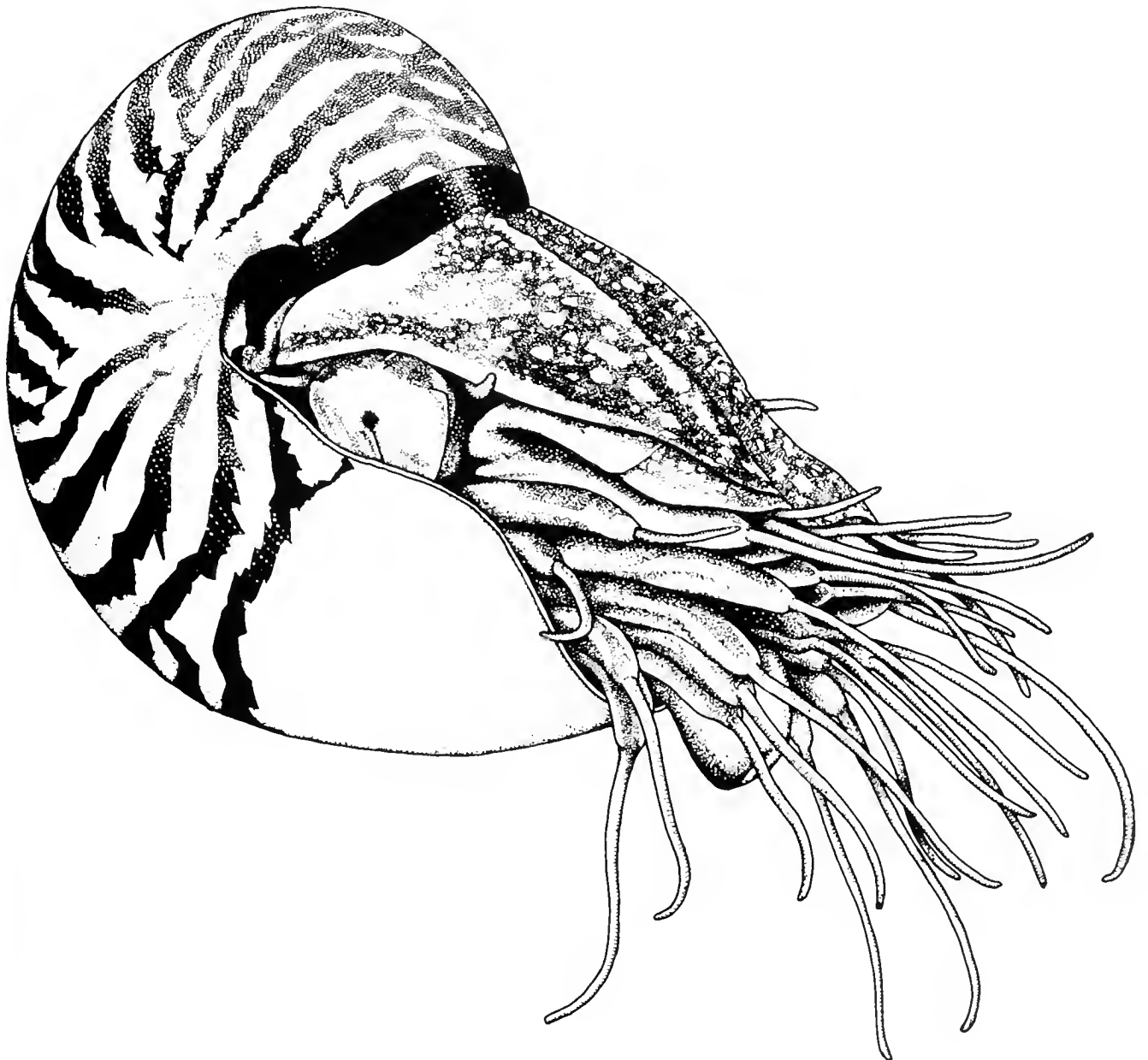


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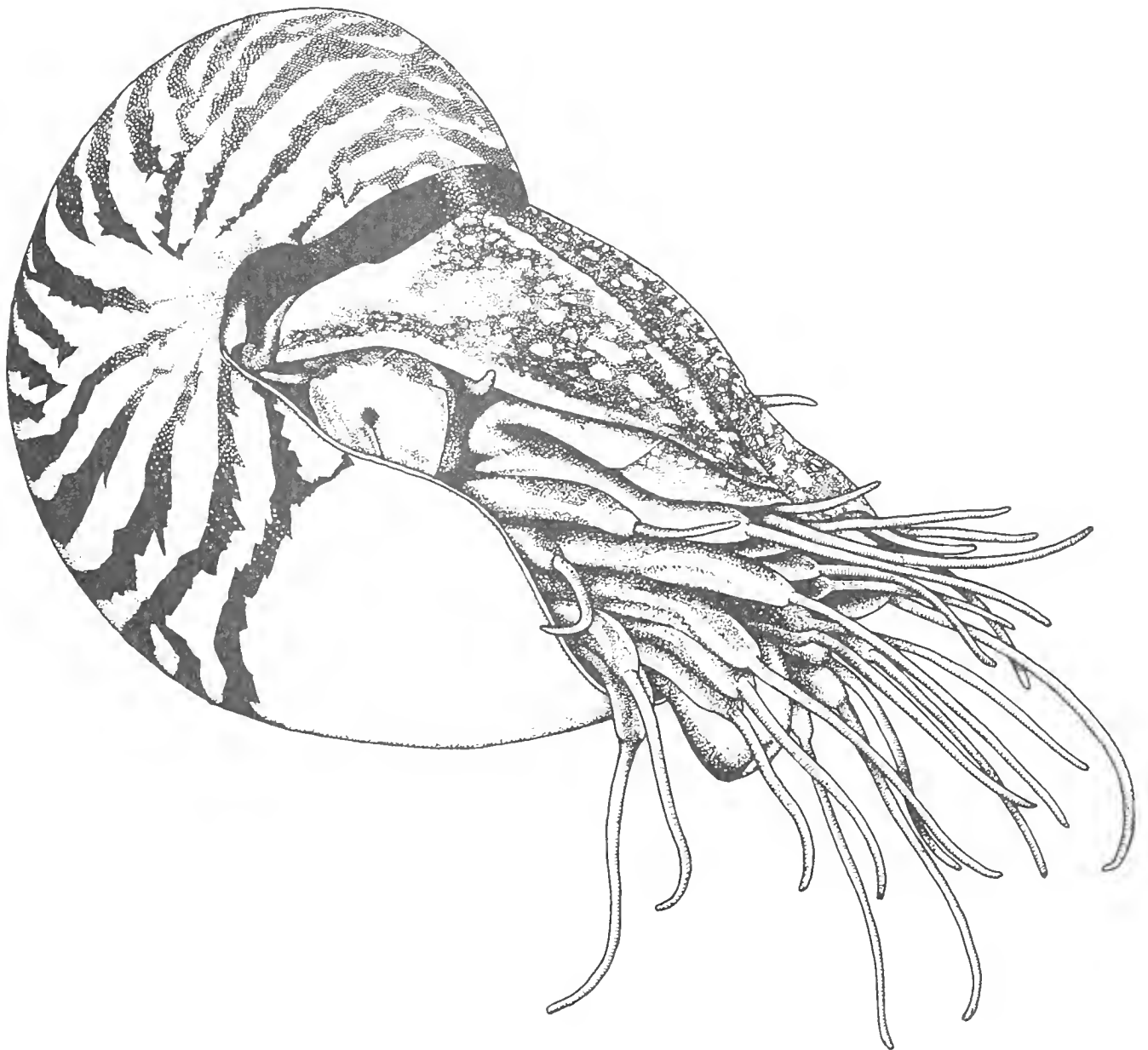
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Systematic Revision of *Allochroa* Ancey, 1887 (Pulmonata: Ellobiidae), with an Account of the Anatomy of *Allochroa layardi* (H. & A. Adams, 1855) and the Description of Two New Species

António M. de Frias Martins

Departamento de Biologia
Universidade dos Açores
P-9502 Ponta Delgada codex
São Miguel, Açores, Portugal

ABSTRACT

Of the nominal species of *Allochroa* Ancey, 1887 described to date, only two are recognized: *A. bronni* (Philippi, 1846), endemic to the Hawaiian Islands, and *A. layardi* (H. & A. Adams, 1855), distributed throughout the Indo-Pacific. Examination of the USNM collection revealed two additional species, *A. nana* Martins, n. sp. and *A. tenuis* Martins, n. sp., herein described. The anatomy of *A. layardi* is described and serves as the basis for determining the relationships of this genus within the Ellobiidae. *Allochroa* has a monaulic, entirely glandular pallial gonoduct and a wide visceral nerve ring with a long right parieto-visceral connective, confirming placement in the Pythiinae. Its close relationship to the Mediterranean and Eastern North Atlantic genus *Ovatella* Bivona, 1832 is indicated by similar apertural dentition, protoconch morphology of *A. tenuis*, and by the internal structure of the penial complex, where the penis appears as the development of one of the pilasters.

Key Words: Ellobiidae, Pythiinae, *Allochroa*, systematics, anatomy

INTRODUCTION

The Ellobiidae are a group of primitive, mostly halophilic pulmonate mollusks, commonly found near and above the hightide limit of mangroves, salt marshes, and boulder and cobble beaches. Morphologically very diverse and ranging in length from barely 1 mm (*Leuconopsis*) to about 100 mm (*Ellobium*), they nevertheless share basic shell characters and body features that allow them to be considered within a single family. Pfeiffer (1853) was the first to attempt a subfamilial organization, based on shell characters alone. He assigned those species with a thick, reflected outer lip to the Auriculae [=Ellobiinae], while he included the species with sharp outer lip in the Melampea [=Melampodinae]. Utilizing radular and also some anatomical characters, Odhner (1925) recognized a more complex subfamilial arrangement and redistributed the ellobiid genera among four additional

subfamilies: Carychiinae, Pedipedinae, Pythiinae and Cassidulinae. Odhner's outline was supported on conchological features by Zilch (1959). The first detailed use of anatomical characters, in a review that included species belonging to 11 genera, was by Morton (1955). His study supported Odhner's classification, but the Cassidulinae were included in the Pythiinae, on the basis of similarities of the reproductive system. In a study of species belonging to 17 of the 23 genera currently recognized in the Ellobiidae, Martins (in press a) clarified Morton's (1955) findings by redefining the subfamilial morphological patterns of the reproductive and nervous systems.

Preserved specimens of *Allochroa layardi* (H. & A. Adams, 1855) are used here as the basis for detailed anatomical investigations of the family extending the preliminary findings reported in Martins (in press b). Insight on the anatomy of *A. layardi* provided information needed to define the phylogenetic relationships of *Allochroa* Ancey, 1887 within the Pythiinae. The present work reviews the taxonomy of the species of *Allochroa* and describes the anatomy of *A. layardi*. Examination of the Mollusk collection at the National Museum of Natural History, Smithsonian Institution, consisting of only dry material, revealed the existence of two new species, herein described.

MATERIALS AND METHODS

This taxonomic revision is based primarily on dry specimens of *Allochroa* in the USNM collection. Four specimens of *A. layardi*, collected on Henderson Island in 1991, were provided for anatomical work. The fully retracted animals were preserved in alcohol and, except for the eyes and the tip of the tentacles, appear to have lost all other pigmentation. Two specimens were dissected under a binocular microscope and drawn using a camera lucida.

Shells with protoconchs were mounted using double-

coated tape. Radulae were stretched across a cover slip after cleaning with KOH solution. Both structures were mounted on stubs and examined and photographed using a Cambridge Stereoscan 250 Mk2 Scanning Electron Microscope.

Acronyms for specimen repositories are as follows:

ANSP:	The Academy of Natural Sciences, Philadelphia
BMNH:	The Natural History Museum, London
MCZ:	Museum of Comparative Zoology, Harvard University, Cambridge
MNHN:	Muséum National d'Histoire Naturelle de Paris
USNM:	National Museum of Natural History, Smithsonian Institution, Washington, D.C.

KEY TO THE SPECIES OF *ALLOCHROA* ANCEY, 1887:

- | | |
|--|--------------------|
| 1. Shell thick | 2 |
| Shell thin | 3 |
| 2. Aperture oval elongated (base narrow) | <i>A. brononii</i> |
| Aperture auriculate (base expanded) | <i>A. layardi</i> |
| 3. Shell length at least 4 mm | 4 |
| Shell length less than 4 mm | 5 |
| 4. Protoconch width less than .5 mm | <i>A. layardi</i> |
| Protoconch width at least .6 mm | 5 |
| 5. Protoconch without umbilicus and with apertural lip not reflected | <i>A. nana</i> |
| Protoconch with umbilicus and with apertural lip slightly reflected | <i>A. tenuis</i> |

SYSTEMATICS

Class GASTROPODA Cuvier, 1797
 Subclass PULMONATA Cuvier, 1817
 Order Archaeopulmonata Morton, 1955
 Family Ellobiidae H. & A. Adams in Pfeiffer, 1854
 Subfamily Pythiinae Odhner, 1925
 Genus *Allochroa* Ancey, 1887

Allochroa Ancey, 1887:288. Type species by original designation. *Auricula brononii* Philippi, 1846.

Description: Shell length to 12 mm, oval-conic, fragile to somewhat solid, sometimes hirsute. Umbilicus absent. Spire with up to 7.4 flat to slightly convex whorls, sculptured with more or less marked spiral lines; body whorl 55 to 80% of shell length, usually with three chestnut spiral bands over a whitish to light-brown background, the band just above the aperture consistently strongest, the one near the suture sometimes faint, the one near the columella largest, sometimes coalescing with the median band. Aperture about 50 to 60% of shell length, oval-elongated to semi-circular, angled posteriorly, rounded anteriorly, inner lip slightly reflected over the columella, with three more or less equidistant teeth: one oblique columellar tooth, a more or less horizontal anterior parietal tooth, and a sometimes strongest, oblique

posterior parietal tooth; outer lip sharp, usually with one prominent fold entering the aperture at about the level of the parietal teeth, forming a somewhat marked anal canal. Protoconch bulbous, smooth, with up to 1.3 whorls visible.

Radula: Central tooth narrow, base deeply emarginate, with two median flaring arms, unicuspid; lateral teeth with elongated, sinuous base with two projecting asymmetric arms, inner arm lower, crown large and long, subquadrangular; marginal teeth with sharp endocone gradually becoming as long as mesocone as row progresses outward, developing a sometimes conspicuous basal ectocone.

Anatomy: Reproductive system monaulic, pallial gonoducts entirely glandular, pallial gland present. Central nervous system with wide visceral ring; right parieto-visceral connective as long as left.

Remarks: The name *Allochroa* was proposed by Ancey (1887) to replace the supposedly preoccupied "*Laimodonta* des auteurs [H. & A. Adams, 1853] (non Nuttall)" (type species *Auricula brononii* Philippi, 1846). "*Laimodonta* Nuttall", wrongly taken as an emendation of *Laemodonta* Philippi, 1846, was restricted to a different assemblage (type species *Auricula striata* Philippi, 1846), following Nevill (1878). A more detailed account of the synonymy of *Laemodonta* and *Laimodonta* is presented elsewhere (Martins, in press a).

Ancey (1887) also made clear that *Marinula* King, 1832, very similar to *Pedipes* Scopoli, 1777, was not an eligible group for his new assemblage, and that *Monica* H. & A. Adams, 1855 [= *Ovatella* Bivona, 1832], although decidedly conchologically closely related, is restricted to Mediterranean and West Atlantic species.

Allochroa is conchologically characterized by the presence of an outer lip internal lamella which, in conjunction with the anterior parietal tooth, divides the aperture into two roughly equal halves: a posterior portion, where the shell is thinner; an anterior, thickened half, sometimes with an additional internal fold on the outer lip. The inner lip of the aperture is typically pythiine, i.e., roughly equidistantly tridentate, with one small columellar tooth and two parietal teeth. The lamellar, outer lip tooth readily separates this genus from the closely related *Laemodonta*, which usually has two round tubercles on the outer lip, and also from *Ovatella*, where the outer lip lamellae are much shorter. The single columellar tooth sets *Allochroa* apart from *Pedipes* which, as in *P. mirabilis* (Mühlfeld, 1816) and *P. pedipes* (Bruguière, 1789), has a strong, crest-like outer lip fold penetrating inside the aperture. In *Pedipes*, the single parietal tooth is very strongly pronounced.

The six species assigned by authors to *Allochroa* are here synonymized into two: the Hawaiian *Allochroa brononii* (Philippi, 1846) and the Indo-Pacific *Allochroa layardi* (H. & A. Adams, 1855). Two additional new species are described herein.

Kuroda and Habe (1952) listed *Pedipes affinis* Férussac, 1821, under *Allochroa*, owing probably to the presence of a strong lamella inside the outer lip. Férussac

(1821), however, had mentioned a bidentate columella as characteristic of *Pedipes*, and Ancey (1857) also used this feature of *P. affinis* to separate it from *Laemodonta*, where Jickeli (1874) had erroneously placed it. Following the above reasoning, I concur with Ancey (1857) in considering Férussac's species a *Pedipes*.

Similarly, the New Caledonian *Pedipes forestieri* Souverbie and Montrouzier, 1864, has been erroneously assigned to *Allochroa* (Franc, 1954; Smith, 1992). In the original description Souverbie and Montrouzier (1864a) mentioned the presence of two columellar teeth, stating that their observations were based on a single, probably juvenile specimen. In a later paper (1864b) the same authors, reacting to the epistolary comment of L. Pfeiffer on that subject "*Spec. nov., sed Marinula*", changed the taxonomic combination to "*Marinula* (an *Pedipes*?)", cautiously justifying, however, their original generic choice by pointing out features such as "1) shell positively striated transversely; 2) two positively columellar folds; 3) external border of the columellar lip contouring behind the upper columellar fold as in *Pedipes mirabilis*, Mühlf., which we possess." The accompanying figure (Souverbie & Montrouzier, 1864a: pl. X, fig. 1) appropriately illustrated their reasoning. Franc (1954) claimed to have found an adult specimen of Souverbie and Montrouzier's species in the Jousseume collection at the MNHN, and assigned it to *Allochroa*. The redescription of *Pedipes forestieri* provided by Franc (1954), mentions the presence of a spiral fold inside the outer lip characteristic of *Allochroa*, but corroborates the presence of "two columellar folds closer to each other than to the parietal", a feature diagnostic of some pedipedine genera, namely *Pedipes* and *Marinula*. Taking into account Souverbie and Montrouzier's (1864a, b) insistence on the pedipedine characteristics of the apertural dentition, a feature confirmed by Franc (1954), and in my inability to examine the type material, I consider the assignment of *Pedipes forestieri* to *Allochroa* to be unwarranted.

The similarity of the basic patterns of shell morphology and color throughout the genus creates some difficulties in separating species. Larger specimens of the highly variable, widely distributed *A. layardi* overlap in shape and color with smaller specimens of the Hawaiian *A. bronnii* (compare Figs. 1 and 5). At the other extreme, thin, less distinctly banded forms of *A. layardi* could be confused with lighter specimens of *A. tenuis*, n. sp. (compare Figs. 10 and 19). However, species can be readily separated on the basis of other conchological characters such as the ratio number of whorls/shell length or using protoconch features.

Allochroa bronnii (Philippi, 1846)

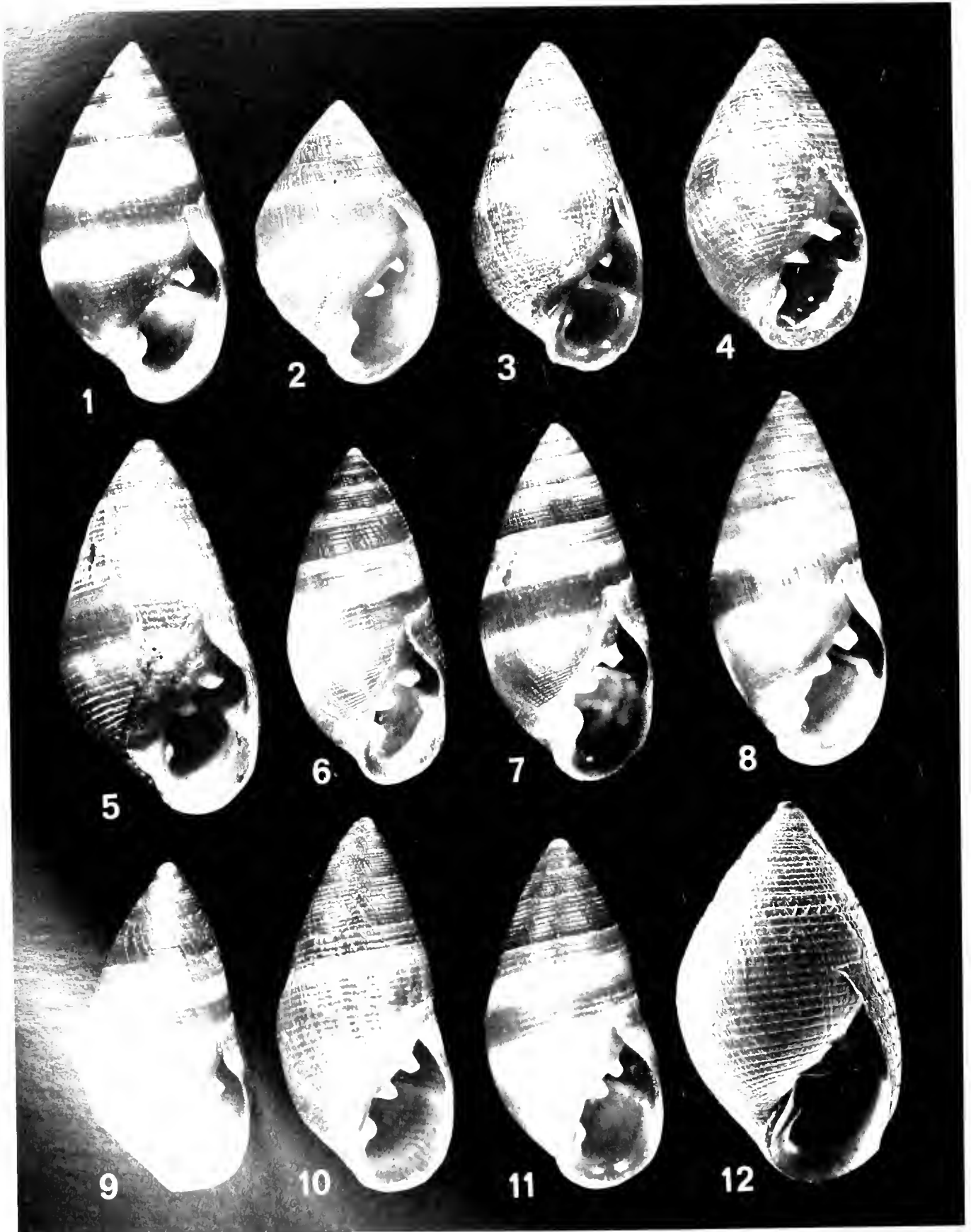
Figures 1–2, 21, 31–32

Auricula bronnii Philippi, 1846:98 [Hawaiian Islands; location of type unknown]. *Auricula sandwichiensis* Souleyet, 1852: 524, pl. 29, figs. 29–32 [Hawaiian Islands; type not found, supposedly at BMNH (Gray, 1855)]. *Ophicardelus (Laimodonta) sandwichiensis* (Eydoux & Souleyet). H & A. Adams, 1855a: 34 [misspelling of *sandwichiensis*]. *Melam-*

pus bronnii (Philippi). Pfeiffer 1854:147. *Ellobium brownii* (Philippi). H. & A. Adams, 1855b:237 [misspelling of *bronnii*]. *Laimodonta sandwichiensis* (Eydoux & Souleyet). H. & A. Adams, 1855b:246, pl. 83, figs 1, 1a [misspelling of *sandwichiensis*]. *Melampus sandwichiensis* (Souleyet). Pfeiffer, 1856:50. *Ophicardelus sandwichiensis* (Eydoux). J. E. Gray in M. E. Gray, 1859:(3), pl. 304, fig. 2, (4):118. *Laemodonta bronnii* (Philippi). Martens & Langkavel, 1871: 57. *Marinula (Laemodonta) bronnii* (Philippi). Nevill, 1878: 220. *Allochroa bronnii* (Philippi). Ancey, 1887:288. *Tralia (Laemodonta) bronnii* (Philippi). Crosse, 1894:321. *Melampus (Laimodonta) bronnii* (Philippi). Kobelt, 1898: 200, pl. 23, figs. 1, 2. *Laimodonta bronnii* (Philippi). Dautzenberg & Fischer, 1905: 107.

Description: Shell (Figs. 1–2, 21) length to 12 mm, ovate-conical, somewhat solid; violet-brown to light-brown, banded. Spire moderately high with up to 7.4 flattened whorls, with marked spiral striae crossed by irregular growth lines that give the surface a matte appearance; one light-brown subsutural band, a median white band followed by a dark-brown band. Body whorl averaging 60% of shell length, sculptured as spire; coloration pattern showing a subsutural light-brown band followed by a marked, white, narrow band halfway between the suture and the aperture, a wide, dark-brown band extending just below the posterior apertural angle, a whitish to brownish band as wide as the previous one gradually merging with the dark-brown, anteriormost band that extends to the anterior tip of the aperture. Aperture oval-elongated, rounded anteriorly, acute posteriorly; inner lip with three subequidistant teeth: one oblique columellar tooth faintly continuous with a callus that runs along the anterior border of the aperture and connects to the tip of the outer lip tooth; two parietal teeth, the anterior one half the length of the aperture, perpendicular to the columellar axis and continuing inward; the posterior one usually strongest, not continuing inward; outer lip sharp, with a ridge-like tooth about opposite the anterior parietal tooth, penetrating inside the aperture for about half a whorl; a wide callus develops anterior to the outer lip tooth. Protoconch 235x155 μm , whitish, smooth, somewhat inflated, barely over one whorl, with elongated, narrowing lip (Fig. 21).

Radula: (Figs. 31–32) Formula [3]+24+1+24+31] $\times 100+$. Central tooth slightly above the plane of the lateral teeth; base narrow, subquadrangular, deeply emarginate with medial lateral projections flaring out; crown less than half the length of the lateral teeth, narrow, unicuspid; mesocone somewhat sharp. Lateral teeth 24, base elongated, slightly bent medially, with lateral projections flaring out asymmetrically, the inner projection smaller, at about the first third of the base, the outer one at about mid-length of the base; crown covering three quarters of base, quadrangular, with a longitudinal depression in the middle. Marginal teeth 31; basis barely longer than crown, diminishing gradually to completely disappear under crown, developing a basal ectocone; crown bicuspid, endocone sharp, short on first teeth, gradually elongating towards the end of the row, mesocone long and narrow, blunt at tip.



Remarks: The Hawaiian *Allochroa brononii* is the largest species of the genus, sometimes reaching 12 mm in length (Souleyet, 1852; USNM 131288). It has been confused with larger forms of the highly variable *Allochroa layardi*, an Indo-Pacific species (Dautzenberg & Fischer, 1905). They can be set apart by the narrower base of the aperture in *A. brononii*, whereas shells of identical size of *A. layardi* have a wider apertural base (see Figs. 1 and 5). In Hawaii, where both species overlap, they are morphologically very distinct (see Figs. 1, 2, 4). Although size alone seems to be sufficiently diagnostic to separate these two species, *A. brononii* shows also a proportionally smaller number of whorls for the length of the shell. However, anatomical studies are needed to ascertain better the differences between these two closely related species.

Habitat Notes: "Found seaward of *Melampus*, *Pedipes*, and *Laemodonta*, often buried in gravel in high tide pools and along rocky shores" (Kay, 1979).

Range: *Allochroa brononii* is endemic to the Hawaiian Islands.

Material Examined: (Sample size in parenthesis). HAWAIIAN ISLANDS: [USNM 20795 (5), 31582 (4), 98175 (6), 98176 (9), 98178 (3), 131288 (1), 319528 (4), 346615 (11)]; HAWAII ISLAND: Keei, near Napoopoo, Kona Coast [USNM 767596 (1)]; OAHU ISLAND: Honolulu [USNM 159574 (1)]; Pearl City, Honolulu [MCZ 55989 (1)]; 1935 dredgings, Hickham Air Force Base, Pearl Harbor [USNM 484416 (3)]; Kaneohe Bay [USNM 887316 (8)].

Allochroa layardi (H. & A. Adams, 1855)
Figures 3–14, 22–27, 30, 33–35, 39–45

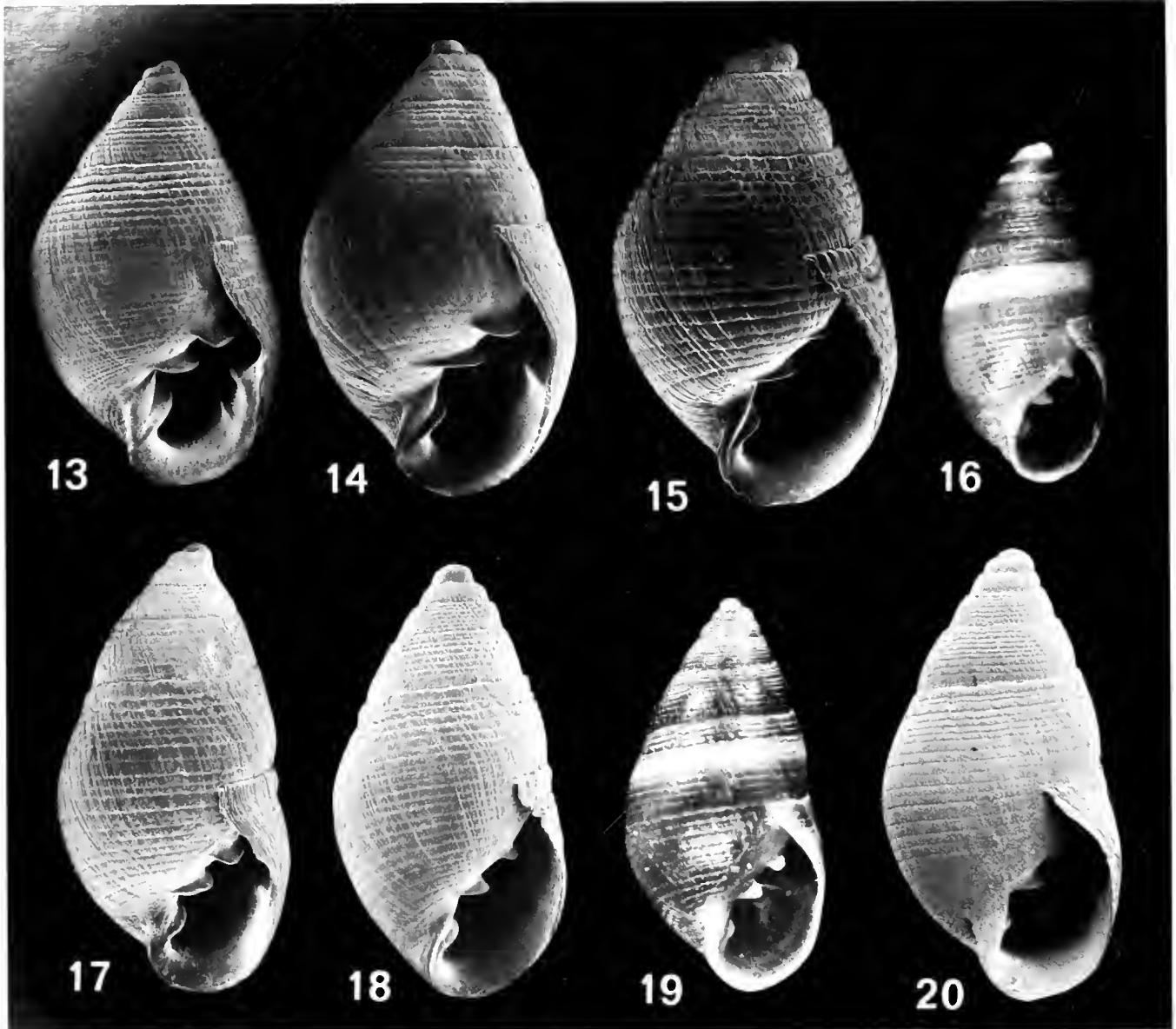
Melampus layardi 'Ads.' Pfeiffer, 1854:147. *Nomen nudum*.
Ophicardelus (*Laimodonta*) *layardi* H. & A. Adams, 1855a: 35 [Ceylon; lectotype herein selected BMNH 196980/1 (Fig. 3); two paralectotypes BMNH 196980/2–3]. *Laimodonta layardi* (H. & A. Adams). H. & A. Adams, 1855b: 246. *Laimodonta pfeifferi* Dunker in Pfeiffer 1860: 201 [Japan; location of type unknown]; Dunker, 1861:25, pl. 2, fig. 19. *Laimodonta conica* Pease 1863: 242 [Pacific Islands; lectotype selected by Kay (1965) BMNH 1964292 (Fig. 4); five paralectotypes BMNH 1964293]. *Laimodonta conica* Pease. Pease, 1868:101, pl. 12, fig. 15 (misspelling of *Laimodonta*). *Laimodonta anaensis* Mousson, 1869: 63 [Anaa Island, Paumotu group; location of type un-

known]. *Laemodonta conica* (Pease). Martens & Langkavel, 1871:57. *Pleotrema anaensis* (Mousson). Paetel, 1873:114. *Laimodonta bronii* var. *conica* (Pease). Jickeli, 1874:178, pl. 7, fig. 3. *Melampus pfeifferi* (Dunker). Pfeiffer, 1876:319. *Melampus conicus* (Pease). Pfeiffer, 1876:319. ?*Melampus anaensis* (Mousson). Pfeiffer, 1876:320. *Marinula* (*Laimodonta*) *conica* (Pease). Nevill, 1878:220. *Marinula* (*Laemodonta*) *conica* (Pease). Martens, 1880: 208. *Laimodonta conica* var. *conicooides* Tapparone Canefri, 1883:240 [Arn Island, New Guinea, location of type unknown]. *Laemodonta* (*Tralia*) *layardi* (H. & A. Adams). Crosse, 1894:321. *Melampus* (*Laimodonta*) *conicus* (Pease). Kobelt, 1898:224, pl. 26, fig. 14. *Melampus* (*Laimodonta*) *anaensis* (Mousson). Kobelt, 1898:228, pl. 27, figs. 10–11. *Laimodonta bronni* var. *producta* Dautzenberg & H. Fischer, 1905:108, pl. IV, figs. 20, 21 [Anse du Crâne, Balïe d'Along, Tonkin; syntypes MNHN (Fig. 5)]. *Enterodonta conica* (Pease). Germain, 1921:264. *Allochroa conica* (Pease). van Benthem Jutting, 1941:283. *Allochroa pfeifferi* (Dunker). Kuroda & Habe, 1952:38. *Allochroa layardi* (H. & A. Adams). Franc, 1954:365.

Description: Shell (Figs. 3–14, 22–27) length to 8 mm, ovate-conical, fragile to somewhat solid; chestnut-brown to pale-yellow, banded. Spire moderately high, whorls 6.0 to 6.5, plano-convex, with spiral striae crossed by irregularly marked longitudinal growth lines which give the surface a faint granulose appearance. Body whorl about 70% shell length, sculptured as the previous whorls; color pattern showing a faint subsutural light band, a marked whitish band halfway between the suture and the aperture, also visible on the two previous whorls, sometimes with a third, wider pale-yellow band gradually becoming dark-brown anteriorly. Aperture auriculate; inner lip tridentate; one oblique columellar tooth not reaching the border of the lip; two parietal teeth, anterior lamellar, transverse, continuing inwards, posterior largest, thick and bifid in larger individuals, slightly elongated but not continuing inwards; outer lip sharp, with a ridge-like tooth about halfway along the length of the aperture, penetrating deep inside the aperture; a wide callus may develop anteriorly, as a continuation of the outer lip tooth, also penetrating inwards; a second outer lip tooth is sometimes present over the callus, located at a level between the anterior parietal tooth and the columellar tooth. Juveniles pilose, the hairs distributed along the spiral striae (Fig. 12). Protoconch 210–235 x 150–175 μ m whitish, smooth, somewhat inflated, a little over one whorl, with rounded peristome (Figs. 22–27).

←
Figures 1–2. *Allochroa brononii* (Philippi); **1.** Hawaii, USNM 98175, sl = 8.2 mm; **2.** Pearl City, Honolulu, Hawaii, MCZ 55989, sl = 3.5 mm.

Figures 3–12. *Allochroa layardi* (H. & A. Adams); **3.** Lectotype, Ceylon, BMNH 196980.a, sl = 7.0 mm; **4.** Lectotype of *Laimodonta conica* Pease, Pacific Islands [Hawaii], BMNH 1964292, sl = 4.2 mm; **5.** Holotype of *Laimodonta bronni* var. *producta* Dautzenberg & Fischer, Balïe d'Along, Anse du Crâne, Tonkin, China, MNHN (not numbered), sl = 8.0 mm; **6.** Paumotu [Tuamotu] Islands, specimen illustrated in Pease (1868, pl. 12, fig. 15), ANSP 22610 [type written in label], sl = 7.0 mm; **7.** Mataira Island, Raroia, Tuamotu Islands, USNM 698771, sl = 5.8 mm; **8.** North Beach, Henderson Island, Pitcairn Islands, R. C. Preece coll., sl = 6.1 mm; **9.** Lijeron Island, Jaluit Atoll, Marshall Islands, USNM 660035, sl = 4.6 mm; **10.** Lugbon Island, Philippines, USNM 201147, sl = 5.5 mm; **11.** Riu Kiu Islands, Japan, USNM 345877, sl = 5.0 mm; **12.** Hirado, Hizen, Japan, USNM 345878, sl = 4.1 mm. sl = shell length.



Figures 13–14. *Allochroa layardi* (H. & A. Adams), Mataira Island, Raroia, Tuamotu Islands, USNM 698771, sl = 3.5, and 2.5 mm

Figures 15–18. *Allochroa nana* Martins, n. sp., Eninman Island, Bikini, Marshall Islands; **15, 17–18** paratypes, USNM 585963, sl = 2.2, 3.7, and 3.0 mm, **16**, holotype, USNM 585963 a, sl = 3.2 mm **Figures 19–20.** *Allochroa tenuis* Martins, n. sp., Noumea, New Caledonia, **19**, holotype, USNM 724374 a, sl = 4.1 mm, **20**, paratype, USNM 724374, sl = 3.5 mm sl = shell length.

Radiata (Figs. 33–35) formula [26+23+1+23+26] × 115. Crown tooth slightly above the plane of the lateral teeth; bases deeply emarginate, with lateral projections flaring out at mid-length, gradually tapering to neck region; crown full length of that of lateral teeth, narrow, unicuspid, mesocone somewhat sharp. Lateral teeth 23, base elongated, slightly bent medially, a rounded inner prominence arises on the lower third, an outer projection flares out at mid-length and tapers towards neck; crown covering two thirds of base and as wide as the latter, unicuspid, cusp rounded. Marginal teeth 26, bases of first teeth barely longer than crown, gradually diminishing

to completely disappear underneath crown, developing a conspicuous lateral basal cusp on the last 13 teeth; crown bicuspid; endocone, sharp, short on first teeth, gradually elongating to about three quarters of mesocone; mesocone as long as that of last lateral teeth, rounded at tip.

Visceral mass: Conical, not following external winding of shell, with whorl impressions weakly insinuated, indicating the extensive resorption of the inner whorls of the shell.

Digestive system: Mandible (Fig. 39) with fibrous appearance, tripartite, median portion roughly quadran-

gular with extremities abruptly tapering posteriorly, lateral portions of sparse, loose fibers, tapering on both extremities. Salivary glands long, cylindrical. Stomach (Fig. 40) tripartite; cardiac region dilated, thin, receiving at its base the duct of anterior diverticulum; mid-portion comprising most of the stomach's volume, muscularized; gastric caecum thin, pouch-like, receiving posterior diverticulum; pyloric region small, thin.

Reproductive system: (Fig. 30, 41–44) Ootestis of long, inverted claviform acini embedded in the conical posterior lobe of the digestive gland, connecting with a collecting duct by their thinner ends, the broader, dark-red dotted extremities appearing at the surface of the digestive gland as an irregular, winding band; proximal half of the hermaphroditic duct thin, relatively straight, distal half forming a greatly convoluted and somewhat dilated seminal vesicle; pallial gonoduct hermaphroditic to the vaginal aperture; albumen gland beneath the anterior lobe of digestive gland and intestinal convolutions; posterior mucus gland tightly convoluted; anterior mucus gland and prostate gland covering entire length of pallial spermoviduct; bursa spherical, fitting under posterior mucus gland; bursa duct nearly equal in length to spermoviduct, emptying near vaginal opening. Pallial gland long, sharply bent about midlength, anterior portion more dilated and slightly longer than posterior one, emptying at the female genital opening. Penial complex relatively short, proximal third dilated; vas deferens adhering to penial sheath, entering penial structure at the distal end of the proximal quarter; penis oval-oblong, blunt, constituted of a thickened, sharply bent, compactly folded muscular pilaster, lodged in the thin, membranous dilation of the penial sheath; internal wall of the penial sheath with fine, radiating grooves at the site of the dilation, with two irregularly grooved longitudinal folds running forward to the aperture, one of them connecting distally to the penis, the other originating at the level of the tip of the penial papilla; penial retractor about as long as the penial complex, relatively thick.

Nervous system: (Fig. 45) Cerebral commissure short, about half the width of a cerebral ganglion; left cerebropleural connective twice the length of the right one; right cerebro-pedal connective somewhat longer than the left one; pleural ganglia small; right pleuro-parietal connective very short, about one-third of the left one; left parietal ganglion as small as pleural ganglia, right one three times larger, with a thick pneumostomal nerve from where a rudimentary osphradial ganglion buds off; parieto-visceral connectives relatively long, the left one somewhat longer.

Remarks: *Allochroa layardi* was described by H. & A. Adams (1855a) from specimens from Ceylon [Sri Lanka], in the Cuming collection. H. & A. Adams' manuscript, although submitted for publication in 1854, was not published until January 1855 (see Duncan, 1937; Trew, 1992). Pfeiffer, who had access to the manuscript of the Adams brothers, listed their new species in his Synopsis (1854), giving credit to the original author(s) and placing the species under the genus *Melampus*. Pfeiffer, however,

did not add any descriptive notes; for this reason, the name "*Melampus layardi* 'Ad.' Pfeiffer" should be treated as *nomen nudum*. The Adams brothers' name was apparently ignored in the various subsequent descriptions of taxa here considered as synonyms of *A. layardi*, and comparisons referred rather to *A. bronni*. Such was the case of *Laimodonta pfeifferi*, from Japan, and of *Laimodonta bronni* var. *producta* from China (see Fig. 5). *Allochroa layardi*, however, has a more slender overall shape and is smaller than *A. bronni*, mainly in Hawaii where both species coexist. Pease (1863) described *Laimodonta conica* from the Hawaiian Islands (Fig. 4); five years later, however, Pease (1868) figured his Hawaiian species using a specimen from Paumotu [Tuamotu Islands], almost twice the size and more elongated than the type specimens (Fig. 6). Mousson (1869) described and figured the larger Tuamotu shells from Anaa Island as *Laemodonta anaensis*, commenting on their clear relationship with *A. bronni*, but at the same time calling attention to the smaller size of his species relative to the latter; his measurements (8 mm), however, are the largest known for *A. layardi*.

Very variable across the Indo-Pacific, *A. layardi* is usually markedly striated, although some specimens can be extremely smooth (Fig. 8). It also varies in shell thickness, the thick specimens sometimes showing an additional internal lamella on the outer lip (Figs. 7, 9, 13), which Tapparone Canefri (1883) considered to be the variety *conicoides* of *Laimodonta conica* [= *A. layardi*]. The color pattern remains basically the same throughout; however, the banding delimitation may sometimes lack sharpness (Fig. 10). The shape and size of the protoconch are consistently homogeneous throughout the distributional range of the species (Figs. 22–27). *Allochroa bronni* (Fig. 21) possesses a protoconch similar to that of *A. layardi*, also stressing the close affinities of the two species. However, as pointed out before, the size and ratio between the number of whorls and the length of the shell justify their taxonomic separation.

Only one radula of each species was studied. It appears that the base of the central tooth of *A. layardi* is decidedly triangular (Fig. 33), whereas that of *A. bronni* is narrowly quadrangular (Fig. 31). The crown of the lateral teeth of *A. bronni* seems to be narrower and longer than that of *A. layardi*.

Habitat Notes: Gassies (1863) stated that this animal appears to be completely marine, and that Montrouzier found it under stones near the shore, together with columbellids, ranellids and tritons. Preece (personal communication) found them in crevices of exposed rocks at about high tide level.

Range: *Allochroa layardi* is widely distributed throughout the Indo-Pacific; it has been reported from Mauritius (Morelet, 1882), Sri Lanka, India (Nevill, 1878), China, Japan, Philippines, New Guinea, Australia, New Caledonia, Marshall Islands, Tuamotu Islands, Hawaii.

Material Examined: (Sample size in parenthesis) CEYLON [SRI LANKA] [BMNH 196980/1 (lectotype),

196980/2–3 (paralectotypes of *Ophicardelus (Laimodonta) layardi*). CHINA: Bah e d'Along, Anse du Cr ne, Tonquin [MNHN, not numbered, holotype and paratype of *Laimodonta bronni* var. *producta*]. JAPAN: Hirado, Iizen [USNM 345878 (30)]; Riu Kiu Islands [USNM 345877 (56)]; Loo Choo Islands [USNM 30811 (12), 161507 (2)]; Nago, Okinawa Island, Loo Choo Islands [USNM 363720 (1)]. PHILIPPINE ISLANDS: Bohol Island [USNM 302973 (4)]; off Point Origan, Tablas [USNM 281503 (1)]; Lugbon Island [USNM 201147 (7)]; Point Hinayang, Leyte [USNM 887317 ex Chicago Academy of Sciences (3)]; Sogod Bay, Leyte [USNM 283799 (1)]; off Point Dumurug, Masbate [USNM 274834 (1)]; off Adyagan Island, E Masbate [USNM 281808(1)]; Ragay Gulf, off Arena Point, Luzon [USNM 284250 (1)]; off Matacot Point, W Louzon [USNM 259939 (1)]; off Pescador Island, Tanon Station [USNM 281169 (1)]; off Capitancillo Island, N Cebu [USNM 287800 (1)]; off Lanis Point, E Cebu [USNM 290562 (2)]; Pujada Bay, E Mindanao [USNM 255647 (1), 276398 (2)]; Tilig, Lubang Island [USNM 229914 (1)]. NEW CALEDONIA: Lifu [USNM 422639 (1), 422640 (1), 423167 (4)]. AUSTRALIA: [USNM 887318 (1)]; mouth of Bigota Creek, Barrow Island [USNM 691788 (1)]. COOK ISLANDS: Tupapa, E of Avarua, Rarotonga [USNM 721509 (1)]. MARSHALL ISLANDS: N end of Lijeron Island, Jaluit Atoll [USNM 660035 (8)]. TUAMOTU ISLANDS: [USNM 98177 (3), 711465 (6)]; RAROIA ISLANDS: Ngarumaoa Island [USNM 697524 (1), 697767 (1), 698079 (2), 720349 (17)]; S end of Ngarumaoa Island [USNM 697593 (3)]; Mataira Island [USNM 698771 (8), 711673 (1)]; Kumekumo Island [USNM 698492 (5)]; Teteu Island [USNM 722685 (1), 722687 (1)]; S end of Teteu Island [USNM 722756 (50)]; Havana Island [USNM (1 fragment)]; Okaea Island [USNM 722834 (1)]; S end of Opakea Island [USNM 722554 (79), 723548 (1)]; Oneroa Island [USNM 720768 (2)]; Ohava Island [USNM 720503 (19)]; Otikaheru Island [USNM 720684 (1)]; Vahi Tahi [USNM 613207 (1)]; Te-mao Harbor, Makatea [USNM 629788 (1)]; NE side of Tepukamarua Island, Takumo [USNM 723724 (1)]; Motu Taraurua, Mangareva Island [USNM 638224 (4)]. PITCAIRN ISLANDS: E end of North Beach, Henderson Island [R. C. Preece collection (4)]. HAWAIIAN ISLANDS: [BMNH 1964292 (lectotype), 1964293 (5 paralectotypes)]; USNM 15157 (2), 20796 (3), 20797 (12), 857319 (4)].

Allochroa nana Martins, new species

Figures 15–18, 28

Description: Shell (Figs. 15–18, 28) length to 3.7 mm, ovato-conical, fragile, spirally striated, dark-brown to golden-brown, banded. Spire moderately high, 5 plano-convex, dark-brown to brown whorls, sometimes with a faint equatorial lighter band; spiral striae undulated due to crossing by marked growth lines which are predominant on the early whorls of teleoconch. Body whorl about 70% of shell length, sculptured as previous whorls; banded color pattern as follows: a light-brown, fine band from

the suture to the first spiral stria, a darker band on the next two striae, a wider, white band covering the next 3–4 striae, a dark-brown band extending to the posterior end of the aperture, frequently continuing to the anterior tip of the shell, sometimes broken up by a diffuse, lighter band extending from the posterior end of the aperture to about the level of the anterior parietal tooth. Aperture semicircular, oblique; inner lip equidistantly tridentate: one small, oblique columellar tooth, two parietal teeth, the anterior strongest and perpendicular to the columellar axis, the posterior about as strong as columellar tooth; outer lip sharp, very rarely with an elongated thickening opposite the anterior parietal tooth and weakly projecting inside the aperture (Fig. 17). Juveniles pilose (Fig. 15). Protoconch 285x210 μ m, bulbous, light-brown, with growth lines showing as faint narrow bands, with elongated, somewhat widening lip (Fig. 28).

Type Locality: Eninman Island, Bikini, Marshall Islands. From drift line along tide pool at N end of island, outer reef side.

Material Examined: (Sample size in parenthesis) MARSHALL ISLANDS: Eninman Island, Bikini [USNM 585963 (holotype), 887320 (64 paratypes)]; Rojoa Island, Enewetak [USNM 587120 (1)]; Pujiyuru Island, Enewetak [USNM 587101 (1)]; N end of Bock Island, Rongerik [USNM 594920 (2)].

Etymology: *nanus*, *i* = dwarf.

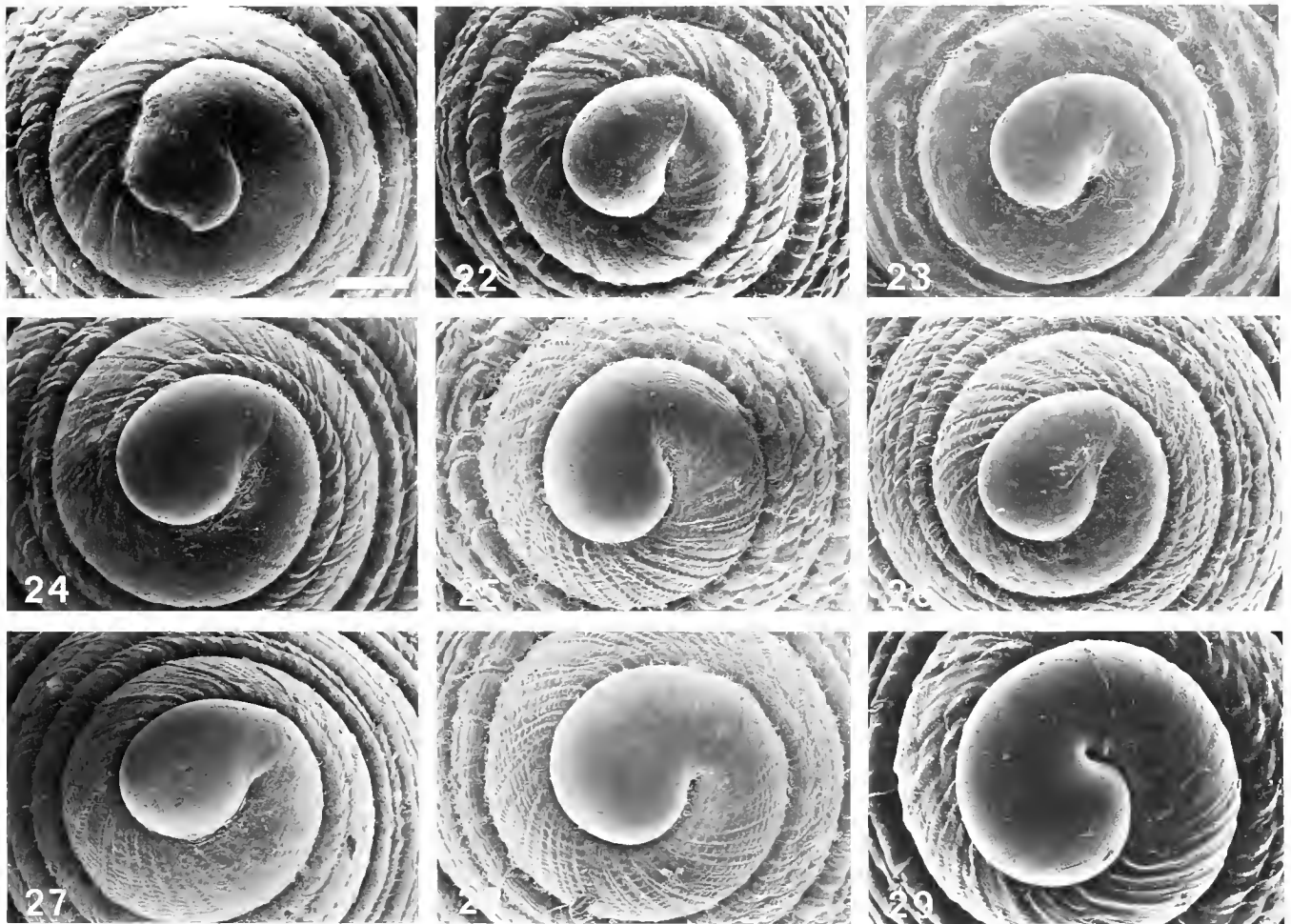
Range: Known from Bikini, Enewetak and Rongerik, in the Marshall Islands.

Remarks: *Allochroa nana* is the smallest species of the genus, and size alone will easily distinguish it from the previously described species. It is, however, best characterized by its large protoconch with faint colabral bands marking the growth lines and with a somewhat widening lip (Fig. 28).

Allochroa tenuis Martins, new species

Figures 19–20, 29, 36–38

Description: Shell (Figs. 19–20, 29) length to 4.6 mm, ovato-conical, fragile, spirally striated, purple-brown to brown, banded. Spire moderately high, 5.5 plano-convex, spirally striated, dark-brown whorls, the last one darkest, usually purple-brown. Body whorl about 70% of shell length, sculptured as previous whorls; banded color pattern as follows: a gradually darkening brown band extending from the suture to the third stria, a marked white band over the next three striae, and a more or less homogeneous brown region extending to the tip of the shell, sometimes broken up by a diffuse, lighter band between the end of the aperture and the posterior parietal tooth. Aperture ovate; inner lip equidistantly tridentate; one columellar tooth, oblique, not reaching the border of the aperture lip, two parietal teeth, the anterior strongest and perpendicular to the columellar axis, the posterior about as strong as columellar tooth; outer lip sharp, rarely with an elongated thickening opposite the anterior pa-



Figures 21–29. Protoconchs of *Allochroa* species. **21.** *Allochroa brononii* (Philippi), Hawaii, USNM 98175. **22–27.** *A. layardi* (H & A. Adams); **22.** Hawaii, USNM 20797; **23.** paralectotype, Ceylon, BMNH 196980; **24.** Henderson Island, Pitcairn Islands (R. C. Preece); **25.** Lugbon Island, Philippines, USNM 201147; **26.** Riu Kiu, Japan, USNM 345877; **27.** Mataira Island, Raroia, Tuamotu Islands, USNM 698771 (specimen shown in fig. 14). **28.** *A. nana* Martins, n. sp., Eninman Island, Bikini, Marshall Islands, lectotype, USNM 585963. **29.** *A. tenuis* Martins, n. sp., Noumea, New Caledonia, lectotype, USNM 724347. Scale bar = 100 μ m.

rietal tooth and weakly projecting inside the aperture (Figs. 19–20). Protoconch $385 \times 240 \mu\text{m}$, bulbous, light-brown, showing 1.3 whorls, with somewhat reflected lip creating an umbilical slit (Fig. 29).

Radula: (Figs. 36–38) Formula [17+14+1+14+17] $\times 100+$. Central tooth barely above the plane of the lateral teeth; base deeply emarginate, with lateral projections flaring out at mid length; crown small, with narrow, pointed mesocone. Lateral teeth 14, base elongated with lateral projections asymmetrical, the inner lower and serving as “point d’apui” for the articulation with the outer basal projection of the next tooth in the row (see Fig. 36); crown subquadrangular, long, with rounded mesocone. Marginal teeth 17, with one sharp endocone becoming longer towards the end of the row; mesocone becoming sharper towards the end of the row.

Type Locality: Lighthouse island opposite Noumea, New Caledonia. From crevices on undersides of coral slabs, outer reef.

Material Examined: (Sample size in parenthesis) NEW CALEDONIA: Lighthouse island opposite Noumea [USNM 724374 (holotype), 887321 (117 paratypes)]; N side of N’Go Bay [USNM 725042 (1)]; Touaourou [USNM 724628 (1), 724722 (1)]. PHILIPPINES: Pujada Bay, E Mindanao [USNM 887322 (1)].

Etymology: *tenuis*, *e* = thin.

Range: Known from New Caledonia and Mindanao, Philippines.

Remarks: *Allochroa tenuis* is readily distinguished from all other species in the genus on the basis of its thinner, darker shell and its large protoconch with flaring lip (see Fig. 29). The smaller, lighter but equally thin *Allochroa nana*, described above, also has a large protoconch, but without a flaring lip. The shape of the protoconch of *A. tenuis*, although unique among the known *Allochroa*, strongly resembles that of *Ocatella acqualis* (Lowe, 1832).

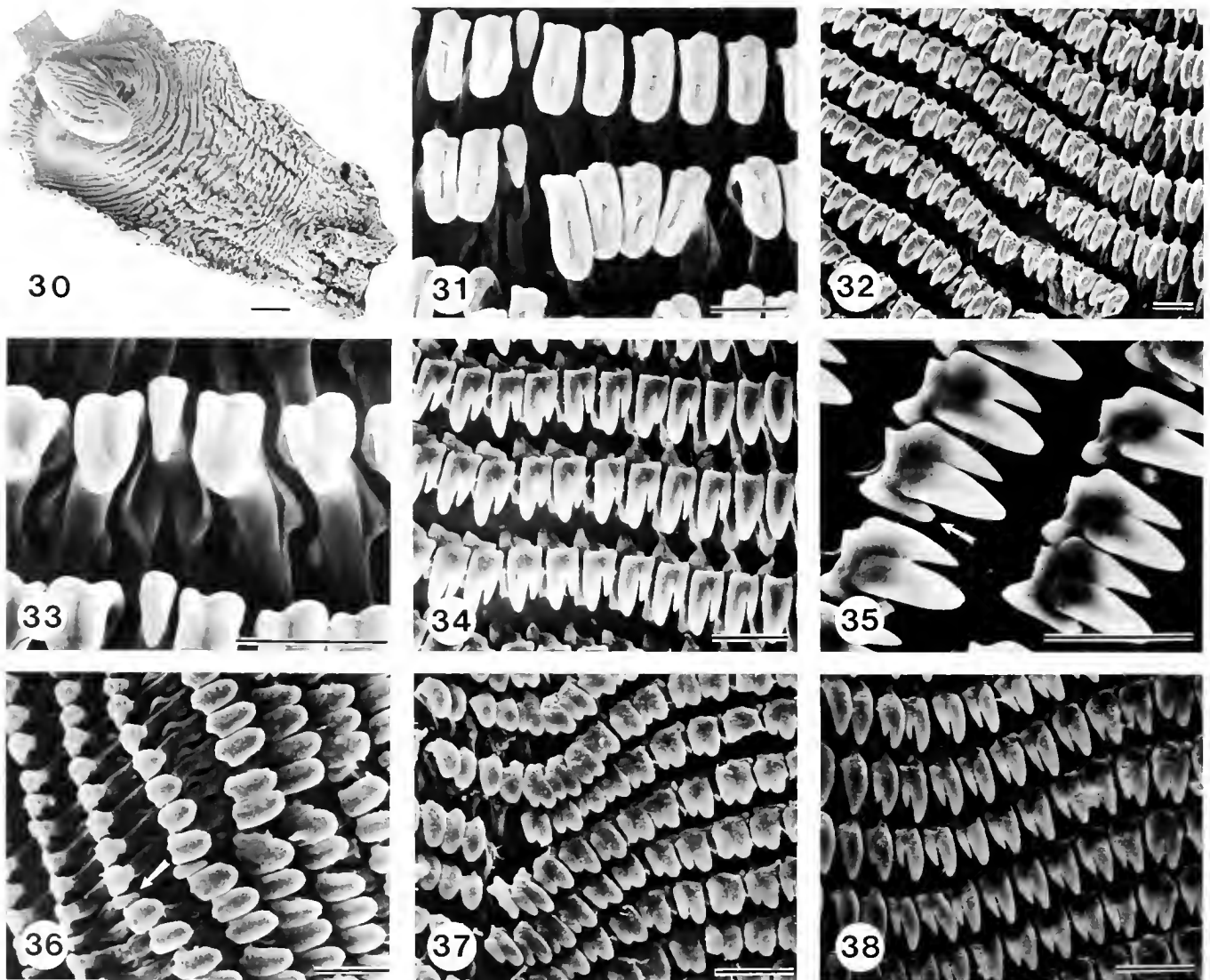


Figure 30. Internal structure of the penial complex of *Allochroa layardi* (H. & A. Adams), Henderson Island, Pitcairn Islands. **Figures 31–38.** Radulae of *Allochroa* species. **31–32.** *A. brononii* (Philippi), Hawaii; **31.** central tooth and first lateral teeth; **32.** last lateral teeth and marginal teeth. **33–35.** *A. layardi* (H. & A. Adams), Henderson Island, Pitcairn Islands; **33.** central tooth and first lateral teeth; **34.** last lateral teeth and marginal teeth; **35.** marginal teeth showing basal cusp (arrow). **36–38.** *A. tenuis* Martins, n. sp., Noumea, New Caledonia; **36.** central tooth (arrow) and lateral teeth; **37.** last lateral teeth and marginal teeth in a worn region; **38.** last lateral teeth and marginal teeth in a fresh region. Scale bar = 100 μm for Fig. 30, 10 μm for all others.

The relationships of *Allochroa* with this European genus are therefore strengthened.

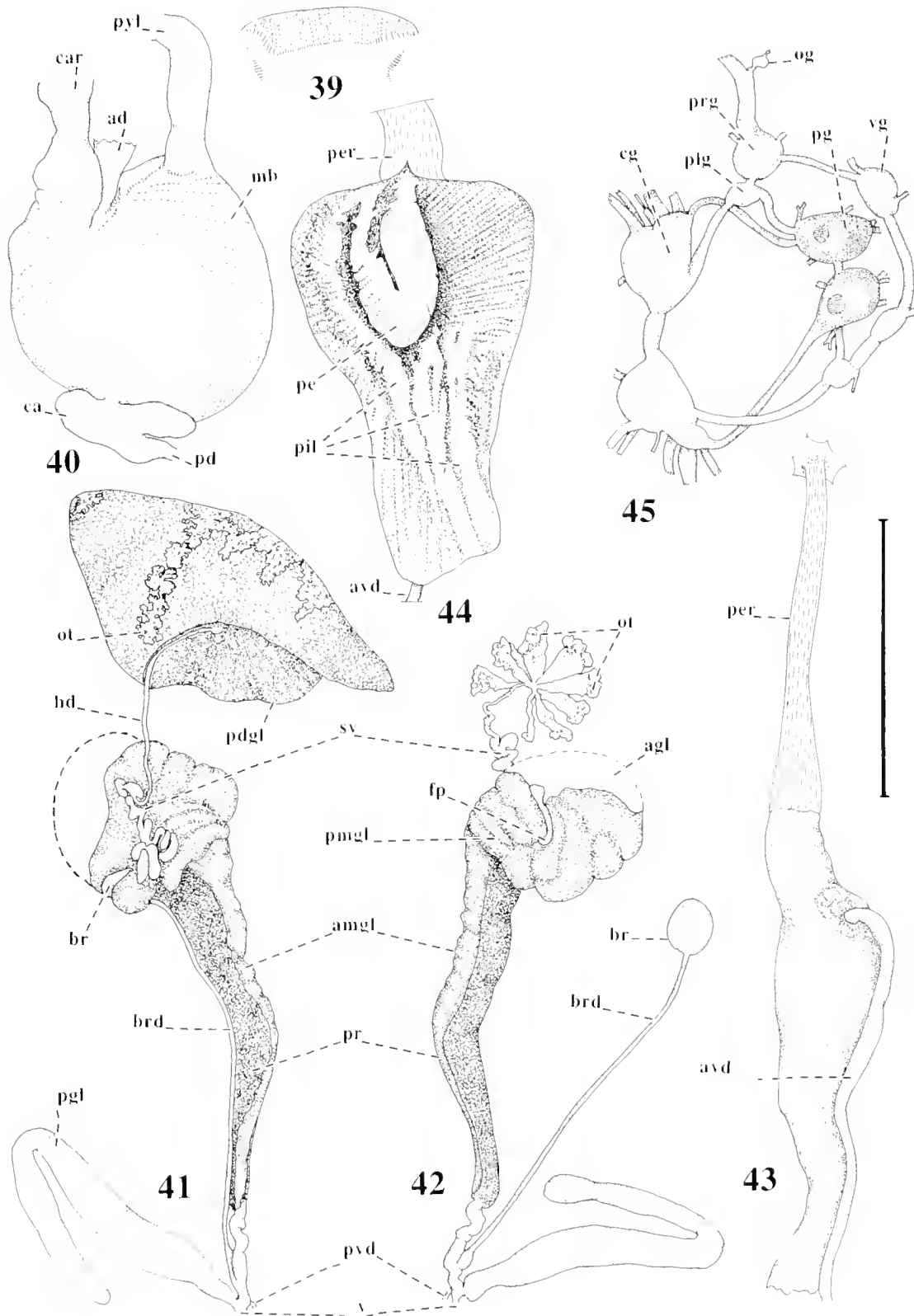
RELATIONSHIPS WITHIN THE ELLOBIIDAE

Since the studies of Odhner (1925) and Morton (1955) the subfamilial division of the Ellobiidae has been based

on anatomical characters, mainly on those of the reproductive system. Martins (in press a, b), studying the characteristics of the central nervous system, concurred with Morton's (1955) conclusions and provided a more complete subfamilial characterization. The Pythiinae, the most primitive subfamily, have a monaulic, entirely glandular, pallial gonoduct and a wide visceral nerve ring

Figures 39–45. Anatomy of *Allochroa layardi* (H. & A. Adams), Henderson Island, Pitcairn Islands, **39.** mandible; **40.** stomach; **41, 42.** reproductive system, **43.** penial complex, **44.** internal structure of penial complex; **45.** central nervous system. Scale bar = 2 mm for Figs. 41–42, 1 mm for all others

ad, anterior diverticulum; agl, albumen gland, amgl, anterior mucus gland, avd, anterior vas deferens, br, bursa; brd, bursa duct; ca, stomachal caecum; car, cardiac region of stomach, cg, cerebral ganglion; fp, fertilization pouch; hd, hermaphroditic duct, mb,



muscular band; og, oesophageal ganglion; ot, ovotestis; pd, posterior diverticulum; pdgl, posterior lobe of digestive gland; pe, penis; per, penial retractor muscle; pg, pedal ganglion; pgl, pallial gland; pil, penial pilasters; plg, pleural ganglion; pmgl, posterior mucus gland; pr, prostate gland/spermiduct; prg, parietal ganglion; pvd, posterior vas deferens; pyl, pyloric region of stomach; sv, seminal vesicle; v, vagina; vg, visceral ganglion

with a long right parieto-visceral connective. The Ellobiinae have a diaulic reproductive system with entirely glandular pallial gonoducts; the visceral nerve ring is wide and has a short right parieto-visceral connective. The Carychiinae have a monaulic reproductive system with the prostate concentrated distally on the gonoduct and a central nervous system of the ellobiine type. The Pedipedinae possess a monaulic or incipient semi-diaulic pallial gonoduct where only the proximal half is glandular and a concentrated visceral nerve ring. The Melanpodinae are characterized by an advanced semi-diaulic reproductive system with non-glandular pallial gonoducts and by concentration of the visceral nerve ring.

Taking into account the preceding arrangement, *Allochroa* must remain within the Pythiinae in view of its monaulic, entirely glandular pallial gonoducts and the wide visceral nerve ring with a long right parieto-visceral connective.

Within the Pythiinae, *Allochroa* shows strongest affinities with the Mediterranean and Eastern North Atlantic *Ovatella*, based primarily on the presence of an internal lamella inside the outer lip, the protoconch of *A. tenuis* which, although different from all others in the genus, is very similar to that of *Ovatella*, and the configuration of the internal structure of the penial complex, where the penis appears as the development of one of the pilasters (Martins, in press b).

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A remarkable species richness of the Barleeidae (Gastropoda: Rissoacea) in the Eastern Atlantic

Serge Gofas

Muséum National d'Histoire Naturelle
55 rue Buffon
F-75005 Paris, France

ABSTRACT

The family Barleeidae, hitherto known in the Eastern Atlantic from two European and Northwest African species of *Barleecia* and two species of *Tropidorissoia* from São Tomé, is found to be represented by 18 species, 14 of which (8 *Barleecia*, 3 *Pseudodiala*, 3 *Lirobarleecia*) are here described as new. Three new species share several shell or radular characters with the type species of *Pseudodiala* and not with *Barleecia*. For this reason *Pseudodiala* is considered to be a valid genus. There are four centers of diversity: Senegal (3 species), the Cape Verde Islands (3 species), São Tomé and Príncipe (6 species) and Southern Angola (6 species), together making the Eastern Atlantic the second most species-rich area after Western America, and the area with the highest diversity at the genus level.

Key words: Barleeidae, western Africa, new species, species diversity, biogeography

INTRODUCTION

The Barleeidae is a family of minute prosobranchs that typically live on intertidal or shallow subtidal hard bottoms of temperate to tropical areas. Many species live within coralline algae, or on "maerl", deposits of living calcareous algal concretions. The genera of the Barleeidae have been reviewed by Ponder (1983), who then considered the Anabathrinae as a subfamily of the Barleeidae but later raised them to full family status (Ponder, 1988).

Western America, from California to Panama and the Galapagos Islands, is the area with most described species of Barleeidae: 25 species are recognized as valid by Ponder (1983). The family is also represented in the Caribbean, eastern South America, East and South Africa, South-east Asia, Australia and New Zealand, and Japan, but generally with low (1–5) species richness.

The family is known hitherto in the Eastern Atlantic by four species: the mainly European *Barleecia unifasciata* (Montagu, 1803), a less well known species *B. gougueti* (Michaud, 1830) from NW Africa, and two species of *Tropidorissoia* from the Island of São Tomé, in the Gulf of Guinea (Tomlin & Shackleford, 1915; Rolán & Templado, 1994). Several species that may be assigned

to the Barleeidae were described from the island of St. Helena (Smith, 1890), but the systematic position of most of them remains uncertain until living animals are examined.

Recent collecting in Angola by the author, and other collectors' material from West Africa in Muséum National d'Histoire Naturelle of Paris and Museo Nacional de Ciencias Naturales, Madrid, has shown that there are a number of undescribed species of Barleeidae on the mainland coast of West Africa, the Cape Verde Islands, São Tomé and Príncipe, making this area one of the centers of species diversity for the family. No species assignable to the Anabathridae has been found in this material, with the exception of the southernmost records of the European species *Nodulus contortus* (Jeffreys, 1856) in Mauritania.

The material examined has the following origins:

—dredgings and shore collecting by I. Marche-Marchad, 1953–1956, mostly from Senegal (MNHN).

—intertidal collecting in the Canary Islands (1981) and Mauritania (1983) by P. Bouchet (MNHN).

—the author's collecting in Angola and São Tomé, 1981–1987, and in Europe (MNHN).

