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Note

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Recent eastern Pacific species of *Sanguinolaria* and *Psammotella* (Bivalvia: Psammobiidae)

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ABSTRACT

There are three Recent eastern Pacific species of *Sanguinolaria*, *S. ovalis* Reeve, 1857, *S. tellinoides* A. Adams, 1850, and *S. tenuis* Olsson, 1961, and one species of *Psammotella*, *P. bertini* (Pilsbry and Lowe, 1932). A neotype for *P. bertini* and lectotypes for *S. tellinoides* and its junior synonym *S. purpurea* are designated herein. The distributions of the species are documented, along with their fossil occurrences and their relationships to other Recent and to fossil species.

INTRODUCTION

Having discussed the eastern Pacific representatives of the genera *Heterodonax* (Coan, 1973: 46–46) and *Gari* (Coan, 2000), I herein complete the review of the family Psammobiidae with treatment of four species that have previously been assigned to the genus *Sanguinolaria*.

Previous reviews of *Sanguinolaria* are those of Reeve (1857) and Bertin (1880). Tryon (1869) listed the then-known species. Dall (1898, 1900: 978–979) and Willan (1993) discussed the genera of the Psammobiidae.

Thus far, there are no papers on the anatomy or biology of *Sanguinolaria* or *Psammotella*.

MATERIALS AND METHODS

In the following treatment, each valid taxon is followed by a synonymy, information on type specimens and type localities, notes on distribution and habitat, and an additional discussion.

The synonymies include all major accounts about the species, but not most minor mentions in the literature. The entries are arranged in chronological order under each species name, with changes in generic allocation from the previous entry, if any, and other notes given in brackets.

The distributional information is based on Recent specimens I have examined, except as noted. Habitat information is scant, because most material has been collected in beachdrift. Fossil occurrences are taken from the literature.

References are provided in the Literature Cited for all works and taxa mentioned.

Morphological Characters: A combination of shell shape and color, and various aspects of the shape of the pallial sinus suffice to distinguish among the four species discussed here; these are detailed in the descriptions and in Table 1.

Abbreviations: The following abbreviations are used in the text: ANSP, Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania, USA; BMNH, British Museum (Natural History) collection, The Natural History Museum, London, England; CAS, California Academy of Sciences, San Francisco, California, USA; ICZN, International Commission on Zoological Nomenclature; LACM, Natural History Museum of Los Angeles County, California, USA; PRI, Paleontological Research Institution, Ithaca, New York, USA; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; MNHN, Muséum national d'Histoire naturelle, Paris, France; SBMNH, Santa Barbara Museum of Natural History, Santa Barbara, California, USA; SDMNH, San Diego Museum of Natural History, San Diego, California, USA; UMML, University of Miami Marine Laboratory, Rosenstiel School of Marine and Atmospheric Science, Miami, Florida, USA; USNM, United States National Museum collection, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; ZMC, Zoologisk Museum Copenhagen, Denmark.

Material in the private collections of Carol C. Skoglund, Phoenix, Arizona, USA, and Kirstie L. Kaiser, Puerto Vallarta, Jalisco, Mexico, was also examined.

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Table 1. Key differentiating characters, size, and frequency of Eastern Pacific *Sanguinolaria* and *Psammotella*

	Color	Shape	Pallial sinus	Maximum size, mm	No. lots studied
S. ovalis	white, with pink beaks	equivalve, ovate, equilateral	greatly expanded, pointed dorsally, meets pallial line at approx. 50° angle	34	20
S. tellinoides	purplish red	equivalve, ovate-elongate, longer posteriorly	expanded dorsally, meets pallial line at 90° angle	72	79
S. tenuis	white	equivalve, ovate-elongate, longer anteriorly	greatly expanded, pointed dorsally, meets pallial line at approx. 75° angle	34	1
P. bertini	purplish red	right valve more inflated, elongate, longer posteriorly	elevated, rounded dorsally, meets pallial line at approx. 30° angle	93	98
				Total lots studied	198

SYSTEMATICS

Family Psammobiidae Fleming, 1828
Genus *Sanguinolaria* Lamarck, 1799

Sanguinolaria Lamarck, 1799: 84.
Type species (by monotypy): *Solen sanguinolentus* Gmelin, 1791: 3227.

Description: Equivalve, with a narrow posterior gape. Periostracum thin. Pallial sinus deep, moderately to very elevated dorsally, its dorsal line with an expanded muscle attachment area just anterior to posterior adductor. Posterior cruciform muscle scar without a small anterior satellite scar. Hinge narrow to moderate in width; teeth small; nymph weak.

Sanguinolaria ovalis Reeve, 1857
Figures 1, 2, 9

Sanguinolaria ovalis Reeve, 1857: pl. 1, fig. 2; Mörch, 1860: 185; Carpenter, 1864: 563 [1872 reprint: 49] [as a possible synonym of *S. miniata*]; Tryon, 1869: 78; Bertin, 1880: 84; Dall, 1898: 61 [as a synonym of *S. tellinoides*]; Keen, 1958: 188–189, fig. 460 [as a separate species]; Keen, 1971: 243, fig. 610: 244 [not to be confused with *Hiatula ovalis* Bertin, 1880: 92, pl. 4, fig. 5a, b, a species of *Soletellina* described from an unknown locality].

Sanguinolaria vespertina Pilsbry and Lowe, 1932: 90–91, 141 [as *Semele vespertina*], pl. 12, figs. 3–4; Hertlein and Strong, 1950: 220; Keen, 1958: 188 [as a synonym of *S.* [illegible]]; Olsson, 1961: 349, 558, pl. 85, fig. 5 [as a separate [illegible]]; Keen, 1971: 244 [as a synonym of *S. ovalis*]; [illegible] 41.

Description: [illegible] equivalve, thin, approximately equilateral [illegible] 48–50% from anterior end), anterior end [illegible] posterior end acutely rounded, without [illegible] Pallial sinus large, much extended and po[illegible] meeting pallial line at an approximately [illegible] adhering a short extent of non confluent [illegible] of line commarginal striae. Color pa[illegible] becoming white toward ventral margin [illegible] both exteriorly and interiorly. Length to 3[illegible] PRI 25921, Guánico, Panama.

Type Material and Localities:

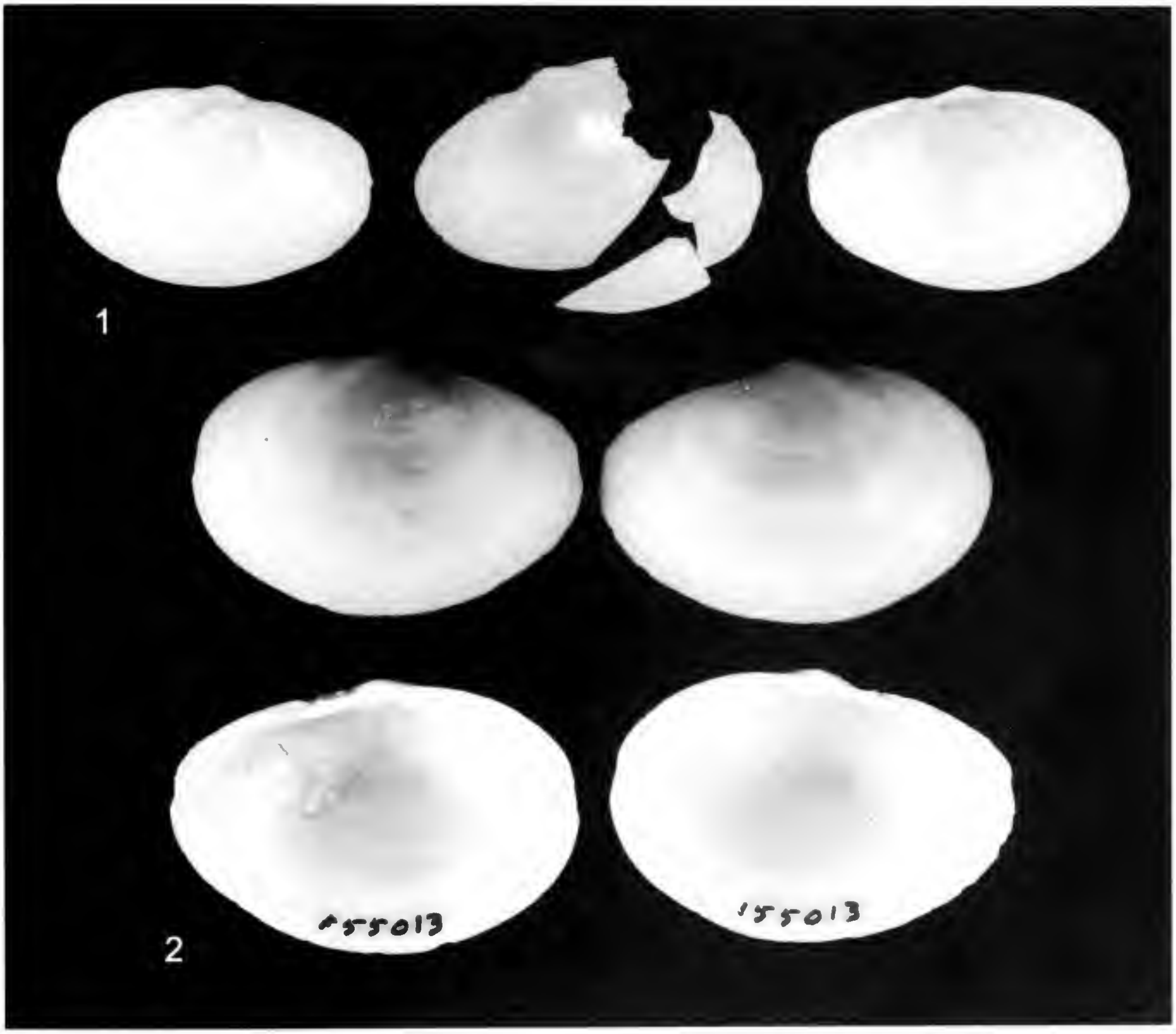
Sanguinolaria ovalis—BMNH 1957.7.15.1, holotype, with broken right valve; length, 22.2 mm; height, 14.0 mm; width (left valve), 3.1 mm (Fig. 1), "Central America", Hugh Cuming. **The locality is here clarified as being San Juan del Sur, Rivas Province, Nicaragua** (11.3°N), following ICZN *Code* Recommendation 76A.1.4.

Sanguinolaria vespertina—ANSP 155013, holotype, pair; length, 31.1 mm; height, 20.9 mm; width, 11.3 mm (Fig. 2). ANSP 398873, paratype; length, 26.4 mm. SDNHM 50773, paratypes, 6 pairs, 2 valves, San Juan del Sur, Rivas Province, Nicaragua (11.3°N), H.N. Lowe, 1931. ANSP 154663, paratype, left valve; length, 29.7 mm, Corinto, Chinandega Province, Nicaragua (12.5°N); H. N. Lowe, 1931.

Distribution: Guaymas, Sonora, México (27.9°N) [CAS 154369], to Guánico, Los Santos Province, Panama (7.2°N) [PRI 25921]; from the intertidal zone to 37.5 m. Material examined: 20 lots.

Material from the Golfo de Panamá that has been misidentified as this species [USNM 96283, 96287, 96353, 96361, 96383], or labeled as *Sanguinolaria sp.* [Kaiser collection], while closely resembling a *Sanguinolaria*, has conspicuous lateral teeth, a low, elongate pallial sinus, and slightly oblique commarginal sculpture. This material is instead *Tellina* (*Hertellina*) *nicoyana* Hertlein and Strong, 1949 (pp. 85–86, 97, pl. 1, figs. 23–26) (see also: Olsson, 1961: 409).

Discussion: This species is very similar to its western Atlantic homologue, *S. sanguinolenta* (Gmelin, 1791: 3225—as *Solen*) [synonyms: *Solen fucatus* Spengler, 1794: 111; *Tellina rubicunda* Röding, 1798: 186; *Sanguinolaria rosea* Lamarck, 1801: 125; *Lobaria rosacea* Schumacher, 1817: 122–123, pl. 6; *Sanguinolaria nivea* Mörch, 1853: 10], which occurs from Florida and Texas, through the West Indies to Brazil. *Sanguinolaria ovalis* differs in being more rounded and less pointed posteriorly, in having a narrower hinge plate and finer hinge teeth, and in not attaining as large a size (*S. sanguinolenta* can attain at least 43.4 mm in length). Additionally, the pallial sinus of *S. sanguinolenta* meets the pallial line at a 90° angle, and it does not rise as far dorsally, without



Figures 1, 2. *Sanguinolaria ovalis* Reeve. **1.** Holotype of *S. ovalis*, length 22.2 mm. **2.** Holotype of *S. vespertina* Pilsbry and Lowe, length 31.1 mm.

as sharp an angle at its summit (Figure 10). This western Atlantic species may also develop thicker shells than any eastern Pacific material of *S. ovalis*. *Sanguinolaria rosea* Lamarck is not preoccupied by *Solen roseus* Gmelin, 1791 (p. 3227), which was based on a figure in Chemnitz (1782: pl. 7, fig. 55) that seems to be a *Soletellina*. This species was attributed to the Red Sea by Bertin (1880: 98). It is also not preoccupied by *Tellina rosea* Gmelin, 1791 (p. 3238), which is based on an illustration in Knorr (1771: pl. 9, fig. 3) that may be of a specimen of *Asaphis deflorata* (Linnaeus, 1758: 687, as *Venus*).

Sanguinolaria vitrea Deshayes, 1855 (p. 326), described from an unknown locality (see also Reeve, 1857: pl. 1, fig. 4), has been suggested to be an additional synonym of *S. sanguinolenta*, one based on light-colored material (Cosel, 1989: 715). Cosel based this conclusion on two lots in the MNHN from Veracruz, Veracruz, Mexico. However, if material in the SBMNH (133229, 345687) and the CAS (152575) from near Veracruz is correctly identified as *S. vitrea*, this is a different species. Indeed, Dall (1898: 58) gave the distribution of *S. vitrea* as being from Texas to Colon, Panama, but this needs to be verified. The SBMNH and CAS material is white and translucent, with pallial sinuses that are not very dorsally extended and that meet the pallial line almost vertically (Figure 11); the largest specimen is 52.4 mm in length. The type lot of *S. vitrea* in the BMNH should be examined to be certain the species has been correctly interpreted.

Sanguinolaria aureocincta Martens, 1879 (p. 744

synonym *S. africana* Cosel, 1989: 714–715; pl. 1, fig. K, pl. 7, figs. 26, 27), is a similar West African species. A still earlier name that may apply to this species is *Tellina achatina* Spengler, 1798: 100.) In describing *S. africana*, Cosel (1989) differentiated it from *S. sanguinolenta* as being larger and more elongate, with less brightly colored beaks. These characters would also separate *S. aureotincta* from *S. ovalis*.

Sanguinolaria tellinoides A. Adams, 1850
Figures 3–6, 12

Sanguinolaria tellinoides A. Adams, 1850: 170, pl. 6, fig. 6; Reeve, 1857: pl. 1, fig. 3; Carpenter, 1857a: 286, 301; 1857b: 31; Mörch, 1860: 185; Carpenter, 1864: 563 [1872 reprint: 49]; Tryon, 1869: 78 [as "*S. tellinides*"]; Bertin, 1880: 84; Dall, 1898: 58; Hertlein and Strong, 1950: 219–220; Keen, 1958: 188, 189, fig. 162; Olsson, 1961: 348, 550, pl. 77, figs. 10, 11; Keen, 1971: 244, 245, fig. 611

Tellina miniata Gould, 1851: 90; 1853: 397, pl. 16, fig. 1; Gould and Carpenter, 1857: 199; Carpenter, 1857a: 226, 231, 245, 301; 1857b: 547 [in Appendix as a senior synonym of *S. purpurea*]; Mörch, 1860: 185 [as "*mineacea*" and a synonym of *S. tellinoides*]; Gould, 1862: 212; Carpenter, 1864: 537, 541, 543, 549, 563, 668 [1872 reprint: 23, 27, 29, 35, 49, 154]; Tryon, 1869: 78 [as a synonym of *S. tellinoides*]; Bertin, 1880: 84; Dall, 1898: 16 [as a synonym of *S. tellinoides*]; Hertlein and Strong, 1950: 219 [as a synonym of *S. tellinoides*]; Johnson, 1964: 110; Keen, 1971: 244 [as a synonym of *S. tellinoides*]

Sanguinolaria purpurea Deshayes, 1855: 346; Reeve, 1857: pl. 1, fig. 5; Gould and Carpenter, 1857: 199 [as a synonym of *S. miniata*]; Carpenter, 1857a: 226, 231, 245, 301, 352; 1857c: 31, 548; 1864: 563 [1872 reprint: 49]; Tryon, 1869: 78 [as a synonym of *S. tellinoides*]; Dall, 1898: 61 [as a synonym of *S. tellinoides*]; Hertlein and Strong, 1950: 219, 251, pl. 2, figs. 5, 8 [as a separate species]; Keen, 1958: 188, 189, fig. 161; Keen, 1971: 244 [as a synonym of *S. tellinoides*]

Sanguinolaria tellinoides elongata Mörch, 1860: 185; Hertlein and Strong, 1950: 220 [not preoccupied by *Gari* (*Psammotaena*) *elongata* (Lamarck, 1818: 514—as *Psammobia*), which is widespread in the Indo-Pacific (Willan, 1993: 61–64)]

Description: Ovate elongate, equivalve, somewhat thicker shelled than *S. ovalis* at a similar size, becoming thick [illegible] specimens; posterior end somewhat lon[illegible] [illegible] from anterior end); anterior end [illegible] somewhat produced, set off by [illegible] approximately two-thirds dis[illegible] [illegible] most evident in large speci[illegible] [illegible] ed and pointed dorsally, [illegible] its ventral margin thus [illegible] line (Figure 12). Sculp[illegible] [illegible] muscle scars [illegible] color pink to purple [illegible] radial color bands; inter[illegible] [illegible] length to 71.5 mm (ANSP [illegible] Mexico).

Type Material and Localities:

Sanguinolaria tellinoides—BMNH 1966540/1, pair, **lectotype here designated**; length, 32.6 mm; height, 19.2 mm; width, 8.4 mm (Figure 3). BMNH 1966540/2, paralectotype; length, 32.5 mm. Gulf of California. **The locality is here clarified as being Guaymas, Sonora, Mexico** (27.9°N), following ICZN *Code* Recommendation 76A.1.4.

Tellina miniata—MCZ 169258, holotype, pair; length, 51.0 mm; height, 33.0 mm; width, 14.3 mm (Figure 4). San Juan [del Sur, Rivas Province, Nicaragua] (11.3°N); Lieut. T. P. Green. The locality was mistakenly given by Johnson (1964: 110) as being in Orange County, California.

Sanguinolaria purpurea—BMNH 1966539/1, **lectotype here designated**, pair; length, 50.0 mm; height, 31.7 mm; width, 15.1 mm (Figure 5). BMNH 1966539/2, 3, paralectotypes, pairs, lengths, 48.4 mm, 44.4 mm. The original specimens came from the collection of Hugh Cuming, but the type locality was given as unknown and is **here clarified as being Guaymas, Sonora, Mexico** (27.9°N), following ICZN *Code* Recommendation 76A.1.4.

Sanguinolaria tellinoides elongata—ZMC unnumbered, holotype, pair; length, 52.4 mm; height, 30.2 mm; width, 13.3 mm (Figure 6). "Realejo" [Corinto, Chinendega Province, Nicaragua] (12.5°N); A. S. Oersted, 1846–1848.

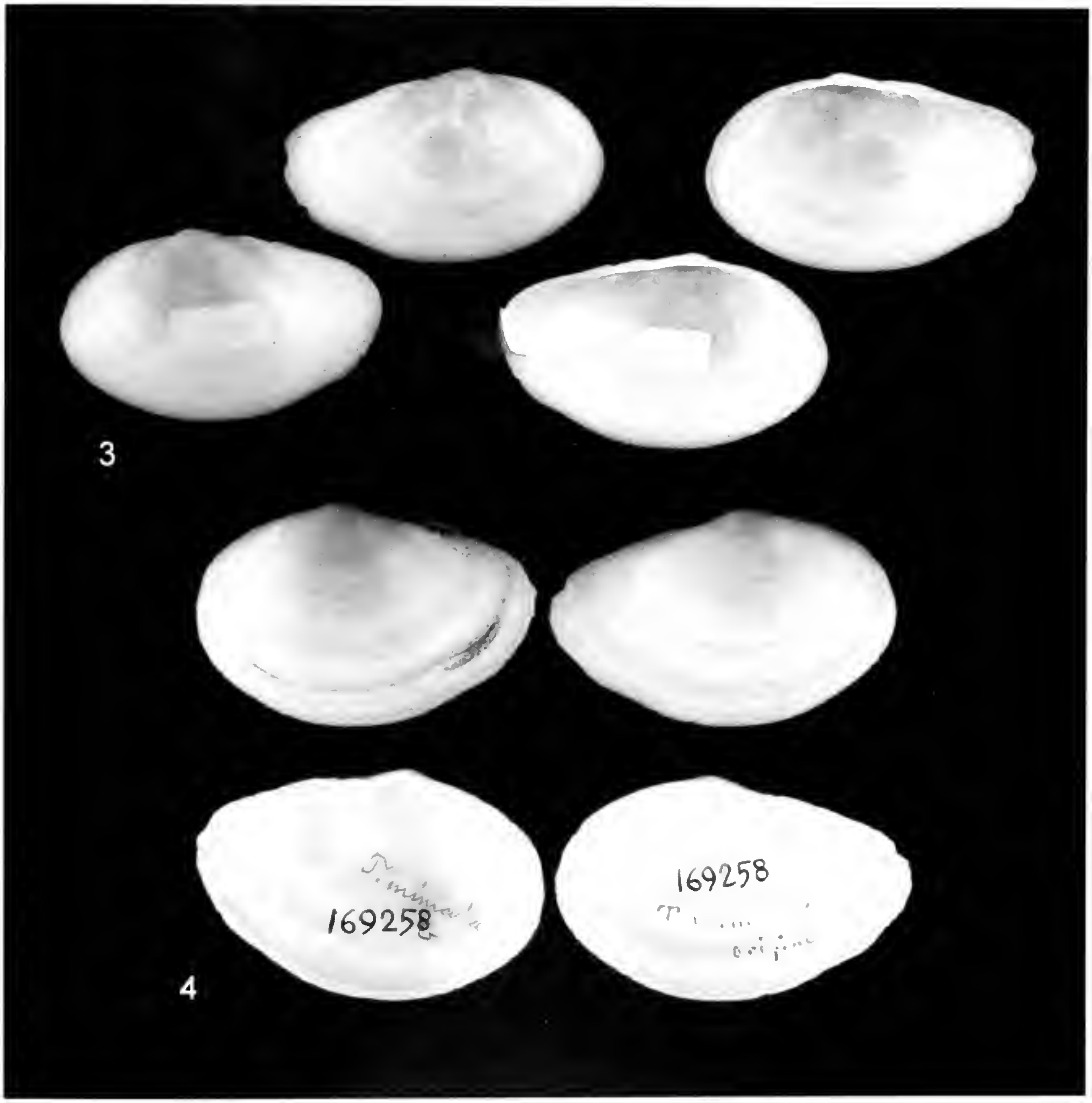
Distribution: Punta Pescadero, Pacific coast of Baja California Sur (23.3°N) [USNM 22964], into the Golfo de California as far north as Punta Diggs, Baja California (30.9°N) [CAS 150381], and Puerto Libertad, Sonora (29.9°N) [ANSP 184183], Mexico, to Cojimíes, Esmeraldas Province, Ecuador (0.4°N) [PRI 25920B]; intertidal zone to 14 m. Material examined: 79 lots. *Sanguinolaria tellinoides* has been reported from the Pliocene Jama Formation at Puerto Jama, Manabí Province, Ecuador (0.2°S) (Pilsbry and Olsson, 1941: 72), and (as "*aff.*") from the late Miocene Gatun Formation on the Atlantic coast of Panama west of Colón (Woodring, 1982: 673, pl. 115, fig. 12).

Discussion: The pallial sinuses of this species become more dorsally pointed in large specimens. This species can be distinguished from *Psammotella bertini* in being equivalve, and by its more rounded outline, less attenuate posterior end, and more dorsally extended and pointed pallial sinus.

Sanguinolaria tenuis Olsson, 1961
Figure 7, 13

Sanguinolaria tenuis Olsson, 1961: 349, 558, pl. 85, fig. 6; Keen, 1971: 244 [as a synonym of *S. ovalis*; not a homonym with *Psammobia tenuis* Deshayes, 1855: 320, a synonym of the Indo-Pacific *Gari anomala* (Deshayes, 1855: 320—as *Psammobia*) (Willan, 1993: 22), nor with *Soletellina tenuis* (Deshayes, 1855: 349—as *Capsa* (*Capsella*)) from the Philippine Islands (Willan, 1993: 77)]

Description: Ovate-elongate; equivalve; anterior end somewhat longer (beaks at 44% from anterior end); anterior end rounded; posterior end rounded, with a slight trace of a radial sulcus at two-thirds of way to posterior end. Pallial sinus large, extended dorsally, meeting pallial at an approximate 75° angle (Figure 13). Sculpture of

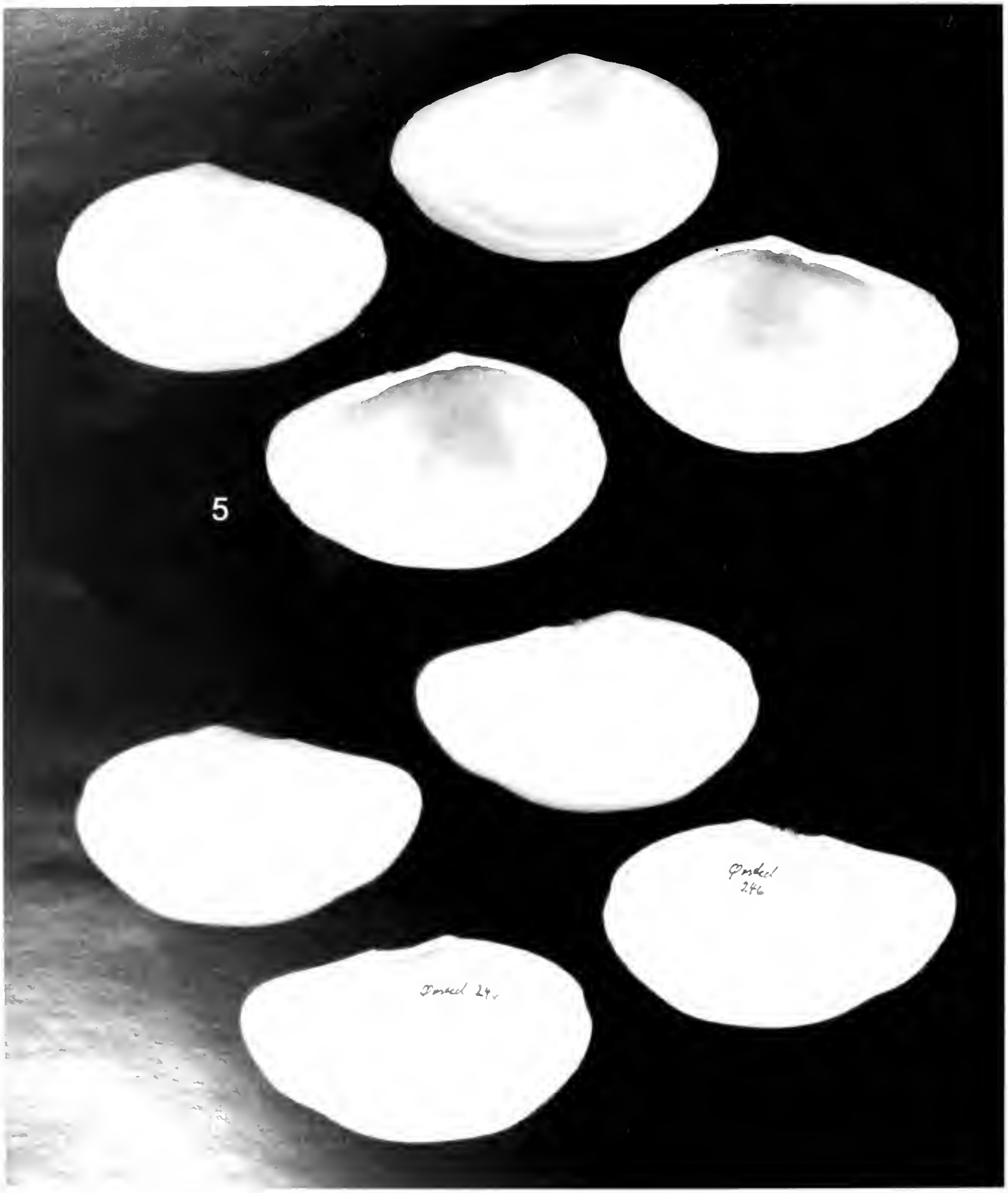


Figures 3, 4. *Sanguinolaria tellinoides* A. Adams. **3.** Lectotype of *S. tellinoides*; length 32.6 mm. **4.** Holotype of *Tellina miniata* Gould; length, 51.0 mm.

fine commarginal striae. Exterior color white, with a light pink radial band a little anterior of midline, white interiorly. Length to 33.8 mm (holotype).

Type Material and Locality: ANSP 218911, holotype, pair, length, 33.8 mm, height 26.1 mm, width 10.9 mm (Figure 7); Canoa, Manabí Province, Ecuador (0.5°N), A. A. Olsson, 1958. An additional fragmentary specimen cited by Olsson (1961) from Punta Montañita, Guayas Province, Ecuador (1°S), would be a paratype; it has not been located in the UMML. Unfortunately none of Olsson's specimens of *Sanguinolaria* have yet been located in the UMML (N. Voss, e-mail, 2–3 May 2001).

Distribution: Thus far known only from the original specimens (Canoa, Manabí Province (0.5°N) (holotype); presumably to Punta Montañita, Guayas Province (1°S) (specimen missing), Ecuador). Both specimens were collected in beachdrift.



Figs A. Adams. **5.** Lectotype of *S. purpurea* Deshayes, length 50.0 mm. **6.** Holotype of S.

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Figures 7, 8. **7.** *Sanguinolaria tenuis* Olsson, holotype, length 55.8 mm. **8.** *Psammotella bertini* Pilsbry and Lowe, neotype of *Tellina hanleyi* Bertin, length 67.5 mm.

Discussion: This is the rare South American ally of *S. ovalis*. It differs in not having rose-colored beaks, in being thicker shelled, and in having a more rounded posterior end.

Genus *Psammotella* Herrmannsen, 1852

Psammotella Herrmannsen, 1852: 114, *ex* "Psammotelle" Blainville, 1828: 541 [vernacular].

Type species (by monotypy): "*T. rufescens* Chemn.", = *Tellina rufescens* Dillwyn, 1817: 85, *ex* Chemnitz ms. = *Tellina cruenta* [Lightfoot], 1768: 40 [as *Tellina "cruentae"*], 58 [as *T. cruenta*]; first reviser: Rehder, 1967: 7. Recent, western Atlantic. [*non Psammotella* H. Adams and A. Adams, 1856: 393, *ex* Deshayes ms. = *Psammotellina* P.-H. Fischer, 1887: 1105, new name, a subgenus of *Gari* and perhaps a senior synonym of *Psammotaena* Dall, 1900: 976 (Willan, 1993: 60)].

Description: Shell inequivalve; right valve more inflated; posterior gape narrow. Pallial sinus deep, moderately elevated dorsally, without an expanded muscle attachment anterior to posterior adductor muscle scar. Posterior cruciform muscle scar with a small anterior satellite scar. Hinge moderately heavy; teeth small; nymph weak.

Discussion: I here rank this New World taxon as a genus because of its major differences from *Sanguinolaria*—conspicuous differences between left and right valves, plus differences in its pallial sinus and cruciform muscle scars.

Psammotella bertini (Pilsbry and Lowe, 1932)
Figures 8, 14

Tellina hanleyi Bertin, 1878: 268–269 [*non Tellina hanleyi* Dunker, 1853: 53–54, pl. 10, figs. 4–6].

Sanguinolaria bertini Pilsbry and Lowe, 1932, new name for *Tellina hanleyi* Bertin, 1880, *non* Dunker, 1853; Pilsbry and Lowe, 1932: 91, 143, pl. 10, figs. 7, 8. Hertlein and Strong, 1950: 220–221. Keen, 1958: 188, 189, fig. 459. Olsson, 1961: 349, 550, pl. 77, fig. 8. Keen, 1971: 244, [illegible] Hertz, 1986: 36.

[illegible] Chemnitz", *auctt.*, *non T. rufescens* Dillwyn, [illegible] Chemnitz ms.; Hanley, 1846: 307–308, 332, pl. [illegible] Carpenter, 1857b: 32. Römer, 1872: 111–112, [illegible] *Tellina rufescens* Dillwyn, 1817: 85, [illegible]

Desc[illegible] right valve conspicuously more [illegible] rior end longer (beaks at 40–48[illegible] terior end rounded, posterior en[illegible] radial sulcus near end in right valve, tip truncate; posterior end sinuous in right valve, tip subtruncate. Pallial sinus deep, its dorsal margin in right valve elevated, rounded to bluntly angular; ventral margin of sinus meeting pallial line at an approximate 30° angle, confluent with pallial line for approximately 75% of its length (Figure 14). Sculpture of fine, irregular commarginal striae, strongest on posterior slope; right valve with radial striae, strongest along ventral margin and in large specimens. Cruciform muscle scars bulbous in large specimens. Color pink to purple, sometimes with darker commarginal bands. Length to 92.8 mm (LACM 71-179.12, Punta Pequeña, Baja California Sur, Mexico).

Type Material and Locality: *Tellina hanleyi* Bertin was based on the figure of *Tellina rufescens* "Chemnitz" in Hanley (1846; see above), which presumably came from the only locality mentioned—Tumbes, Tumbes Province, Peru (3.5°S). This specimen has not been located in the BMNH (J. Pickering, e-mail, 7 June 2001), nor in the Leeds Museum, present location of a substantial amount Hanley's material (A. Norris, e-mail, 13 June 2001). The specimen selected by Pilsbry and Lowe (1932) as "holotype" of their new name—ANSP 152068 from Acapulco, Guerrero, Mexico (16.9°N) (Figure 8)—would normally have no type status, because the type of a renamed junior homonym remains the original type of that taxon (ICZN *Code* Art. 72.7). However, because (1) *Tellina rufescens* was long used to refer both to the western Atlantic species now known as *Psammotella cruenta* and to the eastern Pacific *P. bertini*, (2) we cannot ascertain which of these two species Hanley actually illustrated, (3) there is no good material of the eastern Pacific species in collections from Tumbes, Peru, and (4) Pilsbry and Lowe's "type" is a fine specimen long accorded type status, **this specimen is here designated neotype** of *Tellina hanleyi* Bertin. It is a pair of valves measuring 67.5 mm in length, 28.1 mm in height, and 12.4 mm in width.

Distribution: Laguna Ojo de Liebre [Scammon's Lagoon], Baja California Sur (27.8°N) [ANSP 225928], La Paz, Baja California Sur (24.2°N) [SBMNH 24586, 24587], and Empalme, Sonora (27.9°N) [SBMNH 135133], Mexico, to Máncora, Tumbes Province, Peru (4.1°S) [CAS 154370, SBMNH 125767], and evidently as far south as Colán, Piura Province, Peru (5.0°S) (Paredez and Cardozo ms: Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru); intertidal zone to 17 m. Material examined: 98 lots.

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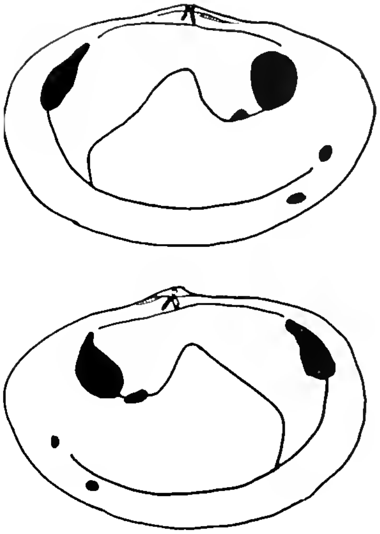
Figures 9–15. [illegible] of shells of *Sanguinolaria* and *Psammotella* showing hinge, pallial sinus, and adductor scars of left and [illegible] CAS 150375, Acapulco, Guerrero, Mexico, length 26.2 mm. **10.** *S. sanguinolenta* [illegible] Gmelin), CAS 152[illegible] Brazil, length 46.1 mm. **11.** *S. vitrea* Deshayes, CAS 152576, Boca del Río, Veracruz, Veracruz, Mexico, le[illegible] *ales* A. Adams, ANSP 220326, Acapulco, Guerrero, Mexico, length 44.5 mm. **13.** *S. tenuis* Olsson, holoty[illegible] *mmotella bertini* (Pilsbry and Lowe), CAS 150380; Acapulco, Guerrero, Mexico; length, 66.6 mm. **15.** *P.* [illegible] Panama Province, Panama, length 61.6 mm.



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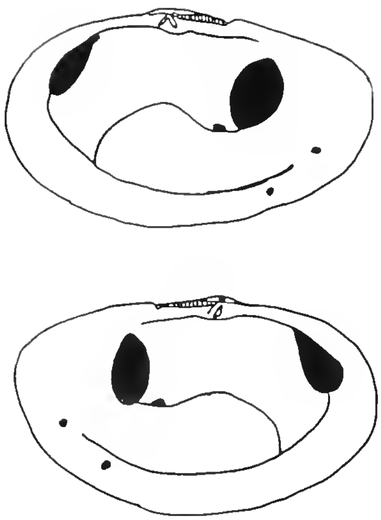

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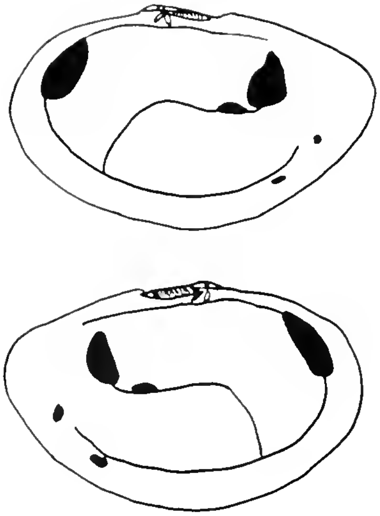

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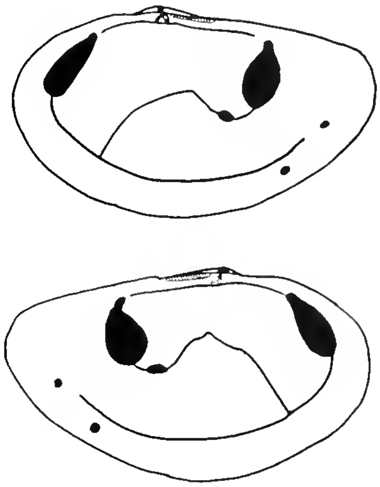

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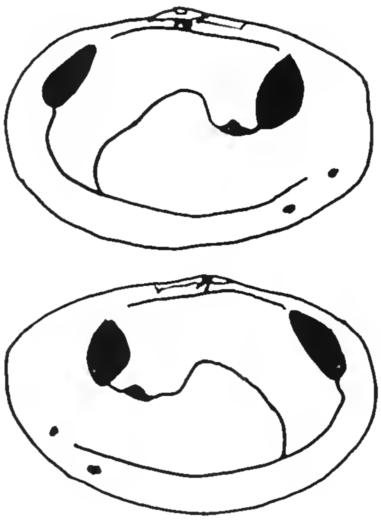

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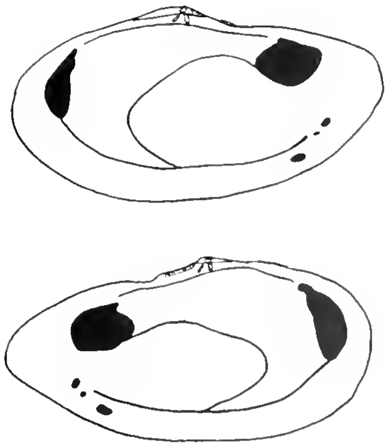

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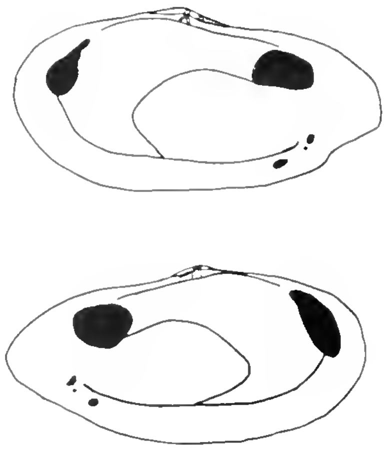

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Discussion: *Psammotella bertini* is very similar to its western Atlantic homologue, *P. cruenta* ([Lightfoot], 1786; see under genus [synonyms: *Tellina operculata* Gmelin, 1791: 3235 (as "*T. operculatas*" in Lugduni printing); *Tellina rufescens* Dillwyn, 1817: 85, *ex* Chemnitz ms]. The last synonym is *non T. rufescens* Gmelin, 1791: 3238, which was based on Gualtieri (1742: pl. 25, fig. C), seemingly a *Venerupis*, perhaps best regarded as one of the many synonyms of *V. decussatus* (Linnaeus, 1758, 690—as *Venus*), as suggested by Carpenter (1857b: 32). *Psammotella cruenta* occurs throughout the Caribbean to Brazil. *Psammotella cruenta* differs from *P. bertini* in being more inequilateral, with a flattener left valve and a more inflated right valve, and a less dorsally expanded pallial sinuses in both valves (Figure 15). Other supposed differences that have been suggested vary too much among populations to be useful. For example, Hertlein and Strong (1950) throught that *P. cruenta* is narrower posteriorly, but this does not seem to be the case if enough lots are studied. They also said that the pallial sinuses of *P. cruenta* were "more arched posteriorly" (?extending further posteriorly) and "confluent with the pallial line for a greater distance," but I can't see much difference in these parameters.

Psammotella smithwoodwardi (Maury, 1917: 393–394 [= 229–230], pl. 64 [= 38], figs. 1, 2—as *Sanguinolaria* (*Psammotella*)), from the late Miocene Cercado Formation of the Dominican Republic is presumably ancestral to these two species. Maury pointed out its affinity to *P. bertini*, but did not compare them. The original figures are insufficiently clear to see any differences from either Recent species. Weisbord (1964: 372) noted that this Miocene species differs from Recent material in lacking radial striae in the right valve.

Psammotella alonata Olsson (1922: 432–433 [= 260–261], pl. 32 [= 29], figs. 5, 6—as *Sanguinolaria* (*Sammotella*) [sic] from the late Miocene Gatun Formation at Banana Hill on the Atlantic coast of Costa Rica, was based on two poorly preserved valves. The species was said to be more elongate posteriorly than *P. cruenta* and to lack radial striae in the right valve. Weisbord (1964: 372–373) added that the anterodorsal margin of the right valve and the posterodorsal margin of the left valve were more concave than in *P. cruenta*. Both of these fossil species are thus far too poorly known to draw any useful conclusions.

For a comparison with *Sanguinolaria tellinoides*, see [illegible] species.

[illegible] D TAXA

[illegible] Conrad, 1837 (p. 231, pl. 17, [illegible] *nom. null.*), is a synonym of [illegible] 1758, 677 (as *Tellina*) of some authors, is a synonym of *Macoma balthica* (Linnaeus, 1758) (Coan et al., 2000: 417).

S. grandis Carpenter, 1857, *ex* Gould ms, a *nomen nudum* in Carpenter (1857a: 228, 349), is regarded as a probable synonym of *Nuttallia nuttallii* Conrad, 1837 (Coan et al., 2000: 426).

S. nuttallii Conrad, 1837 (pp. 230–231; pl. 17, fig. 6) is now placed as *Nuttallia nuttallii* (Conrad, 1837) (Coan et al., 2000: 426).

S. [illegible] is now regarded as a synonym [illegible] Conrad, 1837: 230–231, pl. 17, fig. [illegible]

S. fusca (Sa[illegible] *obia*) a combination

S. pacifica (Conrad, 1837: 241, pl. 18, fig. 13—as *Psammobia*) is a combination by some authors for the species now known as *Heterodonax pacificus* (Conrad, 1837) (Coan et al., 2000: 428).

S. rubroradiata Carpenter, 1860 (p. 1), *ex* Nuttall or Conrad ms, is a *nomen nudum* now regarded as a probable synonym of *Gari californica* (Conrad, 1849: 121) (Coan et al., 2000 426; Coan 2000: 3).

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LITERATURE CITED

Adams, A. 1850. Descriptions of new species of shells from the Cumingian collection. Proceedings of the Zoological Society of London for 1849 (200): 169–170, pl. 6 [reprinted in Annals and Magazine of Natural History (2)7(37): 69, 1851]

Adams, H. and A. Adams. 1856 [1853–1858]. The genera of Recent Mollusca; arranged according to their organization. Van Voorst, London [pp. 381–412, Nov. 1856]

Bertin, V. 1878. Révision des tellinidés du Muséum d'Histoire Naturelle. Nouvelles Archives Muséum national d'Histoire naturelle (2)1: 201–361, pls. 8, 9.

Bertin, V. 1880. Révision des garidées du Muséum d'Histoire Naturelle. Nouvelles Archives Muséum national d'Histoire naturelle (2)3: 57–129, pls. 4, 5.

Blainville, H. M. D. de. 1828. Tellina. F. G. Levrault, ed., Dictionnaire des Sciences Naturelles, ... 52: 528–559. Levrault, Strasbourg and Paris.

Carpenter, P. P. 1857a. Report on the present state of our knowledge with regard to the Mollusca of the west coast of North America. Report of the British Association for the Advancement of Science 26[for 1856]: 159–368 + 4 pp., pls. 6–9.

Carpenter, P. P. 1857b. Catalogue of the collection of Mazatlan Shells, in the British Museum: collected by Frederick Reigen. London (British Museum): xii + 552 pp. [some copies as i–iv + ix–xvi] [also published simultaneously as Catalogue of the Reigen Collection of Mazatlan Mollusca in the British Museum. Oberlin Press, Washington: viii + xii + 552 pp.] [reprinted: Paleontological Research Institution, 1967.]

Carpenter, P. P. 1860. Check lists of the shells of North America. Smithsonian Miscellaneous Collections 2(128): No. 1(a), West coast: Oregonian and Californian province, 4 pp; No. 2(b), West coast: Mexican and Panamic province, 13 pp.

Carpenter, P. P. 1864. Supplementary report on the present state of our knowledge with regard to the Mollusca of the west coast of North America. Report of the British Association for the Advancement of Science 33 [for 1863]: 517–686. [reprinted: Carpenter, 1872: 1–172.]

Carpenter, P. P. 1872. The mollusks of western North America. Embracing the second report made to the British Association on this subject, with other papers; reprinted by permission, with a general index. Smithsonian Miscellaneous Collections 10(252): xii + 325 + 13–121.

Chemnitz, J. H. 1782. Neues systematisches Conchylien-Cabinet 6. Nürnberg. 375 pp., 36 pls.

Coan, E. V. 1973. The northwest American Psammobiidae. The Veliger 16: 40–57, 4 pls.

Coan, E. V. 2000. The eastern Pacific Recent species of the bivalve genus *Gari* (Tellinoidea: Psammobiidae), with notes on western Atlantic and fossil taxa. Malacologia 42: 1–29.

Coan, E. V., P. Valentich Scott and F. R. Bernard. 2000. Bivalve seashells of western North America. Marine bivalve mollusks from Arctic Alaska to Baja California. Santa Barbara Museum of Natural History Monograph 2. Santa Barbara. viii + 764 pp.

Conrad, T. A. 1837. Descriptions of new marine shells from Upper California, collected by Thomas Nuttall, Esq. Journal of the Academy of Natural Sciences of Philadelphia 7: 227–268, pls. 17–20.

Conrad, T. A. 1849. Description of two new genera and new species of Recent shells, &c. Proceedings of the Academy of Natural Sciences of Philadelphia 4[for 1848–1849]: 6: 121.

Cosel, R. von. 1989. Taxonomy of tropical west American bivalves. II. Psammobiidae. Bulletin Muséum national d'Histoire naturelle (A)(4)11(4): 693–731, pls. 1–7.

Dall, W. H. 1898. Synopsis of the Recent and Tertiary Psammobiidae of North America. Proceedings of the Academy of Natural Sciences of Philadelphia 50 [for 1898]: 57–62.

Dall, W. H. 1900. Contributions to the Tertiary fauna of Florida, with especial reference to the silex beds of Tampa and the Pliocene beds of the Caloosahatchie River, including in many cases a complete revision of the generic groups treated of and their American Tertiary species. Part V. Teleodesmacea: *Solen* to *Diplodonta*. Transactions of the Wagner Free Institute of Science of Philadelphia 3(5): 949–1218, pls. 36–47.

Deshayes, G. P. 1855. Descriptions of new shells from the collection of Hugh Cuming, Esq. Proceedings of the Zoological Society of London for 1854 22[279]: 317–320; [280]: 321–336; [281]: 337–352; [282]: 353–368; [283]: 369–371.

Dillwyn, L. W. 1817. A descriptive catalogue of Recent shells, arranged according to the Linnaean method ... John and Arthur Arch, London. xii + 1092 + 29 pp., 5 pls.

Dunker, W. B. R. H. 1853. Index molluscorum, quae in itinere ad Guineam inferiorum collegit Georgius Tams Med. Dr. Fischer, Cassells. vi + 74 pp., 10 pls.

Fischer, P. H. F. 1887 [1880–1887]. Manuel de conchyliologie et de paléontologie conchyliologique ou histoire naturelle des mollusques vivants et fossiles ... Savy, Paris. xxiv + 1369 pp., 23 pls. [pp. 1009–1369, June 1887].

Fleming, J. 1828. A history of British animals, exhibiting the descriptive characters and systematical arrangement of the genera and species of quadrupeds, birds, reptiles, fishes, Mollusca, and Radiata of the United Kingdom ... Bell and Bradfute, Edinburgh, and Duncan, London. xxiii + 565 + [1] pp.

Gmelin, J. F. 1791. Caroli a Linné ... Systema naturae per regna tria naturae ... editio decima tertia, aucta, reformata 1(6). Beer, Leipzig. pp. 3021–3910.

Gould, A. A. 1851. Descriptions of a number of California shells, collected by Maj. William Rich and Lieut. Thomas P. Green, United States Navy. Proceedings of the Boston Society of Natural History 4: 87–93.

Gould, A. A. 1853. Descriptions of shells from the Gulf of California and the Pacific coasts of Mexico and California. Boston Journal of Natural History 6(3): 374–408, pls. 14–16.

Gould, A. A. 1862. Otia conchologica: descriptions of shells and mollusks from 1839 to 1862. Gould and Lincoln, Boston. [ii] + 256 pp.

Gould, A. A. and P. P. Carpenter. 1857. Descriptions of shells from the Gulf of California, and the Pacific coasts of Mexico and California. Part II. Proceedings of the Zoological Society of London for 1856 24[313]: 198–208.

Gualtieri, N. 1742. Index testarum conchyliorum quae adservantur in Museo N. Gualtieri ... et methodice distributae exhibentur tabulis ... xxiii + 110 pls.

Hanley, S. C. T. 1846. Monograph of the genus *Tellina*. G. B. Sowerby II, ed., Thesaurus conchyliorum, or monographs of genera of shells 1(6): 221–336, pls. 56–66.

Herrmannsen, A. N. 1852. Indicis generum malacozoorum supplementa et corrigenda. Fischer, Cassells. v + 140 pp.

Hertlein, L. G. and A. M. Strong. 1949. Eastern Pacific expeditions of the New York Zoological Society. XL. Mollusks from the west coast of Mexico and Central America. Part VII. New York Zoological Society, Zoologica 34(2): 63–97, 1 pl.

Hertlein, L. G. and A. M. Strong. 1950. Eastern Pacific expeditions of the New York Zoological Society. XLII. Mollusks from the west coast of Mexico and Central America. Part IX. New York Zoological Society, Zoologica 35(4): 217–252, 2 pls.

Hertz, C. M. 1986. Herbert Nelson Lowe 1880–1936. A gifted amateur malacologist from southern California. The Festivus 18(3): 26–43.

Hinds, R. B. 1842. Descriptions of new shells. Annals and Magazine of Natural History (2)10(63): 81–84, pl. 6.

Johnson, R. I. 1964. The Recent Mollusca of Augustus Addison Gould. Bulletin of the United States National Museum 239: 1–182, pls. 1–45.

Keen, A. M. 1958. Sea shells of tropical west America: marine mollusks from Lower California to Colombia, 1st edition. Stanford University Press, Stanford. xii + 624 pp., 10 pls. [repr. 1960].

Keen, A. M. 1971. Sea shells of tropical west America: marine mollusks from Baja California to Peru, 2nd edition. Stanford University Press, Stanford. xiv + 1064 pp., 22 pls. [repr. 1984 with only 12 pls.]

Knorr, G. W. 1769–1771. Vergnügen der Augen und des Gemüths in Vorstellung einer allgemeinen Sammlung von Schnecken und Muscheln und andern Geschöpfen welch in Meer gefunden werden. Nürnberg. Vol. 4: 48 + 14 pp., 30 pls., 1769; vol. 5: 46 + 13 pp., 30 pls., 1771.

Lamarck, J. B. P. A. de M. de. 1799. Prodrome d'une nouvelle classification des coquilles. Mémoires de la Société d'Histoire Naturelle de Paris 1: 63–90.

Lamarck, J. B. P. A. de M. de. 1801. Système des animaux sans vertèbres, ou tableau général des classes, des ordres et des genres de ces animaux: . . . . Chez l'auteur and Deterville, Paris. viii + 432 pp.

Lamarck, J. B. P. A. de M. de. 1818. Histoire naturelle des animaux sans vertèbres, . . . Verdière, Deterville and chez l'auteur, Paris. 612 pp.

Lightfoot, J. | 1786. A catalogue of the Portland Museum, lately the property of the Duchess Dowager of Portland, deceased: which will be sold at auction, by Mr. Skinner and Co. . . . London. viii + 3–194 pp. [concerning: Rehder, 1967].

Linnaeus, C. 1758. Systema naturae per regna tria naturae . . . editio decima, reformata. Vol. 1. Animalia. L. Salvii, Stockholm, 824 + iii pp.

Martens, K. E. von. 1879. Übersicht der von Herrn W. Peters von 1843 bis 1847 in Mossambique gesammelten Mollusken. Monatsberichte der Königlichen Preussischen Akademie der Wissenschaften zu Berlin for 1879: 727–749.

Maury, C. J. 1917. Santo Domingo type sections and fossils. Bulletins of American Paleontology 5(29–30): 165–459 [illegible] 1–252, 1–43], pls. 27–65 [= 1–39].

Mö[illegible] O. A. L. 1853. Catalogus conchyliorum quae reliquit D. Alphonso d'Aguirra & Gadea Comes de Yoldi, . . . Vol. 2. Acephala, Annulata, Cirripedia, Echinodermata. Klein, H[illegible] 76 pp.

[illegible] 1859–1861. Beiträge zur Molluskenfauna [illegible] Amerikas. Malakozoologische Blätter 6(4): [illegible] 7(2): 66–96, (3): 97–106, (4): 170–192 [illegible] 1861].

Ol[illegible] Miocene of northern Costa Rica with [illegible] stratigraphic relations. Bulletins of American Paleontology 9(39): 1–309 [= 173–481], pls. 4–35 pls. [= 1–32].

Olsson, A. A. 1961. Mollusks of the tropical eastern Pacific particularly from the southern half of the Panamic-Pacific faunal province (Panama to Peru). Panamic-Pacific Pelecypoda. Paleontological Research Institution, Ithaca. 574 pp., 86 pls.

Pilsbry, H. A. and H. N. Lowe. 1932. West Mexican and Central Americana mollusks collected by N. N. Lowe, 1929–31. Proceedings of the Academy of Natural Sciences of Philadelphia 84: 33–144, pls. 1–17.

Pilsbry, H. A. and A. A. Olsson. 1941. A Pliocene fauna from western Ecuador. Proceedings of the Academy of Natural Sciences of Philadelphia 93 [for 1941]: 1–79, pls. 1–19.

Reeve, L. A. 1857. Monograph of the genus *Sanguinolaria*. L. A. Reeve, ed. Conchologia iconica: or, illustrations of the shells of molluscous animals 10. 1 pl.

Rehder, H. A. 1967. Valid zoological names of the Portland catalogue. Proceedings of the United States National Museum 121 (3579): 51 pp.

Röding, P. F. 1798. Museum Boltenianum . . . pars secunda contiens conchylia sive testacea univalvia, bivalvia & multivalva. Trappii, Hamburg. viii + 109 pp.

Römer, H. C. 1872 [1841–1873]. Die Familie der Tellmuscheln, Tellinidae. Systematisches Conchylien-Cabinet von Martini und Chemnitz 10(4): 292 pp., 52 pls. Bauer and Raspe, Nürnberg [pls. 1–3, first issue, 1841, by H. C. Küster; pp. 1–32, pls. 4–6, 8, 10, 16, 1870; pp. 33–176, pls. 7, 9, 11–15, 17–33, 1871; pp. 177–256, pls. 34–38, 40–52, 1872; pp. 257–291, pl. 39, 1873].

Say, T. 1822. An account of some of the marine shells of the United States. Journal of the Academy of Natural Sciences of Philadelphia 2(2): 221–248, 257–276, 302–325.

Schumacher, C. F. 1817. Essai d'un nouveau système des habitations de vers testacés. Schultz, Copenhagen. [iv] + 287 pp., 22 pls.

Spengler, L. 1794. Noiere bestemmelse og udvidelse af det Linneiske genus *Solen*. Skrivter af Naturhistorie Selskabet 3(2): 81–114.

Spengler, L. 1798. Over det toskallede slaegt tellinerne. Skrivter af Naturhistorie Selskabet 4(2): 67–121, pl. 12.

Tryon, G. W., Jr. 1869. Catalogue of the family Tellinidae. American Journal of Conchology 4(5) [Appendix]: 72–126.

Weisbord, N. E. 1964. Late Cenozoic pelecypods from northern Venezuela. Bulletins of American Paleontology 45(204): 564 pp., 59 pls.

Willan, R. C. 1993. Taxonomic revision of the family Psammobiidae (Bivalvia: Tellinoidea) in the Australian and New Zealand region. Records of the Australian Museum, Supplement 18: 1–132.

Woodring, W. P. 1982. Geology and paleontology of Canal Zone and adjoining parts of Panama. Description of Tertiary mollusks (pelecypods: Propeamussiidae to Cuspidariidae; additions to families covered in P 306-E; additions to gastropods; cephalopods). United States Geological Survey Professional Paper 306F: iv + 541–759, pls. 83–124.

The anatomy and functional morphology of *Tivela ventricosa* (Gray, 1838) (Bivalvia: Veneridae)

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ABSTRACT

A detailed study of shell, organs of the mantle cavity, siphons, and digestive tract of *Tivela ventricosa* is presented, and followed by comparisons with other species of *Tivela*. *Tivela ventricosa* occurs from Espírito Santo State in Brazil to La Paloma in Uruguay. Individuals live in sandy bottoms exposed to pounding surf, where usually a large amount of material in suspension is present. The anatomy and functional morphology of *T. ventricosa* are compared with those of congeneric species occurring off the coast of southeastern Brazil. The siphons of *T. ventricosa* are of type B of Yonge, the ctenidia of type C-1 of Atkins, the relation between the labial palps and the ctenidia belong to category II of Stasek, and the stomach to type V of Purchon.

INTRODUCTION

The Veneroidea is a large superfamily of bivalves that has radiated broadly worldwide, typically into soft, usually intertidal sediments. The genus *Tivela* Link, 1807, occurs on the Atlantic and Pacific coasts of the American continent (Abbott, 1974; Coan et al., 2000).

Isolated references to *Tivela ventricosa* (Gray, 1838) are found mainly in regional checklists (Lange de Morretes, 1949; Gofferjé, 1950; Buckup, 1957; Rios, 1970, 1975, 1985, 1994), but there are no reports on the functional morphology of the species. *Tivela ventricosa* occurs from southeastern Brazil to Uruguay (Rios, 1994). Along the Brazilian littoral, the species is recorded in the states of: Espírito Santo (Rios, 1970), Rio de Janeiro (Rios, 1970), São Paulo (Rios, 1970), Paraná (Gofferjé, 1950; Rios, 1970) and Rio Grande do Sul (Buckup, 1957; Rios, 1970, 1994). The species was recorded by Rios (1970, 1975, 1985, 1994) from the littoral of Uruguay and Broggi (1970) collected fossil representatives of the species from the Querandino Formation, Uruguay, and described the distribution of the living animal from Santos (Brazil) to La Paloma, Rocha (Uruguay). *Tivela ventricosa* was not recorded by Carcelles (1944) and Carcelles and Williamson (1951) from the coast of Argentina.

Although not sold in the commercial seafood markets, the species is an important food item for coastal populations, tourists, and campers on the coast of São Paulo State, Brazil. The main goal of the present paper is to provide basic information on the anatomy and some aspects of the biology of the species.

MATERIALS AND METHODS

Living specimens of *T. ventricosa* (Figure 1) were collected on the intertidal region of beaches in the localities of São Vicente, Bertioga, and Ubatuba, all on the coast of São Paulo, Brazil. Specimens were found buried at depths of approximately 5 cm in sand or muddy-sand substrates, in areas with strong disturbance of bottom deposits, which end up suspended in large amounts in the water column. Specimens were collected during low tide, when they could be detected, at the surface of the substrate, by a little circular mound deposited around the tips of the siphons. Some of the study animals were kept alive up to 4 months.

Drawings were made from relaxed and preserved specimens. Magnesium sulphate was used as a relaxing agent. Ciliary currents were studied with the use of Carborundum, carmine suspensions, or suspensions of Aquadag. Organs and tissues were fixed in Bouin's fluid, and sections 6–8 μm in thickness stained with Ehrlich's haematoxylin and eosin, Azan, and Mallory's triple stain.

Voucher specimens are deposited in the Museu de Zoologia, Universidade de São Paulo, MZSP 32948, 32949.

