<table>
<thead>
<tr>
<th>CONTENTS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fred E. Wells</td>
</tr>
<tr>
<td>Diego G. Zelaya, Cristián Huarte</td>
</tr>
<tr>
<td>Gary W. Schmelz, Roger W. Portell</td>
</tr>
<tr>
<td>Guido Pastorino</td>
</tr>
<tr>
<td>Richard C. Willan, Robert Burn</td>
</tr>
</tbody>
</table>

| Book Review | 29 |

| Notice | 30 |
Sponsored in part by the State of Florida, Department of State, Division of Cultural Affairs, the Florida Arts Council and the National Endowment for the Arts.
Ecological separation of the mudwhelks *Terebralia sulcata* (Born, 1778) and *T. semistriata* (Mörch, 1852) (Gastropoda: Potamididae) from northern Australia

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ABSTRACT

Until recently, two species were recognized in the potamidid genus *Terebralia*: *T. pulstris* (Linnæus, 1767) and *T. sulcata* (Born, 1778). Honbrink (1991) separated *T. semistriata* (Mörch, 1852) from *T. sulcata*, based on a detailed examination of shells, radulae, anatomy, and geographical distributions. The present paper provides comparative data on geographical distribution along the Australian coast, habitat, size frequency characteristics, and densities of the two species, which provides further confirmation that separate specific status is warranted.

Additional key words: Cerithioidea, mangroves, taxonomy, ecology.

INTRODUCTION

The Potamididae is one of the dominant families of mollusks in mangroves in the Indo-West Pacific region. In particular, mudwhelks of genera *Terebralia* and *Telsecopium* are among the largest and most visible of mangrove mollusks, and are key components of the ecosystem (McNae, 1967; 1968; Plaziat, 1977; 1981; Wells and Lalli, in press). In a series of studies in the Bay of Rest, northwestern Australia, and in Hong Kong, Wells (1980, 1983, 1984a, 1984b, 1986, 1990) demonstrated the importance of *Terebralia* as the Bay of Rest population was identified in the papers as *T. sulcata* but is now considered to be *T. semistriata*. For example, *Terebralia semistriata* comprised 55% of the biomass of all invertebrates in the Avicennia zone of the mangroves in the Bay of Rest. Both *T. pulstris* and *T. semistriata* can attain significant densities (often above 100 m⁻²) within mangroves, but populations reach to the edge of the Avicennia pneumatophores and no further (Wells, 1986).

In recent years there has been an increase in studies of *Terebralia*, including their general biology (Socin-dharnoo and Kastoor, 1977; Ramanbu et al., 1987), feeding (Nishihara, 1983; Shin et al., 1997), early growth (Rao, 1938; Hashimoto and Nishijima, 1987), historical declines in populations (Ohgaki and Karozuma, 2000), comparative ecology (Wells, 1980), and relationship to canopy cover (Grove, 1997; Grove and McMahon, 1997).

Until 1991, all ecological studies recognized only two species of *Terebralia*: *T. pulstris* (Linnæus, 1767) and *T. sulcata* (Born, 1778). In a major revision of the group, Honbrink (1991) recognized a third species of *Terebralia*, separating *T. semistriata* (Mörch, 1852), a taxon previously considered to be a synonym of *T. sulcata*. The work was based on a wide combination of characters, including shells, radulae, anatomy, and geographical distributions. Wilson (1993) considered the division of *T. sulcata* into two closely related species required confirmation based on ecological separation of the species. The present paper compares the ecology of *T. semistriata* and *T. sulcata*, confirming that separate specific status is warranted.

MATERIALS AND METHODS

*Terebralia semistriata* and *T. sulcata* were found to occur in separate portions of the same mangrove systems during a collecting expedition made to Darwin Harbour, Northern Territory, in June 1986. The two species were tagged for growth studies at Mandorah (12°51' S, 130°32' E) in May and December 1990 respectively and were monitored at approximately six monthly intervals. The comparative study of the two species reported here was made from 21 to 26 May 2001, on the last visit for the growth studies.

The two species were readily identified in the field using shell characters described by Honbrink (1991). The shell of *Terebralia semistriata* is larger and heavier than *T. sulcata*, has weaker sutures, is weakly sculptured with flattened spiral cords, and lacks axial ribs.

A 50 m transect tape was placed perpendicular to the shoreline at the front of the mangroves (*Terebralia sulcata*) and at the back of the mangroves (*T. semistriata*). A 1 m² quadrat was searched every 2 m from the seaward or landward fringe of the mangroves until the limit...
creek. Fifty animals were counted in each habitat. To be considered to be on the mangrove, the snail had to have the shell apex off the ground; animals lying on the mud surface with their foot attached to a mangrove were considered to be on the sediment.

Shore heights of the populations were determined on the afternoon of 22 May 2001. The time when the lower portion of the Teredalia salcata population became covered on the rising tide was noted, and the tide followed up the shoreline. Shore heights were determined by comparison with the Australian National Tide Tables (Department of Defence, 2000) for Darwin Harbour. Tides in the harbour are predominantly semidiurnal with a maximum range during the year of 7.8 m. The mean neap tidal range is 1.9 m, while springs average 5.5 m.

Data on geographic distributions of the two species were obtained by examining specimens in the Australian Museum, Sydney, AMS. The Natural History Museum, London, BMNH; National Museum of Natural History, Smithsonian Institution (USNM); Western Australian Museum (WAM), and the Zoological Museum, Copenhagen (ZMC).

RESULTS

Populations of the two species - Figures 1, 2 - were clearly separated in the mangroves at Mandorah. Teredalia salcata occupies the seaward zone of the mangroves at a mid-tidal level of 19 to 5.3 m (Table 1). The site is near a channel behind an intertidal sand beach, and is occupied by a mixed mangrove assemblage, including two large Avicennia marina trees, one of which is approximately 6 m high, small ~ 2 m Ceriops australis, and isolated trees of Rhizophora stylosa. The mangroves vary in size from small saplings to a few centimeters tall to full grown R. stylosa. The channel bank slopes steeply up to the mangrove zone, where the shore levels off. The muddy sand is then relatively flat, with shore height increasing by 0.1 m over a horizontal distance of about 25 m. This flat area is occupied by T. salcata. Shoreward

Table 1. Comparison of the nudibranchs Teredalia salcata and T. semistrata in the mangroves at Mandorah, Darwin Harbour, Northern Territory. The difference between habitats occupied to the east and west of the tidal creek was statistically significant $\chi^2 = 19.6, p = 0.05$

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Teredalia salcata</th>
<th>Teredalia semistrata</th>
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</thead>
<tbody>
<tr>
<td>Position in mangroves</td>
<td>Seaward margin</td>
<td>Shoreward margin</td>
</tr>
<tr>
<td>Shore height</td>
<td>19 - 5.3 m</td>
<td>64 - 6.6 m</td>
</tr>
<tr>
<td>Habitat</td>
<td>On sediment surface, also climbs mangrove trees, shrubs, and pneumatophores to a height of up to 60 cm</td>
<td>On sediment surface, never climbs up mangroves</td>
</tr>
<tr>
<td>Density</td>
<td>Mean 0.4 ± 0.1 m</td>
<td>Mean 1.3 ± 0.3 m</td>
</tr>
<tr>
<td>Size frequency distribution</td>
<td>Small: Mean length of population 28.5 ± 0.7 mm n = 196, range 13.44 mm Adults: Mean length 33.7 ± 0.4 mm n = 82, range 26.45 mm</td>
<td>Large: Mean length of population 10.5 ± 0.8 mm n = 198, range 13.89 mm Adults: Mean length 60.6 ± 0.3 mm n = 113, range 51.89 mm</td>
</tr>
<tr>
<td>Other pulliulans present</td>
<td>None</td>
<td>Teredalia pullula, Telescopium telescopium Cerithidea largeliert</td>
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Figures 1, 2. Shell of Teredalia salcata (1) and T. semistrata (2) from the mangroves at Mandorah, Darwin Harbour, Northern Territory. Scale bar = 30 mm.
the mangrove becomes a monospecific forest of large R. stylosa.

_Terebraha sulcata_ occur both on the sediment surface and on the lower trunks and leaves of the mangroves to a height of 60 cm, though most occur at less than 50 cm from the surface of the mud. A difference was found between locations of _T. sulcata_ on mangroves to the east and west of a shallow tidal creek. The creek is approximately 20 m wide at high tide, but only 5 m at low tide. The eastern side, where the bank is steep, contains a small, monospecific stand of Ceriops australis. Seventy-eight percent of the _T. sulcata_ were on the trees when surveyed at low tide (Table 2). The animals secrete mucus, which binds them to the mangrove. If the underlying surface is flat, the mucus can form a complete seal and function as an epiphragm. More commonly, the mucus acts to attach only the inner part of the shell aperture to the mangrove. Both adults and juveniles are found on the mud surface and on the mangroves; however, there is a tendency for juveniles to predominate on the mangroves and adults on the mud surface.

To the west of the small tidal creek, where the transects were made, _Terebraha sulcata_ were most common on the mud surface, with 66% occurring on the mud. The difference between habitats occupied to the east and west of the tidal creek was statistically significant. While no quantitative measurements were made, _T. sulcata_ under _Avicennia marina_ were largely on the sediment surface, while those in _Rhizophora stylosa_ or _Ceriops australis_ tended to be on the mangroves.

In contrast to _Terebraha sulcata_, the population of _T. semistriata_ occurs at the landward fringe of the mangroves, approximately 100 m to the northwest. The habitat is a sand surface with a mixture of mangrove species, including predominantly _Rhizophora stylosa_ and _Avicennia marina_, at a tidal height of 6.1 to 6.6 m. An upper intertidal sand beach commences at a shore height of 6.6 m, forming the upper limit of the population of _T. semistriata_. While some individuals of _T. semistriata_ occur among the _R. stylosa_ most are on the open mud surface among the _A. marina_ pneumatophores. The locations of the snails change somewhat over a two-week tidal cycle as they seek protection from desiccation among the mangrove roots during the neap tides. However, they never climb the mangroves as occurs in _T. sulcata_. Exposed flat rocks in the centre of the mangroves limit the seaward extent of the _T. semistriata_ population.

Separation of the two living populations is complete. A total of 741 _Terebraha sulcata_ were measured during the tagging experiments; no living individuals of _T. semistriata_ were found in the _T. sulcata_ population. A total of 2250 _T. semistriata_ were measured; only a single living _T. sulcata_ was found in the _T. semistriata_ population.

There are also differences in the densities of the two populations of _Terebraha_. _Terebraha sulcata_ has a very low density of only 0.4 ± 0.1 m⁻² and did not co-occur with other potamid species. The mean density of _T. semistriata_ was 1.3 ± 0.3 m⁻². Three other potamids occurred in the transects with _T. semistriata_ _Terebraha palustris_ and _Telecopium telecopium_ (Lamark, 1795) had mean densities of 6.1 ± 1.2 m⁻² and 1.6 ± 0.6 m⁻² respectively. A single specimen of Cerithidea largelberti (Philippi, 1849) was also found.

There is a clear difference in the size-frequency characteristics of _Terebraha sulcata_ and _T. semistriata_ at Mandorah (Table 1; Figure 3). The mean size of adult _T. sulcata_ is 33.7 ± 0.4 mm, with a maximum size of 13 mm. In contrast, the mean size of adult _T. semistriata_ is 60.6 ± 0.3 mm, with a maximum of 69 mm. Thus, the smallest adult _T. semistriata_ was 8 mm larger than the largest adult _T. sulcata_.

Examination of specimens in museums shows that the Australian distributional data provided for _Terebraha sulcata_ by Honbrink (1991) are inaccurate. Essentially Honbrink assumed the two species had the same geographical range on the north coast of Australia; from Shark Bay, Western Australia, to southern Queensland. _Terebraha semistriata_ is in fact widely distributed along the north coast of the continent from Shark Bay, Western Australia, to Keppel Bay on the east coast of Queensland (Figure 4). _Terebraha sulcata_ also extends south to Keppel Bay, Queensland, but it is restricted to the Kimberley, from Broome northward, in Western Australia. In the text of his paper, Honbrink (1991) refers to specimens of _T. sulcata_ from more southerly localities in Western Australia. Rowley Shoals (USNM 847084) and Bay of Rest, North West Cape (USNM 801606). Specimens of both lots were re-examined for the present paper. The label for USNM 847084 clearly states the specimens of _T. sulcata_ were collected in Broome by the Rowley Shoals Expedition. Limited collecting was done in Broome before sailing for the Rowley Shoals. The shoals are open ocean coastal reef atolls and no _Terebraha_ occur there (Wells and Slack-Smith, 1986). The specimens from the Bay of Rest (USNM 801606) was apparently first considered to be _T. sulcata_ by Honbrink. He later changed his mind and included the specimen in _T. semistriata_ in the Smithsonian collection, but apparently neglected to change his written notes. That specimen and all others collected in the Bay of Rest are in fact _T. semistriata_.

**DISCUSSION**

The present paper demonstrates _Terebraha semistriata_ and _T. sulcata_ are clearly separated ecologically. There
are substantial differences in their geographical distributions. Honbrink (1991) examined numerous specimens of *T. sulcata* from a wide range in the western Pacific Ocean, including Malaysia, Vietnam, Indonesia, Papua New Guinea, Philippines, China, Ryukyu Islands, and the Caroline Islands. In contrast *T. semistrata* is limited to the north coast of Australia and southern New Guinea.

In northern Australia, *Terebralia sulcata* is limited to the coast between Broome, Western Australia, and Keppel Bay, Queensland. *Terebralia semistrata* occurs in the entire range occupied by *T. sulcata* in northern Australia, but is also common in the large stretch of coast between Shark Bay and Broome, Western Australia. In the region between Broome and Keppel Bay, the two species of *Terebralia* are sympatric in that they inhabit the same mangrove systems, but they occupy separate areas of the mangroves. Where the two species live in the same mangrove, *T. sulcata* lives in the seaward, mid-intertidal portions of the mangroves, while *T. semistrata* lives in the shoreward, upper portions of the mangroves. *Terebralia sulcata* lives both on the mud surface and also climbs up to 60 cm up the mangroves; in contrast, *T. semistrata* are always on the sediment surface and never climb up the mangroves. Shells of *T. semistrata* are significantly larger than those of *T. sulcata* from the same mangroves.

Information on the segregation of the two species at Mandorah was collected incidentally to a major tagging program conducted to study growth in all three species of *Terebralia*. Expeditionary surveys of mollusks in the Kimberley region of Western Australia and near Gove in the Northern Territory (Wells, unpublished) have found a number of mangroves where similar segregation occurs between populations of *T. sulcata* and *T. semistrata*. Because of the considerable expense of working in remote areas, only the Mandorah populations could be examined in detail.

**ACKNOWLEDGMENTS**

Dr. J. R. Hanley, then of the Northern Territory Museum, provided detailed knowledge of Darwin Harbour and my early expeditions to the area and extensively discussed *Terebralia* with me. My subsequent research on this genus has benefited greatly from these discussions. I thank the curators and staff of the Mandorah Beach Hotel for their warm hospitality during my visits to Mandorah. Dr. M. G. Harasewych kindly arranged access to the mollusk collections of the Smithsonian Institution; Ms. Kathie Way to those of the BMNH; and Dr. Jorgen Kunde to the Zoological Museum, Copenhagen. Mr. Ian Loch and Dr. Winston Ponder generously provided distributional information from the Australian Museum, Sydney. Mr. Clay Bryce and Mr. Corey Whisson provid-
ed technical support in the preparation of the manuscript.

LITERATURE CITED


Two new species of Neolepton Monterosato, 1875 (Bivalvia: Neoleptonidae) from South Georgia Islands, South Atlantic Ocean

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ABSTRACT

Two new neoleptonid species from South Georgia Islands are described. Neolepton georgianum new species is characterized by a medium size shell, smooth shell surface, and ovate shell outline, slightly pointed at anterior end. Neolepton holubergi new species is a small size species, sculptured with well-marked and regularly spaced commarginal ribs. Moreover, the record of Neolepton parvelli from South Georgia Islands is brought into question.

Additional key words. Systematics, South Atlantic Ocean.

INTRODUCTION

Neolepton Monterosato, 1875, is a shallow-water worldwide genus of small Neoleptonidae bivalves. Recently, Salas and Gofas (1998) provided a comprehensive systematic revision of the genus, including a detailed anatomical description of the type species, Neolepton sulcatum Jeffreys, 1859.

Five Neolepton species are known from the Magellanic Region: Neolepton robbi (Cooper and Preston, 1910), Neolepton bennetti (Preston, 1912), Neolepton concentricum (Preston, 1912), Neolepton impet Soo-Ryen, 1957, and Neolepton Falklandicum Dell, 1964. None of these species have been reported from South Georgia Islands (Bernard, 1993; Salas and Gofas, 1998; Valdivinos-Zargues, 1999).

Dell (1964) described Neolepton parvelli from Macquarie Island and allocated specimens from South Georgia Islands to that species despite slight differences in shell outline and hinge details between the two localities. In the same paper, Dell (1964) misidentified neoleptonid specimens from Shag Rocks, near South Georgia Islands, as Neolepton parasiticum (Dall, 1876), a species belonging in the genus Waldo Nicol, 1966 (Nicol, 1966) and excluded from the Neoleptonidae. Salas and Gofas, 1998; Zelaya and Iturute 2002.

In the present paper two new neoleptonid species from South Georgia Islands are described.

MATERIALS AND METHODS

The studied material was collected by the RV Eduardo L. Holmberg from the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP) during the April 1996 cruise to South Georgia Islands arranged by the Instituto Antártico Argentino (Figure 1). Samples were taken with a drag net, fixed in 10% buffered formalin and transported to the laboratory where bivalves were sorted from sediments using a stereoscopic microscope and preserved in ethanol.

The studied species were fully described and illustrated using scanning electron microscope (SEM) pho.

Figure 1. Location map showing the type locality * for Neolepton georgianum new species and N. holubergi new species.
Hinge plate strong, narrowing moderately below the beaks. Left valve: cardinal 2a relatively short, straight, greatly enlarged at posterior half, cardinal 2b relatively long, forming a hook with 2a, posterior lateral PH short, strong and well outstanding from dorsal margin. Right valve: cardinal 1 high, with distal cusp and short base nearly perpendicular to anteroposterior axis. 3a slender and low. 3b quite short and very thin. PI well developed, elongate, with distal cusp.

Inner and outer demibranchs present; the outer demibranch, shorter, represents approximately the half of the inner one. Branchial filaments of outer and inner demibranchs sloping toward the anterior end. Inhalant aperture and exhalant siphon bordered by a single row of short tentacles. Large glandular cells of the mantle edge at both sides of the pedal aperture were present and well visible by transparency.

**Type Material:** Holotype, MLP 6733-1; Paratypes: 20 MLP 6733-2, 10 MACN 35290; 10 MNHN unnumbered; all from the type locality, RV Eduardo L. Holmberg, 8 April 1996.

**Other Material Examined:** >60 specimens from the type locality (MLP 6733-3, MACN 35290).

**Type Locality:** 54°18' S, 35°30' W, South Georgia Islands, 94 m.

**Distribution:** The species is only known from the type locality.

**Etymology:** The species is named after the South Georgia Islands, the type locality.

**Remarks:** Neolepton georgianum new species resembles Neolepton hupel in shell outline, differing by its smaller, higher, and more inequilateral shell. Hinge teeth, particularly the cardinal 1, are more delicate in N. georgianum than in N. hupel. The color of periostracum, pinkish in N. georgianum and whitish in N. hupel is also a distinctive character. Neolepton georgianum is also similar to Neolepton holmbergi new species, from which it differs in having a less inflated shell, shell outline with a pointed anterior end, and smooth shell surface. Both species are characterized by their pinkish periostracum.

Neolepton georgianum differs from N. cebbi, N. Bennettii, and N. concentricum by its quite ovate shell outline and smooth shell surface; the more inequilateral shell and the lower and not prominent beaks clearly separate Neolepton georgianum from N. falklandicum. Neolepton georgianum also differs from N. powelli in having a more ovate shell outline, a consistently more acute anterior end and more curved dorsal and ventral margins. Neolepton powelli was described from Macquarie Island in the same paper Dell (1961) also referred several specimens from South Georgia Islands to this species. Taking into account the narrow distribution ranges that characterize many Neolepton species, as inferred from the generic revision by Salas and Gofas (1998), it is not unlikely that the specimens from South Georgia Islands

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**Figure 10. Neolepton georgianum new species. A partially dissected specimen.**

- **L.** = 3.3 mm, showing details of soft parts anatomy; **f.** foot; **g.** gland cells of the mantle edge; **id.** inner demibranch; **od.** outer demibranch.

- **Epanography.** Hinge teeth terminology follows Bernard (1895, 1898) and Salas and Gofas (1998). Shell measurements were recorded according to the following criteria: shell length (**L.**); maximum anteroposterior distance; shell height (**H.**); maximum dorsoventral distance, perpendicular to length; shell width (**W.**); maximum distance across valves. Morphometric ratios **H/L** and **W/H** were calculated. In the text, number of specimens measured (**n**), mean, and standard deviation are given. Voucher specimens were deposited in Museo de la Plata, La Plata (MLP), Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires (MACN) and Museo National d'Histoire Naturelle, Paris (MNHN).

For comparative purposes, types of Neolepton hupel from the Swedish Museum of Natural History, Stockholm (SMNH), and photographs of the holotype of *N. powelli* from the Natural History Museum, London (NHM) were used.

**SYSTEMATICS**

*Neolepton georgianum* new species

**Figures 2-10**

**Description:** Shell delicate, medium sized; maximum **L.** = 3.4 mm, not inflated; ratio **W/H** = 0.34 ± 0.03, **n** = 12, shell outline ovate, somewhat elongate; high ratio **H/L** = 0.33 ± 0.02, **n** = 12; somewhat inequilateral, posterior end larger and wider than anterior one, which is slightly pointed; anterior and posterior half of dorsal margin only slightly curved, ventral margin evenly and widely arcuate; anterior margin short, acute, posterior margin widely and evenly curved. Beaks very small, sharply triangular, slightly displaced forward, clearly outstanding from shell surface and well visible above dorsal margin. Protoconch well-marked, smooth, not much inflated, about 300 μm long. Shell surface brilliant, periostracum pinkish, finely sculptured with very low, irregularly spaced, commarginal ribs.
Figure 19. *Neolepton holmbergi* new species. A partially dissected specimen, L = 2.7 mm, showing details of soft parts anatomy. f: foot; g: gland cells of the mantle edge; id: inner demibranch; od: outer demibranch.

reported by Dell (1964) as *N. powelli* would represent a different *Neolepton* species, possibly *N. georgianum*.

**Neolepton holmbergi** new species

**Figures 11-18.**

**Description:** Shell delicate, small sized (maximum L = 2.8 mm), somewhat inflated (ratio W/H = 0.66 ± 0.03, n = 14), shell outline ovate, somewhat elongate, high ratio H/L = 0.55 ± 0.02, n = 14), somewhat inequilateral, posterior end expanded, larger than anterior one; dorsal margin extended in a wide curve, tending to be straight at posterior half; posterior margin curved, ventral margin evenly arcuate, anterior margin short and curve. Beaks subcentral, usually eroded. Protoconch well-marked, smooth, not inflated, about 300 μm long. Shell surface dull shining or silky, sculptured with well-marked commarginal ribs, evenly spaced; periostracum pinkish.

Hinge plate solid, narrowing moderately below the beaks and at posterior half. Left valve: cardinal 2a relatively long, slender, enlarged at posterior end; cardinal 2b solid; posterior lateral PH elongated, hardly discernible from dorsal margin. Right valve: cardinal 1 high, with sharply triangular distal cusp and large base; 3a slender, long and low, 3b quite short, weak, PI well developed, elongate, with distal cusp.

Inner and outer demibranchs present; the outer much shorter, slightly overlapping the inner one and representing about the third of its length. Filaments of outer demibranch nearly horizontal. Inhalant aperture and exhalant siphon bordered by a single row of short tentacles. Glandular cells of the mantle edge present at both sides of the pedal aperture.

**Type Material:** Holotype, MLP 6734–1; paratypes: 20 MLP 6734–2, 10 MACN 35291, 10 MNHN unnumbered; all from the type locality, 8 April 1996, R.V. *Eduardo L. Holmberg*.

**Other Material Examined:** 50 specimens from the type locality. MLP 6734–3, MACN 35292.

**Type Locality:** 54°18′ S, 35°30′ W, South Georgia Islands, 94 m.

**Distribution:** The species is only known from the type locality.

**Etymology:** The species is named after the RV *Eduardo L. Holmberg*, aboard of which this species was collected.

**Remarks:** The general shell outline and the shell surface sculpture of well-marked commarginal regularly spaced ribs are diagnostic features of *Neolepton holmbergi* new species. *Neolepton holmbergi* is most similar to *Neolepton georgianum* new species, differing in having a more inflated shell, not much inflated protoconch and shell surface with stronger and regularly spaced commarginal ribs. The more triangular shell outline with nearly equally arcuate anterior and posterior ends is also distinctive for *N. holmbergi*. The hinge in *N. holmbergi* differs in having a high cardinal 1, with a wider base and triangular distal cusp.

*Neolepton hupeli,* another similar species, clearly differs from *N. holmbergi* by its larger size, smooth shell surface, stronger hinge teeth and whitish periostracum.

*Neolepton holmbergi* differs from *Neolepton Falklandicum* by its well-marked shell surface sculpture and not prominent beaks. *N. holmbergi* differs from the other Magellanic *Neolepton* species (*N. cobbii*, *N. concentricum* and *N. bennetti*) in being smaller, having a relatively lower and markedly ovate shell outline.

**ACKNOWLEDGMENTS**

The authors wish to thank A. Warén and K. Sindemark (SMNH) for allowing the study of types of *Neolepton hupeli* and K. Way and A. Campbell (NHM) for sending photographs of the holotype of *N. powelli*. D. Nahabedian kindly made available the specimens collected by the RV *Eduardo L. Holmberg*. The authors are members of the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET). This work was partially supported by a grant from Fundación Antorchas to D. Z.

**LITERATURE CITED**


A new species of *Metula* (Gastropoda: Colubrariidae) from the Lower Miocene Chipola Formation of Florida

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**ABSTRACT**

*Metula mioecenica*, a new species described from the Lower Miocene Chipola Formation of northern Florida, is known only from the holotype that was extracted from an ancient reef deposit along Tennille Creek in Calhoun County. Comparison of the new species reveals similarities with fossil congener *Metula johnsoni* Solander, 1766, from Eocene deposits of England and *Metula pilsherti* Olsson, 1912, from the Plio-Pleistocene Charco Azul Group of western Panama and Costa Rica.

Additional key words: Buceinoida, Neogene, Tertiary, fossil.

**INTRODUCTION**

A number of Recent and fossil species of the genus *Metula* are recorded from around the world, but most are rare. With few exceptions, nearly all living species occur in deep-water environments. The oldest known *Metula* comes from the Eocene, but most of the reported fossil species come from the late Tertiary. In Florida, two species occur in Neogene deposits. *Metula roberti* Olsson, 1967, has been collected from the Pliocene Pinecraft beds (upper Tamiami Formation) along the Kissimmee River and from quarries in Sarasota County, and a second species, described herein, has been recently discovered in the Lower Miocene Chipola Formation in northern Florida. The new species was collected from an ancient reef environment along Tennille Creek in Calhoun County.

Type and figured specimens referred to in this paper are deposited in the Invertebrate Paleontology Division of the Florida Museum of Natural History, University of Florida (UF), Gainesville.

**SYSTEMATICS**

Family Colubrariidae Dall, 1904  
Genus *Metula* H. and A. Adams, 1853  
Subgenus *Metula* H. and A. Adams, 1853  
*Metula* (*Metula* mioecenica new species  
Figure 1)

**Description:** Shell elongate-fusiform. Protoconch glossy. 2 1/2 whorls. Teleconch whorls 7, slightly convex. First two whorls with cancellate sculpture, axial sculpture becoming prominent on third and fourth whorls and with 2 to 3 distinct beaded spiral cords appearing below suture. Surface of remaining whorls generally smooth, exhibiting only very faint cancellate pattern, and spiral cords below shell suture losing their beaded sculpture. Aperture narrow, elliptical, slightly less than 1/2 shell length. Posterior portion of aperture attenuated, and canal region slightly raised, with lirations on inner surface of outer lip. Columella and parietal wall of aperture with callus wash.

**Type Material:** Holotype, UF 110275, length 24.2 mm, width 8.9 mm.

**Type Locality:** Tennille Creek, about 0.75 kilometers west of Chipola River (SE1/4, Sec. 12, T10N, R10W), Calhoun County, Florida (Tahlequah University locality TU 951), Chipola Formation.

**Distribution:** Known only from the type locality.

**Etymology:** Named for the epoch from which the species was collected.

**Discussion:** The oldest species of the genus *Metula* in the United States come from Eocene deposits in Maryland (Clark and Martin, 1901) and Mississippi and Louisiana (Palmer and Brann, 1966). There are no recorded specimens of *Metula* from the Eocene or Oligocene of Florida. Different species of *Metula* have also been recovered from Eocene deposits in France and England. For comparison purposes a specimen of *Metula johnsoni* (Solander, 1766) from the Upper Eocene Barton Beds in Hampshire County, England is illustrated (Figure 3) below the newly described *Metula* (*Metula* mioecenica (Figure 1). The similarity in sculpture and shape between *M. johnsoni* and *M.* (*M.*) mioecenica and to other fossil and Recent *Metula* found in the Caribbean suggests an evolutionary linkage between the European and New World species.

Neogene *Metula* are known from numerous locations including New Hebrides (Ladd, 1976, 1982), Fiji (Ladd, 1977), Trinidad (Jung, 1969), Costa Rica (Olsson, 1922);
10) material, lhibers inia- than a Mctula the laatt'd Figure siS), Mctula Sioinni short W. as- i'anania. •'';< the kcnisis aii<l Sralc 5 his cca bar rohcrti part Fii;iii'c'. w. KKJriiii^ Fii;iland. 
(1964) in incomplete earli'i'St'. am Insti 1. inr^tli 23. That Neogene Mctula 
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i'niiiiinaii (OLsson, 1942) as a synonym for Mctula. They also reclassified Mctula (Minitula) minor Olsson and Bayer, 1972, the type species of the sub- genus Minitula, into the family Columbellidae. Because of the attenuated posterior aperture and liminations on the inner surface of the outer lip, the Chipola Mctula is assigned to the subgenus Mctula.

There has been considerable uncertainty about the correct family classification of Mctula. In a review of this controversy, Boucliet (1988) noted that some investigators opted to keep the genus in the family Buccinidae, while others felt that certain anatomical features of the radula justified assignment to the family Columbellidae. Ben and Maxwell (1987) in an extensive revision of the Columbellidae and related genera, classified Mctula Colum- bellina, and several related genera in the subfamily Pisaniinae into the Buccinidae. Verniquet (2001) in his review of the subfamily Pisaniinae, supported the placement of Mctula in the Colubrariidae, which he maintained as a separate family near Buccinidae. His decision was based upon anatomical characteristics, shell morphology, and ecological factors. Commensurate with his findings, herein we follow Verniquet's assignment.

Mctula (Mctula) mioecenica comes from the Lower Miocene Chipola Formation, which has an age range of 15 to 18 million years. Jones et al., 1993). Therefore, this newly discovered species is the oldest Neogene Mctula thus far reported. In general form it bears a stronger similarity to M. jincera from the Upper Eocene Barton Beds of England (Figure 3) than to the more recent Florida Pleiocene species Mctula (Mctula) roberti (Figure 2). Among Neogene species, M. (M) mioecenica is similar to Mctula (Mctula) pilsbryi Olsson, 1942, from the Pleis- stocene Chapar Azul Group in western Panama and Costa Rica. However, M. (M) mioecenica is about half the size of M. (M) pilsbryi and lacks the well-defined cancellate sculpturing on all but the first two whorls of the teleoconch. Mctula (M) kerrisia Ladd, 1976, from Pleistocene deposits in New Hebrides is also similar to M. (M) mioecenica. Both have approximately the same

Figures 1-3. Florida fossil Mctula and an Eocene counterpart from England. 1. Mctula mioecenica, new species, Holotype. UF 110275, length 242 mm, width 8.0 mm. 2. Mctula roberti Olsson, 1967, Selected specimen from Kassimnee Canal, UF 62412, length 23.8 mm, width 9.5 mm. 3. Mctula jun- cea Solander, 1766. Selected specimen from Barton Beds, England. UF 1228, length 17.2 mm, width 6.2 mm. Scale bar = 10 mm.
shell dimensions and contours and both possess a very faint cancellate sculpture on the lateral whorls. However, M. M. miocenica has two to three prominent spiral bands that appear just below the sutures and in the early whorls there is also a more prominent cancellate sculpture pattern. Among extant Caribbean species M. (M. miocenica) is most similar to Metula (Metula) elleni Olson and Bayer, 1972. Both have approximately the same body dimensions and shape and both have fine to smoothly cancellate body sculpturing. Metula (M. miocenica), however, is more slender, has a more elevated spire, and the body whorl is more sharply angled toward the base.

ACKNOWLEDGMENTS

The authors extend a special note of thanks to Cecil Sexton (Calhoun County, FL) for granting permission to collect on his property. Richard Petit (North Myrtle Beach, SC) and Greg Herbert (University of California at Davis, CA) kindly assisted with the acquisition of relevant literature. George Hecht (UF) and José H. Leal (The Bailey-Matthews Shell Museum, FL) provided photographic support and a specimen loan, respectively. This is the University of Florida Contribution to Paleobiology 541.

LITERATURE CITED


A new species of Ancillariinae (Gastropoda: Olividae) from the southwestern Atlantic Ocean

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ABSTRACT
A new species of the ancilliid genus Analida is described from the southwestern Atlantic off Brazil, Uruguay, and Argentina. Analida joscarlosi new species was identified as Ancilla dimidiata and A. tankervilli by previous authors. Detailed study of the type material and other specimens of the two latter taxa allowed for the recognition of the new species. Adults and juveniles of Analida joscarlosi new species from several localities along the southwestern Atlantic coast are illustrated, described and compared to other living congers.

INTRODUCTION
The genera Analida, Ancilla, and several other Ancillariinae from the southeastern Atlantic were thoroughly studied by Kilburn (1977, 1980, 1981, 1993). Kilburn and Bonechet (1988) also studied the genus Analida from New Caledonia describing four new species and one subspecies. Besides Analida joscarlosi new species, there are four species of Ancillariinae in the southwestern Atlantic: Ancilla fanatost Matthews, Matthews and Dijek, 1980, A. (Hesperanilla) matthewsi Burch and Burch, 1967 and Eburne buernautii (Bernardi, 1859).

Analida tankervilli (Swainson, 1825) occurs only off northern South America (i.e. Isla Margarita, Venezuela). Rios (1994) expressed doubts about the presence of this species off Brazil. There is not, however, a systematic treatment of the subfamily for the species occurring in the southwestern Atlantic.

Dall (1900) mentioned young and dead specimens of Analida tankervilli off Río de La Plata (Argentina) and the Brazilian coast collected by the Albatross expedition at stations 2764 and 2762, respectively. Perhaps influenced by the latter record, Fernández (1965) also cited Ancilla tankervilli, a Venezuelan species and type of the genus Analida H. and A. Adams, 1854, from off Argentina. Scarabino (1977) considered this record as Ancilla dimidiata and extended the known range of this species to San Matías Gulf, Río Negro Province, Argentina (~41°S). Previously, Strebel (1908), based on material of the Swedish Svalbard Expedition, illustrated what he identified as A. dimidiata from the southern coast of the Brazilian state of Rio Grande do Sul. Marcus and Marcus (1968) studied the anatomy and mentioned of specimens supposedly of Ancilla dimidiata but based the name on specimens identified by Klappenbach from the littoral of Rio de Janeiro State, Brazil (Ubatuba and Angra dos Reis). The specimens studied by Marcus and Marcus are herein assumed to belong to the new species.

In his original description of Ancilla dimidiata, G. B. Sowerby II (1859), gave Red Sea as the type locality. Later, E. A. Smith (1915: 96) challenged that locality and mentioned that G. B. Sowerby III's record (1892) of A. dimidiata from South Africa was probably incorrect. This latter opinion was confirmed by Kilburn (1981: 108) who synonymized A. dimidiata (G. B. Sowerby III, 1892) with G. B. Sowerby II, 1859) with Ancilla maravonata (Reeve, 1864). The present report includes, in addition to the description of the new species of Analida a study of the synonyms of Ancilla dimidiata G. B. Sowerby II, 1859), the holotype of Ancilla tankervilli Swainson, 1825, and several other relevant lots of these species.

MATERIALS AND METHODS
The specimens examined in this study are deposited in the collections of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires (MACN), Museo de La Plata, La Plata, Argentina (MLP), and the Museo Nacional de Historia Natural Montevideo, Uruguay (MNHN). Two syntypes of Ancilla dimidiata and the holotype of Ancilla tankervilli are housed in the Natural History Museum, London (BMNH), BMNH 1975/32 and BMNH 1975/24 respectively. Reference material from Brazil housed at the Museu de Zoolgia da Universidade de Sao Paulo, Brazil (MZSP) and at the J. C. Tarasconi collection - Porto Alegre, Brazil were also studied.

Dissections were performed on ethanol-preserved specimens. The radulae were prepared according to the
method described by Solem (1972). Most photography was taken using a digital camera. All images were digitally processed.

Most of the terminology used in the description of the species followed Kilburn (1977, 1981), Marcus and Marcus (1968), and Vokes (1991). However, the posterior groove, a typical line of Marcus and Marcus (1981), is here defined as the narrow and weak groove of the last whorl, which starts in the parietal callus, runs parallel to the ancillid groove, and ends in the labrum. The area between the posterior groove and the ancillid groove is here referred to as the last whorl middle band. A data matrix based on 26 shells was prepared including their maximum length and width and the length of the region between the posterior groove and the ancillid groove when both grooves reach the edge of the labrum (see Table 1). Figures 22-25 show the different shell terminologies.

### SYSTEMATICS

Class Gastropoda Cuvier, 1791
Order Neogastropoda Wenz, 1938
Family Olividae Lapreille, 1825
Subfamily Ancillariinae Swainson, 1840

**Remarks:** I follow Kantor and Bouchet (1999), who showed that Ancillariinae Swainson, 1840, has priority over Ancilliidae H. and A. Adams, 1853.

**Genus Ancilla H. and A. Adams, 1853**

**Type Species:** *Ancilla tankervilii* Swainson, 1825, by subsequent designation of Vokes, 1939.

### Ancilla josecarnosi new species

**Figures 1-14.**

*Ancilla tankervilii* Dall, 1900: 310.  
*Ancilla dimidriata* Stehl, 1900: 25, pl. 1, figs. 2a-c.  
*Ancilla tankervilii* Fernández, 1965: figs. 1-4, Castellanos, 1970: 121, pl. 9, fig. 7, non Swainson, 1825.

**Diagnosis:** Shell small, elliptic ovate, spine low, covered by primary callus, secondary callus tongue-shaped, aperture thin, with labral denticle subterminal, conspicuous. Columellar pillar straight, 3-1 oblique pleats, posterior groove starting at the parietal callus, slightly adaxial to the posterior angle, ending gradually below the middle part of labrum. Adult specimens show sudden change in direction of posterior groove toward anterior edge of labrum. Shell bright-white, adult specimens with faint, darker subterminal line visible under spire glaze and comprising a region delimited by the posterior groove and the ancillid groove; last whorl middle band darker.

| Table 1. Shell measurements—mm of Ancilla josecarnosi new species and A. dimidriata syntypes. |
|------------------|------------------|------------------|
| Ancilla josecarnosi new species | | |
| | Shell length | Shell width |
| MACN 6319 | 17.6 | 8 |
| Paratype | 15.4 | 7 |
| Paratype a | 15.6 | 6.8 |
| Paratype b | 15.8 | 6.8 |
| Paratype c | 19.5 | 8.9 |
| Paratype d | 21.3 | 9.6 |

**Description:** Shell small, up to 22 mm in length, elliptic-ovate, somewhat fusiform, with five smooth, flat whorls. Protoconch with 2.5 whors, completely smooth, translucent. Suture impressed, visible only in the first whorls of young specimens, covered in adult specimens by primary callus, except on protoconch. Secondary tongue-shape callus extends from the middle of the penultimate whorl, over the posterior angle of the aperture and the posterior part of the labrum, to the beginning of the columellar pillar. Last whorl slightly shouldered. Aperture triangular, posterior end strongly angled, la-
brum very thin, sharp, curved; basal denticle subterminal, conspicuous; labral base projects beyond base of columnella base. Siphonal notch deep. Columnella pillar straight, with 3–4 oblique pleats, the posterior larger reaching the parietal callus, anterior fasciolar groove fairly deep, anterior and posterior fasciolar band ("opaque area" of Marcus and Marcus, 1984) of similar width and divided by a weak median ridge; posterior fasciolar groove very weak. Posterior groove starting slightly above the posterior angle of the aperture and ending gradually always abapically to the middle part of labrum. Adult specimens show sudden change of direction of posterior groove toward the anterior edge of the labrum (Figure 5). Ancillid groove shallow, ancillid band narrow.
Growth lines covering entire shell, very conspicuous on last whorl, forming a brown color pattern. Microskagreen sculpture ("microscopic pistules" sensu Kilburn, 1981) regularly packed in both calices and less dense on columellar pillar and adapertural part of labrum. Color bright white; some specimens (usually adults) with a subsurface dark but faint line under spine or groove. Region delimited by the posterior groove and the ancillid groove ("basal groove" of Marcussen and Marcussen, 1966, herein referred to as "last whorl middle band") brownish or dark tinted. Operculum delicate, pale-yellow, ovate-elliptical, somewhat oblong, nucleus subterminal, attachment area on left side (Figures 13–14).

Radula is rachipogonate; rachidian teeth with three cusps, the central one shorter than the laterals. One denticle between the central cusp and the laterals; sometimes an extra obsolescent, asymmetric denticle is visible, see Figure 12, always arising from the base of the rachidian tooth. Marginal teeth curved with a thick attachment area.

It is interesting to remark that the short central cusp of the rachidian in radula is a recurring character in the genus *Amalda* (as far as it can be seen on *A. lemairei*, *A. crassieri* and *A. jemuri*, all Kilburn, 1977). However *Amalda Hesperinclita matthewsi* Burch and Burch, 1967 (according to Kilburn, 1981:450 figure 239) has also the same kind of rachidian teeth. The full significance is unknown.

**Type Material (Table 1):** Holotype: MACN 6519. P. H. Bruno Videla and A. Poozi coll., May 1946, dead shell. Paratypes: two shells, MACN 23489, 34°40' S 55°18' W, 100 m depth, 18 Sep 1938, one shell, MACN 9364-57, Mar del Plata, Mar. 1915; two shells + one live-collected specimen, MACN 15355-6, 34°40' S 53°59'30" W, 29.3 m depth, Mar. 1925; one shell, MACN 5587-16, ABA (research vessel) Polyxena, Station 60, off Mar del Plata; one shell, MACN 10707, Mar del Plata: one shell, MLP 1451. Miramar, Buenos Aires: one shell, MNHN 94111, Cabo Polonio, Departamento Rocha, Uruguay, fishing boat, 3 Nov 1938.