—intertidal and SCUBA collecting in the Cape Verde Islands by the "1a expedición Científica Iberica a Cabo Verde", August 1985 (MNCN).

—intertidal and shallow subtidal collecting by E. Rolán in São Tomé, Príncipe and the Cape Verde Is. (MNCN and private collection of E. Rolán, Vigo).

Radulae have been examined using SEM for a number of species. Radular morphology has been found informative for classification at the family and genus level, but not for the discrimination of closely related species.

ABBREVIATIONS

AMS	= Australian Museum, Sydney.
CER	= private collection of Emilio Rolán, Vigo.
MNHN	= Muséum National d'Histoire Naturelle, Paris.
MNCN	= Museo Nacional de Ciencias Naturales, Madrid.
UAN	= Universidade Agostinho Neto, Luanda.
cat.	= catalogue number.

leg.	= "legit", collected by.
spec., specs.	= live-collected specimen(s).
sh.	= shell(s).
juv.	= juvenile(s).
SEM	= Scanning electron micrograph(s).
*	denotes specimens in the wet collection.

SYSTEMATICS

Family BARLEEIDAE Gray, 1857

The family is diagnosed by having: a pitted protoconch, a groove on the sole of the metapodium reaching its posterior end, and a single-layered operculum with an inner peg. This last character differentiates the Barleeidae from the Anabathridae. Pallial and metapodial tentacles are typically absent. The reader is referred to Ponder (1983) for a detailed account of the family.

Genus *Barleecia* Clark, 1855

Type species: *Turbo ruber* Adams, 1797 (= *Turbo unifasciatus* Montagu, 1803), non *Turbo ruber* von Salis, 1793, by monotypy.

Shell with smooth, solid teleoconch in all species considered, non-umbilicate or very narrowly umbilicate, generally with reddish tinge. Aperture ovate, slightly prosocline to orthocline, with smooth lip thickened at some distance inside, and then beveled to a thin edge. Head-foot typically pigmented with black and yellow. Operculum with an internal peg, a smooth nucleus on the columellar side, and fine growth lines on the remainder of the external surface; a conspicuous external ridge along the columellar side, overrunning the nucleus.

Radula (Ponder, 1983 and herein, Fig. 71–72): central tooth with a large rectangular median cusp and 2–3 small lateral denticles, one sharp basal denticle on each side, separated by a broad, hardly prominent lamella. Lateral teeth (one pair) with a rather broad base, terminating with a large, rather trapezoidal cusp flanked by 2–3 smaller cusps to the inner side and the outer side; with a U-shaped projection beneath those. Marginal teeth (two pairs) narrow, hook-shaped, with small, unipectinate cusps towards the distal end.

Barleecia unifasciata (Montagu, 1803)
(Figures 1, 29–30)

Turbo ruber Adams, 1797:66, pl. 13 fig. 21–22 (non *Turbo ruber* von Salis, 1793). Type locality: Pembrokeshire (British Isles).

Turbo unifasciatus Montagu, 1803:327–328. Type locality: Southampton, and Island of Burrow, Devon (British Isles).

Rissoa fulva Michaud, 1830:12 (repr. 1832:15), pl. 1, fig. 17–18. Type locality: not specified, localities mentioned: Agde, Sète (Mediterranean France) and Corsica.

Sabanaca binghamiana Leach, 1852:154. Type locality: Torbay, Devon (British Isles).

Barleecia rubra var. *elongata* Bucquoy, Dautzenberg & Dollfus, 1884:316, pl. 32, fig. 23. *Barleecia elongata* "n. sp." Locard,

1886:272 and 576. Type locality: Roussillon (Mediterranean France).

Material examined: (collected by the author unless otherwise stated; all in MNHN) **Europe:** Guernsey, Vazon Bay, at low tide among corallines, 1000+ specs., 9.1994; Guernsey, Rocquaine Bay, 1000+ specs., 9.1994. Ploumanac'h (Finistère), at low tide on *Corallina*, 300 specs. (many juv.); Lampaul-Ploudalmezeau (Finistère), on *Corallina*, 1000+ specs. (mostly juv.; adults 2.3 × 1.3 to 2.8 × 1.8 mm); Ile de Sein (Finistère), 300 specs.; Guéthary (Pyrénées-Atlantiques), 54* spec. (2.9 × 1.7 to 3.3 × 2.0 mm); St. Jean de Luz (Pyrénées Atlantiques), 30*+ 150 specs. (2.4 × 1.4 to 3.2 × 1.8 mm); Hendaye (Pyrénées-Atlantiques), 200 specs.; San Sebastián (Guipuzcoa), 1000+ specs.; Ondarroa (Guipuzcoa), 1000+ specs.; Calahonda (Málaga), 200 specs.; Los Escullos (Almería), 7 specs. **Strait of Gibraltar, Ceuta:** Benzú, low tide, 4 specs. **Morocco:** Punta Cires, intertidal in algae, 100 specs.; Tangier Bay, El Ghandouri, 20 specs.; Rabat, near Lahlou, 12 specs.; Mohammedia (=Fedala), 30 sh.; Near Tarfaya, 35 specs., Ortea leg. 8.1987 (2.5 × 1.5 to 2.7 × 1.7, pattern of foot checked on rehydrated specimen). **Mauritania:** Baie de l'Etoile, 250 specs. (1.8 × 1.2 to 2.5 × 1.5 mm), Bouchet leg. 1983; Cap Blanc, exposed rocky shore, 18 specs. (16 juv.), Bouchet leg. 1983; Pointe des Maures, 100+ specs., Bouchet leg. 1983. **Senegal:** Dakar area, 500 sh., Marche-Marchad leg.; Anse Bernard, 5 specs., Marche-Marchad leg. **Tenerife, Canary Islands:** Playa Santo Domingo, 75 specs. (50 juv.), Bouchet leg. 7.1981; Punta del Hidalgo, 200 specs. (30 juv.), Bouchet leg. 7.1981; La Tejita, intertidal, 34 sh. (10 juv.), Bouchet leg. 7.1981; Palm-Mar, intertidal, 25 specs., Bouchet leg. 1981.

Description: Shell conical, solid, adults 2.3 × 1.3 to 3.3 × 2.0 mm. Protoconch dome-shaped (450–500 μ in diameter) of 1½ to 1¾ whorls, with very minute spiral rows of pits. Teleoconch of 3¼ to 3½ whorls. Spire whorls rather flat, body whorl rounded and imperforate. Outer lip slightly prosocline, beveled inside to a thin edge. Color of shell reddish brown, paler towards the parietal insertion of the body whorl; plain or with whitish spiral bands, subsutural, median on body whorl and/or periumbilical, rarely entirely of a pale, wax-like color. Operculum dark crimson. Head-foot with superficial plain black pattern on upper part of head, snout, sides of foot and opercular lobes, upper part of propodium with black area extending on the edges, and grading to a broad axial white area; sole entirely colorless. Yellow axial bar on tentacles, large, triangular yellow granular masses behind each eye.

Habitat: On rocky shores, among red algae (preferably *Corallina*) at low water mark or in tidal pools (Southgate, 1982; Borja, 1986a, 1986b, 1987); in shallow photophilous algal mats in the Mediterranean.

Distribution: From the British Isles to Senegal, the Canary Is. and in the Mediterranean (including the Adriatic and the Eastern Mediterranean, but not the Black Sea).

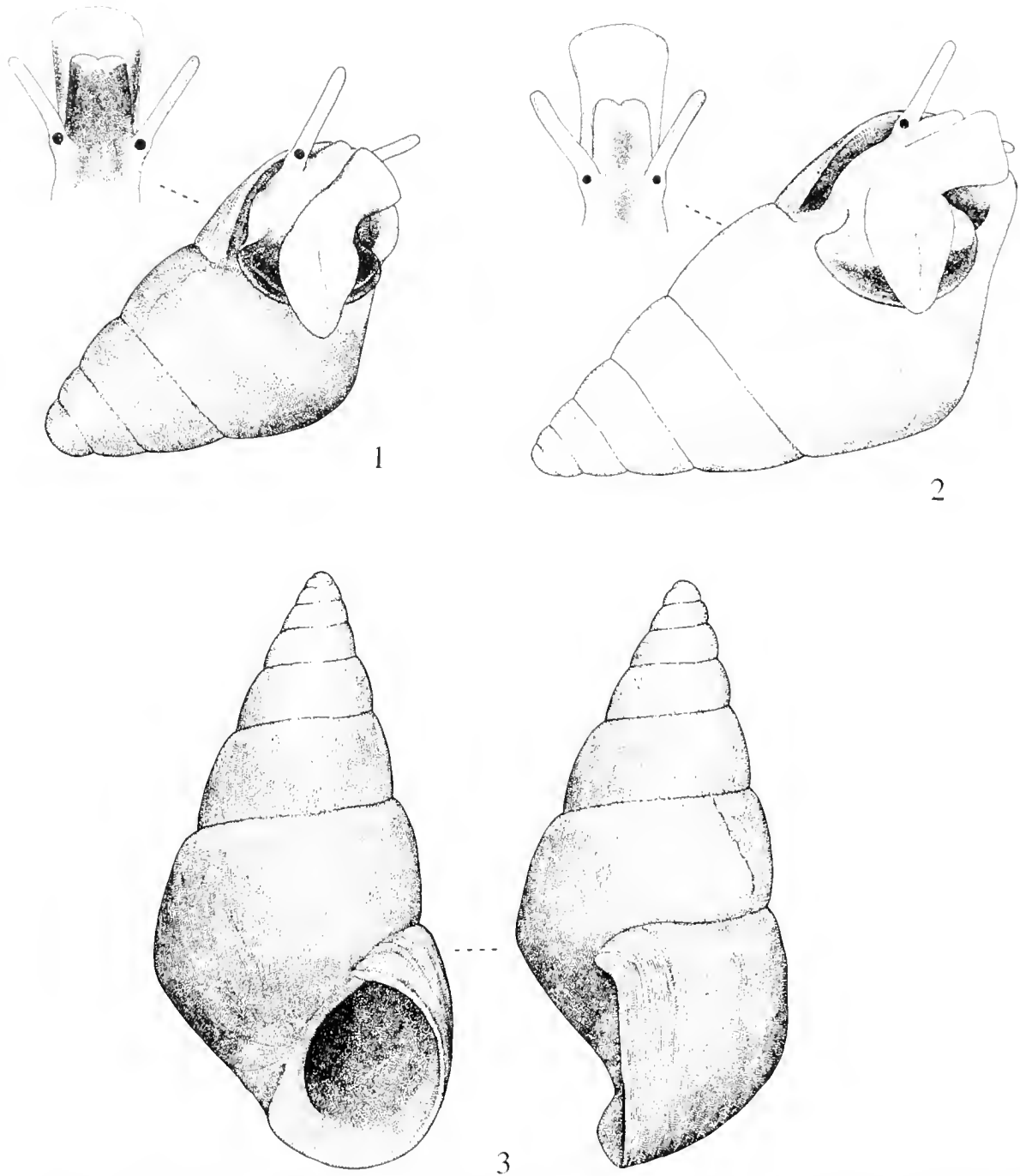


Figure 1. *Barleeia unifasciata* (Montagu, 1803), living animal from Centa. Length of shell 2.6 mm. Figure 2-3. *Barleeia gougeti* (Michaud, 1830). 2. Living animal from Centa. Length of shell 4.3 mm. 3. Specimen from Dakar, length 5.6 mm.

Remarks: The above description is based on specimens from Western Europe and Morocco; such typical *B. unifasciata* are found as far south as Tafaya, Morocco. The populations examined from Baie de l'Étoile, Mauritania and from Senegal are smaller, paler, with more variable profile, but are tentatively assigned to *B. unifasciata* pending further study.

Bellon-Humbert (1974) has figured *Barleeia unifasciata* from Morocco as "*Barleeia minuscula* Montero-

sato", and the sympatric *B. gougeti* as "*B. rubra*"; Monterosato's (1889) description and indication of size (1.5 mm) for *B. minuscula*, although laconic, fit *Coriandria fulgida* (Adams, 1797), a common species on the entire Atlantic coast of Morocco. I consider *Barleeia minuscula* a synonym of *Coriandria fulgida*, a view further supported by the fact that Monterosato lists both *B. rubra* and *B. gougeti* but no species referable to *Coriandria*.

Populations from the Canary Islands cannot be distin-

guished conchologically from those of Western Europe, and are thus treated as conspecific although it is likely that very little, if any, genetic exchange occurs. The head-foot of Canarian specimens is darker, and the entire propodium is black.

Barleeia gougeti (Michaud, 1830)
(Figures 2–3, 31–32)

Rissoa gougeti Michaud, 1830:9, pl.1, hg 7–8. Type locality: Senegal.

Hydrobia compacta Jeffreys, 1883:120, pl.9, hg 9 (non *Hydrobia compacta* Carpenter, 1864). Type locality: Tangiers (Morocco).

? *Barleeia majuscula* Monterosato, 1884:69. Type locality: not specified, localities mentioned: Ognina (Sicily), Alger (Algeria), Lampedusa (Sicily channel).

Barleeia gougeti var. *unicolor* Monterosato, 1889:34 (Casablanca, Morocco).

Barleeia gougeti var. *cerca* Monterosato, 1889:34 (Casablanca, Morocco).

Barleeia carrozzai van Aartsen & Giannuzzi-Savelli, 1991 (replacement name for *Hydrobia compacta*)

Material examined: (collected by the author unless otherwise stated; all in MNHN) **Spain:** Tarifa, intertidal, 3 specs. (3.5 × 2.1 mm). **Strait of Gibraltar, Ceuta:** Punta Almira 35–40 m, 38* + 12 specs. (4.3 × 2.3 to 5.5 × 2.8 mm), Bouchet leg. 5.1986; Benzú, 8 sh. (white). **Morocco:** Temara, low tide, 10 spec.; Mouth of Oued Yquem (= Rose-Marie), S. of Rabat, 31 spec., de Lepiney leg.; Mohammedia (= Fedala) 50 sh.; El Jadida (= Mazagan), low tide, 400 specs.; Essaouira (= Mogador), 300 specs. (2.7 × 1.6 to 6.1 × 3.0 mm); Near Tarfaya, 12 specs., Ortea leg. 8.1987. **Mauritania:** Baie de l'Etoile, 140 specs. (2.9 × 1.7 to 4.3 × 2.3 mm), Bouchet leg. 1983. **Senegal:** Dakar, 8 specs. (5.0 × 3.1 to 5.9 × 3.2 mm), Nicklès leg. 1946; Gorée, 7 sh. (pale periumbilical zone), H. Fischer collection; Gorée, baie de St. Jean, 50 specs., Delais leg. 1.1962; Gorée 20 m, 10 specs., Pin leg. 1994, Bel-Air near Dakar, 6–8 m, 59 specs. (3.1 × 1.8 to 5.0 × 2.7 mm, with attached *Crepidula*), Marche-Marchad leg.; Dakar, Anse Bernard, 9 specs., Marche-Marchad leg.; Dakar-ville, 10 specs., Pin leg. 1994.

Description: Shell conical, solid, adults 2.7 × 1.6 to 6.1 × 3.0 mm. Protoconch dome-shaped (500 μ in diameter), of 1½ to 1¾ whorls, with very minute spiral rows of pits. Teleoconch of 4 to 5 whorls. Spire whorls rather flat, profile of body whorl very faintly carinate and imperforate. Outer lip strongly prosocline near its parietal insertion, then nearly orthocline. Columella protruding anteriorly, more pronounced in juveniles, only slightly in adults where the aperture is more rounded. Color of shell reddish brown, paler towards the parietal insertion of the body whorl; plain or with periumbilical whitish spiral zone; sometimes entirely of a pale, wax-like color. Operculum dark crimson. Head-foot with superficial plain black pattern on upper part of head, snout, and opercular lobes; upper part of propodium and sole entirely colorless. Yellow axial bar on tentacles, large, yellow granular

masses behind each eye and (most often) in each opercular lobe anteriorly to the black markings.

Habitat: On hard bottoms with algal concretions, low intertidal to 40 m.

Distribution: From the Strait of Gibraltar to Senegal.

Remarks: This large species occurs sympatrically with *B. unifasciata* all along the coast of NW Africa, from the Strait of Gibraltar southwards. *Barleeia gougeti* is usually subtidal and is restricted to the lowermost part of the tidal zone, whereas *B. unifasciata* is essentially an intertidal species. The relative abundance of both species is variable, with *B. gougeti* the most abundant species south of Rabat in Morocco.

The ranges of sizes in the two species overlap, and the boundary cannot be clearly placed with only conchological characters. The most obvious distinctive character is the pigmentation pattern of the propodium, which has lateral black areas in *B. unifasciata* (a non-variable feature in Brittany and the Basque country where *B. unifasciata* occurs alone), and is white in *B. gougeti*. The columella of *B. gougeti* is more protruding than in *B. rubra*. Populations where an entirely pale shell is the dominant pattern are common in *B. gougeti*.

Barleeia verdensis Gofas, new species
(Figures 4, 33–34)

Type material: Holotype and 120 paratypes (MNCN cat. 15.05/20526); 120 paratypes (MNHN) collected alive from the type locality.

Type locality: Salmanza, São Vicente, Cape Verde Islands, (16°54'N, 24°57'W).

Material examined: (collected by E. Rolán except specimens with date 8.1985 collected by "la expedición ibérica", or where otherwise stated) **Cape Verde Islands, Boavista:** Derrubado, 13 juv. sh. (CER); Rife de Chaves 4 m, 4 sh. + 25* specs. 5.1988 (CER); Baia Teodora 2 m, 32 + 12* specs. 4.1988 (CER); Morro da Areia, 5.1986 (MNCN); Sal Rei, 40 sh., 5.1986 (MNCN) and 38 sh. (CER). **Brava:** Furna, 8 sh. (CER). **Sal:** Mordeira, 3 specs., 5.1986 (MNCN) and 20 sh. (CER); Fontona, 125 specs. (mostly juv.), 8. 1985 (MNCN); Curral do Dado, 14 specs. (10 juv.) (MNCN); Joaquim Petinha, 157 specs., 8.1985 (MNCN); Parda, 1 spec. (MNCN); Palhona, 40 sh. + 4* specs., 5.1987 (CER); Sal (without further precision), 44 sh. (CER); Serra Negra, 4* specs., 5.1987 (CER); Calheta Fonda 2–5 m, 15* specs., 5.1988 (CER); Palmeira, 2 + 65* specs., 8.1985 (CER); Rigona, 7 specs., 8.1985 (MNCN). **São Nicolau:** Tarrafal, 3 sh., 8.1985 (MNCN). **Santiago:** Tarrafal, 38 sh. (CER). **São Vicente:** Salmanza, intertidal, 10 specs., Cosel leg. 12.1978 (MNHN); the type material (2.7 × 1.6 to 3.3 × 1.8 mm) and 100+ specs., 8.1985 (MNCN); 12 specs., 5.1987 (CER); Calhau, 4 sh. (CER).

Description: Shell conical with rather tall spire, very solid, adults 2.7 × 1.6 to 3.3 × 1.8 mm (holotype 3.2 ×

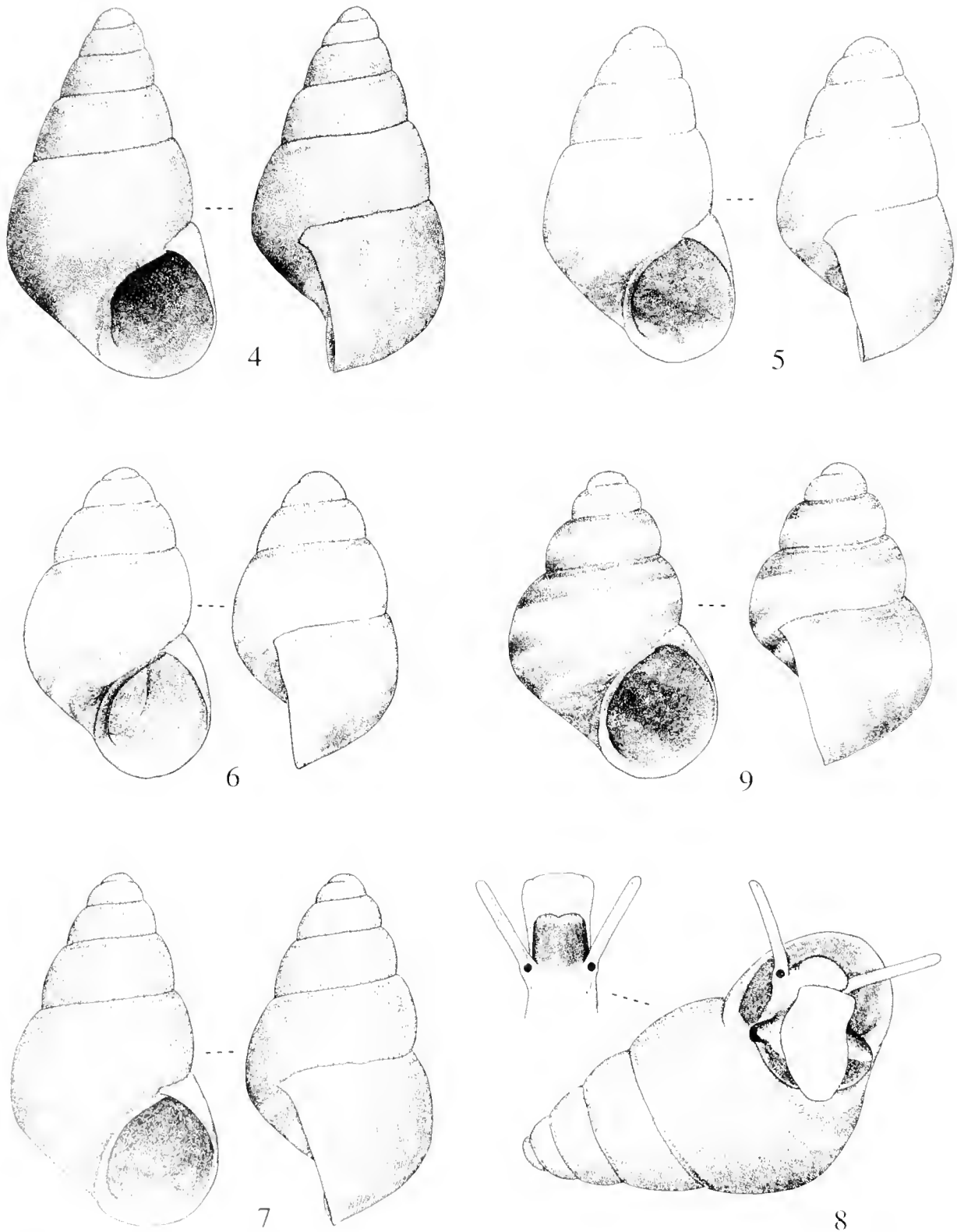


Figure 4. *Barlecia vidensis* Gofas, new species, holotype from Salmanza (São Vicente, Cape Verde Is.), length 3.2 mm **Figure 5.** *Barlecia acemuli* Gofas, new species, holotype from Saragasa (São Vicente, Cape Verde Is.), length 1.7 mm **Figure 6.** *Barlecia chejue* Gofas, new species, holotype from Rile de Chaves (Sal, Cape Verde Is.), length 1.3 mm **Figures 7–8.** *Barlecia tomensis* Gofas, new species **7.** Holotype from Praia das Conchas (São Tomé), length 2.1 mm **8.** Living specimen from Praia das Conchas (São Tomé), length 2.1 mm **Figure 9.** *Barlecia taeniolata* Gofas, new species, holotype from Santa Ana (São Tomé), length 1.6 mm

1.8 mm). Protoconch dome-shaped (350–400 μ in diameter), of $1\frac{1}{4}$ whorls, with very minute pits arranged in crowded spiral rows. Teleoconch with 4 whorls. Spire whorls rather flat, body whorl rounded, imperforate. Outer lip slightly prosocline, beveled both outside and inside to a thin edge; parietal callus narrow. Color of shell dark reddish brown, rather uniform except for a paler area towards the parietal insertion of the body whorl and a poorly defined paler band around the columellar area. Head-foot black except for the sole, the sides of the snout, and the tentacles. Yellow axial bars formed by crowded granules on tentacles; yellow granular masses on opercular lobes.

Habitat: Intertidal or shallow subtidal, among algae.

Distribution: Cape Verde Islands.

Remarks: This species resembles *B. unifasciata* and has been identified as "*B. rubra*" in the literature (e.g. Cosel, 1982 and references therein). It is distinguished by its smaller protoconch, with more crowded rows of pits, taller spire, and peculiar profile of the body whorl, due to the fact that the aperture is beveled not only inside as in other *Barleeia*, but also outside. It is distinguished from *B. gougeti* by its smaller size and less protruding columella.

Barleeia aemilii Gofas, new species
(Figures 5, 35–36)

Type material: Holotype and 40 paratypes (MNCN cat. 15.05/20527); 40 paratypes (MNHN) collected alive from the type locality.

Type locality: Saragasa, São Vicente, Cape Verde Islands (16°49'N, 24°52'W).

Material examined: (collected by E. Rolán, except specimens with date 8.1985 collected by "1a expedición ibérica") **Cape Verde Islands, Boavista:** Sal Rei, 2 sh. (MNCN); Rife de Chaves, 4 m, 1 sh., 5. 1988 (CER). **Santa Luzia:** Praia Francisa, 3 sh. (CER). **Sal:** (without precision) 3 sh. (CER); Joaquin Petinha, intertidal, 9 specs., 8.1985 (MNCN) and 1 spec. (CER); Mordeira, 1 sh., 8.1985 (CER); Serra Negra, 1* spec., 5.1987 (CER); Palhona, 4 sh. (CER); Palmeira, on wharf, 8.1985, 2 specs. (MNCN) + 1* spec. (CER); Rigona, 1 spec., 8.1985 (MNCN); Rabo de Junco, 20 sh., (CER). **Santiago:** S of Tarrafal, 7 specs. + 16 sh. (CER); Prainha, Praia, 6 specs. (CER). **São Vicente:** Calhau, 11 sh. (CER); Saragasa, the type material, 8.1985 (1.4 \times 0.85 to 1.75 \times 1.0 mm); Salmanza, intertidal, 8.1985, 1 spec. (MNCN) + 30 specs., 5.1987 (CER) + 4* specs. (CER); Mindelo, Baía Matiota, 1 spec., Cosel leg. 12.1978 (MNHN).

Description: Shell conical, solid, adults 1.4 \times 0.85 to 1.8 \times 1.0 mm (holotype 1.7 \times 0.95 mm). Protoconch dome-shaped with flattened top (280–300 μ in diameter), $1\frac{1}{4}$ whorls, with very minute spiral rows of pits. Teleoconch of 3 to $3\frac{1}{4}$ whorls. Spire whorls rather flat, body whorl

very slightly angulated. Outer lip slightly prosocline, beveled inside to a thin edge; parietal callus narrow, detached over a tiny umbilical chink. Color of shell pale orange brown, paler towards the parietal insertion of the body whorl; with a sharply defined paler band along the angle of the body whorl, and a less clear pale band around the umbilical chink. Parietal callus tinged with brown. Shell of some individuals entirely of a pale, orange-brown color. Periostracum dull. Operculum reddish brown, more intense along the ridge and edges. Head-foot pale, with yellow axial bars on tentacles; greenish, iridescent buccal mass visible in the head by transparency.

Habitat: Intertidal or shallow subtidal, among algae.

Distribution: Cape Verde Islands.

Remarks: This species is readily distinguished from the previous one by its smaller size, banded color pattern and more pupoid profile. It is most closely related to *B. chefciae* n.sp., which is still smaller, has a more rounded periphery of the body whorl, and has a glossy periostracum rather than the dull, opaque texture found in *B. aemilii*. This species is dedicated to Dr. Emilio Rolán, of Vigo (Spain), a distinguished amateur who has been involved in most of the recent collecting in the Cape Verde Islands.

Barleeia chefciae Gofas, new species
(Figures 6, 37–38)

Type material: Holotype (live collected) and 2 paratypes (sh.) from the type locality (MNCN cat. 15.05/20528), 12 paratypes (sh.) from Porto Ferreiro (MNCN cat. 15.05/20529), 24 paratypes (sh.) from Sal Rei (12 MNCN cat. 15.05/20530, 12 MNHN).

Type locality: Rife de Chaves, Boavista, Cape Verde Islands, in 4 m.

Material examined: (collected by E. Rolán except specimens with date 8.1985 collected by "1a expedición ibérica") **Cape Verde Islands, Boavista:** Derrubado, 2 sh. (CER); Baía Teodora, 1 sh. (CER); Porto Ferreiro, 4 m, 12 sh. (paratypes); Rife de Chaves, 4 m, the holotype, 2 paratypes (sh.) and 6 sh., 5.1988; Sal Rei, 24 sh. (paratypes), 8.1985. **Brava:** (no further details), 39 sh. (CER); Furna, 8 specs. (CER). **Santa Luzia:** Praia Francisa 1 m, 4 sh. (CER). **Santiago:** Tarrafal, 2 sh. (CER). **Sal:** Palhona, 1* spec. (CER). **São Vicente:** Saragasa, 2 specs., 8.1985 (MNCN); Pedrinha 2 sh. (CER).

Description: Shell pupoid, moderately solid, translucent, adults 1.1 \times 0.7 to 1.3 \times 0.75 mm (holotype 1.3 \times 0.75 mm). Protoconch dome-shaped with flattened top (260–270 μ in diameter), $1\frac{1}{4}$ whorls, with very minute spiral rows of pits. Teleoconch of 3 to $3\frac{1}{4}$ whorls. Spire whorls rather flat, body whorl rounded. Outer lip very slightly prosocline, beveled inside to a thin edge; parietal callus narrow, detached over a tiny umbilical chink. Color of shell brownish, with two sharply defined paler bands along the periphery of the body whorl, and around the

umbilical chink, and a broad, ill-defined pale area running along the whorls almost from suture to suture; a dark subsutural line ("false suture") corresponds to the inner surface of the whorl seen by transparency. Parietal callus and periumbilical area dark. Operculum colorless, translucent. Animal not observed.

Habitat: Shallow subtidal, among algae.

Distribution: Cape Verde Islands.

Remarks: This species is closely allied to the previous one, but has a distinctive, *Coriandria*-like appearance with its small size, glossy, pupoid shell and distinct banding pattern. It is also distinguished from all other species treated here by the colorless, translucent operculum. The correct placement in *Barleeia* is ascertained by the characters of the protoconch, operculum and radula.

This species is dedicated to Maria Josefa "Chefi" Alvarez Aza, Dr. Rolán's wife and a companion of the Cape Verde expeditions.

Barleeia tomensis Gofas, new species
(Figures 7–8, 39–40)

Type material: Holotype (MNHN) and 24 paratypes (12 MNHN, 12 MNCN cat. 15.05/20531) collected alive from the type locality.

Type locality: Praia das Conchas, São Tomé (00°24.7'N, 06°38.0'E), at low tide.

Material examined: São Tomé: Esprainha, 50* + 58 specs., Gofas and Fernandes leg. 11.1985 (MNHN); Praia das Conchas, the type material, Gofas and Fernandes leg. 11.1985; Praia das Conchas, 13 sh., Rolán leg. (CER); Mutamba, 28 specs., Fernandes leg. 12.1986 (MNHN); Mutamba, 53 sh., Rolán leg. (CER); Lagoa Azul, 5 sh., Rolán leg. (CER); Praia Morro Peixe, 2 specs., Gofas leg. 11.1983 (MNHN); Santa Ana, 2 m, 11 specs., Rolán leg. (CER).

Description: Shell conical, solid, adults 1.8 × 1.1 to 2.4 × 1.3 mm (holotype 2.1 × 1.2 mm). Protoconch high dome-shaped (350 μ in diameter) of 1½ to 1¾ whorls, with very minute spiral rows of pits. Teleoconch with 3¼ to 3½ whorls. Spire whorls moderately convex, body whorl rounded and imperforate. Outer lip slightly prosocline, beveled inside to a thin edge; parietal callus rather thin. Color of shell reddish brown, paler towards the parietal insertion of the body whorl; typically with two periumbilical spiral bands on body whorl. Operculum dark crimson. Head-foot with superficial black pattern covering the snout, fading behind the head; on opercular lobes and anteriorly on the sides of the epipodial folds; whitish-yellow axial bar on tentacles, whitish/yellow granular masses behind each eye, on the tip of the snout, on the sole of the foot and the propodium, and on the opercular lobes anteriorly to the black markings.

Habitat: Intertidal to shallow subtidal on rocky shores with clear water; in algal growth of coralline and encrusting red algae.

Distribution: Only known from the Islands of São Tomé and Príncipe.

Remarks: This species was cited by Tomlin and Shackelford (1914) and Fernandes and Rolán (1993) as *Barleeia rubra*. The spotted sole of the foot distinguishes it from *B. gougeti* and *B. unifasciata*, which always have a colorless sole. The high spire recalls that of *B. verdensis* n. sp., but *B. tomensis* has a constant, characteristic double pale band around the umbilicus, and does not have the aperture beveled outside.

Barleeia taeniolata Gofas, new species
(Figures 9, 41–42)

Type material: Holotype and 5 paratypes (MNCN cat. 15.05/20532), empty shells from the type locality. 5 paratypes (sh.) from Lagoa Azul (MNHN).

Type locality: Santa Ana, São Tomé (00°15.5'N, 06°45'W), 2 m.

Material examined: São Tomé: Santa Ana, 2 m, 6 sh., Rolán leg. (holotype and paratypes MNCN); Baía de Ana Chaves, 2 m, 5 sh., Rolán leg. (CER); Praia das Conchas, 5 m, 1 sh., Rolán leg. (MNHN); Praia das Conchas, 2 sh., Gofas leg. (MNHN); Lagoa Azul, 4 m, 14 sh., Rolán leg. (paratypes MNHN; CER); Mutamba, 4 m, 21 sh., Rolán leg. (CER). Príncipe: Santo Antonio, 6–10 m, 1 sh., Rolán leg. (CER).

Description: Shell conical, rather translucent, holotype 1.6 × 1.05 mm. Protoconch high dome-shaped (300 μ in diameter) of 1¼ whorls, with very minute spiral rows of pits. Teleoconch with 3 whorls. Spire whorls convex, body whorl rounded and imperforate. Outer lip slightly prosocline, thin; parietal callus rather thin. Color of shell of a pale horny color, with two brown bands on the spire whorls and two more on the body whorl, one continuing the suture and one periumbilical; the two central bands on the body whorl commonly fused to form one broad band. Operculum and animal unknown.

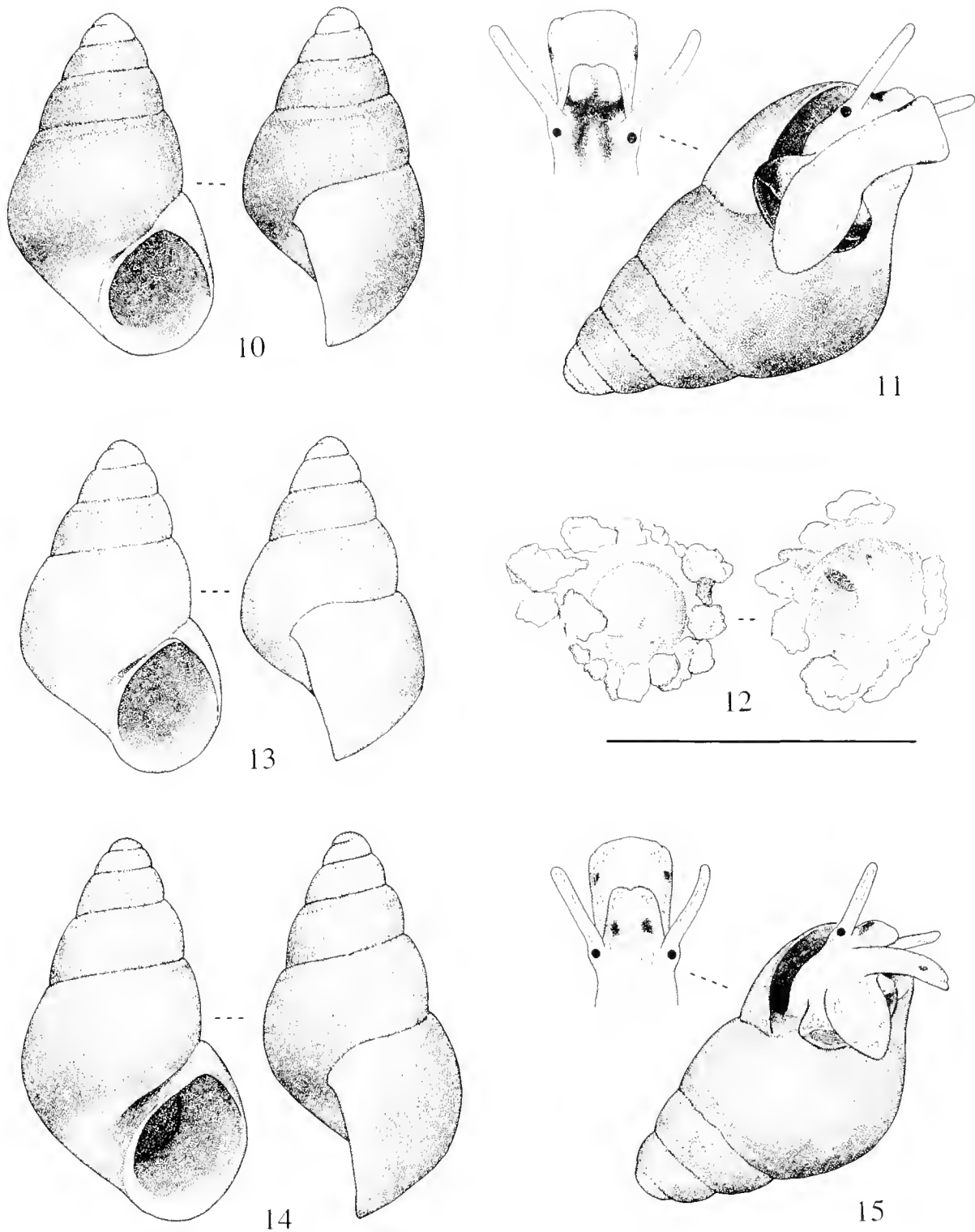
Habitat: Unknown, presumably sublittoral in shallow water.

Distribution: Only known from the Islands of São Tomé and Príncipe.

Remarks: The pitted protoconch of this species is characteristic of *Barleeia* although the shell resembles a *Coriandria* at first glance. It is easily separated from juvenile *B. tomensis* by the shorter spire, more convex whorls, and different color pattern. *Barleeia taeniolata* always has a pale area separating the suprasutural and subsutural brown bands on the whorls, whereas *B. tomensis* only has periumbilical pale bands.

Barleeia pervulgata Gofas, new species
(Figures 10–15, 47–52, 71–72)

Type material: Holotype (MNHN) and over 2000 paratypes (500, of which 100 are juveniles, in each of the



Figures 10–12. *Barleeia pervulgata* Gofas, new species. **10.** Holotype from Chapeu Armado (Angola), length 2.2 mm. **11.** Living animal from Chapeu Armado (Angola), length of shell 2.7 mm. **12.** Egg capsule containing a larva ready to hatch, from Chapeu Armado (Angola). Scale bar 1 mm. **Figures 13–15.** *Barleeia cf. pervulgata* Gofas, new species. **13.** Specimen of a “pale” morph from Santa Maria (Angola), length 2.1 mm. **14.** Specimen of a subtidal morph from Santa Maria (Angola), length 2.4 mm. **15.** Living animal of a subtidal morph from Porto Alexandre (Angola), length of shell 1.7 mm.

following: AMS cat. C.305091, MNCN cat. 15.05/20533, MNHN, UAN) collected alive from the type locality.

Type locality: Chapeu Armado, province of Namibe, Angola (14°27'S, 12°21'E), intertidal.

Material examined: (collected by the author; all MNHN except paratypes specified above) **Angola:** (*typical form*) Caotinha, 2800+ specs. (1.8 × 1.1 to 2.4 × 1.4 mm); Limagens, 800 specs., 12.1981 (1.7 × 1.0 to 2.2 × 1.3 mm); Santa Maria, intertidal, 1000 specs., 12.1981 (1.8 × 1.1 to 2.2 × 1.3 mm, many pale specs.); Santa Maria, dredged 8–10 m, 200 sh.; Lucira (Bissonga), 37 specs. (1.7 × 1.0 to 2.1 × 1.3 mm); Baía das Pipas, 300* specs., 2.1983 (2.4 × 1.5 to 2.9 × 1.7 mm); São Nicolau, 22* + 100* specs., 2.1983 (2.1 × 1.3 to 2.9 × 1.7 mm); Chapeu Armado, the type material (1.9 × 1.2 to 2.7 × 1.6 mm); Praia das Conchas, 200 specs. (2.2 × 1.4, to 2.8 × 1.7 mm); Praia Amelia, 400 + 18* specs., 2.1983 (1.6 × 1.0 to 2.5 × 1.4 mm, some white specs.). (*pale, banded form*) Caotinha, 2 specs. + 8 sh.; Limagens, 130 specs., 12.1981 (1.6 × 1.1 to 2.3 × 1.4 mm); Santa Maria, 0–2 m, 1 sh.; Sta Maria, 8–10 m, 12.1981 on calcareous algae: 50 specs. + 8 sh. (2.4 × 1.4 to 1.8 × 1.2 mm); Lucira (Bissonga), 2 specs.; São Nicolau, 7* + 25 specs. (2.1 × 1.2 to 2.2 × 1.3 mm); Chapeu Armado, 9 specs. + 24 sh. (2.0 × 1.3 to 2.7 × 1.6 mm); Praia Amelia, 19 specs. + 1 sh.; Baía dos Tigres, in mussel bed, 12* + 3000 specs., 8.1985. (*more delicate form from deeper water*): Santa Maria, 8–10 m, 12.1981 on calcareous algae, 600 specs.; Baía da Lucira (Cesar), 10 m, 10 sh.; Santa Marta, 40 m in shell sand, 100 sh.; Praia Amelia, 40–60 m, 25 sh.; off Porto Alexandre, 5* + 2 specs. (1.7 × 1.1 to 2.2 × 1.3 mm).

Description: Shell conical, very solid, adults 1.7 × 1.0 to 2.9 × 1.7 mm (holotype 2.2 × 1.3 mm). Protoconch dome-shaped (350 μ in diameter) of 1½ to 1¾ whorls, with very minute spiral rows of pits, sometimes also with ill-defined spiral sculpture. Teleoconch with 3¼ to 3½ whorls. Spire whorls rather flat, body whorl rounded and hardly umbilicate. Outer lip slightly prosocline, beveled inside to a thin edge; parietal callus thickened in adults, tending to form a ridge. Color of shell reddish brown, paler towards the parietal insertion of the body whorl; plain or with whitish spiral bands, subsutural, median on body whorl and/or periumbilical; rarely entirely of a pale, wax-like color. Operculum dark crimson. Head-foot with superficial black pattern on upper part of head generally forming a V-shaped pattern pointing forwards, then extending over the snout to the sides and axially; two small black spots on the sides of the propodium, sometimes also a pair of larger, blurred, black to grayish spots on the axial part of the propodium; opercular lobes black. Yellow axial bar on tentacles; yellow granular masses behind each eye, on each lobe of the tip of the snout and on opercular lobes anteriorly to the black areas; sole of foot circled by a line of yellow granules.

Habitat: Intertidal to shallow subtidal on rocky shores with clear water; in algal mats, mainly of coralline algae.

Distribution: Known only from the provinces of Benguela and Namibe, Southern Angola.

Remarks: This is by far the commonest *Barleecia* of Southern Angola. It somewhat resembles the European species *B. unifasciata* but is readily diagnosed by the yellow patterns on the foot, absent in the former.

The egg capsule (Fig. 12) has been observed in Chapeu Armado, and is very similar to that of *B. unifasciata* (Lebour, 1934; Southgate, 1982). It is spherical, contains a single developing larva, and is attached to the algal mat and embedded sand grains.

The above description (and Figs 10–11) is based on the populations commonly found in the intertidal zone from Caotinha to Praia Amelia. Besides this, there are two forms which may be distinguished morphologically and are sympatric in most localities:

(1) One form has a paler, commonly banded shell, with slightly more convex whorls and more distinct umbilical clink (Fig. 13). Such specimens also commonly have a taller protoconch, with more conspicuous spiral pattern. They are found on the shore at slightly lower levels than typical *B. pervulgata*, which is restricted to the shore. These forms look quite different at first glance, but many individuals cannot be convincingly separated within microsympatric populations; the sample from Limagens (intertidal) contains many banded forms of ambiguous morphology (e.g. with banded pattern but not with convex whorls). Also, the color pattern of the animal, usually a useful character at species level, varies within the same limits in both forms.

(2) A second form with a more delicate, taller, plain brown shell, occurring always subtidally on soft bottoms with calcareous algal concretions (Figs 14–15). This form never occurs microsympatrically with typical *B. pervulgata*, but is found in Santa Maria together with the above "paler" form in 5–10 m, where both forms cannot be convincingly separated. The color pattern of the animal is not very different from that of palest intertidal morphs.

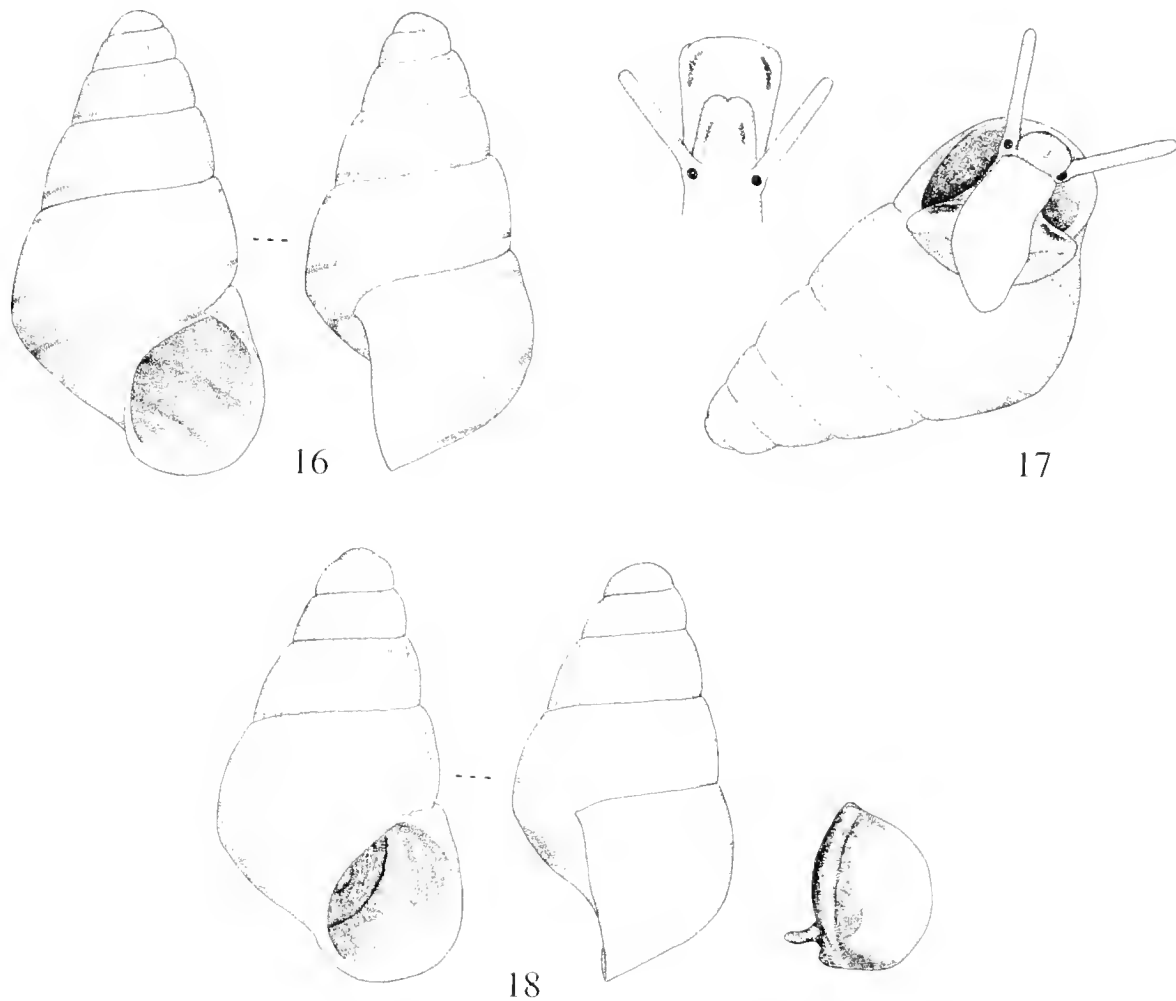
More study (e.g. using allozyme electrophoresis) may be necessary to determine whether the differences are merely ecophenotypic variation, or if there are more than one species with overlapping variation and/or limited introgression.

Barleecia cinguloides Gofas, new species
(Figures 16–17, 43–44)

Type material: Holotype (MNHN) and 64 paratypes (16 of which 4 juv., in each of the following: AMS cat. C.305092, MNCN cat. 15.05/20534, MNHN, UAN) collected alive from the type locality.

Type locality: Praia Amelia, province of Namibe, Angola (15°13'S, 12°07'E), intertidal.

Material examined: (collected by the author; all MNHN except paratypes specified above) **Angola:** Baía de Santa Maria 8–10 m, 5 sh.; Santa Marta, 40 m, 2 sh.; Baía das Pipas, 53* specs., 2.1983 (2.2 × 1.2 to 2.4 × 1.4 mm);



Figures 16–17. *Barleeia cinguloides* Gofas, new species. **16.** Holotype from Praia Amelia (Angola), length 2.4 mm. **17.** Living specimen from Praia Amelia (Angola), length of shell 2.4 mm. **Figure 18.** *Barleeia picta* Gofas, new species, holotype from Santa Maria (Angola), and operculum seen from outer side; length of shell 1.8 mm

Praia Amelia, intertidal, the type material (adults 2.2×1.3 to 2.5×1.4 mm) and 50 specs. (juv.).

Description: Shell high conical, quite solid, translucent, adults 2.2×1.2 to 2.5×1.4 mm (holotype 2.4×1.3 mm). Protoconch high dome-shaped (350μ in diameter) of $1\frac{1}{2}$ to $1\frac{3}{4}$ whorls, with spiral rows of relatively coarse pits, some of them irregularly fused along one row. Teleoconch with $3\frac{1}{4}$ to $3\frac{1}{2}$ whorls. Spire whorls rather flat, body whorl with a faint but sharp keel continuing the suture, imperforate. Outer lip nearly orthocone except for the parietal insertion where it is prosocline, beveled inside to a thin edge; parietal callus moderately thickened. Color of teleoconch pale buff, with narrow brown lines, one subsutural, one suprasutural on the spire and running just above the keel on body whorl, and one periumbilical. Operculum pale brown, external surface shagreened with hardly visible growth lines. Head-foot with superficial black pattern forming two patches anteriorly on each side of propodium, two longitudinal

streaks on the snout and patches on opercular lobes. A solid yellow bar on tentacles, yellow granular masses behind eyes, small yellow spots on each lobe of the snout, and on the sides of propodium; sole colorless.

Habitat: Intertidal on rocky platforms, among rocks covered with coralline algae and lying on coarse, clean sand

Distribution: Known only from the provinces of Benguela and Namibe, Southern Angola.

Remarks: This species recalls the European rissoid *Cingula cingillus* (Montagu, 1803) in shape, color pattern, and even the intertidal habitat in sand under stones. It is readily distinguished from other Barleeidae by its color pattern: banded forms of *B. pervulgata* never have such narrow lines and lack the peripheral keel. The most closely related species is *B. picta* n. sp., similar in shell shape and in having coarse punctures on the protoconch, but colored with flames instead of spiral lines.

Barleeia picta Gofas, new species
(Figures 18, 45–46)

Type material: Holotype (MNHN) and 37 paratypes (9 AMS cat. C.305093, 9 MNCN cat. 15.05/20535, 10 MNHN, 9 UAN) collected alive from the type locality.

Type locality: Baía de Santa Maria, province of Benguela, Angola (13°35'S, 12°33'E), on calcareous algal bottom in 8–10 m.

Material examined: (collected by the author; all MNHN except paratypes specified above) **Angola:** off Ambrizete, 45 m, 7 sh. (2.2 × 1.4 to 2.6 × 1.6 mm, subfossil?); off Ilha de Luanda, 120 m: 1 sh (subfossil); Santa Maria, the type material (1.8 × 1.1 to 2.3 × 1.3 mm); Lucira (Santa Marta), 12 sh. (1.5 × 0.9 to 1.7 × 1.0 mm); Lucira (Cesar), 1 sh.; São Nicolau, 15 sh (1.8 × 1.0 to 1.9 × 1.1 mm); Ponta Albina/Baía dos Tigres, 40 m, 12 sh.

Description: Shell conical, translucent, adults 1.5 × 0.9 to 2.3 × 1.3 mm (holotype 1.8 × 1.0 mm). Protoconch dome-shaped (300 μ in diameter) of 1½ to 1¾ whorls, with ill-defined, flat spirals and covered with spiral rows of rather coarse, pits. Teleoconch with ¾ to 4 whorls. Spire whorls flat, body whorl faintly angulated along a line continuing the suture, non-umbilicate. Outer lip orthocone, with very thin edge, thickened in the adult at some distance from its edge. Color of shell very pale buff to pinkish on apical whorls; two last whorls with a series of very faint subsutural flames, a colorless zone around the periphery of the body whorl; another series of faint flames on periumbilical area, matching the subsutural ones or merged into a continuous darker periumbilical band. Operculum dark crimson, along the ridge and edges, pale yellowish on distal surface; external surface shagreened with hardly distinct growth lines. Patterns of animal not observed in life, seen on rehydrated specimens to have black markings on opercular lobes and on the snout.

Habitat: On bottoms of calcareous red algae ("maerl") in a few meters depth and clear water.

Distribution: Known only from Angola; live-taken only in the province of Benguela, Southern Angola.

Remarks: This species shares with *B. cinguloides* the sculpture of very coarse pits in the protoconch. Shells found on the continental shelf of Northern Angola are similar, but larger. They are presumably derived from Pleistocene deposits which occur in 50–120 m; the material in such samples contains many littoral species, including some now restricted to the south.

Genus *Pseudodiala* Ponder, 1967

Type species: *Diala acuta* Carpenter, 1864, by original designation.

Shell with smooth, rather thin teleoconch, very narrowly umbilicate, generally whitish; spire whorls rather flat, body whorl with a faint peripheral keel. Aperture ovate,

with a thin, opisthocline outer lip. Operculum as in *Barleeia*.

Radula (Ponder, 1983 and herein, Fig. 73–74): central tooth with a large median cusp with blunt tip, and 2–3 small lateral denticles; one sharp basal denticle on each side, separated by a broad U-shaped projection. Lateral and marginal teeth as in *Barleeia*.

Ponder (1983) synonymized *Pseudodiala* with *Barleeia*, but *P. niso* n. sp. shares with the type species of *Pseudodiala*, *P. acuta*, the opisthocline aperture (see Fig. 19) and the narrow central cusp of the radula. The West African species assigned to *Pseudodiala* also stand apart from *Barleeia* by their habitat on soft bottoms of the shelf rather than in intertidal or shallow subtidal hard bottom biota. These are retained as a separate group on these grounds.

Pseudodiala niso Gofas, new species
(Figures 19, 53–54, 73–74)

Type material: Holotype collected alive (MNHN) and 55 paratypes (15 AMS cat. C.305094, 20 MNCN cat. 15.05/20536, 20 MNHN), empty shells from the type locality.

Type locality: Senegal, off Gorée, 50 m (14°32'N, 17°25.5'W).

Material examined: (all MNHN except paratypes specified above) **Senegal:** off Gorée, 50 m, the holotype and 55 paratypes (sh.), Marche-Marchad leg.; Cap de Naze, 25 m, from fish stomach, 3 spec. (3.2 × 1.8 to 3.5 × 2.0 mm), Marche-Marchad leg.; Off Saloum, 50 m, 28 sh., Marche-Marchad leg.; "Petite côte" (i.e. coast between Dakar and the Saloum estuary), 32 m, 1 spec., Leung-Taek leg.

Description: Shell conical, translucent, adults 2.7 × 1.5 to 3.5 × 2.0 mm (holotype 2.7 × 1.7 mm). Protoconch stub-shaped with rounded top (400 μ in diameter) of 1½ to 1¾ whorls, with imperforate surface, ill-defined, flat spirals and a very definite suprasutural keel. Teleoconch with 3½ to 4½ whorls. Spire whorls hardly convex, body whorl carinate along a line continuing the suture, distinctly umbilicate. Outer lip strongly opisthocline, beveled to a quite thin edge, parietal callus separating from the body whorl in adults. Color of shell uniformly whitish to grayish. Operculum dark crimson, with a faint external ridge along the columellar side. Animal not observed.

Habitat: On the continental shelf, 30–100 m.

Distribution: Known only from Senegal.

Remarks: The imperforate protoconch of this species is atypical in the Barleidae, but this character state is bridged to the more usual pitted protoconch by the tiny punctures of the next species *P. acquinotialis* n. sp. The faint suprasutural keel in the protoconch of *P. niso* is homologous to the stronger suprasutural spiral ridge in *P. acquinotialis*, and the overall similarity in protoconchs indicates a close relationship between these spe-

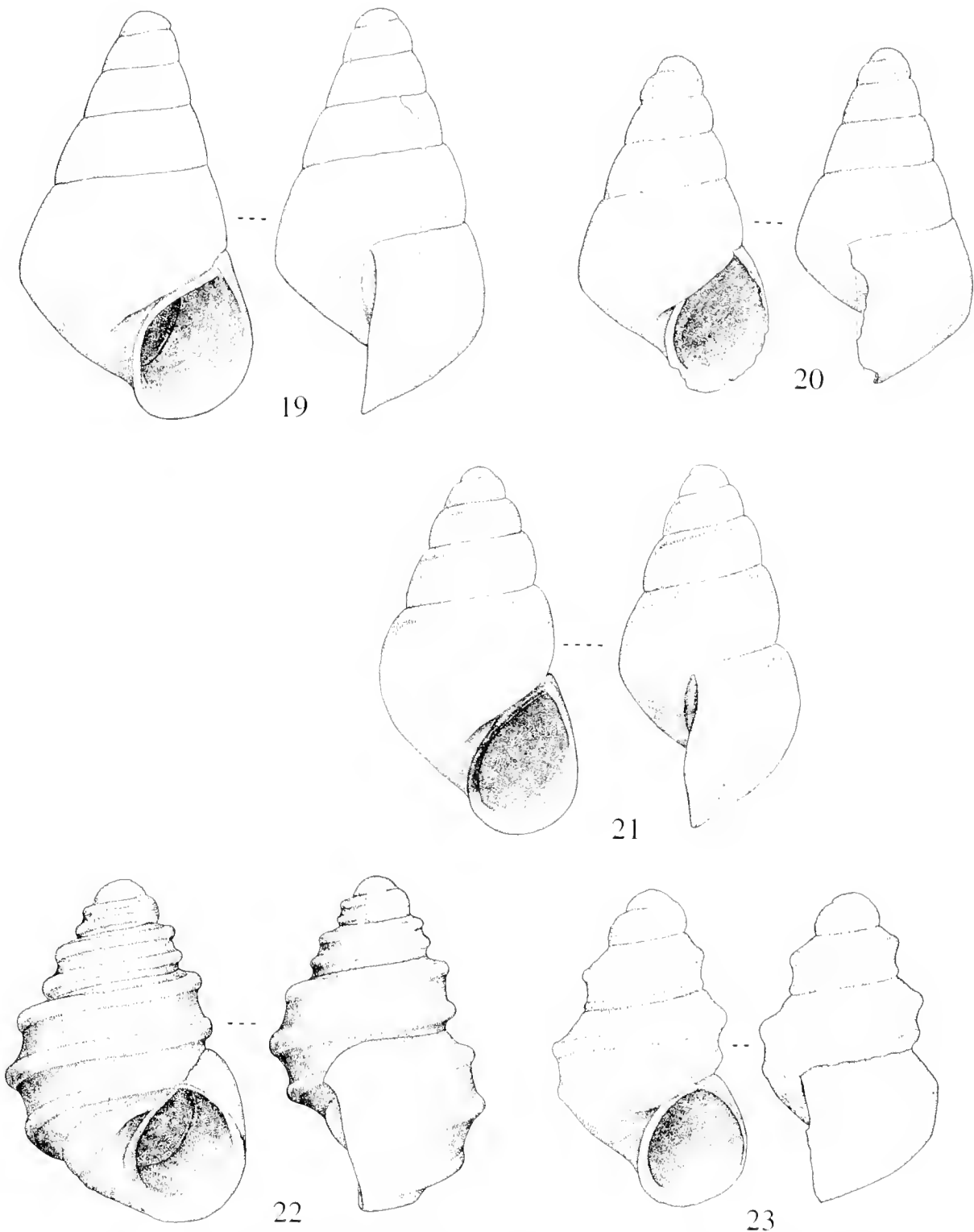


Figure 19. *Pseudodiala niso* Gofas, new species, holotype from off Gorée (50 m), Senegal, length 2.7 mm **Figure 20.** *Pseudodiala acquinotialis* Gofas, new species, holotype from off Equatorial Guinea (150 m), length 1.6 mm **Figure 21.** *Pseudodiala corollaria* Gofas, new species, holotype from Santa Ana, São Tomé, length 1.7 mm **Figure 22.** *Tropidorissoia taphrodes* Tomlin & Shackelford, 1915, specimen from Praia das Conchas, São Tomé, length 1.7 mm **Figure 23.** *Tropidorissoia secunda* Rolán & Templado, 1994, paratype (MNHN) from Praia Emilia, São Tomé, length 1.1 mm

eres. The name is allusive to the resemblance with the eulimid genus *Niso*.

Pseudodiala aequinoctialis Gofas, new species
(Figures 20, 55–56)

Type material: The holotype (MNHN).

Type locality: Equatorial Guinea (01°40'N, 09°25'W), 150 m.

Material examined: Equatorial Guinea: the holotype. **Príncipe:** Santo Antonio, 6–10 m, 21 sh., Rolán leg. (CER); Baía das Agulhas, 8 m, 21 sh., Rolán leg. (CER).

Description: Shell conical, translucent, adults 1.6 × 1.0 to 2.4 × 1.3 mm (holotype 1.6 × 0.9 mm). Protoconch globular with rounded top (300 μ in diameter) of 1½ whorl, with broad spiral ridges, the lowermost of which forms a suprasutural keel, and tiny punctures evenly distributed without lineations. Teleoconch with 3½ whorls, externally smooth, sometimes with irregular internal punctures seen by transparency. Early spire whorls somewhat convex, body whorl carinate along a line continuing the suture, distinctly umbilicate. Outer lip strongly opisthocline, thin. Color of shell uniformly whitish to grayish. Animal and operculum not observed.

Habitat: Unknown, holotype collected as an empty shell on the continental shelf (150 m depth), from a geotechnical core for petroleum exploration, additional material dredged in 6–10 m on soft bottoms around the island of Príncipe.

Distribution: Known from Equatorial Guinea and the island of Príncipe.

Remarks: This species is allied to *P. niso*, with which it shares the general shape, opisthocline lip (broken on all specimens but inferred from the growth lines), the keeled and umbilicate body whorl. It is readily distinguished from *P. niso* by its protoconch with distinct spirals and tiny perforations. It is distinguished from the next species *P. corollaria* n. sp. by lacking the brown color on the parietal side of the aperture, by its larger size, higher spire, flatter whorls and by the profile of its last whorl, which is slightly angulose (more conspicuously in immature specimens).

The holotype, collected in a box core, is slightly immature and possibly derived from a Pleistocene deposit, but is the best preserved specimen. On some specimens from Príncipe, some tiny and evenly distributed punctures can be seen by transparency inside the spire whorls. This feature may be restricted to some specimens and could not be seen on the holotype.

Pseudodiala corollaria Gofas, new species
(Figures 21, 57–58)

Type material: Holotype (MNCN cat. 15.05/20536) and 7 paratypes collected alive from the type locality. 3 paratypes (MNHN) collected alive from Praia Mutamba.

Type locality: Santa Ana, São Tomé (00°15.5'N, 06°45'W), 2 m.

Material examined: (all collected by E. Rolán) **São Tomé:** Santa Ana, 2 m, 8 specs., (holotype and paratypes MNCN) and 3 sh. (CER); Praia Mutamba, 4 m, 3 specs., (paratypes MNHN); Lagoa Azul, 4 m, 5 sh. (CER); Praia das Conchas, 5 m, 6 sh. (CER).

Description: Shell conical, translucent, adults 1.4 × 0.8 to 1.8 × 1.0 mm (holotype 1.7 × 1.0 mm). Protoconch globular with rounded top (300 μ in diameter) of 1½ whorl, with broad spiral ridges, and tiny irregular pits, very loosely arranged along spiral rows. Teleoconch with 3 to 3½ whorls, externally smooth, sometimes with irregular internal punctures seen by transparency. Spire whorls quite convex, body whorl rounded, distinctly umbilicate. Outer lip strongly opisthocline, thin. Color of shell whitish to grayish, translucent, with the parietal edge of the aperture strongly tinged with brown. Protoconch generally more opaque, tinged with yellowish or reddish. Operculum dark crimson. Animal not observed; remains of a black mantle seen attached to the interior of the shell.

Habitat: On soft bottoms of muddy sand in shallow subtidal sites.

Distribution: Known from the Island of São Tomé.

Remarks: This species differs from the closely related *P. aequinoctialis* by not being carinate at any stage, by its smaller size and more convex whorls, by the more distinctly pitted protoconch, and by the dark columellar edge of the aperture.

Genus *Tropidorissoia* Tomlin and Shackleford, 1915

Type species: *Tropidorissoia taphrodes* Tomlin and Shackleford, 1915, by monotypy.

Shell with stout, solid teleoconch and strong spiral keels, very narrowly umbilicate, generally tinged with brown. Aperture ovate, slightly prosocline to orthocline, with smooth inner lip, thickened at some distance inside and then beveled to a thin edge. Protoconch with spiral series of pits, with or without superimposed spiral cords. Head-foot pigmented with black and/or yellow. Operculum as in *Barleecia* except for pale brown color. Radula (Fig. 75–76) as in *Barleecia*.

All the species from St. Helena (*Rissoa aqua*, *R. perfecta*, *R. platia*, *R. varicifera*, *R. vaga*, *R. wallichi*, *R. simulans*, all of Smith, 1890) classified or tentatively classified in *Tropidorissoia* by Tomlin and Shackleford (1915) were referred or tentatively referred by Ponder (1985) to his new rissoid subgenus *Lirocingula*, on the basis of conchological similarity with the South African type species *L. winslowae* (Bartsch, 1928). Data on the soft parts, radulae and opercula are at present wanting for a definitive placement.

Tropidorissoia taphrodes Tomlin and Shackleford, 1915 (Figures 22, 59–60, 75–76)

Tropidorissoia taphrodes Tomlin and Shackleford, 1915 pl.5, fig. 5.

Type material: Holotype (live collected) in British Museum (Natural History); 15 paratypes in National Museum of Wales, Cardiff, cat. 1955.158.1121.

Type locality: Island of São Tomé.

Material examined: São Tomé: Esprainha, 19* + 30 specs., Gofas and Fernandes leg. 11.1985; Praia Mutamba, 9 specs., Fernandes leg. 12.1986; Praia Mutamba, 6 sh., Rolán leg. (CER); Lagoa Azul, 5 m, 5 sh., Rolán leg. (CER); Praia das Conchas (Guadalupe), 19* + 40 specs., Gofas & Fernandes leg. 11.1985; Praia das Conchas, 11 sh., Rolán leg. (CER); Baía de Ana Chaves, 4 sh., Rolán leg. (CER); Santa Ana, 3 specs. Rolán leg. (CER). **Príncipe:** Santo Antonio, 6–10 m, 41 specs. Rolán leg. (CER); Baía das Agulhas, 8 m, 19 specs., Rolán leg. (CER).

Description: Shell conical, solid, adults 0.8×0.5 to 1.2×0.7 mm. Protoconch dome-shaped (350μ in diameter) of $1\frac{1}{2}$ whorl, with strong spiral cords and superimposed minute spiral rows of pits. Teleoconch of 2 to $2\frac{1}{2}$ whorls, with two strong, rounded keels on the spire whorls and with a third similar keel on the body whorl; a spiral thickening around the small umbilical chink. Outer lip slightly prosocline, thickened deep inside, then beveled to a thin edge. Parietal callus moderately developed, detached from the umbilical chink. Color of shell reddish brown, sometimes pale yellowish. Operculum yellow, translucent, with an internal peg. Head-foot with superficial gray pattern on the snout and opercular lobes. Opaque yellowish white flecks axially on tentacles, triangular opaque yellowish-white granular masses behind each eye. Reddish buccal mass clearly seen by transparency. Foot white, with tiny opaque white flecks on the sole; metapodium not conspicuously cleft as in *Barleeia*.

Habitat: Intertidal to shallow subtidal on rocky shores with clear water; in algal mat, mainly of coralline algae.

Distribution: Known only from the islands of São Tomé and Príncipe.

Remarks: Fernandes and Rolán (1993) noted a difference in the populations from Príncipe, these having frequently a pale shell whereas all specimens from São Tomé are uniformly reddish-brown. In the material examined, 36 out of 41 specimens from Santo Antonio and all 19 specimens from Baía das Agulhas are pale.

The protoconch has a peculiar sculpture, quite different from that of most *Barleeia*, but similar to that of "*Barleeia*" *congenita* Smith, 1890 from St. Helena Island (Fig. 63–64).

Tropidorissoia secunda Rolán and Templado, 1994 (Figures 23, 61–62)

Tropidorissoia secunda Rolán and Templado, 1994 237–242, fig. 1–4

Type material: Holotype (MNCN cat. 15.05/6975); Paratypes (3 MNHN, 3 British Museum (Natural History), 3 American Museum of Natural History, 10 CER, 10 private collection of F. Fernandes, Luanda).

Type locality: Praia Emilia, São Tomé ($00^{\circ}21.7'N$ – $06^{\circ}43.5'E$).

Material examined: (collected by E. Rolán) São Tomé: The MNHN paratypes; Praia das Conchas, 6 sh. (CER); Lagoa Azul, 4 m, 25 sh., (CER); Baía de Ana Chaves, 1 sh. (CER). **Príncipe:** Santo Antonio, 6–10 m: 17 sh. (CER); Baía das Agulhas, 8 m, 25 sh. (CER).

Description: Shell conical, solid, adults 0.8×0.5 to 1.2×0.7 mm. Protoconch dome-shaped (220μ in diameter) of $1\frac{1}{2}$ whorl, with minute spiral rows of pits. Teleoconch of 2 to $2\frac{1}{2}$ whorls, with a strong median keel on the spire whorls and with a suprasutural cord which extends on the body whorl to form another keel. Outer lip slightly prosocline, beveled inside to a thin edge. Parietal callus moderately developed, detached to form an umbilical chink. Color of shell white to pinkish. Operculum yellow, translucent. Head-foot with superficial plain black pattern on the snout and opercular lobes. Opaque white axial bar on tentacles, large, triangular opaque white granular masses behind each eye. Pink buccal mass visible by transparency.

Habitat: Subtidal in a few meters depth.

Distribution: Only known from the islands of São Tomé and Príncipe.

Genus *Lirobarleeia* Ponder, 1985

Type species: *Alvania nigrescens* Bartsch & Rehder, 1939 (*Alvania galapagensis* Bartsch, 1911 sensu Ponder, 1983), pending decision of ICZN (see Hertz, 1994 for a discussion of the type species).

Shell with elongate, solid teleoconch and spiral sculpture in all species considered, non-umbilicate or very narrowly umbilicate, generally tinged with brown. Protoconch with minute pits loosely arranged in a spiral direction in the species considered herein; with strong spiral ridges and no pits in the type species. Outer lip opisthocline like in most *Rissoina* species. Head-foot pigmented with black and/or yellow. Operculum as in *Barleeia*.

