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Hamiota, a new genus of freshwater mussel (Bivalvia: Unionidae) from the Gulf of Mexico drainages of the southeastern United States

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ABSTRACT

Hamiota, a new genus of freshwater mussel containing four species formerly assigned to the genus *Lampsilis* Rafinesque, 1820, is described. In addition to the genus *Lampsilis*, members of *Hamiota* had previously been placed in the genera *Villosa* Frierson, 1927, and *Ligumia* Swainson, 1840. Several characters including the packaging of their larvae in a superconglutinate lure to attract host fishes, placement and shape of the marsupia, and release of glochidia through the excurrent siphon, support the recognition of these species as a distinct genus.

INTRODUCTION

Following the discovery in 1988 by Robert Butler of the first superconglutinate lure ensnared on a snag in a tributary of the Choctawhatchee River, a number of publications (e.g., Haag et al., 1995; Hartfield and Butler, 1997; O'Brien and Brim Box, 1999; Blalock-Herod et al., 2002) have confirmed through direct observation the supposition that these unique lures are produced by four species of freshwater mussels endemic to the Gulf of Mexico drainages of the southeastern United States. Herein, we confirm earlier published suggestions that these four species represent a distinct genus of freshwater mussels (Fuller and Bereza, 1973; O'Brien and Brim Box, 1999). The recognition of this genus is based on several characters including the production of the superconglutinate lure, and the unique shape and placement of the marsupia (the region of the demibranchs where female unionoid mussels brood developing larvae), and is supported by molecular evidence (Roe et al., 2001). Use of marsupial features is consistent with previous designations of unionid "divisions" initiated by Simpson (1900a) and continued by Heard and Guckert (1970). The designation of *Hamiota* increases the number of North American unionids genera to 50 (Turgeon et al., 1998).

MATERIALS AND METHODS

A list of specimens examined is included in Appendix 1. Acronyms used in the text are: Academy of Natural Sciences of Philadelphia (ANSP), Delaware Museum of Natural History (DMNH), Florida Museum of Natural History (UF), United States National Museum (USNM), University of Alabama Unionid Collection (UAUC), and Mississippi Museum of Natural Science (MMNS). Abbreviated synonymies are presented for each taxon and include novel combinations and publications with illustration. Measurements were taken to the nearest 0.05 mm using dial calipers.

SYSTEMATICS

Family Unionidae Rafinesque, 1820
Tribe Lampsilini von Ihering, 1901

Hamiota new genus. Type species: *Hamiota subangulata* (Lea, 1840) by original designation

Diagnosis: A monophyletic group of freshwater bivalves (Roe et al., 2001) in which all of the glochidia are released simultaneously encased in mucous packages that are referred to as superconglutinates (Haag et al., 1995, fig. 1). The superconglutinate lure exits the mantle cavity via the excurrent opening and is encased within a transparent mucous tube (Hartfield and Butler, 1997; O'Brien and Brim Box, 1999). When acted upon by water currents the superconglutinate mimics the movements of a swimming fish, and has been shown to elicit attacks from fishes (Haag and Warren, 1999). The marsupium is restricted to the ventral portion of the outer demibranchs of female mussels (Figure 1). The precise shape and pigmentation of the marsupia, as well as the degree of posterior mantle margin development, varies across species.

Description: Members of this genus are small- to medium-sized freshwater bivalves, and adult valves generally are between 45–100 mm in length. Shells range from ovate to elliptical in outline, and are somewhat

Figures 1, 2. Inner mantle and outer demibranchs of gravid superconglutinate-producing mussels in the genus *Hamiota* and inner mantle and outer demibranchs typical of non-superconglutinate-producing mussels of the genera *Lampsilis, Ligumia,* and *Villosa.* **1.** Female *Hamiota australis.* **2.** Female *Villosa vibex.*

compressed to moderately inflated. Shell thickness ranges from heavy to thin. Sexes display some degree of dimorphism in shell shape. Shells of male mussels are typically more acutely pointed posteriorly, whereas shells of female mussels display an expanded posterior margin. Periostracum is typically smooth, but can be very glossy in some species. Background color ranges from dark-brown and black through chestnut-brown to straw-yellow. Black to bright green rays of variable width are often present and may be limited to the posterior slope, or cover the entire disk. Nacre color is typically white although other colors such as salmon or blue may be seen as well, particularly in the beak cavities or the posterior margins. The marsupia are often asymmetrical in shape; the anterior portion is typically broadest, tapering toward the posterior end. The ventral margin of the marsupium is darkly pigmented in gravid females. Pigmentation of marsupia varies across species and populations and colors may include purple, red, black, or white. In females, the mantle margins anterior to the branchial opening are elaborated to varying degrees. The morphology of the glochidial valves of members of *Hamiota* is similar to that of members of *Lampsilis* or *Villosa* (O'Brien and Brim Box, 1999).

Etymology: *Hamiota* = angler. Derived from the Greek word *hamus,* meaning hook. This name refers to the means by which members of this genus attract host fishes by packaging their parasitic larvae in a lure that mimics a small fish.

Remarks: Species of *Hamiota* generally have been treated as *Lampsilis* due to the similarity in shape and coloration of their shells. Some authors also have included these species in the genus *Villosa* or *Ligumia,* due to shell shape, thickness, and/or ornamentation of the mantle flap. The shells of *Hamiota* species are indeed similar to the shells of these genera, and the mantle flap may exhibit characters of both *Lampsilis* and *Villosa*. However, in *Hamiota*, the marsupia is restricted to the ventral half of the posterior portion of the outer demibranchs, while in *Lampsilis*, *Ligumia*, and *Villosa* the marsupium fully occupies the water tubes of the posterior portion of the outer demibranchs (Figure 1). Unlike members of *Lampsilis*, which release larvae through pores in the ventral edge of the demibranchs, members of *Hamiota* release the superconglutinate lure through the excurrent opening. The placement and shape of the marsupium and the extraordinary method of glochidial release and host fish attraction, the superconglutinate, are uniquely derived characters in the Lampsilini that warrant genus-level recognition.

Hamiota altilis (Conrad, 1834) new combination

Unio altilis Conrad, 1834; Conrad, 1834: 43, pl. 2, fig. 1; Chenu, 1845: 21, pl. 1, fig. 1; Reeve, 1865: pl. 23, fig. 109.
Margarita (Unio) altilis (Conrad, 1834); Lea, 1836: 24.
Margaron (Unio) altilis (Conrad, 1834); Lea, 1852a: 27.
Lampsilis altilis (Conrad, 1834); Simpson, 1900a: 529; Parmalee and Bogan, 1998: 125, pl. 47.
Unio clarkianus Lea, 1852; Lea, 1852b: 251; Lea, 1852c: 273, pl. 21, fig. 30; Lea, 1852d: 29, pl. 21, fig. 30.
Margaron (Unio) clarkianus (Lea, 1852); Lea, 1852a: 27.
Lampsilis clarkianus (Lea, 1852); Simpson, 1900a: 532.
Unio gerhardtii Lea, 1862; Lea, 1862a: 168; Lea, 1862b: 208, pl. 31, fig. 277; Lea, 1862c: 30, pl. 31, fig. 277.
Margaron (Unio) gerhardtii (Lea, 1862); Lea, 1870: 35.
Lampsilis (Lampsilis) gerhardtii (Lea, 1862); Simpson, 1900a: 532.
Unio doliaris Lea, 1865; Lea, 1865: 88; Lea, 1868: 260, pl. 32, fig. 75; Lea, 1869: 20, pl. 32, fig. 75.
Margaron (Unio) doliaris (Lea, 1865); Lea, 1870: 42.
Lampsilis (Lampsilis) doliaris (Lea, 1865); Simpson, 1900a: 533.

Description: Described by Conrad (1834) as sub-oval, thin, and inflated. The periostracum was described as "rugose" and "blackish" with rays and "numerous short vermicular lines on the posterior slope," and the nacre as whitish and iridescent. The periostracum of specimens of *H. altilis* is typically brown to chestnut-brown in color with a variable number of dark green rays. The left valve has two heavy, spatulate pseudocardinal teeth, the smaller above the larger. The right valve has two nearly equally sized triangular teeth, the larger anterior to the smaller. The lateral teeth are short but blade-like, two in the right valve, and one in the left.

The posterior mantle margin of the female is expanded into a well-developed flap with papillae along the border. Coloration, number, and size of papillae vary somewhat between populations. In general, however, the interior mantle flap is colored red to dark red or brown with darker spots, while the exterior of the flap is brown to black, often with vertical lighter bars, and with a small, but prominent dark "eye spot" on the posterior end. Small papillae are present along the mantle flap, usually becoming more robust anteriorly. In males, the mantle flap is typically not expanded and is reddish in color. Marsupia of *H. altilis* are finely tapered at each end when immature, becoming broadly rounded on the ends in most populations, tapering anteriorly in others. Marsupia color is a dark reddish-brown or black along the margin and white above. The anus is usually pigmented red and the incurrent and excurrent siphons are reddish-brown to black. The glochidia of *H. altilis* are described by Haag et al. (1999).

Type Material: *Unio altilis* Conrad, 1834, Lectotype ANSP 56419 (Figures 3, 4) here designated. Type locality: Alabama River, near Claiborne [Monroe Co., Alabama].
Unio clarkianus Lea, 1852, Type not found. Type locality: Williamsport, [Maury Co.], Tennessee; Georgia or Alabama.
Unio doliaris Lea, 1865, Lectotype USNM 84936, here designated. Type locality: Etowah River, Georgia.
Unio gerhardtii Lea, 1862, Holotype USNM 25711 by monotypy. Type locality: Chattanooga, Georgia.

Remarks: The most variable species included in *Hamiota*, *H. altilis*, is endemic to the Mobile River Basin. Some of the conchological variation is undoubtedly ecophenotypic in nature, although the extent and nature of the variation in shell shape and pigmentation has not been adequately explored.

Conrad (1834) in his original description did not identify a primary type. Johnson and Baker (1973) identified ANSP 56419 as the figured holotype, although the specimen label indicates the locality as "Ogeechee R., Ga." Johnson and Baker (1973) state that the label is in error, and "probably was mixed with ANSP 46418, which is labeled 'Claiborne, Alabama', by error." Conrad (1834) clearly indicated that the specimen(s) of *U. altilis* described were collected from the "Alabama River, near Claiborne." Conrad (1834) did not specifically designate a holotype and according to the ICZN recommendation 73F and Article 74.5 the holotype designation of Johnson and Baker (1973) is deemed invalid. In order to preserve stability of nomenclature, we herein designate specimen ANSP 56419 as the lectotype of *U. altilis*. In accordance with ICZN Article 74.7, we herein designate the specimen USNM 84936 as the lectotype of *U. doliaris* Lea in order to maintain taxonomic stability and because this specimen appears to be that figured by Lea (1868). *Hamiota altilis* is considered threatened by the United States Fish and Wildlife Service (USFWS, 1994).

Life History: Mature gravid females have been reported from March through June. *Hamiota altilis* have also been observed releasing glochidia in a superconglutinate (Haag et al., 1999). Large centrarchid fishes, including *Micropterus coosae* Hubbs and Bailey, 1940, *M. punctulatus* (Rafinesque, 1819), *M. salmoides* (Lacepéde, 1802), and *Lepomis cyanellus* Rafinesque, 1819, have been confirmed as suitable hosts (Haag et al., 1999).

Range: *Hamiota altilis* was historically reported

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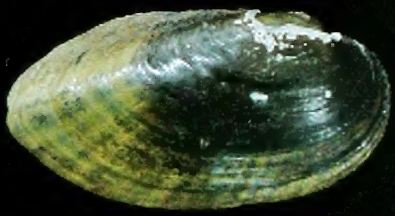

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Figures 3–10. Type material of species of *Hamiota*. Photographs are of the interior of left valve and exterior of right valve. **3, 4.** Lectotype of *H. altilis* ANSP 56419. **5, 6.** Holotype of *H. australis* USNM 150473. **7, 8.** Lectotype of *H. perovalis* ANSP 56416. **9, 10.** Lectotype of *H. subangulata* USNM 85801.

throughout the Mobile River Basin, including the Tombigbee, Black Warrior, Cahaba, Alabama, Tallapoosa, and Coosa River drainages in Alabama, Georgia, Mississippi, and Tennessee. The species is currently restricted to localized portions of the Cahaba, Coosa, and Tallapoosa rivers and some of their tributaries (USFWS, 2003).

Hamiota perovalis (Conrad, 1834) new combination

Unio perovalis Conrad, 1834; Conrad, 1834: 43, pl. 2, fig. 2; Chenu, 1845: 21, pl. 1, fig. 2; Küster, 1861: 257, pl. 87, fig. 2; Reeve, 1866: pl. 38, fig. 209.

Margarita (*Unio*) *perovalis* (Conrad, 1834); Lea, 1836: 24.

Margaron (*Unio*) *perovalis* (Conrad, 1834); Lea, 1852a: 27.

Lampsilis perovalis (Conrad, 1834); Simpson, 1900a: 531.

Unio spillmanii Lea, 1861; Lea, 1861: 39, Lea, 1862d: 98, pl. 15, fig. 246; Lea, 1862e: 102, pl. 15, fig. 246, Reeve, 1868: pl. 82, fig. 435.

Margaron (*Unio*) *spillmanii* (Lea, 1861); Lea, 1870: 42.

Lampsilis (*Lampsilis*) *spillmani* (Lea, 1861); Frierson, 1927: 69 [misspelling].

Description: Conrad (1834) described this species as oval and inflated with a moderately thick shell. He noted two color varieties, one in which the periostracum was olivaceous and obscurely rayed with white nacre and another in which the periostracum was reddish-brown with "rose colored" nacre. The periostracum of specimens of *H. perovalis* is generally lighter in color than *H. altilis* and range from straw-yellow to light brown. The number of rays is variable and can cover the entire disk. The left valve contains two robust equal sized pseudocardinal teeth. The right valve has two pseudocardinals and the anterior tooth is smaller than the posterior tooth. The lateral teeth are elongate, two in the left, one in the right.

The mantle margins of female *H. perovalis* are expanded into well-developed flaps, pigmented red on the interior and darker red to brown or black on the exterior. No eyespot is present and short papillae are present along the mantle edge. Males possess a rudimentary mantle margin with weak pigmentation and few papillae. The marsupia of *H. perovalis* are pisciform in shape, broader anteriorly and narrowly tapering posteriorly. The marsupium is reddish or darker along the margin, often with a darker spot of pigment on the broader anterior end that resembles an eyespot in the superconglutinate lure. The anus can be pigmented red and black, and the incurrent and excurrent siphons are usually reddish or brown in color.

Type Material: *Unio perovalis* Conrad, 1834, Lectotype ANSP 56416 (Figures 7, 8), here designated. Type locality: Alabama River, at Claiborne [Monroe Co., Alabama].
Unio spillmanii Lea, 1861, Lectotype USNM 84925, here designated. Type locality: Luxpalila Creek, near Columbus, Mississippi.

Remarks: There has been some question as to the distinctiveness of *H. perovalis* from *H. altilis*, perhaps because both were described from practically the same locality. An examination of mitochondrial DNA sequences by Roe et al. (2001) recovered these two taxa as a clade, but failed to resolve them into reciprocally monophyletic groups. Hurd (1974) considered *perovalis* a junior synonym of *altilis*, as did Burch (1975). Frierson (1927) considered *U. doliaris* (Lea, 1865) a synonym of *perovalis*, although Parmalee and Bogan (1998) include *U. doliaris* as a synonym of *altilis*. Based on the collection locality and the appearance of the type specimen, we place *U. spillmanii* Lea, 1861 as a synonym of *H. perovalis*. As with *U. altilis*, Conrad (1834) did not specifically designate a holotype for *U. perovalis*, therefore, according to the ICZN Article 74.5 and recommendation 73F the holotype designation of Johnson and Baker (1973) is deemed to be in error. In an effort to maintain nomenclatural stability we herein designate ANSP 56419 the lectotype for *U. perovalis*. According to ICZN Article 74.7, the specimen USNM 84925 is here designated as the lectotype of *U. spilmanii* in order to fix the name and maintain nomenclatural stability. This species is listed as threatened by the United States Fish and Wildlife Service (USFWS, 1994).

Life History: Discharge of superconglutinates was first observed in *H. perovalis* (Haag et al., 1995). Glochidia mature and are discharged between March and June, with releases concentrated in early April (Hartfield and Butler, 1997). *Micropterus coosae*, *M. punctulatus*, and *M. salmoides* have been identified as suitable host fishes for the orange-nacre mucket (Haag and Warren, 1999).

Range: *Hamiota perovalis* was historically known from the Mobile Basin's Alabama, Tombigbee, Black Warrior, and Cahaba rivers and their tributaries in Alabama and Mississippi. The species has apparently become extirpated from the main channels of the larger rivers, but continues to survive in some tributaries of all four drainages (USFWS, 2003).

Hamiota subangulata (Lea, 1840) new combination

Unio subangulatus Lea, 1840; Lea, 1840: 287; Lea, 1842a: 209, pl. 13, fig. 23; Lea, 1842b: 47, pl. 8, fig. 23; Küster, 1861: 278, pl. 94, fig. 2; Simpson, 1892: 415, pl. 58, fig. 1; Reeve, 1868: pl. 65, fig. 327.

Margaron (*Unio*) *subangulatus* (Lea, 1840); Lea, 1852a: 29.

Lampsilis subangulatus (Lea, 1840); Simpson, 1900a: 556; Clench and Turner, 1956: 196, pl. 2, fig. 2.

Ligumia subangulata (Lea, 1840); Haas, 1969: 443.

Villosa subangulata (Lea, 1840); Heard, 1979: 44.

Unio kirklandianus S. H. Wright, 1897; S. H. Wright, 1897: 136.

Lampsilis kirklandianus (S. H. Wright, 1897); Simpson, 1900a: 557; Simpson, 1900b: 76, pl. 1, fig. 7.

Description: A medium-sized mussel that reaches approximately 85 mm in length (Brim Box and Williams, 2000). Specimens are generally elongate; the posterior ridge is rounded and the posterior slope is usually concave. Periostracum color is variable in this species. Individuals range from straw-yellow to chestnut-brown in color with a variable number of black to bright emerald green rays of variable width. These rays emanate from the umbo and radiate across the disk. Most shells are shiny, although some populations exhibit an extremely glossy periostracum. This species has been described as one of the most beautiful of all North American freshwater mussels (S. H. Wright, 1897; Clench and Turner, 1956).

Wright (1897) described *U. kirklandianus* from the Ochlockonee River in Leon County, Florida and remarked that his specimens were more polished and had broader rays than typical of *U. subangulatus*, and that the shells were "deeper and broader." The right valve has two somewhat spatulate pseudocardinal teeth, the smaller nearly directly above the other. The left valve has two pseudocardinal teeth, the anterior one much larger than the other. Lateral teeth are thin, but not delicate, two in the left and one in the right valve. Examination of specimens from across the range of this species reveals substantial variation in shell color and size. The mantle margins in females are only slightly expanded into a modest flap. The flaps are light brown in coloration on the interior and freckled-brown on the exterior, and no eyespot is present. Short papillae are present along the margin of the flap, becoming larger anteriorly. In males, the mantle is only slightly expanded, without pigment, and with very short papillae. The marsupia are pisciform in shape, broader anteriorly and tapered behind, and darkly pigmented along the margin often with a darker spot of pigment anteriorly. The anus is unpigmented and the siphons are brownish. Glochidia were figured and described by O'Brien and Brim Box (1999).

Type Material: *Unio subangulatus* Lea, 1840, Lectotype USNM 85801 (Figures 9, 10) designated by Clench and Turner (1956). Type locality: Chattahoochee River, Columbus, [Muscogee Co.,] Georgia.
Unio kirklandianus S. H. Wright, 1897, Paratype USNM 149648. Type locality: Oclocknee River, Leon Co., Florida.

Remarks: *Hamiota subangulata* is listed as an endangered species (USFWS, 1998). The analysis of Roe et al. (2001) resolved this taxon as monophyletic and in a clade with *H. australis*.

Life History: Discharge of superconglutinate lures has been documented by O'Brien and Brim Box (1999) from late May through early June. *Micropterus punctulatus* and *M. salmoides* appear to be primary hosts for the species (O'Brien and Brim Box, 1999).

Range: *Hamiota subangulata* was found throughout the Apalachicola River Basin and the Ochlockonee River drainage (Brim Box and Williams, 2000). Currently the species continues to survive in some small streams and headwater rivers (USFWS, 1998).

Hamiota australis (Simpson, 1900) new combination

Lampsilis australis Simpson, 1900; Simpson, 1900a: 544; Simpson, 1900b: 75, pl. 2, fig. 2; Clench and Turner, 1956: 199, pl. 2, fig. 3.
Ligumia australis (Simpson, 1900); Haas, 1969: 432.
Villosa australis (Simpson, 1900); Heard, 1979: 44.

Description: Simpson (1900b) described the shells of this species as "long and elliptical . . . moderately inflated." The periostracum was described as "smooth, shinning, greenish yellow, rayed with green" and the nacre as "bright bluish white." Specimens examined were elliptical to elongate oval and often terminate in a blunt point. Specimens are almost always stained black, with some green rays visible on the posterior slope. The periostracum is often glossy. The right valve contains two pseudocardinal teeth, the smaller above the larger. The left valve has two compressed pseudocardinal teeth. Lateral teeth are elongate and slightly curved, two in the left valve and one in the right. Posterior mantle flaps are poorly developed with a streak of red stain along the margins. There is no eyespot on the mantle flap, and only a few very small papillae. The marsupia are pisciform, broadly rounded anteriorly and tapering behind (Figure 1). Color of the marsupium is white along the margin and black above. The anus is unpigmented and the incurrent and excurrent siphons are reddish in color. Glochidia were described and figured by Blalock-Herod et al. (2002).

Type Material: *Lampsilis australis* Simpson, 1900, Holotype USNM 150473 by original designation (Figures 5, 6). Type locality: Little Patsiliga Creek, southeastern Alabama.

Remarks: Fuller and Bereza (1973) stated that this species represented an "undescribed lampsiline genus" and that its marsupium allied it closely with *Ptychobranchus*. This species was incorrectly synonymized with *Ptychobranchus jonesi* (van der Schalie, 1934) by Clench and Turner (1956). The phylogenetic analysis of Roe et al. (2001) clearly placed this species with the other superconglutinate producers.

Life History: Superconglutinate releases have been documented in this species by Blalock-Herod et al. (2002). *Micropterus* spp. are likely hosts (Blalock-Herod et al., 2002).

Range: *Hamiota australis* was known historically from the Escambia, Yellow, and Choctawhatchee River systems. It continues to survive in some river and stream segments within these systems. This species is not currently protected under the Endangered Species Act.

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APPENDIX 1

SPECIMENS EXAMINED

Hamiota altilis

ALABAMA

Alabama River: USNM 25948; Alabama River, near Claiborne: ANSP 56419 [Lectotype *U. altilis* Conrad, 1834], ANSP 56418; Big Swamp Creek, Macon Co.: USNM 361723; Jackson Shoals, Choccolocco Creek: ANSP 103834, ANSP 103871; Beaver Creek: ANSP 103863; Coosa River: ANSP 41120, DMNH 130623; Coosa River, Coosa Valley: ANSP 103771; Higgin's Ferry, Coosa River, Chilton Co.: USNM 218118; McGowen's Ferry, near Wilsonville, Coosa River: USNM 521359; Weduska Shoals, Coosa River: ANSP 48001, DMNH 075252, DMNH 150037, DMNH 150038, USNM 348970, USNM 452169; Coosa River, [incomprehensible handwriting] Shoals, Shelby Co.: ANSP 341399; Shoal Creek, Pine Glen Recreational Area, Cleburne Co.: MMNS 7743, MMNS 8084, MMNS 8085, UAUC 120, UAUC 121, UAUC 125; Yellowleaf Creek, Jumbo, Chilton Co.: ANSP 89031; Cane Creek, West of CR 65, 2 mi. West CR 78 Jct., T15S, R11E, sec 3: UAUC 3292, MMNS 8081; Little Cane Creek, at CR 78, East of Edwardsville: UAUC 3293; Chewacla Creek at CR 22, ~4 mi. East of Tuskeegee, Macon Co.: UAUC 246, UAUC 247, UAUC 248; Uphappee Creek, 0.5 mi. upstream of Hwy. 29, Macon Co.: MMNS 8082; Cahaba River: USNM 152026; Cahaba River: ANSP 126054; Little Cahaba River, 0.5 mi. below Cahaba Beach Rd. bridge, Jefferson Co.: UAUC 149; Coosa River, Weduska Shoals, Shelby Co.: UF 3255; Coosa River at Fort William Shoals, Talladega Co.: UF 65420; Hurricane Creek, Cherokee Co.: UF 175098; Chewacla Creek, 8 mi. ESE of Tuskeegee Co. Rd. 22, Macon Co.: UF 202249; Shoal Creek, St. Clair Co.: UF 245989; Tuskeegee National Forest, Macon Co.: UF 266048; Cahaba River: UF 269576; Shoal Creek, St. Clair Co.: MMNS 8083.

GEORGIA

Etowah River: USNM 84936 [Lectotype, *U. doliaris* Lea, 1865]; Chattooga River: ANSP 89102; Chattooga

River, Chattooga Co.: USNM 59527; Chattanooga: USNM 25711 [Holotype, *U. gerhardtii*, Lea, 1862]; Fish Creek at Highway 278/ GA State Rt. 6, ~3.9 air mi. West of Rockmart, Polk Co.: UAUC 538, UAUC 539; Conasauga River at Tibbs Bridge Murray CR 109 (Whitfield CR100), Murray/Whitfield Co's.: UAUC 515, MMNS 8092; Conasauga River, Muskrat Midden, Tritogonia Shoals (CRM 46.70), Whitfield/Murray Co's.: UAUC 376; Conasauga River, south of state line, Murray Co.: MMNS 8090; Conasauga River: DMNH 150124, USNM 84937, USNM 348969; Etowah River: USNM 123202.

Tennessee

Conasauga River: DMNH 014683; Conasauga River, Conasauga: ANSP 341305, ANSP 347949; Conasauga River, Polk Co.: MMNS 8091.

Hamiota perovalis

Alabama

Alabama River: ANSP 56416 [Lectotype *U. perovalis* Conrad, 1834], ANSP 333496; Alabama River, Claiborne: USNM 84938; Coosa River: ANSP 56415; Coosa River, Gadsen: ANSP 126051; Coosa River, Talladega Co.: ANSP 126048; Black Warrior River: ANSP 88483; Mulberry River [Fork, Black Warrior River]: ANSP 88485; Rush Creek [Black Warrior River Dr.], FS Rt. 245, Winston Co.: MMNS 7745, MMNS 8088, UAUC 426; Flannigan Creek at FS Rd. 229, Lawrence Co.: MMNS 7744, UAUC 423, UAUC 424, UAUC 425; Toadvine, Valley Creek, Black Warrior River Dr., Jefferson Co.: UF 65302, UF 65304; Forks of the Warrior River, Walker Co.: UF 65305; North River, near Hagler's Mill, Black Warrior Dr., Tuscaloosa Co.: UF 65306; Sipsey Fork at N.F. 234, Bankhead National Forest, Winston Co.: UF 79069, UF 79072, UF 79082, UF 79085, UF 79136, UF 79137; Brushy Creek above Brushy Lake Recreational Area, Bankhead National Forest, Winston Co.: UF 79094; Capsey Creek, 50 mi. from Jct. with Brushy Creek, Bankhead N.F., Winston Co.: UF 79115; Sipsey Fork at mouth of Hurricane Creek, Bankhead National Forest, Winston Co.: UAUC 95; Brown Creek, Bankhead National Forest, Winston Co.: UAUC 1774; Alabama: ANSP 126049; North River, near Samantha [Black Warrior River], Tuscaloosa Co.: UAUC 107; Buttahatchee River, Hamilton: ANSP 100657, DMNH 075231; Tuscaloosa Co. Alabama: DMNH 146496; Black Warrior River, Jefferson Co.: UF 269609; Squaw Shoals, Black Warrior River, Jefferson Co.: UF 65298, UF 65299, UF 65300, UF 65303, UF 65307, UF 65429, UF 269518; Garden City, Mulberry Fork: UF 69207, UF 244558; Banks of Brushy Creek, at N.F. Rd. 255, Bankhead N.F. Winston Co.: UF 69269, UF 79177, UF 79178, MMNS 7748, MMNS 8089; Sipsey Fork, 1 mile N. of AL Hwy. 33 crossing, Winston Co.: UF 69279; Brushy Creek at N.F. Rd., Bankhead N.F., Winston Co.: UF 79076; Sipsey River at Sipsey Recreational Area, Bankhead N.F., Winston Co.: UF 79089; Borden's Creek, 1 mi., upstream of from Jct. Sipsey Fork, Sipsey Wilderness, Bankhead National Forest, Winston Co.: UF 79092, UF 79181; Sipsey Fork at N.F. Rd., 234, Bankhead National Forest, Winston Co.: UF 79139; Limestone Creek, 6.3 mi WNW of Monroeville, Monroe Co.: UF 197636; Blackwater Creek upstream from Harris bridge, Walker Co.: UF 266369; Sipsey River, 1.6 mi N. of Pleasant Ridge, Greene Co.: UF 197671; North River at Co. Hwy. 30, Fayette Co.: UF 197686; Sipsey River, 200 m. below Co. Hwy 23, Greene Co.: UF 197552; Sipsey River, 4–6 mi. below Co. Hwy. 2, Greene Co.: UF 197566; Sipsey River at CR 2, downstream of boat ramp, Pickens Co.: UAUC 156; Tombigbee River: ANSP 126053; Elrod, Sipsey River, Tombigbee R.: DMNH 146493; Lubbub Creek, at CR 24, 3.25 mi. Northeast of Aliceville, Pickens Co.: UAUC 67; Tombigbee River: USNM 159989; Lubbub Creek, 1.8 mi SSE of Aliceville above Hwy 14: UF 197619, UF 197632; Sipsey River, 3.6 mi. W. of Jena downstream of CR 2, Greene Co.: UF 197697; Sipsey River near confluence with Carpenter's Creek, Greene Co.: UF 197801; Sipsey River, 5.7 mi. NNE of Mantua, Greene Co.: UF 197857, UF 197862; Sipsey River, near Elrod, Tuscaloosa Co.: UF 269559, UF 65301; Trussels Creek at CR 19 bridge, Greene Co.: MMNS 8087.

Mississippi

Luxpalila Creek, near Columbus: USNM 84925 [Lectotype, *U. spillmanii* Lea, 1861], USNM 123279; Columbus, Lowndes Co.: UF 269560.

Hamiota subangulata

Alabama

Uchee Creek, Russell Co.: UAUC 116.

Florida

Chipola River, Look-Tremble Falls near Alpha, Calhoun Co.: ANSP 175750; Chipola River, near Pole Bluff landing, Calhoun Co.: ANSP 175751; Chipola River: ANSP 84324; Ochlockonee River: DMNH 150098; Ochlockonee River, Leon Co.: USNM 149648 [Paratype, *U. kirklandianus* S. H. Wright, 1897]; Ochlockonee River, Tallahassee, Leon Co.: ANSP 156892, ANSP 341307; Ochlockonee River, 7 mi. west of Tallahassee: ANSP 157553; Ochlockonee River, 10 mi. west of Tallahassee, Leon Co.: ANSP 159126; Ochlockonee River, 11 mi. northwest of Tallahassee: DMNH 119506; Ochlockonee River, 2 mi. west of Bloxham, Liberty Co.: ANSP 360553; Spring Creek, Marianna: ANSP 160210; State Rt. 167, 1 mi. north of Marianna, Chipola River, Jackson Co.: ANSP 349631; Spring Creek, Reynoldsville, Seminole Co.: UF 177; 1 mi. north Marianna, Chipola River: UF 390; 3.5 mi. east of Quincy, Little River: UF 415; ca. 2

mi. east of Clarksville, Chipola River, Calhoun Co.: UF 418; Chipola River, 9.2 km ENE Kinard, 12.5 km NW Lewis, 16.4 km N. Ida, Calhoun Co.: MMNS 8099.

GEORGIA

Chattahoochie River: ANSP 56477; Chattahoochie River, Columbus: USNM 85081 [Lectotype, *U. subangulatus* Lea, 1840]; ANSP 126272; Cooleewahee Creek, 0.9 mi. NE of Newton, Baker Co.: USNM 853746; Cooleewahee Creek at GA Rt. 91, Baker Co.: MMNS 8095; Abram's Inlet, Flint River: ANSP 190294; Mill Creek, Flint River, several mi. north of Albany: ANSP 267572; Kinchafoonee Creek at GA Rt. 41 crossing, just south of Preston, Webster Co.: UAUC591; Kinchafoonee Creek at GA Rt. 49 bridge ~9 air mi. northeast of Dawson, Terrell/Sumter Co's.: UAUC 602, UAUC 603, UAUC 604; Kinchafoonee Creek at GA Rt. 32, Lee Co., GA: MMNS 8096; Chickasawhatchee Creek at CR 130 bridge ~4 air mi. SW of Chickasawhatchee, Terrell Co.: UAUC 1753; Muckalee Creek at GA Rt. 195 bridge ~3.5 air mi. Northeast of Leesburg, Lee Co.: UAUC 312; Whitewater Creek on Morgan Mill Rd., Fayette Co.: UAUC 645; Ochlockonee River: DMNH 173390; Ochlockonee River, 7 mi. S. of Cairo: ANSP 194640, DMNH 048538, UF 412; Mimsville: ANSP 47892, DMNH 075151; Georgia: ANSP 126273; Calvary: ANSP 47891; Ochlockonee River, Thomas/Grady Co's. Georgia: MMNS 8101; Spring Creek at GA Rt. 84, Decatur Co.: MMNS 8094, MMNS 8100; Line Creek at GA Rt. 85/74 bridge, Coweta/Fayette Co.: MMNS 8097; Ichawaynochaway Creek at GA Rt. 216, Baker Co.: MMNS 8098.

Hamiota australis

ALABAMA

Andrews fish trap, Pea River, Barbour Co.: UF 65309; 7 mi. east of Brundidge, Pea River, Pike Co.: UF 123284; Bozemans landing, Conecuh River, near Crenshaw Co. line, Covington Co.: UF 65313; Lightwood Knot Creek, 1.6 mi. west of Opp, Covington Co.: ANSP#; Little Patsaliga Creek: USNM 150473 [Holotype, *Lampsilis australis*, Simpson, 1900]; West Fork Choctawhatchee River at Blue Spring State Park, Barbour Co.: UAUC 134, UAUC 511, UAUC 512, UAUC 513, UAUC 514; Little Choctawhatchie Creek, near Drian bridge, Houston Co.: UF 229532; Conecuh River on CR 28 ~1 mi. east of Goshen, Pike Co.: UAUC 510; Flat Creek at AL Hwy 153, near Flat Creek Church, Geneva Co.: UAUC 547; Five Runs Creek, Conecuh N. F., Covington Co.: MMNS 8086.

FLORIDA

Shoal River at Hwy 85, 1 mi. south of I-10 Jct. in Crestview, Okaloosa Co.: UAUC 550, UAUC 551, UAUC 552, UAUC 643, UAUC 644; Shoal Creek, ca. 1 mi. above U. S. Highway 90, Okaloosa Co.: UF 261852; Limestone Creek, Walton: MMNS 7746, MMNS 7747.

Consideration of genetic relationships in management decisions for the endangered Anthony's riversnail, *Leptoxis crassa anthonyi* (Redfield, 1854) (Gastropoda: Pleuroceridae)

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ABSTRACT

Anthony's riversnail, *Leptoxis crassa anthonyi,* is a federally endangered pleurocerid restricted to three natural populations in the Tennessee River drainage. Recovery plans organized the three populations into two management units, and called for specific numbers of populations for downlisting or delisting. Given that nothing was known about the genetic structure of these populations and that individuals were being randomly transplanted, we examined each population using COI mtDNA sequences. All three populations possessed unique sequence haplotypes, and the two units identified in the recovery plan did not group the populations accurately in a phylogenetic context. Potential management decisions in light of our findings are discussed.

INTRODUCTION

Anthony's riversnail, *Leptoxis crassa anthonyi* (Redfield, 1854), is a pleurocerid gastropod currently listed as endangered by the United States Fish and Wildlife Service (USFWS) under the Endangered Species Act of 1973 as amended (USFWS, 1994). Adult shells of *L. crassa anthonyi* are large compared to sympatric pleurocerids, globose to ovate, greenish to greenish-brown in color, often with purple bands. The body whorl may be sculptured with low, indistinct tubercles, giving the shell a bumpy appearance. The aperture is ovate with a thin outer lip, and the columellar lip is reflected so that it covers a prominent umbilicus (Tryon, 1873). Historically, *L. crassa anthonyi* had been documented from the Tennessee River drainage in Alabama, Georgia and Tennessee, including the lower reaches of some of the larger tributaries (Burch and Tottenham, 1980; Bogan and Parmalee, 1983). Most populations of the species were extirpated when much of the Tennessee River and its tributaries were impounded by the Tennessee Valley Authority. Natural populations of *L. crassa anthonyi* persist at three localities: a small, scattered population in the main channel of the Tennessee River near the Alabama and Tennessee state line; a large population in Limestone Creek, Limestone County, Alabama; and a small population limited to a single stretch of the Sequatchie River, Marion County, Tennessee (Garner, 1994; Jenkinson, 1994; USFWS, 1997; Figure 1).

Two morphologically similar snails have occurred within the historic range of *Leptoxis crassa anthonyi.* The species often occurs sympatrically with *L. praerosa* (Say, 1821), and adults of *L. praerosa* are easily confused with juveniles of *L. crassa anthonyi* (Dillon and Ahlstedt, 1997). The other taxon, *L. crassa crassa* (Haldeman, 1841), was described as being similar to *L. crassa anthonyi* but with larger, more prominent tubercles on the body whorl, is presumed extinct (Turgeon et al., 1998). *Leptoxis crassa anthonyi* shells are most easily recognized as juveniles, given their saucer shape and the presence of a heavy carina that disappears with age (Dillon and Ahlstedt, 1997). The distinctness of *L. crassa anthonyi* has been supported by both allozyme (Dillon and Ahlstedt, 1997) and mitochondrial sequence data (Holznagel and Lydeard, 2000).

In 1997, USFWS published their recovery plan (USFWS, 1997) for *L. crassa anthonyi.* The plan identified two "populations" of *L. crassa anthonyi*: individuals from the Sequatchie and Tennessee Rivers as one population; and individuals from Limestone Creek as the other. Recovery criteria for *L. crassa anthonyi* were to protect the extant populations and to successfully re-establish other populations. If a total of four "populations" could be established, the species could be downlisted to threatened status; if six "populations" could be established, the species would be delisted entirely. Though the plan treated the three localities as two "populations," no effort had been made to determine if they were genetically homogeneous (i.e., a single genetic population) or genetically variable (i.e., two or three separate populations). In order to reach the stated goals of the recovery plan, the number of genetically distinct populations within the species needed to be determined. A working baseline of genetic information about each population was even more important due to reports of snails

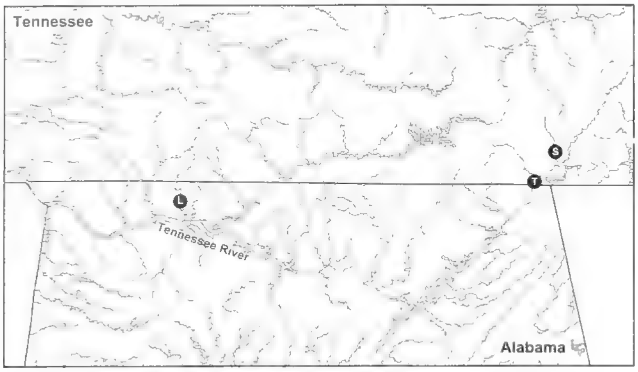

Figure 1. Map showing the locations of the three extant natural populations of *Leptoxis crassa anthonyi*. L = Limestone Creek; S = Sequatchie River; T = Tennessee River.

being translocated into existing populations and moved to new localities in the Tennessee River drainage (J. Garner and D. Hubbs, pers. comms.). In this study, we used mitochondrial DNA sequence data to conduct a comparative genetic analysis of extant *L. crassa anthonyi* populations to examine the degree of genetic differentiation among the three populations. Knowledge of the genetic structure would help direct management efforts in determining which populations could and should serve as sources for augmentations and reintroductions if desired.

MATERIALS AND METHODS

Adult specimens of *L. crassa anthonyi* from the three natural populations were collected under an endangered/threatened species subpermit (SA99-13). The maximum allowed number of specimens were collected, twenty from Limestone Creek, and five each from the Sequatchie and Tennessee Rivers (see Appendix 1). For comparative purposes, a reduced data set from previous analyses (Minton and Lydeard, 2003) was used to place *L. crassa anthonyi* in the proper systematic context. Fifteen individuals of *L. crassa anthonyi* from Limestone Creek and five each from the other two populations were included in the genetic study, along with four *L. praerosa,* each from different river drainages, and one each of the other taxa used in the previous study (Appendix 1).

Mitochondrial DNA sequences for a 1 kb portion of the cytochrome oxidase subunit I gene (COI) were generated using published methods (Minton and Lydeard, 2003) for genomic isolation, PCR amplification, and genetic analysis that followed. Sequences were aligned by eye (Hall, 1999) and phylogenetic hypotheses generated by PAUP* 4.0b10 (Swofford, 2002) under maximum parsimony with the following options: 50 replicates of heuristic search with random addition, uninformative characters were ignored, branches with minimum zero length collapsed, and minimal length trees kept. This gene fragment showed significant phylogenetic signal and no base composition bias or sequence saturation in a more inclusive pleurocerid dataset (Minton and Lydeard, 2003). Internal branch stability was assessed by jackknife (Farris et al., 1996) and Bremer support (Bremer, 1994).

RESULTS

Aligned sequences resulted in a data matrix of 890 characters, of which 222 were parsimony-informative. Each population of *Leptoxis crassa anthonyi* possessed a unique haplotype, and all individuals from a population shared the same haplotype. Maximum parsimony analysis yielded two trees (Figure 2, strict consensus). All specimens of *L. crassa anthonyi* constituted a monophyletic group. Uncorrected p-distances were 1.46% between the Limestone Creek and Sequatchie River spec-

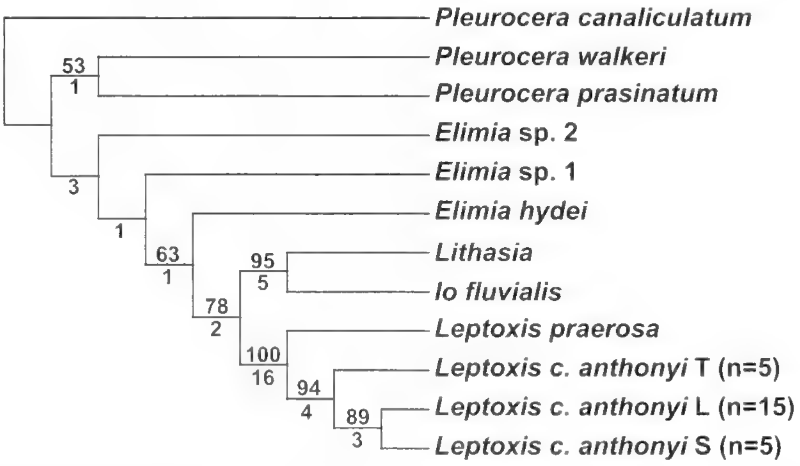

Figure 2. Strict consensus of two most parsimonious trees (TL = 718, CI = 0.54) based on mitochondrial COI sequences. *Leptoxis crassa anthonyi* specimens identified as in Figure 1. Jackknife values >50% above branches, Bremer values below. Composition of *Leptoxis* and *Lithasia* clades are given in Table 1; both clades were monophyletic with jackknife support >50% and Bremer support >1

imens, 2.02% between the Limestone Creek and Tennessee River specimens, and 3.03% between the Sequatchie and Tennessee River specimens. The *L. crassa anthonyi* clade was sister to a clade of *L. praerosa* specimens. Most clades were well supported by jackknife and Bremer values, as were the relationships within each clade.

DISCUSSION

Our results further support the validity of *Leptoxis crassa anthonyi* and its distinctiveness from *L. praerosa*, and show each of the three populations of *L. crassa anthonyi* to be genetically unique based on COI haplotypes. Uncorrected pairwise genetic differences between the three populations of *L. crassa anthonyi* were consistent with published intraspecific differences seen in other pleurocerids using COI sequences (Minton and Lydeard, 2003). The USFWS recovery plan calls for the presence of no fewer than four viable populations of *L. crassa anthonyi* before any change in listing status can occur. For establishment of new populations, introductions of each haplotype to new areas within their current river system would be preferred in order to avoid mixing of unique evolutionary entities and possible elimination of the current genetic diversity.

The USFWS has designated *Leptoxis crassa anthonyi* from the Sequatchie and Tennessee Rviers as a single population. Based on that assumption, their management efforts might target one of the populations as a source for augmenting the other. If translocations are to be used, our analysis suggests that the Limestone Creek population would be a better option for augmenting the Sequatchie River population due to lower genetic difference. Additionally, if a single population is to serve as a source of new introductions and augmentations, recent survey work (J. Garner, pers. comm.) indicates that Limestone Creek would be preferred because of its large population size. Regardless, controlled experimental populations should be established, either in the field or laboratory, that could be monitored genetically and for population growth and be compared with non-augmented populations to determine whether fitness has been enhanced or diminished from the introduction of unique haplotypes from other populations. This measure would be especially prudent given that haplotypes are being randomly introduced through human activity. Any recovery plan that involves translocation of *L. crassa anthonyi* should use juveniles, as they are more easily identified by their strong keel. This will help ensure the movement of *L. crassa anthonyi* and potentially prevent the introduction of adult, non-endemic *L. praerosa*.

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Appendix 1. Systematic list of taxa and specimens used in this study. Complete locality information is available from the authors. UAG = University of Alabama gastropod collection.

Taxon	Locality	UAG voucher	Genbank accession
Genus *Elimia*			
E. hydei	Black Warrior River, Tuscaloosa Co., AL	UAG 584	AF435775
Elimia sp. 1	Green River, Hart Co., KY	UAG 574	AF435759
Elimia sp. 2	Collins River, Warren Co., TN	UAG 407	AF435761
Genus *Io*			
Io fluvialis	Clinch River, Hancock Co., TN	UAG 585	AF435776
Genus *Leptoxis*			
L. crassa anthonyi	Limestone Creek, Limestone Co., AL	UAG 581	AF435772
	Sequatchie River, Marion Co., TN	UAG 582	AF435773
	Tennessee River, Jackson Co., AL	UAG 583	AF435774
L. praerosa	Harpeth River, Davidson Co., TN	UAG 404	AF435779
	Shoal Creek, Lawrence Co., AL	UAG 560	AF435780
	Sequatchie River, Marion Co., TN	UAG 588	AF435781
	Tennessee River, Jackson Co., AL	UAG 589	AF435782
Genus *Lithasia*			
L. armigera	Harpeth River, Cheatham Co., TN	UAG 555	AF435739
L. geniculata fuliginosa	Red River, Robertson Co., TN	UAG 398	AF435754
	Duck River, Maury Co., TN	UAG 403	AF435749
	Buffolo River, Humphreys Co., TN	UAG 406	AF435747
L. lima	Bear Creek, Colbert Co., AL	UAG 570	AF435757
L. verrucosa	French Broad River, Knox Co., TN	UAG 576	AF435767
	White River, Woodruff Co., AR	UAG 577	AF435771
Genus *Pleurocera*			
P. canaliculatum	Duck River, Maury Co., TN	UAG 590	AF435783
P. prasinatum	Yellowleaf Creek, Shelby Co., AL	UAG 591	AF435784
P. walkeri	Shoal Creek, Lauderdale Co., AL	UAG 592	AF435785

Fallen into oblivion—the systematic affinities of the enigmatic *Sulcospira* Troschel, 1858 (Cerithioidea: Pachychilidae), a genus of viviparous freshwater gastropods from Java

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ABSTRACT

Sulcospira Troschel, 1858, is not only the taxonomically oldest but also one of the most poorly known genera of Southeast Asian Pachychilidae. It serves as an instructive case study as to how the puzzling systematics of freshwater Cerithioidea has hampered a deeper understanding of their phylogeny and evolution. The genus has been established for the Javan freshwater gastropod *Melania sulcospira* Mousson, 1849, on the grounds of its round, multispiral operculum and an elongated main cusp in the central radula teeth. Although of great systematic significance, this taxon has been widely ignored by subsequent authors. We here recapitulate the taxonomic history of the genus and describe and evaluate the morphological properties of the type species *S. sulcospira* on basis of the limited existing material, in order to facilitate a better understanding of pachychilid systematics. In addition, in an attempt to clarify its systematic affinity, we compare the properties of another allegedly related species from Java, *S. martini* (Schepmann, 1898). We show that these two viviparous species exhibit different protoconch morphologies, which are indicative of reproductive strategies distinct from other pachychilids. Finally, we outline preliminary suggestions as to the systematics of *Sulcospira* within the family Pachychilidae.

MATERIALS AND METHODS

MATERIALS

This study is based on the examination of material from various museum collections worldwide (see repositories). All of these samples comprise dry shells only, which as a rule were empty. Only few shells contained fragmentary soft parts; some of them were re-hydrated for examinations. However, these bodies generally did not facilitate morphological examinations except for the extraction of small radula fragments. We have not tried to extract DNA from dried tissues because earlier attempts with comparable material of *Brotia* failed. In order to acquire fresh material, collecting trips have been undertaken in 2000 and 2002. We have searched rivers and creeks in different sectors of there course (i.e. upstream, midstream, downstream) for a period of altogether 7 days in West Java (along the roads between Jakarta and Serang, Bogor and Sukabumi, Sukabumi and Pelabuhan Ratu, Bogor and Cipanas, Bogor and Cianjur, in the Botanical Garden Bogor) and for 3 days in East Java (between Taksimalaya, Cipatujah, and Pangadaran). During these trips we were not able to find any material of *Sulcospira*, though.

Because freshwater biotopes on Java are facing dramatic devastation by a multitude of causes related to the dense population on this island such as pollution, flow regulation, drainage, impoundment and a general degradation of collecting areas by agriculture, industry and settlements (own observations; see also Dudgeon, 2000, for SE Asia in general), we believe that *S. sulcospira* has become extinct in vast areas on Java. It remains unclear whether and at which localities populations of this species still exist.

REPOSITORY INSTITUTIONS

Voucher material is housed with the following museums: Natural History Museum, London (BMNH), Museum of Comparative Zoology, Cambridge, Mass. (MCZ), Muséum d'Histoire Naturelle, Genève (MHNG), Muséum National d'Histoire Naturelle, Paris (MNHN), Natural History Museum Naturalis, Leiden (RMNH), Senckenbergmuseum, Frankfurt/Main (SMF), Zoölogisch Museum, Amsterdam (ZMA), Museum für Naturkunde, Berlin (ZMB).

We were not able to locate material in the following museum collections: Academy of Natural Sciences, Philadelphia (ANSP), United States National Museum, Washington (UNSM), Zoologisches Institut und Museum, Universität Hamburg (ZMH), Zoologische Staatssammlung, München (ZSM).

Morphological Examinations

Dimensions of all shells were measured to 0.1 mm precision. The shell height (H) is the maximum dimension parallel to the axis of coiling, breadth (B) the maximum dimension perpendicular to H, including the aperture. The length of the aperture (LA) is the greatest length from the junction of the outer lip with the penultimate whorl to the anterior lip, the width (WA) the greatest length perpendicular to LA. The height of the body whorl (BW) is the distance from the base of the shell to the upper suture of the first whorl exactly above the junction of the outer lip with the penultimate whorl. Morphometrical parameters used in the analyses, beside the shell dimensions, were: H/B, H/LA, H/BW, H/LA and B/BW. These shell parameters were statistically analyzed by performing t-tests, one-way ANOVA, and a discriminate analysis.

Protoconchs removed from dried adults were cleaned by soaking in 10% KOH solution, flushed in distilled water, and sonicated to remove residual contaminations prior to scanning electron microscopy. Radulae were taken from dried shells or from historic preparations. Radulae from dried shells were enzymatically cleaned as described by Holznagel (1998); an old radula embedded in Canada balsam was cleaned with xylene followed by sonication. Radulae and juvenile shells were mounted on aluminum specimen stubs using adhesive carbon tabs or double-sided tape, respectively, and coated with gold-palladium for 120 s at 20 mA for examination under a scanning electron microscope (LEO 1450 VP) at 10 keV.

Nomenclatorial Remarks

Some species-group names introduced by Troschel (1857–1858) are open to discussion. Bouchet (pers. comm.) argued that the usage of the names Bithyniae, Lithoglyphi, Hydrobiae, Ancyloti, Thiarae, and Pachychili by Troschel (op. cit.) contrasts with the rest of his work (Troschel, 1856–1863), in which he stated the ranks of the categories he used and formed names with endings -idea, -ina, or -acea. Because Troschel stated explicitly that he refrained from allocating these groupings at family rank given the somewhat ambiguous morphological data he was faced with, it was suggested that one should ignore these names (Bouchet, pers. comm.). However, some of these names, such as Bithyniidae, Thiaridae, or Hydrobiidae, have been usually published with Troschel (1857–1858) as author. Unless otherwise stipulated, we prefer to refer to Troschel (1857–1858) as author of these names not only because we regard them as available and valid but also in order to maintain stability in their usage; for a statement to the contrary see Bouchet and Rocroi (submitted).

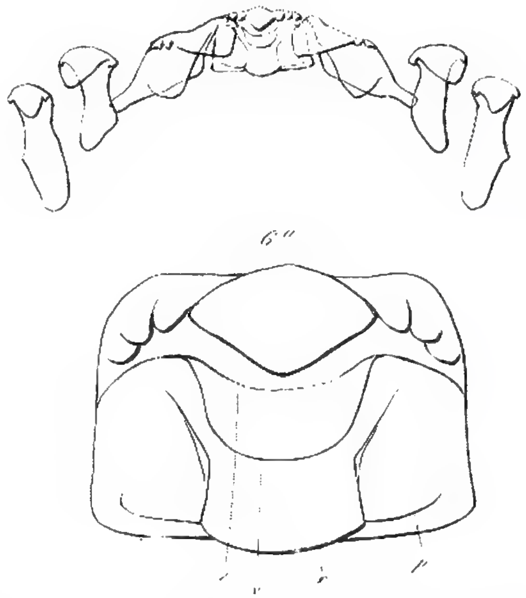


Figure 1. Original drawing of the radula of "*Sulcospira typica* (*Melania sulcospira* Mousson)" by Troschel (1858: pl. 9, fig. 6). In the upper part of the figure a row of teeth is shown comprising a rachidian flanked on each side by a lateral tooth and an inner and outer marginal tooth; a magnified representation of the rachidian is shown below. Characteristics that are typical for Pachychilidae are, e.g., the enlarged main cusp of the rachidian and lateral teeth, respectively, which is flanked by three (or two) smaller cusps on each side that taper in size; the presence and shape of the glabella (or ramp); and marginal teeth possessing two cusps.

Nomenclatorial aspects raised in this paper refer to the stipulations of the 4th edition of the International Code of Zoological Nomenclature ("ICZN") issued by the International Commission of Zoological Nomenclature (1999).

RESULTS

Sulcospira Troschel, 1858

Sulcospira Troschel, 1858: 117–118; Brot, 1874: 56; Thiele, 1929: 190; Morrison, 1954: 381.

Diagnosis: *Sulcospira* possesses a rather conical shell sculptured by spiral lirae; axial sculptural elements are lacking. Protoconchs possess a smooth sculpture with a fine granular texture or faint growth lines.

Type Species: *Melania sulcospira* Mousson, 1849, by monotypy.

Nomenclature and Systematics: The genus *Sulcospira* was described by Troschel (1858) for the Javan species *M. sulcospira* exhibiting certain characteristics that were held to be peculiar of this species, namely a round, multispiral operculum with four regular whorls and the radula with an enlarged main cusp of the rachidian (Figure 1, 17–18). Troschel (1858: 114) based his description on material received from August Brot in Genève, i.e.,

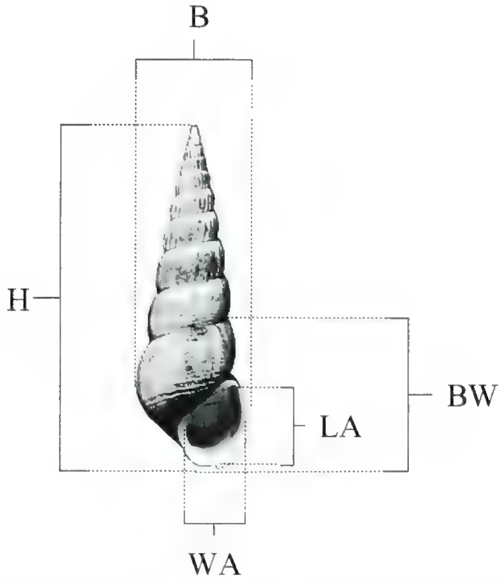


Figure 2. Shell dimensions. B: breadth; BW: weight of the body whorl; H: height; LA: length of the aperture; WA: width of the aperture.

on material that is likely housed at MHNG today (see Material Examined).

Sulcospira represents the oldest available generic name established for representatives of the Southeast Asian Pachychilidae and is here considered valid. However, the diagnosis of Troschel (1858) is not sufficient to characterize the taxon unambiguously. Neither a round and multispiral operculum with four whorls nor the possession of a pronounced main cusp of the rachidian are considered as diagnostic features of *Sulcospira* alone (see discussion). Nonetheless, these features characterize *Sulcospira* as a member of the Pachychilidae (Glaubrecht, 1996, 1999; Köhler and Glaubrecht, 2001, 2002, 2003).

In more recent literature *Sulcospira* has been widely ignored. Thiele (1929) suggested subdividing *Sulcospira* into two subgenera, *Sulcospira* and *Tylomelania* F. and P. Sarasin, 1898. According to Thiele, *Sulcospira* would include *Paracrostoma*, *Acrostoma* Brot, 1870, and *Brotella* Rovereto, 1899, as junior synonyms, consequently comprising two species: *S. sulcospira* from Java and *S. huegeli* (Philippi, 1843) from South India. *Tylomelania*, however, was considered to encompass a small number of species restricted to Sulawesi.

This concept of Thiele (1929) led Subba Rao (1989: 107) to wrongly assume that *M. huegeli* would be the type species of *Sulcospira*, which it is not (see Troschel's original designation).

Later authors had different taxonomic views. Morrison (1954) followed Abbott (1948) but not Thiele (1929) and treated *Acrostoma*, *Brotella*, and *Paracrostoma* as synonyms of *Brotia*, while considering *Tylomelania* as a genus on its own. He also claimed that our understanding of *Sulcospira* is not satisfactory. Based on some superficial similarities with *Brotia*, but also with *Tylomelania* and *Balanocochlis* (a thiarid), Morrison (1954) proposed the allocation of *Sulcospira* "tentatively to the *Melanoides* complex". Since *Melanoides* is a thiarid, this allocation is rejected here.

All these classification schemes were suggested in absence of phylogenetic analyses of morphological characters. In addition to the type species, other taxa have been assigned to the genus by previous authors, although this has not been done consistently (Table 1). The various opinions led also to different assumptions on the species circumscription and diversity of this taxon. For example, Brot (1874) subsumed a number of taxa under *Sulcospira*, of which we currently only consider two to be actually pachychilids: *Melania spadicea* Reeve, 1860, and *M. hainanensis* Brot, 1872. Yen (1939) added two more taxa, *M. ebenina* Brot, 1883, and *M. biconica* Brot, 1886. Boettger (1890), Oostingh (1932), and Adam and Leloup (1838) treated *M. testudinaria* von dem Busch, 1842, as member of *Sulcospira* but did not mention the former taxa. In contrast, other authors assigned those taxa to *Brotia* instead (Rensch, 1934; Benthem-Jutting, 1956, 1959; Knipper, 1958; Dudgeon, 1982, 1989; Köhler and Glaubrecht, 2001, 2002). Eventually, Benthem-Jutting (1956) assumed that *S. sulcospira* is the only representative of the genus.

In order to clarify the puzzling taxonomy and systematics, a revision of *Sulcospira* with an evaluation of its anatomical characters is needed. A sound classification has to be based on autapomorphic features, which is lacking to date. Unfortunately, a comprehensive description of the morphology of *Sulcospira* suffers from the

Table 1. Comparison of previous views on the systematics and circumscription of *Sulcospira*.

	Authors			
	Brot (1874)	Thiele (1929)	Morrison (1954); Benthem-Jutting (1956)	Köhler and Glaubrecht (2002)
Taxonomy at generic level	*Melania* (*Sulcospira*)	*Sulcospira* (*Sulcospira*), *Sulcospira* (*Tylomelania*)	*Sulcospira*	*Sulcospira*
Included taxa	*M. sulcospira*, *M. spadicea*, *M. hainanensis*, and other non-pachychilid taxa	*S. sulcospira*, *S. huegeli*, *T. neritiformis*, *T. carbo*, *T. porcellanica*	*S. sulcospira*	*S. sulcospira*, *S. spadicea*

Table 2. Shell parameters [mm] of *S. sulcospira* and *S. martini*. Abbreviations: B: breadth; BW: weight of the body whorl; H: height; LA: length of the aperture; m: median; N: number of whorls; No: number of shells; sd: standard deviation; WA: width of the aperture.

Lot		No	H	B	LA	WA	BW	N
***S. sulcospira* (total)**	**m**	**26**	**19.3**	**10.1**	**9.5**	**4.9**	**14.3**	**4.7**
	sd		**2.5**	**1.3**	**1.0**	**0.6**	**1.9**	**0.5**
Holotype *M. sulcospira*		1	23.2	12.0	9.7	5.0	15.2	4.0
S. sulcospira (ZMA)	m	21	19.5	10.2	9.5	4.9	14.4	4.6
	sd		2.2	1.2	0.9	0.5	0.6	0.6
S. sulcospira (MNHN)	m	4	18.7	9.9	9.3	4.9	14.1	4.8
	sd		3.6	1.8	1.5	0.9	2.9	0.4
***S. martini* (total)**	**m**	**58**	**27.6**	**12.0**	**11.0**	**5.9**	**17.7**	**6.0**
	sd		**4.5**	**1.5**	**1.3**	**0.8**	**2.1**	**1.0**
Syntypes *M. spadicea* (BMNH 19990497)	m	3	25.5	11.6	10.2	5.2	16.1	6.0
	sd		0.7	0.2	0.9	0.6	0.9	0.5
Syntypes *M. junghuhni* (RMNH, ZMA)	m	22	29.9	12.4	11.6	6.0	18.4	6.3
	sd		4.6	1.8	1.4	0.9	2.4	0.7
Syntypes var. *flammulata*, var. *fasciata* (RMNH)	m	16	28.7	12.3	11.7	6.1	17.9	6.6
	sd		2.9	1.2	1.1	0.7	1.7	0.6
S. martini (ZMB 4.074)	m	17	23.8	11.2	11.0	5.7	16.9	4.9
	sd		2.9	1.3	1.0	0.5	1.7	0.7

lack of well-preserved material of the type species. We compile below the anatomical data based on the material of *S. sulcospira* available.

Sulcospira sulcospira (Mousson, 1849)

Melania sulcospira Mousson, 1849a [1848]: 269; Mousson, 1849b; 68, pl. 9, fig. 3; Martens, 1897: 245 (*partim*); Leschke, 1914: 251.

Sulcospira typica Troschel, 1858: 117, 118, pl. 9, fig. 6 [introduced as replacement name for *M. sulcospira* Mousson, 1849].

Pachycheilus sulcospira [sic].—H. and A. Adams, 1858: 299.

Melania (*Sulcospira*) *sulcospira*.—Brot, 1870: 277; Brot, 1874: 56–57, pl. 6, fig. 11; Boettger, 1890: 245.

Sulcospira sulcospira.—Morrison, 1954: 381; Köhler and Glaubrecht, 2002: 149, fig. 3 L.

Diagnosis: Shell relatively small (Table 2), conical with spiral lirae, and a subsutural depression; aperture elongately ovate, abapically flared. Radula with squarish rachidian exhibiting a straight upper and lower rim, the cutting edge of all teeth with one very pronounced main cusp of triangular shape.

Description: *Shell* (Figures 3–5): small, ovate to conical, solid, spire with eroded apex and up to six flattened whorls, separated by a narrow suture; sculpture consisting of fine, regular spiral lirae that are most prominent at the base and may almost lack on upper whorls, and faint growth lines; whorls with a subsutural depression; color from yellowish to olive or dark brown. Aperture elongately ovate, abapically flared, peristome sharp; columella slightly bent and thickened.

Protoconch (Figures 19–20): Relatively large, compared to the adult; with height of about 1.2 mm comprising one and a half whorl; generally smooth. Apical whorl inflated, dome-shaped, with a granular surface sculpture, transition in sculpture visible on first whorl from granular to faint growth lines. One sample of four specimens housed at MNHN (ex coll. Staat) has a label stating that "about 140 embryos were obtained from the large specimen". However, the fate of these protoconchs is unknown.

Operculum: With four whorls regularly increasing in diameter and a sub-central nucleus.

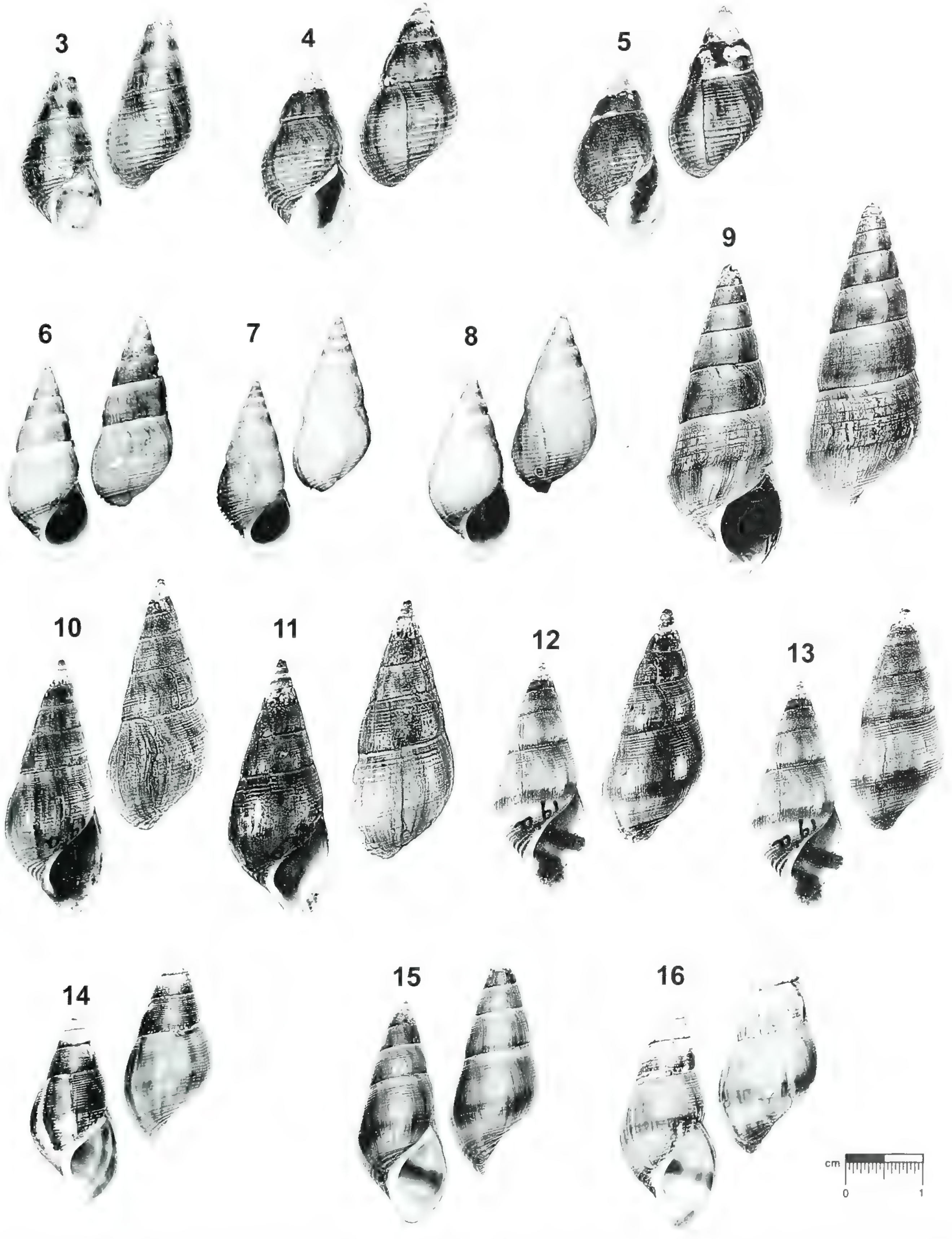
Radula (Figures 16–17): Rachidian tooth squarish with a straight upper and lower rim, cutting edge with one heavily enlarged main cusp of triangular shape, flanked by two, much smaller accessory cusps on each side; glabella well developed, rather rectangular with a rounded basal margin not exceeding the lower rim of the rachidian tooth, lateral margins straight and not well defined. Lateral teeth with one heavily enlarged main cusp, and considerably smaller accessory cusps, one at the outer side, two or three at the inner side. Inner and outer marginal teeth with two cusps, the outer one being very large, triangular in shape, and the inner one being pointed and small. Inner marginal teeth broader than outer marginals. Outer lateral flange inconspicuous.

Anatomy: Unknown.

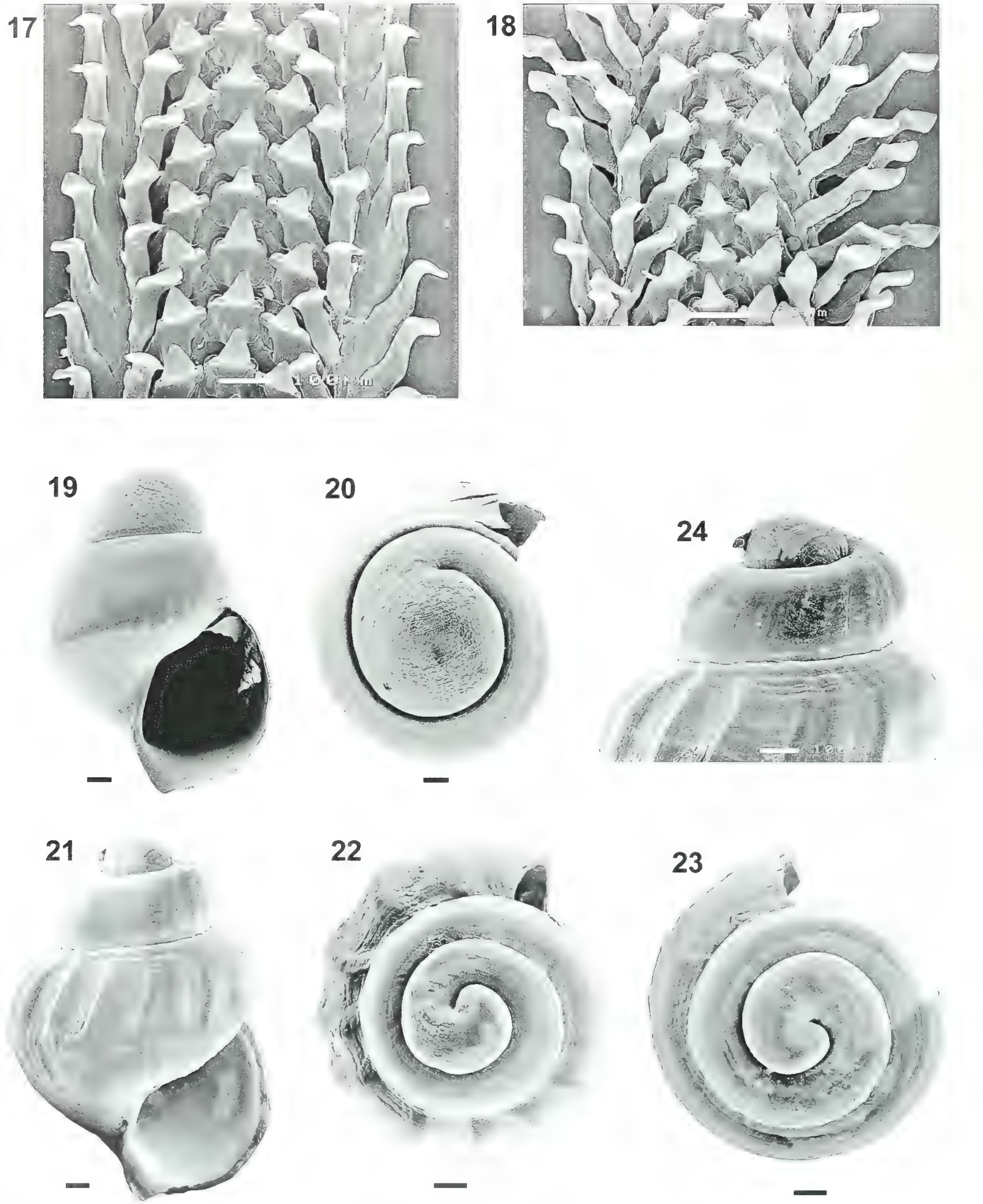
Type Material: Indonesia: Holotype ZMZ 522306, Indonesia: Java, leg. Zollinger (Figure 3) [Mousson, 1849b refers to "das einzige Exemplar dieser Art . . ." = the only specimen of this species . . .].

Type Locality: "Java", Indonesia.

Other Material Examined: Indonesia: Java (MHNG; MNHN; MNHN, ex coll. Staat; ZMA (2 lots); ZMB 200.101) (if not stated otherwise, a single lot from each collection, mostly without reference number, was examined); museums without material: ANSP, BMNH, MCZ, RMNH, SMF, USNM, ZMH, ZSM.



Figures 3–16. Shell morphology of *Sulcospira sulcospira* (**3–5**) and *S. martini* (**6–16**) (apertural and abapertural, respectively **3.** *S. sulcospira*. Holotype (ZMZ 522306). **4–5.** *S. martini*. Two shells from Java (ZMA). **6.** Lectotype of *M. spadicea* (BMNH 19990497/A). **7–8.** Two paralectotypes of *M. spadicea* (BMNH 19990497/B). **9.** Lectotype of *M. junghuhni* (RMNH 71326). **10–11.** Two syntypes of *M. junghuhni* var. *flammulata* (RMNH 71327). **12–13.** Two syntypes of *M. junghuhni* var. *fasciata* (RMNH 71328). **14–16.** Three shells from Java, Malangbong (ZMB 4.074). Scale bar = 10 mm



Figures 17–24. SEM images of the radula and juvenile shells removed from dry shells of *S. sulcospira* (**17–20**) and *S. martini* (**21–24**). *S. sulcospira*: **17.** Radula (ZMA). **18.** Radula (ZMB 200.101). **19.** Juvenile shell, apertural view (ZMA). *S. martini*: **20.** Juvenile shell, apical view (ZMA). **21.** Juvenile shell, apertural view (ZMB 4.074). **22–23.** Apical view. **24.** Detail of the apical portion. Scale bars = 100 μm.

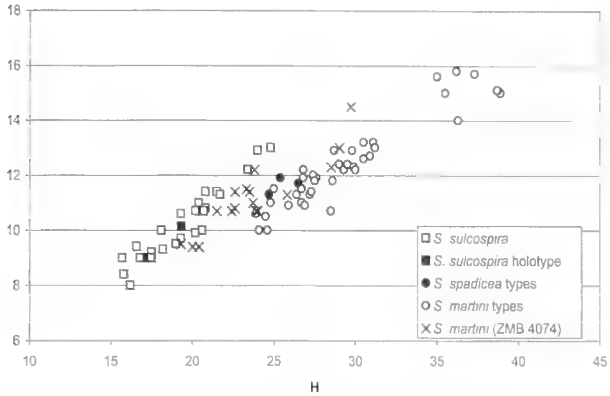


Figure 25. Comparison of the shells of *S. sulcospira* and *S. martini* based on shell parameters height (H) and breadth (B).

Distribution: Indonesia: Java. More precise localities were given by Boettger (1890: Bogor Botanical Garden) and Martens (1997: Jakarta, Malangbong, Cipanas). However, the material of Boettger could not be traced (SMF?), and Martens misidentified material of *Melanoides tuberculata* (Cipanas) and *S. martini* (Malangbong; ZMB 4.076); no voucher material was found from Jakarta.

Nomenclature and Systematics: *Melania sulcospira* is the type species of the genus *Sulcospira* by original designation. When describing the new genus, Troschel (1858), mentioned *M. sulcospira* as the "typical species", and introduced the name *S. typica* for the same taxon as a new, unnecessary substitute name meant to replace an older available name (*nomen novum*). Thus, *S. typica* is a junior synonym of *S. sulcospira* (ICZN Art. 72.7.). *Sulcospira typica* is invalidated as potential type name (ICZN Art. 68.4.) making *M. sulcospira* the type by absolute autonomy. Martens (1897) assumed that *M. spadicea* is a synonym of this species, which was rejected by Leschke (1914) and Benthem-Jutting (1956: 373), stating that Martens (1897) had misidentified specimens of *Melanoides tuberculata* for *M. spadicea.*

Remarks: Compared to *Sulcospira martini*, *S. sulcospira* is more conical in shape; the former lacks a conspicuous subsutural depression. Most conspicuously, both species differ in their protoconch morphology. Shells of *B. testudinaria* are more elongated in shape, attain a larger size (between 25 to 40 mm in shell height), lack a subsutural depression, and exhibit a different radular morphology: e.g., rachidian with inflated and rounded upper corners, a smaller main cusp, marginal teeth possess two equally shaped cusps.

Given the scarcity of material and imprecise earlier locality data for this material, we tried to restrict the type locality from historical accounts. The Swiss malacologist Albert Mousson (1805–1890) based his descriptions on material collected by the Swiss botanist Heinrich Zollinger (1818–1859), who traveled in Indonesia between 1842 and 1848. However, as Zollinger collected not only in West Java, but later also in East Java, and on some other islands (Wanner, 1984), it turned out that a restriction of the type locality is not possible and "Java" remains as the only known reference.

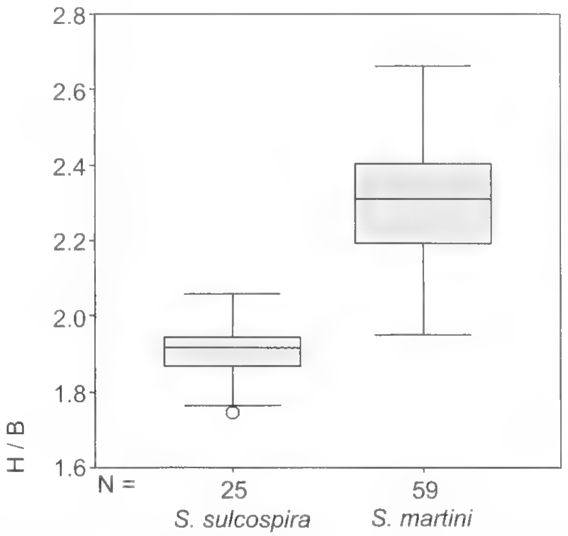


Figure 26. Comparison of *S. sulcospira* and *S. martini* based on shell parameters ratio H/B. Box plot diagram showing the median, the 25%- and 75%-percentile and largest non-extremes (less than 1.5 times of box height).

Sulcospira(?) *martini* (Schepmann, 1898)

Melania spadicea Reeve, 1860: pl. 19, species 132 (not *Melania spadicea* Philippi, 1849); Brot, 1870: 277.

Melania (*Sulcospira*) *spadicea.*—Brot, 1874: 57–58, pl. 6, fig. 12.

Brotia spadicea.—Benthem-Jutting, 1956: 372–373, fig. 75.

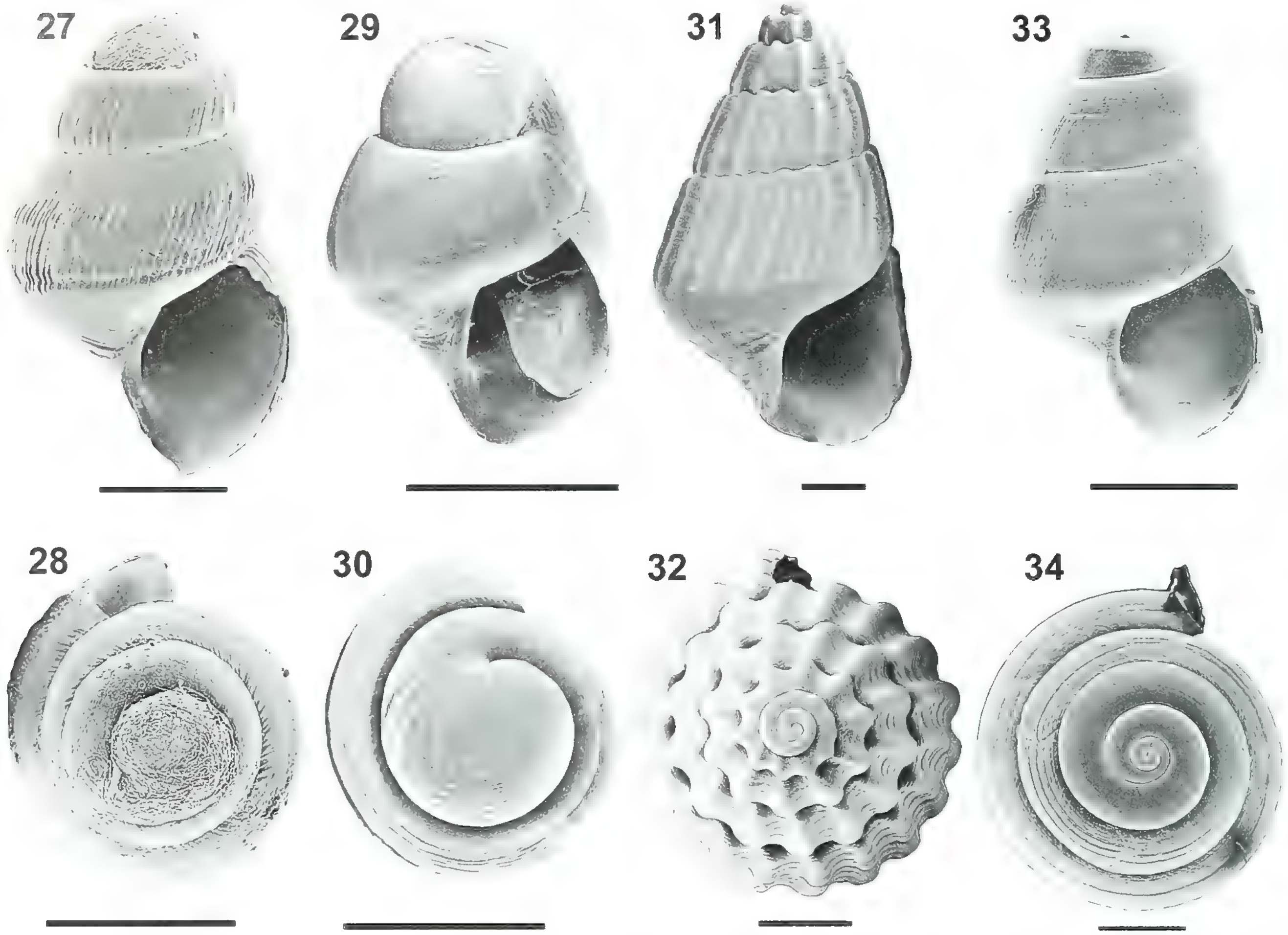
Sulcospira spadicea.—Köhler and Glaubrecht, 2002: 148, fig. 3G.

Melania junghuhni Schepman, 1896: 135–136, pl. 2, fig. 1. ("Java"; lectotype and 41 paralectotypes RMNH 71326; 24 paralectotypes ZMA; two paralectotypes SMF 292406; var. *flammulata*: 16 syntypes RMNH 71327; 3 syntypes MCZ 96926, var. *fasciata*: 18 syntypes RMNH 71328; 24 syntypes ZMA; 8 syntypes MCZ 96898) (not *M. junghuhni* Martin, 1879); Leschke, 1914: 251; Benthem-Jutting, 1929: 84.

Melania martini Schepmann, 1898: 84.

Brotia testudinaria.—Köhler and Glaubrecht, 2001: 301–304 (*partim*); Köhler and Glaubrecht, 2002: 140, 141, 150 (partim).

Diagnosis: Conical shell with convex to flattened whorls sculptured with fine spiral ridges. Protoconch with about 2.5 regular whorls; apical whorl not inflated, no transition in shell structure is visible in the first two whorls. Axial ribs may be present in the juvenile shell from the second whorl on. Most conspicuously distinguished from all other pachychilids by its protoconch morphology (Figures 27–34); distinguishable from *S. sulcospira* by its more elongated and larger shell (Figure 26); though adult shell not distinguishable from *B. testudinaria*.



Figures 27–34. Comparison of protoconchs of different southeastern Asian Pachychilidae (apertural and apical view, respectively). **27–28.** *Brotia costula*. **29–30.** *Brotia hainanensis*. **31–32.** *Tylomelania patriarchalis* (with kind permission of Thomas von Rintelen). **33–34.** *Pseudopotamis semoni*. Scale bars = 100 μm.

Description: *Shell* (Figures 6–16): Small to medium sized (Table 2), ovate to conical, spire with eroded apex and eight to ten flattened whorls; sculpture consisting of fine, closely spaced regular spiral lirae, may lack almost completely, and faint growth lines; color yellowish brown to olive, brown spiral band or patches may be present. Aperture elongated ovate, produced below, peristome sharp.

Protoconch (Figures 21–24): Height of about 1.2 mm comprising 2½ whorls; apical whorl not inflated, corresponding to the regular diameter of the subsequent whorls; first two whorls smooth, only faint growth lines visible, without transition in sculpture, from the second whorl on smooth axial ribs may be present.

Operculum: Consisting of three whorls and a sub-basal nucleus Brot (1874).

Anatomy and Radula: Unknown.

Type Material: Indonesia, Java: Lectotype and 41 paralectotypes of *M. junghuhni*, RMNH 71326, leg. Junghuhn (Figure 9), designated by Köhler and Glaubrecht (2002); 24 paralectotypes, ZMA; two paralectotypes, SMF 292406; 16 syntypes of *M. junghuhni* var. *flammulata*, RMNH 71327; three syntypes, MCZ 96926, 18 syntypes of *M. junghuhni* var. *fasciata*, RMNH 71328; eight syntypes, MCZ 96898. Without locality: Lectotype of *M. spadicea*, BMNH 19990497/A, Cuming collection, designated by Köhler and Glaubrecht (2002); two paralectotypes, BMNH 19990497/2.

Type Locality: "Java", Indonesia.

Other Material Examined: Without locality (ZMA; MHNG); Indonesia: Java (MHNG), Malangbon (ZMB 4.074) (a single lot from each collection, mostly without reference number). No material was found in the following museums: ANSP, MNHN, SMF, USNM, ZMH, ZSM.

Nomenclature and Systematics: *Melania spadicea* Reeve, 1860, is a primary homonym of *M. spadicea* Philippi, 1849 (ICZN Art. 53.3) and, as such, is permanently invalid (ICZN Art. 57.2). The next available names are *M. junghuhni* Schepmann, 1896, *M. junghuhni* var. *flam-*

mulata Schepmann, 1896, and *M. junghuhni* var. *fasciata* Schepmann, 1896. However, the first is a primary homonym of *Melania junghuhni* Martin, 1879, a fossil species from Java, as stated by Schepmann (1898). The other two are junior primary synonyms of *Melania flammulata* von dem Busch in Philippi, 1843, and *Melania fasciata* Menke, 1828, respectively.

Schepmann (1898) suggested *Melania martini* as a replacement name for *M. junghuhni*, which is the valid name for this taxon. The two color morphs described by Schepmann (1896), *fasciata* and *flammulata*, are not considered here to represent extant evolutionary entities and therefore are treated as junior synonyms of *M. martini*.

The classification of this species by former authors is inconsistent. Benthem-Jutting (1956) considered it to be a member of *Brotia*; but unaware of the fact that *M. spadicea* Reeve, 1860, is not valid she assumed that this name had priority over *M. martini*. Köhler and Glaubrecht (2002) assumed that *M. martini* and *M. spadicea* are distinct and treated the former as a synonym of *B. testudinaria* and the latter as a species closely related to *S. sulcospira* as was suggested earlier by Brot (1874).

Distribution: Java, as the only known locality. Malangbon in Central Java, east of Bandung, is the only known exact locality (ZMB 4.074, catalogued in 1859).

Analyses of Shell Morphometry: *Sulcospira martini* can be distinguished from *S. sulcospira* by its higher shell and more slender shape (see analyses of shell parameters below). However, to differentiate between shells of "*M. sulcospira*" and "*M. martini*" is no easy task; contradictory statements on their taxonomy abound in earlier accounts (Brot, 1874; Benthem-Jutting, 1956; Köhler and Glaubrecht, 2002). In fact, shells exhibit a very similar shape, sculpture, and coloration. However, the two taxa can be distinguished by statistical analyses of shell morphometry. We used one-way ANOVA and t-test for two independent groups of variables to discriminate specimens that were assigned beforehand either to *S. sulcospira* or to *S. martini* according to their shell morphology. The t-test showed that both taxa vary significantly by the following parameters ($P<5\%$): H, N, H/B, H/LA, and H/BW; the one-way-ANOVA yielded corresponding results.

The shells of the only lot from Java with precise locality data (ZMB 4.074) is identified here as *S. martini* given its elongated shell (while the original label states "*M. sulcospira*" instead). The statistical test has been employed to explore whether these shells can significantly be discriminated either from shells of *S. sulcospira* or *S. martini* in regard to shell morphometry. Comparison of shells of the lot ZMB 4.074 with shells of *S. sulcospira* (MNHN, ZMA, ZMB 200.101, ZMZ 522306) by t-test reveals that both groups differ significantly in the parameters H/LA, H/BW, and with a weak support ($P = 0.51$) for H/B, whereas no significant differences were found when comparing the lot ZMB 4.074 with other shells of *S. martini* (BMNH 19990497, RMNH 71326-8).

Table 3. Results of the discriminate analysis of shell parameters.

Predicted group membership	*S. sulcospira*	*S. martini*
S. sulcospira	25 (100.0%)	0 (0.0%)
S. martini	1 (1.7%)	59 (98.3%)

A graphic comparison of the two taxa by means of selected shell parameters is shown in Figures 25–26. Shells assigned to each of the two taxa according to their morphology were found to be correctly classified by a discriminate analysis of morphometric data with good statistical support (Table 3). It is concluded that shells of *S. sulcospira* are smaller and more conical in shape than shells of *S. martini* (Table 1, Figure 26).

DISCUSSION

I. Evaluation of Morphological Characters of *Sulcospira*

The operculum and radula of *S. sulcospira* led Troschel (1858) to describe a new genus for this species. However, among the Pachychilidae the operculum is known to be relatively conservative in its general organization (that is, to be multispiral, rounded or ovate) but quite variable in relation to their number of whorls and increase in diameter, even within a single genus (Köhler and Glaubrecht, 2001, for *Brotia*; Köhler and Glaubrecht, 2003, for *Jagora*; Glaubrecht and Rintelen, 2003, for *Pseudopotamis*; Rintelen, 2003, for *Tylomelania*; Köhler, 2003). Consequently, an operculum possessing four regular whorls might be typical for *S. sulcospira*, but only at the species level. The possession of a round to oval, multispiral operculum led Sarasin and Sarasin (1898) to group several taxa within the so-called "palaeomelanians", as contrasted with the so-called "neomelanians", which exhibit a paucispiral operculum. In fact, this grouping coincides well with the modern concept of the Pachychilidae and Thiaridae, respectively (Glaubrecht, 1996, 1999; Köhler and Glaubrecht, 2001, 2002, 2003). Therefore, operculum morphology in *S. sulcospira* corroborates the placement of the taxon within the Pachychilidae. This, however, represents a plesiomorphic character state among the representatives of this family, and is not a suitable character to establish generic distinction.