**Type Locality:** Golfo San Matías, Río Negro Province, Argentina (~44°1' S).

**Other Material Examined:** One shell, MACN 10295, Mar del Plata: Buenos Aires: one live-collected specimen, MLP unnumbered, Mar del Plata: Figures 7–8, this is probably the same specimen mentioned and dissected by Fernández, 1965; she did not, however, report the collection number and, as far as information on the label goes, the material has no special nomenclatural standing; four live-collected specimens, Tarasconi collection, southern coast of São Paulo State, Brazil, 20–40 m depth, December 1986, five live-collected specimens, Tarasconi collection, off Laguna, Santa Catarina State, Brazil, 60–80 m depth, Apr. 2000, three live-collected specimens, MZSP 328883, off Angra dos Reis, Rio de Janeiro State, Brazil, Mar 1969.

**Distribution:** From Espíritu Santo, Brazil (~89°20' W to 33°05'–51°10' W (south of Rio Grande do Sul State, Brazil), 50 m depth, station 4 of the Swedish South Pole Expedition, as *Amalda dimidiata*; Scarabino (1977) cited this species (also as *Amalda dimidiata*) from off Bahía San Antonio, Golfo San Matías (~41°5' S in sandy bottom). Dall's material from the Albatross Expedition originally identified as *Amalda tankervilli* (A. tankervilli of Dall) and later identified by M. A. Klappenbach as *Amalda dimidiata* (A. Kabat pers. comm.); USNM 96128, Station USFC 2762, 111.6 m depth, 20°08' S, 41°34' W (30 Dec 1897); USNM 96169, Station USFC 2764, 21.0 m depth, Samborombón Bay, 36°42' S, 56°23' W (12 Jan 1888); both stations published in Dall (1890); and USNM 221495 and 68651 are from station USFC 2766, 19.2 m depth, Samborombón Bay, 36°47' S, 56°23' W (1 Dec 1888) (Kabat, pers. comm.).

**Etymology:** Named after my friend and serious collector Jose Carlos Tarasconi from Porto Alegre, Brazil.

**Comments on Literature Records:** Strehbl (1908), 33°05'–51°10' W (south of Rio Grande do Sul State, Brazil), 50 m depth, station 4 of the Swedish South Pole Expedition, as *Amalda dimidiata*. Scarabino (1977) cited this species (also as *Amalda dimidiata*) from off Bahía San Antonio, Golfo San Matías (~41°5' S in sandy bottom). Dall's material from the Albatross Expedition originally identified as *Amalda tankervilli* (A. tankervilli of Dall) and later identified by M. A. Klappenbach as *Amalda dimidiata* (A. Kabat pers. comm.); USNM 96128, Station USFC 2762, 111.6 m depth, 20°08' S, 41°34' W (30 Dec 1897); USNM 96169, Station USFC 2764, 21.0 m depth, Samborombón Bay, 36°42' S, 56°23' W (12 Jan 1888); both stations published in Dall (1890); and USNM 221495 and 68651 are from station USFC 2766, 19.2 m depth, Samborombón Bay, 36°47' S, 56°23' W (1 Dec 1888) (Kabat, pers. comm.).

**DISCUSSION**

*Amalda josecarlosi* new species was confused with *A. dimidiata* and *A. tankervilli* by various authors (Dall, 1900; Strehbl, 1908; Fernández, 1965; Castellanos, 1970; Scarabino, 1977; among others). Kilburn (1977) provided a short diagnosis of the genus *Amalda* that was adopted herein; however, the definition of a new character was necessary in order to clarify the shell morphology of the new species as well as the type. Subgeneric assignment was avoided because as Kilburn remarked subgenus "are in urgent need of revision".

*Amalda tankervilli* (Figures 15–17) from Venezuela, mentioned by Dall (1890) from off Rio de la Plata and erroneously identified by Fernández (1965), is a species large for the genus, which reaches more than 75 mm, with an almost smooth columella pillar and a thin fringe between the posterior groove and the ancilliid groove, defined here as the last whorl middle band. Coloration is also very different, distinct shades of pale orange for *A. tankervilli* and whitish for the new species. Dall (1890), Fernández (1965), and Marcussen and Marcussen (1968), among other authors, used an encumbered version of the spelling of this species, *A. tankervilli*. However, according to the Articles 32.3 and 32.5 of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature, 1999) the original incorrect latinization is not considered an error and therefore does not warrant emendation.

Two syntypes of *A. dimidiata* housed at the BMNH apparently have never been illustrated after the original description. Unfortunately, soft parts were not preserved. They are similar to the new species here described, but has a thinner profile, the columella pillar
Figure 26. Scatter diagram showing the relation between length of the field between the apical line and anterior band vs. shell length/width of Anllda joscerclosi new species and subtypes of Amalda dimidiata – N = 20

is straighter and with less conspicuous plats, and the anterior fascial groove is deeper. The posterior groove in both subtypes of A. dimidiata always reaches the labrum above its middle point. On the other hand, in all the specimens studied (more than 20 at different ontogentic stages and from different localities), the apical line of the new species always reaches the labrum anterior to its middle point, particularly in adult specimens. The scatter diagram (Figure 26) showing a plot of the length of the last whorl middle band at the edge of the labrum (the band between the posterior groove and anterior groove) vs. the shell length/width clearly shows the difference between the two subtypes of A. dimidiata and several specimens of A. joscerclosi new species. As far as I know, the geographical distribution of A. dimidiata does not include waters off Argentina. Due to the large and poorly explored Brazilian shelf, its presence or absence off this country could not be verified. Kilburn (pers. comm.) considered the Red Sea as an erroneous locality. The real range of A. dimidiata remains uncertain.

Voskul (1991) redescribed and illustrated the recent species of the genus Eburna Lamarck, 1801, including two species from the southern Caribbean, E. glabra (L., 1758) (type species of Eburna) and E. balteata (Swainson, 1825) and one from off northern Brazil, E. henardi (Bernardi, 1859). In addition, Kilburn discussed the diagnostic characters of the genus Anllda. He pointed out the definition of Amalda of some recent authors better fits some species of Baryspira than A. tankerrillii, type species of Anllda. According to Voskul (1991) the diagnosis of Anllda followed by Chayan (1965) and Kilburn (1977) was based on species of Baryspira rather than on A. tankerrillii. Voskul finally concluded that Anllda should be considered as a subgenus of Eburna. I agree that the Anllda species described by Kilburn and Bouchet (1988) and Kilburn (1993) present several distinct characters that are somewhat far removed from those in A. tankerrillii. Perhaps future research will show that Anllda deserves further taxonomic division.

The morphology of the umbilicus of the species included in Eburna are in fact a conclusive character that should warrant full generic status. However, Anllda (type species Anllda tankerrillii) should also be considered as a fully-fledged genus with two species in the southwestern Atlantic.

According to the literature, most of the species of Ancillariae occur outside the New World, South Africa, the Arabian Peninsula, New Caledonia, and Indonesia appear to be the regions with the largest number of species. Anllda joscerclosi new species is the only species of the subfamily living in Argentina. In addition, despite the good development of Tertiary deposits in Patagonia, there is no record of fossil representatives of this genus. Therefore, Anllda joscerclosi new species, the southernmost living species of the subfamily, is probably derived from the Caribbean stock in which the type species of the genus presently occurs.

ACKNOWLEDGMENTS

I am grateful to R. Kilburn (Natal Museum, South Africa) for sharing information about the geographical distribution of species of Anllda. A. Kubat (USNM) provided essential data about Dall's material. A. Tabiño (MACN) and C. Irurti (MLP) kindly gave access to malacological collections. L. Simone (Museu de Zoologia, USP, Brazil) provided information and specimens from Brazil. José C. Tarasconi (Porto Alegre) as usual kindly provided specimens from his extensive collection. Fabrizio Scarahino (INAPE, Uruguay) provided beneficial criticism. Two excellent reviewers improved the original manuscript considerably. This work was supported in part by the Project PICT No. 01-04321 from the National Agency for Scientific and Technological Promotion, Argentina.

LITERATURE CITED


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On the publication date, authorship, and type species of *Unbraculum* and *Tyldodina* (Gastropoda: Opisthobranchia: Tyldoinoidea): a rejoinder

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ABSTRACT

Further review of the literature reveals that type designations earlier than, or different from, those proposed by Valdés (2001) are available for *Unbraculum* Schumacher, 1817, and three of its synonyms *Unbraculum* Lamarck, 1819; *Gastroplax* Blainville, 1819; and *Unbraculum* Férussac, 1822. The type species of *Unbraculum* is *U. chinense* and the specific name should be attributed to Lamarck, 1801 (who called it *Unbraculum* chinense). This species is a junior synonym of *Patella unbraculum* Lightfoot, 1786, a name introduced in an anonymous work. The neuter gender of *Unbraculum* must be reflected in the names of attributed species. Rafinesque’s descriptions of his genera *Tyldodina* and *Ogyne* are reproduced from his 1814 work. In the interests of nomenclatural stability, it is recommended that *Unbraculumidae* be accorded the status of *nonmen protection* in favour of *Tyldodinaidae* for the monophyletic higher taxon (with the rank of superfamily) encompassing the families *Unbraculidae* and *Tyldodinidae*.

INTRODUCTION

Stimulated by the recent synthesis by Ángel Valdés (2001) of nomenclatural problems associated with the genera *Unbraculum* and *Tyldodina*, the present paper attempts to determine the valid name, exact dates of publication, and type species of these two mollucan genera and their synonyms. Close scrutiny of the literature reveals several earlier overlooked type designations, and provides a different interpretation of the correct name of the type species of *Unbraculum*. The original 1814 descriptions by Rafinesque of his genera *Tyldodina* and *Ogyne* are reproduced from this rare work. Adamson’s (1757) “Le Liri” from Senegal, the basis of *Patella perstera* Gmelin, 1791, is briefly reviewed and commented upon.

DISCUSSION

*Unbraculum*: Its Type Species and Valid Name

Schumacher (1817) included only one species in his new genus *Unbraculum*: the "Parasol Chinese" *Unbraculum chinense*. That is, the type species was clearly established by monotypy. Schumacher’s text can be easily mis-read, as the genus is diagnosed on page 53 and described on page 177, with the type species designation on the top line of page 178 where it looks more like a running head rather than the first line of text for that page.

The question next to determine is to which author should the species name be attributed. Schumacher is the obvious choice as author of the species name *chinense* because it was he who correctly latinized and cited the "*Unbraculum chinense*" of [the non-bi-nominal] Clemmitz (1788) as first among his references. Indeed, both Pilshy (1896) and Sherborn (1930) attributed the species name in the binomen *Unbraculum chinense* to Schumacher (1817), Harris (1930) went a little further, allocating authorship of the species name to "Schumacher (ex Martinus)", that is Clemmitz (1788). However, to quote Valdés (2001: page 30), "*Unbraculum chinense* of Clemmitz (1788), was published in binominal form by Lamarck (1804) as *Unbraculum chinense*" when Lamarck published it in the synonymy of his new species of supposed bivalve *Avarde umbella* [Deshayes (1827) effectively removed *Avarde* from mollusc literature by pointing out that it was an "epiphise de vertébres de Cétacés."] Nowadays, names first published in synonymy are not available (ICZN 1999: Article 11.6). If, however, a junior synonym introduced into the literature has been treated as an available name before 1961 and adopted as the name of a taxon, it is made available with author and date from its first introduction as a synonym (ICZN Articles 11.6.1 and 50.7). In this instance, *Unbraculum* was not adopted as the name of a taxon except by Delle
Umbrellidae and Umbrellae: The Synonyms

When Dall (1889) pointed out the priority of Umbrellum Schumacher, 1817, over Umbrella Lamarck, 1819, he also introduced the family name Umbrellidae, which today is in constant and consistent use by malacologists worldwide. Pilsbry (1896) was the first subsequent author to accept and use both Umbrellum and Umbrellae. The earliest family name appears to be the vernacular "Les Ombrelles" of Férotte (1822), the formal latinization of which has never taken place. The first properly latinized family name was Umbrellidae by Gray, 1827. Operculatidae was established by H. and A. Adams, 1851; Dautzenberg and Bonge, 1933, seem to have been the last authors to use Umbrellae, though as late as 1951, Barnard still called the genus Umbrella Odhner, 1939, created the subordinal rank Umbrellulacea to include the two families Umbrellidae Dall, 1889, and Tylolepididae Gray, 1847. Names of higher rank than superfamily are not governed by the Code of Zoological Nomenclature (ICZN, 1999); therefore the correct authorship at subordinal rank is Umbrellulacea Odhner, 1939. Ordinal rank has been accorded the group by Minchin and Starobogatov, 1978, and by Hatamian (2000) with the names Umbrellulidae and Umbrellulomorpha, respectively. When this higher rank name is ranked as a superfamily i.e., Umbrellaidea, it is subject to the "Principles of Co-ordination" (ICZN, 1999).

As early as July 1823, Children, 1823a, but no author's name appears on the actual works, and again later that same year, Children, 1823b. Children wrote: "Umbrella Type Umbrella indica. Patella umbellata. Gmel. Indian umbrella, commonly called the Chinese parasol." This type designation is valid, and must stand. Kentnard et al., 1931. Children also directed attention to the synonymy of Lamarck's indica with the earlier Patella umbellata Gmel., 1791. Pilsbry (1896) later selected the name prior P. sinica Gmel, 1791 as the better name to use for this species. Page xix of Férotte (1821-1822) appeared as part of the text as "Auchenorhinus" published on 14 April 1822. Kentnard, 1942: Umbrella Férotte therefore dates to 1822; its type species, Umbrella indica (Lamarck, 1819), was subsequently designated by O'Donoghue (1929). Thus, the type designations by Valdes (2001) for Umbrella and Umbrellula are both unnecessary.
O Donoghue accepted Operculatum as a genus name introduced by H. and A. Adams (1851) and designated as type one of the included species, O. mediterraneum (Lamarck, 1819). However, it was Mörch (1852) who validly introduced this genus name, at which time mediterraneum was not among the original included species. Valdés (2001) rectified this situation by selecting Umbrella indica (Lamarck, 1819), one of the species listed, albeit as a synonym, in Mörch's paper, O. sp. (Blackmore), a binomen originally used by Linnæus (1753), in a non-binominal, pre-Linnean work, was, like Umbella chinensis, latinized and introduced in the synonymy of Patella sinica (Gmelin, 1791) by de Roissy (1804) and again in the synonymy of Patella umbellata (Gmelin, 1791) by Dillwyn (1817). Fortunately, the genus name was not adopted as a valid taxon except by Mörch (1852, 1855) and H. and A. Adams (1854) who, when it was already the junior synonym of U. thebaidica, Umbrella, Gastroplax, and Umbrella. The specific name bière has never been adopted, except by Mörch (1852).

Blainville (1819) included only the non-binominal species "Patella umbraica" in his new genus Gastroplax in 1820 he latinized the name as Patella umbraica. Chemnitz (1788) actually called his species "Der chinesische Sommensehurn", and his Latin description read "Umbella chinensis, testa integra, subrotund, diaphana, albida, depressa, planinclusa, verte, latero, cavitate lineis radiatis, flavescens, margine altissimo".

Nowhere does "umbraica" or umbraica appear. Whilst Blainville's generic description is valid (ICZN 1999, Article 12.2.7), inclusion of a non-existent species name from a non-binominal work does not constitute designation of a type species by monotypy, contrary to the statement of Valdés (2001). Unless, of course, Gastroplax and "Patella umbraica" could be considered as a combined description of a new nominal genus and single new nominal species (ICZN 1999, Article 12.2.6); in which case Blainville (1819) would be the author of both names. However, Blainville himself did not consider this to be the case, because in 1820 he named the species upon which he based his genus, Gastroplax tuberculatus, whereupon it became type species by subsequent monotypy (ICZN 1999, Article 69.3).

At the same time, Blainville (1820) introduced in synonymy the binomen Patella umbraica, attributing it to Chemnitz. Patella umbraica is both a primary homonym and junior synonym of Patella umbraica (Röding, 1798), and is of no further concern. Curiously, Röding's (1798) authorship of the species name umbraicum has been unnecessarily revived by Sabelli et al. (1999).

The earliest available name for the type species of Umbraicum is Patella umbraica (L. 1758). Foster (1758) introduced in an anonymous work, and it is generally accepted that all species names proposed for the "Parasol clímato" are synonyms (Rehder 1967). Lightfoot (1758) correctly combined Patella, feminine in gender with umbraicum, neuter, as a noun in apposition. He did not write Patella umbraica as used by Valdés (2001), though this spelling was utilized in the early days by Röding (1798) and Blainville (1820). The genus name Umbraicum too is neuter in gender, hence its included species should all agree if the species names are adjectival in origin. The recently described fossil species U. sanctipauliensi Valdés and Lorenzo, 2000, and the fossil species with which it is compared in that work, U. landrincus Melville, 1813, e.g., must be corrected to sanctipaulianum and landrincus respectively.

Burn (1959) suggested that there is only one Recent, worldwide, pantropical/warm temperate species in the genus Umbraicum, but this hypothesis has yet to be tested. There are twelve Recent nominal species of Umbraicum; Marcus and Marcus (1967) and Marcus (1985) retained the name U. plicatula (von Martens, 1851) for warm-water western Atlantic specimens, and Thompson (1970) U. mediterraneum (Lamarck, 1819) for those from the Mediterranean Sea. From the Olgerse beds of northern Germany, there has been described a somewhat doubtful fossil species Umbrella plicatula von Koenen, 1892, which, if correctly assigned, would be a primary homonym of von Martens’ species. U. petechium Lin, 1981, from Hainan Island, southern China, with no characters to separate it, is the most recent synonym of U. umbraicum.

In summary, the synonymy of Umbraicum now reads:

**Umbraicum Schumacher, 1817**: 177-179. Type species Umbraicum chinense Lamarck, 1801. [= Umbraicum umbraicum Lightfoot, 1758]. by monotypy

+ Umbrella Lamarck, 1819: 339-343. Type species Umbrella indica Lamarck, 1819. [= Umbraicum umbraicum Lightfoot, 1758], subsequent designation by C. Blainville (1823).

+ Gastroplax Blainville, 1819: 182. Type species Gastroplax tuberculatus Larin, 1820. [= Umbraicum umbraicum Lightfoot, 1758], subsequent designation by Blainville (1820).

+ Umbrella Fersaas, 1818-19. Type species Umbrella indica Lamarck, 1819. [= Umbraicum umbraicum Lightfoot, 1758], subsequent designation by O. Donoghue (1829).


**TYPOLINA AND OLYMPOS**

Though unable to consult a complete copy of Rafinesque (1814), Valdés (2001) claimed quite correctly that "Tylodina was originally and validly introduced by Rafinesque in 1814." The title of "Ann. XII" of Rafinesque (1814) [we have had access to the copy in the library of the Academy of Natural Sciences of Philadelphia], includes the date "1 Dicembre 1814." Only pages 161 and...
162 of that work deal with Mollusca, including descriptions of five new genera. Three of them, 
Blepharillium, 
Opisthos and Dichotoma, have disappeared from mollusk literature, but two others, 
Tylodina and Oxyloc, are in everyday use. The work is so scarce, only a few copies not being lost with the rest of Rafinesque's possessions in a series of shipwrecks, and the wording so significant, we feel it is essential to reprint verbatim the original descriptions of these two genera here. The original descriptions, in Italian, read: [page 162]

IV. OXYLOC. Corpo repent, con una grande conchiglia dorsale esterna, bulliforme, spirale semplice; ventre stretto colli brachic intorno e stiata, mantilla allargata in gneale, due tentacoli sprognati e fissa. Differisce dal g. Sigarum per la sua conchiglia esterna, tentacoli sprognati + c. 1 sp. O olivacea.

V. TYLODINA. Corpo repent, con una piccola conchiglia esterna sopra il dorno, membranosa, senti spira, ovale, e colla punta callosa, quattro tentacoli e due posteriori allungati e più grandi brachic sotto la conchiglia, al suo lato destra, uno al lato destra del colla. Differisce dal g. Linum, perché ha una conchiglia esterna e dal g. Helix perché non ha spira. 4 sp. T punctulata.

These descriptions were reproduced, in French, by Rafinesque 1814, whose paper is better known from its inclusion in the Binney and Tryon 1864 reprint of Rafinesque's conchological writings. The French descriptions are an exact translation of this earlier 1814 Italian text, extended only by brief notes on each species, and reduced by shortening the comparison for Oxyloc, and by removing the comparisons with Linum and Helix altogether from Tylodina.

The description of Tylodina is remarkably extensive, and accompanied, however improbable it may seem to present-day opisthobranch workers, by a generic comparison. A single species, T punctulata, is denominated though not described. This combined description meets the requirements of the present International Code of Zoological Nomenclature (ICZN 1999). Article 12.2.6.1, by which both genus and species are to be attributed to Rafinesque, 1814. Tylodina punctulata Rafinesque, 1814 is thus the type species by monotypy of Tylodina Rafinesque, 1814. The family name Tylodiniidae was published by Gray, 1847, who wrote It Woodwana. The early history of this name, including its brief placement in the Pyramidellidae by Gray, 1853, is summarised by Bertsch 1980.

An exactly similar situation occurs with Oxyloc with original combined description of a new genus and single new nominal species. Thus O olivacea Rafinesque, 1814 is the type species by monotypy of Oxyloc Rafinesque, 1814. The earliest use of a family name based upon this genus appears to be Oxylocidae Stoliczka, 1868, correctly written these days as Oxylocidae.

Fischer-Piette 1913 examined and figured the actual specimen upon which Adanson, 1757 based his "Le Lari" from Senegal, and which Gaéona, 1791 formally named Patella percesa. Fischer-Piette 1913 transferred P percesa to Tylodina, declaring it the senior synonym of T citrina Foerster, 1853), the name then in use for this Mediterranean species. Since that date (i.e., 1913), the name Tylodina percesa has been used exclusively. In his description of the animal of "Le Lari," Adanson, 1757, was impressed by the fact that the body projected forward from the end of the shell further from the apex, whereas in the patelliform species described in great detail on the preceding pages, the head was at the end closer to the apex. He commented upon this relationship between shell apex and head of animal as "mais dans un sens contraire." This undoubtedly explains Gaéona's choice of percesa [Latin: turned wrong way round] for the name of this species.

ACKNOWLEDGMENTS

Angel Valdés's paper (2004) provoked one of us (RB) to commit to paper nomenclatural information gathered slowly over more than forty years of amateur opisthobranch enthusiasm. Malacologists, museums, and libraries in Australia, Europe and North America graciously provided access to their resources or copies of pertinent works. The Academy of Natural Sciences of Philadelphia serendipitously revealed to us the elusive 12th part of Rafinesque's Specilia (1814). To each and all, we give grateful thanks.

LITERATURE CITED


Wiljan, R. C. 1984. Bibliography of publications on New Zea-
Book Review

Invertebrate Zoology: The Mid-eastern Invertebrate Fauna. Part II: The Coelomates.


This is the second volume of Dr. Gamil Soliman's work on the invertebrate fauna of the Middle East, including Egypt. This volume covers 17 phyla with major sections devoted to the Mollusca and the Arthropoda. Volume 2 devotes 140 pages in 4 chapters to the mollusks and 176 pages in 4 chapters to the Arthropoda, the two largest phyla of animals. The examples and illustrated animals are drawn for those native to the Middle East. The taxonomy used in this volume is a synthesis of all information available. Each phylum is introduced in a short description, followed by a summary of the higher classification within the phylum, anatomy, respiration, nervous system, reproduction, a summary, key terms, ending with a discussion of the phylogeny of the phylum. The sections vary in length due to the amount of knowledge available on each phylum or class. The text also includes boxes, expanding on topics of special interest, e.g., types of gastropod radulae, gastropod egg masses, pearl formation, bivalve hinge types, growth and molting in arthropods, and comparison of Proteostomia and Deuterostomia. The excellent text figures are complemented by eight plates of color photographs of representative animals of the phyla covered in this volume.

Dr. Soliman worked on these two volumes at the Academy of Natural Sciences of Philadelphia part of each year since 1984. During his yearly visits, he worked completing his research and writing the text of these two volumes as well as drafting the numerous excellent illustrations. It was my great pleasure and inspiration to watch as the numerous figures took shape, to see the text filled out and the two volumes come together. I had the pleasure of reading drafts of most of the chapters, and I am pleased to see the finished volume. This work is not just your average university level invertebrate zoology textbook. Soliman's volume represents a summation of his life work. He is a malacologist by training, as well as an accomplished artist. This can be seen in the expanded treatment of the Mollusca in this second volume. The attention to detail and anatomy clearly shows his love of this group. He has chosen as the representative for the Bivalvia, Spatulopsis rubens (Unionidae: Tridacnidae), to be discussed in detail. This is the most comprehensive published treatment of the anatomy of a species of the family Tridacnidae of Africa. He similarly uses Septa saginata as the representative of the Cephalopoda to illustrate the anatomy and reproduction of this class of Mollusca.

This textbook will be a great aid to the teaching of invertebrate zoology and also will also serve as a major resource volume. I especially like, in addition to the overview of the classification and detailed anatomy, the summary section in numbered bullet format and the listing of key terms. These sections are important for any student of invertebrates. The section on phylogeny pulls together the latest morphological and genetic data on the relationships within and between phyla. I would recommend that this volume along with its companion volume be on the bookshelves of all invertebrate biologists.

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Notice

THE 2003 R. T. ABBOTT VISITING CURATORSHIP

The Bailey-Matthews Shell Museum is pleased to invite applications for the 2003 R. T. Abbott Visiting Curatorship. The Curatorship, established originally in accordance with the wishes of the late Dr. R. Tucker Abbott, Founding Director of the Shell Museum, is awarded annually to enable mollusk systematists to visit the museum for a period of one week. Abbott Fellows will be expected, by performing collection-based research, to assist with the curation of portions of the Museum’s collection and to provide one evening talk for the general public. The Museum collection consists of marine, freshwater, and terrestrial specimens. A large percentage of our holdings have been catalogued through a computerized database management system. A substantial portion of the time will be available for research in the collection, but field work in southwest Florida can be arranged. The R. T. Abbott Visiting Curatorship is accompanied by a stipend of $1,500.

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

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

Applications for the 2003 Visiting Curatorship should be sent no later than May 30, 2003. The award will be announced by late June. Questions about the Visiting Curatorship should be sent to the e-mail address above, or by phone at: (239) 395-2233; fax (239) 395-6706.
INSTRUCTIONS TO AUTHORS

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

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

The sequence of sections should be: title page, abstract page, introduction, materials and methods, results, discussion, acknowledgments, literature cited, tables, figure captions, figures. The title page should include the title, author's name(s) and address(es). The abstract page should contain the title and abstract, which should summarize in 250 words or less the main results and conclusions of the paper. All references cited in the text must appear in the literature cited section and vice versa. In the literature cited section, all authors must be fully identified and listed alphabetically. Follow a recent issue of THE NAUTILUS for bibliographic style, noting that journal titles must be unabbreviated. Information on plates and figures should be cited only if not included in the pagination. Tables must be numbered and each placed on a separate sheet. A brief legend must accompany each table. Captions for each group of illustrations should be typed on a separate sheet and include a key to all lettered labeling appearing in that group of illustrations.

All line drawings must be in black, high quality ink, clearly detailed and completely labeled. Photographs must be on glossy, high contrast paper. All figures are to be consecutively numbered (figs. 1, 2, 3, ...; NOT figs. 1a, 1b, 1c, ... NOR plate 1, fig. 1, ...). Illustrations must be arranged in proportions that will conform with the width of a page (6½ inches or 171 mm) or a column (3½ inches or 82 mm). The maximum size of a printed figure is 6½ by 9 inches or 171 by 228 mm. All illustrations must be fully cropped, mounted on a firm, white backing, numbered, labeled and camera ready. The author's name, paper title and figure number(s) should appear on the back. Original illustrations must be between one and two times the desired final size. It is the author's responsibility that the line weight and lettering are appropriate for the desired reduction. Original illustrations will be returned to the author if requested. Color illustrations can be included at extra cost to the author.

Voucher Material: Deposition of type material in a recognized public museum is a requirement for publication of papers in which new species are described. Deposition of representative voucher specimens in such institutions is strongly encouraged for all other types of research papers.

Processing of Manuscripts: Upon receipt, every manuscript is acknowledged and sent for critical review by at least two referees. These reviews serve as the basis for acceptance or rejection. Accepted manuscripts are returned to the author for consideration of the reviewers' comments.

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

Proofs: After typesetting, two sets of proofs are sent to the author for corrections. Changes other than typesetting errors will be charged to the author at cost. One set of corrected proofs should be sent to the editor as soon as possible.

Reprints and Page Charges: An order form for reprints will accompany the proofs. Reprints may be ordered through the editor. Authors with institutional, grant, or other research support will be billed for page charges at the rate of $60 per printed page.

Manuscripts, corrected proofs and correspondence regarding editorial matters should be sent to: Dr. José H. Leal, Editor, The Nautilus, P.O. Box 1580, Sanibel, FL 33957, USA.
CONTENTS

Rudo von Cosel
Bruce A. Marshall

Two new species of large mussels (Bivalvia: Mytilidae) from active submarine volcanoes and a cold seep off the eastern North Island of New Zealand, with description of a new genus .......................................................... 34

Eugene V. Coan

The tropical eastern Pacific species of the Condylocardidiidae (Bivalvia) .......................................................... 17

William P. Leonard
Lyle Chichester
Kristiina Ovaska

Prophysaon dubium Cockerell, 1890, the papillose taildropper (Gastropoda: Arionidae): distribution and anatomy .......................................................... 62

Erratum ........................................................................ 68
Two new species of large mussels (Bivalvia: Mytilidae) from active submarine volcanoes and a cold seep off the eastern North Island of New Zealand, with description of a new genus

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ABSTRACT

Two new species and a new genus of large mussels from off northern New Zealand are described. Bathymodiolus tangaroua new species from seeps (presumably methane-rich) off Cape Turnagain and Cape Kidnappers at 920–1205 m. and Gigantidites gladius new genus and new species from active submarine volcanoes on the southern Kermadec Ridge at 216–575 m. Gigantidites gladius is anatomically closer to the small wood-associated species of Iris Jeffreys, 1876, than to any of the large mussels currently known from hydrothermal vents or seeps. A polychaete of the genus Branchipolygna Petilhorne, 1984 was found within the mantle cavity of every specimen of Gigantidites gladius.

INTRODUCTION

Following the discovery of a number of species of large mussels associated with seeps and hydrothermal vents from the eastern Pacific, Japan, Fiji, the Caribbean, the Gulf of Mexico, and the Mid-Atlantic Ridge (Kenk and Wilson, 1985; Cosel et al., 1994; Hashimoto and Okutani, 1994; and references therein), examples of a related species were obtained by commercial fishing at two sites off the east coast of the North Island of New Zealand (Lewis and Marshall, 1996) (Figure 1A). This mussel, here referred to as the genus Bathymodiolus Kenk and Wilson, 1985, occurs on slope ridges landward of the accretionary prism of the convergent Pacific-Australian plate.

A second, much larger species was obtained subsequently by dredging during surveys of active submarine volcanoes present along the southern Kermadec Arc off northeastern North Island (Parson and Wright, 1996; Wright, 1994, 1997; de Ronde et al., 2001; and references therein) by the National Institute of Water and Atmospheric Research, Wellington (Figure 1B).

Institutional abbreviations used in the text are: MNHN, Muséum National d'Histoire Naturelle, Paris; NMNZ, Museum of New Zealand Te Papa Tongarewa; Wellington; NIWA, National Institute of Water and Atmospheric Research, Wellington.

SYSTEMATICS

Superfamily Mytiloidea Rafinesque, 1815  
Family Mytilidae Rafinesque, 1815  
Genus Bathymodiolus Kenk and Wilson, 1985


Bathymodiolus tangaroua new species  
(Figures 1–13, 15–18, Table 1)

aff. Bathymodiolus sp.—Lewis and Marshall, 1996: 183; 186, fig. 4, 187
Bathymodiolus sp. II—Cosel, 2002: table 1

Description: Shell large, up to almost 200 mm long, elongate, somewhat adniform, rather thick and solid, externally with well-developed, irregular growth lines; dull-whitish beneath periostracum; internally nacreous-ivory. Beaks subterminal, at about one-seventh total shell length in adults; umbones very broad, flattened. Height gradually increasing posteriorly, markedly curved dorsoventrally, most inflated at about mid-length, equivalent length/height ratio 2.5–3.2. Few specimens somewhat twisted. Anterior part short, rather narrow, protruding nose-like anteriorly; anterior margin narrowly but evenly rounded; ventral margin markedly concave over anterior half. Posterior margin evenly rounded ventrally, convex dorsally; postero-dorsal angulation well-defined, rounded, situated above posterior adductor scar, close to posterior margin. Prodissoconch unknown. Periostracum thick, hard, dark brown, smooth, glossy to somewhat dull, no periostracal hairs (byssal endplates of other specimens scattered over valves). hinge (adults) toothless, anterior hinge margin weakly protruding ventrally. Ligament opisthodetic, very strong, extending over
Figures 1-5. *Bathymodiolus tangaroa* new species. Holotype: Madden Basin; shell length 199.6 mm, NMNZ M 158284. 1, 2. Exterior and interior of right valve. 3, 4. Interior and exterior of left valve. 5. Dorsal view.
Figures 6-9. *Bathymodiolus tangarou* new species. 6, 7. Paratype S. Madden Basin shell length 140.5 mm, NMNZ M.158227 S. Exterior and interior of right valve, S. 9. Paratype 3. Cape Kidnappers (shell length 165.8 mm, NMNZ M.117890) C. Lateral and oblique ventral view of interior of right valve, with muscle scars and pallial line highlighted.
Figures 10–14. *Bathymodiolus tangaroi* new species and *Gigantidae gladius* new species, half-schematic drawings. 10, 11. *Bathymodiolus tangaroi* paratype 3, off Cape Kidnappers; shell length 167.8 mm, NMNZ M.1178063. 10. Sketches of foot-bysseal retractor complex in left lateral 110° and dorsal 114° view and its situation in the shell. 12. *Bathymodiolus tangaroi* paratype 5, off Cape Kidnappers; shell length 164.3 mm, NMNZ. Interior of right valve, showing muscle scars and pallial line. 13. *Bathymodiolus tangaroi* paratype 1, Menden Basin; shell length 177.9 mm, NMNZ M.58227. Dorsally opened stomach (scale bar = 5 mm). 14. *Gigantidae gladius*, paratype 3, Bumble V; shell length 271.3 mm, NMNZ M.154988. Dorsally opened stomach (scale bar = 5 mm); big, beginning of intestinal groove; dd, digestive diverticula duct entrance; ig, intestinal groove; lp, left pouch; oe, esophagus.
about five-sixths of postero-dorsal margin in front of postero-dorsal corner, and ending abruptly posteriorly; ligament plate weakly to strongly convex. Subligamental shell ridge well developed, in some specimens divided into a secondary ridge that extends from under umbo for about a third of ligament length; primary ridge extending posteriorly behind umbo, between ligament and secondary ridge, and becoming obsolete shortly before posterior end of ligament (visible only from ventral perspective). Adductor scars well defined. Anterior adductor scar short, situated just in front of umbo. Posterior adductor scar rather large, more or less rounded, united with most posterior scar of posterior pedal and byssus retractor muscle complex; anterior scar of this complex well separated, very long and itself divided into isolated impressions, extending posteriorly from under middle of ligament. Anterior byssus retractor muscle scar situated deep under beak on anterior part of umbal cavity (visible only from ventral perspective). Pallial line curving parallel to ventral margin.

Anatomy: Ctenidia long, narrow, about 75% of shell length (125 mm long and 13 mm wide in 167 mm specimen), outer and inner demibranchs of equal length, filaments broad and fleshy, food-groove not detected (probably because of poor fixation). Ascending lamellae of outer demibranch anteriorly fused to mantle for a very short distance, those of inner demibranch fused to visceral mass. No muscular longitudinal ridges on mantle and visceral mass where dorsal edges of the ascending lamellae attach, nor connection bars between free edges and gill axes. Inner mantle folds separate along entire ventral margin length from anterior adductor to posterior margin; edges slightly frilled over most of length, more undulate along posterior 30-50 mm; terminating anteriorly over anterior adductor, folded back directly onto muscle and continuing over it as a thin, delicate, inconspicuous membrane. Vacular siphonal membrane short and thin, without median papilla. Foot-byssus retractor muscle complex moderately elongate; anterior retractor rather short, very broad, inserted in anterior part of long umbal cavity, most anterior point under beaks (larval shell). Posterior byssus retractor comprising several diverging muscle bundles with common base at base of byssus; anterior part comprising 3 bundles attached to very long scar at about middle of valves, at about a right angle (most anterior bundle) and about 50 and 60° to longitudinal shell axis (second and third bundle); posterior part consisting of 4-5 bundles passing towards 2 attachment points, most posterior bundle just before posterior adductor. Posterior foot retractor long and thin, arising from anterior side of base of foot behind base of anterior retractor muscles, passing parallel to longitudinal shell axis towards anterior bundle of posterior byssus retractor, then bent dorsally to attachment point, where closely appressed to anterior bundle of posterior byssus retractor. Foot relatively small, 35 mm long (byssal orifice included) in a specimen of 167 mm shell length. Two pairs of labial palps present, anterior pair relatively small, posterior pair long and narrowly triangular (respectively 7 mm and 12-13 mm long in a 160 mm specimen). Intestinal tract narrow. Stomach situated just behind middle of anterior half of shell length, simple, thin-walled, anterior chamber ill-defined; posterior chamber longer. Diverticulae entrances 13, 7 in anterior chamber, and 6 in posterior chamber. Depression on posterior left side corresponds to left pouch. Midgut

Figures 15-17. Bathymodiolus tanganen new species. 15. 16. Paratype 3. Cape Kidnappers (shell length 167.8 mm, NMNZ M 117890). 15. Ventral view of anterior end, showing thin, transverse part of inner mantle fold, and ventrally grooved foot. 16. Ventral view of posterior end, showing valvular siphonal membrane (arrow) without median papilla. 17. Paratype 6. Cape Kidnappers (shell length 169 mm, NMNZ M 117890). Ventral view of anterior end, showing labial palps (arrows).
running posteriorly straight and medially from the stomach, under ventricle and entering ventricle just in front of ostia, without any loop or curve; behind heart, intestine passing over posterior adductor and ventrally on its posterior side; anus at mid-diameter of posterior adductor. Heart rather broad, situated in the posterior half of shell length, anterior extremity of ventricle at mid-shell mantle length. Annules long, fused posteriorly just in front of the posterior adductor, and stretching out forward in narrow lobes to the anterior bundle of the posterior retractor.

Table 1. Bathymodiolus tangarau new species. Shell measurements (mm) and proportions. Paratypes 3, 5, and 6 from off Cape Kidnappers, others from type locality.

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<td>51.0</td>
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<td>50.7</td>
<td>2.54</td>
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<td>2.67</td>
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<td>101.7</td>
<td>40.3</td>
<td>46.8</td>
<td>2.54</td>
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</table>

Type Material: Holotype (pair) NMNZ M 155284, and 5 paratypes (pairs) NMNZ M 155227. 1 pair NIWA F1291. 1 pair MNHN; from type locality, alive, 26 May 2004, FV Tysman Viking (semi-pelagic "orange roughy" trawl that accidentally engaged bottom), presented by S. Donker. Paratypes: South Richey Bank, NE of Cape Kidnappers, North Island, New Zealand, 40 00.8' S, 178 46.0' E, alive, 1170 m, 1994, FV Say Monsieur (semi-pelagic "orange roughy" trawl that accidentally engaged bottom), leg. M. Friar (paratypes 3 and 6, pairs, NMNZ M 111890; paratype 5, pair, MNHN). 1

Type Locality (Figure 18): South side of Mudge Basin, off Cape Turnagain, eastern coast of North Island, New Zealand, 40 26.49' S, 176 58.13' E, 920–1205 m.
Distribution (Figure 18): Off southeastern North Island, New Zealand, living at 920-1205 m.

Biotopy: On hard bottom on the slope ridges landward of the accretionary prism of the convergent Pacific-Australian plate, where plumes of sonar-reflective water, presumably rich in hydrocarbons, rise from the seafloor (for details, see Lewis and Marshall, 1996) (Figure 18). We presume that the mussels live at these emission sites and are nourished by methane-utilizing symbiotic bacteria concentrated in their enlarged gills (Childress et al., 1986; Fisher et al., 1987; Tsumitada, 1991; Rio et al., 1992; and references therein).

Etymology: Named after the Maori sea-god Tangaroa.

Remarks: Bathymodiolus tangaroa is strongly characterized by its markedly curved shell and distinctively elongated-elliptical outline; no other species has this shape. Bathymodiolus hekurenei Gustafson et al., 1998, from the Gulf of Mexico, is of similar size range but more slender and less curved, with thinned-walled valves. Bathymodiolus boomingeri Cosel and Ohn, 1998, from the Barbados Accretionary Prism, is thinner-walled, more elongate, and considerably larger. Bathymodiolus breviset Cosel et al., 1994 (Lau Basin and North Fiji Basin), B. platyconus Cosel et al., 1994 (Mid-Atlantic Ridge), and B. marsalis Haseimoto, 1994 (Rodriguez Triple Junction), are shorter and stout than B. tangaroa, with a markedly broader anterior margin. Bathymodiolus childressi Gustafson et al., 1998, from the Gulf of Mexico has the eumiform shape of B. tangaroa, but is much shorter with almost terminal umbones.

Bathymodiolus tangaroa differs from Bathymodiolus species for which anatomy is known in that the inner mantle fold is much thinner, more delicate, and less conspicuous where it extends transversely over the anterior adductor. Bathymodiolus tangaroa differs from all species other than the group comprising B. childressi, B. platyconus Haseimoto and Okutani, 1994, B. marsalis Haseimoto and Okutani, 1994, and an undescribed species from Barbados (currently under study by R. A. C.), by its multi-bundle foot-bysus-retractor complex. The posterior retractor in B. tangaroa, however, is much longer than the anterior one, rather than vice versa as in B. childressi (see Gustafson et al., 1998, fig. 13) and the undescribed species from Barbados (condition unknown in B. platyconus and B. marsalis). Another common feature of B. childressi, the undescribed Barbados species, and B. tangaroa is the lack of a papilla in the middle of the posterior of the valvular siphonal membrane. Thus, B. tangaroa cannot be assigned to any of the four informal subgroups of Bathymodiolus defined by Cosel (2002), specifically the B. thermophilus group (one species), the B. breviset group (five species), the B. hekurenei group (two species) and the B. childressi group (four species).

Of the 11 specimens examined, one (length 177.9 mm; paratype MNHN) contained a polychaete worm of the genus Branchipolyce Petuhiv, 1984 (length 32.5 mm), which was situated in the mantle cavity above the byssus.

Gigantid new genus

Type Species: Gigantid gladius new species; Recent, New Zealand.

Diagnosis: Shells containing very large size length up to 316 mm, extremely slender. Umbose at about 20% of total shell length. Juvemales (<5 mm) with periostracal bristles. Animal with very long, rather narrow, fleshy teuthiia. Inner mantle folds entirely separate, terminating anteriorly over anterior adductor, edges frilled along posterior 3/4 of shell length. No valvular siphonal membrane. Inner mantle folds below posterior adductor with a deep cleft between left and right mantle lobes. Foot very small, anterior retractor inserting on shell directly above anterior adductor, well in front of umbonal cavity, both muscles forming a common scar.

