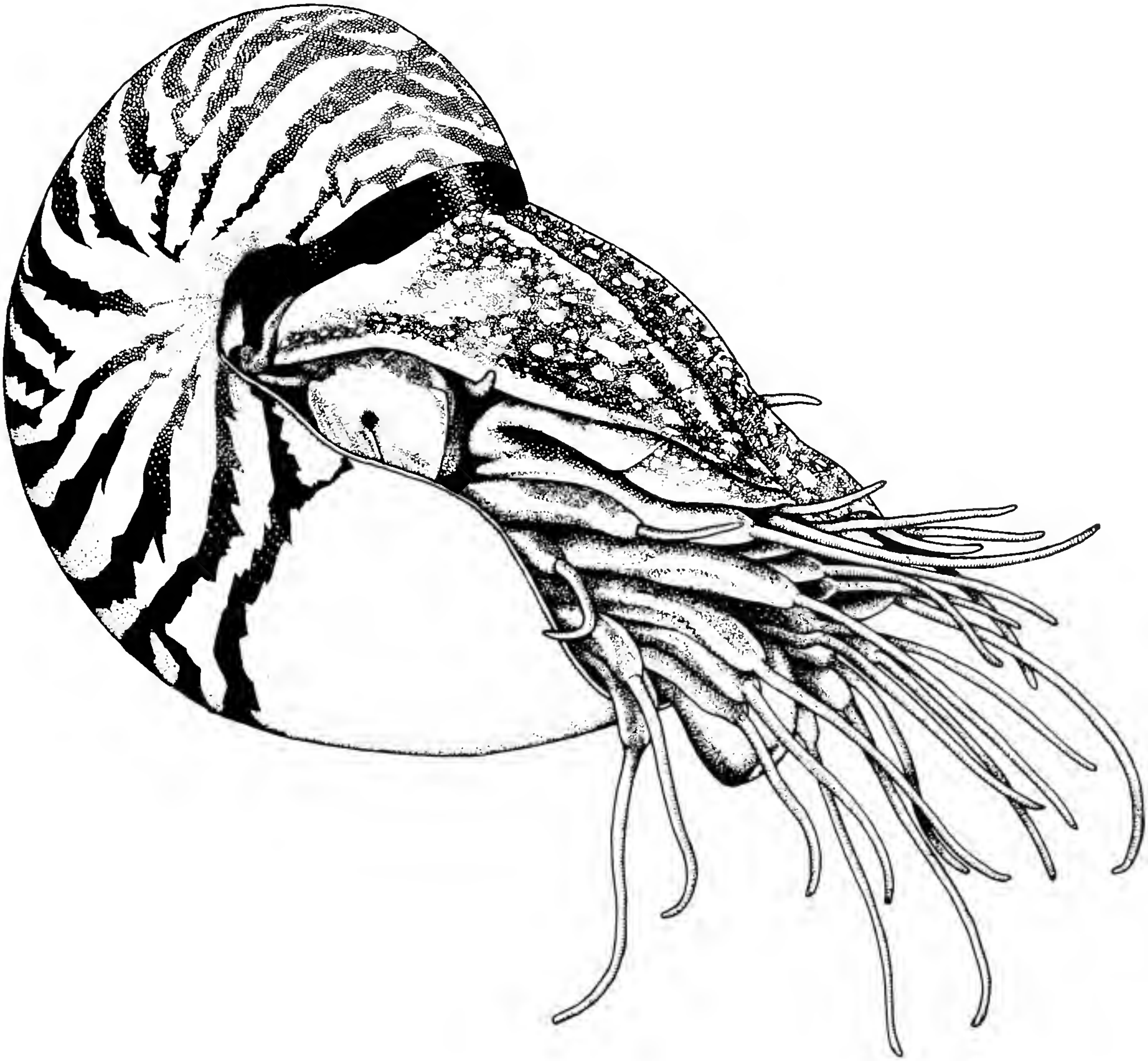
# THE NAUTILUS

Volume 104
1990



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# THE NAUTILUS

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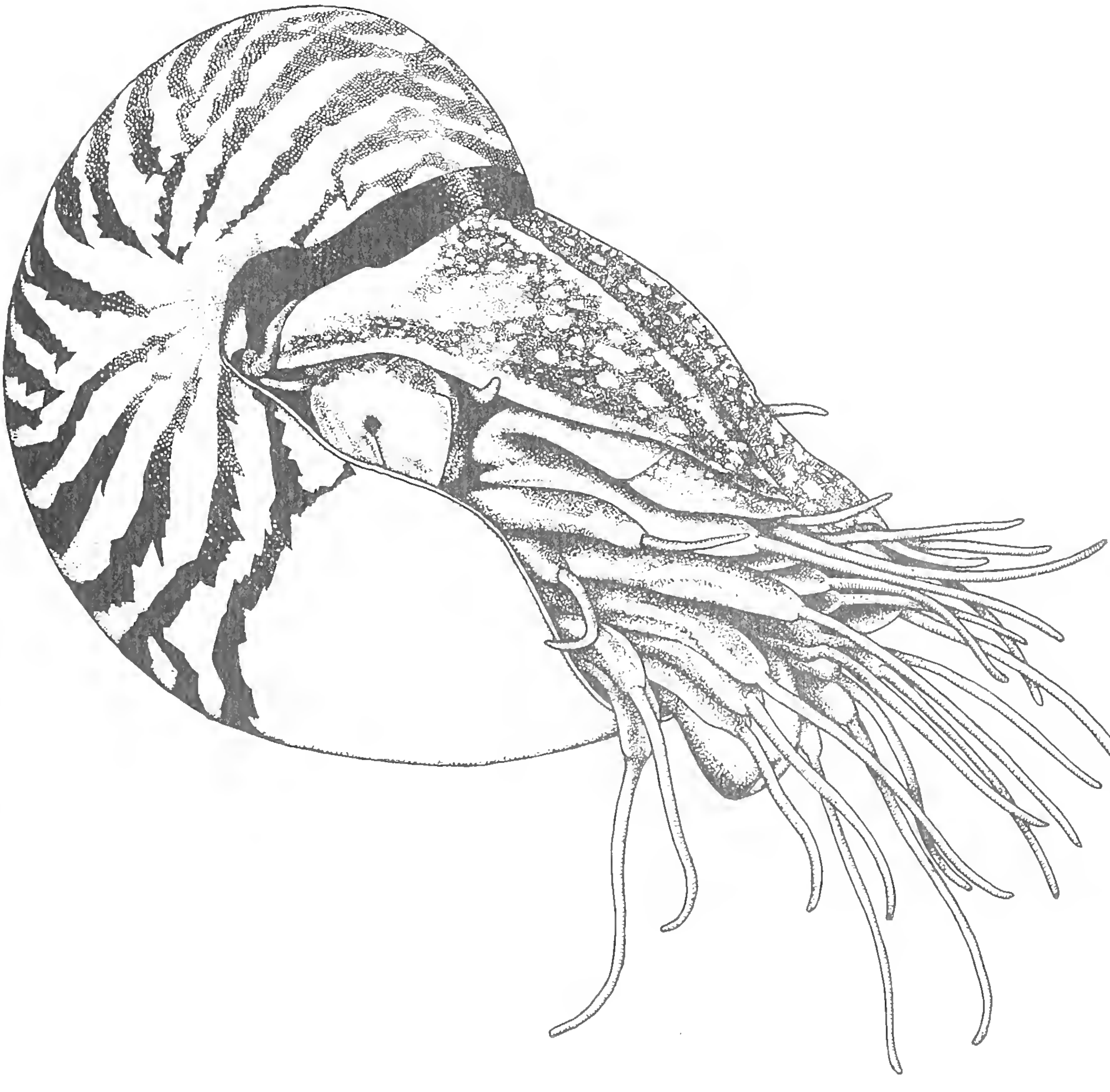

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# THE NAUTILUS

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# WESTERN SOCIETY OF MALACOLOGISTS
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# A New Species of *Latirus* from the Philippine Islands (Gastropoda: Fasciolariidae)

**William K. Emerson**
**Walter E. Sage, III**
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New York, NY 10024, USA

## ABSTRACT

*Latirus deynzerorum* new species is described from specimens obtained in tangle nets set off Bogo, NE Cebu Island, Philippine Islands and elsewhere in the central Philippine Archipelago.

## INTRODUCTION

During the past ten years many new species or otherwise significant specimens of marine mollusks have been collected by fishermen from tangle nets set in moderately deep water in the channels off the central Philippine Islands, mostly in the region of Cebu and Bohol. Specimens of the new species of *Latirus* described herein were obtained several years ago from these sources by Major Al Deynzer of Showcase Shells, Sanibel, Florida, who recently submitted the specimens for study. We take pleasure in describing this new taxon in honor of Bev and Al Deynzer, who, as avid students of mollusks, have generously shared their discoveries with us and others through the years.

## SYSTEMATIC ACCOUNT

Family Fasciolariidae Gray, 1847
Subfamily Peristerniinae Tryon, 1880
Genus *Latirus* Montfort, 1810

**Type species:** by monotypy, *Latirus aurantiacus* Montfort, 1810 [= *L. gibbulus* (Gmelin, 1791)], Recent, Indo-Pacific.

*Latirus deynzerorum* new species
(figures 1–3)
"*Latirus* sp." Springsteen, 1985:4, 7, fig. 4.

**Diagnosis:** A medium-size latirid, ornamented with prickled varices. Shell somewhat resembles *Latirus maculata* (Reeve, 1847: *Turbinella* species 70, pl. 13:70a, 70b) from the Indo-Pacific (Springsteen & Leobrera, 1986: 181, pl. 48:22). It differs from Reeve's taxon in having a larger, more angular shell, with a much longer and more recurved siphonal canal and by distinctive sculptural characters and color patterns. *Peristernia cremnochione* Melvill (1891:397, pl. 2:9), a smaller species attaining 24 mm in length, from Mauritius, more closely resembles this new taxon in the outline and color pattern of the shell. Melvill's taxon, however, lacks a siphonal fasciole, and has a short, straight siphonal canal, characteristic of *Peristernia*.

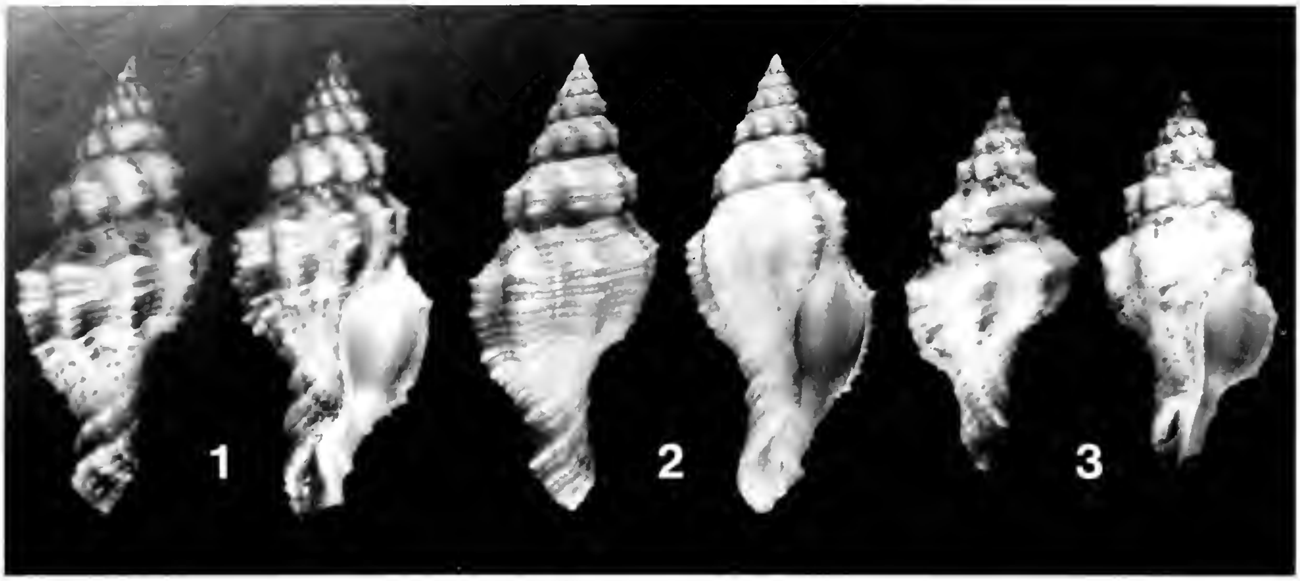
**Description:** Shell solid, fusiformly elongate, attaining 40+ mm in length, whorls angularly rounded, axially ribbed and crossed by conspicuous spiral lirae forming small prickle-like protusions medially on varices, siphonal canal narrowly elongated and recurved, outer lip thin, edge of labrum lirate.

Protoconch glossy, smooth, consisting of 1½ embryonic whorls; postnuclear whorls 6 to 6½ in number, with 8 to 9 widely spaced, rounded axial ribs, crossed by about 14 strong spiral cords on the body whorl posterior to the siphonal canal. Suture partially obscured by fluted axial riblets. Dorsal surface of siphonal canal with 2 prominent spiral ridges and numerous lesser intervening lirae. Aperture widely ovate, outer lip with weak lirations; columella smooth, with inner margin raised to form a thin detached edge anteriorly, extending to near the terminal end of the narrow, recurved siphonal canal; siphonal fasciole well-formed and strongly corded. For measurements, see table 1. Radula and soft parts not seen.

**Color:** Protoconch light tan; base color of shell orange buff, early whorls of spire grayish brown, subsequent whorls with broken bands of brown forming prominent blotches (figure 1); some specimens weakly blotched or entirely lacking blotches (figures 2, 3); fasciole stained dark brown above and within the groove; aperture pinkish white.

**Type locality:** Off Bogo, NE Cebu Island (11°03'N, 124°E), from tangle nets set in moderately deep water, May, 1981.

**Type depository:** Holotype AMNH 232138, 4 paratypes AMNH 232139; 2 paratypes in the Deynzer collection.



**Figures 1–3.** Type specimens of *Latirus deynzerorum* new species. **1.** Holotype AMNH 232138; **2, 3.** Paratypes AMNH 232139, × 1½.

**Range:** Known from the type locality in the central Philippine Islands; also off Panglao Island (9°35′N, 123°48′E), October, 1985, in "deep water," tangle nets, AMNH 239585 (2 specimens, ex-F. J. Springsteen coll.); and off Punta Engaño, Mactan Island, NE Cebu, in tangle nets (Springsteen, 1985:4).

**Remarks:** Our knowledge of the taxonomic relationships of the multitude of latirid-like species that are referable to Peristerniinae genus-group taxa has not progressed much since the appearance of the early reviews of Kiener (1840), Küster and Kobelt (1844–1876), Reeve (1847), Tryon (1880, 1881), Cossmann (1889) and Melvill (1891, 1911). At the present time (see Boss, 1982:1016, 1017; Vaught, 1989:50), most of these species are assigned to either the genus *Latirus sensu lato* (with several non-nominate subgenera), or to the genus *Peristernia* Mörch (1852:99), type species (by subsequent designation: Cossmann 1889:166), *Turbinella crenulata* Reeve (1847, pl. 4, fig. 24). Based on shell characters alone, however, generic placement of these species is largely arbitrary, without knowledge of the radular morphology. For example, the type of *Fusolatirus* Kuroda and Habe (1971: 182), *Fusolatirus pilsbryi* (Kuroda and Habe, 1971:183, pl. 50, figs. 1, 2), was described as having ". . . the shell of *Latirus*-form and the radula of *Peristernia*-formula." Therefore, the precise generic allocation of the new species described herein must remain provisional until the nature of the radula is known.

Table 1. *Latirus deynzerorum* new species. Shell measurements of specimens in mm and number of postnuclear whorls; widths measured including varices. n = 9. Specimens deposited in the AMNH collection unless otherwise stated

| | Length | Width | No. whorls |
|---|---|---|---|
| Holotype figure 1 | 39.6 | 17.3 | 6½ |
| Paratype figure 2 | 39.4 | 16.4 | 6½ |
| Paratype | 33.1 | 15.3 | 6 |
| Paratype | [illegible] | 15.7 | 6 |
| Paratype | 33.9 | 15.0 | 6 |
| Paratype | [illegible] | 14.4 | 6 |
| Paratype | [illegible] | 12.8 | 6 |
| Referred [illegible] | [illegible] | 16.1 | 6½ |
| AMNH 2[illegible] | [illegible] | 13.3 | 6 |

## ACKNOWLEDGEMENTS

In addition to Major Deynzer, we thank F. J. Springsteen for contributing comparative material. We also thank Andrew S. Modell and Stephanie Crooms of the American Museum of Natural History, respectively, for the photography and word-processing.

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# Growth Rates of the Asiatic Clam, *Corbicula fluminea,* in the Upper and Middle St. Johns River, Florida

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## ABSTRACT

Growth rates and population densities of *Corbicula fluminea* were studied over a two year period in the Upper and Middle St. Johns River, Florida. Measured growth rates were compared with published data from other systems, and factors influencing growth rates were identified. Growth rates of *C. fluminea* were affected by flow rate and sediment type, and ranged between 0.0043 and 0.0437 mm/day in this study. *Corbicula* were found to dominate the sandy sediment regions, usually characterized by higher flow rates, while unionid mussels inhabited the more flocculent organic sediments present in slower moving water. Of the 1,650 bivalves collected from dredge samples, 79.3% were *C. fluminea* and 20.7% were unionids. Unionid growth was adversely affected by the presence of *Corbicula*, as mussel growth rates decreased when numbers of *C. fluminea* increased.

## INTRODUCTION

*Corbicula fluminea* (Müller, 1774) has spread rapidly throughout the United States and has become a species new to many freshwater systems throughout the country (McMahon, 1982). It appears that the great success of *C. fluminea* is primarily due to its lack of predators, resistance to environmental stresses, tolerance of many substrates, high reproductive ability, rapid growth, and ability to filter large volumes of water (McMahon, 1977; Mattice, 1979; Graney *et al.*, 1980; Rodgers *et al.*, 1980; Gottfried & Osbourne, 1982). Population density and growth rate data from various aquatic systems have been well documented (Gardner *et al.*, 1976; O'Kane, 1976; [illegible] 1976; Britton *et al.*, 1979; Eng, 1979, Buttner & [illegible] 1980; Scott-Waslik *et al.*, 1983; Welch & Joy, [illegible]

[illegible] tebrate surveys noting the presence [illegible] were conducted in the Upper [illegible] and Belanger (1979), Buzzi [illegible] 1980) and Llibre (1982), little is [illegible] dynamics and growth rate [illegible] system. The purpose of this research was to determine population densities, distributions, and growth rates of *C. fluminea* in the Upper and Middle St. Johns River so that comparisons with other aquatic systems could be made and possible factors influencing growth rates could be identified. A secondary purpose was to investigate the effect of *C. fluminea* on the growth of indigenous unionid bivalves.

## STUDY AREA

The St. Johns River basin encompasses 18,290 sq. km and is one of the few large rivers in the world that flows from south to north. The river originates in the dense marshes of St. Lucie County and flows approximately 300 km north to the Atlantic Ocean, east of Jacksonville, Florida. The topography of the study region is relatively flat, resulting in a shallow river-lake system. This study considered the upper and middle sections, with sampling sites extending from Zig-Zag Canal, Brevard County, to Lake Monroe, Seminole County (figure 1).

## MATERIALS AND METHODS

Clams were collected at all sites from August 1983 through May 1984. Caged clams were maintained in the field during three separate periods, September 1983 to July 1984, August 1984 to February 1985, and February 1985 to July 1985. Each clam was measured to the nearest 0.05 mm for length (greatest anterior–posterior distance), width (greatest distance through the valves), and height (greatest dorso-ventral distance perpendicular to the the hinge line), using vernier calipers. Clams were measured before being placed in the cages and after retrieval. Cages were constructed from 19-liter plastic buckets and approximately 100 holes 1 cm in diameter were drilled in the sides of each container. The bottom of each cage was filled with acid-washed sand to a depth of 25 cm and the cage fitted with a locked lid. Ten (first and second study periods) to 15 clams (third study period) were placed in each cage. In addition, five cages were placed

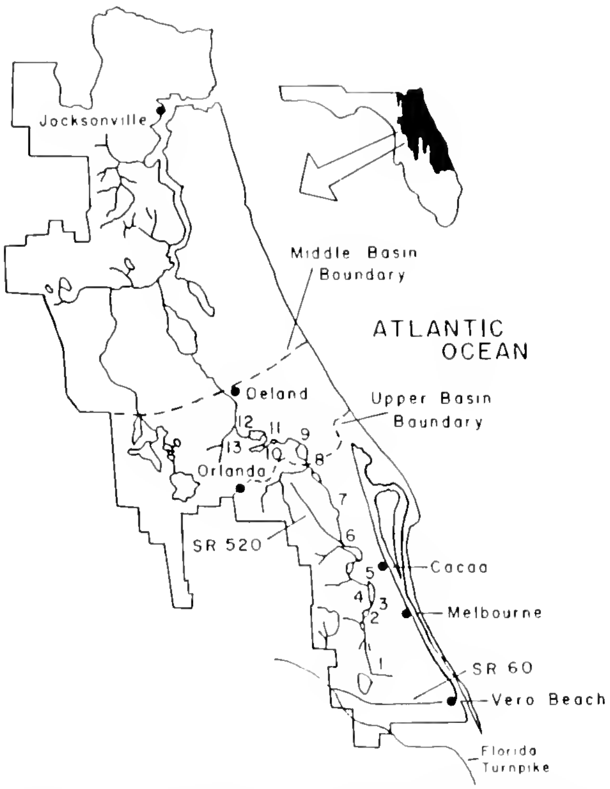

**Figure 1.** The St. Johns River basin with location of sampling sites. 1 = Zig-Zag Canal*; 2 = Lake Sawgrass Outlet; 3 = Camp Holly (Route 192)**; 4 = Lake Washington; 5 = Lake Washington Outlet**, 6 = Lake Poinsett Outlet; 7 = Route 50 Bridge; 8 = Lake Harney Inlet Bridge; 9 = Lake Harney Outlet, 10 = Lake Jessup Outlet, 11 = Lake Monroe Inlet*; 12 = Lake Monroe Outlet*; 13 = Lake Monroe Power Plant Outfall; * = sampling and cage site; ** = cage site only.

at the Lake Washington site to determine the effect of *Corbicula fluminea* populations upon the growth rates of unionid mussels. In this experiment, ten unionid mussels (*Elliptio* sp.) were placed in each cage together with *C. fluminea* in densities equivalent to 500, 1,000, 2,000 or 3,000 clams/m². After five months, the unionid mussels were retrieved and measured to determine growth rates. Water quality parameters (depth, dissolved oxygen [D.O.], water temperature, flow rate, pH, and percent sediment volatile solids) were measured routinely (at least bimonthly) using standard techniques (A.P.H.A., 1980). The mean values for these parameters at the sites are presented in table 1.

## RESULTS AND DISCUSSION

### POPULATION DENSITY AND DISTRIBUTION

**Table 1.** Mean physical and chemical data from routine sampling at selected sites in the Upper and Middle St Johns River. Data were collected at least bimonthly from August 1983 through May 1984

| Site | Depth (m) | D.O.* (mg/l) | Temp.* (°C) | Flow rate* (ft/sec) | pH | Sediment vol. solids (%) |
|---|---|---|---|---|---|---|
| 1 | 2.9 | 3.0 | 20.0 | 0.09 | 6.69 | 13.72 |
| 2 | 2.0 | 4.7 | 21.0 | 0.20 | 7.19 | 18.20 |
| 4 | 1.5 | 5.6 | 23.0 | 0.01 | 7.70 | 3.34 |
| 6 | 2.5 | 6.1 | 22.0 | 0.30 | 7.42 | 2.00 |
| 7 | 3.4 | 4.9 | 22.0 | 0.19 | 7.04 | 4.73 |
| 8 | 2.6 | 5.3 | 20.7 | 0.47 | 7.24 | 2.13 |
| 9 | 2.7 | 8.0 | 19.5 | 0.29 | 7.71 | 7.35 |
| 10 | 2.4 | 8.2 | 20.4 | 0.20 | 8.74 | 3.70 |
| 11 | 4.3 | 5.7 | 23.2 | 0.39 | 7.88 | 4.74 |
| 12 | 4.4 | 5.8 | 24.3 | 0.16 | 8.23 | 11.42 |
| 13 | 4.6 | 5.5 | 20.9 | 0.17 | 8.30 | 3.14 |

* Measured near sediment-water column interface

Population densities of *Corbicula fluminea* varied widely along the St. Johns River system. Of the 11 sites sampled, only one site (Site 12) was completely devoid of clams. With the exception of the Lake Jessup site (Site 10), clams were found in densities greater than 100/m² at least once during the nine sampling events. Four sites contained densities greater than 1,000/m², with Lake Harney Inlet (Site 8) exhibiting the maximum density of 2,700 individuals/m² in November, 1984. Table 2 lists the population densities of *C. fluminea* recorded throughout the study. Only juveniles were found in Zig-Zag Canal (Site 1), where they did not become established.

When only adult populations are considered, some generalities may be drawn from the data. *Corbicula fluminea* were most abundant in sandy sediment with low organic content, such as the Lake Harney Inlet site (Site 8), where the highest mean monthly density of 839 clams/m² was recorded. Sandy substrates were favorable for *C. fluminea* growth from Lake Washington (Site 4) downstream to the Lake Harney Inlet (Site 8), and clams from

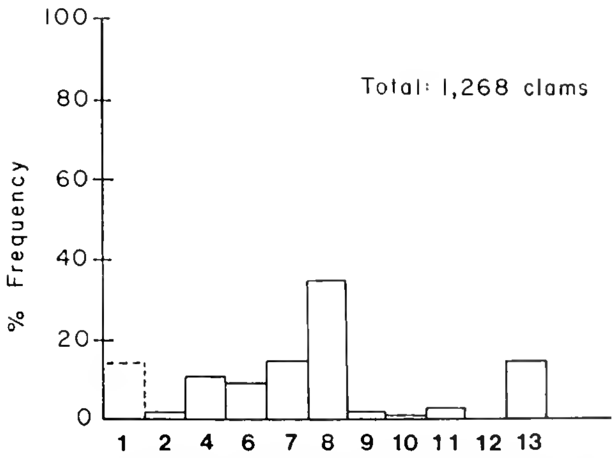

**Figure 2.** *Corbicula fluminea* population distributions, at the Upper and Middle St. Johns River sampling sites, 1983–84 (% frequency = *Corbicula* percentage of total collected invertebrates at each site; dotted line = only juvenile clams)

Table 2. *Corbicula fluminea* population densities (no./m²), from sampling sites in the Upper and Middle St. Johns River (August 1983–May 1984).

| | 1983 | | | | 1984 | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Site | Aug | Sep | Oct | Nov | Jan | Feb | Mar | Apr | May | Mean | SD |
| 1 | — | — | *1,417 | *233 | *250 | — | — | — | — | *211 | 464 |
| 2 | — | — | 33 | — | 150 | — | — | — | — | 20 | 50 |
| 4 | 600 | 567 | 217 | 117 | 217 | 17 | 67 | 433 | 17 | 250 | 229 |
| 6 | 183 | 67 | 33 | 117 | 700 | 383 | 583 | — | — | 230 | 263 |
| 7 | 200 | 283 | 117 | 117 | 433 | 517 | 1,033 | 183 | 217 | 344 | 292 |
| 8 | — | — | 2,217 | 2,700 | 233 | 17 | 2,217 | 167 | — | 839 | 1,166 |
| 9 | — | — | — | — | — | 17 | 17 | — | 100 | 15 | 33 |
| 10 | — | 33 | — | 17 | 17 | — | — | — | — | 7 | 12 |
| 11 | 117 | 367 | 267 | — | — | — | — | — | — | 188 | 162 |
| 12 | — | — | — | — | NS | NS | NS | NS | NS | — | — |
| 13 | NS | NS | NS | NS | — | 783 | 1,083 | 50 | 1,217 | 627 | 572 |

* — Juvenile clams only
NS —Not sampled

these sites represented 68% of the total clams collected. Belanger *et al.* (1985) reported similar results and suggested that rivers with fine, well-oxygenated sand substrates would be optimal for the establishment of *C. fluminea* populations in newly colonized sites.

The distribution of *C. fluminea* in the Upper and Middle St. Johns River (figure 2) is primarily related to sediment type and flow rate. The distribution of *C. fluminea* varied from 34.2% of the total fauna at the Lake Harney Inlet site (Site 8) to 0% at the Lake Monroe Outlet site (Site 12), where deep deposits of organic sediment occurred. Also, few clams were observed in the upper reaches of the study area (Sites 1 and 2), as peat sediments, low flow rates and low dissolved oxygen conditions predominated.

Although it was found that both sediment type and flow rate affected the density of *C. fluminea* populations, results from this study indicated sediment type was the most important limiting factor, as high flow can be ineffective if the sediment type is unsuitable. For example, samples taken from organic muck and peat sediments revealed only small numbers of *C. fluminea*, even though flow rate was often suitable. The reverse situation, sandy sediment and no flow, was encountered at the Lake Washington site (Site 4) where an average clam density of 250/m² was found. Flow rate is an important factor because it is responsible, in part, for the transport of essential materials to the clams, such as food and oxygen. It is also important for the dispersal of waste products and clam larvae. However, it appears that a very high flow rate can limit *C. fluminea*. At Camp Holly, approximately 1 km upstream of the Lake Washington site, the flow rate averaged 1.0 ft/sec over sandy substrate during sampling trips but no clams were found. Observations using SCUBA revealed that the high current had scoured the sediment surface, exposing hard-packed sand. Under these sediment and flow conditions it is very difficult for clam larvae to become established in the riverbed. Instead, they are generally swept downstream to sites where the current velocity has decreased, enabling them to settle out. The natural spread of *C. fluminea* is limited by the nonswimming larval stage, thus river cur-

Table 3. *Elliptio* sp. population density (no./m²) at the sampling sites, 1983–84.

| | 1983 | | | | 1984 | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Site | Aug | Sep | Oct | Nov | Jan | Feb | Mar | Apr | May | Mean | SD |
| 1 | [illegible] | *1,866 | — | — | — | — | — | — | — | *541 | 1,622 |
| 2 | 100 | — | 67 | 133 | 67 | — | — | — | — | 41 | 52 |
| 4 | [illegible] | [illegible] | 50 | 17 | — | 17 | 50 | — | 33 | 19 | 21 |
| [illegible] | [illegible] | [illegible] | 17 | 17 | — | — | — | — | — | 4 | 8 |
| [illegible] | [illegible] | — | 17 | — | — | — | — | — | — | 2 | 6 |
| [illegible] | [illegible] | [illegible] | [illegible] | — | — | — | — | — | — | — | — |
| [illegible] | [illegible] | [illegible] | — | [illegible] | 17 | — | — | — | — | 2 | 6 |
| [illegible] | [illegible] | [illegible] | — | 50 | — | — | — | — | — | 6 | 17 |
| [illegible] | [illegible] | [illegible] | — | — | — | — | — | — | — | — | — |
| [illegible] | [illegible] | [illegible] | — | — | NS | NS | NS | NS | NS | — | — |
| [illegible] | [illegible] | [illegible] | NS | NS | — | — | — | — | — | — | — |

* [illegible]
NS [illegible]

rent can be an important dispersal mechanism leading to rapid down-river range expansion (McMahon, 1982).

*Corbicula fluminea* population densities in the St. Johns River are intermediate to the ranges reported in other areas of the United States. Hall (1984) reported densities as high as 6,663 clams/m$^2$ in the littoral zone of Lake Norman, North Carolina. Eng (1979) found *C. fluminea* population densities in sand bars in the concrete lined Delta–Mendota Canal in California to be between 10,000–20,000 clams/m$^2$. Population densities of *C. fluminea* were noted to be greatest in fine sand (452 clams/m$^2$), followed by sand/gravel substrata (177 clams/m$^2$) in the New River, Virginia (Belanger *et al.*, 1985). In a study on the Wekiva River, Florida, Gottfried and Osbourne (1982) reported population densities of 1,210 clams/m$^2$. Gardner *et al.* (1976) reported the *C. fluminea* population density increased from 0 to 10,000 clams/m$^2$ from 1971 to 1974 in the Altamaha River, Georgia.

## EFFECTS OF *CORBICULA* DENSITIES ON UNIONIDS

Unionid mussels (*Elliptio* sp.) were observed in much lower population densities than *Corbicula fluminea*. Although mussels occurred in high density (4,866 clams/m$^2$) at the Zig-Zag site, this number represented only larval mussels and neither *C. fluminea* nor *Elliptio* sp. became established at this site during the study. The largest adult population of unionids was found at the Lake Sawgrass site (Site 2) in November, when 133 unionids/m$^2$ were collected. All other sites contained densities of 50 unionids/m$^2$ or less, and adult populations were found at only six of the eleven sites. Table 3 shows the mean population densities of unionids at the sampling sites and indicates that density decreases downstream, with few mussels occurring downstream of the Lake Poinsett site (Site 6).

*Elliptio* sp. population densities were inversely correlated to those of *Corbicula fluminea* (F test; $p < 0.05$). As the mean *C. fluminea* population density increased in a downstream direction through the first six sites, *Elliptio* sp. mean population densities decreased to zero. Of 1,600 bivalves collected from dredge samples, 79.3% were *C. fluminea* and 20.7% were of the family Unionidae (*Elliptio* sp.). Only in the upper reaches of the river, where peat sediments dominated, were *Elliptio* sp. population densities greater than those of the Asiatic clam. In sandy regions where both bivalves occurred, *C. fluminea* predominated. Thus, *Elliptio* sp. predominated only where the sediment type was limiting to *C. fluminea*.

SCUBA diving observations at Lake Harney Inlet (Site 8) showed that unionids do exist at the site, even though no individuals were captured in the dredge samples, and revealed the distributional relationships of the two bivalves under natural conditions. In general, *Corbicula fluminea* outnumbered *Elliptio* sp. in the central region of the channel where sandy sediments and measurable flow existed. Toward shore, the sediments changed from sand to silt-covered sand, and then to sand covered with heavy accumulations of silt and detritus. Increasing organic silt accumulations near the river banks were accompanied by increasing numbers of unionids. In contrast, the number of *C. fluminea* decreased as silt accumulation increased. It appeared that *C. fluminea* could not tolerate silt accumulations deeper than 0.5 to 1.0 cm. As the silt depth increased beyond 1 cm, only unionid mussels were observed. The size and shape of the shell of *Corbicula fluminea* may contribute to its preference for sandy substrates. *Corbicula fluminea* shells are more circular in comparison to the elliptical shape of the *Elliptio* sp. Unionid bivalves, being elliptical and usually larger, may extend their shells and siphons beyond the silt while still remaining within the firm sandy substrate below. In the case of *C. fluminea*, only large specimens would be able to accomplish this. Smaller *C. fluminea*, such as those found at Site 8 (20–25 mm size class), would not be able to extend their siphons beyond the silt or muck layer to the more oxygenated flowing river water. The 20–25 mm and 15–20 mm shell-length size classes were the dominant groups collected in the St. Johns River, comprising 46% and 23% of the *C. fluminea* found, respectively.

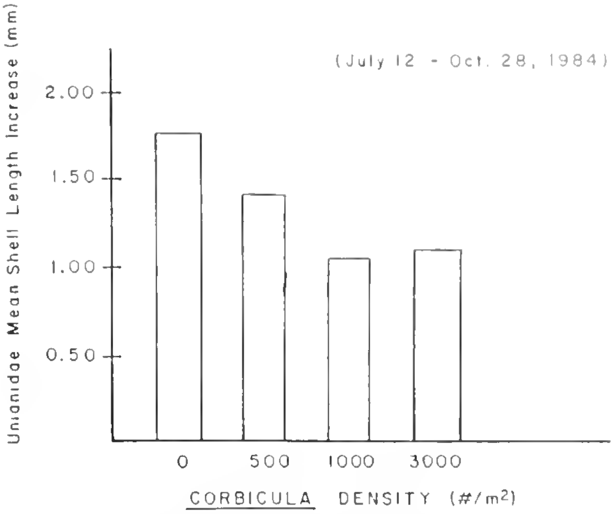

**Figure 3.** Cage experiments data showing the effect of *Corbicula fluminea* densities on growth of *Elliptio* sp.

Several investigators have reported that *Corbicula fluminea* can outcompete native unionid and sphaeriid bivalves (Boozer & Mirkes, 1979; Cooper & Johnson, 1980; Taylor & Hughart, 1981). In this study, growth of *Elliptio* sp. and *C. fluminea* were observed together to confirm previous observations that unionid population densities are inversely correlated with *C. fluminea* population densities. *Elliptio* sp. mussels, placed in control cages, increased their shell length by an average of 1.76 mm during the period between July 12 and October 28, 1984. *Elliptio* sp. growth rates in cages that contained various densities of *C. fluminea* were reduced and the reductions in growth were related to the population density of the Asiatic clams in each particular cage. Figure 3 shows the

Table 4. *Corbicula* growth rates from representative areas of the United States

| Site | Measurement period | Growth rate (mm/day) | Reference |
|---|---|---|---|
| St. Johns River, FL | | | |
| Lake Washington | 10/28/84–2/22/85 | 0.03 | This Study[1] |
| Lake Monroe Inlet | 8/15/84–2/23/85 | 0.0197 | |
| Lake Monroe Outlet | 8/15/84–2/23/85 | 0.0296 | |
| Lake Washington | 2/23/85–7/22/85 | 0.0112 | |
| Lake Harney Inlet | 2/23/85–6/30/95 | 0.0437 | |
| St. Johns River, FL | | | |
| Zig-Zag Canal | 1/8/84–7/2/84 | 0.0063 | |
| Camp Holly | 9/15/83–7/2/84 | 0.0273 | |
| Lake Washington | 1/8/84–7/2/84 | 0.0060 | |
| Lake Monroe Outlet | 11/13/83–7/2/84 | 0.0043 | |
| Southern Illinois Fish Pond | | | |
| Summer | 7/20/79–9/22/79 | 0.012 | Buttner and Heidinger (1980)[2] |
| Winter | 12/6/79–1/16/80 | 0.003 | |
| Selected Texas Reservoirs | 1975 | 0.044 | O'Kane (1976) |
| Altamaha River, GA | 1975 | 0.072 | Sickel (1976) |
| Delta–Mendota Canal, CA | 2/20/73–6/25/73 | 0.0516 | Eng (1979) |
| Lake Benbrook, TX | | | |
| Sandbar Specimens | 6/7/75–9/9/77 | 0.056 | Britton *et al.* (1979)[1] |
| Container Specimens | 6/14/77–9/30/77 | 0.054 | |
| Kanawha River, WV | | | |
| Container Specimens | 3/12/83–12/16/83 | 0.094 | Joy (1985)[3] |
| Lake Erie, OH | 6/82–9/82 | 0.114 | Scott-Wasilk *et al.* (1983) |
| Kanawha River, WV | | | |
| Container Specimens | Summer, 1983 | 0.136 | Welch and Joy (1984)[3] |

1 = 19 liter containers (cages)—with covers, placed on the bottom
2 = Open top cages, 0.3 m² and 9 cm deep, placed on the bottom
3 = Floating units (each unit consisted of 5 cages).

effect of *C. fluminea* population densities on the growth rates of *Elliptio* sp. The reductions in growth rates were: 19.3% when the *C. fluminea* population density was 500 clams/m²; 40.9% for a density of 1,000 clams/m² and 37.5% at a density of 3,000 clams/m². The steady decrease in *Elliptio* sp. growth is evident at *C. fluminea* population densities up to 1,000 clams/m². Beyond this point, for reasons unknown, growth rate reduction seemed to level off. The decreases in growth rate of the Unionidae may have been due to increased competition for essential requirements such as food or oxygen.

In summary, the growth and distribution of *Corbicula fluminea* in the St. Johns River seems to be related to substratum and flow rate. *Elliptio* sp. growth was adversely affected by the presence of *C. fluminea*. However, the adaptability of this unionid mussel to organic [illegible]ment types which are generally uninhabitable by C. [illegible] may serve to protect it from the dangers of [illegible] r the possibility of becoming replaced [illegible] ulations of the Asiatic clam.

[illegible]

A [illegible] *fluminea* growth rates at the cage [illegible] with growth rates reported from other areas of the United States, are presented in table 4. Fastest growth was seen at Lake Harney Inlet (Site 8) during the third sampling period (0.0437 mm/day), as all conditions for growth were favorable at this site (high flow, high D.O., sandy sediment). In general, growth rates in this study were intermediate in comparison to rates reported in other areas of the United States (table 4), although very low rates were measured at the Zig-Zag (Site 1), Lake Washington (Site 4) and Lake Monroe Outlet (Site 10) sites. The average growth rates reported by Eng (1979) from concrete lined canals in California, were 0.45 and 0.70 mm for the months of March–May in 1974 and 1976, respectively. By comparison, the St. Johns River *C. fluminea* grew an average of 0.70 mm and 1.00 mm during the same months in 1984 and 1985. The data in table 4 were collected from many different aquatic systems with site specific variations in habitat conditions which undoubtedly affect growth rates. Britton *et al.* (1979) reported on clams grown in lake environments in northern Texas, while the St. Johns River clams inhabit humic-colored waters under both lake and river conditions. The most important factors leading to slower *C. fluminea* growth in the St. Johns River than in many other areas were probably the lack of food due to low flow rates, periodic low oxygen levels in the water column and the predominance of organic sediment in the river.

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# Multiseasonal Tissue Growth Trends in *Corbicula fluminea* (Bivalvia: Corbiculidae) from the New River, Virginia

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## ABSTRACT

Juvenile and adult *Corbicula fluminea* were collected monthly in 1985 from the New River in Narrows, Virginia. Shell length, shell height, shell inflation, and soft tissue dry weight were recorded for each individual. Regression analyses among all pairs of data sets were calculated monthly. All comparisons among shell dimensions and between shell dimensions and dry tissue weight generated coefficients of determination ($R^2$) $\geq 0.801$. In all instances, comparisons between shell dimensions and the cube root of dry tissue weight generated higher $R^2$ values than comparisons between shell dimensions and dry weight. A comparison of monthly regression lines generated between shell secretion and the cube root of dry weight suggests that shell accretion and tissue growth are not equivalent for all individuals in a population and are dependent on initial size of an individual and on season.

*Key words:* *Corbicula fluminea*; Asiatic clam, shell dimensions, tissue weight; regression analysis.

## INTRODUCTION

Studies assessing the growth of *Corbicula fluminea* (Müller, 1774) have been conducted previously to establish energy budgets for juveniles (Foe & Knight, 1986a), determine the effect of various artificial and algal diets and suspended sediment on growth (Dauble *et al.*, 1985; Foe & Knight, 1985), or monitor growth rates of clams under natural conditions (Welch & Joy, 1984; Joy, 1985). In general, these studies monitored individually marked clams or narrow size ranges of clams in the laboratory [illegible] defined durations (usually ≤30 days) or in the field [illegible] 1 years. Potential applications for data [illegible] studies include use of growth rates as a sublethal monitor for exposure of clams to toxic effluents and chemicals (Belanger *et al.*, 1986a,b; Foe & Knight, 1986b), estimation of soft tissue mass based on shell size in aquaculture efforts (Joy & McCoy, 1975; Buttner, 1986), calculation of condition indices to determine levels of physiological fitness (Joy, 1985), and perhaps as a means by which decisions may be reached concerning optimal periods for chemical control efforts in fouling populations. Few, if any, of these studies addressed growth of both shell and soft tissue simultaneously over a continuum of clam sizes in a natural population. The present study was undertaken to document relationships in tissue weight and shell size in a natural population of *C. fluminea* for a minimum of 1 year to determine if the two parameters provided equivalent conclusions concerning growth in *C. fluminea*.

## MATERIALS AND METHODS

Specimens were collected from the New River at Narrows, Giles County, Virginia, on the last Monday of each month during 1985. Clams were sampled by means of a 3-m handled dredging cage (mesh size = 7.0 mm), permitting collection of individuals as small as 6 mm in shell length (SL). Clams were returned to the laboratory within 2 hr of collection for measurement of shell dimensions and dry tissue weights (DW) of 100 individuals. Voucher samples of intact clams have been deposited with the Department of Malacology at the Academy of Natural Sciences in Philadelphia (ANSP A12516).

Shell dimensions measured included shell length (SL), the maximum anteroposterior dimension; shell height (SH), the distance between dorsal and ventral margins of the shell measured at the apex of the umbo; and shell inflation (SI), the lateral thickness of a bivalve (Britton & Morton, 1982). Shell dimensions were measured with vernier calipers to the nearest ±0.05 mm on the intact animal. Prior to shucking the soft tissues from the shell,

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[1] [illegible] Research Corporation, Merrill Lane [illegible]

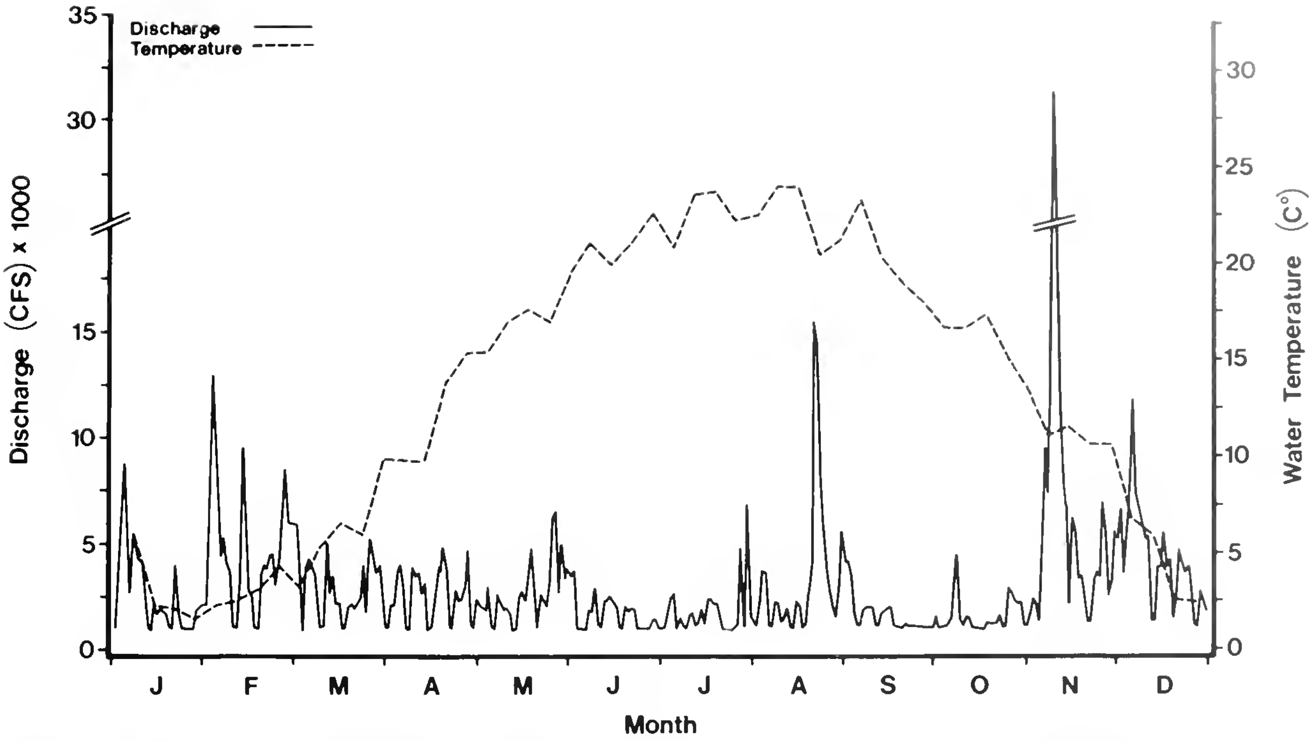


**Figure 1.** Mean weekly water temperature (Narrows) and mean daily discharge rate (Radford) for the New River, Virginia, in 1985

mantle cavity water was drained from the clam by severing the shell adductor muscles and standing the clam on the ventral edges of its shell over absorbent paper toweling. Soft tissues were scraped from the shell, transferred to preweighed aluminum pans, and dried in a drying oven at 80 °C for 48 hr. Pans with tissues were weighed on a Mettler balance to the nearest ±0.5 mg. Abiotic data available at the time of the study included New River water temperatures and discharge levels provided by a local industry and federal agency, respectively (figure 1).

Least squares regression (LSR) analyses were performed monthly among shell dimensions (SL, SH, SI), between individual shell dimensions and DW, and between individual shell dimensions and the cube root of tissue dry weight (CRDW). Regressions of CRDW against a shell dimension resulted in a linearization of the allometric relationship between the untransformed variables (Schmidt-Nielsen, 1984). Generation of LSR analyses was facilitated by programs (general linear models) of the Statistical Analysis System (SAS Institute, Inc., 1982). Coefficients of determination ($R^2$) were generated in conjunction with the LSR analyses as a feature of the computer programs employed.

## RESULTS

All comparisons among shell dimensions and between shell dimensions and tissue weights generated a $R^2 \geq 0.801$ (table 1). The highest $R^2$ values were generated between SH and SL for shell dimension comparisons and between SH and CRDW for comparisons between a shell dimension and dry tissue weight. Values for $R^2$ ranged from 0.988 to 0.996 and 0.895 to 0.970, respectively. Linear regressions of CRDW against shell dimensions always generated better lines of best fit than regressions between untransformed variables.

Intermonthly comparisons of regressions between SH and CRDW revealed marked seasonal trends in weight gain and loss relative to a constant shell size (figures 2–5; table 2). The monthly regression lines are presented

**Table 1.** Coefficient of determination ($R^2$) ranges for comparisons among all potential pairings of shell dimensions and untransformed as well as transformed dry tissue weights for all collections in 1985.

| Parameters compared* | Minimum $R^2$ | Maximum $R^2$ |
|---|---|---|
| SH, SL | 0.988 | 0.996 |
| SL, SI | 0.980 | 0.990 |
| SH, SI | 0.922 | 0.992 |
| SL, DW | 0.826 | 0.953 |
| SL, CRDW | 0.884 | 0.958 |
| SH, DW | 0.832 | 0.949 |
| SH, CRDW | 0.895 | 0.970 |
| SI, DW | 0.801 | 0.935 |
| SI, CRDW | 0.865 | 0.953 |

* CRDW = cube root dry weight, DW = dry weight, SH = shell height, SI = shell inflation, SL = shell length

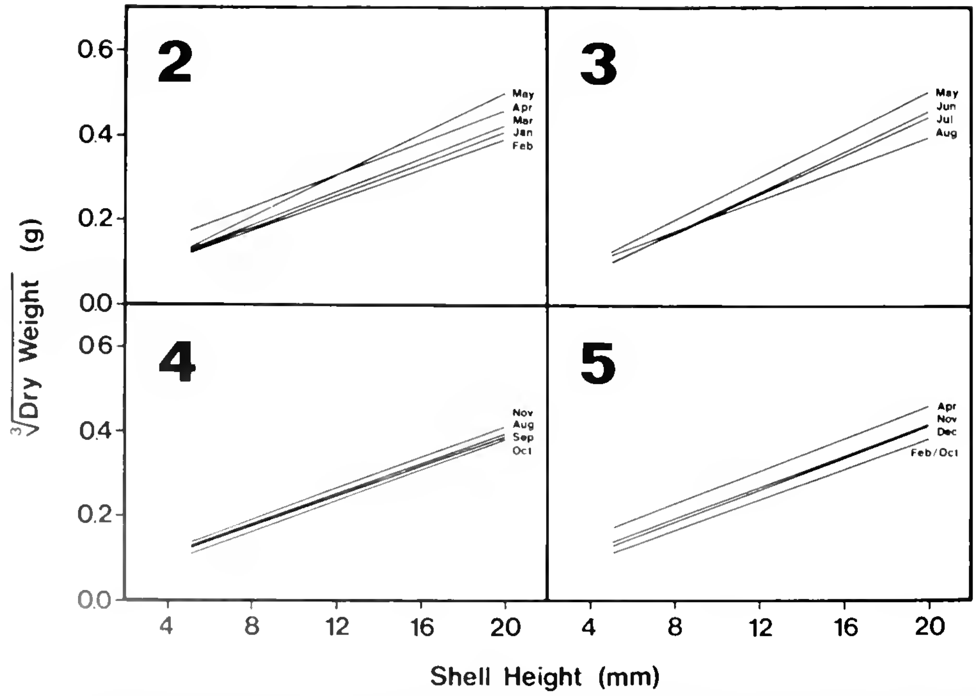
Table 2. Regression parameters and coefficients of determination (R²) for lines of best fit equations predicting the cube root of dry weight from shell height for clams collected on a monthly basis in 1985 from the New River, Virginia, at the collection temperatures listed

| Month | Slope | Y-Intercept | $R^2$ | Collection temperature (°C) |
|---|---|---|---|---|
| January | 0.0185 | 0.034 | 0.955 | 2.0 |
| February | 0.0178 | 0.033 | 0.914 | 5.0 |
| March | 0.0194 | 0.037 | 0.924 | 7.8 |
| April | 0.0195 | 0.073 | 0.895 | 15.0 |
| May | 0.0258 | −0.018 | 0.970 | 19.4 |
| June | 0.0230 | −0.009 | 0.960 | 22.5 |
| July | 0.0215 | 0.005 | 0.935 | 22.0 |
| August | 0.0191 | 0.017 | 0.939 | 22.0 |
| September | 0.0182 | 0.026 | 0.956 | 17.0 |
| October | 0.0178 | 0.028 | 0.943 | 16.0 |
| November | 0.0188 | 0.033 | 0.960 | 9.5 |
| December | 0.0192 | 0.028 | 0.960 | 2.0 |

in chronological order in figures 2, 3, and 4 to illustrate the month-to-month progressions. Selected monthly regression lines are presented in figure 5 to illustrate comparisons between seasons. Although there was a trend towards declining dry weight in all clams in February relative to the initial collection in January, CRDW increased among all clams through April (figure 2). This was demonstrated by progressively higher Y-intercepts, indicating that increases in tissue mass surpassed increases in SH (table 2). As a point of reference, a 15-mm (SH) adult possessed 81.5% more tissue (DW) in April than it did in February. The relationship between CRDW and SH shifted in May from that previously observed, as demonstrated by an increase in the slope of the regression line. Larger individuals (>13 mm SH) possessed more tissue mass relative to SH than in previous months, while smaller individuals (<13 mm SH) had less tissue relative to SH in May than in previous months (figure 2; table 2). Declining slopes and increasing intercept values were observed from May through October (figures 3, 4; table 2) until a distinct increase in CRDW relative to SH was observed in November and December (figures 4, 5). This shift in the regression lines coincided with major flooding of the New River in early November (figure 1). As a point of reference, a 15-mm (SH) adult possessed 22 and 23% more tissue (DW) in November and December, respectively, than it did in October.

## DISCUSSION

Regressions among shell dimensions and between shell dimensions and tissue dry weights generated high R² values that were comparable to the findings of other investigators. The approach to analysis of the data generated in this study differed from that used by others, in that some investigators failed to transform their data (Joy & McCoy, 1975; Rodgers *et al.*, 1977) while others utilized a log-log transformation prior to generating lines



[illegible] best fit for the cube roots of tissue dry weight regressed against shell height for *Corbicula fluminea* [illegible] New River, Virginia, in (2) January, February, March, April, and May; (3) May, June, and August; [illegible] and November, and (5) February, October, April, November, and December, 1985.

of best fit through regression analysis (Sickel, 1979; Aldridge & McMahon, 1978; Kennedy & Heukelem, 1985; Foe & Knight, 1986a, 1987). Comparisons between a shell dimension and either viscera wet or dry weight reveal a curvilinear relationship that is not appropriately analyzed by linear regressions. While log-log transformations do provide a linearization of the relationship between these variables, we believe that use of a cube root transformation may be more biologically appropriate, because body weight is a function of volume and height is a measure of a single, linear dimension. Transformation of weight to its cube root permits a simpler linear regression comparison between shell dimensions and tissue weight rather than regressions between log-log transformed variables. Previously, Dauble *et al.* (1985) utilized a similar approach by regressing the square root of clam weight against SL. One other factor distinguishing our study from those previously reported is that all of the above cited studies used either SL or SI in regressions against tissue weight. Our data demonstrate a lower degree of variability in measurements of SH and, therefore, greater precision in the estimation of tissue weights.

Regressions of CRDW against SH (figures 2–5; table 2) demonstrated that no single monthly or quarterly estimate of tissue mass based on SH can be extrapolated to all other periods of the year. Consistent slopes for the relationships from January through April suggested that the individuals from all size classes were responding to environmental variables in a proportionately common fashion through either the loss (January to February) or accumulation (February through April) of tissue. While the manner in which the data were collected prohibits statements concerning actual shell growth rates, the fact that Y-intercepts declined and increased demonstrates active soft tissue degradation and growth, respectively, at rates not comparable to shell growth. The slope of the regression line describing the relationship rose markedly in May, documenting a change in the relationship among different size clams. Larger individuals were apparently accumulating tissue at a rate proportionately greater than previously observed. Smaller individuals were most likely continuing to accumulate tissue, but the apparent reduction in tissue mass relative to SH probably signified a rapid increase in rate of shell growth.

The increase in tissue mass in larger individuals (~15 mm and greater) in May was most likely in preparation for reproductive activities, while the marked decrease in slope of the regression line from May to June could have reflected initiation of spawning. Reproductive effort in this population for 1984 was greatest during June and July (Doherty *et al.*, 1987). This interpretation is consistent with the observations of Morton (1982). He reported a 42% decline in the slope of the regression line between DW and SL for groups of *Corbicula fluminialis* collected both prior to and after spawning. In contrast, Aldridge and McMahon (1978) did not find significant differences for regressions between log transformed variables of SL and DW for 28 groups of *Corbicula fluminea* collected over a 16-month period. The gradual reduction in slope from June to October may have reflected a continuing release of juveniles by adults, although the need for increased energy expenditure during the warmest period of the year may have also contributed to the decline.

The changes in CRDW relative to SH for smaller clams (~10 mm or less) between April and May were probably a reflection of increased shell secretion rather than tissue loss or resorption. If clams of this size were sexually immature, they would not require a massive increase in tissue to accommodate reproductive efforts. An overlap of the April and May regression lines for clams ranging in size from ~10 to 14 mm may indicate that physiological activities are allocated equally to shell secretion and tissue growth. This interpretation also suggests that size of an individual at the time of spawning dictates the total number of veligers released by that individual.

Increases in the slopes and Y-intercepts for November and December could have been due to tissue growth, resulting from an abundance of nutritive material associated with high river discharge from locally heavy flooding (figure 1). Doherty *et al.* (1987) hypothesized that high river discharges provided high levels of nutrients that permit more than two spawning episodes per year while Foe and Knight (1985) concluded that suspended sediments, up to a concentration of 150 mg/liter, do not adversely affect growth of the Asiatic clam. Since lower temperatures during these months might result in reduced metabolic demands, the potential for growth and maintenance of tissue mass could have been enhanced.

These data also support earlier observations by other investigators that an inverse relationship exists between growth rate and initial size of an individual (Britton *et al.*, 1979; Dreier & Tranquilli, 1981; Welch & Joy, 1984). For example, a 6-mm (SH) juvenile had a dry weight of 2.7 mg in February, whereas the dry weight of an individual of similar shell size had a dry weight 154% greater in April. The increase in tissue mass for a 20-mm (SH) adult was only 68% between February and April (59 and 99 mg dry tissue weight, respectively).

Similarly, the magnitude of the difference between regression lines between any two months is unequal, supporting observations by other investigators that growth is seasonally influenced. Both Fuji (1957) and Joy (1985) observed no growth (SL) in clams maintained at water temperatures <10 °C. Measurable growth was observed when temperatures rose above 14 °C, while the greatest rates of growth were observed at 24 to 30 °C. Britton *et al.* (1979) reported a slowing of shell deposition in clams with shell ≥10 mm in length during winter, while McMahon and Williams (1986) found growth rates of *Corbicula fluminea* individuals to be characterized by large seasonal variation. Mattice and Wright (1986) observed varying growth rates for the Asiatic clam in field studies and suggested that temperature played a major role in growth determination. These conclusions, though, were formulated from observations of shell growth rate. Our study demonstrates that growth of tissue can occur at temperatures below those which appear to be necessary for measurable increases in shell height, length, or inflation (February to April; October to November; table 2). Russell-Hunter *et al.* (1984) have reported comparable observations for populations of freshwater pulmonate snails. Comparisons between pre- and post-winter surviving individuals of *Helisoma trivolvis* and *Lymnaea palustris* revealed reductions in soft tissue ranging from 19–169% based on predictive equations between shell and tissue mass for pre-winter snails.

This study demonstrates that shell growth as defined by increases in shell height, length, or inflation is not equivalent to, and does not necessarily parallel, tissue growth. Initial size, reflective of the reproductive maturity of an individual, and season, reflective of temperature and food availability among other things, are possibly major factors in determining whether shell or tissue growth will predominate. These data imply that regressions between a shell dimension and soft tissue mass generated at one time of the year are not applicable to the same population in other months or seasons.

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# Geological Substrate and Human Impact as Influences on Bivalves of Lake Lewisville, Trinity River, Texas

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## ABSTRACT

The bivalve fauna of Lake Lewisville (Elm Fork Trinity River), Denton County, Texas, consists of 16 species. Present are the introduced Asian clam and 15 native unionids. Relative abundances of species in different areas of the reservoir are related to inundation history and geological substrate. Inundation has locally extirpated some species while other species have flourished. Utilization of shell material for the cultured pearl industry is documented. Ecological, taxonomic, and zoogeographical notes are presented for each species.

*Key words:* Freshwater bivalves, Lake Lewisville, Trinity River, faunal changes, commercial utilization.

## INTRODUCTION

Little is known of the detailed distributions of the freshwater mussels of Texas. Two comprehensive lists have been published (Singley, 1893; Strecker, 1931), but these compilations are in need of updating. Even recent treatments of North American unionids (Burch, 1973, 1975) do not adequately cover the Texas fauna. The only studies of freshwater bivalves from north central Texas localities cover Lake Texoma (Valentine & Stansbery, 1971; White and White, 1977) and Lake Arrowhead (Neck, 1989b). Murray (1972, 1978) has summarized the unionids present in two reservoirs in central and southern Texas. Localized faunal surveys of freshwater bivalves of other portions of Texas have been published recently (Neck, 1986, 1987, 1989a, Neck & Metcalf, 1988).

Below is a summary of a survey of the mussel fauna of Lake Lewisville, a reservoir in north central Texas on the Elm Fork of the Trinity River (figure 1). The purposes of this survey were to determine relative abundance of resident species, intra-reservoir distributions of various species, and human impact upon this fauna. Justifications for the nomenclature used are provided where proper [illegible] has been unclear, nomenclature follows Turgeon [illegible] 88).

[illegible] rts of freshwater bivalves from the upper [illegible] drainage have been published. Flook and [illegible] reported nine species from a single locality [illegible] ville. Strecker (1931) reported fourteen species from the Elm Fork of the Trinity River "near Lewisville, Denton County." The naiad fauna of Dallas County (which borders the southern edge of Denton County) was studied by Read (1954; Read & Oliver, 1953). A survey of unionids of several reservoirs of Tarrant County (Fort Worth, to the west of Dallas County) is available (Mauldin, 1972).

## STUDY AREA

Lake Lewisville (figure 2) is located in north central Texas in central Denton County, approximately 24 kilometers southeast of Denton and 35 kilometers northwest of Dallas. Impounded watercourses include the mainstem and lower reaches of some tributaries of the Elm Fork of the Trinity River. The Elm Fork of the Trinity River is formed from the coalescence of many small tributaries in Cooke, Montague, Clay, and Archer Counties to the west of Denton County.

Lake Lewisville has a dual history; information below is from Dowell and Breeding (1967). The original impoundment (Lake Dallas) was created by Garza Dam built during 1924 through 1927; deliberate impoundment of water began 16 February 1928. The area of the original impoundment was 44.5 km$^2$ at spillway elevation. Original capacity was 2.4 million cubic meters (drainage area 3,018 km$^2$). Accumulation of sediment became a severe problem in the original Lake Dallas. By 1952, capacity of the reservoir had decreased 19.3% to 1.9 million cubic meters. Hydrochemical and vegetational conditions of Lake Dallas were reported by Harris and Silvey (1940).

Construction of a second dam downstream near Lewisville was begun in November 1948 and completed in August 1955. Impoundment of water began 1 November 1954. Following a prolonged filling period during a severe drought, a passageway was created through Garza Dam on 28 October 1957. The combined reservoir system has a surface area of approximately 94.28 km$^2$ at conservation pool level (156 meters above mean sea level). Surface area of the flood pool (161 m msl) is 158.17 km$^2$. Capacity of the combined reservoir system is 5.7 million cubic meters at conservation pool and 12.2 million cubic

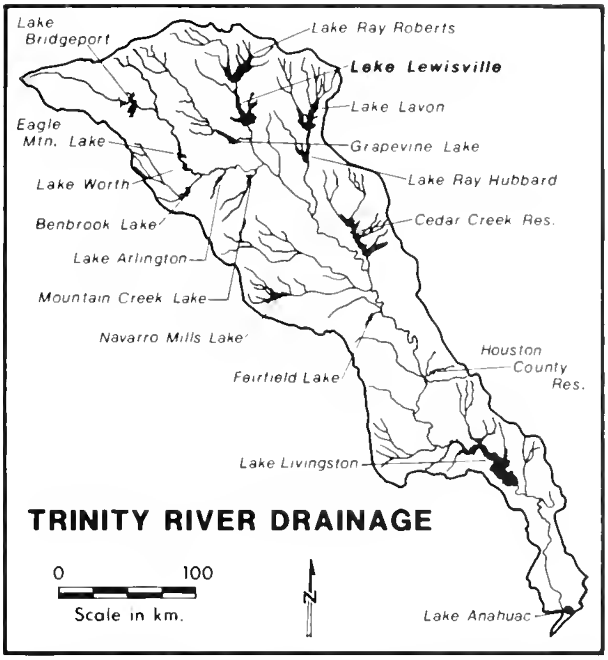

**Figure 1.** Map of Trinity River drainage, Texas, showing location of Lake Lewisville and other reservoirs.

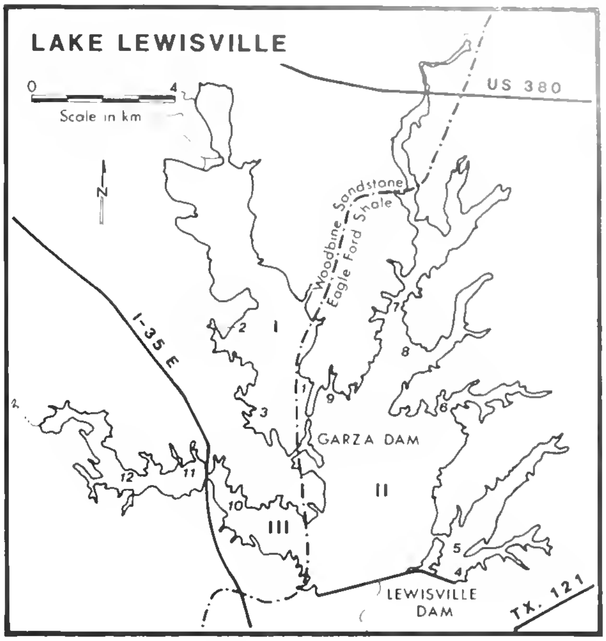

**Figure 2.** Map of Lake Lewisville, Texas, showing geological substrate, reservoir subdivisions (Roman numerals), and collecting localities (Arabic numbers).

meters at spillway level. Drainage area above the dam is 4,300 square kilometers. Shoreline of the conservation pool is approximately 295 kilometers. Primary purposes of the reservoir are flood control, municipal/industrial water supply, and recreation.

More recently Smith (1973) studied the physicochemistry of Lake Lewisville. Variation in water physiochemical parameters was found to be due more to the original characteristics of the basin rather than the length of impoundment. Algal species composition was fairly uniform throughout the surveyed portions of the reservoir. Water temperature varied seasonally from 5.0 °C to 28.5 °C and pH varied from 7.3 to 8.4. Alkalinity varied from 90 to 107 mg/L (mostly bicarbonate) for area II and from 116 to 151 mg/L for area I. Nitrate levels varied from 0.354 to 3.588 mg/L, while phosphate levels ranged from 0.017 to 0.165 mg/L. The Lake Dallas basin (area I) had greater turbidity and higher nutrient enrichment (phosphate and bicarbonate) than area II.

This reservoir has suffered from a lack of name standardization. Originally both the combined impoundment and the dam structure were known as Garza-Little Elm Reservoir and Garza-Little Elm Dam. In 1955 the name of the dam was changed to Lewisville Dam although the reservoir name was unaltered. Subsequently the U.S. Army Corps of Engineers (which operates the dam and reservoir) has changed the name of the reservoir to Lake Lewisville.

The surface geology of the area covered by Lake Lewisville is rather simple (Winton, 1925). The eastern portion is underlain by the Eagle Ford Formation and alluvial deposits, whereas the western portion is underlain by the Woodbine Formation and limited alluvial areas. All deposits are Upper Cretaceous except for the Pleistocene and Recent alluvial terraces. The Eagle Ford consists of a series of black oily shales with a few thin ledges of sandstone. The Woodbine is somewhat variable (Winton, 1925); several layers of indurated sandstone are separated by softer sandstone, loose sand, and clay layers. The Eagle Ford/Woodbine contact is aligned approximately along a NNE to SSW line and passes very close to the axis of Garza Dam, which formed Lake Dallas.

Climate of the study area is transitional between maritime-subtropical and continental-temperate. The nearest recording weather station is at Denton, where the average monthly temperature varies from 7.2 °C in January to 29.3 °C in August. Extreme temperatures recorded are 45 °C and −19.4 °C. Annual precipitation averages 804 mm, but has varied from 384 mm in 1963 to 1,433 mm in 1957. The growing season is 226 days (27 March to 8 November). Weather records for any particular year often are far from the mathematical "norms" because this region is characterized by dramatic year-to-year fluctuations. Fluctuations in precipitation usually are larger than those in temperature. Major droughts occurred in the 1930's and 1950's.

Drought during the mid 1950's was severe enough that 1.2 million cubic meters (98,470 acre-feet) of water were diverted from the Red River into Lake Dallas. Water was pumped from the Red River in Cooke County into Pecan Creek through which the water flowed by gravity into the Elm Fork of the Trinity River (Dowell & Breeding, 1967:36).

## METHODS

Twelve survey sites (Appendix) were chosen in a manner that all major areas of the reservoir were sampled. Most of the sites were located in various recreation parks built by the U.S. Army Corps of Engineers. Time of sampling activities (Winter 1977 through Fall 1978) coincided with an extended drought, which resulted in substantial lowering of the reservoir level. Many hectares of reservoir bottom were exposed to air. Bivalve shells were extremely abundant and readily counted.

Survey transect areas were four meters wide along the water edge for varying distances. Length of transects varied from 50 to 70 meters, but some were lengthened beyond 70 meters in order to increase sample number. Counts should not be taken as relative densities, but as estimates of relative species occurrence at particular sites. Only paired valves were counted in order to reduce the effect of water movement of "dead" valves to localities unsuitable for the species. Such movement is believed to be of minimal significance because most valve pairs lay *in situ*, partially covered with sediment at the place of death. After counts along the pre-selected transect were completed, additional lengths of adjacent reservoir edge were walked. Additional species at times were added to the list of species occurring at a given sampling area. Such occurrences are not recorded in the relative counts for a particular site (tables 1 and 2).

Representative specimens collected during this study have been deposited in the Dallas Museum of Natural History.

## BIVALVE FAUNA

A total of 16 species were observed at the various sampling stations around the reservoir shore (table 1). All but one, *Corbicula fluminea*, are native members of the Unionidae. No fingernail or pea clams (family Sphaeriidae) were observed during this study. Below is a list of species recovered from Lake Lewisville with nomenclatorial discussion, published habitat notations, and habitat occurrences in Lake Lewisville.

*Corbicula fluminea* (Müller, 1774) was not abundant in Lake Lewisville; no living specimens were found. Favorable habitat areas (moving water over sand or gravel substrate) were in small creeks feeding into the reservoir. A few young shells (7 mm length) were found on sand at Fish-O-Rama (private commercial development). All specimens from Lake Lewisville were referable to the "white form" (Hillis & Patton, 1982).

*Anodonta grandis* Say, 1829, is an extremely variable taxon as several names have been applied to different [illegible]enotypes. Read (1954) reported this species to be the [illegible] abundant and widely distributed species in Dallas [illegible] referred his specimens to *A. corpulenta* [illegible] Strecker (1931) called all specimens *A.* [illegible] Lewisville specimens tended toward the [illegible] The largest specimen measured 148.3 [illegible] *A. grandis* was a common species in Lake Lewisville; 106 specimens were taken, and all 12 reservoir localities were represented (table 1).

