CONTENTS

Eugene V. Coan
Recent eastern Pacific species of Sanguinolaria and Psamotella (Bivalvia: Psamohiidae).......................... 1

Walter Narchi
The anatomy and functional morphology of Tivela ventricosa (Gray, 1838) (Bivalvia: Veneridae)..... 13

Fábio di Dario
Bernd R. Schöne
David Bentley
Use of HMDS (hexamethyldisilazane) to dry organic microstructures in etched bivalve mollusk and barnacle shells.................................................. 25

Philippe Bouchet
Gone with the wind: a pelagic marine species described as an endemic land snail from the Bahamas........ 32

Note

Michael Rex
Biogeography of the deep-sea gastropod Palazzia planorbis (Dall, 1927): an uncommon form of rarity... 36

Notice.................................................................................................................. 24
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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, 1964, 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 *Heterolunax* (Coan, 1973: 46–46) and *Gatri* (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 (1850). 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 synonomy includes 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 beach drift. 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; SBMNHL, Santa Barbara Museum of Natural History, Santa Barbara, California, USA; SDMNH, San Diego Museum of Natural History, San Diego, California, USA; UMM, 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.
Table 1. Key differentiating characters, size, and frequency of Eastern Pacific Sanguinolaria and Psammodella

<table>
<thead>
<tr>
<th>Species</th>
<th>Color Description</th>
<th>Shape Description</th>
<th>Pallial sinus Details</th>
<th>Maximum Size, mm</th>
<th>No. Lots Studied</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>S. ovalis</em></td>
<td>white, with pink beaks</td>
<td>equivelar, ovate,</td>
<td>greatly expanded, pointed dorsally, meets pallial line at</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>equilateral</td>
<td>approx. 50° angle</td>
<td>34</td>
<td>20</td>
</tr>
<tr>
<td><em>S. tellinoides</em></td>
<td>purplish red</td>
<td>equivelar, ovate-elongate, longer posteriorly</td>
<td>expanded dorsally, meets pallial line at approx. 75° angle</td>
<td>72</td>
<td>79</td>
</tr>
<tr>
<td><em>S. tenus</em></td>
<td>white</td>
<td>equivelar, ovate-elongate, longer anteriorly</td>
<td>greatly expanded, pointed dorsally, meets pallial line at approx. 75° angle</td>
<td>34</td>
<td>4</td>
</tr>
<tr>
<td><em>P. burti</em></td>
<td>purplish red</td>
<td>right valve more inflated, elongate, longer posteriorly</td>
<td>elevated, rounded dorsally, meets pallial line at approx. 30° angle</td>
<td>93</td>
<td>98</td>
</tr>
</tbody>
</table>

Total lots studied: 198

SYSTEMATICS

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

*Sanguinolaria* Lamarck, 1799, S4.
Type species by monotypy: *Solen sanguinolentus* Gmelin, 1791:3227.

**Description:** Equivelar, with a narrow posterior cape. *Periodinacfum* thin. Pallial sinus deep, moderately to very elevated dorsally, its dorsal line with an expanded muscle attachment area just anterior to posterior adductor. Posterior crumiform muscle scar without a small anterior satellite scar. Hinge narrow to moderate in width; teeth small; nympha weak.

*Sanguinolaria ovalis* Reeve, 1857

Figures 1, 2, 9

*Sanguinolaria ovalis* Reeve, 1857; pl. 1, fig. 2; Mörch, 1860. 185; Carpenter, 1864: 563 [1862 reprint: 49] [as a possible synonym of *S. minutissima*]; Tryon, 1869: 75; Beria, 1880: 84; Dall, 1895: 61 [as a synonym of *S. tellinoides*]; Keen, 1958: 188, 189, fig. 140 [as a separate species]; Keen, 1974: 243, fig. 164. 244 [not to be confused with *Bittadia ovalis* Beria, 1889: 92 pl. 1, fig. 5a, b, a species of *Solettia* described from an unknown locality].


**Description:** Oval, equivelar, thin, approximately equivalent in size; 18-50% from anterior end; anterior end rounded, posterior end acutely rounded, without a radiate process. Pallial sinus large, much extended and pointed posteriorly meeting pallial line at an approximately 50° angle, producing a short extent of non-confluence of the mantle, of fine commarginal striae. Color pink, with orange becoming white toward ventral margin; color both exteriorly and interiorly. Length to 312 mm; PRI 25921: Guanacaste, Panama.

**Type Material and Localities:**

*Sanguinolaria ovalis*—BMNH 1957.7.15.1, holotype, with broken right valve, length: 222 mm, width: 140 mm, left valve, 31 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 vesperina*—ANSP 150013, holotype pair, length: 311 mm, width: 209 mm, length: 11.5 mm [Fig. 2]. ANSP 398778, paratypes, length: 26.4 mm, SDNHM 5077.5, paratypes, 6 pairs, 2 valves. San Juan del Sur, Rivas Province, Nicaragua (11.3° N, HN. Lowe, 1931). ANSP 154065, paratypes, left valve, length: 207 mm. Cornito, Guanacaste Province, Nicaragua (12.5° N, H. N. Lowe, 1931).

**Distribution:** Guanacaste, Sonora, Mexico (27.9° N) [CAS 154569], to Guanacaste, 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, 96363], or labeled as *Sanguinolaria sp. [Kaiser collection]*, while closer resembling a *Sanguinolaria*, has conspicuous lateral teeth, a long, elongate pallial sinus, and slightly oblique commarginal sculpture. This material is instead *Tellina (Hertella) nigrovittata* Hertlein and Strong, 1949 (pp. 53-56; 97, pl. 1, figs. 23-26) (see also: Olsson, 1961: 40).

**Discussion:** This species is very similar to its western Atlantic homologue, *S. sanguinolenta* (Gmelin, 1791: 3225—as *Solen*) [synonyms: *Solen fluxuus* Spengler, 1791; 111; *Tellina ritchaduna* Röding, 1798: 186; *Sanguinolaria rosae* Lamarck, 1801: 125; Lobaria roseaera Schumacher, 1817: 122-123, pl. 6; *Sanguinolaria nitric* Mörch, 1853: 410], 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 such a large size (S. sanguinolenta can attain at least 13.1 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
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. *Sanguinolatoria rosea* Lamarck is not preoccupied by *Solen roseus* Gmelin, 1791 (p. 3227), which was based on a figure in Cuvier (1782: pl. 14, fig. 55) that seems to be a *Solenellina.* This species was attributed to the Red Sea by Bertin (1840: 98). It is also not preoccupied by *Tellina rosea* Gmelin, 1791 (p. 3228), which is based on an illustration in Knorr (1771: pl. 9, fig. 3) that may be of a specimen of *Asaphis deflorata* (Linnaeus, 1758: 657, as Venus).

*Sanguinolatoria vitrea* Deshayes, 1855 (p. 326), described from an unknown locality (see also Reeve, 1857: pl. 1, fig. 1), 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, Mexico. However, if material in the SBMN11: 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 SBMN11 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.

*Sanguinolatoria aureocincta* Martens, 1879 (p. 744)
Sanguinolaria tellinoides A. Adams, 1850
Figures 3-6, 12


Description: Ovate-elongate, equivale, somewhat thick-shelled than S. oralis at a similar size, becoming more thickened in large specimens; posterior end somewhat long-lasting without a distinct area anterior end somewhat rounded and produced, set off by a rounded median ridge as approximately two-thirds distance from anterior end, a most evident in large species, in other cases indistinct and pointed dorsally, becoming pointed at the end of the ventral margin thus completing the oval outline (Figure 12). Sculptural columnar are with ovate oval or rounded oval muscle scars in large specimens, the color pink to purplish, sometimes the shell has a marginal color band, internal pallial color extending length to 71.5 mm (ANSP 259203; from the Philippine islands Willan, 1993: 61).

Type Material and Localities:
Sanguinolaria tellinoides—BMNH 19665401, pair, lectotype here designated, length 32.6 mm, height 19.2 mm, width 8.4 mm (Figure 3). BMNH 19665402, 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 76.A.1.4. T.2ellina miniata—MCZ 169255, holotype, pair length 51.0 mm, height 33.0 mm, width 14.3 mm (Figure 4). San Juan del Sur, Rivas Province, Nicaragua (11.7°N); Lichten, T. P. Green, 1964: 110 as being in Orange County, California.

Sanguinolaria purpurea—BMNH 19665391, lectotype here designated, pair, length 50.0 mm, height 31.7 mm, width 15.1 mm (Figure 5). BMNH 19665392, 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 76.A.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, Chinandega Province, Nicaragua] (12.5°N); A. S. Oersted, 1846-1848.

Distribution: Punta Pescadero, Pacific coast of Baja California Sur (23.5°N) [USNM 229641], into the Gulf of California as far north as Punta Diggs, Baja California (30.9°N) [CAS 150031], and Puerto Libertad, Sonora (29.9°N) [ANSP 184183], Mexico, to Cojimíes, Esmeraldas Province, Ecuador (0.4°N) [PRI 259208]; intertidal zone to 14 m. Material examined: 79 lots. Sanguinolaria tellinoides has been reported from the Phoeoeana James Formation at Puerto Luna, Manabi Province, Ecuador (0.2°S) (Pilsbry and Osborn, 1941: 72), and as "aff. c") from the late Miocene Catan Formation on the Atlantic coast of Panama west of Colon (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 Psemnomella bertinni in being equivale, and by its more rounded outline, less attenuate posterior end, and more dorsally extended and pointed pallial sinuses.

Sanguinolaria tenuis Osborn, 1961
Figure 7, 13


Description: Ovate-elongate; equivale; anterior end somewhat longer than the other at 41% 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 sinuses large, extended dorsally, meeting pallial at an approximate 75° angle (Figure 13). Sculpture of...
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 (1.8°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 (1.8°S, specimen missing), Ecuador. Both specimens were collected in beach drift.
Figure 5. 6. 5. Lectotype of *S. purpurea* Deshaves. length 50.0 mm. 6. Holotype of *S.*
Figures 7, 8. 7. *Sauguinoloria tenuis* Olsson; holotype, length 33.8 mm. 8. *Psammotella bertini* Eilinsky and Lowe; neotype of *Tellina baileyi* Bertin; length, 63.5 mm.
Discussion: This is the rare South American ally of S. orallis. It differs in not having rose-colored beaks, in being thicker shelled, and in having a more rounded posterior end.

Genus *Psammotella* Herrmannsen, 1852


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; nysthm weak.

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

*Psammotella bertini* (Pilsby and Lowe, 1932)

Figures 8, 14

*Tellina bertini* Bertin, 1878: 268–269 [nor *Tellina bertini* Dunker, 1853: 53–54, pl. 10, figs. 1–6].


Description: Shell inequivalve, right valve more inflated; posterior end rounded; beaks at 40–18°; posterior end rounded; posterior cilia, anterior cilia with radial sulci 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 line, 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 92.5 mm (LACM 71–179.12, Punta Pequeña, Baja California Sur, Mexico).

Type Material and Locality: *Tellina bertini* was based on the figure of *Tellina refuscens* "Chemnitz" in Hanley (1846; see above), which presumably came from the only locality mentioned—Tunibes, Tunibes 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 Pilsby 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 refuscens* 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 Tunibes, Peru, and (4) Pilsby and Lowe’s "type" is a fine specimen long accorded type status, *this specimen is here designated neotype of Tellina bertini*. 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 (27.5°N) [ANSP 225928], La Paz, Baja California Sur (24.2°N) [SBMN 1965: 24586, 24587], and Empalme, Sonora (27.9°N) [SBMN 1965: 15579], Mexico, to Mancora, Tumbes Province, Peru (4.1°S) [CAS 154570, SBMN 1956: 12566], and evidently as far south as Colón, Piura Province, Peru (5.0°S) (Paredes and Cardozo ms; Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru); intertidal zone to 17 m. Material examined: 98 lots.

Figures 9–15.

1. Figures 9–15, shells of *Sangunolalaria* and *Psammotella* showing hinge, pallial sinus, and adductor scars of left and right valves.

Guatemala: CAS 150375, Acapulco, Guerrero, Mexico; length, 26.2 mm. 10, S. *sangunolalaria* Gmelin, CAS 150375, Acapulco, Guerrero, Mexico; length, 26.2 mm. 10, S. *sangunolalaria* Gmelin, CAS 150375, Acapulco, Guerrero, Mexico; length, 26.2 mm. 10, S. *sangunolalaria* Gmelin, CAS 150375, Acapulco, Guerrero, Mexico; length, 26.2 mm. 10, S. *sangunolalaria* Gmelin, CAS 150375, Acapulco, Guerrero, Mexico; length, 26.2 mm.