Remarks: The large size and biotopy of Gigantid gladius invites immediate comparison with large mussels of the genus Bathymodiolus, from all of which, however, it differs by the absence of a well-developed valvular siphonal membrane at the posterior end, and the absence of a continuous shell fold across the anterior adductor from one valve to the other. Moreover, unlike Bathymodiolus species, the attachment point of the anterior retractor is not situated somewhere within the umbonal cavity but well in front of it, on the narrow anterior part of the valves close to the antero-dorsal margin. Bathymodiolus, the anterior adductor and retractor muscles are situated close together at their attachment point, especially in species with terminal umbose but remain well separated through ontogeny (Figure 16; see also Cosel et al., 1999, figs. 13, 12, 3, 5, 50, 60, 61). In Gigantid gladius both muscles are in contact at their insertion point and form a common scar. Very young specimens of G. gladius have periostracal bristles on the postero-dorsal part, whereas these have never been recorded from Bathymodiolus species at any stage of growth (e.g. Cosel et al., 1994; Haseimoto and Okutani, 1994; Cosel and Ohn, 1999; Cosel et al., 1999).

The attachment point of the anterior retractor in very young specimens of G. gladius (<5 mm) is in the umbonal cavity as in adult Bathymodiolus species, but with increasing shell size it progressively shifts antero-wards from the anterior part of the umbonal cavity to a position under the antero-dorsal margin, remaining very close to the anterior adductor throughout ontogeny. The only other large mussel known in which the anterior retractor scar is situated in front of the umbonal cavity closely adjacent to the anterior adductor scar, is an undescribed species from the Kii-kata Seamount, Japan. According to Hashimoto and Horikoshi (1989) illustration, the retractor scar in the Japanese species is very close to the adductor scar but not in contact with it, and the two bundles of the posterior retractor are well separated. The Japanese
species, which may thus belong in Gigantidias, is smaller and more strongly curved than G. gladius, and was found burrowing in sediment on a dormant submarine volcano.

Anatomically, G. gladius most closely resembles the much smaller mussels of the genus *Indus* Jeffreys, 1876 (type species *Largentae* Jeffreys, 1876; North Atlantic) *L japonica* up to 8.9 mm long), which live at similar depths associated with decaying wood and whale bones, and *Beuthomodiola* Dall, 1927 (type species *B. lignicola* Dall, 1927; New Zealand) length up to 17.3 mm), which lives on decaying wood. In the absence of animals of the type species of *Indus* for comparison, we have had to base our comparison on specimens of the New Zealand *Indus* species identified by Dall (1927) as *L japonica* (Habe, 1926) (NMNZ M175022). This species and *G. gladius* share a similarly-shaped posterior end of the inner mantle fold, with a short, narrow, deep cleft between the left and right mantle lobes, and no valvular siphonal membrane; and lack of tubular prolongation of the exhalent siphon. Periostracal bristles are present in both species, though only in juveniles of *G. gladius* *Beuthomodiola lignicola* and *G. gladius* both have periostracal bristles, and lack a valvular siphonal membrane, and a tubular prolongation of the exhalent siphon. *Gigantidias* thus differs from *Indus* primarily in the exceptional size and the biotope of the type species, and in the migration of the insertion of the anterior retractor to a position in front of the unbones.

Species of *Adipicola* Duttenberg, 1927, which attain up to 31.3 mm in length, are also similar in gross facies. Sucer soft parts of the type species *Mollusca pelagoicum* Woodward, 1854 were not available for study, we used New Zealand species referred to them by Dall (1927, 1935), for comparison, notably *A. arcuatus* Dall, 1927, a species with a slender, curved shell, living on whale bones. In contrast to *G. gladius*, the inner mantle folds of *A. arcuatus* are much thinner and less frilled, but at the posterior end, especially over the posterior adductor, they are much more broadened to form a long, thin lobe that extends posteriorly below the exhalent siphon. In contrast to the conditions in *L japonica* and *G. gladius*, a valvular siphonal membrane is present in *A. arcuatus*, but reduced to a narrow, transversely very short rim without a papilla. Moreover, *A. arcuatus* has a long, tubular exhalent siphon and no periostracal bristles at any stage of growth. *Adipicola esocella* (also associated with whale bones) lacks periostracal bristles too, and has a tubular exhalent siphon, though shorter than in *A. arcuatus*.

From the sum of similarities and differences, we conclude that there is a close relationship between *Gigantidias* *Indus* and *Beuthomodiola*, that *Adipicola* has closer affinities with *Beuthomodiola*, and that all of these genera form a single phylogenetic radiation within the Mollusca.

*Gigantidias gladius* new species (Figures 14, 19-43; Tables 2, 3)

Description: Shell exceptionally large for a mussel, up to 316 mm long, 54 mm high and 56 mm broad, extremely long and slender, rather thin for the size but solid, dull-white beneath dark periostracum, interior maceous-white. Outline somewhat variable, irregular, fully grown specimen elongate-subcylindrical, slightly curved dorso-ventrally, most inflated about middle or shortly behind it, equivalent length height ratio 1.5-6.2. Half-grown specimens already slender and bean-shaped, very young (length < 60 mm) specimens more or less straight. Beaks in adult specimens at about anterior quarter, anterior part narrow, strongly protruding anteriorly, anterior margin narrowly rounded, ventral margin straight to very slightly concave over anterior half; middle zone of ventral margin markedly concave, straight posteriorly, and slightly convex in posterior fifth. Posterior margin broadly rounded, postero-dorsal margin weakly convex, postero-dorsal corner broadly rounded or not defined, highest part of the valve situated there. Exterior dull, with well-developed, irregular commarginal growth lines. Rounded, pronounced posterior angulation running from umbo towards ventral part of posterior margin, but becoming obsolete on flattened and broader posterior part situated at about 1/5th of shell length. Similar but much shorter anterior angle from umbo to ventral part of anterior margin. Umbo extremely elongated, rather prominent. Fine radial striae running from beaks to anterior, ventral and postero-ventral margins, visible mostly on ventral part of valves, sometimes slightly changing direction at commarginal growth lines. Radial striae weakly reflected on shell anterior, mostly ventrally. On postero-dorsal slope striae replaced by low, broad longitudinal waves that bifurcate towards both dorsal margin and posterior angle (Figure 35). Posterior angle smooth. In dorsal or ventral view, broadest part of shell formed by posterior angle. Second broadest part at anterior angle; section under umbo between anterior and posterior angle about same width as anterior angle, in large specimens even slightly constricted there (Figure 27). In some specimens whole shell often more or less spirally twisted. Lagament plane almost straight to slightly convex. Periostracum strong, dark brown, umbonal region and area under umbo light brown, glossy to somewhat dull, smooth; very young specimens (3-6 mm), however, with short periostracal bristles. Chalys endplates of other specimens commonly scattered over surface of valves. Hinge in very young specimens up to about 5 mm long with row of small denticles of similar size, extending posteriorly from ligament to postero-dorsal angulation, toothless in larger specimens. Anterior hinge margin hardly protruding towards ventral, if at all. Lagament opisthode, strong, extending almost whole of postero-dorsal margin and ending posteriorly 10-20 mm (specimens 200-270 mm shell length) in front of postero-dorsal corner, either abruptly or in a rather short
taper. Subligamental shell ridge well developed from under umbo to about one-half of ligament length, then becoming gradually obsolete, visible under the beaks only from ventral perspective. Adductor scars clearly defined. Anterior adductor scar rather large, arched, situated well in front of umbo, near antero-dorsal margin, united with anterior retractor muscle scar. Posterior adductor scar large, rounded to subangular, united with posterior scar of posterior pedal and byssus retractor muscle scar. Anterior scar of posterior retractor well separated, situated between third and last quarter of ligament length. Anterior byssus retractor muscle scar directly above anterior adductor scar and united with it, well in front of umboes. Pallial line almost parallel to ventral margin. Prodissoconch with glossy, ovate, pinkish purple, sharply delineated, prodissoconch I 83–100 μm wide, prodissoconch II 150 μm wide (development planktotrophic).

Anatomy: Clamidia very long and narrow, length more than 75% of shell length, 578% in shell 271 mm long. 84% in 316 mm specimens; 14 mm broad (outer demin-

branch in a 270 mm specimen: outer and inner demibranchs of equal length, filaments broad and fleshy. Ascending lamellae of outer demibranch anteriorly fused to mantle for a very short distance (about 5 mm), those of inner demibranch fused to visceral mass. Ventral edge of each demibranch with a well-marked food-groove, broader on inner demibranch. No muscular longitudinal ridges on mantle and visceral mass where dorsal edges of the ascending lamellae attach, and no connection bars between free edges and gill axes. Inner mantle folds separate along whole length of ventral margin from anterior adductor to posterior margin, their edges frilled along posterior fifth of shell length or even less, becoming smooth towards anterior, terminating anteriorly over an-
Figures 31–38. *Gigantidus gladius* new species. Half-schematic drawings. 31–33. Paratype 3 (shell length 271.3 mm, NMNZ M.154988(3). 31–32. Sketches of foot-lyssus retractor complex in left lateral (31) and dorsal (32) view and its situation in the shell. 33. Interior of right valve showing muscle scars and pallial line. 34. Paratype 11 (shell length 206.5 mm, NMNZ M 154988(11). Interior of right valve showing muscle scars and pallial line; location of concealed anterior bundles arrowed. 35. Paratype 7 (shell length 245.5 mm, NMNZ M 154988(7). Exterior of left valve showing orientation of fine sculpture. 36–38. Right valves of juvenile paratypes. Rumble III lengths 72.8 mm (36), 39.8 mm (37) and 34.7 mm (38); NMNZ M 158285.
terior adductor and folding back directly onto adductor but not continuing transversally over it as a rim to meet mantle fold of opposite side. Valvular siphonal membrane absent; however, inner mantle fold folded ventrally and becoming very strong and strongly frilled, with a deep cleft between those of right and left valve. Foot very small; length 34 mm (byssus office included) in a specimen of 270 mm shell length. Foot-byssus retractor muscle complex very elongated, but anterior retractor rather short. Anterior retractor in adults inserting immediately above anterior adductor, near antero-dorsal margin and well in front of umbo. Cavity in very young specimens <5 mm long; attachment point is well within anterior part of umbo but still close to anterior adductor, attachment point migrating anteriorly with increasing size. Posterior byssus retractor comprising 2 principle diverging muscle bundles with common base at base of byssus; anterior bundle broadest, descending at a very low angle to longitudinal shell axis from attachment point at about mid-shell length to posterior bundle thinner, extremely long, extending about parallel to longitudinal shell axis to attachment point just in front of posterior adductor. Two additional very thin bundles attached between anterior and posterior bundles; attachment points varying somewhat from specimen to specimen. Posterior foot retractor very long, passing from anterior side of foot base, behind base of anterior retractor muscles, towards anterior bundle of posterior byssus retractor, reaching attachment point closely appressed to bundle for only a very short part of its length. Labial palps irregular, narrow-triangular, very small in adult specimens (anterior palps 2-5 mm long and posterior pair about 8 mm long in a 270 mm specimen, relatively slightly larger in juvenile and half-grown specimens (posterior palps about 3.5 mm long in a 77 mm specimen). Intestinal tract narrow. Stomach situated between first and second quarters of shell length, small in relation to shell size; rather simple, thin-walled, with a small, rather poorly defined anterior chamber; posterior chamber longer and broader; 8 di-
gestive diverticulum entrances visible, 3 at end of anterior chamber, 5 in posterior chamber (specimen examined contained mucus only). Style sac and midgut conjoined. Major typhlosole passing from midgut along floor of posterior chamber to somewhat behind anterior chamber; shallow depression corresponding to left pouch on posterior left side. Gastric shield not detected. Midgut extending posteriorly straight and medially from stomach, passing under ventricle, then turning upwards and entering ventricle without any coiling or loop, passing behind heart over posterior adductor and on posterior side of adductor turning ventrally, anus at mid-diameter of adductor. Heart rather narrow, situated well posteriorly, its long arteries fused posteriorly just in front of posterior adductor, extending anteriorly in long and narrow lobes to midpoint of shell mantle length.

**Type Material:** Holotype NIWA 41.790 (pair, preserved in alcohol) and paratypes NMNZ M.154088 (5), NIWA P.12346 (7), MNNX 2 (2), all from type locality 24 May 2001, RV Tangaroa (stn 107/230). Paratypes: Rumble III submarine volcano, S Kermadec Ridge, 35°14'47"
Figure 43. *Gigantidus gladius* new species in situ on Rumble III volcano. 386 m. 22 May 2001. NIWA sta. TAN 107/152. The largest mussels in the foreground at lower right and at top left centre are 250–300 mm long. The starfish is a new genus and species of the Astereidae (D.G. McKnight, pers. comm.). From color photograph taken by remote camera (courtesy NIWA).

Table 2. *Gigantidus gladius* new species. Shell measurements mm. and proportions.

<table>
<thead>
<tr>
<th>Length</th>
<th>Height</th>
<th>Tumidity</th>
<th>Length</th>
<th>Height</th>
<th>Specimen</th>
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<td>5.78</td>
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</tr>
<tr>
<td>233.5</td>
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<td>5.39</td>
<td>Paratype 5 MNINZ (by broken)</td>
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</tr>
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<td>217.8</td>
<td>13.8</td>
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S. 178°29.4' E. alive. 216–460 m. 2 Nov. 2000. RV *Kvarøy* many juveniles. MNINZ M158266, NIWA P1245. KAI111 21, MNINZ.

Type Locality: Rumble V submarine volcano, southern Kermadec Ridge off northeastern North Island, New Zealand. 36°08.18' S. 178°11.70' E. 755–360 m.

Table 3. Polychaete worms, *Branchipolygus* sp., associated with *Gigantidae gladius* new species.

<table>
<thead>
<tr>
<th>Shell length (mm)</th>
<th>Worm length (mm)</th>
<th>Location of worm within mussel, and pathology</th>
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<tr>
<td>346.0 mm</td>
<td>33 mm</td>
<td>In front of foot between right and shell length</td>
</tr>
<tr>
<td>284.0 mm</td>
<td>15 mm</td>
<td>Below posterior adductor</td>
</tr>
<tr>
<td>276.0 mm</td>
<td>39 mm</td>
<td>Anterior half with one end at mid-shell length</td>
</tr>
<tr>
<td>420.0 mm</td>
<td>35 mm</td>
<td>Posterior end, Worm posterior against posterior adductor</td>
</tr>
<tr>
<td>339.5 mm</td>
<td>40 mm</td>
<td>Right side between byssus and eumida lesions on eumida both sides</td>
</tr>
<tr>
<td>240.0 mm</td>
<td>34 mm</td>
<td>Between anterior tip of foot and anterior adductor</td>
</tr>
<tr>
<td>244.0 mm</td>
<td>37 mm</td>
<td>Third end at mid-shell length, head posterior</td>
</tr>
<tr>
<td>245.5 mm</td>
<td>30 mm</td>
<td>Near mouth, with head touching palp (lesion)</td>
</tr>
<tr>
<td>231.0 mm</td>
<td>34 mm</td>
<td>Between tip of foot and anterior adductor (lesion on right mantle edge)</td>
</tr>
<tr>
<td>216.5 mm</td>
<td>31 mm</td>
<td>In opening above mouth, about 15 mm from projecting posteriorly</td>
</tr>
<tr>
<td>206.5 mm</td>
<td>23 mm</td>
<td>Above eumida on right side at byssus level</td>
</tr>
</tbody>
</table>

Distribution (Figure 12): Submarine volcanoes, Kermadec Ridge, NE New Zealand, 216–755 m, shallowest occurrence nuclear (obtained by dredging upslope), though certainly as shallow as 350 m.

Biotope: High population densities at sulphur-rich hydrothermal springs on active submarine volcanoes (Figure 12). Dredge hauls containing this mussel included elemental sulphur and smelled strongly of it, suggesting that the mussel’s nourishment involves chemosynthesis by sulphur-oxidizing symbiotic bacteria concentrated in the extremely enlarged gills.

Etymology: So named because of its blade-shaped valves (Latin).

Remarks: *Gigantidae gladius* is currently the second largest living mytilid known, being only slightly surpassed in length by *Bathymodiolus* boonei (shell length 316 mm, vs. 370 mm). *Bathymodiolus* boonei, however, is a true *Bathymodiolus* species with a siphonal membrane and a posterior retractor with only two muscle bundles, and is much higher posteriorly and more strongly curved anteriorly. Other major distinguishing characteristics of *G gladius* are the attachment of the anterior retractor well in front of the mussel cavity directly above the anterior adductor, rather than somewhere within the umbilical cavity as in *Bathymodiolus* species, and the uniting of the anterior adductor and retractor scars, which are separate in *Bathymodiolus* species.

All 11 intact adult type specimens of *G gladius* contained a polychaete of the genus *Branchipolygus*. On opening the mussels, the worm was found situated at various sites within the mantle cavity (Table 3), some causing lesions on the mantle edge or in the mouth region. One mussel even had a worm projecting from the opening into the dorsal mantle cavity above the month. Thus the mussel is often traumatized by the polychaete Britayev et al., 2000.

ACKNOWLEDGMENTS

We are grateful to Steve O’Shea and Malcolm Clark, National Institute of Water and Atmospheric Research, Wellington, for loan and gift of material, to Malcolm Clark for the *in situ* photograph, and to his co-workers Keith Lewis and Ian Wright for information on geology of collecting sites, and Richard Garlick for the distribution maps. The specimens of *Gigantidae gladius* were obtained in connection with the following programs funded by the New Zealand Foundation for Research, Science and Technology: “Seamounts: importance to fisheries and marine ecosystems” (COX002S), and “Consequences of earth ocean change” (COX0023). Two anonymous referees are thanked for helpful comments on the manuscript.

LITERATURE CITED


Dell, R. G. 1975. *Mollusca* of the Family *Mytilidae*: *Bivalvia* associated with organic remains from deep water off New Zealand with revisions of the genera *Adhipica* Dautzen-


The tropical eastern Pacific species of the Condylocardiidae (Bivalvia)

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ABSTRACT

There are at least ten minute species of Condylocardiidae in the tropical eastern Pacific: eight species assigned to Condylocardia and two to Carditella. Eight of these taxa are described here for the first time: Condylocardia sparsa new species, Condylocardia formidabilis new species, Condylocardia kloskae new species, Condylocardia chungata new species, Condylocardia kavaro new species, Condylocardia grigi new species, Carditella galapagona new species, and Carditella marina new species. Many of the new species seem to be endemic to islands.

INTRODUCTION

The Condylocardiidae is a group of minute marine bivalves that brood their young within their mantle cavity. F. Bernard (1897: 205) suggested that they derived by neoteny from the Carditidae, however, the family may be polyphyletic, with some currently included taxa derived from other groups. There also remain some significant unresolved questions about which genera constitute the Condylocardiidae. For example, Chayan (1969: 549–550) placed Carditella, which has an external ligament as well as a central resilifer, in the Carditidae, but allocated Cardita, which has only a central resilifer, in the Condylocardiidae (op. cit., p. 558), they are otherwise very similar. Probably only molecular evidence will resolve this and similar questions, because miniaturization may have occurred more than once in the Carditidae, which, at least in substantial part, are brooders.

The Condylocardiidae is unexpectedly diverse, and in recent years many new species have been described, a significant number of them endemic to small geographic areas, particularly islands animal. Salas and C Josel, 1991; Hayami and Kase, 1993; Muddelhart, 2000, 2001, 2002a, b).

The purpose of the present study is to put on record the diversity of the Condylocardiidae in the tropical eastern Pacific, where there are several undescribed species, based on material that has recently become available.

All the species discussed here are under 3.1 mm in length, with most under 2 mm. Consequently, light photography is difficult, and the illustrations here were prepared with scanning electron microscopes at the California Academy of Sciences, the University of Southern California, and the Natural History Museum of Los Angeles County.

In the following treatment, each valid taxon is followed by a synonymy, description, information on type specimens and type localities, notes on distribution and habitat, the etymology of the new species names, and an additional discussion. The synonymies include all major accounts about the species, but not minor mentions in the literature. The distributional information is based on Recent specimens I have examined, except as noted. The only fossil occurrence was taken from the literature. References are provided in the Literature Cited for all works and taxa mentioned.

ABBREVIATIONS

The following abbreviations are used in the text: AM, Australian Museum, Sydney, Australia; CAS, California Academy of Sciences, San Francisco, California, USA; ICZN, International Commission on Zoological Nomenclature; INBio, Instituto Nacional de Biodiversidad, Santo Domingo, Heredia, Costa Rica; LACM, Natural History Museum of Los Angeles County, California, USA; PRI, Paleontological Research Institution, Ithaca, New York, USA; MNHN, Muséum National d'Histoire Naturelle, Paris, France; SBMNH, Santa Barbara Museum of Natural History, Santa Barbara, California, USA; UMi, Marine Invertebrate Museum, Rosenstiel School of Marine and Atmospheric Sciences, Miami, Florida, USA; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; ZMC, Zoologisk Museum, Copenhagen, Denmark. Material in the private collections of Carol C. Skoglund,
Table 1. Some key characters of eastern Pacific Condylocardiidae

<table>
<thead>
<tr>
<th>Species</th>
<th>Shape</th>
<th>Radial commarginal ribs</th>
<th>Prodissocusch</th>
<th>Hinge</th>
</tr>
</thead>
<tbody>
<tr>
<td>Condylocardia digueti</td>
<td>narrow-trigonal</td>
<td>6–11 broad radial commarginal bars</td>
<td>mucronate, with radial ribs, strongly demarcated</td>
<td>posterior lateral in LV low</td>
</tr>
<tr>
<td>Condylocardia hoppopus</td>
<td>trapezoidal</td>
<td>7–8 radial, largest anteriorly moderate commarginals</td>
<td>mucronate, with radial ribs, strongly demarcated</td>
<td>posterior lateral in LV large</td>
</tr>
<tr>
<td>Condylocardia sparsa</td>
<td>trapezoidal</td>
<td>4–5 radial, posterior slope mcsulptured commarginal striae</td>
<td>mucronate, with radial ribs, strongly demarcated</td>
<td>posterior lateral in LV large</td>
</tr>
<tr>
<td>Condylocardia fernandina</td>
<td>broad-trigonal</td>
<td>7–8 low radial/strong commarginals</td>
<td>mucronate, with radial ribs, strongly demarcated</td>
<td>posterior lateral in LV large</td>
</tr>
<tr>
<td>Condylocardia koolae</td>
<td>ovate</td>
<td>15–16 radial moderate commarginals</td>
<td>small, pointed, not set off tip indented</td>
<td>short posterior lateral in LV</td>
</tr>
<tr>
<td>Condylocardia elongata</td>
<td>elongate</td>
<td>9–10 radial, smallest medially fine commarginals</td>
<td>pointed, not set off tip indented</td>
<td>short posterior lateral in LV</td>
</tr>
<tr>
<td>Condylocardia kaiseriana</td>
<td>oblique-trapezoidal</td>
<td>13–14 radial, wider anteriorly moderate commarginals</td>
<td>pointed, not set off tip indented</td>
<td>short posterior lateral in LV</td>
</tr>
<tr>
<td>Condylocardia geigeri</td>
<td>ovate-trigonal</td>
<td>18 radial broad radial crossbars ventrally</td>
<td>mucronate, set off pristinolose</td>
<td>posterior larger in LV small specimens</td>
</tr>
<tr>
<td>Carditella galapagoensis</td>
<td>trapezoidal</td>
<td>16 nodose radial/fin commarginals</td>
<td>pointed, not strongly demarcated, pristinolose</td>
<td>posterior lateral in LV large</td>
</tr>
<tr>
<td>Carditella marietii</td>
<td>trapezoidal</td>
<td>11 nodose radial/fin commarginals</td>
<td>small, strongly demarcated, with fine radial sculpture</td>
<td>posterior lateral in LV large</td>
</tr>
</tbody>
</table>

Phoenix, Arizona, USA; and Kirstie L. Kaiser, Puerto Vallarta, Jalisco, Mexico, was also examined.

MORPHOLOGICAL CHARACTERS

Aside from the fundamental difference in hinge morphology between the Condylocardia and Carditella, a combination of shell shape, external sculpture, prodissocusch morphology, and aspects of the definition suffice to differentiate the species, these are detailed in the descriptions and the most important of them summarized in Table 1. Differences in shell color are also noted in the descriptions of some taxa.

Some of the taxa discussed here are provisionally placed in Condylocardia and may eventually merit the description of additional genera. Middelfart, personal communication, December 2002, a task beyond the scope of the present treatment (see also Discussion at end).

SYSTEMATICS

Condylocardiidae E. Bernard, 1896
Condylocardinae F. Bernard, 1896

Condylocardia E. Bernard, 1896


Diagnosis: Ligament in a central resiliere; no external ligament present. Prodissocusch bounded by a rim that is raised in most, and which has faint radial ribs in most. To 3.1 mm.

Condylocardia digueti E. Bernard, 1896
Figures 1–7


Description: Shell narrow-trigonal, longer anteriorly; anterior end rounded to slightly pointed; posterior end rounded. Prodissocusch large, set off by raised rim; mucronate, with fine radial ribs. Lamellae and esculenther broad. Shell with 6–11 broad radial ribs with narrow interspaces. Radial ribs crossed by commarginal bars. Pos-
E. V. Coan, 2003

Figures 1-7. *Conchilocardia digueti* 1-3. External view of left valve; internal views of left and right valves, Bahía Magdalena, Pacific coast of Baja California Sur, Mexico, 1-11 m. LACM 71-18343, length = 1.6 mm. 4. External view of right valve, Bahía Pulmo, Baja California Sur, Mexico, 6 m. LACM 66-201, length = 1.5 mm. 5. External view of left valve, Isla Santa Margarita, Pacific coast of Baja California Sur, 0-2 m. LACM 66-S-24, length = 1.5 mm. 6. External view of left valve, Punta Aguon, Galápagos, Ecuador, intertidal zone, LACM 70-12410, length = 1.2 mm. 7. Bahía San Gabriel, Isla Espíritu Santo, Baja California Sur, Mexico, syntype, MNHN, left valve, length = 1.5 mm.

terior-most portion of posterior slope with commarginal bars only. White to light tan or yellow. Right valve with large anterior cardinal and small, dorsally positioned posterior cardinal, the resilifer between them; elongate anterior lateral on submarginal ridge, separated from shell margin by serrate groove for anterior margin of left valve; posterior margin serrate, slightly raised distally into lateral tooth. Left valve with small, dorsally positioned anterior cardinal and large posterior cardinal, the resilifer between them; pit anterior to anterior cardinal for anterior cardinal of right valve; anterior margin with serrate lateral ridge; raised distally into low lateral tooth;
posterior margin with low lateral tooth on submarginal ridge separated by serrate groove for posterior margin of right valve. Length to 1.6 mm. Two specimens from Bahía Magdalena LACM 74-153.13 (Figures 1–3), one specimen each from Bahía Pulmo LACM 66-20.1 (Figure 1) and Isla Santa Margarita LACM 66-8.24 (Figure 5), both Baja California Sur, México, and one specimen from Punta Aucón, Guayas, Ecuador LACM 70-12.10 (Figure 6), are figured here to show the range in shapes of this species.

Type Material: MNHN (no number), syntypes, 3 closed pairs, 2 right valves, 2 left valves. M. L. Digniet, 1914, from type locality. The largest left valve measures: length, 1.5 mm; height, 1.5 mm (Figure 7).

Type Locality: Bahía San Gabriel, Isla Espíritu Santo, Baja California Sur, México (24.4° N, 110.4° W).

Distribution: NE end of Isla Cedros, Pacific coast of Baja California, 28.3° N [LACM 71-151-19, 71-152-31], into the Golfo de California as far as Punta la Gringa, Bahía de Los Angeles, Baja California, 29.1° N [LACM 86-195.4], and Cabo Hato, Guayas, Sonora, 27.8° N [CAS 1507-33], México, to SE end of Punta Aucón, Peninsula de Santa Elena, Ecuador, 2.3° S [LACM 70-12.40], SMNH 34087; Isla de Malpelo, Colombia (Kaiser Collection); Isla San Cristóbal, 0.9° N [LACM 34-267.2, 34-269.3, 34-185.3] and Isla Santa Marta, 1.3° N [LACM 34-297.3], Islas Galápagos, Ecuador; intertidal zone to 97 m (mean = 19.1 m; n = 57), in rubble. Lots examined: 91.

Discussion: The species is by far the most abundant and widespread in the eastern Pacific and exhibits considerable variability in shape and number of ribs. Most specimens, such as the figured syntype, are almost triangular, whereas others are more rounded, such as the specimen from Bahía Pulmo figured here. Available material fully bridges these extremes.

Condyliscardia hippopus (Mösch, 1861) (Figures 8–11)


Condyliscardia panamensis Olsson, 1942: 156–457. [issn pagination = 34–35, 210 = 88], pl. 37, fig. 3, figs. 9, 10. Herdmann and Strong, 1948: 106. Olsson, 1961: 140–191, 150 pl. 77, fig. 1 Keen, 1966: 8, 1971: 110 (as a synonym of C. hippopus) PRH 1090, holotype; left valve, length: 1.55 mm; PRH 1091 paratypes; neither lot examined. Zone of unconformity at base of Pleistocene, Punta de Piedra, Peninsula de Barú, Chiriquí Province, Panama S 2° N 82° W.

Description: Shell trapezoidal, longer posteriorly, anterior end sharply rounded, posterior end narrow, pointed. Prodiosocorne large, set off by raised rim, micronate, with fine radial ribs. Lamelle broad, concave, escutcheon broad, less concave. Shell with 4–5 broad radial ribs on the anterior and central slopes; interspaces of approximately half-rib width; posterior slope with only faint traces of radial ribs; ribs crossed by commarginal growth striae. Beaks and anterior slope brown, blue anteriorly brown in some specimens. Right valve with moderate anterior cardinal and tiny, dorsally positioned posterior cardinal, the resilifer between them; posterior smaller radial rib posterior to these; posterior-most portion posterior slope without radial ribs. Radial ribs crossed by moderate commarginal ribs, forming bars on surfaces of radial ribs. White, sometimes with brown patches. Right valve with large anterior cardinal and small, dorsally positioned posterior cardinal, the resilifer between them; anterior end with large lateral tooth on submarginal ridge separated by serrate groove for margin of right valve; postero-dorsal margin serrate, swollen into low lateral tooth distally, with small submarginal shelf below it. Left valve with small, dorsally positioned anterior cardinal and large anterior cardinal, the resilifer between them; anterior to anterior cardinal is pit for anterior cardinal of right valve; antero-dorsal margin serrate, slightly raised distally into lateral tooth, with small submarginal shelf below it; posterior end with lateral on small submarginal ridge separated from hinge margin by serrate groove for hinge margin of right valve. Length to 2.4 mm (LACM 72-42.60). Bahía Ballena, Puntarenas Province, Costa Rica. Two specimens from Bahía Puerto, Guanacaste Province, Costa Rica (LACM 72-38.28), are figured here (Figures 8–10).

Type Material: UZM no number, syntypes, one closed pair, one broken left valve, one intact left valve, one unusually thickened right valve, A. S. Oersted, 1848, from type locality, "in Margaritiferis" [text], "in Balan" [label]. The intact left valve is figured here, length: 2.0 mm; height: 1.9 mm (Figure 11). An external view of the right valve of the pair was given by Keen (1966: 7, figure 4).

Type Locality: Puntarenas, Puntarenas Province, Costa Rica, 10.0° N, 84.9° W.

Distribution: Bahía Jobo, Guanacaste Province, 11.1° N [LACM 72-17.43], to Isla del Caño, Puntarenas Province, 8.3° N [LACM 72-63.78], Costa Rica; Búcaros, Los Santos Province, Panamá, 7.4° N [Olsson, 1961]; specimens not located in UMML (N. Yoss, personal communication, 18 September 2001); Isla Tiboga, Panamá Province, 8.8° N [LACM 39-262.1], Panamá; Isla Marena, Islas Galápagos, Ecuador, 0.3° N [LACM 34-285.7]; 3.99 m (mean = 23.7 m; n = 24), in rubble. Lots examined: 25.

Condyliscardia sparsa new species (Figures 12–14)

Description: Shell trapezoidal, longer posteriorly, inflated, anterior end produced, pointed; posterior end pointed. Prodiosocorne large, set off by raised rim, micronate, with fine radial ribs. Lamelle broad, concave, escutcheon broad, less concave. Shell with 4–5 broad radial ribs on the anterior and central slopes; interspaces of approximately half-rib width; posterior slope with only faint traces of radial ribs; ribs crossed by commarginal growth striae. Beaks and anterior slope brown, blue anteriorly brown in some specimens. Right valve with moderate anterior cardinal and tiny, dorsally positioned posterior cardinal, the resilifer between them; posterior...
to posterior cardinal is pit for posterior cardinal of left valve; anterior end with elongate lateral on submarginal ridge separated from hinge margin by serrate groove for margin of left valve; posterodorsal margin raised into lateral tooth distally, with very short submarginal shelf directly below it. Left valve with tiny, dorsally positioned anterior cardinal and moderate posterior cardinal; the resilifer between them; anterior to anterior cardinal is pit for anterior cardinal of right valve; anterior end with lateral tooth on hinge margin and very short submarginal shelf directly below it; posterior end with large lateral on submarginal ridge separated from hinge margin by serrate groove for margin of right valve. Length to 2.2 mm (LACM 80-60,16).

**Type Material:** LACM 2918, holotype, pair; length.
Figures 15-23. Condylorocochia species. 15-17. Condylorocochia fernandina new species, paratypes, external view of right valve, internal views of left and right valves. Isla Marchena, Islas Galápagos, Ecuador, 12 m. LACM 2921, locality 66-125, lengths = 19 mm (external view); 17 mm internal view. 18-20. Condylorocochia kooi new species, paratypes, external view of left valve, internal views of left and right valves. Isla Wolf, Islas Galápagos, Ecuador, 271 m. LACM 2925, locality 31-264, lengths = 19 mm. 21-23. Condylorocochia elongata new species, paratypes, external view of left valve, internal views of left and right valves. Isla Fernandina, Islas Galápagos, Ecuador, 15-30 m. LACM 2925, locality LACM 72196, lengths = 19 mm (external view); 20 mm internal views.

Type Locality: Punta Penca, N of Bahía Potrero, Guanacaste Province, Costa Rica, 10° 29' 15" N, 85° 18' 53" W. LACM locality 72-38; 8-12 m; Stomather station 126.
Distribution: Isla Meanguera, El Salvador, 13.2° N, to Punta Quepos, Costa Rica, 9.4° N; intertidal zone to 35 m (mean = 12.4 m; n = 11).

Other Material Examined: El Salvador: Kaiser Collection and LACM 2001-15, Isla Meanguera, La Unión Province, El Salvador, 13.2° N, 1 m, 3 pairs, 8 valves; Kaiser Collection, Isla Meanguera, La Unión Province, El Salvador, 13.2° N, 5 m, 17 pairs, 5 valves; Kaiser Collection and SBMNH 346013, Isla Meanguera, La Unión Province, El Salvador (13.2° N), 12 m, 53 pairs, 52 valves; Nicaragua: LACM 74-86, El Velero, Leon Province, Nicaragua, 12° N, 2 m, 3 brachioworm valves; Costa Rica: LACM 80-60.16, Cabo Santa Elena, Puntarenas Province, Costa Rica, 10.5° N, intertidal zone, 1 pair; Type lot, near Bahía Potrero, Guanacaste Province, Costa Rica, 10.5° N, LACM locality 72-38, 8-12 m; INBio 0003404072, Cabo Blanco, Puntarenas Province, Costa Rica, 9.6° N, 20-50 m, 1 pair, 4 valves; INBio 0001494961, Punta El Flor, near Cabo Blanco, Puntarenas Province, Costa Rica, 9.6° N, 14 m, 1 pair, 2 valves; SBMNH 346088, Bahía Ballena, Puntarenas Province, Costa Rica, 9.7° N, 12-14 m; LACM 72-5-5, Punta Quepos, Puntarenas Province, Costa Rica, 9.4° N, 9-23 m, 12 pairs, 1 valve (plus one pair now in AM C.403166); LACM 72-59.29, Punta Quepos, Puntarenas Province, Costa Rica, 9.4° N, 23 m, 1 pair.

Etymology: The specific name refers to the few radial ribs on this species.

Discussion: This species is most similar to the sympatric C. hippocaps, differing in being more trapezoidal, more inflated, and with relatively unsculptured posterior slope. Condylorhadrina sparse also has fewer radial ribs, which are crossed by commarginal striae rather than ribs.

Condylorhadrina fermandina new species
(Figures 15-17)

Description: Shell broad-trigonal, subequilateral, anterior end pointed, posterior end sharply rounded. Prodissoconch large, set off by raised rim, unornamented, with fine radial ribs. Umbilical broad, concave; escenthecon broad, flat. Shell with 7-8 low, broad radial ribs, often with small radial rib anterior to these; interspaces narrow, the anterior-most wider; ribs crossed by dense, moderately strong commarginal ribs; shell white to brown. Right valve with moderate anterior cardinal and very small, dorsally positioned posterior cardinal, the resilifer between them; posterior to posterior cardinal is pit for posterior cardinal of left valve; anterior end with lateral on submarginal ridge separated from shell margin by serrat groove for margin of left valve; posterior margin serrat, elevated distally into lateral tooth, with short submarginal shell directly below it. Left valve with tiny, dorsally positioned anterior cardinal and moderate posterior cardinal, the resilifer between them; anterior to anterior cardinal is pit for anterior cardinal of right valve; anterior margin serrat, raised distally into lateral tooth, with short submarginal shelf directly below it; posterior margin with strong lateral on submarginal ridge, separated from shell margin by serrat groove for posterior margin of right valve. Length to 2.1 mm.

Type Material: LACM 2920, holotype, pair, length 1.9 mm, height, 1.8 mm; LACM 2021, paratypes, 7 pairs, 14 valves; AM C.403167, paratype, left valve, James H. McLean, 11 May 1984, from type locality. Two paratypes are figured here (Figures 15-17).

Type Locality: Punta Espojo, E side of Isla Margarita, Isla Galápagos, Ecuador 0°19.5° N, 90°24° W, LACM locality 84-26, 12 m, rock and coarse sand.

Distribution: Isla Galápagos, Ecuador, from 1.4° N to 1.4° S; not counting the uncertain lot from Isla Wolf, 0°-110 m (mean = 33.1 m; n = 8).

Other Material Examined: Restricted to the Isla Galápagos, Ecuador: LACM 34-264.6, Isla Wolf, 1.4° N, 274 m, 1 pair; specimen tentatively assigned to this species; LACM 84-39.33, 8 anchorage, Isla Pinta, 0.6° N, intertidal zone, rocks and sand, 1 pair; LACM 84-11.19, S side of Isla Pinta, 0.5° N, 15-24 m, rocky slope, 3 valves; LACM 84-26.16 type lot, Isla Margarita, 0.3° N, 12 m, LACM 66-125, 34 N of Punta Espojo, Isla Fernandina, 0.3° S, 0-3 m, 1 pair; CAS 42344, Bahía Conway, Isla Santa Cruz, 0.5° S, depth not recorded, 12 pairs, 17 valves; LACM 34-281, Bahía Academy, Isla Santa Cruz, 0.8° S, 25 m, 7 valves; LACM 34-267, Bahía Wreck, Isla San Cristóbal, 0.9° S, 40 m, 1 pair; LACM 33-161.2, Hancock Bank, NE of Isla Santa María, 1.0° S, 110 m, 1 valve; LACM 34-283.10, Isla Española, 1.4° S, 55 m, 1 pair, 7 valves.

Etymology: The specific name is taken from Isla Fernandina, Islas Galápagos, where the species was first noted.

Discussion: The lot from Isla Wolf consists of a single, worn pair that is thinner, broader, and flatter than the rest of the referred material. Of eastern Pacific species, Condylorhadrina fermandina is most similar to C. digueti, differing from it in attaining a larger size, in being nearly equilateral, broader, with more pointed ends. The sculpture is similar but heavier, the radial ribs being more raised. The commarginal sculpture is much finer and denser. The prodissoconch is more unornamented. Of western Atlantic species, it is most similar to C. smithi (Dall, 1896: 16-17, pl. 1, figure 4, as Carditella), described from Bermuda, in having a trigonal shape and dense, lamellar sculpture, but it differs in being larger and in having fewer, more prominent ribs. Based on examination of USNM 762506 from Bermuda.

Condylorhadrina kindsac new species
(Figures 18-20)

Description: Shell ovate, longer anteriorly; anterior end rounded; posterior end subtruncated, sharply rounded posteriorly. Umbilical broad, prodissoconch small, pointed, set off by an inscpien-
Sculpture of 15–16 radial ribs, broadest just anterior to posterior slope; interspaces widest towards ends, with moderate commarginal ribs, forming knobs on radial ribs; posterior-most portion of posterior slope with commarginal striae only. White. Right valve with elongate anterior cardinal and minute, dorsally positioned posterior cardinal, the resilifer between them; anterior lateral on submarginal ridge separated by groove for lateral of left valve; posterior margin slightly elevated into lateral tooth distally, with short submarginal shelf below it. Left valve with elongate anterior cardinal, fitting above that of right valve, and minute, dorsally positioned posterior cardinal, the resilifer between them; anterior shell margin slightly elevated distally into lateral tooth, short submarginal shelf below it; short posterior lateral present on submarginal ridge separated from shell margin by groove for margin of right valve. Length to 2.2 mm.

Type Material: LACM 2924, holotype, pair, length 2.2 mm; height 1.9 mm. LACM 2925, paratypes, 5 pairs, 11 valves; AM C.106169, paratype, right valve, Victoria III, Alan Hancock Foundation station BS 130, 11 January 1934, all from type locality. Two of the LACM paratypes are figured here (Figures 18–20).

Type Locality: Isla Wolf, Islas Galápagos, Ecuador, 1°23' N, 91°19' W; Alan Hancock Foundation station BS 130, LACM locality 34-264, 271 m, mud. This is the same station as the type locality of Carditaella galapagana.

Distribution: Known only from Isla Wolf, Islas Galápagos, Ecuador, 1°4' N, 183–271 m (mean = 228.5 m; n = 2).

Other Material Examined: Type lot, Isla Wolf, Islas Galápagos, Ecuador, 1°4' N, LACM locality 34-264, 271 m; LACM 34-263.7, same locality, 183 m, 3 pairs, 3 valves.

Etymology: This species is named after Elizabeth Knoll of the California Academy of Sciences, who has helped on this and many other projects.

Description: In this species and C. elongata, unlike in other eastern Pacific species of Condylocardia, the larger tooth in the left valve is the anterior one, which fits above the anterior cardinal of the right valve.

Condylocardia elongata new species
Figures 21–23

Description: Shell elongate, longer anteriorly; anterior end rounded; posterior end truncate. Prodissorochen small pointed, unsulptured, set off by an inconspicuous rim, tip indented. Lamellae elongate, of moderate width; e ventricum broad, slightly concave. Sculpture of 9 to 10 strong radial ribs on anterior and central slopes; ribs with narrower interspaces medially; radial ribs crossed by fine commarginal striae, but with nodes on posterior-most radial rib. Posterior-most portion of posterior end with commarginal striae only. White to light tan. Right valve with narrow anterior cardinal and minute, dorsally positioned posterior cardinal, the resilifer between them; anterior end with triangular lateral on submarginal ridge separated from shell margin by serrate groove for anterior margin of left valve; posterdorsal margin elevated into low lateral tooth. Left valve with narrow anterior cardinal, fitting above that of the right valve, and minute, dorsally positioned posterior cardinal, the resilifer between them; anterior end serrate, with low lateral tooth on hinge margin, and tiny submarginal ridge; posterdorsal margin with lateral tooth on submarginal ridge separated from hinge margin by groove for posterior lateral of right valve. Length to 2.4 mm (a paratype).

