is available here only for two of the five species of the genus (of course one of them is a Pliocene fossil), some systematic inferences can be made based on the scenario given in the literature the Verticordiidae and related families (Allen and Turner, 1974, and others, e.g., Fisher, 1860, 1862b; Pelseneer, 1888; Nakazima, 1967; Allen and Morgan, 1981). Besides the conchological characters discussed above, some anatomical features are possibly restricted to *Spinosipella*, such as: the wide lithodesma (Figures 93, 96–104, lt); the simplified siphonal tentacles (Figure 108), which normally have secondary papillae; the papilla on the roof of the excurrent chamber (Figures 78–80, 85, 94: pi); the absence of incurrent valve in infraseptal chamber. However, wide lithodesma have been reported for *Policordia lisbetae* Knudsen, 1970 (fig. 90), which has very different shell and pallial tentacular characters. The study on the incurrent siphonal structures is of particular importance in septibranchs, as the modified incurrent siphon is the main structure used in prey capture (Morton, 1987).

On the other hand, some features appear to be characteristic of Verticordiidae, such as: elongation of lateral region of kidneys; the muscular stomach (see also Purchon, 1956, 1963); the separation between testis and ovary. By the proximity of the esophagus from anterior adductor muscle, by the lack of incurrent valve, and by the simplified buccal structures, e.g., lack of buccal cavity and tongue, it is possible to suggest that *Spinosipella* is a basal taxon inside Verticordiidae. Unfortunately, no member of the genus was analyzed in the recent comparative studies on anomalodesmatans (Harper et al, 2006).

ACKNOWLEDGMENTS

The authors are grateful to the researchers who loaned the material for this study: Winston Ponder and Ian Loch (AMS) for types of *Spinosipella ericia*; Néstor E. Ardila (MHNMC) and Emilio Garcia (EGC) for *S. agnes* (Colombia) and *S. deshayesiana* (Philippines); Harry G. Lee for *S. agnes* (Florida) (MHNMC) for a large lot of *S. agnes* (Colombia); and especially to Philippe Bouchet and Philippe Maestrati, MNHN, for the loan of a huge quantity of lots coming from several places of the world, mostly from the Indo-Pacific. For thorough comments and additional information about *S. acuticostata* we thank Rafael La Perna. For material of *Haliris fisheriana* we thank to Daniel Mansur Pimpão (PPG-BAN, UFRGS). For help with SEM procedures, we thank Lara Guimarães (MZSP). For Rachel Collin, Smithsonian Institution at Panama, we thank for the help in the text and language. We thank also both referees and the Editor for the thoughtful correction on the manuscript. This project is supported by FAPESP (Fundação de Amparo a Pesquisa do Estado de São Paulo), procs. no. 03/05860-6, 04/02333-8, and a "Treinamento Técnico 3" grant, under the supervision of Antonia Cecília Z. Amaral and Luiz R.L. Simone.

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Late Eocene *Conus* (Neogastropoda: Conidae) from Florida, USA

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ABSTRACT

The neogastropod genus *Conus* is likely the most diverse marine animal genus, but has an Eocene to Pleistocene fossil record that remains poorly understood. We discuss the fossil record of Eocene *Conus* from Florida and recognize three species: *Conus sauridens* Conrad, 1833, and two new species, *Conus palmerae* and *Conus alleni*. We also re-describe *C. sauridens*, identify its likely synonyms, and add new information about its geographic range. The new species *C. palmerae* is restricted to the upper Eocene Ocala Limestone of Florida, while *C. alleni* new species occurs in the upper Eocene Ocala Limestone of Florida and the upper Eocene Moodys Branch Formation of Louisiana.

Additional Keywords: Mollusca, Fossil, Gastropoda, Ocala Limestone

INTRODUCTION

With over 1500 described fossil and extant species, *Conus* Linnaeus, 1758 (cone snails) may be the most diverse marine animal genus (Röckel et al., 1995). Molecular sequence data have offered valuable insights into the relationships of extant *Conus* species (e.g., Duda and Kohn, 2005), but the deep evolutionary history of *Conus* remains unclear: although about 1000 fossil species have been described (Röckel et al., 1995), many of these are likely synonymous (e.g., see Hendricks, in press). Many fossil *Conus* species are based only upon type specimens and/or were described without reference to comparable material from nearby, contemporaneous fossil faunas. Unraveling the early evolutionary history of *Conus* will only be possible by careful examination and interpretation of its rich and well-preserved fossil record.

Some of the oldest substantiated *Conus* fossils are from the early Eocene (Ypresian) of England and France, and possibly Pakistan (Kohn, 1990). Occurrence records of middle Eocene *Conus* in North America show that the genus had achieved a wide geographic distribution soon after its first appearance in the fossil record. For example, Table 1 (which is derived in large part from Kohn and Anderson, 2008) lists names that have been applied to Eocene *Conus* from the southeastern United States. Our purpose is not to revise the systematics and describe the fossil record of all of these taxa, but rather to focus on those species occurring in Florida, which have thus far received only preliminary attention (Richards and Palmer, 1953). This lack of attention is likely related to the preservational nature of these Floridian specimens, almost all of which are preserved as internal and/or external molds rather than shell material. While we focus on *Conus* fossils from the upper Eocene Ocala Limestone of Florida, we also consider likely synonyms of *Conus sauridens* Conrad, 1833, a widespread and temporally persistent taxon that will require additional future attention.

GEOLOGICAL BACKGROUND

Formally named by W. H. Dall (in Dall and Harris, 1892), the Ocala limestone represented all limestones exposed in central Florida at that time. A late Eocene age was not determined for the Ocala limestone, however, until Cooke (1915) correlated the unit with deposits in Mississippi and Alabama. Based on lithology and microfauna, Applin and Applin (1944) divided the Ocala Limestone into an upper member and lower member. Vernon (1951) redefined the Ocala Limestone by restricting it to Applin and Applin's (1944) upper member and placed their lower member in the Moodys Branch Formation. Further, Vernon (1951) subdivided the Moodys Branch Formation (as pertaining to Florida) into the basal Inglis Member and overlying Williston Member. Puri (1953) renamed Vernon's (1951) Ocala Limestone (restricted) as the Crystal River Formation. Later, Puri (1957) elevated the Ocala Limestone to group status (Ocala Group)—consisting, from oldest to youngest, of the Inglis, Williston, and Crystal River formations—and eliminated the Moodys Branch Formation designation for Florida Eocene deposits. Based on macro- and microfossils, Toulmin (1977: 117) correlated the Inglis Formation with the lower Moodys Branch Formation in

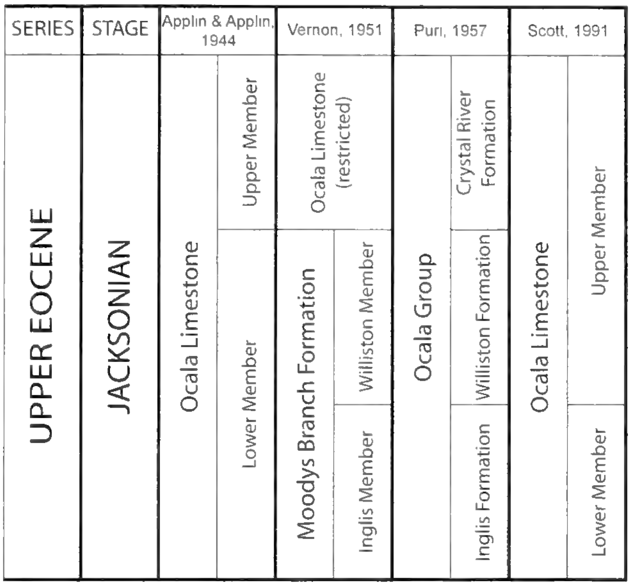
Table 1. Names applied to Eocene *Conus* from the U.S. Coastal Plain, including names of some younger species that are here considered synonyms of Eocene taxa. Type specimen abbreviations: **H,** holotype; **L,** lectotype; and **F,** figured.

Taxon	Type	Type locality	Present disposition according to this study
C. sauridens Conrad, 1833	ANSP 14854 (**L**)	Claiborne, Alabama	*C. sauridens*
C. claibornensis I. Lea, 1833	Lost	Claiborne, Alabama	*C. sauridens*?
C. gyratus Morton, 1834	ANSP 211 (**H**)	South Carolina, locality unknown	*Nomen dubium*
C. parvus H. C. Lea, 1841	ANSP 13161 (**L**)	Claiborne, Alabama	*C. sauridens*
C. mutilatus Tuomey, 1852	None	Wilmington, North Carolina	*Nomen dubium*
C. tortilis Conrad, 1855	ANSP 13196 (**H**)	Jackson, Mississippi	*C. sauridens*
C. alveatus Conrad, 1865	ANSP 13446 (**L**); See MacNeil and Dockery (1984, Pl. 38, Fig. 26)	Vicksburg, Mississippi	*C. sauridens*
C. subsauridens Conrad, 1865	ANSP 53812 (**H**)	Probably Claiborne, Alabama	*C. sauridens*
C. pulcherrimus Heilprin, 1879	AMNH-FI 10175 (**H?**)	Claiborne, Alabama	*Eosurcula pulcherrimus* (a turrid)
C. jacksonensis Meyer, 1885	Unknown, but specimen purported to be holotype figured by Harris and Palmer (1947, pl. 62, fig. 17)	Jackson, Mississippi	*C. sauridens*
C. deperditus var. *subdiadema* de Gregorio, 1890	PRI 26436 (**H**)	Claiborne, Alabama	*C. sauridens*
C. improvidus de Gregorio, 1890	Lost (see Palmer and Brann, 1966)	Claiborne, Alabama	*Nomen dubium*
C. (Conospirus) granopsis de Gregorio, 1890	Lost (see Palmer and Brann, 1966)	Claiborne, Alabama	*Nomen dubium*
C. smithvillensis Harris, 1895	BEG 34656 (**H**)	Smithville, Texas	*C. smithvillensis*
C. cormacki Harbison, 1944	ANSP 16415 (**H**)	Santee Cooper Canal, South Carolina	*Nomen dubium*
C. (Leptoconus) santander Gardner, 1945	USNM 495181 (**H**)	Moseleys Ferry, Texas	*C. sauridens*?
C. (Leptoconus) haighti Gardner, 1945	USNM 495182 (**H**)	Arroyo Veleno, Texas	*C. haighti*
"*Conus* sp. A" Palmer in Richards and Palmer, 1953	UF 108683	Gulf Hammock, Florida	Unidentifiable
"*Conus* sp. B" Palmer in Richards and Palmer, 1953	UF 108858 (designated here as holotype of *C. palmerae*, new species; formerly FL Geol. Survey I-7634)	Gulf Hammock, Florida	*C. palmerae,* new species
C. cracens Hoerle, 1976	USNM 220109 (**H**)	Calhoun County, Florida	*C. sauridens*?
C. alveatus spiralis Dockery in MacNeil and Dockery, 1984	USNM 376678 (**H**)	Smith County, Mississippi	*C. sauridens*
C. (Lithoconus) smithvillensis var. Dockery, 1980	MGS 590 (**F**)	Near Newton, Mississippi	*C. smithvillensis*?
C. (Lithoconus) nocens Garvie, 1996	UT-TMM 962TX22 (**H**)	Bastrop County, Texas	*C. sauridens*?
C. (Lithoconus) smithvillensis var. Dockery, 1980 in Campbell (1995)	UNC 15448 (**F**)	Near Cross, South Carolina	*C. smithvillensis*?

Alabama, Mississippi, and Louisiana. He also correlated the Williston Formation with the upper Moodys Branch Formation in Alabama, Mississippi, and Louisiana. For detailed correlations, see the Correlation of Stratigraphic Units of North America—Gulf Coast Region (1988).

Based on lithology, Scott (1991)—in order to follow the North American Stratigraphic Code (North American Commission on Stratigraphic Nomenclature, 1983)—reduced the Ocala Group to formational rank and returned to the terminology used by Applin and Applin (1944). Therefore, current designations used by the Florida Geological Survey and United States Geological Survey are: lower member of the Ocala Limestone (formerly Inglis Formation) and upper member of the Ocala Limestone (formerly Williston and Crystal River formations). See Figure 1 for a brief history of stratigraphic divisions of the Ocala Limestone in Florida.

In outcrop and shallow subsurface, the Ocala Limestone occurs in northwestern peninsular Florida and a small area of the Florida panhandle adjacent to Georgia and Alabama. Lithologically, the Ocala Limestone is a relatively pure carbonate. Non-carbonate minerals



SERIES	STAGE	Applin & Applin, 1944		Vernon, 1951		Puri, 1957		Scott, 1991	
UPPER EOCENE	JACKSONIAN	Ocala Limestone	Upper Member	Ocala Limestone (restricted)		Ocala Group	Crystal River Formation	Ocala Limestone	Upper Member
			Lower Member	Moodys Branch Formation	Williston Member		Williston Formation		
					Inglis Member		Inglis Formation		Lower Member

Figure 1. History of stratigraphic divisions of the Ocala Limestone in Florida (modified from Oyen and Portell, 2001).

(quartz, chert, and clay minerals) represent less than 5% of the rock volume in the lower member and less than 10% in the upper member (Oyen, 1995). The lower member (formerly Inglis Formation) is primarily a clean packstone and grainstone that represents a higher energy, subtidal environment while the upper member (formerly Crystal River Formation) has a lithology of muddy packstone and wackestone interpreted to signify a lower energy (below wave base), deeper subtidal deposit (Fenk, 1979).

The Ocala Limestone contains diverse and abundant, shallow water marine invertebrate fossils consisting primarily of foraminifera, mollusks, and echinoids. Taxa with calcitic shells are preserved as body fossils, while taxa that had aragonitic shells typically occur as internal and external molds, although on rare occasions they can be found as pseudomorphs of calcite or silica. Most of the calcitic shelled mollusks (e.g., oysters and scallops) and those found as pseudomorphs have been well documented (Harris, 1951; Richards and Palmer, 1953). Few of the many moldic Ocala Limestone mollusks, however, have received the critical attention that they need (Portell and Vokes, 1997).

MATERIALS AND METHODS

Most of the specimens examined in this study are from the Florida Museum of Natural History (FLMNH) Division of Invertebrate Paleontology at the University of Florida (UF) and locality details for individual UF specimen lots listed below can be accessed online via the FLMNH Invertebrate Paleontology database at http://www.flmnh.ufl.edu/invertpaleo/search.asp. Besides UF specimens, some type specimens from the Academy of Natural Sciences, Philadelphia (ANSP), the Texas Natural Science Center at the University of Texas (specimens carry the acronym TMM for Texas Memorial Museum), and the Texas Bureau of Economic Geology (BEG; specimens now at the Texas Natural Science Center) were also examined. Other specimens referred to in the text are from the Geological Survey of Alabama (GSA), the American Museum of Natural History (AMNH), the Mississippi Geological Survey (MGS), the Paleontological Research Institution (PRI), the University of North Carolina (UNC), and the United States National Museum of Natural History (USNM).

Morphospecies were recognized from museum specimens (primarily those at the FLMNH) using the criteria discussed by Smith (1930), Röckel et al. (1995), and Hendricks (in press) and morphological terminology and measurements collected follow those authors. Two terms are introduced here that relate to characters states of the subsutural flexure, which is "the backward curving or bending of the shell aperture below the suture of whorl contact" and "[b]eing a feature of the apertural margin it is strikingly manifest in the growth lines [on the sutural ramp] of well-preserved cones" (Smith, 1930: 284). These two terms are: symmetrically curved subsutural flexure and diagonal subsutural flexure. A symmetrically curved subsutural flexure (also see the more generalized "curved type" described by Smith, 1930) has a maximum point of curvature centered between the margins of the sutural ramp. A diagonal subsutural flexure forms a straight or nearly-straight line that crosses diagonally (abaxioventrally) across the sutural ramp. Also see Muñiz-Solís (1999) for illustrations of different subsutural flexure morphologies.

Measurements were collected using digital and dial calipers and include: shell length (SL), maximum diameter (MD), aperture height (AH), height of maximum diameter (HMD), and spire angle (SA). From these measurements, the following morphometric ratios (developed by Röckel et al., 1995) were computed to characterize shell shape: relative diameter (RD; RD = MD / AH); position of maximum diameter (PMD; PMD = HMD / AH); and relative spire height (RSH; RSH = [SL – AH]/SL). Recognized Floridian morphospecies were compared with previously described species of Eocene *Conus* from the southeastern United States.

Although the simple internal molds of *Conus* fossils offer little taxonomically relevant information, room temperature vulcanizing (R.T.V.) silicone rubber casts made from external molds are often very useful for recognizing species. The external molds discussed herein were first gently cleaned to remove loose debris and then impregnated with polyvinyl butyral (Butvar-76), if needed, to consolidate the limestone. Once dried, clay dams were constructed around the outside of the limestone blocks containing the external molds. Then, de-aerated R.T.V. silicone rubber was slowly poured into and above the molds and again de-aerated in a vacuum chamber. Later, the cured rubber casts were carefully lifted from the molds. For more information regarding this technique see Chaney (1989) or visit http://paleo.cc/casting/silsum.htm.

SYSTEMATICS

Our examination of Eocene *Conus* fossils from Florida resulted in the recognition of one distinctive morphospecies that was first described by Conrad (1833) as *C. sauridens*, and two new species (*C. palmerae* and *C. alleni*) which are described below.

Family Conidae Fleming, 1822
Genus *Conus* Linnaeus, 1758

Conus sauridens Conrad, 1833
(Figures 2–10, 15–22; Table 2)

Conus sauridens Conrad, 1833: p. 33; Conrad, 1835: pl. 15, fig. 7. For comprehensive synonymy listings, see Palmer (1937), Harris and Palmer (1947), and Palmer and Brann (1966).
?*Conus clabornensis* I. Lea, 1833: 186.
Conus parvus H. C. Lea, 1841: 103, pl. 1, fig. 24.
Conus tortilis Conrad 1855: 260, pl. 15, fig. 5.
Conus alveatus Conrad, 1865: 148, pl. 11, fig. 4.
Conus subsauridens Conrad, 1865: 148, pl. 11, fig. 9.
Conus jacksonensis Meyer, 1885: 466.
Conus deperditus var. *subdiadema* de Gregorio, 1890: 20, pl. 1, figs. 56–58.
?*Conus* (*Leptoconus*) *santander* Gardner, 1945: 251, pl. 26, figs. 5, 9, 10, 14.
?*Conus cracens* Hoerle, 1976: 14, 16, pl. 3, figs. 1–3.
Conus alveatus spiralis Dockery in MacNeil and Dockery, 1984: 165, pl. 59, figs. 3, 4.
?*Conus nocens* Garvie, 1996: 90, pl. 19, figs. 9, 10.

Diagnosis: Early postnuclear whorls tuberculate, later teleoconch whorls smooth; shell often widest below shoulder; shoulder typically ridge-like; sutural ramps with raised spiral threads; incised spiral grooves at base of shell.

Description: Shell medium to large-sized (up to 116 mm). Last whorl conical to broadly and ventricosely conical; outline typically convex near shoulder, nearly straight below. Shell often widest below shoulder. Shoulder typically broadly carinate and forming pronounced ridge, less often angulate; smooth. Spire of low to moderate height, spire angle (SA) typically obtuse; outline typically straight to concave in smaller specimens, usually sigmoidal in larger shells. Larval shell multispiral, with at least three whorls. Early postnuclear whorls tuberculate. Subsutural flexure symmetrically curved, depth about 2.5× width. Teleoconch sutural ramps typically sigmoidal (rarely flat or convex), with raised spiral threads (typically three to seven; number increases with shell size) and intervening grooves; ornamentation begins on earliest postnuclear whorls as a single incised spiral groove. Aperture opening of approximately uniform width from base to shoulder. Some large specimens bear a pronounced siphonal fasciole. Last whorl with incised spiral grooves at base, sometimes extending weakly to near center of whorl and occasionally to shoulder in small shells; spiral grooves obsolete in some large shells.

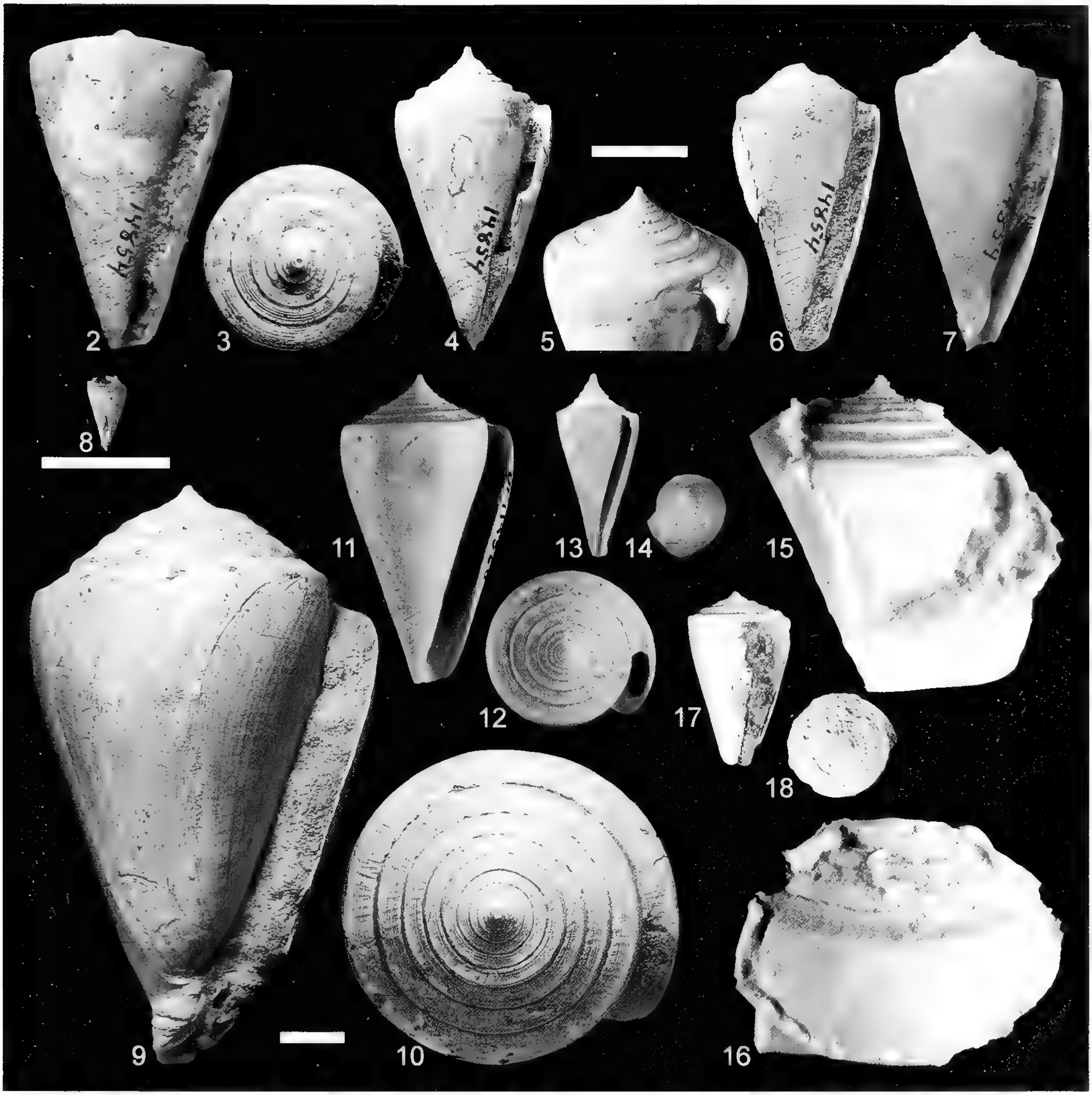
Shell Morphometrics: Thirteen shells of type and non-type specimens of *C. sauridens* were measured and morphometric ratios were computed from these measurements (Table 2): relative diameter (RD) ranges from 0.57–0.74 (average = 0.67); position of maximum diameter (PMD) ranges from 0.83–0.95 (average = 0.91); and relative spire height (RSH) ranges from 0.09–0.21 (average = 0.17).

Type Specimens: Type specimens examined include: ANSP 14854, lectotype of *Conus sauridens* (Figures 2, 3); ANSP 53813, three paralectotypes of *C. sauridens* (Figures 4–6); ANSP 53812, holotype of *C. subsauridens* (Figure 7); ANSP 13161, holotype of *C. parvus* (Figure 8); and ANSP 13196, holotype of *C. tortilis* (Figures 9, 10). See Table 2 for measurements of type specimens.

Type Locality and Occurrence: Conrad (1833) described the species from specimens collected at Claiborne, Alabama. Palmer (1937: 10) designated the type locality and stratum of *Conus sauridens* as PRI station 104: " 'Ferruginous sand' bed at Claiborne, on the Alabama River, Monroe County, Ala. Gosport sand" (Palmer, 1937: 10). The Gosport Sand is the uppermost formation of the Claiborne Group and is late middle Eocene (Bartonian) in age (Dockery, 1980). This species has been previously reported from numerous Paleogene U.S. Gulf Coast strata, including the middle Eocene Claiborne Group, as *C. tortilis* in the upper Eocene Jackson Group, and as *C. alveatus* in the lower Oligocene Vicksburg Group (the reader is directed to the following sources for detailed discussions of specific occurrence records: Palmer, 1937; Harris and Palmer, 1947; Palmer and Brann, 1966; and MacNeil and Dockery, 1984). *Conus sauridens* also occurs in the upper Eocene Ocala Limestone of Alachua, Suwannee, and Jackson counties, Florida. This species also questionably occurs as *C. cracens* in the lower Miocene Chipola Formation of northern Florida.

Other Material Examined: In addition to the type specimen lots listed above, 28 specimen lots containing *C. sauridens* were examined (over 80 specimens). These include: UF 283, UF 290, UF 2292, UF 8647, UF 14706, UF 16726, UF 16661, UF 18874, UF 57713, UF 57733, UF 100693, UF 101995, UF 114376, UF 115875, UF 119912, UF 119913, UF 119918, UF 119962, UF 120021-UF 120027, UF 120032, UF 122384, and UF 126927.

Discussion: *Conus sauridens* was the third fossil *Conus* species to be described from North America, and the first from the Paleogene (Green described the Neogene species *C. deluvianus* and *C. marylandicus* in 1830; see Kohn, 1992). As such, this species has received much attention in the literature, particularly with regards to its



Figures 2–18. Specimens of *Conus sauridens* Conrad, 1833 (**2–10, 15–18**), *C. cracens* Hoerle, 1976 (**11, 12**), and *C. nocens* Garvie, 1996 (**13, 14**). See text and Table 1 for locality information. All scale bars equal 1 cm. Scale bar above Figure 5 pertains to Figures 2–7 and 11–14. Scale bar below Figure 8 pertains only to that figure. Scale bar between Figures 9 and 10 pertains to Figures 9–10 and 15–18. **2–3.** Lectotype (ANSP 14854) of *C. sauridens*, shell length 33.4 mm, maximum diameter 21.1 mm. **4.** Paralectotype (ANSP 53813-3) of *C. sauridens*, shell length 31.9 mm. **5.** Paralectotype (ANSP 53813-1) of *C. sauridens*, maximum diameter 22.3 mm. **6.** Paralectotype (ANSP 53813-2) of *C. sauridens*, shell length 30.2 mm. **7.** Holotype (ANSP 53812) of *C. subsauridens* Conrad, 1865, shell length 33.4 mm. **8.** Holotype (ANSP 13161) of *C. parvus* Lea, 1841, shell length 6 mm. **9–10.** Holotype (ANSP 13196) of *C. tortilis* Conrad, 1855, shell length 90.0 mm, maximum diameter 53.0 mm. **11–12.** Paratype (UF 119560-1) of *C. cracens* Hoerle, 1976, shell length 32.2 mm, maximum diameter 17.8 mm. **13–14.** Holotype (TMM-962TX22) of *C. nocens* Garvie, 1996, shell length 19.2 mm, maximum diameter 8.7 mm. **15.** R.T.V. silicone rubber cast from external mold of *C. sauridens* (UF 120026). **16.** R.T.V. silicone rubber cast from external mold of *C. sauridens* (UF 122384). **17–18.** Highly leached, heavily pitted, and slightly silicified shell of *C. sauridens* (UF 120027), shell length 27.4 mm, maximum diameter 16.5 mm.

Table 2. Measurements (in mm) and morphometric ratios of type and non-type specimens examined. Some measurements could not be collected from casts made from molds; other measurements (and associated ratios) are not accurate because of shell damage (indicated by an asterisk, °). Morphological abbreviations: **SL,** shell length; **MD,** maximum diameter; **AH,** aperture height; **HMD,** height of maximum diameter; **SA,** spire angle (in degrees); **RD,** relative diameter; **PMD,** position of maximum diameter; and **RSH,** relative spire height. Specimen abbreviations: **H,** holotype; **L,** lectotype; **P,** paratype; and **PL,** paralectotype.

Specimen	SL	MD	AH	HMD	SA	RD	PMD	RSH
Type Specimens of *Conus sauridens* Conrad, 1833								
ANSP 14854 (**L,** *C. sauridens*, Figures 2, 3)	33.4	21.1	30.3	28.9	143	0.70	0.95	0.09
ANSP 53813-1 (**PL,** *C. sauridens*, Figure 5)	43.6	22.3°	36.5	33.6	106	0.61°	0.92	0.16
ANSP 53813-2 (**PL,** *C. sauridens*, Figure 6)	30.2°	15.0	26.2	24.5	110	0.57	0.94	0.13°
ANSP 53813-3 (**PL,** *C. sauridens*, Figure 4)	31.9°	16.7	25.9	23.5	101	0.64	0.91	0.19°
ANSP 53812 (**H,** *C. subsauridens*, Figure 7)	33.4°	17.3	28.2	26.2	115	0.61	0.93	0.16°
ANSP 13161 (**H,** *C. parvus*, Figure 8)	~6	—	—	—	—	—	—	—
ANSP 13196 (**H,** *C. tortilis*, Figures 9, 10)	90.9	53.0	75.1	62.1	100°	0.71	0.83	0.17
Non-Type Specimens of *Conus sauridens* Conrad, 1833								
UF 283	37.59	22.4	30.3	27.7	110	0.74	0.91	0.19
UF 290-1	24.43	11.87	19.3	17.3	90	0.62	0.90	0.21
UF 8511-1	48.83	27.38	40.5	35.6	109	0.68	0.88	0.17
UF 8647	41.44	24.31	33.1	30.6	109	0.73	0.92	0.20
UF 16726	22.95	12.36	19.5	18.0	110	0.63	0.92	0.15
UF 115875	33.45	19.86	28.4	25.7	119	0.70	0.90	0.15
UF 120022	116.11	69.15	95.2	84°	121	0.73	0.88°	0.18
Conus palmerae new species								
UF 108858 (**H,** *C. palmerae*, new species, Figures 23, 24)	22.0°	11.5°	14.6°	13.7°	77	—	—	—
UF 15886 (**P**)	—	22.3°	—	—	103		-	—
UF 18599 (**P**, Figure 25)	50.1°	—	—		—		—	—
UF 18711 (**P**)	12.0°		—				—	—
UF 18719 (**P**)	24.9°	–		—	—	—	—	—
UF 18737 (**P**, Figure 26)	56.1°	—		—	—	—	—	—
UF 57018 (**P**)	50.3°	21.5°	—	—	—	—	—	—
UF 66738 (**P,** Figure 27)	—	14.2°	—	—	101	—	—	—
UF 68306 (**P,** Figure 28)	—	19.3	—	—	98	–	—	—
UF 74473 (**P,** Figures 29, 30)	—	19.0°	—	—	98		—	–
UF 110360 (**P**)	65.0°	28.4°	53.8°	—	—		—	–
UF 111327 (**P**)		11.3	—	—	108	–	—	—
UF 112981 (**P**)	—	12.4	—	—	108	–	—	—
Conus alleni new species								
UF 119920 (**H,** Figures 31, 32)	36.2	20.7°	31.3	28.6	121	0.66°	0.91	0.14
UF 119919 (**P,** Figure 34)	33.2°	17.3°	—	—	92	—	—	—
UF 119976 (**P,** Figure 35)	34.5°	17.2°	—	—	—	–	—	—
UF 119977 (**P,** Figure 33)	35.1°	16.8°	—	—	112°		–	—
Other Type Specimens								
ANSP 16145 (**H,** *C. cormacki*, Figure 39)	28.7	22.3				–	—	
UF 119560-1 (**P,** *C. cracens*, Figures 11, 12)	32.2	17.8	27.5	24.0	113	0.65	0.87	0.15
UF 76798-1 (**P,** *C. cracens*)	68.0	37.3°		—	—	-	–	—
TMM-BEG 35656 (H, *C. smithvillensis*, Figures 36-38)	42.1	14.8°	28.6	26.9°	53	0.52°	0.94°	0.32
TMM-962TX22 (**H,** *C. nocens*, Figures 13, 14)	19.2	8.7°	15.1	14.3	87	0.58°	0.95	0.21
TMM-962TX23 (**P,** *C. nocens*)	19.4	8.7°	15.4	14.5	87	0.56	0.94	0.21

morphological variation and probable synonyms. Much of the following was derived from discussions in Palmer (1937), Harris and Palmer (1947), and Palmer and Brann (1966).

Timothy Conrad (1833) described *C. sauridens* from shells that he collected at Claiborne, Alabama. According to Palmer (1937: 461), the "Conradian collection of *sauridens* consists of 5 specimens" which were apparently glued to one card, cataloged as ANSP 14854. Palmer (1937: 461) goes on to state that the "type of *Conus subsauridens* Con. [see below] is also on the card with the *Conus sauridens* collection." These two passages suggest that Conrad's Claiborne collection originally consisted of six specimens. The collection now consists of five specimens: the lectotype (ANSP 14854; Figures 2, 3) of *C. sauridens*, three paralectotypes (ANSP 53813; Figures 4–6), and the holotype of *C. subsauridens* (ANSP 53812; Figure 7); the location of any possible sixth specimen is not known. One low-spired specimen in the type series (ANSP 14854; Figure 2) closely resembles Conrad's (1835, pl. 15, fig. 7) original figure of *C. sauridens*. Palmer (1937) alluded to this specimen in her text as matching Conrad's figure, but did not formally designate it as the lectotype. Kohn (1992)—following Moore (1962) and Palmer and Brann (1966)—considered this specimen to be the lectotype and we accept his conclusion.

Palmer (1937) argued that the matrix filling the apertures of the shells in Conrad's *Conus sauridens* series suggests that the shells do not likely share the same geological provenance. The matrix filling the lectotype is orange and appears to be sand from the Gosport Formation (Palmer, 1937). The matrix filling the three paralectotypes is light-gray. The matrix filling the holotype of *C. subsauridens* is orange, resembling that of the lectotype of *C. sauridens* (Palmer [1937: 461] described the matrix filling the holotype of *C. subsauridens* as "a red, silicified matrix resembling that of the Orangeburg" material from South Carolina). It is important to note, however, that these differences in matrix color may be due to diagenetic weathering of the original matrix material.

The lectotype (ANSP 14854; Figures 2, 3) of *C. sauridens* differs from the paralectotypes (ANSP 53813; Figures 4–6)—which, with the holotype of *C. subsauridens* (see below), are of the much more common morphology—in the following respects: it has flat to slightly convex sutural ramps with more raised spiral threads (about 6) than is typical, the shoulder is angulate rather than forming a carinate ridge, the widest point of the last whorl is nearly at the shoulder rather than beneath it, and the spire is lower than in most other specimens of the species (see Table 2); further, the lectotype does not provide definite evidence of tubercles on the early postnuclear whorls, though these are highly eroded on this specimen.

Isaac Lea (1833) described *Conus claibornensis* from materials sent to him by Judge Charles Tait of Claiborne, Alabama, but lost his only specimen before it could be figured (Kohn, 1992). His description suggests that his specimen was a *C. sauridens*, a name that has priority by three months (Kohn, 1992). Harris (1895), Palmer (1937), and Palmer and Brann (1966) synonymized *C. claibornensis* with *C. sauridens*, while de Gregorio (1890), Dall (1896), and Kohn (1992) regarded this taxon as a *nomen dubium*. Given that no available evidence suggests that more than one fossil *Conus* species is present at Claiborne, Alabama, we agree with the former authors that *C. claibornensis* is equivalent, while questionably, to *C. sauridens*. For a historical overview of interactions between I. Lea, T. A. Conrad, and C. Tait, see Wheeler (1935).

In 1841, H. C. Lea (I. Lea's father) described *Conus parvus* on the basis of a single, small, damaged shell (ANSP 13161; Figure 8) from the Gosport sand at Claiborne, Alabama. We agree with Dall (1896), Palmer (1937), and Palmer and Brann (1966) that *C. parvus* is a juvenile *C. sauridens*. Features uniting the holotype of *C. parvus* with *C. sauridens* include: tuberculate early postnuclear whorls, raised spiral threads on the sutural ramps, and incised spiral grooves on the anterior half of the last whorl.

Conrad (1855) described *Conus tortilis* from one large specimen (ANSP 13196; Figures 9, 10) from Jackson, Mississippi and differentiated it from *C. sauridens* by its "more prominent and convex spire, in the large twisted callus at base, & c." (p. 260). Dall (1896) and Palmer (1937) both considered *C. tortilis* synonymous with *C. sauridens* and Palmer (1937) described *C. tortilis* as representing "the maximum growth of the species" (p. 459). We agree with these authors that specimens of *C. tortilis* are large *C. sauridens*.

Conrad (1865) described two additional species of Eocene *Conus*: *C. subsauridens* and *C. alveatus*. Conrad stated that *C. subsauridens* was from "the Burrstone, probably, of Alabama"; we assume (see above) that the holotype (ANSP 53812) is from Clairborne. We inspected the type of *C. subsauridens* (Figure 7) and agree with Dall (1896) and Palmer (1937) that it is a junior synonym of *C. sauridens*.

The type locality for *Conus alveatus* is Vicksburg, Mississippi; MacNeil and Dockery (1984) suggested that the lectotype (ANSP 13446; MacNeil and Dockery, 1984, pl. 38, fig. 26) and paratype (ANSP 13494) are probably from the Byram Formation. Conrad (1865: 148) differentiated *C. alveatus* from *C. sauridens* by its "less elevated and . . . more profoundly carinated spire, and the revolving lines on the spire are less numerous than in the former [*C. sauridens*]." Dall (1896) and Palmer (1937) recognized *Conus tortilis* and *C. alveatus*, respectively, as the Jacksonian (upper Eocene) and Vicksburgian (lower Oligocene) forms of the older, Clairbornian (middle Eocene), *C. sauridens*. MacNeil and Dockery (1984), however, continued to recognize *C. alveatus* as a distinct Oligocene species occurring in Mississippi and Mexico; they did not compare *C. alveatus* (or Dockery's subspecies *C. alveatus spiralis*; in MacNeil and Dockery, 1984) with *C. sauridens*. MacNeil and Dockery's (1984) figures of *C. aleveatus* (including the lectotype; pl. 38, fig. 26) appear consistent with *C. sauridens* as circumscribed here.

Meyer (1885) described—but did not figure—*Conus jacksonensis* from Jackson, Mississippi, and described the species as similar to *Conus protracta* Meyer, 1885 (an Oligocene taxon from Vicksburg and Red Bluff, Mississippi that we accept, but do not consider further here; see MacNeil and Dockery, 1984 for details), but "with revolving lines on the spire" (p. 466). Meyer [1886] presented *C. protracta* as *C. protractus* and the latter spelling is the one most commonly seen in the literature. Harris and Palmer (1947: pl. 62, fig. 17) figured a specimen (unnumbered, but said to be from the collections of the Geology Department of Johns Hopkins University) that they regarded as the holotype of *C. jacksonensis*. This specimen "consists of the apical whorls" and is 3.5 mm in size (Harris and Palmer, 1947: 446). Harris and

Palmer (1947) considered this taxon a junior synonym of *C. sauridens* and we agree, particularly because of the presence of tuberculate early postnuclear whorls and the presence of raised spiral threads on the sutural ramp.

De Gregorio (1890) described *Conus deperditus* var. *subdiadema* from Claiborne, Alabama. Palmer and Brann (1966) considered this subspecies equivalent to *C. sauridens* and, based upon our inspection of de Gregorio's (1890) figures, we agree. We have not, however, viewed the holotype of *C. deperditus* var. *subdiadema*, which Palmer and Brann reported as PRI 26436.

Gardner (1945: 252) described *Conus santander* as including "those species from the western Gulf that have formerly been included under *Conus sauridens* Conrad, described from Claiborne." Gardner's figures of the holotype (USNM 495181; Moseleys Ferry, Burleson County, Texas) of *C. santander* appear consistent with *C. sauridens* and we consider this taxon a probable synonym.

Hoerle (1976) described *Conus cracens* (see paratype in UF 119560, Figures 11, 12) from the lower Miocene Chipola Formation of northern Florida and noted its strong similarity to *C. sauridens*: "*C. cracens* appears to be a descendant of the widespread (Alabama, Mississippi, Texas) middle Eocene to Oligocene species, *C. sauridens* Conrad" (p. 16). She differentiated *C. cracens* from *C. sauridens* on the basis of several characters: the "nodes on the spire whorls persist for a greater number of turns on *C. cracens*, also it is larger, more slender, with stronger and more opisthocyrt growth lines and more pronounced basal ornament" (p. 16). We examined Hoerle's paratypes at the FLMNH and could not find any discrete morphological characters separating the two taxa. Given the vast amount of geological time separating the species (over 12 million years), however, we questionably synonymize *C. cracens* with *C. sauridens*. Resolving the relationship between these two taxa will require additional study.

Finally, Garvie (1996) described *Conus nocens* on the basis of two small specimens from the Reklaw Formation of Bastrop County, Texas: TMM-962TX22 (holotype; erroneously published as UT-TMM 84822; Figures 13, 14) and TMM-962TX23 (paratype, erroneously published as UT-TMM 84823). In addition to these two specimens, Garvie (1996) reported that he examined 25 additional specimens of *C. nocens* from the Weches Formation and over 100 specimens from the Cook Mountain Formation. While we did not observe these additional, stratigraphically younger specimens, the holotype and paratype of *C. nocens* appear consistent with *Conus sauridens*. They each have raised spiral threads on the sutural ramp, symmetrically curved subsutural flexures, and incised spiral grooves on the anterior half of the last whorl. Further, both have last whorl shapes similar to *C. sauridens*. The early postnuclear whorls of the holotype are tuberculate, but most appear smooth on the paratype. Garvie (1996: 90) stated that four characters separate *C. nocens* from *C. sauridens*: "the flat sides, the sharp unridged carina, the coarse, strong, spiral basal lines, and the lack of strong growth lines on the ramp." We do not consider these characteristics—in isolation or combination—sufficient to discriminate *C. nocens* from *C. sauridens* (as circumscribed above), especially because TMM-962TX22 and TMM-962TX23 are both shells of juveniles. Since, however, we have not seen the other specimens of *C. nocens* mentioned by Garvie (1996), we consider our synonymy of *C. nocens* with *C. sauridens* tentative. Regardless of their taxonomic identity, TMM-962TX22 and TMM-962TX23 are important specimens because of their likely stratigraphic position in the Reklaw Formation. The Reklaw Formation is thought to span the early-middle Eocene (or, Ypresian-Lutetian) boundary and has a relative age equivalent to nannoplankton biochronozone NP14 (Zachos and Molineux, 2003: fig. 2), which has an absolute age of about 49.7 to 47.3 Ma (Berggren and Pearson, 2005). This age would make these two specimens the oldest known *Conus* fossils from the United States Coastal Plain, and only slightly younger than the oldest *Conus* in general (Ypresian of England and France; Kohn, 1990). This oldest regional occurrence record is tempered, however, by the fact that the position of the original collection locality of TMM-962TX22 and TMM-962TX23 ("Devil's Eye, Colorado R."; station 11 of the Geological Survey of Texas and locality 11-T-36 of the Texas Bureau of Economic Geology) is uncertain (Zachos et al., 2005) and may no longer exist (Garvie, 1996). Further, no additional specimens of *Conus* from the Reklaw Formation have yet been found in the collections of the Texas Natural Science Center (A. Molineux, personal communication to JRH, July 11, 2007).

Most of our knowledge of Eocene *C. sauridens* in Florida is from R.T.V. silicone rubber casts of external molds in limestone (e.g., UF 120026, Figure 15; UF 122384, Figure 16), though UF 120027 (Figures 17, 18)—which is a highly leached, heavily pitted, and slightly silicified shell—is an exception. *Conus sauridens* is present in upper Eocene Ocala Limestone of Jackson (UF 18874, UF locality JA002; UF 120026, UF locality JA018; UF 119912, UF locality JA027; and UF 119918, UF locality JA031), Alachua (UF 120027, UF locality AL001), and Suwannee (UF 122384 and UF 120032, both UF locality SU003) counties. Finally, one additional specimen (UF 119913) that may be *C. sauridens* is from the lower Oligocene Bumpnose Limestone of Jackson County (UF locality JA025). Besides these records, the only other known record of this taxon (as recognized here) in Florida is Dall's (1916: 4489) account of *C. tortilis* in the "Ocala." *Conus sauridens* co-occurs in the Eocene of Florida with the new species *C. palmerae* and *C. alleni*; characteristics that distinguish the new species from *C. sauridens* are discussed below.

A complete review of the fossil record of *Conus sauridens* is beyond the scope of this paper, though the preliminary observations we have made here support earlier demonstrations (Palmer, 1937) that *C. sauridens* was a morphologically variable, geographically widespread, and temporally persistent species. While the oldest known (early Eocene) *Conus* fossils were small (<35 mm in shell length), larger species (ca. 70 mm in shell length) have previously been reported from the middle Eocene (Kohn, 1990). During this study, we recognized a very large (shell length, 116.1 mm) specimen (UF 120022; Figure 19) of *C. sauridens* from the upper Eocene Moodys Branch Formation of Grant Parish, Louisiana (UF locality ZL004). This specimen may be the largest *Conus* yet known from the Eocene of the U.S. Coastal Plain. The large geographic range of *C. sauridens* could be related to its developmental mode, which was likely planktotrophic based upon its multispiral larval shell (Figures 20–22), though testing this hypothesis within the context of Shuto's (1974) model of the relationship between developmental mode and larval shell morphology (also see Kohn and Perron, 1994) will require additional study. While not necessarily useful as a guide fossil, shells of *C. sauridens* (as circumscribed here) have recently been utilized in several isotopic studies (Kobashi et al., 2001; Kobashi and Grossman, 2003; Kobashi et al., 2004) of Paleogene climate and have proven to be geologically useful in this regard.

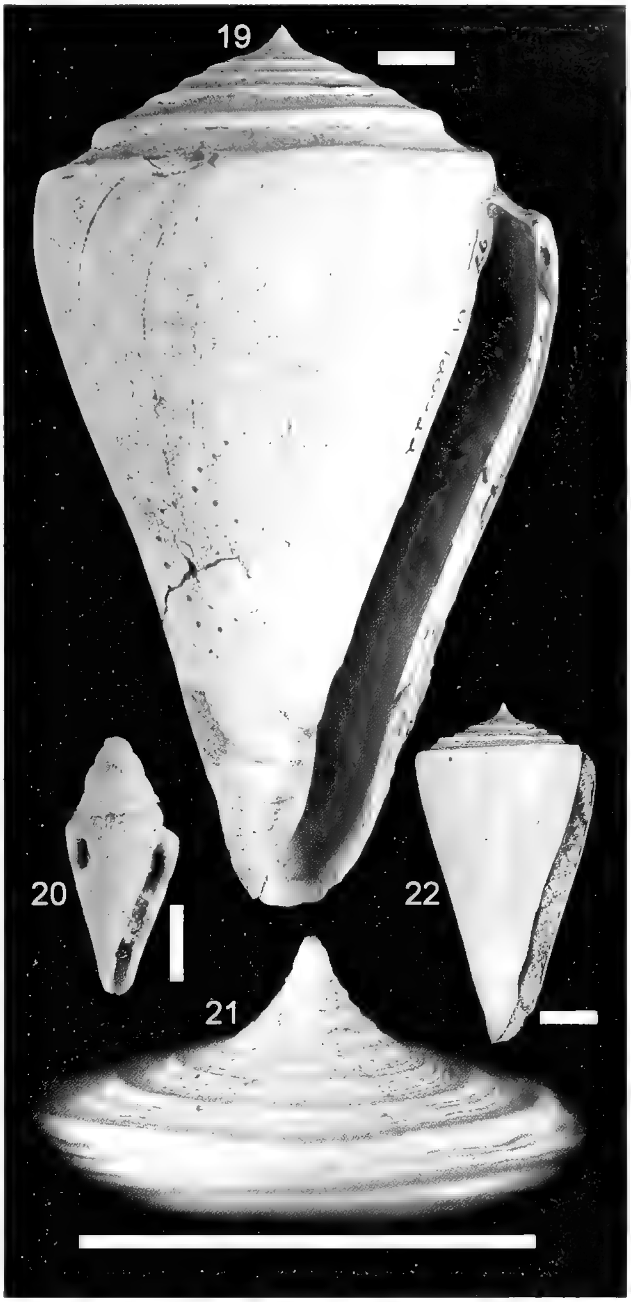
Conus palmerae new species
(Figures 23–30, Table 2)

Conus sp. B, Palmer in Richards and Palmer, 1953: 40, pl. 2, fig. 14.

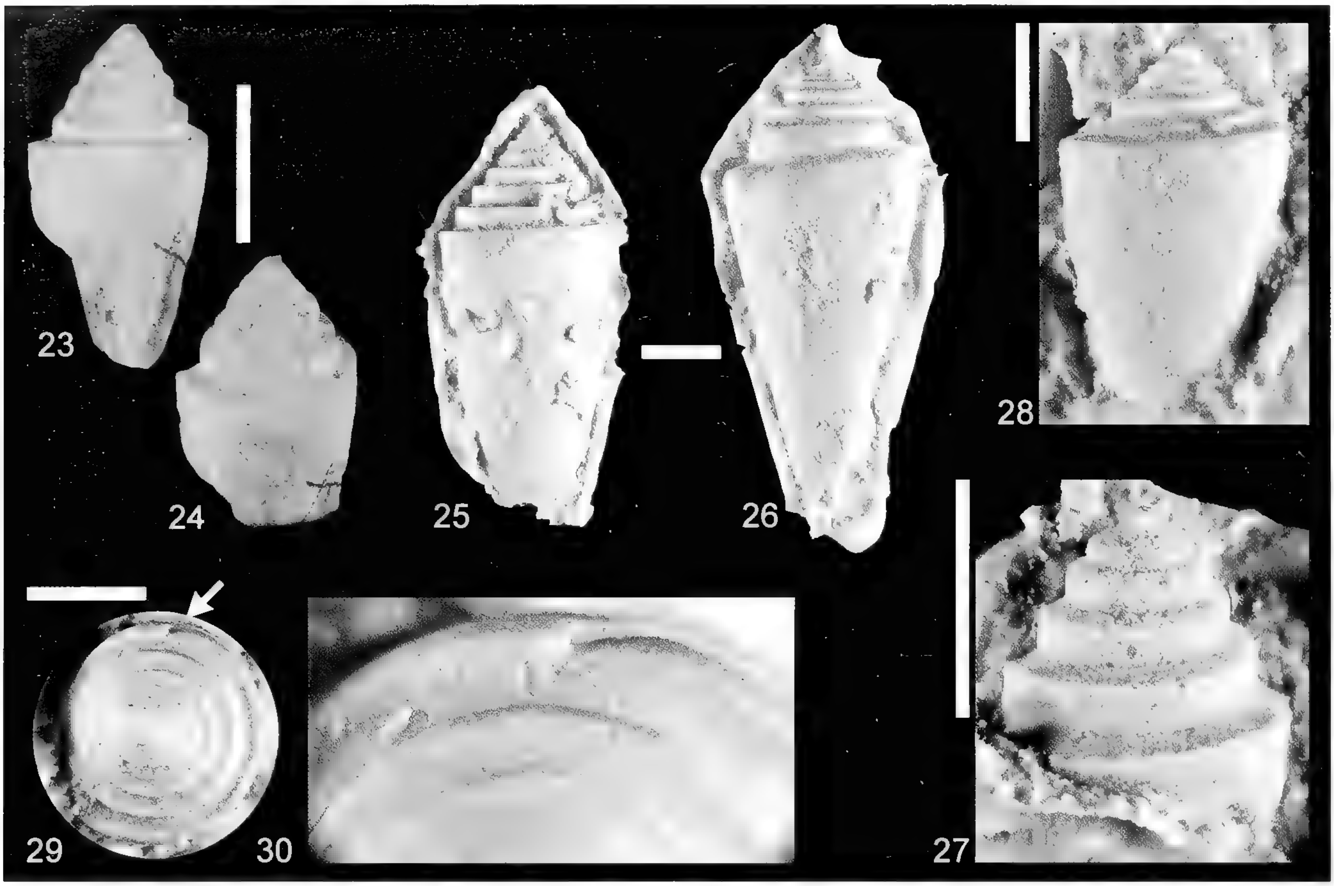
Diagnosis: Teleoconch whorls stepped; early postnuclear whorls smooth; sutural ramps typically smooth; last whorl smooth.

Description: Shell small to moderately large-sized (up to about 65 mm in length). Last whorl conical; outline slightly concave. Shoulder sharply angulate, smooth. Spire of moderate height; outline concave to straight. Teleoconch whorls stepped; spire angle of early whorls typically obtuse relative to later whorls. Larval shell unknown. Early postnuclear whorls smooth. Subsutural flexure symmetrically curved. Teleoconch sutural ramps concave and typically smooth, though occasionally 2 or 3 weak spiral threads are present. Aperture morphology unknown. Last whorl typically smooth, though fine spiral lines may cover the last whorl of some small specimens.

Type Specimens: Holotype UF 108858 (Figures 23, 24), a specimen originally described as "*Conus* sp. B" by Palmer in Richards and Palmer (1953: 40, pl. 2, fig. 14). The holotype is preserved as a calcite-replaced shell. All paratypes are moldic (consisting of just external or external and internal molds) and include: UF 15886, UF 18599 (Figure 25), UF 18711, UF 18719, UF 18737 (Figure 26), UF 57018, UF 66738 (Figure 27), UF 68306 (Figure 28), UF 74473 (Figures 29, 30), UF 110360, UF 111327, and UF 112981. See Table 2 for measurements of these specimens.



Figures 19–22. Specimens of *Conus sauridens* Conrad, 1833. **19.** Largest known specimen (UF 120022) of *C. sauridens*, shell length 116.1 mm, Moodys Branch Formation, UF locality ZL004 (Montgomery Landing 01), Grant Parish, Louisiana; scale bar equals 1 cm. **20.** Juvenile shell (UF 126927), shell length 3.4 mm, Moodys Branch Formation, UF locality ZL004 (Montgomery Landing 01), Grant Parish, Louisiana; scale bar equals 1 mm. **21–22.** Shell (GSA.2007.005), shell length 60.5 mm, Moodys Branch Formation, Montgomery Landing, Grant Parish, Louisiana; Figure 21 shows the larval shell and early postnuclear whorls of this specimen, which is also shown in Figure 22 (both scale bars equal 1 cm).

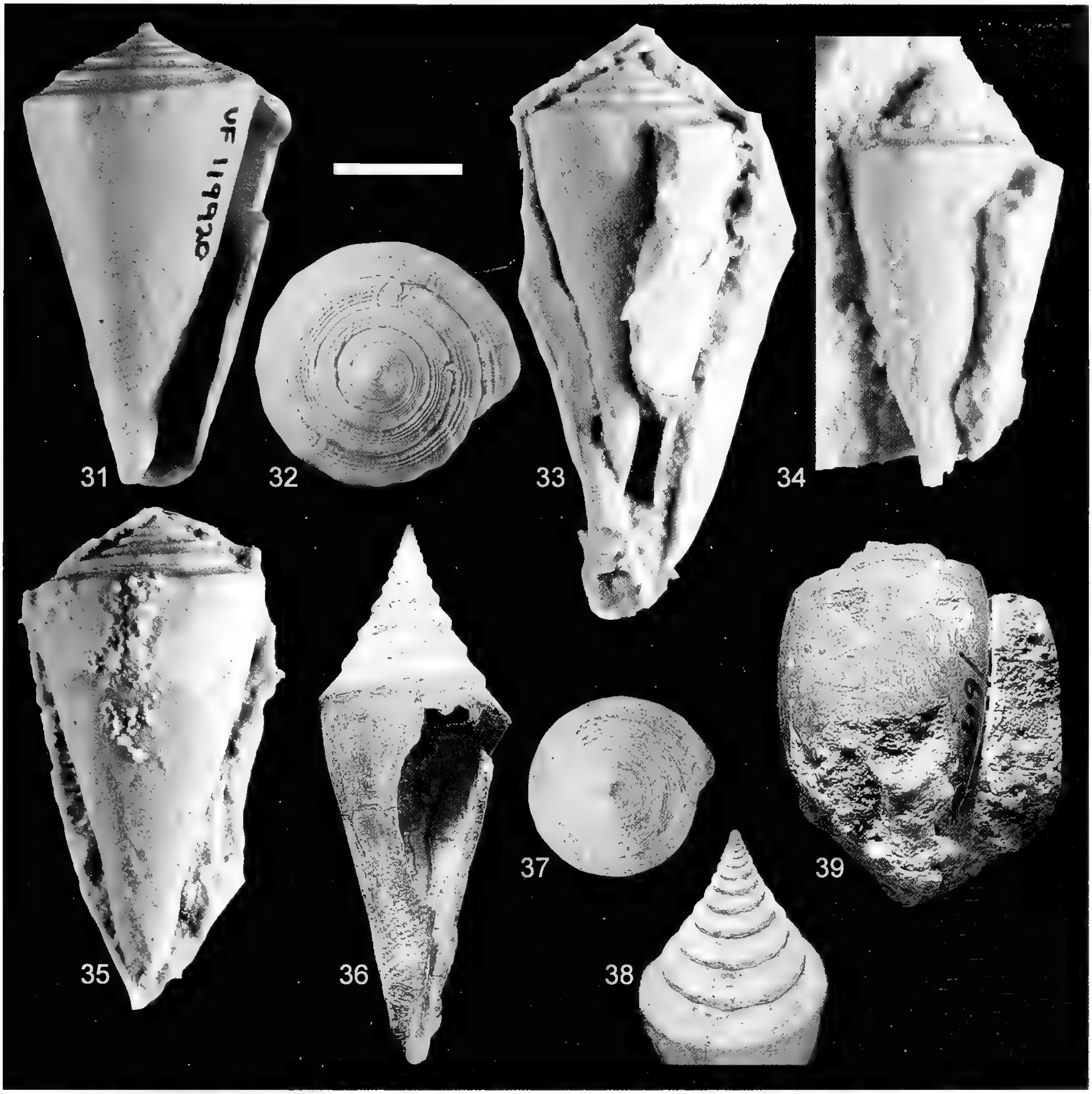


Figures 23–30. Specimens of *Conus palmerae* new species. All scale bars equal 1 cm. **23–24.** Holotype (UF 108858), preserved shell length 22.0 mm, preserved maximum diameter 11.5 mm, lower member of the Ocala Limestone (formerly Inglis Formation), UF locality LV014 (Gulf Hammock 02), Levy County, Florida. **25.** R.T.V. silicone rubber cast of paratype (UF 18599), preserved shell length 50.1 mm, preserved maximum diameter 23.4 mm, Ocala Limestone, UF locality AL016 (S.M. Wall Quarry 01), Alachua County, Florida. **26.** R.T.V. silicone rubber cast of paratype (UF 18737), preserved shell length 56.1 mm, preserved maximum diameter 24.1 mm, Ocala Limestone, UF locality LF001 (Dell Limerock Mine), Lafayette County, Florida. **27.** R.T.V. silicone rubber cast of paratype, (UF 66738), maximum diameter 14.2 mm, Ocala Limestone, UF locality AL028 (Newberry 03), Alachua County, Florida. **28.** R.T.V. silicone rubber cast of paratype (UF 68306), maximum diameter 19.3 mm, Ocala Limestone, UF locality AL004 (Dickerson Limerock Mines), Alachua County, Florida. **29–30.** R.T.V. silicone rubber cast of paratype (UF 74473), preserved maximum diameter 19.0 mm, Ocala Limestone, UF locality AL004 (Dickerson Limerock Mines), Alachua County, Florida; the topmost portion (indicated by arrow) of Figure 29 is magnified 3.5× in relation to Figure 30 to show details of the sutural ramps.

Type Locality and Occurrence: The holotype (UF 108858; Figures 23, 24) is from the lower member of the Ocala Limestone (formerly the Inglis Formation) at UF locality LV014, Gulf Hammock 02, Levy County, Florida. Richards and Palmer (1953: 5) described the locality (R. O. Vernon's L-93) as a "road metal pit 2.9 miles south of the north limits of the town of Gulf Hammock just southwest of State Road 55 in the southwest quarter of Section 34, Township 14 South, Range 16 East." The paratype specimens are from Alachua County UF 68306, UF 74473, UF 111327, and UF 112981, UF locality AL004, Dickerson Limerock Mines, Ocala Limestone; UF 18599, UF locality AL016, S.M. Wall Quarry 01, Ocala Limestone; UF 15886, UF locality AL017, Newberry Corporation Pit 01, Ocala Limestone; and UF 66738, UF locality AL028, Newberry 03, Ocala Limestone and Lafayette County (UF 18711, UF 18719, UF 18737, UF 57018, and UF 110360, UF locality LF001, Dell Limerock Mine, Ocala Limestone). Thus, all specimens of *C. palmerae* are from the upper Eocene, Jacksonian Ocala Limestone of Florida.

Etymology: This species is named in honor of Katherine V. W. Palmer (1895–1982), second director of the Paleontological Research Institution (Ithaca, NY), who was the first to recognize this form as a new, undescribed species and for her important contributions to Cenozoic paleontology (see Caster, 1983).

Discussion: Palmer (1953) did not describe UF 108858 as a new taxon because she did not consider this single damaged shell adequate for this purpose. Newly collected specimens (all molds) are consistent with the gross morphology of Palmer's fossil, but offer new mor-



Figures 31–39. Specimens of *Conus alleni* new species (**31–35**), *C. smithvillensis* Harris, 1895 (**36–38**), and *C. cormacki* Harbison, 1944 (**39**). Scale bar equals 1 cm. **31–32.** Holotype (UF 119920) of *C. alleni*, shell length 36.2 mm, preserved maximum diameter 20.7 mm, Moodys Branch Formation, UF locality ZL004 (Montgomery Landing), Grant Parish, Louisiana. **33.** Paratype (UF 119977) of *C. alleni*, preserved shell length 35.1 mm, Ocala Limestone, UF locality LF002 (Mill Creek Quarry), Lafayette County, Florida. **34.** Paratype (UF 119919) of *C. alleni*, preserved shell length 33.2 mm, Ocala Limestone, UF locality SU014 (Suwannee American Cement), Suwannee County, Florida. **35.** Paratype (UF 119976) of *C. alleni*, preserved shell length 34.5 mm, UF locality LF002 (Mill Creek Quarry), Lafayette County, Florida. **36–38.** Holotype (TMM-BEG 35656) of *C. smithvillensis*, shell length 42.1 mm, preserved maximum diameter 14.8 mm, Weches Formation, Colorado River at Smithville, Bastrop County, Texas. **39.** Holotype (ANSP 16145) of *C. cormacki* (not a *Conus*; see text), preserved shell length 28.7 mm, Santee Cooper Canal, South Carolina

phological details that now justify description of this species.

Conus palmerae co-occurs in the Ocala Limestone with two other late Eocene *Conus* in Florida: *C. sauridens* Conrad, 1833, and *C. alleni* new species. *Conus palmerae* may be distinguished from both of these species by its stepped teleoconch whorls, smooth early postnuclear whorls, smooth sutural ramps, and smooth last whorl.

Conus alleni new species
(Figures 31–35, Table 2)

Diagnosis: Shoulder undulate; subsutural flexure diagonal; last whorl with raised spiral cords on anterior half.

Description: Shell medium-sized (up to about 36 mm in length). Last whorl conical; outline straight to slightly sigmoidal (convex near shoulder). Shell widest at shoulder. Shoulder angulate and with large tubercles resulting from weak undulations. Spire of moderate height; outline straight to slightly concave. Larval shell unknown. Early postnuclear whorls tuberculate. Subsutural flexure diagonal, depth about 1.5× width. Teleoconch sutural ramps concave with several raised spiral cords. Aperture opening about as wide at base as at shoulder. Last whorl with pronounced raised spiral cords on anterior half, sometimes extending weakly as threads to shoulder.

Type Series: Holotype, UF 119920 (Figures 31, 32). The three paratypes consist of external molds and include UF 119977 (Figure 33), UF 119919 (Figure 34), and UF 119976 (Figure 35). See Table 2 for measurements of these specimens.

Type Locality and Occurrence: The holotype (UF 119920, Figures 31, 32) was collected by J. E. Allen from the Jacksonian Moodys Branch Formation at Montgomery Landing (UF locality ZL004), Grant Parish, Louisiana. The paratypes are all from the Ocala Limestone of Florida, including two specimens from Lafayette County (UF 119976, UF 119977, UF locality LF002, Mill Creek Quarry) and one specimen from Suwannee County (UF 119919, UF locality SU014, Suwannee American Cement).

Etymology: This species is named in honor of James E. Allen (1914–1997) of Alexandria, Louisiana, who was an enthusiastic collector and scholar of Gulf Coast Eocene mollusks.

Discussion: *Conus alleni* co-occurs in the Eocene of Louisiana with *C. sauridens* and in the Ocala Limestone of Florida with *C. palmerae* new species and *C. sauridens*. *Conus alleni* can be readily differentiated from both species by its undulate shoulder and spiral cords on the anterior half of the last whorl (raised spiral threads on the last whorl may also be present on small shells of *C. palmerae*, but if so are much weaker).

Conus alleni shares some resemblance with a moldic Oligocene fossil (USNM 166720) from Decatur County, Georgia that Dall (1916) described as *C. vaughani*. Dall's (1916: pl. 86, fig. 1) figure of the cast shows a specimen (partially obscured by matrix) with an obtuse spire angle, undulate shoulder, and raised spiral threads on the sutural ramps that are similar to the teleoconch morphology of *C. alleni*. The presence of rows of spiral beads on the last whorl, the fact that the shell is widest below the shoulder (rather than at the shoulder, as in *C. alleni*), and the fact that the anterior end of the shell appears completely obscured by matrix prevents us, however, from considering these two forms equivalent.

The only known shell material of *Conus alleni* is the holotype (from Grant Parish, Louisiana); the other three specimens are from Florida and all consist of external molds. This taxon was apparently rare, especially outside of Florida. We recognized this new form from the moldic Floridian material before we—by chance—discovered the similar shell from Louisiana in the FLMNH collections. We chose to designate the shell as the holotype, rather than one of the paratype external molds, because of its greater number of characters available for observation.

Other Records of Eocene *Conus* from the U.S. Coastal Plain

Unidentifiable internal molds of *Conus* are common in the Eocene Ocala Limestone of northern Florida. We examined 54 such lots (over 440 specimens) from Alachua, Citrus, Jackson, Lafayette, Marion, and Suwannee counties. These include: UF 15884, UF 15892, UF 15905, UF 17831, UF 17832, UF 17879, UF 17947, UF 17950, UF 17967, UF 18423, UF 18759, UF 18848, UF 18864, UF 18896, UF 18955, UF 18962, UF 19140, UF 19174, UF 19204, UF 19215, UF 20744–20746, UF 46435, UF 68270, UF 107265, UF 119900–UF 119904, UF 119906–119911, UF 119914–119917, UF 119921, UF 120027, UF 120032–120040, UF 120047, and UF 126926.

During the course of this work, we became aware of several other Eocene Coastal Plain *Conus* species that are likely distinct, but are not known to occur in Florida and will require additional investigation; these include: *Conus smithvillensis* Harris, 1895; *C. smithvillensis* var. Dockery, 1980 (also see *C. smithvillensis* var. Dockery in Campbell, 1995); and *Conus haighti* Gardner, 1945.

Harris (1895) described *C. smithvillensis* from the Colorado River at Smithville, Bastrop County, Texas (Weches Formation according to TMM records). The holotype (TMM-BEG 35656; Figures 36–38) shares some characteristics with *C. sauridens* (including a multispiral protoconch, tuberculate early postnuclear whorls, spiral threads on the sutural ramp, growth lines showing a deep and symmetrically curved subsutural flexure, and incised spiral grooves near the base of the last whorl), but has a very different overall shell shape: the spire is much higher (spire angle: 53°, Table 2; in mature individuals of *C. sauridens*, the spire angle is typically over 100°), the conical last whorl has straight sides, and the sutural ramps are flat. Dockery (1980) figured a shell (MGS 590) from the slightly younger Cook Mountain Formation of Mississippi that he described as a variety of *C. smithvillensis*. His figured shell appears to bear many of the discrete characteristics of *C. smithvillensis* described above, though has a lower spire (ca. 76°) and the last whorl is sigmoidal in profile. *Conus smithvillensis* is not at all similar in form to *C. palmerae*. While it bears some of the shell characteristics of *C. alleni*, it lacks *C. alleni*'s distinctive raised spiral cords at the base of the last whorl. Campbell (1995) attributed an external mold (UNC 15448) from the Santee Limestone near Cross, South Carolina to Dockery's (1980) variety of *C. smithvillensis*. Campbell (1995: 146) stated that this form is the "most common *Conus* in the Santee Limestone" and that it "has a nodose shoulder and a taller, more tabulate spire than the widespread *Conus* (*Lithoconus*) *sauridens*." Further study will be required to determine whether these varieties are indeed consistent with Harris's taxon.

Gardner (1945) described *C. haighti* from the Laredo Formation of Zapata County, Texas. She did not figure her holotype (USNM 495182), but her figured (pl. 26, fig. 7) paratype specimen (USNM 495183) has a convex spire profile and rounded shoulder that appear distinct from those characters in *C. sauridens*, *C. palmerae*, and *C. alleni*. Gardner's other figured (pl. 26, fig. 2) specimen of *C. haighti* lacks this distinctive spire form.

NOMINA DUBIA

The following species of *Conus* described from the Eocene of the U. S. Coastal Plain should be regarded as *nomina dubia: Conus gyratus* Morton, 1834; *Conus mutilatus* Tuomey, 1852; *Conus improvidus* de Gregorio, 1890; and *Conus cormacki* Harbison, 1944. *Conus gyratus* (holotype, ANSP 211) is an internal mold of a shell of uncertain provenance from South Carolina (also see Kohn, 1992); Campbell (1995) suggested that it could be an internal mold of the purported variety of *C. smithvillensis* presented by Dockery (1980). *Conus multilatus* was described (but not figured) by Tuomey from casts found near Wilmington, North Carolina. De Gregorio (1890) described *C. improvidus* from Claiborne, Alabama, but his holotype is reportedly lost (Palmer and Brann, 1966) and Palmer (1937: 465) considered the taxon "of doubtful status as an American species." *Conus cormacki* Harbison, 1944 was described from the Eocene Santee Formation of South Carolina, but the holotype (ANSP 16415, Figure 39, Table 2) is clearly not a *Conus*. Campbell (1995: 146) stated that *C. cormacki* "is actually a broken volutid."

Several other Eocene *Conus* species are also problematic. *Conus pulcherrimus* Heilprin, 1879 (type, AMNH-FI 10175) was recognized by Harris (1895) as a turrid (see Palmer and Brann, 1966). The type specimen of *Conus* (*Conospirus*) *granopsis* de Gregorio (1890) is lost (Palmer and Brann, 1966) and Dall (1896) and Palmer (1937) suggested that the small shell figured by de Gregorio (1890) may be the juvenile of another species. Given that the type specimen is lost and that the shell is likely a juvenile specimen, *C. granopsis* is a name that should probably be disregarded.

Finally, along with *Conus* sp. B (described here as the new species *C. palmerae*; holotype, UF 108858), Palmer in Richards and Palmer (1953) also noted a *Conus* sp. A. She said, "species A . . . is a broad (21 mm.), low-spired (7 mm.) shell with sharp angulation of the shoulder of the whorls; the surface was apparently smooth. The specimen is a fragment, 25 mm. high" (Palmer, 1953: 40). We located this specimen (UF 108683), which—like UF 108858—is also a calcite pseudomorph from UF locality LV014, Gulf Hammock 02, Levy County, Florida (lower member of the Ocala Limestone). UF 108683 is poorly preserved and is too fragmentary (more than half of the spire is eroded away and much of the last whorl is missing) to either assign to a known species or to describe as new species.

ACKNOWLEDGMENTS

Sable Allen (Alexandria, Louisiana) graciously donated to the FLMNH the large, well-documented Eocene Gulf Coast mollusk collection of her late husband, James E. Allen. Larry Rogers (Limestone Products), Wayne Beaver (Denali Limerock Mine), Joe Horton (Suwannee American Cement), and Leon Brooks (Hi-Cal Quarry) kindly allowed access to collect in their Florida mines. Paul Callomon (Academy of Natural Sciences, Philadelphia) and Ann Molineux (Texas Memorial Museum) are thanked for allowing access to type specimens. Ann Molineux also provided helpful discussions on Eocene stratigraphy in Texas. Bushra Hussaini and Sandy Ebersole furnished information pertaining to an American Museum of Natural History specimen and a Geological Survey of Alabama specimen, respectively. Alan Kohn provided helpful discussions of and suggestions for terminology related to the "subsutural flexure" of cone shells. Sean Roberts (Florida Museum of Natural History) assisted us with some of the digital photography using a Sony DSC R1 camera (10.3 megapixel resolution). We thank Alan Kohn and an anonymous reviewer for comments that improved the quality of this manuscript. JRH's contributions to this work were supported by the Brayfield Award of the South West Florida Fossil Club and NSF EAR 0518976. RWP's contribution to this work was supported by the McGinty Endowment of the Florida Museum of Natural History, by Barbara and Reed Toomey, and by the late David Nicol whose $1000 grant allowed RWP to permanently transfer the Florida Geological Survey Eocene mollusk collection from the Paleontological Research Institution (where it was under study by Katherine V.W. Palmer) to the Florida Museum of Natural History. This is University of Florida Contribution to Paleobiology 602.

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Synonymization of *Neohyalimax* Simroth, 1896, and *Omalonyx* d'Orbigny, 1837, with a redescription of *Omalonyx brasiliensis* (Simroth, 1896) (Gastropoda: Succineidae)

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ABSTRACT

Neohyalimax was established as a monotypic genus for *N. brasiliensis*. Characters of the reproductive system prompted authors to subsequently treat the taxon as a subgenus of *Omalonyx*. Examination of the holotype and discussion of these characters allowed *Neohyalimax* to be synonymized with *Omalonyx*. *Omalonyx brasiliensis* remains a valid species based solely on the holotype.

Additional Keywords: Mollusca, Pulmonata, Brazil, Rio Grande do Sul

INTRODUCTION

The genus *Omalonyx* d'Orbigny, 1837, comprises succineids slugs of West Indies, Central and South American and Juan Fernandez, with a reduced, flat and fingernail-like shell. *Omalonyx* has commonly been classified with two subgenera (e.g., Patterson, 1971; Tillier, 1981), namely *Omalonyx* sensu stricto and *Neohyalimax* Simroth, 1896. Zilch (1959–1960) and Thiele (1992) indicated that the separation between the subgenera *Omalonyx* and *Neohyalimax* is based on the mantle covering either only the margin or the entire shell and the spire being small or scarcely indicated. The monotypic subgenus *Neohyalimax*, type-species *Neohyalimax brasiliensis* Simroth, 1896, was described from a unique specimen collected from Rio Grande do Sul, Brazil. In revising the family Succineidae Beck, 1837, Patterson (1971) discussed the similarities of *Omalonyx felina* (Guppy, 1872) [= *O. matheroni* (Potiez and Michaud, 1835), according to Tillier, 1981] and *N. brasiliensis*, and brought attention in particular to details of the original description of the latter species (namely the number of seminal vesicles and cephalic tentacles) that suggested recognition of *Neohyalimax* at the subgeneric level. It should be noted, however, that Patterson (1971) did not examine the type of *N. brasiliensis*, nor made a direct comparison with *O. unguis* (d'Orbigny, 1837), the type species of *Omalonyx*. In a revision of the South American and Juan Fernandez succineid slugs, Tillier (1981) similarly did not examine the type of *N. brasiliensis*, but accepted Patterson (1971) assessment of taxonomic status based on the original description provided by Simroth (1896). In support of recognition at the subgeneric rank, Tillier (1981: 144) noted 'an altogether different way of life (terrestrial), a plesiomorphic radula (marginal teeth still longitudinally elongated) and slug-like characters more apomorphic than in *Omalonyx sensu stricto*'.

Simroth (1896) mentioned that the type specimen of *N. brasiliensis* was deposited with the "Berlin Museum". Indeed there is a specimen in Museum für Naturkunde der Humboldt Universität zu Berlin (ZMB 45.913) labeled *Neohyalimax brasiliensis*, but it bears no indication of type status. That the specimen corresponds well with the description given by Simroth (including most details of the internal anatomy) and that no other specimen of this species has been located, the ZMB specimen is here considered to be the holotype.

With the recent rediscovery of Simroth's type specimen, we take the opportunity to redescribe *N. brasiliensis* and reassess its taxonomic status.

MATERIALS AND METHODS

The following lots were examined: GUADELOUPE, Pointe-à-Pitre, *Omalonyx matheroni*, 4 spec., 27.IX.1972, Pointier leg. (MNHN); *O. matheroni*, 11 spec., S. Tillier det. 1979, (MNHN); FRENCH GUIANA, along the road Cayenne-Kourou, 17 km SE Kourou bridge, *O. matheroni*, 5 spec., Tillier leg. (MNHN); PARAGUAY, *O. unguis* (lectotype designated by Tillier, 1981), 1 shell. (MNHN); Asunción, Asunción, *O. unguis*, 1 spec., canje F.H. Schade. (MACN19968, it is labeled as *Hom. unguis* d'Orb.); ARGENTINA, Formosa, Villafañe (26°14.17′ S 59°07.08′ W, Arroyo Bellaco, Estância La Marcela), *O. unguis*, 2 spec., 30.X.2004, Cristián Ituarte leg. (MLP 11878); BRAZIL, Rio Grande do Sul, *Neohyalimax brasiliensis* Simroth, 1 spec. (ZMB 45.913); Cachoeirinha, *O. convexus*, 34 spec., 29.IV.2006, A. Paladini and J. O. Arruda leg., J. O. Arruda det. (MCP 8839); Pelotas (Estrada Pelotas–Rio Grande, 31°45′53.1″ S 52°22′48.2″ W), *O. convexus*, 48 spec., 18.III.2006, A. Paladini and J. O. Arruda leg., J. O. Arruda det. (MCP 8836).

Based on examination of the holotype of *Neohyalimax brasiliensis*, we redescribed the reproductive system (Figure 1). The specimen had been previously dissected, with a sagittal cut from its head to the mantle edge, which then continues towards the left side of animal's tegument. The reproductive system was separated in two parts: one including the vagina (previously dissected and with the papillae on its internal surface exposed), the gametolitic gland duct and its gland and the free oviduct; the other including the pallial oviduct, prostate, albumen gland, fertilization complex, ovulispermduct, ovariotestis, deferent duct, epiphallus and evertophallus (= penis).

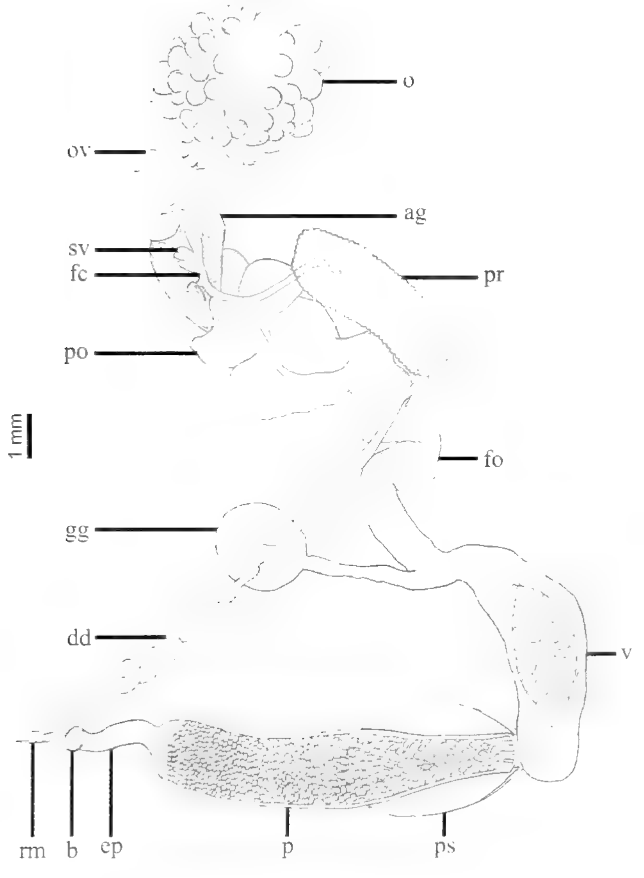

Figure 1. Reconstruction of the reproductive system of *Omalonyx brasiliensis* (Simroth, 1896) (ZMB 45.913). Abbreviations: **ag**, albumen gland; **b**, epiphallial bulb; **dd**, deferent duct; **ep**, epiphallus; **fc**, fertilization complex; **fo**, free oviduct; **gg**, gametolitic gland; **o**, ovariotestis; **ov**, ovulispermduct; **p**, evertophallus; **po**, pallial oviduct; **pr**, prostate; **ps**, evertophallus sheath; **rm**, retractor muscle; **sv**, seminal vesicles; **v**, vagina.

Institutional abbreviations: MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" e Instituto Nacional de Investigacion de las Ciencias Naturales (Buenos Aires, Argentina), MCP, Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul (Porto Alegre, Brazil); MLP, Museo de La Plata (La Plata, Argentina), MNHN, Muséum national dHistoire naturelle (Paris, France) and ZMB, Museum für Naturkunde der Humboldt Universität zu Berlin (Germany).

SYSTEMATICS

Order Heterurethra Pilsbry, 1900
Superfamily Succineoidea Beck, 1837
Family Succineidae Beck, 1837

Genus *Omalonyx* d'Orbigny, 1837

Type Species: *Succinea (Omalonyx) unguis* d'Orbigny, 1837: 229 (year according Sherborn and Woodward, 1901), by original designation.

Diagnosis: Shell very flat, fingernail-shaped, obtuse and small spire, body whorl and aperture very large and elongate-oval, animal body twice the shell length; evertophallus exceptionally long.

Omalonyx brasiliensis (Simroth, 1896)

Neohyalimax brasiliensis Simroth, 1896: 39–45; Morretes, 1949: 130; Simone, 2006: 237.
Omalonyx (Neohyalimax) brasiliensis.—Zilch, 1959–1960: 202; Patterson, 1971: 187; Tillier: 1981.
Homalonyx (Neohyalymax) brasiliensis.—Thiele, 1992.
Omalonyx brasiliensis.—Salgado and Coelho, 2003: 153.

Diagnosis: A species of *Omalonyx* with a thick-walled vagina with robust diamond shaped papillae on its internal surface.

Holotype: ZMB 45.913

Type Locality: Brazil, Rio Grande do Sul.

Redescription: The shell is thin, oval and highly flattened (it is fragmented, which precludes its measurement).

The jaw and radula are missing (see Discussion below). Within the reproductive system, the epiphallus is approximately one fourth of the length of the evertophallus. The former possesses a thick wall, a smooth outer face and a bulb, and its internal surface has transverse folds. The opening of the epiphallus into the evertophallus is a simple opening, without any papilla.

The evertophallus has a thick, wide wall, and the internal surface is covered with aligned diamond shaped papillae. At its proximal extremity, the papillae are smaller and discoid. At its distal extremity there are small longitudinal folds. The evertophallus sheath, thick and muscular, covers practically the entire distal half of the evertophallus. It gradually becomes a thin and transparent membrane, which covers the other half of the evertophallus and the epiphallus. The evertophallus retractor muscle inserts at the junction of the deferent duct with the epiphallus.

The prostate is long and the section of the deferent duct that is embedded in the prostate has small orifices throughout its length within the gland.

The vagina is approximately half of the length of the evertophallus. It has a thick wall and aligned, diamond shaped papillae on its internal surface. These papillae are similar to those on the evertophallus, but more robust. The gametolitic gland is spherical, with a diameter approximately half the length of its duct. The gametolitic gland duct is slim and about two thirds the length of the vagina.

The free oviduct is long, thick, and convoluted with rippled longitudinal folds on its internal surface. The pallial oviduct, approximately half the length of the lower oviduct, is very inflated and convoluted.

The albumen gland is small, bean-like and about one third the length of the prostate. The ovulispermduct is slightly convoluted and more inflated in its distal portion. The ovariotestis is spherical and large.

The pallial cavity and the nervous and digestive systems are damaged.

DISCUSSION

Simroth (1896: 40, pl. V, Fig. 3) characterized the shell as 'a small flat plate of 9 mm in length and 6 mm in breadth. Beneath the light-yellowish periostracum the lime was deposited in concentric rings, with an excentric nucleus to the left of the posterior end. The nearer the nucleus, the thicker is the shelly matter. The periphery is solid, surrounded, near the posterior right-hand margin, by a brown conchiolin line. The nucleus is somewhat thickened; the shell throughout is perfectly flat, and therefore does not enclose any of the soft parts'. The shell, according to Simroth (op. cit.), would place the species close to the genus *Hyalimax* H. & A. Adams, 1855. However, that author recognized that the shell 'In *Hyalimax* it is slightly arched (Fischer)'. Simroth (1896: 41) described the jaw as 'brown and [it] has a sharp edge, with a slight median process (*oxygnath*) and a lighter-coloured palatal plate (*elasmognath*), the two posterior corners of which are somewhat prominent. This plate is finely sculptured, the thread-like markings converging towards the median projection'

Simroth (1896: 41) described the radular teeth as follows: 'the median tooth is tricuspid, the middle cusp being very large. In the lateral teeth the median cusp is still larger, and directed obliquely towards the middle line of the radula; the inner cusp is reduced in size, whilst the outer one is duplicated. In the marginal teeth the inner cusp increases in size, whilst the exterior outer cusp subdivides, giving rise to three outer cusps'.

In the description of *O. felina*, Guppy (1872) indicated that the shell was usually covered by the mantle, but when retracted, it occasionally exposed the central region of the shell. Gibbons (1879), however, repeatedly observed living specimens of *Omalonyx* and never noticed more than a limited portion of the shell border covered by the mantle. In observations of live specimens of *Omalonyx* from the states of Rio Grande do Sul and Minas Gerais, Brazil, we found that the mantle covered the shell in different degrees, and although the shell was well covered in some, in none presented its shell completely covered by the mantle. Based on Guppy (1872) and on our observation of live specimens of *Omalonyx*, the character "mantle covering partially or totally the shell", indicated by Zilch (1959–1960) and Thiele (1992) for the separation of the subgenre *Omalonyx* and *Neohyalimax*, are unjustifiable. The other character, "small spire or extremely small spire" is not a systematic character.

Patterson (1971), using Simroth's description of *Neohyalimax brasiliensis* as reference, indicated that it has similarities with *Omalonyx felina* concerning the general body's shape, the mantle pigmentation and the anatomy of the reproductive system. Because the reproductive system of *Neohyalimax brasiliensis* is similar to that in *Omalonyx* s.s and different from that in *Hyalimax*, which resembles *Succinea* Draparnaud, 1801, Patterson considered *Neohyalimax* as a subgenus of *Omalonyx*. However, Patterson also noted that *Neohyalimax brasiliensis* has one seminal vesicle, whereas there are two in *O. felina*, and that *N. brasiliensis* has only one pair of tentacles, while *O. felina* has two. We verified the presence of two vesicles and one fecundation pouch in *N. brasiliensis*, which contradicts its original description by Simroth (1896) and concurs with the observations of Patterson (1971) for *Omalonyx* sensu stricto.

Simroth (1896) observed only one pair of tentacles in *N. brasiliensis*, the ommatophores. Patterson (1971), however, stated that *Omalonyx* sensu stricto has two pairs of tentacles. Through an external ventral view exam of the anterior region of *N. brasiliensis*, we could observe that the lower tentacles are present, very close to the animal's mouth opening.

Simroth (1896) did not mention the presence of an epiphallus in *N. brasiliensis*. However, we verified the presence of this structure, which is slightly narrower than the evertophallus and is also present in the other species of *Omalonyx* s.s. We also observed small longitudinal folds at the distal extremity of the evertophallus, which are present in all *Omalonyx* species with known anatomy.

Barker (2001) noted the placement of the genital aperture in *Neohyalimax* immediately adjacent to the right tentacle. We confirmed that this does not differ from its position in other species of *Omalonyx* sensu stricto.

In the state of Rio Grande do Sul, type locality of *O. brasiliensis*, no specimens with the characteristics of this species were found, despite extensive investigation and collecting. In the municipalities of Cachoeirinha, Pelotas and other localities in Rio Grande do Sul, only *Omalonyx convexus* (Heynemann, 1868) was found, suggesting its overlapping geographical area with *O. brasiliensis*. The reproductive systems of these species are distinct. In *O. convexus*, the ovariotestis is hemispherical or discoidal; the lower oviduct is generally half the length of the upper oviduct; half of the proximal region of the evertophallus is generally a little wider than the rest, and its internal surface has longitudinal folds in the wider proximal region and cordiform papillae in the distal region; the internal surface of the vagina has smooth longitudinal folds. In *O. brasiliensis*, the ovariotestis is spherical and large; the lower oviduct is approximately twice the length of the upper oviduct; the internal surface of the evertophallus has diamond shaped papillae and the vagina has similar but more robust papillae.

The reproductive system of *O. brasiliensis* resembles that in the studied specimens of *O. matheroni* (Potiez and Michaud, 1835), which agrees with the meticulous description of Tillier (1981), with the exception of the internal surface of the vagina. According to our observations and to Tillier, the vagina in *O. matheroni* has irregular longitudinal folds, inconsistent in number or shape, whereas *O. brasiliensis* has papillae instead of folds, similar to the ones in its evertophallus. Despite the reproductive system similarities of these species, they do not have overlapping ranges. Tillier (1981) considered the probable range of *O. matheroni* to be the entire Amazon basin, the eastern coastal regions of South America from Caracas (Venezuela) to Rio de Janeiro (Brazil) and part of the Lesser Antilles. *Neohyalimax brasiliensis* has been reported only once, from Rio Grande do Sul (Brazil).

When compared to the *O. unguis* (d'Orbigny, 1837) type species, *O. brasiliensis* presents specifics different characteristics such as a smooth external surface of the epiphallus, the internal surface of the evertophallus and vagina has diamond shaped papillae, more robust in the latter, the length of the gametolitic gland corresponds to approximately a half the length of its duct and the lower oviduct, which is little convolute, is generally two times the length of the upper oviduct. In *O. unguis*, according to Arruda et al. (2006), the external surface of the epiphallus has a looped fold, the internal surface of the evertophallus has discoidal papillae, the internal surface of the vagina has inflated elliptic papillae, the length of the gametolitic gland corresponds to approximately a quarter the length of its duct and the lower oviduct, which is convolute, is approximately three times the length of the upper oviduct.

CONCLUSION

Considering the foregoing discussion regarding the number of seminal vesicles, the number of tentacles and the position of the genital aperture, as well as the observations of the reproductive system, we here consider *Neohyalimax* Simroth, 1896 as a junior synonym of *Omalonyx* d'Orbigny, 1837. *Omalonyx brasiliensis* (Simroth, 1896) remains a valid species, based on the only known specimen, which we consider to be the holotype.

ACKNOWLEDGMENTS

We thank the reviewers, Dr. Gary Barker and Dr. Robert Cowie, for their great contribution with very good criticisms and improving the English; Alejandro Tablado (MACN), Cristián Ituarte (MLP), Lúcia Maria Z. Richinitti (MCP), Virginie Héros (MNHN) and Matthias Glaubrecht (ZMB) for loaning material; Guacira Gil for comments and suggestions; Luiz Augusto F. Araújo for the translation from Portuguese to English; to Conselho Nacional de Desenvolvimento Científico e Tecnológico for financial support (CNPq 131716/2005-0 for JOA, 500032/2003-3 for JWT).

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Rehabilitation of *Ergalatax martensi* (Schepman, 1892) (Gastropoda: Muricidae), senior synonym of *Ergalatax obscura* Houart, 1996, and description of *Ergalatax junionae*, new name for *Morula martensi* Dall, 1923

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ABSTRACT

Ergalatax junionae nomen novum is proposed as replacement name for *Morula martensi* Dall, 1923, from the Gulf of Oman and the Persian Gulf. The latter name is a junior secondary homonym of *Pentadactylus martensi* Schepman, 1892, from the Red Sea, of which *E. obscura* Houart, 1996, is here considered as a junior synonym. *Ergalatax junionae* nomen novum is compared with *Ergalatax martensi* (Schepman) and *E. margariticola* (Broderip, 1833). The geographical distribution of *E junionae* and *E. martensi* is updated and the introduced Mediterranean species is identified as *E. junionae*.

Additional Keywords: Mollusca, Gastropoda, Muricidae, Gulf of Oman, Persian Gulf, Red Sea, Mediterranean Sea, homonymy, synonymy, new name.

INTRODUCTION

Some years ago (Houart, 1996: 13), I described *Ergalatax obscura*, a muricid from the Red Sea. Shortly after that paper was published, R. G. Moolenbeek (in litt.) told me about a name introduced by Schepman (1892), *Pentadactylus martensi*, which he also described from the Red Sea. Having then examined a syntype of that species from ZMA (Figure 14), I concluded that *P. martensi* Schepman, 1892, was a junior synonym of *Ergalatax margariticola* (Broderip, 1833).

However, after recently requesting additional information about the other syntypes of *P. martensi* in NMNL, I received digital images that illustrate the remaining three specimens (Figures 18–23), among them the 17 mm long specimen that probably served for the description (Figures 18–19). Those syntypes are undoubtedly conspecific with *E. obscura*, while the ZMA syntype represents *E. margariticola*.

For many years (Houart, 2001), I had identified an introduced eastern Mediterranean species as *Ergalatax obscura* Houart, 1996 [= *E. martensi* (Schepman, 1892)]. However, this concerns yet a third species, which occurs primarily in the Gulf of Oman and in the Persian Gulf. The species was first wrongly illustrated as *Purpura (Ricinula) siderea* Reeve (a buccinid) by von Martens (1874: 95, pl. 5, fig. 49). Later, Dall (1923: 304) provided a new name for that species, naming it *Morula martensi*. Unfortunately, both species, *Pentadactylus martensi* Schepman, 1892, and *Morula martensi* Dall, 1923, are now included in *Ergalatax*, and Dall's name becomes *ipso facto* a junior secondary homonym and needs to be replaced.

I personally mixed both species because of their close relationship and the presence of some related forms (compare Figures 30 and 35). First (in litt.), I provisionally identified the Mediterranean specimen as *E. martensi* (Dall, 1923), but afterwards I erroneously considered it as conspecific with *E. obscura* [= *E. martensi* (Schepman, 1892)] from the Red Sea and the Gulf of Aden (Houart, 1996: 12).

Abbreviations used herein are: AMS: Australian Museum, Sydney, Australia; MNHN: Muséum national d'Histoire naturelle, Paris, France; NMNL: National Museum of Natural History Naturalis, Leiden, The Netherlands; RH: collection of the author; ZMA: Zoologisch Museum, University of Amsterdam, The Netherlands; ZMB: Museum für Naturkunde der Humboldt Universität zu Berlin, zoologisches Museum, Germany. Terminology for shell spiral cords (after Merle, 1999 and 2001) given in Figure 1.

SYSTEMATICS

Subfamily Muricoidea Rafinesque, 1815
Family Muricidae Rafinesque, 1815
Subfamily Ergalataxinae Kuroda, Habe and Oyama, 1971
Genus *Ergalatax* Iredale, 1931

Type Species: *Ergalatax recurrens* Iredale, 1931, Australia (Figure 17) [?= *E. contracta* (Reeve, 1846)] by original designation.

TELEOCONCH WHORLS	
SP:	Subsutural cord
IP :	Infrasutural primary cord (primary cord on shoulder)
adis :	adapical infrasutural secondary cord (shoulder)
abis :	abapical infrasutural secondary cord (shoulder)
P :	Primary cord
s :	secondary cord
t :	tertiary cord
P1 :	Shoulder cord
P2-P6 :	Primary cords of the convex part of the teleoconch whorl
s1-s5 :	secondary cords of the convex part of the teleoconch whorl
example: s1 = secondary cord between P1 and P2; s2 = secondary cord between P2 and P3, etc	
SIPHONAL CANAL	
ADP :	adapertural primary cord on the siphonal canal
MP :	median primary cord on the siphonal canal
APERTURE	
ID:	Infrasutural denticle
D1 to D5:	Abapical denticles

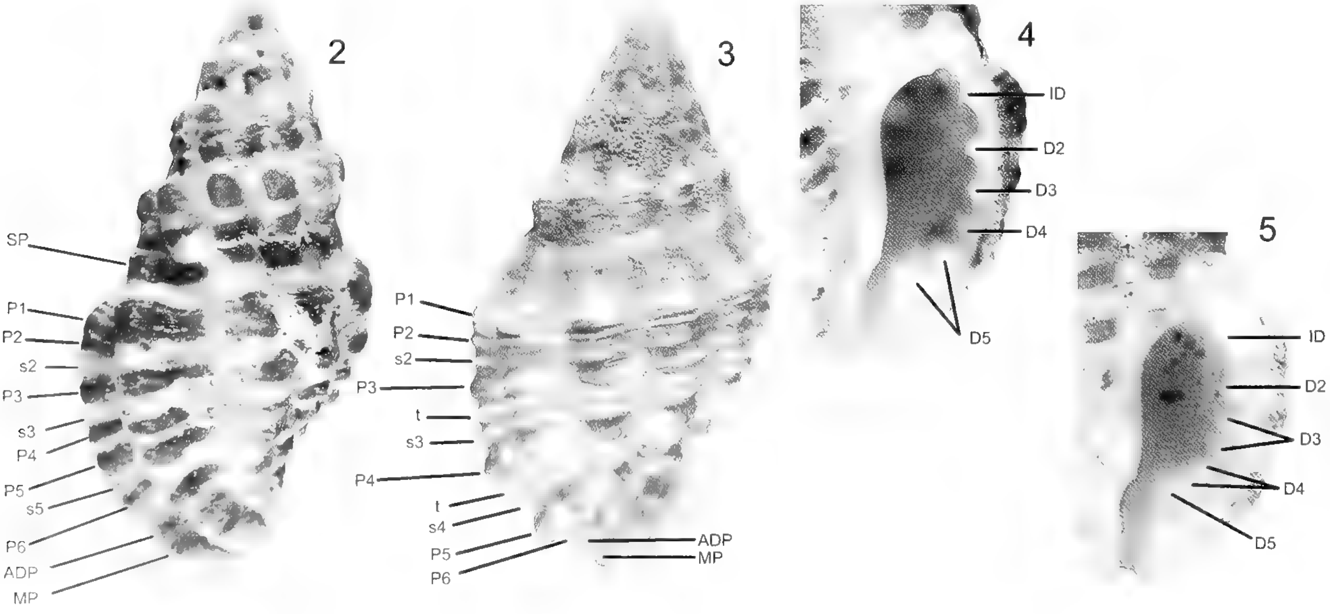
Figure 1. Terminology used to describe the spiral cords (after Merle, 1999 and 2001) (sporadic sculpture is shown in parentheses).

Ergalatax martensi (Schepman, 1892)
(Figures 3, 5, 6, 11, 13, 18–30, 46)

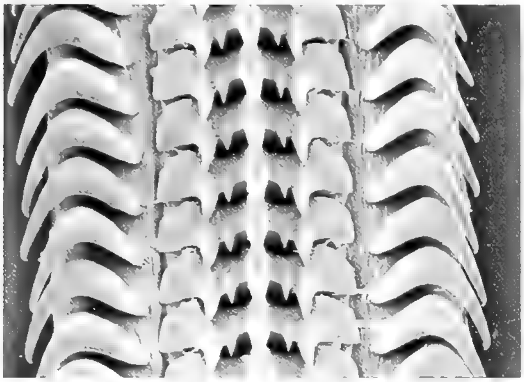
Pentadactylus (Morula) martensi Schepman, 1892: 104.
Cronia martensi Dall.—Sharabati, 1984: pl. 19, fig. 9, 9a, 9b; Singer and Mienis, 1991b: 58, fig. 19; Coulombel, 1994: 73, text fig. (not *Morula martensi* Dall, 1923); Verbinnen and Dirkx, 2000: 69, fig. 9 (not *Morula martensi* Dall, 1923).
Drupella rugosa.—Singer and Mienis, 1991a: 18, fig. 6 (not *Murex rugosus* Born, 1778).
Ergalatax obscura Houart, 1996: 13, figs 1, 3–6; Houart, 2001: 108 (in part), figs 17, 31, 106 and 449 only; Heiman and Mienis, 2003: 22–23 (text fig.).
Not *Morula martensi* (Schepman, 1892) –Tan, 1995: 160, figs 52, 192 g, h (= *Ergalatax junionae* nom. nov.).
Not *Ergalatax obscura*.—Houart, 2001 (in part): 108 (in part), figs 31 and 450–451 only; Delongueville and Scaillet, 2007: 57, fig. 31 (= *Ergalatax junionae* nom. nov.)

Description: Shell medium sized for the genus, up to 25.5 mm in length at maturity. Length/width ratio 1.39–1.92. Heavy, stout. Spire high with 3+ protoconch whorls (tip partially broken), and up to 7 broad, strongly shouldered teleoconch whorls. Suture adpressed. Protoconch conical, acute, whorls smooth. Axial sculpture of teleoconch whorls consisting of high, rounded, nodose ribs: 10 or 11 from first to penultimate whorl, 6 to 8 on last whorl, rarely 5 or 9. Spiral sculpture of high, strong, primary, secondary and tertiary cords. Last teleoconch whorl with adis, IP, abis, P1, immediately followed by small P2, s2, P3, (t), s3, P4,(t), s4, P5, (s5), P6, ADP, MP. P1 and P2 small, P3, P4 and P5 similar in strength, P6 very small or obsolete.