RESULTS

Shell (Figures 2–4): The shell of *T. ventricosa* is equivalve, equilateral, trigonal, with subcentral umbo

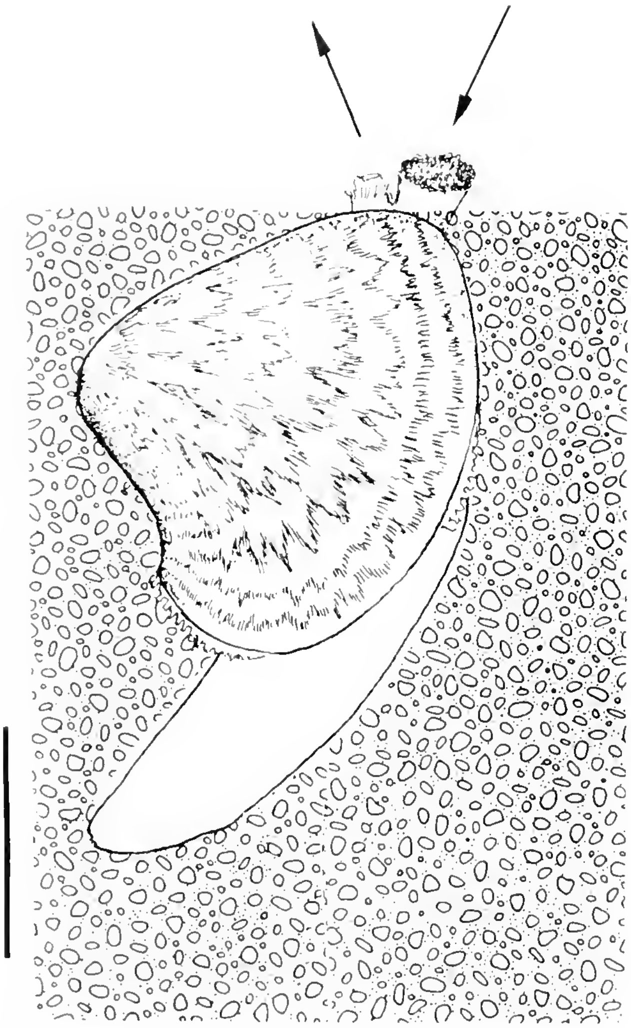

Figure 1. *Tivela ventricosa.* Animal in natural habitat; external view from the left side. Arrows show the direction of the incurrent and excurrent currents. Scale line = 2 cm.

nes and beaks located close to each other. The external surface is smooth, overlaid by a thick, glossy periostracum which gives a varnished appearance to the shell valves. The external color is cream with a variable pattern of radial or zigzag brown streaks (Figure 2). Some [illegible] show alternating unequal rays of straw and [illegible] color, with the ray color on the right valve [illegible] than that on the left. The interior and [illegible] of the shell have a smooth white surface. [illegible] pallial sinus is short, oblique, U-shaped. The [illegible] adductor muscle is oval and more [illegible] posterior one, which is almost circular [illegible]. The hinge is strong, with 3 well [illegible] teeth in each valve (Figure 4). The [illegible] however blade-like; the anterior and [illegible] with the posterior one coarsely [illegible] like anterior lateral tooth on the left [illegible] a deep depression on the right valve. A [illegible] rior dorsal margin of the right valve there is a large groove and a smaller groove is present on the anterior dorsal margin of the left valve. The shell of the largest studied specimen measured 7.9 cm in length, 7.4 cm in height and 5.2 cm in width.

Siphons (Figures 5, 6): The siphons are short and fused at the base. They are formed by fusion of the inner fold with the internal surface of the middle fold of the mantle margin. The aperture of the incurrent siphon is surrounded by branched tentacles, and that of the excurrent siphon has a tapered siphonal membrane with simple tentacles at the basal region.

The incurrent siphon (Figures 5, 6) has about 200 tentacles deployed in 5 sets surrounding the aperture. The tentacles are directed toward the aperture when the animal is pumping water in, which allows for sieve-like trapping of particles. The most external set consists of small, digitiform tentacles, some of which display a bifurcated tip. The four internal sets consist of branched tentacles that decrease in number and increase in length in each succeeding set toward the internal region of the siphonal opening. A U-shaped pigmented dark band is present at the base of the group of three most internal sets of tentacles. The incurrent siphon is very sensitive to touch and vibrations and withdraws in part or completely upon stimulation.

The excurrent siphonal aperture (Figure 6) is smaller than the incurrent siphonal aperture. About 48 simple, external tentacles of milky-white color surround the base of the siphonal membrane. These tentacles are pigmented at their bases.

Siphonal Membranes (Figure 7): A pair of siphonal membranes is present at the basal opening of the incurrent siphon; these membranes contribute to regulate the water flow into the pallial cavity. Two other additional siphonal folds are present and united at the dorsal side of the incurrent siphonal opening; they continue ventrally and in anterior direction as expansions of each mantle lobe.

Organs of the Mantle Cavity (Figures 8, 9): Removal of the left shell valve and respective mantle lobe exposes the organs in the mantle cavity (Figure 8). The ctenidia are dorsally located. The inner demibranch is larger than the outer one; this latter bears a supraxial extension. The inner mantle surface is covered with short cilia, except in a narrow border on its free edges. The mantle edges are fused for a short extension anterior to the incurrent siphon. Dorsally to these fused ventral margins, the highly mobile additional siphonal membranes delimit a canal. The free edge of the mantle has 4 folds and a large number of ramified tentacles, those in the proximal and distal regions of the pedal gape divided into secondary and tertiary branches. These short, simple tentacles may also be absent in the median region of the pedal gape. When the animal is resting, the tentacles on the left side alternate with those on the right side, so that they prevent sand grains from entering the

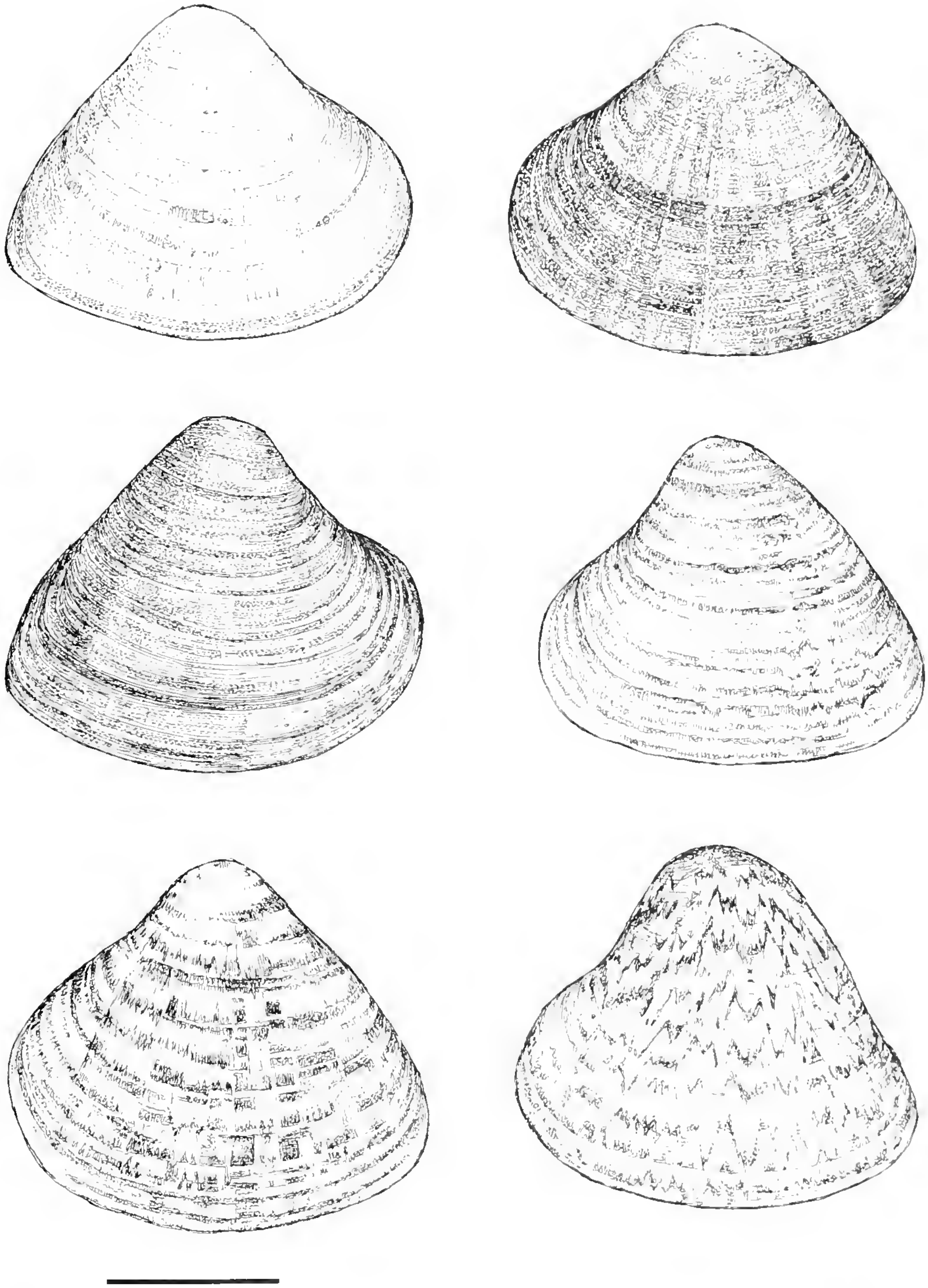

Figure 2. *Tivela ventricosa.* External view of shell valves showing variation in color pattern. Scale line = 2 cm.

mantle cavity. When the foot is protruded, the tentacles touch all its sides, forming a protective lattice-like structure around it.

Ciliary currents on a wide area of the mantle surface are ventrally directed toward two main rejection tracts, one on each ventral margin of the mantle lobes. The main rejection tracts drive and accumulate pseudofaeces into the ventral canal; this latter protects undesirable material from being washed back into the mantle chamber (Figure 9). Upon accumulation of a given amount of pseudofaeces, the adductor muscles suddenly contract to push water out of the mantle cavity causing the siphonal membranes to open and allowing pseudofaeces to be eliminated through the incurrent siphon.

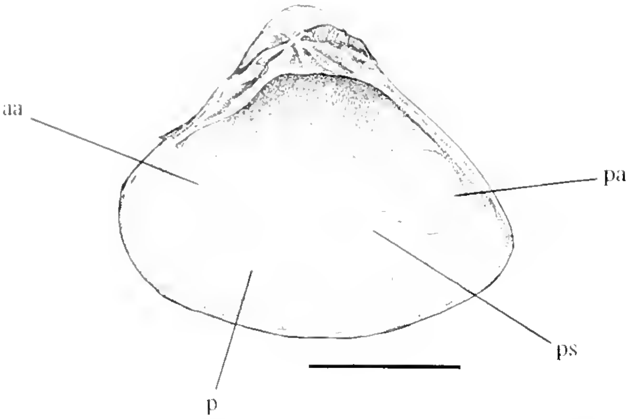

Figure 3. *Tivela ventricosa.* Internal view of the right shell valve, showing the pallial sinus and the scars of the adductor muscles; *aa*, anterior adductor muscle scar; *p*, pallial line; *pa*, posterior adductor muscle scar; *ps*, pallial sinus. Scale line = 3 cm.

Musculature: The anterior adductor muscle is larger than the posterior one. The anterior pedal retractor muscles are inserted into the shell valve posterior to and at a short distance from the anterior adductor muscle. Some of its fibers spread superficially into the anterior and dorsal region of the foot, while most spread in posterior direction; these latter have their extremities in the foot internally to the fibers coming from the posterior pedal retractor muscle. Distally, within the foot, the fibers from both sides join together.

The posterior pedal retractor muscles are inserted in the shell valve in anterior direction and dorsally to the posterior adductor muscle. The retractor muscles on each side unite under the pericardium, where bundles of fibers from the right muscle cross with those from the left one. Where the muscles enter the foot, their bundles once more diverge and their fibers radiate in anterior direction and ventrally into the foot.

The pedal retractor muscles constitute the extrinsic musculature of the foot. In addition to the extrinsic musculature, a varying amount of intrinsic musculature is also present in the proximal and distal portion of the foot. Immediately below the epithelium of the visceral mass in the proximal part of the foot there are circular muscle strands that run in antero-posterior direction and completely surround the visceral mass. The distal free part of the foot is packed with bundles of fibers running transversally, the same occurring in the visceral mass, where transverse fibers are less numerous.

Foot: The foot is large, wedge-shaped, and laterally compressed, which facilitates burrowing in relatively soft substratum, where it digs with rhythmic movements. A

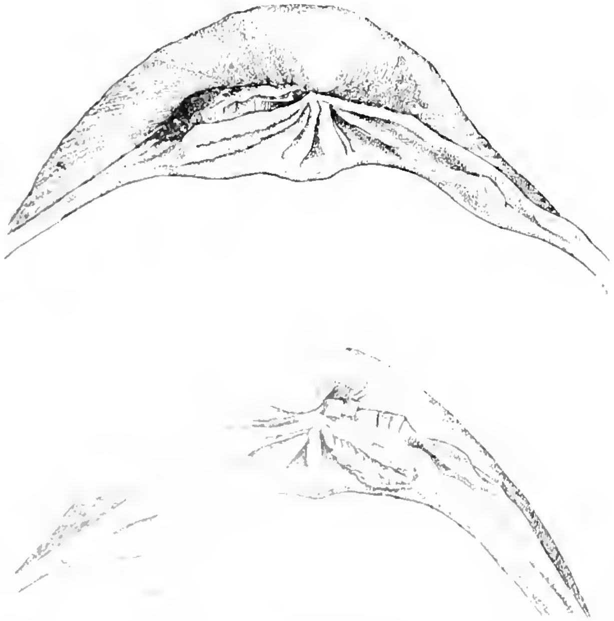

Figure 4. [illegible] d views of the shell valves [illegible] bottom right valve. Scale line [illegible]

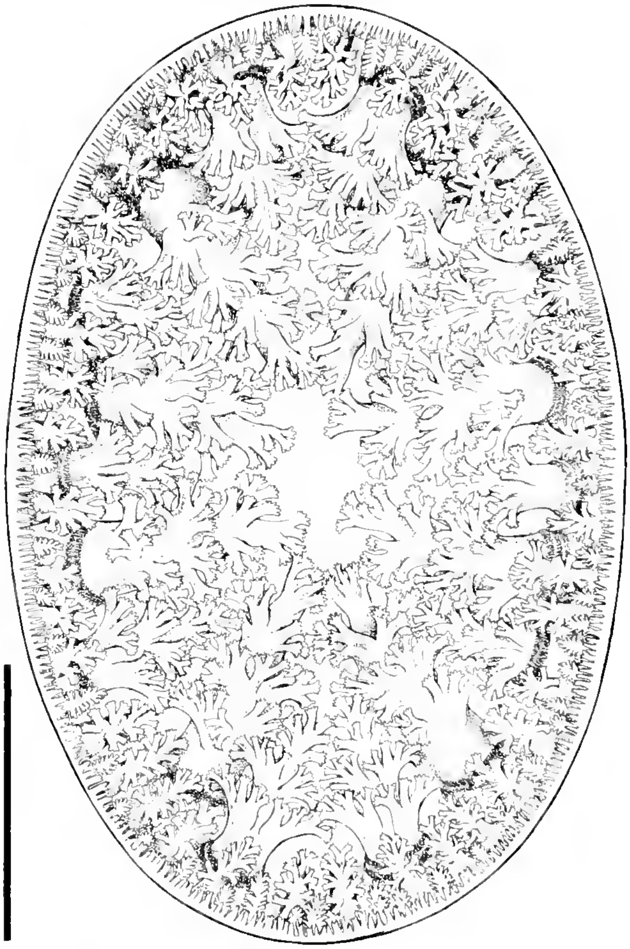

Figure 5. *Tivela ventricosa.* Fully extended incurrent siphon projecting out of the shell valves, showing the intricate disposition of the branched tentacles. Scale line = 0.2 cm.

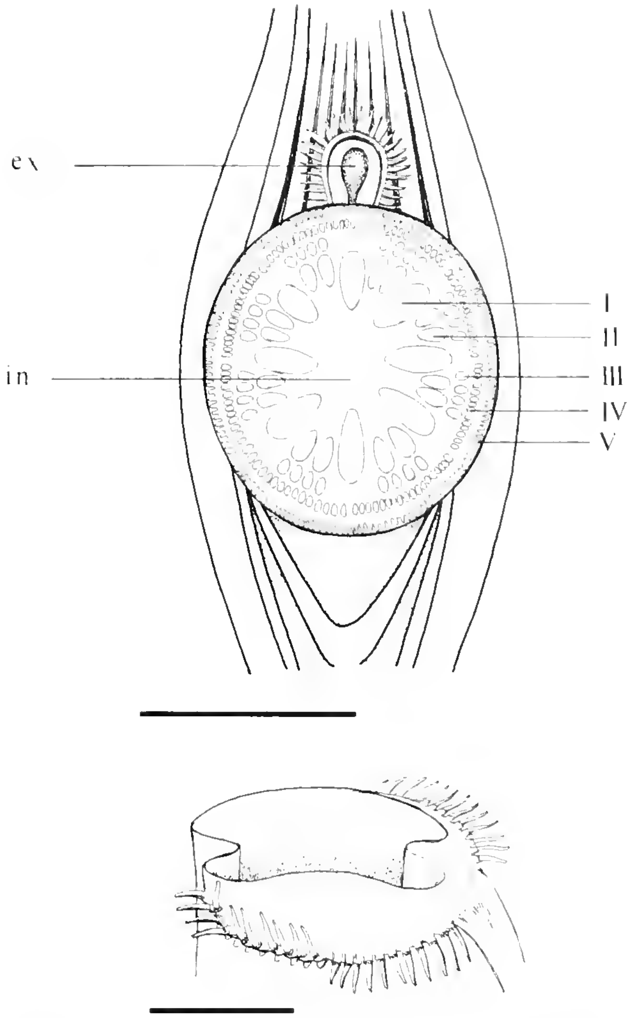

Figure 6. *Tivela ventricosa.* Extended siphons seen from above. Top, diagram emphasizing disposition of the 5 sets of tentacles of the incurrent siphon. *ex*, excurrent siphon; *in*, incurrent siphon; I, II, III, IV, and V sets of tentacles. Scale line = 0.5 cm; bottom, detail of the opening of the excurrent siphon showing the opening membrane and tentacles. Scale line = 0.2 cm.

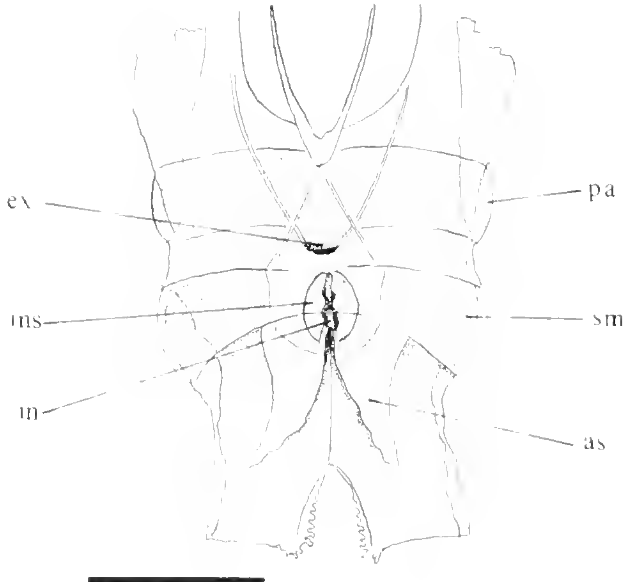

Figure 7. *Tivela ventricosa.* Internal view of the openings of the incurrent and excurrent siphons in the mantle cavity. *as*, additional siphonal membrane; *in*, incurrent siphon; *ins*, incurrent siphonal membrane; *ex*, excurrent siphon; *pa*, posterior adductor muscle; *sm*, siphonal muscle. Scale line = 0.5 cm.

specimen of 4.8 cm shell length buried itself completely in 7 minutes.

Specimens live completely buried at a depth of approximately 5 cm; often specimens can be found with the shell pointing out of the substratum.

Ctenidia (Figures 8, 10–12): The shape of the ctenidia and the current patterns on them are illustrated in Figures 8 and 10. Each ctenidium is formed by two demibranchs, the inner demibranch higher than the outer one, particularly in anterior direction, and grooved along its free margin.

The lamellae of both demibranchs are plicate and heterorhabdic (Figure 11). Plicae are present along the larger part of both lamellae, ranging from a minimum of 29 to a maximum of 69 in the outer and inner demibranchs. The filaments (Figure 12) bear latero-frontal (6 μm long) and frontal cilia (10 μm long), the latter replaced by increasingly longer terminal cilia (up to 40 μm long) in the distal free edge of the filament. Throughout the lateral sides of the filaments lateral cilia produce a powerful respiratory and feeding current.

On the ascending lamella of the outer demibranch, downward ciliary currents were observed on all filaments of the crests and troughs of the plicae. Collected material is mainly conveyed around the free margin of the outer demibranch onto its descending lamellae where frontal cilia carry particles onto an acceptance, mouth-directed current on the ctenidial axes.

There is no food groove along the free edge of the outer demibranch but a group of terminal cilia along the outer face deflects large particles in anterior direction. These particles are carried for a short distance along the free margin, and then transferred to the outer surface of the inner demibranch. On the frontal region of the outer demibranch there are very large cilia that clean the ctenidium by removing particles as large as sand grains.

The frontal ciliary currents on both lamellae of the inner demibranch are almost always directed toward the marginal groove, exception made to the proximal region of the descending lamellae, where cilia beat in dorsal direction to convey material to the acceptance tract along the ctenidium axis.

Labial Palps (Figures 13, 14): The labial palps are flat, triangular, with the inner faces deeply plicate and the outer faces smooth (Figure 13). The ventral tips of

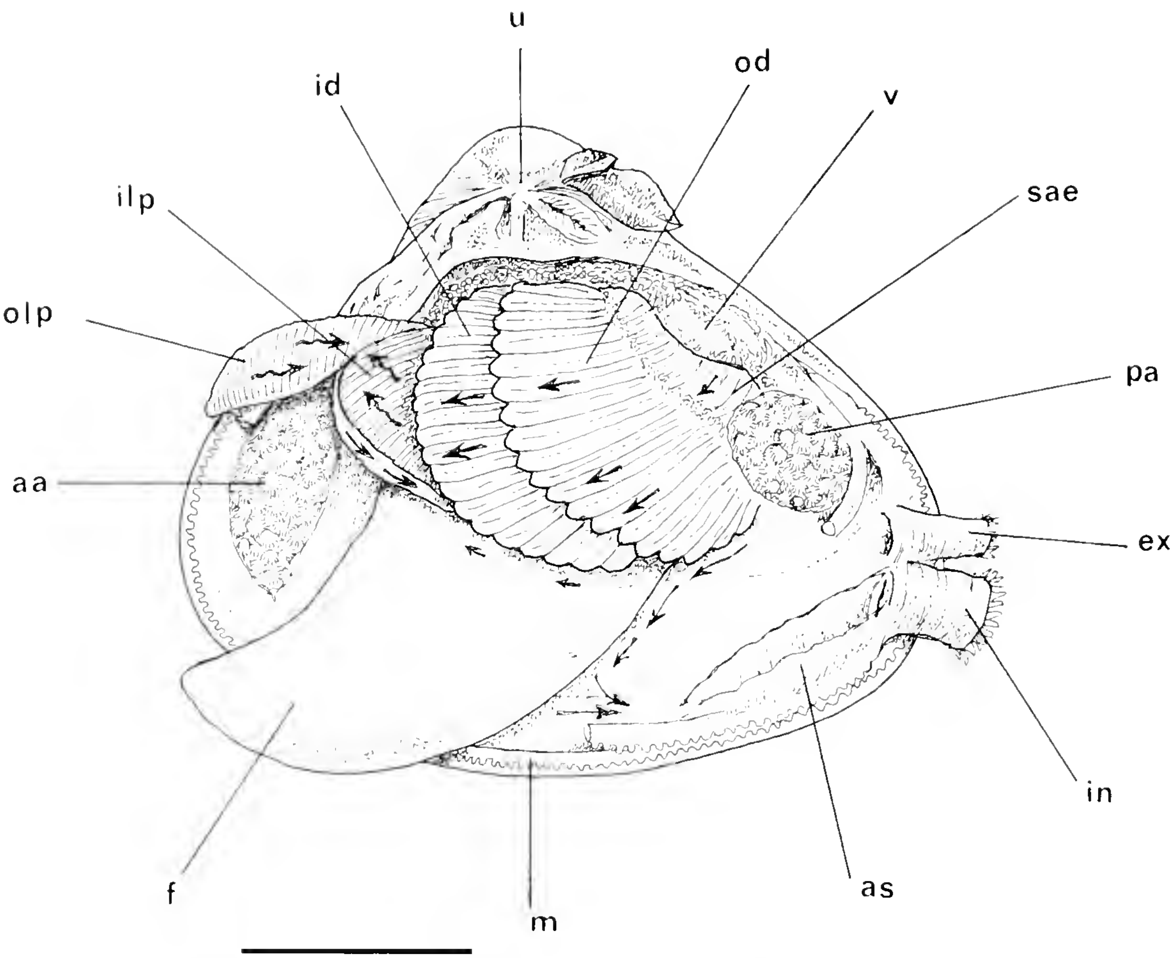

Figure 8. *Tivela ventricosa.* Organs of the mantle cavity viewed from the left side after removal of the left shell valve and left mantle lobe. *aa*, anterior adductor muscle; *as*, additional siphonal membrane; *ex*, excurrent siphon; *f*, foot; *id*, inner demibranch; *ilp*, inner labial palp; *in*, incurrent siphon; *m*, mantle edge; *od*, outer demibranch; *olp*, outer labial palp; *pa*, posterior adductor muscle; *sae*, supra-axial extension of the outer demibranch; *u*, umbo; *v*, ventricle. Arrows indicate the direction of the currents. Scale line = 2 cm.

the most anterior filaments of the inner demibranch are inserted into and fused to the distal oral groove of the palps. On the antero-dorsal region of the external surfaces of the palps, ciliary currents move particles around the dorsal margin to the internal surfaces. The following [illegible] currents on the palps (Figure 11) were recog[illegible]

[illegible] currents (a) that conduct particles to[illegible] one crest of the plicae to the [illegible]ted on the aboral surface of each [illegible] lateral region of the folds, a ven[illegible] is present on the crest of each [illegible]

[illegible] the floor of troughs be[illegible] on the lower half of the side [illegible] are driven onto the smoot[illegible] Here, a strong rejection [illegible] the free tip of the palp.

Muscular [illegible] must be taken into account whe[illegible] palps in sorting food particles is considered. The palps of *T. ventricosa* are relatively active. The plicae on the inner surface may be erected or laid flat, and the palps may be contracted and twisted into a spiral shape, bringing the smooth ventral edge and respective rejection current in contact with the ridged surface.

When small amounts of particles are presented to the palps, little sorting takes place. The ridges are relaxed and overlap. Exposed to the acceptance currents, the majority of particles are carried rapidly toward the mouth.

Large amounts of particles on the palps induce different degrees of muscular activity, which results in optimal sorting efficiency. Excess material causes a muscular reaction by contraction of the organs into a spiral shape and most material to be rejected.

Submitted to moderate amounts of material, the various sorting and rejection currents on the plicae are exposed. Large particles falling into the troughs of the grooves are rejected, while the smaller ones are trans-

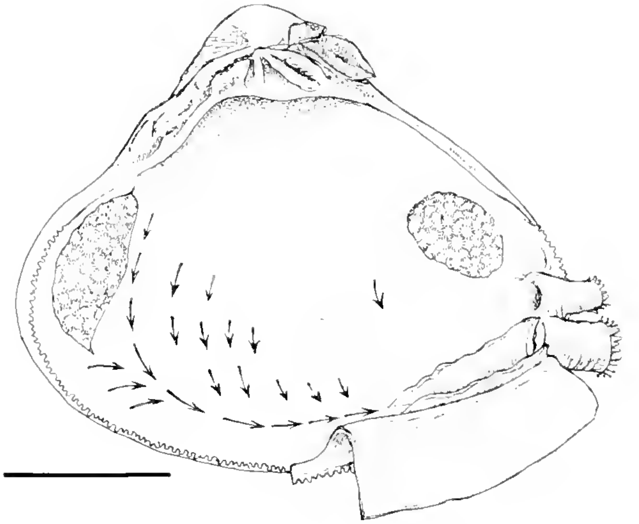

Figure 9. *Tivela ventricosa.* Inner surface of the right mantle lobe after removal of the left shell valve and part of the left mantle lobe showing ciliary cleansing currents and additional siphonal membranes. Arrows indicate the direction of the currents. Scale line = 2 cm.

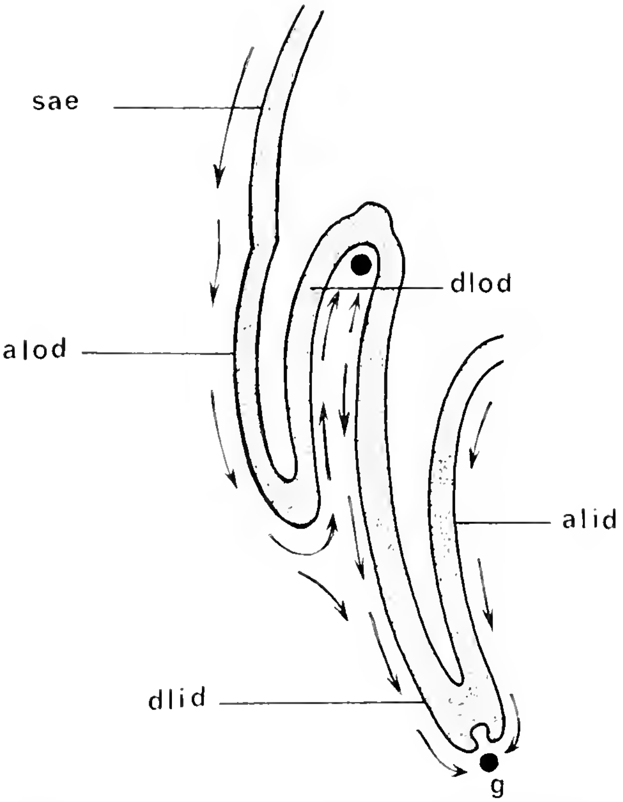

Figure 10. *Tivela ventricosa.* Diagrammatic vertical section through the ctenidia in the style of Atkins (1937b) showing the direction of particle flow by the frontal cilia. *alid*, ascending lamellae of the inner demibranch; *alod*, ascending lamellae of the outer demibranch; *dlid*, descending lamellae of the inner demibranch; *dlod*, descending lamellae of the outer demibranch; g, marginal groove of the inner demibranch; *sae*, supra-axial extension of the outer demibranch. Arrows indicate the direction of the ciliary currents.

ported by the sorting currents; only part of the original material reaches the oral groove between the palps.

Alimentary Canal (Figures 15–16): A short esophagus opens into the anterior wall of the stomach. The combined style sac and intestine opens into the posteroventral region of the stomach, and passes backward and downward as a wider tube into the foot. The midgut continues from the distal end of that wider tube, coils tightly about five times on the ventral side of the stomach, then passes downward and backward to ascend as the hindgut in posterior direction to the style sac. The hindgut passes through the pericardium, where it is surrounded by the ventricle and posterior aortic bulb, and hugs dorsally the posterior adductor muscle, to end in the anal papilla.

The stomach (Figure 16) has its esophageal opening defined by a transverse rim. The minor typhlosole ends on the right side, close to the orifice of the combined style sac and intestine in the floor of the stomach. The major typhlosole, associated with the intestinal groove, penetrates the stomach and passes forward, then downward into the right caecum. The right caecum receives six ducts from the digestive diverticula. Emerging from the right caecum, the major typhlosole passes to the left across the floor of the stomach, forming a flap that projects in dorsal direction toward the esophageal orifice. The major typhlosole then is directed deeply into the left caecum, returns and ends on the caecum opening. The left caecum receives 4 ducts from the digestive diverticula. The origin of the intestinal groove lies on the left anterior floor of the stomach, close to the opening of the left caecum.

Ciliary currents in the left caecum direct particles away from the orifices of the ducts carrying them toward the intestinal groove.

A group of 5 ducts from the digestive diverticula enters the left pouch. A sorting area lying on the floor of this pouch prolongs onto the right side of the stomach, where it expands and forms a beaded swelling. Cilia on this sorting area beat backward along the grooves and away from the openings of the ducts.

A well-developed dorsal hood projects upwards from the roof of the stomach and curves over toward the left side. A sorting area on its roof and anterior wall prolongs over the esophageal opening, then on the right wall of the stomach to finish posterior to the orifice of the right caecum. Material rejected from this sorting area is passed into a rejection tract, which arises within the dorsal hood and discharges into the intestinal groove. The anterior margin of the rejection tract is formed by a fold with several small ridges.

The gastric shield covers an extensive area on the left wall of the stomach, and sends a flange into the opening of the dorsal hood, and another into the left pouch. The

Figure 11. *Tivela ventricosa.* Tranverse sections of the outer demibranch. Top, median plicate, heterorhabdic condition of the ctenidium. Scale line = 0.1 mm; center, detail of the plicate demibranch. Scale line = 0.25 mm; bottom, distal non-plicate condition of the outer demibranch. Scale line = 0.1 mm.

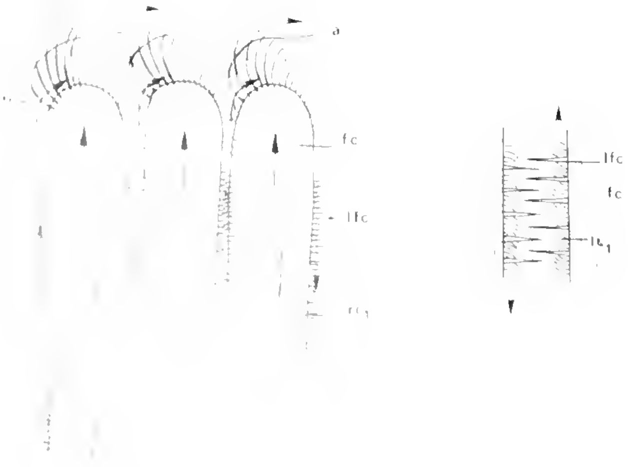

Figure 12. [illegible] on ctenidia. Left [illegible] of the ctenidium; right [illegible] oral cilia; *a*, oral current; *fc*, [illegible] abfrontal cilia; [illegible] large [illegible] indicate the direction of the [illegible].

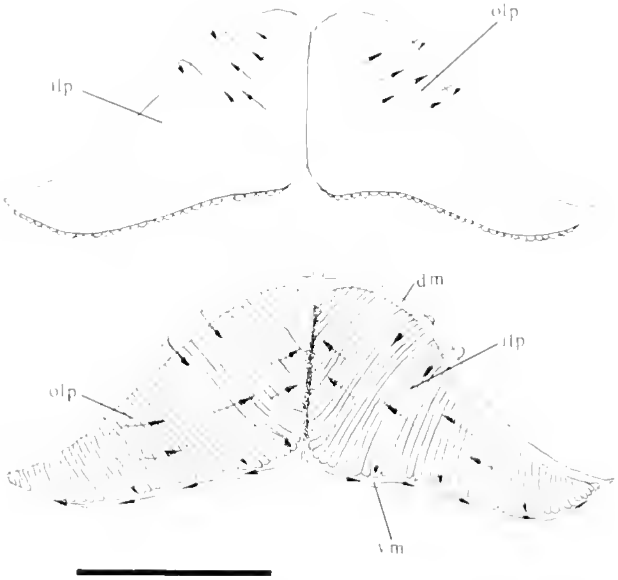

Figure 13. *Tivela ventricosa.* Ciliary currents on the labial palps. Top, external surface of the labial palp; bottom, internal surface of the labial palp; *dm*, dorsal margin; *ilp*, inner labial palp; *olp*, outer labial palp; *vm*, ventral margin. Scale line = 3 cm.

gastric shield has a small tooth-like projection at the anterior end.

There is a sorting area on the anterior wall of the stomach, between the aperture of the esophagus and the transverse section of the intestinal groove. Cilia on this area beat upward toward the esophagus. This sorting area extends to the right caecum, where cilia beat along the grooves from right to left, and probably convey particles toward the dorsal hood.

DISCUSSION

Tivela ventricosa is restricted to sandy beaches directly exposed to wave action. The species is not found in shel-

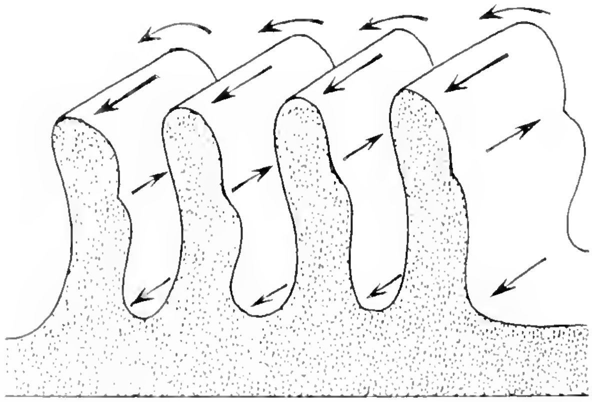

Figure 14. *Tivela ventricosa.* Diagrammatic representation of the ciliary mechanisms on the folded inner surface of the labial palp showing the various ciliary tracts. Anterior is at left.

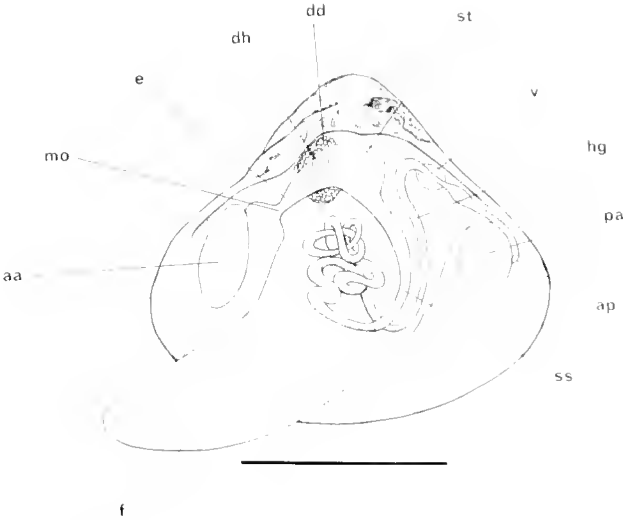

Figure 15. *Tivela ventricosa*. Alimentary canal, seen from the left side; *aa*, anterior adductor muscle; *ap*, anal papilla; *dd*, digestive diverticula; *dh*, dorsal hood; *e*, esophagus; *f*, foot; *hg*, hindgut; *mo*, mouth; *pa*, posterior adductor muscle; *v*, ventricle; *ss*, style sac; *st*, stomach. Scale line = 1 cm.

tered bays or other environments lacking strong wave action. This suggests that a high degree of aeration, made possible by strong mixing at the water/air interface, is essential to the species. Gofferjé (1950) found *T. ventricosa* on open seashores, co-occurring with the venerid bivalve *Amiantis purpuratus* (Lamarck, 1810). *Tivela ventricosa*, like *Tivela stultorum* (Mawe, 1823), as described by Weymouth (1920, 1923), is exposed to constant surf pounding, which its thick shell is able to withstand without cracking. The species apparently thrives in what might be considered as an unfavorable environment.

The large, heavy, massive shell of *T. ventricosa* exceeds in size all other species of *Tivela* occurring off the Brazilian coast. The largest specimen collected during the present study (7.9 cm in length; 7.4 cm in height, and 5.2 cm in width) exceeds the largest one registered by Gofferjé (1950) (3.5 cm in length, 3.0 cm in height, and 0.9 in width).

Armstrong (1965) undertook some experiments with 10 species of bivalves, including *Tivela stultorum*. Studying the position of the animals in relation to the wave front and their behavior in the substratum, that author found that the direction of wave action is related to the *in situ* orientation of that species. Such behavior was not observed in this study for *T. ventricosa*, nor for *T. mactroides* (Born, 1778) studied by Narchi (1972). All following references to *T. mactroides* are from Narchi (1972) unless otherwise noted.

The siphons of *T. ventricosa* are of Type B of Yonge (1948, 1982). The extremely mobile siphonal membrane of the excurrent siphon interferes with the flux of water passing through the ctenidia; when opened and extended outward, the membrane controls and directs the exhalant current. As observed in *T. mactroides*, there is no tentacular ring formed by the median mantle fold around the excurrent and incurrent apertures in *T. ventricosa*.

The siphons of *T. ventricosa* are similar in structure and shape to those described for *T. stultorum* (Weymouth, 1920, 1923) and *T. mactroides*. The incurrent siphon in *T. ventricosa* has branched tentacles disposed in 5 sets surrounding the aperture, unlike *T. mactroides* where they are disposed in 3 sets. The excurrent opening of *T. ventricosa* has about 48 simple tentacles, which are darkly pigmented at their bases, while in *T. mactroides* the excurrent opening tentacles are about 20, and milky white in color.

Narchi and Lopes (1998) recorded for the first time the presence of the additional siphonal membranes in *T. ventricosa*. In this species, the two additional siphonal membranes can be elevated and angled toward each other isolating the pseudofaeces and functioning as a typical waste canal, as Kellogg (1915) described for different species of bivalves.

The siphonal membranes may be raised to freely admit the incurrent stream, or may be drawn downward to direct the stream toward the mantle edges, and away from the gills, such as when much sediment is present. In this last configuration, a relatively large amount of sediment would be deposited ventrally on the mantle, and quickly transported posteriorly.

In *T. ventricosa*, the siphonal membranes control the water current that passes through the mantle cavity, while the additional folds can be elevated and angled toward each other until they meet in the summit of and enclosing the incurrent siphonal opening. This is probably an adaptation to large amounts of suspended sediment in the water by directing particles away from the ctenidia and aiding in their removal.

As seen in some Veneridae (Ansell, 1961), the free edges of the mantle have four folds. According to Yonge (1957) and Ansell (1961), the presence of four folds is accomplished by the duplication of the middle mantle fold.

A large number of branched tentacles in the margin of the mantle was described for *T. crassateloides* (Kellogg, 1915) and *T. mactroides*. In *T. ventricosa* there are also branched tentacles protecting the organs of the mantle cavity from intrusion of large particles of sand and possible injury. Many specimens showed torn or repaired outer demibranchs as apparent consequences of such injury, as Guerón and Narchi (2000) also showed for *Protothaca* (*Leukoma*) *pectorina* (Lamarck, 1818).

The surface of the mantle in *T. ventricosa* has ventrally directed cleansing ciliary currents, similar to that observed by Ansell (1961) in some Veneroidea from England and in *T. mactroides*. In *T. ventricosa* and *T. mactroides*, minor ciliary cleansing currents pass from the free margin of the mantle in the posterior region passing radially inward to join the main rejection tract.

Ansell (1961) described some variation in outer demibranch configuration, between species, and even between specimens of the same species due to the strength

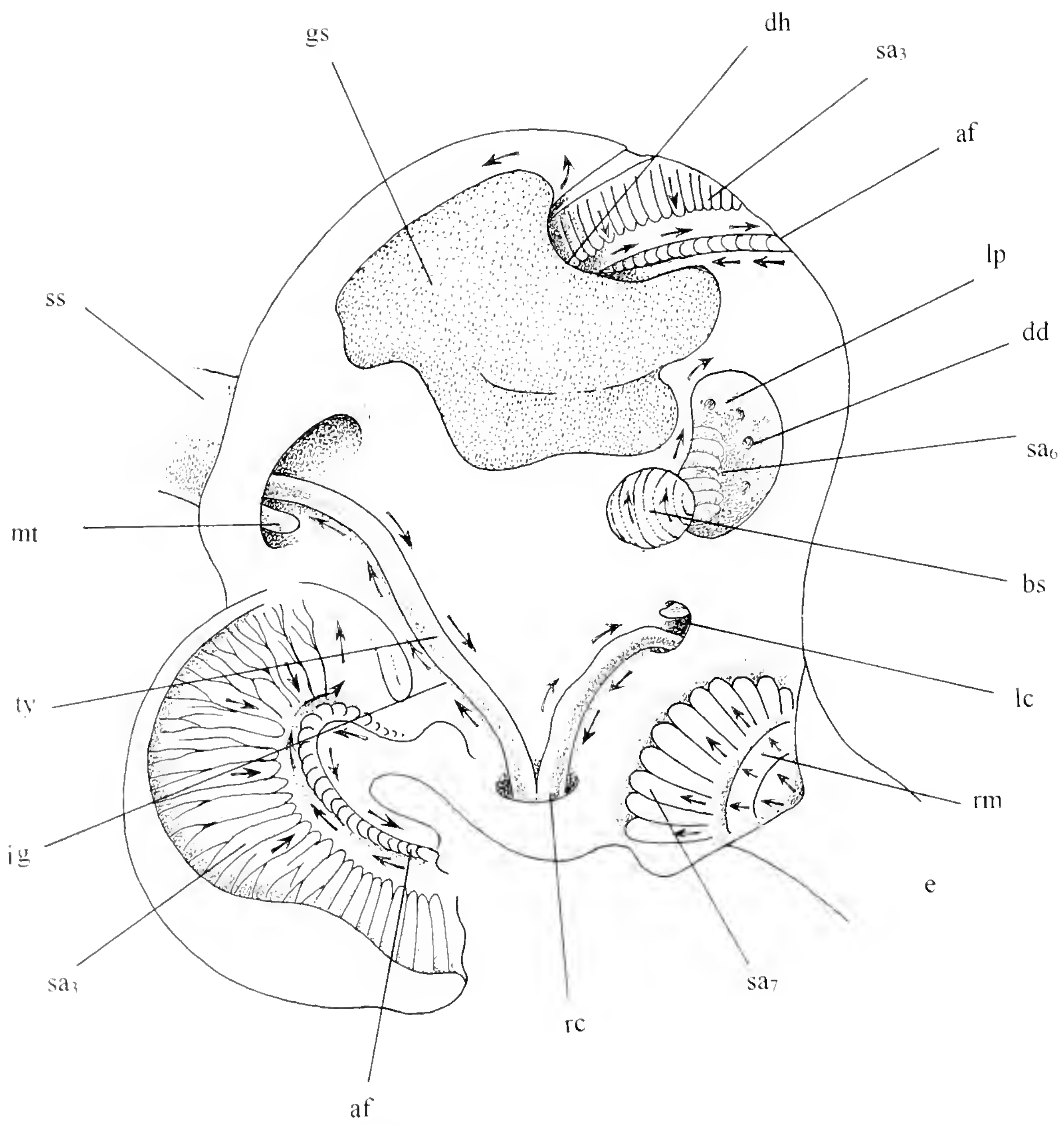

Figure 16. *Tivela ventricosa*. Interior of stomach, seen from right side after opening by incision in the right wall. *af*, anterior [illegible] *b*[illegible]eaded swellings; *dd*, digestive diverticula; *dh*, dorsal hood; *e*, esophagus; gs, gastic shield; *ig*, intestinal groove; *lc*, left [illegible] left pouch; *mt*, minor typhlosole; *rc*, right caecum; *rm*, mouth ring; *sa₃*, principal sorting area of the dorsal hood; *sa₆*, [illegible] left pouch; *sa₇*, sorting area below esophageal orifice; ss, style sac; *ty*, typhlosole.

[illegible] edge carrying particles towards the [illegible] (Ansell, 1961), *Venerupis aurea* (Gmelin [illegible] *rhomboides* (Pennant, 1777), *Mysia* [illegible] and members of *Venus* Linné, 17[illegible] li, 1777, present an incipient [illegible] the mouth at the free edge of the o[illegible]

The pattern a[illegible] ctenidia currents of *T. ventricosa* are [illegible] with the results of Ridewood (1903) and [illegible] b) on the morphology of the ctenidia and their ciliation in some Veneroidea. The ctenidia in *T. ventricosa* belong to Type C(1) of Atkins (1937b), with one groove along the free ventral margin of the inner demibranch, as Narchi (1972) and Narchi and Gabrielli (1980) described for the venerids *Anomalocardia brasiliana* (Gmelin, 1791) and *Chione subrostrata* (Lamarck, 1818), respectively. In *T. mactroides* the ctenidial ciliation is of Type C(2) of Atkins (1937b).

The labial palps of *T. ventricosa* show the same basic features of other species of Veneroidea studied by Thiele (1886), and are also similar in structure and muscular activity to those of *T. mactroides*. The ventral tips of the most anterior filaments of the inner demibranch are inserted into and fused to a distal oral groove; the association of ctenidia and labial palps belong to Category II of Stasek (1963).

The configuration of the alimentary canal of *T. ventricosa* is similar to that of *T. mactroides*, differing mainly by the more convoluted midgut, with 5 closely packed coils in the first, and with only one loose coil in the latter.

Wherever known, the anatomy of the stomach is generally similar throughout the Veneridae. The left and the right caeca of *T. ventricosa* receive 4 and 6 ducts from the digestive diverticula, respectively. Six and 5 ducts were respectively recorded for *T. mactroides*. In *T. ventricosa* another group of five ducts from the digestive diverticula enters the left pouch without being associated with the major typhlosole or the intestinal groove, as described by Purchon (1960) for *Gafrarium minimum* (Montagu, 1847) and *T. mactroides*.

The stomach of *T. ventricosa* has the structure of a typical suspension-feeding eulamellibranch. It is similar to those of the venerids *Glossus humanus* (Linné, 1758), *G. minimum*, *Venus casina* Linné, 1758, and *T. mactroides*, as described by Owen (1953), Purchon (1960), Ansell (1961), and Narchi (1972), respectively. Within the stomach, food particles are kept in motion by the combined action of the rotating crystalline style and the ciliated walls, and are subjected to sorting mainly in the posterior sorting area, as in *T. mactroides*. The stomach of *T. ventricosa* may be capable of handling many particles at one time due to its complexity.

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LITERATURE CITED

Abbott, R. T. 1974. American Seashells. 2nd. Edition. Van Nostrand Reinhold, New York, 663 pp.

Ansell, A. D. 1961. The functional morphology of British species of Veneracea (Eulamellibranchia). Journal of the Marine Biological Association of the United Kingdom 41(2): 489–517.

Armstrong, L. R. 1965. Burrowing limitations in Pelecypoda. The Veliger 7: 195–200.

Atkins, D. 1937a. On the ciliary mechanisms and interrelationships of lamellibranchs. Part II. Sorting devices on the gills. Quarterly Journal of Microscopical Science N.S. 79: 339–373.

Atkins, D. 1937b. On the ciliary mechanisms and interrelationships of Lamellibranch. Part III. Types of lamellibranch gills and their food currents. Quarterly Journal of Microscopical Science N.S. 79: 375–421.

Broggi, J. 1970. Sobre el hallazgo de cinco nuevas especies para el Querandino Uruguayo. Communicaciones de la Sociedad Malacologica del Uruguay 2(18): 427–431.

Buckup, L. 1957. Catálogo dos moluscos do Museu Riograndense de Ciências Naturais. Iheringia 1: 1–40.

Carcelles, A. R. 1944. Catálogo de los moluscos marinos de Puerto Quequén. Revista del Museo de La Plata, Nueva Série, Zoologia 3: 233–309.

Carcelles, A. R. and S. I. Williamson. 1951. Catálogo de los moluscos marinos de la Provincia Magallanica. Revista del Instituto Nacional de Investigacion de las Ciencias Naturales 2(5): 225–383.

Coan, E. V., P. Valentich Scott and F. R. Bernard. 2000. Bivalve seashells of western North America. Marine bivalve mollusks from Arctic Alaska to Baja California. Santa Barbara Museum of Natural History Monograph 2. Santa Barbara. viii + 764 pp.

Gofferjé, C. N. 1950. Contribuição à zoogeografia da malacofauna do litoral do estado do Paraná. Arquivos do Museu Paranaense 8: 221–282.

Guerón, C. O. C. and W. Narchi. 2000. Anatomia funcional de *Protothaca (Leukoma) pectorina* (Lamarck, 1818) (Bivalvia: Veneridae). Revista Brasileira de Zoologia 17: 1007–1039.

Kellogg, J. L. 1915. Ciliary mechanisms of lamellibranchs with description of anatomy. Journal of Morphology 26: 625–701.

Lange de Morretes, F. 1949. Ensaio de catálogo dos moluscos do Brasil. Arquivos do Museu Paranaense 7(1): 5–216.

Narchi, W. 1972. Comparative study of the functional morphology of *Anomalocardia brasiliana* (Gmelin, 1791) and *Tivela mactroides* (Born, 1778) (Bivalvia, Veneridae). Bulletin of Marine Science 22: 643–670.

Narchi, W. and M. A. Gabrielli. 1980. Sobre anatomia funcional de *Chione subrostrata* (Lamarck, 1818). Revista Nordestina de Biologia 3: 25–46.

Narchi, W. and S. G. B. C. Lopes. 1998. On the incurrent siphonal membrane of *Tivela ventricosa* (Gray, 1838) (Bivalvia, Veneridae). *In*: Bieler, R. and P. M. Mikkelsen (eds.) Abstracts of the World Congress of Malacology, Washington, D.C., 1998. Unitas Malacologica and American Malacological Society, Washington. p. 237.

Owen, G. 1953. On the biology of *Glossus humanus* (L.) (*Isocardia cor* Lam.). Journal of the Marine Biological Association of the United Kingdom 32: 85–106.

Purchon, R. D. 1960. The stomach in the Eulamellibranchia; stomach types IV and V. Proceedings of the Zoological Society of London 135(3): 431–489.

Ridewood, W. G. 1903. On the structure of the gills of the Lamellibranchia. Philosophical Transactions of the Royal Society of London Ser. B 195: 147–284.

Rios, E. C. 1970. Coastal Brazilian Seashells. Fundação Cidade do Rio Grande. Fundação Universidade do Rio Grande, Rio Grande. 255 pp., 60 pls.

Rios, E. C. 1975. Brazilian Marine Mollusks Iconography. Fundação Universidade do Rio Grande. Rio Grande. 331 pp., 91 pls.

Rios, E. C. 1985. Seashells of Brazil. 1st. edition. Fundação Cidade do Rio Grande. Fundação Universidade do Rio Grande. Museu Oceanográfico, Rio Grande, 328 pp., 102 pls.

Rios, E. C. 1994. Seashells of Brazil. 2nd. edition. Fundação Cidade do Rio Grande, Instituto Acqua R.J., Museu Oceanográfico Prof. E. C. Rios, Universidade do Rio Grande. Rio Grande, 368 pp., 113 pls.

Stasek, C. R. 1963. Synopsis and discussion of the association of ctenidia and labial palps in the bivalved Mollusca. The Veliger 6: 91–97.

Thiele, J. 1886. Die Mundlappen der Lamellibranchiaten. Zeitschrift für wissenschaftliche Zoologie 44: 239–272, 2 pls.

Weymouth, F. W. 1920. The edible clams, mussels and scallops of California. Bulletin of the California State Fish and Game Commission 4: 3–72, 19 pls.

Weymouth, F. W. 1923. The life-history and growth of the Pismo clam (*Tivela stultorum* Mawe). Bulletin of the California State Fish and Game Commission 7: 5–120.

Yonge, C. M. 1948. Formation of siphons in Lamellibranchia. Nature 161: 198–199.

Yonge, C. M. 1957. Mantle fusion in the Lamellibranchia. Pubblicazioni de la Stazione Zoologica di Napoli 29: 151–171.

Yonge, C. M. 1982. Mantle margins with a revision of siphonal types in the Bivalvia. Journal of Molluscan Studies 48: 102–103.

Notice

THE 2002 R. T. ABBOTT VISITING CURATORSHIP

The Bailey-Matthews Shell Museum is pleased to invite applications for the 2002 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 mollusk systematists 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 2002 Visiting Curatorship should be sent no later than May 30, 2002. 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: (941) 395-2233; fax (941) 395-6706.

Use of HMDS (hexamethyldisilazane) to dry organic microstructures in etched bivalve mollusk and barnacle shells

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ABSTRACT

The organic framework of molluscan and barnacle shells yields clues to biocalcification processes. Slight demineralization of the shells reveals the fragile meshwork of insoluble organic fibers and membranes, which tend to collapse, wrinkle, and shrink when air-dried from water. Comparison of different drying techniques on etched bivalve mollusk (*Chione fluctifraga*) and barnacle shells (*Chthamalus* sp.) reveals that hexamethyldisilazane (HMDS) produced results qualitatively superior to critical point drying or drying from ethyl alcohol or water. HMDS dries structural details of the organic meshwork excellently and facilitates the recognition of faint growth increments for growth pattern analysis (sclerochronology). The HMDS method is cost-effective, saves time and can be used as a routine substitute for drying microstructures in slightly etched molluscan and barnacle shells.

INTRODUCTION

Organic matter plays an essential role in the formation of molluscan and barnacle shells. It has been realized that the organic matrix provides the structural framework ("template"; Clark, 1980) for biomineralization and influences the mineralogical and crystallographic properties (Mann, 1983; Simkiss and Wilbur, 1989; Crenshaw, 1990 and literature therein; Watabe et al., 1993). Demineralization of skeletal hard parts unveils the underlying three-dimensional organic microstructures, which may yield clues to biocalcification processes.

Organic matter is also a major constituent of some growth increments (e.g., Koike, 1986). Slight demineralization of cross-sectioned molluscan and barnacle shells reveals a three-dimensional relief of insoluble organic components and differentially dissolved crystals (as a result of different crystal sizes and orientation). In sclerochronological studies (growth analyses), superficial etching is commonly used to aid in the identification and measurement of internal growth increments in molluscan and barnacle skeletons (Rhoads and Lutz, 1980; Schöne et al., in press). The etching time varies for different species and depends on, for instance, the shell structure, mineralogy, and organic content. Although growth patterns in mollusk shells are the focus of numerous studies, only few papers deal with the growth patterns of barnacles. Unlike most crustaceans, barnacles do not replace their hardparts. Both mollusks (e.g., Davenport, 1938; Pannella and MacClintock, 1968) and barnacles (e.g., Bourget, 1980) grow by periodic accretion of skeletal material producing circadian growth increments (see sketches in Figure 1 and 2; direction of growth). In barnacles, the growth layers are best viewed in the sheath layer (Figure 1), and in most bivalve mollusks in the outer shell layer (Figure 2).

Like most soft tissues, the shell organic framework, including the organic-rich growth increments observed in cross-sections, is prone to collapse, shrinkage, and wrinkling when air-dried (e.g., Anderson, 1951; Nation, 1983; Clark, 1980, 1999). Preventing these unwanted effects requires special chemical treatment, which dehydrates and hardens the fragile organic structures. Several techniques are used to dry biological soft tissues. Although extremely time-consuming and quite dangerous (highly pressurized chamber), critical point drying (CPD) is by far the most common method (Anderson, 1951; using liquid CO$_2$, e.g., Clark, 1980 or Freon 13 as a transitional fluid, e.g., Koike, 1986). On average, preparing one sample by CPD requires full attention over 1.5 hours. The basic CPD equipment costs several thousand dollars. Good results were also achieved with the sublimation dehydrant Peldri II (Kennedy et al., 1989). However, preparation following this technique takes more than twice the time as CPD and Peldri II is no longer available because of environmental hazards. Fluids with low surface tension (acetone or propylene oxide, Boyde and Wood, 1969) sometimes produce reasonable, artifact-free results for biological soft tissues. Some workers prefer the extremely hazardous osmium tetroxide technique (Quattlebaum and Carner, 1980).