Type Material: LACM 2926, holotype, pair, length 2.0 mm; height 1.6 mm. LACM 2927, paratypes, 5 pairs, 21 valves; SEARCHER station 331, 25 January 1972. Two paratypes are figured here (Figures 21–23).

Type Locality: Punta Espinosa, Isla Fernandina, Islas Galápagos, Ecuador, 0°16'57" S, 91°26'20" W; LACM locality 72-196. SEARCHER station 331, 15–50 m.

Distribution: Islas Galápagos, Ecuador, from 1.4° N to 1.3° S, with a possible specimen from Isla La Plata, Fernandina.

Other Material Examined: All from the Islas Galápagos, Ecuador, except the last; LACM 34-264.8, Isla Wolf, 1.4° N, 271 m, 1 valve; LACM 34-263.8, same locality, 183 m, 2 valves; LACM 54-41.20, 8 side of Isla Pinta, 0.3° N, 15–24 m, 1 pair, 11 valves; LACM 54-26.17, Punta Espenyo, E. side of Isla Marchena, 0.3° N, 12 m, 6 pairs, 10 valves; LACM 33-174.9, Bahía Darwini, Isla Genovesa, 0.3° N, 31 m, 4 pairs, 37 valves; LACM 34-262.2, Punta Albemarte, Isla Isabella, 0.2° S, 31 m, 1 pair; Type lot, Punta Espinosa, Isla Fernandina, 0.3° S, LACM locality 72-196, 15–50 m; LACM 34-271.9, Bahía Sullivan, Isla San Salvador, 0.3° S, 37 m, 3 valves; LACM 34-287.8, Bahía Academy, Isla Santa Cruz, 0.8° S, 27 m, 7 valves; LACM 33-193.15, same locality, 0.8° S, 18–37 m, 1 valve; LACM 33-157.7, Bahía Post Office, Isla Santa Maria, 1.3° N, 16 m, 1 valve; LACM 34-283.41, Isla Española, 1.4° S, 55 m, 2 pairs, 10 valves; SBMNH 348089, Isla La Plata, Manabi Province, Ecuador, 1.3° S, 12–50 m, 1 valve [specimen tentatively assigned to this species] Thus, 12–271 m (mean = 58.2 m; n = 13); Lots examined: 13.

Etymology: The specific name refers to the fact that this species is unusually elongate for the genus.

Discussion: Condylocardia elongata and C. kolskeae are unique among eastern Pacific species of Condylocardia in that the larger cardinal tooth in the left valve is the anterior one.

Condylocardia kolskeae new species
Figures 24–27

Condylocardia sp. 1. Kaiser and Bryce, 2001: 15 pl. 7 figures 2 a 2 b.
Figures 24-28. Conchilocardia species. 24-27. Conchilocardia kaiserei new species, paratypes. 24-26. External view of right valve, internal views of left and right valves, Isla Marchena, Islas Galápagos, Ecuador, 12 m, LACM 2929, locality S4-26, lengths = 2.4 mm (external view); 2.1 mm (internal view). 27. External view of left valve, “Tiger Mount,” Isla de Malpelo, Colombia, 11-14 m, SBMN H 346012, length = 2.2 mm. 28. Conchilocardia grigieri new species, paratype, external view of right valve, Isla Santa Cruz, Islas Galápagos, Ecuador, 18 m, LACM 2961, locality S4-296, length = 1.3 mm.

Description: Shell oblique-trapezoidal, much longer posteriorly; anterior end sharply rounded; posterior end broadly rounded. Prodissocoche conical, large, pointed, umbo slightly demarcated by rim, with fine radial ribs, tip indented. Lamellae narrow, esculentum broad, slightly concave. Sculpture of 11-14 radial ribs, widest posterior to midline with wider interspaces, becoming narrower anteriorly, butt also with 1-2 narrow posterior ribs; posterior-most part of posterior slope with commarginal ribs only. Radial ribs crossed by moderate commarginal ribs, forming nodes on radial ribs, slightly scabrose in some specimens. White to light tan; posterior slope with brown patches in some specimens. Right valve with and large anterior cardinal and minute, dorsally placed posterior cardinal, the resilifer between them; antero-dorsal margin with lateral tooth on submarginal ridge, separated from shell margin by groove for shell margin of left valve; posterior margin raised into slightly serrate lateral tooth distally. Left valve with minute, dorsally positioned anterior cardinal and large posterior cardinal, the resilifer between them; anterior margin raised distally into low, serrate lateral tooth, with narrow submarginal shelf for margin of right valve directly below it; posterior end with large lateral on submarginal ridge, separated from hinge margin by groove for margin of right valve. Length to 3.1 mm (Isla Darwin, Islas Galápagos, LACM S4-29,23).

Type Material: LACM 2928, holotype, par length, 2.2 mm, height, 1.7 mm. LACM 2929, paratypes, 21 pairs, 7 valves; AM C 403173, paratypes, 1 right valve, 1 left valve, James H. McLean, 11 May 1984. Two para-
types are figured here (Figures 24-26): SBMN H 346012, paratype; length: 2.2 mm (Figure 27) ["Tiger Mount"; Isla de Malpe, Colombia, 1.0° N, 81.6° W, 1144 m; Kirstie L. Kaiser, 11 March 2000].

**Type Locality:** Punta Espejo, E. side of Isla Murchison, Islas Galápagos, Ecuador, 0.5°19.5° N, 20.2°1 W; LACM locality S4-26; 12 m. rock and coarse sand.

**Distribution:** Isla de Malpe, Colombia, 1.0° N, and Islas Galápagos, Ecuador, as far south as 1.4° S, 12-274 m. mean = 77.4 m; n = 16.

**Other Material Examined:** Material from Isla de Malpe, Colombia: Kaiser Collection, "Tiger Mount". 1.0° N, 9-18 m, 52 pairs, 15 valves; Kaiser Collection and LACM 2000-18041. "Tiger Mount". 4.0° N, 24-34 m, 59 pairs, 10 valves; Kaiser Collection, "Tiger Mount". 4.0° N, 50-56 m, 12 pairs, 16 valves; Kaiser Collection and SBMN H 346012. "Tiger Mount". 1.0° N, 41-44 m, 2 pairs, including the paratype cited above. Material from the Islas Galápagos, Ecuador: LACM S1.29.23. N side of Arch Rock, SE end of Isla Darwin, 1.6° N, 6-9 m. boulders, coral and *Caulerpa*. 2 pairs, 6 valves; LACM S1-263.5, Isla Wolf, 1.4° N, 183 m, 1 pair, 9 valves; LACM S1-264.9, Isla Wolf, 1.4° N, 274 m, 1 pair, 5 valves; LACM S4-33.18, W anchorage, Isla Wolf, 1.4° N, 9-23 m. rocky slope. 1 valve; LACM S4-28.22, Beyond SW anchorage, Isla Wolf, 1.4° N, 23-30 m. sand, 1 pair, 6 valves; LACM S4-26.19, Type locality, Isla Murchison, 0.3° N, LACM locality S4-26, 12 m; LACM S4-13-23. Bahía Stephens, Isla San Cristóbal, 0.8° S, 39.0 m. 2 valves; LACM S3-161.3, Hancock Bank, Isla Santa María, 1.1° S, 119 m. 1 valve; LACM S4-290.5, Bahía Post Office, Isla Santa María, 1.3° S, 16 m. 1 valve; LACM S4-291.8. same locality, 1.2° S, 119 m, 7 valves; LACM S4-292.11, Bahía Gardner, Isla Española, 1.1° S, 64 m, 9 valves; LACM S4-283.9, Isla Española, 1.4° S, 55 m, 2 pairs, 3 valves.

**Eymology:** This species is named for Kirstie L. Kaiser, who has specialized on tropical eastern Pacific island faunas and encountered the first specimens of this species at Isla de Malpe, Colombia.

**Discussion:** It is possible to confuse this species with very small specimens of the humic genus *Ctena*. The latter are longer anteriorly, have somewhat sinuous ligament posteriorly and no central resiliers, two strong cardinal teeth in each valve, subequal anterior and posterior lateral teeth in the left valve, and a bulbous prodissocoche.

*Gondylocardia grigeti* new species (Figure 28)

**Description:** Shell ovate-trigonal, longer anteriorly; anterior end rounded; posterior end truncate. Prodissocoche small set off by raised rim; micromeres, pulsulose, without radial ribs. Lumen broad; esonucleonic broad. Shell with approximately 18 broad radial ribs with narrow interspaces. Radial ribs with cross-bars, most conspicuously ventrally. White to light brown. Right valve with large anterior cardinal and small, dorsally positioned posterior cardinal, the resiliers between them; without pit for posterior cardinal of left valve; anterior end with lateral on short submarginal ridge separated from hinge margin by groove for hinge margin of left valve; posterior dorsal margin slightly pulsulose, raised distally into small lateral tooth. Left valve with small, dorsally positioned anterior cardinal and large posterior cardinal, the resiliers between them; anterodorsal margin slightly pulsulose, raised distally into low lateral tooth; posterior end with small lateral tooth on submarginal ridge, becoming more conspicuous in the largest specimens. Length to 1.9 mm (a paratype).

**Type Material:** LACM 2962, holotype, pair length: 1.3 mm; height: 1.2 mm; LACM 2963, paratypes, 55 pairs, 97 valves; VILLERO III, Van Hancock Foundation station BS 439, 21 January 1934; LACM 2964, paratype, right valve, length: 1.3 mm (LACM locality S4-296); Bahía Academy, Isla Santa Cruz, Islas Galápagos, Ecuador, 0.8° S, 18 m (Fig. 28). 1 closed pair and 5 additional valves specimens from this lot are contained in LACM S4-286.2.

**Type Locality:** Bahía Sullivan, Isla San Salvador, Islas Galápagos, Ecuador, 0.16° S, 90.34° W; Van Hancock Foundation station BS 439, LACM locality S4-271, 37 m.

**Distribution:** Islas Galápagos, Ecuador from 0.2° to 1.3° S, 16-214 m. mean = 51.4 m; n = 18.

**Other Material Examined:** Islas Galápagos, Ecuador: LACM S3-164.4, Bahía James, Isla San Salvador, 0.2° S, 27 m, 9 valves; LACM S4-273.8, same locality, 14 m, 2 valves; LACM S4-263.6, same locality, no depth recorded, 1 valve; LACM S4-298.8, same locality, 29 m, 3 pairs, 20 valves; Type locality, Bahía Sullivan, Isla San Salvador, 0.3° S, LACM locality S4-271, 37 m (LACM S4-174.10, Bahía Darwin, Isla Genovesa, 31 m, 2 valves; LACM S3-175.1, Isla Seymour, 0.4° S, 24 m, 2 pairs, 5 valves; LACM S4-264.1, Isla Seymour, 0.5° S, no depth recorded, 1 pair, 3 valves; LACM S4-292.3, Isla Seymour, 0.5° S, no depth recorded, 2 pairs, 5 valves; LACM S3-169.3, N of Isla Santa Cruz, 0.5° S, 124 m, 1 pair; LACM S4-170.6, same locality, 101 m, 1 valves; LACM S3-171.4, same locality, 64 m, 1 valve; LACM S3-172.3, same locality, 124 m, 3 valves; LACM S3-173.3, same locality, 101 m, 1 pair, 11 valves; LACM S3-166.8, N of Isla Pinzón, 0.6° S, 82 m, 2 valves; LACM S4-194.13, Bahía Cartago, Isla Isabella, 0.6° S, 22 m, 2 valves; LACM S4-286.2, Bahía Academy, Isla Santa Cruz, 0.8° S, 16 m, 1 pair, 5 valves, plus figured paratype; LACM S4-287.9, same locality, 27.5 m, 11 pairs, 26 valves, many juveniles; LACM S4-193.16, same locality, 18-35 m, 5 valves; LACM S4-270.6, Isla San Cristóbal, 0.8° S, no depth recorded, 7 valves; LACM S3-157.8, Bahía Post Office, Isla Santa María, 1.3° S, 16 m, 2 valves.

**Eymology:** This species is named for Daniel L. Geig-
er, a research associate of the Santa Barbara Museum of Natural History, who has been helpful on many projects.

**Discussion:** This species is closest to *Codiilocardia digueti*, differing in having many more radial ribs and in being more ovate.

**Possible Additional Species of *Codiilocardia***

One lot contain specimens that do not fit the species described above, but there is too little material is available to propose an additional new taxon at this time. LACM 84-29.24. N side of Arch Rock, SE end of Isla Darwin, Islas Galápagos, Ecuador (1°6′ N): 6–9 m. Lot contains 1 open pair and 2 valves, all somewhat worn. The shells are slightly longer and somewhat truncate anteriorly, with 12–13 elevated, nodose ribs.

**Carditella E. A. Smith, 1881: 42–43.**

**Type species:** (subsequent designation by Dall 1903: 702). *C. pallida* E. A. Smith, 1881: 43, pl. 5, figure 9–9b. Recent, Estrecho de Magllanes, Chile. Medium sized to minute (up to 5.2 mm). With central resilifier as well as a sunken external ligament that is substantial in some species and minute in others. The following two species are placed in *Carditella* because of their small external ligaments in addition to a resilifier.

**Carditella galapagana** new species
(Figures 29–32)

*Conchocardiidae* sp. 2—Kaiser and Bryce, 2001: 45, pl. 7, figures 3, 3a, 3b.

**Description:** Shell trapezoidal, longer posteriorly; anterior end sharply rounded; posterior end subtruncate. Prodissoconch small, pointed, not strongly demarcated, pustulose, its tip rounded to flattened. Umbilicus narrow, esclerite elongate, wider in right valve. Sculpture of 16–17 strong radial ribs; interspaces half as wide as ribs; radial ribs nodose, crossed by moderate commarginal ribs, forming nodes on rib surfaces. White. Right valve with broad anterior cardinal; resilifier separated from sunken external ligament by low ridge that is slightly swollen dorsally into minute tooth; anterior end with triangular lateral tooth on submarginal ridge, separated from shell margin by groove for margin of left valve; anterior valve margin between beaks and distal lateral tooth granulare. Left valve with large anterior cardiac, which fits above anterior cardinal of right valve, and narrow ridge on anterior border of resilifier; resilifier separated from sunken external ligament by low ridge, swollen dorsally into minute tooth; anterior lateral on hinge margin, the area between it and beaks granular; posteriorodorsal margin with lateral on submarginal ridge separated by serrate groove for margin of right valve. Length to 2.6 mm (a paratype valve).

**Type Material:** LACM 2930, holotype, pair; length, 1.9 mm; height, 1.7 mm. LACM 2931, paratypes, 3 pairs, approximately 108 valves. AM C.403175, paratypes, 1 right valve, 1 left valve; all *Vallejo III*. Alan Hancock Foundation station BS 130, 11 January 1934, from type locality. Two paratypes are figured here (Figures 28–31).

**Type Locality:** Isla Wolf, Islas Galápagos, Ecuador, 1°23′ N, 91°49′ W. Alan Hancock Foundation station BS 130. LACM locality 31–264, 183–274 m, mud. This is the same station as the type locality of *Codiilocardia koosae*. 2

**Distribution:** Isla de Malpelo, Colombia, 4°0′ N; to Islas Galápagos, Ecuador, as far south as 0°5′ S; approximately 29–228 m (mean = 151 m; n = 4).

**Other Material Examined:** Kaiser Collection, "Tiger Mount", Isla de Malpelo, Colombia, 4°0′ N: 24–34 m, 1 valves. Material from the Islas Galápagos, Ecuador: LACM 19–263.6; Isla Wolf, 1°4′ N, 153 m; 2 valves; Type locality, Isla Wolf. L. F. N., LACM locality 34–264, 183–274 m. LACM 34–265.13, Tagus Cove, Isla Isabel, 0°3′ S, 146–153 m, 8 pairs, 90 valves. LACM 34–270.5, Isla San Cristobal, 0°3′ S, no depth recorded, three tiny valves [specimens tentatively assigned to this species].

**Etymology:** The specific name refers to the Islas Galápagos, Ecuador.

**Discussion:** This species is somewhat similar to but has more radial ribs than *C. haucaecis* Dall, Bartsch and Rehder, 1938 (p. 120, pl. 33, figures 5–8), which has only about 11 (Kay, 1979: 553, figure 180E, 554). It differs from the Peruvian-Chilean *Carditella tegulata* (see list below) in being more quadrate and in having more radial ribs. *C. tegulata* has only 10–12 ribs. The four worn valves from Isla de Malpelo are a little more elliptical and elongate than the material from the Islas Galápagos and might come to be regarded as another species when more material becomes available.

**Carditella marietta** new species
(Figures 33, 34)

**Description:** Shell trapezoidal, longer posteriorly; anterior end sharply rounded; posterior end broad, flared. Prodissoconch small, set off by raised rim, with fine radial sculpture and flattened tip. Umbilicus and esclerite narrow. Sculpture of 11–13 strong radial ribs, largest and with wider interspaces posteriorly; radial ribs with scattered nodes. Surface with few brown flecks on white background, especially on posterior slope. Right valve with broad anterior cardinal; resilifier separated from sunken external ligament by low ridge that is swollen dorsally into minute tooth; anterior end with triangular lateral tooth on submarginal ridge, separated from shell margin by groove for margin of left valve; posterior valve margin raised distally into lateral tooth. Left valve with narrow anterior cardinal, which fits above anterior cardinal of right valve; narrow ridge defines anterior border
Figures 29–34. *Carditella* species. 29–32. *Carditella galapagensis* new species, paratypes, external view of left valve, internal views of left and right valves, close-up view of hinge of left valve, Isla Wolf, Islas Galápagos, Ecuador, 274 m, LACM 2931, locality 54-264, length = 2.4 mm, external view; 2.1 mm, internal views; 33, 34. *Carditella marietas* new species, holotype, external view of left valve and internal view of right valve, Islas Marietas, Nayarit, Mexico; CAS 159057, length = 1.6 mm.

of resilifer, resilifer separated from sunken external ligament by low ridge, anterior lateral on hinge margin; posterior end with lateral on submarginal ridge separated from shell margin by groove for margin of right valve. Length to 2.0 mm (Isla San Juanito, Kaiser Collection).

**Type Material:** CAS 159057, holotype, pair; length, 1.6 mm; height, 1.2 mm. Figures 33, 34; CAS 12343, paratypes, 1 broken right valve, 9 closed pairs, mostly small; all formerly Stanford University 52426, Dwyer Expedition, 1965, from type locality, "diving".

**Type Locality:** Islas Marietas, Bahía de Banderas, Nayarit, Mexico, 20.7° N.

**Distribution:** Islas Tres Marias, Nayarit, 21.7° N, to
Islas Revillagigedos, Mexico. 18°3' N; approximately 7-16 m (mean = 20.7 m; n = 7).

Other Material Examined: Mexico: Kaiser Collection, Roata Blanka. Islas San Juanito, Islas Tres Marias, Navarit, 21°7' N, 8-11 m, 6 pairs; Kaiser Collection, Isla Maria Magdalena. Islas Tres Marias, Navarit, 21°5' N, 15-23 m, 1 closed pair; CAS 42335, Isla Maria Magdalena, Islas Tres Marias, Navarit, 21°5' N, depth not recorded, 1 closed pair; LACM 65-12411, E anchorage, Isla Maria Cleofas, Islas Tres Marias, Navarit, 21°4' N, 5-9 m, 18 pairs, all but one tightly sealed; Kaiser Collection, Isla Maria Cleofas, Islas Tres Marias, Navarit, 21°3' N, 16-23 m, 6 sealed pairs; Kaiser Collection, S side, Isla Grande, Islas Marietas, Bahia de Banderas, 20°7' N, 27-40 m, 2 small pairs; CAS 12343, type lot, Islas Marietas, Bahia de Banderas, Navarit, 20°7' N, "diving"; Kaiser Collection, Majahutas, Bahia de Banderas, Navarit, 20°5' N, 6-15 m, 1 small pair; LACM 34-26066, Bahia Sulphur, Isla Clarion, Islas Revillagigedos, 18°3' N, 46 m, 1 valve.

Etymology: The specific name is derived from the Islas Marietas, the type locality.

Discussion: This species differs from Carditella galapagana in that it has a much longer posterior end and fewer ribs, and it is somewhat smaller. This species is similar in shape to Cardioleocardiina kaiserei except that, unlike the latter, it has a small, sinuous external ligament. It is also similar in shape to some juvenile carditids, such as Carditites latiscutata (G. B. Sowerby I, 1839; Broderip and G. B. Sowerby I, 1833; 1895), but can be distinguished by its central resilifier, its larger prodissococheal with a raised rim and radial sculpture, and its wider, less scarose ribs.

Notes on the Southern South American Species of Carditella

There are at least five poorly known species of Carditella that occur on the southern coast of South America:

Carditella cauliata E. A. Smith. 1885 (215). Pl. 15, figure 6, 6a), Estrecho de Magallanes. Chile. Also Tristan da Cunha and Falkland Islands, South Atlantic Ocean. This species is longer posteriorly and is most similar to C. maritima. It has 14 ribs and attains 4 mm in length. See also Dell (1964: 193, 188. figure 3:5).

Carditella maritima (Reeve). 1843 (215). Pl. 9, figure 15, 1844: 194, as Cardita. Areta, Tarapaci Province, to the Estrecho de Magallanes. Chile. This species is longer posteriorly, has 9-10 ribs and attains 4 mm in length. See also Dell (1964: 194, 198, figure 3:4).

Carditella pallida E. A. Smith. 1881. P. 43, pl. 5, figures 9-9b., Estrecho de Magallanes. Chile. The type species of the genus, it is approximately equilateral, has 14-15 ribs, and attains 5.2 mm in length.


Carditella parvulum Dunker. 1861: 36. Non Donovan. 1800: pl. 32, figure 31. Preco, Ica Department, Peru. To Arica, Tarapaci Province. Chile. This species is oval, longer posteriorly, has 14-15 ribs, and attains 5 mm in length.

Carditella tegulata (Reeve). 1843 (215). Pl. 9, figure 18, 1844: 191, as Cardita. Possible synonym: Cardita pigmamum Phil. 1869: 176, pl. 7, figure 3:5; as "Cardita" by Bernard. 1983: 314. Islas Lobos de Tierra, Lambayeque Province, Peru. 6°9' S LACM 38-114.4, to the Estrecho de Magallanes. Chile. Larger specimens are longer posteriorly, have 10-12 ribs, and attain about 4 mm in length. Reeve figured such a specimen, whereas Dell (1964: 191, 188, figure 3:5) illustrated a subtype that is almost equilateral, presumably a smaller specimen. See also Marinovich. 1973: 30, figure 9 and Reid and Osorio (2000: 136-139). figure 7:k.

Carditella parvulum Giesens. 1888 (215). Pl. 6, figures 7:8. Described from the Iquique, Chile, was synonymized by E. B. Sowerby (1833: 184), with Carditella maritima (Reeve. 1843). However, its original measurement (4 mm) is too large to make this plausible, and it might instead be a small specimen of Cyclocardia sornayi (G. B. Sowerby I in Broderip and G. B. Sowerby I. 1833: 195). as Carditella, described from the same locality and which Giesens figure more closely resembles.

Discussion

According to Middelburg (personal communication, December 2002), who has studied the extensive Australian fauna of condiocardiids, only Cardiobecardina elongata, C. kaiserei, and C. koosae match the hinge morphology of the type species of Cardiobecardina, whereas the others are closer to the hinge morphology of Cardiobecardina, though differing in sculpture and prodissococheal shape. Moreover, Cardiobecardina kaiserei, with its very long posterior end, is unlike other species of the genus. Eventually, specialists in this group may wish to propose additional generic taxa to accommodate some of these species.

Acknowledgments

I appreciated the help of the following curators, other personnel and their institutions, who made specimens, literature, and information available: Daniel L. Geiger and Lindsey E. Groves, Natural History Museum of Los Angeles County, Los Angeles, California, USA; Elizabeth Kool, Department of Invertebrate Zoology, California Academy of Sciences, Golden Gate Park, San Francisco, California, USA; Philippe Maestrati, Muséum National d'Histoire Naturelle, Paris, France; Julio Maguña C., Instituto Nacional de Biodiversidad (INBio), Santo Domingo, Heredia, Costa Rica; Tyjana Nichols, National Museum of Natural History, Washington DC, USA; Joan Pickering, The Natural History Museum, London, England, UK; Paul Valentiicht Scott, Santa Barbara Museum of Natural History, Santa Barbara, California, USA; Annie Loun Vedecks, Zoologisk Museum, Copenhagen, Denmark; and Nancy Voss, University of Miami, Miami, Florida, USA; Lyle Campbell, Kirstie L. Kaiser.
and Carol C. Skoglund generously made available material or information from their collections. Peter Middelart of the Australian Museum, Sydney, Australia, and Diego Zelaya of the Museo de La Plata, La Plata, Argentina, provided some information. Alan R. Kabat provided a copy of a scarce paper, Lindsey T. Groves, Kirstie L. Kaiser, and Paul Valentich Scott made helpful comments on the manuscript. Scott Serrata and Sarah Spanning of the California Academy of Sciences and Daniel L. Geiger of the Natural History Museum of Los Angeles County assisted with SEM illustrations. Paul Valentich Scott prepared the plates.

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Prophysaon dubium Cockerell, 1890, the papillose taildropper (Gastropoda: Arionidae): distribution and anatomy

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ABSTRACT

Geographic distributions of many species of native forest slugs in western North America are poorly known. We report on two new records of Prophysaon dubium Cockerell, 1890, from the Rocky Mountains in northern Idaho. These records represent a disjunct population from the remainder of the species range in the Cascade Mountains and along the Pacific coast of northwestern North America, and the easternmost distribution records for the species. The genitalia of the dissected specimens from Idaho were similar to previous illustrations of specimens from Oregon and California and to dissected specimens from Oregon and Washington. We believe that the gross anatomy of the genitalia is sufficiently similar to warrant the treatment of the specimens from all areas as a single species. However, the possibility that the geographically disjunct populations represent cryptic species cannot be ruled out without further study.

INTRODUCTION

The genus Prophysaon Bland and Binney, 1873, consists of nine recognized species of arionid slugs endemic to northwestern North America (Turguen et al., 1995). The genus occurs along the Pacific Coast of North America from southeastern Alaska to northern California, east to the Rocky Mountains in northern Idaho and western Montana (Pilsky, 1948; P. Hendricks, pers. commun.); the portion of the range in the Rocky Mountains is disjunct from the remaining range farther west. Prophysaon anderssoni (J. G. Cooper, 1872) and P. hutnicke Cockerell, 1890 are the only two members of the genus that have been reported to occur in the Rocky Mountains (Smith, 1943; Pilsky, 1948; Frest and Johannes, 2000).

Prophysaon dubium Cockerell, 1890, is a diminutive <20 mm in length when extended and poorly known slug that is reported to range along the Pacific Coast from northwestern Washington south to northern California (Pilsky, 1948; Both and Pressley, 1983; Burke et al., 2000). We report here on an undocumented, disjunct population of P. dubium from the Rocky Mountains in northern Idaho, and provide descriptions of the disjunct genitalia of specimens from the states of Washington, Oregon, and Idaho.

MATERIALS AND METHODS

We searched for terrestrial gastropods on and under woody debris and within leaf litter on the forest floor in a wide range of forested habitats in Washington State, Oregon, and Idaho. We found Prophysaon dubium at 10 localities in Washington State, one in Oregon, and two in northern Idaho. Jim Baugh provided us with specimens from two additional localities in Washington State (Appendix 1).

Seventeen specimens from Washington State (records 1–3 and 5–12 in Appendix 1), two specimens from Oregon (record 13 in Appendix 1) and three from Idaho (record 14 in Appendix 1) were dissected in the current study. Prior to dissection the specimens were photographed live, subsequently drowned in water, and then preserved in 70% ethanol. Our description of the external appearance was based on the examination of live specimens. The external appearance and the genitalia of the specimens were examined under 7.5–60× magnification with a stereo-zoom microscope. The genitalia of specimens from Thurston County, Washington (record 1 in Appendix 1) and Kootenai County, Idaho (record 14 in Appendix 1) were drawn using camera lucida. Additional specimens were preserved in 100% ethanol for use in future genetic studies. Dissected specimens have been deposited in the collection at the Carnegie Museum of Natural History (CMNH, Pittsburgh, Pennsylvania, USA; one specimen has been deposited at the Delaware Museum of Natural History (DMNH, Wilmington, Delaware, USA).

RESULTS

DISTRIBUTION AND HABITAT

In Idaho, we found P. dubium at two sites approximately 30 km apart. At the site in Kootenai County (record 14 in Appendix 1) all eight specimens were within an approximately 100 m × 10 m area along the base of a steep, north-facing slope abutting the floodplain of Beauty Creek. Most individuals (six of eight) were found along the edge of a grassy clearing adjacent to a western hemlock (Tsuga heterophylla)–dominated forest; the two
remaining individuals were on a talus slope beneath closed forest canopy, One individual was on a moss-covered rock, six were under woody debris, and one was on a cardboard sheet placed on the ground to attract gastropods. At the site in Benewah County (record 13 in Appendix 1), the only specimen was found on the underside of a well-decayed birch (Betula papyrifera) log adjacent to Chatolet Lake.

At low-elevation sites in Washington and Oregon, specimens were found in mixed forest, consisting of Douglas-fir (Pseudotsuga douglasii) or western hemlock (Tsuga heterophylla) and bigleaf maple (Acer macrophyllum), with abundant sword ferns (Polystichum munitum) in the understory; specimens also were found at three high-elevation sites, consisting of mountain hemlock (Tsuga mertensiana)-dominated forest with sparse Douglas maple (Acer glabrum). Specimens were found either under woody debris (16 of 44 specimens) or on fallen bigleaf maple leaves (28 of 44 specimens).

**External Appearance and Distal Genitalia**

The external appearance of the specimens from Idaho, Washington, and Oregon is consistent with published descriptions (Pilsbry, 1948; Branson and Pressley, 1983; Kelley et al., 1999) (Figure 1). The background color of specimens includes various shades of brown, reddish-brown, olive, and gray. The mantle is always mottled to some degree with brown or gray pigment, which on some specimens merges to form dark stripes. The foot and to a much lesser extent the mantle are marked by light-brown, orange, copper, and/or gold flecking. The pneumostome is positioned immediately anterior of mid-mantle on the right side. The integument of both the mantle and foot is covered with numerous cone-shaped papillae. Dorsally the foot has a network of dark, longitudinal lines associated with grooves, which, laterally, run obliquely downward to the sole margin. A line of abscission is present on the foot approximately one-third of the animal's extended body length anterior of the posterior end.

Internally, the specimens from Idaho, Oregon, and Washington are similar as well. Specimens from Oregon and Washington display both within and between-site variability in the shape and size of the ejaculatory (distal) portion of the epiphallus. The shape of the distal epiphallus varies from oblong to circular. Each of the three specimens from Idaho displays a sausage-shaped distal epiphallus (Figure 2). None of the specimens examined for this study had an ejaculatory epiphallus that exceeded 2 mm in length and in most individuals the length was barely 1 mm. Shared characteristics among specimens from all three states include a broad and elongated vagina (or free oviduct), a long, slender, and convoluted epiphallus leading up to the distal ejaculatory portion, and a small hairpin-shaped penial loop consisting of a short, slender connecting duct and a slightly thicker-walled penis, which in turn inserts on the atrium. The spermatheca (= bursa copulatrix) and spermathecal duct are similarly proportioned in specimens from all areas, but the length of the duct varied from individual to individual. The small ovotestis consisted of approximately 15-30 lobules, each of which was tipped with black pigment.

**DISCUSSION**

**Distribution**

Previously, *P. dubium* was known from the eastern slopes of the Cascade Mountains to the Olympic Mountains in Washington and south to northwestern California (Cockerell, 1890; Pilsbry, 1948; Branson and Branson, 1984; Both and Pressley, 1983; Kelley et al., 1999; McGraw et al., 2002). Our records from Idaho extend the range of the species westward to the Rocky Mountains (Figure 3). Between the Pacific coastal and Rocky Mountain distributions lies the Columbia Basin, an arid shrub-steppe province in the rain shadow of the Cascade Range (Franklin and Dymsch, 1958; Brunsfield et al., 2001): this area is unsuitable for gastropods that require mesic forest habitats. Consequently, the Rocky Mountain distribution of *P. dubium* appears to be disjunct from Pacific coastal populations, a distributional pattern shared with numerous plants, animals, and fungi (Slater and Shipp, 1940a; b, Krziz, 1958; Briggs, 1971, 1974; Shear, 1976; Enghoff, 1985; Barnosky et al., 1987; John-
son 1987; Lorain 1988; Fender and McKey-Fender 1990; Shelley 1993, 1994a, b, c; Wilson and Larsen 1999; Brunsfeld et al. 2001; Nielson et al. 2001). Varying patterns of differentiation, up to species level, have been documented to accompany this spatial disjunction in different organisms (Brunsfeld et al. [2001] and references cited therein).

**Distal Genitalia**

All specimens that we examined have a very large vagina that is proportionally broader than shown by Pilsbury (1948) for Oregon specimens. Moreover, the epiphallus is approximately the same length as the specimen, not twice its length as reported by Pilsbury (1948); our findings are consistent with those of Ross and Pressley (1983) for a specimen from California.

The genitalia of the three specimens from Idaho are similar to those illustrated by Ross and Pressley (1983). The ejaculatory portion of the epiphallus of these specimens is sausage-shaped and similar, but much smaller proportionally, to that of the specimen from Oregon pictured by Pilsbury (1948). None of our specimens from Idaho, Oregon, or Washington have an ejaculatory portion that exceeded 2 mm in length, which is in sharp contrast with the illustration in Pilsbury (1918: p. 694, fig. 379), in which this structure is shown to be about 5 mm in length.

Some of the specimens from Washington have a small, spheroid- or egg-shaped ejaculatory portion of the epiphallus different from the same structure pictured by both Pilsbury (1948) and Roth and Pressley (1983). Interestingly, the ejaculatory portion of the epiphallus of these Washington specimens is similar in shape and proportions to that drawn by Pilsbury (1948: p. 693, fig. 378) for *P. coerulentum*. Consequently, these Washington specimens easily could be mistaken for *P. coerulentum* were it not for the distinctive external characters of *P. dubium*.

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**Figure 2.** Genitalia of *Prophysum dubium* from Beauty Creek, Kootenai County, Idaho (upper: CM 64155) and Woodard-Ray Natural Resource Conservation Area, Thurston County, Washington (lower: CM 64150). EP: epiphallus; MB: Muscular body of epiphallus; PE: penis; SP: spermatheca; SPOV: spermoviduct; VA: vas deferens; VD: vagina.

**Figure 3.** Distribution of *Prophysum dubium*. Closed circles = specimens examined by us; open circles = records from literature; Cockerell 1890, Filsbry 1948; Branson and Branson 1984; triangles = records that have been reported to us by regional experts; John Applegarth, Steve Dolar, Nancy Duncan, Tom Kogut, and Barry Roth.
such as papillate integument and dark markings on the mantle.

Our description of the features of the genitalia of specimens from Washington represents the mature condition, because the specimen from Woodard Bay (record 12 in Appendix I) deposited a cluster of 14 eggs (approximately 1.3 x 1.2 mm diameter shortly after being laid) in the laboratory on 22 January 2002. Moreover, specimens from Kraus Ridge (record 5 in Appendix I) laid clusters of 6 and 14 eggs (mean egg size = 2.1 x 1.5 mm, SD = 0.2 for both the length and width, n = 9; Figure 4) in the laboratory on 15 December 2003. Although no eggs were obtained from the Idaho specimens, their comparably developed genitalia lead us to believe that these animals were sexually mature as well.

**TAXONOMIC STATUS**

The external appearance and gross anatomy of the reproductive system, which showed only minor individual differences, suggest that our specimens from Idaho, Oregon, and Washington belong to the same species, *Prophysaon dibilitum*. Until molecular studies clarify relationships we suggest that both the coastal populations and the disjunct Idaho populations of *P. dibilitum* should be treated as a single species. We cannot explain the discrepancies between the description of distal genitalia by Pilsbry (1918) and our own observations on 22 dissected specimens from three states, including specimens from the type locality and from a site near one of Pilsbry’s sites in northern Oregon.

Additional field studies are required to establish the distribution and relative abundance of *P. dibilitum* in the Rocky Mountains. Moreover, a range-wide genetics study would provide important information on the degree of differentiation between the Idaho and Pacific coastal populations, and will be crucial to the development of an appropriate conservation strategy for these populations.

**ACKNOWLEDGMENTS**

We thank Jim Baugh, Tom Burke, Vicki and Megan Leonard, Brad Moon, Casey Richart, Robin Shiel, and Joan Ziegler for assistance collecting specimens. We are grateful to John Applegarth, Steve Dolan, Nancy Duncan, Tom Kogut, and Barry Roth for providing additional locality records used to create Figure 3, and both Paul Hendricks (Montana Natural Heritage Program) and Jochen Gerber (The Field Museum, Chicago) for providing information on the distribution of *Prophysaon rotundum* in Montana. We are especially grateful to Casey Richart for making the photograph of *P. dibilitum* eggs used in figure 4. This paper benefited from the thoughtful comments of an anonymous reviewer. Moreover, we are grateful to Tim Pearce for providing comments on an earlier draft of the manuscript and for graciously accepting dissected specimens for the collections at both the Delaware Museum of Natural History and the Carnegie Museum. Kelly Sendall allowed us to use facilities at the Royal British Columbia Museum for the preparation of Figure 2.

**LITERATURE CITED**


**APPENDIX 1**

Specimens of *Prophysaon dubium* examined for this study.

**Washington**

1. Woodard Bay Natural Resource Conservation Area, Thurston County; elevation 15 m above sea level [asl]: 47° 50′ 46″ N, 122° 51′ 04″ W; 17 December 2001, 2 March 2003 (1 specimen collected by R. Shear and J. Ziegler); 1 specimen 13 mm extended length while in movement, collected by W. Leonard; CM 61450, CM 61983.

2. Priest Point Park, Olympia, Thurston County; elevation 20 m asl: 47° 04′ 35″ N, 122° 53′ 30″ W; 5 January 2003, 1 specimen 16 mm extended length while in movement, collected by W. Leonard; CM 61978.

3. Woodland Creek, St. Martin's College, Thurston County; 58 m asl: 47° 02′ 50″ N, 122° 48′ 17″ W; 11 November 2002, and 2 December 2002 (9 specimens collected by W. Leonard); CM 61876.

4. Tolmie State Park, Thurston County; 10 m asl: 47° 07′ 08″ N, 122° 56′ 62″ W; 9 February 2003 (1 specimen 13 mm extended length while in movement, collected by W. Leonard); CM 61876.

5. Schafer State Park, Mason County; 50 m asl: 47° 05′
05.85' N, 123° 27.37' W; 3 January 2003 (11 specimens ranging between 10 and 15 mm extended length [mean = 12.5 mm] while in movement, collected by W. Leonard and C. Richard): CM64979.

6. Headwaters of Porter Creek, Capitol Forest, Thurston County; elevation 350 m asl; 47° 01.33' N, 123° 07.92' W; 20 January 2001 (3 specimens, collected by W. Leonard): DM 221684.

7. 0.6 km west of Omalaska post office, Lewis County; elevation 75 m asl; 46° 34.55' N, 122° 43.53' W; 9 January 2002 (1 specimen, collected by W. Leonard): CM 64419.

8. Centralia, Lewis County; elevation 60 m asl; 46° 43.33' N, 122° 56.62' W; 5 January 2003 (4 specimens ranging between 11 and 15 mm extended length [mean = 14 mm] while in movement, collected by C. Richard): CM64980.

9. South side of State Route 2, 3.2 km west of Stevens Pass summit, Mt. Baker-Snoqualmie National Forest, King County; elevation 1100 m asl; 47° 44.62' N, 121° 7.20' W; 7 May 2001; 27 September 2001 (2 specimens, collected by W. Leonard): DM221686, CM 64154.

10. Toll Creek, Wenatchee National Forest (Interstate 90 site #630), Kittitas County; elevation 747 m asl; 47° 17.63' N, 121° 17.13' W; 2 July 2001 (1 specimen, collected by J. Baugh, maintained in captivity until October 2002): CM 64151.


Oregon

13. Ainsworth State Park Campground, Multnomah County; 70 m asl; 45° 35.88' N, 122° 02.58' W; 11 December 2002 (3 specimens, collected by W. Leonard): CM64982.

Idaho


15. Heyburn State Park, Benewah County; elevation 650 m asl; 47° 21.13' N, 116° 46.68' W; 15 September 2002 (4 juvenile specimen, collected by T. Burke and W. Leonard (specimen used for genetic studies; photographs in personal collection of WL).
Erratum

In the article by Pastorino (2003: 46) the synonymy of *Amalda josexcavati* should read:

*Ancilharia Tankervillei* Swainson.—Dall, 1890: 310.
*Ancilharia diminutata* Sowerby.—Strebel, 1908: 25, pl. 1, figs. 2a–c.
*Ancilla diminutata* (Sowerby).—Smith, 1915: 96, *non* Sowerby, 1859, *nee* Sowerby, 1892; Marcens and Marcens, 1969, figs. 1–9 (anatomy); Rios, 1970: 102, pl. 32; 1975: 111, pl. 33, fig. 472; 1985: 111, pl. 38, fig. 191; 1994: 113, pl. 46, fig. 613; Figueiras and Sicardi, 1973: 264, pl. 15, fig. 193; Scarabino, 1977: 194, pl. 3, fig. 8; Calvo, 1987: 164, fig. 8.
*Ancilla tankervillei* Swainson.—Fernández, 1965: figs. 1–4; Castellanos, 1970: 121, pl. 9, fig. 7, *non* Swainson, 1825.

LITERATURE CITED

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CONTENTS

Luiz Ricardo L. Simone
Carlo Magenta da Cunha

Pseudococculina rinaiia, a new species (Cocculiniformia:
Pseudococculinidae) from off southeastern Brazil ............ 69

Monica A. Fernandez
Silvana Thiengo
Luiz Ricardo L. Simone

Distribution of the introduced freshwater snail Melanoides
tuberculatus (Gastropoda: Thiaridae) in Brazil .................. 78

Carlo Smriglio
Paolo Mariottini

Horatichnus syoerti, a new species (Neogastropoda:
Drilliidae) from the northwestern Indian Ocean ................ 83

Roland Houart

Description of Scabrostrophon inspiratum new species
(Gastropoda: Muricidae) from Vanuatu .......................... 87

Sven N. Nielsen
Daniel Frassinetti

New and little known species of Pseudohividae
(Gastropoda) from the Tertiary of Chile ....................... 91

Notice ........................................................................... 97
Sponsored in part by the State of Florida, Department of State, Division of Cultural Affairs, the Florida Arts Council and the National Endowment for the Arts.
**Pseudococculina rimula**, a new species (Cocculiniformia: Pseudococculinidae) from off southeastern Brazil

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**ABSTRACT**

*Pseudococculina rimula*, new species, is described. It occurs off the state of Rio de Janeiro, in southeastern Brazil, at 350-400 m depth. This is the first report of the genus in the Atlantic Ocean. The main diagnostic characters of the new species are shell high, lacking radial sculpture; snout flat, somewhat involved by oral lappets; posterior odontophore cartilages connected to anterior one in median line; gonoduct connected to posterior end of pallial cavity; a gonoduct running transversally and dorsally in visceral mass; sperm duct mostly closed (tubular); prostate located inside right tentacle; sperm duct opening in a subterminal papilla.