*Anodonta imbecillis* Say, 1829, occurs in the eastern United States, throughout the entire Mississippi system, and southward through the Gulf drainages into Mexico (Simpson, 1914:396; Burch, 1975:15). Mauldin (1972) reported *A. imbecillis* to be more frequent in ponds and small reservoirs than in large reservoirs. Only 18 individuals of *A. imbecillis* from 8 scattered localities were found in Lake Lewisville (table 1). *Anodonta imbecillis* probably was more abundant in backwater sloughs and pools of small creeks that drain into Lake Lewisville.

*Arcidens confragosus* (Say, 1829) is distributed throughout the Mississippi drainage (Murray & Leonard, 1962). In Dallas Co., Read (1954) found *A. confragosus* only in Parson's Slough in shallow water with a "fair current" over a mixed sand and mud substrate. This species was found at 9 reservoir localities, but only 16 individuals appeared in 7 transects (table 1).

*Amblema plicata* (Say, 1817) was the most abundant naiad in Lake Lewisville; 624 specimens (38.8% of total) were counted at 12 transect locations (table 1). This species was the most abundant bivalve at all locations. *Amblema plicata* occurs throughout much of eastern North America, south to the Nueces River, Texas (Burch, 1975). A number of taxa have been established for the *A. plicata* complex in the United States. Read (1954) reported both *A. costata* Rafinesque, 1820, and *A. perplicata* (Conrad, 1841) from the Elm Fork of the Trinity River in Dallas County. Flook and Ubelaker (1972) recorded both *A. plicata* and *A. costata* for Lake Lewisville, but only 4 of 150 were referred to *A. costata*. These two forms are believed to be either genetic morphs or ecophenotypes; in either case no taxonomic rank is recognized herein.

*Quadrula mortoni* (Conrad, 1834) is restricted to the eastern half of Texas (Strecker, 1931). This species is represented in Lake Lewisville by pustulate and non-pustulate forms, which are known from reservoirs in neighboring Tarrant County (Mauldin, 1972). Some of the less angulate specimens, particularly those with a large number of pustules, approach *Quadrula pustulosa* (Lea, 1829). However, specimens similar to *Q. pustulosa* from Lake Lewisville differ from *Q. pustulosa* from southeastern Texas in general shape of shell as well as number, form, and arrangement of pustules. Specimens of *Q. mortoni* differ from *Q. pustulosa* by being broader and somewhat flatter along the dorsal portion of the valves. Individuals of *Q. mortoni* (pustulate and non-pustulate) in Lake Lewisville are most abundant on a sand substrate, even if the sand exists only as a shallow bar over bedrock shale (as in area II).

Shells referred to typical *Q. mortoni* in this study can be keyed to *Q. houstonensis* (Lea, 1859) by using Read (1954), who reported the latter taxon to be "not common in Dallas County," from Elm Fork of the Trinity River on gravel bottom in about a meter of water. Strecker (1931) noted, however, that *Q. houstonensis* from the Elm Fork near Lewisville was "rather inflated and seems peculiar to this branch of the Trinity." Examination of

**Table 1.** Occurrence of bivalves of Lake Lewisville for each collecting locality

| | Area I | | | Area II | | | | | | Area III | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | Total | % | Rank | No. of sites |
| *Corbicula fluminea* | — | * | — | — | — | 2 | 2 | 1 | — | — | 1 | — | 6 | 0.4 | 13 (T) | 5 |
| *Anodonta grandis* | 1 | 13 | 2 | 5 | 2 | 14 | 12 | 14 | 3 | 21 | 7 | 12 | 106 | 6.5 | 4 | 12 |
| *Anodonta imbecilis* | 1 | 3 | — | — | — | 3 | * | 2 | 2 | 3 | 2 | 2 | 18 | 1.1 | 10 | 9 |
| *Arcidens confragosus* | 2 | * | 2 | — | — | 1 | — | 1 | — | 4 | 4 | 2 | 16 | 1.0 | 11 | 8 |
| *Amblema plicata* | 11 | 33 | 54 | 33 | 21 | 89 | 37 | 89 | 32 | 144 | 21 | 30 | 624 | 38.5 | 1 | 12 |
| *Quadrula mortoni* | 2 | * | 1 | 1 | — | — | 2 | 4 | 1 | 1 | — | 1 | 13 | 0.8 | 12 | 9 |
| *Quadrula apiculata* | 21 | 25 | 37 | 1 | 4 | 37 | 29 | 40 | 5 | 54 | 11 | 17 | 281 | 17.3 | 2 | 12 |
| *Tritogonia verrucosa* | — | * | — | — | — | — | — | — | — | — | — | — | * | — | * | 1 |
| *Lampsilis hydiana* | 3 | 9 | 1 | 10 | 7 | 70 | 14 | 18 | 5 | 58 | 11 | 8 | 214 | 13.2 | 3 | 12 |
| *Lampsilis satura* | — | — | — | — | — | — | * | — | — | — | — | — | * | — | * | 1 |
| *Lampsilis teres* | 5 | * | 1 | 2 | 1 | 27 | 2 | 13 | 5 | 15 | 4 | 1 | 76 | 4.7 | 6 | 12 |
| *Leptodea fragilis* | 1 | 2 | * | 5 | 1 | 16 | 1 | 13 | 1 | 4 | 11 | 8 | 63 | 3.9 | 8 | 12 |
| *Potamilus amphichaenus* | 2 | 1 | * | 3 | — | — | 2 | 10 | 1 | 8 | 6 | 7 | 40 | 2.5 | 9 | 10 |
| *Potamilus purpuratus* | 8 | 12 | 6 | 4 | 1 | 14 | 3 | 14 | 7 | 5 | 6 | 8 | 88 | 5.4 | 5 | 12 |
| *Toxolasma parvus* | — | * | — | 2 | 1 | 3 | — | — | — | — | — | * | 6 | 0.4 | 13 (T) | 5 |
| *Truncilla truncata* | 4 | 2 | 4 | 2 | 3 | — | 6 | 18 | 8 | 11 | 1 | 10 | 69 | 4.3 | 7 | 11 |
| Species | 12 | 15 | 11 | 11 | 9 | 11 | 13 | 13 | 11 | 12 | 12 | 13 | 16 | | | |
| Individuals** | 91 (12) | 100 (9) | 108 (9) | 68 (11) | 41 (9) | 276 (11) | 110 (11) | 237 (13) | 70 (11) | 328 (12) | 85 (12) | 106 (12) | 1,620 | 100.0 | — | 12 |

* Species present, but not found in transect

** Number in parentheses is number of species present in transect

(T) = Tie for ranking position

Table 2. Relative counts and percentages of bivalves of Lake Lewisville and subdivisions

| | I | | II | | III | | Total | |
|---|---|---|---|---|---|---|---|---|
| | n | %** | n | % | n | % | n | % |
| *Corbicula fluminea* | * | — | 5 | 0.6 | 1 | 0.2 | 6 | 0.4 |
| *Anodonta grandis* | 16 | 5.4 | 50 | 6.2 | 40 | 7.7 | 106 | 6.5 |
| *Anodonta imbecilis* | 4 | 1.3 | 7 | 0.9 | 7 | 1.3 | 18 | 1.1 |
| *Arcidens confragosus* | 4 | 1.3 | 2 | 0.2 | 10 | 1.9 | 16 | 1.0 |
| *Amblema plicata* | 128 | 42.8 | 301 | 37.5 | 195 | 37.6 | 624 | 38.5 |
| *Quadrula mortoni* | 3 | 1.0 | 8 | 1.0 | 2 | 0.4 | 13 | 0.8 |
| *Quarula apiculata* | 83 | 27.8 | 116 | 14.5 | 82 | 15.8 | 281 | 17.3 |
| *Tritogonia verrucosa* | * | — | — | — | — | — | * | — |
| *Lampsilis hydiana* | 13 | 4.3 | 124 | 15.5 | 77 | 14.8 | 214 | 13.2 |
| *Lampsilis satura* | — | — | * | — | — | — | * | — |
| *Lampsilis teres* | 6 | 2.0 | 50 | 6.2 | 20 | 3.9 | 76 | 4.7 |
| *Leptodea fragilis* | 3 | 1.0 | 37 | 4.6 | 23 | 4.4 | 63 | 3.9 |
| *Potamilus amphichaenus* | 3 | 1.0 | 16 | 2.0 | 21 | 4.0 | 40 | 2.5 |
| *Potamilus purpuratus* | 26 | 8.7 | 43 | 5.4 | 19 | 3.7 | 88 | 5.4 |
| *Toxolasma parvus* | * | — | 6 | 0.7 | * | — | 6 | 0.4 |
| *Truncilla truncata* | 10 | 3.3 | 37 | 4.6 | 22 | 4.2 | 69 | 4.3 |
| Species | 15 | — | 15 | — | 14 | — | 16 | — |
| Individuals*** | 299 (13) | — | 802 (14) | — | 519 (12) | — | 1,620 (14) | — |
| % of Total Sample | 18.5 | — | 49.5 | — | 32.0 | — | 100.0 | — |

* Present, but not recorded in transect

** % of transect sample.

*** Number in parentheses is number of species present in transect

shells at the Strecker Museum (SM) from the Elm Fork near Lewisville identified as *Q. houstonensis* by Strecker (SM 325–329) revealed shells of *Q. pustulosa* that are somewhat more quadrate than typical *Q. mortoni*. No such shells were found in the present survey. Examination of other shells referred to *Q. houstonensis* by Strecker revealed robust shells that appear to represent several species of *Quadrula*.

*Quadrula nodulata* (Rafinesque, 1820) has been reported from various portions of eastern Texas (Strecker, 1931). A single specimen that resembles *Q. nodulata* was found in Lake Lewisville in transect samples. Examination of specimens from Lake Lewisville that resemble *Q. nodulata* indicated that these shells were *Q. mortoni*. These Lake Lewisville specimens did not exhibit nodules on the posterior ridge as in typical *Q. nodulata*; nodules are restricted to the middle of the shell (below the umbo area).

Read (1954) reported *Quadrula metanevra* (Rafinesque, 1820) from adjacent Dallas County. These shells may have been these *nodulata*-like shells or an extremely angulate *Quadrula apiculata*.

*Quadrula apiculata* (Say, 1829) ranges from the Rio Grande through all Texas streams to the Alabama River [illegible] The southern maple-leaf mussel is the sec- [illegible] naiad species in Lake Lewisville; 281 [illegible] ken at all 12 sites (table 1). Read [illegible] phenotypes in Dallas County in- [illegible] the present Lake Lewisville: 1) [illegible] pustules extending to the ven- [illegible] Lea 1859" with pustules only on the more dorsal portions of the valves. Read (1954) reported that both forms prefer sand bottoms; "*speciosa*" tended to be found in shallow water while "*forsheyi*" tended to be found in fairly deep water. These morphological types represent genetic variation in the *Q. apiculata* population, but they may also be the result of reduced rates of pustule formation in older individuals. Neel (1941), who treated *apiculata* as a form of *Quadrula quadrula* (Rafinesque, 1820), presented a discussion of the forms of the *Q. quadrula* group.

*Tritogonia verrucosa* (Rafinesque, 1820) has a wide distribution throughout the Mississippi drainage and other Gulf coastal drainages from Georgia to Texas (Valentine & Stansbery, 1971). In Dallas County, Read (1954) found it only in Elm Fork, where it was "perhaps the most abundant species," on hard gravel or sand in fairly deep water in swift current. This species most often has white nacre; pink and purple nacres become more common in the southern part of its range according to Valentine and Stansbery (1971), who found few specimens in Lake Texoma (all of which had white nacre). All specimens located in this study have white nacre. This species is extremely uncommon in Lake Lewisville; no specimens were encountered in the transect censuses (only one specimen was found, at Graveyard Slough, which is near an incoming creek, which would "freshen" the water quality). The rarity of *T. verrucosa* in Lake Lewisville is the result of its requirement for a rapid current of water.

*Lampsilis hydiana* (Lea, 1838) ranges from eastern Texas and Oklahoma eastward to Arkansas and Alabama

(Burch, 1973:20). *L. hydiana* was reported rare in Dallas County by Read (1954), who found it only in Elm Fork. *L. hydiana* is the third most abundant mussel in Lake Lewisville (but is not common in Area I); a total of 213 individuals were counted in 12 transects (tables 1, 2). Shells exhibit phenotypic variation in details of structure of the pseudocardinal teeth, but this variation tends to be ontogenetic (changing with age). Rays are absent, present on the entire shell, or restricted to the posterior half. Rays may be single and narrow (about 0.1 mm wide) or may coalesce into stripes (whose widths approach 3 mm). Spacing between rays varies such that 80% of the periostracum may be greenish in contrast to the yellowish horn color of the background. Variation in shell morphology may reflect genetic influence by *Lampsilis luteola* (Lamarck, 1819), a species that ranges throughout all of the Mississippi River and southern Canada east of the Rocky Mountains (Burch, 1973:21); *luteola* intergrades with *hydiana* in Louisiana and southern Arkansas (Stansbery, 1983).

*Lampsilis satura* (Lea, 1852), the southernmost species of the *Lampsilis ovata* (Say, 1817) group, is restricted to westernmost Louisiana and eastern Texas (D. H. Stansbery, personal communication). A single shell was found in Lake Lewisville at station 7 (table 1). This specimen is small (47.6 mm, shell length) and had been dead for several years before recovery. The umbo is somewhat higher than those of most *L. satura* from eastern Texas. The recovered specimen probably represents a remnant population (possibly now extirpated) adapted to a free-flowing stream. Read (1954) reported *Lampsilis ventricosa* (Barnes, 1823) as rare in Dallas County; this record probably refers to *L. satura*.

*Lampsilis teres* (Rafinesque, 1820) was reported by Read (1954) as being not very abundant in Dallas County on soft mud substrate, but found in the side of a tight mud bank. *Lampsilis fallaciosa* Smith, 1899, has been utilized to refer to a smaller form with greenish rays (not found in Lake Lewisville but found in Elm Fork below Lewisville Dam during this study). Valentine and Stansbery (1971) suggested that *Lampsilis fallaciosa* may have been replaced by *L. teres* in Oklahoma during the twentieth century after they compared their contemporary collections with those of Isely (1924). White and White (1977) reported the two forms from Lake Texoma in similar habitats but in different arms of the reservoir. *L. teres* was found at every locality sampled in this study; a total of 76 individuals were counted in 11 transects (table 1).

*Leptodea fragilis* (Rafinesque, 1820) occurs throughout most of the eastern United States (Valentine & Stansbery, 1971). Read (1954) found *L. fragilis* widely distributed in Dallas County in soft sand and muck. *L. fragilis* was found at all 12 of my sample sites although only 63 individuals were found in eleven transects (table 1). This species was more abundant on sand than on clay substrates, although I found *L. fragilis* in mud at the base of a terrace cutbank in moving water in the Elm Fork above Lake Lewisville.

*Potamilus amphichaenus* (Frierson, 1898), is known from the Brazos, Trinity and Sabine Rivers of Texas and westernmost Louisiana (Strecker, 1931). Despite Frierson's (1898) statement that *P. amphichaenus* was "one of the most distinct and remarkable Unios," this taxon is little known today. Specimens of *P. amphichaenus* from Lake Lewisville can be separated from specimens of *Potamilus ohiensis* (Rafinesque, 1820) from the Red River to the north by the following characters of *P. amphichaenus*: 1) less compressed laterally; 2) more prominent sinus in the posterior portion of the pallial line; 3) prominent umbo scars; 4) much lower wings, anteriorly and especially posteriorly; 5) large gape between the valves, especially anteriorly; and 6) decreased prominence of pallial line anteriorly.

*Potamilus purpuratus* (Lamarck, 1819) occurs in streams from western Tennessee to Kansas, southward to Louisiana, where it is more common in downstream sites (Valentine & Stansbery, 1971). Read (1954) found it abundant in Elm Fork on gravel, hard clay, mud, and sand. *P. purpuratus* is the fifth most common naiad in Lake Lewisville; 88 specimens were counted in 12 transects, and presence was noted in two additional sites.

*Toxolasma parvus* (Barnes, 1823) is the smallest unionid found in this area. *T. parvus* is found in streams from New York to the Dakotas, southward to Texas and Alabama (Valentine & Stansbery, 1971). Live specimens from Lake Texoma were found on silt or soft mud in areas protected from wind disturbance (White and White, 1977). Read (1954) found *T. parvus* widely distributed in Dallas County on mud bottoms in shallow ponds and sluggish streams. The largest *T. parvus* that I have seen from Lake Lewisville were 24.9 mm in length. Only six individuals were found at three transects; additional specimens were found at three other sites. *T. parvus* is a monomorphic (presumably monoeicious) species in comparison to the larger, dimorphic (presumably dioecious) *Toxolasma texasensis* (I. Lea, 1857), a species not known from Lake Lewisville.

*Truncilla truncata* Rafinesque, 1820, is known from the Mississippi River drainage and westward into eastern Texas (Strecker, 1931; Burch, 1973). *T. truncata* was reported from Elm Fork on soft mud, but occasionally in gravel and sand (Read, 1954). Color of periostracum of Lake Lewisville specimens varies from yellowish brown to dark brown; a few specimens have narrow, faint rays. Sixty-nine individuals were collected from 11 transects.

The bivalve fauna of Lake Lewisville as recorded in this survey consists of 16 species (one corbiculid and 15 unionid species). *Amblema plicata* is the most numerous species at all 12 sampling localities and includes well over one-third of the individuals counted. The seven most abundant species in the transects comprise 89.9% of the sample. The seven least common species comprise the remaining 10.1% of the sample. Seven species were found at all 12 sampling sites; 11 species, 9 or more sites. Except for the two species found at only a single locality, all species were found at five or more sites. No site contained all species, but all sites had at least nine.

## DISCUSSION

### ZOOGEOGRAPHY

The unionid fauna present in Lake Lewisville is typical of the West Gulf Province (Roback *et al.*, 1980; Neck, 1982a), which includes the area drained by rivers west and south of the Mississippi River from the Sabine system through the Rio Grande System. The Trinity River drainage abuts the Mississippi drainage just north of Lake Lewisville, where the Red and Trinity Rivers are separated by a low divide. Little or no recent faunal exchange has occurred because of the very limited number of mussel species in the Red River. Along the Coastal Plain the drainages of the Trinity and the Red are separated by the Sabine Neches system.

The species present in Lake Lewisville represent the "upland" component of those species present in the Trinity River. Strecker (1931) recorded several species in the lower Trinity (but not the Elm Fork) that are not present in Lake Lewisville, because the pre-impoundment conditions of the Elm Fork were not suitable for such large-stream or sand-substrate forms. Species included are *Strophitis undulatus* (Say, 1817), *Fusconaia cerina* (Conrad, 1838), *Megalonaias nervosa* (Rafinesque, 1820), *Plectomerus dombeyanus* (Valenciennes, 1827), *Truncilla donaciformis* (I. Lea, 1828), and *Truncilla macrodon* (I. Lea, 1859).

### INTRA-RESERVOIR DISTRIBUTIONS

Lake Lewisville can be divided into three major subdivisions, which are based upon natural and artificial environmental factors (figure 2). Area I consists of the original Lake Dallas; this area is underlain by the Woodbine Formation. The substrate presently consists of silty clays which have been deposited over the past 50 years. This area receives sewage outfall from the city of Denton (1980 population—48,063) and probably several small towns farther upstream. Area II consists of the larger part of the new reservoir portion of Lake Lewisville which is underlain by thin silty clay terraces that mantle the Eagle Ford Formation (shale). Area III is the Hickory Creek Arm of the new lake portion, which is underlain by the Woodbine Formation. Substantial portions of this area maintain sandy substrates although the upper reaches are covered by recently deposited sediments.

The Denton County soil survey provides information concerning soils now covered by Lake Lewisville (Ford & Pauls, 1980). Soil types presently inundated by the original Lake Dallas (area I) include Callisburg fine sandy loam, Gowen clay loam, and Navo clay loam. Soils pres-[illegible] under area II include Altoga silty clay, Ferris-Hei-[illegible] and Heiden clay. Area III inundates Bastrop [illegible] Birome-Rayex-Aubrey complex (sands), [illegible] sandy loam, and Crockett fine sandy loam. [illegible] data concerning relative percent-[illegible] three major subdivisions of Lake [illegible] areas II and III are more similar [illegible] is to area I (table 2). This relationship indicates that, as a factor in this lake's distribution, similar period of impoundment (II and III) is more important than similar geological substrate (I and III). Also important is unrestricted water and organism movement between II and III whereas an old dam structure with a narrow breach exists between I and II; no direct connection exists between I and III. Shallower water depths and decreased water quality in area I may be additional factors.

Except the stream species that are found only near creek entrances and probably do not reproduce within the reservoir (*Lampsilis satura* and *Tritogonia verrucosa*), no species are restricted to only one of these three subgroups. However, as indicated above, area I stands well apart from the other two in terms of faunal composition. For example, the two most common unionids in Lake Lewisville (*Amblema plicata* and *Quadrula apiculata*) together comprise 55.8% of the entire fauna, and the corresponding values for areas II and III are comparable (53.0% and 53.4%, respectively), but in area I these two species comprise 70.6% of the fauna. Area I supports the least diverse fauna and is the area most dominated by species that are tolerant of environmental disturbance by humans.

In contrast to dominance by abundant taxa, the third most common species, *Lampsilis hydiana*, is distinctly least common in area I. The other species that are least abundant in area I are *Anodonta grandis*, *Lampsilis teres*, *Leptodea fragilis*, *Potamilus amphichaenus* and *Truncilla truncata*. *Potamilus purpuratus* is distinctly most common in area I. *Arcidens confragosus* is more common in areas I and III than in area II; this distribution pattern indicates a preference for sandy substrates, possibly in inflowing streams. Rare in all areas are *Quadrula mortoni*, *Anodonta imbecilis*, *Toxolasma parvus*, and *Corbicula fluminea*.

More individuals and more species occurred in areas with clay rather than sand substrates in Lake Lewisville, although a few species are more abundant on sand substrates (*Leptodea fragilis*, *Quadrula mortoni*, *Arcidens confragosus*, and *Tritogonia verrucosa*). Domination of the fauna by one or two species was frequent in clay substrates and rare in sand substrates. Such relative abundance relationships were also observed at several sites in area II where well-developed sand bars overlay shale bedrock. Within areas of clay substrate, unionids were more common on sites with exposure to wave action. Small sloughs in these areas seldom supported more than a few bivalves.

### FAUNAL CHANGE

Several species reported from the Elm Fork by Read (1954) were not found in Lake Lewisville. *Obliquaria reflexa* Rafinesque, 1820, is a species that requires hard substrates and moderate to fast currents. *Obliquaria reflexa* was reported from Lake Texoma (White & White, 1977) only in riprap gravel substrate and substantial wind-generated water movement; this was the only riverine species found in Lake Texoma. I have found *O. reflexa* in the Elm Fork, below Lewisville Dam; isolated individuals could survive in locally favorable micro-habitats within Lake Lewisville, but periodic drought conditions reduce reservoir elevation and feeder creek flows to such low levels that survival of *O. reflexa* is unlikely.

Only two unionid taxa reported by Strecker (1931) from the Elm Fork at Lewisville were not found during this survey. His *Quadrula houstonensis* apparently represented shells referred to *Quadrula mortoni* in this study (see previous discussion). Read (1954) reported Strecker's *Fusconaia flava undata* to be rare in Dallas County, and found only in the southeastern section. Several other species were reported by Read (1954) in Dallas County, *i.e.*, *Lasmigona costata* (Rafinesque, 1820), *Obovaria subrotunda* (Rafinesque, 1820), *Pleurobema cordatum* (Rafinesque, 1820), *Quadrula metanevra* (Rafinesque, 1820) and *Quadrula petrina* (Gould, 1855). These species are not known to have occurred anywhere in the Trinity River; these records appear to represent misidentifications.

Two species not recorded for the Trinity River at Lewisville by Strecker (1931) have established populations in Lake Lewisville. These species are *Anodonta grandis* and *Anodonta imbecillis*; the former has become the fourth most common bivalve in Lake Lewisville. Increase in abundance of these *Anodonta* has been reported by Murray (1982). Causes of this expansion are not understood but probably involve employing a large number of fish species as hosts during the glochidial stage of the unionid life cycle (Trdan & Hoeh, 1982). Read (1954) suggested that fish stocking activities "probably contributed some species . . . since Strecker," but offered no supporting evidence. Changes in the bivalve fauna of this reservoir are similar to those faunal alterations observed in Lake Springfield, Illinois (Parmalee, 1955; Klippel & Parmalee, 1979).

### Human Utilization of Fauna

An additional human impact upon the unionid fauna of Lake Lewisville was observed during this survey. Unionid valve material is being utilized in the cultured pearl industry. The high-purity calcium carbonate of unionid shells (Nelson *et al.*, 1966) is formed into spheres to provide large "seeds" for cultured pearls (Peach, 1983). In August 1978 individual shell collectors were being paid twenty cents a pound (total wet weight of shell and animal) for shells of *Amblema plicata* and *Quadrula apiculata*. At least one collector sold 500 kilograms (1,100 pounds) in a single day. The preferred species was *A. plicata*, which had to measure about 125 mm in length and could not exhibit worn periostracum on the ridges.

Only *Amblema plicata* from the "new lake" (areas II and III in discussion below) were acceptable as shells from the "old lake" (area I) had thin layers with black or purple coloration. *Amblema plicata* from the "old lake" possessed thinner shells than those from other portions of Lake Lewisville, shell material was often heavily suffused with purple, and shells with white nacre did not possess the bright white nacre seen elsewhere in the reservoir. Stansbery (1971) found that young *A. plicata* on fine substrates (similar to silted portions of the "old lake" bed) grew more slowly than *A. plicata* on coarse substrates.

Individual collectors were experiencing the effects of resource depletion as suitable unionids were "becoming hard to find." Unionids in some isolated coves were reasonably safe from collection, but some collectors used boats to get to these sites. Most collectors gathered unionids in water that was less than two meters deep. Unionids were located visually or tactilely (with hands or feet). In deeper water, diving equipment was used. Neck (1982b) reported amounts of shell removed from various Texas reservoirs, including Lake Lewisville. The 500 kilograms of *A. plicata* reported above consist of approximately 1,430 animals with an average weight of 350 grams.

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## APPENDIX

Below is a list of collecting localities on Lake Lewisville, Denton County, Texas, that were used for this study. Numbers are keyed to those in figure 3.

1. Northeast end of "old" Garza Dam, west or "old" Lake Dallas side.
2. Graveyard Slough, 1.75 km south of Shady Shores community.
3. Willow Grove Park, 1.25 km east of center of city of Lake Dallas.
4. East Hill Park, 1.0 km north of spillway of Lewisville Dam.
5. Stewart Creek Park, 1.5 km north of spillway of Lewisville Dam.
6. Hackberry Park, east side of large cove in southeastern portion of Lake Lewisville State Park, 3.6 km west of FM 423.
7. Little Elm bridge on Farm-to-Market Road (FM) 720, southeast portion 1.5 km southwest of community of Little Elm.
8. Cottonwood Park, 1.8 km south-southeast of Little Elm bridge (FM 720).

9. Northeast end of "old" Garza Dam, east or "new" Lake Lewisville Side.
10. Oakland Park, 0.7 km northeast of Copperas Point (across Hickory Creek Arm).
11. Fish-O-Rama (private commercial development), just southeast of boundary of Hickory Creek Park 0.85 km west of IH 35 E.
12. Sycamore Bend Park, 2.9 km west of Interstate Highway 35E.

# A Reaffirmation of the Nomenclatural Status of *Octopus filosus* Howell, 1868, the Senior Synonym of *Octopus hummelincki* Adam, 1936

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## ABSTRACT

Voss (1962) placed *Octopus hummelincki* Adam, 1936 into the synonymy of *Octopus filosus* Howell, 1868, however, the majority of accounts dealing with this taxon since that time have continued to use the junior synonym. The type material of both taxa were reexamined and their nomenclatural histories traced. *O. filosus* is upheld as the correct senior synonym and a complete synonymy is provided.

*Key words:* *Octopus filosus*, *Octopus hummelincki*, Octopodinae

Howell (1868) described *Octopus filosa* from Santa Cruz Island (= St. Croix in the Virgin Islands). The original description, based on the largest of several live animals Howell had seen, is brief but contains details of body morphometry, arm lengths and the number of adoral, uniserially arranged suckers along each arm. Howell (1868:241) commented that the animal was "remarkable for the long and thread-like terminations to the arms . . .". As part of his description of the coloration of the live animal he also noted (p. 241) that "It changes the color of its spots with great rapidity." Howell illustrated the holotype in ventral whole view. In his monographic work on the Octopodinae, Robson (1929) included *Octopus (Octopus) filosus* based solely on Howell's original description and corrected the gender of the specific epithet.

Adam (1936) described *Octopus hummelincki* from Bonaire, Netherlands West Indies based on three syntypes (1 male, 2 females). He noted the presence of a pair of ocelli located between the eyes and the edge of web. The following year, based on the syntypic series, 1937) expanded his description and provided he whole views of two of the types and illus- e hectocotylus, penis, and funnel organ. ell's description alone, Pickford (1945) us into the synonymy of *O. vulgaris* tion of a lack of a clear morpho- een several Floridian specimens of *O. vulgaris* with attenuate arm tips that approached the condition for *filosus* as described by Howell.

Voss (1962), in a report on the cephalopods in the collections of The Academy of Natural Sciences of Philadelphia, reexamined the holotype of *Octopus filosus* and noted (p. 2) the presence of a "faded but distinct ocellus beneath each eye and scattered thin, thread-like papillae on the dorsum of the head and mantle". Based on this combination of characters, particularly the ocelli (to which Howell's comment regarding the changing colors of the "spots" probably refers), Voss established *O. filosus* as the senior synonym of *O. hummelincki*. Voss further noted that due to the use of the name *filosus* by both Robson (1929) and Pickford (1945) [an additional reference to this taxon by Pickford (1946) apparently was overlooked], its use could not be suppressed by plenary power [e.g., invocation of the 50 year rule as defined by The International Code of Zoological Nomenclature (ICZN, 1985: Art. 79)].

Probably because Voss' 1962 paper is relatively obscure and the nomenclatural situation regarding *Octopus filosus* was mentioned only briefly (one paragraph), Adam's *hummelincki* has been maintained and used routinely as the specific epithet for this taxon in subsequent accounts. In turn, Howell's *filosus* has been relegated to remain among the numerous taxa recognized as junior synonyms of *O. vulgaris* and as such is virtually unknown to a new generation of cephalopod workers.

In order to verify the systematic and nomenclatural disposition of *Octopus filosus* and *O. hummelincki*, I reexamined the types of both taxa. The holotype of *O. filosus* (Academy of Natural Sciences of Philadelphia A6450) is a female (ML 36 mm) with maturing eggs, now in fair condition. Indications of both ocelli are extant and the mantle, head, and basal portions of the arms are covered with thin papillae. Two of the three syntypes of *O. hummelincki* were obtained from the Zoölogisch Museum–Universiteit Van Amsterdam (1 male with spermatophores, 1 female, ML 21 and 18 mm, respectively). Both specimens are in excellent condition, the ocelli are distinct, and the mantle, head and arms are ornamented with tall, thin papillae. The only other octopod with similar ocelli found in the Atlantic Ocean is *O. maya* Voss and Solis, 1966, which is endemic to the Gulf of Campeche, Mexico. In addition it attains large size (to 2.0 kg). My reexamination of the types and the known distribution of ocellated octopods from the Atlantic Ocean support Voss' contention that *O. filosus* and *O. hummelincki* are synonyms.

The name *hummelincki* has appeared in 26 accounts including the original description. Of these, five are species catalogues, three others include *Octopus hummelincki* in a dichotomous key only, and two more cite other papers without the addition of new data. The remaining 16 papers (which include 2 unpublished theses) include new information of a systematic, nomenclatural or biological nature. The name *filosus* has appeared in four systematic-type treatments within the last fifty years (Pickford, 1945, 1946; Voss, 1962; Toll, 1988). Additionally it is listed, without comment, in the synonymy of *O. hummelincki* by Burgess (1966) and Roper *et al.* (1984); however, these accounts do not constitute usage as defined in Article 79c(1)i of the ICZN (1985). As previously noted by Voss (1962), Howell's name cannot be suppressed by the use of plenary power (see ICZN, 1985:Art. 79c). As a result, *O. filosus* is here reaffirmed as the senior synonym of *O. hummelincki* and should be used as such. To be the best of my knowledge, the complete synonymy of *O. filosus* is as follows:

*Octopus filosus* Howell, 1868

*Octopus filosa* Howell, 1868:240.
*Octopus filosus*, Robson, 1929:146.—Pickford, 1945:709; 1946:422.—Voss, 1962:2.—Burgess, 1966:770.—Roper *et al.*, 1984:201.—Toll, 1988:209.
*Octopus* (*Octopus*) *rugosus* (= *Octopus vulgaris* Lamarck, 1798), Robson, 1929 (*pars*, only specimen B.M.1903.9.17.9., *fide* Pickford, 1946:424).
*Octopus hummelincki* Adam, 1936:1, 1937:25. Pickford, 1945:745, 1946:414; 1950:139.—Voss, 1949:3, 1953:73; 1956:279, 1962:2, 1968:657; 1975:351; 1976:77.—Rees, 1950:107.—Burgess, 1966:762.—Voss and Solis, 1966:624.—Palacio, 1977:101.—Cairns, 1976:258.—Wodinsky, 1977:947.—Nesis, 1982:302.—Arocha-Pietri, 1983:37.—Roper *et al.*, 1984:201.—Calow, 1987:360.—Mangold, 1987:182.—Hanlon, 1988:252.—Toll, 1988:209.—Vecchione *et al.*, 1989:20.
*Octopus vulgaris*, Pickford, 1945:708 (*pars*, non *O. vulgaris* Lamarck, 1798).

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# *Coelatura* Conrad, 1853, *Caelatura* Conrad, 1865 and *Coelatura* Pfeiffer, 1877 (Mollusca): A Tale of Two Diphthongs

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## ABSTRACT

*Coelatura* Conrad, 1853 is the valid name for the genus of unionid bivalves emended to *Caelatura* by Simpson (1900). The family-group name Caelaturinae Modell, 1942 must be corrected to Coelaturinae Modell. *Caelatura* Conrad, 1865 is the valid name for the genus of barleeid gastropods renamed *Actaeonema* Conrad, 1865. *Coelatura* Pfeiffer, 1877, *Coelatura* von Martens, 1880, *Caelatura* Germain, 1921 and *Ariocaelatura* Germain, 1921 are objective synonyms of *Plegma* Gude, 1911, a genus of helixarionid gastropods. Confusion among these names has resulted from the difficulty in distinguishing between the "ae" and "oe" diphthongs when they are printed as ligatures. The ligature for "ae" in some typefaces is used as an "oe" in others. The only way to be sure of an author's intentions is to compare words of known spelling.

*Key words:* Barleeidae, *Actaeonema*, *Caelatura*, diphthongs; Helixarionidae, *Plegma*; Unionidae, *Coelatura*.

## INTRODUCTION

During routine curation of the mollusk collection at the Academy of Natural Sciences of Philadelphia, we came across a nomenclatural problem in trying to put specimens identified as *Caelatura* in their proper position in the systematic collection. The name *Caelatura* was in use in both the Bivalvia and the Gastropoda, and subsequent research in the literature revealed further problems with misspellings and emendations affecting taxa in three families. Most of these complications stem from the difficulty of distinguishing the "ae" and "oe" diphthongs when they are printed as ligatures, as they were in the texts in which the names considered here were introduced. We have found that the ligature for "ae" in some typefaces is used as an "oe" in others and that the only way to be sure of an author's intentions is to compare words of known spelling. To sort out the confusion caused by these diphthongs and their ligatures, we rely on the provisions of the *International Code of Zoological Nomenclature* (ICZN, 1985). We note at the outset that *ae* and *oe* are regarded as interchangeable for the purposes of homonymy in species-group names (ICZN Article 58), but not in genus-group names, in which a single letter difference is sufficient to avoid homonymy (Article 56b). We also make use of the ICZN's provisions for determining if subsequent spellings are misspellings or emendations, and for determining if emendations are justified or unjustified.

## TAXONOMY

### *COELATURA* CONRAD (BIVALVIA: UNIONIDAE)

In 1853, Conrad named the genus *Coelatura*, with the single included species *Unio aegyptiacus* Cailliaud, 1827. He used the spelling *Coelatura* twice (p. 267, 268), and the distinction between the "oe" and "ae" ligatures is clear in the text. Simpson (1900) used Conrad's genus for a group of African unionid bivalves, but spelled it "*Caelatura*," (p. 820, 862 and in the index, p. 1004). The instance on page 862 looks like it is spelled with an "oe," because there is little difference between the ae and oe ligatures in the italic typeface in Simpson's work. Inspection of words such as "*aegyptiacus*" (p. 821), "*laevigatus*" (p. 600) and "*coelestis*" (p. 905) shows that he used the spelling "*Caelatura*" throughout. This consistent use qualifies as an intentional emendation (ICZN Article 33b(i)). As there is no evidence in Conrad's text that *Coelatura* is an original misspelling, the emendation is unjustified and introduces the name *Caelatura* Simpson, 1900, which is a junior objective synonym of *Coelatura* Conrad, 1853 (Article 33b(iii)), and is also a junior homonym of *Caelatura* Conrad, 1865 (Gastropoda). Most authors after Simpson incorrectly used the name *Caelatura*, rather than *Coelatura*, exceptions being Vokes (1980:96) and Vaught (1989:124). Modell (1942:190) introduced the subfamilial name Caelaturinae based on the emended spelling of *Coelatura* and Starobogatov (1970:64) used the tribal name Caelaturini. These must be corrected to Coelaturinae Modell, 1942 and Coelaturini Modell, 1942 (Article 35d(ii)).

There is also a question as to the correct spelling of the name of the type species of *Coelatura* Conrad. Cailhaud (1823–1827) rendered it *Unio aegyptiacus* in the text (p. 263), but *Unio egyptiacus* in the plate caption (pl. 61, fig. 5–6). Most authors have used the spelling found in the text, which was published in 1827, but the plate might have been published before then as the atlas was issued in parts between 1823 and 1827 (Sherborn & Woodward, 1901:334). From the available evidence, we cannot prove that the plates were issued before the text, so we retain the spelling "*aegyptiacus*."

### CAELATURA CONRAD (GASTROPODA: BARLEEIDAE)

In 1865, Conrad published a catalogue of Eocene and Oligocene shells of the United States, in which he introduced the name *Caelatura* (Conrad, 1865a). He included the species *Pasithea sulcata* Lea, 1833 and *P. striata* Lea, 1833 in *Caelatura*, which he placed in the Terebridae on page 28. However, he also listed *Caelatura* in the Acteonidae on page 35, including only *Pasithea striata*. Tryon (1865), the editor of Conrad's paper, stated that *Caelatura striata* and *sulcata* both should have appeared on page 35, not on page 28. Later in the year, Conrad renamed *Caelatura* as *Actaeonema* (1865b:147), citing page 35 and not page 28 of his earlier work, and illustrating *Actaeonema striata* (pl. 11, fig. 2). He did not state why he replaced the name. One might assume that he replaced *Caelatura* because of its similarity to the prior *Coelatura*, but Ponder (1983) argued that Conrad meant to restrict the name *Caelatura* to *Pasithea sulcata* on page 28 and to provide a new genus for *Pasithea striata* on page 35. This interpretation is demonstrably incorrect because of Tryon's editorial correction and because Conrad later (1866:9) included both *sulcata* and *striata* in *Actaeonema* and no longer used *Caelatura*. Thus, both *Pasithea sulcata* and *P. striata* Lea, 1833 are originally included species in *Caelatura*, and *Actaeonema* must be regarded as a replacement name for it and therefore an objective synonym.

There is also confusion regarding the type species for *Caelatura* Conrad, 1865. We note that because *Caelatura* and *Actaeonema* are objective synonyms, the first valid type designation for either is a type designation for both (Article 67h). Some authors (Tryon, 1887:53; Fischer, 1885:779) have given *Pasithea striata* as an example of *Actaeonema*, which does not qualify as a type designation. It should be noted that Palmer (1937:154) demonstrated that Conrad (1865b) misidentified *Pasithea striata* Lea, the species he figured (pl. 11, fig. 2) is [illegible] *ellata* Lea, a mathildid. Palmer (1937:68) sug[illegible] *P. striata* Lea is based on a turritellid pro[illegible]tion of the type lot (ANSP 5502) confirms [illegible] is not a barleeid or a mathildid, but [illegible] turritellids are uncertain, as indicated [illegible]. Because Conrad (1865a) cited only *P. striata* and *P. sulcata*, his later (1865b) misidentification of *Pasithea striata* has no bearing on the type species question, a point not realized by later authors. Palmer (1937:156) and Moore (1962:98) treated *Actaeonema striata* as a species described by Conrad, but this is incorrect, as Conrad was merely introducing a new combination. Cossmann (1893:29) stated of *Actaeonema striata* (Lea):

> Il y a lieu de remarquer que ce n'est pas cette espèce qui est le véritable type du genre *Actaeonema*, mais *Pyramis striata*, Conrad, c'est à dire *Pasithea sulcata* ou l'espèce précédente [*Actaeonema sulcatum* (Lea)], de sorte que l'on peut désormais fixer, d'une manière beaucoup plus certaine, les caractéres de ce genre.

Cossmann thus equated Conrad's misidentification of *Pasithea striata* with *P. sulcata* Lea (Conrad had synonymized them as *Pyramis striata* in 1834), but this is incorrect as shown by Palmer (1937). Because Cossmann's statement is ambiguous, it does not qualify as a type designation (ICZN Article 67c(3)). Cossmann later (1921:49) explicitly cited *Pasithea sulcata* Lea as the type species of *Actaeonema*; this is the first valid type designation that we have found. Ponder (1983:244) recognized *P. sulcata* as the type species of *Caelatura*, which he placed in the Barleeidae, but incorrectly considered *P. striata* to be the type of *Actaeonema*.

### COELATURA PFEIFFER (GASTROPODA: HELIXARIONIDAE)

Pfeiffer (1877:8) also named a *Coelatura*, type species, by monotypy, "*H. coelatura* Fér." [= *Helix* (*Helicogena*) *coelatura* Férussac, 1821], a Mascarene land snail. Von Martens (1880:192) used *Coelatura* as a subgenus of *Pachystyla* without attributing authorship to the name, but he included "*Pachystyla caelatura* Férussac (*Helix Helicogena*)," among other species, so it appears at first that he was referring to Pfeiffer's genus. However, von Martens (1881:74) cited himself as having introduced *Coelatura* in 1880. Therefore, we select *Pachystyla caelatura* (Férussac) [= *Helix* (*Helicogena*) *coelatura* Férussac, 1821], by reason of virtual tautonomy, as type species of *Coelatura* von Martens, 1880, making it an objective synonym of *Coelatura* Pfeiffer, 1877. *Coelatura* Pfeiffer non Conrad was replaced by *Plegma* Gude, 1911 and is now placed in the Helixarionidae. (Helicarionidae is a misspelling based on the unjustified emendation of *Helixarion* Férussac, 1821 to *Helicarion* by Férussac (1822) (Kennard, 1942).)

Some authors (*e.g.*, Zilch, 1959:308) consider Pfeiffer's *Coelatura* to have been emended to "*Caelatura*" by Fischer. However, Fischer spelled *Coelatura* correctly in the text (1883:461); it is misspelled in the index (1887:1339), as noted by Schulze *et al.* (1927:482), but this cannot be construed as an emendation, and has no nomenclatural standing. The first author to have emended Pfeiffer's *Coelatura* to *Caelatura* appears to be Germain (1921:103), apparently because he thought that the correct spelling of the type species was *Helix caelatura*, not *Helix coelatura* as given by Pfeiffer (1877:192). However, this is an unjustified emendation because Pfeiffer's *Coelatura* cannot be considered an incorrect original spelling based on evidence in Pfeiffer's text (ICZN Article 32c(ii)). Further complicating matters, Germain (1921: 461), who was unaware of Gude's *Plegma*, introduced *Ariocaelatura* as a replacement for Pfeiffer's name when he realized that it was preoccupied. Thiele (1931:615) and Viader (1937:79) considered *Ariocaelatura* and *Plegma* to be distinct genera although they are objective synonyms. Wenz (1947) introduced the name *Pseudocaelatura* for *Ariocaelatura* "Thiele" non Germain, with type species *Pachystyla scalpta* (von Martens, 1877). Wenz's name is preoccupied by *Pseudocaelatura* Germain, 1921 and was replaced by *Dancea* Zilch, 1960.

There has been confusion as to the correct spelling of the specific name of *Helix* (*Helicogena*) *coelatura* because of inconsistencies in Férussac's work (1819–1832). The species was illustrated on plate 28 (fig. 3, 4), the caption of which was published on 6 April 1821. A second reference to the plate appeared later that year in Férussac 1821a (p. 30 of the quarto edition, p. 34 of the folio), which was published 26 May 1821 (dates from Kennard, 1942:109, 1943:122). In the plate caption, the specific name is spelled "*coelatura*," but from inspection of other words in the captions in the same italic typeface, it is apparent that the typesetter often substituted ligatures, using *oe* for *ae*. For example, *acavae* (pl. 33, 35), *acavoe* (pl. 25, 30, 32, 34, 36); *columellatae* (pl. 11, 15, 17), *columellatoe* (pl. 15, 17, 25, 32); and *perforatoe* for *perforatae* throughout. The vernacular descriptor that Férussac gave this species in the caption is "*ciselée*," meaning carved or sculpted, corresponding in meaning to the Latin *caelatura*. However, *coel-* is sometimes used as an alternate spelling for the Latin root *cael-*, so it cannot be proven from the evidence of the original publication that "*coelatura*" is a misspelling. In 1821a (p. 30) and 1827 (p. 302) Férussac used the spelling "*caelatura*," but these do not qualify as emendations as the spelling appears only once in each work. The spelling "*caelatura*" is repeated four times by Deshayes in Férussac and Deshayes (1850:162), which qualifies as an emendation. (Deshayes continued Férussac's work after the latter's death in 1836). In the complete set of plate captions for the work (Férussac and Deshayes (1851 in 1819–1851)) the spelling "*coelatura*" recurs, presumably copied from the original plate captions. Both spellings have been used with about equal frequency in the literature, as shown in the synonymy by Germain (1921:103). The two most recent references to the species that we have found (Zilch, 1959:308; Groh and Griffiths, 1987:39) use the spelling "*coelatura*." Because "*coelatura*" has priority, cannot be proven to be an original misspelling, and does not threaten nomenclatural stability, *Helix* (*Helicogena*) *coelatura* Férussac, 1821 is the correct citation for the type species of *Plegma*. *Helix caelatura* Deshayes in Férussac and Deshayes, 1850 is an unjustified emendation and an objective synonym of it.

### SUMMARY

We have established the status of the following names: valid names are listed first followed by objective synonyms:

*Coelatura* Conrad, 1853 (Bivalvia: Unionidae) [type species, by monotypy, *Unio aegyptiacus* Cailliaud, 1827]
 + *Caelatura* Simpson, 1900
*Caelatura* Conrad, 1865a (Gastropoda: Barleeidae) [type species, by subsequent designation of Cossmann (1921:49), *Pasithea sulcata* Lea, 1833]
 + *Actaeonema* Conrad, 1865b
*Plegma* Gude, 1911 (Gastropoda: Helixarionidae) [type species, by monotypy, "*H. coelatura* Fér." = *Helix* (*Helicogena*) *coelatura* Férussac, 1821]
 + *Coelatura* Pfeiffer, 1877
 + *Coelatura* von Martens, 1880
 + *Caelatura* Germain, 1921
 + *Ariocaelatura* Germain, 1921

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# *Eduardus* Pilsbry, 1930, a Subgenus of *Praticolella* Martens, 1892 (Gastropoda: Stylommatophora: Polygyridae)

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## ABSTRACT

The purpose of this note is to correct a nomenclatural error that occurs in the literature.

Pilsbry (1930:315) erected *Eduardus* as a section of the subgenus *Polygyra* (*Daedalochila*) Beck, 1837, with *P. martensiana* Pilsbry, 1907, as the type and only member. Later, in a brief note, Pilsbry (1937) transferred *P. martensiana* to the genus *Praticolella* Martens, 1892, based on the genital anatomy of specimens collected in 1934 at "Ingenio Agua Buena, near Tamosopo, S.L.P.," Mexico. Pilsbry (1956:30) continued this assignation in a faunal paper on northern Mexico. Both the note and the faunal paper were apparently overlooked by Zilch (1960:580, fig. 2036), who figured *Praticolella* (*Eduardus*) *martensiana*, but incorrectly gave the name as *Daedalochila* (*Eduardus*) *martensiana*. This error was carried over into Richardson's (1986) catalog of species of the Polygyracea. Both *Eduardus* and *Linisa*, which was introduced on the same page, were omitted from Clench and Turner's (1962) "Names Introduced by Pilsbry."

The shell of *P. martensiana*, with its depressed spire and relatively open umbilicus, is quite distinct from those of all other known members of *Praticolella*. It seems advisable therefore to retain *Eduardus* as a subgenus, pending a generic revision, which is much needed although not presently planned by either author of this note. Thus, *Praticolella* comprises four subgenera: *Eduardus*; *Farragutia* Vanatta, 1915; *Filapex* Pilsbry, 1940, and *Praticolella sensu stricto*. Pilsbry (1940) listed *Filapex* as a section, which is equivalent to a subgenus (International Commission on Zoological Nomenclature, 1985: Article 11e).

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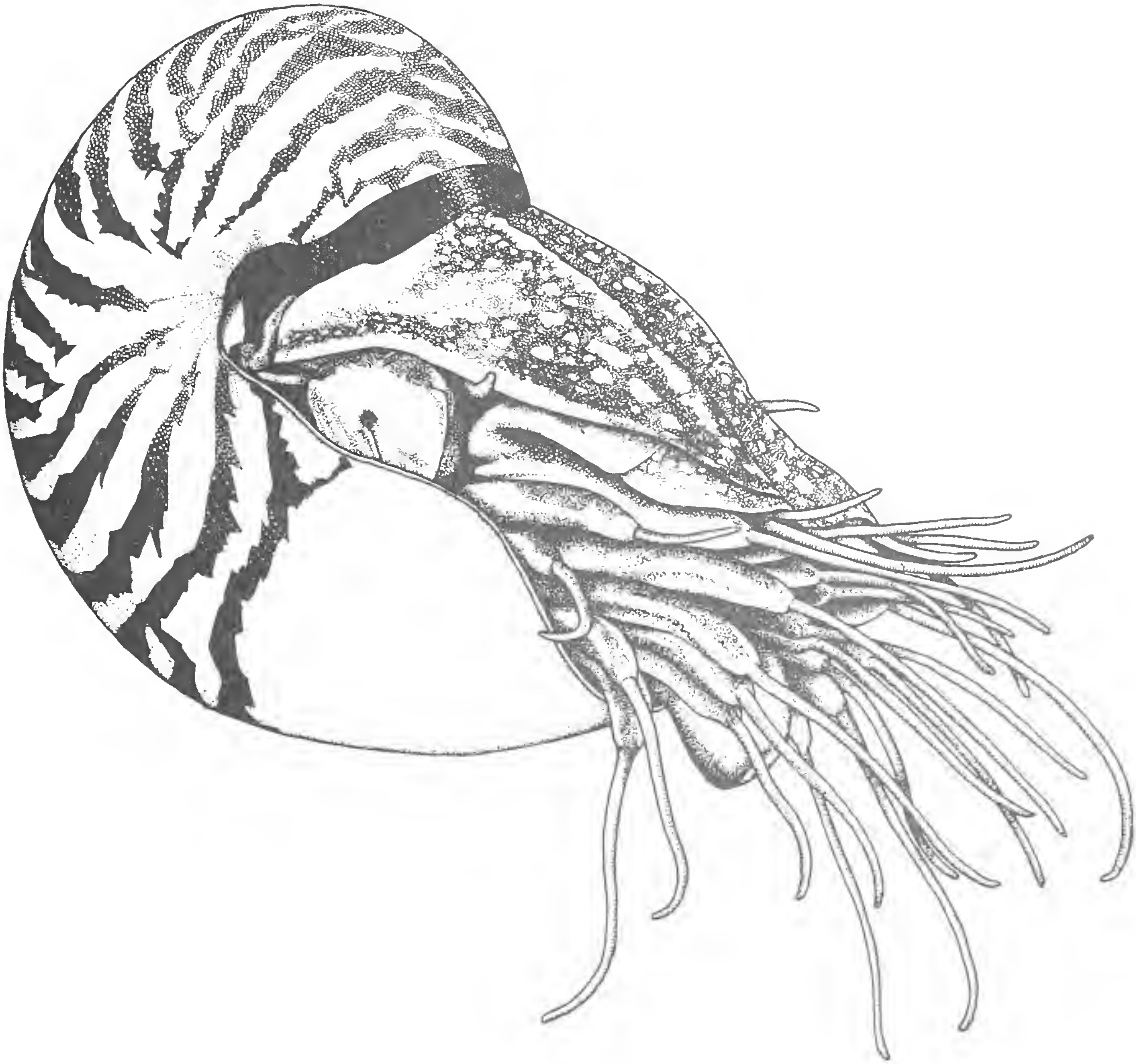

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# Review of the Genus *Colina* H. and A. Adams, 1854 (Cerithiidae: Prosobranchia)

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## ABSTRACT

The types of all nominal *Colina* species were examined as well as numerous specimens in museum collections. Based on this material and gross anatomical study of one species, a diagnosis of the genus is presented. Fourteen species-level taxa have been proposed; of these, three species are recognized herein: the type-species, *Colina macrostoma* Hinds, 1844, *Colina selecta* Melvill and Standen, 1898, and *Colina pinguis* (A. Adams, 1854). The radulae of *Colina macrostoma* and *Colina pinguis* were examined and anatomical features of the latter species were studied for character analysis. Lectotypes for *Colina costatum* and *Colina pinguis* are selected, and *Colina gracilis* is determined a *nomen dubium*. The genus *Colina* is assigned to the family Cerithiidae, subfamily Cerithiinae, near the genera *Bittium*, *Clypeomorus*, and *Cerithium*.

## INTRODUCTION

One of the more poorly known genera of the Family Cerithiidae Ferussac, 1819, is *Colina* H. and A. Adams, 1854. Shells of members of this genus differ considerably from those of all other cerithiids in having an overall pupoid, fusiform, frequently-slender shape, and a markedly constricted body whorl. The genus is not species-rich, but the alpha taxonomy of the group has never been comprehensively reviewed. *Colina* species are not well-represented in museum collections and some appear to be relatively uncommon in their natural habitats. To date, their radular morphology has been obscure and nothing has been published about their soft anatomy.

*Colina* has been assigned to or grouped with a composite mixture of cerithiid and cerithiopsid genera, and its placement among these groups has varied among authors. For example, H. and A. Adams (1856:286) listed *Colina* after *Cerithium* Bruguière, 1789, and *Vertagus* Schumacher, 1817. Tryon (1883:247–248) considered it to be a subgenus of *Cerithium*, placing it between *Cerithioderma* Conrad, 1860 and *Cerithiella* Verrill, 1882. This allocation was obviously based on convergent shell resemblance, as *Cerithioderma* is in Calyptraeoidea, while *Cerithiella* is now considered a member of the Cerithiopsoidea (see Marshall, 1980:85–86). Cossmann (1889:61) believed that the protoconch of *Colina* was unlike those seen in *Cerithium* species and suggested that it was more like that of *Lovenella* Sars, 1878, a cerithiopsoidean. He subsequently pointed out that the name *Colina* was preoccupied and considered it to be a subgenus of *Bezanconia* Fischer, 1884, a fossil taxon, close to *Ataxocerithium* Tate, 1894 (Cossmann, 1906:90). Fossil *Bezanconia* species look very much like living species of *Ataxocerithium*, a group which has been excluded from the Cerithiidae and shown to belong to Cerithiopsoidea (see Houbrick, 1987a). Both Thiele (1929:212) and Wenz (1940:758–759) placed *Colina* within the Cerithiidae, but grouped it with *Ataxocerithium* and other non-cerithioidean taxa. *Colina* was placed after *Vertagus* but before *Campanile* by Fischer (1884:680), thus further linking it with non-cerithioidean taxa (*Campanile* is no longer regarded as a cerithioidean, but has been raised to superfamilial rank, Campanioloidea [see Houbrick, 1989]). Thiele (1929:212) proposed *Ischnocerithium* as a subgenus of *Colina*, but anatomical examination of the type-species of the former taxon shows it to be a typical *Cerithium* representative (Houbrick, pers. obs.).

As seen in the taxonomic history presented above, the composite systematic concept of *Colina* has oscillated between cerithioidean and cerithiopsoidean assignments due to the failure of authors to recognize convergent shell characters in members of both superfamilies. A comprehensive study (Houbrick, in press) of the alpha taxonomy of *Cerithium* Bruguière, *sensu lato*, led to questions about *Colina*, as several species have been attributed to both genera. Examination of the types of the nominal species of *Colina* and study of some preserved anatomical material has revealed a number of interesting characters and has prompted this review, which should expose the genus to more comprehensive studies.

## MATERIALS AND METHODS

The types of all nominal *Colina* species were examined and specimens in major museums were studied to determine the range of variation in shell sculpture. As few preserved samples of *Colina* species were available for anatomical study, the radula and operculum of some species remain unknown. No live specimens of *Colina* were examined. Despite repeated attempts to obtain live-collected, well-preserved specimens, the only available material was unrelaxed, ethanol-preserved specimens of *Colina pinguis*, from eastern Africa. Unfortunately, no adult females were found during the course of this study, and the pallial oviducts could not be studied.

Specimens were dissected under a Wild M-8 dissecting microscope. Radulae and protoconchs were studied using an Hitachi Scanning Electron Microscope.

Abbreviations: AMS, Australian Museum, Sydney; ANSP, Academy of Natural Sciences, Philadelphia; BMNH, British Museum (Natural History); BPBM, Bernice P. Bishop Museum, Hawaii; DMNH, Delaware Museum of Natural History; LACM, Los Angeles County Museum of Natural History; MCZ, Museum of Comparative Zoology; MNHNP, Muséum National d'Histoire Naturelle, Paris; NMW, National Museum of Wales; USNM, United States National Museum; WAM, Western Australian Museum.

As mentioned earlier, morphological characters derived from soft part anatomy are known chiefly from ethanol-preserved specimens of *Colina pinguis* and from one dried specimen of *C. macrostoma*; thus, what follows is incomplete and may be inaccurate, as some anatomical features have been distorted due to poor preservation.

## SYSTEMATIC REVIEW

An overview of the taxonomy, morphology, and the ecology of *Colina* species is presented below. A discussion of the relationship of this genus to other cerithiids and a review of the species follows.

### *Colina* H. and A. Adams, 1854

*Colina* H. and A. Adams, 1854:286, pl. 30, fig. 2 (type species by o.d. *Cerithium macrostoma* Hinds, 1844); Tryon, 1883:247–248, pl. 69, fig. 52, 1887:144, Fischer, 1884:680, Cossmann, 1889:61–62. Thiele, 1929:212, Wenz, 1940:758.

*Colinia* H. and A. Adams, 1858 [emended] Cossmann, 1906: 90–91 (not *Colinia* Nuttall, 1832, Aves); Wenz, 1940:758.

**Diagnosis:** Shell small, elongate, usually decollate, and pupoid with gibbous midwhorls; teleoconch sculptured with axial ribs; body whorl constricted. Columella with strong internal plait. Aperture narrowly ovoid and with expanded outer lip. Operculum corneous, ovoid, paucispiral, with subterminal nucleus. Mantle edge dorsally fringed with papillae. Foot large, having epipodial skirt fringed with papillae and large, posterior operculiferous [illegible] sole with well-developed propodial mucus gland [illegible] centrally located, metapodial mucus gland [illegible] slit like opening. Alimentary system [illegible]ate radula with squarish rachidian [illegible] gland, and stomach with gastric [illegible] Osphradium bipectinate, very broad [illegible] length of mantle cavity and com- [illegible] ments. Pallial gonoducts open. Epiathroid nervous system with long cerebro-pedal connectives.

**Synonymic Remarks:** The name *Colina* was thought to be a secondary homonym of the bird taxon, *Colinus* Goldfuss, 1820, by Cossmann (1906:90–91), who emended the name to *Colinia* (preoccupied by *Colinia* Nuttall, 1832, also Aves). This action was unnecessary, as Article 56b of the *International Code of Zoological Nomenclature* (ICZN, 1985) clearly states that even if the difference between two genus-group names is only one letter, these two names are not homonyms; thus, *Colina* is a valid genus group name, and is not preoccupied.

### *Colina macrostoma* (Hinds, 1844)
(figures 6–44)

*Cerithium macrostoma* Hinds, 1844:27, pl. 26, figs. 11–12 (Holotype [probable]: BMNH 1989181, 10.1 mm; Type locality: Borneo); Sowerby, 1855:877, pl. 184, fig. 219. Sowerby *in* Reeve, 1865: pl. 17, fig. 118; Tryon, 1887:142, pl. 26, figs. 10, 13–15 (in part).

*Colina pupiformis* A. Adams, 1853:176, pl. 20, fig. 14 (Holotype: BMNH 1989182, 13.6 mm, Type locality: Dumaguete, Philippines).

*Cerithium (Colina) costatum* A. Adams *in* Sowerby, 1855:126, pl. 184, fig. 220 (Lectotype, here selected. BMNH 1989180, 11.1 mm; Type locality: not given (not *Cerithium costatum* Defrance, 1817).

*Cerithium pupaeforme* A. Adams. Sowerby, 1855:877, pl. 184, fig. 221; Sowerby *in* Reeve, 1866, pl. 17, fig. 122.

*Cerithium costiferum* (*emd. pro costatum* A. Adams) Sowerby, 1855:896, pl. 184, fig. 220, Sowerby *in* Reeve, 1866: pl. 17, fig. 117.

*Colina gracilis* H. Adams, 1866:150–151 (Type material not located, no figure given. *nomen dubium*).

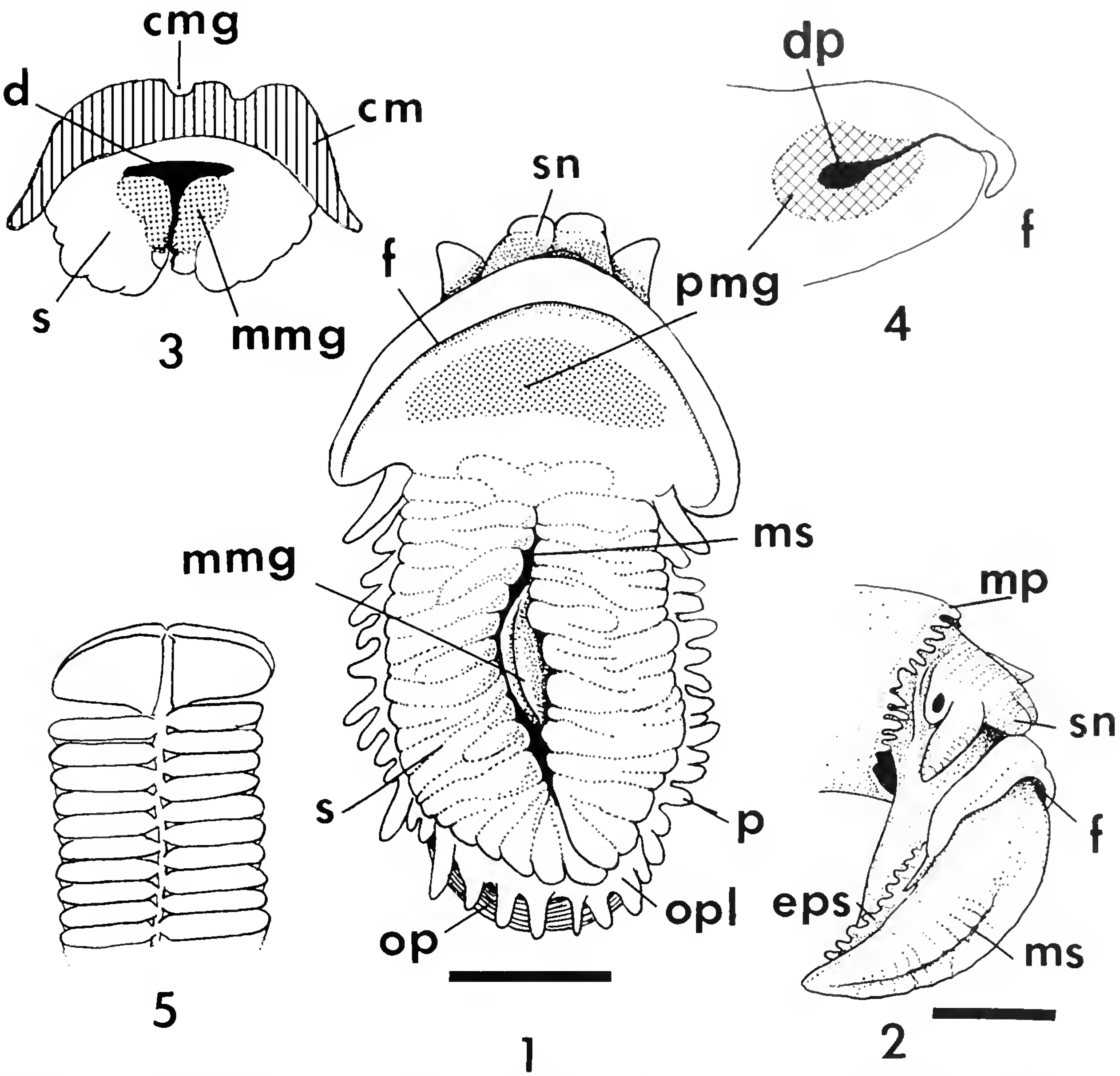
*Colina pygmaea* H. Adams, 1867:308, pl. 19, fig. 20 (Holotype: BMNH 1878.1.28.32, 10.1 mm; Type locality: Borneo).

*Cerithium coarctatum* Sowerby, 1866: pl. 12 [supplementary], figs. 321–322 (Type material not found, Type locality: not given, Sowerby's fig. 32 selected to represent lectotype).

*Cerithium (Colina) macrostoma* Hinds. E. A. Smith. 1884:66–67.

*Cerithium rigens* Bayle, 1880:244 (replacement name for *Cerithium costatum* A. Adams, 1855). Tryon, 1887:142.

**Description:** Shell (figures 6–41): Shell narrowly turreted, elongated, comprising about 15 inflated whorls. Protoconch small, comprising one smooth whorl. Upper teleoconch whorls sculptured with 3 spiral cords and numerous fine axial striae. Adult teleoconch whorls sculptured with about 4 major spiral cords and 4 minor spiral cords; central cord frequently large, carinate; subsutural cord with minute axial pleats. Spiral cords crossed by 12–13 weak to strong axial ribs, forming cancellate sculpture; intersections commonly beaded. Suture moderately impressed, distinct. Body whorl strongly constricted, elongated, sculptured with broad, flattened spiral cords and weak axial striae and incised lines. Aperture ovately elongate with moderately elongate, slightly reflexed canal, concave columella; flaring outer lip of aperture, thick and smooth at edge. Shell color pinkish tan to light brown,

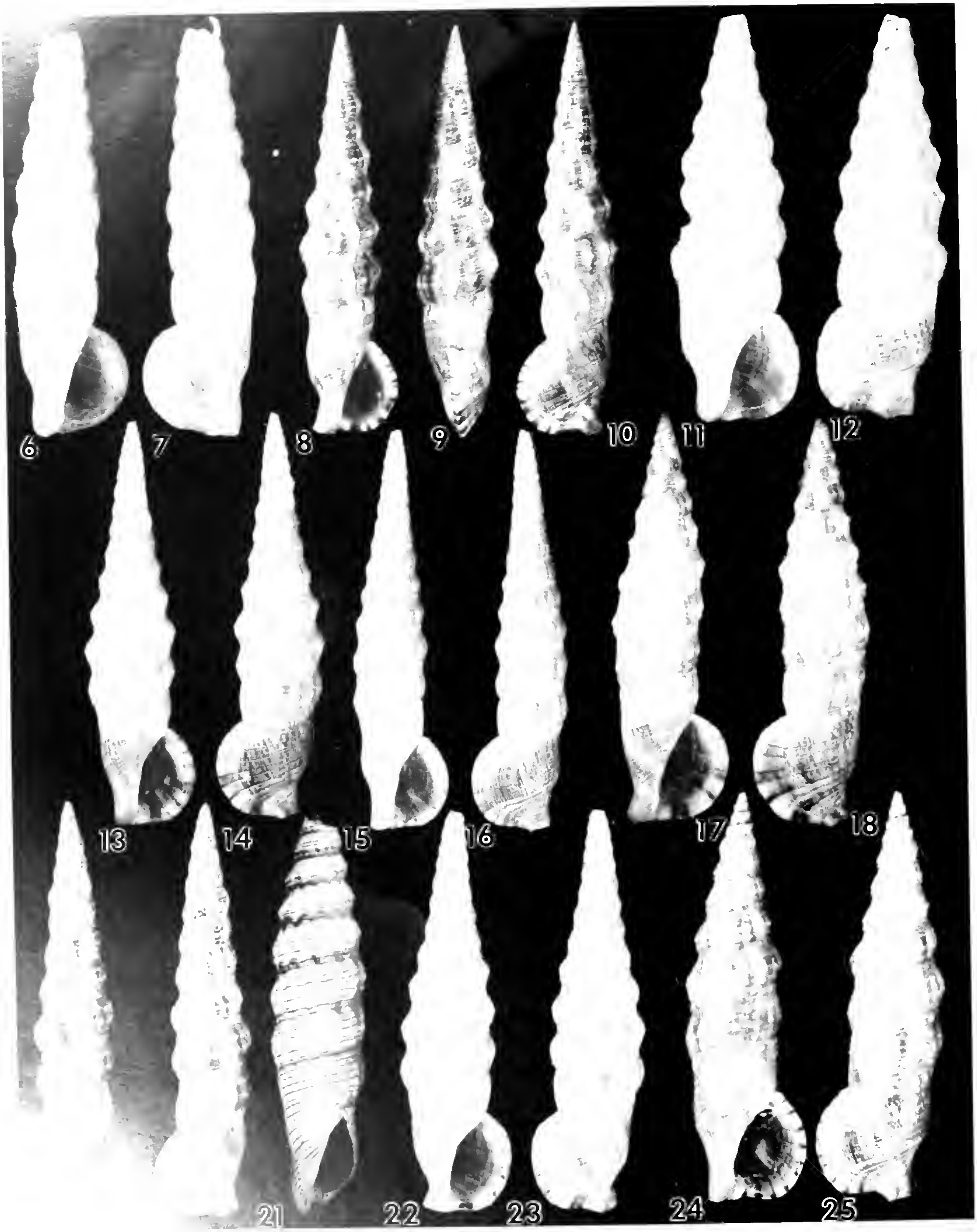


**Figures 1–5.** Anatomical features of *Colina pinguis*. **1.** ventral aspect of the sole of foot, showing crescent shaped propodium, fringing papillae and operculiferous lobe of the epipodial fringing skirt, and two mucus glands, bar = 1 mm; **2.** right lateral aspect showing mantle edge and headfoot, bar = 3 mm; 3, longitudinal cross section through middle of foot showing columella muscle and metapodial mucus gland, **4.** frontal section through propodium showing details of propodial mucus gland; **5.** section of osphradium showing layout of pectens. Abbreviations: cm—columellar muscle; cmg—columellar muscle groove; d—duct of metapodial mucus gland; dp—duct of propodial mucus gland; eps—epipodial skirt; f—flap covering slit into propodial mucus gland, mmg—metapodial mucus gland; mp—mantle papilla; ms—metapodial slit; op—operculum; opl—operculiferous lobe; p—papilla, pmg—propodial mucus gland; s—sole of foot, sn—snout.

with dark brown spiral lines and bands, and blotched with white, especially on beads.

*Radula* (figures 42–44): Radular ribbon small, short, about one-seventh the shell length. Rachidian tooth (Figure 44) with square basal plate having slight median posterior projection and weak lateral fold at each posterior base; cutting edge with median, spade-shaped main cusp flanked on each side by 2–3 pointed denticles. Lateral tooth (figure 44) with rhomboid basal plate having short lateral extension and wide central pillar with small pustule; cutting edge with large pointed main cusp, one inside denticle and 2–3 outside pointed denticles. Marginal teeth (figures 42, 43) spatulate having wide bases and curved tips with long pointed main cusp, 2–3 inner pointed denticles and 2 outer denticles; outer marginal tooth same but lacking outer denticles.

*Animal:* Dried specimen from Japan (ANSP 240281 with papillate mantle edge, moderately long snout and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long, thick cephalic tentacles. Foot long, somewhat tubular in shape, having narrow sole.