Sculpture forming high, nodose knobs at intersection of spiral cords and axial ribs. Aperture relatively small, ovate. Columellar lip with 2 or 3 weak knobs abapically, rim adherent. Anal notch broad, moderately deep. Outer lip weakly crenulate, with 7 strong elongate denticles within [ID, D2 (D1-D2 fused), D3 split, D4, D5 split]. Siphonal canal short, broad, broadly open. Milky white,



Figures 2–5. *Ergalatax* species. Spiral sculpture and apertural denticles. **2, 4.** *Ergalatax junionae* nomen novum (lectotype ZMB). **3, 5.** *E. martensi* (Schepman, 1892) (Red Sea, RH).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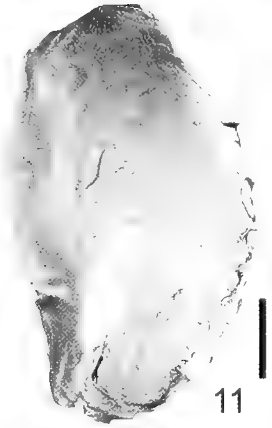
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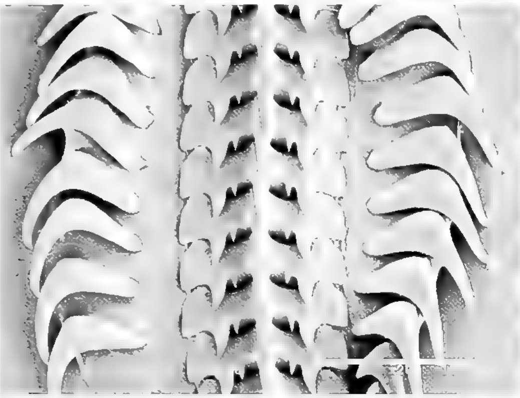
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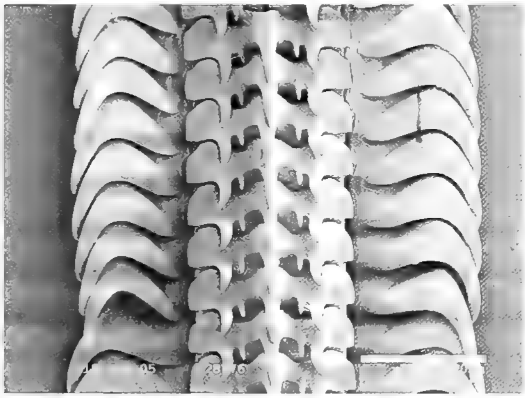
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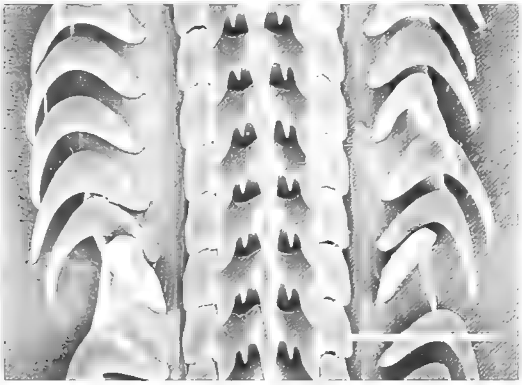
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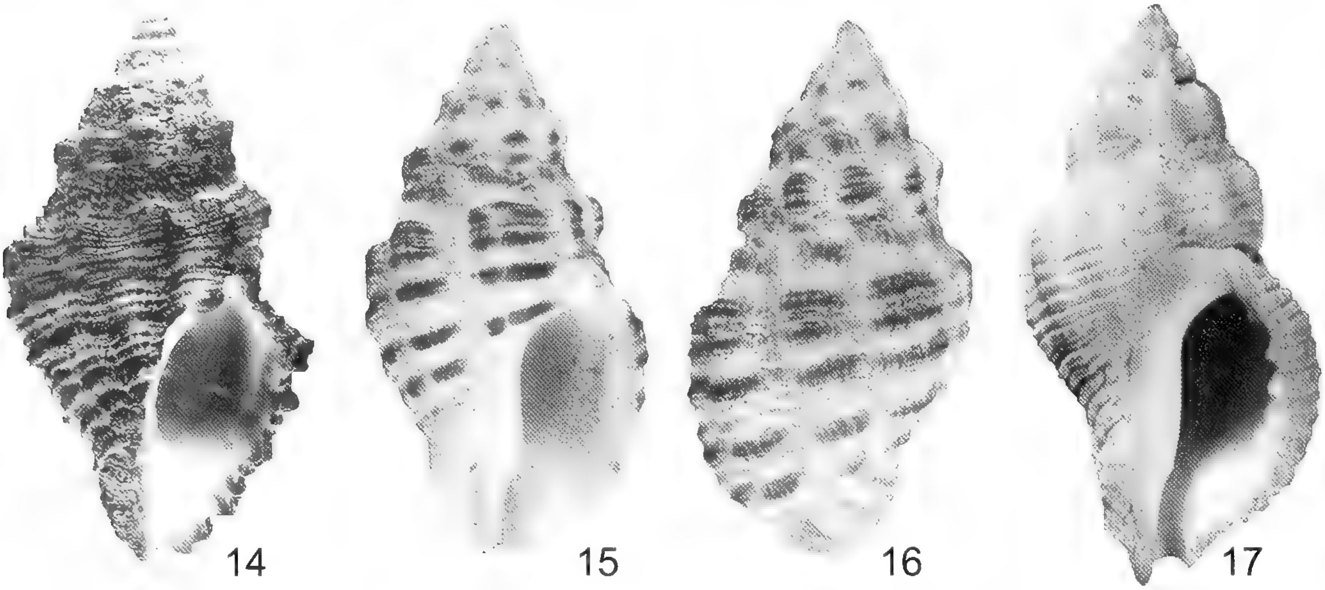
Figures 6–13. *Ergalatax* species. **6.** Radula of *Ergalatax martensi* (Schepman, 1893), Gulf of Aden. Scale bar = 150 μm. **7.** Radula of *E. junionae* nomen novum, Gulf of Iskenderun, Turkey. Scale bar = 120 μm. **8.** Radula of *E. margariticola* (Broderip, 1833), Palau. Scale bar = 120 μm. **9–10.** Radula of *E. contracta* (Reeve, 1846). **9.** Aden, juvenile specimen. Scale bar = 60 μm. **10.** Korea, large adult specimen (lateral denticles worn). Scale bar = 150 μm. **11.** Operculum of *E. martensi* Scale bar = 1 mm. **12.** Operculum of *E. junionae*. Scale bar = 1 mm. **13.** Protoconch of *E. martensi*. Scale bar = 0.5 mm. (Figures 6–11, photos A. Warén).



Figures 14–17. *Ergalatax* species. **14.** *Ergalatax margariticola* (Broderip, 1833). Lectotype of *Pentadactylus (Morula) martensi* Schepman, 1893. "Red Sea, coll. Forskål", ZMA Moll. 2.93.005, 24.8 mm. **15–16.** *Ergalatax junionae* nom. nov. Lectotype of *Morula martensi* Dall, 1923, ZMB 21596, 21.4 mm. **17.** *Ergalatax recurrens* Iredale, 1931. Holotype AMS C57761, 25.5 mm (photo courtesy E. H. Vokes).

creamy white, or tan, usually with some light to dark brown colored spiral cords on shoulder and on more prominent nodes. Aperture cream or pale yellow within.

Operculum ergalataxine (Fig. 11), D-shaped with lateral nucleus in lower right.

Radula (Fig. 6) with a rachidian bearing a long, narrow central cusp, a small, narrow, triangular lateral denticle and a broad, long lateral cusp on each side. Sickle-shaped lateral teeth broad at base and narrow at their end.

Type Material Examined: 3 syntypes NMNL, Red Sea: RMNH.MOL.57165, here selected as lectotype and paralectotypes, 1 syntype ZMA Moll. 2.93.005, Red Sea, here selected as paralectotype; *Ergalatax obscura* Houart, 1996: Perim, Strait of Bab el Mandeb, holotype and 4 paratypes MNHN, 1 paratype RH; Djibouti, Obock, Gulf of Aden, 9 paratypes MNHN; Yemen, Aden, 4 paratypes MNHN, 1 paratype RH.

Othe Material Examined: Djibouti: Obock, Gulf of Aden, 2 RH; Gulf of Aden: 2, RH. **Red Sea:** (no other data), 1 RH; Massawa, Taulud Is., 1 RH; Egypt, Sinai, under stones at low tide, 10 RH; Egypt, Sinai, Sharm El Sheik, 1 RH; Egypt, Sinai, Shark's Bay (marsa umm mureihha), under stones, low tide, 2 RH. Gulf of Aqaba: Israel, Eilat, 0.5–1.0 m, 3 RH; Gulf of Aqaba, Israel, Eilat, under stones, 1–2 m, 4 RH.

Distribution: From the Gulf of Aden to Eilat, Gulf of Aqaba, 0–2 m, on and under stones (Fig. 46).

Remarks: For a comparison with *Ergalatax junionae* see that species below.

Ergalatax junionae nomen novum
Figures 2, 4, 7, 12, 15–16, 31–40, 46)

Morula siderea Reeve.—von Martens, 1874: 95, pl. 5, fig. 49 (not *Ricinula siderea* Reeve, 1846).

Morula martensi Dall, 1923: 304, new name for *Morula siderea* von Martens, 1874, not Reeve, 1846.

Cronia konkanensis.—Bosch and Bosch, 1982: 95, text fig; Smythe, 1982: 60, pl. 1, fig. i; Bosch and Bosch, 1989: 60, text fig. (not *Ricinula konkanensis* Melvill, 1893).

Cronia cf. *konkanensis*.—Giunchi and Tisselli, 1995: 8, text figs.

Ergalatax martens.—Buzzurro, Engl and Tümtürk, 1995: (no pag.), text fig.; Engl, 1995: 46, fig. 10.

Cronia cf. *konkanensis*.—Bosch et al, 1995: 121, fig. 480.

Morula martensi (Schepman, 1892).—Tan, 1995: 160, figs 52, 192 g, h (not *Pentadactylus (Morula) martensi* Schepman, 1892).

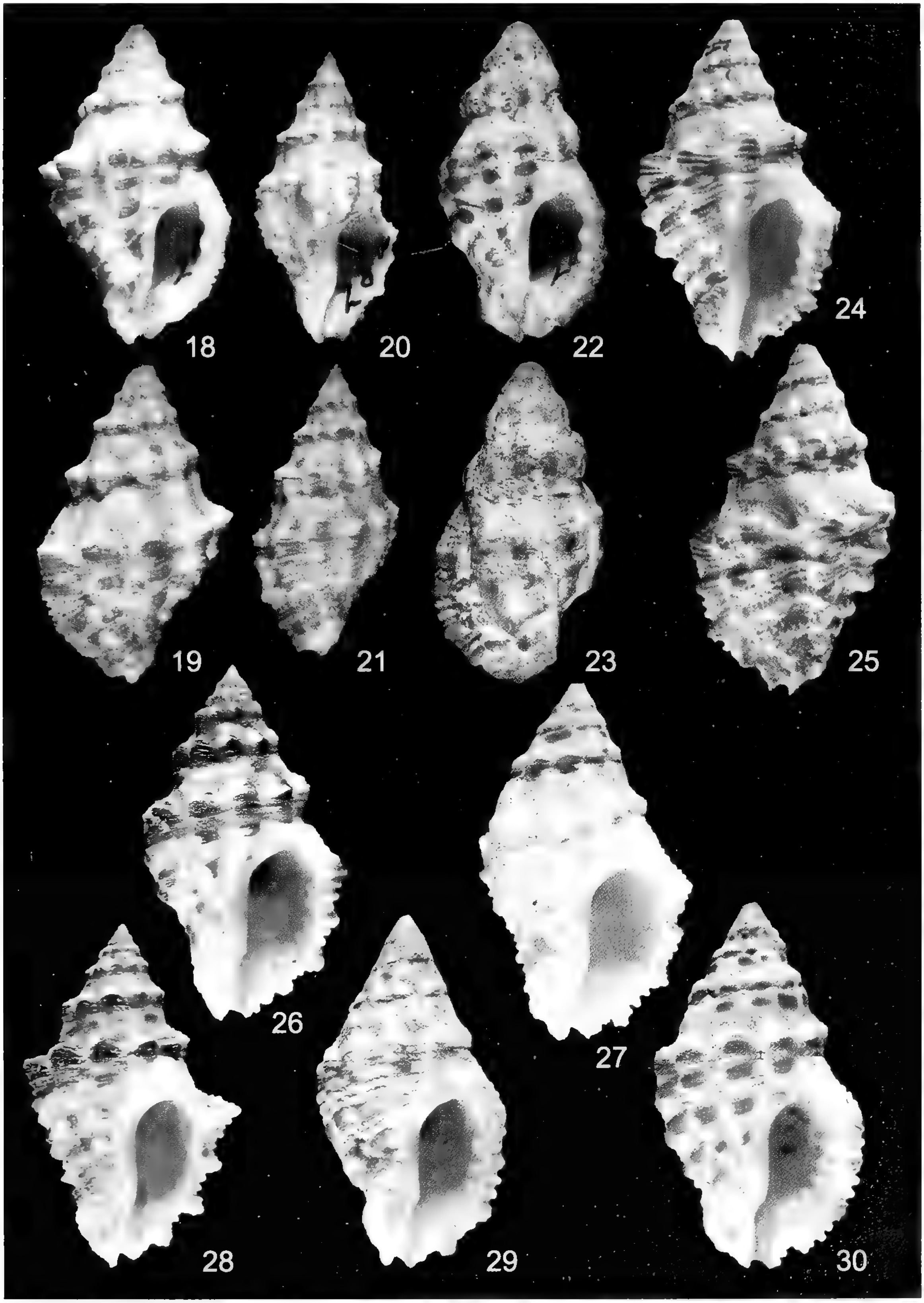
Ergalatax obscura.—Houart, 2001: 108 (in part), figs. 450–451 only; Delongueville and Scaillet, 2007: 57, fig. 31 (not *Ergalatax obscura* Houart, 1996).

Description: Shell medium sized for the genus, up to 29 mm in length at maturity. Length/width ratio 1.91–2.03. Slender, lanceolate, heavy, nodose. Shoulder weakly sloping, concave.

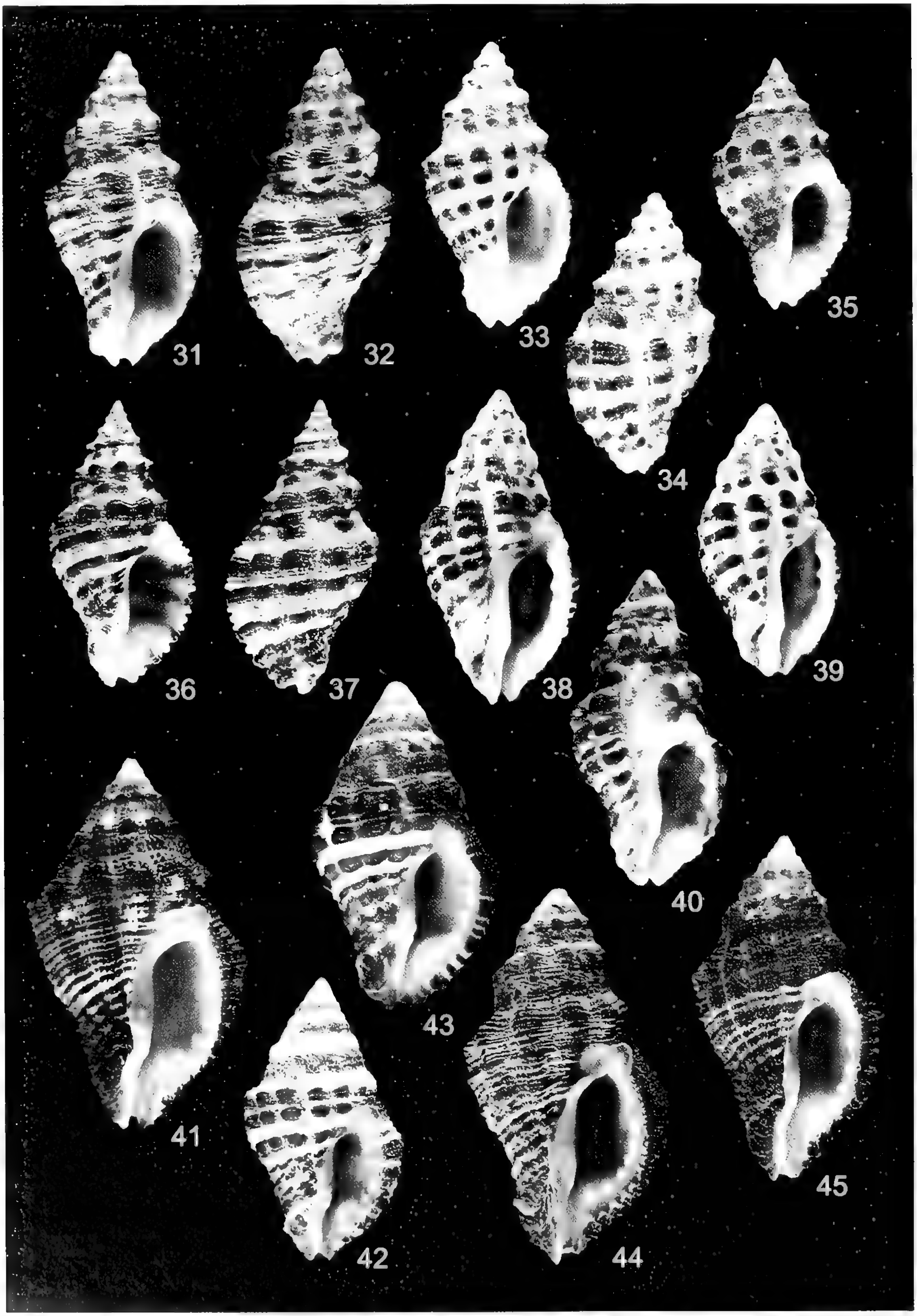
White or creamy white with dark brown or blackish colored primary spiral cords and occasionally s2 or s3. Aperture glossy white.

Spire very high with 3.5 protoconch whorls and teleoconch up to 7 weakly convex, strongly shouldered, nodose whorls. Suture adpressed. Protoconch small, conical, acute; terminal lip raised, of sinusigeral type.

Axial sculpture of teleoconch whorls consisting of high, strong, broad, nodose ribs and erratically placed strong varices. Last teleoconch whorl with 8–11 ribs, occasionally with one or two erratically placed, broad varices. Spiral sculpture of high, strong, nodose and squamose



Figures 18–30. *Ergalatax martensi* (Schepman, 1892). **18–23.** Lectotype and paralectotypes RMNH MOL. 57165 (photo J. Goud). **18–19.** 17.4 mm; **20–21.** 15.7 mm; **22–23.** 17.3 mm. **24–25.** Holotype of *E. obscura* Houart, 1996, Perim, Strait of Bab el Mandeb, MNHN 0159, 24.2 mm (photo MNHN). **26.** Eilat, Israël, RH, 20.8 mm, **27.** Obock, Gulf of Aden, RH, 21.6 mm; **28.** Eilat Israël, RH, 25.1 mm, **29.** Red Sea (no other data), RH, 21.4 mm; **30.** Aden, Gulf of Aden, RH, 21 mm



Figures 31–45. *Ergalatax* species. **31–40.** *Ergalatax junionae* nomen novum. **31–33.** Doha, Wahra, Qatar, RH. **31–32.** 26.5 mm; **33–34.** 22.9 mm. **35.** Yalikent, Iskenderun, Turkey, RH, 17.2 mm; **36–37.** Lebanon, Bay of Jounieh, 19.6 mm; **38–40.** Iskenderun, Bay of Iskenderun, Turkey, RH. **38.** 25.6 mm; **39.** 22.2 mm; **40.** 22.9 mm. **41–45.** *Ergalatax margariticola* (Broderip, 1833). **41.** Raroia, Tuamotu Archipelago, RH, 28.4 mm. **42.** Kai Is., Molluccas, RH, 20.5 mm. **43.** South of New Caledonia, RH, 23.7 mm; **44.** [illegible] Beach, East coast of Singapore, RH, 30.4 mm; **45.** Kwajalein Atoll, RH, 25.9 mm

primary, secondary and tertiary cords. Shoulder of last teleoconch whorl with broad SP, adis, IP, abis, P1, P2, s2, (t), P3, s3, P4,(s4), P5, (s5), P6, ADP, MP: P1 and P2 narrow, P3, P5 and P6 broad, similar in strength, P4 smaller.

Aperture large, narrow, ovate; columellar lip smooth, entirely adherent, with low parietal tooth at adapical extremity; anal notch deep, broad; outer lip weakly erect, with ID, D2-D5. ID largest, broad; D2-D4 decreasing in strength abapically, D5 split; denticles elongate within aperture. Siphonal canal short, broad, dorsally recurved, broadly open.

Operculum (Fig. 12) dark brown, D-shaped, with lateral nucleus in lower right; attached surface with about 8 growth lines and broad, callused rim, about 30–40 % of opercular width.

Radula (Fig. 7) with a rachidian bearing a long, slender central cusp, a small, short lateral denticle and a broad, long lateral cusp on each side. Lateral teeth sickle-shaped, with broad base and narrow end.

Type Material Examined: *Morula martensi* Dall, 1923, lectotype (selected by Houart, 1996) and 6 syntypes ZMB 21596.

Other Material Examined: Persian Gulf: Kuwait, Kuwait City, 4 RH; Qatar, Doha, under rocks, 30 RH; Sharjah, 25°20′ N, 55°21′ E, on rocks, 4 RH; Abu Dhabi, 0.5–1.0 m, 3 RH. Gulf of Oman: Al Hamra, near Qurm, 10 km NW of Muscat, 16 RH; Al Bustan, under rocks, 1 RH. Lebanon: Beirut, harbour entrance, breakwater, max. 15 m, 2 RH; Bay of Jounieh (N), 10–25 m, 2 RH; Batroun, 1–4 m, under stones, 2 RH. Turkey: Gulf of Iskenderun, Iskenderun, under rocks, harbor, 1 m, 8 RH; Kale, beach, 6 RH; Yumurtalik, rock pools, 6 RH; Yalikent, shallow water, on rocks, 1 RH; Bay of Antalya, 6 km off Kemer, 36°39′ N, 30°33′ E, on rocks with mussel banks, 0.5–1.0 m, 7 RH; Fethiye-Oludeniz, on rock at 2 m, 1 RH.

Distribution: Gulf of Oman, Persian Gulf and eastern Mediterranean Sea, intertidal to 4 m, on and under rocks and stones (Figure 46).

Etymology: This species is named in honor of Mrs. Marie-Louise Buyle-Junion (1916–2003), former librarian of the Belgian Malacological Society. She was one of the mainstays of the Society, together with her husband, Jean Buyle.

Remarks: Ships docking at oil terminals in the Gulf of Iskenderun (eastern Turkey) could have introduced the species into the eastern Mediterranean Sea. As noted by Delongueville and Scaillet (2007), the transport via ship hulls or ballast water may be suspected.

The shell morphology of some specimens of *E. junionae* (Fig. 35) is nearly the same to *E. martensi* (Fig. 30), however *E. martensi* differs in having a more strongly shouldered, broader shell, and a yellowish aperture instead of white. with 7 denticles within instead of 6 in *E. junionae*. Moreover, the spiral cords differ in number and strength, as described above and illustrated in Figures 2–5. Twenty-five specimens of *E. martensi* and a few more of *E. junionae* were examined to confirm the stability of these differences.

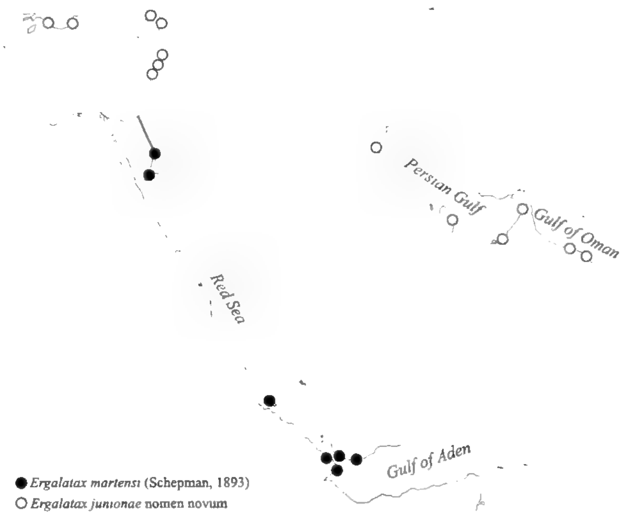


Fig. 46. Distribution of *Ergalatax martensis* and *E. junionae*.

Ergalatax martensi usually has 6–8 axial ribs on the last teleoconch whorl, rarely 5 or 9, compared to *E. junionae* which bears 8–11 ribs and varices on the last whorl.

Ergalatax margariticola (Figures 8, 14, 41–45), a very common Indo-West Pacific species is also related to *E. junionae*, however it is generally stouter and broader, with a wider shoulder, a more squamose spiral sculpture, more uniformly colored shell and different aperture color, being bluish-white, occasionally with a tinge of pink or mauve on the columellar lip *vs.* completely white in *E. junionae*. The shell morphology and color of *E. margariticola* are highly variable, however it is always easily distinguishable from *E. junionae* by one or more differences cited above.

The three species are related to the ergalataxine *Ergalatax contracta* (Reeve, 1845) (Figures 9–10), a probable senior synonym of *Ergalatax recurrens* Iredale, 1931 (Fig. 17), the type species of *Ergalatax*.

Buzzurro, Engl and Tümtürk (1995) were the first to mention the presence of *Ergalatax junionae* [as *Ergalatax martensi* (Dall, 1923)] in the eastern Mediterranean Sea.

Tan (1995:147) in his Ph D. thesis also selected a lectotype for *Morula martensi* Dall, 1923. However, he designated a specimen of *Ergalatax margariticola* (Tan, in litt.) from Kingsmill Is (USNM 52472). Nevertheless, this designation being published in a thesis that does not satisfy Articles 8.1.2 and 8.1.3 of the International Code of Zoological Nomenclature, it is not available as such.

ACKNOWLEDGMENTS

I am very grateful to Jeroen Goud, National Museum of Natural History Naturalis, Leiden for the digital images of the type material of *Pentadactylus martensi* and for his comments, to David Reid, Natural History Museum, London, for providing me useful photocopies and for comments, to Robert G. Moolenbeek, Zoologisch Museum, University of Amsterdam for the loan of the lectotype of *P. martensi*, to the late Prof. R. Kilias, Museum für Naturkunde der Humboldt Universität zu Berlin, for the loan of the specimen illustrated by Martens (1874), lectotype of *Morula martensi* Dall, to Anders Warén, (Natural History Museum, Stockholm) for radula preparation and SEM work of radula and operculum, to E. H. Vokes (Prof. Emeritus, Tulane University, Louisiana) for the photograph of *E. recurrens* Iredale, 1931, to Greg Herbert (University of South Florida, Tampa, USA) for his useful comments and suggestions, and to John Wolff, Lancaster, Philadelphia, for checking the English text.

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Two new deep-sea muricids (Gastropoda) from Argentina

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ABSTRACT

Two new species of muricids belonging in the genus *Trophon* are described from the upper slope off the Atlantic coast of Argentina. Both species have a small size for the genus. The radulae show similarities with those of Antarctic species of the same genus. *Trophon columbarioides* new species has a smooth shell with spines pointed adapically and was collected at 37–38° S, in 209–382 m. *Trophon fasciolarioides* new species has prominent spiral cords and was collected at Burwood Bank in 286–292 m depth and off Bahía Blanca in ca. 1000 m depth.

Additional Keywords: Mollusca, Muricidae, *Trophon*, Southwestern Atlantic, Gastropods, Taxonomy, Patagonia

INTRODUCTION

The genus *Trophon* includes a group of species of undoubtedly austral origin. The older species can be traced as far back as the Oligocene, from Patagonian deposits (Griffin and Pastorino, 2005). Pastorino (2005) redescribed all known living species of *Trophon* from southern South America, and also some new species belonging in the genus. While the subfamilial affinities of this genus are discussed by several authors (e.g. Kool, 1993, 1993a; Vermeij and Carlson, 2000, among others), the genus is firmly established for all fusiform and/or lamellate gastropods—usually with spiral ornamentation—from the southwestern Atlantic. Two of the species characterize the shallow waters along the Patagonian coast, i.e., *Trophon geversianus* and *T. plicatus*. Both are sympatric in the southern part of Argentina; however only *T. geversianus* could be collected intertidally as far North as Buenos Aires province. All the other species are mostly subtidal. *Trophon* species, as far as it is known, are all predators, feeding on the mussel banks and barnacles that are fairly common along the coast of the southern part of South America.

Living in moderately deep waters are *Trophon acanthodes* Watson, 1882, and the recently rediscovered *T. clenchi* (Carcelles, 1953), a rare lamellose and spiny species originally assigned to the genus *Murex* (Pastorino, 2005). Both of them undoubtedly belong in *Trophon*. In addition, Houart (1991) and Pastorino (1999) described *Trophon mucrone* and *T. veronicae* from deep waters off South America. The two species were included in *Trophon* despite some minor but distinctive differences in radulae, protoconchs and penises. Recently Houart (2003) and Houart and Sellanes (2006) described new species from deep waters off Chile.

In this paper two new deep water species from the southwestern Atlantic are described and compared with the other related ones living around the region.

MATERIALS AND METHODS

Specimens of *T. columbarioides* new species studied herein were collected by one of us (FS) on board the Uruguayan R/V ALDEBARAN. The other specimens are from the 2002 cruise to Antarctica of the German R/V POLARSTERN. Additional material was collected by Uruguayan fishing boats. Dissections were performed on these ethanol-preserved specimens to study radulae and male reproductive system when it was available. Radulae were cleaned with commercial bleach and ultrasound, and observed using a Philips XL 30 scanning electron microscope (SEM) at the Museo Argentino de Ciencias Naturales (MACN). Critical point drying of the penises (when available) was prepared at the MACN. Radular terminology follows Kool (1993: fig. 6B). Shell photographs were taken using a digital camera. All images were digitally processed. The material is housed at the MACN and the Museo Nacional de Historia Natural y Antropología, Montevideo (MNHNM).

SYSTEMATICS

Class Gastropoda Cuvier, 1797
Order Neogastropoda Wenz, 1938
Family Muricidae Rafinesque, 1815
Subfamily Trophoninae Cossmann, 1903
Genus *Trophon* Montfort, 1810

Type Species: *Murex magellanicus* Gmelin, 1791. *Trophon geversianus* (Pallas, 1774) by original designation.

Trophon columbarioides new species
(Figures 1–11, 15–18)

Diagnosis: Shell very small, thin, fusiform, chalky; axial ornamentation of 30–35 regular axial lamellae growing along the entire whorl surface, attached to the shell, producing open, long, regularly spaced spines along periphery, pointing upwards. Siphonal canal very long.

Description: Shell small (up to 14 mm), slender, thin profile, chalky, white, somewhat bright; protoconch of two whorls, slightly globose, symmetrical; teleoconch of five oblique, shouldered whorls; spire height less than ¼ of total shell height. Spire angle about 40°; suture impressed; subsutural shelf well defined, oblique; aperture semicircular, interior chalky white; anterior siphonal canal very long (longer than aperture height), narrow, straight, open; outer lip sharp, rounded, inner lip adpressed. Axial ornamentation of 30–35 regular axial lamellae growing along the entire whorl surface, but attached to shell and producing open, long, regularly spaced spines along periphery (almost in the middle of the whorl), pointing adapically; last three whorls with ten lamellae each . A second obsolete series of spines appears to rise at the periphery of older specimens (Figure 11). Spiral ornamentation lacking. Growth lines present throughout shell.

Operculum subtriangular, nucleus terminal. External surface covered by concentric, irregular, growth lines. Inner surface attachment area reaching upper side or center, with horseshoe-shape scars (Figures 17–18).

Rachidian teeth of radula with thin, small central cusp; lateral cusps wider and larger than central cusp; denticle between central and lateral cusp rising from base. Base of rachidian tooth slightly curved. Lateral teeth with single, long cusps; attachment area thick (Figures 15–16).

Type Material: Holotype MACN-In 37380 (Figures 1–3, 7, 9–10) and two paratypes, MACN-In 37381 (Figures 4–6, 8) and MNHNM 15540 (Figure 11).

Type Locality: R/V ALDEBARAN cruise 2003/01, station 37, 37°43′ S, 55°00′ W, 209 m, October 26 2003, 5.3°C of bottom temperature, Piccard dredge; (holotype and one paratype); between 37°05′ S, 54°12′ W in 255 m and 37°02′ S, 54°02′ W in 382 m (one paratype).

Etymology: The general shell morphology reminds some species of the genus *Columbarium* (Caenogastropoda: Turbinellidae), to which it has no close relationship.

Distribution: Known only from three specimens from the type locality and vicinity.

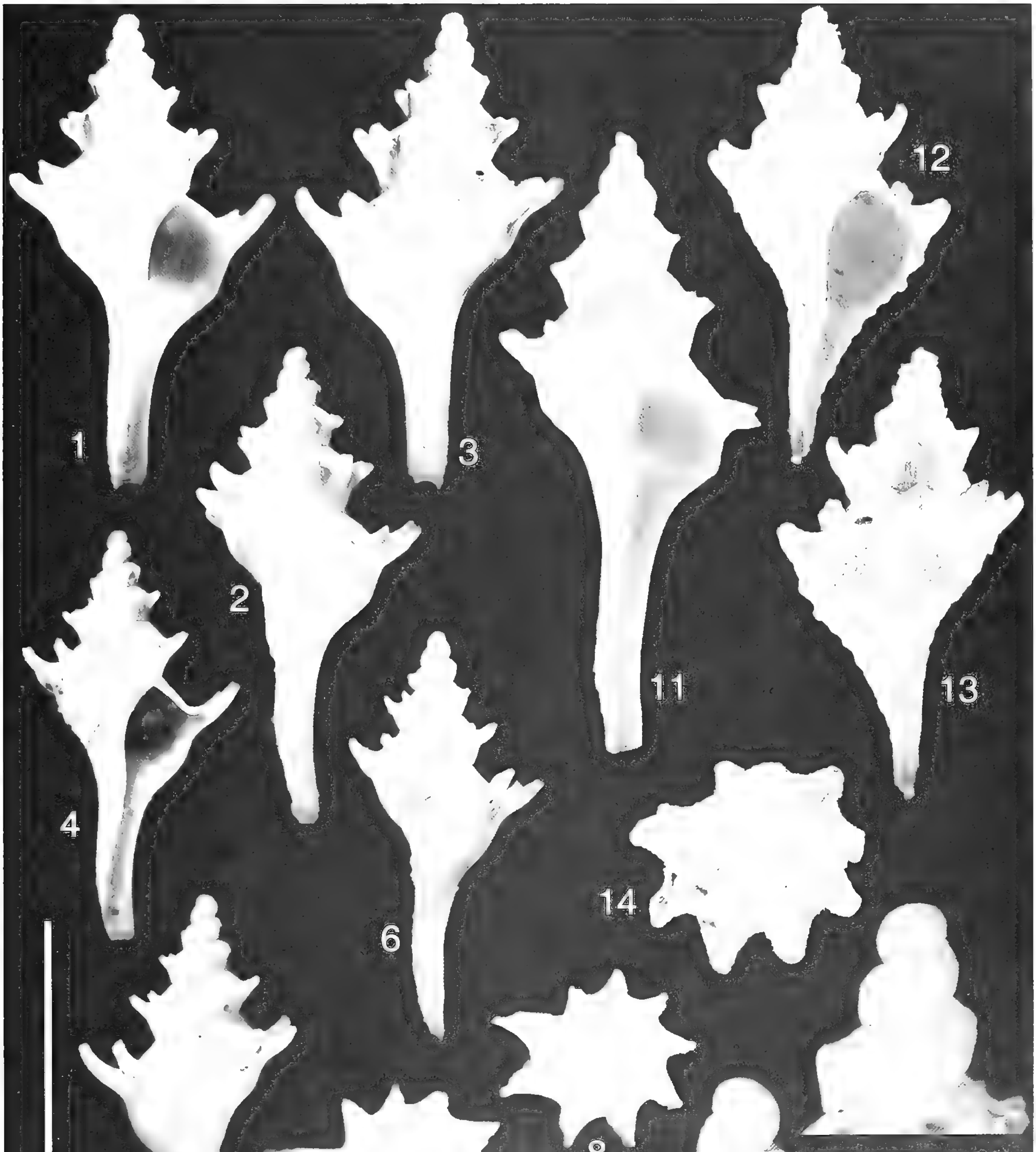
Remarks: At first glance the general morphology of the shell shows some similarities with juveniles of *Trophon acanthodes* Watson, 1882. However the typical spiral cords of the latter appear early in ontogeny (see Figures 12–13) and are completely absent in the new species. In addition both species have clear radular differences (see Pastorino, 2005:69). In addition, *T. plicatus* and *T. clenchi* are comparable species. The latter has unmistakable early developed spiral ornamentation; the former has complete lamellae and a shorter siphonal canal, besides radular differences.

Despite the geographic distance separating them, *Trophon scolopax* and *T. septus* described by Watson (1882) are comparable species. They live around Kerguelen Is., in the southernmost Indian Ocean. As a main difference *Trophon columbarioides* new species has a higher spire and only one series of large and open spines pointing upwards, instead of the three series shown by *T. scolopax* or the triangular upturned ones of *T. septus*.

Trophon echinatus (Kiener, 1840), an extremely variable species (according to Bouchet and Warén, 1985: 141), from deep waters off Northeastern Atlantic and Mediterranean shows a remarkable shell similarity with *T. columbarioides* new species Despite this, we do not support phylogenetic affinities between these and we made the comparison just for showing the existence of specific contrasting differences, particularly at radular level. As far as we can see in the material available there are no signs of spiral cords in the new species which are common in the deeper specimens of the northern one. However, some porcellaneous (not chalky) smooth specimens are in fact comparable. All morphs of *T. echinatus* have a shorter protoconch. Some grown specimens of *T. columbarioides* shows the apparently presence of a second rows of spines while *T. echinatus* has only one. In addition, the radulae (illustrated by Bouchet and Warén, 1985 figs. 333, 335, 336) shows a pair of almost obsolete intermediate denticles between the lateral cusps while in *T. columbarioides* new species they are slightly smaller than the central and lateral cusps. The base of the rachidian is sinuous in *T. echinatus* and somewhat straight in the new species. The intermediate denticles of the rachidian teeth rise from the internal side of the lateral cusps in a way that is typical of the southwestern Atlantic *Trophon* species. The attached portion of the marginal teeth are also different.

Houart (2001) considered *T. echinatus* as belonging in to the genus *Pagodula* Monterosato, 1884 despite the differences that Bouchet and Warén (1985) pointed out with the protoconch of the type species of *Pagodula*: the Pleistocene species *Murex vaginatus* Cristofori and Jan, 1832.

Figures 1–11. *Trophon columbarioides* new species. **1–3.** Holotype, MACN-In 37380, R/V ALDEBARAN cruise 2003/01, station 37, 37°43′ S, 55°00′ W in 209 m. **4–6.** Paratype, MACN-In 37381. Same locality as holotype. **7.** Apical view of the holotype. **8.** Apical view of the paratype. **9–10.** Protoconch of the holotype, scale bar = 1 mm. **11.** Paratype, MNHNM 15540, between 37°05′ S, 54°12′ W in 255 m and 37°02′ S, 54°02′ W in 382 m. **12–14.** *Trophon acanthodes* Watson, 1882, MACN-In 25165-2, 37°35′ S, 54°55′ W, 192 m. Scale bar = 1 cm for all figures except 9–10.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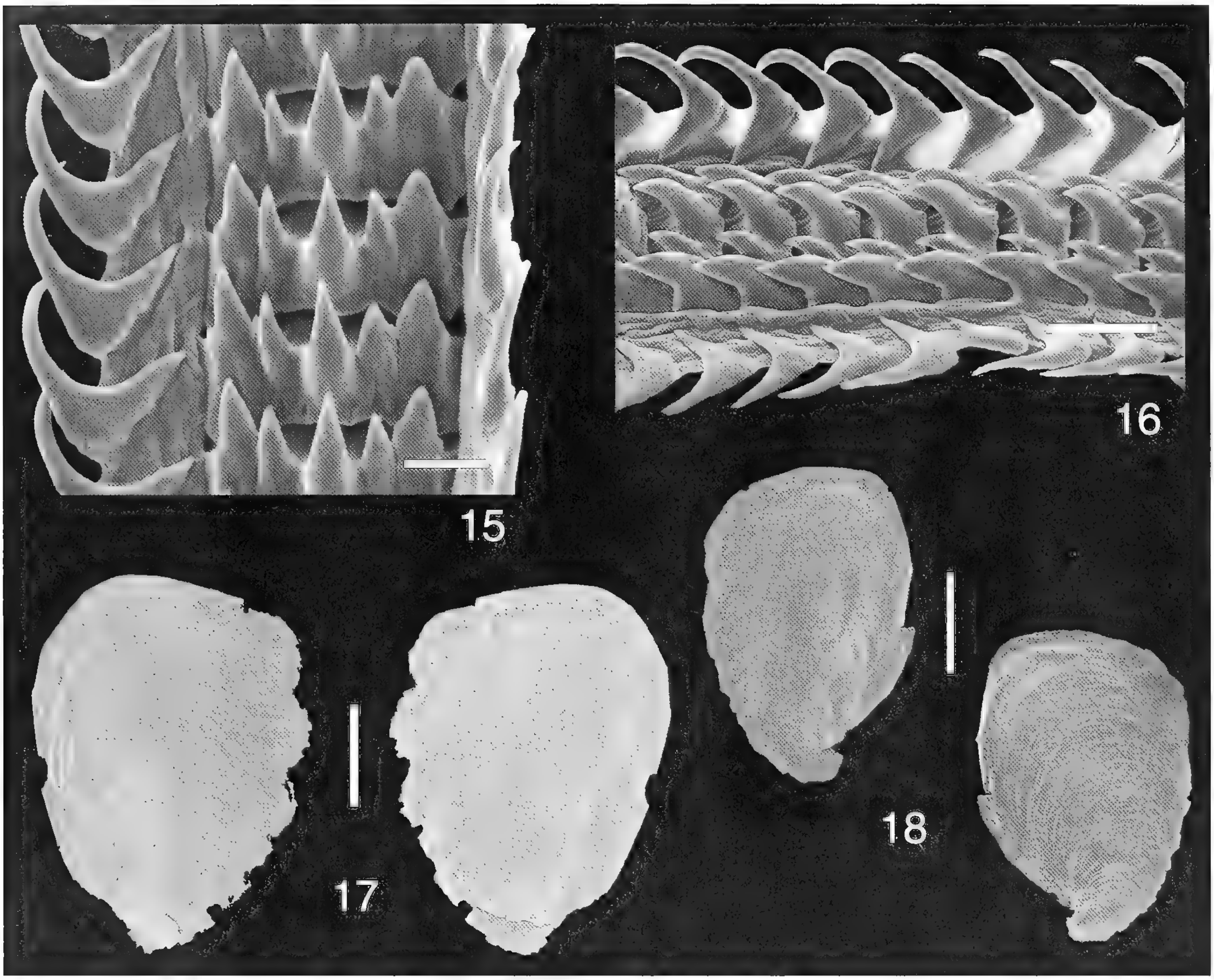


Figures 15–18. *Trophon columbarioides* new species. **15.** Radula frontal view, scale bar = 10 μm. **16.** Radula lateral view, scale bar= 20 μm. **17.** Operculum of the holotype and, **18.** Paratype in figs. 4–6. Scale bars= 1 mm.

Unfortunately both dissected specimens of the new species here described were females so nothing can be said about the morphology of the penises.

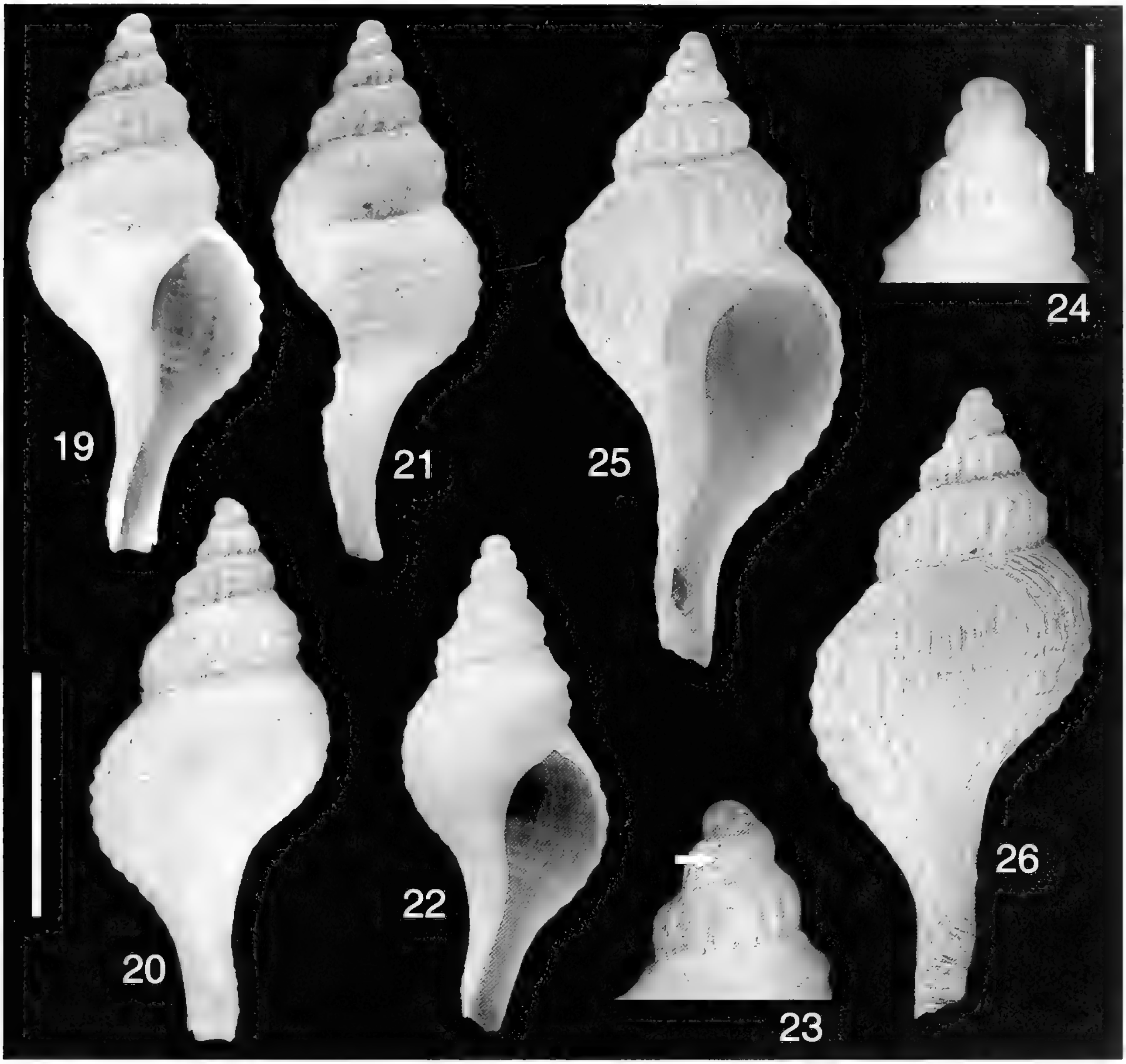
Trophon fasciolarioides new species
(Figures 19–31)

Diagnosis: shell very small, thin, translucid or chalky; very weakly developed axial ornamentation of regular, very low, varices attached to the shell. Spiral ornamentation of 2, 3 and 8 or 9 spiral rounded cords in the second, third and last whorl respectively; cords of similar width; intersection of spiral cords with axial varices conveying a slightly cancellate appearance to shell surface

Description: shell small (up to 12 mm), slender, thin profile, translucid white or chalky; protoconch of 2 whorls, symmetrical; teleoconch of 4½ tabular whorls; spire height less than ⅓ of total shell height. Spire angle about 45°; suture impressed, subsutural shelf very oblique; aperture suboval; anterior siphonal canal long but never longer than aperture height, slightly curved adaxially, open; outer lip sharp, rounded, inner lip adpressed. Axial ornamentation of poorly developed varices, regular, very low, attached to the shell, growing along the entire whorl surface except the siphonal canal. Spiral ornamentation of 2, 3 and 8 or 9 spiral rounded cords in the second, third and last whorl respectively; cords of similar width; intersection of spiral cords with axial varices conveying a slightly cancellate appearance to shell surface; growth lines present throughout shell, becoming scaly at intersection with spiral cords.

Operculum suboval, nucleus terminal. External surface covered by concentric, irregular, extremely thin growth lines. Inner surface attachment area reaching upper side or center, with horseshoe-shaped scars (Figure 31).

Rachidian teeth of radula with thin central cusp, higher than laterals; denticle between central and lateral



Figures 19–26. *Trophon fasciolarioides* new species. **19–21.** Holotype MACN-IN 37382, Banco Burwood, Polarstern St. 150, between 54°30.22′ S, 56°08.58′ W in 286 m and 54°29.64′ S 56°08.09′ W in 292 m. **22.** Paratype MACN-IN 37383, same locality as holotype. **23–24.** Protoconch of the paratype of figure 22, arrow head transition to teleoconch, scale bar = 1 mm. **25–26.** Paratype MACN-In 37384, off Bahía Blanca ca. 1000 m depth. Scale bar = 5 mm for all figures except 23 and 24.

cusp thin and long, rising from the base. Base of rachidian tooth curved. Marginal area with single cusp. Lateral teeth with single, long cusps; attachment area thick (Figures 27–29).

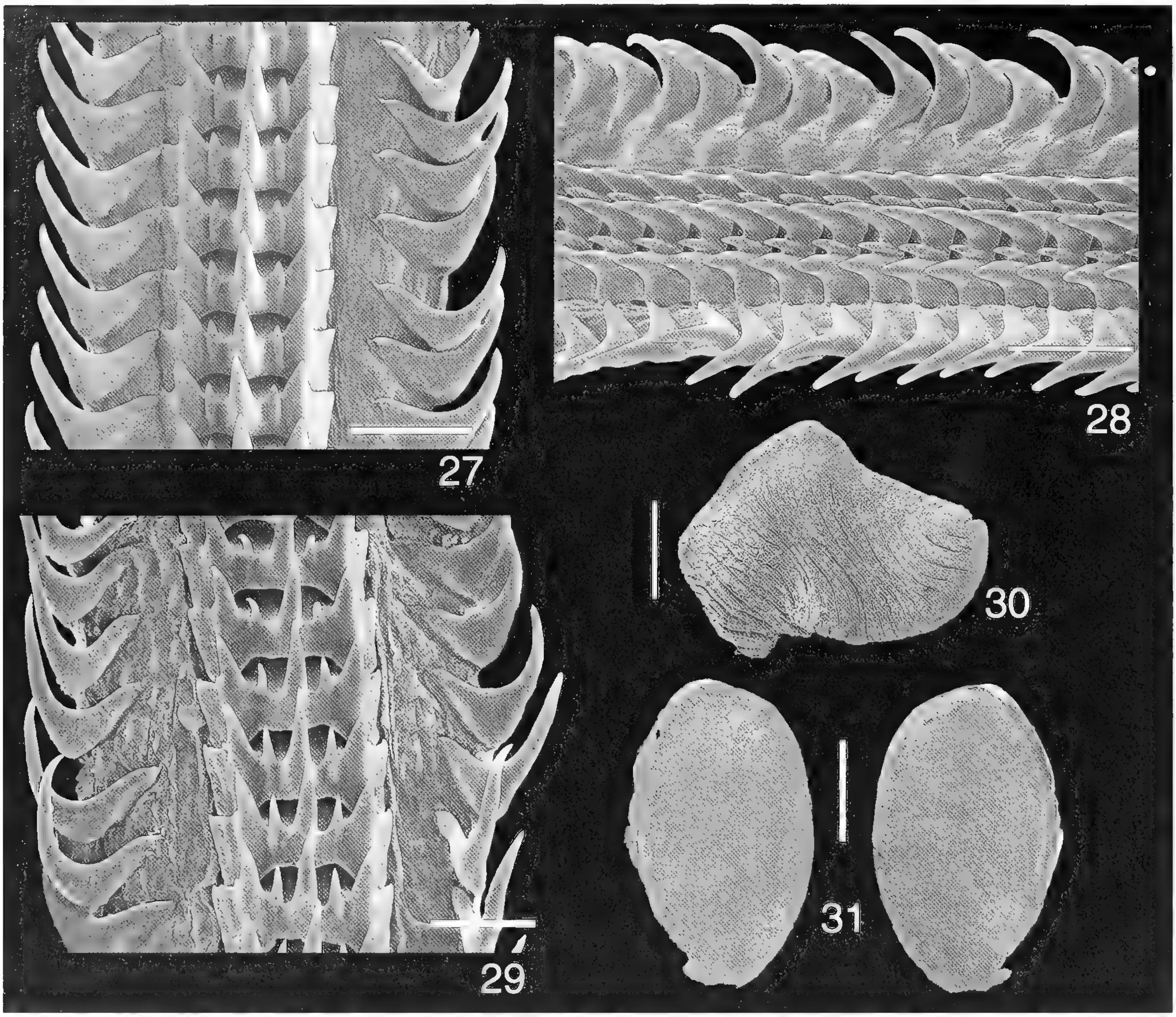
The penis shows an unusual morphology among the Patagonian species of the genus: it is wide, slightly curved and laterally flattened with a small slit at the tip (Figure 30).

Type Material: Holotype MACN-IN 37382 and two paratypes MACN-IN 37383 and MACN-In 37384.

Type Locality: Banco Burwood, Polarstern station 150, 6 Apr. 2002, AGT net, between 54°30.22′ S, 56°08.58′ W in 286 m and 54°29.64′ S, 56°08.09′ W in 292 m.

Etymology: The general shell morphology reminds some species of the genus *Fasciolaria* (Caenogastropoda: Fasciolariidae).

Distribution: known from type locality and approximately off Bahía Blanca in ca. 1,000 m depth (MACN-In 37384).



Figures 27–31. *Trophon fasciolarioides* new species. **27.** Radula of a paratype, MACN-In 37384, frontal view, scale bar = 40 μm. **28.** Lateral view of the same radula as 27, scale bar = 50 μm. **29.** Radula of the paratype MACN-In 37383, scale bar = 20 μm. **30.** Critical point dry of the penis, scale bar = 500 μm. **31.** Two views of the operculum of the paratype of figures 25–26, scale bar = 1 mm.

Remarks: The morphology of the shell and the radula match some of the Patagonian and Antarctic species of the genus *Trophon*. From the first group, *T. ohlini* Strebel, 1904, a rare species from the Magellanic area, has a similar profile. However, its distinctive protoconch points out a clear difference. In addition, the morphology of the penis is far from the typical Patagonian representatives of the genus. *Trophon emilyae* Pastorino, 2002, *T. declinans* Watson, 1882, and *T. cuspidarioides* Powell, 1951, are comparable Antarctic species (Pastorino, 2002a). The first two species differ from the new species in having well developed axial sculpture only. Also *T* *cuspidarioides* has 5½ whorls including the protoconch and five blunt spiral cords in the body whorl, while the new species has a larger spire and 6½ whorls, and 8 or 9 rounded and well defined cords in the last whorl. The axial ornamentation in the new species is very irregular but higher in number than the 25 axials present in *T. cuspidarioides*.

DISCUSSION

In previous papers two groups of species belonging in the genus *Trophon*—i.e., from South America and Antarctica—were pointed out. The main differences between these two groups are several radular and anatomical features (Pastorino, 2002b, 2005). The shell morphology of the two new species described herein agrees with that of *Trophon* living off the South American coast. However,

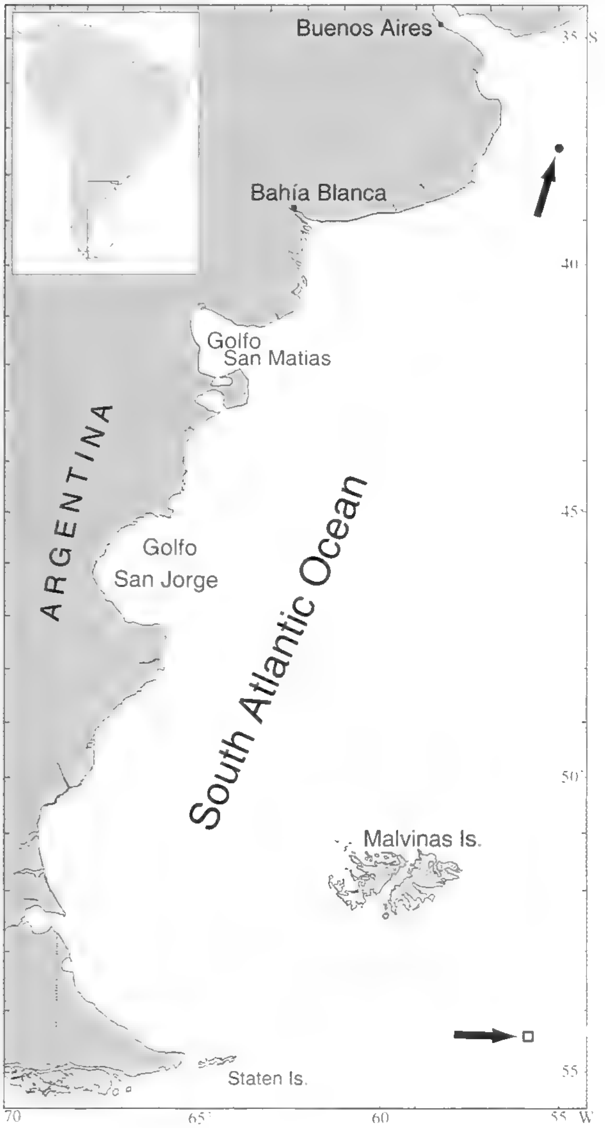


Figure 32. Map showing the type localities of *Trophon columbarioides* new species ● (filled circle) and *Trophon fasciolarioides* new species ☐ (blank square).

the radula has some features found in the Antarctic representatives of the genus—albeit the taxonomic status of the Antarctic species still needs confirmation. Like in the Antarctic group of species, the central cusp of the rachidian teeth is shorter and thinner than the laterals, the internal denticle rise from the base of the rachidian instead of the upper third of the internal side of the lateral cusp, and the lateral teeth have a wide attachment area.

The geographic ranges of species of these two groups do not overlap. Therefore, the morphological features seem to be clearly separated geographically too. However, in the species described herein, this seems not to be the case. While there is no geographic overlapping of species, the morphological features that characterize the Antarctic group do appear in these two new Patagonian species. Contrarily, this does not occur in the case of Patagonian species, the morphological features of which are restricted to South America. Moreover, they are better developed in species from the Magellanic among those described from southern South America (see Pastorino, 2005).

Recently, Houart (2003) introduced three new species he assigned to *Trophon* from off Chile: *T. ceciliae*; *T. condei* and *T. vangoethemi*. The morphology of the radula, only known for the last two species, together with that of *T. mucrone* Houart, 1991, *T. veronicae* Pastorino, 1999 and both new species described here, is that of the Antarctic group, despite the geographic distance separating them. All mentioned species were collected from more than 300 m depth and in most cases they reach more than 1,000 m (see Table 1). Most of the Patagonian species of *Trophon* were collected alive from the intertidal zone to about 300 m depth. Exceptions are some specimens of *T. acanthodes*, *T. clenchi*, and *T. bahamondei* that come from deeper areas. However, there is no Antarctic species—or with their characteristic radular and anatomical features—that live at shallower depths or closer to the continent. Both new species described here were collected from about 300 m depth, which is the shallowest for a *Trophon* with Antarctic features at South American latitudes.

Generic assignment in the whole Trophoninae group is actually under revision. The concept of the genus *Trophon* sensu stricto is easy to apply to the shelf species. However, when deeper species are studied, the presence of several features in common among the shallower species appear somewhat contradictory. Nevertheless, we think that biogeographic boundaries are hard to surpass for species without free larvae as both new species appears to be according to the shape and whorl number of the protoconch. Contrasting historical biogeographic processes must be considered when suggesting affinities between species and therefore comparison with species living far away from the Southwestern Atlantic area can be considered an empty exercise. Some exempli are cases like *T. columbarioides* new species—*T. echinatus* which have very few characters that clearly split both species. In

Table 1. Recently described South American species of *Trophon*.

	Depth (m)	Type locality
T. condei Houart, 2003	900–1350	Ancud, Chile
T. ceciliae Houart, 2003	434–1000, 1300	Antofagasta, Chile
T. vangoethemi Houart, 2003	About 350	Itata, North of Concepcíon, Chile
T. mucrone Houart, 1991	790–1575	Off Río de Janeiro, Brazil
T. veronicae Pastorino, 1999	298–1272	Subantarctic
T. columbarioides new species	209–382	37°43′S, 55°00′W
T. fasciolarioides new species	286–292	Burwood bank

the future molecular characters could add to the understanding of the evolution of morphological features in this group.

ACKNOWLEDGMENTS

We are grateful to L. Paesch and R. Bird (DINARA) for facilities in the collecting of *Trophon* specimens, as well as to J. L. Viggiano and H. Rácz-Lorenz (Montevideo) for the material provided. We thank Miguel Griffin (UNLPam) who helped to improve the English version of the manuscript. R. Houart (Belgium) reviewed this paper; his comments and discussions undoubtedly contributed to enhance the original version despite disagreement on some points. This contribution was supported in part by the project PICT No. 03-14419 from the National Agency for Scientific and Technical Promotion, Argentina. We acknowledge funding by the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) of Argentina, which sponsors the research of G.P.

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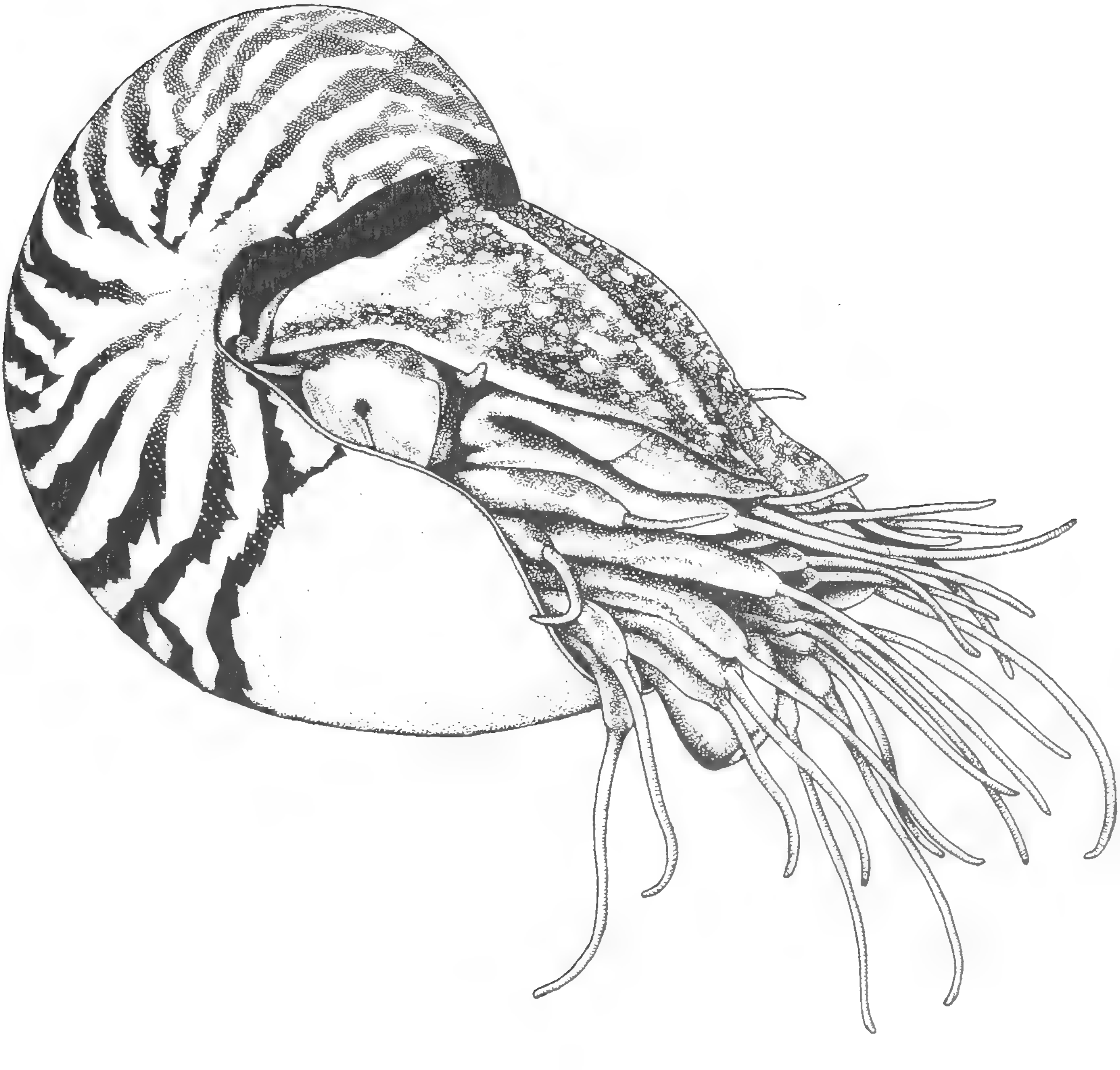
THE NAUTILUS

Volume 122, Number 3
September 26, 2008
ISSN 0028-1344

A quarterly devoted to malacology.



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THE NAUTILUS (ISSN 0028-1344) is published quarterly by The Bailey-Matthews Shell Museum, 3075 Sanibel-Captiva Road, Sanibel, FL 33975.

Periodicals postage paid at Sanibel, FL, and additional mailing offices.

POSTMASTER: Send address changes to: THE NAUTILUS
P.O. Box 1580
Sanibel, FL 33957

THE NAUTILUS

Volume 122, Number 3
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Cretaceous trichotropid gastropods from the Pacific slope of North America: Possible pathways to calyptraeid morphology

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ABSTRACT

Late Cretaceous gastropods belonging to genus *Lysis* Gabb, 1864, from the Pacific slope of North America, bridge the morphologic gap between turbiniform trichotropids and limpet-like calyptraeids. Development of the depressed and broadened inner lip/columella of *Lysis* resulted in a larger aperture that allowed more space for the foot to grasp a hard substrate. Pacific slope species of *Lysis* are represented by five species that collectively span an interval from late Coniacian to late Maastrichtian. They stem from two lineages of the trichotropine genus *Ariadnaria* Habe, 1961. The first lineage, which includes *Ariadnaria ainikta* new species of late Albian to Cenomanian age, *Ariadnaria stibara* new species of Cenomanian age, and *Ariadnaria obstricta* (White, 1889) of late Coniacian? and Santonian age, gave rise to the *Lysis duplicosta* group of neritiform to haliotiform, coarse-ribbed *Lysis*, including *Lysis mickeyi* new species (earliest *Lysis* in the world), *Lysis duplicosta* Gabb, 1864, *Lysis jalamaca* new species, and *Lysis lomaensis* new species. The second lineage of *Ariadnaria* consists of the Turonian *Ariadnaria aldersoni* new species, which gave rise to the *Lysis suciensis* (Whiteaves, 1879) group. Morphologically, this group, which show crepiduliform and fine ribbed shells, appears likely to be a stem group from which Cenozoic *Crepidula*-like genera evolved. *Garzasia* new genus, which ranges from late Campanian or early Maastrichtian age to the mid Maastrichtian, evolved from the *Lysis duplicosta* group and includes *Garzasia intermedia* (Cooper, 1894) and *Garzasia diabla* new species. The very broad, depressed spiraling inner lip of *Garzasia* is suggestive of *Calyptraea* Lamarck, 1799. We propose placement of *Lysis* and *Garzasia* in Lysinae new subfamily of the Trichotropidae. In addition to their occurrence along the Pacific Slope of North America, *Lysis* or *Lysis*-like gastropods are known from middle Santonian to lower Campanian strata in South Africa, upper Campanian in the Congo, and Maastrichtian strata in Mozambique and Japan.

Additional Keywords: Trichotropidae, Lysinae, Calyptraeidae, evolution, paleogeographical occurrence

INTRODUCTION

This study deals with the fossil record of the extinct genus *Lysis* Gabb, 1864, a small group of enigmatic gastropods which has received little or no study regarding its ancestry, point of origin in terms of time and geographic locale, and evolutionary history. Specimens have been found in shallow-marine Cretaceous deposits from southern Vancouver Island and neighboring Gulf Islands, British Columbia, Canada to northern Baja California, Mexico (Figure 1) and, although *Lysis*-like gastropods have been reported at a few locales in the world, its familial placement has been uncertain. This study brings new information about all of these items.

Material for this study included type specimens, additional collections from their type localities, and specimens of Late Cretaceous age (Coniacian to Maastrichtian) from previously unreported-upon localities. Figure 1 provides an index to areas which yielded specimens used in this study.

During the study we discovered undescribed species of the trichotropine genus *Ariadnaria* Habe, 1961, which appear to have given rise to two groups of *Lysis*, a neritiform coarse-ribbed group and a crepiduliform fine-ribbed group. As will be discussed under "Evolutionary Implications," we propose that the neritiform group evolved into *Garzasia* new genus, which appears to be a precursor to calyptraeiform genera.

A total of three genera (one of them new) and 11 species (seven of them new) make up this study. The taxa are: four species of *Ariadnaria* (three of them new), five species of *Lysis* (three of them new), and two species of *Garzasia* (one of them new). The ranges in time of all these species, as well as two recognizable groups of *Lysis*, are plotted on Figure 2. The *Lysis duplicosta* group consists of four species, spanning a total interval of late Coniacian to late Maastrichtian. This group was also the most geographically widespread, with specimens collected from British Columbia to Baja California. The *Lysis suciensis* group is known only from the Campanian to possibly early Maastrichtian, with specimens known from British Columbia to Baja California Sur. *Lysis* persisted for a total of approximately 18 million years in the study area.

The specimens studied here are mainly from fine-

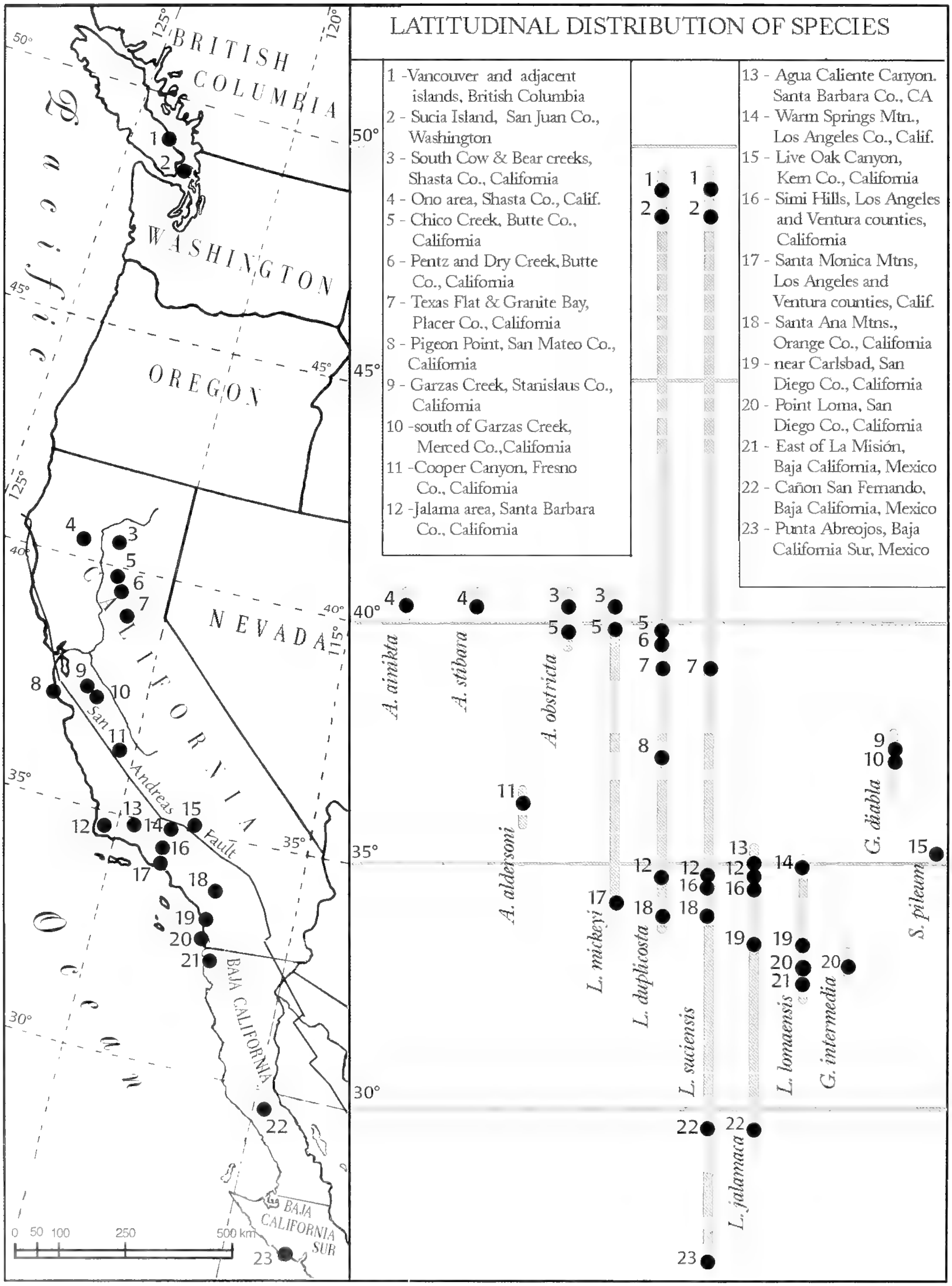


Figure 1. Index map of collecting localities

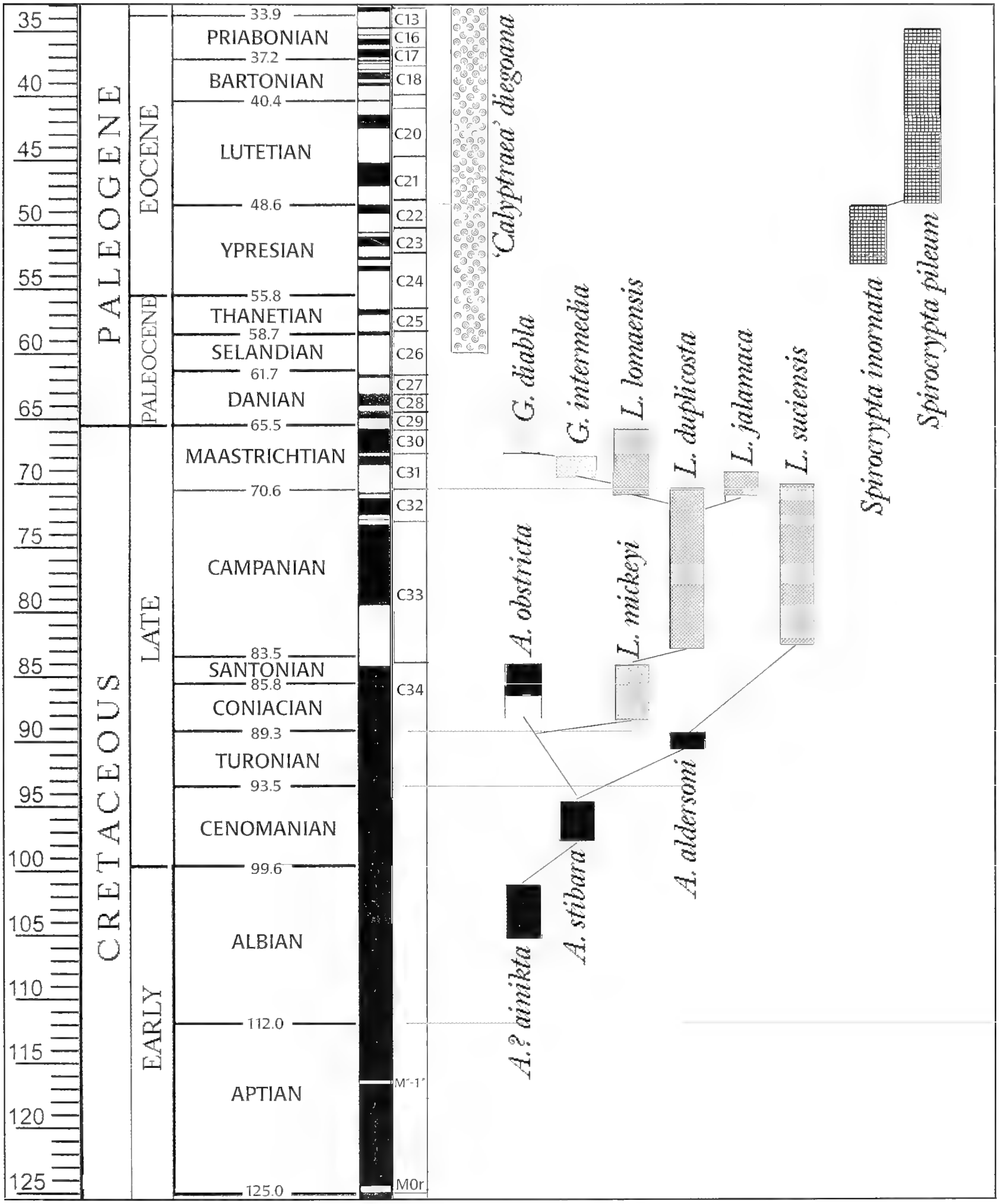


Figure 2. Age ranges of species of *Ariadnaria*, *Lysis*, *Garzasia*, *Calyptraea*, and *Crepidula* discussed in text. Lines connecting the species indicate inferred descent based on morphologic simiarity. *Lysis duplicosta* gave rise to two species one of which, *L. lomaensis*, produced proto-calyptraeform *Garzasia* and the other, *L. jalamaca*, is crepiduliform. An additional crepiduliform line was founded by *L. suciensis*. No known intermediate forms connect these Cretaceous calyptraeiform and crepiduliform gastropods to Tertiary species. The earliest known Pacific Slope calyptraeid, '*C.*' *diegoana* lacks the strong ribbing of *Garzasia*, but crepiduliform *Spirocrypta pileum* differs largely from *L. suciensis* in its small size. Time scale after Gradstein et al. (2004).

grained argillaceous sandstone or siltstone that constitute shelfal deposits that accumulated at depths near or just below wave base.

Specimens are low in number and almost always incomplete. Protoconchs are rarely preserved, the larval shell is in part missing, its shape partially represented by its inner cast in all available specimens. Apertures are usually missing their anteriormost area. Adhering matrix, commonly consisting of well-cemented sandstone usually plugs the aperture, thereby necessitating careful cleaning.

As will be discussed under "Evolutionary Implications," the shape of *Lysis*, with the exception of *L. mickeyi* new species, approaches that of *Crepidula*, resulting from flattening of the aperture, development of a broad shelf, and lateral coiling of the spire. The crepiduliform shape, as well as the *Calyptraea*-like shape of *Garzasia*, pose problems for terminology used for describing certain figures of specimens, as well as for describing certain shell dimensions. For some specimens, a full view of the aperture could only be depicted by having the the shell tipped out of the plane of its axis. The true height of these shells, therefore, is not shown; hence, the "vertical dimension" of the view is given instead, and perpendicular to it is the "horizontal dimension." In most cases, the abapertural view is in the plane of the shell axis; hence, the terms "height" and "diameter" apply.

Abbreviations used in the text are: ANSP: Academy of Natural Sciences of Philadelphia; CAS: California Academy of Sciences, San Francisco; CGS: Geological Survey of Canada, Ottawa; CIT: California Institute of Technology, Pasadena (collections now housed at LACMIP); CSMB: California State Mining Bureau (specimen at CAS); IGM: Instituto de Geología, Universidad Nacional Autónoma de México; LACMIP: Natural History Museum of Los Angeles County; SDNHM: San Diego Natural History Museum; UCLA: University of California, Los Angeles (collections now at LACMIP); UCMP: University of California, Berkeley, Museum of Paleontology; USGS: United States Geological Survey, Menlo Park (collections now housed at UCMP); USNM: National Museum of Natural History, Smithsonian Institution.

PALEOBIOGEOGRAPHIC DISTRIBUTION OF *ARIADNARIA*, *LYSIS*, AND *GARZASIA*

Ariadnaria ranges from late Albian to Recent with its earliest appearance in Pacific slope deposits of North America, where it is found in strata ranging from late Albian to Santonian age. From Japan, Kase (1990) figured, as *Trichotropis*?, a possible *Ariadnaria* species of earliest Maastrichtian age.

Lysis ranges from the late Coniacian to late Maastrichtan, and that is also its range for the Pacific slope of North America. The genus apparently originated in California, with five species known from the Pacific slope of North America. Four additional probable species of *Lysis* are known elsewhere in the world. They are: *Lysis capensis* Rennie, 1930, from the middle Santonian to lower Campanian of South Africa (Kiel and Bandel, 2003); *Lysis congolensis* (Brébion, 1956) from upper Campanian of the Congo, Africa; *Lysis africana* (Cox, 1925) from the Maastrichtian (undifferentiated) of Mozambique; and *Lysis izumiensis* Kase, 1990, from the earliest Maastrichtian of Japan.

Rennie (1935) reported *Lysis caffra* Rennie, 1935, from the Upper Cretaceous near the eastern border of the Eastern Cape Province (Pondoland), southeast Africa, but its swollen naticiform shape with a very large, inflated body whorl and broad, non-depressed inner lip/columellar region, that appears to have a thin callus, are features not found in *Lysis*.

Garzasia ranges from late Campanian or early Maastrichtian to the mid Maastrichtian and is endemic to the Pacific slope of North America.

MODE OF LIFE OF *LYSIS*

Lysis has been found attached to a few specimens of large volutid gastropods. One specimen of *Longoconcha eumeka* Saul and Squires, 2008, from the Point Loma Formation near Carlsbad, California has two specimens of crepiduliform *Lysis jalamaca* new species on its shell, near the outer lip margin (Figure 34), as well as an attachment scar on the abapertural side of the shell. Specimens of *Lysis suciensis* from the Chatsworth Formation near Chatsworth, California, although not found in situ as are the younger Carlsbad specimens, have aperture shapes that could fit on the exterior of a specimen of *Volutoderma* Gabb, 1877. Indication of such an association is absent prior to middle Campanian. Whether the specimens of *Lysis* species were using dead shells as a substrate or had developed an association with living *Volutoderma* is undetermined.

Comparison to probable family members indicates that *Lysis* was a sedentary faculative ciliary feeder. Trichotropines, as well as calyptraeids, are ciliary feeders that live a sedentary life on hard substrates and are protandrous hermaphrodites among whom brooding their young is common (Graham, 1954; Yonge, 1962). These mode-of-life characteristics have historically been used to classify trichotropines as being close to calyptraeids.

SYSTEMATIC PALEONTOLOGY

Superfamily Calyptraeoidea Lamarck, 1809

Discussion: The taxonomy of calyptraeoids, as with most gastropods, was traditionally based on shell morphology and later modified by increasing anatomical knowledge. The inclusion of patelliform Capulidae Fleming, 1822, turbiniform Trichotropidae, and coiled limpet-shaped Calyptraeidae in the superfamily Calyptraeoidea (e.g., Thiele, 1929; Wenz, 1940), has provided calyptraeoids a considerable morphological range and a somewhat complicated classification history (Bandel and Riedel, 1994). In addition to the above three families, Bandel and Riedel (1994), included Hipponicidae Troschel, 1861, in Calyptraeoidea, but Collin (2003: 632) rejected hipponicids from a close relationship with calyptraeids. Ponder and Warén (1988) and Ponder (1998), equated family Capulidae with family Trichotropidae Gray, 1850, on anatomical grounds, reducing the included families to two. Capulids, as exemplified by *Capulus* Montfort, 1810, have limpet-shaped shells; trichotropids, as exemplified by *Trichotropis* Broderip and Sowerby, 1829, usually have coiled shells; and calyptraeids, as exemplified by *Calyptraea* Lamarck, 1799, *Crepidula* Lamarck, 1799, and *Crucibulum* Schumacher, 1817, have limpet-shaped shells with an internal shelf of variable shape.

In her analysis of calyptraeids, Collin (2003a, 2003b) utilized shell characters, anatomical characters, and molecular characters. Collin (2003a) argued that although the so-called echinospira larva of *Capulus* and of *Trichotropis* do not appear to be "true" echinospira, the thickened and elaborate larval shell of these two groups is clearly different from the simple larval shell of extant calyptraeids, and she (Collin, 2003a, 2003b, 2005) has continued to recognize the families Capulidae Fleming, 1822, Calyptraeidae, and Trichotropidae. Collin (2003a) mentioned that despite the detailed studies done on calyptraeids, their taxonomy remains contentious and uncertain. Because specimens studied here show no resemblance to capulids but do, in part, resemble trichotropids, and calyptraeids such as *Calyptraea* and *Crepidula*, we follow Collin in recognizing families Calyptraeidae and Trichotropidae.

Family Trichotropidae Gray, 1850
Subfamily Trichotropinae Gray, 1850

Description: Small to medium sized (usually 15 to 25 mm, but up to 40 mm in height), coiled, high-conic to broad, low-conic, or nearly cap-shaped; spiral sculpture usually better developed than collabral sculpture and represented by distinct cords and/or keels; umbilicus broadly open to slit-like or completely closed; aperture variable in shape, ranging from irregularly triangular and broadly oval to elongate-oval; some forms with more or less attenutated canal; operculum small, horny; radula taenioglossate; periostracum forming combs, bristles, spines usually in places of intersection of spiral and collabral sculpture (from Egorov and Alexeyev, 1998).

Discussion: Trichotropids provide the geologically oldest representatives of the three families Trichotropidae, Capulidae, and Calyptraeidae. We did not follow Ponder and Warén (1988), Ponder (1998), and Bouchet and Rocroi (2005) in placing Trichotropidae in Capulidae because trichotropids, such as the high spired *Ariadnaria* spp. discussed herein, differ distinctly from cap–shaped capulids. Collin (2003b) referred to trichotropids plus capulids as the closest outgroup to calyptraeids, suggesting that she recognized these three as separate families. At present the geologic record finds trichotropids occurring earlier than capulids and also earlier than calyptraeids, and we suggest that based on species described herein, trichotropid-like gastropods gave rise to calyptraeids and that trichotropid specimens reported upon herein demonstrate a progressive development toward either a crepiduliform or a calyptraeiform shell.

Atresius Gabb, 1869, of Early Cretaceous (Valanginien to Hauterivian) age is the earliest trichotropine recognized by Wenz (1940), but its sole named species *A. liratus* Gabb, 1869, is a prominent constituent of chemosynthetic paleocommunities in northern California and probably not a trichotropid. *Lirpsa* Stephenson, 1952, of Cenomanian age from the Woodbine Formation of Texas may be the earliest previously known trichotropine. The earliest reported cap-shaped capulid is *Capulus verus* (Böhm, 1885) of Late Cretaceous (early Campanian) age from Aachen, Germany.

Genus *Ariadnaria* Habe, 1961
[= *Ariadna* Fischer, 1864; *non* Audouin, 1826].

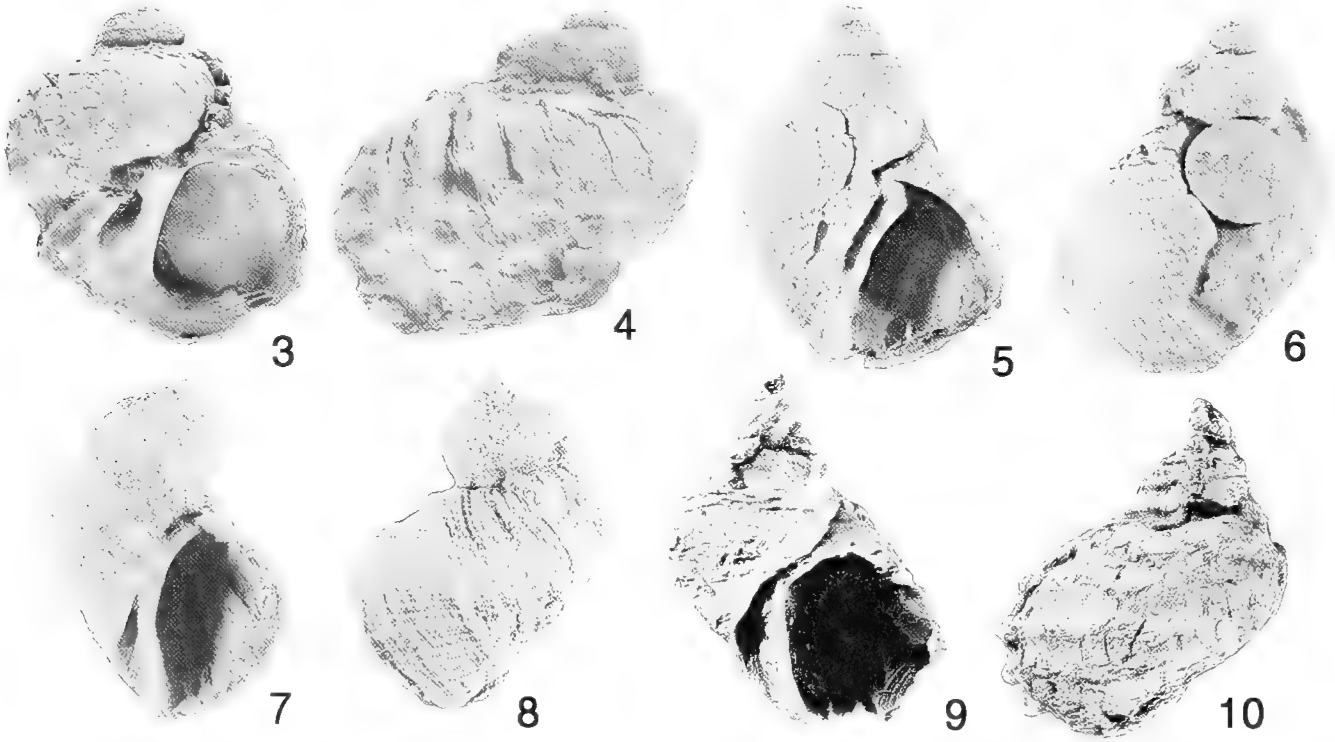
Type Species: *Trichotropis borealis* Broderip and Sowerby, 1829, by monotypy; boreal Arctic circumpolar (Egorov and Alexeyev, 1998) and cool temperate seas: northern North Atlantic south to Northumbria and all Scottish coasts (Fretter and Graham, 1962) and Massachusetts Bay (Emerson and Jacobson, 1976); the Bering Sea and north Pacific south to British Columbia (LACM collection, Forrester Island).

Description: Shell turbiniform (oval-conic) with raised spire; spiral sculpture well developed and consisting of raised cords separated by interspaces of variable width; collabral sculpture consisting of raised growth lines; aperture wide; inner lip slightly concave; canal short and straight; umbilicus slit-like; operculum thin; periostracum forming long, closely spaced bristles on spiral ribs.

Discussion: No prior records of *Ariadnaria* as a fossil were found by us. *Ariadnaria* differs from *Trichotropis* Broderip and Sowerby, 1829, by having an umbilicus. *Turbinopsis* Conrad, 1860, a turbiniform trichotropid of late Campanian or early Maastrichtian age from Mississippi, differs from *Ariadnaria* by having a wider umbilicus (profound according to Conrad, 1860), a last whorl that is more inflated and is tabulate, and having a very oblique fold near the basal margin of the columella.

Ariadnaria ainikta new species (Figures 3–4)

Diagnosis: Medium-size *Ariadnaria* with sturdy shell, rounded whorls, strong sculpture with nine spiral cords widely spaced; collabral sculpture thickly foliate; umbili-



Figures 3–10. *Ariadnaria* species. Specimens coated with ammonium chloride. **3–4.** *Ariadnaria ainikta* new species, holotype CAS 61794.00, CAS loc. 61794, height 20 mm, diameter 17 mm. **3.** Apertural view. **4.** Abapertural view. **5–6.** *Ariadnaria stibara* new species, holotype LACMIP 13371, LACMIP loc. 23464, height 19 mm, diameter 13.5 mm. **5.** Apertural view. **6.** Abapertural view. **7–8.** *Ariadnaria aldersoni*, holotype LACMIP 13372, LACMIP loc. 26370, height 12 mm, diameter 8.5 mm. **7.** Apertural view. **8.** Abapertural view. **9–10.** *Ariadnaria obstricta* (White, 1889), hypotype LACMIP 13373, LACMIP loc. 28717, height 21 mm, diameter 15 mm. **9.** Apertural view. **10.** Abapertural view.

cus elliptical; inner lip broad, expanded anterior and posterior to umbilicus.

Description: Shell medium (approximately 22 mm height), sturdy, turbiniform, spire moderately high, approximately 36% of total shell height; apical angle 110°; most of protoconch missing, remanent low and apparently smooth; teleoconch whorls three, whorls well rounded and enlarging very rapidly; suture appressed but appearing channeled; umbilicus open, deep, and elliptical; growth line prosocline; spiral sculpture consisting of regularly spaced and equally narrow cords; four cords on penultimate whorl; nine cords on last whorl, becoming stronger and more raised near umbilicus; spiral cords on last whorl widely spaced and occasionally with spiral thread in interspaces, especially anterior of periphery; collabral sculpture consisting of thickly foliate ridges coincident with growth checks, especially near outer lip; aperture D-shaped; inner lip broad, expanded anteriorly and posteriorly of umbilicus; abapertural edge of inner lip delineated by sharp ridge; basal lip broadened.

Holotype: CASG 61794.00, height 20 mm, diameter 17 mm, spire height 7.5 mm.

Type Locality: CASG loc. 61794 [=CASG loc. 1346-A].

Distribution: Basal Bald Hills Member of the Budden Canyon Formation, (area 4) Ono area, Shasta Co., California.

Geologic Age: Late Albian.

Discussion: Only the holotype is known. It evidently had a very foliate, thick shell. What remains is riddled with endobiont borings. Remnants of the protoconch are present, there is no clear evidence of an anterior sinus to the aperture, and the shell does not appear to have been nacreous.

The new species most resembles the trichotropid *Turbinopsis hilgardi* Conrad, 1860 (Conrad, 1860: 289, pl. 46, fig. 29; Sohl, 1960: 91, pl. 10, figs. 17, 18) from the upper Campanian/lower Maastrichtian Ripley Formation of Tippah Co., Mississippi, except *A. ainikta* has a smaller umbilicus and narrower cords with much wider interspaces. Additionally, the inner lip of *A. ainikta* is more expanded both anterior and posterior to the umbilicus.

Ariadnaria ainikta and *A. stibara* new species are similar in that there is no ridge separating the umbilicus from the inner lip. *Ariadnaria ainikta* differs from *A. stibara* by having a less elongate shell, wider penultimate whorl, stronger spiral cords with much wider interspaces, a shorter umbilicus that is oval rather than slit-like, foliate collabral sculpture, and no parietal swelling on the inner lip. *Ariadnaria ainikta* differs from *A. aldersoni* new species by being larger, having much stronger spiral cords with much wider interspaces, a well rounded last whorl (not angulate), shorter umbilicus that is oval rather than slit-like, and no ridge separating the umbilicus from the inner lip. *Ariadnaria ainikta* differs from *A. obstricta* (White, 1889) by having a lower spire, wider penultimate whorl, round last whorl (not angulate) more spiral cords, foliate collabral sculpture, shorter umbilicus that is oval rather than slit-like, and no ridge separating the umbilicus from the inner lip. The strong spiral ribbing of *A. ainikta* resembles that of *A. obstricta*.

Etymology: *Ainiktos*, Greek, meaning: baffling, obscure, or enigmatic.

Ariadnaria stibara new species
(Figures 5–6)

Diagnosis: A medium size sturdy *Ariadnaria* with rounded whorls, medium strong sculpture with many spiral cords moderately closely spaced; collabral sculpture very fine and lattice-like on spire whorls; umbilicus chink-like; inner lip with low parietal swelling.

Description: Shell medium small (height approximately 20 mm), sturdy, turbiniform, somewhat elongate, spire high and approximately 50% of total shell height; apical angle approximately 67°; protoconch not present; teleoconch whorls four, whorls well rounded and enlarging rapidly; last whorl tapering anteriorly; suture appressed, appearing channeled, and rapidly descending near aperture; umbilicus narrow, chink-like and present only adjacent to medial and posterior parts of inner lip; growth line prosocline, with several irregularly spaced growth checks near outer lip; spiral sculpture consisting of numerous fine subequal rounded cords; approximately ten closely spaced cords on penultimate whorl with interspaces of nearly equal width; approximately 18 cords on last whorl with interspaces slightly wider than cords; cords strongest, most widely spaced, and occasionally with spiral thread in interspaces on medial and anterior portions of last whorl; collabral sculpture consisting of thin, raised growth lines, forming nearly microscopic lattice-like pattern on spire whorls; aperture D-shaped, moderately large, oblique, narrowed at posterior end by low parietal swelling; inner lip broad, somewhat excavated (concave) medially and flattened anteriorly; abapertural edge of inner lip delineated by low but distinct ridge; basal lip broadened.

Holotype: Holotype LACMIP 13371, height 19 mm (incomplete), diameter 13.5 mm, spire height 9 mm.

Type Locality: LACMIP loc. 23464 is also type locality of *Turrilites dilleri* Murphy and Rodda, 1960.

Distribution: Bald Hills Member (unit IV of Matsumoto, 1960) of the Budden Canyon Formation, (area 4) Ono area, Shasta Co., California.

Geologic Age: Middle Cenomanian.

Discussion: Only the holotype is known, and it lacks the protoconch and the anterior end of the teleoconch. Whether or not an anterior siphonal notch was present is unknown, but the shape of the last whorl suggests that at least a small one was present. The species is assigned to *Ariadnaria* based on shell shape, but it differs from typical *Aradnaria* in its very sturdy shell, the fineness of its sculpture, and the presence of a parietal swelling at the posterior end of the aperture.

Ariadnaria stibara differs from *A. ainikta* by having a more elongate shell, narrower penultimate whorl, much weaker spiral cords with much narrower interspaces, longer and narrower umbilicus, parietal swelling on inner lip, and absence of foliate collabral sculpture. *Ariadnaria stibara* differs from *A. aldersoni* by larger size, less elongate shell, more rounded whorls that are not lax in their coiling, coarser spiral ribs, lattice-like very fine collabral sculpture on spire whorls, parietal swelling on inner lip, less delineated abapertural edge of inner lip, and no fasciole-like flange bounding the umbilicus. *Ariadnaria stibara* differs from *A. obstricta* by having rounded whorls, many more spiral ribs that are much weaker and much more closely spaced, and a less well demarked abapertural edge of the inner lip.

Etymology: Named for its sturdy shell, *stibaros*, Greek, meaning strong or sturdy.

Ariadnaria aldersoni new species
(Figures 7–8)

Diagnosis: Small Ariadnaria with elongate shell and last whorl medially subangulate, coiling stretched axially, whorls bearing many very fine and closely spaced ribs, umbilicus chink-like, spiral sculpture very fine, abapertural edge of inner lip well delineated and raised, umbilicus bordered by fasicole-like flange.

Description: Shell small (approximately 13.5 mm height, estimated); elongately turbiniform, with medially subangulate whorls; upper spire missing; teleoconch whorls enlarging rapidly; suture apparently appressed on earlier whorls, becoming channeled on penultimate whorl, rapidly descending; umbilicus chink-like, bounded by strong rounded fasciole-like ridge; growth line prosocline, well marked with numerous growth welts on last whorl; spiral sculpture consisting of fine, well spaced ribs of unequal strength crossing irregular growth welts; interspaces between ribs wider than ribs; aperture D-shaped, narrowed posteriorly but not angled, with short, broad anterior sinus; outer lip thin, simple; inner lip moderately narrow, abapertural edge raised and well demarked.

Holotype: LACMIP 13372, height 12 mm (incomplete), diameter 8.5 mm.

Type Locality: LACMIP 26370.

Distribution: Panoche Formation, (area 11) Alcalde Hills, Fresno Co., California.

Geologic Age: Late Turonian.

Discussion: Only the holotype is known. It is incomplete, consisting only of the last two whorls, and its small size may indicate that it is not mature. The elongate shape is a distinctive characteristic of this species. *Ariadnaria aldersoni* apparently had a relatively high spire, and the coiling is lax and reminiscent of *Lirpsa* Stephenson, 1952. It somewhat resembles *Lirpsa teres* Stephenson, 1952, but the new species has a narrow, chink-like umbilicus.

Ariadnaria aldersoni is most similar to *A. stibara* and differs by being smaller, having a more elongate shell, angulated whorls that are lax in their coiling, much weaker spiral ribs, abapertural edge of inner lip better delineated, fasciole-like ridge bounding the umbilicus, absence of lattice-like very fine collabral sculpture on spire whorls, and absence of parietal swelling on inner lip. *Ariadnaria aldersoni* differs from *A. ainikta* by being smaller, having much weaker spiral cords with much narrower interspaces, angulate last whorl, longer umbilicus that is slit-like rather than oval, and having a ridge separating the umbilicus from the inner lip. *Ariadnaria aldersoni* differs from *A. obstricta* by being smaller and having fewer and much weaker spiral cords with much narrower interspaces.

In some respects *A. aldersoni* is similar to *Lysis suciensis*. Both have fine ribbing, a relatively high spire, rather lax coiling, and a somewhat slower increase of whorl diameter. Whereas the suture of *A. obstricta* and *Lysis mickeyi* is very close to or at the perimeter of the previous whorl, in *A. aldersoni* and *Lysis suciensis* the suture is usually abapical to the previous whorl's perimeter.