Additional keywords: Anatomy, southwestern Atlantic, Rio de Janeiro.

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**INTRODUCTION**

The Cocculiniformia encompasses taxa with an enigmatic set of primitive and derived features. Its closest groups are yet to be determined, and it is still questionable whether the taxon is monophyletic. They are usually minute, palliform gastropods living in the deep sea.

Two papers have been published dealing with cocculiniform gastropods found in deep waters off Brazil: Simone (1996) described an addisonium, and Leal and Simone (2000) named a pseudococculinid. Both papers provided anatomical information, which is vital for understanding the systematics of the group. Further data on western Atlantic cocculiniformians have been provided by McLean and Harasewych (1995) and Leal and Harasewych (1999).

The present paper describes the description of a third Brazilian species, which was collected by an otter trawl off the coast of São Paulo State, in southeastern Brazil.

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**MATERIALS AND METHODS**

The specimens were dissected using standard techniques, under a stereomicroscope and immersed in fixative. The hard structures (radula and shell) were also examined in a SEM in the Laboratório de Microscopia Eletrônica do MZSP, also using traditional techniques. All drawings were made with the aid of a camera lucida.

Abbreviations used in the figures are: **an**, anus; **ap**, aperture of gonoduct; **an**, atride; **bm**, buccal mass; **br**, subradular membrane; **bs**, blood sinus; **ce**, cerebral ganglion; **cv**, cerebellar vein; **dc**, dorsal chamber of buccal mass; **dd**, duct to digestive gland; **df**, dorsal fold of buccal mass; **dg**, digestive gland; **dl**, diaphragm-like septum separating buccal mass from visceral mass; **ef**, esophageal folds; **ep**, epipodium; **es**, esophagus; **et**, epipodial tentacle; **fl**, foot sole; **ft**, foot; **gb**, gonoduct; **gl**, gill; **go**, gonad; **hc**, head; **hn**, head muscle; **in**, intestine; **jw**, jaw; **kl**, left kidney; **kr**, right kidney; **m1**–**m8**, extrinsic and intrinsic odontophore muscles; **mb**, mantle edge; **me**, mouth sphincter; **mf**, mantle fold; **mj**, jaws, buccal, and oral tube muscles; **ms**, mouth; **oc**, anterior odontophore cartilage; **od**, odontophore; **ol**, oral lappet; **oy**, ovary; **pe**, pericardium; **po**, posterior odontophore cartilage; **pp**, papilla of copulatory tentacle; **pt**, prostate; **pu**, pedal ganglion; **ra**, radula; **rn**, radular muscle; **rs**, radular sac; **rt**, rectum; **se**, subradular cartilage; **sd**, sperm duct; **se**, chamber originating esophagus and separating odontophore in buccal mass; **sm**, shell muscle; **sn**, snout; **st**, stomach; **te**, cephalic tentacle; **tg**, integument; **tp**, copulatory right cephalic tentacle; **ts**, testeis; **ve**, ventricle; **vm**, visceral mass.

Institutional abbreviations used are: MNHN, Muséum National d'Histoire Naturelle, Paris, France; MNRI, Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; MZSP, Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil.

**SYSTEMATICS**

**Genus** *Pseudococculina* Schepman, 1908

**Type species:** *Pseudococculina rugosoaplicata* Schep-
Pseudococculina rimula new species

Figures 1-30

Diagnosis: Shell high, anterior region strongly concave. Sculpture of concentric modulations and threads. Snout flat, surrounded by oral lappets, jaw plates thin. Posterior odontophore cartilages connected to anterior one along median line. Gonad connected to posterior end of pallial cavity by a gonoduct that runs transversally and dorsally in visceral mass. Sperm duct mostly closed (tubular) opening in a subterminal papilla, prostate inside right tentacle.

Description: Shell (Figures 1-4, 6-10) patelliform, length up to 3 mm, high (50% of length), white, relatively thick. Protoconch (Figures 6, 7) with one whorl, planispiral, coiled towards ventral region, with a papilla-like projection on each side oriented along direction of coiling; outer surface smooth, opaque. Teleoconch opaque, sculpture of strong, concentric growth lines and threads. Apex high, curved ventrally and posteriorly, situated along median line of shell, closer to posterior region. Anterior region convex, posterior region weakly concave. Inner surface glossy. Muscular scar horseshoe-shaped, concavity anterior (Figures 9, 10), narrow posteriorly, thick anteriorly; anterior ends curved toward dorsal and posterior regions.

Head-foot (Figures 2, 14-18): Head protruded, occupying about 1/3 of total volume of head-foot. Snout well developed, somewhat flat, edges broad, extending externally (Figures 14-15). Oral lappets (lateral expansions on snout) large, covering most of anterior half of animal body. Cephalic tentacles asymmetrical, right tentacle 50% larger than left tentacle (Figures 16, 17), acting as copulatory organ (details below). Foot sole, or mesopodium, flat, thick, occupying most of ventral surface. Figures 2, 14: anterior edge with a very narrow and shallow furrow. Epipodium about 3/4 of shell length, forming a flat flap, inserted between mesopodium and mantle; free edge with 2 pairs of tentacles on each side; inner tentacles longer and slender, outer tentacles shorter and broader (Figure 18). Shell muscle horseshoe-shaped, posterior region narrow (Figure 15), right half broader and thicker than left half; shell muscle gradually becomes thicker toward anterior region; on posterior region of head, shell muscle turns abruptly, first in dorsal, then in posterior direction. Paired head muscles originate as continuations of the antero-dorsal end of shell muscle (Figure 15); right muscle slightly flatter and broader than left muscle; both run toward mid-anterior region immersed in tegument, forming a V-shaped structure; both muscles attach spreading out, into median region of head wall (Figure 20).

Mantle Organs (Figures 5, 16-17, 19): Pallial cavity shallow, shorter than 1/3 of animal length. Mantle edge simple, weakly bilobed. Gill relatively small, with about 15-20 filaments, left end close to inner edge of left branch of shell muscle; gill narrows gradually towards right, curving posteriorly, running between mantle and right branch of outer edge of shell muscle, up to about mid-length of animal. Gill filaments low, triangular, rod narrow, located in anterior edge. Ctenidial vein contouring anterior part of gill edge. Low and long glandular fold present left half of gill and mantle edge. Rectum and pericardial structures located in posterior region of roof of pallial cavity, just posterior to gill, as described below.

Visceral Mass (Figure 15): Compressed ventrally by foot and shell muscle. Stomach occupying central region, surrounded by digestive gland and intestine. Gonad located in postero-ventral region, between two intestinal loops. Digestive gland pale-brown, with small spots forming a net-like mosaic. Gonad cream-colored. A thin diaphragm-like membrane separates buccal mass from remaining posterior structures. Figure 20, di: this membrane inserted in haemocoele surrounding buccal mass; only esophagus, anterior aorta and visceral nerves pass through membrane.

Circulatory and Excretory Systems (Figures 5, 15, 19): Pericardium and both kidney's flattened dorso-ventrally, situated in roof of pallial cavity, between Gill and posterior end of this cavity. Pericardium broad, about twice heart area, located between left end of Gill and left branch of shell muscle. Auricle triangular, its right side attached to pericardium cavity, contouring gill end with a concavity; insertion of ctenidial vein somewhat broad in its anterior region; connection with ventricle narrow, posterior, Ventricle small and thick, muscular, located posterior to auricle, close to rectum. Yorta very small, posterior and at left from ventricle. Left, anterior kidney elliptical, flattened, solid; located between Gill posterior region and rectum, touching this latter. Right, posterior kidney, longer and narrower, situated on other side of rectum at same level of left kidney, extending little beyond it toward right.

Digestive System (Figures 20-30): Mouth a transversal slit located on antero-ventral region of snout (Figures 14, 20). Buccal splanchn (Figure 23, ne) well-developed and thick. Buccal mass very large, about half of haemocoele length. Oral tube very short, broad, walls thick, muscular; inner surface with low transversal folds. Buccal mass V-shaped, odontophore and esophagus representing respectively ventral and dorsal branches. Inner surface of dorsal wall of buccal mass with pair of broad dorsal folds (Figure 28); that unite anteriorly, edges higher in their mid-region. Dorsal chamber (de) delimited by both dorsal folds relatively deep and broad; inner surface smooth. Jaw plates very thin, color pale brown; anterior end rounded, situated just anterior to connection of dorsal folds (Figures 21, 23, 28); posterior end inconspicuous, gradually weaker in posterior direction up to posterior level of odontophore insertion. Odonto-
Figures 1-10. *Pseudocucullina vimula* new species. 1-3. Dorsal, ventral, and lateral left views of holotype prior to extraction of specimen from shell. Scale bar = 0.50 mm. 4. Paratype, young specimen, SEM dorsal view, scale bar = 0.20 mm. 5. Roof of pallial cavity and adjacent portion of pericardial structures, ventral view, light micrograph, carmine stain. Scale bar = 0.25 mm. 6. Protoconch, SEM dorsal view. Scale bar = 0.05 mm. 7. Same, lateral right side view, scale bar = 0.02 mm. 8-10. Paratype adult specimen, SEM lateral, left side, oblique right, and ventral views. Scale bar = 0.50 mm.
phore pear-shaped, occupying most of buccal mass volume. Odontophore muscles (Figures 23-30): m1, series of small and thin muscles connecting buccal mass to adjacent inner surface of haemocoel, more concentrated around mouth; m1a, pair of narrow jugal muscles, originating in antero-ventral region of inner surface of snout, running in postero-dorsal direction and inserted in ventral-posterior region of odontophore on lateral region of posterior cartilages; mj, pair of muscles moving oral tube and jaws, originating in mid-ventral region of odontophore, contouring anterior edge of posterior cartilages, running toward anterior region, insertion spread out between oral tube and dorsal wall of buccal mass; m3, single transversal muscle, very thin, located just ventral to origin of esophagus in buccal mass, uniting both sides of postero-dorsal surface of odontophore; m4, large pair of dorsal tensor muscles of subradular membrane, originating in latero-ventral surfaces of anterior cartilages, running toward dorsal region, surrounding these cartilages and covering most of their surfaces, inserting along subradular membrane in its exposed functional region; a short portion also originates from posterior cartilages, in their latero-ventral surfaces. m5, pair of ventral tensor muscles of radula, originating in posterior edge of posterior cartilage, running toward meso-dorsal region, contouring posterior edge of anterior cartilage, inserting in ventral surface of radular ribbon in posterior half of its exposed region. m6, a continuation of m1 m6, horizontal muscle, single, thin, uniting both anterior cartilages along their inner ventral edges; m8, pair of approximator muscles of cartilages, connects anterior and posterior pairs of cartilages originating from relatively large areas of ventral surface of anterior cartilages, inserting in anterior and inner edge of posterior cartilage; m11a, pair of narrow ventral tensor muscles of radula, originating in median corner of posterior cartilages, running toward anterior region on ventral surface of odontophore close to its median line, inserting in ventral end of subradular membrane. Other odontophore non-muscular structures: oc, anterior pair of cartilages, elliptical, flat, soft, slightly shorter than odontophore length, anterior end broadly pointed, posterior end blunt; po, posterior pair of cartilages, length about 1/4 of anterior cartilages, somewhat circular, flat, outer surface convex, inner surface concave, covering postero-external surface of anterior cartilages; both pairs of cartilages fused with each other along their median corner (Figure 20); br, subradular membrane, included in radular sac and extending beyond it, covering exposed surface of odontophore within buccal cavity, connecting with lining of oral cavity; sc, subradular cartilage, a thin, transparent but strong membrane connected to subradular membrane, covering part of exposed portion of odontophore in buccal cavity (Figure 21). Radular sac with about same length of odontophore, curved in its middle portion, located in middle-right region of visceral mass (Figures 20, 21). Radular nucleus covered by a conspicuous membrane surrounding a blood sinus (Figure 23), located in left-ventral region of visceral mass.

Radula asymmetrical, teeth rows offset by 1/2 row height; rachidian teeth apparently in level of right half rows. Radular teeth (Figures 11-13): 1 R4 Rachidian anterior-posteriorly long, laterally narrow, base flat, with edges slightly elevated; distal cutting edge concave, low, curved inward; 2 Lateral teeth in five pairs. 2a First lateral tooth triangular, as long as rachidian, base broad, flat, slanted; remaining region narrowing gradually; tip broadly pointed, curved inward; 2b second, third, and
Figures 14-17. *Pseudocoecilia rimula* new species, anatomy. 14. Head-foot and adjacent mantle edge, ventral view. 15. Whole animal extracted from shell, dorsal view, roof of pallial cavity partially removed. 16. Whole animal, anterior view, roof of pallial cavity sectioned at on right side then deflected to expose inner structures. 17. Head and adjacent pallial structures, anterior (but slightly from right side) view, roof of pallial cavity deflected. Scale bars = 0.5 mm.

fourth lateral teeth equal to each other, first tooth slightly smaller, approximately half size of rachidian, situated at same level of broader region of first lateral tooth; base somewhat narrow and short, situated at some distance from adjacent teeth in same row; lateral edge high, curved obliquely, tip sharply pointed, high, curved inward. 2c) outermost lateral tooth as long as rachidian, thick, cylindrical; base narrow, increasing gradually towards distal end, distal end expanding abruptly, with three sub-terminal, low, inward-turned, stubby cusps located on thicker region, concave region located opposite to cusps, nested in base of corresponding tooth of adjacent row; 3). Marginal teeth in 60–65 pairs, all similar; inner teeth larger, gradually decreasing toward edge of ribbon; larger teeth about 1.5 × rachidian length; base slender and flat; middle region long, rod-like, tall, straight, tip strongly curved inwards, apex sharply pointed, preceded by 6–8 pairs of small, slender, pointed cusps along both sides of broader area of tip.

Origin of esophagus marked by a sudden constriction of dorsal chamber of buccal mass (Figures 21–23). Esophagus narrow, inner surface with pair of low and narrow longitudinal folds (Figure 28), a continuation of dorsal folds of buccal mass. Esophagus runs contouring postero-lateral left surface of odontophore toward postero-ventral region, beyond which it surrounds mid-ven-
Figures 18–22. *Pseudocerulina ranula* new species, anatomy. 18. Whole animal extracted from shell, posterior view, mantle edge deflected. 19. Posterior region of pallial roof, dorsal view, depicted by transparency. 20. Head, ventral view, foot removed, haemocoel exposed with inner structures as in situ. 21. Digestive tube as in situ, dorsal view, structures posterior to esophagus slightly deflected. 22. Same, lateral, left side view. Scale bars = 0.5 mm.

Tral surface of foot along a broad curve, after this esophagus runs toward mid-dorsal region, in direction of shell apex, where it inserts in stomach. Figures 21, 22.

Stomach somewhat narrow and long, located transversally in middle region of visceral mass; its dorsal half broader and spherical (Figures 21, 22), with esophageal connection located in its posterior region. Duct to digestive gland narrow, inserted in left region of esophageal connection. Stomach ventral half flattened and long, narrowing gradually. Inner surface of stomach iridescent, greenish. Digestive gland surrounding stomach for most of its area. Intestinal loops complex, as shown in Figures 21 and 22.

Intestine originates at flattened portion of stomach and is included in mid-ventral region of visceral mass. Intestine is convoluted; after its origin in stomach it runs
obliquely toward dorso-lateral region, surrounding ventral surface of stomach; in latero-dorsal right region of visceral mass intestine describes broad curve toward posterio-ventral region, runs down to mid-ventral region of visceral mass, touching inner surface of foot and surrounding middle portion of esophagus; in this region intestine curves broadly, returning to its previous location. running parallel to it but in opposite direction; in latero-dorsal right region of visceral mass intestine describes yet another broad loop ventral to the previous loop, turning along horizontal plane toward left; in latero-anterior left region of visceral mass it curves abruptly toward right region, surrounding odontophore; this last loop runs obliquely toward latero-anterior right region.
of roof of pallial cavity. Aims located on latero-posterior right region of roof of pallial cavity roof (Figure 15).

Reproductive System (Figure 15) Conal located in latero-posterior left region of visceral mass, just dorsal to shell muscle. Testis more anterior, with smooth, uniform surface. Ovary occupying mid-posterior region of gonad, with granulose surface. Gonad with short projection running along right edge of rectum. Gonad gradually becomes a gonoduct along middle portion of rectum. Gonoduct with thin, transparent walls, running obliquely on surface of visceral mass along side rectum; opens in pallial cavity posterior end, posterior to right (posterior) kidney (Figures 15, 19). A shallow furrow runs from this aperture, contouring latero-posterior right corner of pallial cavity to aperture of sperm duct (Figure 17). Posterior aperture of sperm duct directed to left, protected by a pair of diverging folds. Sperm duct very narrow, thin-walled, entirely closed (tubular), running along right edge of floor of pallial cavity to an area anterior to right tentacle, where it folds abruptly toward left and penetrates base of right tentacle. Sperm duct runs along right cephalic tentacle, its basd 2/3 intensely coiled and with thick glandular walls, thicker in its middle portion, then gradually narrows; its distal 1/3 very narrow and almost straight (Figure 17). Sperm duct opening in tip of subterminal papilla: papilla cylindrical, short, nestled in a small concavity (which may indicate possible ability to retract).

Central Nerve System (Figure 21) Ganglia relatively small and separated from each other. Paired cerebral ganglia relatively distant from each other, located in medially in latero-dorsal region of buccal mass. Pedal ganglia relatively close to each other, situated between middle and anterior portions of ventral surface of buccal mass (Figure 20). Remaining ganglia not studied in details.

Shell Measurements, Length, Width, and Height in mm: MZSP 35349. Paratype #4: 3.0 by 2.5 by 1.7; #5: 3.3 by 2.7 by 1.7; #6: 3.1 by 2.6 by 1.9.

Type Material: Holotype MZSP 35348; Paratypes MZSP 35319, 12 specimens; MNRI 5965, 3 specimens (1 without shell); MNHN, 3 specimens (1 without shell), all from type locality, otter trawl, C. Magenta leg., Apr. 2002.

Type Locality: Off southern Rio de Janeiro State, Brazil. 330-400 m depth, rocky bottom.

Distribution: Known only from type locality.

Habitat: Rocky bottom.

DISCUSSION

The generic allocation of the new species is mainly based on the diagnosis of the genus provided by Marshall 1985:222 and Haszprunar 1988: tab. 2 p 175, with addition of further data from other authors (e.g., McLean and Harasewych, 1995). Pseudococculina rima appears to be the first occurrence of the genus in the Atlantic.

Pseudococculina rima differs from the remaining congeners species in having a high shell and by lack of radial sculpture. Pseudococculina rima resembles P. gregaria Marshall, 1985, from New Zealand, but differs by having higher shell, narrower radular rachidian, and by different characters of the copulatory right tentacle, such as uncoiled sperm duct and absence of papilla.

The anatomy of the new species fits the general plan described for the family (Haszprunar, 1987, 1988). Anatomical characters defining the family are gonad divided into testis and ovary and right cephalic tentacle as copulatory organ. However, the new species possesses some peculiarities, as, e.g., the apparent absence of salivary glands (glands are sometimes poorly developed in cocculiniform limpets), the ventricle free from the rectum, the presence of a short opened portion in the sperm duct running on pallial floor, and the presence of a visceral gonoduct. The gonoduct has been regarded as a modification of the right kidney, but, if so, it is only part of the kidney underwent modification, since there is a detectable right kidney. The presence of a very long right kidney, in the P. rima gonoduct, is found in the comparable topology of Vaginalbyssus caryi McLean, 1988 (Haszprunar, 1988: fig. 2). The muscles of the odontophore differ from those of Kulilobysias venezuelensis (McLean, 1985; Haszprunar, 1988: fig. 3), in lacking oral tube muscle and dorsal retractors of cartilages, and by a greater development of the buccal sphincter, differ from those of Coecropygia hispida Marshall, 1986 (Haszprunar, 1987: fig. 3) in lacking buccal dilators and ventral protractors of cartilage, and also by the great development of the buccal sphincter; differ from Cocculina nipporensis Kuroda and Habc, 1919 (Sasaki, 1989: fig. 79) in lacking the pair of ventral tensor muscles of radial sac, lacking the pair of median protractor muscle of subradular membrane, and in having the pair of posterior cartilages.

LITERATURE CITED


Distribution of the introduced freshwater snail *Melanoides tuberculatus* (Gastropoda: Thiaridae) in Brazil

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ABSTRACT

This article describes the alarming spread and current distribution of the introduced thiarid gastropod *Melanoides tuberculatus* in Brazil. The first record of this species in Brazil was in 1987 in Santos, state of São Paulo, and since then it has been recorded in the states of Goiás, Distrito Federal, Minas Gerais, Paraná, Santa Catarina, Bahia, Espírito Santo, Goiás, Mato Grosso, Mato Grosso do Sul, Pará, Pernambuco, Piauí, Rio Grande do Norte and Tocantins. Records concerning the latter states are reported for the first time. *M. tuberculatus* has been studied as the intermediate host of some diseases, and is known as displacing native species. The rapid spread of this species, the lack of any control or monitoring, and the scarce knowledge of the Brazilian freshwater mollusks indicate that serious damage to the ecosystem with probable implications to public health are to be expected. Two other detected species of invasive freshwater mollusks in Brazil are the bivalves *Corbicula fluminea* and *Limnoperna fortunei*.

Additional keywords: Invasive, invading, molluscs, Mollusca, South America, Neotropical.

INTRODUCTION

Research on introduced species have received special attention in the last few years due both to the increasing number of invasions and to the economic, environmental, and human health problems they have caused throughout the world.

South America has been especially hard hit by invasive freshwater species such as *Corbicula fluminea* (Müller, 1771) (Bivalvia: Corbiculidae), *Limnoperna fortunei* (Dunker, 1857) (Bivalvia: Mytilidae), and *Melanoides tuberculatus* (Müller, 1774) (Gastropoda: Thiaridae). The two first species were introduced into South America respectively in the 1970s and in 1991, probably in ballast water of ships originating from southeastern Asia (Darrigran and Ezenira de Drago, 2000).

In North America, *C. fluminea* may have caused some populations of native bivalves to decline, but other native populations seem to coexist with it (Strayer, 1999). In Argentina, *L. fortunei* is well established in the Plata Basin and, in addition to altering the diversity of native molluscan communities, its high-density populations are causing economic problems because they restrict water intake and flow through sewage treatment plants, power plants, and industrial facilities (Darrigran, 2002). In Brazil, economic and environmental problems caused by *L. fortunei* occur at least in the municipalities of Caiuá and Viamão, state of Rio Grande do Sul, according to Mansur et al. (2003).

Reports on the introduction the Afro-Asian thiarid *M. tuberculatus* in Latin America started in the 1960s and it is now distributed in all countries of this region (Brown, 1994). In this paper the current distribution of this invasive species in Brazil is reported as well as its impact on both human health and the environment. The goal is to provide the first complete report of the distribution of the species, based on field studies (result of several projects), three major malacological collections in Brazil, and the literature. This report shall provide the background for future control and monitoring the spread of the species.

MATERIALS AND METHODS

The main source of data is the institutional collections, which contain voucher material of field projects, mainly those involving the authors. The institutions are: Instituto Oswaldo Cruz, Rio de Janeiro (FIOCRUZ), Museu Nacional da Universidade Federal do Rio de Janeiro (MNRJ), and Museu de Zoologia da Universidade de São Paulo (MZSP). Additionally, published reports on the occurrence of *M. tuberculatus* were also examined.
RESULTS


In Brazil, the first record of *M. tuberculatus* was in Santos, state of São Paulo, in 1967 (Vaz et al., 1986). Subsequently, it has been recorded in the states of Minas Gerais (Silva et al., 1994), Paraná (Paz et al., 1995); Rio de Janeiro (Thiebo et al., 1998, 2001, 2002a, 2002b; Giovannelli et al., 2001); Ceará (Melo and Cordeiro, 1999); Paraná (Pereira, 2000); and in the Federal District, Brasilia (Vaz et al., 1986; Gareez and Martins-Silva, 1997).

In addition to the above-mentioned reports, we searched for additional material of *M. tuberculatus* in Brazil. They are listed below and in represented in Figure 1. State of Pará: Itaituba, Tocantins; São Félix do Tocantins and Peixã; Parnamirim; Ceará: Crato, Paraíba; Campina Grande, João Pessoa, Santa Luzia, São Maneudo, and Sousa; Pernambuco; Macaparana and São Lourenço da Mata; Rio Grande do Norte: Pendências, Bahia: Cariranga, Coaraci, Itjuque and Salvador; Federal District, Brasilia: Goiás, Barro Alto, Campinorte, Campinaçu, Colinas do Sul, Formosa, Minaçu, Niquelândia, Nova Iguaçu de Goiás, Padre Bernardo, Santa Rita do Novo Destino, Uruçu and Vila Boa; Mato Grosso: Guiaíba, Nobres, Rosário Oeste and Várzea.

DISCUSSION

The origin of the introduction of Melanoïdes tuberculatus to Brazil remains unknown, but it is probably linked to the plant and freshwater ornamental fish trade. This route of introduction and spreading of freshwater snails had been previously reported i.e., Covic (2002). Marks and Frandsen (1989) and Pointier (1989). The first record of M. tuberculatus in the state of São Paulo was in an aquarium hobbyist store in the city of Santos (Vaz et al., 1956). Thieugue et al. (1995) reported its introduction by local fish farmers and rapid colonization in fish tanks in Guapimirim, Rio de Janeiro, probably in the 1970s. In the states of Minas Gerais, Rio de Janeiro and São Paulo, where more extensive surveys have been done, this species has been collected from almost all hydrographic basins, inhabiting lotic, lentic, polluted or clean water environments, often in dense populations. Melanoïdes tuberculatus has since spread from few points in São Paulo to all Brazilian regions in the course of three decades.

The biological and parthenogenic reproductive characteristics of M. tuberculatus make this species a good invader (Pointier and Delay, 1995). Its adaptability to a wide range of environmental conditions and high reproductive capacity has encouraged its use, mainly in the French West Indies, in the biological control of the host snails of Schistosoma mansoni Sambon, 1907. Field and laboratory experiments undertaken in Desirade, Guadeloupe, Martinique and Santa Lucia revealed the ability of this species to limit and even exclude species of Biomphalaria in these islands (Pointier, 1993; Pointier et al., 1989, 1991, 1993). In Brazil, studies on the impact of exotic species are scarce: Giovanielli et al. (2001) observed that in Sumidouro, an area of low endemicity for schistosomiasis, M. tuberculatus had substantially reduced Biomphalaria glabrata (Say, 1818) populations, indicating a process of competitive exclusion; in Betim and Prudente de Morais, Guimarães et al. (2001) reported marked reduction in populations of B. glabrata and B. straminea (Dunker, 1848) in two lakes, after the arrival of this snail, followed by complete disappearance of the former species eight years later. During the last three years, our group (unpublished data) has been performing a quantitative study of M. tuberculatus, B. straminea and Lymnaea columella (Say, 1817) populations in a large reservoir in Minaçu. Goiás. Preliminary data indicated that native populations of the snail Atyauchumia tenmalabris (Reeve, 1860), previously abundant in the Tocantins River, have been replaced by dense populations of M. tuberculatus. Fernandez et al. (2001) documented the displacement and decline of B. glabrata and Lymnaea chavells (Spix, 1827) populations in a small stream on the campus of Fundação Oswaldo Cruz, Rio de Janeiro, after the introduction of M. tuberculatus. This data is already sufficient for demonstrating that native species, suffering declines from pollution and destruction of their natural habitats, are now being impacted by M. tuberculatus.

Morphological and conchological studies on samples of M. tuberculatus from Brazil are being performed in order to detect the occurrence of distinct morphs as observed in the Caribbean islands. Conchological characteristics and spatial distribution provide evidence that morphs of M. tuberculatus exist in Martinique and that new morphs of this species develop in rapid succession (Pointier, 1989; Pointier et al., 1993). Recently, Simone (2001) included samples of M. tuberculatus in the phylogenetic analyses of Cerithioidea, based on comparative morphology, and has not found any evidence for differentiating morphs.

Regarding medical and veterinary importance, M. tuberculatus acts as potential intermediate hosts of Paragonimus westermani (Kehlert, 1878); Clonorchis sinensis (Cobbold, 1875), and Centrocestus formosanus Nishigori, 1924 helminths responsible respectively for paragonimiasis, clonorchiasis and centrocestiasis transmission (Anaya-Huerta and Almeyda-Artigas, 1999; Pointier, 1999). Until recently M. tuberculatus had never been recorded harboring larval forms of those trematodes in Brazil. A recent report by Boaventura et al. (2002) found specimens from Maricá and Guapimirim shedding Plerocercoides cercariae.

We believe that the ability of M. tuberculatus to spread rapidly and colonize new natural and man-made habitats alike, generally resulting in high-density populations, threatens the native mollusc fauna and should be closely monitored and documented.

Considering the lack of substantial taxonomic and ecological studies on our freshwater mollusc fauna and the environmental impact caused by alien species, in
spite of extensive areas endemic for schistosomiasis in Brazil, and the possible effectiveness of M. tuberculatus as a competitor of planorbid intermediate hosts of S. mansoni, expansion of this species must be thoroughly monitored and controlled, which has not been done.

LITERATURE CITED


Horaiichalus sysoevi, a new species (Neogastropoda: Drilliidae) from the northwestern Indian Ocean

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ABSTRACT

Horaiichalus sysoevi, a new gastropod species of the family Drilliidae, is here described from the northwestern Indian Ocean. The new species, consisting of four shells collected during the John Murray Expedition (1933–34), has previously been misidentified in the literature as Horaiichalus splendidus (A. Adams, 1867), type species of the genus Horaiichalus Oyama, 1954. Horaiichalus sysoevi is conchologically similar to H. splendidus, but differs in having a bigger size, a shell outlineless cylindrical, teleoconch whorls more convex, a smaller number of axial ribs, a higher number of spirals, a narrower and longer siphonal canal. The new species is compared with other members of the genus Horaiichalus from the Japan. With this note, the geographical distribution of Horaiichalus is expanded.

Additional keywords: Gastropoda, Horaiichalus splendidus, Goto Islands, Gulf of Aden.

INTRODUCTION

The familial position of the genus Horaiichalus Oyama, 1954, is still uncertain, as pointed out by Sysoev (1996) who followed Shuto (1979, 1983) in assigning this genus to the family Drilliidae Morrison, 1966. The type locality of Horaiichalus splendidus (A. Adams, 1867), type species of the genus and herein illustrated for comparative purposes, is Goto Islands (Japan). According to Sysoev (1996) Horaiichalus maderensis Shepman, 1913, is conchologically very similar to H. splendidus and should be treated as a subspecies. In this paper we describe a new species of Horaiichalus, Horaiichalus sysoevi, new species from the Gulf of Aden. The new species, represented by four shells collected during the John Murray Expedition in 1933–34, was figured by Sysoev (1996: 2, figs. 20–21) as H. splendidus. The holotype of H. splendidus is housed in the British Museum (Natural History, London); the holotype of H. sysoevi is housed in the John Murray Expedition collection, also at The Natural History Museum. Acronyms used in the text are: The Natural History Museum of London (BMNH), John Murray Expedition (JME). Comparison with other known species of the genus Horaiichalus is presented. With this report the geographical distribution of Horaiichalus is expanded.

SYSTEMATICS

Superfamily Conoidea Rafinesque, 1815
Family Drilliidae Morrison, 1966
Genus Horaiichalus Oyama, 1954

Horaiichalus Oyama, 1954, p. 52.

Type Species: Mangelia splendidus A. Adams, 1867, p. 309, pl. 19, fig. 24, holotype BMNH 196645.

Description: Shell of medium size for family, slender, fusiform, turritate with tall spire. Protoconch panceiral, dome-shaped, smooth, with 1–2.5 convex whorls, bluntly rounded. Teleoconch with 8–9 convex whorls, last whorl ovate. Sculpture of weak axial collateral ribs that extend from suture to suture, crossed by faint spiral lines. Siphonal canal broad and short. Aperture narrow, ovate, and elongate, without distinct sinuses on anterior or posterior regions.

Horaiichalus splendidus (A. Adams, 1867)
(Figures 1–3, 6–8)

Description: Shell of medium size, up to 30 mm length, fusiform, spire tall. Protoconch panceral, of 1.5 whorls, dome-shaped, about 650–700 μm in maximum diameter, smooth, color light-brown. Transition to teleoconch not well marked. Teleoconch elongate and turritate, consisting of 8–9 convex whorls, slightly angled on shoulder (8 whorls in the holotype). Sculpture of weak, equally spaced, wavy collateral axial ribs that extend from suture to suture. 11–13 ribs on the earlier whorls, 16–18 on the last whorl. Axial ribs crossed by very faint spirals, 35–45 on last whorl, more evident near

**Remarks:** *Horatilus* was considered in the past as an Indo-Pacific genus. The type species is from Goto Islands (Japan) and the shells from the JME are from the Gulf of Aden (northwestern Indian Ocean). In addition to its broad geographic distribution, this genus seems to have a considerable bathymetric range, at least from 50–732 m, as reported by Kuroda, Habe and Oyama (1971: 212) and Syslo (1996: 2). As for its systematic position, we agree with Syslo (1996) who, "until

C. Smiriglio and P. Mariottini, 2003


the examination of the radula", has conservatively followed Shuto (1975, 1983) in assigning Horaiclarus to the Drillidae. Horaiclarus maderensis (Schepman, 1913) has been considered by Sysoev (1996) as a subspecies of H. splendidus. The original description and figure of H. maderensis (Schepman, 1913: fig. 41) strongly corroborate this point of view, with the shell of this latter species being only somewhat broader and shorter than that of H. splendidus. For a better comparison of these two taxa, the original drawing of H. maderensis is depicted (Figures 4-5).

Horaiclarus sysocii new species
(Figures 9-16)

Description: Shell of medium size, up to 33 mm length, fusiform, spire tall. Protoconch paucispiral, of 2.5 whorls, dome-shaped, about 450-500 μm in maximum
diameter, smooth, color cream. Transition to teleoconch not well marked. Teleoconch elongate and lanceolate, with 8-9 whorls. Sculpture of weak, equal spaced, wavy collabral axial ribs, 10-11 on earlier whors, 12-13 on last whorl, extending from suture to suture. Spiral lines 35-65, regularly spaced and of about same size, overriding axial ribs on last whorl. Suture well-defined. Aperture narrow and ovate, anterior and posterior striaes not distinct, about one third of the entire height, inner color cream. Siphonal canal short and narrow, Columella curved, smooth. Outer lip thick, inner surface smooth. Shell color uniformly cream with brownish tinges. Soft parts unknown.

**Type Locality:** Gulf of Aden, northwestern Indian Ocean, 13°13′18″ N, 17°56′4″ E to 13°16′00″ N, 17°50′42″ E, 533 m, JME (1933-34), HEMS MaruM iss station 188.

**Type Material:** Holotype: BMNH 20010405, length 32.3 mm, from type locality. Paratypes A-C, BMNH 20010404A-C, Gulf of Aden, northwestern Indian Ocean, 12°04′06″ N, 50°35′56″ E, 752 m, JME (1933-34), HEMS MaruM iss station 176.

**Etymology:** This species is named in honor of Dr. Alexander V. Sysoev (Zoological Museum of Moscow State University, Russia), recognized scientist who has greatly contributed to the knowledge of the malacology.

**Remarks:** *Horaielaus syooci* is herein described from four shells collected during the JME (1933-34) that were already reported and in part figured by Sysoev (1996: 2, figs. 20-21) under the name *H. splendida*. We have been able to examine the holotype of *H. splendida* from the H. Cuming collection and the four shells from JME. This has led us to unquestionably separate that lot of shells from *H. splendida*. The new species is similar to *H. splendida*, but clearly distinguishable by diagnostic features. *Horaielaus syooci* exhibits more lanceolate and less cylindrical body shape, bigger size, smaller and higher spired protoconch, more convex teleoconch whors, small number of axial ribs, higher number of spirals, narrower and longer siphonal canal, different shell color. The new taxon is easily distinguishable from other members of the genus *Horaielaus*: *H. shitoensis* Oyama 1951: p. 21, figs. 33-33a, Kuroda, Habe and Oyama 1971: 213, figs. 12-13, Oyama (1973-50, fig. 7) and Tsuchida and Kurozumi (1996: 11, fig. 5, 1-3) is much smaller (about 10 mm length), the teleoconch is less elongate and lanceolate, with only 5-6 whors, stronger axial ribs and spiral sculpture. We provide the original drawing of *H. shitoensis* for comparison (Figure 17). *Horaielaus syooci* also differs markedly from *H. jahneatus* Smith, 1882, this latter species being smaller (about 10 mm length), with a teleoconch more biconical and much less elongated, with only 5-6 whors, stronger and fewer axial ribs, and the aperture about half of shell length, as can be observed in the pictures reported by Kuroda, Habe and Oyama (1971: 213, figs. 19) and Tsuchida and Kurozumi (1996: 41, fig. 5, 1-3). These authors figured also another species of *Horaielaus* (op. cit., p. 41, fig. 5) that is somewhat similar in size and teleoconch shape to *H. shitoensis* but completely different from *H. syooci*. With this note the geographical distribution of *Horaielaus* is expanded, now ranging from the Japan Sea to the northwestern Indian Ocean.

**ACKNOWLEDGMENTS**

We would like express our deep gratitude to Ms. Kathie Way, Dr. John Taylor, and Mrs. Joan Pickering (all from BMNH) for kindly forwarding the type material of *Horaielaus splendida* and *H. syooci* and relevant literature. We are deeply indebted to Dr. Kurozumi *Natural History Museum and Institute*, Chiba, Japan, for sending valuable references related to *Horaielaus* spp. Sincere thanks are due to Dr. Antonio Bonifito, Laboratorio di Malacologia, Università di Bologna, Italy, and Dr. Paul Callomon (Department of Malacology, Academy of Natural Sciences, Philadelphia, USA) for help with literature. We also want to thank Dr. Marco Oliverio (Università di Roma “La Sapienza”, Italy) for critical comments and advice.

**LITERATURE CITED**


Description of *Scabrotrophon inspiratium* new species (Gastropoda: Muricidae) from Vanuatu

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ABSTRACT

*Scabrotrophon inspiratium* new species is described from Vanuatu and compared with S. *scarlatoi* Golikov and Sirenko, 1992 from the Kurile Islands and with S. *regium* Honart, 1985 from the Philippine Islands. The three species are illustrated.

Additional keywords: Neogastropoda, Muricidae, southwest Pacific Ocean.

INTRODUCTION

The muricids collected during the MUSORSTOM 8 cruise to Vanuatu have been enumerated and discussed by Honart (2001). Twenty-six species have been recorded, of which three remained unidentified and two were described as new. The material studied here was already known at that time, however it was then considered as a possible Coralliophilinae by the author. Reconsideration of my previous analysis and comparison with the additional material prompted the description of *Scabrotrophon inspiratium* new species herein. This brings the total number of muricids (excluding Coralliophilinae) collected during the MUSORSTOM 8 cruise to Vanuatu to 27 of these, three still remain unidentified. Text abbreviations: MNHN: Muséum national d'Histoire naturelle, Paris, France; ZISP: Zoological Institute of Russian Academy of Sciences, St. Petersburg, Russia; dd: dead-collected specimen; lv: live-collected specimen. For other abbreviations see Table 1.

SYSTEMATICS

Family Muricidae Rafinesque, 1815
Genus *Scabrotrophon* McLean, 1996

Type species: *Trophon matsuzani* Kobelt and Küster, 1978; northeastern Pacific, by original designation.

Remarks: The genus *Scabrotrophon* was introduced to include a few species previously allocated to *Nipponotrophon* Kuroda and Habe, 1971; *Radvin and D'Attilio*, 1976; *Myers and D'Attilio*, 1980; *Broth*, 1981; *Honart*, 1985; *Tiba* and *Kosuge*, 1985; McLean (1996) originally included five species and nine taxa have been added by Honart and Lan (2001).

*Scabrotrophon inspiratium* new species (Figures 1, 3–7)

Description: Shell medium sized for the genus, up to at least 11.9 mm in length at maturity (paratype MNHN), broadly biconical, spinose, lightly built. Protoconch whorls unknown (broken). Spire high, up to 6. Suture impressed. Sculpture of teleoconch whorls consisting of low, narrow axial lamellae, each with broad, flattened primary spines. Shoulder spine longest. Other axial sculpture of numerous growth striae. First whorl damaged, second and third with 15 lamellae, fourth with 15–18, fifth with 15, last whorl with 15–15 lamellae. Spiral sculpture of high, strong, narrow, primary cords. Convex part of teleoconch whorl with P1 and P2 visible on early whorls, P1 more conspicuous. Last whorl with P1–P4, S1, P5, S5, P6, ADP. P1 and P2 more broadly spaced than P2, P3, and P4; S4 absent in paratype. Primary cords producing long, broad, flat, weakly labiaform projections at...

Type Material: Holotype, 39.20 length × 22.70 mm width, and one paratype, both MNHN, unnumbered odd. N.O. Mus. Cruise MUSORSTOM S, station GP 1110, Bouchet and Richer de Forges coll. 08 Oct. 1991, both from the type locality.

Type Locality: Northeast of Espiritu Santo Island, 156.00 m, 14° 19′ S, 167° 15′ E, Vanuatu, southwestern Pacific Ocean.

Ectymology: Latin inspiratum, inspired; in connection to the type locality, northeast of Espiritu Santo Island.

Remarks: Seabrotrophon inspiratum new species differs from S. scurlatot, Golikov and Sirenko, 1992 (Figures 2, S-91 from the Kurile Islands in having a more ovate aperture and a broader siphonal canal, narrower and more widely spaced primary cords giving rise to sharp, flat, broad spine-like projections instead of rounded ones in S. scurlatot. P2 is less apparent on early teleoconch whorls in S. inspiratum new species. The spines of P4 are less upwardly curved and comparatively longer, while those of P5 and P6 are less downwardly curved in S. inspiratum new species. The new species differs from Seabrotrophon regina (Houtard, 1985) Figure 10 from the Philippines in having more strongly keeled whorls, a longer siphonal canal, lower spiral cords, and narrower, longer spine-like projections with lower axial lamellae between the spines. Moreover, there is no primary spiral shoulder cord (P4) and no secondary cords (except S4) in S. inspiratum, while S. regina has a shoulder cord and S2, S3, and S4, respectively between P2 and P3. P3 and P1, P4 and P5. Other species of Seabrotrophon are strongly dissimilar and do not need to be compared herein. 