Veracruz, Mexico: length, 66.6 mm. 15, *Psammotella* bertini Pilsby and Lowe, CAS 150390, Acapulco, Guerrero, Mexico; length, 66.6 mm. 15, *Psammotella* bertini Pilsby and Lowe, CAS 150390, Acapulco, Guerrero, Mexico; length, 66.6 mm. 15, *Psammotella* bertini Pilsby and Lowe, CAS 150390, Acapulco, Guerrero, Mexico; length, 66.6 mm. 15, *Psammotella* bertini Pilsby and Lowe, CAS 150390, Acapulco, Guerrero, Mexico; length, 66.6 mm. 15, *Psammotella* bertini Pilsby and Lowe, CAS 150390, Acapulco, Guerrero, Mexico; length, 66.6 mm.
Discussion: *Psammotella bertini* is very similar to its western Atlantic homologue, *P. cruenta* ([Lightfoot](https://www.jstor.org/stable/20308510), 1786), see under genus. [Synonyms: *Tellina operculata* Gmelin, 1791; 3235—*T. operculatus* in Linnaeus printing; *Tellina fuscata* Dillwyn, 1817, 55, ex Chenuitz ms]. The last synonym is non *T. fuscata* Gmelin, 1791: 3235, which was based on Galtieri (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 (1837b: 32). *Psammotella cruenta* occurs throughout the Caribbean to Brazil. *Psammotella cruenta* differs from *P. bertini* in being more inequilateral, with a flatter 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) thought 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 smithii* (Murray, 1917: 303–304 | = 229–230], pl. 64 | = 38], figs. 1, 2—as *Sanguinoloria* (*Psammotella*), from the late Miocene Cercado Formation of the Dominican Republic is presumably ancestral to these two species. Murray 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 albata* Olsson (1922: 432–433 | = 260–261], pl. 32 | = 29], figs. 5, 6—as *Sanguinoloria* (*Psammotella*) [sic] from the late Miocene Catun 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 comparison with *Sanguinoloria tellinoides*, see species.

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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 Yonie, the eulaema of type C 1 of Atkins, the relation between the labial palps and the eulaema belong to category II of Stasek, and the stomach to type V of Panchen.

**INTRODUCTION**

The Veneridea 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; Goos et al., 2000).

Isolated references to *Tivela ventricosa* (Gray, 1838) are found mainly in regional checklists (Lange de Morre, 1949; Goffé, 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 (Goffé, 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 Carbomaronium F4, 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 equivale, equilateral, trigonal, with subcentral umbo-
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 incumbent 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 incumbent 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 incumbent siphon is very sensitive to touch and vibrations and withdraws in part or completely upon stimulation.

The excurrent siphon aperture (Figure 6) is smaller than the incumbent siphon 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 incumbent 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 incumbent 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 supraventral 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 incumbent siphon. Dorsally to these fused ventral margins, the highly mobile additional siphonal membranes delimit a canal. The free edge of the mantle has 1 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...
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 incumbent siphon.

Figure 2. *Tixela ventricosa*. External view of shell valves showing variation in color pattern. Scale line = 2 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.
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 heterorhabdite (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 axis.

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 ctenidial 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
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 ciliary currents on the palps (Figure 11) were recognized:

- Acceptance currents: currents that conduct particles towards the oral opening of the mouth. These currents are present on the crest of each palp.
- Sorting currents: currents that sort particles into different grooves. These currents are present on the floor of troughs between the grooves on the lower half of the palps.
- Rejection currents: currents that reject particles into the groove. These currents are present on the crest of each palp.

Additional currents that must be taken into account when considering the function of the palps in sorting food particles are considered. The palps of *T. ventricosa* are relatively active. The pleats 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 palps are exposed. Large particles falling into the troughs of the grooves are rejected, while the smaller ones are trans-
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 posterior-ventral 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 musle, 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
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**

*Tirlea ventricosa* is restricted to sandy beaches directly exposed to wave action. The species is not found in shel-
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. Goffené (1950) found *T. ventricosa* on open seashores, co-occurring with the venerid bivalve *Amiantis purpurata* (Lamarck, 1810), *Ticela ventricosa*, like *Ticela saltorum* (Lamarck, 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 *Ticela* 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 Goffené (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 *Ticela saltorum*. 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 flow 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 incumbent apertures in *T. ventricosa*.

The siphons of *T. ventricosa* are similar in structure and shape to those described for *T. saltorum* (Weymouth, 1920, 1923) and *T. mactroides*. The incumbent 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 58 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 pseudobranchs 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 incumbent stream, or may be drawn downward to direct the stream toward the mantle edge, and away from the gills, such as when much sediment is present. In this latter 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 incumbent 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. crusataeoides* (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 Garcia and Narchi (2000) also showed for *Protothaca.Leukoma.pictorum* (Lamarck, 1818).

The surface of the mantle in *T. ventricosa* has centrally directed cleansing ciliary currents, similar to that observed by Ansell (1961) in some Veneridae 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. _Tivda ventricosa_ Interior of stomach, seen from right side after opening by incision in the right wall. af, anterior fold; bs, beaded swellings; dd, digestive diverticula; dh, dorsal hood; e, esophagus; gs, gastric shield; ig, intestinal groove; lc, left caecum; ls, left pouch; ml, minor typhlosole; n, right caecum; mt, mouth ring; sa, principal sorting area of the dorsal hood; sa3, sorting area of the left pouch; sa7, sorting area below esophageal orifice; ss, style sac; ty, typhlosole.

of the free edge carrying particles towards the mouth. As noted by Vasell (1961), _Venerupis aurea_ (Gmelin, 1791) and _Mysiva ventricosa_ (Pennant, 1777) and members of _Venus_ Linne, 1758 and _Mytilus_ Linné, 1758, present an incipient current directed toward the mouth at the free edge of the outer lip.

The pattern and morphology of the ctenidia and their ciliation in some Veneroida. The ctenidia in _T. ventricosa_ belong to Type C1 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 brasiliensis_ (Gmelin, 1791) and _Chione subrostata_ (Lamarck, 1818), respectively. In _T. ventricosa_ the ctenidial ciliation is of Type G(2) of Atkins (1937b).

The labial palps of _T. ventricosa_ show the same basic
features of other species of Veneroidae 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 associated 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 right ceca 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 phyllosome or the intestinal groove, as described by Purdon (1960) for Gastrothoa minimum (Montagu, 1817) and T. mactroides.

The stomach of T. ventricosa has the structure of a typical suspension-feeding lamellibranch. It is similar to those of the venericides Glossus lamnaus (Linnaeus, 1758), G. mimimum, Venus casusa Linneus, 1758, and T. mactroides, as described by Owen (1953), Purdon (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


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's 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 $4,500.

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 mollusks (Chione fluctifrons) and barnacle shells (Chthalamus 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 (Maun, 1983; Simkiss and Willbur, 1989; Grencher, 1988 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, 1984). 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 analysis), superficial etching is commonly used to aid in the identification and measurement of internal growth increments in molluscan and barnacle skeletons (Rhoads and Lutz, 1950; 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 molluscan 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 hard parts. Both mollusks (e.g., Davenport, 1939; 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, 1990). 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 CO₂, e.g., Clark, 1980 or Freon 113 as a transitional fluid, e.g., Koike, 1984). 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 H, Kennedy et al. (1989). However, preparation following this technique takes more than twice the time as CPD, and Peldri H is no longer available because of environmental hazards. Fluids with low surface tension (acetone or propylene oxide, Boyle and Wood, 1969) sometimes produce reasonable, artifact-free results for biological soft tissues. Some workers prefer the extremely hazardous osmium tetroxide technique (Quattrellmann and Garner, 1980).

A reliable and simple drying technique, which produces results qualitatively comparable or superior to
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 (CH₃)₃SiNH, 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, 1963; Rumph and Turner, 1999), soft tissues of mollusks (Leal and Simone, 1998), vertebrates (Heegaard et al., 1996; Weyra et al., 1990), microorganisms (Dekker et al., 1991; Hochberg and Litwatt, 2000) or pollen (Chissoci 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 mollusk 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 55), specimen no. ST11-A18; three Chione fluctuifraga Sowerby, 1853) specimens collected alive at North Orca in November 1999 (N31 32 60, W114 52 75), specimen no. NO3-A105, NO3-A106, NO3-A108; and three C. fluctuifraga specimens from Isla Sacatosa (N31 29 60, W114 50 55), 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 matrix, rinsed with water and dehydrated with ethyl alcohol. 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. fluctuifraga shells no. ST12-D1, -D2, and -D3. Figure 2, using a low speed Buchler™ 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 shells. In this study we focused on the composite prism and shell layer of C. fluctuifraga, because they are of primary concern in sclerochronological studies. In the cross-sectioned shells of C. fluctuifraga 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 Al₂O₃ powder), and polished on laps (9, 6, and 0.3 μm Al₂O₃ 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. fluctuifraga 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 (ethylenediamine 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. fluctuifraga and Chthamalus sp. Schöne et al., 2002, and unpublished data. For the presentation of microstructures in C. fluctuifraga 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

Figures 1, 2. Positions in the shells, where the samples Figures 3-16 were taken. dog = direction of growth, direction in which subsequent growth increments were added. 1. Cross-section through the parietal 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 fluctuifraga shell. Samples for Figures 6-9 were taken from the growing edge of the inner shell surface. Samples for Figures 10-16 from the outer shell surface. In radial cross-sections, growth patterns become apparent in the outer shell layer. Figures 9-13.
the samples were rinsed in a series of graded EtOH (40%, 60%, 80%, 100%, 30 min each). The HMDS technique includes immersion of the dehydrated samples in 97% hexamethyldisilazane (Aldrich™ chemical; two times for 30 min each) followed by 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 CO2 allowed to enter the chamber. Free alcohol was flushed from the chamber until dry ice was seen exiting. The sample remained in CO2 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 CO2 = 32°C). CO2 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 kV. 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 periostracum (Figure 1) shows partly dissolved calcite crystals in a crisp three-dimensional mesh of organic fibers when dried from HMDS (Figure 2). CPD results in a less well-dried organic framework (Figure 3). 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 4). Some growth layers disappear partially or entirely when immediately air-dried after etching (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 AR 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 Chione fluctifera (see Schöne et al., 2002). CPD 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, multilayered organic network when dried from HMDS (Figure 14). Growth lines cannot be seen any more. Applying the ALC 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
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 fail 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 a vacuum chamber like in the CPD apparatus. Furthermore, by diffusion constraints, HMDS drying is less prone to artifacts, like CPD, because it does not require high vacuum processing which may represent some danger and to the operator.

**Disadvantages of the HMDS technique:** Thick organic material: These artifacts may result from HMDS itself or from the high molar concentration of the sol. The latter problem may be solved by using ALC and Pd/Pt treated soft tissues. It is not clear if additional dehydration and dehydration and HMDS treatment may enhance and harden the organic meshwork (Wilson and Denny 1993) and dentine with formalin reported to harden the structural arrangement of the organic fabric (Carvalhio 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.

**ACKNOWLEDGMENTS**

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

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ABSTRACT

Abacornia naufragia (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 Lituopidae melanostoma Rang, 1829 (Gastropoda, 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 (Darcinia, Kalotho, Troctropoma) or potentially valid (Hypnina), one (Brandilia) has been suppressed by the ICZN, and the other five (Abacornia, Africornia, Amaplocannus, Bullinopera, Pseudobolama) are synonyms.

INTRODUCTION

William J. Clench (1938) described Leptinaria (Abacornia) naufragia as a new subspecies and species in the pulmonate family Subulinidae, based on specimens collected by J.C. and C. Greenaway 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 Cujana 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 Abacornia is not mentioned at all by Zilch (1959-60) in the pulmonate volume of the standard Handbuch der Paläozoologie. Abacornia has recently been elevated to genus level by Clench (1989: 513, fig. 666), and classified as a member of the family Subulinidae.

In the original publication, Clench noted that "this species is completely different from all others known to him in the pulmonate. The remarkably acute apex and the sculpture from axial on the first whorl to the shoulder of the remaining whorls is sharply different from the species and the thickening of the shell and aperture is unique to the genus." He speculated that Leptinaria naufragia and two other endemic pulmonate snails are remnants of a much older fauna and speculated on the relationships. However, examination of the type material in MCZ-Figs. 1-3) reveals that Abacornia naufragia is not a subulinid, and not even a pulmonate, but a synonym of Lituopidae melanostoma, a circumtropical pelagic cerithoid (Figs. 4-6). Clench and Schlyevo had properly described the apical sculpture of Abacornia, but had failed to recognize its identity. The protoconch of Lituopidae melanostoma consists of four whorls with strong axial ribs, abutting axially on the preceding whorl and interrupted by a smooth band on the shoulder. The protoconch teleoconch discontinuity is marked by a sinuigera notch (Buque et al., 1988: 182, fig. 1, 4).

Lituopidae 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 (Buque et al., 1988).

SYSTEMATICS

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

New synonym:
Abacornia Clench, 1938. Type species: Leptinaria (Abacornia) naufragia Clench, 1938. by original designation

New synonym:
Lituopidae melanostoma Rang, 1829

New synonym:
Leptinaria (Abacornia) naufragia Clench, 1938. 321, pl. 24, figs 1-2.

Abacornia naufragia - Schlyevo, 1999: 541, fig. 666.

Type Material: Holotype MCZ 116705; 4 paratypes, MCZ 116706; 1 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-
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 molluscans literature is problematic, and it may be useful to take the case of the Abaco 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 (Digoniopsis), one (Brondelia) has been suppressed by the ICZN, and the other five (Abacoa, Afrocanidea, Anaplocamus, Bullinomopalia, Pseudohabitatia) are synonyms.