By and large, the same can be stated for the radula. The molluscan radula is generally considered a conservative character (Fretter and Graham, 1994). The pattern described and depicted by Troschel (1858) (Figure 1) is commonly found among pachychilids (Köhler and Glaubrecht, 2001, 2002, 2003; Glaubrecht and Rintelen, 2003; Rintelen and Glaubrecht, 1999, 2003). This had been already noticed by Troschel (1858), when allocating taxa such as *Pachychilus* and *Sulcospira* (but also *Me-*

lanopsis) under the "Pachychili". However, we have been unable to identify a single radular character peculiar to *Sulcospira*, based on the limited anatomical features discussed here. An enlarged main cusp is also found in other pachychilid species, such as *B. pagodula* (Köhler and Glaubrecht, 2001). Moreover, it is evident that radular characters may especially be prone to adaptation, parallelism, and convergence and that intraspecific variability and plasticity in general may be considerable, as described, e.g., for littorinid gastropods (Padilla, 1998; Reid and Mak, 1999; Reid, 2000). Thus, possession of an elongated cusp alone is not considered a characteristic suitable for the diagnosis of *Sulcospira*.

Gross anatomy of *S. sulcospira* and *S. martini* remains unknown, due to the lack of ethanol-preserved specimens. It has been shown for other pachychilids, though, that particularly characters of the reproductive organs (pallial oviduct, gonads, brooding structures) and the protoconch may bear essential systematic information (Köhler and Glaubrecht, 2001, 2003).

Juvenile shells extracted from dried adults (Troschel, 1858; and own observations) deliver circumstantial evidence that *Sulcospira* is viviparous. Furthermore, as made evident from the following comparison, the protoconchs of *S. sulcospira* are similar to those of some species we have primarily assigned to the "*Brotia-testudinaria*-group" (Köhler and Glaubrecht, 2001, e.g., *Brotia testudinaria* and *B. hainanensis*; Figures 29–30). In contrast, other taxa constituting the genus *Brotia* sensu stricto (denominated the "*Brotia pagodula* group" by Köhler and Glaubrecht, 2001) have juveniles with an irregularly wrinkled sculpture of the apical whorl of the protoconch (Figures 25–26). Protoconchs of *Tylomelania* and *Pseudopotamis* exhibit yet another fine morphology (Figures 27–34). They attain a relative large size and exhibit a relatively small apical whorl with a smooth shell as well as regularly increasing whorls (Rintelen and Glaubrecht, 1999, 2003; Glaubrecht and Rintelen, 2003).

As discussed in some detail by Köhler and Glaubrecht (2001), distinct protoconch morphologies of several pachychilid genera are correlated with different reproductive strategies. For example, *Brotia* possesses a subhaemocoelic brood pouch while representatives of *Tylomelania* and *Pseudopotamis* are characterized by an eu-viviparous mode of reproduction utilizing a modified oviduct as brood pouch (= uterine brood pouch; Rintelen and Glaubrecht, 1999; Glaubrecht and Rintelen, 2003). Females of the latter two taxa retain a small number of embryos in the uterus that are nourished by secretions produced by the albumen gland.

The protoconchs of *Sulcospira* correspond to those of the so-called "*Brotia testudinaria* group" (Köhler and Glaubrecht, 2001), which indicates to us that *S. sulcospira* possesses a subhaemocoelic brood pouch as well.

II. COMPARISON OF *S. SULCOSPIRA* AND *S. MARTINI*

Sulcospira martini, which has tentatively been allocated to the genus by Köhler and Glaubrecht (2002), can be distinguished by its shell, but much more conspicuously by its different protoconch morphology, which is unique among the Pachychilidae.

Because the protoconch morphology is related to the mode of reproduction, it is assumed that *S. martini* exhibits reproductive features (e.g. incubatory structure, reproductive strategy) that may be distinct from those known from any other pachychilid taxon.

III. SYSTEMATIC CONCLUSIONS

Shell, operculum, and radula of *S. sulcospira* (and also of *S. martini*) are typically pachychilid; a basally well rounded and flared aperture, a round to oval, multispiral operculum, and a rachidian tooth with an enlarged main cusp flanked by up to three accessory cusps that taper in size are diagnostic characters of this family. However, these characters are symplesiomorphic and, thus, uninformative at the generic level. Soft body morphology, which could bear crucial information, is not known. Still, some systematic conclusions can be drawn based on the evaluation of protoconch morphology, which is considered to be more or less constant at the generic level: First, species of *Brotia* (Figures 27–28), *Tylomelania* (Figures 31–32), and *Pseudopotamis* (Figures 33–34) are not congeneric with *S. sulcospira* (see Figures 19–20) since they exhibit each a distinct protoconch, which is testimony to a different reproductive strategy as discussed above. The same holds true for *Jagora* (Köhler and Glaubrecht, 2003). All these pachychilid genera have been shown to represent independent monophyletic lineages characterized by morphological features, such as peculiar reproductive morphologies. Second, the protoconch of *S. sulcospira* is very similar to that known from species of the "*Brotia-testudinaria*-group" denominated by Köhler and Glaubrecht (2001) (Figures 29, 30 for *B. hainanensis*). Hence, *Sulcospira* Troschel, 1858, being available and valid, might be an appropriate generic name for this species group under the precondition that it can be shown that a protoconch with a smooth and dome-shaped apical whorl is a character possessed by the members of this group and derived by shared ancestry. However, the alternative explanation that a similar protoconch represents an ancestral state that is present in two different lineages has to be ruled out. Otherwise, inferring generic relationship in absence of a phylogenetic evaluation could lead to the erection of paraphyletic taxa when the characters considered are plesiomorphic. Before we cannot show by phylogenetic analyses of morphological or molecular data that *S. sulcospira* and species of the "*Brotia testudinaria* group" indeed belong to the same taxon, we therefore refrain from a respective taxonomic suggestion.

Third, we conclude that *S. martini* can be recognized as a species and that it does not represent a synonym of *S. sulcospira*. Furthermore, it is clear that the morphology of the protoconch of *S. martini* does resemble neither of the known pachychilid genera very closely (Figures 27–34) including that of *S. sulcospira* (Figures 19–

20). Just based on this single feature, it could be deduced that *S. martini* might be a representative of a yet undescribed genus. However, as has been stated for *S. sulcospira,* a sound decision on its systematics should rely on a more comprehensive data set.

For the time being, we suggest to maintain *Sulcospira* as a monotypic genus endemic to Java. Furthermore, we refrain from a taxonomic decision on the generic relationship of "*Sulcospira*" *martini.* It likely is not a member of one of the described pachychilid genera, but its true relationships remain unknown.

Irrespective of our anticipation that both species dealt with in this paper may have already become extinct in large parts of their original distribution area, we still hope that suitable material will turn up, eventually allowing to find an answer to the remaining questions and to solve another of the many puzzling aspects of pachychilid phylogeny and systematics that long hampered a deeper understanding of the evolution of this intriguing and instructive case study among the lymnic Cerithioidea.

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Six new species of *Paryphantopsis* (Gastropoda: Pulmonata: Charopidae) from the Papuan Peninsula of New Guinea

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ABSTRACT

Six new species of *Paryphantopsis*, a genus of charopid snails endemic to New Guinea, are described from the geologically complex eastern terminus of the Papuan Peninsula. All descriptions are based on material collected in 2002–2003 and include information on shell, genital, and radular anatomy. Of the 14 previously described species, genital anatomy was known for three and radular morphology for only one species. Examination of these under-utilized character sets has uncovered taxonomically useful interspecific variation. The six new species appear to have distributions limited to particular mountain groups on the extreme eastern terminus of the Papuan Peninsula. Species in close proximity or sympatry share unique shell, genital and radular characters suggesting local speciation and poor dispersal ability. Diversity in *Paryphantopsis* has been underestimated and it is likely that there are many species yet to be discovered with narrow geographic and ecological ranges in the under-explored mountains of New Guinea.

INTRODUCTION

Paryphantopsis, a genus of charopid snails endemic to New Guinea, are found at moderate and high altitudes (600–4000 m) and are distributed from Western Papua (Irian Jaya) to the Louisiade Archipelago. The genus contains fourteen previously described species: *P. arcuata* Jutting, 1964, *P. dualoensis* Solem, 1970, *P. elegans* (Fulton, 1902), *P. filosa* Jutting, 1964, *P. fultoni* (Coen, 1922), *P. globosa* (Hedley, 1890), *P. lamelligera* (Thiele, 1928), *P. latior* Jutting, 1964, *P. louisiadarum* (Möllendorff, 1899), *P. platycephala* Jutting, 1964, *P. pygmaea* (Bavay, 1908), *P. sculpturata* Jutting, 1964, *P. similis* (Thiele, 1928), and *P. striata* (Fulton, 1902). Solem (1970) reviewed the genus, redescribing all species except those then recently described or reviewed by Jutting (1964). Most *Paryphantopsis* species are known from small samples of shells, often only from their type localities, and data on genital morphology are limited to three species, and on radular morphology to only one species (Solem, 1970, Wiktor, 2003). *Paryphantopsis* has not been reported previously east of longitude 148° E on the relatively poorly sampled eastern part of New Guinea, which is known as the Papuan Peninsula. The eastern end of the peninsula includes the Cloudy Mountains to the south, and the disjunct terminus of the Owen Stanley Range to the north, separated from the main Owen Stanley uplands by extensive lowlands west of Mount Suckling. The geologically complex Papuan Peninsula is formed largely by the East Papua Composite Terrane (EPCT), a tectonic province composed of at least 4 separate geological units with differing ages, origins, and histories. These units appear to have assembled northeast of modern New Guinea during the Paleocene, 62–57 Myr ago, and fused to the main body of the island in the Late Oligocene to Early Miocene, 28–22 Myr ago (Pigram and Davies, 1987). Because of its likely initial offshore amalgamation, the EPCT may have developed a distinct and largely endemic biota. This is the first in a series of papers describing the results of ten weeks of field surveys that took place during April–May, 2002 and January–March, 2003. These surveys explored the extreme eastern terminus of the Papuan Peninsula where two geological units lie in close proximity, the Cloudy Mountains of the Port Moresby Terrane and eastern terminus of the Owen Stanley Range of the Kutu Terrane (Figure 1).

MATERIALS AND METHODS

Specimens were hand-collected or sifted from samples of leaf-litter. Live collected animals were drowned overnight and then preserved in 75% ethanol. Gross anatomical dissections were made under 75% ethanol using a dissecting microscope. Radulae were isolated from dissected buccal masses using a saturated KOH solution. Scanning electron micrographs of radulae were made using a field emission SEM. Drawings of the genital anatomy were made with the assistance of a *camera lucida*, and measurements were taken using an ocular micrometer. Shell measurements were made as follows. Whorl count (W) was measured from the suture of the first whorl to the body whorl and fractions of a whorl were determined with the aid of a cardboard circle divided into 10 equal parts of 36° (Figure 2, line 1–2.9). Spire

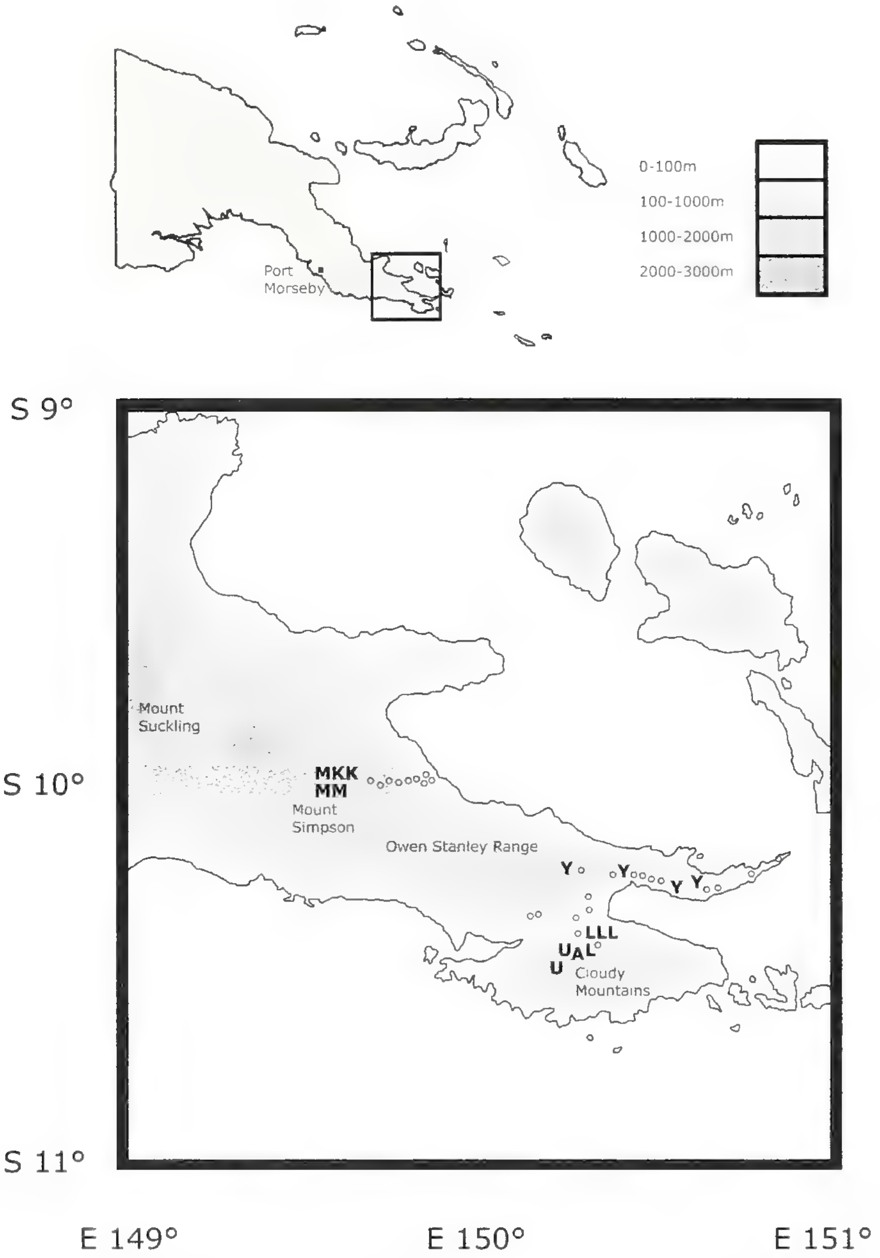
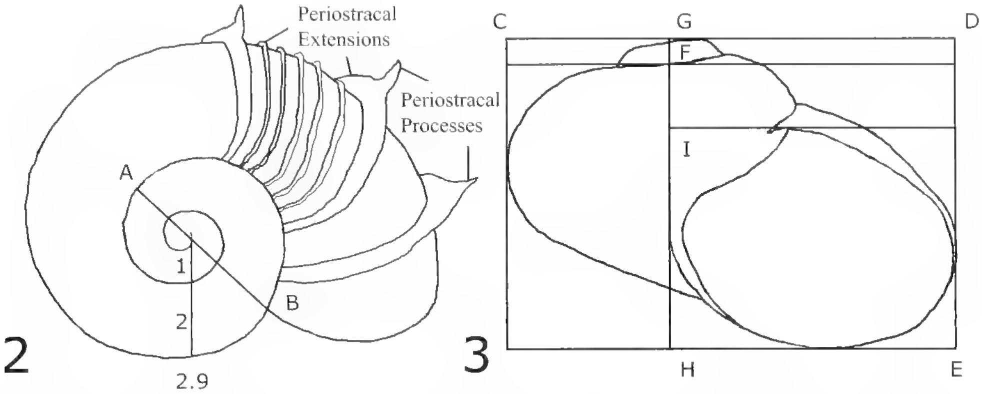


Figure 1. Distribution of *Paryphantopsis* on the eastern terminus of the Papuan Peninsula, Papua New Guinea between 9° S, 149° E and 11° S, 151° E. A = *P. abstrusa*, K = *P. koragae*, L = *P. lebasii*, M = *P. matawanensis*, U = *P. ubwamensis*, Y = *P. yawii*, O = other sites sampled.

diameter (SD) was the length of a straight line passing from the apertural edge of the suture through the middle of the apex to the opposite suture (Figure 2, line A–B). Diameter (D) was the greatest width of the shell perpendicular to the shell axis (Figure 3, line C–D). Height (H) was the greatest distance between the apex and the base of the aperture measured parallel to the shell axis (Figure 3, line D–E). Spire height (SH) was measured from the top of the body whorl to the apex of the shell (Figure 3, line F–G). Aperture width (AW) was the greatest distance from the columellar edge to the outer edge of the aperture (Figure 3, line E–H). Aperture height (AH) was measured from the suture to the base of the aperture, parallel to the shell axis (Figure 3, line H–I). The lengths of radular teeth were measured from the top of the mesocone to the posterior edge of the basal plate. The widths of radular teeth were measured as the greatest width of the cusps, not the basal plate. The following abbreviations are used in figures of genital anatomy: AT = atrium, DI = diverticulum, EP = epiphallus, OV = free oviduct, PE = penis, PG = prostate gland, PP = penial pilasters, PR = penial retractor muscle, SD = spermathecal duct, SP = spermatheca, VA = vagina, VD = vas deferens, VP = vergic



Figures 2–3. Diagram of shell measurements. **2.** Whorl count (line 1–2.9), spire width (line A–B). **3.** Diameter (line C–D), height (line D–E), spire height (line F–G), aperture width (line E–H), aperture height (line H–I).

papillae. Specimens are deposited in the following institutions: Bernice P. Bishop Museum, Honolulu (BPBM), Florida Museum of Natural History, Gainesville (UF), Papua New Guinea National Museum, Port Moresby (PNGNM), Wroclaw University Museum of Natural History (MNHW).

SYSTEMATICS

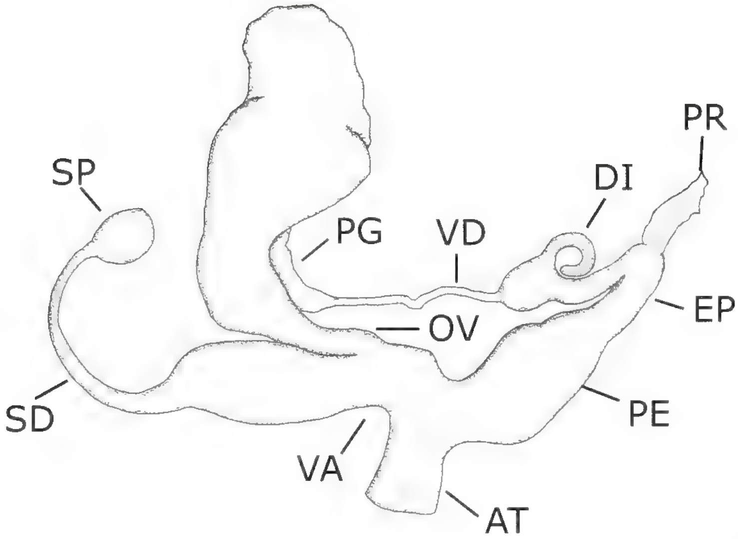
Family Charopidae Hutton, 1884
Genus *Paryphantopsis* Thiele, 1928 (Type species: *Flammulina* (*Paryphantopsis*) *lamelligera* Thiele, 1928, by original designation.)

Description: Moderate to large-sized charopid snails with loosely coiled shells of approximately three whorls. Shell shape varies among species from globose to depressed with an elevated to flat spire and a rounded to keeled margin. The umbilicus, usually covered by an expansion of the peristome, is sometimes perforate. Nuclear whorls (protoconch) are sculptured with spiral rows of small pits that become weaker and less regular on later whorls. Postnuclear whorls (teleoconch) are usually sculptured with growth lines accentuated with short periostracal extensions punctuated with occasional longer extensions at regular intervals. These longer extensions can bear additional processes at the shell margin (Figure 2). A few species do not have longer periostracal extensions and some species do not bear any extensions. Body color is usually yellow in life. The epiphallus is apically inflated, often with an apical diverticulum. The penis is textured with convoluted pilasters of varying complexity. Central teeth of the radula are tricuspid and of similar size to the tricuspid and slightly assymetrical lateral teeth. The many lateral teeth become shorter and less symmetrical, grading in shape with the marginal teeth. Marginal teeth are usually assymetric, their endocones longer than their ectocones. Endocones and ectocones and less often mesocones can bear accessory cusps.

Paryphantopsis abstrusa new species
(Figures 4–10, Table 1)

Description: The adult shell is small for the genus, 4.4–4.8 mm (mean = 4.6) in diameter and 3.5–3.8 mm (mean = 3.6) in height, with 2.9–3.0 (mean = 3.0) rapidly expanding whorls (Figures 4–6, Table 1). The spire is elevated 0.3 mm. Postnuclear whorls descend regularly and the shell height/diameter ratio is 0.76–0.81 (mean = 0.79). The shell has 1.3 evenly rounded nuclear whorls, sculptured with 12 spiral rows of small pits. The postnuclear whorls bear weak and irregular malleations, most readily visible at the base, and indistinct and irregular striae on the apical surface. The postnuclear whorls are also sculptured with weak growth lines. Approximately every fourth growth line is accentuated by a periostracal extension. The periostracal extensions bear small (0.15 mm) trigonal processes at the periphery. These processes occur on every periostracal extension for the first two whorls, then become less regular and finally absent from the final ½ whorl. The fragile processes are often partially worn from the earlier whorls of adult shells. The nuclear whorls are white, the postnuclear whorls brown. The umbilicus is closed by a reflection of the peristome. The aperture is large, ovate to nearly circular, with an aperture-diameter to aperture-height ratio of 0.54–0.67 (mean = 0.63).

The body color is uniform bright yellow-white in life, fading to cream in specimens preserved in ethanol. The vas deferens narrows rapidly from the prostate gland and remains narrow to the swollen head of the epiphallus (Figure 7). A long coiled diverticulum inserts laterally on the epiphallus soon after the junction with the vas deferens. The epiphallus narrows slightly after the diverticulum and widens towards the junction with the penis. The penis is half the length and three times the width of the epiphallus, robust, widest centrally, and narrowing slightly at each end. Apically there are several small convoluted pilasters and one much larger convoluted pilaster that extends to near the base (Figure 8). The penial retractor muscle is robust, originating from



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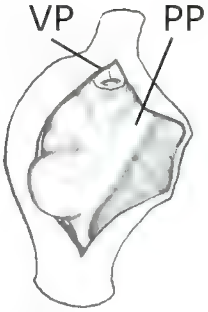

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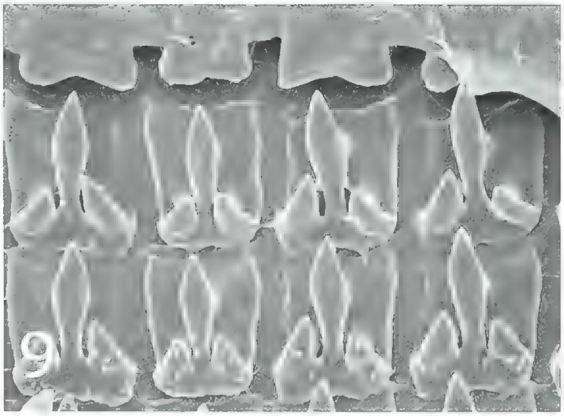
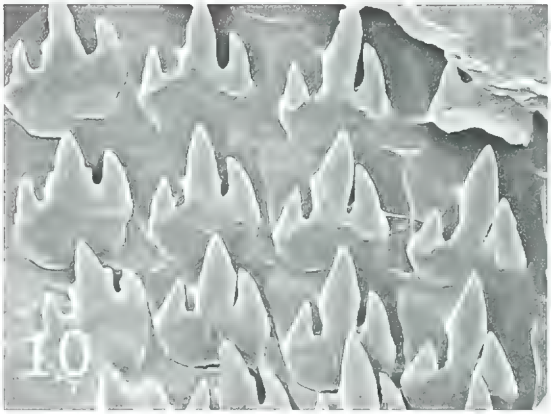




Figures 4–10. *Paryphantopsis abstrusa.* **4–6.** Photographs of shell, Holotype UF 308235, diameter 4.6 mm. **7–8.** Camera lucida drawing of genitalia, UF 299677, maximum width 7.2 mm. **9–10.** Scanning electron micrograph of radula, UF 299677, field width of central and lateral teeth 41 μm, marginal teeth 42 μm

Table 1. Measurements in mm of undamaged adult shells of six species of *Paryphantopsis*, N = count, H = height, D = diameter, SH = spire height, SD = spire diameter, AH = aperture height, AD = aperture diameter, W = number of whorls.

Species	N		H	D	SH	SD	AH	AD	W
P. abstrusa	3	mean ± SD	3.6 ± 0.2	4.6 ± 0.2	0.3 ± 0.0	2.1 ± 0.0	2.6 ± 0.2	2.8 ± 0.1	3.0 ± 0.1
		range	3.5–3.8	4.4–4.8	0.3–0.3	2.0–2.1	2.4–2.7	2.7–2.9	2.9–3.0
P. koragae	3	mean ± SD	2.9 ± 0.1	4.2 ± 0.0	0.2 ± 0.0	1.6 ± 0.1	2.1 ± 0.1	2.6 ± 0.1	2.8 ± 0.1
		range	2.8–3.0	4.1–4.2	0.1–0.2	1.5–1.7	2.0–2.1	2.5–2.7	2.7–2.8
P. lebasii	41	mean ± SD	3.6 ± 0.2	6.8 ± 0.5	0.1 ± 0.1	2.5 ± 0.2	2.8 ± 0.2	4.3 ± 0.4	2.8 ± 0.1
		range	3.3–4.0	6.1–7.5	0.0–0.2	2.3–2.8	2.4–3.0	3.9–4.9	2.7–2.9
P. matawanensis	5	mean ± SD	4.5 ± 0.5	7.0 ± 0.4	0.1 ± 0.1	2.6 ± 0.3	3.6 ± 0.5	4.5 ± 0.4	2.9 ± 0.2
		range	4.0–4.9	6.6–7.3	0.0–0.1	2.2–2.8	3.2–4.1	4.1–4.8	2.7–3.0
P. ubwamensis	3	mean ± SD	5.0 ± 0.2	7.1 ± 0.7	0.3 ± 0.1	3.0 ± 0.3	3.8 ± 0.3	4.3 ± 0.5	3.0 ± 0.1
		range	4.8–5.1	6.4–7.7	0.2–0.4	2.7–3.3	3.6–4.1	3.9–4.9	2.9–3.1
P. yawii	55	mean ± SD	3.1 ± 0.3	5.9 ± 0.4	0.2 ± 0.1	2.2 ± 0.3	2.3 ± 0.3	3.7 ± 0.4	2.7 ± 0.1
		range	2.6–3.6	5.0–6.5	0.1–0.3	1.9–2.6	2.0–2.7	3.2–4.1	2.6–2.8

the diaphragm and inserting at approximately mid-point on the epiphallus. The spermathecal duct is robust, narrowing abruptly at mid-point and remaining narrow until joining the relatively small, ovate spermatheca. The free oviduct joins the moderate length vagina above the atrium.

The central teeth of the radula (second row from left) are tricuspid, 8–9 µm wide and 11–12 µm long, roughly the same shape as, but smaller than, the first lateral teeth, which are 9–10 µm wide and 12–13 µm long (Figure 9). The mesocones of both the central and first lateral teeth are tall, slender, and blade-shaped, joining the rectangular basal plates close to, but not on, their posterior edge. The mesocones of the central teeth barely project beyond the anterior edge of the basal plates, those of the lateral teeth project well beyond the edge. The ectocones are trigonal and short only one third of the height of the mesocones, joining the posterior edge of the basal plates. The lateral teeth are asymmetrical, their endocones are slightly taller then their ectocones. The marginal teeth are dorsoventrally compressed and tricuspid to multicuspid, 8–9 µm wide and 11–12 µm long (Figure 10). The endocones of the marginal teeth are half the height of the mesocones and only slightly taller than the ectocones. The mesocones of the marginal teeth often bear small cusps near the mid-point.

Type Material: Holotype: UF 308235, J. Slapcinsky, 16 April 2002; Paratypes: UF 299667 (2 specimens), UF 303588 (4 specimens), type locality, J. Slapcinsky, 16 April 2002.

Type Locality: Papua New Guinea, Milne Bay Province, Cloudy Mountains, Ubwam Mountain, headwaters of the Watuti River, 10° 29.8′ S, 150° 14.02′ E, 670 m altitude.

Habitat: Observed crawling near the base of trees with smooth bark, in native forest, during wet weather at 670 meters altitude.

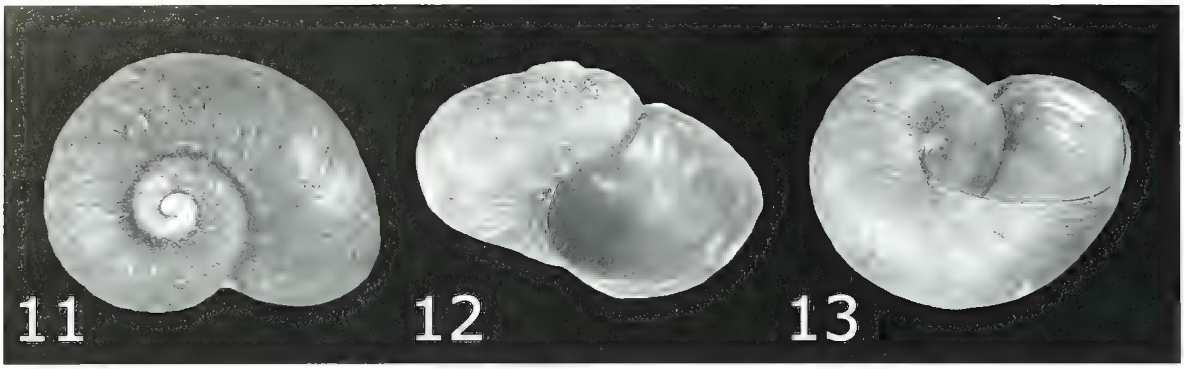
Etymology: From the Latin *abstrusa*, a feminine adjective meaning hidden, concealed and reserved, alluding to the difficulty finding this species and to its subtle almost concealed periostracal processes.

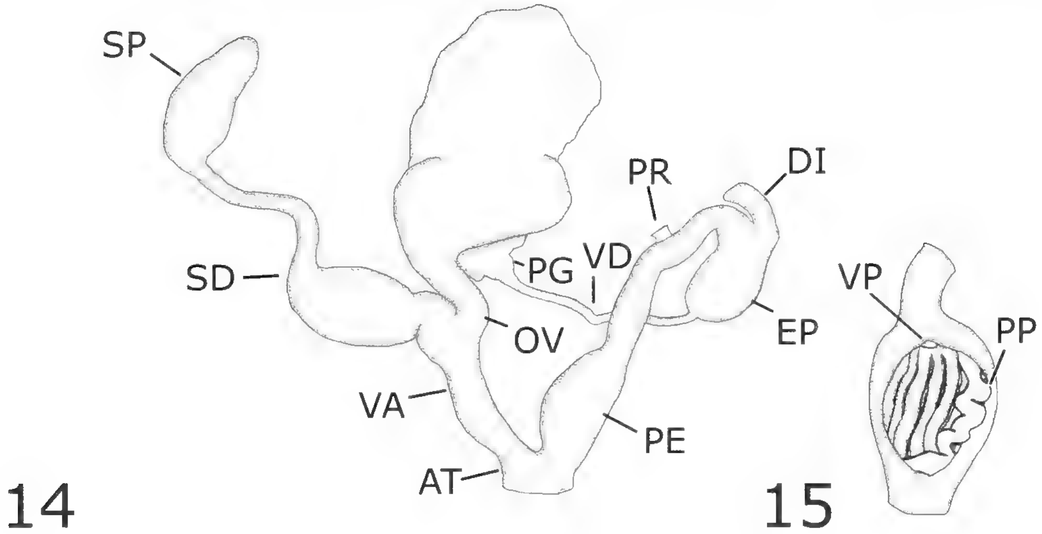
Remarks: *Paryphantopsis abstrusa* differs from most other *Paryphantopsis* smaller than 5 mm in diameter by having periostracal extensions with processes at their margins. *Paryphantopsis similis* is the only other small species with periostracal extensions. It is more depressed, with a height/diameter ratio of 0.70 compared to a height/diameter ratio of 0.79 in *P. abstrusa*.

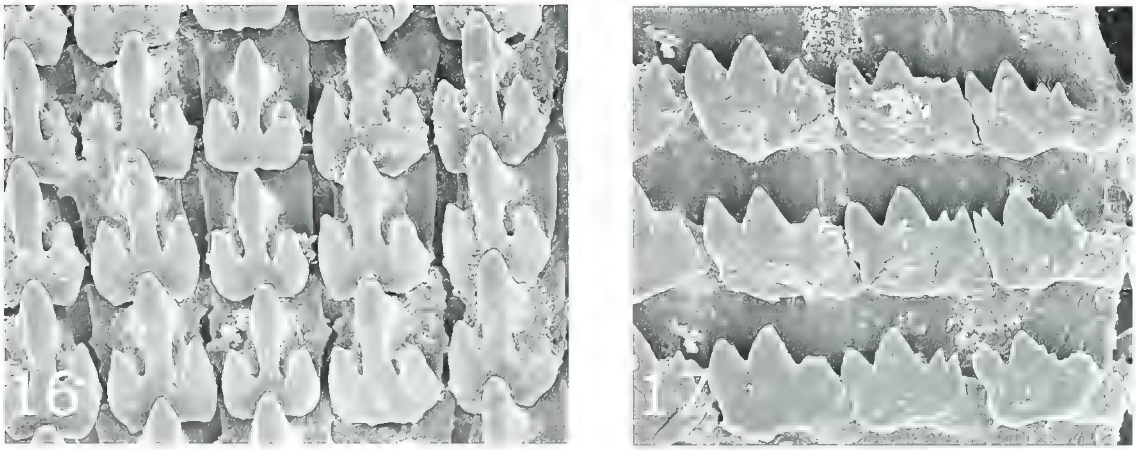
Paryphantopsis koragae new species
(Figures 11–17, Table 1)

Description: The adult shell is small for the genus, 4.1–4.2 mm (mean = 4.2) in diameter and 2.8–3.0 mm (mean = 2.9) in height, with 2.7–2.8 (mean = 2.8) rapidly expanding whorls (Figures 11–13, Table 1). The spire is slightly elevated, 0.1–0.2 mm (mean = 0.2), postnuclear whorls descend slowly and regularly. Shell height/diameter ratio is 0.67–0.71 (mean = 0.69). There are 1.1 evenly rounded nuclear whorls, sculptured with 12 spiral rows of small pits that are not continued on the postnuclear whorls. The postnuclear whorls have regular growth wrinkles with irregular, short, periostracal extensions that are slightly weaker basally. None of the periostracal extensions extend further than the others. The nuclear whorls are white, the postnuclear whorls are dark brown. The umbilicus is closed by a reflection of the peristome. The aperture is large, flattened apically and slightly angled at the periphery and base of the columella. The aperture-diameter to aperture-height ratio is 0.78–0.80 (mean = 0.79).

The body color is uniform yellow in life, fading to cream in specimens preserved in ethanol. The vas deferens narrows rapidly after the prostate gland and remains narrow until entering the swollen, ovate head of the epiphallus (Figure 14). The interior of the head of the epiphallus bears two strong pilasters that enter the short broad diverticulum, which is roughly one quarter of the length of the epiphallus. The epiphallus is two to three times longer than the penis and one third narrower







Figures 11–17. *Paryphantopsis koragae.* **11–13.** Photographs of shell, Holotype UF 308237, diameter 4.2 mm. **14–15.** Camera lucida drawing of genitalia, UF 303586, maximum width 6.3 mm. **16–17.** Scanning electron micrograph of radula, UF 303586, field width of central and lateral teeth 55 µm, marginal teeth 41 µm.

at the junction with the penis. The very short penial retractor muscle originates on the diaphragm and inserts near the mid-point of the epiphallus. The interior of the penis bears several smooth, low, regular pilasters and one much larger convoluted pilaster (Figure 15). The spermatheca is oblong-ovate, its duct is apically narrow and widens abruptly at the mid-point. The free oviduct is relatively robust, joining the long vagina well above the atrium.

The central teeth of the radula (center row) are tricuspid, 9–10 μm wide and 12–13 μm long, slightly smaller than the first lateral teeth, which are 10–11 μm wide, 13–14 μm long (Figure 16). The mesocones of both central and lateral teeth barely project beyond the basal plate. The ectocones of the central and lateral teeth are about one half the height of the mesocones. The lateral teeth are tricuspid and very slightly assymetric with the endocone of each lateral slightly taller than the ectocone. The marginal teeth are dorsoventrally compressed and tricuspid or weakly and irregularly multicuspid, 8–13 μm wide and 8–10 μm long (Figure 17). The endocones of the marginal teeth are nearly the height of the mesocones and can have very weak secondary cusps; the ectocones are shorter and unicuspid to irregularly multicuspid.

Type Material: Holotype: UF 308237, J. Slapcinsky, 20 February 2003; Paratypes: Papua New Guinea, Milne Bay Province, Mount Matawan (Mount Simpson): UF 303586 (2 specimens), UF 303587 (2 specimens), type locality; UF 303584 (1 specimen), plateau ENE of summit, 10°2.1′ S, 149°34.6′ E, 2567 m altitude, J. Slapcinsky, 17 February 2003; UF303585 (1 specimen), Bunisi Village, 10°1.1′ S, 149°36.2′ E, 1450 m altitude, J. Slapcinsky, 16 February 2003.

Type Locality: Papua New Guinea, Milne Bay Province, Mount Matawan (Mount Simpson): NE of summit, 10°1.7′ S, 149°34.7′ E, 2100 m altitude.

Habitat: Active on plants and leaf litter usually near the ground. Observed aestivating in suspended leaf litter within 1.5 m of the ground in tropical hardwood forest and cloud forest from 1450 m to 2600 m altitude.

Etymology: This matronym honors Ms. Helen Korage, Councelor for the Village of Ikara, who facilitated our access to the Mount Matawan area.

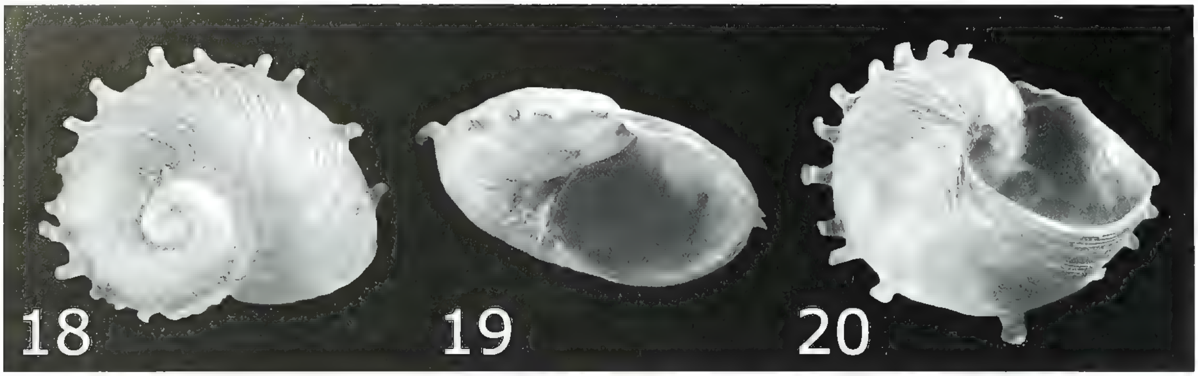
Remarks: *Paryphantopsis koragae* differs from other species of *Paryphantopsis* in being sculptured with growth lines accentuated with very short periostracal extensions. All other small species (≤ 5 mm diameter), including *P. filosa, P. pygmaea, P. arcuata, P. sculpturata, P. similis, P. platycephala,* and *P. abstrusa* have occasional longer periostracal extensions. The anatomy of only one *Paryphantopsis* species of similar size has been figured previously: *P. filosa* from Karkar Island near Madang (Wiktor, 2003, fig. 9). This species differs from *P. koragae* in not having a diverticulum on the epiphallus.

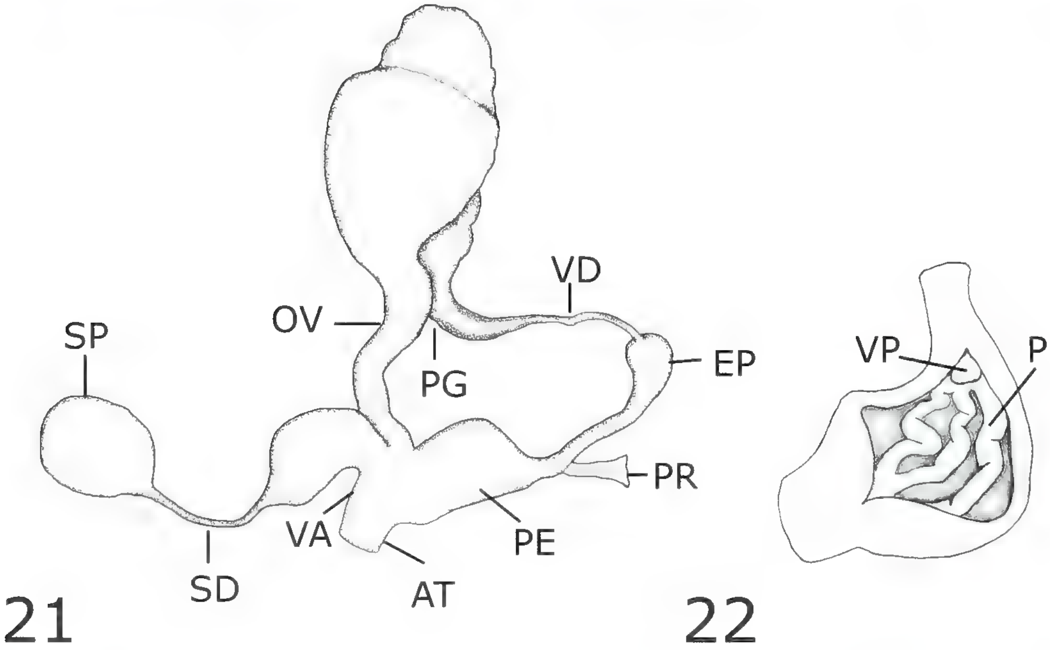
Paryphantopsis lebasii new species
(Figures 18–24, Table 1)

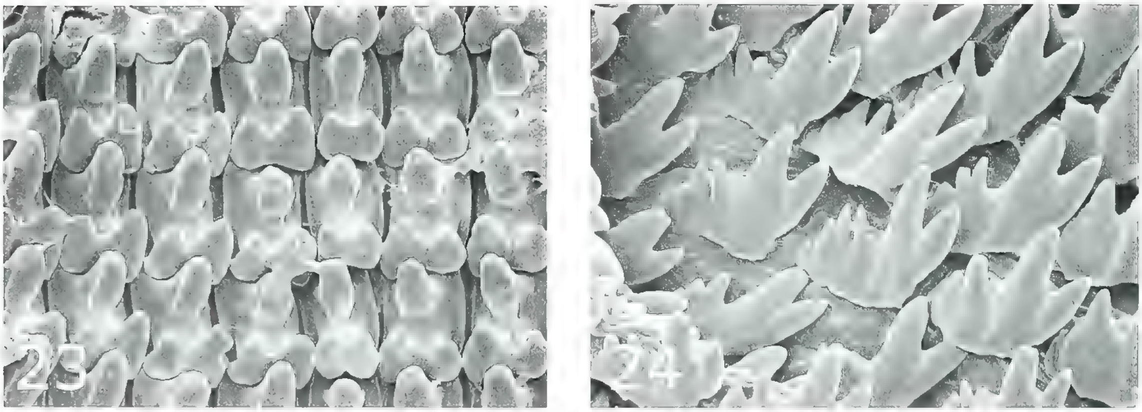
Description: The adult shell is slightly larger than average for the genus, 6.1–7.5 mm (mean = 6.8) in diameter and 3.3–4.0 mm (mean = 3.6) in height, with 2.7–2.9 (mean = 2.8) rapidly expanding whorls (Figures 18–20, Table 1). The spire is flat to slightly elevated, 0.0–0.2 mm (mean = 0.1). Postnuclear whorls descend slowly and regularly and shell height/diameter ratio is 0.45–0.61 (mean = 0.53). There are 1.3 nuclear whorls, with weak, peripheral and supraperipheral angles, and sculptured with about 12 spiral rows of small pits. These pits become larger and less regular on the postnuclear whorls, where they are visible through the periostracum as weak malleations. The sculpture of spiral rows of oblong pits is clearer where the periostracum is removed. The shell periphery is weakly keeled. Apical surface of the whorls is broadly rounded or with a very weak supraperipheral angle. Regular growth wrinkles accentuated with short periostracal extensions are present on the postnuclear whorls. On the apical surface, these extensions are folded along their length towards the aperture and are weakly appressed to the shell. Approximately every fifth periostracal extension protrudes about 0.5 mm beyond the shell margin forming large rectangular processes. These processes overlap each other on the penultimate whorl, but not on the body whorl. They are approximately equally spaced, rectangular, distally rounded, and of approximately equal length. Periostracal extensions of the growth lines are shorter, erect, and less prominent basally. Nuclear whorls are white; postnuclear whorls pale yellow brown. The umbilicus is perforate or, less often, closed, covered to varying degrees by a reflection of the peristome. The aperture is large, depressed-ovate with an aperture-diameter to aperture-height ratio of 0.51–0.75 (mean = 0.65).

The body color is uniform bright creamy-yellow in life, fading to creamy-white in specimens preserved in ethanol. The vas deferens narrows to the junction with the ovate head of the epiphallus (Figure 21). The epiphallus is approximately one quarter the diameter of the penis and does not bear a diverticulum. The penial retractor muscle is a little less than half the length of the epiphallus, originating from the diaphragm and inserting at the base of the epiphallus. The robust penis is a little shorter than the epiphallus, with three strong pilasters that run its entire length (Figure 22). The atrium is short, expanding slightly toward the junction with the penis and vagina. The spermathecal duct is massive at the base, tapering rapidly at mid point, the remainder is relatively narrow until its junction with the spherical spermatheca. The free oviduct is slightly coiled and narrow, joining the very short vagina just above the atrium.

The central teeth of the radula (fifth row from left) are symmetrically tricuspid, 8–9 μm wide and 13–14 μm long, and are similar in shape and length to the slightly wider (9–10 μm), and slightly asymmetrical lateral teeth (Figure 23). The bluntly conical and erect mesocones of







Figures 18–24. *Paryphantopsis lebasii.* **18–20.** Photographs of shell, Holotype UF 308233, diameter 6.5 mm. **21–22.** Camera lucida drawing of genitalia, UF 299671, maximum width 6.7 mm. **23–24.** Scanning electron micrograph of radula, UF 299671, field width of central and lateral teeth 67 μm, marginal teeth 38 μm

the central and lateral rows join their basal plates centrally and barely project beyond the anterior of their basal plates. The ectocones of both the central and lateral rows are trigonal and short, about half the height of the mesocones; they join the posterior edge of their basal plates at a low buttress. The endocones of the lateral teeth are slightly larger but otherwise of similar shape to their ectocones. The marginal teeth are dorsoventrally compressed, multicuspid, about 9–10 μm wide and 10–11 μm long (Figure 24). The endocones are nearly the same height as the mesocones while the ectocones are much shorter, about one half to one third the height of the mesocones and divided into three cusps.

Type Material: Holotype: UF 308233, J. Slapcinsky, 9 April 2002; Paratypes: Papua New Guinea, Milne Bay Province: UF 299676 (1 specimen); UF 299699 (5 specimens), Cloudy Mountains, Ubwam Mountain, headwater of the Watuti River, 10°29.8′ S, 150°14.0′ E, 675 meters altitude, J. Slapcinsky, 16 April 2002; UF 299674 (8 specimens); UF 303593 (4 specimens), Pini Range, Duabo Mission Station, 10°25′ 05″ S, 150°18′ 24 E, 325 meters altitude, J. Slapcinsky, 9 April 2002; BPBM (2 specimens); MNHW 978 (2 specimens); PNGNM 004-105 (2 specimens); UF 299671 (19 specimens); UF 303591 (1 specimen), 30 April 2002; UF 303590 (7 specimens), 2 March 2003, Pini Range, E of Duabo Mission Station, 10°25.0′ S, 150°18.6′ E, 325 meters altitude, J. Slapcinsky; UF 299677 (1 specimen), 30 April 2002; UF 303592 (1 specimen), 1 May 2002, Pini Range, abandoned logging road W of Duabo Mission Station, 10° 24.9′ S, 150° 18.3′ E, 325 meters altitude, J. Slapcinsky.

Type Locality: Papua New Guinea, Milne Bay Province, Pini Range, Duabo Mission Station, 10°25′ 04.7″ S, 150°18′ 24.4″ E, 325 meters altitude.

Habitat: Found on logs, mossy rocks and wet ground, usually near streams in disturbed and undisturbed broadleaf forest in hilly terrain from 325 to 700 meters altitude. Observed active during the day.

Etymology: This patronym honors Mr. Biga Lebasi, our host and guide at Duabo Mission Station, the type locality.

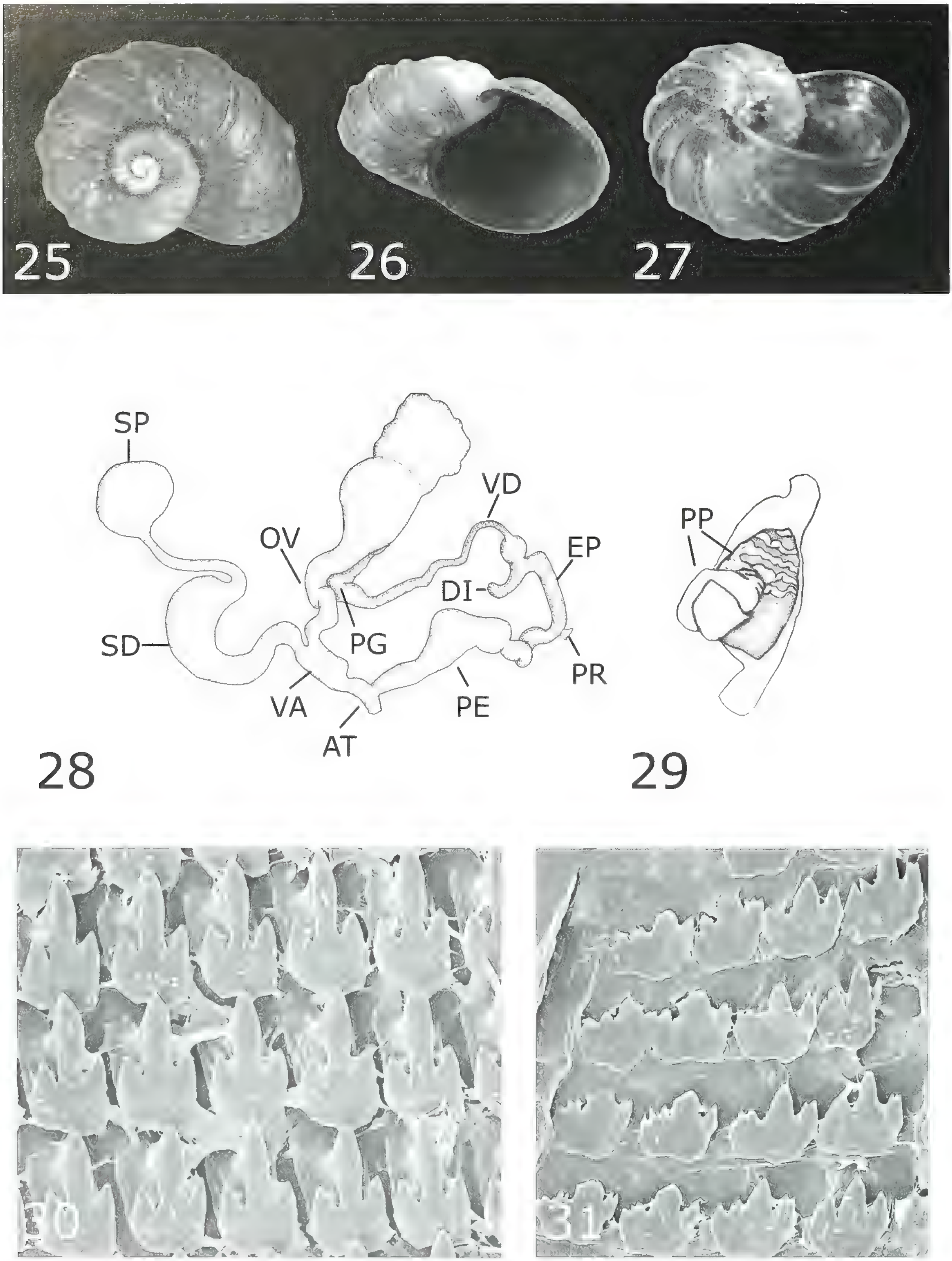
Remarks: Only four other *Paryphantopsis* species, *P. elegans*, *P. fultoni*, *P. yawii*, and *P. lamelligera* have weak to strong peripheral keels. *Paryphantopsis lebasii* is unlike all species *except P. yawii* and *P. fultoni*, in having large, rectangular periostracal extensions oriented parallel to the keeled shell margin. These peripheral extensions are all of equal length, unlike in *P. fultoni*, and do not overlap on the body whorl, unlike in *P. yawii*.

Paryphantopsis matawanensis new species
(Figures 25–31, Table 1)

Description: The adult shell is larger than average size for the genus, 6.6–7.3 mm (mean = 7.0) in diameter and 4.0–4.9 mm (mean = 4.5) in height, with 2.7–3.0 (mean = 2.9) rapidly expanding whorls (Figures 25–27, Table 1). The spire is flat or very slightly elevated, 0.0–0.1 mm (mean = 0.1). Postnuclear whorls descend regularly and shell height/diameter ratio is 0.61–0.69 (mean = 0.64). There are 1.3 rounded nuclear whorls, sculptured with 6 spiral rows of small pits that grade into weak, spiral striae on the penultimate whorl; shell sculpture is obscured by periostracum on the body whorl. The shell is wider and slightly angular below the mid-point. The postnuclear whorls have regular growth wrinkles accentuated with low periostracal extensions that alternate with several much longer extensions approximately every 10 growth-lines. The grouping of several longer extensions appears like a single very thick periostracal extension to the naked eye. The nuclear whorls are white, the postnuclear whorls are dark brown to red-brown. A reflection of the peristome closes the umbilicus. The aperture is large, depressed-ovate, with an aperture-diameter to aperture-height ratio of 0.54–0.67 (mean = 0.63).

In life the body color is bright-yellow with lateral patches of dark purple-brown, the yellow fades to cream in specimens preserved in ethanol. The vas deferens narrows toward the junction with the inflated spherical head of the epiphallus. Immediately after, and perpendicular to the head of the epiphallus, there is a finger-shaped diverticulum that is roughly one quarter the length, and slightly narrower than the diameter of the epiphallus (Figure 28). The remainder of the epiphallus is somewhat twisted and approximately the same length as the penis. The penial retractor muscle is short, originating from the diaphragm and inserting on the basal third of the epiphallus. The epiphallus is roughly half the diameter of the penis. The penis expands for its apical third and then tapers basally to its junction with the similarly sized atrium. The penis apex bears several regular pilasters oriented perpendicular to the length of the penis (Figure 29). At the penis mid-point there is one very large and convoluted pilaster that extends basally. The wall of the base of the penis is thin, bearing regular small pustules. The atrium is short and narrow expanding slightly towards the junction with the penis and the long vagina. The base of the spermathecal duct is relatively narrow, about the same diameter as the base of the penis and free oviduct; it triples in size to its mid-point then narrows abruptly for the remaining third before joining the spherical spermatheca. The free oviduct is narrow, joining the long vagina well above the atrium.

The central teeth of the radula (center row) are tricuspid, 11–12 μm wide and 18–19 μm long, roughly the same size and shape as the first lateral teeth (Figure 30). The mesocones of both the central and first lateral teeth are tall and sharp, tapering apically and narrowing basally. Mesocones are attached to their basal plates along their entire length, except for their apical quarter that extend beyond the anterior margin of the basal plates. The ectocones of the central teeth and the symmetric ectocones and endocones of the lateral teeth are trigonal, about half the height of the mesocones. The mar-



Figures 25–31. *Paryphantopsis matawanensis.* **25–27.** Photographs of shell, Holotype UF 308236, diameter 7.3 mm. **28–29.** Camera lucida drawing of genitalia, UF 303581, maximum width 11.7 mm. **30–31.** Scanning electron micrograph of radula, UF 303581, field width of central and lateral teeth 63 μm, marginal teeth 59 μm.

ginal teeth are dorsoventrally compressed and irregularly multicuspid, 11–12 μm wide and 10–12 μm long (Figure 31). The ectocones of the marginal teeth are slightly shorter than their endocones, which are slightly shorter than their mesocones. Both the ectocones and endocones are irregularly multicuspid, the mesocones are broadly trigonal to broadly rounded.

Type Material: UF 308236, J. Slapcinsky, 19 February 2003; Paratypes: Papua New Guinea, Milne Bay Province, Mount Matawan (Mount Simpson): UF 303581 (9 specimens), UF 303582 (3 specimens), type locality; UF 306529 (1 specimen), NE of summit, 10°2.1′ S, 149°34.4′ E, 2700 m altitude, J. Slapcinsky, 18 February 2003; UF 303583 (1 specimen), NE of summit, 10°1.7′ S, 149°34.7′ E, 2100 m altitude, J. Slapcinsky, 20 February 2003.

Type Locality: Papua New Guinea, Milne Bay Province, Mount Matawan (Mount Simpson), ridge top E of summit, 10°2.5′ S, 149°34.6′ E, 2700 m altitude.

Habitat: All specimens were collected in cloud forest from 2100 to 2700 m altitude. Individuals were observed from 1–2 m above ground, crawling on a variety of cloud forest vegetation in wet or foggy weather. In drier weather specimens were observed in leaf litter that was suspended in trees, especially in the crowns of *Pandanus* sp.

Etymology: Named for the type locality and known range of this species: Mount Matawan (Mount Simpson).

Remarks: Of the other larger (>6 mm diameter) species of *Paryphantopsis*, *P. globosa*, and *P. louisiadarum* do not have periostracal extensions on the growth lines, unlike *P. matawanensis*. Of the species with periostracal extensions, *P. latior*, *P. lamelligera*, *P. fultoni*, and *P. striata* do not have a repeating pattern of approximately 10 short periostracal extensions followed by several longer extensions. *P. matawanensis* further differs from *P. lamelligera* and *P. fultoni* in not having peripheral processes on the periostracal extensions. The genital anatomy of *P. matawanensis* differs from *P. lamelligera* in having a diverticulum.

Paryphantopsis ubwamensis new species
(Figures 32–38, Table 1)

Description: The adult shell is large for the genus, 6.4–7.7 mm (mean = 7.1) in diameter and 4.8–5.1 mm (mean = 5.0) in height, with 2.9–3.1 (mean = 3.0), rapidly expanding whorls (Figures 32–34, Table 1). The spire is elevated, 0.2–0.4 mm (mean = 0.3), the postnuclear whorls descend relatively rapidly, especially near the aperture. The shell height/diameter ratio is 0.66–0.75 (mean = 0.70). The 1.2 nuclear whorls are evenly rounded and sculptured with 12 spiral rows of small pits. These pits do not continue on the postnuclear whorls, which are sculptured only with weak growth lines that do not bear periostracal extensions. The whorls are inflated, the sutures deeply impressed, and the periphery evenly rounded. The nuclear whorls are white, the postnuclear whorls brown, with irregular lighter patches. The umbilicus is perforate, narrowed by a reflection of the peristome. The aperture is large, ovate, with an aperture-diameter to aperture-height ratio of 0.79–0.93 (mean = 0.85).

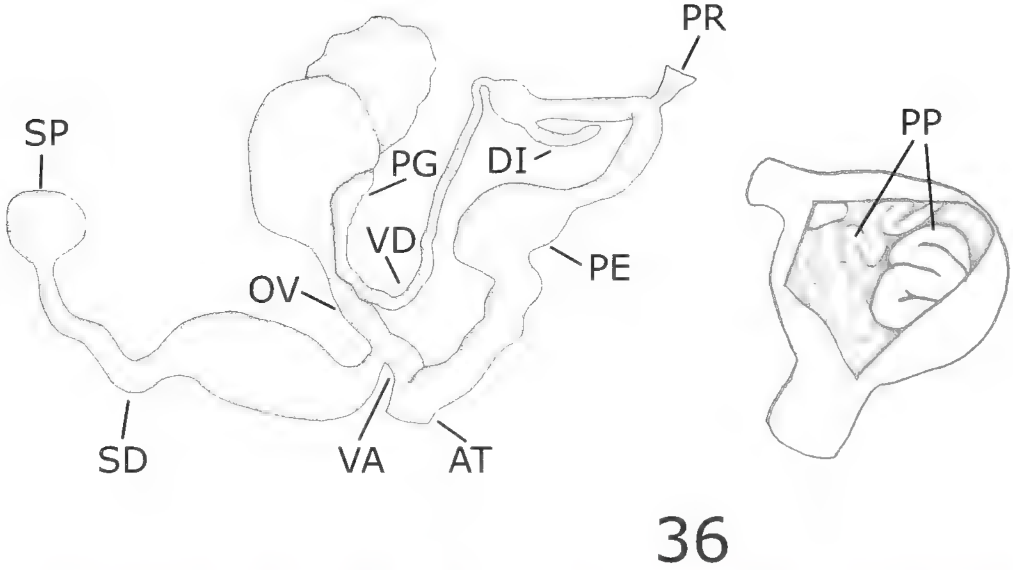
The body color is uniform yellow in life, fading to cream in specimens preserved in ethanol. The vas deferens is wide at the prostate gland, narrowing rapidly and remaining narrow until the junction with the inflated ovate tip of the epiphallus (Figure 35). The epiphallus bears a long (approximately a quarter of the length of the epiphallus), finger-shaped diverticulum just after the junction with the vas deferens. The epiphallus is about one third the diameter of the apex of the penis. The penis is broad apically, narrowing abruptly to half its apical diameter slightly before mid-point and remaining the same diameter to the junction with the atrium. The penis is sculptured with several slightly convoluted pilasters that extend in an arc from near basally to near apically, and one much larger and more convoluted pilaster near the penis mid-point (Figure 36). The penial retractor muscle originates from the diaphragm and inserts at the mid-point of the epiphallus. The spermathecal duct is basally robust and narrows at mid-point, remaining narrow until the junction with the spherical spermatheca. The free oviduct is narrow joining the moderate length vagina above the atrium.

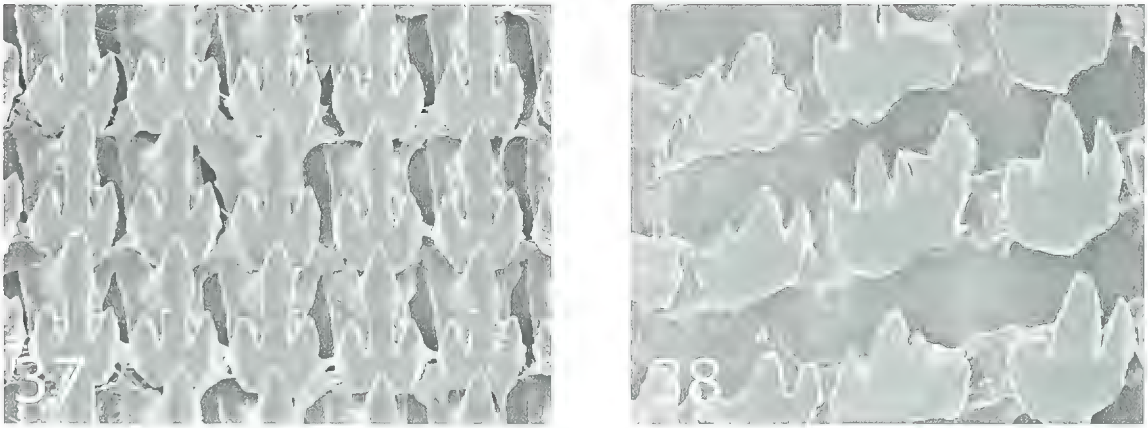
The central teeth of the radula (center row) are tricuspid, 10–11 μm wide and 15–16 μm long, roughly the same width and shape as, but a little shorter than, the first lateral teeth, which are 18–19 μm long (Figure 37). The mesocones of both the central and lateral teeth are long, slender and blade shaped, projecting slightly beyond the basal plate. The ectocones and endocones of the lateral teeth are symmetrical and half the height of the mesocones. The marginal teeth are dorsoventrally compressed and irregularly tricuspid-multicuspid, 12–15 μm wide and 13–15 μm long (Figure 38). The endocones are tall, large to very large and sometimes irregularly multicuspid. The ectocones are unicuspid.

Type Material: Holotype: UF 303589, J. Slapcinsky, 22 April 2002; Paratypes: Papua New Guinea, Milne Bay Province, Cloudy Mountains, Ubwam Mountain: UF 299666 (1 specimen), type locality; UF 299668 (2 specimens), headwaters of the Watuti River, 10°29.8′ S, 150°14.02′ E, 670 m altitude, J. Slapcinsky, 16 April 2002.

Type Locality: Papua New Guinea, Milne Bay Province, Cloudy Mountains, Ubwam Mountain, summit, 10°30.4′ S, 150°13.5′ E, 1000 m altitude.

Habitat: This species was found crawling on a moss-covered rotting log in cloud forest at 1000 meters. Dead shells were also found at 670 meters in leaf litter at the base of a tree with smooth bark.





Figures 32–38. *Paryphantopsis ubwamensis.* **32–34.** Photographs of shell, Holotype UF 303589, diameter 7.7 mm. **35–36.** Camera lucida drawing of genitalia, UF 299666, maximum width 10.1 mm. **37–38.** Scanning electron micrograph of radula, UF 299666, field width of central and lateral teeth 66 μm, marginal teeth 45 μm.

Etymology: This species is named for the type locality, Ubwam Mountain, and indirectly for one of our guides who is named after the mountain.

Type Material: Holotype: Papua New Guinea, Milne Bay Province, Cloudy Mountains, Ubwam Mountain, summit, 10°30.4′ S, 150°13.5′ E, 1000 m altitude, J. Slapcinsky, 22 April 2002 (UF 303589); Paratypes: Papua New Guinea, Milne Bay Province, Cloudy Mountains, Ubwam Mountain: type locality (UF 299666, 1 specimen); headwaters of the Watuti River, 10°29.8′ S, 150°14.02′ E, 670 m altitude, J. Slapcinsky, 16 April 2002 (UF 299668, 2 specimens).

Paryphantopsis yawii new species
(Figures 39–45, Table 1)

Description: The adult shell is average in size for the genus, 5.0–6.5 mm (mean = 5.9) diameter, and 2.6–3.6 mm (mean = 3.1) height with 2.6–2.8 (mean = 2.7) rapidly expanding whorls (Figures 39–41, Table 1). The spire is elevated, 0.1–0.3 mm (mean = 0.2). Postnuclear whorls descend slowly and regularly. Shell height/diameter ratio is 0.47–0.55 (mean = 0.53). The 1.2 nuclear whorls bear rounded peripheral and supraperipheral ridges; sculptured with about 15 spiral rows of small pits. These pits become larger and less regular on postnuclear whorls but usually are obscured by the periostracum. However, pits are visible in areas where the periostracum is removed, and within the aperture. The shell has a peripheral keel and blunt supraperipheral ridge; the surface between is flattened. Postnuclear whorls are sculptured with regular growth wrinkles that are accentuated with periostracal extensions. On the apical surface of the shell, periostracal extensions are folded along their length toward the aperture and appressed to the shell except at the keeled margin where they form rectangular processes that extend about 0.5 mm beyond the shell margin. The large, distally rounded processes overlap, forming a continuous periostracal fringe of uniform length at the shell periphery. Periostracal extensions on the growth lines extend basally but are short and erect. Nuclear whorls are white, postnuclear whorls yellow brown. The umbilicus is closed by a reflection of the peristome. The aperture is large, depressed-ovate, with an aperture-diameter/aperture-height ratio 0.53–0.66 (mean = 0.63).

The body color is uniform bright creamy-yellow in life, fading to creamy-white in specimens preserved in ethanol. The vas deferens narrows toward the junction with the slightly inflated head of the epiphallus (Figure 42). The epiphallus is approximately three times longer and one quarter of the diameter of the penis and does not bear a diverticulum. The penial retractor muscle is long, about two thirds the length of the epiphallus, originating from the diaphragm and inserting on the basal third of the epiphallus. The penis is short and robust with poorly defined pilasters in the apex (Figure 43). The atrium is short and narrow, expanding slightly towards the junction with the penis and the short vagina. The base of the spermathecal duct is massive, tapering slowly but remaining broad for more than one third of its length; the remainder is relatively narrow until the junction with the spherical spermatheca. The free oviduct is slightly coiled and narrow, joining the short vagina just above the atrium.

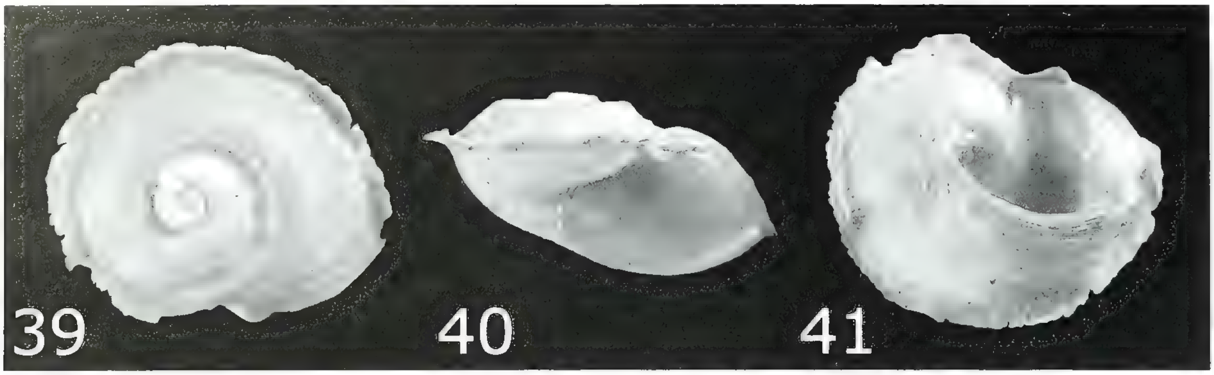
The central teeth of the radula (fifth row from left) are tricuspid, 9–10 μm wide and 14–15 μm long, roughly the same size and shape as the first lateral teeth (Figure 44). The mesocones of both the central and first lateral teeth are short, conical and erect, joining the rectangular basal plates nearly centrally and barely projecting beyond the plates' anterior margin. The ectocones are trigonal and short, only one third of the height of the mesocones, joining the posterior edge of the basal plates. The lateral teeth are asymmetrical; their endocones are slightly taller then their ectocones. The marginal teeth are dorsoventrally compressed, tricuspid to multicuspid, 8–10 μm wide and 10–12 μm long (Figure 45). The endocones of the marginal teeth are nearly the same height as the mesocones while the ectocones are much shorter, only one half to one third of their height and often divided into three cusps.

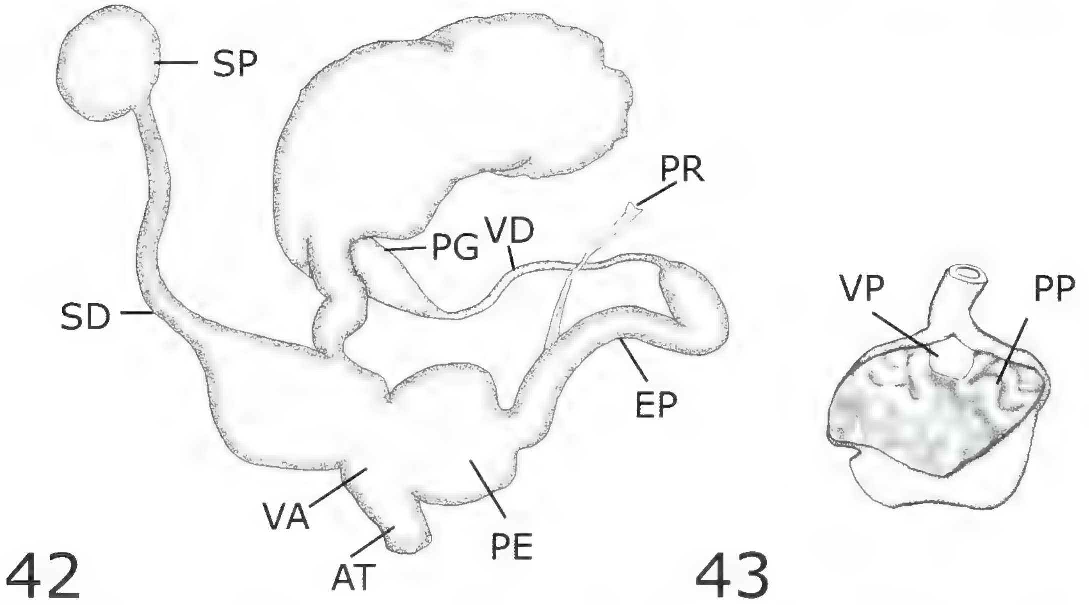
Type Material: Holotype: UF 308238, J. Slapcinsky, 6 April 2002; Paratypes: Papua New Guinea, Milne Bay Province: UF 299675 (2 specimens), UF 303594 (2 specimens), Wowow Mountain, W of Naura, 10°16.9′ S, 150°9.9′ E, 635 m altitude, J. Slapcinsky, 8 May 2002; UF 299673 (1 specimen), UF 303595 (1 specimen), 4 April 2002, UF 303598 (1 specimen), 27 February 2003, waterfall on Upalai Creek, 3 km WNW of Watunoa, 10°19.6′ S, 150°34.6′ E, 60 m altitude, J. Slapcinsky; UF 299670 (3 specimens), UF 299672 (6 specimens), 6 April 2002, UF 303596 (13 specimens), 7 March 2003, headwater of Goilayoli River at road crossing, 30 km ENE of Alotau, 10°18.7′ S, 150°37.3′ E, 275 m altitude, J. Slapcinsky; BPBM (4 specimens), MNHW 977 (4 specimens), PNGNM 004-104 (4 specimens), UF 303597 (45 specimens), small waterfall on Kinahidamadamana River near Budo Village, 10°17.1′ S, 150°26.7′ E, 125 m altitude, J. Slapcinsky, 4 March 2003.

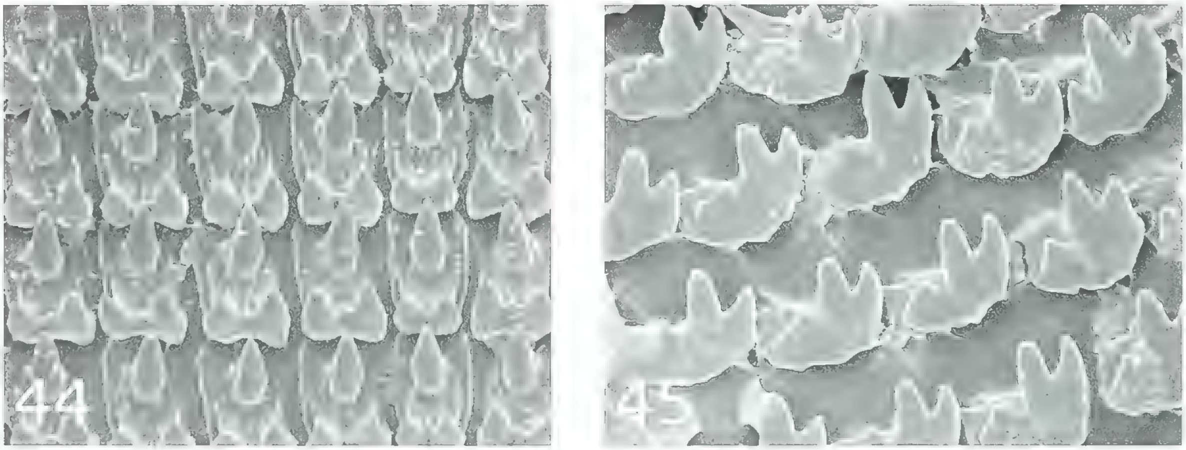
Type Locality: Papua New Guinea, Milne Bay Province, headwater of Goilayoli River at road crossing, 30 km ENE of Alotau, 10°18.7′ S, 150°37.3′ E, 275 m altitude.

Habitat: This species was active during the day in native forest on rocks and logs with moss and algae, and on moist soil near streams. It was encountered in hilly terrain at relatively low altitudes for the genus, ranging from 60 to 635 meters.

Etymology: This patronym honors Mr. Benjamin Yawi of Budo Village, Milne Bay Province, Papua New Guinea. He and his family located, arranged permission to visit, and helped to collect at many of the sites where this species was found.







Figures 39–45. *Paryphantopsis yawii.* **39–41.** Photographs of shell, Holotype UF 308238, diameter 6.5 mm. **42–43.** Camera lucida drawing of genitalia, UF 299672, maximum width 6.4 mm. **44–45.** Scanning electron micrograph of radula, UF 299672, field width of central and lateral teeth 63 μm, marginal teeth 48 μm.

Remarks: Peripheral keels are unusual among known *Paryphantopsis* species and are found only in *P. elegans*, *P. fultoni*, and to a lesser extent in *P. lebasii* and *P. lamelligera*. *Paryphantopsis yawii* is unlike all other species, except for *P. lebasii* and *P. fultoni*, in having large, rectangular periostracal extensions oriented parallel to the keeled shell margin. These peripheral extensions are all of equal length, unlike in *P. fultoni* and they overlap, forming a continuous periostracal fringe, unlike in *P. lebasii*.

DISCUSSION AND CONCLUSIONS

The family Charopidae was previously considered to be a minor component of the terrestrial molluscan fauna of New Guinea, with relatively few species and genera, and to lack the spectacular radiations exhibited by this and the related Endodontidae in the oceanic islands of the Pacific (Solem, 1983: 305). Ongoing surveys indicate that this is not the case; inadequate sampling, rather than low diversity, is the cause of the perceived low number of charopid species in New Guinea. Likewise, reports of low generic diversity of charopids in New Guinea are more likely the result of insufficient sampling and may reflect the paucity of anatomic material available to define generic units (Solem, 1970: 241). Despite the short duration and limited geographic scope of the current survey, six new species of *Paryphantopsis* are reported here, increasing the known diversity of the genus by almost 50%. In addition to *Paryphantopsis*, species belonging to several other charopid genera were also collected; these will be treated in later publications.

On the eastern terminus of the Papuan Peninsula, *Paryphantopsis* species that occur in close proximity or sympatry share unique shell, genital, and radular characters. For example, both species from the Mount Matawan area, *P. matawanensis* and *P. koragae*, have unusually short penial retractor muscles, long vaginas and angled apertural margins. Species in the uplands of the Cloudy Mountains, *P. ubwamensis* and *P. abstrusa*, are unusually tightly coiled and globose. The two lowland species, *P. lebasii* and *P. yawii*, share distally rounded rectangular periostracal processes and the unusual origin of their mesocones from the center of their basal plates. These unusual characters shared by different species in close proximity or sympatry suggest that *Paryphantopsis* species have speciated locally on a fine geographic scale; speciation in these cases is presumably facilitated by their poor dispersal ability. Because much of New Guinea remains under-explored, the true diversity of the islands' *Paryphantopsis*, other charopids, and land snails in general is almost certainly greatly underestimated.

The geographic distribution of the six *Paryphantopsis* species appears to be limited to particular mountain ranges on different terrains, despite the proximity of these mountains to each other (Figure 1). Three species, *P. matawanensis*, *P. koragae*, and *P. yawii* are restricted to the Owen Stanley Range, part of the Kutu Terrane, while three others, *P. abstrusa*, *P. lebasii*, and *P. ubwamensis*, are restricted to the Cloudy Mountains of the Port Moresby Terrane. These distinct suites of endemic species are consistent with the terrane-accretion hypothesis (Davis et al. 1997) proposed for the formation of the East Papua Composite Terrane and suggest that the low vagility and high diversity of charopids and other land snails may make them ideal to test hypotheses of terrain accretional history.

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First record of *Akera* Müller, 1776, from the eastern Pacific, with the description of a new species

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ABSTRACT

The description of the new species *Akera julieae* is based on a complete specimen collected from southern California and three empty shells from Costa Rica. These specimens constitute the first record of *Akera* in the eastern Pacific. *Akera julieae* is distinguishable from the widespread Indo-Pacific species *Akera soluta* by its radular and jaw morphology; the rachidian teeth of *A. soluta* are more solid with larger cusps and flanking denticles, the mid-lateral teeth of *A. soluta* are denticulated, whereas in *A. julieae* they are smooth, and the outermost lateral teeth of *A. julieae* are proportionally more elongate and straighter than those of *A. soluta*; the jaws of *A. soluta* are well developed and composed of a number of rows of strong rodlets, whereas in *A. julieae* the jaws are more rudimentary with only five rows of fragile-looking rodlets. There are no consistent differences between these two species in gizzard plate and adult shell morphology, but the protoconch of *A. soluta* is slightly larger and more elongate. The western Atlantic species *Akera bayeri* is distinguishable from *A. julieae* by having a more elevated shell spire and stronger radular teeth with denticles on all lateral teeth.

INTRODUCTION

The opisthobranch family Akeridae Mazzarelli, 1891, includes opisthobranchs with an external, cylindrical shell into which the animal cannot retract completely. It contains the single genus *Akera* Müller, 1776, and only a few Recent valid species distributed throughout tropical and temperate regions. The type species, *Akera bullata* Müller, 1776, has been reported from the northeast Atlantic, from the Baltic shores of Denmark and Norway to the British Isles, continuing on to the Atlantic and Mediterranean costs of continental France and Spain (Thompson, 1976), Italy (Rinaldi, 1988), and the Canary Islands (Ortea et al., 2001).

In the Indo-Pacific, the widespread species *Akera soluta* (Gmelin, 1791) has been reported from South Africa and Mozambique to Australia, Marshall Islands, and the Philippines (Gosliner, 1987). Both *Akera bicincta* (Quoy and Gaimard, 1833), from Australia, and *Akera constricta* Kuroda 1947, from Japan, have been regarded as junior synonyms of *A. soluta,* see Wells and Bryce (1993) and Hamatani (2000) respectively. This expands the known range for *A. soluta.* Other nominal Indo-Pacific species, *Akera tumida* (A. Adams in Sowerby, 1850), *Akera tasmanica* Beddome, 1882, and *Akera aperta* Hedley, 1899, were all described from the southwestern Pacific, and are poorly known. They are likely synonyms of *A. soluta*, but because they were described based solely on shell morphology, their identities are unclear and in need of revision. In the western Atlantic, Olsson and McGinty (1951) reported for the first time a species of *Akera* from Florida under the name "Akera thompsoni." Because the animal was figured but not described, this species name is a *nomen nudum* in accordance with Article 13.1 of the International Code of Zoological Nomenclature (ICZN, 1999). The first available name for the western Atlantic *Akera* is *Akera bayeri* Ev. Marcus and Er. Marcus, 1967, which has been reported from the southwestern Caribbean Sea and Brazil (Ev. Marcus, 1970).

There are no Recent species of *Akera* known from the eastern Pacific. *Akera maga* Vokes, 1939, the only known species from this area, was described from the lower to middle Eocene, Domengine Formation, Fresno County, California (Vokes, 1939). Squires (2001) reported this species from the Llajas Formation (also lower to middle Eocene), Ventura County, California. In the present paper we describe the first occurrence of Recent *Akera* in the eastern Pacific based on a complete specimen collected in the Channel Islands, California and three shells from Guanacaste, Costa Rica.

MATERIALS AND METHODS

The specimen from California was collected as part of the Southern California Bight 1998 Regional Marine Monitoring Survey (Bight, 1998) conducted in the summer of 1998. Infaunal samples were taken with a 0.1 m^2 Van Veen grab sampler and screened through a 1 mm mesh. The sample was then placed in a relaxant solution of Epsom salts (magnesium sulfate heptahydrate—

Table 1. Comparative material examined in this study. The specimen marked with an asterisk (*) was collected alive and included soft parts.

Species	Locality	Date	Depth	Number
Akera soluta	Kii, Japan	—		LACM 153414*
	Uala Reef, Quezon, Philippines	May 1959	3–15 m	LACM 073035
	New Zealand	—	—	LACM 153415
	Hardwick Bay, South Australia	—	—	LACM 157942
	Hardwick Bay, South Australia	—	—	LACM 153416
	Hardwick Bay, South Australia	—	—	LACM 153417
	Phuket, Thailand	—	—	LACM 046386
Akera bullata	Finmark, Norway	—	—	LACM 153418

$MgSO_4 \cdot 7H_2O$) and freshwater for a minimum of 30 minutes. The sample was then fixed in 10% buffered formalin and preserved in 70% ethanol. The preserved whole animal was photographed using a digital camera mounted on a dissecting scope (Wild Epimarkroskop® M450).

The Costa Rican shells were collected during the Searcher 401 Expedition of the Natural History Museum of Los Angeles County.

Several additional specimens and shells belonging to other species of *Akera* were examined for comparison purposes. These specimens are listed in Table 1.

The shell is very fragile and could not be dissected intact from the specimens examined, which rendered the description below incomplete. Once the shell was removed, the internal organs were dissected and drawn using a Nikon SMZ 1000 microscope equipped with a drawing tube. The radula, jaws, and gizzard plates were dissected and photographed using a Hitachi S-3000N Scanning Electron Microscope (SEM). The apical region of the shell was separated from the rest of the shell and mounted for SEM photography.

SYSTEMATICS

Akeridae Mazzarelli, 1891
Akera Müller, 1776

Type Species: *Akera bullata* Müller, 1776, by monotypy.

Diagnosis: Shell external, fragile, translucent, cylindrical to slightly bulloid. Spire flattened to elevated with a partially embedded protoconch. Aperture equal to the length of the spire or slightly shorter. Thin periostracum forming a raised flange at the keel. Animal unable to retract fully into the shell, but can stretch over twice its length; with a posterior pallial tentacle. Parapodia extending laterally, meeting mid-dorsally over the shell. Radula with rachidian tooth having a median cusp and smaller denticles on either side. Rachidian tooth flanked by 21–52 lateral teeth. Gizzard with a number of irregular plates arranged in three tiers.

Akera julieae new species
(Figures 1–4)

Akera sp.—Behrens, 2004: 18, pl. 1D.

Holotype: LACM 3033, from type locality.

Paratypes: 3 shells, southeastern corner of Bahía Jobo, off sand beach west of Bahía de Salinas, Guanacaste Province, Costa Rica (11°02′22″ N, 85°45′16″ W), 14 Feb. 1972, 1.5–10.7 m depth (LACM 3034).

Type Locality: Southwestern corner of Santa Catalina Island, California, USA (33°18′24″ N, 118°22′05″ W), 24 Jul. 1998, 40.6 m depth, in gray colored silt and clay (LACM 3033).

External Morphology: The body is oval, 10 mm long in the preserved holotype. The cephalic shield is triangular, comprising about ¼ of the body length in the preserved specimen (Figures 1A, 2A). The parapodia are narrow and do not reach the midline of the body (Figures 1A–C, 2A). The gill is unipinnate, with 11 simple lamellae (Figure 2B). The color of the living animals is unknown; the preserved holotype is grayish white.

Shell Morphology: The shell is bullomorph, fragile, well-calcified (Figure 1). The protoconch is smooth, and only the outer whorl is visible externally (Figure 3C). Its maximum diameter is 200 μm. The whorls are separated by a deep, channelled suture, which is shallower on the apical whorls. The periphery of the whorls, near the apex, is angulated and forms a conspicuous keel, which divides the whorls into two parts (Figure 1D, 3C). The inner part has a characteristic pattern of strong, curved wrinkles. The whorls are attached to the preceding whorl just below the periphery of this whorl. The apical region is flattened and the external whorls overlap the most internal. The whorl sides are clearly curved, convex. The aperture is broad below and narrow above, where it extends into a deep sinus along the suture of the upper lip. There is a thin callus in the columella. The sculpture consists of numerous, low and thin spiral ribs and axial growth lines. The shells are covered with a thin brownish periostracum.