Radula (Ponder, 1983 and herein, Fig. 77–78): central tooth with a large rectangular median cusp, one large triangular denticle on each side of it, and sometimes one or two very small denticles flanking these on the sides of the tooth; one sharp basal denticle on each side, separated by a broad, prominent lamella. Lateral teeth (one pair) with a rather broad base, terminating with a large, rather trapezoidal cusp flanked by slightly smaller cusps to either side; with a U-shaped projection beneath those. Mar-

ginal teeth (two pairs) narrow, hook-shaped, with uniplicate small cusps towards the distal end.

I have included the three species described here in *Lirobarleeia* despite important differences in both protoconch and teleoconch sculpture. They are congeneric with *L. albolirata* (Carpenter, 1864) and *L. kelseyi* (Dall & Bartsch, 1902), two West American species that Ponder (1983) included in *Lirobarleeia* notwithstanding the same differences. The radula of the two species described here in agrees fairly well with those illustrated by Ponder (1983), although lateral outermost denticles are wanting in the central tooth of *L. sublaevis* n. sp. The specimen figured by Ponder (1983) to illustrate the designated type species *Alvania galapagensis* Bartsch, 1911 has been shown by Hertz (1994) to belong to *Alvania nigrescens* Bartsch & Rehder, 1939, and this case of misidentification should be settled by a decision of ICZN. The actual *A. galapagensis* is a rare species from deeper water and may be a pickworthiid.

The type species of *Fictonoba* Ponder, 1983 also resembles the species dealt with here, but differs in having a very different central tooth on the radula.

Lirobarleeia elata Gofas, new species
(Figures 24, 65–66)

Type material: Holotype (MNHN) and 200 paratypes (50 AMS cat. C.305095, 50 MNCN cat. 15.05/20538, 50 MNHN, 50 UAN) collected alive from the type locality.

Type locality: Baía de Santa Maria, province of Benguela, Angola (13°35'S, 12°33'E), on calcareous algal bottom in 8–10 m.

Material examined: (collected by the author; all MNHN except paratypes specified above) **Angola:** Caotinha, 1 sh.; Baía de Santa Maria, the type material; Baía da Lucira (Cesar) on calcareous algal bottom 10 m, 1 spec. and 12 sh.; Santa Marta, dredged 40 m on shell sand, 25 sh.; Chapeu Armado, 1 sh.; Praia Amelia, 40–60 m, 3 sh.

Description: Shell elongate, solid, adults 3.2 × 1.6 to 6.2 × 2.6 mm (holotype 5.1 × 2.3 mm). Protoconch dome-shaped (500 μ in diameter) with 1 to 1¼ whorl, apparently smooth at low magnification, with very minute, irregular pits, arranged in spiral bands so as to suggest a faint spiral sculpture. Teleoconch with 5¼ to 6 whorls, with spiral sculpture of very unequal, sharp cords (15–20 on penultimate whorl). Early spire whorls rather flat, the later ones moderately convex, body whorl rounded, hardly umbilicate, with its latest part wider and salient from the profile. Outer lip opisthocline in adults, thickened at some distance in the last ¼ whorl and beveled inside to the edge; parietal callus moderately developed, detached anteriorly in adults. Color of shell pale brown to whitish, with very faint, delicate axial flames starting from the suture; paler towards the termination of the body whorl; inside of aperture whitish to brown, often with two brown streaks on the lip. Operculum dark crimson. Patterns of animal not observed in life, seen on

rehydrated specimens to have black markings on opercular lobes and on the snout.

Habitat: On bottoms of calcareous red algae ("maerl") or coarse, clean shell gravel in a few meters depth in sheltered bays with transparent waters.

Distribution: Only known from Angola.

Remarks: There is some similarity with *Rissoa glypta* Smith, 1890 from St. Helena, which is smaller, has weak axial folds and somewhat carinate whorls. *Lirobarleeia elata* is the largest of the Angolan *Lirobarleeia*; it is distinguished from both *L. pupoides* n. sp. and *L. sublaevis* n. sp. by its more acute apical spire angle, and coarser sculpture; from *L. sublaevis* also by the black markings on the animal and by the protruding lip of the aperture in the adults.

Lirobarleeia sublaevis Gofas, new species
(Figures 25–26, 67–68, 77–78)

Type material: Holotype (MNHN) and 450 paratypes (120 of which 20 juv. in each of the following: AMS cat. C.305091, MNCN cat. 15.05/20540, MNHN, UAN) from the type locality, live collected.

Type locality: Praia das Conchas, province of Namibe, Angola (15°07.0'S, 12°06.7'E), in large tidal pools.

Material examined: (collected by the author; all MNHN except paratypes specified above) **Angola:** Caotinha, 8 specs.; Limagens, 4 sh.; Baía de Santa Maria, 8–10 m, 500 sh.; Lucira (Cesar) 8–10 m, 150 sh. (2.6 × 1.4 to 4.3 × 2.2 mm); Lucira (Bissonga) intertidal 12* + 18 specs.; Santa Marta, 3 sh.; São Nicolau 14* specs. + 30 sh., 2.1983. Chapeu Armado, 100 specs. (many juv.); Praia das Conchas, the type material and 8* specs. (2.8 × 1.4 to 4.6 × 2.3 mm); Praia Amelia, 52 specs. (2.5 × 1.4 to 3.6 × 1.6 mm).

Description: Shell elongate, very solid, adults 2.5 × 1.4 to 4.6 × 2.3 mm (holotype 3.0 × 1.5 mm). Protoconch dome-shaped (400 μ in diameter) of 1¼ whorls, apparently smooth at low magnification, with extremely minute, irregular pits, loosely arranged along a spiral direction. Teleoconch of 3½ to 4½ whorls, with faint, flat spiral threads, the intervals of which show spiral series of punctures (only visible under SEM). Whorls moderately convex, body whorl rounded, slightly constricted, hardly umbilicate. Outer lip orthocline, thickened at some distance in the last ¼ whorl and beveled inside to the edge; parietal callus rather thin, detached anteriorly. Color of shell whitish or pale orange brown with subsutural area paler; occasionally with two blurred spiral orange brown bands on a whitish background. Operculum dark crimson. Head-foot with yellow axial bars on tentacles, yellow granular masses behind each eye, on the tip of the snout, on each side of the anterior part of the propodium. Pink buccal mass clearly visible by transparency.

Habitat: Intertidal, in pools or flats with rocks embedded in clean, coarse sand and algal overgrowth.

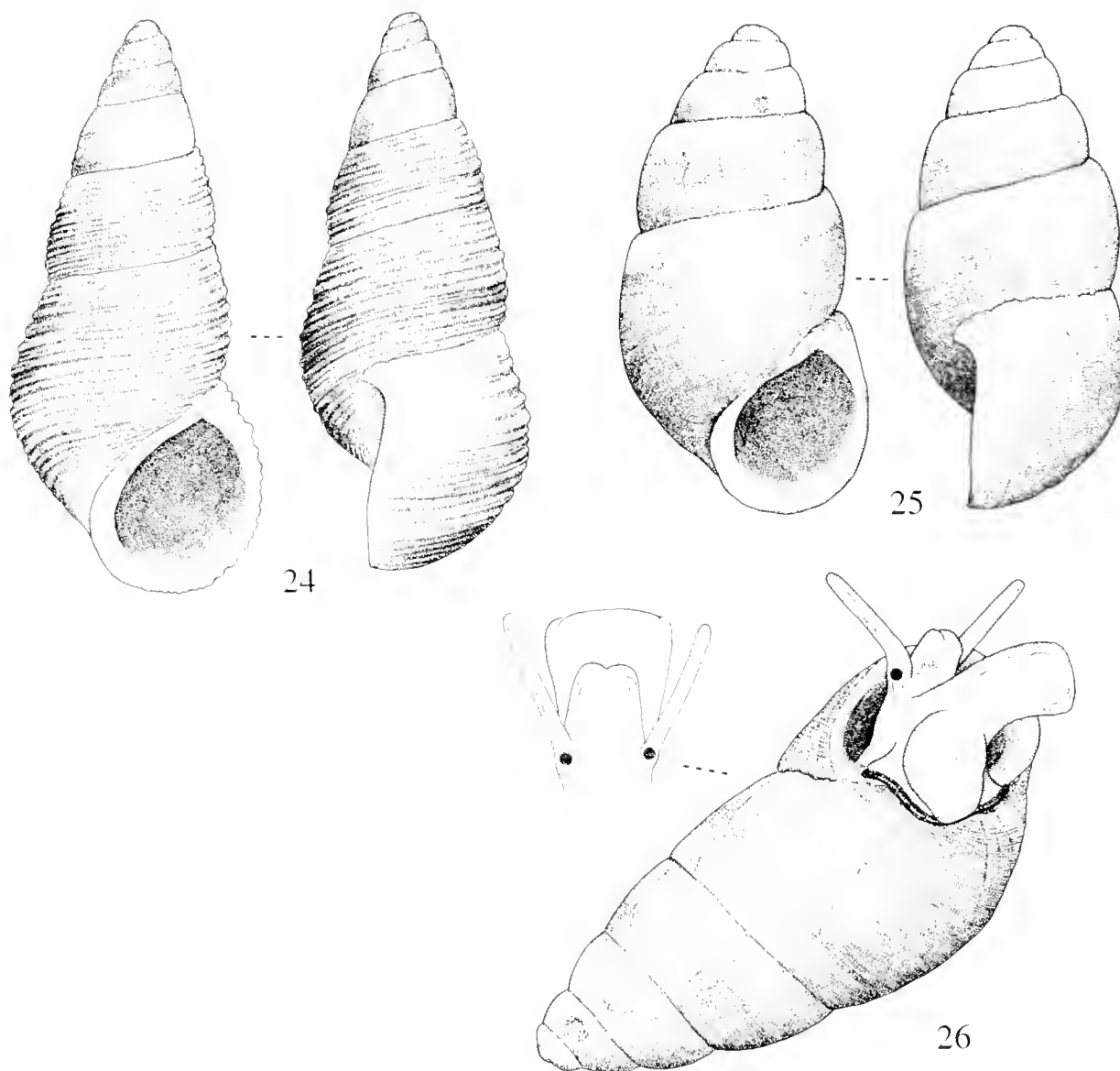


Figure 24. *Liobarleecia clata* Gofas, new species, holotype from Santa Maria (Angola), length 3.1 mm **Figures 25–26.** *Liobarleecia sublaevis* Gofas, new species. **25.** Holotype from Praia das Conchas (Angola), length 3.0 mm. **26.** Living specimen from Caotinha (Angola), length 3.1 mm

Distribution: Only known from Angola.

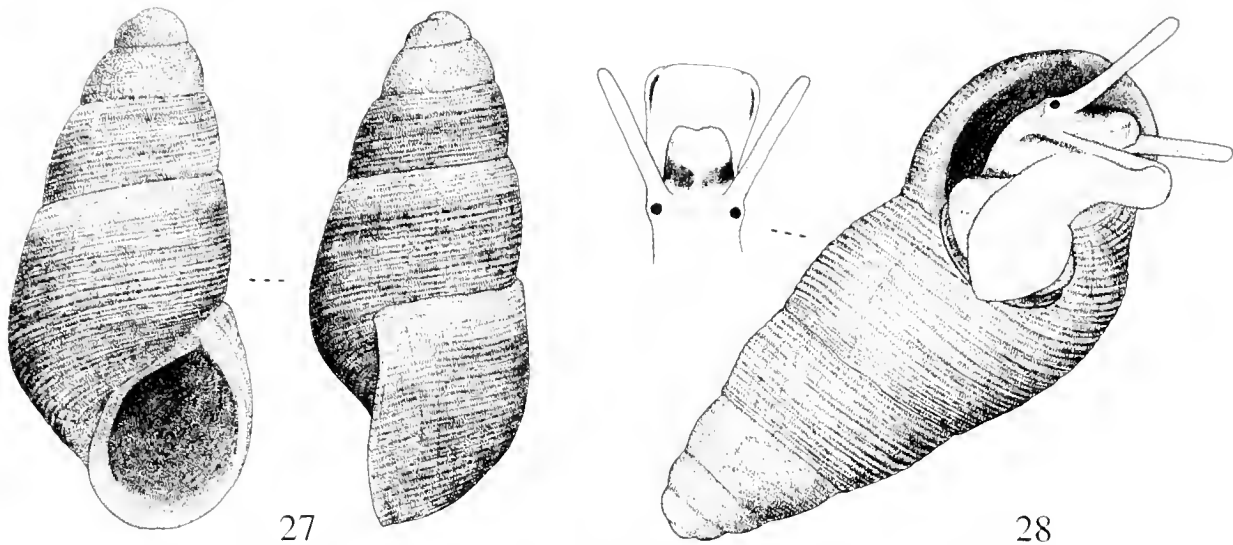
Remarks: *Liobarleecia sublaevis* may resemble some very smooth specimens in the population from Corimba, referred to *L. pupoides* n. sp., but may be distinguished by its lack of black patterns on the head-foot, the absence of any pigmentation on its opercular lobes, and the regularly fusiform profile of its shell, which lacks the protruding body whorl.

Liobarleecia pupoides Gofas, new species
(Figures 27–28, 69–70)

Type material: Holotype (MNHN) and 200 paratypes (50 AMS cat. C.305096, 50 MNCN cat. 15.05/20539, 50 MNHN, 50 UAN) collected alive from the type locality.

Type locality: Corimba, province of Luanda, Angola (8°50'S, 13°09'E), on shell gravel bar in 20 m depth.

Material examined: (collected by the author; all MNHN except paratypes specified above) **Angola:** Corimba, the type material (2.2 × 1.1 to 3.8 × 1.5 mm); Corimba, Praia Etambar in shell sand: 34 shells (2.5 × 1.1 to 3.4 × 1.5). (*Liobarleecia* cf. *pupoides*) Baia dos Tigres, 8* + 31 specs., 8.1985. (2.4 × 1.1 to 2.8 × 1.2 mm).



Figures 27–28. *Lirobarlecia pupoides* Gofas, new species. 27. Holotype from Corimba (Angola), length 2.6 mm. 28. Living specimen from Corimba (Angola), length 3.0 mm.

Description: Shell pupoid, elongate, moderately solid, adults 2.2×1.1 to 3.8×1.5 mm (holotype 2.6×1.2 mm). Protoconch dome-shaped (400μ in diameter) of $1\frac{1}{4}$ whorl, apparently smooth at low magnification, with extremely minute, crowded, irregular pits, loosely arranged along a spiral direction. Teleoconch of $3\frac{1}{2}$ to $4\frac{1}{2}$ whorls, with flat spiral threads, the intervals of which show spiral series of punctures (only visible under SEM), and with very faint axial wrinkles. Whorls flat to moderately convex; body whorl rounded, hardly umbilicate. Outer lip orthocline, beveled inside to the edge which is quite rounded in adults; parietal callus moderately developed, somewhat detached anteriorly and posteriorly. Color of shell orange brown to pale yellowish, occasionally with two blurred spiral bands inside the aperture. Operculum dark crimson. Head-foot with superficial black blotches on each side of the snout, occasionally confluent and extending over the head; black on opercular lobes and anteriorly on the sides of the propodium; yellow axial bar on tentacles, yellow granular masses behind each eye, on the tip of the snout, on the anterior part of the propodium, and on the opercular lobes anteriorly to the black markings.

Habitat: In coarse shell sand, shallow subtidal.

Distribution: Only known from Angola.

Remarks: Very smooth specimens from Corimba may resemble the previous species, *L. sublaevis* in having a similar protoconch and teleoconch microsculpture. *Lirobarlecia sublaevis* generally has a thicker and larger shell, a more fusiform profile without a protruding lip and lacks any black pattern on the head-foot and the opercular lobes. Old shells, possibly subfossil, collected on the beach at Corimba, are larger (up to 4.3×1.5 mm) and have a coarser spiral sculpture on the teleoconch, approaching that of *L. elata* n. sp. They never-

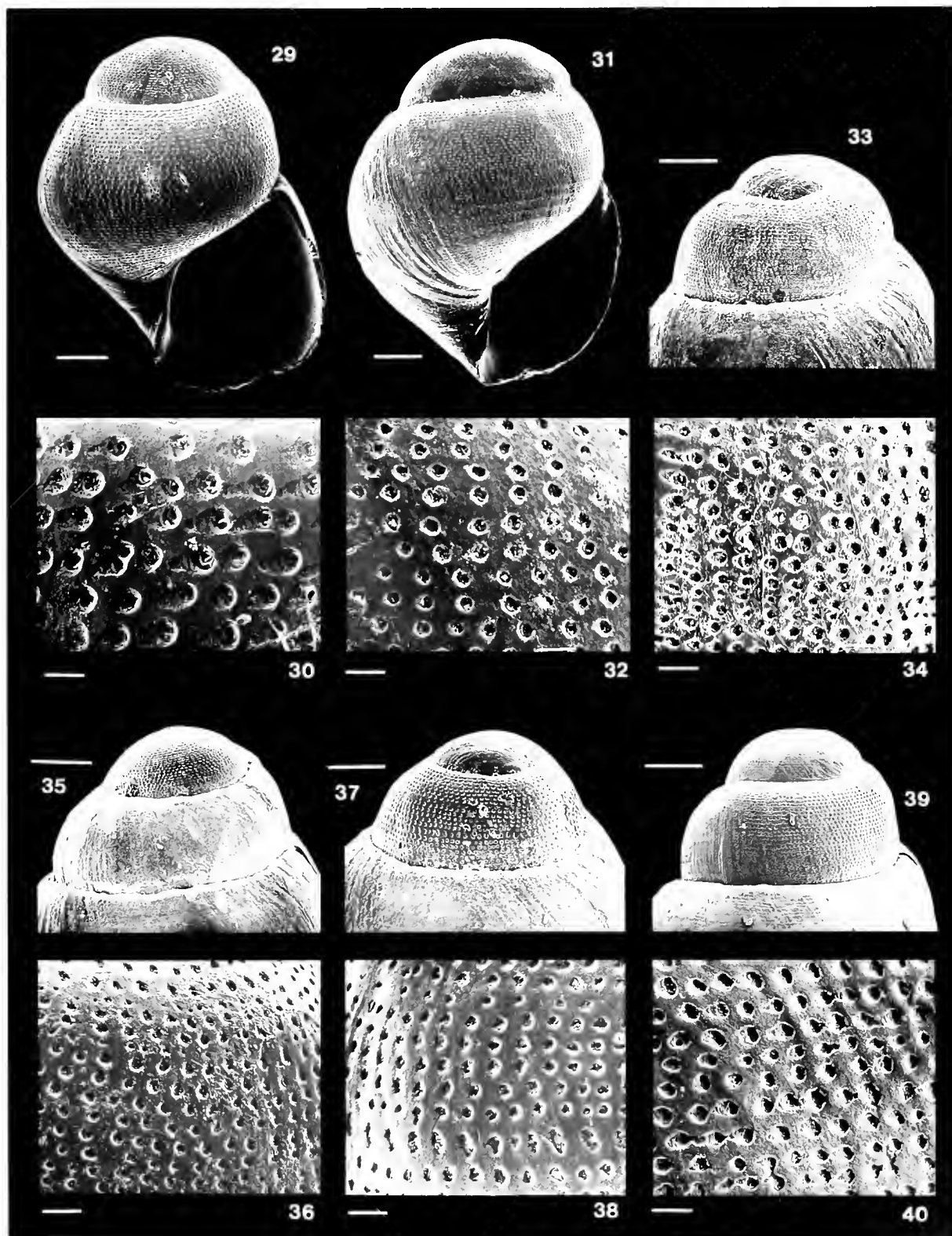
theless retain the pupoid outline that is typical of this species. In the extreme South of Angola, in Baía dos Tigres, there is a local population of *Lirobarlecia* resembling that of Corimba both in shell morphology and color pattern of the head-foot, and also living in ca. 10 m depth on a coarse shell sand. It is not clear, from the material available, if it is the same species with a disjunct range, occurring where adequate substrate exists, or if it is a sister species derived independently from an ancestral stock.

DISCUSSION

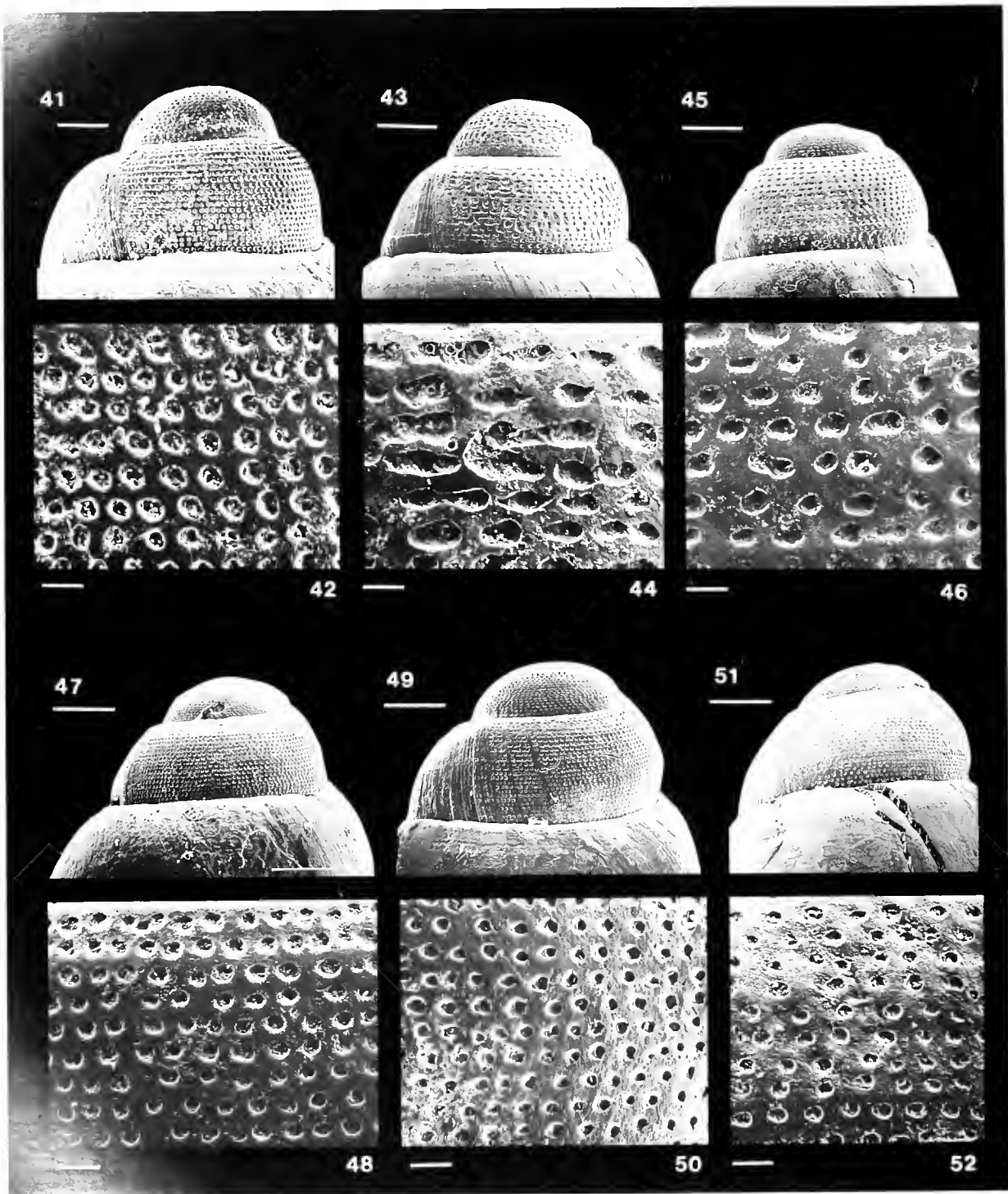
At the local level, sympatric species of Barleceidae may show differentiation in size, or in habitat. The NW African species *Barlecia unifasciata* and *B. gougeti* may be microsympatric and have distinct, although overlapping size ranges. The three Cape Verde Islands species described herein (*B. verdensis* n. sp., *B. acmilii* n. sp., *B. chefae* n. sp.) and the two *Barlecia* from São Tomé (*B. tomensis* n. sp., *B. taeniolata* n. sp.) also exhibit size differentiation among microsympatric species.

The sympatric occurrence of several species (up to four in Baía de Santa Maria, Angola) is accompanied by a segregation in habitat. Among the Angolan species, *Barlecia pervulgata* n. sp. (the typical form) is found intertidally in algal tufts, *B. cinguloides* n. sp. intertidally among stones lying on coarse sand, while *B. picta* n. sp. occurs subtidally among algal concretions together with *Barlecia* cf. *pervulgata* and *Lirobarlecia elata* n. sp. The two Southern species of *Lirobarlecia* are also segregated, *L. sublaevis* n. sp. occurring together with *B. cinguloides* or in tidal pools, while *L. elata* is always subtidal. There is a preference for soft bottoms among *Lirobarlecia* and *Pseudodiata*, and for hard bottoms among *Barlecia*.

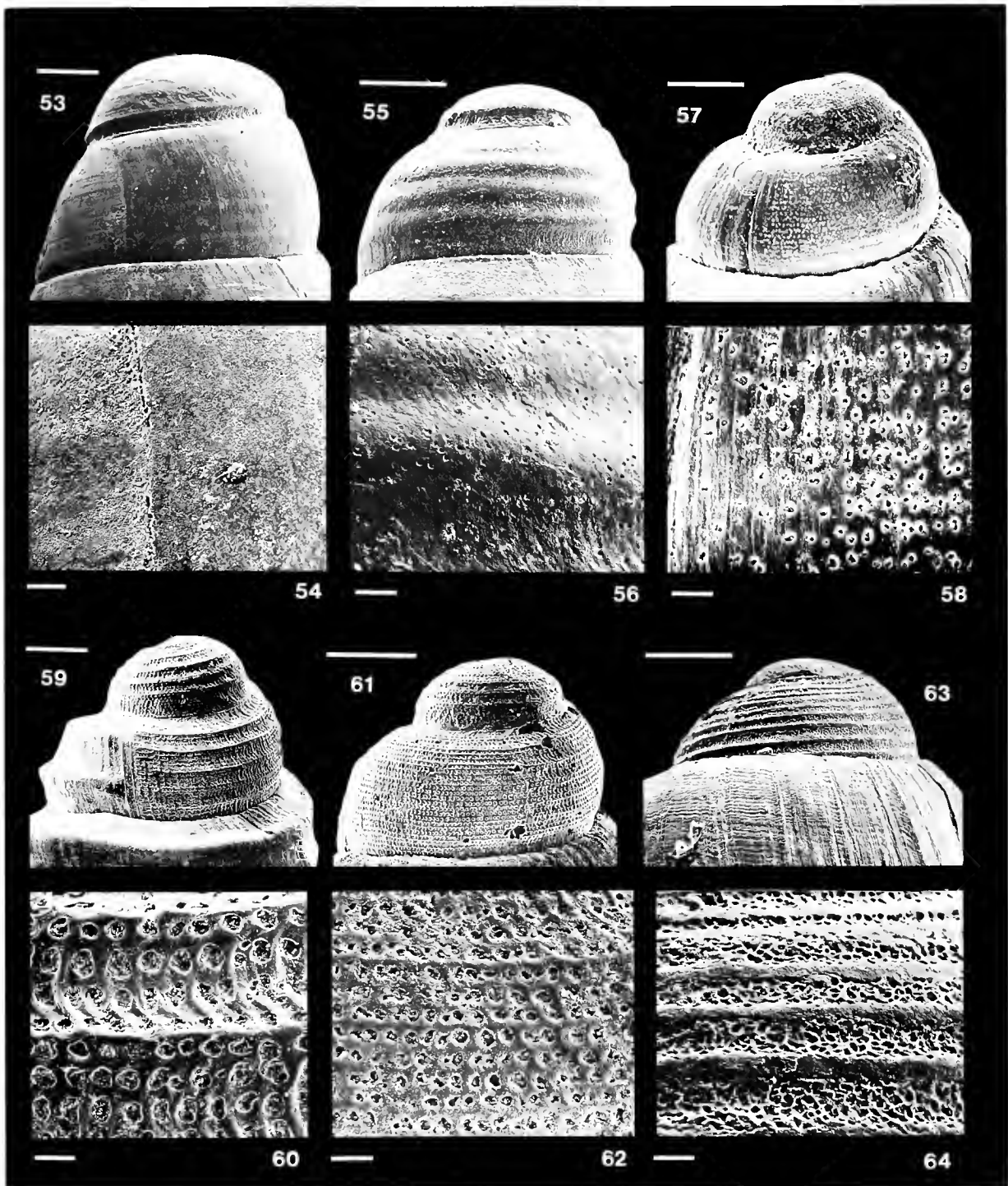
Thus far, the coast of Western America was known as



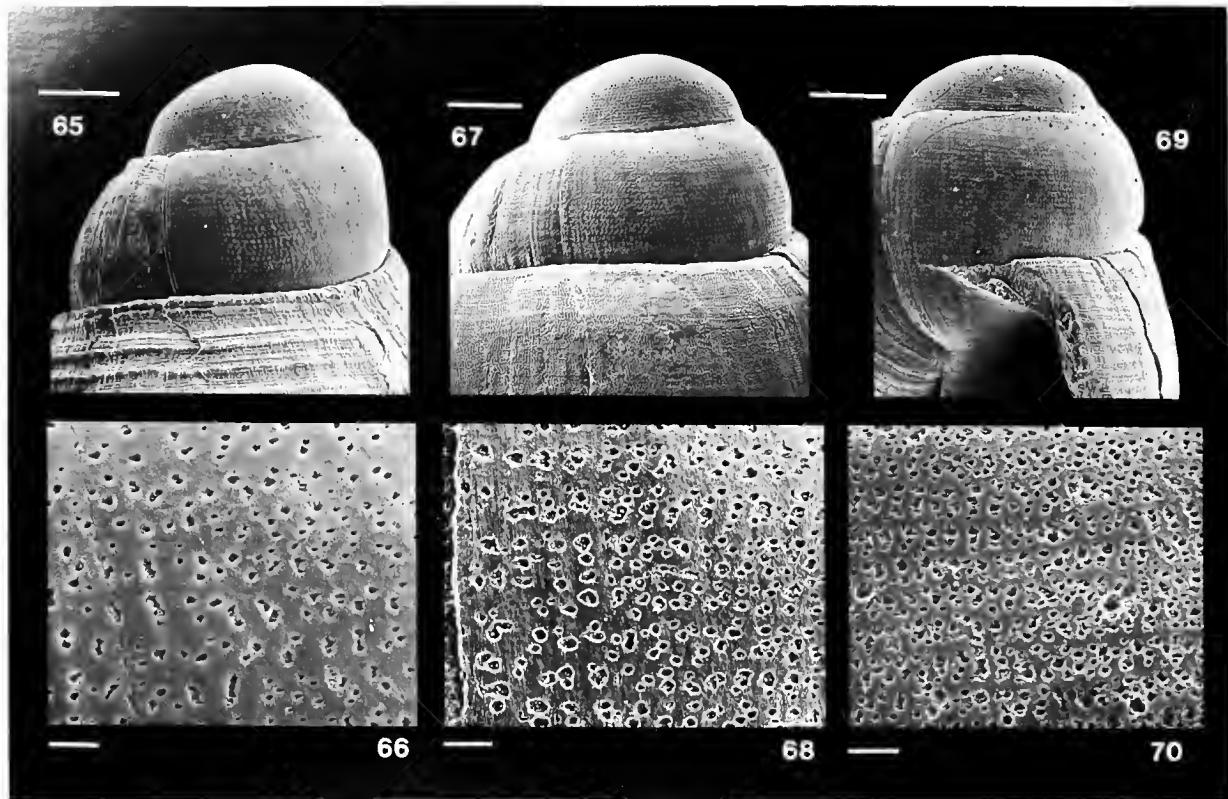
Figures 29–40. Protoconchs of *Barlecia* – general views (scale bars 100 μ) and enlarged portions of the surface (scale bars 10 μ), the latter all to scale: 29–30, *Barlecia unifasciata* (Montagu, 1803), Ploumanac’h (France); 31–32, *Barlecia gougeti* (Michaud 1830), Essaouira (Morocco); 33–34, *Barlecia verdensis* Gofas, new species, paratype, Salmanza (São Vicente, Cape Verde Is.); 35–36, *Barlecia acmili* Gofas, new species, Salmanza (São Vicente, Cape Verde Is.); 37–38, *Barlecia chefiac* Gofas, new species, paratype, Sal-Rei (Boavista, Cape Verde Is.); 39–40, *Barlecia tomentis* Gofas, new species, paratype, Praia das Conchas (São Tomé)



Figures 41-52. Protoconchs of *Barleccia*: general views (scale bars 100 μ) and enlarged portions of the surface (scale bars 10 μ), the latter all to scale. 41-42, *Barleccia taeniolata* Gofas, new species, paratype, Santa Ana (São Tomé). 43-44, *Barleccia cinguloides* Gofas, new species, paratype, Praia Amelia (Angola). 45-46, *Barleccia picta* Gofas, new species, paratype, Santa Maria (Angola). 47-48, *Barleccia pervulgata* Gofas, new species, Caotinha (Angola). 49-50, *Barleccia pervulgata* Gofas, new species, paratype, Chapout Armado (Angola). 51-52, *Barleccia cf. pervulgata* Gofas, new species, Porto Alexandre (Angola).



Figures 53–64. Protoconchs of *Pseudodiala*, *Tropidorissoia* and "*Barlecia*", general views (scale bars 100 μ) and enlarged portions of the surface (scale bars 10 μ), the latter all to scale. 53–54. *Pseudodiala niso* Gofas, new species, off Saloum (Senegal). 55–56. *Pseudodiala acquinocialis* Gofas, new species, holotype, Equatorial Guinea. 57–58. *Pseudodiala corollaria* Gofas, new species, paratype, Santa Ana (São Tomé). 59–60. *Tropidorissoia taphrodes* Tomlin & Shackleford, 1915, Praia das Conchas (São Tomé). 61–62. *Tropidorissoia secunda* Rolán & Templado, 1994, Praia das Conchas (São Tomé). 63–64. "*Barlecia*" *congenita* Smith, 1890, St. Helena.



Figures 65–70. Protoconchs of *Lirobarlecia*: general views (scale bars 100 μ) and enlarged portions of the surface (scale bars 10 μ), the latter all to same scale. 65–66. *Lirobarlecia clata* Gofas, new species, paratype, Santa Maria (Angola). 67–68. *L. sublaevis* Gofas, new species, paratype, Praia das Conchas (Angola). 69–70. *L. pupoides* Gofas, new species, paratype, Corimba (Angola).

the part of the world with the highest species richness in the family Barleecidae. Ponder (1983) recognized 13 species of *Barleecia* (including one *Pseudodiala*) distributed between California and Panama, and 12 species of *Lirobarlecia*, distributed in the same mainland area but also in the Galapagos and Clarion islands.

The description of species from West Africa brings attention to other centers where the family is well represented (Fig. 79). The inner part of the Gulf of Guinea hosts six species representing three genera. The absence of records from Annobón or Fernando Poo islands reflects the lack of data, rather than a real difference between islands.

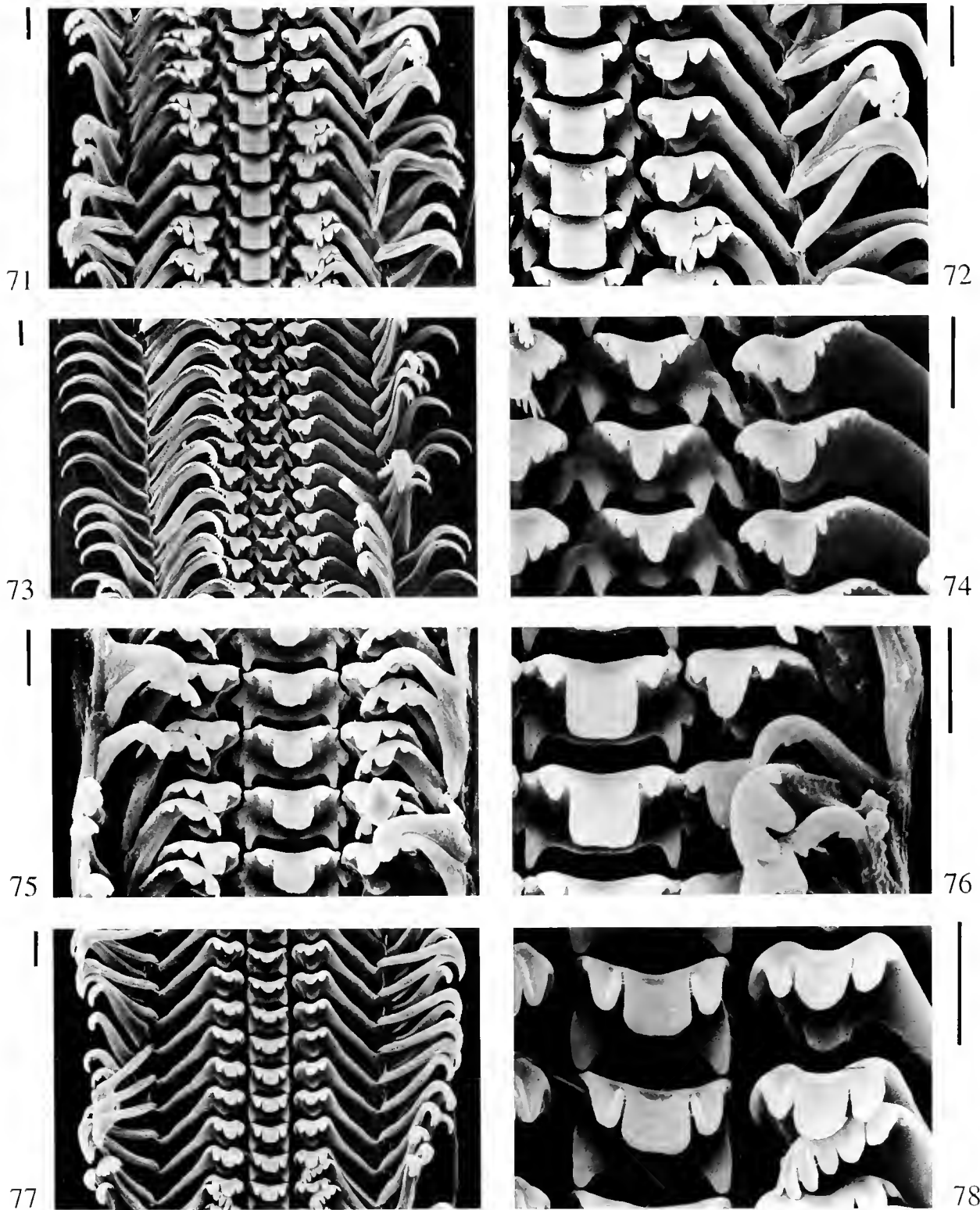
Southern Angola, with six species representing two genera, is another center of richness. The northern limit of five species in Angola coincides with the shift from a rocky coast with clear, cool waters, to a prevalently sandy coastline with warmer, turbid waters north of the city of Benguela. Rocky shores with a well developed cover of small photophilous algae (including *Corallina* spp.) are well represented in the south, unlike the north where hard substrates are scarce and where high turbidity of waters would smother a dense algal cover. The sampling effort has been well balanced between both areas, and the lack of records of *Barleecia* in northern Angola is not a sampling artifact. This supports the view that the gaps

between Angola and the Gulf of Guinea islands, and between the Gulf of Guinea and Senegal, are real. The distribution of *Barleecia* in West Africa may thus reflect the breakdown of a formerly more continuous range.

To the south, the fauna of Namibia remains virtually unknown, but some of the Angolan species, or related ones, may be present there; both *Barleecia* and *Lirobarlecia* are present in the southernmost Angolan sample, less than 100 km from the Namibian border. Despite being a temperate area with rocky shores, South Africa has only two poorly known species, *Barleecia caffra* (Sowerby, 1897) and *B. smithi* Bartsch, 1915, which are definitely outside the West African radiation.

The island of St. Helena may host a number of species of Barleecidae. However, the systematic position of most of the species described by Smith (1890) remains uncertain. *Barleecia congenita* Smith, 1890 lacks spiral sculpture and superficially resembles true *Barleecia*, but its protoconch sculpture (Fig. 63–64) is similar to that of *Tropidorissoia taphrodes*. The species described by Smith as *Rissoa* and tentatively referred by Tomlin and Shackelford (1915) to *Tropidorissoia* may be either rissoids or barleecids (see under *Tropidorissoia*).

Considering the Gulf of Guinea and Angola together, there are fewer species (12 species) than in West America but these are more diverse at the generic level: *Tropi-*



Figures 71–78. Radulae, general views of several complete rows (left) and enlarged views of central and lateral teeth (right, all scale bars 10 μ). 71–72. *Barlecia pervulgata* Gofas, new species, Chapeu Armado (Angola). 73–74. *Pseudodiala niso* Gofas, new species, Cap de Naze (Senegal). 75–76. *Tropidorissoia taphrodes* Tomlin & Shackleford, 1915, Praia das Conchas (São Tomé). 77–78. *Lirobarlecia sublaevis* Gofas, new species, Praia das Conchas (Angola).

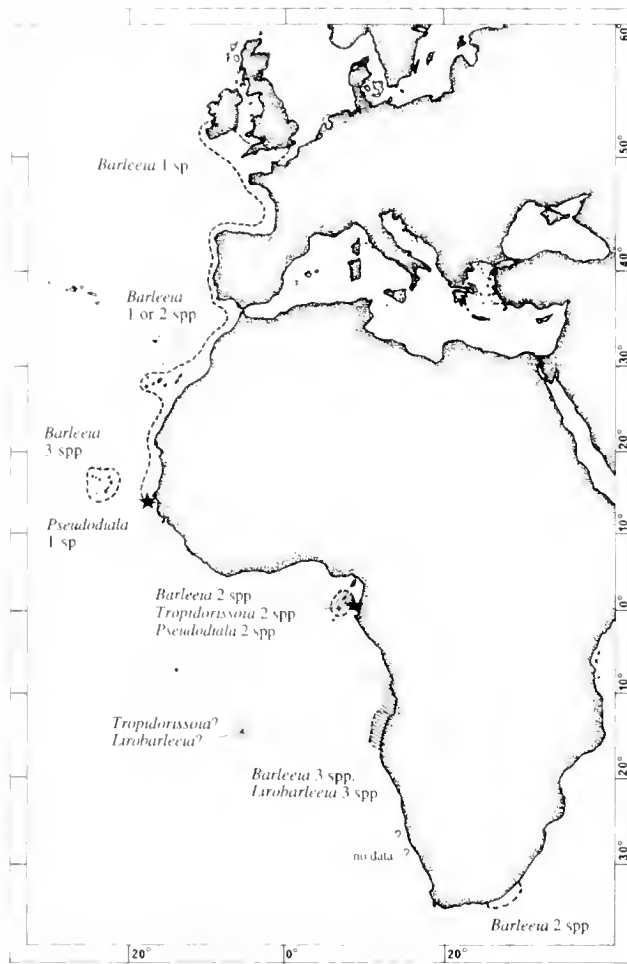


Figure 79. Distribution of the Barleeidae in the Eastern Atlantic: dashed contour, *Barleeia*, hatched, *Tropidorissoia*, and *Lirobarleeia*, stars, *Pseudodiala*

dorrissoia is present in addition to the three genera found in West America. Thus, West Africa as a whole is the area of the world with the highest number of genera in the family. The representation in Senegal (three species, two genera) and in the Cape Verde Islands (three species, all congeneric) is less spectacular.

Larval development without a planktonic stage has been observed only in *B. unifasciata* and in *B. pervulgata* n. sp., but can be extrapolated to all the other species with similar protoconch characters. Despite this constraint, the insular species are able to disperse between moderately distant islands. The three *Barleeia* species from the Cape Verde were collected on six islands 10 to 100 km apart, and would probably have been found everywhere in the archipelago had all ten islands been sampled. The two species of *Tropidorissoia* and *Barleeia tomensis* described from São Tomé were also found in Príncipe, at a distance of 150 km (Fernandes and Rolán, 1993). Conversely, there seems to be an allopatric distribution for *Pseudodiala aequinoctialis* n. sp., found in the inner part of the Gulf of Guinea, and *P. corollaria*

found in São Tomé. This implies that an efficient alternative to dispersal during pelagic larval development is used by some barleeids. The most likely scheme is that the egg capsules of *Barleeia*, which are very light and attached to algae in shallow subtidal environments, are easily torn off the substrate and float away.

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Shell Growth and Decollation in Terrestrial Gastropods

Edmund Gittenberger

Nationaal Natuurhistorisch Museum
P.O. Box 9517
NL 2300 RA Leiden, Netherlands
[2nd address, see Povel]

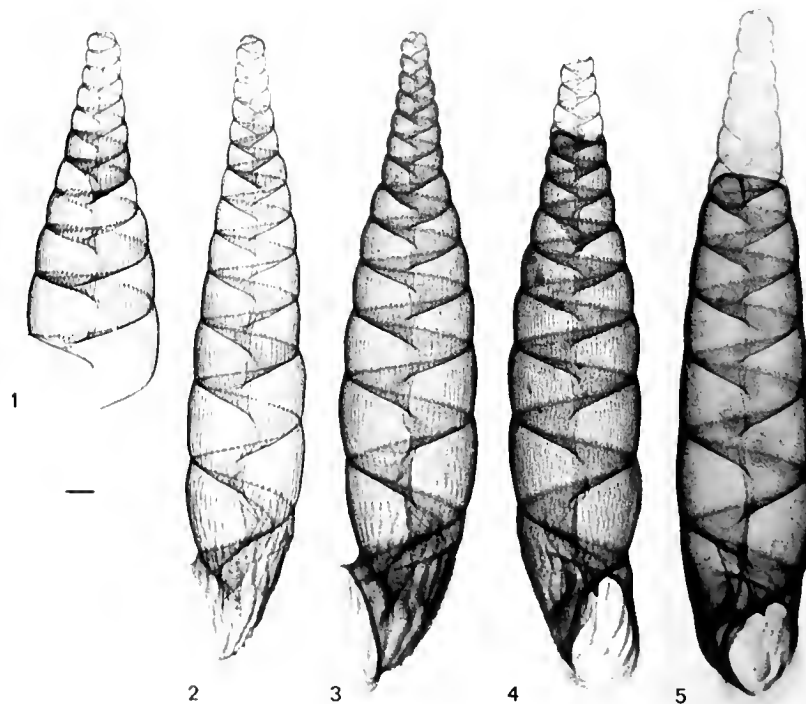
G. David E. Povel

Institute of Evolutionary and
Ecological Sciences
Rijksuniversiteit Leiden
P.O. Box 9516
NL 2300 RA Leiden, Netherlands

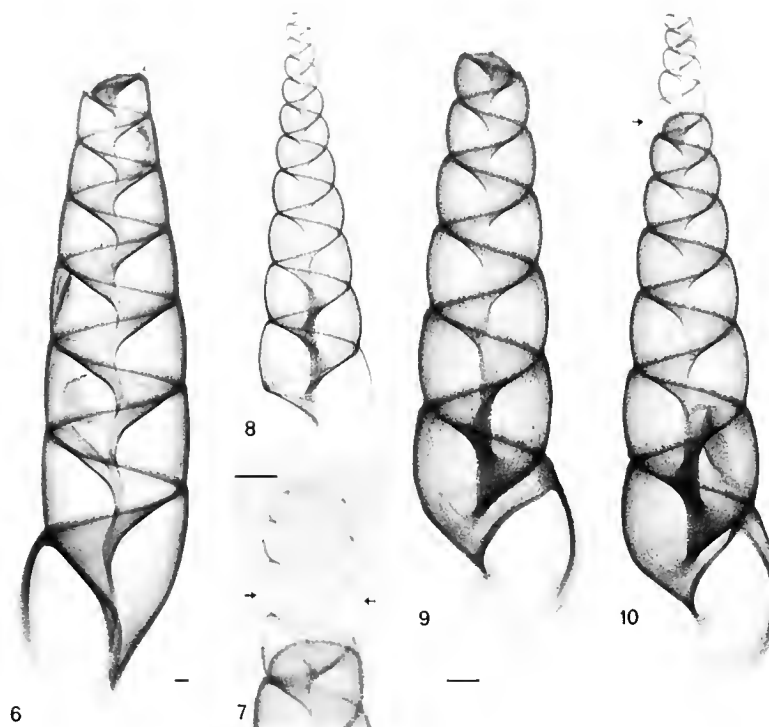
Vermeij (1993:34) described decollation of snail shells as: "... resorption of the inner shell wall in the early part of high-spired snail shells makes the shell so thin in this region that the apical whorls drop off. The remainder of the shell is then plugged by an apical wall or pad." A more refined mechanism has been described for the terrestrial pulmonate snail *Rumina decollata* (Linné, 1758) (Pulmonata: Subulinidae), in which shell wall resorption occurs only locally, resulting in small areas of the shell being predisposed to breaking; prior to the actual decollation, an internal septum is formed just below the weakened part of the shell (Hochpöchler & Kothbauer, 1975). While studying shells belonging to the terrestrial, mainly Greek, genus *Albinaria* Vest, 1867 (Gastropoda Pulmonata: Clausiliidae), using X-rays, a different mode of decollation was discovered in some species.

X-ray radiographs were made with an "Enraf Nonius Diffractis 581", using an Agfa-Gevaert Osray 50DW X-ray film, with an exposure time of 10 seconds at 16mA and 30 KV. To facilitate comparisons of individual shells for shell wall thickness, up to c. 50 specimens were photographed simultaneously on a single negative.

A comparison of conspecific specimens of various sizes revealed that all juvenile shells, irrespective of the actual number of whorls, as well as some specimens that appeared to be adults, were equally thin-walled (Figures 1, 2). Shells with relatively thick walls were never juveniles, they always appeared to be fully grown. When an apical septum was present in such shells, either separating the apical whorls from the lower ones or sealing the upper part of the shell in cases where the apical whorls were missing, such shells had thick walls only



Figures 1–5. Specimens of *Albinaria spratti* (1–4) and *A. rebchi* (5), showing various stages in shell growth and development. 1. Juvenile shell. 2. Fully-grown thin-walled shell. 3. Undamaged shell. 4. Apically damaged, secondarily thickened shell. 5. Shell with the very rare combination of intact, thin, apical whorls and a secondarily thickened wall below a septum. Scale bar (below figure 1) = 1 mm.



Figures 6–10. 6,7. *Perrieria clausiliaeformis*. 6. Fully-grown, partly decollated shell 7. Detail of another specimen, with the protoconch present, showing an extremely thin area (arrows) above the septum 8–10. *Tahaitia heinrichi* 8. Juvenile. 9. Decollated and 10. non-decollated adult shells (arrow indicating extremely thin area). Scale bars = 2 mm

below the septum. Above the septum, the shell whorls, or what remained of them in partially decollated specimens, were always as thin as in conspecific juvenile specimens.

These observations suggest that, in a first phase, these snails produce all the shell whorls, one after the other, of about equal thickness. Once the shell wall has been formed, there is no additional thickening in this initial phase of shell growth, which ends with the formation of the characteristic body whorl, thought to be indicative of adult size. In a second phase, either the entire shell is thickened from within (Figure 3), or an apical septum is formed and the secondary thickening is restricted to the whorls below this septum (Figure 4). The latter category contains shells with relatively thin-walled apical whorls, prone to irregular breaking, usually resulting in conspicuously decollated shells (Figure 4: slightly decollated).

In *Albinaria*, septum formation is usually followed by decollation, as it is in *A. rebeli* Wagner, 1924. This species occurs abundantly in a small valley in Crete, where the snails can easily be observed, hanging on the rock-faces. Among hundreds of full-grown, decollated specimens, six adult shells with the apical whorls still present were collected. These were X-rayed. All of them contained an apical septum, above which the whorls are thinner than below it (Figure 5). No traces of shell wall resorption were seen.

Septum formation may also be related to incidental damage of the apical whorls, as is most probably the case in *A. spratti* (Pfeiffer, 1846). Upon X-ray examination, an apical septum was observed in 68 of 208 shells of this species. Either decollation or fairly serious damage to the uppermost whorls was observed in these specimens. The remaining 140 specimens were undamaged and lacked a septum. Fully grown specimens of *A. spratti* may have a relatively thick shell wall from the body whorl up to the protoconch (Figure 3).

In both *A. rebeli* and *A. spratti*, septum formation might be hypothesized to be a mechanism to protect against desiccation by evaporation. In *A. rebeli* septum formation might be either an autonomous development or triggered by a specific, relatively high permeability of the uppermost whorls. In *A. spratti* it might be indicative of repair, resulting from an accidentally damaged apical portion of the shell.

Relatively thin apical whorls, due to partial secondary shell thickening below a septum, and often resulting in decollation, also occur in *Perrieria clausiliaeformis* Taparone Canefri, 1878 (Figures 6,7) and *Tahaitia heinrichi* Gittenberger, 1989 (Figures 8–10), two terrestrial snail species from New Guinea. They belong to the families Megaspiridae [after Zilch, 1959:376] or Coelocidae [after Nordsieck, 1986:111] (Pulmonata) and Truncatellidae (Prosobranchia), respectively. In *Perrieria clausiliaeformis*, multiple septa are formed during the lifespan

of an individual, resulting in repetitive decollation, as in *Rumina decollata*. We studied adult, but not fully decollated specimens of both species, in which shell whorls were present above the septum. Extremely thin shell walls were observed just above the septum, suggesting that local resorption had occurred there prior to septum formation (Figures 7,10).

In view of the low number of gastropod shells studied with X-rays, we may expect that the decollation mechanism reported here might be more widely spread among gastropods.

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Cannibalism in the Terrestrial Slug *Deroceras laeve*

Jianming Shen

Department of Zoology
University of Tennessee
Knoxville, TN 37996 USA

Cannibalism occurs in many taxa of animals under diverse contexts (Elgar & Crespi, 1992). Whatever the causes of its evolution, cannibalism often has significant influences on population dynamics and may incur changes in developmental, morphological, behavioral, and life history characteristics of a species (reviewed in Fox, 1975; Polis, 1981; Elgar & Crespi, 1992). Cannibalism in gastropods was recently reviewed by Baur (1992), who classified it into three categories: "(1) adult and juvenile gastropods preying on conspecific adults and juveniles; (2) adult gastropods preying on conspecific eggs; (3) larvae and newly hatched snails preying on conspecific eggs" (Baur, 1992: 103). In that review, Baur described cannibalism in the terrestrial slug *Deroceras laeve* (Müller, 1774) as adults preying on conspecifics, citing Rollo and Wellington (1979). However, although describing it as a very aggressive species, Rollo and Wellington (1979) made no remark on cannibalism in *Deroceras laeve*. Anecdotal notes similarly seem to suggest that cannibalism in *Deroceras laeve* occurs as adults or juveniles cannibalizing other adults and juveniles. For example, Karlin and Naegele (1960:14) noted that "it was impossible to hold more than a few specimens of *laeve* in a rearing cylinder since they exhibited strong cannibalistic tendencies" and that "on several occasions, an individual of this species was actually seen to attack and feed upon a smaller slug of the same species". Pillard (1985:14) also observed "members of *Deroceras laeve* feeding on conspecifics".

During the past few years, while raising a large number of *Deroceras laeve* in the laboratory for other purposes, I observed numerous cases of cannibalism in this species. In this note, I describe these observations with respect to Baur's three categories noted above.

1. Adults or juveniles cannibalizing other adults or juveniles. Although this is the form of cannibalism that has been described by previous authors as occurring in *Deroceras laeve*, I observed it only once when one larger juvenile (extended body length ~ 17 mm) killed a much smaller juvenile (extended body length ~ 8 mm) and subsequently consumed most of the victim. There was no food available in the container. As suggested by Karlin and Naegele (1960), this form of cannibalism may be due to overcrowding or an inadequate diet. On the other hand, I also observed numerous attacks, sometimes repetitive attacks, among adults and juveniles held in the same container, supporting previous observations by Rollo and Wellington (1979) that *Deroceras laeve* is very aggressive. However, such aggression rarely led to cannibalism since most victims were able to escape the attacks very quickly. While high proportions (as high as

56%) of slugs collected from the field were observed with severe wounds, I do not interpret these as indications of cannibalism in natural populations of this species.

2. Adults (and juveniles) cannibalizing eggs. In captivity, this typically occurs when the diet is nutritionally unbalanced or when food is not available. Most slugs described here were raised in petri dishes with 3–5 mm of potting soil on the bottom. Under such rearing conditions, adults or juveniles rarely consumed eggs present, provided that food (fresh lettuce) was available. Only on a few (<5) occasions, was a slug found to have consumed one of the eggs it just laid when plenty of fresh food was present. On the other hand, when slugs were raised in petri dishes lined with only wet Kimwipes, 14 of the 16 slugs observed for longer than 3 weeks consumed provided eggs as well as lettuce. Juveniles that ate both eggs and lettuce grew much faster than those that ate only lettuce (unpublished data).

3. Hatchlings cannibalizing eggs. This is the most common form of cannibalism that I observed in *Deroceras laeve*. I discovered that newly hatched slugs (1–3 weeks old) of field collected parents often ate their sibling eggs. I also observed this in the hatchlings of laboratory raised, isolated slugs. Egg cannibalism by *Deroceras laeve* hatchlings occurred regardless of rearing conditions. The propensity for cannibalism seems to vary both among populations and among individuals from the same population. Some hatchlings appeared to prefer eggs to fresh lettuce. Of 25 hatchlings supplied with both eggs and lettuce, four consumed eggs first. Others readily consumed both eggs and lettuce. In an experiment where hatchlings were fed only with eggs, however, 5 of a total of 23 hatchlings died after 5–14 days without eating an egg. While it is unclear whether trophic or nurse eggs exist in *Deroceras laeve*, cannibalistic hatchlings often consumed eggs that did not have a developing embryo. A few hatchlings consumed eggs that had early developing embryos. Contaminated or infected eggs were never consumed.

Cannibalistic hatchlings of *Deroceras laeve* display a typical behavioral pattern when consuming eggs. They first break the outer coat of the egg, then eat their way into the inside of the egg and gradually eat part or all of the egg from the inside out. Sometimes a hatchling moves its whole body inside the egg and eats from the inside. It typically takes more than one hour for a new hatchling to consume most of an egg that is about the same mass or slightly larger than the hatchling. A cannibalistic hatchling may abandon an egg at any time.

Table 1. Weight comparison between cannibalistic and non-cannibalistic hatchlings of *Deroceras laeve*. Means and standard deviations (in parentheses) of the weight at hatching and the weight one week after hatching are presented along with the difference between the two measurements (i.e., weekly growth rate).

	Cannibalistic (n = 15)	Non-cannibalistic (n = 8)	T-test p-value
Weight at hatching (mg)	1.240 (0.269)	1.388 (0.247)	0.2130
Weight after a week (mg)	5.507 (2.514)	3.325 (1.536)	0.0369
Difference (mg)	4.267 (2.344)	1.938 (1.400)	0.0182

especially if it is disturbed during the beginning or ending stages of egg consumption.

DISCUSSION

Egg cannibalism by hatchlings is the main form of cannibalism in *Deroceras laeve*. Adults and juveniles cannibalizing other adults and juveniles or eggs may occur, but probably only under severe conditions. As described above, egg cannibalism by hatchlings does not seem to be induced by abnormal conditions. Therefore, it could be common in natural populations. In species such as *Deroceras laeve*, however, it may be difficult to observe egg cannibalism by hatchlings in the field. Eggs of *Deroceras laeve* are not only small (mean ~ 3 mg) but also typically buried in the soil or laid beneath boards and other objects, and hatchlings usually do not emerge to the surface immediately after hatching.

Egg cannibalism by hatchlings is also known in several other terrestrial gastropods (Baur 1992). For example, newly hatched snails of *Arianta arbustorum* (Linné, 1758) and *Helix pomatia* (Linné, 1758) feed exclusively on eggs (Baur, 1987a, 1988). Baur (1992) suggested that the age specificity of egg cannibalism in gastropods may be associated with an age-specific occurrence of digestive enzymes. Cannibalistic hatchlings often gain considerable nutritional and energetic benefits. In *Arianta arbustorum* and *Helix pomatia*, such benefits are apparently so significant that cannibalistic hatchlings do not distinguish between sibling and non-sibling eggs (Baur, 1987b, 1990a, 1990b). My observations indicate that cannibals in *Deroceras laeve* enjoy a similar nutritional advantage: cannibalistic hatchlings were more than 1.6 times larger than non-cannibalistic ones a week after hatching, and the growth rate of cannibals was on average 2.2 times the growth rate of non-cannibals. As shown in Table 1, both of these values are statistically significant ($p < 0.05$). It also seems that cannibalistic hatchlings of *Deroceras laeve* do not distinguish between kin and non-kin eggs (unpublished data).

Many questions may be asked about cannibalism in *Deroceras laeve*. How common is cannibalism in natural populations of this species? How variable is the propensity of cannibalism both within and among populations? Does this variation of cannibalistic propensity have a genetic basis? What are the costs and benefits of cannibalism, and what might be its evolutionary consequences? Experimental investigations are needed to answer these questions.

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Division of Mollusks
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Dr. Edward J. Petuch
Department of Geology
Florida Atlantic University
Boca Raton, FL 33431

Dr. David H. Stansbery
Museum of Zoology
The Ohio State University
Columbus, OH 43210

Dr. Ruth D. Turner
Department of Mollusks
Museum of Comparative Zoology
Harvard University
Cambridge, MA 02138

Dr. Geerat J. Vermeij
Department of Geology
University of California at Davis
Davis, CA 95616

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Revision of the Supraspecific Classification of Marginelliform Gastropods

Gary A. Covert
Holly K. Covert

Dayton Museum of Natural History
2600 DeWeese Parkway
Dayton, Ohio 45414 USA

ABSTRACT

The supraspecific classification of marginelliform gastropods, formerly treated as the single family Marginellidae, is revised. This revision is based on all available information for all Recent species plus a representative sampling of the fossil fauna, and includes all Recent and fossil genus-group names. All published information is summarized, and additional dissections, concentrating on the foregut and radular morphology, are reported, nearly doubling the number of species known anatomically. Fundamental differences between two groups of marginelliform gastropods are discussed. Cystiscids have internal shell whorls partially resorbed and columellar plications reduced internally. Their radular morphology differs fundamentally in having narrower, more numerous rachidian plates, a different subradular membrane structure, separate odontophoral cartilages, and in the plate development on the posterior end. They differ anatomically in the possession of a typical neogastropod radular sac. True marginellids have unmodified internal whorls and columellar plications continuous internally. Their radulae are shorter and broader, odontophoral cartilages are fused anteriorly, and a marginellid buccal pouch is present. The Olividae have the same specializations as the cystiscids and these two groups are considered to have a common ancestry. On this basis, the Cystiscidae is recognized as a valid family and not considered to be closely related to the Marginellidae. The ancestry of the Marginellidae is discussed and the family is considered to be related to the Volutidae. The Cystiscidae is divided into four subfamilies, three of which are described as new. Nine Recent genera, plus one fossil genus, are recognized. *Plesiocystiscus*, new genus, is described on the basis of a triserial radula and other primitive characters. The Marginellidae is divided into two subfamilies and three tribes, two of which are new. A total of 22 Recent genera are recognized in this family, plus nine fossil genera. *Serrataginella*, new genus, is described on the basis of its unique radular and shell morphology. A systematic section lists synonyms and type species of each genus, along with a diagnosis, description, and summaries of the distribution and fossil record. The phylogeny of both families is discussed, and keys to Recent genera in both groups are presented.

Key words: Cystiscidae, Marginellidae, marginelliform gastropods, systematics, supraspecific classification, new genera, new subfamilies, anatomy.

INTRODUCTION

The best classifications are thus based on the widest possible variety of comparative data.

Richard E. Blackwelder (1964:25)

The higher classification of the family Marginellidae has long been in a state of confusion. Especially useful for an overview of the taxonomic history are the papers of Coan (1965) and Coomans (1976). The early monographs of G. B. Sowerby II (1846), Reeve (1864-1865), Weinkauff (1878-1879), and Tryon (1882-1883), as well as Tomlin's (1917) catalog, treated all members of this family under the single genus *Marginella*. Many popular works still treat all of them under this single genus, while others use generic names inconsistently or erroneously, basing them primarily on superficial similarities of the shell. Coan's (1965) important reclassification was a major improvement, but is now outdated by new information. The confusion over the classification stems from the fact that shell characters alone were used in the early classifications, or were largely used in later classifications. Although many good conchological characters exist, they have generally been misinterpreted, or, in some cases, unrecognized. Information on radulae and external anatomy was widely scattered in the literature, and internal anatomical data, only recently available, is represented by a very small sample.

The senior author has spent the last 13 years working toward a revision of the supraspecific classification of the family Marginellidae on a world-wide basis, studying all aspects of these animals, including shell characters, external anatomy, radulae, internal anatomy, and observations of live animals, including egg capsules. During this process, many new characters were discovered. We feel enough information has finally been gathered that a stable supraspecific classification can be presented, summarizing this research and presenting a complete classification, including complete synonymies of all Recent and fossil genus-group names, along with an interpretation of the phylogeny of this group.

MATERIALS AND METHODS

Since most species were originally described on the basis of the shell, this character complex is of primary importance. Because the eventual aim is to completely monograph this group at the species level, initial work involved acquiring every original description for each Recent species named, as well as all significant subsequent descriptions. A comprehensive species list was compiled from the main catalogs of the family (i.e. Redfield, 1870; Tomlin, 1917; Wagner & Abbott, 1978) and all issues of *The Zoological Record* and other standard nomenclators were consulted, resulting in the publication of a comprehensive bibliography (Covert, 1988e). This body of information primarily dealt with the shell, and much effort was expended on studying and analyzing the conchological characters of all Recent species (Covert, 1988d). The type species of all genus-group taxa were closely scrutinized (Covert, 1986a, 1986b, 1986d, 1986e, 1987a, 1987c, 1987d, 1987f, 1987h, and 1988b). A vast amount of information was accumulated, including the original descriptions of every nominate species, most subsequent descriptions, a large number of photographs of type specimens and other material, drawings, tabular sheets recording locality data and shell measurements for thousands of specimens, keys to species groups, graphs of morphometric shell data, comparative charts, and personal observations and notes. All taxa were provisionally determined to be valid, synonymous, or undescribed, and subsequently assigned to a genus. Further research refined these synonymies and generic allocations. From this large database, a comprehensive species catalog of every valid Recent species was compiled, basing all generic allocations and synonymies on the work outlined herein, not on previous assignments. The generic descriptions, diagnoses, and species counts contained in the systematic section of this paper are summarized from this database. A total of 766 valid Recent species, including 77 undescribed species, is currently recognized for this entire group.

Literature on fossil species was not as comprehensively studied as that on the Recent fauna, but the original descriptions of all genus-group names were studied and a clear determination of each type species was made. A large sampling of additional literature on fossil species was obtained and studied, representing all regions worldwide. Specimens and descriptions of fossil species from the western Atlantic were particularly well represented. Generic allocations of fossil species are based on our own work, and do not necessarily agree with previous assignments. Our approach to the fossil fauna is conservative. Only specimens or literature personally examined were included in our database. A good representation of the fossil fauna has been obtained, and is presumed complete as far as genus-group names are concerned.

During this 13-year period, shell specimens from a wide variety of sources, including a large number of museums and individuals (see acknowledgements), were studied, largely concentrating on the Recent fauna.

Shell measurements, including maximum length parallel to the axis and maximum width perpendicular to the axis, were made with a Spencer AO binocular dissecting microscope using a calibrated optical reticle for minute to small shells under 5 mm. For larger shells, an electronic digital Max-Cal caliper was used with a resolution to 0.01 mm. Internal plications were initially studied by noting internal features on shells with gastropod drill holes or breakage. More detailed studies were conducted by grinding a hole on the ventral surface of the shell with a fine metal file. Some shells were transversely sectioned with a fine jeweler's saw, ground to a smooth surface on a fine-grit whetstone, then polished on a glass plate with toothpaste as a fine abrasive.

Methods used for the extraction, illustration, and analysis of radulae are given in complete detail in Covert and Covert (1987) and only summarized here. Most radulae were extracted without damaging the shell by soaking and flushing the shell with a solution of 10% potassium hydroxide (KOH) using a micropipette. After rinsing with acidic water, radulae were transferred to a microscope slide and mounted in glycerin jelly. Drawings were made using an optical reticle grid in a standard light microscope. Radular data, reported for each genus in the systematic section, includes a shell length to radular width ratio plus the Radular Index. The Radular Index is derived by dividing the number of rachidian plates by the number of cusps per plate, and requires a complete radular ribbon, which was not always available. Routine extraction using KOH destroys many details of the delicate subradular membrane, especially in true marginellids. For a detailed study of these features, radulae were removed during dissection without the use of KOH and studied in glycerin before mounting (see below). Study of the developing posterior end of the radula was made from previously mounted material. All personally prepared material, totalling 224 specimens of 97 species, was mounted using glycerin jelly and studied with a standard microscope. Through the courtesy of Dean Hewish, SEMs of radulae from 99 specimens of 67 mostly Australian species, with complete locality, shell, and morphometric data, were made available. A review and summary of published information is given in Covert (1989b), with additional radular data presented in Covert and Covert (1990). A combined total of 190 radulate species, plus an additional 30 species known to lack a radula, have been studied in detail.

The external anatomy from published sources was summarized in Covert (1987g). Many photographs and drawings, provided by colleagues, were also studied. Live material was examined using a Spencer AO binocular dissecting microscope, then carefully drawn in color. In more remote localities, a Rupen wide-field 16 X hand lens was used. Photographs were taken when possible. Data on the external anatomy of 183 species is summarized in this paper.

All published data on the internal anatomy was studied in great detail. Charts of potentially useful taxonomic characters of all 13 anatomically known species were

constructed, patterned after those in Harasewych and Kantor (1991). Using this information as a guide, and carefully choosing taxa to augment this published data, dissections were completed on 11 additional species, plus one previously reported species that lacked sufficient data. We concentrated on features of the foregut, as these were determined to be of most value taxonomically. Specimens were dissected using a Spencer AO binocular dissecting microscope. Gross dissections were completed on multiple specimens of a species when available, with a total of 26 specimens being dissected (Table 1). Detailed, annotated drawings were made during all stages of dissection. Preservation varied among material due to a wide range of sources and preservatives. Larger animals were extracted from shells with a fine jet of water after briefly soaking them in liquid dish soap. Smaller shells were first measured, then cracked using a small hand vice. Odontophoral cartilages were carefully extracted from the buccal mass of radulate species, manually cleaned of adherent tissue, and mounted on microscope slides using glycerin jelly as a mounting medium. The subradular membranes of these radulae were cleaned of extraneous tissue after extraction and studied in glycerin prior to permanent mounting in glycerin jelly. Potassium hydroxide was not used in the preparation of these cartilages or radulae at any stage. A list of the dissected material, with locality data, shell measurements, and other details, is presented in Table 1.

The following revision is based on all available information of every Recent species plus a representative survey of the fossil fauna. Most importantly, the type species of all marginelliform genus-group names, both Recent and fossil, were studied and fully clarified. Genera are based on groups of related species, not just their type species. A very conservative attitude was taken towards recognition of higher taxa. Shared, derived characters were searched for to unite groups rather than using minor differences to split groups. The rank of subgenus is not utilized in the classification presented as this would require additional research and necessitate formal recognition of additional taxa. We prefer the useage of informal "species groups." The proposal of new taxa has been avoided unless strongly supported.

ABBREVIATIONS AND CONVENTIONS

The following abbreviations and conventions are used in the systematic section and text:

=?	synonymy questioned (species)
?	synonymy questioned (genus)
†	(preceding genus), denotes extinct genus
†	(following species), denotes fossil species
<i>aff.</i>	<i>affinis</i> , having affinity with but not identical with
AMNH	American Museum of Natural History
AMS	Australian Museum, Sydney

ANSP	Academy of Natural Sciences, Philadelphia
BM(NH)	British Museum of Natural History
DMNH	Delaware Museum of Natural History
GAC	collection of Gary A. Coovert
ICZN	International Code of Zoological Nomenclature
M	original designation by monotypy
MHNG	Muséum d'Histoire Naturelle, Genève
MNHP	Muséum national d'Histoire naturelle, Paris
NMV	National Museum of Victoria
OD	original designation
OD (M)	original designation as type species, but also monotypic
OD (T)	original designation as type species, but also tautonomous
SD	subsequent designation as type
SD (M)	subsequent designation as type species, but also monotypic
<i>sic</i>	to signify exact transcription
T	original designation by tautonomy
TS	type species
USNM	National Museum of Natural History, Smithsonian Institution

In the systematic section, the following sequence is used for each generic synonym:

- Genus in original combination, followed by author, year, page number(s)
- TS as cited by original author of genus (or if not originally cited, as cited by author of SD)
- TS in original combination of author of species, if different from above
- Senior synonym if applicable
- Designation of type species (i.e. M, OD, OD (M), OD (T), SD, SD (M), T); SD followed by author, year, page number(s)

In the systematic section, *nomina nulla* (misspellings) are not included. Most *nomina nuda*, unless they have a direct bearing, are also not included. Citing these is undesirable because it imparts a false sense of validity. The comments in Tomlin (1917:242) are applicable.