Etymology: The species is named for John M. Alderson who collected the holotype from Cooper Canyon.

Ariadnaria obstricta (White, 1889)
(Figures 9–10)
Stomatia obstricta White, 1889: 18–19, pl. 4, figs. 10–11.

Diagnosis: Medium size *Ariadnaria* with high spire and angulate last whorl, sculpture of a few widely spaced strong cords, umbilicus chink-like or covered.

Description: Shell medium size (approximately 21.4 mm height), elongate turbiniform; whorl profile rounded with slight angulation at third strong cord on last whorl; spire high and approximately 50% of total shell height; apical angle approximately 67°; protoconch missing; teleoconch whorls four, enlarging rapidly and last whorl tapering anteriorly; suture appressed, anterior to subangulate periphery; umbilicus chinklike or covered by inner lip expansion; bounded abaperturally by strong ridge; growth line prosocline; sculpture of three strong, widely spaced cords on spire, five or six on body whorl; interspaces commonly with mid thread; aperture large and ovate with abapertural edge raised and sharply demarked; outer lip apparently simple; inner lip somewhat expanded and standing high along umbilical chink; basal lip barely drawn out into slight spout-like sinus.

Holotype: USNM 20124.

Type Locality: Little Cow Creek but additional specimens have not been found there. The species is abundant at some localities along South Cow Creek, Shasta Co., California.

Hypotype: LACMIP 13373, height 20 mm, diameter 15 mm from LACMIP loc. 28717.

Distribution: Redding Formation, Bear Creek Sandstone Member, especially (area 3) along South Cow Creek and Bear Creek, Shasta Co.; Chico Formation, Musty Buck Member, (area 5) Chico Creek, Butte Co., California.

Geologic Age: Late Coniacian? to Santonian.

Discussion: The above description is based on 16 specimens; all but one are from LACMIP loc. 28717. Most specimens are poorly preserved, and specimens with the shell surface preserved are difficult to find. The primary cords are strong and almost flange-like.

White's species is here assigned to *Ariadnaria* based on shell shape, sculpture, umbilicus, and presence of a small spout-like sinus in the aperture. This would be the earliest unquestioned occurrence of this genus that previously was known only from the Recent (Wenz, 1940).

In shape and probably sculpture (preservation makes comparison difficult) *A. obstricta* resembles illustrations of *Trichotropis*? sp. in Kase (1990: 568, figs. 2.26, 2.27). Kase's specimen was from the Izumi Group of Japan of early Maastrichtian age.

Ariadnaria obstricta is very similar to *Lysis mickeyi* new species, but *A. obstricta* has more regular spiral ribs, a slighly higher spire, the strong spiral delimiting an umbilical chink, and a free standing inner lip. *Ariadnaria obstricta* differs from *Ariadnaria ainikta* by having a higher spire, narrower penultimate whorl, angulate last whorl, fewer spiral cords, shorter umbilicus that is slit-like rather than oval, ridge separating the umbilicus from the inner lip, and an absence of foliate collabral sculpture. *Ariadnaria obstricta* differs from *A. aldersoni* by being larger, having fewer spiral cords that are much stronger and much more widely spaced, and lacking a fasciole-like ridge bounding the chink-like umbilicus. *Ariadnaria obstricta* differs from *A. stibara* by having angulate whorls, fewer spiral ribs that are much stronger and much more widely spaced, and a more demarked abapertural edge of the inner lip.

Subfamily Lysinae new subfamily

Description: Small to moderately large (15 to 80 mm in height), low turbiniform to almost haliotiform, barely siphonate shells with spiral ribbing. Final whorl somewhat to greatly enlarged; spire very short; aperture large, nearly circular to elongate oval; columella and inner lip flattened, expanded, and depressed to form a shelf within the aperture; some with shelf that spirals into an "umbilicus."

Discussion: The subfamily Lysinae includes *Lysis*

Gabb, *Garzasia* new genus, and probably *Spirogalerus* Finlay and Marwick, 1937. These gastropods are intermediate in form between trichotropines and calyptraeids. If their characteristics were better known, some other species such as those discussed under Global Distribution of Cretaceous Lysiform Gastropods, probably could be included here, some as *Lysis* or *Garzasia* others in as yet undescribed genera.

Genus *Lysis* Gabb, 1864
Tropidothais Cox, 1925: 213–214.

Type Species: *Lysis duplicosta* Gabb, 1864, by monotypy (Stewart, 1927: 345); Campanian of Pacific slope of North America.

Description: Turbinate to crepiduliform gastropods with a rapidly expanding whorl diameter having the columella/inner lip flattened, expanded, and submerged to form a narrow to broad shelf or deck. Shell sculptured by spiral cords or smooth. Nonumbilicate. Aperture with very slight anterior siphonal notch.

Discussion: *Lysis* differs from *Trichotropis* and *Ariadnaria* in having the inner lip completely appressed to the columella. Typical *Lysis* (i.e., the group of *L. duplicosta*) has a carinated whorl in the juvenile stage and a few moderately strong to strong spiral cords. The stronger spirals are typically scaly. Included in this group is *L. duplicosta* and the following new species: *Lysis mickeyi*, *L. jalamaca*, and *L. lomaensis*. The group of *Lysis suciensis* has a more rounded whorl profile and more subdued, finer spiral sculpture; included in it is *L. suciensis*.

Group of *Lysis duplicosta*

The genus *Lysis* was proposed by Gabb (1864) for a low-spired, turbiniform gastropod with a depressed inner lip. He had only immature specimens of a single species (i.e., the type species) and did not recognize their similarity to genus *Crepidula* Lamarck, 1799. He gave no indication of the familial affinities of *Lysis*, other than stating the general form is like genus *Stomatia* Helbling, 1779.

During the last 127 years, *Lysis* has been placed in at least 11 families scattered among "archaeogastropods" to the neogastropods. A review of this placement history is given here. Species that were eventually placed in *Lysis* were originally placed in *Stomatia* of the Stomatellidae Gray, 1840, by Whiteaves (1879, 1903) and White (1889). Stoliczka (1867–1868: 157–158) suggested that *Lysis* should be placed near *Separatista* Gray, 1847, in the Trichotropidae Gray, 1850, in the event that *Lysis* does not belong in either the Naticidae Guilding, 1834, or the Velutinidae Gray, 1840. Fischer (1885) placed *Lysis* in the Naticidae near *Eunaticina* Fischer, 1885. Tryon (1884: 112) did not hesitate to refer *Lysis* to the Muricidae Rafinesque, 1815 (as *Murexia*) [= Purpuradae Children, 1823], but on page 208 Tryon suggested a relationship to *Velutina* Fleming, 1821, of the Lamellariidae d'Orbigny, 1841. Cossmann (1903) wrote that *Lysis* could not be a muricid but must be placed near *Fossarus* Philippi, 1841, presumably in the Fossaridae Adams, 1860, where Stewart, 1927, Rennie (1930), Wenz, 1940, and Anderson (1958) also put it. Cossmann (1925) considered *Lysis* to be a subgenus of *Micreschara* Cossmann (1891) in the family Vanikoroidae Gray, 1840. Dall in Eastman (1913) and Packard (1922) placed *Lysis* in the "Thaisiidae" (=Thaididae) Suter, 1909. Saul (1959) and Saul and Alderson (1981) placed *Lysis* in Calyptraeidae, and, in 1990, Saul included it in superfamily Calyptraeoidea. Kase (1990) discussed previous taxonomic treatments of *Lysis* and suggested that, based on its inner lip shelf, the genus should be placed within the Calyptraeidae Lamarck, 1799. Bandel and Riedel (1994) and Kiel and Bandel (2003) supported this placement. Cox (1925) named and described genus *Tropidothais* Cox, 1925, which is a junior synonym of *Lysis*. He based *Tropidothais* on *T. africana* Cox, 1925, from the Maastrichtian of Mozambique [formerly Portuguese East Africa] and tentatively placed his genus in the Thaididae Jousseaume, 1888. Upon realizing its similarity to *Lysis*, Cox (in Rennie, 1935) synonomized the two genera and placed *Lysis* in the Stomatellidae. In this present paper, we place *Lysis* in the family Trichotropidae, subfamily Lysinae because *Lysis* appears to have evolved from trichotropids by expanding the columella/inner lip area (width and length) to form an interior shelf suggestive of the calyptraeid *Crepidula*.

Lysis mickeyi new species.
(Figures 11–16)

Diagnosis: A relatively high spired *Lysis* with eight or nine strong cords on last whorl; shelf moderately broad, somewhat depressed, and shallowly concave.

Description: Shell medium small (height approximately 20 mm), turbiniform; whorl profile overall rounded with medial angulation on last whorl; spire moderately low and approximately 30% of total shell height; apical angle approximately 90°; protoconch 1.5 whorls, low and smooth; teleoconch whorls 3.5, moderately expanding and last whorl tapering anteriorly; suture abutting and becoming laxly channeled on later whorls; sculpture of strongly raised cords, either moderately closely spaced or widely spaced; penultimate whorl with two to six and last whorl with eight or nine strong spirals, with variable number (two to five) of finer spirals in interspaces; both cords and interspaces crossed by fine collabral ribs, producing beaded appearance; angulation moderately strong on last whorl, coincident with strongest spiral cord; spiral cord anterior to angulation nearly same strength, thereby producing bicarinate appearance to medial part of last whorl; aperture large, oblique, barely notched anteriorly; outer lip simple; shelf moderately broad, somewhat depressed, and shallowly concave.

Holotype: LACMIP 13374, height 13 mm, diameter 9.5 mm, spire height 5 mm.

Paratypes: LACMIP 13375 from LACMIP loc. 23617 and 13376 and 13377 from LACMIP loc. 10757.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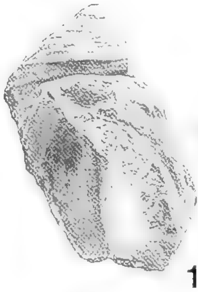
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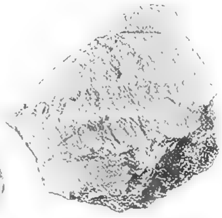
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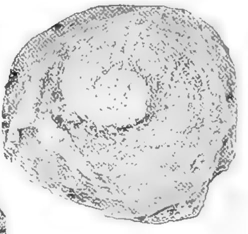
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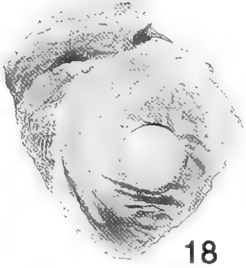
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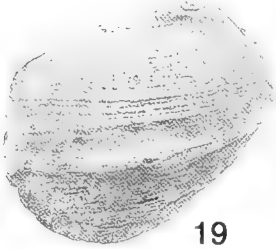
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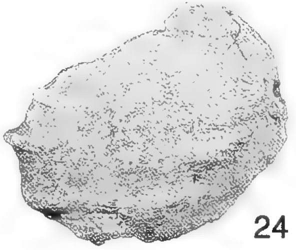
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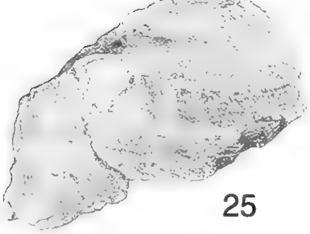
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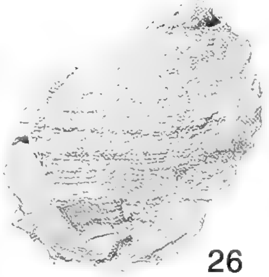
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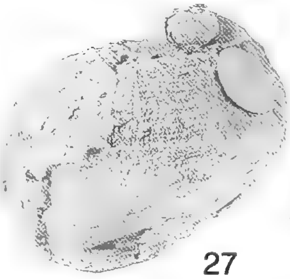
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Figures 11–28. *Lysis* species. **11–16.** *Lysis mickeyi* new species. **11–12.** Paratype LACMIP 13375, LACMIP loc. 23617, height 21 mm, diameter 16 mm. **11.** Apertural view. **12.** Right-lateral view. **13.** Paratype LACMIP 13376, LACMIP loc. 10757, left-lateral view, height 9 mm, diameter 11 mm. **14.** Holotype LACMIP 13374, LACMIP loc. 10757, abapertural view, height 13 mm, diameter 9.5 mm. **15–16.** Paratype LACMIP 13377, LACMIP loc. 10757, height 5 mm, diameter 9 mm. **15.** Left-lateral view. **16.** Apical view. **17–28.** *Lysis duplicosta* Gabb, 1864. **17.** Plasto-lectotype of *Stomatia suciensis carinifera* Whiteaves, 1879, CGS 5772, height 10 mm, diameter 19.5 mm. **18–19.** Hypotype LACMIP 13378, LACMIP loc. 24128. **18.** Apertural view, vertical dimension 27 mm, horizontal dimension 21 mm. **19.** Abapertural view, height 22 mm, diameter 26.5 mm. **20–21.** Hypotype LACMIP 13379, LACMIP loc. 24340. **20.** Apertural view, vertical dimension 28 mm, horizontal dimension 25 mm. **21.** Lateral view, vertical dimension 13 mm, horizontal diameter 29.5 mm. **22–23.** Hypotype LACMIP 13380, LACMIP loc. 24340, height 19 mm, diameter 18 mm. **22.** Apertural view. **23.** Abapertural view. **24.** Hypotype LACMIP 13381, LACMIP loc. 24340, abapertural view, vertical dimension 28 mm, diameter 37.5 mm. **25.** Hypotype LACMIP 13382, LACMIP loc. 24349, abapertural view, height 17 mm, diameter 22 mm. **26.** Hypotype LACMIP 13383, LACMIP loc. 10095, crushed specimen, abapertural view, height 24 mm, diameter 22.5 mm. **27.** Hypotype LACMIP 13384, LACMIP loc. 26951, abapertural view, height 21 mm, diameter 25 mm. **28.** Hypotype LACMIP 13385, LACMIP loc. 24340, abapertural view, height 7.5 mm, diameter 12 mm.

Type Locality: LACMIP loc. 10757.

Distribution: Redding Formation, Bear Creek Sandstone Member of Haggart (area 3) on Bear Creek, Shasta Co.; Chico Formation, top of Ponderosa Way Member and Musty Buck Member (200 m to 650 m above the base of the section) (area 5) on Chico Creek, Butte Co.; basal Tuna Canyon Formation (area 17) at head of Garapito Creek, Santa Monica Mountains, Los Angeles Co., California.

Geologic Age: Early Coniacian to Santonian.

Discussion: The above description is based on 80 specimens; most of these are from LACMIP locs. 10846 and 23617. Most specimens are internal molds. Many show endobiont boreholes, especially on the spire whorls. Two specimens show the protoconch. The oldest specimen is from LACMIP loc. 26967 in the Santa Monica Mountains.

Lysis mickeyi resembles *Lysis suciensis* (Whiteaves, 1879) in height of spire but is closer to *L. duplicosta* in sculpture. *Lysis mickeyi* differs from *L. duplicosta* in having a higher spire, less expanding last whorl, much less expanded shelf, more oval aperture, and thinner spiral cords. *Lysis mickeyi* greatly resembles *Trichotropis obstricta* (White, 1889), but on *L. mickeyi* the spiral ribs are less regular, and its spire is slightly lower. In addition, *L. mickeyi* lacks an umbilical chink and a free-standing inner lip.

Lysis mickeyi is the earliest known *Lysis* from anywhere in the world.

Etymology: Named for Mickey of Mickey's House on Chico Creek near the locality, LACMIP 23617, from which the species was first recognized.

Lysis duplicosta Gabb, 1864
(Figures 17–28)

Lysis duplicosta Gabb, 1864: 138, pl. 21, fig. 98a–98c; Tryon, 1883: 112, pl. 44, fig. 25–26; Cossmann, 1903: 70; Stewart, 1927: 345–346, pl. 21, figs. 7, 7a; Anderson, 1958: 169.
Stomatia suciensis variety *carinifera* Whiteaves, 1879: 128–129, pl. 16, fig. 5.
Lysis oppansus White, 1889: 17, pl. 4, figs. 14–15; Anderson, 1958: 169.
Lysis suciensis var. *carinifera* (Whiteaves).—Whiteaves, 1903: 367, pl. 45, fig. 4.
Micreschara (*Lysis*) *duplicosta* (Gabb).—Cossmann, 1925: 173, pl. 9, figs. 6, 21.
Lysis duplicostata Gabb.—Wenz, 1940: 880, fig. 2587 (reprint of Stewart, 1927); Elder and Saul, 1993: pl. 2, figs. 14–15.
Lysis carinifera (Whiteaves).—Anderson, 1958: 170.
? *Lysis duplicosta carinifera* (Whiteaves).—Dailey and Popenoe, 1966: 6.
Not *Lysis duplicosta* Gabb.—Saul and Alderson, 1981: 35–36, pl. 3, figs. 3–4 [= *Lysis suciensis* (Whiteaves) *fide* Saul, 1990].

Diagnosis: Variably sculptured *Lysis*, with many fine cordlets or with six to eight strong cords, including prominent (often flange-like) carina on periphery; columella and inner lip depressed and expanded to form crescentic shelf, occupying at least one third of aperture in larger specimens.

Description: Shell medium size (height up to approximately 26 mm), neritiform to crepiduliform; spire moderately low, approximately 20% of total shell height; protoconch 1.5 whorls, low and smooth; teleoconch approximately two whorls, overall rounded, enlarging very rapidly, and medially carinate; sculpture consisting of spiral ribs, generally six to eight prominent ones, but highly variable in number, spacing, and strength; periphery always demarked by very strong (occasionally flange-like) carina, located anteriorly of medial position on spire whorl and located medially on last whorl; remainder of whorls covered by spiral sculpture, ranging from numerous closely spaced fine cordlets to several widely spaced moderately strong (can alternate in strength) cords, with interspaces smooth or bearing many cordlets or threads; cords just anterior and, to a lesser degree, just posterior of medial carina on last whorl commonly approaching strength of medial carina, thereby imparting either a bicarinate or tricarinate appearance to whorl profile; aperture circular with a scarcely discernable anterior canal notch; abapertural edge of aperture sharply demarked by raised edge; inner lip and columella flattened, and expanded to form shelf; shelf moderately wide (occupying at least one third of aperture in larger specimens), submerged within the aperture, wrapping far past suture and attached to inside of outer lip; medial part of outer lip digitate.

Lectotype: Of *Lysis duplicosta* UCMP 11975, height 10 mm, diameter 19.5 mm. Gabb (1864) did not indicate a holotype. Merriam (1895) recognized UCMP 11975 as the figured specimen. Stewart's (1927) statement that this is the type specimen is taken as designation of lectotype.

Paralectotype: Of *Lysis duplicosta* ANSP 4242.

Syntypes: *Stomatia suciensis* variety *carinifera* Whiteave's, 1879, CGS 5772, a–d (Bolton, 1965). Whiteaves (1903: pl. 16, fig. 5) figured one of the five syntypes CGS 5772.

Holotype: Of *Lysis oppansus* White, 1889, USNM 20115.

Hypotypes: Of *Stomatia suciensis carinifera*, CGS 5939 (Whiteaves, 1903); Of *Lysis duplicosta* LACMIP 13378–13385; USNM 468585, 468586.

Type Locality: Of *Lysis duplicosta*, Texas Flat, near Rock Corral, from a mine shaft at a depth of 12 m [40 ft.], near the Placer-Sacramento Co. line, Placer Co., northern California; Of *Stomatia suciensis carinifera*, Sucia Island, San Juan Co., Washington. Of *Lysis oppansus*, Pentz Ranch, Butte Co., northern California.

Distribution: Cedar District Formation, Nanaimo Basin, (area 1) Vancouver Island area, southern British Columbia and (area 2) Sucia Island, San Juan Co., Washington; Chico Formation, Ten Mile Member on (area 5)

Chico Creek and Musty Buck Member along (area 6) Dry Creek, near Pentz, Butte Co., California; Chico Formation, (area 7) Granite Bay and Texas Flat, Placer Co., California; Pigeon Point Formation, southern sequence, (area 8) north of Pigeon Point, San Mateo Co., California; Jalama Formation, (area 12) western Santa Ynez Mountains, Santa Barbara Co., California; Ladd Formation, uppermost Holz Shale Member and Williams Formation, Schulz Member, (area 18) Santa Ana Mountains, Orange Co., California.

Geologic Age: Campanian.

Discussion: The above description is based on 101 specimens; most of these are from the Pentz area (LACMIP loc. 24340). At any locality, most of the specimens are internal molds. Some show endobiont boreholes. One specimen, LACMIP 13385 (Figure 28), shows the shape of the protoconch.

The holotype of *Lysis duplicosta* is a juvenile and had not yet developed the wider deck of an adult. The largest specimens of this species thus far found are from the Musty Buck Member of the Chico Formation at LACMIP loc. 24340 near Pentz (area 6). The specimens are from a matrix-supported pebble conglomerate richly fossiliferous in places. The fauna, which includes scraps of cypraeids, suggests warm, shallow water. *Lysis duplicosta* is very rare in the coeval Ten Mile Member on Chico Creek (area 5) which probably represents deeper water than at LACMIP 24340, and the specimen from LACMIP loc. 23639 on Chico Creek may have been transported downslope.

The strength of the cords, especially of the strongest one, varies greatly between individuals. Gabb's specific name refers to a doubled appearance of each major cord, but Gabb's (1864) sharp, deep channel along the strong ribs results from the wearing or breaking off of the scales on the ribs.

Dailey and Popenoe (1966: fig. 3) listed *Lysis duplicosta carinifera* from the Jalama Formation at LACMIP loc. 24128. This somewhat distorted specimen (Figures 18, 19) has some stronger ribs as in *L. duplicosta*, but may represent a strong ribbed variant of *L. jalamaca*. If *L. duplicosta*, it is the geologically youngest specimen of this species.

Rennie (1930: 1935) described two species of *Lysis* from the Umzamba Formation of the Eastern Cape Province (formerly Pondoland), South Africa, one of which *Lysis capensis* Rennie, 1930, is very similar to *L. duplicosta*. According to Klinger and Kennedy (1980), the lower Umzamba Formation at its type locality is latest Santonian or earliest Campanian in age and, therefore, similar in age to the Chico Formation near Pentz, Butte Co., California, where *L. duplicosta* is common. Rennie apparently had only two specimens of *L. capensis* which he said had six stout, sharp, spiral ribs. His holotype is small, similar in size to the holotype of *L. duplicosta*, and both apparently have a relatively narrower deck than is found in large specimens of *L. duplicosta*.

Kase's (1990) report of *L. duplicosta* in the Chatsworth Formation is based on a misidentification of *L. suciensis* in Saul and Alderson (1981).

Lysis jalamaca new species
(Figures 29–36)
Lysis duplicosta Gabb.—Dailey and Popenoe, 1966: 6.
Not *Lysis duplicosta* Gabb, 1864.

Diagnosis: A *Lysis* with sculpture of fine spiral cordlets of alternating strength and within the aperture the shelf wrapping considerably past suture.

Description: Shell medium size (height up to 26 mm), crepiduliform, with rapidly expanding whorls; spire low, and approximately 30% of total shell height; protoconch 1.5 whorls, low and smooth; teleoconch approximately two whorls, well rounded; whorls flattened adjacent to suture; periphery near mid-whorl height; suture abutting just below periphery; growth line prosocline, occasionally forming collabral wrinkles; sculpture consisting of numerous closely spaced fine spiral cordlets alternating in strength and somewhat scaly; cordlets strongest at and near periphery where two or three can be stronger becoming cords and the scales bead-like, with approximately three cordlets in interspaces; aperture ovoid, its abapertural margin sharply demarked and steeply descending; inner lip and columella flattened and expanded to form shelf; shelf narrow anteriorly becoming moderately wide medially, submerged within aperture, wrapping past suture and attached to inside of outer lip.

Holotype: LACMIP 13386, height approximately 35 mm, diameter 34 mm.

Paratypes: LACMIP 13387 (LACMIP loc. 24137) -13388 (LACMIP loc. 24122) and SDNHM 114595, 114596 (SDNHM loc. 3405).

Type Locality: LACMIP loc. 24137, Jalama Formation.

Figures 29–39. *Lysis* species. Specimens coated with ammonium chloride. **29–36.** *Lysis jalamaca* new species. **29–30.** Holotype LACMIP 13386, LACMIP loc. 24137. **29.** Apertural view, vertical dimension 34 mm, horizontal dimension 30 mm. **30.** Abapertural view, vertical dimension 27 mm, diameter 34 mm. **31–32.** Paratype LACMIP 13387, LACMIP loc. 24137. **31.** Left-lateral view, height 18 mm, horizontal dimension 19 mm. **32.** Lateral view, vertical dimension 11.5 mm, diameter 28 mm. **33.** Paratype LACMIP 13388, LACMIP loc. 24122, abapertural view, height 11 mm, diameter 13 mm. **34.** Paratypes SDNHM 114595 and 114596, SDNHM loc. 3405 on outer lip of volute gastropod *Longoconcha eumeka* Saul and Squires, 2008 (SDNHM 70974), SDNHM loc. 3405, height 133 mm, diameter 33 mm. **35–36.** Posteriormost paratype SDNHM 114596 on volute shown in previous figure. **35.** Abapertural view, height 13 mm, diameter 20 mm. **36.** Oblique apical view, vertical dimension 17 mm, diameter 20 mm. **37–39.** *Lysis lomaensis* new species, holotype SDNHM 67150, SDNHM loc. 3403, height 22 mm, diameter 23 mm. **37.** Apertural view. **38.** Abapertural view. **39.** Apical/lateral view, vertical dimension 8 mm, diameter 23 mm.


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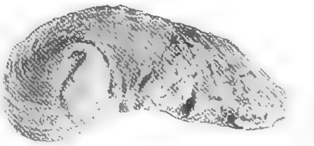
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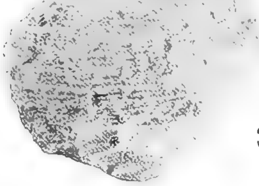
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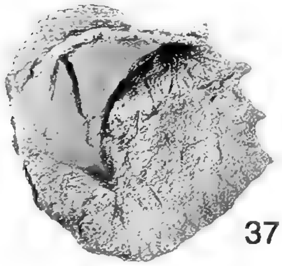
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Distribution: Jalama Formation, (area 12) western Santa Ynez Mountains, Santa Barbara Co.; Debris Dam Sandstone, (area 13) Agua Caliente Canyon, San Rafael Mountains, Santa Barbara Co., California; Chatsworth Formation, upper part (area 16) at Lang Ranch, Ventura Co., California; Point Loma Formation, (area 19) near Carlsbad, San Diego Co., California; Rosario Formation, (area 22) Cañon San Fernando, northwestern Baja California, Mexico.

Geologic Age: Late Campanian and early Maastrichtian.

Discussion: The above description is based on 13 specimens. The best preservation occurs in the Point Loma Formaton near Carlsbad.

Lysis jalamaca is similar to *L. suciensis* but has coarser, more scaly costae than *L. suciensis*, and available specimens of *L. jalamaca* are smaller and less elongate than are large specimens of *L. suciensis*. *Lysis jalamaca* is also similar to *L. duplicosta* in having variable sculpture and in having the strongest cords on the periphery, but *L. jalamaca* is less angulate at the periphery and has weaker cords there. In addition, *L. jalamaca* differs from *L. duplicosta* by being more elongate, having finer sculpture, and having the shelf broader posteriorly. The specimen (LACMIP 13378, Figures 18, 19) from the Jalama Formation has ribbing similar to *L. duplicosta*, but its shelf appears to wrap farther onto the interior of the outer whorl than is usual for *L. duplicosta*.

Etymology: The specific epithet, a name in apposition, reflects the new species occurrence in the Jalama Formation, Santa Barbara Co., California.

Lysis lomaensis new species
(Figures 37–39)

Diagnosis: *Lysis* with low spire and last whorl bearing numerous flanged carinae separated by wide interspaces bearing several spiral threads.

Description: Shell medium size (up to 17 mm height and 30 mm diameter, same specimen), neritiform (last whorl rapidly expanding); spire very low, approximately 10 to 15% of shell height; protoconch 1.5 whorls, low and smooth; teleoconch 2 to 2.5 whorls, very carinated; suture abutting just anterior to periphery; sculpture consisting of up to 11 strong cords; cord at periphery and next three cords posterior of periphery very thin, flanged, and protruding (with cord at periphery protruding most); posteriormost part of last whorl (in vicinity of suture) with approximately three low scaly cordlets; up to three beaded to lowly spinose cordlets anterior to medial carina at periphery; interspaces between all cords wide and bearing up to seven spiral threads (occasional thread can locally develop into small flanged cord); area anterior to medial carina can be covered with only fine cordlets; aperture circular with margin sharply demarked by raised edge; shelf moderately wide, wrapping past suture and attached to inside of outer lip; posterior half of outer lip digitate.

Holotype: SDNHM 67150, height 22 mm, diameter 23 mm.

Paratype: SDNHM 67152 from SDNHM loc. 4071.

Type Locality: SDNHM loc. 3403.

Distribution: Basal San Francisquito Formation, (area 14) Warm Springs Mountain, Los Angeles Co.; Point Loma Formation, (area 19) San Diego Co., California; Rosario Formation, (area 21) five miles east of La Misión, northwestern Baja California, Mexico.

Geologic Age: Latest Campanian to late Maastrichtian.

Discussion: Five specimens were studied. Preservation is generally excellent for three specimens from the Point Loma Formation near Carlsbad, although the protoconch of the holotype is imperfectly preserved. The incomplete, crushed specimen from Warm Springs Mountain is from beds of latest Maastrichtian age at the base of the San Francisquito Formation (LACMIP loc. 14310). Although the abapertural side is not available, the flatness of the apical whorls suggests that it is probably *L. lomaensis*.

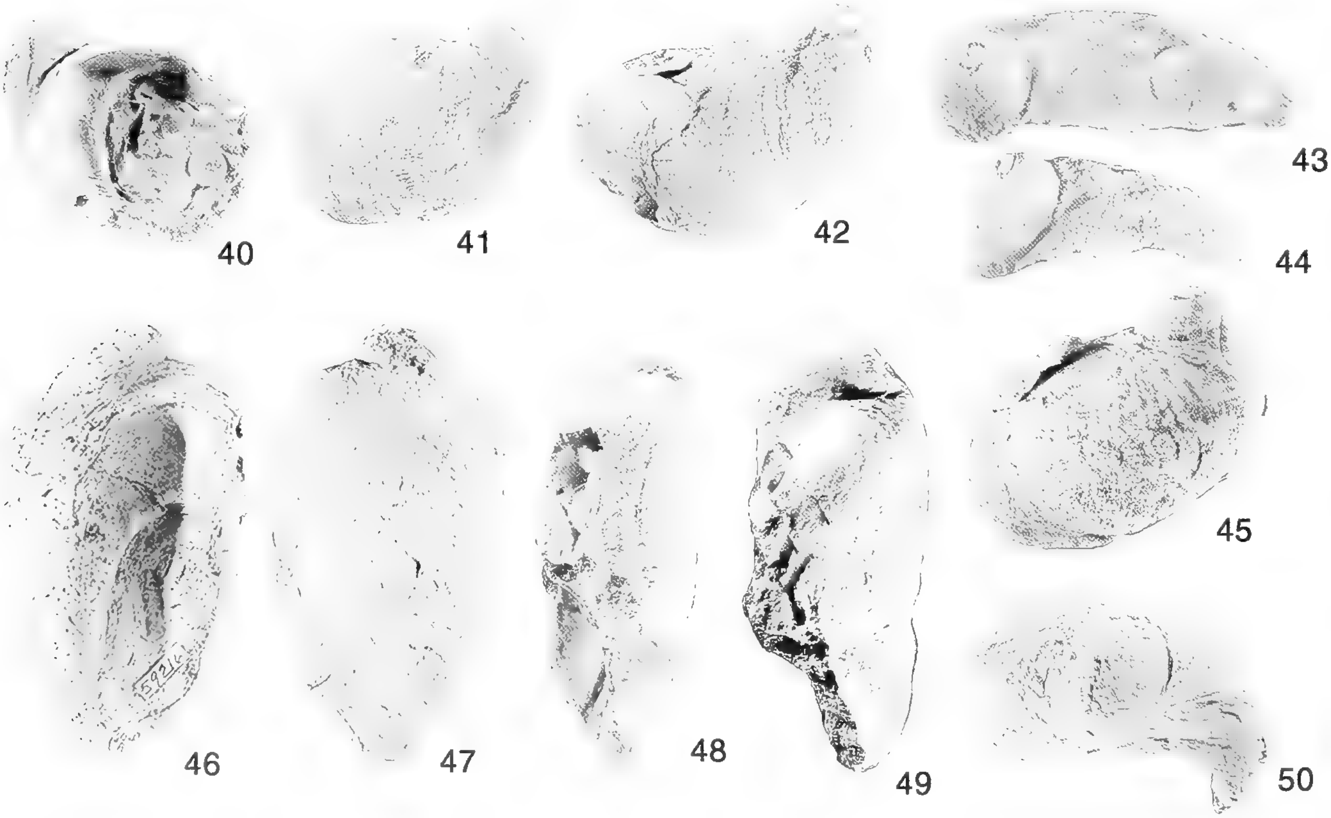
The new species is most similar to *Lysis duplicosta* but available specimens are smaller than a large *L. duplicosta*. *Lysis lomaensis* also has a lower spire, more carinate last whorl (especially posterior to the medial carina), and spiral threads on interspaces between carinae.

Abaperturally, *L. lomaensis* is similar in shape and sculpture to *Garzasia intermedia*, but *L. lomaensis* has a lower spire and in the apertural view the shelf margin is less arcuate, not sigmoid, and the shelf does not spiral into the umbilicus.

Group of *Lysis suciensis*

The group of *L. suciensis* differs from that of *L. duplicosta* in having a more elongate aperture and finer spiral sculpture.

Lysis suciensis (Whiteaves, 1879)
(Figures 40–50)



Figures 40–50. *Lysis suciaensis* (Whiteaves, 1879). Specimens coated with ammonium chloride. **40–41.** Hypotype LACMIP 13389, LACMIP loc. 26020. **40.** Apertural view, vertical dimension 44 mm, horizontal dimension 40 mm. **41.** Abapertural view, height 25 mm, diameter 43 mm. **42–43.** Hypotype LACMIP 13390, LACMIP loc. 10711. **42.** Abapertural view, height 18 mm, diameter 26.5 mm. **43.** Lateral view, vertical dimension 8 mm, diameter 26.5 mm. **44.** Hypotype LACMIP 13391, LACMIP loc. 10095, lateral view, vertical dimension 5 mm, diameter 12.5 mm. **45.** Hypotype LACMIP 13392, Cañon San Fernando, 32 km southeast of El Rosario, Baja California, Mexico, abapertural view, height 18 mm, diameter 21 mm. **46–50.** Hypotype LACMIP 10495, LACMIP loc. 26020. **46–47.** Vertical dimension 70 mm, horizontal dimension 38 mm. **46.** Apertural view. **47.** Abapertural view. **48.** Right-lateral view, vertical dimension 70 mm, horizontal dimension 25 mm. **49.** Slightly oblique right-lateral view, vertical dimension 70 mm, horizontal dimension 27 mm. **50.** Lateral view, vertical dimension 25 mm, horizontal dimension 36 mm.

Stomatia suciensis Whiteaves, 1879: 128–129, pl. 16, fig. 4.
Lysis suciensis (Whiteaves).—Whiteaves, 1903: 367, pl. 45, fig. 3. Stecheson, 2004: 60–62, pl. 2, figs. 4–5.
Lysis californiensis Packard, 1922: 431, pl. 37, figs. 2–3; Stadum, 1973: pl. 2, fig. 12.
Lysis duplicosta Gabb.—Saul and Alderson, 1981: 36, pl. 3, figs. 3–4. Not. *Lysis duplicosta* Gabb, 1864.

Diagnosis: Medium to large *Lysis*, shell elongate with fine, usually wavy cordlets, sculpture obsolete on large specimens.

Description: Medium to large (height up to 84 mm), crepiduliform, elongately expanded; spire moderately high to low, approaching horizontal coiling, and approximately 30 to 35% of total shell height; protoconch approximately 1 to 1.5 whorls, low and smooth; teleoconch approximately 1.5 to 2 whorls, whorls subcarinate to rounded; periphery near one-third whorl height; suture abutting just anterior to periphery, descending; growth line slightly to moderately parasigmoidal, with sinus at posterior end of outer lip on large, smooth individuals; sculpture consisting of fine narrow cordlets, usually wavy, alternating in strength, with narrow interspaces; aperture elongate ovoid, its abapertural margin sharply demarked and steeply descending; inner lip and columella flattened and expanded to form crescentic and moderately wide deck submerged within aperture, posterior end attached to inside of outer lip; inner deck margin concavely curved.

Syntypes: Of *Stomatia suciensis* CGS 5771, a–d.

Lectotype (here chosen): Of *Stomatia suciensis* CGS 5771, height 66 mm.

Paralectotypes: Of *Stomatia suciensis* CGS 5771a–CGS 5771d.

Holotype: Of *Lysis californiensis* UCMP 12287.

Paratype: Of *Lysis californiensis* UCMP 12288.

Type Locality: *Stomatia suciensis*, Sucia Island, San Juan Co., Washington. Of *Lysis californiensis*, UCMP loc. 2167, Santa Ana Mountains, Orange Co., California.

Figured Specimens: LACMIP 10495, 13389, from LACMIP loc. 26020; LACMIP 13390 from LACMIP loc. 10711; LACMIP 13391 from LACMIP loc. 10095; LACMIP 13392 from the Rosario Formation, (area 22) 26 km east of coastline at elevation 200 m on west side of Cañon San Fernando, 15 km north of Mesa San Carlos, approximately 32 km. southeast of El Rosario, Baja California, Mexico.

Distribution: Upper Cedar District Formation, (area 1) Denman Island, Gulf Islands, British Columbia; Lower Cedar District Formation, (area 2) Sucia Island, San Juan Co., Washington; Chico Formation, (area 7) Granite Bay, Placer Co.; Jalama Formation, (area 12) western Santa Ynez Mountains, Santa Barbara Co.; Chatsworth Formation, (area 16) Bell Canyon and Dayton Canyon, Simi Hills, Ventura Co., California; Ladd Formation, upper Holz Shale Member, (area 18) Santa Ana Mountains, Orange Co., California; Rosario Formation (area 22) at Cañon San Fernando, 26 km SE of El Rosario Baja California; Valle Formation, (area 23) 10 km north from Punta Abreojos, Baja California Sur, Mexico.

Geologic Age: Late early Campanian and early Maastrichtian.

Discussion: The above description was based on 107 specimens. The deck of smaller specimens is rather narrow and attaches to the base of the previous whorl. Small specimens are rounded, larger specimens more elongate. In larger specimens the shelf is broader and its posterior end attaches to the inside of the outer lip. Several specimens, especially the larger specimens, have an obtusely biangulate whorl abapical to the periphery. Most specimens from Sucia Island are of small size and badly weathered, but Whiteaves's largest specimen (1879: 129, pl. 16, fig. 4), here designated as lectotype, was indicated by him to be "two inches and a half in length" (i.e., 66 mm). The specimen from Bell Canyon (area 16) of Figures 46–50, lacking its spire and with its outer lip broken, is 75 mm high.

The ribbing on larger specimens from the Chatsworth Formation in Bell and Dayton canyons, Simi Hills (area 16) tends to become fainter toward the outer lip especially on the posterior slope. The specimen figured (Figures 40, 41) retains ribbing around the periphery, but the ribs fade posteriorly toward the aperture. Height range of the smoother specimens is 45 to 76 mm (incomplete), making these the largest specimens thus far found of *Lysis*. The largest of these specimens are larger than representatives of most species of *Crepidula*; only *Grandicrepidula princeps* (Conrad, 1856), attains a larger size.

Genus *Garzasia* new genus

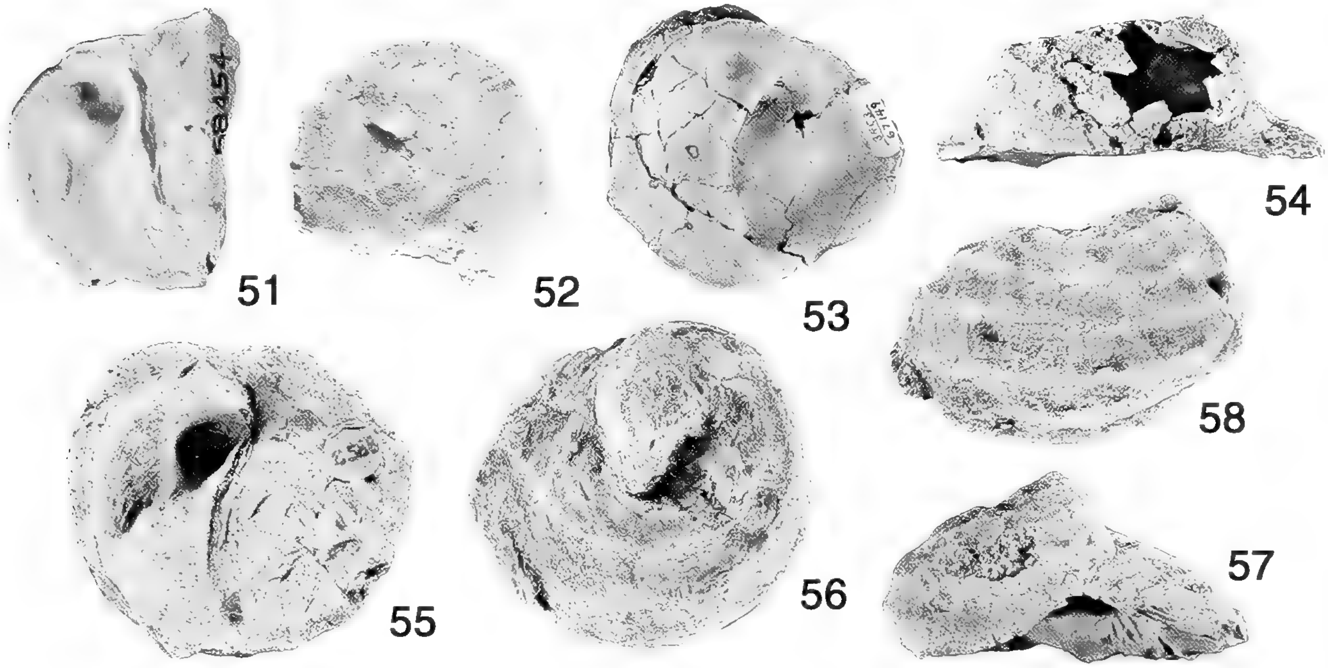
Type Species: *Garzasia diabla* new species from the "Garzas Sand" Member of the Moreno Formation, Stanislaus Co., California; mid Maastrichtian.

Description: Very low to moderately high spired, *Calyptraea*-like shell with weak to strong spiral cords, aperture very broadly expanded and forming base of shell, shelf attached marginally, surrounding the umbilicus, and spiralling into it.

Discussion: *Garzasia* is most similar to *Lysis* but differs from the latter in that the deck surrounds and spirals into an umbilicus somewhat as in *Calyptraea* but with a wider more open umbilicus. It differs from *Calyptraea* in having a sturdier shelf attached marginally as in *Trochita*. It differs from *Trochita* (Figure 71) in having the shelf crescentic with an arcuate to slightly sigmoidal shelfal edge, the axis of spiraling of its shelf off center, and external ribbing spiral rather than protractive.

Etymology: The genus *Garzasia* is named for the "Garzas Sand" and Garzas Creek, Stanislaus Co., California.

Garzasia intermedia (Cooper, 1894)
(Figures 51–54)



Figures 51–58. Species of *Garzasia* new genus. **51–54.** *Garzasia intermedia* (Cooper, 1894). **51–52.** Plasto-lectotype of CASG 609, Point Loma Formation. **51.** Apertural view, vertical dimension 21.5 mm. **52.** Apical view, diameter 19 mm. **53–54.** Hypotype SDSNH 67149, SDSNH loc. 3403. **53.** Apertural view, vertical dimension 61.5 mm, diameter 64 mm. **54.** Left-lateral view of spire above posterior part of aperture, height 20 mm, diameter 64 mm. **55–58.** *Garzasia diabla* new species. **55–57.** Holotype LACMIP 13393, LACMIP loc. 22588. **55.** Apertural view, vertical dimension 36 mm, diameter 37 mm. **56.** Abapertural view, vertical dimension 34 mm, diameter 37 mm. **57.** Side view of spire above posterior part of aperture, height 18 mm, diameter 37 mm. **58.** Paratype LACMIP 13394, LACMIP loc. 26353, slightly oblique left-lateral view (partial specimen), height 29 mm, diameter 9 mm.

Stomatia intermedia Cooper, 1894: 46, pl. 3, fig. 43 [refigured in Yates, 1903: pl. 3, fig. 43].
Lysis intermedia (Cooper).—Anderson, 1958: 170; Coan, 1981: 165, fig. 12 [reprint of Cooper's pl. 3].

Diagnosis: Large *Garzasia*, haliotiform, carinate on periphery, sculpture elsewhere consisting of several low spiral cords separated by wide interspaces bearing up to 10 spiral threads, shelf very broad, with arcuate to slightly sigmoidal margin.

Description: Large size (height up to 37 mm, diameter 68 mm, same specimen); haliotiform with very rapidly expanding last whorl; protoconch unknown; spire highly variable in elevation, ranging from 50 to 85% of total shell height; suture abutting below periphery; growth line prosocline; sculpture consisting of commonly five spiral cords; periphery carinate and bearing strongest cord; peripheral carina located anteriorly of medial position on spire whorl but medially on last whorl; adapical to medial carina two to three medium-strong cords with wide interspaces bearing up to 10 spiral threads; just abapical to medial carina several closely spaced and scaly medium strong cords; aperture circular; inner lip and columella flattened to slightly concave and expanded to form very wide crescentic shelf submerged within aperture; posterior end of shelf surrounds umbilicus and spirals into it.

Lectotype: CAS 609 (formerly CSMB 13742), height 6.4 mm, diameter 22.6 mm (incomplete).

Type Locality: Point Loma, San Diego Co., California.

Figured Specimen: SDSNH 67149 from SDSNH 3403.

Distribution: Point Loma Formation, (area 19 and 20) San Diego Co., California.

Geologic Age: Latest Campanian and early Maastrichtian, *Baculites lomaensis* zone.

Discussion: The above description was based on six specimens, of which preservation is generally good to excellent.

Cooper's (1894) figure 43 line drawing is actually a combination of three specimens. The lectotype (CASG 609) is designated by us and is photographed here (Figure 51) for the first time.

Garzasia intermedia differs from *G. diabla* new species in achieving larger size, having weaker carinae with the medial carina being most prominent, and having spiral threads in interspaces between carinae.

Garzasia intermedia is somewhat similar to *Sigapatella* Lesson, 1830, some species of which [e.g., *Sigapatella novaezelandiae* (Lesson, 1830)] have spiral sculpture, an off-centered apex, and a well-developed "false" umbilicus. The umbilicus of *Garzasia* appears to form as the widely expanded, flattened columella is attached medially around the axis of coiling forming a broad shelfal area. In the holotype of *G. intermedia* and some other specimens this area is an open, funnel shape, but in others the area is more or less filled, resulting in shelves with differing "umbilical" development from a moderate to deep depression. The shelfal edge of *Garzasia* differs from that of *Sigapatella* in being sigmoidal rather than arcuate.

A large specimen SDNHM 67149/3403 has faint markings at each end of the shelf which resemble muscle scars.

Garzasia diabla new species
(Figures 55–58)

Diagnosis: Medium sized, *Calyptraea*-like, with moderately high spire, having three to four equal-strength carinate ribs with wide interspaces.

Description: Medium to moderately large size (up to 30 mm in height), *Calyptraea*-like shell with rapidly expanding last whorl; spire moderately high, approximately 40 to 50% of total shell height; protoconch missing; teleoconch approximately 1.5 whorls, carinate; periphery near one-half whorl height; suture abutting at periphery; sculpture consisting generally of three to four equal-strength and equally spaced carinae with very wide interspaces; aperture circular with its abapertural margin sharply demarked and steeply descending; inner lip margin slightly sigmoidal; posterior end attached to inside of outer lip directly beneath suture; shelf spiraling into umbilicus.

Holotype: LACMIP 13393, height 18 mm, diameter 37 mm.

Paratype: LACMIP 13394 from LACMIP loc. 26353.

Type Locality: LACMIP loc. 22588.

Distribution: Moreno Formation, "Garzas Sand" Member, (area 9 and 10) Merced and Stanislaus counties, California.

Geologic Age: "Mid" Maastrichtian.

Etymology: The species is named for its occurrence in the eastern foothills of the Diablo Range, Merced and Stanislaus counties, California. The specific epithet *diabla* is used as a name in apposition.

Discussion: The above description is based on eight specimens. Preservation of the known specimens of this species is poor. Except for the holotype, all the specimens are internal molds.

This species is very similar to *G. intermedia* from which it differs in having a generally lower but more roundly inflated, spire that is apparently not variable in height, higher last whorl, much stronger sculpture, and the basal flange wrap into the aperture to meet the apertural edge of the shelf.

EVOLUTIONARY IMPLICATIONS

The presence of both fine-ribbed and coarse-ribbed *Ariadnaria* and *Lysis* suggests that species of *Lysis* may have been derived from *Ariadnaria*. During the evolution of *Lysis*, the inner lip broadened (as did the columella) and apparently moved deeper into the aperture, thereby allowing more room for the foot to grasp hard substrate. These changes, assumed to be a function of the rapid expansion of the aperture, were necessary in order that the aperture could accommodate a larger foot for attachment to a hard substrate. The resultant shell shape was crepiduliform. Modern trichotropids studied by Yonge (1962) in Puget Sound thrive on unstable shell beds. If some Cretaceous trichotropids resembled the modern trichotropids in (1) being filter feeders, (2) living on firm substrates, and (3) being protandrous hermophodrites, they would have had characteristics that allowed them to evolve toward the less vagile calyptraeids or crepidulids.

The inner lip of trichotropids is homologous to the internal deck or shelf of calpytraeids, and the development of the shelf in *Lysis* serves as a pattern for the development of the flat shelf in *Crepidula* Lamarck, 1799, and of the shelf in *Garzasia* for the spiral shelf in *Calyptraea* Lamarck, 1799. Trichotropid and crepidulid sculpture is predominantly spiral (i.e., in the direction of coiling), but some calyptraeid sculpture is radial or protractive.

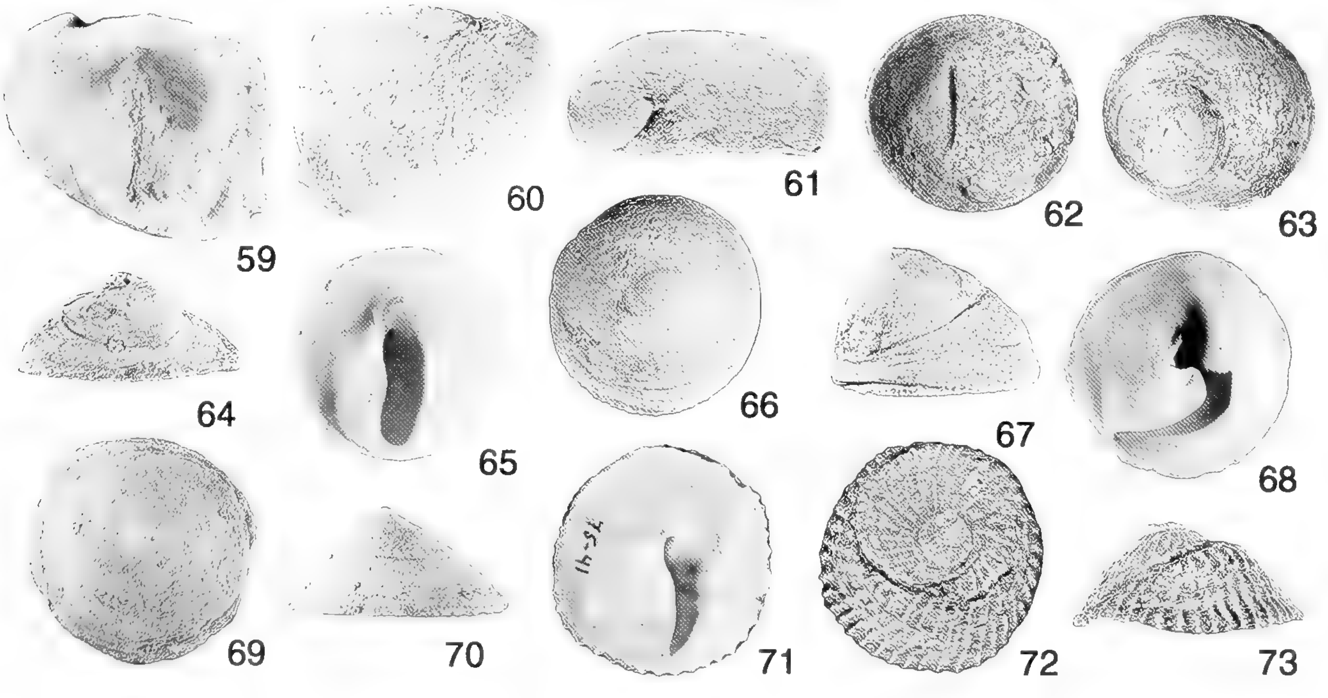
The shell exterior of *Lysis suciensis* group (i.e., *Lysis suciensis* lineage) is fine-ribbed to relatively smooth; interiorly the columella and inner lip are flattened and broadened into a crescentic shelf which, as it lengthened posteriorly, came to resemble a shelf of *Crepidula*. Except for its large size, *Lysis suciensis* resembles the earliest species from the Pacific slope usually assigned to *Crepidula*; namely, '*Crepidula*' *pileum* (Gabb, 1864), which ranges from middle Eocene to Oligocene in California to Washington. Stewart (1927) and Hoagland (1977) slightly extended the range of '*C.*' (*Spirocrypta*) *pileum* by synonymizing with it the late early Eocene *Spirocrypta inornata* (Dickerson, 1916) and the middle to late Eocene *Spirocrypta dickersoni* (Weaver and Palmer, 1922), but Vokes (1939) considered *Spirocrypta inornata* of "Domengine" age to have "a funnel-like process due to the upward curving of the posterior portion of the septa" (Vokes, 1939, pl. 13, fig. 7) rather than the less apparent "umbilicus" of *S. pileum* (see discussion below).

Gabb (1864) originally placed '*Crepidula*' *pileum* in the invalid genus *Crypta* Humphrey, 1797 (a synonym of *Crepidula*), and subgenus *Spirocrypta* Gabb, 1864, of which '*C.*' (*S.*) *pileum* is the type species. '*Crepidula*' (*S.*) *pileum*, which is common in the Tejon Formation of middle Eocene age in Live Oak Canyon, Kern Co., California, has been figured several times (e. g., Gabb, 1864: pl. 29, figs. 233, 233a–b; Stewart, 1927: pl. 29, figs. 2–3; Anderson and Hanna, 1925: pl. 13, fig. 7; Clark, 1938: pl. 4, fig. 19; Wenz, 1940: figs. 2660a, b [reprint of Stewart]. A large specimen from the late Eocene is figured by

Kleinpell and Weaver (1963, pl. 24, fig. 11). Weaver's (1943: 724, pl. 71, fig. 16) illustration of *Calyptraea diegoana* (Conrad) is a lapsus and is a posterior-end-up, apertural view of '*Crepidula*' *pileum*. On page 356 he correctly lists the figure as *Crepidula pileum*. Gabb's (1864: pl. 29, fig. 233a) and Stewart's (1927, pl. 29, fig. 3) show the shelf. Gabb's figure is a fascimile and Stewart's is a photograph that has been reproduced in other discussions of *Spirocrypta* (e.g., Wenz, 1940: 903, fig. 2660a). Gabb's and Stewart's figures are based on lectotype ANSP 4221, but, unfortunately, the shelf of this specimen is broken. Both figures create the false impression that there is a sinus near both ends of the shelf and that the middle part protrudes and is concave. An additional representative specimen (hypotype LACMIP 13395) was cleaned by the senior author and is illustrated in Figures 59–61. Its shelf (Figure 59), which is unbroken, is slightly sigmoidal and long on the left side (or anterior end) and shorter on the right side (or posterior end). There is also a slight convexity of the somewhat sinuous shelf as it approaches the posterior end of the aperture and the shelf margin spirals over slightly to form an indication of an umbilicus. In addition, the shelf is also narrower and closer to the shell margin on the left/anterior and noticeably farther from the shell margin (deeper into the aperture) on the right/posterior. The shelf of '*C.*' *pileum* thus, as noted by Gabb (1864), spirals inward toward the apex. Gabb's figure (pl. 29, fig. 233b) in part illustrates this, as does Figure 59. Although Stewart (1927) synonomized *Spirocrypta* with *Crepidula*, Gabb's description of *Spirocrypta* recognizes this very important characteristic, which helps to distinguish *Spirocrypta* from *Crepidula*. In modern *Crepidula fornicata*, the shelf does not spiral into the whorl apex.

Aperture/shelf features of *Spirocrypta pileum* and *S. inornata* resemble those of the early Paleocene *Spirogalerus lamellaria* Finlay and Marwick, 1937, from New Zealand, in that the shelf of *S. lamellaria* is also narrower and closer to the shell margin on the left/anterior and noticeably farther from the shell margin (deeper into the aperture) on the right/posterior.

Our proposed evolutionary relationship between trichotropines and calyptraeids differs from any previous author's proposal. Hoagland (1977), for example, in her study of *Crepidula* Lamarck, 1799, rejected trichotropids as direct ancestors of calytraeids and crepidulids. Hoagland (1977) opined that although *Trichotropis* Broderip and Sowerby, 1829, and *Crepidula* had a common an-



Figures 59–73. Fossil Calyptraeidae. **59–64.** Comparative Eocene *Crepidula* and *Calyptraea* species. **59–61.** *Spirocrypta pileum* (Gabb, 1864), hypotype LACMIP 13395, LACMIP loc. 22386, vertical dimension 3 mm, diameter 9 mm. **59.** Apertural view. **60.** Abapertural view. **61.** Lateral view. **62–64.** '*Calyptraea*' *diegoana* (Conrad, 1855), hypotype LACMIP 13458, LACMIP loc. 22340. **62.** Apertural view, vertical dimension 29 mm, diameter 31 mm. **63.** Apical view, diameter 31 mm. **64.** Right lateral view, height 13 mm, diameter 31 mm. **65–67.** '*Calyptraea*' *aperta* Solander *in* Brander, 1766, hypotype LACMIP 13396, LACMIP loc. 7333. **65.** Apertural view, vertical dimension 11 mm, diameter 11 mm. **66.** Apical view, diameter 11 mm. **67.** Right-lateral view, height 7 mm, diameter 11 mm. **68–70.** *Calyptraea chinensis* (Linnaeus, 1758), Recent, type-species, hypotype LACM 161651, Cherbourg (Manche), Normandie, France. **68.** Apertural view. vertical dimension 15 mm, diameter 14.5 mm. **69.** Apical view, diameter 14.5 mm. **70.** Right-lateral view, height 6 mm, diameter 14.5 mm. **71–73.** *Trochita trochiformis* (Born, 1778), Recent, type-species, LACM loc. lot 75-41, Pumalin, west of Isla Telcon, Gulf of Corcovado, Chiloe Province, Chile – intertidal. **71.** Apertural view, vertical dimension 40 mm, diameter 38 mm. **72.** Apical view, diameter 38 mm. **73.** Right-lateral view, height 18 mm.

cestor, *Trichotropis* has no direct relationship to *Crepidula* because *Trichotropis* is boreal, living in cold and deep water and has rough sculpture, whereas *Crepidula* had its origin in the Panamic region and is relatively smooth sculptured. Her implications that *Trichotropis* is a deep, cold-water gastropod and that *Crepidula* is a shallow, warm-water gastropod are misleading. Modern *Trichotropis cancellata* (Hinds, 1843) is intertidal in Alaska, British Columbia, and Washington to depths of 104 m off Alaska, 165 m off British Columbia, and 274 m off Washington (LACM Malacology collection). In the southern part of *T. cancellata*'s range, it is in cool-temperate, not boreal waters. The question is, however, not where trichotropids live now but where they were during the Late Cretaceous, when there were no polar ice caps and the subtropical and temperate zones were much wider. Trichotropids and calyptraeid-like gastropods co-existed during the Late Cretaceous in the study area, and both forms lived in relatively warm, shallow waters. Although the Coniacian-Santonian faunas of northern California are noticeably cooler than Turonian faunas (Saul and Squires, 2008) of that area, they would have been temperate. Hoagland (1977) mentioned that anatomical features of *Trichotropis* suggest affinities to calyptraeids, but she believed that similarities of life history and niche between *Trichotropis* and *Crepidula* are convergent. She suggested that *Crepidula* is derived from some form of "calyptraeid stock" that, in turn, was derived from *Trochita* Schumacher, 1817, reported by Wenz (1940) to range from Eocene to Recent. She did not provide any geologic time parameters as to when these derivations took place, but indicated that Shimer and Shrock (1959) recorded the first calyptraeids as "lower Cretaceous." The "lower" seems to be a minor lapsus; all printings of Shimer and Shrock from first 1944 to last 1989 list range of *Calyptraea* and *Crepidula* as "U. Cret.–Recent" and *Crucibulum* as "Tert.–Recent." Wenz (1940: 902), however, questionably included the peculiar looking genus *Galericulus* Seeley, 1861 from the Upper Greensand (Lower Cretaceous upper Albian) of England in calyptraeids. It does not resemble any calyptraeid we have studied. Seeley (1861) named *Crepidula cooksoniae* also from the Upper Greensand, but Hoagland (1977: 395) found it "unconvincing" as a calyptraeid.

The Campanian to Maastrichtian *Damesia* Holzapfel, 1888, of Europe and Tennessee, has been regarded as a calyptraeid by some workers (e.g., Sohl, 1960), but Dockery (1993) assigned *Damesia* to the pyramidelloids.

Bandel and Riedel (1994) reviewed placement and content of Calytraeoidea, and in comparison to Hoagland's (1977) study, they arrived at a different familial content and different relationships between the families. Their Calyptraeoidea consisted of two families: Calyptraeidae containing genera *Calyptraea*, *Crucibulum*, and *Crepidula*; and Hipponicidae containing *Cheilea*, *Hipponix*, *Neojanaca*, and *Thylacus*; but both families excluded trichotropids. According to Bandel and Riedel (1994), all genera in Calyptraeidae lack a probosis and are obligatory filter feeders. However, in Hawaii Ulbrick (1969) reported algae grazing, in addition to filter feeding by *Crucibulum spinosum* Sowerby, 1824.

Cretaceous trichotropines probably had several characteristics that lysines would have inherited from them: 1) filter feeding, 2) living epifaunally, probably on a hard substrate, 3) brooding egg capsules from which planktotrophic larvae hatch, and 4) being protandrous hermaphrodites. Characteristics the lysines would pass on to calyptraeids. Lysines' first recognizable difference from the trichotropines is the increase in expansion rate of the whorl, especially of the last whorl, resulting in an enlarged aperture in which the columella is broadened. The earliest broadening and enlargement were moderate and only become striking as geologically younger species began to have a very distinctive morphology. Until connected with its ancestry, *Lysis* was difficult to classify. The shell also became more flattened and limpet-like, as the aperture enlarged.

Hoagland (1977) credited *Crepidula hochstetteriana* Wilckens (1922: 5–6, pl. 1, figs. 9a, b) as being the earliest *Crepidula* because it was reported from the calcareous conglomerate stratigraphic unit of the Lower "Amuri Group" in the "Amuri Bluff" area, northeastern South Island, New Zealand (Wilckens, 1922: Warren and Speden, 1978). Modern spelling of "Amuri" is Haumuri, and the Cretaceous strata are referred to the Mata Series. Woods (1917) reported that these strata at Haumuri Bluff contain the bivalves *Inoceramus australis* Woods, 1917 and *Inoceramus pacificus* Woods, 1917, which according to Wellman (1959) are limited to the Piripauan Stage of latest Coniacian to Santonian age.

Warren and Speden (1978) noted "problems" with the early collections from this area but nevertheless, listed *Maoricrypta hochstetteriana* (Wilkens, 1922) from the Campanian Okarahia Sandstone of the Mata Series. Described conditions of collecting suggested a strong possibility of co-mingling of material from different strata and that the only known specimens of *M. hochstetteriana* might not be from the Mata Series. In search of the type specimen, we contacted three extraodinarily helpful New Zealanders: A. G. Beu, A. Grebneff, and J. D. Stilwell. Their email communications (2006) indicated that *M. hochstetteriana* is not from the Okarahia Sandstone, and is not of Cretaceous age. Beu found the type specimen (GNS TM2608) in the New Zealand Geological Survey collections. Fortunately, the type specimen was in a large enough block of matrix to take a sample for microfossil dating. He enlisted the aid of G. Wilson who dated the dinoflagellates as late Oligocene, at the oldest. Ian Raine, who looked at the rich spore-pollen assemblage also from the sample, found *Acacia* pollen, which is not known earlier than Miocene in New Zealand. Miocene strata crop out above the Mata Series, and some of the original material sent to Wilkens was apparently from beach boulders derived from younger strata overlying the Cretaceous Mata Series. This Neogene age for Wilckens' species is much more likely considering that the shelf covers nearly one-half of the aperture (Hoagland, 1977: 380).

Hoagland published more papers on *Crepidula* and, in 1986, she revised several items of her 1977 paper but did not design a new evolutionary pathway. We differ from Hoagland (1977) in that we believe it is difficult to go from the centrally oriented apex plan of *Trochita* (Figure 71) or *Calyptraea* (Figure 68) with its spiraling shelf and get to *Crepidula* with its eccentric spire and apparently unspiraled deck. Whether or not *Lysis* species are ancestral to any modern *Crepidula*, younger species of *Lysis* achieved a crepiduloid form with a respectable shelf by wrapping the posterior end of the shelf onto the inside of the outer whorl. Furthermore, from this, the calyptraeid form appears to have evolved with the development of an "umbilicus" in *Garzasia intermedia* making Cooper's specific name remarkably prescient.

At about the Campanian/Maastrichtian boundary, development of the spiral shelf of *Garzasia* resulted in a shelf that appears to be a pattern for development of shelves in *Calyptraea* and perhaps *Crucibulum*. The very broad, depressed spiraling inner lip of *Garzasia* appears to provide a likely pattern for development of the shelf of *Calyptraea* or *Crucibulum*, not for the more decklike shelf of *Crepidula*.

The earliest reported *Calyptraea* on the Pacific slope is *'Calyptraea' diegoana* (Conrad, 1855) which ranges from middle Paleocene to Oligocene and occurs from California to Washington and easternmost Russia (Squires, 1987). A representative specimen from the Tejon Formation Eocene is shown in Figures 62–64. Figure 62 displays the shelf of this species, which is similar to that of *'Calyptraea' aperta* Solander in Brander, 1766 from the Eocene of Europe (Figures 65–67). Both of these species have often been referred to *Trochita* Schumacher, 1817 (type species *Turbo trochiformis* Born, 1778), but their shelves (Figures 62 and 65) spiral from an off-center position roughly a quarter of the diameter in from the aperture edge. A so-called pseudoumbilicus at the upper end of the shelves in Figures 62 and 65 could result from reduction of an umbilicus such as that of *Garzasia*. The shelves of *'C.' diegoana* and *'C.' aperta* are narrower than shelves of *Garzasia* and expand across about one third of the aperture. They differ distinctly from that of *Trochita* (Figures 71–73), which has a sturdy spiraling internal shelf extending from the centered axis of coiling to the outer shell margin, giving the impression of dividing the circular aperture in half.

'Calyptraea' diegoana does not appear to be a direct descendent of *Garzasia*. Its similarity to *'C.' aperta* suggests an ancestor in the Old World Tethyan Sea and, like many of the other Early Cenozoic mollusks (Squires, 1987, 2003), it probably arrived onto the Pacific slope via a circum-equatorial current. These species *'C.' diegoana* and *'C.' aperta* do not have shelves similar to that of *Calyptraea chinensis* (Linnaeus, 1758), the type species of *Calyptraea*. In *C. chinensis*, the thin fragile shelf (Figure 68) occupies about a quarter of the apertural circle. It arises from the apex with a folded-over edge that forms the umbilicus. At the open end of the umbilicus, the shelf edge abruptly veers counter to coiling direction and approaches the apertural margin at an acute angle. The total shelfal edge is sickle-shaped with a short handle (the umbilical edge) and a long curved blade (the outer margin of the shelf). This leaves a deep notch between the attachment of the shelf to the shell and a delicate, lobate shelf.

Trochita is present in modern eastern Pacific slope faunas from Mazatlan, Mexico to Valpariso, central Chile. It occurs in lower to middle Miocene strata as far north as the La Panza Range, San Luis Obispo Co., is present in the Kern River section, Kern Co. (Addicott, 1970) and the Topanga Formation, Santa Monica Mountains, Los Angeles Co., California. It has a thick shell with protractive ribbing and, as mentioned above, a sturdy shelf.

GLOBAL DISTRIBUTION OF CRETACEOUS LYSIFORM GASTROPODS

Both *'Crepidula'* and *'Calyptraea'* have been reported from Campanian and Maastrichtian age strata from throughout the world. Preservation of most specimens makes identification of them problematical. Some of these gastropods have proven to belong to other families or not to be of Cretaceous age. Others need verification. Our tally of occurrences is doubtless incomplete.

Although stated above as "throughout the world," these gastropods are recovered from areas that were probably temperate to tropical. Verified lysines are all younger than Turonian and older than Eocene. Classing *Spirogalaerus* as a lysine provides the only Paleocene record of this subfamily. Late Cretaceous occurrences suggest that the calyptraeids developed in several geographic places from widely distributed trichotropids evolving into Lysinae. An example of this is the evolving shape of *Lysis*. Although on the Pacific Slope calyptraeiform calyptraeoids developed from a crepiduliform calyptraeoid, the calyptraeiform has been recognized more widely geographically, but not earlier than Coniacian.

Cretaceous calyptraeiform calyptraeoids are more widely recognized geographically than are crepiduliform calyptraeoids. Europe has calyptraeiform occurrences but no crepiduliform occurrences. Africa has calyptraeiform occurrences in the north and crepiduliform occurrences in the south. African occurrences are close in time to those of the Pacific Slope. North America (exclusive of the Pacific Slope) has a very few reports along the Gulf Coast of calyptraeiform specimens. The Pacific Slope has both calyptraeiform *Garzasia* and crepiduliform *Lysis*. South America has calyptraeiform species. Japan somewhat mirrors the Pacific Slope. Its known lysine is of early Maastrichtian age, but the additional presence of a trichotropid (Kase, 1990) similar to *A. obstricta* suggests that lysines were developing there roughly synchronously with those along the Pacific Slope. New Zealand has no

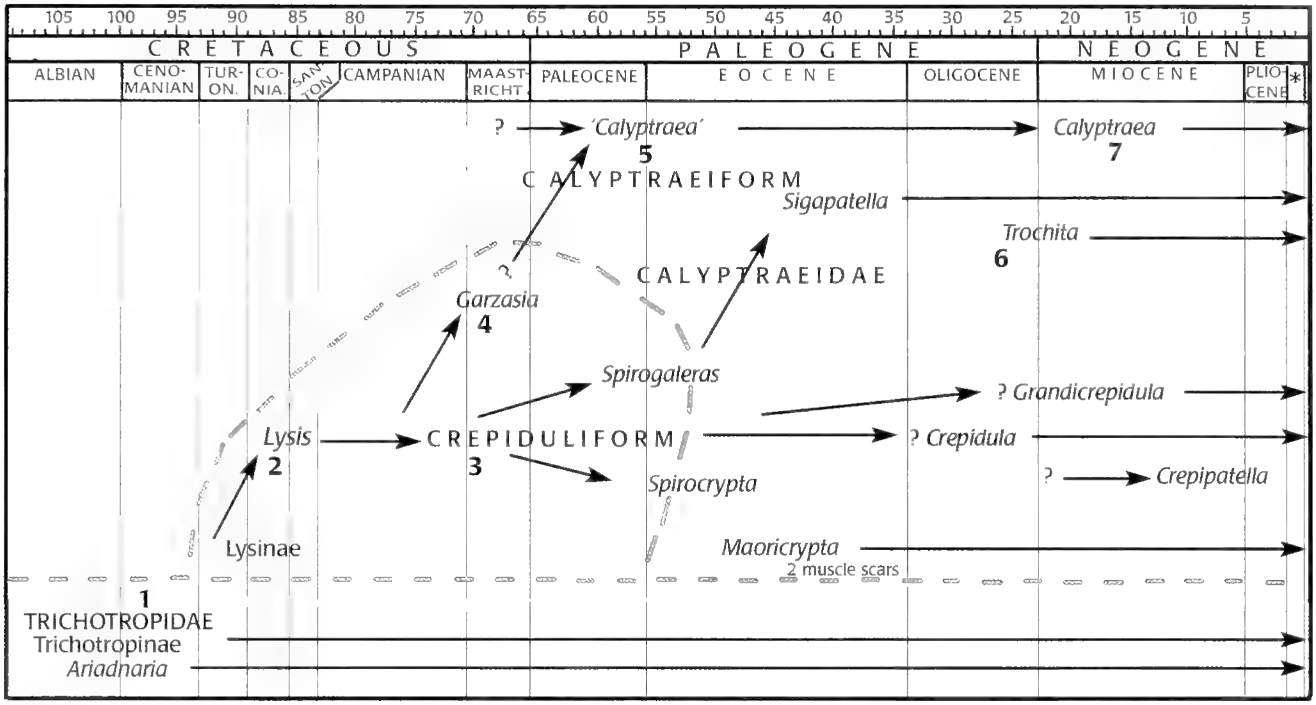


Figure 74. Generalized proposed evolutionary trends of calyptraeoids. Time scale after Gradstein et al., 2004. Calyptraeids and crepidulids probably evolved from several trichotropids. *Lysis* or *Lysis*-like fossils of Coniacian to Maastrichtian age have been described from California, and from Campanian to Maastrichtian age from southern Africa and Japan. **1.** Turriculate gastropods having gill capable of filter feeding, sedentary adult life on hard substrate. Probably capable of copulation, protandrism, and brooding of young. **2.** Broadening of columella and inner lip. Enlarging final whorl. **3.** Attachment of posterior shelf end to interior of outer lip to develop crescentic shelf. **4.** Some species developed "umbilicus" in spiraling shelf as in *Garzasia*. **5.** "Umbilicus" closed or nearly so in Eocene '*Crepidula*' and moving toward more central position in more circular base. **6.** Broad shelf, spiraling from near center of base. Shelf edge nearly straight. **7.** Spiral shell with low spire, round base. Shelf edge extremely sigmoidal. * = Pleistocene. Stages abbreviated are Turonian, Coniacian, Santonian, Maastrichtian.

known Cretaceous lysines but does have the youngest known calyptraeiform lysine.

EUROPE: *Crepidula mytiloidea* Bellardi and Michelotti, 1840 from Villavernia near Tortona Italy was listed among Nomina Dubia by Hoagland (1977) as being from the Cretaceous. Bellardi and Michelotti were describing a Tertiary fauna. Because the specimen and illustrations are so small, Hoagland could not verify that this species was a *Crepidula*.

Calyptraea cretacea (d'Orbigny, 1842: 390, pl. 234, figs. 1–3) [*Infundibulum*] was examined by Kollmann (2005) who determined that d'Orbigny's material was from Campanian of Charente-Maritime, southern France, and that the specimen identified as *C. cretacea* by Delpey (1942: 165, fig. 1) was from Maastrichtian of southwestern France. Poor preservation of d'Orbigny's type caused Kollmann (2005: 172, pl. 18, fig. 18) to refer to it as "*Calyptraea s. lato cretacea* (d'Orbigny, 1843), *species dubia*." Delpey's illustration shows no shelf. Kollmann considered both specimens to be only *Calyptraea* sensu lato. These specimens expand their whorl diameter much less rapidly and have much higher spires than specimens of *Lysis* and *Garzasia* from the Pacific Slope of North America.

Calyptraea depressa Delpey, 1942 (p. 165, fig. 2) from Maastrichtian southwestern France, has a spiraling shelf similar to that of Eocene '*Calyptraea*' *aperta* except that its shelfal margin is concavely arcuate between rim and whorl center.

Kollmann and Odin (2001: 446, pl. 1, figs. 18–19) recorded *Calyptraea* sp. of Maastrichtian age from southwestern France, but the preservation of the specimens appears to be too poor to allow positive generic identification.

AFRICA: As figured, '*Calyptraea*' *bouéi* (Pervinquière, 1912: 10–11, pl. 1, figs. 7–11) from the Maastrichtian of Tunisia externally resembles some forms assigned to '*C.*' *aperta*. The shape of the shelf of '*C.*' *bouéi* shown in figure 9 is difficult to determine, but appears to have a straight edge and probably resembles that of '*C.*' *aperta*.

Galerus libyca Quaas, 1902, was described from upper Maastrichtian/ possibly Danian strata (*Exogyra overwegi* beds) from the Ammonite Hills, Great Sand Sea, Egypt (Quaas, 1902: 238, pl. 25, figs. 26–29). It has been reported also from the Congo (Dartevelle and Brébion, 1956: 29–30, pl. 1, figs. 9–10), and from Libya, Egypt, Congo, and Madagascar (Bandel and Riedel, 1994: 339–340, pl. 7, figs. 2–3). Bandel and Riedel reported Quaas' original specimens lost in World War II and figured the exterior of a subsequently collected specimen of 'Calyptraea' *libyca* which resembles '*C.*' *aperta*. They did not figure the shelf, but described it too briefly as "a flat spiral shelf like that of modern *Calyptraea*."

A *Crepidula* chain was reported by Brébion (1956) in describing *Crepidula congolensis* Brébion, 1956, from the upper Campanian of the Congo, Africa. This African species resembles a *Lysis* more than it does a modern *Crepidula*, in that *C. congolensis* has coiling similar to *Lysis* and a depressed inner lip that barely wraps onto the labral side of the aperture. *Lysis*? *congolensis* (Brébion, 1956: 89, fig. 1; pl. 1, fig. 7a, 7b) is most similar to *L. jalamaca* in shape and sculpture but appears to have much finer ribbing than *L. jalamaca*.

'*Calyptraea*' *primogenita* Kiel and Bandel (2003: 460, fig. 4.14–4.16) and *Lysis capensis* (Rennie, 1930) illustrated by Kiel and Bandel (2003: 460, fig. 6.1–6.2) are from the upper Santonian/lower Campanian, Umzamba Formation. '*Calyptraea*' *primogenita* was described from a single worn and broken specimen. Its ribbing (except on last quarter-whorl) is protractive as in *Trochita*, and it has a thick shell as does *Trochita*. Its whorl shape is more trochiform than in *Trochita* or *Calyptraea*, it consists of more whorls than a *Trochita* or a *Calyptraea*, the last whorl lacks the notable enlargement of a *Trochita* or a *Calyptraea*, and unlike *Trochita* or *Calyptraea*, it has a small open umbilicus and "the columellar lip bears a strong plate" (Kiel and Bandel, 2003).

Lysis capensis is very similar in shape and sculpture to *L. duplicosta*, but its inner lip seems narrower and more similar to that of *L. mickeyi*. *Lysis duplicosta* is generally lower spired and has a broader inner lip/columella.

Rennie (1945: 50, 116, pl. 3, fig. 10) figured a *Calyptraea* sp. from the Upper Cretaceous Senonian of Angola, Africa. A more precise age is unknown and, although the shape and angle of suture in the figure resemble *Calyptraea*, the base and aperture are not illustrated, thereby making generic assignment indeterminate.

NORTH AMERICA (exclusive of the Pacific Slope): *Crucibulum*? sp. of Sohl (1960: pl. 10, fig. 21) is an immature, incomplete specimen from the upper part of the Ripley Formation (Maastrichtian) in Mississippi. Sohl indicated that its incomplete shell suggested a close relationship to *Crucibulum*, and that it definitely appeared to belong in the Calyptroidea. The specimen is too incomplete to determine its genus, its similarity to *Crucibulum* could be a result of the way it is broken, but its spire does suggest Calyptraeoidea.

Sohl (1960) classed *Thylacus cretaceous* Conrad, 1860 in Capulidae, but Dockery (1993) moved it to Calyptraeidae and Bandel and Riedel (1994) included Conrad's species in Hipponicidae. It apparently lived attached to the columella within the aperture of empty gastropod shells. It differs from *Lysis* and *Garzasia* in the way *Thylacus* muscles were attached. At the end of juvenile coiling and beginning of expansion of the last whorl, *Thylacus* deposited left and right prongs instead of modifying the inner lip/columella into a shelf as in *Lysis*. Sohl (1960: pl. 10, fig. 4) and (Dockery (1993: pl.18, figs. 1 and 4) provided good illustrations of the early development which does seem more hipponicid than calyptraeid. When developed to maturity a horseshoe-shaped muscle scar resulted. Dockery's (1993) specimens were from the Coffee Sand of Campanian age and Sohl's (1960) from the Ripley Formation of Maastrichtian age.

SOUTH AMERICA: '*Calyptraea*' *aperta* (Solander *in* Brander, 1766), a European Eocene species (see Figures 65–67 for a representative late Eocene specimen from the Paris Basin, France), was identified by Olsson (1944: 248–249, pl. 9, figs. 10–13) from northern Peru. Olsson's placement of the Tortuga fossil beds below his Radiolite sandstones with *Baculites* suggests a Maastrichtian age. As he provided only exterior views and no description of the shelf, this identification needs further verification. Specimens identified as '*Calyptraea*' *aperta* from Europe and the American Gulf Coast range widely as to whorl height and sculpture which varies from smooth to spinose. The Peruvian specimens increase in diameter at a slower rate and they have more strongly impressed sutures than Eocene specimens, suggesting that the Peruvian specimens are probably not '*C.*' *aperta*.

Calyptraea laevis (Philippi, 1887) from Maastrichtian of central Chile was described as *Trochita laevis* Philippi (1887: 92, pl. 11, fig. 3; referred to *Galeropsis* by Wilckens (1904: 195–196, pl. 17, figs. 9a, b) because of its high spire, and to *Calyptraea* (*Trochita*) by Bandel and Stinnesbeck (2000: 763–764, pl. 1, fig. C). Bandel and Stinnesbeck provided a view of the exterior only, and described the shelf as "a flat concave shell like that of modern *Calyptraea*." Although "flat concave shell" might partially describe a *Trochita* shelf, it is not an acurate description of the shelf in *Calyptraea chinensis* (Figure 68). Wilckens (1907: 13, pl. 3, fig. 6) also reported *Calyptraea* aff. *laevis* Philippi of Maastrichtian age from southern Patagonia, but the preservation of the specimen appears to be too poor to allow positive generic identification.

Calyptraea pileolus d'Orbigny, 1841 was indicated by Hoagland (1977: 354) to have been recorded from Lower Cretaceous strata of Argentina by von Ihering (1907), but the species was listed by Feruglio (1937: 187) from the Patagoniano (Tertiary) of Lago Argentino, Argentina.

JAPAN: As noted earlier, *Lysis izumiensis* Kase, 1990 has been described from the earliest Maastrichtian of Japan. It resembles the group of *Lysis duplicosta* and appears from the illustrations (Kase, 1990: figs. 2.11–2.12) to be most similar to *L. duplicosta* in strength of sculpture and development of innerlip/columellar expansion. Kase (1990) also recorded a trichotropid similar to *Ariadnaria obstricta* from the Izumi Group in Japan.

NEW ZEALAND: The early Paleocene (Danian) *Spirogalaerus* Finlay and Marwick, 1937, from New Zealand is *Lysis*-like, especially as to growth line, and this similarity requires further study to determine whether it results from common ancestry, convergent evolution, or parallel evolution. Finlay and Marwick (1937) assigned *Spirogalerus* to family Calyptraeidae and based their genus on *Spirogalerus lamellaria* Finlay and Marwick, 1937, which resembles *L. suciensis* except that *L. suciensis* lacks the "pseudoumbilicus" described for *Spirogalerus*. Finlay and Marwick (1937) and Boshier (1960) opined that *Spirogalerus lamellaria* could represent the evolutionary link between crepidulids and calyptraeiform *Sigapatella* Lesson, 1830.

Classification of *Spirogalerus* has been inconsistent. Wenz (1940) made it a subgenus of *Calyptraea* Lamarck, 1799. Beu and Maxwell (1990) made *Spirogalerus* a subgenus of the calyptraeid *Sigapatella* Lesson, 1830, but Stilwell and Zinsmeister (1992) separated *Sigapatella* from *Spirogalerus* because the latter has a strongly exerted spire. Collin (2003a) noted that *Sigapatella* has a shell and anatomy similar to the calyptraeid genera *Calyptraea*, *Trochita* Schumacher, 1817, and *Zegalerus* Finlay, 1926. Collin (2003b) considered *Sigapatella* to be monophyletic but did not mention *Spirogalerus*. Marshall (2003) recognized *Sigapatella* (=*Zegalerus*) as a distinct genus based on its shelf edge being broadly and evenly concave instead of sigmoidal. This is a very different shelf than that of *Calyptraea chinensis* (Figure 68). The differences between *Spirogalerus* and *Sigapatella* are similar to those found between *Lysis* and *Garzasia*, and the New Zealand forms also record an evolutionary pattern of enlargement of the last whorl and the aperture, with broadening of the columella/inner lip area into a shelf within a limpetiform shell. Thus, these two genera were probably not links from actual crepidulids, but represent links from lysines to calyptraeids.

ACKNOWLEDGMENTS

We mention again the extraordinary assistance of the New Zealanders in documenting a Tertiary age for a specimen mistakenly recorded as Cretaceous. Malcolm G. Laird, University of Canterbury, Christchurch, New Zealand, and Jeffrey D. Stilwell, Monash University, A. Grebneff, Otago University, Dunedin, New Zealand, and A. G. Beu, GNS Science, New Zealand, provided help in researching the age of the New Zealand Cretaceous units. They recruited micropaleontologists Graeme Wilson, GNS Science, New Zealand, who provided an age range based on the diatoms, and Ian Raine, GNS Science, New Zealand, who recognized the Acacia pollen and reported its maximum age in New Zealand. Raymond Graham, Royal British Columbia Museum, Victoria, Canada provided information on the occurrence of *Lysis duplicosta* in the Gulf Islands area. Lindsey Groves, LACM Malacology, provided specimens of *Calyptraea chinensis* and *Trochita trochiformis* and assistance in finding several obscure references. We also thank an anonymous reviewer and S. Kiel of University of Leeds, U.K. for improvements in the text.

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APPENDIX 1

LOCALITIES CITED

Localities are LACMIP, unless otherwise noted. All quadrangle maps are U. S. Geological Survey maps. Bracketed numbers are areas shown on Figure 1.

[4] CASG 61794. [= CAS 1346-A]. In conglomeratic sandstone 1.6 km (1 mi.) above mouth of Huling Creek, North Fork Cottonwood Creek, Ono Quadrangle (15 minute, 1952), Shasta Co., California. Budden Canyon Formation, Bald Hills Member. Late Albian.

7333. Le Fayel, Paris Basin, France. Late Eocene (Bartonian Stage).

[18] 10095. [=CIT 83]. Fine sandstone just above shale, sectionline fence gate on old road 0.4 km (1/4 mi.) W of Schulz Ranch, 122 m (400 ft.) S. of northeast corner of section 19, T. 5 S, R. 7 W, El Toro Quadrangle (7.5 minute, 1968), south side of Williams Canyon, Santa Ana Mountains, Orange Co., California. Coll.: B. N. Moore, 1 January, 1926. Ladd Formation, uppermost Holz Shale Member. Early Campanian.

[16] 10711. [=CIT 1158]. Approximately 1.84 km (1.5 mi.) due west of Los Angeles-Ventura Co. line on the boundary (extended) between T. 1 N and T. 2 N, north bank of Bell Canyon, southeast slope of Simi Hills, Calabasas Quadrangle (7.5 minute, 1952), Ventura Co., California. Coll.: W. P. Popenoe, 18 July, 1935. Chatsworth Formation. Middle Campanian.

[3] 10757. [=CIT 1593]. Massive sandstones in bed of North Fork Bear Creek, approximately 777 m (2550 ft.) south and 533 m (1750 ft) east of northeast corner of section 5, T. 31 N, R. 1 E, Whitmore Quadrangle (15 minute, 1956), Shasta County, California. Coll.: W. P. Popenoe and W. M. Tovell, 12 Sept., 1941. Redding Formation, Bear Creek Sandstone. Coniacian.

[5] 10846. [=CIT 1014]. Concretions in sandstone, right bank of Chico Creek about 1.6 km (1 mi.) upstream from the little bridge across creek below Mickey house and about 4.16 km (2.5 mi.) N6°W of 14-mile house on Humboldt Road, NW 1/4, SE 1/4 of section 1, T. 23 N, R. 2 E, Paradise Quadrangle (15 minute, 1953), Butte Co., California. Coll: W. P. Popenoe and D. W. Scharf, 16 August, 1931. Chico Formation, top of Ponderosa Way Member. Late Coniacian or early Santonian

[23] 11944. Approximately 10 km N of Punta Abreojos (SW of San Ignacio), in first ridges N of arroyo that crosses Punta Abreojos road (dirt) just S of Campo Rene turnoff, approx. 2 km NW of road. Approx. 2–3 km up ravine, hill .5 km to east is pachydiscid loc., Viscaiano Peninsula, Baja California Sur, Mexico. Coll.: R. Demetrion, 1987, 1989. Valle Formation. Middle? Campanian, with *Hoplitoplacenticeras*?

[14] 14310. About 450m north and 70m west of lookout at summit of Warm Springs Mountain at elev. of 1052 m (3450 ft.), at base of Kirby's (1991, M. A. Thesis) measured section no. 2, Warm Springs Mountain Quadrangle (1958), Los Angeles County, California. Coll.: M. X. Kirby. Basal San Francisquito Formation. Late Maastrichtian.

22340. Gritty conglomeratic sandstone lenses in fine-grained sandstone and shales, east side Grapevine Canyon about 0.8 km (0.5 mi.) south of its north end, about 0.4 km (0.25 mi.) east of, and 30.48 m (100 ft.) above the abandoned highway roadbed on east side of canyon, at about 648 m (2100 ft.) contour, about 91 m (300 ft.) northwest of Tejon/granite fault contact. Locality is 3048 m (10,000 ft.) N24°W of 3174 ft. BenchMark at old Fort Tejon, Tejon Quadrangle, Kern County, California. Coll: W. P. Popenoe, 9 December, 1946. Tejon Formation. Middle Eocene.

22386. Prominent shell bed at crest of ridge on east side of Live Oak Canyon, about 0.4 m (0.25 mi.) south of its mouth, T 10 N, R 19 W, Pastoria Creek Quadrangle, 7.5', 1958, photorevised 1974, Kern County, California. Coll.: W. P. Popenoe, 13 March, 1947. Tejon Formation, Metralla Sandstone Member. Middle to upper Eocene ("Tejon Stage").

[10] 22588. About 2/3 of the way to the top of a gully on southwest slope of a northwest-trending hill on south side of Garzas Creek, where the creek enters the San Joaquin Plain, approximately 610 m south and 183 m west of northeast corner of section 19, T 8 S, R 8 E, Howard Ranch Quadrangle, 7.5', 1953, photorevised 1971, west side of San Joaquin Valley, Stanislaus Co., California. Coll.: W. P. Popenoe and T. Susuki, April, 1950. Moreno Formation, "Garzas Sand" member. Middle Maastrichtian.

[4] 23464. [PR1] Up small creek from Sulivan Ranch Rd. crossing, and 1.28 km (0.8 mi.) north of ranch, near Gas Point Rd., 701 m (2300') N 75°E from mouth of Huling Creek, 579 m (1900') S, 488 , (1600') E of NW corner of section 16, T. 30 N, R. 6 W, Ono Quadrangle (15 minute, 1952), Shasta Co., California. Coll.: P. U. Rodda and M. A. Murphy, May 1955. Budden Canyon Formation, Bald Hills Member, unit iv in Matsumoto, (1960). Middle Cenomanian, probably *Turrilites costatus* Zone

[5] 23617. Fossil in hard, blue-gray concretion in gray-weathering buff sandstone approximately 15.2 m (50 ft.) below highest conglomerate, approx. 0.8 km (0.5 mi.) upstream from Mickey house on west side of Chico Creek, 1.52 m (5 ft.) above stream, 716.28m (2350 ft.) north, 609.6 m (2000 ft.) west of southeast corner of section 1, T. 23 N, R. 2 E, Paradise Quadrangle (15 minute, 1953), Butte Co., California. Coll.: R. B. Saul, 14 August, 1955. Chico Formation, top of Ponderosa Way Member. Late Coniacian or early Santonian.

[5] 23639. In concretions in massive, greenish-gray sandstone, east bank of Chico Creek, west of meadow with large flat-topped, lava block at north edge near road, 373.38 m (1225 ft.) south and 292.6 m (960 ft.) west of northeast corner of section 23, T. 23 N, R. 2 E, Paradise Quadrangle (15 minute, 1953), Butte County, northern California. Collectors: L. R. Saul and R. B. Saul, 20 August, 1952. Chico Formation, lowermost part of Ten Mile Member. Early Campanian.

[12] 24122. Fine- to coarse grained buff sandstone; 76.2 m (250 ft.) north of jeep trail in Jalama Canyon; elevation 190 m (625 ft.), 6.58 km (4.11 mi.) east and 1.1 km (0.69 mi.) south of Jalama Ranch Headquarters; 0.93 km (0.58 mi.) west and 0.66 km (0.41 mi.) north of southeast corner of topo, Lompoc Hills Quadrangle (7.5 minute, 1959), Santa Barbara Co., California. Coll.: D. Dailey, August, 1959. Jalama Formation. Late Campanian–early Maastrichtian

[12] 24128. Dark gray conglomerate in first small canyon east of Ramajal Canyon, elevation 167.6 m (550 ft.), 0.54 km (0.34 mi) south, 3.25 km (2.03 mi.) east of Jalama Ranch Headquarters, 1.22 km (0.76 mi.) north 4.27 km (2.67 mi.) west of southeast corner of Lompoc Hills Quadrangle (7.5 minute, 1959), Santa Barbara Co., California. Coll : D

Dailey, August 1958. Jalama Formation. Late Campanian–early Maastrichtian.

[12] 24237. Medium-grained, buff, arkosic sandstone, 396.2 m (1300 ft.) north of Jalama Creek, elevation 160 m (525 ft.), 0.48 km (0.30 mi.) south, 3 km (1.88 mi.) east of the Jalama Ranch Headquarters, 1.28 km (0.80 mi.) north, 4.59 km (2.87 mi.) west of southeast corner of Lompoc Hills Quadrangle (7.5 minute, 1959), Santa Barbara Co., California. Coll.: W. P. Popenoe, September 1938. Jalama Formation. Late Campanian–early Maastrichtian.

[6] 24340. Penz vicinity, conglomerate beds cropping out just below a drainage canal, southeast side of new Oroville Hwy, about 1.2 km (0.75 mi.) northeast of intersection with Pentz-Magalia-Oroville road, 426.7 m (1400') S., 182.9 m (600') W of the northeast corner of section 36, T. 21 N, R. 3 E, Cherokee quad. (7.5 minute, 1949), Butte Co., California. Coll.: W. P. Popenoe, 1960. Chico Formation, Musty Buck Member. Early Campanian.

[8] 24349. [=USGS M8601 and USGS M8745]. In place? large angular block of sandstone surrounded by sand at shoreline in covelet on north side of elongate seaward-pointing rock; approx. N30°W of Pigeon Point lighthouse, just south of Bolsa Point, Pigeon Point Quadrangle (7.5 minute, 1952), San Mateo County, California. Coll.: L. R. and R. B. Saul, October 11, 1960. Pigeon Point Fm. Middle Campanian.

[16] 26020. [=CIT 1158]. Hard sandstone slabs in fine-grained sandstone, cropping out on high bare cliff, north bank of Bell Canyon, just east of mouth of large gully, and 152.4 m (500') S, 2743.3 (9000') west of northeast corner of section 4, T. 1 N, R. 17 W, Calabasas Quadrangle (7.5 minute, 1952), Simi Hills, Ventura Co., California. Coll.: W. P. Popenoe, 11 Feb., 1972. Chatsworth Formation. Middle Campanian

[10] 26353. Approximately 1.2 km south of Garzas Creek, 671 m south and 114 m east of northwest corner of section 20, T 8 S, R 8 E, Howard Ranch Quadrangle, 7.5', 1953, photorevised 1971, Stanislaus County, California. Coll.: R. B. Stewart and W. P. Popenoe, 1944. Moreno Formation, "Garzas Sand" member. Late early to early late Maastrichtian.

[11] 26370. Reworked fossiliferous Turonian blocks in upper Campanian conglomerate lens in shale, northeast side of Cooper Canyon, approx. 411.5 m (1350') n, 670.6 m (2200') W of southeast corner of section 2, T. 21 S, R. 14 E, Alcalde Hills Quadrangle (7.5 minute, 1969), Alcalde Hills, Fresno Co., California. Coll.: J. Alderson, 18 June, 1977. Panoche Formation, "Alcalde Shale" Member. Late Turonian (with juvenile *Subprionocyclus* sp.).

[18] 26951. Small sandstone lens approx. 6.1 m (20 ft.) above road in roadcut on north side of Silverado Truck Trail, 274.3 m (900 ft.) south of northeast corner of section 18, T. 5 S, R. 7 W, El Toro Quadrangle (7.5 minute, 1949), Orange Co., California. Coll.: A. A. Almgren, 4 Dec., 1981. Ladd Formation, uppermost Upper Holz Shale Member. Late early Campanian.

[17] 26967. Small exposure of coarse-grained, poorly sorted sandstone at bottom of northwest-flowing tributary to main fork of Garapito Creek, 449.6 m (1475 ft.) and 2835 m (9380 ft.) east of northwest corner of section 5, T. 1 S, R. 16 W, Topanga Quadrangle (7.5 minute, 1952, photorevised, 1981), Santa Monica Mountains, Los Angles County, California. Coll.: J. M. Alderson, 31 Dec., 1981. Tuna Canyon Formation. Coniacian.

[3] 28717. South Cow Creek Valley, sandstone associated with conglomerate, lower South Cow Creek Valley, about 152.4 m (500 ft.) downstream from old bridge site across creek, and about 1.6 km (1 mi.) due west of buildings on Hunt Ranch, NE 1/4 of section 17, T. 31N, R. 2W, Millville Quadrangle, Shasta Co., California. Coll.: W. P. Popenoe, 27 Oct., 1971. Redding Formation, Oak Run Conglomerate Member of Haggart, 1986. Late Santonian.

[19] SDNHM 3403. Taylor Made Golf Facility at Salk Drive and College Blvd., elevation 45.1 m (148 ft.) along College Blvd., lat. 33°8'25′ N, long. 117°16'56′ W, [in general = SDNHM 3402, 3404, 4071, 4073], Carlsbad Research Center, Site 29, San Luis Rey Quadrangle 7.5' (1968), San Diego Co., California. Coll.: B. O. Riney, 26 April, 1987. Point Loma Formation. Late Campanian/?early Maastrichtian.

[19] SDNHM 3405. Carlsbad Research Center, 1.6 km north and 2.7 km west of southeast corner of San Luis Rey Quadrangle 7.5' (1968), indicated area along west side of College Blvd, starting about 0.32 km from intersection with El Camino Real extends southward for 0.15 km, San Diego Co., California. Coll.: B. O. Riney, 1987. Point Loma Formation. ?Late Campanian/early Maastrichtian.

[18] UCMP 2167. 3.2 km (2 mi.) N 10°W of BM 1271, Corona Quadrangle (1902), at a gate about 0.8 km (0.5 mi) below Modjeska Springs in Williams Canyon, Santa Ana Mountains, Orange Co., California. Ladd Formation, uppermost Holz Shale. Middle? Campanian.

Feeding behavior, phylogeny, and toxinology of *Conus furvus* Reeve, 1843 (Gastropoda: Neogastropoda: Conidae)

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ABSTRACT

The Indo-Pacific cone snail *Conus furvus* Reeve, 1843, is shown to be molluscivorous, based on four lines of evidence: (1) Specimens of *Conus furvus* maintained in aquaria were directly observed to attack and devour other gastropods, including other cone snails; (2) Its radular teeth share morphometric characteristics with other known molluscivorous *Conus* and differ from those of vermivorous and piscivorous species; (3) Molecular phylogeny places *Conus furvus* within a clade of molluscivorous species; (4) Sequences of two peptide toxins are most similar to conotoxins previously characterized from molluscivorous *Conus* species; one of these closely related peptides was previously shown to block molluscan L-type Ca channels. Similar to molluscivorous species such as *Conus omaria* and *C. victoriae*, *C. furvus* varies widely in shell shape and color pattern, even within its relatively restricted geographic range.

Additional Keywords: Conoidea, snail-hunting cone snail, radular morphology, conotoxins, RT-PCR, phylogeny.

INTRODUCTION

Cone snails are venomous marine gastropods (Kohn, 1959; Röckel, Korn, and Kohn, 1995), and the major biologically active components of their venoms are the conotoxins (Olivera, 2006), typically small (12–35 amino acid residues), highly constrained peptides. Many conotoxins discriminate between closely related molecular isoforms of a particular ion channel family (Terlau and Olivera, 2004); this property makes them valuable tools in neuroscience, and confers their therapeutic potential. The estimated ~100,000 different pharmacologically active peptides present in living *Conus* venoms comprise a very substantial neuropharmacological resource. The systematic study of conotoxins is a seemingly daunting task considering the enormous number of peptides. As the conotoxin sequence database expands, it is becoming clear that certain types are likely to be produced by species that specialize on particular prey and that belong to particular *Conus* clades (Olivera, 2002, 2006). Thus, establishing both the prey and the phylogenetic relationships of *Conus* species provides an important guidepost for searching for conotoxins with certain types of physiological activities.