**Daronia A. Adams, 1861.** Based on a specimen from the Cuming Collection, Cyclostroma. *Daronia spirula A. Adams, 1861,* was described as a new subgenus and species of marine gastropod from the Philippines. Warén and Bouchet (1985) showed that it is a South American species of the land snail family Poteriidae. *Daronia A. Adams, 1861,* being a senior synonym of *Buckleya Higgins, 1872.*

**Brondelia Bourguignat, 1862.** Described as a new genus of Ancyliidae, with two species, *B. droniata Bourguignat, 1854,* 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-
cyllidae until Marshall (1981) recognized it as identical with the marine pulmonate Williamia Monterosato, 1884 [family Siphonariidae]. Incidentally, the name *Brotula* 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 *Cerithoides* Férussac, 1814 [family Cerithiidae], and by Schileyko (1999) as a full genus.

**Pseudolobania Stefani, 1879.** *Dandybardiaria tarentina* Stefani and Fantanelli, 1879, was described as a land snail from the hills near Taranto in southern Italy. It was made the type species of a section Pseudolobanja Stefani, 1879, of *Dandybardiaria* Hartmann, 1821 (family Dendrobardiidae), later elevated to full genus by Foreca (1950). Zilch (1959) has shown that *D. tarentina* is a synonym of *Susiana testulata* Cantraine, 1835, and *Pseudolobania* a synonym of *Susiana* Gray, 1857 [family Pleurobranchiidae].

**Teretropoma Rochebrune, 1881.** Immediately after its description, based on live-taken specimens from the *Doliolidae* of the Senegal of *Teretropoma perrieri* by Rochebrune, 1881, as a new genus and species of *Cypraeidae*. This was a new subfamily *Teretropomidae*, but it was not recognized as an architectonic subfamily until 1892. *Teretropoma* is current, but its type species is *Heteropsis* from *Cypraeidae*, *Teretropoma* was the type material of *Heteropsis* from the Atlantic subspecies of *Heteropsis* by Foreca (1950).

**Digoniopsis Jouy., 1881.** *Digoniopsis iouscena* Jouy. (1881) was described as a new genus and species in the family Cerithiidae. It was described by Zilch (1959). Schileyko (1999) revised the type material and labeled it as a land snail of the family *Ferussacidae*.


digoniopsis bourguignatii was as marine family *Pterinoiidae*. Although Schileyko (1999), referring to Neubert, suggested that only an anatomical study would establish firmly the systematic position of *Digoniopsis*, the heterostrophic protoclit leaves no doubt that it is indeed a pyramidellid.

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

**Afrocarnidea Connolly, 1929.** *Afrocarnidea gemma* Connolly, 1929, was described as a new genus and species of *Buccinidae*, reputedly from Shimbhi Hills, Kenya, but the holotype was shown to be a larval shell of *Cymatium murchison* (Röding, 1798) [family *Buccinidae*], with *Afrocarnidea* Connolly, 1929, ending up in synonymy of *Guttarmen* Mörich, 1852—Ben, 1999.

**Bullinopersilia F. Nordsieck, 1972.** Based on a single empty shell, *Bullinopersilia sphaceloides* F. Nordsieck, 1972 was described as a new genus and species of *Acetoniidae* from shallow water off the Ballestas, in the western Mediterranean. Schirrigio and Mariotti (1990) recognized it as a juvenile of the land snail *Ferussacia follicula* (Gmelin, 1791) [family *Ferussacidae*].

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**In Memoriam**

Tadashige Habe 1916-2001

Russel H. Jensen 1918-2001
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 (Warten 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. Warten (1991, 1993) subsequently reported the species from west of Iceland at 241 m and in the eastern North Atlantic off the British Isles from 2081–2895 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 (Grasse 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-sea abyssal plain at 5216 m.

While the shell sculpture of *Palazzia planorbis* appears to be unique among planispiral deep-sea microgastropods, there is individual variation in the expression of the axial ribs and the extent of branching. The extent of geographic variation throughout its range is unknown because of the scarcity of material and the combination of sampling localities (Table 1). However, the specimen from the eastern tropical Atlantic shown in Figure 1 is remarkably similar to those figured by Warten (1991, 57 fig. 3) and also collected in the western and eastern portions of the Mid-Atlantic Ridge from 3259 m shallower and 15° to 70°N.

Its enormous geographic 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 (Bieder 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 (1985) referred to low relative abundance throughout a species range as insuffusive 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 *Pristigonia nitens* and *P. alba* (Sanders and Allen, 1973), and *Voldiella 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. *Palazza 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.

...Terms of 2001...termed diffusive rarity. The incidence of rare deep-sea gastropods occupying broad geographic ranges is still uncertain since most taxonomic syntheses, such as Bouget 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.

Table 1. Locality data for *Palazza 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 Mariscal, 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.

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<td>3797</td>
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Figure 2. The distribution of *Palazzia planorbus* in the Atlantic; see Table 1 for station data. Circled numbers represent the number of samples yielding *P. planorbus* in that region. Circles without numbers represent individual samples.

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I thank Andrea Etter, Ron Etter, Anders Warén, Philippe Bouchet, and Carol Stuart for their comments on this paper. Jack Cook for the map of the Atlantic and Maria Papaga for helping to prepare the manuscript. The material from the Woods Hole Benthic Sampling Program was provided by Howard Sanders, and from the Atlantic Continental Slope and Rise Study by James Blake. This research was supported by the National Science Foundation Grant OCE-9301687 and by the University of Massachusetts.

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CONTENTS

Russell L. Minton
A cladistic analysis of Lithasia (Gastropoda: Pleuroceridae) using morphological characters ........................................... 39

Ricardo Vega
Rodolfo Vega
Angel A. Luque

Coraliophila kaoforum, a new species (Gastropoda: Coralliophilidae) from the Canary Islands living on Antipathes wollastonii (Cnidaria: Anthozoa: Antipatharia) ........................................... 50

Martin Avery Snyder
Fusinus dorcedeli, a new species (Gastropoda: Fasciolariidae) from the Red Sea, and range extension for two other species .................................................. 56

Helena Fortunato
The systematic position of Strombina (Ostrea: Ostreiidae) Pfeiffer, 1858 (Gastropoda: Columbellidae) .......................................................... 59

H. Lee Fairbanks
The reproductive anatomy, taxonomic status, and range of Oreohelix alpina Elrod, 1901 (Gastropoda: Pulmonata: Oreohelicidae) .................................................. 62

Notes

Bruce A. Marshall
Authorship and date of publication of Ostrea chatenensis Philippi in Kuster, 1844 (Bivalvia: Ostreidae) ........................................... 66

Paul Callomon
Tadashige Habe (1916–2001) .................................................. 67

Book review ................................................................. 69
A cladistic analysis of *Lithasia* (Gastropoda: Pleuroceridae) using morphological characters

Russell L. Minton

Department of Biological Sciences
University of Alabama
Tuscaloosa, AL 35487, USA

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 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 be 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 callos 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. genericata* Haldeman, 1840, as the type for the genus and later erected *Aegitrema* (1841). Presence of posterior and anterior calluses united *Aegitrema and Lithasia*. The primary characters separating the genera were that *Aegitrema* shells were spinous and had apertures with an anterior sinus, while *Lithasia* shells lacked sculpture and the aperture was not distinctly channelled in front as the typical *Aegitrema* (Tryon, 1873). Goodrich (1921) supported Pilsbry and Brehm’s 1896 reduction of *Aegitrema* under *Lithasia*, and *Lithasia* subsequently has stood as a single genus. Goodrich (1940) realized 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 *L. Davis, 1974* or *L. pleuroceri* (Stansby, 1971; Stein, 1975; Burch and Tottenham, 1980). Recognized *Lithasia sensu stricto and Aegitrema* as subgenera in *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 recognize *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 conical 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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yses of the implications of employing modern techniques is prudent. Many approaches of phylogenetic systematics have shown that some morphological traits do not support historically monophyletic mollusk classifications (Graf, 2000; Lydeard et al., 2000). Analyses of morphological characters do support some of taxonomic hypotheses, then the classification of these groups can be stabilized. If not, our approach to select diagnostic characters for these groups must change. Phylogenetic 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 pterygoids, 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 31 other species are presumed extinct (Stein, 1976; Bogdan et al., 1993; Lyeard and Mayden, 1995; Lyeard 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, 1998) was included. Specimens of selected taxa representing five other extant pleurocerid genera (Elminia, Io, Juga, Leptosia, Pleuroceras) 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 using maximum parsimony with NONA 2.0 (Goloboff, 1998) using the following settings: unordered data, 100 replicates, with Juga silicula and Melanides tuberculata Müller, 1774, as outgroups. Juga is basal to the rest of the North American Pleuroceridae (Holznagel and Lyeard, 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 0.9.99b24 (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 comprising of two subgenera, Lithasia sensu stricto and Angitremia, sensu Burch and Tottenham (1990). This classification is commonly used as a starting point in pleurocerid studies (e.g., Lyeard et al., 1997; Holznagel and Lyeard, 2000). Burch and Tottenham's (1990) 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 nodular sculpture (Goodrich, 1940). Lithasia hubrichti Goodrich, 1965, has yet to be described and is included in Group 3 based on Chench (1965) allaying it to Lithasia verrucosa (Rafinesque, 1820).

D. taxa presently included in Lithasia belong to one of three genera: Lithasia, Angitremia, or Angitrea, sensu Tryon (1873). In this case, the original descriptions of Lithasia and Angitremia are used to group taxa based on shell characters. Tryon failed to include Lithasia curta (Lea, 1868), and Lithasia hubrichti had yet to be described. Both species are included in Tryon's Angitremia based on their nodular shell sculpture, Lithasia genericula pinguis (Lea, 1852) = Angitremia pinguis.

E. taxa presently included in Lithasia should be considered species of Io based on developmental characters, sensu Davis (1974), Lea, 1868; and Lithasia hubrichti has yet to be described. Both species are included in Tryon's Angitremia based on their nodular shell sculpture, Lithasia genericula pinguis (Lea, 1852) = Angitremia pinguis.

A sixth scheme, Stein's (1978) recommendation that all Lithasia be considered Pleuroceras, 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 Pleuroceras acutus the type species of the genus. Mobile, 1981; see discussion in Bogdan 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 genericula pinguis in the clade of Leptosia species and the placement of Lithasia oborata (Say, 1829) in a polytomy of Io + some Elminia + ( pinguis + Leptosia) + remaining Lithasia. Analysis of all characters yielded 20 trees of 107 steps that rendered Lithasia non-monophyletic. Figure 10. Lithasia genericula pinguis specimens were basal to a clade of Leptosia species supported by a tandem-shaped apertura, and Lithasia oborata was nested between clades of Pleuroceras and Elminia species near the base of the tree. The remaining Lithasia taxa formed a clade with Io supported by three characters.
Figure 9. Closterium. Strict consensus of the 172 most parsimonious trees, 17 steps, CI = 0.74, generated using shell characters. 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 = 0.371, generated using shell and radula characters combined. Jackknife values ≥ 63% above nodes; number of unambiguous synapomorphies below nodes.
luniform 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, *Elminia*, *Leptaxis*, 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 Turgonev et al. (1998). Tryon's (1953) 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, *Elminia*, *Leptaxis*, and *Pleurocera* taxa all grouped in their respective genera. Only two *Lithasia* taxa grouped away from the others, suggesting that these two species may be misplaced. *Lithasia* *geniculata pinguis* was placed in *Leptaxis* = *Aurulna* by Tryon (1961), and subsequently placed in *Lithasia*, where it has represented the headwaters form of the *geniculata geniculata-faluginea-pinguis* complex. Based on the morphological characters examined here, *L. geniculata pinguis* should be classified as a species of *Leptaxis*.

*Lithasia obvara* is the only species in the genus that occurs in the Green River drainage of Kentucky, and has included in its nominal forms that are unquestionably *Lithasia*. *L. obvara* shells lack the calluses on the aperture, fusiform aperture, and have radulae most similar to *Elminia* species. Though, the phylogenetic analysis suggests allocation of *L. obvara* to a separate genus, I believe the addition of more taxa and pleurocerid species or more morphological characters in the analysis would resolve its generic designation. Considering *Lithasia* species would be considered *Io* to the least name for that clade.

As such, *Io* would be recovered by having a fusiform aperture (2:2), posterior callus on columella (6:1), and formation of canal of the aperture (8:1). This change would reflect the opinions of Davis et al. (1997) regarding the two genera. Within *Lithasia*, however, individual 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 (1952) 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 *obvara 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 pleurocerid genera to date, Tryon (1953) 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 (1953) believed that these characters seem to unite pleurocerids but do little to separate constituent genera and species. It is true that gastropod radulae (Padilla, 1995) 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, 1985) and in phylogenetic reconstructions shell characters often are less homoplasic 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; Holztagl and Lydeard, 2000) to identify pleurocerid genera. In these works, *Elminia* and *Pleurocera* represent natural groups, and the morphological characters support both genera. However, Lydeard et al. (1997) and Holztagl and Lydeard (2000) showed that *Lithasia* and *Leptaxis* are non-monophyletic, though the combined morphological analysis given here supports the recognition of *Leptaxis* 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.