A reliable and simple drying technique, which produces results qualitatively comparable or superior to

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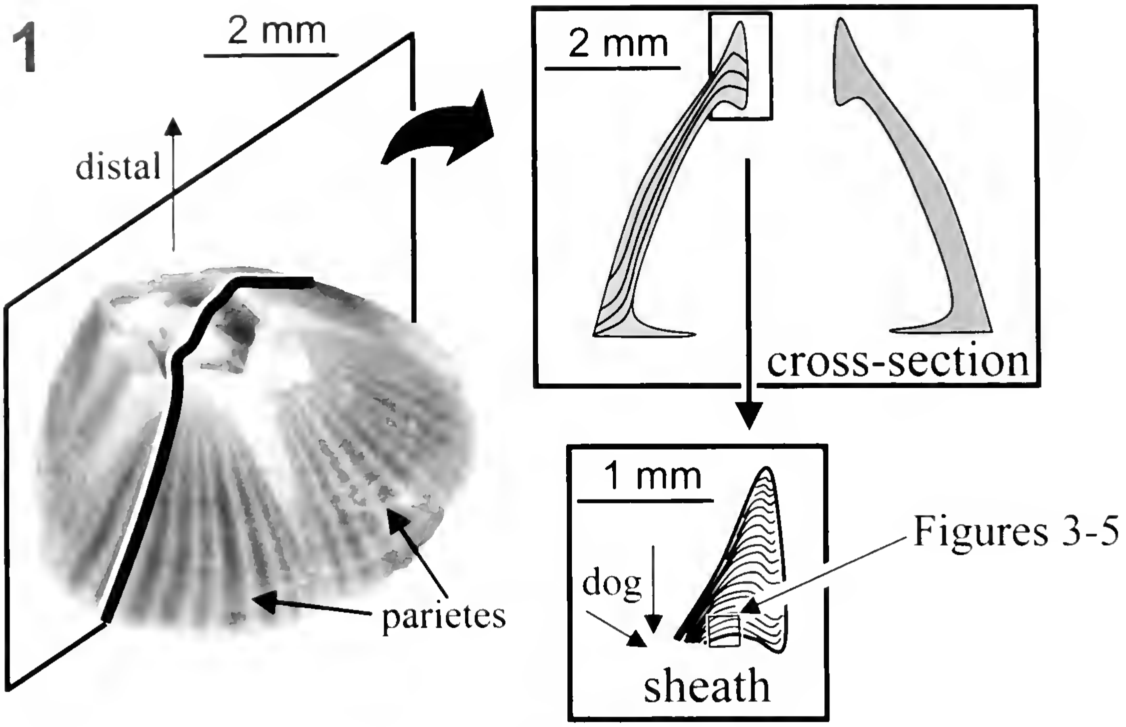
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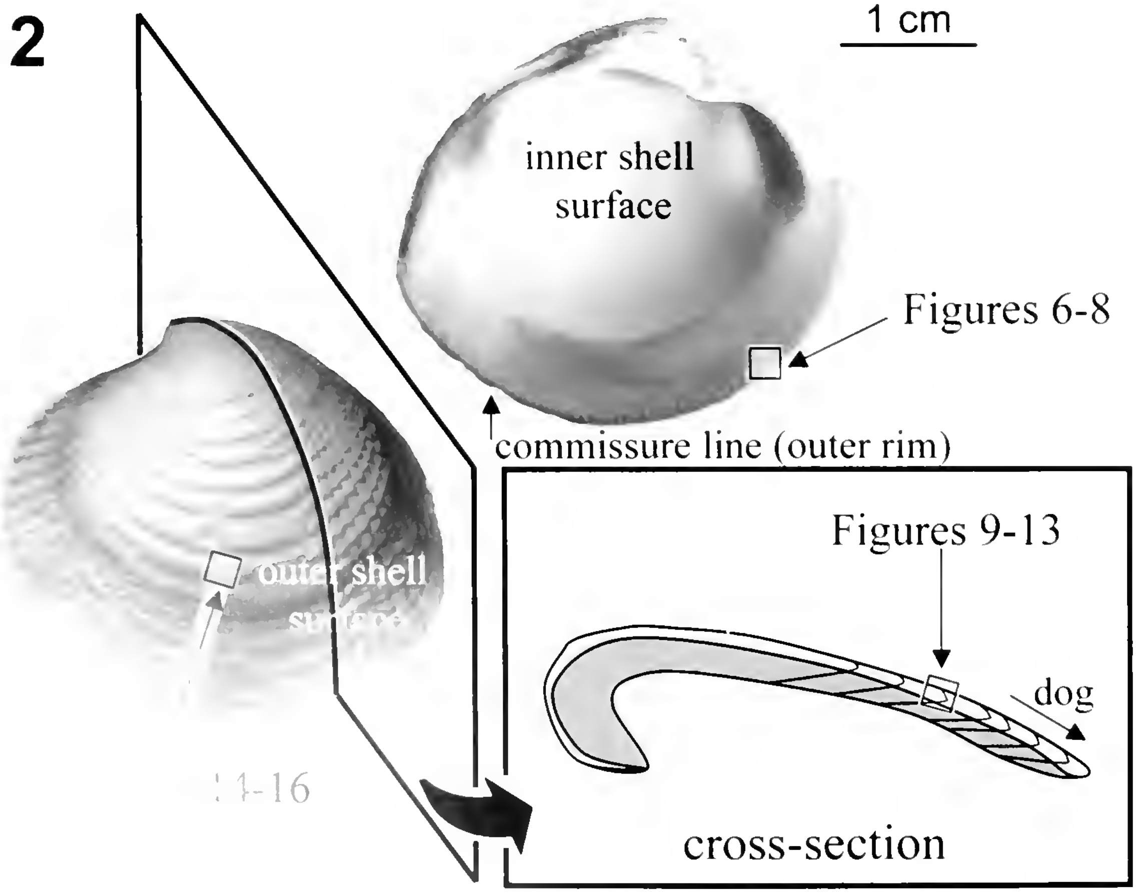
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Figures 6-8
commissure line (outer rim)
outer shell
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14-16
Figures 9-13
dog
cross-section

CPD, was introduced by Nation (1983). After dehydration in a series of graded ethanol solutions, the samples are immersed in hexamethyl-1, 1, 1, 3, 3, 3 disilazane (hexamethyldisilazane, HMDS), an organic reagent with the chemical formula $[(CH_3)_3Si]_2NH$, for approximately five to 30 minutes, and allowed to air-dry at room temperature. The low-cost HMDS drying technique does not require full attention during processing. It was successfully applied to dry various kinds of soft parts in different organism groups, e.g., in insects (Nation, 1983; Rumph and Turner, 1998), soft tissues of mollusks (Leal and Simone, 1998), vertebrates (Heegaard et al., 1986; Wervha et al., 1990), microorganisms (Dekker et al., 1991; Hochberg and Litvaitis, 2000) or pollen (Chissoe et al., 1994). Although applied to demineralized human teeth (Perdigao et al., 1995; Carvalho et al., 1996), to our knowledge HMDS has not been used as a transitional solvent for drying molluscan and barnacle shell microstructures.

This study evaluates the usefulness of HMDS for drying microstructures in etched barnacle and bivalve mollusk shells using scanning electron microscopy (SEM). Special emphasis is given to the use of HMDS in sclerochronological studies. We compare the HMDS technique to 1) the CPD method, 2) air-drying immediately after etching (AIR), and 3) a combination of dehydration in a series of graded alcohol baths and air-drying (ALC).

MATERIALS AND METHODS

Material and general preparation: During field trips in 1999 and 2000, we collected barnacles and bivalve mollusks in the intertidal zone of the northern Gulf of California, Mexico. For this study, we used one barnacle specimen (*Chthamalus* sp.) collected alive at Isla Sacatosa in December 2000 (N31 29.60, W114 50.85; specimen no. ST11-A18), three *Chione fluctifraga* (Sowerby, 1853) specimens collected alive at North Orca in November 1999 (N31 32.60, W114 52.78; specimen no. NO3-A105, NO3-A106, NO3-A108), and three *C. fluctifraga* specimens from Isla Sacatosa (N31 29.60, W114 50.85; specimen no. ST12-D1, ST12-D2, ST12-D3, December 2000). All specimens are housed at the Department of Geosciences, The University of Arizona, Collection Flessa, Subcollection Schöne.

After removal of the soft parts, all specimens were cleaned in Chlorox (5.25% sodium hypochlorite) to dissolve remaining superficial organic matter, rinsed with water and dehydrated with ethyl alcohol (EtOH). Coating with J-B KWIK Weld™ provides a protecting cover for the shells during cutting. The fragile barnacle required embedding in J-B Epoxy. J-B Epoxy is not adversely affected by immersion in EtOH or HMDS.

Cross-sections of barnacle and bivalve mollusk shells: We obtained three cross-sectioned slabs (thickness 0.5 mm) from the barnacle shell (ST11-A18, Figure 1) and from the left valve of each of the three *C. fluctifraga* shells no. ST12-D1, -D2, and -D3 (Figure 2) using a low speed (Buehler™ Isomet) saw. Use of an ultrathin saw blade (0.4 mm thickness) assured that the effects of different preparation techniques (see below) on the organic microstructures could be studied on almost identical portions of the shell. In this study we focus on the composite prismatic shell layer of *C. fluctifraga*, because they are of primary concern in sclerochronological studies. In the cross-sectioned shells of *C. fluctifraga* growth increments are clearly developed and easy to measure. Moreover, etching and drying results may vary with respect to different types of shell microstructure. Focusing on one type of shell layer allows comparisons of the effectiveness of different drying techniques on similar shell microstructures. The cross-sections were mounted on petrographic slides, ground on glass plates (600 and 1000 grit Al_2O_3 powder), and polished on laps (9, 6, and 0.3 µm Al_2O_3 powder). Ultrasonic cleaning between each polishing step assured that no grinding powder was left on the surface.

Inner and outer shell surfaces of the bivalve: Shell fragments of three *C. fluctifraga* specimens (NO3-A105, -A106, and -A108) were mounted on a petrographic slide to expose the growing surface at the inner shell edge. Two shell fragments of specimen ST12-D3 were mounted on petrographic slides with the outer surface exposed.

Chemical treatment: etching and drying: All samples were then etched in a 0.25 mol EDTA solution (ethylene diamine tetraacetate, pH 7.95, buffered with NaOH) and carefully rinsed in de-ionized water. The shells were etched for varying amounts of time (Table 1) to obtain different degrees of demineralization: slight superficial etching and decalcification of the upper 1 mm of shell material. In previous studies we carried out a series of tests and analyzed the effects of an array of etching times and EDTA concentrations on shells of *C. fluctifraga* and *Chthamalus* sp. (Schöne et al., 2002, and unpublished data). For the presentation of microstructures in *C. fluctifraga* and *Chthamalus* sp. the approach used herein proved to be most appropriate. We compared the following four drying techniques (Table 1): air-drying from water (AIR), drying from EtOH (ALC), drying from HMDS and CPD. For ALC, HMDS, and CPD

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Figures 1, 2. Positions in the shells where the samples (Figures 3–16) were taken (d.g. = direction of growth, direction in which subsequent growth increments were added). **1.** Cross-section through the parietes (shell plates) of the barnacle *Chthamalus* sp. The sheath layer (distal portion of the parietes) exhibits faint daily growth structures (Figures 3–5). **2.** *Chione fluctifraga* shell. Samples for Figures 6–8 were taken from the growing edge of the inner shell surface, samples for Figures 14–16 from the outer shell surface. In radial cross-sections, growth patterns become apparent in the outer shell layer (Figures 9–13).

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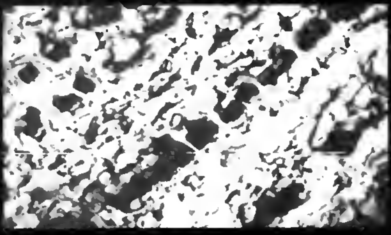

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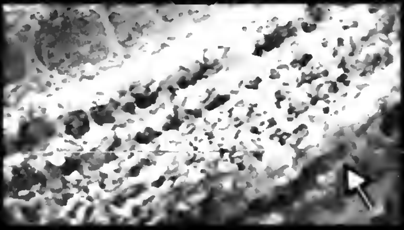

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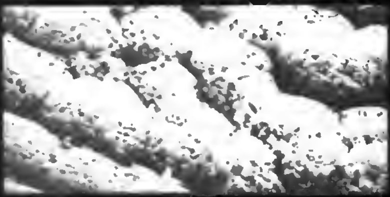

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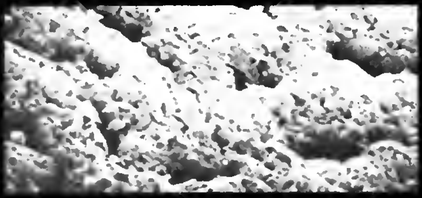

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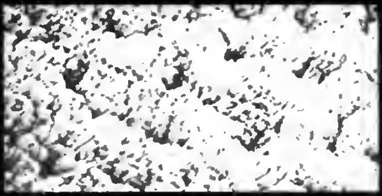

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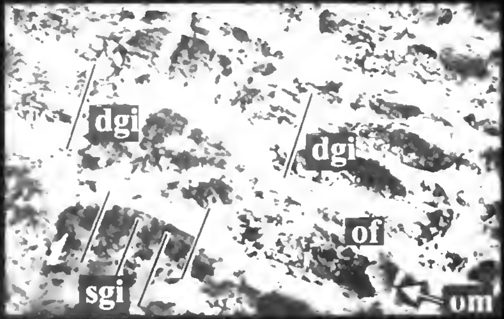

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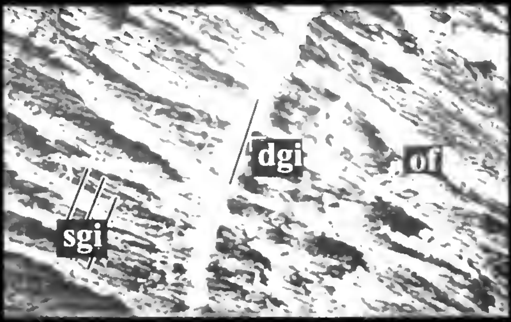

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the samples were rinsed in a series of graded EtOH (40%, 60%, 80%, 5 min each; two times 100%, 30 min each). The HMDS technique includes immersion of the dehydrated samples in 97% hexamethyldisilazane (Aldrich™ chemical; two times for 30 min each) and subsequent air-drying. CPD was performed in a Polaron CPD E3200 apparatus. The dehydrated samples were placed in the CPD apparatus with alcohol, the chamber cooled to 10°C, and CO_2 allowed to enter the chamber. Free alcohol was flushed from the chamber until dry ice was seen exiting. The sample remained in CO_2 for 45 minutes flushing the chamber every 15 minutes. At the end of the exchange, the chamber was sealed and the temperature raised above 35°C (critical temperature for CO_2 = 32°C). CO_2 vapor was then released.

Coating for SEM and photographic documentation: Aluminum stubs were glued to the petrographic slides. The samples were sputter coated immediately with a 30 nm gold layer in a Bio Rad Polaron Division SEM coating system. The samples were studied with a Cambridge Instruments Stereoscan 120 SEM at acceleration voltages of 15 and 25 keV. Black and white photographs were taken on Polaroid Positive/Negative 4×5″ Type 55 Instant Sheet Film for documentation.

RESULTS

Barnacle shell microstructure: Under 750× magnification, the 15-min-etched cross-section of the sheath portion of the barnacle parietes (Figure 1) shows partly dissolved calcite crystals in a crisp three-dimensional mesh of organic fibers when dried from HMDS (Figure 3). CPD results in a less well-dried organic framework (Figure 4). Apparently, some delicate organic fibers collapsed resulting in a slightly blurred image. Even worse is the drying in ALC samples. Presumably, as a result of a complete collapse of the organic matrix, single crystals can barely be discerned (Figure 5). Some growth layers disappear partly or entirely when immediately air-dried after etching (Figure 5).

Bivalve shell microstructure:

Inner shell surface near the commissure: HMDS treatment of the slightly etched growing surface at the inner shell surface (Figure 2) reveals a thin organic meshwork residue in between and on top of the polygonal pattern of the composite prismatic structure (Figure 6). CPD-treated shells are not depicted, because the results are comparable to the HMDS desiccation. ALC produces a somewhat collapsed organic framework (Figure 7). The rod-like surface is completely covered in AIR samples (Figure 8).

Cross-section, outer composite prismatic shell layer: A cross-section etched for 15 min and dried from HMDS clearly shows the composite prismatic structure of the outer shell layer (Figures 2, 9). Organic membranes of daily and even subdaily growth layers are intersected by perpendicular running fibrous membranes (Figure 9; for experimental studies on the timing of growth pattern formation in *C. fluctifraga* see Schöne et al., 2002). CDP dries the organic meshwork less well (Figure 10).

At lower magnification (375×) the differences between the HMDS (Figure 11) and CPD (Figure 12) techniques are less obvious. A reliable counting and measurement of narrow daily growth increments laid down during hot summer conditions can be conducted on HMDS and CPD samples, but barely accomplished on the sample treated with the ALC method (Figure 13). In the latter case the collapsed organic matter covers most parts of the faint growth patterns and does not allow for detailed growth pattern analysis.

Outer shell surface: Outer shell surfaces exposed for twelve hours to the 0.25 mol buffered EDTA solution reveal a well-dried, dense, multi-layered organic network when dried from HMDS (Figure 14). Growth lines cannot be seen any more. Applying the AIR method, the organic framework collapses and covers the shell's microstructures as a mass without clear structures (Figure 15). During the vacuum in the sputter coater

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Figures 3–16. SEM (scanning electron microscopy) images of etched barnacle *Chthamalus* sp. (Figures 3–5) and bivalve mollusks shells (*Chione fluctifraga*) (Figures 6–16). Working distance in mm (WD), acceleration voltage in keV (AV), etching time in min (ET), and scale are provided in each figure. **3.** Best drying of the organic meshwork (N) and single crystals (cs) is achieved when the etched barnacle shells are immersed in HMDS prior to air-drying. Prominent ridges are daily growth lines (dgl). **4.** CPD (critical point drying) dries the organic network partly, but the single crystals cannot be discerned well. **5.** All structural details are gone when using ALC (air-drying from ethyl alcohol). Some faint growth lines fell over to adjacent growth lines (arrow). **6.** The growing edge of the inner surface exhibits crisp polygonal crystal structures in the HMDS treated specimen. **7.** CPD dries most of the faint structures as well. **8.** ALC results in a blurred image. **9.** Daily and subdaily (sgi) growth increments, organic membranes (om) as well as perpendicular running organic fibers (of) are well dried in HMDS-treated cross sections of *Chione fluctifraga*. **10.** but less well in CPD samples. **11.** Daily growth lines (dgl) laid down during hot summer are best viewed in HMDS or **12.** CPD prepared cross-sections. **13.** ALC does not allow for a detailed analysis, because organic structures collapse. **14.** Outer shell surfaces of *Chione fluctifraga* reveal a dense, three-dimensional insoluble organic meshwork when immersed in HMDS prior to air-drying. **15.** AIR (air-drying) results in an undifferentiated mass of collapsed organic structures. **16.** HMDS treated samples may shrink and wrinkle under vacuum during the coating process or in the SEM (nes = non-etched shell surface; don = demineralized organic network).

Table 1. Overview of sample treatment

			Preservation technique			
Species	Specimen #	Etching time	HMDS	CPD	ALC	AIR
Chthalamus fissus	ST11-A18	15 min	Figure 3	Figure 4	Figure 5	
Chione fluctifraga	NO3-A105	3 min	Figure 6			
	NO3-A108	3 min			Figure 7	
	NO3-A106	3 min				Figure 8
	ST12-D1	15 min	Figures 9, 11	Figures 10, 12	Figure 13	
	ST12-D3	12 h	Figures 14–16			Figure 15

and the SEM, however, the organic network sheet wrinkles and shrinks (Figure 16).

DISCUSSION

Advantages of the HMDS technique: Immersion in HMDS prior to air-drying dries more clearly the true arrangement of the insoluble organic microstructures in etched bivalve mollusk and barnacle shells than does the commonly used CPD technique. Generally, the organic framework of slightly etched cross-sections or etched surface samples is well preserved in its original three-dimensional condition when dried from HMDS. This drying quality allows high precision analysis of the structural organic framework in the shells.

Growth patterns in HMDS-treated, slightly demineralized shells appear much clearer than in AIR or ALC processed specimens. In the latter cases, narrow growth increments are completely covered by collapsed organic material. Under the burden of the collapsed organic meshwork, fine and organic-rich increments may fall over to adjacent growth increments. These adverse effects prevent sclerochronologists from counting and measuring the growth increments correctly. In specimens dried from HMDS, even sub-daily growth patterns can be recognized with ease.

HMDS drying does not require expensive lab equipment or additional skills like CPD. Sample preparation is easy, takes only a few minutes and does not require constant monitoring during the immersion or the drying process. Moreover, the sample size is not restricted by [illegible] mm chamber like in the CPD apparatus, [illegible] diffusion constraints. HMDS drying is less [illegible] CPD because it does not require high [illegible] processing, which may represent some [illegible] to the operator.

D[illegible] HMDS technique: Thick or[illegible] These artifacts may re[illegible] HMDS itself or from the high [illegible] SEM. The latter problem [illegible] and Peldri II treated soft tis[illegible] It is not clear if additional [illegible] prior to dehydrating and HM[illegible] and harden the organic mesh[illegible] with formalin reported [illegible] the structural arrangement of the organic fabric (Carvalho et al., 1996). We assume that longer infiltration and drying times may reduce the aforementioned, unwanted effects.

HMDS is a hazardous chemical. Its potential effects on humans and on the environment are barely known (Material Safety Data Sheet). It is strongly advised to use the chemical only under a fume hood and to prevent inhaling or skin contact.

CONCLUSIONS

HMDS drying is a very useful, low-cost, easy-to-apply and time saving alternative to other known drying techniques for soft tissues. This publication demonstrates the applicability of this fast drying solvent in sclerochronology and for the study of organic microstructures in some bivalve mollusk and barnacle shells. With HMDS, we achieved results qualitatively superior to the widely applied CPD. Further studies should determine if the HMDS method can be used as a routine technique in drying organic structures of etched molluscan and barnacle shells and if the HMDS method can also be applied to etched accretionary hard parts of other marine or terrestrial organisms.

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LITERATURE CITED

Anderson, T. F. 1951. Techniques for the preservation of three-dimensional structure in preparing specimens for the electron microscope. Transactions of the New York Academy of Sciences 13: 130–134.

Bourget, E. 1980. Barnacle shell growth and its relationship to environmental factors. In: D. C. Rhoads and R. A. Lutz, (eds.) Skeletal growth of aquatic organisms. Plenum Publishing Corp., New York. Topics in Geobiology 1: 469–491.

Boyde, A. and C. Wood. 1969. Preparation of animal tissue for surface electron microscopy. Journal of Microscopy 90: 221–249.

Carvalho, R. M., M. Yoshiyama, P. D. Brewer and D. H. Pashley. 1996. Dimensional changes of demineralized human dentine during preparation for scanning electron microscopy. Archives of Oral Biology 41: 379–386.

Chissoe, W. F., E. L. Vezey and J. J. Skvarla. 1994. Hexamethyldisilazane as a drying agent for pollen scanning electron microscopy. Biotechnic & Histochemistry 69: 192–198.

Clark, G. R. II. 1980. Techniques for observing the organic matrix of molluscan shells. In: D. C. Rhoads and R. A. Lutz, (eds.). Skeletal growth of aquatic organisms. Plenum Publishing Corp., New York. Topics in Geobiology 1: 607–612.

Clark, G. R. II. 1999. Organic matrix taphonomy in some molluscan shell microstructures. Paleogeography, Paleoclimatology, Paleoecology 149: 305–312.

Crenshaw, M. A. 1990. Biomineralization Machanisms. In: J. G. Carter (ed.) Skeletal Biomineralization: Patterns, Processes and Evolutionary Trends. Volume I. Van Nostrand Reinhold, New York, pp. 1–9.

Davenport, C. B. 1938. Growth lines in fossil pectens as indicators of past climates. Journal of Paleontology 12: 514–515.

Dekker, N. P., C. J. Lammel and G. F. Brooks. 1991. Scanning electron microscopy of piliated *Neisseria gonorrhoeae* processed with hexamethyldisilazane. Journal of electron microscopy technique 19: 461–467.

Heegaard, S., O. A. Jensen and J. U. Prause. 1986. Hexamethyldisilazane in preparation of retinal tissue for scanning electron microscopy. Ophthalmic Research 18: 203–208.

Hochberg, R. and M. K. Litvaitis. 2000. Hexamethyldisilazane for scanning electron microscopy of *Gastrotrichia*. Biotechnic & Histochemistry 75: 41–44.

Kennedy, J. R., R. W. Williams and J. P. Gray. 1989. Use of Peldri II (a fluorocarbon solid at room temperature) as an alternative to critical point drying for biological tissues. Journal of Electron Microscopy Techniques 11: 117–125.

Koike, H. 1986. Microstructure of growth increments in the shell of Mercenaria mercenaria (Linne). Transactions and Proceedings of the Palaeontological Society of Japan, New Series 141: 289–295.

Leal, J. H. and L. R. L. Simone. 1998. *Propilidium curumim*, a new species of Lepetidae (Gastropoda: Patellogastropoda) from off southern and southeastern Brazil. Bulletin of Marine Science 63: 157–165.

Mann, S. 1983. Mineralization in biological systems. Structure and Bonding 54: 125–174.

Nation, J. L. 1983. A new method using hexamethyldisilazane for preparation of soft insect tissues for scanning electron microscopy. Stain Technology 58: 347–351.

Pannella, G. and C. MacClintock. 1968. Biological and environmental rhythms reflected in molluscan shell growth. Paleontolological Society, Memoir 42: 64–81.

Perdigao, J., P. Lambrechts, B. van Meerbeek, G. Vanherle and A. L. B. Lopes. 1995. Field emission SEM comparison of four postfixation drying techniques for human dentine. Journal of Biomedical Materials Research 29: 1111–1120.

Rhoads, D. C. and R. A. Lutz. 1980. (eds.) Skeletal growth of aquatic organisms. Plenum Publishing Corp., New York. Topics in Geobiology 1: 1–750.

Rumph, J. A. and W. J. Turner. 1998. Alternative to Critical Point Drying for soft-bodied insect larvae. Annals of the Entomological Society of America 91: 693–699.

Schöne, B. R., K. W. Flessa, D. L. Dettman, D. H. Goodwin and P. D. Roopnarine. In press. Sclerochronology and growth of the bivalve mollusks *Chione (Chionista) fluctifraga* and *C. (Chionista) cortezi* in the northern Gulf of California, Mexico. The Veliger Jan. 2002.

Simkiss, K. and K. M. Wilbur. 1989. Biomineralization. Cell Biology and Mineral Deposition. Academic Press, San Diego, pp. 1–337.

Quattlebaum, E. C. and G. R. Carner. 1980. A technique for preparing *Beauveria* spp. for scanning electron microscopy. Canadian Journal of Botany 58: 1700–1703.

Watabe, N., R. J. Kingsley and T. Kawaguchi. 1993. Functions of organic matrices in some invertebrate calcifying systems. In: I. Kobayashi, H. Mutvei and A. Sahni (eds.) Structure, Formation and Evolution of Fossil Hard Tissues. Tokai Univ. Press, Tokyo, pp. 3–11.

Werÿha, G., L. Marchal, J. Leclere, G. Grignon and P. Hartemann. 1990. Scanning electron microscopy (SEM) of the human thyroid gland: a technical improvement for follicular cell observation. Journal of Submicroscopic Cytology and Pathology 22: 459–464.

Gone with the wind: a pelagic marine species described as an endemic land snail from the Bahamas

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ABSTRACT

Abaconia naufraga (Clench, 1938), hitherto assumed to represent a monotypical genus and species of Subulinidae (Gastropoda, Pulmonata) endemic to the Bahamas, is shown to be a synonym of the marine pelagic snail *Litiopa melanostoma* Rang, 1829 (Caenogastropoda: Litiopidae). Instances of genera of land and freshwater gastropods originally mistakenly described as marine, and vice versa, are reviewed. Of the 10 names involved, four are valid (*Daronia*, *Karolus*, *Teretropoma*) or potentially valid (*Digoniaxis*), one (*Brondelia*) has been suppressed by the ICZN, and the other five (*Abaconia*, *Afrocanidea*, *Anaplocamus*, *Bullinopersilia*, *Pseudolibania*) are synonyms.

INTRODUCTION

William J. Clench (1938) described *Leptinaria* (*Abaconia*) *naufraga* as a new subgenus and species in the pulmonate family Subulinidae, based on specimens collected by J.C. and G. Greenway and himself in the Bahamas in April 1936. The description was accompanied by black and white photographs. The journal where the description was published (Memorias de la Sociedad Cubana de Historia Natural) may have contributed to the lack of attention that these new taxa have subsequently received in the literature: in fact, the name *Abaconia* is not mentioned at all by Zilch (1959–60) in the pulmonate volume of the standard *Handbuch der Paläozoologie*. *Abaconia* has recently been elevated to genus level b[illegible] (1999: 513, fig. 666), and classified as a m[illegible] [illegible] Subulininae.

In the [illegible] ation Clench noted that "this spec[illegible] ably from all others known to him [illegible] ana. The remarkably acute apex an[illegible] sculpture from axial on the first fou[illegible] the remaining whorls is sharply diffe[illegible] cies, and the thickening of the shell is [illegible] s genus". He speculated that *Leptinaria* [illegible] and two other endemic pulmonat[illegible] a remnant of a much older fauna [illegible] relationships. However, examination of the [illegible] in MCZ (Figures 1–3) reveals that *Abaconia naufraga* is not a subulinid, and not even a pulmonate, but a synonym of *Litiopa melanostoma*, a circumtropical pelagic cerithioid (Figs 4–6). Clench and Schileyko had properly described the apical sculpture of *Abaconia*, but had failed to recognize its identity. The protoconch of *Litiopa melanostoma* consists of four whorls with strong axial ribs, abutting adaxially on the preceding whorl and interrupted by a smooth band on the shoulder; the protoconch/teleoconch discontinuity is marked by a sinusigera notch (Luque et al., 1988: 182, figs 1, 4).

Litiopa melanostoma is abundant in the midst of floating *Sargassum*, and it is easy to imagine how they can be washed ashore and blown inland after the seaweed fronds have been sun-dried. The species is known to occur off the Bahamas (Luque et al., 1988).

SYSTEMATICS

Class Gastropoda Cuvier, 1797
Superfamily Cerithioidea Fleming, 1822
Family Litiopidae Gray, 1847
Genus *Litiopa* Rang, 1829

New synonym:

Abaconia Clench, 1938. Type species: *Leptinaria* (*Abaconia*) *naufraga* Clench, 1938, by original designation.

Bombyxinus Bélanger [in Lesson], 1835 is another already recognized synonym of *Litiopa*.

Litiopa melanostoma Rang, 1829

New synonym:

Leptinaria (*Abaconia*) *naufraga* Clench, 1938: 324, pl. 24, figs 1–2.

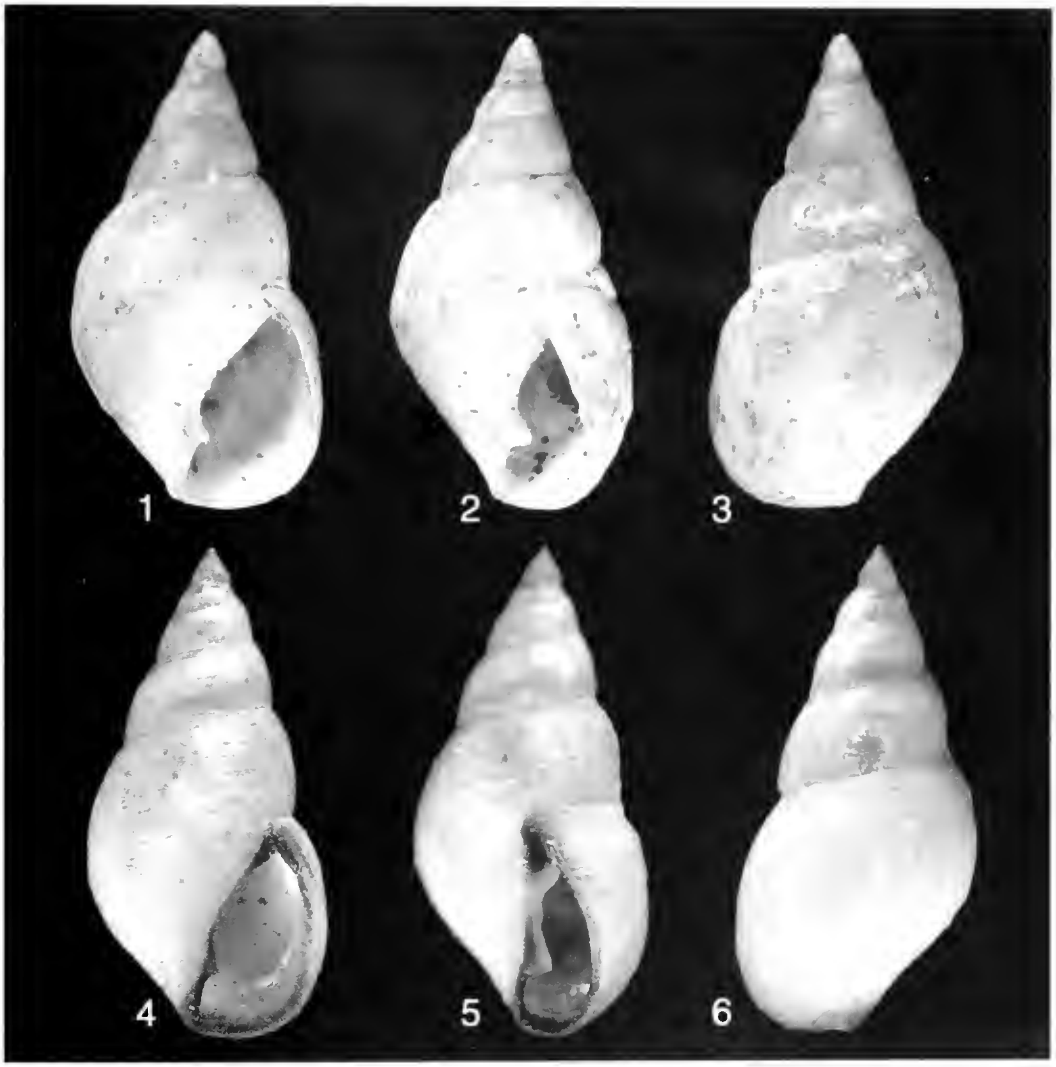
Abaconia naufraga.—Schileyko, 1999: 514, fig. 666.

Type Material: Holotype MCZ 116705; 34 paratypes, MCZ 116706, 4 paratypes MCZ 116707.

Type Locality: Sand Bank, Crossing Bay, Great Abaco Island, Bahamas. Paratypes from the type locality (MCZ 116706) and Mores Island (MCZ 116707).

DISCUSSION

Shells of land and freshwater snails are occasionally washed to the sea and have not infrequently been de-



Figures 1–6. *Litiopa melanostoma* Rang, 1829. **1–3.** Holotype of *Leptinaria* (*Abaconia*) *naufraga* Clench, 1938, MCZ 116705, Sand Bank, Crossing Bay, Great Abaco Island, Bahamas. Height 4.2 mm. **4–6.** One of five syntypes of *Litiopa melanostoma* Rang, 1829, MNHN [uncatalogued], "Atlantic Ocean", Rang coll., 1834. Height 4.6 mm.

scribed as marine gastropods, but the reverse has also occasionally happened. The awareness of these situations across the traditional boundaries of marine and non-marine molluscan literature is problematic, and it may be useful to take the case of the *Abaconia* to draw the attention of taxonomists to names that might have escaped their attention. These are presented below in the chronological order they were described, and summarized in Table 1. Two of the genera involved even became the types of new family-group names, Teretropomidae Rochebrune, 1881, and Anaplocamidae Dall, 1921, and it is probable that, if they had not been mistaken about their habitat, Rochebrune and Dall would not have failed to recognize them as representatives of the families Architectonicidae and Pleuroceridae, respectively. Of the 10 genera involved, four are valid (*Daronia*, *Karolus*, *Teretropoma*) or potentially valid (*Digoniaxis*), one (*Brondelia*) has been suppressed by the ICZN, and the other five (*Abaconia*, *Afrocanidea*, *Anaplocamus*, *Bullinopersilia*, *Pseudolibania*) are synonyms.

***Daronia* A. Adams, 1861.** Based on a specimen from the Cuming Collection *Cyclostrema* (*Daronia*) *spirula* A. Adams, 1861 was described as a new subgenus and species of marine gastropod from the Philippines. Warén and Bouchet (1988) showed that it is a South American species of the land snail family Poteriidae, *Daronia* A. Adams, 1861, being a senior synonym of *Buckleyia* Higgins, 1872.

***Brondelia* Bourguignat, 1862.** Described as a new genus of Ancylidae, with two species, *B. drouetiana* Bourguignat, 1851 (originally described based on material from the Cuming collection from "North America") and *B. gibbosa* Bourguignat, 1862, said to be living on damp rocks in the forest of Edough, near Bône in Algeria. *Brondelia* remained in the freshwater family An-

Table 1. Nominal genera of marine gastropods (arranged alphabetically) originally described as land snails and vice versa.

Nominal genus	Described as	Revised position	Reference
Abaconia Clench, 1938	Subulinidae	Litiopidae	this paper
Afrocanidea Connolly, 1929	freshwater Buccinidae	Ranellidae	Beu (1998)
Anaplocamus Dall, 1896	Trichotropidae	Pleuroceridae	Rehder (1942)
Brondelia Bourguignat, 1862	Ancylidae	Siphonariidae	Marshall (1981)
Bullinopersilia F. Nordsieck, 1972	Acteonidae	Ferussaciidae	Smriglio and Mariottini (1996)
Daronia A. Adams, 1861	Cyclostrematidae	Poteriidae	Warén and Bouchet (1988)
Digoniaxis Jousseaume, 1889	Ferussaciidae	Pyramidellidae	Neubert (1998)
Karolus de Folin, 1870	Acteonidae	Ferussaciidae	Zilch (1959)
Pseudolibania Stefani, 1870	Dandebardiidae	Pleurobranchidae	Zilch (1985)
Teretropoma Rochebrune, 1881	Cyclostomatidae	Architectonicidae	Crosse (1882)

cylidae until Marshall (1981) recognized it as identical with the marine pulmonate *Williamia* Monterosato, 1884 [family Siphonariidae]. Incidentally, the name *Brondelia* is the senior synonym, but it was subsequently suppressed and placed on the Official Index of Rejected and Invalid Generic Names in Zoology by the ICZN (1986, Opinion 1410).

***Karolus* de Folin, 1870.** *Karolus primus* de Folin, 1870, was described as a new genus and species of marine snail from off Vera Cruz on the Pacific coast of Central America. *Karolus* was not originally placed in a family, and was omitted from standard textbooks and treatises for nearly a century. It was treated by Zilch (1959) as a valid subgenus of *Cecilioides* Férussac, 1814 [family Ferussaciidae], and by Schileyko (1999) as a full genus.

***Pseudolibania* Stefani, 1879.** *Daudebardia tarentina* Stefani and Pantanelli, 1879, was described as a land snail from the hills near Taranto in southern Italy. It was made the type species of a section *Pseudolibania* Stefani, 1879, of *Daudebardia* Hartmann, 1821 [family Daudebardiidae], later elevated to full genus by Forcart (1950). Zilch (1985) has shown that *D. tarentina* is a synonym of *Susania testudinaria* Cantraine, 1835, and *Pseudolibania* a synonym of *Susania* Gray, 1857 [family Pleurobranchidae].

***Teretropoma* Rochebrune, 1881.** Immediately after [illegible] based on live-taken specimens from the D[illegible] Senegal [illegible] of *Teretropoma perrieri* [illegible] a new genus and species of "Cy-[illegible] a new subfamily Teretropom-[illegible] recognized it as an architecton-[illegible] 1842. *Teretropoma* is cur-[illegible] of *Heliacus* d'Orbigny, 1842 [illegible] an Atlantic subspecies of *H.* [illegible] 1791 (Bieler, 1993).

Digoniaxis [illegible] *Digoniaxis bourguignati* Jousse[illegible] bed as a new genus and species [illegible] as a land snail of the family Ferussa[illegible] d by Zilch (1959: 342). Based on a [illegible] type material, Neubert (1998) real[illegible] same family Pyramidellidae. Although Schileyko (1999), refering to Neubert, suggested that only an anatomical study would establish firmly the systematic position of *Digoniaxis*, the heterostrophic protoconch leaves no doubt that it is indeed a pyramidelloid.

***Anaplocamus* Dall, 1896.** *Anaplocamus borealis* Dall, 1896, was described as a new genus and species of Trichotropidae from Alaska, and later even became the type of the monotypic family Anaplocamidae Dall, 1921. Rehder (1942) discovered that this was in fact a synonym of the freshwater snail *Anculosa dilatata* Conrad, 1835 [now *Leptoxis dilatata*; family Pleuroceridae], from eastern United States, which had been erroneously labelled as from a marine Alaska locality.

***Afrocanidea* Connolly, 1929.** *Afrocanidea gemma* Connolly, 1929, was described as a new genus and species of freshwater Buccinidae, reputedly from Shimbi Hills, Kenya, but the holotype was shown to be a larval shell of *Cymatium muricinum* (Röding, 1798) [family Ranellidae], with *Afrocanidea* Connolly, 1929, ending up in synonymy of *Gutturnium* Mörch, 1852 (Beu, 1998).

***Bullinopersilia* F. Nordsieck, 1972.** Based on a single empty shell, *Bullinopersilia sphaeroides* F. Nordsieck, 1972 was described as a new genus and species of Acteonidae from shallow water off the Baleares, in the western Mediterranean. Smriglio and Mariottini (1996) recognized it as a juvenile of the land snail *Ferussacia folliculus* (Gmelin, 1791) [family Ferussaciidae].

LITERATURE CITED

Beu, A. 1998. Indo-West Pacific Ranellidae, Bursidae and Personidae (Mollusca: Gastropoda). A monograph of the New Caledonian fauna and revisions of related taxa. Mémoires du Muséum national d'Histoire naturelle 178: 1–255.

Bieler, R. 1993. Architectonicidae of the Indo-Pacific (Mollusca, Gastropoda). Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg, new series, 30: 1–377.

Clench, W. J. 1938. Land and freshwater mollusks of Grand Bahama and the Abaco Islands, Bahama Islands. Memorias de la Sociedad Cubana de Historia Natural 12(4): 303–333, pl. 24–25.

Crosse, H. 1882. [Book review of] Sur un type nouveau de la famille des Cyclostomacea par le Dr. A. T. de Rochebrune. Journal de Conchyliologie 30: 249–250.

Forcart, L. 1950. Systématique des Mollusques en forme de *Daudebardia* et révision des espèces d'Anatolie et de l'île de Crète. Journal de Conchyliologie 90: 107–117.

Luque, A. A., Templado, J. and L. P. Burnay. 1988. On the systematic position of the genera *Litiopa* Rang, 1829 and *Alaba* H. and A. Adams, 1853. Malacological Review, suppl. 4: 180–193.

Marshall, B. A. 1981. The genus *Williamia* in the western Pacific (Mollusca: Siphonariidae). New Zealand Journal of Zoology 8: 487–492.

Neubert, E. 1998. *Digoniaxis bourguignati* Jousseaume 1889, a genus and species of the Pyramidellidae (Gastropoda Heterostropha). Archiv für Molluskenkunde 127(1–2): 103–106.

ICZN [International Commission on Zoological Nomenclature]. 1986. Opinion 1410. *Williamia* Monterosato, 1884 (Mollusca, Gastropoda): conserved. Bulletin of Zoological Nomenclature 43: 249.

Rang, S. 1829. Notice sur le Litiope (*Litiopa*), genre nouveau de Mollusque gasteropode. Annales des Sciences Naturelles 16: 303–307.

Rehder, H. A. 1942. A note on the genus *Anaplocamus* Dall. The Nautilus 56: 49–50.

Schileyko, A. A. 1999. Treatise on Recent terrestrial pulmonate molluscs. Part 4. Ruthenica suppl. 2: 435–564.

Smriglio, C. and P. Mariottini. 1996. Central Tyrrhenian Sea Mollusca XI. Description of *Callostracon tyrrhenicum* sp. nov. (Gastropoda Acteonidae) and remarks on the other Mediterranean species of the family Acteonidae d'Orbigny 1835. Basteria 60: 183–193.

Warén, A. and P. Bouchet. 1988. A new species of Vanikoridae from the western Mediterranean, with remarks on the northeast Atlantic species of the family. Bollettino Malacologico 24(5–8): 73–100.

Zilch, A. 1959–1960. Teil 2. Euthyneura. In: O. H. Schindewolf (ed.), *Handbuch der Paläozoologie, Band 6, Gastropoda*. Borntraeger, Berlin, xii + 835 pp.

Zilch, A. 1985. *Daudebardia tarentina* und *Pseudolibania* (Nudibranchia Notaspidea Pleurobranchidae). Archiv für Molluskenkunde 115(4–6): 291–300.

In Memoriam

Tadashige Habe

1916–2001

Russel H. Jensen

1918–2001

Note

Biogeography of the deep-sea gastropod *Palazzia planorbis* (Dall, 1927): an uncommon form of rarity

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Palazzia planorbis (Dall, 1927) is a minute deep-sea gastropod of uncertain phylogenetic affinity, possibly residing in one of the groups that were once included in the Archaeogastropoda (Warén 1991, 1993). It has a planispiral shell bearing distinctive axial ribs that branch midway toward the outer whorl margins (Figure 1). Like many deep-sea species, its natural history is unknown. Moore (1971) first noted that *P. planorbis* occupies an unusually broad geographic distribution in the western North Atlantic, having been dredged at 2967 m off Labrador and at 538 m off Florida. Warén (1991, 1993) subsequently reported the species from west of Iceland at 241 m and in the eastern North Atlantic off the British Isles from 2081–2898 m. Here, I provide additional records for the western and eastern North Atlantic, tropical Atlantic, and the western South Atlantic (Table 1). These new locality data come from my examination of material provided by the Woods Hole Benthic Sampling Program (Sanders, 1977) and the Atlantic Continental Slope and Rise Study (Grassle and Maciolek, 1992). *Palazzia planorbis* is revealed to have an extraordinarily broad geographic distribution that spans Southern and Northern Hemispheres from 43°33′S to 65°06′N, and includes both the eastern and western corridors of the deep Atlantic (Table 1, Figure 2). Its bathymetric range is similarly impressive, extending from the uppermost reaches of the continental slope (241 m) to the deep abyssal plain (5210 m).

While the shell sculpture of *Palazzia planorbis* appears to be [illegible] among planispiral deep-sea microgastropods, [illegible] individual variation in the expression [illegible] axial ribs and the extent of branching [illegible] geographic variation throughout its [illegible] because of the scarcity of mat[illegible] of sampling localities (Table [illegible] the specimen from the eastern [illegible] in Figure 1 is remarkably sim[illegible] figured by Warén (1991: 77 [illegible] collected in the western and east[illegible] to 3259 m shallower and 45° to 70° [illegible]

Its enormous geog[illegible] ranges are especially notable because *Palazzia planorbis* is very rare, and is included among the smallest gastropods. Specimens from the Woods Hole Benthic Sampling Program (Table 1) were all collected by using epibenthic sleds (Hessler and Sanders, 1967), which are typically towed for one kilometer on the bottom and yield samples that represent about 1000 linear m² of seafloor. As a rough approximation, the data in Table 1 suggest a median density of one individual per 1000 m², with a maximum of 17 individuals per 1000 m² in the western South Atlantic. This is rare, even for deep-sea gastropods which usually exist at low abundance (Rex et al., 1990; Rex and Etter, 1998). With a shell diameter reaching only between one and two millimeters, it is also an extremely small gastropod—both for the Gastropoda as a whole (Bieler and Mikkelsen, 1998) and for the deep-sea fauna (Rex and Etter, 1998).

Relationships among geographic range size, abundance and body size are central to macroecology. Although a great deal of variation has been observed, abundance and body size are generally related to one another negatively, and related to range size positively (Gaston, 1994; Brown, 1995; Gaston and Blackburn, 2000). Thus the combination of low density, large geographic range and small body size observed in *Palazzia planorbis* is exceptional. Rabinowitz (1981) proposed a three-way classification of rarity based on geographic distribution, habitat specificity and local population size. *Palazzia planorbis*, with its extensive geographic range in the Atlantic, occupation of different habitats (depth zones) and small local populations, represents one of the most uncommon forms of rarity in the Rabinowitz scheme. Schoener (1987) referred to low relative abundance throughout a species range as suffusive rarity, and showed that this pattern is an extreme end-member of the rarity continuum.

Widely distributed rare species are also known among deep-sea protobranch bivalves. Examples include *Pristigloma nitens* and *P. alba* (Sanders and Allen, 1973), and *Yoldiella fabula* (Allen et al., 1995). Other bivalves are common in one or more deep-sea basins and rare elsewhere (Allen and Sanders, 1996), a pattern that Schoe-

Figure 1. *Palazzia planorbis* collected from station 195 in the eastern tropical Atlantic (see Table 1 for locality data). The specimen measures 1.24 mm in maximum diameter.

ner (1987) termed diffusive rarity. The incidence of rare deep-sea gastropods occupying broad geographic ranges is still unclear since most taxonomic syntheses, such as Bouchet and Warén's (1980) excellent monograph, have been regional in scope.

Studies of rarity and range delineation are fraught with uncertainty and methodological difficulties (Gaston 1994). It should be cautioned that the apparent abundance of *Palazzia planorbis* (Table 1) may be partly due to sampling error. The mesh size of the collecting net used on epibenthic sleds deployed in the Woods Hole Benthic Sampling Program is 1.0 mm. This is fine enough to capture adults. Smaller juveniles could pass through the mesh, but some do in fact appear in samples. The sieve size used to sort the macrofauna is 420 µm, which should retain all but the smallest post-larval individuals of this species. Earlier sampling, however, used larger mesh and sieve sizes, suggesting that recovery of *P. planorbis* was happenstance. Since the samples are widely separated and represent only five regions of the Atlantic (Table 1, Figure 2), we cannot document the full geographic range or know relative abundance throughout the range. It is possible that *P. planorbis* has an unrecognized center of high density and shows diffusive rather than suffusive rarity (*sensu* Schoener, 1987). Finally, it should be pointed out that, while *P. planorbis* appears to be a coherent morphospecies, some phenotypically uniform deep-sea mollusks show strong population structure at the genetic level (Etter et al., 1999). *P. planorbis* may be a complex of genetically divergent populations or species. Even considering these potential problems, the combination of a Pan-Atlantic distribution, conserved morphology, low abundance and small size would seem to represent an extremely unusual form of rarity for marine mollusks.

Table 1. Locality data for *Palazzia planorbis* in the Atlantic. Where the source of data is not indicated, it refers to this study. ACSAR refers to the Atlantic Continental Slope and Rise Study (Grassle and Maciolek, 1992). WHOI refers to the Woods Hole Benthic Sampling Program (Sanders, 1977), and is followed by the name of the vessel and cruise number. Please see references listed under source for information on other collecting expeditions.

Region	Source	Expedition	Station	Depth (m)	Latitude	Longitude	Specimens
Western North Atlantic	Warén, 1993	Jón Bógason, Coll.	—	241	65°06′ N	26°42′ W	1
	Moore, 1971	Bulldog	—	2967	55°36′ N	54°33′ W	1
		WHOI Chain 106	334	4400	40°43.3′ N	46°14.2′ W	6
		ACSAR	13	1250	39°18.35′ N	70°54.94′ W	1
		WHOI Atlantis II 24	126	3806	39°37.25′ N	66°45.55′ W	1
		WHOI Knorr 35	340	3310	38°16.0′ N	70°21.55 W	1
		WHOI Atlantis II 40	175	4680	36°36.0′ N	68°30′ W	1
	Moore, 1971	Albatross	2668	538	30°58′ N	79°38′ W	1
Eastern North Atlantic	Warén, 1993	INCAL	DS01	2091	57°59.5′ N	10°40.5′ W	1
	Warén, 1993	INCAL	DS02	2081	57°58.7′ N	10°48.9′ W	1
	Warén, 1993	INCAL	DS05	2503	56°27.9′ N	11°11.8′ W	1
	Warén, 1993	INCAL	DS06	2494	56°26.3′ N	11°10.6′ W	1
	Warén, 1991	INCAL	CP05	2884	55°00.4′ N	12°30.2′ W	1
	Warén, 1993	Challenger II	190	2898	54°41′ N	12°18′ W	1
		WHOI Chain 106	323	3347	50°08.3′ N	13°52.3′ W	1
Western Tropical Atlantic		WHOI Knorr 25	295	1011	8°04.2′ N	54°21.3′ W	2
		WHOI Atlantis II 31	159	887	7°58.0′ S	34°22.0′ W	1
Eastern Tropical Atlantic		WHOI Atlantis II 42	198	1563	10°26.5′ S	9°06.5′ E	1
		WHOI Atlantis II 42	197	1596	10°29′ S	9°04′ E	4
		WHOI Atlantis II 42	195	3797	14°45′ S	9°55′ E	2
Western South Atlantic		WHOI Atlantis II 60	239	1670	36°49.0′ S	53°15.4′ W	1
		WHOI Atlantis II 60	247	5216	43°33.0′ S	48°58.1′ W	17

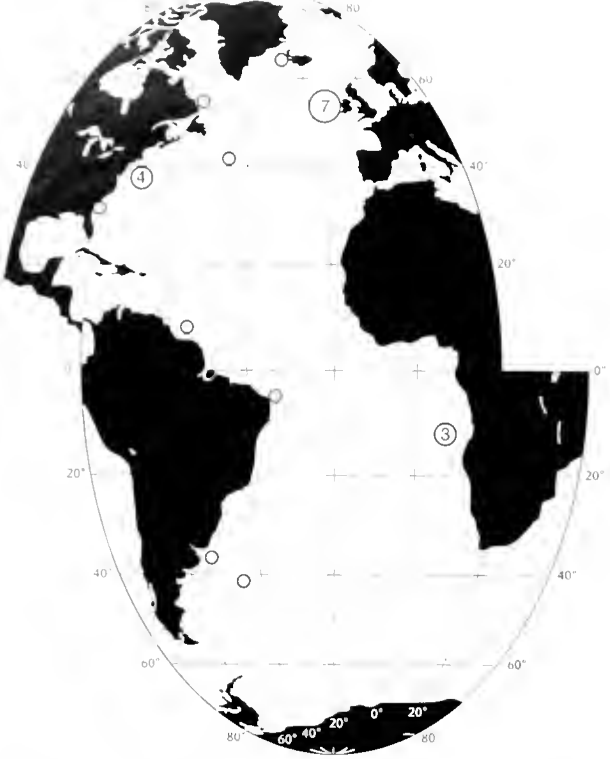

Figure 2. The distribution of *Palazzia planorbis* in the Atlantic (see Table 1 for station data). Circled numbers represent the number of samples yielding *P. planorbis* in that region. Circles without numbers represent individual samples.

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LITERATURE CITED

Allen, J. A. and H. L. Sanders. 1996. The zoogeography, diversity and origin of the deep-sea protobranch bivalves of the Atlantic: The epilogue. Progress in Oceanography 38: 95–153.

Allen, J. A., H. L. Sanders and F. J. Hannah. 1995. Studies on deep-sea Protobranchia (Bivalvia : the subfamily Yoldiellinae. Bulletin of the British Museum (Natural History), Zoology 61: 11–90.

Bieler, R. and P. M. Mikkelsen. 1998. *Ammonicera* in Florida: notes on the smallest living gastropod in the United States and comments on other species of Omalogyridae (Heterobranchia). The Nautilus 111: 1–12.

Bouchet, P. and A. Warén. 1980. Revision of the north-east Atlantic bathyal and abyssal Turridae (Mollusca, Gastropoda). The Journal of Molluscan Studies, Supplement 8: 1–119.

Brown, J. H. 1995. Macroecology. University of Chicago Press, Chicago, 269pp.

Etter, R. J., M. A. Rex, M. C. Chase and J. M. Quattro. 1999. A genetic dimension to deep-sea biodiversity. Deep-Sea Research I 46: 1095–1099.

Gaston, K. J. 1994. Rarity. Chapman and Hall, London, 205 pp.

Gaston, K. J. and T. M. Blackburn. 2000. Pattern and process in macroecology. Blackwell Science, Oxford, 377 pp.

Grassle, J. F. and N. J. Maciolek. 1992. Deep-sea species richness: regional and local diversity estimates from quantitative bottom samples. American Naturalist 139: 313–341.

Hessler, R. R. and H. L. Sanders. 1967. Faunal diversity in the deep-sea. Deep-Sea Research 14: 65–78.

Moore, D. R. 1971. A deep water *Omalogyra* in the western Atlantic. The Nautilus 84: 113–117.

Rabinowitz, D. 1981. Seven forms of rarity. *In*: Synge, H. (ed.) The biological aspects of rare plant conservation. pp. 205–217. Wiley, New York.

Rex, M. A. and R. J. Etter. 1998. Bathymetric patterns of body size: implications for deep-sea biodiversity. Deep-Sea Research II 45: 103–127.

Rex, M. A., R. J. Etter and P. W. Nimeskern, Jr. 1990. Density estimates for deep-sea gastropod assemblages. Deep-Sea Research 37: 555–569.

Sanders, H. L. 1977. Evolutionary ecology and the deep-sea benthos. *In*: Goulden, C.E. (ed.) The changing scenes in natural sciences 1776–1976. pp. 223–243. Academy of Natural Sciences Special Publication, Philadelphia.

Sanders, H. L. and J. A. Allen. 1973. Studies on the deep-sea Protobranchia (Bivalvia): Prologue and the Pristiglomidae. Bulletin of the Museum of Comparative Zoology 145: 237–262.

Schoener, T. W. 1987. The geographical distribution of rarity. Oecologia 74: 161–173.

Warén, A. 1991. New and little known Mollusca from Iceland and Scandinavia. Sarsia 76: 53–124.

Warén, A. 1993. New and little known Mollusca from Iceland and Scandinavia. Part 2. Sarsia 78: 159–201.

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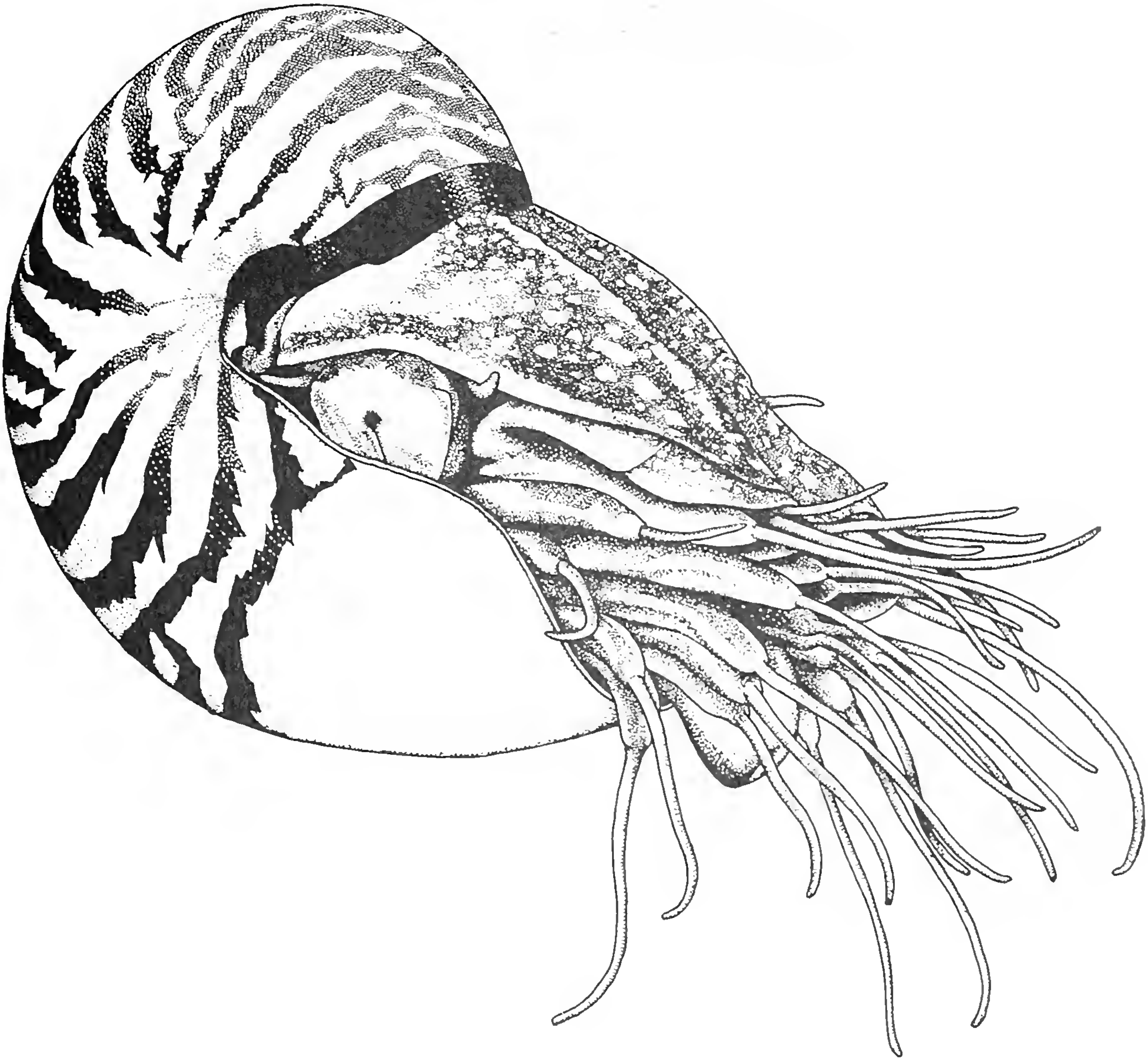

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A cladistic analysis of *Lithasia* (Gastropoda: Pleuroceridae) using morphological characters

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ABSTRACT

The classification of pleurocerid snails and other freshwater mollusks has historically been based on morphological characters. Despite years of taxonomic work on pleurocerids, no single work includes all recognized taxa from a given group and only a few systematic treatments of the family or individual genera exist. Modern methods of phylogenetic systematics have shown that some morphological traits do not support historically accepted mollusk classifications. If analyses of morphological characters do support current taxonomic hypotheses, then the classification of these groups can be considered as stable. If not, our approach regarding diagnostic characters for these groups must change. This paper uses 25 shell and radular characters in a cladistic analysis of the pleurocerid genus *Lithasia*, and compares the findings to previously suggested classifications of the group. Cladistic analyses do not support any current or historical classification of *Lithasia*. However, these morphological characters are found to roughly delineate *Lithasia* and other extant pleurocerid genera, challenging previous works that suggest such characters have limited utility.

INTRODUCTION

Historically, the classification of freshwater mollusks has relied heavily on morphological features such as shell, soft anatomy, and reproductive structures (e.g., Tryon, 1873; Heard and Guckert, 1970; Davis and Fuller, 1981; Burch and Tottenham, 1980). This is particularly evident for pleurocerid snails, where shell features account for the majority of diagnostic characters used in the taxonomy and classification of the group. One group of pleurocerids that has been classified on the basis of shell characters is *Lithasia* Haldeman, 1840, a genus of large river snails found throughout the Cumberland, Ohio, Mississippi, and Tennessee River drainages.

Species of *Lithasia* possess conic to ovate-conic shells with fusiform apertures, a posterior callus on the parietal wall, and frequently some degree of sculpture on the body whorl (Burch, 1982). Most species were described initially as *Melania* and classified according to shell characteristics such as shape and sculpture. Haldeman (1840) erected *Lithasia* and designated *L. geniculata* Haldeman, 1840, as the type for the genus and later erected *Angitrema* (1841). Presence of posterior and anterior calluses united *Angitrema* and *Lithasia*. The primary characters separating the genera were that *Angitrema* shells were spinous and had apertures with an anterior sinus, while *Lithasia* shells lacked sculpture and the aperture was not as distinctly channeled in front as the typical *Angitremae* (Tryon, 1873). Goodrich (1921) supported Pilsbry and Rhoad's (1896) reduction of *Angitrema* under *Lithasia*, and *Lithasia* subsequently has stood as a single genus. Goodrich (1940) recognized four separate groups within *Lithasia*, based primarily on peculiarities of shell sculpture. In the 1970s, authors suggested taxonomic revisions of the genus, placing all members in *Io* (Davis, 1974) or *Pleurocera* (Stansbery, 1971; Stein, 1978). Burch and Tottenham (1980) recognized *Lithasia sensu stricto* and *Angitrema* as subgenera of *Lithasia* based on position of sculpture on the body whorl (Burch, 1982), and not according to the original diagnosis, while Turgeon et al. (1998) followed Burch in recognizing *Lithasia* as one genus.