**Synonymic remarks:** The type lot of *Cerithium macrostoma* Hinds originally consisted of five specimens glued to boards. The one surviving specimen is labeled "probable holotype": it is the figured specimen in Sowerby's *Thesaurus Conchyliorum* (fig. 219) and in *Conchologia Iconica* (pl. 17, figs. 118a,b). The type of *Colina gracilis* H. Adams has not been found. Considering that the description is ambiguous and no figure was presented, it seems prudent to regard this taxon as a *nomen dubium*. H. Adams (1866) noted its close resemblance to *Colina macrostoma* and later remarked (1866:308) that "The species I lately described as *C. gracilis* I find has been since described by Mr. G. B. Sowerby under the name of *C. coarctata*." Although the type of *Cerithium coarctatum* has not been found, Sowerby's figures adequately represent it, and indicate close resemblance to *Colina macrostoma*. The many synonyms of this species have resulted from the failure of authors to appreciate the wide range of intraspecific shell characters. Recognition of the variability of *Colina macrostoma* was first noted by E. A. Smith (1884:66–67), who suggested that *Colina costata*, *C. costiferum*, *C. pygmaea*, and *C. pupiformis* were all ". . . mere variations of one and the same shell," and who noted the variation in whorl number and shape due to loss of the upper spire. While it may be difficult to believe that extreme phenotypes such as the shells of the nominal species shown in figures 6–41 are conspecific, examination of many museum specimens and the types of the nominal species listed in the above synonymy reconfirms E. A. Smith's conclusion.

*Colina selecta* Melvill & Standen, 1898 (Figures 46, 47), is conchologically very close to *Colina macrostoma*, and may be a synonym of this species, but this remains unresolved, due to lack of comparative material.

**Discussion:** This species is highly variable in shell shape and sculpture. Older adult shells have a truncated, pupate appearance due to decollation of early whorls and erosion of the apex, and these look very different from nondecollate shells (see figures 37, 38, 40, 41). Some specimens lose more of the early whorls than do others. When the apex of the spire has been broken off, the animal closes the opening with a spiral plug and frequently this is inset deeply within the old whorl (figures 33–36).

There is a great intraspecific difference in whorl number and in the number and strength of the axial ribs. A range of phenotypes, from those having extremely slender shells (figures 8–10, 13–16, 19, 20) to those with highly inflated midwhorls with wide axial ribs on their shells (figures 29–34, 37, 38), may occur within the same population. Shell sculpture is highly variable, but generally comprises 4–6 spiral cords of which the dominant one frequently forms a keel on the middle of the whorl. Spiral cords are crossed by 12–14 strong axial ribs presenting an overall cancellate appearance (figures 19, 20, 39). Some phenotypes have small nodes at the intersections (figures 8, 9, 13, 14, 17, 18, 22, 23). The subsutural spiral cord has many minute axial pleats. The body whorl cords are flat and weakly sculptured with about 10 incised spiral lines (figure 39). There is seldom any axial sculpture on the body whorl except for the axial pleats beneath the suture. Shell color varies from light tan to pinkish-brown, the body whorl and especially its incised spiral lines, frequently being brown. These show through on the inside of the outer apertural lip.

Shells from Japan and the Philippines (figures 6–25) are slender and highly elongate, while those from Australia and the Indian Ocean (figures 26–41) tend to be shorter, broader, and more pupate. These shorter phenotypes have been given the names *Colina pupiformis* and *Colina pygmaea*. Initially, I was inclined to recognize these nominal species as a subspecies of *Colina macrostoma* because their shorter, more stocky shells tend to occur in more southern and western geographical regions. However, there are intergrades (figure 39), and non-decollate specimens from these regions bridge the gap. Specimens from these parts of the range are frequently badly eroded and uncommon in collections: when more material is available for study, this putative geographic trend in morphology may become better documented. Currently, there is insufficient material to unequivocally resolve this issue, and it seems best to be conservative and regard these nominal taxa as phenotypes of *Colina macrostoma*.

There is little information about the specific microhabitat of *Colina macrostoma*. In Japan and the Philippines, the habitat appears to be shallow, subtidal sea grass beds (USNM 343907, 273627). Although spawn and larvae of *Colina macrostoma* are unknown, its protoconch morphology (Figure 28) suggests a lecithotrophic type of development (see Robertson, 1974; Jablonsky and Lutz, 1980).

**Geographic distribution (figure 45):** This species appears to be confined to the Indo-West-Pacific, having a distribution from Japan south through the Philippines, Indonesia and tropical Australia, and into the Indian Ocean as far west as eastern India and Ceylon

**Specimens examined:** INDIA: W of Mandapam, Gulf of Mannar (ANSP 302283). CEYLON: (USNM 91248).

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**Figures 6–25.** *Colina macrostoma* (Hinds). **6–7.** lectotype of *Cerithium macrostoma* Hinds, Borneo, BMNH 1989181, length 10.1 mm; **8–10.** Port Douglas, Queensland, Australia, LACM 116089, length 18.9 mm; **11–12.** lectotype of *Cerithium* (*Colina*) *Costatum* A. Adams, BMNH 1989180, length 11.1 mm; **13–18.** Sulu Archipelago, Philippines, LACM 76874, length 15.5 mm, 16.5 mm, 11.6 mm, respectively; **19–20.** Shimoda, Shizuoka Pref., Japan, LACM 93102, length 19.0 mm; **21.** holotype of *Colina pupiformis* A. Adams, Dumaguete, Philippines, BMNH 1989182, length 13.6 mm; **22–23.** Sulu Archipelago, Philippines, LACM 76874, length 15.3 mm; **24–25.** Honshu, Japan, ANSP 240281, length 12.0 mm


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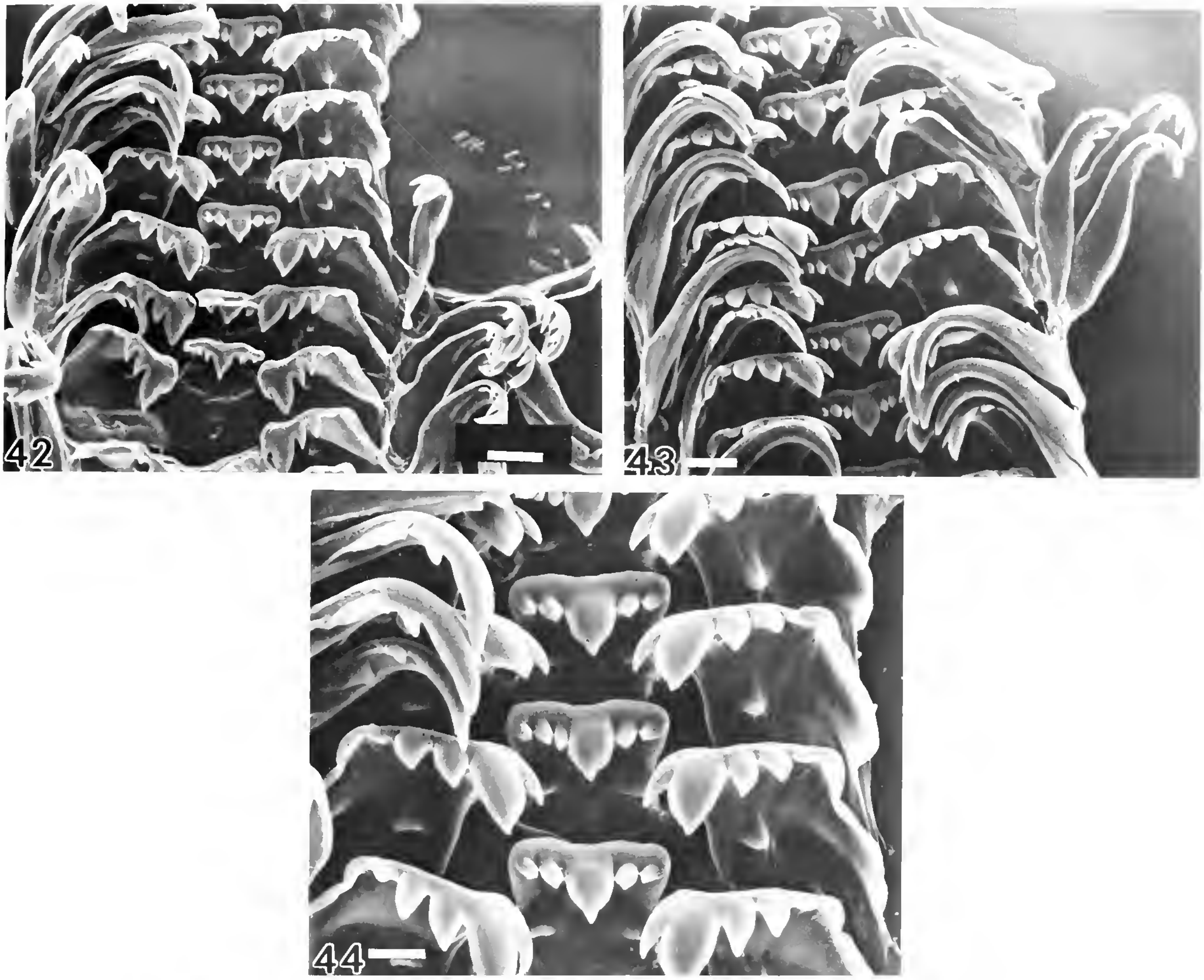

**Figures 42–44.** *Colina macrostoma*, scanning electron micrographs of radula. **42.** portion of radula with marginal teeth spread open, bar = 40 μm; **43.** portion of radula with folded marginal teeth, bar = 40 μm; **44.** detail of lateral and rachidian teeth, bar = 20 μm.

BORNEO. (type-specimen, Borneo (BMNH). JAPAN: Shirahama, near Shimoda, Kii, Shizuoka Pref., Honshu (LACM 93102); Ikenedan (BPBM 229662); Shirahama, Kii, Shizuoka Pref., Honshu (MCZ); Oshima, Osumi, Honshu (USNM 343907, 273627, MCZ); Hachijo Shima, off Tokyo (ANSP 240281, 240158, 240223); Kanada Bay, Kyushu (USNM 91115); Banda, Boshiu (ANSP 65275, MCZ); Hirado, Hizen, Kyushu (USNM 343908, ANSP 1217). RYUKYUS: Loo Choo Ids (ANSP 195629); Ada Village, Kumigami Prov., Okinawa (ANSP 320695). PHILIPPINES: Laminusa, Siasi, Sulu Archipelago (LACM 76874). WESTERN AUSTRALIA: North West Cape Reef, Yardie Creek to Tantabiddi (WAM 1020-84); Mangrove Bay, North West Cape (WAM 1021-84). QUEENSLAND, AUSTRALIA: Gray's Bay, Bowen, Queensland (AMS C117180); 2 mi N of Ellis Beach, Queensland (AMS C117178); Mission Beach, Queensland (AMS C17177); Clump Pt, N Mission Beach, Queensland (BMNH); Dunk Id, Queensland (ANSP 140135, 140136); Four Mile Reef, 4 mi S of Port Douglas (AMS C117175); headland between Kings & Queens Beaches, Bowen (AMS C117169, 117173); Lindeman Ids, N of Mackay (AMS

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**Figures 26–41.** *Colina macrostoma* (Hinds). **26–27.** holotype of *Colina pygmaea* H. Adams, Borneo, BMNH 1878 1.28.32, length 10.1 mm; **28.** protoconch and early whorls, AMS C117177, total length 3 mm; **29–30.** N Mission Beach, Queensland, Australia, BMNH, length 10.7 mm; **31–34.** Ellis Beach, Queensland, Australia, AMS C117178, lengths 9.5 mm, 9.9 mm, respectively. **35–36.** N. Mission Beach, Queensland, Australia, BMNH, length 8.3 mm; **37–38.** Ellis Beach, Queensland, Australia, AMS C117178, length 9.6 mm; **39.** Port Douglas, Queensland, Australia, AMS C117177, scanning electron micrograph, length 9.8 mmm; **40–41.** Hinchenbrook Id., Queensland, Australia, AMS, length 9.3 mm

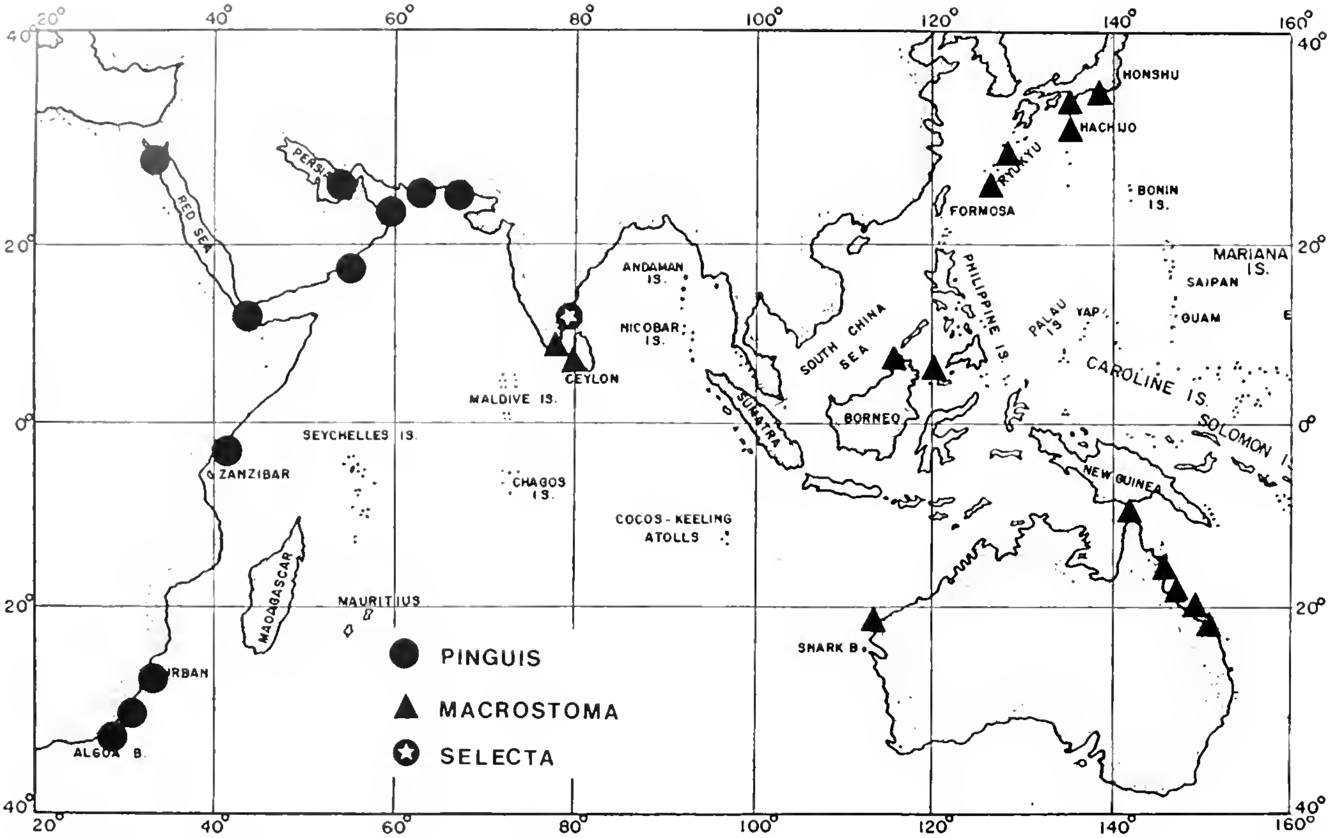


**Figure 45.** Geographic distribution of *Colina* species.

C178174); Hinchenbrook Id, Queensland (AMS); Thursday Id, Torres Strait, Queensland (BMNH 8212697).

### *Colina selecta* Melvill & Standen, 1898
(figures 46, 47)

*Colina selecta* Melvill & Standen, 1898:31, pl. 1, fig. 2 (Holotype: Manchester Museum, 15.1 mm; Type locality: Madras, India).

**Description:** Shell (figures 46, 47): Shell turreted, elongate, narrow comprising about 12 convex whorls having overall cancellate sculpture. Protoconch unknown. Early teleoconch whorls with 3–4 four spiral cords. Adult teleoconch whorls sculptured with 5 spiral cords crossed by 14–15 axial ribs and with subsutural cord pleated axially. Suture impressed. Body whorl elongate, constricted, with about 10 flattened spiral cords, but lacking axial sculpture. Aperture narrow, ovate, with slight siphonal constriction and short, reflected canal and smooth outer lip. Columella concave with slight callus. Shell color [illegible] gray to tan. Operculum, radula and animal un-

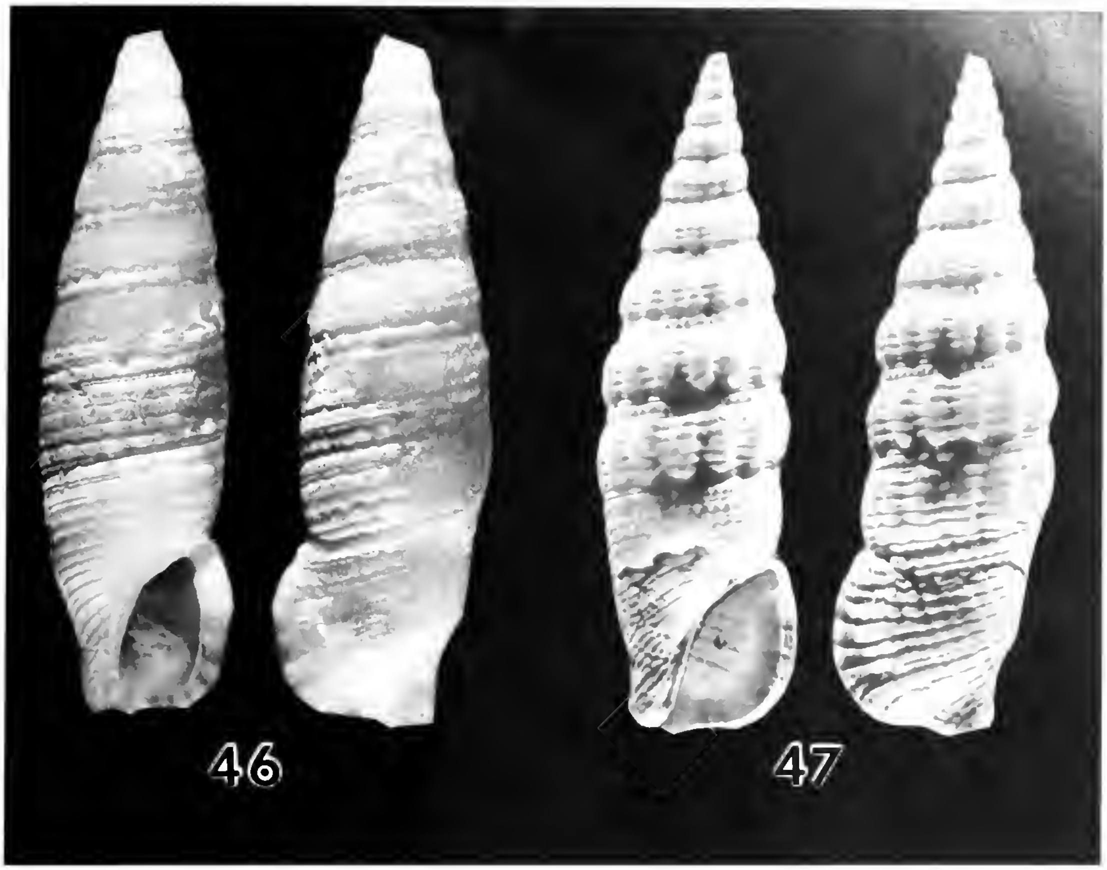
[illegible] species is based solely upon the type [illegible] ng two specimens. It is morphologi- [illegible] *a macrostoma* with which it is geo- [illegible] in India. Melvill & Standen (1898: [illegible] lance of *Colina selecta* to *Colina macrostoma* (cited as *C. taeniatum*), but noted that it was not as pupiform in shape, and not as nodulated transversely. *Colina selecta* has highly cancellate sculpture, a greater number of axial ribs, and an unflaring aperture. Considering the extreme phenotypic variation observed in *Colina macrostoma*, it is not unreasonable to suggest that *Colina selecta* may be merely another variation of the former species. However, *Colina selecta* is known only from a few specimens, and as no specimens of *Colina macrostoma* with intermediate shell sculpture bridging the gap have been seen, it seems best to regard *Colina selecta* as a good species until evidence is presented suggesting otherwise.

**Geographic distribution (figure 45):** The range of this species is limited to the type locality in Madras, India.

**Specimens examined:** INDIA: Madras (type-specimen, Manchester Museum); Krusadi, Madras (paratype, NMW 55158).

### *Colina pinguis* (A. Adams, 1854)
(figures 48–76)

*Cerithium pinguis* A. Adams, 1854:86 (Lectotype, here designated: BMNH 1989200/1, 17.7 mm, 4 paralectotypes, BMNH 1989900/2–5. Type locality: Philippines [in error], here corrected to Cape Natal, South Africa);

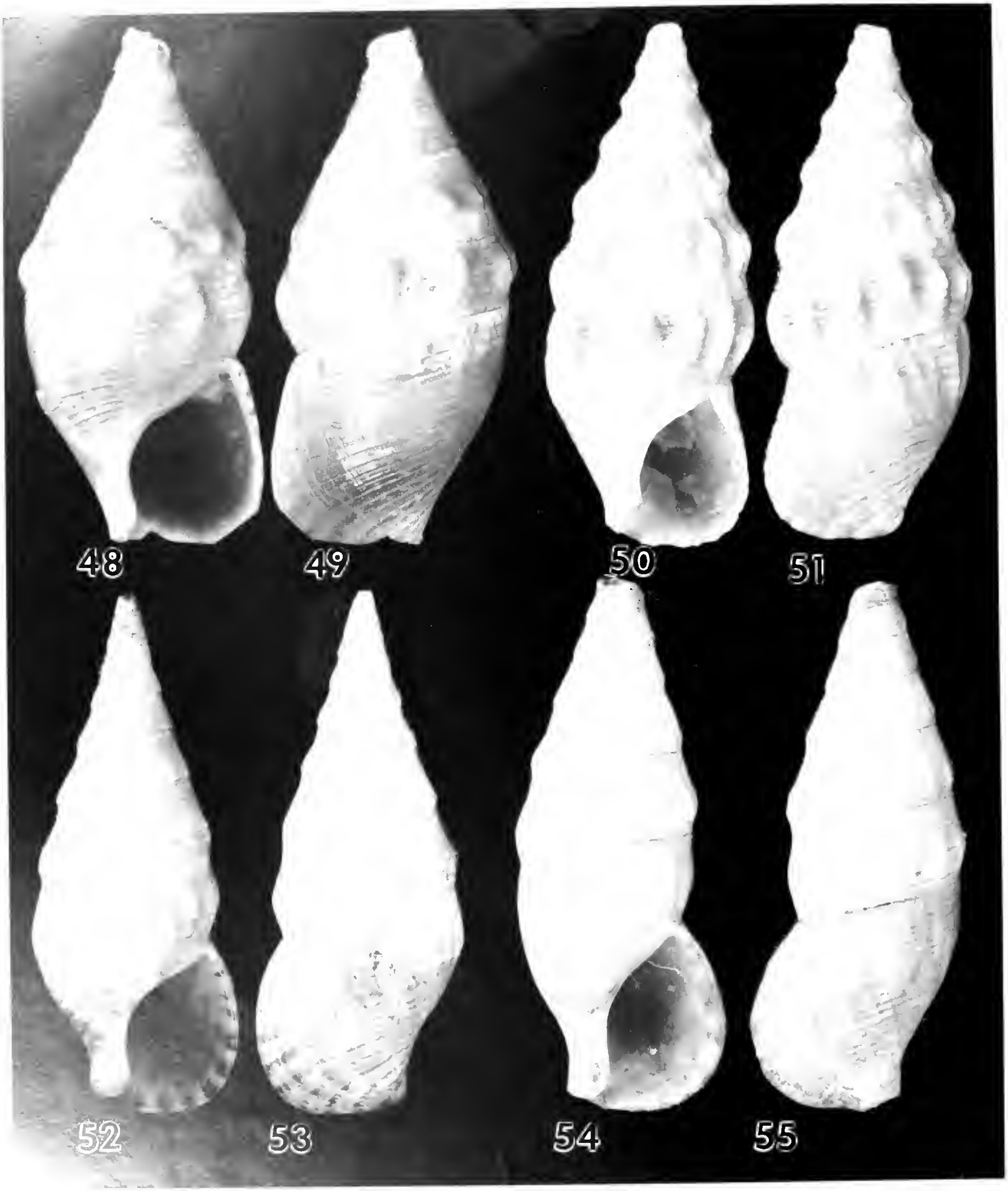


**Figures 46–47.** *Colina selecta* Melvill & Standen. **46.** holotype, Madras, Manchester Museum, 15.1 mm length; **47.** paratype, NMW 55158, 10.5 mm length.

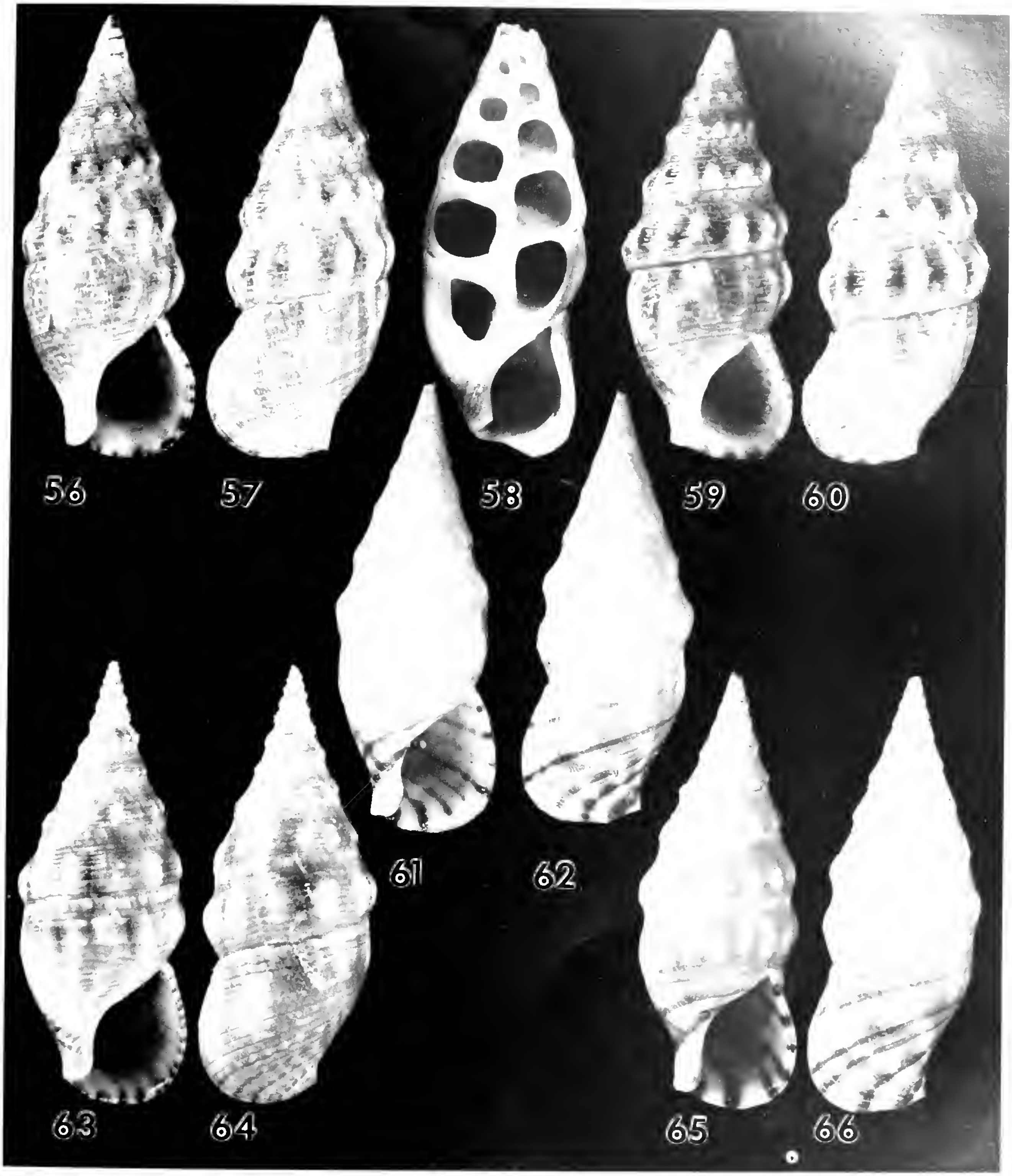
*Cerithium pingue* A. Adams. Sowerby, 1855:877, pl. 184, fig. 217; Sowerby in Reeve 1866: pl. 17, fig. 121.
*Cerithium* (*Colina*) *pingue* A. Adams. Tryon, 1887:141, pl. 26, figs. 8,9,11; Abrard, 1942:61, pl. 6, fig. 28
*Cerithium taeniatum* Sowerby *in* Reeve, 1866: pl. 17, fig. 119 (Holotype: BMNH 1989199; Type-locality: Cape Natal, South Africa, 16 mm (not *Cerithium taeniatum* Quoy and Gaimard, 1834:113); Sowerby, 1866: pl. 17, fig. 320; 1866, pl. 12 [supplementary], fig. 320
*Cerithium contractum* Sowerby, 1855:877, pl. 184, fig. 218 (Holotype: BMNH 1907.10.28.129, 17 mm; Type locality unkown; not *Cerithium contractum* Bellardi, 1850); Sowerby in Reeve, 1866. pl. 17, fig. 120
*Cerithium crumena* Bayle, 1880:245–246 (replacement name for *Cerithium contractum* Sowerby, 1855).
*Colina perimensis* Jousseaume, 1930:285–286 (replacement name for *Cerithium taeniatum* Sowerby, 1866).

**Description:** Shell (figures 48–73): Shell moderately elongate, decollate (adults usually missing 3–4 whorls), adults with plug-like apex; upper whorls with concave outline, convex, swollen middle whorls, and constricted body whorl. Shell shape pupate due to decollation of early whorls and formation of secondary apex. Protoconch comprising about 2 unsculptured smooth whorls with slightly sinuous apertural lip. Early teleoconch whorls sculptured with 3–4 spiral striae; teleoconch whorls concave, pendant; penultimate whorl convex. Adult whorls with overall sculpture of fine spiral striae and incised lines and with 10–14 large axial plicae or ribs on lower half. Body whorl large, elongate, tightly constricted, and weakly sculptured with subsutural plicae and spiral cords. Suture moderately impressed. Aperture narrowly ovoid with short, broad weakly reflexed anterior canal, and smooth dilated outer lip. Columella concave, smooth with slight wash at aperture; 2 internal columellar plaits extending up pillar. Shell color white, with large tan to brown blotches or maculations; thin brown stripes on body whorl appearing as stripes or brown checks at aperture inner lip; axial ribs frequently white. Periostracum tan, thin. Operculum (Figures 67, 68) corneous, ovate, paucispiral with eccentric nucleus.

*Animal* (figures 1–5): Body comprising about four whorls. Long, wide columellar muscle 2 whorls in length; anterior columellar muscle with 2 deep grooves (figure 3, cmg) corresponding to columellar plaits of shell pillar. Cephalic tentacles moderately elongate, but fat and very broad with large peduncular eyes (figure 2); snout moderately elongate, bilobed at tip. Inhalant siphon slightly protruding, with large papillae at edge and darkly pigmented undersurface. Foot large; epipodial skirt fringed with many short papillae (figure 1, p) and having large posterior operculiferous lobe (figure 1, opl); sole with



[illegible] pinguis and types of nominal species. 48–49. lectotype of *Cerithium pinguis* A. Adams from Cape Natal, [illegible] BMNH 1989200/1, 17.7 mm length. 50–51. paralectotype of *Cerithium pinguis*, Cape Natal, South Africa, BMNH [illegible] length. 52–53. holotype of *Cerithium taeniatum* Sowerby, Cape Natal, South Africa, BMNH 1989199, [illegible] 55. holotype of *Cerithium contractum* Sowerby, BMNH 1907.10.28.129, 17.0 mm length.



**Figures 56–66.** *Colina pinguis*, showing variation in pattern and sculptural morphology. **56–57.** Port Alfred, South Africa, DMNH 16073, 17.3 mm length, **58.** shell cut axially to show weak columellar fold, 16.0 mm length, **59–60.** Port Alfred, South Africa, DMNH 16073, 18.5 mm length, **61–62.** Djibouti, Djibouti, MNHNP, 18.5 mm length, **63–64.** Port Alfred, South Africa, DMNH 16073, 16.9 mm length, **65–66.** Djibouti, Djibouti, MNHNP, 15.8 mm length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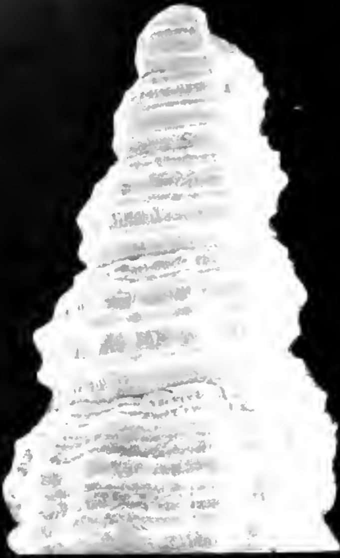
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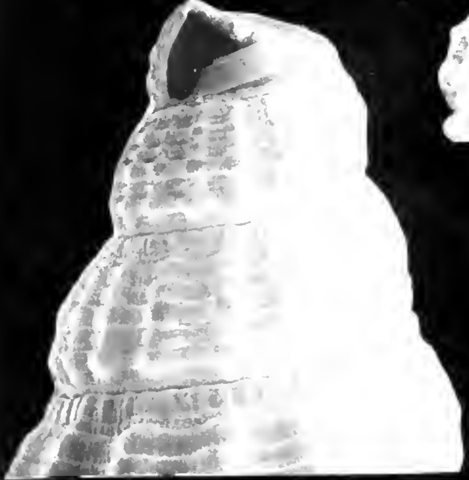
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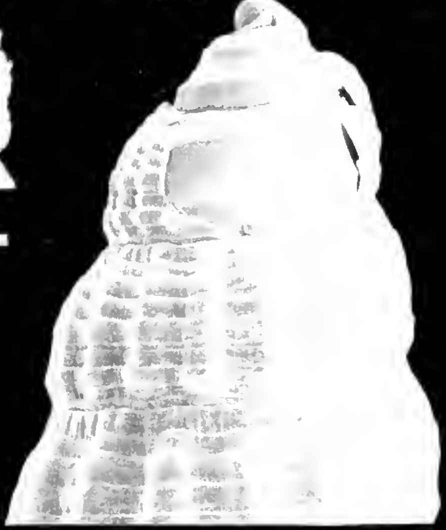
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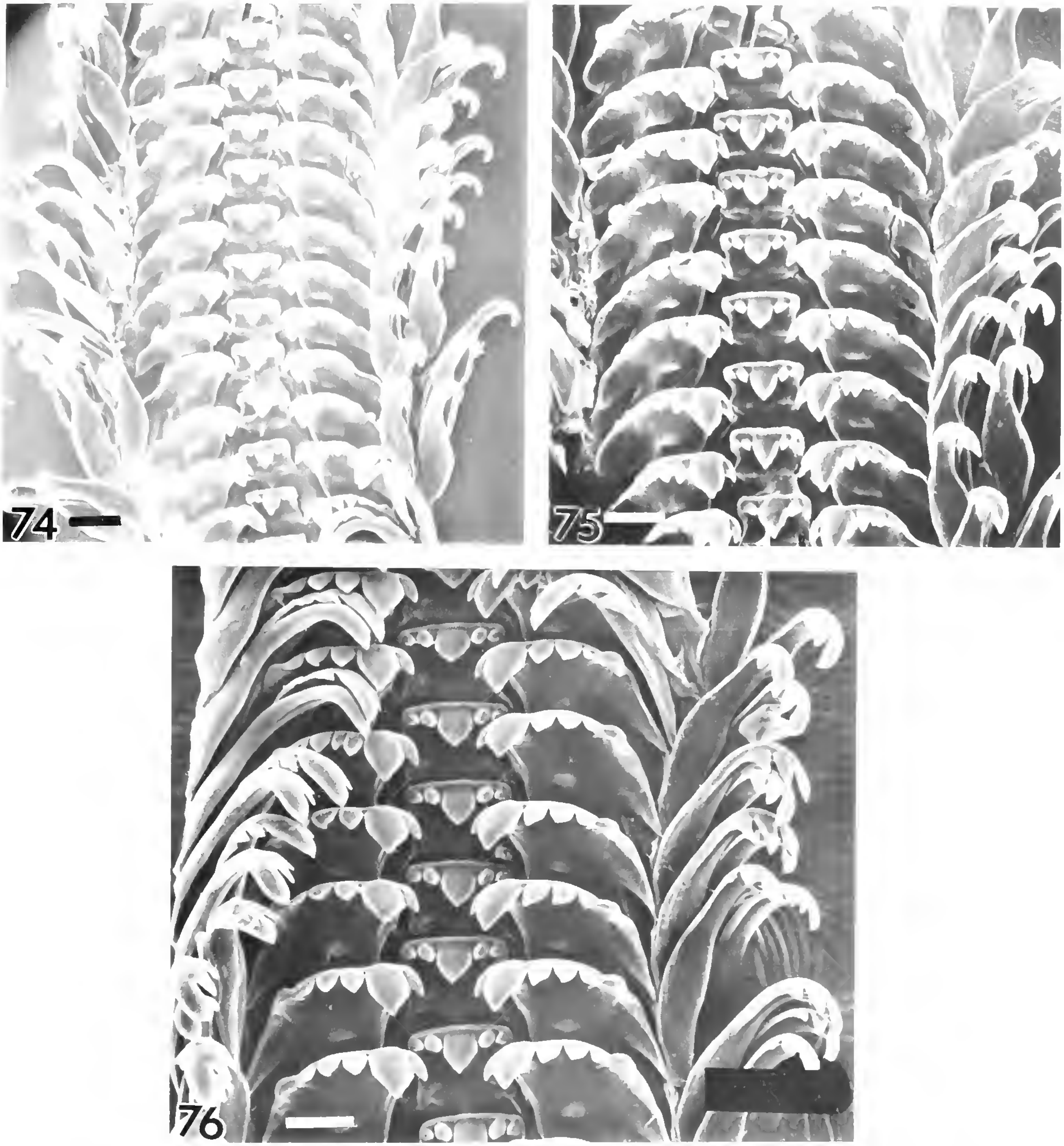

**Figures 74–76.** *Colina pinguis*, scanning electron micrographs of radula (Port Alfred, South Africa, DMNH 16073). **74.** general view of ribbon with marginal teeth spread open, bar = 6 μm, **75.** half row, bar = 6 μm, **76.** detail of lateral and rachidian teeth, bar = 40 μm

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**Figures 67–73.** *Colina pinguis*, scanning electron micrographs of shell and operculum (Oman, BMNH). **67–68.** attached and free sides of the operculum, respectively, bar = 0.9 mm, **69.** early juvenile whorls (protoconch missing), bar = 0.5 mm, **70–73.** lateral and apical views of decollate shell apices, showing broken original shell and replacement plugs, bar (70, 72) = 0.9 mm, bar (71, 73) = 0.5 mm.

[illegible] centrally-located, slit-like metapodial mucus gland (figure 1, mmg) extending deeply within central foot. Propodial mucus gland (figures 1, 4, pmg) crescent shaped, slit-like, extending deeply into front edge of foot, and overlain by thin epithelial flap.

*Radula* (figures 74–76): Radula about one-fifth the shell length. Rachidian tooth (figure 76) with square basal plate having small central bottom projection and with slightly raised fold at each lateral edge; cutting edge convex, with large, central spade-shaped cusp flanked on each side with 2, sometimes 3 small, blunt denticles. Lateral tooth (figure 76) rhomboid-shaped with moderate lateral extension and having wide posterior pillar-shaped extension with small bead; cutting edge comprising small inner denticle, large pointed cusp and 3 small outer denticles. Marginal teeth (figure 76) spatulate, broad at middle, curved at tips; inner marginal tooth with 2 inner denticles, long pointed central cusp and 2 outer denticles; outer marginal tooth same but lacking outer denticles.

**Synonymic remarks:** This species has four synonymous names. The type lot of *Colina pinguis* comprises five specimens, which vary greatly in sculpture and shape. The largest specimen (figures 48, 49), which corresponds to Sowerby's (1855) fig. 217 in the *Thesaurus*, also appears to be the figured specimen of *Colina pinguis* in *Conchologia Iconica* (1866: pl. 17, fig. 121) and is here designated as the lectotype. The second largest specimen of the type lot (figures 50, 51; paralectotype) was figured by Sowerby (1866) in *Conchylogia Iconica* on the same plate (fig. 120), and named *Cerithium contractum*, but this name is preoccupied. The holotype of *Colina taeniatum* (name preoccupied) is a weakly sculptured, non-decollate specimen (figures 52, 53) of *Colina pinguis*, which shows some brown spiral stripes not seen in the type lot. Both *Colina taeniatum* and *Colina contractum* were given replacement names by Jousseaume (1930) and Bayle (1880), respectively.

**Discussion:** *Colina pinguis* is easily distinguished from its congener, *Colina macrostoma*, by its larger, wider, and heavier shell. Its upper whorls are concave and pendant, sculpture is not usually as cancellate as in *Colina macrostoma*, and it never attains the narrowly elongate form of that species. There is no geographical overlap between the two species.

Examination of many lots of *Colina pinguis* from South Africa and from more northern locations reveals considerable sculptural variety within populations (see figures 48–66). Moreover, older, decollate individuals (figures 48–55) have a fatter, more squat aspect than younger, more fusiform individuals with retained spires (figures 56–66). Specimens from the Red Sea (figures 61, 62, 65, [illegible] and northwestern Indian Ocean appear to be more [illegible] colored than those from South Africa.

[illegible]es, commonly recorded from South Africa, [illegible]s in suitable habitats all along the north- [illegible] coast, which is more poorly known. Spec- [illegible] indicate that southern populations are probably continuous with more northern ones in the Red Sea. *Colina pinguis* lives gregariously in lower midtidal pools, chiefly in clumps of coralline algae (Kilburn & Rippey, 1982:54). A label accompanying specimens from Oman in the British Museum (Natural History) collection also cites coralline algae as the habitat. Bosch and Bosch (1982:49) record *Colina pinguis* occurring on sand and algae at low tide in Oman.

The spawn of *Colina pinguis* has been briefly described and illustrated by Kilburn and Rippey (1982:55, fig. 20), who recorded that it is deposited among branches of coralline algae, and consists of a gelatinous mauve string. Their depiction of the egg ribbon shows that it is small, about 10 mm in length, and contains few, moderately large eggs. This feature, plus the unsculptured protoconch, and the patchy, nearly disjunct geographic distribution of the species suggest a direct type of development, but this needs confirmation.

**Fossil records:** This species has been recorded from the Pleistocene of Somalia (Abrard, 1942:61, pl. 6, fig. 28).

**Geographic distribution (figure 45):** *Colina pinguis* occurs along the eastern African coast from South Africa north to Kenya, and then jumping north to the Red Sea, the Gulf of Oman, and Persian Gulf, extending eastward to Pakistan. The single records from Suez and the Persian Gulf need reconfirmation.

**Specimens examined:** RED SEA: Suez, Egypt (USNM 23227). AFFARS & ISSAS: Djibouti (MNHNP). OMAN: Muscat (USNM 798223); Wadi Haart, near Salalah (BMNH); Slud, near Salalah (BMNH). PERSIAN GULF (MNHNP). IRAN: Chah Bahar (MNHNP). PAKISTAN: Manani Rocks, Karachi (BMNH). KENYA: Mombassa (USNM). SOUTH AFRICA: Albany (USNM 97995); Port Alfred, Eastern Cape (USNM 186801, DMNH 16073); Port Gonubie (USNM 845781); Cape Natal (BMNH).

## DISCUSSION

**Shell Morphology and Anatomy:** There are several notable diagnostic shell features of *Colina* species. This genus is easily identified by its unusual fusiform, frequently slender, pupate shell having inflated midwhorls and a highly constricted body whorl. Early whorls are concave in outline, while adult midwhorls are inflated and usually sculptured with large axial ribs. The body whorl is constricted and narrow, relatively weakly sculptured, and has an elongate, ovate aperture. In addition, the upper whorls are frequently decollate and a secondary apex (figures 70–73) is added as a plug, enhancing the pupate shape.

The truncated apex is a distinctive feature of the shell of *Colina* species. Although decollation and formation of a secondary apex occurs in shells of *Cerithidea* species, family Potamididae (Houbrick, 1984), this phenomenon is not seen in other genera of the Cerithiidae nor in members of other cerithioidean families.

The protoconch of *Colina macrostoma* (figure 28) is smooth, comprises one whorl, and is indicative of direct development. It differs totally from the elaborately sculptured protoconchs of litiopids (see Houbrick, 1987b:12, figs. 8, 10) and is unlike those of most *Bittium* and *Cerithium* species that have pelagic veliger larvae. However, *Cerithium* species with direct development have protoconchs similar to those in *Colina* (see Houbrick, 1973; 1974). Cossmann's (1889:61) assertion that the protoconch of *Colina* was unlike those of cerithiids and more like those of cerithiopsids such as *Lovenella*, is probably due to his mistaken notion that the secondary apex of decollate *Colina* individuals (see figures 70–73) he examined was the real protoconch.

Early whorls of *Colina* species are sculptured with three to four spiral cords (figure 69), the two anterior ones being strongest. Kilburn and Rippey (1982:55, fig. 19) noted that "Juveniles resemble very narrow, very high-spired trochids, with a flattened base and short, sharp siphonal spout." Immature *Colina pinguis* shells have a concave outline, and look very much like adult *Trochocerithium* species (see Houbrick, in press).

Of the three *Colina* species recognized herein, *Colina pinguis* has the largest, widest shell (figures 48–66). In contrast, *Colina macrostoma* (figures 6–41) commonly is highly elongate and slender, some morphs attaining almost a nail-like shape (figures 8–10, 14–16, 19–20). This species also has the most variable shell sculpture within the genus. The shell of *Colina selecta* (figures 46, 47) has a sculpture that closely resembles *Colina macrostoma*, but is more finely cancellate.

**Anatomy:** Most of the anatomical knowledge about *Colina* species has been derived from an examination of *Colina pinguis*; thus, anatomical characters may be augmented and/or redefined as the soft parts of other species become known.

Externally, the animal has an overall certithiid aspect and comprises about four whorls. The visceral coils consist of a typical digestive gland and gonad, a stomach about one whorl in length, and a moderately large kidney. The columellar muscle (figure 3, cm) is long and broad, extending nearly two whorls in length, and has two deep anterior grooves (figure 3, cmg) that correspond to the columellar plaits of the shell. The long, broad columellar muscle seen in *Colina* species does not occur in *Bittium* species or in litiopids. The dorsal mantle edge is fringed with papillae (figure 2, mp).

The large foot has an epipodial skirt (figure 2, eps) fringed with papillae along its lateral edges and has a large, posterior papillate operculiferous lobe (figure 1, opl), similar to that seen in many *Bittium* species. The operculum (figure 1, op) overlies the operculiferous lobe. The foot is probably longer and more slender than depicted in figure 1, and the epipodial papillae more tentacular in living snails. The epipodial papillae are short (at least in preserved specimens), and do not appear to be as elongate as in litiopids. In this respect, they are more like the epipodial papillae observed in some *Bittium* species (Houbrick, pers. obs.). The operculigerous lobe of the posterior epipodium of *Colina* species is also similar to that observed in *Bittium* species (see Marcus & Marcus, 1963:75, fig. 80; Houbrick, pers. obs.).

The propodium is crescent shaped (figure 1) and has a long papilla at each side followed by the smaller papillae (figure 1, p) of the epipodial skirt. The leading edge of the propodial sole has a deep slit along its leading edge overlain by a thin propodial flap (figures 1, 2, 4, f). This slit leads into a large deep propodial mucus gland (figures 1, 4, pmg) in the front of the foot. The morphology of the propodial mucus gland of *Colina pinguis* is nearly identical to that of litiopid and *Bittium* species.

The sole of the foot (figures 1, 3, s) is highly glandular, having many transverse furrows and a deep longitudinal slit (figures 1, 2, ms) beginning at the middle of the foot and extending back to its posterior edge. The slit marks the entrance to a massive metapodial mucus gland (figures 2, 3, mmg) having a large duct (figure 3, d) that extends deep into the headfoot to the pedal ganglia. Similar metapodial mucus glands also occur in litiopids (see Houbrick, 1987b:12, figs. 7, 12) and in some *Bittium* species (Marcus & Marcus, 1963:75, fig. 80; Houbrick, pers. obs.). In litiopids and in some *Bittium* species, this gland produces a strong mucus thread, anchoring the animal to the substrate, as seen in *Colina pinguis*. It is therefore reasonable to infer that it has the same function in other *Colina* species.

The ovate, corneous, paucispiral operculum (figures 67, 68) is similar to the opercula of cerithiid species such as *Bittium* Gray, *Cerithium* Bruguière, *Clypeomorus* Jousseaume, *Rhinoclavis* Swainson, and *Pseudovertagus* Vignal, differing only in having a subterminal nucleus.

The cephalic tentacles are very fat, wide, and stubby, each bearing a large eye at its peduncular base. The snout (figures 1, 2, sn) is short and has a bilobed tip. Both the snout and cephalic tentacles are probably longer in living animals.

The dorsal mantle margin has a double fringe, but is smooth ventrally. The upper dorsal part of the double fringe is smooth, while the lower part bears long papillae. This fringed dorsal mantle edge occurs among all members of the Cerithiidae, but is absent in litiopids. The exhalant siphon protrudes slightly, and the dorsal mantle edge adjacent to the inhalant siphon is marked by a deep, left-central cleft, which has enlarged, protruded papillae and a darkly pigmented undersurface.

The mantle cavity is deep and spacious. A very broad bipectinate osphradium (figure 5), comprising tall pectens, tapers posteriorly and extends nearly the full length of the ctenidium. The ctenidium is as long as the mantle cavity, twice as broad as the osphradium, and comprises long, tall leaflets, narrow at their left leading edges and becoming long and shallow to the right. The hypobranchial gland is thick and glandular and as broad as the ctenidium. The rectum is half as wide as the hypobranchial gland and is filled with many white, ovoid stacked fecal pellets. The male pallial gonoduct is open, typically cerithioid, and has many transverse glandular folds along its entire length. These probably comprise the prostate and possibly a spermatophore forming organ, respectively. No spermatophores were found, but as they are typical of cerithioideans, they probably occur in this group as well. The female pallial oviducts are unknown. Although the mantle cavity organs of *Colina pinguis* are typically cerithioid, the very broad bipectinate osphradium is unusual, especially in such a small snail; otherwise, it is typical of those seen in *Cerithium* species (Marcus & Marcus, 1964). In litiopids (Houbrick, 1987b: 13) and some *Bittium* species (Marcus & Marcus, 1963: 78–79, fig. 88, y) the osphradium is monopectinate, while in other *Bittium* species it is a simple ridge (Houbrick, pers. obs.). The morphology of the ctenidial filaments in *Colina pinguis* is very similar to those seen in litiopid and *Bittium* species.

The buccal mass is moderately large, filling the short snout. There are two semilunar shaped prismatic jaws. A pair of thin, tube-like salivary glands coil tightly in front of the nerve ring, but extend through and originate behind it. The taenioglossate radula (figures 42–44 & 74–76) of *Colina* species is of moderate size, about one-seventh the shell length. The rachidian tooth is square, having a cutting edge with a large pointed central cusp flanked by two blunt denticles on each side. The basal plate of the rachidian tooth has a small median posterior extension and a weak raised fold at each lateral edge. The lateral tooth is rhomboid-shaped, having a wide, posterior pillar-shaped extension on the basal plate and a moderate lateral extension. The marginal teeth are spatulate with curved serrated tips. The shape and dentition of the rachidian tooth of the radula of *Colina* species (figures 44, 76) are unlike those of litiopids and many *Bittium* species, which have hourglass-shaped basal plates (see Houbrick, 1987b:12, figs. 13–14; 15, figs. 18–19; Marcus & Marcus, 1963:75, fig. 81): in *Colina* species, the rachidian is more squarish, as in many *Cerithium* species.

The stomach and anterior alimentary tract of *Colina pinguis* are typical of cerithiids and litiopids. Immediately behind the nerve ring, the midesophagus is twisted and expands to form a large esophageal gland whose inner epithelium is thrown into many transverse ridges. Esophageal glands also occur in *Cerithium*, *Clypeomorus* and *Bittium* species (Houbrick, 1974, 1985, in press) and in litiopids (Houbrick, 1987b). The posterior esophagus is a narrow straight tube. The large stomach is lined interiorly with many small ridges and grooves forming complex sorting areas. A raised central pad divides the sorting area; a cuticular gastric shield and a short, but distinct, style sac are present. Although a crystalline style was not observed in preserved specimens, short style sacs and styles occur in *Cerithium* and *Clypeomorus* species Houbrick, 1985). Examination of fecal pellet contents, [illegible] he morphology of the radula and alimentary system, [illegible] ly the sorting surface, gastric shield, and style [illegible] tomach, suggest that members of this genus [illegible] gous herbivores.

[illegible] system is epiathroid. The right cerebral [illegible] are closely joined, but there are very [illegible] connectives. The pedal ganglia lie deep in the foot, each having a statocyst on its inner side. The supraesophageal connective is very long. The ganglia of the nervous system are thus typically cerithioid in layout, but the long cerebro-pedal connectives are notable.

The kidney extends posteriorly, about one-half of a whorl in length. Only one lobe was discerned, and there is a large kidney opening into the posterior mantle cavity.

**Ecology:** Very little has been recorded about the habitats and life histories of *Colina* species. In the original description of the genus, H. & A. Adams (1854:286) remarked that "The species known are inhabitants of deep water, living in coarse sand. . . ." This statement appears to be erroneous, as museum records of all species examined cite intertidal to shallow subtidal habitats. The few data available from collection records indicate that *Colina* species are closely associated with weedy or algal substrates.

*Colina* species appear to use a thread of mucus produced by the large metapodial mucus gland to anchor themselves to their algal substrate in much the same way that litiopids (Houbrick 1987b:11) and some *Bittium* species do (Houbrick, pers. obs.). This phenomenon has been observed by Kilburn and Rippey (1982:55), who recorded that *Colina pinguis* ". . . anchors itself with elastic threads."

**Conclusions:** *Colina* is not a speciose genus and does not have an extensive fossil record, only one Pleistocene record being recorded (Abrard, 1942:61). Although some external anatomical characters such as the epipodial skirt fringed with papillae, a large papillate operculiferous lobe, and deep propodial and mesopodial mucus glands are similar to those seen in species of *Alaba* H. & A. Adams 1853, and *Litiopa* Rang, 1829, family Litiopidae (see Houbrick, 1987b), the combination of shell and other anatomical features are more like those observed in members of the Cerithiidae, especially in *Bittium* species. In addition, some *Bittium* species have a mesopodial mucus gland. These include a shell with a distinct siphonal canal and a protoconch similar to those *Bittium*, *Cerithium*, and *Clypeomorus* species with direct development. The attached surface of the operculum of *Colina* (Figure 67) does not have the spiral ridge seen in litiopid species (see Houbrick, 1987b:10, fig. 1), but is more like those of the cerithiids (see Houbrick, 1974; 1985). Other anatomical characters of *Colina*, absent in litiopids, include the fringed papillate dorsal mantle edge, a long broad columellar muscle, short, fat cephalic tentacles (which may be artifactual), a squarish rachidian tooth, and coiled salivary glands (straight tubes in litiopids). With the exception of the long, broad columellar muscle and short, fat, cephalic tentacles, these characters are present in *Bittium*, *Cerithium*, and *Clypeomorus* species.

As the female pallial oviduct anatomy of *Colina* is unknown, comparison of pallial oviducts of cerithiid genera thought to be closely related to it is not possible. Nevertheless, the known shell, radular, and anatomical characters of *Colina* species clearly suggest an assignment of this genus to the Cerithiidae, subfamily Cerithiinae Ferussac, 1819, close to the general *Bittium* Gray, 1847, *Cerithium* Bruguière, 1789, and *Clypeomorus* Jousseaume, 1888. As more knowledge of the smaller-sized and obscure cerithiid genera is accumulated, these data, along with those from *Colina*, can be utilized in a more complete cerithioidean phylogenetic analysis (see Houbrick, 1988). Only then will the generic relationships become clearer and have a more substantial basis.

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# Two Unusual Gastropods From Late Pliocene Lakes in Northeast Nebraska

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ABSTRACT

*Lymnaea (Acella) haldemani* Binney 1867 and *Acroloxus coloradoensis* (Henderson 1930), rare as living species and unusual as fossils, are found in a late Pliocene lacustrine assemblage in northeast Nebraska in association with two extinct taxa, *Omalodiscus pattersoni* (F. C. Baker, 1938) and *Deroceras aenigma*, Leonard 1950. Climatic interpretation, based on the remaining molluscan fauna, suggest the late Pliocene climate, immediately preceeding the first glacial advance, approximated that of the present

During the 1988 field season, Dr. R. G. Goodwin, Department of Geology, University of Nebraska–Lincoln, discovered fossiliferous lacustrine sediments in Knox County, Nebraska associated with a volcanic ash and underlying a glacial till. Dr. M. R. Voorhies, Curator of Vertebrate Paleontology, University of Nebraska State Museum, quarried and processed approximately one metric ton of sediment from the locality now known as the Clark Mills Local Fauna, UNSM KX 143 (figure 1). Mammals recovered indicated a late Blancan age (2.0–2.5 MA) for the fauna, and paleomagnetic analyses indicate that the sediments were deposited in a reversed magnetic field (Matuyama Reversed Epoch) (Voorhies & Goodwin, 1989). On this basis, the ash is identified as Pearlette Type B, fission-track dated at 1.97 MA (Boellsdorf, 1973:39), hence, of late Pliocene age.

In addition to the mammals, an unusually diverse fish fauna was recovered, to include such northern species as walleye (*Stizostedion vitreum*), northern pike (*Esox*, cf. *E. lucius*), muskellunge (*Esox*, cf. *E. masquinongy*), and an undetermined trout (Salmonidae, Gen. et sp. indet.) (Voorhies, pers. comm.). The mollusks recovered while sorting for vertebrates were given to me for study. Further collection of material from this locality in 1989, collected at controlled stratigraphic intervals, was processed specifically for mollusks and ostracods. The larger gastropods were somewhat crushed, but all taxa were identifiable with confidence. A generally typical cool water fauna was identified, suggesting that cool, pluvial conditions existed at time of deposition (table 1). This fauna differed from the typical Pleistocene faunas occurring during pluvial intervals on the High Plains, suggesting additional investigations involving other known fossiliferous deposits in the immediate area. A second locality, some 6.5 kilometers (4 s.m.) north of the Clark Mills Locality, the Nickles Gravel Pit, UNSM KX 109 (Figure 1), was sampled, largely on the report of a late Blancan microvertebrate fauna, an associated ash, and an overlying till (Voorhies, pers. comm.). Samples processed from this locality produced a second molluskan fauna, which matched very well the Clark Mills fauna,

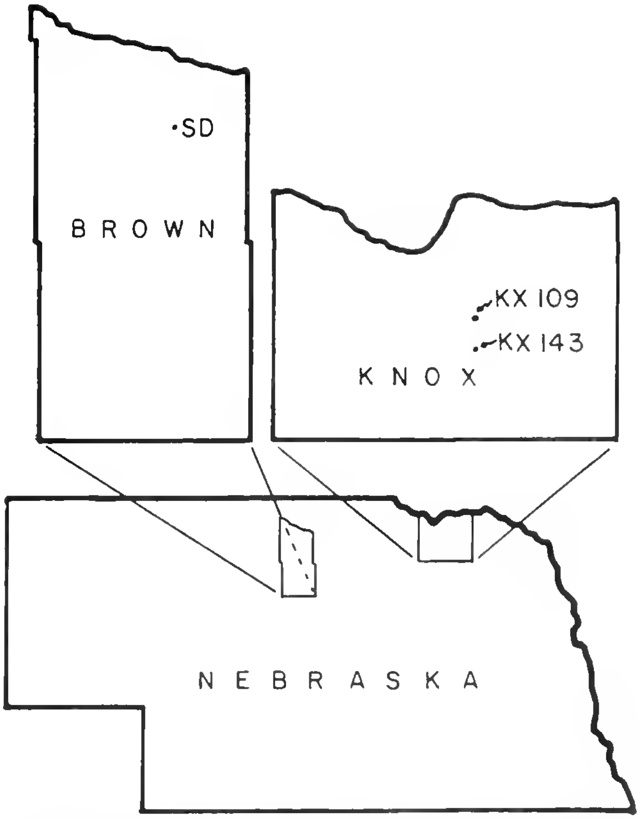


Figure 1. Locality map of Clark Mills Locality (KX 143), Nickles Pit Locality (KX 109), both Knox County, Nebraska and Sand Draw Locality (SD), Brown County, Nebraska

Table 1. Comparison of faunas of the Clark Mills Locality (KX 113), Nickles Pit Locality (KX 109) and Sand Draw Locality 6. Frequency data: VR = 1, R = 2–5, F = 6–15, C = 16–50, A = 51–200, VA = >200. X = Reported by Taylor, 1960, from Sand Draw but not his complete list. * = Extinct taxa, or taxa not known with certainty to still exist locally.

| Faunal list | KX 113 | | KX 109 | Sand Draw |
|---|---|---|---|---|
| | Lower | Upper | | |
| **Gastropods** | | | | |
| **Aquatic** | | | | |
| Valvatidae | | | | |
| *Valvata lewisi* Currier 1868 | F | | | A |
| *V. tricarinata* (Say 1817) | C | | A | R |
| Planorbidae | | | | |
| *Gyraulus parvus* (Say 1817) | A | R | A | A |
| *Promenetus exacuous* (Say 1821) | C | F | A | A |
| *P. umbilicatellus* (Cockerell 1887) | | F | C | VA |
| *Omalodiscus pattersoni* (F. C. Baker 1938)* | R | | | C |
| *Planorbula armigera* (Say 1818) | | VA | VA | X |
| *Planorbella trivolvis* (Say 1817) | C | C | C | |
| *H. anceps* (Menke 1830) | | | R | X |
| Lymnaeidae | | | | |
| *Lymnaea humilis* Say 1822 | A | F | C | A |
| *L. palustris* (Muller 1774) | | | F | C |
| *L. bulimoides* Lea 1841 (?) | | R | R | |
| *L. haldemani* Binney 1867* | R | | | |
| Physidae | | | | |
| *Physella gyrina* Say 1821 | R | A | C | F |
| *P.* sp. (*anatina*?) | | | R | X |
| *Physa jennessi skinneri* (Taylor 1954)* | VR | | R | F |
| Ancylidae | | | | |
| *Acroloxus coloradoensis* (Hend. 1930)* | F | | F | X |
| *Ferrissia meekiana* (Stimpson 1863)* | | | R | X |
| **Terrestrial** | | | | |
| Carychiidae | | | | |
| *Carychium exiguum* (Say 1822) | | | F | X |
| Limacidae | | | | |
| *Deroceras aenigma* Leonard 1950* | R | | R | F |
| Gen. & sp. indet. | R | | R | |
| Succineidae | | | | |
| cf. *Succinea* | R | R | F | X |
| *Oxyloma* sp. | | | F | |
| Pupillidae | | | | |
| *Gastrocopta pentodon* (Say 1821) | | VR | C | F |
| *G. armifera* (Say 1821) 'abbreviata' | | | R | R |
| *G. contracta* (Say 1822) | | | VR | |
| *G. holzingeri* (Sterki 1889) | | | R | |
| *Vertigo ovata* Say 1822 | | | R | F |
| *V. milium* (Gould 1840) | | | VR | R |
| *Pupilla muscorum* (Linn. 1758)* | | | VR | |
| *Pupoides albilabris* (C. B. Adams 1841) | VR | | | F |
| Valloniidae | | | | |
| *Vallonia pulchella* (Muller 1774) | | | VR | X |
| *[illegible] parvula* Sterki 1893 | | | R | |
| [illegible] | | | | |
| *[illegible]minuscula* (Binney 1840) | | | F | R |
| [illegible] (Pilsbry 1890) | | | R | X |

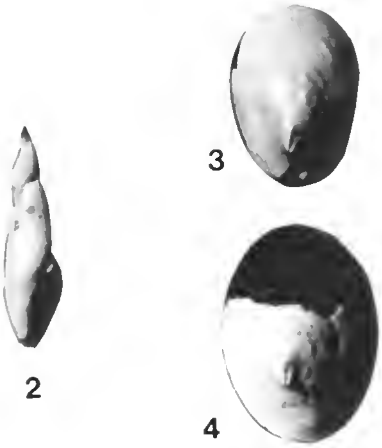
**Table 1.** Continued

| Faunal list | KX 143 Lower | KX 143 Upper | KX 109 | Sand Draw |
|---|---|---|---|---|
| Bivalves | | | | |
| Unionidae | | | | |
| Gen. & sp. indet | | | VR | |
| Sphaeriidae | | | | |
| *Pisidium*, cf. *P. walkeri* Sterki 1895 | A | | C | |
| *P.*, cf. *P. ventricosum* Prime 1851 | C | | C | |
| *Sphaerium partumeium* (Say 1822) | F | F | A | A |
| *S.*, cf. *S. simile* (Say 1816) | | VR | | |
| Ostracodes | A | | F | |
| Large candonid | C | | F | |
| Plant | | | | |
| Chara sp., oogonia | C | | F | |
| *Rhus* sp., sumac nutlets | VA | | | |
| *Celtis* sp., hackberry nutlets | F | | | |

and included a good sampling of the terrestrial gastropods that were poorly represented in the Clark Mills fauna. Table 1 compares these two faunas and a fauna collected at Taylor's (1960:34) Sand Draw Locality 6, Brown County Nebraska, which is supplemented by other taxa reported by Taylor from Sand Draw Localities.

Two unusual gastropod species make the Knox County faunas remarkable. The fauna of the oldest lacustrine section at the Clark Mills Locality, beneath the ash, included three incomplete (2.5–4 whorls), but readily identifiable *Lymnaea (Acella) haldemani* Binney, 1867 (figure 2) and eleven *Acroloxus coloradoensis* (Henderson, 1930) (figures 3, 4). Although no *L. haldemani* were recovered at the Nickles Pit Locality, that fauna did include *A. coloradoensis*. Two extinct species were also found, *Omalodiscus pattersoni* (F. C. Baker 1938), recovered only at the Clark Mills locality, and *Deroceras aenigma* Leonard 1950, found at both localities. For *L. haldemani*, this represents a considerable extension in range, both geographic and stratigraphic. Records of living specimens are restricted to the Great Lakes drainages and the Hudson River system (F. C. Baker, 1928:270; LaRocque, 1968:456). Fossil occurrences have been uncommon, restricted to latest Pleistocene (Wisconsinan) of Ohio (LaRocque, 1968:456), and from two medial Pleistocene (Illinoian) localities in Illinois (Leonard *et al.*, 1971:6). *Acroloxus coloradoensis* is even less common, currently known to exist only in a very few lakes of river systems tributary to the Arctic Ocean or Hudson Bay (Clarke, 1973:263; Mozley, 1926:56), and in a remote mountain lake in Colorado (Walker, 1925:1). Fossil occurrences are only two, the Sand Draw Local Fauna, Brown County, Nebraska, and the Dixon Local Fauna, Kingman County, Kansas (Taylor, 1960:32–40), both of late Pliocene age (late Blancan, 2.2–3.0 MA).

Comparison of the faunas of these two Knox County localities with nearby modern faunas is most instructive. With the exception of the four aforementioned species, over 90% of the mollusks listed in table 1 are currently found living within an approximately 160 kilometers (100 s.m.) radius in northeastern Nebraska, southeastern South Dakota, southwestern Minnesota or northwestern Iowa. The two trees and the fish are also found locally, or within a similar radius. It can, therefore, be inferred that the climate of northeast Nebraska during the late Pliocene, immediately preceding the first glacial advance, was quite similar to, but slightly cooler than, that of today. The presence of lakes in an area presently lacking lakes suggests either greater annual precipitation, or lessened evaporation due to cooler summer maximum temperatures.



Figures 2–4. Unusual Gastropods from the late Pliocene of northeastern Nebraska. 2. *Lymnaea (Acella) haldemani*, KX-143, aperture broken back about ½ whorl. 3–4. *Acroloxus coloradoensis*, broken specimens, 3. KX-143, 4. KX-109. All 10 ×.

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# A New Molluscan Faunule from the Caribbean Coast of Panama

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## ABSTRACT

The Carribbean coast of Panama, particularly the area around the San Blas Archipelago, has been found to represent part of a new subregion of the Caribbean Molluscan Province, and harbors an endemic gastropod fauna. This new faunal division, referred to here as the Blasian Subregion (for the San Blas Archipelago), characteristically contains a large number of Panamic-Caribbean cognate species pairs, and has a distinctive Panamic appearance. Being predominantly a coralline area in an otherwise muddy region of the Caribbean, the Blasian Subregion also contains numerous taxa that are closely related to coral reef-dwelling species from the Bahamas and Florida. The Blasian Subregion ends abruptly at the Golfo de Uraba, on the Panama–Colombia border and, based on peripheral data, may extend northward to the Costa Rica–Nicaragua border. Sixteen new Blasian species are described, including *Turritella marianopsis* n.sp., *Chicoreus hilli* n.sp., *Dermomurex* (*Trialatella*) *cuna* n.sp., *Murexiella edwardpauli* n.sp., *Latirus cuna* n.sp., *Mitra* (*Nebularia*) *leonardi* n.sp., *Prunum leonardhilli* n.sp., *Voluta lacertina* n.sp., *Falsilyria ernesti* n.sp., *Conus brunneofilaris* n.sp., *Conus ernesti* n.sp., *Conus hilli* n.sp., *Conus portobeloensis* n.sp., *Conus rosemaryae* n.sp., *Fusiturricula sunderlandi* n.sp., and *Knefastia hilli* n.sp., and three new Blasian subspecies are described, including *Murex rubidus panamicus* n.subsp., *Oliva* (*Strephona*) *reticularis ernesti* n.subsp., and *Conus granarius panamicus* n.subsp.

*Key words:* Caribbean; Panama; gastropods; San Blas Archipelago

## INTRODUCTION

The southern Caribbean region contains one of the least studied molluscan faunas in the Recent western Atlantic. Although originally thought to house a typical Caribbean tropical molluscan fauna (Valentine, 1973:356), the coastlines of eastern Central America and northern South America are now known to harbor geographically discrete faunules, each differing from one another in species composition (Petuch, 1988). Two of these faunules, one along northern Honduras and eastern Nicaragua, and the other along northern Colombia and the Gulf of Venezuela, were found to contain numerous living archaic genera and species complexes that previously were thought to have been extinct since the late Pliocene (Petuch, 1980, 1981, 1982). These geographically sharply-defined pockets, each with its own characteristic molluscan assemblage, demonstrate that the southern Caribbean is not a faunistically homogeneous region but is, instead, a biogeographical mosaic of small, distinctive faunules.

While the gastropod faunas of coastal Honduras and Nicaragua, and northern Colombia and the Gulf of Venezuela are now better known (Petuch, 1987, 1988), the intervening Caribbean coasts of Costa Rica and Panama have been, to date, poorly studied. Only a single large detailed work has ever been published on the molluscan systematics of this area (Olsson & McGinty, 1958). That paper, however, concentrated on the micromollusca and small macromollusca that were collected in beach drift near Bocas del Toro and Colon, Panama. Nevertheless, the authors described a number of unusual new species (some of which are listed later in this paper) and demonstrated that the Panama coast did not have a typical West Indian-type Caribbean fauna. Houbrick (1968) further showed that several of Olsson and McGinty's new Panama species were also present at Portete, Costa Rica. These range extensions indicate that the Caribbean coasts of Panama and Costa Rica harbor a fourth Central American–northern South American faunal subregion. A year later, Radwin (1969) published a species list of macromollusks that had been collected from dredged spoil piles near Colon. By incorporating the taxa of Olsson and McGinty, this smaller work became the first, and only, compendium of the molluscan fauna of this fourth faunal subregion.

Unlike the Honduran and Colombian mainlands, which have large areas of muddy coastline (*i.e.*, the Gulf of Uraba), the Caribbean coasts of Panama and Costa Rica contain large areas of coral reefs and coralline algal rubble bottoms. Typical of these carbonate areas are the reef platform and coral cays of the San Blas Archipelago and the massive coralline algal reefs and ridges along the Portobelo coast and at Moro Tupo (Vermeij, 1978:88–89). While working with local fishermen who trawl offshore of these carbonate areas, several Panamanian malacologists, in particular Mr. James Ernest of Balboa, have recently collected numerous and important new species of macrogastropods. Since the ranges of the microgastropods of the Caribbean are still very poorly known, the biogeographical implications of Olsson and McGinty's micromollusks, as indicators of a new faunal subregion, are too tenuous. On the other hand, the ranges of the Caribbean macrogastropods, particularly those of the eighteen eutropical index families (Petuch, 1988:6–7), are much better known. In this case, the macrogastropods collected by Mr. Ernest are excellent biogeographical indicators, especially since the ranges of their congeners in Honduras, Nicaragua, Colombia, and Venezuela have recently been established (Petuch, 1987, 1988).