Throughout the remainder of this paper, the term marginellid will be used in the strict sense for the family Marginellidae as defined and restricted in the systematic section herein. The term cystiscid will be used for the family Cystiscidae as defined in the systematic section herein. The term marginelliform will be used in the broad sense of marginellid, equivalent to the traditional concept of the family Marginellidae as conceived by previous authors, and including both marginellids in the strict sense and cystiscids.

Terminology pertaining to shell morphology, radular morphology, and anatomy has been used differently and without standardization by previous authors. Consistency and uniformity are important enough to warrant careful selection and concise definition of terms. In addition, several new terms are introduced and defined.

Table 1. Sex, voucher number, locality data, comments, and shell measurements of dissected material. All dissected specimens, including shells and slide preparations, have been retained in the collection of Gary A. Coovert

Species	Sex	Vouchers	Locality: Comments	Shell	
				Length (mm)	Width (mm)
<i>Bullata bullata</i> (Born, 1778)	male	GAC Acc. #16-90	Bahia de Todos Santos, Bahia State, Brazil, 5 meters depth, ex E. C. Rios; ex isopropyl alcohol. Note 1	52.1	27.8
<i>Dentimargo chburneola</i> (Conrad, 1834)	female	GAC 1177A	Stock Island, on N. side of U.S. Rt. 1, E. end of island, Monroe Co., Florida, under algae covered rocks in 0.3 m, Sept. 7, 1984, collectors G. A. & H. K. Coovert; ex isopropyl alcohol	6.9	3.1
<i>Dentimargo chburneola</i> (Conrad, 1834)	male	GAC 1448	Stock Island, on N. side of U.S. Rt. 1, E. end of island, Monroe Co., Florida, hand-dredged in sea grass beds in 0.3 m, Nov 30, 1988, collectors G. A. & H. K. Coovert, ex isopropyl alcohol	—	—
<i>Hyalina pallida</i> (Linné, 1758)	male	GAC Acc. #4-94 C	(no data); ex Robert Lipé; ex ethyl alcohol, animal only	—	—
<i>Marginella glabella</i> (Linné, 1758)	female	GAC M2548	"Banco Canario-Saharia," (apparently a fishing bank between Spanish Sahara and the Canary Islands), March 20, 1991, ex José Aguiar Morales; ex methyl alcohol, subsequently softened with trisodium phosphate (same data as above)	41.8	23.8
<i>Marginella sebastiani</i> Marchad & Rosso, 1979	male	GAC M2549A	(same data as above)	38.8	21.4
<i>Marginella sebastiani</i>	female	GAC M2549C	(same data as above)	39.8	23.4
<i>Persicula interruptolineata</i> (Megerle von Mühlfeld, 1816)	male	GAC 1581A	N. end of Playa La Galera, Isla de Margarita, Venezuela, NE side of bay, hand-dredged on sandy mud with small patches of Turtle Grass, Oct. 22, 1992, collectors G. A. & H. K. Coovert; ex isopropyl alcohol	14.7	9.6
<i>Persicula interruptolineata</i>	female	GAC 1581B	(same data as above)	12.5	8.4
<i>Persicula interruptolineata</i>	female	GAC 1581C	(same data as above)	12.2	7.9
<i>Persicula interruptolineata</i>	female	GAC 1581D	(same data as above)	11.6	7.5
<i>Persicula interruptolineata</i>	female	GAC 1581E	(same data as above)	13.5	8.4
<i>Persicula mastrana</i> Roth & Pettit, 1972	2 males	GAC Acc. #4-94 A, B	Masirah Island, Oman, shallow water, low tide, collector Donald T. Bosch, ex Robert Lipé; ex ethyl alcohol, animals only	—	—
<i>Prunum</i> aff. <i>aletes</i> Roth, 1978 Note 2	male	GAC 1518A	small island just off Tamarindo Beach, S. of Tamarindo Diria Hotel, Guanacaste Province, Costa Rica, under rocks, low tide, Oct. 18, 1989, collector Peter Bright; ex isopropyl alcohol	18.8	12.1
<i>Prunum</i> aff. <i>aletes</i>	female	GAC 1518B	(same data as above)	19.4	12.2
<i>Prunum</i> aff. <i>aletes</i>	male	GAC 1518C	(same data as above)	20.4	13.4
<i>Prunum guttatum</i> (Dillwyn, 1817)	male	GAC Acc. #2-89	Airport Reef, Utila Island, Bay Islands, Honduras, shallow water under rocks, ex Robert Lipé, ex isopropyl alcohol, animal only	—	—
<i>Prunum guttatum</i>	male	GAC 1172A	channel behind Lagoon Motel, Marathon, Key Vaca, Monroe Co., Florida, under rocks, snorkeling in 0-1 m, Sept. 5, 1984, collectors G. A. & H. K. Coovert, ex isopropyl alcohol	16.5	9.7
<i>Prunum guttatum</i>	male	GAC 1170B	(same data as above); Sept. 4, 1984, late juvenile	14.8	8.0
<i>Prunum prunum</i> (Gmelin, 1791)	female	GAC 1582	Mata Redonda, Isla de Margarita, Venezuela, shallow sand and mud flats with scattered Turtle Grass, low tide, Oct. 24, 1992; ex John Wolfe, ex isopropyl alcohol	30.7	15.8

Table 1. Continued

Species	Sex	Vouchers	Locality / Comments	Shell	
				Length (mm)	Width (mm)
<i>Prunum roosevelti</i> (Bartsch & Rehder, 1939) Note 3	male	GAC Acc. #26-SSA	Walkers Cay, Bahamas, snorkeling at 1 m, grass and algae, night, June 17, 1988, collector Robert Lipe; ex isopropyl alcohol; animal only	—	—
<i>Prunum roosevelti</i>	male	GAC Acc. #26-SSB	(same data as above)	16.9	11.0
<i>Volvarina</i> aff. <i>avena</i> (Kiener, 1834) Note 4	male	GAC 1172B	channel behind Lagoon Motel, Marathon, Key Vaca, Monroe Co., Florida, under rocks, snorkeling in 0-1 m, Sept. 5, 1984, collectors G. A. & H. K. Coovert; ex isopropyl alcohol	11.3	5.0
<i>Volvarina</i> aff. <i>avena</i>	female	GAC 1170C	(same data as above); Sept. 4, 1984	11.3	5.0
<i>Volvarina</i> aff. <i>avena</i>	female	GAC 1170E	(same data as above); Sept. 4, 1984	10.1	4.5

Note 1: Radula figured in Coovert and Coovert (1990:2, fig. 1).

Note 2: Shells were significantly larger and much more brilliantly and differently colored than the nominate deep-water form (from 3 to 82 m). More research is necessary to establish the status of this taxon.

Note 3: The radula of this species is closest to *P. carneum* (Storer, 1837), the animals greatly differing in the external coloration. The radulae are very distinct from the conchologically very similar *Prunum amabile* (Redfield, 1852), also from the Bahamas, whose radula was described in Coovert and Coovert (1990:5-6).

Note 4: See comments in Coovert and Coovert (1990:35) regarding the status of the Florida form of this species.

COMPARATIVE ANALYSIS OF SHELL MORPHOLOGY

Contrary to the opinion of many previous authors, there are many conchological characters that are very useful in the classification of marginelliform gastropods. Those most useful for higher categories are emphasized.

External varix: The external varix or "margin," for which these shells are named, is one of the more important shell characters. Other authors have used the terms "margin," "marginal varix," "varix," "labial varix," "outer varix," or "varical callus," not clearly differentiating between a true external varix and a merely internally thickened lip. The term external varix is herein used in preference over the above terms as it more clearly makes this differentiation. A shell with an external varix has a weakly to distinctly raised margin of callus deposited externally along the labial edge, easily seen by close dorsal examination of the shell.

In all marginelliforms, the outer lip is at least somewhat strengthened or thickened internally in the adult, but many genera completely lack an external varix. This fact has received very little attention in the literature and most original descriptions fail to mention the presence or absence of this important character. Shells lacking a varix are even and smooth along the external labial edge, without a discernable raised margin of callus. The outer lip in such shells is usually marked by a change in angle when viewed from the apex and is often a different color. Presumably, a strengthened lip, either internally, externally, or both, imparts adaptive value in protecting the snail from predation.

Most cystiscid genera, including "*Cystiscus*" (the group with a triserial radula), *Cystiscus* s. str., *Crithe*, *Gibberula*, and *Canalispira*, completely lack an external varix. Only the cystiscid genus *Persicula* varies in this character, with some species possessing a well-developed external varix, whereas others completely lack it. *Granulina* and *Pugnus* are the only cystiscid genera that always possess a strong external varix. Because the very strong axial costae in *Extra* resembles varices, the presence of this character is indeterminate. Based on other conchological characters, *Extra* has been placed with *Crithe* and *Cystiscus*, both non-varicose genera.

Marginellid genera, as opposed to cystiscid genera, nearly always possess a strong external varix. *Hyalina*, a notable exception, usually lacks an external varix. The genera *Prunum* and *Volvarina* vary in this character, some species possessing a strong varix, some a weak varix, and other species completely lacking it. The remaining marginellid genera always possess at least a weak external varix. This usually very strong, distinct varix often continues around the anterior edge of the siphonal canal. A few species have an extremely thickened external varix that is doubled or "duplicate."

Ontogenetic lip development, from initial formative stages in the juvenile, through subadult, to the fully adult stage, has seldom been reported in the literature. We have studied late juvenile and subadult shells for many years in an attempt to ascertain stages of labial development. The external varix is initially formed by an outward upturning of the thin lip edge in most species with a varicose adult shell. Callus deposition subsequently occurs internally and externally, resulting in the thick-

ened. adult varix. We have observed this sequence in the cystiscids *Persicula cingulata* (Dillwyn, 1817) and *P. persicula* (Linné, 1758), and in the marginellids *Eratoidea margarita* (Kiener, 1834), *Marginella rosea* Lamarck, 1822, and *Clabella adansoni* (Kiener, 1834). Because the situation in *Prunum* and *Volvarina* is more complex, we transversely sectioned, polished, and studied many shells from these genera. Preliminary results indicate that some varicose species of *Prunum*, but not *Volvarina*, form the varix as described above. This can often be seen in cross-sections, with the initial varix and subsequent concentric growth rings showing clearly. Other varicose species of both *Prunum* and *Volvarina* initially curve the thin, fragile, developing lip edge inwardly, subsequently adding further callus deposits internally to strengthen and thicken the edge. Only later are significant external callus deposits added in those species with a varicose adult shell. Preliminary results with shell cross-sections of *Prunum* and *Volvarina* indicate a difference in how this occurs. Varicose *Prunum* species with an initially incurved lip produce the varix by adding shell material to both surfaces while extending the growing edge. This can be seen in cross-section as very fine concentric growth rings centered around an initial growing point. Varicose *Volvarina* species, on the other hand, produce the varix by callus deposition internally and externally, without much elongation of the labial edge and lack obvious concentric growth rings. The same difference appears to exist between non-varicose *Prunum* and *Volvarina* species, but the external varix simply does not form in these taxa. Additional study of this character is needed before definite conclusions can be drawn, but preliminary results indicate the existence of a potentially useful taxonomic character.

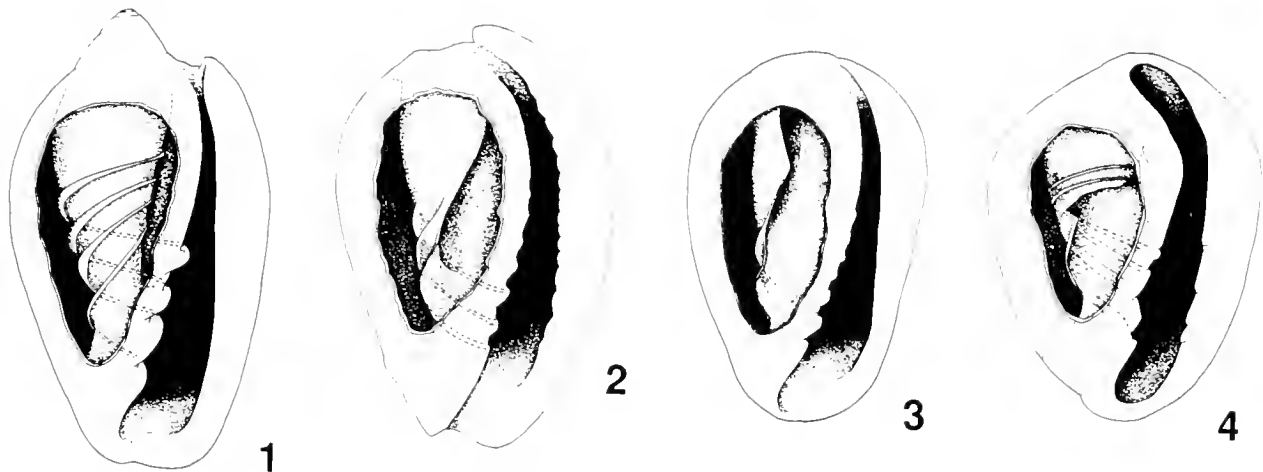
Labial Denticles: Many marginelliform shells have an outer lip with distinct denticles, referred to herein as labial denticles or denticulate lip. This is preferred over such terms as "teeth," "crenulations," or "crenate." Presence or absence of labial denticles is sometimes of generic value but is usually only of specific value. Lirae are a different type of labial structure and are very useful taxonomically. They are usually erroneously referred to as "denticles" or "teeth" in the literature, but the difference is very important. Denticles are small bumps or tooth-like projections on the inside edge of the outer lip and generally do not extend into the aperture. Lirae are thin spiral ridges on the inside of the outer lip oriented perpendicularly to the lip edge and extending well inside the aperture. They resemble denticles only at the outer edge of the lip. The only marginelliforms possessing lirae (but not in all species) are the cystiscid genera *Persicula*, *Canalispira*, and *Gibberula*. These lirate genera usually lack an external varix.

Columellar Plications: Another extremely important character complex is the number and formation of columellar plications. The terms "fold," "plica," and "plait," used by other authors, are considered inappropriate for a spirally wound ridge of shell material that is deposited

upon the columella and is not an actual fold of shell material. The term columellar plication is thus preferred. The anteriormost plication of marginelliform shells does not differ fundamentally from the adjacent plication, and is thus not differentiated by a separate term, such as "siphonal fold" or "basal fold." This anteriormost plication is herein considered the first plication, thus counting anterior to posterior. In many animal groups, serial features are likewise counted in a standard anterior to posterior direction. A few authors, mostly of older works, numbered plications from posterior to anterior, resulting in the anteriormost plication being variously numbered. A survey of marginelliform gastropods reveals that the first columellar plication borders the anterior edge of the columella in all cases (usually continuing and merging with the external varix) except *Afrivoluta*, which has a very volute-like columella. Two fundamentally different plicational conditions occur in marginelliform species. These are correlated with the type of internal whorls present.

Internal Whorls: One group has typical neogastropod internal whorls that are simply previous body whorls subsequently enclosed by additional whorls without further modification. The columellar plications remain unmodified for their entire length. This type of plicate internal whorl has also been observed in the families Turbinellidae, Cancellariidae, Mitridae, Costellariidae, and Volutidae. The internal whorls in true marginellids are maintained at their original thickness with no apparent resorption or further modification and are herein termed unmodified internal whorls (figure 1). Taxa with unmodified internal whorls have columellar plications remaining at their original strength and number throughout subsequent whorls. These plications can be found intact internally upon the entire length of the columella. They are here termed continuous columellar plications and are normally oriented nearly perpendicular to the shell axis. The usual number of plications in this group is four, but varies from two to six among different species, although not normally varying within a species. In those species with five or six plications, the fifth and sixth continue internally for at least a half whorl, and often are fully continuous. These are also considered continuous plications in this paper. In some species, a weak "false fifth plication" (or less commonly a "false fourth" or "false sixth") is present. This may be either a parietal lira that does not continue into the aperture for more than an eighth of a whorl, or a denticle, but neither are true plications because they are not continuous. Within marginelliform gastropods, unmodified internal whorls and continuous columellar plications are found only in species herein assigned to the Marginellidae s. str.

Another group has extremely thin, largely resorbed internal whorls, often partially missing due to complete local resorption or breakage. Proceeding inward, the first three (anterior) columellar plications in the aperture are quickly reduced to two, the third simply diminishes within a half whorl internally. The remaining two are further reduced to a single, sharp, very oblique columellar edge



Figures 1–4. Internal shell whorls. 1. *Prunum prunum* (Gmelin, 1791), showing unmodified internal whorls. GAC, no data. Length 30.9 mm. 2. *Persicula persicula* (Linné, 1758), showing cystiscid internal whorls. GAC Acc. # 54–87, Joal River, Senegal, on sand flats at mouth of river. Length 20.0 mm. 3. *Plesiocystiscus jewettii* (Carpenter, 1857), showing cystiscid internal whorls. GAC Acc. # 14–90, California. Length 5.7 mm. 4. *Granulina hadria* (Dall, 1889), showing modified cystiscid internal whorls. GAC 824, Tampa Bay, Pinellas Co., Fla., 0.3–0.6 m, shallow grass flats. Length 2.0 mm.

within one full internal revolution. This single, sharp columellar edge essentially becomes the axis of the shell. The shape of the internal whorls are very different from the original juvenile body whorls that were subsequently resorbed after being enclosed by the next whorl. Original juvenile shell color, patterns, and apertural columellar plications, generally more than two, are all completely resorbed. Among marginelliform gastropods, this type of internal whorl is found only in species here assigned to the Cystiscidae. They are here termed cystiscid internal whorls (figures 2, 3). Columellar plications in species possessing cystiscid internal whorls differ fundamentally from the continuous plications found in species with unmodified internal whorls, primarily because they are quickly reduced to a single columellar edge, and are not continuous internally. They are here termed internally reduced columellar plications. Posterior to the three internally reduced columellar plications are one to ten parietal lirae superficially resembling columellar plications. These were not differentiated from columellar plications by most previous authors. Parietal lirae are somewhat smaller and weaker than the three anterior plications, do not continue into the aperture for more than a quarter turn, and gradually diminish posteriorly. This results in a total of up to 13 “plications,” of which only the anterior three are considered true, but highly modified, plications. This columellar arrangement, composed of internally reduced columellar plications plus parietal lirae, is herein termed multiplicate. This term has been used by some previous authors, but was not clearly defined. In a few cases, there may be parietal denticles posterior to the parietal lirae, but these are even shorter. A very few species of *Cystiscus* have only two columellar plications (one species, possibly not a cystiscid, is reported to have only a single plication).

A modification of the cystiscid internal whorl has been

studied in species herein assigned to the genus *Granulina*. This modified type is characterized by the first two columellar plications (proceeding inwardly) abruptly ending within one full revolution internally. At this point, a thin, axially oriented edge begins much as in species with cystiscid internal whorls. However, the two posterior columellar plications continue and are situated at the anterior edge of the more bulbous portion of the mostly resorbed internal whorl. These usually translucent internal whorls are extremely thin and fragile and break very easily. The anterior end of these whorls appears to be open. We believe that this is a modification of the cystiscid internal whorl and is herein referred to as a modified cystiscid internal whorl (figure 4). The four columellar plications of *Granulina* superficially resemble continuous plications, but because the first two quickly terminate, they are considered to be internally reduced columellar plications typical of all other cystiscids. The posterior two continue, and are herein referred to as pseudo-continuous plications because they apparently do not continue for more than a whorl or two internally. Members of the genus *Granulina* lack the gradually weakening parietal lirae posterior to the columellar plications, and thus they do not have a multiplicate columella typical of other cystiscids.

Apertural Characters: The extent to which the aperture is occupied by the columellar plications is useful taxonomically. Genera with a multiplicate columella usually have more than half the apertural length occupied by the plications plus parietal lirae. *Marginella*, *Glabella*, *Dentimargo*, and *Eratoidea* have four strong, continuous columellar plications occupying more than half the apertural length, as do *Austroginella* and many of its relatives. Most remaining typical marginellids have four plications occupying less than half the apertural length.

In a few genera, though, the plications are crowded anteriorly. Columellar plications are also very useful taxonomically at the species level. In addition to the number of plications, other useful characters include their height, thickness, shape in cross-section, extent of protrusion from the aperture, their angle, whether they are fused or separate, and whether or not they are excavated inside the aperture. Very little use has been made of these features in the literature.

Another feature of the aperture is its relative width, which can often be compared to the lip thickness as a readily available reference. Most genera have an aperture that is widest anteriorly, but in some the aperture is broadest medially.

Siphonal Notch: The presence or absence of a siphonal notch is an important shell character. Called "anterior notch," "notched anterior canal," or "siphonal canal" by various authors, the term siphonal notch is preferred, as it relates to the function of this feature. A distinct siphonal notch is present in *Persicula* and *Gibberula*, but absent in the related *Canalispira*. This notch is a typical character of *Glabella* and most *Marginella* s. str. The genera *Afrivoluta* and *Marginellona* possess a siphonal notch, although it is weak in *Marginellona*. *Austroginella* has a distinct siphonal notch, but in the related *Mesoginella* the notch is very weak to absent (Coovert, 1988b). In all remaining marginelliform genera the notch is very weak or absent.

Posterior Notch: A weak to distinct posterior notch is sometimes developed at the junction or commissure between the body whorl and the posterior end of the lip. The posterior end of the lip generally forms an abrupt angle just prior to joining the body whorl, leaving a broad to narrow notch between the lip and body whorl. Less commonly, this notch forms as a weak to distinct groove in the posterior end of the lip itself. Various terms "posterior notch," "posterior sinus," "posterior canal," "anal canal," or "anal sulcus," posterior notch is preferred, because it is consistent with "siphonal notch." The terms "anal canal" or "anal sulcus" imply a functional aspect not borne out anatomically. The presence or absence of this character is often obscure, reducing its taxonomic importance. However, many *Persicula*, *Gibberula*, and *Canalispira* have a distinct posterior notch formed at the junction of the body whorl and posterior end of the lip. The posterior notch in *Persicula* is often accentuated by an adjacent callus deposit on the body whorl. The deeply channeled, narrow notch in *Canalispira* is diagnostic. *Protoginella* has a posterior notch formed in the posterior corner of the lip itself.

Spire: Spire height is often important taxonomically. Several groups have a completely immersed spire and thus an easily recognizable shell shape. In this paper, a low spire is defined as having a length less than $\frac{1}{4}$ the shell length (figures 43, 44, 48, 55). A spire of medium height ranges from $\frac{1}{4}$ up to $\frac{1}{2}$ the shell length (figures 57, 73), whereas a tall spire is more than $\frac{1}{2}$ the shell length (figures 49, 70). Spire height often varies consid-

erably within a genus and is thus more important at the species level. Spire height is determined by the insertion point of the posterior end of the lip, and can be referenced by whether or not the posterior end of the lip joins the body whorl at, above, or below the previous suture. This is a very useful character within *Volvarina*, for example.

Shape: Shell shape is another useful feature, and although somewhat subjective, should be carefully described using standard shape names. Marginelliform shells vary from a nearly round, globose outline to elliptic, obovate, obconic, conic, biconic, subtriangular, pyriform, elongate-ovate, subcylindrical, cylindrical, and other combinations. The shape of the shoulders is very important in determining overall shell shape, and can be gently curved to strongly rounded or carinate.

Size: Shell size is often very valuable as a species-level character and, in a general way, for higher categories. Shell size is here reported as minute for shells up to 2.4 mm in length, small for shells over 2.4 mm up to 6.0 mm, medium for shells over 6.0 mm up to 13.0 mm, moderately large for shells over 13.0 mm up to 25.0 mm, large for shells over 25.0 and up to 50.0 mm, and very large for shells over 50.0 mm in length.

Surface Features: Shell texture is another very useful conchological feature. Although most marginelliform shells are perfectly smooth and glossy, some have very characteristic weak to strong axial costae. This term is preferred over "axial ribs" or "longitudinal ribs." This character is often useful at the genus or the species level. Pronounced surface texture is very rare in the family, but *Pugnus* and a few *Granulina* have a minutely sculptured surface. *Rivomarginella* species have minute pustules ventrally that are part of the callus deposit. Many other species have callus deposits ranging from a thin parietal wash to distinct deposits on the spire, posterior parietal area, or anteroventrally. *Afrivoluta* has a very distinctive callus pad (Coovert, 1987a). The placement of callus deposits is species specific and thus diagnostic in the *Persicula cornea* group (Coovert, 1987b). Many *Granulina*, *Crithe*, and other species have a characteristic callus deposit here termed a collabral parietal callus ridge (figures 55, 56). This is a narrow ridge of callus deposited parallel to the lip and usually lying just outside the aperture. It often intersects the columellar plications, causing them to appear excavated. Heavier callus deposits at vulnerable points are interpreted as a protective adaptation against predatory boring. Preliminary observations suggest a strong correlation between typical bore hole locations in uncallused species and locations of callus deposits in related species.

Color: Shell color and pattern are also useful taxonomic characters. Most small species are translucent to opaque white. Most larger species are white, but some range from gray or greenish-gray, to brown, amber, flesh-colored, yellow, orange, pink, rose, or even red. The base color may be overlain with various pattern elements of

a different color. These can consist of spots, irregular blotches, spiral lines or bands, axial or oblique bands or streaks, oblique lines, or various combinations of these features.

COMPARATIVE ANATOMY OF MARGINELLIFORM GASTROPODS

External Anatomy: Features of the external anatomy of 82 species of marginelliform gastropods have been reviewed and summarized (Coovert, 1987g). Since then, a number of additional species have been reported in the literature (Coovert, 1988e:37). Our additional research, plus notes and excellent photographs of the living animals shared by others, provided a clearer picture of the external anatomy of this group. Data on 183 species are summarized in this paper. The four basic morphologic types are summarized first, along with a discussion of general features of the external anatomy. Further details of the external anatomy of each genus can be found in the systematic section.

The four distinct animal "types" delineated and summarized in Coovert (1987g) are based primarily on features of the head. The most common marginelliform animal is termed a "Type 2 animal," which has a simple, unmodified head described by some authors as "bifurcate" (figures 7, 8). The long, slender tentacles emerge from the anterior end of the head, resulting in a bifurcate appearance. Viewed from above, as most photographs are oriented, this bifurcation is not readily apparent. The long, slender tentacles have an eye located on a slight swelling at their bases. The siphon, as in all marginelliform gastropods, is a simple tube formed by the inrolled edges of an elongated expansion of the mantle edge. The siphon in Type 2 animals is moderately long to very long, and simple or weakly notched distally. A few cystisid and most marginellid genera have a Type 2 animal, which is considered to be the generalized type.

Type 1 animals, represented by *Afrivoluta* and *Marginellona*, are characterized by a broad head with a longitudinal medial furrow or channel (figures 5, 6). This channel was described by Harasewych and Kantor (1991: 10) as a "deep tubular channel along dorsal mid-line of head," apparently formed by the ventral fusion of the tentacle bases. These same authors (op. cit., p. 13) noted that this medial channel had not been reported in *Afrivoluta*, but our careful examination of a color transparency of *Afrivoluta pringlei* (ex. W. R. Liltved) has revealed that both genera share this feature. Type 1 animals are further characterized by relatively short tentacles, a simple, moderately long siphon, and a distinct, subtriangular lateral lappet on each side of the head. A small red eye is present on each lateral lappet in *Afrivoluta*. Eyes are completely lacking in *Marginellona*.

Type 3 animals are characterized by an elongate head that is longitudinally split dorsally, with the anterior end bifurcate (figures 9, 10). This configuration could be described as either having the tentacles fused ventrally, resulting in a longitudinal dorsomedial channel, or al-

ternatively, as having a longitudinally split head completely lacking tentacles. A detailed anatomical study is needed to clarify this situation. The siphon is either very short and not readily apparent, or completely absent. Eyes are located on the sides of the head, usually in a conspicuous bulge. Type 3 animals are represented by the genus *Cystiscus* and probably also *Crithe*.

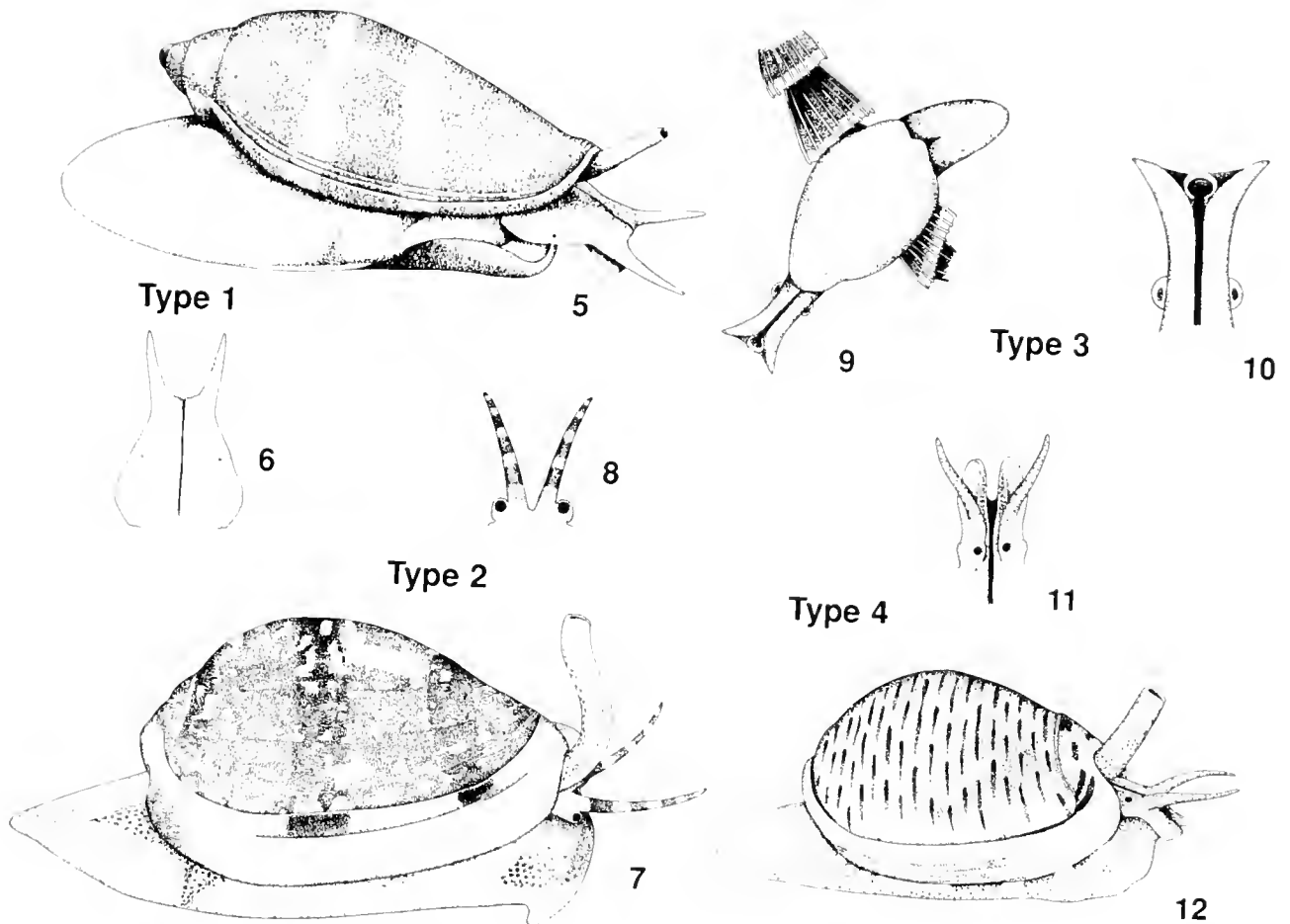
Type 4 animals have a somewhat flattened, longitudinally split head, normally with tentacles (figures 11, 12). The anterior half of the head is completely split, usually with the anterior tips pointed and divergent, but capable of closing together. These two lobes are very flexible and capable of much movement. The posterior half is only split dorsally, and fused ventrally. Tentacles, which are rarely absent, are short to long. The eyes are located on the sides of the head, slightly below the tentacle bases. The siphon is short to long, simple, and protrudes through the siphonal notch at the anterior end of the shell when the animal is active. Type 4 animals are represented by the genera *Persicula* and *Gibberula*. *Canalispira* animals differ from the typical Type 4 animal in lacking tentacles and a visible siphon (cf. Systematic section for more detail).

The siphon of most marginelliform gastropods emerges from the left side of the head, but has been described as fused to the head in *Marginellona* by Harasewych and Kantor (1991:table 3), although these authors stated that the siphon is "fused to head just left of posterior margin of mid-line channel" (op. cit., p. 10). It was described as fused to the mid-dorsal line of the head in *Prunum marginatum* by Graham (1966:135). All species studied by us (Table 3) have a siphon fused to the left side of the head. There seems to be some difference in interpretation, but probably all marginelliforms have a siphon fused to the head at least slightly left of center.

The mantle is another external anatomical feature that is useful taxonomically. Within higher taxa, the degree of mantle extension over the external shell surface varies from none to complete coverage. Extended mantles can be smooth, have low, rounded tubercles or pustules, or possess elongate papillae that are either simple or branched. The terms pustulose and papillose are used here.

Most marginelliform gastropods have a broad, flat foot, although it may be very narrow in a few species. The relative size and length of the foot may have some value taxonomically. Some species have a medially indented foot, and some (e.g. *Hyalina hyalina*, *H. pallida*, and *Prunum martini*) have an anterior, transverse pedal groove. As far as is known, females have a medial, anteroventral pedal gland on the sole of the foot. In some *Gibberula* species, the anterolateral edges of the foot are raised and laterally rolled, forming what Gofas and Fernandes (1988:22) described as "parapodia." All these characters may have taxonomic value and need further study.

Animal coloration is very useful at the species level, but has limited value for higher classification. Gofas and Fernandes (1988) and Gofas (1989a, 1990, 1992) provid-



Figures 5-8. Marginellid external anatomy. **5, 6.** *Afrivoluta pringlei* Tomlin, 1947, example of Type 1 animal. After Liltved (1985) plus pers. obs. of photos (ex. W. R. Liltved). Off Danger Point, western Cape Province, at 246 m. Ca. X 0.65. **5.** Animal viewed from right side. **6.** Dorsal view of head. **7, 8.** *Prunum* aff. *aletes* Roth, 1975, example of Type 2 animal. GAC 151S, small island just off Tamarindo Beach, S. of Tamarindo Diria Hotel, Guanacaste Province, Costa Rica, under rocks, low tide. Shell length 19.4 mm. **7.** Animal viewed from right side. **8.** Dorsal view of head. **Figures 9-12.** Cystiscid external anatomy. **9, 10.** *Cystiscus minutissimus* (Tenison-Woods, 1876), example of Type 3 animal. After Murray (1970) and Coleman (1975). **9.** Animal viewed from above. Ca. 9.0 X. **10.** Dorsal view of head. Ca. 18 X. **11, 12.** *Persicula interruptolineata* (Megerle von Mühlfeld, 1816), example of Type 4 animal. GAC 1581, N. end of Playa La Galera, isla de Margarita, Venezuela, NE side of bay, hand-dredged on sandy mud with small patches of Turtle Grass. Length 14.7 mm. **11.** Dorsal view of head. **12.** Animal viewed from right side.

ed color plates of live animals, making excellent use of coloration or "polychromatism" for species differentiation.

Radula: The radulae of very few species (20 *vide* Coovert, 1989b) were known at the time of the last generic revision of this group (Coan, 1965). Much additional radular information has been subsequently published (see Coovert, 1989b for summary; Coovert and Coovert, 1990). This published data, combined with our unpublished data and observations of SEMs (ex. Dean Hewish), brings the number of species studied to 190. An additional 30 species are known to be non-radulate. Of the 31 Recent genera recognized in this revision, the radulae of only two are unknown.

Three basic radular patterns of marginelliform gastropods have long been recognized by the senior author.

In addition to non-radulate species, the radulate species fall into two different groups. One group has a relatively long, narrow radula, the other group has a shorter, wider radula. The most fundamental differences between these two groups were not apparent until recently. In fact, Coovert (1989b:31) erroneously assigned the genera allied to *Austroginella* to the long, narrow radulate group based solely on radular width.

The first major difference noted between these two groups was the discovery of paired, wing-like extensions of the subradular membrane, found only in species with a long, narrow radula (and not in genera allied to *Austroginella*). These structures, which persist in routine maceration with KOH, were first noticed by Dean Hewish (pers. comm.), and later confirmed by us in a number of species. They were originally called "membranous wings," and appeared to be attached anteriorly to the

radular ribbon at the bending plane. They are not readily visible after permanent mounting on microscope slides.

We follow Coan (1965) in usage of the term rachidian plate rather than "rachidian teeth" because of the wide, multicusped nature of these structures in marginelliform radulae.

We discovered that two different conditions of rachidian plate development occur on the posterior end of the radula where plates are initially secreted. Species with a long, narrow radula have a series of at least 6, and up to 12 or more, gradually formed rachidian plates at the posterior end, which are enclosed in a radular sac. These plates, initially narrower and rudimentary, are extremely thin, clear, and very difficult to discern in slide preparations. Progressing anteriorly, these plates become wider and more visible, first developing medially, with lateral portions forming next, finally followed by full cusp development. We refer to these separate undeveloped plates as nascent rachidian plates, and the gradually developing series as a developmental series. Just anterior to the nascent plates, a series of up to 40 or more fully formed plates are distinctly brown-tinged, followed by fully developed, clear, normal-appearing plates. In contrast, species with a short, wide radula have only one or two nascent plates posteriorly. These plates are fully formed with completely developed cusps, but are extremely thin, clear, and often very difficult to discern in microscope slide preparations. The first plate often appears as a "ghost image." We term these preformed nascent rachidian plates. Just anterior to these nascent plates, a series of 4 to 5 fully formed brown-tinged plates are followed by fully developed, clear, normal-appearing plates. The buccal pouch, characteristic of marginellids in the strict sense (see Internal Anatomy section), contains the posterior end of the radula in this group. Thus, two fundamentally different conditions exist in both overall structure and development of the posterior end of marginelliform gastropod radulae.

In our search for taxonomic characters of marginelliform radulae, we noted that Ponder (1970:70) reported two completely separate odontophoral cartilages in *Gibberula* (as *Diluculum* sp.). A pair of anteriorly fused odontophoral cartilages (described as a single cartilage in *Volvarina taeniolata*, see Fretter, 1976:329) were described from all other studied species. None have been illustrated. We dissected *Persicula interruptolineata* (Megerle von Mühlfeld, 1816), a close relative of *Gibberula*, to confirm the presence of separate odontophoral cartilages. Rather than underlying the radular ribbon as in typical marginellids, the two separate odontophoral cartilages of *Persicula* each fit into one of the "membranous wings" that flank the radular ribbon (figures 15, 16). Further work determined the shape and attachments of these wing-like membranous structures. These paired, hood-like extensions of the subradular membrane (more accurately termed the cuticle, see Hyman, 1967:236), which serve to receive the odontophoral cartilages, are here referred to as odontophoral cartilage hoods (figures 13-16). Nothing resembling these structures has been

Table 2. Anatomical character states utilized in Table 3.

1. Buccal pouch	0—absent 1—present
2. Neogastropod radular sac	0—present 1—absent
3. General radular type	0—cystiscid 1—marginellid 2—absent
4. Specific radular type	0—absent 3—Type 3 radula 5—Type 5 radula 6—Type 6 radula 6m—modified Type 6 radula 7—Type 7 radula
5. Odontophoral cartilages	0—separate 1—anteriorly fused 2—fused both anteriorly and posteriorly 3—absent
6. Siphon	0—attached left of head 1—fused to head
7. Valve of Leiblein	0—present, no bypass tube 1—present, with bypass tube 2—absent
8. Esophageal caecum	0—absent 1—present
9. Gland of Leiblein	0—small, narrow gland, no terminal bulb 1—large, sacculate gland, no terminal bulb 2—with terminal bulb and long, convoluted duct
10. Duct of gland of Leiblein	0—empties into esophagus posterior to nerve ring 1—passes through nerve ring, emptying into anterior end of proboscis either into buccal cavity or anterior end of anterior esophagus
11. Paired salivary glands	0—acinous 1—tubular
12. Paired salivary gland attachment	0—attached to esophagus 1—free of esophagus
13. Paired salivary glands, ducts	0—embedded in walls of esophagus 1—attached to esophagus 2—free of esophagus
14. Accessory salivary glands	0—absent 1—single gland present

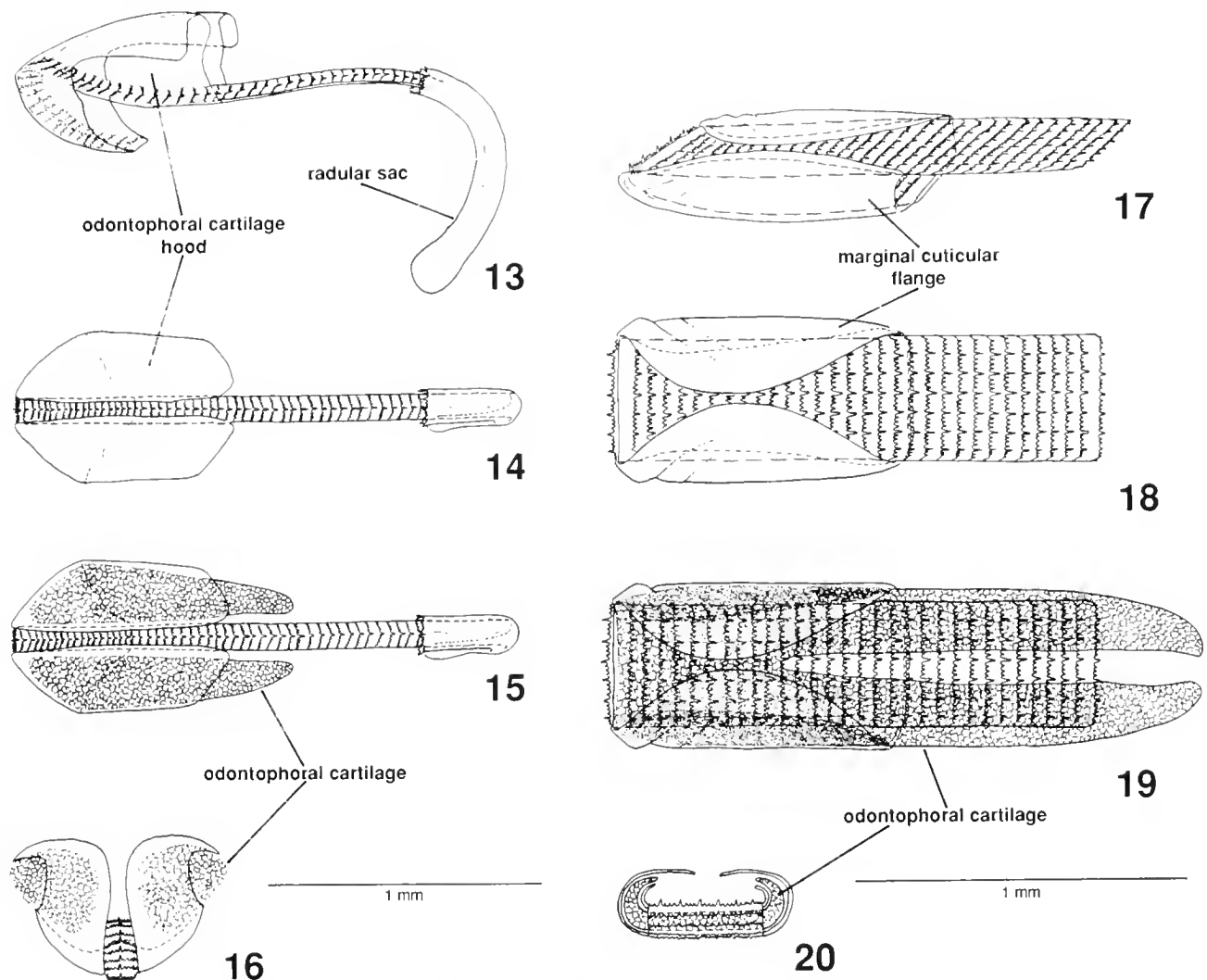
reported in marginellids with a short, wide radula. A radula from a specimen of *Prunum* aff. *aletes* Roth, 1978, which was not macerated in KOH, revealed anterolateral extensions of the radular ribbon cuticle. These, however, were narrower lateral flanges that differ functionally from the odontophoral cartilage hoods of *Persicula*. These extensions of the cuticle apparently help hold the radular ribbon in correct alignment with the underlying odontophoral cartilage. We term these structures marginal cuticular flanges (figures 17-20). Unlike odontophoral cartilage hoods, they are lost during routine maceration

Table 3. Summary of anatomical features of marginelliform gastropods. Character states given in Table 2. Sources of data given in Table 4. ? indicates character state unknown or uncertain.

	Character states													
	Buccal pouch 0-absent, 1-present	Xcogastropod radular sac 0-present, 1-absent	General Radular Type 0-cylindrical, 1-marginal	Specific Radular Type 0-absent, 1-present	Odontophoral cartilages 0-1, 2, 3, 4, 5, 6, 7	Siphon 0-1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14	Valve of L. blem 0-1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14	Esophageal caecum 0-absent, 1-present	Gland of L. blem 0-1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14	Duct of L. blem 0-post, 1-nerve ring, 2-nerve bulb	Paired salivary glands 0-1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14	Paired salivary glands 0-1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14	Paired salivary glands 0-1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14	Access. salivary glands 0-abs, 1-single gland, 2-pairs
Cystiscidae	1	2	3	4	5	6	7	8	9	10	11	12	13	14
<i>Persicula interruptolineata</i>	0	0	0	3	0	0	0	0	0	0	0	0	1	1
<i>Persicula masirana</i>	0	0	0	3	0	0	0	0	0	0	0	0	1	1
<i>Gibberula</i> sp.	0	0	0	3	0	0	1	0	0	0	1	0	0?	1

Marginellidae

<i>Marginellona gigas</i>	1	1	1	7	?	1	0	0	1	0	1	1	2	0
<i>Serrata mustelina</i>	1	1	1	6m	1	0	1	0	2	0	1	0	0	1
<i>Austroginella johnstoni</i>	1	1	1	5	1	?	1	0	2	0	1	0	0	0
<i>Austroginella muscaria</i>	1	1	1	5	1	?	1	0	2	0	1	0	0	0
<i>Mesoginella pygmaea</i>	1	1	1	5	1	0	1	0	2	0	1	0	0	0
<i>Volvarina avena</i>	1	1	1	6	2	0	2	1	2	1	0	1	1	1
<i>Volvarina taeniolata</i>	1	1	1	6	2	?	2	1	2	1	0	1	2	1
<i>Prunum aletes</i>	1	1	1	6	1	0	2	1	2	1	1	1	2	0
<i>Prunum guttatum</i>	1	1	1	6	1	0	2	1	2	1	0	1	1	0
<i>Prunum marginatum</i>	1	1	1	6	?	1	2	1	2	1	0	1	2	0
<i>Prunum martini</i>	1	1	1	6	?	0	2	1	2	1	1	1	2	0
<i>Prunum prunum</i>	1	1	1	6	2	0	2	1	2	1	1	1	1	1
<i>Prunum roosevelti</i>	1	1	1	6	2	0	2	1	2	1	1	1	2	0
<i>Bullata bullata</i>	1	1	1	6	?	0	2	1	2	1	?	?	?	?
<i>Hyalina hyalina</i>	0	1	2	0	3	0	?	?	2?	1?	1	?	?	?
<i>Hyalina pallida</i>	0	1	2	0	3	0	2	1	2	1	1?	1	2	1
<i>Dentimargo cairoma</i>	0	1	2	0	3	0	2	0	2	1	1	1	2	1
<i>Dentimargo eburneola</i>	0	1	2	0	3	0	2	0	2	1	0	1	2	1
<i>Marginella desjardini</i>	0	1	2	0	3	0	2	0	2	1	?	1	?	1
<i>Marginella glabella</i>	0	1	2	0	3	0	2	0	2	1	1	1	2	1
<i>Marginella sebastiani</i>	0	1	2	0	3	0	2	0	2	1	1	1	2	1



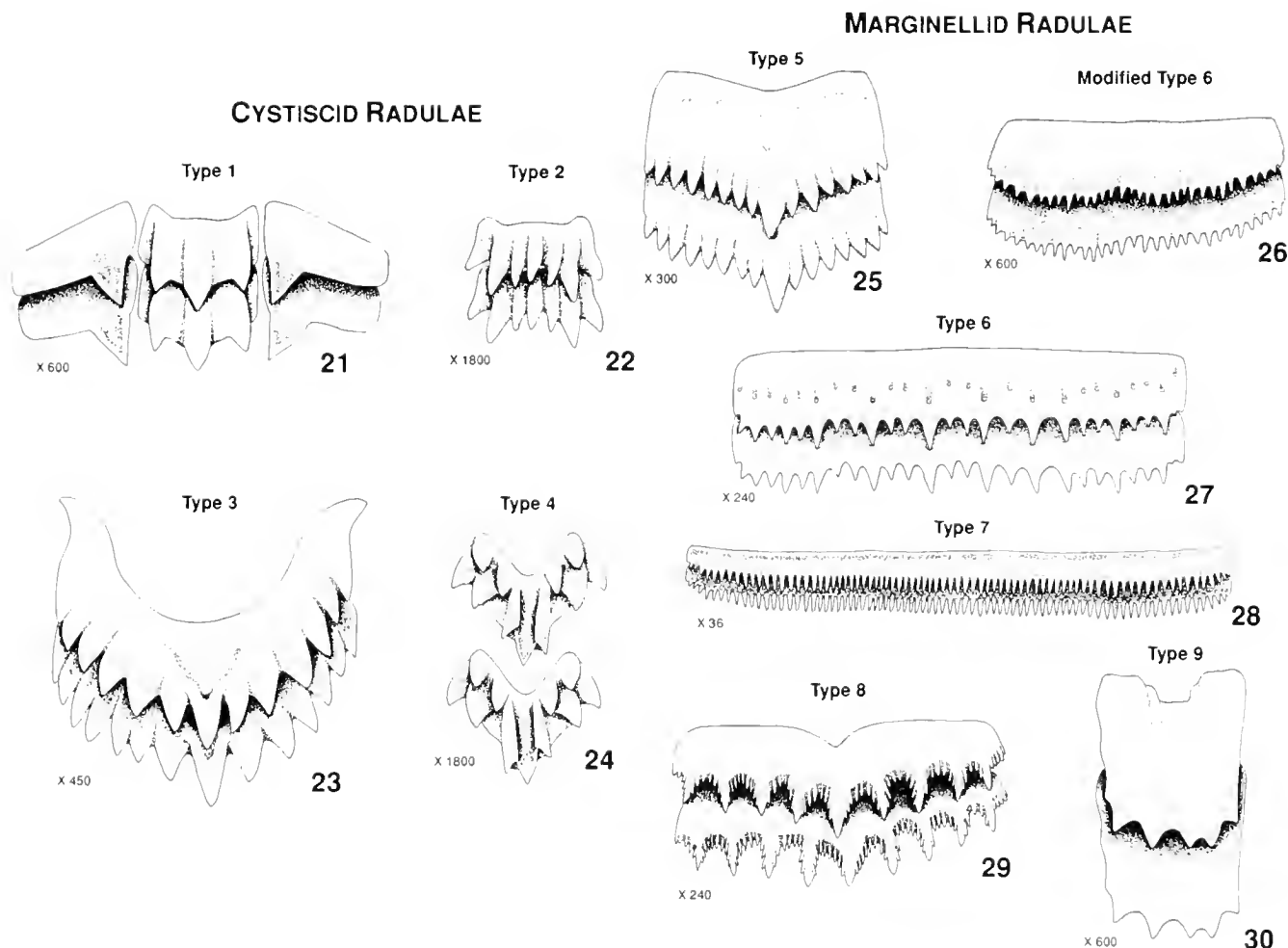
Figures 13–16. *Persicula interruptolineata* (Megerle von Mühlfeld, 1816), showing details of cystiscid radular morphology. GAC 1581, data in Table 1. Rachidian width enlarged 150% for clarity. **13.** Left lateral view, odontophoral cartilages removed, only posterior end of radular sheath shown. **14.** Same, dorsal view. **15.** Dorsal view, odontophoral cartilages in place, muscles and connective tissue removed. **16.** Same, anterior view. **Figures 17–20.** *Prunum aff. aletes* Roth, 1978, showing details of marginellid radular morphology. GAC 1518, data in Table 1. **17.** Left lateral view, odontophoral cartilage removed. **18.** Same, dorsal view. **19.** Dorsal view, odontophoral cartilage in place, muscles and connective tissue removed. **20.** Same, anterior view.

in KOH, suggesting additional differences in composition.

Morphological evidence suggests that there are two fundamentally different types of radulae. The first type has a very long, triserial or uniserial, C-shaped radula, composed of 80 to 200 or more very narrow, usually overlapping, arched rachidian plates, with relatively few (3 to 15) cusps. This type of radula has a pair of odontophoral cartilage hoods, each receiving a separate odontophoral cartilage, which flank the radular ribbon anteriorly. The posterior end of the radula begins as a developmental series of nascent plates and is enclosed in a typical neogastropod radular sac. This type of radula is found in all species here assigned to the Cystiscidae and is termed a cystiscid radula (figures 13–16). The second type has a uniserial, J-shaped ribbon composed

of 10 to 80 broad, overlapping, flat rachidian plates, usually with numerous cusps (9 to 80, rarely 4 to 7). This type of radula has marginal cuticular flanges, and the odontophoral cartilages are fused anteriorly into a single structure underlying the radular ribbon. The posterior end of this type of radula starts with 1 or 2 preformed nascent rachidian plates and is enclosed in a marginellid buccal pouch. This second type is found in all radulate species here assigned to the Marginellidae s. str., and is termed a marginellid radula (figures 17–20).

Coovert (1989b:31–33) divided marginelliform radulae into seven distinct types based on characters of the rachidian plates and the presence or absence of lateral teeth. In addition to these seven types, which are discussed below, two new types are recognized. The orientation of rachidian plates refers to the large, dorsal



Figures 21–24. Cystiscid radular types. **21.** *Plesiocystiscus jewettii* (Carpenter, 1857), example of Type 1 radula. GAC radula no. 093, Pirates Cove, San Luis Obispo, California, intertidal. Ex. M1823, shell length 4.9 mm. **22.** *Cystiscus angasi* (Crosse, 1870), example of Type 2 radula. Hewish radula U, Lonsdale Bight, Victoria, Australia. Ex. NMV F53748, shell length 1.7 mm. **23.** *Persicula persicula* (Linné, 1758), example of Type 3 radula. GAC radula no. 183, Nioidior, Senegal. Ex. AMNH 173759, shell length 19.8 mm. **24.** *Granulina hadria* (Dall, 1889), example of Type 4 radula. GAC radula no. 038, Tampa Bay, Pinellas Co., Florida, sand and mud. Ex. GAC Acc. # 27–82, shell length 2.2 mm. **Figures 25–30.** Marginellid radular types. **25.** *Austroginella muscaria* (Lamareck, 1822), example of Type 5 radula. GAC radula no. 181, Lakes Entrance, Victoria, Australia. Ex. DMNH 12435, shell length 13.3 mm. **26.** *Serrata translata* (Redfield, 1870), example of Modified Type 6 radula. GAC radula no. 304, Raiatea, French Polynesia. Ex. GAC Acc. # 2–91, shell length 4.3 mm. **27.** *Prunum apicinum* (Menke, 1828), example of Type 6 radula. GAC radula no. 147, Sunshine Key, Florida Keys, Monroe Co., Florida. Ex. Peggy Williams colln., shell length 9.5 mm. **28.** *Marginellona gigas* (Martens, 1904), example of Type 7 radula. After Thiele (1904 pl. 9, fig. 64). Ex. Holotype, shell length 80–100 mm. **29.** *Serrataginella spryi* (Clover, 1974), example of Type 8 radula. GAC radula no. 305, off Nacala Bay, N. Mozambique, dredged in 20–30 m, sand. Ex. GAC Acc. # 6–93, shell length 8.0 mm. **30.** *Hydroginella tridentata* (Tate, 1878), example of Type 9 radula. GAC radula no. 306, Margaret River, Western Australia, in sand, 4.6 m. Ex. GAC Acc. # 13–90, shell length 7.8 mm.

section of the ribbon, not the ventrally folded anterior end. This orientation is such that the cutting edge of each rachidian plate is posterior, and the basal edge, where the plate is attached to the membrane, is anterior.

Type 1 through Type 4 radulae are all cystiscid radulae, possessing the characteristics previously defined.

Type 1 (“Triserial Type”) radulae (figure 21) are triserial, with simple, thin, weak, lateral teeth that narrow to a single, posteriorly-pointed cusp. The long, narrow radula is composed of 66 to 103 rows of overlapping rachidian

plates. These plates are very narrow, weakly arched, with 3 to 7 sharp cusps along cutting edge. The basal edge of each rachidian plate is slightly concave, resulting in a weakly U-shaped plate. Odontophoral cartilage hoods were noted by us as well as by Dean Hewish (pers. comm.), but the nature of the odontophoral cartilages is unknown. The genus previously referred to as “*Cystiscus*” (Covert, 1989b), described herein as new, is the only one to possess a Type 1 radula (radulae of 3 species studied).

Type 2 radulae (figure 22) are uniserial, consisting of a

long, narrow series of over 80 to 220 rachidian plates. These plates are overlapping (rarely separate), very narrow, weakly to strongly arched, with 4 to 15 very strong cusps along cutting edge. The basal edge of each plate is slightly concave, nearly straight, or convex medially, resulting in a crescent-shaped, subrectangular, or asymmetrically V-shaped plate. Odontophoral cartilage hoods were noted in many species of *Cystiscus*, but were unknown and unobserved at the time *Crithe* radulae were extracted. The nature of the odontophoral cartilages is unknown. *Cystiscus* (radulae of 14 species studied) and *Crithe* (radulae of 1 species studied) both have a Type 2 ("*Crithe* / *Cystiscus* Type") radula. The radula of *Extra* is unknown, but presumed to be similar.

Type 3 radulae (figure 23) are uniserial, consisting of a long, narrow series of over 80 to 209 rachidian plates. These moderately to strongly overlapping plates are narrow, moderately to strongly arched, with 5 to 14 sharp cusps along cutting edge. The central cusp is often the strongest. The basal edge of each plate is strongly concave, resulting in a U- or V-shaped plate. The reports of wishbone-shaped rachidian plates (Barnard, 1962:14-15; Ponder, 1970:70; Ponder, 1973:fig. 2) are inaccurate and due to an artifact of observation (see discussion in Coovert, 1989b:12-13). Odontophoral cartilage hoods were noted in all three included genera, with a pair of separate odontophoral cartilages noted in *Persicula* and *Gibberula*. *Persicula* (radulae of 14 species studied), *Gibberula* (radulae of 21 species studied), and *Canalispira* (radulae of 2 species studied) all have a Type 3 ("*Persicula* Type") radula.

Type 4 radulae (figure 24) are uniserial, consisting of a long, narrow series of at least 90 to 159 rachidian plates. These usually completely non-overlapping plates are narrow, moderately arched, with 9 to 12 clustered, raised denticles located in staggered positions on the dorsal surface, with a single (or asymmetrically paired) strong central cusp protruding on the cutting edge. The basal edge of each plate is weakly concave, resulting in a weakly V-shaped plate. The rachidian plates are asymmetrical and alternate as mirror images (figure 24). Although odontophoral cartilage hoods have not been observed in representatives of this group, their radulae are otherwise typically cystiscid. A broad, membranous flange on either side and extending the whole length of the radula, effectively doubling the width, has been observed (Dean Hewish, pers. comm.) when using the enzyme Pronase for maceration. This is a less destructive method than the use of KOH. This flange is certainly homologous to odontophoral cartilage hoods, but the nature of the odontophoral cartilages is unknown. No further anatomical information is available. *Granulina* (radulae of 12 species studied) and *Pugnus* (radulae of 2 species studied) both have a Type 4 ("*Granulina* Type") radula.

Type 5 through Type 9 radulae are all marginellid radulae, possessing the characteristics as previously defined.

Type 5 radulae (figure 25) are uniserial, consisting of a

relatively short, broad ribbon of 19 to 75 rachidian plates. These usually overlapping plates are moderately wide, weakly arched, with 8 to 22 strong cusps along cutting edge. The central cusp is often the strongest. There are often pits on adjacent plates to receive the tips of some of the cusps, especially the central. The basal edge of each rachidian plate is generally slightly concave, resulting in a rectangular to chevron-shaped plate. The odontophoral cartilages in *Mesoginella* and *Austroginella* were described as fused anteriorly (Ponder, 1970:62; Ponder & Taylor, 1992:320), but no detailed data exists as to marginal cuticular flanges. *Protoginella* (radula of 1 species studied), *Alaginella* (radulae of 9 species studied), *Austroginella* (radulae of 5 species studied), *Mesoginella* (radulae of 16 species studied), *Ovaginella* (radulae of 2 species studied), and *Balanetta* (radula of 1 species studied) all have a Type 5 ("*Austroginella* / *Mesoginella* Type") radula. The radula of *Closia* is unknown, but presumed to be similar.

Type 6 radulae (figure 27) are uniserial, consisting of a relatively short, broad ribbon of 24 to 75 overlapping rachidian plates. These plates are broad, nearly flat, with 9 to 45 (exceptionally 5) sharp cusps along cutting edge. There are often pits on adjacent plates to receive the tips of some or all of the cusps. The basal edge of each plate is generally straight, resulting in an elongate, rectangular "comb-like" plate. The odontophoral cartilages are fused anteriorly. They are fused posteriorly in most species (but not in *Prunum* aff. *alates* and *P. guttatum*), leaving a narrow, medial, longitudinal posterior slit in most *Prunum* and *Volvarina* (figures 38-42). (See following section on internal anatomy.) A single cartilage was described for *Volvarina taeniolata* (cf. Fretter, 1976:329). The marginal cuticular flanges of *Prunum* aff. *alates*, described above, are very similar in other species of *Prunum* we examined. *Prunum* (radulae of 23 species studied), *Volvarina* (radulae of 42 species studied), *Rivomarginella* (radulae of 2 species studied), *Bullata* (radula of 1 species studied), and *Cryptospira* (radulae of 4 species studied) all have a Type 6 ("*Prunum* / *Volvarina* Type") radula. Most of these are discussed and figured in Coovert and Coovert (1990).

Modified Type 6 radulae (figure 26) are similar to typical Type 6, but differ in having a shorter ribbon composed of only 13 to 35 plates, averaging more cusps (22 to 59) that project from a somewhat sinuous posterior edge, and in often having thinner and more fragile rachidian plates. Pits on adjacent plates to receive cusp tips were not observed as in many typical Type 6 radulae. The odontophoral cartilages of *Serrata* (as *Haloginella*) were described by Ponder (1970:66) as fused except for a very short posterior portion. Marginal cuticular flanges are unknown. *Serrata* (radulae of 8 species studied) is the only genus to have a Modified Type 6 ("*Serrata* Type") radula.

Type 7 radulae (figure 28) are uniserial, consisting of a relatively short, very broad ribbon of 56 to 80 overlapping rachidian plates. These plates are very broad, nearly

flat, with numerous (58 to 85) sharp cusps along cutting edge. The basal edge of each plate is generally straight, resulting in an elongate, rectangular "comb-like" plate. Odontophoral cartilages and marginal cuticular flanges are unknown. The monotypic genera *Marginellona* and *Afrivoluta* both have a Type 7 ("Afrivoluta Type") radula.

Type 8 radulae (figure 29), here described, are uniserial, consisting of a relatively short, broad ribbon of 38 overlapping rachidian plates. These plates are broad, nearly flat, with 9 to 10 sharp cusps on the cutting edge. The entire posterior edge, including all edges of the main cusps, with numerous (total of ca. 70) small, secondary cusps, giving the main cusps a serrated appearance. Pits for reception of adjacent cusp tips were not observed. The basal edge of each plate is slightly indented medially, resulting in a very shallowly V-shaped plate. Odontophoral cartilages and marginal cuticular flanges are unknown. The Type 8 ("Serrataginella Type") radula is unlike any others known, and is represented by "*Marginella*" *spryi* Clover, 1974, type species of a monotypic genus herein described as new.

Type 9 radulae (figure 30), first described by Bouchet (1989:79, fig. 3), are uniserial, consisting of a very short, narrow, greatly reduced ribbon of 10 to 30 rachidian plates. These weak plates overlap and are nearly flat, with 4 to 7 cusps on the cutting edge. Pits for reception of adjacent cusp tips are absent. The basal edge of each plate is straight, resulting in a subquadrate plate. Odontophoral cartilages and marginal cuticular flanges are unknown. *Hydroginella* (radulae of 4 species studied) is the only genus to have a Type 9 ("Hydroginella Type") radula. One species is known to be parasitically associated with fishes (Bouchet, 1989). Judging from the very similar radulae of other species, it seems likely that all may have such an association.

A third major group, comprised of non-radulate species, completely lacks a buccal mass, odontophore, and radula. This was confirmed by dissections of species in the following genera: *Dentimargo* (Ponder, 1970:67, plus species reported herein), *Marginella* s. str. (Graham, 1966:139, Coan & Roth, 1976:220, plus species reported herein), *Clabella* (Coan & Roth, 1976:220), and *Hyalina* (Coan & Roth, 1976:220, and herein). Other species have been subsequently reported to lack a radula, some based on unsuccessful radular extraction with KOH (see Coover, 1989b for review). Thus, a total of 31 species have been inferred or demonstrated to lack a radula. We have attempted routine radular extraction on separate occasions from two specimens of the type species of *Eratoidea*, *E. margarita* (Kiener, 1834), and have not found a radula. Although not definitive, it is suggested that this genus is also non-radulate. This assemblage of non-radulate genera is an artificial group, with *Hyalina* belonging to a different lineage (see discussion in systematic section).

Internal Anatomy: Prior to our studies, only 13 species of marginelliform gastropods had been studied anatomically.

Harasewych and Kantor (1991:tables 2, 3) summarized anatomical data of the 11 species known at that time. Ponder and Taylor (1992) subsequently presented data for two species of *Austroginella*. Few taxonomic conclusions could be drawn from such a relatively small sample because the anatomy varied so greatly. Our dissections added anatomical data for 11 additional species, and further data for one previously reported species (Tables 1–4). Combined with conchological and radular data, this greatly expanded body of anatomical information enabled taxonomic groupings to become evident, making a reliable and stable classification possible. Details of the foregut were emphasized because of their greater taxonomic value. Our primary objective is a presentation of the higher classification, therefore, more detailed reports on the anatomy of individual species will be published elsewhere. A discussion of foregut anatomy follows, along with a summary of known anatomical information for these 24 species.

The proboscis of marginelliform gastropods is relatively short and pleurembolic. The retractor muscles are inserted on the sides of the proboscis, resulting in the basal portion being invaginated, forming a proboscis sac (Fretter & Graham, 1962:150). The proboscis varies somewhat in shape among genera. The small mouth is always situated terminally at the anterior end. Most genera have a proboscis that is rounded or blunt distally, and, when retracted, is generally about two-and-one-half to four times as long as broad. When feeding, the proboscis may be extended to a length approximating the length of the shell in at least some species (Fretter, 1976:329). Both species of *Dentimargo* studied have a distally pointed proboscis about four times as long as broad when retracted (figure 33). *Serrata* aff. *mustelina* has a more bulbous, distally rounded proboscis about one-and-a-half times as long as broad. *Gibberula* and *Persieula* (figures 35, 79) both have a short, broad proboscis about two times as long as broad.

The mouth opens directly into the buccal cavity. No jaws have been observed in any marginelliform species. In radulate species, the buccal cavity leads posterodorsally to the anterior esophagus and posteroventrally to the buccal mass. In non-radulate species, the buccal cavity leads with little or no differentiation to the anterior esophagus.

The most significant hallmark of the family Marginellidae, in the strict sense, is the possession of a "buccal pouch" or "buccal caecum" in radulate species. Both Fretter (1976:333) and Harasewych and Kantor (1991:16) recognized the significance of this structure and its presence only in marginellids and toxoglossans. The buccal pouch (figure 31), the term we prefer for this structure, was first discovered and named by Graham (1966:137), who noted that "in marginellids the most interesting feature of the gut is the situation of the buccal mass, wholly withdrawn into a caecum from its typical place on the floor of the buccal cavity (op. cit., p. 147)." The buccal mass, described as "rather reduced" by Graham (1966:137) and consisting of the odontophoral cartilages,

Table 4. Sources of anatomical data utilized in Table 3

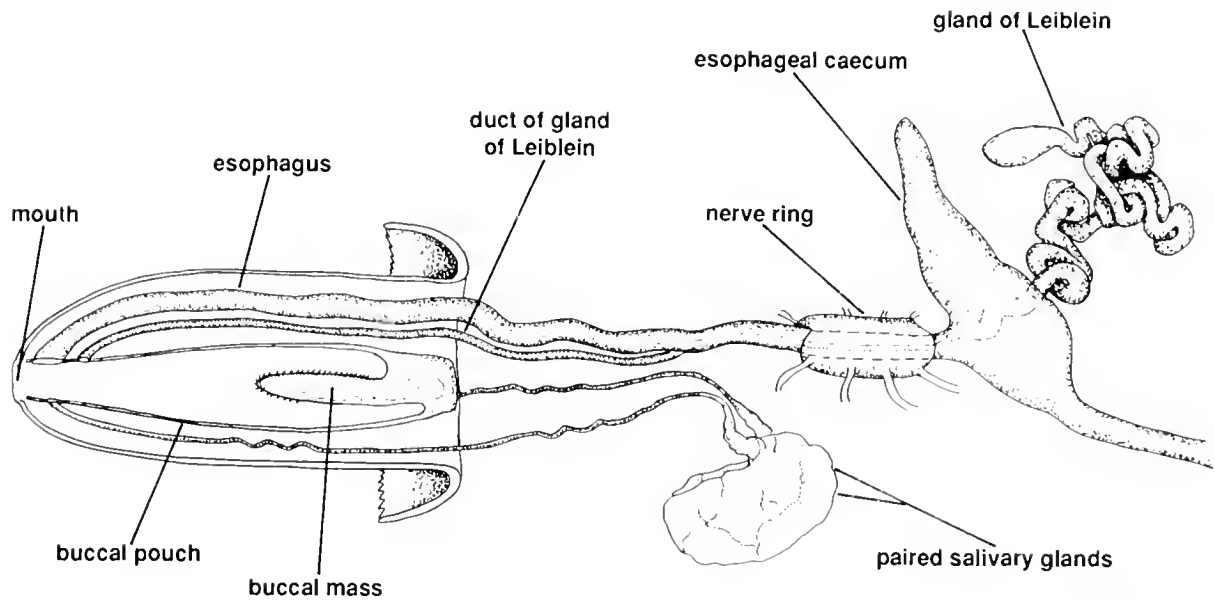
Species (current nomenclature)	Source
Cystiscidae	
<i>Persicula interruptolineata</i> (Megerle von Mühlfeld, 1816)	herein; see Table 1 for data
<i>Persicula masirana</i> Roth & Petit, 1972	herein; see Table 1 for data
<i>Gibberula</i> sp.	Ponder (1970), as <i>Diluculum</i> sp
Marginellidae	
<i>Marginellona gigas</i> (Martens, 1904)	Harasewych and Kantor (1991)
<i>Serrata</i> aff. <i>mustelina</i> (Angas, 1871)	Ponder (1970), as <i>Volvarina</i> (<i>Haloginella</i>) <i>mustelina</i> ; the New Zealand species differs from the Australian species; see Coovert (1989b:16) for comments
<i>Austroginella johnstoni</i> (Petterd, 1884)	Ponder and Taylor (1992)
<i>Austroginella muscaria</i> (Lamarck, 1822)	Ponder and Taylor (1992)
<i>Mesoginella pygmaea</i> (G. B. Sowerby II, 1846)	Ponder (1970), as <i>Mesoginella</i> (<i>Simuginella</i>) <i>pygmaea</i>
<i>Volvarina</i> aff. <i>avena</i> (Kiener, 1834)	herein; see Table 1 for data
<i>Volvarina taeniolata</i> Mörch, 1860	Fretter (1976)
<i>Prunum</i> aff. <i>alates</i> Roth, 1978	herein; see Table 1 for data
<i>Prunum guttatum</i> (Dillwyn, 1817)	herein; see Table 1 for data
<i>Prunum marginatum</i> (Born, 1778)	Graham (1966), as <i>Marginella marginata</i>
<i>Prunum martini</i> (Petit, 1853)	Marcus and Marcus (1968), as <i>Marginella fraterculus</i>
<i>Prunum prunum</i> (Gmelin, 1791)	herein; see Table 1 for data
<i>Prunum roosevelti</i> (Bartsch & Rehder, 1939)	herein; see Table 1 for data
<i>Bullata bullata</i> (Born, 1778)	herein; see Table 1 for data
<i>Hyalina hyalina</i> (Thiele, 1913)	Eales (1923), as <i>Marignella hyalina</i>
<i>Hyalina pallida</i> (Linné, 1758)	Coan and Roth (1976) plus herein; see Table 1 for data
<i>Dentimargo cairoma</i> (Brookes, 1924)	Ponder (1970), as <i>Volvarinella cairoma</i>
<i>Dentimargo eburneola</i> (Conrad, 1831)	herein; see Table 1 for data
<i>Marginella desjardini</i> Marche-Marchad, 1957	Graham (1966)
<i>Marginella glabella</i> (Linné, 1758)	herein; see Table 1 for data
<i>Marginella sebastiani</i> Marche-Marchad & Rosso, 1979	herein; see Table 1 for data

radula, and associated connective tissue and muscles, is contained in the buccal pouch. What characterizes the buccal pouch is the sphincter at its anterior opening into the buccal cavity and the fact that it is a separate caecum or sac that is blind posteriorly, where the radula is initially secreted. This is further discussed by Graham (1966:138), who noted that radular formation occurs "at the innermost end of the pouch, which therefore corresponds to the radular sac of more normal gastropods." Ponder (1970:76) also noted that the buccal pouch is derived from the radular sac. Fretter (1976:329) observed that the "teeth arise at the innermost end of the pouch where there is no clear demarcation of the radular sac typical of prosobranchs." The blind end of a buccal pouch thus corresponds to the posterior end of the radular sac. Our observations of *Prunum*, *Volvarina*, and *Bullata* species confirmed the presence of a buccal pouch. The genera *Serrata*, *Mesoginella*, and *Austroginella*, dissected by Ponder (1970) and Ponder and Taylor (1992), likewise possess a true marginellid buccal pouch. In the true marginellids, the odontophore extends beyond the posterior end of the radula.