ACKNOWLEDGMENTS

I am most indebted to Philippe Bouchet (Muséum national d'Histoire naturelle, Paris) for giving me the opportunity to study the material collected during the numerous MUSORSTOM-MNHN expeditions and for reading the manuscript. I am also very grateful to Boris I. Sirenko (Zoological Institute of the Russian Academy of Sciences) for the loan of the holotype of S. scurlatot, to Didier Merle for his comments on spiral sculpture morphology, and to Marco Oliverio (Università di Roma "La

Sapienza", Rome for having compared the new species with coralliphilids and for his comments.

LITERATURE CITED


Figures 8–10. *Sebulrostrophon* species continued. 8–9. *Sebulrostrophon scinclitor* Golikov and Sirenko, 1992: Kurile Islands, eastward from Iturup Island, 44°20' N, 148°41' E, 414 m, holotype (v), ZISPb 57625; 24.7 mm length. 10. *Sebulrostrophon regina* (Horvat, 1953): Philippine Islands, 13°44' N, 120°31.6'E, 682–770 m, holotype (v), MNHN 51 mm length.


New and little known species of Pseudolividae (Gastropoda) from the Tertiary of Chile

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ABSTRACT

Two new species of Pseudolividae, Maceron vermeiji and Truncaphis maturulancensis, are described and figured from Miocene deposits of the Navidad Formation, central Chile. Both are among the oldest known representatives of their respective genera. Juvenile specimens of the Miocene species Testallium cepa (Sowerby, 1846) and the holotype of the Eocene Sulcolucinum retusum (Philippi, 1857) are figured for comparison. One of the three syntypes of Monoceros optimum Hopé, 1854, and the holotype of Monoceros labiata Hopé, 1854, both previously considered synonyms of Testallium cepa, are figured for the first time and synonymy is confirmed.

INTRODUCTION

The earliest descriptions of Tertiary gastropods of Chile were by d’Orbigny (1842), Sowerby (1846), Hopé (1854), and Philippi (1857). Subsequently, a major revision of Pliocene-Pleistocene faunas was conducted by Herm (1969). New collections of Miocene gastropods from Chile made by the senior author and Klaus Bandel (Hamburg, Germany) and collections housed in the Museo Nacional de Historia Natural (Santiago, Chile) made by the junior author and the late Vladimir Cuyacevich (Santiago, Chile), include a number of undescribed species, among them the two new pseudolivid species described herein. The family Pseudolividae was recently revised by Vermeij (1998) who presented a reevaluation of the entire family based on shell characters of Recent and fossil species and his classification is followed herein. Vermeij (1998) attributed the family-name Pseudolividae in his abstract to Cossmann (1901) and in the systematic section to Fischer (1844). However, it was de Gregorio (1880, p. 104) who first introduced this name and the family is consequently attributed to him.

Although there is a continuous pseudolivid record in South America since the Late Cretaceous, few species have been described (Vermeij, 1997, 1998). Only three Chilean Tertiary species are known (Vermeij and DeVries, 1997): the Eocene Sulcolucinum retusum (Philippi, 1857), the Miocene Testallium cepa (Sowerby, 1846), which also occurs in Peru, and the Pliocene Testallium scattonia Vermeij and DeVries, 1997.

Sulcolucinum retusum comes from strata near the village of Algarrobo (Figure 1), north of San Antonio, Chile. From an intertidal platform of that village, Eocene and Late Cretaceous sediments are known. Because no material other than the holotype is known, and the genus Sulcolucinum d’Orbigny, 1850, is known from the Campanian onward (Vermeij, 1998), the age of the species remains unclear. However, Vermeij (1998) regarded this species as of early Eocene age. Gastriodarium retusum Philippi, 1857, was reassigned to Buccinum Conrad, 1865, by Vermeij and DeVries (1997), a genus later considered to be a synonym of Sulcolucinum (Vermeij, 1998). However, the holotype of G. retusum (Figures 13–14, SGO PI 765, height 53 mm) has never been figured since the original drawing was published by Philippi (1857). The remaining species reported here come from the Navidad Formation (Figure 1).

ABBREVIATIONS

MNH-LG: Museum national d’Histoire naturelle, Laboratoire de Géologie, Paris, France; SGO PI: Museo Nacional de Historia Natural, Departamento de Paleontología de Invertebrados, Santiago, Chile; SMF: Senckenberg Museum, Frankfurt, Germany.

SYSTEMATIC PALEONTOLOGY

Family Pseudolividae de Gregorio, 1880
Genus Maceron H. and A. Adams, 1853

Type Species: Pseudoliva kellettii A. Adams, 1855 = Buccinum asthops Reeve, 1847 = Recent, West Mexico.

Maceron vermeijii new species
(Figures 7, 8, 10, 11)

Description: Shell medium-sized, ovate, spire low, consisting of five to six whorls. Height-to-width ratio
1.25. Whorls separated by narrow suture. Last whorl large, comprising 53% of total shell height, rounded, constructed basally above siphonal fasciole. Pseudolivid groove situated low on last whorl, terminating in distinct labral tooth. Spiral sculpture consisting of three cords below pseudolivid groove and very faint threads above, axial sculpture absent except for faint growth lines. Protoconch unknown. Outer lip planar. Anterior notch present, reflected as groove inside last quarter of last whorl. Interior of outer lip hirate. Columellar callus cutting deeply into former whorl, having two weak folds at entrance to siphonal canal. Columella with two weak folds at entrance to siphonal canal. Siphonal fasciole prominent, bounded above by keel. Anterior notch deep, no umbilicus.

Type Material: Holotype SGO.PL.5988 (height 21 mm, width 19 mm, paratype SGO.PL.3714 (height 22.5 mm; together with nine juvenile specimens of Testallium cepa). Early late Miocene (Tortonian). Navidad Formation.

Type Locality (Figure 1): About one kilometer north of Matanzas, Chile. Early late Miocene (Tortonian), Navidad Formation (see Frassinetti and Covacevich 1993) for more details on the locality.

Occurrence: Specimens of the new species of Macron were collected on an intertidal platform about 1 km north of the village of Matanzas as described by Frassinetti and Covacevich 1993 and from a fossil-bearing lens about 2 m higher in the section. That lens, however, was severely eroded the following year. It has been dated as Tortonian (upper Miocene) based on Foraminifera (Finger et al., 2003). The accompanying gastropod fauna indicates mainly a shallow-water environment but some possible deep-water species are present (Nielsen and DeVries, 2002), such as Xenophora paulinae. Nielsen and DeVries, 2002. A deep-water environment is also indicated by benthic Foraminifera, the ostracod assemblage (Finger et al., 2003), and the presence of otoliths of fish species in the genus Steindachneria (Nolf, 2002). This contrasting evidence may be due to slumping of shallow-water sediments into deeper water, a model supported by the presence of reworked mudstone clasts. The sedimentology of these deposits was discussed elsewhere (Encinas et al., 2003).

Etymology: Named in honor of G. J. Vermeij (University of California, Davis, Geology) who contributed greatly to the knowledge of the Pseudolividae.

Discussion: Another possibly conspecific specimen is SGO.PL.766 (Figure 5, height 30.9 mm) from Navidad. Other species from the Tertiary of Chile resembling Macron vermeij are the Eocene Sulcobilina retusa, and the Miocene Testallium escalonia. Sulcobilina retusa has the pseudolivid groove situated high on the last whorl and is smooth inside the outer lip. Juvenile specimens of Testallium cepa (Figures 4, 6, 9, 12, both part of SGO.PL.3714) of about the same size as presumably adult Macron vermeij differ in not having hirac inside the outer lip, in having more numerous spiral elements below the pseudolivid groove, and in having the columellar callus secreted onto former whorls, rather than cutting deeply into them. Most of the larger specimens of Testallium cepa (Figures 2, 3, part of SGO.PL.3714, height 16 mm) have additional spiral elements above the pseudolivid groove and a more globose appearance, characters that are even more prominent in adults. The Miocene Testallium escalonia has a higher spire, stronger spiral sculpture and no hirac inside the outer lip.

The spire of Macron vermeij is relatively much lower than that of any previously known species of Macron (height-to-width ratio 1.25 in Macron compared with 1.9 to 1.1 in other species) and its last whorl is relatively larger (83% of total shell height compared with 68 to 74% in other species) so that the diagnosis of the genus given by Vermeij (1998) must be emended to include this species.

Macron vermeij extends the geographic distribution of the otherwise strictly northern Pacific genus Macron into the southeastern Pacific. It is the lowest-spired species of Macron and thus closely resembles species of Pseudolina Swainson, 1840, from which it mainly differs by the hirate interior of its outer lip. It is not only intermediate in shell-form but also comes from an area geographically between the main northeast Pacific Macron and the South African Pseudolina. These genera have their origins in the (lower) Miocene of Venezuela (Macron; Gibson-Smith et al., 1997) and Madeira (Pseudolina, Vermeij, 1998).

Figure 1. Type localities of Macron vermeij and Triunphis maitenhauensis and other localities mentioned in the text.
Genus *Testallium* Vermeij and DeVries, 1997

**Type Species:** *Gastrium cepa* Sowerby, 1846; Miocene, Chile.

*Testallium cepa* (Sowerby, 1846) (Figures 2–4, 6, 9, 12, 15, 17, 18, 20)

**Discussion:** *Testallium cepa* has been discussed in detail by Vermeij and DeVries (1997) and it is present at most Miocene localities from southern Peru (DeVries and Frassinetti, 2003) to Isla Stokes, southern Chile (Frassinetti, 2001) and abundant in the Navidad Formation. However, juvenile specimens (Figures 4, 6, 9, 12) have not been figured and the three subtypes of *Monoceros optimum* Hupé, 1854 (Figures 15, 17; MNHN-LG Gg2002.70; height 58 mm) and the holotype of *Monoceros lability* Hupé, 1854 (Figures 18, 20, MNHN-LG Gg2002.77; height 50 mm) put into synonymy with *Testallium cepa* by Vermeij and DeVries (1997), were unavailable at that time because the location of the collection described by Hupé was unknown. Rediscovery of Hupé’s types in the MNHN-LG allows us to figure those specimens herein, confirming the inferred synonymy. According to new data its stratigraphic range is lowermost Miocene (DeVries and Frassinetti, 2003) to upper Miocene (Finger et al., 2003).

Genus *Triumphis* Gray, 1857

**Type Species:** *Buccinum distortum* Wood, 1828; Recent, Caribbean Sea.

*Triumphis mauchlealnensis* new species (Figures 16, 19)

**Description:** Shell moderately large with stepped whorl profile. Protoconch unknown. Whorls with steep, almost straight, slightly concave sides. Last whorl with strong, ridge-like shoulder. Whorl slightly constricted below shoulder, forming a concave area followed by convex, globose region. Whorl anteriorly constricted and thus well defining short, slightly twisted siphonal canal. Broad, flat primary spiral cords present on whole whorl, two to three finer secondary cords between them. Axial sculpture of low, blunt nodes between suture and periphery present on early whorls, becoming obsolete on last whorl. Aperture oval, columella smooth with weak fold at opening of siphonal canal. Outer lip unknown. Siphonal fasciole strongly developed. Pseudumbilical furrows in fasciole and inner lip might be an artifact caused by erosion. Height 29 mm.

**Type Material:** Holotype SGO.PI.5523.

**Type Locality (Figure 1):** Early Late Miocene (Tortonian), Navidad Formation. At the coastal cliff about 500 m south of the Estero Mauchle, Chile to the north of Rio Rapel, at locality 1409764 of Covacevich and Frassinetti (1986).

**Occurrence:** The new species of *Triumphis* was collected about 500 m north of Estero Mauchle to the north of Rio Rapel at the upper margin of Figure 1. This specific locality has been dated, but nearby localities indicate a Tortonian upper Miocene age (Finger et al., 2003).

**Etymology:** Named after the type locality near the Estero Mauchle, Chile.

**Discussion:** *Triumphis* has been included in the family *Buccinidae Raffinesque, 1815* by most workers (e.g., Keen, 1971), but Vermeij (1998) transferred it to *Pseudovulvaria* and this is followed here. Apart from the recent type species, *Triumphis distorta*, only one poorly preserved specimen of *Triumphis* sp. from the middle Miocene of Kern County, California has been reported (Addicott, 1970). *Triumphis mauchlealnensis* differs from *Triumphis distorta* in being constricted below the ridge-like shoulder, in having subequal spiral ornament, and in having a well-defined siphonal canal. It differs from species of the similar genus *Nicema* Woolfing, 1964, by having its ridge-like shoulder as an anterior projection of the posterior notch at the suture and not below the notch and suture. *Nicema* was considered to belong to the *Buccinidae* subfamily *Photinaceae Troschel, 1867*, by Vermeij (1998). *Triumphis mauchlealnensis* could be an intermediate species between *T. distorta* and the genus *Nicema*; however, as Vermeij (1998) adequately observed, "anatomical data and molecular sequences will be needed to confirm the phylogenetic affinities of *Triumphis*" (p. 73), and "anatomical observations on the living *N. subrostata* will be needed to confirm assignment of *Nicema* to the *Photinaceae*" (p. 74).

**ACKNOWLEDGMENTS**

Klaus Baudel is thanked for discussions and companionship in the field. S. Kiel for comments on an early draft of the manuscript, and E. Viny for taking some of the photographs (all Geologisch-Paläontologisches Institut und Museum, Universität Hamburg, Germany). Alan G. Ben (Lower Hutt, New Zealand) made very valuable comments including those of a linguistic nature. Philippe Bouchet confirmed attribution of *Pseudovulvaria* to de Gregorio. Comments by T. J. DeVries and two anonymous reviewers are gratefully acknowledged. This work was financially supported by the Deutsche Forschungsgemeinschaft (DFG) grant Ba 675/25, a grant of the University of Hamburg and a COLPARSIST grant to study the collections in Paris.

**LITERATURE CITED**


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Notice

70th Annual Meeting
American Malacological Society
Sanibel Island, Florida
31 July–4 August 2004

I am glad to announce that the 70th Annual Meeting of the American Malacological Society will take place on beautiful Sanibel Island, Florida, from Saturday, July 31, to Wednesday, August 4, 2004. Sanibel Island is a world-renowned, nature-oriented travel destination that is also famous for its bountiful molluscan resources. The event will be hosted by The Bailey-Matthews Shell Museum and will have as its main venue the Sundial Beach Resort, located on the eastern part of the island.

The American Malacological Society is a dynamic international society of individuals and organizations with an active interest in the study and conservation of mollusks. AMS covers a wide range of subjects in the field of molluscan studies, and its meetings, symposia, sessions, posters, and special events reflect that.

A symposium on the Relationships of the Neogastropoda will be convened by M. G. Harasewych of the National Museum of Natural History at the Smithsonian Institution. Special sessions will include Biodiversity of Marine Mollusks (organized by Gustav Panlay, Florida Museum of Natural History); Coastal Molluscan Assemblages as Environmental Indicators (Michael Savarese, Assumption University, and Greg Tolley, Florida Gulf Coast University); Systematics of Freshwater Gastropods (Russel Minton, Louisiana State University); Global Marine Bivalve Database Workshop (Gustav Panlay, Florida Museum of Natural History); Paul V. Scott, Santa Barbara Museum of Natural History; and Graham Oliver, National Museums and Galleries of Wales), and Terrestrial Mollusks as Agricultural and Environmental Pests (David Robinson, United States Department of Agriculture/Academy of Natural Sciences of Philadelphia). In addition, a special forum organized by Ken Hayes, Anna Bass, and Amy Wethington, all graduate students in malacology, will focus on and discuss common issues and problems faced by soon-to-be professionals in the field.

The 70th Annual Meeting will be sponsored by the American Malacological Society, The Bailey-Matthews Shell Museum, and the Sanibel-Captiva Shell Club, with additional support from the Sanibel-Captiva Chamber of Commerce, Sundial Beach Resort, J. N. "Ding" Darling
National Wildlife Refuge, Florida Gulf Coast University, and Captiva Cruises.

The Sanibel-Captiva Shell Club will sponsor the Shell Museum Open House on Sunday, August 1. The closing banquet will be a dinner-cruise aboard Captiva Cruises's Lady Chadwick, a two-deck vessel holding 250 passengers.

Specially priced rates at the Sundial Beach Resort will be available for meeting participants at $110/night for regular rooms, $125 for the Gulf View rooms, and $175 for two-bedroom suites. Sundial is willing to accommodate up to 6 students per suite, which will help decrease the cost of accommodations for participants on a low budget.

Three field trips are planned for the last day of the meeting, Wednesday, August 4: A nature-watching visit to J. N. "Ding" Darling National Wildlife Refuge on Sanibel, guided by professional ornithologist and Shell Museum volunteer Dr. Jon Greenlaw; a daylong boat trip to Cayo Costa State Park guided by senior Shell Museum staff located on isolated and undeveloped Cayo Costa, the park offers pristine views of the Gulf, dunes, lagoons, and opportunities for shell collecting; no live-mollusk collecting is allowed in the park or elsewhere in Lee County; and a visit to a Plio-Pleistocene fossil pit in Sarasota County guided by Roger Portell, invertebrate paleontologist at the Florida Museum of Natural History.

Pliocene fossil assemblage in Sarasota County

More than 24 airlines service Southwest Florida International Airport in neighboring Fort Myers (30 minutes from Sanibel). The Lee Island Coast region offers many opportunities for side trips on your own, depending on your interest: Edison-Ford Winter Estates, Miracles baseball games, and Everglades National Park, to name a few.

More information check the meeting Web site: www.shellmuseum.org/AMS/index.htm

Cordially,

José H. Leal, PhD
President, American Malacological Society
INSTRUCTIONS TO AUTHORS

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

Manuscripts: Each original manuscript and accompanying illustrations should be submitted in triplicate. Text must be typed on one side of 8½ x 11 inch white paper, double spaced throughout (including literature cited, tables and figure captions), with at least 1 inch of margin on all sides. All pages must be numbered consecutively. If printed on a word processor, the right margin should be ragged rather than justified. Authors should follow the recommendations of the Scientific Style and Format—The CBE Manual for Authors, Editors, and Publishers, which is available from the Council of Science Editors, Inc., 11270 Roger Bacon Drive, Suite 8, Reston, VA 20190, USA (http://www.cbe.org/cbe). The first mention of a scientific name in the text should be accompanied by the taxonomic authority including year. Latin names and words to be printed in italics must be underlined; leave other indications to the editor. Metric and Celsius units are to be used.

The sequence of sections should be: title page, abstract page, introduction, materials and methods, results, discussion, acknowledgments, literature cited, tables, figure captions, figures. The title page should include the title, authors' names and addresses. The abstract page should contain the title and abstract, which should summarize in 250 words or less the scope, main results and conclusions of the paper. All references cited in the text must appear in the literature cited section and vice versa. In the literature cited section, all authors must be fully identified and listed alphabetically. Follow a recent issue of THE NAUTILUS for bibliographic style, noting that journal titles must be uncapped. Information on plates and figures should be cited only if not included in the pagination. Tables must be numbered and each placed on a separate sheet. A brief legend must accompany each table. Captions for each group of illustrations should be typed on a separate sheet and include a key to all lettered labeling appearing in that group of illustrations.

All line drawings must be in black, high quality ink, clearly detailed and completely labeled. Photographs must be on glossy, high contrast paper. All figures are to be consecutively numbered (figs. 1, 2, 3, . . .). NOT figs. 1a, 1b, 1c, . . . NOR plate 1, fig 1. Illustrations must be arranged in proportions that will conform with the width of a page-6½ inches or 171 mm, or a column 3¼ inches or 82 mm. The maximum size of a printed figure is 6¾ by 9 inches or 171 by 228 mm. All illustrations must be fully cropped mounted on a firm, white backing, numbered and camera ready. The author's name, paper title and figure number should appear on the back. Original illustrations must be between one and two times the desired final size. It is the author's responsibility that the line weight and lettering are appropriate for the desired reduction. Original illustrations will be returned to the author if requested. Color illustrations can be included at extra cost to the author.

Voucher Material: Deposition of type material in a recognized public museum is a requirement for publication of papers in which new species are described. Deposition of representative voucher specimens in such institutions is strongly encouraged for all other types of research papers.

Processing of Manuscripts: Upon receipt, every manuscript is acknowledged and sent for critical review by at least two referees. These reviews serve as the basis for acceptance or rejection. Accepted manuscripts are returned to the author for consideration of the reviewers' comments.

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

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### Contents

<table>
<thead>
<tr>
<th>Author(s)</th>
<th>Title</th>
<th>Pages</th>
</tr>
</thead>
<tbody>
<tr>
<td>Patricia Miloslavich, E. Klein, P. E. Penchasadze</td>
<td>Reproduction of <em>Crepidula nucicola</em> March, 1877 and <em>Crepidula aphysoides</em> Reeve, 1859 (Caenogastropoda) from Morrocoy and La Restinga Lagoon, Venezuela</td>
<td>121</td>
</tr>
</tbody>
</table>

*THE* **NAUTILUS**

Volume 117, Number 4
December 25, 2003
ISSN 0028–1344
STATEMENT OF OWNERSHIP, MANAGEMENT AND CIRCULATION

1. Publication Title, THE NAUTILUS.
4. Issue Frequency, Quarterly.
5. No. of Issues Published Annually, Four.
7. Complete Mailing Address of Known Office of Publication, 3075 Sanibel-Captiva Road, Sanibel, FL 33957.
8. Complete Mailing Address of Headquarters, same as 7.
   Editor, Dr. José H. Leal, address as above.
   Managing Editor, Christina Ajuria, address as above.
10. Owner, Shell Museum and Educational Foundation, Inc., address as above.
11. Known Bondholders, Mortgages, and Other Security Holders Owning or Holding 1 Percent or More of Total Amount of Bonds, Mortgages, or Other Securities, None.
12. The purpose, function, and nonprofit status of this organization and the tax exempt status for federal income tax purposes has not changed during the preceding 12 months.
13. Publication Name, THE NAUTILUS.

15. Extent and Nature of Circulation

| A. Total Number of Copies | 520 | 520 |
| B. Paid Circulation |  |  |
| 1. Paid Requested Outside-County Mail Subscriptions | 390 | 399 |
| 2. Paid In-County Subscriptions | 0 | 0 |
| 3. Sales Through Dealers and Carriers, Street Vendors, Counter Sales, and Other Non-USPS Paid Distribution | 0 | 0 |
| 4. Other Classes Mailed Through the USPS | 25 | 25 |
| C. Total Paid and/or Requested Circulation | 415 | 121 |
| D. Free Distribution by Mail |  |  |
| 1. Outside-County | 32 | 32 |
| 2. In-County | 0 | 0 |
| 3. Other Classes Mailed Through the USPS | 0 | 0 |
| E. Free Distribution Outside the Mail | 0 | 0 |
| F. Total Free Distribution | 32 | 32 |
| G. Total Distribution | 447 | 456 |
| H. Copies not Distributed | 73 | 64 |
| I. Total | 520 | 520 |
| J. Percent Paid and/or Requested Circulation | 93% | 93% |
Kaicher's Card Catalogue of World-Wide Shells: A collation, with discussion of species named therein

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ABSTRACT

Kaicher's Card Catalogue of World-Wide Shells is a series of cards illustrating gastropod mollusks, with one species being shown on each card. More than 8,500 cards illustrating about 23,000 species were issued in 60 "packs" between 1973 and 1992. These cards are especially important as many show type specimens. All packs and the range of the cards included in each are collated, as are changes and corrections to the cards made by Kaicher, other authors, and herein. The status of missing card numbers is clarified; some were accidentally skipped; others were removed by Kaicher before publication. Nine species were inadvertently named in the Card Catalogue; all have short descriptions and therefore are not under names. Type material for eight of these is detailed, with designation of six lectotypes. Callistonina vincentii Kaicher, 1986, probably is a synonym of Callistonomella naturalis (Philippi, 1836). Trochidae; Notitia puciaria Kaicher, 1981, becomes Notocerithia puciaria (Naticidae): new combination; Anaea teneraechti Kaicher, 1980, is A. Sellaithi (scevegezzi) Glaubert, 1845. Kuroda and Habe, 1967: Epitominae: new synonym: Helix truncata Kaicher, 1980, is Deiathis orbis Caillet, 1791: Muricidae: new synonym: Bocoaria delici Explicita Kaicher, 1981, is T. alta (Gray, 1831: Trochidae): new synonym: Complex ammonites Kaicher, 1977. Conchidae: the valid name for C. naussia Tročjan, 1975, non C. nausia (Sowerby, 1833) and its replacement name, C. trocıan Tročjan, 1978: new synonym: Complex ammonites Kaicher, 1977, is the valid name for C. mellus Kaicher, 1945, non C. mullus (Sowerby, 1798: a Conus), and its replacement name, Conus megalicus d. Motta, 1901: new synonym: Complex lobatus Kaicher, 1977, is C. fuscolineatus Sowerby, 1965: new synonym: and Conus meg- ladric Kaicher, 1977, is the valid name for C. globifer O. Beukel and Riedel, 2000: new synonym, A first reviser's choice is made for the spelling of Epitominae (Dionysius) 1957, which is judged not to be a senior synonym of Anaea sierio-

INTRODUCTION

Sally Diana Kaicher (1922–1999) was a professional illustrator and writer who worked at various times at the Academy of Natural Sciences in Philadelphia (ANS), the National Museum of Natural History at the Smithsonian Institution (USNM), and the United States Department of Agriculture. She authored or illustrated several popular works on natural history, including Kaicher (1956–1957), Reid (1967), Epple (1969) and Reid et al. (2001), which is a revision of Reid (1967). She authored two scientific papers: Kaicher (1972) and Lyons and Kaicher (1978). She also illustrated and in some cases authored about twenty 35 mm filmstrips for classroom instruction, including one on mollusks (Kaicher, 1968). German and Lyons (1999) published a bibliographic sketch giving details of her career as well as photographs. Epple (1980) published biographical notes and Lamprell (1999) and Rice (1999) published obituaries.

In 1973 Kaicher began publishing the Card Catalogue of World-Wide Shells. The Card Catalogue is a series of 3" × 5" (7.6 × 12.7 cm) glossy cards, each card illustrating a single species of gastropod mollusk with one or more black and white photographs. They were issued in "packs" of 97 to 106 cards, most packs being restricted to species of a single family. In addition to the species cards, each pack had a cover card and one or two introductory and acknowledgment cards. Production of the packs was irregular but continued until 1992. A total of 60 packs and 6,137 cards were issued, including 6,316 cards illustrating specimens, 60 cover cards, 60 acknowledgment cards, and one card, in Pack 31, discussing ovoviviparity in Nassaarius. All of the species illustrated are prosobranchs, and almost all are marine, exceptions being freshwater or brackish species of Nerita (Neritidae), Clea (Buccinidae), and Rissomarginella (Marginellidae). Callomon (1990a) published on the Internet a list of the species illustrated in each part of the Card Catalogue and an index to the specific names (1999b).

About 5,800 distinct species are illustrated, the total being less than the number of cards because some sub-species and varieties were illustrated, and Kaicher reissued cards for some species or corrected their identifications. Kaicher issued replacement cards at different times for a variety of reasons. A small slip enclosed with Pack 16 announced that "some of these cards are unacceptably dark" and that those cards "will be reprinted and sent to you . . . without charge." At least 16 cards in Pack 16 were later replaced and mailed
with Pack 17 - 10 cards and Pack 18 - 6 cards). The replacements were noted only by a small typed slip with Pack 17 stating “Muriciidae replacements . . . more with next pack.” If a card was replaced because of poor image quality, the replacement card bears the same number. If a card was replaced to update the taxonomy or illustrate a better specimen, the replacement card has the original and new numbers separated by a slash [/], sometimes with the addition of “A” to the original number.

Kaicher published the Card Catalogue as an aid to both shell collectors and to professional malacologists. It is now routinely used as a tool by molluscan systematists and has been cited in numerous scholarly works. Many of the shells illustrated on the cards are type specimens never before illustrated photographically. Kaicher photographed many thousands of specimens, some in her own collection, others borrowed from private and institutional collections, and many during her travels to numerous major museums, both in America and abroad. Kaicher bequeathed her collection of Nassariidae to ANSP. Her family subsequently donated to ANSP the remainder of her shell collection, and her photographic negatives, notebooks, and correspondence.

As often happens when type material is illustrated or discussed, some lectotype designations were inadvertently made in the Card Catalogue. In part because of this, Kabat (1996) petitioned the International Commission on Zoological Nomenclature to suppress the Card Catalogue for nomenclatural purposes. Comments on the petition by various workers were published in Bulletin of Zoological Nomenclature 53: 273-277 and 54: 39-66, with the result that in Opinion 1903 (1998), the Commission ruled that the Card Catalogue is nomenclaturally available. We note that the fourth edition of the International Code of Zoological Nomenclature clarifies that lectotype designations made by inference of a holotype have standing only if “the original description neither implies nor requires that there were syntypes” (Article 71.6). Thus in some cases in which Kaicher had been thought to have inadvertently designated a lectotype, it will be found she did not in fact do so.

Because the Card Catalogue is available for nomenclatural purposes, it is important to have a collation, so that citations of nomenclatural actions therein can be made accurately. In cover notes that accompanied the packs, Kaicher corrected mistakes made in numbering the cards and others errors, mostly in spelling or identification. As recipients did not necessarily retain these notes, we have detailed them in our collation included are all changes suggested by Kaicher in cover notes and elsewhere. We have not attempted to review all notes or to bring the names up to date although we have noted some necessary changes. The Marginellidae species treated by Kaicher in Packs 1, 26, and 60 have been extensively reviewed and brought up to date by Covert (1999). Covert notes that 150 of 305 Marginellidae cards illustrate type specimens. In the References Cited we give the full citation for each pack, taking into account missing and duplicated numbers.

RESULTS

Validated Names

Nine manuscript names attributed to various authors appear to have been inadvertently validated in the Card Catalogue. In each case, Kaicher seems to have taken the name from a label in a collection, and in each case she provided a short description. The International Code of Zoological Nomenclature (ICZN, 1999) does not prescribe any minimum length for a description, so these are not valid names as has been maintained by some authors, e.g., Boletin and Reckel (2000), Boletin and Ryall (2000). Also, Kaicher used the Card Catalogue to illustrate species that she considered to be valid, thereby fulfilling the requirement of ICZN Article 11.5, that a name be used as valid when proposed. In the context of the Card Catalogue, Kaicher provided comparative illustrations of many congeneric or conspecific species for each of the validated names. Although Kaicher was unaware that she was the first to validly introduce these names into the literature, ICZN Article 16.1 does not require that names published before 2000 be explicitly indicated as new. We therefore attribute authorship of these names to Kaicher. We have located type material for eight of the nine names: six at the United States National Museum, Smithsonian Institution (USNM) on August 16, 2000, one in the type collection of The Natural History Museum, London (BMNH), one at The Academy of Natural Sciences, Philadelphia (ANSP).

Calliostoma vincentae Kaicher, 1986 - Figure 1, 9-11. Attributed to “tuttelant” on Card 1911. Shells of this species have been sold for many years as “Calliostoma vicenta Rutihls” being listed, for example, by Rice (1952, 2000), but had not been formally published before Kaicher’s treatment. Dr Juan Rutihls y Bassetts of Melilla, Spanish Morocco, was a member of the Malacological Society of London from 1947 until 1934 or 1932, his name appearing in the membership list published in the Society’s Proceedings in 1951 (vol. 28, p. 238), but not in the one published in 1953 (vol. 29, pp. 259-265). He distributed specimens with the manuscript name Calliostoma vicenta” as noted by Muenz (2002), whose research shows that Rutihls did not publish on mollusks, Rice (2000) spelled the name “victena” and Santos Galindo 1977, where it is a made-up name, attributed it to “Rutihls”.

The type lot is ANSP 19899, which is labeled as “Calliostoma vicenta Rutihls. Melilla arraste J. F. Ojeda,” 1936 Spanish Morocco. The original label gives the name as “Calliostoma victenta Rutihls.” The lot contains two specimens, to fix the identity of the name, we here designate the figured specimen as the lectotype. Figure 1, 9-11, height 13.7 mm, the paratype is 13.4 mm in height. Two opercula and crumpled dried animals are also in the lot, but it is not possible to determine what is part of the lectotype and what part of the paratype.

Although the manuscript name was “victenta,” Kaicher validated it as “victenta,” a spelling that must stand. Popp and Goto 1991 and Muenz 2002 synonymized it with Calliostoma tenuis (Philippi, 1846).

Natica variolosa Kaicher, 1984 - Figure 2, 12-14. Attributed to Reeliz on Card 2904. Reeliz introduced this name in
the synonymy of Natica fabel Recluz, 1844 (ex Adamson, 1757; non-binomial) in the original description of that species, Reeve (1855) and Tryon (1867) listed it as a synonym of Natica pellistigra. Dixon and Ravil (1985, pp. 13–14) stated that “…[Natica variolaria] has been used correctly in its West African context by several authors within the last twenty years,” but gave no references. Similarly, Verbeek (1985) and “About twenty years ago, the name Natica variolaria Recluz, 1844 was introduced as the valid name for this species.” Correspondence with Verbeek (through A. Verbeeken, in e-mail to RE 30 January 2000), failed to reveal a reference to this vintage. The only such use we have found is by Santos-Calino (1977), where Natica variolaria is a male name. Since the name was not used as valid before 1961, it cannot be attributed to Recluz, where it first appeared in synonymy (ICZN Article 11.6). Kaicher (1984) apparently was the first to use the name as valid and provide a description, and therefore must be attributed with the authorship.

The type lot, cited by Kaicher, is USNM 90570, and is labeled as “Natica pollys-tigrina Chem. W. Africa. Wesleyan Mus.” and which contains a single specimen. The name “Natica variolaria” does not appear on the label. Kaicher may have inferred the name from the position in the USNM collection, where the species is currently filed as Notocorhlis variolaria, attributed to Recluz. 1844. Kaicher may have seen a second lot, adjacent in the collection: USNM 272970, with USNM label “Natica variolaria Re. Cabon, Africa. Devolle” and original label with “Natica variolaria Re. Cabon,” handwritten and “Emile Devolle 16, rue de Bac, Paris.” It is not clear to us that these two specimens are conspecific with the lectotype: their spires are lower and have stronger axial ribbing below the sutures.

Natica variolaria was first published in synonymy of Natica fabel Recluz, 1844 (ex Adamson, 1757; non-binomial), which is preoccupied by Coelis fabel Röding, 1799 if the latter is classified as a Natica. Fernandes and Rolán (1993) synonymized Röding’s taxon with Natica helvacea Martyn, 1784, a non-binomial name conserved in ICZN Opinion 1662 in 1992. Natica fabel Recluz, 1844 is a synonym of the West African Natica reequigissa Fischer-Piette, 1942 according to Fernandes and Rolán (1993), but an earlier name, based on Adamson’s taxon, is Natica multipunctata de Blainville, 1825, as noted by Verbeek (1985) and Kabat, Finet and Way (1987). Natica variolaria Kaicher, however, is not conspecific with Natica multipunctata, having a sparser pattern and a broader cord in the umbilicus. Alan Kabat (pers. comm. to GR 21 July 2001) confirms that he considers this species to be a Notocorhlis as reflected in the arrangement of the USNM collection.

Anuma teramachii Kaicher, 1980 (Figures 3. 15–17), attributed to Kuroda on Card. 2358, but he did not publish the name: it is not listed by Hamshin Shell Club (1986) or Higo et al. (1999). The name has appeared in print several times as a male name attributed to Kuroda MS (e.g. Azuma 1960. Higo 1975). Weil et al. (1999) treat the species as valid, attributing the name to Kuroda and Habe, 1955, but do not provide a bibliographic reference. It is not listed among Habe’s taxa by Okamoto (2001). Specimens have been distributed under this manuscript name for at least 50 years: ANSP 189370, identified as A. teramachii on the original label was purchased from Shigeo Hashimoto and catalogued in October 1952. The name must be attributed to Kaicher, the first author to provide a description and illustration.

The type lot, cited by Kaicher, is USNM 607185, with USNM label “Anuma splendida de Bonny, Tosa, Shikoku, Japan, 100 fins. ex. J. H. Webb, 1033, 1901” and original label “Anuma splendida Bonny Tosa 100 fins. Japan”; it contains a single specimen. The name “Anuma teramachii” does not appear on the label. Kaicher may have inferred the name from the position in the USNM collection, where the species is currently filled under that name, attributed to Kuroda, 1952. Kaicher likely saw a second lot, also with a single specimen, adjacent in the collection: USNM 607176, with USNM label “Anuma teramachii Kuroda, Tosa, Japan, 150 fins. 1345” and original label “Anuma teramachii Kur. Tosa 150 fins. vary [sic] rare”. To fix the identity of the name, we here designate Kaicher’s figured specimen, USNM 607185, as lectotype (height 15.8 mm; USNM 607176 is a paralectotype (height 15.6 mm).

Kaicher compared Anuma teramachii to Anuma eirea Masahito, Kuroda and Habe, 1971, but that species is currently placed in Clathroscala whereas Anuma teramachii belongs in the subgenus Scalina Conrad, 1850, of which four species are currently recognized from Japan (Higo et al., 1999). It differs from A. (S.) gageoides Kuroda and Habe in 1961, in having a less elongate body whorl and from A. (S.) splendida (Masahito, Kuroda and Habe, 1971) in being larger, less slender, and having more spiral cords per whorl, and from A. (S.) splendida Bonny, 1915 in having finer sculpture. It is most similar to A. (S.) sericozona (Masahito, Kuroda and Habe, 1971), from which Weil et al. (1999) distinguish it as having “more numerous spiral cords of varying strengths”. Their illustrations of these species (figs. 242 and 362), however, do not support this difference, nor does examination of eight additional specimens identified as Anuma teramachii ANSP 189370 231720 243251 243242. We therefore consider A. teramachii to be a synonym of Anuma sericozona.

Tsukada (2000) synonymized Anuma sericozona with A. oaysonasensis Ozaki, 1958, which was named as a Paleocene fossil. Examination of Ozaki’s illustration of the holotype shows that it has a channelled suture defined by a strong spiral cord with the other cords uniformly weaker. In Anuma oaysonasensis, the whorls are of uniform strength near the suture, but stronger below the periphery, particularly on the spire, which gives the early whorls an angular profile. Anuma oaysonasensis also tapers more rapidly than does Anuma sericozona; the width of the anterior whorl of the holotype is about 3.8 mm, the comparable measurement in Anuma sericozona of the same height 15.5 mm, and number of whorls (+) would be about 6.7 mm. We therefore reject the synonymy of Anuma sericozona with Anuma oaysonasensis.

The heading of the original description is Euplotion (Clathroscala) oaysonasensis (Ozaki, 1958, p. 112), but the spelling “oaysonasensis” is used earlier on p. 142, in the plate caption (pl.15, fig. 23), and in the index, p. 180. The name refers to the Osaka or Oyasu Shori. Current either specific name is acceptable nonnaturally. If Oyasu is
latimized, then an "n" is added, following the pattern of Latin words ending in "-io" (e.g., dictio, dictiosis), which yields "ogyaisiosis"; if the word is not latimized, "euis" is added directly to the Japanese word, resulting in "ogyaisiosis". We select ogyaisiosis as the correct original spelling, judging it likely to be the better known because of its use by Tsuchida (2000).

_Haustrium ventricosum_ Kaicher, 1980 (Figure 4, 21-25). Attributed to Tate on Card 2470, but not described by him; the name does not appear in any of his papers on Australian marine or fossil mollusks in the bibliography by Blake (1902).

The type lot, cited by Kaicher, is USNM 304495, the USNM label says "Porpura ventricosa Tate, G. of Spencer, South Australia. Bednall"; the original label says "Porpura ventricosa, Tate G. of Spencer. Aus." The lot contains a single specimen, height 33.6 mm, which is the holotype.

The operculum is part of the lot (Figure 24-25). The specimen is _Dichatilus orbiculatus_ (Gmelin, 1791), a common and highly variable species in southern Australia. This identification was suggested by Dr. Winston F. Pond er, who examined the holotype on 16 August 2000.

_Terebra delicata_ Kaicher, 1981 (Figure 5, 18-20). Attributed to Preston on Card 2752, but Preston did not publish such a name; it is not listed by Adam (1971) or Bratcher and Cernohorsky (1987).

The holotype is in the type collection at BMNH catalogue number 1911.82.22.273 (cited by Kaicher: the type locality is Martintine.

We consider this name to be a junior subjective synonym of _Terebra alba_ Gray, 1834. Gray's name was recognized as valid by Bratcher and Cernohorsky (1987): Kaicher appears to be the first modern author to have recognized the taxon as a good species, although she did not discover the oldest name for it.

_Conus alexandrinus_ Kaicher, 1977 (Figure 6, 30-32). Attributed to "Pais-da Franca" [sic] on Card 1203. Connaas, Moolenberk and Wils (1980) stated that name was found on dealers' lists but was not published by Pais-da Franca. They, Rolin and Rockel (2000) and Filmer (2001) considered it a nomen introduced by Kaicher, but Kaicher does provide a brief description.

Kaicher did not cite an institution or catalogue number, however, we found the figured specimen in USNM 506331. The USNM label says "Conus tevesi Trovão, 1978, Costa Bay, Angola, 1976: In sand under rocks, 1-2 m. Acc. 340672." The original, handwritten by Ed Petuch, says "Conus tevesi Trovão, 1978 - musivus Trovão, 1975, non Sowerby! In sand under rocks, 1-2m depth, Costa Bay, Benguela, Angola. 1976." To fix the identity of the name, we here designate the figured specimen, height 23.6 mm, as the lectotype - Figure 5, 30-31. A second specimen in the lot, height 24.1 mm is a paralectotype (Figure 32).

In the cover sheet to Card Pack 11, Kaicher synonymized the species with _Conus musivus_ Trovão, 1975. Trovão 1975 replaced this name with _C_ tevesi considering it a homonym of _C_ musivus Sowerby, 1833. However, "musivus" is a noun meaning mosaic; it would be a homonym of the adjective "mosaic" only in a neuter genus, according to the examples provided in ICZN Article 38, concerning single letter differences between specific epithets. One of us (GR) posted this matter on the ICZN listserver (http://lyns.bishopmuseum.org/cgi-bin/lyris.pl?enter=iczn-list) on 29 August 2002. Replies indicated that commissioners favor amending Article 38 (under Article 78.3.3.), which is on the agenda for the next meeting of the International Commission on Zoological Nomenclature. Therefore we consider _Conus musivus_ Trovão to be preoccupied by _C_ musivus Sowerby, 1833. _C. alexandrinus_ Kaicher, 1977 to be the valid name for the species, and _C. tevesi_ Trovão, 1975 to be a junior objective synonym.

Edward J. Petuch (pers. comm. to GR, 26 January 2000) confirms that the specimens of this and the three following species were in his personal collection when Kaicher photographed them. Later he donated his specimens to the USNM.

_Conus lineoconicus_ Kaicher, 1977 (Figure 7, 26-29). Attributed to Trovão on Card 1299, but not published by him: it is not listed by Kohn et al. 1955. Apparently this is a dealer's name; it is listed by Rice (1977). Kaicher did not cite an institution or catalogue number, however, we found the figured specimen in USNM 506368. The USNM label says: "Conus lineoconicus Trovão, 1976, off Baina dos Elefantes, Angola, 1965-20 m. Acc. 340672." the original label, handwritten by Ed Petuch says: "Conus lineoconicus Trovão, 1976 - gattatus Kiener. 1849 non Rodig. 1798. Trawled 20 m depth off Baina dos Elefantes, Benguela, Angola. 1965 - sand bottom." To fix the identity of the name, we here designate the figured specimen, height 38.1 mm, as the lectotype (Figure 7, 26-29. A second specimen in the lot, height 34.7 mm, is a paralectotype (Figure 26).