The new taxa described in this paper help to demarcate yet another biogeographical subregion of the Caribbean Molluscan Province. This new subdivision is spatially bounded by the Honduran and Colombian-Venezuelan Subregions (Petuch, 1988; figure 42) and includes the coasts of Costa Rica and Panama. Since the San Blas Archipelago of Panama is the ecological and faunistic archetype, I here refer to this new biogeographical entity as the "Blasian Subregion". Unlike the Honduran and Colombian-Venezuelan Subregions, which contain numerous Pliocene Caribbean relictual taxa, the Blasian Subregion characteristically contains numerous Panamic-Caribbean cognate species pairs (*sensu* Radwin, 1969). Of the nineteen new Blasian taxa described here, seven represent previously-unknown cognate pairs. The other twelve taxa include endemic Blasian members of Caribbean species complexes. Nine gastropod families are represented by the new species, and all of these higher taxa can be used for provincial subdivisional analysis (Petuch, 1988:5–8). Future collecting along the Panama–Costa Rica mainland may uncover sufficient faunistic data to support the elevation of the Blasian Subregion to subprovincial status. At present, not enough information exists concerning the total molluscan fauna and, because of this lack, I prefer to refer to the area as a "subregion".

## THE BLASIAN GASTROPOD FAUNA

As pointed out by Radwin (1969), the Blasian gastropod fauna bears a striking resemblance to the Panamic fauna of western Central and South America, and in particular, the Bay of Panama. For example, unlike the faunas of the adjoining Honduran and Colombian regions, the Blasian area contains a species of the turrid genus *Knefastia* Dall, 1919 (described here), which is normally considered a classic Panamic group. Of particular interest in the Blasian area is the presence of the bizarre vermetid genus *Stephopoma* Mörch, 1860 (Olsson & McGinty, 1958; Houbrick, 1968; Radwin, 1969). Like *Knefastia*, this characteristic Panamic gastropod is found in the Caribbean only within the Blasian subregion. The small, encrusting vermetid, *Stephopoma myrakeenae* Olsson and McGinty, 1958, lives embedded within the coralline algal ridges along Colon and the San Blas Archipelago, and at Portete, Costa Rica, and is characteristic of the unique Blasian lithothamnion community.

The new Blasian members of gastropod cognate pairs are of particular importance in that they underscore the faunal ties to the Panamic–Eastern Pacific areas. Some newly discovered examples of Caribbean-Panamic cognates, based on new taxa proposed in the systematic section of this paper, include: *Turritella marianopsis* n.sp. and *T. mariana* Dall, 1908; *Dermomurex* (*Trialatella*) *cuna* n.sp. and *D.* (*Trialatella*) *cunninghamae* (Berry, 1964); *Murexiella edwardpauli* n.sp. and *M. keenae* Vokes, 1970; *Latirus cuna* n.sp. and *L. centrifugus* (Dall, 1915); *Mitra* (*Nebularia*) *leonardi* n.sp. and *M.* (*Nebularia*) *sphoni* Shasky and Campbell, 1964; *Prunum leonardhilli* n.sp. and *P. curtum* (Sowerby, 1833); and *Knefastia hilli* and *K. olivacea* (Sowerby, 1833).

The Atrato Seaway, the last connection between the Pacific and Atlantic Oceans, closed at the end of the Pliocene (Whitmore & Stewart, 1965; Woodring, 1966; Petuch, 1988), and had its eastern opening along what is now the San Blas Archipelago and the Golfo de Uraba. This area, which was the last to be exposed to the Pacific molluscan fauna, would be expected to have the most Panamic-appearing molluscan assemblages in the Caribbean. The recent discovery of whole suites of new cognate gastropods living along the Blasian area supports this hypothesis. The enclave of Panamic mollusks in the Caribbean, however, is geographically small, ranging from near San Juan del Norte, Nicaragua (near the Nicaragua–Costa Rica border) in the west to the Golfo de Uraba in the east. The broad Honduras-Nicaragua continental shelf, which contains the Honduran Subregion, narrows and ends at San Juan del Norte. At that point, the muddy environment of the Nicaraguan coast shifts to the cleaner carbonate environments of Costa Rica and Panama. A similar situation takes place at the western edge of the Golfo de Uraba, indicating that substrate type is the major limiting factor in the configuration and distribution of the southern Caribbean molluscan subregions. The substrate and bathymetric preferences of some of the new taxa are discussed under the individual descriptions in the systematic section. The entire Blasian Subregion, with its attendant faunule appears to occupy a stretch of coastline of only slightly over 800 km.

The following is a listing of some of the macrogastropods that are presently known to be confined to the boundaries of the Blasian Subregion. Most of these belong to key tropical biogeographical index families (as outlined by Petuch, 1988). Several smaller macrogastropods that were described by Olsson and McGinty (1958) are also listed.

Turbinidae-Liotiinae
  *Arene bitleri* Olsson and McGinty, 1958
Turritellidae
  *Turritella marianopsis* Petuch, n.sp.
Vermetidae
  *Stephopoma myrakeenae* Olsson and McGinty, 1958
Cerithiidae
  *Cerithium caribbaeum* M. Smith, 1946

Muricidae
***Chicoreus emilyae* Petuch, 1987
*Chicoreus hilli* Petuch, n.sp.
*Dermomurex cuna* Petuch, n.sp.
*Murexiella edwardpauli* Petuch, n.sp.
*Murex rubidus panamicus* Petuch, n.sp.
Fasciolariidae
*Latirus cuna* Petuch, n.sp.
Columbellidae
*Nassarina dubia* Olsson and McGinty, 1958
Olividae
*Oliva reticularis ernesti* Petuch, n.subsp.
*Olivella chiriquiensis* Olsson, 1956
*Olivella marmosa* Olsson and McGinty, 1958
Marginellidae
*Gibberula bocasensis* Olsson and McGinty, 1958
*Persicula weberi* Olsson and McGinty, 1958
*Prunum leonardhilli* Petuch, n.sp.
Mitridae
*Mitra* (*Nebularia*) *leonardi* Petuch, n.sp.
Volutidae
*Falsilyria ernesti* Petuch, n.sp.
*Voluta lacertina* Petuch, n.sp.
*Voluta lindae* Petuch, 1987
Conidae
*Conus brunneofilaris* Petuch, n.sp.
*Conus ernesti* Petuch, n.sp.
*Conus granarius panamicus* Petuch, n.subsp.
*Conus hilli* Petuch, n.sp.
*Conus portobeloensis* Petuch, n.sp.
*Conus rosemaryae* Petuch, n.sp.
Turridae
*Fusiturricula sunderlandi* Petuch, n.sp.
*Knefastia hilli* Petuch, n.sp.

## SYSTEMATIC SECTION

The type material of the following new species is deposited in the collection of the Division of Mollusks, National Museum of Natural History, Smithsonian Institution, Washington, D.C., and bears USNM numbers:

Gastropoda
Prosobranchia
Caenogastropoda
Cerithiacea
Family Turritellidae
Genus *Turritella* Lamarck, 1799

### *Turritella marianopsis* new species
(figures 1–3)

**Material examined:** Holotype—Length 58 mm, trawled by commercial fishermen from 65 m depth off Portobelo, Panama, USNM 860523; Paratypes 1–3—same locality and depth as holotype, lengths 52, 44 and 47 mm, USNM 860524.

**Description:** Shell tightly coiled, very elongated, classically turritelliform; whorls with 2 large cords, with the anterior cord being better developed and projecting farther from shell than posterior cord; 2 large cords strongly beaded, giving shell rough appearance; 2 smaller, thin, beaded threadlike cords present between 2 large cords, and 1 thin beaded cord present between posterior cord and suture; shell color brownish-tan with numerous closely-packed, thin, darker brown longitudinal flammules; early whorls pale whitish-tan; beaded cords with alternating light tan and dark brown spots, giving shell speckled appearance; base of shell light tan with scattered tan flammules; aperture wide, slightly rectangular in shape.

**Etymology:** Named for the new species' resemblance to the Panamic *Turritella mariana* Dall, 1908 (. . . "looking like *mariana*").

**Discussion:** *Turritella marianopsis* is morphologically closest to the Panamic *T. mariana* Dall, 1908, especially in shell shape, color pattern, and number of spiral cords, but differs primarily in being more coarsely sculptured, with larger beading and stronger, more elevated spiral cords. Otherwise, the two species are very similar and form an excellent example of a Panamic-Caribbean cognate pair. According to local collectors, *T. marianopsis* is an abundant species at depths of around 60 m, and apparently forms solid beds off the Portobelo coast.

Muricacea
Muricidae
*Chicoreus* Montfort, 1810

### *Chicoreus hilli* new species
(figures 4, 5)

**Material examined:** Holotype—Length 26 mm, trawled by commercial fishermen from 65 m depth off Portobelo, Panama, USNM 860525; Paratypes 1, 2—lengths 24 and 26 mm, same locality and depth as holotype, Leonard Hill collection; Paratype 3—length 24 mm, same locality and depth as holotype, USNM 860526.

**Description:** Shell small for genus, fusiform in shape, thin and delicate; 3 well developed varices per whorl; each body varix ornamented with 4 spines—one large spine on shoulder, one small spine at midbody, and 2 small spines clumped together at body whorl-siphonal canal junction; large spine on shoulder 4 times length of smaller spines; small, scalelike spines sometimes present

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* *Note*: Due to an error in my field notes, I incorrectly gave the type locality of *Chicoreus emilyae* as "off Punta Patuca, Honduras" (Petuch, 1987:65). This erroneous type locality is here emended to "Bocas del Toro, Panama", the locality of the paratype. The other paratypes that came from "off Roatan Is., Honduras", appear to represent another, undescribed *Chicoreus* species, and not *E. emilyae*. *Chicoreus emilyae* has now been found to be a true Blasian endemic. This is probably the "*Chicoreus florifer*" listed by Radwin (1969:231).

between larger spines on varix; varical spines open, cupped, ramose; intervarical areas ornamented with one large, elongated knob; body whorl sculptured with 12–13 thin, raised spiral cords, one or more very fine secondary threads present between cords; siphonal canal very elongated, narrow, ornamented with 3 large, flattened spines per varix; spiral cords and threads on body whorl and siphonal canal minutely scaled; aperture proportionally large, ovate; shell color light brownish-tan, with varices and intervarical knobs being of darker chestnut brown

**Etymology:** Named for Mr. Leonard C. Hill of Miami, Florida, who recognized the species as new and who kindly donated the type material.

**Discussion:** *Chicoreus hilli* is closest to *C. mergus* Vokes, 1974 from Florida, the West Indian Arc, and northern South America, but differs in being a smaller, thinner, more elongated shell with proportionally much larger spines. The varices of *Chicoreus mergus* are very thick and rounded, giving the shell a compact, squat appearance. The varices of *Chicoreus hilli*, on the other hand, are much thinner and sharper, giving the shell a more elongated, graceful appearance. The siphonal canal of *C. hilli* is also much narrower and proportionally much longer than that of *C. mergus*. The shoulder spine of *C. hilli* is also proportionally at least twice as long as the shoulder spine of *C. mergus*.

*Chicoreus hilli* is also similar to *Chicoreus bullisi* Vokes, 1974, from off Nicaragua, but differs in being a much smaller, much more delicate shell with smaller and less-developed varical spines. The varices of *C. bullisi*, like those of *C. mergus*, are also much thicker, wider, and more rounded than those of *C. hilli*. The new species is the smallest known *Chicoreus* in the western Atlantic, and appears to be restricted to the coralline algal and carbonate rubble areas off Portobelo and the San Blas Archipelago.

### *Dermomurex* Monterosato, 1890
### *Trialatella* Berry, 1964

### *Dermomurex* (*Trialatella*) *cuna* new species
(figures 9, 10)

**Material examined:** Holotype—Length 14 mm, trawled by commercial fishermen from 65 m depth off Portobelo, Panama, USNM 860527; Paratype 1—length 13 mm, same locality and depth as holotype, Leonard Hill collection, Miami, Florida

**Description:** Shell elongated, fusiform, thin and fragile; early whorls with 6 small thin varices per whorl, body whorl and penultimate whorl with 3 large, thin, winglike varices per whorl; body whorl ornamented with 6 low flattened cords with cord along shoulder being strongest and best developed; cords extend onto winglike varices, producing slightly scalloped edges; cords of intervarical areas ornamented with small, evenly-spaced nodules; siphonal canal elongated, well developed, slightly recurved; aperture proprotionally large, oval in shape; entire shell covered with thick, cream-white, pebbled intritacalx; surface of intritacalx of varices finely striate.

**Etymology:** Named for the Cuna Indians of the San Blas Archipelago.

**Discussion:** *Dermomurex* (*Trialatella*) *cuna* is the fifth-known member of its three-winged subgenus to be found in the western Atlantic. The other species include *D. abyssicola* (Crosse, 1865) from Guadeloupe, French Antilles, *D. glicksteini* Petuch, 1987 from southeastern Florida, *D. kaicherae* Petuch, 1987 from Venezuela, and *D. oxum* Petuch, 1979 from the Abrolhos Archipelago, Brazil. Of the Atlantic species, *D. cuna* is closest to *D. kaicherae*, but differs in being a more broad-shouldered shell with a proportionally lower spire, and in being a smoother, less sculptured shell lacking the broad, thick intervarical cords and knobs of *D. kaicherae* (Petuch, 1987: plate 24, figures 17, 18). Of the known *Trialatella* species, *D. cuna* is closest to the Panamic *D. cunninghamae* (Berry, 1964), the type of the subgenus, and the two form an obvious cognate pair. The new Caribbean species differs from its Panamic cognate in being a more elongated, slender shell with a proportionally higher spire and less developed winged varices. The form and number of the body whorl cords and the structure of the intritacalx of the two species, however, are very similar.

Vokes (1975: plate 4, figures 3a,b) illustrated a smaller specimen of *D. cuna* from "Holandes Cay, off Cape San Blas, Panama, 22 fathoms" but referred it to the Lesser Antilles species *D. abyssicola*. She later reillustrated the same specimen (Vokes, 1985: figures 13a,b), but this time referred the Panamanian shell to the Brazilian *D. oxum*. This now well-known specimen of *D. cuna*, however, is a juvenile (with 6 varices) of only 9 mm length, and does not exhibit the adult proportions. Fully mature, three-winged specimens of *D. cuna* (approximately 13 mm) and *D. oxum* (holotype 12.5 mm) are quite different, with *D. oxum* being a much broader, stockier shell with wider body whorl cords and elongated intervarical knobs. Although similar to, and often confused with *D. abys-*

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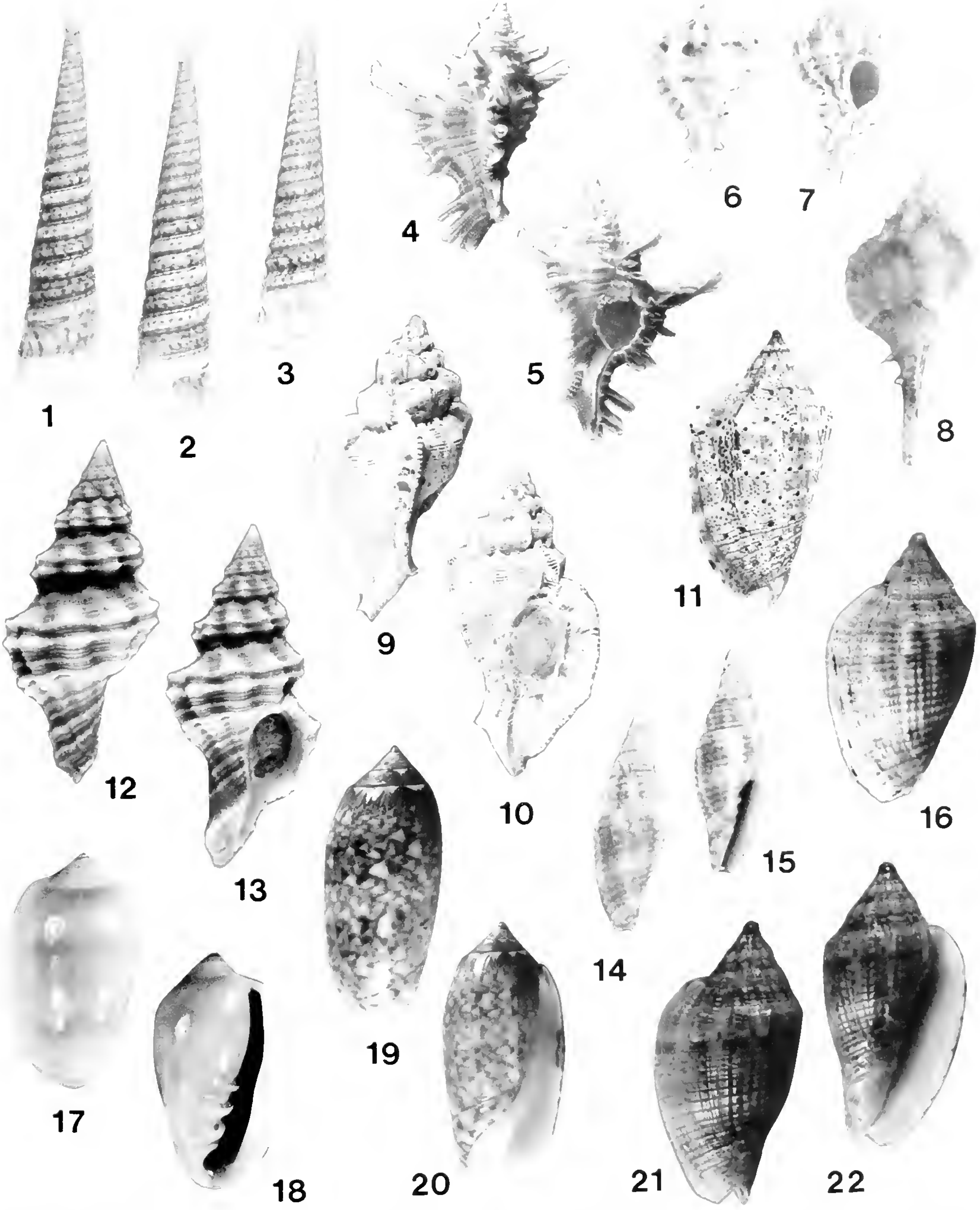
**Figures 1–22.** New gastropods from the Caribbean coast of Panama **1, 2.** *Turritella marianopsis* new species, holotype, length 58 mm, USNM 860525 **3.** *Turritella marianopsis* new species, paratype, length 52 mm, USNM 860524 **4, 5.** *Chicoreus hilli* new species, holotype length 26 mm USNM 860525 **6, 7.** *Murexiella edwardpauli* new species, holotype, USNM 860529 **8.** *Murex rubidus panamicus* new subspecies holotype length 26 mm, USNM 860528 **9, 10.** *Dermomurex* (*Trialatella*) *cuna* new species, holotype, length 14 mm, USNM 860527 **11.** *Voluta virescens* Lightfoot, 1786, 43 mm specimen from Cartagena, Colombia, for



comparison with *Voluta lacertina*. **12, 13.** *Latirus cuna* new species, holotype, length 46 mm, USNM 860531 **14, 15.** *Mitra* (*Nebularia*) *leonardi* new species, holotype, length 22 mm, USNM 860533. **16.** *Voluta lacertina* new species, paratype, length 29 mm, USNM 860538. **17, 18.** *Prunum leonardhilli* new species, holotype, length 19 mm, USNM 860536. **19, 20.** *Oliva* (*Strephona*) *reticularis ernesti* new species, holotype, length 38 mm, USNM 860535 **21, 22.** *Voluta lacertina* new species, holotype, length 31 mm, USNM 860537.

*sicola*, *D. cuna* is a larger, broader shell with a higher, more obviously stepped spire. The siphonal canals of both *D. oxum* and *D. abyssicola* are neither as elongated nor as well developed as that of *D. cuna*, and are not recurved.

In the fossil record, *D. cuna* is most similar to *D. antecessor* Vokes, 1975 from the early Pleistocene of Costa Rica (Moin Formation) and southern Florida (Bermont Formation). This possible Pleistocene ancestor, however, differs from the Recent Blasian species in being a more elongated species with less developed varices and coarser corded body whorl sculpture.

*Murex* Linnaeus, 1758

*Murex rubidus panamicus* new subspecies
(figure 8)

**Material examined:** Holotype—Length 26 mm, trawled by commercial fishermen from 50 m depth off Portobelo, Panama, USNM 860528; Paratype 1—length 27 mm, same locality and depth as holotype, Leonard Hill collection, Miami, Florida.

**Description:** Shell small for genus, with fusiform body; spire high, elevated; body whorl and varices rounded; 3 large, thick varices per whorl; 2–3 narrow, elongated knobs in intervarical areas; body whorl, intervarical knobs, and varices ornamented with 12–14 large, raised spiral cords; thin spiral threads often present between spiral cords; siphonal canal extremely long and narrow, equal to length of shell body; base of siphonal canal ornamented with 2 small spines; aperture small, rounded; peristome ornamented with numerous large white teeth; shell color bright orange with 2 darker orange-tan bands, one around shoulder and one around body whorl-siphonal canal junction; posterior half of siphonal canal brown; anterior half of siphonal canal pale orange-white.

**Etymology:** Named for Panama, the country of the type locality.

**Discussion:** *Murex rubidus* Baker, 1897 is now known to have a split distribution within the Caribbean region, with the nominate subspecies, *M. rubidus rubidus*, being found along the southeastern and western coasts of Florida and the northern Bahamas (Radwin and D'Attilio, 1976:71), and with a small, isolated population, *M. rubidus panamicus*, being found along Caribbean Panama. Both populations may be relicts of a once wide-ranging Pleistocene species that has become biogeographically bisected and spatially reduced since the late Pleistocene. Several other Blasian species also share close morphological similarities with Bahamian gastropods. Included are the Blasian *Chicoreus emilyae* Petuch, 1987 and the Bahamian-Floridian *C. florifer* Reeve, 1846 and the Blasian *Conus hilli* [illegible] and the Bahamian *Conus jucundus* Sowerby, 1887 (= *C. abbotti* Clench, 1942).

*Murex rubidus panamicus* differs from the nominate subspecies in being a much more slender, more fusiform shell with a much higher, more protracted spire. The body whorl of *M. rubidus rubidus* is rounded and globose, while the body whorl of *M. rubidus panamicus* is narrower and elongated

*Murexiella* Clench and Farfante, 1945

*Murexiella edwardpauli* new species
(figures 6, 7)

**Material examined:** Holotype—Length 15 mm, trawled by commercial fishermen from 50 m depth off Portobelo, Panama, USNM 860529; Paratype 1—length 15 mm, same locality and depth as holotype, USNM 860530.

**Description:** Shell small for genus, thin, delicate, with globose, inflated body; 6 varices per whorl, varices thin, with 6 large, recurved spines; intervarical areas ornamented with 6 large spiral cords; intervarical cords and varices minutely squamose; siphonal canal proportionally very elongated, ornamented with 3 large, flattened spines per siphonal varix; shell consistently pinkish-tan colored with 2 darker tan bands, one around shoulder and one around midbody; shoulder of body whorl slightly angled; aperture proportionally large, oval in shape.

**Etymology:** Named for Mr. Edward D. Paul of Miami, Florida.

**Discussion:** *Murexiella edwardpauli* is closest to *Murexiella macgintyi* (Smith, 1938) from Florida and the Bahamas, but differs in being a much smaller, more delicate species with a much more globose body whorl, less angled shoulder, and proportionally longer and narrower siphonal canal. *Murexiella edwardpauli* is also similar to *M. leonardhilli* Petuch, 1987 from Brazil, but differs in being a much smaller shell with thinner, less crassate varices. In the eastern Pacific, *M. edwardpauli* is very similar to *M. keenae* Vokes, 1970, but differs in being a smaller shell with a proportionally longer siphonal canal. Based on shell morphology, *M. keenae* and *M. edwardpauli* can be seen to be very closely related and represent Panamic-Caribbean cognates.

Fasciolariidae
Peristerniinae
*Latirus* Montfort, 1810

*Latirus cuna* new species
(figures 12, 13)

**Material examined:** Holotype—Length 46 mm, trawled by commercial fishermen from 60 m depth off Portobelo, Panama, USNM 860531; Paratype 1—length 42 mm, same locality and depth as holotype, USNM 860532; Paratype 2—length 45 mm, same locality and depth as holotype, collection of Leonard Hill, Miami, Florida.

**Description:** Shell elongately fusiform, with high, scalariform spire and narrow protracted siphonal canal; shoulder sharply angled, with rounded, spikelike knobs; whorls with 8 narrow, raised axial ribs per whorl; axial ribs overlaid with 5 large, thick spiral cords; 2 spiral cords at shoulder largest and best developed, projecting farthest from shell body; areas between large cords ornamented with numerous very fine cords and spiral threads; siphonal canal ornamented with 4 large spiral cords; areas between large siphonal cords ornamented with numerous fine cords and threads; interior of aperture with 10–12 large, beaded cords; edge of lip finely crenulated, with crenulations corresponding to fine spiral cords and threads on shell surface; narrow umbilicus present; shell color bright orange-tan; large cords of body whorl, spire, and siphonal canal white; interior of aperture orange.

**Etymology:** Named for the Cuna Indians of the San Blas Islands.

**Discussion:** *Latirus cuna* somewhat resembles the widespread Caribbean *L. cariniferus* Lamarck, 1822, but differs in being a more slender, elongated shell with a narrower, more protracted siponal canal, and in having a more sharply-angled shoulder with proportionally larger and sharper shoulder knobs. The new Blasian species is also similar to the Panamic *L. centrifugus* (Dall, 1915), but differs in being a more slender, elongated shell with a proportionally longer siphonal canal. Otherwise, both *L. centrifugus* and *L. cuna* share the same type of sharply-angled shoulder, large shoulder knobs, and strongly projecting shoulder cords. I feel it is safe to assume that *L. cuna* and *L. centrifugus* form a cognate species pair.

Volutacea
Mitridae
*Mitra* Lamarck, 1798
*Nebularia* Swainson, 1840

*Mitra* (*Nebularia*) *leonardi* new species
(figures 14, 15)

**Material examined:** Holotype—Length 22 mm, trawled by commercial fishermen from 60 m depth off Portobelo, Panama, USNM 860533; Paratype 1—length 20 mm, same locality and depth as holotype, USNM 860534.

**Description:** Shell narrow and elongated, fusiform; spire high, protracted, scalariform; suture indented, producing narrow shoulder area and stepped spire whorls; body whorl ornamented with 12 large, thick spiral cords; columella with 4 plications, with posteriormost plications being largest; shell color white, heavily overlaid with wide, reddish brown vertical flammules; reddish-brown flammules often coalesce into large, longitudinal patches; some specimens (holotype) with thin white band around midbody; aperture thin, narrow, roughly one-half length of shell.

**Etymology:** Named for Mr. Leonard C. Hill of Miami, Florida who kindly donated the type material.

**Discussion:** In the Caribbean, *Mitra leonardi* is closest to *M. semiferruginea* Reeve, 1845, from the Bahamas, but differs in being a smaller, much narrower shell with a proportionally larger aperture. The two species also differ in color; with *M. semiferruginea* being colored bright yellow with dark, blackish-brown flammules and with *M. leonardi* being white with reddish-brown flammules. In the eastern Pacific, *M. leonardi* is closest to *M. sphoni* Shasky and Campbell, 1964, especially in size and color, but differs in having a more scalariform, stepped spire. *Mitra sphoni* and *M. leonardi*, together, are another example of a Panamic-Caribbean cognate species pair.

Olividae
*Oliva* Bruguiere, 1789
*Strephona* Mörch, 1852

*Oliva* (*Strephona*) *reticularis ernesti* new subspecies
(figures 19, 20)

**Material examined:** Holotype—Length 38 mm, trawled from 40 m depth on silty sand bottom off Portobelo, Panama, USNM 860535; Paratypes 1–3—lengths 37–41 mm, same locality and depth as holotype, Petuch collection.

**Description:** Shell average size for subgenus, cylindrical, with only slightly rounded shoulder; spire low; body whorl colored yellowish-tan, overlaid with dense, close-packed pattern of small, dark brown triangles and zigzags; 2 wide bands of darker brown triangles present around body whorl, one around anterior one-third and one around area just posterior of midbody line; sutural area marked with large, evenly-spaced yellow patches and numerous fine black hairlines; spire whorls glazed-over with dark purple-brown enamel; aperture and columellar area white; columella with 15–20 thin plicae; fasciole yellow-tan marked with 2 rows of large dark brown checkers; protoconch proportionally small, colored dark purple-brown.

**Etymology:** Named for Mr. James Ernest of Balboa, Panama, who collected the type lot.

**Discussion:** *Oliva reticularis ernesti* from the Blasian area differs from *O. reticularis reticularis* Lamarck, 1810, from the Bahamas and West Indian Arc, in being a more straight-sided, cylindrical shell with a much lower spire. The new subspecies is also a darker-colored shell with a finer and denser pattern of triangle markings. *Oliva reticularis ernesti* occurs with, and has often been confused with, *Oliva bewleyi* Marrat, 1871. That species, however, is a much larger shell (av. 55 mm) with a proportionately higher spire and larger protoconch. *Oliva bewleyi* has a much more diffuse color pattern, with the triangle markings and zigzags having a "smeared" look. The triangle markings of *O. reticularis ernesti*, on the other hand, are consistently clear and distinct. Although *O. bewleyi* is now known to range from Panama to Santa Marta, Colombia (Petuch & Sargent, 1986:126), *O. reticularis ernesti* appears to be restricted to the Blasian area

Marginellidae
*Prunum* Hermannsen, 1852

*Prunum leonardhilli* new species
(figures 17, 18)

**Material examined:** Holotype—Length 19 mm, trawled from 60 m depth by commercial fishermen, off Portobelo, Panama, USNM 860536. Paratypes 1, 2—lengths 18 mm and 19 mm, same locality and depth as holotype, Leonard Hill collection.

**Description:** Shell elongated, ovate, somewhat inflated; base of shell flattened anteriorly, bordered by thickened parietal callus that connects with thickened outer lip around anterior end; margins of shell thickened; spire relatively low; columella with 4 very large plications that extend beyond aperture region onto shell base; aperture narrow, slightly wider at anterior end; shell pale bluish-gray color with 2 darker gray bands; thickened lip and basal callus white; junction of body whorl and lip marked by thin yellow line; body whorl-lip junction area suffused with pale yellow color; interior of aperture bright orange-brown; protoconch and early whorls pale orange-tan.

**Etymology:** Named for Mr. Leonard C. Hill of Miami, Florida, who kindly donated the holotype.

**Discussion:** *Prunum leonardhilli* is very similar to *P. curtum* (Sowerby, 1832) from the coasts of Ecuador and Peru, as both species share the same shell shape, shell size, and form of the columellar plications. *Prunum curtum*, however, is a yellow shell with a pale orange outer lip, while *P. leonardhilli* is basically a blue-gray shell with a white outer lip. Regardless of color, the two species appear to be cognates. In the Caribbean *P. leonardhilli* is closest to *P. prunum* (Gmelin, 1791), which is abundant and widespread along the coasts of Colombia and Venezuela. The new Panamanian species differs from the common *P. prunum*, however, in being a smaller, more globose, and less elongated shell, with much larger columellar plications. The columellar plications of *P. prunum* do not extend as far onto the shell base as do those of *P. leonardhilli*. The two species also appear to be ecologically exclusive, with *P. prunum* preferring the organic-rich coastal muds and *P. leonardhilli* preferring fine particulate carbonate bottoms in offshore areas. *Prunum leonardhilli* is sympatric with another Blasian marginellid endemic, *Persicula weberi* Olsson and McGinty, 1958.

Volutidae
Volutinae
*Voluta* Linnaeus, 1758

*Voluta lacertina* new species
(figures 16, 21, 22)

**Material examined:** Holotype—Length 31 mm, trawled by commercial fishermen from 100 m depth off Portobelo, Panama, USNM 860537; Paratype 1—length 29 mm, same depth and locality as holotype, USNM 860538; Paratype 2—length 30 mm, same depth and locality as holotype, Leonard Hill collection.

**Description:** Shell very small for genus, averaging only 30 mm in length; shell outline broadly fusiform, tapering toward anterior end; spire elevated; shoulder rounded, ornamented with 10–12 low, riblike knobs; body whorl ornamented with 20–24 horizontally-arranged, deeply incised spiral sulci and numerous thin longitudinal plicae; sulci and plicae intersect to produce strong cancellate sculpture pattern; intersection of pair of sulci and plicae producing large, raised bead, giving entire surface of body whorl pebbly appearance; subsutural area ornamented with 6 large spiral cords; shell color yellowish-tan overlaid with numerous minute brown dots and 3 bands of large light brown rectangular patches, one along suture, one below shoulder, and one around anterior end; protoconch proportionally large, composed of 2 whorls, flattened and somewhat discoidal; protoconch asymmetrical in form, with first whorl projecting dorsally out of alignment with second whorl; protoconch light brown in color; aperture wide, yellow to pale orange in interior; columella with 10 large, thin, smooth plications; thin, small, secondary plications sometimes present between anteriormost primary plications; outer lip of adults thickened, marked with 10–12 small brown spots; operculum unknown.

**Etymology:** "Little lizard", in reference to the new species' beaded appearance, which resembles lizard skin.

**Discussion:** *Voluta lacertina* is the smallest-known *Voluta* s.s. and is also the deepest-dwelling, having been trawled from 100 m depth. All other *Voluta* s.s., and members of the closely-related *Falsilyria* Pilsbry and Olsson, 1954 species complex, prefer depths of 30 to 50 m and some are often collected by SCUBA diving (such as *Falsilyria sunderlandi* Petuch, 1987 from 10 m depth off Utila Island, Honduras). At Cartagena, Colombia, the closely-related *Voluta virescens* Lightfoot, 1786 is found in shallow subtidal depths and frequently is collected as beach specimens.

*Voluta lacertina* is most similar to the other Blasian endemic volute, *V. lindae* Petuch, 1987 (figure 23), but differs in being a smaller, more heavily scuptured shell with a more rounded shoulder. The sculpture pattern of the two species also differs, with *V. lacertina* having a pebbly, beaded surface texture and with *V. lindae* having stronger longitudinal plicae that give the shell a wrinkled look. The shoulder knobs of *V. lacertina* are weak and rounded, while those of *V. lindae* are strong, angled, and sharply pointed. *Voluta lindae* is also a more brightly colored shell, being an intense yellow or yellow-orange and having large, dark brown spots in rows around the body whorl. *Voluta lacertina*, on the other hand, is a

**Figures 23–41.** New Volutes (Volutidae), Cones (Conidae), and Turrids (Turridae) from the Caribbean coast of Panama. **23.** *Voluta lindae* Petuch, 1987, 4[illegible] mm holotype from Bocas del Toro, Panama, for comparison with *Voluta lacertina*. **24, 25.** *Falsilyria ernesti* new species, holotype, length 54 mm, USNM 860539. **26, 27.** *Conus granarius panamicus* new subspecies, holotype, length

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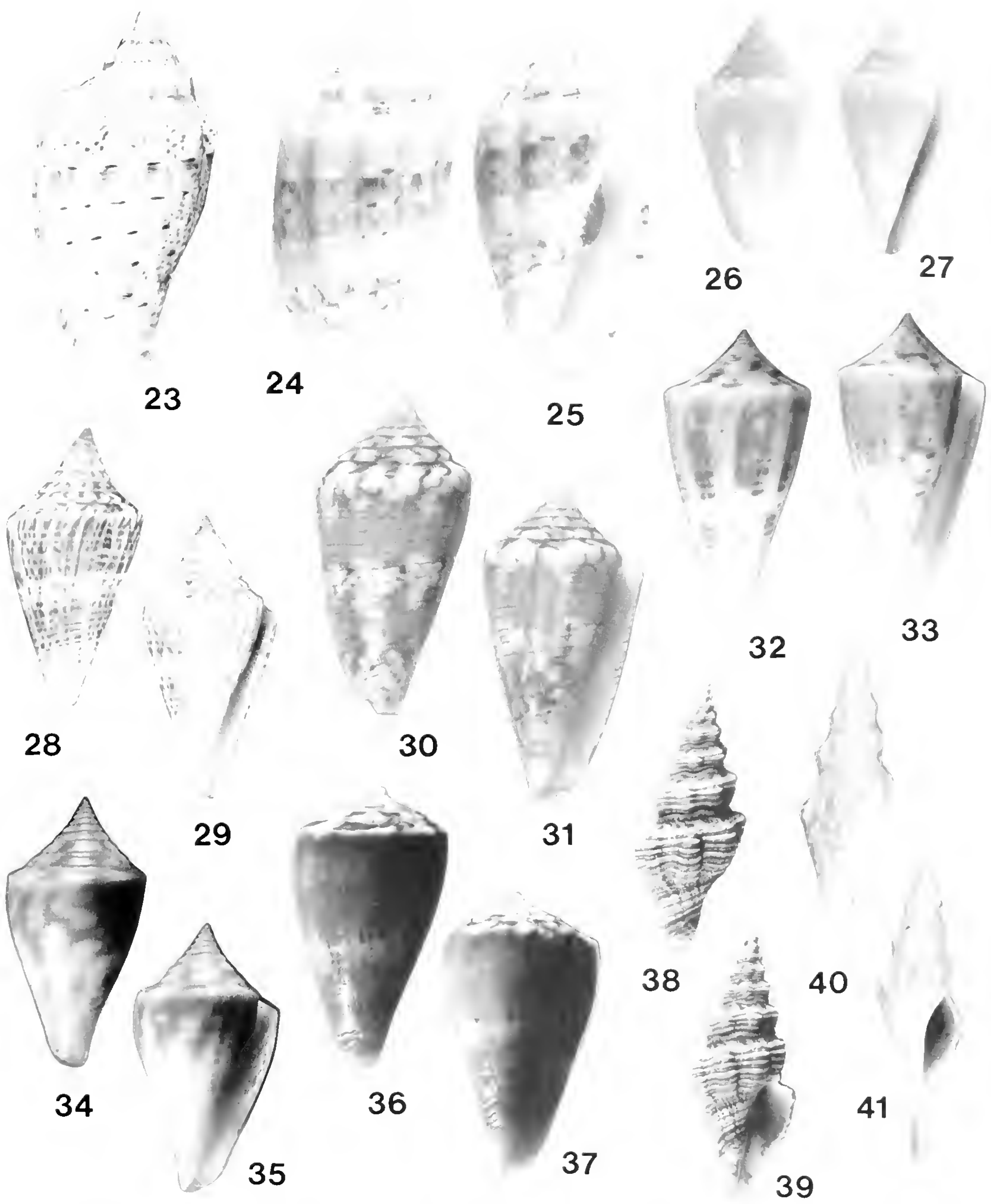

24 mm, USNM 860543 **28, 29.** *Conus ernesti* new species, holotype, length 29 mm, USNM 860542 **30, 31.** *Conus brunneofilaris* new species, holotype, length 14 mm, USNM 860541 **32, 33.** *Conus portobeloensis* new species, holotype, length 31 mm, USNM 860545 **34, 35.** *Conus rosemaryae* new species, holotype, length 25 mm, USNM 860546 **36, 37.** *Conus hilli* new species, holotype, length 21 mm, USNM 860544 **38, 39.** *Knefastia hilli* new species, holotype, length 50 mm, USNM 860548 **40, 41.** *Fusiturricula sunderlandi* new species, holotype, length 33 mm, USNM 860547.

drab little shell, being a pale tan or yellowish-tan and lacks the large, scattered brown spots seen on *V. lindae*. Both species, however, have the same fine-dotted pattern that covers the entire shell, although the dots of *V. lindae* are proportionally larger and darker. The protoconchs of the two species also differ significantly, with that of *V. lindae* being inflated and cylindrical in form, while that of *V. lacertina* is flattened and asymmetrical. Bathymetrically, the two species also differ, with *V. lacertina* living at depths of 100 m or deeper and with *V. lindae* preferring much shallower areas of 20 to 50 m depth.

*Voluta lacertina* is also similar to the well known *V. virescens* (figure 11), which ranges from off Nicaragua to Santa Marta, Colombia, and the two species appear to represent a pair of bathymetric siblings. As in *V. lindae*, *V. virescens* prefers shallower depths, ranging from 5 to 35 m. The substrate preferences of these three closely-knit species also appear to differ, with *V. lacertina* and *V. lindae* preferring coralline algal rubble and carbonate bottoms and with *V. virescens* preferring muddy, organic-rich bottoms. *Voluta virescens* from the organic detrital and reducing substrates within the Golfo de Uraba, on the Panama–Colombia border, are stained black from reduced iron compounds and are often encrusted with iron sulfide. *Voluta lindae* and *V. lacertina*, from the cleaner carbonate substrates of the Blasian area, are usually shiny and uncoated by iron compounds.

Morphologically, *V. virescens* differs from *V. lacertina* in being a larger shell with a smooth shell sculpture that lacks the pebbly beading. The basic shell coloring also differs between the two species, with *V. virescens* being a characteristic green or greenish-gray while *V. lacertina* is a pale yellow-tan. The protoconch of *V. virescens* is proportionally smaller than that of *V. lacertina*, being narrow and cylindrical in form. The protoconch of *V. lacertina* is large for such a small shell, and is flattened and almost discoidal in form. Interestingly enough, although *V. virescens* is the largest species of the Panamanian-Colombian *Voluta* species complex, it has a proportionally much smaller protoconch than those of its diminutive relatives, *V. lindae* and *V. lacertina*.

*Falsilyria* and Pilsbry and Olsson, 1954

*Falsilyria ernesti* new species
(figures 24, 25)

**Material examined:** Holotype—Length 54 mm, trawled by commercial fishermen from 65 m depth off Portobelo, Panama, USNM 860539; Paratype 1—length 55 mm, same locality and depth as holotype, USNM 860540; Paratype 2—length 54 mm, same locality and depth as holotype, Leonard Hill collection, Miami, Florida.

**Description:** Shell narrow, elongated, fusiform, thick and heavy, spire elevated, protracted, spire whorls slightly convex in outline, whorls ornamented with 8–10 large, rounded, axial plications; large plications overlaid with numerous thin, riblike plications; shoulder angled, bordered by single large spiral cord; subsutural areas sculptured with 3 large spiral cords; subsutural spiral cords intersect with thin axial riblets to produce beaded texture on shoulder and spire; body whorl shiny, polished; anterior end sculptured with 5–6 large spiral cords; columella slightly arcuate, with 11–12 thin, smooth plications; outer lip of adults thickened, projecting posteriorward; protoconch proportionally large, rounded, domelike; shell color pale salmon-yellow with 2 wide bands of brown and pale purple checkers and spots, one around midbody and one around anterior end; midbody band overlaid with 4–6 brown spiral hairlines and numerous tiny brown vertical flammules; anterior band similarly marked with 5 brown hairlines and tiny vertical flammules; salmon-yellow areas between wide colored bands completely overlaid with closely-packed, tiny orange-brown speckles; protoconch light tan; columella and interior of aperture pale salmon; edge of lip yellowish-white, marked with evenly-spaced dark brown spots.

**Etymology:** Named for Mr. James Ernest of Balboa, Panama, who collected the type lot.

**Discussion:** Of the *Fasilyria* species complex, *F. ernesti* is the southernmost known member, and its discovery came as a surprise to me. Previously (Petuch, 1987:62), I had stated that the genus was restricted to the coasts of Honduras and northern Nicaragua. The new Blasian species, therefore, represents a considerable range extension for the complex. Of the eight known *Falsilyria* species, *F. ernesti* is most similar to *F. demarcoi* (Olsson, 1965) from Honduras, but differs in being a much smaller, more slender and elongated shell, with a much more sharply-angled shoulder. The Honduran *F. demarcoi* is also a much more brightly colored shell, having a deep orange base tone. The Blasian *F. ernesti*, on the other hand, is a less colorful shell, having a base tone of pale salmon-yellow. In shape and in having a small adult size, *F. ernesti* is also similar to *F. harasewychi* Petuch, 1987, from off Roatan Island. The new species differs from *F. harasewychi*, however, in having a salmon-yellow base color instead of white, and in lacking the wine-red flammules and black and white checkered bands of *F. harasewychi*. The Roatan species has distinctive, characteristic beaded columellar plications, while those of *F. ernesti* are smooth.

Conacea
Conidae
*Conus* Linnaeus, 1758

*Conus brunneofilaris* new species
(figures 30, 31)

**Material examined:** Holotype—Length 14 mm, trawled by commercial fishermen from 65 m depth off Portobelo, Panama, USNM 860541.

**Description:** Shell small, elongately conical, thin, fragile; shoulder sharply angled, carinated; carina faintly undulating; spire moderately elevated, with stepped whorls; body whorl shiny and polished; anterior tip encircled with 6 small spiral cords; aperture narrow, slightly wider at anterior end; protoconch proportionally large, mammillate; shell color bright golden-tan with wide midbody band of large white patches and dark brown flammules; anterior tip marked with large white flammules; golden-tan and white base color overlaid with 21 extremely fine, hairlike, dark brown spiral lines; shoulder and spire white with large, evenly-spaced, dark brown flammules; spire flammules extend over edge of shoulder carina onto body whorl; interior of aperture white; protoconch and early whorls bright yellow.

**Etymology:** "Brown threaded", in reference to the prominent, evenly-spaced, thin brown lines that encircle the body whorl.

**Discussion:** *Conus brunneofilaris*, with its distinct brown spiral lines, resembles no other known Caribbean or Panamic cone shell. In shape and size, this unusual new species is most similar to *C. magnottei* Petuch, 1987 from Roatan Island, Honduras, but differs in having a bright golden-tan base color instead of the pink and purple color of *C. magnottei*, and in having the overlay color pattern of brown lines, which is lacking in the Honduran species. The spire flammules of *C. magnottei* are also larger and more irregular than those of *C. brunneofilaris* and do not extend onto the body whorl.

### *Conus ernesti* new species
(figures 28, 29)

**Material examined:** Holotype—Length 29 mm, trawled by commercial fishermen form 65 m depth off Portobelo, Panama, USNM 860542; Paratype 1—length 31 mm, same locality and depth as holotype, Kevan Sunderland collection.

**Description:** Shell slender, tapering rapidly toward anterior tip; shoulder wide, sharply angled; spire high, elevated, scalariform; shell smooth, polished, with deeply-impressed spiral sulci around anterior end; aperture straight, narrow; shell color white with 12–20 rows of small brown dots and dashes; rows of dots often aligned to form large brown vertical flammule; dotted pattern overlaid with variable amounts of amorphous lighter brown patches; clear band, with only one or two rows of dots, present around midbody; some specimens (holotype) with brown patches coalescing into 2 broad bands, one above, and one below, midbody; anterior tip of shell white; spire whorls white with numerous, evenly-spaced crescent-shaped flammules; early whorls brown; interior of aperture white.

**Etymology:** Named for Mr. James Ernest of Balboa, Panama, who collected the holotype.

**Discussion:** *Conus ernesti* is most similar to *Conus cingulatus* Lamarck, 1810 from the Caribbean coast of Colombia, but differs in being a smaller, lighter colored shell with a much higher, scalariform spire. The lower-spired *Conus cingulatus* is a rough-textured shell, with the body whorl being heavily sculptured with incised sulci and raised spiral threads. *Conus ernesti*, on the other hand, is a smooth, almost polished shell, with incised sulci only on the anterior end. The dark purple-brown *C. cingulatus* has a purple aperture, whereas the white and light brown *C. ernesti* has a white aperture.

The new species is also similar to *C. garciai* daMotta, 1982 from the Caribbean coast of Honduras, but differs in being a much smaller shell with rows of brown dots. Like *C. cingulatus*, *C. garciai* is also a rough-textured shell, heavily ornamented with raised threads, and differs greatly from the smooth *C. ernesti*. Together, *C. garciai*, *C. ernesti*, and *C. cingulatus* form an interesting species complex, with each being restricted to a separate molluscan assemblage.

### *Conus granarius panamicus* new subspecies
(figures 26, 27)

**Material examined:** Holotype—Length 24 mm, trawled by commercial fishermen from 40 m depth off Portobelo, Panama, USNM 860543; Paratype 1—length 28 mm, same locality and depth as holotype, Leonard Hill collection.

**Description:** Shell subpyriform, tapering abruptly toward anterior end; shoulder sharply angled, subcarinated; spire very high, elevated, protracted; shoulder periphery and spire whorls heavily ornamented with numerous large, rounded beads, producing distinctly coronated spire; body whorl shiny, ornamented with 15–18 evenly-spaced rows of tiny pustules; shoulder and subsutural area flattened, producing pronounced stepped spire; shell color pale lilac, often overlaid with large, vertically-oriented, light tan patches; interior of aperture violet.

**Etymology:** Named for Panama, country of the type locality.

**Discussion:** *Conus granarius panamicus* may represent an isolated population of the wide-ranging *C. granarius granarius*, which ranges from northern Colombia into the Gulf of Venezuela. The new subspecies differs from the nominate subspecies in being a smaller, stumpier, more biconically-shaped shell with a proportionally higher and more scalariform spire. *Conus granarius panamicus* also lacks the spiral rows of dots that characterize the color pattern of *C. granarius granarius*, and is a much paler, less colorful shell. Some specimens of *C. granarius panamicus* are uniformly pale lilac (like the holotype), while others have large tan patches. Although the nominate subspecies appears to prefer muddy, siliciclastic sediment bottoms with large amounts of organic matter, *C. granarius panamicus* prefers coralline rubble and carbonate sand bottoms.

It is conceivable that *C. granarius panamicus* may, in fact, be a full species, closely related to, but distinct from, *C. granarius granarius*. The new taxon may be part of a Honduras-Panama-Colombia species complex, much as in the case of *Conus garciai-ernesti-cingulatus*. This species complex, then, would comprise the Honduran *C. harlandi* Petuch, 1987, the Panamanian *C. panamicus*, and the Colombian *C. granarius*, with each being part of a localized, endemic faunule.

*Conus hilli* new species
(figures 36, 37)

**Material examined:** Holotype—Length 21 mm, trawled by commercial fishermen from 26 mm depth off Portobelo, Panama, USNM 860544.

**Description:** Shell stocky, broad across shoulder; spire low, flattened; shoulder sharply-angled, subcarinated; shoulder and spire whorls obsoletely coronated, with low, evenly-spaced undulations along periphery; body whorl very smooth, polished, shiny; anterior tip with 10 small, slightly raised spiral cords; shell color deep purple-blue with blotchy, light blue band around midbody; light blue midbody band marked with 4 rows of tiny, closely-spaced reddish-brown dots; spire whorls white with evenly-spaced, large dark brown crescent-shaped flammules; protoconch mammillate, protracted, light orange in color; aperture narrow, purple within.

**Etymology:** Named for Mr. Leonard C. Hill of Miami, Florida.

**Discussion:** *Conus hilli* is most similar to, and apparently is a close relative of, *Conus kulkulcan* Petuch, 1980 from the Bay Islands of Honduras. The new species differs from *C. kulkulcan*, however, in having a lower, flatter spire, and in having a squatter, less elongated shape. The spire whorls and shoulder of *C. kulkulcan* are marked with numerous fine, dark brown hairlines, but these are absent on *C. hilli*. *Conus kulkulcan* is also a textured shell, having spiral rows of tiny pustules around the body whorl. *Conus hilli*, on the other hand, is an untextured shell, having a highly polished, shiny body whorl. As in the case of the last two new cones in this paper, *Conus hilli* forms an interesting species trio with closely-related Honduran and Colombian species. This complex, then, includes *C. kulkulcan* from Honduras, *C. hilli* from Panama, and *C. colombianus* Petuch, 1987 from northern Colombia. Other related species in this close-knit Caribbean complex include *C. jucundus* Sowerby, 1887 (= *C. abbotti* Clench, 1942) and *C. inconstans* E. A. Smith, 1877 from the Bahamas, *C. arangoi* Sarasua, 1977 from Cuba, Cay Sal, and Turks and Caicos, *C. cardinalis* Hwass, 1792 and *C. cidaris* Kiener, 1845 from Hispaniola and the West Indian Arc, *C. mayaguensis* Nowell-Usticke, 1968 from the Dominican Republic and Puerto Rico, *C. harasewychi* Petuch, 1987 from Palm Beach, Florida, and possibly *C. abrolhosensis* Petuch, 1987 from the Abrolhos Archipelago of Brazil.

*Conus portobeloensis* new species
(figures [illegible])

**Material examined:** Holotype—Length 31 mm, trawled by commercial fishermen from 30 m depth off Portobelo, Panama, USNM 860545.

**Description:** Shell elongate, subpyriform, with low spire; earliest, postnuclear spire whorls protracted, becoming flattened during ontogeny; shoulder sharply angled, edged with small but distinct carina that projects beyond shoulder margin; body whorl smooth and shiny, with 20 large, raised cords around anterior quarter; spire whorls smooth; shell color white, marked with intermittent longitudinal flammules of pale orange-tan; longitudinal flammules, in turn, overlaid with scattered darker tan dots and dashes; anterior end of body whorl pale yellow-orange; spire white, with scattered amorphous flammules of dark orange-tan; midbody marked with clear white band; interior of aperture white; protoconch and early whorls dark orange; periostracum thin, tan, silky in texture.

**Etymology:** Named for the city of Portobelo, off of which the holotype was collected.

**Discussion:** At first glance, *Conus portobeloensis* appears to be related to the *C. garciai-ernesti-cingulatus* species complex, particularly in color pattern. Based upon the presence of a shoulder carina and a subpyriform body form, however, *C. portobeloensis* appears to be more closely related to *C. commodus* A. Adams, 1854 (reillustrated by Petuch, 1987: plate 10, figures 18, 19) from off Roatan Island, Honduras, and may be the Panamanian analogue. *Conus portobeloensis* differs from the Honduran species in being a larger, more elongated shell and in having a color pattern of orange-tan flammules and dots. The new Panamian species is also similar to *C. paraguana* Petuch, 1987 from the Gulf of Venezuela, as both species have an orangish dashed color pattern and both have a clear white midbody band. *Conus portobeloensis* differs from *C. paraguana*, however, in being a much larger, broader species with a wider and more sharply angled shoulder.

*Conus rosemaryae* new species
(figures 34, 35)

**Material examined:** Holotype—Length 25 mm, trawled by commercial fishermen from 85 m depth off Portobelo, Panama, USNM 860546; Paratype 1—length 24 mm, same depth and locality as holotype, Leonard Hill collection, Miami, Florida.

**Description:** Shell small for genus, extremely pyriform, turnip-shaped, wide across shoulder; shoulder carinated; spire moderately protracted, with concave whorls; body whorl polished and shiny, faintly ornamented with numerous low threads; spire whorls smooth; anterior third of body whorl sculptured with 10 deeply-impressed wide spiral sulci; body whorl white, overlaid with dense network of large, amorphous, bright yellow-orange flammules; some specimens (paratype) overlaid with scattered rows of dots; spire whorls white with scattered large, amorphous yellow-orange patches and flammules; anterior tip of shell pale orange; protoconch and early whorls orange; interior of aperture white; periostracum thin, transparent tan, smooth.

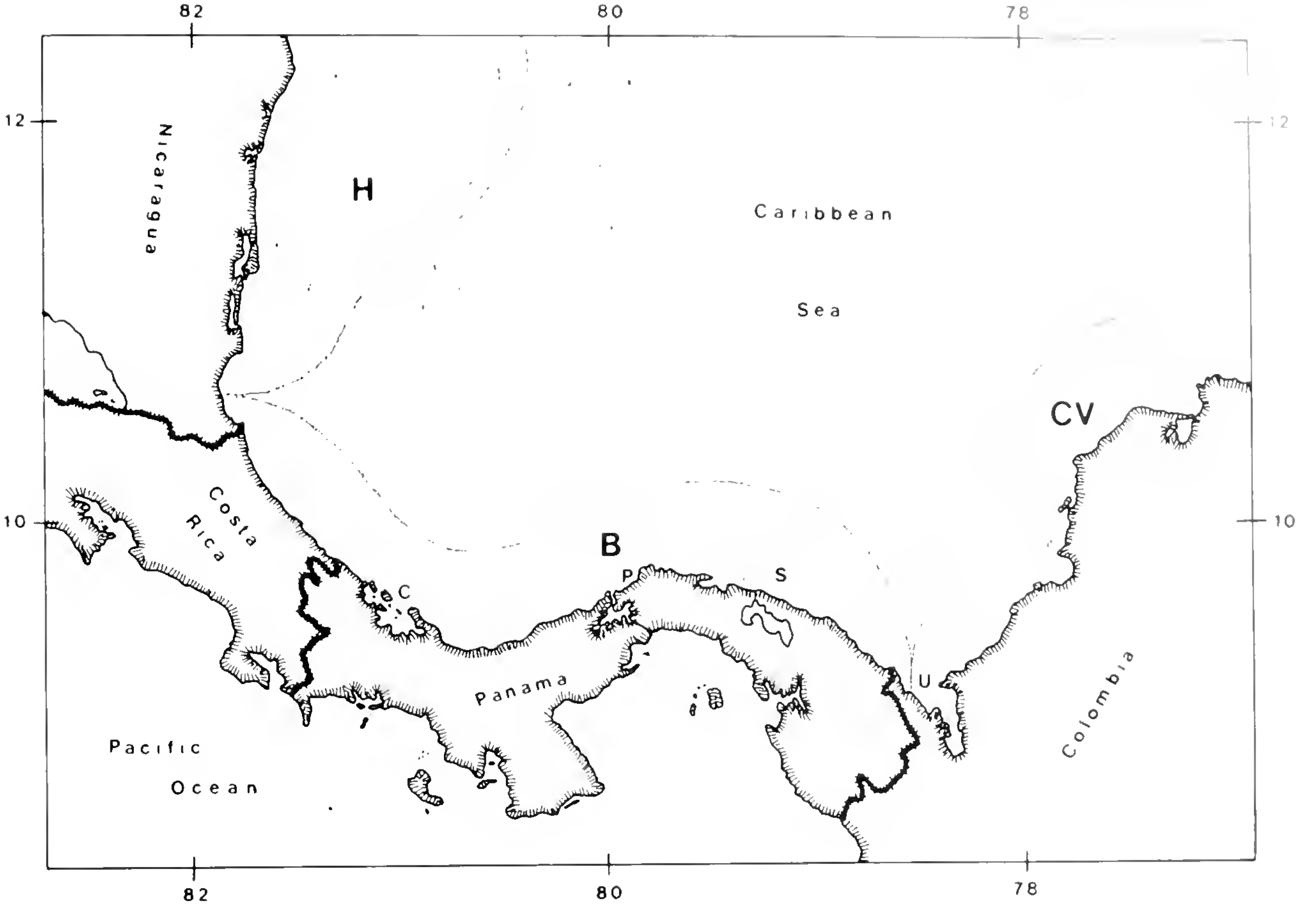

**Figure 42.** Map of the southwestern Caribbean Sea and the Panamanian Isthmus, showing the distribution of Caribbean molluscan faunal subregions. H = Honduran Subregion; B = Blasian Subregion; CV = Colombian-Venezuelan Subregion (taken, in part, from Petuch, 1988). Blasian geographical landmarks include the Laguna de Chiriqui (C), Portobelo (P), San Blas Archipelago (S), and the Golfo de Uraba (U). As shown here, the Blasian Subregion may extend northward to the Costa Rica–Nicaragua border area, in the vicinity of San Juan del Norte, Nicaragua.

**Etymology:** Named for Ms. Rosemary Adams of Sunnymead, California, who assisted Mr. James Ernest in the collection of the new Blasian species.

**Discussion:** Of the known Blasian Conidae, *Conus rosemaryae* is certainly one of the most distinctive. The pyriform turnip shape of this new species is unique among the Caribbean Panamanian cones. In general body form, *C. rosemaryae* most closely resembles *C. gibsonsmithorum* Petuch, 1986 from the Goajira Peninsula of Colombia and the Gulf of Venezuela, but differs in being a larger shell with a more elongated, tapered body whorl, and in being narrower across the shoulder. Although both *C. gibsonsmithorum* and *C. rosemaryae* have color varieties with rows of dots, *C. rosemaryae* is a more heavily patterned, more colorful species, with large orange flammules (as in the holotype) covering most of the shell. The new species is also similar to *C. sennottorum* Rehder and Abbott, 1951 from the Gulf of Mexico off Yucatan, but differs in being a smaller, more slender, and more brightly colored shell.

Turridae

*Fusiturricula* Woodring, 1928

*Fusiturricula sunderlandi* new species
(figures 40, 41)

**Material examined:** Holotype—Length 33 mm, trawled by commercial fishermen from 70 m depth off Portobelo, Panama, USNM 860547.

**Description:** Shell extremely elongated, slender, and fusiform; spire very elevated and protracted, turriculate; shoulder sharply-angled, with 12 oval-shaped knobs per whorl along periphery; subsutural area sloping; body whorl below shoulder knobs ornamented with 10 large beaded spiral cords; subsutural area ornamented with numerous extremely fine spiral threads; margin of suture bordered by bands of small, closely-packed oblong pustules; siphonal canal elongated, narrow, straight, ornamented with numerous fine, beaded, spiral threads, shell color uniformly pinkish-tan; aperture and columella white.

**Etymology:** Named for Mr. Kevan Sunderland of Fort Lauderdale, Florida, who kindly donated the holotype.

**Discussion:** *Fusiturricula sunderlandi* is most similar to the Panamic species, *F. armilda* (Dall, 1908), but differs in being a more slender, fusiform shell with a more elongated body whorl. In *F. armilda*, the body whorl pinches-in abruptly at the junction with the siphonal canal, while in *C. sunderlandi*, the body whorl tapers gradually into the siphonal canal. The two species possibly form a cognate pair.

### *Knefastia* Dall, 1919

### *Knefastia hilli* new species

(figures 38, 39)

**Material examined:** Holotype—Length 50 mm, trawled by commercial fishermen from 70 m depth off Portobelo, Panama, USNM 860548.

**Description:** Shell large, robust, fusiform; spire very high, elevated, distinctly turriculate and scalariform; subsutural area flattened, producing stepped spire whorls; whorls ornamented with 8 large, rounded, elongated, varix-like axial knobs; body whorl ornamented with 12 large, pustulated spiral cords with one or two fine, pustulated secondary cords in between; pustulated cords overlie large axial knobs; siphonal canal short, stubby, ornamented with 8 large, pustulated cords; fine cords and threads present between main siphonal cords; outer lip with numerous lirae along inside edge; anal notch small, narrow; shell color orange-brown with darker brown knobs; primary cords on spire, body whorl, and siphonal canal white or light tan; body whorl-siphonal canal junction marked with wide, dark brown band; anterior end of siphonal canal circled by wide, dark brown band; aperture and columella pale orange-tan.

**Etymology:** Named for Mr. Leonard C. Hill of Miami, Florida.

**Discussion:** *Knefastia hilli* is the first-known living Atlantic species of this primarily Panamic genus. *Knefastia hilli* is most similar to *K. olivacea* (Sowerby, 1833), which ranges from the Gulf of California southward to southern Ecuador. The new Caribbean species differs from *K. olivacea* in being a smaller shell with larger and more pronounced axial knobs, and in having finer and more numerous spiral cords. The two species, however, are very similar and, no doubt, represent Panamic-Caribbean cognates.

## ACKNOWLEDGEMENTS

I thank Mr. Leonard Hill of Miami, Florida, for the donation of the valuable research material collected by Mr. James Ernest. Thanks also to Mr. Kevan Sunderland, Fort Lauderdale, Florida, for the donation of the new *Fusiturricula* species. Special thanks go to Mrs. Cynthia Mischler, Department of Geology, Florida Atlantic University, for patiently typing the manuscript and to Mr. William Lyons, Division of Marine Resources, Florida Department of Natural Resources, for valuable oceanographic data and critical review.

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# Morphological Comparisons of the Species of *Megapallifera* (Gastropoda: Philomycidae)

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ABSTRACT

Specimens of all three species of *Megapallifera*: *M. mutabilis*, *M. wetherbyi*, and *M. ragsdalei*, were collected from their type localities. The external morphology and reproductive system anatomy of each of these species was compared. Mantle color and pattern of *M. mutabilis* is different from those of *M. wetherbyi* and *M. ragsdalei*. Differences among the three species in penial anatomy and in morphology of the lobes in the upper atrium support taxonomic separation of the three species.

*Key words:* Philomycidae; *Megapallifera*, morphology; reproductive-system anatomy.

## INTRODUCTION

The Philomycidae are a family of terrestrial slugs native to the eastern and south-central United States and eastern Asia. There are three genera in the family: *Philomycus*, *Pallifera*, and *Megapallifera*. The slugs in the genus *Philomycus* are large and have a dart sac and dart, those in the genus *Pallifera* are small and lack the dart sac and dart. The slugs in the genus *Megapallifera* also lack the dart sac and dart and were first placed in the genus *Pallifera*. Hubricht (1956) established *Megapallifera* as a subgenus of *Pallifera*, and cited five characteristics for its species: (1) gray or white foot margins, (2) ribbed jaw, (3) large size, (4) chevron-shaped transverse bands on the mantle, and (5) a pilaster extending from the lower vagina into the upper atrium. The latter three characteristics separated *Megapallifera* from *Pallifera*. Hubricht (1976) elevated *Megapallifera* to generic rank, with *M. mutabilis* (Hubricht, 1951), as the type species, and included *M. wetherbyi* (Binney, 1874) and *M. ragsdalei* (Webb, 1950). Webb (1950, 1951) discussed the reproductive-system anatomy of *M. wetherbyi* and *M. ragsdalei* (as a species and subspecies respectively of *Eumelus*), but data concerning the internal anatomy of the atria and penes were incomplete or absent. When Hubricht described *M. mutabilis*, he did not figure the reproductive-system anatomy. Branson (1962) synonomized *M. mutabilis* with *M. ragsdalei*, apparently on the basis of external morphology, without providing supporting data. No comparative studies have been conducted involving all three species of *Megapallifera*.

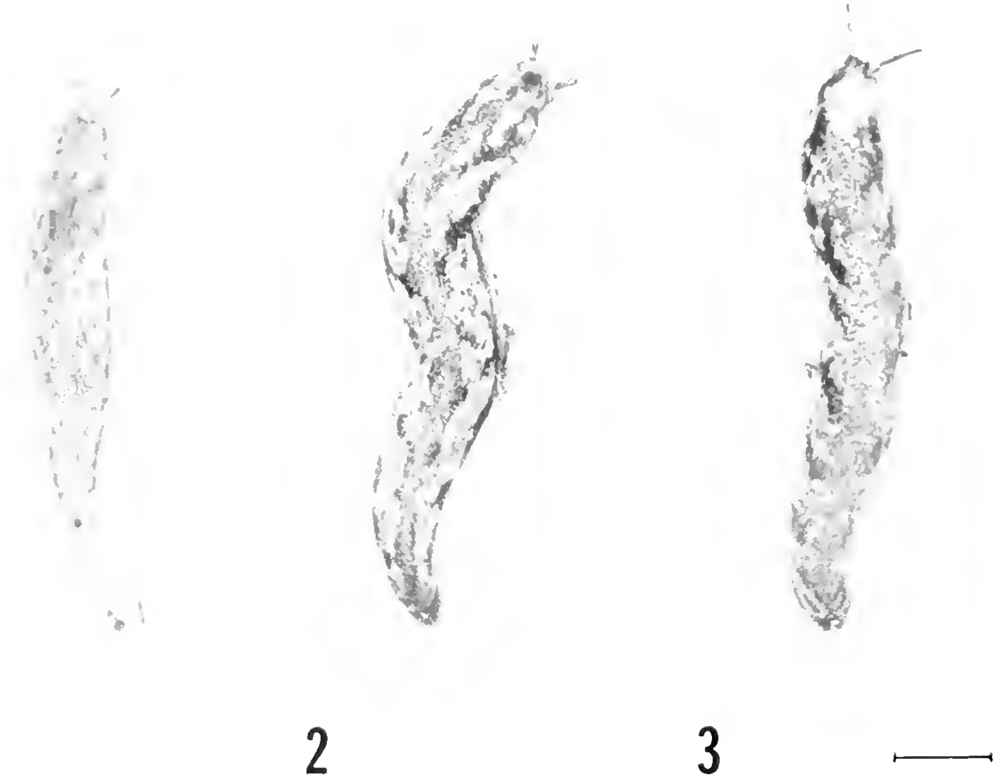
The objectives of this investigation were: (1) to characterize and compare the external morphologies of each of the species of *Megapallifera* and (2) to compare the reproductive systems of these species in order to determine species specific characters.

## METHODS AND MATERIALS

Specimens of *Megapallifera mutabilis* were collected on 18 May 1989 at the type locality (just west of Schoolfield, Pittsylvania County, Virginia), elevation approximately 150 meters, under loose bark of dead trees. Specimens of *M. wetherbyi* were collected on 23 May 1987 and 16 May 1989 at the type locality (near the mouth of the Laurel River, Whitley County, Kentucky), elevation approximately 245 meters, on sandstone cliffs. One specimen of *M. ragsdalei* was collected on 3 April 1988 from the type locality (9.5 kilometers east of Calico Rock, on State Route 56, Izard County, Arkansas), elevation approximately 125 meters, under moss on a sandstone cliff. Additional specimens of *M. ragsdalei*, collected 25 April 1982, at Devils Den State Park, Crawford County, Arkansas (preserved in ethanol) were obtained on loan from the Field Museum of Natural History, Chicago, Illinois (FMNH 210285).

External characteristics were compared with species descriptions to ensure correct identification of all specimens. Mantle color, mantle pattern and foot margin color were compared among species. The live specimens were drowned in distilled water and immediately dissected. The reproductive systems of the specimens dissected were removed and opened so that the internal structure of the atrium and penis could be described. Measurements were taken of eight reproductive structures (length of penis, length of apical chamber of penis, length of penial retractor muscle, length of spermathecal duct, length of vagina, length of oviduct, length of vas deferens, and length of hermaphroditic duct). All material was preserved in 70% ethanol subsequent to dissection. Drownings and dissections of the live specimens were conducted during the same time period (1–12 June) in each year to control for differences in anatomy attributable to phases of the life cycle.

All drawings are tracings of the systems or organs



**Figures 1–3.** Mantle patterns. **1.** *Megapallifera mutabilis*. **2.** *Megapallifera wetherbyi*. **3.** *Megapallifera ragsdalei*. Scale bar equals 10 mm.

**Table 1.** Length comparisons of eight reproductive structures (means with ranges in parentheses) and results of analysis of variance tests. Measurements in millimeters.

| | *M. mutabilis* (N = 3) | *M. wetherbyi* (N = 2) | *M. ragsdalei* (N = 3) | F | p[1] |
|---|---|---|---|---|---|
| Length of slug[2] | 60.0<br>(55.0–65.0) | 71.5<br>(68.0–75.0) | 50.0[3]<br>— | — | — |
| Penis | 11.6<br>(10.7–12.6) | 16.7<br>(16.1–17.3) | 13.1<br>(11.2–15.0) | 8.22 | 0.026[4] |
| Apical chamber | 1.7<br>(1.6–1.8) | 2.6<br>(2.2–3.0) | 1.7<br>(1.5–2.0) | 6.74 | 0.038[4] |
| Penial retractor | 14.6<br>(10.0–20.3) | 7.8<br>(6.8–8.8) | 8.3<br>(6.7–10.8) | 3.00 | 0.139 |
| Spermathecal duct | 10.3<br>(8.6–11.5) | 13.2<br>(11.8–14.6) | 10.9<br>(10.8–11.0) | 3.11 | 0.132 |
| Vagina | 1.7<br>(1.5–1.9) | 1.6<br>(—) | 1.6<br>(1.0–2.7) | 0.04 | 0.966 |
| Oviduct | 9.1<br>(6.8–12.6) | 15.8<br>(12.2–19.3) | 9.4<br>(6.8–11.4) | 2.87 | 0.148 |
| Vas deferens | 18.7<br>(15.1–32.2) | 34.5<br>(29.9–39.1) | 28.1<br>(23.5–35.2) | 5.48 | 0.055 |
| Hermaphroditic duct | 28.9<br>(23.8–32.2) | 40.0<br>(34.4–45.5) | 23.3<br>(20.8–25.5) | 7.35 | 0.032[4] |

[illegible] freedom 2 and 5

[illegible] specimen was obtained
[illegible] at 5% level

**Table 2.** Results of the Modified Duncan Multiple Range Tests Means (in millimeters) underscored by the same line are not significantly different at the 5% level. A, *Megapallifera mutabilis*, B, *Megapallifera wetherbyi*, C, *Megapallifera ragsdalei*.

| Species | A | C | B |
|---|---|---|---|
| Length of penis | 11.57 | 13.01 | 16.70 |
| Length of apical chamber | 1.67 | 1.73 | 2.60 |

| Species | C | A | B |
|---|---|---|---|
| Length of hermaphroditic duct | 23.33 | 28.93 | 39.95 |

figured. The reproductive system was traced from a specimen pinned out in a wax-bottom petri dish and projected, via an overhead projector, onto 8½ × 11 paper. The atrial and penial figures are tracings of photographic slides projected onto 8½ × 11 paper. Voucher specimens have been deposited in the National Museum of Natural History, Smithsonian Institution (USNM 854012 for *Megapallifera ragsdalei*; USNM 854013 for *M. wetherbyi*; USNM 854014 for *M. mutabilis*).