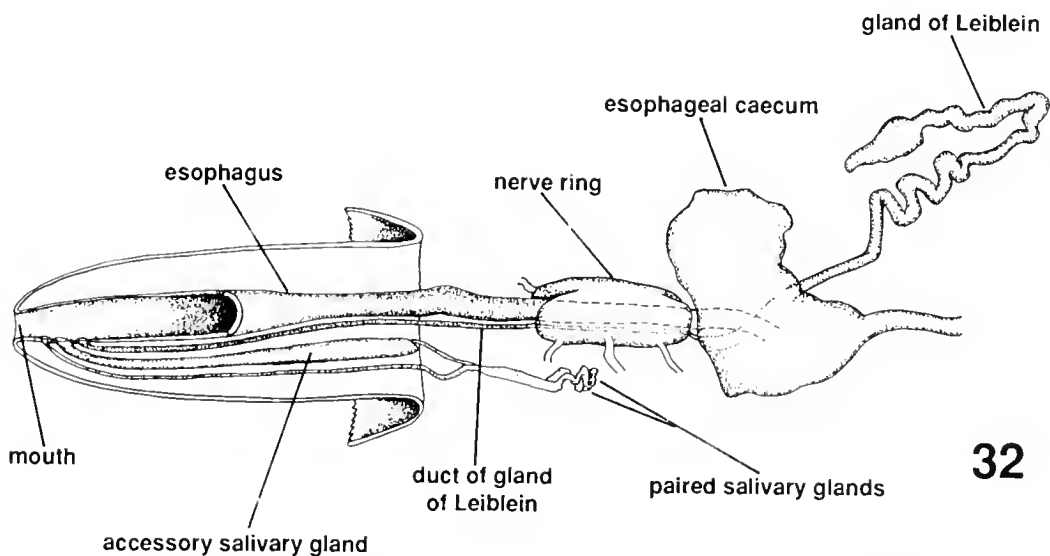
The absence of a buccal pouch in non-radulate species has been confirmed by dissections of species of *Hyalina*, *Dentimargo*, and *Marginella* (figures 32–34). Graham (1966:139) described what he believed to be a vestigial buccal pouch in *Marginella desjardini*. Ponder (1970:

76) considered this to be the accessory salivary gland. Our dissections of *Marginella glabella* (figure 34) and *M. sebastiani*, both close relatives of *M. desjardini*, confirmed this contention, because an accessory salivary gland was found in both species, but neither had a vestigial buccal pouch. Ponder's (1970: fig. 3B) dissection of *Dentimargo cairoma*, and our dissection of *D. eburneola* (figure 33), show the complete absence of a buccal pouch. There is insufficient information about *Hyalina hyalina* in Eales (1923) to draw any conclusions. Coan and Roth (1976:220) likewise did not provide sufficient detail for *H. pallida*, although they did mention the absence of a radula and odontophore. Our dissection of *H. pallida* (figure 32), confirms the absence of a buccal pouch.

A typical neogastropod radular sac enclosing the posterior end of the radula was found in both species of *Persicula* we dissected (figure 35). In *Persicula interruptolineata* and in the *Gibberula* studied by Ponder (1970:fig. E, r.s.), the radular sac is readily distinguished because it protrudes from the posterior end of the proboscis in a characteristic downward curve (figures 35, 79). It is further characterized by a slightly bulbous posterior end which encases the nascent end of the radular ribbon (q.v. previous section). The radular sac extends well behind the odontophore and is an extension of the radular sheath, formed from the subradular membrane. The buccal mass in *Persicula masirana* is morphologi-



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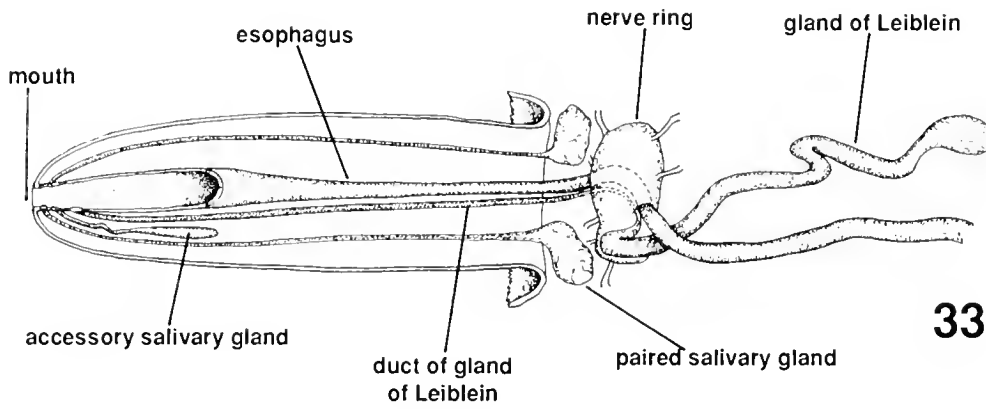
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Figures 31-32. Anatomical features of the foregut of Prumini. Data in Table 1. 31. *Prunum aff. aletes* Roth, 1978. 12.4 X. 32. *Hyalina pallida* (Linné, 1758). 15.3 X.

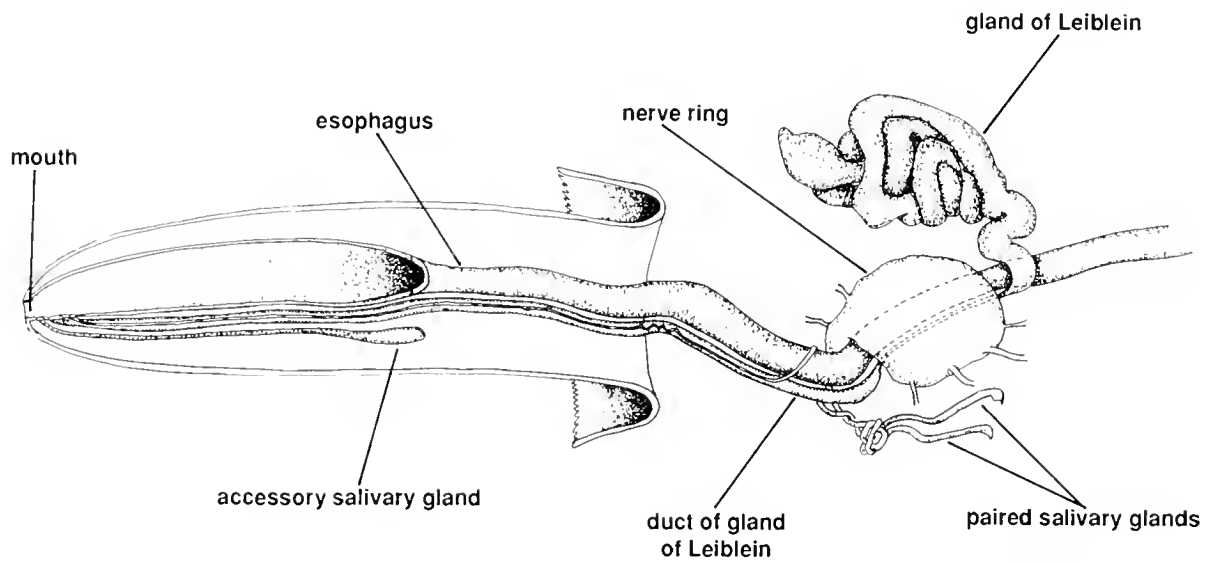
cally the same but the proboscis is simply longer, completely containing the radular sac. The characteristic shape and protrusion of the radular sac seems to be fairly typical for most Neogastropods (including Olividae), with the prominent exception being the Marginellidae, s. str. The radular sac thus differs in several respects from the buccal pouch of marginellids, especially in the lack of an anterior sphincter. All cystiscid genera studied have the same general type of radula, previously termed a cystiscid radula (q.v.). Based on the similar nascent ends of their radulae, all cystiscid genera are assumed to pos-

sess a true radular sac similar to that found in *Persicula* and *Gibberula*. A radular sac has actually been observed in several incompletely cleared cystiscid radulae, including the triserial group "*Cystiscus*," named as a new genus herein.

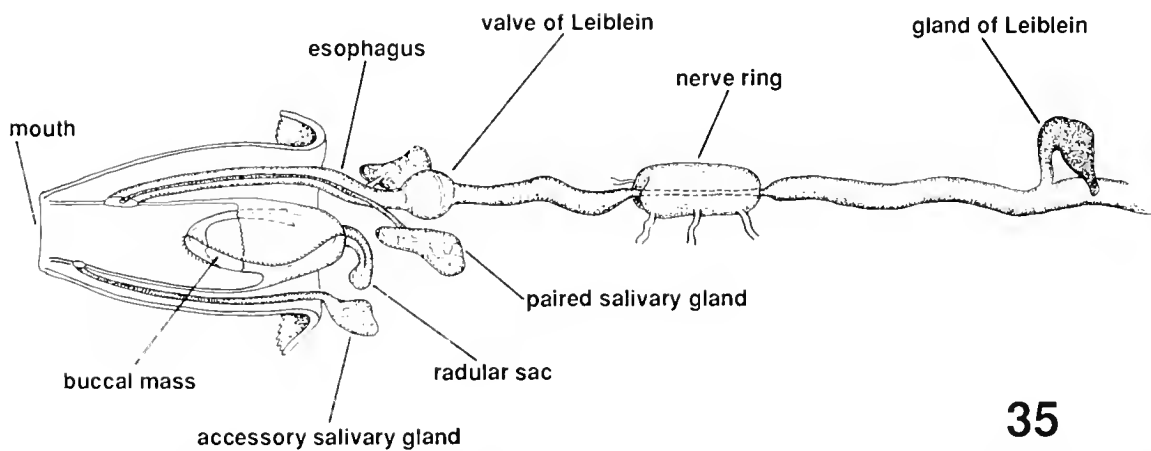
Odontophoral cartilages, which we prefer over "bolsters," "odontophore," or "cartilages," is a more specific term and clearly differentiates these structures from the odontophore, which is often used as a general term for the entire radular mass. These cartilages support and stiffen the radular mass and are composed of large Ley-



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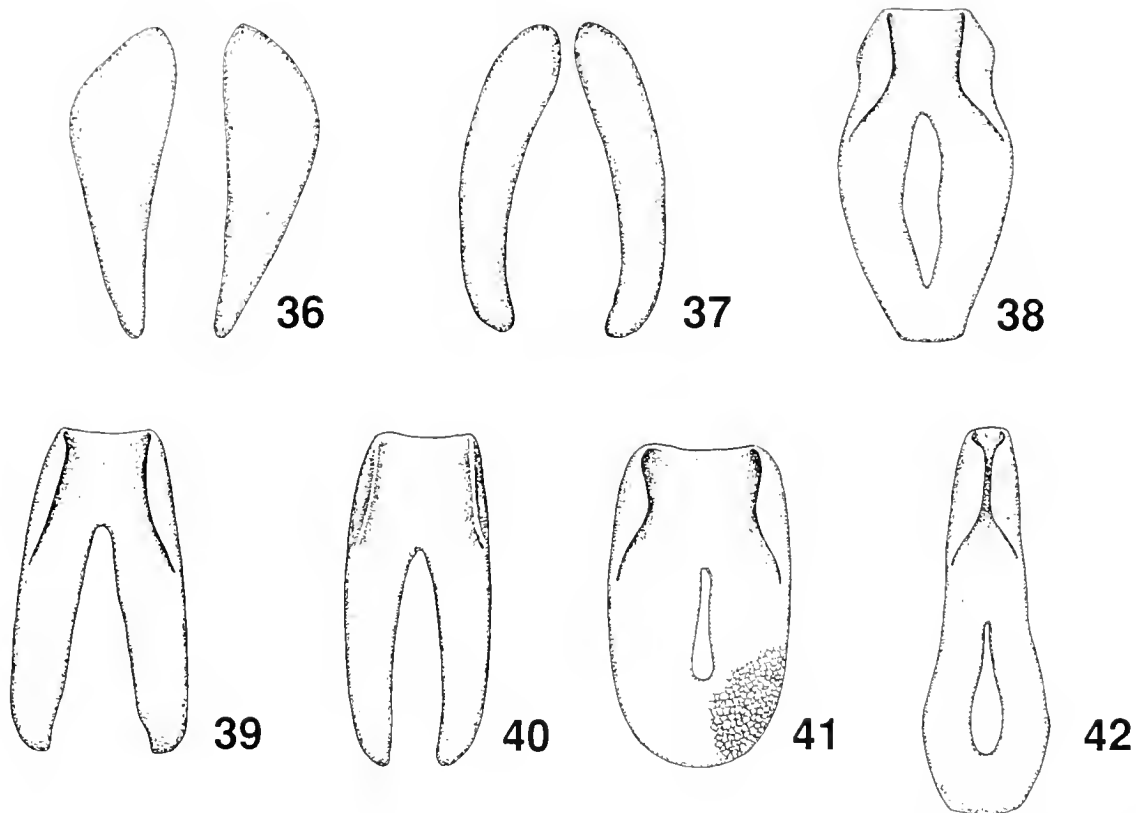


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Figures 33–35. Anatomical features of the foregut of Marginellini and Persiculinae. Data in Table 1. 33. *Dentimargo eburneola* (Conrad, 1834). 22.4 X. 34. *Marginella glabella* (Linné, 1758). 5.2 X. 35. *Persicula interruptolineata* (Megerle von Mühlfeld, 1816). 16.8 X.



Figures 36–42. Odontophoral cartilages of cystiscids and marginellids. Data in Table 1. **36.** *Persicula interruptolineata*. GAC 1581A. Length 0.97 mm. **37.** *Persicula masirana*. GAC Acc. # 4–94B. Length 1.01 mm. **38.** *Volvarina aff. arena*. GAC 1172B. Length 0.88 mm. **39.** *Prunum aff. aletes*. GAC 1518B. Length 1.50 mm. **40.** *Prunum guttatum*. GAC 1172A. Length 0.75 mm. **41.** *Prunum prunum*. GAC 1582. Length 2.12 mm. **42.** *Prunum roosevelti*. GAC Acc. # 26–88A. Length 1.67 mm.

dig cells (chondroid tissue) by which they are easily recognized. Two fundamentally different conditions also exist in this character complex.

In all true marginellids examined, the two odontophoral cartilages are fused at least anteriorly, effectively functioning as a single structure underlying the radula. Ponder (1970:62) described the odontophoral cartilages in *Mesoginella pygmaea* as “fused into a single structure in the front half of the odontophore but posteriorly are connected by a transverse muscle in the usual way.” Ponder (1970:66) described similarly fused cartilages in *Serrata aff. mustelina*, which are separated for only a short distance posteriorly. The two species of *Austroginella* discussed by Ponder and Taylor (1992:320) are likewise described as having anteriorly fused cartilages. The odontophoral cartilages in *Marginellona* were not described by Harasewych and Kantor (1991). Fretter (1976:329) simply described a single cartilage for *Volvarina taeniolata*. Our dissection of *V. aff. arena* revealed a pair of cartilages fused both anteriorly and posteriorly (figure 38). They are slightly bowed medially, leaving a medial slit about half the length of the entire structure, with the anterior margins raised and thickened, and truncated anteriorly. We suspect that *V. taeniolata* may be similarly structured. The closely related genus *Prunum* shows a similar condition. These struc-

tures were insufficiently described in Graham (1966) and Marcus and Marcus (1968) to draw any conclusions. Our dissections of four species of *Prunum* revealed that they all have strongly raised, thickened anterolateral margins, effectively forming a trough or channel for the radular ribbon (figure 20). The odontophoral cartilages in *P. roosevelti* (figure 42) are relatively narrow, rounded anteriorly, completely fused on the very long and narrow anterior half, and slightly bowed and narrowly fused posteriorly, confining a medial slit to the posterior half. The odontophoral cartilages in *Prunum prunum* (figure 41) are relatively short and broad, fused anteriorly and posteriorly, with a narrow medial slit. The anterior end is shallowly emarginate. *Prunum guttatum* (figure 40) and *P. aff. aletes* (figure 39) differ because their odontophoral cartilages are V-shaped, and narrowly fused anteriorly, but not posteriorly. The fused cartilages in *P. guttatum* (figure 40) have the posterior tips slightly convergent but not touching, with the anterior end truncate. In *P. aff. aletes* (figure 39), the anterior end is truncate to shallowly emarginate, and the posterior tips are divergent, forming a distinct V-shape, but in situ (figure 19) connective and muscle tissue hold these posterior tips closer together. In all cases, this fused pair of odontophoral cartilages underlies the main part of the radula (figures 19, 20). The radula wraps around the anterior

end of the odontophore, this point being effectively termed the bending plane. The shorter anterior portion of the radular ribbon, often showing broken cusps, thus lies under the anterior end of the odontophore, giving it the characteristic J-shape. Our data indicates that the odontophoral cartilage shape is consistent within each species, but differs between them, and may prove to be a useful taxonomic character.

All cystiscid genera examined have two completely separate odontophoral cartilages. Each cartilage fits into one of the lateral odontophoral cartilage hoods of the subradular membrane, flanking and not underlying the radula (figures 15, 16). Ponder (1970:70) described the odontophoral cartilages and muscle attachments for a species of *Gibberula*. Our dissections of *Persicula interruptolineata* (figure 36) revealed two separate subtriangular cartilages that are broad and rounded anteriorly, and narrowed posteriorly. In *P. masirana* (figure 37), the separate cartilages are elongate, rather uniform in width throughout, and pointed anteriorly. The radulae of nearly all other cystiscid genera have been described earlier in this paper, and most have odontophoral cartilage hoods. On this basis, we infer that they possess two separate odontophoral cartilages.

The anterior esophagus in radulate genera is situated dorsally within the proboscis, the buccal mass lying below it. In non-radulate species, the anterior esophagus is more centrally placed. Upon exiting the retracted proboscis posteriorly, the esophagus generally makes a sharp S-bend prior to passing through the nerve ring. A valve of Leiblein, when present, is located anterior to the circum-esophageal nerve ring. Ponder and Taylor (1992:321) described the valve of Leiblein in *Austroginella* as being partially encased in the nerve ring anteriorly (figure 80). *Serrata* and *Mesoginella* have a well-developed valve located just anterior to the nerve ring. These three genera have a narrow, non-glandular bypass tube that is adherent ventrally to the valve of Leiblein. *Marginellona* has a large valve of Leiblein situated anterior to the nerve ring (figure 80). The two *Persicula* species we dissected also have a distinct valve of Leiblein, placed well anterior to the nerve ring (figure 35). No bypass tube was found. *Gibberula* has a similarly placed valve of Leiblein, but has a separate glandular tube that bypasses the valve (figure 79). *Volvarina*, *Hyalina*, *Prunum*, *Bullata*, *Dentimargo*, and *Marginella* all lack a valve of Leiblein. Marcus and Marcus (1968:65) discussed an "individually inconstant valve of Leiblein" in *Prunum martini*. In some *Prunum* species we dissected, what at first appeared to be a possible valve of Leiblein simply turned out to be food lumps in the esophagus that were inconsistent in their location or occurrence. We believe that the so-called "individually inconstant valve of Leiblein" in *Prunum martini* were simply food lumps in the esophagus of some individuals.

The esophagus narrows upon entering the nerve ring anteriorly, resuming its original size after exiting posteriorly. A much enlarged sac-like esophageal caecum was found just posterior to the nerve ring in all species

of *Volvarina*, *Prunum* (figure 31), and *Bullata* studied. This structure was first described in *Prunum marginatum* as an "oesophageal caecum" (Graham, 1966:135, fig. 1). Eales (1923) did not mention this structure in *Hyalina hyalina*, nor was it mentioned by Coan and Roth (1976) for *H. pallida*. Our dissection of *H. pallida* (figure 32) revealed a thin-walled, but very distinct, esophageal caecum. An esophageal caecum is absent in all other marginelliform genera that have been studied anatomically.

The most conspicuous foregut gland is the gland of Leiblein, also called the "unpaired gland," "unpaired foregut gland," or "poison gland." This gland occurs in three different forms. In *Persicula* (figure 35) and *Gibberula* (figure 79), this gland is a small, short, often slightly folded gland emptying directly into the posterior end of the mid-esophagus, well posterior to the nerve ring. In *Marginellona* (figure 80), the gland of Leiblein is extremely large, sacculate, broad anteriorly and tapering posteriorly (Harasewych and Kantor, 1991:11). It also empties directly into the mid-esophagus posterior to the nerve ring. All the remaining marginelliform genera studied anatomically have a gland of Leiblein with a long, convoluted duct. The gland in these genera ends distally in a terminal bulb that is either rounded or weakly to distinctly pointed distally. The terminal bulb is narrow, elongate, and rounded distally in *Dentimargo* (figure 33). In *Marginella*, it is shorter, more swollen, and ends in an acuminate, pointed tip (figure 34). In *Serrata*, *Mesoginella*, and *Austroginella* (figure 80), the relatively large duct from the gland of Leiblein, which is about the same diameter as the esophagus, empties into the posterior end of the mid-esophagus just posterior to the nerve ring but does not pass through the nerve ring. These three genera also possess a well-developed valve of Leiblein with a ventral by-pass tube. In *Prunum* (figure 31), *Bullata*, *Volvarina*, *Hyalina* (figure 32), *Dentimargo* (figure 33), and *Marginella* (figure 34), the long, convoluted duct from the gland of Leiblein narrows as it passes through the nerve ring, then continues as a very narrow tube to the anterior end of the proboscis. These six genera all lack a valve of Leiblein. The duct from the gland of Leiblein empties either into the buccal cavity or into the extreme anterior end of the anterior esophagus, which is usually in very close proximity to the point where the ducts of the paired salivary glands empty into the buccal cavity. Ponder (1970:77, 79) described this duct in *Marginella desjardini* as opening "ventrally into the oesophagus a little in front of the nerve ring." This is in error because Graham (1966:139) clearly described this duct as opening "to the gut at almost the same level as that at which the salivary ducts reach the same position," which is at the "extreme anterior end of the proboscis, where they discharge, ... into the buccal cavity." This is mentioned because apparently a figure in Ponder (1973:fig. 3N) is based on this misconception. This does not weaken Ponder's hypothesis for the formation of the poison gland (Ponder, 1970:77-80), but it indicates that this intermediate stage is presently unknown.

All marginelliform genera have either tubular or ascinous paired salivary glands associated with the esophagus. In many cases, tubular and ascinous salivary glands appear to be found in different species of the same genus, and thus may be of limited taxonomic value in these genera. In all cases, the paired glands send fine, narrow ducts to the anterior end of the proboscis, where they empty into the buccal cavity. The placement of the glands and the attachment of ducts differ between species. In *Marginellona*, the paired salivary glands are found dorsal to the gland of Leiblein (figure 80), their ducts running anteriorly along the floor of the proboscis, free of the esophagus. *Serrata*, *Mesoginella*, and *Austroginella* all have glands that are attached to the esophagus just anterior to the valve of Leiblein, the ducts embedded in the esophageal walls for their entire length. *Volvarina taeniolata* has the glands free in the body cavity and the ducts free of the esophagus. In *V. aff. avena*, the paired salivary glands are relatively large and fully contained within the retracted proboscis, the ducts attached anteriorly to the esophagus. In *Prunum*, the paired salivary glands are free of the esophagus. In *P. prunum* and *P. guttatum*, the ducts are attached to the walls of the esophagus. In the other *Prunum* species studied, the ducts lay ventrally along the floor of the proboscis, free of the esophagus. Details on the salivary glands of *Bullata bullata* are unknown. The ducts in *H. pallida* are free of the esophagus, the glands apparently tubular but poorly preserved in the specimen studied. Both *Dentimargo* species have the glands largely contained within the proboscis. They are presumed to be tubular in *D. cairoma*, but are ascinous in *D. eburneola*. Oddly, these glands are not placed laterally in *D. eburneola* as is usual, but instead are placed dorsally and ventrally, one gland situated above the esophagus, the other below the accessory salivary gland (figure 33). In both species, the glands and their ducts lay free. The paired salivary glands of the three species of *Marginella* are located outside the proboscis near the nerve ring, free from the esophagus. In *M. glabella*, the ducts are attached to the duct of the gland of Leiblein (figure 34), unlike those of *M. sebastiani*. The paired salivary glands in *Persicula* and *Gibberula* are attached to the esophagus just anterior to the valve of Leiblein (figure 35). The ducts of *Persicula* are attached to the outside walls of the esophagus, but in *Gibberula* this is unknown. Ponder's illustration (1970: fig. 3E) seems to indicate that these ducts are embedded. Information on these glands and their ducts is summarized in Table 3.

The accessory salivary gland, when present, is always single and empties into the buccal cavity. It is present in all cystiscids studied, being ascinous in both species of *Persicula*, but tubular in *Gibberula*. Within marginellids, a tubular accessory salivary gland is present in *Serrata*, but absent in *Austroginella* and *Mesoginella*. A large, ascinous gland is present in *Volvarina aff. avena*, but appears to be tubular in *V. taeniolata* as described by Fretter (1976:329). Both species of *Hyalina* possess an accessory salivary gland, which is tubular in *H. hy-*

alina and apparently so in *H. pallida* (unreported in Coan & Roth, 1976 and poorly preserved in our specimen). An accessory salivary gland is present in only one species of *Prunum*, being tubular in *P. prunum*. The gland is present and tubular in *Dentimargo* and *Marginella*, but absent in *Marginellona*. Further work, including histology, is needed. See Table 3 for a summary of the occurrence of this gland.

Our primary objective was to discern useful taxonomic characters, and we feel that the most useful features are those of the foregut. Thus, the remainder of the digestive system was not studied in any greater detail by us, nor was the reproductive system. A brief summary of published information on these other systems follows.

The presence or absence of an anal gland should be further investigated. This structure was reported as present and extremely large in *Marginellona gigas* by Harasewych and Kantor (1991:11). *Serrata aff. mustelina*, *Mesoginella pygmaea*, *Dentimargo cairoma* (cf. Ponder, 1970), *Austroginella johnstoni*, *A. muscaria* (cf. Ponder & Taylor, 1992:322), and *Volvarina taeniolata* (cf. Fretter, 1976:329) were all reported as having an anal gland. The only marginelliform reported to lack an anal gland is the species of *Gibberula* reported by Ponder (1970: 71). Published accounts of the remaining species did not report the presence or absence of this structure.

Main features of the reproductive system were summarized in Harasewych and Kantor (1991:tables 2, 3). Published information on the reproductive system is incomplete for a number of species described anatomically. Probably of most interest in the female reproductive system is the presence of three glandular structures or seminal receptacles joining the pallial oviduct between the albumen gland and capsule gland in *Dentimargo cairoma* (cf. Ponder, 1970:74), whereas only one is present in *Gibberula* (op. cit., p. 75). Two such structures are the usual number, as recorded in *Mesoginella pygmaea* and *Serrata aff. mustelina* by Ponder (1970:74), *Marginellona gigas* by Harasewych and Kantor (1991:11), *Marginella desjardini* by Graham (1966:140), and *Volvarina taeniolata* by Fretter (1976:fig. 2A). Information is lacking for the other species. In the male reproductive system, the penis is normally simple, lacking appendages or lobes. But Ponder (1970:72, fig. 4C) described a bilobed penis for *Dentimargo cairoma* that has a sharply pointed posteroapical appendage, which he termed a sheath. Our dissection of *D. eburneola* likewise revealed a sharply pointed apical appendage, but the penis was not bilobed. The penis in *Bullata bullata* is an extremely large, simple, flattened, spatulate structure, about two-thirds the body length. All other species studied have a simple, unlobed penis. Refer to Harasewych and Kantor (1991:tables 2, 3) for a summary of additional characters.

Published information on marginelliform egg capsules was reviewed in Covert (1986c and 1988e:42). Most marginelliform gastropods produce plano-convex or hemispherical egg capsules, but in *Persicula cornea* (Lamarck, 1822) and *Marginella goodalli* (G. B. Sowerby I, 1825) they are stalked. In most cases, each egg capsule

contains a single embryo, but *Prunum apicinum* (Menke, 1828) and *Dentimargo cairoma* sometimes have a second embryo, while egg capsules of *Volvarina avena* contain about five embryos. Development is direct in all known cases. All marginelliform species have a paucispiral protoconch indicating direct development.

Discussion: The division of marginelliform gastropods into two fundamentally different groups became obvious during the course of our research. These two groups were initially differentiated on gross radular features, but further research revealed differences in radular structure, anatomy, and internal columellar plications. In fact, these two groups can be differentiated on the basis of their internal shell whorls alone. These distinctly different groups are the cystiscids and the true marginellids. A brief summary of the differences follows.

Cystiscids have a shell that possesses what we have termed cystiscid internal whorls (figures 2, 3), or modified cystiscid internal whorls in *Granulina* (figure 4). These internal whorls are mostly resorbed by the animal, resulting in extremely thin, modified whorls. The anterior two or three columellar plications are reduced internally to a single, axially oriented, sharp edge. Within the aperture, the columella bears parietal lirae posterior to these plications, thus the columella is multiplicate. In *Granulina*, the posterior two columellar plications continue internally for a whorl or two and does not have a multiplicate columella. Cystiscid radulae (figures 13–16) are long, narrow, and C-shaped, with over 80 and up to 200 or more rachidian plates (with lateral teeth in one genus). The narrow rachidian plates have few cusps and are weakly to distinctly arched. The two odontophoral cartilages each fit into an anterolateral odontophoral cartilage hood (modified in *Granulina*), which flank the radula (figures 15, 16). The posterior end of the radula begins as a series of nascent rachidian plates. It is encased and secreted in a typical neogastropod radular sac, which extends beyond the end of the odontophore (figures 15, 35).

True marginellids, on the other hand, have unmodified internal whorls (figure 1). The plications are continuous internally and the columella is not multiplicate. Marginellid radulae (figures 17–20) are a much shorter, usually broad, uniserial, J-shaped ribbon with 10 to 80 rachidian plates. These moderately to very broad, flat to weakly arched plates usually have many cusps. The subradular membrane is weakly expanded anterolaterally into marginal cuticular flanges, which help hold the radula in correct alignment with the underlying, anteriorly fused odontophoral cartilages (figures 19, 20). The posterior end of the radula begins with only one or two preformed nascent rachidian plates which are secreted in the blind end of a buccal pouch. The odontophore extends past the posterior end of the radula (figure 19).

After discerning the two fundamentally different groups of marginelliform gastropods, we searched for possible relationships among other neogastropod families. This revealed that all of the above cystiscid char-

acters are shared with the Olividae. Thus, we feel that the cystiscids have a shared ancestry with that family, and not with the Marginellidae (see final Discussion section for more details). We have come to the conclusion that the cystiscids and the true marginellids are not closely related and must be considered as separate and distinct families. A systematic section, outlining the classification of these two groups, follows.

SYSTEMATICS

KEY TO THE FAMILIES OF MARGINELLIFORM GASTROPODS

- 1a. Columellar plications not continuous internally, at least anterior two columellar plications reduced to one nearly axially oriented columellar edge within one full revolution internally; columella usually multiplicate with 3 (rarely 2) plications, plus often up to 14 parietal lirae posteriorly, but may have only 1 or 2 pseudocontinuous plications posterior to the anterior 2 internally reduced plications; internal whorls cystiscid or modified cystiscid type (figures 2, 3, 4) very thin and often partially missing due to partial resorption family CYSTISCIDAE
- 1b. Columellar plications continuous internally, not reduced; columella with 2 to 6 plications, at least the first 4 continuing internally, the 5th and 6th often not continuing internally (and are thus parietal lirae); internal whorls unmodified type (figure 1) complete and of original thickness, without evidence of resorption family MARGINELLIDAE

Family CYSTISCIDAE Stimpson, 1865:55

Diagnosis: Shell minute to large, white, uniformly colored, or patterned; surface smooth, sculptured, or axially costate; spire flat to immersed, or low to tall; protoconch paucispiral; lip thickened, smooth or denticulate; external varix present or absent; siphonal notch present or absent; posterior notch present or absent; columella multiplicate, with combined total of 2 to 13 plications + parietal lirae or with 2 internally reduced columellar plications + 1 or 2 pseudo-continuous plications; internal whorls cystiscid or modified cystiscid type. Type 2, 3, or 4 animal; operculum absent. Cystiscid radula, Type 1, 2, 3, or 4. Mantle cavity with monopectinate ctenidium and bipectinate osphradium. Proboscis pleurembolic; jaws absent; typical radular sac present.

Remarks: The family was erected by Stimpson (1865: 55) for a single included species based on unusual features of the head and radula. Subsequent authors included this group in the Marginellidae. Coan (1965:186) recognized this group as a subfamily, again based on unusual features of the head and radula, but did not include such genera as *Gibberula* (in part), *Persicula*, and *Canalispira*. Rules of priority require this name to be used, which is unfortunate because the type specimen of the type species

is lost (Covert, 1986d) and the species is otherwise poorly known. We currently recognize 283 species in the Cystiscidae, of which 26 are undescribed.

Key to the Recent Genera of the Family Cystiscidae

- 1a. Distinct siphonal notch present; spire low to immersed; shell minute to small 2
- 1b. Siphonal notch absent, anterior end rounded; spire immersed, low, or distinctly produced; shell minute to large 3
- 2a. Adult shell completely lacking an external varix; spire low to nearly immersed, but never completely immersed; shell usually white, uniformly colored in some, rarely with a few narrow spiral bands *Gibberula*
- 2b. Adult shell completely lacking an external varix or with an obscure to distinct, raised external varix; spire usually completely immersed, rarely very low; shell usually uniformly colored or with distinctive pattern of spots, tear-drop markings, longitudinal or oblique streaks or zig-zag lines; narrow spiral bands, if present, very numerous; rarely white, if so, with pattern *Persicula*
- 3a. External varix completely absent; columella multiplicate, with combined total of 2 to 17 plications + parietal lirae; with cystiscid internal whorls . . . 4
- 3b. External varix present, distinct, raised, usually strong; columella with 2 internally reduced anterior plications + 1 or 2 pseudo-continuous plications; with modified cystiscid internal whorls . . . 8
- 4a. Posterior corner of aperture sharply, narrowly, and deeply channeled; aperture usually lirate, smooth in some; sutures often channeled or impressed, if filled with callus, then still distinct; spire distinctly produced *Canalispira*
- 4b. Posterior corner of aperture rounded, not channeled; aperture smooth or denticulate, not lirate; sutures callused over, indistinct; spire immersed or low 5
- 5a. Shell with very strong, sharply crested axial costae; strongly developed parietal callus "shield" present; spire sunken, but not immersed, with nuclear whorls visible; 5 columellar plications present; lip heavily thickened, flared posteriorly, not denticulate *Extra*
- 5b. Shell lacking strong axial costae, although may have very weak axial growth lines or very faint wrinkles; parietal callus wash often present, but lacking strongly developed parietal "shield"; spire produced or completely immersed, but not as above; combined total of 2 to 17 columellar plications + parietal lirae; lip narrowly to strongly thickened, smooth or weakly denticulate 6
- 6a. Suture of last whorl expanding rapidly for final half whorl, then abruptly swept posteriorly just before lip, giving characteristic shape to shell; spire nearly flat to low, not immersed; shell shape

- usually cylindrical, elliptic, or oblong
 *Plesiocystiscus*
- 6b. Suture of last whorl not unusually expanding or narrowing; spire low to completely immersed; shell shape rarely cylindrical, usually elliptic, obovate to broadly obovate, or subtriangular 7
- 7a. Spire usually immersed; plications usually square in cross-section, often appearing excavated due to collabral parietal callus ridge, which intersects them just outside of aperture *Crithe*
- 7b. Spire usually at least slightly produced; plications usually rounded in cross-section, rarely appearing excavated, if so, not due to collabral parietal callus ridge *Cystiscus*
- 8a. Shell usually smooth, if sculptured, very obscure; spire immersed; shell elongate to broadly elliptic, obovate, subtriangular, or pyriform, not cylindrical *Granulina*
- 8b. Shell with distinct, punctate sculpture; spire flat to immersed; shell broadly cylindrical and abruptly narrowed anteriorly to broadly subtriangular *Pugnus*

Subfamily PLESIOCYSTISCINAE Covert and Covert, new subfamily

Diagnosis: Shell minute to small, white, hyaline; last whorl rapidly expanded then lip abruptly swept posteriorly giving characteristic shape; spire flat to low; lip thickened posteriorly, smooth, lacking lirae or denticulation; external varix absent; siphonal notch absent; posterior notch absent; columella multiplicate with combined total of 3 to 8 plications + parietal lirae; internal whorls cystiscid type. Type 2 animal; tentacles and siphon moderately long; mantle translucent, in some species not readily extending over external shell surface; foot relatively narrow. Type 1 radula. Internal anatomy unknown.

Genus *Plesiocystiscus* Covert and Covert, new genus (figures 3, 21, 43)

Type species: *Marginella jewettii* Carpenter, 1857a; OD, herein (figure 43).

Diagnosis: Same as for subfamily.

Description: Shell (figures 3, 43) minute to small, (adult length 1.5–6.0 mm). Color white, hyaline; surface smooth, glossy. Shape cylindrical, elliptic, or obovate; weakly to distinctly shouldered. Suture rapidly descending on last half of last whorl, then abruptly sweeping upward just before lip, giving characteristic shape to adult shell. Spire nearly flat to low. Aperture moderately narrow, broader anteriorly. Lip thin anteriorly, gradually thickening toward shoulder, smooth, lacking denticulation or lirae, external varix absent. Siphonal notch and posterior notch absent. Shell often with a weak parietal callus wash or weak parietal callus deposits. Columella multiplicate, with combined total of 3–8 plications + parietal lirae, usually

occupying less than half to slightly more than half the aperture length. Shell with cystiscid internal whorls.

External anatomy: 4 species studied. Type 2 animal, with moderately long tentacles; eyes at base of tentacles; siphon simple, moderately long; mantle translucent and barely visible, possibly not extending over external shell surface in some species; foot relatively narrow, about as wide as shell and 1½ times shell length; animal variously marked with tiny dots of various colors, pattern of internal mantle showing through translucent shell.

Internal anatomy: Unknown.

Radula (figure 21): 3 species studied. Type 1, triserial, with simple, thin, weak laterals that narrow to a single cusp. Ribbon long, narrow, composed of 66–103 rows of plates. Rachidian plates overlapping, very narrow (0.017–0.028 mm wide), weakly arched, with 3–7 sharp cusps on posterior edge. Anterior edge of rachidian plate slightly concave, resulting in weakly U-shaped plates. Shell length: radular width ratio (based on rachidian plate width) = 159–200. Radular Index = 10.9–34.3.

Included species: *P. abbotti* (Jong & Coomans, 1988), *P. atomus* (E. A. Smith, 1890), *P. bubistae* (Fernandes, 1987), *P. cincreus* (Jousseau, 1875), *P. consanguineus* (E. A. Smith, 1890), *P. gutta* (Gofas & Fernandes, 1988), *P. jansseni* (Jong & Coomans, 1988), *P. jewettii* (Carpenter, 1857), *P. josephinae* (Fernandes & Rolan, 1992), *P. larva* (Bavay, 1922), *P. palantirulus* (Roth & Coan, 1968), *P. politulus* (Dall, 1919), plus 4 undescribed species.

Distribution and Habitat: Indo-Pacific (1 species), E. Pacific (4 species), western Atlantic (5 species), W. African (6 species). Intertidal to 80 m.

Fossil Record: Eocene of France, Miocene and Pliocene of Florida, and Pleistocene of California, to Recent.

Nomenclature, Synonymy: Photographs of the syntypes of the type species, *Marginella jewettii*, were published by Palmer (1958:pl. 24, figs. 19–21). A lectotype was designated and illustrated in Coan and Roth (1966:pl. 51, fig. 66). The genus name is derived from the Greek *plesios*, near, in the sense of plesiomorphic, of characters near the ancestor, combined with *Cystiscus*. This indicates the relationship to (and previous inclusion in) the genus *Cystiscus*, type genus of the family. The triserial radula, found in many other neogastropod families, but unknown in any other cystiscids, is the most primitive in this family. Gender masculine.

Remarks: This is the only genus of marginelliform gastropods (previously referred to as “*Cystiscus*”) with a triserial radula. This group is considered to be the most primitive in the family based on the radula and possession of a generalized Type 2 animal. Radular and shell features, including presence of odontophoral cartilage hoods, possession of cystiscid internal whorls, and lack of an external varix, place this group in the Cystiscidae.

Gofas and Fernandes (1988:19) described the mantle of *P. gutta* (Gofas & Fernandes, 1988) as “translucent and hardly visible when it extends over the shell.” Roth and Coan (1968:66) observed that “the mantle was never extruded over the top of the shell of *C. jewettii*” and Behrens (1984:241) likewise described the mantle as not covering the shell in the same species. Additional observations on this point would be useful.

Subfamily CYSTISCINAE Stimpson, 1865:55

Diagnosis: Shell minute to small, white; spire immersed to low; surface smooth or axially costate; lip thickened, smooth or denticulate; external varix absent; siphonal notch absent; posterior notch absent; columella multiplicate, with combined total of usually 2 to 8 plications + parietal lirae; internal whorls cystiscid type. Type 3 animal; mantle smooth, at least partially extending over external shell surface. Type 2 radula. Internal anatomy unknown.

† Genus *Topaginella* Laseron, 1957

Topaginella Laseron, 1957:288

Type species: *Marginella octoplicata* Tenison-Woods, 1877 †; OD (M)

Diagnosis: Shell minute, pyriform, strongly narrowed anteriorly; spire low; lip thickened, strongly denticulate; external varix absent (?); distinct axial costae present; siphonal notch absent; columella multiplicate, with combined total of usually 8 plications + parietal lirae.

Fossil Record: Miocene of Australia.

Nomenclature, Synonymy: The type species, *T. octoplicata*, was figured in Cotton (1949:pl. 18).

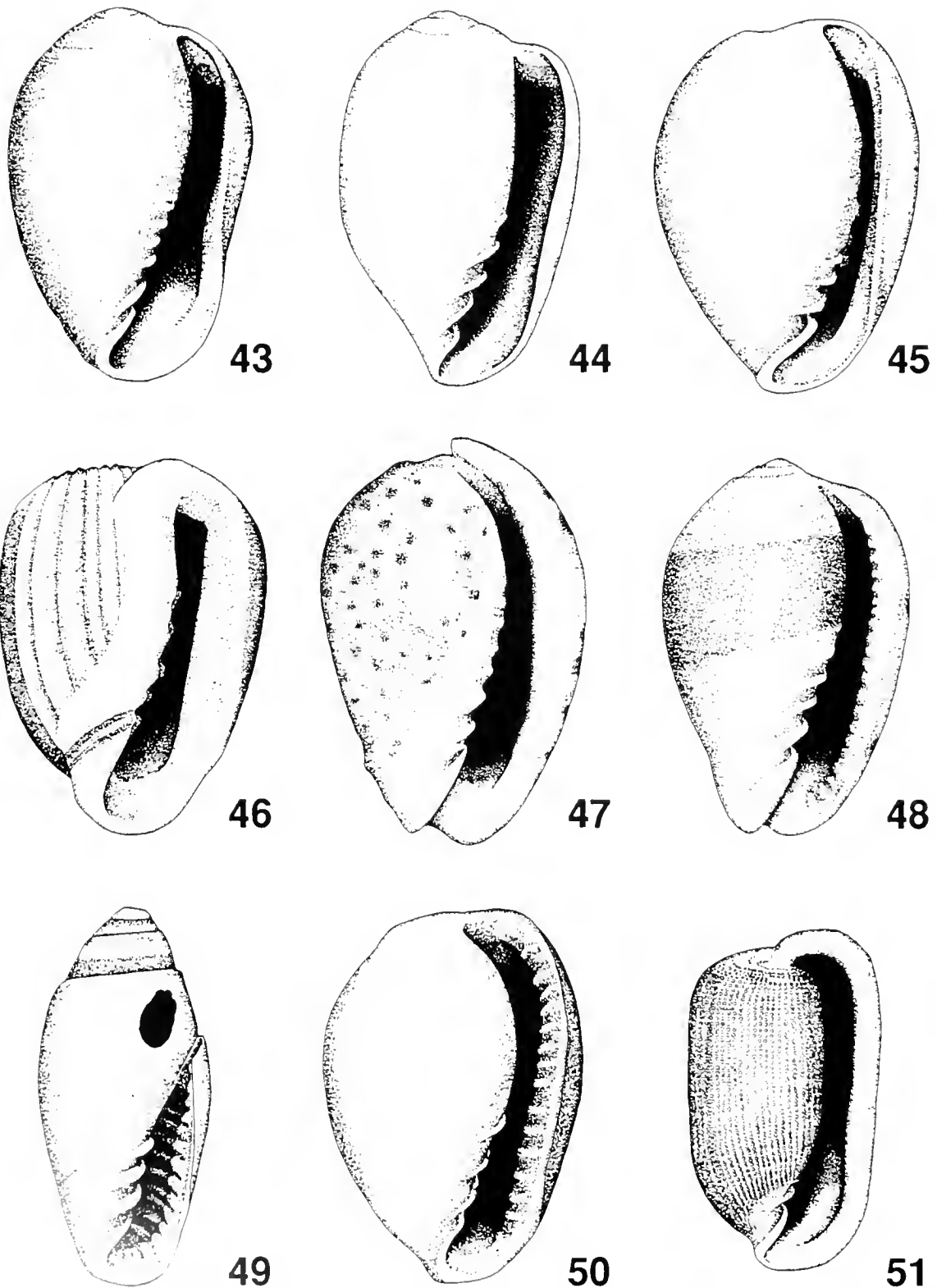
Remarks: The type species seems to be unique. The multiplicate columella and lack of a siphonal notch place it near *Cystiscus*, but the pyriform shape, exerted spire, denticulate lip, and fine axial costae (“striated growth lines” of Cotton, 1949:218) render it distinct. The absence of an external varix needs to be confirmed.

Genus *Cystiscus* Stimpson, 1865
(figures 9, 10, 22, 44)

Cystiscus Stimpson, 1865:55
Euliginella Laseron, 1957:282 [TS: *Marginella angasi* Crosse, 1870; OD]

Type species: *C. capensis* Stimpson, 1865 (non *Marginella capensis* Krauss, 1848), = *Marginella cystiscus* Redfield, 1870 (nom. nov.); M (figure 44).

Diagnosis: Shell minute to small, white, hyaline; spire immersed to low; lip thickened, smooth or weakly denticulate; external varix absent; siphonal notch absent; posterior notch absent; lacking collabral parietal callus ridge; columella multiplicate, with combined total of



Figures 43–51. Shells of type species of cystiscid genera, ventral views. 43. *Plesiocystiscus jewettii* (Carpenter, 1857). GAC M1823, Pirates Cove, San Luis Obispo, California, intertidal. Length 5.3 mm. 44. *Cystiscus cystiscus* (Redfield, 1870). Holotype (destroyed), False Bay, Cape of Good Hope, South Africa, 37 m, on gorgonians. After Stimpson (1865:pl. 8, fig. 2). Length 3.6 mm. 45. *Crithe atomaria* Gould, 1860. ANSP 307869, 1.6 km W.S.W. of Pulau Blankang Matti, Singapore, Malaya. Length 2.0 mm. 46. *Extra extra* Jousseaume, 1894. P. W. Clover collu., Perim, South Yemen. Length 0.9 mm. 47. *Persicula persicula* (Linné, 1758). GAC

usually 2 to 8 plications + parietal lirae, 1st plication usually strong and raised. Type 3 animal; mantle smooth, at least partially extending over external shell surface.

Description: Shell (figure 44) minute to small (adult length 1.0–6.0 mm). Color white, hyaline; surface smooth, glossy. Shape rarely cylindrical, usually elliptic, obovate, or subtriangular; weakly shouldered. Spire completely immersed to low. Aperture narrow to broad, usually wider anteriorly. Lip slightly to distinctly thickened, flared posteriorly in some species, smooth on inside edge to weakly denticulate, lacking lirae, external varix absent. Shell lacking a siphonal notch and posterior notch. Shell with weak parietal callus wash or weak parietal callus deposits in some species, but lacking collabral parietal callus ridge. Columella multiplicate, with combined total of 2–8 plications + parietal lirae, rarely up to 17 in which the posteriormost are denticles; one species with only 1 plication. Plications usually occupying less than half the length of the aperture, but most of the aperture in some. Plications excavated just inside aperture in a few species, usually evenly rounded, first plication usually raised and very strong. Shell with cystiscid internal whorls.

External anatomy (figures, 9, 10): 13 species studied. Type 3 animal with eyes at side of head, usually on lateral swelling; mantle smooth, at least partially extending onto external shell surface, in some species nearly covering shell; foot relatively narrow, about as wide as shell and 1–1.5 X shell length; head and mantle usually uniformly colored, often bright red, orange, or yellow, or brown or black, internal mantle color pattern often showing through translucent shell.

Internal anatomy: Unknown.

Radula (figure 22): 14 species studied. Type 2, uniserial, ribbon long, narrow, composed of 80–200 plates. Rachidian plates overlapping (rarely separate), very narrow (0.009–0.036 mm wide), weakly to strongly arched, with 5–15 very strong cusps on posterior edge. Anterior edge of rachidian plate slightly concave, resulting in crescent-shaped plates. Shell length: radular width ratio = 94–217. Radular Index = 10.7–25.7.

Distribution and Habitat: Neozelanic (1 species), So. Australian (21 species), Indo-Pacific (11 species), W. Atlantic (2 species), South African (23 species). Intertidal to 370 m.

Fossil Record: Eocene of France, Miocene and Pliocene of Australia, to Recent.

Nomenclature, Synonymy: The type species *C. cystiscus* is discussed and figured in Coovert (1986d) and here-

in (figure 44). The radula of this species, along with three others, was reviewed in Coovert (1989b:5–6). SEMs of an additional eight Australian species (Dean Hewish, pers. comm.), including *C. angasi*, the type species of *Euliginella*, have been examined by us. All these species are considered congeneric based on similar radulae and shell characters. *Euliginella* was considered synonymous by Coan (1965:190).

Remarks: Originally described in its own family by Stimpson, apparently based on the radula and unusual features of the head, this genus again becomes the nominate genus of a now more clearly defined family.

Genus *Crithe* Gould, 1860
(figure 45)

Crithe Gould, 1860:354
Microvulina Habe, 1951:105 [TS: *M. nipponica* Habe, 1951: OD]

Type species: *C. atomaria* Gould, 1860; M (figure 45)

Diagnosis: Shell minute to small, white, hyaline; spire usually immersed, rarely low; lip thickened, smooth, lacking denticulation; external varix absent; siphonal notch absent; posterior notch absent; columella multiplicate, with combined total of 6–8 plications + parietal lirae, plications usually excavated inside aperture due to collabral parietal callus ridge. Presumably a Type 3 animal.

Description: Shell (figure 45) minute to small (adult length 1.6–3.2 mm). Color white, hyaline; surface smooth, glossy. Shape narrowly to broadly obovate or subtriangular; weakly to moderately strongly shouldered. Spire usually completely immersed, rarely low. Aperture narrow, wider anteriorly. Lip moderately thickened, especially posteriorly, thinner anteriorly, smooth on inside edge, lacking denticulation and lirae, external varix absent. Shell lacking a siphonal notch and posterior notch. Shell usually with a distinct collabral parietal callus ridge that intersects plications. Columella multiplicate, with combined total of 6–8 plications + parietal lirae, usually occupying about two-thirds the aperture length. Plications usually appearing excavated just inside aperture due to callus deposits from anterior end of collabral parietal callus ridge. Shell with cystiscid internal whorls.

External anatomy: Presumably a Type 3 animal; mantle extension undetermined; generally uniformly colored, bright yellow, rose, or orange-red, or black with 2 zones of yellow on internal mantle.

←
M1558, Dakar, Senegal, West Africa, in sand, low tide. Length 20.0 mm. **48.** *Gibberula oryza* (Lamarck, 1822). Neotype, MHNG, Senegal. After Gofas (1990 fig. 2). Length 6.5 mm. **49.** *Canalispira olivellaformis* Jousseaume, 1875. Lectotype, MHNP, locality unknown. After photos in Kilburn (1990:fig. 5). Length 4.2 mm. **50.** *Granulina isseli* (G. & H. Nevill, 1875). GAC Acc. # 53–57, Red Sea coast of Egypt between El Ghurdaga and 80 km south of El Quseir. Length 1.6 mm. **51.** *Pugnus parvus* Hedley, 1896. GAC M2135, east of North Pt., Flinders Island, Bass Strait, Australia, 39°43'S, 148°36'E. Length 2.0 mm.

Internal anatomy: Unknown.

Radula: 1 species studied (3 specimens). Type 2, uniserial, ribbon long, narrow, composed of 189–220 plates. Rachidian plates overlapping, very narrow (0.007–0.008 mm wide), weakly arched, with 4 strong cusps on posterior edge. Anterior edge of rachidian plate slightly concave, resulting in an asymmetrically V-shaped plate. Shell length: radular width ratio = 23.4–27.0. Radular Index = 47.2–55.0.

Distribution and Habitat: Indo-Pacific (6 species). Intertidal to 58 m.

Fossil Record: Pliocene of Australia to Recent.

Nomenclature, Synonymy: The type species of *Crithe* and *Microvulina*, and their generic synonymy, were discussed in Coover (1986e and 1987c). The holotype of *C. atomaria* was figured in Johnson (1964:pl. 8, fig. 12) and Coover (1986e:fig. 1).

Remarks: The columellar plications, which are square in cross-section and excavated due to the collabral parietal callus ridge, and the usually immersed spire, serve to differentiate this group. The radulae are diagnostic.

Genus *Extra* Jousseume, 1894
(figure 46)

Extra Jousseume, 1894:98, 101

Type species: *E. extra* Jousseume, 1894; M (figure 46)

Diagnosis: Shell minute, white, semitranslucent; prominent axial costae present; spire sunken but not immersed; lip strongly thickened, smooth, lacking denticulation, flared posteriorly; siphonal notch absent; posterior notch absent; distinct parietal callus "shield" present; columella multiplicate, with combined total of 5 plications + parietal lirae, plications slightly excavated inside aperture due to parietal callus deposits.

Description: Shell (figure 46) minute (adult length 1.3–1.4 mm). Color white, body whorl semitranslucent, surface with 17–20 prominent, sharply crested axial costae. Shape obovate, truncate posteriorly; strongly shouldered. Spire sunken but not immersed. Aperture narrow, slightly wider anteriorly. Lip very strongly thickened, especially posteriorly, arched above apex and flared posteriorly, smooth on inside edge, lacking denticulation and lirae, apparently lacking an external varix. Shell lacking a siphonal notch and posterior notch. Shell with a distinct parietal callus "shield" that is free anteriorly with slight chink behind. Columella multiplicate, with combined total of 5 plications + parietal lirae occupying about $\frac{3}{4}$ the aperture length. Plications slightly excavated just inside aperture due to callus deposits from the parietal callus shield. Internal whorls unknown but presumed to be cystiseid type.

External anatomy: Unknown.

Internal anatomy: Unknown.

Radula: Unknown.

Distribution and Habitat: Indo-Pacific (1 species), recorded only from the western Indian Ocean. Apparently shallow water.

Fossil Record: Known only from the Recent.

Nomenclature, Synonymy: See Coover (1987d) for discussion.

Remarks: This monotypic genus is provisionally placed in the Cystiscinae based on the 5 excavated plications and lack of labial denticulation. The last strong axial costa has the appearance of an external varix, which, if present, might eliminate this genus from the Cystiscinae. The slightly sunken but non-immersed spire and the parietal "shield" of this group appear to be unique.

Subfamily PERSICULINAE Coover and Coover, new subfamily

Diagnosis: Shell minute to large, white, uniformly colored, or patterned; spire immersed or low to tall; lip thickened, smooth or lirate; external varix present or absent; siphonal notch present or absent; weak to distinct posterior notch present; columella multiplicate with combined total of 3–13 plications + parietal lirae; internal whorls cystiseid type. Type 4 animal; tentacles short to long, rarely absent; siphon short to long; eyes situated laterally on head slightly below the base of the tentacles; mantle usually not extending over external shell surface. Type 3 radula. Odontophoral cartilages separate; valve of Leiblein present, with or without bypass tube; esophageal caecum absent; gland of Leiblein short, small, emptying directly into posterior end of esophagus; paired salivary glands ascinous or tubular, attached to esophagus just anterior to the valve of Leiblein, ducts attached to walls of esophagus; single accessory salivary gland present, ascinous or tubular; anal gland absent.

Genus *Persicula* Schumacher, 1817
(figures 2, 11–16, 23, 35–37, 47)

Persicula Schumacher, 1817:235

Pachybatron Gaskoin, 1853:356 [TS. *P. margelloideum* Gaskoin, 1853, = *Erato cypracoides* C. B. Adams, 1845, SD (M) Tryon, 1885:270]

Persicula, subg. *Rabicea* Gray, 1857:37 [TS. *P. interrupta* (Lamarck, 1822), = *Margincella interrupta* Lamarck, 1822, = *Voluta interruptolineata* Megerle von Mühlfeld, 1816, M]

Type species: *P. variabilis* Schumacher, 1817, = *Voluta persicula* Linné, 1758; M (figure 47)

Diagnosis: Shell small to large, uniformly colored, or white to colored and patterned, moderately thick to thick-shelled; spire usually immersed; lip thickened, weakly to strongly lirate; external varix present or absent; distinct siphonal notch present; posterior notch present; columella multiplicate with combined total of 4–13 plications

+ parietal lirae. Type 4 animal; tentacles long; siphon usually long; mantle apparently not extending over external shell surface.

Description: Shell (figures 2, 47) small to large (adult length 4.5–34.0 mm). Color white, tan, pinkish- or yellowish-tan, to gray, with pattern of spiral lines, rows of dots or tear-drop shaped markings, or longitudinal wavy or zig-zag markings which often form triangular peaks, less often uniformly flesh-colored or nearly white due to pattern reduction; surface smooth, glossy, few species with weak axial costae. Shape narrowly to broadly obovate, or narrowly to broadly elliptic; weakly to moderately strongly shouldered. Spire usually completely immersed, rarely slightly produced. Aperture narrow, slightly wider anteriorly. Lip moderately thickened, especially posteriorly, thinner anteriorly, very weakly to strongly lirate, completely lacking an external varix or with strong to weak external varix. Shell with a distinct siphonal notch and a very weak to very distinct posterior notch. Moderately-thick to thick-shelled, some species with distinct parietal or apical callus deposits, a few with a very strong parietal callus "shield." Columella multiplicate, with combined total of 4–13 plications + parietal lirae usually occupying more than half the aperture length. Shell with cystiscid internal whorls.

External anatomy (figures 11, 12): 15 species studied. Type 4 animal with moderately long to long tentacles; siphon simple, moderately short to usually very long; mantle apparently not extending over external shell surface; foot narrow to moderately broad, about as wide as shell to considerably broader and about 1½ times shell length; animal variously marked with tiny dots, spots, blotches, flecks, or streaks of opaque white, black, or various colors.

Internal anatomy (figures 35–37): 2 species studied. As in family diagnosis. Valve of Leiblein without bypass tube, paired salivary glands ascinous, single accessory salivary gland ascinous.

Radula (figures 13–16, 23): 14 species studied. Type 3, uniserial, ribbon long, narrow, composed of 80–209 plates. Rachidian plates overlapping, narrow (0.011–0.093 mm wide), moderately to strongly arched, with 6–14 sharp cusps on posterior edge, the central cusp usually the strongest. Anterior edge of rachidian plate strongly concave, resulting in U- or V-shaped plates. Shell length: radular width ratio = 146–572. Radular Index = 6.7–21.8.

Distribution and Habitat: S. Australian (3 species), Indo-Pacific (11 species), E. Pacific (7 species), W. Atlantic (20 species), W. African (9 species), South African (1 species).

Fossil Record: Eocene of France and Alabama, upper Oligocene and Miocene of W. Atlantic, to Recent. Intertidal to 370 m.

Nomenclature, Synonymy: The type species of *Rabicea*,

V. interruptolineata, is congeneric with *P. persicula*, based on similar shell, radular (Coovert, 1989b:22), and external anatomical features. Coan and Roth (1966:282) discussed this synonymy. *Pachybathron* has been treated as a valid genus by many recent authors, including Coomans (1972), who discussed the group, its early confused familial placement, the type species, and its synonymy. The cited example in Adams and Adams (1853:194) does not constitute a type fixation. Tryon (1855:270) thus provided the earliest type fixation by subsequent designation. The features of the external anatomy, radula, and the brown triangular markings of the shell indicate a close relationship to some of the other small western Atlantic *Persicula*. The parietal callus shield is considered to be no more than a species-group character. Thus, *Pachybathron* is here treated as a synonym. Subgeneric recognition may eventually be justified, but this would necessitate formal recognition of other species groups, a step considered unwise at this time.

Remarks: Erroneously reported to have a Type 2 animal (Coovert, 1987g, 1987i) based on strictly dorsal views, closer examination of several species revealed the split head typical of a Type 4 animal (figure 11). The two halves of the head are capable of closing together at will, thus appearing unsplit. The long siphon usually distinguishes this group anatomically from the closely related *Gibberula*. The shell of *Persicula* is usually patterned, often has a distinct external varix, and the spire is usually immersed. These conchological features serve to separate the two groups and are presented in the key to Recent genera. See Coovert (1987b) for a discussion of the *Persicula cornea* group.

Genus *Gibberula* Swainson, 1840 (figures 48, 79)

Gibberula Swainson, 1840:323

Granula Jousseaume, 1875:167, 246 [TS. *G. bensoni* (Reeve, 1865), = *Marginella bensoni* Reeve, 1865, SD (M) Coan, 1965:190]

Kogomea Habe, 1951:103 [TS. *Marginella novemprouncialis* (Yokoyama, 1928), = *Erato novemprouncialis* Yokoyama, 1928, OD]

† *Dentiginella* Laseron, 1957:288 [TS. *Marginella metula* Cotton, 1949 †, OD (M)]

Epiginella Laseron, 1957:279 [TS. *E. abhta* Laseron, 1957, OD]

† *Lataginella* Laseron, 1957:288 [TS. *Marginella kitsomi* Chapman, 1921 †, OD (M)]

Phyloginella Laseron, 1957:280 [TS. *P. compressa* Laseron, 1957, OD]

† *Vetaginella* Laseron, 1957:288 [TS. *Marginella doma* Cotton, 1949 †, OD (M)]

Diluculum Barnard, 1962:14 [TS. *D. mopmatum* Barnard 1962, = *Marginella bensoni* Reeve, 1865, OD]

Type species: *G. zonata* Swainson, 1840, = *Volvaria oryza* Lamarek, 1822; M (figure 48)

Diagnosis: Shell minute to medium size, white or colored, some species with spiral bands; spire low to medium height, not immersed; lip thickened, weakly to strongly

lirate; smooth in some species; external varix absent; distinct siphonal notch present; posterior notch present but often weak; columella multiplicate with combined total of 3–8 plications + parietal lirae. Type 4 animal; tentacles short; siphon short; mantle not usually extending over external shell surface.

Description: Shell (figure 48) minute to medium in size (adult length 1.8–8.5 mm). Color usually white, hyaline, less commonly tan, yellow, or orange, some species with spiral lines or bands or sutural band, rarely with oblique markings; surface smooth, glossy, rarely with fine, weak axial costae. Shape narrowly subcylindrical to usually elliptic, obovate, or subpyriform; weakly to strongly shouldered, some species with weakly raised sutures. Spire low to medium height, not immersed. Aperture narrow to moderately broad, wider anteriorly. Lip moderately thickened, especially posteriorly, thinner anteriorly, usually weakly to strongly lirate but absent in some species, completely lacking an external varix. Shell with distinct siphonal notch and very weak to distinct posterior notch. Shell with apical callus deposits in some species, rarely with elongate collabral parietal callus deposits. Columella multiplicate, with combined total of 3–8 plications + parietal lirae occupying $\frac{1}{3}$ to nearly the full aperture length. Shell with cystiscid internal whorls.

External anatomy: 26+ species studied. Type 4 animal, with short tentacles, which are rarely absent; siphon simple, short, barely extending above the dorsal edge of the siphonal notch; mantle apparently not extending over external shell surface or with a small lobe on the left side in some species; foot narrow to moderately broad, about as wide to slightly wider than shell and usually about $1\frac{1}{2}$ times shell length; some species with anterolateral edges of foot weakly to strongly raised to form "parapodia"; animal variously marked with tiny dots, spots, or blotches, but not striped or lineated, markings of opaque white, brown, yellow, orange, or green.

Internal anatomy (figure 79): 1 species studied. As in family diagnosis. Valve of Leiblein with bypass tube; paired salivary glands tubular; single accessory salivary gland tubular.

Radula: 21 species studied. Type 3, uniserial, ribbon long, narrow, of 80–153 plates. Rachidian plates overlapping, narrow (0.008–0.042 mm wide), moderately to strongly arched, with 5–11 sharp cusps on posterior edge. The central eusp is usually the strongest. Anterior edge of rachidian plate strongly concave, resulting in U- or V-shaped plates. Shell length: radular width ratio = 118–309. Radular Index = 9.1–21.9.

Distribution and Habitat: Neozelanic (2 species), S. Australian (4 species), Indo-Pacific (26 species), E. Pacific (6 species), W. Atlantic (9 species), Mediterranean (10 species), W. African (25 species), South African (7 species). Intertidal to 3,300 m.

Fossil Record: Paleocene and Eocene of France and W. Atlantic, Miocene and Pliocene of Italy, Australia,

W. Atlantic, and Japan, and Pleistocene of W. Atlantic and California, to Recent.

Nomenclature, Synonymy: *Gibberula oryza*, type species of this genus, is valid and distinct from *G. miliaria* (Linné, 1758). Coan (1965:189) (questionably) and Dodge (1955:79–82) considered these two species synonymous. But Gofas (1990:117) clearly differentiated the two species based on shell and external anatomical characters, and designated a neotype (figure 48) and lectotype respectively. The genus *Granula* and its type species *M. bensoni* differ from *Gibberula* (type species *G. oryza*) only in size and very minor, species-level shell characters. *Granula* was synonymized under *Gibberula* by Cossmann (1899:96) and Wenz (1943:141). *Kogomea*, likewise differing only in minor characters, was synonymized by Roth and Coan (1971:579) and Rehder (1980:85). *Diluculum* was discussed and synonymized by Kilburn and Rippey (1982:113, 214). Barnard (1962) described *Diluculum* and its type species simply because the radula was known, whereas other species "are merely names given to the shells of molluscs whose anatomy is unknown (op. cit., p. 14)." This is clearly untenable. The wishbone-shaped radula was an error in observation, likewise made by Ponder (1970:70, fig. 3F). This error was discussed in Coovert (1989b:12). Gofas (1989a) correctly figured a number of radulae from *Gibberula*, drawn from SEMs. The five Laseron (1957) genera were all based on species-level characters, and are here synonymized with *Gibberula*. The type species of all these genera show a distinct siphonal notch. The type species of *Phyloginella* was figured by Kaicher (1992: #6211). Powell (1979:222) synonymized *Lataginella* under *Kagomea* (sic).

Remarks: *Gibberula cucullata* Gofas and Fernandes, 1988, with strongly developed "parapodia," has a highly modified head. The bifurcated tips of the head taper into divergent anterior lobes. These tips can be interpreted as being either the anterior lobes of the head and thus lacking tentacles, or the tentacles themselves and lacking the anterior lobes. Based on the sharply pointed tips and relative position of the eyes, we interpret these tips as being the anterior lobes of the head, the animal lacking tentacles. Gofas and Fernandes (1988:25) suggested that this species "may deserve separate generic status." *Gibberula subbulbosa* (Tate, 1878) (based on unpubl. data ex. R. Burn and D. Hewish) has a similarly constructed head but apparently lacks the strongly developed "parapodia." Until the external anatomy of the type species of all related genus-group names are known, it is considered unwise to place these species in a different genus-level group.

This large, widely distributed group is well characterized by radular, external anatomical, and conchological characters. See *Persicula* for additional discussion.

Genus *Canalispira* Jousseaume, 1875
(figure 49)

Canalispira Jousseaume, 1875:168, 270

Baroginella Laseron, 1957:286–287 [TS: *B. infirma* Laseron, 1957; OD]

Type species: *C. olivellaeformis* Jousseau, 1875; M (figure 49)

Diagnosis: Shell minute to medium size, white, hyaline, rarely with faint pattern, cylindrical-biconic to obovate or obconic; sutures usually impressed to channeled; spire medium to tall; lip thickened, smooth or lirate; external varix absent; siphonal notch absent; deeply channeled posterior notch present; columella multiplicate with combined total of 3–6 plications + parietal lirae. Modified Type 4 animal; tentacles absent; siphon not visible; foot split anteromedially, covering external shell surface anterolaterally.

Description: Shell (figure 49) minute to medium in size (adult length 2.2–10.3 mm). Color usually white, hyaline, rarely with faint brown maculations, fine oblique lines, or weak axial streaks; surface smooth, glossy. Shape cylindrical-biconic to narrowly obovate or obconic; usually very weakly to weakly shouldered. Sutures distinctly to weakly channeled, deeply impressed, or completely callused over. Spire medium to tall. Aperture narrow to moderately broad, wider anteriorly. Lip moderately thickened, especially posteriorly, thinner anteriorly, outer edge incurved on posterior half, usually weakly to strongly lirate but smooth and lacking lirae in some species, completely lacking an external varix. Shell lacking a siphonal notch but with a sharply, narrowly, and deeply channeled posterior notch. Parietal callus wash usually confined to aperture. Columella multiplicate, with combined total of 3–6 plications + parietal lirae occupying half or more of the aperture length. Shell with cystiscid internal whorls.