Anatomy: The buccal bulb is oval; it connects posteriorly to the long esophagus and the salivary glands (Fig-

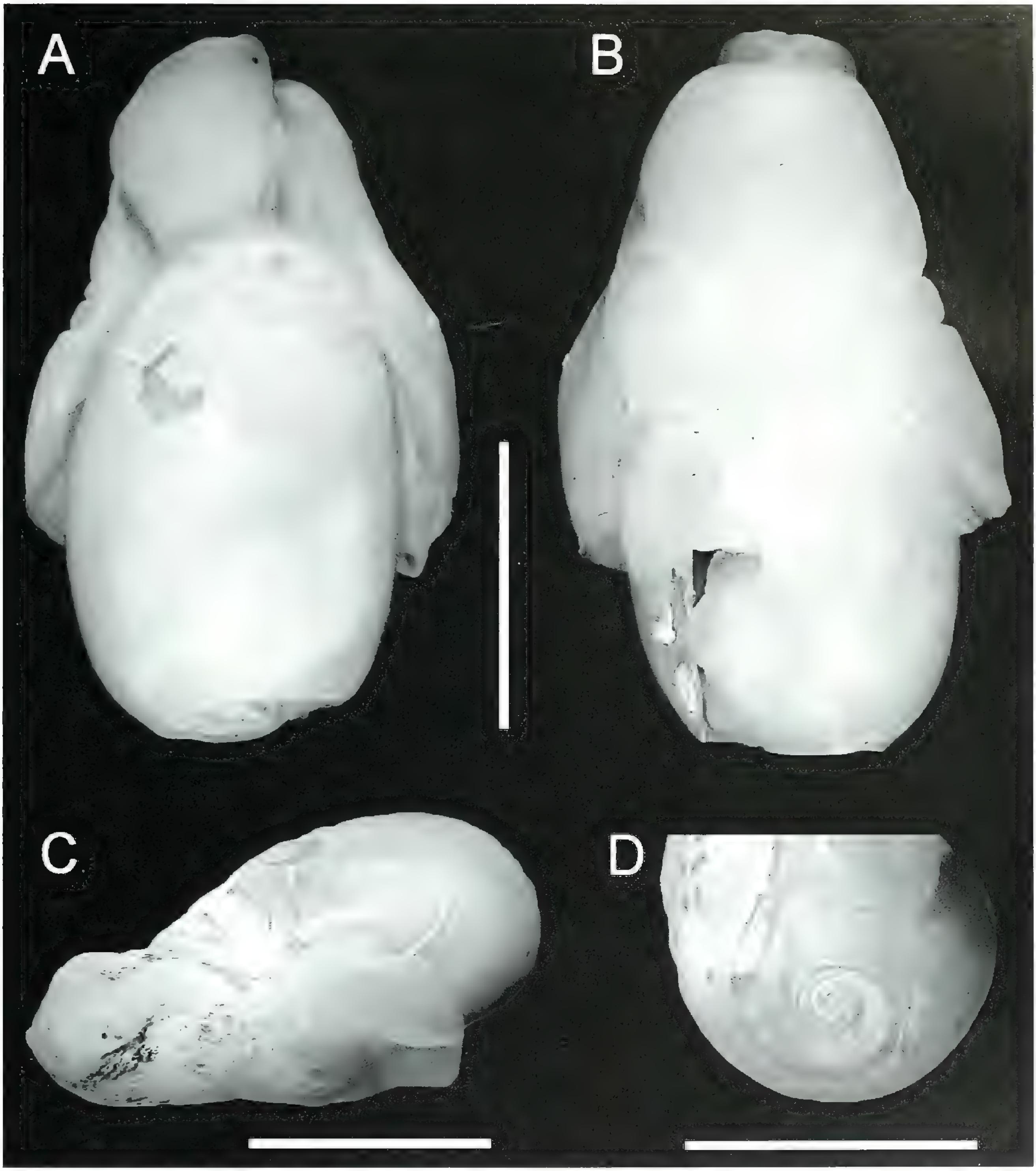

Figure 1. *Akera julieae* new species, photographs of the preserved holotype (LACM 3033). **A.** Dorsal view. Scale bar = 5 mm. **B.** Ventral view. Scale bar as in A. **C.** Lateral view. Scale bar = 5 mm. **D.** Apical view of the shell. Scale bar = 5 mm

ure 2C). Two strong retractor muscles attach laterally to the buccal bulb. The radular formula is 19×23.1.23 in the holotype. The rachidian teeth are broad, with a triangular based, basally concave, and a pointed central cusp (Figure 4A). There are 3–5 denticles on each side of the cusp varying in shape and size. The two innermost teeth on each row have a long and narrow base and a conspicuously wider cusp bearing denticles on the [illegible]

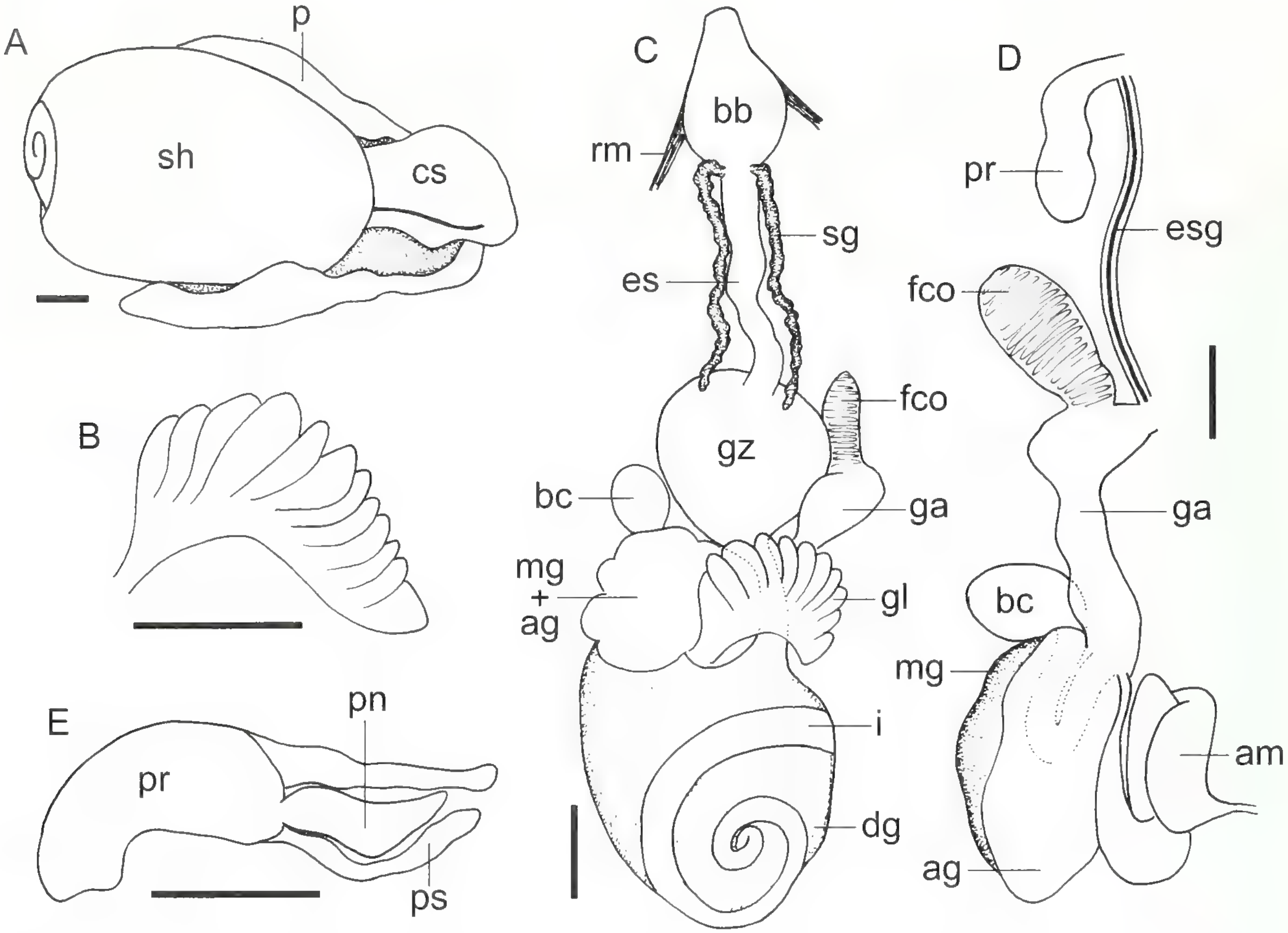

Figure 2. *Akera julieae* new species, drawings of the preserved holotype (LACM 3033). **A.** Dorsal view of the complete body. Scale bar = 1 mm. **B.** Detail of the gill. Scale bar = 1 mm. **C.** General view of the anatomy. Scale bar = 1 mm. **D.** General view of the reproductive system. Scale bar = 0.5 mm. **E.** Penis and prosate. Scale bar = 0.5 mm. Abbreviations: ag, albumen gland; am, ampulla; bb, buccal bulb; bc, bursa copulatrix; cs, cephalic shield; dg, digestive gland; es, esophagus; esg, external seminal groove; fco, female copulatory organ; ga, genital atrium; gl, gill; gz, gizzard; i, intestine; mg, mucous gland; pn, penis; pr, prostate; ps, penial sheath; rm, retractor muscle; sh, shell; sg, salivary gland; sr, seminal receptacle.

and outer sides. The rest of the lateral teeth are hook-shaped, with a long and narrow cusp and lack denticles (Figure 4B). In the outermost teeth the base is shorter and the cusp proportionally longer than in the mid-laterals (Figure 4C). The jaws are composed of 6 rows of simple, elongate rodlets (Figure 3B). The esophagus opens into a large muscular gizzard, which contains several gizzard plates. The gizzard plates vary in shape and size; they are irregular with angular edges (Figure 3A).

The reproductive system is monoaulic (Figure 2D). The ampulla is long and convoluted; it opens into the genital atrium at the same point where the albumen and mucous glands open. The bursa copulatrix is oval; it connects with the genital atrium through a wide and curved duct. The genital atrium is long and is connected to a complex female copulatory organ near the opening. From the gonopore an open seminal groove runs in anterior direction to the protrusible cephalic penis and the prostate. The penis is long and externally enclosed in a sheath (Figure 2E). The prostate is short and simple, and connects proximally to the penis.

Etymology: Dedicated to Julie Barwick, the daughter of the junior author.

DISCUSSION

Akera julieae has been included in *Akera* because of the presence of a fragile, cylindrical external shell, a flattened spire, and a partially embedded protoconch. The radula of this species has a single broad, triangular rachidian tooth, with a median cusp and smaller denticles on either side, as well as several hamate lateral teeth. The gizzard contains a number of irregular gizzard plates arranged in three tiers. All these characteristics are diagnostic of the genus *Akera* (see above).

This is the first record of *Akera* in the eastern Pacific. Behrens (2004) cited this species as *Akera* sp., based on

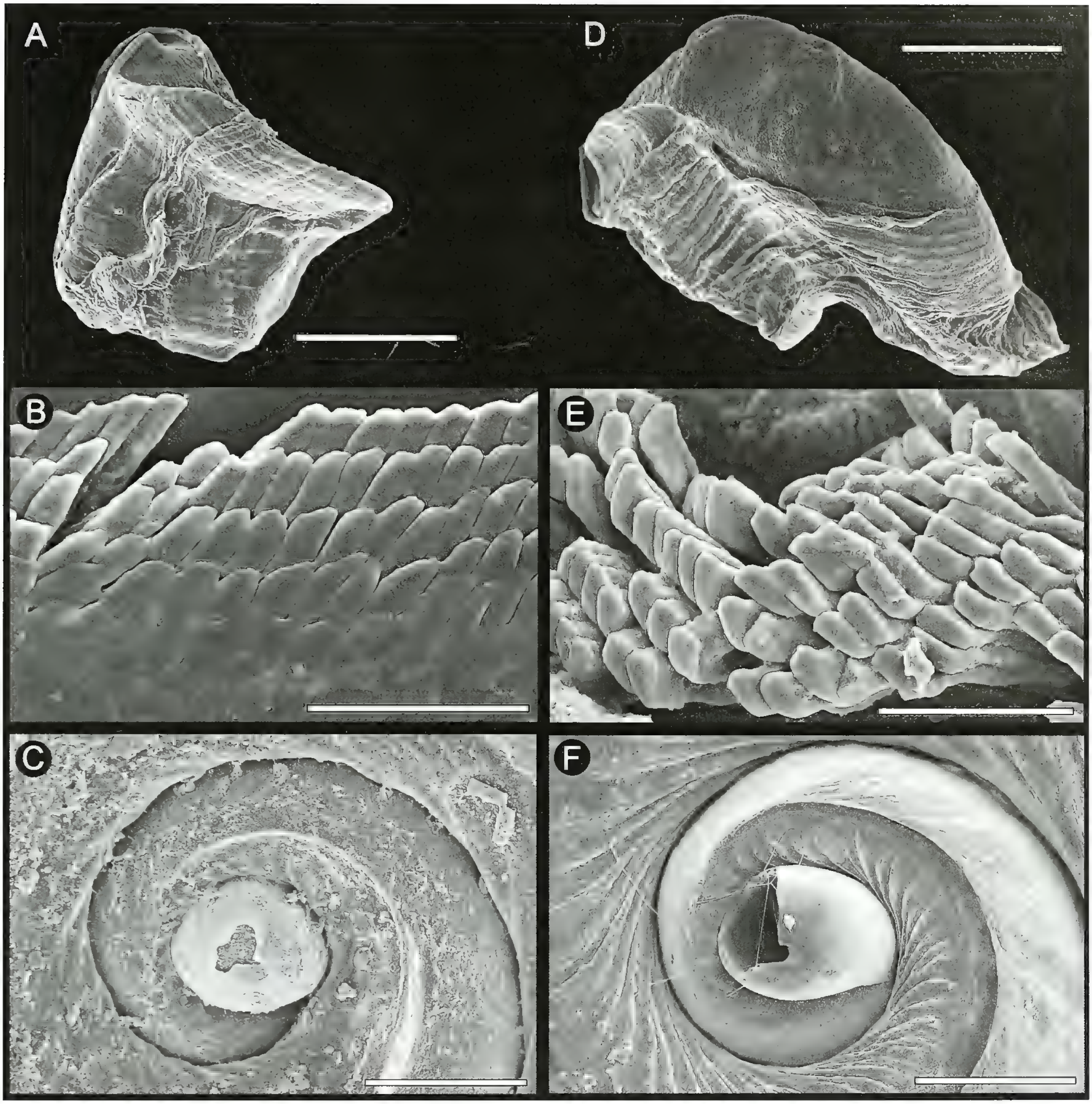

Figure 3. *Akera juliae* new species and *A. soluta* (Gmelin, 1791). **A–C.** *Akera julieae*, scanning electron micrographs of the preserved holotype (LACM 3033). **A.** Gizzard plate. Scale bar = 300 μm. **B.** Jaw. Scale bar = 50 μm. **C.** Protoconch. Scale bar = 200 μm. **D–E.** *Akera soluta* (Gmelin, 1791), scanning electron micrographs of a specimen from Japan (LACM 153414). **D.** Gizzard plate. Scale bar = 300 μm. **E.** Jaw. Scale bar = 50 μm. **F.** Protoconch. Scale bar = 200 μm.

the material here examined and information, photographs, and descriptions provided by the junior author. The description of the new species is mainly based on the holotype, collected from California, but the three empty shells collected from Costa Rica seem to belong to the same species. However, this needs to be verified when complete specimens from Costa Rica become available.

Akera julieae differs from other described species of the genus. Several shells and one specimen of the Indo-Pacific *Akera soluta* were examined for comparison (see Table 1) confirming the presence of several external and internal differences between these two species. For instance, the rachidian radular teeth of *A. soluta* are more solid with larger cusps and flanking denticles (Figure 4D). The three innermost lateral teeth have wide cusps

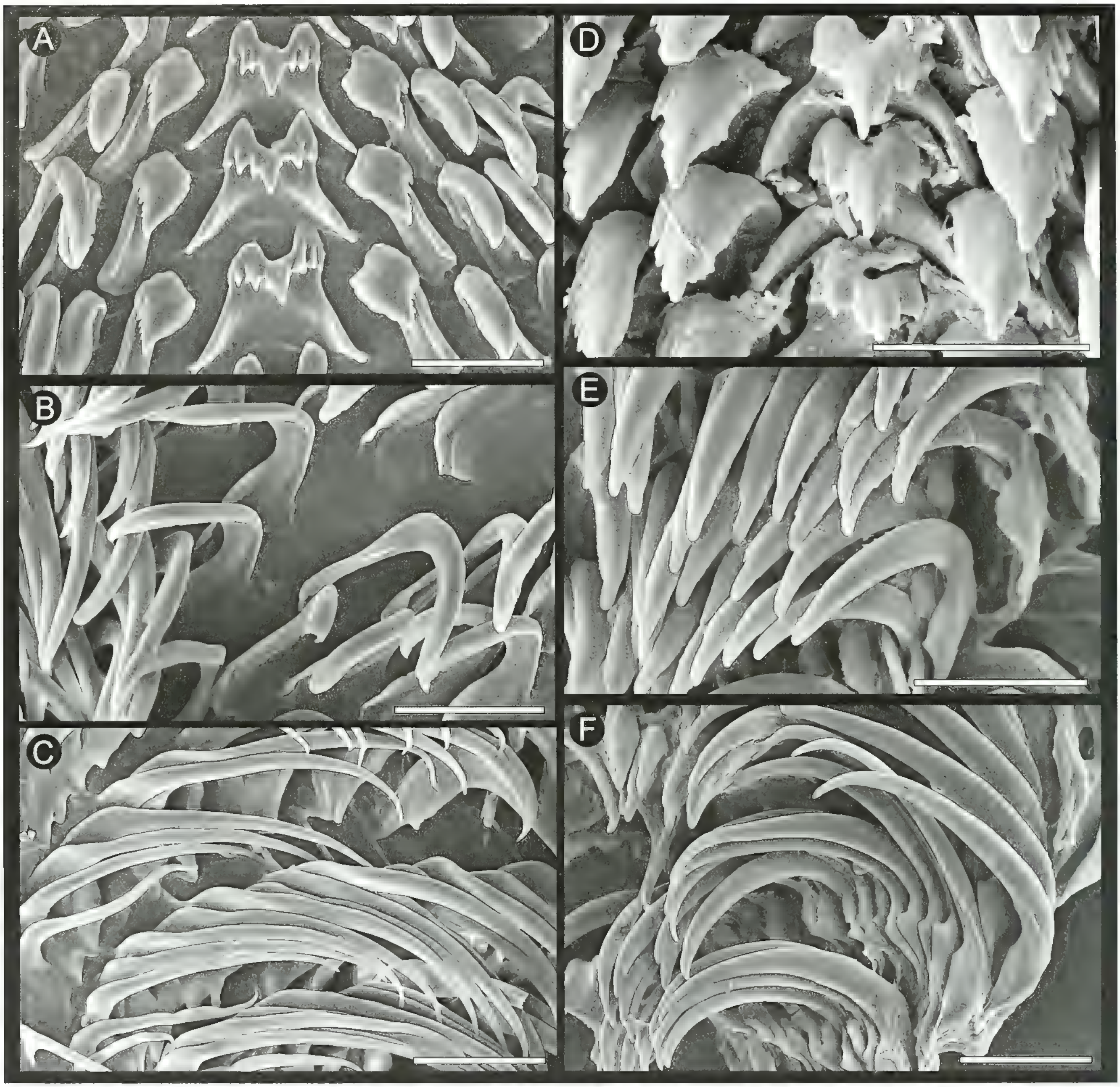

Figure 4. *Akera juliae* new species and *A. soluta* (Gmelin, 1791). **A–C.** *Akera julieae*, scanning electron micrographs of the radula of the holotype (LACM 3033). **A.** Rachidian and innermost lateral teeth. Scale bar = 50 µm. **B.** Mid-lateral teeth. Scale bar = 50 µm. **C.** Outermost lateral teeth. Scale bar = 50 µm. **D–F.** *Akera soluta*, scanning electron micrographs of the radula of a specimen from Japan (LACM 153414). **D.** Rachidian and innermost lateral teeth. Scale bar = 50 µm. **E.** Mid-lateral teeth. Scale bar = 50 µm. **F.** Outermost lateral teeth. Scale bar = 50 µm.

with denticles in *A. soluta*, whereas only the two innermost teeth of *A. julieae* have similar characteristics. The mid-lateral teeth in *A. soluta* also have denticles (Figure 4E), whereas they are smooth in *A. julieae*. The outermost lateral teeth of *A. julieae* are proportionally more elongate and straighter than those of *A. soluta* (Figure 4F). More importantly, the jaws of *A. soluta* are well developed and composed of a number of rows of strong rodlets (Figure 3E), whereas in *A. julieae* the jaws are more rudimentary with only 5 rows of fragile-looking rodlets. There are no consistent differences between the gizzard plates of *A. julieae* and *A. soluta* (Figures 3A, 3D). Externally, *A. soluta* has a slightly larger and more elongate protoconch. The adult shells of these two species are indistinguishable due to the morphological variability in *A. soluta*.

Akera bayeri is the only other species of *Akera* known from the Americas. The external morphology and anatomy of this species was described in detail by Marcus and Marcus (1967) and Marcus (1970). *Akera bayeri* differs from *A. julieae* in two important regards. The shell of *A. bayeri* has a more elevated spire and the radular teeth are stronger with denticles on all lateral teeth, whereas in *A. julieae* the lateral teeth are smooth.

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Description of *Calliotropis pulvinaris* new species (Gastropoda: Trochidae: Eucyclinae: Calliotropini) from West Madagascar

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ABSTRACT

Calliotropis pulvinaris new species is described from West Madagascar and compared with similar species in the trochid subfamily Eucyclinae, particularly with *C. patula* (Martens, 1904), *C. concavospira* (Schepman, 1908), *C. blacki* Marshall, 1979, and *C. vaillanti* (Fischer, 1882). The new species can be separated from these by a rather depressed spire, a rounded periphery, tumid whorls bearing four spiral cords of which nodules decrease in size and increase in number from adapical cord to abapical cord, and five spiral cords on the base.

INTRODUCTION

The malacofauna of this area remains poorly known, despite earlier surveys (1971–1973) by ORSTOM (Office de la Recherche Scientifique et Technique Outre-Mer, now IRD: Institut de Recherche pour le Développement) on the continental slope of Madagascar (Crosnier and Jouannic, 1973). Independently of the inherent economic interest, this endeavor yielded abundant zoological material, more particularly mollusks now deposited at the MNHN (Muséum national d'Histoire naturelle, Paris).

Commercial fishing boats have trawled for deep-water shrimp off Madagascar. The commercial dredging off West Madagascar from these last years brought various specimens of trochid species, some of them described in the past (Watson, 1886; Martens and Thiele, 1904; Thiele, 1925; Barnard, 1963), others recently named as new species (Vilvens, 2001 and 2002). Two years ago, Guido T. Poppe entrusted me with trochid shells collected in deep water. These shells, originally labeled as *Calliotropis patula* (Martens, 1904), are conspecific with material trawled by French expeditions and deposited at MNHN in the 1970s. Closer examination and comparison with the type of the supposed species leads me to conclude that all these shells belong to an unnamed species that is described here as new.

Text abbreviations used are: IRSNB: Institut royal des Sciences naturelles de Belgique, Bruxelles, Belgium; MNHN: Muséum national d'Histoire naturelle, Paris, France; NMNZ: Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand; ZMA: Zoölogisch Museum, Amsterdam, The Netherlands; ZMB: Zoologisches Museum of Berlin, Germany; P1, P2, P3, P4: primary cords (P1 is the most adapical); stn: station; dd: no live specimens present in sample.

I follow below the classification of Hickman and McLean (Hickman and McLean, 1990) at the suprageneric level.

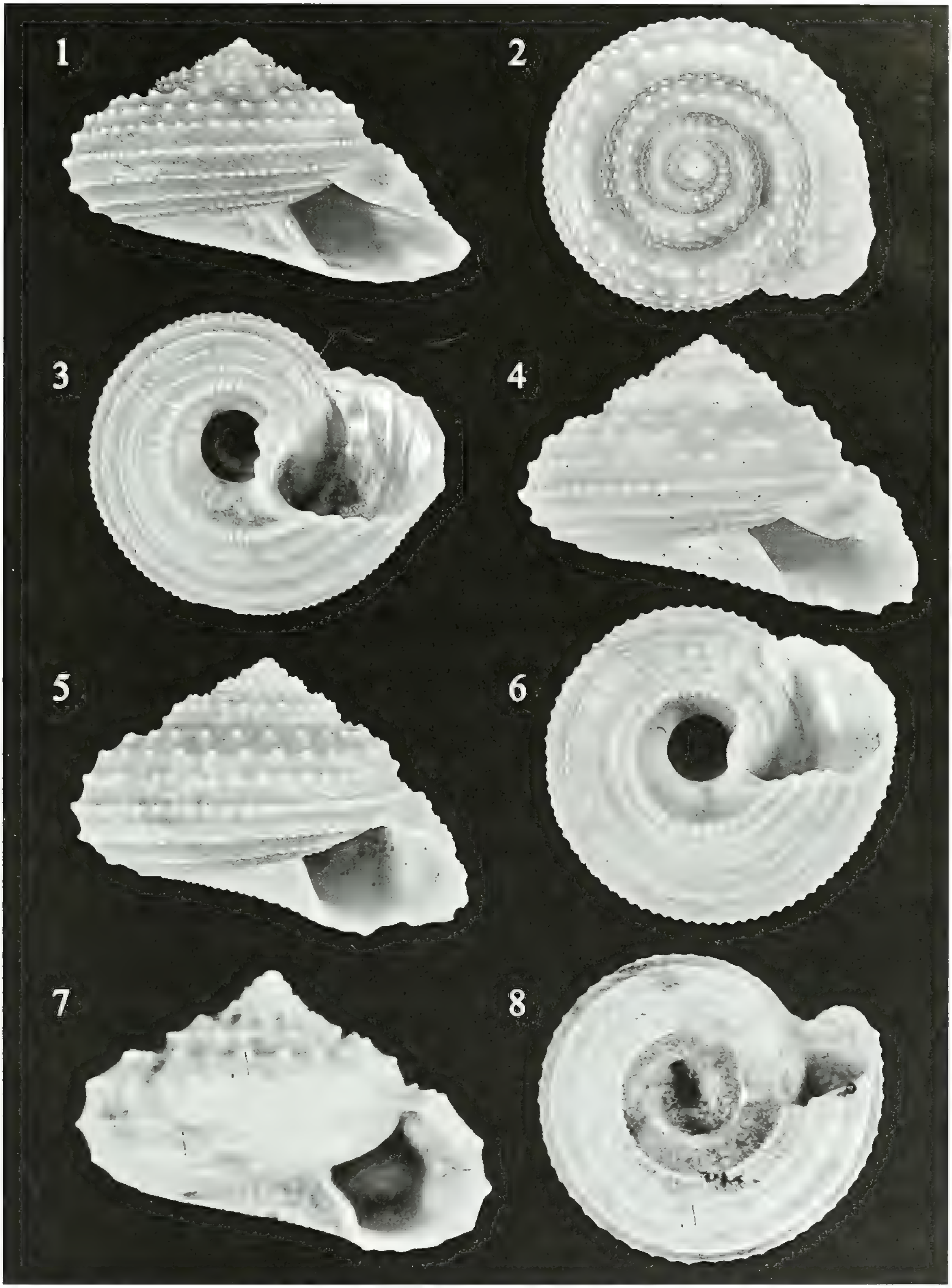
SYSTEMATICS

Family Trochidae Rafinesque, 1815
Subfamily Eucyclinae Koken, 1897
Tribe Calliotropini Hickman and McLean, 1990
Genus *Calliotropis* Seguenza, 1903

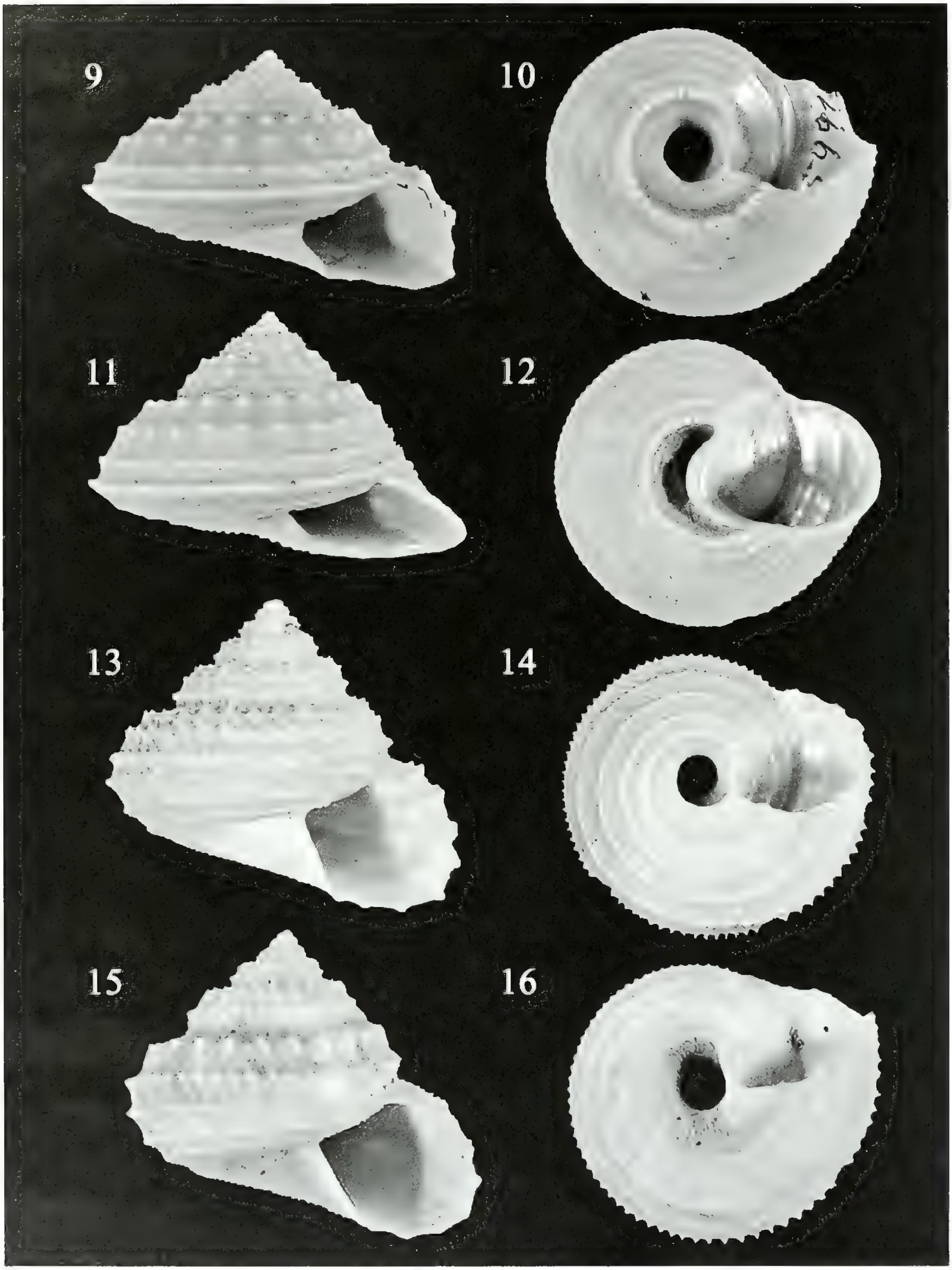
Type Species: *Trochus ottoi* Philippi, 1844, Pliocene–Pleistocene, Italy; by original designation.

Calliotropis pulvinaris new species
(Figures 1–6)

Description: Shell rather long for genus (height up to 18.3 mm, width up to 29.0 mm), rather depressed, rather thin, cyrtoconoidal; spire rather low, height 0.6–0.7×width, height 2.3–4.5×aperture height; umbilicus deep and large. Protoconch about 300 μm wide, with about 1 whorl, partially damaged on available specimens, remaining part smooth. Teleoconch of up to seven convex whorls, bearing four spiral granular cords and prosocline threads; nodules from cords produced by intersections with axial folds on four first whorls; additional axial threads not connecting nodules on last whorls. Suture visible, impressed, not canaliculated. First teleoconch whorl convex, sculptured by about 18–20 prosocline smooth riblets, interspace between riblets twice as wide as riblets; primary spiral cords P2 and P3 appearing almost immediately, evenly spaced, similar in size and shape, bearing rounded nodules produced by intersection with axial riblets. On second whorl, P2 and P3 stronger, P1 appearing at end of whorl, close to P2. On third whorl, nodules of P1 and P2 becoming sharp, with weak-



Figures 1–8. *Calliotropis* species. **1–6.** *Calliotropis pulvinaris* new species. **1–3.** Holotype MNHN, northwestern Madagascar, 18.1×29.0 mm. **4.** Paratype IRSNB, West Madagascar, 18.1×26.6 mm. **5–6.** Paratype, collection C. Vilvens, West Madagascar, 18.3×25.4 mm. **7–8.** *C. concavospira* (Schepman, 1908), syntype ZMA, Indonesia, 6.0×8.7 mm.



Figures 9–16. *Calliotropis* species. **9–12.** *Calliotropis patula* (Martens, 1904). **9–10.** Syntype ZMB 55919, between Zanzibar and Brawa, 16.2×25.1 mm. **11–12.** Syntype ZMB 109933, Somaly, 19.0×27.2 mm. **13–14.** *C. blacki* Marshall, 1979, holotype NMNZ M226932, Raoul Island, Kermadec group, 11.3×13.0 mm. **15–16.** *C. vaillanti* (Fischer, 1882), MNHN, Azores Islands, 10.6×12.2 mm.

Table 1. *Calliotropis pulvinaris*. Shells measurements in mm for all types cited and type material (n=8). H: height; W: width; HA: aperature height; TW: number of teleoconch whorls.

	Measurement					
	TW	H	W	HA	H/W	H/HA
Range	5.75–7.00	15.4–18.3	21.8–29.0	4.00–6.90	0.60–0.70	2.30–4.50
Mean	6.69	17.11	24.7	5.71	0.69	3.10
Standard deviation	0.41	0.97	2.13	0.93	0.03	0.70

ly adapically oriented tip; P4 partially covered by succeeding whorl, with nodules smaller and more numerous than ones on other cords. From fourth whorl on nodules on cords decrease in size and sharpness, and increase in number from P1 to P4; cords evenly distributed on whorl; axial threads in area between cords remain thin, distance between threads similar to threads width. On last whorl, P4 peripheral; no secondary spiral cords; periphery rounded.

Aperture almost circular, forming angle at junction of inner and outer lips; this angle almost rounded and outer lip slightly flared in fully mature specimens; inner lip flanged in a curved arc projecting weakly over umbilicus; parietal lip forming thin, transparent glaze. Columella slightly curved, without tooth, abapical part prosocline. Base moderately convex, with 5 granular spiral cords, innermost one stronger than others and bordering umbilicus; interspace between cords twice as wide as cords, smaller for two innermost cords on young adult specimens; very fine axial lamellate threads between cords, poorly visible. Umbilicus wide, funnel shaped, diameter about 35% of shell diameter, with very fine crowded axial lamellae and no spiral cord within. Color of protoconch and teleoconch pinkish white, with no maculations; first two whorls somewhat brownish.

Type Locality: West Madagascar, 22°17.0′ S, 43°02.2′ E, 640–660 m, Indian Ocean.

Type Material: Holotype MNHN unnumbered (dd), Chalutages *Vauban*, stn. CH 112, coll. A. Crosnier, from type locality, 18.1×29.0 mm; Paratype 1 MNHN unnumbered (dd), 12°50′S, 48°09′E, 580–585 m, northwestern Madagascar, coll. A. Crosnier; Paratypes 2 MNHN (dd), 1 IRSNB (IGnr 30 185) (dd), 1 ZMB (Moll. 108.519) (dd), 1 G. T. Poppe collection (dd), 1 C.Vilvens collection (dd), all from West Madagascar, off Mahajanga (formerly Majunga), commercial trawlers said to be from 800 m.

Etymology: Of a cushion (Latin); with reference to the soft and oval form of the shell, without angulations.

Remarks: *Calliotropis pulvinaris* new species is similar to *C. patula* (Martens, 1904) (Figures 9–12) from East Africa (off Somalia and Zanzibar, 977–1019 m), but this species differs from the new species by having a subangulated periphery, less tumid whorls, four spiral cords on base (instead of 5) and also by the nodules of P1 and P2 that become bigger than those of P3 much later (4th whorl).

The new species weakly resembles *C. concavospira* (Schepman, 1908) (Figures 7–8) from Indonesia (also deep water from 835 to 883 m), but this smaller species has only three cords on the whorls and these whorls are more angulated.

Calliotropis pulvinaris new species may also be compared to *C. blacki* Marshall, 1979 (Figures 13–14), from Kermadec Islands, but this Indo-Pacific species is smaller for a similar number of whorls, has a more elevated spire and only four spiral cords on the base.

The new species is also superficially similar to *C. vaillanti* (Fischer, 1882) (Figures 15–16) and *C. ambigua* (Dautzenberg and Fischer, 1896), both from eastern Atlantic, and to *C. actinophora* (Dall, 1890) from western Atlantic, but these three species have a more elevated spire, only 3 spiral cords on the whorls and only four spiral cords on the base.

ACKNOWLEDGMENTS

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Notice

THE 2005 R. T. ABBOTT VISITING CURATORSHIP

The Bailey-Matthews Shell Museum is pleased to invite applications for the 2005 R. T. Abbott Visiting Curatorship.

The Curatorship, established originally in accordance with the wishes of the late Dr. R. Tucker Abbott, Founding Director of the Shell Museum, is awarded annually to enable malacologists to visit the museum for a period of one week. Abbott Fellows will be expected, by performing collection-based research, to assist with the curation of portions of the Museum's collection and to provide one evening talk for the general public. The Museum collection consists of marine, freshwater, and terrestrial specimens. A large percentage of our holdings have been catalogued through a computerized database management system. A substantial portion of the time will be available for research in the collection, but field work in southwest Florida can be arranged. The R. T. Abbott Visiting Curatorship is accompanied by a stipend of $1,500.

Interested malacologists are invited to send a copy of their curriculum vitae together with a letter detailing their areas of taxonomic expertise and research objectives, and to provide a tentative subject for their talk. Send materials to:

Dr. José H. Leal, Director
The Bailey-Matthews Shell Museum
P.O. Box 1580
Sanibel, FL 33957
jleal@shellmuseum.org

Applications for the 2005 Visiting Curatorship should be sent no later than May 30, 2005. The award will be announced by late June. Questions about the Visiting Curatorship should be sent to the e-mail address above, or by phone at:

(239) 395-2233; fax (239) 395-6706

INSTRUCTIONS TO AUTHORS

THE NAUTILUS publishes papers on all aspects of the biology and systematics of mollusks. Manuscripts describing original, unpublished research as well as review articles will be considered. Brief articles, not exceeding 1000 words, will be published as notes and do not require an abstract. Notices of meetings and other items of interest to malacologists will appear in a news and notices section.

Manuscripts: Each original manuscript and accompanying illustrations should be submitted in triplicate. Text must be typed on one side of 8½ × 11 inch white paper, double spaced throughout (including literature cited, tables and figure captions), with at least 1 inch of margin on all sides. All pages must be numbered consecutively. If printed on a word processor, the right margin should be ragged rather than justified. Authors should follow the recommendations of the *Scientific Style and Format—The CBE Manual for Authors, Editors, and Publishers*, which is available from the Council of Science Editors, Inc., 11250 Roger Bacon Drive, Suite 8, Reston, VA 20190, USA (http://www.cbe.org/cbe). The first mention of a scientific name in the text should be accompanied by the taxonomic authority, including year. Latin names and words to be printed in italics must be underlined; leave other indications to the editor. Metric and Celsius units are to be used.

The sequence of sections should be: title page, abstract page, 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). The abstract page should contain the title and abstract, which should summarize in 250 words or less the scope, main results and conclusions of the paper. All references cited in the text must appear in the literature cited section and vice versa. In the literature cited section, all authors must be fully identified and listed alphabetically. 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 in the pagination. Tables must be numbered and each placed on a separate sheet. A brief legend must accompany each table. Captions for each group of illustrations should be typed on a separate sheet and include a key to all lettered labeling appearing in that group of illustrations.

All line drawings must be in black, high quality ink, clearly detailed and completely labeled. Photographs must be on glossy, high contrast paper. All figures are to be consecutively numbered (figs. 1, 2, 3, . . . , NOT figs. 1a, 1b, 1c, . . . NOR plate 1, fig. 1 . . .). Illustrations must be arranged in proportions that will conform with the width of a page (6¾ inches or 171 mm) or a column (3¼ inches or 82 mm). The maximum size of a printed figure is 6¾ by 9 inches or 171 by 228 mm. All illustrations must be fully cropped, mounted on a firm, white backing, numbered, labeled and camera ready. The author's name, paper title and figure number(s) should appear on the back. Original illustrations must be between one and two times the desired final size. It is the author's responsibility that the line weight and lettering are appropriate for the desired reduction. Original illustrations will be returned to the author if requested. Color illustrations can be included at extra cost to the author.

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Final Manuscript Submission: Authors of accepted manuscripts will be required to submit an electronic version of the manuscript correctly formatted for THE NAUTILUS. The formatted manuscript may be sent as an e-mail attachment to nautilus@shellmuseum.org or in a diskette, preferably prepared using an IBM PC-compatible text processor. Original illustrations may be submitted separately by regular mail or as digital files (zip disks or CDs), preferably in TIFF or BMP formats. The original resolution of digital images at final (printing) size should be at least 600 dpi for halftones and 1200 dpi for line drawings.

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Manuscripts, corrected proofs and correspondence regarding editorial matters should be sent to: Dr. José H. Leal, Editor, The Nautilus, P.O. Box 1580, Sanibel, FL 33957, USA, jleal@shellmuseum.org, (239) 395-2233.

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A revision of the genus *Trophon* Montfort, 1810 (Gastropoda: Muricidae) from southern South America

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ABSTRACT

The genus *Trophon* from southern South America is revised and restricted to ten valid species from among the 36 nominal species still currently used. In addition, a new species, *Trophon parodizi* from Patagonian waters, is described. Adult specimens of the new taxon are illustrated, described and compared with other living species of the same genus and similar geographic distribution. Redescription and re-illustration of types, based on material from several institutions around the world are provided for *Trophon geversianus* (Pallas, 1774), *T. plicatus* (Lightfoot, 1786), *T. patagonicus* (d'Orbigny, 1839), *T. acanthodes* Watson, 1882, *T. pelseneeri* Smith, 1915, *T. amettei* Carcelles, 1946, *T. clenchi* (Carcelles, 1953), *T. wilhelmensis* Ramirez-Bohme, 1981, and *T. bahamondei* McLean and Andrade, 1982. In addition, "*Trophon*" *malvinarum* Strebel, 1908, assigned to *genera incerta*, is also redescribed and illustrated.

INTRODUCTION

Among many groups of marine gastropods from South American waters in need of a modern comprehensive revision, the high diversity and abundance exhibited by the muricid genus *Trophon* Montfort, 1810, renders it particularly interesting. Early collections include a large and varied array of specimens obtained by 19th century expeditions from shallow waters of a vast area including more than 5,000 km of coast in Argentina. A taxonomic revision of these gastropods revealed that a large number of names should be placed in synonymy. The taxonomy and nomenclature thus clarified is sure to improve the usefulness of this genus and its species as tools for biogeographic and evolutionary interpretations, without forgetting that clear specific delimitation is crucial to other uses such as the commercial exploitation of the type species (*Trophon geversianus*) in southern Chile.

The subfamily Trophoninae is one of the most conspicuous groups of marine gastropods living presently around the southern tip of South America. The southern origin of the group seems to be beyond doubt, as discussed by Griffin and Pastorino (2005), when revising the numerous extinct species appearing in the fossil record since the late Oligocene.

This article constitutes a review of all living species of *Trophon* from both coasts of southern South America. The study involves only those taxa living in environments associated with the continental shelf. Accordingly, *T. mucrone* Houart, 1991, from 1500–1575 m off Brazil and the subantarctic *T. veronicae* Pastorino, 1999, are not considered herein. These two deep-water species seem to belong in a different group according to data available on the radula, protoconch, and penis of *T. veronicae*. Such anatomical data remain unknown for *T. mucrone*. In addition, *T. ohlini* Strebel, 1904, with a distinct protoconch and radula, different from those of other Patagonian species and resembling the boreal *Boreotrophon truncatus*, will be the subject of a future paper. Finally, *T. triacanthus* Castellanos et al., 1987, recently described under *Trophon*, is also considered as belonging to a different genus—possibly *Apyxistus*—according to several differences in protoconch and shell morphology.

Houart (2003) recently described three new species under the genus *Trophon* sensu lato from dredgings more than 1000 m in depth. No radular, anatomical, or protoconch information is included in the descriptions. However, enough differences can be observed in the shells that, as mentioned by Houart himself, a new genus may be granted for these species. A similar situation is true for "*Trophon*" *malvinarum*; however, as there are no accurate illustrations or recent descriptions of this species I decided to include it in this work as belonging to an indeterminate genus.

For each of the species considered herein, adult specimens, operculum, gross anatomy, radula, protoconch, and ultrastructure of the shell are described whenever enough material was available. This work is part of a complete revision of the genus including all species from South America and Antarctica.

MATERIALS AND METHODS

All the material examined is housed in the collections of the Museo Argentino de Ciencias Naturales "Bernardino

Rivadavia", Buenos Aires (MACN-In); Museo de La Plata, La Plata (MLP); National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM) and American Museum of Natural History, New York (AMNH). Part of the type material is housed in the following museums: The Natural History Museum, London, (BMNH); Zoologisches Institut und Zoologisches Museum der Universität Hamburg, (ZMH); Swedish Museum of Natural History, Stockholm, (NHRM); Museum national d'Histoire naturelle, Paris (MNHN); Museo Nacional de Historia Natural, Santiago, Chile (MNHNS); Museo Nacional de Historia Natural, Montevideo, Uruguay (MNHNM); Academy of Natural Sciences of Philadelphia (ANSP) and Los Angeles County Museum of Natural History (LACM). Finally, several historical specimens from the Auckland Institute and Museum, New Zealand (AK) were examined for comparative purposes. Material from the USNM originates from the United States Antarctic Program (USAP) and was mostly collected by two ships: R/V HERO and R/V ELTANIN. Material collected by the Uruguayan ship R/V ALDEBARAN is also included.

Dissections were performed on ethanol-preserved specimens for study of gross anatomy, with emphasis on the morphology of the anterior alimentary system, and the pallial portions of the male and female reproductive systems. Radulae were prepared according to the method described by Solem (1972) and observed using a LEO 440 scanning electron microscope (SEM) at the USNM and a Philips XL 30 at MACN. Radular terminology follows Kool (1993, fig. 6B). Shell ultrastructure data were procured from freshly fractured colabral sections taken from the central portion of the lip on the last whorl of two individuals per taxon, whenever sufficient material was available.

Photographs were taken using a digital scanning camera. Several images were scanned from black and white 35 mm negatives using a slide scanner. All images were digitally processed.

For the convenience of the reader in the Additional Material Examined sections, "D" means that the specimens were collected dead and "A" means alive.

SYSTEMATICS

Class Gastropoda Cuvier, 1791
Subclass Ortogastropoda Ponder and Lindberg, 1996
Superorder Caenogastropoda Cox, 1959
Order Sorbeoconcha Ponder and Lindberg, 1996
Infraorder Neogastropoda Wenz, 1938
Family Muricidae da Costa, 1776
Subfamily Trophoninae Cossmann, 1903
Genus *Trophon* Montfort, 1810

Type Species: *Murex magellanicus* Gmelin, 1791 (=*Buccinum geversianus* Pallas, 1774) by original designation. *Polyplex* Perry, 1811 (type species *Polyplex bulbosa* Perry, 1811 =*Buccinum geversianum* Pallas, 1774) and *Muricidea* Swainson, 1840 (type species *Murex magellanicus* Chemnitz, 1780 (*nomen nudum*) =*Murex magellanicus* Gmelin, 1791 =*Buccinum geversianum* Pallas, 1774) are synonyms.

Description: Shells variable in size, ranging from about 1 to more than 10 centimeters high, fusiform, subquadrate to elongate. Protoconch paucispiral, with 2 to 2½ asymmetrical, smooth, slightly globose, and regularly convex whorls. Spire of about 4 whorls, equal or slightly shorter than aperture height, never higher. Subsutural ramp generally present, variously developed and slightly inclined posteriorly, defining a conspicuous keel. Axial sculpture variable, from weak growth lines to strong lamellae—in some instances even growing over the subsutural ramp; axial sculpture generally better developed than spiral sculpture. Lamellae along keel sometimes growing into fairly strong, always open, spines, which may even curve backwards. Spiral ornamentation variably developed; sometimes missing, but generally consisting of slightly rounded and equally developed cords, wider than interspaces and sometimes accompanied by weaker secondary intercalated ones. Spiral ornamentation usually restricted to surface abapical to keel, while missing along subsutural ramp and in some cases only present in the earliest whorls. Aperture subovoid; outer lip sharp, sometimes slightly reflected, but always smooth throughout. Siphonal canal always present and open, although variably developed in length, sometimes curved. Umbilicus variable, usually open, wide, although in some species totally absent or represented by a chink.

Shell ultrastructure arranged invariably in 2 layers: innermost layer of crossed lamellar aragonite, outer layer of amorphous calcite. Relative thickness of both layers variable according to species or—within a given species—latitude at which the population lives.

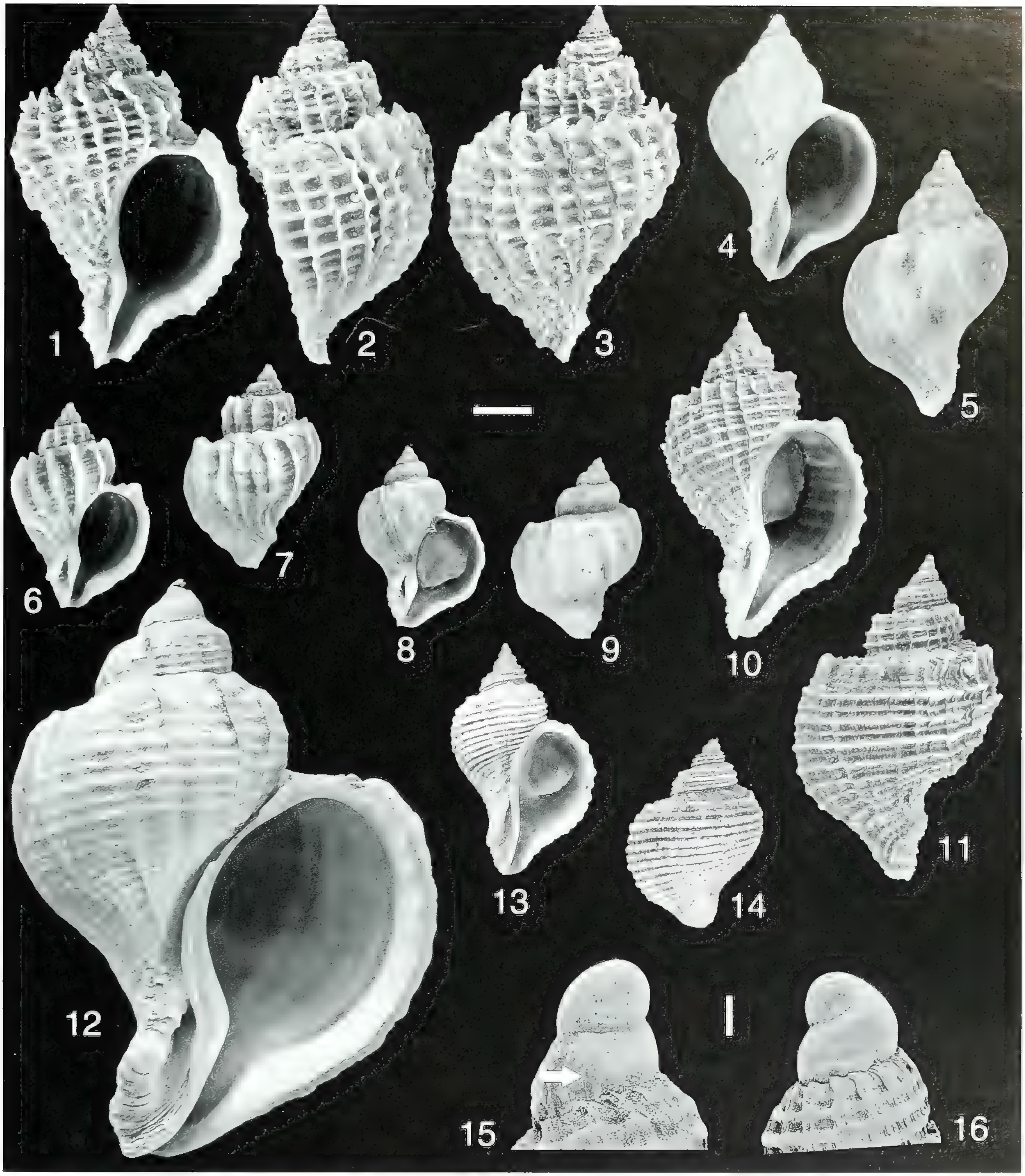
Radulae rachiglossate, rachidian teeth with 3 median cusps, the central one the larger and the lateral ones with a denticle, sometimes obsolete but always present, attached to the interior margin (never free). Rachidian base always sinuous and with the base offset under the proximal tooth. Marginal cusps always single, never bifid. Lateral teeth always thin, with the attachment area also thin. Operculum circular or suboval tear-shaped, attachment area with horseshoe shaped scars.

Accessory salivary glands always developed, tubular, single or coiled and unfilled. Esophagus with a loop running along the left side of the gland of Leiblein; esophageal glands externally invisible.

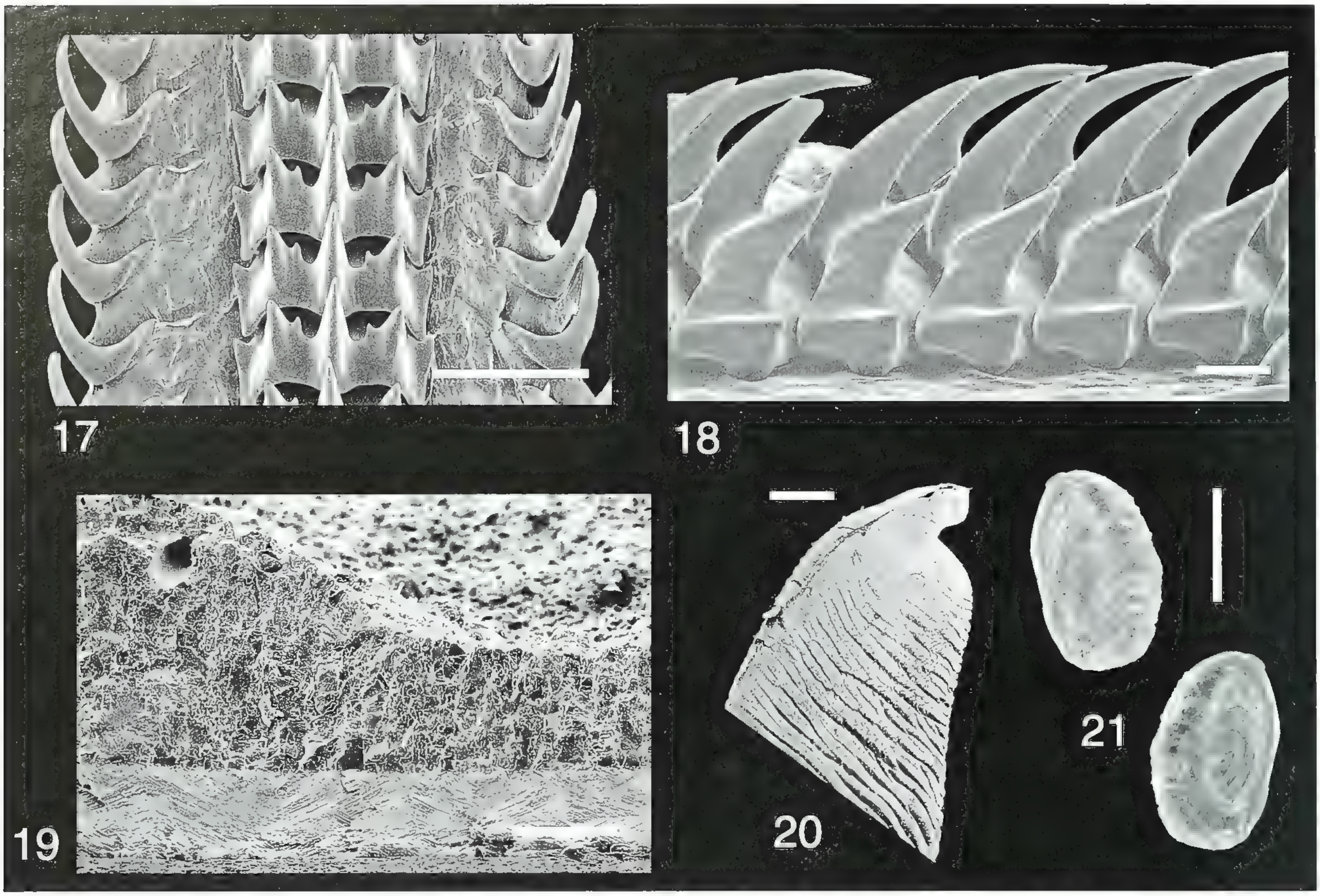
Egg-capsules always erect, never lenticular, usually with nurse eggs.

Trophon geversianus (Pallas, 1774)
(Figures 1–21)

"Purpurschnecken" Knorr, 1769: 47, pl. 30, fig. 2.
"Buccin feuilleté" Knorr, 1770: 53, pl. 30, fig. 2.
Buccinum geversianum Pallas, 1774: 33, pl. 3, figs. 1, 2.
Buccinum foliaceum multifariam frondosum Chemnitz, 1780: 130, pl. 139, fig. 1297 [non-binominal, rejected by Opinion 184 (ICZN, 1944) [Lectotype of *Murex magellanicus* Gmelin, 1791 (Beu, 1978)].



Figures 1–16. *Trophon geversianus* (Pallas, 1774). **1–3.** MACN-In 36036, Punta Cavendish, Puerto Deseado, Santa Cruz province in 5 m. **4–5.** MACN-In 36042, Cueva del Indio, Puerto Deseado. **6–9.** MACN-In 36041, Sierra Grande, Río Negro province, in tide pools. **10–11.** MACN-In 36037, Punta Peñas, San Julián, Santa Cruz Province in 2 m. **12.** MACN-In 36043, Bahia Almanza, Puerto Harberton, Tierra del Fuego, in 3 m. **13–14.** MACN-In 36038, both specimens from Playa La Mina, San Julián, Santa Cruz Province intertidal. Scale bar for all shells = 1 cm. **15–16.** Two views of protoconch, arrow head the transition to teleoconch. Scale bar = 500 μm



Figures 17–21. *Trophon geversianus* (Pallas, 1774). **17.** Radula, frontal view. Scale bar = 100 μm. **18.** Lateral view of the same radula. Scale bar = 30 μm. **19.** Ultrastructure of the shell. Scale bar = 100 μm. **20.** Penis, critical-point dried. Scale bar = 800 μm. **21.** two views of the operculum. Scale bar = 1 cm.

Buccinum fimbriatum Martyn, 1784: fig. 6.
Murex magellanicus Gmelin, 1791: 3548 *partim* (var. β excl.); d'Orbigny 1841: 451; Wood, 1828: 127, pl. 26, fig. 90; Hanley, 1856: 132, pl. 26, fig. 90.
Neptunea foliacea Röding, 1798: 116.
?*Murex ventricosus* Molina, 1810: 178.
Polyplex bulbosa Perry, 1811: pl. 9, fig. 5.
Murex foliatus Schumacher, 1817: 215, sensu Vokes 1971.
Fusus magellanicus Lamarck. Gray, 1839: 118.
?*Murex varians* d'Orbigny, 1839: pl. 42, figs. 4–7; d'Orbigny, 1841:452.
T. geversianus Pallas.—Montfort, 1810: 483, fig.; H. and A. Adams, 1853: 77, pl. 8, fig. 3 c.; Tapparone-Canefri, 1874: 15; Kobelt, 1878: 205, pl. 72, fig. 1–3; pl. 73, fig. 1; Sowerby II, 1880: pl. 404, figs. 7,8; Tryon, 1880: 144, pl. 32, figs. 337–340, 343–347; pl. 70, figs. 433; Watson, 1886: 164; Rochebrune and Mabille, 1889: H.53; Strebel, 1904: 173, pl. 4, figs. 11–23; pl. 5, figs. 24–42; pl. 6, figs. 43–52. Lamy, 1906: 3; Ihering, 1907: 404; Melvill and Standen, 1907: 106; Strebel, 1908: 37, pl. 6, figs. 94 a, b.; Carcelles, 1946: 60, figs. 1–5; 1946: 69, figs. 6a,b; 7a,b,c,d; 8; Powell, 1951: 151, fig. L, 81; N, 107; Castellanos, 1970: 76, pl. 5 fig. 2; Dell, 1971: 210; Harasewych, 1984: 13, figs. 1–3, 19–25; Vokes, 1991: 7, fig.; 1992: 3, figs 1c, d; 3c, d; Kool, 1993: 47, figs. 9–14, 30–31; Castellanos and Landoni, 1993: 3, pl. 1 figs. 1–15, 18–21
Fusus intermedius Hupé in Gay, 1854: 166, pl. 4, fig. 6, *non* Cristofori and Jan, 1832 *nomen nudum*; *nec* A. J. Michelotti, 1846 *nomen nudum*; *nec* G. Michelotti, 1847; Rochebrune and Mabille, 1889: H.53.
F. geversianus Pallas.—Hupé in Gay, 1854: 167; Gould, 1861: pl. 16, fig. 277 a, b.
Trophon geversianus var. *calva* Kobelt, 1878: 305, pl. 75; fig. 1.
T. geversianus var. *lirata* Kobelt, 1878: 305, pl. 76, fig. 1, 2.
T philippianus Dunker in Kobelt, 1878: 277, pl. 72, figs. 4, 5; Melvill and Standen, 1907: 107; Powell, 1951: 152.
T. .philippinarum Dunker. Sowerby II, 1880: pl. 405, fig. 21.
?*T. varians* (d'Orb.).—Carcelles, 1943: 431, figs. 1, 2, 3, 6, 7; Castellanos, 1970: 75, pl. 5, fig. 3, 4; Vokes, 1992: 3 fig. 4c.
T plicatus (Lightfoot).—Calvo, 1987: 135, fig. 99.
Trophon sp. Vokes 1991: 9, figs. 1–13.

Description: Shell large (up to 100 mm) and extremely variable, fusiform, subquadrate profile, chalky, whitish; protoconch of 2 whorls, smooth, cylindrical, slightly globose, slightly asymmetrical; teleoconch of 4 shouldered whorls, spire less than ⅓ of total shell height. Spire angle about 50°; suture impressed; subsutural shelf straight, aperture ovoid, interior glossy pinkish; anterior siphonal canal moderately long (half the height of aperture); umbilicus closed or deep, some specimens with a pseudoumbilical chink; outer lip rounded, with reflected edges; inner lip curved, adpressed.

Axial ornamentation of irregular, low lamellose varices on first whorls, becoming 8–10 well-defined lamellae on last ones. Lamellae growing across entire whorl, attached to the shell, sometimes curving adaxially. Lamellae ending in shallow peripheral spine, in some specimens growing adapically.

Spiral ornamentation of about 15 cords beginning at periphery of whorls. Smooth specimens common in intertidal pools and mytilid banks. Coloration varying from creamy white to dark brown. Growth lines regularly spaced, present throughout shell. Geographic variation conspicuous from north to south and from intertidal to infralittoral specimens, expressed as a series of smooth to profusely ornamented specimens according to area of collection.

Shell ultrastructure composed of two layers; innermost layer (50% shell thickness) of colabrally aligned crossed lamellar aragonite, outer layer (50% shell thickness) with amorphous calcite.

Operculum oval, brownish, with terminal nucleus. External surface covered by concentric, irregular, growth lines. Inner surface attachment area with 3 horseshoe-shaped scars, thick glazed rim present in all specimens.

Anatomical and radular characters as described by Harasewych (1984) and Kool (1993).

Type Material: The type material upon which Pallas (1774) based *Buccinum geversianum* could not be located. It could not be found at the Zoological Institute of the Russian Academy of Sciences (ZIL) St. Petersburg, where most of the material studied by that author is housed (B. Sirenko, pers. comm.).

Additional Material Examined: 53°39′ S, 70°55.5′ W, 5 A, R/V Hero Cruise 702, Sta. 466, 25 April 1970, 20 m (USNM 901605); 53°39′ S, 70°55.5′ W, 6 A, R/V Hero Cruise 702, Sta. 473, 26 April 1970, 15–18 m (USNM 901609); 53°30′48″ S, 70°50′33″ W, 4 A, R/V Hero Cruise 692, Sta. 69-11, 24 April 1969, intertidal, (USNM 901604); 53°24.8′ S, 69°39.2′ W, 1 D, R/V Hero Cruise 702, Sta. 481, 27 April 1970, 18 m, (USNM 901605); 53°17′ S, 68°13′ W, 1 A, R/V Hero Cruise 712, Sta. 71-2-6, 21 April 1971, 1 m, (USNM 886739); 53°51′32″ S, 70°25′52″ W, 1 A, R/V Hero Cruise 692, Sta. 69-22, 13 May 1969, 2–3 m (USNM 886187); 53°37.9′ S, 70°14′ W, 1 D, R/V Hero Cruise 702, Sta. 486, 28 April 1970, 292–296 m (USNM 901602); 54°59′ S, 64°53′ W, 1 D, R/V Eltanin Cruise 11, Sta. 970, 11 February 1964, 586–641 m (USNM 870515); 53°48.7′ S, 70°24.1′ W, 1 D, R/V Hero Cruise702, Sta. 489, 29 April 1970, 13–18 m (USNM 901601); 54°27′ S, 66°12′ W, 2 D, R/V Eltanin Cruise 6, Sta. 453, 21 January 1963, 31 m (USNM 901600); 53°26′ S, 68°35′ W, 6 A, R/V Eltanin Cruise 21, Sta. 297, 12 January 1966, 0 m (USNM 901607); 53°35′ S, 70°50′ W, 1 D, 1 A, R/V Eltanin Cruise 21, Sta. 292, 8 January 1966, 0 m (USNM 901606); 53°17′ S, 68°13′ W, 3 D, R/V Eltanin Cruise 712, Sta. 71-2-6, 21 April 1971, 0–1 m (USNM 901608); Puerto Basil Hall, Isla de los Estados, 10 A, 21 May 1971, 0–1 m (MLP 4243); Buen Suceso Bay, Tierra del Fuego, 4 A, 23 October 1941 (MLP 27218); San Julián, Punta Peñas, 6 A, 1 March 1924 (MLP 526 *partim*); Puerto Lobos, Chubut, 12 A, 2 February 1938 (MLP 2021); Puerto Golondrina, Ushuaia, 9 A, January 1962 (MLP 27201); Puerto Pirámides, Chubut, 1 A (MLP 4715); San Julián, 8 A (MLP 1583); Puerto Hoppner, Isla de los Estados, 7 A (MACN-In 22547); Punta Cavendish, Puerto Deseado, 7 A, 6 February 1961 (MACN-In 26171); Punta Cavendish, Puerto Deseado, Santa Cruz province, 5 m (MACN-In 36036); Chubut, 6 A (MACN-In 4097); Tierra del Fuego, 4 A (MACN-In 5777-1); Cueva del Indio, Puerto Deseado (MACN-In 36042); Sierra Grande, Río Negro province, in tide pools (MACN-In 36041); Punta Peñas, San Julián, Santa Cruz province, 2 m (MACN-In 36037); Playa La Mina, San Julián, Santa Cruz province intertidal (MACN-In 36038); Bahia Almanza, Puerto Harberton, Tierra del Fuego, 3 m (MACN-In 36043); San Antonio Oeste, Río Negro, intertidal, 3 A (MACN 35387); 54°47′36″ S, 64°22′35″ W, 1 A, R/V Eltanin Cruise 712, Sta. 71-2-44, 24 May 1971, intertidal (USNM 881127); 54°46′12″ S, 64°24′42″ W, 1 A, R/V Eltanin Cruise 712, Sta. 71-2-46, 21 May 1971, intertidal (USNM 881131); 54°4536″ S, 64°02′36″ W, 1 A, R/V Eltanin Cruise 7151, Sta. 869, 23 October 1971, intertidal (USNM 881132); 54°45′45″ S, 64°09′55″ W, 1 A, R/V Hero Cruise 712, Sta. 71-2-40, 21 May 1971, intertidal (USNM 881130); 54°47′48″ S, 65°16′ W, 1 A, R/V Hero Cruise 712, Sta. 71-2-8, 23 April 1971, intertidal (USNM 881126); 54°48′, 65°14′ W, 1 A, R/V Hero Cruise 712, Sta. 71-2-14, 25 April 1971, intertidal (USNM 881129); Punta Arenas, Cabeza de Mar, Chile (ANSP 101444); Ushuaia (ANSP 316762); Malvinas Is. (ANSP 277535 and 277538); Cape Fairweather, Santa Cruz province, Argentina (ANSP 78080); Straits of Magellan (ANSP 36241 and ANSP 366497); Puerto San Julián (ANSP 312324); Santa Cruz River (ANSP 101445); Puerto Gallegos (ANSP 312319); Golfo San Jorge (ANSP 178645); Puerto Madryn, Chubut (ANSP 170471); Puerto Parry, Isla de los Estados, 54°46′ S, 64°23′ W (ANSP 402810); mouth of Santa Cruz River (ANSP 88536); Punta Arenas (ANSP 88549); Puerto Madryn (ANSP 170474); Punta Arenas, Chile (ANSP 199711).

Distribution: *Trophon geversianus* has the widest geographic range of all species of *Trophon,* i.e., from Buenos Aires province to Burdwood Bank in the southwestern Atlantic, Tierra del Fuego and Malvinas Is., and the Magellan Strait in Chile. Literature records from around Antarctica are almost certainly wrong assignments, probably mistaking it for *Trophon nucelliformis* Oliver and Picken, 1984, *T. macquariensis* Powell, 1957, or *T. albolabratus* Smith, 1875.

Remarks: *Trophon geversianus* is the best-known species of the entire genus. The great morphological variation can be appreciated from the large number of names proposed for the different morphological variants in this species. Zaixso (1973) and Penchaszadeh (1976) both studied the egg capsules of this species but only the latter confirmed the existence of short-lived nurse eggs in the capsules.

Trophon varians is a dubious species described by d'Orbigny from material he collected in northern Patagonia (*"au sud du Rio Negro"*). This species has no lamellae, weak spiral cords, and its shell is unusually thick. Houart (1998) illustrated a paralectotype (as syntype) housed in Paris and Aguirre (1993) designated and figured the lectotype (BMNH 1854.12.4.539) from 13 syntypes from the BMNH collection. According to d'Orbigny's illustration (Plate 42, figs. 4, 5) and the lectotype and the paralectotype housed in Paris, it appears that its distinctive characters are the thickness of the shell and absence of lamellae. However, despite this difference between *T. geversianus* and these primary types of *T. varians,* the rest of the paralectotypes are very similar to other thin-shelled specimens of *Trophon geversianus* usually found exposed during low tides in northern Patagonia, Golfo San Matías and around the Valdés Peninsula. The anatomy and radula of the latter are identical to those of *T. geversianus.* The specimens with heavy shells are characteristic of the mouth of Rio Negro. Nothing is known about the anatomy and radula of these heavy specimens. Perhaps these characters may prove that it is only a local variation of *Trophon geversianus,* as it was suggested originally by d'Orbigny himself (1841: 452). D'Orbigny (1841: 452; 1839, plate 42, figs. 6–7) also described and illustrated the egg-capsules from what he supposed were *T. varians.* The illustration agrees better with capsules of *Urosalpinx haneti* (Petit, 1856).

Trophon plicatus (Lightfoot, 1786)

(Figures 22–42)

Le Sabot Magellanique Favanne, 1780: 342, pl. 79, fig. I., *nomen nudum.*
Buccinum laciniatum Martyn, 1784: fig. 42, *nomen nudum.*
Murex plicatus Lightfoot, 1786: 104.
M. lamellosus Martyn.—Gmelin, 1791: 3536; Wood and Hanley, 1856: 133, pl. 27, fig. 100
Polyplex gracilis Perry, 1811: pl. 9, fig. 4.
Fusus laciniatus Martyn.—Reeve, 1847: spec. 14, figs. a, b, c.; Hupé *in* Gay, 1854: 168; Gould, 1861: pl. 16, fig. 278.
Trophon laciniatus Martini.—H. and A. Adams, 1853: 77, pl. 8, figs. 3 a, b.; Kobelt, 1878: 280, pl. 72, figs. 6, 7; Tryon, 1880: 143, pl. 31, figs. 330–332. Rochebrune and Mabille, 1889: H.53; Strebel, 1904: 199, pl. 3, figs. 1–8; Lamy, 1906: 3; Strebel, 1908: 37; Castellanos, 1970: 74, pl. 5, fig. 1.
?*Trophon antarcticus* Philippi, 1868: 225 (sensu Tryon 1880).
T. lacineatus Martyn. Sowerby II, 1880: pl. 404, fig. 13.
T. (Stramonitrophon) laciniatus (Martyn).—Powell, 1951: 156, fig. L, 86.
T. (Stramonitrophon) lamellosa (Gmelin).—Dell; 1971: 212.
T. plicatus (Lightfoot, 1786).—Rehder, 1967: 20; Cernohorsky, 1977: 117, fig. 18; Vokes, 1991: 7, fig.; 1991b: 9, figs. 14–16; 1992: 3, figs. 2, b, c, d.; Castellanos and Landoni, 1993: 5, figs. 16, 15, 22.

Description: Shell of medium to large size (to 50 mm), smooth, fusiform, thin, somewhat chalky; protoconch smooth of 2½ whorls; teleoconch of 6 shouldered whorls, spire less than ½ of total shell height. Spire angle about 50°; suture impressed; subsutural ramp straight, aperture small, ovoidal, interior pale brownish; anterior siphonal canal long (more than half height of the aperture), narrow, curved, open; umbilicus absent; outer lip rounded with reflected edges; inner lip curved, adpressed. Axial ornamentation of irregular, low lamellose varices in the first whorls, that become 8–10 real lamellae in the last ones. Lamellae growing over the entire whorl, but attached to the shell, sometimes curving adaxially. Lamellae ending in a peripheral spine, in some specimens growing adapically. Spiral ornamentation poorly developed to almost smooth, sometimes consisting of 6 weak cords on the base of the last whorl and the back of the siphonal channel. Regular, very weak growth lines present throughout shell.

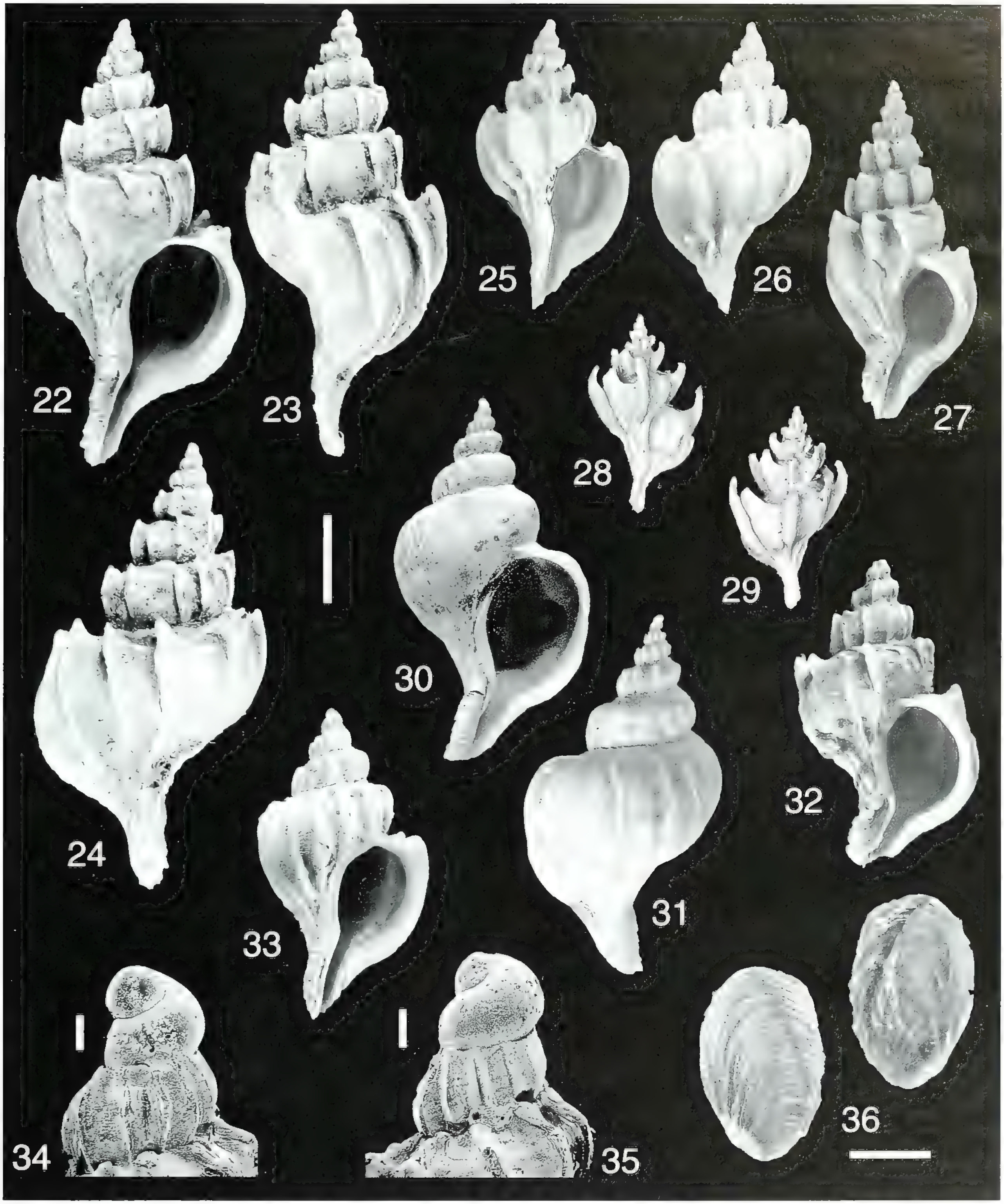
Shell ultrastructure composed of two layers; innermost layer (25% of shell thickness), composed of colabrally aligned crossed lamellar aragonite, outer layer thick (75% of shell thickness) with amorphous calcite (Figure 42).

Operculum oval, with terminal nucleus. External surface covered by concentric, irregular, growth lines. Inner surface attachment area with two or three horseshoe-shaped scars, glazed rim present in all specimens (Figure 36).

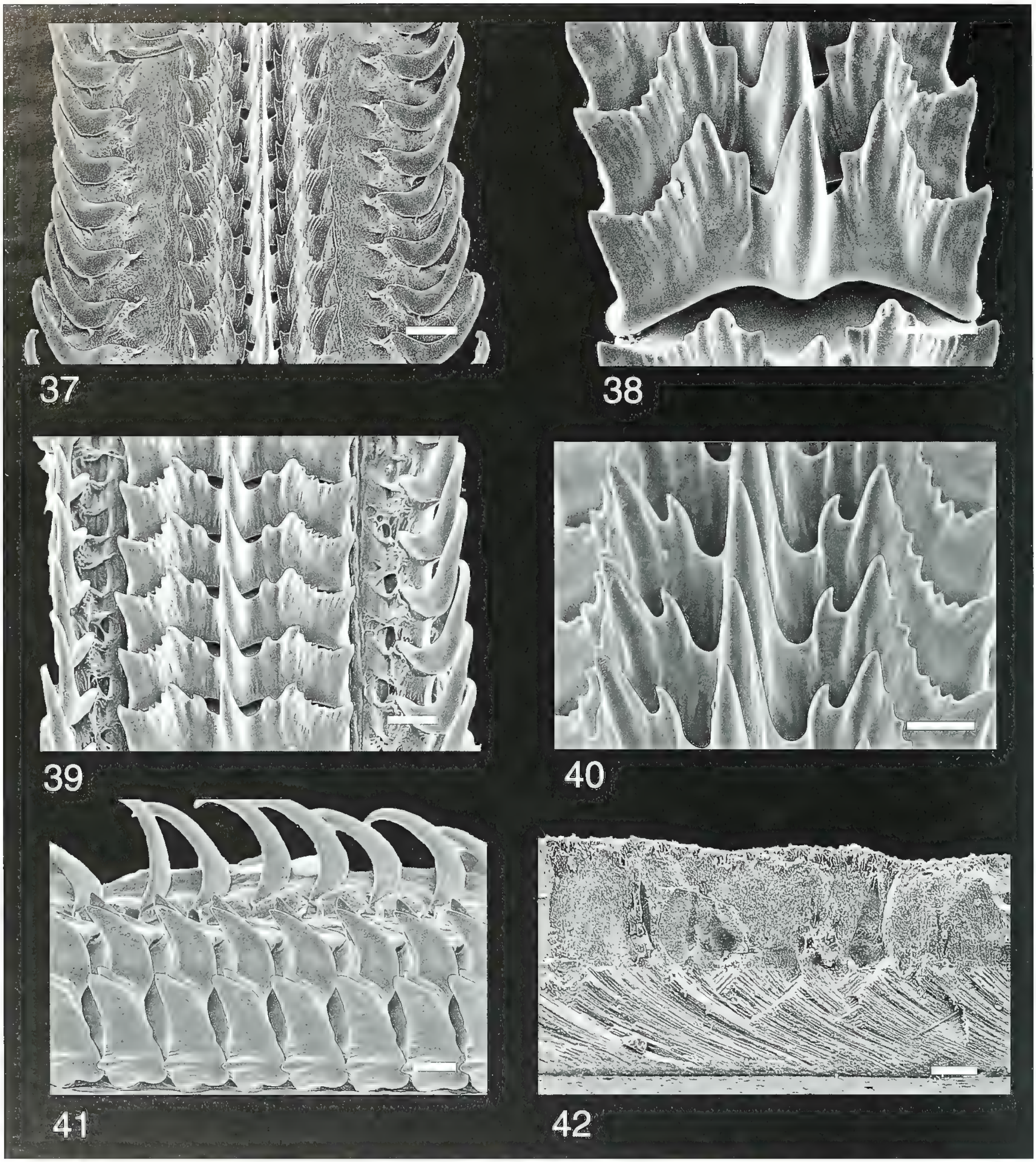
Animal of medium size relative to shell. Mantle large, mantle roof thin. Cephalic tentacles broad in basal half, flat, blunt, with rounded large black eyes in the middle; mantle edge thickened, smooth; pallial organs arranged as in other rachiglossans; brown osphradium less than half of ctenidium length, slightly asymmetrical, with 50–55 leaflets per side; ctenidium as wide as osphradium, containing triangular leaflets. Hypobranchial gland brownish and inconspicuous, rectum to the right of hypobranquial gland.

Proboscis pleuroembolic, long, broad. Radular ribbon extending beyond rear of buccal mass, long (0.69 × aperture height vs. 0.78 × aperture height in *Trophon geversianus*). Esophagus loops beneath buccal mass, where esphagus receives embedded ducts of salivary glands anterior to a small Leiblein valve. Esophagus curving distinctly and running along entire side of gland of Leiblein. Esophageal glands (*"Glandule framboise"*) whitish in color, posterior to nerve ring slightly marked on the external side of the esophagus. Large salivary glands enveloping Leiblein valve and accessory salivary glands. Accessory salivary glands distinctly large, sometimes dark-colored, tubular, compact, coiled, embedded in salivary glands. Gland of Leiblein conspicuous, brown, ending in a medium size blind duct and very small ampulla.

Radula rachiglossan with rachidian teeth wide (~150 μm), central cusp thin, large; lateral cusps wider and slightly shorter than central cusp, with inner edge straight; with sharp straight denticle in upper third of internal edge of lateral cusp, external edge with 6 very



Figures 22–36. *Trophon plicatus* (Lightfoot, 1786). **22–24.** MACN-In 36033, Bahia Ensenada, Ushuaia, Tierra del Fuego, Argentina. **25–26.** MACN-In 9032-16, Comodoro Rivadavia, Chubut province, Argentina. **27.** BMNH 19990384, 45°55.219′ S, 73°39.522′ W. intertidal. Islet NE shore of Isla Huemules, Golfo Elefantes, Chile. **28–29.** AK 133035, Station WS788 Discovery, 45°07′ S, 65°W. **30–31.** MACN-In 36034, Punta Peñas, San Julián, Santa Cruz province, Argentina. **32.** Same lot as Figure 6. **33.** MLP 27202, Bahia Golondrina, Ushuaia, Tierra del Fuego. **34–35.** Two protoconchs, scale bars = 400 μm. **34.** USNM 870535 52°30′ S. 67°14′ W. in 82 m. **35.** USNM 901620. 53°35′ S. 69°45′ W. 1 D. R/V Hero Cruise 692. Sta. 404. 37–46 m. **36.** MLP 27232, operculum, external (left) and internal (right) views, scale bar = 1 cm. Scale bar for all shells = 1 cm



Figures 37–42. *Trophon plicatus* (Lightfoot, 1786). **37.** MLP 27232, Dorsal view of radular ribbon. Scale bar = 50 μm. **38.** MLP 526, San Julián, Punta Peñas, 1 March 1924, rachidian teeth. Scale bar = 30 μm. **39.** Variations of rachidian teeth, Rocamora, Ushuaia, 1 A, 8–10 m (MACN-In 36053). Scale bar = 30 μm. **40.** MLP 27202, Bahia Golondrina, Ushuaia, Tierra del Fuego, Argentina, detail of the rachidian teeth. Scale bar = 20 μm. **41.** Same specimen as 40, lateral view of rachidian teeth, scale bar = 30 μm. **42.** USNM 870535, 52°30′ S, 67°14′ W, in 82 m, shell ultrastructure, fracture surface commarginal. Scale bar = 30 μm.

well defined denticles, always present. Base of rachidian tooth sinuous, sliding beneath base of next tooth. Marginal area with single conspicuous cusp. Lateral teeth with single, long and narrow cusp, slightly attached basal plate. Cusps of rachidian teeth pyramid-like in lateral view (Figures 38–40).

Male and female organs as in *Trophon geversianus* (see Harasewych, 1984).

Type Locality: Islas Malvinas.

Type Material: Probably lost. According to Dance (1966) part of the material from the Portland Catalogue is in London (BMNH), however this is not the case of *T. plicatus*.

Additional Material Examined: 52°30′ S, 67°14′ W, 2 D, R/V Eltanin Cruise 11, Sta. 980, 14 February 1964, 82 m (USNM 870535); 53°35′ S, 69°45′ W, 1 D, R/V Hero Cruise 692, Sta. 404, 37–46 m (USNM 901620); 52°56′ S, 75°00′ W, 1 D, R/V Eltanin Cruise 11, Sta. 958, 5 February 1964, 92–101 m (USNM 870423); 53°06′ S, 67°04′ W, 3 D, R/V Hero Cruise 702, Sta. 450, 5 March 1970, 86 m (USNM 901622); 53°39′24″ S, 70°55′30″ W, 1 D, R/V Hero Cruise 702, Sta. 467, 25 April 1970, 24 m (USNM 901623); 52°35′ S, 65°08′ W, 1 D, R/V Eltanin Cruise 11, Sta. 976, 13 February 1974, 128 m (USNM 870525); 46°04′ S, 83°55′ W, 1 A, R/V Eltanin Cruise 25, Sta. 326 9 October 1966, 298 m (USNM 901621); 53°48.7′ S, 70°24.1′ W, 1 D, R/V Hero Cruise 702, Sta. 489, 29 April 1970, 13–18 m (USNM 901624); 53°32′ S, 64°57′ W, 2 A, R/V Eltanin Cruise 11, Sta. 974, 12 February 1964, 119–124 m (USNM 881960); 53°39′ S, 70°55.5′ W, 1 A, R/V Hero Cruise 702, Sta. 466, 20 m (USNM 901754); Bahia Golondrina, Ushuaia, 1 A, (MLP 27202); Rocamora, Ushuaia, 1 A, 8–10 m (MACN-In 36053); Bahía Ensenada, Ushuaia, Tierra del Fuego, (MACN-In 36033); 45°07′ S, 65°W, 1 A, Discovery Station WS788, 13 December 1931, 82–88 m (AK 133035) illustrated in figs. 28–29; Comodoro Rivadavia, 17 D (MACN-In 9032-16); 54°34′ S, 64°00′18″ W, 1 D, 1 A, R/V Hero Cruise 715, Sta. 870, 24 October 1971, 84 m (USNM 881128); Bahía Buen Suceso, 1 A, 23 October 1941, (MLP27230); Cabo Colnett, Isla de los Estados, 1 A, R/V Hero Cruise 712, Sta. 853, 20 October 1971, 91 m (USNM 869720); 2 D, 78 m (USNM 96176); Orange Harbor (USNM 5676); Paso Richmond, Tierra del Fuego 55 m, (MACN-In 24940); 55°7′ S, 66°33′ W, 82 m (MACN-In 23938); Tierra del Fuego (MACN-In 5240-2); Punta Peñas, San Julián, Santa Cruz province, Argentina, 4 A (MLP 27232); Punta Peñas, San Julián, Santa Cruz, Argentina, 1 A (MLP 27212); Puerto San Julián, Santa Cruz province, Argentina (49°15′ S, 67°39′ W), 4 A, 2–3 m (MACN-In 36034); 45°55.219′ S, 73°39.522′ W intertidal, Islet NE shore of Isla Huemules, Golfo Elefantes, Chile (BMNH 19990384).

Distribution: This is a typical species from the Magellanic province. It has been recorded from Peninsula Valdés to Tierra del Fuego in Argentina and Chile to 49°S in the north (Reid and Osorio, 2000).

Remarks: The authorship of the name according to Dance (1962) and Rehder (1967) should be credited to J. Lightfoot, the anonymous compiler of the "Catalogue" where the name was used for the first time, not to Solander.

There is an interesting range of conchological variation in *Trophon plicatus*, from almost smooth specimens to highly lamellate. However, the profile is always slender. *Trophon bahamondei* McLean and Andrade, 1982, is a morphologically similar species, with peripheral spines and shallow lamellae. On the other hand, *T. bahamondei* has no spiral ornamentation and *Trophon plicatus* has 6 weak cords on the base of the last whorl and the back of the siphonal canal.

The gross anatomy is that customary for most Patagonian Trophoninae. However, a distinctive anatomical feature is the morphology of the accessory salivary glands, which are compact, tubular, somewhat coiled and large, and completely embedded in the salivary glands. Most Patagonian Trophoninae (e.g., *T. bahamondei* as well as *T. geversianus*), have small, kidney-shaped, accessory salivary glands.

Radular features of *T. plicatus* are clearly different from *T. bahamondei* (see Figures 26–27). The latter has a distinctive small cusp on the outer margin of the lateral cusp on the rachidian teeth. In addition, the rachidian base is thinner and wider.

Trophon antarcticus Philippi, 1868, is probably a synonym according to Tryon (1880); however, the type material is missing and the description is rather obscure.

Powell (1951) described the subgenus *Stramonitrophon* to include only *T. plicatus* [(as *T. laciniatus* Martyn, *nomen nudum* rejected by Opinion 456 (ICZN, 1957)] a species with *Stramonita*-like radula, i.e., rachidian teeth with three cusps, where the marginal side of the lateral cusps bears several denticles. This radula illustrated by Powell (1951: 194, fig. L, 86) was dissected from the specimen illustrated in figs. 28–29. The radular morphology of *T. plicatus* is different from that of *T. geversianus*. However, *Coronium coronatum* (Penna-Neme and Leme, 1978) and *T. acanthodes* Watson, 1882, bear the same denticles on the lateral cusps of the rachidian teeth. This appears to be a common feature in several Trophoninae from the southwestern Atlantic.

The shell of *Trophon iarae* Houart, 1998, shows some similarity with some specimens of *T. plicatus*. It was based on only two specimens collected by fishing boats apparently from Brazil and off Uruguay. The anatomy and soft parts of *T. iarae* remain unknown. The radula apparently has been illustrated by Calvo, 1987 (although according to Houart, 1998: 127, there is no certainty about the identity of the specimen from where this radula was taken). In any event, this illustration does not allow for a detailed comparison with other species. Further comments about the validity of this species or its affinity with other species of *Trophon* mostly depends on anatomical data which are not available.

Houart (1998: 127) mentioned the specimen of *T. plicatus* illustrated by Cernohorsky (1977) from Lively Is. (Malvinas Is.) as belonging to his new species, *T. iarae*. However, Cernohorsky's specimen could be easily included in the range of geographic distribution and morphological variation of *T. plicatus*. He also illustrated two specimens of *T. patagonicus* as *T. plicatus* (Figures 8–10 in Houart, 1998).

Trophon patagonicus (d'Orbigny, 1839)
(Figures 43–65)

Murex patagonicus d'Orbigny, 1839: pl. 62, figs. 2–3; 1941: 452 *non Fusus patagonicus* Sowerby, 1846 (=*Trophon*).
Trophon necocheanus Ihering, 1907: 404, pl. 16, fig. 106.
Trophon laciniatus (Martyn).—Carcelles, 1946: 70–72, figs. 6 a, b, 7 a–d, 8.
Trophon plicatus (Lightfoot, 1786).—Rios, 1985: 88, pl. 31, fig. 386; 1994: 114, pl. 37, fig. 483; Houart, 1998: 130, figs. 8–10 *non* Lightfoot, 1786.

Description: Shell large (up to 72 mm), biconic, heavy, chalky or glossy white, sometimes brownish grey, opaque; protoconch smooth of 2¼ (~2.0 × 1.5 mm) asymmetrical whorls; transition to teleoconch well defined; teleoconch of 7 shouldered whorls, spire less than ⅓ of total shell height. Spire angle about 70°; suture impressed; aperture oval, interior glossy white; anterior siphonal canal rather long for the genus (half height of aperture), narrow, open; pseudoumbilicus deep and widely open; outer lip reflexed. Axial ornamentation of irregular strong, sharp lamellae covering entire whorl surface, numbering 9–12 in the last whorl. Continuum of morphologies present from completely smooth shells with no axial ornamentation (Figures 53–56), to some incipient lamellae along peripheral keel (Figures 48–50), to strongly developed lamellae (Figures 43–45). Spiral ornamentation missing, except on first teleoconch whorl which bears 3–4 invariably present spiral cords (Figures 62–63). Irregular growth lines present throughout shell surface. Some uncommon specimens have about three weak greenish or dark spiral lines on the last three or four whorls.

Shell ultrastructure arranged invariably of two layers; innermost layer (25% shell thickness), composed of crossed lamellar aragonite, outer layer very thick (75% shell thickness) of amorphous calcite (Figure 61).