Authors have historically assembled pleurocerid genera based on grouping taxa with shared shell characters. Such is the prevalent approach found in the literature published over a period of 150 years, and no analyses of these characters exists for *Lithasia* or any other pleurocerid genus. This may be a result of the lack of uniform information found in the literature. Different authors rarely provided comparable levels of qualitative or quantitative data in their original descriptions, and seldom used terms and expressions that may or may not have the same descriptive connotations (e.g., tapering versus broadly conic shells), making it difficult for readers to draw comparisons between works. Many descriptions were based on one or a few shells, juveniles, or partial shells given to the author, and radulae were not included in these descriptions. Finally, descriptions were subjective based on the experience of the author, the amount of variation they accepted, and their understanding of the other taxa in the literature. Given the current state of freshwater mollusk taxonomy in general and pleurocerids specifically, and the fact that morphological characters are still used to confirm taxon identity, anal-

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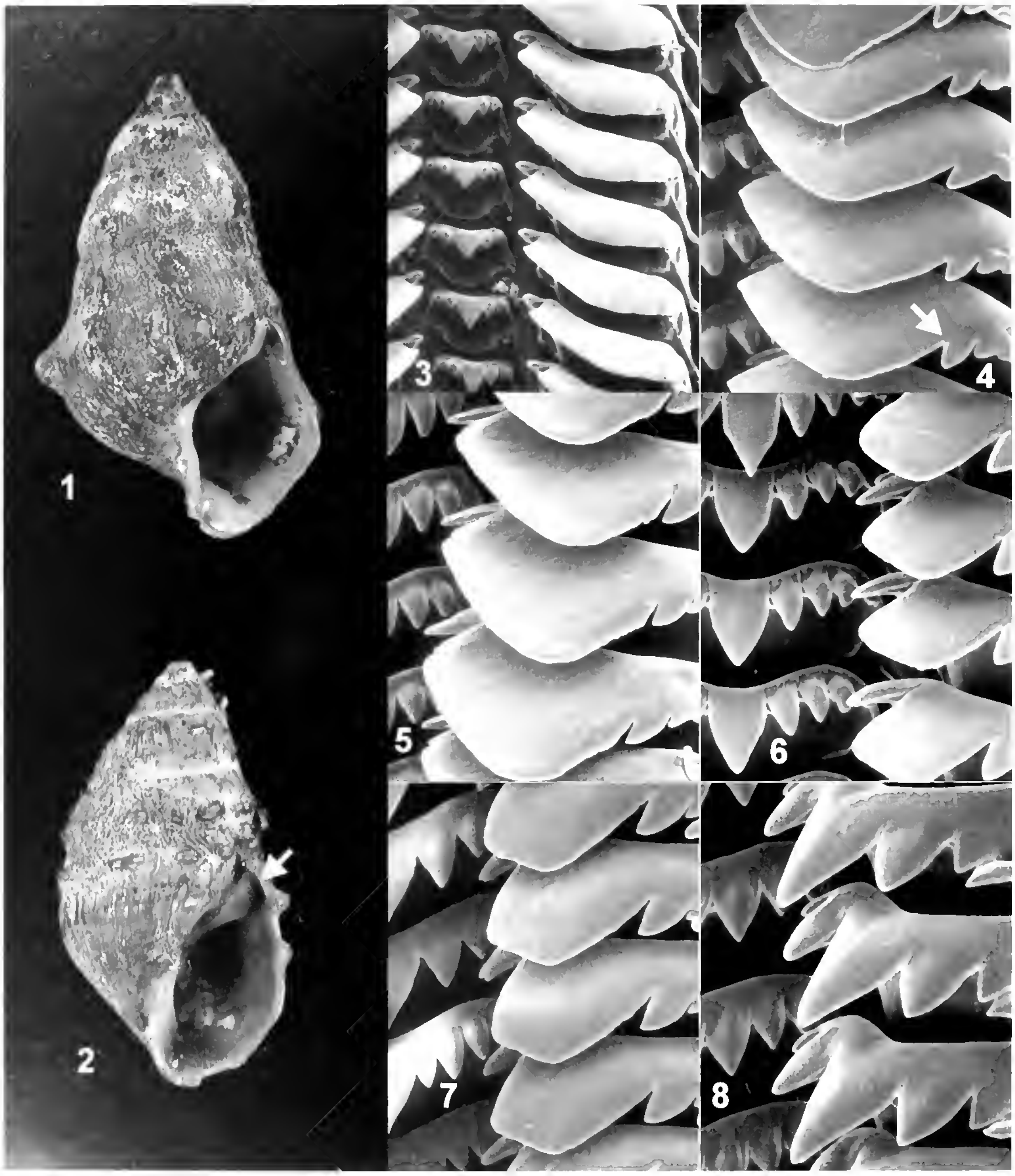

Figures 1–8. Illustrations of selected characters and character states used in the cladistic analysis of *Lithasia*. **1.** *Lithasia armigera* [illegible] aperture (2:2) and presence of anterior (7:1) and posterior (6:1) calluses on the columella. **2.** *Lithasia verrucosa* [illegible] body whorl (5:1) and posterior lengthening of aperture (arrow, 10:1). **3.** Absence of cusp next to lateral tooth [illegible]. **4.** [illegible] cusp next to lateral tooth (arrow, 13:1). **5.** Lamellar main lateral cusp (19:0). **6.** Rectangular main lateral [illegible] [illegible]al main lateral cusp (19:2). **8.** Triangular main lateral cusp (19:3).

[illegible] employing modern techniques [illegible] of phylogenetic systematics have sho[illegible] [illegible]ological traits do not support histori[illegible] [illegible]ask classifications (Graf, 2000; Lydeard [illegible] [illegible]alyses of morphological characters d[illegible] [illegible] taxonomic hypotheses, then the classifica[illegible] [illegible]oups can be stabilized. If not, our approach [illegible] [illegible]gnostic characters for these groups must change [illegible] [illegible]netic taxonomies of this kind have been advocated in several studies (e.g., de Queiroz and Gauthier, 1990, 1992, 1994; Bryant, 1996; Sereno, 1999; Lydeard et al., 2000).

Further complicating this problem is that pleurocerids, in a similar fashion to what happens to many other freshwater invertebrate groups, are experiencing declines in their number of species and individuals caused by river impoundment, habitat degradation, and poor land-use practices (Stein, 1976; Bogan et al., 1995; Lydeard et al., 1997). For example, in the Mobile Basin, one genus (*Gyrotoma*) and approximately 34 other species are presumed extinct (Stein, 1976; Bogan et al., 1995, Lydeard and Mayden, 1995; Lydeard et al., 1997). Even with the loss of diversity in the family, only five of 156 recognized pleurocerid species (Turgeon et al., 1998) are listed as either endangered or threatened as of May, 2001 (U.S. Fish and Wildlife Service). If morphology alone is to be used in identification of these imperiled taxa, then analyses of these characters gain even more importance. A lack of such analyses can hinder efforts to recognize, manage, and conserve distinct taxa (Waples, 1991; Mayden and Wood, 1995) within these affected groups.

The goal of this study is to compile shell and radula characters from *Lithasia*, analyze them using cladistic techniques in order to test historical and modern classifications of the genus and its species composition, and to determine possible relationships of the genus and its taxa to other pleurocerids based on those analyses. Potential changes to the taxonomy of *Lithasia* based on these analyses and the utility of using these characters in pleurocerid classification are discussed.

MATERIALS AND METHODS

Specimens for the study were either collected live or borrowed from museum collections (Appendix 1). Shell characters were taken directly from specimens. Radulae were extracted, cleaned, and prepared according to the method described by Holznagel (1998), viewed using a Hitachi S-2500 scanning electron microscope, photographed, and analyzed. For *Lithasia*, at least one representative from each recognized species and subspecies (Burch and Tottenham, 1980) was included. Specimens of selected taxa representing five other extant pleurocerid genera (*Elimia*, *Io*, *Juga*, *Leptoxis*, *Pleurocera*) were also included (Appendix 1). Data consisted of a matrix of 25 characters (Appendix 2, Figures 1–8) coded as either binary or multi-state (Appendix 3), and analyzed phylogenetically under maximum parsimony with NONA 2.0 (Goloboff, 1998) using the following settings: unordered data, 100 replicates, with *Juga silicula* and *Melanoides tuberculata* Müller, 1774 as outgroups. *Juga* is basal to the rest of the North American Pleuroceridae (Holznagel and Lydeard, 2000) and *M. tuberculata* was chosen as a more distant outgroup. Jackknife analysis (37% deletion, 1000 iterations of 10 replicates each) was performed in XAC (Farris, unpublished, Farris et al., 1996) to test the stability of the data. A strict consensus tree mapped with characters was produced with Winclada 0.9.99m24 (Nixon, 1999). The analysis was run twice, once using shell characters alone and once with all characters combined. Because most previous classifications (e.g., Tryon, 1873; Goodrich, 1940) were based on shell characters only, they were analyzed separately and combined with radula data.

Once the classification hypothesis was established, it was compared to five different classification schemes proposed by previous authors (Appendix 1).

A. Lithasia represents a single genus. This assumption follows the current (Turgeon et al., 1998) view of the genus.
B. Lithasia represents a single genus comprised of two subgenera, *Lithasia sensu stricto* and *Angitrema*, *sensu* Burch and Tottenham (1980). This classification is commonly used as a starting point in pleurocerid studies (e.g., Lydeard et al., 1997; Holznagel and Lydeard, 2000). Burch and Tottenham's (1980) genera and subgenera differ in species composition from those of Tryon (1873).
C. Lithasia represents a single genus comprised of four species groups based on peculiarities of the nodulous sculpture (Goodrich, 1940). *Lithasia lubrichti* Clench, 1965 had yet to be described and is included in Group 3 based on Clench (1965) allying it to *Lithasia verrucosa* (Rafinesque, 1820).
D. Taxa presently included in *Lithasia* belong to one of three genera: *Lithasia*, *Angitrema*, or *Anculosa*, *sensu* Tryon (1873). In this case, the original descriptions of *Lithasia* and *Angitrema* are used to group taxa based on shell characters. Tryon failed to include *Lithasia curta* (Lea, 1868), and *Lithasia lubrichti* had yet to be described. Both species are included in Tryon's *Angitrema* based on their nodulous shell sculpture. *Lithasia geniculata pinguis* (Lea, 1852) = *Anculosa pinguis*.
E. Taxa presently included in *Lithasia* should be considered species of *Io* based on developmental characters, *sensu* Davis (1974). *Io* Lea, 1831, has precedence over *Lithasia* Haldeman, 1840, and *Angitrema* Haldeman, 1841.

A sixth scheme, Stein's (1978b) recommendation that all *Lithasia* be considered *Pleurocera*, is not treated here as it is nomenclatural, not taxonomic, and has since been resolved by the International Commission on Zoological Nomenclature's decision to make *Pleurocera acutus* the type species of the genus (Melville, 1981, see discussion in Bogan and Parmalee, 1983). Characters supporting relationships in the parsimony analysis were compared to characters that grouped species in the other classifications.

RESULTS

Maximum parsimony analysis of shell characters alone yielded 372 trees of 27 steps (Figure 9). *Lithasia* was rendered non-monophyletic by the placement of *Lithasia geniculata pinguis* in the clade of *Leptoxis* species and the placement of *Lithasia obovata* (Say, 1829) in a polytomy of (*Io* + some *Elimia* + *pinguis* + *Leptoxis* + remaining *Lithasia*). Analysis of all characters yielded 20 trees of 107 steps that rendered *Lithasia* non-monophyletic (Figure 10). *Lithasia geniculata pinguis* specimens were basal to a clade of *Leptoxis* species supported by a teardrop-shaped aperture, and *Lithasia obovata* was nested between clades of *Pleurocera* and *Elimia* species near the base of the tree. The remaining *Lithasia* taxa formed a clade with *Io* supported by three characters

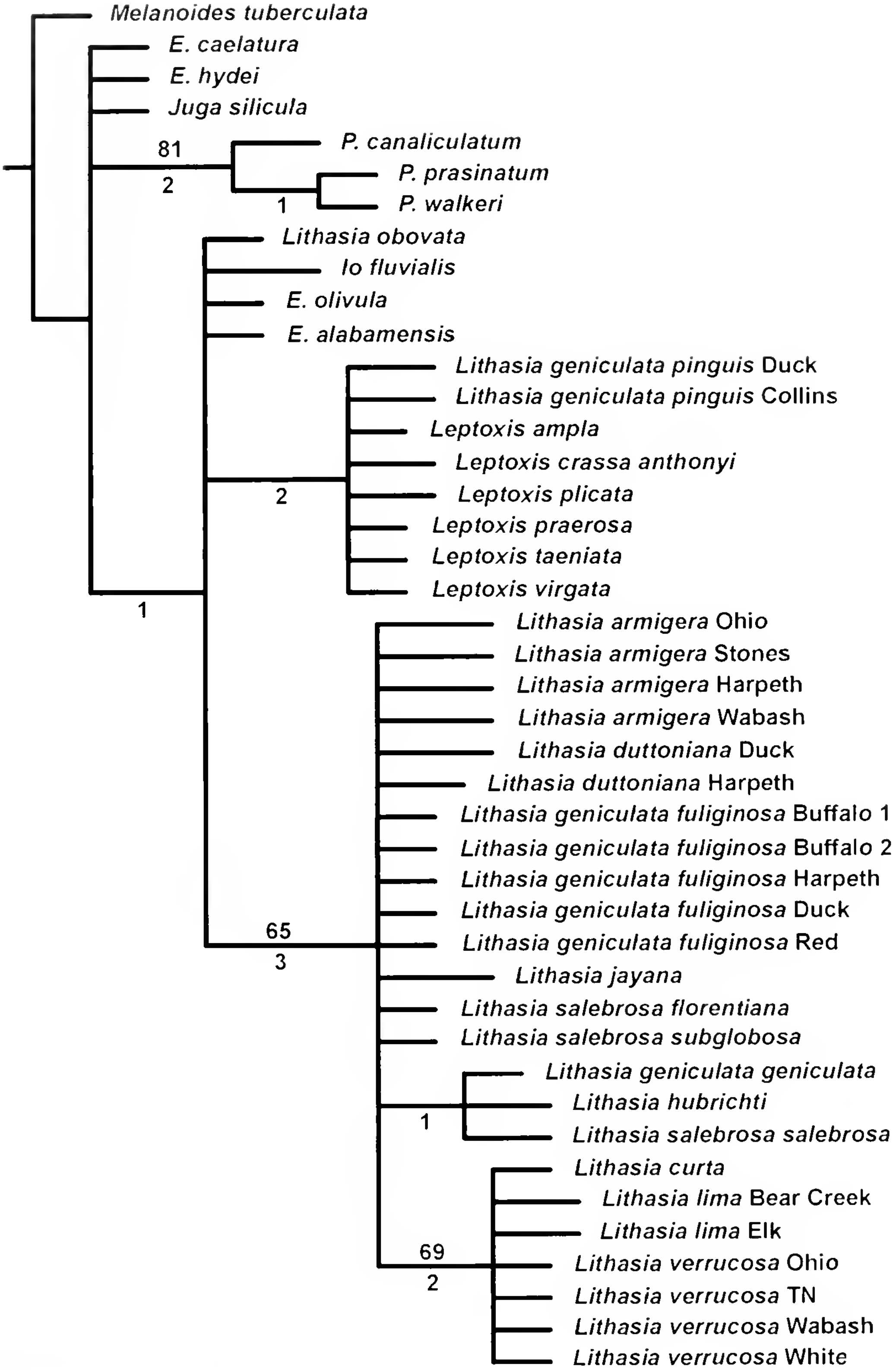

Figure 9. C[illegible] *[illegible]a*. Strict consensus of the 372 most parsimonious trees (27 steps; CI = 0.74) generated using shell character[illegible] [illegible] values > 63% above nodes, number of unambiguous synapomorphies below nodes.

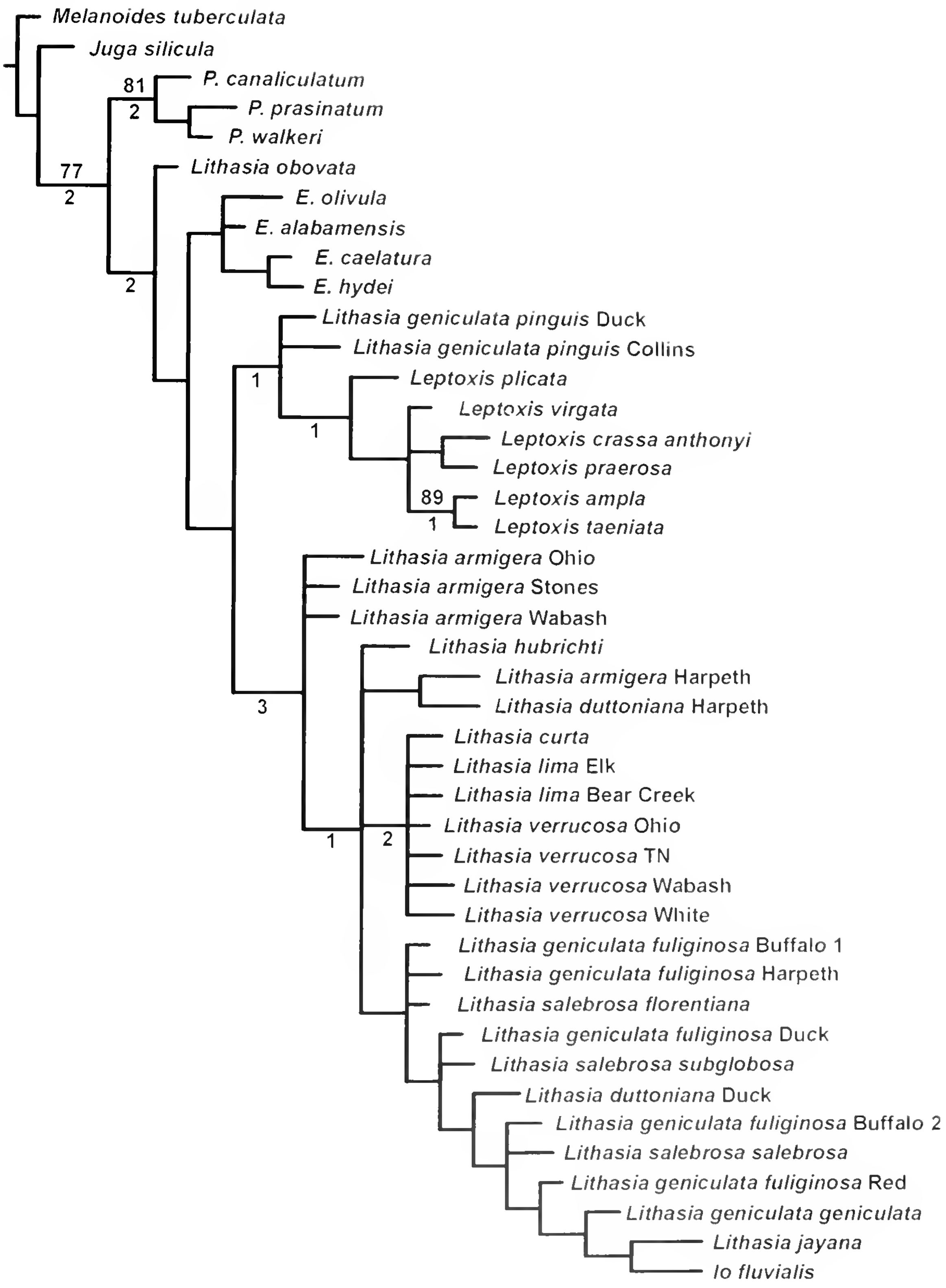

Figure 10. Cladistic analysis of *Lithasia*. Strict consensus of the 20 most parsimonious trees (107 steps, CI = 0.374) generated using shell and radula characters combined. Jackknife values ≥ 63 (above nodes), number of unambiguous synapomorphies below nodes.

fusiform aperture (character 2: state 2), posterior callus on aperture (6:1), and slight anterior canalization of the aperture (8:1). Despite being well resolved, little support for any clade existed as evidenced by low jackknife values. Three other pleurocerid genera, *Elimia*, *Leptoxis*, and *Pleurocera*, were all recovered as monophyletic.

DISCUSSION

The current taxonomy of pleurocerids is based on shell characteristics, and most work on the family has focused on these characters. An extensive literature exists for the family, with most works being either wholly descriptive or taxonomic shuffling taxa among groups. This study stands as the first cladistic treatment of all currently recognized *Lithasia* species and their relationships to other pleurocerids based on shell and radula characters.

Neither analysis completely recovered the five classifications being compared. In both phylogenetic treatments *Lithasia* taxa did not form a single group, which refutes the taxonomies of Burch and Tottenham (1980), Goodrich (1940), and Turgeon et al. (1998). Tryon's (1873) groupings of the currently recognized species of *Lithasia* was also not supported, as sculptured and smooth taxa did not group separately. Davis's contention that *Lithasia* species should be considered as members of *Io* was partially supported in the parsimony analysis of all characters, where *Io* was nested deep in a clade containing most *Lithasia* taxa.

The consensus trees suggest that shell characters alone do not recover currently or historically recognized groups. However, shell and radula characters combined can be used to recover pleurocerid genera, but do not resolve species level identity well. In the total character analyses, *Elimia*, *Leptoxis*, and *Pleurocera* taxa all grouped in their respective genus. Only two *Lithasia* taxa grouped away from the others, suggesting that these two species may be misplaced. *Lithasia geniculata pinguis* was placed in *Leptoxis* (*Anculosa*) by Tryon (1864), and subsequently placed in *Lithasia*, where it has represented the headwaters form of the *geniculata geniculata-fuliginosa-pinguis* complex. Based on the morphological characters examined here, *L. geniculata pinguis* should be classified as a species of *Leptoxis*. *Lithasia obovata* is the only species in the genus that occurs in the Green River drainage of Kentucky, and has included [illegible] nominal forms that are questionably *Lithasia*. [illegible] lls lack the calluses on the aperture, fusiform [illegible] have radulae most similar to *Elimia* species. [illegible] logenetic analysis suggests allocation of *L.* [illegible] parate genus. I believe the addition of [illegible] *Pleurocera* species or more morphological [illegible] lysis would resolve its generic design[illegible] *Lithasia* species would be considered *Io* [illegible] lest name for that clade. As such, *Io* wou[illegible] having a fusiform aperture (2:2), poste[illegible] lumella (6:1), and formation of canal of the [illegible] 2). This change would reflect the opinions of Da[illegible] garding the two genera. Within *Lithasia*, howev[illegible] idual species were not recovered, and continued analysis is required to elucidate diagnostic characters at the species level. None of the five current and historical classifications of *Lithasia* evaluated in this study are completely consistent with the analysis. Only the diagnosis of Burch (1982) is partially supported. A posterior callus on the columella (6:1) and the formation of anterior canal of the aperture (8:1–2) unite all *Lithasia* (minus *geniculata pinguis* and *obovata* plus *Io*) in the combined character analysis.

This study offers evidence refuting previous notions that shell and radula characters have limited utility in recognizing pleurocerid groups and supports the use of these characters in defining pleurocerid genera. In the most inclusive treatment of pleurocerids to date, Tryon (1873) offered an extensive discussion on the use and validity of shell characters in separating the various genera and species in the group. Tryon recognized that shell characters can vary greatly and looked towards the use of other anatomical characters to separate "natural genera" and discover corroborative shell characters for these groupings. Goodrich (1940: 1) noted that shell characters "once. . .considered immutable have proved to be secondary and more or less evanescent". Tryon (1873: liii–lv) figured some of Troschel's illustrations of radulae and commented on Stimpson's observations that shell and radula characters seem to unite pleurocerids but do little to separate constituent genera and species. It is true that gastropod radulae (Padilla, 1998) and freshwater mollusk shell characters can be plastic, often exhibiting clinal variations (e.g., Adams, 1900, 1915, Ortmann, 1920), and therefore potentially contributing homoplasy to phylogenetic analyses. Adding soft anatomy characters to a study such as this might theoretically improve the resolution of the analyses, but many characters frequently used to delineate taxa vary little among pleurocerids (Dazo, 1965) and in phylogenetic reconstructions shell characters often are less homoplastic than anatomical characters (Schander and Sundberg, 2001).

The results given here are consistent with studies employing molecular methods (Lydeard et al., 1997; Lydeard et al., 1998; Holznagel and Lydeard, 2000) to identify pleurocerid genera. In these works, *Elimia* and *Pleurocera* represent natural groups, and the morphological characters support both genera. However, Lydeard et al. (1997) and Holznagel and Lydeard (2000) showed that *Lithasia* and *Leptoxis* are non-monophyletic, though the combined morphological analysis given here supports the recognition of *Leptoxis* as a natural group. A thorough molecular study of *Lithasia*, including all of its nominal species and forms, will provide valuable information on the species composition of *Lithasia*, and subsequent character analysis will help define the diagnostic features of the genus.

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LITERATURE CITED

Adams, C. C. 1900. Variation in *Io*. Proceedings of the American Association for the Advancement of Science 49: 208–225, pls. i–xxvii.

Adams, C. C. 1915. The variations and ecological distribution of the snails of the genus *Io*. Memoirs of the National Academy of Sciences 12(2): 1–92, pls. 1–60.

Anthony, J. G. 1855. Descriptions of new species of *Ancylus* and *Anculosa*, from the western states of North America. Annual Report of the Lyceum of Natural History of New York 6: 158–160, pl. 5, figs. 20–23.

Bogan, A. E. and P. W. Parmalee. 1983. Tennessee's Rare Wildlife Volume 2. The Mollusks. 123 pp.

Bogan, A. E., J. M. Pierson and P. Hartfield. 1995. Decline in the freshwater gastropod fauna in the Mobile Basin. pp. 249–252. In: LaRoe, E. T., G. S. Farris, C. E. Puckett, P. D. Doran, & M. J. Mac (eds.). Our Living Resources: A report to the Nation on the distribution, abundance, and health of U.S. plants, animals, and ecosystems. U.S. Department of the Interior, National Biological Service, Washington, 530 pp.

Bryant, H. N. 1996. Explicitness, stability, and universality in the phylogenetic definition and usage of taxon names: a case of the phylogenetic taxonomy of the Carnivora. Systematic Biology 45: 174–189.

Burch, J. B. and J. L. Tottenham. 1980. North American Freshwater Snails. Species list, ranges and illustrations. Walkerana 1: 81–215.

Burch, J. B. 1982. North American Freshwater Snails. Identification keys, generic synonymy, supplemental notes, glossary, references, index. Walkerana 1: 217–365.

Clench, W. J. 1965. A new species of *Lithasia* from Mississippi. The Nautilus 79: 30–33.

Conrad, T. A. 1834a. Description of some new species of fresh water shells from Alabama, Tennessee. American Journal of Science and Arts 25(2): 338–343.

Conrad, T. A. 1834b. New freshwater shells of the United States, with coloured illustrations, and a monograph of the genus *Anculotus* of Say; also a synopsis of the American naiades. Judah Dobson, Philadelphia. 76 pp.

Davis, G. M. 1974. Report on the rare and endangered status of a selected number of freshwater Gastropoda from southeastern U.S.A. Unpublished report submitted to the Fish and Wildlife Service, U.S. Department of the Interior, Washington. 51 pp. plus maps.

Davis, G. M. and S. L. H. Fuller. 1981. Genetic relationships among recent Unionacea (Bivalvia) of North America. Malacologia 20: 217–253 + 2 appendices.

Dazo, B. C. 1965. The morphology and natural history of *Pleurocera acuta* and *Goniobasis livescens* (Gastropoda: Cerithiacea: Pleuroceridae). Malacologia 3: 1–80.

de Queiroz, K. and J. Gauthier. 1990. Phylogeny as a central principle in taxonomy: phylogenetic definitions of taxon names. Systematic Zoology 39: 307–322.

de Queiroz, K. and J. Gauthier. 1992. Phylogenetic taxonomy. Annual Review of Ecology and Systematics 23: 449–480.

de Queiroz, K. and J. Gauthier. 1994. Toward a phylogenetic system of biological nomenclature. Trends in Ecology and Evolution 9: 27–31.

Farris, J. S., V. A. Albert, M. Kallersjo, D. Lipscomb and A. G. Kluge. 1996. Parsimony jackknifing outperforms neighbor-joining. Cladistics 12: 99–124.

Goloboff, P. A. 1998. NONA 2.0. Software published by the author. Tucuman, Argentina.

Goodrich, C. 1921. Something about *Angitrema*. The Nautilus 35: 58–59.

Goodrich, C. 1928. *Strephobasis*, a section of *Pleurocera*. Occasional Papers of the Museum of Zoology, University of Michigan, 192: 1–15, pls. 1–2.

Goodrich, C. 1940. The Pleuroceridae of the Ohio River drainage system. Occasional Papers of the Museum of Zoology, University of Michigan. 417: 1–21.

Gould, A. A. 1847. [Descriptions of *Melania*, from the collection of the Exploring Expedition.] Proceedings of the Boston Society of Natural History 2: 222–225.

Graf, D. L. 2000. The Etherioidea revisited: a phylogenetic analysis of hyriid relationships (Mollusca: Bivalvia: Paleoheterodonta: Unionoida). Occasional Papers of the Museum of Zoology, University of Michigan 729: 1–21.

Haldeman, S. S. 1840. A monograph of the Limniades and other freshwater univalve shells of North America. Supplement to No. 1. Dobson, Philadelphia. 3 pp.

Haldeman, S. S. 1841. A monograph of the Limniades and other freshwater univalve shells of North America. No. 3 [Limnea]. J. Dobson, Philadelphia. 16 pp.

Heard, W. H. and R. H. Guckert. 1970. A re-evaluation of the Recent Unionacea (Pelecypoda) of North America. Malacologia 10: 333–355.

Holznagel, W. E. 1998. A nondestructive method for cleaning gastropod radulae from frozen, alcohol-fixed, or dried material. American Malacological Bulletin 14: 181–183.

Holznagel, W. E. and C. Lydeard. 2000. A molecular phylogeny of North American Pleuroceridae (Gastropoda: Cerithioidea) based on mitochondrial 16S rDNA sequences. Journal of Molluscan Studies 66: 233–257.

Lea, I. 1831. Description of a new genus of the family Melaniana of Lamarck. Transactions of the American Philosophical Society 4: 122–124.

Lea, I. 1841a. New fresh water and land shells. Proceedings of the American Philosophical Society 2(16): 11–15.

Lea, I. 1841b. Continuation of Mr. Lea's paper on fresh water and land shells. Proceedings of the American Philosophical Society 2(19): 81–83.

Lea, I. 1842. Description of new freshwater and land shells. Transactions of the American Philosophical Society 8: 163–250 + 23 plates.

Lea, I. 1845. Description of new freshwater and land shells. Proceedings of the American Philosophical Society 4: 162–168.

Lea, I. 1852. Description of a new genus (*Basistoma*) of the family Melaniana, together with some new species of American Melaniae. Transactions of the American Philosophical Society 10: 295–302.

Lea, I. 1861a. Description of new species species of *Schizostoma*, *Anculosa* and *Lithasia*. Proceedings of the Academy of Natural Sciences of Philadelphia 13: 54–55.

Lea, I. 1861b. Description of forty nine new species of the genus *Melania*. Proceedings of the Academy of Natural Sciences of Philadelphia 13: 117–123.

Lea, I. 1868. New Unionidae, Melanidae, etc., of the Unit

States. Journal of the Academy of Natural Sciences 6: 340–341.

Lydeard, C. and R. L. Mayden. 1995. A diverse and endangered aquatic ecosystem of the southeastern United States. Conservation Biology 9: 800–805.

Lydeard, C., W. E. Holznagel, J. Garner, P. Hartfield and M. Pierson. 1997. A molecular phylogeny of Mobile River drainage pleurocerid snails (Caenogastropoda: Cerithioidea). Molecular Phylogenetics and Evolution 7: 117–128.

Lydeard, C., J. H. Yoder, W. E. Holznagel, F. G. Thompson and P. Hartfield. 1998. Phylogenetic utility of the 5'-half of mitochondrial 16S rDNA gene sequences for inferring relationships of *Elimia* (Cerithioidea: Pleuroceridae). Malacologia 39: 183–193.

Lydeard, C., R. L. Minton and J. D. Williams. 2000. Prodigious polyphyly in imperiled freshwater pearly-mussels: a phylogenetic test of species and generic designations. In: Harper, E. M., J. D. Taylor and J. A. Crame (eds.) The Evolutionary Biology of the Bivalvia. Geological Society of London. Special Publication 177, pp. 145–158.

Mayden, R. L. and R. M. Wood. 1995. Systematics, species concepts, and the evolutionary significant unit in biodiversity and conservation biology. American Fisheries Society Symposium, 17: 58–113.

Melville, R. V. 1981. Opinion 1195. *Pleurocera* Rafinesque, 1818 (Gastropoda): the type species is *Pleurocerus acutus* Rafinesque in Blainville, 1824. Bulletin of Zoological Nomenclature 38: 259–265.

Müller, O. F. 1774. Vermium terrestrium et fluviatilium, seu animalium infusoriorum, helminthicorum et testaceorum, non marinorum, succincta historia. Vol. 2. xxxvi. Heineck et Faber, Havniae et Lipsiae, 214 pp.

Nixon, K. C. 1999. Winclada (BETA) ver. 0.9.9. Software published by the author, Ithaca.

Ortmann, A. E. 1920. Correlation of shape and station in freshwater mussels (Naiades). Proceedings of the American Philosophical Society 59(4): 269–312.

Padilla, D. K. 1998. Inducible phenotypic plasticity of the radula in *Lacuna* (Gastropoda, Littorinidae). The Veliger 2: 201–204.

Pilsbry, H. A. and S. N. Rhoads. 1896. Contributions to the zoology of Tennessee, No. 4. Mollusks. Proceedings of the Academy of Natural Sciences of Philadelphia 48: 487–506.

Rafinesque, C. S. 1820. Annals of nature, or annual synopsis of new genera and species of animals, plants, etc. discovered in North America. Pp. 10–11.

Redfield, J. H. 1854. Descriptions of new species of shells. Annual Report of the Lyceum of Natural History of New York 6: 130–132.

Reeve, L. A. 1860. Conchologia Iconica: or illustrations of the shells of molluscous animals. Lowell Reeve, London.

Say, T. 1821. Descriptions of the univalve shells of the United States. Journal of the Academy of Natural Sciences of Philadelphia 2(1):149–179.

Say, T. 1825. Descriptions of some new species of fresh water and land shells of the United States. Journal of the Academy of Natural Sciences of Philadelphia 5(3–4): 119–131.

Say, T. 1829. Descriptions of new terrestrial and fluviatile shells of North America (continued). New Harmony Disseminator 2(19): 291–293.

Schander, C. and P. Sundberg. 2001. Useful characters in gastropod phylogeny: soft information or hard facts. Systematic Biology 50: 136–141.

Sereno, P. C. 1999. Definitions in phylogenetic taxonomy: critique and rationale. Systematic Biology 48: 329–351.

Stansbery, D. H. 1971. Rare and endangered freshwater mollusks in Eastern United States. In: Jorgenson, S. E. and R. E. Sharp (eds.) Proceedings of a symposium on rare and endangered mollusks (naiads) of the U.S. U.S. Fish and Wildlife Service, Department of the Interior, Washington, pp. 5–18f, 50 figs.

Stein, C. B. 1976. Gastropods. In: Endangered and threatened species of Alabama. Bulletin of the University of Alabama Museum of Natural History No. 2. Tuscaloosa, pp. 21–41.

Stein, C. B. 1978b. Comments on the proposed designation of a type species for *Pleurocera* Rafinesque, 1818. Bulletin of Zoological Nomenclature 34: 196–197.

Tryon, G. W. 1864. Synonymy of the species of Strepomatidae, a family of fluviatile Mollusca, inhabiting North America. Proceedings of the Academy of Natural Sciences of Philadelphia 16: 24–48, 92–104.

Tryon, G. W. 1873. Land and Freshwater Shells of North America. Part IV. Strepomatidae. Smithsonian Miscellaneous Collections 16(253), pp. i–lv + 1–435.

Turgeon, D. D., J. F. Quinn Jr., A. E. Bogan, E. V. Coan, F. G. Hochberg, W. G. Lyons, P. M. Mikkelsen, R. J. Neves, C. F. E. Roper, G. Rosenberg, B. Roth, A. Scheltema, F. G. Thompson, M. Vecchione and G. D. Williams. 1998. Common and scientific names of aquatic invertebrates from the United States and Canada. Mollusks (2nd edition). American Fisheries Society Special Publication 26, 526 pp. U. S. Fish and Wildlife Service Threatened and Endangered Species System. http://endangered.fws.gov. Queried May 8, 2001.

Waples, R. S. 1991. Pacific salmon, *Oncorhynchus* spp., and the definition of "species" under the Endangered Species Act. Marine Fisheries Review 53: 11–22.

Appendix 1. Systematic list of taxa used in the cladistic analysis of the genus *Lithasia* (n = 1 for each taxon). Classification follows Turgeon et al. (1998); taxa are named as in Burch (1980). Complete locality information is available from the author. FMNH = Field Museum of Natural History; INHS = Illinois Natural History Survey; NCSM = North Carolina State Museum of Natural Sciences; UAG = University of Alabama Gastropod Collection; UMMZ = University of Michigan Museum of Zoology.

Taxon	Locality	Collection number
Family Pleuroceridae		
Genus *Elimia*		
E. alabamensis (Lea, 1861b)	Coosa River, Coosa Co., AL	NCSM-P 4658
E. caelatura caelatura (Reeve, 1860)	Choccolocco Creek, Calhoun Co., AL	NCSM-P 4659
E. hydei (Conrad, 1834b)	Black Warrior River, Jefferson Co., AL	NCSM-P 4663
E. olivula (Conrad, 1834a)	Alabama River, Monroe Co., AL	NCSM-P 4664
Genus *Io*		
Io fluvialis (Say, 1825)	Holston River, Sullivan Co., TN	NCSM-P 4667
Genus *Juga*		
J. silicula (Gould, 1847)	Oak Creek, Benton Co., OR	NCSM-P 4670
Genus *Leptoxis*		
L. ampla (Anthony, 1855)	Little Cahaba River, Bibb Co., AL	NCSM-P 4671
L. crassa anthonyi (Redfield, 1854)	Sequatchie River, Marion Co., AL	NCSM-P 4672
L. plicata (Conrad, 1834b)	Black Warrior River, Jefferson Co., AL	NCSM-P 4674
L. praerosa (Say, 1821)	Harpeth River, Davidson Co., TN	NCSM-P 4675
L. taeniata (Conrad, 1834b)	Choccolocco Creek, Talladega Co., AL	NCSM-P 4676
L. virgata (Lea, 1841a)	Clinch River, Hancock Co., TN	NCSM-P 4677
Genus *Lithasia*		
L. armigera (Say, 1821)	Wabash River, White Co., IL	INHS 23628
	Ohio River, Massac Co., IL	INHS 23632
	East Fork Stones River, Rutherford Co., TN	UAG 397
	Harpeth River, Cheatham Co., TN	UAG 572
L. curta (Lea, 1868)	Tennessee River, Lauderdale Co., AL	UMMZ 242200
L. duttoniana (Lea, 1841a)	Duck River, Maury Co., TN	UAG 402
	Harpeth River, Davidson Co., TN	UAG 405
L. geniculata geniculata (Haldeman, 1840)	Caney Fork, Dekalb Co., TN	UMMZ 51563
L. geniculata fuliginosa (Lea, 1842)	Buffalo River, Humphreys Co., TN (1)	UAG 406
	Red River, Robertson Co., TN	UAG 398
	Duck River, Maury Co., TN	UAG 403
	Buffalo River, Perry Co., TN (2)	UAG 395
	Harpeth River, Davidson Co., TN	UMMZ 55253
L. geniculata pinguis (Lea, 1852)	Collins River, Warren Co., TN	UAG 407
	Duck River, Coffee Co., TN	UAG 392
L. hubrichti Clench, 1965	Big Black River, Hinds Co., MS	FMNH 137751
L. jayana (Lea, 1841b)	Duck River, Humphreys Co., TN	UAG 573
L. lima (Conrad, 1834a)	Elk River, Limestone Co., AL	UAG 571
	Bear Creek, Colbert Co., AL	UAG 570
L. obovata (Say, 1829)	Green River, McLean Co., KY	FMNH 46219
L. salebrosa salebrosa (Conrad, 1834a)	Tennessee River, Lauderdale Co., AL	UAG 565
L. salebrosa florentiana (Lea, 1841a)	Tennessee River, Hardin Co., TN	UAG 425
L. salebrosa subglobosa (Lea, 1861a)	Tennessee River, Hardin Co., TN	UAG 416
L. verrucosa (Rafinesque, 1820)	Wabash River, White Co., IL	INHS 23629
	Ohio River, Massac Co., IL	INHS 23651
	Tennessee River, Hardin Co., TN	UAG 427
	Tennessee River, Lauderdale Co., AL	UAG 568
Genus *Pleurocera*		
P. canaliculatum filum (Lea, 1845)	Duck River, Maury Co., TN	NCSM-P 4686
P. prasinatum (Conrad, 1834a)	Yellowleaf Creek, Shelby Co., AL	NCSM-P 4689
P. walkeri Goodrich, 1928	Shoal Creek, Lauderdale Co., AL	NCSM-P 4692
Family Thiaridae		
Genus *Melanoides*		
M. tuberculata (Muller, 1774)	Drainage ditch, Gainesville, Alachua Co., FL	NCSM-P 4682

Appendix 2. Morphological characters and character states used in the cladistic analysis of the genus *Lithasia*.

1. Shell shape. (0) globose, (1) conic, (2) ovately conic.
2. Aperture shape. (0) teardrop, (1) ovate, (2) fusiform.
3. Sculpture on posterior body whorl. (0) none, (1) carinate, (2) tubercles.
4. Sculpture medially on body whorl. (0) none, (1) sharp angle on body whorl, (2) tubercles.
5. Sculpture on entire body whorl. (0) none, (1) even lateral rows of small nodules, (2) costate.
6. Posterior callus on columella. (0) absent, (1) present.
7. Anterior callus on columella. (0) absent, (1) present.
8. Length of anterior canal of aperture. (0) none, (1) slight, (2) elongate.
9. Twisting of aperture anteriorly. (0) absent, (1) present.
10. Lengthening of aperture posteriorly along body whorl. (0) absent, (1) present.
11. Sculpture limited to body whorl. (0) yes, (1) no, (2) absent.
12. Length of aperture. (0) less than one-half shell length, (1) one-half shell length, (2) more than one-half shell length.
13. Cusp next to lateral tooth exteriorly. (0) absent, (1) present.
14. Shape of upper rachidian margin. (0) convex, (1) straight.
15. Length/width ratio of rachidian. (0) tooth as long as wide, (1) tooth longer than wide.
16. Length/width ratio of central rachidian denticle. (0) length and width equal, (1) longer than wide.
17. Shape of central rachidian denticle. (0) pointed, (1) blunt.
18. Location of cutting edge on main lateral cusp. (0) edge restricted to medial quarter, (1) edge restricted to medial half, (2) edge present on entire tooth.
19. Shape of main lateral cusp. (0) lamellar, (1) rectangular, (2) trapezoidal, (3) triangular.
20. Width of main lateral cusp. (0) less than one-third of cutting edge, (1) less than one-half but more than one-third of cutting edge, (2) greater than one-half of cutting edge.
21. Length/width ratio of main lateral cusp. (0) length and width equal, (1) length greater than width, (2) width greater than length.
22. Shape of leading edge of main lateral cusp. (0) pointed, (1) rounded, (2) straight.
23. Shape of marginal teeth. (0) pointed, (1) round.
24. Number of inner marginal teeth. (0) 1–4, (1) 5–8, (2) more than 8.
25. Number of outer marginal teeth. (0) 1–4, (1) 5–8, (2) more than 8.

Appendix 3. Cladistic analysis of the genus *Lithasia*. Data matrix of taxa and character states. River names follow appropriate taxon names where needed.

Lithasia armigera Ohio	[illegible]
Lithasia armigera Stones	[illegible]
Lithasia armigera Harpeth	[illegible]
Lithasia armigera Wabash	[illegible]
Lithasia curta	[illegible]
Lithasia duttoniana Duck	[illegible]
Lithasia duttoniana Harpeth	[illegible]
Lithasia geniculata fuliginosa Buffalo 1	[illegible]
Lithasia geniculata fuliginosa Buffalo 2	[illegible]
Lithasia geniculata fuliginosa Duck	[illegible]
Lithasia geniculata fuliginosa Harpeth	[illegible]
Lithasia geniculata fuliginosa Red	[illegible]
Lithasia geniculata geniculata	[illegible]
Lithasia geniculata pinguis Duck	[illegible]
Lithasia geniculata pinguis Collins	[illegible]
Lith[illegible]	[illegible]
Litha[illegible]	[illegible]
Litha[illegible]	[illegible]
Litha[illegible]	[illegible]
Lithasia [illegible]	[illegible]
Lithasia sale[illegible]	[illegible]
Lithasia salebr[illegible]	[illegible]
Lithasia salebrosa	[illegible]
Lithasia verrucosa [illegible]	[illegible]
Lithasia verrucosa [illegible]	[illegible]
Lithasia verrucosa Wab[illegible]	[illegible]
Lithasia verrucosa White	[illegible]
Io fluvialis	[illegible]

Appendix 3. Continued

Leptoxis ampla
Leptoxis crassa anthonyi
Leptoxis plicata
Leptoxis praerosa
Leptoxis taeniata
Leptoxis virgata
Elimia alabamensis
Elimia caelatura
Elimia hydei
Elimia olivula
Juga silicula
Pleurocera canaliculatum filum
Pleurocera prasinatum
Pleurocera walkeri
Melanoides tuberculata

Appendix 4. Genus *Lithasia*. Classification schemes used in comparison to cladistic hypotheses. Taxa marked with a * were not treated by the original author but are included in the groups based on their works; see text for explanation.

Turgeon et al. 1998	Burch and Tottenham, 1980	Goodrich, 1940	Tryon, 1873	Davis, 1974
Genus *Lithasia*	Genus *Lithasia*	Genus *Lithasia*	Genus *Anculosa*	Genus *Io*
L. armigera	Subgenus *Lithasia*	Group 1	*L. geniculata pinguis*	*Io fluvialis*
L. curta	*L. geniculata geniculata*	*L. armigera*	Genus *Angitrema*	*L. armigera*
L. duttoniana	*L. geniculata fuliginosa*	*L. duttoniana*	*L. armigera*	*L. curta*
L. geniculata	*L. geniculata pinguis*	*L. jayana*	*L. curta*	*L. duttoniana*
L. hubrichti	*L. obovata*	*L. lima*	*L. duttoniana*	*L. geniculata geniculata*
L. jayana	*L. salebrosa salebrosa*	Group 2	*L. geniculata geniculata*	*L. geniculata fuliginosa*
L. lima	*L. salebrosa florentiana*	*L. geniculata geniculata*	*L. hubrichti**	*L. geniculata pinguis*
L. obovata	*L. salebrosa subglobosa*	*L. geniculata fuliginosa*	*L. jayana*	*L. hubrichti*
L. salebrosa	Subgenus *Angitrema*	*L. geniculata pinguis*	*L. lima*	*L. jayana*
L. verrucosa	*L. armigera*	*L. salebrosa salebrosa*	*L. salebrosa salebrosa*	*L. lima*
	L. curta	*L. salebrosa florentiana*	*L. verrucosa*	*L. obovata*
	L. duttoniana	*L. salebrosa subglobosa*	Genus *Lithasia*	*L. salebrosa*
	L. hubrichti	Group 3	*L. geniculata fuliginosa*	*L. salebrosa florentiana*
	L. jayana	*L. curta*	*L. obovata*	*L. salebrosa subglobosa*
	L. lima	*L. hubrichti*	*L. salebrosa florentiana*	*L. verrucosa*
	L. verrucosa	*L. verrucosa*	*L. salebrosa subglobosa*	
		Group 4		
		L. obovata		

Coralliophila kaofitorum, a new species (Gastropoda: Coralliophilidae) from the Canary Islands living on *Antipathes wollastoni* (Cnidaria: Anthozoa: Antipatharia)

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ABSTRACT

A new species of *Coralliophila* from the Canary Islands living on the antipatharian *Antipathes wollastoni* is described. The new species differs from its closest Eastern Atlantic relative *Coralliophila brevis* (Blainville, 1832) by its smaller size and spiral cords of similar width, and from the Western Atlantic *Coralliophila caribaea* Abbott, 1958, by having a thinner shell and narrower aperture and by the sculpture and smaller size of the protoconch. Additional remarks on the taxonomy and feeding of some Eastern Atlantic and Mediterranean Coralliophilidae are included.

INTRODUCTION

The family Coralliophilidae comprises tropical to temperate, shallow- to deep-water marine species that live and feed on cnidarians. The conchological characters may vary greatly within the family, and there are different grades of interspecific and intraspecific variation. Shell variability, together with the rarity of most of the species due to their restricted habitat (specially those living in deep water), the absence of radula, the absence of protoconch (usually eroded in adults and even in some specimens) and the poor knowledge of anatomy and biology have led to a confused taxonomy of the family that [illegible] the generic allocation of species difficult. The Coralliophilidae has been traditionally considered [illegible] closely related to Muricidae, but Pon[illegible] [illegible] without further discussion propose[illegible] [illegible] as a subfamily of Muricidae. This ta[illegible] [illegible] been adopted by some subsequent au[illegible] [illegible] Riedel, 2000). However, Kantor (1995) [illegible] [illegible]ugh differences in foregut anatomy to [illegible] [illegible]on into two different families. Since th[illegible] [illegible] of the Coralliophilidae is currently [illegible] [illegible]e prefer to use the traditionally accepted ranking of the taxon at the family level.

No critical revisions of the family have been published except for that of Massin (1982) for the genera *Magilus* and *Leptoconchus*, but two catalogues (D'Attilio, 1978; Kosuge and Suzuki, 1985) consider about 200 Recent species. At least 27 genera have been described, but the actual number is probably smaller (D'Attilio and Bertsch, 1979; Kosuge and Suzuki, 1985); a large number of species (about 80) are included in the genus *Coralliophila* H. and A. Adams, 1853, but this genus still needs to be better defined. Most coralliophilids feed on scleractinian corals, but there are also species that feed on Gorgonacea, Corallimorpharia, Zoanthidea (Miller, 1981; Robertson, 1970, 1981; Wicksten and Wright, 1993), Actiniaria (Spada, 1979; Oliverio, 1989a), and Alcyonacea (Lorenz, 1996). Only two species of *Rhizochilus* (*Rhizochilus antipathum* Steenstrup, 1850, and *Rhizochilus* sp.) and *Coralliobia cumingii* (H. and A. Adams, 1863) are known to feed on Antipatharia in the Indo-Pacific (Kay, 1979; Poorman, 1981; Kosuge and Suzuki, 1985; D'Attilio and Kosuge, 1988). The type of feeding and the degree of association with anthozoans vary from boring, endobiotic, almost parasitic, highly host-selective species (*Magilus*, *Leptoconchus*, *Reliquiaecava*) (Massin, 1982, 1983, 1987, 1988, 1990), to less selective species with a relatively high mobility (*Coralliophila*) (Miller, 1981).

References to Eastern Atlantic coralliophilids are scattered in publications from different areas: Mediterranean and European Atlantic (Sabelli and Spada, 1980; Oliverio, 1989a, b; Poppe and Goto, 1991), continental West Africa (Knudsen, 1956; Bernard, 1984; Talavera, 1975; Gofas, Pinto-Afonso and Brandão, 1985; Kosuge and Fernandes, 1988; Smriglio and Mariottini, 2000), deep waters of the northeastern Atlantic (Bouchet and Warén, 1985), Cape Verde Islands (Cosel, 1982), São Tomé Island (Kosuge and Fernandes, 1989; Rolán and Fernandes, 1990), Saint Helena Island (Smith, 1890), and Tristan da Cunha Island (Watson, 1886). Four spe-

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cies were recorded from the Canary Islands by Nordsieck and García-Talavera (1979): *Coralliophila meyendorffii* (Calcara, 1845), *C. brevis* (Blainville, 1832), *Babelomurex cariniferus* (G. B. Sowerby, 1834) (as *Coralliophila babelis* (Réquien, 1848)), and *Coralliophila richardi* (P. Fischer, 1882) (as *C. lactuca* (Dall, 1889)). In addition to *C. richardi*, two additional deep-sea species are known from the Canary Islands: *C. squamosa* (Bivona, 1838) and *C. basileus* (Dautzenberg and Fischer, 1896) (Bouchet and Warén, 1985). Finally, *Coralliophila fontanangioyi* Smriglio and Mariottini, 2000, has been recently described from Tenerife.

During SCUBA-diving sampling around the island of Tenerife (Canary Islands), a coralliophilid living on the black coral *Antipathes wollastoni* (Gray) has been found. This third species of the family known to live on antipatharians is described here as a new species, since it shows clear differences from the previously known coralliophilids from the Atlantic Ocean.

Institutional abbreviations used in this work are: BAU, Dipartimento di Biologia Animale e dell'Uomo, "La Sapienza" University, Rome, Italy; MNCN, Museo Nacional de Ciencias Naturales, Madrid, Spain; MCNT, Museo de Ciencias Naturales de Tenerife, Tenerife, Spain; DBUA, Departamento de Biología, Universidad Autónoma, Madrid, Spain.

SYSTEMATICS

Superfamily Muricoidea Rafinesque, 1915
Family Coralliophilidae Chenu, 1859
Genus *Coralliophila* H. and A. Adams, 1853

Type species: *Fusus neritoideus* Lamarck, 1816, by subsequent designation (Iredale, 1912). Recent, Indo-Pacific.

Coralliophila kaofitorum new species
(Figures 1–7)

Description: Shell (Figures 1–4) up to 24.6 mm of length, 15.5 mm width, solid but rather thin, ovoid-fusiform; spire high, conical, with up to 7 convex whorls, shoulder slightly angulate; suture well defined with undulate narrow groove. Shell color uniformly yellowish- or pale-brown, milky-white when cleaned. Protoconch (Figures 5–7) of about 3½–4 whorls, 1 mm length, 940 µm width, and diameter of first whorl 280 µm. Protoconch indicative of planktotrophic larval development. Protoconch nucleus (Figure 7) smooth except for small scattered pustules, subsequent whorls with two strong spiral keels, crossed by axial ribs forming nodules at intersections and scattered, small pustules (Figure 6). Thick varix indicates limit between protoconch and teleoconch. Protoconch color pink to reddish- or pale-brown. Protoconch lacking or usually eroded in adult specimens, but when present is frequently somewhat tilted in relation to shell axis. Teleoconch with 5–7 convex whorls, somewhat angulate at shoulder on earlier whorls. Last whorl large, convex, more or less angulate at shoulder, then narrowing toward base, representing almost 3/4 of total shell length. Aperture large, oval, lirate and white within; but one specimen with inner side of aperture pinkish. Outer lip thin, with finely serrated outer margin (margin rippled internally); inner lip slightly angulate in middle. Siphonal canal broad, moderately elongate, open, slightly recurved. Umbilical aperture absent. Axial sculpture of 9–11 (on specimens longer than 10 mm) or 8–9 (on smaller specimens) broad, elevated axial ribs on last whorl, and usually 10 axial ribs on penultimate whorl. Axial ribs less marked toward end of body whorl in longest specimens, but clearly marked in smaller (younger) specimens. Spiral sculpture on last whorl of up to 18–19 cords of rounded cross-section, all of similar width, and bearing prominent densely packed, fine and long, scale-like lamellae. Spiral cords 8–9 on the penultimate whorl. Shell usually covered by encrusting organisms (*Miniacina*, bryozoans, serpulid polychaetes, two different small species of bivalves, sponges and calcareous algae were observed on a single specimen). Living animal white or whitish, including tentacles and siphon, with densely-packed, yellow speckles, which form a ring on distal part of the siphon. Operculum brown, mahogany-, or reddish-brown.

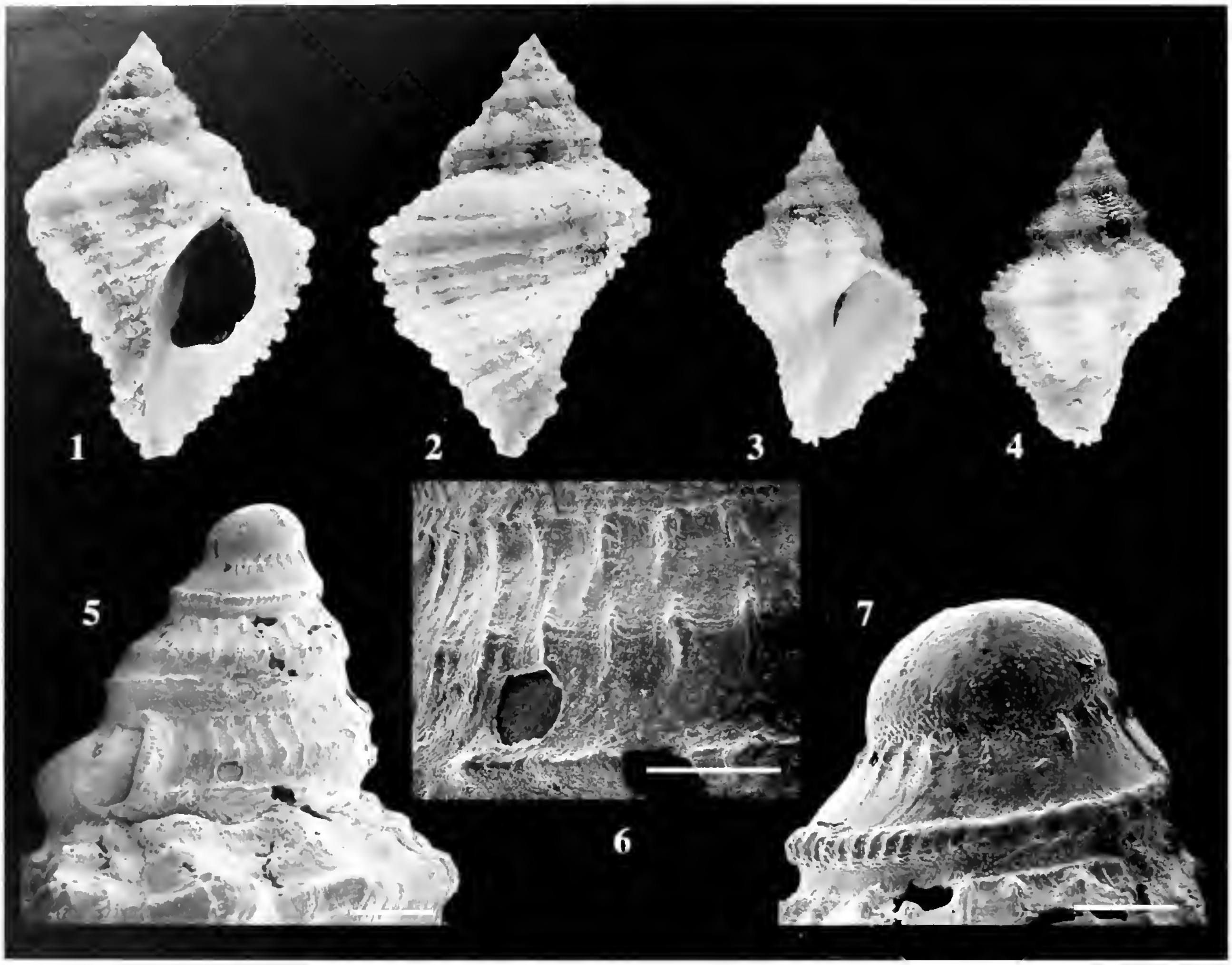
Type Material: Holotype (Figures 1–2) MNCN 15.05/32583, 20.0 mm length × 13.5 mm width; five paratypes, MNCN 15.05/32583; two paratypes, MCNT TFMCBMMO/000277 and TFMCBMMO/000278; two paratypes, DBUA, 15.05/18. All from type locality, attached to black coral *Antipathes wollastoni* (Gray), Nov.–Dec. 1994.

Type Locality: Punta de Teno, Tenerife, Canary Islands, 28°20′ N, 17°55′ W, depth 22–24 m.

Other Material Examined: Twelve specimens from the type locality, Ricardo and Rodolfo Vega Collection, type locality, R. and R. Vega coll., Nov.–Dec. 1994; 18 specimens, BAU (Punta de Teno); 12 specimens, BAU (Diente de Ajo); 21 specimens, BAU (Veril de Masca) (all Tenerife, Canary Islands, M. Oliverio coll.); one specimen, 20.9 mm length × 13.6 mm width, R. and R. Vega Collection (La Bombilla, Palma Island, Canary Islands), collected alive on *Antipathes wollastoni*, 40 m depth, D. R. Galloway coll., 24 Aug. 1996.

Distribution: Known only from the type locality, Punta de Teno, two other nearby points on the Tenerife Island (Diente de Ajo and Veril de Masca), and from La Palma Island (La Bombilla, David Roig Galloway leg.). The planktotrophic type of development indicated by the protoconch of *Coralliophila kaofitorum* suggests a wider distribution than that currently known, but the species has not yet been found in other Macaronesian Islands, the West African coast or the Mediterranean.

Habitat: All collected and observed specimens were found attached near the base of colonies of the black coral *Antipathes wollastoni* (Gray) or near the major branch nodes in the case of very large colonies, between



Figures 1–7. *Coralliophila kaoptorum* new species. **1, 2.** Holotype MNCN 15.05/32583, 24.6 × 15.5 mm, Punta de Teno, Tenerife, Canary Islands. **3, 4.** Paratype 1, MNCN 15.05/32583, from the type locality, 14.9 × 9.6 mm. **5, 6, 7.** Protoconch of paratype 1. **5.** General view. Scale bar: 200 µm. **6.** Detail of the sculpture of the last whorl. Scale bar: 100 µm. **7.** Detail of the nucleus and the first whorl. Scale bar: 100 µm.

18–30 m (Punta de Teno and Diente de Ajo) and 42–48 m (Veril de Masca). An average number of 5–6 specimens per antipatharian colony were observed in Punta de Teno (with a maximum of 10–12 specimens, and up to 20 on a single antipatharian colony in Veril de Masca. Of 27 specimens checked for their position on three colonies, [illegible] with the siphon directed upwards and 7 downwards [illegible] pers. comm.). No observations of feeding [illegible] have been made.

Etymology: [illegible] name combines to the nicknames of [illegible] two authors: Kao (Ricardo) and Ohto [illegible].

Remarks: *C*[illegible]*rum* is tentatively assigned to the genus [illegible] because it resembles other species (*C*[illegible]) that are presently included in that genus [illegible] generic revision of the family.