Traditional cone snail taxonomy is based on shell morphology; this has proved difficult because of the absence of resolution and possible convergence of shell characteristics. None of the infragenic classification schemes primarily based on shell shape and sculpture, shell color patterns, and radular morphology has received widespread acceptance (Duda, Kohn, and Palumbi, 2001). Thus, these traditional criteria need to be complemented by other types of data.

The specific focus of this study, *Conus furvus* ("the

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dark cone") is unusual in several respects. Although it is found over a relatively restricted area of the tropical Indo-Pacific (almost all specimens have been collected in the Philippines, where it is quite common in some localities), its shell shape and color pattern vary widely (Figure 1). In most localities, the typical form of *Conus furvus* has a brown and white shell. However, in the Southwestern Philippines, a remarkable diversity of forms occurs, particularly along the island of Palawan and in the Sulu Sea (Figure 1). As new localities are explored, additional variations are being discovered. In the comprehensive treatment of Indo-Pacific *Conus* species by Röckel et al. (1995), the number of taxa synonymized with *Conus furvus* was probably among the highest for any species. The authors discussed about a dozen distinct forms which they regard as geographic variations. Röckel et al. (1995) concluded that *Conus furvus* "appears to be characterized by isolation of local populations." In general, the occurrence of sinistral specimens in any *Conus* is exceedingly rare; another notable feature of *C. furvus* is that most sinistral *Conus* specimens collected in the Philippines belong to this species (an example is shown in Figure 1).

In a study using the calmodulin intron sequence as a phylogenetic marker, Duda and co-workers (Duda et al., 2001; Duda and Kohn, 2005; Duda and Palumbi, 2004) grouped *C. furvus* with *C. litteratus* in their phylogenetic tree. They inferred that the two species diverged only at the beginning of the Pliocene; since *C. litteratus* is a well-established vermivorous species that feeds on capitellid polychaetes (Kohn and Nybakken, 1975), with a fossil record going to the Lower Miocene, this strongly suggested that *C. furvus* is a vermivorous *Conus*.

Purchasers of *Conus furvus* in the Guimaras Islands public market, in the Philippines, make a soup by boiling the snails with tomatoes, onions, and lemongrass. Only the portions of *C. furvus* near the foot are eaten; apparently the sections near the hepatopancreas have a bitter taste and grainy texture. An alternative culinary use of the snails is as an ingredient for a local dish prepared with noodles. Various other snails are typically sold with it: *C. radiatus*, a piscivorous species, is the most common other *Conus* found for sale with *C. furvus* at this locality.

In this paper we present data on prey capture behavior by *C. furvus*, the morphometric characteristics of its radular teeth, a phylogenetic analysis based on standard mitochondrial sequences, and the first conotoxin sequences obtained from this species. These data consistently support the conclusion that *Conus furvus* is a molluscivorous species.

MATERIALS AND METHODS

Specimen Collection and Dissection: Specimens of *C. furvus* for DNA extraction were purchased in a public market in Guimaras Island, Philippines. The snails were dissected to remove the hepatopancreas for total genomic DNA extraction and the venom duct for RNA extraction. A few specimens were maintained in an aquarium. Specimens for radular tooth analyses were collected in Coron Harbor and Bobok Island, Palawan, Philippines, and preserved in alcohol. The shells are deposited in the Field Museum of Natural History, Chicago, FMNH 300120, 300121, and 300122. The body of specimen No. 300121 is preserved in the Bernice P. Bishop Museum, Honolulu, Hawaii, BPBM 248751.

Analysis of Radular Teeth. The radular sacs of four specimens were dissected and 4–6 teeth from each mounted permanently in polyvinyl lactophenol medium on slides. Barb and blade lengths were measured from the tip of a tooth as described by Kohn et al. (1999), using an ocular micrometer and Nomarski differential interference contrast optics.

Genomic DNA Extraction: The total genomic DNA was extracted using the Xanthogenate DNA Extraction Protocol (Tillet and Neilan, 2000), a method based on the use of the polysaccharide solubilizing chemical xanthogenate. The method is non-toxic and requires no enzymatic or mechanical steps to break cells.

RNA Extraction: Frozen venom duct in RNA*later* (Ambion, Austin, Texas) was thawed in ice prior to RNA extraction, and a sample of the tissue (10–15mg) was homogenized in 1 mL Trizol reagent (Invitrogen, Carlsbad, California). The total RNA was extracted according to the manufacturer's recommendation.

Amplification of the Mitochondrial 12S and 16S rRNA and mtCOI Genes: For PCR amplification, primer pairs designed to hybridize to a segment of 12S, 16S rRNA genes and mtCO1 genes were used. The primer sequences used for the amplification are listed in Table 1. PCR amplifications of the three mitochondrial genes were carried out in a 10 μL reaction mixture containing 1X reaction buffer (200mM Tris HCl, 500mM KCl, pH 8.4), 0.7 mM of each dNTPs, 0.7 mM of both primers, 0.4 unit Taq DNA Polymerase, 3.0 mM $MgCl_2$, and approximately 50.0 ng of template DNA. PCR amplification was carried out for 40 cycles. Denaturation was carried out at 94 °C, annealing at 48°–55 °C and extension at 72 °C. The PCR products were visualized on 1% agarose gel containing 0.1 mg EtBr/mL. Multiple or smeared PCR products were further purified using the WIZ Prep DNA purification kit (Promega, Madison, Wisconsin), otherwise, the terminated reaction was directly sequenced. These sequences have been deposited at GenBank.

12S Accession Numbers: *ammiralis* EU682274, *aulicus* EU682275, *bandanus* EU682277, *dalli* EU682281, *episcopatus* EU682283, *flavus* EU794315, *furvus* EU682284, *geographus* EU794316, *kintoki* EU794317, *litteratus* EU794318, *magus* EU794319, *marmoreus* EU682288, *monachus* EU794320, *obscurus* EU794321, *omaria* EU682289, *textile* EU682296, *tulipa* EU794322, *virgo* EU794323; 16S Accession numbers: *ammiralis*

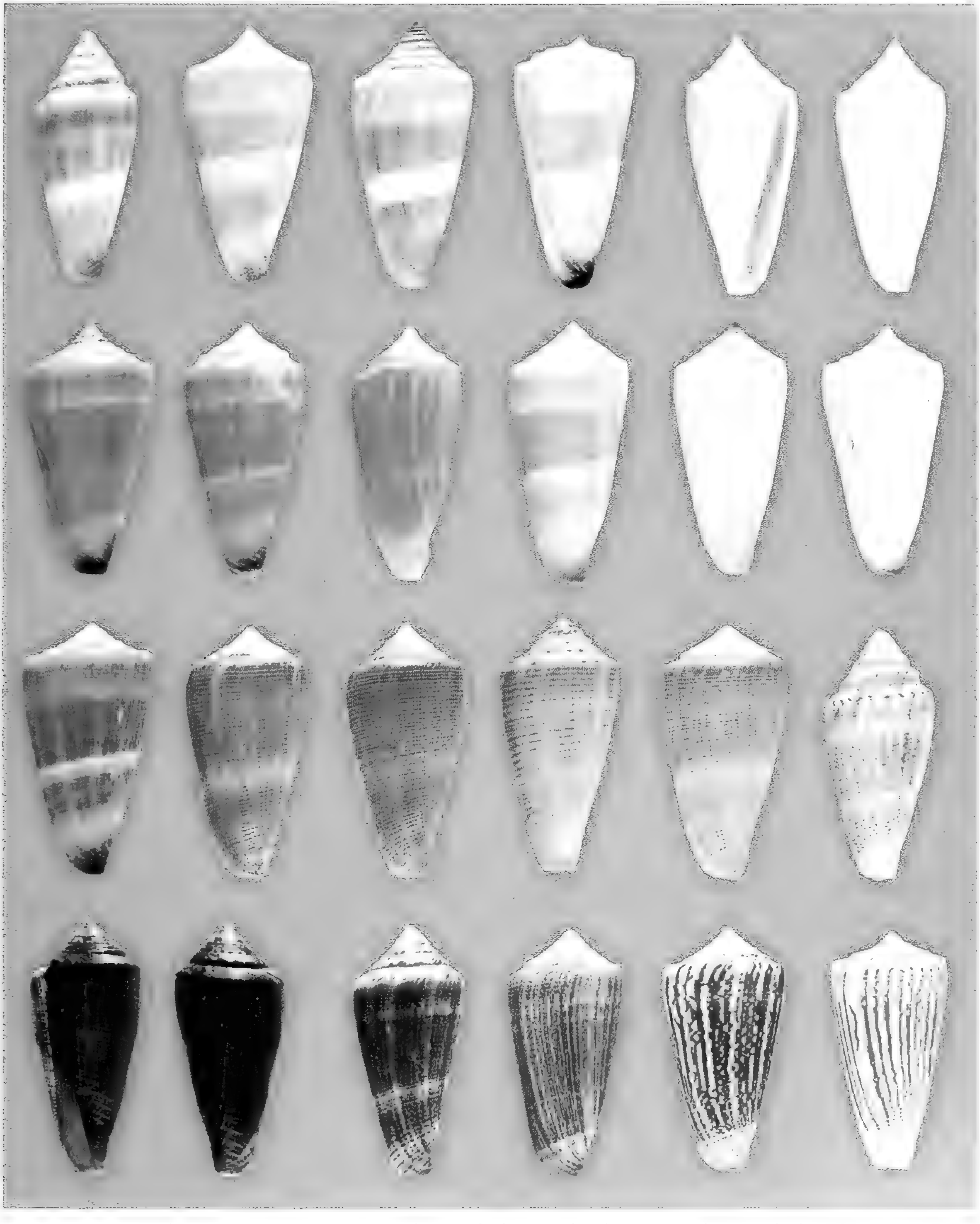

Figure 1. Some of the different variations of *Conus furvus*. The brown colored specimens shown in the bottom row, center, are similar to those used for this research. Note the sinistral specimen in the lower left hand corner.

Table 1. Primer pairs used for the amplification of the 12S, 16S rRNA gene and mtCO1 gene.

	12S	16S	mtCO1
Upstream primer	5′ AGAG(C/T)G(A/G) CGGGCGATGTGT 3′	5′ GTTTACCAA AAACATGGCTTC 3′	5′ GGTCAACAA ATCATAAAGATATTGG 3′
Downstream primer	5′ TGCCAGCAG (C/T)CGCGGTTA 3′	5′ CCGGTCTGA ACTCAGATCACGT 3′	5′ TAAACTTCAGGG TGACCAAAAAATCA 3′

EU682299, *aulicus* EU794324, *bandanus* EU794325, *dalli* EU078935, *episcopatus* EU078937, *flavus* EU794326, *furvus* EU682301, *geographus* EU794327, *kintoki* EU794328, *litteratus* EU794329, *magus* EU078939, *marmoreus* EU794330, *monachus* EU078938, *obscurus* EU794331, *omaria* EU794332, *textile* EU078936, *tulipa* EU794333, *virgo* EU794334.

RT-PCR of M and O-superfamily Conotoxin Genes: Single-stranded cDNA was synthesized from the total RNA extracted from the snail's venom duct using oligodT primers and Superscript II (Invitrogen, Carlsbad, California) and following the manufacturer's protocol. Double-stranded cDNA was synthesized using primers targeted to the conserved regions of the M- and O-superfamily genes. The product of the synthesis was visualized in a 1% agarose gel containing EtBr (0.1 mg/mL). The terminated reaction containing the PCR product of the correct size (~0.4Kb) was used for the cloning reaction. The cloning reaction followed the manufacturer's protocol for the TOPO-TA cloning kit (Invitrogen Life Technologies, Carlsbad, California). The clones were screened for inserts of the correct size and were cultured on a selective medium and incubated overnight with shaking (200 rpm) at 37 °C. The plasmids from these clones were extracted and sequenced.

Phylogenetic Analysis: 12S and 16S rRNA sequences were aligned using ClustalX, v1.8 (Jeanmougin, Thompson, Gouy, Higgins, and Gibson, 1998). The alignments were refined by eye using MacClade 4.08 (Maddison and Maddison, 2001). Trees were optimized using the individual rRNA alignments and the concatenated alignments (presented herein). To account for the complexity of sequence evolution, final analyses were restricted to model-based maximum likelihood (PAUP4b10, (Swofford, 2002)) and Bayesian inference (Huelsenbeck and Ronquist, 2001). Each method used maximum likelihood parameters describing sequence evolution that were optimized with a GTR+I+G model that includes six possible substitution types (GTR) and allows some sites to be invariant (I), allows across-site rate heterogeneity (G) and allows unequal base frequencies.

The Bayesian analysis ran for 100,000 generations (sampled every 100 generations) with the first 25,000 generations discarded as burn-in trees. Two MCMCMC runs (metropolis-coupled Monte-Carlo markov-chain), using four chains each, were used to thoroughly explore tree space. Convergence of the likelihoods was judged adequate by monitoring the MrBayes output describing the average standard error of the difference (ASED) in split frequencies between the two runs and by comparing plots of the tree log-likelihood trees from generation 50,000 to 100. By the last generation, the ASED was less than 0.004; the plot of likelihoods versus generation had stabilized. Furthermore, the PSRF (Potential scale reduction factor) reached 1.00 for the total tree length and for each model parameter.

RESULTS

Feeding Observations: Individuals of *Conus furvus* were frequently observed to prey on other cone snails in the aquarium. Most observations were made with *C. radiatus* as the prey. Upon introduction of prey into an aquarium tank with *C. furvus*, immediate behavioral responses were observed both from predator and prey. The prey immediately crawled away from *C. furvus* and attempted to bury itself in the sand. At almost the same time, *C. furvus* pointed its siphon toward the retreating snail and crawled in its direction. While still relatively far away from the prey, *C. furvus* extended its proboscis, and inserted it into the body of its prey with one jerking motion. Immediately the prey was observed to stop moving. *Conus furvus* then maneuvered the immobilized prey so that its aperture was turned upwards, away from the sand, after which *C. furvus* commenced feeding on the upturned *C. radiatus*.

Analysis of Radular Teeth: Radular tooth length ranged from 6.4 to 8.9% of shell length (mean = 7.5%) in the four specimens examined. Each tooth is armed with a barb that extends for 5% of the tooth length from the tip (range 4.6–5.4%), and a blade that extends for 9% of the length from the tip (range 8.9–9.3%). This morphometric data clearly identifies the teeth as those of a molluscivorous species, as noted by Nybakken (1990; see also Kohn, et al., 1999; Nishi and Kohn, 1999). However, these workers did not present details of *C. furvus* tooth morphometry, which differs markedly from previously examined molluscivorous *Conus* species. Nishi and Kohn (1999) divided the eleven species they studied into three groups based on both discrete and quantitative characters. The former, i.e. presence of one barb, one blade, and continuous serration clearly place *C. furvus* in Group A, with *C. araneosus*, *C. bandanus*, and *C. marmoreus*. Groups B and C have teeth with two barbs and no blade (Table 2). However, *C. furvus* differs from the Group A species in its quantitative characters. Its teeth are more than twice as long relative to shell length, thus matching the members of Group C rather than Group A (Table 2). The *C. furvus* teeth also differ from Group A and more

Table 2. Comparison of *Conus furvus* radular teeth with those of other molluscivorous species according to qualitative (discrete) and quantitative (continuous) characters. N, Number of specimens measured. Qualitative characters: B1, First barb; B2, Second barb; BL, Blade; SE, Serration; +, present; –, absent; C, Continuous; D, Discontinuous. S_L, Shell length; T_L, Tooth length; $B1_L$, Barb length; B_L, Blade length; SE_L, Serration length; BA_W, Base width; SH_W, Shaft width. All dimensions are in mm. Data on Groups A, B, and C from Nishi and Kohn (1999).

			Qualitative characters				Quantitative characters						
Group	Species	N	B1	B2	BL	SE	T_L/S_L	$B1_L/T_L$	$B2_L/T_L$	BL_L/T_L	SE_L/T_L	BA_W/T_L	SH_W/T_L
	C. furvus	4	+	–	+	C	0.07	0.05	—	0.09	0.70	0.06	0.04 (0.04–0.05)
A	*C. araneosus*	3	+	–	+	C	0.03 (0.026–.033)	0.08 (0.07–0.08)	—	0.13 (0.13–0.14)	0.49 (0.33–0.68)	0.11 (0.09–0.12)	0.05 (0.04–0.5)
	C. bandanus	5											
	C. marmoreus	15											
B	*C. ammiralis*	4	+	+	–	C	0.05 (0.03–0.08)	0.04 (0.03–0.05)	0.06 (0.05–0.09)	—	0.74 (0.62–0.81)	0.05 (0.04–0.08)	0.03 (0.02–0.05)
	C. canonicus	17											
	C. nodulosus	5											
	C. textile	15											
	C. victoriae	4											
C	*C. episcopatus*	11	+	+	–	D	0.07 (0.07–0.08)	0.05 (0.04–0.05)	0.08 (0.07–0.09)	—	0.68 (0.67–0.69)	0.07 (0.06–0.08)	0.05 (0.04–0.05)
	C. omaria	9											
	C. pennaceus	30											

closely resemble Groups B and C with respect to all four other quantitative characters that they share (Table 2).

PCR Amplification and Phylogenetic Reconstruction: A phylogenetic tree based on two standard markers, 12S and 16S rRNA was constructed as described under Methods. *Conus furvus* clustered on the same branch with species previously shown to feed on other mollusks (Figure 2). In contrast, *Conus furvus* was well-resolved from *C. litteratus*, the worm-hunting species postulated previously to be *C. furvus's* closest relative. The hypothesis that *C. furvus* is closer to the *C.litteratus* than to the other mollusk hunting snails is significantly rejected ($p<0.0001$) using Kishino-Hasegawa (Kishino and Hasegawa, 1989) and Shimodaira-Hasegawa (Shimodaira and Hasegawa, 1999) tests comparing the respective log-likelihood scores. The hypothesis that *C. furvus* and *C. litteratus* are sister species is significantly rejected by these tests using the 12S and 16S data alone. Because of the great variation of forms presently assigned to *Conus furvus*, we also obtained a "bar code" sequence (CO1 gene) from the specimens analyzed, which is deposited in GenBank.

Mapping Radular Tooth Characters to the Molecular Phylogenetic Tree: Morphometric data on radular teeth were available for seven of the nine molluscivorous species on the molecular tree (Figure 2), and the values of the seven quantitative morphometric characters for these species shown on the right side of Table 2 were entered into a discriminant function analysis. A phylogenetic tree generated from the proximity matrix calculated from the centroids of the first two canonical variates they accounted for 99.6% of the variance) (Figure 2B) was completely congruent with the conotoxin gene-based tree (Figure 2A).

O- and M- Superfamily Genes from *C. furvus*: Primer pairs designed to hybridize to the conserved regions of the O- and M-superfamily conotoxins successfully amplified conotoxin genes from the *C. furvus* venom duct. Translation of the amplified sequences resulted in amino acid sequences characteristic of the canonical arrangement of conotoxin precursors. Both of the sequences have a hydrophobic N–terminal signal sequence, which is highly conserved among conotoxins belonging to the same superfamily, an intervening pro region, and the mature toxin region at the C–terminus.

An O-superfamily conotoxin (Fr7.1) from *C. furvus* was successfully amplified and sequenced, and a 264-base sequence containing an open reading frame coding for the conotoxin was obtained. A 302-base sequence coded for a second conotoxin from *C. furvus* (Fr3.1) that belongs to the M-superfamily was also cloned and sequenced.

The O-superfamily conotoxin from *C. furvus* (Fr7.1) was strikingly similar to an ω–conotoxin isolated from *Conus textile* (Fainzilber et al., 1996), ωTxVII (Figure 3A). Alignment of the amino acid sequences shows 82.1% similarity. ωTxVIIA has previously been shown to target L-type Ca channels in mollusks; given the high sequence similarity, Fr7.1 is likely a voltage-gated Ca channel antagonist. A comparison of the M-superfamily conotoxins from *C. furvus* (Fr3.1) with M–superfamily conotoxins from *C. textile* (Tx3.5) and *C. marmoreus* (Mr3.5) also shows a high degree of similarity (Figure 3.B). Alignment of Fr3.1 with Tx3.5 shows the sequences to be 84.4% identical while Fr3.1 aligned with Mr3.5 shows the sequences to be 67.2% identical. The

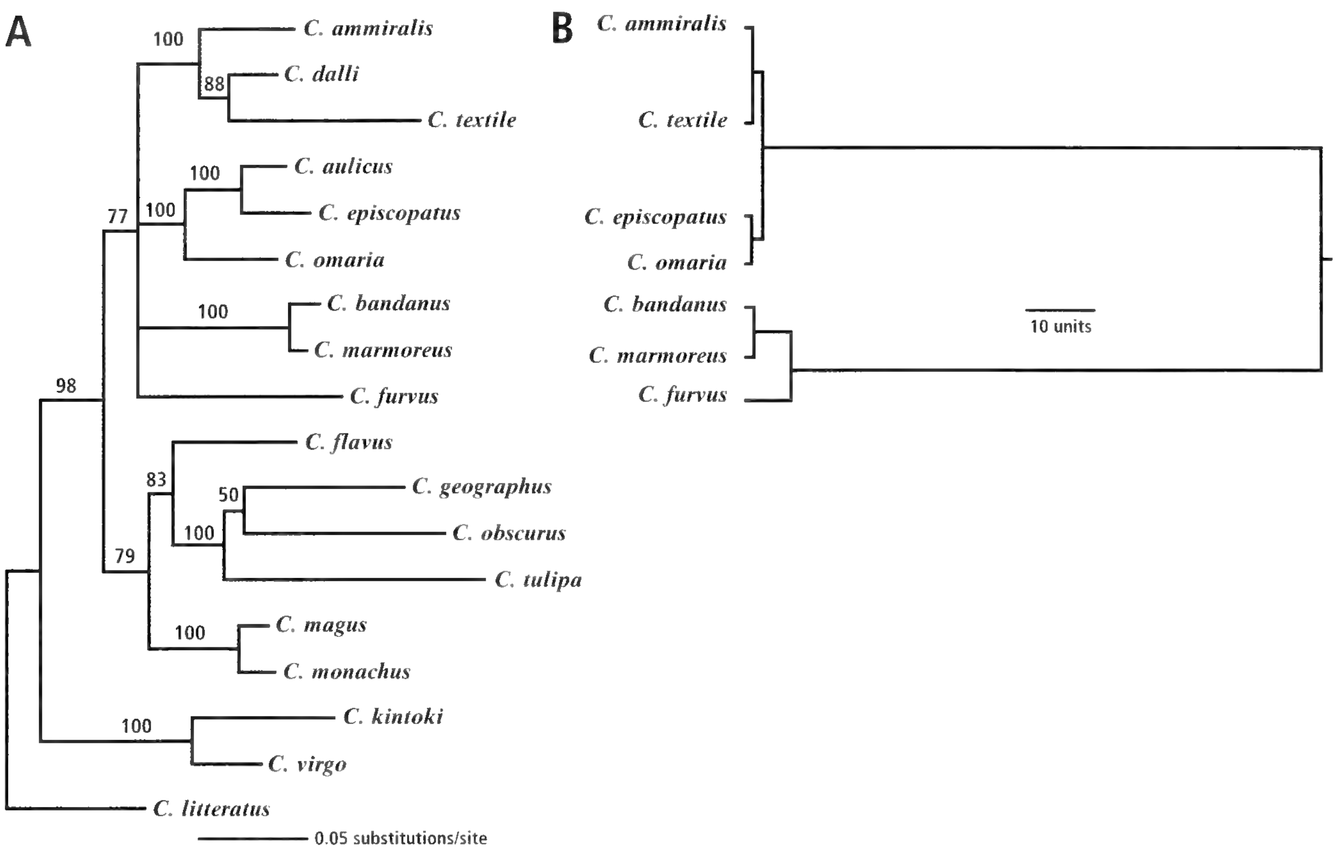

Figure 2. A. Optimal maximum likelihood tree from a Bayesian analysis of 12SrRNA and 16SrRNA sequences estimating the evolutionary relationship among some *Conus* species. The uppermost clade, from *Conus ammiralis* to *C. furvus*, comprises molluscivorous species. Branch labels are Bayesian support values summarizing confidence in each split. B. Neighbor-joining UPGMA tree from analysis of radular tooth morphometry, based on euclidean distance matrix of centroids of canonical variates 1 and 2 determined from discriminant function analysis of 7 radular tooth variables, measured as in Nishi and Kohn (1999).

Fr3.1 sequence clearly belongs to the m-3 branch of the M-conopeptide superfamily, which is characteristic of molluscivorous *Conus* species (Corpuz *et al.*, 2005). The two *C. furvus* conotoxin sequences are most similar to conotoxins from other molluscivorous species, consistent with the behavioral observations made above and with the phylogenetic tree shown in Figure 2.

DISCUSSION

In the central Philippines, *Conus furvus* occurs on rocky intertidal habitats. At low tide, individuals can be found in depressions on the substrate, together with other mollusks; this is where *C. furvus* is generally collected by fishermen in Guimaras Island, to be sold with other commercial shellfish at the public market. *Conus furvus* was formerly abundant along the shores of Guimaras Island, but an oil spill in the area in August 2006 threatened the marine life; *C. furvus* became much more scarce at this locality after the spill, but the population appears to be recovering.

From the results presented above, we conclude that *Conus furvus* is a molluscivorous species. This conclusion is based on direct observation of *C. furvus* attacking gastropod prey, on morphometric characteristics of the radular teeth that are shared with other molluscivorous *Conus*, by the high degree of sequence similarity between toxin precursors in the venom duct of *Conus furvus* and previously described conotoxins from other molluscivorous *Conus*, and by its phylogenetic proximity to them based on molecular markers. A previous molecular result suggesting that *C. furvus* might be vermivorous (Duda et al., 2001; Duda and Kohn, 2005) is probably erroneous.

An unusual feature of the *Conus furvus* attack on *C. radiatus* is that the prey was apparently injected with venom only once; multiple stinging was never observed. All other molluscivorous *Conus* species previously observed attack prey using multiple injections of venom before starting to feed on the immobilized prey (Yoshiba, 1983, 1987; Kohn, 2003). The reason for this behavioral difference is unclear, but the venom composition could well reflect it. A further biochemical characterization of *Conus furvus* venom is in progress (S. Espino and G. Concepcion, unpublished results).

The phylogenetic relationship between *C. furvus* and other *Conus* species evaluated for 12S and 16S rRNA gene sequences (Figure 2) is consistent with *C. furvus*

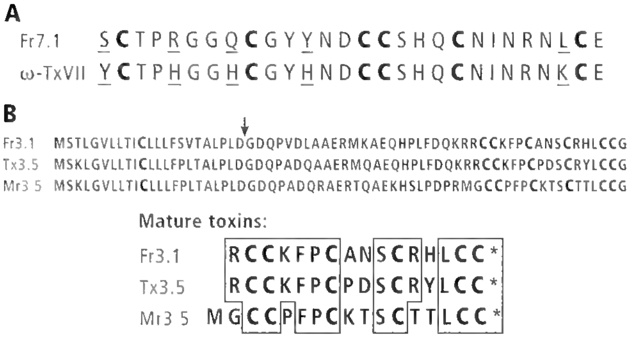

Figure 3. A. Alignment of the toxin region of Fr7.1 from *Conus furvus* and ωTxVII from *Conus textile* (GenBank Nuc. Acc. No. DD012770). B. Alignment of Fr3.1 from *Conus furvus* with other M-superfamily precursors highlighting the conserved amino acids. Tx3.5 and Mr3.5 were from *Conus textile* and *Conus marmoreus*, respectively (Corpuz et al., 2005). The predicted mature toxins are also shown; the asterisk denotes an amidated C-terminus.

being more closely related to the mollusk hunting *Conus* species than to *C. litteratus* (Bayesian clade support = 98), a vermivorous species. The several clades of molluscivorous *Conus* probably have a common ancestor. Using the tree based on molecular data in Figure 2A, the well supported groups can be referred to, using the subgenera of Marsh (1964) as clade names) as the *Conus* clade (with *Conus marmoreus* as the type), the *Cylinder* clade, (with *Conus textile* as the type), and the *Darioconus* clade (with *Conus omaria* as the type). Although *Conus furvus* belongs within the larger mollusk hunting clade, including these three groups, its position within the clade remains unresolved. Given its lack of a tented pattern, it has an unusual shell pattern for a molluscivore. However, some specimens of smaller, usually tented species such as *Conus barbieri* and *Conus victoriae* occasionally have plain brown shell variants, not unlike typical specimens of *Conus furvus*.

A more comprehensive molecular analysis of molluscivorous *Conus*, including *C. furvus*, has recently been carried out; these results will be presented elsewhere. Additional phylogenetic markers, such as ITS-2 sequences, were used for this study. This has led to greater refinement of the phylogenetic tree and supports the basic conclusion that *C. furvus* is a molluscivore.

ACKNOWLEDGMENTS

This work was supported in part by GM48677 from the U.S. National Institutes of General Medical Services (to BMO). The support of the University of the Philippines in the Visayas for a fellowship award to S.E. to pursue graduate studies in Chemistry is gratefully acknowledged. NSF Grant 0316338 partly supported the research of AJK. The late J.E. Norton contributed the *C. furvus* specimens for radular tooth morphometry, and Dr. M. Nishi assisted in the data analysis.

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Two new species of *Mitrella* (Gastropoda: Neogastropoda: Columbellidae) from the lower Miocene Chipola Formation of northwestern Florida

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ABSTRACT

Two new species of *Mitrella* from the lower Miocene Chipola Formation of are described. *Mitrella hayesorum* new species and *Mitrella phyllisae* new species are found primarily in Chipola Formation exposures along Farley Creek in northwestern Florida, USA. Placement of the new species in the genus *Mitrella* is tentative.

Additional Keywords: Neogene, ultraviolet light, gastropod, *Astyris*

INTRODUCTION

Species assigned to the genus *Mitrella* are widely distributed in the warm and shallow waters of the Recent seas of the world (Gardner, 1947, 1948). The exact origin of *Mitrella* is not clear, but some of the earliest representative of the genus from the southeastern portion of North America appeared in the Eocene (MacNeil and Dockery III, 1984; Palmer, 1937). Maury (1910) described three *Mitrella* (as *Astyris*) from the Chipola Formation. These were originally deposited in the Cornell University collection at Ithaca, New York, and now deposited at PRI. With more specimens than Maury had at her disposal, Gardner (1947) described 13 species and two subspecies of *Mitrella* from the Chipola Formation.

Mitrella have been found in all exposed facies of the Chipola Formation on the Chipola River, Tenmile Creek and Farley Creek, in the Chipola River drainage in Calhoun County, Florida. They are also present in the Chipola Formation exposed in the lower bed at Alum Bluff in Liberty County, Florida. The two new species described herein have been collected only in the Chipola Formation exposures in the Chipola River drainage, primarily at Farley Creek. Vokes (1989) stated the Chipola facies along Farley Creek where the two new species are most prevalent is a bivalve-rich miliolid lime-sand with many calcareous algae and coral heads, and assumed it was a shallow back-reef environment.

Some specimens were photographed under ultraviolet light (UV) to facilitate visualization of color patterns. Institutional abbreviations are: UF: Florida Museum of Natural History (FLMNH for locality records), University of Florida, Gainesville; PRI: Paleontological Research Institution, Ithaca; ANSP: The Academy of Natural Sciences, Philadelphia; AMNH: American Museum of Natural History, New York.

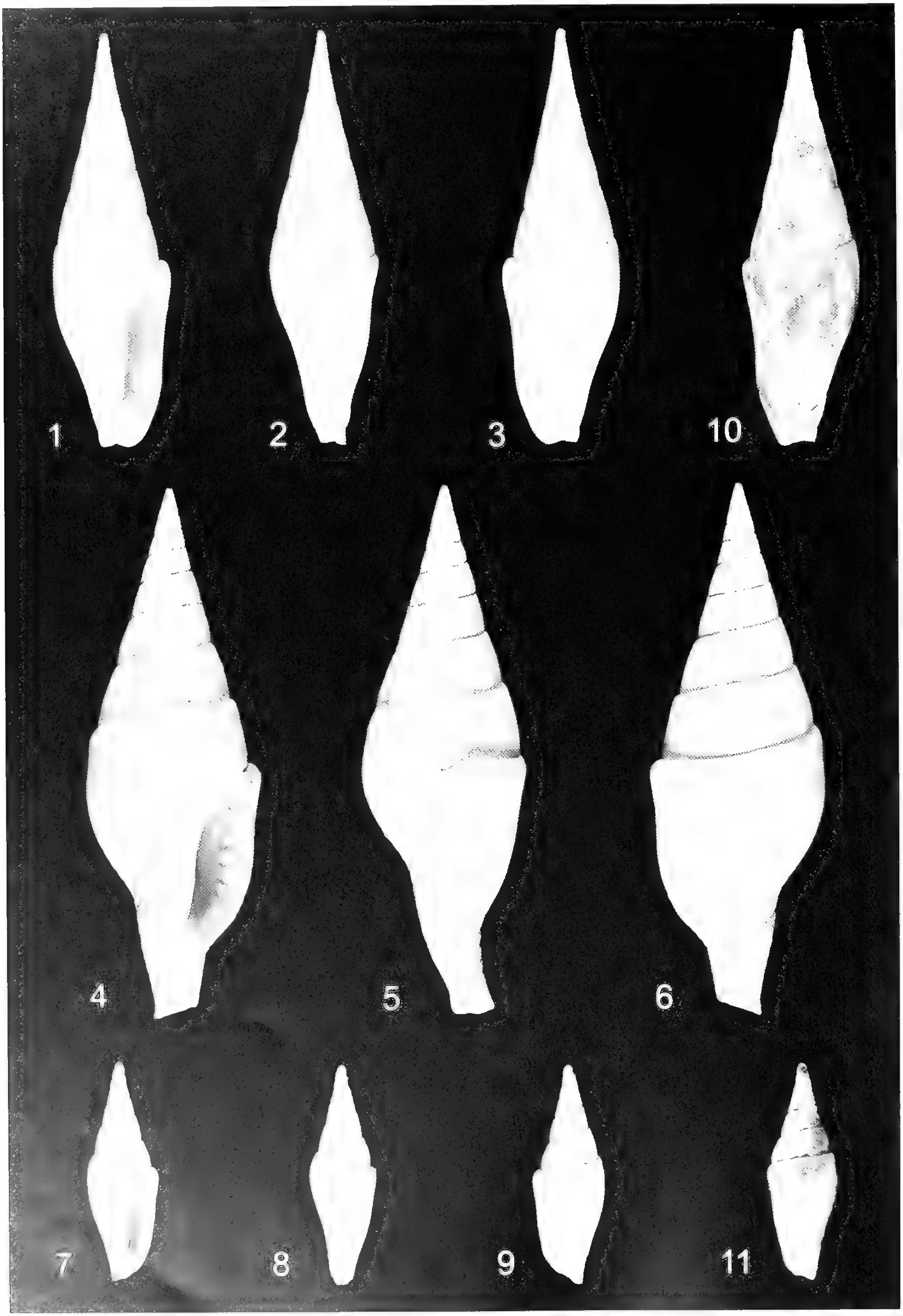
SYSTEMATICS

Superfamily Buccinoidea Rafinesque, 1815
Family Columbellidae Swainson, 1940
Genus *Mitrella* Risso, 1826

Diagnosis: Small to very small, smooth, fusiform shells. Sculpture, if present, of incised spiral lines. Spiral sculpture is generally restricted to the anterior end near the base: axial sculpture is, with few exceptions, entirely absent. The outer lip is dentate in adult specimens (Diagnosis according to Campbell [1993] and Keen [1971]).

?*Mitrella hayesorum* new species
(Figures 1–3, 10)

Description: Shell fusiform, narrow. Height of holotype 19.8mm. Protoconch mammillated, with about two smooth, rounded whorls, the second expanded, with no perceptible protoconch/teleoconch transition. Teleoconch with ten slightly convex, shiny whorls with microscopic irregular spiral grooves, axial sculpture lacking. Spire elevated with somewhat concave sides. Suture distinct. Aperture elongated, less than half the length of the entire shell. Outer lip sinuous, varicose externally, margin thin and sharp. Basal lip extending slightly beyond pillar. Posterior canal produced and thickened externally. Denticles present on inner surface of outer lip, ten to 12 in number, weak on anterior third, strongest on central third, frequently absent on posterior third. Parietal wall with two axial ridges, outer ridge weak with small raised beads reflecting underlying sculpture on pillar. Inner ridge prominent with median notch, adapical half of ridge strong, abapical half tapering and completely disappearing abapically. Base of pillar with about nine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oblique grooves with a rounded summit between grooves. Dark band about one third width of penultimate whorl appears below suture on last three whorls of holotype. Band has irregular narrow, oblique, light colored lines, some forming u- or v-figures.

Type Material: Holotype: UF 119655, height 19.8mm, width 5.6mm; Paratypes: ANSP-IP 81324, one specimen; AMNH-FI 43312, one specimen; PRI 8382, one specimen; Diegel-Duerr collection, one specimen. All from type locality.

Type Locality: FLMNH locality Farley Creek 07 (CA022), Farley Creek east of SR 275, Calhoun County, Florida (to protect privacy rights of landowners, specific locality information is available only to qualified researchers upon written request to the author or the Invertebrate Paleontology Division of the FLMNH), Chipola Formation.

Distribution: Chipola Formation along Tenmile and Farley Creeks and the Chipola River, Calhoun County, Florida.

Etymology: Named to honor the forestry-oriented Hayes family who have graciously granted the author, and others, permission to collect on their property.

Remarks: The species currently placed in *Mitrella* comprise a complex group and may have been differently assigned to the genera *Alia, Astyris, Nitidella* by different authors (Keen, 1971). The taxonomic position of *M. hayesorum* is questionable and its current assignment to *Mitrella* is tentative. *Mitrella hayesorum* has unique characters, such as the bulbous second whorl of the protoconch, extended slightly concave spire and wide siphonal canal extending below the pillar, and cannot be confused with any other known *Mitrella*. Although no specimens of *Mitrella dalli* (Maury, 1910), the species in the Chipola Formation closest in form to *M. hayesorum*, were available for study, Maury's figure of *M. dalli* (1910: pl. 6, fig. 2) indicates a smaller shell (12 mm), a shorter, stouter spire, and a narrower anterior canal than *M. hayesorum*. The nearest European fossil congener of *Mitrella hayesorum* is *Mitrella (Macrurella) nassoides* (Grateloup, 1827) (Figures 4–6) from the early Pliocene of Italy, which is larger, wider at the midbody, and has a narrow anterior canal. The maximum height of all specimens of *Mitrella hayesorum* examined is 19.93 mm, minimum height is 18.17 mm. Exposure of *M. hayesorum* to ultraviolet light (Figure 10) reveals a fluorescent pattern of axial flammules in addition to the narrow band below the suture on the anterior whorls of the new species. Seven specimens of the most common *Mitrella* in the Chipola Formation, *Mitrella ischna* Gardner, 1947, a more robust species than *M. hayesorum*, were examined under UV light and revealed fine filamentous lines covering all teleoconch whorls. Three specimens of *Mitrella asema* Gardner, 1947, a shorter species than *M. hayesorum*, exhibits, under UV light, narrow axial bars running from suture to suture, offset in alignment from previous whorls, with four per whorl on most teleoconch whorls.

?*Mitrella phyllisae* new species
(Figures 7–9, 11)

Description: Shell small, fusiform. Height 7 mm, width 2.2 mm. Protoconch with two smooth whorls, second whorl enlarged. Teleoconch with five smooth, convex whorls, without axial sculpture. Spire sides slightly concave. Suture impressed. Aperture less than half the length of entire shell. Outer lip with slight varix, margin thin and sharp, usually dentate within. Thin parietal wash present. About seven impressed oblique grooves cross base of pillar, separated by narrow bands with rounded summits. Faint round spots, eight on last whorl of holotype, appear on last three whorls. Spots about one-quarter the height of penultimate whorl in diameter rest just above median line of the whorls.

Type Material: Holotype, UF 119656, height 7.0 mm, width 2.2 mm; Paratypes, ANSP-IP 81325, one specimen; AMNH-FI 43313, one specimen; PRI 8383, one specimen; Diegel-Duerr collection, one specimen. All from type locality.

Type Locality: FLMNH locality Farley Creek 07 (CA022), Farley Creek east of SR 275, Calhoun County, Florida, (to protect privacy rights of landowners, specific locality information is available only to qualified researchers upon written request to the author or the Invertebrate Paleontology Division of the FLMNH), Chipola Formation.

Distribution: Chipola Formation along Tenmile and Farley Creeks and the Chipola River, Calhoun County, Florida.

Etymology: Named for Phyllis Diegel, the author's companion and a knowledgeable conchologist and paleontologist.

Remarks: As with *Mitrella hayesorum*, the assignment of *M. phyllisae* to *Mitrella* is tentative. A cursory inspection would indicate *Mitrella phyllisae* to be a dwarf *M. hayesorum*. Closer examination reveals that *M. phyllisae*

Figures 1–11.—*Mitrella* species. **1–3.** Apertural, lateral, and abapertural views of the holotype of *Mitrella hayesorum* new species, UF 119655, height 19.8 mm, width 5.6 mm, Burdigalian Miocene. **4–6.** Apertural, lateral, and abapertural views of *Mitrella nassoides* (Grateloup, 1827) UF 119657, height 25.5 mm, width 8.6 mm, Zanclean Pliocene, from Liguria County, Ceriale, Italy, for comparison with *M. hayesorum*. **7–9.** Apertural, lateral, and abapertural views of the holotype of *Mitrella phyllisae* new species, UF 119656, height 7.0 mm, width 2.2mm, Burdigalian Miocene. **10, 11.** *Mitrella* exposed to UV light **10.** Holotype of *Mitrella hayesorum* (same specimen as Figure 3) showing UV exposed pattern. **11.** Holotype of *Mitrella phyllisae* (same specimen as Figure 9) showing UV exposed pattern.

differs from the much larger *M. hayesorum* by the shorter spire, the slightly more impressed suture, and fewer oblique incised lines on the base of the shell. A series of dots about 1 mm in diameter are visible on *M. phyllisae* encircling all teleoconch whorls, one-third the length of the whorl below the suture, eight on the last whorl. Exposure to UV light reveals (Figure 11), in addition to the larger dots, a field of minute dots covering the entire teleoconch, somewhat reminiscent of the pattern on the Recent *Mitrella ocellata* (Gmelin, 1791) from the western Atlantic. Also, the anterior portion of the outer lip of *M. phyllisae* is less developed than that of *M. hayesorum,* which is wider and extends beyond the pillar. The height of all specimens of *M. phyllisae* examined varies less than 1.0 mm, from a maximum of 7.4 mm to a minimum of 6.8 mm.

ACKNOWLEDGMENTS

The author extends his appreciation to Roger Portell, FLMNH, for providing the plates and commenting on an earlier draft of the manuscript. Digital images were prepared by Sean Roberts, FLMNH. Thanks also to Marc Grigis, Belgium, for donation of a specimen of *Mitrella nassoides*, to Dr. Bernard Landau, Portugal, for encouragement and advice, and to Burke and Brooks Hayes and also Archie and Vicki Whittington for permission to collect on their respective properties in North Florida. Pamela McBride provided secretarial assistance. I am indebted to two anonymous reviewers whose comments and suggestions improved the manuscript.

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Catalogue of the type material of mollusks deposited at the Zoology Museum, University of Costa Rica

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ABSTRACT

This catalogue compiles the basic data for mollusk type material deposited at the Zoology Museum of the University of Costa Rica. It includes 62 holotypes and 151 paratypes, representing 68 species and 41 genera. The species, authors, date of publication, bibliographic references, type locality, catalogue number, number of specimens, state of preservation, and related information are indicated for each taxon. In some cases, remarks on the current taxonomic status and other useful information are provided. For all species, except for opisthobranchs, the shell of either the holotype or one of the paratypes is illustrated.

Additional Keywords: Holotype, paratype, Mollusca, mollusk collection

INTRODUCTION

The Zoology Museum of the University of Costa Rica (MZUCR) was founded in 1960 by UCR professors Douglas C. Robinson and William Bussing. The collection consists of both invertebrates and vertebrates, and includes birds, fishes, mammals, reptiles, amphibians, tunicates, decapods, sipunculids, sponges, corals, and mollusks, among other groups. The specimens come from a wide variety of research projects, and donations from national and international researchers, as well as amateur naturalists. Most of the material is preserved in a wet collection (70% ethanol), but there is also a dry collection.

THE MOLLUSK COLLECTION AT THE UNIVERSITY OF COSTA RICA

Former UCR curator Carlos Villalobos and a great number of other researchers started the mollusk collection at the Museum in 1964. Since then, UCR staff and visiting scientists have continuously added to the collection. In addition, a significant amount of material has been donated to the Museum. Some examples include the collections of malacologists George Richard, from University of La Rochelle, France (mainly specimens of the family Conidae and other material from the Indo-Pacific), Kristie L. Kaiser, associated with the Santa Barbara Museum of Natural History (material from Cocos Island, Costa Rica), and the Latin American collection of independent scientist Dwight W. Taylor (including terrestrial and freshwater mollusks as well as type material); and amateur naturalists Michael Montoya (a valuable collection of marine mollusks from the Mesoamerican region, Cocos Island, and the Caribbean), Mary Yost (marine mollusks from Guanacaste, Costa Rica), Robert Nishimoto and others in 1969 (marine mollusks from Puntarenas, Costa Rica), and Jerry Wellington in 1972 (marine mollusks from both the Pacific and the Atlantic). In 2005, the collection increased in size considerably, having absorbed the mollusk collection of the Costa Rican National Biodiversity Institute (INBio), which closed its Malacology Department in September 2004. Currently, the collection is comprehensive, including more than 37,670 lots and 216,587 specimens representing the molluscan fauna of the Pacific Coast of North, Central, and South America (however, there is also material from the Indo-Pacific, France, and Africa).

The collection is divided into two main categories: a dry collection consisting mainly of the shells of bivalves and gastropods, and a wet collection comprising cephalopods, gastropods, bivalves, polyplacophorans, and terrestrial and freshwater mollusks preserved in alcohol.

Considering that this collection is the most important in the country and perhaps in all of Central America, and due to the recent increase in the amount of type material, it is important to compile this information and publish a catalogue that addresses in detail the literature available for the type material, its location, and illustrations of the shell of each type represented. We hope to facilitate the future work of taxonomists and help locate type material, contributing in this respect to their research.

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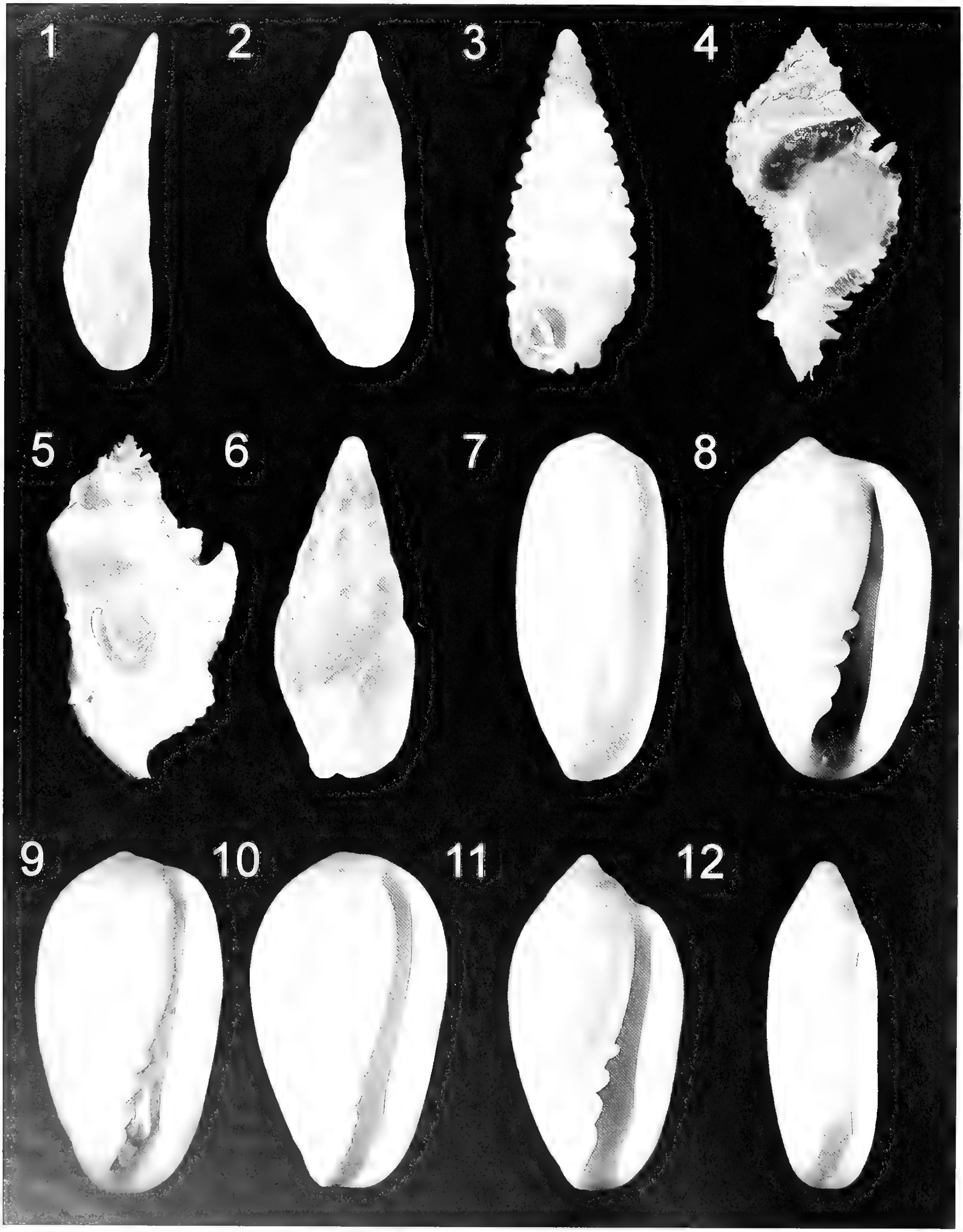
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TYPE COLLECTION

This catalogue includes 62 holotypes and 151 paratypes, representing 68 species and 41 genera. All types are listed alphabetically by species epithet. Photographs of opisthobranch types are not included, although they are listed in this catalogue. For each taxon, the following information is included: the name of the species cited exactly as it was published in the original description, the author(s), date of publication, bibliographic references, type locality, catalogue number, number of specimens, state of preservation, and related information (SEM stubs, microscopy slides, egg masses of the specimens). In some cases, remarks on the current taxonomic status and other useful information are provided. We also indicate whether the specimen is preserved complete (including the shell and soft parts) or when only the shell remains in the dry collection.

In a few cases, the information in the original publication about the location of the type material is not accurate, and we clarify this in the remarks. For each species, either the holotype or one of the paratypes is photographed, and the figure number is properly indicated beside the specimen.

Although the original publications on some type material (*Noumea regalis* Ortea, Caballer and Moro, 2001; *Dentimargo argonauta* Espinosa and Ortea, 2002; *Ticocystiscus iberia* Espinosa and Ortea, 2002; *Cratena piutaensis* Ortea, Caballer, and Espinosa, 2003; *Milleria ritmica* Ortea, Caballer, and Espinosa, 2003; *Phidiana adiuncta* Ortea, Caballer, and Moro, 2004; and *Costoanachis cascabulloi* Espinosa and Ortea, 2004) stated that the material was deposited at INBio, in fact, the material was never deposited there or at the University of Costa Rica. Although attempts have been made to clarify the location of this material with the authors, none has been successful. Abbreviation used in the text: m.a.s.l. = meters above sea level.

CATALOGUE OF TYPE MATERIAL

academica, *Okenia*, Camacho-García and Gosliner, 2004: 431–438, figs. 1–3. Type locality: Playa Tamarindo, Tempisque Conservation Area, Puntarenas, Costa Rica (9°03′58″ N, 85°51′08″ W), 0 m depth. HOLOTYPE: MZUCR-INB0003118102 (specimen), MZUCR-INB0003764988 (radula and jaw, SEM stubs), PARATYPE: MZUCR-INB0001496648, San Miguel, Reserva Natural Absoluta de Cabo Blanco, Tempisque Conservation Area, Puntarenas, Costa Rica (9°34′53″ N, 85°08′26″ W), 0 m depth.

aeci, *Philinopsis*, Ortea and Espinosa, 2001b: 41, pl. 2C, 3A. Type locality: Punta Mona, Manzanillo, Limón, Costa Rica (9°6′37″ N, 82°66′08″ W), 6 m depth. HOLOTYPE: MZUCR-INB0001495781. PARATYPE: MZUCR-INB0003721981. Same locality data as holotype. Remarks: Paratype said to be deposited at the Instituto de Oceanología, Habana, Cuba, but was deposited at INBio.

alfiopivai, *Plesiocystiscus*, Espinosa and Ortea, 2002: 102–106, figs. 1–3, pl.1. Type locality: Manzanillo, Limón, Costa Rica (9°39″ N, 82°39″ W), 20–24 m depth. HOLOTYPE: MZUCR-INB0003754713 (shell, Figure 21).

anulatus, *Janolus*, Camacho-García and Gosliner, 2006: 1295–1305, figs. 1–7. Type locality: Isla Ballena, Parque Nacional Marino Ballena, Puntarenas, Costa Rica (9°06′24″ N, 83°43′35″ W), 6 m depth. HOLOTYPE: MZUCR-INB0001495772 (specimen), MZUCR-INB0003764958 (SEM stub with jaw), MZUCR-INB0003764987 (SEM stub with radula), MZUCR-INB0003765066 (slide preparation with labial plate). PARATYPES: MZUCR-INB0003764915 (1 specimen). Same locality data as holotype; MZUCR-INB0003836171 (1 specimen), SW side of Isla Plata, Guanacaste, Costa Rica (10°26′48″ N, 85°48′20″ W), 10 m depth.

arleyi, *Melanella*, Espinosa, Ortea and Magaña, 2001: 123–124, fig. 3. Type locality: Punta Mona, Manzanillo, Limón, Costa Rica (9°37″ N, 82°37″ W), 10–12 m depth. HOLOTYPE: MZUCR-INB0003138455, (shell, Figure 1).

awapa, *Doto*, Ortea, 2001a: 21–23, pl. 2G, fig. 9. Type locality: Punta Mona, Manzanillo, Limón, Costa Rica (9°37″ N, 82°37″ W), 10 m depth. HOLOTYPE: MZUCR-INB0001497507 (specimen and egg mass).

beatrix riopejensis, *Helicina* ("*Gemma*"), Richling, 2004: 303–308, figs. 133–138. Type locality: SW of Liverpool (about 24 km of Puerto Limón) along Río Peje, Limón, Costa Rica (90°55′46″ N, 83°13′15″ W), 135 m.a.s.l. HOLOTYPE: MZUCR-INB003542625 (shell, Figure 30). PARATYPE: MZUCR-INB0003542626 (shell). Same locality data as holotype.

boeckereli, *Alcadia* (*Microalcadia*), Richling, 2001: 6–7, figs. 9–12. Type locality: Guanacaste National Park, about 10 km S of Santa Cecilia, Volcán Orosí, near field station Pitilla, beginning of Sendero Orosilito, primary forest, Guanacaste, Costa Rica (10°59′18″ N, 85°25′34″ W), 700 m.a.s.l., HOLOTYPE: MZUCR-INB0003404980 (shell, Figure 24). Remarks: species was assigned to *Alcadia* in Richling, 2004: 374–377, figs. 257–262; previously in *Helicina*.

bramale, *Hoplodoris*, Fahey and Gosliner, 2003: 198–201, figs. 17E, 28–30. Type locality: Puerto Escondido, Manuel Antonio National Park, Puntarenas, Costa Rica (9°23′ N, 84°08′ W), 0 m depth. HOLOTYPE:

Figures 1–12. 1. Holotype of *Mellanela arleyi*, 2.1 mm. **2.** Holotype of *Melanella zugnigae*, 1.1 mm. **3.** Holotype of *Triphora orteai*, 2.0 mm. **4.** Paratype of *Chicoreus* (*Phyllonotus*) *eversonii*, 137 mm. **5.** Paratype of *Typhisopsis carolskoglundae*, length 19 mm, diameter, 11mm. **6.** Paratype of *Mitrella loisae*, 4.9 mm. **7.** Holotype of *Hyalina chicoi*, 9.1 mm. **8.** Holotype of *Prunum cahuitaensis*, 12.5 mm. **9.** Holotype of *Prunum chumi*, 18.2 mm. **10.** Holotype of *Prunum holandae*, 19.5 mm **11.** Holotype of *Prunum lizanoi* 13.2 mm. **12.** Holotype of *Volvarina socoae*, 11.8 mm.

MZUCR-INB0003572316. PARATYPES: MZUCR-INB0003572306 (6 specimens), Punta Uvita, Marino Ballena National Park, Puntarenas, Costa Rica (9°08′ N, 83°45′ W), 0–2 m depth; MZUCR-INB0001498550 (1 specimen), 0 m depth. Same locality data as the other paratypes.

bribri, *Gibberula*, Espinosa and Ortea, 2000: 100–101, pl 1, fig. 4. Type Locality: Punta Mona, Manzanillo, Limón, Costa Rica (9°38′ N, 82°37′ W), 10–15 m depth. HOLOTYPE: MZUCR-INB0003349908 (shell, Figure 16). PARATYPES: MZUCR-INB0003349905, MZUCR-INB0003349906, MZUCR-INB0003349907 (1 specimen each, shells). Locality data for all paratypes same as holotype.

caballeri, *Philine*, Ortea, Espinosa and Moro, 2001: 38–40, figs. 9–10, pl. 2B. Type locality: Punta Mona, Manzanillo, Limón, Costa Rica (9°37′ N, 82°37′ W), 9 m depth. HOLOTYPE: MZUCR-INB0003138445.

cabecar, *Doto*, Ortea, 2001a: 34–37, figs. 16–17, pl. 2M. Type Locality: Punta Mona, Manzanillo, Limón, Costa Rica (9°39′ N, 82°37′ W), 20 m depth. HOLOTYPE: MZUCR-INB0003449742.

cahuitaensis, *Prunum*, Magaña, Espinosa and Ortea, 2003: 122–124, figs. 1, 2A–B, pls. 1A, 2A. Type Locality: 1 km E from Puerto Vargas Station, Cahuita National Park, Limón, Costa Rica (9°43′33″ N, 82°48′31″ W). HOLOTYPE: MZUCR-INB0003718203 (shell, Figure 8). PARATYPE: MZUCR-INB0003718204 (shell). Same locality data as holotype.

caribetica, *Gibberula*, Espinosa and Ortea, 2002: 113–114, fig. 10, pl.1. Type locality: Punta Mona, Manzanillo, Limón, Costa Rica (9°37′ N, 82°37′ W), 8 m depth. HOLOTYPE: MZUCR-INB0003718205 (shell, Figure 17).

carolskoglundae, *Typhisopsis*, Houart and Hertz, 2006: 56–58, figs. 17–25, 47–49, 59, 63. Type locality: Playas del Coco, Guanacaste, Costa Rica (10°55′53″ N, 85°69′81″ W), 24–37 m depth, on mud bottom. PARATYPE: MZUCR-6153, (shell, Figure 5). Boca de la Honda, Veraguas, Panamá (7°27′ N, 80°51′ W), in white sand. Remarks: The coordinates and the collecting locality of this paratype appear to be incorrect since these coordinates plot inland.

chicoi, *Hyalina*, Espinosa and Ortea, 1999a: 167–169, figs. 1A–C, 2A, 3A–D. Type locality: Manzanillo, Limón, Costa Rica (9°38′ N, 82°39′ W), 5–12 m depth. HOLOTYPE: MZUCR-INB0003350839 (shell, Figure 7). Remarks: Paratype said to be deposited at INBio in the original publication, but never sent to INBio or the University of Costa Rica.

chiquitica, *Oligyra*, Richling, 2001: 1–2, figs. 1– 2. Type Locality: 9 km W of Matina, a little stream up the Río Barbilla from the crossing of the road Siquirres to Limón, along a tributary of Río Barbilla, Limón, Costa Rica (10°03′29″ N, 83°22′24″ W), 70 m.a.s.l. HOLOTYPE: MZUCR-INB0003404977 (soft parts and shell, Figure 32). PARATYPE: MZUCR-INB0003404981 (shell and soft parts).

chumi, *Prunum*, Espinosa and Ortea, 2000: 107–108, figs. 8–9. Type locality: Manzanillo, Limón, Costa Rica (9°38′ N, 82°39′ W), 10–15 m depth. HOLOTYPE: MZUCR-INB0003349912 (shell, Figure 9). PARATYPES: MZUCR-INB0003349913, MZUCR-INB0003349914, MZUCR-INB0003349915 (1 specimen each, shells). Locality data for all paratypes same as holotype.

convenientis, *Eubranchus*, Caballer and Ortea, 2002: 81–85, figs. 2, 3, 7 pl. 1B. Type locality: Manzanillo, Limón, Costa Rica (9°38′ N, 82°39′ W), 0 m depth. HOLOTYPE: MZUCR-INB0003576832.

corcovadensis, *Cryptostrakon*, Cuezzo, 1997: 1–8, figs. 1–14. Type locality: Corcovado National Park, Sirena Station, Sendero a Río Los Patos, Puntarenas, Costa Rica (8°30′ N, 83°35′ W), 10 m.a.s.l. HOLOTYPE: MZUCR-INB0001468087 (shell, Figure 37; SEM stub with radula). PARATYPE: MZUCR-INB0001468080 (shell and soft parts). Remarks: Paratype locality data same as holotype. In the publication, the holotype and paratype catalogue numbers mistakenly written INB000468087 and INB000468080, respectively.

costacubensis, *Janolus*, Ortea and Espinosa, 2000: 80–83, figs. 1–2. Type locality: Miramar, N coast of La Habana, Cuba (23°7′21″ N, 82°25′10″ W), 20–25 m depth. PARATYPE: MZUCR-INB0001497432 (1 specimen), collecting locality Manzanillo, Limón, Costa Rica (9°38′ N, 82°39′ W), 20–25 m depth.

cruzmoralai, *Dentimargo*, Espinosa and Ortea, 2000: 110–113, fig. 11, pl. 2. Type locality: reefs from Manzanillo, Limón, Costa Rica (9°38′ N, 82°37′ W), 12–15 m depth. HOLOTYPE: MZUCR-INB0003349903 (shell, Figure 14).

curere, *Doto*, Ortea, 2001a: 17–18, fig. 7, pl. 2C. Type locality: Puerto Viejo, Limón, Costa Rica (9°38′ N, 82°39′ W), 6 m depth. HOLOTYPE: MZUCR-INB0001496453.

destinyae, *Cuthona*, Hermosillo and Valdés, 2007: 119–124, figs. 1C, 4, 5. Type locality: La Godornia, Zihuatanejo, Guerrero, México (17°37.854′ N, 101°33.562′ W). PARATYPES: MZUCR-INB0003118106 (4 specimens), Playa Avellanas, Guanacaste, Costa Rica (10°13.583′ N, 85°50.433′ W).

duao, *Doto*, Ortea, 2001a: 28–30. figs. 12– 13, pls. 2A, 2K. Type locality: Punta Mona, Manzanillo, Limón, Costa Rica (9°37′ N, 82°37′ W), 10–19 m depth. HOLOTYPE: MZUCR-INB0003138803.

echandiensis, *Helicina*, Richling, 2004: 271–277, figs. 77–84. Type locality: La Amistad National Park, Las Alturas Sector, Southern Cordillera de Talamanca, S of Cerro Echandi, Campamento Echandi, Puntarenas, Costa Rica (09°01′33″ N, 82°40′12″ W), 2840 m.a.s.l. HOLOTYPE: MZUCR-INB0003542520 (soft parts and shell, Figure 26). PARATYPES: MZUCR-INB0003574064 (1 specimen, soft parts and shell), MZUCR-INB0003542521 (1 specimen, soft parts and shell), MZUCR-INB0003428246 (19 specimens, shell and soft parts). Locality data for all paratypes same as holotype.

elizabethae, *Adrana*, Ortea and Espinosa, 2001e: 61–64, fig. 17. Type locality: in front of Gandoca beach, Limón, Costa Rica (9°36′ N, 82°35′ W), 10–15 m depth. HOLOTYPE: MZUCR-INB0003449558 (shell, Figs. 38–39).

escondida, *Helicina* (*"Gemma"*), Richling, 2004: 348–357, figs. 210–218. Type locality: 9 km W of Matina, a little stream up the Río Barbilla from the crossing of the road from Siquirres to Limón, along a tributary of Río Barbilla, Limón, Costa Rica (10°03′29″ N, 83°22′24″ W), 70 m.a.s.l. HOLOTYPE: MZUCR-INB0003542623 (soft parts and shell, Figure 27), PARATYPE: MZUCR-INB0003542624 (soft parts and shell). Locality data same as holotype.

espinosai, *Ancula*, Ortea, 2001b: 49, pl. 2D. Type locality: Punta Mona, Manzanillo, Limón, Costa Rica (9°37′ N, 82°37′ W), 9 m depth. HOLOTYPE: MZUCR-INB0003188764.

eugeniae, *Elysia*, Ortea and Espinosa, 2002: 130–133, figs. 1–2, pl. 1A. Type locality: Manzanillo, Limón, Costa Rica (9°38′ N, 82°39′ W), 16 m depth. HOLOTYPE: MZUCR-INB0001497478.

eversonii, *Phyllonotus*, D'Attilio, Myers and Shasky, 1987: 162–164, figs. 1–2. Type Locality: SW side of Isla Manuelita, Isla del Coco, Costa Rica (5°33′ N, 87°03′ W, 66 m depth. PARATYPE: MZUCR 4934 (shell, Figure 4).

gandocaensis, *Rissoella*, Ortea and Espinosa, 2001a: 36, pl. 2A. Type locality: Punta Mona, Manzanillo, Limón, Costa Rica (9°37' N, 82°37' W), 9 m depth. HOLOTYPE: MZUCR-INB0003323831. Remarks: shell destroyed, only dry soft body present, not figured here.

genecoani, *Plesiocystiscus*, Espinosa and Ortea, 2000: 96–97, fig. 1, pl. 1. Type locality: Manzanillo, Limón, Costa Rica (9°39′ N, 82°37′ W), 25 m depth. HOLOTYPE: MZUCR-INB0003349916 (shell, Figure 22). PARATYPES: MZUCR-INB0003349917 (2 specimens, shells). Locality data same as holotype.

goslineri, *Cylichnella*, Valdés and Camacho-García, 2004: 459–497, figs. 4D–F, 5. Type locality: Sector Playitas, Golfo Dulce, Puntarenas, Costa Rica (8°44′19″ N, 83°21′57″ W), 0 m depth. HOLOTYPE: MZUCR-INB0001497964 (shell, Figure 23). PARATYPES: MZUCR-INB0003718957 (15 specimens, shell and soft parts, lateral gizzard plate and radular teeth in SEM stubs). Locality data same as holotype.

hojarasca, *Alcadia (Microalcadia)*, Richling, 2001: 5–6, figs. 6–8. Type locality: cordillera de Tilarán, about 9 km N of Santa Elena, near Mirador Gerardo, Guanacaste, Costa Rica (10°22′19″ N, 84°48′25″ W), 1450 m.a.s.l. HOLOTYPE: MZUCR-INB0003404979 (shell, Figure 25). Remarks: species was assigned to *Alcadia* in Richling, 2004: 370–374, figs. 249–255; it was previously *Helicina*.

holandae, *Prunum*, Espinosa and Ortea, 1999b: 175–176, fig 1H. Type locality: Cayos Limón, Islas San Blas, Colón, Panamá (9°33′00″ N, 78°53′30″ W). HOLOTYPE: MZUCR-5750 (shell, Figure 10). PARATYPE: MZUCR-INB0003350838 (shell), Punta Uvita, Manzanillo, Limón, Costa Rica (9°38′ N, 82°41′ W). Remarks: According to the original publication the holotype was deposited at the Instituto de Oceanología de la Habana, Cuba, but in fact it was deposited at INBio. The paratype was erroneously assigned the catalogue number INBI0CR1001501498 in the original publication. Also, the locality for the paratype, Punta Uvita, was misspelled in the original publication as Punta "Ubitas."

inbiotica, *Trapania*, Camacho and Ortea, 2000: 317–321, figs. 1–3. Type locality: San Miguel Station, Reserva Absoluta de Cabo Blanco, Tempisque Conservation Area, Puntarenas, Costa Rica (9°34′49″ N, 85°08′28″ W), 1 m depth. HOLOTYPE: MZUCR-INB0001500889.

iugula, *Doto*, Ortea, 2001a: 26–27, fig. 11, pl. 2J. Type locality: Punta Mona, Limón, Costa Rica (9°39′ N, 82°37′ W), 25 m depth. HOLOTYPE: MZUCR-INB0003449604.

kekoldi, *Doto*, Ortea, 2001a: 18–21, fig. 8, pl. 2 E–F. Type locality: Punta Mona, Limón, Costa Rica (9°38′ N, 82°37′ W), 9 m depth. HOLOTYPE: MZUCR-INB0003449587 (soft body and egg mass).

leopoldoi, *Eubranchus*, Caballer, Ortea and Espinosa, 2001: 55–56, fig. 14, pl. 2E. Type locality: Punta Mona, Manzanillo, Limón, Costa Rica (9°38′ N, 82°37′ W), 6 m depth. HOLOTYPE: MZUCR-INB0003138799.

lizanoi, *Prunum*, Magaña, Espinosa, and Ortea, 2003: 124–126, figs. 2C, 3, pls. 1B, 2 B. Type locality: Bahía Junquillal Wildlife Refuge, Golfo de Santa Elena, Guanacaste, Costa Rica. HOLOTYPE: MZUCR-INB0003481195 (shell, Figure 11). PARATYPES: MZUCR-INB0003481192 (1 specimen, shell, including a slide with radula), MZUCR-INB0003476231 (1 specimen, shell and soft parts).

loisae, *Mitrella*, Pitt and Kohl, 1979: 467–468, figs. 2A–B, 3A–B. Type locality: N side of Punta Coralillo, Bahía de Caldera, about 20 km S of the city of Puntarenas, Puntarenas, Costa Rica (9°54′ N, 84°44′ W). PARATYPES: MZUCR 2363 (2 specimens, shell, Figure 6).

magagnai, *Dendrodoris*, Ortea and Espinosa, 2001d: 52–53, fig. 13, pl. 3E. Type locality: Manzanillo, Limón, Costa Rica (9°38′ N, 82°39′ W), 20 m depth. HOLOTYPE: MZUCR-INB0001497496.

manzanilloensis, *Polycera*, Ortea, Espinosa, and Camacho, 1999: 161–163, fig. 3. Type locality: Manzanillo, Limón, Costa Rica (9°38′ N, 82°39′ W), 8 m depth. HOLOTYPE: MZUCR-INB0001496124.

marioi, *Gibberula*, Espinosa and Ortea, 2000: 101–102, fig. 5, pl. 1. Type locality: coral reefs of Manzanillo, Limón, Costa Rica (9°39′ N, 82°39′ W), 30 m depth. HOLOTYPE: MZUCR-INB0003371977 (a slide preparation with radula).

millenae, *Cuthona*, Hermosillo and Valdés, 2007: 124–128, figs. 1D, 6, 7. Type locality: Los Arcos, Bahía de Banderas, Jalisco, México (20°32.855′ N, 105°17.340′ W), 19 m depth. PARATYPE: MZUCR-INB0003836263, Playa Real, NE Punta Roble, Guana-

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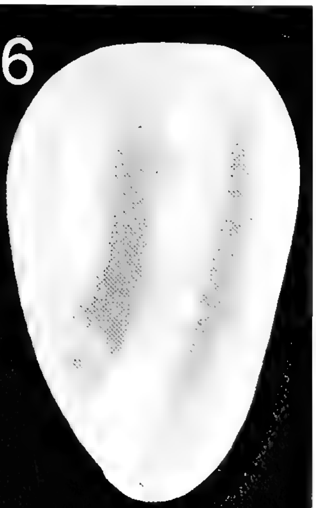

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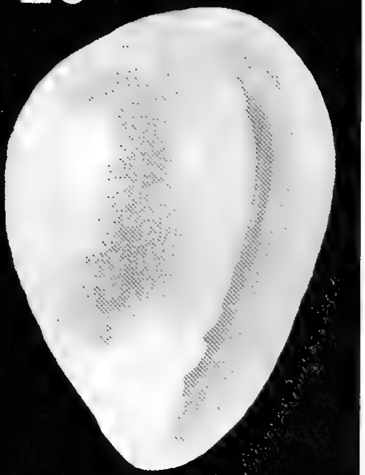

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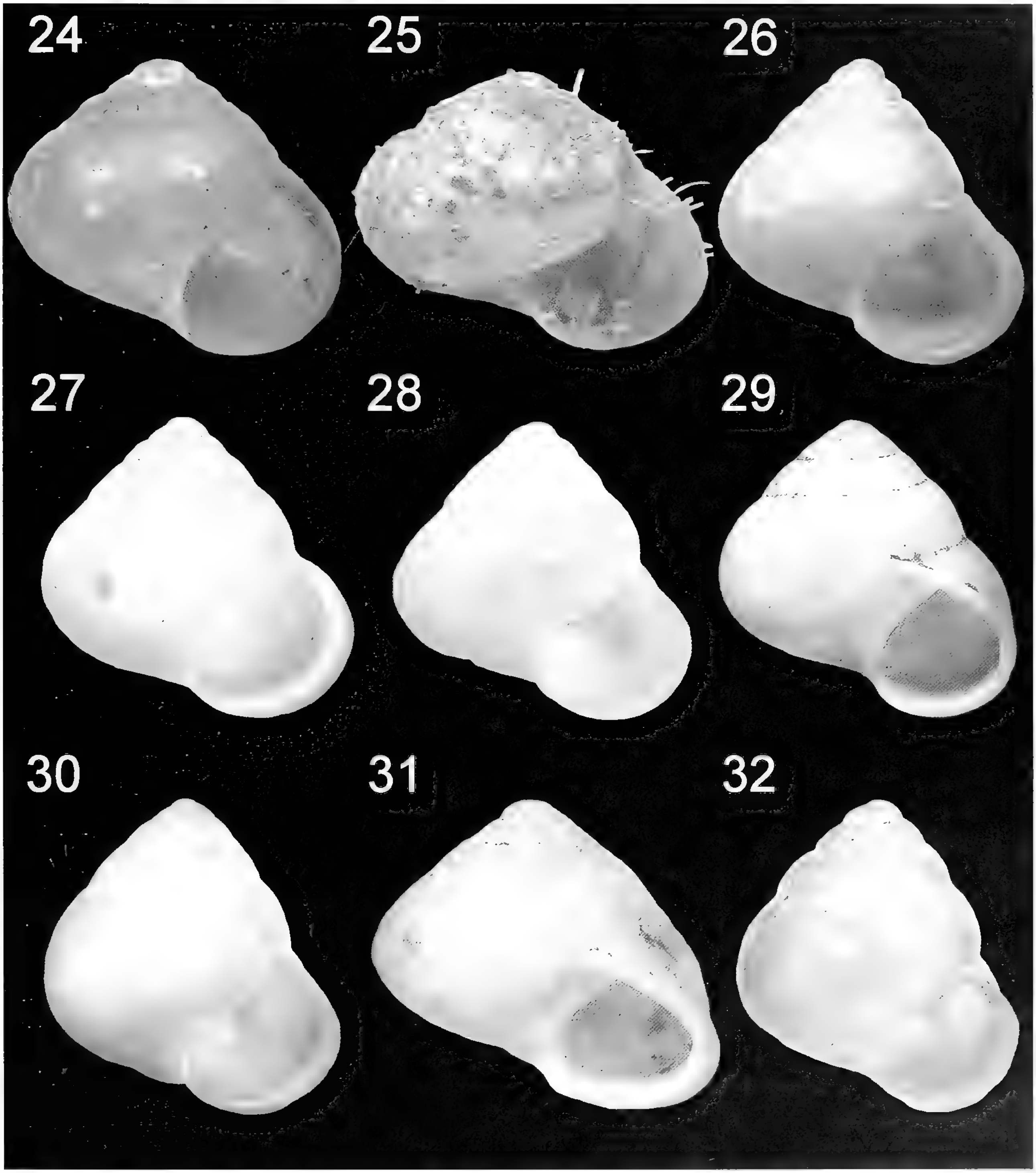

Figures 24–32. **24.** Holotypes of *Alcadia* (*Microalcadia*) *boeckereli*, 2.2 mm. **25.** *Alcadia* (*Microalcadia*) *hojarasca*, 2.4 mm. **26.** *Helicina* ("*Tristramia*") *echandiensis*, 7.2 mm. **27.** *Helicina* ("*Gemma*") *escondida*, 6.2 mm. **28.** *Helicina* ("*Gemma*") *monteverdensis*, 6.6 mm. **29.** *Helicina* ("*Gemma*") *talamancensis*, 9.2 mm. **30.** *Helicina* ("*Gemma*") *beatrix riopejensis*, 7.8 mm. **31.** *Helicina* ("*Tristramia*") *punctisulcata cuericiensis*, 5.9 mm. **32.** *Oligyra chiquitica*, 4.8 mm

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Figures 13–23. **13.** Holotypes of *Volvarina yolandae*, 6.2 mm. **14.** *Dentimargo cruzmoralai*, 2.5 mm. **15.** *Dentimargo zaidettae* 2.5 mm. **16.** *Gibberula bribri*, 11.0 mm. **17.** *Gibberula caribetica*, 6.0 mm. **18.** *Gibberula sierrai*, 2.1 mm. **19.** *Gibberula ubitaensis* 1.8 mm. **20.** *Granulina minae*, 1.0 mm. **21.** *Plesiocysticus alfiopivai*, 1.9 mm. **22.** *Plesiocysticus geneeoani*, 2.2 mm. **23.** *Cylichnella goslineri* 4.5 mm

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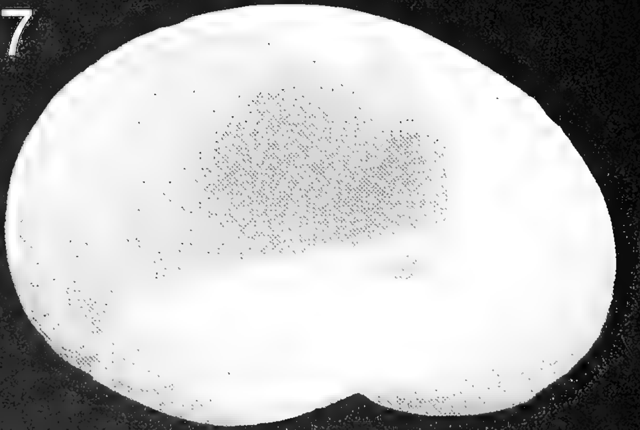

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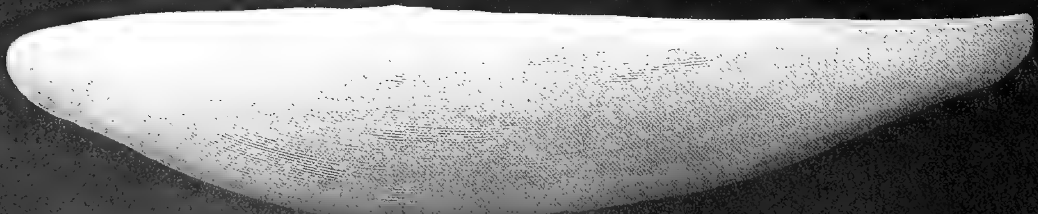

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caste, Costa Rica (10°23.200′ N, 85°50.733′ W), 5 m depth.

minae*, *Granulina, Espinosa and Ortea, 2000: 103, fig. 6, pl. 1. Type locality: Punta Mona, Manzanillo, Limón, Costa Rica (9°37′ N, 82°37′ W), 12–15 m depth. HOLOTYPE: MZUCR-INB0003349904 (shell, Figure 20).

monteverdensis*, *Helicina (*"Gemma"*), Richling, 2004: 334–348, figs. 183–199. Type locality: Cordillera de Tilarán, near Monteverde, Zona Protectora Arenal-Monteverde, Reserva Biológica Bosque Nuboso Monteverde, Sendero Bosque Nuboso, Puntarenas, Costa Rica (10°18′08″ N, 84°47′41″ W), 1550 m.a.s.l. HOLOTYPE: MZUCR-INB0003542627 (shell, Figure 28). PARATYPE: MZUCR-INB0003542628 (shell). Locality data same as holotype.

orteai*, *Cyerce, Valdés and Camacho-García, 2000: 445–456, figs. 1–5. Type locality: Playa Cabuya, Cabuya, Cóbano, Puntarenas, Costa Rica (9°39′ N, 85°11′ W), 0 m depth. HOLOTYPE: MZUCR-INB0001500521. PARATYPE: MZUCR-INB0001500644. Locality data same as holotype.

orteai*, *Triphora, Espinosa, 2001: 21–22, fig. 7. Type locality: Punta Mona, Manzanillo, Limón, Costa Rica (9°37″ N, 82°37″ W), 10–15 m depth. HOLOTYPE: MZUCR-INB0003138795 (shell, Figure 3).

osae*, *Jorunna, Camacho-García and Gosliner, 2008: 165–167, figs. 21–22. Type locality: Playa Gallardo, Golfito, Osa Conservation Area, Costa Rica (8°38′33″ N, 83°13′40″ W), 0 m depth. HOLOTYPE: MZUCR-INB0003701453, MZUCR-INB0003799440 (radula and jaw, SEM stubs).

pacifica*, *Chiapaphysa, Taylor, 2003: 170–171, fig. 168, pl. 8.8. Type locality: Río Tenorito, Hacienda La Pacífica, Guanacaste, Costa Rica (10°29.02′ N, 89°09.58′ W), 100 m.a.s.l. PARATYPES: MZUCR-INB0003382239 (10 specimens, shells, Figure 33).

proranao*, *Doto, Ortea, 2001a: 23–25, fig. 10, pl. 2H. Type locality: Punta Mona, Manzanillo, Limón, Costa Rica (9°37′ N, 82°37′ W), 9 m depth. HOLOTYPE: MZUCR-INB0003138763.

punctisulcata cuericiensis*, *Helicina, Richling, 2004: 277–283, figs. 87–96. Type locality: Cordillera de Talamanca, Estación Cuericí, 4.5 km E of Villa Mills, Sendero al Mirador, Cartago, Costa Rica (9°33′28″ N, 83°40′13″ W), 2700 m.a.s.l. HOLOTYPE: MZUCR-INB0003542622 (shell, Figure 31). PARATYPE: MZUCR-INB0003542541 (shell and soft parts). Other locality data same as holotype (09°33′19″ N, 83°40′13″ W, 2600 m.a.s.l.).

sanctijohannis*, *Mayabina, Taylor, 2003: 102–104, fig. 85, pls. 3.5, 3.6. Type locality: Barra del Colorado, Limón, Costa Rica (10°46.37′ N, 83°35.27′ W). PARATYPES: MZUCR-INB0003382237 (10 specimens, shell), MZUCR 69-01 (10 specimens, shell, Figure 34). Locality data for all paratypes same as holotype.

selva*, *Ercolania, Ortea and Espinosa 2001c: 45–47, fig. 11. Type locality: Manzanillo, Limón, Costa Rica (9°39′ N, 82°39′ W), 0 m depth. HOLOTYPE: MZUCR-INB0003138832. PARATYPE: MZUCR-INB0003449624. Locality data same as holotype.

sierrai*, *Gibberula, Espinosa and Ortea, 2000: 99–100, fig. 3, pl. 1. Type locality: Punta Mona, Manzanillo, Limón, Costa Rica (9°38′ N, 82°37′ W), 10–15 m depth. HOLOTYPE: MZUCR-INB0003349909 (shell, Figure 18).

sinusdulcensis*, *Tropinauta, Taylor, 2003: 110–111, figs. 91–94. Type locality: small stream in pasture 3 km SE of Golfito, Puntarenas, Costa Rica (8°36.68′ N, 83°8.48′ W). PARATYPES: MZUCR-INB0003382246 (5 specimens, shells, Figure 36).

socoae*, *Volvarina, Espinosa and Ortea, 1999b: 171–172, figs. 1E, 2D–E. Type locality: Manzanillo, Limón, Costa Rica (9°39′ N, 82°45′ W), 1.0–1.5 m depth. HOLOTYPE: MZUCR-INB0003350887 (shell, Figure 12). PARATYPE: MZUCR-INB0003350888 (shell). Remarks: in the original publication the holotype and paratype were erroneously assigned the catalogue numbers INBIOCR001496127 and INBIOCR1001496128, respectively.

talamancensis*, *Helicina (*"Gemma"*), Richling, 2001: 3–5, figs. 3,4. Type locality: Fila Costeña, N of Bajo Bonito, N of Río Claro, Puntarenas, Costa Rica (8°44′41″ N, 83°02′09″ W), 980 m NN. HOLOTYPE: MZUCR-INB0003404978 (shell, Figure 29). PARATYPES: MZUCR-INB0001494642 (8 specimens, shell), MZUCR-INB0001487761 (2 specimens, shell and soft parts), 3.5 km from Escuela de Llano Bonito Carretera a San Vito, Puntarenas, Costa Rica (8°44′27″ N, 83°02′04″ W), 840 m m.a.s.l., MZUCR-INB0001494509 (1 specimen, shell and soft parts), 3.5 km NE from Escuela de Llano Bonito, Puntarenas, Costa Rica (8°44′54″ N, 83°02′04″ W), 920 m m.a.s.l. Remarks: species was assigned to *Helicina* in Richling, 2004: 308–318, figs. 140, 142–148; it was previously *Olygira talamancensis*. The paratype MZUCR-INB0003389580 (1 specimen, shell, locality data same as MZUCR-INB0001494509) is said to be deposited at INBio but is not present.

tempisquensis*, *Jorunna, Camacho-García and Gosliner, 2008: 167–170, figs. 23–24. Type locality: Cabo Blanco, Costa Rica (9°34′50″ N, 85°08′26″ W), 0 m depth. HOLOTYPE: MZUCR-INB0003542376. PARATYPES: MZUCR-INB0003542377 (2 specimens).

tempisquensis*, *Mayabina, Taylor, 2003: 109–111, fig. 90, pl 4.4. Type locality: edge of marshes, 100 m E of W end of airstrip, Palo Verde National Park, Guanacaste, Costa Rica (10°20.68′ N, 85°20.60′ W). PARATYPES:

Figures 33–39. 33. Paratype of *Chiapaphysa pacifica*, 6.1 mm. **34.** Paratype of *Mayabina sanctijohannis*, 6.7 mm (UCR 69-01). **35.** Paratype of *Mayabina tempisquensis*, 7.5 mm. (INB0003382244). **36.** Paratype of *Tropinauta sinusdulcensis*, 5.5 mm. **37.** Holotype of *Cryptostrakon corcovadensis*. 4 mm. **38.** Holotype of *Adrana elizabethae*, (left valve dorsal view) 32.5 mm. **39.** Holotype of *Adrana elizabethae*. (left valve ventral view) 32.5mm

MZUCR-INB0003382244 (10 specimens, shell, Figure 35), MZUCR 70-01 (10 specimens, shell).

tica, *Furcilla*, Espinosa and Ortea, 2000: 105–107, fig. 7, pl. 1. Type locality: coral reefs of Manzanillo, Limón, Costa Rica (9°39′ N, 82°39′ W), 30 m depth. HOLOTYPE: MZUCR-INB0003371976 (including a slide with radula).

tica, *Mexichromis*, Gosliner, Ortea, and Valdés, 2004: 589–593, figs. 1A, 2, 3. Type locality: Bajo del Diablo, Isla del Caño, Puntarenas, Costa Rica (8°42′04″ N, 83°53′20″ W), PARATYPES: MZUCR-INB001486639 (2 specimens).

ubitaensis, *Gibberula*, Espinosa and Ortea, 2000: 97–99, fig. 2, pl. 1. Type locality: Punta Uvita, Manzanillo, Limón, Costa Rica (9°38′ N, 82°41′ W), 12–15 m depth. HOLOTYPE: MZUCR-INB0003349902 (shell, Figure 19). Remarks: the Type locality, Punta Uvita, was misspelled in the original publication as "Ubita."

yolandae, *Volvarina*, Espinosa and Ortea, 2000: 108–110, fig. 10, pl. 1. Type locality: Manzanillo, Limón, Costa Rica (9°39′ N, 82°39′ W), 10–25 m depth. HOLOTYPE: MZUCR-INB0003350843 (shell, Figure 13). PARATYPES: MZUCR-INB0003350841 (1 specimen, shell), MZUCR-INB0003350842 (1 specimen, shell). Locality data same as holotype. Remarks: according to the original publication, the paratype MZUCR-INB0003350841 was deposited at the Instituto de Oceanología de la Habana, Cuba, and the paratype MZUCR-INB0003350842 was deposited at Museo de Ciencias Naturales de Tenerife, Canary Islands; however, both are deposited at MZUCR.

zaidettae, *Dentimargo*, Espinosa and Ortea, 2000: 113–114, fig. 12, pl. 2. Type locality: Punta Mona, Manzanillo, Limón, Costa Rica (9°38′ N, 82°37′ W), 12–15 m depth. HOLOTYPE: MZUCR-INB0003349911 (shell, Figure 15). PARATYPE: MZUCR-INB0003349910 (1 specimen, shell). Locality data same as holotype. Remarks: According to the original publication the paratype was deposited at the Instituto de Oceanología de la Habana, Cuba, but in fact it is deposited at MZUCR.

zugnigae, *Melanella*, Espinosa, Ortea and Magaña, 2001: 26–27, figs. 8C, D. Type locality: Punta Mona, Manzanillo, Limón, Costa Rica (9°37′ N, 82°37′ W), 10–15 m depth. HOLOTYPE: MZUCR-INB0003138456 (shell, Figure 2).

ACKNOWLEDGMENTS

We are very grateful to Alvaro Morales and Ingo Werthmann for their logistic support during the elaboration of this paper. The photographs were taken at the facilities of Centro de Investigación en Ciencias del Mar y Limnología (CIMAR) at the University of Costa Rica. Eugene V. Coan and David Butvill made constructive comments on this manuscript.

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Dilemma japonicum new species (Bivalvia: Anomalodesmata: Poromyidae): A new record of the genus from the Northwest Pacific

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ABSTRACT

The fourth species of the bivalve genus *Dilemma* Leal, 2008, is described from disarticulated valves collected off central Japan. The discovery of these specimens represents a significant range extension for the genus to the Northwest Pacific. The new species is distinguished from the other three known species by its surface sculpture, shape of escutcheon, and hinge. The prodissoconch, indicative of lecithotrophic development, and shell microstructure, with outer homogeneous and inner nacreous layers, are illustrated for the first time for a species of the genus.

Additional Keywords: Septibranchia, Poromyoidea, Japan, nacreous layer, prodissoconch

INTRODUCTION

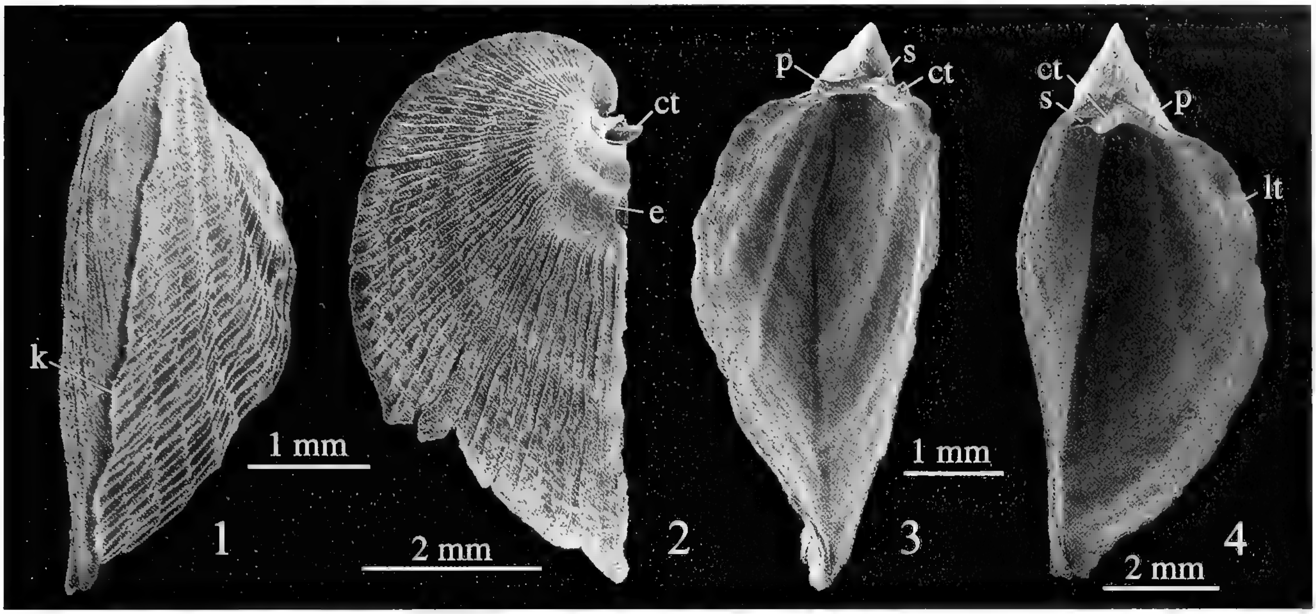
Dilemma is a recently established, unusual genus of Anomalodesmata (Leal, 2008). The first described species of the genus, *D. inexpectatum* (Crozier, 1966), was dredged from bathyal depths off northern New Zealand and originally assigned to *Corculum*, family Cardiidae (Crozier, 1966) due to general similarities in shell shape. However, its original familial allocation was questionable from habitat and depth alone, because *Corculum* species inhabit shallow lagoons of tropical waters and utilize photosynthesis-derived energy by symbiotic dinoflagellates (Farmer et al., 2001). Subsequent discovery of obviously related species with preserved soft parts allowed Leal (2008), using details of the macroanatomy, to demonstrate (1) that *Corculum inexpectatum* and the other, then newly found species are related and deserved grouping under a new genus, (2) that the new genus should be included in the Poromyidae, and (3) that species of *Dilemma* are carnivores. In fact, carnivory is a feeding habit that is common in the Anomalodesmata, a group of bivalves mostly present in the deep sea.

Three species were originally (Leal, 2008) assigned to the genus: (1) *Dilemma frumarkernorum* Leal, 2008, from off Key West Florida, 229 m, (2) *D. spectralis* Leal, 2008, from off Vanuatu, 950–961 m, and (3) *D. inexpectatum* (Crozier, 1966) from off Three Kings Islands, New Zealand, 805 m. Their geographic distribution is disjunct, but shell morphology is surprisingly similar between the species of Florida and Southwest Pacific.

During a research cruise off central Japan, in 2000, the senior author collected small unpaired valves of *Corculum*-like bivalves, but its locality (240–273 m) was obviously too deep for *Corculum*. In addition, the inner shell layer is iridescent, indicating presence of a nacreous layer. This conchological feature alone precluded inclusion of this new species in the Cardiidae. However, lack of soft parts prevented a better resolved familial or suprafamilial placement of the new taxon. The publication by Leal (2008) allowed allocation of the unknown bivalve in that newly established genus of the Poromyidae. In this paper, we describe this most interesting new species and report a new record of the genus from the Northwest Pacific.

MATERIALS AND METHODS

Four unpaired valves were sorted from sediments dredged from southeast of Kamogawa, Chiba Prefecture, Japan, with a biological dredge (R/V TANSEI-MARU, cruise KT-00-05, station 1, 240–273 m, 34°59.963′ N, 140°27.159′ E– 35°00.020′ N, 140°28.427′ E, May 17, 2000). All specimens were dead and disarticulated. The shells were coated with platinum and vanadium and photographed with a scanning electron microscope (Hitachi S-2250N), following a standard method (see Geiger et al., 2007). The holotype and two paratypes are deposited in the Department of Historical Geology and Paleontology, The University Museum, The University of Tokyo (UMUT), and one paratype in The Bailey-Matthews Shell Museum, Sanibel, Florida (BMSM).



Figures 1–4. *Dilemma japonicum* new species. **1.** Lateral view. **2.** Posterior view. **3–4.** Interior view. **1–3.** Left valve. **4.** Right valve. **1.** Holotype, UMUT RM 29689. **2.** Paratype 1, UMUT RM29690, **3.** Paratype 2, UMUT RM29691, **4.** Paratype 3, BMSM 17983. Abbreviations: **ct** = cardinal-like tooth; **e** = escutcheon; **k** = keel; **lt** = lateral tooth; **p** = projection in hinge; **s** = socket.

SYSTEMATICS

Superfamily Poromyoidea Dall, 1886
Family Poromyidae Dall, 1886
Genus *Dilemma* Leal, 2008

Type Species: *Dilemma frumarkernorum* Leal, 2008, by original designation.

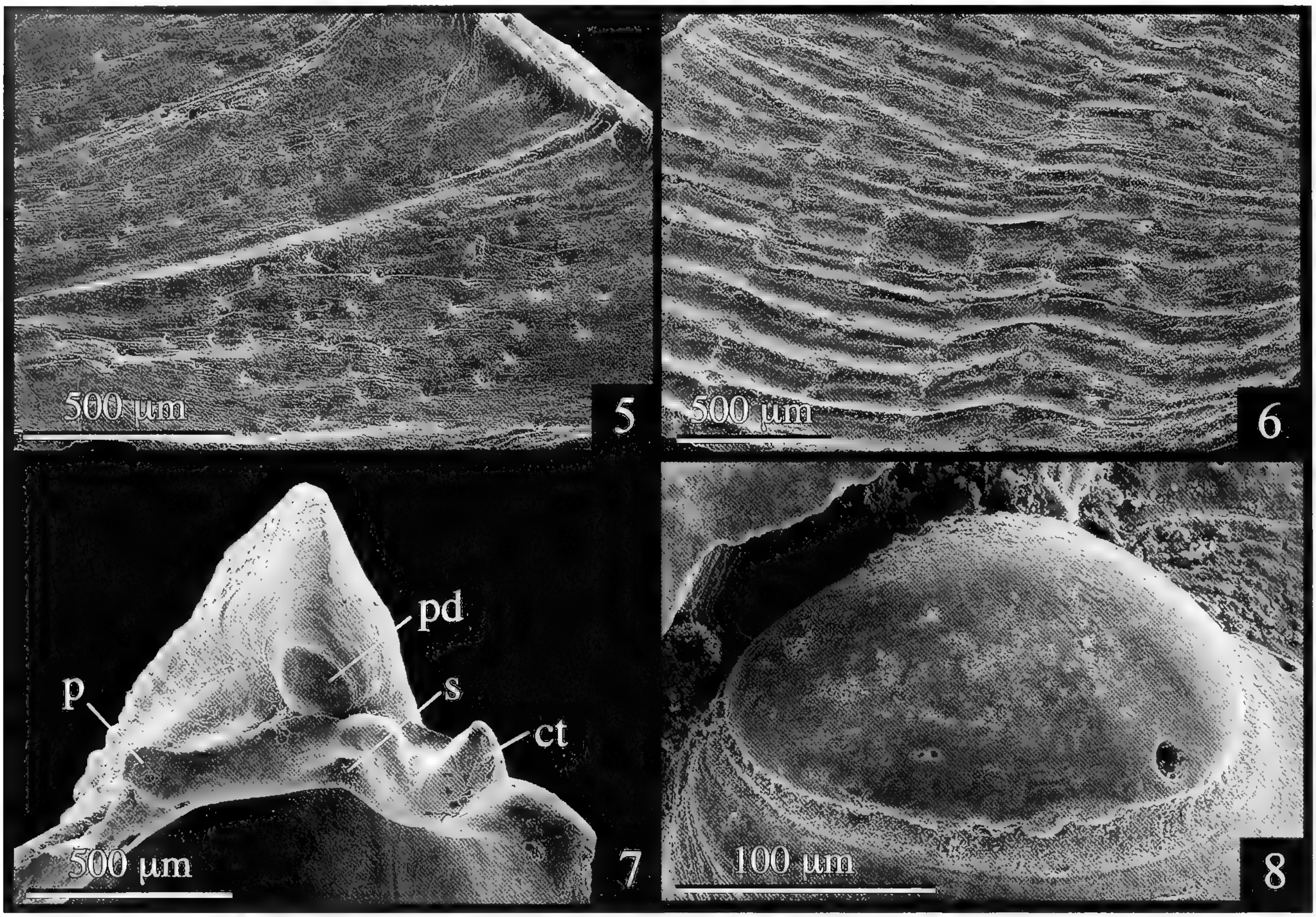
Diagnosis: Shell compressed anteroposteriorly and expanded laterally; lateral outline of articulated valves cardioid; umbones projecting dorsally and located anteriorly; sharp oblique carina dividing anterior and posterior regions; maximum growth axis having ca. 30° against anteroposterior axis; hinge axis short with cardinal-like tooth and socket in each valve; lateral tooth reduced, present only in right valve; ligament external, double-layered; lithodesma absent; shell interior lined with sheet-like nacreous layer. See Leal (2008) for anatomical characters.

Dilemma japonicum new species
(Figures 1–12)

Diagnosis: Posterior region of shell sculptured by rough, lamellate, thin, commarginal ribs; surface irregularly punctate on anterior region but puncta radially arranged on posterior region; escutcheon not distinctly demarcated; prominent projection present in posterior region of hinge.