Operculum oval, with terminal nucleus. External surface covered by concentric, irregular, growth lines. Inner surface attachment area with two or three horseshoe-shape scars.

Rachiglossan radula with rachidian teeth distinct, central cusp thin, large; lateral cusps slightly shorter than central cusp, sharp straight denticle in the upper third of the internal edge of the lateral cusp, external edge of lateral cusps smooth. Base of rachidian tooth sinuous, sliding beneath base of next tooth. Marginal area with single conspicuous cusp. Lateral teeth with single, long and narrow cusp, attached to basal plate (Figures 64–65).

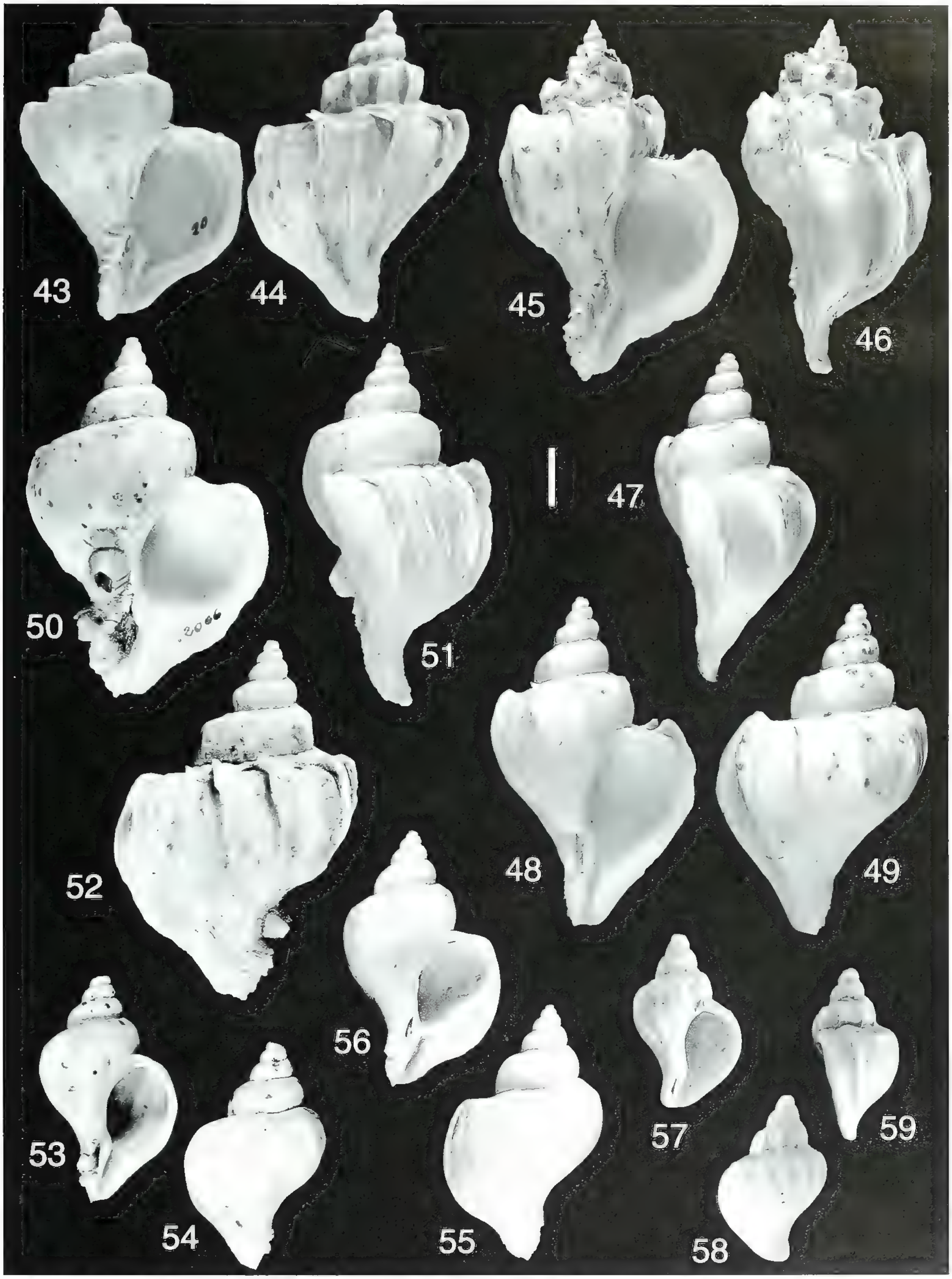
Penchaszadeh (1976) described the egg capsules of *T. patagonicus* [identified as *T. laciniatus* (Martyn) and *T. varians* (d'Orbigny)].

Type Material: Four syntypes are housed in the Natural History Museum, London under the number 1854.12.4.538, from "*Baie de San Blas, Patagonie*". One of them is herein illustrated (Figures 43, 44).

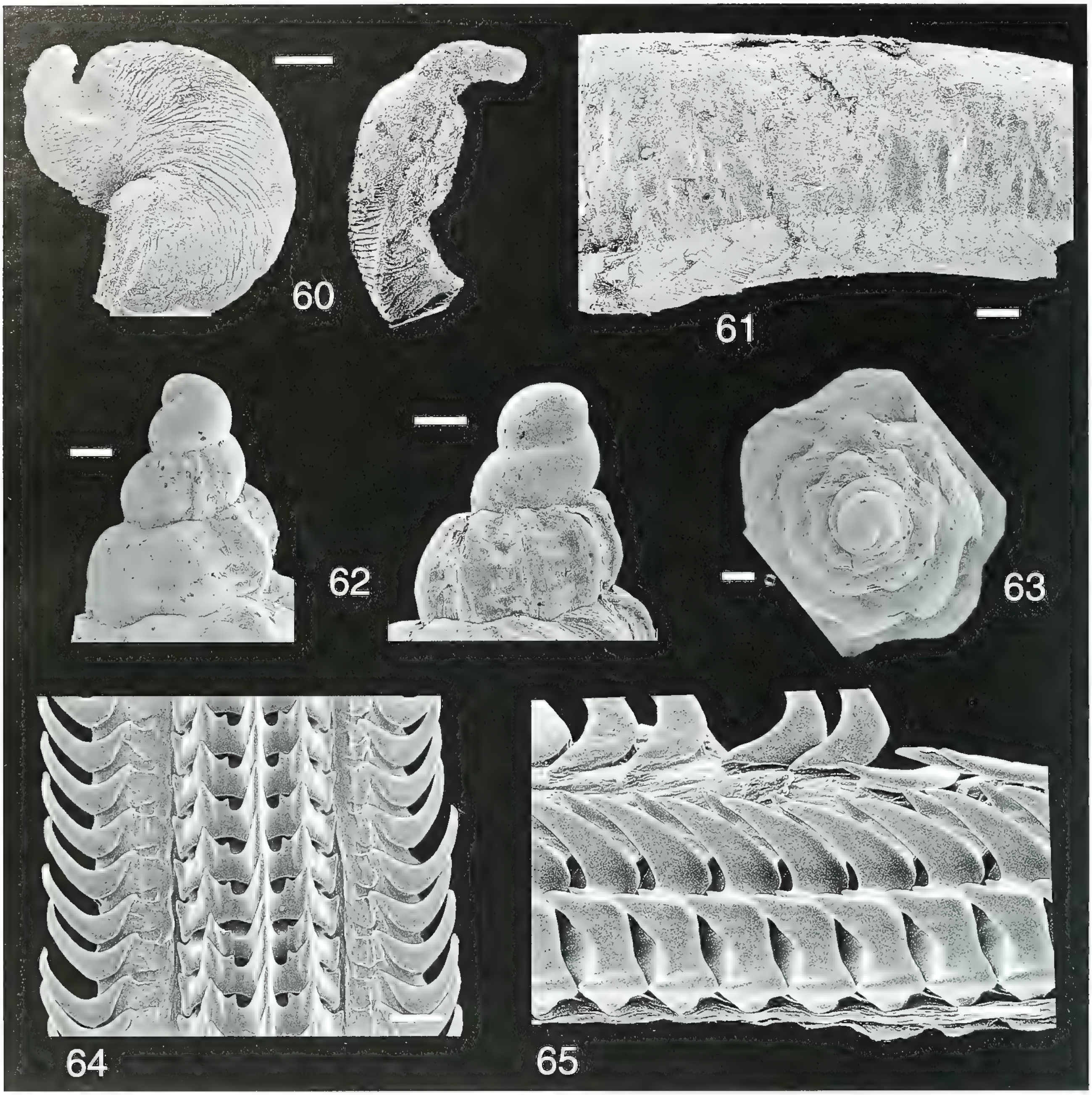
Additional Material Examined: Puerto Quequén, Buenos Aires province, 3 A (MLP 26309); Miramar, Buenos Aires province, 1 A, 1 D (MLP 417); Necochea, Buenos Aires province, 3 A, 30 m (AMNH 173640); Necochea, 1 A, 30 m (AMNH 181220); Puerto Quequén (ANSP 236034 and 236032); 18 miles off Puerto Quequén, 4 D (MACN-In 20441); 37°20′ S, 56°50′ W, 4 D, 55 m (MACN-In 15104); Mar del Plata, Buenos Aires province, Argentina (MACN-In 10289; 12902; 2 D, 45 m, 9361-51; 7 D, 11374; 11587; 11587-1; 4 D, 10249; 10320; 2 D, 10742; 11118; 3 D, 12066; 3 A, 25775; 9361-53; 5 D, 10290; 10190; 10248; 12216); 36°25′ S, 54°38′ W, 54 m, 1 D (MACN-In 23426); 34°40′ S, 52°18′ W, 1 A, 100 m (MACN-In 23491); Fondos de Querandí, Buenos Aires province, 5 A (MACN-In 14334); 25 miles off Puerto Quequén, 22 D (MACN-In 21138); Fondos de Querandí, 1 D (MACN-In 25774); Necochea, 2 D, 40–50 m (USNM 710024); Mar del Plata, 4 D, 1 D (USNM 568240; USNM 346826); off Necochea, 1 A, 30 m (USNM 876123, Bledsoe collection); Mar del Plata, 1 D (USNM 363768); Uruguay, 1 D (USNM 346786); 1 D, 36°30′ S, 54°44′ W, 26 m (MACN-In 24259).

Distribution: This species is common on the mussel banks off southern Uruguay and Buenos Aires province in depths of 25–40 m.

Remarks: *Trophon patagonicus* is a variable species, endemic to the littoral of Buenos Aires province and the Uruguayan coast. The species has had quite a confusing taxonomic history. Those specimens with well-developed lamellae have been usually identified as *T. plicatus*, and those with smooth shells and no ornamentation as *T. geversianus* or *T. varians*. Specimens collected on the same location were identified as two different species according to the presence or absence of lamellae. However, some specimens (Figures 50–52) are clearly intermediate forms, and no another anatomical feature seems to separate them. There is no reason to consider them as two different species. The whole lot of specimens studied by Carcelles (1946) shows clearly that he confused d'Orbigny's species with *T. plicatus*. Such a mistake was also made by Rios (1985, 1994) and several other authors. *Trophon plicatus* is a typical magellanic species with a thinner and more cylindrical profile, medium size (never reaching more than 50 mm high). Specimens of *T. plicatus* here identified were never collected at latitudes north of 45°S. Its protoconch is always smooth and with fewer whorls, and the lamellae along the keel usually develop into strong triangular projec-



Figures 43–59. *Trophon patagonicus* (d'Orbigny, 1839). **43–44.** Syntype BMNH 1854.12.4.538, Bahía San Blas, Argentina. **45–46.** MACN-In 36040, Puerto Quequén, Buenos Aires. **47–49.** MLP 417, Miramar, Buenos Aires, in 54 m. **50–52.** MACN-In 12066, Mar del Plata, Buenos Aires. **53–56.** MACN-In 36031, Puerto Quequén. **57–59.** MACN-In 21047, "Carmen de Patagones" Buenos Aires. Scale bar for all figures = 1 cm.



Figures 60–65. *Trophon patagonicus* (d'Orbigny, 1839). **60.** Penis, critical-point dried. Lateral and frontal view. Scale bar = 1000 μm. **61.** Shell ultrastructure, fracture surface commarginal. Scale bar = 300 μm. **62–63.** MACN-In 11374, protoconch, three views, Mar del Plata, Buenos Aires province. Scale bar for all figures = 600 μm. **64.** Dorsal view of radular ribbon. Scale bar = 50 μm. **65.** Lateral view of rachidian teeth. Scale bar = 50 μm.

tions approximately parallel to the coiling axis. The aperture is larger and subcircular in *T. patagonicus*, very different from the smaller and almost circular one on *T. plicatus*. *Trophon geversianus* usually has strong spiral ornamentation on the entire shell surface, a feature also observed in *T. varians*.

Ihering (1907) described *T. necocheanus* based on (Quaternary?) specimens collected at Necochea, Buenos Aires province, Carmen de Patagones, Buenos Aires province, and Sierra Laziar, Santa Cruz province ("*Formation araucanienne*"). Most of the type material is lost, but the remaining types fall within the range of variation of *T. patagonicus*. One of the specimens, from a lot of three, with uncertain locality (MACN-In 21047, relabeled "Carmen de Patagones?") is here illustrated (Figures 57, 59). This specimen was acquired through an exchange with Museu Paulista, São Paulo, Brazil (where Ihering worked for most of his professional life) and is part of the original type series. All of the specimens fit well in the original description of *T. patagonicus* and there is no doubt that is the same species described by d'Orbigny.

Sowerby II (2nd of name) described in 1846 *Fusus patagonicus* from the Tertiary of San Julián (Santa Cruz province, Argentina), a species that clearly belongs in *Trophon*. Therefore, as the two species are quite distinct, d'Orbigny's name has priority over Sowerby's (Griffin and Pastorino, 2005).

Trophon acanthodes Watson, 1882
(Figures 66–78)

Trophon acanthodes Watson, 1882: 386; 1886: 166, pl. 10, fig. 6; Cernohorsky, 1977: 112, fig. 9 (holotype); Pain, 1980: 8, fig.; Rios, 1985: 88, pl. 31, fig. 388; Castellanos, 1986: 22, fig.; Castellanos and Landoni, 1993: 8, pl. 2, fig. 28.
Fusus acanthodes (Watson).—Carcelles, 1947: 12, pl. 2, figs. 1, 2; pl. 3, figs. 3, 4 (not figs. 5, 6 which is *Coronium coronatum*).
Pagodula acanthodes (Watson).—Kaicher, 1980: fig. 2599.
"Fusinus" acanthodes (Watson).—Calvo, 1987: 153, fig. 127.
"Trophon" acanthodes Watson.—Rios, 1994: 37, pl. 37, fig. 486.

Description: Shell large, about 125 mm high, thick, slender in profile, chalky white; protoconch worn in all specimens; teleoconch of 7 shouldered whorls; spire less than ⅓ of total shell height. Spire angle about 45°; suture impressed, subsutural shelf oblique, somewhat convex, aperture small, subcircular, interior glossy white; anterior siphonal canal very long (longer than aperture height) deep, straight or curved, always open; outer lip rather reflected, rounded, inner lip adpressed. Axial ornamentation of 12–15 regularly spaced, axial lamellae, slightly raised, almost attached along the entire whorl, producing open, conspicuous, regularly spaced spines at periphery; spines becoming more closely packed on last whorl. Spiral ornamentation of 4–5 weak rounded threads on the lower part of the first whorls, becoming more than 20 in last one. Growth lines present throughout shell, producing wrinkly surface by intersection with spirals.

Operculum elliptical, nucleus terminal, older specimens tear-shaped. External surface covered by concentric, irregular, growth lines. Inner surface with a conspicuous marginal rim; attachment area covering almost the whole operculum but the rim; horseshoe-shaped scars present.

Rachidian teeth wide (~130 μm), central cusp large; lateral cusps wider and shorter than central cusp, inner edge with an almost obsolete denticle (particularly in adult specimens), external edge with 5–6 denticles decreasing in size towards the edge. Base of rachidian tooth curved, somewhat sinuous, sliding beneath base of next tooth. Marginal area with single cusp. Lateral teeth with single, long cusp, slightly attached basal plate.

Shell ultrastructure composed of two layers: innermost layer (55% of total thickness of shell) composed of crossed lamellar aragonite, outer layer (45%) of amorphous calcite.

Animal as in other *Trophon* species but with some size differences. Tentacles long and well defined, joined at base; eyes deeply marked. Salivary and accessory salivary glands as in *T. plicatus*. Osphradium a bit more than one third of ctenidium length, asymmetrical, with about 112 leaflets, ctenidium with about 250 leaflets twice as large as osphradium. Typical pleuroembolic proboscis, shorter than in *T. geversianus*, valve of Leiblein also smaller; gland of Leiblein large with a long blind duct. Radula long; digestive tract with the usual loop on the left side of the gland of Leiblein, before the duct to the gland.

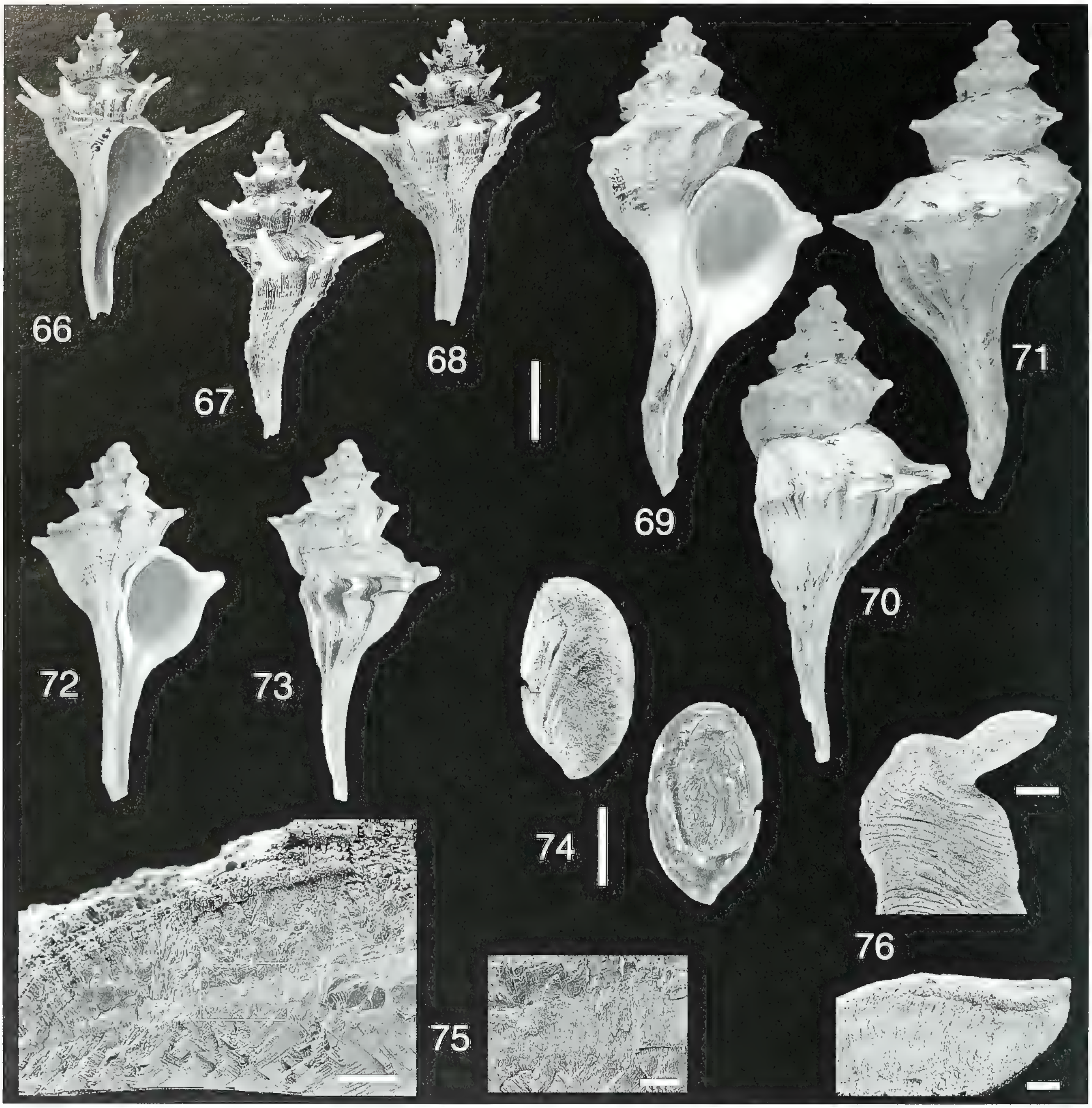
Male and female organs similar to *T. geversianus*.

Type Material: BMNH 1887.2.9.568, holotype 50°8′30″ S, 74°41′ W, 229 m (illustrated by Cernohorsky, 1977, fig. 9).

Additional Material Examined: 52°53′ S, 74°05′ W, 3 D, R/V Eltanin Cruise 23, Sta. 1605, 1 April 1966, 522–544 m (USNM 901756); off Mar del Plata, 5 A, January 1962 (MLP 26283); 52°41′ S, 74°35′ W, 1 D, R/V Eltanin Cruise 21, Sta. 290, 6 January 1966, 188–247 m (USNM 870115); 51°56′ S, 56°39′ W, 1 D, R/V Eltanin Cruise 7, Sta. 557, 14 March 1963, 855–866 m (USNM 870345); 52°52′ S, 75°18′ W, 1 D, R/V Eltanin Cruise 21, Sta. 288, 119–329 m (USNM 901758); 52°51′ S, 74°13′ W, 1 D, R/V Eltanin Cruise 21, Sta. 291, 523–539 m (USNM 901757); 52°53′ S, 74°05′ W, 2 D, R/V Eltanin Cruise 23, Sta. 1605, 1 April 1966, 522–544 m (USNM 897615); 40°15′ S, 57°40′ W, 1 A (MACN 18425); 40°03′ S, 57°00′ W, 1 D, 50 fathoms (91.5 m) (MACN 15699); 30 miles off Mar del Plata (ANSP 262989 and 236028); off Mar del Plata, 1 A, 2 D (MACN 17671 and 16449); 39°26′ S, 56°40′ W, 1 A, 1 D, 90 m (MACN 17040); 39°02′ S, 56°46′ W, 1 A, 1 D; East of Punta Médanos (39°–39°30′ S), 4 D, 50 fathoms (91.5 m) (MACN 14386); 39°55′ S, 57°50′ W, 1 D, 51 fathoms (93 m); 38°25′ S, 56°30′ W, 3 D (MACN 16798); 39°35′ S, 57°10′ W, 1 A, 1 D (MACN 18342); 39°50′ S, 57°18′ W, 4 A, 52 fathoms (95 m) (MACN 21741); 39°00′ S, 57°10′ W, 2 D, 45 fathoms (82 m) (MACN 15216); 37°15′ S, 54°50′ W, 1 A, R/V Aldebaran, March 2000, commercial otter trawl, 111 m (MACN-In 36032); 36°37′ S, 54°14′ W, 1 A, R/V Aldebaran, March 2000, otter trawl, 104 m (MACN-In 36031); 39°02′, 57°02′ W, 2 D, 46 fathoms (84.1 m) (MACN-In 25118); 37°35′ S, 54°55′ W, 1 D, 105 fathoms (192 m) (MACN-In 25165-2).

Distribution: Off Rio Grande do Sul state in Brazil (Rios, 1994), Uruguay, to Tierra del Fuego, Argentina.

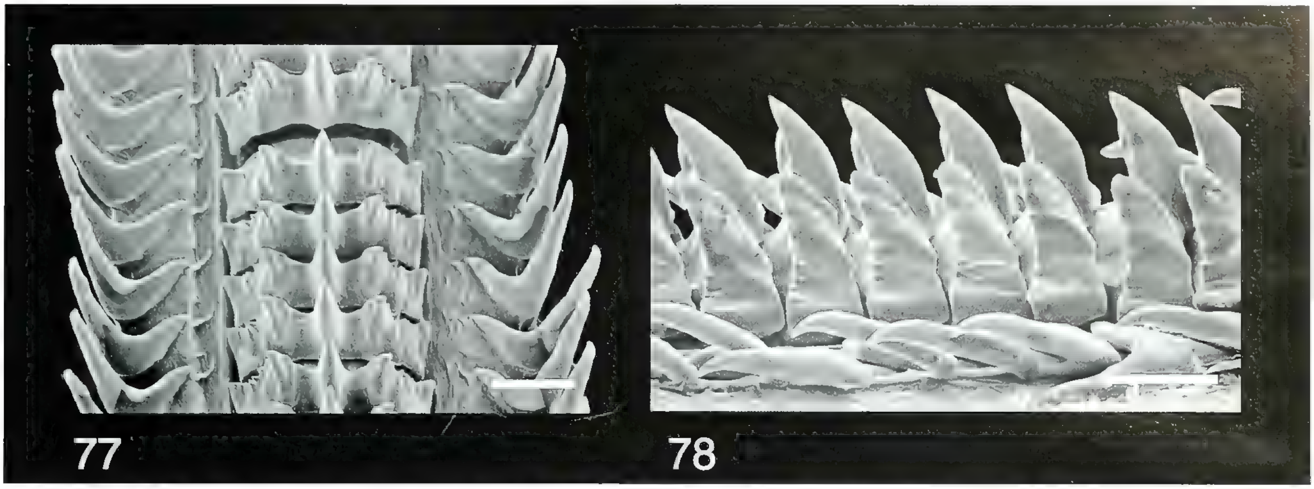
Remarks: The shell of *Trophon acanthodes* is somewhat similar to that of *Coronium coronatum*, which in fact could be granted that generic position. The operculum and the radula are different in both species. The operculum is somewhat triangular in *Coronium* with a weak rim instead of the characteristic thicker one of the *Trophon* species. The radula of *Trophon acanthodes* presents the intermediate cusp between the central and the lateral



Figures 66–76. *Trophon acanthodes* Watson, 1882. **66–68.** MACN-In 25118, 39°02′, 57°02′ W, 46 fathoms (84.1 m). **69–71.** MACN-In 36031, 37°15′ S, 54°50′ W in 111 m. **72–73.** MLP 26283, Mar del Plata. Scale bar for all shells = 1 cm.**74.** Two views of the operculum of the specimen in Figures 69–71. Scale bar = 1 cm. **75.** Ultrastructure of the shell. Scale bar = 200 µm; detail, large quadrangle. Scale bar = 50 µm. **76.** Penis, critical-point dried (scale bar = 600 µm) with detail of the efferent conduct (scale bar = 150 µm).

one of the rachidian teeth almost obsolete, while in *Coronium coronatum* it is very conspicuous. Castellanos (1986) drew a stereotyped radula of *T. acanthodes* where denticles are wrongly placed on the margin of the rachidian tooth instead of the inner edge of the lateral cusp.

The protoconch in *Coronium* is multispiral and extremely pointed, distinctive of the genus. All the studied specimens of *T. acanthodes* are worn; however, some of them show the sinuated line of a typical *Trophon* protoconch.



Figures 77–78. *Trophon acanthodes* Watson, 1882. **77.** MLP 26283, off Mar del Plata Radula of a large specimen, frontal view. Scale bar = 50 µm. **78.** Lateral view. Scale bar = 50 µm.

Trophon pelseneeri Smith, 1915
(Figures 79–93)

Trophon pelseneeri Smith, 1915: 92, pl. 2, figs. 6, 7; Rios, 1994: 115, pl. 38, fig. 484; Houart, 1991: 33.
Trophon sp.—Carcelles, 1944: 253.
Trophon orbignyi Carcelles, 1946: 81, pl. 12; Castellanos, 1970: 73, pl. 5, fig. 6.

Description: Shell small to medium in size (up to 35–40 mm), fusiform, slender, chalky, pinkish with 2 weak, diffuse reddish bands along the edge of last whorl lamellae; protoconch symmetrical, cylindrical, smooth, of 2½ whorls; teleoconch of 7 rectangular whorls, spire ⅓ of total shell height. Spire angle about 45°, suture impressed, subsutural shelf straight, aperture small, circular, interior glossy white; anterior siphonal canal long, open, straight, with the tip adaxially curved, equal to aperture height; umbilicus slightly open, sometimes only a narrow slit; outer lip reflexed to form lamellae; inner lip curved, with white adpressed callus. Axial ornamentation of 9–11 regular, low lamellae, covering entire whorl surface; lamellae forming a back-turned spine at periphery. Spiral ornamentation of 2 to 3 very weak threads in first whorls becoming more than 7 in last one, sometimes only visible along edge of last whorl lamellae. Siphonal fasciolae slightly oblique, always present.

Operculum triangular (tear-shaped), with terminal nucleus. External surface covered by irregular growth lines. Inner surface attachment area with horseshoe-shaped scars; glazed rim weak but present (Figure 88).

Radula rachiglossate with rachidian teeth wider than high, central cusp thin, in a different plane than laterals; lateral cusps wider and shorter than central cusp, with inner edge oblique; sharp straight denticle in the upper third of the internal edge of the lateral cusp, external edge with almost obsolete denticles numbering 3–4. Base of rachidian tooth slightly sinuous, sliding beneath base of next tooth. Marginal area with single conspicuous cusp. Lateral teeth with single, long and narrow cusp, slightly attached basal plate (Figures 92–93).

Type Material: [*T. pelseneeri*] BMNH 1915.4.18.276–7, two syntypes from west of Malvinas Is. in 229 m (Figures 79–82) and [*T. orbignyi*] MACN-In 24421, Puerto Quequén, Buenos Aires, holotype (Figures 83–85) and 10 paratypes.

Additional Material Examined: Macaé, Rio de Janeiro, Brazil, August 1969, 2 A, 55 m (USNM 846550); Macaé, Rio de Janeiro,, Brazil, 1 A, 30 m (AMNH 187586); Rio de Janeiro, Brazil, 1 A (AMNH 241045); off Rio de Janeiro, Brazil (ANSP 289807); 34°48′7″ S, 54°21′9″ W, 1 A, R/V ALDEBARAN, Cruise 9901, Sta. 25, 27 January 1999, 25 m, with Piccard trawl (MNHNM 15400).

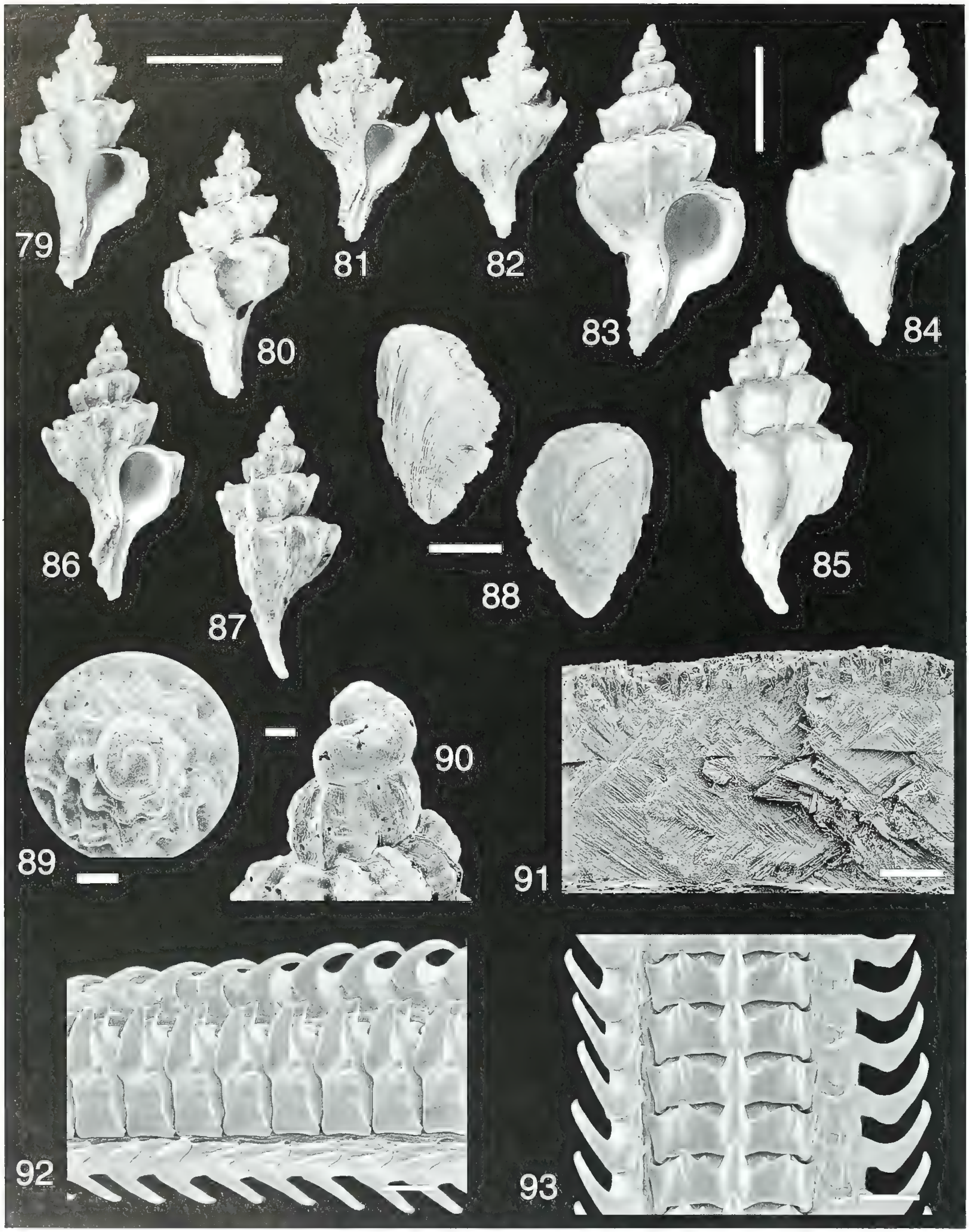
Distribution: Rio de Janeiro, Brazil, to Uruguay and Buenos Aires province, Malvinas Is. Rios (1994) cited it from dredgings from 55 to 225 m off the Brazilian coast.

Remarks: This is a rare species occasionally collected by fishermen on the mussel banks off Buenos Aires province. It was originally described from Sta. 38 of the British Antarctic ("Terra Nova") Expedition, west of Malvinas (Falkland) Islands in 125 fathoms depth. However, together with this species, the author mentioned several others not reported before or since from this latitude, but which occur at Station 42 of the same expedition, off Rio de Janeiro. This leads to the supposition that the material from these stations could have been mixed up (Scarabino, 2003: 199).

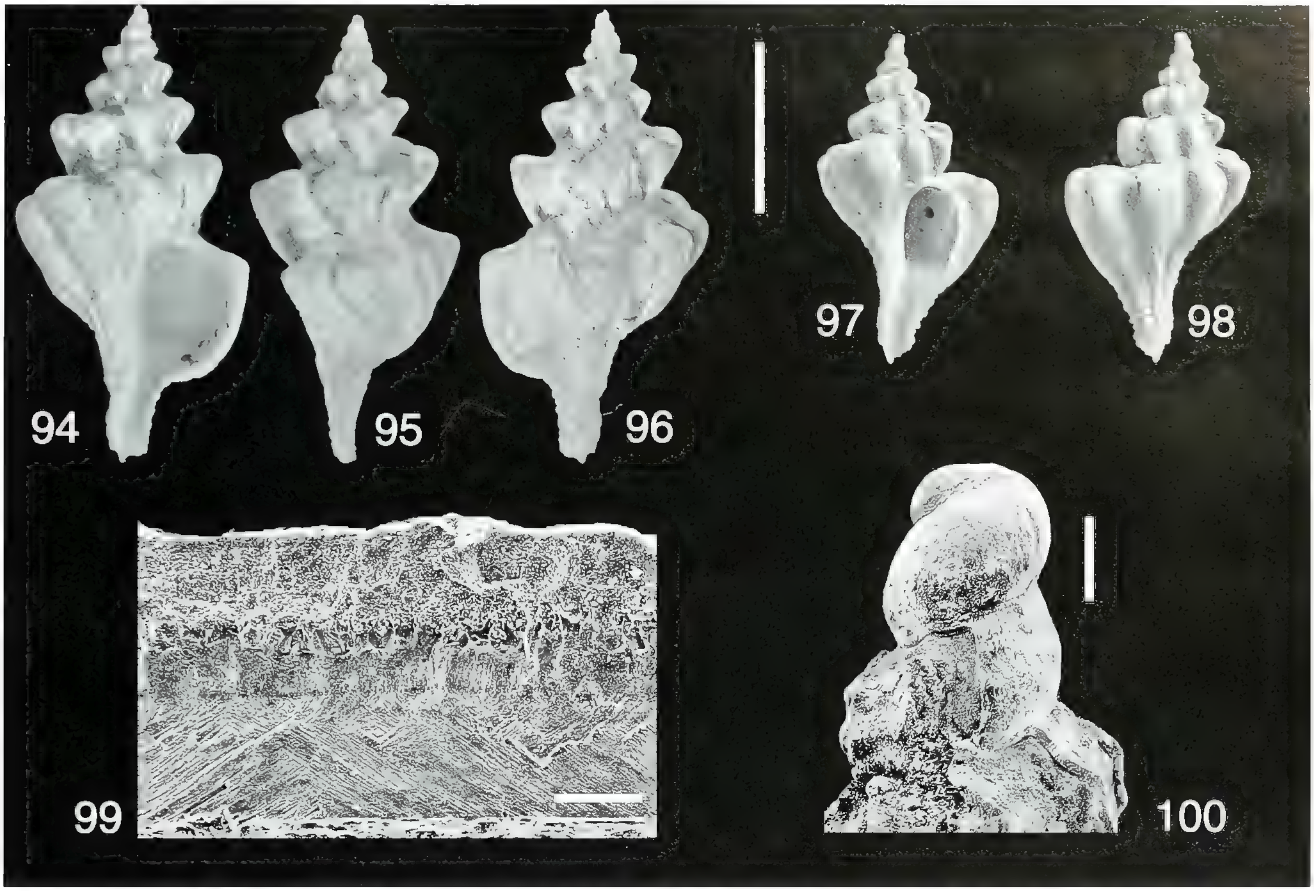
Trophon amettei Carcelles, 1946
(Figures 94–100)

Trophon amettei Carcelles, 1946: 84, fig. 13; Carcelles and Williamson, 1951: 287

Description: Shell small in size (up to 30 mm), fusi-



Figures 79–93. *Trophon pelseneeri* E. A. Smith, 1915. **79–80.** BMNH 1915.4.18.276-7 syntype. **81–82.** BMNH 1915.4.18.276-7, other syntype. **83–85.** *T. orbignyi* Carcelles, MACN-In 24421 holotype. **86–87.** MNHNM 15400, B/I ALDEBARÁN, 34°d48′7″ S, 54°21′9″ W, in 25 m. Scale bar = 1 cm. **88.** Two views of the operculum of the specimen in Figures 86–87. Scale bar = 2 mm. **89–90.** USNM 846550, apical and lateral view of the protoconch. Scale bars = 400 and 300 μm respectively. **91.** Detail of the ultrastructure of the shell. Scale bar = 100 μm. **92–93.** Dorsal and lateral view of the radula of the specimen in Figures 86–87. Scale bars = 30 μm



Figures 94–100. *Trophon amettei* Carcelles, 1946. **94–96.** MACN-In 23810, holotype, 45°09′ S, 66°27′ W in 11.28 m. **97–98.** MACN-In 23810, paratype. Scale bar = 1 cm. **99.** MACN-In 23810, ultrastructure of the shell. Scale bar = 30 μm. **100.** MACN-In 23810, protoconch, uncoated SEM picture. Scale bar = 300 μm.

form, biconic, chalky whitish; protoconch elongate, smooth, of 2¼ whorls; teleoconch of 6 strongly shouldered whorls, spire less than ½ of the total shell height. Spire angle about 45°, suture impressed; subsutural shelf short but straight, aperture small, ovoid, interior glossy white; anterior siphonal canal comparatively long, almost same height as aperture, open and straight; umbilicus closed, inner lip adpressed. Axial ornamentation of 8 regular concave lamellae per whorl. Lamellae growing attached to entire whorl surface and producing concave spine along periphery. Spiral ornamentation of 2 cords in first teleoconch whorls that soon become obsolete on subsequent whorls. Last whorl with 6–10 cords on lower part. Shell ultrastructure composed of two layers, similar to *T. geversianus*. Operculum and soft parts unknown.

Type Material: Holotype and 15 paratypes (MACN-In 23810) all from 45°09′ S, 66°27′ W anchorage Restinga Aristizábal, Chubut province, in 8 fathoms (11.28 m), rocky bottom associated with the calyptraeids *Crepidula cachimilla* and *Calyptraea pileolus*.

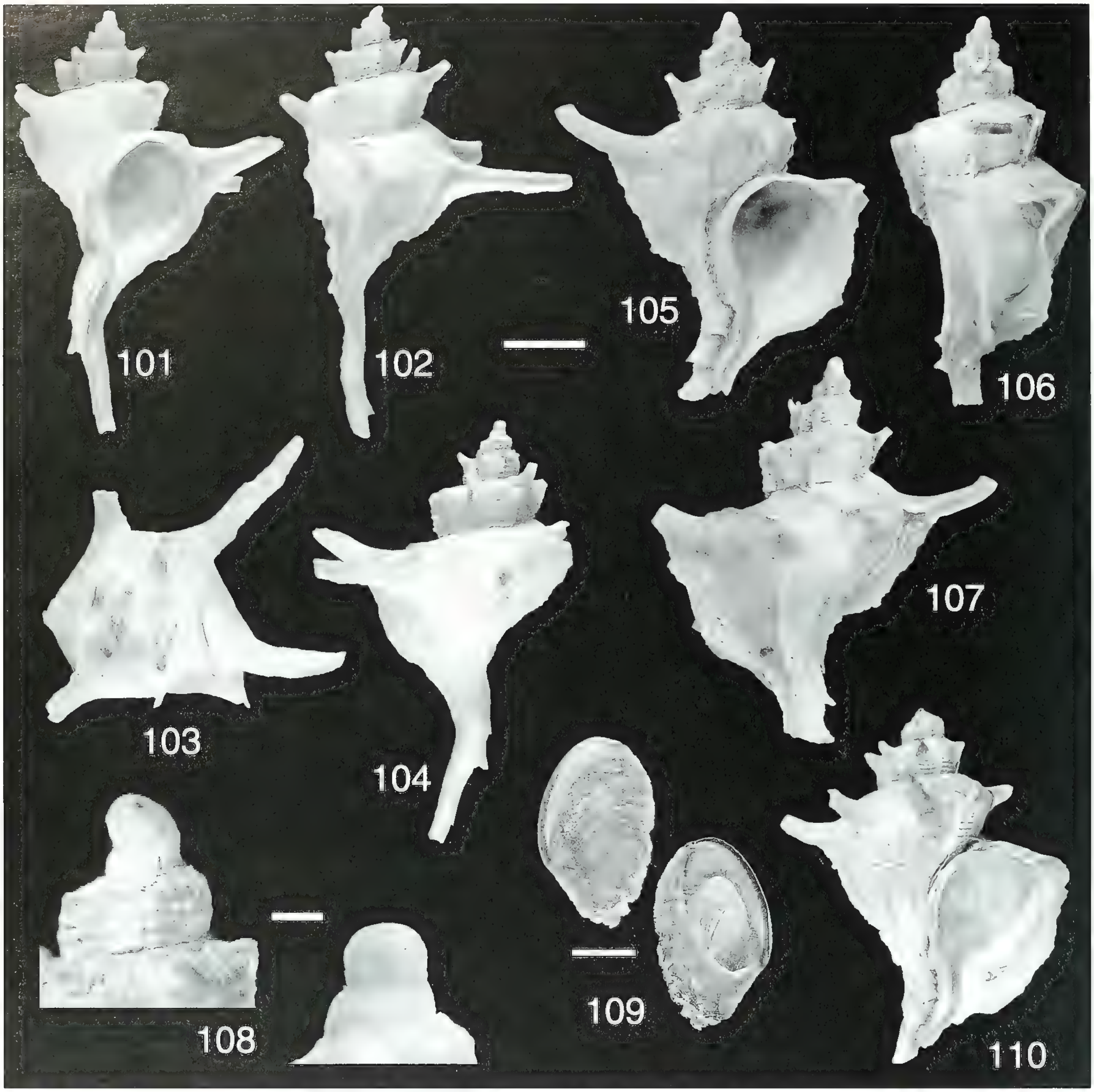
Remarks: This is a rare species known only from the type locality. It has not been found again. The regular concave lamellae, are in fact, unusual for the genus. The protoconch resembles those usually found in the genus *Fuegotrophon*, however the typical fimbriate spiral ornamentation is absent. *Trophon pelseneeri* has a comparable profile, however it is easily segregated: where the latter has lamellae forming a back-turned spine at periphery, *T. amettei* presents a characteristic and unique concave lamellae. In addition *T. pelseneeri* has a slightly open umbilicus while in *T. amettei* it is invariably closed. Examination of the radula may beget a new generic allocation for this species.

Trophon clenchi (Carcelles, 1953)
(Figures 101–114)

Murex clenchi Carcelles, 1953: 7, figs. 23–28; Castellanos, 1970: 80, pl. 5, fig. 7; Fair, 1976: 31, fig. 15; Vokes, 1992b: 24; Rios, 1994: 115.

Poirieria (Poirieria) clenchi (Carcelles).—Vokes, 1970: 18.

Description: Shell medium in size, delicate, thin, chalky, translucent white; protoconch known only from the holotype, asymmetrical, globose, of 2–2½ whorls; teleoconch of 5 shouldered whorls; spire short, less than ¼ of total shell height. Spire angle about 45° (without spines); suture impressed, subsutural shelf short,

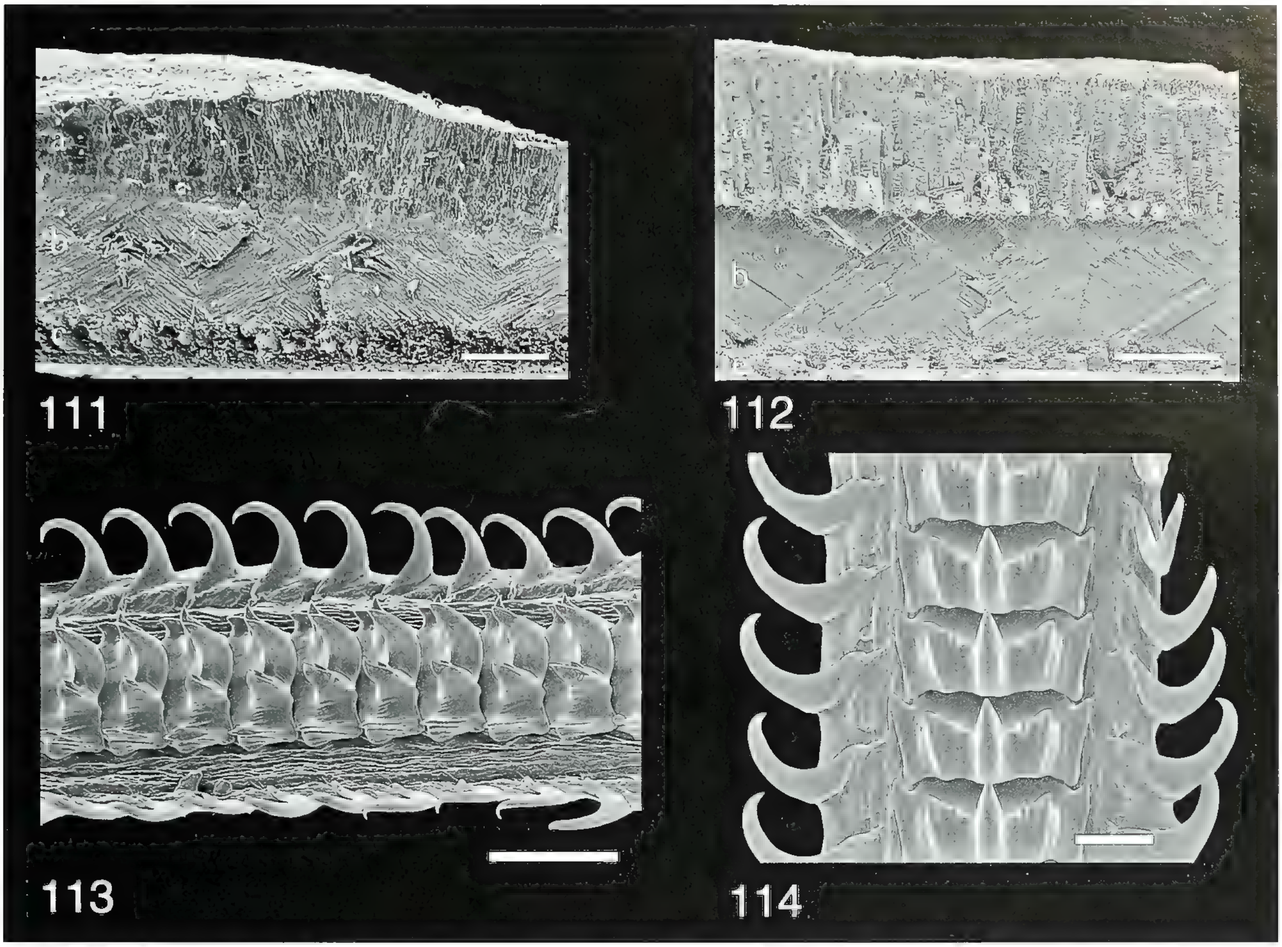


Figures 101–110. *Trophon clenchi* (Carcelles, 1953). **101–104.** MACN-In 25146, holotype, 38°24′ S, 55°36′ W in 89.61 m. **105–107.** MACN-In 36269, aproximately 45°10′ S, 57°20′. Scale bar = 1 cm. **108.** Holotype, protoconch. Scale bar = 1000 μm. **109.** External and internal views of operculum of specimen in Figures 105–107. Scale bar = 0.5 cm **110.** MACN-In 25146, paratype.

straight; aperture suboval, interior glossy white; anterior siphonal canal very long (longer than the aperture height), deep and slightly curved in the beginning and then straight, open but narrow; outer lip sharp, inner lip somewhat protruding, adpressed. Axial ornamentation of 7–9 regular axial lamellae growing across entire whorl surface, but attached to shell producing open, long and regularly spaced spines along periphery. Spiral ornamentation of 4–5 rounded cords on lower half of first whorls, becoming more than 20 in the last. Delicate growth lines present on entire shell surface.

Shell ultrastructure composed of two layers following the common pattern of the genus: innermost layer (40% of total thickness of shell) composed of crossed lamellar aragonite, outer layer (50%) of amorphous calcite. Sometimes, depending on the fracture mode, a basal aragonitic layer can be observed.

Radulae rachiglossate, rachidian teeth with three me-



Figures 111–114. *Trophon clenchi* (Carcelles, 1953). **111.** USNM 901774, 51°58′ S, 56°38′ W, R/V ELTANIN Cruise 7, Sta. 558, 646–845 m, ultrastructure of the shell. Scale bar = 100 μm. **112.** *Poirieria zelandica*, ultrastructure, commarginal fracture surface. Scale bar = 100 μm. **113.** *Trophon clenchi* MACN-In 36269. Lateral view of radula ribbon. Scale bar = 100 μm. **114.** Dorsal view of radular ribbon. Scale bar = 50 μm.

dian cusps, the central one the larger and the lateral ones with a denticle, attached to the upper third of the interior margin of the lateral cusp; external margin with 2–3 obsolete denticles. Rachidian base sinuous, with the base offset under the proximal tooth. Marginal cusps single, never bifid. Lateral teeth curved, thin, with attachment area also thin (Figures 113–114).

Operculum triangular or suboval tear-shaped, attachment area elliptical, with horseshoe shape scars.

Type Material: 38°24′ S, 55°36′ W, off Mar del Plata, in 89.6 m, holotype and paratype (MACN-In 25146).

Additional Material Examined: 51°58′ S, 56°38′ W, 3 D, R/V ELTANIN Cruise 7, Sta. 558, 646–845 m (USNM 901774). 41°51′ S, 57°34′ W, collected by Uruguayan fishermen, June 2002, 1062 m, 1A, MACN-In 36270; approximately 45°10′ S, 57°20′ Uruguayan fishermen, 1 A, MACN-In 36269; 54°50′ S, 63°50.5′ W, 2.5 miles south Punta Fallows, Isla de los Estados, Tierra del Fuego, 1 A, R/V HERO Cruise 715, Sta. 715/879, 28 October 1971, in 342–353 m (LACM 71-331).

Distribution: Known from off Buenos Aires province, Patagonia and Isla de los Estados, in 90–1050 m depth.

Remarks: Carcelles (1953) described *Murex clenchi* from two shells he received from the crew of the ARA BAHÍA BLANCA, an Argentine Navy ship that occasionally collected material for the collection of the Museo Argentino de Ciencias Naturales (MACN). Both holotype and paratype were collected from the continental shelf off Buenos Aires province. This material remained housed at the MACN until it was sent on loan and it appears to have been lost for almost 30 years (see Castellanos, 1986). The return of the material to MACN made the type material again available for studies. Perhaps because of these facts, the ordinary quality of the illustration and the absence of soft parts, the species was always reluctantly considered as the southernmost representative of the genus *Murex*.

E. H. Vokes, in a fundamental paper published in 1970, stated that *Murex clenchi* belongs in the genus *Poirieria* sensu stricto. Rios (1994) considered *M. clenchi* as an anomalous specimen of *Trophon acanthodes* Watson, a species that slightly resembles some specimens of *M. clenchi* (e.g., the paratype).

The morphology of the shell as well as the radula and penis of *Murex clenchi* allow the allocation in the genus *Trophon*. In fact, this was already suggested by E. H. Vokes (1992b). After studying the material of *T. acanthodes* housed at the MACN she proposed that *M. clenchi* belongs to *Trophon* sensu lato and not to *Poirieria*. It bears no relationship with *Poirieria* despite some apparent shell similarity. As it is shown in Figure 112, *Poirieria zelandica*, type species of *Poirieria*, has no calcitic layer on the shell but a thick aragonitic one instead (Figure 112a). In contrast, the entire group of Patagonian *Trophon* (*T. clenchi* in particular), shows different degrees of development of the typical calcitic layer on the distinct species.

The range of the very few lots studied falls within the geographic distribution of other species of *Trophon*. *Trophon clenchi* was known from two quite different geographic and bathymetric areas: off Buenos Aires province (in about 90 m) and the slope off Patagonia. A new lot is recorded here from Isla de los Estados, which significantly increases the range of distribution of the species. It is possible that like other Patagonian species of the genus, *T. clenchi* would be associated to hard bottoms, thus hampering the collection of material. Its fragility, size, and inadequate sampling of the area adds other reasons for the scarcity of records. It is suggested that these variables accounts for the disjunt recorded distribution of this species. In fact, this species started to be repeatedly collected recently, when the fishery of the Patagonian toothfish (*Dissostichus eleginoides*) on the Argentinean slope provided the opportunity to catch accidentally entangled specimens (F. Scarabino, pers. comm.).

Trophon wilhelmensis Ramirez-Bohme, 1981
(Figures 115–119)

Trophon (*Enixotrophon*) *wilhelmensis* Ramirez-Bohme, 1981: 6, fig. 1a, b.

Description: Shell of medium size, about 52 mm high, slender in profile, chalky white; protoconch unknown; teleoconch of 6 shouldered whorls; spire less than ⅓ of total shell height. Spire angle less than 45°; suture impressed, subsutural shelf straight, aperture small, subcircular, interior glossy white; anterior siphonal canal very long (longer than aperture height) deep, straight or curved, always open; outer lip rather reflexed, rounded, inner lip adpressed. Axial ornamentation of 12–15 regularly spaced, axial lamellae, slightly raised, almost attached along the entire whorl, producing open, conspicuous, regularly spaced spines at periphery; spines becoming more closely packed on last whorl. Spiral ornamentation of 4–5 weak rounded threads on the lower part of the first whorls, becoming more than 20 in last one. Growth lines present throughout shell, producing wrinkly surface by intersection with spirals.

Operculum elliptical, nucleus terminal. External surface covered by growth lines. Inner surface with marginal rim; attachment area, horseshoe-shaped scars present.

Rachidian teeth of about 90 μm wide, central cusp large; lateral cusps shorter than central cusp, inner edge with conspicuous denticle, external edge with 5 denticles of equal size. Base of rachidian tooth straight, somewhat sinuous, sliding beneath base of next tooth. Marginal area with single cusp. Lateral teeth thin with single, long cusp, slightly attached basal plate.

Type Material: Holotype in MNHN (unnumbered), 41°51′ S, 74°30′5″ W West of Chiloé Island in 250 m.

Additional Material Examined: Boca del Guafo, 43°39′36″ S, 73°51′11″ W, southern Chile, 6 July 2002, 1 A, 200 m (MNHN unnumbered).

Distribution: Known only from the holotype and another lot, both from the same area and depth, around the Chiloe Is., Chile.

Remarks: *Trophon wilhelmensis* was recently described from Chile with no mention of the similarity with *T. acanthodes*. Both species are actually quite similar. The species, known only from the holotype and another specimen, may be distinguished from *T. acanthodes* mainly by the upturned spines (compare Figures 66–73 with Figures 115–117). In addition, slight differences in the morphology of the rachidian teeth allow for further differentiation of the two species. Notwithstanding, future studies of specimens from intermediate localities could demonstrate that these represent but a single species.

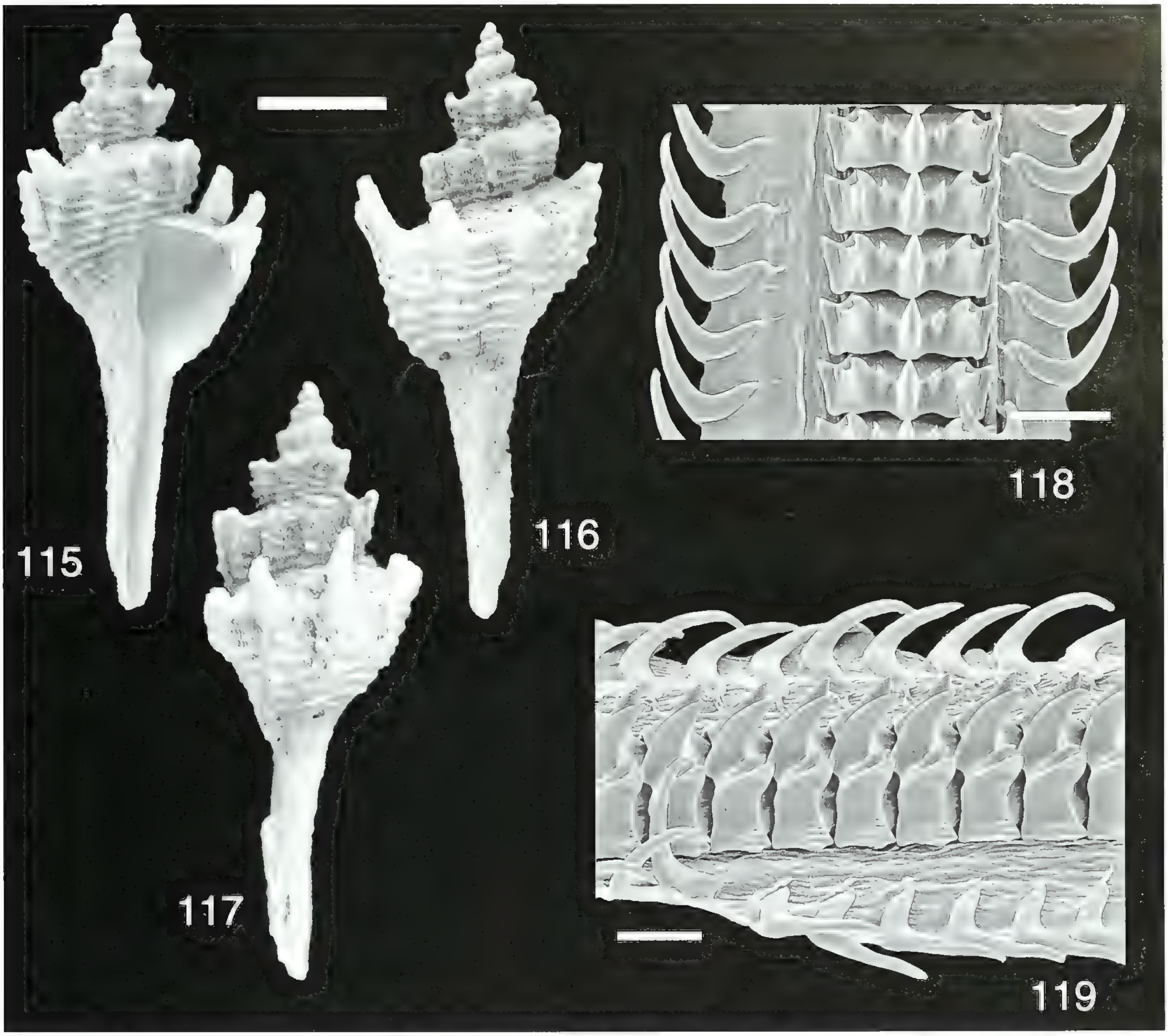
Trophon bahamondei McLean and Andrade, 1982
(Figures 120–125)

Trophon bahamondei McLean and Andrade, 1982: 10, figs. 24–25.

Description: Shell of medium size, up to 50 mm, slender, with narrow profile, chalky or creamy white; protoconch unknown (worn in all specimens); teleoconch of 6 shouldered whorls; spire less than ½ of total shell height. Spire angle about 45°; suture impressed, subsutural shelf well defined, straight; aperture subcircular, interior chalky white; anterior siphonal canal very long (equal to aperture height), narrow, and curved, open; outer lip sharp, rounded, inner lip adpressed. Axial ornamentation of 11–13 regular axial lamellae growing on entire whorl surface, but attached to the shell and producing open, short and regularly spaced spines along periphery. Spiral ornamentation lacking. Growth lines present throughout shell.

Operculum elliptical, nucleus terminal. External surface covered by concentric, irregular growth lines. Inner surface attachment area reaching upper side or center, with horseshoe-shaped scars (Figure 123).

Radula with rachidian teeth very wide (~114 μm), with narrow base, central cusp thin, large; lateral cusps



Figures 115–119. *Trophon wilhelmensis* Ramirez-Bohme, 1981. **115–117.** MNHNS unnumbered, Boca del Guafo, 43°39′36″ S, 73°51′11″ W, southern Chile, 6 July 2002, 200 m. Scale bar = 1 cm. **118–119.** Radula of the specimen on Figures 115–117, **118.** Frontal view. Scale bar = 50 μm. **119.** Lateral view. Scale bar = 40 μm.

wider and shorter than central cusp, inner edge with sharp, curved denticle, external edge with denticles decreasing in size toward lateral edge where they disappear. Base of rachidian tooth sinuous, inserted in part under base of subsequent tooth. Marginal area with single conspicuous cusp. Lateral teeth with single, long and very narrow cusp, slightly attached basal plate. Central cusps of rachidian teeth curved back in lateral view (Figures 124–125).

Animal very similar to *T. plicatus.* Osphradium less than half ctenidium length, asymmetrical, with 60–70 leaflets. Ctenidium with 140 leaflets less than two times larger than those of osphradium. Tentacles well defined; eyes deeply marked. Same type of accessory salivary glands, twisted and non-compact.

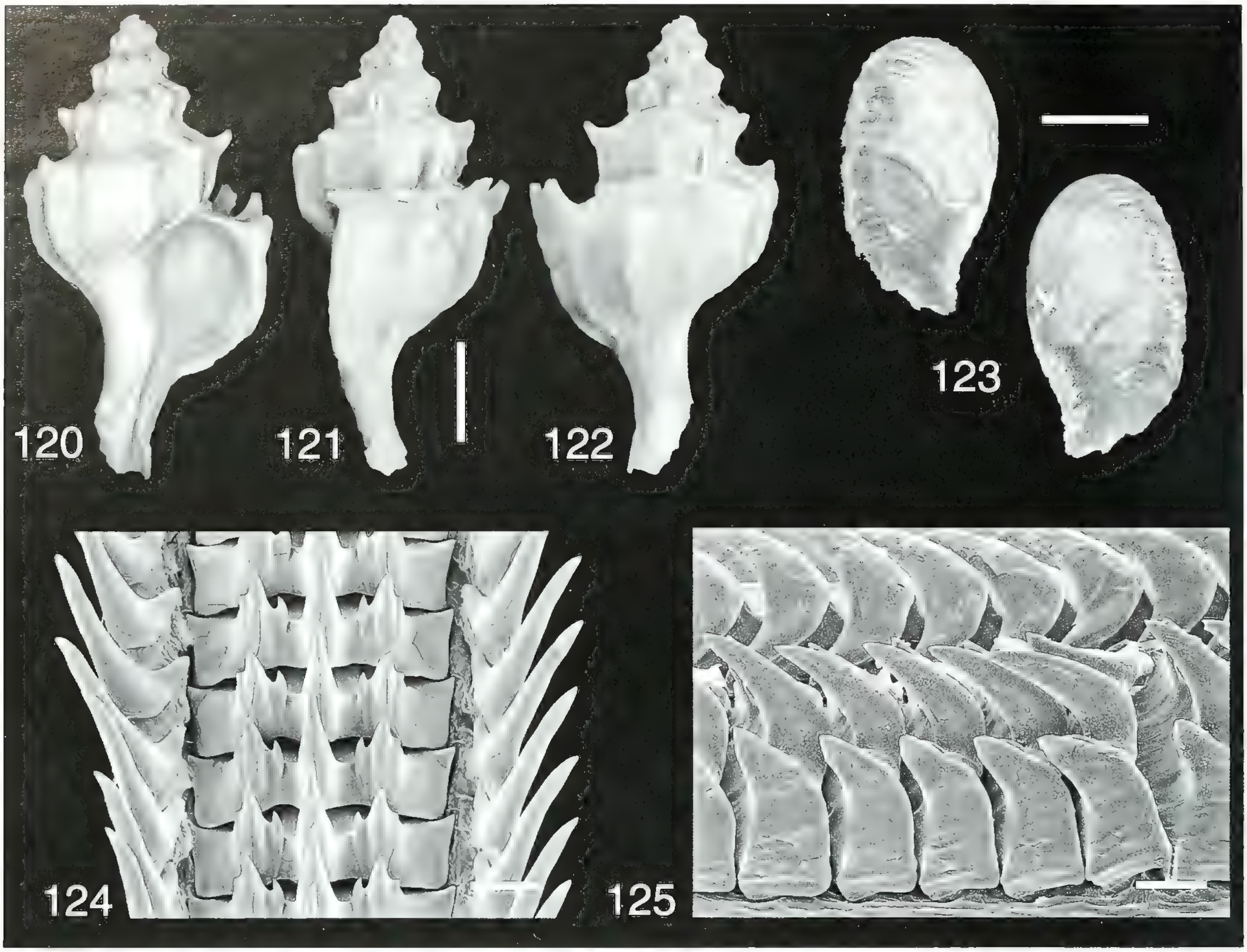
Male unknown, all specimens studied were females. Female similar to *T. geversianus.*

Type Material: Holotype from off Pichilemu, Chile, 34°27′ S, 340 m (LACM 1982, but apparently on loan) and two paratypes, 34°27′ S, 71°54′ W, 25 May 1976, 200–450 m (USNM 784739).

Additional Material Examined: 31°56′ S, 71°54′ W, off Los Vilos, Chile, 2 A, 8 March 1977, 240–350 m (LACM 72491); off Playa Blanca, Coquimbo, Chile, 400 m (ANSP 291065); off Coquimbo, Chile (LACM 75-88).

Distribution: This is a deep water *Trophon* known from latitudes 30° to 34° S off the coast of Chile.

Remarks: *Trophon bahamondei* is apparently a very



Figures 120–125. *Trophon bahamondei* McLean and Andrade, 1982. **120–122.** Paratype USNM 784739, 34°27′ S, 71°54′ W, Pichilemu, Chile, in 200–450 m. Scale bar = 1 cm. **123.** Operculum, external (right) and internal (left) views. Scale bar = 1 cm. **124.** Dorsal view of radular ribbon. Scale bar = 30 μm. **125.** Lateral view of rachidian teeth. Scale bar = 30 μm.

consistent species from the morphological standpoint. It was only recently described despite its apparently widespread presence in shrimp trawls. The deeper water habitat of species (more than 200 m) probably rendered the species less accessible in the past.

General morphology of shell and gross anatomy shows at first glance some similarities with those of *T. plicatus*; however close examination of shell and radula confirms the presence of a different species.

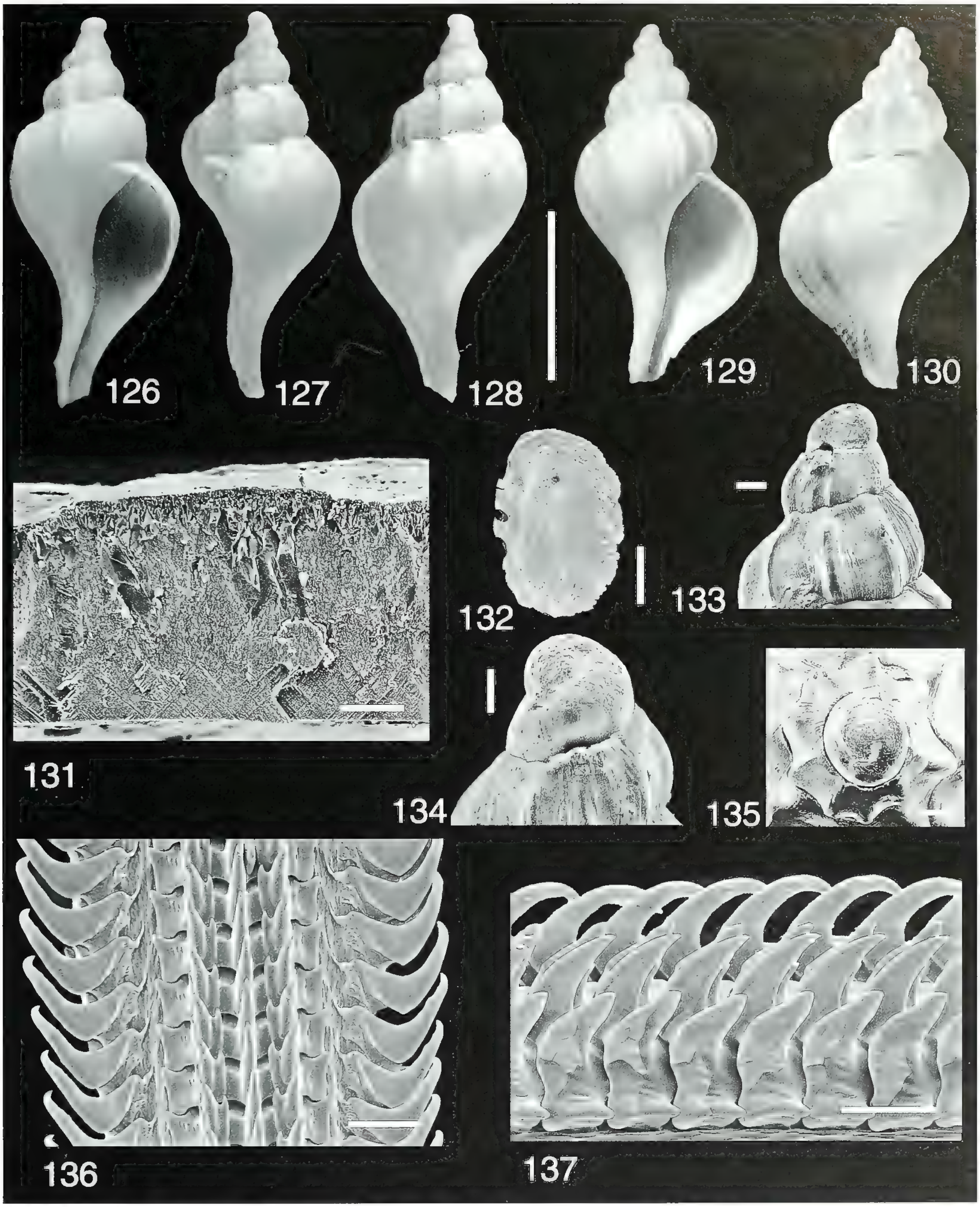
Trophon parodizi new species
(Figures 126–137, Table 1)

Description: Shell medium in size (up to 23 mm), very thin, chalky; protoconch smooth, of 1½ (1.41 × 1.39) very asymmetrical whorls; transition to teleoconch well defined; teleoconch of 4 convex whorls, spire less than ⅓ total shell height. Spire angle about 40°; suture impressed; aperture subovoid, interior glossy white; anterior siphonal canal medium in size (less than half height of aperture), narrow, open; umbilicus absent; outer lip rounded. Axial ornamentation of irregular, low, rounded ridges occupying entire whorl surface, numbering up to 9 in early whorls, but vanishing and undulate on last whorl. Spiral ornamentation poorly developed or almost smooth, when present consisting of obsolete, weak cords mostly developed on last whorl. Irregular growth lines present throughout shell.

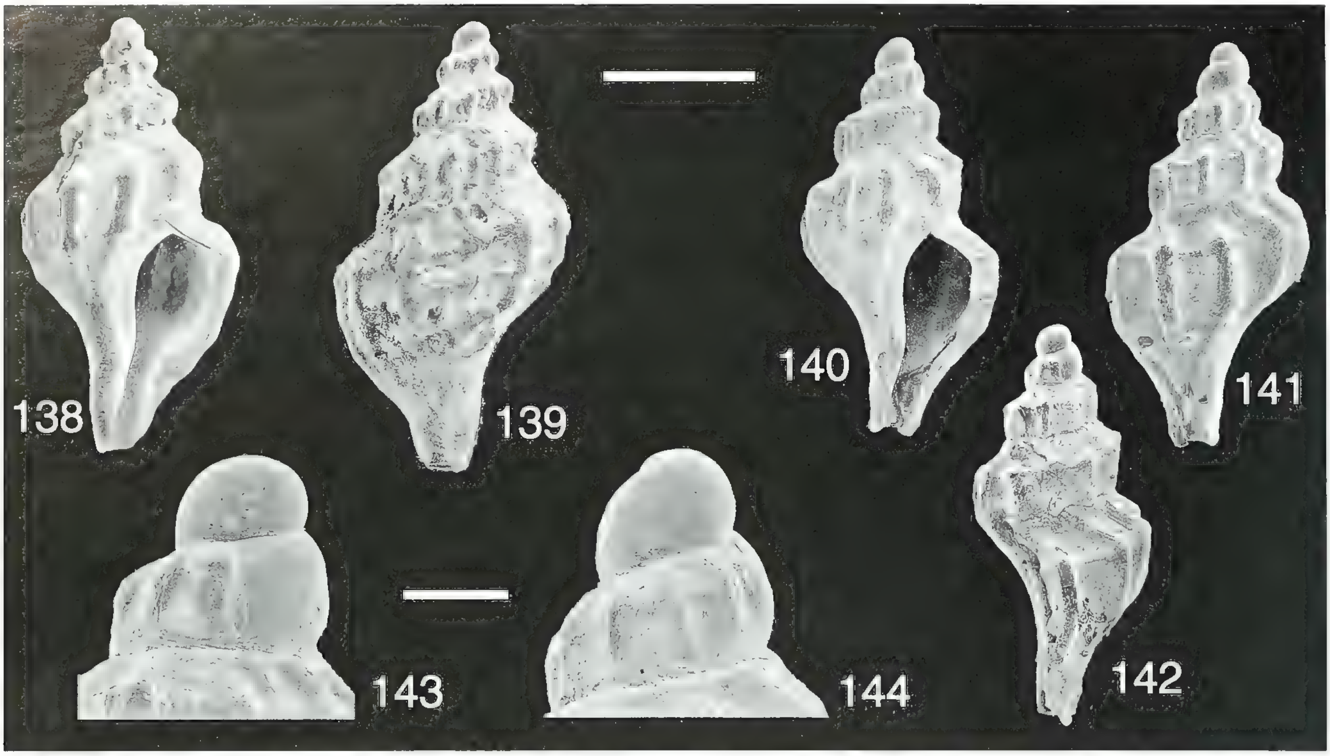
Shell ultrastructure composed of two layers; innermost layer thin (35% of shell thickness), composed of colabrally aligned crossed lamellar aragonite, outer layer thick (65% of shell thickness) with amorphous calcite.

Operculum oval, with terminal nucleus. External surface covered by concentric, irregular, growth lines. Inner surface attachment area with two or three horseshoe-shape scars. Animal unknown.

Radula rachiglossan with rachidian teeth distinctive, central cusp thin, large; lateral cusps almost same size as central cusp, sharp denticle on upper third, irregular external denticles present. Base of rachidian tooth sin-



Figures 126–137. *Trophon parodizi* new species. **126–128.** USNM 896397, holotype, 54°56′ S, 65°03′ W, in 229–265 m. **129–130.** USNM 896397, paratype, coated with ammonium chloride. Scale bar = 1 cm. **131.** Ultrastructure, fracture surface commarginal. Scale bar = 20 μm. **132.** USNM 896397, operculum, external view. Scale bar = 0.5 cm. **133–135.** Protoconch of the paratype, three views. Scale bar for all figures = 400 μm. **136.** Dorsal view of radular ribbon. Scale bar = 40 μm. **137.** Lateral view of rachidian teeth. Scale bar = 40 μm.



Figures 138–144. "*Trophon*" *malvinarum* Strebel 1908. **138–139.** NHRM 1041, holotype, 52°29′ S, 60°36′ W. **140–142.** MACN-In 23944-2, 55°07′ S, 66°33′ W. **143–144.** Protoconch. Scale bar = 400 μm.

uous, sliding beneath base of next tooth. Marginal area with a conspicuous cusp. Lateral teeth with single, long cusps and narrow, slightly attached basal plate.

Type Material: Holotype and one paratype from 54°56° S, 65°03° W, Le Maire Strait, R/V Eltanin Cruise 11, Sta. 969, 10 February 1964, 229–265 m, Blake trawl (USNM 896397) (Map 1).

Material Examined: Only holotype and paratype.

Distribution: Known only from the type locality.

Etymology: This species is named after Juan José Parodiz, one of the pioneers of malacology in Argentina, Curator Emeritus at the Carnegie Museum, Pittsburgh, and a good friend.

Remarks: *Trophon parodizi* is an unusual species within *Trophon*. The small, very thin shell, almost completely smooth and devoid of lamellae, is an exception for the Patagonian *Trophon*. However, the radula and protoconch match those typical of the genus. The radular morphology resembles that of *T. plicatus* where the denticles of the lateral cusp of the rachidian teeth are placed along the entire external edge of the lateral cusp. In *T. parodizi* the lateral cusp is thinner and the denticles are more clearly separated from it and placed mainly along the marginal area as in *T. bahamondei*. In addition—a character also present in *T. bahamondei*—most internal denticle lies against the lateral cusp and is clearly differentiated from the rest.

"*Trophon*" *malvinarum* Strebel, 1908
(Figures 138–144)

Trophon malvinarum Strebel, 1908: 44, figs. 16 a–c; Carcelles and Williamson, 1951: 289; Castellanos and Landoni, 1993: 10, pl. 2, fig. 29.

Description: Shell small, up to 30 mm, thick, fusiform, profile slender, chalky, whitish; protoconch globose, somewhat cylindrical, with two whorls; teleoconch of 4½ shouldered whorls, spire less than ⅓ of total shell height. Spire angle about 45°; suture impressed; subsutural shelf abaxially oblique, aperture subquadrate, anterior siphonal canal moderately long (same height as aperture); umbilicus closed, outer lip polygonal to rounded; inner lip slightly curved, adpressed. Axial ornamentation of 8–9 regular, distinct low varices, which never develop into full-fledged lamellae. Spiral ornamentation of about 3 cords, filling interspaces between consecutive varices, and beginning at periphery of whorls.

Radula and anatomy unknown.

Table 1. Measurements of the type specimens of *Trophon parodizi* new species in mm.

Species	Length	Width	Whorls
T. parodizi			
Holotype	23	11	4
Paratype	21.1	10.6	4

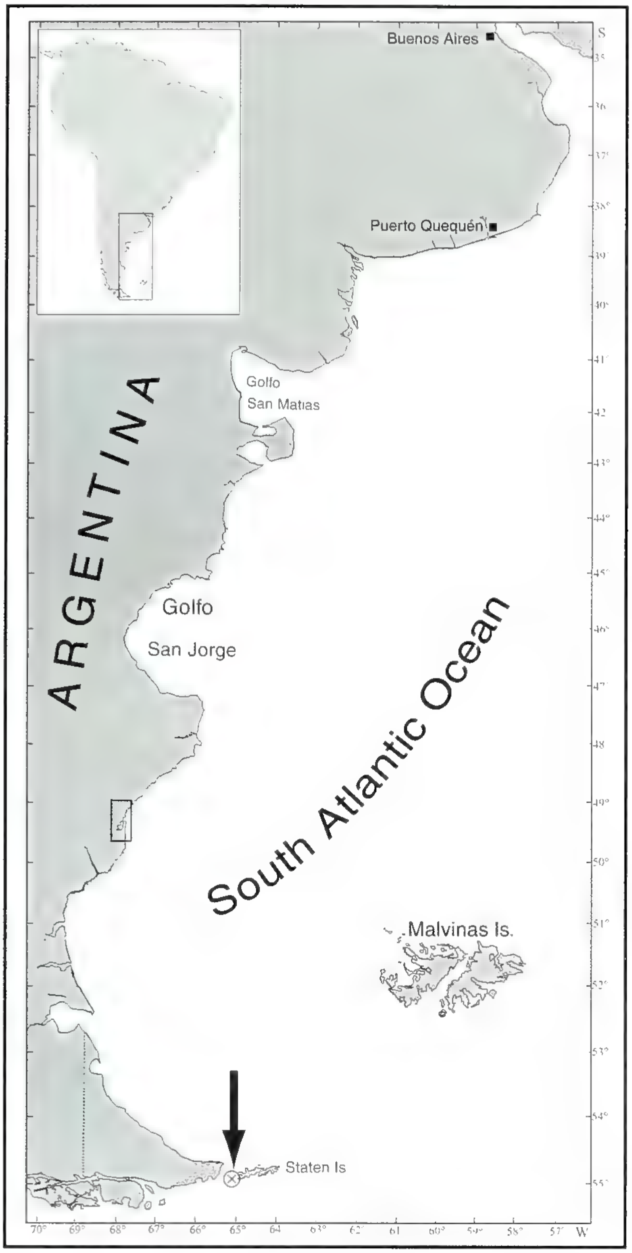


Figure 145. Map showing the type locality of *T. parodizi* new species (◆).

Type Material: 52°29′ S, 60°36′ W, West Falkland (Malvinas) Is., Svenska Sudpolar Expedition, 11 September 1902, Sta. 58, 197 m (NHRM 1041).

Additional Material Examined: 55°07′ S, 66°33′ W, 1 D. 83 m (MACN-In 23944-2).

Distribution: Around Malvinas Is. and the Magellanic region.

Remarks: *"Trophon" malvinarum* is a rare species known from only one specimen other than the holotype. It was originally described in the genus *Trophon*; however, the protoconch is somewhat shorter and symmetrical and the shell never develops true lamellae but low varices. It probably could be better assigned in the genus *Urosalpinx*. Assessment of its real affinities must wait until specimens with soft parts preserved can be studied.

CONCLUDING REMARKS

The geographic distribution of the species of the genus *Trophon* sensu stricto is restricted to the southwestern Atlantic and the southeastern Pacific Oceans. This distribution is certainly a consequence of their larval biology. Planktonic larval development is unknown to occur in the genus. Moreover, the larvae do not need to move any significant distance either for feeding or reproductive purposes—those from shallow water habitats live on mussel banks on which they feed and mate. Such a condition is reflected in the enormous morphological variation shown by the shells of the different species, particularly in *T. geversianus*. While most of the species are well known, some others were only collected in a single location (e.g., *T. amettei*) and therefore their range of variation remains to be known.

Radular and anatomical features suggest that the entire *Trophon* group from Patagonia is very homogeneous. All the species included in this genus have several common radular features. The most remarkable are: the intermediate denticle attached to the upper third of the internal edge of the lateral cusp of the rachidian teeth; a single marginal denticle in the external edge of the base of the rachidian teeth; the attachment area of the marginal teeth are always (no exceptions known) narrow, thin, with the free part of same thickness, and the central cusp of the rachidian is always thin and larger than the laterals (see also Pastorino, 2002).

The Antarctic species so far assigned to *Trophon* and the boreal ones recently included in the genus *Boreotrophon* (see Egorov, 1993) have the inner denticle between central and lateral cusp of the rachidian teeth always free, attached to the base of the teeth. In addition, most of the radulae of these northeastern Atlantic species—according to Bouchet and Warén's revision (1985)—have a broad attachment of the marginal teeth.

Conchological features are so variable that I considered them as secondary. However, the protoconchs are actually very different and allow for the division in at least two clearly defined groups. There is no ornamentation on the protoconchs of Patagonian representatives of *Trophon*, whereas most of the boreal species of *Boreotrophon* have a delicate pattern of irregular threads. The Antarctic species have also no ornamentation in the protoconch with only one exception: *T. scotianus* Powell, 1951 which has apparently the same pattern observed in North Atlantic *Boreotrophon* species.

There are several anatomical features that characterize the group of species living along the South American coast. The accessory salivary glands, when known, are usually tubular; the esophagus produces a typical esophageal loop after the valve of Leiblein and posteriorly runs appressed to the left side of the gland of Leiblein;

the esophageal glands in the mid-esophagus are inconspicuous, not externally visible; and finally, the penises are always dorso-ventrally flattened, with a large papilla and a simple *vas deferens* either closed by the overlapping sides of the penis or open.

The features mentioned above and the geological story of the two areas, Antartica and Patagonia, allow for the clear differentiation of these two groups.

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Latitudinal trends in shell characters of the neogastropod *Olivancillaria urceus* (Gastropoda: Olividae) in the temperate southwestern Atlantic Ocean

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ABSTRACT

Variation in shell characters of the neogastropod *Olivancillaria urceus* (Röding, 1798) was analyzed at the central part of its geographical range. Nine shell dimensions were measured from specimens from seven localities between 32°10′ S and 40°33′ S along the Atlantic coast of South America. Significant effects of collection site were detected on all measured variables. The first three components in principal component analysis together explained nearly 80% of the observed variance in morphometric measures. Variables also differ in their allometric trajectories among localities: all measured shell dimensions displayed both positive and negative allometric coefficients along the latitudinal axis. Allometric effects were then removed to allow for determination of size-free variation in shape. High-spired, elongated forms occurred more frequently in higher latitudes. Spire width, maximum width, maximum width/height and shell thickness decreased as latitude increased. Spire length measured on the apertural side showed an opposite trend. No relationship with latitude was found for fasciolar-band length and spire length (measured along the abapertural shell side). The existence of extreme forms within the analyzed sample showed high phenotypic and ecological plasticity in the populations assigned to *O. urceus*.

INTRODUCTION

Gastropod shell shape reflects a trade-off among functional requirements, energetics of construction and maintenance, rules governing growth, and the imprint of evolutionary ancestry. The result of the interactions between these factors on the realized shell is also affected by environmental features and tied to architectural constraints (Vermeij, 1993). Phenotypic plasticity in shell characters appears to exert a strong influence on small and large-scale morphological variation in marine snails (Trussel and Etter, 2001).

Different patterns in shell variation are found as different spatial scales and taxonomical or ecological hierarchies are considered: well-disseminated eco-geographical rules, suitable for many taxa, predict that animals at high latitudes should have larger body sizes and life spans than at low latitudes (Mayr, 1956; Atkinson and Sibly, 1997). In most mollusks growth is faster at high temperatures and in the presence of food than in cold, nutrient-poor conditions (Vermeij, 1993).

Latitudinal variation in shell characters was detected in northern hemisphere gastropods assemblages. This variability was related to efficiency of calcium carbonate utilization. It was shown that more heavily calcified and ornamented shells occur with decrease in latitude (Grauss, 1974).

When considering variation in shell features at the intraspecific level, it could be interpreted as a response to environmental conditions, which may include biotic and abiotic factors. Biotic interactions have been proposed as driving forces for morphological changes. Certain shell characters interpreted as anti-predatory features such as low spire and elongate aperture were found to be significantly different between comparable gastropod assemblages from both sides of the tropical Atlantic and Indo-West Pacific (Vermeij, 1978).

Within-location variation in shell shape and shore-level size gradients have been found for several species of intertidal mollusks (Vermeij, 1972). This intra-populational variability is often coupled with shifts in shell growth and has been related experimentally with food supply and density-dependant processes: specimens of *Littorina littorea* (Linnaeus, 1758) with plentiful supply of seaweed grow faster and develop low-spired shells than other group maintained under crowded conditions; in the latter growth was slower and higher spired shells were developed (Kemp and Bertness, 1984). De Wolf et al. (1998) documented large-scale patterns of shell variation in *Littorina striata*, a planktonic-developing periwinkle from Macaronesia, confirming expectations based

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Figure 1. Map showing parts of the Atlantic coast of Brazil, Uruguay, and Argentina that include the collection sites of *Olivancillaria urceus*

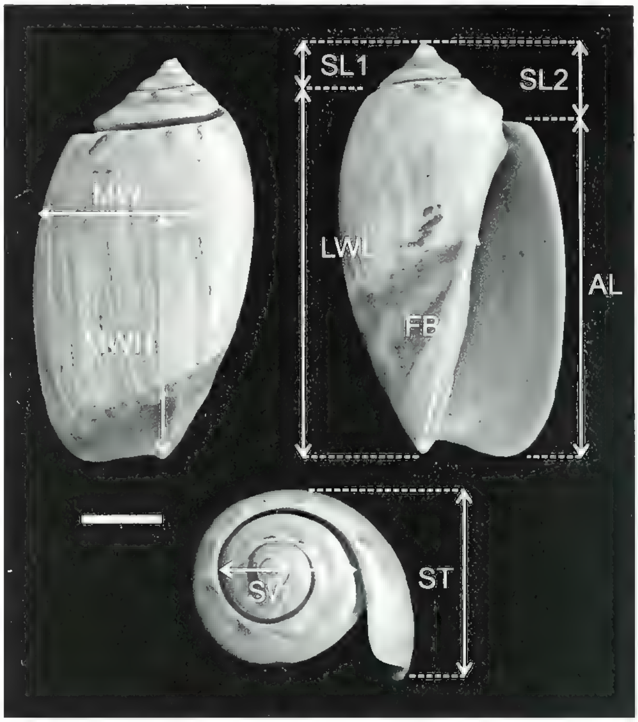

Figure 2. Dorsal, ventral, and apical view of *Olivancillaria urceus* showing measurements taken for statistical analysis. Scale bar = 1 cm. Abbreviations: LWL: last whorl length from suture to anterior end; AL: aperture length, distance along outer lip from suture to anterior end; FB: distance between anterior and posterior ends of fasciolar band along internal side of the aperture; MW: maximum linear distance from outer lip to opposite side; MWH: maximum linear distance perpendicular to MW to anterior end; ST: shell thickness; SW: diameter of spire base from tip of callus above aperture to opposite point on suture; SL2: lateral spire length from tip of callus above aperture to protoconch tip on outer lip side in ventral view, parallel to growth axis; and SL1: same length measured on the opposite side

on morphological patterns observed among other prosobranchs for increasing shell size and weight in southern sites.

There is also ontogenetic related variation due to allometric increase of spire length relative to other shell dimensions (Vermeij, 1993). In this context, remotion of allometric effects is needed in order to detect changes in shell shape.

However, most of the studies dealing with morphological variability in gastropods are restricted to intertidal rocky-shore snails, in particular those belonging to Littorinidae. We know of no attempt made to analyze or even describe patterns of intraspecific variation in neogastropod shell features along a latitudinal axis in the Southern Hemisphere.