**ACKNOWLEDGMENTS**

I would like to thank S. Alksteid, J. Garner, and D. Neely for specimens, M. Glanbrecht, P. Harris, C. Lydeard, and F. Strong provided helpful comments on the manuscript.
LITERATURE CITED


Appendix 1. Systematic list of taxa used in the cladistic analysis of the genus *Lithia* (n = 1 for each taxon). Classification follows Turgeon et al. (1988); taxa are named as in Burch (1989). 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.

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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 columnella. (0) absent, (1) present.
7. Anterior callus on columnella. (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) lamellate, (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) rounded.
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. Continued

- Leptoxis amphi
- Leptoxis crosa anthonyi
- Leptoxis pleata
- Leptoxis praeusa
- Leptoxis tarmata
- Leptoxis virgata
- Elimia abalamaensis
- Elimia calendura
- Elimia hopkei
- Elimia olivula
- Jaga siliula
- Pleurocera canaliculatum filum
- Pleurocera prosimianum
- Pleurocera walkeri
- Melanoles 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.)

<table>
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<tr>
<th>Turgon et al., 1998</th>
<th>Burch and Tottenham, 1980</th>
<th>Goodrich, 1940</th>
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Coralliophila kaofitorum, a new species (Gastropoda: Coralliophiliidae) from the Canary Islands living on Antipathes wollastonii (Cnidaria: Anthozaa: Antipatharia)

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ABSTRACT

A new species of Coralliophila from the Canary Islands living on the antipatharian Antipathes wollastonii 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 cayenae 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 Coralliophiliidae are included.

INTRODUCTION

The family Coralliophiliidae 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 protococh usually eroded in adults and even in young specimens, and the poor knowledge of anatomy and biology, have led to a confused taxonomy of the family that makes the generic allocation of species difficult. The Coralliophiliidae has been traditionally considered as a subfamily closely related to Muricidae, but Ponder (1970) and Kantor (1985, 1995) have proposed Coralliophiliidae as a subfamily of Muricidae. This taxon has not been accepted by some subsequent authors (i.e., Riedel 2000). However, distinctions in fore and gill anatomy to previously assign the coralliophiliids into two different families. Since the taxonomic positions of the Coralliophiliidae is currently uncertain, we 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 Maglin and Leptocochus, 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). Only a large number of species (about 50) are included in the genus Coralliophila, and Adams, 1853, but this genus still needs to be better defined. Most coralliophiliids feed on scleractinian corals, but there are also species that feed on Gorgonacea, Corallimorpharia, Zanichellidae, Miller, 1981; Robertson, 1970, 1981; Wicksten and Wright, 1993; Actinaria (Spada, 1979; Oliverio, 1989a, b; Poppo and Goto, 1991), continental West Africa (Kinsela, 1956; Bernard, 1984; Takacera, 1975; Gócas, Pinto-Afonso and Brandão, 1985; Kosuge and Fernandes, 1988; Smigliolo and Mariottini, 2000), deep waters of the northeastern Atlantic (Bonete and Walen, 1985), Cape Verde Islands (Cesel, 1982), São Tomé Island (Kosuge and Fernandes, 1988), the Ryukyus, and the Philippines and the Red Sea (Kosuge and Fernandes, 1989, 1990), Saint Helena Island (Smith, 1980), and Tristan da Cunha Island (Watson, 1986). Four spe-
cies were recorded from the Canary Islands by Nord- 
sieck and García-Talavera (1979): Coralliophila meyen- 
dorffii (Calcare, 1845); C. brevis (Blainville, 1832); 
Babelomorpha carinaferus (G. B. Sowerby, 1834) (as Cor-
alliophila bubels) (Rénquen, 1849); and Coralliophila rich- 
ardi (P. Fischer, 1852) (as C. lactea (Dall, 1889)). 
In addition to C. richardi, two additional deep-sea spe-
ies are known from the Canary Islands: C. squamosa 
(Bivona, 1838) and C. basilis (Dantzenberg and Fi-
scher, 1896) (Bouchet and Warén, 1985). Finally, Cor-
alliophila fontanangiyo Smirghio and Mariottini, 2000, 
has been recently described from Tenerife.

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

Institutional abbreviations used in this work are: BAU, 
Dipartimento di Biologia Animale e dell'Como, “La 
Sapienza” University, Rome, Italy; MCNB, Museo Na-
cional de Ciencias Naturales, Madrid, Spain; MCNT, 
Museo de Ciencias Naturales de Tenerife, Tenerife, 
Spain; DBUA, Departamento de Biologia, Universidad 
Autónoma, Madrid, Spain.

SYSTEMATICS

Superfamily Muricoidea Rafinesque, 1815
Family Coralliophilidae Chou, 1859
Genus Coralliophila H. and A. Adams, 1853

Type species: Fusus wrighti Lamark, 1816, by 
subsequent designation (Iredale, 1912). Recent, Indo-
Pacific.

Coralliophila kaefitorum 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-
form; 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 3 1/2–4 whorls, 1 mm length, 940 
µm width, and diameter of first whorl 280 µm. Proto-
conch indeterminate or planktotrophic larval develop-
ment. Protoconch nucleus (Figure 7) smooth except for small, 
scattered pustules, subsequent whors with two strong 
spiral keels, crossed by axial ribs forming nodules at in-
tersections and scattered, small pustules (Figure 6). 
Thick varix indicates limit between protoconch and 
teleconch. Protoconch color pink to reddish- or pale-
brown. Protoconch lacking or usually eroded in adult 
specimens, but when present is frequently somewhat til-
ted in relation to shell axis. Teleconch with 5–7 convex 
whorls, somewhat angulate at shoulder on earlier whors. 
Last whorl large, convex, more or less angulate at shoul-
der, then narrowing toward base, representing almost 3– 
4 of total shell length. Aperture large, oval, binate and 
white within; but one specimen with inner side of ap-
erture pinkish. Outer lip thin, with finely serrated outer 
margin (margin rippled internally); inner lip slightly an-
gulate in middle. Siphonal canal broad, moderately elo-
gate, 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 penulti-
mate 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 encrust-
ing organisms (Miniaster, bryozoans, serpulid polych-
chates, two different small species of bivalves, sponges 
and calcareous algae were observed on a single speci-
men). Living animal white or whitish, including tentacles 
and siphon, with densely-packed, yellow spicules, which 
form a ring on distal part of the siphon. Operculum 
brown, mahogany, or reddish-brown.

Type Material: Holotype (Figures 1–2), MCNB 
15.05/32583, 20.0 mm length × 13.5 mm width; five 
paratypes, MCNB 15.05/32583, two paratypes, MCNT 
TFM/CMOIO 0000277 and TFM/CMOIO 0000278, two 
paratypes, DBUA, 15.05/18. All from type locality, at-
tached to black coral Antipathes wollaustoni (Gray) 

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, 
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 speci-
men, 20.9 mm length × 13.6 mm width; R. and R. Vega 
Collection. La Bombilla, Palma Island, Canary Islands, 
collected alive on Antipathes wollaustoni 40 m depth. D. 

Distribution: Known only from the type locality, Pun-
ta 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 kaefitorum suggests a 
widder distribution than that currently known, but the 
species has not yet been found in other Macaronian 
Islands, the Western African coast or the Mediterranean.

Habitat: All collected and observed specimens were 
found attached near the base of colonies of the black 
coral Antipathes wollaustoni (Gray) or near the major 
branch nodes in the case of very large colonies, between
18-30 m (Punta de Teno and Diente de Ajo) and 42-48 m (Veril de Mascot). 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 in a single antipatharian colony in Veril de Mascot. Offshore, specimens were collected on three colonies with the siphon directed upwards and 7-10 mm long (pers. comm.). No observations of feeding were made.

Etymology: The specific name combines to the nicknames of the first two authors, Kao (Ricardo) and Otero (Rodolfo).

Remarks: Coralliophila kaojiloni is tentatively assigned to the genus Coralliophila because it resembles other species (Coralliophila brevis) that are presently included in that genus. Future generic revision of the family.

Coralliophila kaojiloni differs 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 crittendeni) and red (L. ruberrima) gorgonians, off Puerto de la Cruz, at 30-32 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, Emicella stricta, Lophogorgia sarmentosa) (Olive- rio, 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.

Figures 1-7. Coralliophila kaojiloni new species. 1, 2. Holotype, MNCN, 15.05/32583, 21.6 × 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.
It lives on a variety of anthozoans including scleractini- 
as gorgonaceans, zoanthideans and Corallimorpharia. 
(Well & Lamb, 1977; Miller, 1981; De Jong and Com- 
mann, 1985). The embryonic shell of Coralliphila cari-
iba was illustrated by Bandel (1975), and the proto-
conch and larval shell by De Jong and Coomans (1985) 
and Lead (1991). The protoconch of C. cariba has its 
nucleus densely covered by small pastules, is somewhat 
longer (4.5 whors, 1.2 mm length), and has more promi-
"ently nodules than that of C. kasdorum. Presently 
molecular investigation is in progress by Marco Oliverio to 
assay the relationships of the new species with Coralliph-
illa brevis and Coralliphila cariba.

The new species also differs from Coralliphila mey-
endorfii (Calcar, 1945), another littoral species of the 
Canary Islands widely distributed along the Mediterr-
anean and Eastern Atlantic, which has a longer up to 
10 mm) and more solid shell, with 5–6 tellococon whors 
about 13–15 spiral cords and 8–10 strong axial ribs, 
canal rather short, and umbilical aperture. In the Canary 
Islands, C. meyendorfii preys on Anomia sulcata 
(Pérez-Sánchez and Moreno-Batet, 1991), and in the 
Mediterranean the species is known to prey on An-
omia sulcata, Chalacora caspitosa, and Balanophylla 
europaea (Sabella and Spada, 1980; Oliverio, 1980).

The Atlantic-Mediterranean Coralliphila squamosa 
(Bivona, 1833) 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 lamellae 
cordlets, the siphonal canal is of medium length and the 
unbifurcation aperture evident (Bouchet and Warén, 1985; 
Oliverio, 1980). Coralliphila squamosa preys on Gorgo-
amce or deep-sea scleractinians (Oliverio, 1980). 
Coralliphila monterosatoi (Locard, 1907), from Spain, 
and Coralliphila profundilus Huis, 1949, from Ber-
muda, should be considered junior synonyms of C. squa-
mosa, according, respectively, to Bouchet and Warén 

Coralliphila basilicae (Dautzenberg and H. Fischer, 
1896) reaches up to 27 mm, has a thinner shell and 
broad 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.

Coralliphila richardi (P. Fischer, 1882) is a deep-sea 
(bathy) species that lives (and probably preys) on the 
scleractinians Madrepora coralata 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 Coralliphila, with 8–10 axial foliate varices in-
stead of solid ribs and with relatively less spiral cords 
without the characteristic saphra sculpture. Coralliphila 
richardi is included by Kosuge and Suzuki (1985) in the 
genus Emozamia Iredale, 1929, along with the similar 
Coralliphila jardi Kimdean, 1956, found from Sierra Le-
one to Angola.

Coralliphila fontanunguijji Snirghio and Mariottini, 
2000, described from Tenerife Island, is smaller 
(up to 7.5 mm) and has a solid biconal shell. It lives 

on the scleractinian Madrepora aspera Milne-Edwards 
and Haime, 1850. Pérez-Sánchez and Moreno-Batet, 
1991; Snirghio and Mariottini, 2000 authors' observations 
in Tenerife), which probably is a Macaronesian endemic 
(Zibrowius, 1980). According to Snirghio and Mariottini 
(2000), Coralliphila fontanunguijji is similar to 
Coralliphila altbongamanta (E. A. Smith, 1890) from 
St. Helena Island, Coralliphila barro-caeruleus Kosuge 
and Fernandes, 1989, from São Tomé; Coralliphila pat-
 casa Petch, 1957. from Florida, and Coralliphila curta 
Sowerby, 1801, from Marthas Island; all of them clearly 

differ from C. kasdorum by the smaller size and dif-
rent shell shape.

The remaining coralliphilids 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 Su-
zuki, 1985; Richter and Lecque, in press). This species 
preys on the scleractinian Phyllanthus monstezi authors' 
observations), whereas in the Mediterranean it preys on 
Chelaora caspitosa. Asteoides calcubareis and Poly-
ejthus nanclarc (Oliverio, 1998), and authors' observa-
tions) of these latter species, only Polyjeathus nanclarc might possibly be found in the Canary 
Islands (Zibrowius, 1980).

One other, probably undescribed littoral species of 
coralliphilids is found in the Canary Islands living on the 
scleractinian Dendrophyllia ramea from Lanzarote, 40– 
50 m, Castaro Pérez Dionis and Marco Oliverio, pers. 
comm. It is a large up to 10 mm solid shell, very 
similar to that illustrated as Coralliphila et. jardi from 
Gabon by Bernard (1984: pl. 29, fig. 120).

The remaining Mediterranean species of Coralliphila 
are all very different. Coralliphila panormitana 
Monte salts, 1969) is solid, with 10 axial ribs and 22–24 spi-
cal cords with small scales. This species lives at the base 
of Paracarinaria chamaeleon and associated to Corallium 
subulatum (Oliverio, 1998b) or Epizoanthus arcuacens 
(Temple et al., 1993). Coralliphila ophiophia (Arada 
and Boppert, 1856) has a solid, more or less globose shell, 
similar to Coralliphila squamosa in size, and lives in 
bottoms with strong coralligenous component; its diet 
is unknown (Oliverio, 1998).