Description: Shell thin, fragile, compressed anteroposteriorly; shell height larger than shell length. Anterior and posterior regions clearly demarcated by sharp keel (Figure 1, **k**); anterior region narrower and less inflated than posterior. Surface of anterior region smooth, flattened in macroscopic view, but microscopically punctate (Figure 5). Surface of posterior region sculptured by several weak radial ribs (Figure 3), and more prominently so by dense commarginal ribs, also punctate in enlarged view, but puncta arranged neatly in radial direction unlike on anterior region (Figure 6). Umbo angulated by keel and rib along posterior margin (Figure 7); umbonal cavity deep; umbo involute (Figure 3). Prodissoconch simple, flattened, shield-like, ca. 200 μm in length, without prominent sculpture or division into prodissoconch I and II (Figure 8). Hinge provided with single cardinal-like tooth and socket on each valve (Figures 3–4, 7, **ct, s**); cardinal-like tooth located anterior to socket on left valve (Figure 3), their position reversed on right valve (Figure 4). Lateral tooth small, present only on right valve (Figure 4, **lt**). Single sharp projection (Figures 3–4, 7, **p**) prominent on posterior side of hinge in similar position and size in right and left valves. Ligament and outlines of muscle scars not observed in disarticulated valves. Shell margin consisting of two layers, outer homogeneous structure and inner nacreous structure (Figure 9–10, **OL, IL**). In outer layer elongate granules arranged vertically but lacking clear boundary. In inner layer suboval tablets fusing in growth region (Figure 11), numerous sheet-like layers forming nacre (Figure 12).

Type Material: Holotype, 4.7 mm (height: SH) × 2.0 mm (length: SL), UMUT RM29689 (Figure 1); Paratype 1, 5.6 mm (SH) × 2.4 mm (SL), UMUT RM29690 (Figure 2); Paratype 2, 6.0 mm (SH) × 3.0 mm (width), UMUT RM29691 (Figure 3); Paratype 3, 9.3 mm (SH) × 4.0 mm (SL), BMSM 17983 (Figure 4).



Figures 5–8. *Dilemma japonicum* new species. **5–6.** Detail of surface sculpture. **5.** Anterior slope. **6.** Posterior slope. **7.** Detail of hinge. **8.** Prodissoconch. **5–6.** Holotype, UMUT RM29689. **7–8.** Paratype 2, UMUT RM29691. Abbreviations: **ct** = cardinal-like tooth; **p** = projection in hinge; **pd** = prodissoconch; **s** = socket.

Type Locality: Southeast off Kamogawa, Chiba Prefecture, Japan. 240–273 m, 34°59.963′–35°00.020′ N, 140°27.159′–140°28.427′ E.

Distribution: Known only from the type locality.

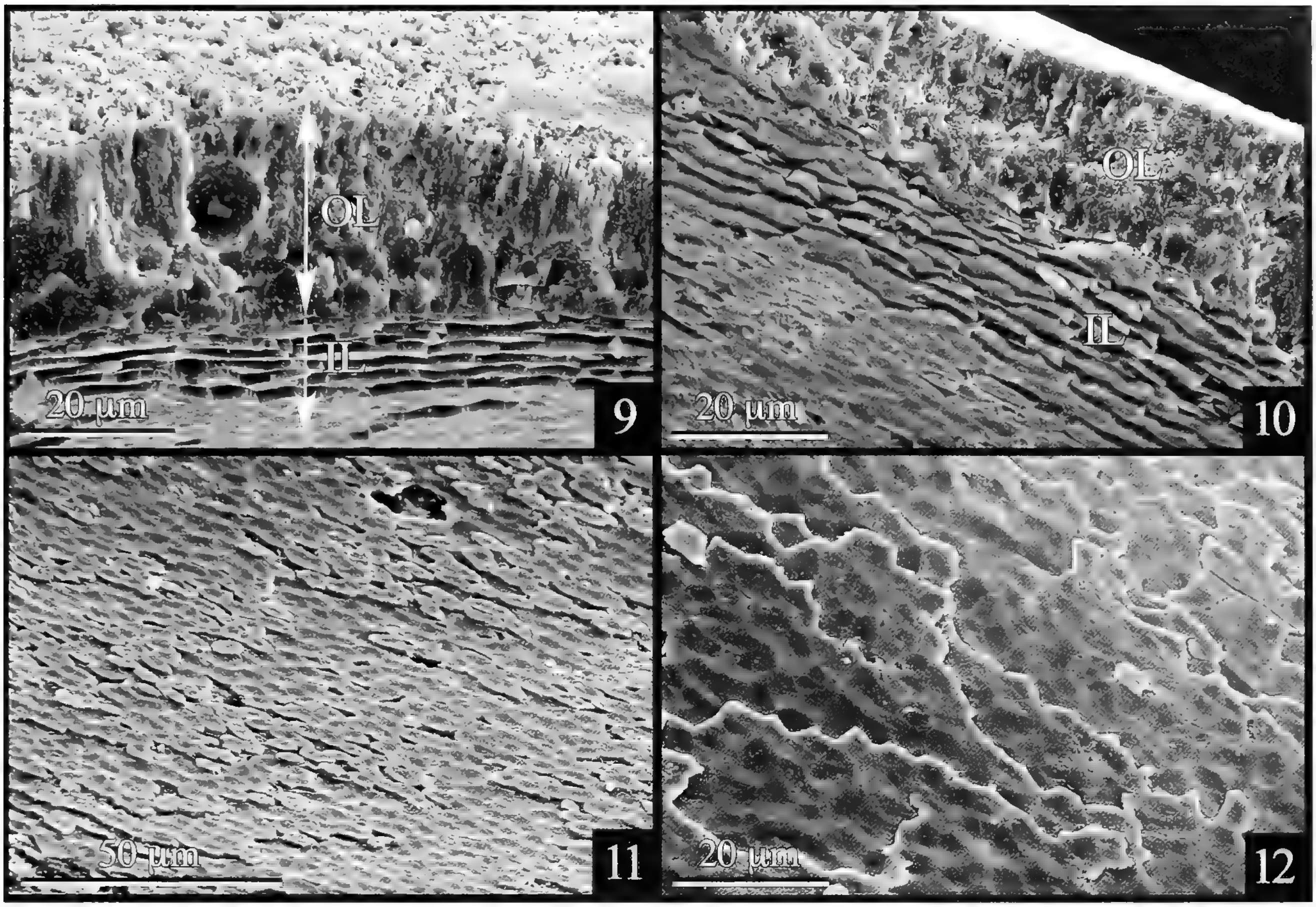
Etymology: The species epithet recognizes the country of the type locality. The epithet *japonicum* agrees in gender with the name *Dilemma*, a late-Latin neuter noun derived from the Greek. Of the previously named species in the genus, *inexpectatum* is a neuter gender epithet, *frumarkernorum* has a genitive ending that is not to be influenced by the gender of the genus, and *spectralis* is an epithet originally used by Leal (2008) as a noun in apposition.

DISCUSSION

The inclusion of the new species in the genus *Dilemma* is well supported by the presence of the diagnostic shell characters of the genus: anteroposteriorly compressed shell, cardioid outline in articulated valves, sharp carina dividing the shell into the anterior and posterior regions, cardinal-like tooth and socket in each valve, and nacreous shell interior. Obviously there is no other group having a combination of these characters in bivalves.

From the three previously known species of the genus, *Dilemma inexpectatum* (Crozier, 1966) from northern New Zealand is most similar to the new species in having rough commarginal sculpture in the posterior region. However, the two species differ in two characters: the rows of pores are absent and the escutcheon is distinct in *D. inexpectatum*. As summarized in Table 1, the four species in the genus can be distinguished among themselves by four shell characters: sculpture in the posterior region; the presence or absence of small pits; the distinctness of the escutcheon; and the presence or absence of the posterior projection of the hinge. The paired posterior projections are present only in *D. japonicum*; they are not part of the hinge teeth system, because they do not articulate as a tooth and a socket between the right and left valves. Unfortunately, the outlines of muscle scars were unclear in the specimens of the new species.

The original description of *Dilemma* mentioned "Shell apparently nacreous internally . . ." (Leal, 2008: 3), but did not offer any detailed descriptions or discussions



Figures 9–12. *Dilemma japonicum* new species. Shell microstructure. **9–10.** Observed at small broken part of shell margin, vertical section of homogenous structure in outer layer (**OL**) lined by nacreous structure in inner layer (**IL**). **11–12.** Oblique (11) and horizontal (12) views of nacreous layer at inner shell surface. Paratype 2, UMUT RM29691.

on the shell microstructure of the three originally included species. The description of the inner nacreous shell layer in the present study confirms its presence in *Dilemma*.

A shell consisting of outer homogeneous and inner nacreous layers (Figure 9–12) supports inclusion of the new species in Anomalodesmata (Taylor et al., 1973; Prezant, 1998). The microstructure of the outer layer is somewhat similar to a simple prismatic structure in that elongate granules are arranged vertically. The outer layer is identified as a homogeneous structure, because, unlike typical prismatic structure, crystals lack sharp boundaries. It should be observed, however, that environmental changes can alter otherwise organized shell microstructures to appear irregular, smoothed, and homogeneous (R. Prezant, pers. comm.).

Table 1. Shell characters and distribution of the four *Dilemma* species.

	D. frumarkernorum	*D. spectralis*	*D. inexpectatum*	*D. japonicum* new species
Sculpture in posterior region	Dense, coarse growth lines	Smooth	Rough commarginal ribs and grooves	Rugose, lamellate commarginal ribs
Small pits on exterior surface	Absent	Present	Absent	Present
Escutcheon	Not clearly separated	Not clearly separated	Clearly defined	Not clearly separated
Projection posterior to beak	Absent	Absent	Absent	Present
Distribution	Off Key West Florida, USA, 229 m	Off Vanuatu, Southwestern Pacific, 930–961 m	Off Three Kings Islands, New Zealand, 805 m	Off central Japan, Northwest Pacific, 240–273 m (dead

The prodissoconch of *Dilemma japonicum* new species indicates non-planktotrophic, lecithotrophic development. It measures ca. 200 μm in length (Figure 8), a size that fits into the predicted size range (135–230 μm) of prodissoconchs of bivalves with lecithotrophic development (Ockelmann, 1965; Jablonski and Lutz, 1983). The developmental modes of the other species of the genus are unknown.

Although two of the other live-collected species of *Dilemma* were found attached to hard substrata, the microhabitat of the new species is unknown. The bottom sediment from the type locality contained numerous dead shells and other biogenic fragments such as those of bryozoans and sponges. Because most bivalves were dead and disarticulated, large part of samples in the dredge haul was inferred to be transported and accumulated. Specifying the actual microhabitat of the species is an interesting target for future sampling.

The description of *Dilemma japonicum* extends the geographic range of the genus to the Northwest Pacific, in addition to previous records from off Florida and the Southwestern Pacific (off Vanuatu and New Zealand). The genus has a broad geographic range, extending across the Panama land bridge and Eastern Pacific barrier. Future sampling of deep-sea hard substrates may yield additional records of *Dilemma* species from other locations in the Pacific and in other oceans.

ACKNOWLEDGMENTS

The authors are indebted to the reviewers, Rüdiger Bieler, Robert S. Prezant, and Richard C. Willan, for their comments and suggestions. Richard Willan and Rüdiger Bieler helped with etymologies and confirmed the gender of the name *Dilemma*. The samples of the new species became available with the kind assistance of Dr. Suguru Ohta (formerly Ocean Research Institute, University of Tokyo), other colleagues on board and crew of R/V TANSEI-MARU (Japan Agency for Marine-Earth Science and Technology, formerly Ocean Research Institute, University of Tokyo) during the cruise KT-00-05.

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On the genus *Heteroschismoides* Ludbrook, 1960 (Scaphopoda: Gadilida: Entalinidae), with descriptions of two new species

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ABSTRACT

Heteroschismoides is a deep-sea genus characterized by shells being between 10 and 20 mm as adults, sculptured by 9 to 10 prominent primary ribs and a unique deep irregular apical fissure on dorsal side, considered until now to include a single species: *Dentalium subterfissum* Jeffreys, 1877. During revision of material from several expeditions carried out by the Museum National d'Histoire Naturelle, Paris, two new species were identified and are here described: *H. meridionalis* new species and *H. antipodes* new species In addition, designation of the lectotype of *H. subterfissus* is proposed, as well as new records for this species in the northeastern Atlantic ocean are given. *Heteroschismoides meridionalis* new species is closely related to *H. subterfissus*, but the first has a smaller maximum diameter of shell and smaller apical aperture diameter. *Heteroschismoides antipodes* new species from Solomon Islands is smaller than other two species for both, shell length and fissure extension. The distance of point of maximum curvature from the apex in *H. antipodes* new species is located nearer to the apex than in *H. meridionalis* new species and *H. subterfissus*. The results here obtained considerably enlarge the geographical distribution of the genus and suggest a worldwide bathyal and abyssal distribution for this genus.

Additional Keywords: Heteroschismoides subterfissus, Heteroschismoidinae, tusk shell, lectotype, new species, Brazil, Solomon Islands, deep-sea

INTRODUCTION

The genus *Heteroschismoides* was proposed by Ludbrook in 1960 to include the deep sea species *Dentalium subterfissum* Jeffreys, 1877 (for further supraspecific information see Steiner and Kabat, 2001). The most re markable character of the genus is a unique, deep and irregular apical fissure at the dorsal side of shell not present among other Scaphopoda (Chistikov, 1982; Scarabino, 1995). Since Chistikov (1982), this genus has been considered as monospecific and restricted to the Atlantic Ocean. During the revision of material from several expeditions carried out by the Muséum national d'Histoire naturelle, Paris, in the northeastern and southwestern Atlantic Ocean (Brazil) as well as off Solomon Islands in the Pacific, a number of specimens corresponding to the genus were identified. In a preliminary sorting, Brazilian specimens were placed under *H. subterfissus*, but the unexpected finding of representatives in the tropical Pacific, decided us to undertake the present revision. Here, we propose the lectotype of *Heteroschismoides subterfissus* and describe two new species, extending considerably the geographical distribution range of the genus.

MATERIALS AND METHODS

The material was collected during several expeditions carried out by the MNHN and IFREMER, known as BIOGAS I to XII (1972–1981), THALASSA (1970–73) and INCAL (1973): in the Gulf of Gascony; ABYPLAINE (1982): off Portugal and Spain; NORATLANTE (1969): large coverage of the North Atlantic; BIAÇORES (1971): off Azores; BIOVEMA (1977): VEMA Trench; MD55 (1987): Southeastern Brazil; and SALOMON 2 (2004): off Solomon islands.

In view to better define the species, a morphometric analysis was attempted based on selected undamaged shells of the three species. Shell measurements were taken according to Shimek (1989), Steiner (1999) and Steiner and Linse (2000), including length (L); maximum diameter (Max), that is in this case equal to the anterior aperture diameter; maximum curvature (Arc); distance of point of maximum curvature from the apex (Larc); apical aperture diameter (Apd). Besides those measurements, we also estimated the extension of the apical fissure (Fiss) located at dorsal side of shell. To assure independence among variables, we performed a preliminary correlation analysis among all variables with strongly correlated variables ($r > 0.70$) being excluded. The nonparametric Kruskal-Wallis test was employed to examine for differences of each morphometric parameter (untransformed data) between species. Dunn's multiple comparisons test was used *a posteriori* to assess significant differences between species. A multivariate approach was carried out utilizing Discriminant Function (DF) Analysis to integrate all morphometric data in a single analysis. To perform this analysis, we standardized the morphometric data following Romesburg (1984).

Institutional abbreviations used in the text are: BMNH: The Natural History Museum, London; IFREMER: Institut Français de Recherche pour l'Exploitation de la Mer; MNRJ: Museu Nacional, Rio de Janeiro, Brazil; MNHN: Muséum national d'Histoire Naturelle, Paris; USNM: National Museum of Natural History, Smithsonian Institution, Washington, DC, USA. Other abbreviations are: CP: beam trawl; DC: "Charcot" dredge; stn: station; lv: live-collected; dd: shell only.

SYSTEMATICS

Order Gadilida Starobogatov, 1982
Suborder Entalimorpha Steiner, 1992
Family Entalinidae Chistikov, 1979
Subfamily Heteroschismoidinae Chistikov, 1982
Genus *Heteroschismoides* Ludbrook, 1960

Type Species: *Dentalium subterfissum* Jeffreys, 1877 (by original designation). Recent, northeastern Atlantic Ocean.

Description (Modified from Scarabino, 1995: 302): Shell up to 20 mm length, slightly curved, regularly tapering. Translucent grey when the animal is alive, opaque to polished white or cream when empty. Longitudinally sculptured by 9–10 primary ribs that reach the anterior aperture or vanish towards it. Intercostals spaces convex or straight, smooth or finely striated longitudinally by 8 to 14 lines. Secondary ribs, predominantly a single one, can be present in each intercostal space. Apex with a long and wide irregular fissure on dorsal side early observed in late embryonic stages and juvenile shells. Section polygonal, more notorious at the central zone of shell, fading or not towards the slightly laterally compressed thin oral aperture in adult specimens. Shell fractures and repairs are frequently observed, as well as twisting of shell.

RADULA: Rachidian tooth with anterior margin rounded and lateral margins thick; laterals with sharp pointed primary cusps and 4 important denticles; marginal slightly curved with conspicuous lateral processes, better observed in light microscope.

Distribution: Recent, Atlantic Ocean and tropical Pacific Ocean, bathyal-abyssal.

Remarks: Scarabino (1995: 302) mentioned by mistake "10–12 primary ribs"; in the light of new information this number is here corrected as 9 to 10 primary ribs. Molecular data of *H. subterfissus* has been published by Steiner and Dreyer (2003).

Heteroschismoides subterfissus (Jeffreys, 1877)
(Figures 1–6, 15)

Dentalium subterfissum Jeffreys, 1877: 154; 1883: 660, pl. 49, fig. 3; Watson, 1879: 516; 1886: 10, pl. 1, fig. 10; Pilsbry and Sharp, 1897: 61, pl. 7, figs. 15–19; Warén 1980: 53.
Dentalium (Heteroschisma) subterfissum: Henderson, 1920: 58.
Dentalium (Dentalium) subterfissum: Nicklès 1979: 47, fig. 5a b.
Heteroschismoides subterfissus: Chistikov, 1982: 675, figs. 3, 5; Steiner 1998: 78; Steiner and Kabat, 2001: 446; 2004: 651.

Description: Shell up to 9.2 mm length, slightly curved, regularly tapering. Translucent shiny grey, presenting fractures and repairs. Longitudinal sculpture of nine primary notorious ribs and a single secondary one in between, more notorious in the dorsal half, all reaching the thin oral aperture. Intercostals spaces convex, finely striated longitudinally by eight lines. Apex with a 2.3 mm long, wide, irregular fissure on dorsal side. Transversal section polygonal, slightly compressed laterally, less apparent at apex.

Type Material: Lectotype, here selected (see remarks), the largest (9.2 mm) of the three specimens of lot USNM 175018, Ireland, 54°19′ N,11°50′ W, 1180 fms [2158 m] (Porcupine 1869 stn 16); other paralectotypes: USNM 175017, Off West coast of Ireland, (Porcupine 1869 stn 19a), 2 specimens; USNM 175019, Greenland, 56°11′N 37°41′W, 1450 fms [2646 m], Valorous stn 12, 1 specimen; USNM 175020, 55°40′N 12°46′W, 1476 fms [2694 m], Porcupine 1869 stn 21, 3 specimens; off Azores, Challenger Expedition stn 78, 37°26′ N 25°13′ W, Azores, 1000 fathoms [1825 m], 7 specimens and 3 fragments, BMNH 1887.2.9.36–40. Two other paralectotypes from Porcupine expedition are deposited at BMNH under code 1885.11.5.1393–4, with a mention "further syntypes in USNM 175017-020".

The fact of the species has been partially described on the base of a young specimen (see Remarks) and that the specimen illustrated was not found in the collections revised, lead us to designate the lectotype based on an adult shell.

Measurements of Lectotype (mm): Length 9.20, oral aperture 1.00, apex 0.12, arc 0.42 at 1.9 from apex.

Type Locality: West of Ireland, 54°19′N, 11°50′W, 1489 m, Porcupine 1869, stn 16 (here selected).

Other Material Examined: Off Gabon (Africa), 2°32′ S, 8°18′ E, stn DS20, 2514 m (1 dd); Gulf of Guinea, 4°40′N, 5°39′2E); stn DS30, 3109 m (8 dd) (both WALDA Expedition, CNEXO, Nicklès, 1979), all MNHN.

Figures 1–14. *Heteroschismoides* species. **1–6.** *H. subterfissus* (Jeffreys, 1977). **1.** Lectotype USNM 175018, 9.2 mm. **2.** Paralectotype. **3.** Detail of the apical fissure. **4.** Specimens showing embryonic shell. **5.** Detail of longitudinal ribs. **6.** Detail of microsculpture on the outer surface of intercostals space. **7–10.** *H. meridionalis* new species. **7.** Holotype, MNHN, 14 mm. **8.** Paratype, detail of apex. **9.** Detail of sculpture. **10.** Detail of microsculpture on the outer surface of intercostals space. **11–14.** *Heteroschismoides antipodes* new species. **11.** holotype, MNHN, 9.95 mm. **12.** Detail of apex. **13.** Detail of sculpture. **14.** Detail of microsculpture on the outer surface of intercostal space.


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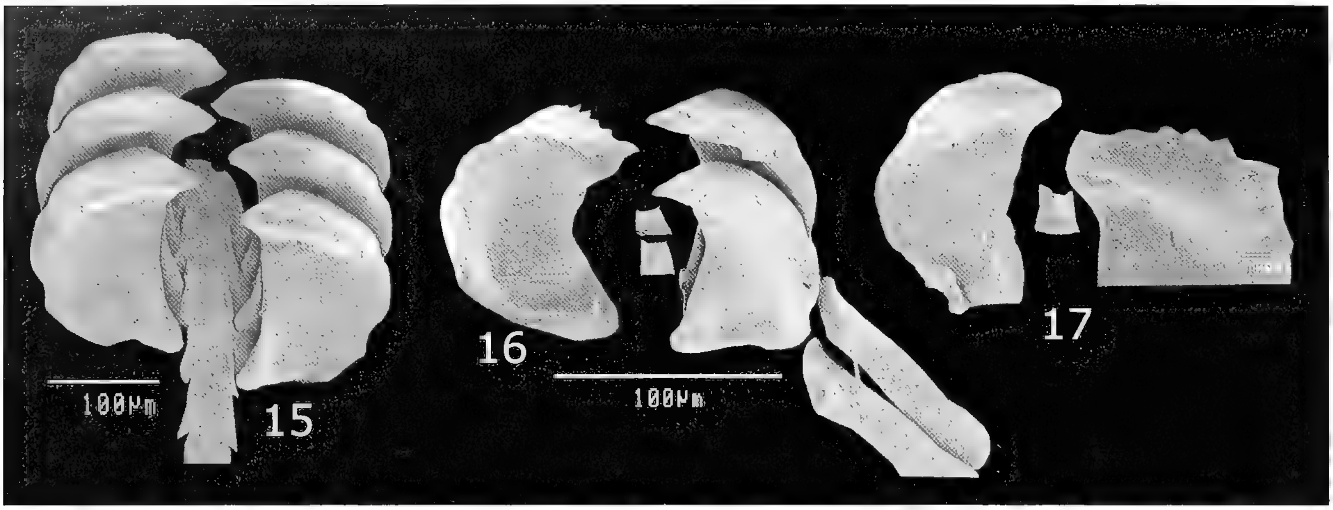

Figures 15–17. Radulae of *Heteroschismoides* species. **15.** *H. subterfissus*, rachidian and lateral teeth, internal view. **16.** *H. antipodes* new species, external view of lateral tooth (left), rachidian, lateral, and marginal teeth (right), in internal view. **17.** *H. meridionalis* new species: rachidian and lateral teeth, internal view.

New Records: Central Atlantic Ocean: Azores Islands: Biaçores 1971: stn DS 54, 38°12′ N, 28°15′ W, 1810 m, 2 dd, stn DS 165, 37°33′ N, 25°58′ W, 2085–2050 m, 1 dd, DS 173, 37°57′ N, 26°08′ W, 3225 m, 1 dd; Noratlante 1969: stn 02, 53°55′ N, 17°52′ W, 2456 – 2420, 3 lv; stn 84, 36°21′ N, 08°43′ W, 2871–2875 m, 3 lv, 3 dd; stn 85, 36°25′ N, 08°48`, 2573–2580 m, 2 lv, 3 dd; Thalassa 1971, Stn X 336, 44°11′ N,05°10′ W, 1850–2050 m, 1 lv, 1 dd; Eastern Atlantic Ocean: Incal 1976: stn. DS 01, 57°59′ N, 10°40′ W, 2091 m, 56 lv, 7 dd; stn. DS 02, 57°59′ N, 10°49′ W, 2081 m, 51 lv, 3 dd; stn. DS 05, 56°28′ N, 11°12′ W, 2503 m, 24 lv, 7 dd; stn. DS 07, 55°01′ N, 12°31′ W, 2884 m, 4 lv, 1 dd; stn. DS 07, 56°27′ N, 11°11′ W, 2884 m, 5 lv, 1 dd; stn. DS 08, 55°02′ N, 12°35′ W, 2891–2884 m, 3 lv, 2 dd; stn. DS 09, 55°08′ N, 12°53′ W, 2897 m, 2 lv, 2 dd; stn. CP 01, 57°58′ N, 10°55′ W, 2040–2068 m, 12 lv; stn. CP 02, 57°58′ N, 10°42′ W, 2091 m, 2 dd; stn. CP 03, 56°38′ N, 11°06′ W, 2466 m, 3 lv, 1 dd; stn CP 04, 56°33′ N, 11°11′ W, 2438–2513 m, 7 lv, 7 dd; stn CP 05, 56°00′ N, 12°29′ W, 2884 m, 1 dd; stn CP 06, 55°02.3′ N, 12°40′ W, 2888–2893 m, 3 lv, 1 dd; stn CP 07, 55°03′ N, 12°46′ W, 2895–2897 m, 1 dd; stn CP 09, 50°15′ N, 13°16′ W, 2659–2691 m, 2 lv; stn WS 01, 50°19′ N, 13°08′ W, 2550–2539 m, 5 lv; stn WS 02, 50°19′ N, 12°55′ W, 2498–2505 m, 1 lv; stn WS 03, 48°19′ N, 15°23′ W, 4829 m, 2 dd; stn WS 09, 47°28.8 N–47°27.9′ N, 09°34′ W, 4277 m, 1 dd.; stn OS 01, 54°14′ N, 13°11′ W, 2634 m, 1 lv; Biogas II: stn DS 32, 47°32′ N, 08°05′ W, 2138 m, 3 lv, 3 dd; Biogas III: stn DS 37, 47°32′ N, 08°35′ W, 2110 m, 2 dd; Biogas IV: stn DS 52, 44°06′ N, 04°22′ W, 2006 m, 2 dd; stn DS 51, 44°11′ N, 04°15′ W, 2430 m, 1 lv; stn DS 58, 47°34′ N, 09°08′ W, 2775 m, 3 dd; stn DS 62, 47°33′ N, 08°40′ W, 2175m, 1 dd; stn DS 64, 47°29′ N, 08°35′ W, 2156m, 4 lv, 1 dd; BIOGAS V: stn CP 07, 44°09.8′ N, 04°16.4′ W, 2170 m, 5 dd; Biogas VI: stn DS 61, 47°34.7′ N, 08°38.8′ W, 2250 m, 1 lv, 1 dd; stn DS 62, 47°33′ N, 08°40′ W, 2175 m, 1 dd; stn DS 63, 47°33′ N, 08°35′ W, 2126 m, 1 lv; stn CP 08, 47°03′ N, 08°39′ W, 2177 m, 2 lv, 1 dd; stn CP 09, 47°33′ N, 08°44′ W, 2171 m, 1 lv; stn CP 24, 44°08′ N, 04°16′ W, 1995 m, 3 dd; stn DS 71, 47°34′ N, 08°34′ W, 2194 m, 3 lv, 5 dd; stn DS 86, 44°04.8′ N, 04°18.7′ W, 1950 m, 1 dd; stn DS 87, 44°05′ N, 04°19′ W, 1913 m, 3 lv; Biogas VII: stn CP 26, 47°33′ N, 08°34′ W, 2115 m, 1 lv; Biogas VIII: stn KG 145, 47°33′ N, 08°39′ W, 2170 m, 1 dd; stn KG 147, 47°33.40′ N, 08°40.70′ W, 2190 m, lv, dd; stn KG 149, 47°33′ N, 08°39′ W, 2165 m, 1 dd; stn KG 151, 47°34′ N, 08°39′ W, 2205 m, 1 lv; Biogas IX: stn CP 34, 47°32′ N, 08°25′ W, 1970 m, 1 dd; Biogas XI: stn CP 37, 47°34′ N, 08°41′ W, 2175 m, 2 lv.

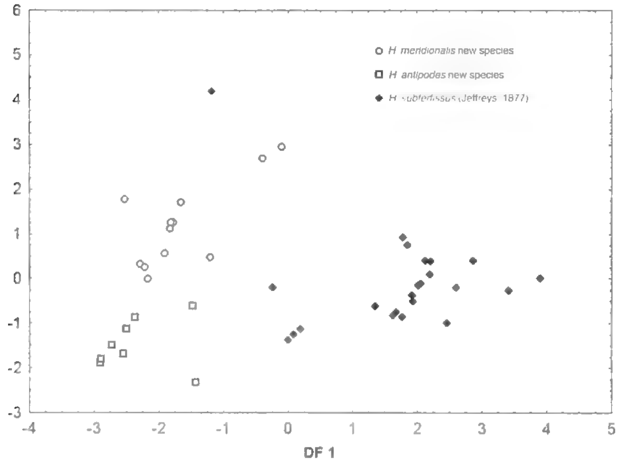

Figure 18. Discriminant function analysis of shell morphometric parameters of *Heteroschismoides* species.

Distribution: Eastern Atlantic Ocean: Greenland, off West Ireland, Gulf of Gascony, off Spain and Portugal to Gulf of Guinea, West Africa (Jeffreys, 1877; Watson, 1879, 1886, Locard, 1898; Nicklès, 1979). Alive in 940

2987 m, shells down to 4829 m (present paper). Richest depth for live material: 2040–2503 m (present paper).

Remarks: Jeffreys partially described the species based on a juvenile specimen, since he mentioned "... posterior end bulbous" and illustrated this morphology in plate 49, fig. 3. However, no juvenile specimen was detected among the type material. In addition, he wrote that the slit is in the "under or ventral side", which in fact corresponds to the dorsal side in normal position of the animal. Jeffreys also mentioned the presence of 12 to 16 ribs, but we did not find any specimens with that number of ribs. However, it is possible that secondary ribs and intercostal striae might have been, in part, counted inappropriately for the original description. To clarify, in the description we enumerated only the primary ribs because the number of secondary ribs varies with age and among specimens but the number primary ribs is constant among specimens and through the life of the specimen. Specimens with embryonic shell are often observed.

Heteroschismoides subterfissus was also mentioned in the CHALLENGER expedition from "stn 120 - 8°37′ S 34°28′ W, Pernambuco, South America 675 fathoms [1232 m] red mud" (Watson, 1886). The lot in which this reference was based was not located in BMNH collections by the senior author. In the distribution paragraph, Watson (1886) wrote "Habitat.- Davis Strait. 1785 fathoms. North Atlantic; various Stations off the West Coast of Ireland. 1180 to 1476 fathoms (Jeff.)." He did not mention Pernambuco.

The material from Pernambuco may belong to the new species described below or, as suggested by Henderson (1920: 58), could also correspond to specimens of *Pertusiconcha callithrix* (Dall, 1889), since young specimens of this species, specially those with a broken apex, can easily be misidentified as species of *Heteroschismoides* (Scarabino, pers. observ).

Heteroschismoides meridionalis new species
(Figures 7–10, 17)

Description: Shell 14 mm length, slightly curved, regularly tapering, opaque white. Longitudinal sculpture composed of nine rounded-edge primary ribs, all reaching but fading towards the oral aperture. No secondary ribs. Intercostal spaces concave in posterior three quarters and straight to convex at the anterior fifth, presenting 12 very faint, fine striae throughout. Apex with a 2 mm long, wide irregular fissure on dorsal side. Cross-section polygonal, less angular at apex and at the slightly laterally compressed anterior aperture.

Measurements of the Holotype (mm): Length 14.0, oral aperture 1.0, apex 0.1, arc 0.8 at 6.7 from apex.

Type Material: Holotype (lv) MNHN 20902 and 14 paratypes (dd), 13 MNHN 20903–20906, 1 MNRJ 12707.

Type Locality: Off Espírito Santo, Brazil, 18°59.1′ S, 37°47.8′ W, 1540–1550 m [MD 55 stn DC 70].

Material Examined: Southwestern Atlantic Ocean: MD 55 stn CP 68, 18°55.6′ S, 37°49.1′ W, 1200–1500 m, 1 dd (paratype MNHN 20903); stn DC 70, 18°59.1′ S, 37°47′8 W, 1540–1550 m, 1 lv (holotype MNHN 20902), 26 dd (7 paratypes MNHN 20904, 1 paratype MNRJ 12707); stn DC 72, 19°00.4′ S, 37°48.8′ W, 950–1050 m, 4 dd (paratypes MNHN 20905); stn CB 77, 19°40.6′ S, 37°48.1′ W, 790–940 m, 9 dd (2 paratypes MNHN 20906); stn. CB 79, 19°01.8′ S, 37°47.8′ W, 1500–1575 m, 10 dd; stn CB 106, 23°54.2′ S, 42°10.5′ W, 830 m, 15 dd; stn. CB 107, 24°00.3′ S, 42°14.4′ W, 1020 m, 11 dd.

Etymology: *Meridionalis*: Southern. Name refers to the taxon's distribution in the Southern Hemisphere.

Distribution: Brazil: Espírito Santo and São Paulo. Alive in 1540 m, shells in 790–1540 m depth.

Heteroschismoides antipodes new species
(Figures 11–14, 16)

Description: Shell to 9.95 mm length, slightly curved at the apex, regularly tapering. Opaque white. Longitudinal sculpture of ten primary ribs, all reaching the oral aperture. Intercostal spaces concave and smooth. Apex with a wide irregular fissure 1.7 mm long on dorsal side. Cross section polygonal, less obvious at apex, slightly laterally compressed at the anterior aperture.

Measurements of Holotype (mm): Length 9.95, oral aperture 0.9, apex, 0.1, arc 0.4 at 2.76 from apex.

Type Material: Holotype (dd) MNHN 20907 and 10 paratypes (7 lv, 3 dd) MNHN 20908–20910

Type Locality: Solomon Islands, 07°49.3′ S, 157°41.2′ E, 1045–1118 m [SALOMON 2 Stn. CP2217].

Material Examined: Solomon Islands. SALOMON 2: stn CP2182, 08°47.0′ S, 157°37.9′ E, 762–1060 m, 16 dd; stn CP2197, 08°24.4′ S, 159°22.5′ E, 897–1057 m, 2 lv, 2 dd (3 paratypes MNHN 20909); stn CP2217, 07°49.3′ S, 157°41.2′ E, 1045–1118 m, 1 lv, 3 dd (holotype MNHN 20907 and 3 paratypes MNHN 20908), stn CP2218, 07°56.3′ S, 157°34.6′ E, 582–864 m, 4 lv (paratypes MNHN 20910) 14 dd; stn CP2253, 7°26.5′ S, 156°15.0′ E, 1200–1218 m, 10 dd.

Etymology: From Greek *antipodes*, meaning those living on diametrally opposed places on Earth.

Distribution: Solomon Islands, alive in 1200 m; shells 762–1200 m depth.

MORPHOMETRIC RESULTS AND DISCUSSION

Table 1 lists the mean, standard deviation, minimum, and maximum values for each morphometric parameter for the three species. Significant differences in all morphometric parameters were observed between the species (Kruskal-Wallis test; $p<0.01$), except for the maximum curvature (Arc). This univariate comparison showed that *H. meridionalis* new species and *H. subter-*

Table 1. Shell morphometric parameters with minimum (min), maximum (max), mean values and standard deviation (±SD) for the three new species of *Heteroschismoides.* L: length; Max: maximum diameter (= anterior aperture diameter); Arc: maximum curvature; Larc: distance of point of maximum curvature from the apex: Apd, apical aperture diameter; Fiss: fissure length. KW: Kruskal-Wallis test); *ns:* not significant; °p<0.001. The horizontal lines at Dunn's test represents absence of statistical differences.

	H. meridionalis (n=12)		*H. antipodes* (n=8)		*H. subterfissus* (n=23)			
	mean (±SD)	min–max	mean (±SD)	min–max	mean (±SD)	min–max	KW	Dunn's test
L	13.3 (1.6)	11.1–16.5	8.9 (0.8)	7.9–10.7	14.2 (2.6)	10.0–19.0	19.19°	st sb an ├───┤ ├─┤
Max	1.0 (0.05)	0.9–1.1	1.0 (0.07)	1.0–1.2	1.4 (0.16)	1.0–1.7	29.76°	st an sb ├───┤ ├─┤
Arc	0.5 (0.4)	0.1–1.2	0.5 (0.1)	0.4–0.7	0.5 (0.1)	0.2–1.0	0.82 *ns*	st sb an ├───────┤
Larc	6.1 (0.8)	4.8–7.2	3.5 (0.6)	2.1–4.0	5.4 (2.5)	2.2–11.4	14.98°	st sb an ├───┤ ├─┤
Apd	0.1 (0.05)	0.1–0.2	0.2 (0.00)	0.2–0.2	0.2 (0.05)	0.2–0.3	20.15°	st an sb ├───┤ ├───┤
Fiss	2.1 (0.5)	1.5–3.1	1.4 (0.2)	1.1–1.5	1.9 (0.5)	1.2–3.0	13.32°	st sb an ├───┤ ├─┤

fissus are more similar, differing significantly only in maximum diameter (Max) and apical aperture diameter (Apd) (Table 1). *Heteroschismoides meridionalis* new species is also less shiny and the intercostal spaces are more densely striated: 12–15 striae (observed on stained or coated specimens due to the difficulty to be observed without any treatment) against 8–10 in *H. subterfissus* (well observed under lens) (these data was obtained from counting 10 specimens of each species).

Individuals of *Heteroschismoides antipodes* new species are significantly smaller than individuals of the other two species for both shell length and fissure extension. The distance of point of maximum curvature from apex (Larc) in *H. antipodes* new species specimens is located nearer to apex than in specimens of both *H. meridionalis* new species and *H. subterfissus* (Table 1). In addition, *H. antipodes* specimens are opaque, due to their coarsest surface microsculpture. Specimens of this species have smooth intercostal spaces without secondary ribs and striae, and the primary ribs are more apparent.

The multivariate discriminant function analysis was able to distinguish three groups among the specimens we examined that correspond to three species (Wilks' Lambda = 0.12; $F_{6,76} = 24.27$; $p < 0.0000$). This analysis classifies about 97% of the cases correctly (only 1 out of 43 specimens were incorrectly classified) (Figure 3). The model was constructed with 3 parameters (Max, L : Max, Larc). The variable L, which was highly correlated with Larc ($r = 0.80$) and Fiss ($r = 0.74$), was excluded. The Discriminant Functions (DF) based on the raw coefficients of canonical variables are shown below:

$$\mathrm{DF1} = 2.5439\mathrm{Max} + 1.0378\mathrm{L} : \mathrm{Max} - 0.7366\mathrm{Larc}$$

$$\mathrm{DF2} = 0.7249\mathrm{Max} + 2.1404\mathrm{L} : \mathrm{Max} - 0.8328\mathrm{Larc}$$

The radulae of the three species, here illustrated, are quite similar and further studies would be necessary to test the existence of interspecific differences, as it is the case in most Scaphopoda. Finally, the findings of *Heteroschismoides* in the Solomon Islands show the genus to have worldwide distributed instead of being confined to the eastern Atlantic Ocean. However, better sampling of areas of the Indian Ocean (one of the less known tropical areas for scaphopod diversity) could eventually confirm whether the genus is also represented in that ocean.

ACKNOWLEDGMENTS

The authors want acknowledge the support and help received from Philippe Bouchet, Virginie Héros, and Philippe Maestrati (MNHN), Ellen Strong (USNM), Kathie Way (BMNH), and Anders Warén (Swedish Museum of Natural History, Stockholm). Ronald Shimek is also gratefully acknowledged for his constructive comments on the manuscript.

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Parasitism of *Monogamus minibulla* (Olsson and McGinty, 1958) (Gastropoda: Eulimidae) on the red sea-urchin *Echinometra lucunter* (Linnaeus, 1758) (Echinodermata: Echinometridae) on the Caribbean coast of Mexico

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ABSTRACT

Eulimids are gastropod mollusks parasites of echinoderms. Intertidal red sea-urchins, *Echinometra lucunter*, collected along the Mexican Caribbean shores were examined for the presence of those ectoparasitic gastropods. The analysis of 206 sea-urchins resulted in 56 having eulimids on them (27% prevalence), mostly living in pairs, with about 7 eulimid pairs per sea-urchin. The eulimid gastropods found are *Monogamus minibulla* (Olsson and MacGinty, 1958), described from Panama. Its host was unknown. This article consists of the first record of this host-parasite relationship. A short description of the shell structure and some details of the biological relationship are given. The females are much larger than the males, and the latter are usually attached to the female bodies. Most female eulimids live inside the hypertrophied foot, which this allows for partial enveloping of the entire body. A few females, however, were found living fixed directly on the echinoderm integument. The position of the gastropod on the sea-urchin is fixed via boring through the skeleton. Anchoring is achieved via the proboscis. Some females had egg capsules (0.9–1.5 mm) fixed to their bodies; each is a spherical structure attached to the body by a short stalk. Egg capsules contained 14–15 embryos in different stages of development. The only previously published account of this type of relationship involves a similar species living on *Echinometra mathaei* (Blainville, 1825) from the Red Sea.

Additional Keywords: Rosenia, Echinometra mathaei, Monogamus interspinea

INTRODUCTION

The red sea-urchin *Echinometra lucunter* (Linnaeus, 1758) is frequently found on shallow water rocky-bottoms along the Mexican Caribbean shores, and occasionally in sea-grass beds. In that region, some specimens living in the reef lagoons host one or more tiny whitish eulimid gastropods firmly attached to their bodies.

Ecological associations including eulimids gastropods have been recognized (Warén, 1983). The original description of the eulimid *Rosenia minibulla* Olsson and McGinty, 1958, was made from an empty shell found on the beach of Isla Bocas, Panama; however at that time, its host was unknown.

Lützen (1976) studied the sea urchins *Echinometra mathaei* (Blainville, 1825) from the Red Sea and the Western Pacific Ocean and found eulimid parasites on them. He named a new genus as *Monogamus* because he found these eulimids always living in pairs; he included two different species, one (*M. entopodia* Lützen, 1976) living inside the hypertrophied tube feet of *E. matthaei* from the Red Sea, and another one (*M. interspinea* Lützen, 1976) living on the integument of *E. matthaei* from several localities in the Western Pacific Ocean.

Warén (1983) established *Rosenia* Schepman, 1914, as a junior synonym of *Pelseneeria* Koehler and Vaney, 1908. However, the transfer of *Rosenia minibulla* to *Monogamus* was informally proposed by Warén and Moolenbeek (1989), perhaps because both share internal growth lines in the body whorl. In addition, the former author had found individuals of the species living on *E. lucunter*.

The faunal associations of the red sea-urchin were studied in the southern Caribbean Sea by Schoppe and Werding (1996), but these authors did not find eulimids associated with the red sea-urchin in the study localities. In this contribution, my objectives are to report the parasitism of the eulimid *Monogamus minibulla* (Olsson and McGinty, 1958), on the red sea-urchin *Echinometra lucunter* (Linnaeus, 1758), found along the Caribbean coast of Mexico, and to describe some aspects of the relationship between the two species.

MATERIALS AND METHODS

The material was collected along several places in the Caribbean coast of Quintana Roo, Mexico: Isla Contoy

(21°30′8.4″ N, 86°47′45.3″ W, 28/II/01); Playa Paraiso, Cozumel (20°35′21.5″ N, 86°43′44″ W, 24/III/01); Playa Ana and José (19°54′22.4″ N, 87°26′14.5″ W, 2 km S from the junction to Boca Paila, 18/II/01); Majagual (18°43′28″ N, 87°42′05″ W, 22/III/00); Punta Herradura (18°32′23″ N, 87°44′32″ W, 27/VI/00); and Buenavista (18°30′42″ N, 87°45′30″ W, 15/V/99).

Sea-urchins were counted and those with eulimids fixed, sorted and kept individually, and identified according to Hendler et al. (1995). The number of eulimids per sea-urchin was counted to determine the prevalence: the relationship between the number of infested hosts (sea-urchins) and the total number of hosts; and the intensity: number of parasites (eulimids) present in infected host (Margolis et al. 1982). Voucher specimens were deposited in the Swedish Museum of Natural History, Stockholm, Sweden, SMNH 27858, and in the Reference Collection of El Colegio de la Frontera Sur (ECOSUR), Chetumal, Mexico).

RESULTS

Monogamus minibulla (Olsson and McGinty, 1958)

Description: Mean shell length: 1.85 mm (range 1.5–2.5), width 1.15 mm (range 1.0–1.5). Females are easily distinguished due to their body-size, being twice as large as males. The shell is tiny, spherical, fragile, and transparent. The spire is low, the nuclear apex is long and erect like a stump (mucro). The shell color is white with glossy texture, with a very fine suture line. There are two post-nuclear whorls; the first one is small and convex, with a small shoulder close to the suture, which is better seen on the aperture side. The body whorl is large, and inflated, polished, with some delicate growth lines. The aperture is wide, the outer lip thin, expanded along its median part. There is no operculum. When the animal is alive, the mantle and visceral mass are deep-red. There are two distinct black eyes. Tentacles were not observed.

Parasitism: From a total of 206 sea-urchins, 56 were infested with eulimids. The prevalence was of 0.27 (presence of the parasite in 27% of the specimens). The intensity was of 7.03: there was an average of 7.03 eulimid pairs per sea-urchin (including only those that were infested by at least one eulimid [Table 1]).

Attachment Locations of Parasites on Hosts: Many parasites have a preference for the oral side of the host, although some were located on the dorsal side (periproct); in only two cases parasites were found on the peristomial membrane (buccal tube foot). Most eulimids invade the tube feet, becoming inserted in its integument. This invasion can produce a hypertrophy of that tube foot. Often, the deformation is such that when the eulimid grows into adulthood, the tube feet are modified beyond recognition. The eulimids, in particular juveniles with a single teleoconch whorl, use the skin of the tube as a protective hood; later, as the animal grows, its own mantle (the pseudopallium) covers the fragile shell, except for the apical part, which is left uncovered (Figure 1).

Another attachement site is the interambulacral zone. Eulimids that are not covered by the pseudopallium are attached by the snout (plus pharyngeal anchor). Few others may be found adhering to the integument at the base of spines, where according to stage of shell growth, it may be collapsed, broken, and later disappear, leaving an open space where the "eulimid-scar" becomes evident.

Eulimids may bore the sea-urchin test: this may be seen clearly when detached specimens were placed on a host. They may also enlarge the pore associated with the foot tube: a typical feeding pattern of ectoparasitic eulimids involves insertion of the proboscis through the tube pore followed by suction of coelomic contents of the sea-urchin.

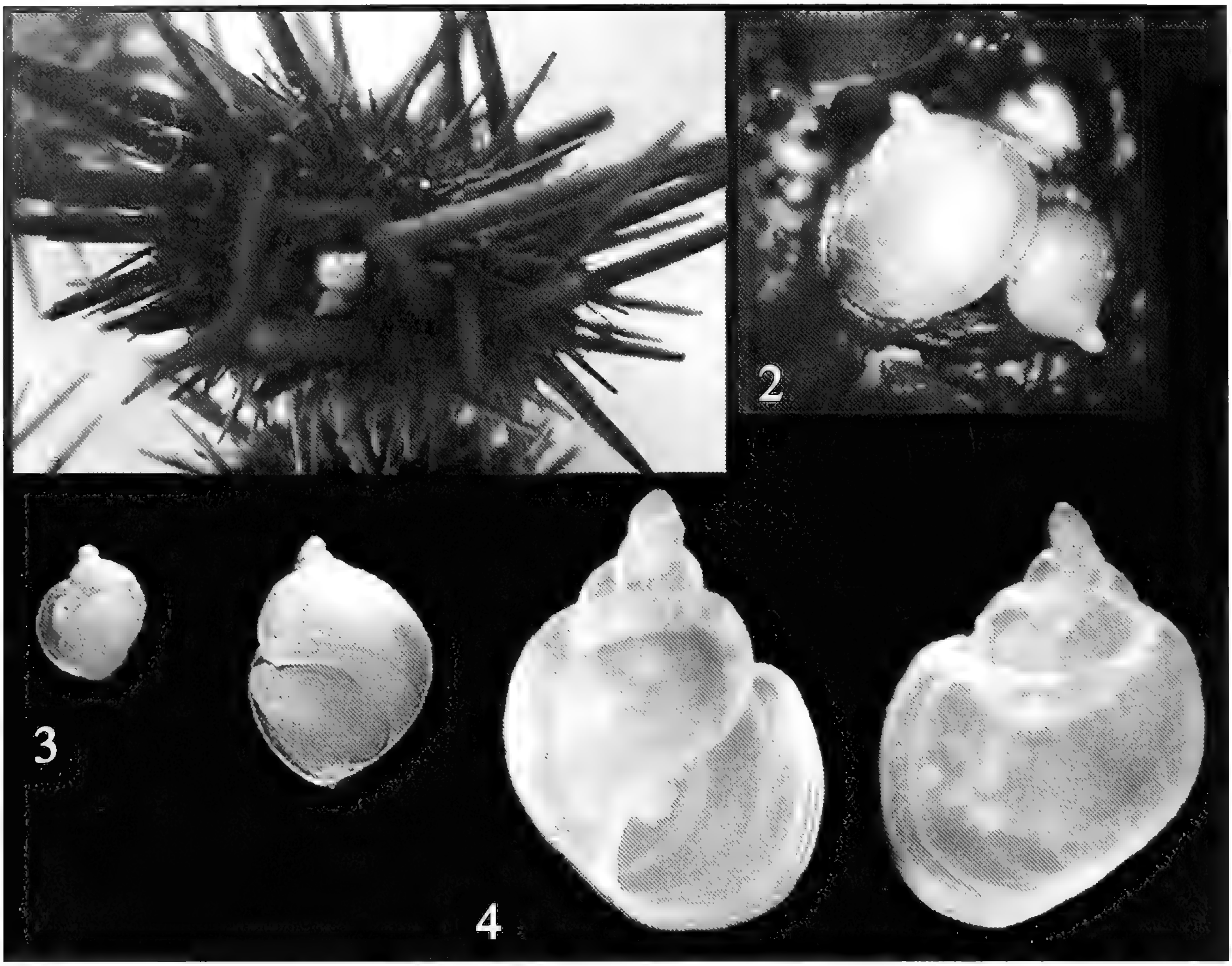
The gastropods were found mostly in pairs, but, less frequently, two or three males were found associated with a single larger female. These pairs look like irregularly shaped protrusions of the body wall, each with one or two circular openings through which the eulimid shell tips may project. Egg capsules were observed packed in globular sacks (3–5), attached for a short stalk to the body of the female, and partially or completely covered by the pseudopallium. Each capsule (size 0.09–1.5 mm in length) contained 14–15 embryos. Egg capsules contained all stages from early egg stage to small juveniles ready to hatch.

DISCUSSION

Olsson and McGinty (1958) described *Monogamus minibulla* based on an empty shell. In the present study details of the shell morphology are presented based on several alive specimens and those fixed on the sea-urchins. Warén in Warén and Moolenbeek (1989) briefly pointed out the presence of *M. minibulla* associated to

Table 1. Intensity and prevalence of *Monogamus minibulla* on *Echinometra lucunter* on the Caribbean coast of Mexico.

Localities	Sea urchins	With parasites	Eulimid females	Intensity	Prevalence
Isla Contoy	27	13	268	20.61	0.48
P. Paraíso	3	1	1	1.00	0.30
P. Ana y José	51	14	114	8.14	0.27
Majagual	120	23	9	0.39	0.19
P. Herradura	3	3	2	0.66	1.00
Buenavista	2	2	1	5.50	1.00



Figures 1–4. *Monogamus minibulla.* **1.** On *Echinometra lucunter* (host test = 16.54 mm diameter × 8.72 mm height); **2.** *In situ.* **3.** Male (left, 1.5 mm) and female (right, 2.5 mm). **4.** Female, anterior and lateral views (1.8 mm height × 1.4 mm width.)

Echinometra lucunter. However, they only recorded the dimensions of the shell (1.5 mm of longitude and a larval shell of 1.0 mm), because their contribution was focused mainly in the relationship of the eulimid *Trochostilifer eucidaricola* (Warén and Moolenbeek, 1989) associated with the pencil sea-urchin *Eucidaris tribuloides* (Lamarck, 1816). This study constitutes the first report of the relationship of *Monogamus minibulla* with *Echinometra lucunter* for the Mexican Caribbean region.

Lützen (1976) reported the presence of *Monogamus entopodia* in the tube feet of the Red Sea sea-urchin. In the Mexican Caribbean, *M. minibulla* infests the tube feet, but was also observed attached to the epidermis host, using its snout and tissues of the host but without being covered or protected with the pseudopallium. The two different patterns were rarely observed on the same sea-urchin. Lützen (1976) had found the same patterns but on sea urchins collected in different localities and regarded them as belonging to two different species. Further, *Echinometra* from the Indian and western Pacific oceans have been found to belong to three different morphospecies that might be reproductively isolated from each other as well (Arakaki and Uehara, 1999). Thus, it seems that Caribbean sea-urchins have not diverged as much as those present in the Indo-Pacific Oceans.

Few studies have detailed the prevalence and intensity of eulimids parasites, Salazar and Reyes (1998) studied the relationship of *Thyca callista* Berry, 1959, and the starfish *Phataria unifascialis* (Gray, 1840), finding that the association was more frequent in two sites of the Gulf of California where human influence was more accentuated. In this case, only one of the localities (Playa Ana and José) is heavily influenced by development, and is a protected, semi-enclosed embayment, with many residences and tourists. That locality presented two sea-urchins that had unusually high infestations of about 100 eulimids each. Most of the sea-urchins were adjusted close to the average of about 7 eulimid pairs per sea-urchin.

Warén (1983) pointed out that many tropical eulimids that attach their egg capsules to their shells to or to their hosts, have almost invariably been found with spawn, an indication that spawning might be continuous. On the other hand, Lützen (1976) suggested for *M. entopodia* that the presence of different developmental stages found simultaneously in samples of egg capsules indicates continual production of eggs, which is similar to what happens in *M. minibulla*.

A thorough study of the association is required to elucidate the mechanisms of feeding, including histology. There is need to clarify whether the proboscis sucks of part of the liquid fraction of the host's coelom or, as Lützen (1976) pointed out for *M. entopodia*, the eulimid feeds exclusively of the area adjacent to attachment on the sea-urchins.

To determine the specificity of this association it is necessary to do experiments and observations in the collection place, to determine whether, as Warén (1983) pointed out, there is lack of specificity of the parasite on a single species guest. Although I had opportunity to examine some specimens of *Echinometra viridis* Agassiz, 1863, and I did not observe any attached eulimids, it could be said that if some preference exists in this case, but also this would have to corroborate it. Further, in 2001 I had examined about 50 specimens belonging to *E. lucunter* from Guana Island, but none had any associated eulimid parasite.

ACKNOWLEDGMENTS

Many thanks to Anders Warén (Swedish Museum of Natural History), who always answered my questions about eulimids and is always ready to help. To Sergio Salazar-Vallejo and Maria Ana Tovar, who reviewed previous drafts of the manuscript and to colleagues at ECOSUR for collecting the sea urchins for the present study. The careful reviews by Anders Warén and an anonymous referee enhanced the clarity of this contribution. Humberto Bahena helped improve the quality of the photographs.

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Erratum

Due to an editorial lapse, the article by Simone and Cunha (2008) in the most recent issue of The Nautilus incorrectly listed "FMNH" instead of the correct form "UF" as the collection acronym for the Florida Museum of Natural History.

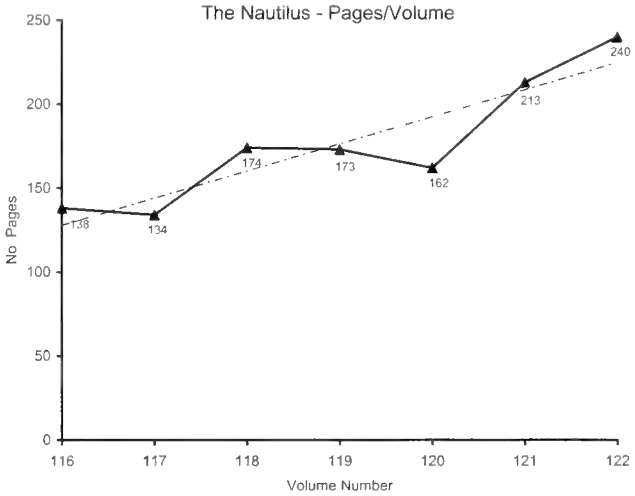
LITERATURE CITED

Simone, L. R. L. and C. M. Cunha. 2008. Revision of the genus *Spinosipella* (Bivalvia: Verticordiidae), with descriptions of two new species from Brazil. The Nautilus 122: 57–78.

Notices

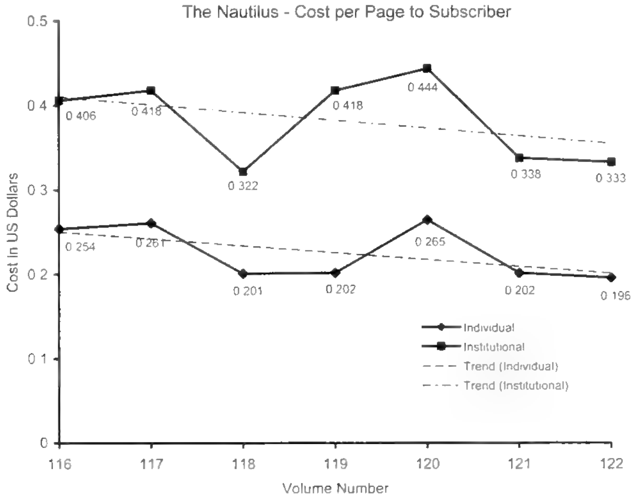
Subscriptions rates for The Nautilus will increase slightly for 2009. Individual and institutional subscriptions will change respectively to $50 and $85. Shipping costs will remain the same. These adjustments are necessary given increases in production, materials, and mailing costs.

The Nautilus staff has been making a concerted effort to increase the quality and quantity of articles published in the journal. The graph below shows the number of pages published in the last seven volumes (the number of pages for current volume 122 is projected). The increase in number of pages has been steady, and we intend to keep this positive rate for the next volumes.



Given the increase in number of pages, the cost of one page to subscribers has actually declined in the past seven years, from $0.25 in 2002 [volume 116] to $0.19 in 2008 [volume 122], to individual subscribers, and from $0.40 to $0.33 to institutional subscribers.

The graph below shows the price per page to individual and institutional subscribers and relevant trends for the past seven years based on subscription costs and number of pages. Please consider these figures and trends when renewing your subscription!



The Nautilus has signed an agreement with the Biodiversity Heritage Library (BHL) Project. Ten major natural history museum libraries, botanical libraries, and research institutions have joined to form BHL. The agreement entails digitizing back issues of The Nautilus for open electronic access to the entire journal except for the last three volumes. One of the participating members of BHL, the National Museum of Natural History (Smithsonian Institution) Library in Washington, DC, started digitizing the journal.

The Nautilus will be posted in the BHL portal (www.biodiversitylibrary.org) and in The Bailey-Matthews Shell Museum web site (shellmuseum.org/nautilus). Accordingly, BHL will receive 29 volumes of the journal previously scanned by friends of the journal. The Nautilus and its editor want to acknowledge the time and effort contributed by David Campbell, Wayne Harland, Fabio Moretzsohn, Richard E. Petit, and Colin Redfern in that first phase of the electronic access project.

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THE NAUTILUS

Volume 122, Number 4
December 22, 2008
ISSN 0028-1344

A quarterly devoted to malacology.

SUBSCRIPTION INFORMATION

The subscription rate for volume 123 (2009) is US $50.00 for individuals, US $85.00 for institutions. Postage outside the United States is an additional US $10.00 for regular mail and US $25.00 for air delivery. All orders should be accompanied by payment and sent to: THE NAUTILUS, P.O. Box 1580, Sanibel, FL 33957, USA, (239) 395-2233.

Change of address: Please inform the publisher of your new address at least 6 weeks in advance. All communications should include both old and new addresses (with zip codes) and state the effective date.

THE NAUTILUS (ISSN 0028-1344) is published quarterly by The Bailey-Matthews Shell Museum, 3075 Sanibel-Captiva Road, Sanibel, FL 33975.

Periodicals postage paid at Sanibel, FL, and additional mailing offices.

POSTMASTER: Send address changes to: THE NAUTILUS
P.O. Box 1580
Sanibel, FL 33957

THE NAUTILUS

Volume 122, Number 4
December 22, 2008
ISSN 0028-1344

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STATEMENT OF OWNERSHIP, MANAGEMENT, AND CIRCULATION

1. Publication Title, THE NAUTILUS.
2. Publication No., 0028-1344.
3. Filing Date, September 24, 2008.
4. Issue Frequency, Quarterly.
5. No. of Issues Published Annually, Four.
6. Annual Subscription Price, US $80.00.
7. Complete Mailing Address of Known Office of Publication, 3075 Sanibel-Captiva Road, Sanibel, FL 33957 USA.
8. Complete Mailing Address of Headquarters, same as 7.
9. Full Names and Complete Mailing Addresses of Publisher, The Bailey-Matthews Shell Museum, 3075 Sanibel-Captiva Road, Sanibel, FL 33957 USA.
   Editor, Dr. José H. Leal, address as above.
   Managing Editor, Mary Jo Bunnell, address as above.
10. Owner, Shell Museum and Educational Foundation, Inc., address as above.
11. Known Bondholders, Mortgagees, and Other Security Holders Owning or Holding 1 Percent or More of Total Amount of Bonds, Mortgages, or Other Securities, None.
12. The purpose, function, and nonprofit status of this organization and the tax exempt status for federal income tax purposes has not changed during the preceding 12 months.
13. Publication Name, THE NAUTILUS.
14. Issue Date for Circulation Data Below, September 26, 2008.

15.	Extent and Nature of Circulation	Average 12 months	Single Issue
A.	Total Number of Copies	420	420
B.	Paid Circulation		
	1. Paid/Requested Outside-County Mail Subscriptions	309	319
	2. Paid In-County Subscriptions	0	0
	3. Sales Through Dealers and Carriers, Street Vendors, Counter Sales, and Other Non-USPS Paid Distribution	0	0
	4. Other Classes Mailed Through the USPS	16	15
C	Total Paid and/or Requested Circulation	325	334
D.	Free Distribution by Mail		
	1. Outside-County	12	12
	2. In-County	0	0
	3. Other Classes Mailed Through the USPS	0	0
E	Free Distribution Outside the Mail	0	0
F	Total Free Distribution	12	12
G	Total Distribution	337	346
H.	Copies not Distributed	83	74
I	Total	420	420
J	Percent Paid and/or Requested Circulation	97%	97%

New species of scissurellids from the Austral Islands, French Polynesia, and the Indo-Malayan Archipelago (Gastropoda: Vetigastropoda: Scissurellidae, Anatomidae, Larocheidae)

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ABSTRACT

Four new species of Scissurellidae, Anatomidae, and Larocheidae are described from the Austral Archipelago, French Polynesia and the Indo-Malayan Archipelago: *Sinezona danieldreieri* new species, *S. wiley* new species (both Scissurellidae), *Anatoma rapaensis* new species (Anatomidae) and *Trogloconcha lozoueti* new species (Larocheidae). One of the species is currently only known from the Austral Islands *T. lozoueti*), while the others seem to show a broad Indo-Malayan Archipelago to western Pacific distribution. Shells of all species and the radulae of *S. danieldreieri*, *T. lozoueti*, and *A.rapaensis* are illustrated with scanning electron micrographs.

Additional Keywords: Mollusca, Rapa Island, radula

INTRODUCTION

The present contribution describes some microgastropods in the families Scissurellidae, Anatomidae, and Larocheidae known from the Austral Islands and beyond. The impetus stems from a French expedition to the southeastern-most Austral island, Rapa (see Lozouet et al., 2004; 2005 for details); for the species found at Rapa, additional material from other localities located in various institutional collections has also been included. This article is part of a series describing the biodiversity of this remote archipelago (e.g., Schwabe and Lozouet, 2006).

Scissurellidae sensu lato comprises lineages of small basal marine snails in Vetigastropoda (Geiger et al., 2008). The phylogenetic position of Anatomidae is currently unsettled. Whereas Geiger and Thacker (2005; unpublished data) resolved a *Lepetodrilus* (Lepetodrilidae) + *Scissurella*, *Sinezona*, *Sukashitrochus* (Scissurellidae sensu stricto) clade with more distantly related *Anatoma* (Anatomidae), Kano (2008) using the same three genes (Histone 3, COI, 18S) recovered in some of his analyses a clade uniting all three of these lineages (*Lepetodrilus, Sinezona, Anatoma*). Scissurellidae and Anatomidae are characterized by a slit or foramen in the shell (lacking in Larocheidae), a rhipidoglossate radula, and a lack of nacre. Approximately 140 species are currently described with an additional 90 remaining to be formally recognized (Geiger, 2003; 2008). To date, no species in these families have ever been recorded from the Austral Islands. The species described herein are all new to science, one with its range restricted to the Austral Islands, and three others known from several localities in the broad Indo-Pacific.

MATERIALS AND METHODS

Standard methods for scanning electron microscopy (SEM) were employed as detailed in Geiger (2006a, b, c) and Geiger et al. (2007). Terminology for shell morphology and details on method of whorl count have been given elsewhere (Geiger, 2003; Geiger and Sasaki, 2008). Specimens cited are dry lots; ": complete" indicates wet-preserved lots with animals. All depth indications refer to bottom depth.

Institutional abbreviations used in the text are: BRC: Bret Raines Collection, Kansas City, USA; DLG: Daniel L. Geiger Collection, Los Angeles, USA; JTC: Jean Tröndlé Collection, Paris, France; LACM: Los Angeles County Museum of Natural History, Los Angeles, USA; MNHN: Muséum national d'Histoire naturelle, Paris, France; SBMNH: Santa Barbara Museum of Natural History, Santa Barbara, USA; USNM: United States National Museum of Natural History, Washington (DC), USA; ZMA: Zoological Museum, Amsterdam, The Netherlands.

Other abbreviations used in text are: M: Monotypy OD: Original designation; SEM: Scanning electron microscope/microscopy/micrograph.

SYSTEMATICS

Scissurellidae Gray, 1847
Sinezona Finlay, 1926

Type species: *Schismope brevis* Hedley, 1904 (OD).

Remarks: The genus has recently been treated by Marshall (2002) and Geiger (2003).

Sinezona danieldreieri new species
(Figures 1–9)

Description: Shell small (to 0.77 mm), trochiform. Protoconch of 1 whorl, with strong axial sculpture not reaching apical suture, apertural varix not connected to smooth embryonic cap, apertural margin straight. Teleoconch I of 0.875 whorls, suture at periphery, approximately 9–15 strong, raised axial cords; first spirals after 0.5 whorls. Teleoconch II of 0.6 whorls, approximately four fine spiral cords at onset of selenizone between selenizone and deep suture below periphery, descending noticeably on last 0.25 whorls; shoulder slightly concave, approximately 13–20 axial cords, raised near suture, as high as wide towards selenizone; approximately 10 spirals, distinct cords near suture, diminishing to very fine cords near selenizone; interstices with fine irregular growth lamellae. Base with constriction below selenizone, approximately 15 elevated spiral cords, crossed and run over by approximately 16 fine spiral lines. Umbilicus cone-shaped, moderately wide, wall smooth, at distinct angle to base. Aperture D-shaped, roof overhanging. Selenizone above periphery, keels quite strong, moderately elevated, distinct lunules, elongated foramen closed anteriorly.

Operculum: Thin, flexible, multispiral, with central nucleus.

Radula (Figures 8–9): Rachidian tooth triangular cusp with approximately five equal sized denticles. Lateral teeth 1–3 similar; outer edge of cusp with 4–5 denticles. Lateral tooth 4 reduced in size, hook-shaped. Lateral tooth 5 enlarged by broadening, approximately six, large denticles on inner edge, 1–2 small ones on outer edge. Central denticle of inner marginal teeth large, approximately three denticles on inner edge, four on outer

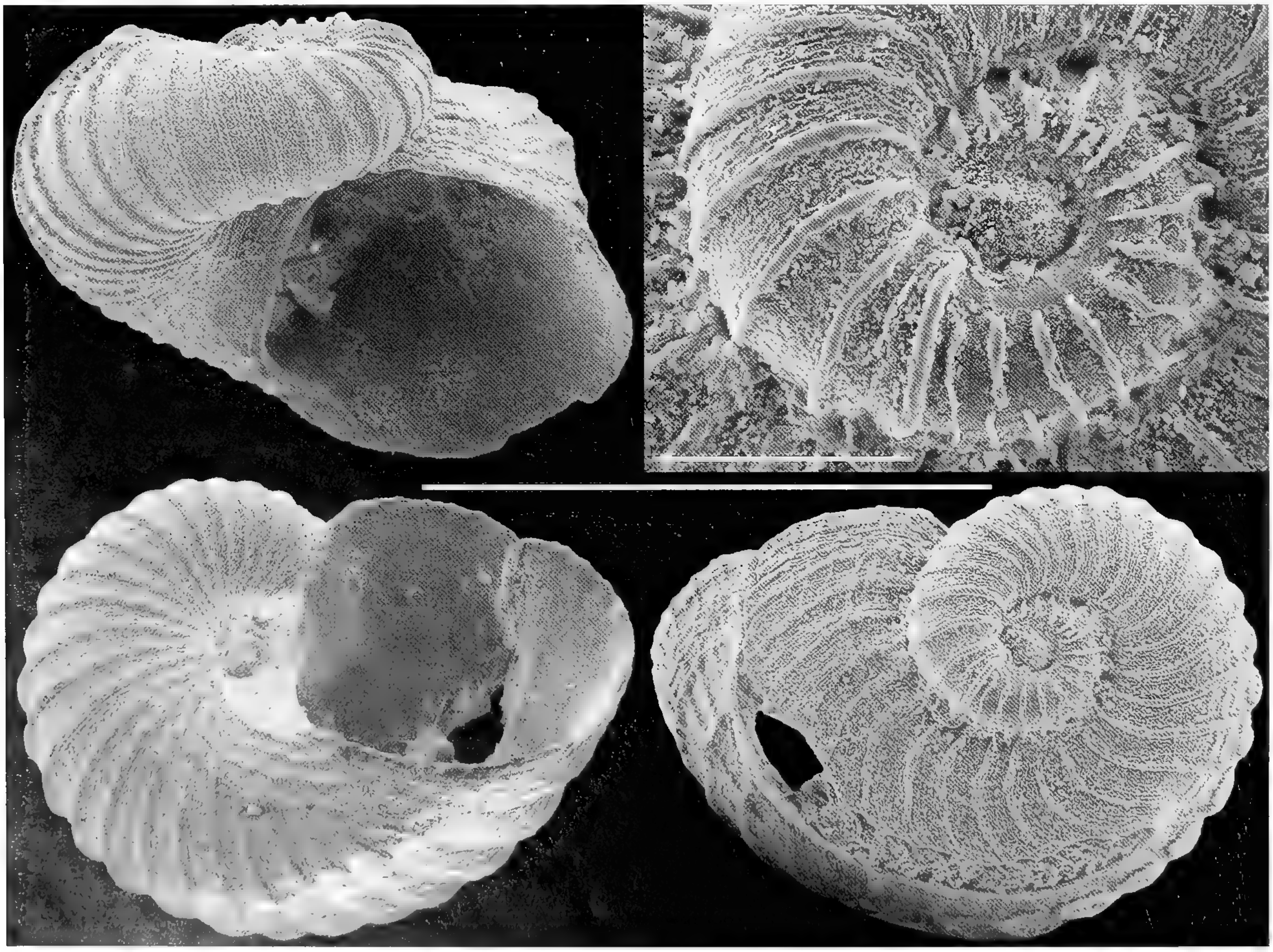


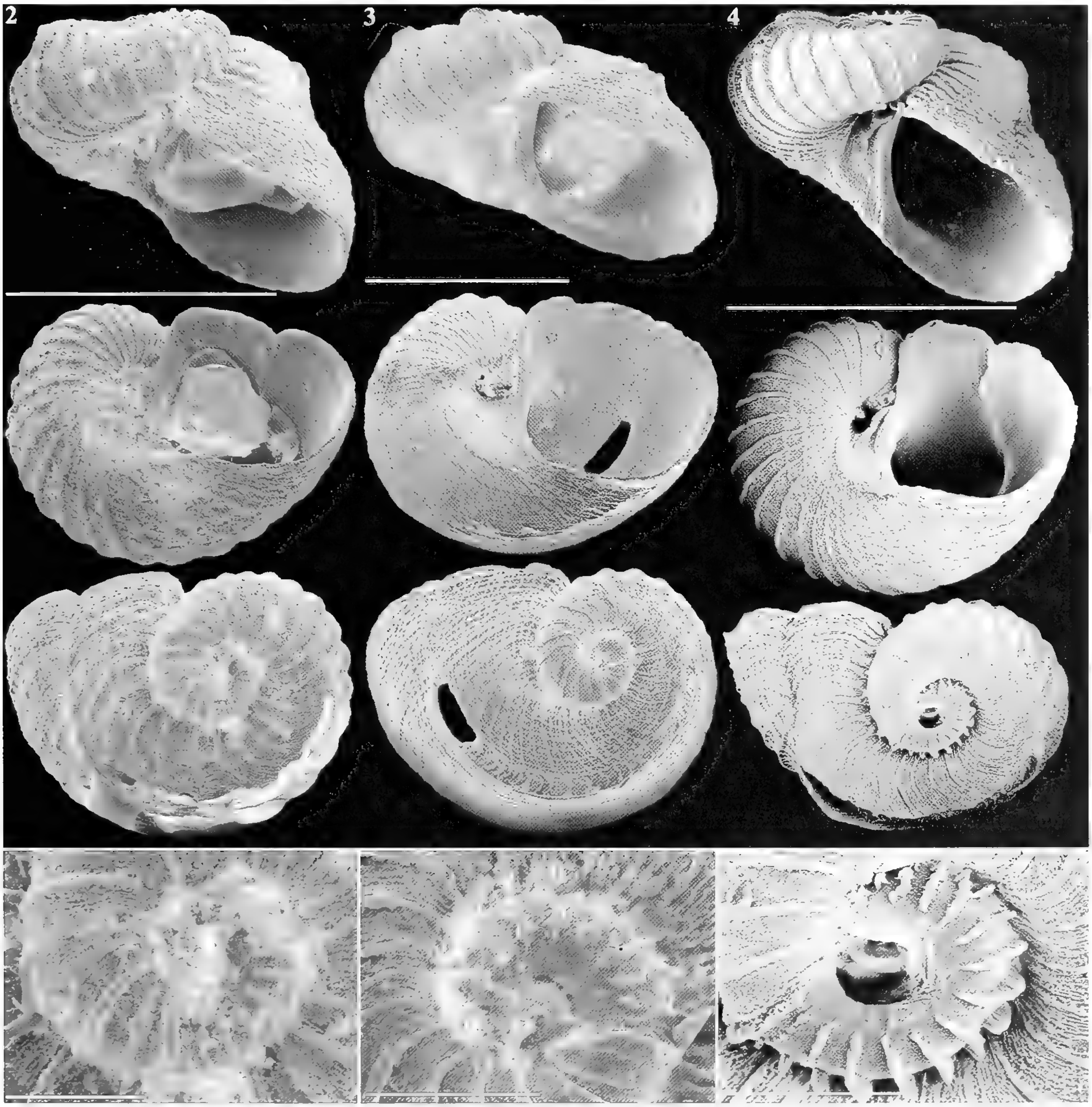
Figure 1. Holotype of *Sinezona danieldreieri* new species. (SBMNH 83540). Lumu Reef, Kimbe Bay, New Britain, Papua New Guinea, 5.283° S, 150.131° E, 0–5 m. Scale bar, shell = 500 μm. Scale bar, protoconch = 100 μm.

edge; outer marginal teeth spoon-shaped, bilaterally symmetrical with approximately a dozen fine denticles on each side. Radular interlock moderate.

Type Material: Holotype: SBMNH 83540: Figure 1. 24 Paratypes: 3–4 m, Little Santa Cruz Island, Mindanao, 6.884° N, 122.04° E (USNM 812453, 1: Figure 2). 1.5 m, Okinawa, Oku, Japan, 26.847° N, 128.287 E (LACM 77–61, 3: one illustrated Figure 3). 20 m, Off Bohol Is, Pamilacan Island, 9.5° N, 123.917° E (AMS 406342, 1: Figure 4).

Type Locality: 0–5 m, Lumu Reef, Kimbe Bay, New Britain, Papua New Guinea, 5.283° S, 150.131° E. Col. D. L. Geiger Oct. 2005.

Etymology: The name honors Daniel Dreier, son of Douglas and Hanna Dreier of Santa Barbara, who have

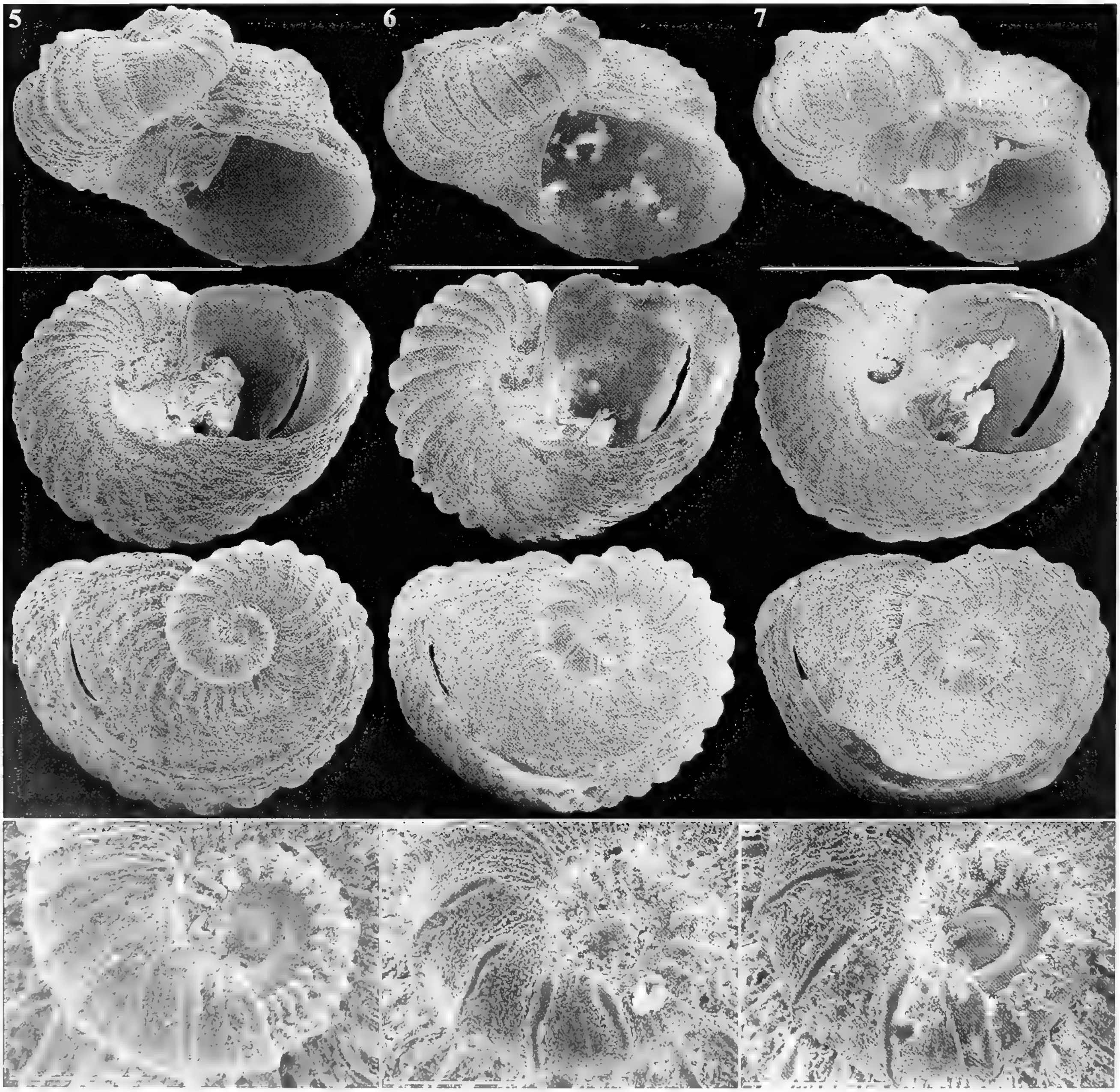


Figures 2–4. Paratypes of *Sinezona danieldreieri* new species **2.** Little Santa Cruz Island, Mindanao, Philippines, 6.884° N, 122.04° E. 3–4 m (USNM 812453, 1). **3.** Okinawa, Oku, Japan, 26.847° N, 128.287° E, 1.5 m (LACM 77-61, 3). **4.** Off Bohol Island. Pamilacan Island. Philippines, 9.5° N, 123.917° E. 20 m (AMS 406342, 1). Scale bars, shell = 500 µm. Scale bars, protoconch = 100 µm

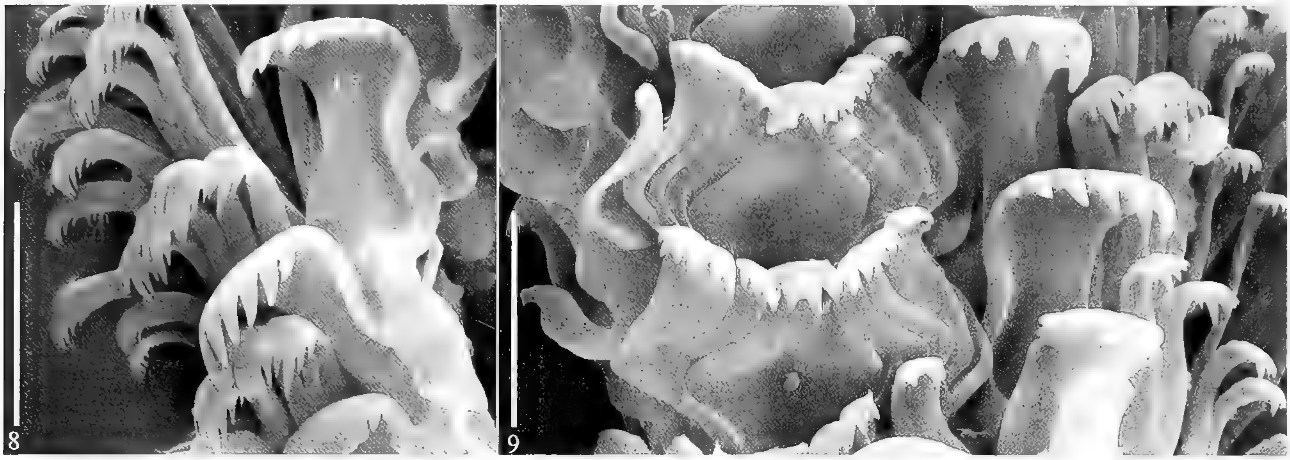
made generous contributions to the Santa Barbara Museum of Natural History.

Distribution: Indo-Malayan Archipelago to southern Polynesia; shallow reef environments.

Other Material Examined: French Polynesia: 0 m, Rapa Iti Island, Rapa, Austral Islands, 27.622° S, 144.302° W (MNHN, 1). 0 m, Kotuaie Point, Tupuaki Bay, Rapa, Austral Islands, 27.577° S, 144.343° W (MNHN, 1). 2 m, North of Pukitarava, Rapa, Austral Islands, 27.597° S, 144.227° W (MNHN, 4: two illustrated Figures 5–6). 2–4 m, N of Aturapa Island, Rapa, Austral Islands, 27.572° S, 144.350° W (MNHN, 4). 2 m, N of Rapa Iti Island, Rapa, Austral Islands, 27.620° S, 144.303° W (MNHN, 1). 2 m, N of Anatakuri Bay, Rapa, Austral Islands, 27.623° S, 144.307° W (MNHN, 15). 3–24 m, Hiri Bay, Rapa, Austral Islands, 27.622° S, 144.370° W (MNHN, 4). 5 m, Anarua Bay, Rapa, Austral Islands, 27.605° S, 144.378° W (MNHN, 7: one illustrated Figures 7, 8–9 [radula]). 6 m, Mei Point,



Figures 5–7. *Sinezona danieldreieri* new species. **5–6.** North of Pukitarava, Rapa, Austral Islands, French Polynesia, 27.597° S, 144.227° W, 2 m (MNHN). **7.** Anarua Bay, Rapa, Austral Islands, French Polynesia, 27.605° S, 144.378° W, 5 m (MNHN). Radula of specimen is shown in Figures 8–9. Scale bar, shell = 500 μm. Scale bar, protoconch = 100 μm.



Figures 8–9. Radula of *Sinezona danieldreieri* new species, from specimen shown in Figure 7. Anarua Bay, Rapa, Austral Islands, 27.605° S, 144.378° W, 5 m. **8.** Lateral teeth 4 (L4) and 5 (L5) plus marginal teeth. **9.** Half width of radula with central field. Scale bars = 10 μm.

Rapa, Austral Islands, 27.637° S, 144.303° W (MNHN, 1; MNHN, 1). 6 m, SW of Gotenaonao Point, Rapa, Austral Islands, 27.645° S, 144.320° W (MNHN, 3). 15–20 m, Vavai, Rapa, Austral Islands, 27.590° S, 144.381° W (MNHN, 1; MNHN, 1). 16–20 m, Mei Point, Rapa, Austral Islands, 27.637° S, 144.303° W (MNHN, 2). 18 m, Rarapai Island, Rapa, Austral Islands, 27.572° S, 144.368° W (MNHN, 1). 27 m, Kauira Point, Rapa, Austral Islands, 27.592° S, 144.347° W (MNHN, 1). 30 m, NW of Tauna Island, Rapa, Austral Islands, 27.605° S, 144.303° W (MNHN, 17). 36 m, around Rukuaga Point, Rapa, Austral Islands, 27.568° S, 144.368° W (MNHN, 8).

PHILIPPINES: Canipo Island, Cuyo Islands, Palawan Province, 11° N, 120.948° E (USNM 808195, 1).

GUAM: 0.7 m, Ajayan Bay, S. Guam, 13.245° N, 144.717° E (LACM 77-19, 2).

Remarks: The protoconch sculpture shows some intraspecific variability in the material examined. More specifically, the strong axial cords are sometimes discontinuous. This character is not restricted to the present species, hence, it does not seem to be of any systematic value. Those axial cords are also somewhat variable in width, the thickenings occasionally seeming to form some faint spiral elements. Given the intra- and interspecific variability of protoconch sculpture at this level of detail, the presence/absence of faint spiral elements is considered irrelevant for systematic purposes. Discrete differences can be observed between strong and weak axial cords as utilized previously in a systematic context (Geiger, 2003).

Sinezona plicata (Hedley, 1899) from the Indo-Pacific has an overall wider and larger shell (2.3 mm; Geiger and Jansen, 2004b), more pronounced but fewer raised axial cords, and a protoconch with spiral lines. *Sinezona ferriezi* (Crosse, 1867) (? = *S. hoernesi* Semper, 1865: whereabouts of Semper types unknown, original illustration lacking detail) with broad Indo-Malayan Archipelago distribution, is about twice as large, has a smooth protoconch with a distinct apertural varix, and >1 teleoconch I whorls. *Sinezona globosa* Geiger, 2006, from New Caledonia and Wallis Island is more rounded in overall appearance, lacks the elevated spiral cords, is larger (3.1 mm; Geiger, 2006a), and has spiral sculpture on the protoconch. *Sinezona macleani* Geiger, 2006, with broad Indo-Malayan distribution is more globular in overall outline, larger (2.3 mm; Geiger, 2006a), has a protoconch with flocculent sculpture, lacks the raised axial lines and has a wider umbilicus. All the above species grow to much larger size and would be immature with open slit at the maximum size of *S. danieldreieri*.

Sinezona wileyi new species
(Figures 10–16)

Description: Shell medium size (up to 1.08 mm) trochiform turreted. Protoconch slightly sunken in, with 1 whorl, fine irregular axials, no apertural varix, apertural margin straight. Teleoconch I with 0.6–0.7 whorls, suture at periphery, usually with approximately 14–22 faint to distinct fine axial cords, usually without spiral lines (occasionally faintest spiral threads only visible by SEM [Figure 11]), interstices with irregular thickenings. Teleoconch II with up to 1.25 whorls, suture below periphery. Shoulder with approximately 32–44 barely perceptible to distinct fine commarginal axial cords, stronger near suture becoming less distinct towards selenizone; approximately eight barely perceptible to very indistinct spiral cords, concentrated on middle of shoulder; occasional specimens with predominant spiral sculpture (Figure 11). Base distinctly constricted below selenizone, axial cords of same strength and density as on shoulder, starting in lower portion of constriction below selenizone; approximately 17 fine, irregularly spaced spiral cords, starting in lower portion of constriction with onset of axial lines. Umbilicus wide, walls straight.

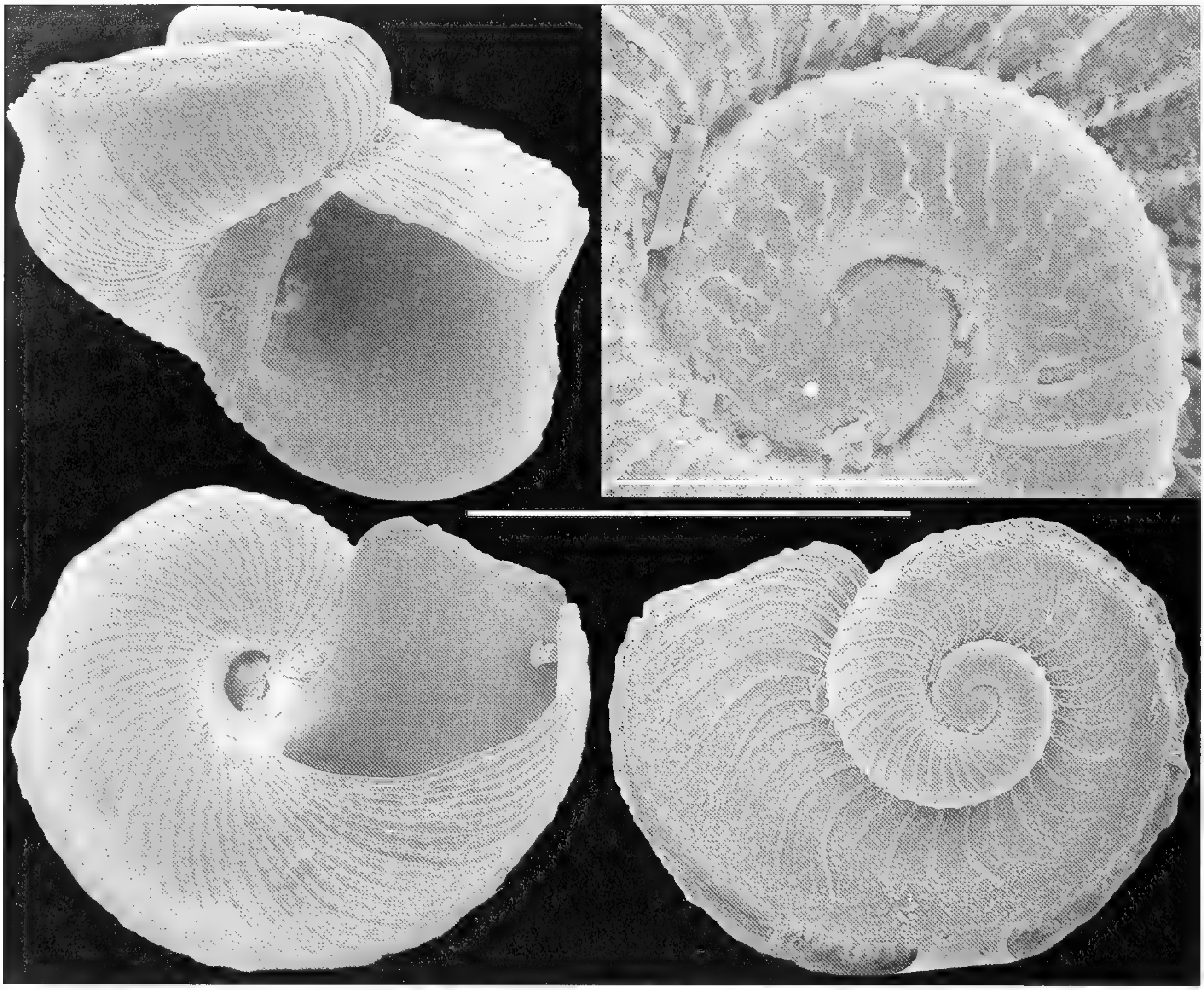


Figure 10. Holotype of *Sinezona wileyi* new species. Lumu Reef, Kimbe Bay, New Britain, Papua New Guinea, 5.283° S, 150.131° E, 0–5 m, (SBMNH 83541). Scale bar, shell = 500 µm. Scale bar, protoconch = 100 µm.

smooth, periphery at distinct angle to base, bordered by carina. Aperture subquadratic, D-shaped, roof overhanging. Selenizone above periphery, keels moderately strong, quite elevated, lunules distinct at regular interval; foramen narrow, elongated, margins converging and touching, without raphe. Animal unknown.

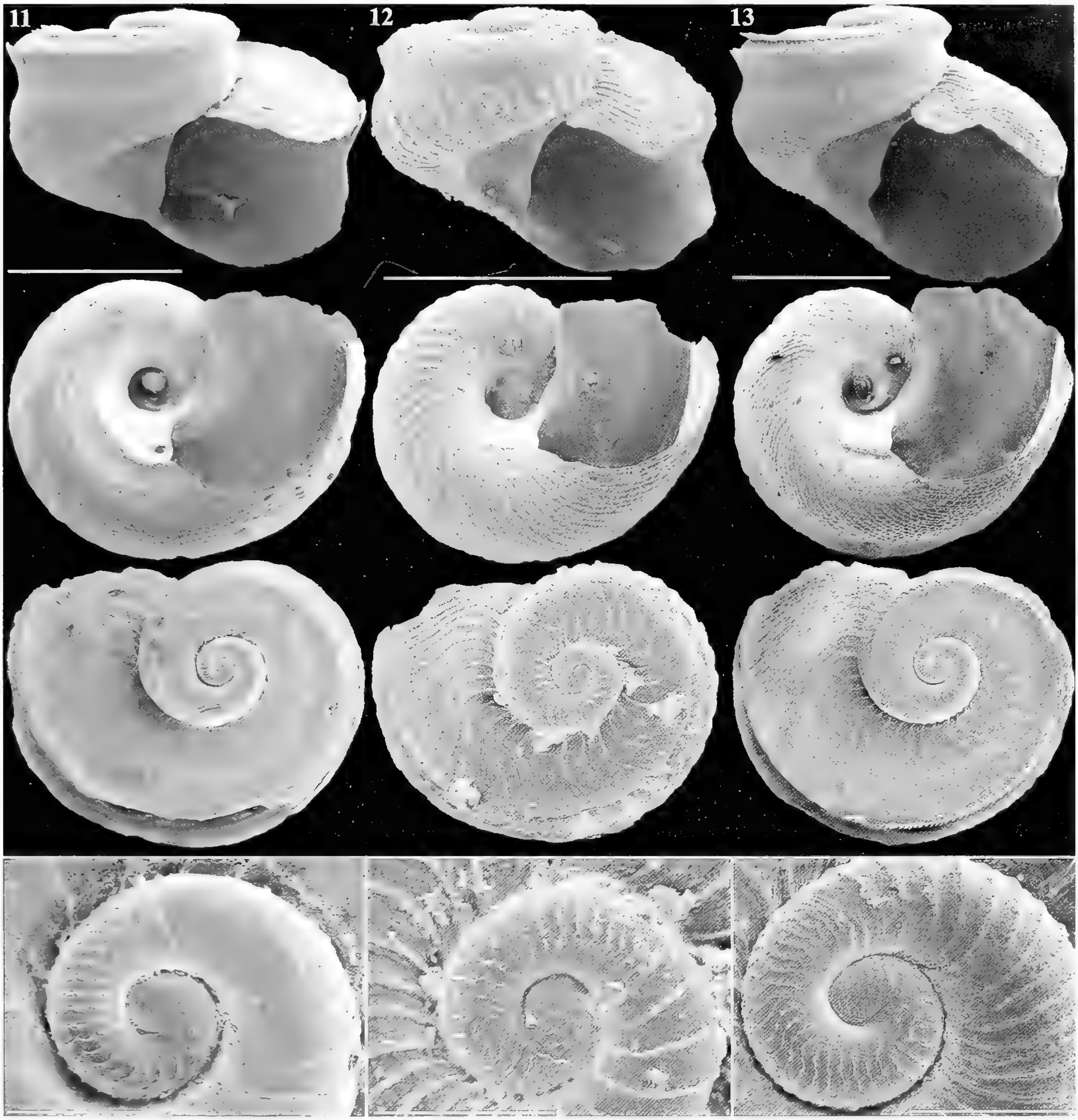
Type Material: Holotype: SBMNH 83541 (Figure 10). 35 Paratypes: 0–5 m, Lumu Reef, Kimbe Bay, New Britain, Papua New Guinea, 5.283° S, 150.131° E (DLG 639, 19: one illustrated in Figure 15). Laisse de plage extérieure, Mururoa, Tuamotu, French Polynesia, 21.842° S, 138.895° W (JTC, 2: one illustrated in Figure 12). 20 m, Herald Pass, W of Ndravuni Island, NW end of Great Astrolabe Reef, Fiji, 18.767° S, 178.467° E (LACM 85-135, 2: one illustrated in Figure 14). 20 m, Herald Pass, W of Ndravuni Island, NW end of Great Astrolabe Reef, Fiji, 18.767° S, 178.467° E (LACM 85-135, 2). 10–20 m, Off Francis Island in Beqa Lagoon, just off of Beqa Island (south of Viti Levu), 18.300° S, 178.067° E (DLG 279, 10: one illustrated in Figure 16).

Type Locality: 0–5 m, Lumu Reef, Kimbe Bay, New Britain, Papua New Guinea, 5.283° S, 150.131° E.

Etymology: The name honors the collector of the first known specimens of the species Tony Wiley of Riverside, California, USA.

Distribution: Tropical Indo-Malayan Archipelago; shallow shelf.

Other Material Examined: French Polynesia: 36 m, Around Rukuaga Bay, Rapa, Austral Islands, 27.568° S, 144.368° W (MNHN, 20: Figures 11, 13). 2–4 m, N of Aturapa Island, Rapa, Austral Islands, 27.572° S, 144.350° W (MNHN, 1). 5 m, Anarua Bay, Rapa, Austral Islands, 27.605° S, 144.378° W (MNHN, 4). 45 m, Haurei Bay, Rapa, Austral Islands, 27.613° S, 144.305° W (MNHN, 1).



Figures 11–13. *Sinezona wileyi* new species. **11–12.** Around Rukuaga Bay, Rapa, Austral Islands, French Polynesia, 27.568° S, 144.368° W, 36 m (MNHN, 20). **13.** Laisse de plage extérieure, Mururoa, Tuamotu, French Polynesia, 21.842° S, 138.895° W (Paratype: JTC, 2). Scale bars, shell = 500 µm. Scale bars, protoconch = 100 µm

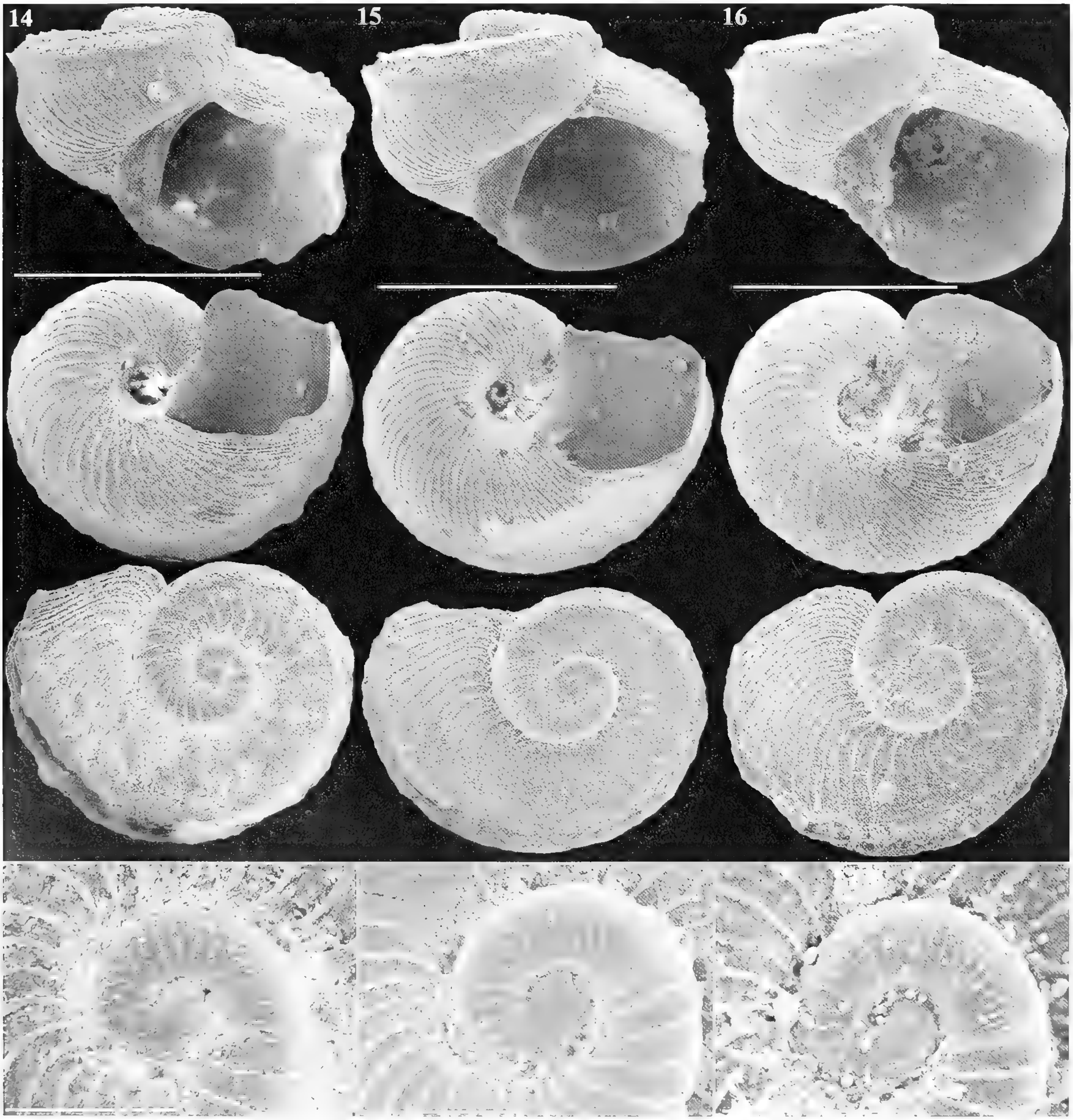
New Caledonia: 25–30 m, Santal Bay, Lifou, 20.822 S, 167.173° E (MNHN, 1). 55–57 m, Koumac Sector, 20.672° S, 164.195° E (MNHN, 1). 5–25 m, Touho Sector, 20.878° S, 165.325° E (MNHN, 1). 8 m, Touho Sector, 20.742° S, 165.265° E (MNHN, 1).