Coralliophila kaoptorum [illegible] from its closest relative *Coralliophila brevis* (Blainville, 1832), which is also present in the Canary Islands and has been collected at the base of the yellow (*Lophogorgia viminalis*) and red (*L. ruberrima*) gorgonians, off Puerto de la Cruz, at 20–32 m depth, and off the northern side of the Teno Peninsula, in identical environmental conditions. *Coralliophila brevis* is a longer species (up to 30–40 mm), very variable, especially in spire length and shape of the aperture and the siphonal canal; the spiral sculpture consists of 15–25 often markedly imbricate, alternating broad and thin cords; frequently one or two more swollen cords on the upper part of the spire accentuate the carene of the whorl. In the Mediterranean, *Coralliophila brevis* lives also on gorgonians (*Paramuricea chamaeleon*, *Eunicella stricta*, *Lophogorgia sarmentosa*) (Oliverio, 1989b; Poppe and Goto, 1991).

Coralliophila caribaea Abbott, 1958, from the Western Atlantic is a similar species, but it is somewhat solid and has a wider aperture usually purple on the inside.

It lives on a variety of anthozoans including scleractinians, gorgonaceans, zoanthideans and Corallimorpharia (Wells and Lalli, 1977; Miller, 1981; De Jong and Coomans, 1988). The embryonic shell of *Coralliophila caribaea* was illustrated by Bandel (1975), and the protoconch and larval shell by De Jong and Coomans (1988) and Leal (1991). The protoconch of *C. caribaea* has its nucleus densely covered by small pustules, is somewhat longer (4.5 whorls, 1.2 mm length), and has more prominent nodules than that of *C. kaofitorum*. Presently molecular investigation is in progress by Marco Oliverio to assay the relationships of the new species with *Coralliophila brevis* and *Coralliophila caribaea*.

The new species also differs from *Coralliophila meyendorffii* (Calcara, 1845), another littoral species of the Canary Islands widely distributed along the Mediterranean and Eastern Atlantic, which has a longer (up to 40 mm) and more solid shell, with 5–6 teleoconch whorls with about 13–15 spiral cords and 8–10 strong axial ribs, canal rather short, and umbilical aperture. In the Canary Islands, *C. meyendorffii* preys on *Anemonia sulcata* (Pérez-Sánchez and Moreno-Batet, 1991), and in the Mediterranean the species is known to prey on *Anemonia sulcata*, *Cladocora caespitosa*, and *Balanophyllia europaea* (Sabelli and Spada, 1980; Oliverio, 1989b).

The Atlantic-Mediterranean *Coralliophila squamosa* (Bivona, 1838) has a longer (up to 40–50 mm) and more solid shell, with 8–10 axial ribs and 12–20 major spiral cords, alternating with the same number of lamellose cordlets, the siphonal canal is of medium length and the umbilical aperture evident (Bouchet and Warén, 1985; Oliverio, 1989b). *Coralliophila squamosa* preys on Gorgonacea or deep-sea scleractinians (Oliverio, 1989b). *Coralliophila monterosatoi* (Locard, 1897), from Spain, and *Coralliophila profundicola* Haas, 1949, from Bermuda, should be considered junior synonyms of *C. squamosa*, according, respectively, to Bouchet and Warén (1985), and Kosuge and Suzuki (1985).

Coralliophila basileus (Dautzenberg and H. Fischer, 1896) reaches up to 27 mm, has a thicker shell and broader siphonal canal. It is found on the upper part of the insular slopes around Azores and the Canary Islands (Bouchet and Warén, 1985); its prey/host is unknown.

Coralliophila richardi (P. Fischer, 1882) is a deep-sea (bathyal) species that lives (and probably preys) on the scleractinians *Madrepora oculata* and *Lophelia pertusa* in other Eastern Atlantic localities (Bouchet and Warén, 1985; Oliverio, 1989b, and observations of the third author). The shell of this species is very different from typical *Coralliophila*, with 8–10 axial foliate varices instead of solid ribs and with relatively few spiral cords without the characteristic scaly sculpture. *Coralliophila richardi* is included by Kosuge and Suzuki (1985) in the genus *Emozamia* Iredale, 1929, along with the similar *Coralliophila jarli* Knudsen, 1956, found from Sierra Leone to Angola.

Coralliophila fontanangioyi Smriglio and Mariottini, 2000, described from Teno, Tenerife Island, is smaller (up to 7.5 mm) and has a solid biconical shell. It lives on the scleractinian *Madracis asperula* Milne-Edwards and Haime, 1850 (Pérez-Sánchez and Moreno-Batet, 1991, Smriglio and Mariottini, 2000, authors' observations in Tenerife), which probably is a Macaronesian endemism (Zibrowius, 1980). According to Smriglio and Mariottini (2000), *Coralliophila fontanangioyi* is similar to *Coralliophila alboangulata* (E. A. Smith, 1890) from St. Helena Island, *Coralliophila raramaculatus* Kosuge and Fernandes, 1989, from São Tomé, *Coralliophila pacei* Petuch, 1987, from Florida and *Coralliophila curta* Sowerby, 1894 from Mauritius Island; all of them clearly differ from *C. kaofitorum* by the smaller size and different shell shape.

The remaining coralliophilid species found in the Canary Islands, *Babelomurex cariniferus* (G. B. Sowerby, 1834) is included in a different genus on the basis of conchological and anatomical features (Kosuge and Suzuki, 1985, Richter and Luque, in press). This species preys on the scleractinian *Phyllangia mouchezi* (authors' observations), whereas in the Mediterranean it preys on *Cladocora caespitosa*, *Astroides calycularis* and *Polycyathus muellerae* (Oliverio, 1989b, and authors' observations); of these three latter species, only *Polycyathus muellerae* might possibly be found in the Canary Islands (Zibrowius, 1980).

One other, probably undescribed littoral species of coralliophilid is found in the Canary Islands living on the scleractinian *Dendrophyllia ramea* (from Lanzarote, 40–50 m, Gustavo Pérez Dionis and Marco Oliverio, pers. comm.). It is a large (up to 40 mm) and solid shell, very similar to that illustrated as *Coralliophila* cf. *jarli* from Gabon by Bernard (1984, pl. 29, fig. 120).

The remaining Mediterranean species of *Coralliophila* are all very different. *Coralliophila panormitana* (Monterosato, 1869) is solid, with 10 axial ribs and 22–24 spiral cords with small scales. This species lives at the base of *Paramuricea chamaeleon* and associated to *Corallium rubrum* (Oliverio, 1989b) or *Epizoanthus arenaceus* (Templado et al., 1993). *Coralliophila sophiae* (Aradas and Benoit, 1876) has a solid, more or less globose shell, similar to *Coralliophila squamosa* in size, and lives in bottoms with strong coralligenous component; its diet is unknown (Oliverio, 1989b).

Among the eastern Atlantic species, *Coralliophila aedonius* (Watson, 1886) from Nightingale Island (Tristan da Cunha) has a strong shell, with a high, scalariform spire, relatively small aperture and umbilicus. *Coralliophila giton* (Dautzenberg, 1891) from the Cape Verde Islands and São Tomé is a smaller species (up to 20 mm), with a thick elongate fusiform shell usually eroded and incrusted, 7–9 broad axial ribs and about 27 spiral cords on the last whorl (Kosuge and Fernandes, 1989, Rolán and Fernandes, 1990). *Coralliophila atlantica* (E. A. Smith, 1890) from St. Helena Island is a solid, small species (17.2 mm), with low axial ribs and spiral cords with weak sculpture. *Coralliophila erythrostoma* (E. A. Smith, 1890), also from St. Helena is solid, sub-rhomboidal, and has a reddish aperture and evident umbilicus. *Coralliophila patruelis* (E. A. Smith, 1890) from St.

[illegible] is small (10.5 mm). As far as we know, the three latter species are only known from type material, illustrated and briefly described by Kosuge and Suzuki (1985).

Coralliophila kraemmeri Knudsen, 1956, from Nigeria, and *Coralliophila marrati* Knudsen, 1956, from Liberia, have solid, umbilicated shells, the first one has 16 axial ribs and 14 spiral ridges on the body whorl, whereas *C. marrati* has rounded ribs and only 8 prominent spiral ridges (Knudsen, 1956).

Coralliophila occidentale Kosuge and Fernandes, 1988, from Angola is a small (up to 9.4 mm) and rather solid species. *Coralliophila adansoni* (Kosuge and Fernandes, 1989) from São Tomé is also solid and has the inner side of the aperture denticulate. Finally, *Coralliophila knudseni* Smriglio and Mariottini, 2000, from Ivory Coast and *Coralliophila schiottei* Smriglio and Mariottini, 2000, from Sierra Leone, are smaller and have biconical and more solid shells than *Coralliophila kaofitorum*.

The remaining western Atlantic species of *Coralliophila* are also different. *Coralliophila aberrans* (C. B. Adams, 1850) has a thick, globose shell with strong spiral cords. *Coralliophila galea* (Reeve, 1846) also has a more solid shell and wider aperture. *Coralliophila salebrosa* H. and A. Adams, 1863, has an ovate-fusiform shell, with angulate spire, and *Coralliophila scalariformis* (Lamarck, 1822) has a scalariform profile.

RECOMMENDATION

The host of *Coralliophila kaofitorum*, the anthipatarian *Antipathes wollastoni*, forms in the Canary Islands a characteristic community on walls below 50 m of depth, but it can be found at shallower depths (18–24 m) in caves or overhangs at certain sites (Pérez-Sánchez and Moreno-Batet, 1991). A similar assemblage occurs in the Caribbean islands with other antipatharian species (*Antipathes* spp. Humann, 1993). *Antipathes wollastoni* is only known with certainty from Madeira, Selvagem and Canary Islands, but it is probably also present in the Cape Verde Islands (A. Brito pers. comm.). It is pro[illegible] protection in the Canary Islands and included [illegible] Red List (Bacallado et al., 1989) and [illegible] Marine Fauna List (Bonnet-Fernández-[illegible]-Fernández, 1992). We strongly [illegible] mental authorities of the Canary [illegible] include *Coralliophila kaofitorum* [illegible] since it is up to now only [illegible] and is strictly associated [illegible]

ACK[illegible]

We [illegible] for information about the [illegible] to him and Al[illegible] [illegible] on the manuscript [illegible] on coralliophilids from the [illegible] Bedoya (MNCN) for SEM photographs, and to Rogelio Sánchez and Jesús Muñoz (MNCN) for photographs; to Alberto Brito and Rogelio Herrera for information about conservation. This work was supported by Fauna Ibérica IV project (DGICYT PB95–0235).

LITERATURE CITED

Bacallado, J. J., T. Cruz, A. Brito, J. Barquín and M. Carrillo. 1989. Reservas Marinas de Canarias. Publicaciones de la Consejería de Agricultura y Pesca, Gobierno de Canarias, 200 pp.

Bandel, K. 1975. Embryonalgehäuse karibischer Meso- und Neogastropoden (Mollusca). Akademie der Wissenschaften und der Literatur Mainz Abhandlungen der mathematisch-naturwissenschaftlichen Klasse 1975(1): 1–133.

Bernard, P. A. 1984. Coquillages du Gabon. Pierre A. Bernard, Libreville, Gabon, 140 pp.

Bonnet-Fernández-Trujillo, J. and Á. Rodríguez-Fernández. 1992. Fauna marina amenazada en las Islas Canarias. ICONA, Colección Técnica. Ministerio de Agricultura Pesca y Alimentación, Madrid, 296 pp.

Bouchet, P. and A. Warén. 1985. Revision of the Northeast Atlantic bathyal and abyssal Neogastropoda excluding Turridae (Mollusca, Gastropoda). Bollettino Malacologico supplemento 1: 123–296.

Cosel, R. von. 1982. Marine Mollusken der Kapverdischen Inseln. Übersicht mit zoogeographischen Anmerkungen. Courier Forschung-Institut Senckenberg 52: 35–76.

D'Attilio, A. 1978. Superfamily Muricacea: Catalogue of the family Coralliophilidae. The Festivus 10(10): 69–96.

D'Attilio, A. and H. Bertsch. 1979. Preliminary account of three generic taxa in the Muricacean family Coralliophilidae. The Festivus 11(3): 21–25.

D'Attilio, A. and S. Kosuge. 1988. Descriptions of new species of the genera *Coralliobia* and *Favartia* from the Philippine Islands (Gastropoda Coralliophilidae and Muricidae). Bulletin of the Institute of Malacology Tokyo 2(7): 109–112.

De Jong, K. M. and H. E. Coomans. 1988. Marine Gastropods from Curaçao, Aruba and Bonaire. E. J. Brill, Leiden, 261 pp.

Gofas, S., J. Pinto-Afonso and M. Brandão. 1985. Conchas e Moluscos de Angola. Universidade Agostinho Neto/Elf Aquitaine Angola, 144 pp.

Haas, F. 1949. On some deepsea mollusks from Bermuda. Butlletí de la Institució Catalana d'Història Natural 37: 3–7.

Humann, P. 1993. Reef coral identification. Florida, Caribbean, Bahamas. New World Publications Inc., Jacksonville, 240 pp.

Kantor, Yu. I. 1995. On the morphology of the digestive system of *Latiaxis* (*Babelomurex*) (Gastropoda, Coralliophilidae) with notes on the phylogeny of the family. Ruthenica 5: 9–15.

Kantor, Yu. I. 1996. Phylogeny and relationships of Neogastropoda. In: J. D. Taylor (ed.) Origin and evolutionary radiation of the Mollusca. Oxford University Press, London, pp. 221–230.

Kay, E. A. 1979. Mollusca. In: Reef and shore fauna of Hawaii, section 4. Bernice P. Bishop Museum Special Publication 64. Bernice P. Bishop Museum Press, Honolulu, 653 pp.

Knudsen, J. 1956. Marine Prosobranchs of Tropical West Africa (Stenoglossa). Atlantide Report 4: 7–110.

Kosuge, S. and F. Fernandes. 1988. Report on the family Coralliophilidae from West Africa with the description of a new species (Gastropoda). Bulletin of the Institute of Malacology Tokyo 2: 96–97.

Kosuge, S. and F. Fernandes. 1989. Description of two new species of the genera *Ocinebrina* and *Coralliophila* from São Tomé Island, West Africa, with some discussion on *Purpura giton* (Gastropoda, Muricidae and Coralliophilidae). Bulletin of the Institute of Malacology Tokyo 2: 132–136.

Kosuge, S. and M. Suzuki. 1985. Illustrated catalogue of *Latiaxis* and its related groups Family Coralliophilidae. Institute of Malacology of Tokyo, Special Publication No. 1, 83 pp.

Leal, J. H. 1991. Marine Prosobranch Gastropods from oceanic islands off Brazil. Universal Book Services, Oegstgeest, 419 pp.

Lorenz, F. 1996. L'habitat di alcune specie di Coralliophilidae in Tanzania. La Conchiglia 278: 22–24.

Massin, C. 1982. Contribution to the knowledge of two boring gastropods with an annotated list of the genera *Magilus* Montfort, 1810 and *Leptoconchus* Rüppell, 1835. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie 53(17): 1–28.

Massin, C. 1983. Note on the genus *Leptoconchus* Rüppell, 1835 (Mollusca, Gastropoda, Coralliophilidae) with the description of two new species, *Leptoconchus vangoethemi* sp. n. and *Leptoconchus cyphastreae* sp. n. from Papua New Guinea. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie 55: 1–16.

Massin, C. 1987. *Reliquiaecava*, a new species of Coralliophilidae. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie 57: 79–90.

Massin, C. 1988. Boring Coralliophilidae (Mollusca, Gastropoda): coral host relationship. Proceedings of the 6th International Coral Reef Symposium 3: 177–184.

Massin, C. 1990. Biologie et écologie de *Leptoconchus peronii* (Lamarck, 1818) (Gastropoda, Coralliophilidae) récolte en Papouasie Nouvelle-Guinée, avec une description de l'espece. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie 60: 23–33.

Miller, A. C. 1981. Cnidarian prey of the snails *Coralliophila abbreviata* and *C. caribaea* (Gastropoda: Muricidae) in Discovery Bay, Jamaica. Bulletin of Marine Science 31: 932–934.

Nordsieck, F. and F. García-Talavera. 1979. Moluscos Marinos de Canarias y Madera (Gastropoda). Aula de Cultura de Tenerife, Tenerife, 208 pp.

Oliverio, M. 1989a. Note sull'ecologia di *Coralliophila meyendorffi* (Calcara, 1845) (Gastropoda: Prosobranchia). Atti Prima Giornata di Studi Malacologici CISMA, pp. 215–220.

Oliverio, M. 1989b. Famiglia Coralliophilidae Chenu 1869 in Mediterraneo. La Conchiglia 21(246–249): 48–55.

Pérez-Sanchez, J. M. and E. Moreno-Batet. 1991. Invertebrados Marinos de Canarias. Ediciones del Cabildo Insular de Gran Canaria, Las Palmas de Gran Canaria, 335 pp.

Ponder, W. F. 1998. Superfamily Muricoidea. In: Beesley, P. L., G. J. B. Ross and A. Wells (eds.), Mollusca: The Southern Synthesis. Fauna of Australia Vol. 5. CSIRO Publishing: Melbourne, Part B, pp. 819–820.

Ponder, W. F. and A. Warén. 1988. Classification of the Caenogastropoda and Heterostropha—a list of the family group and higher category names. In: Ponder, W. F. (ed.), Prosobranch Phylogeny. Malacological Review, suppl. 4: 288–326.

Poorman, L. H. 1981. *Rhizochilus* in the Gulf of California (Neogastropoda ? Coralliophilidae). The Veliger 24: 165–166.

Poppe, G. T. and Y. Goto. 1991. European Seashells, volume I. Verlag Christa Hemmen, Wiesbaden, 352 pp.

Richter, A. and A. A. Luque. In press. Current knowledge on Coralliophilidae (Gastropoda) and phylogenetic implications of anatomical and reproductive characters. Bollettino Malacologico.

Riedel, F. 2000. Ursprung und Evolution der "höheren" Caenogastropoda. Berliner geowissenschaftliche Abhandlungen E32: 1–240, pls. 1–21.

Robertson, R. 1970. Review of the predators and parasites of stony corals, with special reference to symbiotic prosobranch gastropods. Pacific Science 24: 43–54.

Robertson, R. 1981. *Epitonium millecostatum* and *Coralliophila clathrata*: two prosobranch gastropods symbiotic with Indo-Pacific *Palythoa* (Coelenterata: Zoanthidae). Pacific Science 34: 1–17.

Rolán, E. and F. Fernandes. 1990. *Coralliophila adansoni* Kosuge and Fernandes, 1989, new name for *Ocinebrina adansoni*. Bollettino Malacologico 26(5–9): 143–144.

Sabelli, B. and G. Spada. 1980. Guida illustrata all'identificazione delle conchiglie del Mediterraneo. Fam. Coralliophilidae. Bollettino Malacologico 16(7–8) suppl.: 3 pp.

Smith, E. A. 1890. Report on the marine molluscan fauna of the island of St. Helena. Proceedings of the Zoological Society of London 1890: 247–317.

Smriglio, C. and P. Mariottini. 2000. Description of three new Coralliophilidae from the Eastern Atlantic ocean. La Conchiglia 296: 11–18.

Spada, G. 1979. Guida pratica alla formazione di una raccolta di conchiglie marine. Bollettino Malacologico 15(1–2), suppl.: 73–80.

Talavera, F. G. 1975. Moluscos de sedimentos de la plataforma continental de Mauritania. Boletín del Instituto Español de Oceanografía 192: 1–18.

Templado, J., A. Guerra, J. Bedoya, D. Moreno, J. M. Remón, M. Maldonado and M. A. Ramos. 1993. Fauna marina circalitoral del sur de la Península Ibérica. Resultados de la Campaña Oceanográfica Fauna I. Museo Nacional de Ciencias Naturales, Consejo Superior de Investigaciones Científicas, Madrid, 138 pp., 45 pls.

Watson, R. B. 1886. Report on the Scaphopoda and Gastropoda collected by H. M. S. Challenger during the years 1873–76. Report of the Challenger Expedition, Zoology 15(42): 756 pp., 50 pls.

Wells, F. E. and C. M. Lalli. 1977. Reproduction and brood protection in the Caribbean gastropods *Coralliophila abbreviata* and *C. caribaea*. Journal of Molluscan Studies 43: 79–87.

Wicksten, M. K. and R. T. Wright. 1993. Predation by *Latiaxis eldredi* (Gastropoda: Coralliophilidae) on *Corynactis californica* (Anthozoa: Corallimorphidae). The Veliger 36: 92.

Zibrowius, H. 1980. Les Scléractiniaires de la Méditerranée et de l'Atlantique nord-oriental. Mémoires de l'Institut Océanographique, Monaco 11: 1–227.

Fusinus dovpeledi, a new species (Gastropoda: Fasciolariidae) from the Red Sea, and range extension for two other species

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ABSTRACT

Fusinus dovpeledi new species from the Red Sea is described. The new species is distinguished by shell characters from the similar Red Sea species *F. leptorhynchus* (Tapparone-Canefri, 1875) and from *F. colus longicauda* (Lamarck, 1801) from southeastern Africa. New range records are provided for *F. bifrons* (Sturany, 1900) and *F. arabicus* (Melvill, 1898).

INTRODUCTION

A new species in the genus *Fusinus* is described from the Red Sea and taxonomic affinities are discussed. Most *Fusinus* are subtidal burrowers, although some species are found in deep water. The discovery and description of this new species is part of a trend in recent years in which a number of new fasciolariids have been named (e.g., Gofas, 2000; Hadorn and Rogers, 2000; Snyder, 2000, Snyder and Snyder, 1999; and others). Specimens of the new species described herein have been collected by fishermen at a depth of 300 m. Additionally, the rediscovery of *Fusinus bifrons* (Sturany, 1900), another Red Sea species, with a range extension to the Indian Ocean, is reported. A probable range extension is also reported for *Fusinus arabicus* (Melvill, 1898). The abbreviation USNM National Museum of Natural History, Smithsonian Institution, Washington DC, is used here.

SYSTEMATICS

Family Fasciolariidae Gray, 1853
[illegible] Fusinae Wrigley, 1927
[illegible] Rafinesque, 1815

[illegible] *colus* Linnaeus, 1758, Recent, [illegible] monotypy.

[illegible]

Descrip[illegible] size moderate for genus, length [illegible] long, slightly undulated, apex subtending an angle of approximately 29°. Sculpture of axial ribs and spiral cords, ribs forming prominent angular knobs on later whorls, with knobs falling approximately at the center of whorl. Body whorl with 11–13 ribs, penultimate and early whorls with 12–14 ribs. Early whorls of paratype (only) lightly sculptured with axial ribs, becoming evanescent. Axial ribs crossed by numerous spiral cords, some brown on later whorls; strong brown cords alternate with weaker uncolored cords on body whorl. Penultimate whorl with 12 strong cords, becoming evanescent toward the suture, and numerous weak, fine, axial lines, visible only under magnification, between axial ribs. Aperture typically ovate and elongate; parietal shield shiny, waxy white, extending onto siphonal canal. Spiral cords beneath shield raised to form lirate sculpture. Canal long, thin, somewhat sinuous. Operculum claw-like, light brown. Protoconch, periostracum, and radula unknown.

Type material: Holotype USNM 903651, length 107 mm, width 24.4 mm, spire height 40 mm, live-collected. Paratype, Peled Collection (damaged), length 72.8 mm, width 22.8 mm, spire and siphonal canal broken, dead-collected, from type locality.

Type locality: Red Sea off Neviot (Egypt), 75 km south of Elat (Israel), 300 m depth on sandy bottom.

Etymology: The species is named after Dov Peled (Tivon, Israel), a student, collector and dealer in the shells of the Red Sea area.

Distribution and habitat: Known only from type locality.

Discussion: *Fusinus dovpeledi* is most closely related to *F. leptorhynchus* (Tapparone-Canefri, 1875), which is well illustrated in Sharabati (1984: pl. 23, fig. 7). The knobs on *F. leptorhynchus*, formed by the axial ribs, are fewer, numbering just 9, and are more square than those on *F. dovpeledi*. The operculum of *F. leptorhynchus* is distinctively reddish brown, and the shell is smaller, typically ranging between 75 and 80 mm, with a proportionately shorter siphonal canal. These differences are sufficient to rule out *F. dovpeledi* being a deeper-water

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[1] Research As[illegible]

Figures 1–4. Species of *Fusinus*. **1, 2.** *Fusinus* [illegible] **1.** [illegible] USNM [illegible] bottom off Neviot, Egypt, 75 km south of Elat, Israel [illegible] **2.** [illegible] from type locality. **3.** *Fusinus bifrons* Sturany, 1900. Fehse Coll[illegible] Red Sea [illegible] 400 m. **4.** *Fusinus arabicus* Melvill, 1898. Snyder Collection [illegible] Egypt, depth 32–40 m.

form of *F. leptorhynchus*. Comparison can also be made with *F. colus longicauda* (Lamarck, 1801) from the east coast of southern Africa (Cernohorsky, 1972: pl. 48, fig. 1a); that species has 10 axial ribs on the penultimate whorl. However, whereas the number of axial ribs increases toward the posterior end of the spire of *F. dorpeledi*, the opposite is true in *F. colus longicauda*. The axial ribs are not nearly so pronounced on the body whorl in *F. colus longicauda* as in *F. dorpeledi*; the former grows to approximately 200 mm.

Fusinus bifrons (Sturany, 1900)
(Figure 3)

Sturany (1900:197) introduced a deep-water species, *Fusus bifrons*, dredged in depths of 490–900 m in the Red Sea. He compared this axially ribbed species to *F. forceps* (Perry, 1811), *F. multicarinatus* (Lamarck, 1822), *F. toreuma* (Deshayes, 1843) (a synonym of *F. colus* (Linnaeus, 1758)), and *F. leptorhyncus* (Tapparone-Canefri, 1875), and he named a smooth variety of his new species "form *paucicostata*." Later, Sturany (1903: pl. 1) illustrated *F. bifrons* and erroneously referred to the taxon *paucicostata* at specific rank. According to R. Janssen of the Senckenberg Museum, Frankfurt (reported privately by R. Hadorn), the type material of this "form" differs from that of the nominate species only in sculpture and this "form" should be considered a synonym of *F. bifrons*.

Two freshly-collected specimens of the smooth form of *F. bifrons* were examined, one 99.9 mm long, 26.6 mm width, with broken siphonal canal (Peled Collection, from the Red Sea), the other 106.5 mm long, 26.9 mm width (Snyder Collection, from the Indian Ocean). The smaller specimen was dredged on a sandy bottom at 350–400 m off Neviot (Egypt), 75 km south of Elat (Israel), Red Sea. The larger specimen was collected by Russian research expeditions to the Saya de Malha Bank in the Indian Ocean (Bondarev and Roeckel, 1992; Sirenko, 1995). The larger specimen was illustrated by Sirenko (1995: fig. 7). This represents a significant range extension for this species from the Red Sea to the Indian Ocean.

bicus Melvill, 1898)

tension of *Fusinus arabicus* (Mel-
orted. This species, previously known from the Gulf of Arabia, is figured in Bosch et al. (1995: 136, species 578). Two specimens were trawled by fishermen in the 1980s off El Tur, Gulf of Suez (Egypt), in depths of 32–40 m. Both specimens were trawled as dead shells and hence this range extension is stated without absolute certainty. Even though taken by commercial trawlers, with notoriously vague collecting data, it is virtually certain that the specimens were collected in the Red Sea rather than the Arabian Sea. These two dead-collected specimens are identical in almost all respects to Arabian Sea specimens of *F. arabicus* (Melvill, 1898).

LITERATURE CITED

Bondarev, I. and D. Roeckel. 1992. The shells of Saya de Malha Bank. La Conchiglia 262: 21–38.

Bosch, D. T., S. P. Dance, R. G. Moolenbeek and P. G. Oliver. 1995. Seashells of eastern Arabia. Motivate Press, Dubai, 296 pp., col. pls.

Cernohorsky, W. O. 1972. Marine Shells of the Pacific, II. Pacific Publications, Sydney: 411 pp., 68 pls.

Gofas, S. 2000. Four species of the family Fasciolariidae (Gastropoda) from the north Atlantic seamounts. Journal of Conchology 37: 7–16, figs. 1–3.

Hadorn, R. and B. Rogers. 2000. Revision of recent *Fusinus* (Gastropoda: Fasciolariidae) from tropical western Atlantic, with description of six new species. Argonauta 14(1): 5–57, pls. 1–16.

Sharabati, D. 1984. Red Sea Shells. Routledge & Kegan Paul, London: 128 pp., 49 pls.

Sirenko, B. I. 1995. On the fauna of shell-bearing molluscs in the Saya de Malha Bank, Indian Ocean (part 2). La Conchiglia 276: 20–24, figs. 1–15.

Snyder, M. A. 2000. *Latirus beckyae*, a new species of Fasciolariidae (Gastropoda: Neogastropoda) from Brazil. The Nautilus 114: 161–163, figs. 1–3.

Snyder, M. A. and N. C. Snyder. 1999. A new species from Columbia, South America, *Fusinus columbiensis* n.sp. (Gastropoda: Fasciolaridae). La Conchiglia 291: 21–22, figs. 1–4.

Sturany, R. 1900. Diagnosen neuer Gastropoden aus dem Rothen Meere. Anzeiger der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe 37(17): 197–201.

Sturany, R. 1903. Gastropoden des Rothen Meeres. Berichte der Commission für Oceanographische Forschungen. Expeditionen S. M. Schiff 'Pola' in das Rothe Meer nördliche und südliche Hälfte 1895/96–1897/98. Zoologische Ergebnisse 23. Denkschriften der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe 74: 209–283, pls. 1–7, 1 text fig. (Also issued as a separate, pp. 1–75.)

The systematic position of *Strombina* (*Cotonopsis*) *lindae* Petuch, 1988 (Gastropoda: Columbellidae)

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ABSTRACT

The systematic position of *Strombina lindae* Petuch, 1988, is discussed and revised. The species should be allocated in the columbellid genus *Cotonopsis* Olsson, 1942. The shell characteristics that define the two known *Cotonopsis* subgenera, *C.* (*Cotonopsis*) and *C.* (*Turrina*), are itemized and contrasted. The holotype of *S. lindae* is re-illustrated and the protoconch figured for the first time.

INTRODUCTION

In his revision of the *Strombina* group, Jung (1989) gave *Cotonopsis* Olsson, 1942, generic status and recognized two subgenera, *Cotonopsis sensu stricto* Olsson, 1942, and *Cotonopsis* (*Turrina*) Jung, 1989. *Cotonopsis* is represented by 18 species, two of them known only as fossils, and 16 extant. The majority of the living species (12) are found in the eastern Pacific. Two species are found in the Caribbean Sea (Houbrick, 1983; Petuch, 1988); one species in West Africa (Emerson, 1993), and a fourth species in the Andaman Sea (Kosuge, Roussy and Muangman, 1998; Kronenberg and Dekker, 1998, 1999). As noted by Kronenberg and Dekker (1998) this distribution might indicate an earlier origin of this genus, i.e. prior to early Pliocene as proposed by Jung (1989). On the other hand, both the West African and the Asian species may be part of separate lineages, the rank of which can only be addressed pending anatomical and molecular data.

The aims of this paper are to correct the systematic position of *Strombina* (*Cotonopsis*) *lindae* Petuch, 1988, to discuss the subgeneric position of this species, and to re-illustrate the holotype deposited in the National Museum of Natural History, Smithsonian Institution (USNM 859942), with special attention to the protoconch. This latter task was prompted by both the poor quality of the original illustrations and the lack of information on the morphology of the protoconch in the original description.

SYSTEMATICS

Family Columbellidae Swainson, 1840
Genus *Cotonopsis* Olsson, 1942

Cotonopsis Olsson, 1942: 227, 75. Type species, by original designation: *Strombina* (*Cotonopsis*) *panacostaricensis* Olsson, 1942; Olsson, 1942: 75, pl. 10, fig. 10.

Description: Shell small to large (11–56 mm), general shell shape varying from fairly stout to slender. Most species lightly sculptured with axial ribs predominantly on early teleoconch whorls. Outer lip usually weakly thickened; both columellar and parietal callus usually present, weakly to well developed. Parietal ridge and posterior canal present, prominent in several species. Recurved and well-developed anterior canal. Protoconch smooth with 1½ to 3 whorls (according to Jung, 1988).

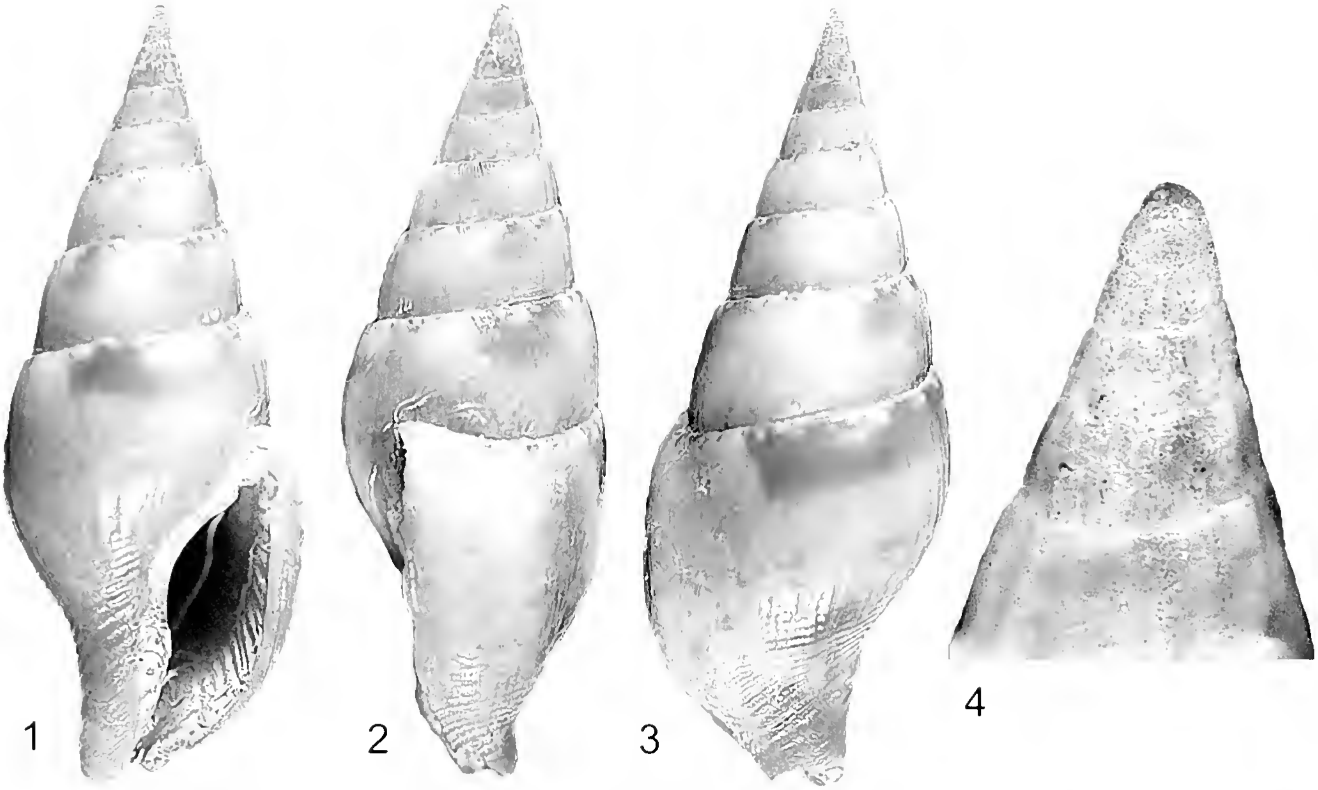
Subgenus *Cotonopsis sensu stricto*

Description: Stout shells, inflated body whorl, axial ribs on early teleoconch, well developed parietal and columellar callus, weakly developed parietal ridge and posterior canal, and smooth protoconch with 1 ½ to 3 whorls.

Cotonopsis (*Cotonopsis*) *lindae* (Petuch, 1988), new combination
(Figures 1–6)

Strombina (*Cotonopsis*) *lindae* Petuch, 1998: 161–162, pl. 38, figs. 15, 16. Off St. James, Barbados, trawled 70 m depth.

Description: Shell small, stout (up to 22.9 mm in length), inflated body whorl, axial ribs on the early teleoconch, relatively well developed columellar and parietal



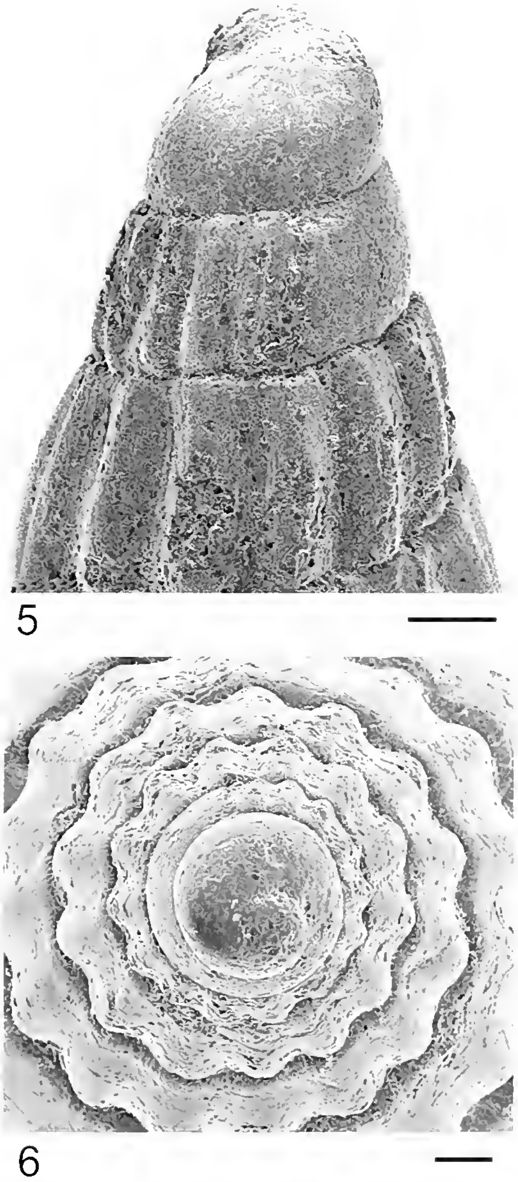
Figures 1–4. *Cotonopsis* (*Cotonopsis*) *lindae*, holotype, USNM 859942, height 22.88 mm, width 9.00 mm. **1.** Apertural view. **2.** Lateral view, right side. **3.** Abapertural view. **4.** Protoconch and early teleoconch whorls.

calluses. Protoconch smooth, with 1¾ whorls and about 700 µm diameter.

Discussion: The two subgenera recognized by Jung (1988) differ in several morphological features. In contrast to the characters above described for *Cotonopsis sensu stricto*, species of *Cotonopsis* (*Turrina*) have smooth, mostly slender shells, with well- and sometimes heavily developed parietal ridge and posterior canal; parietal and columellar calluses missing or very weak, and a smooth protoconch with 2 ¾ to 3 whorls. Based on shell characteristics, *C. lindae* is best placed in the subgenus *Cotonopsis sensu stricto*.

Cotonopsis (*Turrina*) seems to be restricted to the [illegible] Pacific and has no known fossil record. *Coton*[illegible] *stricto* has a much wider distribution, in[illegible] Pacific, the Caribbean Sea, the West [illegible] Andaman Sea. Stratigraphically, [illegible] the early Pliocene of Esmeraldas, [illegible] Peninsula Burica, Costa Rica. [illegible] mentioned above, the recent dis[illegible] seems to indicate an origin [illegible] This [illegible] species reported from outside the eastern Pacific. *Cotonopsis lindae* resembles *C. phuketensis* (Kosuge, Roussy and Muangman, 1998) from the Andaman Sea in its reduced sculptural elements, but the latter is a much larger species, with an incised suture and a protoconch with a larger number of whorls. *Cotonopsis argentea* Houbrick, 1983, from the Dominican Republic and *Cotonopsis monfilsi* Emerson, 1993, from Senegal are also much larger, with heavier sculptured teleoconch whorls. Besides, *C. monfilsi* lacks axial ribs, bearing instead spiral lines. Its protoconch has three whorls. The protoconch of *C. argentea* is similar to that of *C. lindae* in size, but the former has a weaker columellar callus.

Among the eastern Pacific species, the dimensions of *C. lindae* are similar to *Cotonopsis mendozana* (Shasky, 1970) from the Gulf of Fonseca, El Salvador, but the latter has a much less recurved siphonal canal, more heavily sculptured early teleoconch whorls, well-developed columellar callus, and inconspicuous lirae on its outer lip. Similarly to *C. lindae*, *Cotonopsis esmeraldensis* (Olsson, 1964) from the Esmeraldas province, Ecuador, also lacks heavy sculpture and has almost the same dimensions, but its siphonal canal is longer and it has a more strongly developed columellar callus.



Figures 5–6. *Cotonopsis* (*Cotonopsis*) *lindae* holotype, USNM 859942. **5.** SEM of protoconch, showing a slightly sigmoid lip, and the sculpture of the early teleoconch whorls. **6.** Same, apical view. Scale lines = 200 µm.

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LITERATURE CITED

Emerson, W. K. 1993. A new species of columbellid gastropod from the old world tropics. The Nautilus 106: 147–151.

Houbrick, R. S. 1983. A new *Strombina* species (Gastropoda: Prosobranchia) from The tropical Western Atlantic. Proceedings of the Biological Society of Washington 96: 349–354.

Jung, P. 1989. Revision of the *Strombina*-Group (Gastropoda: Columbellidae), fossil and living. Distribution, biostratigraphy and systematics. Mémoires Suisses de Paleontology 111: 1–298.

Kosuge, S., P. H. Roussy and P.-P. Muangman. 1998. Report on the fauna of Thailand (I) with the description of a new species (Columbellidae and Buccinidae). Bulletin of the Institute of Malacology of Tokyo 3(5): 75–76.

Kronenberg, G. C. and H. Dekker. 1998. A new species of *Cotonopsis* Olsson, 1942 from an unexpected locality (Gastropoda Prosobranchia: Columbellidae). Vita Marina 45(3–4): 11–16.

Kronenberg, G. C. and H. Dekker. 1999. *Cotonopsis vanwalleghemi* Kronenberg & Dekker, 1998, a junior synonym of *Strombina phuketensis* Kosuge, Roussy & Muangman, 1998, with some notes on the generic position and colour pattern (Gastropoda Prosobranchia: Columbellidae). Vita Marina 46(1–2): 69–72.

Olsson, A. A. 1942. Tertiary and Quaternary fossils from the Burica Peninsula of Panama and Costa Rica. Bulletins of American Paleontology 27(106): 153–258 (1–106), pls. 14–25 (1–12).

Petuch, E. J. 1988. Neogene history of tropical American mollusks. The Coastal Education & Research Foundation (CERF). Charlottesville, 1–217 pp.

The reproductive anatomy, taxonomic status, and range of *Oreohelix alpina* (Elrod, 1901) (Gastropoda: Pulmonata: Oreohelicidae)

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ABSTRACT

The reproductive anatomy of specimens of *Oreohelix alpina* from the type locality in the Mission Mountains of western Montana is figured and compared with that of specimens collected in the Swan Mountains, approximately 20 kilometers to the east. It appears that *O. alpina* is found in both the Mission Mountains and the Swan Mountains, which constitutes a range extension for the species. In addition, the reproductive anatomy of *O. alpina* is compared with that of *O. subrudis apiarium*. *Oreohelix alpina* has been incorrectly placed in Pilsbry's *O. subrudis* group of species and should be included in the *O. strigosa* group.

INTRODUCTION

The genus *Oreohelix* (Pilsbry, 1904) is composed of a large number of species found throughout the Rocky Mountains from southern Canada to southern Arizona and New Mexico. A large amount of intraspecific variation in shell shape and color is present in the genus, and it is often difficult to determine whether the cause of the variation is environmental or genetic (Pilsbry, 1939). There is, however, little variation in reproductive anatomy; Pilsbry (1939) found no relevant interspecific variation in the morphology of the reproductive system. Nonetheless, that author based in part upon the ratio of the plicate (ridged) portion to the pustulose portion of the internal surface of the penis, allocated species of *Oreohelix* to one of three groups, the *O. strigosa* [illegible] group, or the *O. yavapai* group.

[illegible] *Oreohelix alpina* from the Mission [illegible] Montana on the basis of the shell [illegible] of the internal anatomy of that spec[illegible]tively placed *O. alpina* in the *O. subrud*[illegible] *O. subrudis* occurs at lower elevations [illegible] range and because no members of the [illegible] in the area.

Specimens of [illegible] from the type locality had not been coll[illegible] 50 years. Recently, however, Hendricks (1998) [illegible]d and reported on several specimens from the [illegible]lity, some of which he sent to me for dissection. The goals of the study were (1) to figure the reproductive anatomy of *O. alpina* and (2) to determine its taxonomic position relative to Pilsbry's three *Oreohelix* groups. A third goal was to compare additional specimens similar to *O. alpina* from a locality in the Swan Mountains to those from the type locality in the Mission Mountains, which is located approximately 20 kilometers to the west.

MATERIALS AND METHODS

Specimens of *Oreohelix alpina* were collected (Hendricks, 1998) from the southeast ridge of St. Marys Peak which is near the type locality on the southwest ridge of St. Marys Peak, T18N R18W S21 (Township, Range, and Section from USGS topo map), Mission Mountains, Lake County, Montana, elevation approximately 2800 meters, on 27 Aug. 1997 (Figure 1). Additional specimens of *Oreohelix*, similar to *O. alpina*, were collected by Bill Hammer, on 7 Aug. 1974 above Rumble Lake, Swan Mountains (T20N R16W S2), Missoula County, Montana, elevation approximately 2400 meters (Figure 1). Two topotypes and three specimens from the Swan Mountains were dissected and their reproductive systems removed. For comparative purposes, the reproductive systems of three specimens of *O. subrudis apiarium* Berry, 1919, collected on 2 Aug. 1975, at Yellow Bay, Flathead Lake (T24N R19W S4), Lake County, Montana, elevation approximately 890 meters), were used. The reproductive system of each specimen was traced from the monitor of a dissecting microscope/video system. The penis of each specimen was then dissected to allow for tracing of their internal surface. Measurements of the plicate and the pustulose portions of the internal penial surface were made using an ocular micrometer. The drawings of one specimen were used as representative of the population. The diameter, height of shell, and number of whorls of the specimens from the type locality and those from the Swan Mountains were measured. Voucher specimens of *O. alpina* from the type locality and from the Swan Mountains are de-

Figure 1. Western Montana showing the locations of the Mission and Swan mountains. Scale bar = 20 km.

posited in the collection of mollusks at the National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA (USNM 1002352 and USNM 1002353).

RESULTS

Figures 2–3. Shells of *Oreohelix alpina*. **2.** From the type locality in the Mission Mountains. **3.** From the Swan Mountains. Scale bar = 5 mm.

Table 1. Shell measurements for *Oreohelix alpina*. Measurements in millimeters.

	Diameter of shell	Shell height	Number of whorls
Mission Mountains			
Specimen A	8.0	4.5	3.3
Specimen B	7.9	4.6	4.0
Specimen C	7.5	*	3.5
Specimen D	8.4	4.6	4.0
Mean	7.95	4.57	3.70
Swan Mountains			
Specimen A	11.1	6.4	4.3
Specimen B	8.5	5.0	4.25
Specimen C	9.0	5.0	4.0
Specimen D	8.6	5.2	4.0
Mean	9.3	5.4	4.15

* Shell was damaged during the taking of measurements. Height could not be obtained.

Shells from the Mission Mountains and from the Swan Mountains are shown in Figures 2 and 3; their measurements are given in Table 1. The gross reproductive anatomy of individuals from all three localities are shown in Figures 4–6, and the internal penial anatomies are shown in Figures 7–9. Table 2 summarizes the measurements of the internal penial anatomy. The plicate portion of the internal penial surface of the Mission Mountains (Figure 7) and the Swan Mountains (Figure 8) specimens was less than 50% of the total length in contrast to that of *O. subrudis aparium* which was greater than 50%.

DISCUSSION

The reproductive organs of *Oreohelix alpina* from the type locality (Figures 4 and 7) are typical of the genus, and no diagnostic characters at the specific level were detected.

Pilsbry (1939) noted that in the *O. strigosa* group the plicate portion of the penis was " . . . decidedly less than

Table 2. Measurements of the plicate portions and pustulose portions of the internal surfaces of the penises of *Oreohelix alpina* and *O. subrudis apariun*. Measurements in millimeters.

	Total length	Pustulose portion	Plicate portion	Percent plicate
O. alpina, Mission Mountains				
Specimen A	7.5	4.1	3.4	45
Specimen B	10.0	5.6	4.4	44
O. alpina, Swan Mountains				
Specimen A	7.5	4.4	3.1	41
Specimen B	7.5	4.6	2.0	39
Specimen C	6.5	4.0	2.5	38
O. subrudis apariun				
HLF39-1	17	7.5	9.5	56
HLF39-2	15.5	7.0	8.5	55
HLF39-3	14.5	6.5	8.0	55

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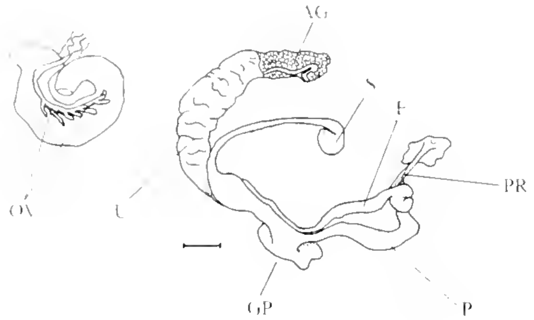

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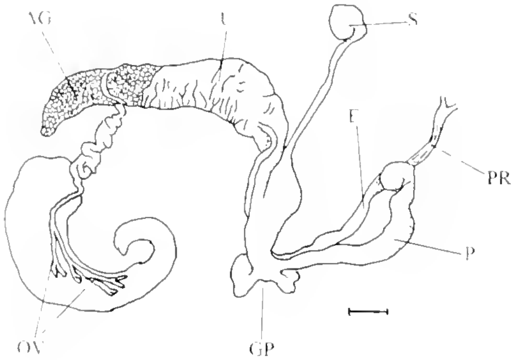

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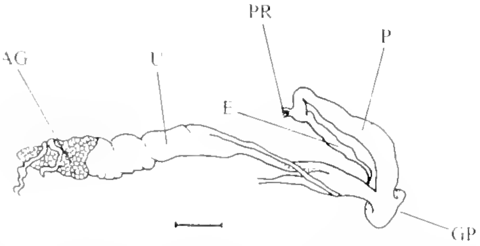

Figures 1–6. Reproductive systems of species of *Oreohelix*. **4.** *O. alpina* from the Mission Mountains. **5.** *O. alpina* from the Swan Mountains. **6.** *O. subrudis apiarium* from the Mission Mts. AG = albumin gland; E = epiphallus; GP = genital pore; OV = ovotestis; PR = penial retractor muscle; P = penis; S = spermatheca; U = uterus. Scale bars: Figures 4 and 5 = 1 mm, Figure 6 = 5 mm.

half [illegible] the total penial length but greater than half the total penial length in both the *O. subrudis* group and the *O. yavapai* group, these two groups then being separated on the basis of whether the anterior half of the penis [illegible] decidedly swollen . . ." or not.

Pilsbry [illegible] placed *O. alpina* in the *O. subrudis* group [illegible] from the other groups (*O. stri-*

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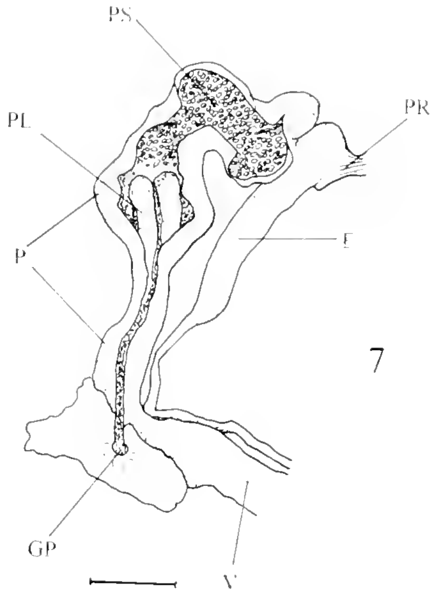

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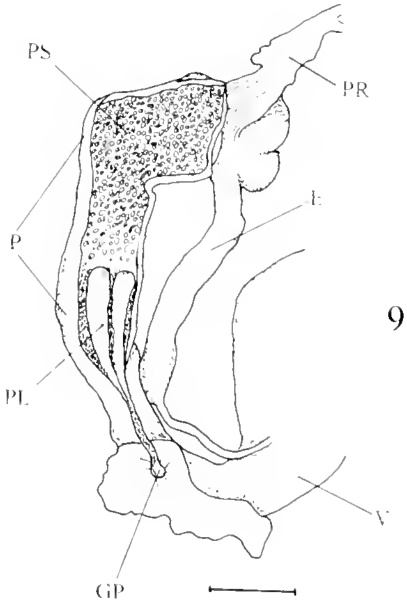

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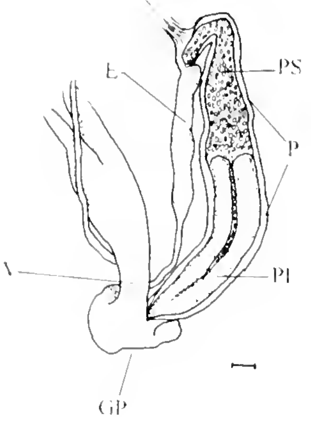

Figures 7–9. Int[illegible] of species of *Oreohelix*. **7.** *O.* [illegible] from the M[illegible] Mountains. **8.** *O. subrudis apiarium* from the M[illegible] Mountains. **9.** *O. alpina* from the Swan Mountains. E = epiphallus; GP = genital pore; PR = penial retractor muscle; P = penis; PL = plicate surface; PS = pustulose surface; V = vagina. Scale bars = 1 mm.

gosa and *O. yavapai*) are found in the Mission Mountains. However, the length of the plicate portion of the penis of *O. alpina* was less than 1/2 total penis length, whereas the plicate portion of *O. subrudis apiarium*, also from the Mission Mountains, was greater than 1/2 total penial length (Table 2). In the *O. yavapai* group the plicate portion of the penis is also greater than 1/2 total penial length, but in addition the proximal portion of the penis is enlarged, which is not the case for *O. alpina* (Figure 4). Therefore, if the grouping system of Pilsbry (1939) is to be followed, I suggest placement of *O. alpina* in the *O. strigosa* group.

The shells of *Oreohelix alpina* from the Mission Mountains and the shells from the Swan Mountains (Figure 1) could not be separated morphologically (Figures 2 and 3). Comparisons of reproductive system measurements for these two populations (Table 2) did not appear significantly different. Therefore, it appears that these two populations belong to the same species, and this represents a range extension for *O. alpina*.

LITERATURE CITED

Berry, S. S. 1919. Mollusca of Glacier National Park, Montana. Proceedings of the Academy of Natural Sciences of Philadelphia 71: 195–209.

Elrod, M. J. 1901. Montana shells. Rocky Mountain Magazine 2: 691–697.

Hendricks, P. 1998. Rediscovery of *Discus brunsoni* Berry, 1955 and *Oreohelix alpina* (Elrod, 1901) in the Mission Mountains, Montana, with comments on *Oreohelix elrodi* (Pilsbry, 1900). The Nautilus 112: 58–62.

Pilsbry, H. A. 1904. General Notes. The Nautilus 17: 131.

Pilsbry, H. A. 1939. Land Mollusca of North America (North of Mexico). Volume 1, Part 1. The Academy of Natural Sciences of Philadelphia, Monographs Number 3, Philadelphia, xvii + 573 + ix [index] pp.

Notes

Authorship and date of publication of *Ostrea chilensis* Philippi *in* Küster, 1844 (Bivalvia: Ostreidae)

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Ostrea chilensis, a commercial oyster of New Zealand and Chile (Buroker *et al.*, 1983; Chanley and Dinamani, 1980; Jeffs and Creese, 1996; Ó Foighil et al., 1999; Ó Foighil and Taylor, 2000), consistently has been dated from 1845 under authorship of Philippi in all references seen. The few authors who cite the original reference for *O. chilensis* (Dall, 1909; Hanley, 1856; Lamy, 1929) refer to Küster's edition of *Systematisches Conchylien-Cabinet von Martini und Chemnitz*, p. 74, pl. 13, fig. 7, 8, in volume 7, part 1. The text describing *O. chilensis* ("Philippi in Lit.") is part of Lieferung 186, issued in 1868 (Küster, 1868) (Johnson, 1968: 366; Smith and England, 1937: 97; Welter-Schultes, 1999: 185). The taxon *Ostrea chilensis* (as "O. [strea] *chilensis* Philippi") in fact originates from the list of species depicted on the plates included in Lieferung 45 printed on the wrapper thereof (Küster, 1844), which bears the imprinted date 1844 and is assumed to have been issued then in the absence of evidence to the contrary (ICZN, 1999: Article 21.3). Here *Ostrea chilensis* stands technically as a *nomen nudum*, for at the foot of the list is the statement "Wegen Krankheit des Kupferstechers kann Taf. XIII erst mit der nächsten Lieferung ausgegeben werden" ("Because of the engraver's illness, Plate 13 will be distributed with the next delivery.") In the absence of evidence to the contrary it is appropriate to accept that plate 13 was indeed issued in the next Lieferung (which is [illegible] 1844 and assumed to have been issued then [illegible] name *O. chilensis* became available from the [illegible] standpoint at the time of issue of that [illegible] that pl. 13 was erroneously attributed [illegible] Lieferung 45 erroneously dated 18[illegible] 1999: 185) but the latter correctly [illegible] compilation.) Although wrappers [illegible] intended to be discarded, and [illegible] duced on them with reference [illegible] criteria for availability (ICZN Articles 8.1, 12 [illegible] placed on these wrappers were accepted as pub[illegible] C. D. Sherborn (in Smith and England, 1937: S[illegible] *et figura*"), who failed, however, to include *Ostrea chilensis* in *Index Animalium* (Sherborn, 1922–1933). The authorship and date of publication of *O. chilensis* are thus Philippi *in* Küster, 1844 (Küster, 1844).

ACKNOWLEDGMENTS

For checking accession records for parts of *Systematisches Conchylien-Cabinet von Martini und Chemnitz* and other works, I am grateful to R. Janssen (Senckenberg Museum, Frankfurt), A.L. Kabat (Washington, D.C.), D.G. Reid (The Natural History Museum, London), A.H. Swann (Wheldon and Wesley Ltd., Leighton Buzzard), A. Warén (Swedish Museum of Natural History, Stockholm), and F. W. Welter-Schultes (Universität Göttingen). Special thanks to S. Jordan (La Habra Heights, California), who supplied a photocopy of a wrapper of Lieferung 45, and to P. Bouchet (Museum National d'Histoire Naturelle, Paris) and A. L. Kabat for extensive comments on the subject.

LITERATURE CITED

Buroker, N. E., P. Chanley, H. J. Cranfield, P. Dinamani. 1983. Systematic status of two oyster populations of the genus *Tiostrea* from New Zealand and Chile. Marine Biology 77: 191–200.

Chanley, P. and P. Dinamani. 1980. Comparative descriptions of some oyster larvae from New Zealand and Chile, and a description of a new genus of oyster, *Tiostrea*. New Zealand Journal of Marine and Freshwater Research 14: 103–120.

Dall, W. H. 1909. Report on a collection of shells from Peru, with a summary of the littoral marine Mollusca of the Peruvian zoological province. Proceedings of the United States National Museum 37: 147–294.

Hanley, S. 1842–1856. An illustrated and descriptive catalogue of Recent bivalve shells. Williams and Norgate, London, xviii + 392 pp.

ICZN (International Commission on Zoological Nomenclature). 1999. International Code of Zoological Nomenclature. Fourth Edition. International Trust for Zoological Nomenclature, London, 306 pp.

Jeffs, A. G. and R. G. Creese. 1996. Overview and bibliography of research on the Chilean oyster *Tiostrea chilensis* (Philippi, 1845) from New Zealand waters. Journal of Shellfish Research 15: 305–311.

Johnson, R. I. 1968. Martini and Chemnitz (Kuester's edition) Systematisches Conchylien-Cabinet, 1837–1920: a complete collation. Journal of the Society for the Bibliography of Natural History 4: 363–367.

Küster, H. C. 1844. Inhalt [list of species depicted on plates included in Lieferung 45, pl. 13, however, evidently issued in Lieferung 46, 1844]. Systematisches Conchylien-Cabinet von Martini und Chemnitz (Küster, H. C., ed.) 7 (4): 45 (wrapper). Bauer and Raspe, Nürnberg. (Photocopy in Mollusca Section library, Museum of New Zealand Te Papa Tongarewa.)

Küster, H. C. 1868. Conchifera. Zweischalige Mollusken. Conchifera monomyaria. Muschelthiere mit einem Schliessmuskeln. Systematisches Conchylien-Cabinet von Martini und Chemnitz (Küster, H. C., ed.) 7 (4): 186: 50–84. Bauer and Raspe, Nürnberg.

Lamy, E. 1929. Révision des *Ostrea* vivants du Muséum National d'Histoire Naturelle de Paris. Journal de Conchyliologie 73: 1–46.

Ó Foighil, D., B. A. Marshall, T. J. Hilbish and M. A. Pino. 1999. Trans-Pacific range extension by rafting is inferred for the flat oyster *Ostrea chilensis*. Biological Bulletin 196: 122–126.

Ó Foighil, D. and D. J. Taylor. 2000. Evolution of parental care and ovulation behavior in oysters. Molecular Phylogenetics and Evolution 15: 301–313.

Sherborn, C. D. 1922–1933. Index Animalium 1801–1850. British Museum (Natural History), London: Longmans, Green and Co., B. Quaritch, Dulau, Oxford University Press, Wheldon and Wesley, and Oliver and Boyd.

Smith, E. A. and H. W. England. 1937. Martini and Chemnitz (Kuester's edition) Systematisches Conchylien Cabinet 1837–1918. Journal of the Society for the Bibliography of Natural History 1: 89–99.

Welter-Schultes, F. W. 1999. Systematisches Conchylien-Cabinet von Martini und Chemnitz (1837–1920), bibliography of the volumes in Göttingen. Archives of Natural History 26: 157–203.