Among the eastern Atlantic species, Coralliphila ac-
donis (Watson, 1886) from Nightingale Island Tristan da 
Cunha has a strong shell, with a high, scalariform 
spire, relatively small aperture and umbilicus. Corall-
iphila 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 
incrubed, 7–9 brocal axial ribs and about 27 spiral cords 
on the last whorl Kosuge and Fernandes, 1989; Robin 
and Fernandes, 1990; Coralliphila atlantica E. A. Smith, 
1890; from St. Helena Island is a solid, small 
species 17.2 mm, with low axial ribs and spiral cords 
weak sculpture. Coralliphila atrophrostoma E. A. Smith, 
1890, also from St. Helena is solid, sub-bioidal, and has a reddish aperture and evident umbil-
icus Coralliphila patrich E. A. Smith, 1890, from St.
Helena, 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 1955.

*Coralliophila kraemeri* Knudsen, 1956, from Nigeria, and *Coralliophila marrati* Knudsen, 1956, from Liberia, have solid, uncalcified shells; the first one has 16 axial ribs and 14 spiral ridges on the body whorl, whereas *C. marrati* has rounded ribs and only 5 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 adansonii* Kosuge and Fernandes, 1989, from São Tomé is also solid and has the inner side of the aperture dentinulate. Finally, *Coralliophila knudseni* Smirgho and Mariottini, 2000, from Ivory Coast and *Coralliophila schiatti* Smirgho and Mariottini, 2000, from Sierra Leone, are smaller and have biconical and more solid shells than *Coralliophila kaoforum*.

The remaining western Atlantic species of *Coralliophila* are also different. *Coralliophila aberrans* (C. B. Adams, 1850), has a thick, globular 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 kaoforum*, the antipatharian *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, 1991. *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 proposed for protection in the Canary Islands and included in the Preliminary Red List (Bacallado et al., 1989) and the FAO and Marine Fauna List (Bonnet-Fernández-Humann and Rodríguez-Fernández, 1992). We strongly encourage the environmental authorities of the Canary Islands to include *Coralliophila kaoforum* in the Preliminary Red List of species, since it is up to now only known from the Canary Islands and is strictly associated 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


Kosuge, S. and E. Fernandes, 1988. Report on the family Cor-


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

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ABSTRACT
Fusinus dorseledi new species from the Red Sea is described. The new species is distinguished by shell characters from the similar Red Sea species F. leptorychhus (Tapparone-Canefri, 1875) and from F. colus longicolor (Lamarck, 1801) from southeastern Africa. New range records are provided for F. bifrons (Sturany, 1900) and F. arabicus (Melville, 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 (Melville, 1898). The abbreviation USNM, National Museum of Natural History, Smithsonian Institution, Washington DC, is used here.

SYSTEMATICS
Family Fasciolariidae Gray, 1855
Subfamily Fusininae Wrigley, 1927
Genus Fusinus Lamarck, 1819
Type species, F. colus Lamarck, 1758, Recent, India.

Description: Species size moderate for genus, length to height ratio long, slightly undulate, 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, periostoma, 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 Nuweiba, Egypt, 75 km south of Elat (Israel), 300 m depth on sandy bottom.

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

Distribution and habitat: Known only from type locality.

Discussion: Fusinus dorseledi is most closely related to F. leptorychhus (Tapparone-Canefri, 1875), which is well illustrated in Sharabati (1984: pl. 23, fig. 7). The knobs on F. leptorychhus formed by the axial ribs, are fewer, numbering just 9, and are more square than those on F. dorseledi. The operculum of F. leptorychhus 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. dorseledi being a deeper-water
Figures 1–4. Species of Fusinus. 1, 2. fusinus doupeledi new species. 1. Holotype. USNM 903651. 107 mm length. from sandy bottom off Nefiot (Egypt). 75 km south of Elat (Israel). Red Sea. depth 300 m. 2. Paratype. Peled Collection. 72.5 mm length from type locality. 3. fusinus bifrons (Sturany, 1900). Peled Collection. 99.3 mm length from Elat. Red Sea, Israel. depth 350–400 m. 4. fusinus arabicus (Melvill, 1895). Snyder Collection. 96.6 mm length. trawled by fishermen off El Tur, Gulf of Suez (Egypt). depth 32–40 m.
form of *F. leptorhynchus*. Comparison can also be made with *F. colus longicandaa* (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 longicandaa*. The axial ribs are not nearly so pronounced on the body whorl in *F. colus longicandaa* 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, *Fusinus bifrons*, dredged in depths of 490–900 m in the Red Sea. He compared this axially ribbed species to *F. forcerps* (Perry, 1811), *F. multieticatus* (Lamarck, 1822), *F. terebrana* (Deshayes, 1843) (a synonym of *F. colus* (Linnaeus, 1758)), and *F. leptorhynchus* (Tapparoni—Canzoni, 1875), and he named a smooth variety of his new species “form pancicostata.” Later, Sturany (1903: pl. 1) illustrated *F. bifrons* and erroneously referred to the taxon *pancicostata* at that rank. According to R. Jansen 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 Qeiyet (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 Roedel, 1992; Sirenko, 1995). The larger specimen was illustrated by Sirenko (1993: fig. 7). This represents a significant range extension for this species from the Red Sea to the Indian Ocean.

*Fusinus quadricus* (Melville, 1898)  

Extension of *Fusinus arubicus* (Melville, 1898) reported. This species, previously known from the Gulf of Arabia, is figured in Bosch et al. (1995: 163, 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. arubicus* (Melville, 1898).

**LITERATURE CITED**


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. (Turricula), 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 (Turricula)* 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 (Honbrink, 1983; Petuch, 1988); one species in West Africa (Emerson, 1993); and a fourth species in the Andaman Sea (Kosuge, Ronssy and Munngam, 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 59942), 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* panamastriata Olsson, 1942. Olsson, 1942, 75, pl. 10, fig. 10

Description: Shell small to large, 14–50 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 1 1/2 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 1/2 to 3 whorls.

*Cotonopsis (Cotonopsis) lindae* Petuch, 1988: new combination

Figures 1–6

*Strombina (Cotonopsis) lindae* Petuch, 1988, 161. 162 pl. 38, figs. 13–16. Oil St James, Barbados, trawled 70 m depth

Description: Shell small to stout, up to 22.9 mm in length, inflated body whorl, axial ribs on the early teleoconch, relatively well-developed columellar and parietal...
calluses. Protoconch smooth, with 1½ 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 eastern Pacific and has no known fossil record. *Cotonopsis sensu stricto* has a much wider distribution, including the eastern Pacific, the Caribbean Sea, the West Indies, the Andaman Sea, and the early Pleocene of Esmeraldas, Ecuador. The Guatil Peninsula, Baja California, and several species from the Pacific coast of the Americas, as mentioned above, the recent distribution of *C. lindae* seems to indicate an origin outside the eastern Pacific. *Cotonopsis lindae* resembles *C. pluketensis* (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, 1993, from the Dominican Republic and *Cotonopsis moufusi* Emerson, 1993, from Senegal are also much larger, with heavier sculptured teleoconch whorls. Besides, *C. moufusi* 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 mendocina* (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 hair 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 lindae* holotype, USNM 579942. 5. SEM of protoconch, showing a slightly sigmoid lip, and the sculpture of the early teleconch whorls. 6. Same, apical view. Scale lines = 200 μm.

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LITERATURE CITED


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 was 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. subulatus argentum* *Oreohelix alpina* has been incorrectly placed in Pilsby's *O. subulatus* group of species and should be included in the *O. striosa* group.

**INTRODUCTION**

The genus *Oreohelix* (Pilsby, 1939) is composed of a large number of species found throughout the Rocky Mountains from southern Canada to northern 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 (Pilsby, 1939). There is, however, little variation in reproductive anatomy. Pilsby (1939) found no relevant interspecific variation in the morphology of the reproductive system. Nonetheless, that author based in part upon the ratio of the plate:ridge portion to the postulose portion of the internal surface of the penis, allocated species of *Oreohelix* to one of three groups, the *O. striosa* group, the *O. subulatus* group, or the *O. yarapa* group.

Fairbanks described *Oreohelix yarapa* from the Mission Mountains of western Montana on the basis of the shell and the reproductive anatomy of that species. Pilsby subsequently placed *O. alpina* in the *O. subulatus* group because *O. subulatus* occurs at lower elevations in the Mission Mountains range and because no members of the *O. striosa* group occur in that area.

Specimens of *Oreohelix alpina* from the type locality had not been collected for over 50 years. Recently, Hendricks (1998) reported and described six specimens from the type locality, 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 Pilsby'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. Mary's Peak which is near the type locality on the southwest ridge of St. Mary's Peak, T18N R18W S2 E1, (Township, Range, and Section from USGS topo map). Mission Mountains, Lake County, Montana, elevation approximately 2500 meters, on 27 Aug. 1997 (Figure 1). Additional specimens of *Oreohelix*, similar to *O. alpina*, were collected by Bill Hamner, 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. subulatus argentum* Berryl, 1919, collected on 2 Aug. 1975, at Yellow Bay, Flathead Lake (T24N R19W S1), 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 postulose 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-
RESULTS

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 anatomy 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. subrubris aparimum 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 (1930) noted that in the O. strigosa group the plicate portion of the penis was "...decidedly less than

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

<table>
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<tr>
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<th>Diameter of shell</th>
<th>Shell height</th>
<th>Number of whorls</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mission Mountains</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Specimen A</td>
<td>8.0</td>
<td>15</td>
<td>3.3</td>
</tr>
<tr>
<td>Specimen B</td>
<td>7.9</td>
<td>14</td>
<td>4.0</td>
</tr>
<tr>
<td>Specimen C</td>
<td>7.5</td>
<td>13</td>
<td>4.5</td>
</tr>
<tr>
<td>Specimen D</td>
<td>8.4</td>
<td>16</td>
<td>1.0</td>
</tr>
<tr>
<td>Mean</td>
<td>7.95</td>
<td>15.3</td>
<td>3.70</td>
</tr>
<tr>
<td>Swan Mountains</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Specimen A</td>
<td>11.1</td>
<td>6.1</td>
<td>4.3</td>
</tr>
<tr>
<td>Specimen B</td>
<td>8.5</td>
<td>3.0</td>
<td>4.25</td>
</tr>
<tr>
<td>Specimen C</td>
<td>9.0</td>
<td>5.0</td>
<td>4.0</td>
</tr>
<tr>
<td>Specimen D</td>
<td>8.6</td>
<td>5.2</td>
<td>4.0</td>
</tr>
<tr>
<td>Mean</td>
<td>9.3</td>
<td>5.4</td>
<td>4.15</td>
</tr>
</tbody>
</table>

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

Table 2. Measurements of the plicate portions and postulate portions of the internal surfaces of the penises of Oreohelix alpina and O. subrubris aparimum. Measurements in millimeters.

<table>
<thead>
<tr>
<th></th>
<th>Total Length</th>
<th>Postulate Portion</th>
<th>Plicate Portion</th>
<th>Percent Plicate</th>
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</thead>
<tbody>
<tr>
<td>O. alpina, Mission Mountains</td>
<td></td>
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<td></td>
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<tr>
<td>Specimen A</td>
<td>7.5</td>
<td>11</td>
<td>3.4</td>
<td>45</td>
</tr>
<tr>
<td>Specimen B</td>
<td>10.0</td>
<td>5.6</td>
<td>4.4</td>
<td>44</td>
</tr>
<tr>
<td>O. alpina, Swan Mountains</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Specimen A</td>
<td>7.5</td>
<td>14</td>
<td>3.1</td>
<td>11</td>
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<tr>
<td>Specimen B</td>
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<td>2.0</td>
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</tr>
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<td>Specimen C</td>
<td>6.5</td>
<td>10</td>
<td>2.5</td>
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<td>O. subrubris aparimum</td>
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<tr>
<td>HLF39-1</td>
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<td>9.5</td>
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<td>8.0</td>
<td>55</td>
</tr>
</tbody>
</table>

Figures 1–3. Western Montana showing the locations of the Mission and Swan Mountains. Scale bar = 20 km.

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.
Figures 4-6. Reproductive systems of species of Oreohelix.
4. O. alpina from the Mission Mountains. 5. O. alpina from the Swan Mountains. 6. O. subrudis apurum 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 = 3 mm.

Hull...the total penial length, but greater than half the total penial length in both the O. subrudis group and the O. purpurai group; these two groups then being separated on the basis of whether the anterior half of the penis was "decidedly swollen..." or not.

Pikry originally placed O. alpina in the O. subrudis group because it arose from the other groups (O. stri-
gosa and O. yatapaia) 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. subradiis apariana, also from the Mission Mountains, was greater than 1/2 total penial length (Table 2). In the O. yatapaia 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 Pilsky (1939) is to be followed, I suggest placement of O. alpina in the O. strigosus group.