The genus *Olivancillaria* d'Orbigny, 1839, is widely distributed along the Atlantic coast of South America. It comprises seven species occurring from tropical areas (Espírito Santo, Brazil) to temperate regions (Golfo San Matías, Argentina) (Burch and Burch, 1964; Klappenbach, 1964; 1965; 1966; Rios, 1994). *Olivancillaria urceus* (Röding, 1798) is distributed along the entire latitudinal range of the genus in subtidal soft bottoms, ranging from the surf zone to at least 35 m depth (Juanicó and Rodríguez-Moyano, 1976; Milstein et al., 1976; Escofet et al., 1979; Scarabino, 1984) and exhibiting conspicuous differences in shell shape as noticed by Baratinni and Ureta (1961). For these reasons, this species is suitable for the examination of patterns of morphological variation in the region.

In this paper we document large-scale variability in shell features of *Olivancillaria urceus* in the temperate sector of it distribution range and analyze this species variability along the latitudinal axis. We also discuss possible ecological implications of the observed pattern.

MATERIALS AND METHODS

A total of 193 specimens collected in seven sites between 32° and 40° S along the Atlantic coast of South America were analyzed. Collection sites were Cassino Beach, Brazil (32°10′ S, 52°20′ W, Site 1), La Coronilla (33° 57′ S, 53°30′, Site 2), La Paloma (34°38′ S, 54°08′ W, Site 3) and Punta del Este (34°36′ S, W 58° 18′ W, Site 4), Uruguay, and Mar del Plata (38°02′ S, 57° 32′ W, Sites 5), Puerto Militar (38°44′ S, 62°10′ W, Site 6) and San Antonio Oeste (40°33′ S, 64°50′ W, Site 7), Argentina (Figure 1). Examined material is deposited at Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (Buenos Aires, Argentina) and Museo Nacional de Historia Natural (Montevideo, Uruguay).

Nine shell dimensions were measured with vernier

Table 1. Sample size, % of variation accounted by PC1 and allometric coefficients for morphometric variables in each collection site. Abbreviations: LWL: last whorl length from suture to anterior end; AL: aperture length, distance along outer lip from suture to anterior end; FB: distance between anterior and posterior ends of fasciolar band along internal side of the aperture; MW: maximum linear distance from outer lip to opposite side; MWH: maximum linear distance perpendicular to MW to anterior end; ST: shell thickness; SW: diameter of spire base from tip of callus above aperture to opposite point on suture; SL2: lateral spire length from tip of callus above aperture to protoconch tip on outer lip side in ventral view, parallel to growth axis; and SL1: same length measured on the opposite side.

	Locality						
Variable	1	2	3	4	5	6	7
Sample size	27	17	39	18	43	21	28
% of variation accounted for by PC1	65.33	67.54	84.36	71.81	94.23	87.82	75.44
Allometric coefficients							
LWL	1.258	0.492	1.098	1.144	1.063	0.985	0.890
AL	1.451	0.374	1.166	0.965	1.072	1.028	1.125
FB	1.544	0.617	1.207	1.086	1.142	1.05	0.948
MW	1.101	0.382	1.12	1.089	1.102	1.134	1.123
MWH	1.386	0.459	1.163	1.041	1.134	1.026	1.062
ST	1.214	0.485	1.143	1.159	1.118	1.043	1.151
SW	1.294	0.760	1.338	1.101	1.136	1.165	1.285
SL1	0.025	2.573	0.426	0.619	0.623	0.750	0.765
SL2	−0.274	2.858	0.340	0.796	0.610	0.819	0.650

calliper, within an accuracy of 0.05 mm. Abbreviations for the variables are as follows: LWL: last whorl length from suture to anterior end; AL: aperture length, distance along outer lip from suture to anterior end; FB: distance between anterior and posterior ends of fasciolar band along internal side of the aperture; MW: maximum linear distance from outer lip to opposite side; MWH: maximum linear distance perpendicular to MW to anterior end; ST: shell thickness; SW: diameter of spire base from tip of callus above aperture to opposite point on suture; SL2: lateral spire length from tip of callus above aperture to protoconch tip on outer lip side in ventral view, parallel to growth axis; and SL1: same length measured on the opposite side (Figure 2). Collection sites were grouped *a priori* for discrimination of differences among samples from different geographic regions. For this we used the non-parametric Kruskall-Wallis ANOVA median test. Allometric coefficients for the seven collection sites were calculated for all variables. The method used was based on Jolicoeur (1963) with additions from Kowalewski et al. (1997). Data were log-transformed and subjected to principal component analysis (PCA). The first principal component (PC1) was regarded as a size axis. Correlation between sampling size and explained variance was examined by means of regression analysis. The allometric coefficient for each original variable was estimated by dividing the PC1 loading for that variable by the mean PC1 loading over all variables. Estimation of 95% confidence intervals for the allometric coefficients was made by bootstrapping specimens (2000 bootstrap replicates were made, not shown).

Size effects were then removed, following Lleonart et al. (2000), by scaling all individual to the same size (mean LWL) adjusting their shape to the one they would have in the new size according to allometric change. PCA was run on transformed data and loads of the eight remaining variables (i.e., all but total length) were calculated. This removal method is one of the most powerful tools available, since it is in turn a theoretical generalization of the technique used by Thorpe (1975, 1976), which was recorded as one of the most efficient methods in the empirical evaluation done by Reist (1985).

A cluster analysis (single linkage, Euclidean distances) was then performed to discriminate among possible morphological groups using site mean value for each variable. The cophenetic correlation coefficient (CCC) was calculated to measure the internal distortion of the cluster analysis following Sokal and Rolf (1962). Finally, possible relationships between latitude and shell characters were examined by regression analysis.

RESULTS

All variables showed significant differences between sites (non–parametric ANOVA: $p < 0.01$). PCA performed with log-transformed data showed that variance explained by PC1 (Factor 1, regarded as size axis) differed among sampling sites and varied between 65.33% (site 1) and 94.23% (site 5). Explained variance was not correlated with sample size (regression analysis, F = :0.010, p-level = 0.922). Allometric coefficients calculated for the nine variables also varied among collection sites. All variables displayed both positive ($b > 1$) and negative ($b < 1$) allometric trajectories (Table 1).

The first three factors in size-free PCA explained together 79.38% of the total variance. Variables MW, MHW, ST, and SW grouped together with positive loads on Factor 1. SL1 and SL2 formed another highly cor-

Table 2. Results of size-free PCA Analysis. % of variance accounted by each factor and loading of each variable are shown. Abbreviations: LWL: last whorl length from suture to anterior end; AL: aperture length, distance along outer lip from suture to anterior end; FB: distance between anterior and posterior ends of fasciolar band along internal side of the aperture; MW: maximum linear distance from outer lip to opposite side; MWH: maximum linear distance perpendicular to MW to anterior end; ST: shell thickness; SW: diameter of spire base from tip of callus above aperture to opposite point on suture; SL2: lateral spire length from tip of callus above aperture to protoconch tip on outer lip side in ventral view, parallel to growth axis; and SL1: same length measured on the opposite side.

	Factor loadings		
Variable	PC1	PC2	PC3
% of variation	41.54	22.9	14.95
AL	0.422	−0.474	0.550
FB	0.173	−0.487	0.716
MW	0.874	0.2125	−0.063
MHW	0.888	0.083	0.034
ST	0.858	0.226	−0.111
SW	0.811	0.246	−0.044
SL1	−0.094	0.815	0.446
SL2	−0.396	0.735	0.399

related group loading positively on Factor 2, and AL and FB did the same on Factor 3 (Table 2).

Two different groups were discriminated when the collection-site mean value for each variable were plotted onto a hierarchical cluster, one of these groups composed by individuals belonging to sites 6 and 7 (Figure 3). The calculated value for CCC was 0.93.

Latitudinal-related patterns of variation were found in variables MW, MHW, ST, AL, and SW. This group of variables showed a decreasing trend with increasing latitude. On the other hand, SL2 tend to increase with latitude, whereas SL1 and FB displayed no relationships. The coefficient of determination (r^2) explained less than 30% for all variables (Figure 4).

DISCUSSION

The present work documents shell shape variation in *O. urceus* along a latitudinal gradient. The results show that shell features vary between sites. The analyses presented above show that northern forms are stunt, low-spired, and conical, whereas southern specimens (mostly those from sites 6 and 7) are high-spired, narrower and elongated.

Within location variation may be due to local differences in habitat conditions, for example, contrasting beach morphodynamics, which are in turn associated with different sediment features. However, the poor geographical definition of collection sites did not allow us to assign in all cases a particular individual to a particular habitat. Notwithstanding, intraspecific phenotypic plasticity in a small spatial scale is known to occur in mollusks. For example, observations made on the muricid *Nucella lapillus* (Linnaeus, 1758) showed that specimens from very exposed shores are short-spired when compared with those from sheltered localities (Cooke, 1895; 1915).

When considering variation at a geographic scale, two possible scenarios are suggested to explain the among-collection sites differences. These are either: (1) a gradual response to shifts in environmental conditions along the latitudinal gradient that generate a shape gradient (in this scenario, macro-scale variation in physical parameters such as sea water temperature and calcium carbonate availability could be correlated with the observed variation); or (2) different morphs associated with par-

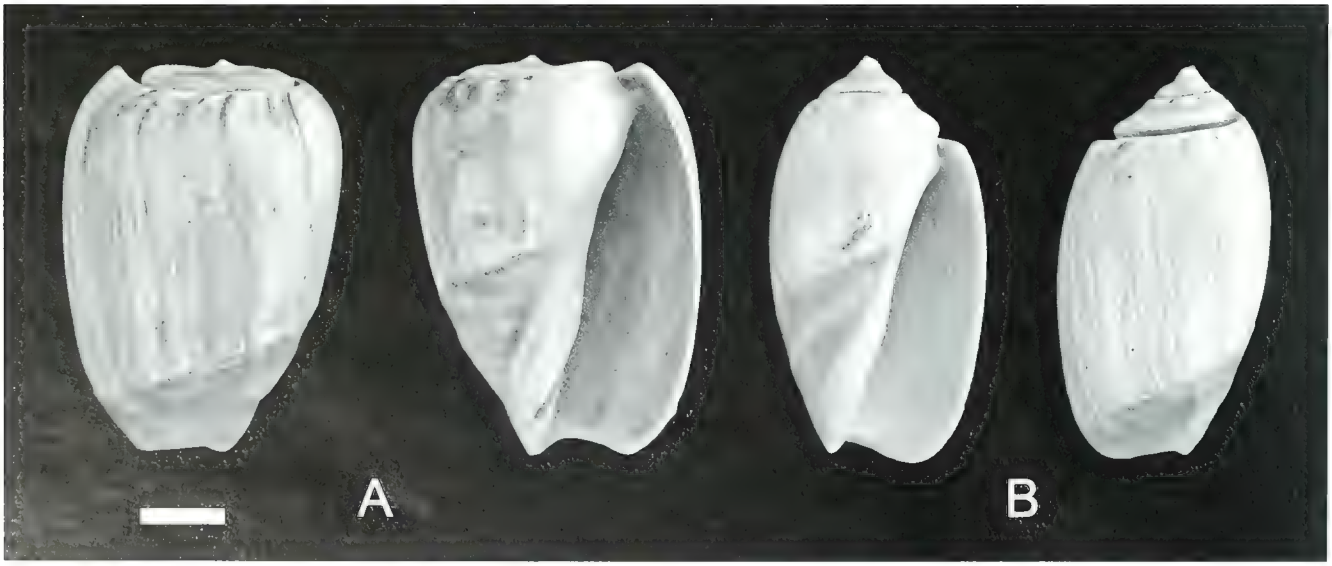

Figure 3. Extreme forms of *Olivancillaria urceus* in the study area **A.** dorsal and apertural view of specimens from site 3. **B.** Dorsal and apertural views of specimens from site 7. Scale bar = 1 cm

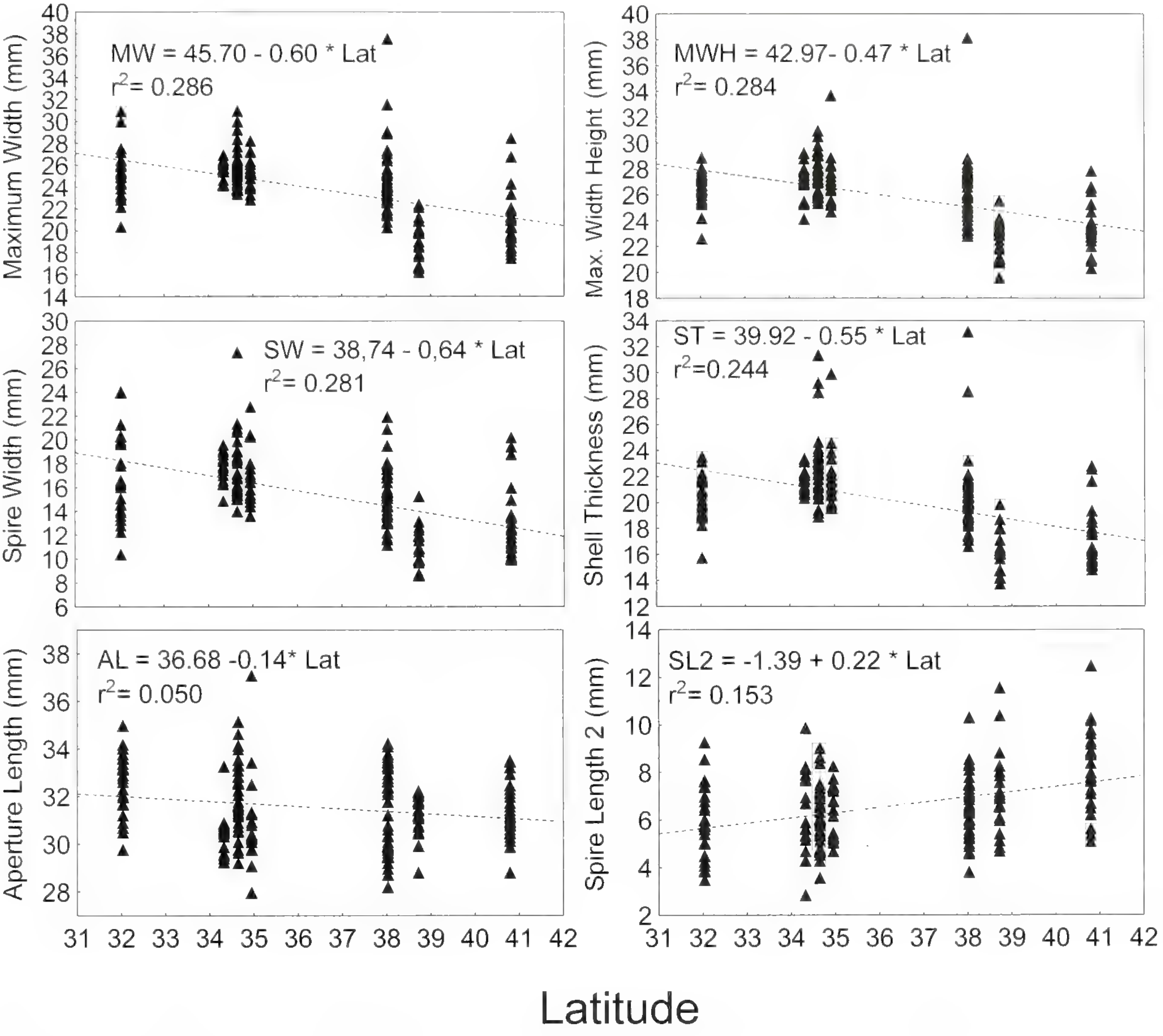

Figure 4. *Olivancillaria urceus,* relationship between standardized shell characters and latitude. Coefficients of determination (r^2) and linear model fitted are shown.

ticular habitats, such as exposed sandy beaches or sheltered bays: broader specimens with short spire in high-energy habitats and high-spired, elongated forms in protected habitats. In this case, likelihood of occurrence of one particular morph depends on environmental characteristics of geographic locations and may be considered local populational phenomena.

A related species, *Olivancillaria vesica* (Gmelin, 1791) also shows two geographical forms, recognized as subspecies, which are easily separable along its distribution range (Klappenbach, 1966). This species shows an opposite latitudinal pattern: northern forms are narrower and longer compared with the broader, "auriculated" (ear-shaped) southern forms. In accordance with (2), the latter form extends along the southern coast of Brazil (Santa Catarina), Uruguay, and Argentina as far as Puerto Quequén, Province of Buenos Aires, the same geographical area in which *O. urceus* displays broader and low spired shells. These broader shell forms could be interpreted as associated with a large foot that enhances its ability of "anchoring" to the substratum in higher energy environments, thus improving individual fitness. However, more study is necessary on the taxonomic status on *O. vesica* forms before any analysis of its morphological variation.

It can be argued that differences in spire length and width reflect shifts in growth patterns associated with the adaptive process. It should be noticed that there is a coincidence between occurrences of high-spired forms (associated with slower growth mode) in higher lati-

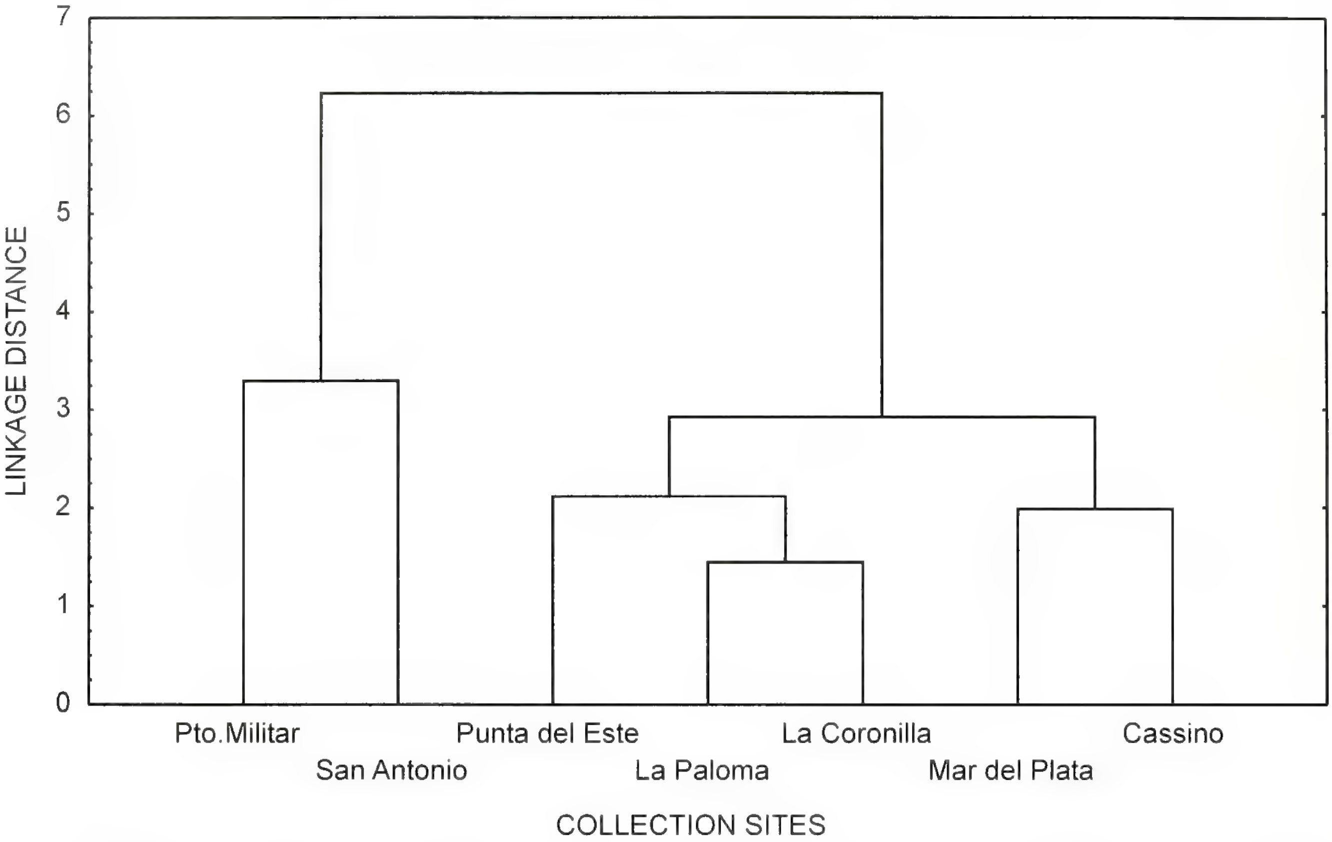

Figure 5. *Olivancillaria urceus*, cluster analysis. Collection sites were grouped on the basis of similarities in the mean value for each morphometric variable.

tudes. This could be supporting the hypothesis that both latitudinal and environmental effects may be coupled together in a combined effect that masks the isolated effects of each factor.

As demonstrated by PCA analysis, nearly half of the variance is explained by PC1 (42% of total variance), which in turn is mainly affected by MW, MWH, ST, and SW. This fact implies that changes in shell shape detected within the analyzed sample are due mostly to differences in its variables. Variation observed in SL2 and SL1 are of much less importance as form determinants when considering total variance components. However, height and shape of the spire and protoconch characters have been regarded as important specific (López et al., 1988) and supraespecific (Tursch, 1988) features, for which these characters deserves further analysis. Nevertheless, it seems that macrogeographic variation in shell morphology strongly depend on local conditions, which make adequate sampling and data treatment very difficult.

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Errata

Due to an editorial lapse, the Introduction section was omitted from Köhler and Glaubrecht's (2005) article in the most recent issue of The Nautilus. The missing Introduction is printed below (literature references are in the main article), with apologies to the authors and readers.

Fallen into oblivion—the systematic affinities of the enigmatic *Sulcospira* Troschel, 1858 (Cerithioidea: Pachychilidae), a genus of viviparous freshwater gastropods from Java

Frank Köhler
Matthias Glaubrecht

INTRODUCTION

The first volume of the well-known work "*Das Gebiss der Schnecken zur Begründung einer natürlichen Klassifikation*" ['Establishing a natural classification of snails from their dentition'] by Franz Hermann Troschel (1810–1882) was published in parts between 1856 and 1863. The work is an important historic landmark in the enduring challenge of zoologists to create a natural classification of the living gastropods. In his work, Troschel (p. 117) described the genus *Sulcospira* within the tribus 'Pachychili' mainly based on features of the operculum and the radula (Figure 1). According to Robertson (1957), that description was published in 1858. Within the non-marine Cerithioidea, *Sulcospira* represents one of the least known genera of Southeast Asian Pachychilidae, a group of viviparous freshwater gastropods we have been focusing on in the last few years.

Recent research aiming to propose a phylogenetic systematics hypothesis and to establish a natural classification of this limnic gastropod family will also allow a better understanding of their evolution, morphology, and ecology (Glaubrecht, 1996; 1999; Köhler and Glaubrecht, 2001; 2002; 2003; Glaubrecht and Rintelen, 2003). Only recently, the Pachychilidae Troschel, 1857, have been shown to represent a monophyletic group clearly distinct from the Thiaridae Troschel, 1857, and from the other limnic Cerithioidea. This new concept has been suggested by analyses of morphological data (e.g. Glaubrecht, 1996; 1999) and is corroborated by molecular data suggesting that Thiaridae (e.g. *Melanoides*, *Thiara*, *Tarebia*) and Pachychilidae (e.g. *Paracrostoma* Cossmann, 1900, *Pachychilus* Lea, 1850) are not very closely related to each other (see phylogenetic reconstruction in Lydeard et al., 2002: figs. 1, 2). This classification conflicts with the traditional view of most earlier authors who treated pachychilid taxa as 'Melaniidae' = Thiaridae (among others, Thiele, 1929; Rensch, 1934; Benthem-Jutting, 1956; Brandt, 1968; 1974) or Pleuroceridae (e.g. Ponder and Warén, 1988; Vaught, 1989).

However, our current knowledge of the phylogeny and systematics of freshwater Cerithioidea in general and the Pachychilidae in particular is still limited, since many taxa remain poorly known. Only recently, systematic studies using morphological as well as molecular genetic data have shed some light on the relationships of several other genera within the Pachychilidae. For instance, Köhler and Glaubrecht (2001) presented comparative morphological data on taxa traditionally assigned to *Brotia* H. Adams, 1866, by various authors, revealing that this genus as previously perceived actually comprises four lineages, each characterized most conspicuously by distinct reproductive morphologies.

Subsequent studies including molecular phylogenetics data put special emphasis on two of these lineages, *Jagora* Köhler and Glaubrecht, 2003, endemic to the Philippines (Köhler and Glaubrecht, 2003) and *Tylomelania* F. and P. Sarasin, 1898, endemic to Sulawesi (Rintelen and Glaubrecht, 1999; 2003), suggesting an independent generic status for each. In addition, the properties of another Australasian pachychilid genus, *Pseudopotamis* Martens, 1894, have been extensively described by Glaubrecht and Rintelen (2003). Hence, a notable portion of crucial biological information on pachychilids has been amassed, helping to facilitate a better understanding of pachychilid systematics, phylogeny, and evolution.

Nevertheless, there remain a number of systematic and taxonomic problems and difficulties related to this group of freshwater snails. One of them will be dealt with in this study: The taxonomy and systematic position of *Sulcospira*.

Among the various generic names that have been introduced for Southeast Asian pachychilid taxa, *Sulcospira* is clearly the oldest one. Its description predates that of other names, such as *Brotia*, *Antimelania* Fischer and Crosse, 1892, or *Pseudopotamis*; a complete annotated list of the introduced supraspecific names within the Southeast Asian Pachychilidae is given in Köhler and Glaubrecht (2002). Consequently, every other supraspecific pachychilid taxon is valid only with the reserve that it is not a junior synonym of *Sulcospira*. In spite of this significant taxonomic role of *Sulcospira*, this taxon has been widely ignored, especially by modern systematists. Thus, another aim of this article is to compile all available information on *Sulcospira* and to provide new data from our own examinations of the limited material from museum collections. In addition, implications for pachychilid taxonomy and systematics are discussed in relation to *Sulcospira*.

LITERATURE CITED

Köhler, F. and M. Glaubrecht. 2005. Fallen into oblivion—the systematic affinities of the enigmatic *Sulcospira* Troschel, 1858 (Cerithioidea: Pachychilidae), a genus of viviparous freshwater gastropod from Java. The Nautilus 119: 15–26.

In the recently published article by Ardila and Valdés (2004), please note the following corrections:

On page 134, caption of Figure 3, replace "*Armina muelleri* Thompson, Cattaneo and Wong, 1990", for "*Armina muelleri* (Ihering, 1886)";

On the same page, the adjacent subsections "**Type Material**" and "**Type Locality**" should be replaced by:

Material Examined: MHNMC INV MOL3901, 32 mm length, alive, from off Salamanca Island, Colombia (11°5′46″ N, 74°40′35″ W), 20 m depth, hard bottom with pennatulaceans (*Renilla reniformis* and *Renilla muelleri*).

LITERATURE CITED

Ardila, N. E. and A. Valdés. 2004. The genus *Armina* (Gastropoda: Nudibranchia: Arminidae) in the southern Caribbean, with the description of a new species. The Nautilus 118: 131–138.

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The Sphaeriidae (Bivalvia) from northwestern Argentina including three new species of *Pisidium*

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ABSTRACT

Knowledge on the Sphaeriidae fauna in southern South America is significantly improved with the description of three new species of the genus *Pisidium* from Salta and Jujuy provinces (northwestern Argentina). This paper provides the first record of sphaeriids in restrictive high-altitude South American environments, particularly from very small water courses found in "vegas", exceptionally localized areas of "cushion vegetation" or "cushion peat bogs" developing between 2000–4000 m altitude in the Argentine pre-Andean ranges. Furthermore, the geographic distribution range of *Pisidium chiquitanum* Ituarte, 2001, only reported to date from the type locality in sub-Andean regions of central Bolivia, is considerably enlarged.

INTRODUCTION

The Sphaeriidae fauna from Argentina is poorly known; the first reports were those by Strobel (1874) on *Musculium argentinum* (d'Orbigny, 1835) and Pilsbry (1911) describing several new species of *Pisidium* C. Pfeiffer, 1821, and *Musculium* Link, 1807, from Patagonia. Later on, Doello-Jurado (1921) described the first species of *Eupera* Bourguignat, 1854, from Argentina, and Ituarte (1989, 1994) and Ituarte and Dreher-Mansur (1993) described three new species of *Eupera* from Iguazú, Uruguay and Paraná River basins in northeastern Argentina. Regarding the species diversity of *Pisidium* C. Pfeiffer, 1821, twelve species are known from Patagonia and Northeastern provinces (Ituarte, 1996, 1999, 2000).

Only two species of Sphaeriidae have been reported from northwestern Argentina: *Sphaerium lauricochae* (Philippi, 1869), from Jujuy Province (Ituarte, 1995) and *Musculium argentinum* from Mendoza Province (Strobel, 1874). The species diversity of *Pisidium* has essentially not been documented. In the present paper, three new species of *Pisidium* from lowland and high-altitude habitats in the pre-Andean mountain ridges are described. Based on new findings the knowledge on the geographic distribution of *Pisidium chiquitanum* Ituarte, 2001, is updated.

MATERIALS AND METHODS

Materials for the present study were obtained during three field trips to Northwestern Argentina (Tucumán and Salta provinces in March 1999, Salta and Jujuy provinces in December 2001 and March 2004, and Catamarca Province in March 2004). Figure 1 shows the location of collecting sites; more detailed information on the source of specimens is given in the Systematics section. The collected specimens were fixed immediately after collecting in 70° alcohol after being relaxed through a short rinse (around 20 seconds) in warm water (about 50°C). Specimens for scanning electron microscopy (SEM) were cleaned by repeated rinsing in distilled water followed by a short treatment (about 5 seconds) in 10% sodium hypochlorite solution. Soft anatomy was studied after decalcification of valves through a 12-hour rinsing in a 5% formaldehyde and 2% acetic acid solution. Linear measurements (shell length [SL], shell height [SH], shell width [SW] and presiphonal suture length [PSS]), shape indices and morphometric ratios (height index [HI= SH/SL], convexity index [Ci= SW/SH], ratio of hinge length [HiL] to shell length [HiL/SL]), were calculated according to the criteria followed by Ituarte (1996). For each calculation (n= 10, unless otherwise stated), mean and standard deviation values are given.

Type specimens are deposited at Museo de La Plata, La Plata (MLP), Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires (MACN), Fundación Miguel Lillo, Tucumán (FML) and Muséum National d'Histoire Naturelle, Paris (MNHN). Types of *Pisidium chiquitanum*, housed at Museo de Historia Natural "Noel Kempff Mercado", Santa Cruz de La Sierra, Bolivia (MHNB) and MLP were also used for comparative purposes.

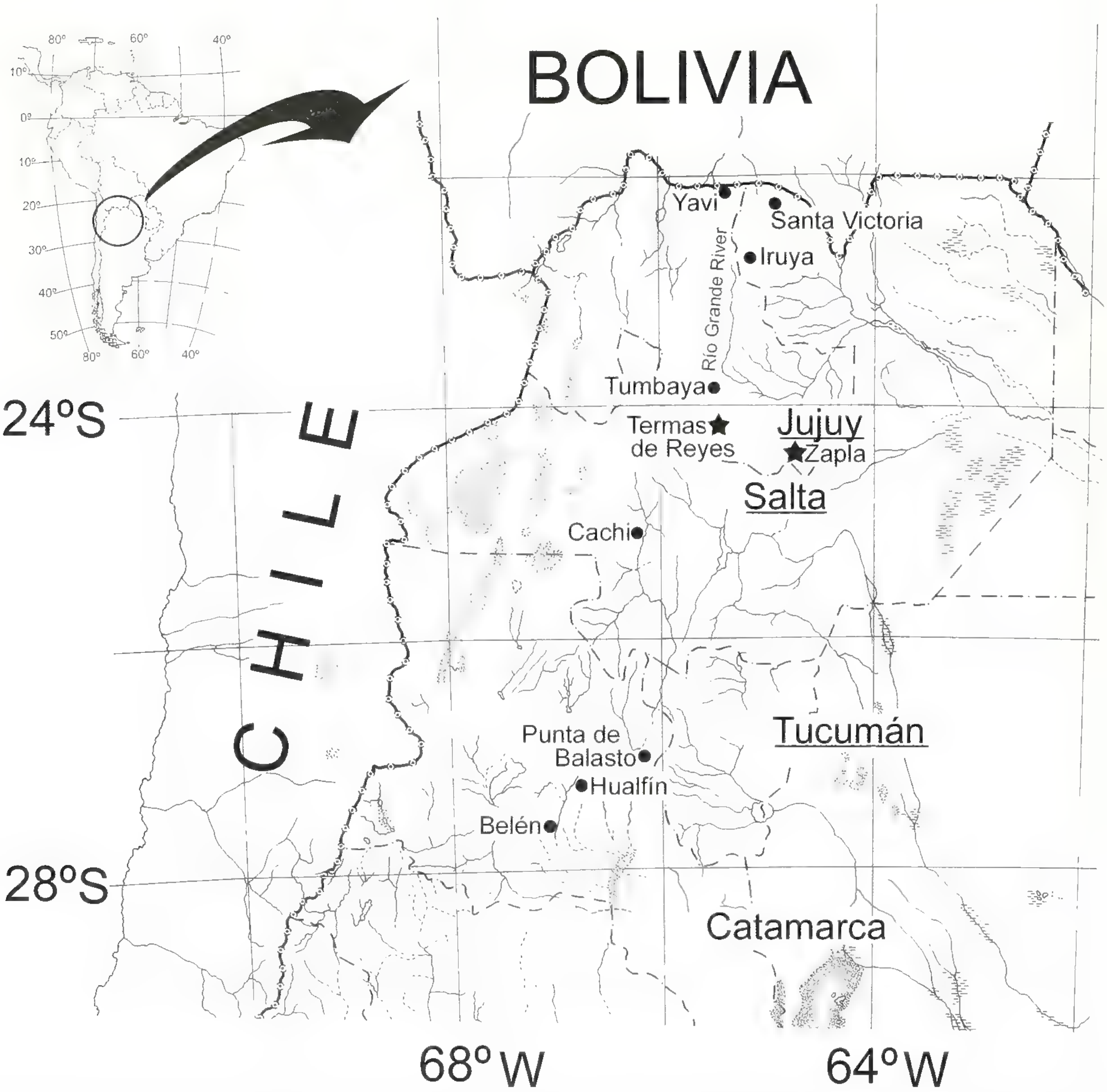


Figure 1. Location map. Stars in black indicate type localities of *Pisidium omaguaca* new species, *Pisidium ocloya* new species, and *Pisidium chicha* new species.

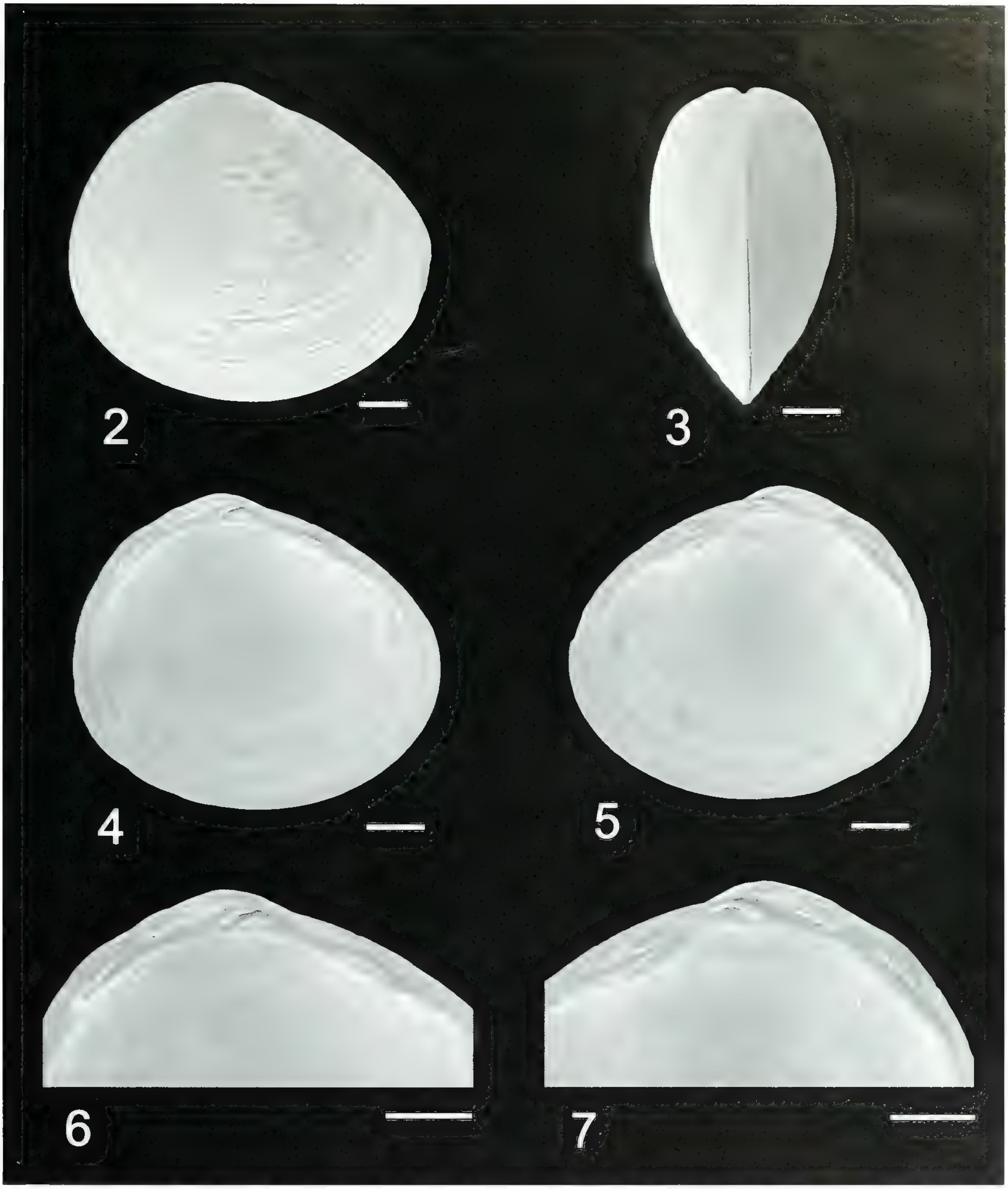
SYSTEMATICS

Pisidium omaguaca new species
(Figures 2–15)

Diagnosis: Shell markedly oval, high and anteriorly produced, beaks depressed, displaced backward, not projecting from shell surface and only barely visible above dorsal margin; ligament internal; anal and branchial mantle openings present; two demibranchs present, nephridia of closed type, with lateral lobe not visible in lateral or dorsal views.

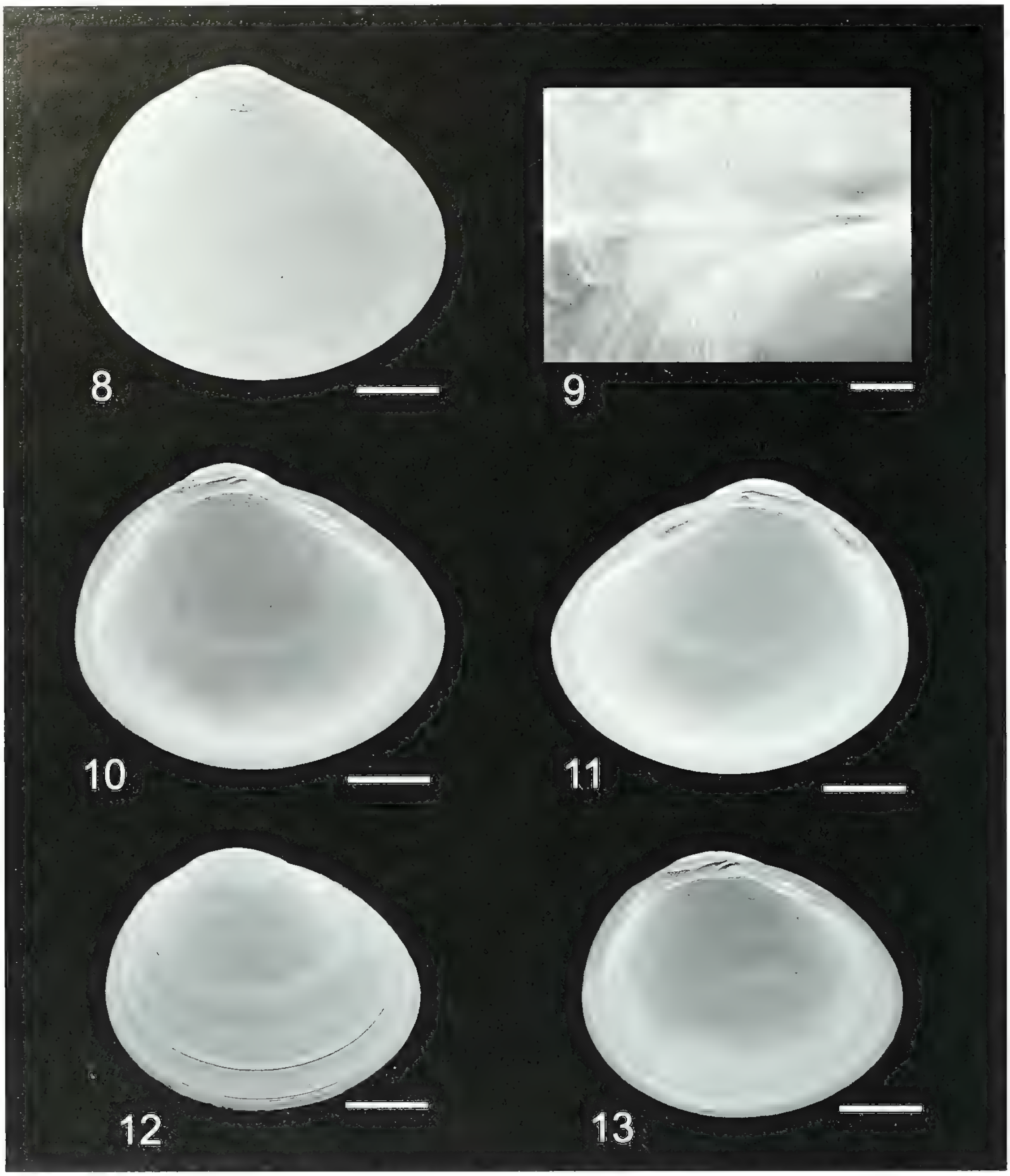
Description: Shell thin, translucent, small to medium size (mean SL = 2.73 ± 0.17, maximum observed size: 3.7 mm), rather high (mean HI = 85 ± 1) (Figure 2), not inflated (mean Ci = 58 ± 3) (Figures 2, 3). Shell outline markedly oval, anteriorly elongated. Anterior end produced in a sharp curve, posterior end short, widely rounded, sometimes slightly truncated and straight (Figures 2, 4, 5, 8). Dorsal margin short, weakly connected with anterior margin, which slopes markedly towards anterior end; sometimes, a gentle angle marks joining point of dorsal and posterior margins (Figure 8). Beaks very low, depressed and wide, not raised from shell surface, only slightly projected above dorsal margin, displaced backward, located at about 59% of SL (Figures 2, 4, 5). Shell surface finely and somewhat irregularly striated, glossy, amber.

Hinge plate strong, hinge line short (HiL/SL = 53 ± 3), strongly curved. Hinge: Left valve (Figures 4, 6): cardinal teeth well-developed, the inner one (C_2) thin, short at base, bent upward, slightly oblique with respect



Figures 2–7. *Pisidium omaguaca* from Termas de Reyes, Jujuy. **2.** Holotype (MLP 5496-1-1): outer view of right valve. **3–7.** Paratypes (MLP 5496-1-2). **3.** Posterior view. **4.** Left valve, inner view. **5.** Right valve, inner view. **6.** Left valve, detail of hinge **7.** Right valve, detail of hinge. Scale bars = 500 μm

to antero-posterior axis, rounded at the tip, outer cardinal tooth (C$_4$) a narrow, slightly wider at posterior end, uniformly curved blade, quite oblique, overlapping C$_3$ at posterior half; anterior lateral tooth (AII) very strong, short, nearly straight, cusp high, pointed, displaced forward; posterior lateral tooth (PII) minute, straight and strong, cusp high, distally displaced. Right valve (Figures 5, 7): cardinal tooth (C$_3$) not strong, somewhat displaced forward, curved in the middle, quite narrow at anterior half, slightly enlarged in a posterior

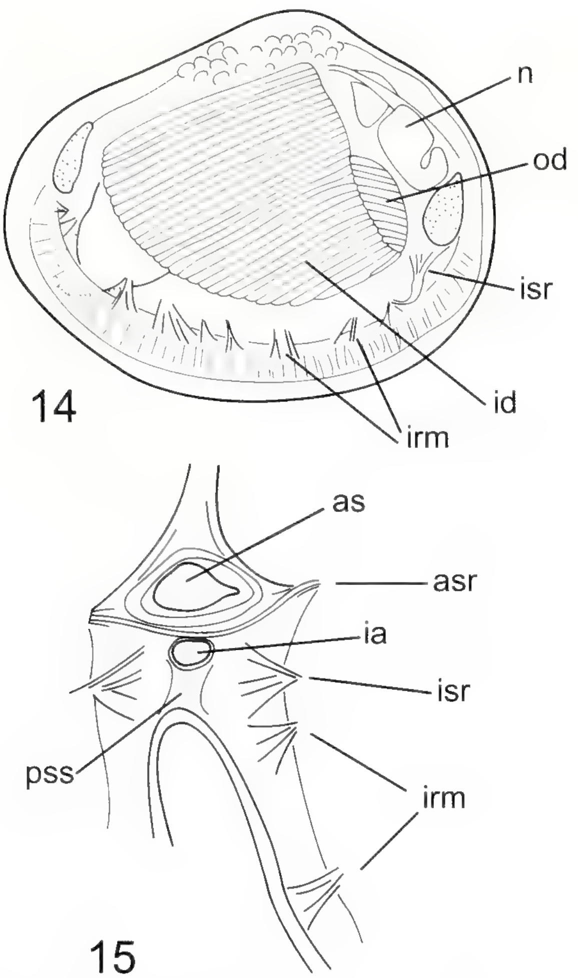


Figures 8–13. *Pisidium omaguaca*. **8.** Paratype (MLP 5485). Right valve, outer view. **9.** Paratype (MLP 5496-1-2). Dorsal view, detail of the escutcheon. **10–11.** Inner view of left and right valves of a specimen from Tiraxi, Jujuy (MLP 6535). **12, 13.** Outer and inner views of right and left valves of a specimen from a "peat bog" between Yavi (Salta) and Santa Victoria (Jujuy) (MLP6559). Scale bars (**8, 10–13**) = 1000 μm; (**9**) = 200 μm.

elongated cup. Lateral teeth short and robust, inner anterior lateral (AI) curved, cusp subcentral or slightly displaced anteriorly; outer anterior lateral tooth (AIII) quite short, cusp distal; inner posterior lateral (PI) nearly straight, short, cusp subcentral; outer posterior lateral (PIII) minute, with distal cusp.

Ligament-pit enclosed, deep, inner margin straight or slightly concave (Figures 6, 7). Ligament relatively short, representing 20 ± 1% of shell length, strong, internal, never visible from outside (Figure 9). Escutcheon inconspicuous (Figure 9).

ANATOMY: Anal siphon and branchial inhalant mantle opening present. Presiphonal suture about 9% of shell length (Figure 15). Eight or nine well-marked muscle scars located away from pallial line correspond to inner radial mantle muscles. Muscle scars corresponding to anal siphon retractors are coalescent with that of



Figures 14–15. *Pisidium omaguaca* new species. **14.** Gross anatomy. **15.** Mantle muscles. (**as:** anal siphon; **asr:** anal siphon retractor; **ia:** inhalant aperture; **id:** inner demibranch; **isr:** inhalant siphon retractor; **irm:** inner radial mantle muscles; **n:** nephridium; **od:** outer demibranch; **pss:** presiphonal suture).

posterior adductor muscle (Figures 4, 5). Bundles of fibers of inner radial mantle muscles strong, converging anteriorly, except for two posterior bundles (Figures 4, 5, 14).

Inner and outer demibranchs present. Outer demibranch much smaller, formed by 10–12 very short descending filaments, reaching back to the 14th filament of inner demibranch (Figure 14). Up to three large embryos (1.3 mm length) were found within each brood pouch of a specimen 3.7 mm L. Nephridia of closed type, dorsal lobe, usually subquadrate, completely covering pericardial part of nephridium (Figure 14).

Type Locality: A small watercourse opening into Reyes River at Termas de Reyes, 24°10′19″ S, 65°29′27″ W, 1754 m altitude, Jujuy Province, Argentina (Figure 1).

Type Material: Holotype (MLP 5496-1-1) and 42 paratypes from the type locality (16 paratypes MLP 5496-1-2; 6 paratypes MLP 5485; 4 paratypes MACN-In 36361; 12 paratypes FML 14506; and 4 paratypes MNHN.

Other Material Examined: Jujuy Province: numerous specimens from the type locality (MLP 5496-1-3); Tumbaya, small pool with vegetations at the side of national road No. 9 (23°47′28″ S, 65°28′37″ W), 2070 m (MLP 6548); small stream flooding from springs in highland areas covered with "cushion vegetation", between Yavi (Jujuy) and Santa Victoria (Salta) (22°07′11″ S 65°13′05″ W), 4150 m (MLP 6559); small pool at the side of Río Grande River (22°58′14″ S 65°27′01″ W), 3950 m (MLP 6530); small springs at side of Manzanito Rivulet, near Huertas (22°14′20″ S 65°00′31″ W), 2740 m (MLP6551); small stream at the side of the road to Yala (24°07′20″ S 65°24′16″ W), 1430 m (MLP 6531). Salta Province: unnamed brook on provincial road No. 57, near Cachi (25°05′24″ S 66°07′33″ W), 2340 m (MLP 6540).

Distribution: Highlands of Jujuy and Salta provinces, Argentina, between 1400 and 4100 m altitude.

Etymology: The name refers to the Omaguacas, ancient aboriginal inhabitants of the Quebrada de Humahuaca, the spectacular 150 km long valley of the Río Grande River (Figure 1), which underwent a major cultural change during the past 10,000 years.

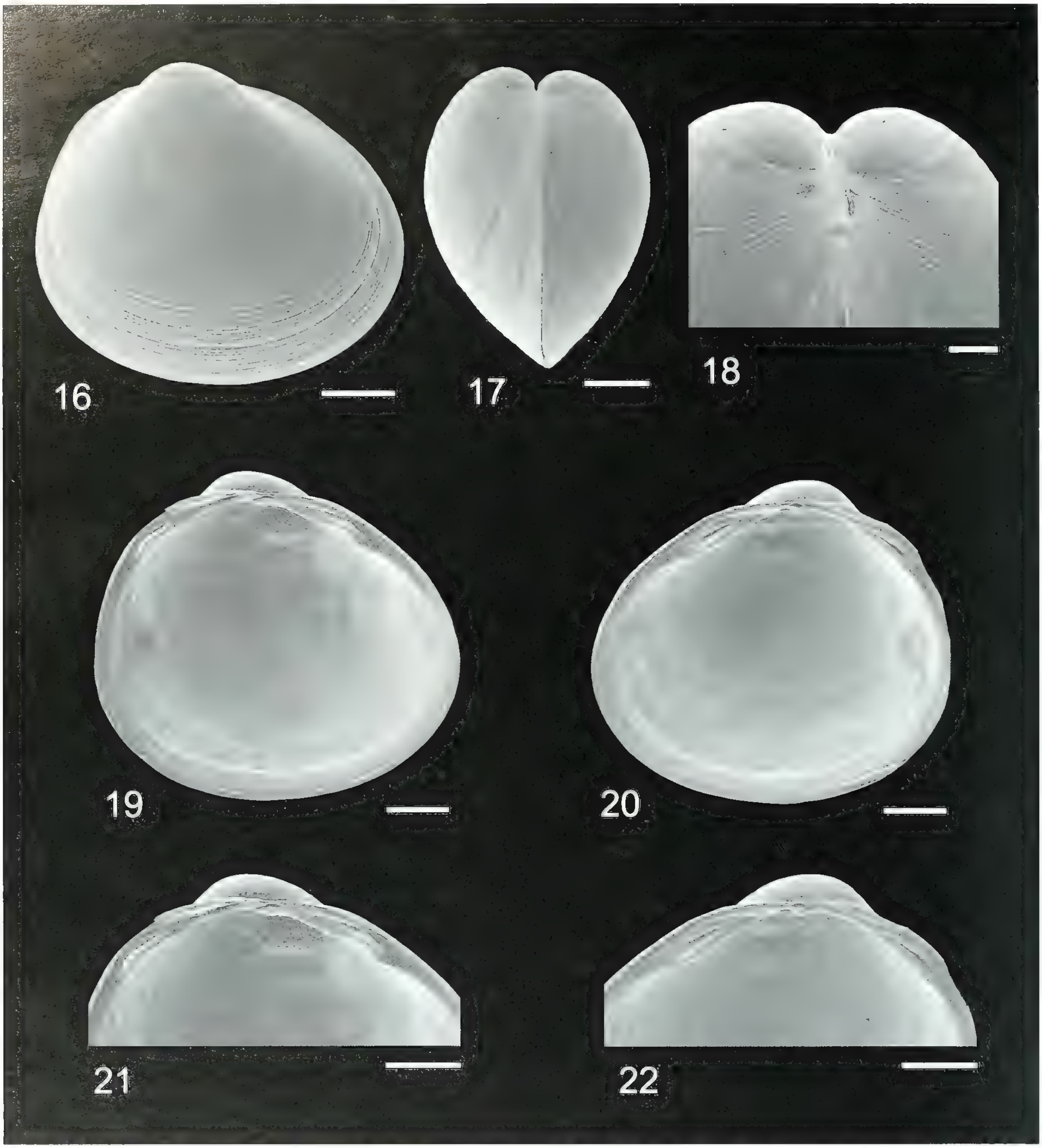
Remarks: *Pisidium omaguaca* new species differs from *Pisidium meierbrooki* Kuiper and Hinz, 1984, in being higher and less obese, having lower and not inflated beaks, and a more broadly rounded posterior end. *Pisidium omaguaca* new species is similar to *Pisidium chiquitanum* Ituarte, 2001, in soft anatomy, but differs in having a more solid and higher shell, with posterior end shorter and anterior half of dorsal margin sloping markedly towards the anterior end.

Pisidium ocloya new species
(Figures 16–33)

Diagnosis: Shell rather trapezoidal and high, small size, presence of only one (anal) mantle aperture and one demibranch.

Description: Shell thin, translucent, of small to medium size (maximum observed SL = 3.2 mm), high (mean HI = 85 ± 2), quite convex (mean Ci = 77 ± 4), shell outline rather trapezoidal. Anterior end somewhat produced in a sharp curve, posterior end short, truncate, somewhat oblique (Figures 16, 17). Beaks full, wide at base, markedly raised from shell surface and projected above dorsal margin, subcentral or slightly displaced backward, located at about 58% of SL (Figures 16, 19, 20). Shell surface finely and irregularly striated (Figures 16, 18), glossy, whitish or yellowish.

Hinge plate not strong, narrow in middle, hinge line rather long (HiL/SL = 56 ± 2), arcuate. Hinge on right valve (Figures 20, 22): cardinal tooth (C_3) delicate,



Figures 16–22. *Pisidium ocloya* new species from Burrumayo River, Jujuy. **16.** Holotype (MLP 5499-1): outer view of right valve. **17–22.** Paratypes (MLP 5499-2). **17.** Posterior view. **18.** Posterior view, detail of ligament. **19.** Left valve, inner view. **20.** Right valve, inner view. **21.** Left valve, detail of hinge. **22.** Right valve, detail of hinge. Scale bars (**16, 17, 19–22**) = 500 μm; (**18**) = 200 μm

rather weak, slightly curved, narrow on anterior half, enlarged into a well-marked, blunt, posterior cup. Lateral teeth robust, inner anterior lateral (AI) well-developed, cusp displaced distally; outer anterior lateral tooth (AIII) shorter and weaker, cusp distal; inner posterior lateral (PI) gently curved, not long, cusp distally displaced; outer posterior lateral (PIII) reduced in size, with distal cusp. Hinge on left valve (Figures 19, 21): cardinal teeth minute, inner one (C_2) short and high, horizontal with respect to antero-posterior axis, outer one (C_4) short, oblique, slightly overlapping C_2 at posterior end; anterior lateral tooth (AII) very strong, cusp high, distal; posterior lateral tooth (PII) shorter and weaker, cusp high, distal.

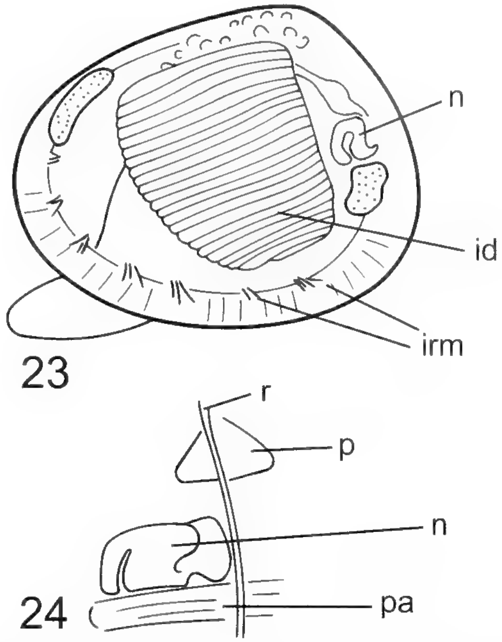
Ligament-pit enclosed, deep, inner margin slightly and evenly curved (Figures 21, 22), Ligament narrow, relatively long, representing 24 ± 1% of shell length, visible from outside and somewhat protruded at anterior half of ligament length. Escutcheon slightly marked by a delicate lanceolate line (Figures 17, 18).

ANATOMY: Only one demibranch (inner) present (Figure 23). Only anal mantle opening present. Inner radial mantle muscles weak, 6–7 bundles of few weak fibers converging anteriorly, attached just above pallial line (Figure 23); sometimes scars corresponding to inner radial muscles coalescent with pallial line (Figures 19, 20). Anal siphon retractors attached immediately ventrally to posterior adductor muscle. Nephridium with lateral loop visible dorsally (Figure 24).

Type Locality: Small flooded areas on the banks of Burrumayo River (24°10′18″ S, 65°22′43″ W), 1201 m altitude, in the neighborhood of Jujuy City, Jujuy Province, Argentina; and unnamed brook opening into Zapla River (24°16′03″ S, 65°07′09″ W), 946 m altitude, Zapla, Jujuy Province, Argentina.

Type Material: Holotype (MLP 5499-1) and 15 paratypes from the outskirts of Jujuy City (6 paratypes MLP 5499-2; 10 paratypes FML 14505; 56 paratypes from Zapla (36 paratypes MLP 6899-2; 10 paratypes MACN-In 36362; 10 paratypes MNHN).

Other Material Examined: Catamarca Province: unnamed brook at national road No. 40 at La Ciénaga de Abajo, between La Ciénaga and Belén (27°31′05″ S, 66°59′08″ W), 1520 m (MLP 7201); Jujuy Province: numerous specimens from the type locality (MLP 7369); unnamed brook on side of provincial road No. 4 at Guerrero (24°11′13″ S, 65°26′51″ W), 1650 m (MLP 7379); small spring on side of provincial road No. 4, near Termas de Reyes (24°10′36″ S 65°28′18″ W), 1730 m (MLP 5497-1, MLP 7370-1); small water course on side of national road No. 9 at Tumbaya (23°51′26″ S, 65°27′57″ W), 2020 m; Los Cedros Rivulet, south to "El Carmen" (24°28′0″ S 65°17′08″ W), 1190 m (MLP 6545-1); small spring near Tiraxi (23°59′57″ S, 65°19′39″ W), 1576 m (MLP 6553); on the road between Termas de Reyes and Laguna Yala, flooded areas at the bottom of hills (24°07′47″ S, 65°28′58″ W), 1920 m (MLP 7371). Salta Province: unnamed brook at national road No. 40 at Molinos (25°18′53″ S, 66°14′58″ W), 2155 m (MLP 6526); small spring at road No. 33 to Cachi at Los Laureles (25°06′27″ S, 65°36′10″ W), 1360 m (MLP 6529); Tucumán Province: flooded areas at side of the Nío River, near Río del Nío City (26°25.60′ S 64°55.60′ W), 886 m (MLP 7403); on side of Medina River, on provincial road No. 305, between El Tipal and Aserradero (MLP 7404-1); small pond on side of Potrero de Las Tablas River, Raco, 880 m (MLP6992), La Angostura dam, on Los Sosa River (26°55′21″ S, 65°41′02″ W), 2000 m (MLP 6897-2).



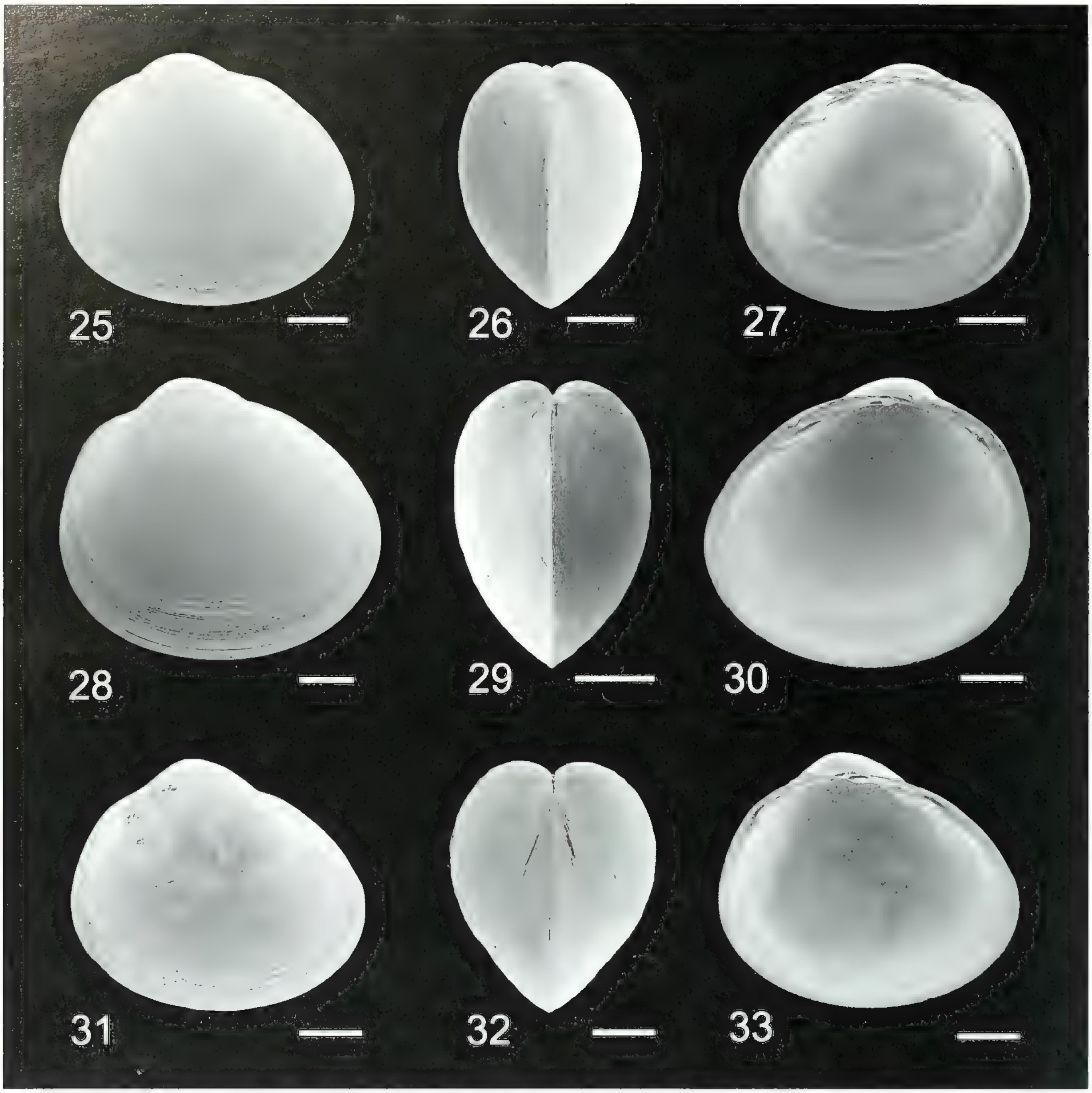
Figures 23–24. *Pisidium ocloya* new species. **23.** Gross anatomy. **24.** Detail of nephridium. (**id:** inner demibranch; **irm:** inner radial mantle muscles; **n:** nephridium; **p:** pericardium; **pa:** posterior adductor; **r:** rectum.

Distribution: Catamarca, Jujuy, Salta, and Tucumán provinces, Argentina, between 880 and 2155 m altitude.

Etymology: The name of the new species refers to the Ocloyas, ancient aboriginal inhabitants of the lands in the surroundings of the type locality.

Remarks: *Pisidium ocloya* new species strikingly differs from other northwestern Argentine *Pisidium* species by its relatively small size and trapezoidal shell outline. Compared with *Pisidium vile* Pilsbry, 1987, a small species from the eastern drainage system of the Río de La Plata Basin, *P. ocloya* new species differs in being larger and comparatively lower. Ituarte (1999) described *Pisidium huillichum* from southern Chile, another small-sized *Pisidium* species with one mantle opening and one demibranch, which differs from *P. ocloya* in having a non trapezoidal shell outline, lower beaks, very strong lateral teeth, and strongly marked commarginal ribs of the shell surface.

The height/length ratio, the convexity index and the degree at which part of the ligament is protruded showed a relatively wide variability in samples of *Pisidium ocloya* from different localities (Figures 25–33); larger specimens were in general more convex with much inflated and pronounced beaks, and more sharply defined trapezoidal outline.



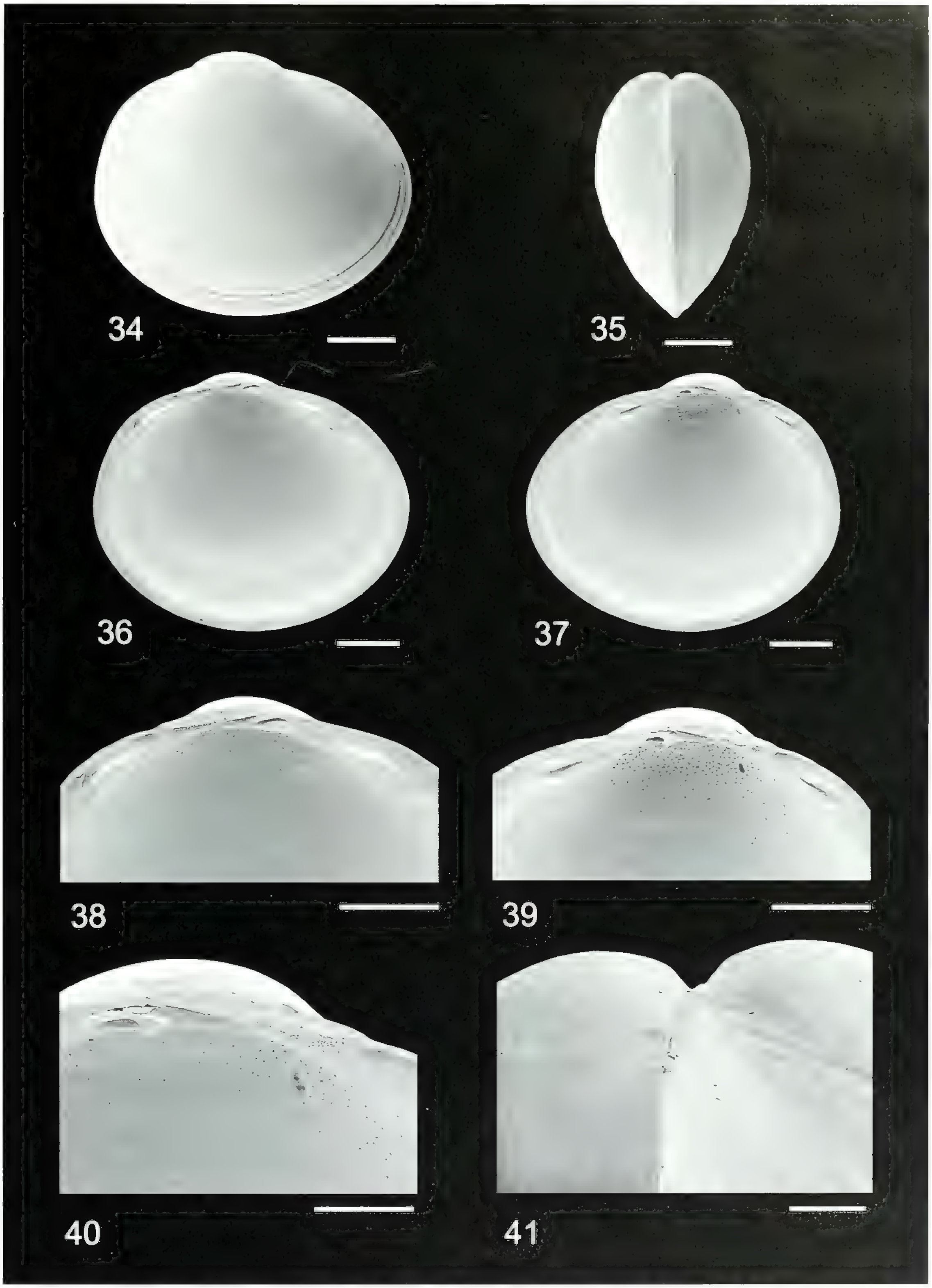
Figures 25–33. *Pisidium ocloya* new species. **25–27.** Specimens from Termas de Reyes, Jujuy (MLP 5497-1). **28–30.** Specimens from Zapla, Jujuy (MLP 6899-2). **31–33.** Specimens from Cachi, Salta (MLP 6529). Scale bars = 500 μm.

Pisidium chicha new species
(Figures 34–43)

Diagnosis: Rather elliptic shell outline, sub-centrally located beaks, somewhat inflated and markedly raised from shell surface, are diagnostic features. The presence of only one mantle aperture and one demibranch is also distinctive.

Description: Shell small, maximum observed shell length 2.7, moderately high (mean HI = 79 ± 1), not convex (mean Ci = 68 ± 5); shell outline strikingly oval. Dorsal and ventral margins broad, dorsal margin, slightly arcuate, ventral margin uniformly curved; anterior end evenly curve and only slightly projected forward, posterior end slightly truncated (Figures 34–37). Beaks wide, widely rounded at tip, somewhat inflated, raised above dorsal margin but low, sub-central, slightly displaced backward, located at about 57–58% of SL. Shell surface glossy, amber, sculptured with well marked fine and rather regularly spaced striae (Figure 34).

Hinge plate narrow, hinge line somewhat short, HiL/SL = 53 ± 3% of SL (n = 8), widely curved. Hinge on left valve (Figures 36, 38): cardinal teeth well-developed, the inner one (C_2) thin, long, straight at base, bent upward distally, parallel with respect to antero-posterior axis, rounded at tip, outer one (C_4) a slender, slightly



Figures 34–41. *Pisidium chicha* new species. **34.** Holotype (MLP 6899-1-1): outer view of right valve. **35–41.** Paratypes (MLP 6899-1-2). **35.** Posterior view. **36.** Left valve, inner view. **37.** Right valve, inner view. **38.** Left valve, detail of hinge. **39.** Right valve, detail of hinge. **40.** Right valve, detail of cardinal tooth and ligament. **41.** Posterior view, detail of ligament. Scale bars (**34–37**) = 500 μm; (**38, 39**) = 200 μm; (**40**) = 250 μm; (**41**) = 100 μm

curved blade, quite oblique, overlapping C_2 on posterior half; anterior lateral tooth (AII) very strong, straight, cusp high, somewhat acute, displaced distally; posterior lateral tooth (PII) short, strong, cusp high, distal. Hinge on right valve (Figures 37, 39, 40): cardinal tooth (C_3) well-developed, narrow, and evenly curved on anterior half, quite enlarged into triangular, slightly grooved cup at posterior end; slightly hanging from inner margin of hinge plate. Lateral teeth short and robust, inner anterior lateral (AI) somewhat curved, cusp displaced forward; outer anterior lateral tooth (AIII) very short, straight, with distal cusp; inner posterior lateral one (PI) short, straight, slender and low, cusp sub-central; outer posterior lateral one (PIII) minute, with distal cusp.

Escutcheon lanceolate, long, outline demarcated by a very delicate line. Ligament-pit enclosed, inner margin gently sinuous (Figures 40, 41). Ligament moderately strong, internal, slightly visible from exterior, but not protruded, representing about 23% of shell length.

ANATOMY: Only one (anal) mantle opening present. Only inner demibranch present (Figure 42). Inner radial mantle muscles weak, inserted just above or coalescent with pallial line. Nephridium with dorsally visible lateral loop (Figure 43).

Type Locality: Unnamed brook flooding into Zapla River in the neighborhood of Zapla City (24°16′01″ S, 65°07′09″ W), 946 m altitude, Jujuy Province, Argentina, and small springs on bank of Manzanito Rivulet, on the road from Santa Victoria East to Yavi near Huertas (22°14′20″ S, 35°00′31″ W), 2740 m, Jujuy Province, Argentina.

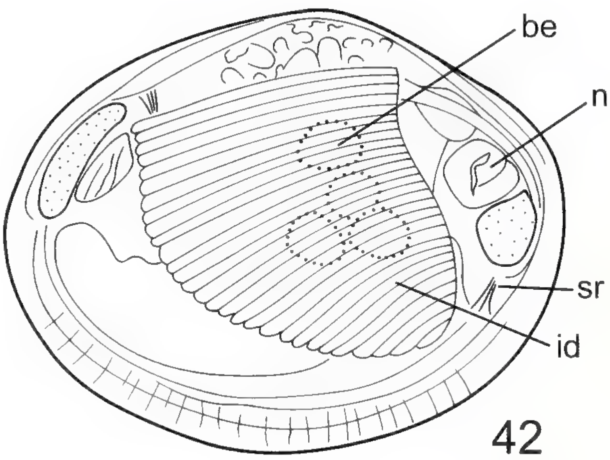
Type Material: Holotype (MLP6899-1-1), 9 paratypes (7 paratypes MLP 6899-1-2; 2 paratypes MACN-In 36363) from 24°16′ S, 65°12′ W; 62 paratypes from 22°14′20″ S, 35°00′31″ W (52 paratypes MLP 6550; 5 paratypes FML 14775; 5 paratypes MNHN).

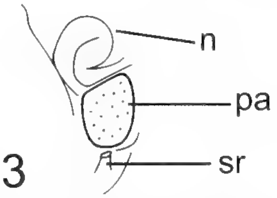
Other Material Examined: Catamarca Province: flooded areas at side of an unnamed river on the road to Singuil, (27°38′25″ S, 65°57′23″ W), 2000 m (MLP7203). Jujuy Province: Los Cedros Rivulet, close to Las Maderas Dam (24°28′40″ S 65°17′08″ W), 1190 m (MLP 6545-2). Tucumán Province: small pools at the side of Medina River, on provincial road 305 between El Tipal and Aserradero (MLP 7404-2).

Distribution: Catamarca, Jujuy and Tucumán provinces, Argentina, between 940 and 2740 m altitude.

Etymology: The name of the new species alludes to the Chichas, a small ethnic group that was a part of the Omaguaca people, who inhabited the lands in the neighborhood of the type locality.

Remarks: The shell shape, quite ovate and nearly equilateral, and the marked sculpture of *Pisidium chicha* new species are distinctive features that allow for easy identification of the new species among other *Pisidium* species from northwestern Argentina. A moderate shell variation was observed: the specimens from Manzanito Rivulet (MLP 6550) show shells slightly more convex and higher than those of the specimens from Zapla (MLP 6899-1); the striae were slightly coarser and more marked in the former group. Specimens from Catamarca Province (MLP 7203) show slightly inequilateral shells, with posterior end slightly shorter. *Pisidium chicha* shares with *P. ocloya* the same number of mantle openings and demibranchs and the nephridium with lateral lobe dorsally visible; but the former species strikingly differs in having a smaller shell with quite an oval shell outline. The presences of only one demibranch and one mantle opening in *P. chicha* clearly separate this species from *P. chiquitanum*. In addition, this latter is a larger species of relatively similar shell outline but that also differs from *P. chicha* in having an almost smooth shell surface, lower, more backward displaced beaks, and somewhat truncated posterior end.





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Figures 42–43. *Pisidium chicha* new species. **42.** Gross anatomy. **43.** Detail of nephridium. (**be:** brooding embryos; **id:** inner demibranch; **n:** nephridium; **pa:** posterior adductor; **sr:** siphon retractor).

Pisidium chiquitanum Ituarte, 2001
(Figures 44–47)

Pisidium chiquitanum Ituarte, 2001: 50; figs. 2–14 (La Siberia, West of Comarapa, Santa Cruz de La Sierra, Bolivia, holotype MHNB 34734).

Diagnosis: Rather elongate shell outline, slightly truncated at posterior end, low and posteriorly located beaks, ligament position, internal but externally visible, presence of branchial and anal openings, two demibranchs on each side and nephridia of closed type.

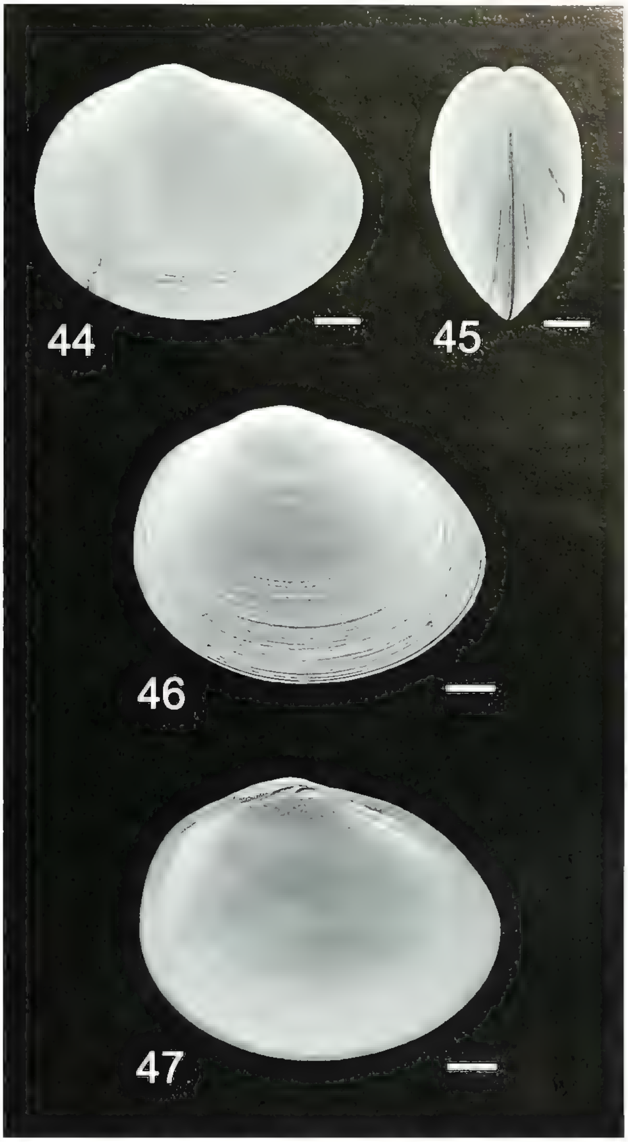
Description: Shell thin, small to medium size (mean SL = 3.9 ± 0.25; maximum observed size: 4.2 mm), not very high (mean HI = 80 ± 1), not convex (mean Ci = 61 ± 4), shell outline markedly oval, elongate, anteriorly produced, posterior end short, widely rounded, or slightly truncated and nearly straight (Figures 44, 46, 47). Beaks low, depressed, slightly projected above dorsal margin, located at about 62% of SL (Figures 44–46). Shell surface dull glossy, straw-yellowish, with fine and low commarginal striae, moderately more accentuated towards the shell margin (Figures 44, 46).

Hinge plate solid, hinge line rather long (HiL/SL = 56 ± 2). Hinge on right valve: Right cardinal tooth (C_3) strongly curved in middle, quite narrow on anterior half, enlarged into gently sulcated, rounded, or somewhat elongate cup. Right lateral teeth robust, inner anterior lateral (AI), widely curved, long, cusp sub-central or slightly displaced forward; outer anterior lateral tooth (AIII) quite short, cusp distal; inner posterior lateral (PI) nearly straight, short, cusp sub-central; outer posterior lateral tooth (PIII) reduced in size with distal cusp. Left valve (Figure 47): cardinal teeth short, inner one (C_2) short, oblique with respect to antero-posterior axis, outer one (C_4) a narrow curved lame, quite oblique, overlapping C_2 on posterior half; anterior lateral tooth (AII) strong, straight, cusp sub-central; posterior lateral tooth (PII) narrow and weak, cusp distal.

Ligament-pit enclosed, deep, inner margin slightly sinuous, concave at posterior end. Escutcheon well marked by a delicate line; ligament long, internal, but visible from outside in anterior half through a very narrow and sometimes rather long gap between valves, never protruded. Ligament length is 23 ± 1% of shell length.

ANATOMY: Anal siphon and branchial mantle opening present. Presiphonal suture rather long, representing 11 ± 2% of SL. Anal siphon well-developed, pair of powerful siphonal retractors present. Inner radial mantle muscles, 8 bundles as rule, inserted away from pallial line, scars of those corresponding to anal siphon retractors coalescent with posterior adductor muscle scars. Inner and outer demibranchs present. Outer demibranch reduced in size, composed of 11–15 very short descending filaments, reaching back to the 14–16th filament of inner demibranch. Nephridia of closed type, dorsal lobe variable in shape, commonly subquadrate, with lateral loop not visible in dorsal view.

Material Examined: Holotype (MHNB 34734) La Siberia, West of Comarapa, Santa Cruz de La Sierra, Bolivia; Tucumán, Argentina: 27°01′24″ S, 65°39′29″ W (MLP 6554): Cerro Muñoz, Santa Cruz, 26°54′ S, 65°46′42″ W, 2400 m (MLP 6991); La Angostura dam, 26°56′ S, 65°41′03″ W, 1800 m (MLP 6527); Jujuy, Argentina: Los Laureles, 25°06′27″ S, 65°36′10″ W, 1360 m (MLP 6528); Los Toldos, Santa Victoria Department, 1770 m (MLP 6993); small brook near Tiraxi (23°59′57″ S, 65°19′39″ W), 1576 m (MLP 6552); small spring at the side of provincial road No. 4, near Termas de Reyes (24°10′36″ S, 65°28′18″ W) (MLP 5497-2).



Figures 44–47. *Pisidium chiquitanum* Ituarte, 2001. **44, 45.** Paratype (MLP 5362). **44.** Outer view of right valve. **45.** Posterior view. **46, 47.** Specimen from Tiraxi, Jujuy (MLP 6552). **46.** Outer view of right valve. **47.** Inner view of left valve. Scale bars = 500 μm.

Distribution: Ranging from sub-Andean regions in Siberia (west of Comarapa) in central Bolivia (1800 m altitude) southward to northwestern Argentina (between 1360 and 2400 m altitude).

Remarks: *Pisidium chiquitanum* can be easily identified among South American *Pisidium* species by its oval shell outline with low beaks and internal (however visible from the outside) ligament. It is also characterized by two, inner and outer, demibranchs on each side, two siphonal openings, and nephridia of closed type

Pisidium chiquitanum resembles *Pisidium meierbrooki* Kuiper and Hinz, 1984, from Peru and Bolivia, which is the only known species from tropical South America with both, branchial and anal, siphonal openings (Ituarte, 1995). *Pisidium meierbrooki* differs from *P. chiquitanum* in having a more convex shell (according to data in Kuiper and Hinz, 1984, the Ci varies between 77 and 80), fuller and more backward displaced beaks. As pointed out by Ituarte (2001)*Pisidium chiquitanum* is similar to specimens from Ecuador and Peru reported by Kuiper and Hinz (1984), as *Pisidium casertanum* (Poli, 1791), an Eurasian species extremely variable in shell shape, currently reported as cosmopolitan (Burch, 1975; Kuiper, 1983; Kuiper and Hinz, 1984; Holopainen and Kuiper, 1982). However, these specimens are larger than *P. chiquitanum*, having more central beaks and less produced anterior end. *P. chiquitanum* also differs from *P. casertanum* in having less convex shell, lower and narrower beaks, decidedly displaced backward. The specimens from northwestern Argentina slightly differ from the ones from Bolivia in being generally higher, with beaks slightly less displaced in posterior direction (Figure 46).

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Mysella pedroana, a commensal bivalve (Lasaeidae) on two decapod crustacean hosts

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ABSTRACT

Mysella pedroana (Dall, 1898), lives commensally on *Isocheles pilosus* (Holmes, 1900), and *Blepharipoda occidentalis* Randall, 1839. Because of their small size at reproductive maturity, specimens attached to *Isocheles pilosus* were previously referred to in the literature as an undescribed species. However, preliminary comparisons between the variability of hinge dentition and internal structure of those specimens and small individuals of *Mysella pedroana* indicate that they represent instead a single species. Variability of characters including size at reproductive maturity and shell morphology suggests that *Mysella pedroana* is a highly variable species.

INTRODUCTION

A small bivalve living attached to hermit crabs has perplexed biologists for over a decade. It was referred to as *Mysella* sp. H by Valentich-Scott and Barwick (2001), as an undescribed species. It was shown to be reproductively mature at 1.0 mm in length.

Bivalves in the family Lasaeidae have been taxonomically problematic (Dall, 1898; Gage, 1966a; 1966b; Ó Foighil and Eernisse 1988; Morton and Scott, 1989). These bivalves combine features of immaturity induced by changes in environmental factors, perhaps due to their commensal nature. *Mysella pedroana* (Dall, 1898), is no exception. It is found both as a commensal and free-living (Scott, 1987); however, due to its prevalence on hosts, it may prefer a commensal habitat.

Mysella pedroana was previously thought to be host-specific and found only on the sand crab *Blepharipoda occidentalis* Randall, 1839, (Burch and Burch, 1944; Boss, 1965a; Lafferty, 1993; Boyko and Mikkelsen, 2002). Originally described by Dall in 1898 from a single valve, *M. pedroana* was then redescribed (Boyko and Mikkelsen, 2002) and associated with *B. occidentalis* as host. The discovery of its occurrence on another host, the hermit crab *Isocheles pilosus* (Holmes, 1900), previously undocumented variation in shell morphology, and small size at reproductive maturity has led to this present study.

Blepharipoda occidentalis (Decapoda: Albuneidae) is found in the northeastern Pacific from Stinson Beach, Marin County, California, USA, to Bahia Santa Rosalia, Baja California, Mexico (Morris et al., 1980) both intertidally and subtidally, burrowing in sand. *Isocheles pilosus* (Decapoda: Diogenidae) ranges from Bodega Bay Harbor, Sonoma County, California, USA, to Estero de Punta Banda, Baja California, Mexico (Rickets et al., 1985). Like *B. occidentalis*, it is intertidal, but also occurs in mud flats, bays and estuaries including depths offshore up to 55 meters. *Isocheles pilosus* most commonly inhabits shells of *Polinices* or *Kelletia* (pers. comm. Scott, 2004) and crawls on the sand or buries with only its eyes and mouth visible (Fager, 1968). *Mysella pedroana* is either attached to the crab's setae or in its branchial chambers.

MATERIALS AND METHODS

Preserved specimens identified by Valentich-Scott and Barwick (2001) as *Mysella* sp. H from the collections in the Santa Barbara Museum of Natural History (SBMNH) were studied. Additional material included SBMNH specimens associated with preserved specimens of *Isocheles pilosus* and *B. occidentalis*, along with specimens from two living *I. pilosus* and one *B. occidentalis* collected at Sands Beach, Santa Barbara. Specimens removed from *I. pilosus* are deposited as SBMNH 351472–351480 and 47635. Material of *M. pedroana* examined includes SBMNH 348251, 345553, 348252, and 348253.

Of the 145 available specimens, 35 were opened and examined for gross anatomy. Characters examined were internal structure, shell dentition, and shape. Measurements were made with vernier calipers and anatomical observations were performed under a dissecting microscope. Scanning electron micrography was performed at SBMNH with a Zeiss EVO 40 XVP with a variable-pressure secondary electron detector.

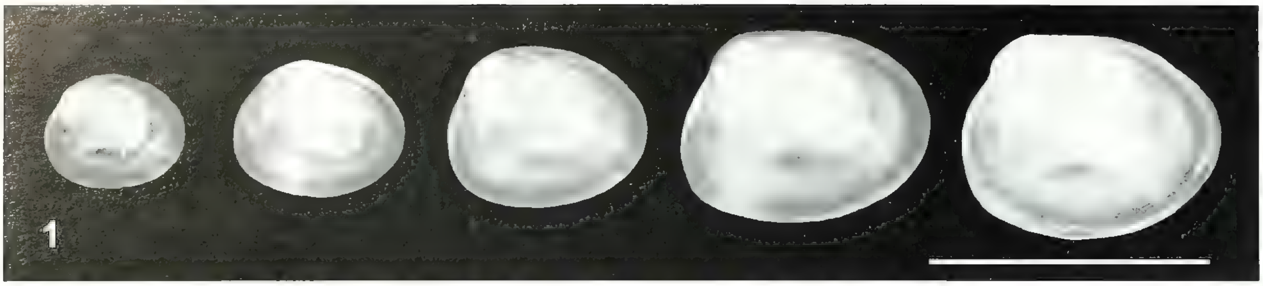


Figure 1. A growth series of commensal *Mysella pedroana*, SBMNH 351473. Scale bar = 1 mm.

Living *Mysella perdroana* were placed in Petri dishes with sea water and coarse sediment for comparison of movement in different media. Specimen with brood was stained with crystal violet in distilled water prior to examination.

RESULTS

Mysella pedroana (Dall, 1898)

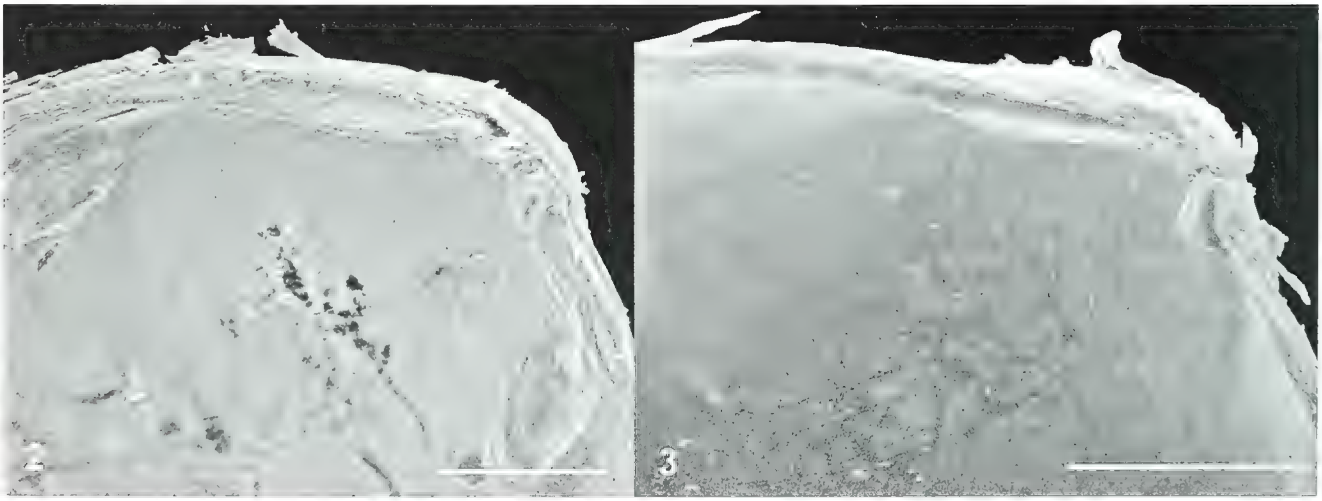
Description: Shell (Figures 1–3): Shell morphology variable from ovate to subtrigonal, thin, more elongate anteriorly; umbones opisthogyrate; beaks range from central to posterior; shell surface white with poorly defined commarginal striae; periostracum thick and yellow, variable in texture, rough and dehiscent to smooth and adherent; prodissoconch line present; maximum shell length 11.0 mm, mean height to length ratio 77% (herein) (SD ±4.8; range 11.0–1.0 mm) to 80% (Boyko and Mikkelsen, 2002).