This is a valid species, synonyms are _Conus gattatus_ Kiener, 1845, _Gaudialis gattatus_ Rodig. 1798 (= _Conus_ ) and _Conus laevigatus_ da Mota, 1901, a replacement for Kiener's name. Rolin and Rockel (2000) and Filmer (2001) considered this a nake name, but it had a brief description. The species that Rockel and Fernandes (1982) noted is "known to collectors as "lineoconicus"" is a different taxon named _Conus micropunctatus_ Rockel and Fernandes, 2000.

_Conus lobitensis_ Kaicher, 1977 (Figure 8, 33-38) Attributed to Pais-da Franca [sic] on Card 1311, but she did not publish the name; it is not listed by Kohn et al. 1955. Apparently this is a dealer's name, but not offered recently according to Rice (1999).

Kaicher did not cite an institution or catalogue number, however, we found the figured specimen in USNM 506331. The USNM label says: "Conus obtusus Kiener, 1849. Armado Bay, Angola, 1975, under rocks, low tide. Acc. 340672." the original label, handwritten by Ed Petuch says: "Conus obtusus Kiener, 1849 Under rocks, low tide. Armado Bay. Mocamedes. Angola. 1975." To fix the identity of the name, we here designate the figured specimen, height 19.0 mm, as the lectotype (Figure 7, 33-35). The locality is thus Armado Bay, Angola, not Lobitos Bay, Angola as might be expected from the name. Three other specimens in the type lot, heights 18.7, 17.1 and 15.1 mm are paralectotypes (Figure 36-38).

Rolin and Rockel (2000) and Filmer (2001) considered this a nake name, but it had a brief description, _Conus lobitensis_ however appears to be a synonym of _Conus fuscolimbatus_ Sowerby, 1905, as illustrated by Rolin and Rockel.
Conus negroides Kaehler, 1977. Attributed to Pas-d'a Franca (sic) on Card 1313, but she did not publish the name; it is not listed by Kohm et al. (1995). Apparently a dealer's name, Conus neoides is attributed to Kaehler, 1977 by Rice (1999).

The location of the type material is unknown; we were unable to locate the figured specimen at USNM. The type locality is Angola, as listed by Kaehler.

Rolán and Röckel (2000) and Filmer (2001) considered this a new name, but it had a brief description. Rolán and Röckel (2000) listed it in the synonymy of their new species Conus giabrielae, which is therefore a junior subjective synonym of Conus negroides.

For completeness, we note that Kaehler coauthored one species published outside the Card Catalogue, Vexilhium Paviae (chicklenaarorum) Lyons and Kaehler, 1978. Leptocoris havartensis "Bartsch and Reider" is a new name introduced by Kaehler (1956, part 5, pl. 5, fig. 6); it is a synonym of Conus saturea. 1844 according to Kay (1979) and Filmer (2001). Rolán and Ryall (2000) listed Conus giabrielae as a new name introduced by Kaehler, but that species was described by Pas-d'a Franca (1957).

List of Packs

Exact dates of publication for the card packs (Table 1) are difficult to determine. Most cover sheets (described below) are dated and we have used this date except where better evidence is available. Kaehler did not mail all packs of a given number at the same time, but posted them in small batches as they were collated. A few of Kaehler's records survive that have been helpful in dating. The cover sheet for Pack 42 is dated August 28, 1983 but it states that the cards would not be received from the printer until September 5. The earliest mailing record we have located for Pack 42 is September 9, and that date is used herein.

Cover Sheets and Errata Slips (Sheets)

Each pack was accompanied by a "cover sheet," indicated by CS herein. These small sheets were of varying sizes (11 to 14 cm wide and 11 to 28 cm long) and were not designed for permanancy. The top of each usually had information about planned future packs and sometimes listed changes to be made on cards in previous packs. The bottom was an order form for the next card pack. In addition to the cover sheet, some packs included an "errata slip," listing changes to be made on cards already issued, indicated by ES herein. These slips were of various sizes, sometimes including only a single line of type, and were obviously not intended for retention after the changes had been made. For reference purposes we have assigned them numbers. All are assumed to have been issued with the like-numbered cover sheets unless otherwise stated but some might have been sent with subsequent packs. The following such slips have been identified:

ES5: stapled to CS5 (Mitridae).
ES23: undated (Epitonidae).
ES29: slip pasted to CS29, with handwritten addition, possibly not to all copies.
ES37: undated (changes in Columbellidae).
ES10: undated, typewritten (magnification of Corallophilus mansfieldi).
ES12a: undated slip with CS12.
ES12b: undated slip with CS43 (wrapped around the replacement cards).
ES19a: dated 10 days after CS49 but sent with it.
ES19b: slip pasted to CS19.
ES55: probably issued with CS59.

Corrections and Annotations

We use the following conventions in the list of corrections and annotations:

1) Where species cards were not numbered, we assign them numbers that were skipped within the same pack, if Kaehler had not already done so.

2) In cases of reidentification, we add authors where Kaehler omitted them and inferred generic names in a few cases where Kaehler did not state them explicitly (e.g., 824), we have given years only if Kaehler gave them, which she sometimes did for recently named species.

3) For generic changes we state the combination if the ending of the trivial name or the use of parentheses changed, even if Kaehler omitted this information; otherwise we cite only the genus.

4) Underlining is changed to italics in quotations of Kaehler.

5) Each error that is corrected is attributed to a source, either a cover sheet [CS#], an errata sheet [ES#], another card [Card #], ourselves [herein] or another published work. For brevity, common errors are assigned the following numbers, to avoid repetitive explanations in the text.

Note 1: Number was inadvertently skipped: 96, 145, 146, 369, 744, 1328, 1526, 1542, 2009, 2178, 2503, 3214, 3239, 3289, 3346, 3259, 3437, 5600, 5661, 5812, 6038, 6070, and 6193; in some cases reassigned to an unnumbered card. In addition, Kaehler removed cards 345, 2275, 2687, 2990, 3013 (in some cases), 3504 and 5757 before release.

Note 2: Number duplicated (745, 1510, 3137, 3288, 3770, 3776-3873, 5253, and 6189): Kaehler noted some of these duplications in her cover sheets, but did not recommend solutions. When the duplicates are in separate packs, the one published later can have "bis" (Latin for "twice") added to its number to distinguish it if desired. There was no order, alphabetic, taxonomic, or geographic, to the cards within a pack as issued, so for duplicate numbers within packs it cannot be determined which was intended to bear the number.

Note 3: Specific name is misspelled.
Table 1. Dates of publication of the Card Catalogue, with subject and range of card numbers included in each pack. Most dates were obtained from the cover sheets issued with the card packs; "KR" in brackets after a date indicates that it was obtained from Kaicher's records; "ES" means errata sheet.

<table>
<thead>
<tr>
<th>Pack</th>
<th>Date of issue</th>
<th>Subject</th>
<th>Card numbers range</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>October, 1973</td>
<td>Marginellidae</td>
<td>1-98</td>
</tr>
<tr>
<td>3</td>
<td>February 15, 1974</td>
<td>Mitridae I</td>
<td>196-292</td>
</tr>
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<td>4</td>
<td>May 26, 1974</td>
<td>Mitridae II</td>
<td>293-399</td>
</tr>
<tr>
<td>5</td>
<td>September 5, 1974</td>
<td>Strombacea</td>
<td>390-497</td>
</tr>
<tr>
<td>6</td>
<td>December 14, 1974</td>
<td>Muricidae II</td>
<td>498-594</td>
</tr>
<tr>
<td>7</td>
<td>March 25, 1975</td>
<td>Terebridae I</td>
<td>595-691</td>
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<td>8</td>
<td>August 15, 1975</td>
<td>Naticidae I</td>
<td>692-787</td>
</tr>
<tr>
<td>10</td>
<td>July 15, 1976</td>
<td>Volutidae</td>
<td>904-1009</td>
</tr>
<tr>
<td>11</td>
<td>November 13, 1976</td>
<td>Comidae I</td>
<td>1010-1115</td>
</tr>
<tr>
<td>12</td>
<td>January 10, 1977</td>
<td>Comidae II</td>
<td>1116-1221</td>
</tr>
<tr>
<td>13</td>
<td>March 17, 1977</td>
<td>Comidae III</td>
<td>1222-1327</td>
</tr>
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<td>June 1, 1977</td>
<td>Comidae IV</td>
<td>1329-1434</td>
</tr>
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<td>17</td>
<td>June 1, 1978</td>
<td>Cymatiidae I</td>
<td>1647-1752</td>
</tr>
<tr>
<td>19</td>
<td>December 6, 1978</td>
<td>Cancellariidae</td>
<td>1859-1964</td>
</tr>
<tr>
<td>20</td>
<td>April 18, 1979</td>
<td>Muricidae IV</td>
<td>1965-2071</td>
</tr>
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<td>21</td>
<td>April 9, 1980</td>
<td>Trochidae I</td>
<td>2072-2177</td>
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<td>22</td>
<td>July 2, 1980</td>
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<td>2179-2284</td>
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<td>Epitonidae I</td>
<td>2285-2391</td>
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<td>24</td>
<td>December 15, 1980</td>
<td>Muricidae V</td>
<td>2397-2503</td>
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<td>25</td>
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<td>2504-2609</td>
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<td>Halotidae</td>
<td>2716-2821</td>
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<td>October 9, 1981</td>
<td>Naticidae II</td>
<td>2822-2927</td>
</tr>
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<td>December 23, 1981</td>
<td>Epitonidae II</td>
<td>2928-3033</td>
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<td>July 21, 1982</td>
<td>Cymatiidae II and Bursidae</td>
<td>3140-3243</td>
</tr>
<tr>
<td>32</td>
<td>November 20, 1982</td>
<td>Oliva I</td>
<td>3244-3345</td>
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<td>March 27, 1983</td>
<td>Nassariidae II</td>
<td>3347-3452</td>
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<td>July 27, 1983</td>
<td>Epitonidae III</td>
<td>3453-3558</td>
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<tr>
<td>35</td>
<td>December 6, 1983</td>
<td>Cassidae and Oocystidae</td>
<td>3559-3664</td>
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<tr>
<td>36</td>
<td>March 26, 1984</td>
<td>Columbellidae I</td>
<td>3665-3770</td>
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<td>August 9, 1984</td>
<td>Columbellidae II</td>
<td>3700-3805</td>
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<tr>
<td>38</td>
<td>November 1, 1984</td>
<td>Turbo I</td>
<td>3826-3921</td>
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<td>39</td>
<td>January 22, 1985</td>
<td>Calliophila I</td>
<td>3922-4027</td>
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<td>April 24, 1985</td>
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<td>Fuscariidae II</td>
<td>4561-4667</td>
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<td>January 8, 1987</td>
<td>Nerita I</td>
<td>4669-4775</td>
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<td>May 10, 1987</td>
<td>Buccinidae III</td>
<td>4781-4887</td>
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<tr>
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<td>August 5, 1987 [ES, 199a]</td>
<td>Oliva I</td>
<td>4889-4995</td>
</tr>
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<td>November 30, 1987</td>
<td>Trochidae IV</td>
<td>4996-5101</td>
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<td>February 20, 1988 [KR]</td>
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<td>December 15, 1988</td>
<td>Fissurellidae I</td>
<td>5313-5419</td>
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<td>October 26, 1989</td>
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<td>5632-5737</td>
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<td>59</td>
<td>May 11, 1992</td>
<td>Marginellidae III</td>
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</table>
Note 4: Specific name is a noun and hence invariant.
Note 5: Specific name is a genitive and hence invariant.
Note 6: Specific name is an adjective in comparative form and hence varies with gender of genus.
Note 7: Generic name is misspelled.

Pack 1—Marginellidae [and Cystiscidae]

28. Pronum marginatum: add "also occurs in the Caribbean" [CS2].
30. Pronum olivaceaformis: not "olivaceaformis" [Card 30: 6192].
39. Pronum gatuanum: "ranges in size from 15-25 mm., not 3 mm" [CS2].
47. Volvarina incepta: preoccupied name replaced by Hyalina discors (Roth) [Card 17:6190].
52. Bulbata matthiessi: not "mattihersi" [CS19].
53. Volvarina tenuidors: synonym of Hyalina pallida (Linne) [Card 53:6198].
60. Volvarina rubella: specimen is V. eversaei [Card 60: 6195]; see Card 61:83.
96. This number was skipped; Käicher included, at least in some packs sold after the original publication date, a handwritten note about its absence.
98. Gramina lavalecarena: not "lavalecarena" [CS2: CS19]; specimen represents an undescribed Giberula species [Cards 61:89, 98:6197].

Pack 2—Muricidae

99. Murex peuten: change name to M. peuten peuten [Card 99:6600].
100. Murex acaulostipes: specimen is M. scolopax Dillwyn [Card 100:6604]; see Card 100:6607.
101. Phyllomotus oculus: not "oculus" [CS3].
102. Murca taeniopristis: specimen is M. spiratixus Ponder and Vokes [Card 102:6604]; see Card 102:6609.
105. Murca scolopax: specimen is M. altispina Ponder and Vokes [Card 60:00]; see Card 102:6604.
111. Murex cuppingeri: reissued as Card 114:6614 with minor changes to text.
114. Murca brevissima: change to M. brevissima brevissima [Card 114:6643].
126. Murca maeggilhorni: change to M. brevissima maeggilhorni [Card 126:6614].
134. Chlorus fulvus: change genus to Hexaplex [CS10].
143. Sistrum antillarum: specimen is S. formosus [Card 143:2575].
145. This number was skipped; assign to unnumbered Chlorus daniornis [Note 1].
146. This number was skipped; assign to unnumbered Chlorus spectrum [Note 1].
151. Murca tribulis: specimen is M. fulisubtilulis Ponder and Vokes [Card 60:10]; see 151:6031.

Pack 3—Mitridae [and Costellariidae]

225. Subeuncella flaminia: specimen is Mitra intercalata Sowerby [ES5], i.e., Zaba intercalata (Sowerby) [CS15]; see Card 225A:1529.
232. Strigatella decorata, not "decorata" [CS19].
234. Strigatella gansupata, not "gansupata" [ES5].
245. Costellaria michani: specimen is C. deshayesi (Reeve) [ES5]; specimen is C. alba (Sowerby) [CS15]; see Cards 245A:1534, 1515, 1516.
261. Pastia hampei, identification questioned [CS15]; see Card 261A:1536.
266. Costellaria styliola: species was transferred tentatively to Latiomitra (Turbinellidae) by Bonchot and Kauer (2000).
269. Pastia paludita: specimen is P. albigloba (C. B. Adams) [ES5, CS15]; see Card 269A:1540.
271. Pastia exigua: specimen is Costellaria sykesi (Mellville) [CS15]; see Card 271A:1539.
287. Pastia hendersoni: change genus to Costellaria [CS15]; see Card 287A:1538.
288. Vexillum demersoni: "Delete taylori amia. Shy from the synonymy . . . . . . The type of taylori amia is a juvenile of another species" [ES5].
290. Zelclania woldemarii, not "woldemarii" [ES5, CS19].

Pack 4—Mitridae [and Costellariidae]

345. Not issued; removed by Käicher [ES4].
369. This number was skipped; assign to unnumbered Pastia amabili [sic. amabili] [Note 1].
370. Cunea aegra: specimen is C. piu (Dohrn) [CS15]; see Cards 370A:1533 and 1507.
385. Strigatella auricularis: specimen is S. assimilis (Pease) [CS15]; see Cards 385A:1535 and 148.

Pack 5—Strombidae

422. Add this number to the card for Varicospira crista [CS6].
434. Strombus gibberulus gibberulus, not "gibberalis" [Note 3].
448. Strombus gibberulus gibberialis, not "gibberalis" [Note 3].
456. Strombus gibberulus albus, not "gibberalis" [Note 3].
466. Add this number to the card for Lambis truncata [CS6].
Pack 6—Muricidae

518. Murex nigrospinous, specimen is M. ternispina Lamarck [Card 102/6049].
521. Mur rex ocella: reissued as Card 524/6042 with minor changes to text.
526. Mur ex malabaricus: see holotype on Card 526/2573.
538. Mur ex trapa: reissued as Card 538/6050 with revised text.
543. Mur ex concinus: reissued as Card 543/6045 with revised text.
572. Poiretia zelandica, not “Poiretia” [Note 7].
575. Hexaplex densus: specimen is H. ptiliens [Card 575/2579]; see Card 2504.
584. Favartia granida: preoccupied name replaced by Favartia cernicornis Radwin and D'Attilio, 1976 [Card 584/2577].
591. Homalocyathus oxyacanthus, not “oxyacanthus” [Note 3].

Pack 7—Terebridae

653. Terebra monile: preoccupied name replaced by Terebra quinquimargi Cernohorsky and Bratcher, 1976 [CS13].

Pack 8—Naticidae

726. Natica brunneolina, not “brunneolus” [Note 4].
739. Tectonatica violacea: change combination to Tecta violacea (Sowerby) [Card 739A/3027].
744. This number was skipped; see 715 below [Note 1].
745. Two cards have this number. Natica grapi and Euprypa pallida: one of them should have been 744, but it cannot be determined which.
773. Tectonatica tecta: change to T. tecta form gemmata (Reeve) [CS30]; see Card 2953.
779. Euprypa pallida: change combination to Natica pallida Philippi; because of white calcareous operculum with three ridges [CS29].
792. Slium minus, not “minor” [Note 6].

Pack 9—Mitridae [and Costellariidae]

824. Costellaria latericulata: syntypes do not match type illustration; use name C. orbiculata McIlvill instead [CS12].
832. Pusia circularis: specimen is P. circulae Milhorsky (CS15); see Cards S32A/1530 and 1514.
857. Costellaria radia: specimen is C. orbiculata Reeve [CS15]; see Cards S67A/1531 and 248.
873. Mitra lienardi: change to M. ferruginea forma lienardi [CS15]; see Card 873A/1537.

Pack 10—Volutidae

904. Lyria kurodai, not “kurodai” [Note 3].

Pack 11—Conidae

1058. Conus havanensis: “I now tend to agree with William Old that this is a synonym of Conus magellanicus Hvass”; see Card 1067 [CS14].

Pack 12—Conidae

1122. Conus seiculus seiculus: specimen is C. algocensis algocensis Sowerby, [CS14].
1156. Conus cinereus: author is Hvass [CS19].
1194. Conus kinoshtaiti, not “kinoshtaiti” [Note 3].

Pack 13—Conidae

1248. Conus zelanius, not “zelanius” [CS19].
1257. Conus sphecalatus, not “sphecalatus” [CS19].
1259. Conus lineopunctatus, change authorship to Kaicher [see above].
1261. Conus cyanostomus, not “cyanostomus” [CS19].
1282. Conus formurensis Blumenbach, not “Blumen- back” [CS19].
1293. Conus alexandrinus, specimen is C. murinus Trovao [CS14]; change authorship of C. alexandrinus to Kaicher [see above]; Paes-da Franca, not “Paes-da Franca” [herein].
1303. Conus kintoki: authors are Habe and Kosuge [CS14].
1311. Conus lobitensis: change authorship to Kaicher; is Conus fuscolineatus Sowerby [see above]; Paes-da Franca, not “Paes-da Franca” [CS14].
1313. Conus negraves: change authorship to Kaicher [see above]; Paes-da Franca, not “Paes-da Franca” [CS14].

Pack 14—Conidae

1328. This number was skipped between Packs 13 and 14 [CS15].
1342. Conus clarus, not “clarius” [CS19].

Pack 15—Mitridae [and Costellariidae]

1489. Pusia crocata, not “crocata” [CS19].
1526. This number was skipped; assign to unnumbered Mitra carinacea [Note 1].
 Pack 16—Muricidae

1510. This number was used in both Pack 15 (Pusia albinaeta) and Pack 16 (Boreotrophon alaskanus) [CS19].

1512. This number was skipped [CS19].

1590. Specimen illustrated is not Ocenebra acicularis [CS20], but Pusia dorbignii [Tate et al. 1826] [herein]; see Cards 1390/4/2005 for Ocenebra acicularis and 4343 for Pusia dorbignii.

1640. Eroksia rufonotata: Eroksia misspelled in text [herein].

 Pack 17—Cymatiidae

1655. Cymaniella galambk; synonym of Sassa sexcostata (Tate) [Card 1655/3337].

1659. Cabestana spengleri: change genus to Cymatium [Card 1659/333].

1663. Fusitriton landanus: change to F. magellanicus landanus [Card 1663/3334].

1665. Gryneus grynium: not “gymnium” [CS19].

1663. Cabestana dolhare: author is Linne [CS19].

1692. Septa acrogra: this printed name changed to Ranula acrogra by self-adhesive label in packs mailed at time of publication. In many packs issued subsequently this card did not receive the corrective label [herein].

1690. „ Monoplex lignarius, not “lignarius” [Note 1]: probably a Septa [CS19].

1702. Ranula acrogra, not “gutturia”: [Note 1].

1703. Fusitriton retiolus: change to F. magellanicus retiolus [CS32].

1706. Fusitriton macrasi: change to E. magellanicius macrasi [CS32].

1707. Monoplex parthenopetra parthenopetra: change genus to Cymatium [Card 1707/3342].

1705. Bispel junada, not “juanda”: magnification is ×2, not ×1 [CS19].

1717. Fusitriton cancellatus: synonym of F. magellanicius (Roding) [CS32].

1719. “Protoconch differences suggest Cabestana keri is a Septa” [CS19].

1731. Nsegzina subdictoria: change genus to Sassa [Card 1731/3343].

1732. Sassa scanitaria: change to S. massaniformis scanitaria [Card 1732/3323].

1744. Gattara lineatissima: change genus to Cymatium [Card 1744/3341].

 Pack 18—Fasciolariidae

1754. Fusinus leptorhynchos, not “leporhynchos” nor “leptohynchos” as in CS16 [Note 3].

1757. Latirus amplustr: not “anphistris” [Note 4].

1766. Granulifusus rufinodeus, not “rufinodeis” [CS16].

1768. Granulifusus suboblitus: change to G. nipponicus suboblitus [CS16].

1787. Latirus melaneamericanus, not “melaneamericanus” [Note 3].

1790. Latirus bairstowii: change combination to Dolicholatius bairstowii (Sowerby) [CS16].

1798. Fusinus allanus: see syntype on Card 1798/4721.

1800. Dolicholatius ernesti: change combination to Teratius ernesti (Melville) [CS18].

1815. Fusinus nigricostatus: synonym of F. tuberosus (Reeve) [CS16].

1820. Fusinus sandwichensis, not “sandwichiensis”: see lectotype on Card 1820/4728. The name was spelled both ways by Sowerby, 1850, the original author; a first reviser’s choice establishing the correct spelling was made by Snyder (2003).

1828. Pleurolophus heyneanus: change to P. lugubris heyneanus [CS46].

1836. Microtus durchk: specimen is M. lineolatus (Crosse and Fischer), which is not synonymous [Card 1836/4720]; see Card 4655.

1851. Fusinus murchison: change to F. diicrus (A. Adams) [Card 1851/4729].

 Pack 19—Cancellariidae

1924. Agatris agassizii: catalogue number is USNM 95711, not 75711 [herein].

1940. Adnec microscopica: catalogue number is USNM 82977, not 32977 [herein].

 Pack 20—Muricidae

1977. Eroksia graji, not “Eroksi” [Note 7].

1983. Trophon gerriswanum, not ”gerriswanum” [Note 3].

1985. Murex chrysonostoma, not “chrystosostoma” [Note 4].

1989. Ocenebra purpurea, not “Ocenebra” [Note 7].

1995. „ Ocenebra purpurea, not “Ocenebra” [Note 7].

2005. Atthesma striata: change name to Atthesma philippiana (Dall), which is not synonymous [Card 2005/2574].

2009. This number was skipped [Note 1].

2010. Risomurex schrammi: specimen is R. deformis (Reeve) [Card 2010/6053].

2014. Marxus nothokienz, not “nothokienz” [Note 3].

2034. Hexoplex cunariens, not “cunariens” [Note 3].

2058. Eroksia ferrugina, not “Eroksia” [Note 7].

2052. Afrithrophus insignis: specimen with adult aperture shown on Card 2052/2576.

2060. Ocenebra acanthophora Montsiazi: there is no such name; Hoarit (2001) considered it an error for O. acanthophora Montorsato, 1875, which is a nede name. Kaicher gave no description, so it remains a nede name [herein]. Hoarit (2001) identified Kaicher’s illustrated specimen as Oce- nebra hispidula (Pallary, 1904).

1590/4/2007. Ocenebra acicularis, not “Oocenebra” [Note 7].
THE NAUTILUS, Vol. 117, No. 4

Pack 21—Trochidae

2135. Trochus satrampus: author is von Martens, not "von Maltzan" [herein].
2167. Calliostoma stenosophala, not "stenosphala" [Note 3].
2177. Calliostoma deceptum, not "deceptum" [Note 3].

Pack 22—Trochidae

2178. This number was skipped between Packs 21 and 22 [Note 4].
2241. Clauclus ovalomorphus, not "ovalomorphus" [Note 3].
2242. Calliostoma ornithophorus: change genus to Clauclus [CS30].
2275. Not issued: removed by Kaicher [CS22].

Pack 23—Epitoniiidae

2285. Epitonium alizonum, not "alizonum" [Note 5].
2289. Epitonium bullatus, not "bullatunum" [Note 4].
2292. Epitonium clathrus, not "clathrum" [Note 4].
2303. This number was skipped [ES23].
2320. Epitonium helicorum, not "helicorum" [Note 4].
2325. Epitonium macrophalbus, not "macrophalbus" [Note 4].
2328. Add this number to unnumbered card for Cicerotoma hilarype [ES23].
2332. Add this number to unnumbered card for Epitonium geniculatum [ES23].
2333. Epitonium melius, not "melior" [Note 6].
2342. Epitonium millecostatum, not "millecostum" [Note 3].
2350. Epitonium rarecosta, not "rarecosta" [Note 4].
2338. Annua teramachii: change authorship to Kaicher: is Annua sericozogae Masalito, Kuroda and Habe [see above].

Pack 24—Thaididae

2418. Azumaonid ula matina, not "Azumaonidu" [Note 7].
2457. Mordula basostoma, not "basostoma" [Note 4].
2470. Hautoidea ventricorum, change authorship to Kaicher, is Didathula optinga Canclini [see above].
2481. Mordula gemnulifera: Pease: No such name was introduced by Pease. The specimen illustrated is conspecific with Eugma gemnulifera Pease 1860, which is a synonym of Mordula echnatia Reeve, 1846 according to Cernohorsky (1979). Therefore, we consider "gemnulifera" to be a lapsus for "echnatia". The alternative is that, because the card contains a description, Kaicher had inadvertently validated a manuscript name of Pease based on a specimen label in a collection. We reject this possibility because Kaicher cited three locations indicating the geographic range of the species: "Sanada Takihi Hawaii". If she had validated a manuscript name, in all likelihood she would have cited only a single locality.

Pack 25—Muricidae

2507. Boreotrophon cepula, not "ceplulus" [Note 4].
2542. Erykosa paucinuta, not "Erykiosa" [Note 7].
2562. Pierogyris hamatus, not "Pierogyris" [Note 7].
2568. Risomurex idios, not "idios" [Note 3].
2588. Straminotrophon longastelli, not "Straminotrophon" [Note 7].
2594. *Erykosa nitens, not "Erykiosa" [Note 7].

Pack 26—Marginellidae [and Cystiscidae]

2634. Cystiscus aphanospira, not "aphanespira" [Note 3]. Covert (1999) erroneously changed it to "aphanespira" [Note 4]: description should read "2 strong concomular folds (trace of smaller one)" [CS26].
2662. Marginellus diadectus: locality should read "supposedly from Indian Ocean and Sunda Strait." (This correction erroneously referred to Card 2709 on CS26) [CS26].
2676. Globella reccova, not "reccova" [CS26].
2686. Volvaria obscura: specimen is misidentified and may represent an undescribed species [Card 2680/619].
2687. Not issued: removed by Kaicher [CS26].
2709. See 2662 above.

Pack 27—Terebridae

2752. Terebra delicatula: change authorship to Kaicher: is Terebra alba Gra [see above].
2768. Parriciterbreria separanda: change family to Columbellidae [Card 2768/1247].
2797. Parriciterbreria thyrsaea Melvill, not "thyrsaea Melv" [herein]: change family to Columbellidae [Card 2797/1248].

Pack 28—Haliootidae

2823. Haliootis orina: specimen is H cyclobates Peron [sic: Peron] [CS29].
2877. Haliootis diversicolor: misprinted as 2077 [herein].

Pack 29—Naticidae

2922. Naticina lincozoa, not "lincozoa" [Note 4].
2938. Anamoropsis morfli, not "morghi" [herein]: species transferred to Epitonidae, as Prohibitina morfli, by Wilson 1993.
2955. Feootamatus tect: specimen matches the neotype [CS30]; see Card 773.
2978. Nucrata vestita, not "vestita" [Note 3].
2959. Eunicina rhodochryta, not "rhodochryta" [Note 4].
2961. Natica variolata: change authorship to Kächer; is a Notocochlis [see above].
2980. Anactopus globulus: species transferred to Epi-
2990. Not issued: removed by Kächer [CS29].
3013. Natica insularum: A postcard postmarked October
26, 1981 asked that this card be destroyed as the
illustrated specimen was misidentified; how-
ever, the card was removed from some packs be-
fore they were shipped [ES29]. Natica insularum
is correctly shown on Card 2998.

Pack 30—Epinouiidae
3049. Epitonium aequatoriale, not “aequatoriale”
[Note 3, 4].
3062. Epitonium chrysi, not “chrysi” [Note 3].
3070. Epitonium platyparema, not “platyparema” [Note
4].
3103. Epitonium laboe, not “laboe” [Note 3].

Pack 31—Nassariidae
Pack cover card. Nassarius consors is not sinus;
negative accidentally “floppe” [CS31].
3135. Two cards have this number. Nassarius brunnae-
cestoma and V. striatus [Note 2].
3184. Nassarius lurcestoma, not “lurestoma” [Note 4].
3214. This number was skipped [CS31].

Pack 32—Cymatidae and Bursidae
3239. This number was skipped between Packs 31 and
32 [Note 1].
3288. Two cards have this number. Bursa granularis
emmingiana and Aegobucinum prodir; one
should have been 3289, but it cannot be detei-
nined which [Note 2].
3289. This number was skipped [Note 1]; see 3288
above.

Pack 33—Olividae
3346. This number was skipped between Packs 32 and
33 [Note 1].
3412. Amalda navaezeleandic form bicolor Angas: Au-
gas did not introduce the name bicolor; it is a
misspelling and misidentification of tricolor Gray,
1847 by Suter 1904 according to Olson (1956),
who lists the name in the synonym of Bayaspis
navaezeleandic. The illustrated specimen is also
mislocalized: the species is endemic to New Zea-
land [herein].

Pack 34—Nassariidae
3458. Nassarius muselina: “the specimen illustrated.
lower right, is the holotype (USNM 24200)’”
[CS34].

3482. Nassarius abysicola, not “abysicola” [Note 4].
3525. Nassarius cinetella: “the ‘life-size’ illustration is
actually about twice life size” [CS34].
3536. Nassarius leptospira, not “leptospira” [Note 4].

Pack 35—Epinouiidae
3570. Epitonium echinocostata, not “echinocostata”
[Note 4].
3615. Epitonium sericifila, not “sericifila” [Note 4].
3626. Epitonium calipephem, not “calipephem” [Note
3].
3637. Epitonium fodiacecosta, not “fodiacecosta”
[Note 4].
3640. Epitonium turritellata, not “turritellata” [Note
4].
3653. Epitonium babylonus, not “babylonus” [Note 4].

Pack 36—Cassididae and Oocorthyidae [and
Harpidae]
3730. Morum sp.: is Morum annulatum Emerson. 1986
[CS16].

Pack 37—Columbellidae
3770. This number was used in both Pack 36 (Echinoc-
ois avarosa) and Pack 37 (Anachis decimdentata)
[Note 2].
3775. Anachis visitsella: habitat previously unknown;
matches shell illustrated as Anachis ceterata from
Puerto Rico in Caribbean Seashells by Warmke
and Abbott (1961) [CS41].
3779. Costaeachis fluctata, change genus to Anachis
[ES37b].
3781. Pseudanachis bisedowi; not “Pseudanachis”
[Note 7].
3812. Mitrella liveseana: may be a Euplia [ES37a].
3822. Columella torturata: change combination to Eup-
lia torturata (Lamarck) [ES37a].
3825. Columella varians: change combination to Eup-
lia varians (Sowerby) [ES37a].
3863. Columella scripta: change combination to Eup-
lia scripta (Lamarck) [ES37a].

Pack 38—Columbellidae
3776–3875: These numbers were used in both Pack 37
and Pack 38 [CS30, Note 2].
3776. Notochila pascala (Herken)
3777. Mitrella dentiventula (Duel.
3778. Anachis cancellata (Caskin).
3779. Astiris perlicuda Dall.
3780. Mitrella densithorata (Carpenter).
3781. Anachis cancellata act. nov. Caskin.
3782. Mitrella dartevelle (Knudsen).
3783. Anachis hirta (E. A. Smith).
3784. Astiris vidua Dall.
3785. Mitrella melilli (Knudsen).
3786. Columbella castanea Sowerby.
3787. Cosmociona nitens (C. B. Adams).
3788. Anachis adelinea (Tyson).
3789. Anachis heresi Skarby.
3790. Anachis emeris (Fischer-Piette and Nickles).
3791. Anachis emeris var.
3792. Mitrella verduniri (Knudsen).
3793. Anachis atramentaria (Sowerby).
3794. Anachis consanguinea (Sowerby).
3795. Mitrella percula (Dunker).
3796. Columbella paddens Lesson.
3797. Mitrella mundicrens (Reeve).
3798. Anachis gaskoini Carpenter.
3799. Microthara eithara (Reeve).
3800. Mitrella bacata (Gaskoin).
3801. Mitrella canariensis (Orbigny).
3802. Mitrella gattata (Sowerby).
3803. Mitrella xenu Dall.
3804. Mitrella lartigoniensis (Reeve).
3805. Nasserina tehuantepecensis (Shaky).
3806. Mitrella tenuis (Gaskoin).
3807. Strombina pacifica Dall.
3808. Mitrella australis (Gaskoin).
3809. Anachis descendens (von Martens).
3810. Mitrella delineata (Reeve).
3811. Nasserina cruciata (Moreb).
3812. Aesopus punctolius: change combination to Parviterella punctolius Pilsky, since it is the type species of the genus, and the genus is recognized on Cards 2768 and 2797 (see above) [herein].
3813. Mitrella virideta Tate.
3814. Mitrella loisae Pitts and Kohl.
3815. Mitrella dictata (Temson Woods).
3816. Anachis incerta (Stearns).
3817. Anachis reedi Bartsch.
3818. Cosmociona palmeri (Dall).
3819. Nasserina helecrina Keen.
3820. ? Euphicsn urina (Duclos).
3821. Mitrella baccalis (Reeve).
3822. Mitrella psilla (Duclos).
3823. Strombina edulenta Dall.
3824. Anachis kirostra (Duclos).
3825. Anachis ragulosa (Sowerby).
3826. ? Pyrene yoldia (Duclos).
3827. Anachis (L. violacea) (Gaskoin).
3828. Zafrona pulchella (Blainville).
3829. Parmataria huponti (Kiener).
3830. Strombina mendozanai Shaky.
3831. Mitrella conspersa (Gaskoin).
3832. Mitrella pulla (Gaskoin).
3833. Astyris appressa Dall.
3834. Astyris procura Dall.
3835. Mitrella vclintata (Sowerby).
3836. Astyris multioculata Dall.
3837. Mitrella baccinalis Sowerby.
3838. Anachis lenta (Hinds).
3840. Aesopus algae (Sowerby).
3841. ? Pyrene ida (Duclos).

3843. Mitrella pyramidalis (Sowerby).
3844. "Pyrene" mimocita Tomlin.
3845. Anachis leptalea (E. A. Smith).
3846. Mitrella apicata (E. A. Smith).
3847. Mitrella smpstomonea (E. A. Smith).
3849. Nasserina bathica (Dall).
3850. Amphissa reticulata Dall.
3851. Euphicsn bidentata (Menke).
3852. Astyris amantiis Dall.
3853. Zafrona ubalosa (Gould).
3854. Mitrella sancticuleana E. A. Smith.
3855. Aesopus chrysalidea (Carpenter).
3856. Aesopus hilum (Hedley), not "hilium" [Note 3].
3857. Aesopus cassandra (Hedley).
3858. Mitrella yorkeana (Crosse).
3859. Nasserina plexa (Hedley).
3860. Aesopus podatilus (Hedley).
3861. Mitrella russelli (Brazier).
3862. Anachis kranusii (Sowerby).
3863. Zafrona diarepceta Pilsky.
3864. Zafrona alternata (Gould).
3866. Aesopus steareus (Tyson).
3867. Zafrona consorubra Behder.
3868. ? Zafrona retiaria (Tomlin), not "retiaria" [Note 3].
3869. Anachis burmani (Tomlin).
3870. Ruthia nazuthamica Shaky.
3871. Mitrella baleuti (E. A. Smith).
3872. Anachis fuscidens Dall.
3874. Anachis mita (Thiele).
3875. Parametaria macrostoma (Reeve).

**Pack 39—Turridae**

3902. Cellepsdrpta radiata: specimen is not USNM 421774 but probably ANSP 300563; see Card 3907 [herein].
3907. Cellepsdrpta elegans: catalogue number 421774 visible on shell is a USNM, not an ANSP, number; see Card 3902 [herein].
3939. Agathostenes castellata, not "costellata" [Note 3].

**Pack 40—Coralliophilidae**

4004. "Coralliophilia" koehimae: change combination to Latusiophila koehimae; change family to Muricidae [Card 4004 08054]. See also Bucinidae 4004 below.
4060. "Coralliophilia" mansfieldi: magnifications are "x2" and "x1" [ES 10].

**Pack 41—Nassariidae**

4103. Nassarius sinuatus, not "sinuarius" [Note 5].
4117. Bullia indusica, not "indusica" [Note 3].
4148. Cyllene unimaculata, not "unimaculata" [ES41].
4155. Bulbia otalicetinus, not "otalicetinus" [ES41].

Pack 42—Columbellidae

4205. Aequus spirala, not "spirala" [Note 4].
4210. Pyrene ogasariarum: removed from Pack 42, reprinted and shipped with Pack 43 [ES42a].
2768/4217. Parviterella separanda, not "separanda" [Note 3]; author is Toulin, not McVick [herein].
2797/4218. Parviterella thyrsea Melvill, not "thyrsea Melvill" [Note 3].
4297. Mitrella phyllina: removed from Pack 42, reprinted and shipped with Pack 43 [ES42a]. Other cards that were reprinted, but not first removed are 4211–4216, 4218–4220, 4225, 4273, 4276, 4292, 4294, 4296, 4299, 4301, 4305.

Pack 43—Buccinidae

4004. Nassaria pusilla form lacerior: misprint for 4404 [herein].
4310. Bapomita canaliculata: change to B. spirata valvulaturn (Swainson) [Card 4635/4310].
4339. Neptunia antiqua: specimen is N. despecta descripsa (Linné) [CS4].
4343. Pismum doriae Pagrandeau: not "Payrandeau" [herein].
4345. Buccinum leucostoma, not "leucostomum" [Note 4].
4356. Buccinulum lineolata, not "lineolatm" [Note 4].
4369. Pholus cingletomastus, not "cingletomastus" [Note 4].
4373. Caitharus melancostoma, not "melanostomus" [Note 4].
4383. Caitharus erythrostoma, not "erythrostomus" [Note 4].
4397. "Caitharus" dentatus: change combination to Eosipho dentatus (Schepman) [Card 4941/4397].
4404. See 4004.

Pack 44—Buccinidae

4417. Metula alba: magnifications x2 and x4, not x1 and x2 [Card 4936/4417].
4440. Polia pastinacea, not "pastinacca" [Note 3].
4469. Chloris polycha: character genus to Engnua [Card 4660/5833].
4870. Scaresia divus, not "Scaresia" [Note 7].
4513. Caitharus albozonatus: author is Kosuge, not "Kosuge and Habe" [herein]; preoccupied name replaced by C. leucostomatus Kosuge, 1985 [Card 4513/5835].

Pack 45—Trochidae

4526. Claudia bertheletii, not "bertheleti" [Note 3].
4614. Callistosoma vienctacae, change authorship to Katcher; probable synonym of Callambonella naturalis Philippi [see above].

Pack 46—Fasciolariidae

4629. Latirus rhodonostomus, not "rhodonostomus" [Note 4].
4654. Latirus croesus, not "croesus" [Note 3].
4655. Microcos rhodonostomi: M. diakeri mentioned in text is Card 4720, not 4719 [herein].
4665. Latirus singularis, not "singulatus" [Note 3].
4671. Latirus elegans: author is A. Adams, not "Gray" [herein].
4674. Latirus manrophonus, not "manrophonus" [Note 3].
4680. Leucoziavia ocellata, not "ocellifera" [Note 3].
4694. Fusius fragilissimus: change genus to Bayeirius; change family to Buccinidae [Card 4694/5834].
4710. Latirus leucolius: change combination to Godfreya leucolius (A. Adams), change family to Buccinidae [Card 4710/5832].
4711. Fusius rufusalbumus: change genus to Exiloidia; change family to Turbinellidae [CS5]; reissued as Card 5628.
4715. Pleurolopha liguriae, not "liguria" [Note 4]; originally spelled "liguria" by Linné (1758), but as "liguria" by Linné 1767. Vokes (1971) noted that the latter was correct Latin, but retained the spelling "liguria" in accordance with the ICZN rules then in effect. As the later spelling "liguria" has remained in prevailing use, attributed to Linné, 1758, it is to be maintained (ICZN Art. 33.3.1) [herein].

Pack 47—Neritidae

4733. Dostia leonine, not "leonii" [Note 3].
4750. Clypeolum subauriculatum, not "subauriculatum" [Note 3].
4756. Clypeolum tanitensis: change X. auriculata in text to C. auriculatum [herein].
4765. Theodoxus elongatus, not "elongatus" [Note 3].
4773. Theodoxus grandimorius valentina: author is Graell, not "Graell" [herein].
4779. Theodoxus pelophomus, not "pelophomus" [Note 3].
4787. Nerita bicornica: author is Troschel, 1878, not Recluz [herein].
4824. Nerita vespertina: change genus to Clypeolum, to agree with placement of C. tanitensis (Card 1756), with which it is compared [herein].

Pack 48—Buccinidae

4851. Metula sp.: is M. africana Bouchet, 1988 [Card 5851/5888].
4862. Caitharus leucodonnus, not "leucodonnus" [Note 4].
4885. Pismum hermaniae, not "hermaniae" [Note 3]; A. Adams (1855) spelled the name "hermaniae", stating "We have named it after M. Hermannsen, who has contributed so materially towards the natural history of the Mollusca, by his
valuable work on Bibliography and Synonyms'. Because it is clear that Adams' intention was to name the species for A. N. Herrmannsen, author of Indicia Generum Malacozoonum Primordiae (1846–1852), the spelling must be corrected to "herrmannsen" under ICZN Article 32.5.1.