The shells of Ovocolelix 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


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; O. Foighil et al., 1999; O. 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 Conchylium-Cabinet von Martini und Chemnitz, p. 74, pl. 13, fig. 7, 8, in volume 7, part 1. The text describing O. chilensis ("Philippi in Lि") is part of Lieferung 186, issued in 1868 (Küster, 1868); (Johnson, 1958: 366; Smith and England, 1937: 97; Welter-Schultes, 1990: 185). The taxon Ostrea chilensis (as "O. [stev] chilensis Philippi") in fact originates from the list of species depicted on the plates included in Lieferung.45 printed on the wrapper thereof (Küster, 1841), 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 21.3.3). 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. 211 erst mit nachst[n]en 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 also referred to 1844 and assumed to have been issued then, and that the name O. chilensis became available from the earliest point at the time of issue of that Lieferung to the inclusion of O. chilensis erroneously dated 1843 in Welter-Schultes 1990: 185), but the latter pointing to some other component of the compilation. Although wrappers for some species were intended to be discarded, and most indeed were so produced on them with reference to illustrations of criteria for availability (ICZN Articles 81.12: 14), produced on these wrappers were accepted as published (C. D. Sherborn in Smith and England, 1957: 59). "Ostrea chilensis," 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 Conchylium-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

Jeffs, V.C. and R.G. Creese, 1996. Overview and bibliogra-
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 Hinki, 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 (Zuho-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 (1961) and Shells of the World in Colour (Vol. 1, 1965, with Kiyoshi Hto; Vol. 2, 1966, with Sadao Kosuge).

Earlier in his career, Dr. Habe worked closely with Takahito 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 specialty 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. B. 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


Book Review


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 (Leaf, 2001, review of Skoglund, 2000) I had wished that the author could provide an equivalent update on the gastropods. That work, also published as a supplement to The Festschrift, 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 superspecific taxa new for the region (indicated in bold-face).

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., Clipperion, Cocos, and Gorgon) 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 "Cocculiniformia" (Cocculiniformia) (pages ii, 23), as a suborder under the subclass Neritimorpha. Skoglund used the correct spelling for the subclass Cocculiniformia in some pages, and I wonder whether the misspelled word was meant to be "Cocculinoida" or a repetition of "Cocculiniformia."

The hierarchical named 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 Vaughan (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. J. 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 air-mail only. Contact the San Diego Shell Club, c/o 3883 Mt. Blackburn Way, San Diego, CA 92111 USA or e-mail Carole Hertz (chdhertz@pacbell.net) for further information.

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CONTENTS

Sven N. Nielsen
Thomas J. DeVries

José Willibaldo Thomé
Suzete Rodrigues Gomes
Rosane Souza da Silva

Kristiina Ovaska
Lyle Chichester
Heike Reise
William P. Leonard
Jim Baugh

Philippe Bouchet
Richard Petit

Guido Pastorino
Pable E. Penchaszadeh

Tertiary Xenophoridae (Gastropoda) of western South America............................................. 74
Redescription of the genus and species Heterococcinia limayana (Lesson, 1830) (Gastropoda: Soleolifera: Veronicellidae) ................................................. 79
Anatomy of the dromedary jumping-shug, Hemphillia dromedarius Branson, 1972 (Gastropoda: Stylommatophora: Arionidae), with new distributional records ......... 89
New species of deep-water Cancellariidae (Gastropoda) from the southwestern Pacific .......................... 95
Spawn of the Patagonian gastropod Parentheria plumbea (Philippi, 1844) (Buccinidae) ................................ 105
The known view of Figure 1 followed Chmiuljcs (1990) KNTRM, sar(fiuces 'hile. basal shallow scales aliont. Xcnophilien 9.SU)5 1990) central fault-bound is New dioiip, ..

Abstract

Three species of Xenophoridae are reported from the Tertiary of western South America: Xenophora carditigera new species from the Oligocene of Peru, Xenophora paludinae new species from the Miocene, Navidad Formation of central Chile, and Stellaria kriegeri-baurhohli new species from the Tertiary of Peninsula Valdez, 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, Onuphis Swainson, 1840, and Stellaria Schmidt, 1832. However, most workers now recognize these as the generic rank (e.g., Kreipl and ME. 1999), a view that is followed here. Where known, the protoconch in Xenophora species consists of about 3.5 low trochospiral whors (Bannell, 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, Ben (1977) reviewed the Cenozoic Xenophoridae of New Zealand which include an Eocene to Miocene species, a Miocene species and a Oligocene 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 murieli 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, fine-grained siltstones with thin-shell valves of Chlamys and fish scales of sardines and anchovies (DeVries, 1998).

Internal molds of probable Xenophora species are also found in a fault-bounded outcrop of pebbly coarse-grained sandstone overlooking the lower Rio Teca 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 Philippy 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 Dremlin (in Herrn, 1969, p. 71) as Lower Miocene (Burdigalian). However, Tsuchi et al. (1990) and Ibaraki

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

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

**Mollusca** Formation, Peninsula Aranco, South- ern Peru

The Mollusca Formation has been defined from cores drilled on Peninsula Aranco. It consists of gray siltstones dated as Tortonian (García, 1968). All similar siltstones of the area usually have been considered to belong in this formation. However, analysis of the molluscan fauna suggests a Miocene age at least for part of these sediments (S. Nielsen, 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 Millongne (Figure 2). These concretionary nodules are washed free by the tide and usually yield specimens of the crab *Cancer araneus* Philippi, 1837. 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 INP); Departamento de Paleontología de Vertebrados, Museo Nacional de Historia Natural, Santiago de Chile (SGO); and Senckenberg Museum, Frankfurt, Germany (SMF). Photographs were taken using a Leica SL2 camera. Images were scanned from Ilford FP4 125 black and white 35 mm negatives using an Acor Scannit 2720S film scanner and processed with Photoshop 6.0.
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 line.

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; colateral 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 line 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 15 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: DA 631 S, northwest of Loma Cuesta Chilcaya, about 1 km north of Comotama–Carhitas road, about 5 km east Playa Carhitas, 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: Othuna Formation, Oligocene, between Paracas and Bahia 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: Tertiary. *Xenophora*. 3-11, *Xenophora carditigera* new species. 3-5, Holotype, SMF 323039, height 17 mm, diameter 36 mm. 6-8, Paratype, SMF 323041, height 13.5 mm, diameter 22.5 mm. 9-11, Paratype, MUSM 18134, height 24 mm, diameter 32.5 mm. 12, *Xenophora paullina* new species, Paratype SGO PI 5991, diameter 154 mm.
**Chelidophora** (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, 1953). 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 cavities in adults. Specimens of *Carditigera* 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* (Benz, 1977), an early to middle Miocene species from New Zealand that may be part of a lineage that includes *X. paratops* (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 lines. Attached camouflaging objects seem to include either high-spined gastropods or concave-side-up bits (axes up to 50 mm wide). Basal aperture 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 134 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. Vásquez 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 paratops* Finlay, 1926 (see Ben, 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 *Trachita 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* Linne, 1764.

**Stellaria kriegerbartholdi** 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, peripheral flange 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 Aranco, south-central Chile.

**Etymology:** Named after Rolf Krieger Barthold, who did the difficult preparation of this specimen.

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

**Discussion:** *Stellaria kriegerbartholdi* 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. kriegerbartholdi* *S. kriegerbartholdi* 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* Dallo, 1892, from Mississippi, which also might be regarded as ancestral to *S. kriegerbartholdi*. *S. conica* has the umbilicus almost obscured by the parietal callos.

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.

Remarks: The concept for *Stellaria* given by Ponder (1983) has to be expanded to include species with a closed umbilicus. In *S. kriegerbartholdi* Ponder (1983) noted that the placement in *S. testigera* "is not completely satisfactory...a concept which is even more appropriate for *S. kriegerbartholdi*. 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.
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 (Ben 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. conchyliphora* 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 Ben 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. kriegerbartholphi* but has an open umbilicus like modern species. Ponder (1983) discussed *S. testicula* as a possible early offshoot while *Stellaria* was still close to *Xenophora*, which may also be true for *S. kriegerbartholphi*. However, characters of the known *Stellaria* species suggest that the fossil record of this genus is very fragmentary.

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LITERATURE CITED


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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* Krans, 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 copulatory bursa is elongated-spheroid, tapering into a distal elongation that folds and joins the bursa duct toward its base, receiving the penial 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 medio region, forming expansions on the sides that mark the beginning of the gland; the penis is longer than the verge and tapers in its distal portion. There is no spatha. All pertinent bibliography is discussed and the synonymization of *Vaginina odlhneri* Hoffmann, 1927, is justified.

**INTRODUCTION**

The Veronicellidae are terrestrial snails 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; Forscal, 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. couraditi* and *V. togensis*, 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. couraditi*, and by a smooth sheath in *V. togensis*.

In his discussion of the nomenclature of the Veronicellidae, Baker (1925) designated *Vaginina odlhneri* as the type species of *Vaginina* Hoffmann, 1925 (accepted *V. couraditi* and synonymized *V. togensis* 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 *Mesoleucininae*, with the following diagnosis: "dark notum, weakly pointed, genital pore almost at mid-length of the hypostome; 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 odlhneri* 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. odlhneri* from *V. togensis* 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 Veronicellidæ, considered Vaginina as a subgenus of Pseudoveronicellula, 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 Pseudoveronicellula (Vaginina) conradii as a valid name. Without discussion and without examining specimens, he also added Pseudoveronicellula (Vaginina) odleri (Hoffmann) to his list as from "probably Africa." He also proposed a new species, Pseudoveronicellula (Vaginina) duparti, 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 tauton Heterovaginina as a subgenus of Vaginina, based on the description of Vaginina (Heterovaginina) peruiana, from Lomas de Atocongo, near Lima, Peru, and included V. odleri due to the similarities of the two species. He excluded V. conradii 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 Deguer (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. peruiana, 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 Deguer (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 peruiana Kraus, 1953, with Vaginula luiyanaless Lessan, 1930, 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 Vaginula odleri, but concluded that this species should be included in the genus Heterovaginina because it occurs in southern Peru. He thus agreed with Kraus (1953a); although he did not go so directly.

Thomé (1953) redescribed the holotype of Vaginina Heterovaginina peruiana Kraus, 1953, deposited in the Senckenberg Museum, Frankfurt-am-Main, without discussing the synonymy. The copulation bursa is, according to Thomé (1953), sac-like and sessile in V. humeri, whereas we know it to be present only in juvenile specimens. Thomé (1953), in a revision of the American genera of Veronicellidæ, recognized and redescribed (still only on the basis of the juvenile type specimen Heterovaginina) keeping it monotypic H. peruiana and with occurrence restricted to Peru. He did not mention V. odleri.

In addition, Thomé (1954) redescribed the holotype of H. odleri, deposited in the Naturhistoriska Riksmuseet of Stockholm, Sweden. According to Thomé (1954), 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 mid-length. An inspection of its illustration, (Figure 15, 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 redescriptions 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 Veronicellidæ occurring in Peru, several specimens, both juvenile and adult, were found in the examined collections. These were positively identified as Heterovaginina luiyanaless (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 (USM), 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; Museo de Ciencias e Tecnología, Pontificia Universidad Católica del 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 1594 and USM 2513b 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 radicial teeth and twenty lateral teeth were calculated. The anatomic, generic and specific,
characteristics are emphasized, following Hoffmann (1925) and Thomé (1975, 1985a, 1985b, 1993).

SYSTEMATICS

Genus Heterovaginina Kraus, 1953
Heterovaginina Kraus, 1953a: 63-65.

Type Species: Vaginina [Heterovaginina] peruiana Kraus, 1953a: 63-65 (= Heterovaginina limayana Lesson, 1830).

Diagnosis: The rectum penetrates the integument near the female genital pore. The thin-tissueed copulation bursa is spheroid, tapering in a distal lengthening that bends and joins the bursa duct toward its base, receiving the duct at the distal 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)

Vaginina limayana Lesson, 1830: 392-393: 471. pl. 11 figs. 14-14
Vaginina limayana Deshayes in Férussac and Deshayes, 1819: 1854. 99-100. pl. SE. fig. 11. exact copy of Lesson, 1830.

Pseudocoroneia Vaginina ovulifera Forcart. 1953: 60.


Vaginina Heterovaginina ovulifera Kraus. 1953a: 63-65.

Heterovaginina limayana. Kraus. 1954: 82-83.

Heterovaginina ovulifera 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 gland. Gland 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 1/3 of the way down the full length of the animal and continuing to the rear without reaching the posterior perinotum. The 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 hypotonum = 4.14, distance from the female genital pore forward = 11.50, 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 palatal, 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 posterior aortic artery meets the nerves near their beginning (on 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 = 418; apart = 16.5; maximum separation = 2.72 mm; meeting of the aortic artery = 1.46 mm from the origins.

Pedal gland (Figure 1) 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 = 4.20; distended (dorsal surface) = 4.14; greatest width = 1.90.

The thin-tissueed copulation bursa, or spermatheca or spermatoalkine gland, of some authors, is spheroid, tapering in a distal lengthening that folds and joins the bursa duct toward its base, receiving the duct at the distal 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 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 and no 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 gland. Gland 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 gland = 1.15; 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 17-20. *Heterospira hungolensis*. 17. Sheath that envelops the penis, opened longitudinally (MUSM 2513). 18. View of the distal portion of the penis sheath, showing the sharp longitudinal folds of the internal tissue (MUSM 2513). 19. Sheath opened longitudinally, showing the presence of a salient globular formation of the internal tissue, similar to that described by Hofmann (1927) for *H. mollaris* as a gland (FMNH 59486). 20. Region of the salient globular formation, greatly enlarged, also showing details of the tissue folds (FMNH 59486). 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 (glândular?) 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 miniscule 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 radidid 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 5.55 mm length by 3.41 mm at the greatest width. The average dimensions of 20 lateral teeth were: length 56.2 μm, width 24.3 μm, distances from the greatest width to the tip 29.45 μm. The average dimensions of 20 radula teeth were: length 32.8 μm, width 12.8 μm, distance from the greatest width to the tip 17.0 μm. Figures 22–23.