Analysis of variance was used to compare the means of measurements of reproductive organs. After the analysis of variance tests were conducted, a modified Duncan Multiple Range Test (Kramer, 1956) was used to determine which means, among those compared in a given ANOVA, were significantly different.

## RESULTS

### External Characters

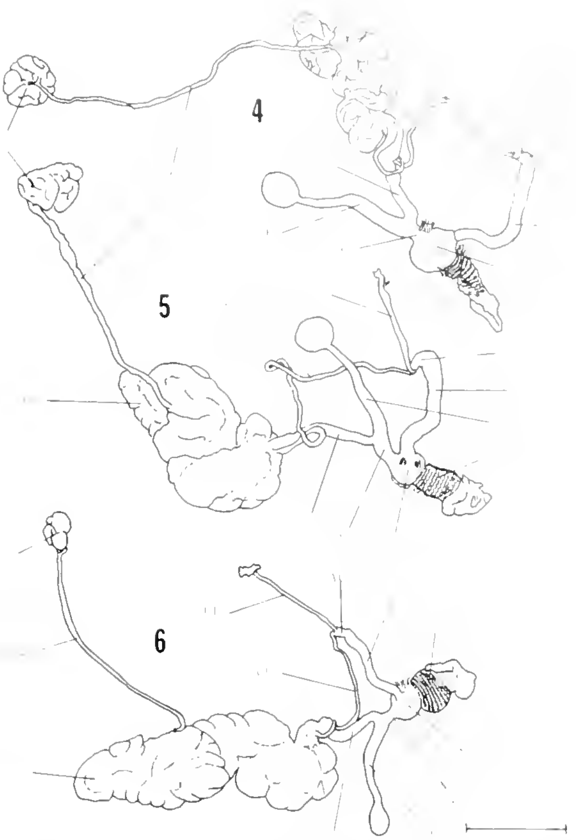
All living specimens attained crawling lengths that varied between 50 and 75 millimeters (figures 1–3). All had some transverse chevron-shaped bands on the mantle (figures 1–3). All had gray or white foot margins.

The mantle color of *Megapallifera mutabilis* was fawn or tan whereas the mantle color of *M. wetherbyi* and *M. ragsdalei* was gray. The "spots" that produce the mantle pattern were light to dark brown in all three species; however, the arrangement of those spots varied among species. Both *M. wetherbyi* and *M. ragsdalei* had broad distinct chevrons in their mantle pattern (figures 2, 3). In *M. mutabilis* the mantle pattern was a series of spots that in some cases produced vague chevrons on the mantle (figure 1).

Observed habitat preferences varied among the species. *Megapallifera mutabilis* preferred old-growth deciduous forest, whereas *M. wetherbyi* and *M. ragsdalei* preferred areas in which sandstone outcrops and cliffs were common.

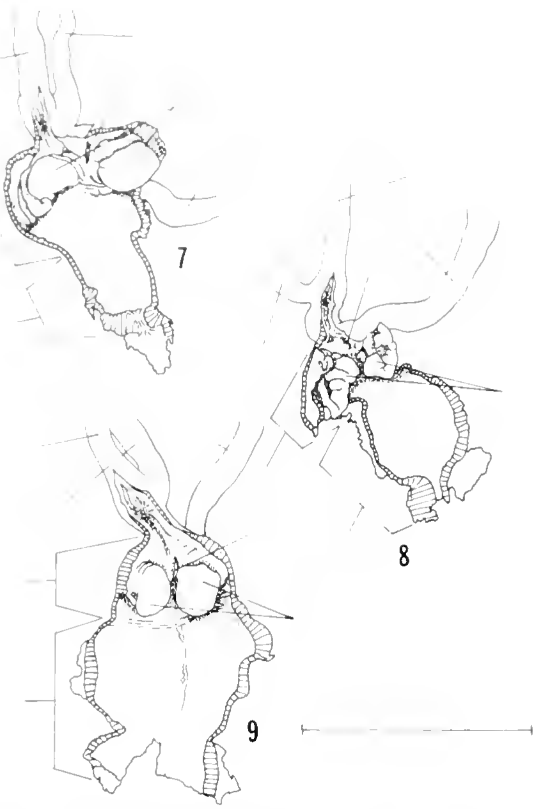
### Reproductive System Characters

Comparisons of length measurements of some reproductive structures are shown in table 1. Analysis of variance tests (table 1) indicated three significant differences among species. For each of these tests, the Modified Duncan Multiple Range Tests (table 2) indicated which of the species were significantly different from the others.

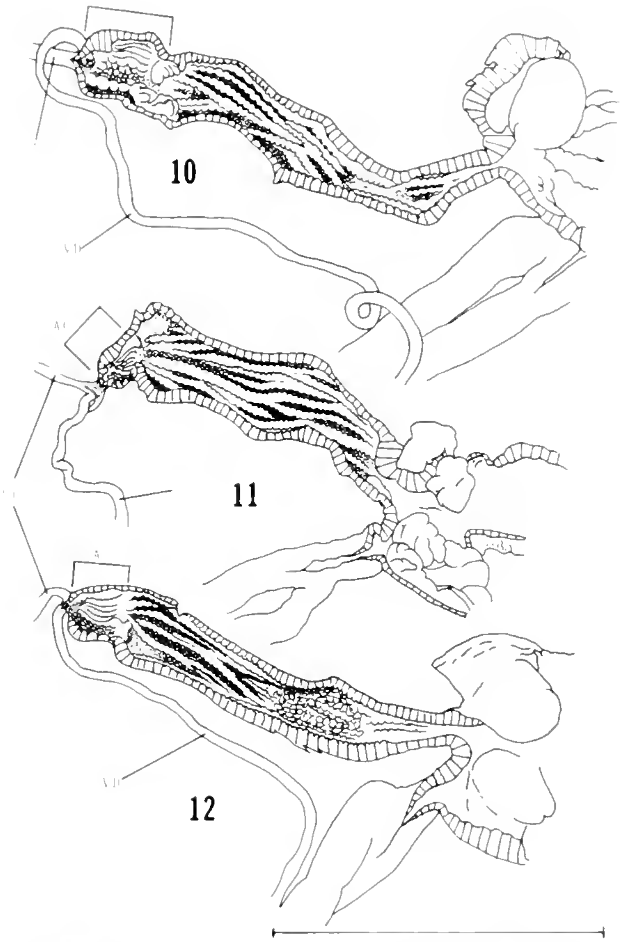


**Figures 4–6.** Genitalia. **4.** *Megapallifera wetherbyi*. **5.** *Megapallifera ragsdalei*. **6.** *Megapallifera mutabilis*. Scale bar equals 10 mm AC, apical chamber, AG, albumen gland, G, gonad, HD, hermaphroditic duct, LA, lower atrium, P, penis, PR penial retractor; SD, spermathecal duct, UA, upper atrium, UV, free oviduct, V, vagina; VD, vas deferens.

All specimens had an atrium with two "parts", a lower atrium and an upper atrium (figures 7–9). The external surface of the lower atrium (lying within the body cavity) was covered with glandular material (figures 4–6), the internal surface was relatively smooth (figures 7–9). The color of the glandular material on the outside surface of the lower atrium varied among species, light orange for *Megapallifera wetherbyi*, white for *M. ragsdalei*, cream for *M. mutabilis*. The external surface of the upper atrium, in all specimens, was nonglandular, and had accessory retractor muscles located near the origin of the vagina (figures 4–6). Internally, the upper atrium contained two labia-like lobes, one on either side of the opening to the penis (figures 7–9). In *M. mutabilis* these lobes were the least complex, having two or three folds that divided a lobe into sublobes (figure 9). In *M. wetherbyi* the primary lobes had two to three folds (figure 7) whereas *M. ragsdalei* had four or five sublobes (figure 8).



**Figures 7–9.** Internal details of the atria. **7.** *Megapallifera wetherbyi*. **8.** *Megapallifera ragsdalei*. **9.** *Megapallifera mutabilis*. Scale bar equals 10 mm. AL, atrial lobes; LA, lower atrium, P, penis, PO, penial opening, SD, spermathecal duct; UA, upper atrium; UV, free oviduct



**Figures 10–12.** Internal detail of the penes. **10.** *Megapallifera wetherbyi*. **11.** *Megapallifera ragsdalei*. **12.** *Megapallifera mutabilis*. Scale bar equals 10 mm. AC, apical chamber; PR, penial retractor; VD, vas deferens

The penes of all specimens had an apical chamber at the vas-deferens end, *i.e.*, a part of the penis set off by an internal constriction (figures 10–12). The size of the apical chamber varied among species (table 1), but internally there was little variation in the pattern of folds and pilasters among species. Internally, below the apical chamber, the penis of *M. mutabilis* had five to seven pustulose pilasters that began at the vas-deferens end and gradually disappeared at approximately the midpoint of the penis (figure 12). The remainder of the penis, internally, was pustulose. The penis of *M. ragsdalei* had seven to nine pustulose pilasters that ran the entire length of the penis (figure 11). The internal penial anatomy of *M. wetherbyi* (figure 10) was similar to that of *M. ragsdalei* (figure 11). All specimens lacked a penial sheath (figures 10–12).

## DISCUSSION

[illegible] characteristics, mantle color and mantle [illegible] *Megapallifera mutabilis* were clearly different [illegible] *M. wetherbyi* and *M. ragsdalei* (figures 1–3). [illegible] the internal morphology of the penis (figures [illegible] and the shape of the upper atrial lobes (figures 7 [illegible] *mutabilis* were different from those of both *M. wetherbyi* and *M. ragsdalei*. Significant differences between the mean lengths of the penis and the apical chamber of the penis (table 2) were demonstrated between *M. mutabilis* and *M. wetherbyi*. These data support the species status of *M. mutabilis*.

External morphological data supporting the separation of *Megapallifera wetherbyi* from *M. ragsdalei* were not conclusive (figures 2, 3). However, internal morphological data supported specific-level separation of these two taxa. Mean lengths of the penis, the apical chamber of the penis, and the hermaphroditic duct for *M. wetherbyi* were significantly greater than those of *M. ragsdalei* (table 2). In addition, the lobes in the upper atrium of the former were different from those of the latter (figures 7, 8). Hubricht (1956) mentioned a pilaster that extended from the lower vagina into the upper atrium. Webb (1950) mentioned a single pilaster or a bilobed pilaster in the upper atrium. Neither author figured the lobes in the uneverted condition. This study has demonstrated that there are two separate lobes located in the upper atrium, one on either side of the opening into the penis and below the opening into the vagina. In addition, these lobes were, in some specimens, quite complex. In these three species the most obvious reproductive-system differences were in these lobes, *i.e.*, all three species were easily separated on the basis of these lobes alone (figures 7–9). Webb (1951) made note of the atrial lobes during studies of the courtship between two *M. wetherbyi*. The lobes were referred to as "hoods", in their everted shape, and they appeared to play a significant role in premating behavior. In view of the apparent function of these lobes it seems appropriate, for these three species, to attach considerable significance to atrial lobe differences.

In summary, this study demonstrated species-specific morphological differences, both external and internal, between *Megapallifera mutabilis*, *M. wetherbyi*, and *M. ragsdalei*.

## ACKNOWLEDGEMENTS

Thanks go to Susan McKee, who was the only person to find a live specimen of *Megapallifera ragsdalei* at the type locality. Thanks also go to Dr. Richard Reeder, who helped locate specimens used in this study, and provided valuable comments concerning the writing of this paper. Financial support for field work was provided by grants from the Research Development Gra[illegible] Pennsylvania State University.

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# Ovophagy in *Anachis avara* (Say, 1822) (Gastropoda: Columbellidae)

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Five strands of egg cases of *Melongena corona altispira* Pilsbry and Vanatta, 1934, were collected in the Indian River, near Wabasso, Indian River County, Florida in July of this year and maintained in a recirculating seawater table together with approximately fifty specimens of *Melongena corona altispira*. When examined after several hours in the seawater table, six specimens of *Anachis avara* (Say, 1822) were found on the egg capsules. The *Anachis* were removed and returned to the table approximately one meter from the egg cases. The capsules were examined and placed in a large bowl, the rim of which extended above the water level in the seawater table by two centimeters. Seawater flowed into the bowl, overflowing the rim into the table.

The following morning (12 hours later) four of the six specimens of *Anachis avara* in the seawater table were again on the flat sides of the egg capsules, each on the terminal capsule of a strand. When examined under a dissecting microscope, the columbellids were observed to have penetrated the walls of the egg cases near the centers of the capsules, and to be feeding on the *Melongena* larvae and on the dense inner layer of albuminous fluid (figure 1). To reach the egg capsules, the *Anachis* had to crawl past two large *Mercenaria mercenaria* that had been cracked open and placed in the tank to feed the *Melongena*.

Although there was not sufficient time to repeat these observations with appropriate controls, it seems clear that *Anachis avara* is capable of locating gastropod egg cases at considerable distances by chemosensory means. It is unclear whether *Anachis avara* showed a preference for egg cases over *Mercenaria mercenaria*, or if it was deterred from feeding on the bivalves by the presence of feeding *Melongena*.

Members of the family Columbellidae have extremely diverse and [illegible] diets that may consist of polychaetes, small crustacea, ascidians, hydroids, algae, organic detritus and carrion (Hatfield, 1979; Taylor *et al.*, 1980). Taylor (1987) reported that six of 16 specimens of *Mitrella scripta* examined contained gastropod eggs in their stomachs. The present observations suggest that gastropod eggs represent a significant dietary item for at least some species of columbellids.

**Figure 1.** *Anachis avara* feeding on larvae of *Melongena corona altispira*

This is contribution number 264 of the Smithsonian Marine Station at Link Port.

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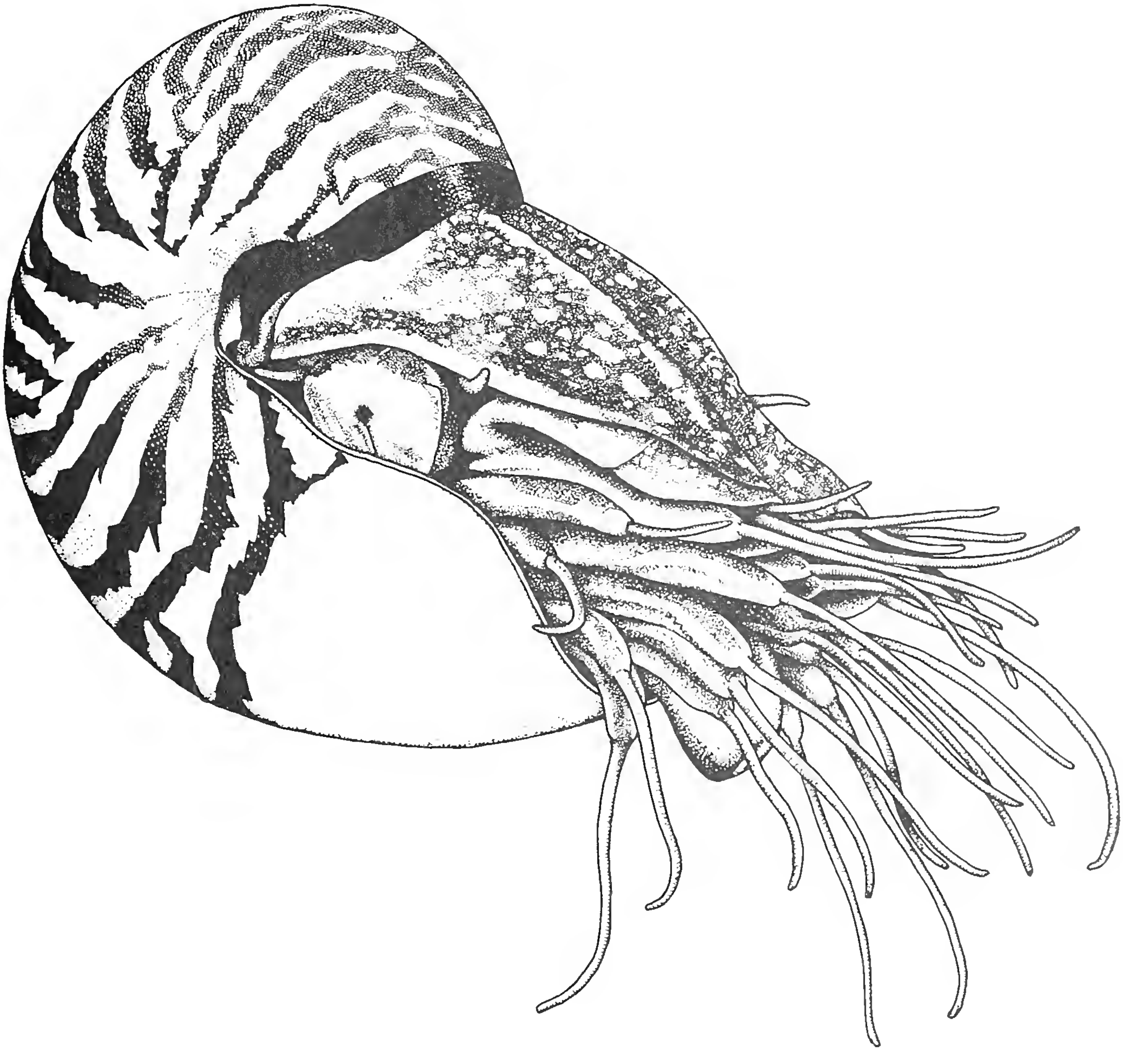

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# A New Genus and Species of Neomphalid Limpet from the Mariana Vents with a Review of Current Understanding of Relationships among Neomphalacea and Peltospiracea

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## ABSTRACT

*Symmetromphalus regularis* new genus, new species, is described from hydrothermal vents of the Mariana Back Arc Basin. It differs from *Neomphalus fretterae* McLean, 1981, in having the opening of the mantle cavity directed anteriorly rather than to the left, more numerous epipodial tentacles, the operculum retained in the adult, and in a deep sperm groove on the left cephalic tentacles of males.

The family Cyathermiidae is here proposed for two coiled members of the superfamily Neomphalacea, the genera *Cyathermia* and *Lacunoides*, both of Warén and Bouchet (1989). The family Cyathermiidae is characterized by: a short snout, a closed sperm groove along the left cephalic tentacle, and two cirri at the tip of the left cephalic tentacle.

Neomphalacea can be associated with Peltospiracea in a suborder Neomphalina, on the basis of shared characters (non-nacreous shell, monotocardian heart, bipectinate gill, lack of ctenidial bursicles, similar radula). As these may be plesiomorphic or convergent characters, further anatomical comparisons are needed to establish additional synapomorphic characters for such a suborder. A fossil record of the newly expanded complex is yet elusive, but should continue to be sought.

*Key words:* Archaeogastropoda, Neomphalacea, *Symmetromphalus*; Cyathermiidae; Peltospiracea; hydrothermal-vent limpets, Mariana Vents.

## INTRODUCTION

*Neomphalus fretterae* McLean, 1981, the largest and most densely aggregated of hydrothermal-vent limpets, was the first vent-limpet to be described (McLean, 1981). Its anatomy was treated in an accompanying paper by Fretter *et al.* (1981). Although I expected that additional species of *Neomphalus* would eventually be found at other sites, none were found until the fauna of the Mariana Back Arc Basin was sampled in 1987, at which time a new, monotypic genus in the family Neomphalidae was discovered. The primary objective of this paper is to provide the formal description of the new genus and species *Symmetromphalus regularis*.

Recently, an affinity with *Neomphalus* was recognized in two coiled genera described by Warén and Bouchet (1989) from Eastern Pacific hydrothermal vents: *Cyathermia* and *Lacunoides*. These small-shelled, monotypic genera are regularly coiled and have many of the diagnostic features common to *Neomphalus*, although they share other unique features, which indicate that they in turn should be segregated within their own family. Accordingly, the family Cyathermiidae is here proposed.

Higher classification of Neomphalacea and the recently proposed and probably related Peltospiracea McLean (1989a) has been discussed by Haszprunar (1988a,b, 1989), Warén and Bouchet (1989), and Fretter (1989). Another objective of this paper is to briefly review the current work that assesses these relationships, noting the gaps in our understanding of anatomy in certain members.

My early interpretation of the possible fossil affinity of *Neomphalus* has generated some controversy; here I take the opportunity to review these criticisms and offer a revised assessment of the potential for a fossil record of the groups treated here.

## MATERIALS AND METHODS

The new species described here was first collected with the deep-submersible *Alvin* in May, 1987, at hydrothermal vents of the mid-Pacific Mariana Back Arc Basin. A general description of the site was given by Hessler *et al.* (1988). Until now, two other gastropods, *Alvinoconcha hessleri* Okutani and Ohta, 1988, and *Pseudorimula marianae* McLean, 1989b, have been described from these vents.

Limpet specimens were collected with the mechanical arm of the *Alvin* in the course of collecting substrate samples and general collecting of all organisms. Material was preserved upon reaching the surface and was originally fixed for 24 hours in 10% seawater formalin buffered with sodium borate, washed in fresh water, and transferred to 70% ethanol (for details of collecting procedures see Turner *et al.*, 1985). Preserved specimens were sorted at Scripps Institution of Oceanography and forwarded to me by Robert R. Hessler.

Radulae were extracted from preserved specimens after dissolution of tissues with 10% NaOH for 48 hours, air dried and coated with gold palladium for SEM examination. Juvenile shells with protoconchs were examined with SEM. Protoconch lengths were taken directly from scale indications for the SEM micrographs.

Repositories of the type material are the Los Angeles County Museum of Natural History (LACM), the United States National Museum (USNM), and the Museum National d'Histoire Naturelle, Paris. All figured specimens are deposited at the LACM.

## SYSTEMATICS

### Superorder ARCHAEOGASTROPODA
Thiele, 1925

Recent authors (Salvini-Plawen, 1980; Salvini-Plawen & Haszprunar, 1987; Haszprunar, 1988a,b; Hickman, 1988) have discussed the problems inherent in the "archaeogastropod" concept, pointing out that Archaeogastropoda, as traditionally constituted (Thiele, 1925; Knight *et al.*, 1960) represents a grade.

Hickman (1988) redefined Archaeogastropoda to include superfamilies Pleurotomariacea, Fissurellacea, and Trochacea, stating that it was thereby synonymous with Haszprunar's concept of Vetigastropoda Salvini-Plawen, 1980. However, Haszprunar (1988a,b) also included Lepetodrilacea McLean, 1988, in Vetigastropoda, which inclusion was overlooked by Hickman (1988) and also by Bieler (1990:380) in his critique of Haszprunar's work. I follow Haszprunar (1988a,b) in retaining the traditional meaning of Archaeogastropoda, allowing it to be expressly indicated in a classification as an orthophyletic grade.

### Superfamily NEOMPHALACEA McLean, 1981

The diagnosis that follows encompasses two families, the Neomphalidae and the Cyathermiidae new family, taking into account the characters of the two coiled genera described by Waren and Bouchet (1989). It will, however, need to be modified once the internal anatomy of all genera becomes known.

**Diagnosis:** Shell regularly coiled or of limpet form, lacking nacre, periostracum thick; first teleoconch whorl with oblique aperture and rounded whorls, regularly coiled in all genera, protoconch with net-pattern surface sculpture, operculum multispiral initially, final volution enlarged, retained at least through the first teleoconch whorl in all members.

Monotocardian; ventricle not penetrated by rectum; left kidney only; ctenidium bipectinate, afferent membrane lacking or very short; gill axis producing sturdy free tip, filaments elongate, skeleton lacking bursicles. Perioral surface with transverse furrow extending to cephalic lappets. Eyes lacking, epipodial and cephalic tentacles non-papillate, left cephalic tentacle of male modified to function as penis, sperm groove open or closed. Gonad with glandular gonoducts, dorsal to digestive gland and intestine; females with seminal vesicle.

Radula rhipidoglossate, cusps of all teeth aligned in descending rows, shaft lengths of all teeth increasing toward edge of ribbon. Rachidian tooth with shaft broad at base and acutely pointed overhanging cusp. Lateral teeth four pairs, inner surfaces excavated to articulate with rachidian or adjacent lateral teeth, overhanging cusps of laterals like those of rachidian tooth. Marginal teeth numerous, shafts wide but incompletely separated at base, tips deeply serrate.

### CYATHERMIIDAE new family

**Diagnosis:** Shell coiled through teleoconch; sculpture smooth to finely reticulate. Neck short; short snout present; cephalic tentacles anterio-laterally directed; enlarged left tentacle serving as penis, sperm groove of enlarged left tentacle closed, tip with two prominent cirri. Afferent ctenidial membrane very short. Cusps of rachidian and lateral teeth finely serrate, cusp of rachidian tooth much longer than those of inner lateral teeth.

**Included genera:** *Cyathermia* Waren and Bouchet, 1989, and *Lacunoides* Waren and Bouchet, 1989. *Cyathermia* is monotypic for *C. naticoides* Waren and Bouchet, which is widely distributed on the East Pacific Rise. *Lacunoides* is monotypic for *L. exquisitus* Waren and Bouchet, known only from the Galapagos Rift.

**Remarks:** Separation of the two monotypic coiled genera from the two monotypic limpet genera is now appropriate at the familial level, given that each of the two groups of genera have synapomorphic characters in common. Diagnostic characters of the Cyathermiidae are the short snout, left cephalic tentacle with closed sperm groove and two cirri at the tip, serration of rachidian and lateral teeth and enlargement of rachidian tooth. See Waren and Bouchet (1989) for more detailed descriptions of these two genera.

### Family NEOMPHALIDAE McLean, 1981

**Diagnosis:** Shell coiled through first teleoconch whorl, changing to limpet form in second teleoconch whorl; sculpture of strong radial ribs. Neck long; snout lacking in adult; cephalic tentacles posteriorly directed; sperm groove of enlarged left tentacle open; cirri at tip of penis lacking. Cusps of rachidian and lateral teeth non-serrate, cusp of rachidian tooth of same length as those of inner lateral teeth.

**Included genera:** *Neomphalus* McLean, 1981, and *Symmetromphalus* new genus. *Neomphalus* is monotypic for *N. fretterae* McLean, 1981, known from the Galapagos Rift (the type locality) and from sites on the East Pacific Rise. *Symmetromphalus* is monotypic for *S.*

*regularis* new species, known only from the Mariana Back Arc Basin vents.

**Remarks:** Diagnostic characters of the Neomphalidae are the limpet form of the mature shell, absence of snout, posterior direction of cephalic tentacles, open sperm groove and lack of cirri on the enlarged left tentacle. See Fretter *et al.* (1981) for a more detailed description of anatomy in *Neomphalus fretterae*.

*Symmetromphalus* new genus

**Type species:** *Symmetromphalus regularis* new species.

**Description:** Shell of limpet form, mantle cavity and horseshoe-shaped muscle open anteriorly; shell outline symmetrical in juvenile, irregular in mature specimens; coiled apical whorl offset to right. Sculpture of finely beaded radial ribs; operculum present in adult. Neck long, perioral surface with transverse furrows extending to cephalic lappets. Cephalic tentacles short, posteriorly directed, left tentacle of male greatly distended, deep dorsal sperm groove connecting with groove on left side of neck. Epipodial tentacles present posteriorly and laterally. Gill bipectinate, afferent membrane lacking, filaments elongate, efferent axis of free tip extended over long neck. Radula rhipidoglossate, four pairs of lateral teeth, cusps similar to those of rachidian teeth, except fourth lateral teeth strongly serrate on outer edge; marginal teeth numerous.

**Remarks:** On characters of external anatomy, *Symmetromphalus* differs from *Neomphalus* in its: anterior rather than leftward opening of the mantle cavity and shell muscle, its evenly distributed rather than posteriorly grouped epipodial tentacles, smaller cephalic tentacles, greater prominence of sperm groove in enlarged left cephalic tentacle, and apparent absence of well-defined food groove. The shell differs in having strong beading on early ribs and lacking the interior ridge. A vestigial operculum is present in mature specimens. The radula is similar in both genera.

Most of these distinctions are regarded as significant at the generic level. Only the sculptural difference (prominent beading rather than smooth ribs) is considered a species-level difference by itself.

Names of both the new genus and species emphasize the regular and symmetrical aspect, in contrast to the leftward shift of the mantle cavity that characterizes *Neomphalus*.

*Symmetromphalus regularis* new species

(figures 1–17)

**Description:** Shell (figures 1–3, 7–10, 17) of medium size for family (maximum length 14.0 mm for females, 10.6 mm for males), white under thick, pale tan periostracum, which projects beyond edge of shell. Profile moderately elevated; juvenile shell nearly symmetrical, outline of mature shell irregular, indicating habitual site of attachment. Apical whorl markedly posterior in juvenile shell (figures 11, 12), closer to center in mature shell. Protoconch (figures 13, 14) length 220 μm, surface sculpture of irregular network of low ridges. First teleoconch whorl rounded, suture deep, coiled through one-half whorl of growth. Limpet form attained after completion of first teleoconch whorl; growth of posterior slope beginning at shell length of 1.5 mm. Radial (spiral) sculpture arising at shell length of 1 mm, consisting of low primary cords on which beading appears at shell length of 2 mm. Secondary cords arise at shell length of about 7 mm, quickly assuming size of primary cords; cords at margin very narrow, retaining beading, interspaces broad. Shell interior glossy white. Muscle scar horseshoe-shaped, open anteriorly, broad throughout, except posteriorly; anterior terminations rounded. Apical pit remaining open.

*Dimension of holotype (female):* Length 12.3, width 10.1, height 5.0 mm; dimensions of illustrated paratype (male): length 8.4, width 6.5, height 3.0 mm.

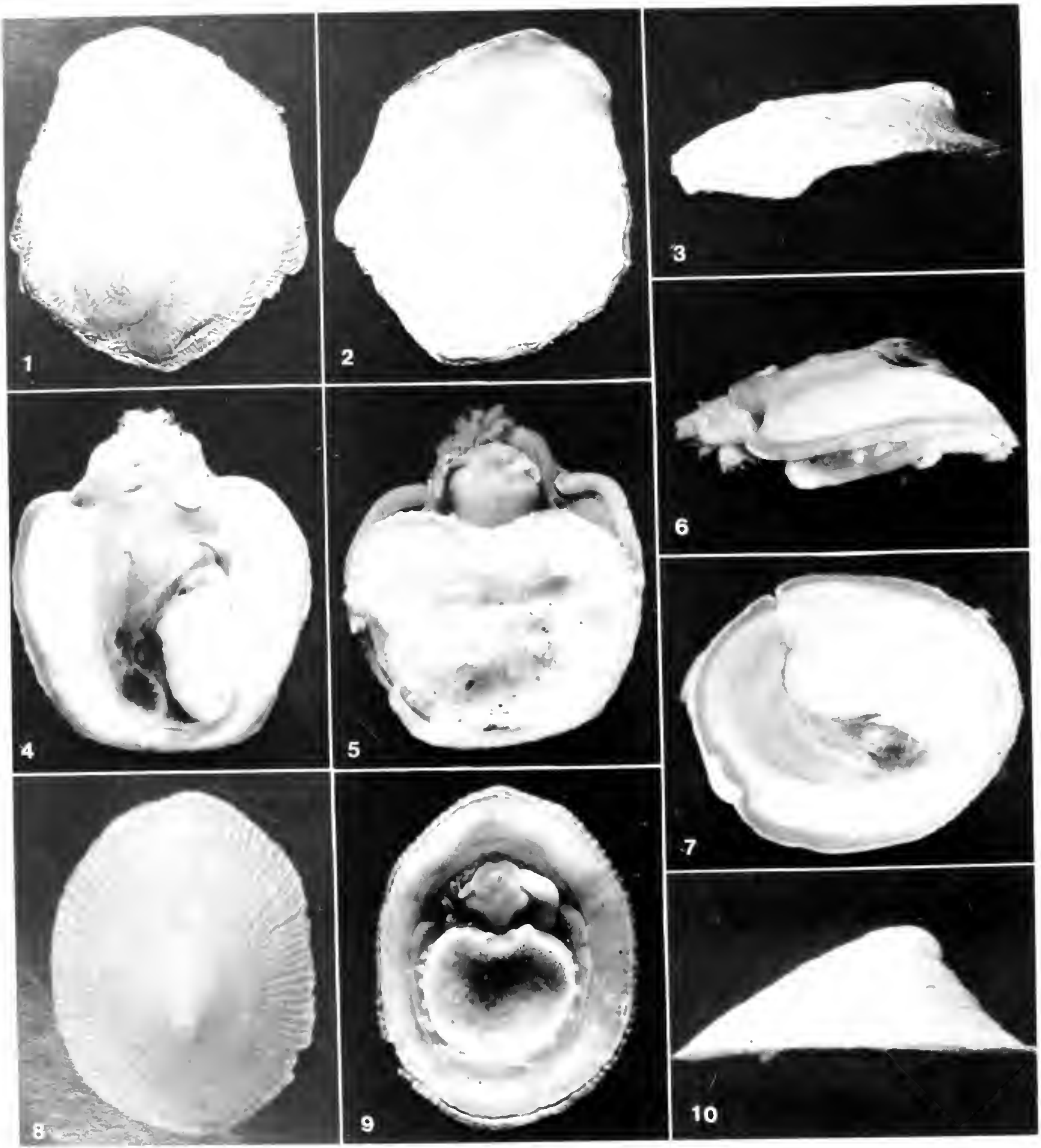
*External anatomy (figures 4–7, 9):* Neck long, wide, dorso-ventrally compressed, lateral edges acutely angulate (except left edge deeply grooved in male). Transverse furrow extending laterally above mouth, delimiting the ventrally positioned oral lappets. Eyes lacking, cephalic tentacles posteriorly directed, equal and relatively short and thin in females (contracted state); left tentacle of male enormously distended, bearing a deep sperm groove dorsally, which is continuous with deep groove on left edge of neck. Females lack groove on left edge of neck.

Mantle cavity deep, extending two-thirds the length of shell muscle on left side. Ctenidium bipectinate, afferent membrane lacking throughout its length, efferent axis arising at posterior of mantle cavity on left; free tip of gill separating above base of neck, its efferent axis massive, extending well anterior of head; gill filaments overlying head, greatly elongate, decreasing in length toward tip.

Mantle margin with fine papillae corresponding to radial ribs. Outline of foot rounded; anterior edge of foot with furrow marking opening of pedal gland. Epipodial ridge encircling foot, extending forward on both sides to join with neck edges; short, contracted epipodial tentacles evenly spaced along ridge, becoming smaller anteriorly, not extending anteriorly beyond position of shell muscle. Operculum (figure 9) very thin, transparent, multispiral, with rapidly enlarging final whorl, edge frayed, shed in some large females (largest operculum about 4 mm diameter).

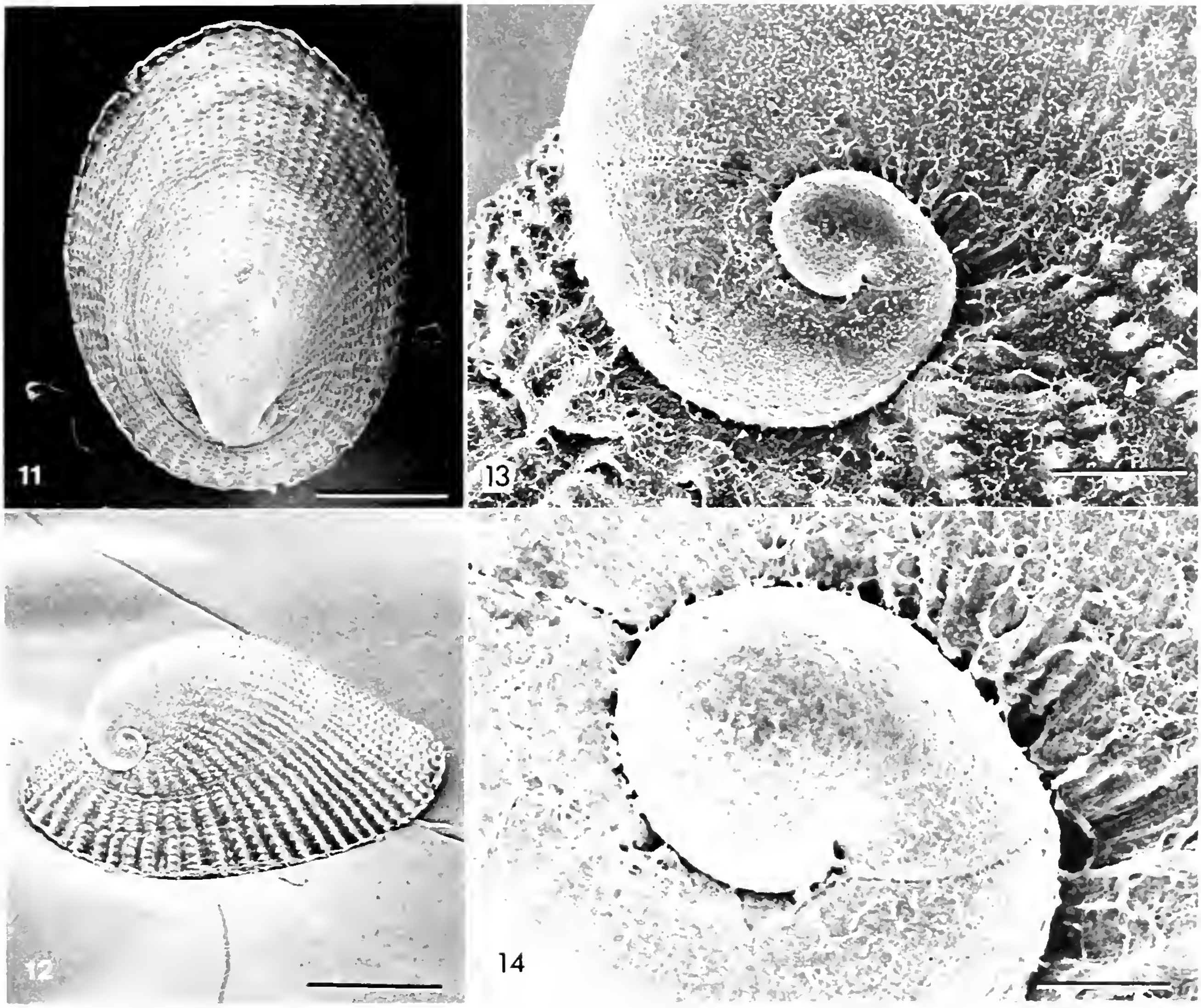
In dorsal view of detached animal, shell muscle arms very broad, except posteriorly, where reaching one-fifth the maximum width; anterior terminations rounded, mantle skirt thin, showing posteriormost extent and outline of ctenidium; pericardium visible as dark structure posterior to gill; gonad and pallial gonoducts large, overlying digestive gland, occupying posterior dorsal area next to right arm of shell muscle (figure 4).

Radula (figures 15, 16) rhipidoglossate, rachidian and



**Figures 1–10.** *Symmetromphalus regularis* new species, from Alice Springs vents, Mariana Back Arc Basin. *Alvin* dive 1843, 3,640 m. Ar[illegible] top in dorsal and ventral views. **1–6.** Holotype (female), LACM 2432, shell length 12.3 mm. **1.** Shell exterior. **2.** Shell inte[illegible] side of shell. **4.** Dorsal view of detached body. **5.** Ventral view of detached body. **6.** Left lateral view of detached body. **7**[illegible] Paratype (male), LACM 2433, shell length 8.4 mm. **7.** Dorsal view of detached body. **8.** Shell exterior. **9.** Ventral view, at[illegible]hed to shell, showing operculum on edge. **10.** Left side of shell.

four pairs of late[illegible] similar morphology, marginal teeth numero[illegible] [illegible]w of all teeth forming circular arc. Base of rac[illegible]h broad, overhanging cusp moderately long, tapered [illegible] acute tip. First lateral tooth slightly less prominent than rachidian tooth, inner base behind that of rachidian tooth. Second, third and fourth lateral teeth similar to each other, their innermost bases behind the base of adjacent lateral teeth; lengths



**Figures 11–14.** *Symmetromphalus regularis* new species. SEM views of juvenile paratype, LACM 2433, shell length 3.5 mm. **11.** Dorsal view. **12.** Oblique, left lateral view. **13.** Protoconch and early sculpture, scale bar = 200 μm. **14.** Protoconch, scale bar = 100 μm.

of shafts and overhanging cusps increasing in length outwardly. Fourth lateral tooth larger than third, its outer edge sharply serrate, its lowermost serration most prominent. Inner marginal teeth with long, broad shafts, cusp edges deeply serrate; shafts of outer marginal teeth incompletely separated.

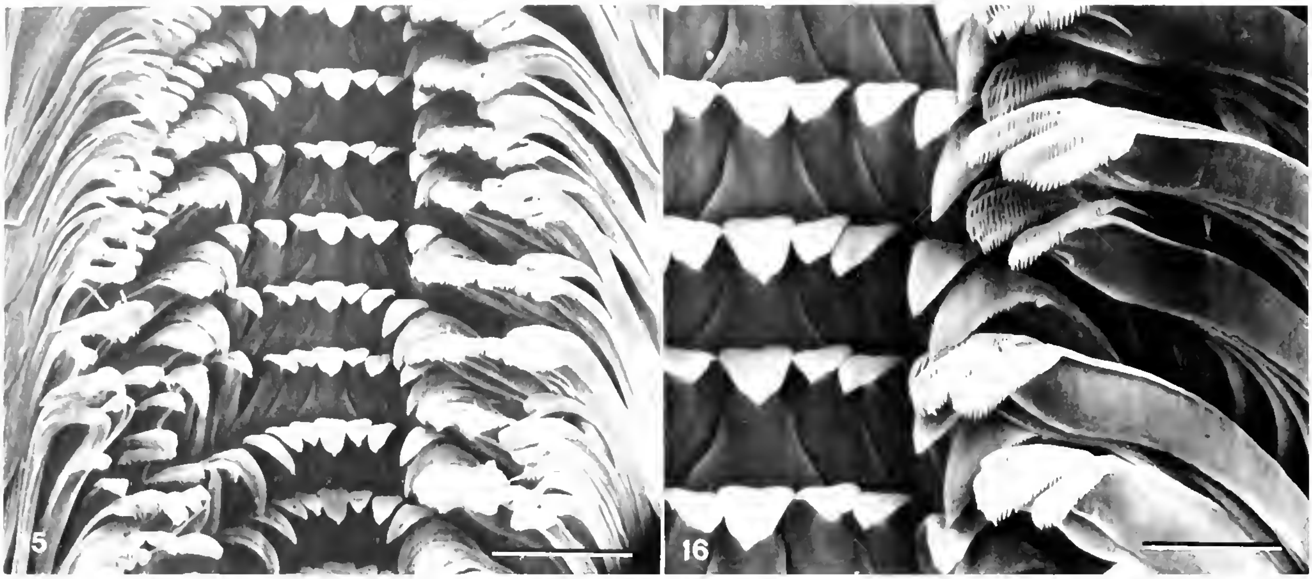
**Type locality:** Alice Springs vents, Mariana Back-Arc Basin (18°12.6′N, 144°42.4′E), 3,640 m. The limpets occur in dense aggregations on the walls of the vents (figure 17). From the photograph it is evident that the limpets are oriented randomly, filling all space on the substrate, but not stacked.

**Type material:** 27 specimens from type locality, *Alvin* dive 1843, 4 May 1987. Holotype LACM 2432, 10 paratypes LACM 2433, 10 paratypes USNM 784763, 6 paratypes MNHN. All specimens have undamaged periostraca, free of biogenic or mineral encrustations. Males are represented by six specimens only, of which the smallest (with broken shell) is approximately 5 mm in length. Twelve specimens under 5 mm in length are too small to sex without sectioning.

## DISCUSSION

### HIGHER CLASSIFICATION

The affinities and the higher classification of the Neomphalacea are yet to be fully resolved and are likely to remain controversial for some time. Fretter *et al.* (1981) affirmed that *Neomphalus* is a highly derived archaeogastropod, but could not relate it to other known living groups. Waren and Bouchet (1989) placed the newly described family Peltospiridae McLean, 1989, in the



**Figures 15, 16.** *Symmetromphalus regularis* new species. SEM views of radula of paratype. **15.** Full width of ribbon, showing rachidian, four pairs of lateral teeth and numerous marginal teeth, scale bar = 40 μm. **16.** Enlarged view of overhanging cusps of rachidian, laterals and marginals, scale bar = 20 μm

Neomphalacea, whereas McLean (1989a), Fretter (1989), and Haszprunar (1988a,b, as hot-vent group A) separated two superfamilies: Neomphalacea and Peltospiracea. Shared characters of both superfamilies include the monotocardian heart, bipectinate ctenidia that lack bursicles, oesophageal features, statocysts with statoliths, and radular similarity. In having the left kidney only and in lacking ctenidial bursicles both groups were placed outside the Vetigastropoda (superfamilies Scissurellacea, Pleurotomariacea, Fissurellacea, Haliotacea, Trochacea, and Lepetodrilacea) by Salvini-Plawen and Haszprunar (1987) and by Haszprunar (1988a,b). Both groups were regarded as generally more primitive than the Vetigastropoda by Haszprunar.

The main argument for separation of Neomphalacea and Peltospiracea concerns the striking differences in external features that are related to feeding modes: in Neomphalacea the neck is long and dorso-ventrally compressed; transverse furrows lead from the recessed mouth to protruding lappets that are ventral to the cephalic

Figure 17. *Symmetromphalus regularis* new species. In situ view of limpets on basalt boulders in path of effluent at Alice Springs, Mariana Back-Arc Basin, 3,640 m. The largest limpets may exceed 14 mm in length. Photo courtesy S. Ohta

tentacles (see Warén & Bouchet, 1989, fig. 23 for *Cyathermia*), and there is a notch for dorsal access to the mouth from the food groove (well-developed only in *Neomphalus*), the bipectinate gill is hypertrophied, the gill filaments elongate and separated for filter feeding in combination with grazing. In contrast, the Peltospiracea are known by the descriptive appellation of 'tapersnouts,' which was first used by McLean (1985) prior to their formal description, because of their long, tapered snouts. The tapered snout was correlated by Fretter (1989) with a well-developed, protrusible subradular organ, enabling the snout to project at great length.

The Peltospiridae include both limpet-shaped and coiled members. Two important papers on anatomy of peltospirids have been published, that of Fretter (1989) on anatomy of the limpets and the subsequent paper of Haszprunar (1989) on the anatomy of the coiled *Melanodrymia*. Unfortunately Haszprunar did not have benefit of access to the manuscript of Fretter (1989), so that comparisons could not be made. *Melanodrymia* is atypical of peltospirids in several respects: having both the left and right tentacles modified for copulation (unlike the peltospirid limpets or other coiled peltospirids), and lacking skeletal rods in the ctenidium. It may be that *Melanodrymia* is not a true peltospirid, although Haszprunar elected not to establish a family for it.

Anatomical comparisons between all supposed peltospirids are needed. The limpet *Hirtopelta* McLean, 1989a, lacks a tapered snout and represents a genus not strictly peltospirid. Another unresolved problem has been noted: there are two different protoconch types (net sculpture and longitudinally ribbed) both in limpet genera and coiled genera (McLean, 1989a; Warén & Bouchet, 1989).

Knowledge of the internal anatomy of *Cyathermia* is also needed. Because it is regularly coiled, it seems evident that *Cyathermia* is less derived and probably a better representation of neomphalacean anatomy than *Neomphalus*, although the Cyathermiidae seem to have more complex reproductive modifications in having cirri at the tip of the copulatory appendage. *Symmetromphalus*, the new genus described here, is less derived than *Neomphalus*, for the reason that its symmetry is typical of all other prosobranch limpets, its torsion not carried through an additional 90 to place its mantle cavity on the left, as in *Neomphalus*. *Neomphalus* is also more derived in having a well-defined food groove and a gill that is larger and thereby more effective than that of *Symmetromphalus*.

Radular similarities between Neomphalacea and Peltospiracea need not indicate close affinity. Hickman (1983) first discussed both radular types, and in 1984 reported that the radula of *Melanodrymia* was similar to that of *Neomphalus* and that both could represent an "unspecialized grade of rhipidoglossate radular evolution." Haszprunar (1989) agreed that radular similarities could be "plesiomorphic and should not be overemphasized in tracing phylogenetic relationships." A similar case of radular uniformity is known in the earliest ontogenetic stages of most trochaceans (Warén, 1990).

One can unite the superfamilies Neomphalacea and Peltospiracea within a suborder Neomphalina based on such shared characters as the similarity of the unspecialized radulae, lack of nacre, and lack of ctenidial bursicles, but these are plesiomorphic, grade defining characters. It is difficult to identify apomorphic characters to define such a suborder. We are left with negative characters that suffice to remove both superfamilies from other well-defined suborders. In spite of the present difficulties in justifying a suborder Neomphalina within a rigorous cladistic framework, I expect that the original hypothesis of Warén and Bouchet (common ancestry for Neomphalidae and Peltospiridae) will eventually be accepted.

An alternative view of the affinity of *Neomphalus* was given by Sitnikova and Starobogatov (1983), in a short, unillustrated paper in which they placed *Neomphalus* in their new suborder "Neomphaloidei" [sic] in the order Vivipariformes Sitnikova and Starobogatov, 1982. A translation of the original Russian has been obtained, courtesy David R. Lindberg. The radula of *Neomphalus* was said to lack a lateromarginal plate and to have marginal teeth that are not distributed in groups of small secondary teeth as in rhipidoglossate radulae of trochid, turbinid, and neritid species. Marginal teeth of *Neomphalus* were said to be more similar to the marginal teeth in the architaenioglossate radula, particularly the genus *Leonia* in Pomatiidae, despite the fact that there are only two pairs of marginal teeth in *Leonia*. Other shared characters cited were elongate mantle cavities and looped pallial gonoducts.

Warén and Bouchet (1989) dismissed the Sitnikova and Starobogatov phylogeny of *Neomphalus* as not to be taken seriously in the absence of detailed evidence, and objected to the placement of *Neomphalus* among the Mesogastropoda. I agree that a more convincing exposition of the theory needs to be presented. The radular argument seems irrelevant to me: why should the neomphalacean radula be structured like that of other known rhipidoglossate groups? Nothing is said to falsify the interpretation that it is a relatively unspecialized rhipidoglossate radula. Recently, Golikov and Starobogatov (1988) introduced 36 new prosobranch suborders while maintaining the order Vivipariformes with suborders Neomphaloidei, Viviparoidei, and Valvatoidei. This was done without knowledge of the later introduction of Peltospiracea (McLean, 1989a; Warén & Bouchet, 1989, Fretter, 1989) and of recent work on Valvatidae (Rath, 1988), which resulted in the placement of Valvatacea in the subclass Heterobranchia by Ponder and Warén (1988).

An article in Japanese entitled "New archaeogastropod superfamily Neomphalacea" by Nakamura (1986) is not to be taken as a proposal of a homonym for the superfamily; rather it is evidently a review note intended for Japanese readers.

### FEEDING BIOLOGY

Haszprunar (1988b) suggested that "*Neomphalus* itself probably does not feed by filter-feeding alone, but possibly by symbiotic chemoautotrophic bacteria and/or by grazing bacterial films like some other molluses of the hydrothermal vents. This is indicated by its radula, which is not like those of typical filter feeders. . . ." Original reports on *Neomphalus* of McLean (1981) and Fretter *et al.* (1981) made it clear that part of its nutrition is derived from grazing, particularly in the younger stages. Symbiotic chemoautotrophic bacteria are associated with most bivalves in the hydrothermal-vent community, but the only vent-associated gastropod for which this relationship is known is *Alvinoconcha hessleri*, as reported by Stein *et al.* (1988). Stein (personal communication) has informed me that other vent limpets have been subjected to biochemical assay (ribulose-1,5-diphosphate carboxylase) for chemoautotrophic symbionts, but the negative results were not published. There is, however, a report by de Burgh and Singla (1984) of bacterial colonization of the gill surface and direct endocytosis of the bacteria in the limpet subsequently described as *Lepetodrilus fucensis* McLean, 1988.

Haszprunar's comment that the radula of *Neomphalus* is not like that of typical filter-feeders is not relevant, because the radulae of filter feeding gastropods in such superfamilies as Trochacea, Cerithiacea, and Calyptraeacea are subject to the phylogenetic constraints of the radular plans typical of each group. A typical filter-feeding radula can therefore not be defined. The radula of a filter-feeding gastropod functions primarily to rake in a food string, for which many possible morphologies are suitable.

## FOSSIL RECORD

A direct fossil record for any neomphalacean or peltospiricean shell morphology remains to be established. In my earlier assessment of *Neomphalus* (McLean, 1981), I suggested that there may be a link between Neomphalacea and the Paleozoic Euomphalacea, which I had (somewhat rashly) emphasized by placing both in a therein proposed suborder Euomphalina. The thrust of my argument was as follows: given that euomphalaceans have been regarded as immobile and therefore potential filter-feeders (references in McLean, 1981), a gill like that of Neomphalacea could have provided the mechanism by which filter-feeding was possible in Paleozoic euomphalaceans.

Although most subsequent authors have ignored my functional argument, Runnegar (1983) took notice of it. He did "not wish to disagree with any of this," but had difficulty with the resulting classification. Batten (1984) found no similarities in shell structure between Neomphalacea and Paleozoic Euomphalacea. Bandel (1988) removed from Euomphalacea all Mesozoic genera mentioned by McLean (1981) as possible links between the [illegible] groups. While the latter two authors have found no [illegible] supporting the connection, it can still be argued [illegible] on to Paleozoic euomphalaceans (or pos- [illegible] through unknown intermediate steps [illegible]. Now that *Cyathermia*, as well as the entire peltospiracean complex, is known, it may be easier to conceive of a connection leading to other living genera.

Sitnikova and Starobogatov (1983) stated that a connection between *Neomphalus* and eumphalaceans was falsified because Euomphalacea had paired gills (on the basis of the spiral keel in some euomphalacean genera), but that rather dogmatic assumption is not generally accepted and to me seems poorly founded and unlikely. The shell of *Cyathermia* has a deep sinus in the outer lip (see Waren & Bouchet, 1989: figs. 6, 7), which is undoubtedly related to projection of the single bipectinate gill. This evidence suggests to me that a hypertrophied single gill like that of Neomphalacea would better correlate with spiral keels or sinuses in the lips of euomphalaceans (see McLean, 1981: fig. 13) than would paired gills.

The coiled genera *Cyathermia* and *Lacunoides* demonstrate that the typical neomphalacean gill and mouth with dorsal access to ctenidial filaments can function in mature, coiled snails. These coiled snails are mobile, but they are also smaller, of a size comparable to the juveniles of *Neomphalus* and *Symmetromphalus*. We have yet to discover a larger, coiled member of the Neomphalacea, but there is no reason to assume that it could not function as a sedimentary filter feeder. However, we are not likely to find such a member of Neomphalacea in the hydrothermal-vent habitat, as it would be more prone to shell crushing by the brachyuran predators in the hydrothermal environment.

Now that we have recognized major radiations comprising the superfamilies Neomphalacea and Peltospiracea, as well as the Lepetodrilacea (see McLean, 1988; Fretter, 1988), which superfamily is not discussed here, I continue to believe it likely that these groups must have had a fossil record in the Paleozoic and early Mesozoic, the time at which all living archaeogastropod superfamilies diverged (more detailed discussion in McLean, 1981, 1985, 1988, 1989a,b). There are numerous extinct gastropod clades of the Paleozoic and Mesozoic, which are assumed to have been rhipidoglossate archaeogastropods, for which the anatomical plan remains conjectural (see Knight *et al.*, 1960). The enormously plastic Peltospiracea and the newly expanded Neomphalacea have only been introduced into the literature for slightly over one year, hardly enough time for paleontologists with interests in Paleozoic and Mesozoic faunas to have searched for connecting links.

## BIOGEOGRAPHIC IMPLICATIONS

The Mariana Back Arc Basin vents are isolated from all other known hydrothermal sites, yet they contain some faunal elements in common with those of other sites, in addition to faunal elements found nowhere else. Only one mollusk, the lepetodrilacean limpet *Lepetodrilus elevatus* McLean, 1988, occurs widely at vents on the Galapagos Rift and at all hydrothermal vent-fields on the East Pacific Rise as well as at the Mariana vents (McLean, unpublished). There is also a faunal connection of the

Mariana vents to the vents of the Mid-Atlantic Ridge: *Pseudorimula* McLean, 1989, has an undescribed congener at the Mid-Atlantic Ridge (McLean, in preparation). Hessler *et al.* (1988) suggested that hydrothermal vents associated with past spreading centers are likely to account for these widely disjunct distributions. Tunnicliffe (1989) discussed the vicariant events that shaped the present distributions of hydrothermal-vent faunas shared by the East Pacific Rise and the Juan de Fuca/Gorda Ridge systems. The vicariant events that would allow interchange between the eastern Pacific ridge systems and the Mariana Back Arc Basin remain to be treated in the literature. Vast amounts of geologic time must surely be involved, in view of the slow, step-by-step dispersal of vent archaeogastropods that is necessitated by their lack of planktotrophic dispersal stages (for review see Lutz, 1988).

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# Shell Dissolution Rate in Freshwater Pulmonate Snails: Influence of Periostracum and Water Chemistry

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## ABSTRACT

The size-specific rate of shell dissolution was measured *in situ* in three Michigan lakes that differed in pH and calcium concentration using shells of two species of freshwater pulmonate snails, *Physella integra* (Haldeman 1841) and *Helisoma anceps* (Menke 1830). Lack of a periostracum resulted in significantly higher rates of dissolution as did exposure to lake water with either low pH and/or low [$Ca^{2+}$]. Three-factor ANOVA indicated significant effects for periostracum condition and site as well as significant two and three-way interactions.

For *H. anceps* (but not *P. integra*) the periostracum appears to greatly reduce the rate of shell dissolution hence may serve to reduce shell damage in acid waters. Adverse water chemistry (low pH and/or low $Ca^{2+}$) has a much greater effect on shell dissolution across species (CD = 81%) than does presence or absence of periostracum (CD = 4%).

Shell dissolution response to water chemistry as well as the degree of periostracum protection differs between these two species of snails. Models of lake acidification involving either $Ca^{2+}$ flux and pool sizes or mollusk population survival may need to consider such differences.

*Key words:* Acidification, pH, calcium; snail, shell; periostracum; dissolution; freshwater

## INTRODUCTION

Freshwater mollusks are known to be more sensitive to acidification of their habitat than other benthic groups (Okland & Okland, 1986). Although shell erosion of adult snails and certain physiological processes are influenced by exposure to acid waters, the egg and juvenile stages are most severely affected (Zischke *et al.*, 1983; Rooke & Mackie, 1984; Burton *et al.*, 1985; Hunter, 1988, 1990). This sensitivity of early developmental stages is also observed in waters of low calcium concentration due to the importance of calcium in normal molluscan physiology (Rooke & Mackie, 1984; Hunter, 1990). It is now evident that the disappearance of mollusk populations from lakes or streams affected by acidic deposition is due to recruitment failure as a result of developmental arrest and poor juvenile survival (Hunter, 1988, 1990; Shaw & Mackie, 1989). In contrast to eggs and juveniles, adult snails are relatively resistant to short-term exposure to moderate (pH 5–6) levels of acidity (Servos & Mackie, 1986); however they commonly develop shell damage, such as pitting, as a result. Longer term exposure at slightly higher (but still subneutral) pH may also result in shell pitting. Evidence of shell dissolution in adult snails may therefore provide an early indication that the population is at risk from recruitment failure (Hunter, 1988). Although it might appear that one could make such a determination based on measurement of ambient physico-chemical parameters (*e.g.*, pH, [$Ca^{2+}$], dissolved inorganic carbon, etc.), such measures are indirect indicators of stress on an aquatic mollusk population hence, at best, are useful only as general indicators. Evidence cited in Okland and Okland (1986) suggests there is a wide range of tolerances to high [$H^+$] among species of freshwater mollusks. This is likely compounded by interpopulation variation in tolerance, making it difficult to predict at precisely what pH level one would expect a particular species-population to begin showing stress.

Results that examine the interaction of pH and [$Ca^{2+}$] in terms of adverse effects on fecundity, development, and juvenile survival in a pulmonate snail have been reported elsewhere (Hunter, 1990). The purpose of this study was to measure the rate of shell dissolution using shells of two species of freshwater pulmonate snails, some with periostracum (proteinaceous outer shell layer), some without it, in lakes with different pH and [$Ca^{2+}$] conditions. Interspecific differences, influence of the periostracum, and lake differences insofar as they might modify the rate of shell dissolution were of particular interest.

## MATERIALS AND METHODS

The shells of two species of freshwater pulmonate snails were used in this study. Shells of *Physella* ("*Physa*") *integra* and *Helisoma anceps* originated from Douglas Lake, Cheboygan Co., Michigan, USA. Empty shells from adult-size animals that had died within the past 24 hours were obtained from aquaria of concurrent culturing experiments. Any remaining debris inside these shells was removed by a jet of distilled water into the aperture after which the shells were air-dried. Such shells had a fully intact periostracum. Living snails were not used because they deposit shell even while previously secreted $CaCO_3$ is undergoing dissolution. Hence the use of gravimetric methods to measure rates of loss would be confounded by simultaneous additions to and removal from the shell mass.

Shells without a periostracum were obtained from assorted shells (probably <5 years old) that had washed up above water level where the periostracum was lost by natural (aerial) weathering. These latter shells contrasted markedly with those having an intact periostracum by lacking most of the characteristic color and glossy sheen of the shells of living snails, instead having a matte, chalky white appearance. Shells that were eroded, pitted, or strongly discolored, were avoided.

The apertures of both kinds of shells were completely sealed with silicone aquarium sealer so as to prevent erosion of shell material from the inner surface (nacreous layer) of the shells. This assured that any shell loss by dissolution would be from the outer surfaces of the shell only. Shells were then dried at 105 ± 5 °C to a constant weight and placed into numbered mesh bags ("bridal veil" of 1 $mm^2$ mesh size). The bags were then enclosed in styrene plastic boxes with screened tops and bottoms and attached to stakes securely driven into the bottoms of three selected lakes. The lakes in which the shells were submerged are identified below along with the means of three calcium and pH measurements (taken near shore at 0.5 m). These study sites were all located on protected (windward) shores.

1. Douglas Lake, Cheboygan Co., MI: high calcium (35.4 mg $Ca^{2+}$/L); high pH (8.59).
2. Vincent Lake, Cheboygan Co., MI: low calcium (3.5 mg $Ca^{2+}$/L); high pH (7.78).
3. Lake Nita, Alger Co., MI: low calcium (3.0 mg $Ca^{2+}$/L); low pH (5.47).

No mollusks are presently found in either Vincent or Nita; however, *H. anceps* (with pitted shells) occurred in Vincent Lake up to a few years ago.

The experimental design was factorial with three sites, two species, and two periostracum conditions giving 3 × 2 × 2 = 12 treatments. Each treatment involved ten replicate shells or 120 total shells. Shells remained *in situ* at 0.25–0.5 m depth for 42 days at Douglas Lake and Vincent Lake and 45 days at Lake Nita, after which they were removed, dried, and weighed. Change in shell mass was computed from weights before and after drying, then (assuming linear weight loss) converted to a rate by dividing by the number of days. Since larger shells lose more $CaCO_3$ per unit time than smaller shells, small differences in starting shell size among treatments were compensated for by dividing dissolution rate by shell size (maximum shell dimension), hence the data are expre[illegible] [illegible]cific dissolution rate which is $\mu g$ $CaCO_3$ dis[illegible] [illegible]ell dimension day.

Data [illegible] treatments were evaluated using one [illegible] ANOVA and Fishers Protected Least Significa[illegible] [illegible] procedure (PLSD). The latter is a two-stage [illegible] an overall test of significance (standard F-test) is followed by pairwise comparisons if the F-test is significant at the chosen alpha level (Koopmans, 1987).

## RESULTS

Figure 1 shows mean size-specific dissolution rate for all twelve treatment groups. Results of a one-factor ANOVA indicated that there were significant differences among treatments ($F_{(11,103)} = 116.99$, $P < 0.0001$). Treatment histograms having a common letter are not significantly different from each other by Fishers PLSD ($\alpha = 0.05$). These data indicate that there are substantial site and periostracum effects; *e.g.*, shell dissolution is minimal at Douglas Lake (<3 $\mu g$/(mm·day) for either species whether the periostracum is present or absent. In contrast, the Vincent Lake site (high pH, low [$Ca^{2+}$]) produced dissolution rates that were intermediate, ranging from 9.7 $\mu g$/(mm·day) for *H. anceps* shells with periostracum to 27.2 $\mu g$/(mm·day) for *H. anceps* shells without periostracum. The highest rates of shell dissolution occurred at Lake Nita (low pH, low [$Ca^{2+}$]) ranging from 17.7 $\mu g$/(mm·day) for *H. anceps* with periostracum to 58.7 $\mu g$/(mm·day) for *H. anceps* without periostracum. Dissolution rates for *P. integra* shells with periostracum were higher than the above rates for *H. anceps*. *Physella integra* shells with periostracum at Vincent Lake lost mass at 15.1 $\mu g$/(mm·day) while those at Lake Nita lost mass at 36.7 $\mu g$/(mm·day). Without periostracum, however, *P. integra* rates were lower than those for *H. anceps*: 19.8 $\mu g$/(mm·day) at Vincent Lake and 39.7 $\mu g$/(mm·day) at Lake Nita.

It can also be seen from figure 1 that absence of a periostracum in *H. anceps* greatly increased the shell dissolution rate of that species, however, in *P. integra* the dissolution rate was only slightly increased by lack of a periostracum, and the difference was not significant. In *H. anceps* the lack of a periostracum resulted in a dissolution rate that is over two (at Vincent Lake) or three times greater (at Lake Nita) than at Douglas Lake.

The degree to which size-specific dissolution rate is influenced by the three main effects (site, species, periostracum condition) is expressed in table 1, which gives the results of a three-factor ANOVA (SPSS-X). Since the data were neither normally distributed nor were the variances of the treatment means equal, a square root transformation was used. Both site and periostracum condition had significant effects on size-specific dissolution rate; for site, $F_{(2,103)} = 712.84$ ($P < 0.001$) and for periostracum condition, $F_{(1,103)} = 63.92$ ($P < 0.001$). There was no significant effect for species; *i.e.*, *P. integra* and *H. anceps* shells had similar rates of dissolution when considered as species groups across the three sites. The size-specific rate of dissolution was influenced more by site differences than by presence or absence of a periostracum. The coefficient of determination for site = 81% whereas that for periostracum condition = 4%.

Table 1 also indicates that there are significant two- and three-way interactions between the main effects.

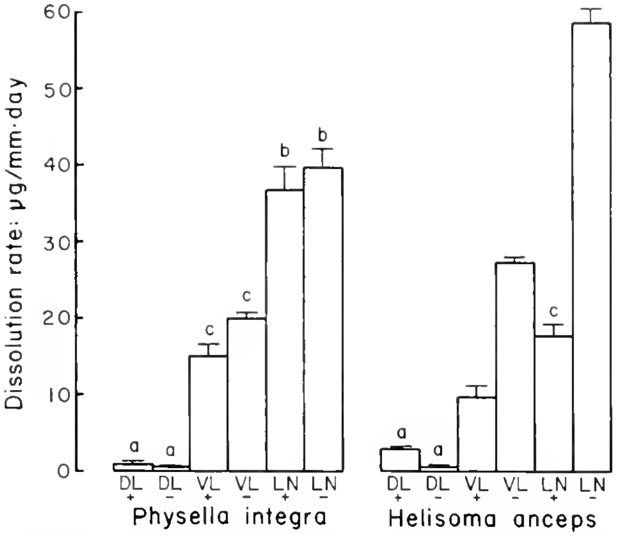

**Figure 1.** Size specific shell dissolution rates ($\bar{x} \pm$ SE) for *P. integra* and *H. anceps* with (+) and without (−) periostracum at three lakes: DL = high pH, high Ca$^{2+}$ site; VL = high pH, low Ca$^{2+}$ site; LN = low pH, low Ca$^{2+}$ site. Histograms with the same letter over them are not significantly different by Fishers PLSD ($\alpha = 0.05$). N = 10 for all treatments.

Specifically, the shell dissolution rate of either species at a particular site is dependent on periostracum condition.

Assuming a constant dissolution rate at summer lake surface temperatures, one can calculate the number of days required for dissolution losses to equal the entire mass of an average size shell. Using a mean dry shell weight of 70.9 mg for *P. integra* and 77.7 mg for *H. anceps*, it would take 8,273 days and 2,472 days, respectively, for a typical adult-size shell, with intact periostracum at Douglas Lake, to completely dissolve. At Vincent Lake, these figures are lowered to 424 days for *P. integra* and 768 days for *H. anceps* (both with periostracum), and at Lake Nita they are further lowered to 178 days for *P. integra* and 368 days for *H. anceps*. The shortest time to complete dissolution would be 118 days for an *H. anceps* shell, without periostracum, in Lake Nita.

## DISCUSSION

The results presented herein suggest that the periostracum of *Physella integra* shells offers little protection against shell dissolution due either to low ambient [Ca$^{2+}$] or to low pH. For *Helisoma anceps*, however, the presence of an intact periostracum substantially reduces shell loss in lakes of low [Ca$^{2+}$]. For example, in Vincent Lake (low [Ca$^{2+}$], high pH), shell loss was reduced by 64.6% when compared to shells without a periostracum. Similarly, at an acid lake (Lake Nita) where both low [Ca$^{2+}$] and low pH occurred, the presence of a periostracum reduced shell dissolution by 69.8%. Hence in *H. anceps* the presence of an intact periostracum may reduce shell damage in slightly acid waters.

**Table 1.** Results of three factor ANOVA on size specific shell dissolution rate data for *Physella integra* and *Helisoma anceps* at three different lakes and with periostracum either present or absent. Data were square root transformed.

| Source of variation | Degrees of freedom | Mean square | F |
|---|---|---|---|
| Main effects | | | |
| Site | 2 | 265.60 | 712.84* |
| Species | 1 | 0.00 | 0.00 ns |
| Periostracum | 1 | 23.82 | 63.92* |
| Two-way interaction | | | |
| Site × species | 2 | 0.71 | 1.91 ns |
| Site × periostracum | 2 | 17.64 | 47.35* |
| Species × periostracum | 1 | 14.49 | 38.88* |
| Three-way interaction | | | |
| Site × species × periostracum | 2 | 9.92 | 26.61* |
| Error | 103 | 0.37 | |
| Total | 114 | 5.78 | |

* $P < 0.001$; ns = $P > 0.05$

The method used to obtain periostracum-free shells was to select weathered shells from debris above the high-water line. These weathered shells had been exposed to sun, drying, freeze-thaw, etc., for a few months/years. It is not known if this weathering did more than simply cause the loss of the periostracum; *i.e.*, does such treatment alter the dissolution rate? If so, the effect is likely to be small based on the fact that for *P. integra* there is no significant difference in dissolution rate between weathered (= periostracum-free) and unweathered (= with periostracum) shells at all three sites (see table 1).

The periostracum is the outermost layer of mollusk shells and is entirely organic, consisting largely of conchiolin, a quinone-tanned protein (Wilbur, 1964). Below this layer lies most of the mass of the shell which is calcium carbonate secreted in a protein matrix.

Most of the references to periostracum function in the literature are to prosobranchs or bivalves (Wilbur, 1964; Digby, 1968; Tevesz & Carter, 1980). Fretter and Graham (1962) suggest that, for prosobranch snails and lamellibranchs, the function is to reduce shell erosion. It is not clear if this is a reference to mechanical abrasion, chemical dissolution or both. In some groups, such as burrowing and boring bivalves, there is a substantial periostracum that apparently protects against mechanical abrasion (Morton, 1964; Yonge & Thompson, 1976). Tevesz and Carter (1980) suggest that the unionacean periostracum is one of the most important adaptations of this group to prevent shell dissolution. A variety of periostracum functions have been suggested for bivalves, including minimization of encrusting by epizooans, resistance to boring and attack by other predators, increased stability in the substratum, and decreased effect of substratum scour (Bottjer & Carter, 1980; Wright & Francis, 1984). Although working with hydrothermal vent bivalves. Hunt (1987) observed that periostraca might, among other functions, provide protection of the mature shell from chemical dissolution. In a study of marine bivalves, Swinehart and Smith (1979:380) suggested that magnesium and iron in the periostracum could "act as a defensive buffer against degradation from acidic conditions."

In freshwater pulmonate snails, the periostracum is relatively thin and generally lacks hair-like projections that are found in certain bivalve groups. There is little in the literature to suggest a function for the periostracum in this group of snails.