Tadashige Habe (1916–2001)

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Tadashige Habe, who died at 85 on December 29, 2001, was one of the most productive and influential zoologists of the twentieth century. He played a major part in the development of malacology in Japan and the western Pacific, and authored a large number of books that set the standards for the study of the systematics and distribution of mollusks from that area of the world.

Dr. Habe was born March 31, 1916, in the village of Hioki, part of what is now Sasayama in Hyogo Prefecture. He attended Ikeda High School in neighboring Osaka Prefecture, staying on to work as an assistant teacher until 1939. Electing to study zoology at Kyoto Imperial University from 1939 to 1941, he then transferred to Seto Marine Laboratory in Shirahama, returning to Kyoto in 1945. Dr. Habe had joined the staff at Kyoto as a junior research assistant in 1942 and became a full research assistant in 1949. From 1946 to 1950 he also served as an adviser to the Natural Resources Section of Allied General Headquarters in Tokyo.

After receiving his doctor of science degree in 1957, Dr. Habe was appointed assistant professor at Kyushu University and moved to the Marine Biological Laboratory on Amakusa Island in western Kyushu. He retained his position at Kyushu University for five years after moving in 1962 to the National Science Museum in Tokyo (NSMT).

Dr. Habe's career at the NSMT lasted from his appointment as researcher in 1962 to his retirement as head of the zoology department in 1980. He then served for four years as a professor at the Ocean Institute of Tokai University, where he remained professor emeritus until 1989. From 1985 to 1988 he was also director of the Tokai University Museum of Natural History. In 1986 Dr. Habe was awarded the Order of the Sacred Treasure (Zuiho-sho) by the Japanese government for his contributions to zoological research in Japan.

Dr. Habe first published formally as co-author of a 1935 report on shell collecting in Manchuria and Korea. For more than fifty years he wrote prodigiously, alone and in co-authorship with all the other senior Japanese malacologists of the post-war period. Several of his books are well known outside Japan, including *Shells of the Western Pacific in Color* (1964) and *Shells of the World in Colour* (Vol. 1, 1965, with Kiyoshi Ito; Vol. 2, 1966, with Sadao Kosuge).

Earlier in his career Dr. Habe worked closely with Tokubei Kuroda (1886–1987), who had arrived at Seto Marine Laboratory in 1940 and was to have a formative influence on the younger man. The two published their first joint book, a synopsis of the Japanese Helicacea, in 1949. This work was followed by the extensive *Illustrated Catalogue of Japanese Shells* (1949–1955) and the landmark *Checklist and Bibliography of the Recent Marine Mollusca of Japan* (1952). The latter was published in part as a result of its Dr. Habe's work for Allied General Headquarters, and provided the first thorough collation of Western and local literature on Japanese Mollusca. In 1971 Kuroda and Habe were joined by Katsura Oyama (1917–1995) in producing the lavish *The Sea Shells of Sagami Bay*. This extensive work owed its existence in part to the favorable relationships all three authors enjoyed with the Imperial household, a connection further reflected in a number of subsequent papers co-authored by Dr. Habe and Prince Hitachi (Masahito), brother of the current emperor.

During the four decades that followed the Second World War, Japanese malacology was to a considerable extent sustained by the sponsorship and participation of a number of keen amateur collectors and authors. Dr. Habe was an enthusiastic advocate of collaboration with amateur collectors, and skillfully helped channel the energy and resources of benefactors such as Tetsuaki Kira and Ryosuke Kawamura into the production of useful publications and scientifically significant collections. He was instrumental in obtaining the vast Kawamura collection for the NSMT, and co-authored an impressive iconography based on it, *World Seashells of Rarity and Beauty* (1991).

Dr. Habe's speciality was taxonomy, and he was the first Japanese malacologist to serve on the council of the International Trust for Zoological Nomenclature. In 1977, he published *Systematics of Mollusca in Japan: Bivalvia and Scaphopoda*, a complete illustrated taxonomical treatment of both groups.

Another important but less well-known facet of Dr. Habe's career was his work in translating and summarizing developments in Western malacology for the benefit of his Japanese colleagues. This took the form of a long series of well-researched biographies of Western malacologists and zoologists as well as reviews of books and monographs and reports on Japanese type specimens in overseas museum collections.

He was well known among malacologists in the West, and traveled overseas more often than many of his contemporaries. During his period with Allied General Headquarters, he worked both with Dr. Alvin Cahn and Dr. Myra Keen of Stanford University. In later years, he was a regular visitor to the United States and a friend in particular of Dr. R. Tucker Abbott, with whom he shared a broad outlook concerning amateur scientists and popular publications. Visitors to the NSMT during Dr. Habe's tenure always benefited from his renowned hospitality.

A member from its early days of the Malacological Society of Japan, Dr. Habe served as vice president from 1963 to 1979, as president from 1979 to 1995 and as emeritus president until his death. In recent years his failing eyesight began to restrict his activities, but he remained an active contributor to conferences and periodicals until the late 1990s.

In the course of his career, Dr. Habe introduced more than a thousand new names to science. Collations of his new taxa were published by Inaba and Oyama (1977) and Okamoto (2001). The latter work is complete, includes a full bibliography and cites 976 new species names and 315 new genera. A partial bibliography was published by Dr. Habe himself in 1980.

LITERATURE CITED

Habe, T. 1980. Bibliography of Tadashige Habe. T. Habe, Tokyo. 47 pp. [Partly in Japanese.]

Inaba, T. and K. Oyama (Eds.) 1977. Catalogue of molluscan taxa described by Tadashige Habe during 1939–1975, with illustrations of hitherto unfigured species. Okinaebisu-kai, Chiba. 185 pp., 7 pls.

Okamoto, M. (ed.) 2001. Molluscan taxa described by Tadashige Habe. Vol. 1. Gastropoda (excluding Heterobranchia): i–viii + 1–891. Vol. 2. Gastropoda (Heterobranchia), Cephalopoda, Bivalvia & Scaphopoda): 892–1630 + xix–xxxix + index 1–42 + xl–xli. Committee for celebrating Dr. T. Habe's eightieth birthday, Tokyo. [Partly in Japanese.]

Book Review

Panamic Province Molluscan Literature: Additions and Changes from 1971 through 2001. III. Gastropoda.

Skoglund, C. 2002. Panamic Province Molluscan Literature: Additions and Changes from 1971 through 2001. III. Gastropoda. The Festivus 33 (supplement): i–xi + 1–286 pp.

Possibly inspired by the immensity of A. Myra Keen's *Sea Shells of Tropical West America* (Keen, 1971) and clearly based on a lifetime of study of the subject, for years Carol Skoglund has been updating the inventory of Panamic mollusks as originally published in Keen's work.

In the conclusion of a recent review of Skoglund's volume on bivalves and chitons (Leal, 2001, review of Skoglund, 2001)[1] I had wished that the author could provide an equivalent update on the gastropods. That work, also published as a supplement to *The Festivus*, is now available. The exhaustive compilation results from years of record keeping, as attested to by the long list of pertinent publications by the author in that periodical, and Skoglund's unquestionable grasp of the subject of Panamic mollusks. The general format follows that adopted for the previous parts. Although most of the updates consists of the inclusion of new species, Skoglund also presents newly adopted use of synonyms, new combinations (these latter two categories indicated by Keen's original species number), as well as the occurrence of supraspecific taxa new for the region (indicated in boldface).

In a similar fashion to the volume on bivalves and chitons, the new publication is spiral-bound and protected by a plastic cover. Although the compilation is not illustrated, reference to original works and existing figures is abundant and seems to be complete.

Like the previous volume, the gastropod update covers the coast, shelf, and slope between 25° N and 6° S. Most welcome bonuses are the extensive treatments of mollusks from oceanic islands in the tropical eastern Pacific, (e.g., Clipperton, Cocos, and Gorgona) and of those associated with geologically active features, such as hydrothermal vents and cold seeps, of the adjacent deep-sea areas. The only oversight I noticed in a brief reading of the suprageneric taxa were the misspellings of "Cocculiformia" [Cocculiniformia] (pages ii, 23), as a suborder under the subclass Neritimorpha. Skoglund used the correct spelling for the subclass Cocculiniformia (same pages), and I wonder whether the misspelled word was meant to be "Cocculinoida" or a repetition of "Cocculiniformia."

The hierarchical ranked arrangement of families and genera generally follows that adopted by Keen. In many cases, however, those were modified through the adoption of more recent taxonomic rearrangements, including some of the groupings ultimately compiled by Vaught (1988) and the inclusion of additional, mostly deep-sea, families and genera that have been introduced in the last 30 years, mainly through the efforts of J. H. McLean and others. The advances in our understanding of gastropod phylogeny over the past few decades (e.g., Ponder and Lindberg, 1996, 1997) have resulted in a higher classification of the Class Gastropoda that differs significantly from that incorporated in earlier works. While this new classification is being adopted in many recent works on gastropods (e.g., Beesley et al., 1998; Higo et al., 1999; Okutani, 2000) the opportunity to update the taxonomic arrangement of Panamic gastropods has been missed in Skoglund's work. This, however, shall not be a major handicap: the author's chief objective is to give a consistent update on the inventory and nomenclature of Panamic gastropods, providing links both to Keen's book and the original references. In my opinion, she has achieved what she set out to do with great success. If you use Myra Keen's work, you must have these updates.

The cost in the US is $35 postpaid (overseas $50, airmail only). Contact the San Diego Shell Club, c/o 3883 Mt. Blackburn Ave., San Diego, CA 92111, USA, or e-mail Carole Hertz (cmhertz@pacbell.net) for further information.

LITERATURE CITED

Beesley, P. L., G. J. B. Ross and A. Wells (eds.) 1998. Mollusca: the Southern Synthesis. Fauna of Australia Vol. 5. CSIRO Publishing, Melbourne, 563 pp. (Part A), pp. 565–1234 pp. (Part B).

Higo, S., P. Callomon and Y. Goto. 1999. Catalogue and Bibliography of the Marine Shell-bearing Mollusca of Japan. Elle Scientific Publications, Osaka, 749 pp.

Keen, A. M. 1971. Sea Shells of Tropical West America. Marine Mollusks from Baja California to Peru. 2nd edition. Stanford University Press, Stanford, xiv + 1064 pp.

Leal, J. H. 2001. Book review. Panamic Province Molluscan Literature. Additions and Changes from 1971 through 2001 [2000]. The Nautilus 115: 37.

Okutani, T. (ed.) 2000. Marine Mollusks in Japan. Tokai University Press, Tokyo, xlviii + 1173 [+2] pp.

Ponder, W. F. and D. Lindberg. 1996. Gastropod phylogeny—challenges for the 90s. In: J. D. Taylor (ed.) Origin and Evolutionary Radiation of the Mollusca. Oxford University Press, Oxford, pp. 135–154.

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[1] Inadvertently, in the title of my review I cited the bivalve and chiton volume as "...from 1971 to 2001" when it should have been "... from 1971 to 2000." My apologies to the author and editor.

Ponder, W. F. and D. Lindberg. 1997. Towards a phylogeny of gastropod molluscs: an analysis using morphological characters. Zoological Journal of the Linnean Society 119: 83–265.

Skoglund, C. 2001. Panamic Province Molluscan Literature. Additions and Changes from 1971 through 2000. I. Bivalvia. 2. Polyplacophora. The Festivus 32 (supplement): i–v + 1–119 (Bivalvia), 1–20 (Polyplacophora).

Vaught, K. C. 1988. A Classification of the Living Mollusca. American Malacologists, Inc., Melbourne (Florida), xii + 189 pp.

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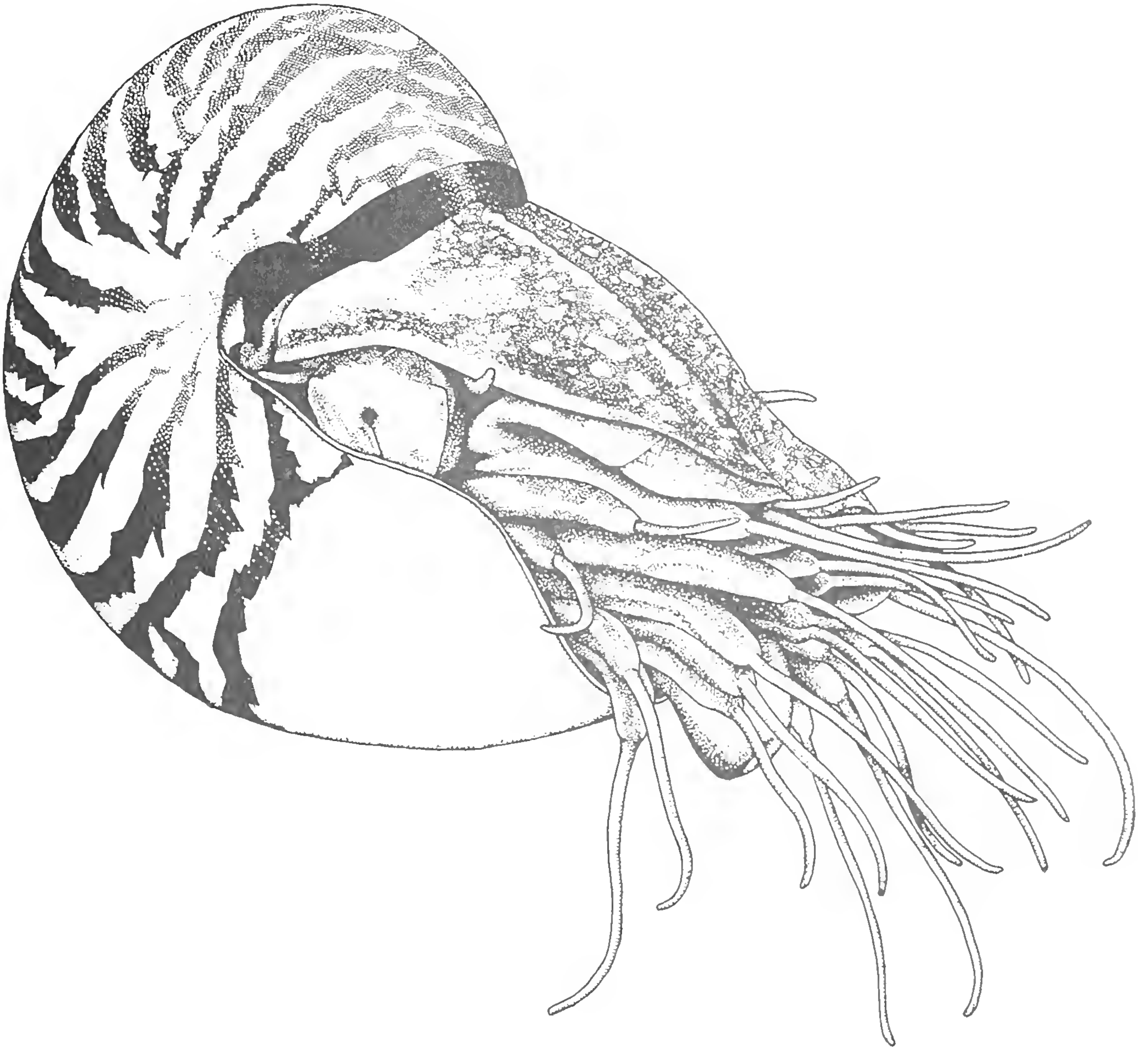

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CONTENTS

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FLORIDA Arts

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Tertiary Xenophoridae (Gastropoda) of western South America

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ABSTRACT

Three species of Xenophoridae are reported from the Tertiary of western South America. *Xenophora carditigera* new species from the Oligocene of Peru, *Xenophora paulinae* new species from the Miocene Navidad Formation of central Chile, and *Stellaria kriegerbartholdi* new species from the Tertiary of Peninsula Arauco, south-central Chile. All of these species are first records of Xenophoridae for the respective countries. The relationship of South American *Xenophora* species with Tertiary New Zealand taxa and the difficulty in identifying a species closely related to the other South American *Stellaria* are discussed.

INTRODUCTION

Xenophoridae are a group of exclusively warm-water marine gastropods. The biology, fossil history, and taxonomy of 25 recent species has been reviewed by Ponder (1983), who recognized the single genus *Xenophora* Fischer von Waldheim, 1807, including the subgenera *Xenophora sensu stricto*, *Onustus* Swainson, 1840, and *Stellaria* Schmidt, 1832. However, most workers now recognize these at the generic rank (e.g., Kreipl and Alf, 1999), a view that is followed here. Where known, the protoconch in *Xenophora* species consists of about 3.5 low trochospiral whorls (Bandel, 1993: pl. 12, fig. 1), a type of morphology that indicates planktotrophic development, which in turn suggests long-distance dispersal.

Ponder (1983) also described Tertiary fossil species from Australia, while in an earlier work, Beu (1977) reviewed the Cenozoic Xenophoridae of New Zealand which include an Eocene to Miocene species, a Miocene species and a Pliocene to Recent species. Until now, Cenozoic Xenophoridae have never been recorded from Peru or Chile.

GEOLOGY OF FOSSIL-BEARING LOCALITIES

PISCO BASIN, PERU

The Pisco Basin of southern Peru (Figure 1) is a forearc basin (Dunbar et al., 1990) with four depositional sequences containing upper Eocene, Oligocene, lower to middle Miocene, and middle Miocene to lower Pliocene shelf and littoral deposits (DeVries, 1998). Specimens of *Xenophora* are most often found in massive, bioturbated, medium-grained sandstones of the Oligocene Otuma Formation between Paracas and Bahía de la Independencia (Figure 1), together with valves of *Cardita newelli* Rivera, 1957. The *Xenophora*-bearing sandstones interpreted as shallow-water nearshore shelf deposits, overlie a basal transgressive sequence of medium bedded coarse-grained sandstones with nearly monospecific molluscan assemblages of *Turritella* or *Ostrea*, and underlie a thick sequence of thin-bedded, tuffaceous, fine-grained siltstones with thin-shelled valves of *Chlamys* and fish scales of sardines and anchovies (DeVries, 1998).

Internal molds of probable *Xenophora* species are also found in a fault-bound outcrop of pebbly coarse-grained sandstone overlooking the lower Río Ica valley (Figure 1). The molluscan fauna associated with the molds suggest a late Eocene age and hence assignment to the Paracas Group.

NAVIDAD FORMATION, CENTRAL CHILE

The Navidad Formation (Darwin, 1846) is known for a rich molluscan fauna that was last reviewed extensively by Philippi (1887). Sediment deposition as indicated by microfossils ranges from intertidal to outer shelf. Most of the specimens of *Xenophora* described here have been recovered from gray deepwater siltstone that today forms the intertidal platform at Punta Perro (Figure 2). These deposits have been dated with foraminifers by Dremel (in Herm, 1969, p. 71) as Lower Miocene (Burdigalian). However, Tsuchi et al. (1990) and Ibaraki

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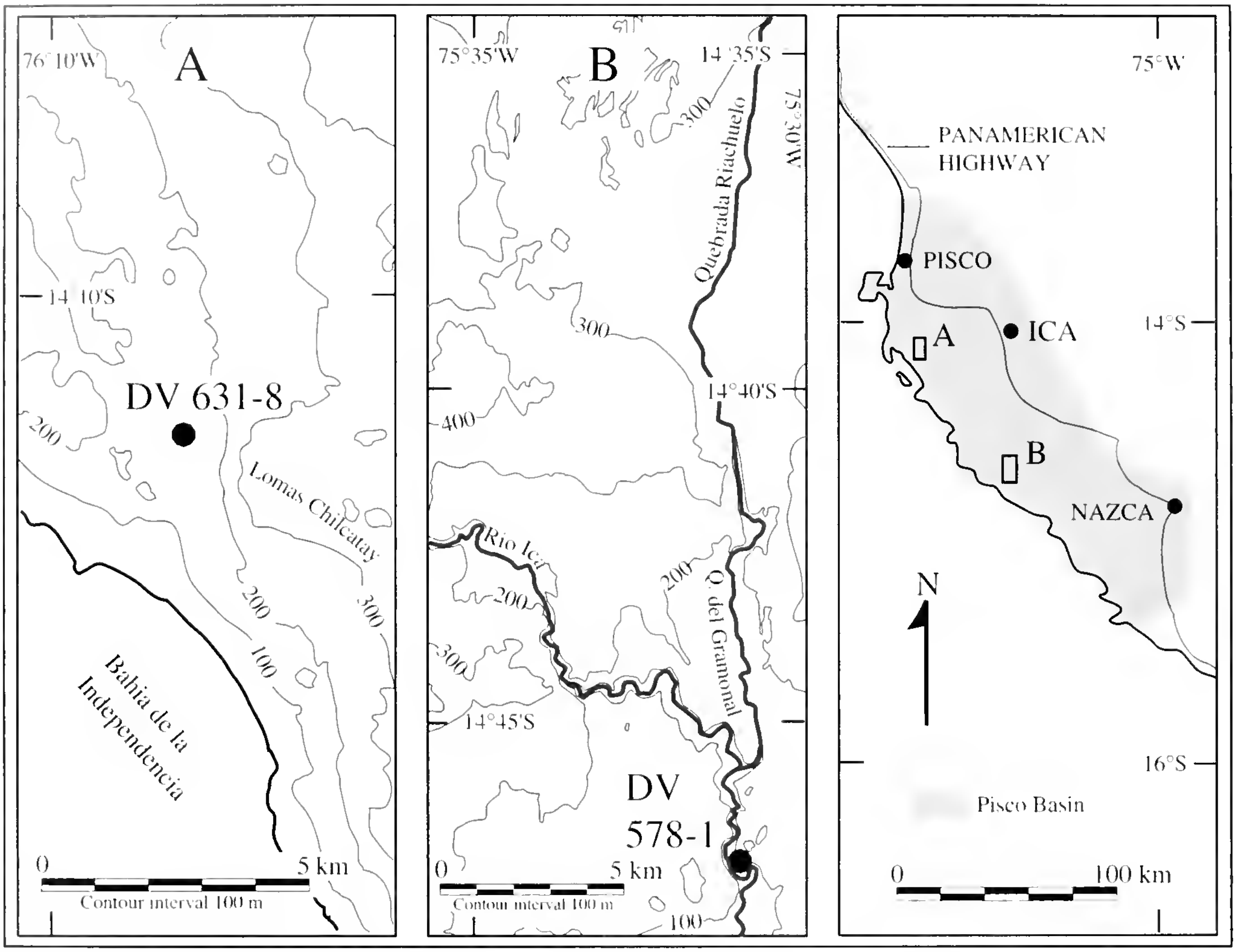


Figure 1. Fossil localities for *Xenophora carditigera* in the Pisco Basin of Peru.

1992) have pointed out that an Upper Miocene age (Tortonian) is more likely.

Additional specimens have been collected north of the Río Rapel and from Matanzas, both also in the area of Navidad (Figure 2). The sediments of these localities are believed to be contemporaneous with those of Punta Perro.

MILLONGUE FORMATION, PENINSULA ARAUCO, SOUTH-CENTRAL CHILE

The Millongue Formation has been defined from cores drilled in [illegible] Arauco. It consists of gray siltstones dated [illegible] (García 1968). All similar siltstones of [illegible] generally have been considered to belong in this [illegible]. However, analysis of the molluscan fauna [illegible] Miocene age at least for part of these sediments [illegible] unpublished data).

The *Stellaria* specimen described herein was found in a concretionary nodule from a coastal cliff with exposures of gray siltstones to the east of Punta Millongue (Figure 2). These concretionary nodules are washed free by the tide and usually yield specimens of the crab *Cancer araucanus* Philippi, 1887. Because this locality has not been dated until now, the age of the *Stellaria* remains uncertain.

MATERIALS AND METHODS

Specimens described or mentioned in this study are deposited in the collections of the following museums: Departamento de Paleontología de Vertebrados, Museo de Historia Natural de la Universidad de San Marcos, Lima, Peru (MUSM INV); 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 camera. Images were scanned from Ilford FP4 125 black and white 35 mm negatives using an Acer ScanWit 2720S film scanner and processed with Photoshop 6.0.

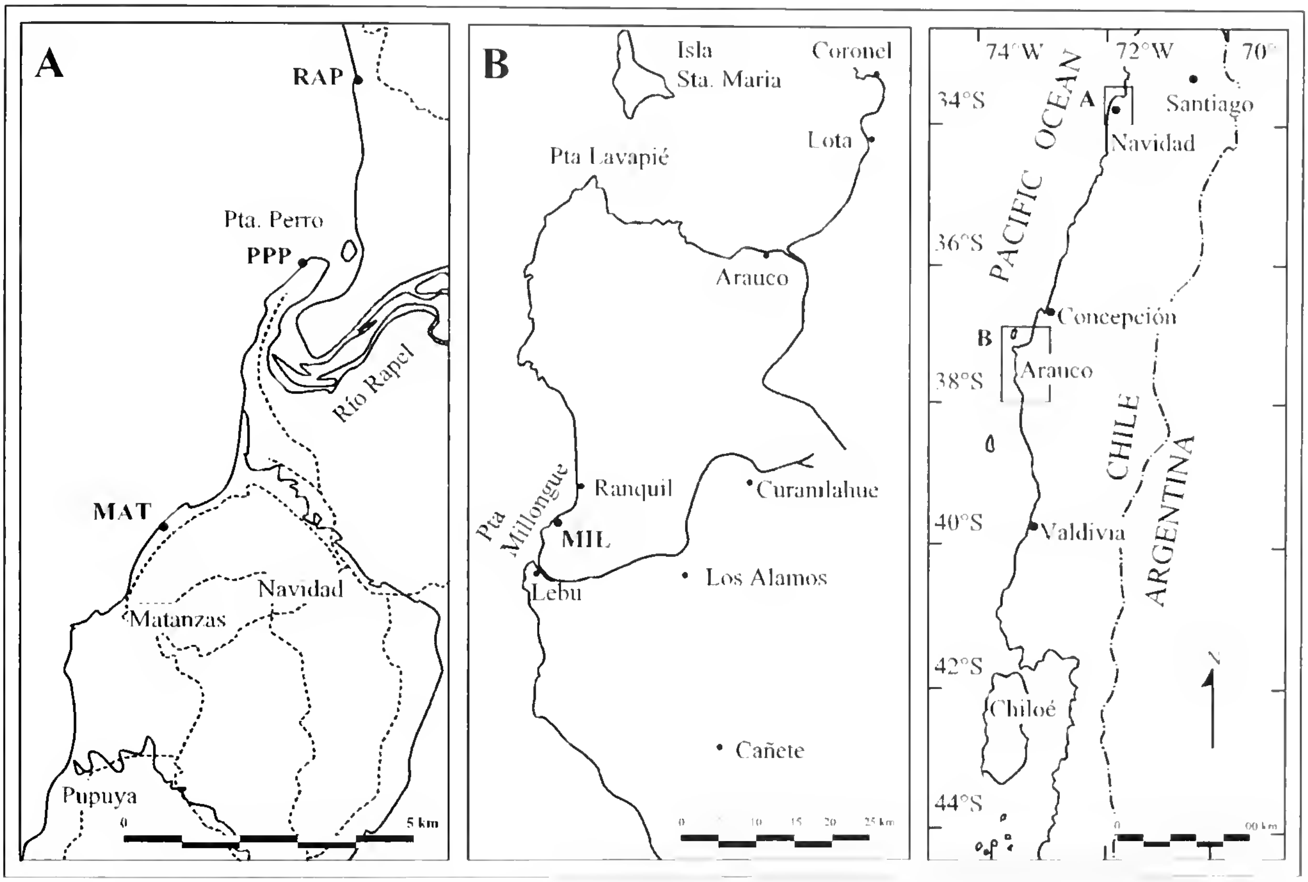


Figure 2. Fossil localities for *Xenophora paulinae* (Navidad area) and *Stellaria kriegerbartholdi* (Peninsula Arauco) in Central Chile.

SYSTEMATIC PALEONTOLOGY

Family Xenophoridae Philippi, 1853
Genus *Xenophora* Fischer von Waldheim, 1807

Type Species: *Xenophora laevigata* Fischer von Waldheim, 1807 (= *Trochus conchyliophorus* Born, 1780)

Xenophora carditigera new species
(Figures 3–11)

Diagnosis: Moderate size, moderately tall spire; base without spiral sculpture; dorsal surface with weakly opisthocline to spiral irregular lirae.

Description: Diameter up to 36 mm. Spire angle 70–90°; whorls and spire flat-sided to very slightly convex. Protoconch poorly preserved. Base flat to slightly concave; neither spiral nor subspiral sculpture (lines, threads, rugae) evident; colabral growth lines and ridges present. No umbilicus in adults; none evident in juveniles; thick columella. Dorsal surface with weak prosocline growth lines and coarse, wavy lirae that are weakly opisthocline to irregularly spiral. No prosocline nor opisthocline axial cords. Cemented objects evenly spaced, about seven per whorl, increasing in size on later whorls, less than 50% of shell covered. Aperture unknown.

Type Material: Holotype SMF 323039 (figures 3–5), height 17 mm, diameter 36 mm. 5 paratypes: SMF 323040, height 16 mm, diameter 30 mm, SMF 323041 (figures 6–8), height 13.5 mm, diameter 22.5 mm, MUSM INV 1 (figures 9–11), height 21 mm, diameter 32.5 mm, MUSM INV 2, height 15 mm, diameter 26.5 mm, MUSM INV 3, height 13 mm, diameter 21.5 mm.

Type Locality: DV 631-8, northwest of Loma Cuesta Chilcatay, about 1 km north of Comotrana-Carhuas road, about 5 km east Playa Carhuas, in ridge-forming sandstone bed, 120.5 m in measured section, 14°11′06″ S, 76°08′17″ W (Punta Grande 1:100,000 quadrangle).

Etymology: Named after *Cardita*, the bivalve most often cemented to this species, and *gera*, the Latin root signifying "to bear or carry."

Occurrence: Otuma Formation (Oligocene), between Paracas and Bahía de la Independencia, Peru. Possibly from the uppermost Eocene.

Discussion: Specimens of *Xenophora carditigera* new species differ in several respects from those of *X. con-*

Figures 3–12. [illegible] 3–11. [illegible] new species. 3–5. Holotype SMF 323039, height 17 mm [illegible] 6–8. [illegible] 041, height 5.5 mm, diameter 22.5 mm. 9–11. Paratype MUSM INV 1, height 21 mm, [illegible] 12. [illegible] species. Paratype SGO.PI 5991, diameter 154 mm.

chyliophora (Born, 1780), a species with a fossil record that may extend back to the Eocene and which is presently found off the coast of both eastern and western North and Central America (Ponder, 1983). The latter species is characterized by rugose cords on the dorsal surface; wavy lirae that are distinctly opisthocline; base with weak spiral sculpture; an umbilicus in juvenile specimens; and a thin columella and umbilical callous in adults. Specimens of *X. carditigera*, in contrast, have neither rugose spiral cords, strongly opisthocline lirae, nor spiral sculpture on the base, and have a thick rather than thin columella.

Xenophora carditigera most closely resembles *X. flemingi* Beu, 1977, an early to middle Miocene species from New Zealand that may be part of a lineage that includes *X. prognata* (Finlay, 1926) (late Eocene to middle Miocene) and *X. neozelanica* Suter, 1908 (early Pliocene to Recent). Specimens of *X. flemingi* are also moderately tall and straight-sided, lack an umbilicus, have weakly developed to obsolete spiral sculpture on the base, and are only partially covered by cemented debris that increases in size towards the aperture. The principal difference between *X. carditigera* and *X. flemingi* is that dorsal lirae on the latter are distinctly opisthocline.

Xenophora paulinae new species
(Figures 12–16)

Diagnosis: Shell large, umbilicus closed, whorl outline concave. Subsutural ramp reaching halfway onto previous whorl. Dorsal surface between cemented objects with coarse wavy lirae and prosocline axial growth lines.

Description: Shell large (holotype diameter 132 mm, height 62 mm), with depressed spire (angle about 105°), peripheral flange unknown. Protoconch unknown. No umbilicus in adults (no juveniles known), whorl outline concave due to subsutural ramp reaching about halfway up onto previous whorl. Dorsal surface between cemented objects with coarse wavy lirae as well as prosocline axial growth lines. Base weakly concave, sculptured with low, narrow, irregular, collabral growth lirae. Attached camouflaging objects seem to include either high-spired gastropods or concave-side-up bivalves (up to 50 mm wide). Basal apertural lip regularly and shallowly curved. Aperture unknown.

Type Material: Holotype SMF 323042 (figures 13–14), height 62 mm, diameter 132 mm, Punta Perro; paratypes SGO.PI 5991 (figure 12), diameter 154 mm, Punta Perro, SGO.PI 5992 (figures 15–16), spire fragment, height 16 mm, Matanzas.

Type Locality: Intertidal platform at Punta Perro, central Chile.

Etymology: Named after Paulina S. Vasquez Illanes, friend and colleague, who found part of the type material.

Occurrence: Navidad Formation, Tortonian, Navidad area, central Chile.

Discussion: *Xenophora paulinae* new species differs from most other species by its large size. The only similarly large species is the Eocene to Miocene New Zealand *Xenophora prognata* (Finlay, 1926) (see Beu, 1977) from which it differs in having concave rather than convex whorls, formed by a subsutural ramp reaching about halfway up onto previous whorl.

Previously, Tavera (1979) stated that his *Trochita gigantea* (also from the Navidad Area) might prove to be a *Xenophora*. However, Tavera (1979) provided no diagnosis to separate his species from other taxa, and he did not figure the specimen. Consequently the name is considered unavailable under ICZN Article 13.1.1.

Genus *Stellaria* Schmidt, 1832

Type species: *Trochus solaris* Linné, 1764

Stellaria kruegerbartholdi new species
(Figures 17–20)

Diagnosis: Spire short, with narrow peripheral flange divided into prominent, blunt digitations. No umbilicus. Base lightly convex, with distinct collabral growth lines.

Description: Short spire, periphery divided into about 10 prominent blunt digitations. No umbilicus. Whorl outline and sculpture unknown, because original shell is dissolved except for periphery and digitations, but outline appears to be weakly convex. Base slightly convex, with distinct collabral growth lines.

Holotype: SGO.PI 5993 (figures 17–20), height 24 mm, diameter with attachments 60 mm, spire angle 95°.

Type Locality: Northeast of Playa Millongue, Peninsula Arauco, south-central Chile.

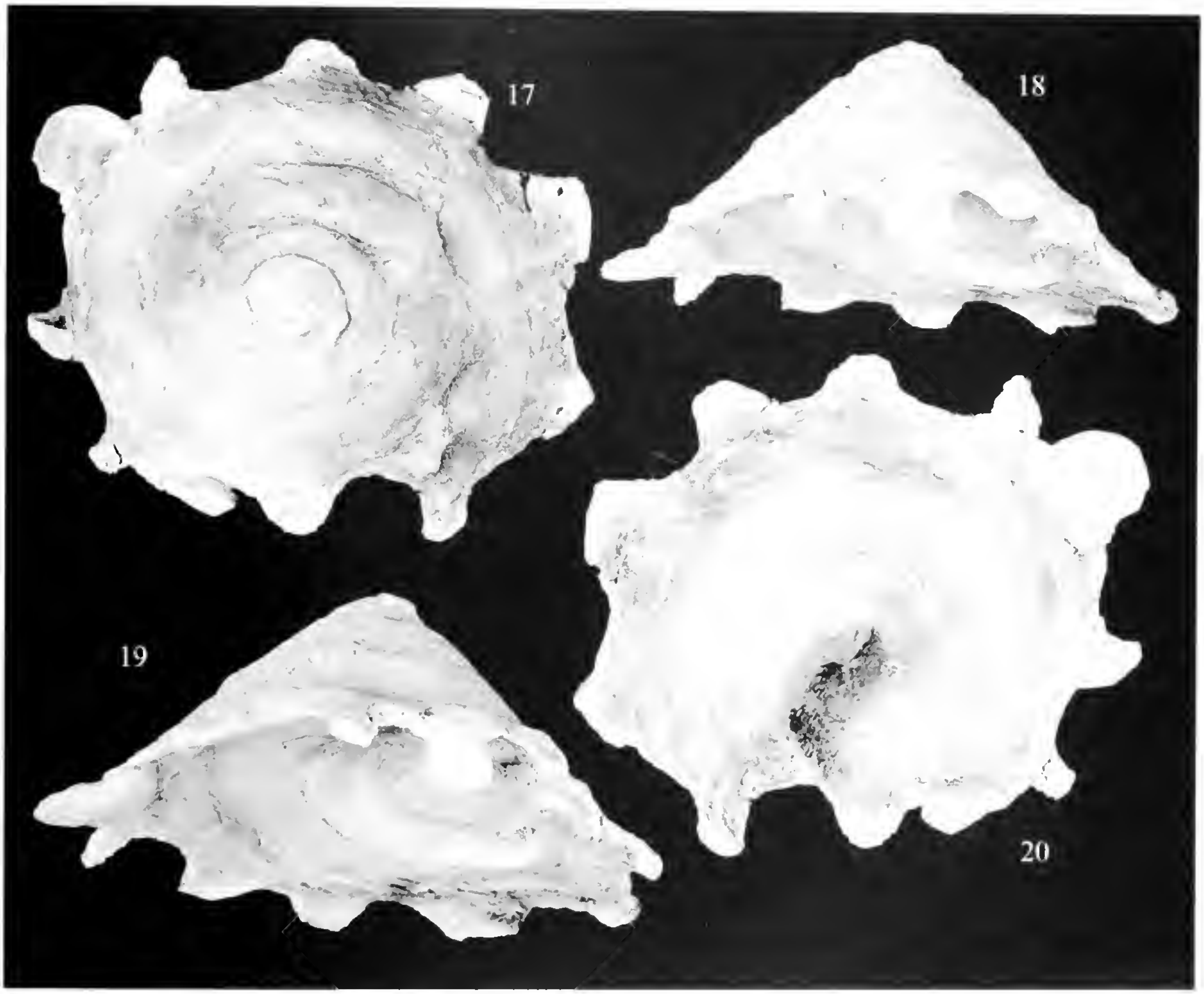
Etymology: Named after Rolf Kruegerbarthold, who did the difficult preparation of this specimen.

Occurrence: Northeast of Punta Millongue, Peninsula Arauco, south-central Chile.

Discussion: *Stellaria kruegerbartholdi* differs from all other species of this genus in having a closed umbilicus. The type species, *S. solaris*, has tubular spines, a feature that cannot be observed in *S. kruegerbartholdi*. *S. kruegerbartholdi* most resembles the Oligocene to Pliocene *S. testigera* (Bronn, 1831) (with its two Recent subspecies) in having a strongly digitate peripheral rim. *S. testigera* lived in the Mediterranean and spread to Atlantic Africa and the Gulf of Aden. As suggested by Ponder (1983), *S. testigera* could have evolved from the Eocene *S. conica* Dall, 1892 from Mississippi, which also might be regarded as ancestral to *S. kruegerbartholdi*. *S. conica* has the umbilicus almost obscured by the parietal callus (McNeil and Dockery, 1984). The completely closed umbilicus would also justify inclusion of this species in *Xenophora*, suggesting that this species or species line lost its camouflaging habit and evolved from a different ancestor than *Stellaria* s.s. However, this view is not followed here.

Figu[illegible] *[illegible]aulam* new species. **13–14.** Holotype SMF 323012, height 62 mm, diameter 132 mm. **15–16.** [illegible] fragment, height 16 mm.

Remarks. [illegible] for *Stellaria* given by Ponder [illegible] 1983) ha[illegible] to include species with a closed umbilic[illegible] *[illegible]bartholdi* Ponder, 1983 [illegible] noted that the p[illegible] *[illegible]stigera*) is not completely satisfactor[illegible] which is even more appropriate for *S. kruegerbartholdi*. It does not seem justified to erect a new genus for this species because a closed umbilicus is also present in *Xenophora* and, therefore, seems to be an old invention of the family. Characters separating *Stellaria* from *Xenophora* are reduced



Figures 17–20. *Stellaria kriegerbartholdi* new species. Holotype SGO.PI.5993, height 24 mm, diameter with attachments 60 mm.

to the presence of spines or digitations, an expanded peripheral flange and a nearly smooth dorsal surface.

CONCLUSIONS

The Cenozoic Xenophoridae of Chile and Peru close a considerable biogeographic gap in the history of the family. Oligocene records of *Xenophora* are few but the genus was already established in Australia (Ponder 1983) and New Zealand (Beu 1977) in the Eocene. In the Miocene the genus was widespread in the Indo-Pacific Region with three species also present in the Caribbean Sea. Today only the type species, *X. conchyliophora* remains in the Americas (Ponder 1983).

Our two species of *Xenophora* seem closely allied with New Zealand species. Similarities between faunas from New Zealand and Argentina have recently been indicated by Beu et al. (1997). Our records of *Xenophora* show that there are even more connections with Pacific South America, a fact which is, of course, not surprising. More trans-Pacific affinities can be expected from further studies of Pacific South American faunas.

Stellaria conica from Eocene beds of Mississippi may be an ancestor of *S. kriegerbartholdi* but has an open umbilicus like modern species. Ponder (1983) discussed *S. testigera* as a possible early offshoot while *Stellaria* was still close to *Xenophora*, which may also be true for *S. kriegerbartholdi*. However, characters of the known *Stellaria* species suggest that the fossil record of this genus is very fragmentary.

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Klaus Bandel is thanked for company in the field and discussion on Chilean geology and biology of *Xenophora*. José H. Leal, Alan Beu, and an anonymous reviewer made valuable comments which helped to improve the manuscript. Fieldwork of SNN was financially supported by the Deutsche Forschungsgemeinschaft (DFG), grant Ba 675/25. Fieldwork of TJDV was financed by himself and in part by a Fulbright Senior Scholarship.

LITERATURE CITED

Bandel, K. 1993. Caenogastropoda during Mesozoic times. Scripta Geologica, Special Issue 2: 7–56.

Beu, A. G. 1977. New Zealand Cenozoic gastropods of the genus *Xenophora* Fischer, 1807. Journal of the Royal Society of New Zealand 7: 229–241.

Beu, A. G., M. Griffin and P. A. Maxwell. 1997. Opening of Drake Passage gateway and Late Miocene to Pleistocene cooling reflected in Southern Ocean molluscan dispersal: evidence from New Zealand and Argentina. Tectonophysics 281: 83–97.

Darwin, C. 1846. Geological observations on South America. Smith, Elder & Co., London, 279 pp.

DeVries, T. J. 1998. Oligocene deposition and Cenozoic sequence boundaries in the Pisco Basin (Peru). Journal of South American Earth Sciences 11: 217–231.

Dunbar, R. B., R. C. Marty, P. A. Baker. 1990. Cenozoic marine sedimentation in the Sechura and Pisco basins, Peru. Palaeogeography, Palaeoclimatology, Palaeoecology 77: 235–261.

García A., F. 1968. Estratigrafía del Terciario de Chile Central. In: Cecioni, G. (ed.): Symposio sobre el Terciario de Chile, Zona Central. Andres Bello, Santiago, pp. 25–57.

Herm, D. 1969. Marines Pliozän und Pleistozän in Nord- und Mittel-Chile unter besonderer Berücksichtigung der Entwicklung der Mollusken-Faunen. Zitteliana 2, 159 pp.

Ibaraki, M. 1992. Planktonic Foraminifera from the Navidad Formation, Chile: their geologic age and paleoceanographic implications; pp. 91–95. In: Ishizaki, K. and T. Saito (eds.): Centenary of Japanese Micropaleontology. Terra Scientific Publishing Company, Tokyo.

Kreipl, K. and A. Alf. 1999. Recent Xenophoridae. ConchBooks, Hackenheim, 148 pp.

McNeil, F. S. and D. T. Dockery, III. 1984. Lower Oligocene Gastropoda, Scaphopoda, and Cephalopoda of the Vicksburg Group in Mississippi. Mississippi Department of Natural Resources, Bureau of Geology Bulletin 124, 415 pp.

Philippi, R. A. 1887. Los fósiles terciarios i cuartarios de Chile. F.A. Brockhaus, Leipzig, 256 pp.

Ponder, W. F. 1983. Xenophoridae of the world. The Australian Museum Memoir 17, 126 pp.

Tavera, J. 1979. Estratigrafía y paleontología de la Formación Navidad, Provincia de Colchagua, Chile (Lat. 30°50'–34° S). Boletín del Museo de Historia Natural Chile 36: 1–176.

Tsuchi, R., T. Shuto, T. Takayama, I. Koizumi, A. Fujiyoshi, M. Ibaraki and Martínez-R. Pardo. 1990. Fundamental data on Cenozoic biostratigraphy of Chile. Supplement. 3. Punta Perro section north of Navidad, central Chile. Reports of Andean Studies, Special Volume 3: 70–71.

Redescription of the genus and species *Heterovaginina limayana* (Lesson, 1830) (Gastropoda: Soleolifera: Veronicellidae)

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ABSTRACT

Based on the examination of 58 specimens deposited in various institutions, we redescribe the genus *Heterovaginina* Kraus, 1953, considering it monotypic and with its range restricted to Peru. The type species, *H. limayana* (Lesson, 1830) is also redescribed, and **a neotype designated** for the species. The anatomy of the hermaphroditic region near the female genital pore is emphasized as characteristic of the genus: the copulation bursa is elongated spheroid, tapering into a distal elongation that folds and joins the bursa duct toward its base, receiving the junctor duct at the tip of the bursa. The rectum penetrates the integument near the female genital pore. There is no penial gland and no accessory gland. The anatomy of the anterior male genital system characterizes the species: smooth penis, with short cylindrical verge that intumesces slightly in its medial region, forming expansions on the sides that mark the beginning of the glans; the penis is longer then the verge, and tapers in its distal portion. There is no spatha. All pertinent bibliography is discussed and the synonymization of *Vaginina odhneri* Hoffmann, 1927, is justified.

INTRODUCTION

The Veronicellidae are terrestrial slugs with worldwide distribution, still poorly known and of uncertain position within the Gastropoda (Hoffmann, 1925; Hyman, 1967; Thomé, 1988a, 1993; Tillier et al., 1996). Among the genera included in the family (Hoffmann, 1925; Forcart, 1953; Thomé, 1975), two share the lack of a penial gland, a structure formed by a papilla and a varied number of tubules, which lies alongside the penis and has systematic importance, although its function is yet not understood.

Of the two genera of the Veronicellidae lacking the penial gland, one occurs in Africa, *Vaginina* Simroth, 1897, and the other, *Heterovaginina*, is restricted to Peru. Simroth characterized *Vaginina* simply by the absence of the penial gland, as opposed to the genus *Vaginula* Berthold, 1827 (a synonym of *Vaginulus* Férussac, 1821), which exhibits that structure. In proposing the genus, Simroth (1897) based it on the examination of two specimens without specific names. Only later, that author (Simroth, 1913) examining the same two specimens, described them as *V. conradti* and *V. togoensis*, both originating from the same West African locality. But they differ by the presence of glandular protuberances on one side of the penis sheath in *V. conradti*, and by a smooth sheath in *V. togoensis*.

In his discussion of the nomenclature of the Veronicellidae, Baker (1925) designated *Vaginina conradti* as the type species of *Vaginina*. Hoffmann (1925) accepted *V. conradti* and synonymized *V. togoensis*, maintaining that the character used by Simroth (1913) would be insufficient to differentiate them, in that he had only two specimens, both collected in the same locality. Hoffmann (1925) included the genus in his then new subfamily Meisenheimerinae, with the following diagnosis: "dark notum, weakly pointed; genital pore almost at mid-length of the hyponotum; with the anterior lobe of the digestive gland behind the anterior loop of the intestine, with the pedal nerves together for a short stretch, parallel and then diverging; with a needle-shaped penis and a basal ringed thickening; without penial gland."

Hoffmann (1927) described *Vaginina odhneri* based on a single specimen of unknown origin, but stating that it was certainly from Africa, despite the fact that *Vaginina*, known only from Africa, was only recorded once. Without discussing the synonyms he had proposed in 1925, he differentiated *V. odhneri* from *V. togoensis* by the shape of the penis (also different from the genus-level morphology he had proposed) and respective sheath and aspects of the copulation bursa and connecting ducts. He adds that in his species the lobe of the digestive gland is in front of the anterior loop of the intestine (also different from the proposed genus level morphology).

Forcart (1953), in his monograph on African Veronicellidae, considered *Vaginina* as a subgenus of *Pseudoveronicella*, stating that it differs from the other subgenera included in the genus by the characteristics of the copulatory organs and the presence of canals and ducts between the rectum and the ureter, without discussing, at neither the genus nor the subgenus level, the absence or presence of the penial gland. Forcart (1953) agreed with the synonymy of Hoffmann (1925) and considered *Pseudoveronicella* (*Vaginina*) *conradti* as a valid name. Without discussion and without examining specimens, he also added *Pseudoveronicella* (*Vaginina*) *odhneri* (Hoffmann) to his list as from "probably Africa". He also proposed a new species, *Pseudoveronicella* (*Vaginina*) *duporti*, observing that this would differ from the others in the subgenus by the presence of the penial gland (which in fact sets the species apart).

Kraus (1953a) proposed the taxon *Heterovaginina* as a subgenus of *Vaginina*, based on the description of *Vaginina* (*Heterovaginina*) *peruviana*, from Lomas de Atocongo, near Lima, Peru, and included *V. odhneri* due to the similarities of the two species. He excluded *V. conradti* because the anterior intestinal loop is anterior to the digestive gland, the copulation bursa has a long duct, and the penis has a much different shape. Kraus (1953b), without any reference to Baker (1925) or to Hoffmann (1925), but mentioning verbal contact with Forcart (Basel, Switzerland) and based on the work of Degner (1934) on the anatomy of *V. togoensis*, raises *Heterovaginina* to the genus level. Kraus stated that, after examining histological sections of a paratype of *H. peruviana*, he found it had a cloaca and lacked the links between the rectum and the fourth ureter, thereby differing from the African genus that, according to Degner (1934), had separate openings for the rectum and the fourth ureter that were connected to each other by a urethral canal and 5 urethral ducts (which were used in the description by Forcart (1953)). Later on, Kraus (1954) synonymized *Heterovaginina peruviana* Kraus, 1953, with *Vaginulus limayanus* Lesson, 1830, considering that, according to personal information from W. Weyrauch, "only one species occurs" in the type locality.

Forcart (1957), after examining Peruvian specimens in the Field Museum of Natural History (now re-examined by us) found them to represent *Vaginina odhneri*, but concluded that this species should be included in the genus *Heterovaginina* because it occurs in southern Peru. He also agreed with Kraus (1953a), although he did not [illegible] directly.

Thomé ([illegible]) redescribed the holotype of *Vaginina* (*Heterovaginina*) *peruviana* Kraus, 1953, deposited in the Senckenberg Museum Frankfurt-am-Main, without discussing [illegible]. The copulation bursa is, according to Thomé ([illegible]), sac-like and sessile in *V.* (*H.*) *peruviana* which [illegible] know to be present only in juvenile specimens. Thomé (1975), in a revision of the American genera of Veronicellidae, recognized and redescribed (still only on the basis of the juvenile type specimen) *Heterovaginina*, keeping it monotypic (*H. peruviana*) and with occurrence restricted to Peru. He did not mention *V. odhneri*.

In addition, Thomé (1984) redescribed the holotype of *H. odhneri*, deposited in the Naturhistoriska Riksmuseet of Stockholm, Sweden. According to Thomé (1984), the copulation bursa is spheroid, seated over a thick cylindrical uniform duct and has a short, slender junctor duct that penetrates the copulation bursa duct at midlength. An inspection of its illustration (Figure 18, p. 44) and knowledge that the material was damaged, lead us to infer that the copulation bursa had actually been pushed down along its duct. Thus, the junctor duct is in part adhering to the bursa duct and does not penetrate it. The junctor duct must, certainly, penetrate the tip of the damaged copulation bursa. The penis is short and broad, with a short, level/convex verge that continues toward the spheroid glans. This latter is transversally widened, with a lateral conical protuberance projecting from the level face of the verge. Thomé et al. (1999) reported a preliminary illustrated redescription of the genus, which is now presented herein in an expanded format.

During the examination of the specimens and of the literature to define the species of the Veronicellidae occurring in Peru, several specimens, both juvenile and adult, were found in the examined collections. These were positively identified as *Heterovaginina limayana* (Lesson, 1830). Based on this material we propose the validity of the genus and the species, with their respective redescriptions and the designation of a neotype.

MATERIALS AND METHODS

Fifty-eight specimens from 26 lots were examined, from the collections of the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos (MUSM), Lima, Peru; Senckenberg Museum (SMF), Frankfurt-am-Main, Germany; Field Museum of Natural History (FMNH), Chicago, USA; British Museum of Natural History (BMNH), London, England; Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul (MCP-PUCRS), Porto Alegre, RS, Brazil; National Museum of Natural History (USNM), Washington, DC, USA (Thomé et al., 1997) and Naturhistoriska Riksmuseet (NRS), Stockholm, Sweden (Thomé, 1984).

For study of the internal anatomy, the specimens were dissected, starting with a posterior to anterior longitudinal ventral incision, following the methodology of Thomé and Lopes (1973) and subsequent improvements. The mandible (= jaw, of some authors) and radula of two specimens from lots MCP 6594 and MUSM 2513-b were extracted under the stereomicroscope and later analyzed and measured under the scanning electron microscope. The averages of length, width, and distance between the region of greatest width and the anterior tip of twenty rachidian teeth and twenty lateral teeth were calculated. The anatomic, generic and specific, characteristics are emphasized following Hoffmann (1925) and Thomé (1975, 1988a, 1988b, 1993).

SYSTEMATICS

Genus *Heterovaginina* Kraus, 1953
Heterovaginina Kraus, 1953a: 63–65.

Type Species: *Vaginina* (*Heterovaginina*) *peruviana* Kraus, 1953a: 63–65 (= *Heterovaginina limayana* (Lesson, 1830)).

Diagnosis: The rectum penetrates the integument near the female genital pore. The thin-tissued copulation bursa is spheroid, tapering in a distal lengthening that bends and joins the bursa duct toward its base, receiving the junctor duct at the bursa tip. The bursa duct, of more rigid tissue, is cylindrical and extremely short in the juvenile animal, but lengthens in the adult, becoming an elongated/spheroid bursa. No accessory gland and no penial gland are to be found.

Distribution: Restricted to Peru, South America.

Heterovaginina limayana (Lesson, 1830)

Vaginulus limayanus Lesson, 1830: 302–303, 471, pl. 14, figs. 1–1A.
Vaginula limaiana Deshayes in Férussac and Deshayes, 1819–1851: 96^{6}–96^{7}, pl. 8E, fig. 11 (exact copy of Lesson, 1830).
Vaginina odhneri Hoffmann, 1927: 26, figs. 11–14; Thomé, 1984: 34–36, figs. 14–19.
Pseudoveronicella (*Vaginina*) *odhneri* Forcart, 1953: 60.
Vaginina (*Heterovaginina*) *peruviana* Kraus, 1953a: 63–65; Thomé, 1969: 357, figs. 29–30, 48.
Vaginina (*Heterovaginina*) *odhneri*: Kraus, 1953a: 63–65.
Heterovaginina limayana: Kraus, 1954: 82–83.
Heterovaginina odhneri: Forcart, 1957: 96.

Diagnosis: Penis smooth, short cylindrical verge that intumesces a little beyond the middle of its length, forming expansions on the sides that mark the beginning of the glans. Glans longer than the verge, tapering in its distal portion; generally curved. There is no spatha.

Redescription: *External Anatomy*. A large portion of the examined material is externally very discolored. However, the color pattern on the notum showed the following general characteristics: specimens with light chestnut colored notum with irregularly distributed black dots and splotches, nevertheless clearly showing two longitudinal black lines that delimit a lozenge-shaped mid-region. Between these two lines a fine light streak occurs centrally in the notum, starting apart from the anterior perinotum at about ¼ of the way down the full length of the animal and continuing to the rear without reaching the posterior perinotum. (Averages of the external dimensions, in 20 specimens (measurements in mm): notum length = 29.20, width = 13.90, height = 7.14; width of the sole = 4.41; width of the right hyponotum = 4.14, distance from the female genital pore forward = 14.50, and behind = 12.90; distance from the female genital pore to the pedal furrow = 0.73.)

Internal Anatomy. Salivary gland well developed, formed by large and prominent acini, some quite loose, others compact. Anterior intestinal loop covered by the anterior lobe of the digestive gland.

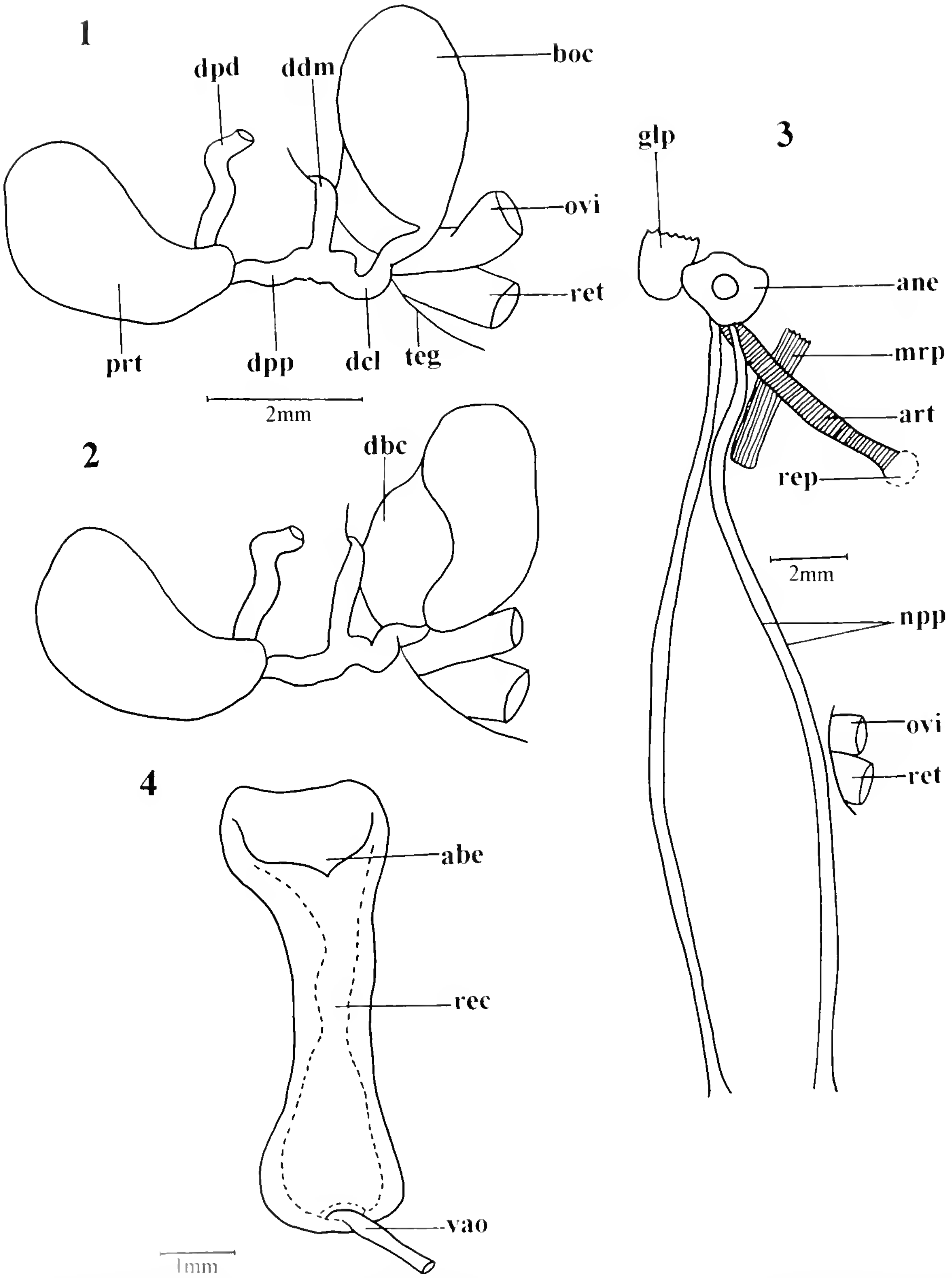
The two nerve pairs, pedal and pallial, originate very close to the respective ganglia of the periesophageal ring and stretch through the central cavity in two sets, right and left, which separate from each other about a fourth of the way from their starting place, continuing thus almost to the end of the central body cavity, where they come slightly closer and penetrate the integument (Figure 3). The anterior aortic artery meets the nerves near their beginning in anterior direction (Figure 3). The posterior pedal branch of the aortic artery was not found. (Average measurements of the nerves in 20 specimens in mm: total length = 29.9; together = 4.48; apart = 16.5; maximum separation = 2.72 mm; meeting of the aortic artery = 1.76 mm from the origin.)

Pedal gland (Figure 4) short, flattened, broad in its proximal portion, narrowing in the middle with the posterior extremity rounded and somewhat broadened, dorsal opening scalloped, longitudinally three areas are visible, a translucent outer one on each side, and a slightly rough central one that is higher, narrower, and yellowish. At the distal extremity of this central area is the penetration scar of the inferior branch of the aortic artery, right under the nerve ganglia. (Average dimension of the pedal gland in 20 specimens (in mm): length in the natural position = 1.20, distended (dorsal surface) = 4.41; greatest width = 1.90.)