Fiji: 10–20 m, Off Francis Island in Beqa Lagoon, just off of Beqa Island (south of Viti Levu), 18.300° S, 178.067° E (DLG 279, 10).

Papua New Guinea: 70 m, off South Ema Reef, Kimbe Bay, New Britain, 5.202° S, 150.152° E (DLG 768, 3).

Remarks: The organization of the foramen in this species seems to be intermediary between the typical open slit in *Scissurella* and the closed foramen in *Sinezona*. Although the margins of the slit are converging and fused anteriorly, a raphe is not evident. The facts that there is a marked downward deflection of the last quarter whorl and that the roof of the peristome attaches below the periphery of the previous whorl demonstrate that those specimens are fully grown and share more similarities with *Sinezona* than with *Scissurella* with an open slit. Accordingly, *S. wileyi* is placed in *Sinezona*.

The species seems to have variable strengths of sculpture. Most specimens have predominant axial sculpture (Figures 10, 12, 14–15), while in occasional specimens (Figure 11) the axial sculpture is barely perceptible and the spiral structures, particularly on the adumbilical part of base, become most prominent. As there are intermediate specimens (Figure 13) with distinct adumbilical



Figures 14–16. *Sinezona wileyi* new species, paratypes. **14.** Herald Pass, W of Ndravuni Island, NW end of Great Astrolabe Reef, Fiji, 18.767° S, 178.467° E, 20 m (LACM 85-135, 2). **15.** Lumu Reef, Kimbe Bay, New Britain, Papua New Guinea, 5.283° S, 150.131° E, 0–5 m (DLG 639, 19). **16.** Off Francis Island in Beqa Lagoon, just off of Beqa Island (south of Viti Levu), Fiji, 18.37° S, 178.067° E, 10–20 m (DLG 279, 10). Scale bars, shell = 500 µm. Scale bars, protoconch = 100 µm.

spiral lines and relatively weak axial lines, combined with identical condition of the protoconch and very small size, these sculptural differences are considered to constitute intraspecific variability.

There are no similar species in the Indo-Pacific. *Sinezona ferriezi* (Crosse, 1867) with broad Indo-Malayan Archipelago distribution is most similar, but is about twice the size of *S. wileyi*, has a smooth protoconch with distinct apertural varix, a teleoconch I with more than whorl, is more rounded overall, and a distinct raphe anterior to the closed foramen. *Sinezona garciai* Geiger, 2006, from the Caribbean, shares the protoconch sculpture, the absence of an apertural varix on the protoconch, the relatively short teleoconch I with 0.6 whorls, and the narrow umbilicus. However, in addition to its occurrence in a separate ocean, *S. garciai* has a more inflated shell with an oval aperture, which connects to the previous whorl barely below the periphery, has only about 0.6 teleoconch II whorls, and bears a distinct raphe anterior to the foramen.

Anatomidae McLean, 1989
Anatoma Woodward, 1859

Type Species: *Scissurella crispata* Fleming, 1828 (M).

Remarks: The genus has recently been treated by Marshall (2002), Geiger (2003), and Geiger and Jansen (2004a).

Anatoma rapaensis new species
(Figures 17–23)

Description: Shell of medium size (to 1.82 mm), trochiform biconical. Protoconch with 0.75 whorls, flocculent sculpture, no apertural varix, apertural margin slightly sinusoid. Teleoconch I with 0.3–0.4 whorls, approximately 9–12 axial cords, interstices with fine flocculent sculpture, occasionally (holotype) flocculent sculpture somewhat concentrated in position of selenizone. Teleoconch II with up to 2.25 whorls, suture immediately below selenizone in early growth, offset by width of selenizone

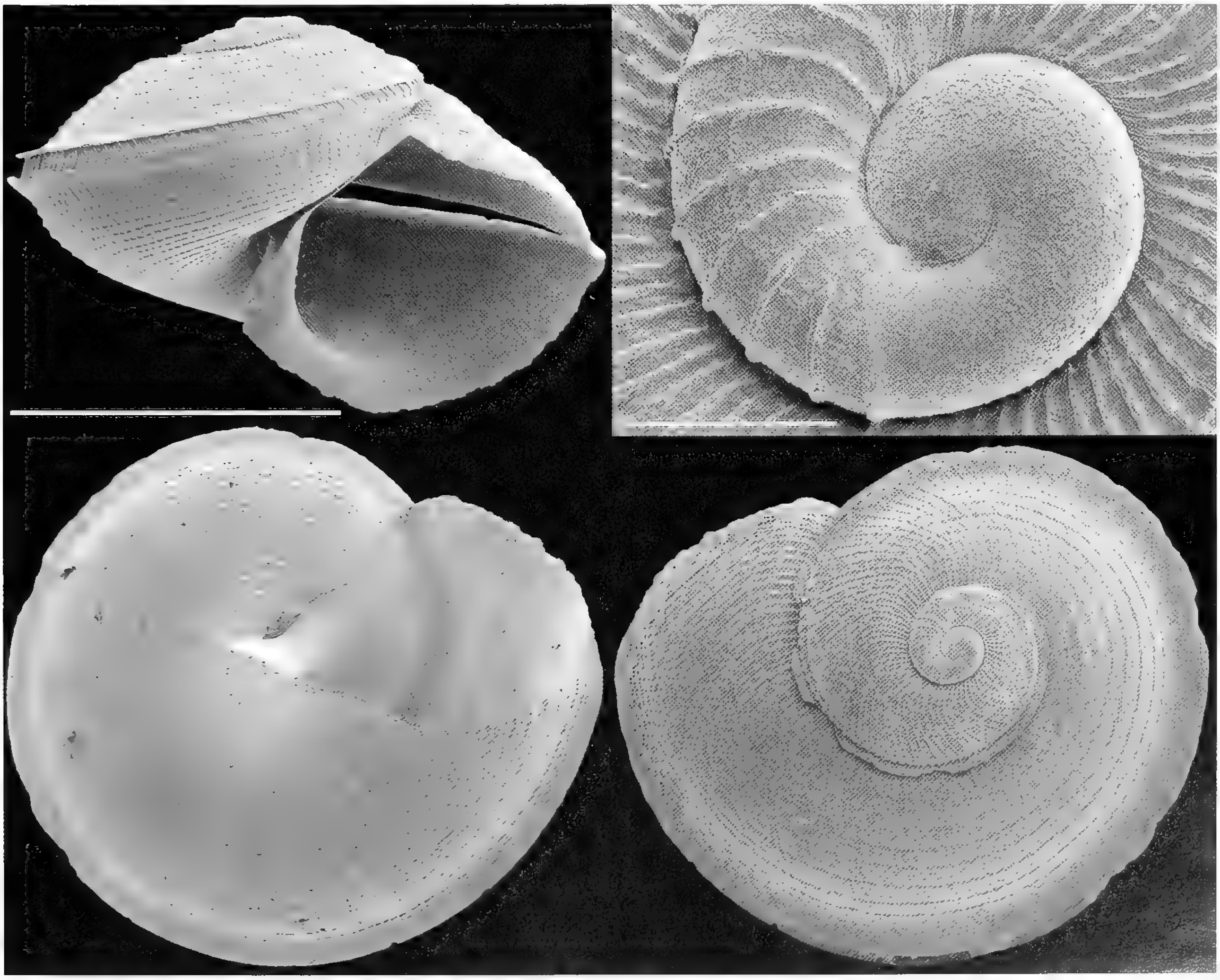
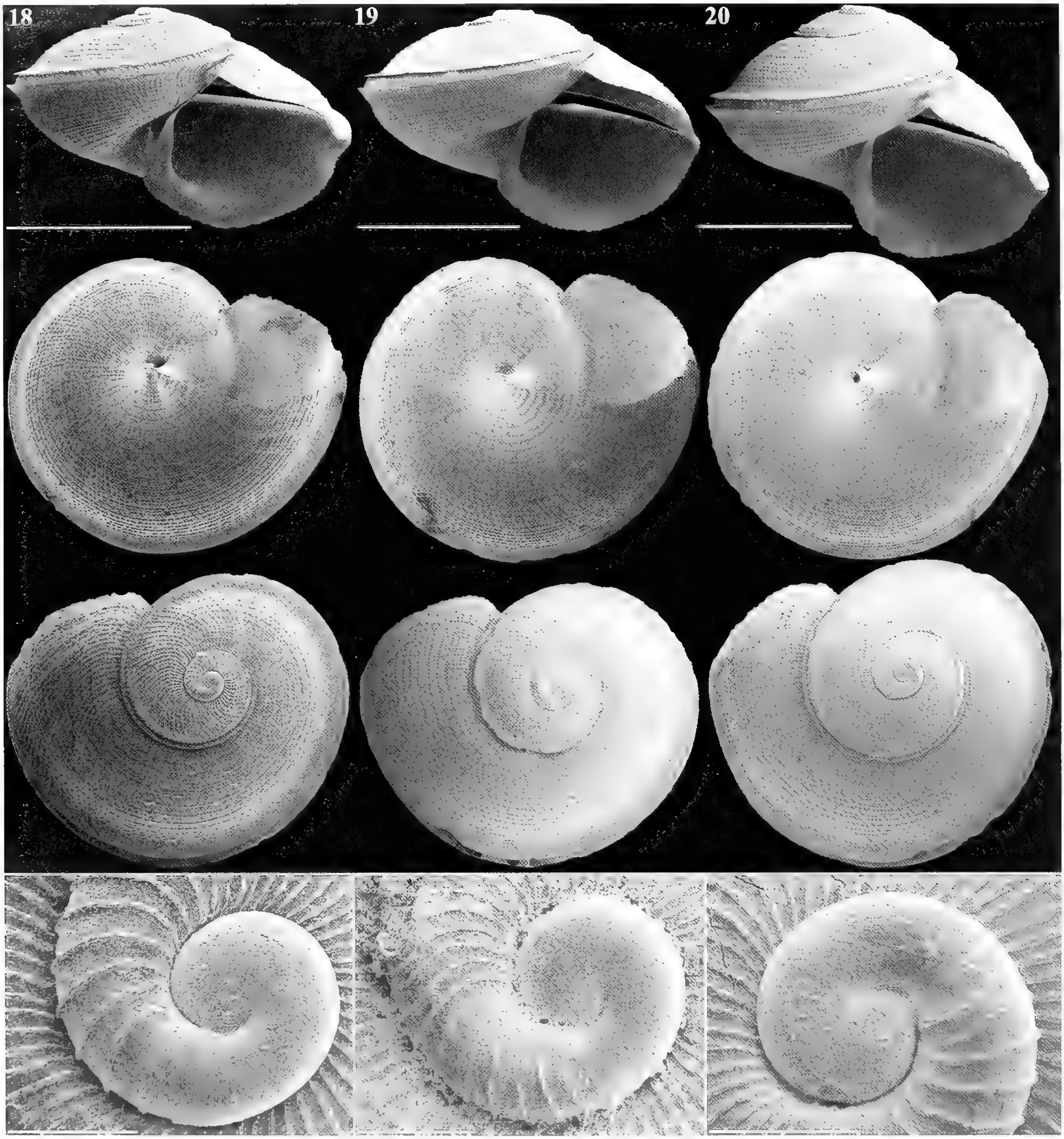


Figure 17. Holotype of *Anatoma rapaensis* new species. St. 43, Haurei Bay, Rapa, Austral Islands, French Polynesia, 27.613° S 144.305° W, 45 m. (MNHN 20823). Scale bar shell = 1 mm. Scale bar protoconch = 100 μm.



Figures 18–20. *Anatoma rapaensis* new species, paratypes (MNHN). **18–19.** St. 43, Haurei Bay, Rapa, Austral Islands, French Polynesia, 27.613° S, 144.305° W, 45 m (MNHN 20824). **20.** St. 48, around Rukuaga Point, Rapa, Austral Islands, French Polynesia, 27.568° S, 144.368° W, 36 m (MNHN, 30). Scale bars, shell = 1 mm. Scale bars, protoconch = 100 µm

in fully grown specimens. Shoulder convex, approximately 53–66 (n = 4) axial cords on first teleoconch II whorl, same density on remaining whorls; first fine spiral cords after 0.125 whorls, approximately 7–10 after one teleoconch II whorl, approximately 15–22 at apertural margin of fully grown specimen, becoming less distinct and more unevenly spaced towards apertural margin; intersections of axial and spiral cords forming minute points. Base continuously sloping with narrow umbilicus; axial cords of same density and strength as on shoulder, approximately 19 spiral cords, fine spiral cords below selenizone turning into low steps from mid-base onwards; intersection of spiral and axial cords with fine points. Aperture ovoid D-shaped, roof overhanging, basal adumbilical portion flared. Selenizone at periphery, keel moderately strong, moderately elevated, slit open, margins converging towards apertural margin.

Operculum (Figure 23): As large as aperture, thin, corneous, nucleus central, multispiral.

Radula (Figures 21–22): Rachidian tooth trapezoid, central denticle with 3–4 denticles on each side. Lateral teeth 1–3 similar, development of cusp reduced peripherally, terminal denticle largest, 4–2 denticles on outer edge. Lateral tooth 4 reduced in size, hook-shaped, with one minute point on each side. Lateral tooth 5 enlarged with four strong denticles on inner margin. Inner marginal teeth elongated, terminal denticle largest, 3–4 smaller denticles on inner margin, three larger denticles on outer margin. Outer marginal teeth with cup-shaped cusp with many small denticles.

Type Material: Holotype: MNHN 20823 (Figure 17). 60 Paratypes: 45 m, RAPA St. 43, Haurei Bay, Rapa, Austral Islands, French Polynesia, 27.613° S, 144.305° W (MNHN 20824, 29; two illustrated in Figures 18–19). 36 m, RAPA St.48, Around Rukuaga Point, Rapa, Austral Islands, 27.568° S, 144.368° W (MNHN, 30; one illustrated in Figure 20). 145 m, MUSORSTOM 9 St. CP 1159, Eiao Island, 7.972° S, 140.728° E (MNHN, 1: Figures 21–23 [radula, operculum]).

Type Locality: 45 m, RAPA St. 43, Haurei Bay, Rapa, Austral Islands, French Polynesia, 27.613° S, 144.305° W.

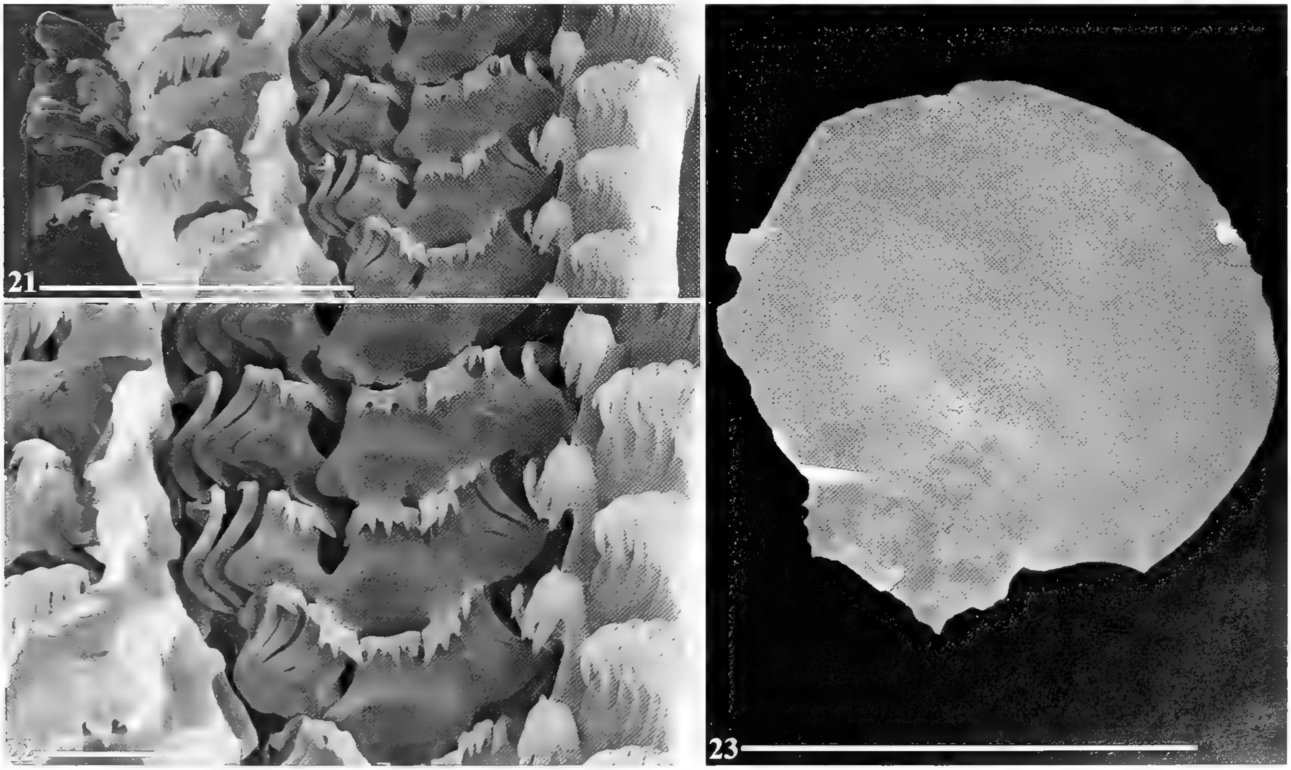
Etymology: The species is named after its type locality, Rapa Island, French Polynesia.

Distribution: Tropical Indo-Malayan Archipelago and Western Pacific; shallow shelf to upper slope.

Other Material Examined: French Polynesia: 10–15 m, Pake Bay, Rapa, Austral Islands, 27.617° S, 144.310° W (MNHN, 2). 30 m, NW of Tauna Island, Rapa, Austral Islands, 27.605° S, 144.303° W (MNHN, 50). 33 m, Haurei Bay, Rapa, Austral Islands, 27.612° S, 144.318° W (MNHN, 10). 52–57 m, SE of Tauna Island, Rapa, Austral Islands, 27.608° S, 144.295° W (MNHN, 50; MNHN, 20). 100 m, North of Raivavae, Austral Islands, 23.828° S, 147.693° W (MNHN, 2).

Philippines: 92–97 m, 12.517° N, 120.650° E (MNHN, 8).

New Caledonia: 105–110 m, Poindimie Sector, 20.817° S, 165.317° E (MNHN, 9). 250–350 m, southern New Caledonia, 22.500° S, 166.400° E (MNHN, 1). 250–350 m, southern New Caledonia, 22.500° S, 166.400° E (MNHN, 1). 495 m, southern New Caledonia, 22.367° S, 166.233° E (MNHN, 3). 600–616 m, northern New Caledonia, 18.817° S, 163.250° E (MNHN, 3).



Figures 21–23. Radula and operculum of *Anatoma rapaensis* new species. Eiao Island, Marquesas Islands, 7.972° S, 140.728° E, 145 m (MNHN, 1). **21–22.** Radula. **23.** operculum. Scale bar, radula Figure 21 = 50 µm. Scale bar, radula Figure 22 = 20 mm. Scale bar, opeculum = 500 µm.

MARQUESAS ISLANDS: 145 m, Eiao Island, 7.972° S, 140.728° E (MNHN, 1: paratype). 200–220 m, Ua Huka Island, 8.900° S, 139.633° W (MNHN, 6). 352–358 m, Hiva Oa Island, 9.850° S, 139.150° W (MNHN, 1).

FIJI: 149–168 m, S of Viti Levu, 18.207° S, 178.552° E (MNHN, 1). 260–305 m, S of Viti Levu, 18.308° S, 178.097° E (MNHN, 6). 275–430 m, S. of Viti Levu, 18.297° S, 177.907° E (MNHN, 1). 441–443 m, S. of Viti Levu, 18.320° S, 177.862° E (MNHN, 1).

Remarks. *Anatoma rapaensis* is characterized by the rather flattened overall shape, the short teleoconch I with less than 0.5 whorls, and the fine reticular sculpture that is axial-dominated on the first half teleoconch II whorl, subsequently becoming spiral-dominated. The most similar species is *Anatoma* (sensu lato) *exquisita* Schepman, 1908, from the Indo-Malayan Archipelago; the comparison is based on SEM imaging of the holotype (ZMA 3.08.101; Figure 24). The shell is slightly taller, the spiral and axial lines are denser, forming more prominent points at their intersection, and the axial lines are slightly stronger than the spiral lines even in larger specimens (specimens 1.8–3.5 mm examined); protoconch and teleoconch I are eroded beyond recognition. *Anatoma paucispiralia* Bandel, 1998, from Satonda, Indonesia, has a smooth protoconch, a shorter teleoconch I (0.125 vs. 0.3–0.4 whorls), and a slightly undulating shoulder profile. All other Indo-Pacific species are either more turreted or have noticeably different sculpture on shoulder and base. The only other documented case of a species that shows a change of sculpture on the teleoconch II is *Anatoma janetae* Geiger, 2006, known from 2,500 m off the west coast of North America (Geiger, 2006c).

Larocheidae Fleming, 1927
Trogloconcha Kase and Kano, 2002

Type Species: *Trogloconcha ohashii* Kase and Kano, 2002 (OD).

Remarks: The genus was recently treated by Geiger (2003).

Trogloconcha lozoueti new species
(Figures 25–30)

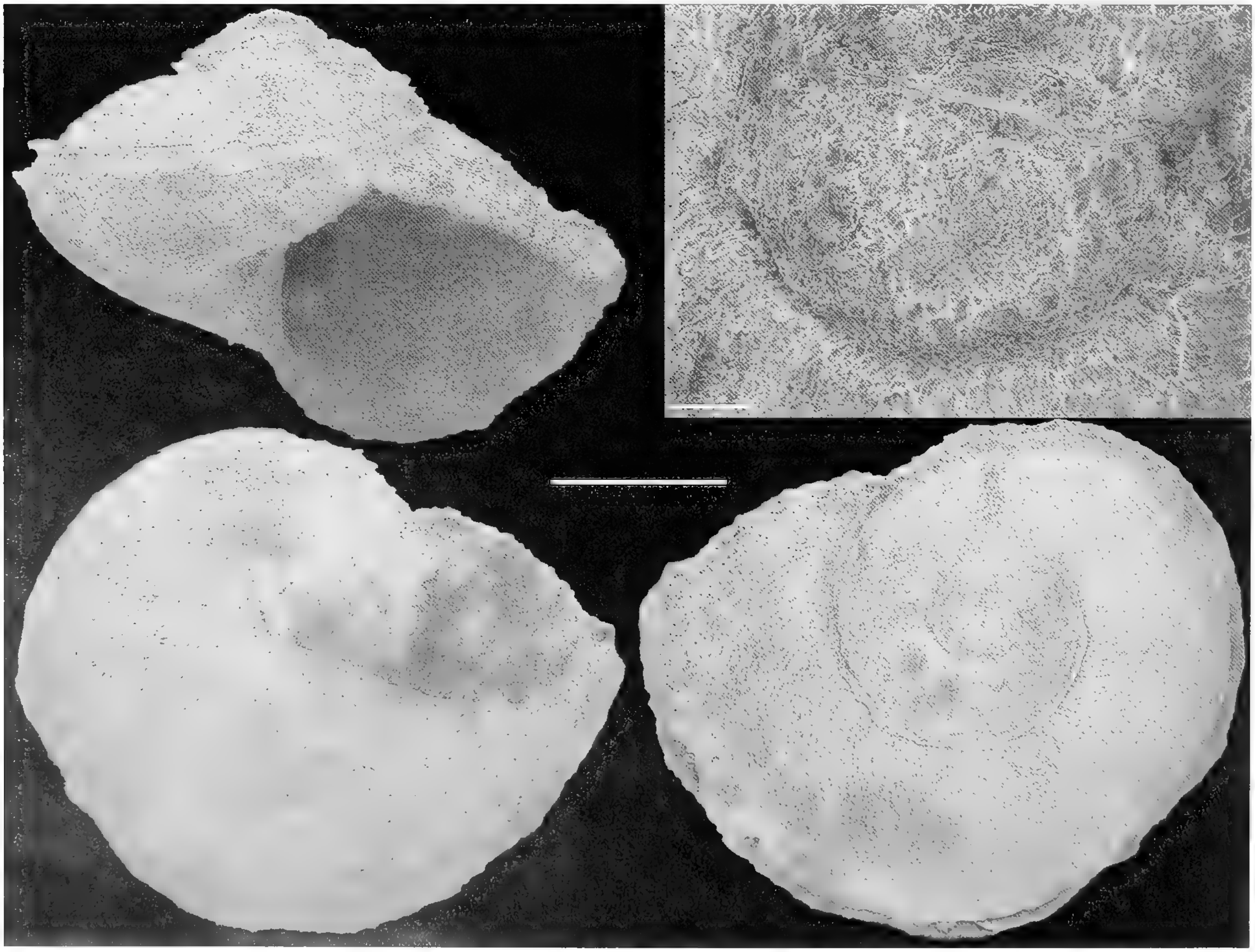
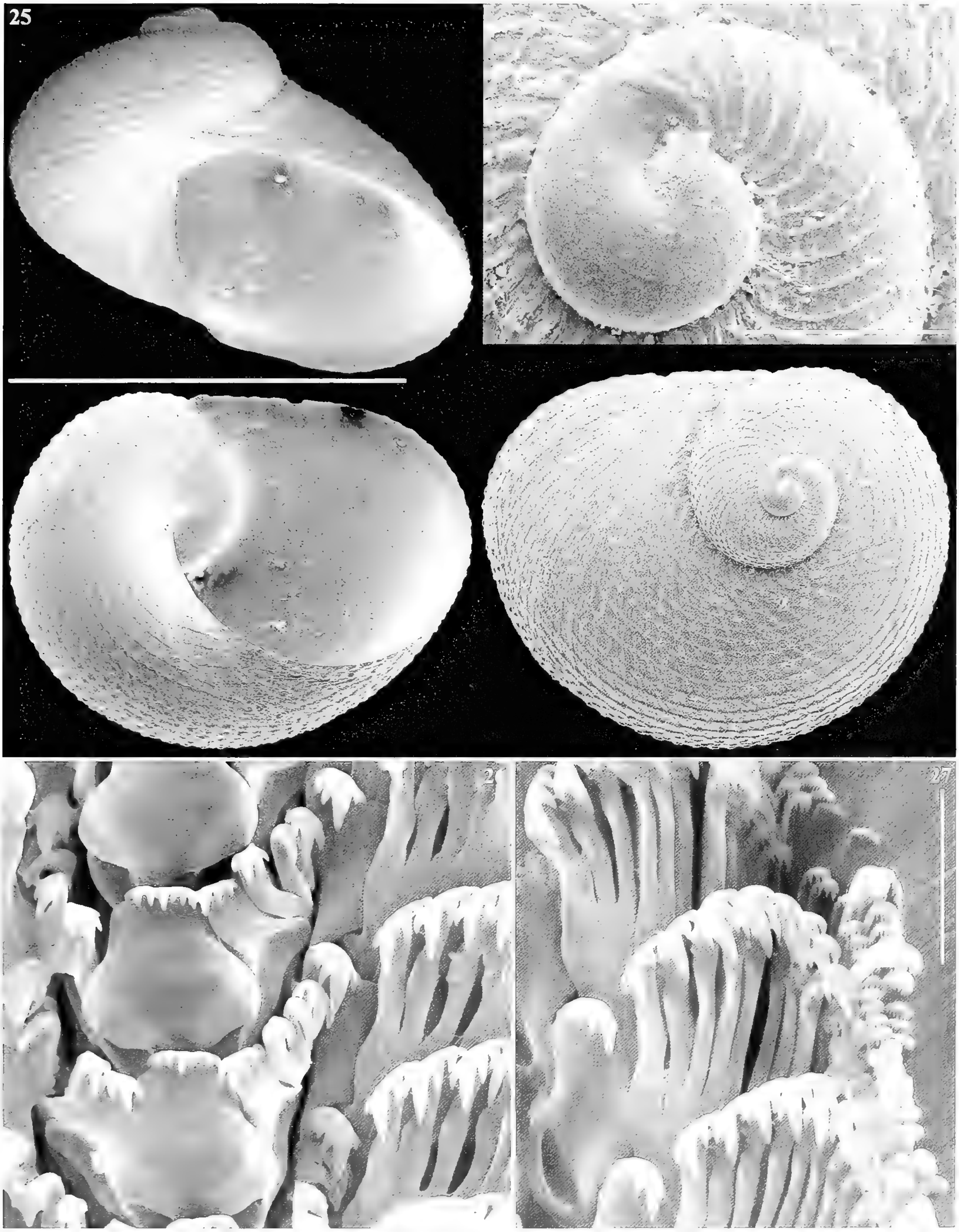
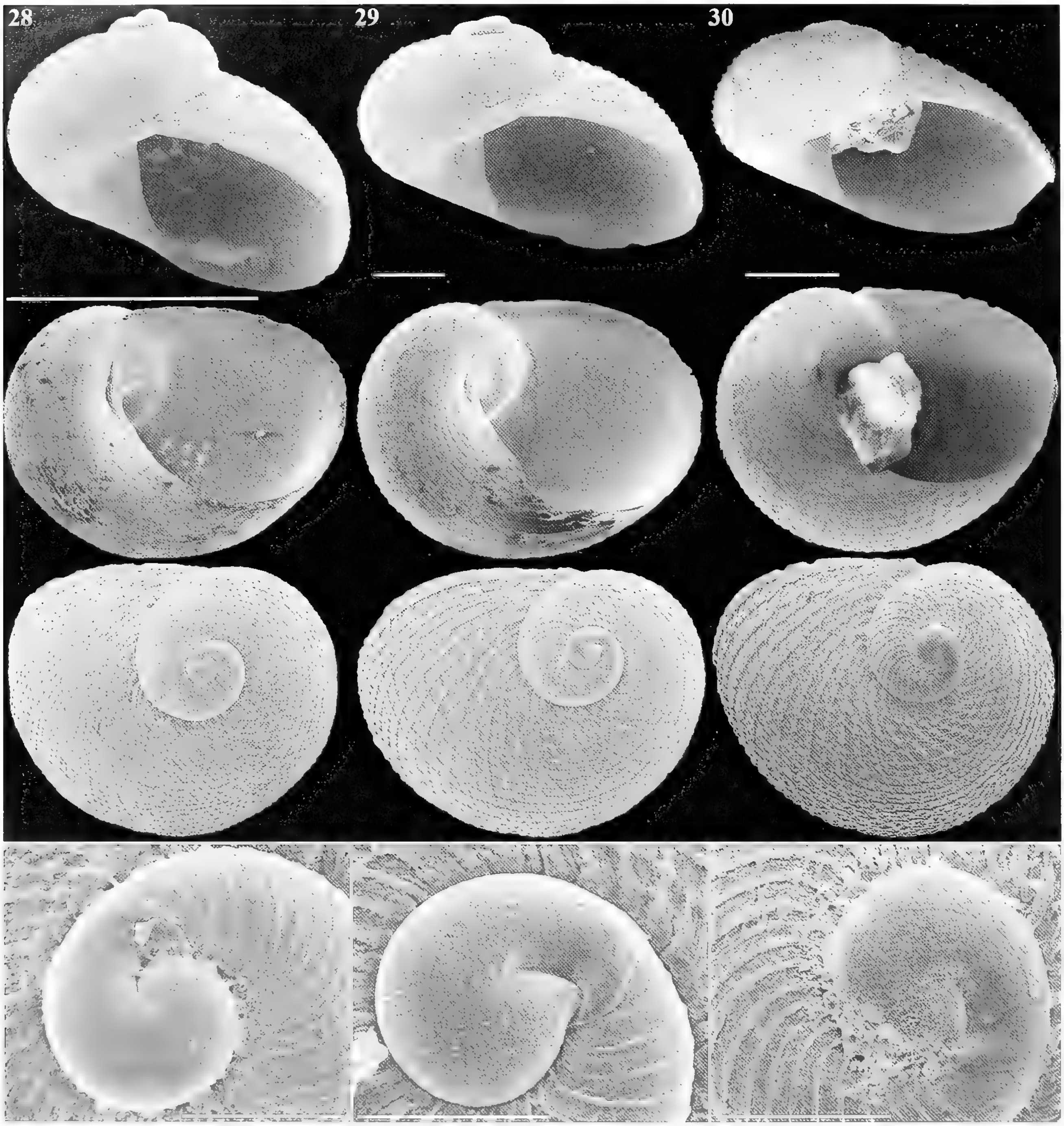


Figure 24. Holotype of *Anatoma exquisita* Schepman, 1908 (ZMA 3.08.101). Siboga Station 95, 5°43.5′ N, 119°40′ E, 522 m [between Sabah, Malaysia, and southeastern Tawitawi Group, Philippines]. Scale bar, shell = 1 mm. Scale bar, protoconch = 100 μm



Figures 25–27. *Trogloconcha lozoueti* new species. **25.** Holotype (Vavai, Rapa, Austral Islands, French Polynesia, 27.590° S, 144.381° W, 15–20 m; MNHN 20825). **26–27.** Radula from specimen shown in Figure 30 (Hiri Bay, Rapa, Austral Islands, French Polynesia, 27.622° S, 144.37° W, 3–24 m; MNHN). Scale bar, shell = 1 mm. Scale bar, protoconch = 100 µm. Scale bar, radulae = 10 µm.



Figures 28–30. *Trogloconcha lozoueti* new species. Paratypes. **28–29.** Vavai, Rapa, Austral Islands, French Polynesia, 27.590° S, 144.381° W, 15–20 m (MNHN 20826). **30.** Hiri Bay, Rapa, Austral Islands, French Polynesia, 27.622° S, 144.37° W, 3–24 m (MNHN. 20). Scale bar, shell 28 = 1 mm. Scale bars, shell 29–30 = 200 µm. Scale bars, protoconch = 100 µm

Description: Shell medium size (to 1.17 mm), trochiform globular, with rapidly increasing whorls. Protoconch with 0.75 whorls, flocculent sculpture somewhat spirally arranged, weak apertural varix, apertural margin convex. Teleoconch with up to two whorls, approximately 15 axial cords on first 0.3–0.5 whorls with no spiral sculpture, interstices with fine flocculent sculpture; onset of spiral cords after 0.5 whorls; approximately 31 spiral cords, from suture to mid-base as fine spiral cords, transitioning to low spiral steps in 5–6 adumbilical spirals; approximately 70 fine axial cords on last whorl, forming distinct points at intersections; overall appearance of shell fine reticulate and spiky. Suture bordered by strong irregularly lamellate thickening on shoulder. Base anomphalus with weak callus in umbilical region. Aperture oval, roof overhanging.

Operculum: Corneous, round, multispiral, with central nucleus, covering only approximately 1/3 of aperture.

Radula (Figures 26–27): Rachidian tooth triangular, cusp with central denticle largest, three denticles on each side, arranged in convex curve. Lateral teeth 1–4 similar, L-shaped, cusp with apical denticle largest, 3–4 denticles on outer margin, 1–3 denticles on inner margin; lateral tooth 5 enlarged by half, apical denticle largest, 3–4 denticles on each side. Inner marginal teeth with elongated shaft central denticle largest, 3–4 denticles on inner margin, 5–6 denticles on outer margin; outer marginal teeth with cup shape cusp, with many fine denticles on each side. Radular interlock of central field strong.

Type Material: Holotype: MNHN 20825. 26 Paratypes: 15–20 m, RAPA St. 32, Vavai, Rapa, Austral Islands, 27.590° S, 144.381° W (MNHN 20826, 6: two illustrated in Figure 28–29). 3–24 m, RAPA St. 9, Hiri Bay, Rapa, Austral Islands, 27.622° S, 144.370° W (MNHN, 20: one illustrated in Figure 30).

Type Locality: 15–20 m, RAPA St. 32, Vavai, Rapa, Austral Islands, French Polynesia, 27.590° S, 144.381° W.

Etymology: Named in honor of Pierre Lozouet (MNHN) for his accomplishments particularly in the field of fossil mollusks including Scissurellidae sensu lato, and his work in connection with the Rapa expedition.

Other Material Examined: French Polynesia: 36 m, Around Rukuaga Point, Rapa, Austral Islands, 27.568° S, 144.368° W (MNHN, 100). 33 m, Haurei Bay, Rapa, Austral Islands, 27.612° S, 144.318° W (MNHN, 6). 52–57 m, SE of Tauna Island, Rapa, Austral Islands, 27.608° S, 144.295° W (MNHN, 20). 30 m, NW of Tauna Island, Rapa, Austral Islands, 27.605° S, 144.303° W (MNHN, 3). 8 m, S of Tarakoi Island, Rapa, Austral Islands, 27.093° S, 144.308° W (MNHN, 1). 52–57 m, SE of Tauna Island, Rapa, Austral Islands, 27.608° S, 144.295° W (MNHN, 9).

Remarks: *Trogloconcha ohashii* from southern Japan has fewer spiral and axial elements that also form elevated points and a wide umbilicus. *Trogloconcha tesselata* Kase and Kano, 2002, from the Indo-Malayan Archipelago has a smooth protoconch and lacks the fine points at the intersection of axials and spirals. *Trogloconcha christinae* Geiger, 2003, from Western Australia lacks spiral sculpture and has flattened-flocculent protoconch sculpture.

The new species is currently only known from the Austral Islands. The radula represents the general vetigastropod pattern (rhipidoglossate) and shows the typical larocheid arrangement of similar lateral teeth 1–4, without reduced, hook-shaped lateral tooth 4; the radula confirms the placement of the species in Larochaeidae. The lack of a brood pouch seen in *Larochaea* and *Larocheopsis* places the species in *Trogloconcha*. Juveniles have a proportionally wider appearance with the suture approximately at the periphery of the previous whorls. Fully grown specimens have a more elevated appearance with the suture connecting well below the periphery of the previous whorl.

DISCUSSION

The new species all belong to recognized genera. They are diagnosed by particular character combinations not known from any described species. The two *Sinezona* species are among the smaller species in the genus, while the *Anatoma* and *Trogloconcha* species are within the usual size range for their respective genera. All species show characters of shell and radular morphology that are known from other species; no new character states were found. The combination of particular features and their particular strength of development, however, are unique for each of the new species.

The distribution of three species reaches beyond the Austral Islands towards the equator (*Sinezona wileyi*, *S. danieldreieri*, and *Anatoma rapaensis*), while one species (*Trogloconcha lozoueti*) is currently only known from Rapa Island. This pattern suggests a closer faunal affinity of the Austral archipelago with the broad Indo-Malayan Archipelago, rather than with the temperate Southern Ocean. The two more widely distributed species *S. danieldrieri* and *S. wileyi* are also those that have been found in deeper water, confirming the idea that deep-water species in general show a wider distribution than those restricted to shallow water.

ACKNOWLEDGMENTS

I thank on behalf of P. Lozouet all colleagues who participated in "RAPA 2002" and especially the mollusk group: R. von Cosel, V. Héros, A. Le Goff , P. Maestrati, J.-L., Menou, S. Schiaparelli and J. Tröndlé. Many thanks also to Claude Payri (University of Papeete, Tahiti), who organized the logistics with the French Navy and the mayor and local council of Rapa. Pierre Lozouet provided helpful criticism on a draft version of the present contribution. Diego Zelaya and an anonymous reviewer improved the manuscript with helpful pointers. Total Foundation funded the expedition within its "Coral Reef Biodiversity Programme." The SEM investigation was supported by NSF MRI-0420706 grant to Henry Chaney, Michael Caterino, and Daniel L. Geiger. Visiting curatorships from AMS and MNHN to DLG are kindly acknowledged.

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Early Pleistocene mollusks of the Tubul Formation, South-Central Chile

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ABSTRACT

Early Pleistocene mollusks of the Tubul Formation are reviewed and 23 species are recognized. These are twelve bivalves, ten gastropods, and one scaphopod. With two exceptions, all of them are known from the Recent. The fauna is compared with Miocene, Pliocene-Pleistocene, and Recent faunas of the Chilean coast. The composition of the Tubul fauna resembles the Recent one of the Magellan Region, suggesting cooler water temperatures for south-central Chile during the early Pleistocene than at present.

Additional Keywords: Mollusca, eastern Pacific, climate

INTRODUCTION

The marine late Pliocene to early Pleistocene of Chile comprises localities distributed along almost the whole length of the coast of Chile (Figure 1). The northern localities attributed to the Pliocene and Pleistocene are exclusively nearshore environment outcrops between Peninsula Mejillones and Coquimbo that have been described in detail by Herm (1969) and Le Roux et al. (2004, 2005, 2006). Herm (1969) described the faunas from these localities and also commented on the fauna of the La Cueva Formation, which overlies the Miocene Navidad Formation of central Chile. Pliocene faunas from southern Chile have been described from the islands Guafo (Frassinetti, 1997, 2000) and Guamblín (Frassinetti and Covacevich, 1995). Another fauna of late Miocene or early Pliocene age from central Chile is known from Lo Abarca near San Antonio (Covacevich and Frassinetti, 1990; DeVries, 2003).

The Tubul Formation (Figure 2) was first described by Feruglio (1949), with its type area located on the southern side of the Gulf of Arauco (37°14′ S, 73°26′ W). Onshore outcrops are limited to the east by the Cordillera de Nahuelbuta and to the west by the Pacific Ocean. Feruglio (1949) described the sediments of the Tubul Formation as light-gray soft tuffaceous sandy mudstones with fossil remains, which can reach a thickness of up to 100 m (García, 1968). Using macrofossils, Brüggen (1950) showed that these sediments can be correlated with those of Coquimbo. From their study of microfossils, Martínez and Osorio (1968) concluded that the basal part of the Tubul Formation corresponds to the middle Pliocene. However, later studies by Martínez (1976) in Caleta Huetón led to the conclusion that the base of the Tubul Formation corresponds to the late Pliocene. Subsequently, Biró-Bagóczky (1979) recognized a lower and an upper member: the lower member has a thickness of approximately 50 m and is formed by very fine, slightly calcareous, dark-gray sandstones, including abundant fossil marine fauna; the upper member also has a thickness of approximately 50 m and is formed by light-gray to olive fine sandstones and mudstones with rare fossils.

According to Pineda (1983, 1986), deposition of the sediments of the Tubul Formation was rapid, in a quiet zone close to the coast, maybe lagoonal. These sediments should correspond to the Plio-Pleistocene-boundary (Pineda, 1983, 1986) and occur at the following localities: Punta Pichicui, Estero Chupalla, Villa Alegre, Los Alamos, Quebrada Raquilco, El Tique, Estero Licauquen, and Minas Trihueco. According to Pineda, the Tubul Formation represents a transgressive sequence. The presence of quartz-sand and a conglomerate at the base of the formation has been interpreted as a former coastal line. Above this level, very fine clayey sandstones have been deposited, which should represent

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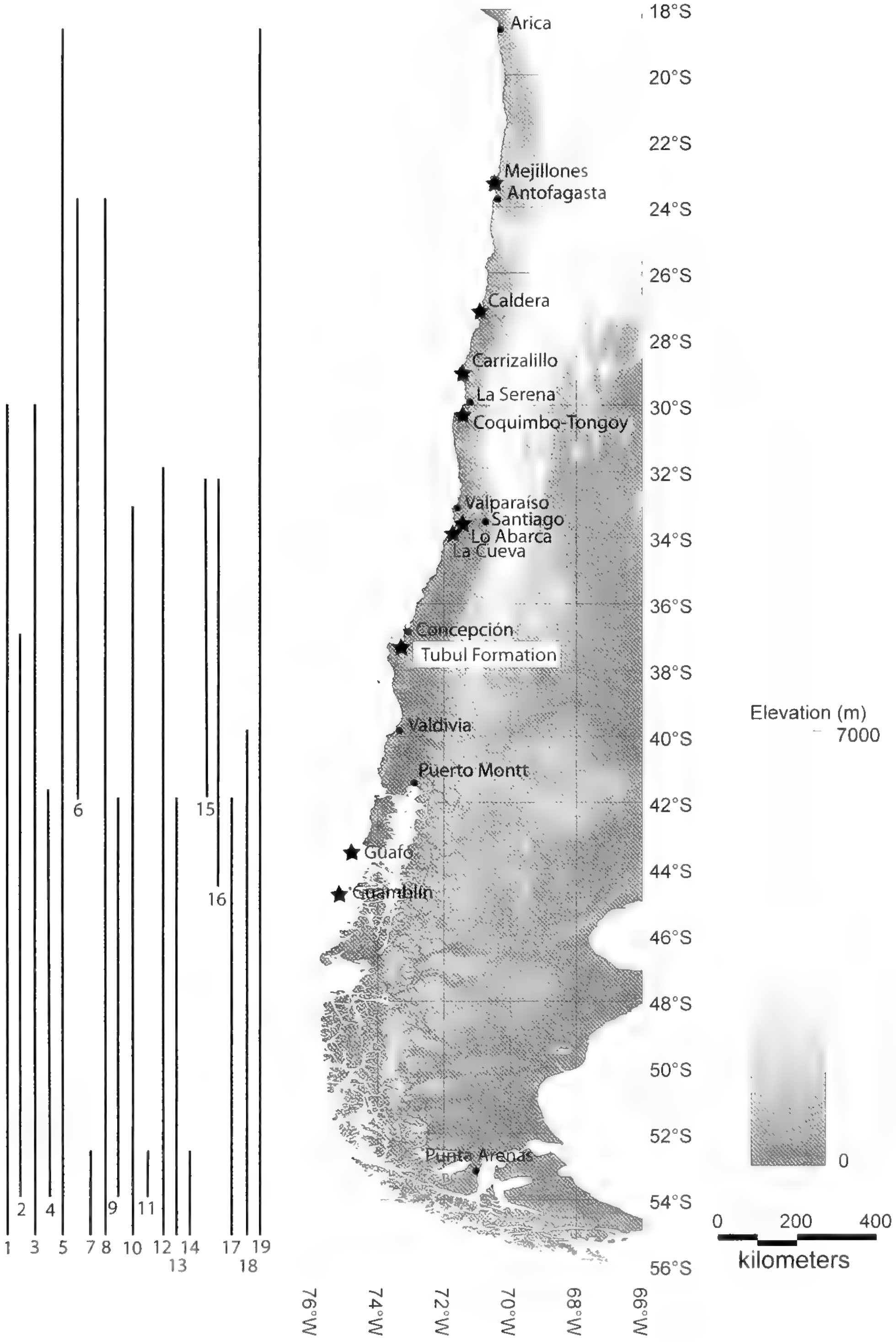


Figure 1. Extant ranges of bivalve and gastropod species occurring at Las Peñas. 1. *Ennucula grayi*. 2. *Tindariopsis sulculata*. 3. *Malletia chilensis*. 4. *Zygochlamys patagonica*. 5. *Cyclocardia velutinus*. 6. *Macoma inornata*. 7. *Darina solenoides*. 8. *Ensis macha*. 9. *Retrotapes exalbidus*. 10. *Pandora cistula*. 11. *Epitonium magellanicus*. 12. *Fusitriton magellanicus*. 13. *Trophon geversianus*. 14. "*Xymenopsis*" *dispar*. 15. *Chorus giganteus*. 16. *Nassarius taeniolatus*. 17. *Adelomelon ancilla*. 18. *Bela paesleri*. 19. *Scaphander interruptus*. Stars indicate Plio–Pleistocene fossil localities.

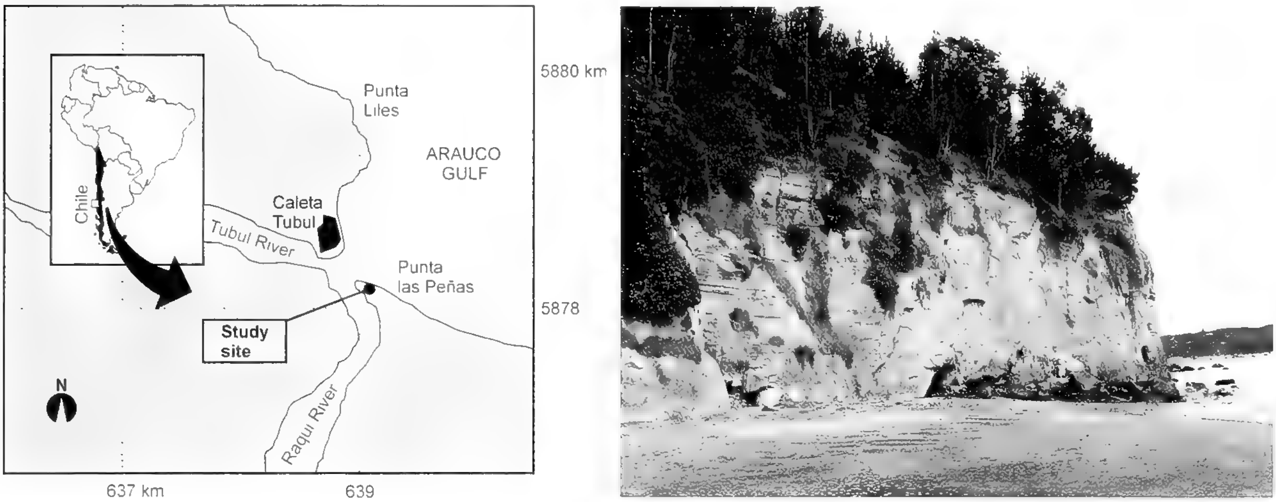


Figure 2. Area of the Tubul Formation and sample site at Las Peñas. Height of coastal bluff about 18 m.

a shallow-marine environment. Radic et al. (2005) cited a thickness of 100 to 500 m for the Tubul Formation based on well data and seismic lines.

The molluscan fauna decribed in this paper comes from the coastal bluffs near Las Peñas (Figure 2), which represent the uppermost part of the Tubul Formation.

MATERIALS AND METHODS

The mollusks described in this study belong to the collection of the late Professor Lajos Biró and are housed in the Departamento de Ciencias de la Tierra, Universidad de Concepción, Chile. The material comes from near Punta Las Peñas (37°14′32″ S, 73°26′02″ W, Figure 2), south of the village Tubul, and is designated by the letter 'T' in the collections. The number of specimens inspected for each species is indicated by a number in parentheses if the number is greater than one. Species are not formally described because all except two are well known, Modern geographic ranges of species are modified from Valdovinos (1999).

SYSTEMATICS

Class Bivalvia Linnaeus, 1758
Family Nuculidae Gray, 1824
Genus *Ennucula* Iredale, 1931

Ennucula grayi (d'Orbigny, 1846)
(Figure 3)

Nucula obliqua Sowerby, 1833: 5, pl. 16, fig. 21.

Nucula grayi d'Orbigny, 1846: vol. 5, 625 (*nomen novum* for *N. obliqua* Sowerby, *non* Lamarck, 1819).

Ennucula grayi (d'Orbigny).–Soot-Ryen, 1959: 13, pl. 1, fig. 8; Villarroel and Stuardo, 1998: 133, figs. 8, 70, 71, 73, 107–109.

Ennucula araucana (Philippi).–Villarroel and Stuardo, 1998: 165 (*partim*), figs. 142–143.

Ennucula valdiviana (Philippi).–Villarroel and Stuardo, 1998: 165 (*partim*), figs. 134–137.

Ennucula lebuensis (Philippi).–Villarroel and Stuardo, 1998: 165 (*partim*), figs. 138–139.

Material Examined: 47 specimens: T/4 (2), T/5 (6), T/7 (5), T/11, T/17, T/204, T/237, T/386, T/1072, T/1276 (3), T/1313, T/1394–1397, T/1537, T/1749–1754, T/1968 (7), T/1969 (2), T/1989–1990, T/2048, T/2090.

Measurements: Width 19.2 mm, length 16.7 mm (T/237).

Occurrence: Recent: Coquimbo to Magellan Region; Plio-Pleistocene: Arauco to ?Isla Guafo.

Remarks: *Nucula barrosi* Philippi, 1887 (=*N. araucana* Philippi, 1887), *N. lebuensis* Philippi, 1887, and *N. valdiviana* Philippi, 1887, are Miocene species from the Navidad, Ranquil, and Sto. Domingo formations of central and southern Chile. However, their generic placement is not known and therefore possible relationships to *E. grayi* remain unclear. The specimens mentioned and figured by Villarroel and Stuardo (1998) belong in *E. grayi* and not in one of these Miocene species. The taxonomic positions of these older species must await a revision of the Chilean Miocene nuculoids.

Genus *Tindariopsis* Verrill and Bush, 1897

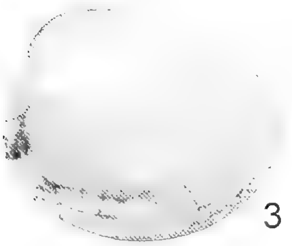
Tindariopsis sulculata (Gould, 1852)
(Figure 4)

Nucula striata King and Broderip, 1832: 337 (*non* Lamarck, 1805).

Nucula sulculata Gould, 1852: 12, 434, pl. 37, figs. 539 a–e (Couthouy MS).

Nucula elegans Hupé, 1854: 305, Conquiliología pl. 5 fig. 7; Philippi, 1887: 189, pl. 31, fig. 6.

Tindariopsis sulculata (Gould).–Dell, 1964: 149; Villarroel and Stuardo, 1998: 144–145, figs. 39–41, 80–82 157–159.



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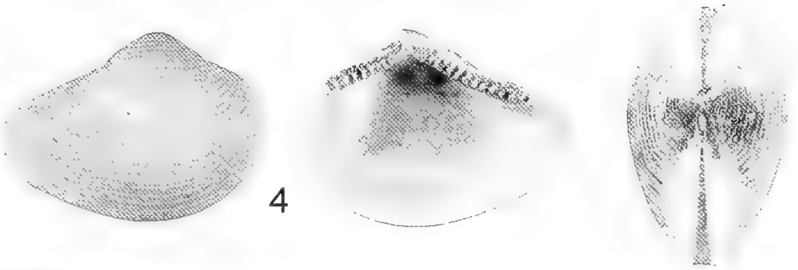

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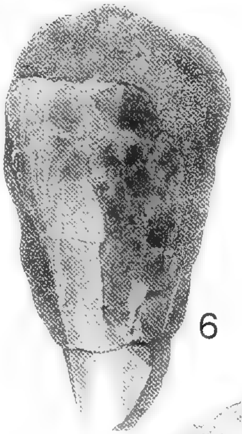

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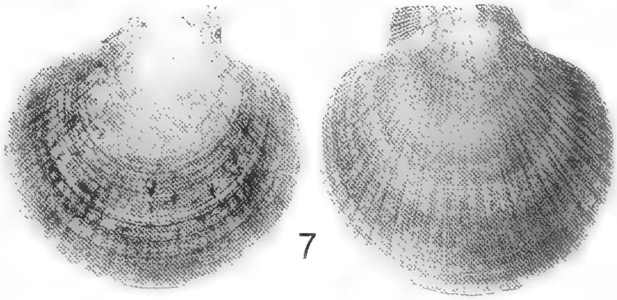

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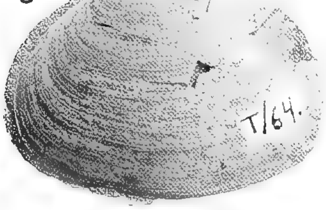

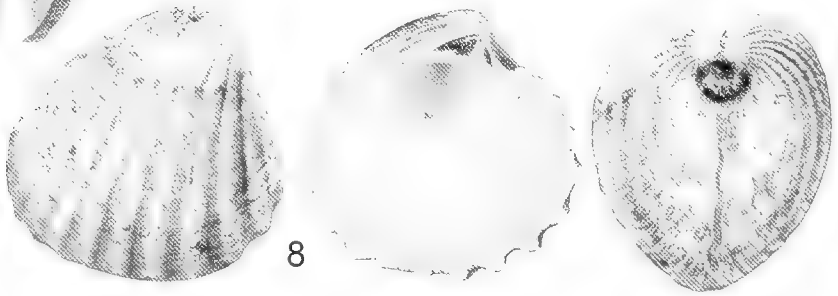

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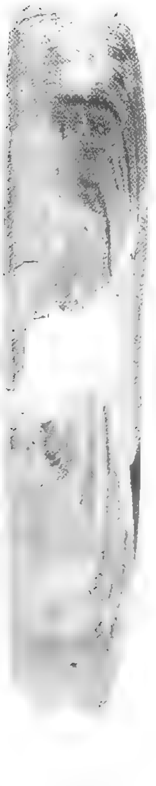

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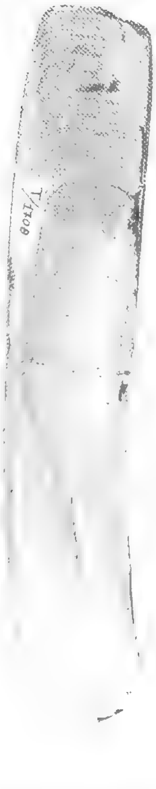

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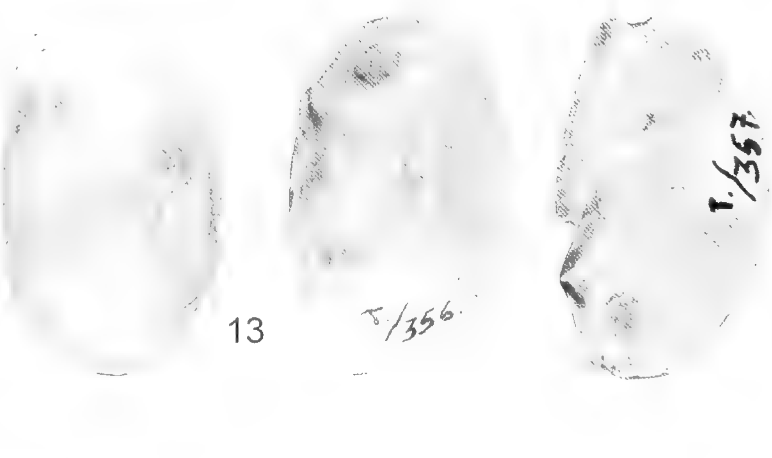

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Nuculana sulculata (Gould).–Dell, 1971: 167, pl. 1, figs. 1–4, pl. 2, fig. 9.
Nuculana elegans (Hupé).–Frassinetti and Covacevich, 1995: 51, text-fig. 3a, pl. 1, figs. 1–5; Frassinetti, 1997: 60, pl. 1, figs. 5–7.
Tindaria sulculata (Gould).–Griffin and Nielsen, 2008: 16, pl. 5, figs. 3–5.

Material Examined: ca. 1850 specimens: T/1 (92), T/8 (24), T/9 (89), T/12 (17), T/13 (36), T/14 (17), T/15 (48), T/16 (9), T/18 (198), T/19 (252), T/32 (10), T/53–54, T/148 (4), T/149 (9), T/164 (2), T/168 (8), T/206, T/207 (4), T/236 (4), T/296 (3), T/542, T/974 (2), T/982–984 (ca. 150), T/1083 (7), T/1182–1187 (ca. 90), T/1235 (6), T/1270 (293), T/1308 (ca. 30), T/1379 (92), T/1518 (11), T/1536 (21), T/1624, T/1681 (ca.45), T/1682 (6), T/1802–1804 (ca. 90), T/1911 (23), T/1912 (ca. 90), T/1913, T/1970 (15), T/2001 (5), T/2009 (23), T/2042 (7).

Measurements: Width up to 16 mm (T/1682).

Occurrence: Recent: Talcahuano to Strait of Magellan; Plio-Pleistocene: Arauco to Isla Guamblín.

Remarks: As for many other species, there are different names for Recent and fossil records of the same species. Villarroel and Stuardo (1998, p. 145), in their review of the Recent and fossil species of Chilean Protobranchia, noted that "The ornamentation of the shell of *T. sulculata* is very similar to that of the fossil species *T. elegans* (. . .). It differs from that by its shorther length and by the truncation of its extreme posterior." However, we do not consider these differences as sufficient for specific separation and regard them as intraspecific variation instead.

Family Malletiidae H. and A. Adams, 1858
Genus *Malletia* Moulins, 1832

Malletia chilensis Moulins, 1832
(Figure 5)

Malletia chilensis Moulins, 1832: 85, pl. 1, figs. 1, 8.
Malletia inequalis Dall, 1908: 219, 383.
?*Malletia* sp. Frassinetti and Covacevich, 1995: 50.

Material Examined: Nine specimens: T/544(2), T/1091–1093, T/1917, T/2176–2178.

Measurements: Figured specimen width 26 mm (T/1092).

Occurrence: Recent: Coquimbo to Magellan Region; Plio-Pleistocene: Arauco to Isla Guamblín.

Remarks: According to Villarroel and Stuardo (1998), there are four or five species of *Malletia* known from Chile, all of which are rather similar to each other. Apart from *M. chilensis,* they recorded *M. patagonica* Mabille and Rochebrune, 1889, *M. inequalis* Dall, 1908, and *M. magellanica* (Smith, 1875). *Malletia hyadesi* Mabille and Rochebrune, 1889 was listed as a probable synonym of *M. patagonica*. *Malletia volckmanni* (Philippi, 1887) most probably is of Miocene age and has not been revised and its placement should be regarded with caution.

Family Mytilidae Rafinesque, 1815
Genus ?*Mytilus* Linnaeus, 1758

Mytilus sp.
(Figure 6)

Material Examined: One specimen: T/106.

Measurements: Length 58 mm (T/106).

Remarks: According to Valdovinos (1999) there are nine species of Mytilidae known from Chile. Based on the main characters of the our shell fragment, such as the pointed morphology of the umbo and fine external growth striae, our specimen may correspond either to the genus *Mytilus* or *Choromytilus*. In southern Chile the species *Choromytilus chorus* (Molina, 1782) and *Mytilus edulis chilensis* Hupé, 1854, coexist, but it is not possible to identify our specimen to species level. Mytilidae of uncertain generic and specific status are known from Miocene through Recent and are in need of a detailed revision.

Family Pectinidae Rafinesque, 1815
Genus *Zygochlamys* Ihering, 1907

Zygochlamys patagonica (King and Broderip, 1832)
(Figure 7)

Pecten patagonicus King and Broderip, 1832, 5: 337.
Pecten tenuicostatus Hupé, 1854: 291, pl. 5, fig. 4; Philippi 1887: 203, pl. 47, fig. 1; Möricke, 1896: 580, pl. 12, figs. 13–16.
Chlamys patagonica patagonica (King and Broderip). –Beu, 1985: 1–11, pl. 1, figs. 1–4.
Zygochlamys patagonica (King and Broderip).–Waller, 1991: 28–30, pl. 2, figs. 13, 14; Griffin and Nielsen, 2008: 37, pl. 16, figs. 5, 6.
Chlamys tenuicostatus (Hupé).–Frassinetti and Covacevich, 1995: 52, text-fig. 3b, pl. 1, figs. 6–9.

Material Examined: 305 specimens: T/63, T/79, T/135, T/147, T/166, T/175, T/180, T/222–223, T/243, T/255, T/256, T/293, T/305, T/307–309, T/311–312, T/329–334, T/361–380, T/387–399, T/432–434, T/491–504, T/577–578, T/725–726, T/728–772, T/775–777, T/806–820, T/1006 -1017, T/1039, T/1074–1077, T/1080–1082, T/1156–1157, T/1160–1166, T/1269.

Figures 3–13. Bivalvia. **3.** *Ennucula grayi* (d'Orbigny, 1846) [length 19.2 mm]. **4.** *Tindariopsis sulculata* (Gould, 1852) [length 16.0 mm]. **5.** *Malletia chilensis* Moulins, 1832 [length 16.0 mm]. **6.** *Mytilus* sp. [length 58.0 mm]. **7.** *Zygochlamys patagonica* (King and Broderip, 1832) [length 75 mm]. **8.** *Cyclocardia velutinus* (E. A. Smith, 1881) [length 18.5 mm]. **9.** *Macoma inornata* (Hanley, 1844) [length 16.0 mm]. **10.** *Darina solenoides* (King and Broderip, 1832) [length 44.0 mm]. **11.** *Ensis macha* (Molina, 1782) [length 97.2 mm]. **12.** *Retrotapes exalbidus* (Dillwyn, 1817) [length 62.0 mm]. **13.** *Pandora cistula* Gould, 1850 [length 23.0 mm].

T/1280–1281, T/1284, T/1309–1310, T/1358, T/1371–1378, T/1380–1386, T/1389–1392, T/1415–1424, T/1514–1516, T/1553–1559, T/1579–1586, T/1632, T/1677–1680, T/1714–1728, T/1827, T/1863–1875, T/1964–1967, T/2003–2008, T/2030–2031, T/2033, T/2037–2038, T/2049, T/2052, T/2055–2056, T/2059–2065, T/2154–2167, T/2181–2192, T/2225–2229.

Measurements: Height 75 mm, width 73 mm (T/223).

Occurrence: Recent: Island of Chiloé to Strait of Magellan; Plio-Pleistocene: Arauco to Isla Guamblín.

Remarks: Because revision of Chilean pectinids is not within the scope of this work, relationships of *Z. patagonicus* to the northern species described by Herm (1969) are not discussed here. *Zygochlamys patagonicus* is the type species of *Psychrochlamys* Jonkers, 2003. However, like Griffin and Nielsen (2008) and Dijkstra and Marshall (2008), we consider *Psychrochlamys* a synonym of *Zygochlamys*.

Family Carditidae Fleming, 1828
Genus *Cyclocardia* Conrad, 1867

Cyclocardia velutinus (E.A. Smith, 1881)
(Figure 8)

Cardita (Actinobolus) velutinus E.A. Smith, 1881: 42, pl. 5, fig. 8.
Cardita volckmanni Philippi, 1887: 167, pl. 37, fig. 4.
Cardiocardita volckmanni (Philippi).–Frassinetti and Covacevich, 1995: 53, text-fig. 3c, pl. 1, figs. 10–17; Frassinetti, 1997: 65, pl. 1, figs. 17–20.

Material Examined: 19 specimens: T/507–510, T/639, T/786–787, T/1546–1552, T/1628–1630, T/1756, T/2256.

Measurements: Width 18.5 mm, length 17 mm (T/508).

Occurrence: Recent: Arica to Beagle Canal; Plio-Pleistocene: Arauco to Isla Guamblín.

Remarks: A number of different *Cyclocardia* species has been reported from southern Chile (Forcelli, 2000).

Family Tellinidae Blainville, 1814
Genus *Macoma* Leach, 1819

Macoma inornata (Hanley, 1844)
(Figure 9)

Tellina inornata Hanley, 1844, 1847: 315, pl. 59, fig. 127.
Tellina tubulensis Philippi, 1887: 134, pl. 32, fig. 7.
Macoma (Psammacoma) inornata (Hanley).–Soot-Ryen, 1959: 62, pl. 4, figs. 34–36.
Macoma tubulensis (Philippi).–Frassinetti, 1997: 72, pl. 2, fig. 6.

Material Examined: Eight specimens: T/64, T/721–724, T/789, T/1236, T/2067.

Measurements: Width figured specimen (T/64) 26 mm

Occurrence: Recent: Atacama to Gulf of Ancud; Plio-Pleistocene: Arauco to Isla Guamblín.

Remarks: Herm (1969, p. 119) described a specimen of *Ardeamya* sp. as the only tellinid from the Pliocene south of San Antonio. Since Herm knew the Philippi collection, it must be assumed that it is not conspecific with the species reported here.

Family Mactridae Lamarck, 1809
Genus *Darina* Gray, 1853

Darina solenoides (King and Broderip, 1832)
(Figure 10)

Erycina solenoides King and Broderip, 1832: 335.
Darina solenoides (King and Broderip).–Smith, 1905: 337.
Mactra sp.–Frassinetti and Covacevich, 1995: 54.

Material Examined: One specimen: T/1238.

Measurements: Width figured specimen (T/1238) 44 mm.

Occurrence: Recent: Strait of Magellan and Tierra del Fuego; Plio-Pleistocene: Arauco to Isla Guamblín.

Remarks: Herm (1969) discussed the problems of related forms appearing in the Pliocene of Coquimbo to San Antonio which he placed in the genus *Mulinia* Gray, 1837.

Family Pharidae H. and A. Adams, 1858
Genus *Ensis* Schumacher, 1817

Ensis macha (Molina, 1782)
(Figure 11)

Solen macha Molina, 1782: 203; Hupé, 1854: 369, pl. 8, fig. 6.
Solen gladiolus Sowerby, 1839: 153, pl. 43, fig. 4.
Solen gladiolus? Sowerby.–Philippi, 1887: 169, pl. 34, fig. 9.
Ensis macha (Molina).–Carcelles, 1944: 292.
Ensis sp.–Frassinetti, 1997: 67. pl. 2, figs. 4–5.

Material Examined: 38 specimens: T/192, T/579–580, T/793–797, T/1084, T/1101–1102, T/1175–1176, T/1285–1290, T/1368–1370, T/1412–1414, T/1694, T/1707–1712, T/1923, T/1972, T/2000, T/2068, T/2226–2227.

Measurements: Up to 97.2 mm (T/1707).

Occurrence: Recent: Caldera to Magellan Region; Plio-Pleistocene: Coquimbo to Isla Guafo.

Remarks: *Ensis macha* is one of the few species which has a very wide geographical range in Pliocene and Recent faunas of Chile. During the Pleistocene it also reached Mejillones (Herm, 1969; own observations).

Family Veneridae Rafinesque, 1815
Genus *Retrotapes* del Río, 1997

Retrotapes exalbidus (Dillwyn, 1817)
(Figure 12)

Venus exalbida Chemnitz, 1795: 225, pl. 202, fig. 2 (*non binom.*); Dillwyn, 1817: 170.
Venus aerea Hupé, 1854: 338.
Venus subalbicans Hupé, 1854: 339.
Venus araucana Philippi, 1887: 117, pl. 17, fig. 6; Tavera and Veyl, 1958: 170, pl. 4, fig. 13c.
Samarangia exalbida (Dillwyn).–Carcelles, 1944: 287, pl. 12, figs. 93, 94.
Eurhomalea araucana (Philippi).–Frassinetti, 1974: 47, figs. 1–2; Frassinetti and Covacevich, 1995: 54, text-fig. 3c, pl. 1, fig. 18; Frassinetti, 1997: 74, pl. 2, fig. 6.
Retrotapes exalbida (Dillwyn).–del Río, 1997: 80–82, figs. 22, 23, 41.
Retrotapes exalbidus (Dillwyn).–Reid and Osorio, 2000: 139, fig. 5J; Griffin and Nielsen, 2008: 7, 35, pl. 1, figs. 2–4, pl. 16, figs. 1–3.

Material Examined: 669 specimens: T/21–25, T/44–49, T/56, T/58–62, T/65–73, T/75, T/78, T/84–109, T/136–140, T/151, T/153–163, T/173–176, T/181–191, T/198–203, T/208–213, T/216–221, T/226–235, T/241–242, T/249–253, T/257–263, T/266–272, T/277–282, T/319–328, T/400–421, T/449–490, T/516–539, T/545–557, T/607–614, T/653–671, T/681–703, T/710–719, T/802, T/829–881, T/901–910, T/919–968, T/978, T/987–989, T/1027–1037, T/1109–1114, T/1128–1134, T/1142–1154, T/1158–1159, T/1194–1197, T/1212–1217, T/1228–1229, T/1237–1268, T/1298–1306, T/1316–1324, T/1333–1356, T/1425–1428, T/1511–1513, T/1534, T/1538–1544, T/1648–1676, T/1781–1796, T/1805–1809, T/1817–1826, T/1835–1862, T/1949–1963, T/2011–2014, T/2035–2036, T/2039–2041, T/2046, T/2058, T/2081, T/2093–2097, T/2140–2147, T/2230–2249.

Measurements: Up to width 62 mm, length 54.5 mm (T/967).

Occurrence: Recent: Chiloé to Strait of Magellan; Plio-Pleistocene: Arauco to Isla Guamblín.

Remarks: A number of different *Eurhomalea* species, most probably now belonging in *Retrotapes*, has been reported from northern Chile (Herm, 1969).

Family Pandoridae Rafinesque, 1815
Genus *Pandora* Bruguière, 1797

Pandora cistula Gould, 1850
(Figure 13)

Pandora cistula Gould, 1850: 217.
Kennerlyia patagonica Dall, 1915: 450.
Pandora sp.–Frassinetti and Covacevich, 1995: 55, pl. 1, fig. 19.

Material Examined: T/141–146, T/345, T/353–354, T/615–634, T/781, T/783, T/784 (3), T/972–973, T/986 (2), T/1273 T/1291–1292, T/1311–1312, T/1405–1411, T/1535 (8), T/1755, T/2175, T/2225.

Measurements: Width 23 mm (T/2225).

Occurrence: Recent: Valparaíso to Magellan Region; Plio-Pleistocene: Arauco to Isla Guamblín.

Remarks: This species is the only living species of *Pandora* recorded in Chile (see Forcelli, 2000).

Class Gastropoda Cuvier, 1795
Family Epitoniidae Berry, 1910
Genus *Epitonium* Röding, 1798
Subgenus *Nitidiscala* de Boury, 1909

Epitonium (Nitidiscala) magellanicus (Philippi, 1845)
(Figure 14)

Scalaria magellanica Philippi, 1845: 46.
Scalaria (Opalia) magellanica Strebel, 1905: 656, pl. 23, figs. 44a–f.
Cirsotrema (Coroniscala) magellanicum (Philippi). – Wenz, 1938: 798, fig. 2322.
Epitonium (Nitidiscala) magellanica(Philippi).–Ramírez, 1987: 70, fig. 82.
Epitonium biroi Frassinetti and Covacevich, 1995: 56, pl. 2, figs. 1–2; Frassinetti, 1997: 135, pl. 1, figs. 4–5.

Material Examined: One specimen: T/2071.

Measurements: Height 20.5 mm.

Occurrence: Recent: Strait of Magellan; Plio-Pleistocene: Arauco to ?Isla Guamblín.

Remarks: A number of different epitoniid species has been reported from southern Chile (Forcelli, 2000). The type material of *Epitonium biroi* Frassinetti and Covacevich, 1995 from Guamblín was not revised, so it remains unclear if it represents a different species or a synonym.

Family Naticidae Guilding, 1834
Genus *Euspira* Agassiz, 1838

Euspira guamblinensis Frassinetti and Covacevich, 1995
(Figure 15)

Polinices (Euspira) guamblinensis Frassinetti and Covacevich, 1995: 57, text-fig. 4a–e, pl. 2, figs. 3–5; Frassinetti, 1997: 135, pl. 1, figs. 6–9.

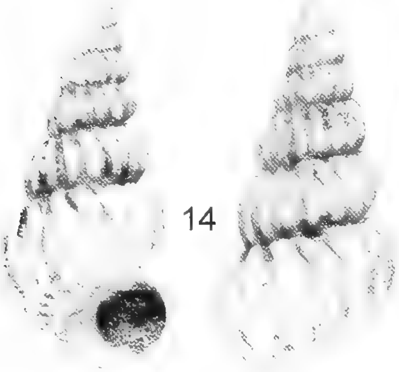
Material Examined: 37 specimens: T/30, T/152, T/215, T/335–337, T/778, T/779, T/976, T/1177–1181, T/1272, T/1279, T/1627, T/1684, T/1696, T/1704, T/1705, T/1777, T/1899, T/1901, T/1902, T/1909, T/1940–1942, T/1991, T/2053, T/2068, T/2151, T/2210–2212, T/2255.

Measurements: Height up to 22.5 mm, figured specimen (T/1909) height 14 mm.

Occurrence: Recent: Extinct; Plio-Pleistocene: Arauco to Isla Guamblín.

Remarks: None of the extant naticid species reviewed by Pastorino (2005a) matches *Euspira guamblinensis* in its callus characters and we regard it as a valid species.

Family Ranellidae Gray, 1854
Genus *Fusitriton* Cossmann, 1903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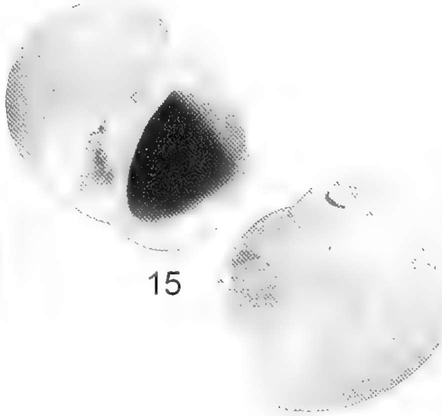
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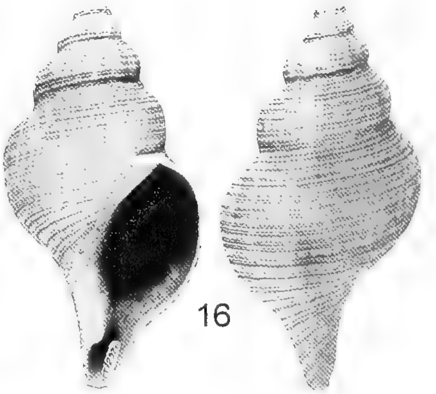
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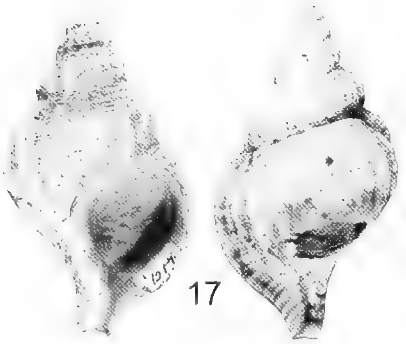
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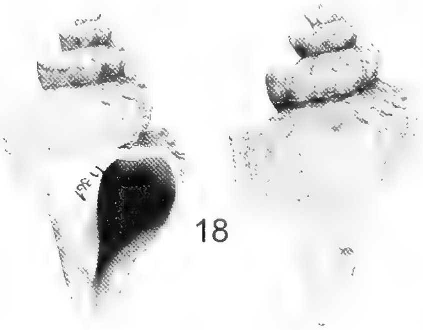
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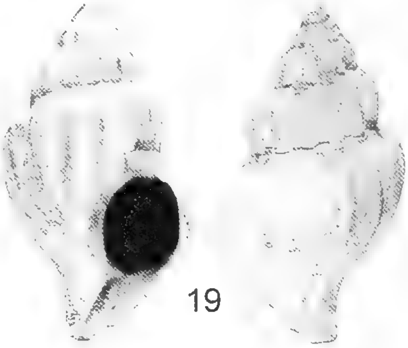
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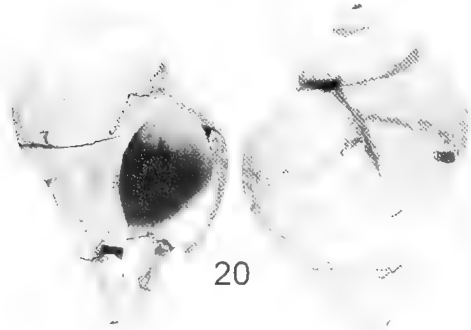
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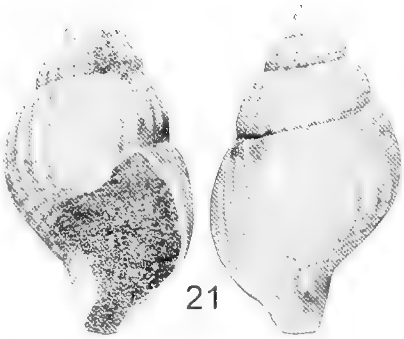
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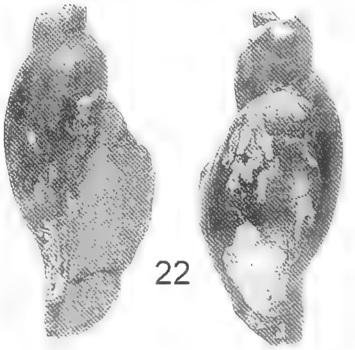
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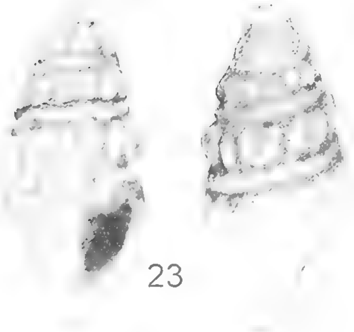
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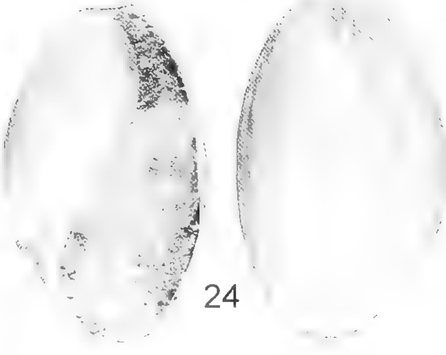
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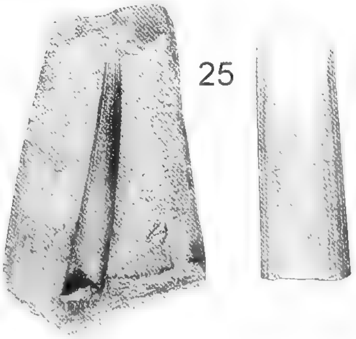
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Fusitriton magellanicus (Röding, 1798)
(Figure 16)

Murex magellanicus Chemnitz, 1788: 275, pl. 164, fig. 1570 (*non binom.*).
Neptunea magellanica Röding, 1798: 116.
Triton cancellatum Lamarck, 1816: 4.
Priene (*Fusitriton*) *cancellatus* (Lamarck).–Cossmann, 1903: 109, fig. 8.
Argobuccinum (*Fusitriton*) *cancellatus* (Lamarck).–Wenz, 1938: 1058, fig. 3022.
Argobuccinum (*Argobuccinum*) *magellanicum* (Röding).–Carcelles, 1944: 247, pl. 2, fig. 23.
Argobuccinum (*Fusitriton*) *magellanicum* (Röding). –Carcelles and Williamson, 1951: 286.
Fusitriton cancellatus (Lamarck).–Smith, 1970: 475, pl. 42, figs. 4–10.
Fusitriton magellanicus (Röding).–Cernohorsky, 1977: 107, fig. 3.

Material Examined: 20 specimens: T/150, T/171, T/178, T/214, T/315, T/340, T/511, T/512, T/572, T/971, T/1100, T/1282, T/1360, T/1575, T/1731, T/2026, T/2039, T/2169, T/2214, T/2252.

Measurements: Figured specimen (T/2026) height 73 mm.

Occurrence: Recent: Los Vilos to Magellan Region and Juan Fernández Archipelago; Plio-Pleistocene: Arauco.

Remarks: This is a well known species that clearly does not present any taxonomic problems.

Genus *Sassia* Bellardi, 1872

Sassia leucostomoides (Sowerby, 1846)
(Figure 17)

Triton leucostomoides Sowerby, 1846: 240, pl. 4, fig. 64.
Sassia leucostomoides (Sowerby).–Frassinetti, 1997: 136, pl. 1, figs. 11–14; Griffin and Nielsen, 2008: 49, pl. 21, figs. 9–14.

Material Examined: Six specimens: T/310, T/574; T/2032, T/2153, T/2196, T/2215.

Measurements: Figured specimen (T/574) height 44.4 mm.

Occurrence: Recent: Extinct; Plio-Pleistocene: Arauco to Isla Guafo.

Remarks: This species was originally described from Guafo (Sowerby, 1846) and this record is the first from another locality.

Family Muricidae Rafinesque, 1815
Genus *Trophon* Montfort, 1810

Trophon geversianus (Pallas, 1774)
(Figure 18)

Buccinum geversianus Pallas, 1774: 33, pl. 3, figs. 1, 2.
Murex magellanicus Gmelin, 1791: 3548.
Fusus geversianus (Pallas).–Hupé, 1854: 167.
Trophon geversianus (Pallas).–Gould, 1852: 227, pl. 6, fig. 227.

Material Examined: Nine specimens: T/513, T/569, T/575, T/640, T/798, T/1361, T/1574, T/2029, T/2253.

Measurements: Height 62 mm (T/640), figured specimen (T/1361) 39 mm.

Occurrence: Recent: Chiloé to Magellan Region; Plio-Pleistocene: Arauco.

Remarks: The Chilean species of the genus *Trophon* present a high intraspecific variability, with many species described as synonyms of *T. geversianus*. A detailed revision of the genus *Trophon*, including *T. geversianus*, was recently provided by Pastorino (2005b).

Genus "*Xymenopsis*" Powell, 1951

"*Xymenopsis*" cf. "*X.*" *dispar* (Rochebrune and Mabille, 1889)
(Figure 19)

Fusus dispar Rochebrune and Mabille, 1889: H57, pl. 2, fig. 3.
Trophon dispar (Rochebrune and Mabille).–Carcelles and Williamson, 1951: 289.
Xymenopsis dispar (Rochebrune and Mabille).–Powell, 1951: 159.

Material Examined: 16 specimens: T/352, T/586 (5), T/588 (7), T/1357, T/2219, T/2245.

Measurements: Figured specimen (T/352) 22 mm.

Occurrence: Recent: Tierra del Fuego; Plio-Pleistocene: Arauco.

Remarks: Pastorino and Harasewych (2000) stated that this species does not belong in *Xymenopsis* but did not provide a more appropriate generic-level placement in the Muricidae.

Genus *Chorus* Gray, 1847

Chorus giganteus (Lesson, 1830)
(Figure 20)

Monoceros giganteus Lesson, 1830: 405, N° 165, pl. 11, fig. 4.

Figures 14–25. Gastropoda and Scaphopoda. **14.** *Epitonium* (*Nitidiscala*) *magellanicus* (Philippi, 1845) [height 25.0 mm]. **15.** *Euspira guamblinensis* Frassinetti and Covacevich, 1995 [height 22.5 mm]. **16.** *Fusitriton magellanicus* (Röding, 1798) [height 73.0 mm]. **17.** *Sassia leucostomoides* (Sowerby, 1846) [height 44.4 mm]. **18.** *Trophon geversianus* (Pallas, 1774) [height 62.0 mm]. **19.** "*Xymenopsis*" cf "*X.*" *dispar* (Rochebrune and Mabille, 1889) [height 22.0 mm]. **20.** *Chorus giganteus* (Lesson, 1830) [height 95.0 mm]. **21.** *Nassarius taeniolatus* (Philippi, 1845) [height 11.0 mm]. **22.** *Adelomelon ancilla* (Ligthfoot, 1786) [height 142.0 mm]. **23.** *Bela paesleri* Strebel 1905 [height 16.0 mm]. **24.** *Scaphander interruptus* Dall, 1889 [height 18.5 mm]. **25.** *Dentalium* sp. [length 72.0 mm]

Monoceros giganteus? Lesson.–Möricke, 1896: 564.
Rapana (*Chorus*) *gigantea* (Lesson).–Wenz, 1941: 1038, fig. 3080.
Chorus giganteus (Lesson).–Carcelles, 1954: 271, pl. 5, figs. 1–11; Herm, 1969: 135, pl. 15, figs. 4a, 4b; DeVries, 1997: 132, pl. 1, figs. 1–4, pl. 4, fig. 4.
Chorus grandis (Philippi).–Herm, 1969: pl. 15, figs. 3a, 3b.

Material Examined: 17 specimens: T/576, T/985, T/1174, T/1193, T/1904–1905, T/1907–1908, T/1910, T/1984, T/2170–2172, T/2208, T/2213, T/2272, one specimen without number.

Measurements: Height up to 95 mm (T/985), figured specimen (T/1905) 80.5 mm.

Occurrence: Recent: Papudo to Calbuco; Plio-Pleistocene: southern Peru to Arauco.

Remarks: The species of *Chorus* have been reviewed by Herm (1969) and DeVries (1997). DeVries (1997) also gave new diagnoses and descriptions. Regarding the stratigraphic range of *Chorus giganteus* cited by DeVries (1997), its presence in the Tubul Formation implies a maximum age of very late Pliocene to early Pleistocene for these deposits.

Family Nassariidae Iredale, 1916
Genus *Nassarius* Duméril, 1806

Nassarius taeniolatus (Philippi, 1845)
(Figure 21)

Buccinum taeniolatus Philippi, 1845: 69; Hupé, 1854: 207, pl. 4, fig. 9.
Nassarius taeniolatus (Philippi).–Keen, 1971: 609, fig. 1313.

Material Examined: Three specimens: T/586 (2), T/1687.

Measurements: 11 mm (T/1687).

Occurrence: Recent: Papudo to Chonos Archipelago; Plio-Pleistocene: Arauco.

Remarks: This species is the only representative of *Nassarius* in southern Chile, while two more species are found living off central and northern Chile (*N. gayi* (Kiener, 1835) and *N. dentifer* (Powys, 1835); see Marincovich, 1973).

Family Volutidae Rafinesque, 1815
Genus *Adelomelon* Dall, 1906

Adelomelon ancilla (Ligthfoot, 1786)
(Figure 22)

Voluta ancilla Lightfoot, 1786: 84.
Voluta gracilis Wood, 1828: 59, pl. 3, fig. 2.
Cimbiola ancilla (Lightfoot).–Pace, 1902: 28, pl. 7, figs. 1–16.
Adelomelon (*Adelomelon*) *ancilla* (Lightfoot).–Wenz, 1938: 1347, fig. 3816.
Adelomelon ancilla (Lightfoot).–Dall, 1906: 143.

Material Examined: One specimen: T/1227.

Measurements: Figured specimen (T/1227) 142 mm.

Occurrence: Recent: Chiloé to Magellan Region; Plio-Pleistocene: Arauco to ?Isla Guafo.

Remarks: It is unclear if *A. reconditus* Frassinetti, 1997, is a different species or a juvenile *A. ancilla*. A large specimen of presumably *A. reconditus* was found on Guafo (coll. Nielsen), but preservation does not allow assignment to a species. The Chilean fossil species of *Adelomelon* were recently revised by Nielsen and Frassinetti (2007a).

Family Turridae H. and A. Adams, 1853
Genus *Bela* Leach in Gray, 1847

Bela paesleri Strebel, 1905
(Figure 23)

Bela paessleri Strebel, 1905: 588, pl. 22, figs. 35, 35a–b.
Mangelia (*Bela*) *paessleri* (Strebel).–Carcelles, 1950: 67.

Material Examined: 14 specimens: T/589 (6, in part), T/590 (7), T/1626.

Measurements: Height 16.7 mm (T/1626).

Occurrence: Recent: Valdivia to Magellan Region; Plio-Pleistocene: Arauco.

Remarks: This species is in need of revision, but because the protoconch is not preserved in these specimens, it is not possible to verify its generic position.

Family Scaphandridae Montfort, 1810
Genus *Scaphander* Montfort, 1810

Scaphander *interruptus* Dall, 1889
(Figure 24)

Scaphander interruptus Dall, 1889, 12: 297, pl. 12, fig. 12.

Material Examined: Six specimens: T/244, T/583, T/584 (2), T/975, one specimen without number.

Measurements: Figured specimen without number, 18.5 mm.

Occurrence: Recent: Panama to Magellan Region; Plio-Pleistocene: Arauco.

Remarks: The Recent and fossil Chilean Cephalaspidea are in need of revision. *Scaphander cosmophilus* (Sowerby, 1846) is known from the Pliocene of Isla Guafo (Frassinetti, 2000) and possibly from Isla Guamblín (Frassinetti and Covacevich, 1995). *Scaphander cosmophilus* was placed in the Genus *Kaitoa* by Griffin and Nielsen (2008). It is not clear if the two species are closely related.

Class Scaphopoda Bronn, 1862
Family Dentaliidae Gray, 1847
Genus *Dentalium* Linnaeus, 1758

Dentalium sp.
(Figure 25)

Material Examined: Two specimens: T/1937–1938.

Measurements: Figured specimen (T/1937) length 72 mm.

Remarks: Dentaliidae are well represented in Chile at least since the Miocene (see e.g., Philippi, 1887; Herm, 1969). A review of the group has never been undertaken.

ASSOCIATED MACROFAUNA

Several taxa outside the mollusks are known from the Tubul Formation. The Biró collection contains about 225 specimens of barnacles, remains of two decapod crabs, bryozoans, about 260 specimens of the brachiopod *Magellania venosa* Solander, 1786, two different echinoids and some shark teeth.

Some of the fauna represented in the collection does not come from the Tubul Formation but from the Miocene Ranquil Formation, most probably from the nearby locality Punta El Fraile (see Nielsen et al., 2004; Finger et al., 2007). Miocene representatives in the Tubul collection include the nautiloid cephalopod *Aturia cubaensis* (Lea, 1841) and the olivid gastropod *Lamprodomina dimidiata* (Sowerby, 1846).

COMPARISON WITH OTHER FAUNAS AND CONCLUSIONS

Underlying the Tubul Formation is the late Miocene to early Pliocene Ranquil Formation (García, 1968; Pineda, 1986; Finger et al., 2007), the fauna of which is similar to that of the Navidad Formation south of Valparaíso (see Philippi, 1887; Groves and Nielsen, 2003; Nielsen, 2004, 2005; Nielsen and Frassinetti, 2003; Nielsen et al., 2004). This fauna has been reworked and is of early to middle Miocene age (DeVries and Frassinetti, 2003; Finger et al., 2007) and contains many tropical to subtropical gastropod genera, such as *Nerita*, *Strombus*, *Xenophora*, *Distorsio*, *Echinophoria*, *Ficus*, *Terebra*, and *Architectonica* (Philippi, 1887; Covacevich and Frassinetti, 1980; Nielsen, 2005; Nielsen and DeVries, 2002; Nielsen and Frassinetti, 2007b), that disappeared from Chile during the late Miocene climate cooling. A number of the gastropod genera described herein (*Epitonium*, *Trophon*, *Chorus*, *Nassarius*) were already present in Chile during the Miocene, but were represented by different species. If and how these are related to the living taxa has yet to be investigated.

The Pliocene to Pleistocene faunas from northern Chile have a different composition than that of the Tubul Formation, containing abundant Trochoidea, *Fissurella*, *Turritella*, *Crucibulum*, *Trochita*, *Crepidula*, different species of Naticidae (including *Sinum cymba*), *Argobuccinum*, *Nassarius*, *Acanthina*, *Chorus*, and *Oliva peruviana* (Herm, 1969; DeVries, 1997, 2003; own data), representing today's coastal fauna of northern to central Chile. However, these are nearshore faunas with many taxa from rocky coasts, while that of Tubul is a soft-bottom fauna from slightly deeper water, missing typical rocky-shore elements such as *Fissurella*, *Acanthina*, and *Concholepas*, which are present in the Plio-Pleistocene deposits of northern Chile and in the modern fauna along the whole Chilean coast (McLean, 1984; DeVries, 1995, 2003).

The Tubul fauna has previously been compared to faunas coming from Guamblín and Guafo islands farther south (Frassinetti, 1997, 2000; Frassinetti and Covacevich, 1995; Table 1). The fauna from Guamblín is close to the Tubul fauna and Frassinetti and Covacevich (1995) and Frassinetti (2000), comparing both faunas directly, cited new Tubul species (*Epitonium biroi*, *Trophon covacevichi*, and *Hindsiclava ignorata*), and suggested that *Epitonium biroi* may be conspecific with *E.* (*Nitidiscala*) *magellanicus*, *Trophon covacevichi* may be conspecific with *Trophon geversianus*, and *Hindsiclava ignorata* may be conspecific with *Bela paesleri*. However, to confirm these synonymies more material should be directly compared.

The fauna described by Frassinetti (1997, 2000) from Guafo contains a mixture of species also present at Guamblín island and Tubul and species known from older deposits, e.g., *Panopea chiloensis*, *Incatella chilensis*, *Echinophoria* sp. (cited as *Semicassis* sp.), *Chorus doliaris*, *Penion* spp., and *Gemmula subaequalis*. It seems likely that these taxa represent a fauna intermediate in age between the older faunas and the Tubul-Guamblín fauna but it is possible that specimens of the older fauna have been reworked from older beds and incorporated into younger sediments as has been demonstrated for the Navidad, Ranquil and Lacui formations of Mio-Pliocene age (Finger et al., 2007). The presence of *Chorus doliaris* and *Incatella chilensis* suggests a latest Miocene age for the Guafo fauna (DeVries, 1997, 2007).

The first appeareance of *Chorus giganteus* in southern Peru during the latest Pliocene (DeVries, 1997) makes this a likely maximum age for the Tubul fauna. Indeed, this agrees well with strontium isotope stratigraphy data from calcitic shells of *Zygochlamys patagonica* coming from the same locality, which confirm an early Pleistocene age (unpublished data). The two apparently extinct species present, *Euspira guamblinensis* and *Sassia leucostomoides*, may well be found living off Chile in the future. Comparison with living ranges of the species found in the Tubul Formation (Figure 1) permits one to identify two regions with 16 species in common. The fauna of the Tubul Formation resembles most closely the present-day faunas of northern Chiloé island and the Magellan Region, whereas northern faunas of Pliocene to Pleistocene age have a composition similar to that of modern northern and central Chile. Water temperatures for the Arauco area are accordingly interpreted to have been colder than today. It is presently not known if the more northern species (Figure 1, numbers 6, 15, 16) previously tolerated cooler waters or if the southern species (Figure 1, numbers 7, 11, 14) tolerated warmer waters. However, it is possible that an additional factor

Table 1. Comparison of mollusk species found at Tubul, Guafo and Guamblín.

	Tubul	Guafo	Guamblín
Bivalvia			
Ennucula grayi	×	? (*barrosi*)	
Tindariopsis sulculata	×	×	
Malletia chilensis	×		? (sp.)
Mytilus sp.	×		
Zygochlamys patagonica	×	? (cf. *hupeanus*)	× (*tenuicostatus*)
Lucinoma sp.		×	
Cyclocardia velutinus	×	× (*volckmanni*)	× (*volckmanni*)
Macoma inornata	×	× (*tubulensis*)	
Darina solenoides	×		× (*Mactra* sp.)
Ensis macha	×	× (sp.)	
Retrotapes exalbidus	×	× (*araucana*)	× (*araucana*)
Pandora cistula	×		× (sp.)
Panopea chiloensis		×	
Gastropoda			
Epitonium magellanicus	×	? (*biroi*)	? (*biroi*)
Turritella chilensis		×	
Euspira guamblinensis	×	×	×
Echinophoria sp.		× (*Semicassis*)	
Fusitriton magellanicus	×		
Sassia leucostomoides	×	×	
Cymatium remotum			×
Trophon geversianus	×	? (*covacevichi*)	? (sp.)
Trophon parcus		×	
"*Xymenopsis*" cf. "*X.*" *dispar*	×	? (*huilliche*)	
Xymenopsis hero			×
Chorus giganteus	×		
Chorus doliaris		×	
Nassarius taeniolatus	×		
Nassarius gayi			×
Phos chilensis		×	
Penion spp		×	
Adelomelon ancilla	×	? (*reconditus*)	
Bela paesleri	×		
Hindsiclava ignorata			×
Cryptogemma senex			×
Gemmula subaequalis		×	
Scaphander interruptus	×	? (*cosmophilus*)	? (*cosmophilus*)
Scaphopoda			
Dentalium sp.	×	? (sp	

independent of water temperature is responsible for these widely separated species triplets today in contrast to their common occurrence during the early Pleistocene.

ACKNOWLEDGMENTS

First of all we express our gratitude to Profesor Lajos Biró-Bagóczky (1929–1993) who, together with others, assembled this collection during more than 15 years. Arturo Quinzio (Departamento Ciencias de la Tierra, Universidad de Concepción, Chile) made this work possible by giving access to this collection. Klaus Bandel (Geologisch-Paläontologisches Institut, Universität Hamburg, Germany) is thanked for discussion on the Tubul Formation and fauna. Daniel Melnick (GFZ Potsdam) helped with the DEM map for the distribution figure. Comments and suggestions by Tom DeVries (Burton, USA) improved the manuscript. Work of SNN was supported financially by Deutsche Forschungsgemeinschaft grant Ni 699/4-1 and 4-2.

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Radula morphology in veined rapa whelks, *Rapana venosa* (Valenciennes, 1846) (Gastropoda: Muricidae) from Chesapeake Bay, USA

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ABSTRACT

Radula length, width, number of transverse rows of teeth, and rachidian tooth dimensions (central cusp height, central cusp base width, and rachidian tooth base width) were examined in relation to leined rapa whelk shell length. Radula length and width increase linearly with whelk shell length. The number of transverse rows of radular teeth increase with whelk shell length. Within an individual, central cusp height of the rachidian tooth increases with increasing distance from the anterior of the radula. Central cusp height of the rachidian tooth, an indicator of tooth wear or use, was least for teeth in rows 1 and 11. Teeth in radular row 21 appear to be in a transition zone from high to low wear or use. Within a radula and within a size class, the ratio of central cusp base width to rachidian tooth base width does not change. Central cusp base width, central cusp height and rachidian tooth base width were significantly smaller in females than in males indicating sexual dimorphism in rachidian tooth shape for rapa whelks. Patterns of wear as indicated by central cusp base width to central cusp height ratio values were not significantly different between sexes and may serve as an indication that feeding strategies and/or prey may be similar between animals of different sex but similar size.