Further evidence that the periostracum provides some protection against shell erosion is derived from casual field observations that pulmonates from stressful environments often have deeply pitted shells. It is likely that once a small area of periostracum has become worn away (usually abraded by mechanical damage) then the exposed underlying shell dissolves more rapidly than unaffected areas nearby. The result is a pit in the shell that, in time, may open into a perforation possibly leading to the death of that individual. Although extensive wear and pitting is often observed in the umbonal region of freshwater bivalves, such wear is likely a result of the physical process of abrasion, rather than of chemical effects (Hinch & Green, 1988). Bivalve shells, which are in contact with interstitial water of the substratum over much of the shell area, are subject to somewhat different (moderated) physico-chemical conditions than are pulmonate snails, which are usually located on the surfaces of stones, vegetation, sediment, etc., hence are more directly exposed to lake or stream water conditions. Hinch and Green (1988) argue that increased shell erosion in bivalves most likely results from physical etching due to water turbulence rather than from chemical dissolution. However, chemical dissolution rates would also be elevated by conditions of water turbulence and should not be ruled out. The same authors found that bivalve shell etching was not related to water chemistry (alkalinity and pH levels) and it may be that the nacroprismatic shell microstructure of unionaceans is substantially more resistant to dissolution than that of freshwater pulmonates (Tevesz & Carter, 1980; Hinch & Green, 1988).

It is not surprising that contact by snail shells with lake water low in calcium or low in both calcium and pH substantially increases the rate of shell dissolution. In a laboratory study, whole animal [$Ca^{2+}$] of *Planorbella trivolvis*, after 53 days of exposure to pH 4.9, decreased 16% on a dry weight basis and 14% on a size-specific basis (Hunter, 1988). In that same study it was reported that ashed shells (essentially $CaCO_3$ without the periostracum or any other organic material) lost $CaCO_3$ about 4.6 times faster than did the shells of live animals. One may envision the shell as a non-living mass of $CaCO_3$ which is in direct contact with and responsive to calcium-deficient or acid water, despite being a part of a living mollusk.

What is perhaps unexpected is that there is such a different response by the shells of the two species involved in this study. Comparing the size-specific dissolution rate of shells exposed to Vincent Lake water (low [$Ca^{2+}$], circumneutral pH) with that of shells exposed to Douglas Lake water (high [$Ca^{2+}$], slightly alkaline water), *P. integra* showed a 43-fold increase and *H. anceps* a 6-fold increase in dissolution rate. In other words, *P. integra* shells with intact periostraca were far more sensitive to dissolution-inducing conditions than were shells of *H. anceps*. Interestingly, *H. anceps* shells were the more sensitive of the two species to the absence of a periostracum. Thus, *P. integra* shells are moderately sensitive to dissolution-inducing conditions, whether the periostracum is present or not. In contrast, *H. anceps* shells with periostracum are less sensitive to dissolution than those of *P. integra*, but without a periostracum, *H. anceps* shells are considerably more sensitive. This study suggests that the periostracum in some snail species (*e.g.*, *H. anceps*) could act as a deterrant to shell dissolution. In populations that are in locations subject to gradual acidification, the life of adults may be prolonged compared to other species (*e.g.*, *P. integra*).

Clearly, either the paucity of $Ca^{2+}$ ions in the water or relatively low pH may result in higher rates of loss of shell mass in pulmonate snails. Data from this study indicate that when both conditions occur (which is typical of acid lakes) that the shell dissolution rate is higher than it is for lakes having low [$Ca^{2+}$] and neutral or alkaline pH. It is not possible from this study to know if pH and [$Ca^{2+}$] are acting synergistically; however data from another study indicate that such is not the case, *i.e.*, effects of low [$Ca^{2+}$] and low pH on growth and fecundity of snails reared in the lab are no more than additive (Hunter, 1990).

This study demonstrates that degree of periostracum protection and shell dissolution rates may differ significantly between species, hence, $CaCO_3$ loss cannot be assumed to be identical for all freshwater snails. Such considerations are of potential interest in the modeling of lake acidification processes either in terms of the disappearance of specific molluscan taxa from the benthos in a regime of continual pH and alkalinity reduction or calcium release by biota to free ion pools.

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# Effect of Experimentally Induced Shell Damage on Mortality, Reproduction and Growth in *Helisoma trivolvis* (Say, 1816)

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## ABSTRACT

We conducted a replicated laboratory experiment to test the potential effect of shell damage (imitating that inflicted by crayfish) on mortality, reproduction, and shell growth of the snail *Helisoma trivolvis* (Say, 1816). During the egg-laying period of the snail, we removed 0, 2, 4 or 9 mm of shell from the aperture. For the subsequent 29 days, we monitored snail egg production, mortality, and shell growth. We predicted that because of physiological trade-offs, snails would either repair their shell and show decreased egg production and mortality (Hypothesis 1), or forego repair and show high egg production and early (or high) mortality (Hypothesis 2).

Results were inconsistent with both hypotheses. Only shell growth differed significantly ($p < 0.05$) among damage treatments, with growth positively related to damage. Our data do not conclusively refute the trade-off assumption. However, the results do strongly suggest that non-lethal shell damage, like that inflicted by crayfish, is unlikely to affect snail population growth.

*Key words:* *Helisoma*, *Orconectes*, predation, damage, trade-off, repair, snails, crayfish.

## INTRODUCTION

Snails and their predators have coevolved in ways that enhance their ability to survive predation and to catch prey, respectively (Vermeij and Covich, 1978). The importance of predation on marine snails is supported by an abundance of observations (Norton, 1988; Raffaelli, 1978; Vermeij, 1979, 1982; Vermeij and Covich, 1978) and experimental evidence (Garrity *et al.*, 1986). Freshwater gastropods, however, have developed far fewer antipredatory shell features than marine gastropods, perhaps because of limited minerals in fresh water, insufficient time for coevolution (due to the relatively young age of most freshwater bodies), and a lower diversity of predators in fresh water (Vermeij and Covich, 1978).

Recent evidence suggests, though, that freshwater snails are readily eaten by both shell-invading predators like leeches (Brown and Strouse, 1988) and shell-crushing predators like redear sunfish (Stein *et al.*, 1984), pumpkinseed sunfish (Osenberg and Mittelbach, 1989), and crayfish (Crowl, 1989; Lodge and Lorman, 1987; Olsen, 1989; Weber and Lodge, 1990). Probably because of their relatively high feeding rate, *e.g.*, 50–200 *Hydrobia* $\cdot$ crayfish$^{-1}$ $\cdot$ day$^{-1}$ (Olsen, 1989), and frequently high densities (Lodge *et al.*, 1987), crayfish (*Orconectes* spp.) appear to be particularly potent predators of snails. Field observations (Weber and Lodge, 1990) and experimental (Lodge and Lorman, 1987; Lodge, unpublished data) evidence suggest that crayfish predation influences abundance and species composition of snails in northern Wisconsin lakes. Indirect effects of predation, such as the non-lethal shell damage documented extensively for marine snails (Geller, 1990; Raffaelli, 1978; Vermeij, 1982; Vermeij *et al.*, 1980; Vale and Rex, 1989; Zipser and Vermeij, 1980), may have an impact on snail populations by reducing individual fitness. An experimental test of this possibility, which has not been previously explored for freshwater snails, is the topic of this paper.

In laboratory experiments in which freshwater *Orconectes* crayfish prey on snails, predation rate differs among snail species (A. P. Covich, personal communication), but intermediate sized shells (6–9 mm) are most often non-lethally damaged (Olsen, 1989). Smaller snails are almost always successfully eaten; larger snails, which have stronger shells, are not handled as easily. In laboratory experiments, *Orconectes rusticus* (Girard, 1852) (31–39 mm carapace length) eat about 7% and non-lethally damage ($\geq 1$ mm shell aperture peeled away) about 25% of 60 *Helisoma* available to single crayfish in one night (Olsen 1989). In this paper, we test the impact on snail mortality, fecundity, and shell growth of experimentally induced damage that mimicked the crayfish-inflicted damage described by Olsen (1989).

Our experiment was designed to test two opposing hypotheses regarding the effects of non-lethal damage on reproductively active snails. Both hypotheses are built

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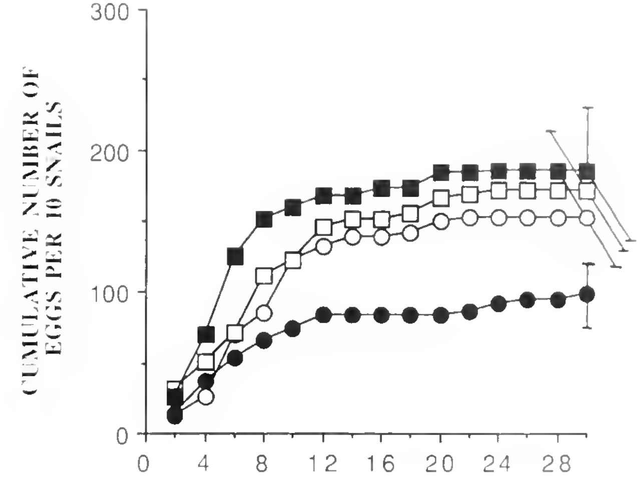
on the assumption that trade-offs (sensu Tilman, 1989) exist in the allocation of resources by individual snails to repair, growth and reproduction. The trade-off assumption, *e.g.*, that energy spent on growth decreases energy available for reproduction, is a critical component in much ecological and evolutionary thought, to the point of becoming a paradigm (Tilman, 1989).

Hypothesis 1 is that a damaged snail will divert energy and nutrients from growth and reproduction to repair its damaged shell. If this occurs, non-lethal shell damage by a predator might limit snail populations even though the snail is not killed. Hypothesis 2 is that a snail would respond to non-lethal damage by foregoing repair and putting all of its energy into reproduction (Kirkwood, 1981). This might be the expected result for semelparous snails, like the *Helisoma* used in our experiment (see Boerger, 1975 for description of *Helisoma* life cycle). If Hypothesis 1 is correct, we predicted damaged *Helisoma* would exhibit low fecundity, and low or delayed mortality. In this case, non-lethal damage might depress snail populations. If Hypothesis 2 is correct, we predicted damaged snails would exhibit fecundity similar to undamaged snails and early, high mortality rates. In this case, non-lethal damage would have a negligible effect on snail populations.

**1**



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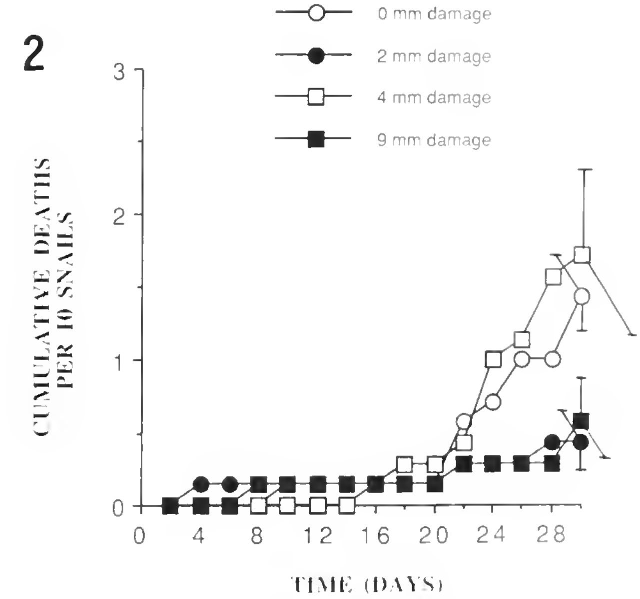

**Figure 1.** Mean (N = 7) cumulative number of eggs per 10 snails as a function of time. No significant difference in total egg production (day 29) existed among treatments (ANOVA p = 0.40). **Figure 2.** Mean (N = 7) cumulative deaths per 10 snails as a function of time. Mean for 0 damage treatment is zero from day 0 through day 8. Differences among treatments in total mortality (day 29) were marginally significant (ANOVA p = 0.052). For figures 1 and 2, ±1 SE is indicated for day 29 only.

## MATERIALS AND METHODS

The experiment was conducted at the University of Notre Dame Environmental Research Center (UNDERC) in the Upper Peninsula of Michigan (46°N, 89°W) during the latter part (1 June–1 July 1989) of the reproductive season of *H. trivolvis* (Boerger, 1975). Adult snails (mean shell diameter of 24.6 mm, range = 21–29 mm) were collected from Mullahy and Ward lakes, two small mesotrophic lakes on UNDERC property.

This size range of snails was used because it was most available. While these snails are larger than those most susceptible to non-lethal damage (Olsen, 1989), we assume response to damage would be similar to that of species whose reproductive size is smaller, *e.g.*, *Helisoma campanulata* (Say).

Shells were artificially damaged by peeling 0, 2, 4, or 9 mm ring of shell from the aperture with forceps. The living tissue of all snails was undamaged. There were seven replicates for each of the four damage treatments. Each of the 28 experimental units was a shallow fiberglass tray (30 × 35 × 8.5 cm deep), filled to a depth of 5 cm with lake water. Snails were randomly assigned to treatments, and trays randomly assigned to a lab bench position. Trays were maintained with natural lighting from windows. Temperature fluctuated in the range 14–21 °C. Each tray contained 10 snails (all with the same degree of damage) and 2–3 periphyton covered rocks (6–10 cm diameter) to provide snail food. Food level was kept as constant as possible throughout the experiment by replacing water and rocks about once per week (three times during the experiment). Snail mortalities and egg sacs were counted every other day. Dead snails were removed. Egg sacs were collected with a scalpel from tray sides, rocks, and shells of snails. Eggs in each egg sac were counted under a dissecting microscope. Every snail was measured for new shell growth near the end of the experiment (24 June).

We tested differences among treatments in egg production, mortality, and shell growth with a separate ANOVA for each response.

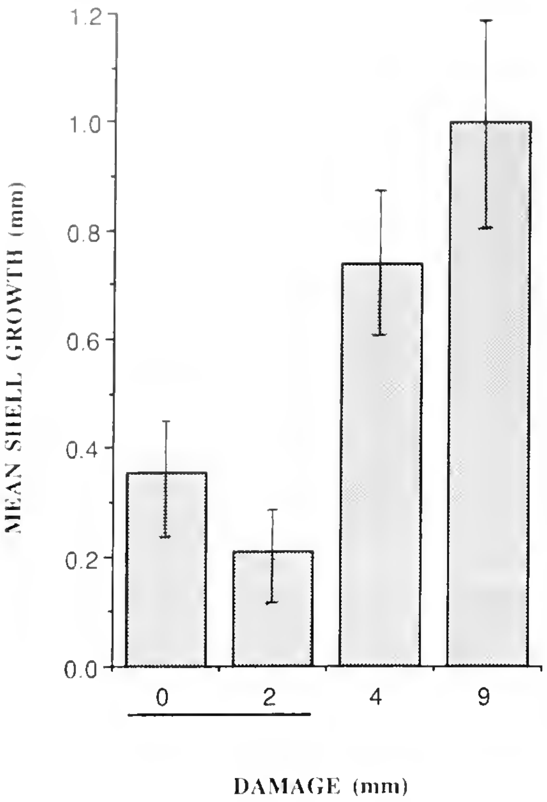

**Figure 3.** Histogram of mean shell growth ($N = 7$) ±2 SE for the four shell damage treatments (ANOVA $p < 0.001$). The horizontal bar connects treatments that did not differ ($p > 0.05$, Tukey's Test).

## RESULTS

For all four damage levels, cumulative egg production increased through about day 12, and began to level off thereafter as egg-laying ceased (figure 1). No differences existed among treatments in total eggs laid (ANOVA $p = 0.40$ for day 29 data).

Mortality was very low in all treatments through the egg-laying period, and began to increase in all treatments after egg-laying ceased (figure 2). On day 29, there was a marginally significant difference among treatments in total mortality (ANOVA $p = 0.052$), but the apparent rank order of mortality was not correlated to inflicted damage levels

Shells in all treatments grew during the experiment, with growth differing among treatments (ANOVA $p < 0.001$) and generally positively related to damage level (figure 3). Regrown shell on damaged snails was very thin compared to the rest of the shell. This, along with the original fracture line, made it easy to measure growth on damaged snails. On control snails, however, new growth often blended in with the old shell, rendering uncertain our growth measurements for the control treatment. Even if control growth data were removed from consideration, the positive relation between damage and growth remains for the three damage treatments

## DISCUSSION

Differences in mortality among damage levels were marginally significant ($p = 0.052$), but probably not biologically meaningful because there is no relationship between the treatment and the apparent response (figure 2). A lack of relation between damage and mortality is consistent with the conclusions of Zipser and Vermeij (1980) that shell damage does not cause mortality in marine snails. More recently, though, Geller (1990) found that damaged *Nucella*, an intertidal snail, have higher mortality than undamaged snails. Like *Helisoma*, however, damaged *Nucella* have more shell growth, and no difference in fecundity relative to undamaged snails (Geller, 1990). In *Helisoma*, the only response that clearly differed significantly among treatments was growth (figure 3), which increased with increasing damage. *H. trivolvis* damaged most severely regrew their shells the most (figure 3, $p < 0.001$), but suffered no decline in fecundity (figure 1) or any increase in mortality (figure 2). Results were therefore inconsistent with both initial hypotheses, and apparently inconsistent with the trade-off assumption underlying both hypotheses.

While this apparent contradiction of the trade-off assumption is intriguing, the limitations of our experiment make it premature to reject the occurrence of physiological trade-offs in these snails. We did not measure responses in energy or other relevant units, nor did we measure other physiological responses that may be involved in trade-offs, *e.g.*, growth of living biomass, egg weight, or egg viability. Results do, however, suggest that shell growth is "hardwired," *i.e.*, it cannot be turned off, even with senescence imminent in semelparous snails.

It is possible that a damaged snail might be more vulnerable to subsequent attacks by predators. We did not test this possibility, but suspect the effect would be minor. In lab experiments where crayfish damaged shells (Olsen, 1989), crayfish appeared to curtail an attack because the remaining shell was simply too strong to break. In addition, the earlier experiments probably enhanced the frequency of shell damage over natural frequencies by enhancing encounter rates between predator and prey. Thus, it seems unlikely that non-lethal shell damage by crayfish would have any impact on snail population growth.

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# New Gastropods from the Bermont Formation (Middle Pleistocene) of the Everglades Basin

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## ABSTRACT

Eight new gastropods are described from the poorly-known basal beds ("Holey Land Unit") of the middle Pleistocene Bermont Formation of the Everglades Basin. The new species include *Cypraea (Macrocypraea) spengleri* n.sp. and *Cypraea (Pseudozonaria) portelli* n.sp. (Cypraeidae), *Melongena (Miccosukea) cynthiae* n.sp. and *Melongena (Miccosukea) holeylandica* n.sp. (Melongenidae), *Scaphella seminole* n.sp. (Volutidae), and *Conus capelettii* n.sp., *Conus griffini* n.sp., and *Conus lemoni* n.sp. (Conidae). Also described is a new subgenus of *Melongena* Schumacher, 1817, *Miccosukea* n.subgen., which represents an endemic Pleistocene species radiation from within the Everglades region.

*Key words:* Gastropods; Pleistocene; Everglades; Florida.

## INTRODUCTION

Of the major surficial stratigraphic units of the Everglades Basin of southern Florida, the middle Pleistocene Bermont Formation is the least known and the most poorly studied. Indeed, the formation did not even receive an official designation until 1974, when DuBar informally named and described this important set of units. Previously (*i.e.*, McGinty, 1970; Hoerle, 1970), the formation was simply referred to as "Unit A" or the "Glades Unit," or, prior to that time, as the "un-named post-Caloosahatchee formation" (*i.e.*, E. Vokes, 1968). Although the formation name still has not been accepted by regional offices of the United States Geological Survey (*fide* Wesley L. Miller, Water Resources Division, USGS, Miami), several workers in the Pleistocene paleontology of southern Florida have adopted its usage and recognize its importance as the "missing link" in the stratigraphic record of the Everglades region (*i.e.*, E. Vokes, 1976, 1984; Petuch, 1988). Since the depositional center of the formation is within the Everglades Basin where there are few sampling sites, only sporadic collections of Bermont material have been made and the molluscan fauna, particularly its gastropod component, is known from only a handful of publications.

In response to increased building and construction in southern Florida, several large new land fill quarries have been excavated within the Everglades region over the last few years. Two of these in particular, the Capeletti Brothers pit #11 in northern Dade County and the Griffin Brothers pit on the Broward-Palm Beach County line, have cut into extremely fossiliferous beds of the Bermont Formation and have uncovered many new and interesting gastropods. Besides new species, both quarries have yielded large numbers of classic Bermont index fossils (as listed by McGinty, 1970; DuBar, 1974; and Petuch, 1988, 1989) such as *Melongena (Rexmela) bispinosa* (Philippi, 1844), *Fasciolaria okeechobeensis* Tucker and Wilson, 1932, *Latirus maxwelli* Pilsbry, 1942, *Vasum floridanum* McGinty, 1940, *Fusinus watermani* (M. Smith, 1940), and *Strombus mayacensis* Tucker and Wilson, 1933, demonstrating the contemporaneous nature of their beds. Several other newly-described index fossils, including *Lindoliva griffini* Petuch, 1988, *Lindoliva spengleri* Petuch, 1988, and *Malea petiti* Petuch, 1989 were also collected in both quarries, indicating that the dredged fossiliferous sediments came from the same stratigraphic horizon.

At both quarries, the Bermont Formation is approximately 10 meters thick and is stratigraphically more complex than had previously been reported (DuBar, 1974). Of particular interest are the basal beds of the formation, which contain a large number of undescribed gastropod species. Although containing the same species at both localities, the basal beds in the Capeletti Brothers pit are marly and unconsolidated whereas the stratigraphic equivalents in the Griffin Brothers pit are indurated into a thick layer of dense limestone. This richly fossiliferous indurated bed (figure 22), which averages 2 meters in thickness and is found at a depth of approximately 15 meters below surface, has also been uncovered at construction sites in the Loxahatchee area of West Palm Beach and south of South Bay, along the North New River Canal in central Palm Beach County. The most numerous and largest blocks of this Bermont limestone, however, have been dredged from the Griffin Brothers pit. Since the Griffin pit and its exposures of Bermont material are adjacent to the Holey Land Wildlife Refuge (named for the numerous shallow craters formed by World War II bombing practice, *fide* Howard

A. Griffin, Jr.), the basal indurated bed has been informally referred to by local paleontologists as the "Holey Land Unit." A cursory survey of the gastropods of the Holey Land Unit has shown that a large percentage of the species appear to be undescribed and that several belong to previously unknown subgenera and species complexes.

In this paper, eight new gastropod species and a new gastropod subgenus are described from the basal beds ("Holey Land Unit") of the Bermont Formation. Included are *Cypraea* (*Macrocypraea*) *spengleri* n.sp. and *Cypraea* (*Pseudozonaria*) *portelli* n.sp. (Cypraeidae), *Melongena* (*Miccosukea*) *cynthiae* n.sp. and *Melongena* (*Miccosukea*) *holeylandica* n.sp. (Melongenidae), *Scaphella seminole* n.sp. (Volutidae), and *Conus capelettii* n.sp., *Conus griffini* n.sp., and *Conus lemoni* n.sp. (Conidae), and the new subgenus of *Melongena*, *Miccosukea* n.subgen. Institutional abbreviations, for the deposition of type material, include: USNM (Department of Paleobiology, National Museum of Natural History, Smithsonian Institution), UF (Florida Museum of Natural History, University of Florida, Gainesville, Florida), CM (Department of Paleontology, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania), and FAU (Department of Geology, Florida Atlantic University, Boca Raton, Florida).

## SYSTEMATICS

Gastropoda
Prosobranchia
Cypraeacea
Cypraeidae
*Cypraea* Linnaeus, 1758
*Macrocypraea* Schilder, 1930

*Cypraea* (*Macrocypraea*) *spengleri* new species
(figures 5, 6)

**Material examined:** HOLOTYPE—Length 107 mm, dredged from 20 m depth in Capeletti Brothers pit #11, 7 km west of Florida Turnpike, due west of Hialeah, northeastern Dade County, Florida, CM 35728; PARATYPES—Length (fragmentary) 105 mm, dredged from 15 m depth in Griffin Brothers pit, 10 km west of US Highway 27, along Palm Beach-Broward County line, Florida, FAU 320; length 120 mm, internal mold, same locality as previous paratype, FAU 321; length 158 mm, same locality as previous two paratypes, Spengler collection, Lantana, Florida; length 83 mm, same locality as holotype, Petuch collection.

**Description:** Shell typical of subgenus, large, inflated, subcylindrical; aperture narrow, widening toward anterior end, arcuate; columella (holotype) with 33 narrow teeth that extend into aperture; lip with 44 narrow teeth; fossula poorly developed, with 9 narrow teeth; base of shell rounded; auricles (extrapolated from damaged type material) well developed, projecting; color pattern (faintly preserved on holotype) composed of numerous small, widely-scattered round spots.

**Etymology:** Named for Mr. John Spengler of Lantana, Florida, who has helped me collect at several important fossil sites in the Everglades.

**Discussion:** *Cypraea spengleri* represents the first new species of the subgenus *Macrocypraea* to be described from the fossil record of the continental United States, and is the largest cowrie known from the Neogene of Florida. The cypraeid fragments from the "Glades Unit" of the Belle Glade pit, listed by Hoerle (1970:63) as "*Cypraea ?cervus* Linne," are probably referable to *C. spengleri*. The "*Cypraea cervus*" from Belle Glade and Ortona Lock, listed by McGinty (1970:55), is also probably *C. spengleri*. Based on the specimen in the Spengler collection (158 mm paratype), I also previously referred the new species to *C. cervus* (Petuch, 1988: plate 24, fig. 10). As molds, *C. spengleri* is relatively common in the Holey Land limestone at the Griffin Brothers pit, but the preservation is poor and most specimens are fragmentary. Complete specimens such as the holotype, however, have only been collected in the unconsolidated marly facies of the Holey Land Unit in northern Dade County.

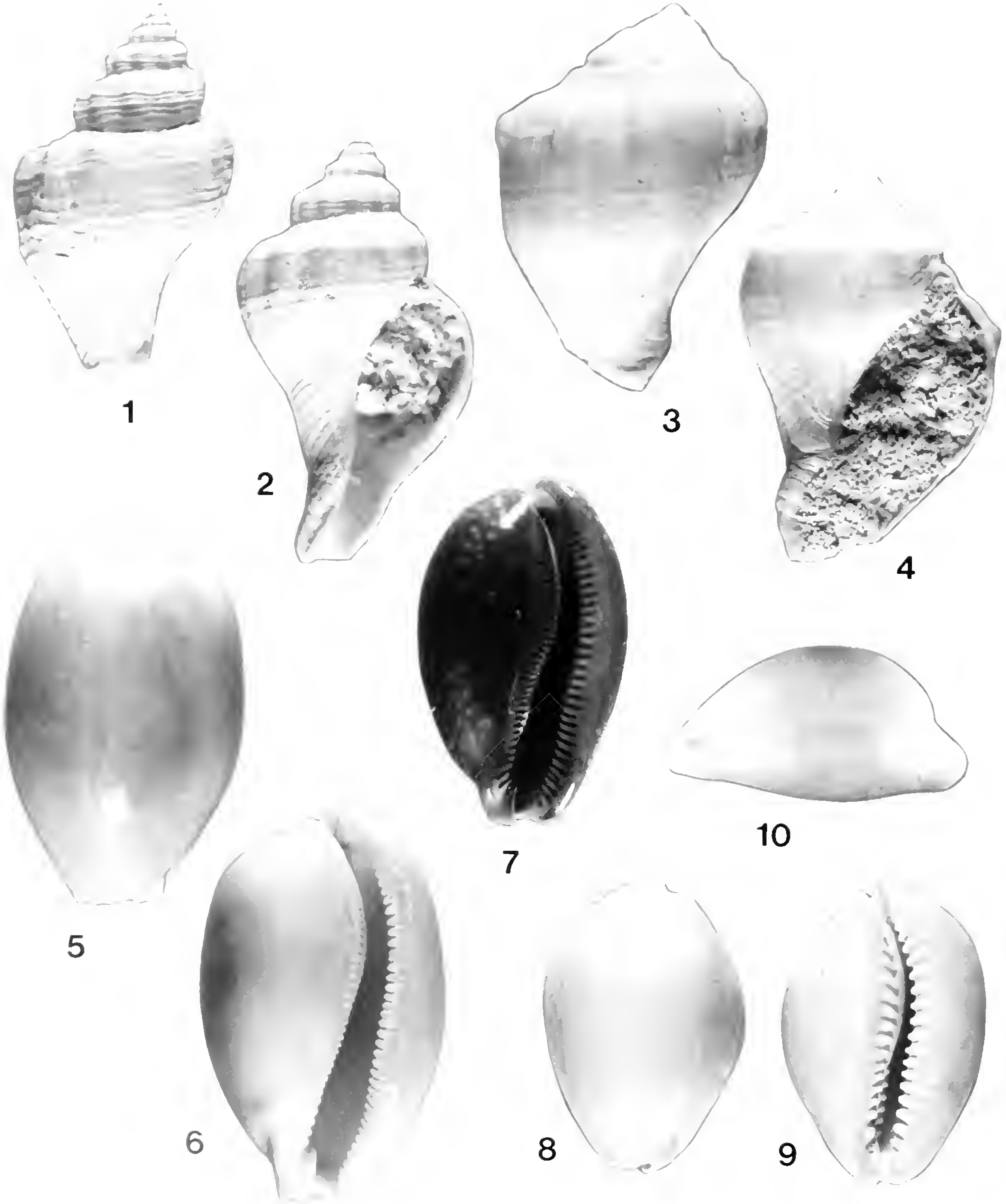
*Cypraea spengleri* is most similar to *C.* (*Macrocypraea*) *cervus* Linnaeus, 1771 from the Carolinian Province and, based on its similar shape and size, is probably the direct ancestor of that well known Recent species. The main difference between the two cowries, however, is seen in the form of the apertural teeth, particularly those of the columella; in *C. cervus*, the columellar teeth are slender and elongated, extending well onto the base of the shell (figure 7), while in *C. spengleri*, the columellar teeth are short and coarse and do not extend onto the base but, instead, terminate along the edge of the columella (figure 6). Likewise, the labial teeth of *C. cervus* are finer and more elongated than those of *C. spengleri*, and also extend farther onto the shell base. The number of apertural teeth also differs between the two species, with *C. cervus* having more teeth (average 37 columellar, 43 labial) than *C. spengleri* (average 33 columellar, 40 labial).

*Pseudozonaria* Schilder, 1927

*Cypraea* (*Pseudozonaria*) *portelli* n.sp.
(figures 8, 9, 10)

**Material examined:** HOLOTYPE—Length 25 mm, dredged from 15 m depth in Griffin Brothers pit, 10 km west of US Highway 27, at Broward-Palm Beach County line, Florida, UF 28985; PARATYPE—Length 25 mm, from 20 m depth in Capeletti Brothers pit #11, 7 km west of Florida Turnpike, northeastern Dade County, Florida, Petuch collection.

**Description:** Shell average size for subgenus, oval in outline, dorsoventrally flattened; beaks well developed, projecting; margins thickened, sharply angulate; base slightly rounded; spire region shallowly indented; aperture narrow, slightly arcuate; teeth blunt and coarse, numbering 15 along columella and 19 along lip (of ho-



**Figures 1–10.** New Melongenids and Cypraeids from the "Holey Land Unit" of the Bermont Formation. **1.** *Melongena* (*Miccosukea*) *cynthiae* n.sp., dorsal view of paratype, length 55 mm; **2.** *Melongena* (*Miccosukea*) *cynthiae* n.sp., ventral view of holotype, length 38 mm. **3, 4.** *Melongena* (*Miccosukea*) *holeylandica* n.sp., dorsal and ventral views of holotype, length 35 mm; **5, 6.** *Cypraea* (*Macrocypraea*) *spengleri* n.sp., dorsal and ventral views of holotype, length 107 mm, **7.** *Cypraea* (*Macrocypraea*) *cervus* Linnaeus, 1771, ventral view of 85 mm specimen, for comparison with *C.* (*Macrocypraea*) *spengleri*. **8, 9.** *Cypraea* (*Pseudozonaria*) *portelli* n.sp., dorsal and ventral views of holotype, length 25 mm; **10.** *Cypraea* (*Pseudozonaria*) *portelli* n.sp., lateral view (left) of holotype.

lotype); color pattern (faintly preserved on holotype) composed of numerous, densely-packed specklings, often fusing together to form longitudinal stripes, on the dorsum and numerous evenly-spaced small spots on margins; anterior and posterior tips each with 2 large patches.

**Etymology:** Named for Mr. Roger Portell, Florida Museum of Natural History, who collected the holotype.

**Discussion:** *Cypraea portelli* represents the first species of its subgenus to be found in the fossil record of the United States. Until now, *Pseudozonaria* was unknown in the Caloosahatchian Province (Miocene to Pleistocene S.E. United States and the Floridian Peninsula), and was thought to have been confined to the Gatunian Province (Miocene to Pleistocene Caribbean, northern South America, and western Central America) (Petuch, 1982; Vermeij & Petuch, 1986). In the Recent, the subgenus is represented by three species from the Panamic Province of the tropical western Americas; *C.* (*Pseudozonaria*) *arabicula* (Lamarck, 1811), *C.* (*Pseudozonaria*) *nigropunctata* Gray, 1828, and *C.* (*Pseudozonaria*) *robertsi* (Hidalgo, 1906). Of the three living species, *C.* (*Pseudozonaria*) *portelli* is most similar to *C. robertsi*, being the same size and having the same type of apertural teeth, shape and form of the aperture, and color pattern. The new species differs from *C. robertsi*, however, in having a broader, more rounded outline and in having angled, thickened margins.

In the fossil record of the Gatunian Province of the Caribbean basin, *C. portelli* is most similar to *C. raymondrobertsi bowdenensis* (Pilsbry, 1922) from the Pliocene of Jamaica and the Dominican Republic. Both species share the same broad, oval shell outline and the same flattened appearance. The apertural teeth of *C. raymondrobertsi bowdenensis*, however, are proportionally much larger and better developed than those of *C. portelli*, and extend much farther across the base of the shell. *Cypraea portelli* was probably the last *Pseudozonaria* to live in the Atlantic.

Buccinacea
Melongenidae
Melongeninae
*Melongena* Schumacher, 1817

*Miccosukea* new subgenus

**Diagnosis:** Shells average-sized for genus, but more elongated and fusiform, generally resembling *Fasciolaria* species in outline; shoulders, especially those of body whorls, rounded, without prominent spines or flutings; shoulders of whorls ornamented with low, rounded knobs or evenly-spaced low, rounded axial ribs; spires and body whorls both heavily sculptured with numerous strong spiral cords; spiral cords finer and more numerous on siphonal canals; siphonal canals very well-developed, elongated; siphonal canals of some species well-differentiated from body whorl, narrow, giving shells appearance of small *Pugilina* or *Busycon* species; aperture wide, flaring, oval in shape; spire height and development variable within subgenus, with some species having elevated, scalariform spires and others having low, slightly-stepped spires; sutures slightly impressed, smooth, without fine fimbriations or crenulations.

**Type species:** *Melongena* (*Miccosukea*) *cynthiae* new species, described here. Lower beds ("Holey Land Unit") of Bermont Formation, Aftonian Stage, Pleistocene, Palm Beach County, Florida (figures 1, 2).

**Other species in *Miccosukea*.** *Melongena* (*Miccosukea*) *holeylandica* new species, described here. Lower beds ("Holey Land Unit") of Bermont Formation, Aftonian Stage, Pleistocene, Palm Beach County (figures 3, 4); *Melongena* (*Miccosukea*) sp., fragmentary, Bermont Formation, Aftonian (Yarmouth?) Stage, Pleistocene, Dade County, Florida.

**Etymology:** The new subgenus honors the Miccosukee Seminole Tribe of the Everglades.

**Discussion:** The new subgenus represents a separate evolutionary line off the *Melongena* Schumacher, 1817 (*sensu stricto*) stock, and appears to have been endemic to southern Florida. This local radiation differs from classic *Melongena* species in containing smaller, more fusiform shells with better-developed and more elongated siphonal canals, and in lacking sutural fimbriations and large shoulder spines. *Miccosukea* also differs from the subgenus *Rexmela* Olsson and Harbison, 1953 in being more fusiform in shape, in having much better developed siphonal canals, in lacking large shoulder spines, and in lacking the "collar" of fimbriations bordering the suture.

At several Bermont localities, *Melongena* (*Miccosukea*) species and *Melongena* (*Rexmela*) species, such as *M.* (*Rexmela*) *bispinosa* (Philippi, 1844), occur together and show that the two subgenera were sympatric.

*Melongena* (*Miccosukea*) *cynthiae* new species
(figures 1, 2)

**Material examined:** HOLOTYPE—Length 38 mm, dredged from 15 m depth in Griffin Brothers pit, 10 km west of US Highway 27, at Broward-Palm Beach County line, Florida, USNM 448813; PARATYPES—Length 55 mm (incomplete), same locality as holotype, FAU 322 (figure 1); lengths 41 and 52 mm, same locality as holotype, FAU 323; length 64 mm, same locality as holotype, Petuch collection.

**Description:** General shell shape and form as for subgenus; spire protracted, scalariform; spire whorls convex; suture impressed; spire, body whorl, and siphonal canal heavily sculptured with numerous large, evenly-spaced spiral cords; smaller secondary cords present between large primary cords.

**Etymology:** Named for Mrs. Cynthia Mischler, Department of Geology, Florida Atlantic University.

**Discussion:** *Melongena cynthiae*, type of the new subgenus, more closely resembles a small *Pugilina* Schumacher, 1817 species than it does other western Atlantic melongenids. Unlike *Pugilina* species, *M. cynthiae* has a distinctly rounded shoulder on the body whorl, rounded and convex spire whorls, and an impressed suture. In having a protracted, scalariform spire, the new species somewhat resembles high-spired forms of *Melongena* (*Rexmela*) *corona* (Gmelin, 1791), such as *altispira* Pilsbry and Vanatta, 1934. *Melongena cynthiae* differs from these high-spired forms, however, in having a much more elongated body whorl and in having a much better developed, and longer, siphonal canal. Being in *Miccosukea*, *M. cynthiae* also lacks the open shoulder spines and fimbriated sutures of *Rexmela* species.

The new species is also similar to the stratigraphically higher *Melongena* (*Miccosukea*) *holeylandica* n.sp. (figures 3, 4), but differs in having a much higher, scalariform spire, in having a longer siphonal canal, and in being more heavily sculptured with strong spiral cords. A large, undescribed *Miccosukea* species has also been collected, although only as fragments, in the uppermost beds of the Bermont Formation in the Capeletti Brothers pit. This un-named species also has a high, scalariform spire, but has a smoother, less sculptured shell. The "Melongenid-new genus, new species" that I previously illustrated (Petuch, 1988: plate 24, figs. 1, 2) is *M. cynthiae*.

*Melongena* (*Miccosukea*) *holeylandica* new species
(figures 3, 4)

**Material examined:** HOLOTYPE—Length 35 mm, dredged from 12 m depth in Griffin Brothers pit, 10 km west of US Highway 27, at Broward-Palm Beach County line, Florida, USNM 448814; PARATYPES—Lengths 48, 51, and 55 mm, same locality as holotype, FAU 324; length 52 mm, same locality as holotype, Petuch collection.

**Description:** General shell shape and form as for subgenus; spire low, rounded, slightly dome-shaped; subsutural area raised to form large, rounded spiral cord; subsutural cord producing minutely canaliculate suture; spire, body whorl, and siphonal canal sculptured with low, faint spiral cords; shoulder of body whorl ornamented with scattered small, low knobs; siphonal canal broad.

**Etymology:** Named for the area adjacent to the type locality, the Holey Land Wildlife Refuge.

**Discussion:** The similarities and differences between *Melongena holeylandica* and the only other named *Miccosukea* species, *M. cynthiae*, are discussed under the preceding description. The "Melongenid-new genus, new species" that I previously illustrated (Petuch, 1988: plate 24, figs. 5, 6) is *M. holeylandica*.

Volutac
Volutida
Scaphellin
*Scaphella* [illegible] 1832

*Scaphella seminole* new species
(figures 18, 19, 20, 21)

**Material examined:** HOLOTYPE—Length 52 mm, dredged from 20 m depth in Capeletti Brothers pit #11, 7 km west of Florida Turnpike, due west of Hialeah, northeastern Dade County, Florida, CM 35729; PARATYPES—Length 53 mm, same locality as holotype, CM 35730 (figures 20, 21); lengths 54, 55, and 56 mm, same locality as holotype, FAU 325; lengths 55, 56 mm, same locality as holotype, Petuch collection.

**Description:** Shell small for genus, fusiform, with rounded, sloping shoulder; spire proportionally low, with sloping whorls; top of shoulder marked with faintly incised, shallow furrow; area between suture and shoulder furrow producing wide, faintly raised subsutural band; protoconch proportionally large, rounded, domelike, with rounded calcarella; first 2 postnuclear whorls heavily sculptured with numerous, evenly-spaced, large axial ribs; axial ribs overlaid with numerous fine spiral threads, producing slightly cancellate appearance; columella with 4 large plications; color pattern, when preserved, composed of 7–9 rows of large, evenly-spaced rectangular checkers.

**Etymology:** Named for the Seminole Indian Tribe of the Everglades region.

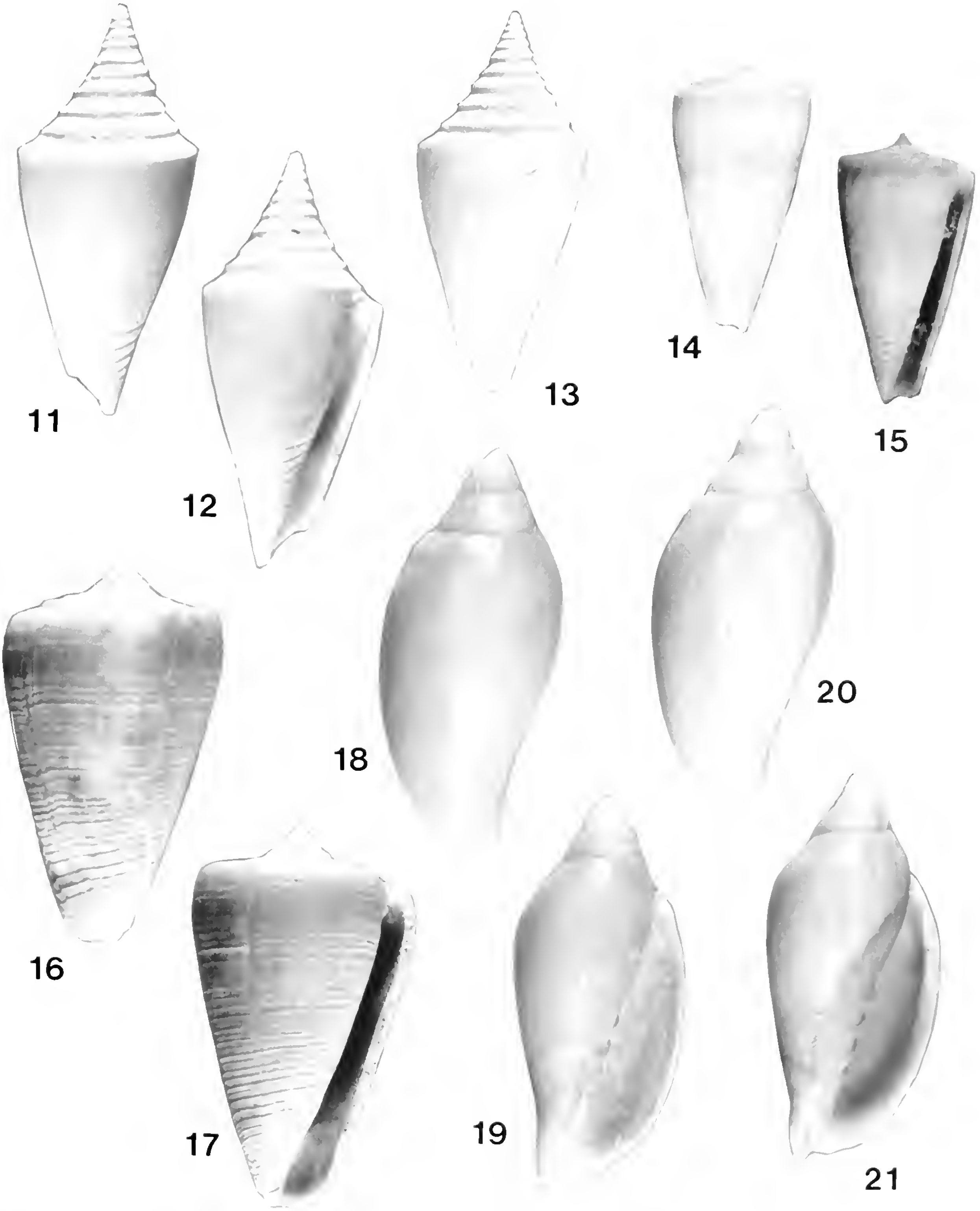
**Discussion:** *Scaphella seminole* is the smallest of the known fossil *Scaphella* species, with the average length of the type lot (all adult specimens with thickened, posteriorly-flaring lips) being only around 54 mm. The new species is similar to the late Pliocene-early Pleistocene Caloosahatchee Formation *S. floridana* (Heilprin, 1886), but differs in having a much smaller, stumpier shell with a much lower, unprotracted spire. The axial ribbing on the postnuclear whorls of *S. floridana* is also coarser and better developed than that of *S. seminole* and extends onto the third whorl.

Conacea
Conidae
*Conus* Linnaeus, 1758

*Conus capelettii* new species
(figures 11, 12, 13)

**Material examined:** HOLOTYPE—Length 38 mm, dredged from 20 m depth in Capeletti Brothers pit #11, 7 km west of Florida Turnpike, due west of Hialeah, northeastern Dade County, Florida, CM 35731; PARATYPES—Length 33 mm, same locality as holotype, CM 35732 (figure 13); lengths 36, 39, 41, and 42 mm, same locality as holotype, Petuch collection.

**Description:** Shell slender, elongately subpyriform, biconic; shoulder sharply angled, carinated; spire very protracted, scalariform; body whorl and spire smooth, with silky texture; anterior end encircled with 8–10 deep, evenly-spaced grooves; aperture narrow, widening slightly



**Figures 11–21.** New Conids and Volutids from the "Holey Land Unit" of the Bermont Formation. **11, 12.** *Conus capelettii* n.sp., dorsal and ventral views of holotype, length 38 mm; **13.** *Conus capelettii* n.sp., dorsal view of paratype, length 33 mm; **14, 15.** *Conus griffini* n.sp., dorsal and ventral views of holotype, length 15 mm; **16, 17.** *Conus lemoni* n.sp., dorsal and ventral views of holotype, length 56 mm; **18, 19.** *Scaphella seminole* n.sp., dorsal and ventral views of holotype, length 52 mm; **20, 21.** *Scaphella seminole* n.sp., dorsal and ventral views of paratype, length 53 mm.

**Figure 22.** Detail of a fossiliferous limestone block from the basal beds ("Holey Land Unit") of the Bermont Formation. This block was dredged from 15 m depth in the Griffin Brothers pit on the Palm Beach-Broward County line in the central Everglades Basin. The lucinids on the left and lower left are approximately 60 mm in diameter.

toward anterior end, color pattern, when preserved, composed of wide longitudinal flammules and zig-zags.

**Etymology:** Named for Mr. Ronald Capeletti, of Capeletti Brothers, Inc., Hialeah, Florida, in thanks for allowing me to collect large suites of Bermont material on his property.

**Discussion:** *Conus capelettii* has the highest, most scalariform spire of any cone shell known from the Plio-Pleistocene fossil record of Florida. Based on shell shape, size, and spire form, the new species appears to be more closely related to *Conus scalaris* Valenciennes, 1832 from the Recent western coast of Mexico than to other western Atlantic cone shells. *Conus capelettii* differs from *C.*

*scalaris*, however, in having a proportionally shorter body whorl with a distinctly more pyriform shape. The new Bermont species is also similar in shape to some slender morphs of the Recent Carolinian Province *C. floridanus* Gabb, 1868, but differs primarily in having a sharper, more carinated shoulder and in having a much higher, scalariform spire.

### *Conus griffini* new species
(figures 14, 15)

**Material examined:** HOLOTYPE—Length 15 mm, dredged from 15 m depth in North New River Canal, along US Highway 27, 30 km south of South Bay, Palm Beach County, Florida, CM 35733; PARATYPE—Length 18 mm, dredged from 15 m depth in Griffin Brothers pit, 10 km west of US Highway 27, at Broward-Palm Beach County line, Florida, Petuch collection.

**Description:** Shell small for genus, slender, straight-sided; shoulder sharply angled, carinated; spire low and flattened; body whorl smooth and shiny; anterior tip encircled with 8–10 low, rounded cords; aperture narrow; protoconch mammillate, projecting above spire line; color pattern, when preserved, composed of single row of small spots around midbody.

**Etymology:** Named for Mr. Howard A. ("Andy") Griffin, Jr., Davy, Florida, in thanks for allowing me to collect on his property over the last eight years.

**Discussion:** *Conus griffini* is the first member of the *C. magellanicus* Hwass, 1792 species complex to be found in the fossil record of continental North America. In the Recent, this complex of small cones is confined to shallow water, coral reef areas of the West Indies, Bahamas, and Caribbean Basin. The new Bermont species is most similar to the Recent *C. kalafuti* DaMotta, 1987 from Roatan Is., Honduras, and both cones have the same small size, flat spire, projecting nipple-like protoconch, and color pattern composed of a checkered midbody band. *Conus griffini* differs from *C. kalafuti*, however, in having a more slender, straight-sided shell and in having stronger spiral cords around the anterior tip. Otherwise, the two species are very similar, and *C. griffini* is most probably the ancestor of the Honduran *C. kalafuti*.

Previously (Petuch, 1988: plate 23, fig. 2), I had illustrated and referred to this new Bermont cone as "*Conus* cf. *eversoni* Petuch, 1987." That species, which is also related to *C. kalafuti* and is also from Roatan Is., Honduras, has a larger and more elongated shell than *C. griffini*. The protoconch of *C. griffini* is also proportionally larger than that of *C. eversoni* and is more prominently mammillate.

### *Conus lemoni* new species
(figures 16, 17)

**Material examined:** HOLOTYPE—Length 56 mm, dredged from 15 m depth in Griffin Brothers pit, 10 km west of US Highway 27, at Broward-Palm Beach County line, Florida, CM 35734; PARATYPES—Length 49 mm, same locality as holotype, CM 35735, lengths 37, 45, 48, and 68 mm, same locality as holotype, FAU 326; length 65 mm, dredged from 20 m depth in Capeletti Brothers pit #11, 7 km west of Florida Turnpike, due west of Hialeah, northeastern Dade County, Florida, Petuch collection.

**Description:** Shell broad, heavy, with wide shoulder; shoulder angled, with rounded edge; spire low, flattened, with early whorls projecting above later whorls; suture indented; spire whorls distinctly canaliculate; body whorl heavily sculptured with numerous, closely-packed, large spiral cords; aperture narrow; color pattern, when preserved, composed of numerous rows of small spots, often arranged in bands, and scattered large axial flammules that often coalesce to form longitudinal stripes; spire marked with evenly-spaced crescent-shaped flammules.

**Etymology:** Named for Dr. Roy Lemon, Department of Geology, Florida Atlantic University.

**Discussion:** *Conus lemoni* is a new member of the *Conus spurius*, 1791 species complex of the Pliocene-to-Recent Caribbean and Floridian regions. Morphologically, the new Bermont species combines the shell characters of two Recent species, *C. spurius atlanticus* Clench, 1942 and *C. lorenzianus* Dillwyn, 1817. In having a broad shell shape, rounded shoulder edge, and low spire, *C. lemoni* resembles the Carolinian *C. spurius atlanticus*. On the other hand, in being heavily sculptured with closely-packed spiral cords and in having a flammulated color pattern, the new Bermont cone resembles the southwestern Caribbean *C. lorenzianus*. It is possible that *C. lemoni* is ancestral to both closely-related species.

In the Florida fossil record, *C. lemoni* is similar to several undescribed subspecies of *C. spurius* from the upper beds of the Bermont Formation and the overlying Fort Thompson Formation (late Pleistocene). The new Holey Land species differs from the younger *C. spurius* subspecies, however, in having distinctly canaliculate spire whorls and in being heavily sculptured with spiral cords.

## ACKNOWLEDGEMENTS

I thank Mr. John Spengler, Lantana, Florida, for assisting me in the collection of Bermont fossils, and Mr. Howard ("Andy") Griffin, Jr., and Mr. Ronald Capeletti for allowing me to collect on their property. Special thanks to Mrs. Cynthia Mischler for patiently typing the manuscript.

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THE NAUTILUS 104(3):105–107, 1990

# *Micropilina tangaroa*, a New Monoplacophoran (Mollusca) from Northern New Zealand

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## ABSTRACT

*Micropilina tangaroa* n.sp., based on a single shell from the Three Kings Rise, northern New Zealand, is the first record of the class Monoplacophora from the western Pacific.

*Key words:* Monoplacophora, New Zealand, *Micropilina*.

## INTRODUCTION

Since the discovery of *Neopilina galathea* in 1952 (Lemche, 1957), 14 Recent species have been added to the class Monoplacophora (Lemche, 1957; Clarke & Menzies, 1959; Menzies & Layton, 1963; Tebble, 1967; Menzies, 1968; Rokop, 1972; McLean, 1979; Moskalev *et al.*, 1983; Bouchet *et al.*, 1983; Warén, 1988, 1989; Warén & Bouchet, 1990). These species are based on material from off Hawaii, the eastern Pacific margin, the western and northern Atlantic, and the Gulf of Aden. The present record extends the range to the southwestern Pacific (figure 1). Recent monoplacophorans are mainly confined to bathyal and abyssal depths, though one species lives at 174–388 m depth off southern California (McLean, 1979). Monoplacophoran morphology and anatomy have been discussed in detail by Lemche and Wingstrand (1959) and Wingstrand (1985), while Menzies *et al.* (1959) and Tendal (1985) have discussed their ecology and diet.

Class **Monoplacophora** Odhner *in* Wenz, 1940

Genus *Micropilina* Warén, 1989:2

**Type species:** *Micropilina minuta* Warén, 1989, by original designation; Recent, northern Atlantic.

**Remarks:** Suprageneric classification of the Monoplacophora has been drastically modified by Moskalev *et al.* (1983) and Starobogatov and Moskalev (1987). These authors placed the 11 Recent species then known into six families and three superfamilies. Unfortunately the anatomy of *Micropilina* is unknown, so it cannot be placed in this hierarchial framework. Despite the lack of supportive anatomical data, *Micropilina* species are undoubtedly monoplacophorans, since their shells exhibit the multiple muscle attachment scars characteristic of many species of the class (figure 3) (Lemche & Wingstrand, 1959; Wingstrand, 1985). The class name is generally credited to Wenz (*in* Knight, 1952), but, as indicated by Warén (1988), it was first introduced by Odhner (*in* Wenz, 1940).

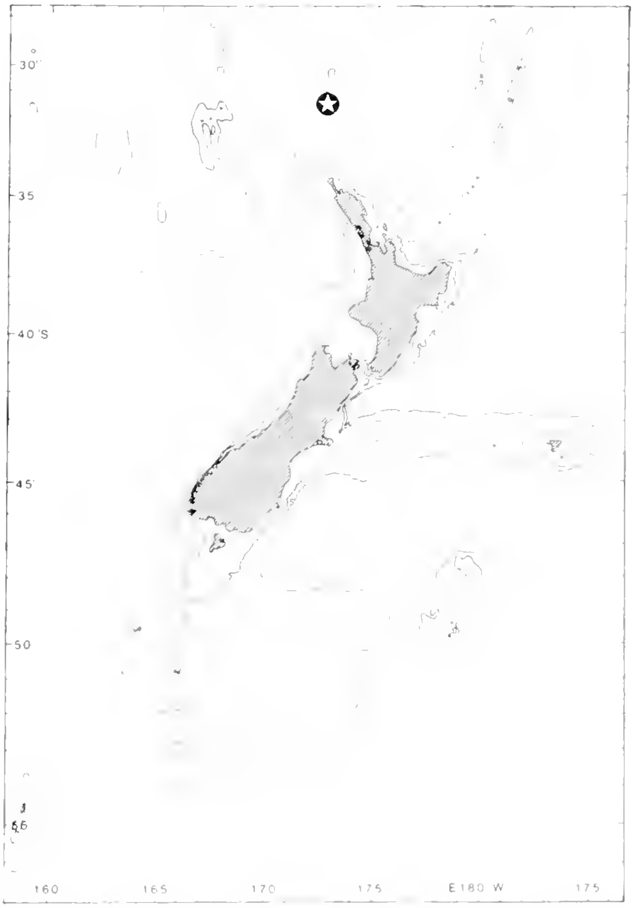

**Figure 1.** Map of New Zealand showing type locality (star) for *Micropilina tangaroa* new species. 200 and 1000 meter contours indicated

Figures 2–5. M[illegible] species. **2.** Left lateral, **3.** ventral, and **4.** dorsal views of holotype (length [illegible] 1.50 mm). 5. [illegible]

*Micropilina tangaroa* new species
(figures 2–5)

**Description:** Shell (holotype) 1.50 mm long, thin, strongly arched capuliform; apertural margin regularly ovate, concave from side to side; rounded apex projecting slightly beyond anterior apertural margin, opaque white. Shell wall apparently lamellar throughout, presumably arganonite. Apical area convex, 0.17 mm long, defined by fine concentric ridge, surface slightly etched. Exterior surface at 0.17–0.30 mm shell length essentially smooth apart from few, fine raised concentric growth lines. Thereafter sculptured with strong concentric ridges and finer radial riblets. Concentric ridges close, sharply defined, broader than high, summits weakly convex, interspaces about half width of each ridge, weaker and less sharply defined beside apertural margin. Radial riblets confined to interspaces of concentric ridges, rounded, interspaces slightly narrower than each riblet, each riblet about as wide as interspace of each concentric ridge. Interior surface encircled by complex series of muscle attachment scars, of which at least 15 pairs are discernable, through precise number of muscle attachment points uncertain, especially over anterior half. Animal unknown.

**Type material:** Holotype New Zealand Oceanographic Institute, Wellington H.555 (length 1.50 mm, width 0.88 mm, height 0.50 mm).

**Type locality:** (Figure 1) Station U.602, 31°30.7′S, 172°49.8′E, northern Three Kings Rise, northern New Zealand, dead 1,216–1,385 m, rocky substratum with pumice, carbonate sand and shell, February 9, 1988, R.V. *Rapuhia*.

**Etymology:** The species is named for the Maori sea god Tangaroa.

**Discussion:** Compared with the north Atlantic species *Micropilina minuta* Warén, 1989, which it most resembles, *M. tangaroa* differs in being larger (length 1.50 mm compared with 1.06 mm), and in having concentric ridges that are much larger both in actual size and in size relative to the size of the radial riblets. Judging from the increasing curvature of the posterior and lateral slopes and the change (presumably senescent) in sculpture beside the apertural margin, the holotype of *M. tangaroa* is evidently an adult. Apical pits recorded by Warén (1988, 1989) were not observed in the present specimen, which is long dead, locally stained by manganese deposition, and slightly etched.

## ACKNOWLEDGEMENTS

I thank curatorial staff at New Zealand Oceanographic Institute, Wellington, for access to sediment samples that yielded the monoplacophoran, New Zealand Geological Survey, Lower Hutt, for scanning electron microscopy, Mark Strange for photographic printing and Kathleen Ryan for word processing.

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# Addenda to "*Distorsio ridens* (Reeve, 1844): A Synonym of *Distorsio clathrata* (Lamarck, 1816) (Gastropoda: Personidae)"

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We are indebted to David Freeman of Cape Town, South Africa for calling our attention (*in litt.*, June 6, 1990) to an error in our recent paper pertaining to the identity of *Distorsio ridens* (Reeve, 1844) (Emerson and Sage, 1990). Through an unfortunate oversight, a photograph of the apertural view of a paralectotype of *D. ridens* [British Museum (Natural History) 1967630, = *D. clathrata* (Lamarck, 1816)], which was correctly cited and illustrated in figure 6, was inadvertently substituted for figure 2. Figure 2 was erroneously labeled the apertural view of the lectotype of *D. ridens* [American Museum Natural History (AMNH) 6369, = *D. clathrata*].

The apertural view of the lectotype was previously illustrated by Lewis (1972:45, figure 48) and an enlargement of the aperture of the lectotype was provided in our paper (Emerson and Sage, 1990, figure 15). To correct our error, the entire view of the ventral aspect of the lectotype is given herein to compare with Reeve's (1844, pl. 12, sp. 46) original figure of *Triton ridens* [= *Distorsio clathrata*]. See figures 1, 2, herein.

Reference also should be made here to the two unidentified species of *Distorsio* trawled in 400 m off Cape Gardafui (Ras Asir), Somalia that were under study by us at the time we were preparing our review of *D. ridens* (Emerson and Sage, 1990:131). One of these was described on March 31, 1990 as *Distorsio somalica* Parth from "North of Mogadishou, dredged in deep water" (Parth, 1990, figure 1; herein figures 9–12). Parth's newly described taxon has some morphological characters that are reminiscent of *Distorsio decipiens* (Reeve, 1844) and *D. reticularis* (Linné, 1758) [= *D. reticulata* Röding 1798, *fide* Beu, 1987:314]. *Distorsio somalica* has a larger, narrower shell with more prominent labial teeth (as well as other differing sculptural features) than that of *D. decipiens*. *Distorsio somalica* resembles somewhat the general shape of *D. reticularis*, but has a narrower shell with weaker sculpture and more prominent labial teeth. In the past *D. reticularis* has been confused with *D. decipiens* (see Springsteen, 1985). Parth (1990:1), however, compared the type specimens of *D. somalica* with *D. perdistorta* Fulton, 1938.

The other Somalian specimens we examined are apparently referable to *D. perdistorta*, a wide-ranging Indo-West Pacific species with populations also in the eastern and western Atlantic Ocean (Beu, 1985:62). Our specimens of *D. perdistorta* from Somalia differ from the shells of the western-Pacific populations by having a wider, more inflated shell, with the expanded outer lip commonly colored with tan rays and the parietal shield covered (in all 4 of the specimens examined) by a brightly colored tan glaze (herein figures 3–6). The "typical" Indo-Pacific specimens of *D. perdistorta*, which have a narrower, less inflated, but a more distorted shell with a whitish parietal shield, however, are also known from off Madagascar in 300–340 meters [N. of Nossi Be, 12°43′S, 48°15′E, Academy Natural Sciences of Philadelphia 352156 (ANSP)], as reported by Lewis (1972:29). The presence of both of these forms in the Indian Ocean suggests that they are likely only morphs of *D. perdistorta*. Compare figures 3–6 with figures 7, 8. *Distorsio reticularis* (Linné, 1758) is also known to occur in the Indian Ocean, as noted by Parth (1990).

## ACKNOWLEDGEMENTS

In addition to the courtesy extended by Mr. Freeman, we are indebted to Mr. John Bernard of Crossville, TN and to Dr. Gary Rosenberg of the Philadelphia Academy of Sciences, PA for kindly providing us with the Somalian and Madagascan specimens of *Distorsio*, respectively, for study and report. Dr. Alan Beu of the New Zealand Geological Survey, Lower Hutt generously contributed

→

**Figures 1, 2.** *Distorsio ridens* (Reeve, 1844). **1.** Copy of original illustration of *Triton ridens* Reeve. **2.** Lectotype of *Triton ridens* Reeve (AMNH 6369). **Figures 3–8.** *Distorsio perdistorta* Fulton, 1938. **3–6.** Off Cape Gardafui, Somalia, ex-John Bernard Collection (**3, 4.** AMNH 232148; **5, 6.** AMNH 232147). **7, 8.** North of Nossi Be, Madagascar (ANSP 352156). **Figures 9–12.** *Distorsio somalica* Parth, 1990 (same locality data as in figures 3–6 (**9, 10.** AMNH 232149, **11, 12.** AMNH 232150). All figures ×1.


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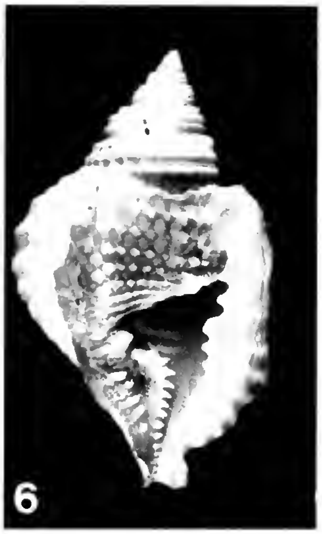
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additional data and expressed his views on the taxonomic status of the specimens from Somalia. We also thank Mr. Andrew Modell and Ms. Stephanie Crooms of the American Museum of Natural History who undertook the photography and the word-processing of the manuscript, respectively.

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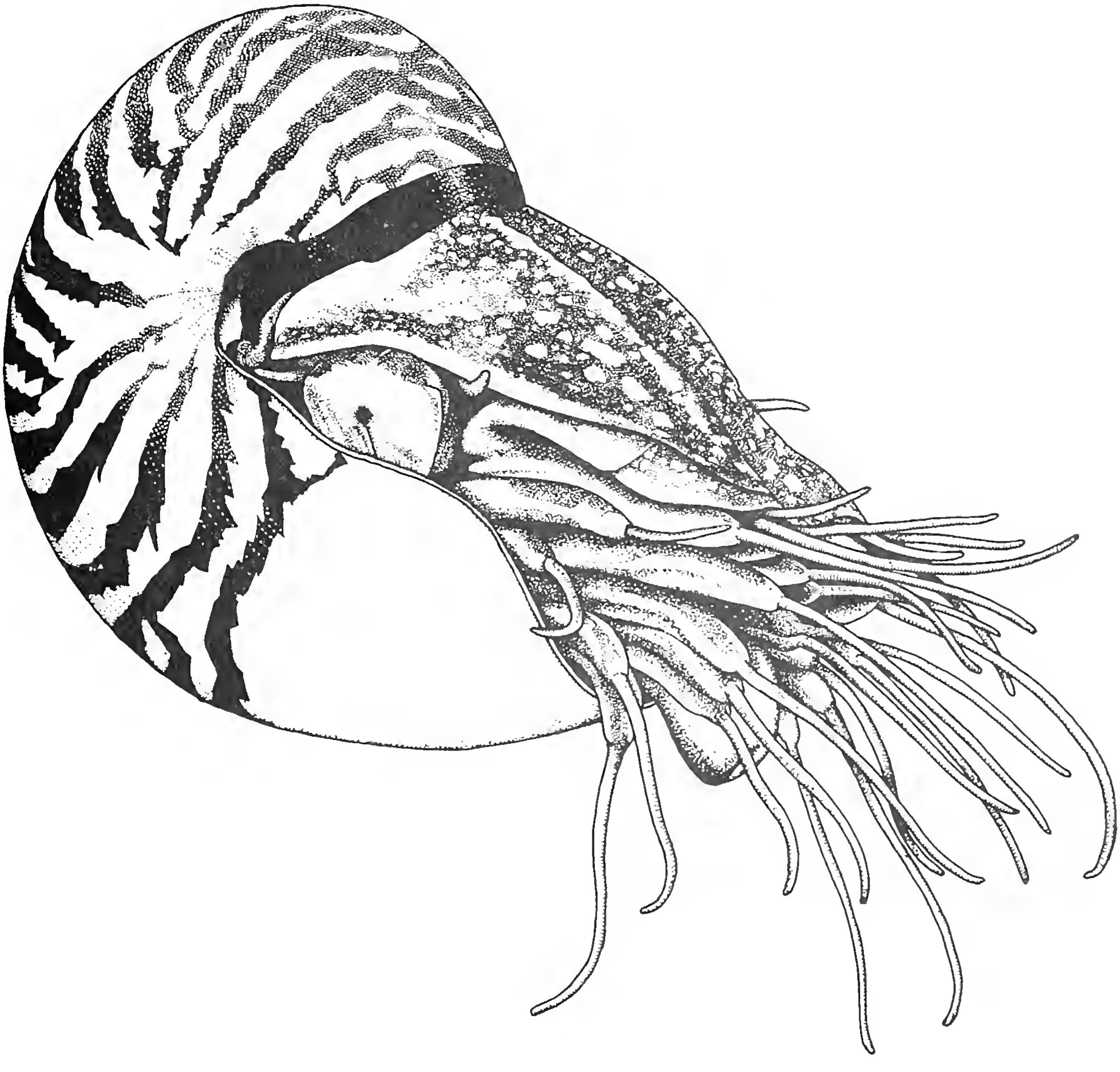

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THE NAUTILUS 104(4):111–119, 1990

# *Procymbulia philiporum* New Species, with a Discussion of the Genus *Procymbulia* Meisenheimer, 1905 (Gastropoda: Thecosomata)

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## ABSTRACT

*Procymbulia philiporum*, new species, is described from submersible collections in the Bahamas. This species retains a coiled shell but exhibits unique characters not known for other pseudothecosomes. It displays an extensive wingplate reminiscent of the family Cymbuliidae and encases its calcareous shell in a voluminous pseudoconch. Thus *P. philiporum* displays key characters of both the Peraclididae and the Cymbuliidae. This species is most appropriately placed in the genus *Procymbulia* Meisenheimer, 1905, within the Family Peraclididae Tesch, 1913, to distinguish its transitional nature.

*Key words:* Pteropod; Thecosomata; *Procymbulia*; *Peraclis*.

## INTRODUCTION

The genus *Procymbulia* Meisenheimer, 1905, was established from observations of a single preserved specimen of the type species, *P. valdiviae* Meisenheimer, 1905, collected in the southern Indian Ocean. This genus is of special interest since even the damaged specimens thus far described display various morphological characters that relate it both to the shelled *Peraclis* Forbes, 1844, and to the shell-less cymbuliids. Thus it has been considered a "missing link" (Meisenheimer, 1905; Tesch, 1913) between the shell-bearing genera of the Thecosomata and genera of the gelatinous pseudothecosomes (Cymbuliidae) which only possess a calcareous shell as larvae (*e.g.*, Lalli and Gilmer, 1989). Approximately 64 specimens from various expeditions and usually from deep tows have been ascribed to this genus (Bonnevie, 1913; Massy, 1932; Tesch, 1913, 1946, 1948; Hubendick, 1951). No species of *Procymbulia* has ever been collected intact. Tesch (1948) obtained sufficient shell remnants from the Dana Expedition material to piece together the shape of what he considered to be the shell of *P. valdiviae* Meisenheimer, 1905. Although the shell differed from those of all previously described *Peraclis* species, Tesch concluded that the morphological differences displayed by his specimens did not warrant the erection of a separate transitional genus.

I here describe the first living, intact specimen of a *Procymbulia* species, which I ascribe to a new species. It was collected alive at 902 m with a manned submersible. The animal exhibits key characters of both the Cymbuliidae and of the Peraclididae. These data warrant the reinstatement of the genus *Procymbulia* Meisenheimer, 1905.

## MATERIALS AND METHODS

In the present description of the new *Procymbulia* species I have assumed that the shell and wingplate axes run anterior-posterior (table 1). This terminology was established by Lalli and Gilmer (1989) for correct orientation of the body of pseudothecosomes (Families: Peraclididae, Cymbuliidae) to the shell and pseudoconch. Live pseudothecosomes are normally oriented with their ventral surface facing up. The proboscis and mouth are situated directly over the apex of the shell (in *Peraclis*) or over the blunt enlarged end of the pseudoconch (in cymbuliids). The median lobe of the wingplate is situated on the margin opposite the proboscis and lies directly over (ventral to) the pallial cavity opening. Thus the axis of the wingplate runs anterior-posterior in relation to the shell. This orientation is displayed by all live pseudothecosomes (excluding *Desmopterus* Chun, 1889) and bears no resemblance to descriptions of preserved specimens of *Peraclis* or *Procymbulia* species (*e.g.*, Meisenheimer, 1906; Tesch, 1948; Spoel, 1976). Preserved specimens are usually contracted and have the mantle cavity displaced laterally, towards the left or "dorsal" side of the shell in a manner that can resemble live specimens of the Limacinidae (Euthecosomata). Thus coiled pseudothecosomes are often erroneously considered analogous with the Limacinidae in regard to their body and shell orientation because of these preservation artifacts.

The single specimen was collected by the JOHNSON SEA-LINK I submersible using a 7.5 liter acrylic sampler

Table 1. Terminology used for orientation of soft part morphology of *Procymbulia* by various authors compared to the present description

| Soft part | Meisenheimer (1905) | Tesch (1948) | This paper |
|---|---|---|---|
| Wingplate axis | dorsoventral | dorsoventral | anterior-posterior |
| Median lobe of wingplate | ventral | ventral | anteroventral |
| Proboscis | dorsal | dorsal | posteroventral |
| Tentacles | dorsal | dorsal | posterior |
| Pallial cavity | ventral | dorsal | anteroventral |
| Gill | — | ventral to right | anterior on midline |
| Anus | right | left | anterior on right |

with lids at either end that move horizontally over the openings to assure gentle collection (Tietze and Clark, 1986). The sampler is sealed when closed so that there is no exchange of water during return to the surface. The specimen was immediately transferred to a 0.5 liter glass dish and maintained at 8 °C on board ship for observation and photography. Photographs were taken using a Zeiss Tessovar macrolens fitted with an Olympus OM-2 camera body and dark field illumination. All photographs were taken with Kodak K-25 color slide film or Panatomic-X black and white film. The specimen was preserved in a 2% final solution of unbuffered glutaraldehyde and transferred to 70% ethanol after two weeks. The specimens was not dissected and is deposited in the National Museum of Natural History, Smithsonian Institution (USNM 860550).