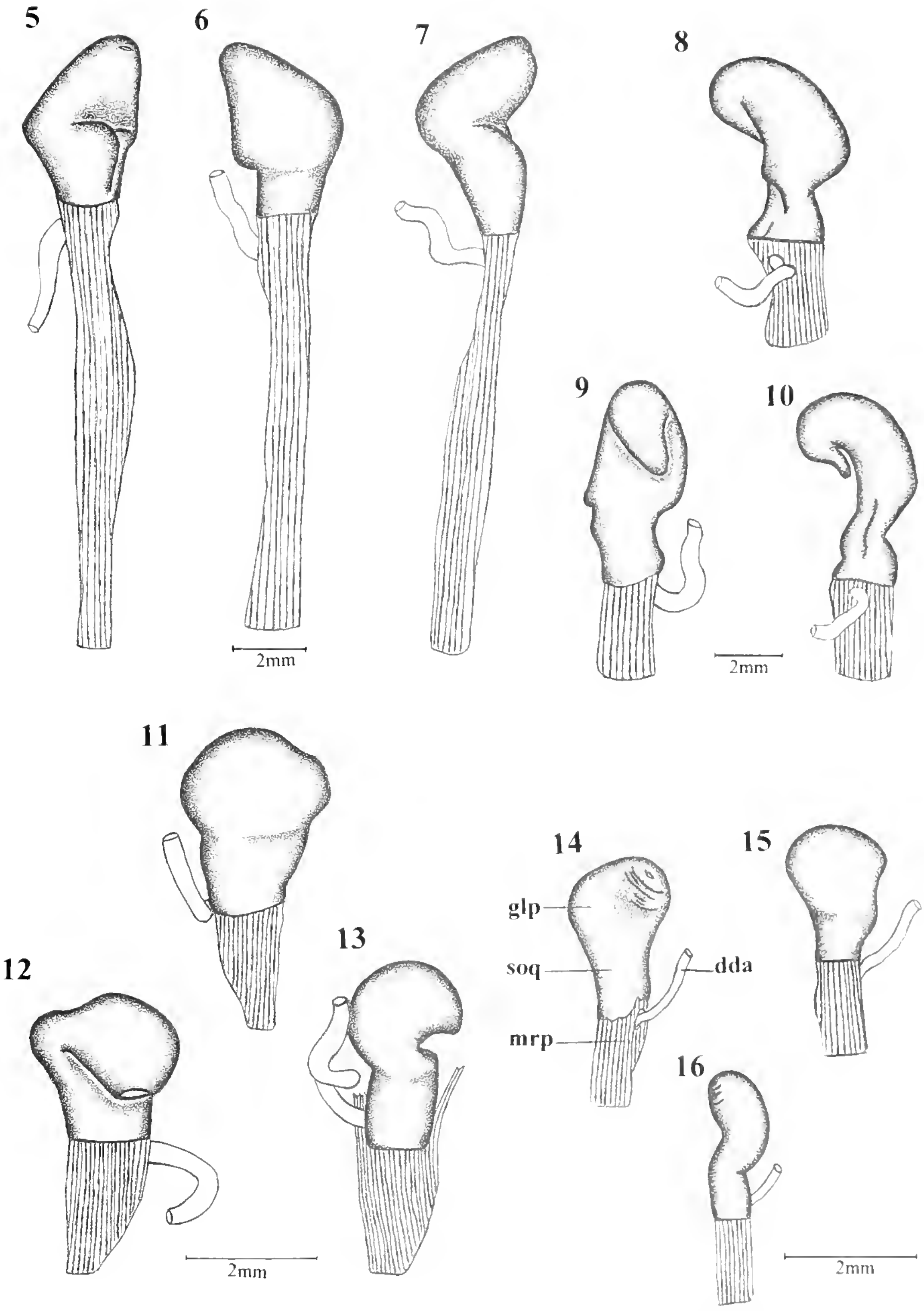
The thin-tissued copulation bursa (= spermatheca or spermatolytic gland of some authors) is spheroid, tapering in a distal lengthening that folds and joins the bursa duct toward its base, receiving the junctor duct (= canalis junctor of some authors) at the bursa tip. The bursa duct, of more rigid tissue, is cylindrical and extremely short in the juvenile animal, but lengthens in the adult, becoming an elongated spheroid bursa. The junctor duct is thick and sinuous, narrowing slightly in its final portion when, after entwining part of the base of the bursa duct, it penetrates into the narrowest part of the copulation bursa itself. The rectum penetrates the integument near the female genital pore (Figures 1, 2). No accessory gland (= accessory bursa of some authors) was found.

Penis smooth, with a short, cylindrical verge, swelling a bit beyond the middle of its full length, forming on the sides two expansions that mark the beginning of the glans. Glans longer than the verge, becoming slender in its distal portion, generally curved. Retractor muscle of the penis very variable in length (Figures 5–16). There is no spatha. (Average dimensions of the penis in 20 specimens (in mm): total length = 2.26; greatest diameter of the glans = 1.45; verge length = 1.02; verge diameter = 1.07.)

The sheath surrounding the penis (Figure 17) has two distinct regions, clearly differentiated by the well defined presence of two different types of tissue. The proximal portion of the sheath, which surrounds the penis



Figures 1–4. [illegible] *limayana*. **1, 2.** Part of the posterior genital organs and of the rectum (MCP 6594). **3.** Arrangement of the pedal ne[illegible] (MCP [illegible]). **4.** Pedal gland (MCP 6594). abe: opening; ane: nerve ring; art: anterior aortic artery; boc: copulation bursa; dbc: copulat[illegible] duct; dcl: junction duct; ddm: middle deferens; dpd: distal posterior deferens; dpp: proximal posterior deferens; glp: part [illegible] pedal gland; mrp: retractor muscle of the penis; npp: pair of pedal and palial nerves; ovi: part of the oviduct; prt: prostat[illegible] region; rep: pericardial region; ret: part of the rectum; teg: integument; vao: part of the inferior branch of the aortic arter[illegible]



Figures 5–16. *Heterovaginina limayana* **5–13.** Three different views of the penis, in 3 adult specimens (respectively MUSM 2513/b (Figures 5–7), MUSM 1458 (Figures 8–10), FMNH 59488/a (Figures 11–13)). **14–16.** Three different views of the penis in one juvenile specimen (FMNH 59486/b). dda: anterior portion of the deferens duct; glp: glans; mrp: retractor muscle of the penis; soq: verge.

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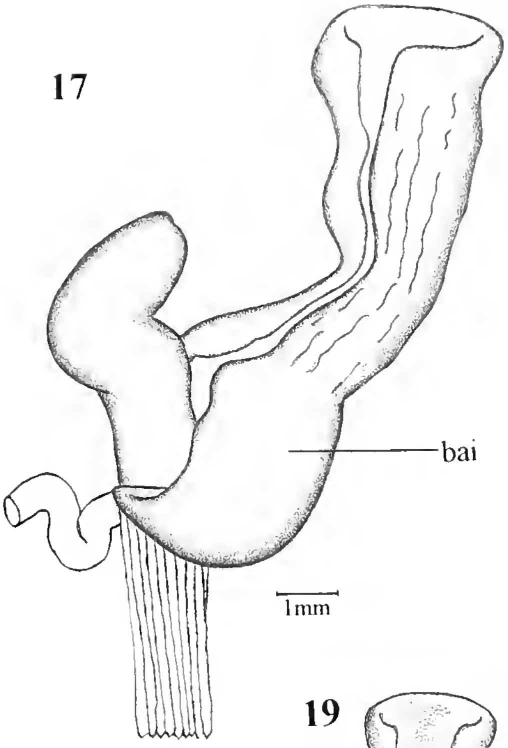

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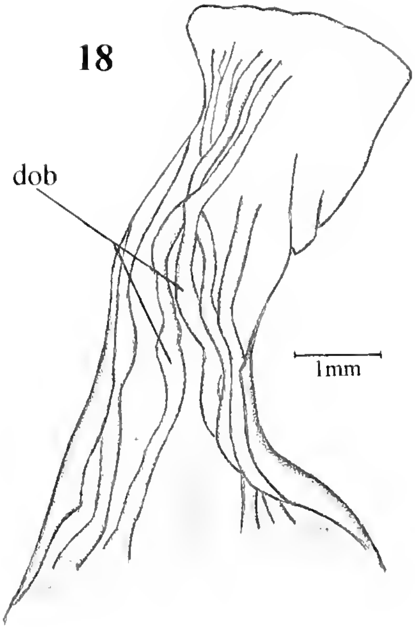

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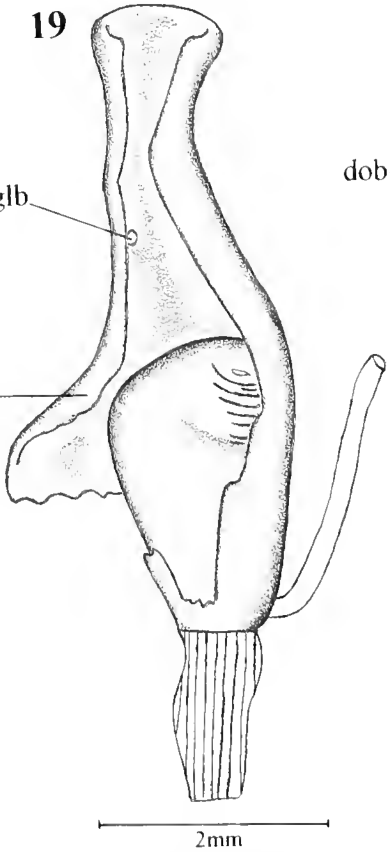

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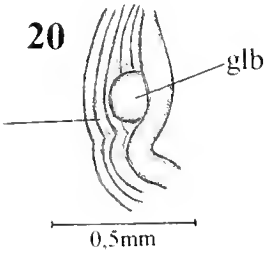

Figures [illegible] *[illegible]una limayana.* **17.** Sheath that envelops the penis, opened longitudinally (MUSM 2513/b). **18.** View of the di[illegible] penis sheath, showing the sharp longitudinal folds of the internal tissue (MUSM 2513/b). **19.** Sheath, opened long[illegible] the presence of a salient globular formation of the internal tissue, similar to that described by Hoffmann (19[illegible] as a gland (FMNH 59486/b). **20.** Region of the salient globular formation, greatly enlarged, also showing details of t[illegible]olds (FMNH 59486/b). bai, sheath; dob, folds; glb, salient globular formation.

is extremely thin, often allowing visualization of the penis by transparency. The distal portion, starting from a significant constriction right after the tip of the penis which is swollen, has numerous longitudinal folds internally and a porous and yellowish (glandular?) aspect. These folds may be more or less tight, neatly arranged, and rectilinear (especially in juvenile specimens) or in disarray (Figure 18). Even in juvenile specimens where the male region is little developed, the minuscule folds (Figure 20) can be seen inside the sheath. The penial gland is absent.

The mandible is formed by an average of 23 laths (= ribs, of some authors), very visible and somewhat separated one from the other. The most central laths are a bit taller than the others. No transverse grooves were noted, perhaps due to the obvious wear. The average length and greatest width of the mandible, in the same lots utilized for extraction of the radulae, were 2.1 mm and 0.5 mm respectively (Figure 21).

The radula has a great number of lateral teeth, distributed rectilinearly in columns parallel to the single, central line of rachidian teeth, which are always smaller. An average of 103 columns and 120 transverse rows were counted, resulting in a calculation of 12360 teeth per radula. The average dimensions of the radula were 5.85 mm length by 3.41 mm at the greatest width. The average dimensions of 20 lateral teeth were: length 56.2 µm, width 24.5 µm, distances from the greatest width to the tip 29.43 µm. The average dimensions of 20 rachidian teeth were: length 32.8 µm, width 12.8 µm, distance from the greatest width to the tip 17.0 µm (Figures 22–23).

Neotype (herein designated): MUSM 4001, from type locality, 24 Jan. 2002, leg. Rina Ramírez and Ulises Zamora.

Type Locality: Peru, Dpto. Lima, Cerro San Cristobal (12°01'45.1" N, 77°00'52.6" W), 215 m above sea level.

Other Material Examined: MUSM 4001 (neotype), Peru, Dpto. Lima, Cerro San Cristobal (12°01'45.1" N, 77°00'52.6" W), 215 m above sea level, 24 Jan. 2002, leg. Rina Ramírez and Ulises Zamora; MUSM 4000, 2 specimens, same data as the neotype; MUSM 1158, 1 specimen, Peru, Dpto. Lima, Bosque Zárate (11°54' N, 76°29' W), 3000 m above sea level, 24 Mar. 1978, leg. Valencia and Franke; MUSM 1160a, 1 specimen, Peru, Dpto. Lima, Bosque Zárate (11°51' N, 76°29' W) (Chourritos II), 2880 m above sea level, 01 Mar.1980, leg. Valencia and Franke; MUSM 1660, 4 specimens, Peru, Dpto. Lima, Lomas de Atocongo (Stemloma) (12°13' N, 76°54' W), 28 Sep. 1951, leg. Koepcke (Kp340m); MUSM 1807a, 3 specimens, Peru, Dpto. Lima, Surco (11°52' N, 76°28' W), leg. Koepcke (Kp1010a); MUSM 2388, 1 specimen, Peru, Dpto. Lima, Surco (11°52' N, 76°28' W), 2100 m above sea level, 17 Aug. 1965; MUSM 2389, 1 specimen, Peru, Dpto. Lima, Distrito de San Borja (Rio Surco) (12°06' N, 77°01' W), 08 Jun. 1986, leg. A. Rossi; MUSM 2513, 3 specimens, Peru, Lima, Huachipa (12°00' N, 76°56' W); MUSM 3251, 2 specimens, Peru, Dpto. Lima, Canta, Culluhuay (11°19' N, 76°33' W), 3550 m above sea level, 24 Mar. 1989, leg. H. Sisniegas; SMF 108548 (holotype of *Vaginina (Heterovaginina) peruviana*), Peru, Dpto. Lima, Lomas do Atocongo (12°13' N, 76°54' W), 28 Oct. 1951, leg. Koepcke; SMF 323293/1, 1 specimen (ex-MUSM 4000), same data as holotype; SMF 140062/7, 7 specimens, Peru, Dpto. Lima, Cerro San Cristobal, leg. W. Weyrauch; FMNH 59486, 8 specimens, Peru, Dpto. Lima, April 1948, leg. W. Weyrauch; FMNH 59487, 6 specimens, Peru, Dpto. Lima, Lomas do Atocongo (12°13' N, 76°54' W), leg. W. Weyrauch; FMNH 59488, 3 specimens, Peru, Oconeque, Puno, 4 Oct. 1941, leg. C. C. Sanborn; FMNH 300744, 1 specimen, (ex-MUSM 4000), same data of the neotype; BMNH 20020126, 1 specimens, (ex-MUSM 4000), same data of the neotype; MCP 6501, 1 specimen, Peru, Dpto. Lima, Bosque Zárate, (11°54' N, 76°29' W), 3000 m above sea level, 24 Mar. 1978, leg. Valencia and Franke; MCP 6502, 3 specimens, Peru, Dpto. Lima, Surco (11°52' N, 76°28' W), 2100 m above sea level, 17 Aug. 1965; MCP 6504, 1 specimen, Peru, Dpto. Lima, Canta, Culluhuay (11°19' N, 76°33' W), 3550 m above sea level, 24 Mar. 1989, leg. H. Sisniegas; MCP 6593, 1 specimen, Peru, Lima, Huachipa (12°00' N, 76°56' W); MCP 6594, 1 specimen, Peru, Dpto. Lima, Apr. 1948, leg. W. Weyrauch; MCP 7988, 2 specimens (ex-MUSM 4000), same data of the neotype; USNM 571941, 1 specimen, Peru; NRS 949/1052 (holotype of *Vaginina odhneri*).

DISCUSSION

Vaginulus limayanus was briefly described by Lesson (1830), who used a few morphological features in his description. Lesson also offered a color plate (probably prepared in Peru), including dorsal and ventral views of the animal. This specimen was not deposited at the Paris Museum, and could not be found, despite our efforts in any other major European Museum. It is very likely that Bérard lost the specimen after the artwork was completed. We conclude that there was never a holotype. The description and figures were used by Deshayes (1830–1832) in Férussac and Deshayes, with no further comments.

Although the holotype *Vaginina (Heterovaginina) peruviana* Kraus, 1953, is an immature specimen, the synonymyzation of this latter species by Kraus (1954) based on information from W. Weyrauch is confirmed after its examination.

Recent collections and observations of live specimens made by our collaborator Rina Ramírez confirm that there is only one species at the type locality and its vicinities.

Therefore, **we herein propose the designation of a neotype for the species** (see above), deposited at the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos (MUSM), Lima, Peru (MUSM 4001) and

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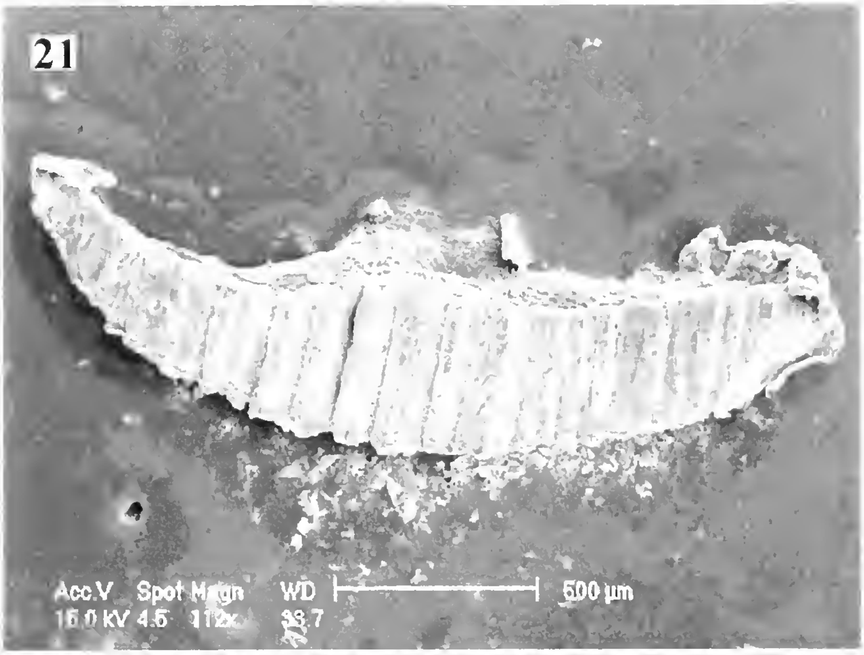

22 **23**

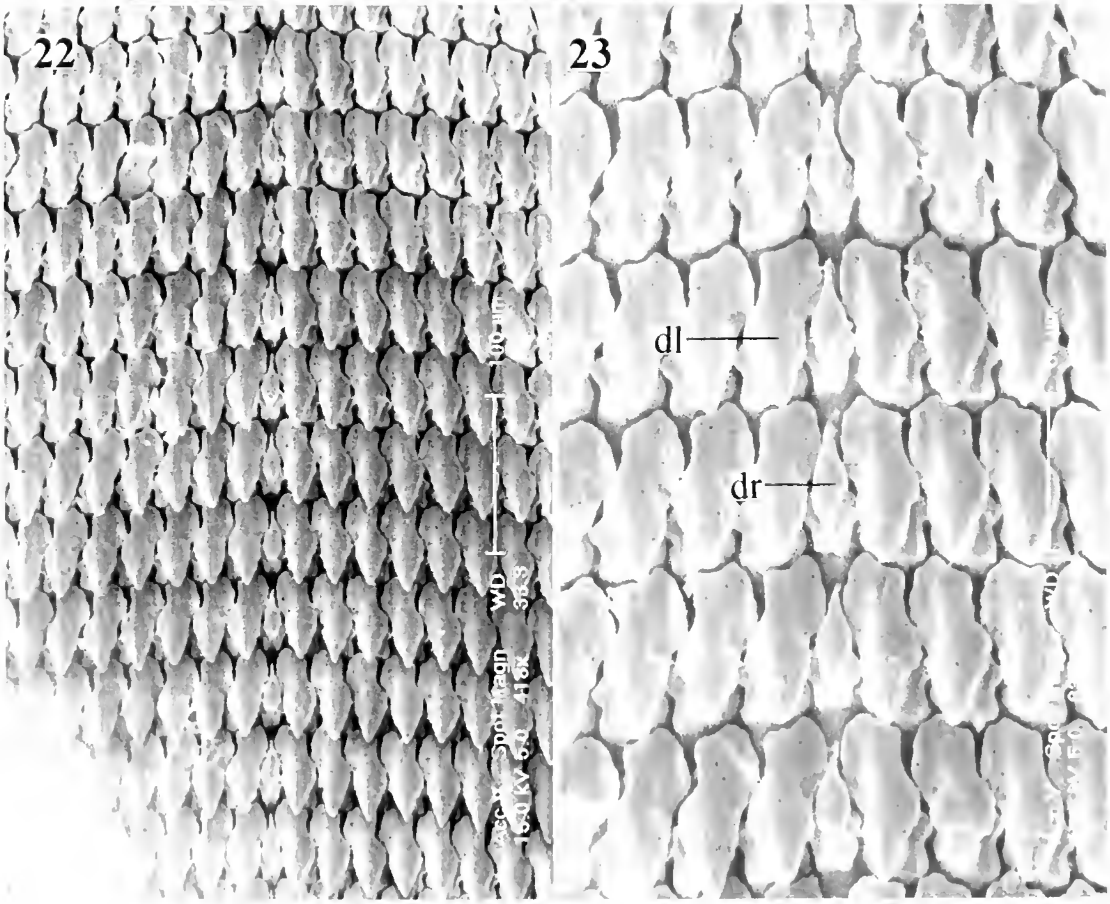

Figure 21. [illegible] *mana*. General view of a mandible. MCP 2513 b.
Figures 22–23. [illegible] *limayana*. Middle region of the radula. **22.** slightly and **23.** greatly enlarged. MCP 2513 b. dl: lateral tooth; [illegible] central.

collected at the original type locality of the species (Cerro San Cristobal.

Hoffmann (1927) proposed the species *Vaginula odhneri*, especially due to the presence in the penis sheath of a glandular protuberance. Thomé (1984) in his redescription of the holotype of *V. odhneri*, made no reference to that distinctive protuberance because the holotype was extensively damaged.

In three juvenile specimens (SMF 108518, MCP 6593, and FMHN 59486/d), among them the holotype of *H. peruviana* (= H. *limayana*), an almost circular protuberance on the inner wall of the penis sheath was found, very similar to that described by Hoffmann (1927) for *H. odhneri* as a "gland". The "gland" described for *H. odhneri*, used to distinguish it from *H. limayana* ("sensu" Kraus), appears to be only a more salient, globular formation of the internal tissue of the sheath, because its texture is the same as this tissue (not a "gland") (Figures 19–20).

Despite the additions and changes made herein, the dichotomous key for determining the American genera, proposed by Thomé (1975), continues to be valid for *Heterovaginina*.

ACKNOWLEDGMENTS

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LITERATURE CITED

Baker, H. B. 1925. Nomenclature of Veronicellidae (Vaginulidae). The Nautilus 39: 13–18.

Berthold, A. A. 1827. Latreille's Natuerliche Familien des Thierreichs, aus dem Franzoesischen mit Anmerkungen und Zusaessen. Weimar, Verg. Gr. H. S. priv. Landes-Industrie-Gomptoirs.

Degner, E. 1934. Westafrikanische Nacktschnecken. I. Streptaxiden, Helicarioniden, Vaginuliden. Zoologische Jahrbücher, Systematik, 65(3/4): 209–308.

Deshayes, G. P. 1830–1832. In: Férussac, D. and G. P. Deshayes (eds.) (1819/1851). Histoire Naturelle Générale et Particulière des Mollusques Terrestres et Fluviatiles. Chez J. B. Baillière, Paris [1830, text: p. 96'–96'; 1832, pl. 8I, fig. 11].

Forcart, L. 1953. The Veronicellidae of Africa (Mollusca, Pulmonata). Annales du Musée du Congo Belge, Sciences Zoologiques 23: 1–110.

Forcart, L. 1957. Was ist *Vaginula odhneri* Hoffmann 1927 (Veronicellidae)? Archiv für Molluskenkunde 86: 96–97.

Hyman, L. H. 1967. The Invertebrates: Mollusca I. McGraw-Hill, New York, 792 pp.

Hoffmann, H. 1925. Die Vaginuliden. Ein Beitrag zur Kenntnis ihrer Biologie, Anatomie, Systematik, geographischen Verbreitung und Phylogenie. In: Fauna et Anatomia Ceylanica III, Nr. 1. Jenaische Zeitschrift für Naturwissenschaft 61(1-2): 1–374.

Hoffmann, H. 1927. Ueber Vaginuliden aus dem Reichsmuseum Stockholm. Arkiv för Zoologi 19A(25): 1–39.

Kraus, O. 1953a. Vaginulidae aus Peru. Archiv für Molluskenkunde 82: 63–65.

Kraus, O. 1953b. Zur Anatomie und systematischen Stellung von *Heterovaginina*. Archiv für Molluskenkunde 82: 153–154.

Kraus, O. 1954. Weitere Veronicellidae aus Peru. Archiv für Molluskenkunde 83: 81–83.

Lesson, R. P. Zoologie. 1830. In: Duperrey, L. I. Voyage autour du monde, exécuté par ordre du Roi, sur la Corvette de S. Magesté, La Coquille, pendant les années 1822, 1823, 1824 et 1825. Arthus Bertrand, Paris, Libr. Ed. v. 2, 1e partie, 471p. + 16pl.

Simroth, H. 1897. Ueber verschiedene Nacktschnecken. Sitzungsberichte der Naturforschenden Gesellschaft zu Leipzig 22–23: 140–154.

Simroth, H. 1913. Ueber die von Herrn Prof. Voeltzkow auf Madagaskar und in Ostafrika erbeuteten Vaginuliden nebst verwandtem Material von ganz Afrika. In: Voeltzkow, A. Reise in Ostafrika in den Jahren 1903–1905 mit – Wissenschaftliche Ergebnisse. Stuttgart, E. Schweizerbart'sche Verlagsbuchhandlung, Naegele & Dr. Sproesser, v. 3, Syst. Abt., Heft 3, p. 127–216, pl. 13–17.

Thomé, J. W. 1969. Erneute Beschreibung neotropischer Veronicellidae-Typen (Mollusca, Gastropoda). II. Arten aus der Sammlung des Senckenberg-Museums in Frankfurt a. M. Archiv für Molluskenkunde 99: 331–363.

Thomé, J. W. 1975. Os gêneros da Família Veronicellidae nas Américas (Mollusca, Gastropoda). Iheringia, série Zoologia (48): 3–56.

Thomé, J. W. 1984. Veronicellidae (Mollusca, Gastropoda) pantropicais: III. Redescrição de 5 espécies, com base no exame dos tipos depositados no "Naturhistoriska Riksmuseet" de Estocolmo, Suécia. Iheringia, série Zoologia (64): 29–46.

Thomé, J. W. 1988a. Recaracterização de *Veronicella sloanei* (Cuvier, 1817) (Mollusca, Gastropoda, Veronicellidae). Iheringia, série Zoologia (67): 15–35.

Thomé, J. W. 1988b. Redescrição dos tipos de Veronicellidae (Mollusca, Gastropoda) Neotropicais: XI. Espécies na Academy of Natural Sciences, Philadelphia. Iheringia, série Zoologia (69): 25–39.

Thomé, J. W. 1993. Estado atual da sistemática dos Veronicellidae (Mollusca; Gastropoda) americanos, com comentários sobre sua importância econômica, ambiental e na saúde. Biociências 1: 61–75.

Thomé, J. W., S. R. Gomes and R. S. Silva. 1999. Recaracterização do gênero *Heterovaginina* Kraus, 1953 (Mollusca, Gastropoda, Veronicellidae). In: Congreso Latinoamericano de Malacología, 06–10 Septiembre 1999, Coquimbo

Chile) Resúmenes. Universidad Catolica Del Norte, Coquimbo, pp. 106–107.

Thomé, J. W. and V. L. R. Lopes. 1973. Aulas práticas de Zoologia I. Dissecação de um molusco gastropode desprovido de concha. Iheringia (série Divulgação) 3: 34–45.

Thomé, J. W., P. H. dos Santos and L. Pedott. 1997. Annotated list of Veronicellidae from the collections of the Academy of Natural Sciences of Philadelphia and the National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A. (Mollusca: Gastropoda: Soleolifera). Proceedings of the Biological Society of Washington 110: 520–536.

Tillier, S., M. Masselot and A. Tillier. 1996. Phylogenetic relationships of the Pulmonate Gastropods from rRNA sequences, and tempo and age of the Stylommatophoran radiation. In: Taylor, J. D. (ed.) Origin and Evolutionary radiation of the Mollusca. Oxford University Press, New York, pp. 267–284.

Anatomy of the dromedary jumping-slug, *Hemphillia dromedarius* Branson, 1972 (Gastropoda: Stylommatophora: Arionidae), with new distributional records

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ABSTRACT

The genus *Hemphillia*, represented by at least 7 species, is a poorly known group of slugs endemic to western North America. We investigated the distribution and habitats of *H. dromedarius* Branson, 1972, and present a redescription of the anatomy of its distal genitalia, used for species identification. We collected specimens from 6 localities on Vancouver Island, British Columbia, Canada, and from 9 localities in Washington State, USA. The Vancouver Island localities represent a northward range extension for the species and first confirmed records from Canada. The species occurred from near sea level to an elevation of 1370 m, with most localities above 700 m. In all dissected specimens (at least 1 per locality) the penis was proximally broad and distally tapered; a well-developed verge was present within the penis sac. Contrary to the original species description, the penis had an accessory sac that inserted distally near the gonopore. Although the anatomy of the genitalia did not match the original description, the dissection of the type material confirmed that our specimens represented *H. dromedarius*.

INTRODUCTION

The genus *Hemphillia* Bland and Binney, 1872 consists of a group of arionid slugs endemic to western North America. Slugs of this genus are characterized by a visceral cavity elevated into a pronounced, dorsal hump, a shell-plate that is partially exposed through a slit in the mantle (Pilsbry, 1948), and a remarkable anti-predatory behavior: they typically exhibit "violent writhing and leaping" in response to molestation (Pilsbry, 1948: 738). Seven species are currently recognized (*H. glandulosa* Bland and Binney, 1872; *H. burringtoni* Pilsbry, 1948; *H. pantherina* Branson, 1975; *H. camelus* Pilsbry and Vanatta, 1897; *H. dromedarius* Branson, 1972; *H. danielsi* Vanatta, 1914; and *H. malonei* Pilsbry, 1917; Turgeon et. al., 1998) but additional, undescribed species may exist (Kelley et al., 1999). The genus has received little attention from either systematists or ecologists, and the taxonomic relationships, distribution, and ecology of all species are poorly known.

Branson (1972) described *H. dromedarius* based on specimens from the Olympic Mountains, Washington. His description was based primarily on external characteristics with little reference to the anatomy of the distal reproductive system, which is often extremely useful or even essential for the identification of slugs (Kerney and Cameron, 1979; Tompa, 1984; Gomez, 2001). Our interest in this species arose after the discovery in 1999 of a large (60 mm in length) jumping-slug from Vancouver Island, British Columbia, Canada; only *H. glandulosa*, a much smaller species, was previously known from the west coast of British Columbia (Pilsbry, 1948; Cameron, 1986) but an early report of a large, unidentified *Hemphillia* (originally misidentified as *H. malonei*) existed from Vancouver Island (Hanham, 1926). Our attempts to verify the identity of the new specimen were frustrated by a lack of published information on the genitalia of *H. dromedarius*, prompting us to examine the type material and to collect additional specimens from Wash ington State, United States, for comparisons. Here we present a description of the distal reproductive anatomy of *H. dromedarius* based on these findings. We also present new distributional records for the species, including a northward range extension and the first confirmed documentation of the species from Canada.

MATERIALS AND METHODS

We collected slugs from forested areas on Vancouver Island, British Columbia, Canada, and in Washington State, United States, between 1999 and 2002 (see Appendix for collection localities and dates). On Vancouver Island, the first specimen of *H. dromedarius* was found incidentally during surveys for terrestrial gastropods in the autumn of 1999, but surveys in subsequent years focused specifically on potential habitats for this species (a total of 104 forested sites were surveyed on Vancouver Island and 38 sites on the mainland of British Columbia). Specimens from Washington were collected either for comparisons with material from Vancouver Island or during opportunistic surveys in various localities. We located slugs by turning over woody debris and by visually searching other potential microhabitats on the forest floor. Specimens collected were killed by drowning and preserved in either 70% ethanol or isopropyl alcohol, and vouchers were deposited in the collection at the Royal British Columbia Museum (RBCM), Victoria, British Columbia, Canada.

We dissected at least one specimen from each locality. The dissection of new material was performed by LC (most specimens) and KO under 7–30 × magnification using a dissecting microscope. Drawings of the reproductive system of selected specimens were made using camera lucida attached to a dissecting microscope. The dissection and examination of the holotype (USNM 577690; National Museum of Natural History, Washington, DC) and two paratypes (FMNH 173022, Field Museum of Natural History, Chicago; DMNH 43029, Delaware Museum of Natural History, Wilmington) was performed by HR.

RESULTS

On Vancouver Island we located *H. dromedarius* at six lo[illegible] from near sea level to an elevation of 1060 [illegible] Appendix). These localities represent a northward ra[illegible] for the species (Figure 1). Habitats consisted [illegible] forest, dominated by western hemlock [illegible] *phylla*), western redcedar (*Thuja plicata*), a[illegible] (*Abies amabilis*); the forest floor was typicall[illegible] thin compact needle litter. Five of the six [illegible] in remnant patches of old growth forest (wi[illegible] 250 years old); one locality (record 3 in Appendix) was in second growth forest with some old trees. All sites contained abundant coarse woody debris, including large diameter logs in advanced stages of decay. In Washington, habitats of *H. dromedarius* consisted of both old-growth and older second-growth coniferous forests dominated by Douglas-fir (*Pseudotsuga menziesii*) and western hemlock; mountain hemlock (*Tsuga mertensiana*) and subalpine fir (*Abies lasiocarpa*) were present at the highest elevation sites. Within these habitats, we found *H. dromedarius* under and within decaying logs and fallen bark, under rocks, and, once, active on the surface of the litter. Most sites were mesic, but at three high-elevation sites on the east slope of the Cascade Mountains (records 10, 11, and 13 in Appendix I) the slugs occurred on drier talus substrates.

Morphology and Internal Anatomy

Externally, all specimens were similar and conformed with the description by Branson (1972) (Figure 2). The predominant color of the mantle and foot was various shades of gray with cream-colored mottling on the sides; the sole of the foot was pale-yellow, orange-yellow, or cream. One individual (from locality 1 in Appendix) was buff brown with a bright yellow sole. The tail-portion of the foot was laterally compressed, keeled, and tipped with a horn-like protuberance (caudal horn), as described by Branson (Figure 2, insert). The nine Vancouver Island specimens ranged from 40 to 60 mm in length; three specimens from Washington (record 9 in Appendix) were 32–37 mm (all measurements from fresh, relaxed specimens after drowning).

Internally, the ovotestis was gray-brown and similar in color to the digestive gland. Close to the entrance of the ducts of the digestive gland there was an intestinal diverticulum of unknown function. The penis was proximally broad and tapering distally, and a well-developed verge was present (Figure 3). The verge filled most of the broad end of the penis sac; there were no other intra-penial structures. The penial retractor muscle inserted at the long and slender epiphallus. The penis had an accessory sac, which consisted of a narrow tube that broadened proximally and irregularly (Figure 3). The tubular base of the accessory sac inserted towards the distal end of the penis near the gonopore. The bursa copulatrix (spermatheca) consisted of a stout tube that broadened proximally into a globular sac, more pronounced in some individuals than in others. The penis, free oviduct, and bursa copulatrix joined close to the gonopore; there was no distinct atrium.

The holotype is a fully adult specimen with a large albumen gland, and its genital anatomy is generally the same as in our specimens. The distal part of the penis is rather narrow, and the proximal part is wide. There is a penial appendix that inserts distally near the gonopore. The retractor inserts at the epiphallus. Internal penis structures were not investigated to minimize damage to the type specimen. Both paratypes are juvenile, and their genitalia are in somewhat unnatural positions, which further hinders the investigation (parts of the distal genitalia of specimen DMNH 43029 are within the right tentacle, and those of specimen FMNH 173022 are partly everted through the genital pore—both probably

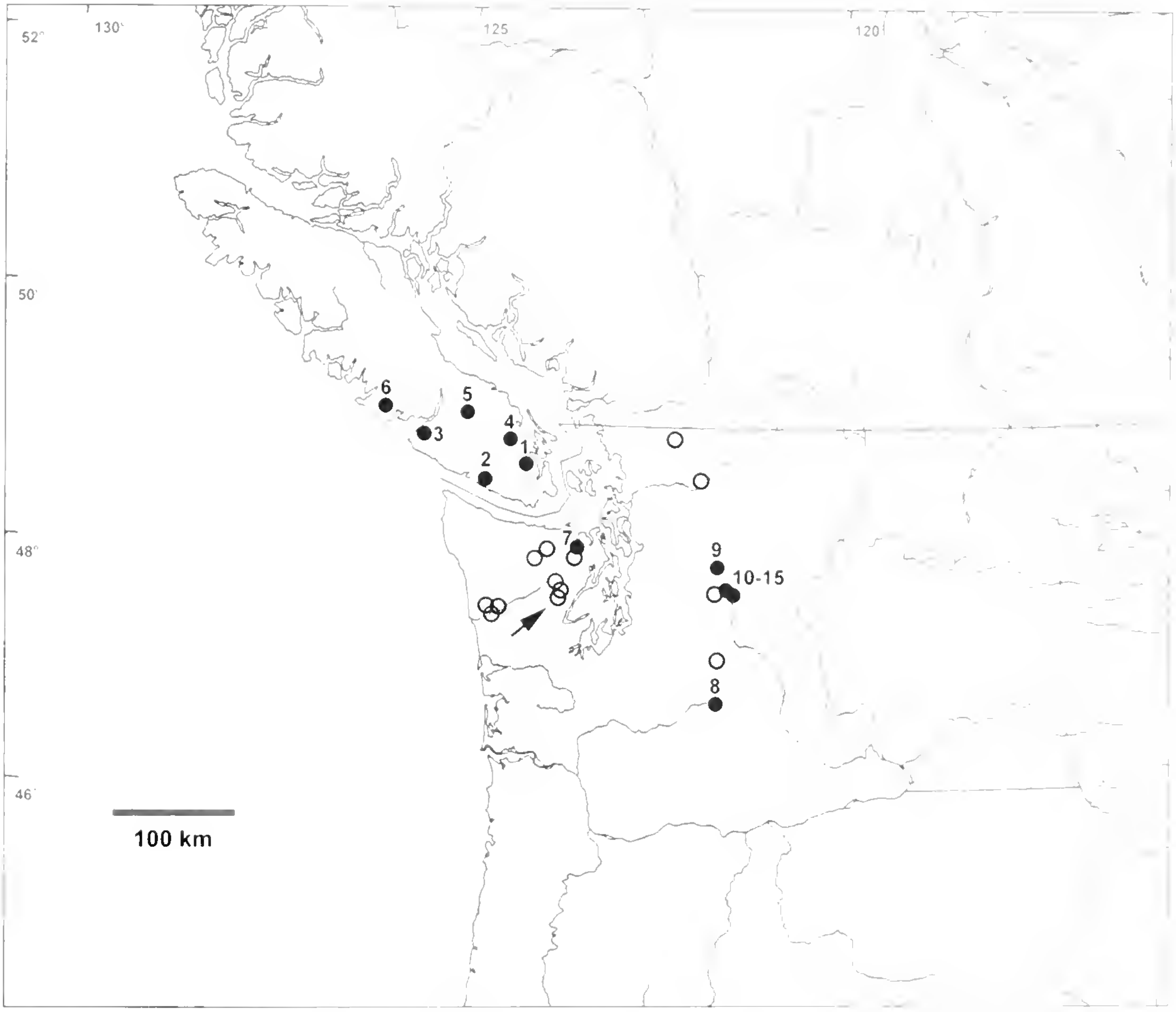

Figure 1. Distribution map for locality records of *Hemphillia dromedarius*. Solid circles: this study (numbers correspond to those in Appendix); open circles: previous localities (Branson 1972, 1977, 1980). Arrow points to the type locality (Branson 1972).

artifacts of killing). Nevertheless, a penial appendix is present at least in specimen DMNC 43029 and the structure of the everted genital complex in specimen FMNH 173022 suggests its presence. All three type specimens have the intestinal diverticulum mentioned above.

DISCUSSION

The geographic distribution of *H. dromedarius*, like that of many other terrestrial gastropods in western North America, is poorly known. Previous published locality records are from the Cascade Range and Olympic Peninsula in western Washington, including the Olympic and Mt. Rainier National Parks and the Mt. Baker and Snoqualmie National Forests (Branson, 1972, 1977, 1980) (Figure 1). In addition, some of the records from western Washington reported by Pilsbry (1948) for *H. maloneі*, prior to the description of *H. dromedarius*, may belong to the latter species. Our records from Vancouver Island represent a northward range extension and first confirmed records from Canada. On the mainland both the northern and southern extent of the species' distribution remain poorly known. The northernmost mainland record is from the Cascade Mountains, Washington (Silver Fir Camp, Mount Baker National Forest; Branson, 1980) close to the Canadian border (Figure 1). The southernmost confirmed locality is from the Gifford Pinchot National Forest (record 8 in Appendix). *Hemphillia* that are similar in size and external appearance to *H. dromedarius* have been found farther south in the Cascade and Coast ranges of northwestern Oregon (Tom Burke, pers. comm. by WPL; Carol Bickford, pers. comm. by WPL), but because these were not dissected, species identification remains uncertain.

We found *H. dromedarius* at six localities on Vancouver Island. A previous report (Hanham 1926: 143) exists of two specimens of a large, black jumping slug from "... the border of a good-sized lake" (most likely Holyoak Lake) on Mt. Brenton, Vancouver Island, at an elevation

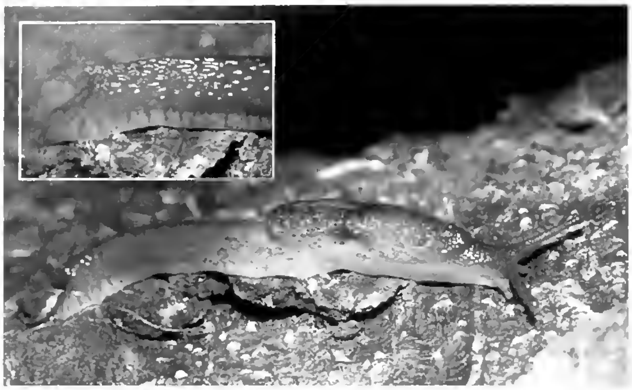

Figure 2. Specimen of *Hemphillia dromedarius* from Loss Creek, Vancouver Island, British Columbia, Canada (locality 2 in Appendix; RBCM 001-00280-001); caudal horn of the same animal (insert). The length of the live animal was 55 mm.

between 3500 and 4000 ft". The slugs were identified as *H. malonei* by Walter J. Eyerdam (of Seattle, Washington), apparently on the basis of Hanham's later description of their color; no specimens were available, as their soft anatomy had disintegrated before the slugs could be preserved (Hanham, 1926). Later authors (Pilsbry, 1948; Kozloff and Vance, 1958) questioned the identification of this record, which has remained enigmatic. We confirmed the presence of *H. dromedarius* near Holyoak Lake (record 4 in Appendix); most likely, the slugs reported by Hanham from the same locality 75 years previously were also of this species.

Our locality records from Vancouver Island were from older forests at elevations from near sea level to 1060 m. All three localities in the drier southeastern and south-central parts of the island were above 700 m in elevation, and the species seemed to be absent from lower slopes and valley bottoms. In contrast, the three localities on the wetter, west coast of the island were near sea-level. In Washington, previous records for the species existed from elevations of 238 m to 1436 m

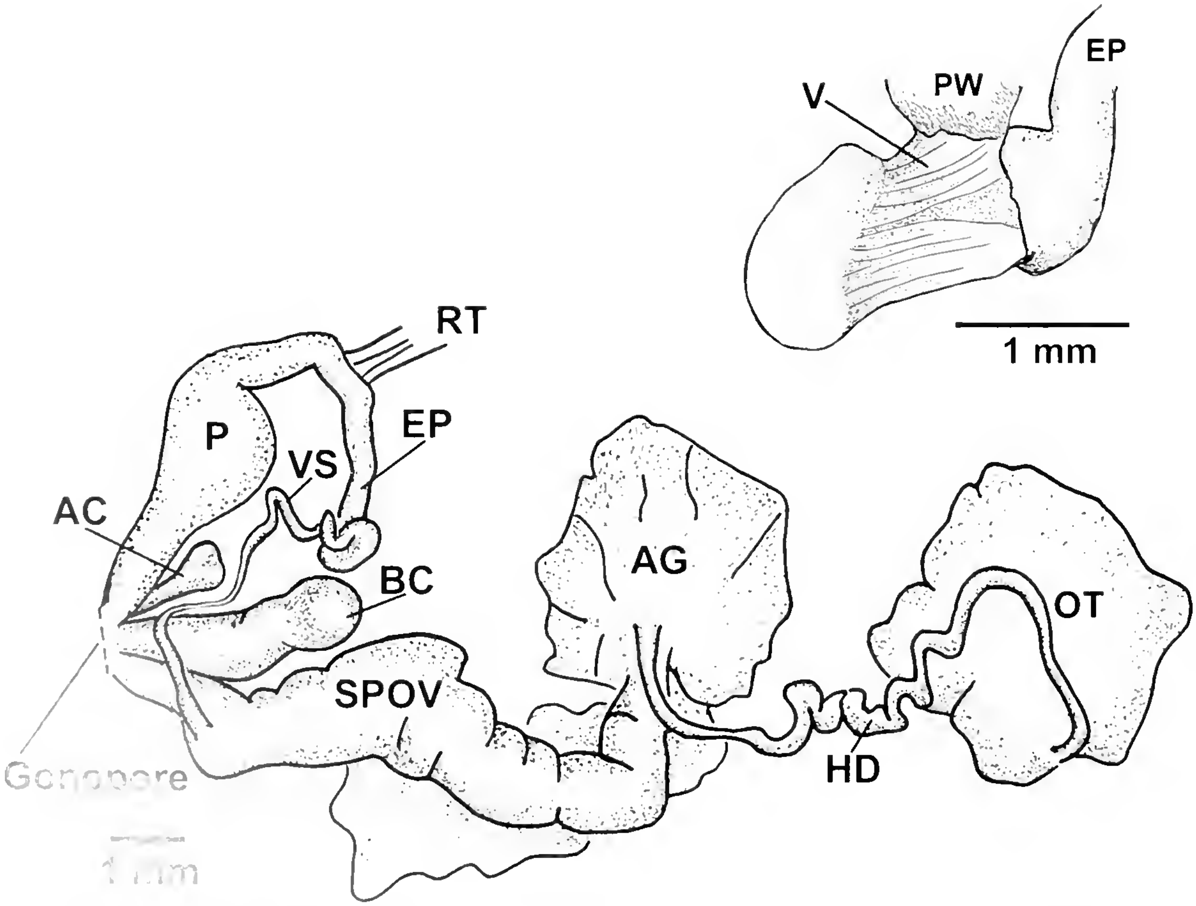

Figure 3. Reproductive system of *Hemphillia dromedarius* drawn from 2 specimens from White Pass, Lewis Co., Washington (RBCM 001-286-00[illegible]; [illegible] Appendix): genitalia of specimen 1 and lateral view of the verge, dissected from the penial sac of specimen 2 (insert). AC: accessory sac of penis; AG: albumen gland; BC: bursa copulatrix (spermatheca); EP: epiphallus; HD: hermaphroditic duct; OT: ovotestis; P: penis; PW: penial wall peeled back; RT: penial retractor; SPOV – spermoviduct; V: verge; VS: vas deferens.

(Branson, 1972, 1980). All but one of our records from Washington (record 7 in Appendix) were from relatively high elevations (744–1370 m). On the east slope of the Cascade Range (records 10–15) the species appears to be confined to wooded mountain peaks amidst drier grass/shrub habitats. Interestingly, at these sites the slugs inhabited sparsely wooded subalpine talus.

Externally our specimens conformed with the description for *H. dromedarius* (Branson, 1972), although our measurements of the length of fresh specimens from Vancouver Island (40–60 mm) were considerably greater than the length (24–31 mm) reported by Branson. As the two juvenile paratypes suggest, most of Branson's specimens might not have been fully grown. Although the anatomy of the genitalia of our specimens differed from the original description, these specimens were comparable with Branson's (1972) type material. The original description referred to the anatomy of the genitalia three times: in the identification key (p. 103): "penis broad, lacking an accessory gland"; in the corroborative description (p. 105): "the inflated penis does not bear an accessory sac"; and in the diagnosis (p. 106): "It [*H. dromedarius*] differs from *H. danielsi* in matters of coloration and in possessing the inflated penis and in lacking an accessory stimulator". We presume that the accessory organ in question refers to the same structure. In the adult specimens investigated by us, only the proximal portion of the penis was broad, whereas its base was long and rather narrow. Also contrary to these statements, in the specimens we examined, including type specimens, a penial accessory sac was always present. However, the holotype as well as the two investigated paratypes had not been dissected by Branson, so it remains unknown what specimen, and therefore species, he might have examined for his anatomical descriptions.

In *H. dromedarius*, there were no intrapenial accessory structures, such as the "stimulator" described for *H. malonei* (Kozloff and Vance, 1958). A more detailed, comparative investigation of the verge and other intrapenial structures among species of *Hemphillia* awaits investigation.

Three other large-bodied (>30 mm in length) species of *Hemphillia* are currently recognized (*H. malonei*, *H. camelus*, and *H. danielsi*). A penial accessory sac is absent in *H. malonei* (Pilsbry, 1948, L.C., unpublished), which is sympatric with *H. dromedarius* in the Olympic Mountains of Washington. Externally, the two species can be distinguished by the absence of a caudal horn and the presence of a prominent, light-colored, mid-dorsal stripe on the tail in *H. malonei*. *Hemphillia camelus* from eastern British Columbia and Washington also lacks both a caudal horn and a penial accessory sac (Pilsbry, 1948). Of the described species, *H. dromedarius* most closely resembles *H. danielsi*, which occurs in Montana (Pilsbry, 1948), and our specimens keyed out to this species using Branson's (1972) identification key. Systematic relationships within *Hemphillia* and among related genera have not been examined recently, and comparative studies of reproductive anatomy and genetics of *Hemphillia* are in order.

ACKNOWLEDGMENTS

The first *H. dromedarius* from Vancouver Island was found during gastropod surveys sponsored by Weyerhaeuser Canada (Nanaimo Office). Subsequent financial support for surveys in British Columbia came from the Endangered Species Recovery Fund (Wildlife Habitat Canada) and Department of Forest Sciences, University of British Columbia (through a Forest Renewal British Columbia grant to John Richardson).

We thank Suzanne Beauchesne, Christian Engelstoft, Robert Forsyth, Brent Haddaway, LeeAnn Hancock, Kelley Jorgensen, Tom Kogut, Brad Moon, Bill Null and Lennart Sopuck for enthusiastic help with the collection of specimens. Robert Forsyth provided literature references and contacts. Glen Dunsworth and David Lindsay provided access to forestry lands. Kelly Sendall and Phil Lambert allowed us to use the facilities at the Royal British Columbia Museum and accepted our specimens. We are also grateful to Robert Hershler, Timothy Pearce, and Jochen Gerber for the loan of type specimens. Ira Willey helped with the imaging of the figures.

LITERATURE CITED

Branson, B. A. 1972. *Hemphillia dromedarius*, a new arionid slug from Washington. The Nautilus 85:100–106.

Branson, B. A. 1977. Freshwater and terrestrial Mollusca of the Olympic Peninsula, Washington. The Veliger 19:319–330.

Branson, B. A. 1980. Collections of gastropods from the Cascade Mountains of Washington. The Veliger 23:171–176.

Gomez, B. J. 2001. Structure and functioning of the reproductive system. In: Barker, G. M. (ed.), The Biology of Terrestrial Molluscs. CABI Publishing, Wallingford. pp. 307–330.

Hanham, A. W. 1926. *Hemphillia malonei* Van. The Nautilus 39:113–114.

Kelley, R., S. Dowlan, N. Duncan and T. Burke. 1999. Field Guide to Survey and Manage Terrestrial Mollusk Species from the Northwest Forest Plan. Bureau of Land Management, Oregon State Office. 114 pp.

Kerney, M. P. and R. A. D. Cameron. 1979. A Field Guide to Land Snails of Britain and North-west Europe. William Collins and Sons, Ltd.: London. 288 pp.

Kozloff, E. N. and J. Vance. 1958. Systematic status of *Hemphillia malonei*. The Nautilus 72:42–49.

Pilsbry, H. A. 1948. Land Mollusca of North America (north of Mexico). The Academy of Natural Sciences of Philadelphia, Monograph 2:521–1113 + xlvii.

Tompa, A. S. 1984. Land snails (Stylommatophora). In Tompa, A. S., N. H. Verdonk and J. A. M. van den Biggelaar (eds.), The Mollusca 7. Reproduction. Academic Press: London and New York. pp. 47–140.

Turgeon, D. D., J. F. Quinn, Jr., J. A. Coan, F. G. Hochberg, W. G. Lyons, P. M. Mikkelsen, R. J. Neves, C. F. E. Roper, G. Rosenberg, B. Roth, A. Scheltema, F. G. Thompson, M. Vecchione, and J. D. Williams. 1998. Common and Scientific Names of Aquatic Invertebrates from the United

States and Canada: Mollusks. Second edition. American Fisheries Society Special Publication 26. 526 pp.

APPENDIX

Localities for *Hemphillia dromedarius* examined for this study.

Vancouver Island, British Columbia, Canada:

1. 5 km northeast of Wild Deer Lake, 9 km southwest of Duncan (logging road L1000); elevation 700 m above sea level (asl); 48°41′ N, 123°46′ W; 8 October 1999 (collected by K. Ovaska, L. Sopuck, and S. Beauchesne; RBCM 001–00279–001).
2. Loss Creek, at Hwy. 14 southeast of Port Renfrew; 48°28′ N, 124°15′ W; elevation 49 m asl; 14 April 2000; (collected by R. Forsyth and K. Ovaska; RBCM 000–00145–001; 15 June 2001 (collected by K. Ovaska and C. Engelstoft; RBCM 001–00280–001) (Figure 2).
3. Bamfield West; 48°50′ N, 125°8′ W; elevation < 20 m asl; 23 July 2000 (collected by K. Ovaska; maintained in captivity until 19 December 2000; RBCM 001–00281–001).
4. Vancouver Island, Mt. Brenton (south end of Holyoak Lake), ca. 8 km southwest of Chemainus; 48°54′ N, 123°50′ W; elevation 1060 m asl; 25 August 2001 (2 specimens collected by K. Ovaska, L. Sopuck, and S. Beauchesne; RBCM 001–00282–001).
5. Mt. Hooper (shores of an unnamed lake), ca. 20 km northwest of Youbou; 48°60′ N, 124°29′ W; elevation 830 m asl; 10 September 2001 (2 specimens collected by L. Sopuck, C. Engelstoft, K. Ovaska, and S. Beauchesne; RBCM 001–00283–001).
6. Indian Creek, ca. 9 km N of Ucluelet on Kennedy Flats; 49°02′ N, 125°32′ W; elevation < 20 m; 18 November 2001 (collected by L. Sopuck, B. Beasley, K. Ovaska, W. Leonard, G. Shreiber, and J. Ziegltrum) (specimen used for genetic studies; photograph in personal files of KO).

Washington State, United States:

7. Clallam Co., 4.8 km south of Blyn (off Woods Road), Olympic National Forest; 47°59′ N, 123°00′ W; elevation 150 m asl; 20 May 2001 (collected by W. Leonard and B. Moon; RBCM 001–00285–001).
8. Lewis Co., Gifford Pinchot NF, 14.5 km west of White Pass (north side of SR 12); 46°40′ N, 121°31′ W; elevation 853 m asl; April 2000 (8 specimens collected by K. Jorgensen and W. Leonard; RBCM 001–00286–001; 12 April 2002 (2 specimens collected by W. Leonard; RBCM 001–286–001).
9. King Co., Mt. Baker-Snoqualmie National Forest, several locations from 0.8 to 1.6 km west of Stevens Pass; 47°54′ N, 121°06′ W; elevation 1100 m asl; April and May 2001 (3 specimens collected by W. Leonard and W. Null; RBCM 001–00287–001).
10. Kittitas Co., Wenatchee National Forest, Ski View; 47°23′ N, 121°22′ W; elevation 1370 m asl; 17 October 2000 (collected by J. Baugh; RBCM 001–00359–001).
11. Kittitas Co., Wenatchee National Forest, Granite Creek; 47°09′ N, 121°05′ W; elevation 927 m asl; 19 October 2000 (collected by J. Baugh) (dissected specimen lost).
12. Kittitas Co., Wenatchee National Forest, Cold Creek; 47°20′ N, 121°22′ W; elevation 808 m asl; 1 November 2000 (collected by J. Baugh; RBCM 001–00361–001).
13. Kittitas Co., Wenatchee National Forest, Mosquito Creek; 47°18′ N, 121°20′ W; elevation 775 m asl; 26 October 2000 (collected by J. Baugh; RBCM 001–00360–001).
14. Kittitas Co., Wenatchee National Forest, Swamp Lake; 47°19′ N, 121°18′ W; elevation 744 m asl; 9 July 2001 (collected by J. Baugh; RBCM 001–00289–001).
15. Kittitas Co., Wenatchee National Forest, Roaring Creek; 47°20′ N, 121°22′ W; elevation 810 m asl; 11 July 2001 (2 specimens; collected by J. Baugh; RBCM 001–00288–001).

New species of deep-water Cancellariidae (Gastropoda) from the southwestern Pacific

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ABSTRACT

One new genus and nine new species of Cancellariidae are described from New Caledonia from depths between 200 and 600 meters. They are *Africotriton adelphus* new species, *Mirandaphera* new genus, *Mirandaphera* [illegible] new species, *Mirandaphera maestratii* new species, *Merica* [illegible] new species, *Sveltia roceron* new species, *Sveltia* [illegible] new species, *Nipponaphera pardalis* new species, *Nipponaphera* [illegible] new species, and *Nipponaphera* [illegible] new species. *Africotriton adelphus* new species is the first species in that genus known from outside South Africa and Australia. The new genus *Mirandaphera* is characterized by its [illegible] shell with very large crenulated axial ribs and axial columella. The genus is composed of the two new species described herein, *Mirandaphera maestratii* new species and *M.* [illegible] new species, and two other species, *M.* [illegible] (Habe, 1961) **new combination** and *M. arafurensis* Verhecken, 1997 **new combination**, from deep water off Japan and the Arafura Sea, respectively. *Trigonaphera* [illegible] Habe, 1961 and *Agatrix nodosivaricosa* Petuch, 1979 are transferred to *Nipponaphera*. New species of *Merica*, *Sveltia*, and *Nipponaphera* are the deepest dwelling known representatives in their respective genera.

INTRODUCTION

The tropical deep-water fauna of the southwestern Pacific was virtually unknown just two decades ago, but considerable advances have since been made both in terms of sampling in the field and taxonomical descriptions of the material collected. Emphasis has been placed on the exploration of the area around New Caledonia, resulting in the description of several hundred new molluscan species (see, among others, Crosnier, [illegible]; Bouchet, 1991; Bouchet, 1995; Bouchet and Marshall, 2001). Although the inventory is still far from complete, it has already been revealed to be one of the most—if not the most—diverse anywhere in the world, with exceptional diversification in such families as Seguenziidae (55 species; Marshall, 1991), Muricidae ([illegible] 200 species; Houart, 2001), or Scaphopoda (75 species; Scarabino, 1995).

Based on the literature, the family Cancellariidae appears poorly represented in the tropical South Pacific, with half a dozen nominal species recorded from shallow water in New Caledonia, to just two reported from Fiji and a single species from the Society Islands. By contrast, the material originating from the recent expeditions in New Caledonia, Vanuatu, Fiji, Tonga, and Wallis and Futuna contains about 50 species of Cancellariidae, about 40 of which are undescribed, mainly from depths between 200 and 600 meters. The purpose of the present paper is to provide descriptions of the most spectacular of the new species. A more comprehensive monograph, describing and illustrating the entire cancellariid fauna of the region, will follow. We restrict ourselves in the present paper to the description of shell morphology and defer to the second article descriptions of radulae (when available) and discussion of patterns of bathymetrical and geographical distributions.

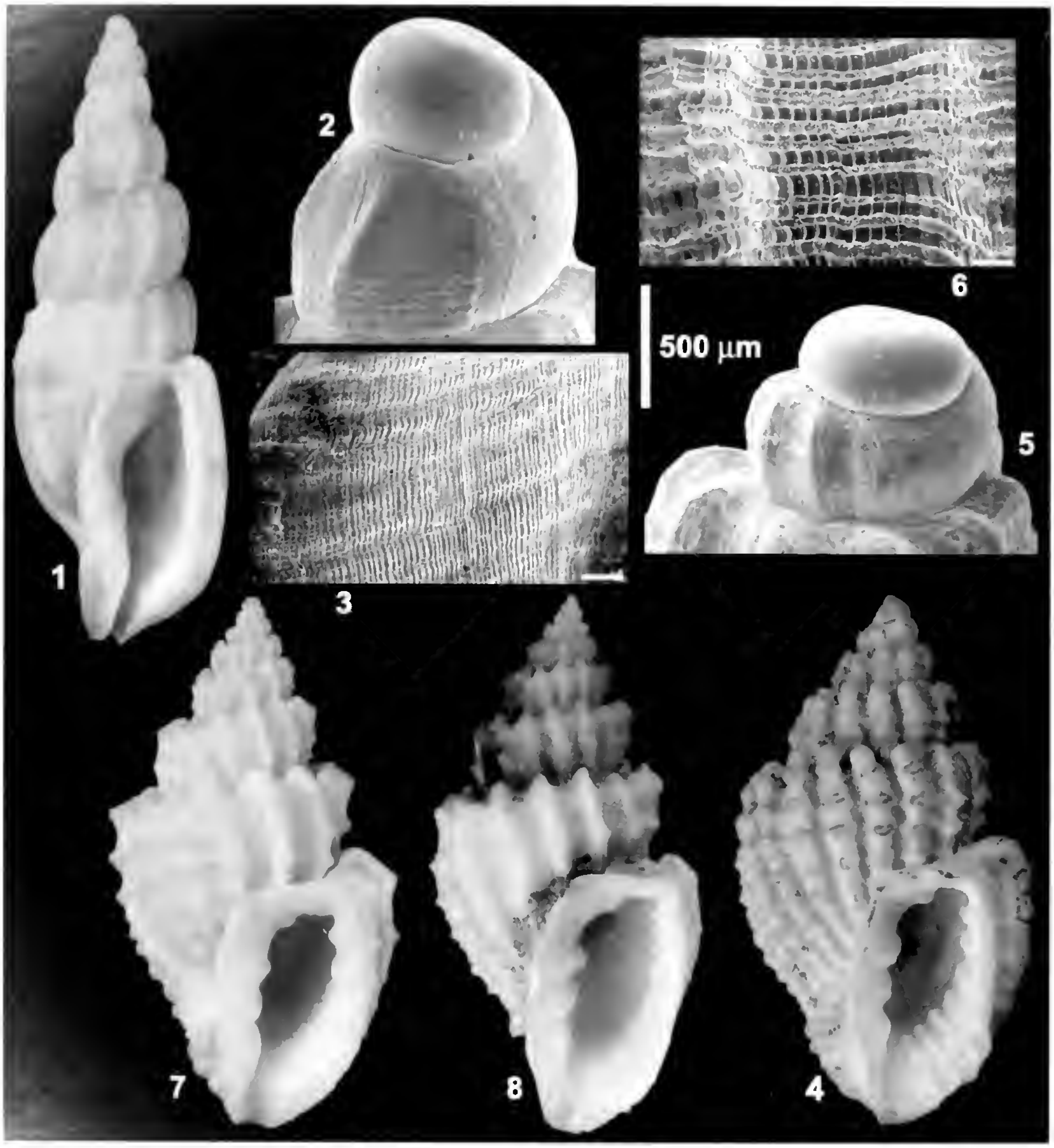
MATERIALS AND TEXT CONVENTIONS

The new species originate from several dredging programs conducted by Dr Bertrand Richer de Forges of Institut de Recherche pour le Développement (IRD, formerly ORSTOM), Nouméa. The context of the programs, narratives of the expeditions and full station lists are presented by Richer de Forges ([illegible]: MUSORSTOM 4), Richer de Forges ([illegible]: LAGON), Richer de Forges ([illegible]: SMIB 5), and Richer de Forges and Chevillon ([illegible]: SMIB 8, BATHUS 2, 3 and 4).