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 10000, 2 specimens, same data as the neotype; MUSM 1458, 1 specimen, Peru, Dpto. Lima, Bosque Zárate (11°54' N, 76°29' W), 3000 m above sea level, 24 Mar. 1979, leg. Valencia and Franke; MUSM 1460a, 1 specimen, Peru, Dpto. Lima, Bosque Zárate (11°54' N, 76°29' W), 3000 m above sea level, 17 Aug. 1965, MCP 6504, 1 specimen, Peru, Dpto. Lima, Cerro San Cristobal, 11°19' N, 76°33' W, 3550 m above sea level, 24 Mar. 1980, leg. H. Sisniegas; MUSM 6595, 1 specimen, Peru, Dpto. Lima, Huachipa (12°00' N, 76°56' W), MCP 6594, 1 specimen, Perú, Dpto. Lima, Apr. 1978, leg. W. Wevran; MCP 7288, 2 specimens, ex-MUSM 4001, same data as holotype; BMNH 519104, 1 specimen, NRS 949 4052, holotype of Vaginina ophideri.

DISCUSSION

Vaginina limayana 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 Béard 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 Féminac and Deshayes, with no further comments.

Although the holotype Vaginina heterogonia peruviana Kraus, 1953, is an immature specimen, the synonymization of this latter species by Kraus (1954) based on information from W. Wevran (2002) may be incomplete.

The holotype Vaginina horderogonia peruviana Kraus, 1953, is an immature specimen, the synonymization of this latter species by Kraus (1954) based on information from W. Wevran (2002) may be incomplete.

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.
Figure 21. *B. m. huangena* General view of a mandible (MCP 2513-b)

Figures 22-23. *B. m. m. huangena*: Middle region of the radula. 22, slightly and 23, greatly enlarged (MCP 2513-b). dl: lateral tooth; dr: radular tooth, central.
collected at the original type locality of the species, Cerro San Cristobal.

Hoffmann (1927) proposed the species *Vagina h olmeri*, especially due to the presence in the penis sheath of a glandular protuberance. Thomé (1984) in his redescription of the holotype of *V. olmeri* made no reference to that distinctive protuberance because the holotype was extensively damaged.

In three juvenile specimens (SMF 108548, MCP 6593, and FMNH 59486d), 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. olmeri* as a “gland”. The “gland” described for *H. olmeri*, 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 *Heterovagina*.

ACKNOWLEDGMENTS

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LITERATURE CITED


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 redescriptions 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 1570 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. burrenicensis* Pilsbry, 1918; *H. pantherina* Branson, 1975; *H. camilus* Pilsbry and Vannatta 1947; *H. dromedarius* Branson, 1972; *H. danieli* Vannatta, 1947, and *H. maloneyi* 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. Kernery and Cameron 1979; Tropa, 1984; Gomez, 2001. Our interest in this species arose after the discovery in 1999 of a large (60 mm) 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. maloneyi* 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-
vington 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 documented occurrence 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 1989 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% ethyl 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, Illinois; 43029, Delaware Museum of Natural History, Wilmington) was performed by HR.

**RESULTS**

On Vancouver Island we located *H. dromedarius* at six locations ranging from near sea level to an elevation of 1060 ft. (Appendix). These localities represent a northward range extension for the species (Figure 1). Habitats consisted of coniferous forest, dominated by western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), and douglas fir (*Abies amabilis*); the forest floor was typically comprised of thin, compact needle litter. Five of the six localities were in remnant patches of old-growth forest with trees > 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) 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 motting 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 FMNH 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 13029, 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 Pilsby (1948) for H. malacor, 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 S 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 *Hemphilla 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. malouei* by Walter J. Eyedam (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, 1918; 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.
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. dromedaris (Branson, 1972), although our measurements of the length of fresh specimens from Vancouver Island (40–60 mm) were considerably greater than the length (21–31 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 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, the only previous 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 these specimens, a penis 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 specimens and therefore species, he might have examined for his anatomical descriptions.

In H. dromedaris, there were no intrapenial accessory structures, such as the “stimulator” described for H. malouci (Kozloff and Vance, 1958). A more detailed, comparative investigation of the verge and other intrapenial structures among species of Hemphilina awaits investigation.

Three other large-bodied (>30 mm in length) species of Hemphilina are currently recognized: H. malouci, H. caeculus, and H. danielisi. A penis accessory sac is absent in H. malouci (Pilsbry, 1914c, L.C., unpublished), which is sympatric with H. dromedaris in the Olympic Mountains of Washington. Internally, 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. malouci. Hemphilina caeculus from eastern British Columbia and Washington also lacks both a caudal horn and a penis accessory sac (Pilsbry, 1948). Of the described species, H. dromedaris most closely resembles H. danielisi, which occurs in Montana (Pilsbry, 1948), and our specimens keyed out to this species using Branson’s (1972) identification key. Systematic relationships within Hemphilina and among related genera have not been examined recently, and comparative studies of reproductive anatomy and genetics of Hemphilina are in order.

ACKNOWLEDGMENTS

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LITERATURE CITED


APPENDIX

Localities for *Hemiphilia 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°25' 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°30' 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 Hoquiam Lake; ca. 5 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. Mount Hoope - shores of an unnamed lake; ca. 20 km northwest of Youbou; 48°60' N, 124°29' W; elevation 550 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. Shreve, and J. Ziegler; specimen used for genetic studies; photograph in personal files of K.O.

**Washington State, United States:**

7. Clallam Co., 4.8 km south of Blyn (off Woods Road); Olympic National Forest; 47°39' 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 53 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 001-00286-001.

9. King Co., Mt. Baker-Snoqualmie National Forest, several locations from 0.8 to 1.6 km west of Stevens Pass; 47°51' 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 509 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 610 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 adolphus, new species; Mirandaphora maculata new species; Mirandaphora maesartii new species; Moraea marinae new species; Stellia rossii, new species; Stellia splendida, new species; Africotriton parvulus, new species; Nipponaphora paradoxoidea new species; and Nipponaphora goniata new species. Africotriton adolphus new species is the first species in that genus known from outside South Africa and Australia. The new genus Mirandaphora is characterized by its broad, non-unilateral shell with very large, crumulated axial ribs and axial collumna. The genus is composed of the new species described herein, Mirandaphora maesartii new species and M. shampoo new species, and two other species: M. tamae, Habe, 1981 new combination and M. arafurae, Verheeken, 1997 new combination, from deep-water off Japan and the Aru Islands respectively. Trinapaula tamae, Habe, 1981, and Xestostomatostomia petuch, 1979 are transferred to Nipponaphora. New species of Moraea, Stellia, and Nipponaphora 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, Croxter and Bouchet, 1991; Bouchet, 1995; Bouchet and Marshall, 2001). Although the inventory is still far from complete, it has already revealed to be one of the most— if not the most— diverse anywhere in the world, with a exceptional diversification in such families as Seguenziidae, 55 species; Marshall, 1991; Muricidae, 90-200 species; Honart, 2001; or Scaphopoda, 73 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 shelf 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 more 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 where available and discussion of patterns of bathymetrical and geographical distributions.

MATERIALS AND TEXT CONVENTIONS
The new species originate from several dredging programs conducted under 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 1990. MUSORSTOM 4, Richer de Forges 1991 Programmes LAGON, Richer de Forges 1993; SMB 5 and Richer de Forges and Chevillon 1997. SMB 8, BATHUS 2, 3, and 4.

In the lists of type and other material examined, individual lots in MNHN are un ambiguously designated by the combination of name or number, and station number. DW refers to dredge hauls, CT to beam trawls. It refers to live-taken specimens and to empty shells spins to commercially obtained specimens. state when dredged is not known.

SYSTEMATICS
Family Cancaliidae Forbes and Hanley, 1851
Subfamily Pleurotominae Ben and Maxwell, 1987
Genus Africotriton Ben and Maxwell, 1987
Genus Stellia Schofield, 1959
Genus Mirandaphora Schofield, 1959
Genus Nipponaphora Ben and Maxwell, 1987
Type Species: 

*Planorbis erubescens* C. B. Sowerby III, 1903, by original designation.

*Afrotriton adelphe* new species (Figures 1-3)

Type Material: 

Holotype: 22.4 mm height × 7.8 mm width [lv. Figure 1] and 3 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 7: sta. DW902].

Other Material Examined: 

Description: Protoconch mammilate, paraphrizal, 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 creations on edge but smooth within. A shield-like callos produced on the inner lip, weak over the parietal area but well produced over the indutural 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 retracted. 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. carin apex Beu and Maxwell, 1987, is from off New South Wales, Australia. The new species differs from A. carin apex in being much more slender with less convex whorls, and in having stronger spiral cords and weaker axial ribs. Africotriton adelphus resembles 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, 1854
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 thinned on outer edge and extending back over the parietal wall as a rounded shield that extends out at the indutural area. No strumoid 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 indutural shelf. Unbilocular absent.

Discussion: Besides the two new species described here, we include Trigonaphera tosaensis Habe, 1964 recently placed in Solatia by Hasegawa, 2001. 553- and Solatia inarafusensis Verheeken, 1997 in Mirandaphera. The resemblance of these taxa to Solatia is only very superficial. The type species of Solatia, S. pisatoria (Gmelin, 1791) has weak collumellar folds, an appressed suture, and a flaring aperture among other differences. Species of Mirandaphera have a superficial resemblance only to high-spired species of Sculpta Fournelle, 1857 from which they differ in having a elongated tabulate shell with very large crenulated axial ribs and a axial col-
nula. 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 apheca. Apehra was introduced as a genus in Cancellariidae and later used as a stem name for various cancellariae genera, all treated as feminine. A search for its origin reveals only a few usage, 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: 138.7 mm height × 19.3 mm width) + v in MNHN (Figure 8).

Type Locality: South of New Caledonia, off Passe de Konaré, 22°49’ S, 166°45’ E, 300–370 m [BATHUS 2: sta. DW731].

Other Material Examined: North of New Caledonia, BATHUS 1: sta. DW902, 19°01’ S, 163°15’ E, 341–351 m, 2 dd (Figure 7; 1; From commercial sources, boat Tui II, off Belep Islands, 3 spms.

Description: Protoconch smooth, of 1.3 whorls, diameter 350 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 11 on penultimate whorl. The ribs are run-
gular on the shoulder over which they reenforce and ex-
tend 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, and in angular. 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 ridlets. Ribs on adult shells sometimes formed as thickened nodes with subsequent growth originating from under the
outer lip. Aperture elongate. Outer lip thick, smooth, with a narrow, smooth shell inside the lip. About 12 strong ribs 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 brownish-yellow.

Etymology: Named for Dr. Patrice Cuvré, 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* (Verheeken, 1997) in having strong ribs 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 northeastern 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°21’ E, 455–512 m, 1 dd; Fiji: MUSORSTOM 10: sta. CP1341, 16°52.5’ S, 177°13.7’ 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 by high narrow axial ribs barely wider than interspaces. Two axial ribs, 14–16 in number, extend over the rounder shoulder and turn down to a narrow subterminal ramp that extends all the way to the moderately impressed siphonal canal. Spiral sculpture of narrow densely packed spiral cords, which become denser and increase in height at region of cords forming head-like nodes on the ribs. There are 10 nodes on the body whorl ribs with approximately 16 cords between centers of nodes. Spiral cords intersected by finer incremental riblets that form an intrinsically-like micromollusc (Figure 6). Final rib is produced as a terminal cusp. Aperture elongate, narrow. Outer lip thickened with 8 ribs 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 mariscus* new species (Figures 9–12).

**Type Material:** Holotype (25.7 mm height × 18.0 mm width) (lv) (Figure 9) in MNHN.

**Type Locality:** Off northeastern coast of New Caledonia, Passe de Hienghène, 20°34’ S, 164°55’ E, 470–490 m (BATHUS 4: sta. CP947).