## SYSTEMATICS

Family: Peraclididae Tesch, 1913
Genus: *Procymbulia* Meisenheimer, 1905

The original characters of this genus based on Meisenheimer's original description of *P. valdiviae* include: a ventral (see table 1) mantle cavity that opens beneath the wingplate opposite the margin bearing the proboscis; a cymbuliid-like gelatinous wingplate with similar muscle pattern; a more elongated proboscis than *Peraclis*; sensory processes bordering the median lobe of the wingplate; no operculum; shell unknown, but presumed to be depressed based on soft part morphology.

### *Procymbulia philiporum* new species
(figures 1–12)

**Description:** Coiled pseudothecosome pteropod but closely resembling *Corolla* Dall, 1871, in general appearance. Wingplate gelatinous, oval, highly patterned with muscle, transparent at margins but becoming thick and light brown near the centerline. Calcareous shell with four whorls, thin, brown colored, sinistrally coiled. Shell depressed; spire and body whorl with prominent growth striae parallel to aperture; aperture broad and drawn out in an elongated manner without a sharply pointed rostrum; columellar lip reduced. Shell internal within a voluminous gelatinous pseudoconch. Pseudoconch oval, *Corolla*-like in shape and consistency, length 1.5 × width, with broadly oval opening coinciding with shell aperture. Proboscis extending at 90° angle to wingplate surface, with darkly pigmented ciliary tracks surrounding mouth. Two unsheathed, equal tentacles on posterior surface of proboscis. Wingplate with distinct median lobe on anterior margin; lateral sensory processes on either side of median lobe but not extending beyond wingplate margin. No operculum present.

**Type locality:** Approximately 3 km SW of Moore Island in the Northwest Providence Channel, Bahamas (26°14.76′N, 77°43.46′W). Depth of collection: 902 m in midwater; time: 2300 hrs; 3 Nov 1989; temperature at collection depth: 6.7 °C; surface temperature: 28.5 °C. One specimen.

**Etymology:** This species in named in honor of Dr. Philip Pugh, the scientific observer, and Mr. Philip Santos, the submersible pilot, who together collected the specimen.

**Dimensions alive:** Wingplate width: 20.2 mm; pseudoconch length: 11.3 mm; pseudoconch maximum width: 7.3 mm; shell height: 7.5 mm, maximum shell width: 4.5 mm. **Dimensions preserved:** Wingplate width: 11.2 mm (highly contracted).

**Remarks:** *Procymbulia philiporum* possesses a finely sculptured, calcareous, sinistrally coiled shell (figures 1–10). It is very fragile and of a uniform chestnut brown color (figures 1, 2), differing considerably in structure from that of *P. valdiviae* as described by Tesch (1948). The shell of *P. philiporum* is distinguished by its well-defined growth striae (figures 1–10) that lie parallel to the aperture on the spire and body whorl. The spire is depressed (figures 9, 10). There are no keels or ribs along the suture and there are no spiral ribs on the body whorl as Tesch (1948) described as the major character of the shell of *P. valdiviae*. The anterior margin of the aperture

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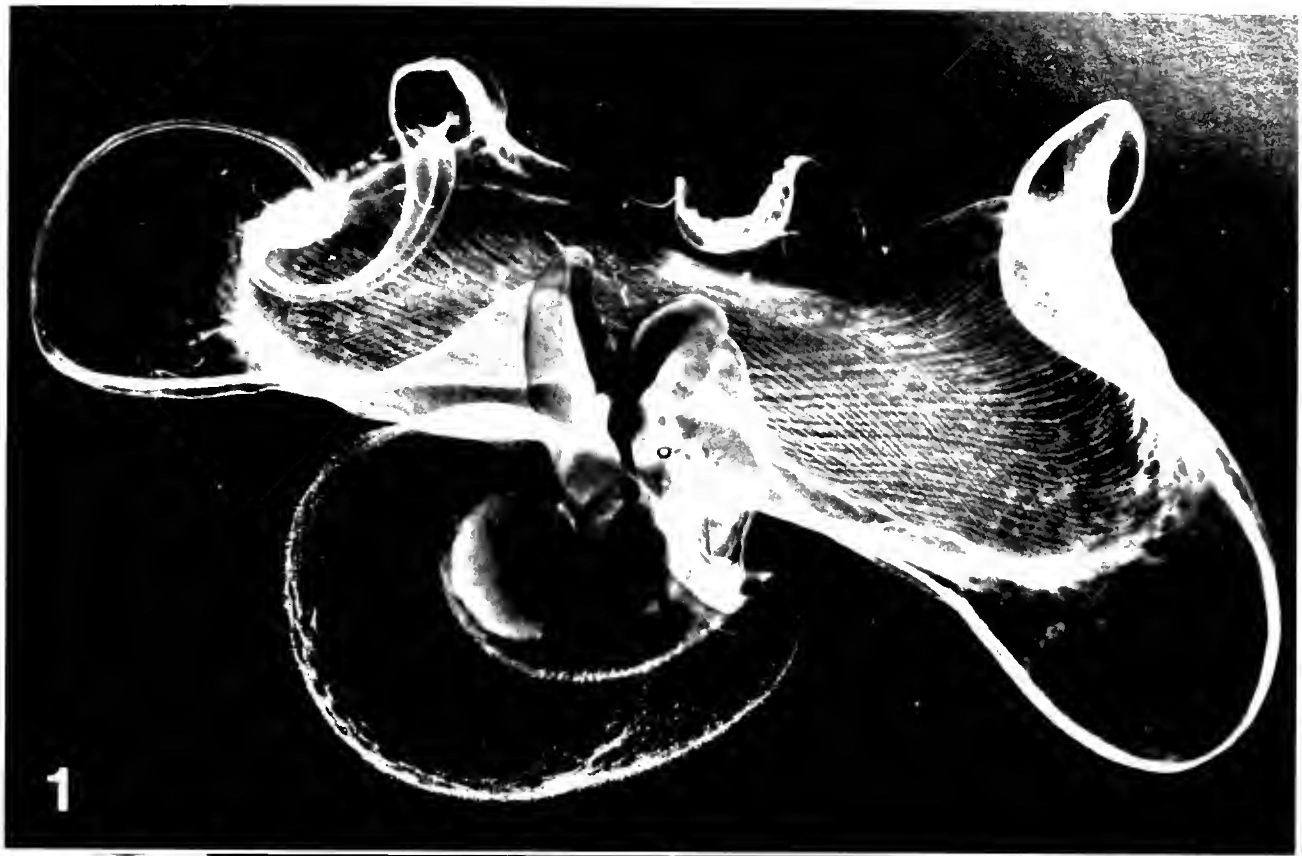
Figures 1–3. *Procymbulia philiporum* new species. **1.** From life, posterior view turned slightly so the left side and ventral surface of the wingplate are exposed. Compare with figure 4 for labels. Magnification ca. 8 ×. **2.** Posterior view, showing close up of shell apex and proboscis; compare with figure 7 for labels. Magnification ca. 12 ×. **3.** Anterior view from the left side showing exposed pallial cavity. The gill and pallial gland are visible; compare with figures 8 and 11 for labels. Magnification ca. 10 ×.



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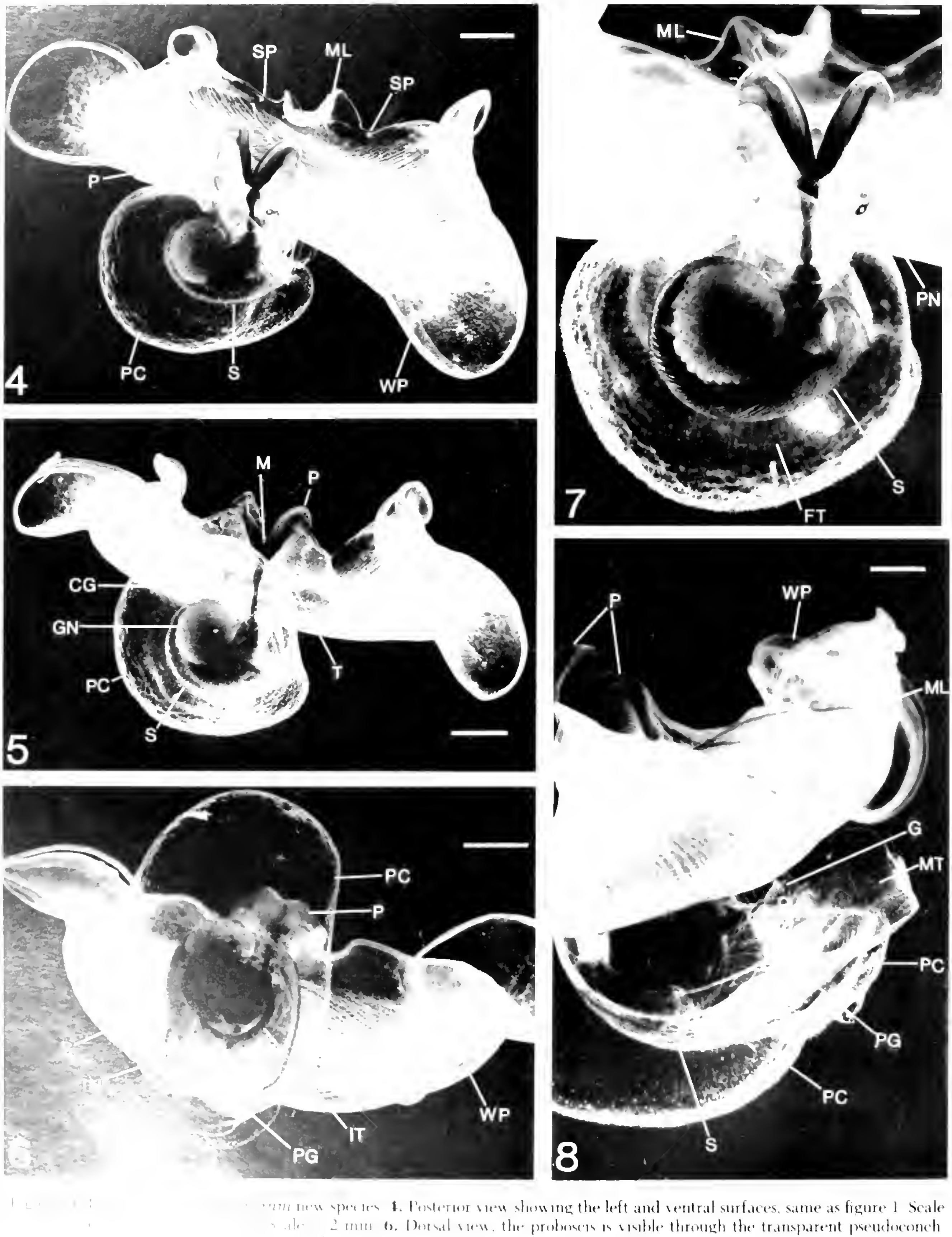
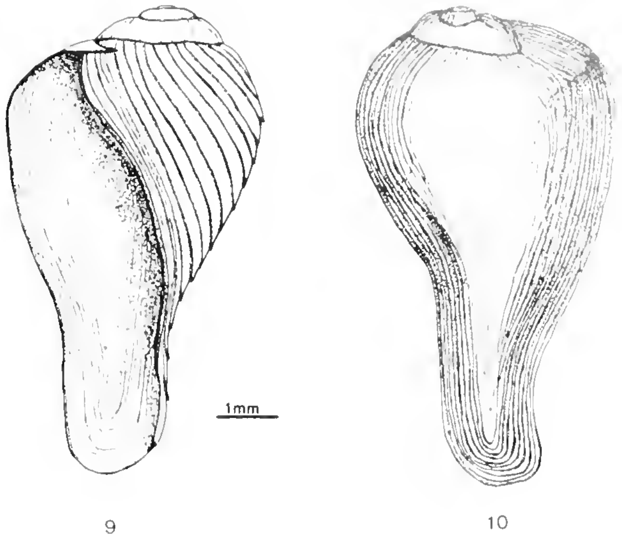


[illegible] *...um* new species. **4.** Posterior view showing the left and ventral surfaces, same as figure 1. Scale [illegible] Scale = 2 mm. **6.** Dorsal view, the proboscis is visible through the transparent pseudoconch [illegible] ...ving close up of shell apex and proboscis. Scale = 1 mm. **8.** Anterior view from the left side (figure 9) is broadly expanded in an elongated manner without a sharply pointed rostrum, in contrast to the pointed rostrum of *P. valdiviae* (*i.e.*, Tesch, 1948) and of all *Peraclis* species. I detected no reticulation on the shell surface. The thin shell could not be removed from the animal without destruction. Consequently it dissolved after several weeks in the preservative.

The shell is enclosed in a large gelatinous pseudoconch (figures 1–8) of the same character and proportional size as those of cymbuliids. The pseudoconch is enclosed within a delicate layer of epithelium that does not appear to bear pigment or chromatophores as is common in the cymbuliids (Lalli and Gilmer, 1989). The pseudoconch appers to be connected to the shell surface by a series of fine threads (figure 7, FT). On the anterior end, there is a pronounced cavity between the shell and pseudoconch (figures 3, 8) that is lined with a dark brown layer of tissue. The pseudoconch also dissolved in the preservative although the epithelial layer that enclosed it remained as a membrane around the visceral nucleus.

The midline of the wingplate is situated directly over the posterior-anterior axis of the shell and pseudoconch (figures 1–7). The proboscis bearing the mouth (figures 4, 5, P) projects ventral-most at 90° from the posterior wingplate margin, directly over the apex of the shell and the blunt, posterior end of the pseudoconch. The expansive wingplate extends laterally and anteriorly, with a large median lobe (figures 4, 7, 8, ML) extending anterior-most, beyond the apertures of both the shell and pseudoconch. On either side of the median lobe, small dense patches occur near the wing border (figures 4, 11, SP) that appear to be concentrations of nerve fibrils and canals that converge from within the wingplate. They are not large, distinct processes as described in *P. valdiviae* (*cf.* Meisenheimer, 1905; Massy, 1932).

The wingplate is thick and heavily cross-patterned with muscle fibers (figures 1–8) which resemble the pattern seen in *Corolla* species (personal observation). The wingplate varies from almost transparent at the margins to light brown near the center line and around the base of the proboscis (figures 2, 7). The ciliated grooves of the lateral foot lobes nearest the mouth are nearly black in color (figures 2, 7), but become almost transparent at their distal margins (figure 1). The unpaired median foot lobe (figure 11, MFL) forms a low border anterior to the mouth and appears as a light brown extension off the wingplate. The paired tentacles (figure 5, T) resemble those of *P. valdiviae* (*cf.* Meisenheimer, 1905). They are of eqnal size, unsheathed, and lie on the posterior surface of the proboscis. The base of each tentacle is darkly pigmented but each terminates in a round, light-colored patch on the tip (figures 2, 7). The penis extends from an opening near the base of the proboscis, below (dorsal to) the left tentacle (figure 7, PN).



**Figures 9–10.** *Procymbulia philiporum* new species. **9.** Shell, ventral view showing aperture. **10.** Shell, dorsal view

The pallial cavity opens broadly across the anterior portion of the shell aperture (figures 3, 8, 11). The anterior end of the pseudoconch is supported by a thick integument (figures 6, 11, IN) that extends from the pallial cavity. This integument appears to be the base of the epithelium that encloses the pseudoconch. Above (ventral to) this integument, a thick layer of the mantle (figures 6, 8, 11, MT) protrudes anteriorly beyond the aperture. The oval-shaped pallial gland is located on the ventral surface of this mantle layer. No "balancer" structure (*cf.* Meisenheimer, 1905) occurs on the mantle border of *P. philiporum*. Ventral to the pallial gland, a large plicate gill (figures 3, 8, 11, 12, G) originates from the right side of the visceral mass and extends anteriorly. When fully expanded in life, the gill protrudes slightly beyond the shell and lies along the midline of the pallial cavity, obscuring the pallial gland. The gill presents a large smooth surface with no deep furrows.

The intestine originates posteriorly, near the gonad (figure 12) and ends anteriorly on the right side of the pallial cavity near the gill. In its course (figure 12), it first encircles the viscera between the gonad and the digestive gland; it next extends anteriorly along the right side of the mantle cavity; it again encircles the anterior portion of the viscera before extending into the pallial cavity. The anus opens to the right of the gill at the end of a long and seemingly unsupported extension of the intestine (figures 11, 12, A). Because the anus and lower

←

showing exposed pallial cavity with gill and pallial gland. Scale = 1 mm. Abbreviations: CG, central ganglion; FT, fine threads connecting shell and pseudoconch; G, gill; GN, gonad; IN, integument supporting anterior end of pseudoconch; IT, intestine; M, mouth; ML, median lobe of wingplate; MT, mantle tissue; P, proboscis; PC, pseudoconch; PG, pallial gland; PN, penis; S, shell; SP, sensory processes; T, tentacle; WP, wingplate.

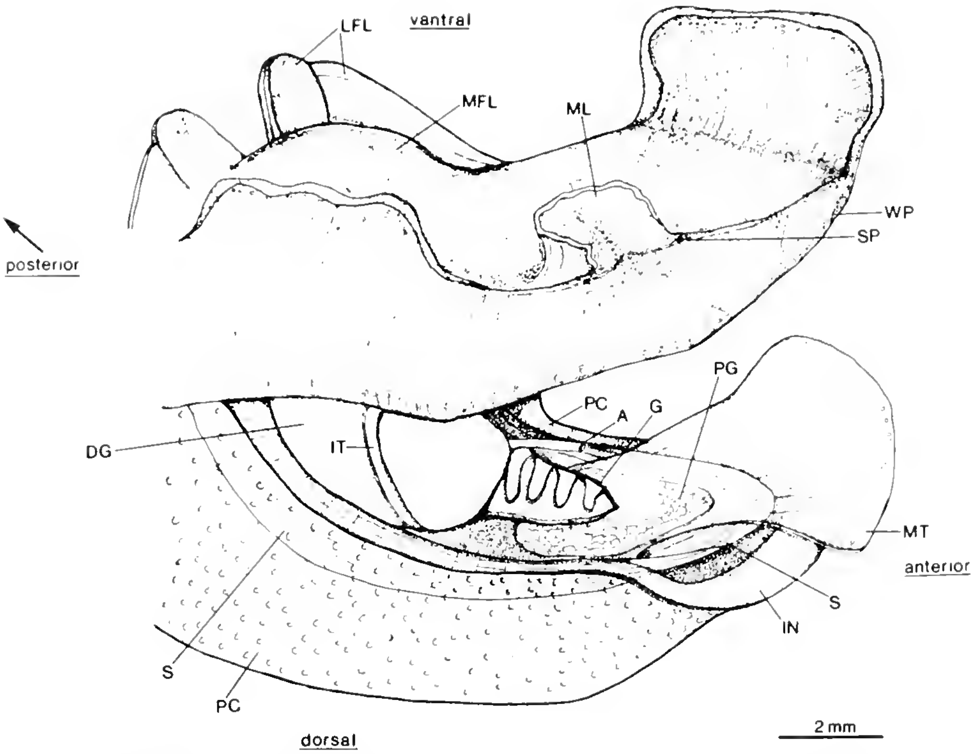


**Figure 11.** *Procymbulia philiporum* new species. Anterior view from the left side showing pallial cavity. Compare with figures 3 and 8. The posterior-anterior and dorsal-ventral axes of the shell are shown. The gill is retracted, but can extend beyond the anterior shell border. A, anus; DG, digestive gland; G, gill; IN, integument supporting pseudoconch; IT, intestine; LFL, lateral foot lobes (paired); MFL, median foot lobe (unpaired); ML, median lobe of wingplate; MT, mantle tissue; PC, pseudoconch; PG, pallial gland; S, shell; SP, sensory processes; WP, wingplate.

intestine have twisted back in a loop to the left side of the mantle cavity in the preserved specimen, the intestinal path of *P. philiporum* resembles the "Type A" diagram of Tesch (1948: figure 34E).

**Live observations:** The animal was neutrally buoyant in the center of the sampler on return to the surface and slowly swam about the container when disturbed. It swam by undulations of the wingplate in the manner of the cymbuliids (Morton, 1964; Lalli and Gilmer, 1989) and appeared to be healthy with no apparent signs of damage. The animal never attempted to retract into the shell even after severe prodding and indeed this would not appear possible given the size of the wingplate.

The intestine appeared to be full throughout its length, and several fecal pellets were produced during observation. The pellets were released into the pallial cavity and discarded off the anterior surface of the body by ciliary currents on the mantle. They were roughly 3 to 4 mm long and 0.5 mm in width. Recognizable contents included broken foraminifera tests, crustacean exoskeleton fragments, and coccolithophores. No particles in the fecal contents were larger than 40 μm.

## DISCUSSION

*Procymbulia philiporum* clearly displays characters of both the Peraclididae and the Cymbuliidae (Table 2), and points to the close affinity between these families. It therefore seems reasonable to reinstate the genus *Procymbulia* Meisenheimer, 1905, to emphasize its transitional nature. *Procymbulia philiporum* clearly shows close affinity to the family Peraclididae with respect to the coiled shell and the orientation of its internal organs. However, several new traits of the Peraclididae are now apparent based on this description: First, the shell can be totally enclosed in a gelatinous pseudoconch, similar to those characteristic of the Cymbuliidae. Secondly, the wingplate can have a broad highly gelatinous nature also similar to the Cymbuliidae. Thirdly, an operculum can be absent and the shell can lack suture ornamentation and a pointed rostrum. Lastly, the animal may not be capable of retraction into the shell.

Meisenheimer (1905) established *Procymbulia* as a transition genus mostly because the pallial cavity of his specimen was comparable in position to that of the cymbuliids and opposed by 180° in comparison to those of either *Peraclis* or *Limacina*. In fact, the pallial cavity and wingplate of living specimens of *Peraclis* species and *P. philiporum* have a similar orientation with respect to their shells and neither resembles the orientation of *Limacina*. More accurate characters on which to distinguish *Procymbulia* are the combined presence of the shell and pseudoconch, and the gelatinous *Corolla*-like wingplate.

Although *Peraclis* and *Procymbulia* have coiled shells, both display an important pseudothecosome trait by

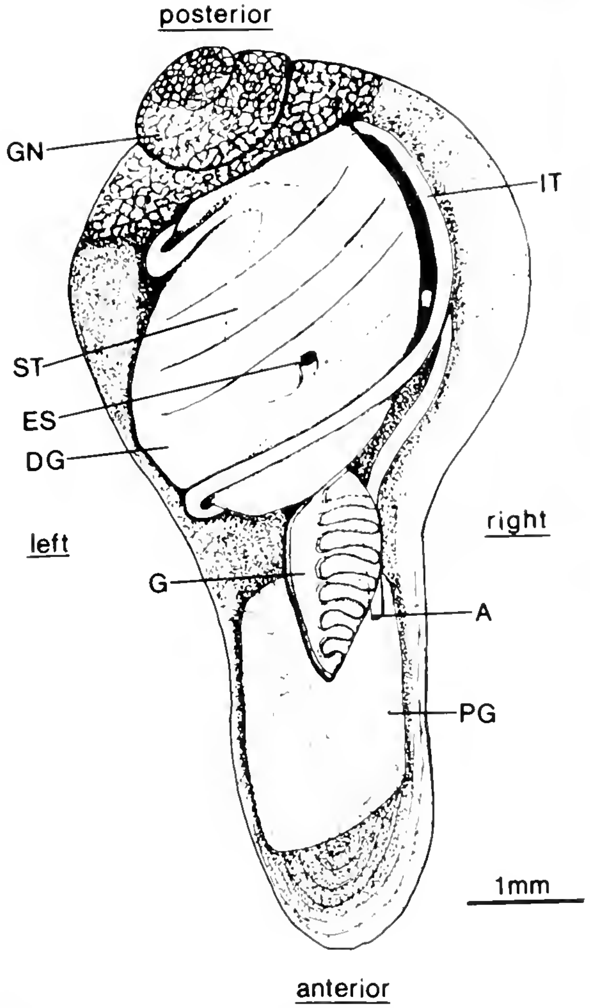


**Figure 12.** *Procymbulia philiporum* new species. Course of intestine (IT), mantle removed. A, anus; DG, digestive gland, ES, esophagus; G, gill, GN, gonad, PG, pallial gland; ST, stomach.

making them functionally internal structures (Gilmer and Harbison, 1986; personal observation). At least three species of *Peraclis* [*P. reticulata* (D'Orbigny, 1836), *P. bispinosa* Pelseneer, 1888 (figure 13), and *P. apicifulva* Meisenheimer, 1906] have mantle tissue that completely encloses the shell in life (personal observation). *Procymbulia philiporum*, however, more closely resembles the cymbuliids by encasing its shell in a pseudoconch, and by its apparent inability to retract into its shell possibly explaining the loss of the operculum. The wingplate of *P. philiporum* is also much more cymbuliid-like in thickness, muscle pattern, and general shape than I have seen in *Peraclis*.

**Figure 13.** *Peraclis bispinosa* from life, posteroventral view, wingplate (WP) fully expanded; mantle covering the shell (MT) is retracted so that the apex is visible. Scale = 2 mm. ML, median lobe of wingplate; P, proboscis, S, shell.

Since Tesch (1948) closely linked *Procymbulia valdiviae* to *Peraclis bispinosa*, I have shown a partially expanded, living specimen of the latter species (figure 13) for comparison with *P. philiporum*. *Procymbulia bispinosa* has a more heavily pigmented wingplate and proboscis than *P. philiporum*, but the wingplate is reduced in thickness, in extent of muscle bands, and in size relative to the shell. The proboscis and gill[1] of *P. bispi-*

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[1] Note: In a previous description of *Peraclis* (Lalli and Gilmer, 1989), we erred in stating that the gill was only retracted mantle tissue. I have now examined the gill in *P. reticulata*, *P. bispinosa*, and *P. apicifulva*.

**Table 2.** Comparison of major traits of the Peraclididae and Cymbuliidae prior to this description of *Procymbulia*.

| Peraclididae | Cymbuliidae |
|---|---|
| Coiled shell present with prolongation of columella | Calcareous shell in larval stage only |
| Shell axis oriented along posterior-anterior body axis | Body highly gelatinous, wingplate up to 2× body length |
| Shell often enclosed by voluminous mantle tissue | Shell replaced in adults by gelatinous pseudoconch |
| Operculum circular, glassy, left handed | Operculum left handed in larval forms |
| Proboscis comprised of three footlobes fused to wingplate | Proboscis similar, capable of great expansion in some genera |
| Anus opens to the right inside pallial cavity | Anus opens to left side of pallial cavity |
| Uniform pallial gland, without transparent bands | Pallial gland usually divided by transparent bands |
| Plicate ctenidium present in pallial cavity | No true ctenidium present |
| Well developed buccal mass present | Buccal mass reduced or absent in most species |
| Retracts completely into shell | No retraction mechanism after larval stage |

*nosa* are remarkably similar in structure to those of *P. philiporum*. Although *P. bispinosa* has extensive mantle that normally surrounds the shell, the live specimen in figure 13 was also carefully collected with the JOHNSON SEA-LINK and shows no evidence of a pseudoconch. In addition, *P. bispinosa* is capable of complete retraction into its shell.

Most descriptions of pseudothecosomes are greatly hampered by the condition of the material. Much of the described variation in *Peraclis* species is due to twisting of the pallial cavity or wingplate (*e.g.*, Tesch, 1948: figure 34a,b), during retraction. The mantle is much more extensive in living specimens than in preserved material which always shows tremendous variation. In addition, the same confusion in *Peraclis* regarding terms used to describe the orientation of the soft parts with the shell (Gilmer and Harbison, 1986; Lalli and Gilmer, 1989) also exists for *Procymbulia* (table 1).

Descriptions of *Procymbulia valdiviae* (Meisenheimer, 1905; Hubendick, 1951) suggest that the body and shell have an orientation similar to those of *P. philiporum*. Whether a pseudoconch is present remains unknown, although Massy (1932) described a firm membrane surrounding the viscera in her specimens. This tissue could be the epithelium that encloses the pseudoconch. It seems doubtful that the shell or pseudoconch of *P. philiporum* would ever survive the rigors of net collection or routine fixation. Both structures on my specimen dissolved within two weeks of preservation. A similar condition could be expected for *P. valdiviae*.

Tesch (1948) provided the most complete description of what he considered to be *Procymbulia valdiviae*. He found it so similar to *Peraclis bispinosa* that he removed its standing as a genus and discounted any transitional status it displayed between the Peraclididae and the Cymbuliidae. However, five facts suggest that the specimens Tesch used to make his determination are probably a new species of *Peraclis* rather than specimens of *P. valdiviae*: 1) the shells bear distinct *Peraclis*-like rostra and suture ornamentation; 2) the shells survived net collection and years of preservation; 3) only his specimens bear an operculum; 4) Tesch's figures show a *Peraclis*-like 90° twisting of the wingplate, indicating partial retraction into the shell. Figures of *P. valdiviae* from Meisenheimer (1905), Bonnevie (1913), Hubendick (1951), and my preserved specimen of *P. philiporum* all have the wingplate situated in its unretracted position (the proboscis over the gonadal whorl) suggesting *Procymbulia* does not display this type of retraction. And finally, 5) Tesch found no lateral processes bordering the median lobe of the wingplate.

*Procymbulia* appears to be cosmopolitan in its distribution and represented by at least two species. Based on the collections of Meisenheimer (1905) and Massy (1932), it would appear that *P. valdiviae* probably occurs in the circumglobal southern oceans, primarily in deep water. As stated above, Tesch's (1948) Indo-Pacific specimens most likely belong to a new species of *Peraclis*. Bonnevie's (1913) description of *P. michaelsarsi* from a single specimen collected in the N.E. Atlantic may be very similar to *P. philiporum*. Based on her brief description, the shape of the gonadal whorl and the orientation and pigmentation pattern of the proboscis resemble *P. philiporum*. Hubendick (1951) and Tesch (1946) may also have collected *P. philiporum*, since all of these Atlantic specimens assigned to *P. valdiviae* lack the large sensory processes on the anterior wingplate margin characteristic of this latter species. Hubendick's figures closely resemble my preserved specimen, and Tesch (1946) described a similar pigment pattern to that of *P. philiporum* but indicated that an operculum was attached to the wingplate of his specimens. My animal shows no scar or other indication of ever having had an operculum. Tesch's specimens were considerably smaller than mine, however, and the operculum may be lost at an early age.

## ACKNOWLEDGEMENTS

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# Studies on Bathyal and Abyssal Buccinidae (Gastropoda: Neogastropoda):
# 1. *Metula fusiformis* Clench and Aguayo, 1941

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## ABSTRACT

Based on the morphology of the radula and shell, *Metula fusiformis* Clench & Aguayo, 1941 is transferred to the predominantly Indo-western Pacific genus *Manaria*. This species occurs in upper continental slope communities (183–578 m) of the Caribbean Sea and the northern coast of South America. The holotype was collected dead in 2,633 m, well below the depth inhabited by this species. The large well-developed gland of Leiblein, a separate sperm ingesting gland between the capsule gland and albumin gland, and three-cusped rachidian teeth are features that *Manaria* shares with other fusiform buccinids (*e.g.*, *Penion*, *Serratifusus*) as well as with primitive members of other families within Muricacea. These features are interpreted as being symplesiomorphic, and suggest that the fusiform buccinids are among the more primitive members of the Buccinidae.

*Key words:* Buccinidae; Caribbean, bathyal, *Manaria; Metula*

## INTRODUCTION

The family Buccinidae comprises one of the most diverse and dominant groups of predatory prosobranch gastropods at high latitudes and at bathyal, abyssal and hadal depths. It is represented in the fossil record of the Lower Cretaceous (Albian), and ranks among the oldest of the neogastropod families (Taylor *et al.*, 1980). Like most predatory prosobranch families, it is believed to have evolved in temperate climatic zones at higher latitudes (Sohl, 1987). Although the majority of these families became predominantly tropical during the Cenozoic, most Buccinidae remained in temperate and polar regions, were the family diversified since the late Miocene (Taylor *et al.*, 1980). The success of Buccinidae at high latitudes and in the deep sea has been attributed to their broad habitats and diets, which are considered to be adaptations to unpredictable resources (Taylor, 1978).

Despite the high diversity and abundance of Buccinidae, the systematics of this group is poorly understood at all taxonomic levels. This is due, in large part, to the fact that the vast majority of taxa are based exclusively on features of the shell and operculum, supplemented occasionally by observations on radular morphology. Shells of Buccinidae tend to be simple, and offer few readily discernible morphological characters. These are subject to convergence, especially in polar regions and the deep sea, where effects of habitat on shell form are most pronounced (Graus, 1974).

Detailed anatomical data are available for comparatively few, mainly shallow-water taxa (*e.g.*, Dakin, 1912; Golikov, 1963, 1980; Kosuge, 1967; Ponder, 1973; Lus, 1981; Kantor, 1990). The lack of well-defined, synapomorphic anatomical features (other than radular morphology), even between the families Buccinidae, Nassariidae, Fasciolariidae, and Melongenidae have led Ponder (1973a) to suggest these groups might all be considered subfamilies of Buccinidae. This arrangement was subsequently adopted by Ponder and Warén (1988).

Bouchet and Warén (1985) revised the deep-water Buccinidae (*sensu* Wenz, 1943) of the northeastern Atlantic Ocean, and later (Bouchet & Warén, 1986) reviewed many of the tropical deep-water species. Despite these significant contributions, most of the nearly 200 supraspecific taxa within Buccinidae (*sensu* Wenz, 1943) are poorly defined, and the assignment of many species to genera remain tentative.

Among the taxa listed by Bouchet and Warén (1986) as "insufficiently known" is *Metula fusiformis* Clench and Aguayo, 1941. The placement of this species in *Metula* was disputed by Olsson and Bayer (1972) who suggested that it had affinities with *Fusinus* or a fusiform buccinid. Abbott (1974) referred this species to the genus *Bartschia*. Bouchet and Warén (1986) considered it to be a buccinid, and commented on its conchological resemblance to *Euthriostoma*.

During a recent dive aboard the research submersible Johnson-Sea-Link I off Navassa Island, situated off the southwestern peninsula of Haiti, the author had the opportunity to observe and collect several living specimens of "*Metula*" *fusiformis*. These observations, together with data from additional material discovered in the USNM collections, form the basis of this report, the first in a series on enigmatic deep-water buccinid taxa.

## MATERIALS AND METHODS

Five specimens of "*Metula*" *fusiformis* Clench and Aguayo, 1941 were observed, recorded on videotape and collected either in (1 specimen) or within 2 meters (4 specimens) of a bucket baited with decomposing octopus and set on an ooze-covered area (slope about 20°) off the west coast of Navassa Island (18°24'42"N, 75°03'00"W) at a depth of 578 m for 50 hours. The specimens, which were moribund upon reaching the surface, were fixed in 10% neutral buffered formalin and stored in 70% ethanol until dissection.

Phenetic analyses were used to assess the relationships of three conchologically similar taxa, each proposed on the basis of a single specimen. All specimens listed in the "material examined" section, as well as the holotype of *Buccinofusus surinamensis* Okutani, 1982 and two specimens of a southern variant of *Buccinum canetae* Clench and Aguayo, 1944, described as *Plicifusus jamarci* Okutani, 1982, were scored for the 11 shell characters listed in table 1. These data were standardized (mean = 0, standard deviation = 1), a Euclidean distance matrix calculated, and a phenogram based on the UPGMA clustering algorithm was produced using SYSTAT version 4.0 (Wilkinson, 1988). A Principle Component Analysis using the same data matrix (25 specimens × 11 characters) was performed, also using SYSTAT, and the individuals plotted using the first two principal components as axes.

Repositories of examined specimens are indicated by the following abbreviations:

MCZ—Museum of Comparative Zoology, Harvard University
NSMT—National Science Museum, Tokyo
USNM—National Museum of Natural History, Smithsonian Institution

## SYSTEMATICS

Family Buccinidae Rafinesque, 1815
Genus *Manaria* E. A. Smith, 1906

### *Manaria fusiformis* (Clench & Aguayo, 1941)
(figures 1–5, 7–17)

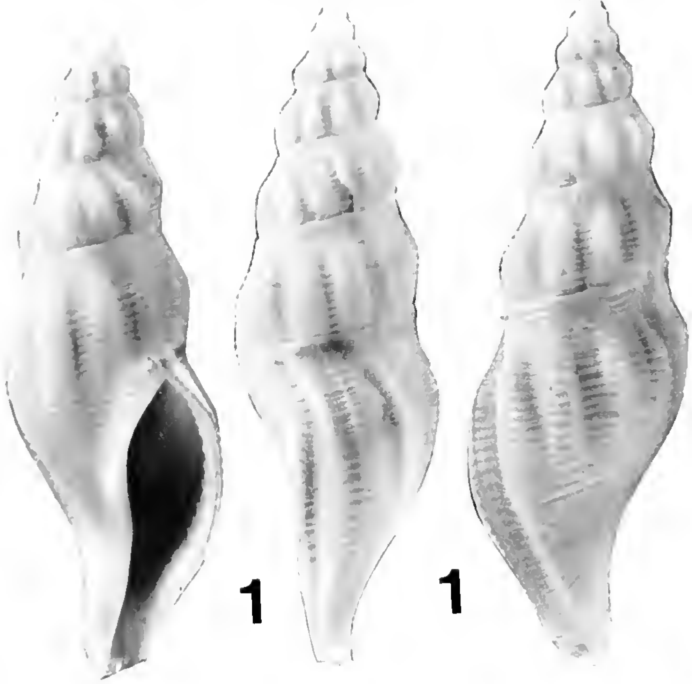
*Metula fusiformis* Clench & Aguayo, 1941:179, pl. 14, fig. 1; Bouchet & Warén, 1986:485, fig. 116
"*Metula*" *fusiformis* Clench & Aguayo.—Olsson & Bayer, 1972:925
*Bartschia fusiformis* (Clench & Aguayo).—Abbott, 1974:217
*Mohnia kaicherae* Petuch, 1987:103, pl. 21, figs. 8, 9

**Table 1.** Shell characters used for phenetic analyses. Characters 1 through 8 describe the geometry of the generalized shell form (Harasewych 1982).

1. Shape of the generating curve of the body cavity (Sbc).
2. Shape of the generating curve of the siphonal canal (Ssc).
3. Relative siphonal length (Rsl).
4. Siphonal angle (β).
5. Angle of the generating curve (θ).
6. Rate of whorl expansion (W).
7. Position of the generating curve relative to the axis (D).
8. Rate of whorl translation (T).
9. Spire angle (α).
10. Number of axial ribs on fourth teleoconch whorl (no. rib).
11. Number of spiral cords on fourth teleoconch whorl (no. cord).

**Shell morphology:** Shell (figures 1, 3, 4, 5) to 69 mm, thick, biconical, fusiform. Protoconch badly eroded or missing on all adult specimens examined. Protoconch of juvenile specimen (figures 7, 8) just over one smooth whorl, with a diameter of 0.75 mm. Transition to teleoconch gradual, marked by formation of axial ribs, followed within ½ whorl by the formation of six fine spiral cords. Teleoconch of up to 8¾ convex whorls, rounded at first, becoming sharply shouldered by the fifth postnuclear whorl. Suture broadly adpressed. Axial sculpture of broad, rounded, regularly-spaced, axial to slightly prosocline ribs that do not extend onto the anteriormost portions of the body whorl or the siphonal canal. Axial ribs number 11–12 on the first and 11–16 on the penultimate whorl. Spiral sculpture of strong cords, as broad or broader than intervening spaces, that overlay axial ribs. Cords number 12–13 between suture and shoulder, 19–21 between shoulder and siphonal canal, 16–18 on siphonal canal. Sixteen to 21 cords remain exposed on penultimate whorl. Aperture elliptical, tapering posteriorly beneath suture to form anal sulcus. Outer lip with 18–23 thin spiral lirae pronounced beneath axial ribs and weak or absent between. Inner lip smooth, with thin, porcellaneous inductura. Columella solid, sinuate, lacking folds. Siphonal canal broad, slightly shorter than aperture, crossing coiling axis. Siphonal fasciole weak, adjacent to columellar edge of siphon. Exterior surface of shell dull ivory to light amber, aperture and columella white. Periostracum (figure 9) thick, straw-colored to brown, consisting of thin, axial blades that are broadest between spiral cords and abraded along their surfaces. Operculum (figures 2, 13, op) thick, elongate, with terminal nucleus (usually abraded), attached along slightly less that ½ of its inner surface, glazed along posterior and left inner margins, fills aperture ¼ whorl from outer lip.

**Shell ultrastructure:** (figure 10) Shell composed of three layers of crossed-lamellar crystals and an outermost prismatic layer. Innermost layer (≈200 μm) with crystal faces oriented at approximately a 35° angle to growing edge of the shell; crystal faces of next layer (≈250 μm) perpendicular to growing edge; outermost crossed-lamellar layer (≈625 μm) parallel to growing edge. Prismatic layer of varying thickness (50–200 μm) outermost, comprising the spiral cords and contains all of the shell color. Inner three layers white.



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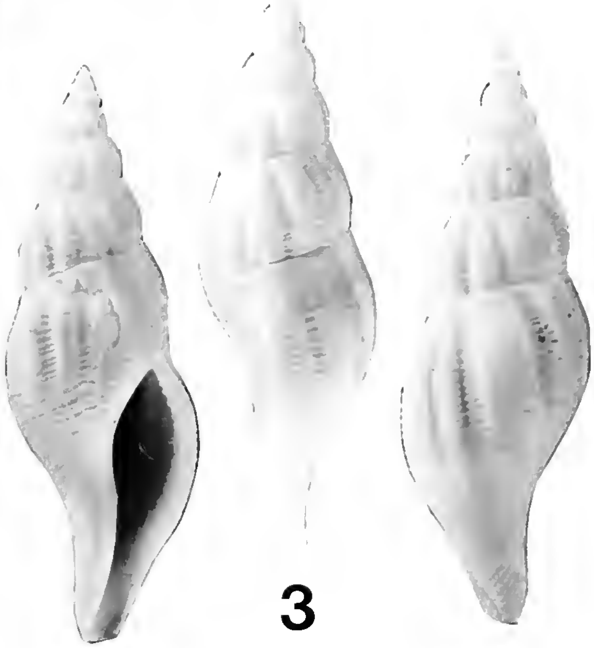

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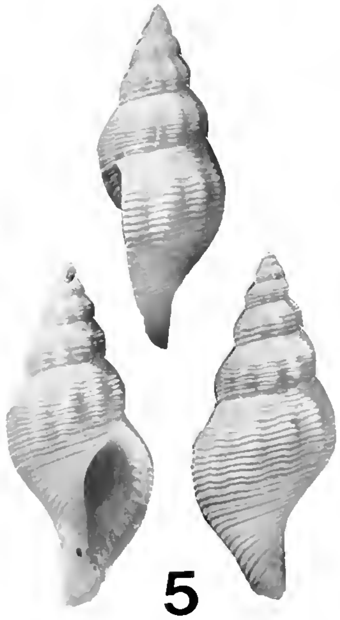

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**External anatomy:** (figure 13) Soft tissues comprise 3½–4 whorls, mantle cavity spans ⅔ whorl, kidney ¼ whorl, digestive gland 2½–3 whorls. Columellar muscle long, narrow, attaching to shell 1⅓ whorl behind mantle edge. Foot small, rectangular (L/W = 1.4) with thin, deep propodial groove along leading edge of sole. Animal uniform khaki to tan in color. Head small, with pair of thin, tapering cephalic tentacles with round black eyes at their bases. Siphon (figure 13, s) short, muscular.

**Mantle cavity:** Arrangement of mantle cavity organs similar to that of *Buccinum undatum* Linné, 1758 (Fretter & Graham, 1962: fig. 180B). Mantle with thick, muscular band (figure 13, mb) along edge, thin, transparent posteriorly. Osphradium bipectinate, large, dark brown, with 70–80 filaments above ganglion and 62–68 below. Ctenidium, twice as long and slightly narrower than osphradium, sharply tapered along anterior edge. Hypobranchial gland (figure 13, hg) broad, thick, viscous and clear in water, solid and opaque in alcohol.

**Alimentary system:** Proboscis (figure 14, pb) long (1.5 × shell aperture length), narrow (1.2 mm), pleurembolic, retracts to rear of cephalic hemocoel, overlying salivary glands anteriorly and gland of Leiblein posteriorly. Buccal mass, as long as introverted proboscis, with radular sac extending slightly from its posterior margin. Radula (figure 12) short (6.0–7.9 mm, n = 3), composed of 102–108 rows of teeth. Rachidian tooth with three cusps of equal length located on central portion of broad, basal plate. Lateral teeth with two cusps, outer cusp 1.5 times as long and broad at its base as inner cusp. Salivary glands (figure 14, sg) large, irregular, with ducts becoming embedded in wall of esophagus (within dorsal folds) anterior to valve of Leiblein (figure 14, vl). Gland of Leiblein (figure 14, gl) long, convoluted, posteriorly tapering, filling posterior ⅔ of cephalic hemocoel, emptying via a thin duct into the posterior region of the mid-esophagus. Stomach (figures 13, 14, sto) simple, U-shaped, with two widely separated ducts to digestive glands. Intestine thin, tubular, with longitudinal folds, rectum (figure 14, r) little expanded, simple. Anal gland absent.

**Female reproductive system:** A narrow oviduct leads from the large yellow-orange ovary to the albumen gland, which lies along the anterior right wall of the kidney. The pallial portion of the female gonoduct (figure 15) consists of a large sperm ingesting gland (figure 15, ig), long, narrow capsule gland (figure 15, cg) and a muscular bursa copulatrix (figure 15, bc) with the female opening (figure 15, fo) situated ventral to the anus (figure 15, a).

**Male reproductive system:** Testis (figures 13, 16, te) orange tan, along right side of digestive gland. Testicular duct (figure 16, td) tubular, about 0.3 mm in diameter, becomes convoluted along adaxial wall of kidney to form seminal vesicle (figure 16, sv). Duct straightens before passing along wall of pericardium and entering rear of mantle cavity (figure 16, rmc). The prostate gland (figure 16, pr) is narrow, and runs along the right wall of the mantle cavity, ventral to the rectum. The tubular vas deferens (figure 16, vd) runs from the prostate gland anteriorly along the floor of the mantle cavity to the base of the penis (figure 16, pen), which is approximately ¾ the length of the mantle cavity, dorsoventrally compressed, truncated, and with a terminal papilla (figure 16, pap) emanating from a depression along its distal lateral wall.

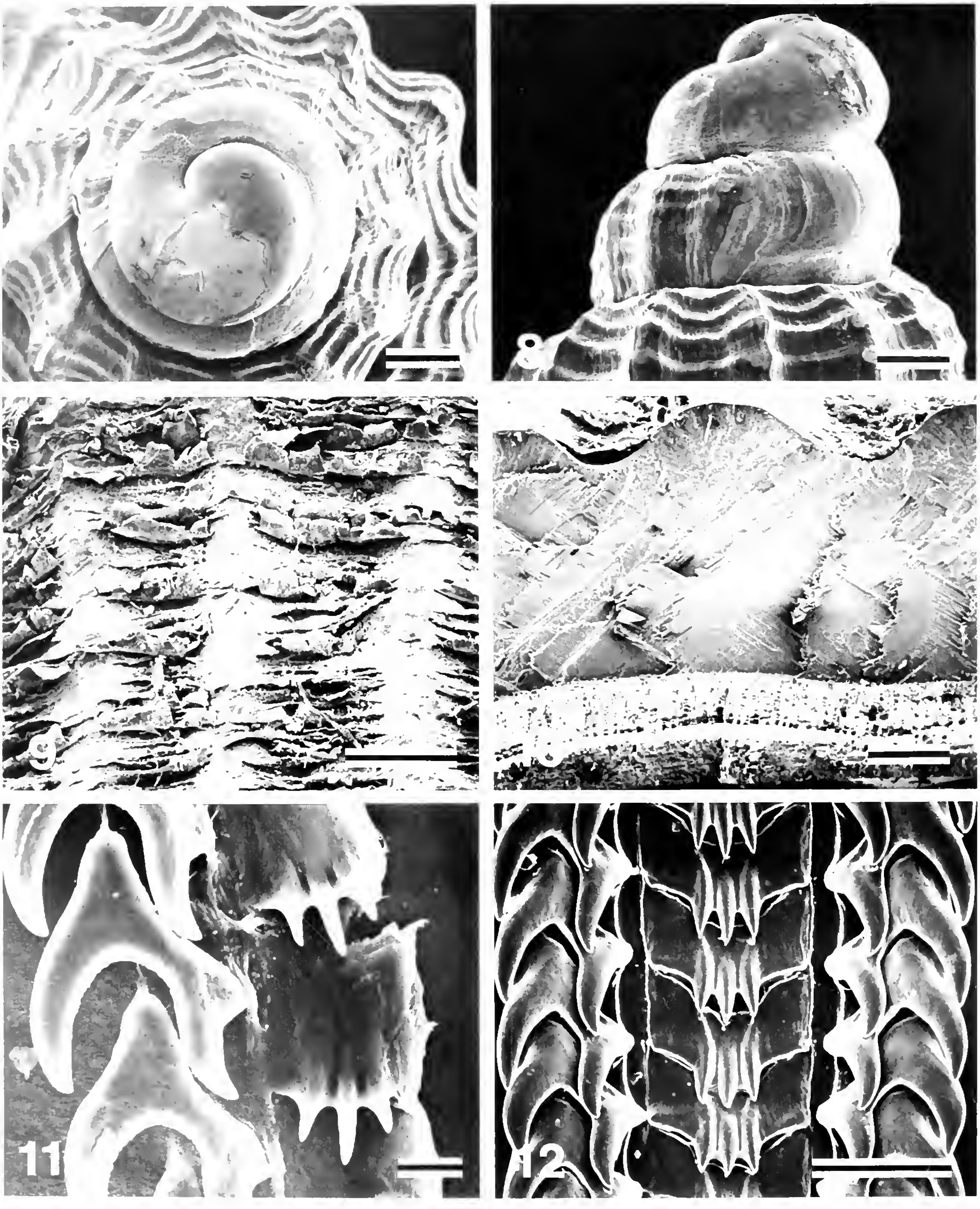
**Material examined:** Holotype, MCZ 135290, Atlantis sta. 3344, trawled off Cienfuegos, Cuba (21°38′N, 80°12′W), in 1,440 fms (2,633 m); Holotype of *Mohnia kaicherae* Petuch, 1987, USNM 859855, off Los Monges Islands, off mouth of Gulf of Venezuela, Venezuela, in 200 m; USNM 875112, Johnson-Sea-Link I sta. 2321, off west coast of Navassa Island (18°24′42″N, 75°03′00″W), in or near carrion-baited bucket left in 570 m for 50 hours [5 specimens]; USNM 854016, Johnson-Sea-Link I sta. 2320, off Lulu Bay, Navassa Island (18°22′42″N, 75°02′44″W), on small tree branch in 530 m [2 juvenile specimens]; USNM 832953, off Long Point, south shore of St. Croix, US Virgin Islands, in 160 fms (293 m) [10 specimens]; USNM 832954, off Salt River Canyon, north shore St. Croix, US Virgin Islands, in 230 fms (420 m) [2 specimens]; USNM 811332, R/V Oregon sta. 4225, 150 miles north of Sao Luís, Maranhao, Brazil (00°18′N, 44°23′W), in 100 fms (183 m) [1 empty shell].

**Ecology:** Like many buccinids, this species is attracted to carrion, and is at least a facultative scavenger. The five specimens of *Manaria fusiformis* were the only gastropods collected in or near the baited trap. Also present in the trap were several dozen isopods (*Booralana tricarinata* Camp & Heard, 1988). The two juvenile specimens were collected from a single fragment of sunken wood that was also inhabited by three chitons, about 20 skeneiform trochids, and that contained teredinids and burrowing sipunculans. Water temperatures at the two Johnson-Sea-Link stations at which this species was collected were 9.7° C (JSL-I-2320) and 9.9° C (JSL-I-2321). Gut contents of three adult specimens were examined, but did not reveal identifiable remains. The bathymetric range of all live-collected specimens was 293–578 m.

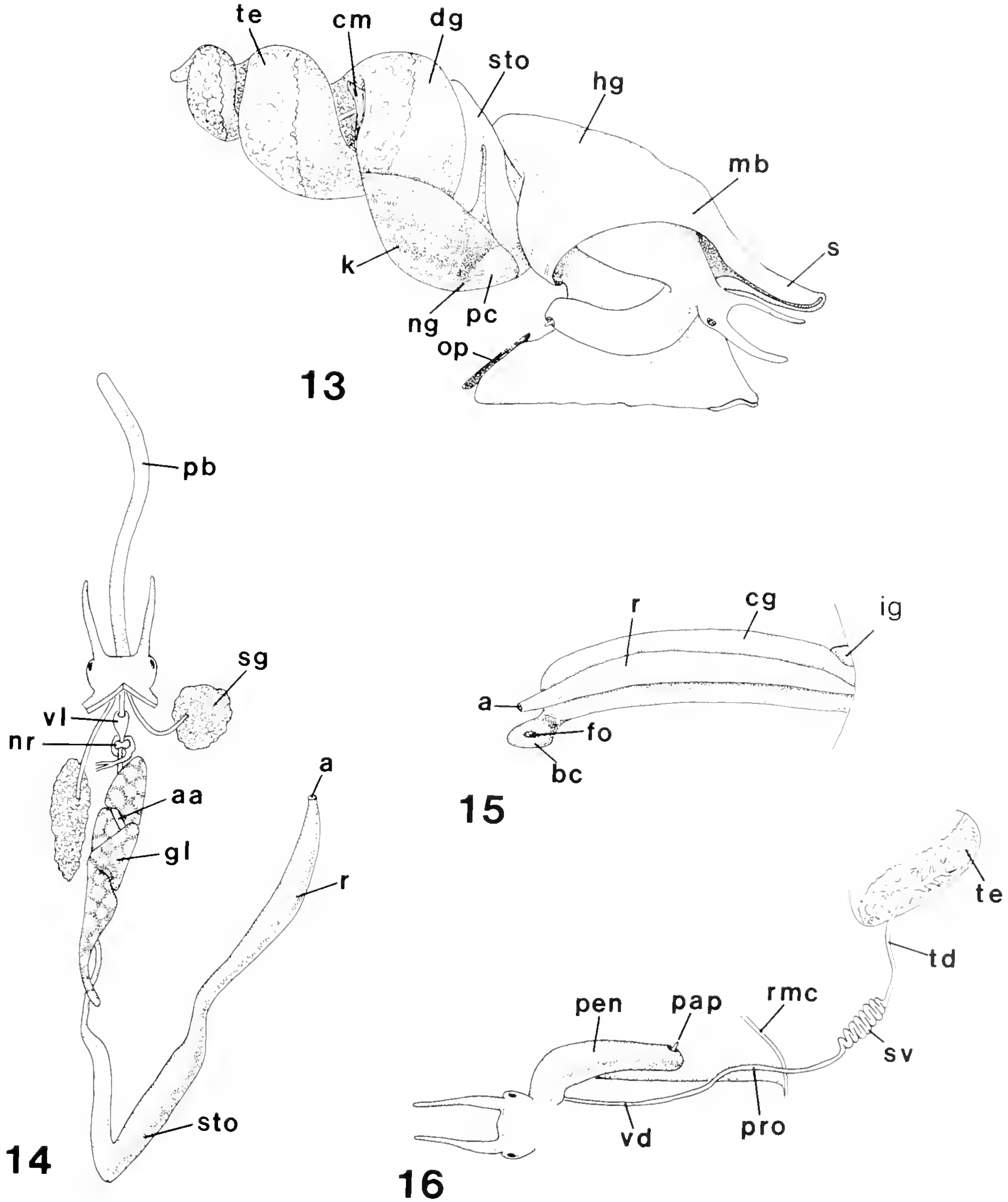
**Geographic range:** (figure 17) This species is presently known only from the northern and eastern Caribbean Sea, and from along the northern coast of South America.

←

**Figures 1–5.** *Manaria fusiformis* (Clench & Aguayo, 1941). **1.** USNM 875112, JSL-I sta. 2321, off west coast of Navassa Island 1.5 × **2.** Operculum of specimen in figure 1. 3.0 × **3.** Holotype of *Metula fusiformis* Clench & Aguayo, MCZ 135290, Atlantis sta. 3344, off Cienfuegos, Cuba in 2,633 m. 1.5 × **4.** USNM 811332, 150 miles north of Sao Luís, Maranhao, Brazil in 183 m. 1.5 ×. **5.** Holotype of *Mohnia kaicherae* Petuch, 1987, USNM 859855, off Los Monges Islands, off mouth of Gulf of Venezuela, Venezuela, 200 m. 1.5 ×. **Figure 6.** *Buccinofussus surinamensis* Okutani, 1982. Holotype NSMT Mo 60028, off Surinam. 1.0 ×



Figures 7–12. *[illegible]* Clench & Aguayo. **7.** Axial view of protoconch of juvenile specimen (USNM 854016). Scale bar [illegible] **8.** [illegible] view of same protoconch. Scale bar = 200 μm. **9.** Periostracum. Scale bar = 500 μm. **10.** Shell ultrastructure, [illegible] edge [illegible] whorl behind lip. Scale bar = 250 μm. **11.** Radular ribbon of juvenile specimen (USNM [illegible] right side. Scale bar = 5 μm. **12.** Radular ribbon of adult specimen (specimen in figure 1[illegible] [illegible]



**Figures 13–16.** Anatomical features of *Manaria fusiformis* (Clench and Aguayo). **13.** Male specimen, lateral view. **14.** Alimentary system. **15.** Female reproductive system. **16.** Male reproductive system. a, anus, aa, anterior aorta; bc, bursa copulatrix, cg, capsule gland, cm, columellar muscle; dg, digestive gland, fo, female opening, gl, gland of Leiblein, hg, hypobranchial gland, ig, ingesting gland, k, kidney; mb, muscular band of mantle; ng, nephridial gland, nr, nerve ring, op, operculum, pap, papilla, pb, proboscis, pc, pericardium; pen, penis; pro, prostate gland, r, rectum; s, siphon, sg, salivary gland, sto, stomach, sv, seminal vesicle, td, testicular duct; te, testes; vd, vas deferens; vl, valve of Leiblein.

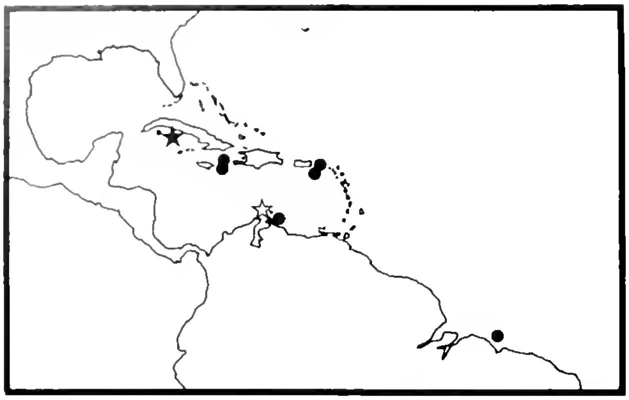


**Figure 17.** Geographic distribution of *Metula fusiformis*. Solid star denotes type locality. Open star denotes type locality of *Mohnia kaicherae*.

## DISCUSSION

Although originally described in the genus *Metula*, the generic placement of *M. fusiformis* Clench and Aguayo, 1941 has undergone considerable, if speculative, peregrination during the intervening decades. The radula of this species, with three-cusped rachidian teeth and two-cusped lateral teeth (figures 11, 12), differs from that of *Metula* H. and A. Adams, 1853 (Bouchet, 1988: fig. 1), and precludes the suggested affinities with *Fusinus* or any fasciolariid (Olsson & Bayer, 1972:925), or with *Euthriostoma* (Bouchet & Warén, 1986:485). This radula most closely resembles those of species in the genera *Eosipho* Thiele, 1929 and *Manaria* Smith, 1906 (Bouchet & Warén, 1986: figs. 13–17, 19–24). Ontogenetic changes in the morphology of the rachidian tooth of *M. fusiformis* include the broadening and lateral expansion of the basal plate, as well as the thickening and redirection of the cusps to a parallel orientation (figures 11, 12). Similar ontogenetic changes in *Manaria lirata* Kuroda and Habe, 1961 have been illustrated (Bouchet & Warén, 1985: figs. 20, 23). The presence of pronounced axial ribs overlaid by thick spiral cords, a spire that is more than half the shell length, and a well differentiated siphonal canal in *M. fusiformis*, in *Manaria thurstoni* Smith, 1906 (the type species of *Manaria*), and in several Japanese species of *Manaria*, as well as the lack of these features in *Eosipho smithi* (the type species of *Eosipho*) support the transfer of *Metula fusiformis* to the genus *Manaria*.

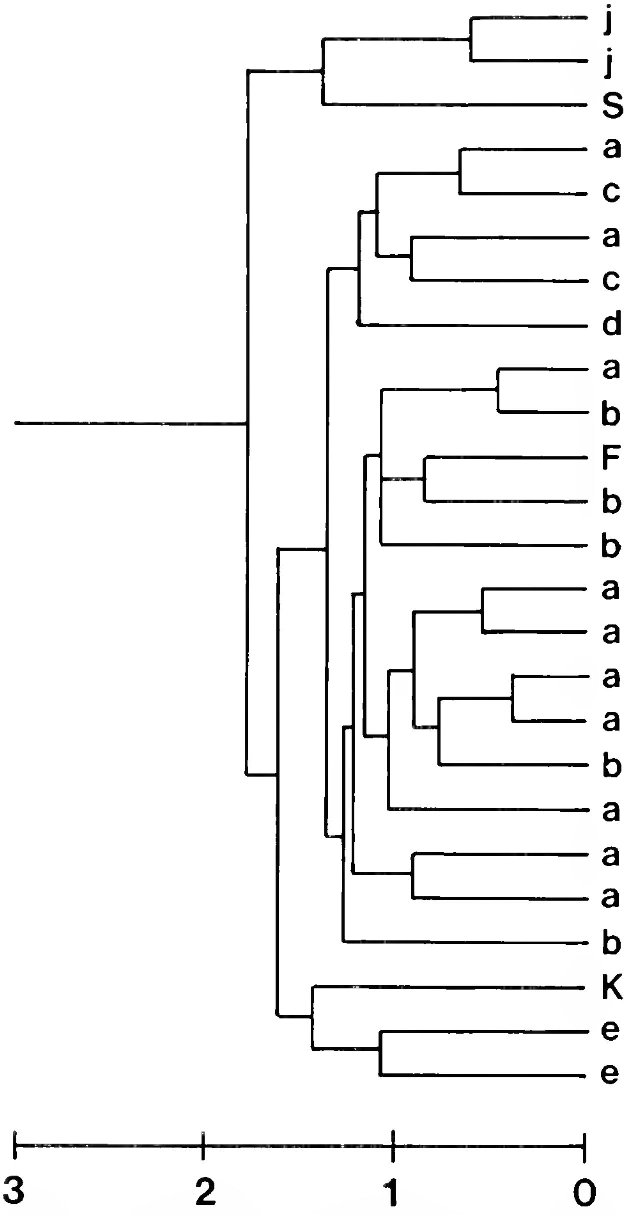


**Figure 18.** Phenogram of UPGMA clustering of Euclidean distances using standardized data. **a–e.** *Manaria fusiformis*. **a.** USNM 832953, St. Croix [10 specimens]. **b.** USNM 875112, Navassa [5 specimens]. **c.** USNM 832954, St. Croix [2 specimens]. **d.** USNM 811332, Brazil. **e.** USNM 854016, Navassa [2 juvenile specimens]. **F.** Holotype of *Metula fusiformis* Clench & Aguayo. **j.** Southern variant of *Buccinum canetae* described as *Plicifusus jamarci*. **K.** Holotype of *Mohnia kaicherae* Petuch. **S.** Holotype of *Buccinofusus surinamensis* Okutani.

A UPGMA phenogram (figure 18) of the 21 available specimens (including the holotype) of *Manaria fusiformis*, the holotypes of *Buccinofusus surinamensis* Okutani, 1982 and *Mohnia kaicherae* Petuch, 1987, as well as two specimens of *Buccinum canetae* (*jamarci* form), together with a plot of scores of the first two principal components for these specimens (figure 19) indicate that the holotype of *Mohnia kaicherae* falls within the range of variation of *Manaria fusiformis*. This holotype (figure 5, 18K, 19K), which has six teleoconch whorls, is intermediate in morphology between the two juvenile specimens of *Manaria fusiformis* (figures 18e, 19e), which have 3.8 and 4.0 teleoconch whorls, and the remaining adult specimens (figures 18, 19a–d), which have between 8.0 and 8.75 whorls. Thus, *Manaria fusiformis* can be seen to undergo allometric growth in shell and radular form.

The holotype of *Buccinofusus surinamensis* Okutani,

**Table 2.** Survey of the subfamilies of Buccinidae (according to Ponder & Warén, 1988) for morphologies of the gland of Leiblein (gL), sperm ingesting gland (ig), and number of cusps on rachidian teeth (rach). gL: 0 = absent, 1 = reduced or modified, 2 = large, glandular. ig: + = present, − = absent; ? = unknown

| | gL | ig | rach |
|---|---|---|---|
| Buccinidae | | | |
| *Manaria fusiformis* (herein) | 2 | + | 3 |
| *Penion* (Ponder, 1973) | 2 | + | 3 |
| *Serratifusus* (Harasewych, 1990) | 2 | + | 3 |
| *Buccinum undatum* (Dakin, 1912, Fretter, 1941) | 1 | + | >3 |
| *Neptunea (Golikov, 1963)* | 1 | − | 2, 3, >3 |
| *Retifusus tenuis* (Kosuge, 1967) | ? | + | 3 |
| *Tacita arnoldi* (Lus, 1981) | 2 | ? | 4 |
| *Volutopsius* (Kantor, 1990) | 0 | ? | 1, 3, >3 |
| *Thalassoplanes moerchi* (Lus, 1973) | 0 | ? | 1 |
| Nassariinae | | | |
| *Illyanassa obsoleta* (Brown, 1969; Fretter, 1941) | 1 | + | >5 |
| Melongeninae | | | |
| *Busycon carica* (Harasewych, 1982a) | 1 | − | 4–8 |
| *Melongena corona* (Harasewych, 1982a) | 0 | − | 3 |
| Fasciolariinae | | | |
| *Leucozonia nassa* (Marcus & Marcus, 1962) | 2 | + | 3 |
| *Microfulgur carinatus* (Ponder, 1970) | 2 | − | 3 |

1982, a species synonymized with *M. fusiformis* by Bouchet and Warén (1986:485), is more similar in shell morphology to *Plicifusus jamarci* Okutani, 1982 than to any specimens of *M. fusiformis*, and is therefore removed from the synonymy of *M. fusiformis*. In addition to being separable on the basis of the continuous characters listed in table 1, both *Buccinofusus surinamensis* and *P. jamarci* differ from *Manaria fusiformis* in having a substantially larger, chalky, white shell with deeply receding spiral lirae along the outer lip of the aperture.

The presence of a large, well-developed gland of Leiblein, simple, three-cusped rachidian teeth, and a female reproductive system with a distinct sperm ingesting gland between the albumen gland and the capsule gland in *Manaria* (herein), *Penion* (Ponder, 1973), and *Serratifusus* (Harasewych, 1990), represents a combination of characters uncommon within Buccinidae (table 2). Each of these features occurs widely throughout the Muricoidea (table 3), suggesting that these are plesiomorphic characters, and that the fusiform buccinids are among the more primitive members of the family Buccinidae.

Finally, it is suggested that the depth at which the holotype of *M. fusiformis* was collected (2,633 m) falls outside the bathymetric range of the species, and represents *post-mortem* transport of the shell into greater depths. All living specimens of *Manaria fusiformis* were taken between 183 m and 578 m, indicating that this species is a member of upper slope communities. Bathymetric zonation along the continental slope has been well documented (*e.g.*, Okutani, 1968), and bathymetric ranges of species have been found to be narrower on the upper slope than on the middle slope (Hecker, 1990).

**Table 3.** Survey of the families of Muricoidea (according to Ponder & Warén, 1988) for morphologies of the gland of Leiblein (gL), sperm ingesting gland (ig), and number of cusps on rachidian teeth (rach). gL: 0 = absent, 1 = reduced or modified, 2 = large, glandular. ig: + = present, − = absent. Reported features are present in some, but not necessarily in all, members of the listed families.

| | gL | ig | rach |
|---|---|---|---|
| Muricidae (Houston, 1976; Harasewych, 1984) | 2 | + | 3 major + minor |
| Turbinellidae (Harasewych, 1987) | 2 | + | 3 |
| Buccinidae | see table 2 | | |
| Columbellidae (Marcus & Marcus, 1962a, Houston, 1976) | 1 | − | 0 |
| Volutidae (Ponder, 1970a) | 2 | + | 3 |
| Olividae (Marcus & Marcus, 1959, Ponder & Darragh, 1975) | 2 | + | 3 |
| Harpidae (Bergh, 1901) | 0 | + | 3 |
| Marginellidae (Ponder, 1970b) | 1 | + | 1–20+ |
| Mitridae (Ponder, 1972, 1973a) | 0 | + | 3 or more |
| Volutomitridae (Ponder, 1972, 1973a) | 1 | + | 1 |
| Costellariidae (Ponder, 1972, 1973a) | 2 | + | 3 or more |

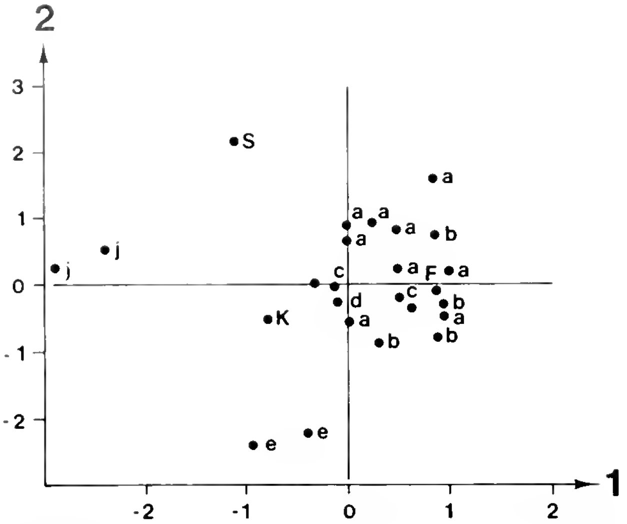


**Figure 19.** Plot of scores of first two principal components. Abbreviations as in figure 18

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# *Bellascintilla parmaleeana* New Genus and Species from the Tropical Eastern Pacific, with a Review of the Other, Ventrally Notched Galeommatid Genera (Bivalvia: Galeommatacea)

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## ABSTRACT

*Bellascintilla parmaleeana*, new genus and species, is described from the tropical eastern Pacific. It differs from *Divariscintilla maoria* Powell, 1932, in the morphology of the cardinal teeth, as well as the internal crenulation of the ventral margin of the valves, prominent exterior radiating sulcus, sculpture of commarginal striae, and in shell ultrastructure.

Four other ventrally notched galeommatids are redescribed on the basis of shell characters and shell ultrastructure: *Vasconiella jeffreysiana* (Fischer, 1873), from the northeastern Atlantic, *Divariscintilla maoria* Powell, 1932, from New Zealand, *Tryphomyax lepidoformis* Olsson, 1961, and *T. mexicanus* (Berry, 1959) from the tropical eastern Pacific. The general shell characters of the latter two species indicate these to be more closely allied with *Galeomma*.

*Divariscintilla yoyo* Mikkelsen and Bieler, 1989, and *D. troglodytes* Mikkelsen and Bieler, 1989, lack a ventral notch and are reassigned to the genus *Phlyctaenachlamys* Popham, 1939, based on shared characters of internal shell and morphology of shell, hinge, ligament, mantle, and ctenidia; however, the "flower-like organ" has not been reported in *Phlyctaenachlamys*.

*Key words:* ventrally notched galeommatids, systematics, anatomy, shell ultrastructure; *Phlyctaenachlamys*.

## INTRODUCTION

Galeommatid bivalves are small and easily overlooked, particularly because the living animals are often commensal with other kinds of animals, such as living attached to the walls of stomatopod burrows. Stomatopod burrows have not been adequately sampled for associated species of Mollusca. Galeommatid shells, however, are reasonably well represented in museum collections and have morphological characters that enable the definition of genera and species based on shell characters alone. One group of galeommatids has the shell ventrally notched in one or both valves. Until now the number of species known with this feature is four, and a total of three generic taxa have been introduced to accommodate them.

The objective here is to describe a new monotypic genus and species that is broadly distributed throughout the Panamic Province. This necessitated comparison with other ventrally notched galeommatids from the same faunal region and other regions of the world. The total number of taxa is sufficiently small to enable a full review of all species.

I have included descriptions of shell ultrastructure in addition to the conventional shell characters, providing an additional character set. The information derived from shell ultrastructure provides finer distinctions in support of the classification adopted here.