Additional Keywords: Neogastropoda, rachidian teeth, allometry, ontogeny

INTRODUCTION

The radula is a chitinous ribbon-like series of nearly colorless transverse tooth rows resting atop the radula membrane (Wu, 1965; Radwin and Wells, 1968). Muricid gastropods use the anterior teeth when drilling holes in bivalve prey (Carriker, 1961, 1981; Fujioka, 1985). As anterior teeth are worn down, they are replaced by younger teeth that are formed in the radular sac and gradually moved forward along the radula (Isarankura and Runham, 1968; Carriker, 1981). Muricid radulae have between 100 and 500 transverse rows of teeth (e.g., Carriker, 1961; Radwin and Wells, 1968; Fujioka, 1985). Each transverse row of teeth consists of a central rachidian (R) tooth and two slender marginal teeth (M) in the tooth formation M + R + M (Carriker, 1969). The central rachidian tooth in each transverse row is responsible for most of the rasping and physical shell removal during drilling while the marginal teeth synchronously tear flesh from prey (Carriker, 1969; Carriker et al., 1974; Krutak, 1977). Thus, the rachidian teeth show more wear, or reduction in size with use, than marginal teeth found in the same transverse rows (Carriker et al., 1974). This trend is particularly evident at the anterior end of the radula where the rachidian cusps in the most anterior row(s) may be completely removed by use (Carriker, 1969, 1974; Fujioka, 1985).

Veined rapa whelks (*Rapana venosa*, Valenciennes 1846, Muricidae) are predatory marine gastropods that, while originally native to Japanese and Korean waters (Tsi et al., 1983), have successfully invaded marine and estuarine habitats in the Black, Adriatic, Aegean, Mediterranean (Mann et al., 2004), and North Seas (Vink et al., 2005) as well as the Rio de la Plata (Pastorino et al., 2000) and Chesapeake Bay, USA (Harding and Mann, 1999). At the present time, the Chesapeake Bay rapa whelk population is the only known population of rapa whelks in North America.

Rapa whelks provide an unusual opportunity to investigate allometric changes in radula morphology across a wide size range of individuals because they reach terminal shell lengths in excess of 170 mm (Wu, 1988; Harding and Mann, 2005). Like other muricids (Paine, 1966), rapa whelks experience ontogenetic shifts in diet (Harding and Mann, 2001) as well as predation strategy and resulting predation signatures in prey valves (Harding et al., 2007). Small (< 35 mm shell length) rapa whelks drill their prey (Harding and Mann, 2001; Harding et al., 2007) including barnacles

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(*Balanus* sp., *Chthamalus* sp.), mussels (*Mytilus* sp., *Geukensia demissa*), soft shell clams (*Mya arenaria*), and oysters (*Crassostrea virginica*). At shell lengths above 35 mm, rapa whelks eat larger bivalves (Harding and Mann, 2001) including oysters and northern quahogs (*Mercenaria mercenaria*) and typically either edge bore their prey or leave no signatures (Morton, 1994; Harding et al., 2007).

We quantitatively describe radula and rachidian tooth morphology for a size range of rapa whelks from Chesapeake Bay, USA. Rachidian teeth in *Rapana* have a large central cusp flanked by two smaller cusps (Arakawa, 1964; Wu, 1965). Shell length, the maximum dimension from the tip of the spire to the bottom of the siphonal canal, is used as the metric of whelk size. Shell length does not fluctuate with season or other factors. Relationships between shell length and radula dimensions are quantitatively described for male and female rapa whelks. Within each radula, rachidian tooth morphology is described along the length of the radula by measuring ratios of rachidian tooth central cusp base width to central cusp height and central cusp base width to rachidian tooth base width. The resulting ratios are compared between teeth along the length of an individual radula and across radulae from male and female whelks as well as from a size range of Chesapeake Bay rapa whelks.

MATERIALS AND METHODS

Rapa whelks with shell lengths (SL) in excess of 70 mm were obtained from the lower Chesapeake Bay, USA as donations to the Virginia Institute of Marine Science (VIMS) rapa whelk bounty program. Rapa whelks less than 70 mm SL were cultured at VIMS, Gloucester Point, Virginia to supplement the lower SL range of rapa whelks because individuals less than 70 mm SL were not available through the bounty program.

At the time of whelk collection, SL was measured in mm and whelks were assigned to shell length classes that were established to evenly categorize the potential SL range (1–180 mm SL). Petite, small, medium, and large classifications corresponded to whelk SL ranges of less than 45 mm, 45.1–90 mm, 90.1–135 mm, and 135.1–180 mm, respectively.

Whelks were frozen after collection and thawed to facilitate dissection and removal of radulae. Whelks were sexed during dissection and distinguished as male or female on the basis of penis length and gonad color after Mann et al. (2006). For the purposes of discussion herein, true females (penis length = 0 mm, bright yellow gonad) and imposex females (penis length <20 mm, bright yellow gonad) are grouped together per Mann et al. (2006) Typically, radulae were dissected out of the whelk proboscis. However, two control radulae were removed by soaking the proboscis for 24 hours in 10% sodium hydroxide to ensure that dissection removed the entire radula intact. Only intact radulae were used in this study

After removal from whelks, images of the complete radula were taken using a digital camera mounted on a dissecting microscope for measurement of total radula length, total anterior to posterior distance (mm) and radula width, the maximum lateral distance across the bases of the marginal and rachidian teeth at the first transverse row of teeth (Figure 1). The odontophore was removed and then the rachidian teeth were systematically removed from every 10th transverse tooth row (e.g., Row 1, 11, 21 etc.) along the radulae moving from anterior to posterior (Figures 2 and 3). Tooth rows were removed with a size 10 scalpel blade for larger individuals, and with sharpened needles for cultured individuals less than 66 mm SL.

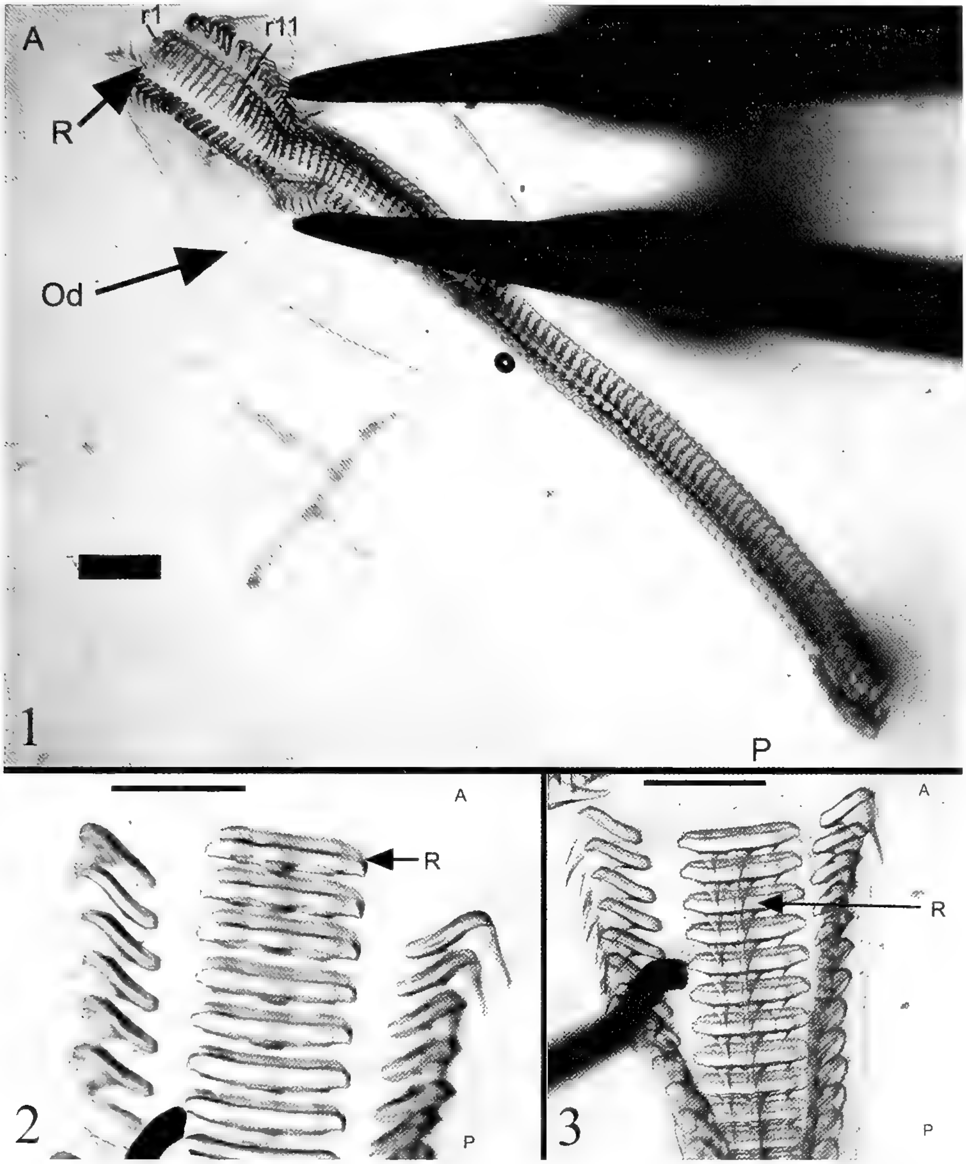
Digital images were taken of each individual rachidian tooth after removal with the tooth positioned convex side down. Typical magnification of individual teeth used for digital images ranged from 50× for whelks with SL greater than 147 mm to 90× for whelks less than 45–50 mm SL. Measurements (mm, Figure 4) of the rachidian tooth central cusp base width (L1), maximum central cusp height (L2) measured from the tip of the central cusp to the midpoint of L1, and the maximum rachidian tooth base width (L3) were made on the resulting images. The terminology used to describe tooth morphology follows that of Kool (1993).

Data Analyses: Significance levels for all statistical tests were set at alpha = 0.05 *a priori*. Fisher's multiple comparison tests were used for *post hoc* comparisons when appropriate.

Radula Allometry and Gross Morphology: Linear and power regression models were used to describe relationships within sexes between rapa whelk shell length and radula length, radula width, and number of rows of transverse teeth per radula. The relationship between radula length and both radula width and the number of transverse rows of teeth within radulae from males and females were also examined with both linear and power regressions. The slopes of all morphological regressions were compared between sexes with t tests (per Zar, 1996) on raw data or on logarithm transformed data if the power model was deemed more appropriate than the linear model.

Rachidian Tooth Dimensions: The relationship between central cusp base width (L1, Figure 4) and size class of the whelk from which it came was evaluated with a three-way ANOVA (whelk size class × tooth row × sex) with the response being the maximum base width of the rachidian tooth. These data satisfied assumptions of homogeneity of variance after the logarithm transformation was applied but not normality.

The relationship between rachidian tooth central cusp height (L2, Figure 4), the size class of the whelk from which it came, and the tooth row was evaluated with a three factor ANOVA (whelk size class × tooth row × sex). These data satisfied neither the assumption of normality nor homogeneity of variance regardless of the



Figures 1–3. Radula of veined rapa whelk. **1.** Radula from an 84.2 mm shell length (SL) whelk showing general morphological features and orientation. **2.** A rachidian tooth from row 1 of the radula from a 134 mm SL whelk showing wear. **3.** An unworn rachidian tooth from row 41 from a 122 mm SL whelk. Scale bar = 1 mm. Abbreviations: **r** = row number; **R** = rachidian; **Od** = odontophore; **A** = anterior; **P** = posterior.

transformation (logarithm, natural logarithm, square root, arcsine).

The relationship between rachidian tooth base width (L3, Figure 4), row number, sex, and size class of the whelk from which it came was evaluated with a three-way ANOVA (whelk size class × tooth row × sex). These data satisfied the assumption of homogeneity of variance without transformation but did not satisfy the assumption of normality regardless of the transformation (logarithm, natural logarithm, square root, arcsine) and were analyzed without transformation.

The ratio of rachidian tooth central cusp base width (L1) to central cusp tooth height (L2) was calculated for each rachidian tooth. Using a ratio that compares base width to tooth height is appropriate in a structure where both the base width and tooth height change along the length of the structure with ontogeny. Not only does the ratio allow for scaling when comparing individual teeth along the radula length, but it can also be used as an index of wear because width does not change with use. In this case a central cusp base width: central cusp tooth height ratio >1 is indicative of wear. The first 81 rows were chosen for analysis because every radula dissected had at least 81 rows. These data satisfied neither the assumption of homogeneity of variance nor normality regardless of the transformation (logarithm, natural

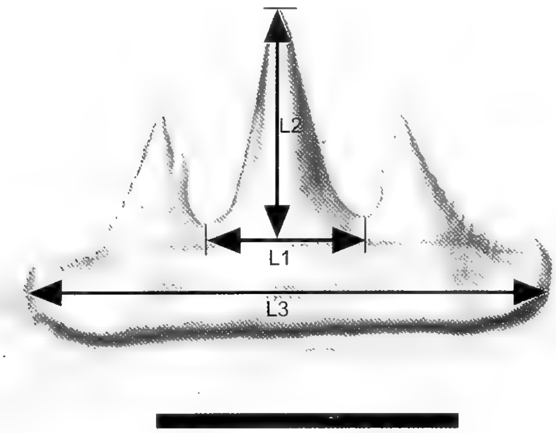


Figure 4. Veined rapa whelk rachidian tooth with the measurements made in this study identified: rachidian tooth central cusp base width (L1), rachidian tooth central cusp height (L2), and rachidian tooth base width (L3). Scale bar = 0.25 mm.

logarithm, square root, arcsine). A three-way ANOVA (whelk size class × tooth row number × sex) was used to evaluate the ratio of central cusp width to central cusp height (L1:L2).

The ratio of central cusp base width (L1) to rachidian tooth base width (L3) for each rachidian tooth was evaluated with a 3 way ANOVA (size class × row × sex) to describe potential changes in tooth shape with ontogeny. Data satisfied assumptions of homogeneity of variance without transformation but not normality (either with or without transformation, e.g., logarithm, natural logarithm, square root, arcsine). Changes in the L1:L3 ratio across whelk size classes reflect ontogenetic changes in tooth morphology that may be related to sexual dimorphism (Fujioka, 1982, 1984) and which may act to disperse relatively greater strike force during feeding in larger whelks.

RESULTS

Only radulae from whelks collected when water temperatures were above 11–12°C and feeding were used (Harding, unpublished data). All radulae examined were intact. Descriptive morphological data were collected from 39 rapa whelk radulae. These radulae were from rapa whelks with shell lengths between 20.2 mm and 174 mm (Table 1, Figure 5). Rapa whelk radula lengths ranged from 4.33 to 51.05 mm with corresponding radula widths of 0.23 to 2.67 mm and total number of transverse rows of teeth of 89 to 210, respectively. Radula length was an average of 21.4% (standard error = 0.61%) of shell length.

Radula Allometry and Gross Morphology: Regression coefficients for the fitted linear and power regression models used to describe relationships between rapa whelk shell length and radula morphology and between rapa whelk radula measurements are given in Table 2A.

The linear model is suggested as a better descriptor of the relationship between rapa whelk shell length (SL) and radula length (RL; Figure 6A) for both sexes since the coefficients of determination from both models are identical (Table 2A) and the linear model provides the simplest description of the data. The slope for the SL–RL relationship in males is significantly higher than that for females (t-test, Table 2B).

The power model more accurately described the relationships between rapa whelk SL and radula width (RW; Figure 6B) by predicting a radula width equal to 0 at a shell length equal to 0. The coefficient of determination for the linear model describing the relationship between shell length and the number of rows of radular teeth was higher (females = 0.63, males = 0.76, Table 2A) than that of the corresponding power model (females = 0.58, males = 0.69, Table 2A) for both sexes and the linear model predicted a positive number of rows of teeth at shell lengths of 0 mm (Figure 6C).

The relationship between radula length (RL) and radula width (RW) was described with a power model for both sexes (Table 2A, Figure 6D) which predicted a radula width of 0 at a radula length of 0 and had a higher coefficient of determination than the corresponding linear model (Table 2A). The linear model describing the relationship between radula length (RL) and number of transverse rows of teeth has a higher coefficient of determination than the corresponding power model

Table 1. Description of rapa whelks used in this study with basic statistics on radulae. Abbreviations used below are as follows: F = female, M = male, Avg = average for female and male whelks combined, SL = shell length, mm, SEM = standard error of the mean in parentheses, RL = radula length, mm, RW = radula width, mm; NRT = number of rows of teeth.

Whelk size class	# of Whelks (F/M)	Avg SL (SEM)	Avg RL (SEM)	Avg RW (SEM)	Avg NRT (SEM)	Avg RL/SL % (SEM)
Petite (<45 mm SL)	F = 5	25.64 (2.64)	5.28 (0.56)	0.48 (0.18)	106 (6.07)	20.59 (0.58)
	M = 5	34.72 (3.07)	7.62 (0.95)	0.71 (0.31)	122.20 (4.78)	21.72 (0.81)
Small (45.1–90 mm SL)	F = 5	70.38 (5.47)	15.93 (2.21)	0.97 (0.15)	133.80 (5.05)	22.38 (1.65)
	M = 6	69.13 (6.21)	17.63 (1.92)	1.22 (0.13)	126.67 (3.86)	25.56 (1.79)
Medium (90.1–135 mm SL)	F = 4	104.75 (5.07)	22.32 (2.52)	1.47 (0.03)	137 (12.71)	21.37 (2.53)
	M = 5	120.2 (5.3)	29.85 (1.58)	2.04 (0.10)	149.2 (7.19)	25 (1.51)
Large (135.1–180 mm SL)	F = 2	153 (10.0)	35.7 (3.2)	1.99 (0.24)	177.5 (16.5)	23.3 (0.57)
	M = 7	153.71 (4.47)	41.12 (2.23)	2.22 (0.10)	182.29 (6.38)	26.76 (1.21)

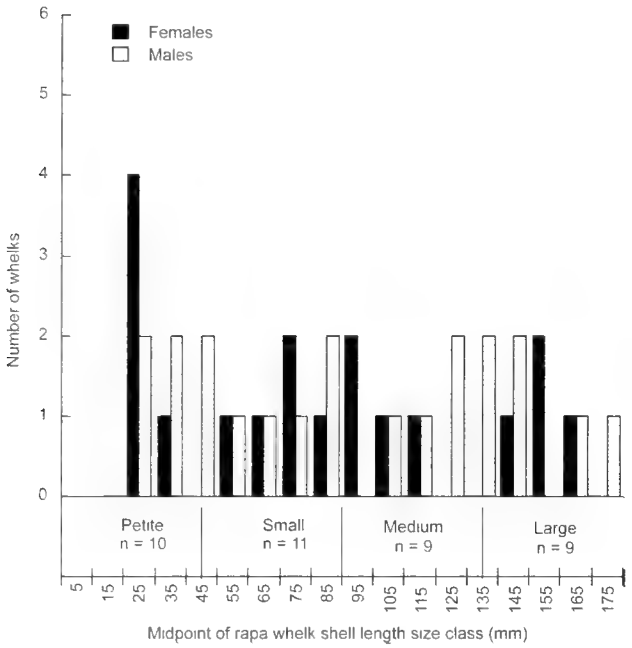


Figure 5. Shell length (mm) frequency distribution for the 39 veined rapa whelks whose radulae were examined in this study.

(females = 0.78 vs. 0.71, males = 0.81 vs. 0.72, Table 2) and predicts a positive number of tooth rows at radula lengths of 0 mm (Figure 6E).

Rachidian Tooth Dimensions: Rachidian tooth central cusp base width (L1, mm; Figure 4) increased significantly with increasing whelk size class (Table 3, Figures 7A and 7D). There were no significant differences in central cusp base width observed between rows within a size class for the 81 rows of teeth that were examined. Central cusp base width was significantly larger in males than in females (Fisher's test, Table 3). Differences between male and female central cusp base width were particularly evident in the medium and large size classes (Figure 7A and 7D).

The height of the rachidian tooth central cusp (L2, mm) varied significantly with size class, row number, and sex (ANOVA, Table 3, Figures 7B and 7E). In general, larger whelks have larger central cusp heights in rows 31 through 81 than whelks of other size classes. Within all size classes and both sexes, central cusp heights from rows 1 and 11 are significantly less than in rows 31 through 81 (ANOVA, Table 3, Figures 7B and 7E). Central cusp heights from rows 1, 11 and 21 in large whelks are significantly different from central cusp heights in petite whelks but similar to cusp heights observed in rows 1 and 21 for medium whelks and row 11 for small whelks (ANOVA, Table 3, Figures 7B and 7E). Female whelks have significantly lower L2 values than male whelks (Fisher's test, Table 3, Figures 7B and 7E).

Rachidian tooth base width (L3, mm) increases significantly with increasing whelk size class (ANOVA,

Table 2A. Summary of regression statistics used to describe rapa whelk radula morphology and wear patterns. The linear model equation was $y = (a * x) + b$. The equation used for the power model was $y = a X^{b}$. Abbreviations used below are as follows: coef = coefficient; SE = standard error, vs. = versus; SL = shell length, mm; RL = radula length, mm; RW = radula width, mm; NRT = number of rows of teeth.

		Females					Males				
Relationship	Model	R^2	Coef a (SE)	Coef b (SE)	F Statistic	p Value Regression	R^2	Coef a (SE)	Coef b (SE)	F Statistic	p Value Regression
SL vs RL	Linear	0.93	0.23 (0.01)	-0.87 (1.47)	186.32	<0.01	0.93	0.27 (0.02)	1.60 (1.80)	273.30	<0.01
	Power	0.93	0.16 (0.08)	1.07 (0.10)	188.72	<0.01	0.93	0.18 (0.08)	1.08 (0.09)	273.17	<0.01
SL vs RW	Linear	0.82	0.01 (0.001)	0.16 (0.13)	63.30	<0.01	0.77	0.01 (0.001)	0.31 (0.17)	69.52	<0.01
	Power	0.81	0.03 (0.01)	0.86 (0.13)	61.29	<0.01	0.78	0.05 (0.03)	0.75 (0.11)	73.75	<0.01
SL vs NRT	Linear	0.63	94.01 (8.73)	0.50 (0.10)	24.20	<0.01	0.76	97.08 (6.87)	0.51 (0.06)	66.41	<0.01
	Power	0.58	47.44 (11.78)	0.24 (0.06)	19.38	<0.01	0.69	40.38 (8.28)	0.29 (0.04)	46.10	<0.01
RL vs. RW	Linear	0.81	0.24 (0.13)	0.05 (0.01)	59.46	<0.01	0.77	0.43 (0.16)	0.05 (0.01)	69.7	<0.01
	Power	0.80	0.13 (0.04)	0.77 (0.12)	57.37	<0.01	0.79	0.19 (0.06)	0.67 (0.10)	78.17	<0.01
RL vs NRT	Linear	0.78	93.28 (6.29)	2.29 (0.32)	50.66	<0.01	0.81	100.17 (5.58)	1.87 (0.20)	92.44	<0.01
	Power	0.71	67.26 (8.59)	0.25 (0.04)	34.28	<0.01	0.72	65.23 (8.09)	0.26 (0.03)	52.76	<0.01

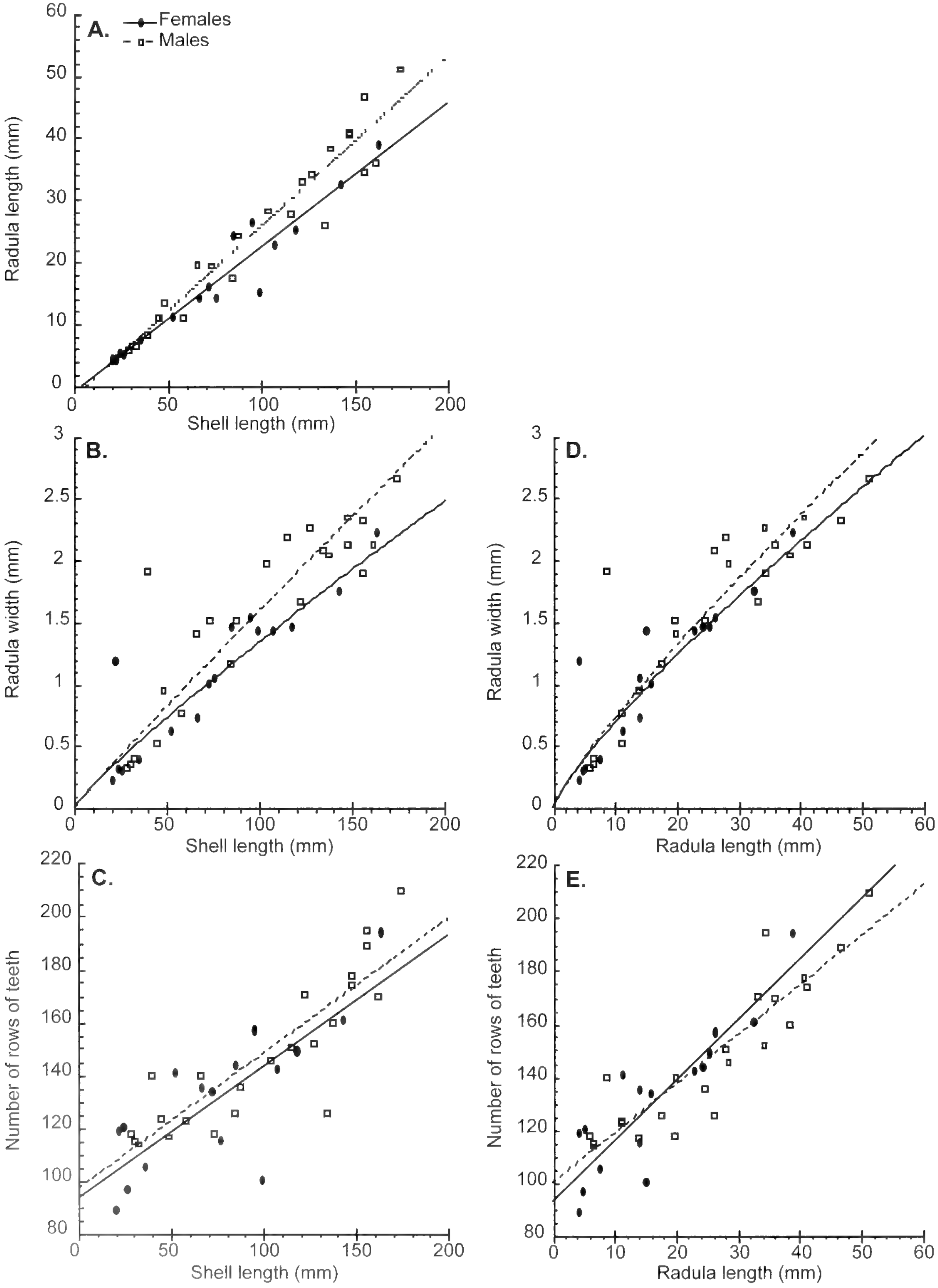

A.
Females
Males
Radula length (mm)
Shell length (mm)
0
10
20
30
40
50
60
0
50
100
150
200
B.
Radula width (mm)
Shell length (mm)
0
0.5
1
1.5
2
2.5
3
D.
Radula width (mm)
Radula length (mm)
0
10
20
30
40
50
60
C.
Number of rows of teeth
Shell length (mm)
80
100
120
140
160
180
200
220
E.
Number of rows of teeth
Radula length (mm)

Table 2B. Summary of t-tests comparing regression equations for female and male whelks given in Table 2A that are recommended for descriptions of these relationships. T-tests were performed for the power model using logarithm transformed data. Abbreviations are the same as those used in Table 2B above.

Relationship	Comparison	Model	p value
SL vs. RL	Female vs. Male	Linear	$<0.05^*$
SL vs. RW	Female vs. Male	Power	>0.05
SL vs. NRT	Female vs. Male	Linear	>0.05
RL vs. RW	Female vs. Male	Power	>0.05
RL vs. NRT	Female vs. Male	Linear	>0.05

Table 3, Figures 7C and 7F). However, no differences were observed in rachidian tooth base widths between radular tooth rows within a whelk size class and within a sex (ANOVA, Table 3, Figures 7C and 7F). Rachidian tooth base width was significantly larger in male whelks than in female whelks and this trend is particularly evident in the medium and large size classes (Table 3, Figures 7C and 7F).

Large whelks had significantly higher ratios of rachidian central cusp base width (L1) to central cusp height (L2) than all other whelk size classes (ANOVA, Table 3, Figure 8). The first row of teeth in the radulae had significantly higher L1:L2 ratios than all other rows (ANOVA, Table 3, Figure 8). The eleventh row of teeth also had an L1:L2 ratio that was significantly higher than that observed in rows 21–81 (ANOVA, Table 3, Figure 8). Since central cusp base to height (L1:L2) ratios >1 are indicative of tooth wear, the anterior 1–11 rows of teeth are more worn than newer teeth occurring in rows 21 and higher. Within each size class and sex, a wide range of L1:L2 values was observed for row 1 and/or row 11 (Figure 8). This variability was the result of one or two individual whelks per size class having very low central cusp heights (extreme wear) in row 1 or row 11, the rows of teeth that are actively used in feeding. Patterns of wear as indicated by L1:L2 ratio values were not significantly different between sexes (Table 3, Figure 8).

The ratio of central cusp base width to rachidian base width (L1:L3) was significantly affected by size class and sex (ANOVA, Table 3, Figure 9). Within a size class and within a sex, the ratio of central cusp base width to rachidian tooth width did not change significantly with row number. Male whelks had greater L1:L3 ratios than female whelks (Fisher's test, Table 3, Figure 9).

DISCUSSION

Radula length, radula width, and number of rows of teeth in the radula increase with increasing rapa whelk shell length. Ontogenetic increases in radula length and the number of rows of teeth with shell length have also been documented for other muricid species (e.g., *Stramonita floridana*, Radwin and Wells, 1968 (as *Thais floridana*); *Cronia margariticola* and *Morula musiva*, Fujioka, 1984; *Thais bronni* and *T. clavigera*, Fujioka, 1985; *Nucella lapillus*, Kool, 1993).

The relationship between rachidian tooth base width and central cusp base width also changes with ontogeny but does not change in relation to the anterior-posterior location on the radula. That is, within an individual and within a size class, rachidian teeth examined from rows 1 through 81 display similar scaling of central cusp base width to rachidian tooth base width. Rachidian teeth in female rapa whelks tend to have smaller central cusp base width as well as tooth base widths when compared to male whelks within the same size class. Fujioka (1982, 1984) describes similar ontogenetic changes in rachidian tooth shape including an increase in central cusp base width for *Cronia margariticola*, *Morula musiva*, and *Drupella* sp. in relation to sexual dimorphism. The observed ontogenetic changes in rachidian tooth shape may reflect morphological shifts designed to accommodate greater rachidian tooth strike force resulting from the scaling of the buccal complex at increased whelk sizes. Presumably there is an ontogenetic scaling relationship in effect to optimize the force provided by the buccal mass musculature and minimize the damage to rachidian teeth through use that is reflected in the shape of the tooth.

Rachidian tooth wear, as indicated by the ratio of central cusp width (L1) to central cusp height (L2), decreases with increasing distance from the anterior (oldest) end of the radula. Rachidian teeth in the first 11 rows of the radula have central cusp heights that are less than central cusp heights in rows 21 through 81 in all size classes. Carriker et al. (1974) describe rachidian cusps that have been worn off leaving only the tooth base in the anterior rows of rachidian teeth of *Urosalpinx cinerea folleyensis*. In laboratory studies with *Thais bronni* and *T. clavigera*, Fujioka (1985) observed that rows of teeth worn by feeding occupy 5–15% of the total number of radular rows. The whelk *Acanthina spirata* uses approximately 8 to 20 teeth in each rasping stroke as these whelks feed on mussels (Hemingway, 1975). These data are consistent with our observations for rapa whelks, where at least the 1st and 11th rows of the radula were used, and the 21st row acted as a transition between the part of the radula the whelk was actively using to feed and the more posterior section that was unused.

The observed changes in rachidian tooth wear may reflect ontogenetic changes in predation strategy, diet, or possibly both. Differences in predation strategy are potentially reflected in the observed changes in

Figure 6. Relationships for female (n = 16) and male (n = 23) veined rapa whelks ranging from 20.2 to 174 mm SL between shell length (SL) and radula length (RL, A), SL and radula width (B), SL and the number of rows of teeth (C), RL and radula width (D and RL and number of rows of teeth (E) with fitted regressions (female = solid, male = dashed) that were used to describe the relationships. Linear regression models are plotted for panels A, C, and E. Power models are presented in panels B and D Regression equations and descriptive statistics are given in Table 2

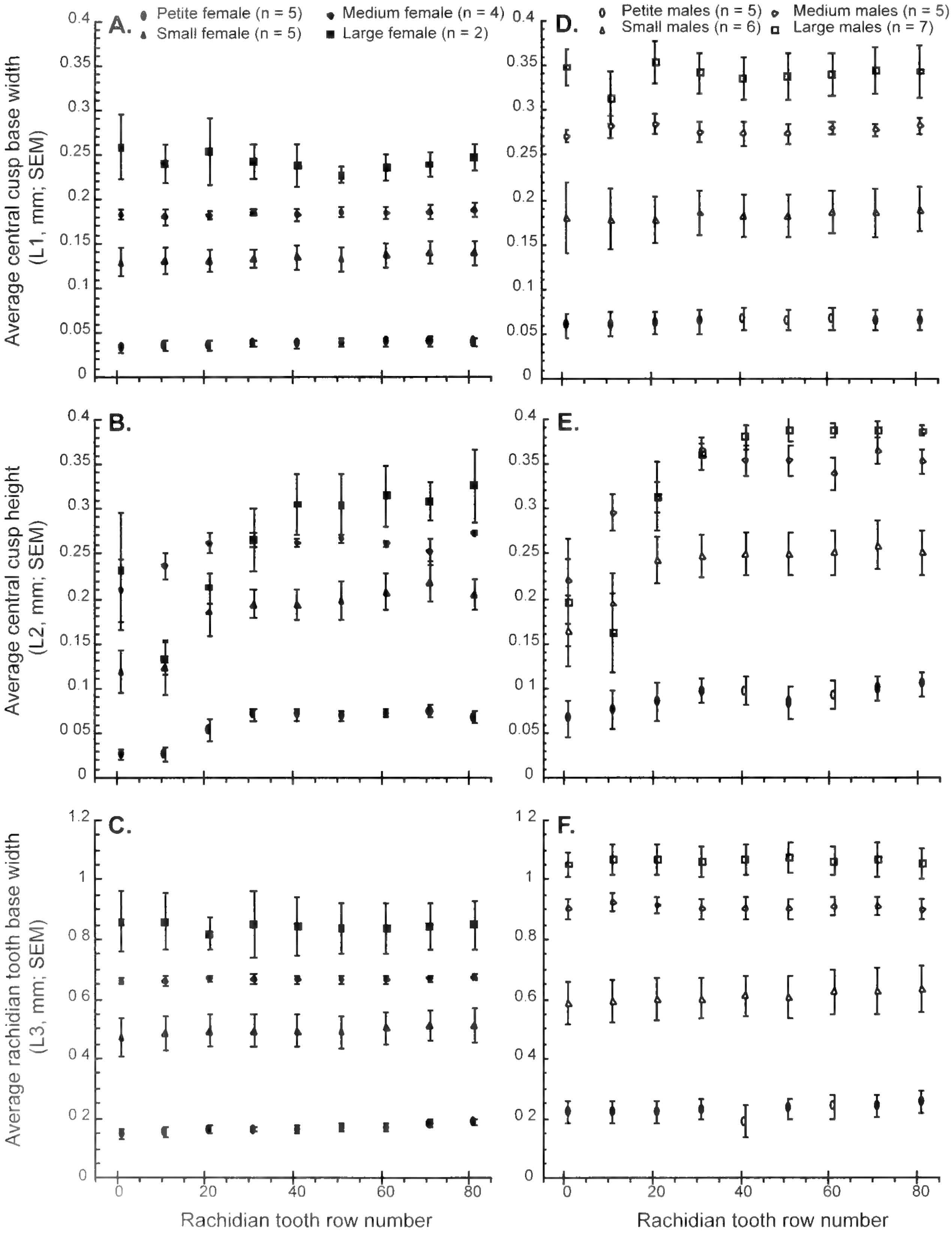


Figure 7. Graphs of rachidian tooth row number in relation to average central cusp width (L1) with error bars (standard error of the mean, SEM) for females (A) and males (D) from all size classes, average central cusp height (L2) with error bars (standard error of the mean, SEM) for females (B) and males (E) from all size classes, and average rachidian tooth base width (L3, SEM) for females (C) and males (F) from all size classes.

Table 3. Summary of ANOVA results comparing tooth morphology across whelk size classes and rows within the radulae. Asterisks indicate statistical significance at an alpha value of 0.05. Abbreviations used below are as follows: 1= petite size class, 2 = small size class, 3 = medium size class, 4 = large size class. NA = Not applicable. Refer to Figure 4 for a description of L1, L2, and L3.

Test	Response	Factors	p value	Fisher's test results
ANOVA	Central cusp base width (L1)	Size class	$<0.01^{*}$	4 > 3 > 2 >1
		Row	0.80	NA
		Sex	$<0.01^{*}$	Male > Female
ANOVA	Central cusp height (L2)	Size class	$<0.01^{*}$	4, 3 > 2 >1
		Row	$<0.01^{*}$	1, 11 < 31–81
		Sex	$<0.01^{*}$	Male > Female
ANOVA	Rachidian tooth base width (L3)	Size class	$<0.01^{*}$	4 > 3 > 2 > 1
		Row	0.99	NA
		Sex	$<0.01^{*}$	Male > Female
ANOVA	Wear (ratio L1/L2)	Size class	0.02^{*}	4 > 3, 2, 4 = 1
		Row	$<0.01^{*}$	1 > 21–81; 11> 31–81
		Sex	0.16	NA
ANOVA	Shape (ratio L1/L3)	Size class	$<0.01^{*}$	4 > 2, 3 > 1
		Row	0.90	NA
		Sex	$<0.01^{*}$	Male > Female

rachidian tooth wear with ontogeny because the rachidian teeth are actively used during shell drilling. Methods of feeding which require penetration of prey valve shells with the radula (e.g., drilling) will leave more wear on the rachidian teeth than non-drilling methods of attack. Therefore, examination of rachidian tooth wear along the radula and differences in wear depending on size class may give an indication as to transitions in feeding strategies of different size classes of rapa whelks (Figure 8). High levels of rachidian tooth wear (L1:L2 ratio >1) in rows 1 and 11 were associated with the petite and large size classes (Figure 8A). The smallest whelks (<45 mm SL) typically leave drill holes (i.e., wall bores) in the valves of their prey (Harding et al., 2007). Although large (>135 mm SL) rapa whelks do not always leave predation signatures in prey valves, edge bore signatures are left instead of drill holes (Harding, Kingsley-Smith, Mann, unpublished data) when signatures are present. The observed L1:L2 values for rows 1 and 11 in the large size class are driven by one male (Figure 8B). It is possible that this individual had been using its radula to penetrate prey shells and that the other large whelks had not. Since the large whelks used herein were wild caught and had unknown feeding histories, we cannot say this with certainty. Relatively less wear (L1:L2 ratio <1.2) in row 11 was observed in rapa whelks with shell lengths of 45 to 135 mm (small and medium size classes) that do not typically drill their prey (Harding et al., 2007, Figure 8). Similar wear patterns (L1:L2 ratio) were observed for males and females and may serve as an indication that feeding strategies and/or prey may be similar between animals of different sex but similar size.

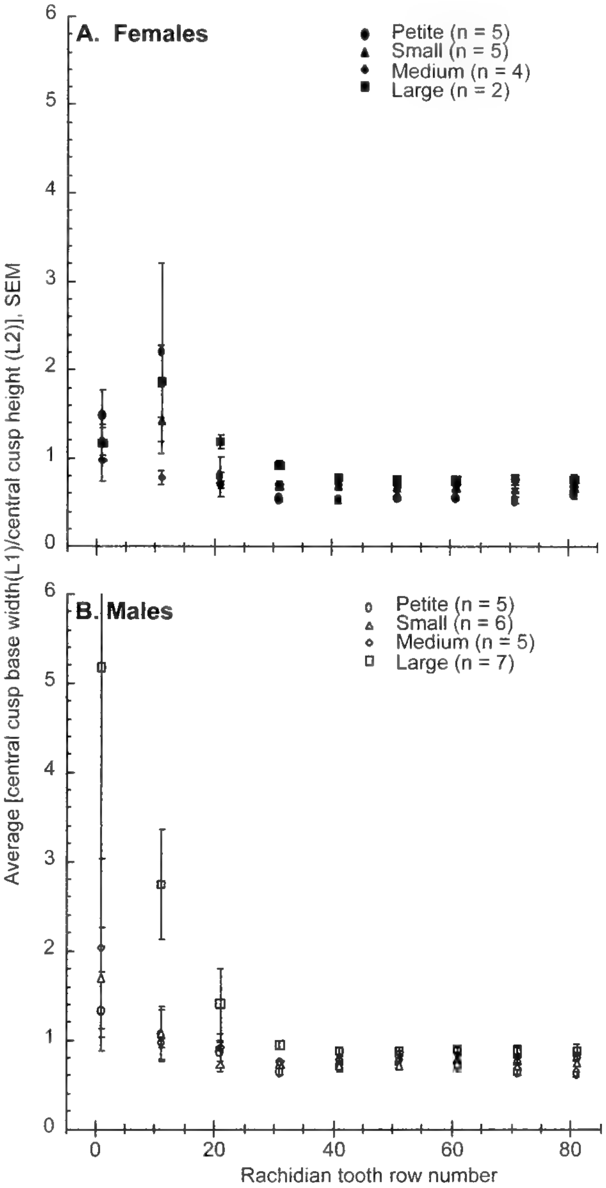


Figure 8. Rachidian tooth wear as indicated by the average ratio of rachidian tooth central cusp base width (L1) to central cusp height (L2) in relation to rachidian tooth row number for females (A) and males (B) from all size classes.

If a whelk is using the radula to penetrate the shell, the chemical composition of the prey shell may affect the level of wear observed on the rachidian teeth. Oyster and mussel shells have more calcite and are relatively softer than other bivalves with predominantly aragonite shells (Carter, 1980). Drilling through aragonite shells has the potential to cause more wear on rachidian teeth than shell penetration of calcite shells. Examination of the radulae from rapa whelks using drilling to consume a species-specific diet is a topic for future research that would provide data to address changes in radula wear with regard to prey shell hardness.

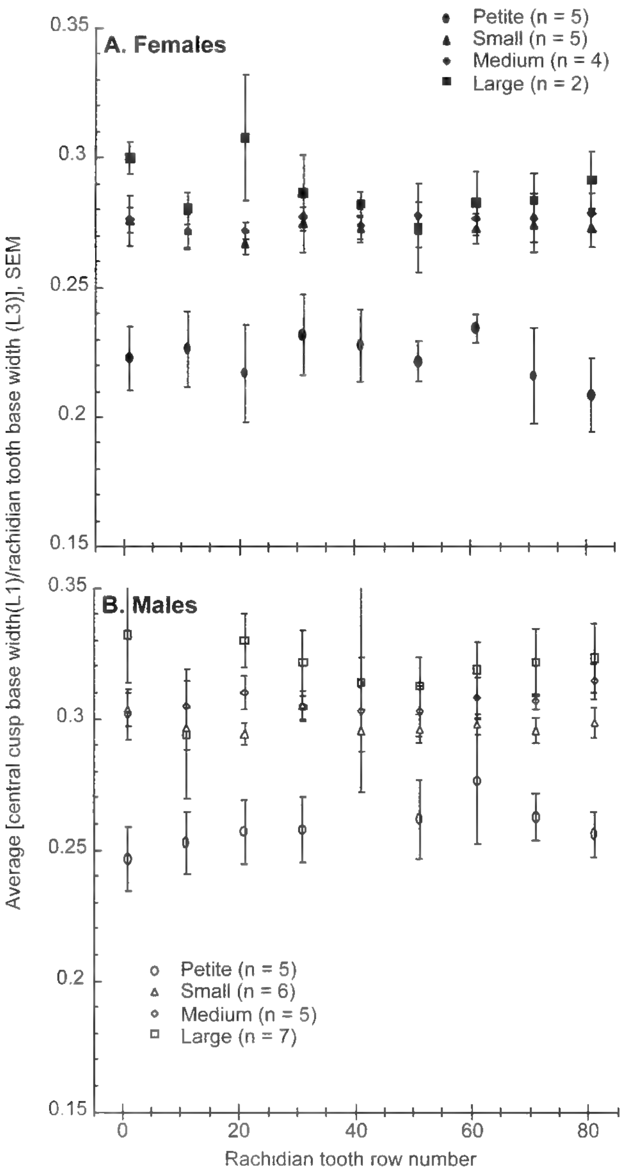


Figure 9. Average ratio of central cusp base width (L1) to rachidian tooth base width (L3, with standard error of the mean, SEM) by rachidian tooth row for females (A) and males (B) from all size classes.

ACKNOWLEDGMENTS

This manuscript is dedicated to the late Dr. Melbourne R. Carriker, whose passion for and detailed work with Muricids serves as both a standard of excellence and an inspiration. Thanks are extended to all local fishermen that have participated in the Virginia Institute of Marine Science rapa whelk bounty program since its inception in 1998. Melissa Southworth, Ethan Jestel, Catherine Ware, Erica Westcott, Steven Goodbred, David Kerstetter, Peter Kingsley-Smith, Amy Bohannon, Meredith Fagan, Meghan Harris, Rhonda Howlett, Rae Marie Johnson, Courtney Harris, Karen Capossella, John Hansen, and Matthew Robinson assisted with whelk collections from local fishermen. Drs. Greg Capelli, Randy Chambers, John Kraeuter, Ms. Melissa Southworth, and an anonymous reviewer provided valuable comments on earlier versions of this manuscript. This work was completed in partial fulfillment of the requirements for an undergraduate Honors degree (SMG) from the Department of Biology, College of William and Mary, Williamsburg, Virginia. This is contribution number 2928 from the Virginia Institute of Marine Science, Gloucester Point, Virginia.

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A new species of *Sphaerium* Scopoli, 1777, from southern Brazil (Bivalvia: Sphaeriidae)

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ABSTRACT

Sphaerium cambaraense new species is described based on samples collected in the beginning of the summer near the headwaters of Taquari River (Jacui River Basin) on the basaltic plateau of southern Brazil. This is the first record for the genus *Sphaerium* in Brazil and in South America outside the Andes. *Sphaerium cambaraense* is characterized by a relatively large and solid shell, a high triangular shell outline and a solid hinge plate. Compared with *Sphaerium forbesi* (Philippi, 1869), *S. cambaraense* has a more strongly triangular shell outline and beaks not prominent. *Sphaerium lauricochae* (Philippi, 1869), another similar species from Bolivia, Chile, and Peru, has a more rounded shell outline.

Additional Keywords: Freshwater, Rio Grande do Sul, South America

INTRODUCTION

According to Dreher-Mansur and Meier-Brook (2000), the family Sphaeriidae is represented by two subfamilies: Euperinae, including the genera *Eupera* Bourguignat, 1854, and *Byssanodonta* d'Orbigny, 1846; and Sphaeriinae with three genera, *Sphaerium* Scopoli, 1777, *Musculium* Link, 1807, and *Pisidium* Pfeiffer, 1821.

Four species of the genus *Sphaerium* are known from South America: *Sphaerium aequatoriale* Clessin, 1879, from Ecuador (Kuiper and Hinz, 1984); *S. forbesi* (Philippi, 1869) recorded from Peru and Bolivia (Haas, 1949), from Bolivia (Haas, 1955), from Colombia, Peru, Bolivian Andes (Kuiper and Hinz, 1984), and Chile (Ituarte, 1995); *S. lauricochae* (Philippi, 1869), from Peru, Bolivia and Chile (Kuiper and Hinz, 1984), and Chile (Ituarte, 1995); *S. titicacense* (Pilsbry, 1924), from Peru and Bolivia (Kuiper and Hinz, 1984). According to these authors, they are concentrated in the Central Andes from Ecuador to North Chile including high-altitude Bolivia, at 2000 to 4700 m altitude; varying in size between 3 and 12.5 mm. Haas (1949) reports *Sphaerium* (*S.*) *boliviense* (Sturany, 1900), from the highlands of Bolivia and from a lake in Junin, Peru. He examined also material of this species collected by Sioli in the regions of the rivers Maué-Açú and Tapajós, tributaries of the Amazon River, which constitutes the first record of *Sphaerium* for Brazil. According to Kuiper and Hinz (1984), *S. boliviense* is a junior synonym of *S. forbesi*.

The record of *Sphaerium observationis* by Mansur et al. (1991) for Mirim Lagoon in southern Brazil is a misidentification, as that species is not a *Sphaerium*. According to the revision by Ituarte (1995), *Pisidium observationis* Pilsbry, 1911, only occurs in the southern Argentina, not in Brazil.

Sphaerium cambaraense new species is the fifth *Sphaerium* species from South America and the first species of the genus described from southern Brazil, in the highlands near the Atlantic Ocean, a location geographically very distant from the Andes and Amazon River.

MATERIALS AND METHODS

Specimens were collected with a plastic sieve with mesh size of about 0.8 mm. Specimens were sorted from the sediment with fine feather tweezers; anesthetized in small vials containing water with menthol crystals, fixed in a 5% formalin solution for 24 hours, rinsed for 24 hours in tap water and preserved in 70% ethanol. Soft parts of specimens for scanning electron microscopy (SEM) were removed with tweezers, shells cleaned with a soft and fine brush and rinsed several times in distilled water. Dried shells were glued on stubs with light-silver glue (Porolon Equipment, Herts) or metallic adhesive tape (TO66 Silver tape 9 mm, Hert-Scotch), coated with gold, and observed either in a Cambridge Stereoscan 250 Mk2 or Philips scanning electron microscopes. Shell microstructure was studied by fracturing shells at the middle of the height, parallel to commarginal ridges. Terminology for shell microstructure follows Dyduch-Falniowska (1983) and Dreher-Mansur and Meier-Brook (2000).

Stomach nomenclature follows Purchon (1958, 1960). The shape indices, height index [I = H/L] and convexity index [Ci = W/H], were calculated according to the criteria followed by Ituarte (1996).

Abbreviations use in the text are: MACN, Museo Argentino de Ciencias Naturales, Buenos Aires; MCN, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre; MCP, Museu de Ciências e Tecnologia da Pontifícia Universidade Católica, Rio Grande do Sul, Porto Alegre, Brazil.

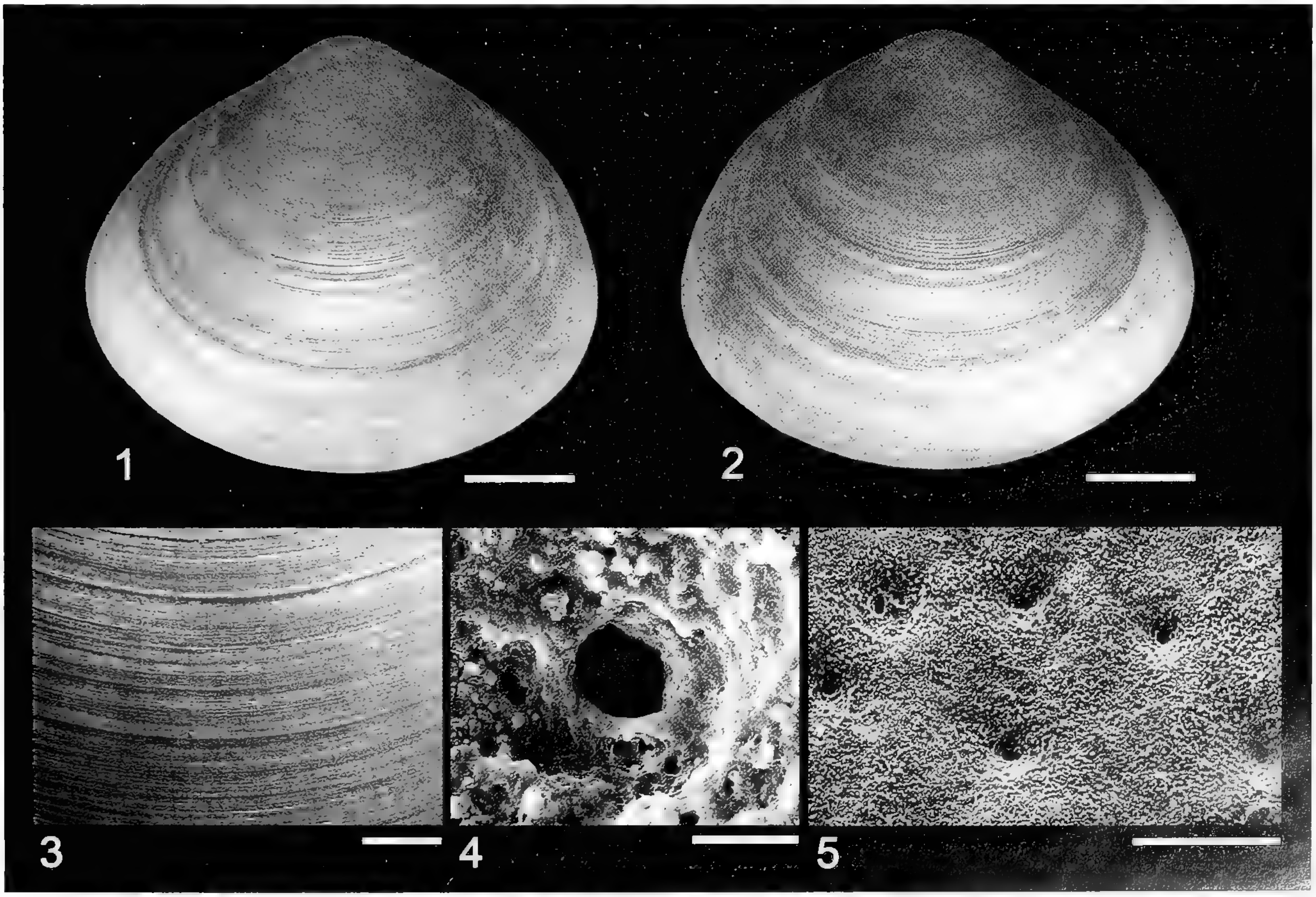
Genus *Sphaerium* Scopoli, 1777

Sphaerium cambaraense new species
(Figures 1–20)

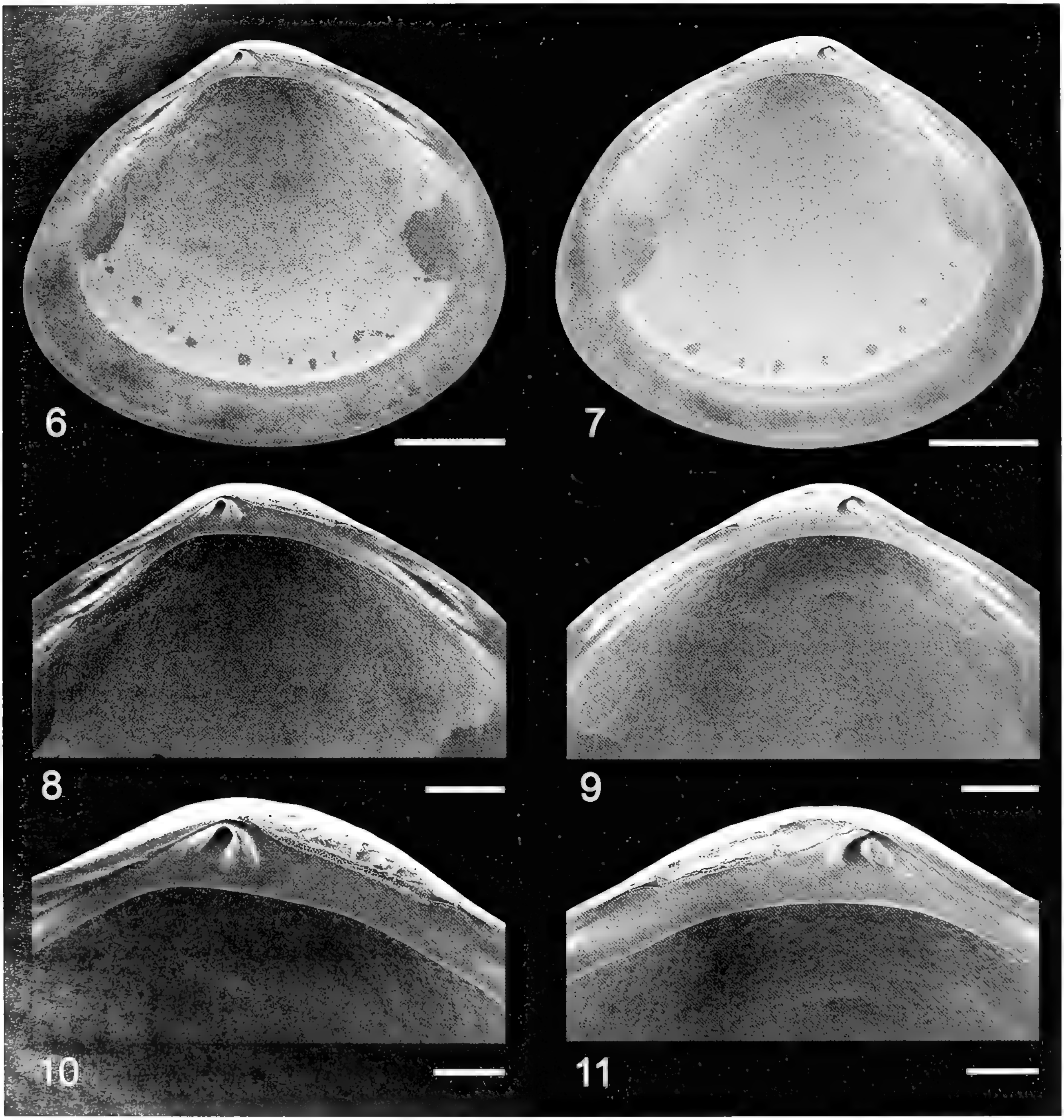
Diagnosis: Distinguished by the relatively large and solid shell with trapezoidal tending to triangular shell outline, low and wide beaks, subcentrally located, without marked nepionic cap, and broad and solid hinge plate.

Description: SHELL: Solid, relatively large (maximum observed L: 11.22 mm), slightly convex (Ci = 53±5). Shell outline high (I = 85±2), trapezoidal tending to triangular. Dorsal margin has pronounced curve. Anterior and posterior margins gradually descending and gently curved below middle of total height, without marked angle. Posterior end slightly truncated, oblique (Figures 1, 2). Ventral margin long and evenly curved. Shell surface silky, glossy, with very fine irregularly distributed radial lines, weaker on beaks and irregular commarginal, sometimes coarse, striae (12 or more per 0.5 mm in the middle of the shell (Figure 3). Outer shell surface light yellowish brown; pale brown at beaks, more ventrally grayish brown with complete or incomplete yellow concentric bands running from anterior to posterior margins; a large yellow band near ventral margin. Beaks without marked embryonic cap. Inner shell surface white, grayish at muscle scars. Beaks slightly prosogyrous, low and wide, slightly raised above dorsal margin, subcentrally located (Figures 1, 2, 6, 7).

Hinge plate strikingly curved, solid, broad, reaching 0.5 mm width in middle region in specimens of 11 mm length, slightly narrower at level of cardinal teeth. Hinge line arched, particularly below cardinal teeth (Figures 6–9). Cardinal teeth strong, close to dorsal margin. Right cardinal tooth, C3, short, strongly curved, posterior end enlarged in a grooved cup (Figure 10). Left cardinal teeth: outer cardinal tooth, C4, thin, strikingly oblique, located immediately behind C2, anterior end slightly overlapping



Figures 1–5. *Sphaerium cambaraense* new species. **1, 2.** Holotype MCP Mol. Outer view of left and right valves. **3.** Detail of outer shell surface. **4, 5.** Inner shell surface, detail of pores. Scale bars: 1, 2 = 4 mm; 3 = 400 µm; 4 = 4 µm; 5 = 40 µm



Figures 6–11. *Sphaerium cambaraense* new species. Paratype (MACN-In 37063). **6.** Inner view of right valve. **7.** Inner view of right valve. **8.** Hinge of right valve. **9.** Hinge of left valve. **10.** Detail of right cardinal tooth (C3) and ligament. **11.** Detail of left cardinal teeth (C2 and C4) and ligament. Scale bars 6, 7 = 2 mm; 8, 9 = 1 mm, 10, 11 = 500 μm

C2; inner cardinal tooth, C2, short, high, columnar, deeply arched into a V-shape (Figure 11). Right lateral teeth somewhat short, strong, with distal cusps (Figure 8); left lateral teeth relatively long, strong, and high (Figure 9). Ligament internal but exteriorly visible, slightly protruded in larger specimens (Figures 10, 11).

Shell Microstructure: Inner shell surface perforated by numerous pores (55/400 μm^2 to 13/160 μm^2) (Figures 4, 5) representing the opening of tubuli that cross entire calcareous part of shell (shown in part in Figure 12). Openings of pores on inner surface surrounded by a funnel-shaped depression and in mouth circled by a rim

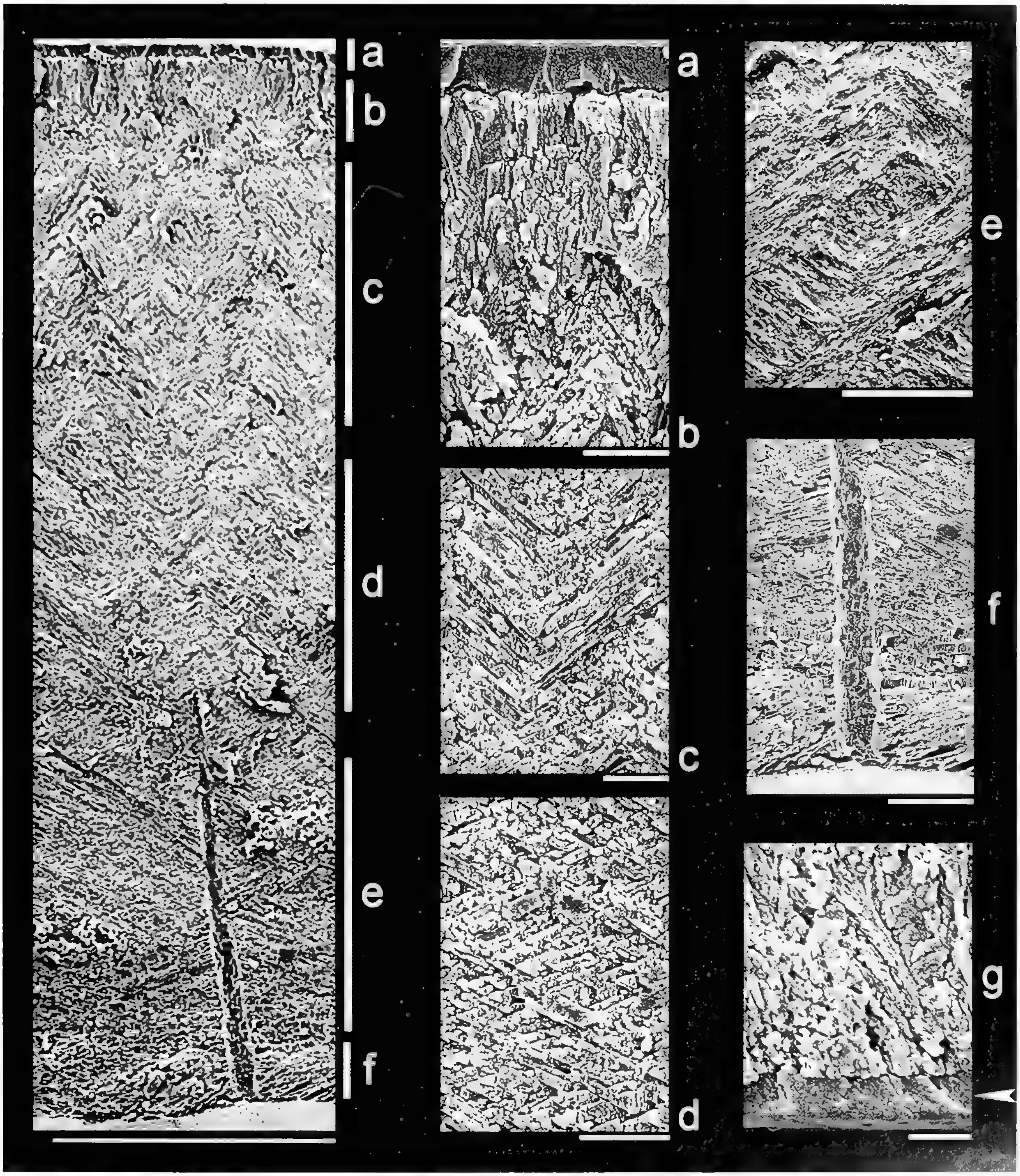
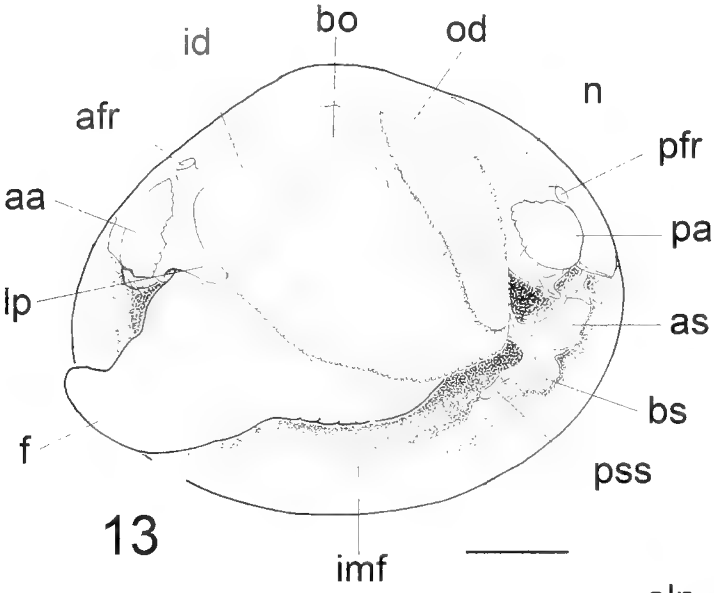


Figure 12. *Sphaerium cambaraense* new species. Shell microstructure from **a:** periostracum (top) to **f:** the endostracum (bottom Inserts **a–g** are details of: **a,** periostracum; **b,** granular layer; **c,** diagonal layer forming a composite prismatic structure; **d,** diagonal layer. crossed structure; **e,** diagonal layer forming a pseudo crossed lamellar structure; **f,** palisade structure; **g,** diagonal layer, and internal surface of the endostracum (arrow). Scale bars: 12 = 50 µm; inserts: a–d = 4 µm; e = 20 µm; f = 10 µm; g = 2 µm



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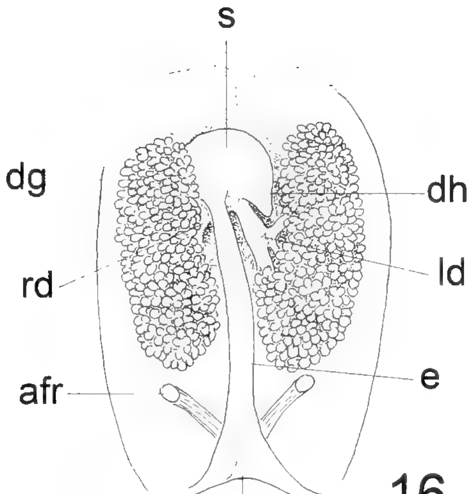

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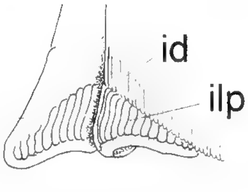

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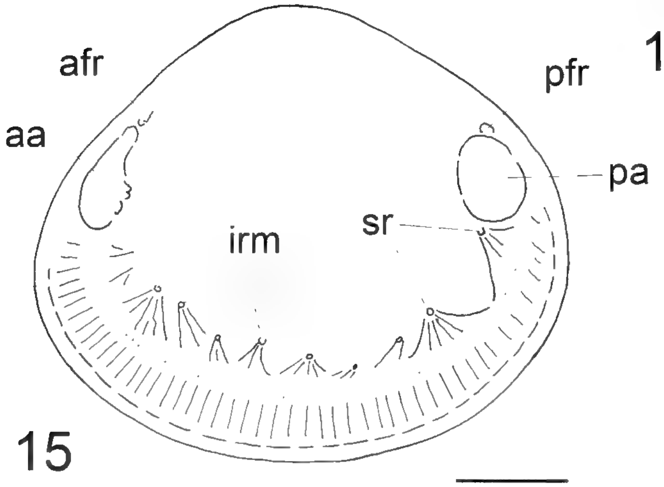

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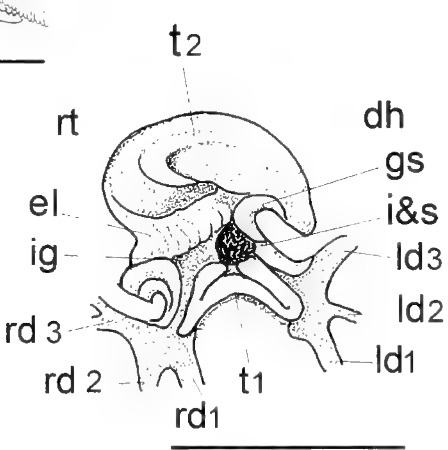

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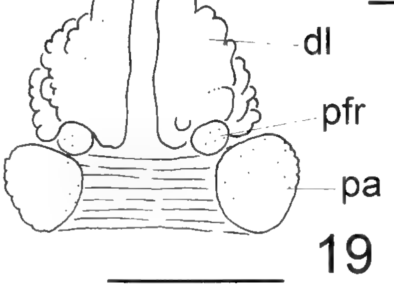

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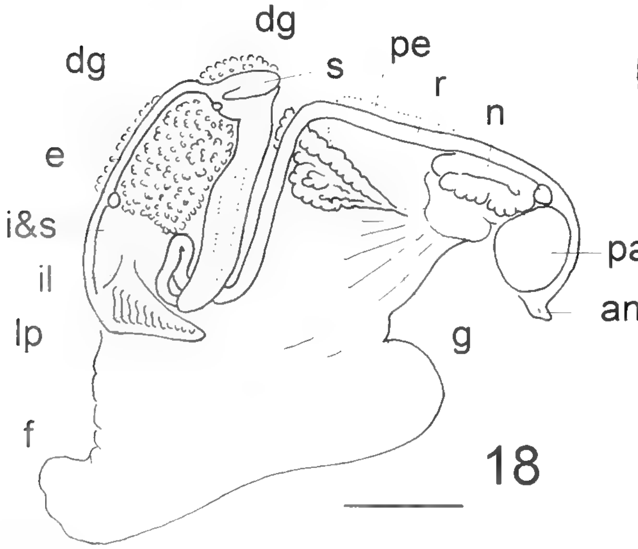

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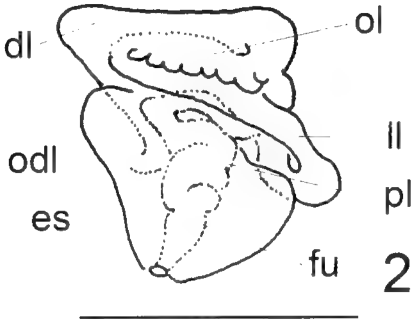

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(Figure 4). Shell relatively thick reaching 200 μm in central area (Figure 12). Shell structure consists of five layers: periostracum, granular layer, diagonal layer, palisade, diagonal layer, and endostracum. Below the 2 μm thick periostracum (Figure 12, **a**), a granular 10 μm thick layer appears (Figure 12, **b**); grains concentrated in some points irregularly and sparsely distributed, looking like cone-shaped bars arranged perpendicularly to shell surface. These change into irregularly and compactly arranged grains of different sizes. More internally, shell structure changes gradually into a diagonal layer (Figure 12, **c, d, e**), where three different patterns may be distinguished: first (about 50 μm thick), composite prismatic structure, showing vertical feather-like pattern (Figure 12, **c**); second (about 40 μm thick), occupies the central part of shell, gradually changing into a cross-lamellar structure (Figure 12, **d**); the third (approximately 60 μm), resembles a pseudo crossed-lamellar structure (Figure 12, **e**). Close to the inner shell surface there are one or two palisade layers, narrow (each about 1 μm thick) (Figure 12, **f**). The palisade structure is followed by a diagonal layer with lamellae oriented in one direction (Figure 12, **g**); below, a very narrow layer, the endostracum (1.0 to 1.5 μm thick) (Figure 12, arrow).

ANATOMY (FIGURES 13–20): Inner and outer demibranchs well-developed, outer smaller demibranch reaching half of height of inner demibranch (Figure 13). Brood sacs occupy anterodorsal part of inner demibranchs, embryos contained in sacs showed different developmental stages, denoting sequential brooding. Up to six developing embryos found in largest examined specimen (≥11 mm length). Largest, tertiary, brood sac contained two embryos (≥1 mm length) (Figure 13); secondary sac located under largest one, contained three or four small embryos. Primary sac attached lower on inner demibranch. (Specimens for this study were collected at the beginning of the Southern Hemisphere summer (January, 1994) and many of the specimens larger than 9 mm showed brood sacs.) Anal and branchial openings extended in diverging short siphons, nearly equal in size. Anal siphon wider at base and more stretched out (Figure 13). Two labial palps (Figure 13, 14) on each side of mouth, triangular-shaped in lateral view; opposite contacting walls with 12 small folds, tapering toward distal ends. Mantle musculature (Figure 15) with relatively short siphonal retractors; inner radial mantle muscles arranged in eight to nine bundles (Figure 15). Fan-shaped stomach (Figures 17, 18) bent to right side, laterally covered by digestive gland. Dorsal hood relatively short and left duct well developed. Stomach internally (Figure 17) shows very simplified structures on dorsal hood and right side such as short gastric shield under dorsal hood; minor typhlosole and rejecting tract beginning at right side after descending from dorsal hood; and an elevation slightly wrinkled between intestinal groove and rejection tract; anterior fold absent. Intestine opening associated to style sac in center of floor; major typhlosole arched in front with two expansions that end respectively at left and right duct openings, not penetrating in ducts, which allocates the stomach to Type IV; left and right duct openings well developed and ramified in three secondary ducts.

Intestine short and simple (Figure 18), anterior part associated to style sac, broad, descending straight to floor of visceral mass; mid-intestine strikingly stretched forming single loop; hindgut straight, ascending and bending toward rectum that ends into an anal papilla. Nephridia of closed type; dorsal and outer lobes fused, impossible to distinguish in dorsal view (Figures 19, 20); external wall of outer lobe ornamented with many small, rounded extrusions; nephridia in young specimens usually of open type and with separated lobes. Funnel relatively long and wide; proximal loop with smooth walls forming three ascending rings then run backward up to posterior adductor muscle, turning laterally in direction to lateral loop. Lateral loop straight, elongated, running along outer side and partially covered laterally by outer lobe. Excretory sac sub-triangular, rounded in front and relatively small. No valve at the entering of the distal loop into excretory sac.

Type Locality: Lajeado da Margarida (50°15.75′ W, 29°0.87′ S; 870–880 m altitude) on Camisa River, Antas River Basin, considered to be the headwaters of Taquari River, the main tributary of Jacuí River, South Atlantic Brazilian Basin.

Type Material: Holotype MCN 38821; Paratypes: MCN 33919 (33 specimens), MCP 9109 (6 specimens), MACN-In 37063 (two specimens), 12 Jan. 1994.

Etymology: The specific epithet refers to the City and Municipality of Cambará, close to the type locality.

Distribution and Habitat: Known only from the type locality. The Municipality of Cambará is situated in northeastern Rio Grande do Sul State, Brazil, in the highest part named Planalto Riograndense. From the physiographic point of view, this region is characterized by a basaltic shield covered by low grass steppes and *Araucaria* Forest mixed with the southeastern limits of the Atlantic Forest. The altitude varies from 850 to 1050 m, and in the winter, temperatures fall below freezing and there is the occasional snow. The rivers that cross the region, flanked by a low gallery forest, have

Figures 13–20. *Sphaerium cambaraense* new species. Schematic drawings of soft anatomy. **13.** Gross anatomy (left mantle lobe removed). **14.** Folded surfaces of inner and outer left labial palps. **15.** Outer view of left mantle lobe showing the inner radial mantle muscles. **16.** Dorsal view of the stomach and digestive gland. **17.** Floor of the stomach after removing the roof. **18.** Inner view of the organs in the visceral mass. **19.** Dorsal view of nephridia, posterior adductor muscle and posterior foot retractors. **20.** Lateral view of left nephridium. Scale bars: 13, 15, 16, 18 = 2 cm; 14, 17, 19, 20 = 2 mm hard bottoms formed by flattened basaltic stones, and currents are strong. The collecting sites were small ponds along the river course, where currents were lower, allowing the accumulation of decayed leaves and very soft, dark, and fine sand deposits, not deeper than 1 m, where specimens settle. Together with the *Sphaerium* samples, many specimens of one species of *Pisidium* sp. (MCN 33918), and one of *Diplodon* sp. (MCN 33920) not yet identified, were found.

DISCUSSION

Sphaerium cambaraense is similar to *Sphaerium forbesi* (Philippi, 1869) (from Bolivia, Chile, and Peru). However, *S. cambaraense* has a more decidedly triangular shell outline, beaks not full with not marked nepionic shell; in addition, *S. cambaraense* is larger than *S. forbesi*. *Sphaerium lauricochae* Philippi, 1869), also reported from Bolivia, Chile, and Peru, differs from *S. cambaraense* by its more rounded shell outline. In relation to shell thickness and microstructure, *S. cambaraense* is similar to the European species *Sphaerium rivicola* (Lamarck, 1818) and *Sphaerium corneum* (Linnaeus, 1758); Dyduch-Falniowska (1983) reported for these species (as well as for *Musculium lacustre* (Müller, 1774) and several *Pisidium* species) six different layers, (1) periostracum, (2) homogeneous-granular layer, (3) granular layer; (4) diagonal layer (composite prismatic structure), (5) palisade structure, and (6) endostracum. Only *S. corneum* and *S. rivicola* showed a different structure for the diagonal layer, referred to as "crossed-lamellar structure" (Dyduch-Falniowska, 1983). This structure was also found in *S. cambaraense*, however, the diagonal pattern of the plates has a different arrangement: in *S. rivicola* the oblique plates show a horizontal herringbone pattern and in *S. cambaraense* some rows of plates are oblique not forming a horizontal pattern. These latter resemble in part the pseudo crossed-lamellar structure found in the Corbiculidae. The periostracum layer in *S. cambaraense* is thinner than in *S. corneum* and the homogeneous granular layer is lacking. The simplified condition of posterior and right side of stomach is quite similar to that found in the Euperinae (Dreher-Mansur and Meier-Brook, 2000).

The nephridium is relatively similar compared to *S. corneum* (Dreher-Mansur and Meier-Brook, 2000), but the excretory sac and proximal loop are shorter and the valve at the insertion of the distal loop into excretory sac is lacking in *S. cambaraensis;* the multilobed surface of lateral lobe is observed for the first time in *Sphaerium*.

Based on the similar morphology of the nephridium, Korniushin (1998) proposed that South American species traditionally assigned to *Sphaerium* actually belong to *Musculium*. According to Park and Ó Foighil (2000), the usefulness of the fine anatomy of nephridium in the family Sphaeriidae is relative, due to its high morphological plasticity. Cooley and Ó Foighil (2000), based on mitochondrial 16S r DNA gene sequences observed that the *Sphaerium/Musculium* clade exhibit moderate to low levels of genetic divergences and the same asynchronous or sequential brooding pattern (i.e., brooding sacs contain more than one developing generations of embryos). Nevertheless, Cooley and Ó Foighil (2000) recognized *Musculium* as a monophyletic group. We allocate the new species in *Sphaerium* until more evidence is available to help with this question. More recently, a phylogenetic analysis of the Sphaeriinae (Lee and Ó Foighil, 2003) based on a molecular study of nuclear (ITS-1) and mitochondrial (16S) gene sequences of 15 species from North and South America, Europe, Asia, and Australia, recovered a strongly supported monophyletic group of sequential brooders (*Musculium* and *Sphaerium*). However, the analyses indicate that *Musculium* and *Sphaerium* sensu lato are not natural groups, proposing a new classification system comprising five subgenera within *Sphaerium*: *Sphaerium* sensu stricto Scopoli, 1777; *Musculium* Link, 1807; *Amesoda* Rafinesque, 1820; *Sphaerinova* Iredale, 1943, and *Herringtonium* Clarke, 1973. As these subgeneric groupings, however well supported by molecular data, are not defined from the morphological point of view, it is not possible at this point to place *S. cambaraense* within the new scheme.

ACKNOWLEDGMENTS

We are grateful to the curators of MCN mollusk collection: Ingrid Heydrich and Silvia D. Hahn for providing the loan of specimens; to Prof. Dr. Cecilia Volkmer Ribeiro for the help in sampling and to Prof. Dr. Wolfgang Maier from Tübingen University, Germany, for SEM sessions; Fabián Tricárico from the MACN SEM unit for his fine work with SEM photography. C.I. is a researcher from the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina.

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THE NAUTILUS 122(4):236–243, 2008

Some remarks on the gross anatomy of *Adelomelon ferussacii* (Donovan, 1824) (Gastropoda: Volutidae) from the coast of Patagonia, Argentina

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ABSTRACT

Specimens of the volutid *Adelomelon ferussacii* (Donovan, 1824) were dissected. These were collected during an extraordinary low tide on February, 2006, at Playa La Mina, Puerto San Julián, Santa Cruz Province, Argentina (49°09′ S, 67°37′ W). The gross anatomy, along with radulae and shell ultrastructure, are described for the first time. Analysis of these features suggests a close relationship with the other species of the genus *Adelomelon* Dall, 1906, and raises doubts about the validity of *Pachycymbiola* Ihering, 1907, a genus in which it has been included by recent authors.

Additional Keywords: Southwestern Atlantic, Mollusca, Patagonia

INTRODUCTION

The family Volutidae includes the most conspicuous species among all endemic mollusks of the Southwestern Atlantic. This is so not only because of their large size, but also because of their interesting reproductive biology (Penchaszadeh, 1976, 1999; Luzzatto, 2006). Volutes live in quite diverse environments (i.e., subtidal to deep water; soft, muddy, sandy, or mixed bottoms; cold, temperate, or warm waters). Several species are extremely rare, while others are quite common. At least two species, particularly in Uruguay, are the subject of extensive commercial fisheries. These are *Zidona dufresnei* (Donovan, 1823) and *Adelomelon brasiliana* (Lamarck, 1811). Other species are likely to be exploited in the near future (Giménez and Penchaszadeh, 2002). In addition, volutids usually are top predators with great ecological importance in the marine realm. Species of volutes studied thus far generally have been found to be predators on other mollusks and/or scavengers.

About 30 names have been applied to Volutidae from the western Atlantic, from Venezuela to Argentina. Of these, 16 are living in Argentine waters. Most are poorly known, with data derived only from their original description, which generally included very little biological information. In addition, the taxonomic status of several names awaits clarification.

Adelomelon ferussacii (Donovan, 1824), a locally common volute similar to *A. brasiliana*, is known only from its shell. Recent findings of egg capsules suggest a completely different reproductive biology (Penchaszadeh and Segade, submitted).

In this paper we provide new anatomical and ultrastructural data for *Adelomelon ferussacii* derived from a large ontogenetic series of live specimens, and compare them with other species of the same genus.

MATERIALS AND METHODS

Specimens used in this study were hand-collected during an extraordinary low tide on February 2006 at Playa La Mina, Puerto San Julián, Santa Cruz Province (49°09′ S, 67°37′ W) (Figure 1). The surface water temperature was 15°C. Animals were relaxed in freezing sea water, preserved in ethanol 70% and dissected under a stereoscopic microscope. Radulae were prepared according to the method described by Solem (1972). Photographs were taken using digital cameras and images were also digitally processed. Shell ultrastructure data were procured from freshly fractured colabral sections taken from the central portion of the lip on the last whorl of several individuals. MACN: Museo Argentino de Ciencias Naturales.

SYSTEMATICS

Family Volutidae Rafinesque, 1815
Subfamily Zidoninae H. Adams and A. Adams, 1853
Genus *Adelomelon* Dall, 1906

Adelomelon ferussacii (Donovan, 1824)

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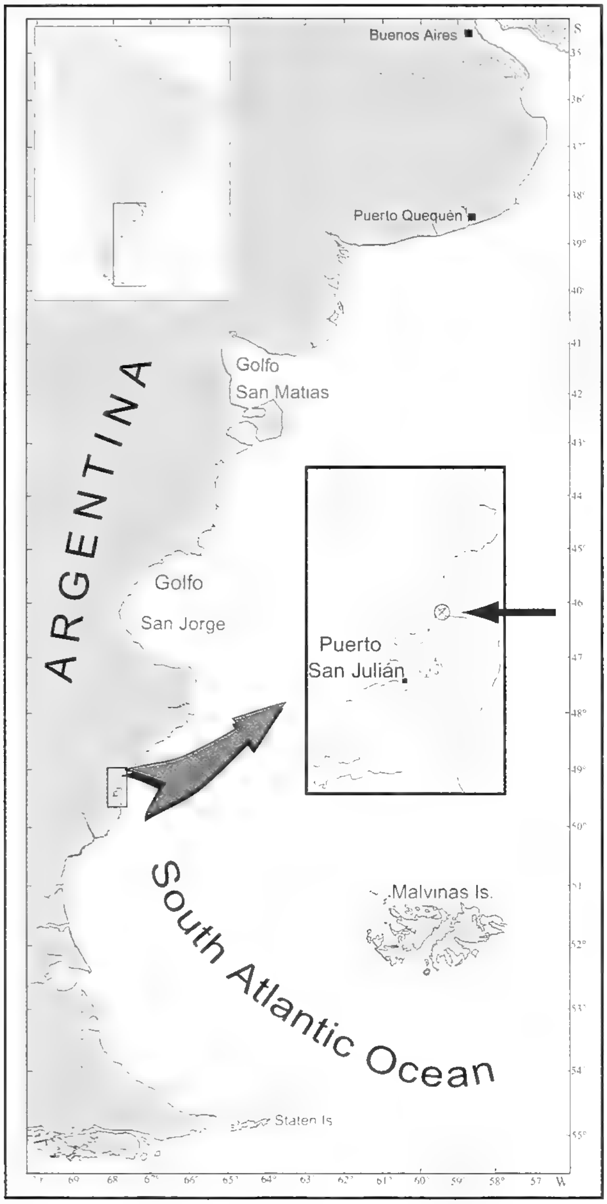


Figure 1. Map showing the study area of Playa La Mina, Santa Cruz, Argentina.

Voluta ferussacii Donovan, 1824, 2, pl. 67; Sowerby, 1846 1: 203, pl. 46, fig. 7; Reeve, 1849 6, pl. 10, fig. 23, spec. 39; Dall, 1907: 362.

Voluta rudis Gray in Griffith and Pidgeon, 1834: 601, pl. 30, fig. 1.

Voluta oviformis Lahille, 1895: 20, pl. 1, figs. 1–2, pl. 2, figs. 53–56, pl. 7, figs. 121–138, pl. 10, figs. 4–9.

Voluta oviformis typica Lahille, 1895: 20.

Voluta oviformis longiuscula Lahille, 1895: 20.

Voluta oviformis fratercula Lahille, 1895: 20.

Voluta (Cymbiola) ferussacii Donovan.—Strebel, 1906: 100, pl. 9, figs. 46, 46a, 48–49.

Adelomelon (?) *ferussacii* Donovan.—Clench and Turner, 1964: 157, Pl. 98, figs. 1–3.

Adelomedon (sic) *ferussacii* (Donovan).—Castellanos, 1970: 110, pl. 8, fig. 7.

Adelomedon (sic) *ferrusacii* [sic].—Castellanos, 1970b: 1, figs. 6, 9.

Adelomelon (Pachycymbiola) ferussacii (Donovan, 1824). —Weaver and DuPont, 1970: 108, pl. 45C, 45D.

Adelomelon ferussacii (Donovan, 1824).—Castellanos and Landoni, 1992: 12, Pl. 1, fig. 8.

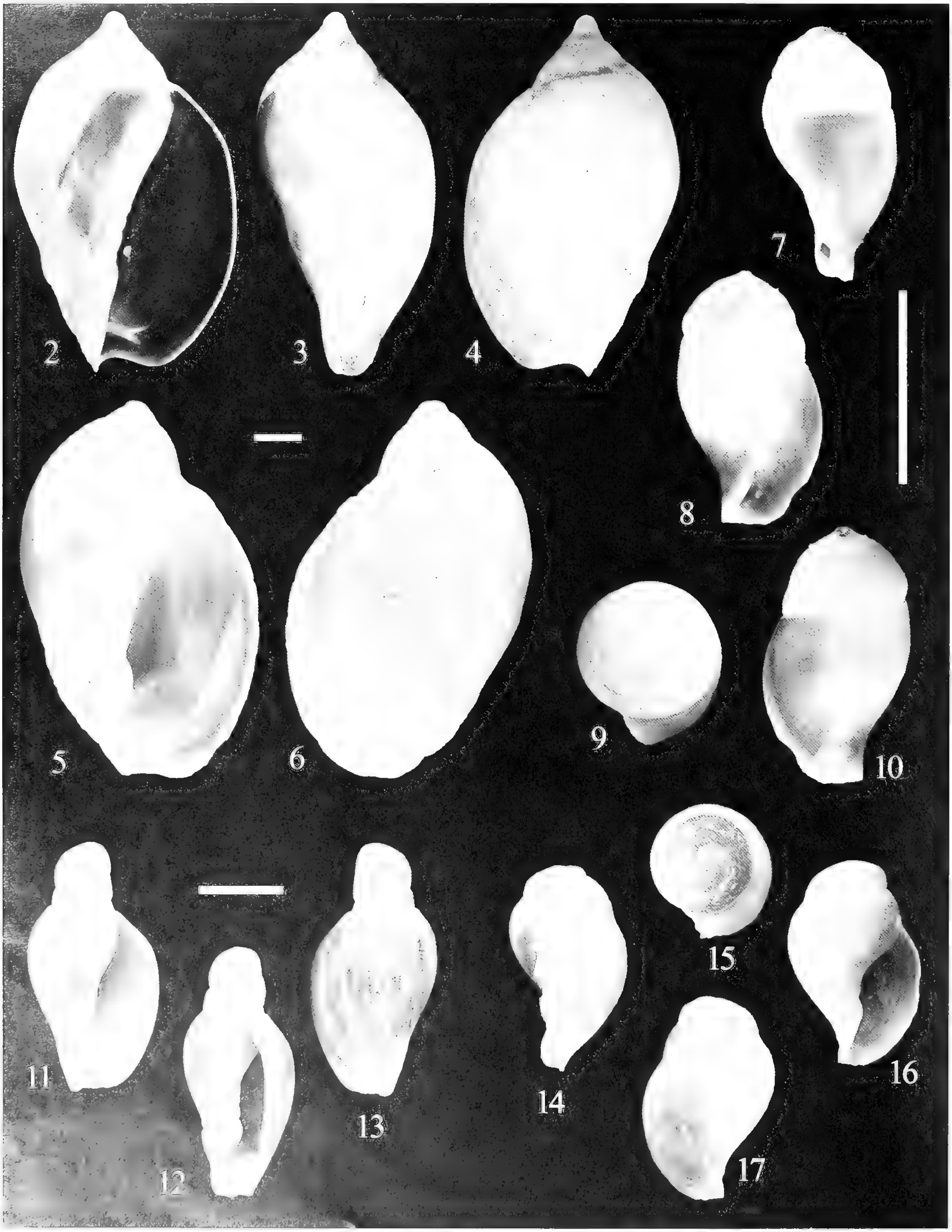
Pachycymbiola ferussacii (Donovan, 1824).—Poppe and Goto, 1992: 116, pl. 38, figs. 3–5.

Description: Shell medium in size, up to 122 mm, solid, fusiform; color grayish-brown. Aperture semicircular, dark-brown within. Protoconch of 1½ smooth whorls; teleoconch of up to 4 slightly convex whorls; spire low, sometimes somewhat upturned; spire angle of 80°, suture well defined. Columella curved, orange, with three to six folds set obliquely to siphonal fasciole, regularly distributed except for the anteriormost one, which is separate from the others. Columellar callus usually weak, but sometimes thick. Siphonal canal fairly broad and shallow. Growth lines span the surface, sometimes producing irregular costae. Shell ultrastructure showing three layers: a crossed-lamellar aragonite layer in which the crystal planes are arranged perpendicularly to the growing edge of the shell, and also perpendicular to the middle layer (25% shell thickness); a middle layer (50% shell thickness) of colabrally aligned crossed-lamellar aragonite, and an outer layer (25% shell thickness) of amorphous calcite (Figure 18). The innermost layer varies in thickness according to the sector of the lip: along the most curved sector it appears thicker, while it is reduced or absent towards the ends of the lip. This arrangement is quite similar to that found in shells of *A. brasiliana* (Figure 19) and *A. beckii* (Broderip, 1836).

Embryonic shells very thin (at hatching stage), whitish in the first whorls and dark brown in the last protoconch whorl. Surface covered by 8–10 regularly spaced spiral threads in the last whorl, no plaits visible. Calcarella reduced, weakly pronounced.

Foot, head, and siphon are finely mottled purple in color. The contact surface of the foot is whitish. Foot and shell length are similar. Operculum absent. Head broad and flattened, with two short tubular tentacles that separate the lateral lappets from the central one. Eyes are very small and located near the base of the tentacles. The penis emerges directly behind the right cephalic lappet (Figure 21). The siphon, also well pigmented, is muscular with paired and symmetrical siphonal appendages emerging from the base of the siphon and spanning half its length.

The bipectinate osphradium has aproximately 100 equal leaflets. The ctenidium is 1½ times as long as the osphradium. The hypobranchial gland is thin. The proboscis shows the same color pattern as the foot, head and siphon. Mouth opening is triangular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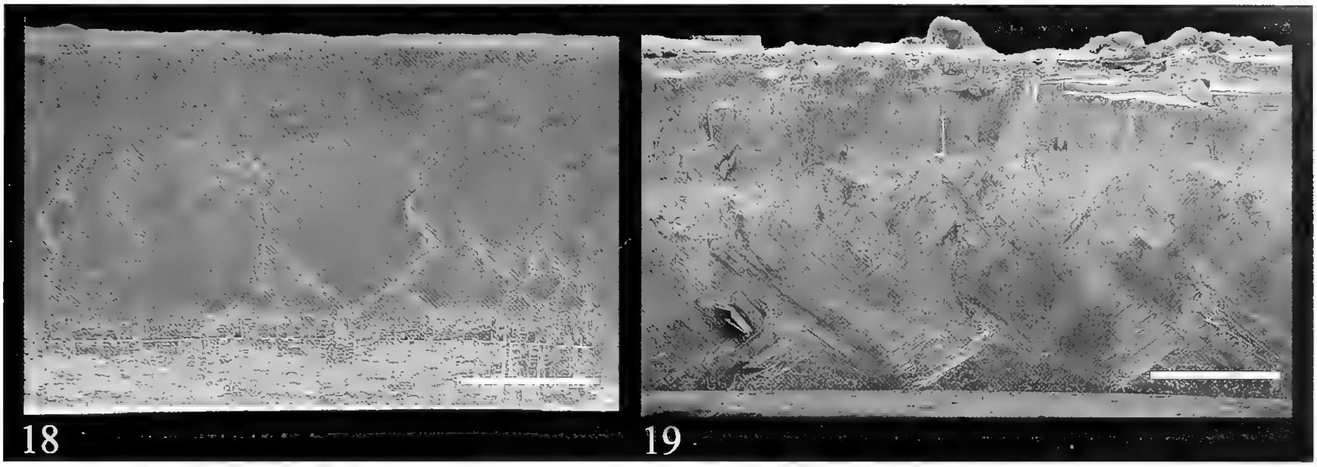


Figures 18–19. Shell ultrastructure. **18.** *Adelomelon ferussacii* (Donovan, 1824). **19.** *Adelomelon brasiliana* (Lamarck, 1811). Scale bars = 500 μm.

Radular ribbon narrow, up to 17.4 mm in length (n = 13; x = 11.7; DS = 1.97), with 49–74 rows (proportional to shell length) with one tricuspid central tooth per row (Figure 22). The radulae increase the number of teeth with age (Figure 32). Central tooth thin and long, anterior profile concave with a ventral-posterior thickening (Figures 23 and 24). Lateral cusps of the rachidian tooth are similar in size to the central one. Each cusp with a dorsal shallow indentation or groove present, where the corresponding previous cusp imbricates (Figures 24–25). Embryonic radulae showing about 15 rows of teeth where lateral cusps are shorter than central cusps (Figure 26; Table 1).

Salivary glands (racemose glands) large and irregularly shaped. Accessory salivary glands (tubular glands) very long and extremely convoluted, distally expanded, overlying dorsal surface of salivary glands. The tubular glands can easily be separated from the racemose glands. Ducts of the accessory salivary glands descend laterally to oesophagus and are sub terminal with respect to the mouth. They never fused and end separately. Ducts of salivary glands become embedded in the oesophagus anterior to small valve of Leiblein. The anterior esophagus runs behind the proboscis, and passes through the nerve-ring where an externally inconspicuous valve of Leiblein is located. The gland of Leiblein is very long and extremely convoluted (Figure 20). The posterior oesophagus continues to the stomach.

Material Examined: (D = specimen was dead when sampled; A = alive) Punta Cavendish, Puerto Deseado, Santa Cruz province, 2 D, collected in 5 m depth (MACN-In 31354); Patagonian coast, 1 D (MACN-In 11385); Playa Cabo San Pablo, Tierra del Fuego, 4 D (MACN-In 12532); Punta Sinaia, Tierra del Fuego, Expedición Facultad, 5 D (MACN-In 12531); Ushuaia, Tierra del Fuego, 1 D (MACN-In 9441); Punta María, Río Grande, Tierra del Fuego, 9 D (MACN-In 35113); Bahía San Sebastián, Tierra del Fuego, 1 D (MACN-In 35393); San Sebastián south, Tierra del Fuego, 4 D, Exp. Facultad de Ciencias (MACN-In 12530); Playa del Río Grande, Santa Cruz province, 1 D, (MACN-In 6647); 52°20′ S, 68°18′ W, Station 28, Cabo Vírgenes.

Table 1. Dimensions (mm) of some adults of *Adelomelon ferussacii* from MACN collection.

Specimen	1	2	3	4	5	6	7	8	9	10	11	12	13
Sex	♂	♂	♀	♂	♀	♂	♂	♀	♀	♀	♀	♀	♀
Shell length (mm) (SL)	76.5	75	58	91	78	85	75	72	76	74.5	76	114	75
Aperture length (AL)	60	57	46	69	60	64	59	56	58	58	56	89	56.5
AL/SL	0.78	0.76	0.79	0.76	0.77	0.75	0.79	0.78	0.76	0.78	0.74	0.78	0.75
Spire angle (°)	80	78	77	83	82	84	89	80	83	78	81	85	82
Radula length (RL)	10.8	11.3	9.5	12.2	12.1	13.1	11.4	10.4	9.6	11.8	12.1	17.4	11.7
Number of radular teeth	56	50	49	53	61	58	56	52	50	60	58	74	57

Figures 2–17. Shells of *A. ferussacii* and *A. brasiliana*. **2–13.** *Adelomelon ferussacii* (Donovan, 1824). **2–4.** MACN-In 37013 Puerto San Julián, Santa Cruz. **5–6.** Holotype of *Voluta rudis* Griffith and Pidgeon, 1834, NHM 19920177. **7–10.** Embryo shells (at hatching stage) MACN-In 37014. Puerto San Julián, Santa Cruz. **11–13.** Juvenile shells MACN-In 37012, 3 km North of Puerto San Sebastián, Tierra del Fuego. **14–17.** *Adelomelon brasiliana* (Lamarck, 1811), embryo shells MACN-In 37015, off Mar del Plata, Buenos Aires. Scale bars = 10 mm.

Santa Cruz province, A.R.A. Bahía Blanca, 1 D, in 11 m (MACN-In 24080); Bahía Laura, Puerto Deseado, Santa Cruz province, 1 D (MACN-In 9199-16); Bahía San Sebastián, Tierra del Fuego, 1 D (MACN-In 21154); Estancia "Viamonte", Río Grande, Tierra del Fuego, 2 D (MACN-In 27219); Isla Quiroga, Puerto Deseado, Santa Cruz province, 1 D (MACN-In 26199); Punta Arenas, Chile, 1 D (MACN-In 9040-27); Río Grande, Tierra del Fuego, 24 D (MACN-In 12529); Playa La Mina, Puerto San Julián, Santa Cruz Province (67° 37′ W, 49° 09′ S), 10 A in low tide (MACN-In 37487).