[illegible] MNHN [illegible] DW [illegible] CP [illegible]

SYSTEMATICS

Family Cancellariidae Forbes and Hanley, 1851
Subfamily Plesiotritoninae Beu and Maxwell, 1987
Genus *Africotriton* Beu and Maxwell, 1987



Figures 1–8. New deep-water Cancellariidae. **1–3.** *Africotriton adelphum* new species. **1.** Holotype, height 22.4 mm; south of New Caledonia, SW of Ile des Pins, 22°47′ S, 167°22′ E, 390 m. **2.** Protoconch of specimen from SW of Ile des Pins, 22°48′ S, 167°[illegible] E, [illegible]45 m [BATHUS 2: sta. DW719]. **3.** Teleoconch microsculpture, same specimen as Figure 2. **4–6.** *Mirandaphera* [illegible] new species. **4.** Holotype, height 14.0 mm; off northeastern coast of New Caledonia, Passe de Hienghène, 20°33′ S, 164°[illegible] E, [illegible] m. **5.** Protoconch of specimen from Wallis and Futuna, 13°19′ S, 176°17′ W, 350 m [MUSORSTOM 7: sta. DW[illegible]]. **6.** [illegible] microsculpture, same specimen as Figure 5. **7–8.** *Mirandaphera cayrei* new species. **7.** Specimen, height 27.[illegible] mm; [illegible] Caledonia, 19°01′ S, 163°15′ E, 311–351 m [BATHUS 4: sta. DW902]. **8.** Holotype, height 38.7 mm; South of N[illegible] Passe de Kouaré, 22°49′ S, 166°15′ E, 300–370 m. Scale lines = 100 µm (3, 6) and 500 µm (2, 5).

Type Species: [illegible] *[illegible]liratus* C. B. Sowerby III, 190[illegible], [illegible]ral designation.

Africotriton adelph[illegible] new species
(Figures 1–3)

Type Material: Holotype 22.4 mm height × 7.8 mm width (lv; Figure 1) and [illegible] paratypes (dd), all from the type locality, in MNHN.

Type Locality: South of New Caledonia, SW of Ile des Pins, 22°47′ S, 167°22′ E, 390 m [MUSORSTOM 4: sta. DW226].

Other Material Examined: South of New Caledonia. BIOCAL, sta. DW44, 22°47′ S, 167°14′ E, 440–450 m, 2 juv. lv, 1 juv. dd.—SMIB 2: sta. DW1, 22°53′ S, 167°13′ E, 438–444 m, 1 juv. lv.—SMIB 3: sta. DW26, 22°55′ S, 167°16′ E, 450 m, 1 lv.—BATHUS 2, sta. DW719, 22°48′ S, 167°16′ E, 444–445 m, 4 lv (Figures 2, 3).

Description: Protoconch mammilate, paucispiral, of 1.1 whorls, diameter 1.25–1.30 mm (Figure 2). Transition to teleoconch marked by onset of closely spaced spiral cords. Teleoconch of seven moderately rounded whorls; spire angle 26°–27°. Prominent orthocline rounded varices that extend above the appressed suture are formed irregularly, but usually at about 240° intervals. Spiral sculpture of over 60 low closely spaced spiral cords. Axial sculpture of widely spaced, rounded non-collabral ribs, 7 between final two varices, with closely packed microscopic growth lines (Figure 3). Aperture narrowly ovate. Outer lip with weak crenulations on edge but smooth within. A shield-like callus produced on the inner lip, weak over the parietal area but well produced over the inductural area and extending over the siphonal constriction. Columella almost axial with a narrow fold at the center. A second, very weak fold posterior to the center fold is visible on some specimens. Siphonal canal narrow, open, strongly recurved. Shell color cream to yellow-brown with 6 or 7 red-brown spiral bands, narrow on small shells but wide on some adults, appearing as weak bands except on the tops of the varices where they appear as narrow stripes.

Etymology: The Greek *adelphos*, brother, utilized to highlight the resemblance of the species to others in the genus; treated here as a Latin adjective.

Remarks: Of the six species included in this genus when introduced, five are from South Africa and the sixth, *A. carinapex* Beu and Maxwell, 1987, is from off New South Wales, Australia. The new species differs from *A. carinapex* in being much more slender with less convex whorls, and in having stronger spiral cords and weaker axial ribs. *Africotriton adelphum* resembles more the South African *A. kilburni* Beu and Maxwell, 1987, but that species has more prominent spiral cords and weaker axial ribs.

Subfamily Cancellariinae Forbes and Hanley, 1851

Genus *Mirandaphera* new genus

Type Species: *Mirandaphera cayrei* new species

Description: Shell relatively large, reaching over 35 mm. Teleoconch of 7–9 whorls. Shell somewhat attenuated with large axial ribs that dominate the shell sculpture. Ribs angled or rounded at the shoulder over which they project as small coronations but rarely extend back to the suture. Sutural ramp depressed. The suture is only slightly impressed. Small nodes are formed where weak spiral cords cross ribs. Spiral cords are much stronger and more evident on the ribs than in the interspaces. Outer lip thick, slightly flared on outer edge and extending back over the parietal wall as a rounded shield that extends out at the inductural area. No stromboid notch visible on outer lip. Columella axial with two strong folds and a third fold which sits on the edge of the siphonal fold before turning away to parallel other folds. Folds do not extend out to the edge of the inductural shelf. Umbilicus absent.

Discussion: Besides the two new species described here, we include *Trigonaphera tosaensis* Habe, 1961 (recently placed in *Solatia* by Hasegawa, 2001: 583) and *Solatia arafurensis* Verhecken, 1997 in *Mirandaphera*. The resemblance of these taxa to *Solatia* is only very superficial. The type species of *Solatia*, *S. piscatoria* (Gmelin, 1791), has weak columellar folds, an appressed suture, and a flaring aperture among other differences. Species of *Mirandaphera* have a superficial resemblance only to high-spired species of *Scalptia* Jousseaume, 1887 from which they differ in having an elongated tabulate shell with very large crenulated axial ribs and a axial columella. *Mirandaphera*, as understood here, is a deep-water genus. No fossil species have been recognized in the literature.

Etymology: The Latin *mirandus*, meaning wonderful or strange, combined with *aphera*. *Aphera* was introduced as a genus in Cancellariidae and later used as a stem name for various cancellariid genera, all treated as feminine. A search for its origin reveals only a few usages, the earliest of which are as the given name of women in England in the mid-17th Century.

Mirandaphera cayrei new species
(Figures 7–8)

Type Material: Holotype (38.7 mm height × 19.3 mm width) (lv) in MNHN (Figure 8).

Type Locality: South of New Caledonia, off Passe de Kouaré, 22°19′ S, 166°45′ E, 300–370 m [BATHUS 2, sta. DW731].

Other Material Examined: North of New Caledonia, BATHUS 4, sta. DW902, 19°01′ S, 163°15′ E, 341–351 m, 2 dd (Figure 7).—From commercial sources, boat Tui II, off Bélep Islands, 3 spms.

Description: Protoconch smooth, of 1.3 whorls, diameter 850 µm. Transition to teleoconch marked by strong axial rib. Teleoconch of about 9 elongate whorls. Axial sculpture of strong rounded ribs (about 12 on body whorl and 14 on penultimate whorl). The ribs are biangular on the shoulder over which they recurve and extend partially onto the otherwise smooth, flat sutural ramp. Suture barely impressed. Spiral sculpture of about 8 primary cords that form prominent nodes where they cross the axial ribs. Nodes strongest on the shoulder, wide biangular. About 4 primary spiral cords visible on penultimate whorl. Numerous fine secondary spiral cords cover the shell, 8 or more between each pair of primary cords with an occasional secondary spiral cord intermediate in strength, not intersected by axial riblets. Ribs on adult shells sometimes formed as thickened varices with subsequent growth originating from under the outer lip. Aperture elongate. Outer lip thick, smooth, with a narrow, smooth shelf inside the lip. About 12 strong lirae extend from lip only a short way into the aperture. A posterior canal is formed under the shoulder and is further delineated by a pustule on the parietal wall. Shield-like parietal callus well-developed. Columella with three strong folds, the anterior one weakest and bordering the distinct siphonal fold before turning to parallel the other folds. Folds do not extend to the end of the inductural callus. Body whorl only slightly constricted behind the siphonal fasciole. Umbilicus absent. Shell color off-white or beige; primary spiral cords slightly darker, light yellow-brown.

Etymology: Named for Dr. Patrice Cayré, head of IRD's Department des Ressources Vivantes, in recognition for his support to taxonomy and biodiversity exploration.

Remarks: *Mirandaphera cayrei* differs from *M. tosaensis* (Habe, 1961) and *M. arafurensis* (Verhecken, 1997) in having strong lirae within the aperture and a more turreted, attenuate shell on which the spiral sculpture is prominent in profile. *Mirandaphera maestratii* has, among other differences, more numerous axial ribs, stronger spiral sculpture, and a more rounded profile.

Mirandaphera maestratii new species
(Figures 4–6)

Type Material: Holotype (14.0 mm height × 8.4 mm width) (dd) in MNHN (Figure 4).

Type Locality: Off northeast coast of New Caledonia, Passe de Hienghène, 20°33′ S, 164°57′ E, 533–610 m [BATHUS 4: sta. DW948].

Other Material Examined: Vanuatu, MUSORSTOM 8, sta. DW1061, 16°15′ S, 167°20′ E, 458–512 m, 1 dd; Fiji: MUSORSTOM 10: sta. CP1341, 16°52.5′ S, 177°43.7′ E, 500–614 m, 1 dd; Wallis and Futuna: MUSORSTOM 7: sta. DW601, 13°19′ S, 176°17′ W, 350 m, 1 dd (Figures 5, 6).

Description: Protoconch prominent, of 1.3 whorls, diameter 850 µm (Figure 5). Onset of teleoconch marked by a strong axial rib. Teleoconch of about 6 whorls ornamented with high narrow axial ribs barely wider than interspaces. [illegible] ribs, 14–16 in number, extend over the [illegible] and turn down to a narrow sutural ramp [illegible] all the way to the moderately impressed [illegible] sculpture of narrow densely packed [illegible] become denser and increase in height at [illegible] forming bead-like nodes on the ribs. [illegible] nodes on the body whorl ribs with approx[illegible] between centers of nodes. Spiral cords intersected by [illegible] incremental riblets that form an intricate [illegible] sculpture (Figure 6). Final rib is produced as a terminal varix. Aperture elongate, narrow. Outer lip thickened with 8 lirae within that extend to the outer edge but do not descend deeply into the aperture. Posterior canal is formed under the shoulder and is further delineated by a pustule on the parietal wall. Parietal callus well-developed but not extending out as a shield. Columella with three strong folds, the anterior one weakest and bordering the siphonal fold before turning to parallel the other folds. Folds do not extend to the outer edge of the inductura. Body whorl slightly constricted behind the small but well-defined siphonal fasciole. Umbilicus absent. Shell color light brownish-yellow.

Etymology: Named for Philippe Maestrati, MNHN museum technician, in appreciation for his dedication to processing and sorting much of the New Caledonia material.

Remarks: *Mirandaphera maestratii* is separable from *M. cayrei* by its closely spaced axial ribs. The spiral cords of *M. maestratii* are also unique, being so closely spaced that the interspaces appear as incised lines. The delicate pattern they form is especially noticeable when there is a varix on which they are visible.

Genus *Merica* H. and A. Adams, 1854

Type species: *Cancellaria melanostoma* Sowerby, 1849, by subsequent designation of Cossmann (1899).

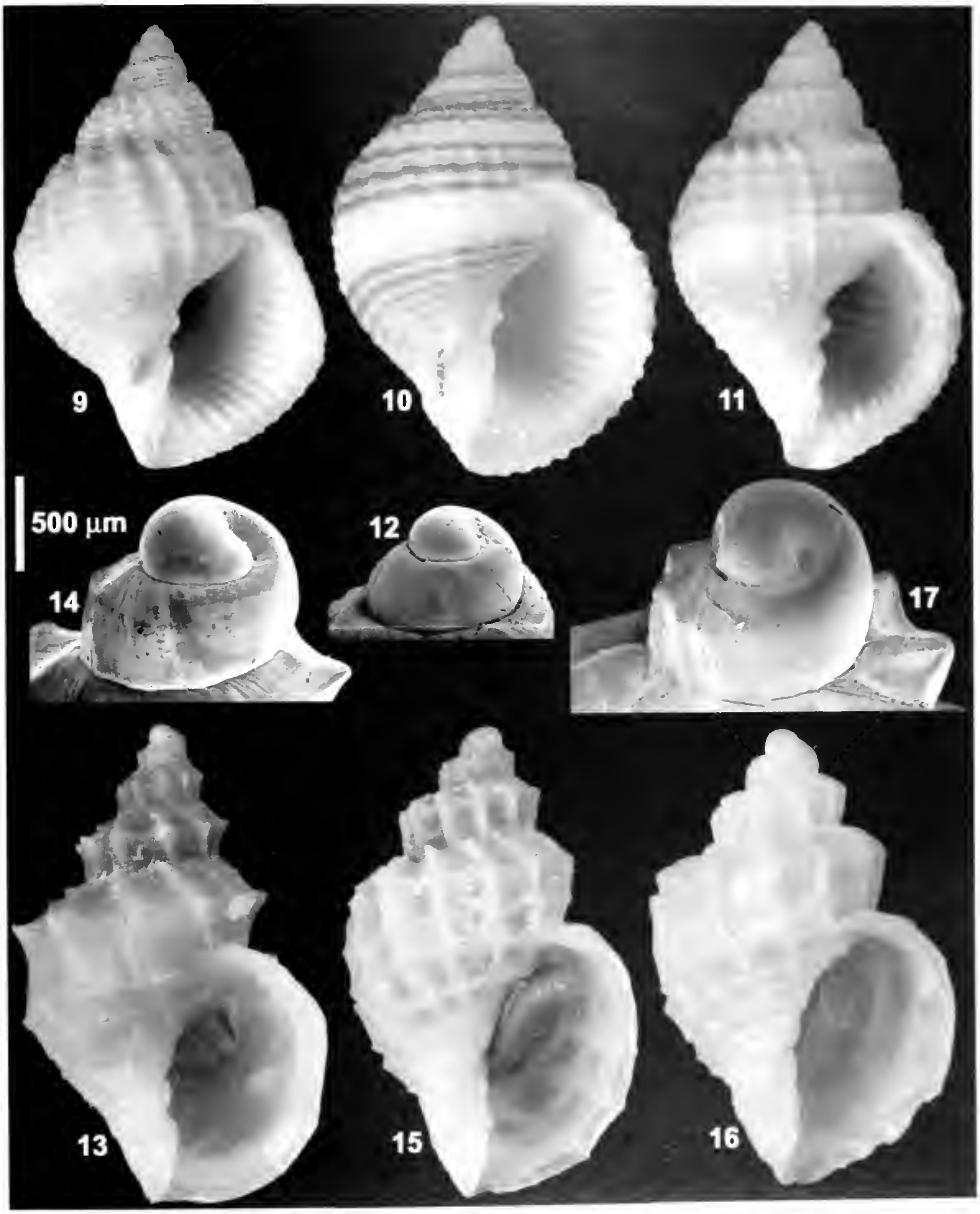
Merica marisca new species
(Figures 9–12)

Type Material: Holotype (25.7 mm height × 18.0 mm width) (lv) (Figure 9) in MNHN.

Type Locality: Off northeast coast of New Caledonia, Passe de Hienghène, 20°34′ S, 164°58′ E, 470–490 m [BATHUS 4 sta. CP947].

Other Material Examined: New Caledonia: BATHUS 4: sta. CP889, 21°01′ S, 164°27′ E, 416–433 m, 1 dd (Figure 12).—HALIPRO 1: sta. CP851, 21°43′ S, 166°37′ E, 314–364 m, 1 lv (Figure 11); Vanuatu: MUSORSTOM 8: sta. CP1136, 15°41′ S, 167°02′ E, 398–400 m, 1 dd (Figure 10).

Description: Protoconch smooth, shiny, with 1.0 whorl (Figure 12). Transition to teleoconch marked by a slight depression and onset of axial and spiral sculptures. Teleoconch of up to 6 rounded whorls. Shoulder small, rounded, sloping back to an impressed suture forming a narrow channel. Axial sculpture of about 14–16 low axial ribs on body whorl of adult; slightly more on earlier whorls. Ribs rounded in profile and narrower than intervening spaces. Periodic internal varices (see Harasewych and Petit, 1982: 111), noticeable on outer surface of shell as thickened axial ribs, each followed by a relatively flat area. Spiral sculpture of strong, broad cords (16–20 on body whorl, 6–7 on penultimate whorl); those on shoulder crowded, others usually with a secondary cord in the interspaces and rarely a tertiary cord. Aperture large with a widely elliptical, prosocline outer



Figures 9–17. New deep-water Cancellariidae. **9–12.** *Merica* [illegible] new species. **9.** Holotype, height 25.7 mm; off the [illegible] coast of New Caledonia, Passe de Hienghène, 20°34′ S, 164°58′ E, 470–490 m. **10.** Specimen from Vanuatu, height [illegible] mm; 15°41′ S, 167°02′ E, 398–400 m (MUSORSTOM 8, sta. CP1136). **11.** Specimen from New Caledonia, height 18.7 mm; 2[illegible]′ S, 166°37′ E, 314–364 m (HALIPRO 1, sta. CP851). **12.** Protoconch of specimen from off the western coast of New Caledonia, 21°01′ S, 164°27′ E, 416–433 m (BATHUS 4, sta. CP889). **13–14.** *Sveltia* [illegible] new species. **13.** Holotype, height 14.[illegible] mm; south of New Caledonia, Norfolk Ridge, Banc Jumeau Ouest, 2[illegible]°20′ S, 168°01′ E, [illegible]–565 m (BATHUS 3, sta. DW8[illegible]). **14.** Protoconch of specimen from south of New Caledonia, SW of Ile des Pins, 23°00′ S, 167°16′ E, 550 m (BIOCAL, sta. DW[illegible]). **15–17.** *Sveltia splendidula* new species. **15.** Holotype, height 11.0 mm; south of New Caledonia, SW of Ile des Pins, 22°50′ S, 167°21′ E, 500–504 m (SMIB 8, sta. DW201). **16.** Paratype, height 10.1 mm; south of New Caledonia, SW of Ile des Pins, 22°5[illegible]′–23°00′ S, 167°21′–167°23′ E, 491–558 m (SMIB 8, sta. DW193–196). **17.** Protoconch of specimen from same locality as Figure 16. Scale line = 500 µm (12, 14, 17).

lip. Outer lip with a finely serrated edge; inner surface with 11 spiral lirae that diminish about a quarter whorl into the aperture. Columella with 3 folds, the posterior one being slightly larger and the anterior one forming the edge of the short, narrow canal. The anterior fold extends to the edge of the inductural callus with smaller fold-like features or pustules sometimes present on outer edge of inductura. Color yellow-brown with a dark red-brown band at shoulder and smaller lines or bands on body whorl. A white band is sometimes present just anterior to the shoulder and just anterior to the periphery.

Etymology: Latin *marisca*, f., a large type of fig.

Remarks: *Merica pirum* has many features in common with the Philippine *Merica ektyphos* Petit and Harasewych, 2000, which has stronger sculpture with heavy nodes formed at intersections of spiral cords and axial ribs. In addition, *M. ektyphos* has a rounded and more solid shell, and the protoconch is ¼ whorl larger than in *M. pirum*. Species of *Merica* live subtidally and on the continental shelf. The bathyal *M. pirum* is apparently the deepest living species in the genus.

Genus *Sveltia* Jousseaume, 1887

Type Species: "*Sveltia varicosa* [sic] Brocc." [= *Voluta varricosa* Brocchi, 1814], by original designation.

Sveltia rocroii new species
(Figures 13–14)

Type Material: Holotype (14.3 mm height × 8.9 mm width) (lv) (Figure 13) and one paratype (dd) from the type locality in MNHN.

Type Locality: South of New Caledonia, Norfolk Ridge, Banc Jumeau Ouest., 23°20′ S, 168°01′ E, 361–365 m [BATHUS 3: sta. DW830].

Other Material Examined: New Caledonia: BIOCAL, sta. DW37, 23°00′ S, 167°16′ E, 350 m, 1 juv. lv. (Figure 14), 1 juv. dd.—MUSORSTOM 4: sta DW181, 18°57′ S, 163°22′ E, 350 m, 1 dd.—BATHUS 4: sta. DW931, 18°55′ S, 163°24′ E, 360–377 m, 1 dd.—From commercial sources, boat Tui II, off Belép Islands, 3 spms.

Description: Protoconch smooth, erect, of 1.0 whorl, diameter [illegible] 30 mm, axis of protoconch tilted to teleoconch [illegible] 14). Transition to teleoconch clearly marked [illegible] like line, angled at the shoulder and foll[illegible] of axial ribs. Teleoconch of about five whorls [illegible] sculpture of low, widely spaced ribs, seven on body [illegible] and ten on penultimate whorl, extending from the suture to the base of the shell. Spiral sculpture of one cord situated midway on whorl and forming an angled shoulder with sharp short spines present at intersections with axial ribs. A weaker spiral cord is sometimes present between the shoulder and the slightly impressed suture. About five weak spiral cords are located anterior to the shoulder, the first anterior one widely spaced from shoulder and forming a slight angle to the body whorl Remaining spiral cords weaker and more closely spaced. Aperture large, oval. Outer lip prosocline, formed by a terminal varix, smooth within. Parietal wall with weak callus, becoming stronger and slightly reflected at the inductura. Columella with three strong folds, the anterior one forming the edge of the short siphonal canal. Shell thin, white, translucent.

Etymology: Named for M. Jean-Paul Rocroi, MNHN, in appreciation of his contribution to molluscan nomenclature.

Remarks: The new species may be compared to only one Recent species other than *Sveltia splendidula*, described herein, is *S. gladiator* (Petit, 1976), which occurs off the Galapagos Islands at a depth of 200 m. Although their protoconchs are entirely different (the protoconch of *S. gladiator* is multispiral indicating planktotrophic larval development), the two species share the "window-like" sculpture below the shoulder formed by the widely spaced cords and ribs. The spines on the shoulder of *S. rocroii* are much shorter than in *S. gladiator*. The European Tertiary species *Calcarata calcarata* (Brocchi, 1814) is startlingly like *S. rocroii* in appearance but that species differs, among other features, in being slightly umbilicate.

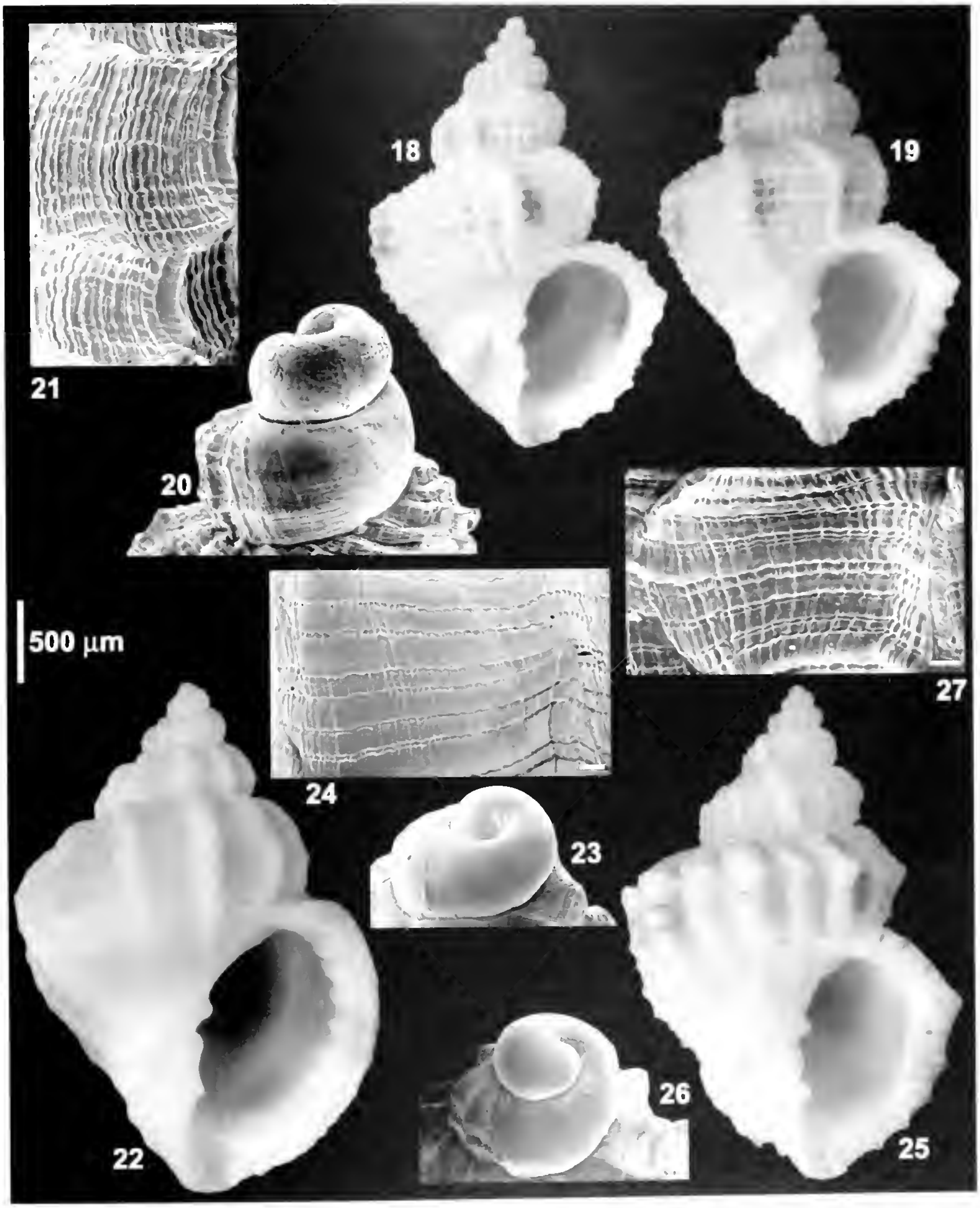
Sveltia splendidula new species
(Figures 15–17)

Type Material: Holotype (11.0 mm height × 6.9 mm width) (lv) (Figure 15) and three paratypes (1 lv, 2 dd) in MNHN.

Type Locality: South of New Caledonia, SW of Ile des Pins, 22°50′ S, 167°21′ E, 500–504 m [SMIB 8: sta. DW201].

Other Material Examined: South of New Caledonia, SW of Ile des Pins: SMIB 8: sta. DW193–196, 22°59′–23°00′ S, 167°21′–167°23′ E, 491–558 m, 1 lv, 2 dd (paratypes; Figures 16, 17).

Description: Protoconch smooth, erect, of 0.9 whorls, diameter 1.20 mm, axis of protoconch tilted to teleoconch (Figure 17). Transition to teleoconch marked by the appearance of an axial rib with angled shoulder. Teleoconch of 3+ rapidly expanding whorls. Axial sculpture of evenly spaced sharp ribs, about 12 on body whorl that are continuous from the suture to the base. The ribs are produced slightly above and over subsequent growth. Spiral sculpture of about seven sharp spiral cords. One cord, somewhat stronger, forms the shoulder over which the axial ribs cross and angle back to a slightly impressed suture. A second strong cord sometimes present at line of sutural attachment. On the final portion of the body whorl the angled shoulder becomes obsolete and the ribs curve smoothly back to an impressed



Figures 18–27. New deep-water Cancellariidae. **18–21.** *Nipponaphera pardalis* new species. **18.** Paratype, height 20.0 mm; north of New Caledonia, Grand Passage, 19°06′ S, 163°29′ E, 230 m (MUSORSTOM 4 sta. DW185). **19.** Holotype, height 25.5 mm; north of New Caledonia, Grand Passage, 19°07′ S, 163°30′ E, 220 m (LAGON sta. 1148). **20.** Protoconch, specimen from South of New Caledonia, Norfolk Ridge, 23°18′ S, 168°05′ E, 311–330 m (SMIB 8 sta. DW181). **21.** Microsculpture of teleoconch, same specimen as Figure 20. **22–24.** *Nipponaphera cyphoma* new species. **22.** Holotype, height 15.1 mm; north of New Caledonia, Grand Passage, 18°55′ S, 163°24′ E, 350–365 m (HALICAL 1 sta. DW01). **23.** Protoconch, same specimen as Figure 22. **24.** Microsculpture of teleoconch, same specimen as Figure 22. **25–27.** *Nipponaphera goniata* new species. **25.** Holotype, height 16.1 mm; south of New Caledonia, Norfolk Ridge, Banc Azteque, 23°41′ S, 168°01′ E, 280 m (SMIB 5 sta. DW76). **26.** Protoconch, specimen from South of New Caledonia, Norfolk Ridge, 24°46′ S, 168°08′ E, 241–245 m (SMIB 8 sta. DW159). **27.** Microsculpture of teleoconch; specimen from south of New Caledonia, Norfolk Ridge, 24°46′ S, 168°08′ E, 235–252 m (SMIB 8 sta. DW154). Scale lines = 100 µm (21, 24, 27) and 500 µm (20, 23, 26).

suture. The spiral cords do not cross over the axial ribs. Aperture large, ovate. Outer lip prosocline, thin, without internal lirations. Parietal area without callus. A small callus is sometimes formed at very base of inductura. Columella with three folds, the posterior one larger and descending. The two anterior folds situated at ends of a shelf-like structure bordering the short siphonal canal. Body whorl slightly constricted behind the weak siphonal fasciole. Shell color white, translucent.

Etymology: Diminutive of the Latin adjective *splendidus* (*-a, -um*), meaning showy or magnificent.

Remarks: *Sveltia splendidula* closely resembles *S. rocroii* from which it differs in possessing more numerous and stronger spiral cords and axial ribs, and in having a much less angular shoulder. The unusual combination of sculpture and translucence gives the shell a shoji-like appearance. The bathymetric distribution of the genus *Sveltia* is unclear due to the confused generic allocation of included species, but *Sveltia splendidula* is apparently the deepest dwelling species in the genus.

Genus *Nipponaphera* Habe, 1961

Type Species: *Nipponaphera habei* Petit, 1972, by ICZN Opinion 1052.

Nipponaphera pardalis new species
(Figures 18–21)

Type Material: Holotype (25.5 m height × 18.0 mm width) (lv) (Figure 19) and one paratype (lv) (Figure 18) in MNHN.

Type Locality: North of New Caledonia, Grand Passage, 19°07′ S, 163°30′ E, 220 m [LAGON: sta. 1148].

Other Material Examined: New Caledonia: MUSORSTOM 4: sta. DW185, 19°06′ S, 163°29′ E, 230 m, 1 lv (paratype, Figure 18).—Sta. DW227, 22°46′ S, 167°20′ E, 300 m, 1 dd.—SMIB 5: sta. DW72, 23°42′ S, 168°01′ E, 400 m, 1 dd [worn; allocation uncertain].—SMIB 8: sta. DW181, 23°18′ S, 168°05′ E, 311–330 m, 1 juv lv (Figures 20, 21).—Sta. DW182-184, 23°18′–23°19′ S, 168°05′ E, 305–367 m, 1 dd.—BATHUS 2: sta. DW744, 22°38′ S, 167°10′ E, 124 m, 1 dd.—BATHUS [illegible] DW942, 19°04′ S, 163°27′ E, 264–270 m, 1 juv [illegible] commercial sources, boat Tui II, off Bélep I[illegible] spms.

Descripti[illegible]ch corroded but apparently consisting of [illegible]orls; teleoconch of 5.2 whorls. Spire high. S[illegible] imbricated axial lamellae and raised spiral cords [illegible] to form squarish intervals. Aperiodical axial [illegible] on final whorl, five on penultimate whorl, and two [illegible] penultimate whorl. Spiral sculpture of about 10 sp[illegible]l cords on penultimate whorl and about 20 on final whorl. Second order sculpture of incremental lines crossing spiral threads and forming finely reticulate sculpture in the squarish intervals (Figure 21). Spire whorls regularly convex, gradually becoming angular at shoulder on final two whorls. Suture deeply impressed. Body whorl only slightly constricted behind siphonal fasciole. Outer lip thin, smooth immediately within but then with about 18 lirations that extend deeply into the aperture. Inner lip reflected as a parietal shield partly extending over the umbilical area in the inductural region. Columella slightly concave with three folds, the anterior two folds close together, much like one large bifurcate fold. Deep umbilicus well developed. Siphonal canal short but distinct. Shell background color creamy-white with brownish blotches on the periphery of the whorls behind varices; primary spiral cords brown on the varices.

Etymology: The Latin *pardalis*, a female panther. To be treated as a noun in apposition. Selected because of the brown blotches behind the varices.

Remarks: The protoconch of the holotype is corroded. The protoconch of the paratype consists of 1.8 whorls, diameter 1.15 mm (Figure 20). Among the species of *Nipponaphera* known at present, this new species most resembles *N. teramachii* (Habe, 1961), **new combination,** which is more distinctly angled at the shoulder, and has coarser sculpture. (The transfer of *Trigonaphera teramachii* to *Nipponaphera* will be discussed in our later monograph.)

Nipponaphera cyphoma new species
(Figures 22–24)

Type Material: Holotype (13.1 height × 9.2 mm width) (dd) (Figures 22–24) in MNHN; 2 paratypes, Petit collection.

Type Locality: North of New Caledonia, Grand Passage, 18°55′ S, 163°24′ E, 350–365 m [HALICAL 1: sta. DW04].

Other Material Examined: From commercial sources, off Bélep Island, dredged at 400 m by boat Tui II, May 2001, 2 spms (paratypes).

Description: Protoconch glassy, white, with 0.9 whorls, diameter 0.93 mm (Figure 23). Transition to teleoconch marked by a small varix-like axial rib followed by spiral and axial sculpture. Spiral sculpture of flat cords of varying sizes. Primary cords normally separated by slightly smaller secondary cords with even smaller tertiary cords in interspaces between the primary and secondary cords. Body whorl with 10–12 primary spiral cords, about 4–5 visible on penultimate whorl. Spiral cords separated by narrow spaces that appear as incised lines instead of spaces (Figure 24). Axial sculpture of rounded ribs, about 8 in number on the body whorl and 11 on the penultimate whorl. Small nodes are present where primary spiral cords cross the axial ribs. On the terminal varix there is a strong shoulder node. Shoulder rounded back to a barely impressed suture. Body whorl rounded but somewhat constricted behind the weak siphonal fasciole. Outer lip thin, weakly serrate. Inner portion of outer lip with a smooth rounded shell followed by about 14 sharp short lirations. Columella with weak callus on inductural area. Columella with three folds that do not extend to the outer edge of the inductura. Posterior fold largest. Two anterior folds situated on ends of a low shelf-like platform with the anteriormost fold becoming the edge of the short well-formed siphonal canal. Umbilicus absent. Shell color mottled white and light brown. Colors arranged in weak bands. Brown bands are located at the shoulder, just anterior to the periphery and at the base.

Etymology: The Greek *kyphoma*, meaning hump, with reference to the sturdy axial ribs of the species. To be treated as a noun in apposition.

Remarks: *Nipponaphera cyphoma* differs from *Nipponaphera nodosivaricosa* (Petuch, 1979), **new combination** (originally in *Agatrix*), in having much finer spiral sculpture, fewer and more widely spaced axial ribs, and a proportionally broader shell. (The transfer of *Agatrix nodosivaricosa* to *Nipponaphera* will be discussed in a future monograph.) The bathymetric distribution of the genus *Nipponaphera* is unclear due to confused generic allocation of described species, but *Nipponaphera cyphoma* is apparently the species with the deepest occurrence in the genus.

Nipponaphera goniata new species
(Figures 25–27)

Type Material: Holotype (16.1 mm height × 11.4 mm width) (dd) (Figure 25) in MNHN.

Type Locality: South of New Caledonia, Norfolk Ridge, Banc Aztèque [also called Banc Antigonia on marine charts], 23°41′ S, 168°01′ E, 280 m [SMIB 5, sta. DW76].

Other Material Examined: South of New Caledonia, Norfolk Ridge. BIOCAL: sta. DW65, 24°48′ S, 168°09′ E, 245–275 m, 1 dd.—CALSUB: dive 21, 22°15′ S, 167°09′ E, 340 m, 1 lv.—CHALCAL 2: sta. DW71, 24°42′ S, 168°10′ E, 230 m, 3 dd.—SMIB 8: sta. DW154, 24°46′ S, 168°08′ E, 235–252 m, 1 dd (Figure 27).—Sta. DW157, 24°46′ S, 168°08′ E, 251–255 m, 1 dd.—Sta. DW158, 24°46′ S, 168°08′ E, 262–290 m, 1 dd.—Sta. DW159, 24°46′ S, 168°08′ E, 241–245 m, 6 dd (Figure 26).—Sta. DW173, 23°41′ S, 168°00′ E, 234–242 m, 1 dd.—Sta. DW174, 23°40′ S, 168°01′ E, 235–240 m, 2 dd.—BERYX 11: sta. DW18, 24°48′ S, 168°09′ E, 250–270 m, 1 dd.

Description: Protoconch smooth, of slightly more than 1 whorl, diameter 1.00 mm (Figure 26). Teleoconch of 5 whorls, spire high, spire angle of 63–66°. Structure of strong lamellate axial ribs reflected adaperturally and much weaker uneven spiral cords. Some axial ribs are stronger than others and form stronger varices. Axial ribs number about 13 on final whorl and 14 on penultimate and antepenultimate whorls. Ribs regularly convex on first two whorls becoming distinctly angular at shoulder. Spiral sculpture of about 8 primary cords on spire whorl and about 15 on body whorl, each with 5–8 secondary cords in intervals. Spiral cords cross the many rib-like growth lines forming finely reticulate reticulate microsculpture (Figure 27). Suture well impressed. Body whorl slightly constricted behind siphonal fasciole. Aperture with about 17 lirae within that do not extend to the edge of the outer lip but extend deeply within. Inner lip forming parietal shield extending slightly over the narrow umbilicus. Columella only slightly concave with three folds, the anterior two close together, much like one large bifurcate fold. Siphonal canal short but distinct. Shell white, mottled with light brown blotches near the periphery. Primary cords brown, especially where they cross the axial ribs on the last 1.5 whorls. Some specimens are completely white.

Etymology: The Latin adjective *goniatus* (*-a, -um*), angulated, in reference to the shell outline.

Remarks: *Nipponaphera goniata* differs from *N. teramachii* (Habe, 1961) by its proportionally higher spire, narrower umbilicus, and its brown maculations. From *N. pardalis* it differs in having thicker ribs that are not imbricate. It also possesses a narrow umbilicus and has a smaller adult size. The two species, *N. pardalis* and *N. goniata*, coexist south of New Caledonia but have never been taken together.

LITERATURE CITED

Adams, H. and A. Adams. 1854 [in 1853–58]. The genera of Recent Mollusca; arranged according to their organization. 2 vols. John van Voorst, London. [1: 1–256, pls. 1–32, 1853; 1: 257–484, 2: 1–92, pls. 33–72, 1854; 2: 93–284, pls. 73–96, 1855; 2: 285–412, pls. 97–112, 1856; 2: 413–540, pls. 113–128, 1857; 2: 541–660, pls. 129–138, 1858.]

Beu, A. G. and P. A. Maxwell. 1987. A revision of the fossil and living gastropods related to *Plesiotriton* Fischer, 1884 (Family Cancellariidae, Subfamily Plesiotritoninae n. subfam.) with an Appendix: Genera of Buccinidae Pisaniinae related to *Colubraria* Schumacher, 1817. New Zealand Geological Survey Paleontological Bulletin 54: 1–140, pls. 1–30.

Bouchet, P. (ed.). 1995. Resultats des Campagnes MUSORSTOM, volume 14. Memoires du Museum National d'Histoire Naturelle 167: 1–654.

Bouchet, P. and B. Marshall (eds.). 2001. Tropical Deep-Sea Benthos, volume 22. Memoires du Museum National d'Histoire Naturelle 185: 1–406.

Brocchi, G. B. 1814. Conchiologia fossile subapennina con osservazioni geologiche sugli Apennini e sul suolo adiacente. Stamperia Reale, Milano. 2 vols. [1: 1–240; 2: 241–712, pls. 1–16.]

Crosnier, A. and P. Bouchet (eds.). 1991. Resultats des Campagnes MUSORSTOM, volume 7. Memoires du Museum National d'Histoire Naturelle, ser. A 150: 1–259.

Gmelin, J. F. 1791. Caroli a Linné Systema Naturae per regna tria naturae. Editio decima tertia. Vol. 1, pt. 6. Vermes: 3021–3910. Lipsiae.

Habe, T. 1961. Coloured illustrations of the shells of Japan (II). Hoikusha, Osaka, 182 pp., Appendix 42 pp., 66 pls. [An English edition was issued in 1964 with a larger page size: Shells of the western Pacific in color. Vol. II. Hoikusha, Osaka, 233 pp., 66 pls.]

Harasewych, M. G. and R. E. Petit. 1982. Notes on the morphology of *Cancellaria reticulata* (Gastropoda: Cancellariidae). The Nautilus 96: 104–113.

Hasegawa, K. 2000. Cancellarioidea. pp. 581–585, pls. 289–291. In: T. Okutani (ed.) Marine Mollusks in Japan. Tokai University Press, Tokyo, 1173 pp.

Houart, R. 2001. *Ingensia* gen. nov. and eleven new species of Muricidae (Gastropoda) from New Caledonia, Vanuatu, and Wallis and Futuna Islands. In: P. Bouchet and B. Marshall (eds.), Tropical Deep-Sea Benthos, volume 22. Mémoires du Muséum National d'Histoire Naturelle, Paris 185: 243–269.

Jousseaume, F. 1887. La famille des Cancellariidae (Mollusques Gastéropodes). Le Naturaliste 9 [= ser. 2, 1]:155–157, 192–194, 213–214, 221–223.

Marshall, B. 1991. Mollusca Gastropoda: Seguenziidae from New Caledonia and the Loyalty Islands. In: A. Crosnier and P. Bouchet (eds.), Résultats des Campagnes MUSORSTOM, volume 7. Mémoires du Muséum National d'Histoire Naturelle, Paris, ser. A 150: 41–109.

Petit, R. E. 1976. Notes on Cancellariidae (Mollusca: Gastropoda) - III. Tulane Studies in Geology and Paleontology 12: 33–43, pls. 1–2.

Petit, R. E. and M. G. Harasewych. 2000. Three new species of the genus *Merica* (Neogastropoda: Cancellariidae) from South Africa and the Philippines. The Nautilus 114: 142–148.

Petuch, E. 1979. Twelve new Indo-Pacific gastropods. Nemouria 23: 1–21.

Richer de Forges, B. 1990. Explorations for bathyal fauna in the New Caledonian economic zone. In: A. Crosnier (ed.), Résultats des Campagnes MUSORSTOM, volume 6. Mémoires du Muséum National d'Histoire Naturelle, ser. A 145: 9–54.

Richer de Forges, B. 1991. Les fonds meubles des lagons de Nouvelle-Calédonie: généralités et échantillonnages par dragages. Pp. 7–148, in: B. Richer de Forges (ed.), Le benthos des fonds meubles des lagons de Nouvelle-Calédonie, volume 1. Etudes et Thèses [ORSTOM, Paris].

Richer de Forges, B. 1993. Campagnes d'exploration de la faune bathyale faites depuis mai 1989 dans la zone économique de la Nouvelle-Calédonie. Listes des stations. In: A. Crosnier (ed.), Résultats des Campagnes MUSORSTOM, volume 10. Mémoires du Muséum National d'Histoire Naturelle 156: 27–32.

Richer de Forges, B. and C. Chevillon. 1996. Les campagnes d'échantillonnages du benthos bathyal en Nouvelle-Calédonie, en 1993 et 1994 (BATHUS 1 à 4, SMIB 8 et HALIPRO 1). In: A. Crosnier (ed.), Résultats des Campagnes MUSORSTOM, volume 15. Mémoires du Muséum National d'Histoire Naturelle 168: 33–53.

Scarabino, V. 1995. Scaphopoda of the tropical Pacific and Indian Oceans, with description of 3 new genera and 42 new species. In: P. Bouchet (ed.), Résultats des Campagnes MUSORSTOM, volume 14. Memoires du Muséum National d'Histoire Naturelle 167: 189–379.

Verhecken, A. 1997. Mollusca Gastropoda: Arafura Sea Cancellariidae collected during the KARUBAR cruise. Mémoires du Muséum National d'Histoire Naturelle 172: 295–323.

Spawn of the Patagonian gastropod *Pareuthria plumbea* (Philippi, 1844) (Buccinidae)

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ABSTRACT

The spawn of *Pareuthria plumbea* (Philippi, 1844) consists of an egg mass of 4–19 egg capsules. The uncleaved egg, in number of 1–5 per capsule, measured about 300 µm. *Pareuthria plumbea* has direct development without nurse eggs, hatching at crawling stage. Extra-vitelline substances in the intracapsular liquid are likely to be the only extravitelline food available for the embryos. Hatching occurs by rupture or dissolution of the capsule wall in a possibly random location on the thin basal membrane. The number of hatchlings varied from 1–5 within the same spawn. Hatchling number and shell size are related.

INTRODUCTION

The genus *Pareuthria* was proposed by Strebel (1905) in his extensive account of the gastropod fauna from the Strait of Magellan. He described six new species under *Pareuthria*. However, the validity of these species remains uncertain.

Pareuthria plumbea (Philippi, 1844) is the oldest name of a very polymorphic species endemic to the Magellanic province (Figures 1–3). It ranges from southern Chubut province (~45°S) in Argentina to 49°S in Chile (Dell, 1971). It is usually found intertidally at low tide under rocks and in tide pools. Gallardo and Penchaszadeh (2001) mentioned *Pareuthria plumbea* as having direct or non-pelagic development.

Buccinids have a wide range of developmental modes from free-swimming planktotrophic veligers (Bandel, 1975, 1976; Amio, 1963) to lack of a larval stage (Fioroni, 1966; Martel et al., 1986; Portmann, 1925; Miloslavich and Dufresne, 1994; Miloslavich and Penchaszadeh, 1994).

In this note, we describe the spawn of *Pareuthria plumbea* (Philippi, 1844), including the number and size of the uncleaved egg, the development pattern and the hatching stage, of a population from Puerto Deseado, Argentina (~46° S) on the Atlantic coast.

MATERIALS AND METHODS

Adults specimens and egg masses of *Pareuthria plumbea* were collected at low tide in Dos Hermanas, Puerto Deseado, Santa Cruz Province, Argentina (47°45′S, 65°55′W) during February 2000. The intertidal area is occupied by mytilids forming banks on rocky platforms. Specimens and spawns of *P. plumbea* were frequently found in crevices and under rocks. Adults specimens and egg capsules were fixed in 5% formalin on sea water. Those with shelled embryos were preserved in 70% ethanol. Most photographs of the eggs, capsules and embryos were taken using a digital scanning camera attached to a Zeiss Stemi 2000 stereoscopic microscope. All images were digitally processed.

RESULTS

We examined 15 egg masses, for a total number of 106 egg capsules. Each egg mass is composed of 4–19 egg capsules ($\bar{X}$ = 8.83, SD = 5.07, n = 15) (Figure 6). *Pareuthria plumbea* has transparent, yellowish, subcircular, bulliform capsules which are often aggregated and partially overlapping each other (Figures 7–10). They are attached to the substrate by a circular basal membrane measuring 4.2–5.2 mm ($\bar{X}$ = 4.96, SD = 0.22, n = 10). Each capsule has its own basal membrane that is not fused with adjacent ones. The capsules measure 3.2–3.8 mm in diameter ($\bar{X}$ = 3.6, SD = 0.18, n = 10). There is a suture line that splits the capsule in two sides (Figures 9, 11). There is no pre-formed apical plate or escape aperture as a plug, nor an escape slit. During hatch-

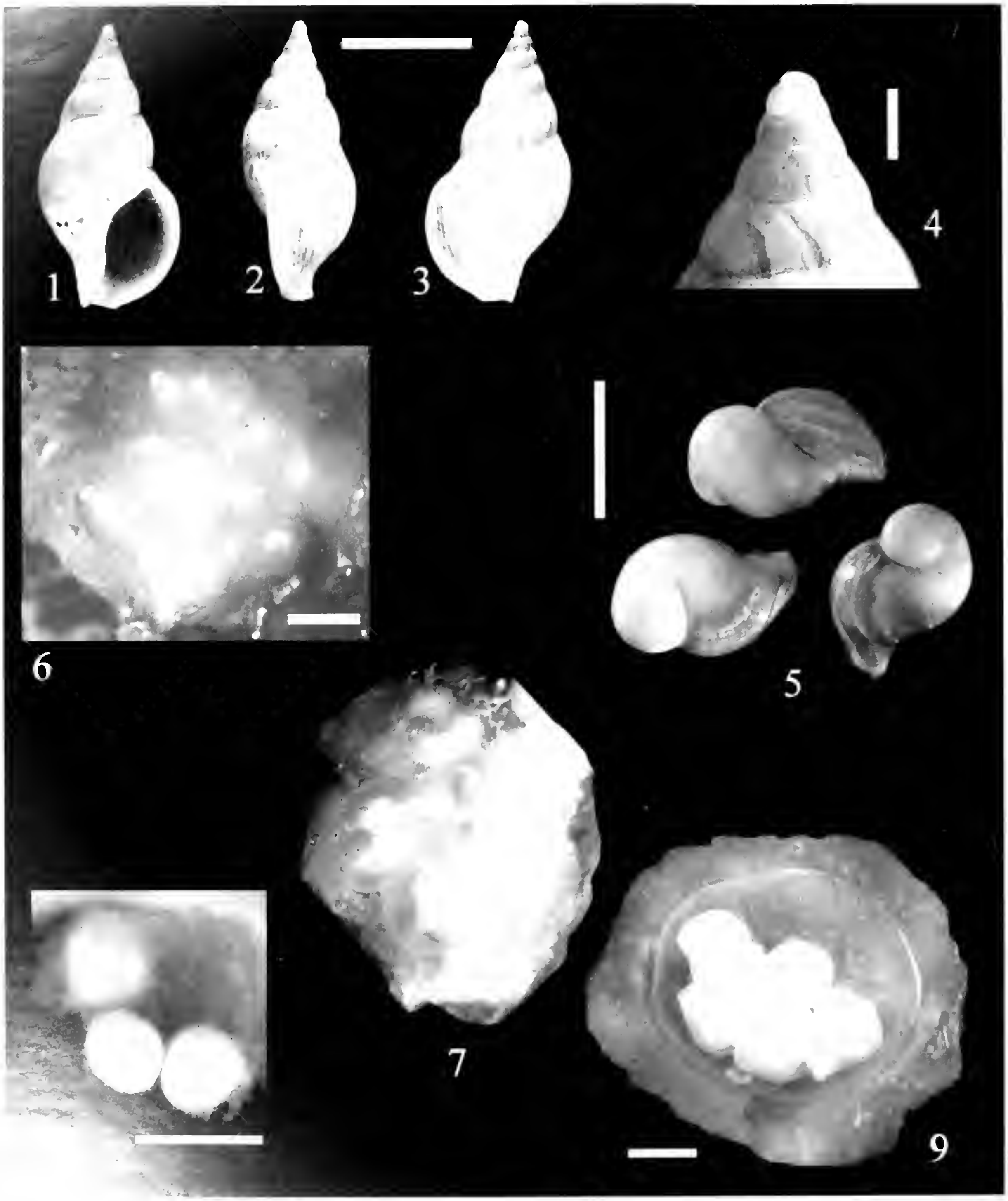

Figure [illegible] Philippi, 1844. **1–3.** MACN 1032, adult specimen from Caleta Coyle, Santa Cruz, Argentina. S[illegible] protoconch. Scale bar = 1 mm. **5.** Three embryos at the pre-hatchling stage. Scale bar = 1 [illegible] **6.** [illegible]ble cluster of eggs. Scale bar = 3 mm. **7.** Several clusters of spawns, the top capsules with the [illegible] **8.** Three eggs from the same capsule. Scale bar = 500 μm. **9.** Isolated capsule with five early [illegible]

Figures 10–12. Egg capsules of *Pareuthria plumbea* (Philippi, 1844). **10.** Cluster of egg capsules. **11.** Isolated capsule. **12.** Middle section showing the capsule profile. Scale bars = 1 mm.

ing the rupture of the basal membrane that is much thinner than the upper wall of the capsule was recorded; this could be an escape way for hatchlings.

The uncleaved eggs measured 280–340 µm in diameter (X = 300, SD = 15.68, n = 14) (Figure 8). They are embedded in a very dense intracapsular liquid that becomes, when preserved in ethyl alcohol, opaque and flocculates like denatured egg whites. This intra capsular liquid is completely translucent at the latest stages of development, suggesting that it contains nutritional substances that would be ingested by the embryos. No nurse eggs were recorded.

The number of embryos was 1–5 within any given spawn. When five are present, one is generally abortive and is probably eaten by the remaining embryos. Hatchling number and shell size are apparently related. When a single embryo developed, the shell length at the prehatching stage was: 2.14–2.19 mm (X = 2.16 mm, n = 4, SD = 0.03), with two embryos the shell length was: 1.79–2.22 (X = 1.99 mm, n = 13, SD = 0.14), with three: 1.60–1.97 (X = 1.81 mm, n = 21, SD = 0.09), with four: 0.79–1.84 mm (X = 1.62 mm, n = 33, SD = 0.17). We did not find capsules at the late pre-hatching stage with five embryos. The embryos hatch as crawling juveniles, with a well-developed foot (Figure 5).

The protoconch has 2½–2¾ convex, somewhat globose, whorls (Figure 4). Whorls are completely smooth and brownish in color. There is a gradual transition to teleoconch. Therefore, changes in the axial ornamentation are usually the only way to recognize features of the adult shell. The first teleoconch whorl has weak and irregular costae that disappear gradually.

DISCUSSION

Development with planktonic larvae has been described for several species within the family Buccinidae, generally from tropical regions (e.g., *Pisania pusio* (Linnaeus, 1758) and *Pusia tincta* (Conrad, 1846) (formerly in the genus *Cantharus*); Bandel, 1975, 1976). In temperate and colder waters there are also examples of hatching of veliger larvae (e.g., *Babylonia japonica* (Reeve, 1842); Amio, 1963, Rivest, 1983). However, the most common mode of development within the Buccinidae involves the lack of free-swimming larval stages, hatching of crawling juveniles, and the presence of nurse eggs. The best-known examples are *Buccinum undatum* Linnaeus, 1758 (Fioroni, 1966; Martel et al., 1986, Portmann, 1925), *B. cyaneum* Bruguière, 1792 (Miloslavich and Dufresne, 1994), *Searlesia dira* (Reeve, 1846) (Rivest, 1983), and *Colus stimpsoni* (Mörch, 1867) (West, 1979), among others.

Other species of Buccinidae, such as *Engoniophos unicinctus* (Say, 1825), have direct development without nurse eggs, hatching at the crawling pediveliger stage (Miloslavich and Penchaszadeh, 1994). In this latter species, albumin in the intracapsular liquid is the most important extra food available for the embryos (Miloslavich, 1999). Given the lack of nurse eggs and the large difference between the uncleaved egg diameter and the shell length at hatching, *Pareuthria plumbea* probably shows the same pattern of embryonic feeding on substances of the intracapsular fluid.

We found several capsules with only one embryo in an early stage of development, and the rest of them at a later stage. The absence of empty shells inside the capsule makes unlikely the possibility of cannibalism at a late developmental stage. The same was observed in *Engoniophos unicinctus* (Miloslavich and Penchaszadeh, 1994).

The fact that clusters formed by several egg masses of *P. plumbea* are common could indicate a gregarious spawning behavior as demonstrated for several other neogastropods (D'Asaro, 1970) and particularly for some buccinids such as *E. unicinctus* (Miloslavich and Penchaszadeh, 1994).

The egg capsules of some buccinids present a preformed exit hole or plug. This is the case, among others, of *Buccinum undatum*, *B. hydrophanum* Hancock, 1846 (Thorson, 1935) and all the species of the genus *Colus* (studied by Thorson, 1935 and 1946 as *Sipho*), including *C. jeffreysianus* (Fischer, 1868) (= *C. howsei* in Lebour, 1937). In other buccinids the escape of hatchlings takes place through a wide slit that is situated in different positions according to the species (e.g., *Neptunea antiqua* (Linnaeus, 1758), *Beringius turtoni* (Bean, 1834)), or by an aperture following the suture line of the egg capsule, as in *E. unicinctus* (Miloslavich and Penchaszadeh, 1994). Despite the presence of a suture line in the egg capsules of *P. plumbea*, the opening does not occur along this line, but by rupture or dissolution of the capsule wall in an apparently random location on the thin basal membrane.

The large egg capsules of *Volutopsius norvegicus* (Gmelin, 1791) and *Pyrulofusus deformis* (Reeve, 1847) do not have any kind of exit hole (Thorson, 1940). This is also the case in *Pareuthria plumbea*, although its egg capsules are clearly smaller.

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LITERATURE CITED

Amio, M. 1963. A comparative embryology of marine gastropods, with ecological considerations. Contribution from the Shimonoseki University of Fisheries 12: 229–358.

Bandel, K. 1975. Embryonalgehause karibischer Meso- und Neogastropoden (Mollusca). Akademie der Wissenschaften und der Literature, Mainz 1: 1–133.

Bandel, K. 1976. Morphologie der Gelege und ökologische Beobachtungen an Buccinaceen (Gastropoda) aus der [illegible] Karibischen See. Bonner Zoologische Beiträge [illegible]

[illegible] 1970. Egg capsules of prosobranch mollusks [illegible] and the Bahamas and notes on spawn- [illegible] Bulletin of Marine Science 20: 414 [illegible]

Dell, [illegible] mollusca of the Royal Society Expe[illegible] Chile, 1958–1959. Records of the Domi[illegible] 253.

Fioroni, P. 1966. Zur morphologie und embryogenese des darmtraktes und der transitorischen organe bei Prosobranchiern (Mollusca, Gastropoda). Revue Suisse de Zoologie 73: 621–876.

Gallardo, C. S. and P. E. Penchaszadeh. 2001. Hatching mode and latitude in marine gastropods: revisiting Thorson's paradigm in the southern hemisphere. Marine Biology 138: 547–552.

Lebour, M. 1937. The eggs and larvae of the British prosobranchs with special reference to those living in the plankton. Journal Marine Biological Association of the United Kingdom 22:105–166.

Martel, A., D. H. Larrivee, K. R. Klein and J. H. Himmelman. 1986. Reproductive cycle and seasonal feeding activity of the neogastropod *Buccinum undatum*. Marine Biology 92: 211–221.

Miloslavich, P. 1999. Nutritional value of the intracapsular liquid of *Engoniophos unicinctus* Say, 1825 (Caenogastropoda: Buccinidae). Journal of Molluscan Studies 65: 522–523.

Miloslavich, P. and P. E. Penchaszadeh. 1994. Spawn and development of *Engoniophos unicinctus* (Say, 1825) (Gastropoda: Prosobranchia) from the southern Caribbean Sea. The Veliger 37: 425–429.

Miloslavich, P. and L. Dufresne. 1994. Development and effect of female size on egg and juvenile production in the neogastropod *Buccinum cyaneum* from the Saguenay Fjord. Canadian Journal of Fisheries and Aquatic Sciences 51: 2867–2872.

Philippi, R.A. 1844–1851. Abbildungen und Beschreibungen neuer oder wenig gekannter conchylien herausgegeben. 2. Cassel.

Portmann, A. 1925. Der einfluss der Nähreier auf die Larven-Entwicklung von *Buccinum* und *Purpura*. Zeitschrift für Morphologie und Ökologie der Tiere 3: 526–541.

Rivest, B.R. 1983. Development and the influence of nurse egg allotment on hatching size in *Searlesia dira* (Reeve, 1846) (Prosobranchia: Buccinidae). Journal of Experimental Marine Biology and Ecology 69: 217–241.

Strebel, H. 1905. Beiträge zur Kenntnis der Molluskenfauna der Magalhaen-Provinz. 3. Zoologischen Jahrbüchern. Abteilung für Systematik, Geographie, und Biologie der Tiere 22: 575–666.

Thorson, G. 1935. Studies on the egg-capsules and development of arctic marine prosobranchs. Meddelelser om Grønland. Kommissionen for Videnskabelige Undersøgelser I Grønland 100: 1–71.

Thorson, G. 1940. Notes on the egg-capsules of some North-Atlantic prosobranchs of the genus *Troschelia*, *Chrysodomus*, *Volutopsis*, *Sipho* and *Trophon*. Videnskalige Meddelelser fra Dansk naturhistorisk Forening i København 104: 251–265.

Thorson, G. 1946. Reproduction and larval development of Danish marine bottom invertebrates with special reference to the planktonic larvae in the Sound (Øresund). Meddelelser fra Komissionen for Danmarks Fiskeri- og Havundersøgelser. Serie: Plankton 4: 1–523.

West, D. L. 1979. Nutritive egg determination in *Colus stimpsoni* (Prosobranchia: Buccinidae). American Zoologist 19: 956.

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