## MATERIALS AND METHODS

Specimens of *Vasconiella jeffreysiana*, *Divariscintilla maoria*, *Tryphomyax lepidoformis*, *T. mexicanus* and of *Bellascintilla parmaleeana* (LACM paratypes 2447 and 2448), were mounted on stubs, gold coated and examined with a Cambridge 360 scanning electron microscope (SEM) set at 20 kilovolts and a working distance of 10 mm. The holotype of *B. parmaleeana* (LACM 2446) was examined uncoated with SEM set at 2 kilovolts and a working distance of 6 mm.

Only a single valve of each genus was examined for shell ultrastructure because the ventrally notched galeommatid species are rare and few specimens are available for study. Examination of shell ultrastructure was conducted on adult valves that were broken radially from hinge line to ventral edge. It was generally possible to follow each of the shell layers described from umbo to ventral margin. Individual shell layers were observed at magnifications of 5,000 × and 10,000 ×. Photomicrographs were made in the central region of the shell that contained all the shell layers. Measurements of shell thickness were made in the central region of the shell,

**Table 1.** Comparison of shell characters of *Vasconiella*, *Divariscintilla*, *Tryphomyax*, and *Bellascintilla*.

| Character | *Vasconiella* | *Divariscintilla* | *Tryphomyax* | *Bellascintilla* |
|---|---|---|---|---|
| Ventral notch | present on right valve | present on both valves | present on both valves | present on both valves |
| Valve congruence | greatly inequivalve | equivalve | equivalve | slightly inequivalve |
| Exterior sculpture | right smooth, left with commarginal striae | smooth | cancellate | commarginal striae |
| Mid-valve sculpture | two radiating ribs fused by suture | radiating rib | radiating rib bound by sulci | two radiating ribs fused by suture |
| Interior sculpture | fine riblets on margin | minutely granulate | radiating ribs | crenulate margin |
| Position of beak & cardinals | central | anterior | central | anterior |
| Cardinals type | tubercular | tubercular | tubercular | cuniform |
| no. left | 2 | 0 | 2 | 2 |
| no. right | 1 | 1 | 1–2* | 2 |
| Laterals | | | | |
| no. left | 1 | 1 | 1 | 1 |
| no. right | 1 | 0 | 1–2* | 2 |
| Adductor | unknown | unknown | unknown | isomyarian |
| Ligament | unknown | amphidetic | resilium | resilium |

* Reflects a species level differentiation

using a vertical point-to-point feature. Characterization of individual layers of shell ultrastructure follows standards defined by Carter and Clark (1985). Shell dimensions were measured using a Zeiss zoom stereomicroscope with optical reticle.

For consistency, revised descriptions are given for each species.

The following institutional abbreviations are used: ANSP, Academy of Natural Sciences of Philadelphia; CAS, California Academy of Science; LACM, Los Angeles County Museum of Natural History; NMNZ, National Museum of New Zealand; SDNHM, San Diego Natural History Museum; SMNH, Swedish Museum of Natural History; USNM, National Museum of Natural History.

## SYSTEMATICS

Bivalvia Linnaeus, 1758
Heterodonta Neumayr, 1884
Veneroida H. & A. Adams, 1856
Galeommatacea Gray, 1840
Galeommatidae Gray, 1840
[= Galeomatidae Nordsieck, 1969]
[= Vasconiellidae Scarlato and Starobogatov, 1979]

Chavan (1969) treated the family Galeommatidae without subfamilial division, recognizing 24 genera (five of these questionably, with four others pronounced *genera dubia*), and 10 subgenera. Of these, only three genera possess a ventral notch at mid-valve position in one, or more commonly, both valves.

The new species described herein differs at the generic level. Its description follows the review of other ventrally notched galeommatids: *Vasconiella jeffreysiana* (P. Fischer, 1873), *Divariscintilla maoria* Powell, 1932, *Tryphomyax lepidoformis* Olsson, 1961, and *T. mexicanus* (Berry, 1959).

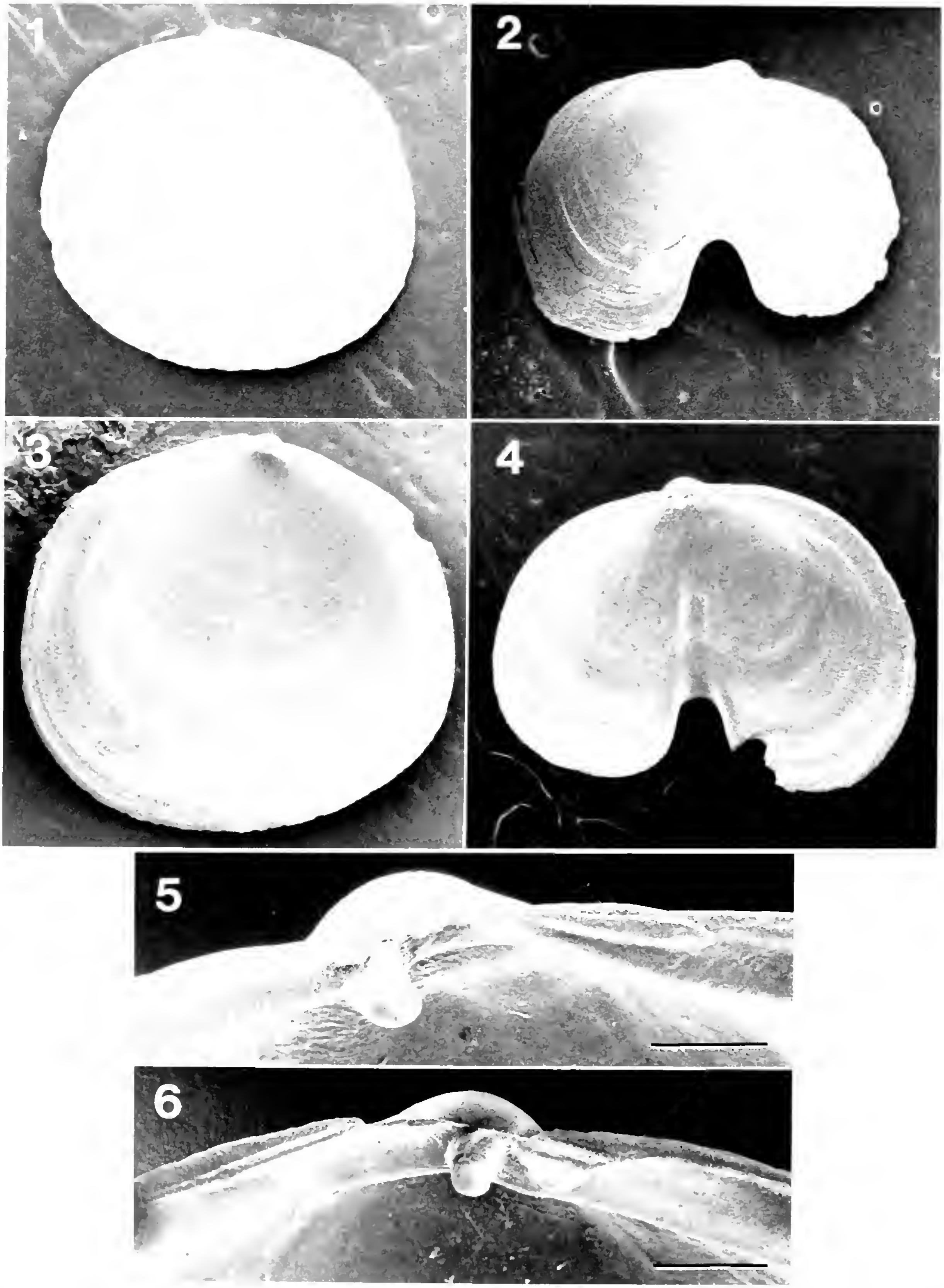
Key to the ventrally notched Galeommatidae:
(See table 1 for additional details)

1. Shell ventrally notched at mid-valve length in right valve only, left valve orbicular in profile . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Vasconiella*
   Both valves ventrally notched at mid-valve length 2
2. Shell exterior smooth, unsculptured, with single, small mid-valve rib; ventral notch broad and shallow . . . . . . . . . . . . . . . . . . . . . . . . . . . *Divariscintilla*
   Shell exterior sculptured, mid-valve rib prominent, ventral notch narrow and deep . . . . . . . . . . 3
3. Shell exterior sculptured with riblets and commarginal striae giving the exterior a cancellate appearance, mid-valve rib bordered on either side by minute sulci . . . . . . . . . . . . . . . . . . . *Tryphomyax*
   Shell exterior sculptured with fine commarginal striae only, mid-valve rib composed of two ribs fused together by a medial suture . . . *Bellascintilla*

### *Vasconiella* Dall, 1899

**Type species by original designation:** *Hindsia jeffreysiana* P. Fischer, 1873. The genus is monotypic.

**Diagnosis:** Highly inequivalve with left valve larger than right valve. Shell ventrally notched at mid-valve length in right valve only, left valve orbicular in profile. Two ribs, fused by a suture, ascend from mid-valve notch of right valve and rise to middle of central slope, left valve without such sculpture. Cardinal teeth tubercular.



**Figures 1–6.** *Vasconiella jeffreysiana* (P. Fischer, 1873) SMNH uncataloged. Sagres, Algarve Prov., Portugal, 17–33 m. **1.** Exterior of left valve, length 3.4 mm, Pontal dos Corvos, 17–22 m. **2–6.** Ponta dos Caminos, 23–33 m, sand. **2.** Exterior of right valve, length 3.5 mm. **3.** Interior of left valve, length 4.0 mm. **4.** Interior of right valve, length 3.8 mm. **5.** Hinge of right valve, scale bar = 200 µm. **6.** Hinge of left valve, scale bar = 200 µm.

one in right valve, two in left valve. One posterior lateral tooth present in each valve.

**Remarks:** The type species of *Vasconiella* was originally described in the genus *Hindsia* Deshayes, 1858, not H. and A. Adams, 1853, in which the type species has a geologic range of Paleocene to Upper Eocene. *Hindsia* was replaced by *Hindsiella* Stoliczka, 1871, and assigned to the Sportellidae by Dall (1899:876). The genus *Vasconia* Fischer, 1873, was another unnecessary new name for *Hindsia*; Fischer (1887) corrected this error. Dall (1899:875) was the first to recognize the need for generic separation of "*Vasconia*" *jeffreysiana*; the name *Vasconiella* was proposed in a provisional classification scheme without discussion.

### *Vasconiella jeffreysiana* (P. Fischer, 1873)
(figures 1–6, 31, 35)

*Hindsia jeffreysiana* P. Fischer, 1873:83, pl. 2, fig. 8, 1887: 1032–1033, fig. 776a,b

*Scintilla crispata* P. Fischer, 1873:83, pl. 2, fig. 7; P. Fischer, 1874:220, P. Fischer, 1878:178, Hildago, 1917:631; Aartsen, 1982:125.

*Vasconia jeffreysiana*; P. Fischer, 1874; de Folin and Perier, 1878:351; P. Fischer, 1878:178, Hildago, 1917:727.

*Lepton lepisma* Monterosato, 1878:314, Warén, 1980:46; Aartsen, 1975:467; 1982:125.

*Vasconiella jeffreysiana*; Dall, 1898:875; Pasteur-Humbert, 1962:53, pl. 19, fig. 75; Montero Aguera, 1971:58; Kisch, 1958:21–24, fig. 1, pl. 3; Nordsieck, 1969:91, pl. 14, fig 51.30, Chavan, 1969:537, figs. 35–7a,b; Aartsen, 1975:466–467; 1982:125; Bruggeman-Nannenga, 1975:14; Dekker, 1975:466; Mienis, 1975:441; 1976:522; Verduin, 1975:422, Bouchet, Danrigal, and Huyghens, 1978:126, pl. 5, fig. 17; Montero Aguera, 1971:58–59, Cornet, 1982:36–43, figs. 2–5; Mikkelsen and Bieler, 1989:189

*Solecardia* (*Scintillorbis*) *crispata*; Montero Aguera, 1971:223–224

**Material examined:** SMNH uncataloged, Pontal dos Corvos, Sagres, Algarve Prov., Portugal (37°01.3′N, 08°58.3′W), 17–22 m, base of cliff, May 1988, one left valve. SMNH uncataloged, Ponta dos Caminos, Sagres, Algarve Prov., Portugal (37°02′N, 08°52′W), 23–33 m, sand, May 1988, five right valves, one left valve. SMNH uncataloged, Sagres Harbor, Algarve Prov., Portugal (37°00.6′N, 08°55.6′W), 9–15 m, May 1988, one left valve. SMNH uncataloged, Baía Baleeira, Sagres, Algarve Prov., Portugal (37°00.7′N, 08°55.0′W), 12–17 m, sand, May 1988, one right valve.

**Description:** Right and left valves highly disparate, inequivalve by virtue of deep notch in ventral shell margin of right valve; ventral shell margin of left valve subcircular. Right valve attaining 4.2 mm in length and 3.0 mm in height; left valve larger, attaining 5.4 mm in length and 4.6 mm in height. Exterior of right valve smooth except for growth rings and two ribs joined together by suture radiating from umbo, becoming more raised where joining notch of ventral shell margin. Interior of right valve with corresponding sulcus radiating of ventral shell margin. Left valve subcircular in outline. Exterior surface smooth, with many evenly spaced commarginal striae on shell exterior from middle of valve to valve margin. Fine radiating riblets faintly impressed on ventral margin of interior of right valve, strongly impressed on ventral margin of interior of left valve. One tubercular cardinal tooth and one short posterior lateral tooth in right valve; two cardinal teeth in left valve, anterior cardinal wedge-shaped, posterior cardinal tubercular; one short posterior lateral tooth.

**Shell ultrastructure (figure 35):** Shell thickness of specimen studied 35 µm, consisting of five distinct layers. Exterior layer of thin, blocky simple prismatic structure, underlain by layer of fine-grained homogeneous structure; median and thickest layer of crossed-lamellar structure, underlain by fine-grained homogeneous structure; innermost layer of thin blocky simple prismatic structure.

**Distribution:** Bay of Biscay and Mediterranean Sea (Franc, 1960) to Morocco (Pasteur-Humbert, 1962), north to Plage de l'Aber, Kerfany les Pins and Quiberon on the French Atlantic coast (Aartsen, 1982).

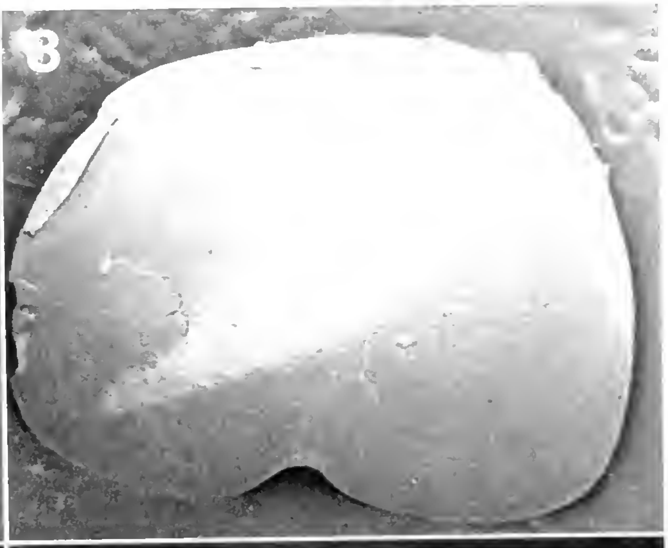
**Remarks:** The notched right valve of *Vasconiella jeffreysiana* was described by P. Fischer (1873) as *Hindsia jeffreysiana* while the unnotched left valve also was described by P. Fischer (1873) as *Scintilla crispata*. Kisch (1958) reported the discovery of to disparate valves joined together in a single specimen; however, he did not associate the name *S. crispata* with the left valve and described and illustrated the left valve as if for the first time. Cornet (1982), in a partial synonymy of *Vasconiella jeffreysiana*, was first to recognize and associate the left valve with the original description of *S. crispata*.

Cornet (1982) illustrated the hinge of both left and right valves and provided additional description of the hinge and exterior "deposit", but stated in error that "there are no true lateral teeth." Scanning electron photomicrographs of the hinge clearly show the presence of a short posterior lateral tooth in the right valve (figure 5), and a short posterior lateral tooth in the left valve (figure 6). The single cardinal tooth of the right valve fits beneath the two cardinal teeth of the left valve, and the lateral tooth of the left valve fits beneath the lateral tooth of the right valve, forming a very effective fulcrum and counterlocking hinge. SEM views of the mid-valve ridge (figure 31) show it to be two ridges fused together by a radial suture.

The anatomy of *Vasconiella jeffreysiana* was described in detail by Cornet (1982). No positive evidence for commensial association with stomatopods has been documented, however, Cornet (1982) noted that the distribution of *Vasconiella jeffreysiana* was congruent with that of *Lysiosquilla eusebia* (Risso, 1816).

### *Divariscintilla* Powell, 1932

**Type species by original designation:** *Divariscintilla maoria* Powell, 1932. The genus is monotypic.



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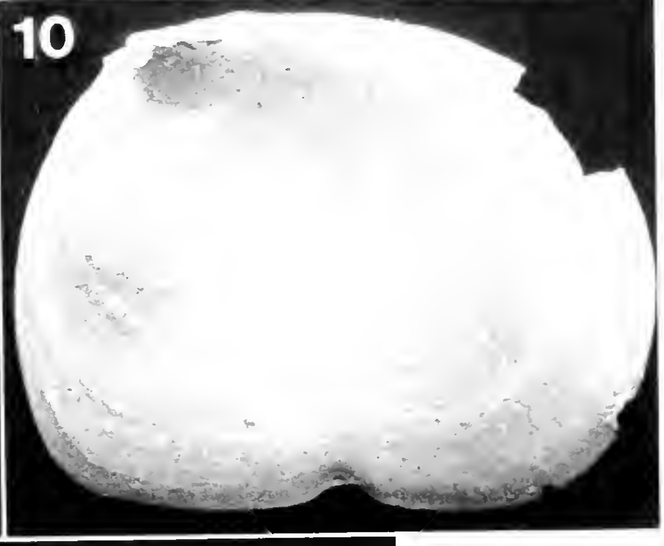

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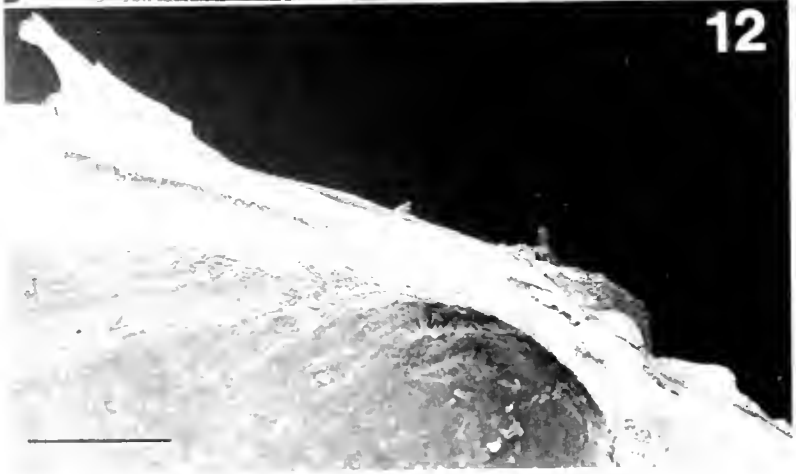

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**Diagnosis:** Both valves ventrally notched at mid-valve length, ventral notch broad and shallow. Shell exterior smooth, unsculptured, with single, small mid-valve rib beginning at mid-valve notch and ending on central slope. Two tubercular cardinal teeth in right valve, left valve without teeth.

### *Divariscintilla maoria* Powell, 1932
(figures 7–12, 32, 36)

*Divariscintilla maoria* Powell, 1932:66–67, pl. 6, fig. 1 [holotype, Auckland Museum]; 1962:122, Judd, 1971:343–353, figs. 1–7; Morton, 1975:365, 368, 1976:32; Mikkelsen and Bieler, 1989:175–195.

*Vasconiella* (*Divariscintilla*) *maoria*; Chavan, 1969:537; Powell, 1976:126.

**Material examined:** NMNZ M.21965, Cheltenham Beach, Auckland, New Zealand, from *Lysiosquilla spinosa* burrows, one left valve, one right valve, and two specimens with paired valves.

**Description:** Shell equivalve, inequilateral. The second largest of the ventrally notched galeommatids with both valves attaining 6.0 mm in length and 4.9 mm in height. Anterior end shorter than posterior as defined by notch on mid-ventral margin. Fine, week rib radiating from umbo to ventral notch in both valves, otherwise shell exterior with commarginal growth lines divaricating at radiating rib. Interior of valves minutely granulate, shell margin smooth; weak interior sulcus radiating from beak cavity to ventral notch and corresponding to external radiating rib. Ligament amphidetic, mostly posterior to beak supported by nymphs. Hinge of right valve with one tubercular cardinal tooth, anterior to large resilium (figure 11). Left valve lacking cardinal teeth, narrow horizontal resilifer under posterior side of beak; lateral tooth posterior to beak, terminating at terminus of nymph.

**Shell ultrastructure (figure 36):** Shell thickness of specimen examined 25 μm. Shell consisting of three distinct layers. Exterior shell layer of fine grained homogeneous structure; median and thickest layer consisting of intersected crossed platy structure; interior shell layer of irregular simple prismatic structure.

**Distribution:** Scattered shells have been found throughout New Zealand (Judd, 1971).

**Remarks:** Powell's (1932) description, although detailed, lacks mention of the following features. The ligament is described as being amphidetic without mention of a nymph. The ligament is primarily posterior to the beak where it is supported by a nymph (figure 12), yet the ligament does pass between the beaks, terminating slightly anterior to them where it is supported by a small nymph. Additionally, no mention [illegible] lateral tooth of the left valve, the granular interior of the valves, or the weak external rib that radiates from the umbo to the ventral notch (figure 32), with a corresponding sulcus on interior of valves.

Judd (1971) documented the anatomy, behavior and commensal relationship of *Divariscintilla maoria* with stomatopods.

### *Tryphomyax* Olsson, 1961

**Type species:** *Tryphomyax lepidoformis* Olsson, 1961 by original designation. The genus *Tryphomyax* presently contains two species: *T. lepidoformis* Olsson, 1961, and *T. mexicanus* (Berry, 1959).

**Diagnosis:** Shell quadrate or subovate with a prominent radial mid-valve rib from mid-valve notch to umbo bound on either side by minute sulci. Cancellate sculpture of exterior produced by radial riblets and commarginal striae. One or two tubercular cardinal teeth in right valve, two in left valve. One or two lateral teeth in right valve, one lateral tooth in left valve.

### *Tryphomyax lepidoformis* Olsson, 1961
(figures 13–16, 33)

*Tryphomyax lepidoformis* Olsson, 1961:240–241, pl. 36, figs. 4, 4a [holotype, ANSP 218922]; Keen, 1971:133–135, fig. 308, Bernard, 1983:30.

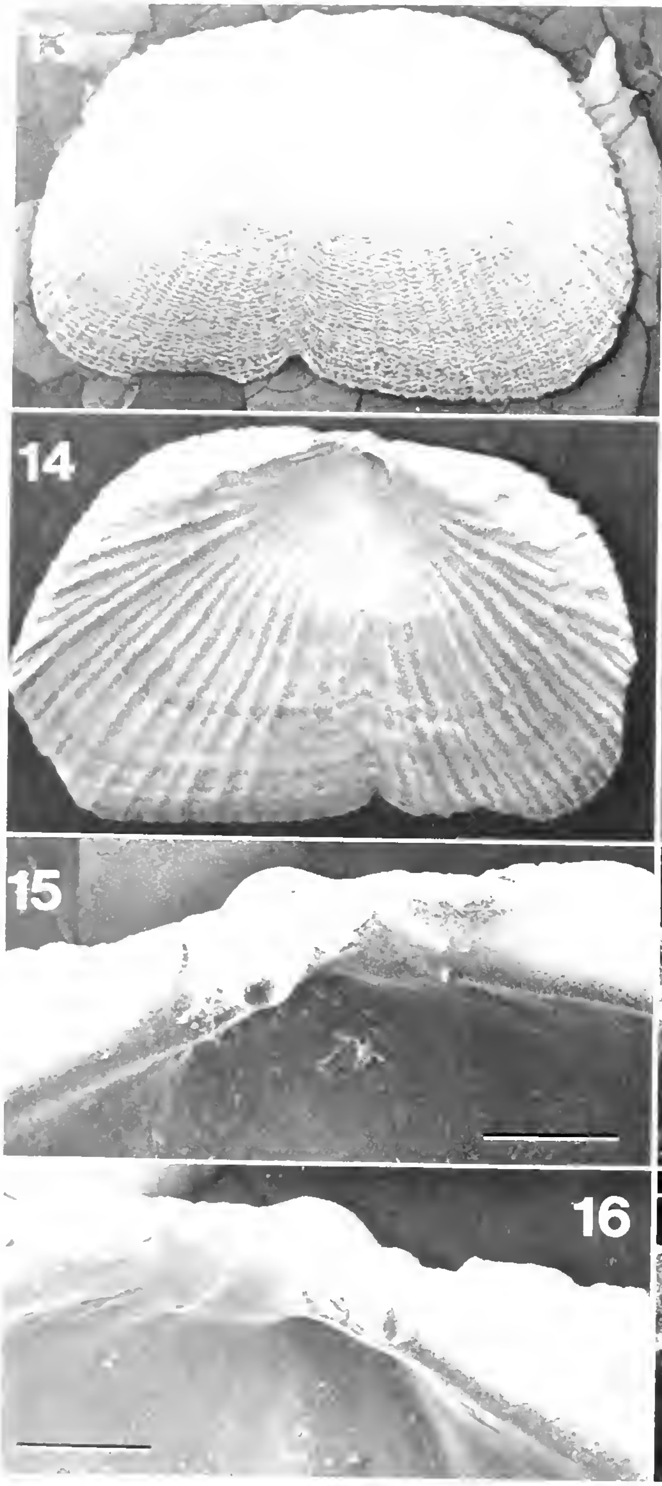
*Tryphomyax lepidoformis laevis* Olsson, 1961:241, pl. 36, figs. 7, 7b [holotype, ANSP 218923].

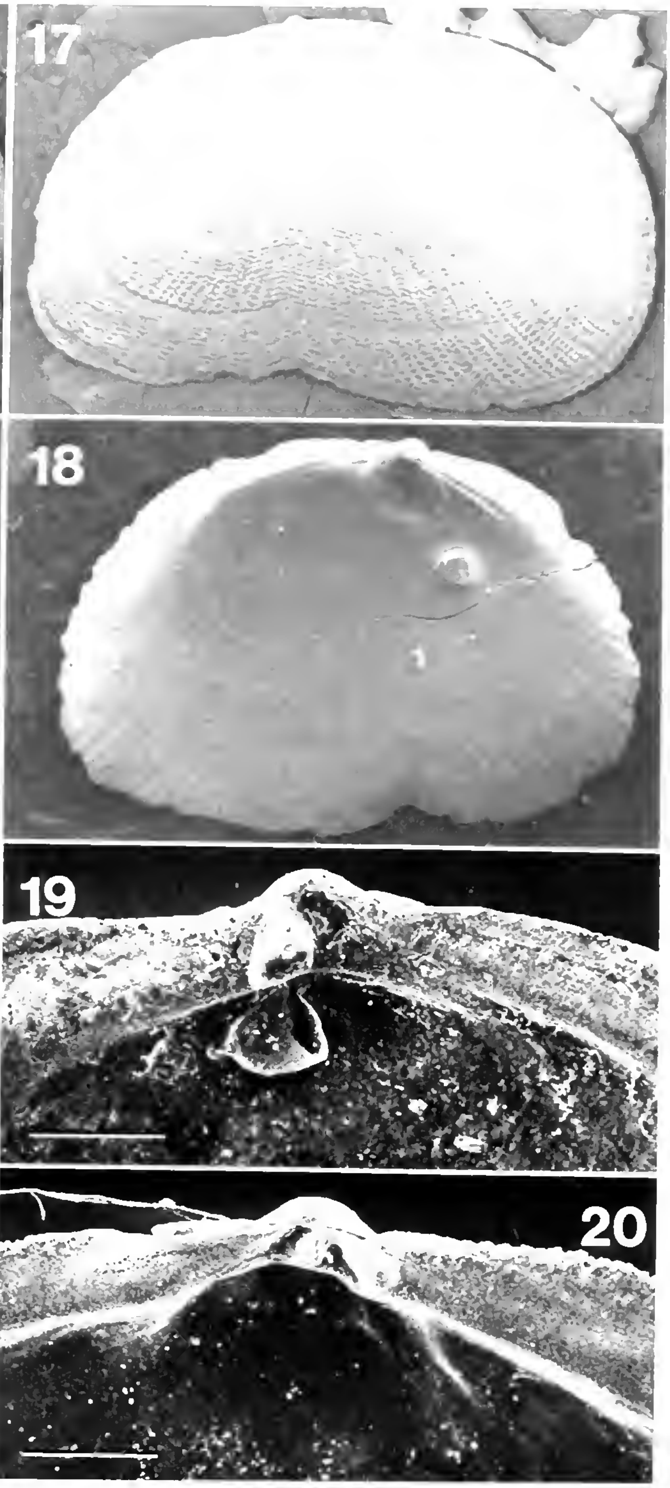
**Material examined:** LACM 77-144.4, Punta Chame, Golfo de Panama, Panama (08°41'N, 79°39'W), shallow dredging, two left valves. LACM 62-22.1, Bahía Cholla, W of Puerto Peñasco, Sonora, Mexico (31°19.6'N, 113°37.7'W), intertidal screenings, one right valve.

**Description:** Shell equivalve, inequilateral. Outline of shell rectangular. Anterior of valves shorter than posterior as defined by notch on mid-ventral valve margin. Wide, pronounced rib radiating from umbo to ventral notch in both valves (figure 33). Exterior of valves with regularly spaced riblets radiating from umbo and densely covered with thin, closely spaced commarginal multicostae. Interior of valves with regularly spaced, pronounced ribs radiating from umbo cavity, becoming slightly divaricated anteriorly; weak interior sulcus radiating from beak cavity to ventral notch and corresponding to external radiating rib. Ligament internal. Hinge of right valve with one large tubercular cardinal tooth and a smaller lamellar cardinal tooth anterior and dorsal to larger tooth; two very short lateral teeth located posterior to cardinal teeth; ventral lateral tooth descend-

←

**Figures 7–12.** *Divariscintilla maoria* Powell, 1932. NMNZ M.21965 Cheltenham Beach, Auckland, New Zealand, from *Lysiosquilla spinosa* burrows. **7.** Exterior of left valve, length 6.1 mm. **8.** Exterior of right valve, length 6.0 mm. **9.** Interior of left valve, length 5.0 mm. **10.** Interior of right valve, length 5.0 mm. **11.** Hinge of right valve, scale bar = 500 μm. **12.** Hinge of left valve, scale bar = 200 μm.





Figures 13–16. *Triphomyax lepidoformis* Olsson, 1961. **13–14, 16.** LACM 77-141.4, Punta Chame, Golfo de Panama, Panama. **13.** Exterior of left valve, length 5.4 mm. **14.** Interior of left valve, length 5.4 mm. **15.** LACM 62-22.1, Bahía Cholla, Sonora, [illegible] Hinge of right valve, scale bar = 200 μm. **16.** Hinge of left valve, scale bar = 200 μm.

Figures 17–20. *Triphomyax mexicanus* (Berry, 1959). **17.** LACM 65-82.1, N end Isla Cerralvo, Gulf of California, Baja California [illegible] valve, exterior, length 5.7 mm. **18, 20.** LACM 71-22.1, S of Punta Arena, Gulf of California, Baja California Sur. **18.** [illegible] of left valve, length 2.9 mm. **19.** LACM 66-21.3, from off Punta Arena, Gulf of California, Baja California [illegible] scale bar = 200 μm. **20.** Hinge of left valve, scale bar = 200 μm.

ing sharply from beak, dorsal lateral tooth approximately parallel to hinge margin; obscure resilifer posterior to tubercular cardinal tooth. Left valve with two cardinal teeth, anterior cardinal tooth tubercular, separated from posterior cardinal tooth by curved fossa, posterior cardinal tooth C-shaped, curved anteriorly; posterior lateral tooth descending sharply from beak, separated from posterior cardinal tooth by resilifer forming triangular fossa with apex reaching beak.

**Distribution:** A single valve is reported here from the head of the Gulf of California. This may have been due to a labeling error, as all other records are from Panama.

**Remarks:** This species is one of the rarest bivalves in the Eastern Pacific. It was reported by Olsson (1961) to occur in association with "worm tubes". Anatomy, behavior, and reproduction are unknown.

Although Bernard (1983) listed *Tryphomyax lepidoformis* Olsson as a synonym of *T. mexicanus* (Berry), both taxa are recognized here as distinct species. Comparisons with *T. mexicanus* are given below.

*Tryphomyax mexicanus* (Berry, 1959)
(figures 17–20, 37)

*Galeomma mexicanus* Berry, 1959 108–109 [holotype, CAS 043981, paratype, SDNHM 42813]; Hertz, 1984 18, fig. 35

*Tryphomyax mexicanus*: Keen, 1971 135, fig. 308, Bernard, 1983:30.

**Material examined:** LACM 69-21.4, W side Isla Miramar, S of Puertecitos, Gulf of California, Baja California, Mexico (30°04.8′N, 114°33.0′W), 15–26 m, sand, one left valve. LACM 69-22.3, W of Isla San Luis, S of Puertecitos, Gulf of California, Baja California, Mexico (29°57.80′N, 114°28.0′W), 26 m, sand, right valve (broken for shell ultrastructure after measurement). LACM 85-21.1, Juncalito, Gulf of California, Baja California Sur, Mexico (25°53′N, 111°20.5′W), beach drift, one right valve, one left valve. LACM 65-82.1, off N end Isla Ceralvo, Gulf of California, Baja California Sur, Mexico (24°23′N, 109°55.5′W), 9 m, one left valve. LACM 66-21.3, off Punta Arena, Gulf of California, Baja California Sur, Mexico (23°32′N, 109°28′W), 18–37 m, sand, one right valve. LACM 71-22.1, Los Tezos Ranch, 1.5 mile S of Punta Arena, Gulf of California, Baja California Sur, Mexico (23°31′N, 109°00′W), 9 m, one left valve.

**Description:** Shell equivalve, inequilateral. Largest of the ventrally notched galeommatids with valves reaching 6.4 mm in length and 4.0 mm in height. Outline of shell oblong and rounded, not rectangular. Anterior of valves shorter than posterior as defined by notch on mid-ventral valve margin. A weak rib radiating from umbo to ventral notch in both valves. Exterior of valves with irregularly spaced riblets radiating from the central slope to the ventral margin; densely covered with thin, closely spaced commarginal multicostae. Interior of valves smooth, except ventral margin, which is crenulate with small radiating riblets. Hinge of right valve with one large tubercular tooth, and posterior fossa for resilifer, both located under beak; one large lateral tooth posterior to resilifer. Left valve with two cardinal teeth; posterior cardinal tooth tubercular, arising from directly under the beak; anterior cardinal tooth lamelliform, descending at an angle from beak. Lateral tooth of left valve horizontal and parallel to dorsal hinge line.

**Shell ultrastructure (figure 37):** Shell thickness of specimen examined 59 μm, with a single distinct layer, consisting of very fine complex crossed-lamellar structure.

**Distribution:** Throughout the Gulf of California. Previously reported only from the head of the Gulf of California (Berry, 1959; Keen, 1971). The distribution is here extended south to Punta Arena, Gulf of California, Baja California Sur, Mexico. The more extensive distribution cited by Bernard (1983) from the head of the Gulf of California to Panama was a result of his synonomy of *T. lepidoformis* with *T. mexicanus*.

**Remarks:** This species differs from *T. lepidoformis* in profile, being rounded rather than rectangular, in both external and internal shell sculpture, and in having a different hinge structure. The posterior lateral teeth in the right valves are different in both number and relative size, *T. mexicanus* having a single large posterior lateral (figure 19 truncates prior to posterior terminus of lateral tooth due to accidental shell breakage) whereas *T. lepidoformis* has two small short posterior lateral teeth in the right valve. The primary distribution is more northern than that of *T. lepidoformis*, the records limited to the Gulf of California. Anatomy, ecology, behavior, and reproduction are unknown.

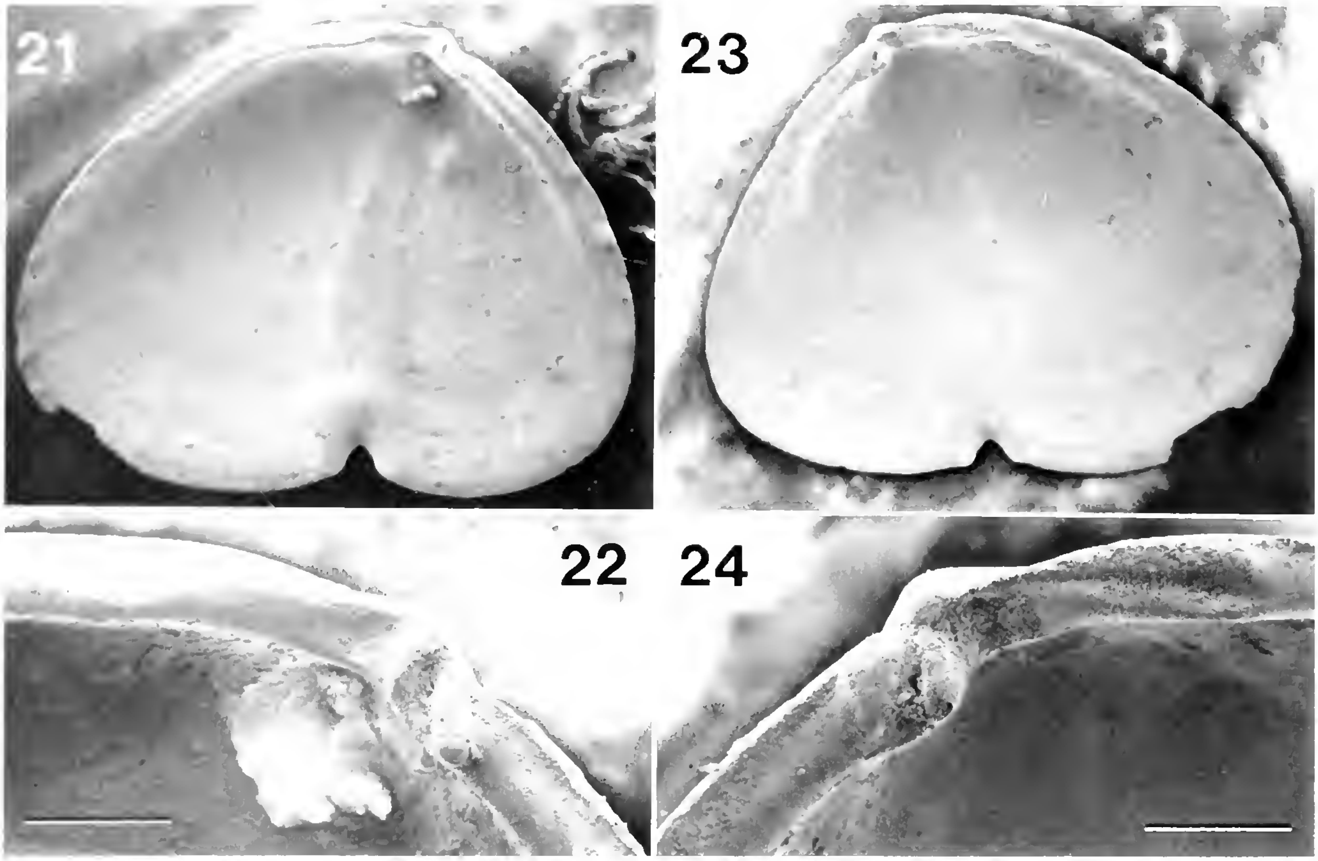
*Bellascintilla* new genus

**Type species, here designated:** *Bellascintilla parmaleeana* new species. The genus is monotypic.

**Diagnosis:** Shell subtriangular in outline with beaks anterior. Two distinct ribs fused together by medial suture arising from mid-valve notch, terminating abruptly on umbo. Shell sculptured with fine commarginal striae that ascends towards mid-valve ribs. Cardinal teeth cuneiform, two in each valve. One posterior lateral tooth in left valve, two posterior lateral teeth in right valve. Resilifer between cardinal teeth and lateral teeth.

**Etymology:** The name is a Latin compound derived from *scintilla*, spark, and *bella*, beautiful

**Remarks:** The smallest of the ventrally notched galeommatids, the shell attaining 4.5 mm in length and 3.5 mm in height. *Bellascintilla* (figure 38) differs from *Divariscintilla* (figure 36) in shell ultrastructure (thickest layer of crossed lamellar structure underlain by fine grained homogeneous structure rather than thickest layer of intersected crossed platy structure underlain by irregular simple prismatic structure as in *Divariscintilla*), being more like that of *Vasconiella* (figure 36), in exterior shell



**Figures 21–24.** *Bellascintilla parmaleeana* new species. Holotype, LACM 2446, off Bahía Herradura, Puntarenas Province, Costa Rica. **21.** Interior of left valve, length 3.2 mm. **22.** Hinge of left valve, scale bar = 200 μm. **23.** Interior of right valve, length 3.1 mm. **24.** Hinge of right valve, scale bar = 200 μm.

sculpture (fine commarginal striae, with small undulating ribs along posterior dorsal margin and ventral margin internally crenulate rather than essentially smooth, featureless sculpture as in *Divariscintilla*); in form and number of the mid-valve ribs (two fused together by suture rather than a single small rib as in *Divariscintilla*); and in the hinge teeth (cuniform rather than tuberculiform). Based on similarity of shell ultrastructure, and the formation of the mid-valve ridge, *Bellascintilla* also requires comparison to *Vasconiella*. These genera differ in left valve profile (triangular and ventrally notched rather than suborbicular and lacking a ventral notch as in *Vasconiella*), and in the morphology of their hinge teeth (cuneiform rather than tuberculiform). *Tryphomyax* and *Bellascintilla* do not share any of the features studied here other than the presence of a ventral notch.

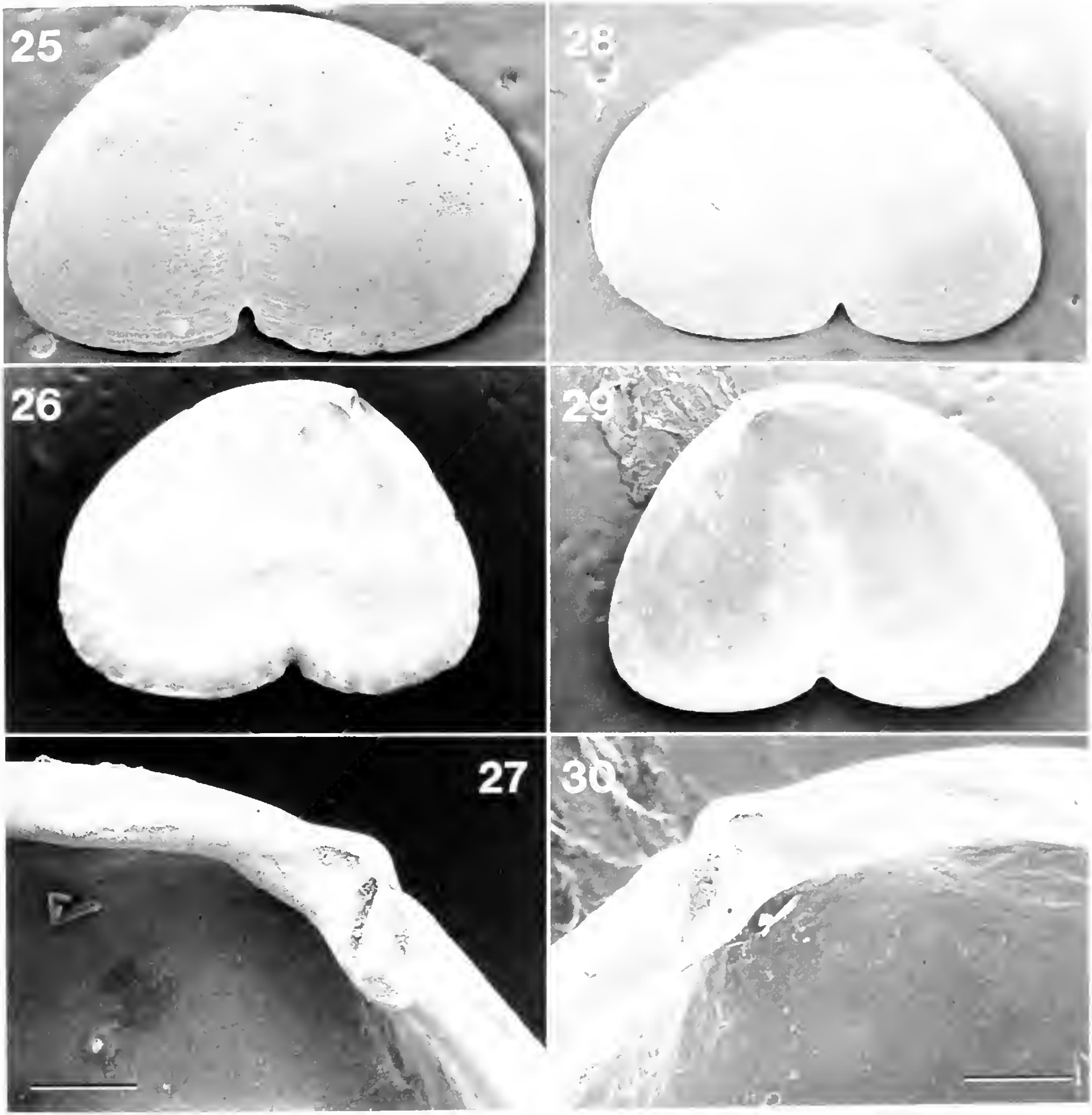
The discovery of a new species that shares with the type species of *Divariscintilla* the presence of a notch in the ventral margin of both valves initially suggested that *Divariscintilla* includes species possessing this specific character. Comparison of shell ultrastructure characters, and the formation of the mid-valve ridge, reveal that *Bellascintilla* is more closely related to *Vasconiella* than to *Divariscintilla*, despite the initial similarity of shell form between *Bellascintilla* and *Divariscintilla*. The hinge teeth of *Bellascintilla* are cuniform rather than tuberculiform as in *Vasconiella*, *Divariscintilla* and *Tryphomyax* suggesting that possession of a notch in the ventral valve margin could be convergent, or that the cuneiform teeth of *Bellascintilla* evolved from tuberculiform teeth of its ancestor.

*Bellascintilla parmaleeana* new species
(figures 21–30, 34, 38)

**Type locality:** Off Bahía Herradura, Puntarenas Province, Costa Rica (9°38.8′N, 84°40.8′W), 37 m (R/V SEARCHER station 451; LACM station 72-54).

**Type material:** Holotype: LACM 2446; articulating pair of valves, left valve length 3.2 mm (figures 21–22), right valve length 3.1 mm (figures 23–24), height both valves 2.4 mm.

LACM 2447, five paratypes, Isla del Cano, Puntarenas Province, Costa Rica (8°44.0′N, 83°52.5′W), 12 m, sand, R/V SEARCHER (LACM station 72-64): specimen *a*, left valve, length 3.6 mm, height 2.6 mm (figure 25); specimen *b*, left valve, length 4.1 mm, height 3.4 mm (figures 26–27); specimen *c*, right valve, length 3.1 mm, height 2.4 mm (figures 28, 34); specimen *d*, right valve length 3.4 mm, height 2.5 mm; specimen *e*, right valve length 3.5 mm, height 2.9 mm.

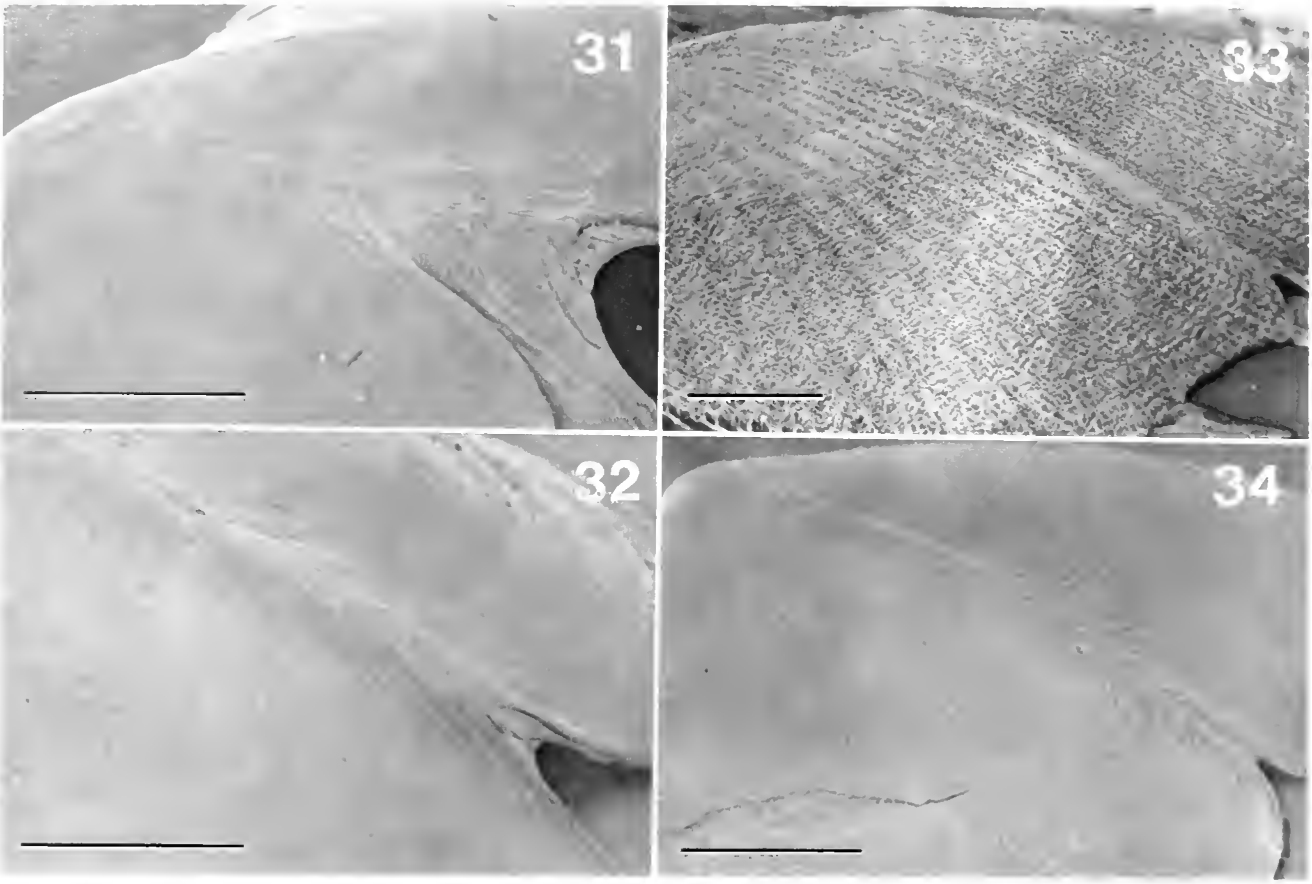


**Figures 25–30.** *Bellascintilla parmaleeana* new species. Paratypes, **25–28.** LACM 2447, Isla del Cano, Puntarenas Province, Costa Rica. **25.** Specimen *a*, exterior of left valve, length 3.6 mm. **26.** Specimen *b*, interior left valve, length 4.4 mm. **27.** Specimen *b*, hinge of left valve, scale bar = 200 μm. **28.** Specimen *c*, exterior of right valve, length 3.4 mm. **29–30.** LACM 2448, off Rancho El Tule and Rancho Palmilla, Gulf of California, Baja California Sur, Mexico. **29.** Interior of right valve, length 4.5 mm. **30.** Hinge of right valve, scale bar = 200 μm.

LACM 2448, paratype, between Rancho El Tule and Rancho Palmilla, Gulf of California, Baja California Sur, Mexico (22°58′N, 109°48′W), 18–37 m, sand (LACM station 66-17), right valve, length 4.5 mm, height 3.5 mm (figures 29–30).

LACM 2449, paratype, Playa Nancite, N side Golfo de Papaguayo, Parque Nacional Santa Rosa, Guanacaste Province, Costa Rica (10°48′N, 85°42′W), beach drift (LACM station 86-26), left valve, length 3.4 mm, height 2.5 mm.

LACM 2450, seven paratypes, Punta Chame, Golfo de Panama, Panama (08°41′N, 79°39′W), shallow dredging (LACM station 77-144), specimen *a*, right valve, length 4.2 mm, height 3.3 mm; specimen *b*, right valve, length 3.4 mm, height 2.7 mm; specimen *c*, right valve, length 3.5 mm, height 2.6 mm; specimen *d*, right valve, length



**Figures 31–34.** Comparison of mid-valve ribs. **31.** *Vasconiella jeffreysiana*, SMNH uncataloged, scale bar = 500 μm. **32.** *Dicariscintilla maoria*, NMNZ M 21965, scale bar = 500 μm. **33.** *Tryphomyax lepidoformis*, LACM 77-144.4, scale bar = 500 μm. **34.** *Bellascintilla parmaleeana* new species, paratype, LACM 2447, specimen *e*, scale bar = 500 μm.

3.3 mm, height 2.7 mm, specimen *e*, right valve, length 2.9 mm, height 2.3 mm; specimen *f*, left valve, length 4.1 mm, height 3.1 mm; specimen *g*, left valve, length 3.5 mm, height 2.9 mm.

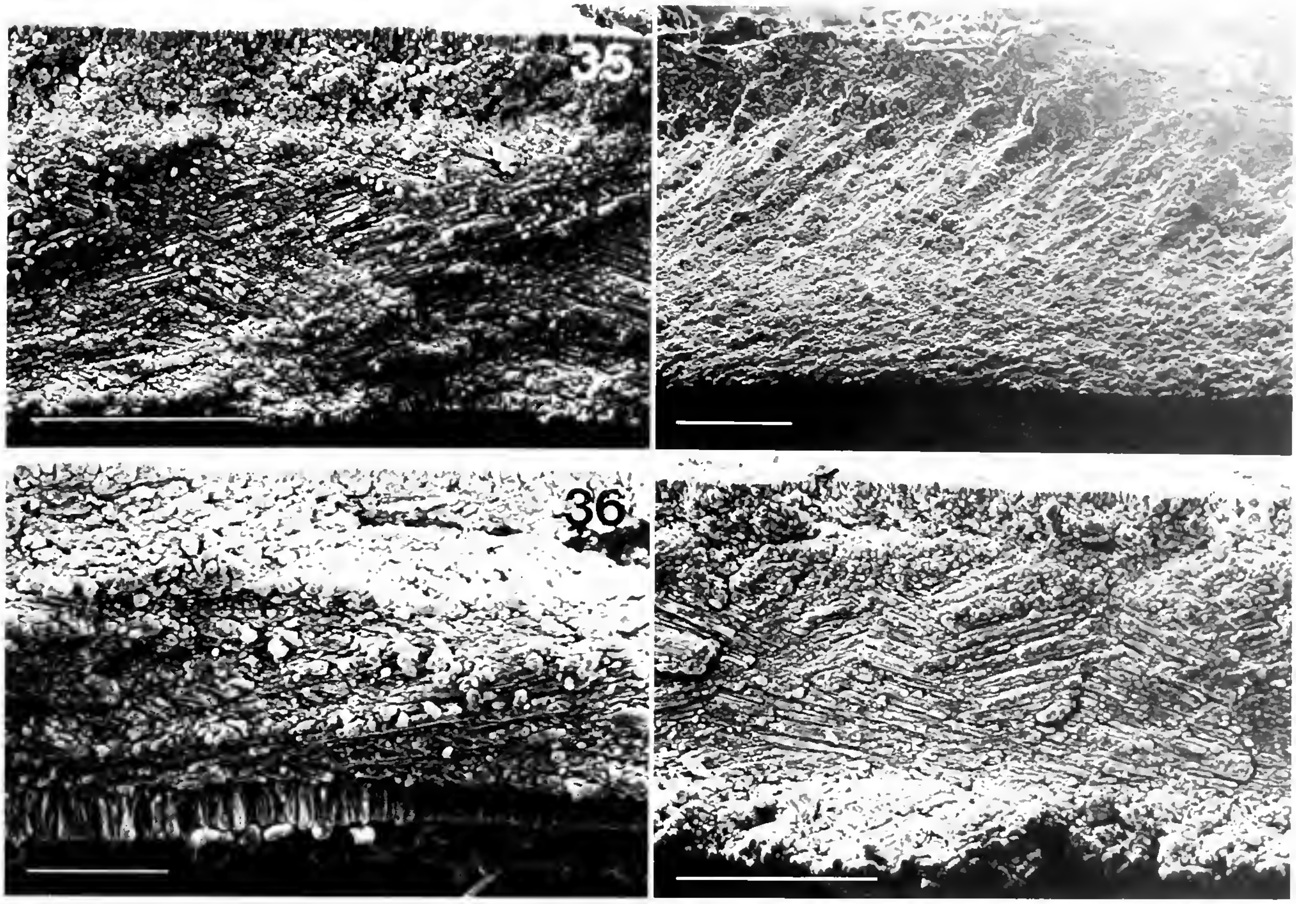
LACM 2451, paratype, N side Isla Salango, Manabi Province, Ecuador (01°35.5′S, 80°53.4′W), 6–12 m, under rocks and coral (LACM station 80-65), left valve, length 2.8 mm, height 2.1 mm.

USNM 859410, paratype from type locality, right valve, length 2.7 mm, height 2.0 mm.

**Description:** Shell inequivalve, inequilateral, very small (to 4.5 mm). Ligament an internal resilium. Left valve slightly longer than right valve. Left valve with two cuneiform cardinal teeth, posterior cardinal low, apex directly under beak, anterior cardinal with apex anterior to beak, widening as it descends, two cardinal teeth separated by narrowly radiating fossa. Resilifer separating cardinal teeth from posterior lateral teeth in both valves. Left valve with single downward curving lateral tooth. Right valve with two radiating cuneiform cardinal teeth, [illegible] immediately below beak, widening as they [illegible] teeth separated by deep fossa that widens as [illegible] Two posterior lateral teeth in right valve [illegible] resilium and cardinal teeth. Posterior and anterior adductor muscle scars equal in size, posterior adductor muscle scar located higher in valves than anterior adductor scar. Ventral margin of shell in both valves internally crenulate. Mid-ventral notch pronounced giving rise to a raised triangular fold that ascends dorsally to umbo. This interior, raised triangular fold corresponds externally to two ribs joined together by suture that arises from mid-ventral notch on ventral margin of exterior shell valve and ascends towards umbo. The fold truncates abruptly within 0.3 to 0.5 mm of umbo. Exterior sculpture of both valves with fine commarginal striae. Small undulating ribs radiating along posterior dorsal margin of shell, less developed along anterior shell margin.

**Shell ultrastructure (figure 38):** Shell thickness of specimen examined 37 μm, consisting of four distinct layers. Exterior layer of very thin, blocky, simple prismatic structure, underlain by layer of fine grained homogeneous structure; median, thickest layer consisting of crossed lamellar structure, underlain by layer of fine grained homogeneous structure.

**Distribution:** Rancho El Tule and Rancho Palmilla, Gulf of California, Baja California Sur, Mexico (22°58′N,



**Figures 35–38.** Comparison of shell ultrastructure. Exterior surface at top. SEM views taken on central slope of valves. **35.** *Vasconiella jeffreysiana*, SMNH uncataloged, scale bar = 20 µm. **36.** *Divariscintilla maoria*, NMNZ M 21965, scale bar = 10 µm. **37.** *Tryphomyax mexicanus*, LACM 69-22.3, scale bar = 20 µm. **38.** *Bellascintilla parmaleeana* new species, LACM 72-54 (from same lot as holotype), scale bar = 20 µm

109°48′W) to Isla Salango, Manabi Province, Ecuador (01°35.5′S, 80°53.4′W).

**Remarks:** Known only from dead valves. This species is the smallest of the ventrally notched galeommatids. Information concerning the anatomy, reproduction, behavior and commensal association, if any, of this bivalve is not available.

**Etymology:** Named in honor of Dr. Paul W. Parmalee, Director of the Frank H. McClung Museum and Professor of Zooarchaeology, Emeritus, University of Tennessee, Knoxville, Tennessee, who first inspired my interest in bivalve mollusks.

## DISCUSSION

The family Vasconiellidae was erected by Scarlato and Starobogatov (1979) to accommodate the ventrally notched genus *Vasconiella* Dall, 1899. Until the anatomy of more of the Galeommatidae has been studied and their relationships better understood, it seems premature to divide the Galeommatidae into subfamilies, much less additional families.

*Tryphomyax* shares with *Vasconiella* and *Divariscintilla* the tuberculiform cardinal teeth. However, the shell ultrastructures of these three genera exhibit major differences. Although the shell ultrastructure of *Galeomma* Turton, 1825, is unknown, the shell of *Tryphomyax* has a basic morphology suggesting affinity with *Galeomma*.

The presence of a ventral notch in the shell margin is the single shell character that genera *Vasconiella*, *Divariscintilla*, *Tryphomyax*, and *Bellascintilla* share in common. What is the purpose of the ventral notch, and does it serve the same function in all four genera? Powell (1932) believed the ventral notch to be "a true ventral byssus-sinus"; however, recent workers have demonstrated no correlation between the ventral notch and the byssus. Cornet (1982) showed that the outer and middle mantle of the right side, adjacent to the ventrally notched right valve of *Vasconiella*, formed a deep indentation whereas the inner mantle fold was straight. In *Divariscintilla* however, Judd (1971) reported that the mantle beneath the "slit" (ventral notch) was not "incised." As the structure of the mantle beneath the notch differs in these two genera, a functional similarity is regarded as unlikely. Judd (1971) demonstrated that the placement of the byssus on the foot of *Divariscintilla* was not anatomically correlated with the location of the ventral notch. He further reported that the ventral notch was completely absent from juveniles less than 2–3 mm in length, and did not develop until the shell was 3.5–4.5 mm. Cox (1969) stated that the byssus of early postlarval stages of many bivalves serves as an anchor and prevents larvae from suffocating by suspending the juveniles above the level of sediment deposition. Most bivalves lack a byssus, or it is vestigial, in the adult stage. The development of the ventral notch in *Divariscintilla* late in its life cycle may be taken as indirect evidence against the ventral notch functioning to accommodate the byssus. Other galeommatids that lack the ventral notch possess either a byssus or a byssal gland in the foot such as reported in *Phlyctaenachlamys* by Popham (1939). The function of the ventral notch in the four genera treated here remains unresolved.

*Tryphomyax* has the thickest shell (maximum thickness observed 59 μm), and is composed of only a single layer, which is structurally different from that of the other three ventrally notched galeommatids. *Bellascintilla* has a thinner shell (maximum thickness observed 37 μm), composed of four layers. The shell ultrastructure of *Vasconiella* is remarkably similar to that of *Bellascintilla*, but is thinner (maximum thickness observed 34 μm), and has an additional structural layer. Thus, *Vasconiella* has the most complex shell ultrastructure of the ventrally notched galeommatids studied to date. *Divariscintilla* has the thinnest shell of this group of galeommatids (maximum observed thickness 25 μm), composed of three layers that are unlike the ultrastructures of the other ventrally notched galeommatid genera. None of these genera conform to the shell ultrastructure reported by Taylor, Kennedy, and Hall (1973) for two species of *Scintilla* in terms of numbers of shell layers, or their composition. In contrast, they report finding two layers, an outer layer composed of crossed lamellar structure and an inner layer of complex crossed lamellar structure in *S. oweni* Deshayes and *S. rosea* Deshayes (Taylor *et al.*, 1973). Further investigation into the comparative shell ultrastructure of galeommataceans is warranted, both to provide characters for phylogenetic analysis as well as to examine possible variation within and between populations and environments.

In addition to a strong similarity in shell ultrastructure, *Vasconiella* and *Bellascintilla* show similarity in the formation of the mid-valve ridge, which in both genera exhibits two radiating ribs fused together with a suture between them. Prior to this study, *Vasconiella*, *Divariscintilla* and *Tryphomyax* were reported to have a single mid-valve radiating sulcus (Fischer, 1873; Olsson, 1961; Powell, 1932). Based on shell ultrastructure and the formation of the fused mid-valve ridges, *Bellascintilla* appears to be more closely related to *Vasconiella* than to either *Tryphomyax* or *Divariscintilla*, despite the differences of shell shape, hinge teeth, and zoogeography.

The hinge of *Bellascintilla* has some features in common with the family Leptonidae Gray, 1847 (*e.g.*, cuneiform cardinal teeth), and could conceivably be a primitive member of either family. It is therefore with some misgivings that I place *Bellascintilla* in the Galeommatidae. A clearer understanding of systematic relationships within the Galeommatacea will result when more information concerning the anatomy and shell ultrastructure of many of the genera becomes available. Because the definitions of the families in the Galeommatacea are not yet clarified (Ponder, 1971; Bernard, 1975), and in part because the anatomy and biology of *Bellascintilla* and *Tryphomyax* are unknown, the relationships of these four genera are subject to change as additional data becomes available.

I recognize a single species of *Divariscintilla*, the type species *D. maoria*. The two species described as *Divariscintilla yoyo* and *D. troglodytes* by Mikkelsen and Bieler (1989) are reassigned here to the genus *Phlyctaenachlamys* Popham, 1939. They share with *P. lysiosquillina* Popham, 1939, the type species of *Phlyctaenachlamys*, major conchological characters, including the unnotched ventral shell margin, hinge teeth and ligament morphology, shell ultrastructure, and anatomical characters including an internal shell, mantle morphology, and ctenidial morphology (see Mikkelsen & Bieler, 1989; Popham, 1939). As in *Phlyctaenachlamys lysiosquillina*, *P. yoyo* and *P. troglodytes* have shells that are equivalve, inequilateral, oval, flattened, and roundly elongate anteriorly. The hinge teeth and ligament are remarkably similar between the three species of *Phlyctaenachlamys*, but are quite different than those of *Divariscintilla maoria* Powell and *Bellascintilla parmaleeana*. The shell ultrastructure of *Phlyctaenachlamys lysiosquillina* is unknown. Mikkelsen and Bieler (1989) illustrate and describe the shell ultrastructure of *P. yoyo* and *P. troglodytes* as "cross-lamellar, with thin homogeneous layer on either side". This is somewhat similar to the ultrastructural arrangement of *Vasconiella* and of *Bellascintilla*, but is very different from the ultrastructural arrangement of *Divariscintilla*, and even more so from that of *Tryphomyax*. The shell of *Phlyctaenachlamys lysiosquillina* is internal (Popham, 1939), as it is in *P. yoyo* and *P. troglodytes* (Mikkelsen and Bieler, 1989). Only the anterior and posterio-dorsal margins of *Divariscintilla maoria* are covered by the mantle (Judd, 1971). The number and placement of mantle tentacles and defensive appendages is strongly similar between *P. lysiosquillina* and those of *P. yoyo* and *P. troglodytes* (see Mikkelsen & Bieler, 1989; Popham, 1939). There are two primary anterior tentacles in *P. lysiosquillina*, *P. yoyo* and *P. troglodytes* as illustrated by Popham (1939) and by Mikkelsen and Bieler (1989), although *P. troglodytes* has a second set of short anterior tentacles. *Divariscintilla maoria* has 6 to 8 large defensive appendages (Mikkelsen & Bieler, 1989) or posterior appendages (Popham, 1939), which are absent from *P. lysiosquillina*, *P. yoyo* and *P. troglodytes*. The ctenidia, usually an important source of phylogenetic information, are smooth in *Divariscintilla maoria*, but pleated in *P. lysiosquillina* (Popham, 1939) and in *P. yoyo* and *P.*

*troglodytes* (Mikkelsen & Bieler, 1989). The unusual "flower-like" organ of *Divariscintilla maoria* and those discovered in *P. yoyo* and *P. troglodytes* by Mikkelsen and Bieler (1989), were not reported by Popham (1939). Whether these "flower-like" organs were overlooked in *P. lysiosquillina*, or simply do not exist in this species, is unknown.

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# Malacology or Conchology?

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The choice of which of these two words to use depends not, as one might suppose, on etymology, priority, or the original intentions of the proposers, but on usage (and emotions!). The purposes of the present paper are to elaborate on these ideas, to record some apparently new insights on this old polemic, and to advocate use of *malacology*. This paper does not concern the pros and cons of studying living animals or shells.

The two competing terms for the study of the phylum Mollusca are *malacology* and *conchology*. To most modern biologists, *malacology* means the study of molluscan animals (soft bodies plus shells if present) and *conchology* means the study of just their shells. The Greek word *malakos* and the Latin word *molluscus* apparently are not cognates, although they both mean soft. The Greek *konche* means *either* snail or shell (whence the English conch). In two editions of an excellent, scholarly book on the history of shell collecting, S. Peter Dance (1966, 1986) has favored *conchology* for the study of whole mollusks. Dance quotes various authors to show that *konche* and its diminutive *konchylion* could mean a shell-bearing mollusk, not only its shell. I give reasons here for favoring the term *malacology*, in answer to Dance (1966, 1986).

The polarity is deep-seated. In the United States there are the American Malacological Union and the Conchologists of America. In the British Isles there are the Malacological Society of London and the Conchological Society of Great Britain and Ireland, etc.

The word *conchyliologie*, anglicized to *conchology* by da Costa (1776), was introduced in 1742 by the aristocratic cabinet naturalist Antoine Joseph Dezallier [or Desallier] d'Argenville in the book *L'Histoire Naturelle éclaircie dans deux de ses parties principales, la Lithologie et la Conchyliologie, dont l'une traite des Pierres et l'autre des Coquillages* (Paris). The book primarily concerns minerals, fossils, and shells. D'Argenville defined *concha* and *coquillage* as an animal with a shell ("coquille") plus its contained soft body or "fish" ("poisson"). Expressly excluded from the book are most "*mollusca*," which to him meant soft-bodied animals without shells. Curiously, d'Argenville illustrated six terrestrial slugs. There are also, besides molluscan shells, illustrations of echinoids, barnacles, organ-pipe coral (*Tubipora*), serpulid worms, etc. There were no illustrations of chitons, octopuses, squids, or cuttlebones.

The word *malacologie*, also French and anglicized in 1836 to *malacology* and apparently a contraction of *malacozoologie*, was one of two terms introduced in 1814, 72 years after d'Argenville, by the controversial and perhaps brilliant field naturalist Constantine Samuel Schmaltz Rafinesque. He meant by the term the study of "Mollusques" as he understood them ("Classe Malacosia"). His second word, *anopologie*, was for a broader study. (One wonders how serious he was.) Rafinesque had no companion term for the shell bearers (or Conchifera). It is likely that Rafinesque had more-or-less the same concept of "Mollusques" as Cuvier (1817), who included chitons and cephalopods in the group, but also ascidians, brachiopods and cirripedes. Characteristically, Rafinesque proposed malacologie in a now-very-rare booklet, this one verbosely entitled *Principes Fondamentaux de Somiologie ou les Loix de la Nomenclature et de la Classification de l'Empire Organique ou des Animaux et des végétaux contenant les Règles essentielles de l'Art de leur imposer des noms immuables et de les classer méthodiquement* (Palermo).

H. M. D. de Blainville (1825), in the text of his ***Manuel de Malacologie*** *et de Conchyliologie* (Paris and Strasbourg), did much to disseminate the word malacologie and to bring about use of the two terms in modern times. In two ways, de Blainville showed his preference for malacologie: his use of the two typefaces, and his stating that malacologie is a part of zoology while conchyliologie is an "art" (title page).

Both terms were proposed before the modern phylum Mollusca was conceptualized. But let us not have a new term! (testaceology, the study of shells, and molluscologie are already extinct).

D'Argenville was pre-Linnaean, but the binomial nomenclatural rule of priority is hardly operative. Original intentions and etymology seem more relevant, but unfortunately do not pertain. The first syllables of *mol*lusk and *mal*acology are conveniently similar. Quite properly, malacozoology had been part of zoology. Also, softness is common to the bodies of all mollusks, while shells are not. Rafinesque came closer to the modern concept of the Mollusca than d'Argenville, who (as shown above)

**Figure 1.** Constantine Samuel Schmaltz Rafinesque (1783–1840), who proposed the term *malacologie* in 1814. The authenticity of this portrait has been questioned (LaRocque, 1964).

**Figure 2.** Antoine Joseph Dezallier d'Argenville (1680–1765), who proposed the term *conchyliologie* in 1742. From the engraving in Favanne and Favanne (1780).

grouped in it a variety of shelly animals. In a later publication, Rafinesque did include cephalopods in his Mollusques. It is admitted that these are slender arguments for *malacology*. But is the case for *conchology* any better? Even though to an ancient Greek malacologia might have meant a discourse on anything soft, to me, a biologist, the term *malacology* is preferable to *conchology* for the modern branch of zoology concerning mollusks. However, the dual usage no doubt will continue.

I thank Professor A. J. Cain (via Dr. A. E. Bogan) for bringing to my attention Rafinesque's apology.

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