External anatomy: 2 species studied. Modified Type 4 animal; tentacles absent; triangular lobes of head pointed anteriorly; the small black eyes medially placed on each triangular lobe; siphon not visible; mantle extension undetermined; foot narrow, about as wide and long as the shell, split anteromedially, covering the anterior end of the shell laterally like “parapodia”; animal white or colorless. (Largely based on unpubl. notes and drawings of an undescribed W. Australian species, ex. P. W. Clover).

Internal anatomy: Unknown.

Radula: 2 species studied. Type 3, uniserial, ribbon long, narrow, composed of 121–136 plates. Rachidian plates overlapping, narrow (0.016–0.033 mm wide), moderately to strongly arched, with 7 sharp cusps on posterior edge. The central cusp is usually the strongest. Anterior edge of rachidian plate strongly concave, resulting in U- or V-shaped plates. Shell length: radular width ratio = 176–270. Radular Index = 17.3–19.4.

Distribution and Habitat: So. Australian (1 species), Indo-Pacific (7 species), W. Atlantic (3 species), South African (2 species). Intertidal to 540 m.

Fossil Record: Pliocene of Australia to Recent.

Nomenclature, Synonymy: The lectotype of *C. olivellaeformis* was figured by Kilburn (1990:fig. 5) and is illustrated here (figure 49). We studied the holotype of *B. infirma* and it is clearly congeneric, differing only in the degree of channeling of the sutures. We regard this character to be of species-level and synonymize *Baroginella* with *Canalispira*.

Remarks: The modified Type 4 animal and lack of a siphonal notch render this group distinct, but the Type 3 radula clearly places this genus in the Persiculini. More study is needed of living animals.

Subfamily GRANULININAE Coovert and Coovert, new subfamily

Diagnosis: Shell minute to small, white, hyaline; surface smooth or sculptured; spire flat to immersed; lip thickened, smooth or denticulate; external varix present; siphonal notch absent; columella with 2 internally reduced columellar plications, plus 1 or 2 pseudo-continuous plications; internal whorls modified cystiscid type. Type 2 animal; tentacles long, slender; siphon moderately long; mantle pustulose, extending over external shell surface; foot long, narrow. Type 4 radula. Internal anatomy unknown.

Genus *Granulina* Jousseau, 1888 (figures 4, 24, 50)

Granulina Jousseau, 1888:191

? † *Cryptospira* (*Cypracolina*) Cerulli-Irelli, 1911:231 [TS: *Voluta clandestina* Brocchi, 1814 †; M]

Merovia Dall, 1921:86 [TS: *Merovia pyriformis* (Carpenter, 1865), = *Volutella pyriformis* Carpenter, 1865, = ? *Marginella margaritula* Carpenter, 1857b; M]

Microginella Laseron, 1957:280 [TS: *Marginella anxia* Hedley, 1909; OD]

Gibberulina auctt., non Monterosato, 1884

Type species: *Marginella pygmaea* Issel, 1869 (non *Marginella pygmaea* G. B. Sowerby II, 1846), = *Marginella isseli* G. & H. Nevill, 1875 (nom. nov.); M (figure 50)

Diagnosis: Shell minute to small, white, hyaline; spire immersed; lip strongly thickened, usually denticulate; external varix present; siphonal notch absent; collabral parietal callus ridge often present; columella with 4 strong plications that are often excavated inside aperture. Type 2 animal; tentacles long, slender; siphon moderately long; foot long, narrow; mantle pustulose, extending over external shell surface.

Description: Shell (figures 4, 50) minute to small (adult length 0.8–3.2 mm). Color white, hyaline; surface smooth, glossy, rarely with fine, weak axial costae or minutely pitted. Shape narrowly to broadly elliptic, obovate, subtriangular, or pyriform; very weakly to weakly shouldered. Spire usually immersed. Aperture narrow to moderately broad, noticeably wider anteriorly and slightly wider posteriorly. Lip moderately to greatly thickened,

especially posteriorly, usually distinctly denticulate, rarely smooth, with distinct external varix. Shell lacking a siphonal notch; posterior notch usually absent, rarely weakly developed. Shell usually with a weak to distinct collabral parietal callus ridge that often intersects columellar plications. Columella with 4 strong plications, third and fourth rarely weak, rarely with weak parietal denticles posterior to plications. Plications often appearing excavated inside aperture due to callus deposits from anterior end of collabral parietal callus ridge. Plications occupying half or less the aperture length. Shell with modified cystiscid internal whorls.

External anatomy: 13 species studied. Type 2 animal, with long, slender tentacles; eyes at base of tentacles; siphon simple, moderately long; mantle pustulose, extending symmetrically over most of external shell surface; foot narrower to slightly wider than shell and about twice the shell length; animal variously marked with tiny dots, spots, or areas of concentrated pigmentation, markings usually black, white, or yellow, but may be orange or turquoise.

Internal anatomy: Unknown.

Radula (figure 24): 12 species studied. Type 4, uniserial, ribbon long, narrow, composed of 90–159 plates. Rachidian plates usually completely non-overlapping, very narrow (0.006–0.012 mm wide), moderately arched, with 9 to 12 raised, clustered denticles located in staggered positions on dorsal surface, with a single (or asymmetrically paired) strong central cusp protruding posteriorly. Anterior edge of rachidian plate weakly concave, resulting in vaguely V-shaped plates. The rachidian plates are asymmetrical and alternate as mirror images. Shell length: radular width ratio = 16.4–35.1. Radular Index = 8.2–13.7.

Distribution and Habitat: So. Australian (3 species), Indo-Pacific (13 species), E. Pacific (3 species), W. Atlantic (12 species), Mediterranean (8 species), W. African (3 species), South African (3 species). Intertidal to 1,285 m (single record at 1,700 m).

Fossil Record: Miocene to Pliocene of W. Atlantic, Pliocene of Italy, Pleistocene of Japan and California, to Recent

Nomenclature, Synonymy: The type species and generic synonymy of *Granulina* was discussed in Coover (1987b). Although the "problem of *Granulina clandestina*" was treated by Gofas (1992:5–6), with a neotype designated and figured (op. cit., fig. 3), several discrepancies remain. Brocchi (1814:642–643, pl. 15, fig. 11) described and figured a shell with 3 columellar plications, a slightly exerted spire, and a pyriform shape. This was considered to be a juvenile by Gofas (1992:5), but juvenile *Granulina* have four plications, an immersed spire, and an ovate or globose shape. More study is needed to resolve these discrepancies. The lectotype of *V. pyriformis*, type species of *Merovia*, was figured by Coan and Roth (1966: pl. 51, fig. 77). Further research is needed to clearly

establish the synonymy of this species with *M. margaritula*. We have studied syntypes of *M. anxia*, type species of *Microginella*, and regard them to be referable to *Granulina*.

Remarks: Absence of a siphonal notch and presence of a distinct external varix distinguish this genus from all other cystiscid genera except *Pugnus*. Shell shape and usual lack of sculpturing will further characterize *Granulina*. The very distinct Type 4 radula, modified cystiscid internal whorls, and Type 2 animal clearly distinguish these two genera as a separate subfamily. For a discussion of *G. hadria* (Dall, 1889), see Coover (1988a).

Genus *Pugnus* Hedley, 1896
(figure 51)

Pugnus Hedley, 1896:105–106
Marginellopsis Bavay, 1911:241 [TS *M. serrei* Bavay, 1911: M]

Type species: *P. parvus* Hedley, 1896; OD (M) (figure 51)

Diagnosis: Shell minute, white, hyaline; surface minutely sculptured; spire flat to immersed; lip thickened, smooth or denticulate; external varix present; siphonal notch absent; columella with 3 or 4 plications. Type 2 animal; tentacles long, slender; siphon moderately long; foot long, narrow; mantle pustulose, extending over external shell surface.

Description: Shell (figure 51) minute (adult length 0.75–2.0 mm). Color white, hyaline; surface sculpture of extremely fine, crossed spiral and axial threads leaving rows of quadrate or hexagonal pits in between, or with spiral or axial rows of beads or short, dashed ridges which are often serpentine or interconnected. Shape broadly cylindrical to broadly subtriangular; weakly to strongly narrowed anteriorly, strongly shouldered. Spire flat to immersed. Aperture moderately narrow to broad, wider anteriorly and slightly wider posteriorly. Lip strongly thickened, especially posteriorly, distinctly denticulate or smooth, with distinct external varix. Shell lacking a siphonal notch and posterior notch. Often with a distinct parietal callus wash extending out of aperture. Columella with 3–4 plications, third and fourth often weak. Plications occupying less than half the aperture length. Shell with modified cystiscid internal whorls.

External anatomy: 1 species studied. Type 2 animal, with long, slender tentacles; eyes at base of tentacles; siphon simple, moderately long; mantle pustulose, extending symmetrically over most of external shell surface; foot narrower than shell and about twice the shell length; animal variously marked with tiny reddish dots and spots on a translucent background. [Based on pers. obs. of photographs of *P. serrei* (Bavay, 1911), ex. Colin Redfern].

Internal anatomy: Unknown.

Radula: 2 species studied. Type 4, uniserial, ribbon long, narrow, of > 124 plates. Rachidian plates usually completely non-overlapping, very narrow (0.006 mm wide), moderately arched, with 11–12 raised, clustered denticles located in staggered positions on dorsal surface, with a single (or asymmetrically paired) strong central cusp protruding posteriorly. Anterior edge of rachidian plate weakly concave, resulting in vaguely V-shaped plates. The rachidian plates are asymmetrical and alternate as mirror images. Shell length: radular width ratio = 161–242. Radular Index = 10.3.

Distribution and Habitat: S. Australian (1 species), Indo-Pacific (1 species), W. Atlantic (2 species). Intertidal to 60 m.

Fossil Record: Known only from the Recent.

Nomenclature, Synonymy: *Marginellopsis* is here synonymized with *Pugnus* on the basis of very similar radulae (pers. obs. of SEMs, ex. Dean Hewish) and similar shell sculpturing between the type species of the two groups. An undescribed species from Brazil has characters of both groups, and *P. maesae* Roth, 1972 is intermediate in shell shape. Special attention should be paid to the distinctive surface sculpturing uniting them all. These differences are provisionally considered to be of specific value only. See Roth (1972:107) for remarks on differing familial placement.

Remarks: For general comments, see remarks under *Granulina*.

Family MARGINELLIDAE Fleming, 1828:328

Diagnosis: Shell minute to very large, white, uniformly colored, or patterned; protoconch paucispiral; lip thickened, smooth or denticulate; external varix present or absent; siphonal notch present or absent; columella with 2–6 plications; internal whorls unmodified type. Type 1 or Type 2 animal; operculum absent. Marginellid radula, Type 5, 6, modified Type 6, Type 7, 8, or 9, or non-radulate. Mantle cavity with monopectinate ctenidium and bipectinate osphradium. Proboscis pleurembolic; jaws absent; marginellid buccal pouch present, absent in non-radulate species; odontophoral cartilages fused anteriorly or both anteriorly and posteriorly; valve of Leiblein present or absent, with or without bypass tube; esophageal caecum present or absent; gland of Leiblein large, sacculate, and emptying directly into posterior end of esophagus, or with long, convoluted duct and a terminal bulb, emptying either into posterior end of esophagus or passing through nerve ring and emptying into anterior end of proboscis; paired salivary glands ascinous or tubular, either attached to esophagus just anterior to the valve of Leiblein, contained within proboscis, or free, ducts either embedded in or attached to walls of esophagus, or free; single accessory salivary gland present or absent, ascinous or tubular; anal gland present.

Remarks: We currently recognize a total of 483 species

in the Marginellidae, of which 51 remain to be described. The two subfamilies were recognized in Coan (1965) but were not clearly based on anatomical characters.

Key to the Recent Genera of the Family Marginellidae

- 1a. Adult shell very large, over 50 mm in length; siphonal notch present, broad, weak to distinct; spire medium height, with large, often somewhat bulbous protoconch; lip narrowly thickened, smooth, without denticulation 2
- 1b. Adult shell minute to large, rarely very large, if over 50 mm, then spire immersed or with strongly thickened, denticulate lip; spire immersed to tall, protoconch not unusually large; lip narrowly to strongly thickened, with or without denticulation 3
- 2a. Columella with 4 very strong, nearly transverse plications; 1st plication well posterior of anterior border of columella; with very distinct parietal callus deposit posteriorly; shell often somewhat dull and crazed or blistered *Afrivoluta*
- 2b. Columella with 2 strong, very oblique plications; 1st plication bordering anterior end of columella; without distinct parietal callus deposits; shell very smooth, glossy . . . *Marginellona*
- 3a. Columella with 4 strong plications occupying more than half the aperture length; if with weak "false 5th" plication, then with distinct posterior notch; spire low, medium, or tall; external varix distinct; often with weak to distinct siphonal notch present 4
- 3b. Columella with 2–6 plications, those with 4 or fewer plications occupying half or less the aperture length; spire immersed, or low, medium, or tall; external varix distinct, weak, or absent; siphonal notch usually absent, if present, with more than 4 plications 12
- 4a. Shell with distinct to weak siphonal notch 5
- 4b. Shell completely lacking a siphonal notch, the anterior end rounded, or notch very weak and obscure 8
- 5a. Shell usually white or uniformly colored yellowish-white to yellowish-orange, rarely with several obscure pale yellow spiral bands; Australian or Neozelanic distribution 6
- 5b. Shell usually with distinct and colorful pattern of spots or dots, numerous spiral lines, mottled, or with axial streaks or lines, or various combinations; eastern Atlantic or western Indian Ocean distribution 7
- 6a. Posterior notch present, sharply defined; lip rapidly thickening posteriorly, narrowed slightly then widening again at posterior ¼; lip smooth, not denticulate; body whorl generally pyriform, strongly narrowed at anterior ¼; usually with heavy ventral callusing; spire whorls convex or shouldered, giving uneven profile; posterior end

- of lip joins body whorl well below suture above; 4th plication not distinctly remote . . . *Austroginella*
- 6b. Posterior notch weak to absent; lip thickest medially, uniformly thickened throughout; lip smooth or weakly denticulate; body whorl obovate, usually straight to convex at anterior ¼; spire whorls evenly contoured, essentially straight in profile; posterior end of lip joins body whorl at or slightly below previous suture; 4th plication often remote (i.e. farther separated than other 3) *Mesoginella*
- 7a. Shell with distinct to obscure axial costae; aperture usually broadest medially; lip strongly denticulate *Glabella*
- 7b. Shell smooth, completely lacking axial costae; aperture usually broadest anteriorly; lip smooth or denticulate *Marginella* (part)
- 8a. Lip flared at shoulder, weakly to strongly alate; shell usually strongly narrowed anteriorly 9
- 8b. Lip not notably flared or alate; shell not usually strongly narrowed anteriorly 10
- 9a. With a strongly marked posterior notch in corner of aperture; columellar plications appear excavated inside aperture due to callus deposits; weak "false 5th" plication present; lip strongly thickened, with distinct denticulation *Protoginella*
- 9b. With at most a weak, broadly rounded posterior notch in corner of aperture; columellar plications rounded, not appearing excavated inside aperture; lacking "false 5th" plication; lip moderately thickened, usually lacking denticulation, if present, usually weak *Alaginella*
- 10a. Shell either with intricate pattern of spiral and axial elements, or shell length > 15 mm *Marginella* (part)
- 10b. Shell usually white or uniformly colored; pattern, if present, consisting of only 1 to 4 narrow spiral bands; shell minute to medium in size, 1.9–12.0 mm in length. 11
- 11a. Labial denticulation always present, subequal throughout; spire low to medium height; shell broadly obconic in shape; some species with weak to distinct axial costae *Eratoidea*
- 11b. Labial denticulation sometimes absent, if present, with either a single strong posterior labial denticle, or posterior denticle distinctly stronger than others; spire medium to tall; shell usually narrowly biconic, rarely broadly biconic in shape; rarely with axial costae *Dentimargo*
- 12a. Spire immersed or nearly so 13
- 12b. Spire low to medium 20
- 13a. External varix extremely weak to absent; columella with 3 plications; shape narrowly cylindrical *Volvarina* (part)
- 13b. External varix strong, distinct, if weak to absent, then with 4 columellar plications; columella with 3–6 plications; shape various 14
- 14a. Columella with 3 plications that are crowded anteriorly; shape cylindrical to narrowly obovate 15
- 14b. Columella with 4–6 plications, that often occupy half or more the aperture length; shape broadly elliptic to obovate, rarely cylindrical to narrowly obovate 16
- 15a. Without labial denticulation; body whorl usually somewhat abruptly narrowed anteriorly *Balanetta*
- 15b. With fine labial denticulation in adult; body whorl gradually narrowed anteriorly *Hydroginella* (part)
- 16a. Columella with 4, 5, or 6 plications; if with only 4 plications, then lip completely lacking denticulation, shell uniformly colored or patterned, and shell moderately large to large *Cryptospira* (part)
- 16b. Columella with 4 plications; lip usually distinctly denticulate; if not denticulate, then shell white, and small to medium in size 17
- 17a. Columellar plications usually thin, sharp, anteriorly crowded; if not, then lacking labial denticulation; Indo-Pacific distribution 18
- 17b. Columellar plications thick, moderately heavy, not crowded anteriorly; western Atlantic distribution 19
- 18a. Labial denticulation strong, distinct; shell usually with distinct color, lip and apical spot darker, rarely grayish-white; columella with 4 thin, sharp, anteriorly crowded plications; western Indian Ocean distribution *Closia*
- 18b. Labial denticulation usually absent, rarely weakly developed; shell white, lacking coloration; columella with 4 thin to moderately heavy plications occupying less than half the aperture length, crowded anteriorly in some; Australian or Neozelanic distribution *Ovaginella*
- 19a. Shell white; unpatterned or with 2 obscure, broken spiral bands *Prunum* (part)
- 19b. Shell distinctly colored; distinctly patterned with spots or numerous spiral bands *Bullata*
- 20a. Columella with 3 plications that are crowded anteriorly; weak to strong collabral parietal callus ridge present posterior to plications, the posterior end often appearing as "false 4th" plication; lip with fine denticulation . . . *Hydroginella*
- 20b. Columella with 2–6 plications that are not crowded anteriorly; usually lacking collabral parietal callus ridge; if present, then lip not denticulate, or with 2nd collabral callus ridge inside aperture and 4 plications; lip with or without denticulation, if present, usually strong 21
- 21a. Columella with 5–6 continuous plications; shell usually solid gray, or gray with spiral lines or a distinct pattern of spiral lines interrupted by longitudinal streaks, but not white and unmarked; spire low, depressed; shell broadly elliptic, obovate, pyriform, or subtriangular; me-

- dium-sized to large, length 6.2–46.0 mm; Indo-Pacific distribution *Cryptospira* (part)
- 21b. Columella with 2–4 plications; if with more than 4 plications, then either (1) with a “false 5th” plication and shell narrow and cylindrical, (2) color pure white, opaque, with a weak siphonal notch, or (3) western Atlantic distribution; otherwise not as above 22
- 22a. Siphonal notch weak but present; Indo-Pacific, Australian, or Neozelanic distribution 23
- 22b. Siphonal notch completely absent; if weak but present, then West African distribution; widely distributed 24
- 23a. Columella with 4 plications, 4th plication often remote; shell translucent white to white, without heavy ventral callus deposits; with distinct external varix; Australian or Neozelanic distribution *Mesoginella* (part)
- 23b. Columella with 5–6 plications; shell opaque milky white with heavy ventral callus deposits; with or without external varix; Indo-Pacific distribution *Volvarina* (part-*monilis* Group)
- 24a. With “false 5th” plication present as a transverse denticle or weak parietal lira, neither extending into aperture appreciably, rarely absent; lip denticulate when fully adult; shell cylindrical or subcylindrical; distinct external varix present; shell colored and multi-banded or white; Indo-Pacific, Australian, or Neozelanic distribution *Serrata*
- 24b. With 4 columellar plications; if 5th present, then continuous, not a “false 5th” or weak parietal lira; lip smooth or denticulate; shell variously shaped; if cylindrical or subcylindrical, then lip smooth, not denticulate; distinct external varix present or absent; widespread distribution 25
- 25a. Collabral parietal callus ridge present, although often weak, plus a collabral callus ridge present inside aperture, both just posterior to 4 strong columellar plications; lip with strong denticulation; external varix present, lip moderately to strongly thickened, especially at anterior third; shape obovate to subpyriform; color translucent white or light orange; East African distribution *Serrataginella*
- 25b. Lacking collabral callus ridge inside aperture; if collabral parietal callus ridge present, then with only 3 columellar plications and lip smooth; otherwise lacking above combination of characters 26
- 26a. Columellar plications 2, 3, or 4, thin and sharp; shell very thin, translucent or hyaline, color white to amber, usually unpatterned, rarely with faint yellowish-white spiral bands; external varix absent, if present, very weak; lip smooth, completely lacking denticulation *Hyalina*
- 26b. Columellar plications 3, 4, or 5, not unusually thin and sharp; if only 3, then joined by short collabral callus ridge posteriorly; shell color various, shell often thicker, not unusually thin and translucent; external varix present or absent, if absent, columellar plications thicker; labial denticulation present or absent 27
- 27a. Shell with ventral and apical callus wash minutely granulated; with distinct external varix; lip smooth, lacking denticulation; aperture broad; freshwater, SE Asian distribution *Rivomarginella*
- 27b. Shell lacking minute granulations ventrally and apically; without above combination of characters; not freshwater, widely distributed 28
- 28a. Labial denticulation present in many species, but may be absent; color uniformly white, cream, or gray, or spotted to streaked in some, but generally not with narrow darker bands alone (bands, if present, of pale background color interrupting darker shell color); columella with 4–5 plications; heavy ventral callusing common, especially callus pad near posterior commissure of lip; if shell white and lacking labial denticulation, then unpatterned, with 4 columellar plications, and western Atlantic distribution *Prunum*
- 28b. Labial denticulation absent; color translucent white to orange or brown, usually with yellow, orange, brown, or reddish-brown narrow bands, which are darker than shell color, rarely axially streaked, not patterned with spots; columella with 3–4 plications; ventral callus deposits weak or absent *Volvarina* (part)

Subfamily MARGINELLONINAE Coan, 1965:186, 191

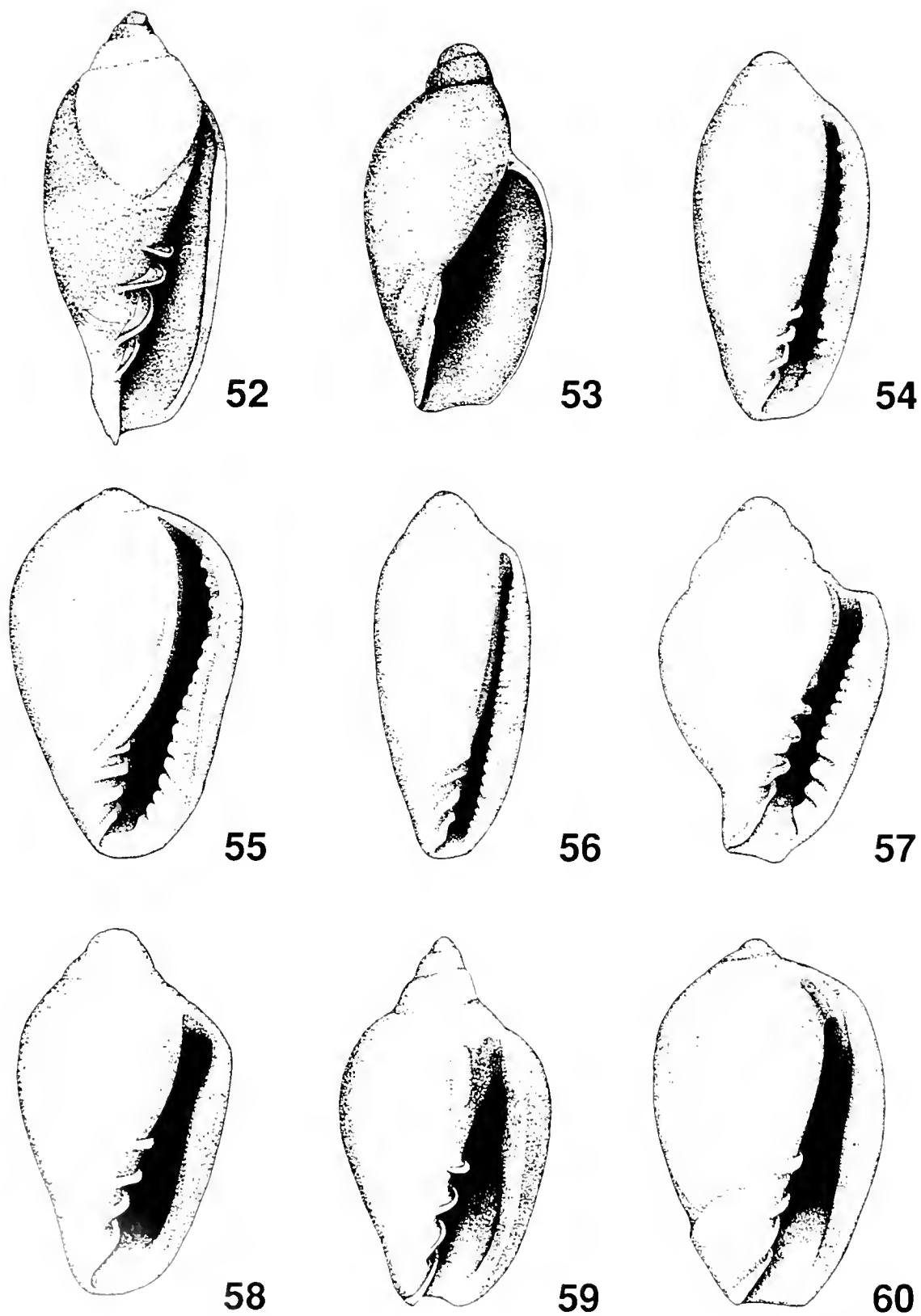
Diagnosis: Shell very large; spire medium height; protoconch large; lip narrowly thickened, smooth, lacking denticulation; external varix present; siphonal notch present; columella with 2 or 4 strong plications. Type 1 animal; tentacles relatively short; eyes reduced or absent; siphon moderately long. Type 7 radula. Marginellid buccal pouch present; valve of Leiblein present, without bypass tube; esophageal caecum absent; gland of Leiblein large, sacculate, emptying directly into posterior end of esophagus; paired salivary glands tubular, free, ducts free along floor of proboscis; single accessory salivary gland absent.

Genus *Afrivoluta* Tomlin, 1947
(figures 5, 6, 52)

Afrivoluta Tomlin, 1947:244

Type species: *A. pringlei* Tomlin, 1947; OD (M) (figure 52).

Diagnosis: Shell very large, volute-shaped; spire medium height; protoconch large; lip narrowly thickened, smooth, lacking denticulation; external varix present; broad, distinct siphonal notch present; distinct parietal callus deposit present; columella with 4 strong, nearly



Figures 52–60. Shells of type species of marginellid genera, ventral views. 52. *Afrivoluta pringlei* Tomlin, 1947. GAC M1819, Agulhas Bank, South Africa, trawled at 110 m. Length 115.4 mm. 53. *Marginellona gigas* (Martens, 1904). Holotype of *Sigaluta pratasensis* Relider, 1967, USNM 237015, W. of Pratas Reef, South China Sea, 20°37'N, 115°43'E, in 380 m, gray mud and sand bottom. After photos in Harasewych and Kantor (1991 fig. 2) and Weaver and DuPont (1970 pl. 40, fig. 11, D). Length 54.1 mm.

transverse plications, 1st plication beginning well posterior of anterior end of columella. Type 1 animal; tentacles relatively short; eyes reduced; siphon moderately long; mantle smooth, extending at least partially over external shell surface.

Description: Shell (figure 52) very large (adult length 84.7–130.9 mm). Color tawny to cinnamon or pinkish-tan. Relatively thin-shelled, surface smooth and semi-glossy with evident growth lines, often crazed or with weak to distinct bubbles or blisters in shell surface. Shape oblong, volute-shaped, broadest at about posterior third, narrowed anteriorly, very weakly shouldered. Spire of medium height, apex swollen, blunt. Aperture broad, wider anteriorly. Lip narrowly thickened inside and rolled externally, producing a distinct external varix with a sharp dorsal margin unconnected to 1st columellar plication. Lip smooth, not denticulate. Siphonal notch broad, distinct; posterior notch poorly defined. Parietal callus deposit near posterior commissure of lip large to moderately large. Columella with 4 very strong continuous plications that are nearly transverse to axis, 1st plication beginning well posterior of anterior end. Plications occupying slightly more than half the aperture length. Internal whorls unmodified.

External anatomy (figures 5, 6): 1 species studied. Type 1 animal; tentacles relatively short; eyes very reduced, red, on lateral lappets close to edge; siphon moderately long; mantle smooth, able to extend over at least anterior left half of external shell surface; foot broad, about 2 X shell width, slightly longer than shell, with posteromedial mound corresponding to parietal callus deposit of shell; animal uniformly colored yellowish-tan. (Based on published data, summarized in Coovert, 1987a and Coovert, 1987g:9; plus personal observations of photographs ex. W. R. Liltved).

Internal anatomy: Unknown.

Radula: 1 species studied. Type 7, uniserial, ribbon short, very broad, composed of 70–80 plates. Rachidian plates overlapping, very broad (1.75–1.90 mm wide), nearly flat, with numerous (70–80) sharp cusps along posterior edge. Anterior edge of rachidian plate generally straight, resulting in elongate, rectangular “comb-like” plates. Shell length: radular width ratio = 61. Radular Index = 0.8.

Distribution and Habitat: South African (1 species). Recorded from depths of 70 to 500 m. Specimens obtained by commercial bottom trawlers.

Fossil Record: Known only from the Recent.

Nomenclature, Synonymy: The type species and genus were discussed by Coovert (1987a). The holotype was figured by Tomlin (1947:244) and Bruggen (1963:fig. 1).

Remarks: This monotypic genus was discussed by Coovert (1987a, 1987e). The genus was correctly assigned to the Marginellidae by Barnard (1963). The type species has a very large, striking shell. The 4 massive columellar plications are distinctive, with the first situated well posterior of the anterior border of the columella. The very prominent posterior parietal callus deposit is characteristic.

Genus *Marginellona* Martens, 1904
(figures 28, 53, 80)

Marginella (*Marginellona*) Martens, 1904:108
Sigaluta Rehder, 1967 182–183 [TS: *S. pratensis* Rehder, 1967,
= *Marginellona gigas* Martens, 1904, OD]

Type species: *Marginella* (*M.*) *gigas* Martens, 1904; M (figure 53)

Diagnosis: Shell very large, smooth and very glossy, narrowly obovate; spire medium height with shouldered whorls; protoconch large; lip narrowly thickened, smooth, lacking denticulation; external varix apparently present; a broad, weak siphonal notch present; lacking parietal callus deposit; columella with 2 strong, very oblique plications, 1st plication bordering anterior end of columella. Type 1 animal; tentacles relatively short; eyes absent; siphon moderately long.

Description: Shell (figure 53) very large (adult length 53.9–157.0 mm). Color translucent tan, yellowish-brown, or greenish-brown, aperture darker brown. Thin-shelled, surface smooth and very glossy. Shape narrowly obovate, weakly shouldered. Spire medium height, with large bulbous protoconch and shouldered whorls, sutures callused over. Aperture very broad, wider and truncate anteriorly. Lip narrowly thickened, smooth, not denticulate, apparently with a narrow external varix. Siphonal notch very broad, weak; posterior notch poorly defined. Shell with a thin parietal callus wash but no large callus deposits. Columella with 2 strong, nearly axially oriented continuous plications occupying slightly less than half the aperture length. Internal whorls unmodified.

External anatomy: 1 species studied. Type 1 animal; tentacles relatively short; eyes absent; siphon moderately

54. *Serrata serrata* (Gaskoin, 1849). Holotype, BM(NH), Mauritius. After photograph in Kaicher (1981:#2690). Length 8.9 mm. 55. *Serrataginella spryi* (Clover, 1974). Holotype, BM(NH) 1973.83, 240 km S. of Porto Amelia, Mozambique, low tide under stones. After photos in Clover (1974:fig. 6) and Kaicher (1981:#2629). Length 9.5 mm. 56. *Hydroginella dispersa* Laseron, 1957. Holotype, AMS 103353, Murray Island, Torres Strait, north Queensland, 4–15 m. Length 5.1 mm. 57. *Protoginella lavigata* (Brazier, 1877). Syntype, Katow, New Guinea, mud bottom 13 m. After Hedley (1901, pl. 16, fig. 5). Length 6.4 mm. 58. *Alaginella ochracea* (Angas, 1871). GAC Acc. # 28–89, Little Bay, New South Wales. Length 3.5 mm. 59. *Austroginella muscaria* (Lamarck, 1822). GAC M1232, Victoria, Australia, on beach. Length 15.3 mm. 60. *Mesoginella turbinata* (G. B. Sowerby II, 1846). GAC M1655, Port Stephens, New South Wales. Length 7.2 mm.

long; mantle extension undetermined; foot broad, about 2 X shell width, slightly longer than shell (Harasewych and Kantor, 1991:10).

Internal anatomy (figure 80): 1 species studied. Same as for subfamily.

Radula (figure 28): 1 species studied. Type 7, uniserial, ribbon short, very broad, composed of 56–80 plates. Rachidian plates overlapping, very broad (1.6–2.5 mm wide), nearly flat, with numerous (58–85) sharp cusps along posterior edge. Anterior edge of rachidian plate generally straight, resulting in elongate, rectangular “comb-like” plates. Shell length: radular width ratio = 43–63. Radular Index = 0.9–1.0.

Distribution and Habitat: Indo-Pacific (1 species). Occurs from the eastern Indian Ocean off the Nicobar Islands and the South China Sea. Recorded from depths of 380 to 1,280 m.

Fossil Record: Known only from the Recent.

Nomenclature, Synonymy: The type species of *Sigaluta* is a synonym of *M. gigas*, the type species of *Marginellona*, thus synonymizing these two groups. See discussion in Harasewych and Kantor (1991). The holotype of *Sigaluta pratensis* is figured herein (figure 53) and in color in Weaver and DuPont (1970:pl. 40, figs. H, I) and Abbott and Dance (1982:220).

Remarks: Harasewych and Kantor (1991) reviewed this monotypic genus. This is the largest marginellid known. The smooth and very glossy shell, 2 very oblique columellar plications, and lack of a parietal callus deposit serve to separate the type species from *Afrivoluta pringlei*, the only marginellid species with which it is likely to be confused.

Subfamily MARGINELLINAE Fleming, 1828:328

Diagnosis: Shell minute to very large, white, uniformly colored, or patterned; lip thickened, smooth or denticulate; external varix present or absent; siphonal notch present or absent; columella with 2–6 plications. Type 2 animal; tentacles long to very long, slender; eyes at base of tentacles on slight swelling; siphon moderately to very long; mantle smooth, pustulose, or papillose, usually at least partially extending over external shell surface. Type 5, 6, modified Type 6, Type 8, or 9 radula, or non-radulate. Marginellid buccal pouch present, absent in non-radulate species; odontophoral cartilages fused anteriorly or both anteriorly and posteriorly; valve of Leiblein present or absent, if present, with bypass tube; esophageal caecum present or absent; gland of Leiblein with long, convoluted duct and a terminal bulb, emptying either into posterior end of esophagus or passing through nerve ring and emptying into anterior end of proboscis; paired salivary glands ascinous or tubular, either attached to esophagus just anterior to the valve of Leiblein, contained within proboscis, or free, ducts either embedded or attached to walls of esophagus, or free;

single accessory salivary gland present or absent, ascinous or tubular.

† Genus *Myobarum* Sohl, 1963

Myobarum Sohl, 1963:750–751

Type species: *M. laevigatum* Sohl, 1963 †; OD (M)

Diagnosis: Shell moderately large, surface smooth, glossy; spire medium to tall; sutures callused over; aperture broad; lip thickened, smooth; external varix weakly developed; weak siphonal notch present; strong, narrow posterior notch present; columella with 2 widely-spaced plications, the anterior one bordering the anterior end of the columella.

Fossil Record: Late Cretaceous (Upper Maestrichtian) of Mississippi and Georgia.

Nomenclature, Synonymy: Photographs of the holotype were figured in Sohl (1963:pl. 90, figs. 19, 20) and Sohl (1964:pl. 44, figs. 15, 16).

Remarks: Apparently monotypic. The two widely-spaced columellar plications are unusual. Although originally placed in the Volutidae, Ponder (1973:331) suggested that this genus might belong in the Marginellidae. Petuch and Sargent (1986:10) mentioned *Myobarum* as a possible ancestor to the Olividae. The general shell shape, glossy, callused surface, anterior plication bordering the anterior end of the columella, and the blunt, paucispiral protoconch all indicate a marginellid. Based on these conchological features, this genus is here included in the Marginellidae, subfamily Marginellinae. Placement to tribe must await further, extensive study of the fossil fauna.

Tribe AUSTROGINELLINI Coover and Coover, new tribe

Diagnosis: Shell minute to moderately large, white, rarely lightly colored or obscurely banded; spire immersed to tall; lip thickened, smooth or denticulate; external varix present; siphonal notch weak or absent; columella with 2–4 plications occupying more than half to less than half the aperture; some species with a “false 4th” or “false 5th” plication. Type 2 animal; siphon moderately long to very long; mantle smooth, pustulose, or papillose, extending over external shell surface. Type 5, modified Type 6, or Type 8 or 9 radula. Marginellid buccal pouch present; odontophoral cartilages fused anteriorly; valve of Leiblein present, with bypass tube; esophageal caecum absent; gland of Leiblein with a terminal bulb and a long, convoluted duct emptying into posterior end of esophagus; paired salivary glands tubular, attached to esophagus just anterior to the valve of Leiblein, ducts embedded in walls of esophagus; single tubular accessory salivary gland present or absent.

"Serrata Group"

Diagnosis: Shell small to medium, white to translucent, uniformly colored or banded in some species; spire immersed or low to medium; lip thickened, finely to coarsely denticulate, rarely smooth; external varix present; siphonal notch absent; some species with collabral parietal callus ridge; columella with 3 or 4 plications occupying less than half the aperture length, often with "false 4th" or "false 5th" plications. Type 2 animal; siphon moderately long; mantle smooth or pustulose, extending over external shell surface. Modified Type 6, or Type 8 or 9 radula. Anatomy as in tribe, single tubular accessory salivary gland present.

† Genus *Conuginella* Laseron, 1957

Conuginella Laseron, 1957:288

Type species: *Marginella inermis* Tate, 1878 †; OD (M)

Diagnosis: Shell medium size, conical, strongly but evenly narrowed anteriorly; spire low; lip narrowly thickened, denticulate, produced or angulate posteriorly; external varix present; siphonal notch absent; columella with 4 plications occupying less than half the aperture length.

Fossil Record: Miocene of Australia.

Nomenclature, Synonymy: This group was placed by Coan (1965:190) as a subgenus of *Serrata*.

Remarks: Related to *Exiginella*, a fossil group synonymized below with *Serrata*. *Conuginella* differs in having only 4 columellar plications, a distinctive conical shape, and a produced posterior corner of the lip. Shared features are the presence of an external varix, denticulate lip, and slender shell shape.

Genus *Serrata* Jousseaume, 1875
(figures 26, 54)

Serrata Jousseaume, 1875:167, 230

Haluginella Laseron, 1957:284 [TS. *Marginella mustelina* (Angas, 1871), = *Hyalina (Volvarina) mustelina* Angas, 1871; OD]

† *Exiginella* Laseron, 1957:289 [TS. *Marginella winterti* Tate, 1878 †; OD]

Type species: *Serrata serrata* (Gaskoin, 1849), = *Marginella serrata* Gaskoin, 1849; T (figure 54)

Diagnosis: Shell small to medium, white to brown, often banded, usually cylindrical; spire low to medium; lip thickened, finely to coarsely denticulate, rarely smooth; external varix present; lacking a siphonal notch; lacking parietal callus deposits and ridge; columella with 4 strong plications plus a weak "false 5th" occupying less than half the aperture length. Type 2 animal; siphon moderately long; mantle smooth or pustulose, extending over external shell surface. Modified Type 6 radula.

Description: Shell (figure 54) small to medium in size (adult length 3.6–13.0 mm). Color white to grayish-white or brown, often with prominent brown spiral bands, or rarely pale orangish-yellow bands; surface smooth, glossy. Shape cylindrical to narrowly elliptic, narrowly subpyriform in one species; weakly to strongly shouldered. Spire low to medium height, rarely very low and obscure. Aperture narrow, usually wider anteriorly. Lip weakly to strongly thickened, finely to coarsely denticulate, rarely smooth, with a weak to distinct external varix. Shell without a siphonal notch or a posterior notch. Shell with a thin parietal callus wash, lacking large callus deposits and collabral parietal callus ridge. Columella with 4 strong, continuous plications, plus a weak to strong parietal lira or "false 5th" plication, which combined occupy slightly less than half, but more than one-third, the aperture length. Internal whorls presumed unmodified.

External anatomy: 2 species studied. Type 2 animal; tentacles long, slender; siphon moderately long; mantle smooth or pustulose, covering shell symmetrically; foot slightly wider than shell, about 1½ X shell length; animal colored with cream, orange, or buff. See summary in Coovert (1987g:13, 20) as *Haluginella*.

Internal anatomy: 1 species studied. Same as for "*Serrata* Group."

Radula (figure 26): 8 species studied. Modified Type 6, uniserial, ribbon short, broad, of 13–35 plates. Rachidian plates overlapping, thin, fragile, broad (0.052–0.120 mm wide), nearly flat, with numerous (22–59) sharp cusps along sinuous posterior edge. Anterior edge of rachidian plate generally straight, resulting in elongate, rectangular "comb-like" plates. Shell length: radular width ratio = 59–117. Radular Index = 0.4–1.6.

Distribution and Habitat: Neozelanic (2 species), S. Australian (7 species), Indo-Pacific (3 species). Intertidal to 370 m.

Fossil Record: Middle Oligocene of New Zealand (*vide* Powell, 1979:217), Miocene of Australia, to Recent.

Nomenclature, Synonymy: The type of *M. serrata* is figured by Kaicher (1981:#2690) and herein (figure 54). Synonymy of *Serrata* and *Haluginella* is based on radular and conchological similarities. The radula of Australian *S. mustelina*, type species of *Haluginella*, has been studied (pers. obs. of SEMs, ex. Dean Hewish) and compared with radulae from *S. translata* (Redfield, 1870), an undoubted congener of *S. serrata*, type species of *Serrata*. These radulae and shells compare very favorably, and the generic groups they represent are herein considered synonyms. For discussion of *Haluginella*, see Coovert (1987f). *Exiginella* is synonymized based on conchological similarity to the other two groups, including a fairly strong 5th columellar plication, denticulate lip, and an external varix.

Remarks: *Haluginella* and *Serrata* had been considered distinct until we extracted radulae of *S. translata*. The

shared possession of a modified Type 6 radula, shell with a weak "false 5th" plication, lack of a collabral parietal callus ridge, and the usually denticulate lip are diagnostic. Coan (1965:190) considered *Haloginella* a subgenus of *Volvarina* and was subsequently followed by others. Anatomical features described by Ponder (1970) clearly place this group, along with *Mesoginella* and *Austroginella*, in a separate tribe, based especially on the presence of a valve of Leiblein, the absence of an esophageal caecum, and the emptying of the duct from the gland of Leiblein into the esophagus posterior to the nerve ring.

Genus *Serrataginella* Coover and Coover, new genus (figures 29, 55)

Type species: "*Marginella*" *spryi* Clover, 1974; OD (M), herein (figure 55)

Diagnosis: Shell medium-sized, translucent white to light orange, unbanded, broadly obovate to subpyriform; spire low; lip strongly thickened, coarsely denticulate; external varix present; lacking a siphonal notch; with collabral parietal callus ridge plus parallel callus ridge inside aperture; columella with 4 strong plications occupying about one-third the aperture length, lacking "false 5th" plication. Type 8 radula.

Description: Shell (figure 55) medium in size (adult length 8.0–9.9 mm). Color translucent white to light orange; surface smooth, glossy. Shape broadly obovate to subpyriform, moderately strongly shouldered. Spire low. Aperture narrow, usually wider anteriorly, narrowest medially due to incurving of lip. Lip moderately to strongly thickened, especially anterior third, coarsely denticulate in adults, denticulation absent in subadults, first developing anteriorly, with a strong external varix. Siphonal notch absent; posterior notch absent. Shell with a weak but distinct collabral parietal callus ridge just outside aperture, plus weak to distinct collabral callus ridge well within aperture, both most distinct just posterior to plications. Columella with 4 strong, continuous plications, lacking parietal lira or "false 5th" plication. Plications occupying about 1/3 aperture length. Internal whorls presumed unmodified.

External anatomy: 1 species studied. Animal reported to be light orange in color (Clover, 1974:215).

Internal anatomy: Unknown.

Radula (figure 29): 1 species studied. Type 8, uniserial, ribbon short, broad, of 38 plates. Rachidian plates overlapping, broad (0.191 mm wide), nearly flat, with 9–10 sharp cusps along posterior edge. The entire posterior edge, including all of the edges of the main cusps, with numerous (total of ca. 70) small, subordinate cusps, giving the main cusps a serrated appearance. Anterior edge of rachidian plate slightly indented medially, resulting in a very shallowly V-shaped plate. Shell length: radular width ratio = 42. Radular Index = 40.

Distribution and Habitat: Indo-Pacific (1 species). Recorded from E. African coast. Intertidal to 30 m.

Fossil Record: Known only from the Recent.

Nomenclature, Synonymy: A photograph of the holotype of the type species was figured by Clover (1974:pl. 8, fig. 6) and Kaicher (1981:#2629). Name derived from *Serrata*, valid marginellid genus to which this new genus is believed to be allied, and *L. serrata*, toothed like a saw, serrated, in reference to the serrated cusps of the radula, combined with *-ginella*, adopted from *Marginella*. Gender feminine.

Remarks: This monotypic genus is characterized by the very distinctive radula, possession of a collabral callus ridge on the parietal area as well as inside the aperture, plus the 4 strong columellar plications and strong labial denticulation. Placement is based on conchological similarities to *Serrata* and *Hydroginella*. See Coomans (1975) for further information. See Key for further differentiation.

† Genus *Stromboginella* Laseron, 1957

Stromboginella Laseron, 1957:289

Type species: *Marginella crassidens* Chapman and Crespin, 1928 †; OD (M)

Diagnosis: Shell medium size, broadly biconic, strongly narrowed and acute anteriorly; spire medium height; aperture very narrow; lip thickened, denticulate; external varix present; siphonal notch absent; columella with 4 plications crowded anteriorly.

Fossil Record: Pleistocene of Australia.

Nomenclature, Synonymy: Coan (1965:189) placed this group as a subgenus of *Marginella*, but the anteriorly crowded plications indicate little relationship.

Remarks: The broadly biconic shell shape strongly narrowing anteriorly and the very narrow aperture are apparently unique features of this monotypic genus. The denticulate lip and general shape indicate placement in *Austroginellini*, "*Serrata* Group," whereas the 4 anteriorly crowded plications indicate close relationship to *Hydroginella*.

Genus *Hydroginella* Laseron, 1957 (figures 30, 56)

Hydroginella Laseron, 1957:284

Neptoginella Laseron, 1957:283 [TS. *N. fascicula* Laseron, 1957; OD]

Pillarginella Gabriel, 1962:197 [TS. *Marginella columnaria* Hedley & May, 1908; OD (M)]

Type species: *H. dispersa* Laseron, 1957; OD (M) (figure 56)

Diagnosis: Shell small to medium, white to orangish-brown or amber, hyaline or translucent, rarely banded,

usually cylindrical, obovate, or subpyriform; spire immersed or low to medium; lip thickened, usually finely denticulate, rarely smooth; external varix present; lacking a siphonal notch, collabral parietal callus ridge usually present; columella with 3 plications plus a weak "false 4th" occupying less than $\frac{1}{4}$ the aperture length. Type 2 animal; siphon moderately long; mantle extension undetermined. Type 9 radula.

Description: Shell (figure 56) small to medium (adult length 3.0–10.3 mm). Color white to orangish-brown to amber, hyaline or translucent, one species with 3 broad pale orange spiral bands; surface smooth, glossy. Shape narrowly to broadly cylindrical or obovate to subpyriform, usually strongly narrowed anteriorly; weakly to strongly shouldered. Spire immersed or low to medium height. Aperture usually narrow throughout, some species moderately broad, often wider anteriorly or narrowest medially due to incurved lip. Lip moderately to strongly thickened, thickest medially or at anterior third, usually finely denticulate in adults, denticulation often weak or absent medially, rarely completely absent, with weak to strong external varix. Siphonal notch absent; posterior notch absent. Shell with weak to strong collabral parietal callus ridge beginning just posterior to plications, appearing at that point as "false 4th" plication, ridge rarely absent. Columella with 3 continuous plications crowded anteriorly, occupying $\frac{1}{4}$ or less of aperture length. Internal whorls unmodified.

External anatomy: 2 species studied. Type 2 animal; tentacles long, slender; siphon moderately long; mantle extension undetermined; foot about as wide as shell, slightly longer, some species with opaque white spots. See Bouchet (1989:79, fig. 2).

Internal anatomy: Unknown.

Radula (figure 30): 4 species studied. Type 9, uniserial, ribbon very short, narrow, greatly reduced, of 10–30 plates. Rachidian plates weak, overlapping, narrow (0.019–0.032 mm wide), nearly flat, with few (4–7) cusps along posterior edge. Anterior edge of rachidian plate straight, resulting in subquadrate plates. Shell length: radular width ratio = 230–391. Radular Index = 2.3–7.5.

Distribution and Habitat: S. Australian (4 species), Indo-Pacific (13 species). Intertidal to 550 m.

Fossil Record: Known only from the Recent.

Nomenclature, Synonymy: Bouchet (1989) discussed *Hydroginella* and *Neptoginella* and figured the holotypes of both type species (note that his captions of figs. d and e were reversed). Although conchological similarities were discussed, these genera were not synonymized. These groups, plus *Pillarginella*, are here considered congeneric based on distinctive conchological features, especially the presence of a collabral parietal callus ridge and only 3 columellar plications. The very distinctive radula is known from four species (Bouchet, 1989:fig. 3;

Hewish, 1990:fig. 2A), including *H. columnaria* (pers. obs. of SEMs, ex. Dean Hewish), the type species of *Pillarginella*. The principle of first reviser (ICZN Art. 24) is employed in choosing *Hydroginella* over *Neptoginella*. These 3 groups form a very distinctive assemblage of species.

Remarks: Bouchet (1989) reported on the parasitism of sleeping fish by *H. caledonica* (Jousseaume, 1877). The very unusual, highly reduced radula, characteristic of this group, suggests a similar behavior in the other species.

"*Austroginella* Group"

Diagnosis: Shell minute to moderately large, white, rarely lightly colored or obscurely banded; spire immersed to tall; lip thickened, smooth or denticulate; external varix present; siphonal notch weak or absent; columella with 2–4 plications occupying more than half to less than half the aperture, some species with a "false 5th" plication. Type 2 animal; siphon long to very long; mantle smooth, weakly pustulose, or papillose, extending over external shell surface. Type 5 radula. Anatomy as in tribe, single accessory salivary gland absent.

† Genus *Mioginella* Laseron, 1957

Mioginella Laseron, 1957:287

Type species: *Marginella regula* Cotton, 1949 †; OD (M)

Diagnosis: Shell medium size, broadly biconic, narrowed anteriorly; spire tall; shoulders angulate or carinate; lip thickened, denticulate; external varix present; weak siphonal notch present; broad posterior notch present; columella with 4 plications, plus a weak 5th, occupying more than half the aperture.

Fossil Record: Eocene of Australia.

Nomenclature, Synonymy: This genus was placed as a subgenus of *Marginella* by Coan (1965:189). The fifth plication is not present in *Marginella* s. str. and the resemblance is superficial.

Remarks: We consider this apparently monotypic genus to be ancestral to *Protoginella* based on the presence of a weak 5th columellar plication, tall spire, and weak posterior notch. Laseron (1957:287) considered this genus to be ancestral to *Carinaginella* based on the carinate shoulders. *Carinaginella* is synonymized here with *Alaginella* because we regard carinate shoulders to be convergent and not expressing a close relationship to members of *Alaginella*, which also has 4 columellar plications. Cotton (1949:218) stated that *M. regula* was related to *M. muscaroides* Tate, 1878, a species we consider to be clearly in *Austroginella* based on the distinctively shaped lip and presence of a strong siphonal notch, and thus not closely related to *Mioginella*.

Genus *Protoginella* Laseron, 1957
(figure 57)

Protoginella Laseron, 1957:285

Type species: *Marginella lavigata* Brazier, 1877, = *Marginella (Prunum) lavigata* Brazier, 1877; OD (figure 57)

Diagnosis: Shell small to medium, white, biconic or subpyriform, strongly narrowed anteriorly; spire medium height; aperture narrow; lip strongly thickened, strongly denticulate, alate posteriorly; external varix present; posterior notch present; siphonal notch absent; columella with 4 strong plications that are excavated inside aperture, plus a "false 5th"; plications occupying more than half the aperture.

Description: Shell (figure 57) small to medium in size (adult length 4.4–7.0 mm). Color white; surface smooth, glossy. Shape biconic, subpyriform, strongly narrowed anteriorly, weakly to strongly shouldered. Spire medium height. Aperture narrow throughout. Lip strongly thickened, posterior corner strongly alate, strongly denticulate, with distinct external varix. Shell without siphonal notch, but anterior end somewhat truncate; posterior notch present at posterior corner of lip. Extent of ventral callusing undetermined. Columella with 4 strong continuous plications excavated inside aperture, plus weak "false 5th" plication or parietal lira; plications occupying 4/5 aperture length. Internal whorls presumed unmodified.

External anatomy: Unknown.

Internal anatomy: Unknown.

Radula: 1 species studied. Type 5, uniserial, ribbon short, broad. Rachidian plates barely overlapping, moderately broad (0.028 mm wide), weakly arched, with 14–15 strong cusps on posterior edge. Central cusp strongest. Anterior edge of rachidian plate moderately concave, resulting in rectangular to chevron-shaped plates. Shell length: radular width ratio = 160.

Distribution and Habitat: Indo-Pacific (2 species). Recorded from 13 to 97 m.

Fossil Record: Eocene and Pliocene of Australia, to Recent.

Nomenclature, Synonymy: A syntype of the type species is figured by Kaicher (1981:#2644) and herein (figure 57). Hedley (1901:123) emended the name to *M. laevigata*, an unjustified emendation. No evidence in the original publication itself exists of "clear evidence of an inadvertent error," and incorrect transliteration is not to be considered an inadvertent error [ICZN Art. 32(e)(ii)]. Thus, there is no homonymy with *Marginella laevigata* Eichwald, 1830. The syntype of *M. baudinensis* Smith, 1899, a synonym, was figured by Kaicher (1981:#2622). Some authors have synonymized *M. valida* Watson, 1886, which is an *Alaginella* and very distinct from *P. lavigata*.

Remarks: Laseron's original concept included *M. geminata* Hedley, 1912. This was based on the presence of a denticulate lip, a character variable in *Alaginella*, in which this species is now placed. This restricted concept of *Protoginella* is based on a strong posterior notch, columellar plications appearing excavated due to callus deposits, presence of a weak "false 5th" plication, and a strongly thickened, denticulate lip.

† Genus *Nudifaba* Eames, 1952

Marginella, subg. *Nudifaba* Eames, 1952:122

Type species: *Marginella (N.) rakhiensis* Eames, 1952 †; OD (M)

Diagnosis: Shell minute, broadly obconic; spire flat; aperture narrow; lip strongly thickened, produced on posterior corner, smooth, lacking denticulation; strong external varix present; strong posterior parietal callus deposit present near posterior commissure of lip, forming weak posterior notch; siphonal notch absent; columella with 4 strong plications occupying slightly more than half the aperture.

Fossil Record: Eocene of Pakistan.

Nomenclature, Synonymy: Currently considered a monotypic genus.

Remarks: The 4 columellar plications, smooth, strongly thickened lip that is produced or alate on the posterior corner, presence of an external varix, and absence of a siphonal notch all indicate placement in the Austroginellini and an ancestral relationship to *Alaginella*. Due to the early occurrence of this group in the Eocene of Pakistan, and the presence of a strong posterior parietal callus deposit, we consider this a separate, valid genus.

Genus *Alaginella* Laseron, 1957
(figure 58)

Alaginella Laseron, 1957:286

Carinaginella Laseron, 1957:286 [TS: *Marginella carinata* E. A. Smith, 1891; OD (M)]

† *Cassoginella* Laseron, 1957:287 [TS: *Marginella palla* Cotton, 1949 †; OD (M)]

Triginella Laseron, 1957:280–281 [TS: *Marginella malina* Hedley, 1915; OD (M)]

Type species: *Marginella ochracea* Angas, 1871; OD (figure 58)

Diagnosis: Shell minute to medium, white, biconic, obovate, or subpyriform, usually strongly narrowed anteriorly; spire low to medium height; aperture narrow to moderately narrow; lip moderately thickened, denticulate to smooth, alate posteriorly; external varix present; posterior notch weak or absent; siphonal notch absent; columella with 4 strong unexcavated plications occupying slightly more than half the aperture, lacking "false 5th" plication. Type 2 animal; siphon long; mantle papillose, extending over external shell surface.

Description: Shell (figure 58) minute to medium in size (adult length 1.7–13.0 mm). Color white; surface smooth, glossy. Shape biconic, obovate to subpyriform, usually strongly narrowed anteriorly; weakly to strongly shouldered, rarely strongly carinate. Spire usually medium height, rarely very low to low. Aperture narrow to moderately narrow, rarely broad, narrowest medially in some species. Lip moderately thickened, thickest medially to posteromedially, posterior corner strongly alate, denticulate to smooth, with a distinct external varix. Shell without siphonal notch, posterior notch weak, poorly defined to absent. Shell without obvious ventral callusing. Columella with 4 strong continuous plications occupying slightly more than half the aperture length. Internal whorls unmodified.

External anatomy: 2 species studied. Type 2 animal; tentacles long, slender; siphon long; mantle covering most or all of external shell surface, papillose with conspicuous, branched papillae; foot nearly as wide as shell, twice as long; animal white, dotted with brown. [Based on description of *A. geminata* (Hedley, 1912) in Cotton (1944: 16) (as *weedingi* Cotton, 1944) plus description of *A. ochracea* (Angas, 1871), ex. unpublished mss., ex. R. Burn and D. R. Hewish].

Internal anatomy: Unknown.

Radula: 9 species studied. Type 5, uniserial, ribbon short, broad, of 20–55 plates. Rachidian plates usually overlapping, moderately broad (0.019–0.040 mm wide), weakly arched, with 11–20 strong cusps on posterior edge. The central cusp usually strongest. Anterior edge of rachidian plate slightly to strongly concave, resulting in rectangular to chevron-shaped plates. Shell length: radular width ratio = 86–174. Radular Index = 1.5–4.4.

Distribution and Habitat: S. Australian (8 species), Indo-Pacific (8 species), South African (9 species). Intertidal to 1,650 m.

Fossil Record: Miocene and Pliocene of Australia, to Recent.

Nomenclature, Synonymy: The types of *M. ochracea*, type species of *Alaginella*, and *M. carinata*, type species of *Carinaginella*, were figured by Kaicher (1981: #2618, #2682). The radulae of these two species, plus *M. malina*, type species of *Triginella*, have been studied (pers. obs. of SEMs, ex. Dean Hewish), and all three species are here considered to be congeneric. Conchological differences are considered to be of specific value only, including the carinate shoulders of *A. carinata*. *M. palla*, the type species of *Cassoginella*, has an axially costate shell. As in other austroginelline genera, this is considered to be of specific value only. The alate posterior end of lip and lack of a siphonal notch place this species in *Alaginella*. The principle of first reviser (ICZN Art. 24) is herein employed in choosing *Alaginella* over the other, more restricted names.

Remarks: The alate, flared shoulder of the aperture and

the anteriorly strongly narrowed shell, combined with the lack of a strong posterior notch and lack of a “false 5th” columellar plication will serve to distinguish this group. The presence or absence of labial denticulation and axial costae are considered to be of specific difference only. The branched mantle papillae may ultimately prove to be a diagnostic character of this genus. The report on the radula in the original description of *Triginella malinoides* Gabriel, 1962, fig. 4 is apparently erroneous. We have examined SEMs of a radula (ex. Dean Hewish) from a shell intermediate between *A. malina* (Hedley, 1915) and *T. malinoides* and it is a typical *Alaginella* radula. In fact, we consider these two species synonymous. The radula figured by Gabriel is clearly not a marginellid radula and is obviously in error.

† Genus *Hiwia* Marwick, 1931

Marginella, subg. *Hiwia* Marwick, 1931:129

Type species: *Marginella (Hiwia) amplificata* Marwick, 1931 †; OD (M)

Diagnosis: Shell small, broadly biconic, strongly narrowed anteriorly; spire medium height; strong axial costae present; shoulders angulate to carinate; aperture narrow; lip thickened, smooth, not denticulate; posterior corner of lip sharply angulate; external varix present; siphonal notch absent; columella with 4 plications occupying more than half the aperture.

Fossil Record: Eocene of Australia, to Oligocene of New Zealand.

Nomenclature, Synonymy: This group was considered to be a valid genus by Coan (1965:189).

Remarks: The two included species (type species and *M. aldingae* Tate, 1878) appear to be closely related, but otherwise form a distinct, valid genus, apparently extinct since the Oligocene. A relationship to the “*Austroginella* Group” and especially *Austroginella* is indicated by the 4 columellar plications occupying more than half the aperture, but this group lacks a siphonal notch and has a narrow aperture.

Genus *Austroginella* Laseron, 1957
(figures 25, 59, 80)

Austroginella Laseron, 1957:285

Plicaginella Laseron, 1957:285 [TS. *Marginella formicula* Lamarck, 1822; OD]

Type species: *Marginella muscaria* Lamarck, 1822; OD (figure 59)

Diagnosis: Shell medium to moderately large, white, yellowish-white, or pale yellowish-orange, biconic, obovate, or subpyriform, usually strongly narrowed anteriorly; spire low to medium height with shouldered whorls; aperture broad; lip smooth, rapidly thickening posteriorly with sharply defined posterior notch; external varix

present; siphonal notch present; heavy ventral callusing usually present; columella with 4 strong plications occupying more than half the aperture. Type 2 animal; siphon long to very long; mantle smooth or weakly pustulose, extending over external shell surface.

Description: Shell (figure 59) medium to moderately large (adult length 6.2–16.3 mm). Color white, yellowish-white, or pale yellowish-orange; surface smooth, glossy, some species with weak to distinct axial costae. Shape biconic, narrowly to broadly obovate, or subpyriform, usually strongly narrowed anteriorly; weakly to strongly shouldered. Spire low to medium height; spire whorls convex or shouldered, giving uneven profile. Aperture broad, especially anteriorly. Lip moderately to strongly thickened, narrow anteriorly, rapidly thickening posteriorly but slightly narrowed at posterior fourth, smooth, lacking labial denticulation, with distinct external varix. Shell with distinct siphonal notch, and strong, grooved posterior notch at the junction of body whorl and posterior commissure of lip. Shell usually with heavy ventral callusing. Columella with 4 strong continuous plications occupying slightly more than half the aperture length. Internal whorls unmodified.

External anatomy: 4 species studied. Type 2 animal; tentacles long, slender; siphon long to very long; mantle smooth or weakly pustulose, covering most or all of external shell surface; foot very broad, 2–3 X as wide as shell, about 2 X as long; animal spotted or blotched with white, dark brown, orange, yellow, red, or green. See summary in Ponder and Taylor (1992).

Internal anatomy (figure 80): 2 species studied. Same as for "*Austroginella* Group."

Radula (figure 25): 5 species studied. Type 5, uniserial, ribbon short, broad, of 29–61 plates. Rachidian plates overlapping, moderately broad (0.029–0.114 mm wide), weakly arched, with 13–20 strong cusps on posterior edge. Central cusp strongest. Anterior edge of rachidian plate slightly to moderately concave, resulting in chevron-shaped plates. Shell length: radular width ratio = 118–162. Radular Index = 1.7–3.5.

Distribution and Habitat: S. Australian (6 species). Intertidal to 27 m.

Fossil Record: Miocene to Pleistocene of Australia, to Recent.

Nomenclature, Synonymy: The nomenclature of these two genus-group names and their type species were discussed in Coover (1988b), in which the presence of axial costae are considered to be of specific value only.

Remarks: This well-characterized group is distinguished by the presence of 4 strong columellar plications occupying more than half the aperture, combined with the presence of a siphonal and a posterior notch, along with the distinctive lip shape. For an account of predatory shell drilling and anatomy, see Ponder and Taylor (1992).

Genus *Mesoginella* Laseron, 1957
(figure 60)

Mesoginella Laseron, 1957:282

Deviginella Laseron, 1957:283–284 [TS: *Marginella brachia* Watson, 1886, = *Marginella (Glabella) brachia* Watson, 1886; OD]

† *Hianoginella* Laseron, 1957:288 [TS: *Marginella physa* Cotton, 1949 †; OD (M)]

Sinuginella Laseron, 1957:282 [TS: *Marginella inconspicua* G. B. Sowerby II, 1846; OD]

Spiroginella Laseron, 1957:283 [TS: *Marginella leia* Cotton, 1944, = *M. turbinata* G. B. Sowerby II, 1846; OD (M)]

† *Urniginella* Laseron, 1957:287 [TS: *Marginella cassidiformis* Tate, 1878 †; OD (M)]

Type species: *Marginella turbinata* G. B. Sowerby II, 1846; OD (M) (figure 60)

Diagnosis: Shell small to medium, white or yellowish-white, rarely brownish-orange or with pale bands, biconic, obconic, obovate, or broadly cylindrical, not strongly narrowed anteriorly; spire low to medium height with evenly contoured whorls; aperture moderately narrow; lip smooth to denticulate, moderately to strongly thickened, thickest medially; external varix present; weak siphonal notch usually present; posterior notch weak to absent; ventral callusing usually absent; columella with 4 strong plications occupying slightly less to slightly more than half the aperture, 4th plication often remote. Type 2 animal; siphon long; mantle smooth or weakly pustulose, extending over external shell surface.

Description: Shell (figure 60) small to medium in size (adult length 2.5–11.0 mm). Color usually white to yellowish-white, semi-opaque to translucent, rarely brownish-orange or with pale yellow bands; surface smooth, glossy, some species with weak to distinct axial costae. Shape narrowly to broadly obovate, obconic, biconic, or broadly cylindrical, not strongly narrowed anteriorly; weakly to strongly shouldered. Spire low to medium height with evenly contoured whorls. Aperture moderately narrow, usually wider anteriorly. Lip moderately to strongly thickened, thickest medially, usually smooth, some species with weak to moderately strong labial denticulation, with distinct external varix. Siphonal notch nearly absent to weak, rarely strong, distinct or completely absent. Posterior notch weak, poorly defined or absent. Shell usually without evident ventral callusing. Columella with 4 strong continuous plications, 4th often remote, rarely with parietal tubercle appearing as "false 5th" plication. Plications occupying slightly less to slightly more than half the aperture length. Internal whorls unmodified.

External anatomy: 5 species studied. Type 2 animal, tentacles long, slender; siphon long; mantle smooth or weakly pustulose, asymmetrically extending over external shell surface; foot narrow to broad, slightly narrower to 1½ X as wide as shell, about 1½ X as long; animal variously spotted, blotched, or with lines of various colors,

including white, yellow, orange, brown, and black. See summary in Covert (1987g).

Internal anatomy: 1 species studied. Same as for "*Austroginella* Group."

Radula: 16 species studied. Type 5, uniserial, ribbon short, broad, of 19–75 plates. Rachidian plates usually overlapping, moderately broad (0.018–0.050 mm wide), weakly arched, with 9–22 strong cusps along posterior edge. The central cusp (or two subcentrals) is the strongest. Anterior edge of rachidian plate slightly to strongly concave, resulting in rectangular to chevron-shaped plates. Shell length: radular width ratio = 101–221. Radular Index = 1.5–7.1.

Distribution and Habitat: Neozelanic (13 species), S. Australian (13 species), Indo-Pacific (7 species). Intertidal to 640 m.

Fossil Record: Miocene, Pliocene, and Pleistocene of Australia, to Recent.

Nomenclature, Synonymy: The nomenclature of *Mesoginella* and *Sinuginella* and their type species were discussed by Covert (1988b). The type of *M. inconspicua* was figured by Kaicher (1981:#2702). *M. brachia*, type species of *Deviginella*, falls well within the limits of *Mesoginella*. The principle of first reviser (ICZN Art. 24) is here employed in choosing the better known *Mesoginella* over *Deviginella*. The holotype of *M. leia* was figured in Hewish and Gowlett-Holmes (1991:64, figs. E-F) and synonymized with *M. turbinata*, thus placing *Spiroginella* in synonymy. The two fossil genera *Hianoginella* and *Urniginella* are here synonymized, based on conchological characters falling within the limits of *Mesoginella*. Laseron (1957:284) used several *nomina nuda* that are apparently manuscript names for genera synonymized here. These should not be further considered.

Remarks: The presence or absence of axial costae are not considered to be a genus-level character in this group. The 4th columellar plication is often remote, i.e. separated farther from the other 3 plications. This is a rather diverse genus but all species possess the same type of radula and conchological characters.

Genus *Closia* Gray, 1857
(figure 61)

Closia Gray, 1857:36

Type species: *Closia sarda* (Kiener, 1834), = *Marginella sarda* Kiener, 1834; M (figure 61)

Diagnosis: Shell medium to moderately large, white or colored, obovate; spire immersed; lip thickened, denticulate; external varix present; siphonal notch and posterior notch absent; columella with 4 thin, sharp plications crowded anteriorly.

Description: Shell (figure 61) medium to moderately

large (adult length 9.9–48.0 mm). Color grayish-white, without other markings; pale rose, pink, or orangish-yellow, with lip and apical spot darker brownish-rose or yellowish-orange; or pale yellowish- to light orange with paler mid-body band and lip darker with tiny white specks. Shell surface smooth, glossy. Shape obovate, weakly to strongly narrowed anteriorly, with rounded to angulate shoulders. Spire immersed. Aperture moderately narrow, wider anteriorly. Lip moderately to strongly thickened, strongly to very strongly denticulate in adults, with a distinct external varix. Shell without siphonal notch or posterior notch. Shell usually with evident ventral callus deposits anteriorly and especially posteriorly. Some with heavy parietal callus wash abruptly ending at entrance to aperture, creating appearance of collabral parietal callus ridge. Columella with 4 thin, sharp, continuous plications, crowded anteriorly, occupying slightly less than $\frac{1}{3}$ to $\frac{1}{4}$ aperture length. Internal whorls presumed unmodified.

External anatomy: 1 species studied. Animal white, semi-transparent. [From description of *C. limpida* Bozzetti, 1992:11, = *C. majuscula* (Martens, 1880)]. Presumed Type 2 animal.

Internal anatomy: Unknown.

Radula: Unknown.

Distribution and Habitat: Indo-Pacific (3 species), restricted to western Indian Ocean. Recorded from 20 to 140 m.

Fossil Record: Known only from the Recent.