4899. **Buccinum** *kiiuokatsugi*, not "kiiuokatsage" [Note 3].

4900. **Prodotia iostoma**: change name to **Prodotia** sp. "A" [Card 4900/5351], wrong protoconch illustrated; see Cards 5526 and 5546 for *P. iostoma* and 5858 for *P. cf. P. iostoma*.

**Pack 49—Oliviidae**

4994. **Olivella** *formicacorsii*, not "formicacorsi" [Note 3; named for Dr. A. Formica Corsi].

5034. **Olivella** *guldfugius*: type locality is St. Vincent [ES91a].

5036. **Olivella** *nitera*: specimen is from Espirito Santo, Brazil; wrong protoconch illustrated [ES91a].

5047. Not issued; removed by Katcher [ES91b].

**Pack 50—Trochidae**

5053. **Cauharidella** *tessellata*: compare to syntax shown on Card 5791/5053; see Card 5712.

5067. **Bathybathix** *acola*: specimen is *B. cf. acola* [Card 5687/5067]; see Card 5688.

5080. **Mierchenich** *sanguinipes* sanguineus, not "Micherchenich" [Note 7].

5095. **Munella** *holwirthana*: authorship is Neville and Nevill, not "Nevill" [herein].

5120. **Mierchenich** *tenebrosas*, not "Micherchenich" [Note 7].

5123. **Mierchenich** *sanguinipes* cryptus, not "Micherchenich" [Note 7].

5117. **Mierchenich** *rojoza*: not "Micherchenich* rofozoa" [Notes 3, 6].

5149. **Mierchenich** *dilatata*, not "Micherchenich" [Note 7].

5152. **Astele** *pulcherrima*: synonym of **Cardiastella punctocostata** [Card 5686/5152].

**Pack 51—Oliviidae**

5253. Two cards have this number. **Olia** *cf. antimena* and *O. acuta* [Note 2].

5259. This number was skipped [Note 1].

**Pack 52—Turbinidae**

5317. **Guldfordia** *triumphus*, not "Guldfordia" [Note 7].

5320. **Guldfordia** *yoka*, not "Guldfordia" [Note 7].

5323. **Microastrea** *pumilula*: not "pumilula" [Note 3].

5326. **Guldfordia** *aculata*, not "Guldfordia" [Note 7].

5329. **Guldfordia** *modifera*, not "Guldfordia" [Note 7].

**Pack 53—Fissurellidae**

5381. **Medusa** *fissurella* *salebrosa*: "type species of Medusa fissurella" [CS53].

5411. **Diodorofissurella** *scutatum*: "type species of Diodora fissurella" [CS53].

5420. **Diodora** *elizabethae*, not "elizabethae" [Note 3].

5437. This number was skipped; assign to unnumbered **Diodora calyculata** [Note 1].

5451. **Fissurella** *pulex*: not that species; identity not determined [CS54].

**Pack 54—Oliviidae**

5502. **Oliva** *miniacea*, not "miniacea" [Note 3].

**Pack 55—Turbinidae**

5660. This number was skipped [Note 1].

5661. This number was skipped [Note 1].

**Pack 56—Trochidae**

5686/5067. **Cardiastella** *punctocostata*: number should be 5686/5152 [herein]; see next item and 5152 above.

5687/5052. **Bathybathix** *acola*: number should be 5687/5067 [herein]; see previous item and 5067 above.

5712. **Cauharidella** *tessellata*, not "tessellata" [Note 3].

5716. **Rossiteria** *nucleus*: not "nucleo" [Note 4].

5721. **Minella** *holwirthana*: authorship is Neville and Nevill, not "Nevill" [herein].

5737. Not issued; removed by Katcher [CS56].

5791/5053. **Cauharidella** *tessellata*, not "tessellata" [Note 3].

**Pack 57—Buccinidae**

5795. **Crassicostubera** *norfolkensis*: size is about 10 mm, not "40 + mm" [herein].

5819. **Scarilia** *fasciobrata*: not "Scarilia" [Note 7].

5823. **Engina** *pulcherrima*: note catalog number is 1966608 not 1966608 on original card 4060 [herein].

5852. This number was skipped; assign to unnumbered **Colubraria** *tortosia* [Note 1].

5848. **Colubraria** *bayeri*: transferred to **Tritonoharpa** (Cardiastellidae) by Harasewych, Pettit and Verheeken 1992.

**Pack 58—Ovulidae**

5914. **Cyphoma** *signatum*: museum number is USNM 599386 [ES58].

5920. **Galora** *acculata*: change genus to Galoratra [ES58].

5926. **Pseudocryptus** *proteinus*: in text discussion, change *P. adanusi* to *P. adamsi* [ES58].

5913. **Sculptura** *barbaricus*: change "Dall" to "Dall" [ES58].
6001–6002. Magnification, omitted from many Muricex sp. cards, is x1 [CS59].
6007. (2) Pygmaeapteryx aleciae, not "Pygmaeapteryx". Unnumbered Potieria kopua erroneously assigned to this number on CS59; on some copies of CS59, Kaucher crossed out 6007 and wrote in 6008, which see.
6016. Potieria primanovae, not "Potieria" [Note 7].
6017. Pygmaeapteryx adexis, not "Pygmaeapteryx" [Note 7].
6038. This number was skipped; assign to unnumbered Potieria kopua [Note 1]; see 6007 above.
6039. Pygmaeapteryx richardbinghami, not "Pygmaeapteryx" [Note 7].
6070. This number was skipped; assign to unnumbered Bisumarex withroi [CS59].
6096. Typhis ocellatus, not "oceanus" [Note 3].

Pack 60—Marginellidae [and Cyrtiscidae]

6105. Homalocantha dorpeledi, not "Homalocantha" [Note 7].
6111. Canalspira attenuata, not "Canalspira" [Note 7].
6130. Deadinargo smithii; museum number is MCZ 207389, switched with Card 6171 (see below) [herein].
6141. ? Perimyella pyramum; change genus to ? Persica [CS60].
6171. Deadinargo idioelida; museum number is ANSP 219511, switched with Card 6130 (see above); Coover (1999) erroneously changed the ending to agree with Deadinargo [Note 4].
6185. Canalspira replicata, not "Canalspira" [Note 7].
6189. Two cards have this number; Gibberula laclavanca of authors and Volvarina perrieri [Note 2].
6193. This number was skipped [Note 1].
6204. Canalspira minor, not "Canalspira" [Note 4].

ACKNOWLEDGMENTS

We wish to thank William G. Lyons (Bill) and his wife Carol for the many hours they spent sorting and conserving material relevant to the production of the Kaucher cards. Bill provided a detailed review of the manuscript, as did Alan R. Kabat. Edward J. Petuch put us on the track of unrecognized type material of Conus species in the USNM mollusk collection. M. G. Harasewych allowed us access to that collection and Paul Greenhall provided information about changes in its organization. Kathleen Way loaned material from the BMMH. Michael Hollmann advised on West African naticids. Heuk K. Menis provided information about Dr. Rahtik. Sarah Watson prepared the plates from digital photographs taken by Gary Rosenberg. Paul Callomon photographed Testa (sic) delicate and added images of it to the plates.

LITERATURE CITED

Pack #18—Fasciolariidae Part I S. D. Kaicher, St. Petersburg, Florida. Cards [i-ii], 1753-1858.


Reproduction of *Crepidula navicula* Mörch, 1877 and *Crepidula aphysioides* Reeve, 1859 (Caenogastropoda) from Morrocoy and La Restinga Lagoon, Venezuela

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ABSTRACT

Brooding specimens of *Crepidula aphysioides* and *Crepidula navicula* were collected from La Restinga Lagoon, Margarita Island, and Las Lomas Bay, Morrocoy, Venezuela at a depth of 0.5–1 m. Individuals of *C. aphysioides* were attached to man-grove oysters and mussels that were attached to the roots of *Rhizophora mangle*, while those of *C. navicula* were attached to the gastropod *Modiola nodulosa*.

Brooding females of *C. aphysioides* measured 9.4–18.2 mm shell length and each female brooded 23.4 ± 4.5 egg capsules. The egg capsules had a triangular shape, with one corner extending to form a stalk that attached the egg capsule to the substrate. The capsule walls were thin and transparent. Egg capsules measured 0.5–2.7 mm length (without the stalk); 0.5–2.7 mm width, and the stalk 0.6 – 3.3 mm length. The number of eggs per capsule varied from 3 to 16. The uncleaved egg measured about 300 µm and all eggs developed. Nurse eggs were not observed. Cannibalism, however, was observed among sibling embryos and the number of hatching was significantly lower by one individual than the number of eggs. Hatching occurred as crawling juveniles measuring about 600 µm in shell length.

Brooding females of *C. navicula* measured 4.9–7.4 mm shell length and each female brooded 8.5 ± 2.2 egg capsules. The egg capsules were very similar to those of *C. aphysioides* but smaller (between 0.5 and 1.3 mm lengthwise) and contained 3–4 eggs each. The uncleaved eggs measured around 330 µm. All eggs developed, cannibalism was observed, and the number of hatchings was significantly lower than the number of eggs. Between 2–4 individuals hatched per capsule as pediveligers measuring 550–1172 µm shell length.

Female size determines fecundity, in terms of juvenile production, on both species. This is accomplished through two different strategies, the first an increase in the number of hatchings per female at larger female sizes *C. aphysioides* and the second that larger females produced larger egg capsules with more hatchings *C. navicula*.

INTRODUCTION

The shells of *Crepidula* Lamarck, 1799 are limpet-like, flat or cup shaped, with a coiled apex at the posterior end, the interior has a shellly platform which is attached to the shell by both sides and covers about half of the internal area (the posterior portion of the soft body), and they have no operculum (Abbott, 1974; Díaz and Puyana, 1994).

Calyptracids in the genus *Crepidula* are very common throughout the North and South American coasts both in the Pacific and the Atlantic. Abbott (1974) reported 13 species from North America, and Hoogland (1986) reported other additional six species. In the Caribbean, Díaz and Puyana (1994) and De Jong and Coumans (1988) reported 3 species from Colombia, the West Indies, Aruba, Curacao, and Bonaire; these are *Crepidula aculeata* Gmelin, 1791, *Crepidula cornexa* Say, 1822, and *Crepidula plana* Say, 1822. Warmke and Abbott (1961) reported three other species for the Caribbean, *Crepidula compta* Say, 1822, *Crepidula protea* d'Orbigny, 1843, and *Crepidula rissei* Dunker, 1877. The taxonomic allocation of species is difficult solely on the basis of conchological characters given the impressive plasticity that these shells have when growing on different substrates. Hoogland (1986) made an advance in the systematics of the genus through the study of egg capsules, larval development, electrophoresis, and anatomy. Collin (2000a) stated that the taxonomy of the species of *Crepidula* with pale, flattened, concave, or recurved shells is particularly difficult and uncertain; she separated the *Crepidula plana* complex from North America into three different species based on morphological, developmental, and molecular mitochondrial cytochrome oxidase I data.

Information regarding reproductive patterns of some species has proved to be very helpful in determining the
systematic placement of these species (Penchasazdeh, 1988). The major review of brood characteristics for Calyptraeidae included 19 Crepidula species (Hoagland, 1986), of which two species, C. plana Say, 1822 and C. convexa Say, 1822 had different data depending on geographic locality. In summary, as are all calyptraeids, Crepidula species are protandric hermaphrodites. They may have small or large lecithotrophic eggs, and as extra-embryonic food sources they may feed on nurse eggs or cannibalize sibling embryos. In consequence, developmental modes are variable and hatching can take place as planktotrophic veligers, pediveligers, or crawling juveniles. Cledón and Penchasazdeh (2001) described the reproduction of Crepidula argentina Simone, Pastorino, and Penchasazdeh, 2000, and also gave a review of some of the reproductive characteristics of South American Crepidula species. Other studies describing the reproductive biology of several Crepidula species are: Kundsen (1950), Bandel (1976), Stone Ament (1979), Chajaroro et al. (1999), Gallardo (1977, 1996) and Collin (2000a, b).

Herein, we describe the egg capsules, intracapsular development of the embryos, and hatching mode of two Crepidula species from Venezuela: C. navicula from Morrocoy National Park, which is located on the northwestern coast of Golfo Triste, and C. aphysiods from Isla de Margarita, an island located approximately 10 km north from the Araza Peninsula, at the northeastern coast of Venezuela. The relationship between female size and the number and size of egg capsules, size of the eggs, and size of hatching was also determined as well as the relationship between capsule size and the number of eggs, embryos, and hatchlings contained therein.

MATERIALS AND METHODS

Specimens

Crepidula navicula: specimens brooding egg capsules were collected in February 1995, September 1996, and February 2002 at Las Luisas, Morrocoy National Park, Falcón State (10°32’ N, 69°16’ W, Figure 1), at 0.2-1.0 m depth. The habitat consists of a turtle grass bed with some patches of sand and the calcareous alga Halimeda monile (Ellis and Solander) Lamour. The specimens were found attached to live Modulus modulus Linnaeus, 1758 (Figure 2), gastropods that were living on leaves of the turtle grass Thalassia testudinum Banks ex-König. The females (Figure 3) and egg capsules collected were observed live. To observe the embryos in the egg capsules during development, the female was carefully removed from the substrate and the underlying brood was observed under the stereoscopic microscope. After the observations, the female was reattached to its brood. This reattachment was usually successful, but when not, the embryos inside the egg capsules remained live for 8 days without the protection of the mother. In addition, we placed microscope slides inside the aquaria and some females spawned using these surfaces to attach their broods, allowing us to observe the egg capsules through the glass without removing the mother. Egg capsules at the different stages of development were fixed in a glutaraldehyde-acetate (GAA) buffer containing 4–6% formalin (Miloslovich and Penchasazdeh, 1997) for at least 24 hours and preserved in ethanol. The photographs were taken from live material. Voucher material consisting of the entire adult individuals preserved in ethanol was deposited in the Field Museum of Natural History, Chi-
Crepidula aspidoides: Brooding specimens were collected in February 2000 and October 2001 and 2002 at La Restinga Lagoon located between 64°2′ W and 64°12′ W, 10°00′ N and 11°2′ N. During the first field trip (February 2000), individuals were found attached to the mangrove oyster Crassostrea rhizophorae Guilding, 1828, that was attached to mangrove roots of Rhizophora mangle Linnaeus at a depth of 0.5–1.0 m. During the second field trip (October 2001), most of the animals had changed their substrate and were now attached to the invading mussel Perna viridis Linnaeus, 1758 (Figure 4) which had been previously reported in the Venezuelan Caribbean but not at this site (Penchaszadeh and Velez, 1995). The females (Figure 5) and egg capsules were observed live as previously described for C. maricula and posteriorly were fixed and preserved in ethanol. Voucher material consisting of the entire indi-

Figure 2-3. Crepidula maricula. 2. Ventral view of the gastropod host Modulus nodulosus with one individual of C. maricula attached. 3. Ventral and dorsal view of C. maricula. Scale bar = 10 mm.

Figure 4-5. Crepidula aspidoides. 4. Valve of host Perna viridis with one individual of C. aspidoides attached. 5. Ventral and dorsal view of C. aspidoides. Scale bar = 10 mm.

viduals preserved in ethanol was deposited in the Field Museum of Natural History, FMNH 293349 and at the Museum of Comparative Zoology, MCZ 304129.

Development

A total of 10 brooding females of C. maricula and 45 of C. aspidoides were collected. The following aspects of the spawn were studied: (1) number and size of egg capsules brooded per female, (2) number and size of eggs and developing embryos within the capsule, (3) observation of the different stages of development, and (4) hatching mode and size of hatching. We studied the relationship between female size and number and size of capsules, number and size of eggs, embryos and hatchlings per capsule as well as the relationship between capsule size and number and size of eggs and hatchlings per capsule using a Pearson product-moment correlation. Given that some samples may not be independent as they come from the same female, we calculated partial Pearson correlations using, when appli-
Table 1. Length, width and height of brooding females of Crepidula navicula and Crepidula aphylodes. Results are reported as mean ± SD. Numbers in parenthesis indicate range minimal and maximal values.

<table>
<thead>
<tr>
<th></th>
<th>Length (mm)</th>
<th>Width (mm)</th>
<th>Height (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>C. navicula</em></td>
<td>5.9 ± 0.6</td>
<td>4.2 ± 0.4</td>
<td>2.2 ± 0.3</td>
</tr>
<tr>
<td></td>
<td>(4.9-7.1)</td>
<td>(3.3-4.8)</td>
<td>(1.7-2.7)</td>
</tr>
<tr>
<td></td>
<td>n = 40</td>
<td>n = 40</td>
<td>n = 40</td>
</tr>
<tr>
<td><em>C. aphylodes</em></td>
<td>12.4 ± 0.2</td>
<td>8.8 ± 1.4</td>
<td>3.0 ± 0.7</td>
</tr>
<tr>
<td></td>
<td>(9.4-15.2)</td>
<td>(7.2-12.2)</td>
<td>(2.8-3.9)</td>
</tr>
<tr>
<td></td>
<td>n = 72</td>
<td>n = 72</td>
<td>n = 72</td>
</tr>
</tbody>
</table>

cable, the variables female volume, capsule area and number of capsules as controlling factors.

Given the growth particularities of the shells of Crepidula in relation to their substrate, instead of considering female size as shell length exclusively, we report female size as the volume of a half spheroid in which the volume is calculated by the following equation:

\[ V = \frac{4}{3} \pi r^2 \text{d} \]  

in which \( b = \) shell height, \( r1 = \) radius 1 (half shell length) and \( r2 = \) radius 2 (half shell width).

All observations of live and preserved material were carried out with a Zeiss stereoscopic microscope and Zeiss microscope; measurements were performed with an ocular micrometer.

Table 2. Statistic results of female size—spawn relationships for Crepidula navicula.

<table>
<thead>
<tr>
<th>Variables</th>
<th>r correlation</th>
<th>P (**)</th>
<th>n</th>
<th>Controlled by (***):</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female volume—number of capsules</td>
<td>0.130</td>
<td>0.364</td>
<td>10</td>
<td>None</td>
</tr>
<tr>
<td>Female volume—capsule area</td>
<td>0.306</td>
<td>0.004</td>
<td>137</td>
<td>Number of capsules</td>
</tr>
<tr>
<td>Female volume—number of eggs per capsule</td>
<td>0.190</td>
<td>0.144</td>
<td>18</td>
<td>Capsule area</td>
</tr>
<tr>
<td>Female volume—number of embryos per capsule</td>
<td>0.009</td>
<td>0.912</td>
<td>137</td>
<td>Capsule area</td>
</tr>
<tr>
<td>Female volume—number of hatchlings per capsule</td>
<td>0.054</td>
<td>0.826</td>
<td>22</td>
<td>Capsule area</td>
</tr>
<tr>
<td>Female volume—egg size</td>
<td>0.02</td>
<td>0.999</td>
<td>75</td>
<td>Number of capsules</td>
</tr>
<tr>
<td>Female volume—hatching size</td>
<td>0.248</td>
<td>0.058</td>
<td>61</td>
<td>Number of capsules</td>
</tr>
<tr>
<td>Capsule area—number of eggs per capsule</td>
<td>0.0635</td>
<td>0.004</td>
<td>18</td>
<td>Capsule area</td>
</tr>
<tr>
<td>Capsule area—number of embryos per capsule</td>
<td>0.577</td>
<td>0.004</td>
<td>137</td>
<td>Female volume</td>
</tr>
<tr>
<td>Capsule area—number of hatchlings per capsule</td>
<td>0.652</td>
<td>0.004</td>
<td>22</td>
<td>Female volume</td>
</tr>
<tr>
<td>Capsule area—egg size</td>
<td>0.131</td>
<td>0.268</td>
<td>75</td>
<td>Female volume</td>
</tr>
<tr>
<td>Capsule area—hatching size</td>
<td>0.245</td>
<td>0.054</td>
<td>61</td>
<td>Female volume</td>
</tr>
<tr>
<td>Number of capsules—hatching size</td>
<td>0.059</td>
<td>0.004</td>
<td>61</td>
<td>Number of capsules</td>
</tr>
<tr>
<td>Number of hatchling per capsule—hatching size</td>
<td>0.135</td>
<td>0.004</td>
<td>61</td>
<td>Number of capsules</td>
</tr>
</tbody>
</table>

* Pearson product—moment correlation  
** Partial Pearson correlation using as controlling factors the variable(s) which showed a significant correlation and controlling by female volume.

RESULTS

Sexual Maturity and Female Size—Spawn Relationships

The shells of brooding females of *C. navicula* measured 1.9-7.4 mm length, 3.3-4.8 mm width, and 1.7-2.7 mm height (Table 1). The female genital papilla was observed in individuals larger than 3.5 mm shell length, while males (with presence of a penis) measured up to 5 mm shell length. Female volume of *C. navicula* was significantly correlated with capsule area (Pearson product moment correlation: \( p < 0.001 \)). No correlation was observed between female volume and the other reproductive parameters. However, a relatively good correlation was found with hatching size (\( p = 0.058 \)). Capsule area was correlated to number of eggs (\( p = 0.004 \)), number of developing embryos (\( p < 0.001 \)) and number of hatchlings per capsule (\( p = 0.001 \); Table 2, Figure 6).

The shells of brooding females of *C. aphylodes* measured 9.1-15.2 mm length, 7.1-12.2 mm width and 2.8-3.9 mm height (Table 1). The female genital papilla was observed in individuals larger than 7.5 mm shell length, while males (with presence of a penis) measured up to 11 mm shell length. In this latter species we observed a significant relationship between female volume and number of capsules (\( p = 0.002 \)), number of eggs per capsule (\( p < 0.001 \)), number of embryos per capsule (\( p < 0.001 \)) and number of hatchlings per capsule (\( p < 0.001 \)). No relationship was observed between female volume and hatching size (\( p = 0.100 \)).
size and hatching size. Capsule area was correlated to number of developing embryos \((p < 0.001)\) and number of hatchlings per capsule \((p < 0.001)\). (Table 3, Figures 7, 8).

**DEVELOPMENT**

*Crepitula navicula*: The females brooded 5–15 egg capsules in the mantle cavity. The egg capsules measured 0.8–1.6 mm width and 0.5–1.3 mm length (from the base of the capsule to the tip), the stalk is thread-like and measures 1.0–1.2 mm length (Table 4).

The number of eggs per capsule varied from 1 to 6 (mean = 3 ± 1, \(n = 157\)). The nucleated eggs were yellow and measured approximately 330 μm in diameter (Figure 9, Table 3). All the eggs developed, gastrulation is by epiboly as the micromeres at the animal pole divide.

**Table 3.** Statistic results of female size–spawn relationships for *Crepitula aphysoides*.

<table>
<thead>
<tr>
<th>Variables</th>
<th>( r ) correlation</th>
<th>( P ) (#)</th>
<th>( n )</th>
<th>Controlled by ¹²³</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female volume—number of capsules</td>
<td>0.4767</td>
<td>0.002</td>
<td>38</td>
<td>None</td>
</tr>
<tr>
<td>Female volume—capsule area</td>
<td>0.2305</td>
<td>0.153</td>
<td>38</td>
<td>Number of capsules</td>
</tr>
<tr>
<td>Female volume—number of eggs per capsule</td>
<td>0.1911</td>
<td>&lt;0.001</td>
<td>37</td>
<td>Capsule area</td>
</tr>
<tr>
<td>Female volume—number of embryos per capsule</td>
<td>0.728</td>
<td>&lt;0.001</td>
<td>70</td>
<td>Number of capsules</td>
</tr>
<tr>
<td>Female volume—number of hatchlings per capsule</td>
<td>0.5705</td>
<td>&lt;0.001</td>
<td>45</td>
<td>Capsule area</td>
</tr>
<tr>
<td>Female volume—egg size</td>
<td>0.0003</td>
<td>0.986</td>
<td>269</td>
<td>Capsule area</td>
</tr>
<tr>
<td>Female volume—hatching size</td>
<td>0.078</td>
<td>0.262</td>
<td>210</td>
<td>Capsule area</td>
</tr>
<tr>
<td>Capsule area—number of eggs per capsule</td>
<td>0.1408</td>
<td>0.021</td>
<td>269</td>
<td>Female volume</td>
</tr>
<tr>
<td>Capsule area—number of embryos per capsule</td>
<td>0.408</td>
<td>&lt;0.0001</td>
<td>315</td>
<td>Female volume</td>
</tr>
<tr>
<td>Capsule area—number of hatchlings per capsule</td>
<td>0.2858</td>
<td>0.0001</td>
<td>210</td>
<td>Female volume</td>
</tr>
<tr>
<td>Capsule area—egg size</td>
<td>0.0185</td>
<td>0.763</td>
<td>277</td>
<td>Female volume</td>
</tr>
<tr>
<td>Capsule area—hatching size</td>
<td>0.1067</td>
<td>0.124</td>
<td>210</td>
<td>Female volume</td>
</tr>
<tr>
<td>Number of capsules—hatching size</td>
<td>0.245</td>
<td>0.725</td>
<td>210</td>
<td>Female volume</td>
</tr>
<tr>
<td>Number of hatchlings per capsule—hatching size</td>
<td>0.1743</td>
<td>0.012</td>
<td>210</td>
<td>Female volume</td>
</tr>
</tbody>
</table>

¹ Pearson product–moment correlation
² Partial Pearson correlation using as controlling factor \( x \) the variables which showed a significant correlation and controlling by female volume.
and overgrow the macromeres at the vegetal pole (Figure 10). The gastrula measured around 350 \(\mu m\) in diameter (Figure 11) and the trophophore (Figure 12) measured around 370 \(\mu m\) including the small velar lobes. The early veliger measured around 430 \(\mu m\) (Figure 13), it had eyes and a small yelum. The veliger (III) stage measured around 160 \(\mu m\) (Figure 14), it was characterized by a round biliated yelum, small cephalic tentacles and the organic matrix of the shell. The foot develops and the intracapsular pediveliger stage (Figure 15) was characterized by a reduced yelum, short and thick cephalic tentacles; the shell of this pediveliger measured around 560 \(\mu m\) and was starting to calcify. Prior to hatching, the soft body showed brown pigmentation and a calcified shell measuring around 580 \(\mu m\) in length (Figure 16). At hatching, the shell measured around 900 \(\mu m\), the hatching was characterized by a small round yelum and a large foot (Figure 17). An interesting observation was the fact that the pediveligers hatched from the egg capsules but remained inside the brooding chamber of the mother for a few days, protected by its mantle cavity and shell (Figure 18). When the pediveligers crawled out of this brooding chamber, their shell had a minimum size of 1000 \(\mu m\) and the yelum had resorbed completely (Tables 5 and 6). The number of hatchlings was significantly lower (by one individual) than the number of eggs (t-test, \(p < 0.001\)). This difference is attributable to cannibalism, which we observed among sibling embryos in a few egg capsules, usually larger embryos feeding on a smaller one.

**Crepidula aphysonides**: Each female broods between 11 and 40 egg capsules (mean = 23.4 \(\pm\) 4.5, \(n = 45\), Figure 19). The egg capsules had a triangular shape, with one corner extending to form a stalk by which all the egg capsules were attached to the substrate at a common point. The capsule walls were thin and transparent. Egg capsules measured 0.5–2.1 mm length (excluding the stalk), 0.7–2.5 mm width and the thread-like stalk measured 0.6–3.3 mm length (Table 1). The number of eggs per capsule varied from 3 to 15. The uncleaved egg measured about 300 \(\mu m\) (Figure 20) and all eggs underwent normal cleavage and developed (Figures 21–24). Development was very similar to *C. naucila*: the gastrula measured around 350 \(\mu m\) diameter (Figure 25). The ciliated trophophore (Figure 26) was very active inside the egg capsule, rotating and moving constantly. These embryos were yellow, measured about 184 \(\mu m\), and had the organic matrix of the shell and eyes. No significant differences were observed between the number of eggs and the number of embryos at this stage (\(p = 0.1472\)) and nurse eggs were not observed. During development, a small round yelum develops (Figures 27–30). Hatching occurs as crawling pediveligers measuring about 600 \(\mu m\) in shell length (Figure 31). These pediveligers had the ability to swim very close to the substrate and when in contact with any surface, they crawled. The number of hatchlings was significantly lower (by one individual) than the number of eggs (t-test, \(p = 0.01597\)). This difference would be due to cannibalism, a phenomenon we observed among sibling embryos in one egg capsule, in which one embryo suddenly lost all its yolk content to the egg capsule and the rest of the embryos started feeding on it immediately. The emptied embryo survived for a few days and then died (Figures 32, 33). We measured the embryonic shell of 12 adult individuals and found that it measured 590 \(\pm\) 39 \(\mu m\) in length which did not differ significantly from the size of the shell at hatching.

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**Table 1**: Egg capsule dimensions of *Crepidula naucila* and *Crepidula aphysonida*. Values represent mean \(\pm\) SD, numbers in parentheses indicate range.

<table>
<thead>
<tr>
<th>Species</th>
<th>Egg capsule shape</th>
<th>Width A</th>
<th>Length B</th>
<th>Stalk C</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Crepidula aphysonida</em></td>
<td><img src="https://example.com/diagram.png" alt="Diagram" /></td>
<td>1.14 (\pm) 0.36</td>
<td>1.12 (\pm) 0.26</td>
<td>1.14 (\pm) 0.54</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.65–2.73</td>
<td>0.50–2.15</td>
<td>0.60–3.32</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(n = 157)</td>
<td>(n = 187)</td>
<td>(n = 176)</td>
</tr>
</tbody>
</table>

| *Crepidula naucila* | ![Diagram](https://example.com/diagram.png) | 1.2 \(\pm\) 0.2 | 0.9 \(\pm\) 0.1 | 10–1.2 |
|                    |                   | 0.8–1.6 | 0.50–1.3 | \(n = 153\) |
|                    |                   | \(n = 153\) | \(n = 153\) | |
DISCUSSION

SIZE AT SEXUAL MATURITY

In these protandric species, the overlap between male and female size is common (Collin, 1995). In nature, the transition from male to female may depend on the availability of a mate and on the relationship between body size and the reproductive demands of each sex. In this study, we observed the genital papilla in specimens of C. aphysoides larger than 7.5 mm in shell length. From the total number of females, only 62.5% of them were brooding egg capsules, this is comparable to results obtained by Collin (2000b) in two Crepidula species from the coast of San Juan Island, Washington State (Pacific coast of North America). The first is Crepidula adunca Sowerby, 1825, which broods throughout the year, with a maximum proportion of 66% brooding females between January and February, and the second is Crepidula lingulata, which reproduces in the summer with a
Table 5. *Crepidula natricula* and *Crepidula aplanthes*. Characteristics of embryos during intracapsular development. Values represent mean $\pm$ SD, numbers in parenthesis indicate range.

<table>
<thead>
<tr>
<th>Stage</th>
<th>Characteristics</th>
<th><em>C. natricula</em> size of embryos (um)</th>
<th><em>C. aplanthes</em> size of embryos (um)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Egg</td>
<td>Unleaved yellow egg</td>
<td>329 $\pm$ 28</td>
<td>317 $\pm$ 59</td>
</tr>
<tr>
<td>Gastrula</td>
<td>Yellow embryos, round with flattened edge at the site of the velar lobes (not developed). Movement</td>
<td>349 $\pm$ 29</td>
<td>350 $\pm$ 19</td>
</tr>
<tr>
<td>Trochophore (preveliger embryo)</td>
<td>Development of small, ciliated velar lobes, rotates around itself</td>
<td>369 $\pm$ 32</td>
<td>352 $\pm$ 33</td>
</tr>
<tr>
<td>Veliger (I)</td>
<td>Eyes, growth of velum</td>
<td>434 $\pm$ 15</td>
<td>No measures</td>
</tr>
<tr>
<td>Veliger (II)</td>
<td>Organic matrix of shell, velum, very small cephalic tentacles, the foot begins to differentiate</td>
<td>460 $\pm$ 41</td>
<td>447 $\pm$ 19</td>
</tr>
<tr>
<td>Veliger (III)</td>
<td>Development of foot begins, non calcified shell, larger velum</td>
<td>446 $\pm$ 56</td>
<td>424 $\pm$ 22</td>
</tr>
<tr>
<td>Pediveliger</td>
<td>Calcification of shell, small foot and short cephalic tentacles, reduction of velum</td>
<td>561 $\pm$ 98</td>
<td>No measures</td>
</tr>
<tr>
<td>Prehatching</td>
<td>Bilobed and round velum, well developed foot, calcified yellow shell, purple-brown pigmentation of foot and mantle</td>
<td>590 $\pm$ 76</td>
<td>450 $\pm$ 38</td>
</tr>
<tr>
<td>Hatching</td>
<td>Similar to prehatching but larger and stronger shell. Operculum was not observed in any stage.</td>
<td>814 $\pm$ 140</td>
<td>619 $\pm$ 95</td>
</tr>
</tbody>
</table>

Table 6. Summary of the reproductive characteristics of *Crepidula natricula* and *Crepidula aplanthes*. Values represent mean $\pm$ SD, numbers in parenthesis indicate range.

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of capsules per female</th>
<th>Capsule length mm $^1$</th>
<th>Eggs per capsule</th>
<th>Hatchlings per capsule</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Crepidula natricula</em></td>
<td>8.5 $\pm$ 2.2</td>
<td>0.92 $\pm$ 0.15</td>
<td>3.9 $\pm$ 1.0</td>
<td>2.8 $\pm$ 0.8</td>
</tr>
<tr>
<td></td>
<td>5-15</td>
<td>0.52-0.13</td>
<td>(3-5)</td>
<td>(1-4)</td>
</tr>
<tr>
<td></td>
<td>n = 40</td>
<td>n = 153</td>
<td>n = 18</td>
<td>n = 22</td>
</tr>
<tr>
<td><em>Crepidula aplanthes</em></td>
<td>23.4 $\pm$ 4.5</td>
<td>1.1 $\pm$ 0.3</td>
<td>7.6 $\pm$ 2.5</td>
<td>6.5 $\pm$ 2.1</td>
</tr>
<tr>
<td></td>
<td>11-40</td>
<td>0.5-2.1</td>
<td>(3-5)</td>
<td>(3-13)</td>
</tr>
<tr>
<td></td>
<td>n = 45</td>
<td>n = 157</td>
<td>n = 58</td>
<td>n = 48</td>
</tr>
</tbody>
</table>
maximum proportion of 61-62% brooding females between June and August.

**FEMALE SHELL LENGTH AND Spawn Relationships**

A correlation between female size and egg capsules per brood is a common feature of calyptraeid species (e.g. Hoagland, 1986; Chaparro et al., 1999; Collin, 2000b). However, our results confirmed this hypothesis to be true only for *C. aphysoidea*. Chaparro et al. (1999) reported that in *C. dilatata* Lamarck, 1822, egg capsule size (height and width), the weight of the capsule wall, and the number of eggs per capsule increased with shell length in females; however, the number of embryos per capsule, egg diameter, and number of capsules per brood were independent of female shell length. In this work we found that female size is an important parameter related to fecundity in *C. aphysoidea*, since it is associated with number of eggs, number of embryos, and number of hatchlings. In *C. navicula*, the same parameter affects capsule size. What seems to be consistently important for both species is the fact that the number of eggs, embryos, and hatchlings contained in each capsule is dependent on capsule size, probably due to space limitations, so if capsule size is limited by female size as is the case of *C. navicula*, the final result is that smaller females are less fecund than larger ones in juvenile production. In the case of *C. aphysoidea*, a difference in size of 5 mm in shell length (around 500 mm in volume) is very significant in terms of juvenile production. A small female produces few capsules with few hatchlings (around 75 hatchlings per female), while a large female produces many capsules with many hatchlings (more than 100 hatchlings). The term “female size” as used in this study involves not only shell length but also shell height and width; this is particularly necessary for *Crepidula* species since they grow on limited-size substrates such as the shell of other small gastropods. In the case of *C. navicula*, we observed small individuals attached to the gastropods *Tritia texellata* Putzev and Michaud, 1958, which is a very small species, and to *Cerithium euclarium* Bruguière, 1792, which has a very irregular surface. These two gastropods inhabit the sand under and around turtle grass, while the main host *M. nodulosa* is epifaunal on the blades of that seagrass. It is possible that some hatchlings fall from the host shell to the bottom where they would actively seek a host shell. Putnam (1964) reported the relationship between *C. adunca* Sowerby, 1825, and its host, the gastropod *Trigula fragilis* A. Adams, 1854. In this species, hatching occurs as crawling juveniles and less than 10% of the brood remain on the parental host, becoming quiescent sooner than those that fall off, which in turn are quite active.

**Development**

*Crepidula* species are usually very productive with respect to the number of capsules brooded by each female. The lowest value reported by Hoagland (1986) was for *C. adunca* and *C. aphysoidea* that brood between 6-12 and 8-14 egg capsules respectively, while the highest value was for *C. fecunda* and *C. formicida* that brood up to 75 egg capsules, a difference that is most likely due to species size. In terms of number of egg capsules brooded per female, we observed a significant trend within the genus *Crepidula*, for smaller species brooding less capsules than larger ones (Pearson correlation: r = 0.510, p = 0.01, n = 22, Figure 34). *Crepidula navicula* broods 5-15 egg capsules, which is lower than the previous report for *C. navicula* (10-20 egg capsules per brood). This value, however, is similar to the fecundity of *C. cf. convexa* from Panama, which broods 7-16 capsules per female (Hoagland, 1986). In the present study, the two species are very similar both morphologically and regarding development. The females of *C. aphysoidea* are larger and produce more egg capsules with more eggs than females of *C. navicula* which, on the other hand, produce larger eggs and larger hatchlings. This coincides with the observations by Hoagland (1986) on calyptraeids: smaller species tend to have larger, fewer, yolkier eggs and fewer egg capsules than larger species.

Development in both species was synchronous: all embryos within one brood were at the same stage of development and hatched at the same time. This is common among other calyptraeids, in several *Crepidula* species (Hoagland, 1986), and in *Cerithium turbinatum* Gmelin, 1791 (Miloslavich and Penchaasand, 2001). However, Putnam (1964) reported that not all egg capsules under a given female of *C. adunca* are necessarily at the same stage of development or hatch at the same time. Adelphophagy or nurse egg ingestion has been reported in at least 7 *Crepidula* species and cannibalism of damaged or abnormal embryos is widespread in the genus (Hoagland, 1986). In our two *Crepidula* species,

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**Figure 19.** Ventrail view of female of *Crepidula aphysoidea* with brood.
nurse eggs were not observed and cannibalism of one or two embryos was observed in few egg capsules. The egg and hatching production of both species is very variable (Table 6). For *C. navicula*, the lowest egg production was 15 eggs per female and the highest 90 (average 33 eggs per female), while the lowest production of hatchlings was 10 per female and the higher was 60 (average 25 hatchlings per female). For *C. aphysoioides*, the production per female is in average 5-6 times greater in comparison to *C. navicula*: in this species, the lowest egg production was 33 eggs per female and the highest 720 (average 166 eggs per female), while the lowest production of hatchlings was 33 per female and the higher was 520 (average 152 hatchlings per female).

The size of the uncleaved egg of *C. navicula* and *C. aphysoioides* is within the size range of other *Crepidula* species, 150–420 μm (Hoagland, 1986). In these two species, egg size is particularly important because yolk would be almost the only food source available for the embryo during intracapsular development, given the absence of nurse eggs and limited cannibalism. Development of *C. navicula* and *C. aphysoioides* is synchronous within and among egg capsules of a single female; however, they reach variable sizes (Table 5) probably depending on the yolk reserves of the egg (which also has variable sizes) (Table 5). Hoagland (1986) reported that for most calyptraeids, larvae develop synchronously, except for those with nurse eggs.

About half of the *Crepidula* species reported by Hoagland (1986) hatch as free-swimming veligers and the other half hatch as crawling juveniles. Of these, most of the tropical Caribbean and Gulf of Mexico species have direct development and lack a free-swimming stage: *C. aculeata*, *C. convexa*, *C. navicula*, and *C. plana* from Florida (Hoagland, 1986) and *C. porcellana* from tropical west Africa (Kamdem, 1950). *C. navicula* from the Bahamas also hatches as a crawling juvenile (Hoagland, 1986). In this paper, the two species hatched as crawling pediveligers with a very limited swimming capability and remain very close to the substrate. This reproductive pattern for tropical calyptraeids would be another exception to “Thorson’s rule” (Thorson, 1946, 1950) that proposes that species with planktonic larvae are predominant in tropical marine environments (see review by Gallardo and Penczak, 2001).

ACKNOWLEDGMENTS

Many people helped in the field and in the laboratory work required to complete this research; we thank them all: Ana Karina Carbonini, Elizabeth Huck, Oliver Corn.
REFERENCES: Blanca Cheletti, Eduardo Losada, Marta Kurek. We also thank Dr. Sheila Marques Podes for the diagram of the species shape and very specially to José Luis Garcia Rondón. Artis Publishers and Ana Karima Carno- 


tin' Tlic for their invaluable help with the photographs. We are also indebted to Dr. Rachel Collin, Smithsonian Tropical Research Institution (STRI) Panama and Dr. Juan Manuel Díaz, Instituto de Investigaciones Marinas y Costeras José Benito Vives de Andrés (INVERMAR, Colommbia) for their help in the identification of the species. This work was partially supported by a Decameto de Investigación y Desarrollo, Universidad Simón Bolívar grant to the Group in Marine Sciences and a Fonacit grant (81-2001-000764) to Patricia Miloslavich.

LITERATURE CITED


NEW TAXA PROPOSED IN VOLUME 117 (2003)

GASTROPODA

Amalda josewateri Pastorino, 2003, new species (Olividae) ................................................... 16
Horridatus syrioii Smirglio and Mariottini, 2003, new species (Drilliidae) ............................... 55
Micraea termergii Nielsen and Frassinetti, 2003, new species (Pseudolividae) ....................... 91
Metalula Metalula miocenica Schmelz and Portell, 2003, new species (Calabridiidae) .............. 12
Neolepton georgianum Zelaya and Huarte, 2003, new species (Neoleptonidae) ...................... 8
Neolepton holmbergii Zelaya and Huarte, 2003, new species (Neoleptonidae) ....................... 10
Pseudococclina rumpei Simone and Magenta, 2003, new species (Pseudolividae) .................. 70
Scabrotriton inspiraturn Huart, 2003, new species (Mariscidae) ........................................... 57
Triumphus maartenholensis Nielsen and Frassinetti, 2003, new species (Pseudolividae) ........ 95

BIVALVIA

Bathymodiolus tangara von Cosel and Marshall, 2003, new species (Mytilidae) ......................... 31
Carditella galapagana Coan, 2003, new species (Conchocardiidae) ....................................... 57
Carditella marieta Coan, 2003, new species (Conchocardiidae) ............................................ 57
Conchocardiidae chungata Coan, 2003, new species (Conchocardiidae) ................................. 54
Conchocardiidae fernandina Coan, 2003, new species (Conchocardiidae) .............................. 53
Conchocardiidae gorgori Coan, 2003, new species (Conchocardiidae) ................................... 56
Conchocardiidae kaisera Coan, 2003, new species (Conchocardiidae) ................................... 54
Conchocardiidae koolae Coan, 2003, new species (Conchocardiidae) ................................... 53
Conchocardiidae sparsa Coan, 2003, new species (Conchocardiidae) .................................... 50
Gigantidus gladius von Cosel and Marshall, 2003, new species (Mytilidae) ................................ 38

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