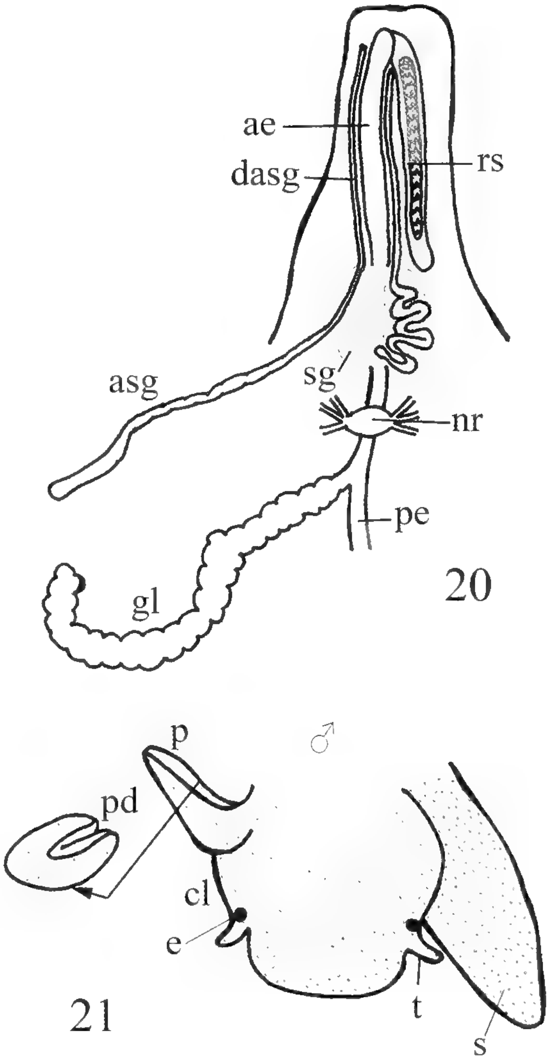
Distribution: *Adelomelon ferussacii* is a typical component of the Magellanic province, ranging from the province of Santa Cruz to Southern Chile. More northern citations of the species (e.g., Clench and Turner, 1964; Castellanos and Landoni, 1992), are here referred to *A. brasiliana*. No specimens of *A. ferussacii* from revised collections (MLP and MACN) were found outside of this range.

Distribution According to Previous Records in the Literature: Puerto Gallegos, Punta Arenas, (Strebel, 1906); Santa Cruz coast, (Lahille, 1895); Southern Patagonia and Magellanic region (Carcelles and Williamson, 1951); Golfo San Matías to Straits of Magellan (Clench and Turner, 1964), however they only examined specimens from the localities of Puerto Deseado, Cabo Buen Tiempo, Río Gallegos, Bahía de la Posesión and San Gregorio in Chile; Golfo San Matias to Magellan Straits (Weaver and DuPont, 1970); Santa Cruz (Castellanos, 1970b); Southern coast of Buenos Aires province to Magellan Straits (Castellanos and Landoni, 1992); Southeastern coast of Argentina, south to the Magellan Straits (Poppe and Goto, 1992).

DISCUSSION

Clench and Turner (1964) suggested the inclusion of *Voluta ferussacii* in the genus *Adelomelon* Dall, 1906, because of shell similarity with *A. brasiliana*. However, at that time they examined no complete specimens to confirm such generic placement. Weaver and Du Pont (1970) mentioned that no live specimens were collected. Later, Castellanos (1970) illustrated the radula confirming the generic placement suggested by Clench and Turner (1964). However, data on the gross anatomy had not previously been reported.

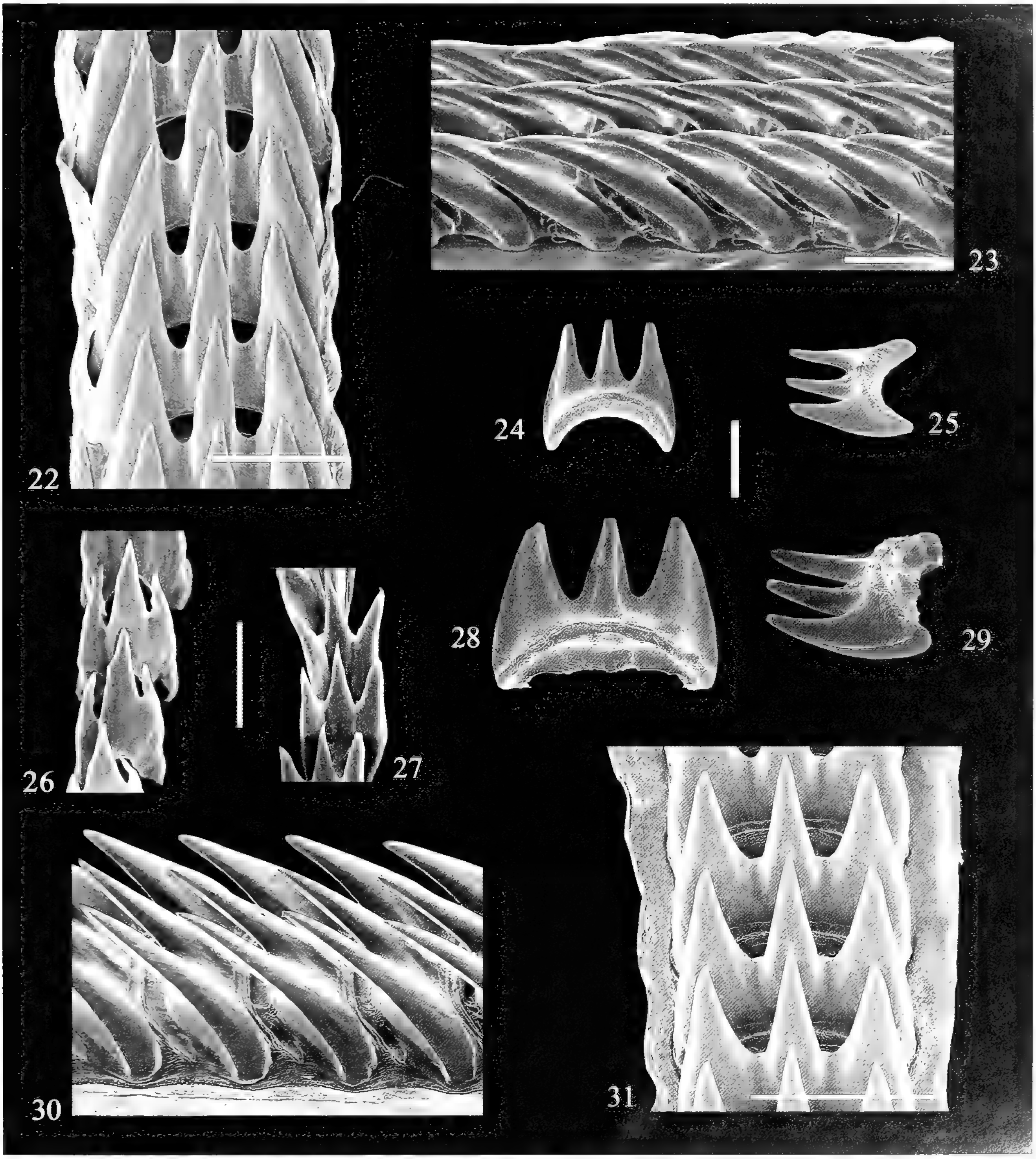
The last comprehensive taxonomic revision of the family Volutidae from the southwestern Atlantic was prepared by Clench and Turner (1964, 1970). They described the new subfamily Odontocymbiolinae and the new genus *Odontocymbiola*, and finally resolved the confusion of previous authors (e.g., Pilsbry and Olsson, 1954) between *Adelomelon ancilla* (Lightfoot, 1786) and *Odontocymbiola magellanica* (Gmelin, 1791). These authors also described two new species: *O. pescalia* and *A. riosi* (Clench and Turner, 1964). The latter was included in the new subgenus *Weaveria*. After their work, several additional new species were described, in particular from Brazil (e.g., Leal and Bouchet, 1989; Leal and Rios, 1990).



Figures 20–21. *Adelomelon ferussacii* (Donovan, 1824). **20.** Anterior alimentary system. **21.** Dorsal view of head, siphon, and penis of a male specimen. **ae,** anterior esophagus; **asg,** accesory salivary gland; **cl,** cephalic lappet; **dasg,** duct accesory salivary gland; **e,** eye; **gl,** gland of Leiblein; **nr,** nerve ring; **p,** penis; **pd,** penial duct; **pe,** posterior esophagus; **rs,** radular sac; **s,** siphon; **sg,** salivary gland; **t,** tentacle.

Most of the literature dealing with southwestern Atlantic volutids is primarily taxonomic. Anatomical data are scarce and usually drawn from one or relatively few specimens, sometimes incomplete. Exceptions are the papers by Novelli and Novelli (1982) and Ayçaguer (2002), particularly the latter, in which the authors described in some detail the anatomy of *Zidona dufresnei*.

Clench and Turner (1964) and Ayçaguer (2002) mentioned that *Adelomelon beckii*, *A. ancilla*, *A. brasiliana*, and *Zidona dufresnei* all have characteristic racemose salivary glands loosely intertwined in the tubular



Figures 22–31. Radulae of *Adelomelon* species. **22–26.** *Adelomelon ferussacii* (Donovan, 1824). **22.** Frontal view. Scale bar 250 µm. **23.** Lateral view. Scale bar = 200 µm. **24–25.** Rachidian teeth. Scale bar = 200 µm. **26.** Radula of an embryo. Scale bar 50 µm. **27–31.** *Adelomelon brasiliana* (Lamarck, 1811). **27.** Radula of an embryo. Scale bar = 50 µm. **28–29.** Rachidian teeth. Scale bar = 200 µm. **30.** Lateral view. Scale bar = 200 µm. **31.** Frontal view. Scale bar = 250 µm.

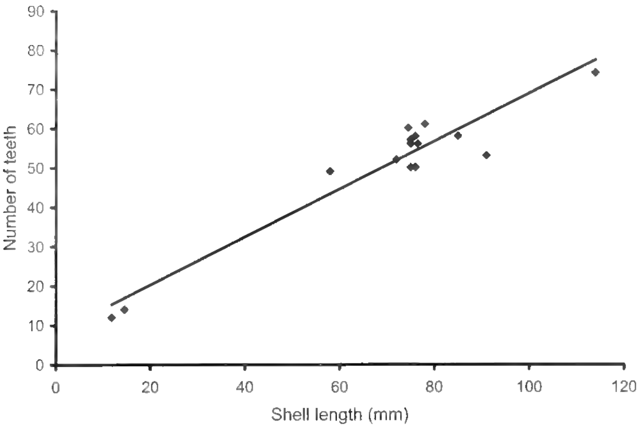


Figure 32. Relationship between radular and shell length (R = 0.9178).

accessory glands. The radula in these species is also rachiglossate with a unique central tricuspid tooth. These characters, together with several shell similarities placed *A. ferussacii* in the Zidoninae subfamily.

Radulae of the species *A. ferussacii* and *A. brasiliana* are quite similar (Figures 22 and 31). However, *A. brasiliana* has a wider and more convex base of the rachidian teeth than *A. ferussacii* (Figures 24 and 28). Lateral cusps of the rachidian teeth are shorter and wider in *A. brasiliana* than in *A. ferussacii*. These differences are probably specific characters and are also present in the embryos of both species (Figures 26 and 27).

The name *Pachycymbiola* was proposed by Ihering (1907: 209) as a subgenus of *Adelomelon* for *A. brasiliana*, which is actually the type species. Pilsbry and Olsson (1954) and later Scarabino et al. (2004) promoted *Pachycymbiola* to generic rank, and mentioned as main characters an ovate shell with a short spire, a free oval egg capsule, and a protoconch without calcarella. Del Río and Martínez (2006) also treated *Pachycymbiola* at the generic rank following the latter authors. They described five Tertiary species, three new, under-this genus, pointing out as main differences from *Adelomelon* the ovate shape of the shell, the short spire and the protoconch without calcarella, in agreement with Scarabino et al. (2004). *Adelomelon brasiliana* has all these features and a large free ovoid ovicapsule, with 9 to 33 embryos per capsule (Penchaszadeh and de Mahieu, 1976; Luzzatto, 2006). On the other hand, *A. beckii* and *A. ancilla*, which belong in the subgenus *Adelomelon*, have smaller egg capsules, always attached to hard substrates (Penchaszadeh et al., 1999). *Adelomelon ferussacii* presents egg capsules similar to those of A. *beckii*, which are globose hemispherical and flexible, with a white opaque color and a leathery texture, attached to a hard substrate such as stones or rocky substrates (Penchaszadeh and Segade, in preparation).

The inclusion of *A. ferussacii* in the subgenus *Pachycymbiola* was first suggested based on some external similarity to *A. brasiliana*. However, the egg capsules do not match those of *A. ferussacii*. In fact they look more similar to those of other species of *Adelomelon*. Also, the gross anatomy revised here does not show conclusive features to include *A. ferussacii* in a different group as suggested previously. The only character that could stand as a difference are those of shell morphology. Pilsby and Olsson (1954), Scarabino et al. (2004) and Del Río and Martinez (2006) concede that shell shape place *A. ferussacii* close to *Pachycymbiola*. They do not mention that a calcarella is reduced, present in the young of *A. ferussacii* (Figures 7–13), but absent in those of *A. brasiliana*. At a closer look even the shell shape is substantially different, since *A. brasiliana* has a more flattened spire and pronounced shoulder tubercles more similar to *A. becki* than *A. ferussacii*. Further detailed anatomical studies will confirm the relationships of these Southwestern Atlantic endemic volutids.

ACKNOWLEDGMENTS

We thank M. Griffin (UNLPam) and F. Scarabino for the suggestions that considerably improved the manuscript. Bronwyn Gillanders helped to improve the English. Two anonymous reviewers made useful suggestions on an early draft of the manuscript.This contribution was supported by Project PICT No. 03-14419 from the National Agency for Scientific and Technical Promotion, Argentina. We acknowledge funding by the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) of Argentina, to which GP belongs.

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A new species and a new record of Muricidae (Gastropoda) from Brazil: genera *Pterynotus* and *Leptotrophon*

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ABSTRACT

Leptotrophon atlanticus, a new species of *Leptotrophon* Houart, 1995, a genus of Trophoninae previously known only from the Indo-Pacific Ocean, is described from the northeastern coast of Brazil, from depths of 240–260 m. *Leptotrophon atlanticus* is very similar to *Leptotrophon kastoroae* Houart, 2001, but has shorter spines, which are brown colored. The shell microsculpture of *L. atlanticus* was studied using scanning electron microscopy, which revealed a protoconch slightly granulated on the last quarter of the whorl and a teleoconch with growth striae crossed by regularly spaced zigzag spiral lines and axial microstriae. The radula of *L. atlanticus* fits the pattern described for the genus, but the lateral/marginal cusps of the rachidian teeth are not as independent of each other, being somewhat fused into a common base. This study reports the first record from the South Atlantic Ocean of the Muricinae *Pterynotus havanensis* Vokes, 1970, previously known only from the Caribbean region.

Additional keywords: Muricinae, Trophoninae, South Atlantic, biodiversity, taxonomy

INTRODUCTION

The family Muricidae is represented in Brazil by 49 species from six subfamilies, of which members of the subfamily Muricinae are most numerous, with 24 species in nine genera (Rios, 1994). Other genera of Muricinae recorded from the western Atlantic have never been recorded from Brazil until now. This includes the genus *Pterynotus*, which is found in deeper-water habitats (Vokes, 1970), with eight species reported from Florida and the Caribbean (Rosenberg, 2005), in addition to mention records from other regions of the world, e.g., Ponder (1972) from Australia, Bouchet and Warén (1985) from the northeast Atlantic, and Houart (2001) from New Caledonia.

The subfamily Trophoninae includes 18 genera (Vaught, 1989). It is represented in the western Atlantic by five genera, of which only *Trophon* Montfort, 1810, occurs in Brazil (Rios, 1994). More recently, Houart (1995) described the genus *Leptotrophon*, whose 26 species are restricted to the Indo-Pacific region, in New Caledonia (Houart, 1995, 2001) and eastern Indonesia (Houart, 1997).

This report presents the first record of the genus *Pterynotus* Swainson, 1833 from Brazil, based on *Pterynotus havanensis* Vokes, 1970, as well as the first record of the genus *Leptotrophon* from the Atlantic Ocean, based on a new species described from northeast Brazil.

MATERIALS AND METHODS

This report is based on a sample collected on the Canopus Bank, State of Ceará, in 2005, from a biogenic substratum, in 240–260 m depth. Identification of the species was based on original and subsequent descriptions. In cases where fragments of soft parts were available, an attempt was made to record some anatomical characteristics using camera lucida, especially of the head-foot and the pallial cavity. Radulae were prepared for SEM according to the methodology described by Bandel (1984).

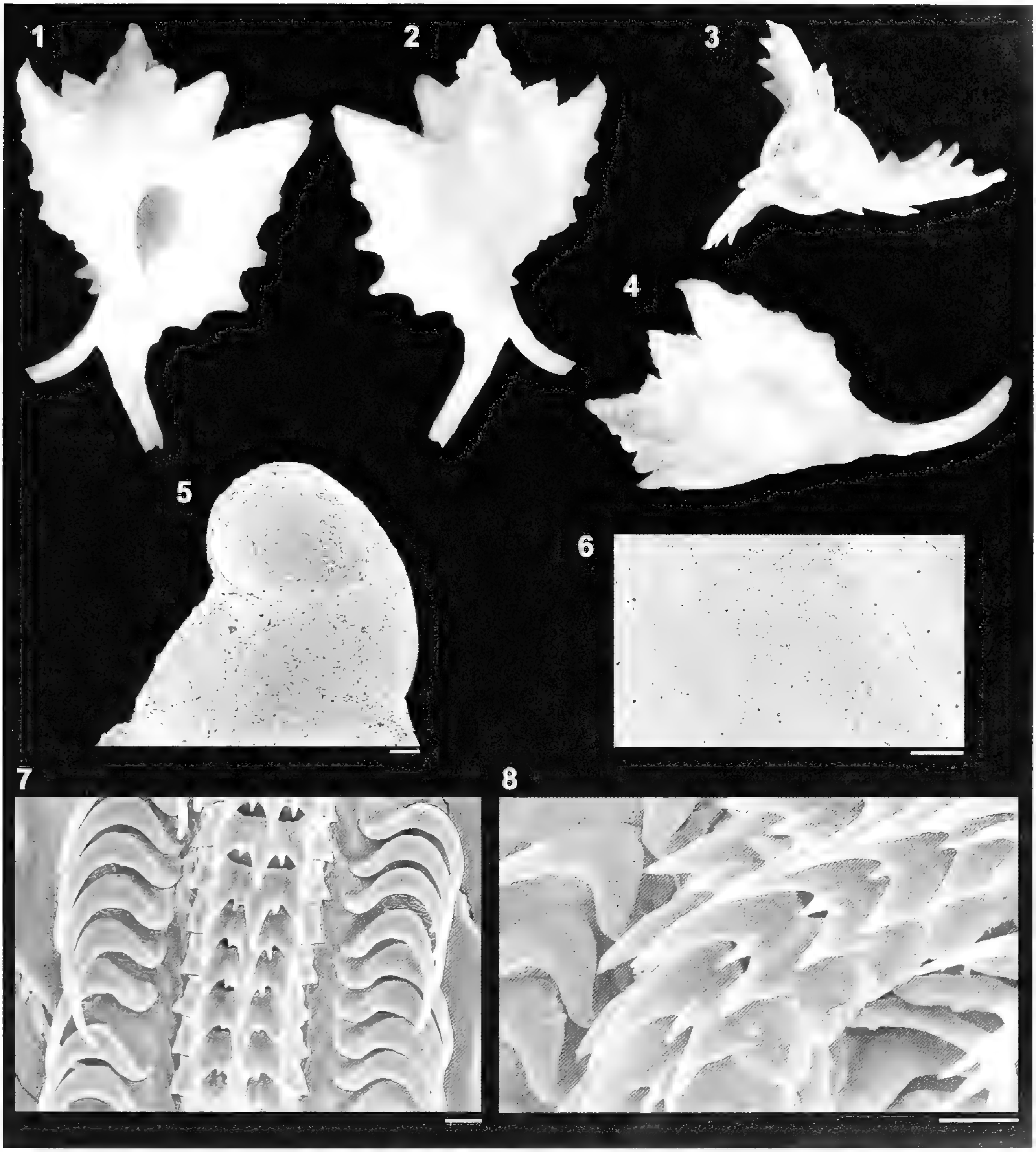
SYSTEMATICS

Family Muricidae Rafinesque, 1815
Subfamily Muricinae Rafinesque, 1815
Genus *Pterynotus* Swainson, 1833

Type Species: *Murex pinnatus* Swainson, 1822 by subsequent designation.

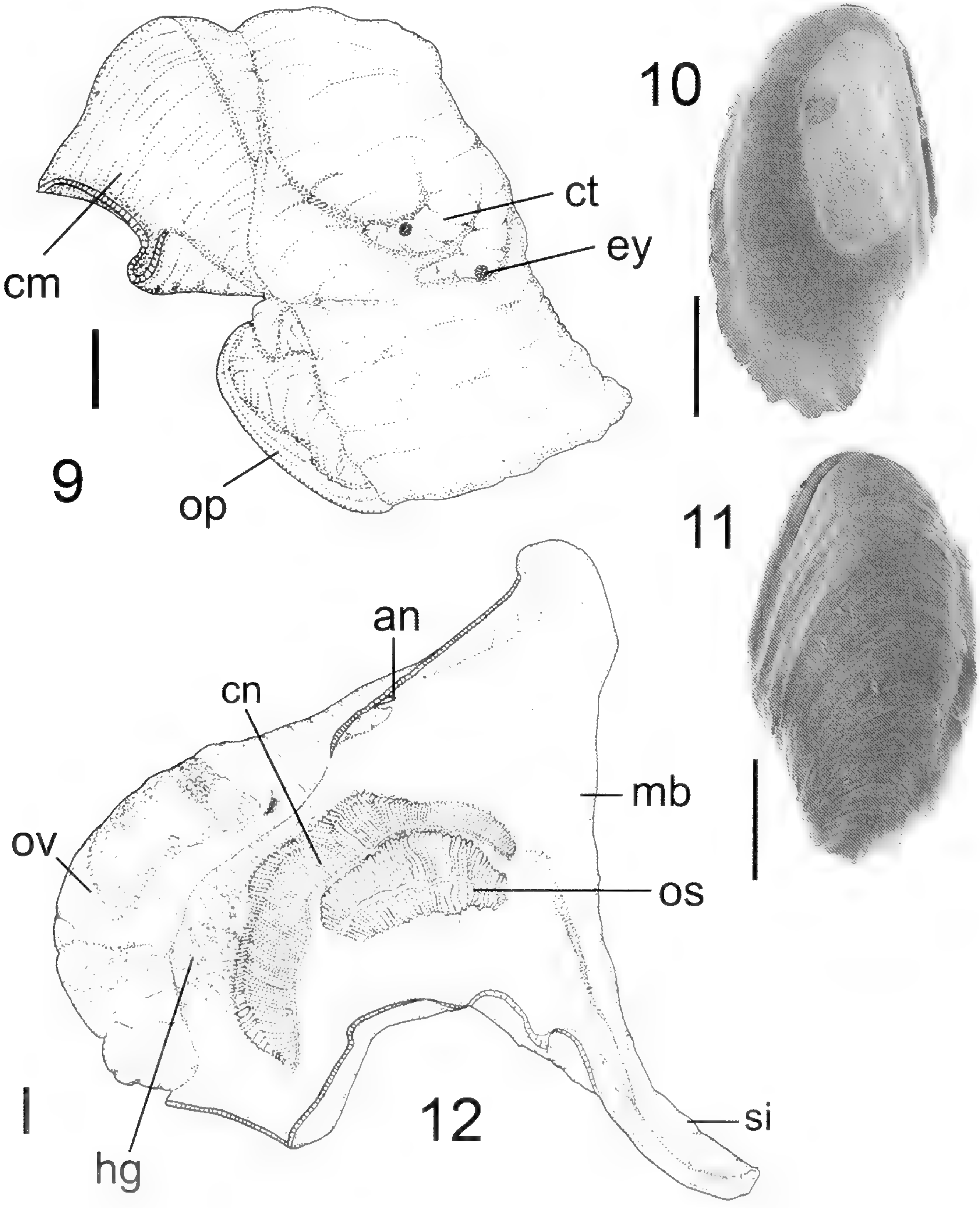
Pterynotus havanensis Vokes, 1970
(Figures 1–12)

Pterynotus (*Pterynotus*) *havanensis* Vokes, 1970 (new name for *Murex tristichus* Dall, 1889, non *Murex tristichus* Beyrich, 1854.)



Figures 1–8. *Pterynotus havanensis* Vokes, 1970: **1–4, 7–8.** MNRJ 11057, length = 24.4 mm, width = 16.5 mm. **5–6.** MNRJ 11003. **1.** Shell in apertural view. **2.** Shell in abapertural view. **3.** Shell in apical view. **4.** Shell in lateral view. **5.** Protoconch **6.** Detail of teleoconch sculpture. **7.** Radulae in dorsal view. **8.** Detail of rachidian teeth. Scale bars: 5–6 = 100 µm; 7–8 = 10.0 µm

Murex (*Pteronotus*) *tristichus* Dall, 1889: 202, pl. 15, fig. 2).
Pteropurpura tristicha.—Dall, 1927: 58.
Murex (*Pterynotus*) *tristichus*.—Clench and Farfante, 1945: 36, pl. 20, figs. 1–4.
Pterynotus phaneus auct.— Abbott, 1974: 175, fig. 1856 (non Dall, 1889).
Pterynotus phaneus Dall.—Radwin and D'Attilio, 1976 100 (in part



Figures 9–12. *Pterynotus havanensis* Vokes, 1970 (MNRJ 11057). **9.** Head-foot in apertural view, female. **10.** Operculum in inner view. **11.** Operculum in outer view. **12.** Palial cavity, female. Scale bars = 1.0 mm. Abbreviations: **an,** anus; **cm,** columellar muscle; **cn,** ctenidium; **ct,** cephalic tentacle; **ey,** eye; hg, hypobranchial gland; **mb,** mantle border; **op,** operculum; **os,** osphradium; **ov,** oviduct; **si,** siphon.

Pterynotus havanensis Vokes.—Fair, 1976: 47, pl. 13, fig. 164.

Pterynotus (*Pterynotus*) *phaneus* auct.—Harasewych and Jensen, 1979: 4, fig. 3 (in part, non Dall, 1889).

Description: Shell of moderate size (up to 25 mm in length), fusiform, thin; color white. Protoconch paucispiral, with 1.5 whorls, glassy, slightly bulbous, ending in a thin varix. Teleoconch with up to five whorls, somewhat convex in outline, with three thin, flaring, backward-curved, wing-like varices per whorl, with 5–6 digitations along margin of last whorl varices. Axial sculpture consisting of fine growth striae, more visible in ventral view of varices, where they cross with spiral threads, giving it a foliaceous appearance; no intervarical nodes present. Spiral sculpture obsolete, barely discernible spiral threads, formed by microscopic shallow furrows, somewhat undulated and irregularly spaced; abapertural view of varices with five–six spiny digitations per varix on the last whorl and two digitations on spire varices; spine on shoulders of whorls largest. Aperture oval, peristome slightly projected, inner lip reflected, attached posteriorly, smooth, with small undulations corresponding to varical digitations; outer lip smooth. Siphon canal rather long, sharply bent abaperturally and to the right side; narrowly open; with previous, old imbricate canal termination, recurved to the left side.

Radula (Female): Rachiglossate type; radula ribbon long and narrow; rachidian teeth with five pointed cusps, central cusp the largest, the second largest at the margins, each area between central and marginal cusps with an acute tiny cusp; marginal edge rectangular and somewhat pointed, base concave; lateral teeth sickle-shaped, broader at the base.

Head-Foot (Female): Head poorly differentiated, eyes located laterally and in middle of somewhat long cephalic tentacles. Foot large. Operculum horny, ovate, covering entire shell aperture; external surface with terminal nucleus and concentric growth lines; inner surface attachment area with single horseshoe-shaped scar, not positioned centrally, covering less than 50% of total area of operculum, with one adventitious layer.

Pallial Cavity (Female): Mantle border smooth; siphon long and narrow, with smooth border, muscle attachment reaching as far as gill. Osphradium bipectinate, unequal, right side about 1.5 times as wide as left, broad and long (about half total ctenidium length). Ctenidium monopectinate, long and narrow. Hypobranchial gland a thin, poorly developed glandular mass covering mantle between anterior end of gill and oviduct. Oviduct occupying about half of pallial cavity length, broad.

Type Locality: Blake Station 51, off Havana, Cuba, between 445 m and 823.5 m.

Material Examined: MNRJ 11003 (one individual and seven empty shells); MNRJ 11067 (one individual); MNRJ 11057 (one individual); all from Canopus Bank, 96 miles off Ceará State, 240–260 m depth, from biogenic substratum.

Geographic Distribution: Off Georgia and Fernandina (Dall, 1927), Key West (Fair, 1976) Florida, USA; Havana, Cuba (type locality); Pleistocene Moín Formation, Costa Rica (Vokes, 1992); Golfo of Urabá, Colombia (Vokes, 1992); Ceará State, Brazil (this study).

Discussion: *Pterynotus havanenis* Vokes, 1970, was originally described as *Murex* (*Pteronotus*) *tristichus* Dall, 1889. The taxon was later included in a long list of synonyms of *Pterynotus phaneus* (Dall, 1889) by Harasewych and Jensen (1979), based on a wide variation found in several shell characteristics such as the axial sculpture, intervarical nodes and outer lip. Vokes (1992) revalidated *P. havanensis*, based on the more numerous varices on the early teleoconch whorls and the smoother shell surface.

The only available published illustrations of *P. havanensis* are those of the holotype (Dall, 1889: pl. 15, fig. 2; Clench and Farfante, 1945: pl. 20, figs. 1–4; Vokes, 1970: pl. 3, figs. 1a,b; Abbott, 1974: fig. 1856; Fair, 1976: pl. 13, fig. 164; Harasewych and Jensen, 1979: fig. 3; Vokes, 1992: pl. 2, fig. 3), in addition to a Pleistocene fossil specimen from Costa Rica (Vokes, 1992: pl. 2, fig. 6). This study provides the first illustrations of Recent specimens (Figures 1–4), except for that of the holotype itself.

The Brazilian specimens herein studied, all from Canopus Bank, about 96 miles off the coast of the State of Ceará (240–260 m depth), are very similar to the holotype illustrations, with little sculpturing between the varices (Figures 1–2, 4), without the intervarical nodes described for *P. phaneus*, in addition to axial and spiral growth lines, the digitations on the margins of the varices and no denticulate outer lip (Figure 1). These characteristics, along with the shape and sculpture of the varices, clearly distinguishes *P. havanensis* from *P. phaneus*.

Vokes (1992) stated that both *P. phaneus* and *P. havanensis* have denticulations on the inner side of the outer lip. However, this detail is not stated in the original or subsequent descriptions of this species, as well as in the holotype illustrations, which show a smooth outer lip, as well as in the specimens from Brazil. Such denticles reported by Vokes (1992) probably correspond to the undulations by the varical digitations. In addition, Vokes (1992) considered that *P. havanensis* bears several varices on the early teleoconch whorls, making reference to the figure in Harasewych and Jensen (1979). Brazilian specimens bear the usual three varices on the first teleoconch whorls.

The radula herein illustrated (Figures 7–8) has some minor differences from the radula of *P. phaneus* illustrated in Harasewych and Jensen (1979: 15, fig. 17). In *P. havanensis*, the central and lateral cusps are longer in relation to the total length of the tooth; also, the two inner cusps are narrower and shorter.

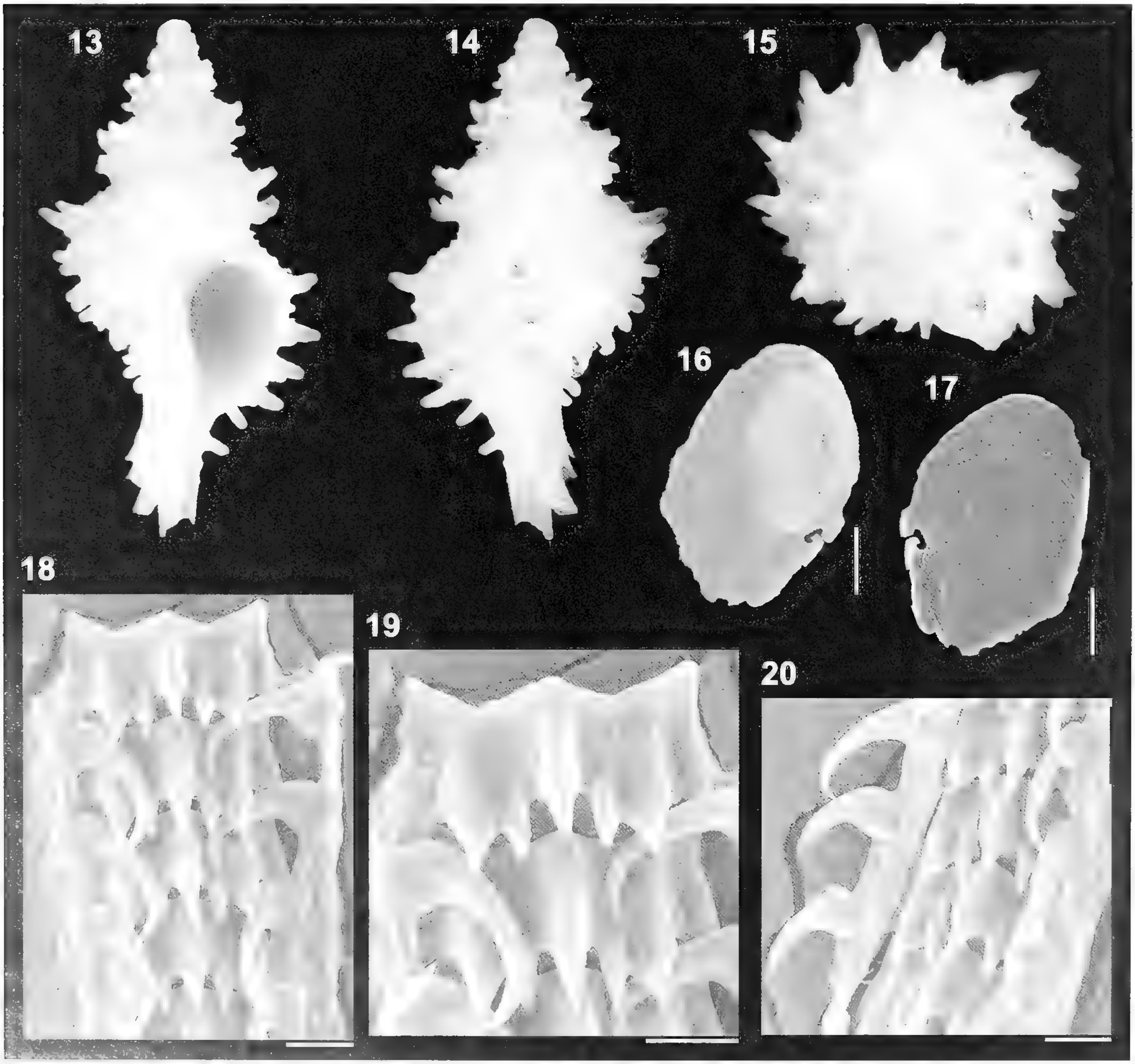
Subfamily Trophoninae Cossmann, 1903
Genus *Leptotrophon* Houart, 1995

Type Species: *Leptotrophon caroae* Houart, 1995, by original designation. Recent, New Caledonia.

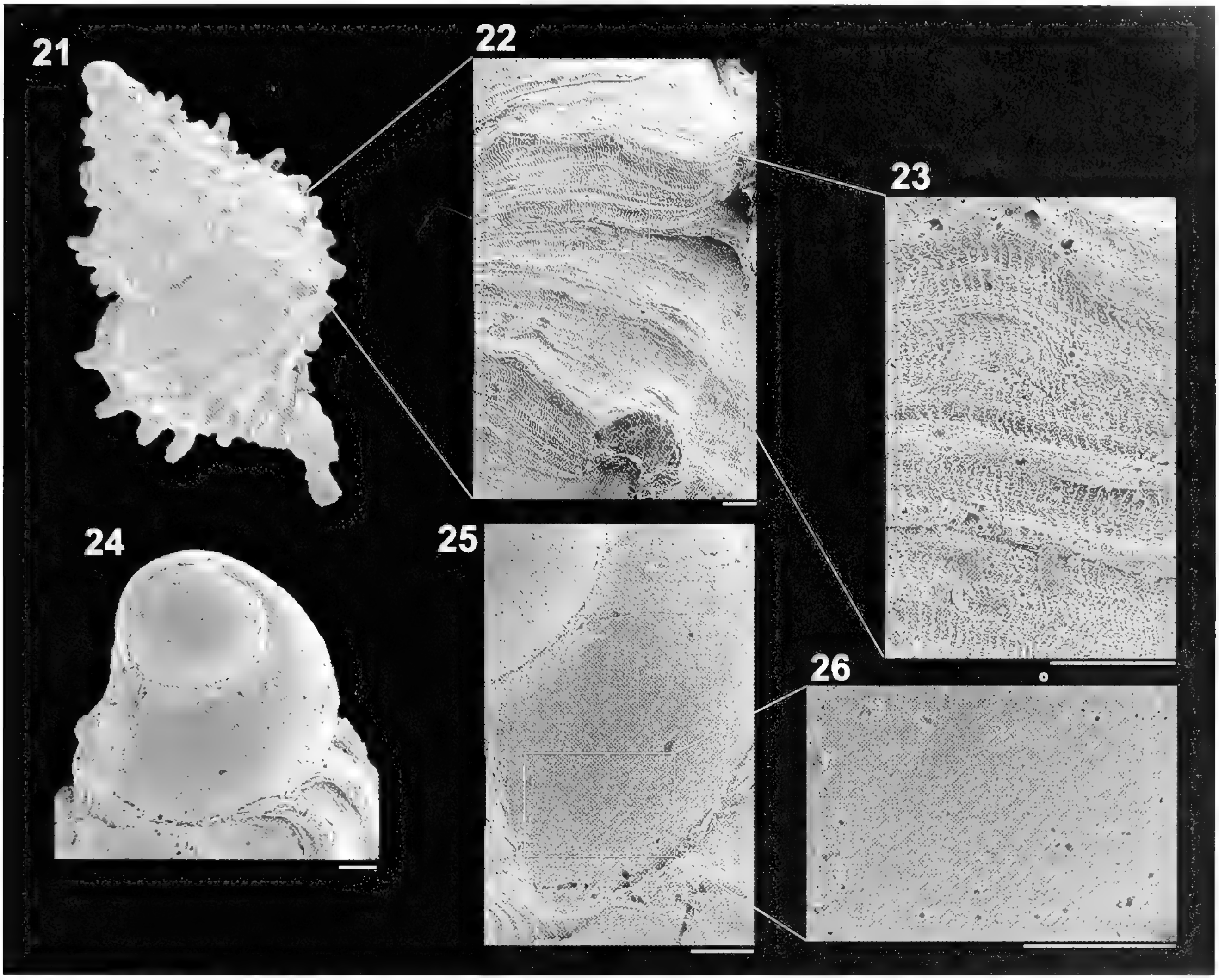
Leptotrophon atlanticus new species
(Figures 13–26)

Diagnosis: Shell densely spiny; color cream white with brown spines; paucispiral protoconch with slight granulated microsculpture on last quarter of last whorl.

Description: Shell up to 8.8 mm in length (holotype), biconic, and densely spiny; spire high. Color creamy white, with light brown spines in live specimens. Protoconch rounded, paucispiral, with 1.50 to 1.75 whorls, with slightly granulated microsculpture, forming faded spiral cords on last quarter of last whorl; terminal varix low. Teleoconch with up to 4.25 slightly shouldered whorls. Suture impressed. Axial sculpture consisting of numerous weak, orthocline lamellate growth striae and spiny varices, regularly spaced, forming spines at interceptions of spiral cords. Spiral sculpture on spire of two



Figures 13–20. *Leptotrophon atlanticus* new species. Holotype, MNRJ 11004, length = 8.8 mm, width = 4.6 mm). **13.** Apertural view. **14.** Abapertural view. **15.** Apical view. **16.** Operculum in inner view. **17.** Operculum in outer view. **18.** Radulae in dorsal view. **19.** Detail of rachidian teeth. **20.** Detail of lateral teeth. Scale bars 16–17 = 500 µm ; 18–20 = 10 µm



Figures 21–26. *Leptotrophon atlanticus* new species. Paratype, MNRJ 11009, length = 8.2 mm, width = 4.4 mm. **21.** Abapertural view. **22.** Detail of sculpture on teleoconch whorl. **23.** Detail of microsculpture on teleoconch whorl. **24.** Protoconch. **25–26.** Detail of protoconch sculpture. Scale bars = 100 μm.

strong cords, the adapical one located at 1/3 of whorl height below the suture; interceptions between axial varices and spiral cords form two primary spines regularly arranged in spiral crowns, each crown with 9–10 spines on last whorl of holotype; spines tall, channeled, commonly adapically and backward-curved, slightly larger at shoulder; spaces between adjacent spines have a squamous appearance, due to crossing of spiral cords with axial growth striae; last whorl with four additional spiral spiny crowns, regularly arranged at the base, along with corresponding spiral cords; secondary squamous small spines appear irregularly arranged, interspaced with primary spines; holotype with a secondary spiral cord appearing between the two primary ones closest to the suture, on the last half of the last whorl. Microsculpture formed by growth striae crossed by regularly spaced zigzag spiral lines and axial microstriae. Aperture slightly oval, rounded adapically with about 1/3 of total shell height. Columellar lip flaring, smooth and adapically adherent. Anal notch indistinct. Outer lip smooth, fragile, primary spiral cords and growth striae visible within. Siphon canal long, narrow, bent backwards, narrowly open and smooth, with seven imbricate old canal terminations.

Radula (Female): of rachiglossate type; radula ribbon long and narrow; rachidian tooth trapezoidal, with five pointed cusps; the two lateral cusps adjacent to central cusp somewhat fused into a bifurcated cusp, outermost cusps slightly larger; marginal edges rectangular well pointed, area between outer cusps and marginal edges with two very small folds; base somewhat sinuous; lateral teeth sickle-shaped, broader at base.

Operculum horny, elliptical, covering entire shell aperture; external surface with terminal nucleus and concentric growth lines; inner surface attachment area with single horseshoe-shaped scar, not positioned centrally covering about 50% of total area of operculum, with one adventitious layer.

Type Material: Holotype: MNRJ 11004 (8.8 mm); three paratypes: MNRJ 11009, all from type locality.

Type Locality: Canopus Bank, 96 miles off Ceará State, 240–260 m depth, from biogenic substratum.

Distribution: Known from type locality only.

Discussion: The allocation of *Leptotrophon* in Trophoninae follows Houart (1995), who, when describing *Leptotrophon*, stated that he was considering Trophoninae in a traditional way, to include typical "*Trophon*-like" species, diagnosed as small, thin spinose shells with a flaring columellar lip. In fact, Kool (1993) stated that Trophoninae is probably a non-monophyletic group and, thus, Houart (1995) considered that future studies would probably show that the genus *Leptotrophon* would have to be transferred from the Trophoninae.

The new species fits very well in the diagnosis of *Leptotrophon*, and is very similar to several species from the Indo-Pacific, including the type species, *L. caroae*.

Leptotrophon atlanticus bears the characteristic spiny sculpture (Figures 13–15), round-ovate aperture, and flaring columellar lip (Figure 13). The radula of *L. atlanticus* (Figures 18–20) fits the pattern described for *Leptotrophon*, but the lateral/marginal cusps are not as independent of each other, being somewhat fused into a common base (Figure 19). In other species referred to *Leptotrophon* by Houart (1995), the lateral/marginal cusps are similar to *L. atlanticus* [e.g., *L. caroae* and *L. acerapex* (Houart, 1986)]. In addition, two small marginal denticles may be seen on the outer base of the marginal cusps (white arrow in Figure 19), a characteristic found in other species of *Leptotrophon* described by Houart (1995).

The protoconch of the species described by Hoaurt (1995) shows considerable variation in shape, with rounded-globose, acuminate, or carinate protoconchs present in different species. The type species has a carinate protoconch, and *Leptotrophon atlanticus* has a rounded-globose protoconch (Figure 24).

The most similar species are *L. kastoroae* Houart, 1997, and *L. perclarus* Houart, 2001. Both species are larger than *L. atlanticus*. *Leptotrophon perclarus* has a taller spire, more acuminate apex, and more inflated last whorl; in addition, it has more numerous and smaller spines. The shell shape of *L. kastoroae* is almost identical to that of *L. atlanticus*, but the spines are longer and are more upward-curved.

Previously to this work, no record of shell microsculpture for any species of *Leptotrophon* was available. The protoconch is always described as smooth. In fact, the protoconch of *L. atlanticus* has an overall smooth appearance (Figure 24), but SEM reveals that only its most apical region is smooth; the last quarter area, close to the varix, bears spiral sets of microscopic granulations (Figures 25–26). A delicate microsculpture also covers the entire teleoconch surface, including the spiral cords and spines, with axial and spiral microstriae forming a somewhat reticulate pattern (Figures 22–23).

The operculum of *L. atlanticus* is similar in its outer surface to those illustrated by Houart (1995) for species of *Leptotrophon* from the New Caledonian region. Houart (1995) did not describe the operculum of *Leptotrophon* internally; the operculum of *L. atlanticus* has one adventitious layer.

In spite of the several common characteristics in the shell and radulae morphology of *Leptotrophon atlanticus* and the species from the Indo-Pacific, the generic allocation herein used should be considered as provisional, due to the wide geographic separation between the new species and the other species in the genus *Leptotrophon*, most of which bearing protoconchs that indicate non-planktotrophic development. All 26 previously described species of *Leptotrophon* are restricted to the Indo-Pacific (Houart, 1995; 1997; 2001); *Leptotrophon atlanticus* new species is the first record of this genus outside that region. The bathymetry of *L. atlanticus*, on the other hand, falls within the bathymetric range reported for the Indo-Pacific species (200–720 m). In the future, direct comparisons with the Indo-Pacific species, especially including characters visible only under SEM, would be most helpful to establish the degree of similarity among these species.

ACKNOWLEDGMENTS

We are grateful to Mr. Roland Houart (Institute Royal des Sciences Naturelles de Belgique) for comments on the taxonomy of the species. Vinicius Padula (MNRJ) and Franklin Noel dos Santos (Universidade Federal do Pará) provided additional bibliography. Dr. Janet Reid revised the English text. Dra. Noemia Rodrigues helped with the SEM photos. We also thank two anonymous reviewers for their comments and suggestions. Special thanks are due to Mr. Antonio Gil Bezerra and Ms. Elisa Gradvohl Bezerra, owners of INACE Shipyard (Indústria Naval do Ceará) for the loan of the fishing boat and to Mrs. José and Marcus Coltro for financial support to the collecting efforts. Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) provided a PROTAX pos-doctoral grant to P.M. Costa.

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THE NAUTILUS 122(4):252–258, 2008

A new species of *Chlamydoconcha* Dall, 1884, from southeastern Brazil (Bivalvia: Chlamydoconchidae)

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ABSTRACT

The second species in the genus *Chlamydoconcha* is described. *Chlamydoconcha avalvis* new species, occurs off the coast of Rio de Janeiro coast, in southeastern Brazil. The new species has very reduced valves and a mantle surrounding the entire body, two features of the genus. The outer surface of the mantle lacks papillae except for a single one located close to the excurrent siphon. These are distinctive characters of *Chlamydoconcha orcutti* Dall, 1884, from the eastern Pacific coast of North America, the single other known species of the genus. Some of the more interesting anatomical characters of the new species are: posterior pair of retractor muscles of foot free from valves, absence of adductor muscles, gastric style sac totally separated from intestine, and the presence of a single (excurrent) siphon.

Additional keywords: Anatomy, western Atlantic, Rio de Janeiro

INTRODUCTION

The genus Chlamydoconcha Dall, 1884 (type species by original designation: *C. orcutti* Dall, 1884) has been known to be monotypic. *Chlamydoconcha orcutti* occurs from California to western Mexico (Carlton, 1979; Morton, 1981). The species is characterized by reduction of the shell, which is restricted to the anterior region of a spherical mantle cover; the mantle outer surface has many, somewhat equidistantly distributed papillae. After the original description, further anatomical studies of *C. orcutti* were done by Bernard (1897) and Morton (1981).

A sample collected by biologist Vinicius Padula on the coast of Rio de Janeiro was sent to the author for study. The analysis of the material revealed a new species of *Chlamydoconcha*, formally described herein. This paper is also the first discovery of the genus in the Atlantic Ocean, representing the second known species in the genus. The present description also includes a detailed anatomy, which is discussed in comparison to *C. orcutti* (Bernard, 1897; Morton, 1981)

The taxonomic allocation of the genus *Chlamydoconcha* has been problematic. It has been included in the Galeommatidae (Morton, 1981), but full family status has been assigned (Chlamydoconchidae, Bernard, 1983), as part of the Galeommatoidea. Full superfamily status was also considered (Chlamydoconchacea, Keen, 1969). The Galeommatoidea, are mostly mollusks with usual bivalve shells, but may also include highly modified, slug-like animals, with internal and reduced shells.

MATERIALS AND METHODS

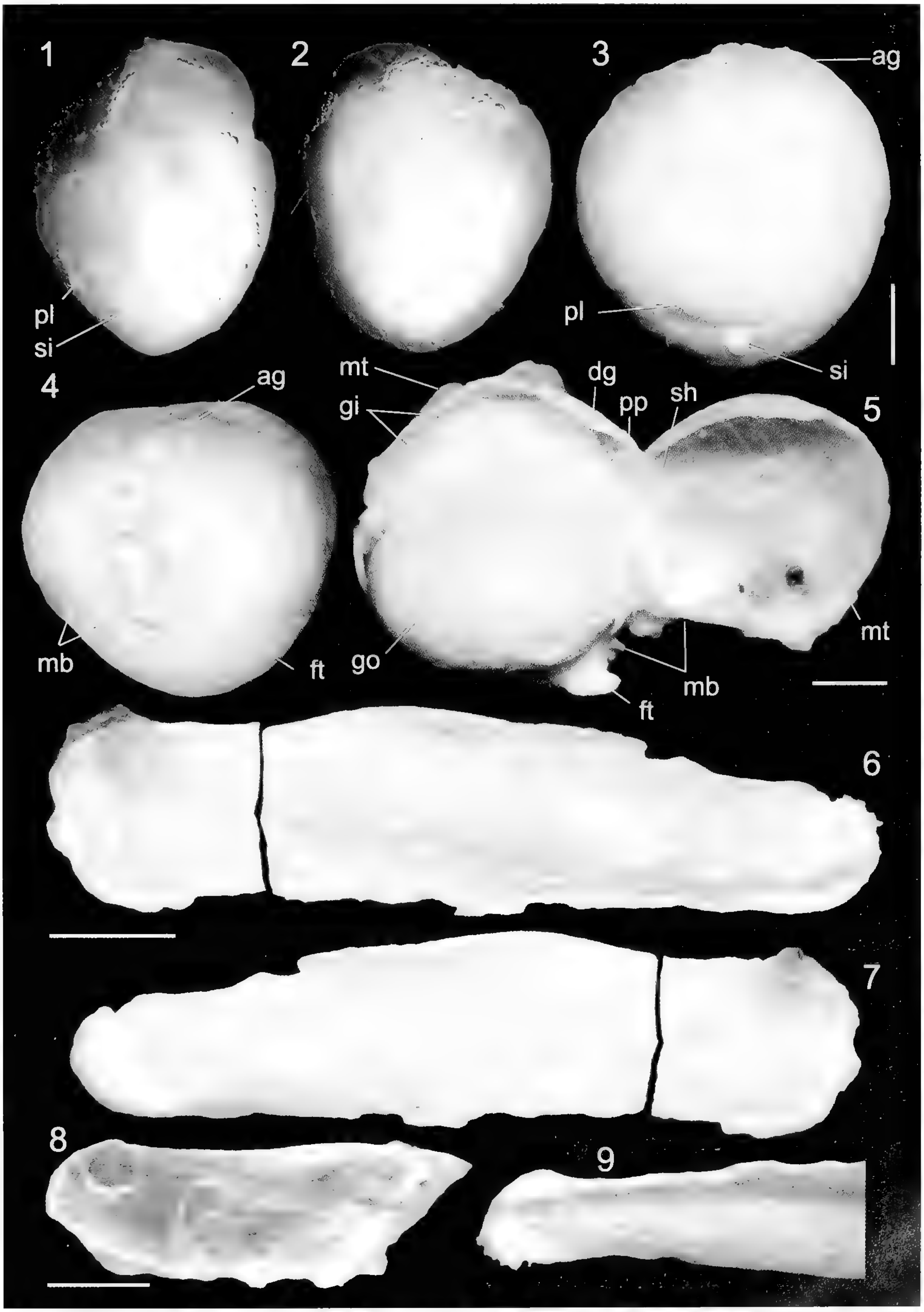
The specimen was delivered preserved in 70% EtOH. A photo of the living specimen was taken before preservation. The dissection of the preserved animal was performed by standard techniques, under a stereo microscope, with the specimen immersed in the alcohol. All dissection steps were also photographed (e.g., Figures 3–5). Drawings were made with aid of a *camera lucida*.

Abbreviations used in figures are: **an**, anus; **au**, auricle; **by**, byssal gland; **cc**, gill ciliary connection; **ce**, cerebral ganglion; **co**, cerebro-visceral connective; **dd**, ducts to digestive diverticulae; **dh**, dorsal hood; **di**, inner demibranch; **do**, outer demibranch; **es**, esophagus; **fg**, gill food groove; **fm**, posterior foot retractor muscle; **fr**, anterior foot retractor muscle; **ft**, foot; **ga**, genital aperture; **gi**, gill; **go**, gonad; **gs**, gastric shield; **in**, intestine; **ip**, inner hemipalp; **ki**, kidney; **mb**, mantle border; **mo**, mouth; **mt**, mantle; **ne**, nephropore; **op**, outer hemipalp; **pa**, pedal aperture of mantle; **pc**, pericardium; **pg**, pedal ganglia; **pl**, pallial papilla; **pm**, pallial muscles; **pp**, palp; **rt**, rectum; **sh**, shell; **si**, excurrent siphon; **ss**, style sac; **st**, stomach; **ty**, typhlosolis; **ve**, ventricle; **vg**, visceral ganglia; **vm**, visceral mass.

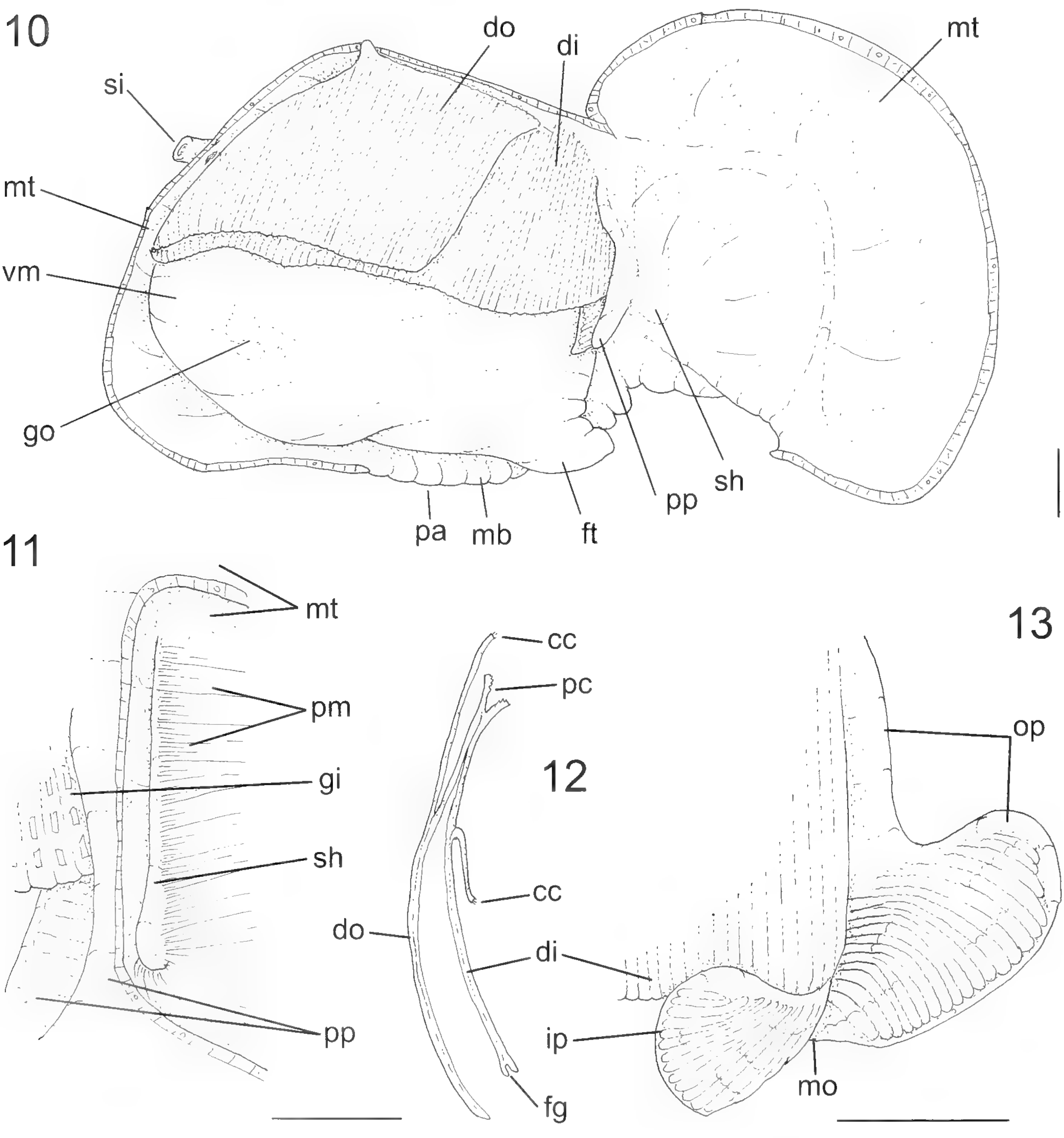
Institutional abbreviation: **MZSP**; Museu de Zoologia da Universidade de São Paulo, Brazil.

SYSTEMATICS

Chlamydoconcha avalvis new species
(Figures 1–20)



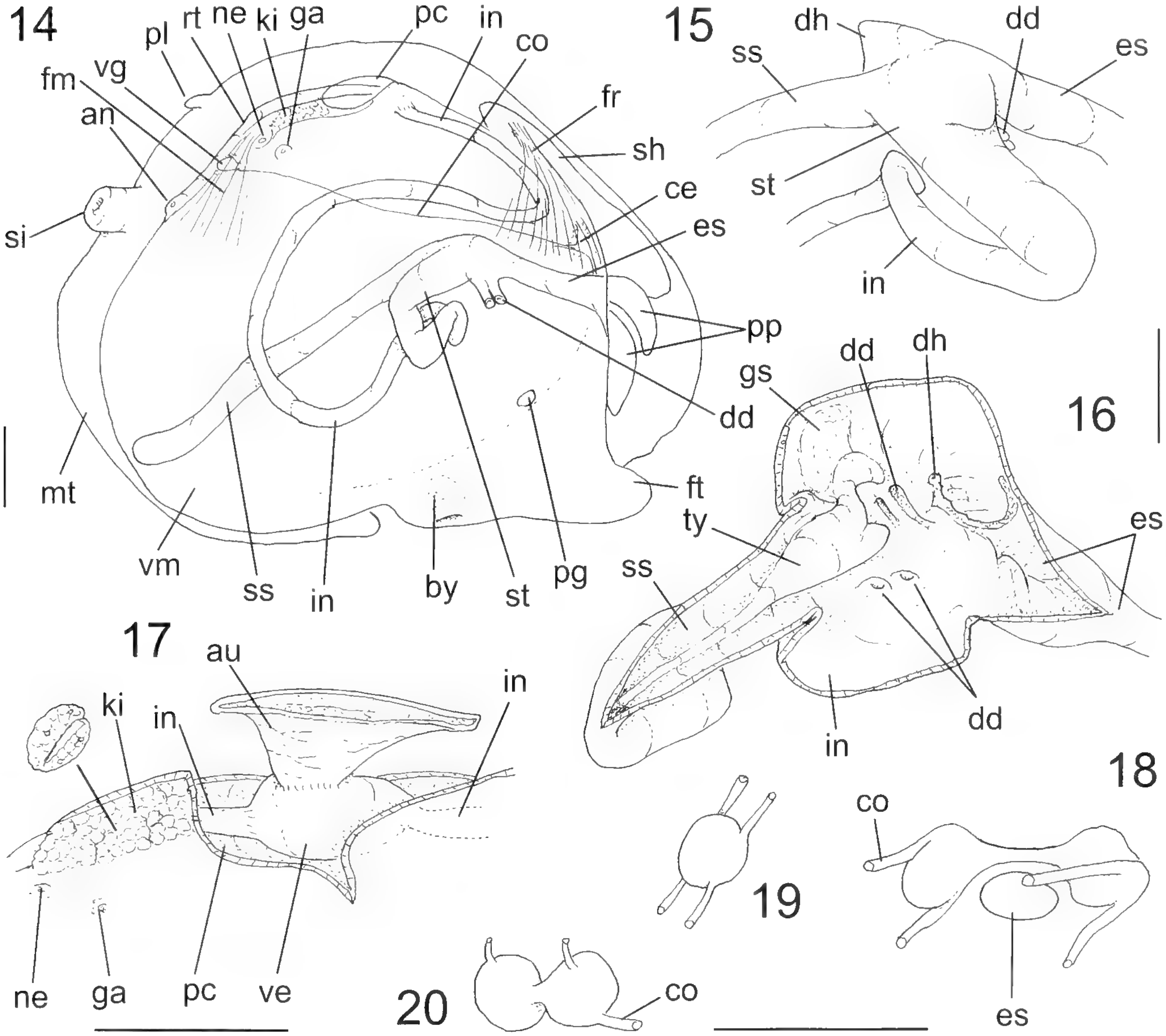
Figures 1–9. *Chlamydoconcha avalvis* Holotype photos. **1–2.** Living specimen, dorsal and lateral views, photo Vinicius Padula **3–5.** Preserved specimen. **3.** Dorsal view. **4.** Ventral view. **5.** Left view, right mantle lobe partially removed and deflected anteriorly, right gill deflected upwards. **6.** Right valve, outer view (transversal section artificially done). **7.** Same, inner view. **8.** Left valve, inner view. **9.** Right valve, ventral view of its posterior, concave region. Scale bars = 1–5 = 2 mm; 6–9 = 0.5 mm



Figures 10–13. *Chlamydoconcha avalvis* anatomy. **10.** Left view of entire animal, right mantle lobe partially removed and deflected anteriorly (right in Figure). **11.** Region of right valve, internal surface of mantle removed, showing pallial muscles (pm) originating in valve, some adjacent structures also shown. **12.** Gill, transversal section in its middle region. **13.** Right palp, outer hemipalp deflected anteriorly, a short portion if inner demibranch also shown. Scale bars = 1 mm.

Diagnosis: Species with a single papilla close to excurrent siphon. Anterior pallial gland shallow. Internal shell size about 10% of mantle surface; with rounded, almost [illegible] posterior end. Anterior pair of pedal retractor muscles with a branch originated from shell. Gastric main chamber and style sac narrow and long.

Description: Shell (Figures 6–9): Reduced, inequivalve, occupying about 1/10 of mantle, embedded into mantle anterior region (Figure 10, **sh**). Length approximately 4 times width. Color white, opaque. Outline softly irregular. Both valves asymmetrical; left valve about ¼ shorter than right valve (Figure 8) (this may be



Figures 14–20. *Chlamydoconcha avalvis* anatomy. **14.** Left view of entire animal emphasizing location of digestive tract and topology of main muscles, ganglia and glands, animal artificially represented as transparent. **15.** Midgut as *in situ*, right view. **16.** Same, slit longitudinally to expose inner surface. **17.** Renopericardial structures and region, right auricle artificially disconnected from gill and deflected upwards, a transversal section of indicated level of right kidney also shown. **18.** Cerebral ganglia, posterior-slightly right view, topology of esophagus also indicated. **19.** Pedal ganglia, right and slightly posterior view. **20.** Visceral ganglia, right and slightly posterior view. Scale bars = 1 mm.

abnormal). Shape somewhat deformed and irregular; flattened, planar. Prodissoconch rounded, sub-terminal: located in middle of anterior fifth of valve length; shape semispherical, with small dorsal bulging portion; 0.26 mm long, 0.31 mm height. Outer surface somewhat irregular with strong commarginal undulations and with rounded, concave impressions; with ventral edge elevated (Figure 9). Calcareous concretions close to periphery on right valve (Figure 8). Periostracum extending about 1/3 beyond calcareous portion of each valve, wider dorsally; color yellowish, transparent. Hinge edentulous. Ligament small, restricted to umbonal region, relatively wide (Figures 6–7), pale brown; resilifer absent. Inner surface glossy. Scar of anterior retractor muscle of foot occupying about 1/5 of inner surface, 3 times longer than wide, located just posterior to umbonal concavity.

MANTLE (FIGURES 1–5, 10): Surrounding body almost completely, spherical in contracted condition (Figures 1–4). Color pale cream, translucent (living and preserved). Outer surface smooth and simple, lacking papillae

Pedal aperture ventral, longer anteroposteriorly (Figures 4, 10); aperture length about half total mantle length. Edges of pedal aperture thick, simple, with undulations, thicker anteriorly. Anterior gland as a blind-sac, located in anterior, median region, about 1/3 of animal height from anterior end of pedal aperture (Figure 4, **ag**); size equivalent to 1/30 of mantle outer surface; its aperture central, with about ¼ of gland size. Excurrent siphon cylindrical, small, papilla-like, located about half of animal height from posterior end of pedal aperture (Figures 3, 10, **si**); length about 1/20 of animal length; internal surface smooth, simple. Single papilla located about 1/5 of animal length dorsal to excurrent siphon (Figures 1, 3, **pl**), on median line, solid, size about half of that of siphon. Pair of small, low, bulging projections slightly dorsal to anterior gland, corresponding with shell umbos. Mantle relatively thick, mostly hollow, sponge-like. Mantle inner surface smooth, simple (Figure 5).

Main Muscle System (Figures 11, 14): Adductor muscle not seen, possibly immersed in thin layer of visceral dorsal muscles. Pair of anterior pedal retractor muscles originate about 1/3 from inner surface of valves (scar described above), and about 2/3 splayed by anterodorsal region of visceral sac; gradually becoming thicker towards ventral, up to anterior half of pedal dorsal region. Pair of posterior pedal retractor muscles somewhat similar to anterior pair; originating in dorsal visceral sac side about ¼ posterior from that of anterior pair. Thin layer of pallial muscles splayed by mantle like a net; mainly concentrated anteriorly, inserting in anterior pair of pedal retractor muscles, in level just anterior to palps.

Foot and Byssus (Figures 4, 5, 10, 14): Foot narrow, longer antero-posteriorly; length about half of animal length; width about 1/5 of animal width; projected anteriorly at about ¼ of animal length. Anterior region somewhat pointed. Byssal gland a narrow furrow located subterminally, in posterior region of foot ventral medial line; about 1/7 of foot length. Byssal gland thin, hollow, chamber depth of about 1/5 of foot length (Figure 14, **by**). No byssus found.

Pallial Cavity (Figures 5, 10–13): Surrounding almost entire space between mantle and visceral sac, except for a dorsal portion correspondent to 1/10 of visceral sac surface connected to mantle. Gill eulamellibranch, heterorhabdic, occupying about half of pallial cavity, mainly in dorsal region (Figure 10), about two times longer than wide. Outer demibranch slightly triangular, about 2/3 of inner demibranch; anterior region becoming abruptly narrow, ending about 1/8 of total gill length-posterior to inner demibranch anterior end. Inner demibranch anterior end slightly rectangular, ending between hemipalps. Gills gradually narrowing towards posterior, up to somewhat pointed posterior end. About 1/4 of each gill (their posterior region) free from visceral mass, connected with each other by cilia. Cilia connect outer lamellae of outer demibranch with mantle and inner lamellae of inner demibranch with visceral sac (Figure 12, **cc**), same ciliary connection between both inner demibranchs in their region posterior to visceral mass. Connection among gill filaments by aligned longitudinal tissue rods equivalent in width to filaments; each longitudinal rod separated from neighbor rods by distance equivalent to 5 filaments. Ventral edge of outer demibranch simple; filaments very thin (about 1/50 of gill width), outer connection mostly dorsal.

Inner demibranch filaments a little shorter than inner demibranch itself; ventral edge with food groove. Inner gill connection to visceral mass dislocated ventrally, separated from remaining dorsal gill connection by distance equivalent to half gill width (Figures 5, 12). Palps (Figure 13) with size equivalent to 1/10 of that of gill; category II (Stasek, 1963). Hemipalps similar to each other; ventral half tall, slightly triangular; dorsal half narrow (about ¼ of ventral half), smooth, surrounding anterior insertion of inner demibranch. Inner surface of palp (ventral half) with uniform, transversal folds, about 20 folds in each hemipalp; more distal folds shorter, weakly arched, folds gradually becoming longer towards medial, dorsal region of folds becoming narrower and strongly arched, forming a folded dorsal furrow in direction to mouth; ventral end of each folds rounded; dorsal end weaker; a smooth, narrow area surrounding entire edges of hemipalps (Figure 13). Both palps separated from each other by a distance equivalent to half of longer portion of palp length. Mouth surrounded by anterior and posterior relatively tall lips, inner surface smooth.

Visceral Mass (Figures 5, 14): Bulging, spherical; separation with foot somewhat distinct. Gonad color cream, surrounding most of visceral structures, occupying about 80% of outer region. Genital aperture a small slit located about 1/20 of visceral height from dorsal edge and from nephropore (Figures 14, 17, **ga**); genital duct not discernible. Digestive diverticula restricted to central area of anterior region; color pale greenish beige. Renopericardial structures occupying about 1/10 of visceral volume, located in posterior region of dorsal surface.

Circulatory and Excretory Systems (Figures 14, 17): Heart of about 1/20 of visceral volume; located anterior to kidney; length about 1/8 of total length. Auricles triangular, insertion with ctenidial veins about ¼ of their length, located in posterior quarter of gill. Connection to ventricle longitudinal, lateral, with about half of ventricle length. Ventricle occupying about entire pericardial length. Kidneys white, extending from pericardium posterior end to area equivalent to pericardial length toward posterior region. Each kidney about three times longer than tall, mostly solid except for inner flattened lumen running longitudinally long central region. Each nephropore a minute slit located just anterior to origin of pair of posterior pedal retractor muscles; inside excurrent chamber of outer demibranch.

Digestive System (Figures 14–16): Palps described above (pallial cavity). Esophagus with about 2/3 of distance between palps in width; length about 1/5 of that of visceral mass; inner surface smooth. Stomach positioned transversal, somewhat perpendicular to esophagus, running towards right; narrowing gradually (Figure 15); estimated volume about 1/20 of that of visceral mass; Type IV (Purchon, 1958). Stomach inner surface with pair of low, narrow folds located transversally in esophageal insertion (Figure 16). Dorsal U-shaped furrow located just posterior to esophageal insertion (concavity posterior). Dorsal hood triangular, located at left side of stomach, with about ¼ of stomach height; its aperture as left end of U-shaped furrow. Ducts of digestive diverticula in two pairs; each pair located in middle region of lateral gastric side; left pair slightly longer than right pair. Typhlosole very wide on origin of style sac, narrowing relatively abruptly, running longitudinally in style sac left side as narrow, low fold. Gastric shield with about 1/8 of internal gastric surface; located inside U-shaped furrow. Style sac totally separated from intestine; long and narrow; width about 70% of that of esophagus; running somewhat straight backwards, ending in posterior wall of visceral mass. Digestive diverticula described above (visceral mass) Intestine originating in right side of style sac origin; inner surface smooth, simple; initially as wide as stomach, gradually becoming narrow up to 1/3 of its original width after a distance equivalent to that of esophagus. Intestine performing tight loops as shown in Figure 14; after this, performing wide, sigmoid loop, in such superior branch edges superior surface of visceral mass, along median line; running towards posterior. Anus sessile, simple; located at base of excurrent siphon.

GENITAL SYSTEM: Gonad described above (visceral mass). Genital pores represented by small slits equivalent in size to nephropore (Figures 14, 17, **ga**), located about 1/20 of total animal length from nephropore, slightly posterior and ventral. No indication on brooding in gills was observed.

CENTRAL NERVOUS SYSTEM (FIGURES 14, 18–20): Cerebral ganglia (Figure 18) located a short distance dorsal to mouth; each one with size equivalent to 1.5× esophagus diameter. Cerebral commissure narrow, length equivalent to each ganglion. Pedal ganglia (Figure 19) located in middle between cerebral ganglia and posterior end of foot; both ganglia completely connected with each other along median line, forming a single, spherical mass of equivalent size of each cerebral ganglion. Visceral ganglia (Figure 20) located just ventral to origins of posterior pair of pedal retractors; size equivalent to about 80% of that of cerebral ganglia, visceral commissure very short, ganglia almost touching each other. Cerebro-visceral connective very narrow, running through gonad (Figure 14, **co**).

Measurements: Animal length = 15 mm; valve = 3.7 by 1.2 mm.

Holotype: MZSP 86318, Vinicius Padula col., 05 March 2006.

Type Locality: Brazil, Rio de Janeiro, Cabo Frio, Ilha Comprida, 22°51′47″ S, 41°56′35″ W, about 6 m depth, under rocks.

Distribution: Only known from the type locality.

Etymology: The specific epithet refers to the apparent absence of the shell valves, which are virtually invisible in the living animal; a combination of the Latin negative prefix *a* and the noun *valvis*.

Comparative Remarks: *Chlamydoconcha avalvis* has the external surface of the highly developed mantle practically lacking papillae (Figures 1–4). This is the main character differentiating the species from the Pacific congener *C. orcutti*, which has a richness of papillae in the outer mantle surface, somewhat equidistantly disposed (Dall, 1884; Bernard, 1897; Williams, 1949; Morton, 1981: fig. 8). However, a single papilla is present in *C. avalvis*, close to the excurrent siphon; *C. orcutti* also possesses a differentiated papilla in the same position (Bernard, 1897: fig. 3), which was named "defensive papilla" by Morton (1981).

Anatomically, both *Chlamydoconcha* show similar organization. Mantle enlargement, foot features, position of the valves and main muscles, and internal features of glands and digestive tubes, are similar in the two species. The main anatomical differences, beyond the above mentioned papillae, are: The shell is proportionally smaller in *C. avalvis* (about 1/10 of mantle, Figure 14) than that of *C. orcutti* (about 1/6 of mantle). Although the prodissoconch (Figures 6–8) is very similar in both species, the posterior end of the shell of *C. avalvis* is more squarish than that of *C. orcutti*; in which the posterior end of the shell is pointed (Bernard, 1897: fig. 13; Morton, 1981, figs. 4–5). The anterior gland of *C. avalvis* is a blind sac, its internal chamber is small and short, practically with the same thickness of the surrounding mantle (Figure 4, **ag**); on the other hand, that of *C. orcutti* (Bernard, 1894: "cheminée dorsale") has a deeper empty chamber directed posteriorly (Bernard, 1894: fig. 19, X), more recently, this gland was designated "pheromone organ" (Morton, 1981, fig. 10), and described with similar characters of *C. avalvis*. The anterior pair of pedal retractor muscles has a branch originated from the inner surface of the valves in *C. avalvis* (Figure 14, **fr**); this is not described for *C. orcutti* (Bernard, 1894: fig. 20, mp), although mentioned by Morton (1981). The midgut organization of *C. avalvis* (Figures 14–16) is quite different from that of *C. orcutti* (Bernard, 1894: figs 9, 19; Morton, 1981, fig. 24) in several details, the main characters are: the narrower and longer gastric style sac of *C. avalvis*, while that of *C. orcutti* is wider and shorter (about 1/3 of visceral sac length); the stomach is also narrower and smaller in *C. avalvis* than that of *C. orcutti*; the intestinal loops are differently performed in both species, and in *C. avalvis* it is apparently narrower

Although the living animal of *C. avalvis* (Figures 1–2) was not observed crawling, it is possible that it also has an anterior projection of the mantle like that of *C. orcutti* (Bernard, 1894: figs.10, 11; Williams, 1949; Morton, 1981), as the mantle arrangement of that region is taller and wavy. The presence of a single siphon close to the anus shows that the siphon is excurrent; as no incurrent siphon is present, the conclusion that water intake takes place through the pedal aperture (Morton, 1981). This feature is also found in other galeommatids, such as *Kellia porculus* Pilsbry, 1904; *Scintilla nitidella* Habe, 1962 (Morton and Scott, 1989, figs. 3, 18).

DISCUSSION

Discovery of the second species in the genus *Chlamydoconcha* fits the description of the genus by Dall (1884). The anatomical characters of the *Chlamydoconcha* species are quite modified, even if considered under the light of the extraordinary suite of modifications exhibited by the Galeommatoidea (Woodward, 1893; Morton, 1981; Bieler and Mikkelsen, 1992). The reduction of the shell of *Chlamydoconcha* is apparently the most extreme in all Bivalvia; its interiorization inside the mantle is also found in other genera, e.g., *Galeomma* Turton, 1825, *Ephippodonta* Tate, 1889 (Woodward, 1893; Lützen and Nielsen, 2005), and *Divariscintilla yoyo* Mikkelsen and Bieler, 1989. All these genera and species, however, have proportionally larger valves. The foot is an important comparative character in Galeommatoidea. The "hanging" foot and the flower-like organ are some of the main characters (Bieler and Mikkelsen, 1992; Jespersen and Lützen, 2006); *Chlamydoconcha* possesses at least the first of these two characters. A molecular study (Ó Foighil et al., 2001) places *Chlamydoconcha* as terminal taxa inside the Galeommatidae, a similar result of the morphological approach (Bieler and Mikkelsen, 1992). A dwarf male has been described for *Chlamydoconcha orcutti* (Morton, 1981), however, one has not been found so far in *C. avalvis*.

ACKNOWLEDGMENTS

A special thank to Vinicius Padula, Museu Nacional, Universidade Federal do Rio de Janeiro, by collect and donation of the lot examined herein. This study is sponsored in part by FAPESP (Fundação de Amparo a Pesquisa do Estado de São Paulo), project no. 04/02333-8.

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Research Note

Sinistral *Campeloma decisum* (Say, 1817) (Gastropoda: Viviparidae) from the Fox River, Illinois

Campeloma (Gastropoda: Viviparidae) are a group of ovoviviparous, prosobranch snails endemic to North America east of the Rocky Mountains (Burch, 1989). These snails are known to burrow in mud or sand in freshwater streams and lakes and feed on carrion (van der Schalie, 1965; Burch, 1989). *Campeloma* spp. from southern North America typically reproduce sexually but those from the northern United States and Canada are parthenogenetic due to the scarcity of males in this region (van der Schalie, 1965). Shells of *Campeloma* are moderately thick, conical, and imperforate with a smooth surface and rounded whorls, and although normally dextral, sinistral specimens are occasionally found (Baker, 1928; Burch, 1989). In fact, Call (1886) pointed out Rafinesque's "type" of *Campeloma crassulum* Rafinesque, 1819, from the Ohio River was sinistral, noting that the shell had "four whorls of the spire reversed." Sinistral individuals show not only a reversal in shell orientation but also in organ placement (Savage, 1938).

Sinistral *Campeloma* have been found throughout eastern North America. Call (1880) recorded *C. decisum* (Say, 1817) (as *C. integrum* and *C. rufum*) from the Erie Canal at Mohawk, New York, Pilsbry (1897) reported sinistral *C. decisum* from the Hudson River at Fort Edward, New York, and Ancey (1897) commented on sinistral *C. decisum* from New York but gave no specific location. Bickel (1966) examined sinistral *C. crassulum* from the Ohio River at Louisville, Kentucky, Goodrich (1939) discussed sinistral *C. geniculum* (Conrad, 1834) from the Ogeechee River in Georgia, and Lee (2008) figured a sinistral *C. limum* (Anthony, 1860) from the Altamaha River at Doctortown, Georgia. Baker (1902) commented on a "reversed" *C. decisum* (as *C. rufum*) in a private collection, gave dimensions of a reversed *C. decisum*, and figured a sinistral *C. decisum* (as *C. subsolidum*), but did not give locality data for any of the specimens examined. Sampson (1916) stated that he had sinistral *C. decisum* (as *C. subsolidum*) in his collection from Flat Creek in Pettis County, Missouri, and Call (1886) referred to sinistral *C. descisum* (as *C. subsolidum*) from a slough near Fort Dodge, Iowa, and figured a reversed *C. decisum* (as *C. obesum*) from Lewis, Iowa. Baker (1928) figured sinistral *C. decisum* (as *C. integrum*, *C. rufum*, and *C. brevispirum*) from three different locations in Wisconsin (Wisconsin River near Merrimack, Sturgeon Bay at Sturgeon Bay, and Mirror Lake presumably near Baraboo), and Haas (1939) reported on a sinistral *C. decisum* (as *C. integrum*) from the Kankakee River near Shelby, Indiana. In Illinois, sinistral *C. decisum* (as *C. integrum* and *C. rufum*) have been reported from the Salt Fork Vermilion River near Homer (van Cleave, 1936), the Des Plaines River in the Chicago area (Lee, 2008), and Jackson Park Lagoon in Chicago (Hand, 1928; Meyer, 1928; Haas, 1939).

Sinistral uterine young in *Campeloma* have been reported by several authors, including Call (1880), Pilsbry (1897), Hand (1928), van Cleave (1936), and Haas (1939). Both dextral and sinistral *Campeloma* produce sinistral embryos (Hand, 1928; Haas, 1939). Sinistrality might result from either embryological disturbances (e.g., crowded uteruses or damaged eggs) that have no genetic basis, or individual mutations destined to disappear in the population because copulation between dextral and sinistral snails is impeded by mechanical incompatibility (Call, 1880; van Cleave, 1936; Cazzaniga and Estebenet, 1990). However, because some degree of assortative mating occurs in gastropods, sinistral snails could become reproductively isolated (Cazzaniga and Estebenet, 1990); also, because many *Campeloma* lineages are parthenogentic, sinistral snails could become unconstrained by mating compatibility (Mattox, 1938; van der Schalie, 1965). There appears to be a progressive reduction in the percentage of sinistral individuals from uterine young to adults with only a few individuals reaching sexual maturity (van Cleave, 1936). This high degree of mortality might occur as the result of morphological or physiological abnormalities (van Cleave, 1936; Bickel, 1966).

We here report on sinistral *C. decisum* from the Fox River basin near Algonquin, Illinois. Nineteen specimens of *C. decisum* from "Mill Pond (near creek), Algonquin, Illinois," were found in the University of Illinois Museum of Natural History Mollusk Collection, Champaign-Urbana (UIMNH 18288); no date was given for this lot but the collector, the Rev. W. A. Nason, died in 1921. In addition, a relict sinistral *C. decisum* shell was collected by JST while conducting a freshwater mussel survey in the Fox River at Buffalo Park Forest Preserve near Algonquin (42.1486° N, 88.2900° W), Kane County, Illinois, on 25 July 2007. This specimen was extracted from silt-compacted gravel in an impounded area of the river and has been deposited in the Illinois Natural History Survey Mollusk Collection, Champaign (INHS 31862).

The Fox River has experienced sub-substandard water quality conditions prior to the passage of the Clean Water Act and has encountered habitat changes (e.g., increased siltation and substrate compaction) due to the presence of lowhead dams (Santucci et al., 2005; Tiemann et al 2007). Because these physicochemical changes have been shown to alter freshwater snail assemblages (Burch, 1989), the population of sinistral *C. decisum* in the Algonquin area might be extirpated. Fieldwork will continue in an attempt to document live individuals.

ACKNOWLEDGMENTS

Funds were provided by the Illinois Department of Transportation. A. Kuhns (INHS) and J. Griesbaum (INHS) assisted in the 2007 sampling. T. Stewart (Iowa State University) assisted in identification of the 2007 specimen. G. Levin (INHS), D. Thomas (INHS), B. Tiemann, and two anonymous reviewers offered constructive criticism.

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THE NAUTILUS 122(4):261–263, 2008

Book Reviews

Freshwater Mussels of Alabama & the Mobile Basin in Georgia, Mississippi & Tennessee

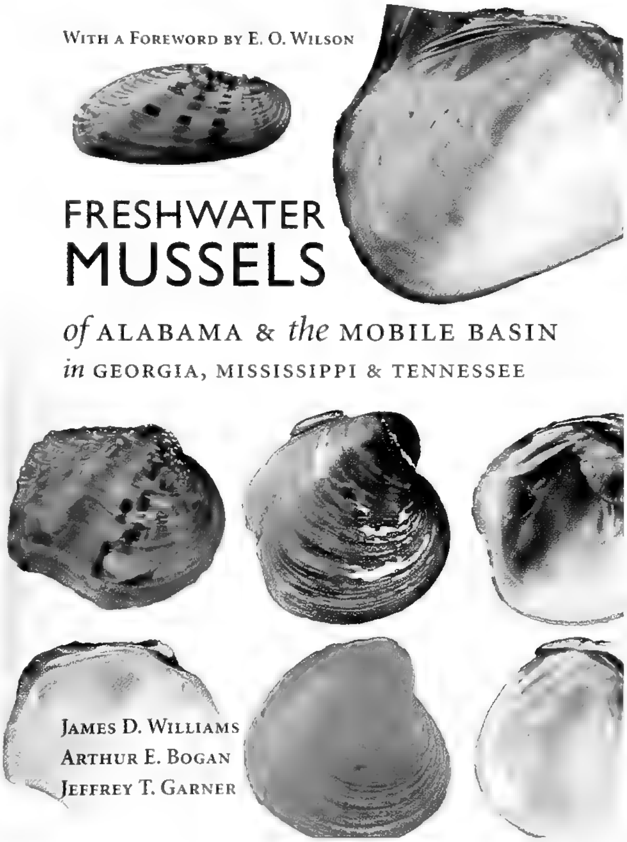
Williams, James D., Arthur E. Bogan, and Jeffrey T. Garner. 2008. Freshwater Mussels of Alabama & the Mobile Basin in Georgia, Mississippi & Tennessee. University of Alabama Press, Tuscaloosa, xv + 1–908, including numerous text figures and maps, many in color. ISBN-13: 978-0-8173-1613-6 (cloth: alk. paper); ISBN-10: 0-8173-1613-6 (alk. paper) 9 × 11.5 inches. Hardback; 10 lbs. $70.00 from publisher and several booksellers; possibly less on eBay.

Over the last decade or two the awareness of the American populace and its policy-makers with the country's indigenous flora and fauna has been stirred to an unprecedented degree. Government has responded to a new culture of concern over environmental change and the conservation of natural communities, and one of the most important consequences of riding this *zeitgeist* has been the commissioning of scientists to elucidate the current state of our biota. Conspicuous among the products of this "green revolution" is a watershed of works treating the naiad fauna of either a political unit (e.g. state) or a major river system. Except possibly for Constantine Rafinesque's epiphany on the banks of la Rivière Ohio has there been such a celebration of this natural resource!

Preceded by recent works treating the biology of pearly freshwater mussels of several eastern American regions, most conspicuously the state of Tennessee and the Appalachicola River system (Georgia, Alabama, Florida), Williams, Bogan, and Garner have tackled the most extensive fauna yet considered, that of Alabama and the entire Mobile Basin, but, based on other works of this contemporary genre, as we shall see, the treatment of those 178 species-level taxa, were it by traditional measure, only partially accounts for the prodigious metrics (e.g. weight) captioned above.

The work is organized into a foreword, acknowledgements, institutional abbreviations, 16 chapters, an appendix (North American naiad type catalogues), a glossary, bibliography, and index. Certain observations can be made as one moves through the work.

Introductory comments place Alabama and its mussel fauna in a broader context and present the grim reality of habitat degradation, resource depletion, extirpation, and extinction. No less than 23 reviewers are acknowledged for vetting this opus; workers in over 30 museums on other institutions were cited as collaborators, and dozens of field workers contributed their labors. Thanks are also offered to molecular geneticists, whose work underpinned many of the taxonomic innovations mentioned later.



With a Foreword by E. O. Wilson

FRESHWATER MUSSELS

of ALABAMA & *the* MOBILE BASIN

in GEORGIA, MISSISSIPPI & TENNESSEE

James D. Williams
Arthur E. Bogan
Jeffrey T. Garner

There follows an historical review of naiad work in the state. The contributions of the feuding Quakers Isaac Lea and Timothy Conrad, of C. T. Simpson, H. H. Smith, and H. D. Athearn, the latter two being the dedicatees of the book, and many others are presented briefly.

Chapter 3 spans 25 pages and presents an analysis of the inland waters of Alabama and the Mobile Basin, which support more aquatic biodiversity than any other area of comparable size on the continent. The geography, geology, hydrology, and, regrettable degradation of these waterways (damming, canalization, etc.) is discussed in detail. The use of archival maps and photographs along with present-day images provides a starkly heuristic backdrop.

Short chapters basically tabulate mussel taxa by constituent watercourse in the post-European and archaeological record. A section on the commercial use of mussels and their pearls is nicely illustrated and again reinforces the theme of resource depletion. Chapter 7 is an historical review of naiad conservation efforts in the state, which have been rather extensive, particularly in the last decade; it concludes with a tabulation of the 48 Alabama species listed as endangered or threatened as of January, 2006, under provisions of the federal Endangered Species Act.

Twenty pages are devoted to the ecology and life history of the naiads. The topics are treated with thoroughness and involve aspects of habitat (and its degradation), feeding, predation, competition, parasitism, and the unique reproductive and larval strategies if these mollusks—including anatomic and behavioral contrivances to optimize host fish infestation. Much recent work is brought to bear on these topics.

Shell morphology and higher (ordinal, suprafamilial, familial) classification are dealt with succinctly; the latter with the most current systematic insights.

Chapter 11 explains the format of the accounts in the taxonomic section. These headings are uniform and clearly indicated: Scientific and Common Name (each epithet initiated in upper case!); Illustrations; Description of Shell, Soft Anatomy, Glochidium, Similar Species; General Distribution; Alabama and Mobile Basin Distribution (a map appears at the end of each entry and is marked with black dot for each recorded occurrence); Ecology and Biology; Current Conservation Status and Protection; Remarks; and Synonymy. The latter includes a caveat indicating that this is far from a chresonymy, being limited to the first usage of a species-level epithet (generic reassignment not considered) considered in synonymy. On the other hand, it is generously, almost exhaustively, illuminated with type figures, in color when available.

The over 700-odd pages devoted to the treatment of two Unionoidean families, 43 genera, and 178 species-level taxa plus short vignettes on five species of hypothetical occurrence, six non-naiad clams (Sphaeriidae is not parsed) including the two non-natives *Corbicula fluminea* and *Dreissena polymorpha*, and finally a newly-diagnosed identity for the spuriously recorded (mislocalized) *Unio decumbens* I. Lea, 1861 [*Trapezoideus exolescens* Gould, 1843) of southeast Asia].

The bibliography contains over 1000 titles, and the index is inclusive with all topics, terms, person- and place-names, and genus-species, species-genus entries, and the same reciprocation for the common names.

A stunning feature of this work is the photography of Richard Bryant, who captures the shells of each species-level taxon in large format, with crispness and color accuracy. The specimens are almost all of the highest quality, sometimes apparently requiring the use of extralimital material. The shells are scrupulously posed with the adductor scar axis horizontal, posterior to the left (as was the custom of the prolific naiadologist-publisher Isaac Lea). Such conventions make it easy on the diagnostic eye.

The marshalling of information in the taxonomic portion, particularly in Ecology and Biology and in the Remarks is staggering and probably indicates a strong collaboration among the authors of this work. Other features such as the thousands of locality indicators, the lifting of hundreds of type figures from classic works, give a dimension to this work that is unprecedented, especially informative, and indicative of a lot of hard [illegible]

There are taxonomic initiatives exercised in this work. A major one of these is dealing with the "*Pleurobema* problem." Tabulations of pages 501–504 indicate the profusion of available names for Mobile Basin and other Alabama species and the synonymies of four prior monographers and in the present work, which has a relatively conservative perception of the diversity. Williams et al. pare the list of Turgeon, Quinn, et al. (1998) by seven species while adding three classic and one post-1998 species. Likewise three *Elliptio* species. are resuscitated from synonymy as are a half dozen other species in five genera. There are three un-named taxa included in the work, *Anodonta* sp., *Epioblasma* sp. cf. *capsaeformis*, and *Toxolasma* sp. Each is, however, provided with vernacular names—a convenient machination.

Although installed in the literature over the last decade, reassignments of long-recognized species to the resurrected *Pleuronaia* Frierson, 1927, and the newly-ordained *Hamiota* Roe and Hartfield, 2005, may surprise the reader. There are another half dozen generic reassignments necessitated by molecular genetic study, perhaps the most surprising of which is the Pistolgrip, *Quadrula verrucosa* (placing *Tritogonia* in synonymy).

Implausible as it may appear in context, there are two rather minor detractions which warrant brief mention. If I had my say in the creation of this *magnum opus*, I would have asked for a discussion of the geological history that provided the state with the isolation of the Mobile Basin system, without which its present naiad diversity would have never reached the unassailable present-day mark. I see no reference to the Tertiary calamity that diverted the Tennessee River from its ancient course southwest past Lookout Mt. and into the heart of Alabama and thence to the Gulf of Mexico. The classic paper by Simpson (1900) on the evolution of the relevant naiad faunas and the geological evidence in support of it (Johnson, 1905a, 1905b; Adams, 1928) seem appropriate for the beginning of Chapter 3. The other little vexation is the persistence of gender-bending binomina in the naiad literature. It is not entirely clear how "*Pleurobema stabilis*" and "*Ptychobranchus subtentum*" became entrenched, but the Code and the original descriptions indicate they should be rendered *Pl. stabile* and *Pt. subtentus*.

Williams, Bogan, and Garner have produced a holistic and exhaustive work, carefully executed and seductively constructed. The taxonomic scope is unprecedented in recent years, covering some 60 percent of the American fauna. Aside from being a precious asset to the malacological community, it will advance the understanding of biodiversity, ecology, and conservation in a much wider audience. To quote from Edward Osborne Wilson's Foreword: "People do care about species of wildlife, however, if they see a picture of it, know its name, and read what is known of its distribution and natural history. In addition to their contribution in mussel biology, this is what the authors have given us."

We applaud Williams, Bogan, and Garner, and we commend the Alabama Department of Conservation, Game and Fish Division as well as Auburn University, whose commitment has helped assure that this prodigious work will be affordable to a wider readership.

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Guide to the Freshwater Molluscs of the Lesser Antilles

Pointier, Jean-Pierre. 2008. Guide to the Freshwater Molluscs of the Lesser Antilles. Conch Books, Hackenheim, Germany, 127 pp. www.conchbooks.de. Retail price: 38.

This small volume covers the freshwater molluscan fauna of the islands of the Lesser Antilles. These islands form a double arc of volcanic islands extending from Anguilla in the north to Grenada in the south along the east edge of the Caribbean Sea. Dr. Philippe Jarne, of Montpellier, France wrote the short preface. A brief history of the study of freshwater mollusks in the Lesser Antilles is also provided.

Pointier reports nine families of gastropods and two families of bivalves; 28 gastropod and three bivalve species from the islands. The gastropods are divided into 19 native gastropod species including the two endemic species, *Neritilia succinea* [Neritiliidae] and freshwater opisthobranch *Tantulum elegans* [Tantulidae], and nine introduced species. Lesser Antilles freshwater bivalve fauna contains the introduced *Mytilopsis leucophaeta* and two endemic species of Sphaeriidae.

This volume has a flow chart key to the families of gastropods and bivalves and is supplemented with a page of figures illustrating the key landmarks, shell sculpture, and types of opercula. Species are treated by family units in the same order as found in the key with discussion of the anatomy and ecology for the members found in the Lesser Antilles. Each of the gastropod species accounts is accompanied by two to five color illustrations of the shells, eggs, live animals, and ecology. The pulmonate species accounts incorporate illustrations of the reproductive anatomy of each species. A section is devoted to aquatic habitats where these mollusks have been collected and includes 44 color photographs of habitats and plants. The figure captions note some of the snail species found on the plants and some plants used as egg-laying sites or food. This volume is based on extensive field work throughout the Lesser Antilles. Species are well illustrated, including close-up color figures of live specimens of all but the freshwater opisthobranch *Tantulum elegans*. "Guide to the Freshwater Molluscs of the Lesser Antilles" is a great companion to the earlier work on the freshwater mollusks of Cuba (Pointier et al., 2005).

I have found this volume very useful and recommend it for anyone working on, or interested in, identification of the freshwater mollusks of the Lesser Antilles. This book will fit nicely in a backpack and will be a handy reference in the field. I would recommend this well illustrated book to anyone interested in freshwater mollusks.

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Pointier, J.-P., M. Yong and A. Gutiérrez. 2005. *Guide to the freshwater molluscs of Cuba*. Conch Books Hackenheim, Germany. 119 pages.

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Notice

Bulletin of Zoological Nomenclature 65(2): 152. June 2008.

OPINION 2197 (Case 3341) of the International Commission on Zoological Nomenclature.

***Cardium egmontianum* Shuttleworth, 1856 (currently *Trachycardium egmontianum*; Mollusca, Bivalvia, CARDIIDAE): current usage conserved.**

Abstract. The Commission has ruled that the current usage of the specific name *egmontianum* for a common and widespread western Atlantic bivalve *Trachycardium egmontianum* (Shuttleworth, 1856) of the family CARDIIDAE is conserved by setting aside all lectotype designations for *Cardium mindanense* Reeve, 1844, prior to that by Vidal (1998).

LITERATURE CITED

Vidal, J., 1998. Taxonomic revision of the Indo-Pacific *Vasticardium assimile* species group (Mollusca, Cardiidae). Apex 13: 111–125.

Errata

A couple of items published in the most recent issue of The Nautilus (volume 122 issue number 3) need correction.

In the article by Villalobos-Rojas et al. (2008), page 155, right-hand column, line 5, the first name of Ms. Kirstie Kaiser was misspelled. In the same article, the complete reference to Pitt and Kohl (1979) was omitted (see below).

In the article by González-Vallejo (2008), page 180, the image representing the female shell on Figure 3, right, was inverted by the authors; that shell is not left-handed.

The editor apologizes to all parties concerned for these editorial blunders.

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González-Vallejo, N. E. 2008. Parasitism of *Monogamus minibulla* (Olsson and McGinty, 1958) (Gastropoda: Eulimidae) on the red sea-urchin *Echinometra lucunter* (Linnaeus, 1758) (Echinodermata: Echinometridae) on the Caribbean coast of Mexico. The Nautilus 122: 178–181.

Pitt, W. and R. Kohl. 1979. A new Panamic *Mitrella* (Mollusca: Gastropoda). The Veliger 21: 467–468.

Villalobos-Rojas, F., A. G. Guzmán-Mora, Y. E. Camacho-García. 2008. Catalogue of the type material deposited at the Zoology Museum, University of Costa Rica. The Nautilus 122: 155–165.

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INSTRUCTIONS TO AUTHORS

THE NAUTILUS publishes articles on all aspects of the biology, paleontology, and systematics of mollusks. Manuscripts describing original, unpublished research and review articles will be considered. Brief articles, not exceeding 1000 words, will be published as notes and do not require an abstract. Notices of interest to the malacological community will appear in a notices section.

Manuscripts: Each original manuscript and accompanying illustrations should be submitted to the editor preferably via e-mail or as hardcopy in triplicate.

Text must conform to the dimensions of 8½ × 11-inch paper, double-spaced, and single-column throughout (including literature cited, tables, and figure captions). Authors should follow the general recommendations of *Scientific Style and Format—The CSE Manual for Authors, Editors, and Publishers*, available from the Council of Science Editors at www.councilscienceeditors.org. The first mention of a scientific name in the text should be accompanied by the taxonomic authority, including year. Latinized names and other words to be printed in italics must be underlined; leave other formatting indications to the editor. Metric, not English, units are to be used. Geochronologic modifiers should be capitalized only when units are formally recognized: for instance, use Late Cretaceous but early Miocene. Likewise, only modifiers of formally recognized chronostratigraphic units are capitalized: use Lower Jurassic but upper Oligocene.

The sequence of sections should be title page, abstract, introduction, materials and methods, results, discussion, acknowledgments, literature cited, tables, figure captions, figures. The title page should include the title, author's name(s) and address(es). If corresponding author is not the senior author, please indicate. The abstract should summarize in 250 words or less the scope, main results, and conclusions of the article. Abstracts should be followed by a list of additional key words. All references cited in the text must appear in the Literature Cited section and vice-versa. Please follow a recent issue of THE NAUTILUS for bibliographic style, noting that journal titles must be unabbreviated. Information on plates and figures should be cited only if not included within the pagination of cited work. Tables must be numbered and each placed on a separate page. If in doubt, please follow a recent issue of the journal for sequence of sections and other style requirements.

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All line drawings must be in black, clearly detailed, and completely labeled. Abbreviation definitions must be included in the caption. Line drawings must be high resolution files at least 600 dpi (dots per inch) resolution at actual size. Standard digital formats for line drawings include .tif, .bmp, .psd, .eps, and .pdf.

Photographs may be submitted in black-and-white or color, preferably in RGB mode if in color. Standard digital formats for photographs include .tif, .psd, .jpg, or .pdf. Photographs must be high resolution files at least 300 dpi resolution at actual size.

If more than one figure is included in an illustration, all figures are to be consecutively numbered (Figures 1, 2, 3, . . . , NOT Figures 1A, 1B, 1C, . . . , NOR Plate 1, Figure 1, . . .). In illustrations with more than one figure, make sure that blank areas between figures is kept to a minimum, thereby allowing for more area for each individual figure.

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Voucher Specimens: Deposition of the holotype in a recognized institutional, public collection is a requirement for publication of articles in which new species-level taxa are described. Deposition of paratypes in institutional collections is strongly encouraged, as is the deposition of representative voucher specimens for all other types of research work.

The Editorial Process: Upon receipt, all manuscripts are assigned a number and acknowledged. The editor reserves the right to return manuscripts that are substandard or not appropriate in scope for THE NAUTILUS. Manuscripts deemed appropriate for the journal will be sent for critical review to at least two reviewers. The reviewers' recommendations will serve as basis for rejection or continuation of the editorial process. Reviewed manuscripts will be sent back to authors for consideration of the reviewers' comments. The revised version of the manuscript may at this point be considered accepted for publication by the journal.

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