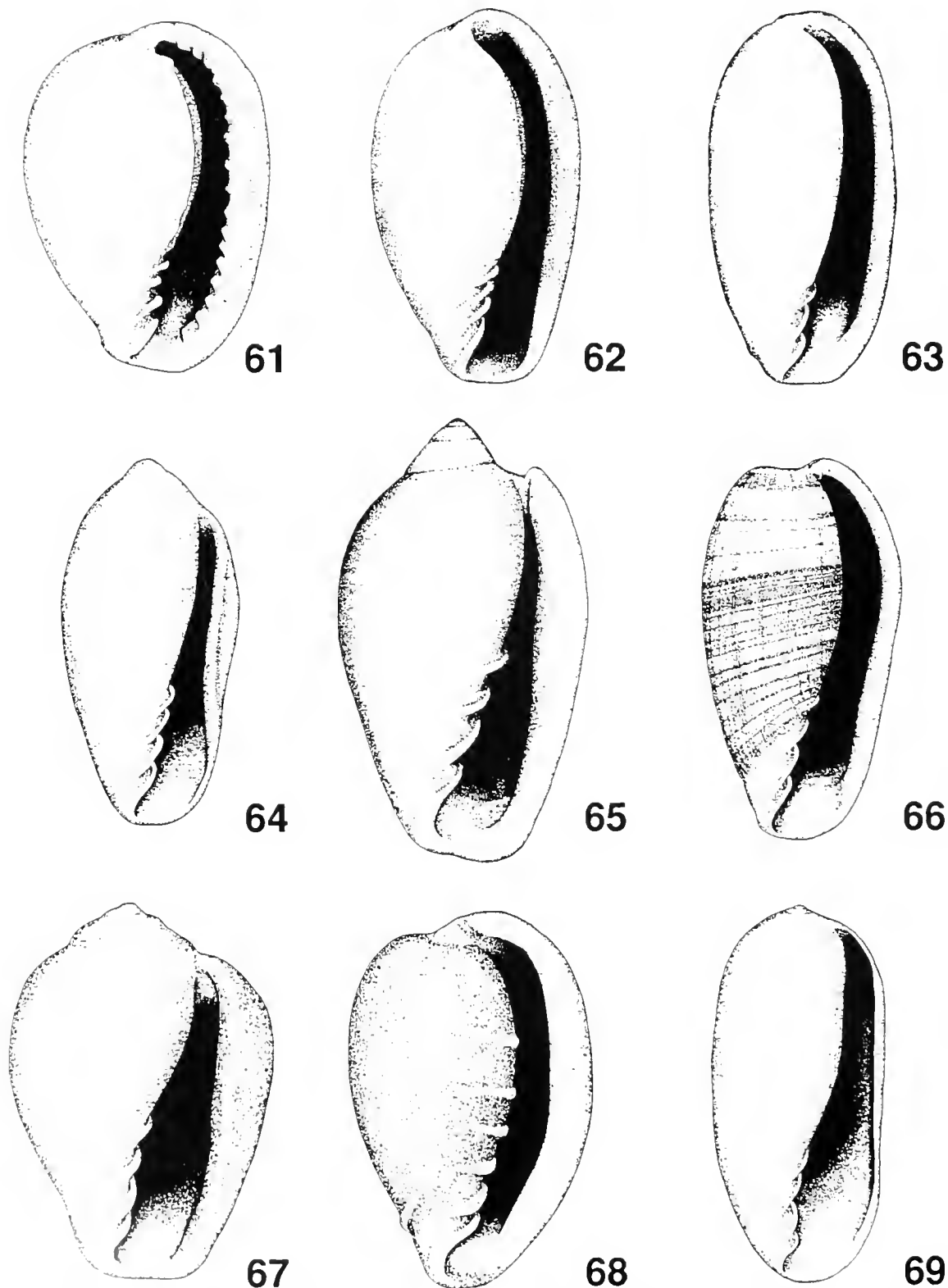
Nomenclature, Synonymy: Coan (1965:189), followed by others, considered this group to be a subgenus of *Bullata*, apparently based on the similarity to *B. lilacina* (G. B. Sowerby II, 1846). *Bullata*, which is included in Prunini based on its radula, anatomy, and fossil ancestry, has a tendency toward heavy ventral callusing and stronger columellar plications that are not nearly as crowded anteriorly as in *Closia*. Although the radula and animal are unknown, we feel that *Closia* is not closely related to *Bullata* and has a different ancestry.

Remarks: *Closia* has been variously associated with *Bullata* and *Ovaginella*. Conchologically, it comes closest to *Ovaginella*, with which it shares shell shape, and thin, sharp, anteriorly crowded columellar plications. The coarser labial denticulation, distinct shell pigmentation, heavier posteroventral callus deposit, and Indian Ocean distribution serve to distinguish it. Until the radula and animal are known, these two groups are provisionally considered distinct.

Genus *Ovaginella* Laseron, 1957
(figure 62)

Ovaginella Laseron, 1957:280

Type species: *Marginella ovulum* G. B. Sowerby II, 1846; OD (figure 62)



Figures 61–69. Shells of type species of marginellid genera, ventral views. **61.** *Closia sarda* (Kiener, 1834). GAC M1341, off Ambanja, N.E. Madagascar, dredged. Length 17.6 mm. **62.** *Ovaginella ovulum* (C. B. Sowerby II, 1846). Type, BM(NH) 80.9.8.5, locality unknown. After photograph in Kästner (1981:#2647). Length ca. 9 mm. **63.** *Balanetta baylei* Jousseaume, 1875. GAC M1607, Margaret River, Western Australia, on beach. Length 10.5 mm. **64.** *Volvarina mitrella* (Risso, 1826). GAC M2533, Salina Bay, Malta, dredged on sandy bottom at 6 m. Length 9.3 mm. **65.** *Prunum prunum* (Gmelin, 1791). GAC M1393, Venezuela. Length 26.9 mm. **66.** *Bullata bullata* (Born, 1778). GAC M1787, Praia de Forte Gragoata, Niterói, Rio de Janeiro, Brazil. Length

Diagnosis: Shell small to medium, white, elliptic to obovate; spire immersed; lip thickened, usually smooth, rarely denticulate; external varix present; siphonal notch and posterior notch absent; columella with 4 anteriorly crowded plications.

Description: Shell (figure 62) small to medium in size (adult length 4.2–10.1 mm). Color translucent to semi-opaque white; surface smooth, glossy. Shape narrowly to broadly elliptic to obovate, weakly to strongly shouldered. Spire immersed. Aperture moderately narrow, slightly wider anteriorly. Lip moderately thickened, usually smooth, rarely weakly denticulate, with distinct external varix. Siphonal notch weak or absent; posterior notch absent. Shell usually without evident ventral callusing. Columella with 4 continuous plications crowded anteriorly, occupying distinctly less than half aperture length. Internal whorls unmodified.

External anatomy: Unknown.

Internal anatomy: Unknown.

Radula: 2 species studied. Type 5, uniserial, ribbon short, broad, of 20–31 plates. Rachidian plates overlapping, moderately broad (0.025–0.035 mm wide), weakly arched, with 8–14 strong cusps along posterior edge. The central cusp is the strongest. Anterior edge of rachidian plate slightly concave, resulting in rectangular to chevron-shaped plates. Shell length: radular width ratio = 170–285. Radular Index = 1.8–3.5.

Distribution and Habitat: Neozelanic (2 species), S. Australian (2 species). Recorded from 3 to 370 m.

Fossil Record: Known only from the Recent.

Nomenclature, Synonymy: The type species of *Ovaginella*, *M. ovulum*, is figured by Kaicher (1981:#2674) and herein (figure 62). Coan (1965:189) placed *Ovaginella* as a subgenus of *Balanetta*, but the latter has only 3 columellar plications and a narrower shape.

Remarks: Although *Balanetta* and *Ovaginella* both have a Type 5 radula, they are considered distinct based on conchological differences.

Genus *Balanetta* Jousseaume, 1875
(figure 63)

Balanetta Jousseaume, 1875 168, 269

Type species: *B. baylei* Jousseaume, 1875; M (figure 63)

Diagnosis: Shell minute to medium, white, cylindrical to narrowly obovate; spire immersed; lip thickened, smooth; external varix present; with weak or absent siphonal notch; posterior notch absent; columella with 2 or 3 plications crowded anteriorly.

Description: Shell (figure 63) minute to medium in size (adult length 1.5–12.0 mm). Color translucent to opaque white or yellowish-white; surface smooth, glossy. Shape cylindrical to narrowly obovate, weakly to strongly shouldered. Spire immersed. Aperture moderately narrow, distinctly wider anteriorly. Lip moderately thickened, smooth, not denticulate, with a distinct external varix. Siphonal notch weak or absent, posterior notch absent. Shell without evident ventral callusing. Columella with 3 continuous plications (one species with 2), crowded anteriorly, occupying less than ¼ aperture length. Internal whorls presumed unmodified.

External anatomy: Unknown.

Internal anatomy: Unknown.

Radula: 1 species studied. Type 5, uniserial, ribbon relatively short, broad, of 29–37 plates. Rachidian plates overlapping, moderately broad (0.027–0.031 mm wide), weakly arched, with 9–14 strong cusps on posterior edge. Central cusp strongest. Anterior edge of rachidian plate slightly concave, resulting in rectangular to chevron-shaped plates. Shell length: radular width ratio = 185–239. Radular Index = 2.6–3.1.

Distribution and Habitat: S. Australian (3 species), Indo-Pacific (1 species). Intertidal to 183 m.

Fossil Record: Known only from the Recent.

Nomenclature, Synonymy: The type species was dedicated to M. Bayle in the original description by Jousseaume (1875:269, 274) but spelled “*baylii*” in the text and “*baylei*” in the figure caption (op. cit., pl. 8, fig. 5). This is to be considered a case of multiple original spellings, which is dealt with in the ICZN [Art. 32(b)(i)]. This section, then, is subject to Section 32(c)(ii), which considers an incorrect original spelling one in which the original publication itself shows clear evidence of an inadvertent error. Because Jousseaume intended the species to be dedicated to M. Bayle, it is clear that the spelling “*baylei*” is the correct one. Tomlin (1917:252) considered “*baylei*” an error.

Remarks: The immersed spire, lack of labial denticulation, and presence of an external varix and only 3 columellar plications, distinguishes this group.

Tribe PRUNINI Coovert and Coovert, new tribe

Diagnosis: Shell small to very large, white, uniformly colored, patterned, or banded; spire immersed, or low to tall; lip thickened, smooth to denticulate; external varix present or absent; siphonal notch usually absent; posterior notch absent; columella with 2–6 plications occupying half or less of the aperture. Type 2 animal; siphon long

57.6 mm. **67.** *Rivomarginella morrisoni* Brandt, 1968. GAC Acc. # 11–89, Prachin River, Kabinburi, Thailand. Length 10.0 mm. **68.** *Cryptospira tricincta* (Hinds, 1844). GAC M1253, Formosa Strait, S.W. Taiwan, dredged at 37 m. Length 23.5 mm. **69.** *Hyalina pallida* (Linné, 1758). GAC M2068, St. Croix, U.S. Virgin Islands. Length 14.3 mm.

to very long; mantle smooth, pustulose, rarely distinctly papillose, usually extending over external shell surface. Type 6 radula or non-radulate. Marginellid buccal pouch present, absent in non-radulate species; odontophoral cartilages present in radulate species, fused anteriorly or both anteriorly and posteriorly; valve of Leiblein absent; esophageal caecum present; gland of Leiblein with long, convoluted duct and a terminal bulb, passing through nerve ring and emptying into anterior end of proboscis; paired salivary glands ascinous or tubular, either contained within proboscis or free, ducts either attached to walls of esophagus or free; single accessory salivary gland present or absent, ascinous or tubular.

Genus *Volvarina* Hinds, 1844
(figures 38, 64)

Marginella, section *Volvarina* Hinds, 1844:75

Type species: *Marginella nitida* Hinds, 1844, = *Marginella (Volvarina) nitida* Hinds, 1844, = *Voluta mitrella* Risso, 1826; SD Redfield, 1870:221 (figure 64)

Diagnosis: Shell small to moderately large, color translucent white, amber, or brown, usually with darker bands; spire immersed, or low to tall; lip thickened, smooth, not denticulate; external varix usually absent, but weak to strong in some species; siphonal notch absent or weak; columella with 3 or 4 plications, some species with weaker 5th or 6th, combined occupying half or less of the aperture. Type 2 animal; siphon long to very long; mantle smooth or usually pustulose, rarely distinctly papillose, usually extending over external shell surface. Type 6 radula.

Description: Shell (figure 64) small to moderately large (adult length 2.6–22.4 mm). Color translucent to opaque white, amber, or brown, usually with yellow, orange, brown, or reddish spiral bands, rarely axially streaked; surface smooth, glossy. Shape elongate to moderately broadly cylindrical, elliptic, narrowly to broadly obovate, or oblong, rarely elliptic-cylindrical with immersed spire; weakly to strongly shouldered. Spire rarely immersed, usually low, medium, or tall. Aperture narrow to moderately broad, rarely broader, usually wider anteriorly. Lip narrowly to strongly thickened, smooth, not denticulate, usually lacking an external varix, some species with weak to strong external varix. Siphonal notch rarely weak, usually absent; posterior notch absent. Ventral callusing usually not evident, present in one species group. Columella usually with 4 continuous plications; rarely with 3 plications and “false 4th” plication that joins short collabral parietal callus ridge; or 5 plications, the 5th not continuous past ½ whorl internally, plus often “false 6th” plication or parietal lira posteriorly. Plications usually occupying less than half, but some species up to half the aperture length. Internal whorls unmodified.

External anatomy: 26 species studied. Type 2 animal; tentacles long, slender; siphon long to very long; mantle smooth or usually pustulose, rarely distinctly papillose,

extending over external shell surface, often nearly completely covering shell; foot moderately broad, about 1½ X shell width, 1½–2 X length; animal variously spotted or mottled in white, black, or various colors.

Internal anatomy (figure 38): 2 species studied. As in tribe. Marginellid buccal pouch present; odontophoral cartilages fused both anteriorly and posteriorly; paired salivary glands ascinous, either contained within proboscis or free, ducts either attached to walls of esophagus or free; single accessory salivary gland present, ascinous or tubular.

Radula: 43 species studied. Type 6, uniserial, ribbon short, broad, of 31–75 plates. Rachidian plates overlapping, broad (0.034–0.562 mm wide), nearly flat, with 10–33 (exceptionally 5) sharp cusps on posterior edge. Anterior edge of rachidian plate generally straight, resulting in elongate, rectangular “comb-like” plates. Shell length: radular width ratio = 25–96. Radular Index = 1.0–4.5.

Distribution and Habitat: Neozelanic (1 species), S. Australian (2 species), Indo-Pacific (33 species), E. Pacific (3 species), W. Atlantic (24 species), Arctic (1 species), Magellanic / Antarctic (3 species), Mediterranean (1 species), W. African (29 species), South African (10 species). Intertidal to 1,780 m.

Fossil Record: Eocene of France, Oligocene to Pleistocene of W. Atlantic, early Miocene of W. Pacific, Miocene to Pliocene of Italy, Pleistocene of California, to Recent.

Nomenclature, Synonymy: As discussed in Gofas (1989b: 160), the correct type species designation, by subsequent designation, is Redfield (1870:221). Mention in Hinds (1844:75) of *M. avena* as a “typical species” does not constitute a type designation, and the Cossmann (1899: 92) designation was preceded by that of Redfield.

Remarks: Apparently the smooth mantle does not readily cover the external shell surface in the narrow, non-varicose species. The broader, varicose West African and Mediterranean species all have a pustulose mantle that more readily covers the external shell surface (see Gofas, 1989b, and Gofas & Fernandes, 1992). Several undescribed Caribbean species, discussed in Covert and Covert (1990) (as *Prunum* sp., red-papillose mantle; and *Volvarina* sp. SW), have a distinctly papillose mantle that readily covers the shell. This is the most widely distributed genus as currently conceived, being found in all marine provinces. See *Prunum* for further discussion.

Genus *Prunum* Herrmannsen, 1852
(figures 1, 7–8, 17–20, 27, 31, 39–42, 65)

Prunum Herrmannsen, 1852:113

† *Volutella*, subg *Microspira* Conrad, 1868:66 [TS: *P. (sic.) oviformis* Conrad, 1868, = *Volutella (M.) oviformis* Conrad, 1868 †, M]

Egouena Jousseaume, 1875:167, 192 [TS: *E. egouen* Jousseaume, 1875, = *Marginella amygdala* Kiener, 1841; T]

† *Porcellanella* Tryon, 1882:16, (*non* White in MacGillivray, 1852) [TS: *P. bella* Conrad, 1868, = *Prunum bella* Conrad, 1868 †; OD (M)] [publ. as *nomen nudum* in Conrad, 1863:564, TS: *P. bella* Conrad, 1863, *nomen nudum*; M]
Marginella, subg. *Volvarina*, section *Leptegouana* Woodring, 1928:237–238 [TS: *Voluta guttata* Dillwyn, 1817; OD]

Type species: *Voluta prunum* Gmelin, 1791; M (figure 65)

Diagnosis: Shell small to large, usually thick, opaque, white or uniformly colored, often patterned, but usually not simply with dark, narrow bands; shell variously shaped; lip moderately to strongly thickened, smooth to denticulate; external varix usually present; siphonal notch usually absent; posterior notch absent; shell usually with heavy ventral callusing; columella with 4 plications occupying half or less of the aperture. Type 2 animal; siphon long to very long; mantle smooth, extending over external shell surface. Type 6 radula.

Description: Shell (figures 1, 65) small to large (adult length 3.3–44.1 mm). Shell usually thick, opaque, rarely translucent, white or colored tan, gray, brownish-gray, orange, or pink; uniformly colored, streaked, or spotted, or with paler spiral bands on colored species, some species with opaque white flecks overlaying other patterns, rarely banded with darker color. Surface smooth, glossy. Shape obovate, oblong, subtriangular, biconic, or rarely sub-cylindrical; weakly to strongly shouldered. Spire rarely immersed, usually low to medium height. Aperture narrow to moderately broad, wider anteriorly. Lip moderately to very strongly thickened, in one group much thinner anteriorly, smooth, often weakly to distinctly denticulate; usually with very distinct, rarely duplicate, external varix that is weak to absent in some species. Siphonal notch usually absent, rarely weakly developed; posterior notch absent. Ventral callus usually heavy, often with strongly produced deposit near posterior commissure of lip. Columella usually with 4 continuous plications, rarely with weak 5th plication. Plications usually occupying half or less of aperture length. Internal whorls unmodified.

External anatomy (figures 7, 8): 17 species studied. Type 2 animal; tentacles long, slender; siphon long to very long; mantle smooth, symmetrically extending over external shell surface, often nearly completely covering shell; foot broad and long, about 1½ X shell width, 2 X shell length; animal variously marked with tiny dots, spots, blotches, or lines of various colors.

Internal anatomy (figures 31, 39–42): 6 species studied. As in tribe. Marginellid buccal pouch present; odontophoral cartilages fused anteriorly or both anteriorly and posteriorly; paired salivary glands ascinous or tubular, free, ducts either attached to walls of esophagus or free; single tubular accessory salivary gland present or absent.

Radula (figures 17–20, 27): 22 species studied. Type 6, uniserial, ribbon short, broad, of 24–59 plates. Rachidian plates overlapping, broad (0.096–0.920 mm wide), nearly

flat, with 16–45 sharp cusps on posterior edge. Anterior edge of rachidian plate generally straight, producing elongate, rectangular “comb-like” plates. Shell length: radular width ratio = 30–103. Radular Index = 0.6–2.9.

Distribution and Habitat: Indo-Pacific (2 species), E. Pacific (7 species), W. Atlantic (52 species), W. African (3 species). Intertidal to 1,840 m.

Fossil Record: Eocene of Mississippi, Oligocene to Pleistocene of W. Atlantic, to Recent.

Nomenclature, Synonymy: The four genus-group names synonymized under *Prunum* differ mainly in degree of callusing, spire development, and degree of thickening and denticulation of the outer lip, all considered to be of specific value only. *Egouena* is in the same species group as *P. prunum* based on its type species *E. egouen*, a junior synonym of *M. amygdala*. This is supported by our observations of specimens of *P. marginatum* (Born, 1778), in which subadults are extremely similar to *P. prunum*, whereas fully adult specimens with heavy callus deposits are obviously close to *P. amygdalum*. All share the same brown apertural coloration and combined with several other species form a closely related species group. The 3 multiple original spellings of *Egouena* were listed and discussed in Coan (1965:189), where Neave (1939:2:199) was listed as the first revisor. The other 3 genus-group names are not quite as closely related, but certainly appear to be congeneric. The holotype of *Volutella oviformis* was figured by Gardner (1937:pl. 47, figs. 11–12). The type of *P. bellum* was figured by Olsson and Harbison (1953:pl. 30, fig. 4). Coan (1965:189) synonymized *Egouena*, *Porellanella*, and *Leptegouana* under *Prunum*. Roth (1978:8) tentatively considered *Egouena* and *Leptegouana* synonyms of *Microspira*. Some of these genus-group names could be employed as subgeneric groups after all *Prunum* and *Volvarina* are fully revised, but this would probably necessitate introducing additional formal names. We feel that recognition of informal species groups would be a better solution. Much research remains to be done along these lines, especially with the anatomy and fossil fauna.

Remarks: The concept of this genus outlined in Coovert (1988c) has been further modified, partially based on the work of Gofas (1989b) and Gofas and Fernandes (1992) on *Volvarina*. These authors placed the majority of West African species, formerly included in *Prunum*, in *Volvarina*. They stated that the separation of these two genera was largely subjective as far as shell features, a contention with which we agree. Species of *Prunum* have a smooth mantle, whereas the West African *Volvarina* have a pustulose or papillose mantle. The group of non-varicose, narrow *Volvarina* often have a smooth mantle, but in at least one species group (“*rubella* group,” see Coovert & Coovert, 1990), their radula distinguish them from *Prunum*. Also, the ontogenetic development of the thickened outer lip in varicose and non-varicose species may further distinguish these genera (cf. section on shell

morphology). The key to genera will serve to identify these two groups based on current concepts.

A satisfactory solution to this complex situation will only be realized through a complete revision of all species groups in both genera, based on shell and anatomical features in combination with a study of the fossil record. We feel that the large group of western Atlantic species assigned to *Prunum*, both varicose and non-varicose, forms a natural assemblage distinct from the western Atlantic species assigned to *Volvarina*. Three major species radiations apparently occurred: eastern Atlantic *Volvarina* with a pustulose mantle; western Atlantic *Prunum* with a smooth mantle; and a much more widespread group of narrow, non-varicose *Volvarina*.

Genus *Bullata* Jousseau, 1875
(figure 66)

Bullata Jousseau, 1875:167, 250

Marginella, subg. *Volutella* Swainson, 1830:(2)1, *Marginella* pl. 1 (non Perry, 1810) [TS: *Marginella bullata* Lamarck, 1822, = *Voluta bullata* Born, 1778; OD]

Gibberulina Monterosato, 1884:139 [invalid emendation, as "nom. sost."]

Type species: *Bullata bullata* (Born, 1778), = *Voluta bullata* Born, 1778; T (figure 66)

Diagnosis: Shell moderately large to very large, colored and banded or patterned, elliptic to oblong or obovate; spire immersed or nearly so; lip thickened, denticulate in adults; external varix present; siphonal notch absent; columella with 4 strong plications occupying less than half the aperture but are not crowded anteriorly. Type 2 animal; siphon long; mantle extension undetermined. Type 6 radula.

Description: Shell (figure 66) moderately large to very large (adult length 16.8–90.0 mm). Color yellowish-orange to orangish- or pinkish-brown, spirally banded or with white spots, lip pink, yellow, or orange, darker than shell color. Shell surface smooth, glossy. Shape elliptic to oblong or obovate, moderately to strongly shouldered. Spire immersed or nearly so. Aperture narrow to moderately broad, wider anteriorly. Lip moderately to strongly thickened, weakly to strongly denticulate in adults, with a distinct external varix. Siphonal notch, posterior notch absent. Parietal callusing weakly to strongly developed, especially posteriorly, absent in type species. Columella with 4 continuous plications occupying less than half the aperture length. Internal whorls unmodified.

External anatomy: 1 species studied. Type 2 animal; tentacles long, slender; siphon long; mantle extension undetermined, foot moderately broad, about 1½ X shell width, slightly longer than shell; animal marked with fine, narrow red lines on cream background. [Based on dissection of *Bullata bullata*].

Internal anatomy: 1 species studied. As in tribe. Marginellid buccal pouch present.

Radula: 1 species studied. Type 6, uniserial, ribbon short, broad, of 47 plates. Rachidian plates overlapping, broad (0.825 mm wide), nearly flat, with 40 sharp cusps along posterior edge. Anterior edge of rachidian plate generally straight, resulting in elongate, rectangular "comb-like" plates. Shell length: radular width ratio = 63. Radular Index = 1.2.

Distribution and Habitat: W. Atlantic (4 species). Recorded from 1 to 60 m.

Fossil Record: Miocene and Pliocene of W. Atlantic, to Recent.

Nomenclature, Synonymy: Nomenclature of *Gibberulina* was discussed in Coovert (1987h:27).

Remarks: The large, patterned shells with an immersed spire and 4 moderately heavy columellar plications not crowded anteriorly serve to distinguish this group. The presence of an esophageal caecum clearly places this genus in the Prunini. As here defined, this group is restricted to the Caribbean province, where it evolved in the Miocene as a direct offshoot of *Prunum*.

Genus *Rivomarginella* Brandt, 1968
(figure 67)

Rivomarginella Brandt, 1968:275

Type species: *R. morrisoni* Brandt, 1968; (OD) M (figure 67)

Diagnosis: Shell small to medium, translucent, lightly colored, shape obconic to subpyriform; spire medium height; aperture broad; lip thickened, smooth; external varix present; siphonal notch absent; with minutely granulated apical and ventral callusing; columella with 4 plications occupying half the aperture length. Type 2 animal; siphon long; mantle smooth, extending over external shell surface. Type 6 radula.

Description: Shell (figure 67) small to medium in size (adult length 5.4–11.3 mm). Color translucent yellowish-white to brownish-white, some species with 1 or 2 obscure spiral bands; surface smooth, glossy. Shape broadly obconic to subpyriform, moderately to strongly shouldered. Spire medium height. Aperture moderately broad to broad, wider anteriorly. Lip moderately thickened, smooth, lacking denticulation, with a distinct external varix. Siphonal notch, posterior notch absent. Shell with minutely granulated ventral and apical callusing. Columella with 4 continuous plications occupying half the aperture length. Internal whorls presumed unmodified.

External anatomy: 2 species studied. Type 2 animal; tentacles long, slender; siphon long; mantle smooth, extending almost completely over external shell surface; foot moderately broad; animal pigmented with blackish-brown, black, or yellow dots or blotches. The penis was described by Brandt (1968:277) as long, simple, and lacking appendages.

Internal anatomy: Unknown.

Radula: 2 species studied. Type 6, uniserial, ribbon short, broad, of 38–47 plates. Rachidian plates overlapping, broad, nearly flat, with 18–29 sharp cusps along posterior edge. Anterior edge of rachidian plate generally straight, resulting in elongate, rectangular “comb-like” plates. No further data available.

Distribution and Habitat: Indo-Pacific (2 species), found in freshwater in S.E. Asia.

Fossil Record: Known only from the Recent.

Nomenclature, Synonymy: See Brandt (1968:pl. 10, fig. 63) for a photograph of the holotype of the type species.

Remarks: Subadult shells show that the lip is first reflected, then gradually thickened by callus deposits. This is unlike *Volvarina*, which initially has the lip curved in. Thus, we consider *Rivomarginella* to be more closely allied to the *Prunum* lineage. *Eratoidea* was considered by Brandt (1968:275) to be the closest relative, but it is apparently non-radulate and has stronger columellar plications occupying more than half the aperture. For further information see Brandt (1974), Coomans and Clover (1972), and Djajasmita and Coomans (1980).

Genus *Cryptospira* Hinds, 1844
(figure 68)

Marginella, section *Cryptospira* Hinds, 1844:76

Type species: *Marginella tricineta* Hinds, 1844, = *Marginella (Cryptospira) tricineta* Hinds, 1844; SD (M) Gray, 1847:142 (figure 68)

Diagnosis: Shell medium to large, opaque, uniformly colored or with bands or patterned; spire immersed or low; lip thickened, smooth or denticulate; external varix present; siphonal notch absent; columella with 4 to 6 plications. Type 2 animal; siphon long; mantle smooth, extending over external shell surface. Type 6 radula.

Description: Shell (figure 68) medium to large (adult length 6.2–46.0 mm). Color usually uniformly opaque gray or flesh-colored to pale brown, many with narrow spiral lines, undulating longitudinal zig-zag lines, longitudinal streaks, or spiral lines crossed by longitudinal streaks, lip often differentially colored. Often relatively thick-shelled, surface smooth, glossy. Shape cylindrical, elongate to broadly elliptic, obovate, pyriform, or subtriangular, moderately to strongly shouldered. Spire immersed or low. Aperture narrow to moderately broad, wider anteriorly. Lip moderately to strongly thickened, smooth or with weak to strong denticulation in adults, with a distinct external varix that is rarely duplicate. Siphonal notch absent or at most very weakly developed; posterior notch absent, weak notch present between posterior parietal callus deposit and posterior lip commissure. Shell often with anterior or posterior ventral parietal callusing. Columella with 4 to 6 continuous plications

occupying distinctly less than half to more than half the aperture length. Internal whorls unmodified.

External anatomy: 4 species studied. Type 2 animal; tentacles long, slender; siphon long; mantle smooth, extending symmetrically or nearly so over external shell surface; foot moderately broad, about 1½ X shell width, 1½ X length; animal uniformly colored or brightly marked with streaks of red on yellow ground color.

Internal anatomy: Unknown.

Radula: 4 species studied. Type 6, uniserial, ribbon short, broad, of 36–50 plates. Rachidian plates overlapping, broad (0.158–0.403 mm wide), nearly flat, with 9–28 sharp cusps along posterior edge. Anterior edge of rachidian plate generally straight, resulting in elongate, rectangular “comb-like” plates. Shell length: radular width ratio = 35–77. Radular Index = 1.4–2.3.

Distribution and Habitat: Indo-Pacific (15 species). Recorded from 0.6 to 123 m.

Fossil Record: Pliocene of Java, to Recent.

Nomenclature, Synonymy: The earliest type species designation is by Gray (1847:142), as noted in Coan (1965:189). Besides being predated by Gray, Cossmann's (1899:94) designation of *Marginella quinqueplicata* Lamarck, 1822, as type species, is invalid because this was not an included species of Hinds. See Palmer (1937:418) for comments on nomenclature, but note that Hinds' usage of division places this taxon as a genus-group name (ICZN, Art. 10e). We do not consider *Euryentome* to be closely related to *Cryptospira*. Coan (1965:189) placed *Cryptospira* as a subgenus of *Bullata*. We consider these two groups to have separate origins, *Bullata* being a direct descendant of Caribbean *Prunum*, whereas *Cryptospira* is restricted to the western Indo-Pacific where it evolved.

Remarks: See Coomans (1969) for further information. The large, thick, colored, frequently patterned shells, often with 5 or 6 columellar plications, serve to differentiate this group. One species group within the genus has distinctively gray-colored shells. As defined and restricted geographically, this genus forms a compact, closely related group.

Genus *Hyalina* Schumacher, 1817
(figures 32, 69)

Hyalina Schumacher, 1817:234

Marginella, subg. *Volvarina*, section *Neovolvaria* Fischer, 1883:602 [TS: *Marginella pallida* (Linné, 1767), = *Bulla pallida* Linné, 1758; M]

Type species: *Hyalina pellucida* Schumacher, 1817, = *Bulla pallida* Linné, 1758; M (figure 69)

Diagnosis: Shell small to large, white to lightly colored, hyaline or translucent, thin-shelled; spire low to medium height; aperture broad; lip thin, smooth; external varix weak to absent; siphonal notch absent; ventral callusing

absent; columella with 2 to 4 plications occupying less than half the aperture. Type 2 animal; siphon long; mantle smooth. Non-radulate.

Description: Shell (figure 69) small to large (adult length 4.0–29.0 mm). Color white, hyaline or translucent, cream to amber or brown, rarely with faint yellowish-white bands or numerous spiral lines. Thin-shelled, surface smooth, glossy. Shape broadly cylindrical to obovate, weakly to moderately shouldered. Spire low to medium height. Aperture moderately broad to broad, usually distinctly wider anteriorly. Lip moderately thin, smooth, lacking denticulation; external varix weak to absent. Siphonal notch, posterior notch, ventral callusing absent. Columella with 2–4 continuous plications occupying distinctly less than half the aperture length. Internal whorls unmodified.

External anatomy: 3 species studied. Type 2 animal; tentacles long, slender; siphon long; mantle smooth, apparently extending over external shell surface; foot moderately broad, about $1\frac{1}{2}$ X shell width, $1\frac{1}{2}$ X length; animal white or translucent, uniformly colored or spotted and flecked with orange and black.

Internal anatomy (figure 32): 2 species studied. As in tribe. Marginellid buccal pouch absent, paired salivary glands tubular, free, ducts free, single accessory salivary gland present, tubular.

Radula: Non-radulate, completely lacking buccal mass, including odontophore. 3 species known or strongly suspected to be non-radulate.

Distribution and Habitat: Indo-Pacific (1 species), W. Atlantic (3 species), Magellanic / Antarctic (2 species), South African (5 species). Intertidal to 1,340 m.

Fossil Record: Pliocene of Florida, to Recent.

Nomenclature, Synonymy: Coan and Roth (1976) gave a complete discussion of *Hyalina* and its type species. They designated (op. cit. fig. 1) the same specimen as neotype for both *Bulla pallida* Linné, 1758 and *Hyalina pellucida* Schumacher, 1817, placing *Neovolvaria* as an objective synonym of *Hyalina*.

Remarks: The complete lack of a radula and buccal mass at first suggested placement of this genus with the non-radulate marginellines, but conchological features did not conform. Subsequent dissection of a specimen of *H. pallida* revealed the presence of an esophageal caecum, a diagnostic feature of the Prunini. The thin, translucent shells, a weak or absent external varix, and 2, 3, or 4 columellar plications will generally serve to distinguish this genus.

Tribe MARGINELLINI Fleming, 1828:328

Diagnosis: Shell minute to very large, white, uniformly colored, or patterned, biconic, obconic, or broadly obovate; spire low to tall; lip thickened, smooth or denticulate; external varix present; siphonal notch present or

absent; columella with 4 or 5 strong plications occupying half or more of the aperture. Type 2 animal; siphon long; mantle smooth or papillose, variably extending over external shell surface. Non-radulate, lacking entire buccal mass, including odontophore and cartilages. Proboscis rounded, blunt, or distally pointed; marginellid buccal pouch absent; valve of Leiblein absent; esophageal caecum absent; gland of Leiblein with a terminal bulb and a long, convoluted duct that passes through nerve ring and empties into anterior end of proboscis; paired salivary glands ascinous or tubular, either contained within proboscis or free, ducts either attached to walls of esophagus or free; single accessory salivary gland present, tubular.

† Genus *Stazzania* Sacco, 1890a

Marginella, subg. *Stazzania* Sacco, 1890a:138 (245); 1890b:26 (318)

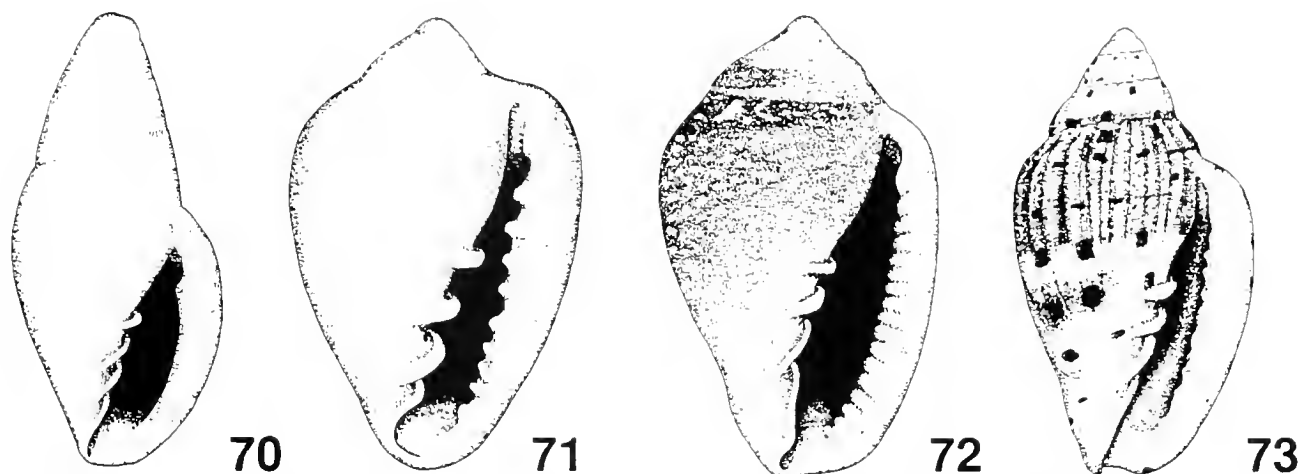
Type species: *Marginella (Stazzania) emarginata* Sismonda, 1847, = *Marginella emarginata* Sismonda, 1847 †; M

Diagnosis: Shell minute to moderately large, narrowly to broadly biconic or broadly obovate; spire medium to tall; aperture narrow; lip thickened, smooth or denticulate, often with stronger or single posterior denticle; external varix present; siphonal notch absent; columella with 4 or 5 strong plications occupying more than half the aperture; collabral parietal callus ridge present, usually connecting with bifurcated outer ends of plications.

Fossil Record: Eocene of France, to upper Miocene of Italy.

Nomenclature, Synonymy: Many European paleontologists synonymize *Dentimargo* under *Stazzania* (e.g. Gougerot & Le Renard, 1979; Nieulande, 1981; Le Renard & Nieulande, 1985), apparently based on similarities in shell shape and the presence of bifurcated columellar plications in some species of both groups. The bifurcated plications in *Stazzania* result from thin, paired callus ridges on their distal ends joining a collabral parietal callus ridge. However, in fossil species we assign to *Dentimargo*, bifurcated columellar plications are fundamentally different, being thick and broad, with a U-shaped notch distally that creates the bifurcate appearance. Species of *Dentimargo* with a collabral callus ridge do not have this ridge intersecting the distal ends of the plications. Most Recent species of *Dentimargo* have simple, unmodified plications. The type species of *Stazzania* is significantly larger than the relatively small Eocene species herein assigned to the same group, but has a very similar shape.

Remarks: *Stazzania* is here considered to be an extinct, separate lineage from the contemporaneous *Dentimargo*. *Dentimargo*, besides differing in plications, is generally narrower with a broader aperture.



Figures 70–73. Shells of type species of marginellid genera, ventral views. **70.** *Dentimargo dentifera* (Lamarck, 1803). GAC Acc. # 35–87, fossil, Lutetian of the Eocene, Paris Basin, Fercourt, France. Length 4.6 mm. **71.** *Eratoidea margarita* (Kiener, 1834). GAC M2079, Water Island, St. Thomas, Virgin Islands. Length 8.0 mm. **72.** *Marginella glabella* (Linné, 1758). GAC M1322, Cape Verde Islands. Length 38.7 mm. **73.** *Glabella faba* (Linné, 1758). GAC M1720, Dakar, Senegal, West Africa, under rocks at 15 m. Length 18.5 mm.

Genus *Dentimargo* Cossmann, 1899
(figures 33, 70)

Marginella, subg. *Marginella*, section *Dentimargo* Cossmann, 1899:90

Volvarinella Habe, 1951:101–102 [TS: *V. makiyamai* Habe, 1951, OD]

Marginella, subg. *Eburnospira* Olsson & Harbison, 1953:201–202 [TS: *Marginella eburneola* Conrad, 1834 †, OD]

Longinella Laceron, 1957:286, (non Gros & Lestage, 1927) [TS: *Marginella maugeana* Hedley, 1915, OD]

Type species: *Marginella dentifera* Lamarck, 1803 †; OD (figure 70)

Diagnosis: Shell small to medium, white or uniformly colored, usually banded, usually biconic; spire medium to tall; aperture moderately broad to broad; lip thickened, smooth or denticulate, often with stronger or single posterior denticle; external varix present; siphonal notch absent; columella with 4 strong plications occupying more than half the aperture. Type 2 animal; siphon long; mantle smooth or weakly papillose, extending over external shell surface.

Description: Shell (figure 70) small to medium in size (adult length 2.4–12.0 mm). Color translucent to subopaque, white, cream, to brown, usually with 1–4 narrow, yellow or brown bands. Shell surface smooth, glossy, rarely with weak to distinct axial costae. Shape narrowly to broadly biconic, rarely narrowly subovate; weakly to strongly shouldered. Spire height medium to tall, rarely stepped. Aperture moderately broad to broad, wider anteriorly. Lip thin to moderately thickened, rarely strongly thickened, smooth to denticulate, often with stronger or single denticle at posterior fourth of lip, with a distinct external varix. Siphonal notch absent, rarely very weakly

indicated; posterior notch usually absent, at most weakly indicated. Ventral callusing usually absent. Columella with 4 strong continuous plications occupying more than half the aperture length. Internal whorls unmodified.

External anatomy: 7 species studied. Type 2 animal; tentacles long, slender; siphon long; mantle smooth or weakly papillose, extending over external shell surface, often nearly completely covering shell; foot moderately narrow to moderately broad, about 1–1½ X shell width, and 1–1½ X length; animal variously spotted or blotched with black, opaque white, or red, or with opaque white lines. Penis with sharply pointed distal or posterodistal appendage.

Internal anatomy (figure 33): 2 species studied. As in tribe. Proboscis pointed distally; paired salivary glands ascinous or tubular, contained within proboscis, ducts free.

Radula: Non-radulate, completely lacking buccal mass, including odontophore. 9 species known or strongly suspected to be non-radulate.

Distribution and Habitat: Neozelanic (10 species), S. Australian (8 species), Indo-Pacific (28 species), E. Pacific (4 species), W. Atlantic (15 species), W. African (2 species), South African (3 species). Intertidal to 1,300 m.

Fossil Record: Eocene of France, Eocene to Pleistocene of W. Atlantic, Oligocene to Pliocene of Australia, Miocene to Pliocene of W. Pacific, to Recent.

Nomenclature, Synonymy: Roth (1978:12) synonymized all of the above genus-group names, a view with which we agree. Powell (1971:223) had previously synonymized *Longinella* under *Volvarinella*. A cotype of *M. maugeana* was figured by Kaicher (1981:#2628), who

placed it in *Dentimargo*, treating *Longinella* as a subgenus. The type of *M. eburneola* was figured in Olsson and Harbison (1953:pl. 30, fig. 8). The characters separating these groups are viewed as specific differences only. The gender of *Dentimargo*, based on the Latin noun *margo* can be treated as either masculine or feminine. Because the combination "*Dentimargo dentifera*" used by Cossmann (1899:pl. 4, fig. 15) is generally considered shorthand for *Marginella (Dentimargo) dentifera*, there is no direct evidence of intended gender for *Dentimargo* by Cossmann [(ICZN Art. 30(a)(1)]. Thus, the name is to be treated as masculine.

Remarks: This is a widely distributed group, both spatially and temporally. Eventually, a thorough revision may enable species groups to be delineated. Until a thorough knowledge of the phylogeny is known, useage of informal species groups is a better solution than recognition of subgenera.

Genus *Eratoidea* Weinkauff, 1879
(figure 71)

Marginella, section *Marginella*, grupe *Eratoidea* Weinkauff, 1879:140

Type species: *Marginella margarita* Kiener, 1834; SD Cossmann, 1899:87 (figure 71)

Diagnosis: Shell minute to medium, white or uniformly colored, rarely banded, broadly biconic; some species axially costate; spire low to medium, often stepped; lip thickened, denticulate; external varix present; siphonal notch absent; columella with 4 strong plications occupying half or more of the aperture. Type 2 animal; siphon long; mantle papillose, extending over external shell surface.

Description: Shell (figure 71) minute to medium size (adult length 1.9–11.0 mm). Color usually translucent to subopaque white, less commonly deep rose, rarely translucent white with 2 narrow brown spiral bands. Shell surface smooth, glossy, some species with weak to distinct axial costae. Shape broadly biconic, weakly to strongly shouldered. Spire low to medium height, often weakly to distinctly stepped. Aperture moderately narrow to broad, not usually distinctly wider anteriorly. Lip weakly to strongly thickened, weakly to distinctly denticulate, with a distinct external varix. Siphonal notch absent; posterior notch usually absent to at most weakly indicated. Shell without evident ventral callusing. Columella with 4 strong continuous plications occupying half to more than half the aperture length. Internal whorls unmodified.

External anatomy: 2 species studied. Type 2 animal; tentacles long, slender; siphon long; mantle papillose with very long papillae in *E. hematita* (Kiener, 1834), extending almost completely over external shell surface, undetermined in *E. margarita* (Kiener, 1834); foot moderately narrow to moderately broad, about 1–1½ X shell

width, 1–1½ X length; animal variously dotted or spotted with brown, yellow, or opaque white. [Based on pers. obs. of photographs ex. W. R. Liltved and R. Lipe].

Internal anatomy: Unknown.

Radula: We have attempted routine extraction of radulae from 2 specimens of *E. margarita* and found no radula. Based on this and conchological affinities with other non-radulate genera, we strongly suspect that this genus is also non-radulate.

Distribution and Habitat: W. Atlantic (9 species). Recorded from 1 to 1,470 m.

Fossil Record: Miocene of Caribbean, to Recent.

Nomenclature, Synonymy: Although Weinkauff (1879) used the single genus *Marginella*, he proposed an outline classification that included the new "grupe" *Eratoidea*. His "section" apparently corresponds to subgenus, whereas "grupe" corresponds to section. This genus was placed as a synonym of *Marginella (Gibberula)* by Coan (1965:189). *Gibberula* is a cystiscid genus completely unrelated to *Marginella* or *Eratoidea*.

Remarks: The 4, strong, continuous plications occupying more than half the aperture, lack of an anterior notch, and strongly denticulate lip serve to distinguish this group and to place it in Marginellini. The type species has variably low, weak axial costae, relating it to the smaller axially costate species.

† Genus *Euryentome* Cossmann, 1899

Cryptospira, subg. *Cryptospira*, section *Euryentome* Cossmann, 1899:95

Type species: *Marginella crassilabra* Conrad, 1833 (non *Marginella crassilabra* Bory de St. Vincent, 1827), = *Marginella silabra* Palmer, 1937 (nom. nov.), = *Marginella anatina* Lea, 1833 †; OD

Diagnosis: Shell medium size; lip strongly thickened, strongly denticulate on its sharp inner edge; strong external varix present; weak siphonal notch present or absent; very deep posterior notch present; columella with 4 continuous plications, often with weak 5th plication, and 4 to 5 parietal lirae in some species.

Fossil Record: Eocene of Alabama and Mississippi, to Miocene of Trinidad.

Nomenclature, Synonymy: The correct name for the type species is *M. anatina* Lea, 1833, the next available name for the junior primary homonym *M. crassilabra* Conrad, 1833. The replacement by Palmer (1937:416–417) was unnecessary and is therefore a junior synonym. Lea's type of *M. anatina* (*vide* Palmer & Brann, 1966: 618) was figured in Palmer (1937:pl. 89, fig. 10).

Remarks: The presence of parietal lirae initially caused us to consider placement in the Cystiscidae, but examination of a shell of *E. columba* (Lea, 1833) revealed

unmodified internal whorls with 4 continuous plications. The 4 strong plications, a very strong posterior notch, and probable relationship to S.E. U.S. Eocene *Dentimargo* cause us to place this genus in the Marginellini.

† Genus *Simplicoglobella* Sacco, 1890b

Marginella, subg. *Glabella*, section *Simplicoglobella* Sacco, 1890b:21 (313)

Type species: *Marginella (Glabella) taurinensis* Michelotti, 1847 †; SD (M) Eames, 1952:119

Diagnosis: Shell medium to large, narrowly to moderately broadly biconic; spire medium to tall; aperture moderately broad; lip thickened, smooth, not denticulate; external varix present; siphonal notch very weak to absent; columella with 4 strong plications occupying more than half the aperture.

Fossil Record: Miocene of Italy.

Nomenclature, Synonymy: Treated as a subgenus of *Marginella* in Coan (1965:189).

Remarks: This group is an extinct lineage related to *Marginella*, differing in its narrower shape and generally taller spire.

Genus *Marginella* Lamarck, 1799
(figures 34, 72)

Marginella Lamarck, 1799:70

† *Marginella*, subg. *Glabella*, section *Denticuloglobella* Sacco, 1890b:25 (317) [TS: *Marginella (Glabella) deshayesi* Michelotti, 1847 †; M]

Cucumis Deshayes, 1830:34 [in synonymy]

Porcellana Gray, 1847:142 (non Lamarck, 1801) [TS: *Voluta glabella* Linné, 1758; OD (M)]

Pseudomarginella Maltzan, 1850:108 [TS: *P. adansoni* Maltzan, 1850, = *Voluta glabella* Linné, 1758; M]

Type species: *Voluta glabella* Linné, 1758; M (figure 72)

Diagnosis: Shell small to very large, white to colored, always patterned, biconic to obconic, lacking axial costae; spire low to medium height; aperture broad; lip thickened, smooth to denticulate; external varix present; siphonal notch usually present; columella with 4 strong plications occupying more than half the aperture. Type 2 animal; siphon long; mantle smooth, usually not readily extending over external shell surface.

Description: Shell (figure 72) small to very large (adult length 3.5–74.1 mm). Color white, cream, tan, gray, or reddish-orange to brown, always with pattern of white to dark dots or spots, spiral lines or bands, or mottled, or with axial streaks or lines, or various combinations. Shell surface smooth, glossy. Shape biconic to obconic, rarely narrowly biconic, weakly to strongly shouldered. Spire low to medium height, rarely tall. Aperture moderately broad to broad, wider anteriorly. Lip moderately thin to strongly thickened, smooth to weakly or strongly den-

ticulate, with a distinct external varix. Siphonal notch usually distinct, absent to weak in some species. Posterior notch absent to weak or distinct. Ventral callusing usually absent, strong parietal callus present in some species. Columella with 4 strong continuous plications occupying more than half the aperture length. Internal whorls unmodified.

External anatomy: 24 species studied. Type 2 animal; tentacles long, slender; siphon long; mantle smooth, apparently not readily extending over external shell surface in most species; foot moderately broad, about 1½ X shell width, and 1–1½ X length; animal variously spotted, mottled, streaked, or lineated with white, black, red, or yellow on a translucent or variously colored background.

Internal anatomy (figure 34): 3 species studied. As in tribe. Proboscis rounded or blunt distally; paired salivary glands tubular, free, ducts attached to walls of esophagus.

Radula: Non-radulate, completely lacking buccal mass, including odontophore. 16 species known or strongly suspected to be non-radulate.

Distribution and Habitat: Indo-Pacific (5 species), W. Atlantic (1 species), W. African (32 species), South African (25 species). Intertidal to 2,083 m.

Fossil Record: Miocene and Pliocene of Italy, to Recent.

Nomenclature, Synonymy: The type species of *Denticuloglobella*, *M. deshayesi*, falls well within the range of *Marginella* and this genus is here synonymized. For a discussion of the "pseudogenus" *Pseudomarginella*, see Cooke (1922).

Remarks: This group is distinguished by the 4 strong plications occupying more than half the aperture, plus the colored, patterned shell and lack of axial costae. For discussion of the *M. musica-diadochus* group, see Covert (1989a).

Genus *Glabella* Swainson, 1840
(figure 73)

Glabella Swainson, 1840:133, 324.

Marginella, section *Phaenospira* Hinds, 1844:72 [TS: *Marginella nodata* (sic.) Hinds, 1844, = *Marginella nodata* Hinds, 1844, SD (M) Gray, 1847:142]

Marginella, subg. *Marginella*, section *Faba* Fischer, 1883:602 [TS: *Marginella faba* (Linné, 1758), = *Voluta faba* Linné, 1758; M]

Type species: *Voluta faba* Linné, 1758; SD (M) Gray, 1847:142 (figure 73)

Diagnosis: Shell medium to large, white to colored, always patterned, biconic, distinct axial costae present; spire medium to tall; aperture narrow to moderately broad; lip thickened, distinctly denticulate; external varix present; siphonal notch present; columella with 4 strong plications occupying more than half the aperture. Type 2 animal; siphon long; mantle extension undetermined.

Description: Shell (figure 73) medium to large (adult length 6.2–35.0 mm). Color white, gray, or yellowish-olive to olive in background, always with pattern of spiral lines or rows of dots, axial lines or streaks, or variously mottled, spotted, or streaked. Shell surface smooth, glossy, with weak to usually distinct axial costae. Shape broadly to narrowly biconic, weakly to strongly shouldered. Spire medium to tall. Aperture moderately narrow to moderately broad, usually widest medially. Lip moderately to strongly thickened, distinctly denticulate, with a distinct external varix. Shell with siphonal notch weak or distinct. Posterior notch absent to weak or distinct. Shell usually without evident ventral callusing. Columella with 4 strong continuous plications occupying more than half the aperture length. Internal whorls unmodified.

External anatomy: 2 species studied. Type 2 animal; tentacles long, slender; siphon long; mantle extension undetermined; foot broad, about $1\frac{1}{2}$ X shell width, $1\frac{1}{2}$ X shell length; animal variously spotted, blotched, or streaked with yellow or reddish-brown. [See summary of *G. adansoni* (Kiener, 1834) in Covert (1987g:12) and figure of *G. lucani* (Jousseaume, 1884) in Gofas & Brandao (1985:85, fig. b)].

Internal anatomy: Unknown.

Radula: Non-radulate, completely lacking buccal mass, including odontophore. 1 known non-radulate species (Coan & Roth, 1976:220).

Distribution and Habitat: Indo-Pacific (4 species), W. African (13 species). Intertidal to 183 m.

Fossil Record: Known only from the Recent.

Nomenclature, Synonymy: Various authors have designated different type species, including *M. prunum* (Gmelin, 1791) by Fischer (1883:602) and *M. bifasciata* Lamarck, 1822 by Redfield (1870:221), but the designation of *M. faba* by Gray (1847:142) was the earliest. A photograph of the type of *G. faba* has been studied (pers. obs. ex. photograph of P. W. Clover). The type of *G. nodata* was figured by Kaicher (1981:#2640). Both fall well within the limits of the genus. *Phaenospira* had previously been synonymized by Coan (1965:189).

Remarks: We consider axial costae to be a species-level character in other genera. In this case, though, *Glabella* seems to form a natural assemblage, albeit closely related to *Marginella*. Besides possessing axial costae, this group always has a strongly denticulate lip and an aperture that is broadest medially.

DISCUSSION

FAMILY RELATIONSHIPS

Previous sections of this paper outlined the fundamental differences between the two families of marginelliform gastropods—the Cystiscidae and the Marginellidae. Shared similarities between each of these two families and other neogastropod families (Table 5), in particular,

characters presumed to be derived, will be examined next.

The Cystiscidae have a number of unusual characters that differentiate them from the Marginellidae. Interestingly, these same characters are shared with the Olividae. The partially resorbed “cystiscid internal whorls” are characterized by being extremely thin, modified in shape, and having the columellar plications reduced to a single, axially oriented, sharp edge internally (figures 2, 3). A very similar type of internal whorl, though, is seen in members of the genus *Oliva*, clearly visible in X-ray photographs in Zeigler and Porreca (1969:8) and confirmed by personal observations of both young and adult shells of *O. sayana* Ravenel, 1834. Similar internal shell construction is found in *Agaronia* (pers. obs.). In *Olivella*, the internal whorls are often nearly completely resorbed rather than modified and thinned. For further discussion, see Olsson (1956:169), Kantor (1991:24, 41–43, 49), and Marcus and Marcus (1959:107–108). The only other gastropod families reported to have internal whorl resorption are Cypraeidae and Conidae, in which whorl walls are greatly thinned, and Neritidae and Ellobiidae, in which the internal whorls are completely resorbed (Moore, 1960:1121; Fretter & Graham, 1962:69). Because internal whorl resorption is uncommon in gastropods, we consider this to be a shared, derived character between the Cystiscidae and Olividae.

The multiplicate columella of cystiscids consists of 1 or 2 anterior columellar plications that are reduced internally, plus parietal lirae posterior to these plications. In the Olividae, true columellar plications are absent, but a sharp, axially oriented columellar edge is found internally. The parietal area often bears distinct lirae. Although similar to the multiplicate columella of cystiscids, the olivid columella lacks anterior columellar plications.

The radular morphology is of particular interest in differentiating the Cystiscidae from the Marginellidae. The long, narrow radula of at least 80 to 200 or more rachidian plates is characteristic of the cystiscids. Lateral teeth are present only in the genus *Plesiocystiscus*, in which the radula closely resembles those of certain olivids (Olsson, 1956:figs. 9, 10). Radulae and subradular membranes of cystiscids were compared with those from: *Oliva sayana* Ravenel, 1834, *Agaronia griseoalba* (von Martens, 1897), and *Olivella (Pachyoliva) semistriata* (Gray, 1839). In all three olivid species, odontophoral cartilage hoods, very similar to those in cystiscids, were found. Separate odontophoral cartilages, each fitting into one of the flanking odontophoral cartilage hoods, were found in *O. sayana* and *A. griseoalba*. These cartilages are very similar in general shape to those of *Persicula* (figures 36, 37). These two olivids also have the posterior end of the radula, which extends beyond the odontophore, encased in a typical neogastropod radular sac and beginning as a developmental series of nascent plates. Both species have lateral teeth, but are otherwise similar in radular morphology to the cystiscid genus *Persicula* (figures 13–16). For further discussion of *Oliva* radular

Table 5. Comparison of major taxonomic characters of marginelliform groups with related neogastropod families. See text for further discussion

Character	Volutidae	Marginelloninae	Marginellinae	Cystiscidae	Olividae
Internal whorls resorbed	no	no	no	YES	YES in most
Labial lirae	absent	absent	absent	PRESENT in some	PRESENT in some
Siphonal notch	YES in some	YES in some	YES in some	YES in some	YES
Plications	continuous	continuous	continuous	multiply	multiply
Head with lateral lappets & dorsomedial channel	PRESENT in some	PRESENT	absent	absent	absent
Shell covered by mantle or foot	mantle in some	mantle (in <i>Afrivoluta</i>)	mantle	mantle in some; foot in <i>Canalispira</i>	foot
Marginellid buccal pouch	absent	PRESENT	PRESENT	absent	absent
Neogastropod radular sac	PRESENT	absent	absent	PRESENT	PRESENT
Odontophoral cartilage hoods	?	absent	absent	PRESENT	PRESENT
Radula with laterals	YES in some	no	no	YES in <i>Plesiocystisc.</i>	YES
Central rachidian tricuspid	YES in some	no	no	YES in 1 genus	YES in some
Length of radular ribbon	moderately short to long	moderately short	moderately to very short	long	long (short in <i>Olivella</i>)
Odontophoral cartilages	separate (in <i>Alcithoe</i>)	?	fused at least anteriorly	separate	separate or fused anter.
Valve of Leiblein	PRESENT	PRESENT	PRESENT or absent	PRESENT	PRESENT
Gland of Leiblein	lg. sacculate, or w/terminal bulb	lg. sacculate	with terminal bulb	short gland, no long duct	short gland, or w/terminal bulb
Duct from Gland of Leiblein	posterior to nerve ring	posterior to nerve ring	posterior or ANTERIOR	posterior to nerve ring	posterior to nerve ring
Anal gland	PRESENT	PRESENT	PRESENT	absent	PRESENT or absent
Development	direct / veliger	direct	direct	direct	most veliger

morphology, see Marcus and Marcus (1959:124-5). *Olivella* has a shorter, broader radula with laterals and separate odontophoral cartilages. Marcus and Marcus (1959:121, fig. 31) and Kantor (1991:26, fig. 5C) further discuss the radular morphology of *Olivella*, including the odontophoral cartilages. The rachidian plates are tricuspid in *Olivella* and *Jaspidella* (Olsson, 1956:169, figs. 9, 10) and their radulae strongly resemble the triserial radulae of some *Plesiocystiscus*. *Plesiocystiscus*, the only cystiscid genus with lateral teeth, is considered to be the most primitive group in the family. Possession of lateral teeth is certainly a primitive feature, as is the tricuspid rachidian plate in cystiscids and olivids (Kilburn, 1981:354). In summary, the entire radular morphology of certain cystiscids and olivids are very similar. Many of these features, such as the formation of the odontophoral cartilage hoods and separate, flanking odontophoral cartilages, are considered to be shared, derived characters. The common possession of a typical neogastropod radular sac is a shared, primitive character.

Additional shell features shared between cystiscids and olivids include the glossy exterior of the shell. The mantle at least partially covers the exterior of the shell in the cystiscid genera *Cystiscus*, *Granulina*, and *Pugnus*. In other cystiscid genera, such as *Plesiocystiscus*, *Gibberula*, and *Persicula*, the shell is apparently not covered by the mantle. In olivids, the foot at least partially covers the shell and affords protection, and therefore, the glossy shell exterior is apparently due to secretion by the foot, not by the mantle. A similar animal has been described for the cystiscid genus *Canalispira*. A glossy shell is apparently convergent in many groups and does not by itself suggest a strong affinity between cystiscids and olivids. A strong siphonal notch is found in the cystiscid genera *Persicula* and *Gibberula* and is very characteristic of olivids, but is also found in many other groups. Lirae on the inner surface of the outer lip are found in many species of *Persicula*, *Gibberula*, and *Canalispira*, and also in the olivid genus *Olivella*. This character is less common than the other conchological characters but still could be due to convergence. A comprehensive study and review of all these features in olivids is needed and a common link between cystiscids and olivids should be searched for in Cretaceous material.

Anatomically, both the Cystiscidae and Olividae have a valve of Leiblein and a short gland of Leiblein (with a long, convoluted duct and a terminal bulb in *Amalda*) that empties into the esophagus posterior to the nerve ring (Ponder, 1973:fig. 3). Both groups have a typical neogastropod radular sac and lack the marginellid buccal pouch. Both families have species that possess a single accessory salivary gland. These characters are also found in other neogastropods. An anal gland is absent in *Gibberula* (Ponder, 1970:71) and present or absent in the Olividae (Kantor, 1991:tables 1,2). Cystiscids have direct development, whereas olivids generally have pelagic larvae (Boss, 1982:1018).

In summary, it is suggested that the Cystiscidae and Olividae have a shared, common ancestry based on char-

acters summarized in Table 5. They have much more in common with each other than do cystiscids and marginellids, which share no derived characters. Our recognition of two families of marginelliform gastropods reflects these conclusions. The erroneous placement of cystiscids and marginellids together was apparently based on superficially similar columellar plications, which we have shown to be completely different, and on externally glossy shells, which are a convergently derived adaptation produced by the extended mantle.

A search for the ancestry of the now restricted family Marginellidae first involves a consideration of the most primitive group within the family. Harasewych and Kantor (1991:17) suggested that the Marginelloninae may be the most primitive group in the family. This is based on the unspecialized features of the foregut, including a large valve of Leiblein lacking a glandular bypass, and the large gland of Leiblein, which lacks a terminal bulb and empties into the esophagus posterior to the nerve ring. We fully concur with this view. All other marginellids show specializations of the foregut, such as possession of a glandular bypass around the valve of Leiblein, development of a long, convoluted duct from the gland of Leiblein which has a terminal bulb, or loss of the valve of Leiblein with the duct from the gland of Leiblein passing through the nerve ring. The features of the head in *Marginellona* and *Afrivoluta*, including possession of lateral lappets and a dorsomedial channel, are features shared with many volutids (Harasewych & Kantor, 1991:13) and are very likely derived characters. The split head in cystiscids is considered to be fundamentally different and unrelated to the dorsomedially channelled head seen in marginellonines. The two genera of the Marginelloninae were originally placed in the Volutidae based on their large shells. Another typical volutid feature in *Afrivoluta* is the placement of the anterior columellar plication which does not border the anterior edge of the columella as in all other marginellids. The presence of a weak to strong siphonal notch in the Marginelloninae is typical of volutids, but is also found in olivids and some cystiscids. All volutids and marginellids have shells with unmodified internal whorls and strong, continuous columellar plications (Moore, 1955:430; Dillon, 1981:14; Abgrall, 1981:9). A valve of Leiblein and an anal gland are present in both families (absent in some Marginellinae). All marginellids and most volutids have a relatively short radular ribbon and have lost the lateral teeth. The broad, comb-like, multiscupid rachidian plate seen in many genera of marginellids is similarly developed in *Voluta* (Weaver and DuPont, 1970:fig. 1). Apparently all marginellids have a mantle covering the external shell surface, a feature seen in some volutids. For these reasons, it is suggested that the Marginelloninae, and thus the rest of the Marginellidae, are allied to the Volutidae (Table 5). The marginellids differ in the presence of a buccal pouch.

Thiele (1929:353-356) recognized only three genera in his treatment of the Marginellidae, namely *Persicula*, *Marginella*, and *Marginellona*. These three genera, with

their included subgenera and sections, correspond very closely to the classification of the Cystiscidae and the two subfamilies of the Marginellidae presented here. The single exception is Thiele's inclusion of *Canalispira* in *Marginella*, which is not surprising due to its superficial resemblance conchologically to certain marginellids. Coan's (1965) classification recognized these three groups in name, but differed in the assignment of genera.

Ponder (1973:331) suggested that the Volutomitridae, which appeared in the Late Cretaceous, possibly arose from a common stem with the Marginellidae. Volutomitrids often have an operculum and their radula has a very odd wish-bone shaped rachidian plate, frequently with lateral teeth. These features, along with a variously sculptured shell, are very different from the marginellids. We believe that this group has little in common with the Marginellidae.

Part of the difficulty in determining familial relationships lies in the abundance of convergent characters within Neogastropoda (Ponder, 1973:302). An overall tendency toward reduction of the number of radular teeth and their cusps is seen throughout the Neogastropoda. Loss of the lateral teeth occurs in some Mitridae, Volutidae, Volutomitridae, Cancellariidae, as well as in Marginellidae and Cystiscidae. Complete loss of the radula occurs in at least some Coralliophilidae, Cancellariidae, Turridae, Terebridae, Colubrariidae, and Marginellidae. The development of a long, convoluted duct and a terminal bulb in the gland of Leiblein is seen in several families, including some Muricidae, Olividae, Volutidae, Marginellidae, and the Conoidea. The reduction or complete loss of the valve of Leiblein is less common, but is seen in some Mitridae and Marginellidae, and all Harpidae and Conoidea. Besides sharing these last two character states, the Conoidea and the Marginellidae also share the development of a buccal pouch and the passage of the duct from the gland of Leiblein through the nerve ring. All of the above characters shared by the Conoidea and Marginellidae are most likely convergent. The parallel evolution of the Conoidean "poison gland" and the gland of Leiblein in the Marginellidae was discussed by Ponder (1970:77-80), Graham (1966:146), and Fretter (1976:333-334). More research on the phylogeny of these groups is needed, as well as more study into the nature of the gland of Leiblein in the Marginellidae and its possible use as a "poison gland" (Fretter, 1976:333-334).

PHYLOGENY OF THE CYSTISCIDAE

Our hypothesis of the relationships of the higher taxa within the family Cystiscidae is summarized in figure 74. Presumed ancestral character states include a Type 2 animal with a cystiscid Type 1 radula, and a shell with cystiscid internal whorls, a multiplicate columella, and lacking an external varix. Additional characters include lack of a siphonal notch, presence of a valve of Leiblein, and presence of a small gland of Leiblein with a short duct emptying into the esophagus posterior to the nerve ring. All these shell and radular characters are present

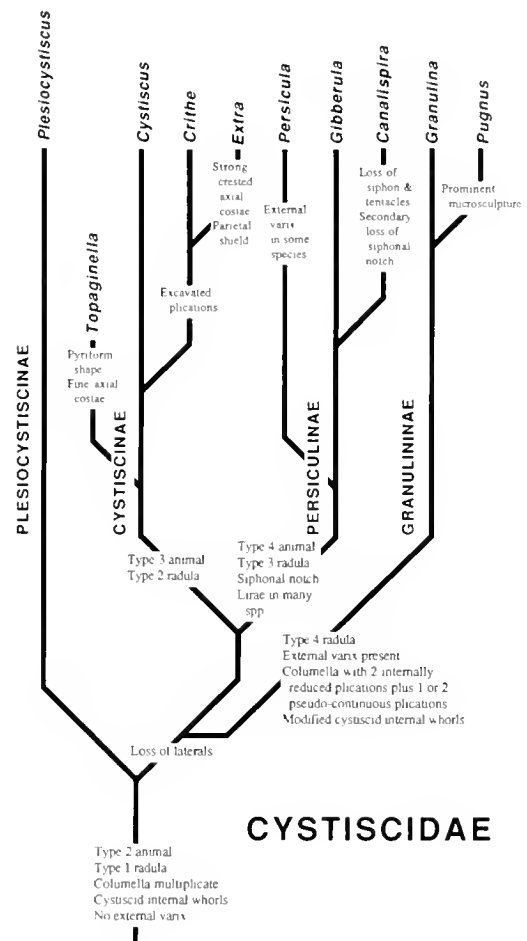


Figure 74. Intuitively derived phylogeny of the Cystiscidae. Characters at base are primitive for the family; all others are major specializations for each lineage.

in the Plesiocystiscinae, here considered to be the most primitive group in this family. The presence of lateral teeth in the radula in this group, undoubtedly a primitive character state, is most significant. Some species of *Plesiocystiscus* have a tricuspid rachidian plate, another primitive feature (Kilburn, 1981:354). Because all other cystiscids have a greater number of cusps along the rachidian plate, an increase in the number of cusps is considered to be a specialization in this family. The remainder of the family have lost the lateral teeth, a derived condition also occurring in several other neogastropod families.

The unique character states that distinguish the Cystiscinae are a Type 3 animal and a Type 2 radula. *Extra* is thought to be a recent divergence from *Crithe*. The extinct genus *Topaginella*, which has a shell with fine axial costae, is likely an early offshoot from this lineage.

Persiculinae are distinguished by the presumed derived character states of a Type 4 animal, a Type 3 radula, presence of a siphonal notch, and presence of apertural lirae in many species. As *Canalispira* is thought to be a recent divergence, the absence of a siphonal notch

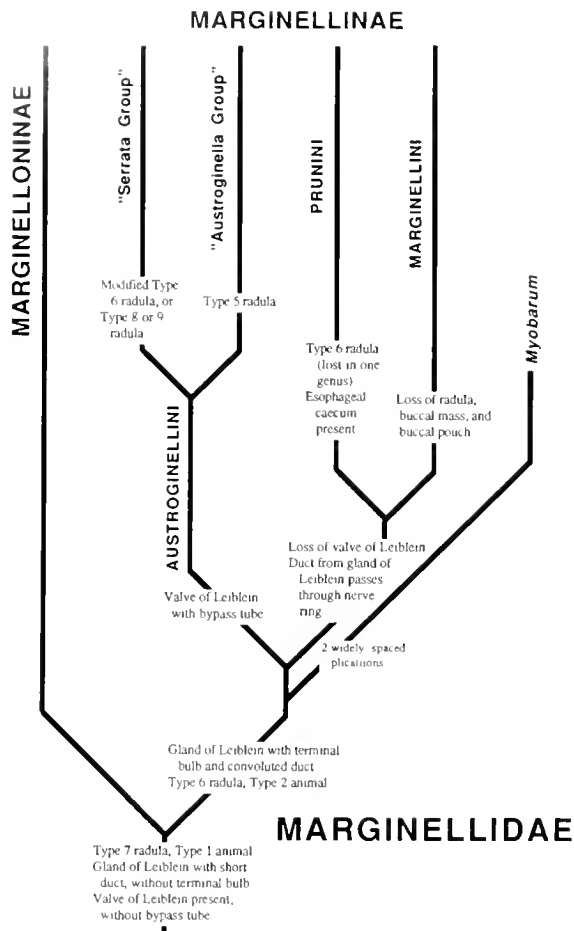


Figure 75. Intuitively derived phylogeny of the Marginellidae. Characters at base are primitive for the family; all others are major specializations for each lineage.

in this genus is hypothesized to be a secondary loss of this character. If absence of a notch is considered to be a retained primitive character, then development of a notch in the much earlier *Gibberula* and *Persicula* would have had to occur twice, which seems less likely. *Canalispira* also has a highly modified animal, lacking a siphon and tentacles. *Gibberula* is distinguished by the development of a glandular tube bypassing the valve of Leiblein, a derived character (figure 79). Development of an external varix in some species of *Persicula* is also a derived character for this family.