Muscle scars apparent in larger specimens with anterior adductor scar elongate and posterior ovate; pallial line entire; hinge with prominent subumbonal resilium; two lateral cardinal teeth on right valve with longer anterior tooth and slight groove, posterior shorter; teeth diverging into an inverted V; left valve with thin grooves (lamellae) that interlock with the right valve. Extensive variation shown in smaller specimens (length 1–3.4 mm), which may exhibit a posterior tubercular tooth on the right valve with a similar posterior tubercular tooth on the left valve.

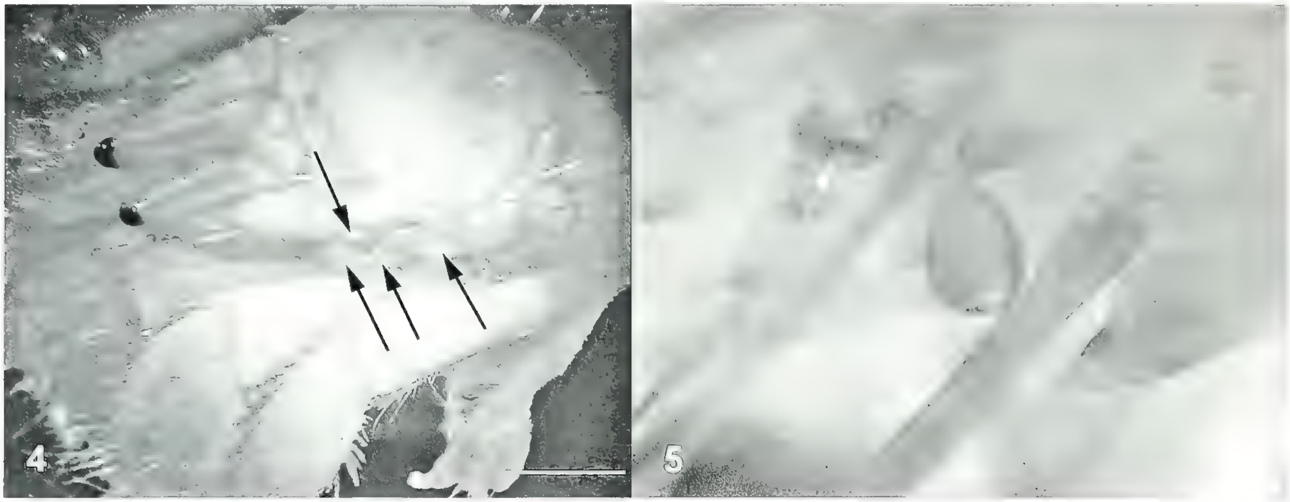
Gross Anatomy: Mantle papillate, more so anteriorly; ctenidium encompasses large area of internal space and serves as a brood chamber; presence of eggs observed in specimens from 1–11 mm in length; labial palps small.

Observations on Live Specimens: Activity was enhanced following regular replacing of cold sea water. Clams were observed crawling on surface of Petri dish with shell positioned vertically, in the manner of a gastropod; dug in sand with anterior end, process took 15–20 sec. Detached *M. pedroana* took 3 min. to reattach to setae on the ventral surface of *I. pilosus*. However, when *I. pilosus* setae were easily accessible and *M. pedroana* was placed next to them, attachment took 30–45 sec.

Host information and prevalence: *Blepharipoda occidentalis* had a carapace length of 4.06–4.55 cm (n = 3) and all three had *Mysella pedroana* present. *Isocheles pilosus* had a carapace length of 1.9–2.57 cm (n = 6) with three of the six crabs having bivalves present.



Figures 2–3. *Mysella pedroana*, hinge dentition. **2.** From host *Isocheles pilosus*, SBMNH 351473, SEM. Scale bar = 200 µm. **3.** From host *Blepharipoda occidentalis*, SBMNH 351478, SEM. Scale bar = 1 mm.



Figures 4–5. *Mysella pedroana*. **4.** Host *Isocheles pilosus* showing attachment between the chela and carapace (arrows), SBMNH 345553, Scale bar = 2.2 mm. **5.** On host *Isocheles pilosus* with byssus (arrow), SBMNH 351472. Scale bar = 0.8 mm.

Three *B. occidentalis* were examined with 100% prevalence. Of the six preserved museum specimens of *I. pilosus*, only one was infested. However, two live *I. pilosus* were examined and fifty-nine *M. pedroana* specimens were retrieved.

The live *B. occidentalis* examined had two *M. pedroana* that were found on the external surface near the antennae and on the second pereopod.

Host *Isocheles pilosus*: *Mysella* specimens on *I. pilosus* were found in the branchial chambers, attached to the chelae, the junction between the chela and carapace, the ventral setae and branchial chambers (Figure 4). The largest specimens were on the chelae (1 mm) with smaller individuals on the ventral surface (0.7–1 mm) and juveniles (<0.7 mm) anteriorly in the right and left branchial chambers. Those on the ventral surface and in the branchial chambers were attached with byssus (Figure 5). The few on the chelae were observed crawling or attached by byssal threads to the surface spines of the chelae. Upon preservation in 70% ETOH *M. pedroana* retained its byssal threads.

DISCUSSION

This study suggests that shell shape of *Mysella pedroana* is more variable than previously appreciated. These variable characteristics include texture of the periostracum (rough and dehiscent to smooth and adherent), dentition, shape of the shell. These differences have been attributed to environmental conditions in other molluscan shells (Wellington and Kuris, 1983; De Wolf et al., 1998).

Shell variation probably led to the redescription of *Mysella pedroana* as *Rochefortia golischi* by Dall in 1916 (Burch and Burch, 1944); these were later synonymized by Scott (1987). However, this variation is also common to many commensal species and makes it difficult to identify them based on shell morphology (Ó Foighil and Eernisse, 1988; Morton and Scott, 1989).

Due to shell variation and the small size at reproductive maturity of *M. pedroana*, these smaller bivalves on *I. pilosus* were thought to be a new species, referred to as *Mysella* sp. H (Valentich-Scott and Barwick, 2001). However, minimum size of brooding adults of *M. pedroana* had been previously reported at 1 mm (Valentich-Scott and Barwick, 2001) and spermatogenesis has been confirmed in specimens of 1.2 mm. Previous observations for individuals of *M. pedroana* undergoing spermatogenesis were 4.7 mm in length (pers. comm. Kevin Lafferty, 2004). Reproductive maturity at small sizes has been reported also for *Pseudopythina macrophthalmensis* at 2.0 mm (Jespersen et al., 2001) and *Mysella bidentata* with egg production at 1.7 mm (Ó Foighil et al., 1984).

The prevalence of *Mysella pedroana* was higher on *B. occidentalis* than on *I. pilosus*. Those on *B. occidentalis* were also larger in the gill chambers compared to only juveniles found in the gills of *I. pilosus*. Further examination of both hosts would be required to see if there is a host preference.

Reattachment to a host is possible for the species. Both Lafferty (pers. comm. 2004) and Valentich-Scott (pers. comm. 2004) noted that individuals could drop their byssus and disassociate from the host if perturbed. Individuals of *M. pedroana* could use this procedure to move from host to host or to become free-living.

The above observations on morphology and symbiont-host relationships permit the identification of this bivalve as *Mysella pedroana*. Previously reported host specificity for commensal bivalves may be due to the scarcity of studies or experimental observations (Boss, 1965b; Morton and Scott, 1989). This species was previously thought to be host-specific (Boyko and Mikkelsen, 2002), an assumption here shown not to be valid.

ACKNOWLEDGMENTS

I would like to thank to Paul Valentich-Scott for his guidance, knowledge and for introducing me to the world of bivalves. The Hearst Foundation Internship through the Santa Barbara Museum of Natural History made this research possible. Scanning electron microscope facilities funded by NSF grant number MRI0420726, Daniel Geiger assisted with SEM images. Michael Caterino, Henry Chaney and Armand Kuris for reviewing preliminary drafts. Shane Anderson provided living crabs, Patricia Sadeghian contributed her knowledge of crustaceans. Paula Mikkelsen and Kevin Lafferty whom offered additional data. Kelvin Barwick contributed many specimens. Two anonymous reviewers offered critical observations which greatly improved the manuscript.

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Coralliophila trigoi (Gastropoda: Muricidae), a new species from the northeastern Atlantic Ocean

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ABSTRACT

Based on shell characters and with further support from molecular data, *Coralliophila trigoi*, a new species of gastropod of the family Muricidea, is here described from the northeastern Atlantic Ocean. The new taxon, consisting of several specimens mainly collected along the Atlantic Spanish coast, has previously been misidentified in the literature as *Coralliophila basilea* (Dautzenberg and H. Fisher, 1896). *Coralliophila trigoi* new species is conchologically similar to *Coralliophila meyendorffii* (Calcara, 1845), and *Coralliophila panormitana* (Monterosato, 1869), but it can be easily separated from them mainly because it is differently sculptured. The new species is compared with other members of the genus *Coralliophila* from the same geographical area and Mediterranean Sea. Molecular sequencing of the internal transcribed spacer 2 region (ITS2) of the nuclear rDNA and part of the mitochondrial gene for 12S rDNA confirm the validity of the new species.

INTRODUCTION

The coralliophilines form a monophyletic group of neogastropods that includes approximately 200–250 described species grouped, based on their shell morphology, in at least 7–10 "genera", distributed worldwide in temperate and tropical oceans. The subfamily Coralliophilinae Chenu, 1859 (for the phylogenetic relationship of this muricoidean groups, see Oliverio and Mariottini, 2001a) includes species invariably associated with cnidarians, which are generally used as food by the gastropods. Shell variability, absence of radula, absence of a preserved protoconch (often eroded in adults and even in young specimens), together with a limited knowledge of the anatomy, represent constrains to the understanding of the taxonomic status of this group of neogastropods. Their classical systematics above the species level is at present far from being stable (Clover, 1982; Bouchet and Warén, 1985; Kosuge and Suzuki, 1985; Oliverio, 1989; Vaught; 1989; Oliverio, in press). Data from mitochondrial and nuclear genes (12S rDNA and ITS2 rDNA, respectively) have been recently utilized in the proposal of a molecular framework for the phylogeny of these muricids (Oliverio and Mariottini, 2001a; Oliverio, Cervelli and Mariottini, 2002). Data from both sequence and secondary structure show that Rapaninae Gray, 1853 (=Thaidinae Jousseaume, 1888) are their sister group (Harasewych et al., 1997; Oliverio and Mariottini, 2001a; Oliverio, Cervelli and Mariottini, 2002), indicating a monophyletic radiation of the Coralliophilinae. The state-of-the-art knowledge about feeding, anatomy, sexual strategies, parental care, and protoconch of coralliophilines was recently reviewed by Richter and Luque (2002). The authors reported the available data on protoconch and larval development of many coralliophilines belonging to ten different genera, including *Coralliophila* H. and A. Adams, 1853. We had the opportunity to examine several shells of a coralliophiline that we could allocate to any of the Atlantic and Mediterranean species of this subfamily. These shells, mostly collected along the coast of Galicia, Spain, were previously misidentified in the literature as *Coralliophila basilea* (Dautzenberg and H. Fisher, 1896) (Rolán, 1983; Rolán, López and Gutiérrez-Garcia, 1995). After comparisons with other species, we realized that they represent an undescribed species, possibly related to *Coralliophila meyendorffii* (Calcara, 1845) and *Coralliophila panormitana* (Monterosato, 1869).

In order to verify the taxonomic validity of *Coralliophila trigoi*, we carried out molecular sequencing of the internal transcribed spacer 2 region (ITS2) of the nuclear rDNA and of part of the mitochondrial gene for 12S rDNA. Genomic DNA was extracted from the dissected foot of two freshly collected individuals with standard methods (SDS-proteinase K digestion, phenol/chloroform extraction, ethanol precipitation (Oliverio and Mariottini, 2001b)). Mitochondrial rDNA was amplified through the polymerase chain reaction (PCR) with primers *12S-I* and *12S-III* (Oliverio and Mariottini, 2001a) Nuclear ribosomal ITS2 was amplified using the primers

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Table 1. Collecting data and DDBJ/EMBL/GenBank accession number for specimens assayed in molecular systematics.

		Accession number	
Species/individuals	Collecting locality and depth	12S	ITS2
Coralliophila neritoidea	Taiwan, 23°10′ N, 120°05′ E, 5 m depth	AJ293679	AJ420258
Coralliophila brevis	La Maddalena Is. (Sardinia, Italy), 41°15′ N, 009°26′ E, 30 m depth	AJ293676	AJ420256
Coralliophila mejendorffii	La Maddalena Is. (Sardinia, Italy), 41°15′ N, 009°26′ E, 3–7 m depth	AJ297517	AJ293661
Coralliophila panormitana	Cape Circeo (Latium, Italy), 41°11′ N, 013°04′ E, 70 m depth	AJ293681	AJ420259
Coralliophila trigoi new species, specim. #1	Camariñas, Galicia, Spain, northeastern Atlantic Ocean, 15–50 m depth	AJ937305	AJ937307
Coralliophila trigoi new species, specim. #2	Camariñas, Galicia, Spain, northeastern Atlantic Ocean, 15–50 m depth	AJ937306	AJ937308

its-3d and *its-4r* complementary to conserved regions of the ribosomal coding portions on the 5.8S and 28S rRNAs (Oliverio and Mariottini, 2001b). PCR-amplified products were directly sequenced by an automated sequencer. Nucleotide sequences were first aligned by hand and the alignment progressively optimized according to secondary structure homology. Phylogenetic analyses were performed using PAUP* 4b10 (Swofford, 2002). GenBank accession numbers (12S and ITS2) of the *Coralliophila trigoi* sequences are reported in Table 1.

Institutional abbreviations used: MNCM, Museo Nacional de Ciencias Naturales, Madrid, Spain; MZB, Laboratorio di Malacologia, Museo di Zoologia dell'Università di Bologna, Italy.

Abbreviations used for collections: CS-PM, Carlo Smriglio and Paolo Mariottini (Rome, Italy); ER, Emilio Rolán (Vigo, Spain); FS, Frank Swinnen (Lommel, Belgium); JT, Juan Trigo (Brion, A Coruna, Spain); MO, Marco Oliverio (Rome, Italy).

SYSTEMATICS

Superfamily Muricoidea Rafinesque, 1815
Family Muricidae Rafinesque, 1815
Subfamily Coralliophilinae Chenu, 1859
Genus *Coralliophila* H. and A. Adams, 1853

Type Species: *Fusus neritoideus* Lamarck, 1816, Ency. Meth., pl. 435, figs. 2a–b. (=*Purpura violacea* Kiener, 1836), by subsequent designation (Iredale, 1912). Recent, Indo-Pacific.

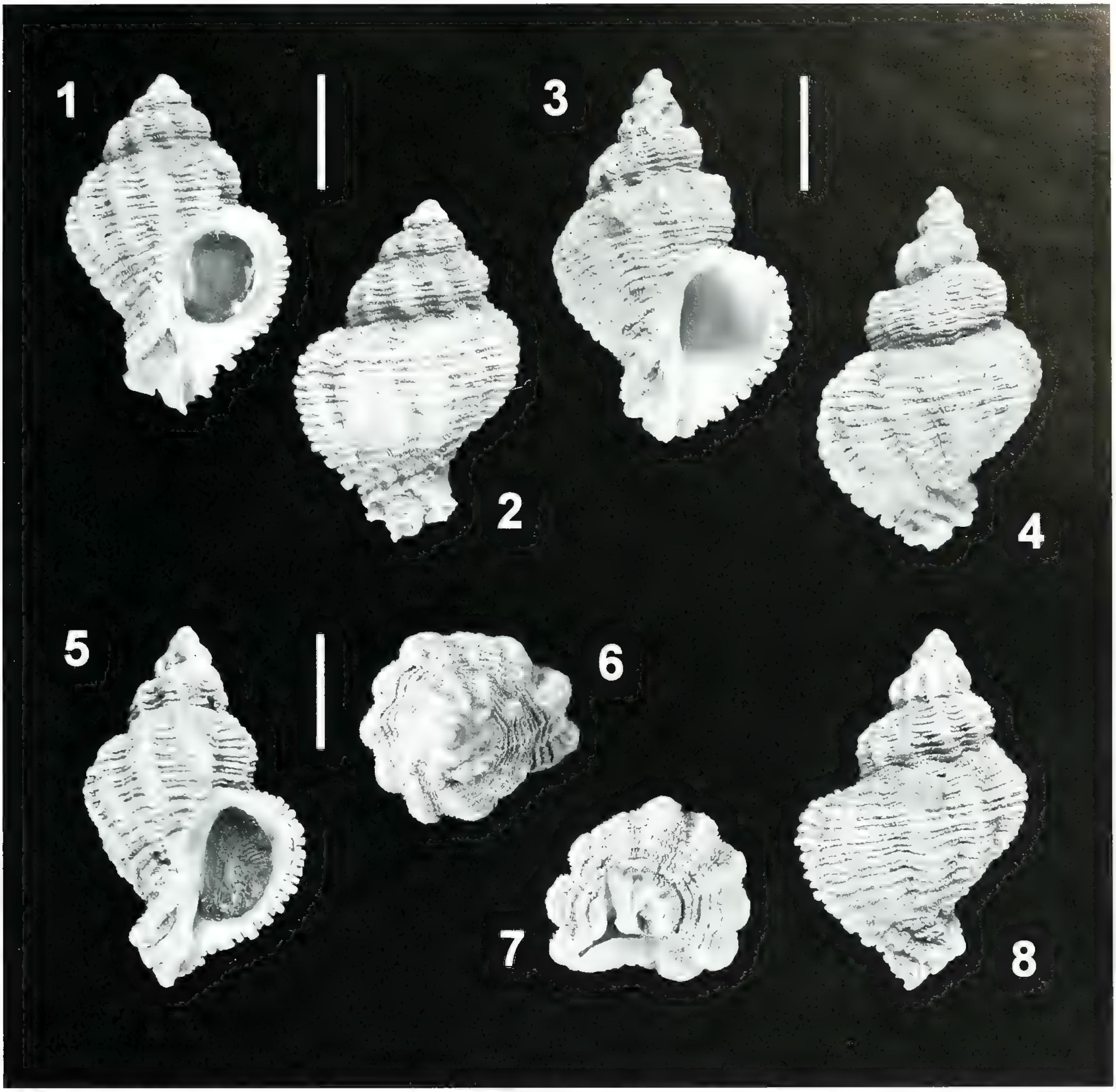
Coralliophila trigoi new species
(Figures 1–8, 13–14, 17–21)

Description: Shell of large size, up to 35 mm length. Protoconch usually eroded in adult specimens (protoconch observed in only one juvenile specimen, albeit worn and lacking the embryonic stage). Protoconch indicative of planktotrophic larval development, multispiral, composed of protoconch I and II. Protoconch II of about 2½ whorls, with a diameter of about 800 μm, showing two strong spiral keels, only one visible above the suture of the first whorl, crossed by axial ribs forming nodules at intersections. The protoconch-teleoconch demarcation is well-defined, marked by a varix. Teleoconch shape biconical, elongate ovoid-fusiform, solid, rather inflated. Spire relatively high, conical, 4–5 rather convex whorls, shoulder rounded. Suture not very evident, partially covered by the sculpture, which is formed of 15–20 spiral cords, regularly ordered, rarely alternating with smaller spiral cords. Spiral sculpture consisting of ribs rounded in cross-section, all of similar width, densely covered with imbricating, fine, and long lamellae. Axial ribs 7−11, large, generally weak, crossing the spiral cords. Siphonal canal short, narrow, open, moderately curved. Aperture large, oval, representing about half of the shell height, white or cream-white inside. Umbilicus absent. Outer lip thin and crenulate. Shell color uniformly reddish- or pale-brown. Operculum oval, oblong, horny, concentric, with lateral-terminal nucleus, reddish-brown.

Type Material (Figures 1–8): Holotype (Figures 1–2), 30.6 × 20.4 mm, MNCN 15.05/46458; paratype A (Figures 3–4), 31.6 × 19.4 mm, MZB 31023; paratype B (Figures 5–8), 27.3 × 16.7 mm, CS-PM; paratype C, 27.4 × 18.2 mm, CS-PM; paratype D, 24.2 × 16.8 mm, ER; paratype E, 26.8 × 16.6 mm, ER; paratypes A–E, from type locality; paratype F, 30.9 × 18.5 mm, ER, Malpica, Spain; paratype G, 23.5 × 16.3 mm, ER, Camelle, Spain; paratype H, 24.8 × 17.3 mm, JT; paratype I, 21.2 × 12.3 mm, JT; paratype L, 26.9 × 17.1 mm, JT; paratype M, 21.4 × 12.3 mm, JT; paratype N, 31.2 × 18.0 mm, JT; paratype O, 18.5 × 12.8 mm, JT; paratype P, 7.4 × 5.1 mm, CS-PM; paratypes H–P from Porto da Baleeira, Sagres, Portugal; paratype Q, 30.2 × 18.1 mm, ER, Lira A Coruña, Spain; paratype R, 26.4 × 17.2 mm, ER, Malpica, Spain; paratype S, 27.3 × 16.2 mm, CS-PM; paratype T, 25.1 × 16.2 mm, CS-PM; paratypes Q–T from Lira A Coruña, Spain; paratype U, 39.2 × 23.2 mm, CS-PM, A Guarda, Spain; paratype V, 30.1 × 18.6 mm, CS-PM, type locality; paratype W, 29.8 × 17.4 mm, CS-PM; paratype Z, 25.8 × 16.2 mm, CS-PM; paratypes W–Z from Malpica, Spain.

Type Locality: Camariñas, Galicia, Spain, northeastern Atlantic Ocean, 15–50 m depth.

Distribution: Known from Galicia, Spain, to Algarve, Portugal, in the Atlantic Ocean, and from Malaga and Almeria (Alboran Sea, Spain) in the Mediterranean.

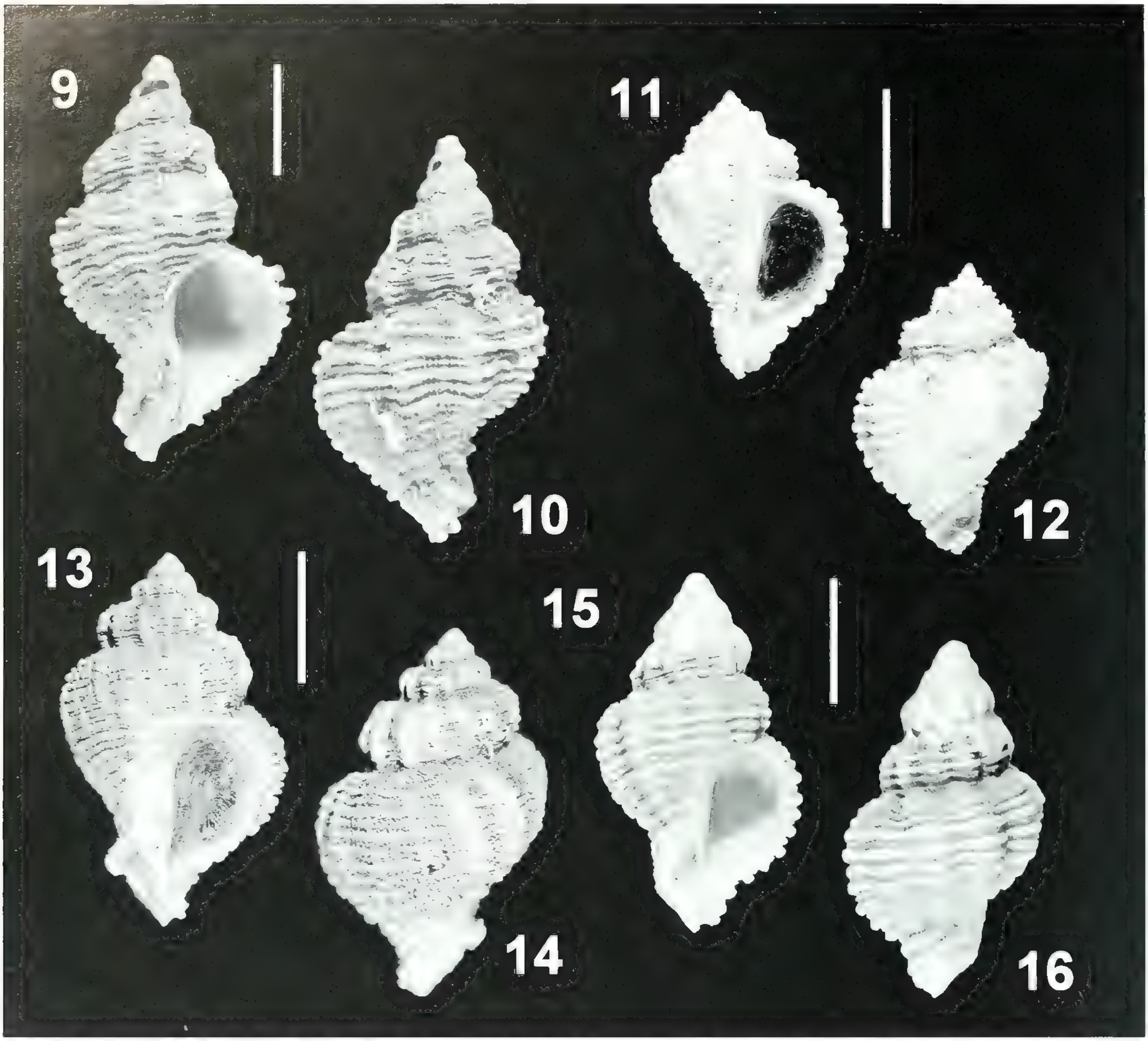


Figures 1–8. *Coralliophila trigoi* new species. **1–2.** Holotype, 30.6 × 20.4 mm, MNCN 15.05/46458. **3–4.** Paratype A, 31.6 × 19.4 mm, MZB 31023. **5–8.** Paratype B, 27.3 × 16.7 mm, CS-PM. From type locality, depth 15–50 m. Scale bars = 1 cm.

Habitat: Several live collected specimens were found attached at the base of host cnidarians *Calliactis parasitica* (Couch) (a sea anemone).

Etymology: This species name is dedicated to our friend Juan Trigo, who supplied some of the specimens of the new species.

Molecular Sequencing: Given the often misleading information conveyed by characters of shell morphology in this group (Oliverio and Mariottini, 2001b), we verified the validity of the new species using a molecular approach. We sequenced the internal transcribed spacer 2 region (ITS2) of the nuclear rDNA and part of the mitochondrial gene for 12S rDNA from individuals of the new taxon and compared them with available sequences of *C. meyendorffii*, *C. panormitana*, and *Coralliophila brevis* (Blainville, 1832), plus *Coralliophila neritoidea* (Lamarck, 1816) as outgroup. Parsimony analysis of the aligned sequences of nuclear and mitochondrial DNA resulted in the tree reported in Figure 27.

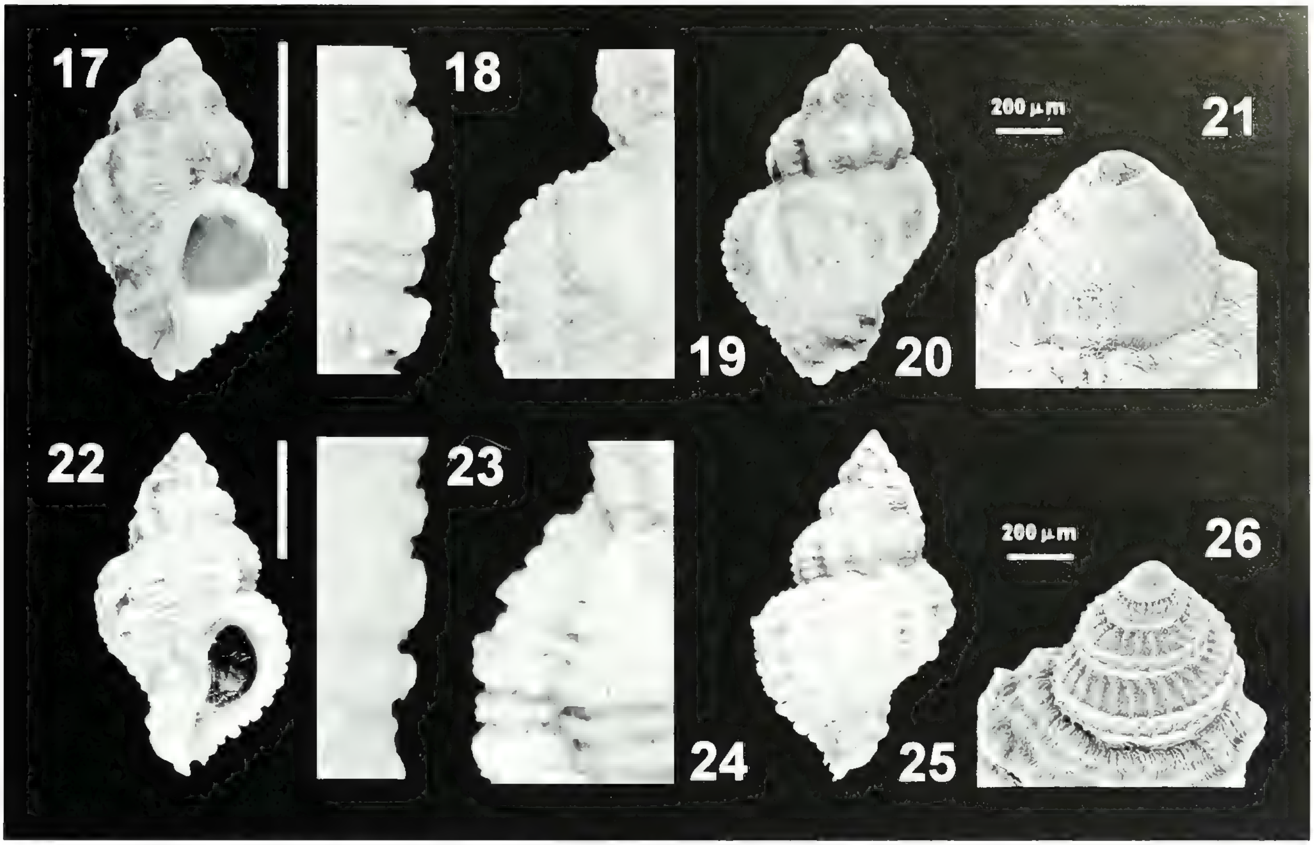


Figures 9–16. Shells of *Coralliophila* species. **9–10.** *Coralliophila squamosa* (Bivona, 1838), 35.9 × 20.9 mm, CS-PM, Camariñas, Galicia, Spain, 15–50 m depth. **11–12.** *Coralliophila panormitana* (Monterosato, 1869), 19.2 × 12.1 mm, CS-PM, Malaga, Spain, 40 m depth. **13–14.** *Coralliophila trigoi* new species, 27.2 × 18.1 mm, MO, Marbella, Spain, 30–50 m depth. **15–16.** *Coralliophila meyendorffii* (Calcara, 1845), 26.8 × 14.7 mm, FS, Punta del Carmen, Lanzarote Isl., Canary Islands, 20 m depth. Scale bars = 1 cm.

The two related species *C. meyendorffii* and *C. panormitana*, were more closely related to each other than to the two specimens of the new species.

Other Material Examined: *Coralliophila trigoi:* 5 spec. from the type locality; 3 spec., Laxe; 1 spec. A Guarda; 3 spec. Camelle; 3 spec. Malpica, Galicia, Spain, ER; 2 spec. Sagres, Algarve, Portugal, CS-PM; 2 spec. Almeria; 3 spec. Marbella, Spain, MO; *Coralliophila meyendorffii:* 10 spec. La Maddalena Isl., Sardinia Island; 1 spec. San Pietro Isl., Sardinia Island; 6 spec. Santa Marinella; 3 spec. Ponza Isl.; 1 spec. Capo Palinuro; 3 spec. Le Castella; 5 spec. Elba Isl., Italy, CS-PM; 6 spec. Punta del Carmen, Lanzarote Isl., Canary Islands, FS; *Coralliophila panormitana:* 5 spec. Marina di Camerota, Italy; 1 spec. Malaga, Spain; 1 spec. Portimão, Portugal, CS-PM; *Coralliophila squamosa:* 23 spec. from the type locality; 6 spec. Laxe; 8 spec. Camelle; 7 spec. Malpica, Galicia, Spain, ER; 10 spec. Ría de Vigo, Galicia, Spain, JT; 1 spec. Malaga, Spain; 1 spec. San Pietro Isl., Sardinia Island; 1 spec. Ventotene Isl.; 1 spec. Marina di Camerata; 2 spec. Le Castella; 2 spec. Civitanova Marche, Italy, CS-PM.

Remarks: Based on shell characters of the teleoconch we take the conservative approach of conserving this



Figures 17–26. Shells of *Coralliophila* species. **17–20.** *Coralliophila trigoi* new species, 23.6 × 14.0 mm, CS-PM, Algarve, Portugal. **18, 19.** Details of shell sculpture. **21.** *Coralliophila trigoi* new species, detail of the larval whorls, paratype P, 7.4 × 5.1 mm, CS-PM, Porto da Baleeira, Sagres, Portugal, 15–25 m depth. **22–25.** *Coralliophila meyendorffii* (Calcara, 1845), 28.6 × 16.0 mm, CS-PM, La Maddalena Isl., Sardinia, Italy, 1 m depth. **23, 24.** Details of shell sculpture. **26.** *Coralliophila meyendorffii*, detail of the larval whorls, specimen size 2.2 × 1.3 mm, CS-PM, La Maddalena Isl., Sardinia, Italy, 1 m depth. Scale bars = 1 cm, except for Figures 21, 26, scale bars = 200 µm.

species in the genus *Coralliophila* s. l., as traditionally formulated (see also Oliverio, in press). The new species was collected in Galicia together with the Atlantic-Mediterranean *Coralliophila squamosa* (Bivona, 1838). This latter species is generally collected in the Mediterranean Sea at depths ranging from 100 to 600 m (Figures 9–10). The new taxon is clearly conchologically distinguishable from all other eastern Atlantic and Mediterranean species of Coralliophilinae. *Coralliophila trigoi* shows a certain resemblance with the Mediterranean *Coralliophila panormitana* (Monterosato, 1869), but the latter is smaller, having a different sculpture that includes a larger number of spiral cords (22–24), with smaller scales (Figures 11–12).

Coralliophila trigoi is similar to *Coralliophila meyendorffii* (Calcara, 1845) (Figures 15–16, 22–26), but it differs by its more rounded shape, by having the length/width and length/aperture length ratios smaller (1.60 and 1.68 vs. 1.72 and 1.86), by possessing a larger number of primary spiral cords (15–20 vs. 13–15), which are narrower in width and differently sculptured, and by a reddish- or pale-brown color (*Coralliophila meyendorffii* is generally milky-white). Furthermore, the protoconch II of *Coralliophila trigoi* shows a number of whorls (2½) and a diameter (800 µm) different from the values on *Coralliophila meyendorffii* (3½ and 650–750 µm, respectively; see Figures 21, 26). The main shell morphological differences between these two species are summarized in Table 2. *Coralliophila meyendorffii* is a littoral, widely distributed species, occurring in the Mediterranean Sea (Figures 22–26), along the Atlantic African coast and Canary Islands (Figures 15–16). It is worth mentioning that *Coralliophila meyendorffii* preys on a variety of anthozoans, including the cnidarian *Calliactis parasitica* (personal observations). Interestingly, *Coralliophila trigoi* seems to be distributed along the Atlantic coast of Spain and Portugal, but restricted to the Alboran Sea (Malaga, Almeria) within the Mediterranean basin. The collecting depth is slightly deeper (50 m) than the bathymetric range (littoral) of *Coralliophila meyendorffii*. Although the planktotrophic mode of development (as indicated by the protoconch) of *Coralliophila trigoi* could bring about a wider geographic distribution than that currently known for the species, the taxon has not yet been found in the Macaronesian Islands and the West African coast.

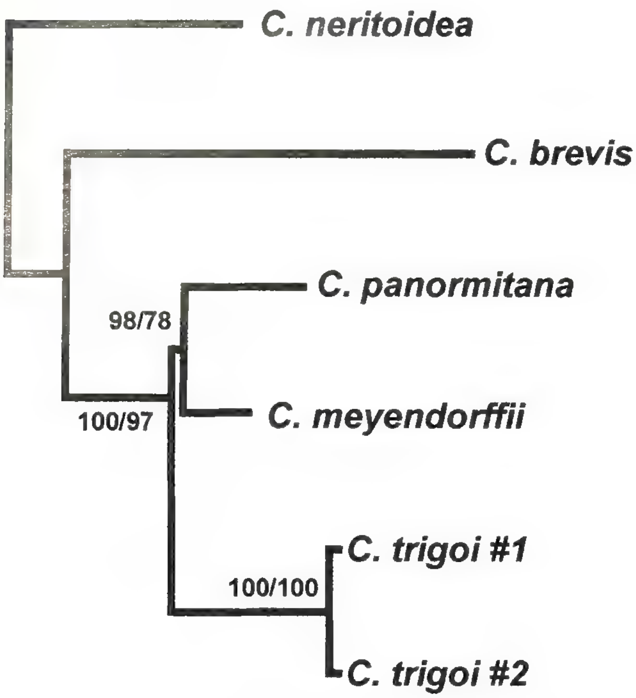


Figure 27. Cladogram of parsimony analysis for the studied coralliophiline taxa. This topology was recovered under maximum parsimony analysis of the 12S + ITS2 dataset (either including or excluding gap positions). Numbers at the branch represent bootstrap support in MP analyses (gap included and gaps as missing). Locality data and GenBank accession numbers (12S and ITS2) are reported in Table 1.

Coralliophila trigoi has been previously misidentified as *Coralliophila basilea* (Rolán, 1983: 236, fig. 210; Rolán, López and Gutiérrez-Garcia, 1995: 30, fig.2), but it is easily distinguishable from this taxon. *Coralliophila basilea* has a more turreted shell and a coarser spiral sculpture. Among the fossil coralliophiline records, the only species that slightly resembles the new taxon is *Coralliophila burdigalensis* (Tournouër, 1874), a species from the Upper Oligocene and Lower Miocene of Aquitaine (France); but the fossil species is smaller and has a different shell outline and sculpture (Lozouet and Renard, 1998: 173, figs. 2. 1–10).

Parsimony analysis of the aligned sequences of nuclear and mitochondrial DNA resulted in the tree reported in Figure 27. Accordingly, the two related species *C. meyendorffii* and *C. panormitana* were more closely related to each other than to the two specimens of the new species. The same results (not shown here) were obtained including additional (yet shorter) sequences of *C. meyendorffii* from other Mediterranean localities (Sardinia, Sicily, and Southern Spain). This is a clear indication that the specimens of the new form constitute a distinct, isolated gene-pool and strongly support our decision to describe it as new.

Table 2. Comparison of shell characters between *Coralliophila trigoi* and *C. meyendorffii.*

Shell characters	*C. trigoi*	*C. meyendorffii*
Protoconch diameter	800 μm	650–750 μm
Protoconch number of whorls	2.5	3.5
Teleoconch primary spiral cords	15–20	13–15
Teleoconch axial ribs	7–11	8–10
Length/width ratio	1.60 ± 0.09	1.72 ± 0.09
Length/aperture length ratio	1.68 ± 0.10	1.86 ± 0.10
Size range	17.6–35.4 mm	19.5–34.3 mm

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LITERATURE CITED

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Book Review

Land Snails of British Columbia

Forsyth, Robert G. 2004. Land Snails of British Columbia. Royal BC Museum Handbook. Royal BC Museum, Victoria, 192 pp. ISBN 0-7726-5218-X. Black and white illustrations, plus a section of color photographs.

Even as "cutting edge" systematics shifts its focus from morphological to molecular data sets, the need for identification manuals based on real-world field marks and accessible characters has never been greater. When zoologists with landcare agencies or environmental consultants ask for references on land snails, it hardly helps to refer them to ponderous, outdated, and hard to find tomes such as Pilsbry (1939–1948). So, manuals like *Land Snails of British Columbia* are a welcome resource.

Land Snails of British Columbia is the latest in a Royal BC Museum series of natural history books that began in 1942. It is the first work to describe and illustrate the 92 species of terrestrial mollusks known to occur in British Columbia, Canada. Because all of the species treated occur outside that province as well, its utility extends beyond those borders. Identification aids include a paragraph of physical description, usually brief, to the point, and adequate; a sentence or two of comparison with other, potentially confusing species; clear illustrations (the line-and-stipple drawings of many of the smaller kinds are noteworthy); and keys to, first, the genera of snails and slugs, and then to the species in each multi-species genus. For slugs, where the diagnostic characters are often internal, excellent, predominantly original, drawings of the distal genitalia are provided. (The simple dissection needed to access these features should be within the range of all to whom this book is directed.) The language of the descriptions is simple and intelligible, and a glossary of technical terms is included. The descriptive material is followed by a summary of each species' distribution, concise comments on natural history, etymology of the generic and specific name, remarks that, among other things, update the species' taxonomic history (e.g., since Pilsbry, 1939–1948) or point out special conservation status, and selected references pointing to the extensive and well researched bibliography. All of this adds up to a highly functional volume that will serve its intended audience well.

A six-page section of color photographs of living snails and slugs, mainly by Kristiina Ovaska, is not only attractive but also helpful, particularly in showing the *habitus* of living slugs, something not always well conveyed by drawings.

The information is amalgamated (the author's word) from published literature, his own observations, scientific collections, and personal communications with other workers. The distributions are based in part on unpublished records from the Royal BC Museum and other collections. Specific localities are not cited; three online resources by the same author (Forsyth, 1999, 2005a, 2005b) provide more detail for specific regions.

A significant innovation is the introduction of *Euconulus* (*Euconulus*) *praticola* (Reinhardt, 1883) to the North American fauna. Its distinctness from *E.* (*E.*) *fulvus* (Müller, 1774) is well documented by characters of shell and external anatomy. The former catchall "Zonitidae" is correctly parsed into Pristilomatidae, Gastrodontidae, and Daudebardiidae for regional genera, in keeping with recent work by Hausdorf and others. *Monadenia*, iconic of northwest American forests, is correctly assigned to Bradybaenidae rather than the redundant and poorly argued Monadeniidae of Nordsieck (1987) and Schileyko (1996). In these and other ways, the author shows himself to be well "booked up" on the current and evolving literature of land snail systematics.

Overall, the taxonomy is simplified, appropriately for a general interest manual. Synonyms are merely listed, not referenced, as few potential users will need that entry into the primary literature. Subspecies are treated in the remarks, not in the major taxon headings or in the taxonomic checklist (pp. 23–28). If experience in California is any guide, upon further study some—perhaps most—nominal subspecies will be shown to be species; and examination of data not available to prior monographers may uncover local endemics, possibly in former glacial refugia such as the Queen Charlotte Islands. For the present, however, this handbook provides a reliable source of biodiversity information. Author Forsyth is fully aware of the dynamic character of taxonomic analysis and astutely states (p. 2), "this book is a work in progress." By clearly showing the state of our knowledge at this time, he has contributed greatly to that process.

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A morphological reanalysis of *Pleurocera acuta* Rafinesque, 1831, and *Elimia livescens* (Menke, 1830) (Gastropoda: Cerithioidea: Pleuroceridae)

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ABSTRACT

Pleurocera acuta and *Elimia livescens* have been the subject of several anatomical and ecological studies and are two of the most thoroughly documented species of North American Pleuroceridae. Yet significant gaps still remain in our understanding of their structure. Consequently, the anatomy of these two species is re-described, allowing a re-interpretation of pallial oviduct homologies; features not previously portrayed in the literature (midgut and kidney) are newly described. These taxa are characterized by the presence of an ovipositor, a kidney with a subdivided internal lumen that invades the pallial roof, a prostate with a highly folded anterior spermatophore-forming region, and a pallial oviduct with spermatophore bursa but lacking a seminal receptacle. This analysis verifies the degree of similarity between the two species, but a number of differences were identified including features of the ovipositor, pallial oviduct, prostate, anterior esophagus, midgut, kidney, pericardium and nervous system. Comparison to other pleurocerids confirms that species distributed in Western North America (*Juga*) and Asia (*Hua*, *Semisulcospira*) share the presence of a seminal receptacle—a feature that is lacking in all described Eastern North American species.

INTRODUCTION

The freshwater Pleuroceridae Fischer, 1885, comprises one of the most species-rich assemblages of limnic mollusks occurring in North America and Eastern Asia. In North America, they are represented by eight genera (*Athearnia* Morrison, 1971, *Elimia* H. and A. Adams, 1854, *Io* Lea, 1831, *Juga* H. and A. Adams, 1854, *Leptoxis* Rafinesque, 1819, *Lithasia* Haldeman, 1840, *Pleurocera* Rafinesque, 1818, and the extinct *Gyrotoma* Shuttleworth, 1845) and estimates of 159 species currently considered valid; of these, 34 are extinct and 59 are listed as critically imperiled (G1) or imperiled (G2) (Johnson et al., 2005).

The current concept of the family Pleuroceridae (e.g. Bouchet and Rocroi, 2005) can be traced to the works of Thiele (1928, 1929) who recognized 6 subfamilies within the heterogeneous "Melaniidae" (an invalid name for Thiaridae Gill, 1871), including the Pleurocerinae. An alternative, highly polyphyletic view promoted by Morrison (1954) caused great confusion for more than four decades concerning the extension and independence of the Pleuroceridae and Pachychilidae P. Fischer and Crosse, 1892 (e.g. Ponder and Warén, 1988). Recent work on the systematics of limnic lineages within the Cerithioidea Fleming, 1822 (e.g. Glaubrecht, 1996, 1999; Köhler et al., 2004) has resolved some of this confusion and supports the distinctiveness of these families on both morphological and molecular grounds. However, molecular data (Lydeard et al., 2002) do not support monophyly of the Pleuroceridae as currently defined, but suggest that a clade of eastern North American species are more closely related to *Melanopsis* (Melanopsidae H. Adams and A. Adams, 1854) than to a clade of western North American (*Juga*) and eastern Asian pleurocerids (*Semisulcospira* Boettger, 1886, *Hua* Chen, 1943).

As noted by Woodard (1934), anatomical data are critical in refining the phylogenetic relationships and classification of these species. However, all taxonomic treatments of the family have been based primarily on conchological characters in the absence of a broad comparative understanding of morphology. Although the subject of numerous ecological studies (e.g. Dillon, 2000) and comparably many descriptions exist for the radula, operculum and life history of North American pleurocerids, surprisingly little is known about their basic biology and anatomy. Scant information on the anatomy (besides radula and operculum) has been provided for *Elimia laqueata* (Say, 1829) (Woodard, 1934), *E. potosiensis* (Lea, 1841) (Jones and Branson, 1964) and *Pleurocera canaliculata* (Say, 1821) (Magruder, 1935b); among western North American forms, only reproductive anatomy is known for several species (Prozorova and Raschepkina, 2004). In addition, the classically cited work of Dazo (1965) on the natural history, ecology, distribution and anatomy of *Pleurocera acuta* Rafinesque, 1831 and *Elimia livescens* (Menke, 1830) has long stood as the most comprehensive morphological study of any pleurocerid gastropod. As such, that study has formed the basis for hypotheses of homology in recent higher-order phylogenetic studies based on morphology (e.g. Houbrick, 1988; Glaubrecht, 1996). Yet, Dazo's study was completed long before our present understanding of the structure, function and homologies of cerithioidean reproductive anatomy was in place, particularly through the work of R. S. Houbrick on marine species. We also have a much more thorough understanding of midgut structure and its utility in revealing phylogenetic affinities of cerithioideans (Glaubrecht and Strong, 1999; Strong and Glaubrecht, 1999, unpublished data).

Given the persistent paucity of anatomical data available for the family, the goal of this contribution is to reevaluate the morphology and putative homologies of the two species described by Dazo, and to place them within the emerging framework now available for limnic cerithioideans. This is critical for ongoing morphological and phylogenetic studies of cerithioidean gastropods, and in particular for clarifying the monophyly and systematic affinity of the family Pleuroceridae.

MATERIALS AND METHODS

This study is based on collections of individuals of *Pleurocera acuta* and *Elimia livescens* living sympatrically in the Mukwonago River at the outflow from Lower Phantom Lake, Mukwonago, Waukesha County, Wisconsin (42°51.402 N; 88°19.767 W). Populations were sampled in May and June; only reproductively mature individuals were used for observations of reproductive anatomy. Individual specimens were cracked, preserved in 95% ethanol and were not relaxed. Voucher material is deposited in the National Museum of Natural History in Washington (USNM).

As stated above, Dazo (1965) provided a rather detailed account of external features (operculum, shell, ovipositor, color patterns of the head-foot) as well as of the radula and all internal organ systems (alimentary, nervous, excretory, respiratory, vascular, and reproductive systems). Baker (1928) also provided information on the operculum, jaw, radulae, and external anatomy of the two species; additional scattered accounts relating to the radula, external anatomy and life history are also available (e.g. Jewell, 1931; Howe, 1938; Goodrich, 1945). As such, the following reanalysis emphasizes anatomy of the soft parts. As the two species are overwhelmingly similar, a thorough account is provided for *Pleurocera acuta* – the type species of the type genus for the family; only details that differ are noted for *Elimia livescens*. However, the internal kidney structure of *P. acuta*, while displaying the same configuration as *E. livescens*, is too occluded with excretory tissue to allow a clear representation. As such, only the internal structure for the latter species is illustrated.

Specimens were examined using a Leica MZ 12,5 binocular microscope with camera lucida; visualization of structures was enhanced through the use of aqueous toluidine blue. Typically four to five specimens were examined for each organ system investigated, especially for those systems showing high levels of individual and/or seasonal variation (i.e. reproductive system); a minimum of two individuals were examined for particularly complex structures (i.e. midgut, nerves). Descriptions of midgut morphology are given with the stomach opened dorsally and the style sac uppermost. Unless otherwise indicated, an incision is made along the extreme right, upper and lower margins, and the roof deflected laterally to the left. Terminology follows Strong and Glaubrecht (2002, 2003).

RESULTS

Pleurocera acuta Rafinesque, 1831

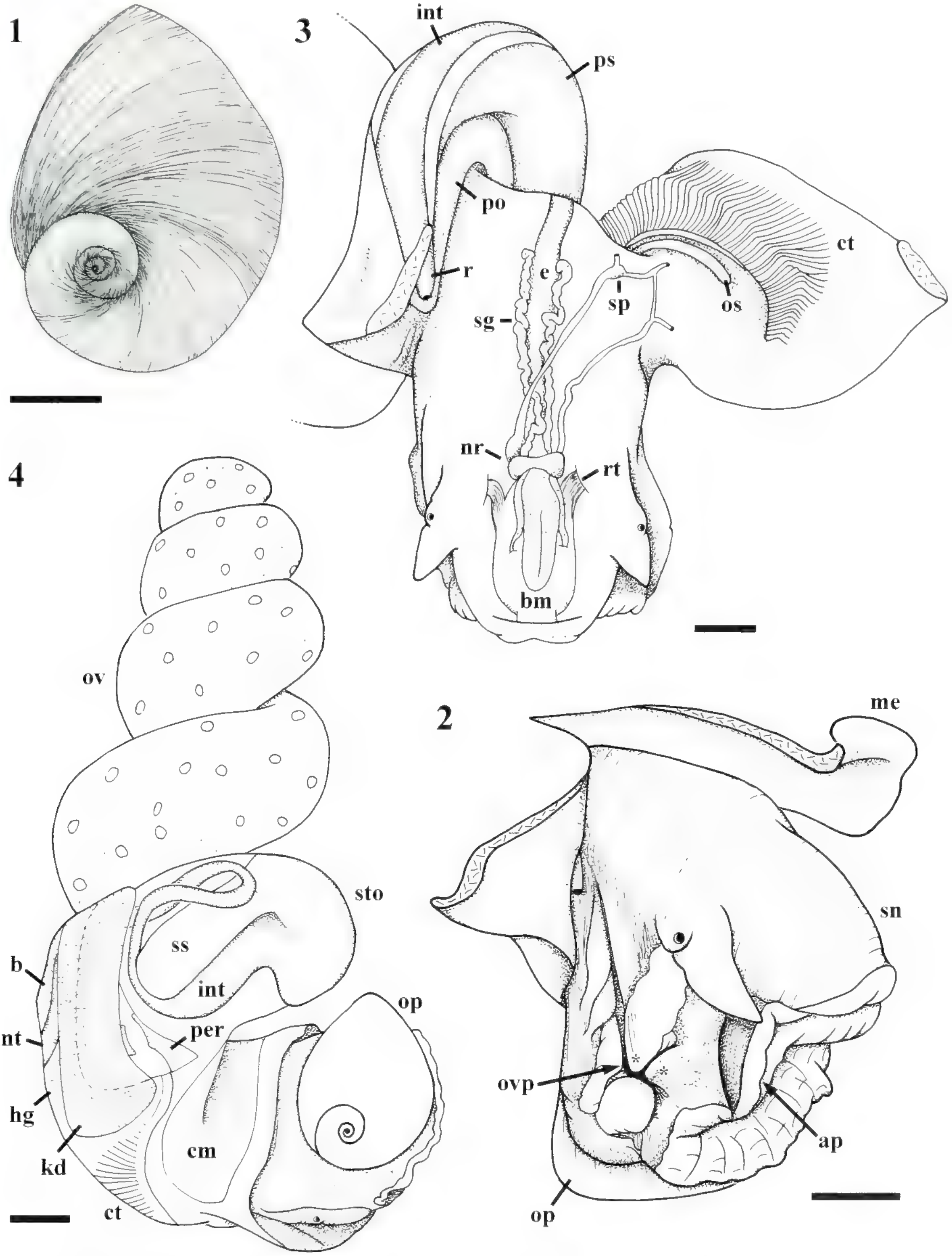
Material Examined: Wisconsin: Mukwonago River: USNM 1081522, 1081524.

External Anatomy: Operculum sub-ovate, corneous, dark reddish-brown in color, with 3.5 whorls; paucispiral with large, eccentric nucleus of approximately 2.75 to 3 whorls (Figure 1). Final whorl moderately inflated. Nucleus occupying slightly under 1/2 (~43%) of total length.

Foot ovate with narrow propodium; anterior pedal gland opening along anterior margin (Figure 2, **ap**). Ovipositor (**ovp**) located on side of neck below right cephalic tentacle. Ciliated egg groove extending short distance up side of neck from ovipositor, shallowing past mantle margin; groove fading near anal aperture. Two, partially juxtaposed, parallel folds, extending into ovipositor pore from aperture (*); one fold at upper posterior edge, second at lower anterior edge of ovipositor (when viewed laterally), forming obliquely flattened H-shaped lumen. Folds unequal in size; anterior fold along floor significantly larger than posterior fold along roof. Ovipositor pore expanding medially into head-foot, then curving and narrowing slightly posteriorly. Two vertical limbs of "H" unequal such that posterior limb forming rather narrow channel along posterior wall. Anterior limb inflated and expanding medially into foot, forming large flattened, subtriangular chamber. Folds diminishing toward blind tip of pore. Short grooved tract extending ventrally from ovipositor aperture toward foot sole, but not reaching edge of foot.

Most individuals with straight osphradium, but some with curved anterior tip (Figure 3, **os**). Hypobranchial gland highly developed with pendulous, transverse folds (Figure 4, **hg**).

Alimentary System: FOREGUT. Buccal mass short and stout, extending to base of cephalic tentacles (Figure 3,



Figures 1–4. Anatomy of *Pleurocera acuta*. **1.** Operculum. **2.** Ovipositor and egg groove. Right lateral view of side of foot. Asterisks (*) indicate folds extending into ovipositor. **3.** Mantle cavity and anatomy of cephalic hemocoel. Dorsal view, anterior is below. Hypobranchial gland removed for clarity. **4.** External view of organs in visceral mass. Dotted line indicates extent of pericardium under main kidney chamber. Abbreviations: **ap,** anterior pedal gland; **b,** bladder; **bm,** buccal mass; **cm,** columellar muscle; **ct,** ctenidium; **e,** esophagus; **hg,** hypobranchial gland; **int,** intestine; **kd,** main kidney chamber; **me,** mantle edge; **nr,** circum-esophageal nerve ring; **op,** operculum; **os,** osphradium; **ov,** ovary; **ovp,** ovipositor; **per,** pericardium; **po,** pallial oviduct; **ps,** peri-intestinal sinus; **r,** rectum; **rt,** buccal mass retractor muscle; **sg,** salivary gland; **sn,** snout; **sp,** supra-esophageal ganglion; **ss,** style sac; **sto,** stomach. Scale bars = 1 mm.

bm). Odontophore occupying majority of buccal cavity with small, glandular subradular organ protruding before radula. Small jaws present at anterior ends of dorsal folds; epithelium of buccal cavity overlying dorsal folds glandular (stippled region). Shallow, non-glandular buccal pouches extending underneath dorsal folds adjacent to buccal ganglia at rear of buccal cavity. Radular sac short, curving upward behind base of buccal mass. Robust buccal retractors (**rt**) inserting onto lateral walls of cephalic hemocoel adjacent to cerebral ganglia (**nr**). Short, glandular mid-ventral fold forming small flap just behind odontophore in anterior esophagus, flanked laterally by two ventro-lateral folds. Ventro-lateral folds converging short distance behind mid-ventral fold and continuing through mid-esophagus (**e**). Mid-esophagus long, bearing paired longitudinal ventral and dorsal folds. Epithelium between dorsal and ventral folds weakly glandular and irregularly striated; septate esophageal gland lacking. Dorsal and ventral folds converging and fusing at distal end of mid-esophagus before continuing into posterior esophagus and subdividing into numerous folds equal in height. Long, tubular salivary glands (**sg**) opening dorso-laterally to buccal cavity alongside odontophore, passing through circum-esophageal nerve ring (**nr**), almost reaching posterior esophagus.

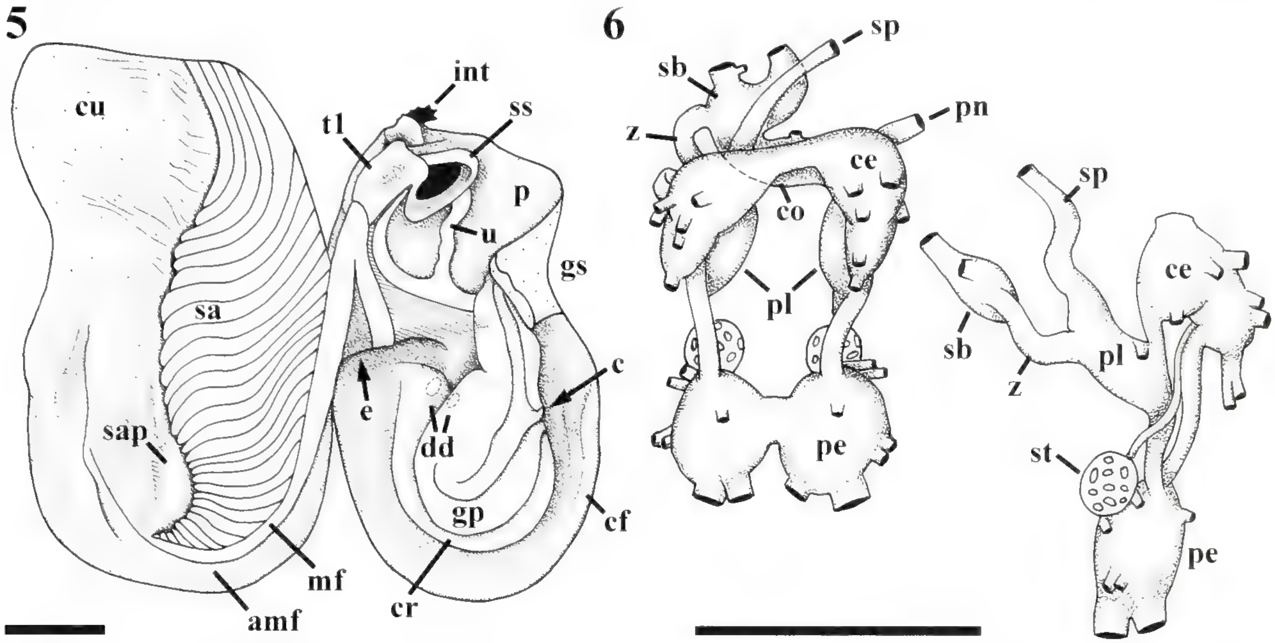
Midgut. Esophagus opening under ledge on left side of midgut floor (Figure 5, **e**). Marginal fold (**mf**) extending anteriorly from esophageal aperture alongside major typhlosole (**t1**), then turning posteriorly bordering right margin of sorting area (**sa**). Groove present along midline of marginal fold (**mf**) for much of its length; groove fading proximally and distally. Sorting area elongate- triangular, tapering posteriorly; posterior tip curving slightly to the left around wedge-shaped sorting area pad (**sap**). Accessory marginal fold (**amf**) emerging from esophageal aperture, paralleling marginal fold and curving around posterior tip of sorting area; fold bifurcating at posterior end of gastric chamber to form two folds. Fine parallel striations extending anteriorly from esophagus up face of major typhlosole. Midgut roof to the left of sorting area coarsely folded and cuticularized (**cu**). Gastric shield (**gs**) small and delicate, strongly concave, with narrow, tubular posterior end and more flaring, flattened anterior end; shield continuous with cuticle of stomach roof and crystalline style pocket (**p**). Glandular pad (**gp**) large and broadly rounded. Crescentic ridge (**cr**), bounding deep crescentic groove, extending from esophageal aperture and fusing to right side of glandular pad. Paired digestive gland ducts (**dd**) opening to deep pocket near proximal tip of crescentic ridge. Shallow caecum (**c**) extending ventrally under glandular pad behind gastric shield. Single longitudinal fold (**cf**) extending from caecum (**c**) around posterior end of gastric chamber. Prominent fold (**u**) extending from right side of style sac lip, along floor of crystalline style pocket, to base of major typhlosole; fold bounding u-shaped depression below lip of style sac (**ss**). Style sac and intestinal groove communicating along entire length. Crystalline style present.

Hindgut. Proximal intestine (Figure 4, **int**) passing below distal tip of style sac (**ss**), then extending posteriorly alongside style sac to main gastric chamber (**sto**). Intestine curving anteriorly, with broad loop overlying proximal style sac. Intestine extending under posterior end of main kidney chamber (**kd**), entering pallial roof alongside bladder (**b**) and pallial gonoduct (Figure 3, **po**), continuing forward to papillate anus near mantle margin (**r**).

Reno-pericardial System: Kidney comprising three interconnected chambers (Figure 4, 17, **kd**, **b**). Main chamber (**kd**) lying along dorsal surface of body whorl, anteriorly surrounding pericardium (Figure 4, **per**), crossing axis of body from right to left and extending short distance into pallial roof at base of mantle cavity. Chamber occluded anteriorly (within pallial roof) with excretory tubules. Posteriorly, main chamber with small, narrow lumen, dorsally enclosing intestine. Second chamber (see exposed chamber in Figure 17) extending between pericardial chamber to right body wall below intestine, forming small bladder (Figure 4, **b**). Chamber mostly occluded by vertical sheets of excretory tissue radiating from afferent renal vessel (see Figure 17, **arv**), and communicating to mantle cavity via large nephropore (**np**). Sheets of excretory tissue branching and anastomosing, and fusing to right lateral floor, roof and walls; vertical sheets highly branched anteriorly and forming comparatively dense honeycomb of excretory tissue. Bladder penetrating connective tissue along right side of body, short distance into mantle roof. Excretory tissue separating small ventral chamber below, within pallial portion (dotted line). Size of ventral chamber, as well as branching pattern and number of excretory sheets of tissue variable between individuals. Small aperture just behind afferent renal vessel connecting main chamber and bladder (arrow). Nephridial gland absent.

Pericardium voluminous (Figure 4, **per**), extending to right side of body (dotted line).

Nervous System: Circum-esophageal nerve ring (Figure 3, **nr**) lying immediately behind buccal mass, at base of cephalic tentacles. Cerebral ganglia (Figure 6, **ce**) connected by short, stout commissure, each producing seven nerves (optic, statocyst, tentacular, and four labial nerves). Buccal connectives short, innervating buccal ganglia lying ventro-laterally at base of buccal cavity immediately behind buccal retractor muscles. Pleural ganglia (**pl**) lying behind and below cerebral ganglia connected to cerebral ganglia by short, thick connectives. Pedal ganglia (**pe**) with two prominent anterior nerves and five smaller accessory nerves. Small statocysts (**st**) with approximately 10–15 statoconia present dorsally alongside pedal ganglia behind pedal connectives. Sub-esophageal ganglion (**sb**) joined to left pleural ganglion by thickened connective (**co**); connec-

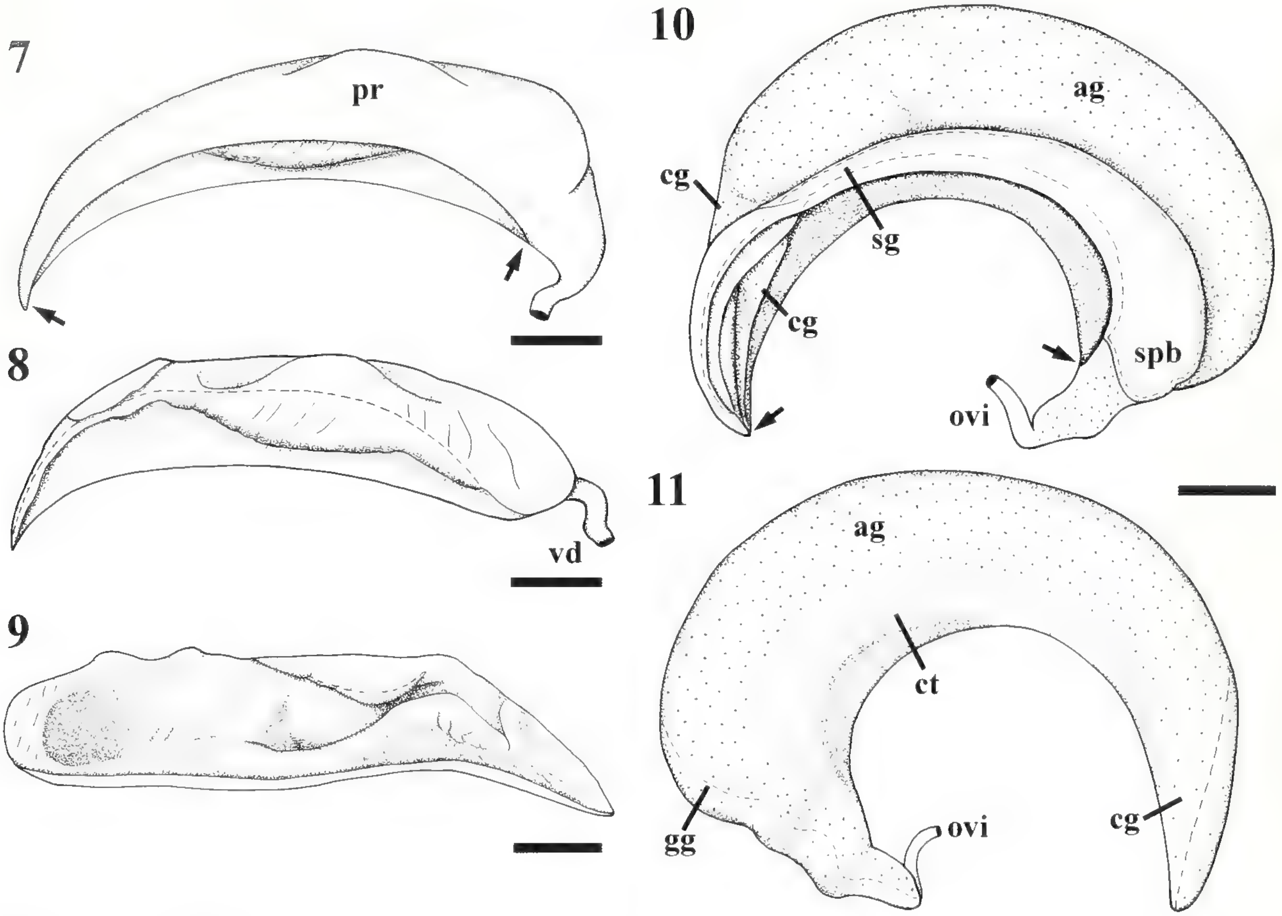


Figures 5–6. Anatomy of *Pleurocera acuta*. **5.** Midgut anatomy. Dorsal view, anterior is uppermost. **6.** Circum-esophageal nerve ring. Frontal view on the left, right lateral view on the right. Abbreviations: **amf,** accessory marginal fold; **c,** caecum; **cf,** caecal fold; **ce,** cerebral ganglion; **co,** thickened connective between left pleural and sub-esophageal ganglia; **cr,** crescentic ridge; **cu,** cuticularized region of stomach roof; **dd,** duct of digestive gland; **e,** esophageal aperture; **gp,** glandular pad; **gs,** gastric shield; **int,** intestine; **mf,** marginal fold; **p,** crystalline style pocket; **pe,** pedal ganglion; **pl,** pleural ganglion; **pn,** pallial nerve from left pleural ganglion; **sa,** sorting area; **sap,** sorting area pad; **sb,** sub-esophageal ganglion; **sp,** connective to supra-esophageal ganglion; **ss,** lip of style sac; **st,** statocyst; **t1,** major typhlosole; **u,** u-shaped fold; **z,** zygoneury. Scale bars = 1 mm.

tive producing 1–3 small nerves (n=2). Zygoneury (**z**) formed between sub-esophageal and right pleural ganglia. In addition to zygoneury (**z**), sub-esophageal ganglion (**sb**) producing one other prominent nerve and connectives to the left pleural (**pl**) and visceral ganglia. Long connective uniting right pleural and supra-esophageal ganglia (Figures 3, 6, **sp**), the latter lying on left side mantle floor near midline of osphradium. Dialyneury formed between pallial nerve of left pleural ganglion and osphradial nerve of supra-esophageal ganglion at junction of mantle roof and floor. Single visceral ganglion present between pericardium and kidney at base of mantle cavity, above posterior esophagus on the right. Ganglion producing two prominent nerves.

Reproductive System: MALE. Narrow vas deferens (Figure 8, **vd**) emerging ventrally from testes, continuing forward along ventral midline of whorl. Short, distal portion of vas deferens thickened and forming straight seminal vesicle. Vas deferens narrowing and curving dorsally to enter posterior end of prostate (Figure 7, **pr**) at base of mantle cavity. Prostate glandular, forming flattened tube, opening to mantle cavity through broad slit along entire length except for a short fused segment at base of mantle cavity (arrows). Lateral lamina epithelium thin along aperture; short distance into lumen, glandular tissue forming flattened longitudinal shelf. Glandular tissue diminishing in thickness at anterior and posterior ends of gonoduct. Shelf undercut along much of its length by flattened sinus (Figure 8, dotted line). Glandular tissue forming central rounded mass flanked by shallow trough along gonoductal groove. Medial lamina unevenly glandular, with irregular troughs and ridges; glandular tissue diminishing in thickness anteriorly and posteriorly (Figure 9). Epithelium of medial lamina posterior 1/5 smooth and concave, partially separated from anterior region by prominent curving ridge; ridge embracing corresponding rounded glandular mass in lateral lamina. Ridge continuous anteriorly with curving trough formed by opposing ridges of tissue. Trough fading anteriorly, and becoming flanked by short, shallow flap running along gonoductal groove.

FEMALE. Gonad (Figure 4, **ov**) dorsally surrounding digestive gland (except for a narrow ventral strip) from tip of visceral mass to posterior end of midgut (**sto**). Oviduct emerging ventrally from ovary. Renal oviduct (Figures 10, 11, **ovi**) deflected dorsally behind mantle cavity before entering base of glandular pallial oviduct. Pallial oviduct, with proximal albumen (**ag**) and distal capsule glands (**cg**). Albumen and capsule glands forming narrow bands with opposing flattened surfaces bounding gonoductal groove (Figure 11, **gg**); non-glandular portions of medial and lateral laminae formed by thickened connective tissue (**ct**). Proximal segment of albumen gland at base of mantle cavity under pallial kidney extension rather short and straight (Figures 10,



Figures 7–11. Reproductive anatomy of *Pleurocera acuta*. **7.** External, left lateral view of prostate. Anterior is to the left. Arrows indicate extent of opening to gonoductal groove. **8.** Internal aspect of prostate lateral lamina. Dotted line designates extent of sinus under glandular shelf. **9.** Internal aspect of prostate medial lamina. Anterior is to the right. Note parallel folds and groove at anterior end, representing presumptive spermatophore forming region. **10.** External, left lateral view of pallial oviduct. Anterior is to the left. Arrows indicate extent of opening to gonoductal groove. **11.** External, right lateral view of pallial oviduct. Anterior is to the right. Abbreviations: **ag,** albumen gland; **cg,** capsule gland; **ct,** connective tissue; **gg,** gonoductal groove; **ovi,** renal oviduct; **pr,** prostate; **sg,** sperm gutter; **spb,** spermatophore bursa; **vd,** vas deferens. Scale bars = 1 mm.

11, **ag**). Anterior to pallial kidney chamber, albumen gland curving under distal tip of bursa to the right, then arcing dorsally. Capsule gland comprising approximately anterior 1/4 of pallial oviduct; externally capsule gland not inflated (Figure 10, **cg**). Broad aperture along entire length of pallial oviduct except for a short fused segment at base of mantle cavity (Figure 10, arrows). Above aperture, sperm gutter (**sg**) opening in medial lamina at anterior tip of pallial oviduct and deepening posteriorly; gutter leading to short, blind spermatophore bursa (**spb**). Seminal receptacle absent.

Elimia livescens (Menke, 1830)

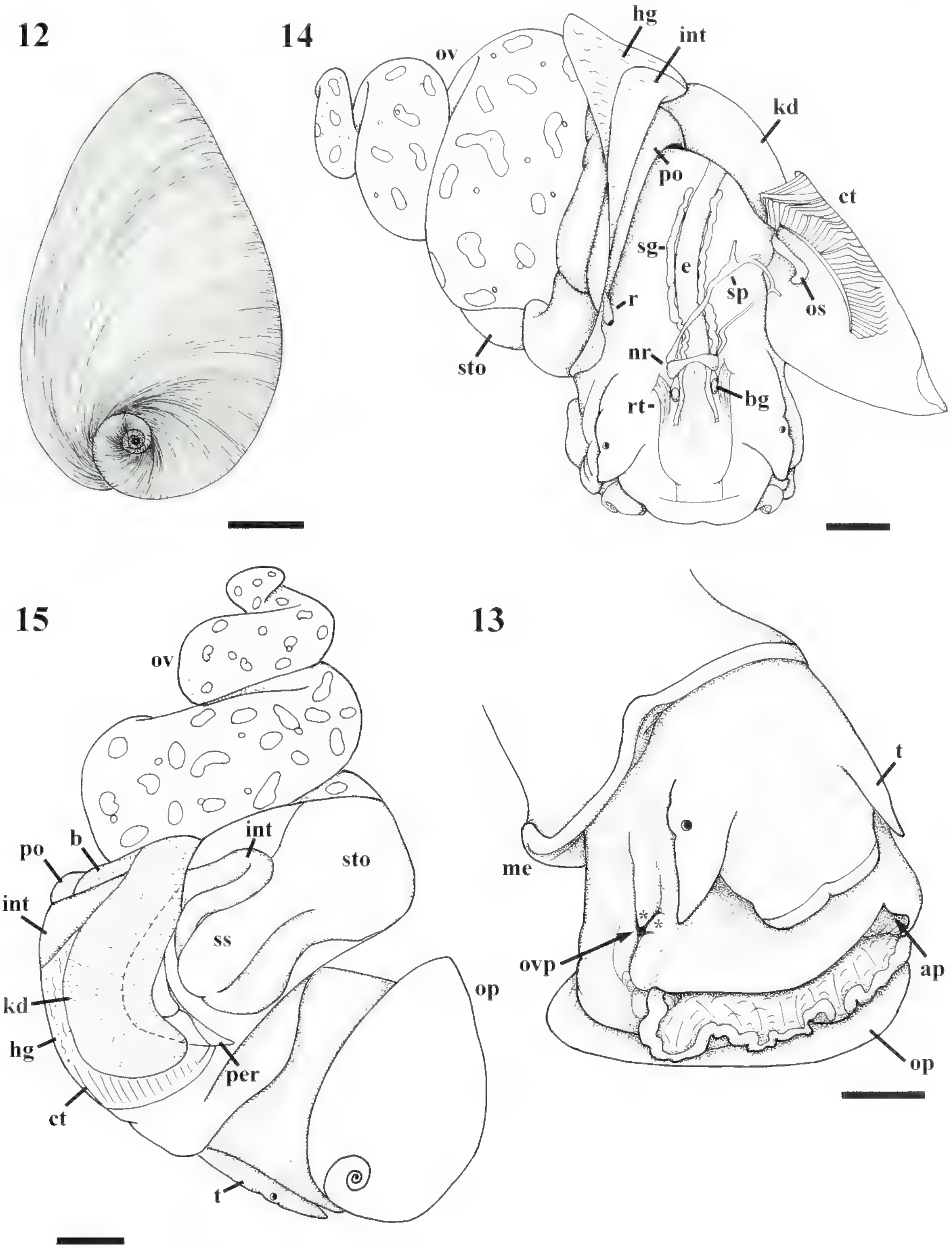
Material Examined: Wisconsin: Mukwonago River: USNM 1081521, 1081523.

External Anatomy: Operculum ovate, corneous, dark reddish-brown in color, with three whorls; paucispiral with small, basal nucleus of approximately 2.5 whorls (Figure 12). Last whorl expanding rapidly. Nucleus comprising approximately 1/5 of total length.

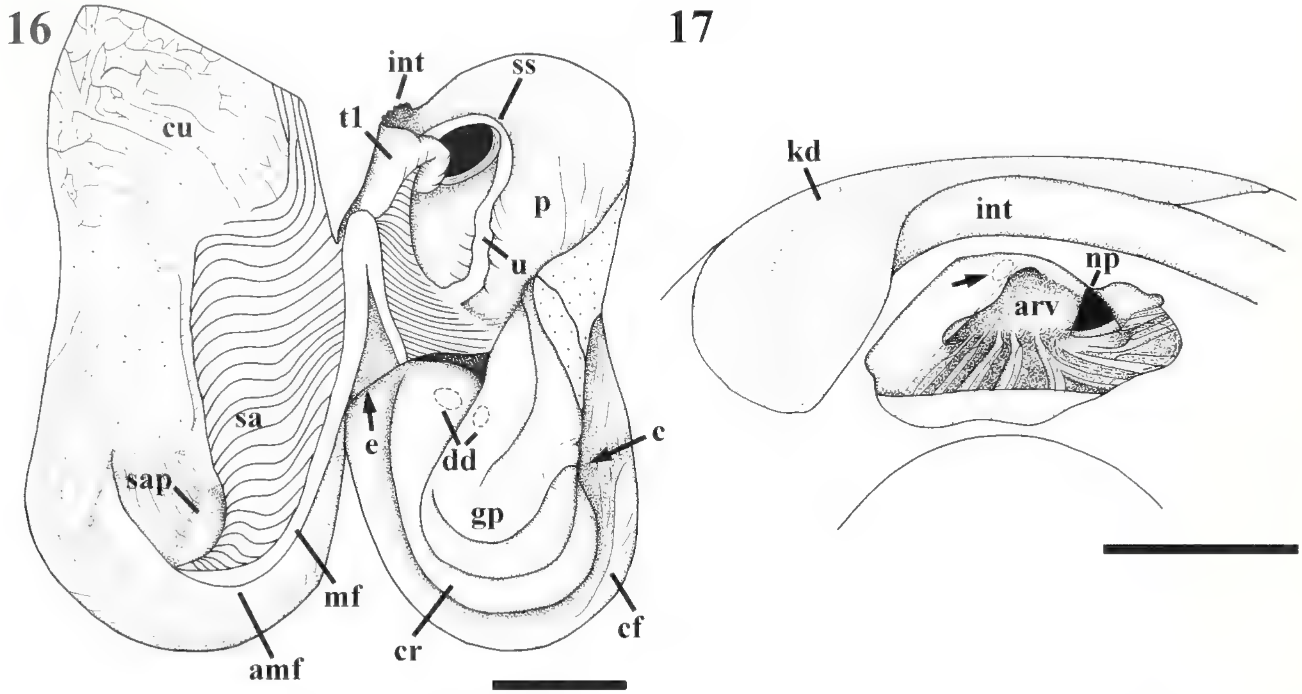
Foot broad and rounded, with wide propodium and long anterior pedal gland along anterior margin (Figure 13, **ap**). Ciliated egg groove extending short distance up side of neck from ovipositor; groove fading near base of tentacle. Parallel folds extending into ovipositor pore from aperture (*) roughly equal in size. Grooved tract extending ventrally from ovipositor to sole of foot at junction of propodium and mesopodium, just behind termination of anterior pedal gland.

Osphradium with curved anterior tip; some individuals with mostly straight osphradium (Figure 14, **os**). Hypobranchial gland well developed with deep, transverse folds (Figures 14, 15, **hg**).

Alimentary System: FOREGUT. Epithelium between dorsal and ventral folds glandular and irregularly to transversely striated. Dorsal and ventral folds diminish-



Figures 12–15. Anatomy of *Elimia livescens*. **12.** Operculum. **13.** Ovipositor and egg groove. Right lateral view of side of foot. Asterisks (*) indicate folds extending into ovipositor. **14.** Mantle cavity and anatomy of cephalic hemocoel. Dorsal view, anterior is below. **15.** External view of organs in visceral mass. Dotted line indicates extent of pericardium under main kidney chamber. Abbreviations: **ap,** anterior pedal gland; **b,** bladder; **bg,** buccal ganglion; **ct,** ctenidium; **e,** esophagus; **hg,** hypobranchial gland; **int,** intestine; **kd,** main kidney chamber; **me,** mantle edge; **nr,** circum-esophageal nerve ring; **op,** operculum; **os,** osphradium; **ov,** ovary; **ovp,** ovipositor; **per,** pericardium; **po,** pallial oviduct; **r,** rectum; **rt,** buccal mass retractor muscle; **sg,** salivary gland; **sp,** supra-esophageal ganglion; **ss,** style sac; **sto,** stomach; **t,** cephalic tentacle. Scale bars = 1 mm



Figures 16–17. Anatomy of *Elimia livescens*. **16.** Midgut anatomy. Dorsal view, anterior is uppermost. **17.** Kidney anatomy. Internal view of bladder. Lateral view, anterior is to the right. Right wall of bladder and adhering sheets of excretory tissue removed to reveal interior; cross-hatching indicates cross-section through sheets of tissue. Arrow indicates opening in septum allowing communication between bladder and main kidney chamber. Dotted line anteriorly indicates extent of ventral chamber. Abbreviations: **amf,** accessory marginal fold; **arv,** afferent renal vessel; **c,** caecum; **cf,** caecal fold; **cr,** crescentic ridge; **cu,** cuticularized region of stomach roof; **dd,** duct of digestive gland; **e,** esophageal aperture; **gp,** glandular pad; **gs,** gastric shield; **int,** intestine; **kd,** main kidney chamber; **mf,** marginal fold; **np,** nephropore; **p,** crystalline style pocket; **sa,** sorting area; **sap,** sorting area pad; **ss,** lip of style sac; **t1,** major typhlosole; **u,** u-shaped fold. Scale bars = 1 mm.

ing at distal end of mid-esophagus (Figure 14, **e**) but continuous into posterior esophagus. Posterior esophagus narrow, bearing numerous folds of equal height. Long, tubular salivary glands (**sg**) just reaching transition to posterior esophagus.

MIDGUT. Groove along midline of marginal fold lacking (Figure 16, **mf**). Single, weak, caecal fold (**cf**) along right side of midgut behind gastric shield, opposite caecum.

HINDGUT. Proximal intestine (Figure 15, **int**) passing below distal tip of style sac (**ss**), then extending posteriorly alongside style sac almost reaching main gastric chamber (**sto**). Intestine curving anteriorly with loop partially overlying proximal style sac. Intestine extending under posterior end of main kidney chamber (**kd**), entering pallial roof alongside bladder (**b**) and pallial gonoduct (**po**), continuing forward to papillate anus near mantle margin (Figure 14, **r**).

Reno-pericardial System: Bladder (Figure 15, **b**) largely occluded by vertical sheets of excretory tissue radiating from afferent renal vessel (Figure 17, **arv**) and fusing to right lateral floor, roof and walls. Sheets of excretory tissue loosely and regularly branching and anastomosing; posterior sheets less branched than those anteriorly.

Pericardium rather narrow and short (Figure 15, **per**), extending to intestinal loop (dotted line).

Nervous System: Buccal ganglia (Figure 14, **bg**) lying dorso-laterally at base of buccal mass between buccal retractor muscles (**rt**) and salivary glands (**sg**). Thickened connective (Figure 18, **co**) between left pleural and sub-esophageal ganglia producing 1–2 nerves (n=2). In addition to zygoneury (**z**) and connectives to left pleural and visceral ganglia, sub-esophageal ganglion producing 2–3 prominent nerves (n=2). Small statocysts (**st**) with approximately 20–30 statoconia.

Reproductive System: MALE. Flattened longitudinal shelf of glandular tissue within lateral lamina diminishing in thickness at anterior and posterior ends of prostate (Figures 19, 20, **pr**). Deep longitudinal cleft opening in glandular shelf along gonoductal groove at midpoint of gonoduct and extending anteriorly; cleft closing a short distance back from anterior tip of gonoduct (Figure 20, **cl**). Medial lamina thinly and rather evenly glandular along its length; glandular tissue slightly diminishing anteriorly (Figure 21). Epithelium of medial lamina posterior third smooth and strongly concave, separated from anterior 2/3 by prominent curving ridge; ridge embracing corresponding groove in glands of lateral lamina at proximal end of cleft. Epithelium of medial lamina anterior 2/3 irregularly and variably crossed by oblique and longitudinal ridges.

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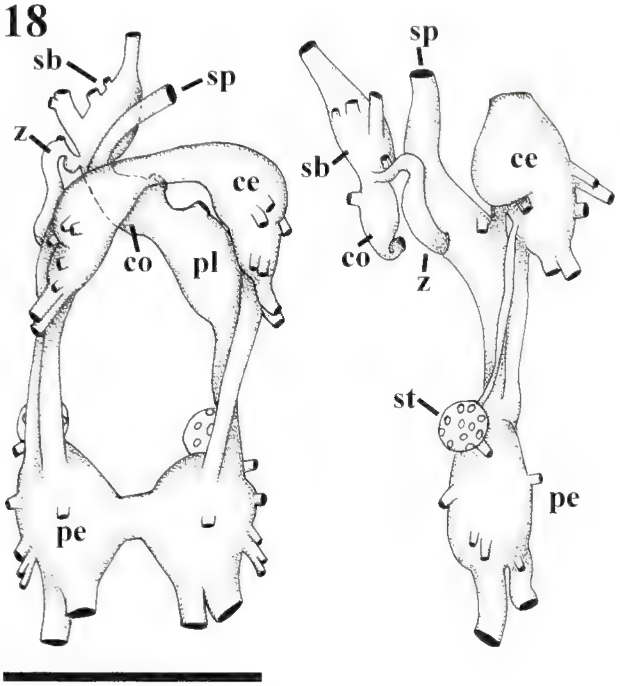


Figure 18. Circum-esophageal nerve ring of *Elimia livescens*. Frontal view on the left, right lateral view on the right. Abbreviations: **ce,** cerebral ganglion; **co,** thickened connective between left pleural and sub-esophageal ganglia; **pe,** pedal ganglion; **pl,** pleural ganglion; **sb,** sub-esophageal ganglion; **sp,** connective to supra-esophageal ganglion; **st,** statocyst; **z,** zygoneury. Scale bar = 1 mm.

Female. Renal oviduct (Figures 22, 23, **ovi**) deflected dorsally behind mantle cavity before entering base of glandular pallial oviduct. Proximal albumen gland rather long and initially curved, then forming straight segment along base of mantle cavity under pallial kidney extension. Capsule gland comprising approximately anterior 1/3 of pallial oviduct; externally capsule gland markedly inflated. Above aperture, short distance back from anterior tip of oviduct (~1/5 of length), sperm gutter (**sg**) opening in medial lamina and deepening posteriorly; gutter leading to short, blind spermatophore bursa (**spb**).

DISCUSSION

Whatever may be discovered in the future regarding the structure and relationships of species currently placed within the Pleuroceridae, given that *Pleurocera acuta* is the type species of the type genus for the family, this description will necessarily remain as the standard for the application of the name.

Comparison of *Pleurocera acuta* and *Elimia livescens*

Baker (1928) commented on the considerable uniformity of structure in the genitalia of these two species and that the soft parts do not seem to show the same degree of differentiation as the shells. Although this statement was based on external observations, Dazo (1965) similarly noted that, except for differences in size, the internal anatomy of the two species is quite similar or often identical in all organ systems; the most significant differences were those relating to size and shape of the operculum, snout, tentacles, foot, and radula.

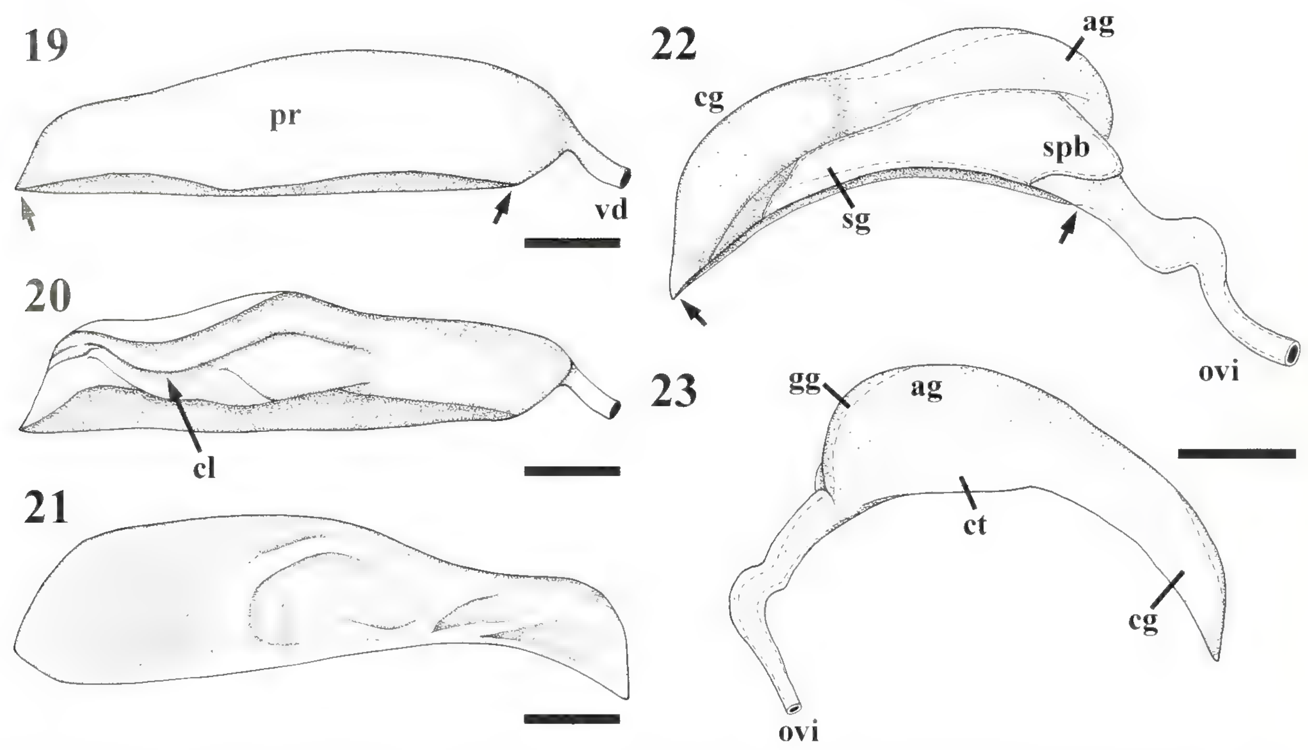
Yet, notions of similarity and how similar two entities must be to be characterized as "identical" are subjective concepts. The thorough documentation of these two species has been provided to allow a more objective means of assessing the degree of similarity between the two. Of course, any anatomical rendering will maintain some element of subjectivity.