**Other Material Examined:** New Caledonia: BATHUS 4: sta. CP951, 21°01’ S, 164°27’ E, 416–433 m, 1 dd (Figure 12).—HawaiIPRO 1: sta. CP551, 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 Harasewycz and Petit, 1982: 111), noticeable on outer surface of shell as thickened axial ribs, each followed by a relatively large 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, *Merian marisea* new species. 9. Holotype. Height 25.7 mm; off northeastern coast of New Caledonia. Passe de Hienghêne. 20°34' S. 164°58' E. 450-490 m. 10. Specimen from Vannatu. Height = 17.9 mm. 15°41' S. 167°02' E. 395-400 m. [MUSORSTOM] sta. CP1136. 11. Specimen from New Caledonia. Height 18.7 mm. 21°13' S. 166°37' E. 314-364 m. [HALIPRO 1] sta. CPS51. 12. Protoconch of specimen from off the western coast of New Caledonia. 21°01' S. 164°27' E. 416-433 m. [BATHUS 4] sta. CPS89. 13-14, *Stellina mecon* new species. 13. Holotype. Height 13.3 mm; south of New Caledonia. Norfolk Ridge. Banc Jumeau Ouest. 23°20' S. 168°01' E. 361-365 m. [BATHUS 5] sta. DWS301. 14. Protoconch of specimen from south of New Caledonia; SW of Île des Pins. 23°00' S. 167°16' E. 350 m. [BIOC.V.M.] sta. DW97. 15-17, *Stellina splendidula* new species. 15. Holotype. Height 11.9 mm; south of New Caledonia; SW of Île des Pins. 22°50' S. 167°21' E. 500-504 m. [SMH S. sta. DW201]. 16. Paratype. Height 10.4 mm; south of New Caledonia; SW of Île des Pins. 22°59' 23°00' S. 167°21'-167°23' E. 491-558 m. [SMH S. sta. DW193-196]. 17. Protoconch of specimen from same locality as Figure 16. Scale line = 500 mm. 12, 14, 17.
lip. Outer lip with a finely serrated edge; inner surface with 14 spiral lines 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 indential callus with smaller fold-like features or pustules sometimes present on outer edge of indutrix. 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 *marica*, f. a large type of fig.

**Remarks:** *Merica pirum* has many features in common with the Philippine *Merica ektaphos* Petit and Harasewych, 2000, which has stronger sculpture with heavy nodes formed at intersections of spiral cords and axial ribs. In addition, *Ektaphos* has a rounded and more solid shell, and the protoconch is 8½ 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 Sclitia** Jousseaume, 1887

**Type Species:** "*Sclitia varicosa* [sic] Broczi." (= *Volita varicosa* Brocchi, 1814), by original designation.

*Sclitia rocroii* new species

(Figures 13-14)

**Type Material:** Holotype (14.3 mm height × 8.9 mm width) (♀) (Figure 13) and one paratype (♂) from the type locality in MNHN.

**Type Locality:** South of New Caledonia, Norfolk Ridge, Bane Jumeau Ouest, 23°20' S, 168°01' E, 361-365 m [BATHUS 3; sta. DWS30].

**Other Material Examined:** New Caledonia: BIO-CM, sta. DW37, 23°00' S, 167°16' E, 350 m, 1 juv. ♀ (Figure 14); 1 juv. ♀ — MUSORSTOM 4, sta. DW151, 23°57' S, 163°22' E, 350 m, 1 ♀ — BATHUS 4, sta. DW931, 18°53' S, 163°24' E, 360-377 m, 1 ♀ — From commercial sources, boat Tui II, off Belép Islands, 5 spines.

**Description:** Protoconch smooth, erect, of 1.0 whorl, diameter 1.0 mm. Axis of protoconch tilted to teleoconch. *S. rocroii* a transition to teleoconch clearly marked by numerous suture lines, the first anterior to the shoulder and followed by 8 to 10 whorls of axial ribs. Teleoconch of about five whorls. Axial sculpture of low, widely spaced ribs, seven on body whorl and ten on penultimate whorl, extending from the aperture to the base of the shell. Spiral sculpture of one whorl 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. Patellal wall with weak callus, becoming stronger and slightly reflected at the indutrix. 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 *Sclitia 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.

*Sclitia splendidula* new species

(Figures 15-17)

**Type Material:** Holotype (11.0 mm height × 6.9 mm width) (♀) (Figure 15) and three paratypes (1 ♀, 2 ♀♂) in MNHN.

**Type Locality:** South of New Caledonia, SW of île des Pins, 22°50' S, 167°21' E, 500-504 m [SMIB 8; sta. DW201].

**Other Material Examined:** South of New Caledonia, SW of île des Pins, SMIB 8; sta. DW193-196, 22°59'-23°00' S, 167°21'-167°23' E, 491-558 m, 1 ♀, 2 ♀♂ (paratypes: Figures 16, 17).

**Description:** Protoconch smooth, erect, of 0.9 whorls, diameter 1.20 mm. Axis of protoconch tilted to teleoconch (Figure 17). 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 of the shell. The ribs are produced slightly above and over subsequent growth. Spiral sculpture of 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 siphonal 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. *Nippomphera paulillus* new species. 18. Paratype, height 204 mm; north of New Caledonia, Grand Passage, 19°06′ S 163°29′ E, 230 m [MUSORSTOM 4 sta. DW185]. 19. Holotype, height 255 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 S sta. DW151]. 21. Microsculpture of teleoconch, same specimen as Figure 20. 22–24. *Nippomphera euphonia* new species. 22. Holotype, height 133 mm; north of New Caledonia, Grand Passage, 18°55′ S 163°21′ E, 350–355 m [HALO sta. 1 sta. DW01]. 23. Protoconch, same specimen as Figure 22. 24. Microsculpture of teleoconch, same specimen as Figure 22. 25–27. *Nippomphera goniata* new species. 25. Holotype, height 161 mm; south of New Caledonia, Norfolk Ridge, Bateau Azteque, 23°41′ S 168°01′ E, 250 m [SMIB S sta. DW76]. 26. Protoconch, specimen from South of New Caledonia, Norfolk Ridge, 24°16′ S 168°08′ E, 215 m [SMIB S sta. DW159]. 27. Microsculpture of teleoconch, specimen from south of New Caledonia, Norfolk Ridge, 24°16′ S 168°08′ E, 235–252 m [SMIB S 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 proscroene, thin, without internal lacations. 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 shell-like structure bordering the short siphonal canal. Body whorl slightly constricted behind the weak siphonal fascicule. Shell color white, translucent.

**Etymology:** Diminutive of the Latin adjective splendidus (-a, -um), meaning showy or magnificent.

**Remarks:** *Svetlia splendidula* closely resembles *S. rocrisi* 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 transversity gives the shell a shoji-like appearance. The bathymetric distribution of the genus *Svetlia* is unclear due to the confused generic allocation of included species, but *Svetlia splendidula* is apparently the deepest dwelling species in the genus.

Genus *Nipponaphera* Habe, 1961

**Type Species:** *Nipponaphera habeí* Petit, 1972, by ICZN Opinion 1052.

*Nipponaphera paralis* new species

(Figures 18-21)

**Type Material:** Holotype (25.5 m height × 18.0 mm width) (k) (Figure 19) and one paratype (k) (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 2 Sta. DW155, 19°06' S, 163°29' E, 230 m, 1 k (paratype, Figure 18).—Sta. DW227, 22°16' S, 167°20' E, 300 m, 1 dld.—SMIB 5; sta. DW72, 23°42' S, 165°01' E, 400 m, 1 dld [worn; allocation uncertain].—SMIB 5; sta. DW81, 23°15' S, 165°05' E, 311–330 m, 1 jmv. k (Figures 20, 21).—Sta. DW182, 23°18'-23°19' S, 168°05' E, 305–367 m, 1 dld.—BATHUS 2; sta. DW711, 22°38' S, 167°10' E, 121 m, 1 dld.—BATHUS 1; sta. DW912, 19°04' S, 163°27' E, 264–270 m, 1 jmv. k (commercial sources, boat Tcii II, off Bélep Island, 2001, 2 spms (paratypes).

**Description:** Protoconch corroded but apparently consisting of about 10 whorls. Teleoconch of 5.2 whorls. Spire high. Shoulder in lacrated axial lamellae and raised spiral cords that cross to form squarish intervals. Aperiodical axial cords set on final whorl, five on penultimate whorl, and two on antepenultimate whorl. Spiral sculpture of about 10 spiral 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 inter-

vals (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 fascicule. Outer lip thin, smooth immediately but then with about 15 lacations 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 peripheral of the whorls behind varices; primary spiral cords brown on the varices.

**Etymology:** The Latin *paralis*, 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 15 whorls, diameter 1.15 mm (Figure 20). Among the species of *Nipponaphera* known at present, this new species most resembles *X. teranachii* (Habe, 1961), *new combination*, which is more distinctly angled at the shoulder, and has coarser sculpture. (The transfer of *Trigona-aphera teranachii* 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 [HALICAM: sta. DW01].

**Other Material Examined:** From commercial sources, off Bélep Island, dredged at 400 m by boat Tcii 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 1–5 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 si-
phonous fasciole. Outer lip thin, weakly serrate. Inner portion of outer lip with a smooth rounded shell followed by about 14 sharp short lamellae. Columella with weak callus on indurated area. Columella with three folds that do not extend to the outer edge of the indurated. Posterior fold largest. Two anterior folds situated on ends of a low shell-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 kyphoma* differs from *Nipponaphera nodosicarinosa* (Fecht, 1979), *new combination* (originally in *Agatella*), in having much finer spiral sculpture, fewer and more widely spaced axial ribs, and a proportionally broader shell. (The transfer of *Agatella nodosicarinosa* 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 kyphoma* 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 Azéé [also called Banc Antigone 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°45' S, 168°09' E, 245–275 m, 1 dd.—CALSUB: dive 21, 22 45° S, 167°09' E, 340 m, 1 kv.—CHALCAL 2: sta. DW71, 24°42' S, 168°10' E, 230 m, 3 dd.—SMIB S: 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.—BELHYX 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 mezan spiral cords. Some axial ribs are stronger than others and form stronger vaurices. 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 5–6 secondary cords in intervals. Spiral cords cross the many rib-like growth lines forming finely reticulate reticulate microsculpture. Figure 27. Surface well-impressed. Body whorl slightly constricted behind siphonal fasciole. Aperture with about 17 flae 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* (= -num, angulated, in reference to the shell outline.

**Remarks:** *Nipponaphera goniata* differs from *X. teramachi* (Kabe, 1961) by its proportionally higher spire, narrower umbilicus, and its brown maculations. From *X. paraldis* 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, *X. paraldis* and *X. goniata*, coexist south of New Caledonia but have never been taken together.

**LITERATURE CITED**


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. Hatching number and shell size are related.

INTRODUCTION

The genus *Pareuthria* was proposed by Strebcl (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 Chilean 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 (Randel, 1975, 1976; Anio, 1963) to lack of a larval stage (Pizzi, 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°33′W) during February 2000. The intertidal area is occupied by mussels forming banks on rocky platforms. Specimens and spawn 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 50% 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 (N = 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 1.2–5.2 mm. N = 196, SD = 0.22, n = 10). Each capsule has an own basal membrane that is not fused with adjacent ones. The capsules measure 3.2–3.8 mm in diameter N = 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-
Figures 1–9. *N. phoebae* Philippi, 1844. 1–3. MACN 1032, adult specimen from Caleta Golfe, Santa Cruz, Argentina. Scale bar = 1 mm. 4. Detail of the protoconch. Scale bar = 1 mm. 5. Three embryos at the pre-hatching stage. Scale bar = 1 mm. 6. Freshly spawned with visible cluster of eggs. Scale bar = 3 mm. 7. Several clusters of spawns, the top capsules with three and two embryos, respectively. 8. Three eggs from the same capsule. Scale bar = 500 μm. 9. Isolated capsule with five early, shelled embryos. Scale bar = 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, opalescent and flocculates like denatured egg whites. This intracapsular 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. Hatching number and shell size are apparently related. When a single embryo developed, the shell length at the pre-hatching 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 = 0.11), 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 pusia* (Linnæus, 1758) and *Pisania 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* (Linnæus, 1758) (Fioroni, 1966; Martel et al., 1986; Portmann, 1925); *Buocyclus Bruguiera*, 1792 (Miroslavich and Dufresne, 1994); *Scalissa diva* (Reeve, 1846); Rivest, 1983), and *Colbus simpsoni* (Mörch, 1867; West, 1979), among others.

Other species of Buccinidae, such as *Engoniophos uncinatus* (Say, 1825), have direct development without nurse eggs, hatching at the crawling pediveliger stage (Miroslavich and Pechasazdeh, 1994). In this latter species, albumin in the intracapsular liquid is the most important extra food available for the embryos (Miroslavich, 1999). Given the lack of nurse eggs and the large difference between the uncleaved egg diameter and the shell length at hatching, *Pareathria phlebeca* 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 uncinatus* (Miroslavich and Pechasazdeh, 1994).

The fact that clusters formed by several egg masses of *P. phlebeca* are common could indicate a gregarious
spawning behavior as demonstrated for several other neogastropods, D'Asaro, 1970 and particularly for some bucecins such as *E. uncinatus* (Miloslavich and Penchasadze, 1994).

The egg capsules of some bucecinids 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 *Siphon*) including *C. jeffreysianus* (Fischer, 1868). In *E. uncinius* (Lebour, 1937), in other bucecinids the escape of hatchlings takes place through a wide slit that is situated in different positions according to the species (e.g., *Neptiinea antiqua* (Linnaeus, 1758), *Beringiunus turtui* (Bean, 1834), or by an aperture following the suture line of the egg capsule, as in *E. uncinatus* (Miloslavich and Penchasadze, 1994). Despite the presence of a suture line in the egg capsule 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 *Volutopsis norvegicu* (Gmelin, 1791) and *Pyrolifes deiformis* (Reeve, 1847) do not have any kind of exit hole (Thorson, 1930). This is also the case in *Parathesia plumbea*, although its egg capsules are clearly smaller.

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