With this in mind, the present analysis confirms that *Pleurocera acuta* and *Elimia livescens* are remarkably similar, both in overall organization and in many details. This level of similarity is perhaps not unexpected given the sister group relationship between the two genera supported in one molecular analysis (Holznagel and Lydeard, 2000). However, it should be noted that monophyly of these genera has not been demonstrated unambiguously (e.g. Sides, 2005), but awaits confirmation within a more comprehensive phylogenetic framework. Thus, the present results may indicate a closer systematic affinity than currently appreciated.

Yet, a number of differences between the two species are apparent. Externally, the two differ in development of the hypobranchial gland, but this is difficult to quantify. They also differ in the position of the ovipositor and its relationship to the foot sole. This is consistent with described differences in the mode of egg capsule transfer to the substrate; in *Pleurocera acuta*, only the everted walls of the ovipositor function in oviposition (van Cleave, 1932), but in *Elimia laqueata*—a species with an ovipositor configuration identical to *E. livescens* (see below)—both the everted lips of the ovipositor and the margins of the finely grooved tract guide the ova to the substrate (Woodard, 1934).

The most significant differences in midgut structure are length of caecal fold, and the presence of a groove along the marginal fold; however, these variations may be attributable to preservation artifacts. The significance of other minor differences (size and/or shape of caecum, glandular pad, major typhlosole, gastric shield, crescentic ridge, field of parallel striations above esophageal aperture) can only be ascertained once a broader sampling of species from both genera have been examined. But these may also be attributable to preservation artifacts and/or intra-specific variation.

Internal structure of the kidney differs only in that the vertical sheets of excretory tissue are more highly and densely branched within the bladder in *Pleurocera acuta*. It was observed that the amount of such excretory tissue varied between individuals in a species and with maturity. Although a highly qualitative character, the degree of difference between the two species surpasses that of intra-specific variation.



Figures 19–23. Reproductive anatomy of *Elimia livescens*. **19.** External, left lateral view of prostate. Anterior is to the left. Arrows indicate extent of opening to gonoductal groove. **20.** Internal aspect of prostate lateral lamina. Note deep cleft at anterior end (**cl**), representing presumptive spermatophore forming region. **21.** Internal aspect of prostate medial lamina. Anterior is to the right. **22.** External, left lateral view of pallial oviduct. Anterior is to the left. Arrows indicate extent of opening to gonoductal groove. **23.** External, right lateral view of pallial oviduct. Anterior is to the right. Abbreviations: **ag,** albumen gland; **cg,** capsule gland; **cl,** deep cleft; **ct,** connective tissue; **gg,** gonoductal groove; **ovi,** renal oviduct; **sg,** sperm gutter; **spb,** spermatophore bursa; **vd,** vas deferens. Scale bars = 1 mm.

The configuration of the nerve ring and visceral loop is largely identical between the two. One difference is the number of nerves issuing from the sub-esophageal/left pleural connective and from the sub-esophageal ganglion. However, given the observed intra-specific variation, these differences likely fall within the range of individual variation.

In contrast to the results presented here, Dazo (1965) reported 9 cerebral nerves, only a single nerve from the visceral ganglion, and an inconstant number of accessory pedal nerves; however, Dazo did confirm the unique thickened left pleural/sub-esophageal connective. Dazo also commented on the unlikely generality of Rosewater's (1961) findings that pleurocerids differ primarily in the lengths of the cerebral commissure and left pleural/sub-esophageal connective (n=6 for 9 species). Indeed, these lengths were found to be sometimes conspicuously different between individuals examined in the present study.

Males of the two species differed in the pattern of folds within the anterior region of the prostate. Regardless, the anterior region is inferred to be the site of spermatophore formation rather than the comparatively smoother posterior region. This conclusion seems justified given the similarity in the configuration of the folds as compared to overall form and shape of the spermatophore (Jewell, 1931; Dazo, 1965). Limnic cerithioideans in the family Paludomidae Stoliczka, 1868, have separated the glands in this anterior region to form a hollow tube that has been implicated in spermatophore formation (Glaubrecht and Strong, 2004). That discovery further supports the notion that sperm packets are produced anteriorly and suggests that this function may be homologous in different lineages.

For a summary of these and other morphological differences, see Table 1.

COMPARISON TO OTHER PLEUROCERIDS

With minor exception, published accounts agree on the main patterns of pleurocerid anatomy. Thus, pleurocerids have long been known to be dioecious and oviparous (except *Semisulcospira*) with an ovipositor involved in the deposition of the egg capsules (Stimpson, 1864). Members of the family are also aphallate, with open gonoducts, a gonad that dorsally surrounds the digestive gland, and produce crescent-shaped spermatophores (e.g. Stimpson, 1864; Jewell, 1931; Woodard, 1934, 1935; Magruder, 1935b; Jones and Branson, 1964; Dazo, 1965). Like other cerithioideans, pleurocerids possess

Table 1. Summary of morphological differences between *Pleurocera acuta* and *Elimia livescens*.

	Pleurocera acuta	*Elimia livescens*
External Anatomy:		
Propodium	Narrow	Broad
Ovipositor ventral groove	Does not extend to foot margin	Extends to foot margin
Curved anterior tip of osphradium	Sometimes present	Often present
Alimentary System:		
Ventral folds at posterior end of mid-esophagus	Fused	Unfused
Groove along marginal fold	Present	Absent
Length of caecal fold	Long	Short
Hindgut loop	Extends to main gastric chamber	Does not reach main gastric chamber
Reno-Pericardial System:		
Bladder excretory tubules	Densely and highly branched	Loosely and regularly branched
Pericardium	Extends to right body wall	Extends to intestinal loop
Nervous System:		
Buccal ganglia	Ventro-lateral	Dorsal
Statoconia	~10–15	~20–30
Nerves from sub-esophageal/left pleural connective	1–3	1–2
Nerves from sub-esophageal ganglion	2 connectives and 2 nerves (including zygoneury)	2 connectives and 3–4 nerves (including zygoneury)
Reproductive System:		
Spermatophore-forming region	Parallel folds and trough in medial lamina	Deep cleft in lateral lamina
Sperm gutter	Extends to anterior tip of oviduct	Does not extend to anterior tip of pallial oviduct
Junction of renal and pallial oviduct	Renal oviduct curves dorsally to straight segment of albumen gland	Renal oviduct ventrally joins curved portion of albumen gland
Proximal albumen gland	Short, straight segment between renal oviduct and posterior end of bursa	Initially curved, with long, straight segment to posterior end of spermatophore bursa

two types of glands within the pallial oviduct – a feature not previously documented among eastern North American species.

The gut is characterized by the presence of tubular salivary glands, a crystalline style and a style sac in restricted communication with the proximal intestine (Magruder, 1935a, b; Itagaki, 1960; Dazo, 1965). The bi-lobed nature of the kidney has been noted before (Magruder, 1935b; Itagaki, 1960), but the internal subdivision of the organ had not been previously documented.

The nervous system is consistent with many other cerithioideans (left dialyneurous, long connective between the right pleural and supra-esophageal ganglia, single visceral ganglion) (e.g. Strong, 2003; Strong and Glaubrecht, 2002, 2003), but is distinguished by the presence of an enlarged connective between the left pleural and sub-esophageal ganglia and a zygoneurous connection on the right—the latter a highly homoplastic character in the Cerithioidea (see review in Houbrick, 1988). However, the presence/absence of zygoneury among pleurocerids requires confirmation as it has been depicted as dialyneury in several other species (Magruder, 1935b; Itagaki, 1960). Only the former study confirmed the presence of the enlarged left pleural and sub-esophageal connective. Additionally, published descriptions (Magruder, 1935b; Itagaki, 1960; Dazo, 1965; present study) disagree on the number of nerves produced by various ganglia, but as noted above, this can be highly variable even within species. However, the number of statoconia reported by Magruder (30–40; 1935b) is significantly more than the number reported herein, possibly exceeding the level of intra-specific variation and, thus may be an informative phylogenetic character.

Several significant discrepancies among previous descriptions of pleurocerid anatomy are now resolved. Woodard (1934, 1935) observed a so-called "cytophore organ" at the base of the mantle cavity, apparently confluent with the sperm duct. Similarly, Dazo (1965) reported the presence of a cytophore organ in males of both *Pleurocera acuta* and *Elimia livescens*. Based on the present analysis and Woodard's description of the internal structure and position of this organ, it is clear that Woodard misidentified the kidney bladder as a part of the reproductive tract. However, it is not clear why the cytophore organ was described as lacking in females. The intimate connection between the bladder and proximal pallial gonoduct was correctly depicted in *Hua* by Prozorova (1990).

Dazo (1965), as well as several other workers (Woodard, 1934; Jones and Branson, 1964), have

Table 2. Summary of morphological differences between *Pleurocera acuta* and *Elimia livescens* compared to other limnic gastropods classified in the Pleuroceridae and Melanopsidae. Details from Itagaki, 1960; Bilgin, 1973; Houbrick, 1988; Nakano and Nishiwaki, 1989; Glaubrecht, 1996; Strong and Glaubrecht, unpubl. data.

	Pleuraceura acuta *Elimia livescens*	*Juga*	*Semisulcospira*	*Melanopsidae*
External Anatomy:				
Ovipositor pore	Simple, weakly glandular	Simple, weakly glandular	Not applicable	Complex, highly glandular
Alimentary System:				
Salivary glands	Tubular	?	Tubular	Tubular/branched
Salivary gland position	Pass through nerve ring	?	Pass through nerve ring	Pass through/anterior to nerve ring
Esophageal gland	Absent	?	Absent?	Present
Digestive gland ducts	2	?	2	1
Caecum	Small	?	Small	Deep and spiral
Reno-Pericardial System:				
Bladder	Small, pallial	?	?	Small, pallial
Nervous System:				
Dialyneury, Zygoneury	Zygoneury	?	Dialyneury?	Zygoneury
Reproductive System:				
Seminal vesicle	Straight	?	Straight	Coiled
Pallial oviduct	Open	Open	Closed	Open
Seminal receptacle	Absent	Present	Present	Present
Reproductive strategy	Oviparous	Oviparous	Viviparous	Oviparous

reported the presence of a seminal receptacle, but no mention of a spermatophore bursa was made. The present study has confirmed that the sperm storage structure in *Pleurocera acuta* and *Elimia livescens* is a bursa based on the presence of unorientated sperm. Examination of specimens of *E. laqueata* (USNM 1081558) confirmed that the structure reported as a seminal receptacle is indeed a bursa—no seminal receptacle is present; judging from the description of Jones and Branson (1964), the same holds true for *E. potosiensis*. The pallial position of the bladder was also confirmed in *E. laqueata* (pers. obs.). It is interesting to note that the sperm gutter extends farther anteriorly in *E. laqueata* than in *E. livescens*. Additionally, the straight segment of the albumen gland between the tip of the bursa and the junction of the renal oviduct is lacking in *E. laqueata*. Instead, the albumen gland arcs dorsally to join the renal oviduct just behind the tip of the bursa. In all other respects, the overall structure of the pallial oviduct in *E. laqueata* is consistent with features described here, as well as in the close association between the ovipositor and the junction of the propodium and mesopodium.

A final discrepancy is the presumed site of spermatophore formation. Woodard (1934, 1935) described the distal prostate as smooth and the highly folded proximal portion as the site of spermatophore formation. Jones and Branson (1964) did not distinguish a spermatophore-forming region in *Elimia potosiensis*. In the present study, it is the highly folded distal region that is inferred to be the site of spermatophore formation.

SYSTEMATICS OF PLEUROCERIDAE

As mentioned above, although confusion has long existed, the distinctiveness of the Pachychilidae from other limnic lineages including the Pleuroceridae has now been clarified based on morphological and molecular data (e.g. Glaubrecht, 1996, 1999; Lydeard et al., 2002; Köhler et al., 2004). However, the paraphyly of eastern and western North American and Asian pleurocerids with respect to the Melanopsidae based on molecular data (Lydeard et al., 2002) remains at issue. The analysis of Houbrick (1988) did not include sufficient taxon sampling to adequately assess monophyly of the two families, but a sister-group relationship between the two was supported.

Although an in depth analysis of monophyly and affinity of the two families is beyond the scope of this study, several morphological features may be informative in clarifying these relationships. As noted by Prozorova (1990) the reproductive anatomy of eastern North American pleurocerids differs from species in western North America (*Juga*) and Asia (*Semisulcospira*) in that both *Juga* and *Semisulcospira* possess a seminal receptacle in addition to a spermatophore bursa. The latter genus has modified the pallial oviduct into a closed brood pouch (Itagaki, 1960; Nakano and Nishiwaki, 1989; Prozorova, 1990; Rashchepkina, 2000; Prozorova and Raschepkina, 2001, 2004).

In addition to the synapomorphies recovered in the analysis of Houbrick (weakly developed hypobranchial gland, zygoneury, long left pleural/sub-esophageal connective), midgut anatomy is broadly congruent in the two families, differing in several significant respects from that of the other limnic lineages (e.g. Paludomidae, Pachychilidae, Thiaridae) (Bilgin, 1973; Köhler and Glaubrecht, 2001; Strong and Glaubrecht, 2002, 2003, unpubl. data). They also share similarities in renopericardial (presence of a bladder) and reproductive anatomy (open pallial gonoducts, presence of a seminal receptacle)—the latter, in particular, are undoubtedly symplesiomorphic. But other aspects of the anatomy are consistent within each family and clearly differentiate the two when sufficient information is available. Thus, in addition to features of the radula and shell, melanopsids may be distinguished by the presence of an esophageal gland, salivary glands that lie anterior to the nerve ring (although variable in the family), a single digestive gland duct and spiral caecum in the midgut, and a coiled seminal vesicle. Of course, the extent to which these features represent shared derived or homoplastic features remains to be discovered in the context of a phylogenetic analysis.

CONCLUSIONS

The present study has provided the first detailed description of the midgut and kidney for any pleurocerid snail, and has clarified the internal structure and homologies of the pallial gonoducts of eastern North American forms. This comparative analysis has confirmed the high degree of morphological similarity between *Pleurocera acuta* and *Elimia livescens*, but has also revealed a number of differences in detail; the extent to which these features support monophyly of the genera remains to be established. The fact that the presence/absence of a seminal receptacle distinguishes eastern and western North American/Asian pleurocerids is confirmed. Pleurocerids and melanopsids are broadly similar in features of the midgut and share a similar configuration of the pallial oviduct, but can be distinguished by anatomical characters of the alimentary (salivary glands, esophageal gland, digestive gland ducts, caecum) and reproductive (seminal vesicle) systems. However, comprehensive anatomical treatments of western North American and Asian pleurocerids are needed to fully assess the morphological distinctiveness of the two families. The clarification of the distribution of these features, within the context of a phylogenetic analysis, should aid in refining the monophyly of the Pleuroceridae and their affinity to other freshwater lineages.

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New Late Cretaceous (Santonian and Campanian) gastropods from California and Baja California, Mexico

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ABSTRACT

Three new genera and six new species of shallow-marine Late Cretaceous gastropods are reported from various formations in California and from one formation in Baja California, Mexico. *Tegula jeanae* new species, of early Campanian age, is the earliest known species of this trochid genus. *Nerita* (subgenus?) *orovillensis* new species is the second known Early Campanian neritid from California. The cerithioid *Bullamirifica* new genus is represented by three species: *Bullamirifica verruca* new species of Coniacian age; *Bullamirifica elegans* new species of early Campanian age; and *Bullamirifica ainiktos* (Dailey and Popenoe, 1966) of middle to late Campanian age. The latter species has the most widespread distribution, with occurrences in southern California and northern Baja California. *Minytropis melilota* new genus and species of Santonian age, and *Paxitropis dicriota* new genus and species of Late Santonian to early Campanian age are high-spired trichotropids. As presently known, *Bullamirifica*, *Minytropis*, and *Paxitropis* were endemic to the study area.

INTRODUCTION

This study is based largely on specimens collected by Eric Göhre of Oroville, California. Over the years, he has amassed a sizeable collection of shallow-marine mollusks from the lower Campanian Pentz Road member of the Chico Formation near Pentz, Butte County, northern California (Figure 1). His collection has yielded several new species of gastropods, and some of these were described by Groves (2004) and Squires and Saul (2004). In part, this present study concerns three additional new species and a new genus of gastropods found in his collection. They are the trochid *Tegula jeanae* new species, the neritid *Nerita* (subgenus?) *orovillensis* new species, and the cerithioid *Bullamirifica elegans* new genus and species.

Inspection of the literature, as well as examination of the collections at the Natural History Museum of Los Angeles County, allowed us to incorporate two additional species into *Bullamirifica*. These are *Bullamirifica verruca* new genus and species from the Coniacian Member IV of the Redding Formation in the Oak Run area, northern California, and *Bullamirifica anikitos* Dailey and Popenoe (1966) new combination from the middle Campanian Pigeon Point Formation southwest of San Francisco, northern California; the middle upper Campanian Punta Baja Formation, Baja California, Mexico; and the upper Campanian Jalama Formation, southern California (Figure 1). "*Cimolithium miyakoense*" (Nagao, 1934) and "*Vicarya* (*Shoshiroia*) *yabei*" Kamada, 1960, reported by Perrilliat-Montoya (1968) from Baja California, Mexico (see Figure 1, formation 6), are judged by us to be synonyms of *Bullamirifica ainiktos*.

Also included in this present study are new trichotropid gastropods found in the collections at the Natural History Museum of Los Angeles County. They are *Minytropis melilota* new genus and species from the Santonian part of the Redding and Chico formations of northern California, and *Paxitropis dicriota*, new genus and species from the of upper Santonian part of the Redding Formation, northern California; the lower Campanian part of the Chico Formation; and the lower Campanian part of the upper Holz Member of the Ladd Formation, southern California (Figure 1).

The geologic age of each new species described in this paper is shown in Figure 2. The entire interval of time that encompasses all these species is Coniacian to late Campanian, or about 19 million years. The new species are locally common, except for *Tegula jeanae*, *Nerita* (subgenus?) *orovillensis*, and *B. verruca*.

The classification system used here generally follows that of Hickman and McLean (1990) for the tegulines, Ponder (1988) for the trichotropids, and Ponder and Warén (1988) for the other taxa.

Study localities are listed in Appendix 1. Abbreviations used in the text are: CAS: California Academy of Sciences,

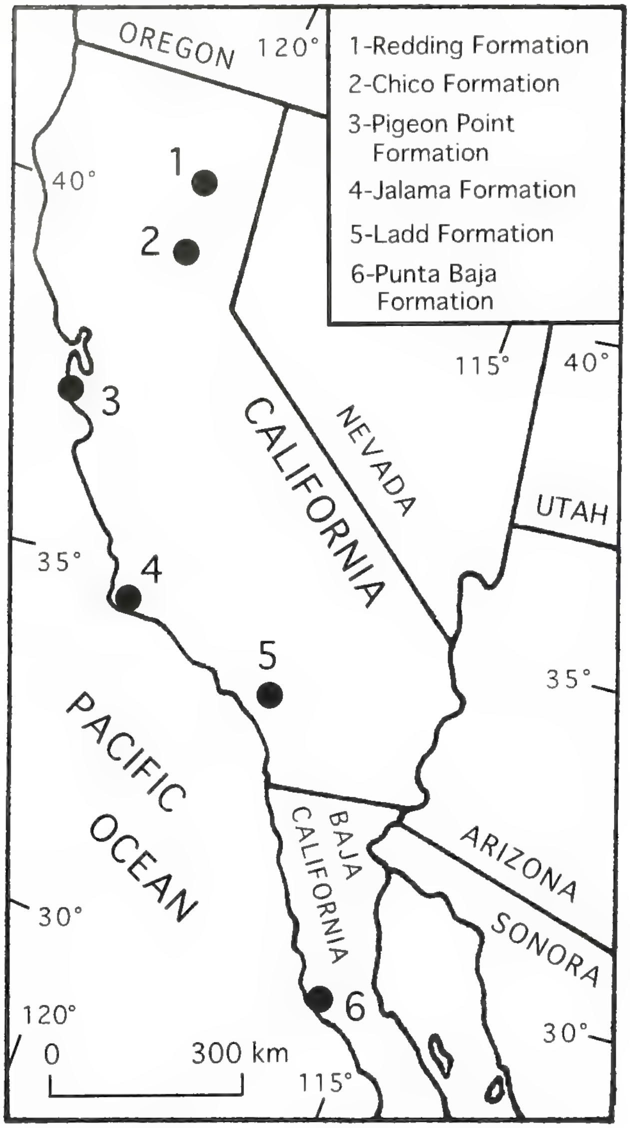


Figure 1. Location of formations bearing the new taxa.

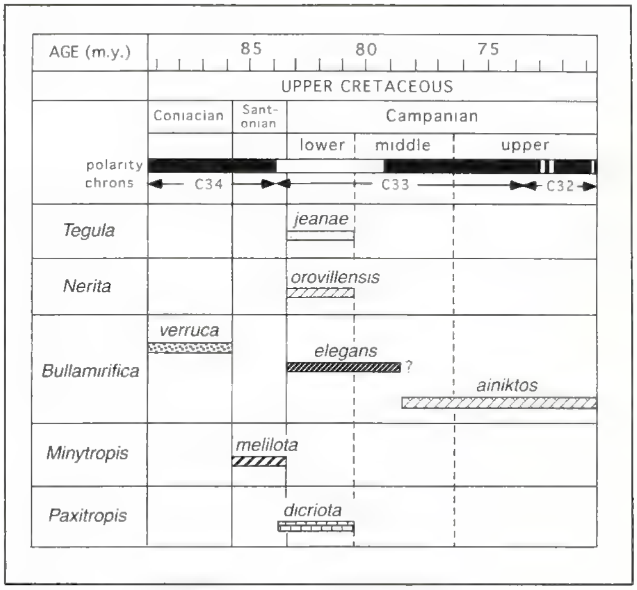


Figure 2. Chronostratigraphic positions of the new taxa. Ages of stage boundaries and magnetostratigraphy from Gradstein et al. (2004, fig. 19.1).

San Francisco; IGM: México Museo del Paleontologia del Instituto de Geologa; LACMIP: Natural History Museum of Los Angeles County, Invertebrate Paleontology Section; UCLA: University of California, Los Angeles (collections now housed at LACMIP); UCMP: University of California Museum of Paleontology (Berkeley); USGS: United States Geological Survey.

STRATIGRAPHY

Except for the Punta Baja Formation, which is discussed below, the ages and depositional environments of all the formations and members containing the new taxa discussed in this paper can be found in the following papers: Member IV of the Redding Formation, Squires and Saul (2003a); Musty Buck Member of the Chico Formation, Saul and Squires (2003); Pentz Road member (informal) of the Chico Formation, Squires and Saul (1997); Ten Mile Member of the Chico Formation, Squires and Saul (2003b); upper Holz Shale of the Ladd Formation, Squires and Saul (2001); Pigeon Point Formation, Elder and Saul (1993) and Squires and Saul (2003b); and Jalama Formation, Squires and Saul (2003b). The locales of these formations are shown in Figure 1. Stratigraphic information mentioned below concerns additional pertinent biostratigraphic details. The age of the Jalama Formation used here is slightly younger than used in our previous papers because we had to adjust its chronostratigraphic position based on the latest published (Gradstein et al., 2004) absolute-time and global-paleomagnetic data correlations.

PUNTA BAJA FORMATION

Perrilliat-Montoya (1968) reported specimens of gastropods, herein assigned to *Bullamirifica ainiktos*, from the "Rosario Formation" at Punta Baja, near El Rosario, northern Baja California, Mexico. The 5–140 m thick Punta Baja Formation (Figure 1) overlies fluvial deposits of the La Bocana Roja Formation, and the angular unconformity between these two formations is canyon-shaped (Boehlke and Abbott, 1986). This canyon is filled with conglomerate, sandstone, and siltstone reported by Kilmer (1963) to have been deposited in shallow-marine depths not exceeding 60 meters. Boehlke and Abbott (1986) have a differing viewpoint and reported that the deposits represent turbidites that accumulated in bathyal depths. They reported, furthermore, that shallow-marine mollusks are common, but Kilmer's collection at UCMP does not contain very many specimens. The Punta Baja Formation is unconformably overlain by terrestrial deposits of the La Escarpa Member of the El Gallo

Formation, which, in turn, is overlain by the Rosario Formation.

Based on molluscan fossils collected by F. H. Kilmer, Saul (1983: 21–22, fig. 9) reported the ammonite *Metaplacenticeras* cf. *pacificum* (Smith, 1900) and the gastropod *Turritella chicoensis pescaderoensis* Arnold, 1908, from the siltstone in the Punta Baja Formation. Although these two mollusks were reported by Saul (1983: 65–66) to be of late Campanian age, more recent biostratigraphic studies (Elder and Saul, 1996: fig. 1) depicted both of these taxa as ranging in age from late middle Campanian to earliest late Campanian. Adjustments for the most recently published (Gradstein et al., 2004) absolute-time and global-paleomagnetic data correlations place these ammonite and turritellid zones in the middle late Campanian. Recent examination by the junior author of additional Punta Baja Formation mollusks revealed three specimens of the bivalve *Calva*. The best preserved specimen is from LACMIP loc. 12582 and is *Calva* (*Egelicalva*) *crassa* Saul and Popenoe, 1992, whose geologic range is early late Campanian to early Maastrichtian elsewhere on the Pacific slope of North America (Saul and Popenoe, 1992). The other two *Calva* specimens are worn and broken, from UCMP loc. B-3388. These two specimens are similar to *Calva* (*Calva*) *peninsularis* (Anderson and Hanna, 1935), whose geologic range is latest Campanian to early Maastrichtian elsewhere on the Pacific slope of North America (Saul and Popenoe, 1992).

Boehlke and Abbott (1986: fig. 4) assigned the age of the Punta Baja Formation to the early Campanian based entirely on calcareous nannofossils. They also reported that the benthic foraminifera in this formation correspond to the F2-lower E foraminifera zones of Goudkoff (1945), but they did not rely on the foraminifera for their age call. Almgren (1986: table 2) reported that the F2-lower E foraminifera zones are essentially correlative to the early Campanian to late Campanian. It is important to mention that the Alcalde Shale in the Coalinga area along the west side of the San Joaquin Valley, central California, is correlative to the E zone (Almgren, 1986: table 3). As depicted in Saul (1983: fig. 10), the Alcalde Shale contains *Metaplacenticeras* cf. *M. pacificum*, and Almgren (1986) assigned the Alcalde Shale to the early late Campanian.

In summary, the *Metaplacenticeras*, *Turritella*, *Calva*, and benthic foraminifera data strongly support a middle late Campanian age for the Punta Baja Formation. The calcareous nannofossils, however, support an early Campanian age. It seems probable that the older calcareous nannofossils are reworked, and this would be consistent with the depositional environment of the formation.

SYSTEMATIC PALEONTOLOGY

Superfamily Trochoidea Rafinesque, 1815
Family Trochidae Rafinesque, 1815
Subfamily Tegulinae Kuroda, Habe and Oyama, 1971
Genus *Tegula* Lesson, 1835

Type Species: *Tegula elegans* Lesson, 1835, by monotypy; Recent, west coast of Central America to the Gulf of California, Mexico.

Discussion: Although Wenz (1938), Keen (1960), and Davies (1971) reported the geologic range of *Tegula* to be Miocene to Recent, Bandel and Stinnesbeck (2000) reported a species of *Tegula* of Late Cretaceous (Maastrichtian) age from central Chile. Kiel and Bandel (2001) reported a tentatively identified *Tegula* from upper Campanian strata in northern Spain. The early Campanian new species described below represents the confirmed earliest record we know of for *Tegula*. For the Pacific slope of North America, the previous earliest record of *Tegula* was given by Addicott (1973: 17, pl. 8, figs. 2, 4), who reported it from the Wygal Sandstone Member of the Temblor Formation, southwestern margin of the San Joaquin Valley, Kern County, central California. Squires (2003: table 2.1, fig. 2.1) placed this member in the lower Oligocene Matlockian Stage.

Tegula jeanae new species
(Figures 3–5)

Diagnosis: A *Tegula* with low to moderate spire. Whorls convex, smooth, and bearing one spiral groove on posterior third of last whorl. Anomphalous. Last whorl with raised lip along basal edge, base sunken between this lip and columellar lip, which bears at least one denticle and one much smaller denticle adapically.

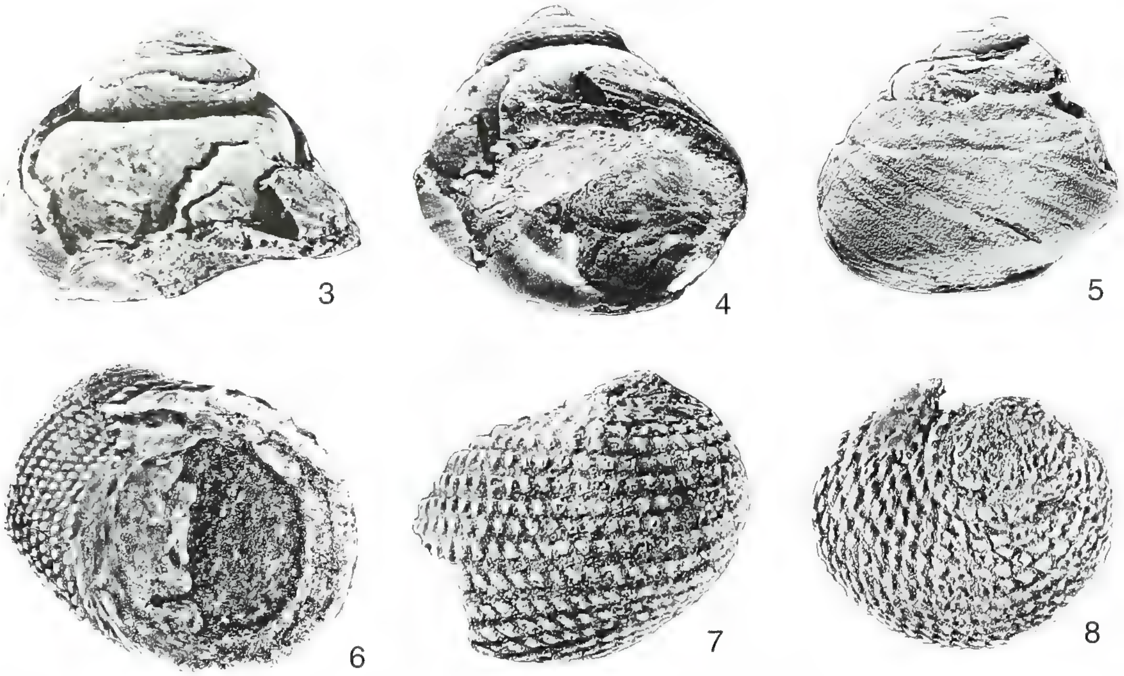
Description: Shell medium (up to 16.6 mm height and 21.7 mm diameter, same specimen). Turbiniform with spire low to moderately elevated. Protoconch unknown. Teleoconch consisting of three whorls. Suture impressed, slightly channeled. Whorls convex, sometimes slightly concave short distance anterior of suture; blunt angulation anterior of medial part of last whorl. Whorls smooth; spiral groove posterior of medial part of last whorl. Aperture oblique, peristome discontinuous. Anomphalous, umbilical area covered by broad callus. Base wide and smooth, peripheral (abaxial) margin coincident with raised lip along edge of last whorl; area depressed between this lip and columella. Outer lip strongly prosocline. Columellar lip with at least one oblique denticle; much weaker second denticle sometimes present immediately posterior of main denticle. Growth lines strongly prosocline, forming wide bands.

Holotype: LACMIP 13322, 18.7 mm in height, 22 mm in diameter.

Paratype: LACMIP 13323.

Type Locality: LACMIP loc. 24337.

Geologic Age: Early Campanian.



Figures 3–8. New tegulid and neritid gastropods. Specimens coated with ammonium chloride. **3–5.** *Tegula jeanae* new species, LACMIP loc. 24337. **3.** Paratype LACMIP 13323, apertural view, height 13.9 mm, diameter 17.9 mm. **4–5.** Holotype 13322, height 18.7 mm, diameter 22 mm. **6–7.** *Nerita* (subgenus?) *orovillensis* new species. **6.** Holotype LACMIP 13324, apertural view, height 11.6 mm, diameter 16.8 mm. **7–8.** Paratype LACMIP 13325, total shell height 10 mm, diameter 13.7 mm. **7.** Abapertural view. **8.** Apical view.

Distribution: Chico Formation, Pentz Road member (informal), near Pentz, Butte County, northern California.

Etymology: Named for Jean Göhre, mother of Eric Göhre, who collected and donated the type material to LACMIP.

Discussion: This new species is known from two specimens, both showing good preservation. The new species is remarkably similar to *Tegula* (*Chlorostoma*) *funebralis* (Adams, 1855), from Pliocene and Pleistocene strata of southern California (Grant and Gale, 1931) and from the Recent of Vancouver Island, British Columbia, to central Baja California, Mexico (McLean, 1978). The new species differs from *T.* (*C.*) *funebralis* by having a smooth shell rather than being ornamented by weak spiral ribs. The similarity between the new species and *T.* (*C.*) *funebralis* is even stronger if the specimens of the latter are worn.

Tegula ovallei (Philippi, 1887: pl. 12, fig. 4; Bandel and Stinnesbeck, 2000: 761, pl. 1, B), the only other positively identified Cretaceous *Tegula* that we know of, is from Maastrichtian strata in central Chile. The new species differs from *T. ovallei* by having a smooth shell rather than being ornamented by granulated spiral ridges

Kiel and Bandel (2001: 139, pl. 1, fig. 1) reported a tentatively identified *Tegula*? *simplex* (Quintero and Revilla, 1966: 49, pl. 8, fig. 3) from upper Campanian strata in northern Spain. The new species differs greatly from *T.*? *simplex* by having a less elevated spire, smooth shell, blunt rather than a sharp angulation anterior of the medial part of the last whorl, broad callus covering the umbilical region, wider aperture, very much stronger denticles on the columella, raised lip along the basal edge of the last whorl, and sunken base between this raised lip and the columellar lip.

Family Neritidae Rafinesque, 1815
Genus *Nerita* Linnaeus, 1758

Type Species: *Nerita peloronta* Linnaeus, 1758, by subsequent designation (Montfort, 1810); Recent, south Florida, West Indies, and Bermuda.

Discussion: *Nerita* sensu lato ranges from Early Cretaceous (Hauterivian), and the earliest record is from the Ono Member of the Budden Canyon Formation, Trinity County, northern California (Saul and Squires, 1997). The new species described below represents the first record of an early Campanian *Nerita* from the study area.

Subgenus?
Nerita (subgenus?) orovillensis new species
(Figures 6–8)

Diagnosis: A *Nerita* with approximately 18 to 19 beaded spiral ribs. Columellar lip with four or five obscure teeth.

Description: Shell medium small (up to 11.6 mm in height and 16.3 mm in diameter, same specimen), broader than high, globose. Last whorl rapidly expanding. Protoconch unknown. Teleoconch consisting of 2.5 to 2.75 whorls. Uppermost spire very low. Suture obscure. Earliest 1.5 teleoconch whorls apparently smooth, rest of teleoconch covered with approximately 18 narrow spiral ribs bearing small beads; interspaces between ribs approximately as wide as interspaces. Beads on ribs becoming smaller and slightly elongate on base of last whorl, especially in parietal region. Spiral rib adjacent to suture can be slightly stronger than other ribs. Aperture large, nearly circular. Outer lip flared, interior smooth. Columellar lip with five somewhat obscure teeth, most posterior tooth widest and longest. Deck area broad, sloping, and sharply demarcated from base of last whorl. Growth lines prosocline.

Holotype: LACMIP 13324, 11.6 mm in height, 16.8 mm in diameter.

Paratype: LACMIP 13325.

Type Locality: LACMIP loc. 24337.

Geologic Age: Early Campanian.

Distribution: Chico Formation, Pentz Road member (informal), near Pentz, Butte County, northern California.

Etymology: Named for Oroville, California.

Discussion: The new species is based on two specimens. The external surfaces are moderately well preserved, but the columellar lip and especially the deck area are poorly preserved.

The new species is remarkably similar to *Nerita* (*Theliostyla*) *crooki* Clark (1938: 700, pl. 4, figs. 1, 2) from the Markley Formation east of San Francisco, Solano County, northern California. Squires (2003: table 2.1, fig. 2.1) assigned this formation to the middle Eocene ("Tejon Stage"). The new species differs from *N.* (*T.*) *crooki* by having fewer and wider teeth on the columellar lip, fewer ribs on the last whorl with relatively wider interspaces, and ribs near the middle of the last whorl not noticeably broader than adjacent ribs.

The new species is also very similar to *Nerita umzambiensis* Woods (1906: 311, pl. 37, figs. 14–15; Bandel and Kiel, 2003: 51–52, pl. 1, figs. 4–5) from the Santonian/Campanian Umzamba Formation in southeastern South Africa. The new species differs from *N. umzambiensis* by having fewer teeth on the columella lip, ribs on the base of the last whorl, and a deck area sharply demarcated from the base of the last whorl.

The new species somewhat resembles *Nerita* (*Theliostyla?*) *kennedyi* Squires and Saul (2002: 185–187, figs. 31–34) from the upper lower to lower middle Eocene ("Domengine Stage") Santiago Formation, northern San Diego County, southern California. The new species differs from *N.* (*T.?*) *kennedyi* by having beads that are not elongate, wider interspaces between the ribs, and fewer, stronger, and wider teeth on the columellar lip.

The only other early Campanian neritid known from the Pacific slope of North America is *Neritina* (*Dostia*) *cuneata* (Gabb, 1864: 137, pl. 21, fig. 97) from lower Campanian strata at Tuscan Springs on Little Salt Creek, Tehama County, northern California. Gabb's species might also be present in 1) upper Campanian and/or lower Maastrichtian strata in the Pozo area, San Luis Obispo County (Vedder, 1977) and 2) Maastrichtian strata along the western edge of the San Joaquin Valley, California (Woods and Saul, 1986). The new species is vastly different from *Neritina* (*Dostia*) and does not have its patelliform shape nor its distinctive collabral sculpture.

Superfamily Cerithioidea Férussac, 1819
Family Indeterminate

Discussion: The new genus described below is most likely a cerithioid, on the basis of its sigmoidal growth lines, high spire, sculpture, short siphonal canal (slightly twisted), smooth columella, and smooth interior of the outer lip. Some specimens of the new genus have a narrow spire, like that found in cerithioids, but other specimens of the new genus have a buccinid-like shell. The strongly sigmoidal growth lines of the new genus, however, are unlike that found on buccinid shells. It is possible that the new genus belongs to a new cerithioid family.

Genus *Bullamirifica* new genus

Type Species: *Bullamirifica elegans*, new species; Early Campanian, Pentz area, Butte County, northern California.

Description: Shell medium (up to 83 mm height and 37 mm diameter, same specimen), fusiform to turreted. Height to diameter ratio 2 to 2.7. Spire high, comprising 41 to 55% of total shell height. Pleural angle 33 to 42°. Protoconch unknown. Teleoconch whorls six to eight. Spire whorls with shoulder angulate; last whorl with periphery angulate. Ramp short to moderately long, concave to rarely straight-sloped. Suture slightly undulatory, weakly impressed. Collabral sculpture consisting of many narrow ribs, closely to moderately widely spaced; interspaces smooth. Collabral ribs slightly opisthocline to opisthocyrt, usually extending from suture to suture. Collabral ribs present on base or obsolete; if present, swollen and elongate. Spiral sculpture consisting of several spiral ribs with variable width and spacing, especially on last whorl. Spire whorls with strongest spiral rib on whorl shoulder, several weak or moderately strong spiral ribs occasionally near anterior suture, and suture coincident with weak spiral rib either bearing weak nodes or without nodes. Last whorl sculpture with three to four widely spaced, strong spiral ribs on periphery and one or two weaker spiral ribs or several spiral riblets on base. Intersections of collabral and spiral ribs producing many nodes or strongly projecting tubercles, either rounded (knob-like) to spinose or narrowly elongate. Nodes and knobs most pronounced on whorl shoulder, especially on last whorl. Intersections also strong on anterior portion of last whorl periphery. Aperture short but moderately wide, comma-shaped; small, narrow arch (canal-like) present where outer lip meets most posterior part of aperture. Columellar lip smooth. Siphonal canal short and spout-like or well developed, moderately short, and can be twisted to left. Outer lip thin, markedly sinuous, interior smooth. Growth lines sigmoidal between suture and shoulder; antispiral sinus coincident with tuberculate spiral rib.

Geologic Age: Coniacian to early late Campanian.

Etymology: Combination of the Latin *bulla*, meaning knob, and the Latin *mirifus*, meaning to cause wonder.

Discussion: Three species can be herein assigned to this new genus. Two of these species, *Bullamirifica verruca* and *Bullamirifica elegans*, are based on entirely new material. The third species was originally tentatively assigned by Dailey and Popenoe (1966) to *Pseudoglauconia* Douvillé, 1921. Dailey and Popenoe (1966) stated that this particular species belongs in a new genus, but they withheld their description until better specimens were obtained. Although representatives of the new genus have sigmoidal growth lines (see Wenz, 1940: 764, fig. 2214) similar to that of *Pseudoglauconia*, *Bullamirifica* differs considerably from *Pseudoglauconia* by having a bucciniform rather than a tapered/conical shape, angulate rather than flat-sided whorls, and tubercles on the sides of the whorls instead of only near the suture, and the suture between the penultimate and last whorl is not extremely deep and widely sunken. Unfortunately, the aperture of *Pseudoglauconia* is not known and none of the apertures on the available specimens of *Bullamirifica* is complete. In spite of the absence of knowledge about the aperture of *Pseudoglauconia*, Wenz (1940) believed this gastropod genus to belong in the Cerithiidae.

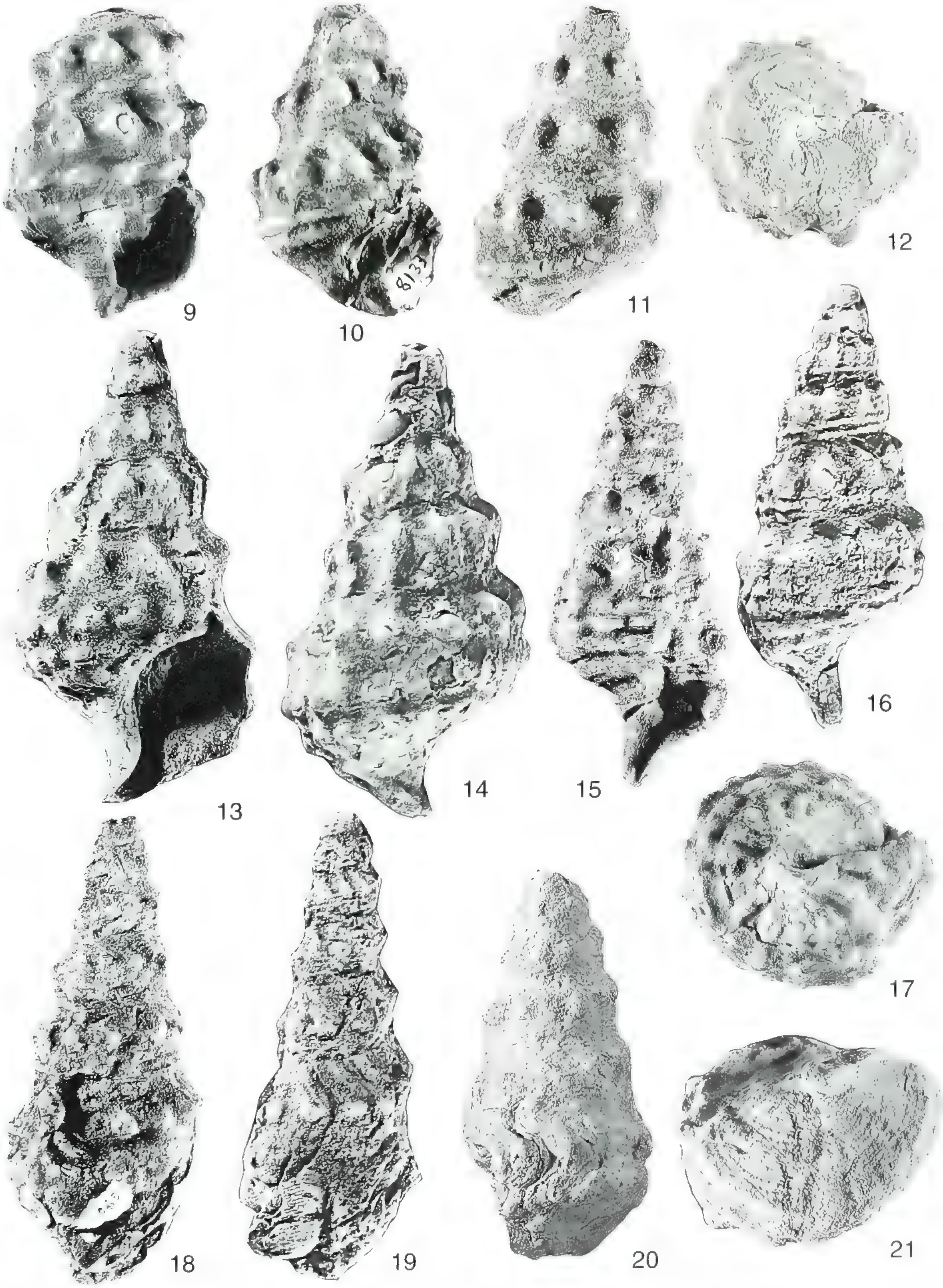
The shape of the growth lines in *Bullamirifica* is similar to that of *Batillaria echinoides clavatulata* (Lamarck, 1804) from the middle Eocene (Lutetian) of the Paris Basin, France. The siphonal canal of this Eocene species is longer than normally found in *Batillaria* Benson, 1842. Ponder and Warén (1988) and Houbrick (1988) placed *Batillaria* in superfamily Cerithioidea, family Batillariidae Thiele, 1929. The similarity in growth-line shape between *Bullamirifica* and *Batillaria* suggests to us that the new genus might be a cerithioid. The high turreted spire of *Batillaria*, however, is quite unlike the lower, more paucispiral spire of *Bullamirifica*.

Bullamirifica has the growth-line shape, shell shape, sculpture, and twisted siphonal canal similar to that of *Pseudorapa* Holzapfel, 1888, a monotypic genus from the Vaals Greensand in the Netherlands and Germany. The age of these strata was determined to be early Campanian by Albers (1976). Wenz (1941: 1083, fig. 3079) illustrated *Pseudorapa*. *Bullamirifica* differs from it by having a less twisted siphonal canal and more variable sculpture, including the possibilities of having spiral ribs and a relatively narrow shell. In addition, *Pseudorapa* has an outer lip that is very crenulate and a spiral band near the base of the last whorl that produces a tooth-like projection on the outer lip.

Bullamirifica verruca new species
(Figures 9–12)

Diagnosis: Small *Bullamirifica* with prominent rounded knobs, nine on shoulder of last whorl. Suture coincident with noded spiral rib. Base of last whorl without elongate collabral ridges. Siphonal canal short and straight.

Description: Small (up to 34 mm estimated height and 16.8 mm diameter, same specimen), fusiform, moderately slender. Height to diameter ratio approximately 2. Spire high, approximately 44% of shell height. Pleural angle approximately 35 to 37°. Protoconch and upper spire unknown. Teleoconch whorls approximately six (estimated). Spire whorls with shoulder angulate, last whorl with periphery angulate. Ramp short, concave. Suture slightly impressed, possibly undulatory. Collabral sculpture consisting of many ribs, widely spaced; interspaces smooth. Collabral ribs slightly opisthocline and extending from suture to suture. Collabral ribs mainly prevalent on ramp. Spiral sculpture consisting of several ribs with variable strength and spacing, especially on last whorl. Intersections of collabral and spiral ribs producing many strongly projecting rounded tuberculate knobs or, less commonly, nodes; knobs and nodes most prominent on shoulder and usually extending posteriorly across ramp and become narrow ridges. Spire whorls with strongest spiral rib on whorl shoulder, very faint spiral riblets present between whorl shoulder and anterior suture. Suture coincident with moderately weak spiral rib bearing small nodes. Penultimate whorl with spiral rib on shoulder bearing nine, moderately closely spaced knobs. Last whorl with three spiral ribs on periphery, strength of ribs progressively decreasing anteriorly: strong rib on shoulder and bearing nine very prominent tuberculate knobs; middle rib moderately strong and bearing more numerous nodes (about half sized of those on shoulder) that tend to become smaller and even obsolete adaxially; and most anterior periphery rib weakest and weak nodes tending to be obsolete adaxially. Base of last whorl usually with one or two spiral ribs, both bearing nodes (best developed near outer lip) or bearing no nodes, and with strength of spiral ribs decreasing anterior in direction; occasionally, anterior region of base with only very weak spiral riblets.



Figures 9–21. New cerithioid? gastropods. Specimens coated with ammonium chloride. **9–12.** *Bullamirifica verruca* new genus and species, LACMIP loc. 8133. **9.** Paratype LACMIP 13327, apertural view, height 27 mm, diameter 19.2 mm. **10–11.** Holotype LACMIP 13326, height 29.7 mm, diameter 17.8 mm. **10.** Apertural view. **11.** Abapertural view. **12.** Paratype LACMIP 13327, basal view, diameter 18.9 mm. **13–17.** *Bullamirifica elegans* new genus and species, LACMIP loc. 24337. **13–14.** Holotype LACMIP 13328, height 66.9 mm, diameter 34.9 mm. **13.** Apertural view. **14.** Abapertural view. **15–16.** Paratype LACMIP 13329, height 60.1mm diameter 25.7 mm. **15.** Apertural view. **16.** Abapertural view. **17.** Holotype LACMIP 13328, basal view, diameter 35.7 mm. **18–21.** *Bullamirifica ainiktos* (Dailey and Popenoe, 1966) new genus. **18–19.** Hypotype LACMIP 13330, LACMIP loc. 10691, height 60 mm, diameter 24.1 mm. **18.** Apertural view. **19.** Abapertural view. **20.** Plasto-holotype LACMIP 40435, LACMIP loc. 24125, right-lateral view, height 58.2 mm, diameter 29.1 mm. **21.** Hyptotype LACMIP 13331, LACMIP loc. 24124, basal view, diameter 16.7 mm

Aperture round with very small posterior "arch." Aperture elliptical, columellar lip smooth, outer lip thin; siphonal canal short and spout-like.

Holotype: LACMIP 13326, incomplete specimen with two whorls (upper spire missing), 29.7 mm height, 17.8 mm diameter.

Paratype: LACMIP 13327.

Type Locality: LACMIP loc. 8133.

Geologic Age: Coniacian.

Distribution: Redding Formation, Member IV, Oak Run area, northern California.

Etymology: Latin *verrucus*, wart.

Discussion: This new species is based on three specimens. It differs from *Bullamirifica elegans* new species below by smaller size and presence of rounded rather than elongate knobs, fewer knobs on shoulder of last whorl, no elongate collabral ridges on base of last whorl, a noded spiral rib coincident with the suture, and a straight siphonal canal. *Bullamirifica verruca* differs from *Bullamirifica ainiktos* by being smaller with a shorter spire and having rounded and much more projecting nodes, many fewer nodes on shoulder of last whorl, much less tendency for elongate collabral ridges on ramp, and much weaker spiral ribs between shoulder and anterior suture.

Bullamirifica verruca is very similar to the cerithioid *Tympanotonus* (*Tympanotonus*) *robustus* Dockery (1993: 47, pl. 7, fig. 1) in the shape of the spire, strong nodes on the spire, and shape of the growth lines next to the outer lip. *Tympanotonus* (*T.*) *robustus*, which is of Campanian age and from Mississippi, however, has no siphonal canal.

Bullamirifica elegans new species
(Figures 13–17)

[?] *Pseudoglauconia*? aff. *P. ainiktos* Dailey and Popenoe.—Elder and Saul, 1993: pl. 2, fig. 11.

Diagnosis: Large *Bullamirifica* with prominent opisthocline collabral ridges on upper spire and base of whorl. Shoulder of last whorl with 11 nodes. Suture coincident with unnoded weak spiral rib. Siphonal canal short but well developed and twisted to left.

Description: Medium large (up to 83 mm estimated height and 37 mm diameter, same specimen), fusiform, moderately wide, rarely slender. Height to diameter ratio approximately 2.2. Spire high, approximately 40% of shell height. Pleural angle approximately 33 to 42°, rarely approximately 30°. Protoconch and uppermost spire unknown. Teleoconch whorls approximately eight (estimated). Whorls with angulate shoulder. Ramp short and slightly concave. Collabral sculpture consisting of many moderately strong, narrow ribs; interspaces smooth. Collabral ribs extending from suture to suture. Collabral ribs sigmoidal between posterior suture and shoulder, opisthocline between shoulder and anterior suture. Collabral ribs somewhat swollen on base of last whorl. Spiral sculpture consisting of several ribs with variable strength and spacing. Intersections of collabral and spiral ribs producing many swollen, axially elongate nodes or, in some cases, rounded tuberculate knobs; nodes and knobs most prominent on shoulder. Spire whorls with strongest spiral rib on whorl shoulder and occasionally two moderately strong, noded spiral ribs between whorl shoulder and anterior suture. Suture coincident with weak spiral riblet. Penultimate whorl with spiral rib on shoulder bearing 11 widely spaced nodes. Last whorl with three or four spiral ribs on periphery, strongest rib on shoulder and bearing 11 nodes. Spiral ribs on periphery of last whorl usually show strength progressively decreasing anteriorly, occasionally rib immediately anterior of shoulder weaker than other ribs on periphery. Growth lines sigmoidal, with antispiral sinus coincident with shoulder. Aperture elliptical, columellar lip smooth, outer lip thin; siphonal canal short but well developed and slightly twisted to left.

Holotype: LACMIP 13328; nearly complete specimen of five whorls (upper spire missing), 66.9 mm height, 34.9 mm diameter.

Paratype: LACMIP 13329.

Type Locality: LACMIP loc. 24337.

Geologic Age: Early Campanian to possibly middle Campanian.

Distribution: Early Campanian: Chico Formation, Pentz Road member (informal), near Pentz, Butte County, northern California; Possibly middle Campanian: Pigeon Point Formation, San Mateo County, northern California.

Etymology: Latin *elegans*, meaning very fine or choice.

Discussion: The new species is based on six specimens from the Pentz area, and preservation is moderately good on all of them. Nearly all the specimens are moderately wide, but a few are somewhat slender, as the specimen illustrated in Figures 15–16.

There might be one specimen of the new species from the Pigeon Point Formation. This museum specimen, which cannot be located, was figured by Elder and Saul (1993: pl. 2, fig. 11). It was identified by them as *Pseudoglauconia*? sp. aff. *P. ainiktos* Dailey and Popenoe, but it has a profile somewhat more like *Bullamirifica elegans* and basal nodes like *B. elegans*. As will be discussed later, there are specimens of *B. ainiktos* from the Pigeon Point Formation. It seems likely that some of the *Bullamirifica* specimens from the Pigeon Point Formation represent transitional forms between *B. elegans* and *B. ainiktos*.

Bullamirifica elegans differs from *Bullamirifica verruca* in having larger size, prominent collabral ribs extending from suture to suture on the spire whorls, swollen collabral ribs on the neck, more nodes on shoulder of the penultimate and last whorls, and siphonal canal longer and slightly twisted to the left. In addition, *B. elegans* occasionally has strong unnoded spiral ribs between suture and shoulder.

Bullamirifica elegans differs from *Bullamirifica ainiktos* by usually having a wider pleural angle, usually a less elevated spire, wider and stronger nodes on shoulder, fewer nodes on shoulder of last whorl, and base with swollen collabral ribs instead of fine spiral ribs. *Bullamirifica elegans* also has variability in morphology, whereas *B. ainiktos* does not.

Bullamirifica elegans is very similar to the cerithioid *Tympanotonus* (*Tympanotonus*) *binodosus* Dockery (1993: 47, pl. 7, fig. 2) in the shape of the spire, strong nodes on the spire, and shape of the growth lines next to the outer lip. *Tympanotonus* (*T.*) *binodosus* of Campanian age and from Mississippi, however, has no siphonal canal.

Bullamirifica ainiktos (Dailey and Popenoe, 1966) new combination
(Figures 18–25)

Pseudoglauconia? *ainiktos* Dailey and Popenoe, 1966: 21–22, pl. 6, figs. 3, 5, 6.
Pseudoglauconia? aff. *P. ainiktos* Dailey and Popenoe.—Elder and Saul, 1993: pl. 2, fig. 10.
Cimolithium miyakoense (Nagao, 1934). —Perrilliat-Montoya, 1968: 20, pl. 4, fig. 2.
Vicarya (*Shoshiroia*) *yabei* Kamada, 1960.—Perrilliat-Montoya, 1968: 21, pl. 6, fig. 1.

Diagnosis: Medium-size *Bullamirifica* with usually slender turreted whorls. Ramp on upper spire short, with narrow collabral ribs crossed by weaker spiral ribs; ramp on later whorls much longer and smooth and concave. Spire whorls concave on posterior half but angulate medially, with moderately strong tubercles. Shoulder of last whorl with 14 nodes. Base of last whorl with many, closely spaced spiral riblets. Siphonal canal short and possibly straight.

Description: Medium, up to 67.5 mm height estimated and 25.4 mm diameter, same specimen. Shell usually slender, turreted, occasionally wide, fusiform. Height to diameter ratio approximately 2.7. Spire high, approximately 55% of total shell height. Pleural angle approximately 33 to 37°. Protoconch unknown. Teleoconch whorls approximately eight (estimated). Spire whorls with shoulder angulate. Ramp usually short and concave, occasionally long and straight-sloped. Suture obscured. Collabral sculpture consisting of many spiral ribs closely spaced and narrow. Collabral ribs opisthocyrt, most prominent on ramp. Spiral sculpture consisting of several ribs, moderately weak and closely spaced. Intersections of collabral and spiral ribs producing many nodes, most prominent and somewhat spinose on shoulder. Spire whorls with strongest spiral rib on whorl shoulder and five moderately strong, non-noded spiral ribs between shoulder and anterior suture; most anterior one of these ribs coincident with suture. Penultimate and last whorls with approximately 14 nodes on shoulder. Last whorl with three spiral ribs on periphery, progressively weaker anteriorly, and bearing nodes. Base of last whorl bearing fine spiral riblets. Siphonal canal short and twisted to left. Columellar lip smooth. Outer lip sinuous; interior smooth.

Holotype: LACMIP 40435, incomplete specimen (tip of spire and siphonal canal missing), 39 mm height, 29 mm diameter.

Type Locality: LACMIP loc. 4125.

Geologic Age: Middle Campanian to Late Campanian.

Distribution: Middle Campanian: Pigeon Point Formation, near Pigeon Point, San Mateo County, northern California. Middle late Campanian: Punta Baja Formation, southwest of El Rosario, Baja California, Mexico. Late Campanian: Jalama Formation, Santa Barbara County, southern California.

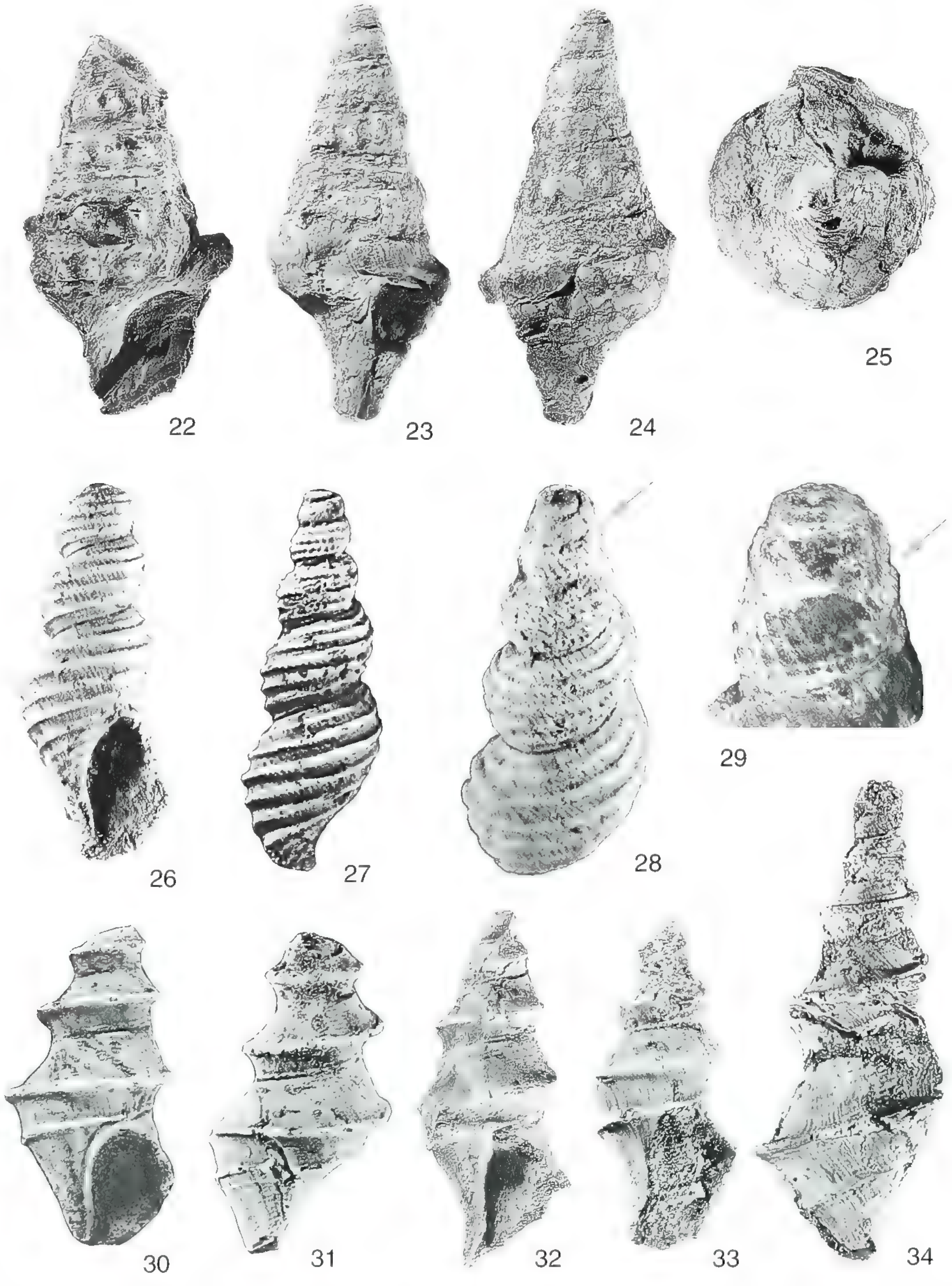
Discussion: Description of the new species is based on 25 specimens: 18 from the Jalama Formation, five from the Pigeon Point Formation, and two from the Punta Baja Formation. The Jalama specimens have poor to moderately good preservation, although the apices are broken off and the siphonal canal missing. The Pigeon Point specimens also have poor to moderately good preservation, but the matrix is very hard to remove. The Punta Baja specimens have poor preservation.

The Pigeon Point Formation specimen illustrated by Elder and Saul (1993: pl. 2, fig. 10) has a whorl profile like that found on *B. ainiktos* but it has wider pleural angle, similar to that found on *B. elegans*. Unfortunately this specimen is missing. As mentioned earlier, it seems likely that some of the *Bullamirifica* specimens from the Pigeon Point Formation represent transitional forms between *B. elegans* and *B. ainiktos*.

Bullamirifica ainiktos differs from *Bullamirifica verruca* by larger size and having less rounded and much lower nodes, more nodes on shoulder of last whorl, much more tendency for elongate collabral ridges on ramp, and much stronger spiral ribs between shoulder and anterior suture.

Bullamirifica ainiktos differs from *Bullamirifica elegans* by smaller size, having a narrower spire, usually a more elevated spire, narrower and weaker nodes on shoulder, more nodes on shoulder of last whorl, and base with fine ribs instead of swollen collabral ribs.

Perrilliat-Montoya (1968) identified one of the Punta Baja Formation specimens (Figures 23–25 herein) of *B. ainiktos* as *Vicarya* (*Shoshiroa*) *yabei* and identified the other specimen as *Cimolithium miyakoense*. With Wenz (1940: 740–741, fig. 2145) as a basis for comparison, we consider that *Bullamirifica ainiktos* differs considerably from the former gastropod by having a non-conical shell,



Figures 22–34. New cerithioid? and trichotropid gastropods. Specimens coated with ammonium chloride, unless otherwise noted. **22–25.** *Bullamirifica ainiktos* (Dailey and Popenoe, 1966) new genus. **22.** Hypotype LACMIP 13332, USGS loc. M-8601, height 35.8 mm, diameter 20 mm. **23–25.** Plasto-hypotype IGM 1325, height 80 mm, diameter 36.9 mm. **23.** Apertural view. **24.** Abapertural view. **25.** Basal view. **26–29.** *Minytropis melilota* new genus and species. **26.** Paratype LACMIP 13334, LACMIP loc. 10787, apertural view, height 7 mm, diameter 2 mm. **27–29.** Holotype LACMIP 13333, LACMIP loc. 10786, abapertural view, height 62 mm, diameter 2.2 mm. **27.** Abapertural view. **28.** Oblique apertural view of tip; arrow indicates where protoconch ends and teleoconch starts. **29.** Protoconch, height 0.5 mm, diameter 0.8 mm; arrow indicates where protoconch ends and teleoconch starts; SEM photomicrograph (uncoated). **30–34.** *Paxitropis dicriota* new genus and species. **30–31.** Paratype LACMIP 13336, LACMIP loc. 23643, height 12.7 mm, diameter 6.8 mm. **30.** Apertural view. **31.** Abapertural view. **32.** Holotype LACMIP 13335, LACMIP loc. 23639, apertural view, height 14.7 mm, diameter 6.6 mm. **33.** Paratype LACMIP 13337, LACMIP loc. 23642, apertural view, height 10.1 mm, diameter 4.4 mm. **34.** Paratype LACMIP 13338, LACMIP loc. 24217, abapertural view, height 11 mm, diameter 4.3 mm

more rows of nodes, and absence of a notch on the outer lip near the suture and not having a thick, extensive callus that covers part of the noded sculpture near the suture on the last whorl. Using Kase (1984: 135–136, pl. 21, figs. 1–9; fig. 20) as a basis for comparison, we consider that *Bullamirifica ainiktos* differs considerably from the latter gastropod by having a much lower spire, more strongly sinuous growth lines, and a well developed, twisted siphonal canal.

Superfamily Capuloidea Fleming, 1822
Family Capulidae Fleming, 1822
?Subfamily Trichotropinae Gray, 1850

Discussion: We include a subfamily name because high-spired capulids, like those described below, are so distinctive from cap-shaped capulids. The subfamily allocation is tentative, pending much-needed taxonomic work on capulids.

Genus *Minytropis* new genus

Type Species: *Minytropis melilota* new species; Late Cretaceous, Santonian, northern California.

Description: Shell very small, estimated maximum height just over 10 mm. Shell thin, narrowly fusiform-elongate. Protoconch flat-topped and smooth, approximately two whorls. Teleoconch whorls rounded. Sculpture consisting of several strong spiral ribs with wide interspaces, both ribs and interspaces crossed by well delineated prosocline growth lines. Aperture oval, produced anteriorly to short, with narrow siphonal canal. Outer lip thin with no varix or inner denticulations. Inner lip callused, narrow.

Geologic Age: Early and Late Santonian.

Etymology: Combination of the Greek *minys*, meaning little, small, or short; and the Latin *tropis*, meaning keel.

Discussion: The placement of *Minytropis* among the trichotropids is suggested by the strongly prosocline and well marked growth lines, strong spiral sculpture, and the short, open siphonal canal. *Minytropis* resembles *Opposirius* Iredale, 1931, which is known only from the Recent of Australia (Wenz, 1940). *Minytropis* differs from *Opposirius* by having a narrower aperture, a longer siphonal canal, and a rounded rather than a bladelike inner lip.

Finlay and Marwick (1937) reported that *Opposirius* is more similar to *Certhioderma* Conrad, 1860, than to any other trichotropid genus. In comparison to *Certhioderma*, *Minytropis* is similar in having a flat-topped, smooth protoconch and in having a short siphonal canal, but *Minytropis* differs by having a much narrower shell, longer and much narrower aperture, stronger spiral sculpture, sculpture not recticulate on adult whorls, and no hint of an umbilicus. Wenz (1940) reported *Cerithioderma* to have a geologic range of Late Cretaceous to Oligocene, but Marwick (1965) reported that this genus is also extant. Dockery (1993) reported *Cerithioderma* from Campanian strata in Mississippi. High-spired trichotropids very similar to *Cerithioderma* are best represented in New Zealand Tertiary strata (Maxwell, 1992). According to Maxwell (1992), *Trichosirius* Finlay, 1926, might be a junior synonym of *Cerithioderma*.

Minytropis melilota new species
(Figures 26–29)

Description: Small, up to 10.2 mm estimated height and 3.5 mm diameter, same specimen. Shell narrowly fusiform-elongate. Spire high, 60% (estimated) of shell height. Pleural angle approximately 22°. Protoconch flat-topped, with two whorls, and smooth (0.5 mm height, 0.8 mm diameter). Teleoconch of approximately seven to eight subangulate whorls, last whorl nearly one-third total height. Suture deeply impressed, nearly coincident with very weak rib. Sculpture nearly cancellate on earliest teleoconch whorl, but four spiral riblets slightly stronger than numerous collabral threads. Sculpture on subsequent whorls progressing into five strong, flat-topped ribs on middle spire, six ribs on lower spire, and approximately eight to nine ribs on last whorl; most posterior spiral rib weak to very weak on all these whorls. Interspaces of nearly equal width on spire whorls but becoming twice as wide as ribs on last whorl. On last whorl, ribs on whorl face equally strong but on base, ribs become much less prominent and more closely spaced. Growth lines strongly prosocline, marked by fine collabral threads strongest on early whorls where they produce slight beading of spiral ribs. Growth lines less prominent and closer-spaced on later whorls; growth lines can be somewhat prominent on base of last whorl. Aperture oval, produced anteriorly to short, narrow siphonal canal. Outer lip thin, arcuate, crenulated by ribs. Columellar lip narrow, weakly callused, and barely forming a pseudo-umbilical chink between base of whorl and indistinct fasciole.

Dimensions of Holotype: Nearly complete specimen (siphonal canal mostly missing), 6.2 mm height, 2.2 mm diameter.

Holotype: LACMIP 13333.

Type Locality: LACMIP loc. 10786.

Paratype: LACMIP 13334.

Geologic Age: Early and Late Santonian.

Distribution: Lower Santonian: Redding Formation, Member V, Clover Creek, Shasta County, northern California. Upper Santonian: Chico Formation, Musty Buck Member, Chico Creek, Butte County, northern California.

Etymology: Latin *melitota*, meaning sweet clover (in reference to the occurrence of the new species near Clover Creek).

Discussion: Description of this new species is based on 29 specimens, most of which represented by small fragments. The better preserved specimens are all from the Redding Formation, however, none of these specimens is as large as the larger ones from the Chico Formation localities. Only two specimens, both from LACMIP loc. 10786, have retained the protoconch. The protoconch of one of these specimens is illustrated in Figures 27–29. The other specimen's protoconch is mostly embedded in hard matrix. The flat-topped protoconch of *M. meliota* supports the position of this gastropod among the Trichotropidae.

The new species can be distinguished from the similar looking *Opposirius idoneus* Iredale (1931: 210, pl. 22, fig. 7; Wenz, 1940: fig. 2631), an extant species in southwestern Australia, by having a narrower shell, one more rib on the spire, two to four more ribs on the base of the last whorl, a much longer siphonal canal, an a rounded columella. *Opposirius idoneus* is the type species of *Opposirius* Iredale, 1931.

Genus *Paxitropis* new genus

Type Species: *Paxitropis dicriota*; Late Cretaceous, late Santonian to early Campanian, northern California.

Description: Shell medium small, narrowly pagodiform. Spire whorls with prominent keel medially. Suture bordered posteriorly by relatively weak spiral rib becoming keel-like on last whorl and, in concert with aforementioned keel, producing bicarinate last whorl. Shell base with several weak spiral riblets. Growth lines prosocline. Columellar lip callused, abaxial margin well-delineated. Siphonal canal short but distinct. Anomphalous.

Geologic Age: Late Santonian to early Campanian.

Etymology: Combination of the Latin *pax*, meaning peace (in reference to the peaceful Pacific coast); and the Latin *tropis*, meaning keel.

Discussion: *Paxitropis* is similar to *Trichotropis* Broderip and Sowerby, 1829, a genus known (Sohl, 1960) from the Late Cretaceous to Recent. The modern distribution of *Trichotropis* is restricted to circum-boreal waters, in both the northern and southern oceans and, as Sohl (1960) noted, this modern distribution is in sharp contrast to its Cretaceous distribution in temperate shallow-water deposits. *Paxitropis* differs from *Trichotropis* by having a smaller size, much narrower shell (including a narrower aperture), a siphonal canal, much lower variability in sculpture, and being anomphalous.

Paxitropis resembles the trichotropid *Icuncula* Iredale, 1924, which is known from the Recent of the Indo-Pacific (Wenz, 1940). *Paxitropis* differs from *Icuncula* by having no hint of an umbilicus, less prominent keels that are unwavy, one less keel on the last whorl, and no axial riblets on the ramp. The aperture of *Paxitropis* is not entirely known.

The new genus has a whorl profile very similar to the turrid *Austrocarina* Laseron, 1954, known only from the Recent of New South Wales and Victoria, southeastern Australia and Tasmania. *Paxitropis*, however, is not a turrid because it does not have the turrid growth lines, which tend to be opisthocline anterior to the notch and across the whorl periphery curving toward prosocline very near the siphonal area.

Paxitropis dicriota new species
(Figures 30–34)

Description: Shell small, up to height estimated 14.5 mm and 6.6 mm diameter. Shell pagodiform. Spire high, approximately 60% of shell height. Pleural angle approximately 30°. Protoconch unknown. Teleoconch approximately six strongly angulated whorls, with wide ramp on middle spire whorls and on last whorl. Sculpture dominated by prominent spiral rib, medially located on shoulder and keel-forming on later whorls. Early teleoconch whorls with two spiral ribs anterior to carina. On mature whorls, these additional ribs become mere threads and equivalent in strength to growth lines, thus producing microscopic cancellate surface, especially on ramp. Suture impressed, nearly coincident with weakly noded subsutural spiral rib located immediately posterior to suture. Subsutural spiral rib relatively weak on spire whorls but becoming keel-like on last whorl. Last whorl with two sharp keels, one just above middle whorl height and second one weaker and occasionally minutely noded, emergent at anterior suture. Shell base with several weak spiral ribs. Growth lines prosocline, most prominent on shell base, near outer lip. Aperture lanceolate and produced anteriorly to short, but distinct siphonal canal. Outer lip thin, angulate, crenulated by ribs. Columellar lip callused, abaxial margin well-delineated. Columellar lip narrow, barely forming pseudo-umbilical chink between base of whorl and indistinct fasciole.

Holotype: LACMIP 13335, 14.7 mm height, 6.6 mm diameter.

Paratypes: LACMIP 13336, 13337, and 13338.

Type Locality: LACMIP loc. 23643.

Geologic Age: Late Santonian to Early Campanian.

Distribution: Upper Santonian: Redding Formation, Member VI, area east of Redding, Shasta County, northern California. Lower Campanian: Chico Formation, Ten Mile Member, Chico Creek, Butte County, northern California; Ladd Formation, upper Holz Shale Member, Santa Ana Mountains, Orange County, southern California.

Etymology: Combination of the Greek *di*, meaning two, and the Greek *criota*, meaning ringed.

Discussion: Twenty incomplete specimens were available, and the six most complete of these are the basis for the above description. The only specimen from the

Redding Formation is geologically the oldest specimen (LACMIP loc. 24217). The only specimen from the upper Holz Shale is from LACMIP loc. 21536.

The new species is very similar to the Pliocene to Recent *Trichotropis bicarinata* (Sowerby, 1825; Pitt and Pitt, 1989: pl. 1, figs. 3–4; Egorov and Alexeyev, 1998: 25, figs. 22–23), which is a Pacific upper boreal Arctic species, occurring in the waters off northern Japan, Kamchatka, southern Chukchi Sea, and Queen Charlotte Islands in British Columbia (Egorov and Alexeyev, 1998). The new species differs from *T. bicarinata* by having a much narrower last whorl and a much narrower aperture. These same differences distinguish the new species from *Trichotropis vokesae* Pitt and Pitt, 1989, which is extremely similar to *T. bicarinata*. *Trichotropis vokesae* is of Pliocene age and from northwestern Ecuador, and the new species differs from *T. vokesae* in the same ways that it differs from *T. bicarinata*.

The new species can be distinguished from the similar looking *Icuncula torcularis* (Tenison-Woods 1879; Wenz, 1940: fig. 2630), an extant species living off the coasts of southeastern Australia and Tasmania, by having less projecting and non-wavy keels, one less keel on the last whorl, and an absence of axial riblets on the ramp. *Icuncula torcularis* is the type species of *Icuncula* Iredale, 1924.

The new species is remarkably similar to the extant *Austrocarina recta* (Hedley, 1903; 1922: 223, fig. 3; Powell, 1966: 34, pl. 3, fig. 2; 1969: 364, pl. 276; Wilson, 1994: 187) but differs from *A. recta* by having a shell approximately 14 mm in height instead of 6 mm, a more projecting and usually wider keel on the shoulder of the adult whorls, several weak spiral ribs on base of last whorl, several spiral ribs on earliest teleoconch whorls, straight rather than a curved profile of the base, columellar lip callused with abaxial margin well-delineated, and no tendency to develop collabral ribs on earliest teleoconch whorls.

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APPENDIX 1

LOCALITIES CITED

Localities are LACMIP, unless otherwise noted. All quadrangle maps listed below are U. S. Geological Survey maps.

10786. Near crest of south slope of divide between Basin Hollow and Clover creeks, at approximately southeast corner of the northwest 1/4 of section 33, T. 32 N, R. 2 W. Lower Santonian. Redding Formation, Member V (lower part). Coll.: W. P. Popenoe and D. W. Scharf, August 8, 1931.

10787. Near crest of north slope of divide between Basin Hollow and Clover creeks, near northeast corner of northwest 1/4 of section 33 and not more than 122 m south of section line, T. 32 N, R. 2 W, Millville Quadrangle (15 minute, 1953), Shasta County, northern California. Lower Santonian. Redding Formation, Member V (lower part). Coll.: W. P. Popenoe and D. W. Scharf, August 8, 1931.

12582. Turritellas and oysters along beach just south of La Bocana Roja Formation outcrop, approximately 2 km north of south tip on west side of Punta Baja, Mexico. Middle upper Campanian. Punta Baja Formation. Coll.: L. R. Saul, October 12, 1990.

21536. Corona Quadrangle, Santa Ana Mountains, Orange County, southern California. Lower Campanian. Ladd Formation, upper Holz Shale Member. Coll.: T. Bear, 1940.

23639. East bank of Chico Creek in concretions in massive, greenish-gray sandstone, 373 m south and 293 m west of northeast corner of section 23, T. 23 N, R. 2 E, Paradise Quadrangle (15 minute, 1953), Butte County, northern California. Lower Campanian. Chico Formation, Ten Mile Member. Coll.: L. R. and R. B. Saul, August 20, 1952.

23642. On W bank of Chico Creek, west of big westward projection of east lava cap and approximately N 27°W of BM 1770, 122 m south and 632 m west of northeast corner of section 26, T. 23 N, R. 2 E, Paradise Quadrangle (15 minute, 1953), Butte County, northern California. Lower Campanian. Chico Formation, Ten Mile Member. Coll.: L. R. and R. B. Saul, August 20, 1952.

23643. Concretionary sandstone on west side of Big Chico Creek, 670 m south and 762 m west of northeast corner of section 26, T. 23 N, R. 2 E, Paradise Quadrangle (7.5 minute, 1953), Butte County, northern California. Lower Campanian. Chico Formation, Ten Mile Member. Coll.: L. R. Saul and R. B. Saul, August, 1952.

24124. Hard, medium-grained, gray, arkosic sandstone, 158 m north of Jalama Creek, 3.3 km west and 0.6 km north of southeast corner of the topographic sheet, Lompoc Hills Quadrangle (7.5 minute, 1947). Upper Campanian. Jalama Formation. Coll.: D. Dailey and J. R. Dorrance, October, 1929.

24125. Hard, fine to medium-grained arkosic sandstone, 2.8 km west and 0.53 km north of southeast corner of the topographic sheet, Lompoc Hills Quadrangle (7.5 minute, 1947). Upper Campanian. Jalama Formation. Coll.: D. Dailey and J. R. Dorrance, October 29, 1929.

24217. Hard sandstone slabs in bed of Clover Creek, 213 m north and 366 m west of southeast corner of section 22, T. 32 N, R. 2 W, Millville Quadrangle (15 minute, 1953), Shasta County, northern California. Upper Santonian. Redding Formation, Member VI. Coll.: W. P. Popenoe and D. Dailey, August 27, 1959.

24337. Along east side of Highway 70, 792 m north and 305 m west of southeast corner of section 36, T. 21 N, R. 3 E, Cherokee Quadrangle (7.5 mintue, 1949), Butte County, northern California. Lower Campanian. Chico Formation, Pentz Road member (informal). Coll.: E. Göhre.

UCMP B-3388. In south-trending arroyo which reaches coast about 2.8 km north of the tip of Punta Baja. Marine invertebrates from massive, chert conglomerate at confluence of this arroyo and northwest-trending tributary about 122 m upstream from confluence. This locality is about 488 m northwest of the Punta Baja road. Middle upper Campanian. Punta Baja Formation. Coll.: F. H. Kilmer, date unknown.

USGS M-8601. In lens in sandstone on beach 0.5 km southeast of Bolsa Point, Pigeon Point Quadrangle, San Mateo County, northern California. Middle Campanian. Pigeon Point Formation. Coll.: W. P. Elder, 1989?

Daffymitra lindae, a new genus and species of Volutomitridae (Neogastropoda) from the Bellingshausen Abyssal Plain

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ABSTRACT

Daffymitra lindae, new genus, new species, is described from the Bellingshausen Abyssal Plain off Ellsworthland, Antarctica. Known only from its shell, this new taxon is included in the family Volutomitridae, but differentiated from all known living genera and species on the basis of its inflated shell shape, with an attenuated anterior and distinctive siphonal canal, as well as by the shape and disposition of its three recessed, obliquely oriented columellar plaits. This new taxon represents the first record of Volutomitridae from abyssal depths. The conchological similarity of *Daffymitra* to the Upper Cretaceous genus *Volutomorpha* raises the possibility that *Daffymitra* may be a surviving descendent of a lineage presumed extinct since the end of the Cretaceous, and suggests that a reassessment of the relationships between the various Cretaceous genera assigned to Volutoderminae and the earliest Volutomitridae.

INTRODUCTION

The Volutomitridae is a small family of rachiglossan neogastropods characterized by: a fusiform shell (reaching 50 mm) with 2–5 columellar plaits, and a paucispiral, mammilate protoconch; a radula with distinctive, wishbone-shaped rachidian teeth and small, needle-like lateral teeth that are present in most species; a mid-oesophagus that is long, convoluted, with a muscular posterior end; a gland of Leiblein that is only partially separated from the mid-oesophagus; and a single accessory salivary gland (Ponder, 1972, 1998; Kantor and Harasewych, 1992; Bouchet and Kantor, 2004). The family ranges into the North Pacific, North Atlantic and the Caribbean, but centers of diversity are concentrated in the southern hemisphere, particularly in the waters surrounding Antarctica, Australia, New Zealand, and especially New Caledonia (Bouchet and Kantor, 2004). Six genera and 50 species are currently recognized in the Recent fauna (Bouchet and Kantor, 2004), with a single genus (*Paradmete*) containing six species represented in the Antarctic and Magellanic fauna (Numanami, 1996; Bouchet and Kantor, 2004). Volutomitrids are known from the sublittoral zone to depths of 1980 m (based on dead specimens), but the majority of species are confined to outer continental shelf and upper continental slope depths (Bouchet and Kantor, 2004: Appendix; see Figure 7 herein).

In the course of our studies of Antarctic and sub-Antarctic neogastropods sampled by the United States Antarctic Program (USAP) and housed in the collections of the National Museum of Natural History (USNM), we encountered a single specimen of a volutomitrid that was collected on the Bellinghausen Abyssal Plain. This specimen represents a new genus and species within the family Volutomitridae, as well as the first record of the family from abyssal depths. This new genus and new species is described herein, and comparisons made with other volutomitrid taxa.

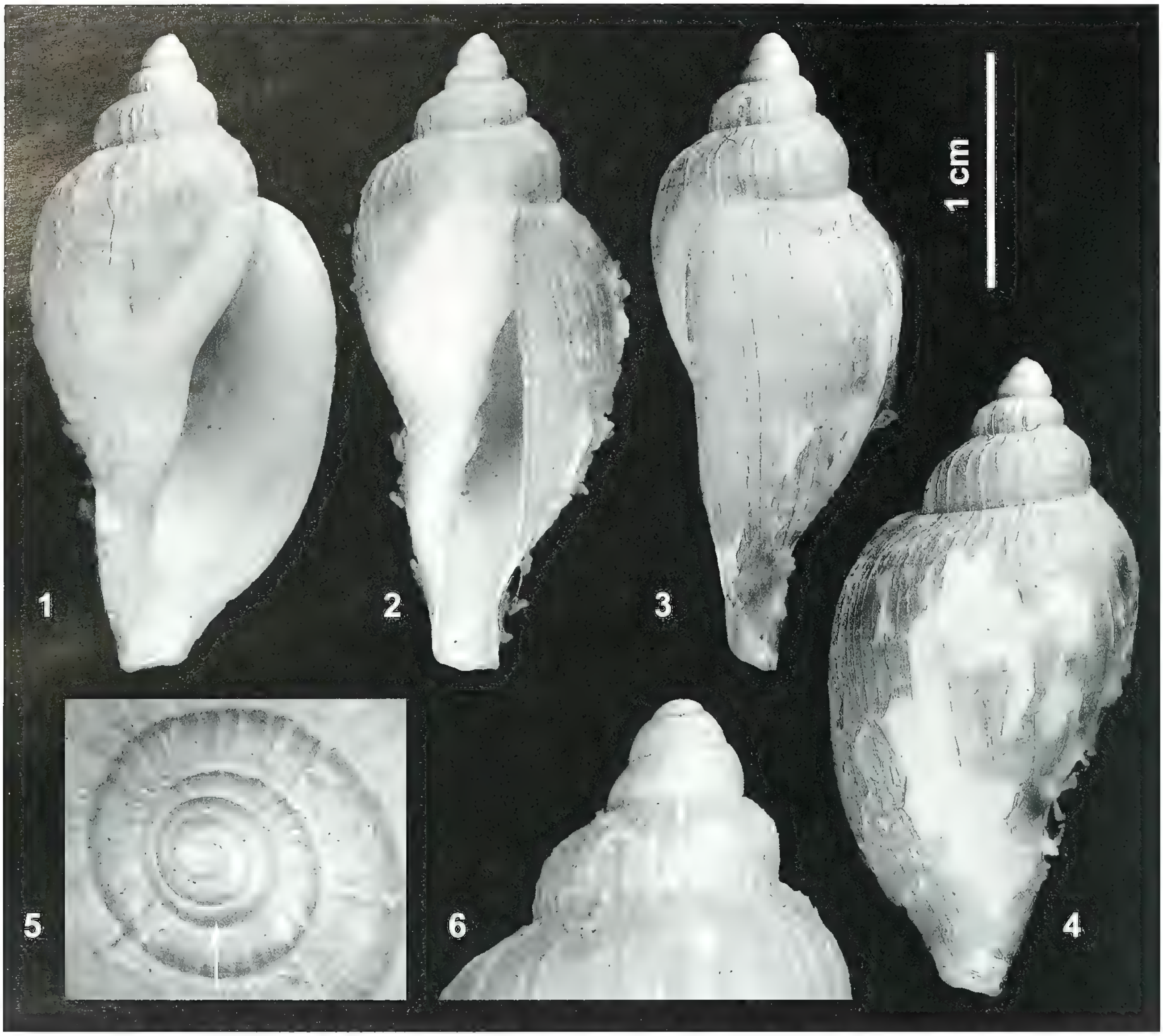
SYSTEMATICS

Class Gastropoda Cuvier, 1797
Order Neogastropoda Wenz, 1938
Family Volutomitridae Gray, 1854
Genus *Daffymitra* new genus

Type Species: *Daffymitra lindae* new species, by original designation.

Description: Shell medium-sized for the family (to 28 mm), with low, conical spire, broadly inflated body whorl. Protoconch conical, large, 2.6 mm in diameter, of 2 5/8 smooth whorls. Teleoconch thin, of about 3 smoothly rounded whorls, with well demarcated, broad siphonal canal. Axial sculpture of distinct, very narrow, broadly spaced ribs that extend from suture to siphonal canal. Spiral sculpture of narrow, cords, alternating in prominence. Aperture high (74% of shell length) broadly ovate. Outer lip thin, smooth. Columella with three columellar folds (central strongest) and siphonal fold. Shell white. Periostracum thin, olive brown. Operculum, anatomy, radula, unknown.

Etymology: This genus is named after Daffy, a tortoiseshell longhair cat that belongs to the senior author's wife Linda.



Figures 1–6. *Daffymitra lindae* new species, holotype. **1.** Apertural view of the shell. **2.** Oblique view, shell is rotated slightly to expose the columellar plaits. **3.** Lateral view of the shell. **4.** Dorsal view of the shell. **5.** Apical and **6.** lateral views of the protoconch. Transition to teleoconch is marked by arrow.

Daffymitra lindae new species
(Figures 1–7)

Description: Shell (Figures 1–4) of moderate size (to 27.9 mm), thin, fragile, with matte surface, inflated, fusiform, tapering anteriorly, with conical spire. Protoconch (Figures 5–6) large, mammilate, 1970 μm in height, diameter increasing from 676 μm to 2570 μm in 2 5/8 convex whorls. Protoconch-teleoconch transition distinct (Figures 5, 6, arrow), marked by onset of weak closely spaced prosocline ribs. Teleoconch of 3 1/8 strongly convex, ovate whorls with rounded shoulder. Suture impressed. Axial sculpture of thin, sharply demarcated, weakly prosocline raised ribs, 42 on last whorl, 34 on penultimate whorl. Ribs closely spaced on first teleoconch whorl, becoming more widely spaced on later whorls, but again closely spaced along final 1/8th whorl. Spiral sculpture of very low, narrow cords, subequal in width, alternating in prominence, covering entire shell surface, about 50 on final whorl, 10 on penultimate whorl. Aperture large (0.74 shell length), broadly oval, smooth, deflected from shell axis by 15°. Outer lip very thin, weakly reflected, edge forming final axial rib, with shallow anal sinus at suture. Columella weakly sinuate, convex posteriorly, distinctly concave medially, and again anterior to 3 obliquely oriented, recessed folds (Figure 2). Central fold most pronounced, anteriormost fold even more obliquely oriented than central and posterior fold. Parietal callus, broad, very thin. Siphonal canal broad, long, well delimited from

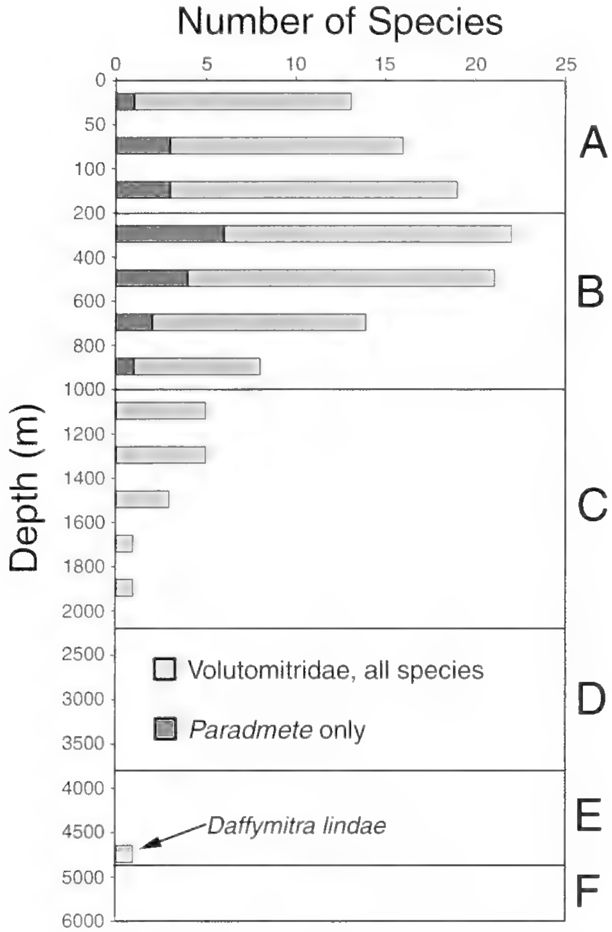


Figure 7. Bathymetric distribution of the Recent species of Volutomitridae, of the Antarctic genus *Paradmete* (data from Bouchet and Kantor, 2004: Appendix), and of *Daffymitra lindae*. A: continental shelf; B: upper continental slope; C: lower continental slope; D: continental rise; E: abyssal plain, F: hadal depths.

aperture. Shell color white. Periostracum thin, olive brown, covering entire shell. Operculum, radula and anatomy unknown.

Type Locality: Bellingshausen Abyssal Plain, 61°27′ S, 94°58′–95°22′ W, in 4419–4804 m [R/V ELTANIN cruise 23, sta. 1621, 10 Apr. 1966].

Type Material: Holotype, USNM 1080443, shell length 27.9 mm, final whorl length 23.4 mm, aperture length 21.5 mm, shell width, 13.5 mm.

Distribution: Known from the type locality only.

Etymology: This species is named for the senior author's wife. Linda Lee Harasewych.

Remarks: Despite the absence of anatomical and radular data, this new species can be unambiguously assigned to the family Volutomitridae on the basis of its distinctive shell shape, sculpture, presence of the diagnostic paucispiral mammilate protoconch, and weak columellar folds.

Seven genera are currently recognized within the family Volutomitridae (Cernohorsky, 1970; Bouchet and Kantor, 2004). The large size, long, broad aperture, and thin shell of this new species, as well as the presence of three obliquely oriented and deeply recessed columellar folds and a siphonal fold preclude its assignment to either the fossil genus *Proximitra* Finlay, 1927, or the Recent genera *Conomitra* Conrad, 1865; *Microvoluta* Angas, 1877; *Peculator* Iredale, 1924; or *Magdalemitra* Kilburn, 1974.

Conchologically, the new species is closer to the genera *Volutomitra* H. and A. Adams, 1853 and *Paradmete* Strebel, 1908, which are considered to be closely related (Powell, 1951: 165; Cernohorsky, 1970: 91). The 13 known species of *Volutomitra* are widely distributed in the World Ocean, ranging from South Africa, Southern Australia, New Zealand and to the Bering Sea in the Pacific, and from Colombia to the northern part of the Atlantic Ocean. *Daffymitra lindae* differs from all known species of *Volutomitra* in having a proportionally shorter spire and inflated rather than fusiform shell, coarse spiral sculpture and sharp, narrow, broadly spaced axial ribs, as well as columellar folds that are weak, recessed within the aperture and obliquely oriented rather than being strong, prominent, and nearly perpendicular to the columellar axis. The only species of *Volutomitra* with pronounced axial sculpture, *V. erebus* Bayer, 1971, from Colombia, has axial ribs that are thicker, more rounded, orthocline, and more densely spaced.

The genus *Paradmete*, contains six species, all confined to Antarctic and sub-Antarctic waters. *Daffymitra lindae* may easily be distinguished from *Paradmete fragillima* (Watson, 1882), the type species, as well as from *P. briedensis* Numanami, 1996, and *P. arnaudi* Numanami, 1996, by its larger size, shorter spire, inflated rather than narrowly fusiform shell, and distinctive narrow, prosocline axial ribs, as well as by its well demarcated siphonal canal. The Magellanic *Paradmete crymochara* (Rochebrune and Mabille, 1885) approaches *Daffymitra lindae* in size, but differs in its elongate, fusiform shape, absence of a distinct siphonal canal, and presence of four columellar folds. The distinctive *Paradmete percarinata* Powell, 1951, can be recognized by its prominent peripheral carina, sharply shouldered shell and pronounced columellar folds that are nearly perpendicular to the columellar axis. Most similar to *Daffymitra lindae* is *Paradmete curta* (Strebel, 1908), which reaches a similar size, has a low spire, and has axial ribs, which, however, are opisthocline rather than prosocline. *Daffymitra* differs in lacking a strong shoulder and in having an inflated shell shape with an attenuated anterior and distinctive siphonal canal.

The shell of *Daffymitra lindae* bears a surprising resemblance to some members of the Mesozoic genus *Volutomorpha*, particularly *V. mutabilis* Wade, 1926 (see Wade, 1926: pl. 37, fig. 10, pls. 40, figs. 6, 9; Sohl, 1964: pl. 39, figs. 1, 2, 6). *Volutomorpha* was restricted to the Upper Cretaceous faunas of the Gulf and Atlantic coastal plains (for a review, see Sohl, 1964: 252–254), and was "the giant of Cretaceous gastropods" (Wade, 1926: 20) with shell lengths extrapolated to exceed 45 cm. Pilsbry and Olsson (1954: 19) included *Volutomorpha* in the Cretaceous subfamily Volutodermatinae, which they placed in the family Volutidae together with Volutomitrinae. More recently, Dzhalilov (1977: 93) proposed a new subfamily Volutomorphinae, also within Volutidae, while Bouchet et al. (2005: 255) considered Volutomorphinae a synonym of Volutodermatinae, which they transferred from Volutidae to the extinct family Pholidotomidae.

While *Daffymitra* is easily distinguished from *Volutomorpha* by its far smaller size, thinner shell, absence of thick axial ribs, and lack of a pronounced shoulder, this conchological similarity raises the intriguing possibility that *Daffymitra* is a "living fossil," a surviving descendent from a group presumed to have become extinct at the end of the Cretaceous. Further research is clearly required to reevaluate the relationships between the various Cretaceous genera assigned to Volutoderminae and the earliest Volutomitridae.

DISCUSSION

The family Volutomitridae has a broad geographic range, but has previously been known only from continental shelf and continental slope faunas, while the genus *Paradmete* has been reported only from shelf and upper slope depths (Figure 7). The greatest diversities for both the family and the genus occur at upper continental slope depths.

Although *Daffymitra lindae* is represented by a single empty shell, the fragility of the shell, the presence of periostracum, and the fact that it was collected below the aragonite compensation depth indicate that the specimen could not have been dead for long, and that the species inhabits the area in which this specimen was collected. Thus, this taxon represents the first record of Volutomitridae from abyssal depths. In a survey of Antarctic and Magellanic Buccinoidea, Harasewych and Kantor (2004) found that the abyssal buccinoidean fauna of the region has no genera in common with the sublittoral or bathyal faunas, but that credible sister taxa and likely origins for at least some of the abyssal genera occur on the adjacent continental slope. Based on shell morphologies, the genera *Volutomitra*, *Paradmete*, and *Daffymitra* appear to represent a lineage within Volutomitridae distinct from the predominantly austral genera *Proximitra*, *Conomitra*, *Microvoluta*, *Peculator*, and *Magdalemitra*. The genus *Paradmete*, a member of the upper slope fauna of Antarctica, is likely the sister taxon of the abyssal genus *Daffymitra*.

ACKNOWLEDGMENTS

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Exilia alanbeui, a new species from the Neogene of central Chile: the first record of *Exilia* (Gastropoda: Ptychatractidae) from South America

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ABSTRACT

A new species of the ptychatractid genus *Exilia*, *E. alanbeui* new species, is described from late Neogene sediments of the Navidad Formation, central Chile. This new species represents the first record, fossil or Recent, of the genus *Exilia* from the South American continent. Given that Recent species of *Exilia* are restricted to bathyal depths, the presence of representatives of the genus in fine siltstones of the Navidad and Ranquil formations lend support to a previous interpretation of bathyal depths for these deposits.

INTRODUCTION

The genus *Exilia* Conrad, 1860, has been placed in the family Turbinellidae by Maxwell (1988) and in the subfamily Ptychatractinae within the Turbinellidae by Kantor et al. (2001). The subfamily Ptychatractinae was removed from the Turbinellidae and raised to family level by Riedel (2000), as was suggested previously by Kantor and Bouchet (1997). Riedel (2000) placed the Turbinellidae together with other columellar plaits-bearing groups in his suborder Volutina while the Ptychatractidae were placed in the suborder Muricina based mainly on radula type and absence of columellar plaits. The most recent classification is that presented by Bouchet and Rocroi (2005), placing Ptychatractidae within Pseudolivoidea. The genus *Exilia* has been revised by Bentson (1940) and more recently by Kantor et al. (2001). The latter authors synonymized nine nominal genera, i.e., *Mitraefusus* Bellardi, 1873, *Mesorhytis* Meek, 1876, *Surculina* Dall, 1908, *Phenacoptygma* Dall, 1918, *Palaeorhaphis* Stewart, 1927, *Zexilia* Finlay, 1926, *Graphidula* Stephenson, 1941, *Benthovoluta* Kuroda and Habe, 1950, and *Chathamidia* Dell, 1956, containing fossil and Recent species with *Exilia* and recognized a total of nine living species. Fossil species were not formally treated by them but a number of species were figured for comparison. Previously, the Recent species of the synonymized genus *Benthovoluta* had been reviewed by Cernohorsky (1973) and Harasewych (1987). Species of *Exilia* are known from the Late Cretaceous (Coniacian) onward and fossil species are known from all continents except Africa and South America, "probably a reflection of insufficient studies of Cretaceous and Tertiary mollusks in these regions" (Kantor et al., 2001, p. 92). Some Cretaceous through Miocene species come from shallow-water deposits while deep-water occurrences are known since the late Eocene (Kantor et al., 2001). Recent species of *Exilia* are restricted to bathyal depths at tropical latitudes and in the New Zealand region (Kantor et al., 2001).

GEOLOGY OF THE FOSSIL-BEARING LOCALITIES

The Navidad Formation (Darwin, 1846) and its equivalents have recently been re-interpreted as late Miocene bathyal basin deposits containing displaced intertidal to outer shelf sediments (Finger et al., 2003; Nielsen et al., 2003). Several fossiliferous sites have been sampled for micro- and macrofossils. Of these, two localities from the Navidad Formation (Figure 1B) and two from the Ranquil Formation (Figure 1C) yielded specimens of *Exilia* described here.

Locality PPP (Figure 1B) is a grey deep-water siltstone that today forms the intertidal platform at Punta Perro. Based on planktonic foraminifera this locality has been dated as late Miocene (Tortonian) by Tsuchi et al. (1990) and Ibaraki (1992), while new dating by Finger et al. (2003) suggests an even younger age. The fauna is of an unusual composition for the Navidad Formation, containing otherwise unknown species of *Struthiochenopus* (Zinsmeister and Griffin, 1995) and *Xenophora* (Nielsen and DeVries, 2002). The specimens coming from Pupuya (Figure 1B) were collected by

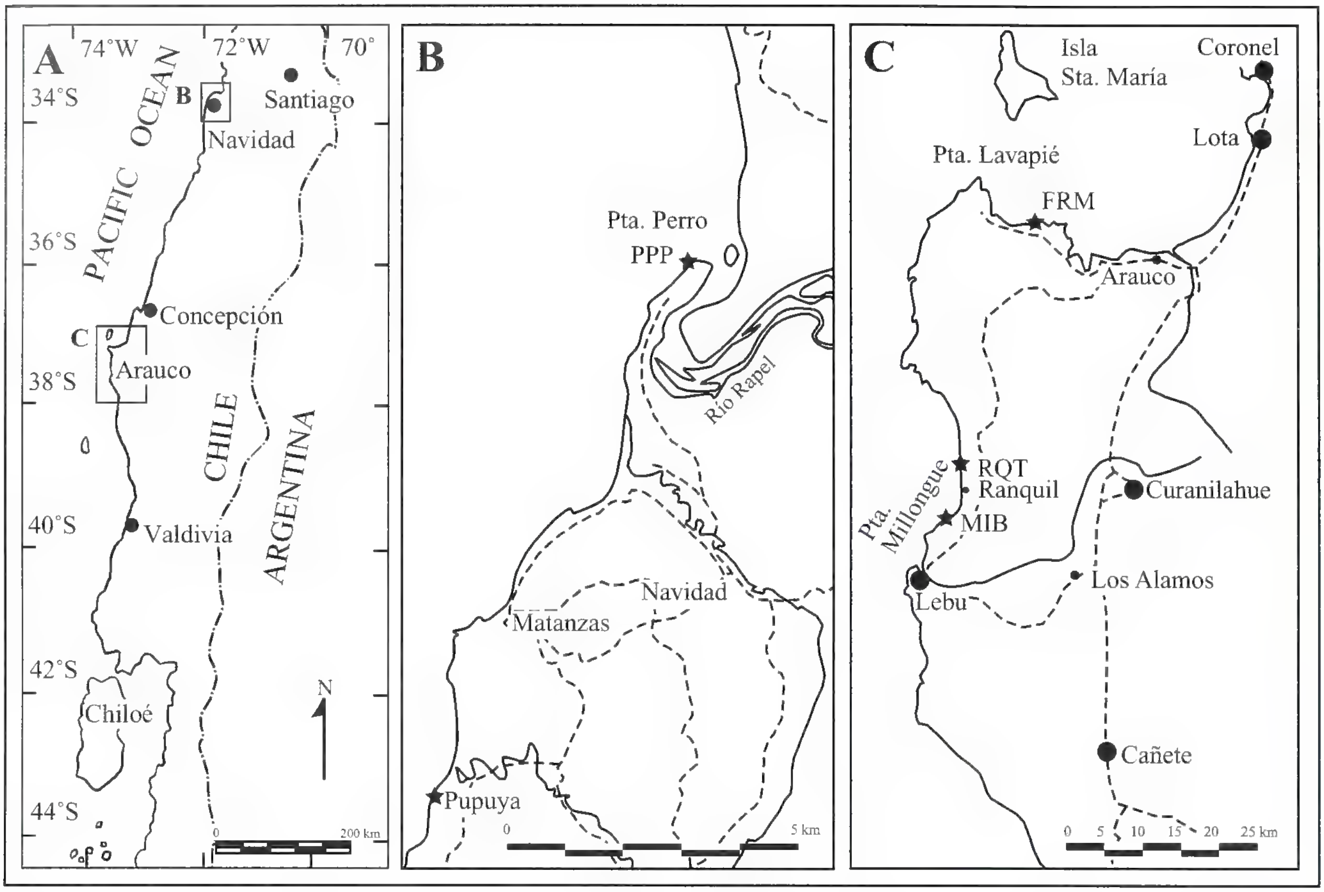


Figure 1. Fossil localities for *Exilia alanbeui* new species, in central Chile. **A.** Location of working areas. **B.** Localities of the Navidad Formation, Platform Punta Perro (PPP), Pupuya. **C.** Localities of the Ranquil Formation, Punta El Fraile (FRM), northern end of Caleta Ranquil (RQT), southwestern end of Caleta Ranquil.

V. Covacevich and D. Frassinetti a little south of the village Pupuya and come from a grey siltstone for which no ages are available. However, the faunal content (e.g., Nielsen et al., 2004) justifies correlation with PPP. The sediment at the type locality Punta El Fraile (FRM, Figure 1C) consists of grey siltstone and underlies a yellowish sandstone typical for the Ranquil Formation. The limit between these two lithological units has been observed to be a sharp, concordant one including some pebbles at the boundary. The sediments at Caleta Ranquil (RQT and MIB, Figure 1C) consist of a grey siltstone similar to that present at Punta El Fraile. The geological relation with other lithologies present at this locality, like reddish sandstone with beds of glauconitic sandstone and coarse light-grey sandstone, are not yet clear. However, both localities of the Ranquil Formation are similar to those of the Navidad Formation in lithology, and faunal content and were also dated as late Miocene by Finger et al. (2003).

MATERIALS AND METHODS

Specimens described in this study are deposited in the collections of the Departamento de Paleontología de Invertebrados Museo Nacional de Historia Natural, Santiago de Chile (SGO.PI) and Senckenberg Museum, Frankfurt, Germany (SMF). Photographs were taken using a Leicaflex SL2 or Olympus Camedia c730 camera. Images taken with the former camera were scanned from Ilford FP4 125 black and white 35 mm negatives using an Acer ScanWit 2720S film scanner. All images were processed with Adobe Photoshop 7.0.

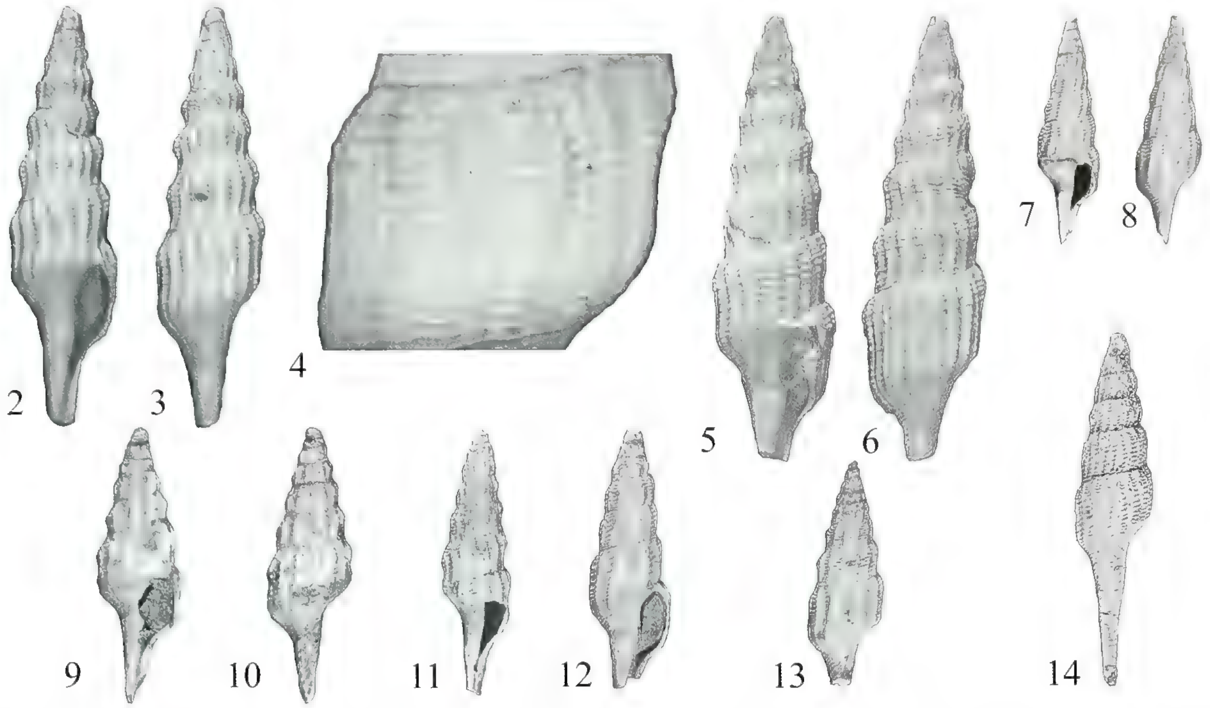
SYSTEMATIC PALEONTOLOGY

Family Ptychatractidae Stimpson, 1865
Genus *Exilia* Conrad, 1860

Type Species: *Exilia pergracilis* Conrad, 1860, by monotypy; Midway Group, lower Eocene, Alabama, USA.

Exilia alanbeui new species
(Figures 2–14)

Description: Shell narrow-fusiform, with spire occupying only little more than half of total height. Protoconch unknown. Teleoconch of about seven straight to slightly convex whorls, lacking pronounced shoulder. Axial sculpture consists of rounded, slightly



Figures 2–14. *Exilia alanbeui* new species. **2–4.** Holotype FRM 019 (height 28.35 mm). **5–6.** Paratype FRM 012-3 (height 30.2 mm). **7–8.** Paratype FRM 012-2 (height 15.46 mm). **9–10.** Paratype FRM 012-1 (height 9.3 mm). **11.** Paratype FRM 012-4 (height 18.03 mm). **12.** Paratype FRM 012-5 (height 17.62 mm). **13.** Paratype FRM 012-6 (height 15.2 mm). **14.** PPP 017 (PPP, height 23.9 mm).

backwards bent, collabral ribs. Penultimate whorl bears about 16 ribs, which become obsolete on base of whorl. Spiral sculpture well and equally defined, consisting of narrow, low, rounded, subequal cords, crossing axial elements unchanged, separated by interspaces of about equal width. Fine secondary spiral threads present in some interspaces. On penultimate whorl 10–14 spiral cords present, 8–9 further cords present on base of last whorl and about 30 weaker, closely spaced cords on siphonal canal. Aperture narrow-elongate. Outer lip thin. Siphonal canal narrow, long, straight. Inner lip smooth. Columella smooth and almost straight, with weak swelling at entrance of siphonal canal.

Etymology: This species is named in honour of Alan G. Beu (Institute of Geological and Nuclear Sciences, New Zealand), who always helps when needed.

Type Material: Holotype SGO.PI.6371 (FRM, height 28.35 mm), paratypes SGO.PI.6372 (FRM, one specimen, height 10.5 mm), SGO.PI.6373 (FRM, 21 specimens), SMF 327749 (FRM, 19 specimens).

Other Material Examined: SGO.PI.6374 (PPP, height 23.9 mm), SGO.PI.6375 (PPP, one specimen), SGO.PI.5303 (Pupuya, four specimens), SGO.PI.6376 (RQT, one specimen, height 9.25 mm), SGO.PI.6377 (MIB, one specimen, height 29.91 mm).

Type Locality: The grey siltstone at Punta El Fraile (FRM), Arauco, southern central Chile.

Occurrence: PPP, Pupuya, FRM, MIB, RQT; Navidad and Ranquil formations, Late Miocene or Early Pliocene, central Chile.

Discussion: *Exilia alanbeui* resembles the type species, *E. pergracilis* (see Bentson, 1940, pl. 2, fig. 25; Kantor et al., 2001, figs. 1 A–D), and *E. lincolnensis* Weaver, 1916, but differs from those North American Eocene species in having a less convex whorl profile, almost straight instead of sinusoidal axial sculpture and a more angulated whorl base. It differs from the New Zealand Miocene species *E. nodulifera* (Marwick, 1931), *E. leachi* (Marwick, 1931) and *E. wellmanni* Maxwell, 1988 (see Maxwell 1988) in having stronger axial sculpture. Most species of *Exilia* have more convex whorls and especially the Recent species have weaker axial sculpture (see Harasewych, 1987 and Kantor et al., 2001). The geographically closest species, *E. cortezi*, has wider whorls and different axial sculpture and is therefore not considered to be closely related to *E. alanbeui*. *Exilia alanbeui* is known only from localities consisting of deep water siltstones which have been dated as probably Messinian in age based on foraminifera (Finger et al., 2003). Therefore, this species is younger than the above mentioned Miocene species from New Zealand. Regarding the similarity of the two species, *E. alanbeui* may prove to be closely related to the New Zealand species *E. wellmanni*.

CONCLUSIONS

The occurrence of *Exilia alanbeui* in central Chile is the first record of the genus from the South American continent (except the Recent *E. cortezi* (Dall, 1908) from the Galápagos Islands) and therefore closes a considerable biogeographic gap. Although shallow water species of *Exilia* are known from Miocene deposits of Europe, the occurrence of *Exilia* in siltstones of the Navidad and Ranquil formations is here interpreted to support microfossil data placing these deposits in a bathyal environment (Finger et al., 2003).

Exilia alanbeui is another Chilean Miocene gastropod species that shows many similarities to New Zealand taxa. Trans-Pacific biogeographic connections between Chile and New Zealand during the Miocene have already been shown for some vetigastropods (Nielsen et al., 2004) and xenophorids (Nielsen and DeVries, 2002).

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Spawn of *Amphissa* sp. and *Cosmioconcha* sp. (Caenogastropoda: Columbellidae) from the Colombian Caribbean

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ABSTRACT

We describe the egg capsules and embryos of *Amphissa* sp. and *Cosmioconcha* sp. collected in the Caribbean Sea off Colombia between 20–160 m depth. *Amphissa* sp. had one layer of 24 egg capsules attached to the shell. *Cosmioconcha* sp. was completely covered by several layers of egg capsules; only the outer layer capsules contained embryos, the rest had the escape aperture open. Egg capsules of both species were translucent, dome-shaped, with an oval escape aperture at the center of the dome top. The surface was smooth, with no ridges nor sutures, and attached to the shell by an oval basal membrane that was surrounded by a thin, irregular flange. Egg capsules of *Amphissa* sp. measured 2 mm in diameter and contained 6 embryos/capsule at the gastrula stage; egg capsules of *Cosmioconcha* sp. measured 1 mm in diameter and contained 25 embryos/capsule at all stages of development (eggs, trochophores, and veliger larvae). Gastrulae of *Amphissa* sp. measured 750–900 µm in length and development in this species is probably direct. Uncleaved eggs of *Cosmioconcha* sp. measured 150 µm in diameter, the veliger had an operculum, a transparent shell measuring 188–219 µm in length, and a small velum; hatching occurs as planktonic larvae. No nurse eggs were observed in the two species but late cannibalism among sibling embryos may occur in *Cosmioconcha* sp.

INTRODUCTION

The family Columbellidae is very diverse in number of species in the Southern Caribbean. In this region, a total of 13 genera (*Columbella* Lamarck, 1799; *Rhombinella* Radwin, 1968; *Amphissa* H. and A. Adams, 1853; *Zafrona* Iredale, 1916; *Anachis* H. and A. Adams, 1853; *Nassarina* Dall, 1889; *Mitrella* Risso, 1826; *Cosmioconcha* Dall, 1913; *Aesopus* Gould, 1860; *Decipifus* Olsson and McGinty, 1958; *Mazatlania* Dall, 1900; *Strombina* Morch, 1852; *Nitidella* Swainson, 1840, and *Pyrene* Röding, 1798) and more than 30 species have been recorded (cf. Radwin, 1877 a, b; 1978; Costa, 2005); however, columbellid classification, as well as the identity and interpretation of the characters that support this classification, is not well resolved (DeMaintenon, 1999). The shells of these species are usually small and fusiform, within a size range of 5 to 24 mm and the outer lip usually bears denticles. The egg capsules and reproduction of several species have been described worldwide: Thorson (1940) summarized the different forms of egg capsules found in species from the Iranian Gulf, Knudsen (1950, 1995) described the egg capsules and development of species of tropical West Africa and the Azores, Amio (1957, 1963) described the eggs, larvae and embryology of Japanese species, DAsaro (1970) described the egg capsules of Panamanian Pacific species, Marcus and Marcus (1962) described the reproductive biology of several species from Brazil and Fortunato et al. (1998) characterized the reproduction of *Bifurcium bicanaliferum* (Sowerby, 1832) from the Pacific coast of Panama. In the Caribbean region, Bandel (1974) described the egg capsules of 10 species of Columbellidae from Santa Marta, Colombia; Penchaszadeh et al. (1983) characterized the reproduction of *Mazatlania consentini* Philippi, 1836 (as *M. aciculata*) (Lamarck, 1822) and Cipriani and Penchaszadeh (1993) that of *Strombina francesae* J. Gibson-Smith, 1974, and *Strombina pumilio* (Reeve, 1859), all three from Venezuela. Despite these studies, egg capsule morphology and developmental mode is still unknown for most of the recognized species.

Bandel (1974) distinguished 6 morphological groups of columbellid egg capsules according to the material he observed in Colombia and the literature. These are: (1) shallow domes on a broad, irregularly rounded disk of adhesion only extending on a narrow rim beyond the capsule walls as in *Mitrella ocellata* (Gmelin, 1791) reported as *Mitrella argus* (d'Orbigny, 1842), (2) cone shaped capsule, the walls rise from the round adhesion disk and end in a projecting edge forming a collar around the escape aperture, which is concave as in *Costoanachis sparsa* (Reeve, 1859), (3) cupola shaped with a suture dividing the capsule in 2 halves, oval base and the basal membrane extends in an irregular rim beyond the capsule walls, the escape aperture is asymmetrically located as in *Columbella mercatoria* (Linnaeus, 1758), (4) flask shaped and oval or round at the base, radial symmetry, the round adhesion disk is smooth and transparent, the capsule is sculptured with ridges as in *Nitidella nitida* (Lamarck, 1822), (5) brick

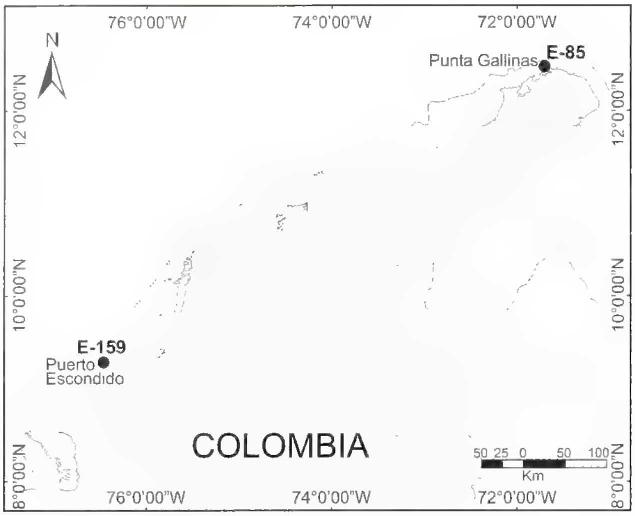


Figure 1. Map of the collecting localities in the Colombian Caribbean.

shaped egg capsules, escape aperture is absent as in *Anachis* sp. and (6) oval shaped standing on a peduncle as in *Columbella tryngas* Pils. A common spawning feature among these species was that they attached the egg capsules to hard substrates such as rocks, stems and algae (*Sargassum*), aquarium walls and hydroid stalks. Another spawning strategy found in the family involves attaching the egg capsules to the shells of conspecific living adults, such is the case of *Mazatlania consentini*, *Strombina pumilio*, *S. francesae* and *Bifurcium bicanaliferum* (Penchaszadeh et al., 1983; Cipriani and Penchaszadeh, 1993; Fortunato et al., 1998). There is no report in the literature for the Columbellid family of females using the shells of other living species as a substrate for egg laying.

In this paper, we describe the egg capsules and embryos of *Amphissa* sp. (*Amphissa* H. and Adams, 1853) and *Cosmioconcha* sp. (*Cosmioconcha* Dall, 1913) two apparently yet undescribed species from the Colombian Caribbean continental shelf. We also report on the number of egg capsules spawned by individual females and some reproductive parameters such as number and size of embryos contained in the egg capsules.

MATERIALS AND METHODS

One specimen of *Amphissa* sp. and three specimens of *Cosmioconcha* sp. were collected during 2001 by the Colombian ship B/I Ancon during an expedition to the Colombian Caribbean shelf (Figure 1). The specimen of *Amphissa* sp. was collected at Puerto Escondido, station E-159 at 158 m in muddy bottom (9°17′ N, 76°26′ W). The three specimens of *Cosmioconcha* sp. were collected at Punta Gallinas, station E-85 at 22 m depth in muddy-sand bottom (12°27′ N, 71°41′ W). Samples were obtained by trawling for 10 minutes with a trawling net type V measuring 12.7 m in total length and with a mesh size of 10 mm (Marinovich Trawl Co. Inc. USA). Samples were washed and separated in a 2 mm mesh seine, observed alive and preserved in ethanol 70%. The material of both species is deposited at the Museo de Historia Natural Marina de Colombia (MHNMC), INVEMAR, catalog numbers INV MOL3746 for *Amphissa* sp. and INV MOL5396 for *Cosmioconcha* sp.

The following reproductive aspects were studied: (1) number and size of egg capsules attached to each specimen, (2) number and size of embryos within each capsule and (3) observation of the different stages of development.

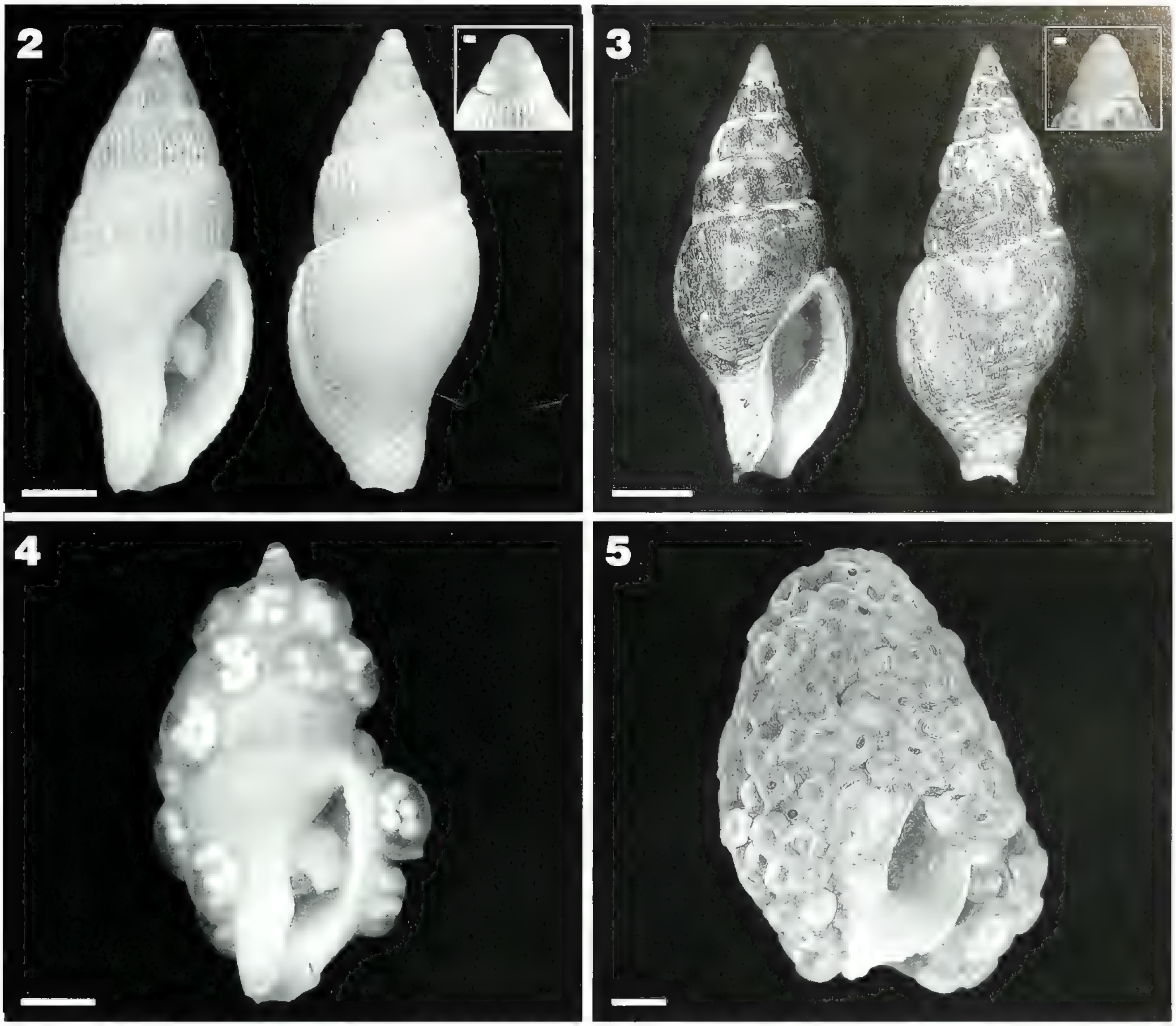
RESULTS

The specimen of *Amphissa* sp. (Figure 2) measured 12.5 mm and 5 mm in shell length and width respectively; the protoconch of this species measured 480 μm in length and had two whorls. A seemingly related species is *A. acuminata* (Smith, 1915) from the southern West Atlantic. Specimens of *Cosmioconcha* sp. (Figure 3) measured between 11 and 12 mm in shell length and between 4.5 and 5 mm in shell width; the protoconch measured 570 μm in length and had 3–3½ whorls. The taxonomic status of this species has to be confirmed.

A total of 24 egg capsules were attached to the shell of *Amphissa* sp. (Figure 4); these were arranged in one layer and covered most of the shell. The three specimens of *Cosmioconcha* sp. were completely covered by egg capsules in several layers that added 3 mm to the size of the shell (from 5 to 8 mm) (Figure 5). The egg capsules of the internal layers had no embryos and had their escape apertures open; the closed capsules containing embryos were limited to the external layer (Table 1).

The egg capsules of *Amphissa* sp. (Figure 6) were translucent, dome-shaped, with an oval escape aperture located on the center of the dome top. The capsule surface was smooth with no ridges nor sutures. They were attached to the shell by an oval basal membrane that was surrounded by a thin, irregular flange. Egg capsules measured around 2 mm in diameter and contained around 6 gastrulae embryos in each capsule. The egg capsules of *Cosmioconcha* sp. (Figure 7) were very similar to those of *Amphissa* sp. but smaller, measuring around 1 mm in diameter and containing around 25 embryos in each capsule at the three developmental stages examined: eggs, trochophore, and veliger larvae (Table 2). No nurse eggs were observed. The open egg capsules were filled with debris composed of organic matter and muddy sediment. Between the egg capsules, within the empty spaces, several specimens of the genus *Turbonilla* were found.

All egg capsules of *Amphissa* sp. contained embryos in the gastrulae stage in a number of six per capsule. The gastrulae were yellow, elongated, measuring 750–900 μm in length and 600–660 μm in width (Table 3). Each egg capsule of *Cosmioconcha* sp. contained embryos in the same stage of development; however, three different stages were identified in the spawn: uncleaved eggs, trochophore and veliger larvae (Table 3).



Figures 2–5. Shells and attached egg capsules. **2**. Adult shell of *Amphissa* sp. and detail of protoconch. Scale bar = 2 mm, detail = 200 μm. **3**. Adult shell of *Cosmioconcha* sp. and detail of protoconch. Scale bar = 2 mm, detail = 100 μm. **4**. Adult shell of *Amphissa* sp. covered by attached egg capsules. Scale bar = 2 mm. **5**. Adult shell of *Cosmioconcha* sp. covered by attached egg capsules. Scale bar = 2 mm. All photos taken from preserved material.

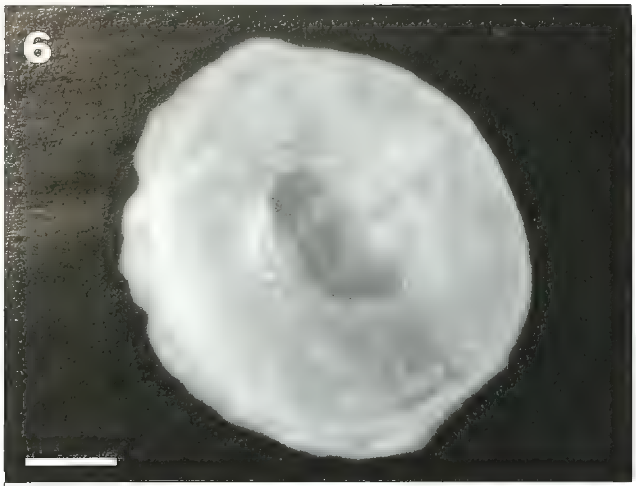
Table 1. *Cosmioconcha* sp. Number of layers and summary of the attached egg capsules for each of the three specimens collected (ND = not determined).

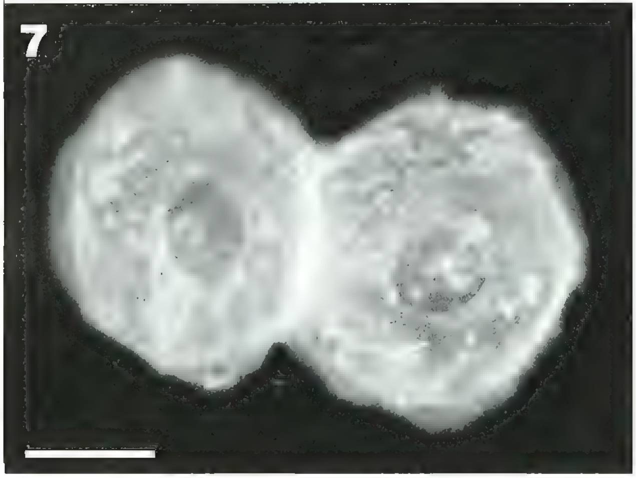
Specimen	1	2	3
Number of layers	4	6	4
Total number of attached capsules	537	775	494
Total number of capsules in external layer	ND	217	157
Number of open empty capsules	447	623	385
Number of closed empty capsules	3	0	1
Number of closed capsules containing embryos	86	152	108
Number of open capsules containing embryos	1	0	0

Empty embryonic shells were observed in a few capsules with embryos at the veliger stage. The uncleaved eggs measured 150 μm in diameter and the trochophore measured 165–212 μm in length. The veliger had an operculum and was characterized by a transparent, fragile shell measuring 188–219 μm in length and 156–194 μm in width. The velum was small, measuring 144–219 μm across from one lobe to the other and 31–94 μm in height; the cilia of this velum were very small, measuring 6–13 μm.

DISCUSSION

Amphissa sp. has not been previously reported in the Colombian Caribbean; the sediment at the locality





Figures 6–7. **6.** Egg capsule of *Amphissa* sp. Scale bar = 500 μm. **7.** Egg capsule of *Cosmioconcha* sp. Scale bar = 500 μm. All photos taken from preserved material.

where the specimen was collected is muddy, suggesting a broader habitat distribution for the species. The shell of this species resembles somewhat that of *A. acuminata* (Smith, 1915), a southwestern Atlantic species (Costa, 2005), but it is not as slender and the whorls are more rounded; the teleoconch consists of six rounded whorls and the sculpture of uniform spiral lirae and fine axial ribs, forming small rounded nodules at the intersections; aperture narrow, suboval; outer lip a little thickened exteriorly, with about five slender, short lirae within. For a detailed description of *A. acuminata*, see Simone and Leme (2001) and Costa (2005). The living species apparently most closely related to *Cosmioconcha* sp. is *Costoanachis helenae* Costa, 1983, whose distribution range is apparently restricted to the tropical sector of the Brazilian coast, from Amapá to Rio de Janeiro, in depths ranging from 8 to 100 m (Rios, 1994; Costa, 2005). We compared the egg capsules of *Cosmioconcha* sp. to those of *C. helenae* collected off Boipeba, an island on coast of the Brazilian state of Bahia (deposited at the Museu Nacional do Rio Janeiro, MNRJ 1029). The specimen measured 11.9 mm in length and 5.2 mm in width. Several spawning events had occurred on this shell since there were two layers of egg capsules, the external with about 30 and the internal with about 15 capsules, a number considerably lower than the number of capsules found in our species of *Cosmioconcha* (see Table 2). The capsules were very similar in shape to those of *Cosmioconcha* sp. but their size was larger; they measured 1.4 mm in length and 1.3 mm in width, and the aperture measured 0.6 mm in length and 0.5 mm in width (n= 10 capsules measured).

Cosmioconcha sp. was previously reported from the Colombian Caribbean as *Anachis* cf. *fraudans* Jung, 1969, a very closely related form from the Miocene-Pliocene of Trinidad (Díaz and Puyana, 1994). It also resembles *C. helenae* (Costa, 1983) in shell size and form, as well as in the number and form of embryonic whorls. However, the latter has a more slender spire, the upper half of its last whorl is sculptured with 11–18 axial ribs and its shell color is pale brown with white spiral bands (Costa, 2005). The last whorl of *Cosmioconcha* sp. lacks axial ribs and the shell is pale yellow under the dark brown periostracum. *Costoanachis helenae* has so far been only recorded from the central Brazilian coast, from Amapá to Rio de Janeiro (Rios, 1994; Costa, 2005).

The reproductive strategy of spawning or attaching the egg capsules to the adult shell of conspecifics is comparable to the spawning of other Caribbean species found in Venezuela, (Penchaszadeh et al., 1983; Cipriani and Penchaszadeh, 1993). However, it was not reported

Table 2. Summary of the egg capsule characteristics of *Amphissa* sp. and *Cosmioconcha* sp. Values represent mean ± SD, numbers in parenthesis indicate range (n = number of egg capsules measured).

Species Shell length (mm)	Capsule length (mm)	Capsule width (mm)	Capsule height (mm)	Aperture length (mm)	Aperture width (mm)	Embryos per capsule
Amphissa sp. 12.5)	2.2±0.1 (2.0–2.4) n=18	2.0±0.01 (1.9–2.1) n=18	0.8±0.2 (0.6–1.0) n=18	0.90±0.04 (0.78–0.93) n=11	0.74±0.07 (0.60–0.90) n=11	5.9±1.2 (4–8) n=11 (Gastrulae)
Cosmioconcha sp. 11–12)	1.15±0.15 (0.75–1.5) n=63	1.01±0.12 (0.75–1.47) n=63	0.36±0.06 (0.24–0.50) n=62	0.35±0.05 (0.27–0.54) n=62	0.27±0.03 (0.02–0.02) n=62	25.0±2.9 (19–31) n=23 (All stages)

Table 3. Size of embryos of *Amphissa* sp. and *Cosmioconcha* sp. during intracapsular development. Values represent mean ± SD and are reported in µm, numbers in parenthesis indicate range (n = number of embryos measured).

Species	Egg	Gastrula	Trochophore	Veliger	Protoconch (in adult)
Amphissa sp.	—	840±74 (750–900) n=6	—	—	500–600
Cosmioconcha sp.	150±0 n=16	—	189±19 (165–213) n=4	200±14 (188–219) n=7	570

for any of the 10 columbellid species studied by Bandel (1974) in the Santa Marta region, which attached the egg capsules to other hard substrates such as rocks, *Sargassum* plants, stalks of hydroids and, when in captivity, to the glass walls of the aquarium. There are no records in the literature of columbellids spawning on the shells of other species, a strategy that has been observed in the sandy beach gastropod *Olivancillaria deshayesiana* Ducros, 1857, from Argentina, which spawns the egg capsules on the adult shells of *Buccinanops monilifer* Kiener, 1834, and *Buccinanops duartei* Klappenbach, 1961, either directly on the adult shell or on top of the egg capsules of these species, which are also attached to the shell of conspecific individuals (Borzone, 1985). The fact that several layers of egg capsules are found, as well as different stages of embryonic development and empty egg capsules, on *Cosmioconcha* sp. suggests that several different events of oviposition have occurred using this specimen as substrate. Penchaszadeh et al. (1983) reported that females of *Mazatlania consentini* (as *M. aciculata*) attach their egg capsules to the shells of other individuals of the population with shells larger than 9 mm, apparently exclusively males, as shown by histological sections of the gonads of bearing individuals (Penchaszadeh, 1981). Fortunato et al. (1998) stated that the egg masses of *Bifurcium bicanaliferum* usually have several layers as well, whereas those of the Venezuelan Caribbean *Strombina pumilio*, *S. francesae*, and *M. consentini* have only one layer of egg capsules attached to the shell as we observed in *Amphissa* sp. Regarding this remarkable difference in the number of egg capsules that a single animal is bearing, we hypothesize that the egg capsules of species that bear few of them on the shell arranged on a single layer are easily detachable since they are usually individually attached, as is the case in *M. aciculata*. In this species, up to 20 egg capsules can be observed at the same time on one single adult shell; these have embryos at different stages of development, which means that not all egg capsules are spawned simultaneously. Once the veliger larvae hatch, the empty capsule usually falls off the shell, sometimes leaving only the basal membrane attached to the shell, and new capsules are spawned (Penchaszadeh, 1981). On the other hand, egg capsules of species with several layers are more resistant since they are attached not only to the adult shell by the basal membrane, but also form a very compact structure of egg capsules attached between them by lateral membranes (*B. bicanaliferum*, *Cosmioconcha* sp.). As pointed out by Pechenik (1986), gastropod egg capsules are structurally and chemically complex, the different layers are composed in general among and other components by protein and carbohydrates (Bayne, 1968; Miloslavich, 1996; Rawlings, 1999). Hunt (1966) also reported that since the capsule walls are extremely resistant to chemical treatment, the protein and carbohydrate components should be strongly linked in a glycoprotein complex and thus stabilized by sclerotization. In this way, the bond between two egg capsules is much stronger than the bond between an egg capsule and a shell.

The description of the egg capsule of *Amphissa* sp. is similar to the description provided by Bandel (1974) for *Zafrona pulchella* (cited as *Anachis pulchella*) in its dome shape. However, the dome of *Amphissa* sp. lacks the division into lower and upper parts separated from each other by one or a few concentric rings, it does not have a suture that continues the axis of the escape aperture and the membrane is not striped nor wrinkled. On the contrary, the surface is very smooth and only very thin imperceptible lines are visible. A comparable feature among both species is that the number of embryos per capsule was very similar and that no nurse eggs nor cannibalism seem to occur.

The egg capsules of *Cosmioconcha* sp. also fit in the first category of egg capsule morphology described by Bandel (1974), a simple dome attached by a rounded base. It is very similar to the capsule of *Amphissa* sp. but half its size in length, width and height. This capsule shape and general morphology are also comparable to the two species of the *Strombina* group from the Caribbean described by Cipriani and Penchaszadeh (1993), which have about the same size than the capsules of *Amphissa* sp., and to *B. canaliferum* from the Pacific coast of Panama described by Fortunato et al. (1998), which has about the same size than the capsule of *Cosmioconcha* sp.

No nurse eggs seem to be present in the two species studied. In comparison to other columbellid gastropods, the reproductive strategy of *Amphissa* sp. is similar to that of *S. francesae* and *S. pumilio*: large egg capsules (more than 2 mm in length), large eggs (more than 500 µm) and few embryos (about 4 to 8) that hatch as large crawling juveniles (larger than 0.9 mm). We did not observe the hatching stage of *Amphissa* sp., but the large size of the gastrula (about 840 µm) indicates that it comes from a large egg which would most probably lead to direct development as in the two species of *Strombina* studied by Cipriani and Penchaszadeh (1993). On the other hand, the reproductive strategy of *Cosmioconcha* sp. is similar to that of *Bifurcium bicanaliferum*, *Anachis sparsa*, and *Cosmioconcha sertulariarum* (d'Orbigny, 1839): small egg capsules (about 1 mm in length), small eggs (about 140–200 µm) and many embryos (more than 20) that hatch as small veliger larvae (about 300 µm) (Fortunato et al., 1998; Marcus and Marcus, 1962). Late cannibalism among sibling embryos inferred from the presence of empty shells inside a few egg capsules of *Cosmioconcha* sp. has also been reported in *B. bicanaliferum* by Fortunato et al. (1998). Although late cannibalism might take place in the egg capsules of *Cosmioconcha* sp., it is very unlikely that this limited extraembryonic food source will allow the larva to grow from 200 µm to 600 µm, which is the protoconch size found in the adult shell. It is most likely that *Cosmioconcha* sp. will hatch as a veliger larva spending some time in the plankton as is also the case of *B. bicanaliferum*, which grows from 1.5 whorls to 2.5 whorls in the planktonic period (Fortunato et al., 1998). In the case of *Amphissa* sp., we can conclude from the size of its protoconch that this species must hatch as a crawling juvenile since the gastrula stage is already as large as the protoconch, a situation similar to what happens with the two *Strombina* species from the Venezuelan Caribbean studied by Cipriani and Penchaszadeh (1993).

We hope that in a near future, and thanks to the collection efforts carried out by INVEMAR in the southern Caribbean, more specimens will be collected. This will not only allow for the proper description of these species through use of traditional characters such as those from adult shell, anatomy, and radular morphology, but may also help increase the number of observations on egg capsules and the development of other embryonic stages.

ACKNOWLEDGMENTS

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Erratum

Due to an editorial lapse in the latest article by Cristián Ituarte (2005), please substitute the last sentence in the Etymology section (page 97, right-hand column, lines 24, 25) as follows:

Replace "..., which underwent a major cultural change during the past 10,000 years."

For: "..., which has been a major pathway for cultural exchange during the past 10,000 years."

LITERATURE CITED

Ituarte, C. 2005. The Sphaeriidae (Bivalvia) from northwestern Argentina including three new species of *Pisidium*. The Nautilus 119: 93–104.

Pterorytis pacanana new species (Gastropoda: Muricidae): circumstantial evidence for late Pliocene El Niño events in southern Peru

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ABSTRACT

Pterorytis pacanana new species was discovered in upper Pliocene bioclastic sandstone near Chala, southern Peru. Although it was found farther south than other *Pterorytis* species from the eastern equatorial Pacific Ocean, *P. pacanana* most resembles *P. roxaneae* Petuch, 1994, from the Pliocene Pinecrest beds of Florida. Its presence among endemic late Pliocene cool-water mollusks from high-energy shoreface paleoenvironments is thermally anomalous in the same sense as the rare occurrence of other species from northern Peru and Ecuador in upper Pliocene and Pleistocene strata from southern Peru. By analogy with modern thermally anomalous mollusks that appear episodically off the coast of southern Peru and Chile, the Pliocene and Pleistocene examples are circumstantial evidence for the occasional southward incursion of warm equatorial waters during former El Niño events.

INTRODUCTION

Pliocene deposits in southern Peru are noted for a variety of muricid gastropods, most belonging to genera still represented by extant species (e.g., *Acanthina* Fischer von Waldheim, 1807; *Chorus* Gray, 1847; *Concholepas* Lamarck, 1801; *Crassilabrum* Jousseaume, 1880; *Muregina* Vermeij, 1998; *Stramonita* Schumacher, 1817; *Xanthochorus* Fischer, 1884), but some from genera entirely or locally extinct (e.g., *Herminespina* DeVries and Vermeij, 1997; *Trophon*, Montfort, 1810) (DeVries, 1995, 1997, 2000, 2003, in press a, in press b; DeVries and Vermeij, 1997). Specimens of most Pliocene muricids are not exceedingly difficult to find.

A well-preserved muricid from Pliocene bioclastic sandstone south of Chala is, literally, the rare exception. None have been found other than a single shell plucked from a roadcut of the Panamerican Highway that overlooks Playa Huacllaco. The lamellar fimbriate varices of the Huacllaco specimen invite comparison with ocenebrines from Ecuador, the southeastern United States, and the northwestern Pacific Ocean. Its lone appearance in a collection of endemic cool-water muricids is another example of a thermally anomalous molluscan species encountered in upper Pliocene and Pleistocene beds of southern Peru (Muizon and DeVries, 1985; DeVries, 1986; Ortlieb et al., 1990). A reasonable hypothesis is that these equatorial species were introduced to higher austral latitudes by warm-water incursions during the Pliocene and Pleistocene comparable to modern incursions that carry Panamic molluscan larvae poleward during El Niño events (DeVries, 1988; Arntz and Tarazona, 1990; Paredes et al., 1998).

GEOLOGY

Bioclastic sandstone and gravel and balanid coquina overlie igneous basement in roadcuts along a series of sweeping curves in the Panamerican Highway where it descends towards the beach at Playa Huacllaco (Figure 1). The sediments represent high-energy foreshore and intertidal paleoenvironments that once flanked steep cliffs. The section, previously published

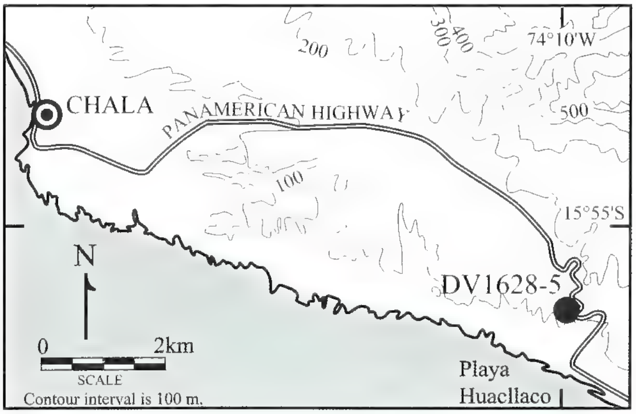

Figure 1. Type locality of *Pterorytis pacanana* new species (DV 1628).

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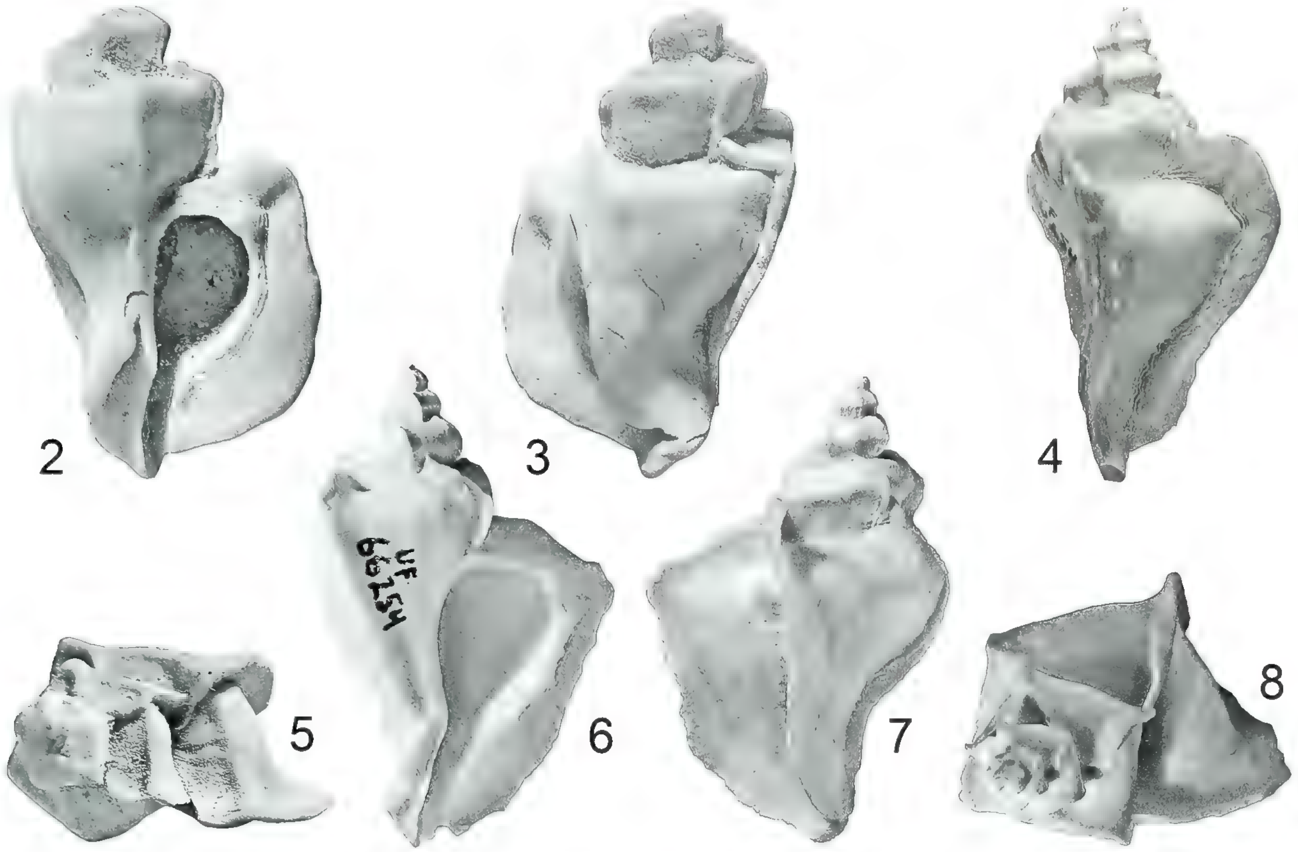

Figures 2–8. *Pterorytis* species. **2, 3, 5.** *Pterorytis pacanana* new species. Upper Pliocene. Holotype, UWBM 97772, length = 30.9 mm, width = 19.6 mm. **2.** Apertural view. **3.** Abapertural view. **5.** Oblique view of spire. **4, 6–8.** *Pterorytis roxaneae* Petuch, 1994. Upper Pliocene. Holotype, Florida Museum of Natural History, Gainesville, UF 66254, length = 33.3 mm, width = 21.5 mm. **4.** Lateral view. **6.** Apertural view. **7.** Abapertural view. **8.** Oblique view of spire.

by DeVries (2003), consists of four stratigraphic units. The ocenebrine specimen was found at the base of Unit III, just below strata where rounded clasts of blackened andesite first appear in great numbers and below beds where specimens of *Concholepas* and *Acanthina* acquire their modern form (DeVries, 2000, 2003).

The age of the Huacllaco beds is bracketed by basal beds with specimens of *Concholepas nodosa* Hupé, 1854, *Acanthina triangularis* DeVries, 2003, and *Herminespina mirabilis* (Möricke, 1896), which collectively indicate an early late Pliocene age (DeVries and Frassinetti, 2003), and the uppermost and oldest of several marine terraces, whose elevation and largely extant taxa suggest a latest Pliocene age (Muizon and DeVries, 1985).

MATERIALS AND METHODS

The specimen from Peru described in this study was found by the author. Dimensions affected by breakage are enclosed by parentheses. The holotype is deposited at the University of Washington's Burke Museum of Natural History and Culture in Seattle, Washington (UWBM).

SYSTEMATICS

Family Muricidae Rafinesque, 1815
Subfamily Ocenebrinae Cossmann, 1903
Genus *Pterorytis* Conrad, 1862
Subgenus *Pterorytis* sensu stricto

Type Species: *Murex umbrifer* Conrad, 1832, by monotypy.

Pterorytis pacanana new species
(Figures 2, 3, 5)

Diagnosis: Shell small; texture waxy, shell thin. Five lamellar, fimbriate varices; intervarical nodes absent. Three spiral cords; shoulder spiral cord strong. Sutural platform horizontal. Labral tooth absent.

Description: Shell 30.9 mm long (first teleoconch whorls missing), quadrate in profile, very thin, with waxy texture. Spire estimated to be about 40 percent of shell length. Siphonal canal about 20–25 percent of shell length. Protoconch and earliest teleoconch whorls missing. Upper sides of whorls planar, vertical; base of body whorl sharply constricted. Shoulder orthogonally angulate, sutures deeply impressed; sutural platform horizontal to slightly concave. Three last whorls with five lamellar varices extending from fasciolar ridge to suture, each varix joining across suture with varix of previous whorl. Lamellae broader basally, narrower adapically, extended adapically at shoulder but not spinose; fimbriate on adapertural face; erect or recurved adaperturally except apertural lamellae, which is weakly recurved abaperturally. Intervarical nodes absent. Spiral sculpture of prominent but ill-defined rounded primary cord at shoulder angulation and two additional broad low spiral cords anteriorly, almost obsolete. Additional broad low secondary cords barely visible adjacent to adapertural face of varices. Lamellar fimbria slightly extended at intersection with primary spiral cords. Aperture with inverted tear-drop shape. Parietal rib, anal sulcus absent; parietal area unexcavated. Columella smooth, inner lip very weakly concave, adherent anteriorly. Outer lip without dentition on inner edge. Labral tooth absent. Siphonal canal open, slightly recurved to right. Siphonal fasciole strongly arched, without rostrae. Pseudo-umbilicus narrow, extending adapically beyond siphonal canal.

Holotype: UWBM 97772, DV 1628-5, lower Upper Pliocene, length (30.9) mm, width 19.6 mm.

Type Locality: Roadcut along the Panamerican Highway, 10 km south of Chala, on a winding descent from a 200 m elevation terrace towards Playa Huacllaco, locality DV 1628, north side of first sweeping outside curve from base of outcrop, south side of road, near outcrop of igneous basement rock (Figure 1), 15°52′ S, 74°10′ W (Chala 1:100,000 quadrangle).

Occurrence: Upper Pliocene, southern Peru.

Etymology: 'Paca,' Quechua for 'high,' and 'nan,' Quechua for 'path,' referring to the horizontal to concave sutural platform bordered above and below by vertical walls of the whorls.

Remarks: *Pterorytis* or *Ocinebrellus* Jousseaume, 1880, is the most appropriate genus in which to place the Huacllaco specimen, which has five varices on at least the last three whorls, consistent with the three to nine varices observed on fossil Atlantic species of *Pterorytis* (Emerson, 1959; Vermeij, 2001), the four to five varices on the modern eastern Pacific *Pterorytis hamatus* (Hinds, 1844) (Emerson, 1985), and three to twelve varices on specimens of *Ocinebrellus* (Amano and Vermeij, 1998a). The ocenebrine genera *Ceratostoma* Herrmannsen, 1846, *Pteropurpura* Jousseaume, 1880, and *Microrhytis* Emerson, 1959, in contrast, have three prominent lamellar varices on all or at least the last two whorls (Vermeij and Vokes, 1997; Amano and Vermeij, 1998a, 1998b). Specimens of *Ceratostoma*, *Pteropurpura*, *Microrhytis*, and some *Ocenebra* Gray, 1847, also have intervarical nodes, which are absent on the Huacllaco specimen and specimens of *Pterorytis* and *Ocinebrellus*.

The absence of a closed siphonal canal does not argue against assignment of the single Huacllaco specimen to *Pterorytis* or *Ocinebrellus*, since juvenile and some adult specimens of the two genera may have an open siphonal canal. The Peruvian specimen, itself partly abraded, might be a juvenile specimen or have a broken siphonal canal.

Distinguishing *Pterorytis* from *Ocinebrellus* for placement of the Huacllaco specimen is problematic. *Ocinebrellus* has four primary spiral cords on the swollen portion of the body whorl, posterior to the labral tooth, if present (Vermeij and Vokes, 1997; Amano and Vermeij, 1998a). *Pterorytis* and the Huacllaco specimen have three primary spiral cords, with an additional weak primary spiral between the shoulder and suture. On smoother specimens of both genera the number of primary spiral cords can be difficult to enumerate, and on strongly sculptured specimens the distinction between primary and secondary spiral cords is unclear if the ontogeny is unknown.

Other features are equally unsatisfactory for distinguishing the two genera. The reflection of lamellar varices is not reliable, since the lamellae may be adaperturally reflected, or not, in *Ocinebrellus* (Amano and Vermeij, 1998a), abaperturally reflected or erect in *Pterorytis* (Vermeij and Vokes, 1997), and erect or reflected in either direction on the Huacllaco specimen. The angularity of the shoulder also fails as a distinguishing character. Most specimens of *Ocinebrellus* have an angulate shoulder and a horizontal sutural platform (as is the case for the Huacllaco specimen), but some have rounded shoulders. Most specimens of *Pterorytis* have broad, planar, steeply sloping sutural platforms, but some have narrower, less inclined sutural platforms more like those of typical *Ocinebrellus* and the Huacllaco specimen.

The presence or absence of a labral tooth is not diagnostic. Some ocenebrines acquire a labral tooth only in adulthood; the Huacllaco specimen might be a juvenile. Species of *Pterorytis* that normally have a tooth (*P. umbrifer* Conrad, 1832; *P. fluviana* Dall, 1890) have specimens lacking a tooth. Specimens of *P. roxaneae* Petuch, 1994, never have a labral tooth (Vermeij and Vokes, 1997). Species of *Ocinebrellus* (sensu Amano and Vermeij, 1998a) that normally lack a labral tooth have specimens with a tooth. (In the more restrictive classification of Houart and Sirenko (2003), species of *Ocinebrellus* do not have a labral tooth.)

Taking into account this taxonomic ambiguity, the Huacllaco specimen is assigned to *Pterorytis*. Species of *Pterorytis* (*P. umbrifer*, *P. fluviana*, *P. roxaneae*) typically have smooth-shelled variants such as the specimen from Huacllaco. Most specimens of *Pterorytis*, like the Huacllaco specimen, feature a prominent primary spiral cord at the shoulder, but nonetheless usually lack spines or angulations typically seen in specimens of *Ocinebrellus*.

Pliocene Ecuadorian specimens assigned to *Ocinebrellus* by Vokes (1988) are smooth, have a prominent shoulder spiral bordering an inclined sutural platform, and have varices that are only weakly angulate; they may be referred to *Pterorytis ecuadoria* (Olsson, 1964). They have a more fusiform profile and greater number of varices than the Huacllaco specimen.

The specimen of *Pterorytis pacanana* most closely resembles specimens of the Pliocene *Pterorytis (Pterorytis) roxaneae* Petuch, 1994, (Figures 4, 6–8) from the Pliocene Pinecrest beds of Florida (Vermeij and Vokes, 1997). Specimens of both species are thin with a waxy texture, have reduced spiral sculpture, and lack a labral tooth. Pinecrest specimens differ from the Huacllaco specimen in having four varices, not five, varical lamellae that are broader adapically, not abapically, and a weak peripheral spiral cord bordering a sloping sutural platform, rather than the strongly defined horizontal sutural platform of *P. pacanana*. Contrary to Vermeij and Vokes (1997), the holotype of *P. roxaneae* is neither excessively worn nor lacking the labral varix.

DISCUSSION

Pterorytis pacanana is the third or fourth species of *Pterorytis* recognized in the eastern Pacific Ocean, after *P. ecuadoria* (Pliocene, Ecuador), *P. hamatus* (Recent, northern Peru [Alamo and Valdivieso, 1997], a species with a protoconch unlike that of *Ocinebrellus* or any other ocenebrine [R. Houart, personal communication, 2005]), and an unnamed Recent ocenebrine from northern Peru (Radwin and D'Attilio, 1976). These taxa define an eastern tropical Pacific complement to a clade of *Pterorytis* species from the southeastern United States whose oldest members date to the late Miocene. *Ocinebrellus*, which may be endemic to the northwestern Pacific (Amano and Vermeij, 1998a; Houart and Sirenko, 2003), extends back to the Early or Middle Miocene. *Ocinebrellus* seems morphologically more similar to *Pterorytis* than other ocenebrine clades, but the trail of fossil species that might lead from Japanese *Ocinebrellus* to Panama and the Caribbean and beyond to Peruvian and Floridian *Pterorytis* has yet to be discovered (Amano and Vermeij, 1998a).

Table 1. Molluscan species associated with *Pterorytis pacanana*, new species, which was found at the base of Unit III of the Upper Pliocene beds above Playa Huacllaco, Peru (* = Extinct).

Unit III+IV (younger)	
	Acanthina unicornis (Bruguière, 1789)
	Cancellaria buccinoides Sowerby, 1832
	Choromytilus chorus (Molina, 1782)
*	*Chorus grandis* (Philippi, 1887) / *C. giganteus* (Lesson, 1846)
*	*Concholepas camerata* DeVries, 2000
	Concholepas concholepas (Bruguière, 1789)
	Crassilabrum crassilabrum (Sowerby, 1834)
	Crepidula dilatata (Lamarck, 1822)
	Eurhomalea lenticularis (Sowerby, 1835)
	Glycymeris ovata (Broderip, 1843)
	Mesodesma donacium (Lamarck, 1818)
	Mulinia edulis (King, 1831)
	Oliva peruviana Lamarck, 1811
*	*Piscoacritia* new species
	Prisogaster niger (Wood, 1828)
	Sinum cymba (Menke, 1828)
	Xanthochorus cassidiformis (Blainville, 1832)
Unit I+II (older)	
*	*Acanthina triangularis* DeVries, 2003
*	Acmaeids
*	*Chlamys* cf. *C. vidali* (Philippi, 1887)
	Choromytilus chorus (Molina, 1782)
*	*Chorus grandis* (Philippi, 1887)
*	*Concholepas camerata* DeVries, 2000
*	*Concholepas nodosa* (Möricke, 1896)
	Fissurella spp.
*	*Herminespina mirabilis* (Möricke, 1896)
	Lithophaga sp.
*	*Piscoacritia collapsa* DeVries and Hess, 2004
*	*Stramonita* new species
*	*Tegula (Chlorostoma)* new species
	Xanthochorus buxeus (Broderip, 1833)
*	*Xanthochorus* new species

The specimen of *Pterorytis pacanana* from 16°S is remarkable for its singular occurrence and equatorial affinity. Associated taxa (Table 1) are entirely endemic or cool-water species that became prevalent after a provincial mid-Pliocene extinction that coincided with a global cooling event (Dowsett et al., 1996; DeVries, 2001). The rare appearance of *Pterorytis* in southern Peru resembles that of a mangrove bivalve, *Anadara* cf. *A. grandis* (Broderip and Sowerby, 1829), whose specimens are found in small numbers in uppermost Pliocene beds at 15°30′ S with cool-water species (Muizon and DeVries, 1985; DeVries, 1986). In a more recent example, specimens of *Chione broggi* (Pilsbry and Olsson, 1943) and *Cerithium stercusmuscarum* Valenciennes, 1833, both living today only as far south as the Sechura coastline of northern Peru (5°S) (Alamo and Valdivieso, 1997), are occasionally found in upper Pleistocene terrace deposits near San Juan de Marcona (15°20′S), Sacaco (15°30′S), and Ilo (17°40′S) (DeVries, 1986, 1988; Ortlieb et al., 1990). Ortlieb et al. (1990) proposed that the late Pleistocene thermally anomalous species were introduced southward from equatorial latitudes during El Niño events. Several such immigrations of equatorial mollusks have been documented during modern El Niños events (Arntz and Tarazona, 1990; Paredes et al., 1998). The rare Pliocene equatorial species in southern Peru were probably introduced in the same manner.

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A new species of *Falsimargarita* (Gastropoda: Vetigastropoda: Trochidae) from the South Atlantic Ocean

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ABSTRACT

A new trochid species, *Falsimargarita stephaniae*, is described from about 1200 m depth off the Malvinas (Falkland) Islands, South Atlantic Ocean. The new species is distinguished from the most similar congeneric ones by its exceedingly large spiral cords located only along the periphery of its shouldered whorls. A re-hydrated specimen allowed for the description of some details of the anatomy of the new species, including head-foot, buccal mass, and radula.

INTRODUCTION

Representatives of the trochid genus *Falsimargarita* Powell, 1951, can be distinguished by shell characters such as external iridescence, well-defined spiral whorls, strong spiral sculpture, opened umbilicus, and thin shell wall. The genus encompasses five species occurring in the cold or freezing deep waters off Antarctica and the Magellanic region of South America. The taxon was more recently revised by Dell (1990), who outlined the diagnostic characters of the genus and described two species.

The analysis of a specimens collected by a boat deep-fishing for king crab and tuna revealed the presence of the new species. This paper is part of a larger project of revision of western Atlantic molluscan species, which at the moment is focused on the study of deep-sea trochids.

MATERIALS AND METHODS

A single specimen with dry soft parts was available for study. Dry soft parts were carefully removed and re-hydrated in physiological solution and 3–4 drops of KOH 20% for 3 h, then transferred to 70% ETOH. Only the head-foot was adequately extracted. The dissection was performed with the specimen immersed under the fixative, in a stereomicroscope. All drawings were done under camera lucida. The radula was removed and cleaned in a boiling solution of KOH for 1 h, then cleaned by sonication in water. The examination was done under a Zeiss electron microscope at the Laboratório de Microscopia Eletrônica of Museu de Zoologia da Universidade de São Paulo.

Institutional abbreviations used in this article are: MORG, Museu Oceanográfico da Fundação Universidade de Rio Grande, Rio Grande, Brazil; MZSP, Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil.

SYSTEMATICS

Genus *Falsimargarita* Powell, 1951

Type species: *Margarites gemma* Smith, 1915; by original designation, Antarctica.

Falsimargarita stephaniae new species
(Figures 1–12)

Diagnosis: Shell with broad spire, 5 prominent large and tall spiral cords restrict to periphery; umbilicus protected by strong plate.

Description: Shell of medium size (16.6 mm), trochoid to turbiform, whitish, iridescent-gray to pale-reddish; wall relatively thin, light. Protoconch of one smooth, glossy whorl. Separation protoconch-teleoconch poorly defined. Spire with 3.5 teleoconch whorls; each whorl highly convex, relatively high and shouldered; superior half weakly descendent, sculptured by 6–7 low and narrow spiral and numerous axial lines, both equally predominating; inferior half abruptly descendent, sculp-

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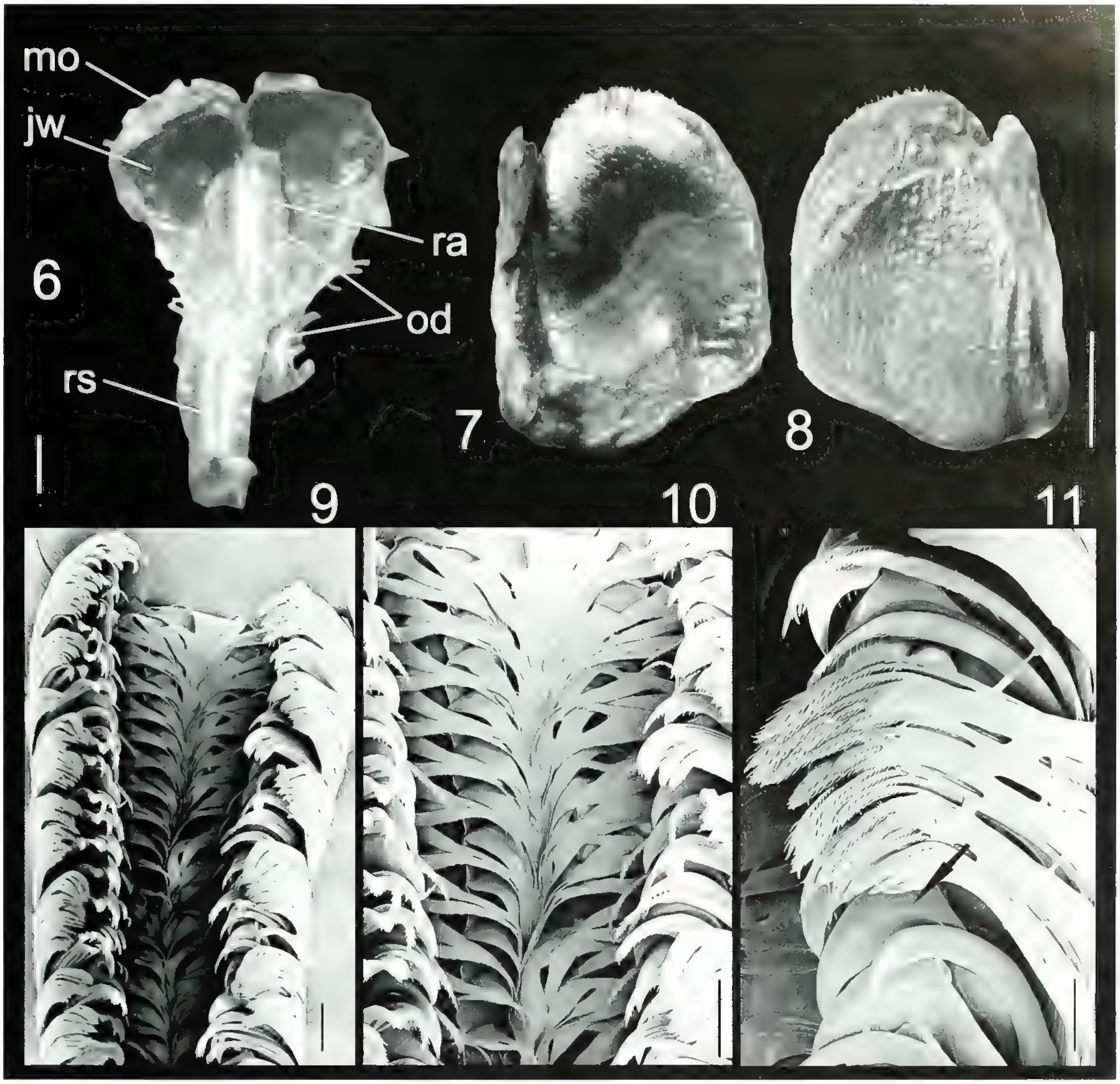
Figures 1–5. *Falsimargarita stephaniae* new species. **1–4.** Shell of holotype, apertural, abapertural, apical, and umbilical views (larger diameter 16.6 mm). **5.** Operculum, outer view.

tured by five strong and prominent spiral cords, two adapical and one abapical cords clearly larger, latter cord coinciding with suture; smooth area bearing only growth lines present between cords of abapical half of whorl. Body whorl about twice spire width, sculptured with five strong spiral cords that continue unchanged from spire; five spiral cords restricted to periphery area of body whorl; base sculptured with 18 spiral lines successively and gradually broader and more spaced toward umbilicus. Body whorl well separated from umbilicus by larger spiral cord, almost a low carina. Umbilicus open, deep, surface with simple growth lines; a strong plate-like expansion of the inner lip separates this latter from umbilicus. Aperture rounded, ample. Inner lip slightly deflected on abapical half, somewhat thick; adapical half marked only by thin glazed area on body whorl; no callus present. Outer lip rounded, thin, with small projections corresponding to spiral sculpture.

HEAD-FOOT: Total length about ½ length of last shell whorl. Head protruded, occupying about ⅓ of total head-foot volume. Snout with about ¼ of foot size,



Figures 6–11. *Falsimargarita stephaniae* new species. **6.** Buccal mass, ventral view, ventral wall opened longitudinally along median line and deflected to expose jaws. Scale bar = 1 mm. **7–8.** Left jaw plate, outer and inner views. Scale bar = 0.5 mm. **9–11.** Radula. **9.** General view; **10.** Detail of central and lateral teeth. Scale bars = 100 μm. **11.** Detail of lateral teeth, arrow indicating fifth lateral tooth. Scale bar = 50 μm. Abbreviations: **jw,** jaw; **mo,** mouth; **od,** odontophore; **ra,** radula; **rs,** radular sac.

cylindrical, broad; distal surface flattened, fully covered with small papillae; each papilla cylindrical, tip rounded; mouth central. Tentacles long (about twice snout length), narrow, tip rounded. Ommatophore with about ¼ of tentacle length and approximately with same width; located just posterior to tentacles; eyes dark, on ommatophore tips. Foot occupying about ⅔ of head-foot volume. Mesopodium constituting most of foot, outline somewhat triangular; sole flat, simple; anterior furrow of pedal glands bordered by thick margins, restricted anteriorly, not protruding beyond lateral edges. Epipodium divided into two apparently symmetrical lateral flaps, covering entire dorsal surface of mesopodium, from snout base to opercular pad; bearing eight pairs of long epipodial tentacles projecting about twice longer than epipodial width, each tentacle protruding on ventral but not on dorsal epipodial surface; each epipodial tentacle bearing papillae at ventral surface of basal region; papillae increasing in number and size toward middle tentacles; some epipodial tentacular papillae bifid at tip. Opercular pad with edges as continuation of epipodium. Columellar muscle thick, encompassing a half whorl.

Operculum: Circular, horny, multispiral; nucleus central; occupying entire shell aperture

Digestive System: Buccal mass somewhat larger than snout internal space. Buccal cavity having a pair of very large, dark-brown jaw plates, outline somewhat ellipti

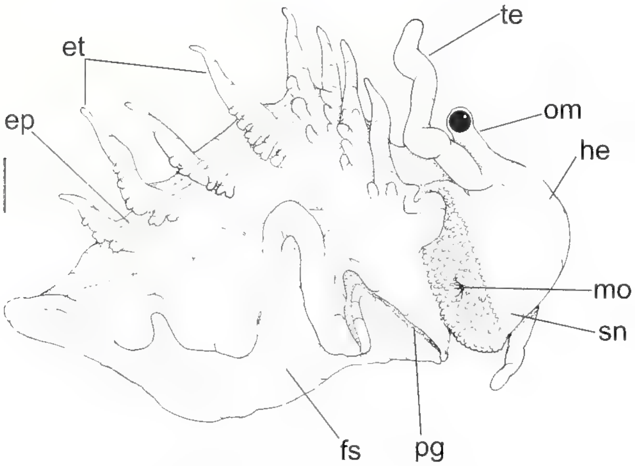


Figure 12. *Falsimargarita stephaniae* new species. Head-foot, ventral to slightly lateral right view, epipodium deflected upward. Scale bar = 1 mm. Abbreviations: **ep,** epipodium; **et,** epipodial tentacle; **fs,** foot (mesopodium) sole; **he,** head; **mo,** mouth; **om,** ommatophore; **pg,** anterior furrow of pedal glands; **sn,** snout; **te,** cephalic tentacle.

both jaws occupying most of dorsal and lateral surfaces of buccal cavity; posterior and lateral regions of jaws low, medial and anterior regions taller, with projected edges; series of small cusps present along anterior and medial edges, each cusp pointed and well separated from each other. Odontophore about half projected into buccal cavity. Radular ribbon about three times odontophore length; about half of radular ribbon projected beyond posterior end of odontophore.

Radula: Rachidian tooth encompassing about ¼ of radular ribbon width, triangular, narrowing somewhat abruptly, strongly curved over its own base; cutting edge sharply pointed, margins with very slender, elongated cusps. First to fourth lateral teeth long, slender, narrowing gradually, curved inward; distal half bearing edges with slender, elongated cusps; tip sharply pointed. Rachidian and four more central lateral teeth thin, flexible. Fiftieth lateral tooth thick, hook-like, curved inward; base broad, thick; distal region arched, resembling a thick scythe. Marginal teeth slender, tall, about 20 pairs per row, slightly broader toward medial region; base ruler-like, weakly curved inward; distal half sharpening gradually, with several slender, elongated cusps along edges about 25 pairs per tooth; tip sharply pointed.

Holotype: MORG 49650 (shell and operculum), MZSP 46559, diameter: 16.6 mm; height: 14.6 mm; includes re-hydrated soft parts and radula.

Type Locality: Argentina, off Islas Malvinas (45°S 58°W), 1200 m depth (fishing boat col., x/2004, Helen Racz leg.).

Distribution: Known only from type locality.

Etymology: The Latinized specific epithet honors the collector's mother, Ms. Teodora Stefania.

DISCUSSION

Although it has been recognized that definitions of generic boundaries in the Trochidae merits further revision, we are reasonably certain of its generic allocation of the new species, because the species possesses the conchological attributes reported in the Introduction for *Falsimargarita*.

There are two other genera also occurring in the South Atlantic Ocean that also exhibit iridescent shells, a character associated with the presence of thin outer shell layers. One of these genera is *Margarella* Thiele, 1893 (see Zelaya, 2004); the new species cannot be allocated into this genus because of its larger size, presence of thin shell wall, and absence of a parietal callus. The other genus is *Gaza* Watson, 1879; *Falsimargarita stephaniae* can not be included in *Gaza* given its taller shell, more rounded spiral whorls, and absence of a flap covering the umbilicus.

Additional comparisons and discussion about *Falsimargarita* is provided by Dell (1990: 93). At first glance, the new species could also be assigned to the Indo-Pacific genus *Otukaia* Ikebe, 1942; however, the new species has lower profile, more elaborate sculpture, and a more widely open umbilicus.

Falsimargarita stephaniae differs from the remaining congeneric species *F. iris* (Smith, 1915), *F. gemma* (Smith, 1915), *F. thielei* (Hedley, 1916), *F. georgiana* Dell, 1990 and *F. benticola* Dell, 1990) by having shouldered whorls, and by the strength of the spiral folds. The other species have a rounded whorl profile and a uniformity of spiral sculpture. Only *F. thielei* possesses differentiable spiral cords resembling those of *F. stephaniae*; however, *F. stephaniae* additionally differs from *F. thielei* by having a larger number of those outstandingly large spiral cords at the shell periphery and a taller spire.

The bathymetry is also a distinctive among *Falsimargarita* species. *Falsimargarita gemma, F. iris*, and *F. thielei* occur in depths to 400 m. *Falsimargarita benthicola* and *F. georgiana* are found in deeper waters around 3000 m, while *F. stephaniae* occurs at intermediary depths, around 1200 m.

Until the discovery of the new species, the only *Falsimargarita* known to occur in latitudes north of 50°S was *F. iris*, which reaches 35°S (Rosenberg, 2004). *Falsimargarita stephaniae* is the second species recorded for these latitudes.

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Notice

BIVALVIA 2006 - INTERNATIONAL CONGRESS ON BIVALVIA, BELLATERRA (BARCELONA), SPAIN, 22–27 JULY 2006

The congress, to be held at the Universitat Autònoma de Barcelona, calls together neontologists and palaeontologists with research interests in bivalve mollusks. Plenary talks include population genetics, evolution of ontogeny, evolutionary paleontology, biomineralization, and freshwater conservation biology, but contributions need not be restricted to these topics. In addition, there will be a planning session for a new bivalve treatise.

Two one-day excursions—one each on recent and fossil bivalves—will be organized.

Interested parties are asked to register and submit abstracts via the congress webpage http://bivalvia2006.uab.es.

Further inquiries may be directed to Niko Malchus (n.malchus@gmx.net). Please include in the subject line "Bivalvia 2006".

Notice

2006 MEETINGS OF THE AMERICAN MALACOLOGICAL SOCIETY AND THE WESTERN SOCIETY OF MALACOLOGISTS, SEATTLE, WASHINGTON, 29 JULY–3 AUGUST 2006

The 72nd annual meeting of the American Malacological Society and the 39th annual meeting of the Western Society of Malacologists will be held jointly in Seattle from 29 July–3 August 2006 under the coordination of AMS and WSM co-president Dr. Roland C. Anderson. The meeting's main venue will be the University of Washington. Reasonably priced housing will be available at the University dormitories and the University Inn Motel. The opening night reception will be held at the Burke Museum, located on campus, and the closing banquet will be at UW's University Club, also on campus. Thursday, 3 August, will be devoted to field trips.

The meeting will include three symposia: one on cephalopod behavior organized by Jennifer Mather of the University of Lethbridge, one on chitons organized by Douglas Eernisse of the California State University at Fullerton, and one on opisthobranchs organized by Sandra Millen of the University of British Columbia, Canada.

There will be a sale of malacological reprints to benefit the student fund of WSM and the traditional spirited auction of books and molluscan memorabilia (no shells) that will benefit the student funds of both organizations. Several notable items of cephalopod art have already been donated as well as a copy of R. T. Abbott's 2nd edition of American Seashells. Bring some of your reprints, books, and molluscan art to benefit this very worthy cause! Reprints and auction items can be sent to Roland Anderson at the address below.

For further information please contact AMS and WSM president:

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The sequence of sections should be: title page, abstract page, 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). The abstract page should contain the title and abstract, which should summarize in 250 words or less the scope, main results and conclusions of the paper. All references cited in the text must appear in the literature cited section and vice versa. In the literature cited section, all authors must be fully identified and listed alphabetically. 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 in the pagination. Tables must be numbered and each placed on a separate sheet. A brief legend must accompany each table. Captions for each group of illustrations should be typed on a separate sheet and include a key to all lettered labeling appearing in that group of illustrations.

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