The Granulininae is, in some ways, the greatest departure in the family. Specializations in this group include the very distinctive Type 4 radula with modified odontophoral cartilage hoods, presence of an external varix, presence of modified cystiscid internal whorls, with the columella possessing 2 internally reduced plications in addition to 1 or 2 pseudo-continuous plications. The mantle covers the shell in this group, apparently another specialization within this family. Primitive characters that are retained include a Type 2 animal and the absence of a siphonal notch. The Granulininae is thought to have diverged from the main branch of the family

(figure 74) after the lateral teeth were lost from the radula. Because this group has a fossil record dating back only to the Miocene, it could also have diverged from the plesiocystiscine line (which shares a Type 2 animal) after the cystiscines and persiculines diverged, but this would imply that lateral teeth were lost twice in this family. *Pugnus* is considered to be a recent offshoot from *Granulina*. Although the Granulininae differs in a number of characters from the other subfamilies, the Cystiscinae and the Persiculinae differ in their radically different animal types. Thus, we feel that all four groups should be accorded equal ranking as subfamilies.

PHYLOGENY OF THE MARGINELLIDAE

Our hypotheses of relationships of the higher taxa within the family Marginellidae are summarized in figures 75 and 80. Assumed ancestral characters for this family include a Type 1 animal with a marginellid Type 7 radula, a gland of Leiblein with a short duct and lacking a terminal bulb, and presence of a valve of Leiblein (figure 80). Additional characters include a shell with unmodified internal whorls, continuous columellar plications, and presence of an external varix. All these ancestral characters have been retained in the subfamily Marginelloninae, which is considered to be the most primitive group in the family. The probable relationship between the Marginelloninae and Volutidae has been discussed previously. Because a number of marginellid groups with specializations of the foregut possess fewer cusps along the rachidian plate, loss of cusps, rather than an increase in cusps (as in the Cystiscidae), is considered to be derived within this family. Further evidence of this is found in the greatly reduced radula of *Hydroginella*, a highly specialized genus, and eventual loss of the radula in two lineages of the Marginellinae. The Marginelloninae is composed of only two genera, *Afrivoluta* and *Marginellona*, which can be easily differentiated by the number and orientation of columellar plications. Lack of eyes, a development for life in deep water, and a very weak siphonal notch further distinguish *Marginellona*.

The remainder of the family is grouped together as the subfamily Marginellinae, based on the shared specializations of the gland of Leiblein, which ends in a terminal bulb and has a long, convoluted duct (figure 80). The animal is the generalized Type 2 with a Type 6 radula. The rachidian plate of the Type 6 radula has fewer cusps than the Type 7 radula. The extinct genus *Myobarum* was probably an early divergence from this main stem of the Marginellinae but could be ancestral to the entire family, based on its appearance in the late Cretaceous. The Marginellinae diverged at this point into two main lineages. The Austroginellini retained the valve of Leiblein but developed a bypass tube (figure 80). Additional characters of the Austroginellini, which are apparently primitive, include attachment of the paired salivary glands to the esophagus in front of the valve of Leiblein, and the ducts from these glands being embedded in the esophageal walls (figure 80). The other lineage,

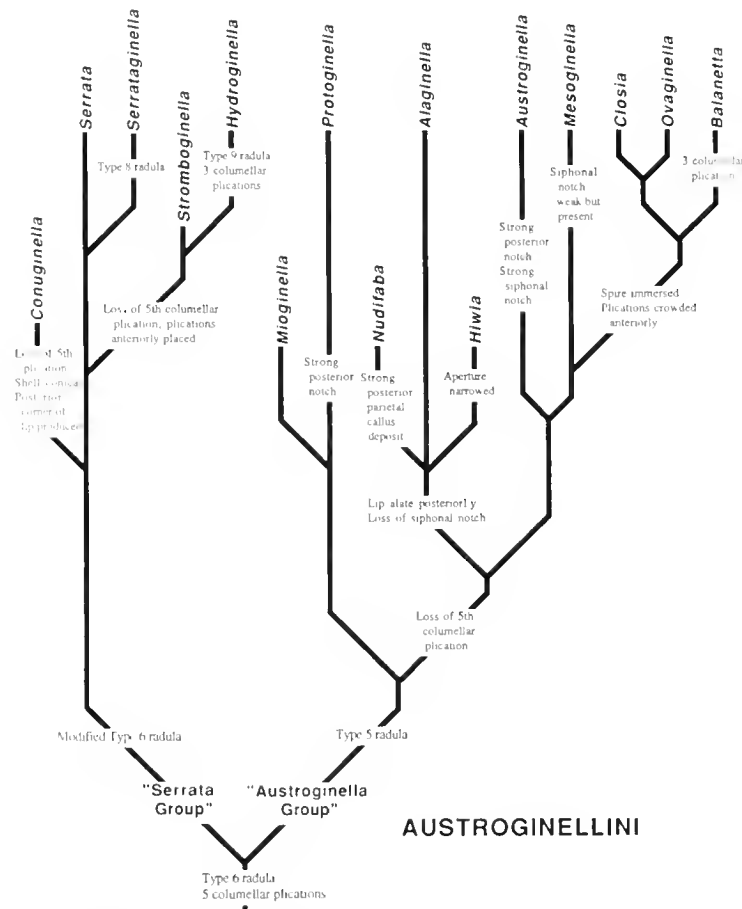


Figure 76. Intuitively derived phylogeny of the Austroginellini. Characters at base are primitive for the tribe; all others are major specializations for each lineage.

composed of the Prunini and Marginellini, lost the valve of Leiblein, but the duct from the gland of Leiblein passes through the nerve ring and empties into the extreme anterior end of the buccal cavity (figure 80). The Prunini and Marginellini are considered to be sister groups based on these shared features, with the Prunini developing an esophageal caecum, a derived character diagnostic for that tribe. Additional characters of the Prunini / Marginellini lineage, which are probably also primitive, include the paired salivary glands being free of the esophagus, and their ducts either attached to the esophagus or free, but not embedded in the walls as in the Austroginellini. The Marginellini is characterized by the complete loss of the buccal mass, including radula and odontophoral cartilages, plus the loss of the buccal pouch (figure 80). This loss also occurred in *Hyalina*, an undoubted member of the Prunini based on its possession of an esophageal caecum as well as shared conchological characters (figure 80). The loss of a radula is therefore considered to have occurred in two independent lines, not three as speculated by Coan and Roth (1976:220).

Intuitively derived phylogenetic relationships within the tribe Austroginellini are summarized in figure 76. Primitive anatomical characters for this tribe have al-

ready been mentioned. Additional conditions presumed to be ancestral include a Type 6 radula and a shell with five plications and a denticulate lip. This tribe diverged into two main lineages at this point. The "Serrata Group" developed a gradually weakening modified Type 6 radula, while the "Austroginella Group" developed a Type 5 radula, which is a narrower, fewer-cusped, chevron-shaped modification of the original Type 6 radula. (Informal groups are preferred at this level to avoid further inflation of taxonomic groupings). Within the "Serrata Group," the genus *Serrata* retained the modified Type 6 radula and most species retained the denticulate lip and at least a weakened fifth columellar plication. *Conuginella*, an extinct Miocene genus, lost the fifth plication and developed a distinctive conical shape and posteriorly produced lip. *Stromboginella*, another extinct genus, diverged in the Pleistocene from the lineage with anteriorly crowded columellar plications and lost the fifth plication. *Hydroginella*, also in this lineage, continued the trend of anterior crowding of plications, with the subsequent reduction to three plications. *Hydroginella* also continued the trend of radular reduction, resulting in a greatly reduced Type 9 radula. An additional specialization for this group is the presence of a collabral parietal callus

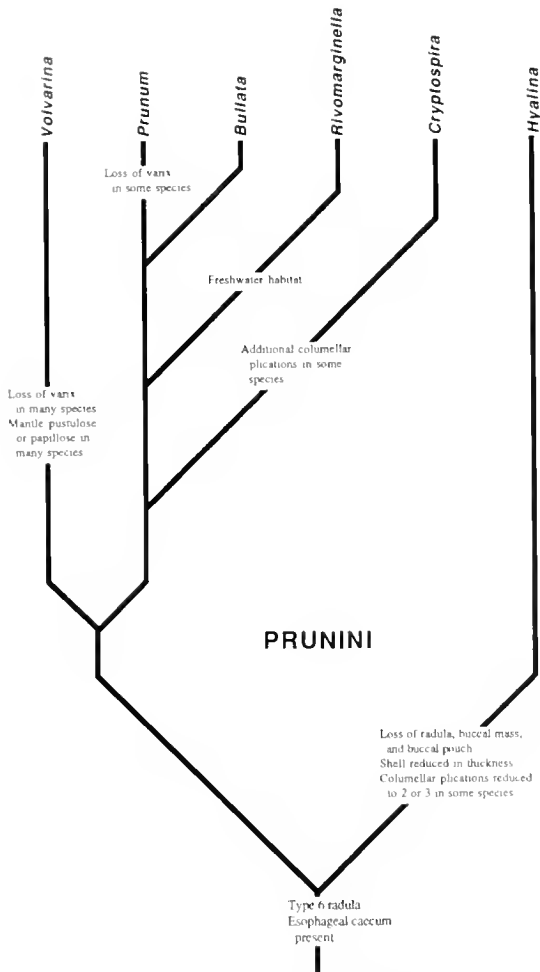


Figure 77. Intuitively derived phylogeny of the Prunini. Characters at base are primitive for the tribe; all others are major specializations for each lineage.

ridge just posterior to the columellar plications, in which the anterior end often superficially appears to be a weak fourth plication. This derived character, along with the distinctive radula, distinguishes this well-defined genus. One species is a known fish parasite. We anticipate that additional species may also share this behavior. Shell shape, as in many groups, is variable and accounts for the many synonyms of *Hydroginella*. The genus *Serrataginella* has a very distinctive and unusual Type 8 radula. The rachidian plate possesses secondary cusps not seen in any other marginellid, giving the main cusps a serrated appearance. Unusual derived shell characters include two collabral callus ridges, one of which is confined to the aperture, and replacement of the fifth plication by a weak denticle. The “*Austroginella* Group,” with a Type 5 radula, radiated into several genera. Possession of five strong columellar plications occupying more than half the aperture is ancestral within this group. *Protoginella* retained the five columellar plications and developed a strong posterior notch. An early offshoot of this branch is the extinct Eocene genus *Mioginella*, which

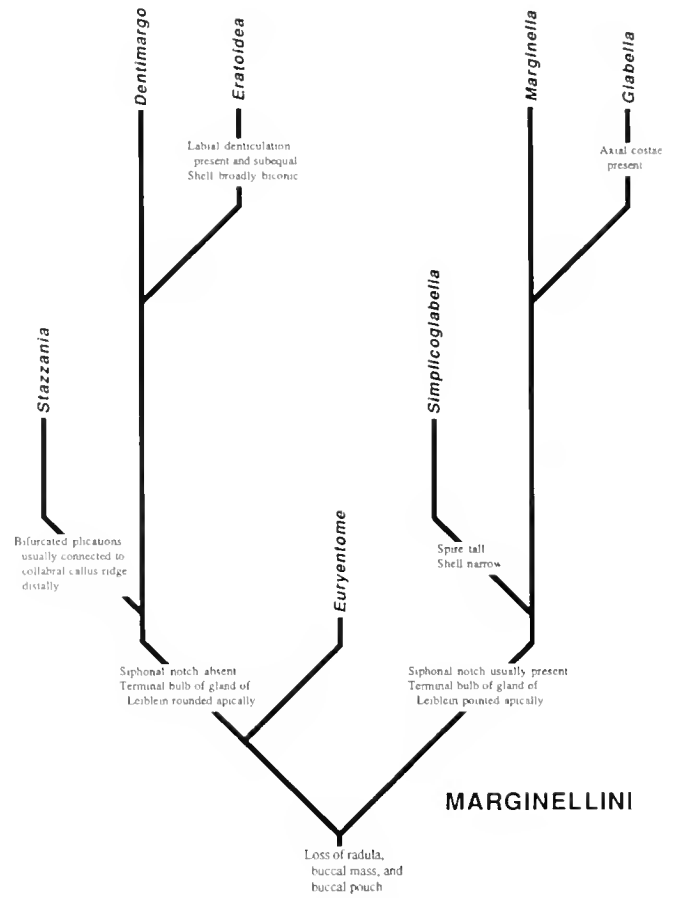


Figure 78. Intuitively derived phylogeny of the Marginellini. Characters at base are primitive for the tribe; all others are major specializations for each lineage.

shares the posterior notch but has carinate shoulders and a weak siphonal notch. The remainder of the “*Austroginella* Group” lost the fifth columellar plication. *Nudifaba* is an Eocene offshoot from the *Alaginella* line. *Alaginella* is characterized by a weakly to strongly alate posterior corner of the aperture, a strongly narrowed shell anteriorly, and general loss of labial denticulation in most species. This group also lacks distinct siphonal and posterior notches. Variable shape and shoulder development in this genus is responsible for the numerous genus-group synonyms. *Hiwia* is an extinct Eocene offshoot with a distinctive shell having strong axial costae and angulate or carinate shoulders. *Austroginella* is characterized by strong posterior and siphonal notches, as well as a distinctively thickened, smooth lip. *Mesoginella* is variable in shell shape and other features, has a weak or absent posterior notch, and the fourth plication is often remote. From this lineage diverged a group of genera with an immersed spire and thin, sharp, anteriorly crowded columellar plications. *Closia* and *Ovaginella* retained four plications. Strong labial denticulation was retained in *Closia*, which developed a colored shell, whereas *Ovaginella* generally lost labial denticulation

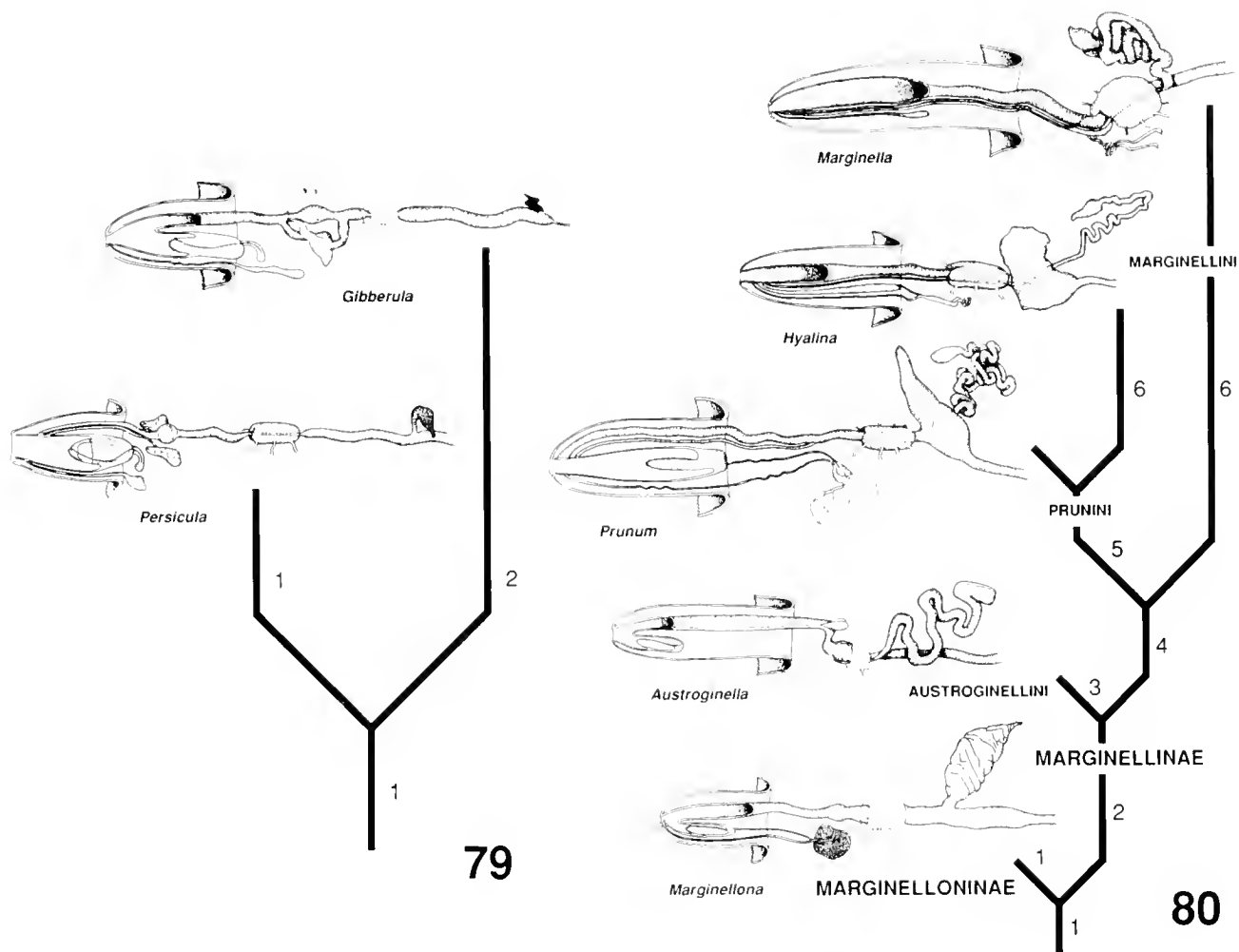


Figure 79. Intuitively derived phylogeny of the Cystiscidae, subfamily Persiculinae as illustrated by features of the foregut. Character states: 1: Valve of Leiblein without bypass tube. 2: Valve of Leiblein with bypass tube. *Gibberula* sp. after Ponder (1970), *Persicula interruptolineata* after figure 35 herein. **Figure 80.** Intuitively derived phylogeny of the Marginellidae as illustrated by features of the foregut. Character states: 1: Gland of Leiblein with short duct emptying posterior to nerve ring, valve of Leiblein present; marginellid buccal pouch present; marginellid radulae present. 2: Gland of Leiblein with terminal bulb and convoluted duct. 3: Valve of Leiblein with bypass tube; paired salivary glands attach to esophagus just anterior to valve of Leiblein; salivary ducts embedded in esophageal walls. 4: Loss of valve of Leiblein; duct from gland of Leiblein passes through nerve ring; paired salivary glands completely free of esophagus; salivary ducts attached or free, but not embedded in esophageal walls. 5: Esophageal caecum developed. 6: Loss of radula, buccal mass, and buccal pouch. *Marginellona gigas* after Harasewych and Kantor (1991), *Austroginella johnstoni* after Ponder and Taylor (1992), *Prunum* aff. *aletes* after figure 31 herein, *Hyalina pallida* after figure 32 herein, *Marginella glabella* after figure 34 herein.

but did not develop shell coloration. *Balanetta*, with a narrower shell, lost the fourth columellar plication.

The phylogeny of the tribe Prunini is summarized in figure 77. Anatomical features of this group have already been discussed, the most significant being the development of an esophageal caecum, a derived character state unique to this tribe. The Type 6 radula is considered primitive and is retained in nearly all genera. The widely distributed *Volvarina* lineage is characterized by loss of the external varix and development of a pustulose or papillose mantle, both occurring in many, but not all, species. The *Prunum* lineage, largely a western Atlantic radiation, has several extant Indo-Pacific species and two

genera that are offshoots. *Cryptospira* developed additional columellar plications in some species, and has a variously colored or patterned shell. *Rivomarginella*, the only freshwater group, is allied to the *Prunum* lineage based on the ontogenetic development of its varix. *Bullata* is a relatively recent offshoot of *Prunum* and is confined to the western Atlantic coast of South America. Much more work is required to fully characterize *Prunum* and *Volvarina*. Attention should be focused on anatomy, including the odontophoral cartilages and radulae, external features of the animal, including coloration and mantle characters, and shell characters. Study of external varix development shows great potential and involves

cutting and polishing shell cross-sections. The final branch of the tribe Prunini is the genus *Hyalina*, characterized by the complete loss of the buccal mass, including odontophore, radula, and buccal pouch. This genus is further characterized by a thin shell and columellar plications that are reduced to two or three in some species.

Our reconstruction of the phylogeny of the tribe Marginellini is summarized in figure 78. This group is characterized by complete loss of the buccal mass and buccal pouch, and lacks the esophageal caecum of the Prunini. Shell features include four strong columellar plications spanning half or more of the aperture. One branch of this tribe is characterized by absence of a siphonal notch, and the gland of Leiblein has the terminal bulb rounded distally. Further anatomical features in *Dentimargo* include a distally pointed penis and possession of three glandular structures or seminal receptacles that join the pallial oviduct between the albumen gland and capsule gland. *Stazzania* is an extinct Eocene offshoot of the *Dentimargo* lineage characterized by the bifurcated ends of the columellar plications joining a collabral callus ridge. *Dentimargo* shells usually have a prominent posterior labial denticle that is characteristic. The shells of *Dentimargo* are also generally narrower and differ in plications, which are usually not bifurcated in Recent species. Where the plications are bifurcated, the ends do not join a collabral callus ridge as they do in *Stazzania*. *Eratoidea* is a Caribbean offshoot with subequal labial denticulation and often weak to distinct axial costae. *Euryentome* is an extinct Eocene group from the western Atlantic with a strong posterior notch and often has parietal lirae posterior to the columellar plications. The second branch of the tribe has the siphonal notch usually present, and the terminal bulb of the gland of Leiblein is pointed distally. Further anatomical differences that may differentiate this group from the *Dentimargo* line include a simple penis and only two glandular structures between the albumen gland and capsule gland. Further work is needed to confirm this in more species. *Simpli-coglabella* is a Miocene offshoot with a narrower shell and a taller spire. *Marginella* is a large genus with a smooth shell, whereas *Glabella* is a well-defined group having distinct axial costae.

EXTRALIMITAL GENERA

The family Cryptochordidae was questionably included as an extinct subfamily of the Marginellidae by Ponder and Warén (1988:306). This family was originally named by Pchelintsev, *et. al* (1960:235) with the genus *Cryptochorda* Mörch, 1858 as type genus, and *Buccinopsis stromboides* Herrmann, 1781 as type species (OD) of the genus. Specimens of *Cryptochorda stromboides* from the Eocene of France were examined and this species is unrelated to either the Cystiscidae or the Marginellidae. This species has a tiny protoconch, a strong siphonal notch, irregularly-spaced axial costae, a weak siphonal fasciole, and the columella is bordered by a sharp edge with no columellar plications otherwise evident. The

glossy shells have some parietal callusing and a sharp posterior sinus. These are all characters of the Harpidae, and we would therefore agree with the assignment of *Cryptochorda* to that family by Palmer and Brann (1966: 616–617). This group can be removed from further consideration in the Cystiscidae or Marginellidae.

Bouchet (1989:82–83) placed the monotypic genus *Tateshia* Kosuge, 1986 (type species *T. yadai* Kosuge, 1986, OD) in the Marginellidae and regarded it as a marginellid with a primitive radula. We initially regarded this genus as a marginellid based on shell morphology but assumed an error had occurred in associating the radula, which is very muricid-like, a fact noted by Kosuge (1986: 78). We have been informed by Dr. Sadao Kosuge (pers. comm.) that radulae were obtained from three specimens and thus it appears no error occurred. This genus was originally placed in the Olividae by Kosuge. We can only conclude that this species, which has a radula unlike any member of the Cystiscidae or Marginellidae, belongs elsewhere. Perhaps further anatomical work will clarify the relationship of this enigmatic genus, which, admittedly, has a very marginellid-like shell.

Argentovoluta Vazquez and Caldini, 1989 (type species *A. bottai* Vazquez & Caldini, 1989) was mentioned by Poppe and Gotto (1992:215) as possibly belonging to the Marginellidae. The columellar plications are clearly volutid and, therefore, this genus can be removed from further consideration in the Cystiscidae or Marginellidae.

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ROBERT TUCKER ABBOTT

1919-1995

Dr. R. Tucker Abbott, former Curator of Mollusks at the National Museum of History, Smithsonian Institution, Curator and holder of the Pilsbry Chair of Malacology at the Academy of Natural Sciences of Philadelphia, Assistant Director of the Delaware Museum of Natural History, and founding Director of the Bailey-Matthews Shell Museum, died on November 3, 1995 on Sanibel Island, Florida after a long illness.

Dr. Abbott was known to the international malacological community as a prolific author of numerous scholarly and popular works on mollusks, and as an editor of *THE NAUTILUS*, *INDO-PACIFIC MOLLUSCA*, and *MONOGRAPHS OF MARINE MOLLUSCA*. An obituary, which will include a listing of his publications and malacological taxa, will appear in volume 110 of *THE NAUTILUS*.

The Evolution of Cold Tolerance in *Corbicula fluminea* (Bivalvia: Corbiculidae)

Brian R. Kreiser

Jeffrey B. Mitton

Department of Environmental,
Population and Organismic Biology
University of Colorado
Boulder, CO 80309-0334 USA

Since *Corbicula fluminea* (Müller, 1774) was first reported in the United States in 1938 (Burch, 1944), it has spread rapidly across the continent. In his review of the distribution of *Corbicula* in the United States, Counts (1986) listed it as occurring in 33 states. At that time, most of the site references were for locations south of 40° latitude. Several workers hypothesized that *Corbicula* appeared to have reached the limit of its ability to extend its distribution northward due to a lack of cold tolerance (e.g. Graney *et al.*, 1980; McMahon, 1982). Several observations supported this hypothesis. Laboratory experiments indicated that the absolute lower temperature limit for *Corbicula* was 2° C (Mattice & Dye, 1976). Likewise, it had been noted that severe cold caused heavy mortality (e.g. Horning & Keup, 1964; Rodgers *et al.*, 1979).

Though *Corbicula fluminea* has become established in numerous northern environments, these locations are protected from winter temperatures by industrial thermal effluents, usually from power plants. As a result, *Corbicula* is now found in association with power plants in Iowa (Ekblad, 1975), Minnesota (Cummings & Jones, 1978), Michigan (Clarke, 1981; French & Schloesser, 1991) and Connecticut (Morgan *et al.*, 1992). Graney *et al.* (1980) suggested that these thermally protected populations may serve as stepping stones in further northern expansion. One exception to the association with power plants was a population reported in Wisconsin on the St. Croix River (Cummings & Jones, 1978). However, there have been no further reports on this location so the success of this population is unknown. These observations suggest that low temperatures are a major restriction on the distribution of *Corbicula* in North America.

Published reports and personal communications reveal that *Corbicula fluminea* is spreading from thermal refuges and expanding its range beyond the limits that had been imposed by a lack of cold tolerance. *Corbicula* is quite common in the Great Lakes in Michigan and is now well established in small lakes within the state (Dr. J. Carlton, pers. comm., 1995). Likewise, *Corbicula* has spread from a power plant in Haddam, Connecticut up

the Connecticut River past Hartford. During severe winters, these populations suffer heavy mortality. Thus, thermal refuges provided by power plants, deep water and possibly spring water inputs are important for the persistence of the clam in the Connecticut River (Dr. D. Morgan, pers. comm., 1995; NUSCO, 1991, 1993, 1994, 1995). *Corbicula* is also appearing in new locations. Freeman and Perkins (1992) reported *Corbicula* in lakes in Lancaster Co. and in the Cozad Canal in Dawson Co., Nebraska. Furthermore, *Corbicula* is currently found in large numbers at river and canal locations along the Platte River from Brady to Cozad, Nebraska (M. Peyton, Central Nebraska Public Power & Irrigation, pers. comm., 1994). *Corbicula* is now resident at Donner Lake, which is at an elevation of 5933 feet in the Sierra Nevada, and is typically covered by snow and ice in the winter (G. Stockwell, Savannah River Ecology Lab, pers. comm., 1994). In Colorado the first recorded population was reported by Nelson and McNabb (1994) at the Cherry Creek Reservoir in Denver. Recently, we learned of another reported location at Highline Lake in western Colorado (Dr. S.-K. Wu, pers. comm., 1995).

We have investigated two of these northern locations. In October 1994, one of us (B.K.) examined an irrigation canal in Lincoln Co., Nebraska (T12N, R26W sec. 30). At that time, a dense population, approximately 120 individuals per square meter, was found in a canal holding only about .3 meters of water. A variety of age classes was present, with individuals ≤ 10 –15 mm shell length being more abundant than older individuals (25–30 mm shell length). In June 1995 we sampled Highline Lake, which is approximately 30 km northwest of Grand Junction, CO at an elevation of 4697 feet. We found only a few shells along the shore. However, a substantial concentration of individuals (about 30 per square meter) was discovered by diving 10–15 meters from shore near a boat launch. Furthermore, these individuals were quite large (30–40 mm shell length) suggesting that this population has been established for some time. Information obtained from conversation with fishermen concurred with these observations. Their remarks placed the clams

as having been established in this reservoir for at least 8 years. Voucher specimens from this site have been deposited at the University of Colorado Museum.

Despite predictions about *Corbicula fluminea*'s distribution limits in North America, this invader continues to move northward. In some of these northern locations, it appears that a thermal refuge is necessary. For example, along the Connecticut River winter mortality can approach 99%. After a severe winter, populations are primarily composed of juveniles, presumably the offspring of inhabitants of thermal refuges (NUSCO, 1994, 1995). However, *Corbicula* is present in other locations without the benefit of an apparent thermal refuge (e.g. the Nebraska irrigation canal & Highline Lake). Unfortunately, we have no data on winter temperatures or any information on the amount of winter mortality experienced. Without this information we are only able to speculate on the apparent cold tolerance of these populations. However, these observations do suggest that this invading species is expanding its range by evolving greater tolerance to cold.

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First Report of the Genus *Proadusta* Sacco, 1894 (Gastropoda: Cypraeidae) from the Western Hemisphere, with a Description of a New Species from the Eocene of Washington

Lindsey T. Groves

Malacology Section
Natural History Museum of Los
Angeles County
900 Exposition Boulevard
Los Angeles, California 90007 USA

Richard L. Squires

Department of Geological Sciences
California State University
18111 Nordhoff Street
Northridge, California 91330-8266
USA

ABSTRACT

A new species of cypraeid gastropod, *Proadusta goedertorum* n. sp., is reported from the middle lower Eocene ("Capay Stage") upper part of the Crescent Formation, Thurston County, Washington. This new species was found at two localities where shallow-water marine deposits are interbedded with rocky shoreline-forming basalt flows. *Proadusta* Sacco, 1894 was previously known only from the lower Eocene to lower Miocene of Europe, Myanmar (= Burma), and Indonesia.

Key words: *Proadusta*, Cypraeidae, Western Hemisphere, Eocene, Washington.

INTRODUCTION

Only five species of the family Cypraeidae are known from the Eocene of the eastern Pacific region (Groves, 1993; 1994a), and *Nucleolaria cowlitziana* Groves, 1994a is previously the only true cypraeid known from the Eocene of Washington. The first appearance of the genus *Proadusta* Sacco, 1894 in the Western Hemisphere is recorded here with the description of *Proadusta goedertorum* Groves and Squires, n. sp. from middle lower Eocene ("Capay Stage") strata in the upper part of the Crescent Formation, Thurston County, Washington. *Proadusta goedertorum* is also one of only two species of the genus found anywhere in the lower Eocene, the other being *P. chevallieri* (Cossmann, 1896) from Ypresian deposits of Liancourt, Oise Department, France.

STRATIGRAPHY

The new species is from the upper part of the Crescent Formation of Arnold (1906) at CSUN localities 1563 and 1564 (= LACMIP localities 16655 and 16848) at Larch Mountain, just west of Olympia, in the Black Hills area in the Washington Coast Ranges (Figure 1). These localities have been the subject of recent studies by Squires and Goedert (1994; in press) involving molluscan paleontology, depositional environment, and geologic age.

Fossil-bearing rocks at both localities consist of a thin section of richly fossiliferous and conglomeratic silty mudstone interbedded with basalt. Extrusion of the basalt caused shoaling and the establishment of a rocky shoreline community where gastropod and bivalved mollusks lived with colonial corals and abundant coralline algae. Shells were transported a short distance seaward where they were deposited as a matrix of coquina that infilled spaces between basalt boulders. Many of the shells in the coquina are small to minute, and their size prevented them from being destroyed during transport. Within the coquina are a few larger shells, like those of the new species, that apparently lived in the shallow-subtidal environment where coquina accumulation took place (Squires & Goedert, 1994; in press).

GEOLOGIC AGE

Based on mollusks and benthic foraminifera, Squires and Goedert (1994; in press) assigned the rocks at both CSUN localities 1563 and 1564 to the middle lower Eocene ("Capay Stage"). Clark and Vokes (1936) were the first to recognize this west coast mega-invertebrate stage. The stage name is informal; therefore, it is placed in quotation marks. Givens (1974) modified the use of the "Capay Stage," and it is in this modified sense that the name is used herein. As discussed in Squires et al. (1992), this stage is equivalent to the west coast benthic foraminiferal Penutian Stage, as used in the emended sense of Almgren et al. (1988). The "Capay Stage" is also equivalent to the middle part of the European Ypresian Stage (Squires, 1987).

ABBREVIATIONS

Abbreviations used for catalog numbers and/or locality numbers are: CSUN, California State University, Northridge; LACM, Natural History Museum of Los Angeles County, Malacology Section; LACMIP, Natural History Museum of Los Angeles County, Invertebrate Paleon-

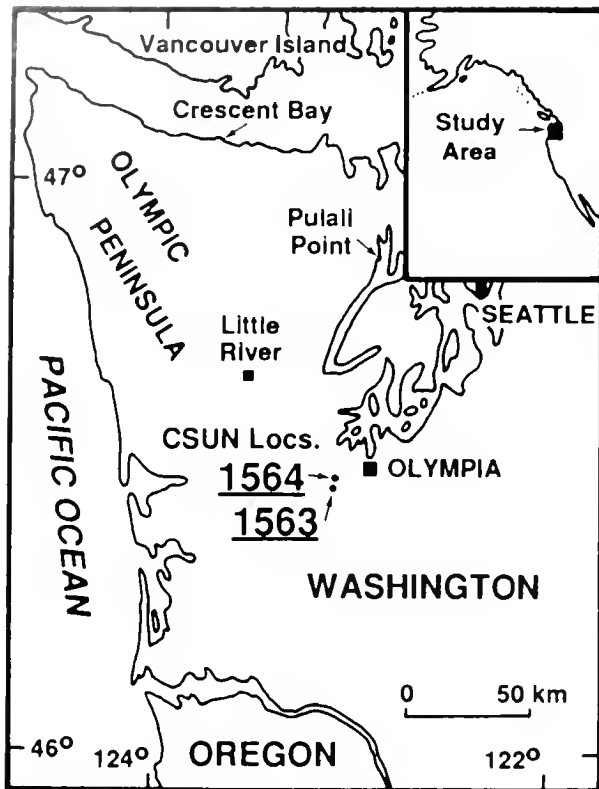


Figure 1. Index map showing localities of the new species described herein (Type locality = CSUN 1563 [= LACMIP 16655]). Localities are described in the "Localities Cited" section.

tology Section. Measurement parameters are defined as follows: length = greatest distance between anterior and posterior ends; width = greatest distance between lateral margins; and height = greatest distance between base and dorsum.

The classification herein follows that of Schilder and Schilder (1971).

SYSTEMATIC PALEONTOLOGY

Superfamily Cypraeacea Rafinesque, 1815
 Family Cypraeidae Rafinesque, 1815
 Subfamily Erosariinae Schilder, 1924
 Tribe Pustulariini Schilder, 1932
 Genus *Proadusta* Sacco, 1894

Type Species: *Cypraea (Proadusta) denticulina* Sacco, 1894 [= *C. (P.) splendens* (Grateloup, 1845) var. *denticulina* Sacco, 1894 (not of Grateloup)] by subsequent designation of Cossmann (1903:156). Lower Oligocene (Lattorfian Stage), Carcare, Liguria Province, northwestern Italy [Note: The Lattorfian Stage of Mayer-Eymar (1893) has been rejected as a standard chronostratigraphic unit of the lowermost Oligocene and may span the interval from the late Middle Eocene to the earliest Oligocene [= Priabonian through earliest Rupelian] (Berggren et al., 1985; Prothero, 1994)].

Original Description: *Testa affinis* Adusta, *sed spira non excavata, plus minusve prominens* (Sacco, 1894:33).

Diagnosis: Shell small to medium in size (19 mm), ovate to pyriform, with produced extremities; aperture curved posteriorly, with narrow deep canals; teeth numerous and fine; fossula wide, shallow, smooth (modified from Wenz, 1941).

Remarks: Schilder and Schilder (1971) recognized at least 18 species and 10 subspecies of *Proadusta* from lower Eocene (Ypresian) through lower Miocene (Aquitanian) strata of Europe and southeast Asia. (Specific ranges include: EOCENE of Belgium, England, France, Germany, Indonesia (Borneo), and Italy; OLIGOCENE of France, Germany, Italy, and Myanmar (= Burma); and MIOCENE of France). *Proadusta goedertorum*, sp. nov. is the first report of this extinct genus in the Western Hemisphere.

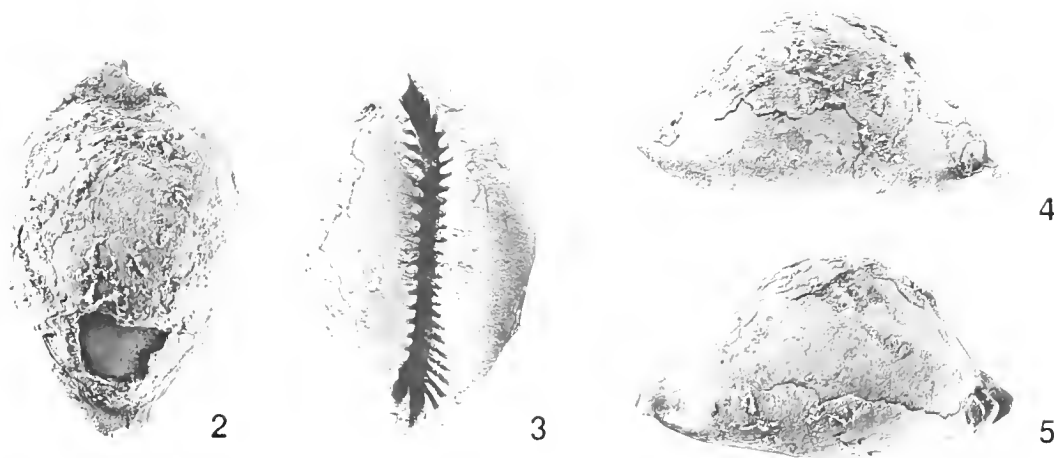
Dolin (1991) described *Cypraeacites blowi* from the upper Eocene (lowermost Jacksonian), Moodys Branch Formation, Montgomery Landing (= Creole Bluff), Grant Parish, Louisiana [U.S. Geological Survey locality 2003]. Groves (1994b) assigned *C. blowi* to the genus *Proadusta* following Schilder (1939) and Schilder and Schilder (1971) who had placed *Cypraeacites* in synonymy with *Proadusta*. Under Article 20 of the ICZN (1985) the genus *Cypraeacites* is not an available name and *blowi* is here assigned to the new world genus *Cypraeorbis* of Conrad (1865) based on similarities of shell shape, terminal ridges, fossula, and dentition, therefore establishing *P. goedertorum* as the first record of the genus *Proadusta* in the Western Hemisphere.

The new species of *Proadusta* described herein from the middle early Eocene of Thurston County, Washington provides additional evidence that tropical conditions existed in this region. Durham (1950) reported that the tropics extended northward of 49°N along the Pacific coast of North America during most of the Eocene. Squires and Groves (1993) also documented an Eocene tropical climate in King County, Washington by the presence of the ovulid species *Sulcocypraea mathewsonii* (Gabb, 1869) from the Tukwila Formation. Groves (1994a) further documented tropical conditions in the Washington Eocene with the description of *Nucleolaria cowlitziana* from the Cowlitz Formation.

Proadusta goedertorum Groves and Squires, new species (Figures 2-5)

Diagnosis: A *Proadusta* of small to medium size with produced extremities, posteriorly curved aperture, fine teeth, and smooth, wide fossula.

Description: Shell ovate shaped, small to medium in size with prominent produced extremities; spire covered; dorsum highly arched and smooth; maximum height slightly posterior of midpoint; slight marginal callus; base convex; aperture curved posteriorly toward columella; labial lip with 26 strong teeth with smooth interstices; columellar lip with 17 weak teeth with smooth interstices; teeth



Figures 2-5. *Proadusta goedertorum* Groves & Squires, n. sp., holotype. 2. Abapertural view. 3. Apertural view. 4. Left-lateral view. 5. Right-lateral view [all $\times 2.57$].

produced at both extremities forming slight anterior marginal ridges, indistinct in posterior canal; fossula wide, smooth, concave; posterior and anterior terminal canals shallow and narrow; columellar lip slightly inflated, shallow pit above posterior terminus at base of dorsum

Type Material: Holotype LACMIP 12375, paratype LACMIP 12376. The holotype measures 19.4 mm in length, 12.3 mm in width, and 10.8 mm in height. The paratype measures 17.1 mm in length, 10.4 mm in width, and 8.9 mm in height. Both specimens display original shell material. A third poorly preserved specimen from CSUN locality 1564 (= LACMIP locality 16848) also displays original shell material.

Type Locality: CSUN locality 1563 (= LACMIP locality 16655), Larch Mountain area, Black Hills, Thurston County, Washington (47°59'09"N, 123°8'12"W). Middle-early Eocene age ("Cpaya Stage"), upper part of the Crescent Formation.

Comparison: The new species is most similar to *Proadusta moloni* (Bayan, 1870) from the middle Eocene (Lutetian Stage) of San Giovanni Ilarione, Veneto District, Italy. *Proadusta goedertorum* has more numerous, finer apertural teeth and less pronounced terminal extensions. The new species also resembles *P. acyensis* (Raincourt, 1876) from upper Eocene (Auversian Stage) of Acy, Oise Department, France but has a less sinuous aperture, narrower posterior and anterior canals, and a wider labial margin.

Discussion: The excellent preservation of the new species allows for its unequivocal generic assignment. *Proadusta goedertorum* is significantly different from all other eastern Pacific cypraeids and is the only representative of this genus in the Western Hemisphere.

Etymology: This new species is named after James L. and Gail H. Goedert, Gig Harbor, Washington, for their numerous valuable contributions to the study of invertebrate and vertebrate paleontology of Washington.

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CSUN 1563 (= LACMIP 16655). At elevation of 680 m (2230 ft.), exposed in roadcut on northeast side of logging road, 47°59'03"N, 123°8'12"W, 300 m north and 50 m east of southwest corner of section 1, T17N, R4W, and 500 m S32°E of Larch Mountain, Capitol Peak U.S. Geological Survey 7.5', provisional edition 1986 quadrangle, Thurston County, Washington, 1:24,000. Middle early Eocene ("Capay Stage"), Crescent Formation. Collectors: J.L. & G.H. Goedert, 1992-1995.

CSUN 1564 (= LACMIP 16548). At elevation of 530 m, roadcut exposure, 800 m (2624 ft.) north and 50 m (164 ft.) west of southwest corner of section 25, T18N, R4W, Summit Lake U.S. Geological Survey, 7.5', 1981 quadrangle, Thurston County, Washington, 1:24,000. Middle early Eocene ("Capay Stage"), Crescent Formation. Collectors: J.L. & G.H. Goedert, 1992-1995.

Perotrochus metivieri, a New Species of Pleurotomariid from the South China Sea (Gastropoda: Pleurotomariidae)

Patrick Anseeuw

Mispelstraat 18
9820 Merelbeke
BELGIUM

Yoshihiro Goto

Yamamoto-Cho Minami 5-1-6
Yao City, Osaka Prefecture 581
JAPAN

ABSTRACT

Perotrochus metivieri, a new species of pleurotomariid, is described from bathyal depths in the South China Sea. It belongs to the thin-shelled group within *Perotrochus* termed "Group B" by Bayer (1965) and "*Perotrochus africanus* - complex" by Wagner and Coomans (1990). Comparisons are made with the other species of *Perotrochus sensu lato* that inhabit this area.

Key words: Pleurotomariidae, *Perotrochus*, new species, South China Sea.

INTRODUCTION

A medium-sized specimen of *Perotrochus*, live-collected but lacking soft parts or operculum, was first brought to our attention by Mr. G. Campanini of Pavia, Italy, who had obtained it indirectly from Russian trawlers operating in the South China Sea off Vietnam. Identification proved problematic as this specimen resembled to a certain extent both juvenile examples of the high-spired form of *Perotrochus africanus* Tomlin, 1848 and large adult specimens of *P. vicdani* Kosuge 1980. A second specimen was obtained by Mr. Donald Dan of Baltimore, USA. The data accompanying this specimen was vague. The shell came from a Russian source and was alleged to have been taken off New Zealand. A third specimen has since been obtained by the junior author.

Close examination and direct comparison of these three specimens revealed consistent differences in a series of characters in shell morphology that allow these specimens to be distinguished from other Recent Pleurotomariidae. This species is herein described as new, even though the locality data supplied with all three specimens is imprecise.

SYSTEMATICS

Superfamily Pleurotomarioidea Swainson, 1840

Family Pleurotomariidae Swainson, 1840

Genus *Perotrochus* P. Fischer, 1855

Perotrochus metivieri Anseeuw and Goto, new species (Figure 1)

Description: Shell (fig. 1) medium-sized for genus (maximum diameter to 68.0 mm, minimum diameter to 59.4 mm, height to 60.4 mm), thin, light, non-umbilicate. Shell profile trochiform with clearly gradate spire. Suture adpressed. Mean spire angle 82° (n = 3), profile of periphery rounded, base moderately convex. Protoconch damaged or worn on all specimens, glassy, of slightly more than 1 whorl, with weakly flared lip. Teleoconch of up to 7+ whorls. Selenizone appears near suture in first 1/4 whorl, descends to mid-whorl by whorl 2, and below mid-whorl by whorl 5. Selenizone flush with whorl surface or slightly concave, margins flush or slightly keeled. Anal slit broad (to 4.4 mm), long, with upper margin spanning up to 100°, lower margin to 72°. Axial growth striae dominant and strongly prosocline between suture and selenizone, weak and prosocyt between selenizone and periphery, opisthocyt on selenizone. Spiral sculpture of thin cords (10-12 between suture and selenizone, 1 on selenizone, 5-6 between selenizone and periphery) well-defined on early whorls, creating distinctly cancellate, finely beaded sculpture above and below selenizone of first 3-4 whorls. After 4th whorl, spiral cords rapidly become obsolete, persisting only as irregularly-spaced threads in area near the suture and between selenizone and periphery. Aperture subquadrate to oval, curve of columella gently sigmoidal, columellar margin nacreous, not thickened, extending 1/5 the distance from axis to periphery. Umbilicus excavated but imperforate. Base weakly convex, with 40-44 fine spiral cords intersected by regular, fine, axial growth lines, producing finely cancellate surface. Protoconch and first teleoconch whorl porcellaneous white; base color of teleoconch buff with occasional darker patches and slight, pinkish suffusion at margins of selenizone. Entire outer surface slightly iridescent due to thinness and translucency of outer shell layer. Interior of aperture (except base of previous whorl) covered by thin nacreous layer, within which the pattern of exterior sculpture is discernible. Nacre covers inner surfaces above and below slit, with extremely thin chamfer of constant width at slit margins. Operculum and soft parts unknown.

Type locality: Trawled in 350 m in the South China Sea off Vietnam.



Figure 1. *Perotrochus metivieri* Anseeuw and Goto, new species. Apertural, lateral, apical and ventral views of the holotype (USNM 880085), off Vietnam, South China Sea. Maximum diameter = 51.1 mm.

Type material: Holotype, USNM 880085, (max. diameter 51.1 mm, min. diameter 44.7 mm, height 43.8 mm), off Vietnam, South China Sea. Paratype 1, Anseeuw collection, max. diameter 68.0 mm, min. diameter 59.4 mm, height 60.4 mm), from the type locality. Paratype 2, Dan Collection, (specimen damaged, max. diameter unknown, min. diameter 59.8 mm, height 56.5 mm) New Zealand (?).

Etymology: This species is named for Dr. Bernard Métiévier of the Laboratoire de Malacologie, Museum na-

tional d'Histoire naturelle, Paris, in recognition of his extensive work in the field of Malacology and his contributions to the knowledge of western Pacific Pleurotomariidae.

Comparative remarks: *Perotrochus metivieri* is readily distinguished from all other species hitherto reported from the South China Sea: *Perotrochus hirasei* Pilsbry, 1903 (Bondarev, 1991), *P. teramachii* Kuroda, 1955 (Lan, 1994; Okutani, 1979), *P. caledonicus* Bouchet and Métiévier, 1982, and *P. vicdani* Kosuge, 1980 (Raybaudi,

1992). In silhouette it most closely resembles the southern Atlantic species *Perotrochus atlanticus* Rios and Mathews, 1968, particularly in the profile of the spire, but is otherwise unmistakable. Of the other species from the western Pacific, *P. tangaroana* Bouchet and Metivier, 1982, is similar in size and construction and similarly lacks a clear color pattern, but can be distinguished from *P. metivieri* by its higher, less gradate spire profile, more inflated base with correspondingly rounder aperture, and shorter, narrower slit. *Perotrochus metivieri* might be confused with juvenile *P. teramachii* Kuroda, 1955, but the former is smaller in adult form, lacks any clear patterning, and has a flatter base than *P. teramachii*. *Perotrochus metivieri* resembles in some respects certain specimens of *P. vicdani* Kosuge, 1980, from the South China Sea, but these differ in having strong coloration and patterning as well as finely beaded sculpture on the teleoconch.

Paratype 1 of *P. metivieri* differs somewhat in shape and appearance from the holotype, in particular by having a distinctly constricted penultimate whorl and slightly taller profile. Constriction of the whorl in mature adult specimens is a phenomenon occasionally observed in other pleurotomariids and may be indicative of a gerontic stage.

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furnished the second paratype as well as valuable advice. The photographs were supplied by Mr. Paul Callomon of Elle Scientific Publications, Osaka, Japan, who also edited and prepared the manuscript. Finally, we thank two anonymous referees for their helpful comments.

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Morphology and Possible Relationships of *Ecphora* (Cenozoic Gastropoda: Muricidae)

Geerat J. Vermeij

Department of Geology and
Center for Population Biology
University of California at Davis
Davis, CA 95616 USA

ABSTRACT

The muricid gastropod genus *Ecphora* Conrad, 1843, comprises Oligocene to Pliocene species from eastern North America and Oligocene to Middle Miocene species from Europe. Earlier workers speculated that it evolved in North America from an Early Oligocene *Tritonopsis*-like ancestor. Evidence from previously unstudied shell characters indicates that *Ecphora* belongs to the subfamily Ocenebrinae, whereas *Tritonopsis* is a subgenus of *Cymia* Mörch, 1860, a member of the Rapaninae. *Ecphora* lacks the parietal rib, lirate outer lip, and adapical extension of the outer lip of *Cymia* and related genera, and may have been derived from an as yet unknown ocenebrine ancestor in which the external shell sculpture was predominantly or exclusively spiral.

Key words: *Ecphora*, *Stenomphalus*, Muricidae, Neogene, Atlantic coastal plain.

INTRODUCTION

The genus *Ecphora* as classically understood by American authors is a distinctive group that was characteristic of Oligocene to Pliocene faunas of the Atlantic Coastal Plain of the United States (Petuch, 1988a,b; Ward, 1992). Its status as a muricid is well established by virtue of its shell morphology and by the fact that very large muricid-type drill-holes are common in bivalves co-occurring with *Ecphora*. These cylindrical holes are too large to have been made by muricids other than *Ecphora* (Vermeij, 1987; Petuch, 1988b; Campbell, 1993). No consensus has emerged, however, about the position of *Ecphora* and its relatives within the Muricidae. Petuch (1988a,b) regarded the group as a distinct subfamily Ecphorinae, which he held to be a New World parallel to the Old World subfamily Rapaninae Gray, 1853. He circumscribed the latter subfamily narrowly around the genus *Rapana* Kool (1993b) tentatively assigned *Ecphora* to the Ocenebrinae, whereas Carter *et al.* (1994) suggested that it is derived from *Tritonopsis*, a taxon assigned by all students of the Muricidae to the Rapaninae as broadly redefined by Kool (1993b), that is, encompassing such genera as *Thais*, *Rapana*, *Morula*, *Nassa*, and their relatives. The purpose of this paper is to review the genus

Ecphora, to discuss the distribution within Muricidae of several shell characters that have not previously been considered in arguments about the taxonomic assignment of *Ecphora* and superficially similar genera, and to argue that *Ecphora* should be referred to the Ocenebrinae.

CRITICAL REVIEW OF PERTINENT GENERA

Ecphora Conrad, 1843

Type species: *Fusus quadricostatus* Say, 1824 (figures 1, 2).

Synonyms:

Stenomphalus Sandberger, 1861 (type species, *Fusus cancellatus* Thomä, 1845, non J. de C. Sowerby, 1826, = *Stenomphalus caerulea* (Römer-Büchner, 1827))

Chesathais Petuch, 1988a (type species, *Chesathais lindae* Petuch, 1988a).

Ecphorosycon Petuch, 1988a (type species, *Ecphora pamlico* Wilson, 1987).

Trisecephora Petuch, 1988a (type species, *Ecphora tricostata* Martin, 1904).

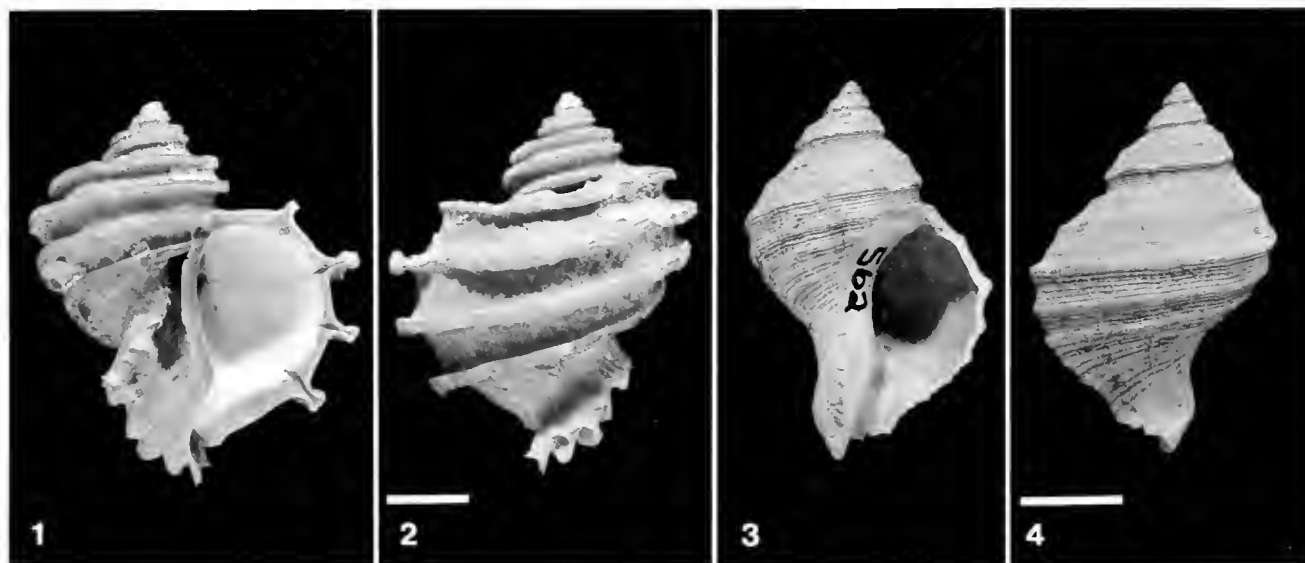
Siphoccephora Petuch, 1988b (type species, *Ecphora* (*Stenomphalus*) *aurora* Wilson, 1987).

Globcephora Petuch, 1994 (type species, *Ecphora floridana* Petuch, 1988b).

Latecephora Petuch, 1994 (type species, *Ecphora bradleyae* Petuch, 1987).

Revised diagnosis: Protoconch multispiral; teleoconch broadly fusiform; suture deep, channeled in adult; false umbilicus present; sculpture consisting of spiral elements only, three to eight prominent cords on last whorl and two on preceding whorl, outer lip planar, thin, crenate at edge, smooth on apertural side; adapical junction of outer lip gradual, without notch or extension; columellar margin smooth, straight; parietal rib absent; most species with thick brown external calcitic layer.

Remarks: *Ecphora* forms a compact group that, because of variations in sculpture and shape, has been divided into a number of subgenera by Petuch (1988a,b, 1994). These subgroups are here treated as subjective junior synonyms of *Ecphora*. The type species, *Ecphora quadricostata*, from the Pliocene Yorktown Formation



Figures 1, 2. *Ecphora quadricostata* (Say, 1824), Yorktown Formation (Pliocene), Virginia; collected by P. W. Signor; Vermeij collection. Ventral (1) and dorsal (2) views; scale bar = 1 cm. **Figures 3, 4.** *Cymia vaughani* (Mansfield, 1937), Haywood Landing Member, Belgrade Formation (latest Oligocene), North Carolina; E. H. Vokes Collection. Ventral (3) and dorsal (4) views; scale bar = 1 cm.

of Virginia (see Campbell, 1993), is characterized by four strong primary cords, and lacks secondary spiral sculpture. Most other species of *Ecphora* as defined here possess secondary cords in addition to the primaries, which number from three to eight depending on the population or even the stage of ontogeny. Primary ribs vary in cross-section from triangular to T-shaped, as well as in width. Other variable characters are the size of the false umbilicus and the length of the anterior siphonal canal. Carter *et al.* (1994) noted that all species of *Ecphora* beginning with the Late Oligocene *E. tampaensis* (Dall, 1915) have an external layer of calcite. The only fully aragonitic species is *E. wheeleri*, Rossbach and Carter, 1991 (Early Oligocene River Bend Formation, North Carolina), the earliest member of the genus in North America.

Petuch's (1988a) genus *Chesathais* was based on his new species *C. lindae* from the Middle Miocene (Serravallian) Choptank Formation of Maryland. Petuch (1988a) characterized this group as having a biconic fusiform shell, lirate outer lip, and a sculpture of fine spiral ribs and threads. This description accords better with *Rapana vaughani* Mansfield, 1937 (figures 3,4) and *R. biconica* Dall, 1915 than with the type species *C. lindae*. Petuch (1988b) included *R. biconica* in *Chesathais*, but made *R. vaughani* the type of *Rapanecephora*, which I consider to be a junior subjective synonym of *Tritonopsis* Conrad, 1865.

As Ward (1992) already pointed out, *Chesathais lindae* is a true *Ecphora*. The type specimen (USNM 424254) has four primary spiral ribs on the last whorl and two on the penultimate whorl. The second cord, counting from the suture, forms the periphery, which is evenly rounded. A secondary cord is situated below the suture,

as well as between cords one to three and in front of the fourth cord. The whole surface, including that of the broad siphonal canal, is covered with fine threads. The columella is smooth and straight. There is neither a parietal rib nor an anal notch, and the outer lip is not adapically extended. The inner surface of the outer lip is coarsely ribbed in accordance with the primary and secondary cords on the shell's exterior. The false umbilicus is very narrow. *Chesathais* is therefore a junior subjective synonym of *Ecphora*. Whether its type species, *Ecphora lindae*, is a subjective junior synonym of *E. meganae meganae* Ward and Gilinsky, 1988, as Ward (1992) contends, must await studies of variation and comparisons of material from the Choptank and Calvert Formations of Maryland.

Until 1987, the name *Stenomphalus* was used for Oligocene and Miocene species from Europe. Besides the type species, these include *S. jauberti* (Grateloup, 1840) from the Burdigalian (Early Miocene) and Helvetian (= Langhian, Middle Miocene) of France; *S. moulinsi* (Brochon, 1849) from the Burdigalian of France; *S. wiechmanni* (von Koenen, 1872) from the Vierland Stage (Early Miocene) of the North Sea Basin; and *S. koeneni* (Görges, 1952) from the Chattian (Late Oligocene) of Germany.

Through the kindness of P. Lozouet, I have examined a specimen of *Stenomphalus moulinsi* from Saucats, France. The broadly fusiform shell has six spiral cords on the last whorl and two on the penultimate whorl. The second cord forms the obtusely angulate periphery. One or more secondary cords and threads of various sizes are situated between the primary cords. The subsutural ramp is vertical. The columella is straight and smooth. The outer lip is smooth on its apertural side, and lacks an anal

notch and an adapical extension. The long siphonal canal is covered with spiral threads. There is a narrow false umbilicus. The posterior end of the aperture lacks a parietal rib or knob. *Stenomphalus jauberti* is said to be similar, but has only three cords on the last whorl and shows partial separation of the adult last whorl from the penultimate whorl (Cossmann & Peyrot, 1924; Wilson, 1987).

I have also examined a lot labeled "*Stenomphalus* sp." in the National Museum of Natural History, Leiden, kindly loaned to me by A. W. Janssen. This lot is of unknown (but probably Early Miocene) age, and comes from a gravel quarry on the Resebergweg, Lübeck-Kücknitz, in Schleswig-Holstein, Germany. Of the six shells, four specimens have four primary ribs, one has three primary ribs, and one has five. Small secondary cords are observable anterior to the primary cords on some specimens. Two primary cords appear on the penultimate whorl. The periphery is marked by the second cord. As in American species of *Ecphora*, the subsutural ramp is vertical, and there is a brown external layer probably composed of calcite.

Cossmann and Peyrot (1924) referred the French species to *Ecphora*, which they considered a subgenus of *Rapana*. Wilson (1987) maintained this placement, but regarded *Ecphora* as a genus and placed the European species in the subgenus *Stenomphalus*. He added a new American species, *E. (S.) aurora*, from the Pungo River Formation (Langhian Miocene) of North Carolina. Petuch (1988b) made this species the type of his new subgenus *Siphoecephora*. This species has a spindle-shaped shell with three very broad grooved spiral ribs on the last whorl, separated by narrow interspaces sculptured by one of two secondary spiral threads. As in the European species, two of the primary cords are visible in the spire whorls, and the subsutural ramp is nearly vertical.

The species that have been assigned to *Stenomphalus* vary in shape and in the number of ribs, and I can find no features that consistently distinguish *Stenomphalus* and *Siphoecephora* from *Ecphora*. Petuch's (1988b) proposal of *Siphoecephora* for *aurora* was supported largely by the mistaken belief that the European species of *Stenomphalus* are small (less than 20 mm long). Although *E. aurora* (length 80 mm) is the largest species assigned to *Stenomphalus*, the Miocene species of that group from Europe are 50 to 75 mm long. As the name implies, species of *Stenomphalus* generally have a small false umbilicus, but so do many American species of undoubted *Ecphora*, especially the older species. I consider *Stenomphalus* and *Siphoecephora* to be junior subjective synonyms of *Ecphora*.

Rapana Schumacher, 1817

Type species: *Rapana foehacca* Schumacher, 1817 (= *Buccinum bezoar* Linnaeus, 1758).

Diagnosis (shell characters only): Protoconch multispiral; teleoconch large (adults greater than 100 mm long),

broadly fusiform; sculpture consists of scaly tuberculated spiral cords, seven or eight on the last whorl, between which are situated numerous fine spiral threads; suture deep; outer lip planar, thin, crenate at edge, lirate on apertural side, adapically extended, without anal notch; anterior to the fifth spiral cord is a spiral groove, which at the outer lip ends in three enlarged and ventrally directed crenations; columella straight, smooth; parietal rib absent; small false umbilicus present; thin external layer of calcite.

Remarks: This genus is here narrowly circumscribed to contain three Recent species and their immediate Pliocene-Pleistocene ancestors. Besides the type species *R. bezoar*, which occurs subtidally from Japan to the Philippines, I include *R. venosa* (Valenciennes, 1846) from the cool-temperate northwestern Pacific, and *R. rapiformis* (Born, 1778) from the Philippines and North Australia to the Red Sea. *Rapana venosa* is a recent immigrant to the Mediterranean and Black Seas. Other fossil species that have been assigned to *Rapana* belong to *Cymia* and *Ecphora*. The Early Miocene Californian *R. vaquerosensis* Arnold, 1907, and the Baja Californian Early Miocene *R. imperialis* Hertlein and Jordan, 1927, may be large ocenebrines related to *Forreria* and *Chorus*.

Cymia (Cymia) Mörch, 1860

Type species: *Cuma sulcata* Swainson, 1840 (= *Buccinum tectum* Wood, 1828)

Diagnosis (shell characters only): Teleoconch thick, biconic; sculpture consisting of many fine scaly spiral threads and a single centrally placed spiral row of tubercles; aperture narrow; outer lip planar, thin, crenate at edge, coarsely lirate on apertural side, with deep adapical notch; columella straight, with strong central fold; parietal rib strong; suture indistinct except at final growth stage, when the last whorl may separate from the preceding one; false umbilicus narrow or absent; thin external layer of calcite present.

Cymia (Tritonopsis) Conrad, 1865

Type species: *Triton subalveatum* Conrad, 1848

Synonyms:

Rapanecephora Petuch, 1988b (type species, *Rapana vaughani* Mansfield, 1937).

Diagnosis: Shell fusiform to biconic; whorls flattened, separated by appressed or canaliculate suture; sculpture consisting of five or more spiral cords and secondary spiral threads; narrow false umbilicus present; aperture relatively broad; outer lip thin, lirate on apertural side, crenate at edge, with adapical extension but without anal notch; columella straight, with central fold that may be obsolete in some species; parietal rib present; calcite layer absent.

Remarks: Vokes (1989) pointed out that the lineage leading to *Cymia tecta*, which lives in the eastern Pacific

from Costa Rica to Peru, extends back to the latest Oligocene or earliest Miocene of Peru (as *C. berryi* Olsson, 1931). Other species are known from the Miocene of Trinidad, Venezuela, Colombia, Panama, and Baja California Sur, and from the Pliocene to the Recent of the tropical eastern Pacific.

A second group of species that Vokes (1989) recognizes as belonging to *Cymia* consists of species that differ from *Cymia* s. s. by having two or more rows of tubercles on the last whorl. These tubercles are situated behind the middle of the last whorl, and the subsutural slope is nearly vertical rather than obliquely sloping as in the *Cymia tecta* group. The shell therefore superficially resembles double-knobbed specimens of the rapanine genus *Stramonita* Schumacher, 1817. This group contains *C. monoplex* (Sandberger, 1861) from the Stampian (= Rupelian, Early Oligocene) of western Europe; *C. grateloupi* (d'Orbigny, 1852) from the Aquitanian (latest Oligocene) of France; *C. calcarata* (Grateloup, 1833) from the Aquitanian and Burdigalian of France; *C. henckeni* Maury, 1917, from the Early Miocene Baitoa and Thomonde Formations of Hispaniola; *C. marcanoi* Vokes, 1989, from the latest Miocene or early Pliocene Cercado Formation of the Dominican Republic; and perhaps *C. pleuriplicata* Cossmann and Peyrot, 1924, from the Burdigalian of France. The anal notch in this group is weak. The outer lip is provided on its apertural side with denticles. Cords are numerous in the American species and in *C. pleuriplicata*, but they number from four to six in *C. monoplex*, *C. grateloupi*, and *C. calcarata*. The central columellar fold is always strong. In *C. calcarata* there are one or two smaller columellar folds immediately anterior to the central fold. A thick parietal rib is invariably present. This group of species may deserve separate subgeneric status. It differs from *Cymia* s. s. by the presence of at least two posteriorly placed rows of tubercles instead of one central row.

The type species of *Tritonopsis*, *Triton subalveatum* Conrad, 1848, from the Mint Spring and Byram Formations of the Vicksburg Group (Early Oligocene) of Mississippi, differs from the two groups of *Cymia* discussed above by lacking an anal notch and by the absence of tubercles. In some individuals, two of the spiral cords are more strongly expressed than the others (MacNeil & Dockery, 1984; Carter *et al.*, 1994). The last whorl is rounded, not shouldered. The outer lip bears nine denticles on its apertural side that extend as lirae further into the aperture. A second species is *C. (T.) woodii* Gabb, 1860, from the Early Miocene Kirkwood Formation of New Jersey. A third undescribed species with an angulate rather than rounded last whorl and with axial swellings between the spiral bands was recorded by Woodring (1973) from the Gatuncillo Formation (Late Eocene) of Panama.

The genus *Rapancephora* Petuch, 1988b was proposed for biconic shells with a low spire, sloping shoulder, and a sculpture of spiral threads and weak peripheral nodes. Petuch (1988b) based his genus on *Rapana vaughani* Mansfield, 1937, from the Tampa Limestone (Aquitanian)

of Florida. Mansfield (1937) described this species on the basis of a cast made from a mold. Only the upper surface of most of the last whorl and part of the spire is visible on the type specimen (USNM 495946). Characters of the aperture therefore remain unknown. The last whorl bears eight or nine weak spiral cords, of which the third (counting from the indistinct appressed suture) forms a weakly noded periphery. Threads are intercalated between the cords.

Specimens from the coeval Haywood Landing Member of the Belgrade Formation of North Carolina have also been assigned to this species under the generic name *Tritonopsis* (Rossbach & Carter, 1991; Ward, 1992; Carter *et al.*, 1994). I have examined beautifully preserved shells from this unit in the E. H. Vokes collection, as well as material sent to me under the name *Tritonopsis vaughani* by J. G. Carter. Most specimens have five primary spiral cords on the last whorl, but a few have six or seven cords. The third cord forms a smooth periphery, which is located well posterior of the midpoint of the last whorl. Between the primary cords are situated many spiral threads and sometimes a very weak secondary cord. The obliquely upturned anterior siphonal canal bears fine spiral threads. Adjacent to it is a very small false umbilicus, which in many specimens is absent. The apertural side of the outer lip bears lirae or sometimes paired elongate denticles. The straight columella is usually smooth, but in some specimens (Figure 2) a trace of a central fold is observable. The suture is narrowly canaliculate. The outer lip is adapically elongated opposite a thick parietal rib; an anal notch is lacking. According to Carter *et al.* (1994), the shell is wholly aragonitic.

Richards (1943) described *Rapana gillettei* from the Silverdale Beds (= Haywood Landing Member of the Belgrade Formation) of North Carolina. Ward (1992) regarded this taxon as distinct from his *Tritonopsis vaughani* from the same formation. According to Ward, *R. gillettei* has weaker spiral ribs and more rounded whorls. I cannot separate *R. gillettei* from shells considered as *T. vaughani* by Ward (1992) and Carter *et al.* (1994). Given the poor preservation of the type of *Rapana vaughani* and the tendency for spiral sculpture to vary in prominence in many rapanines, I consider *Rapana gillettei* Richards, 1943, to be a junior subjective synonym of *Rapana vaughani* Mansfield, 1937, which I consider to be a species of *Cymia* (*Tritonopsis*).

Co-occurring with *C. vaughani* in the Tampa Limestone as well as in the Haywood Landing Member of the Belgrade Formation is *Rapana conica* Dall, 1915. Ward (1992) assigned this species to *Tritonopsis*, and pointed out that Richards (1943) referred to it as *Rapana vaughani*. Petuch (1988b) assigned *R. biconica* to *Chesathais*. The species differs from *Cymia* (*Tritonopsis*) *vaughani* chiefly in having the spiral sculpture consisting of fine spiral threads, a sharp peripheral cord, and sometimes two to three additional cords below the periphery. The siphonal canal is longer and the columella is more curved. No trace of a fold appears in the columella in any specimens I have examined.

Assignment of *Rapana vaughani* and *R. biconica* to *Tritonopsis* (Rossbach & Carter, 1991; Ward, 1992; Carter *et al.*, 1994) is justified by virtue of the spiral sculpture, lirate outer lip, adapical extension of the outer lip, absence of an anal notch, and the presence in at least some specimens of *R. vaughani* of a very weak central columellar fold. *Rapana conica* clearly diverges significantly from the type of *Tritonopsis* in the absence of the columellar fold, but it is morphologically linked to the more typical members of the subgenus by *R. vaughani*.

Vokes (1989) regarded *Tritonopsis* as a synonym of *Cymia*. I believe that separation of the two is warranted on the basis of the absence of an anal notch and of tubercles in *Tritonopsis*. The subgenus ranges from the Late Eocene to the Early Miocene of Atlantic North and tropical America.

Petuch (1988b) included in his genus *Rapanecphora* one additional species besides *Rapana vaughani*. This is the Early Eocene *R. nanjemoyensis* Petuch, 1988b, from the Woodstock Member of the Nanjemoy Formation of Maryland. Carter *et al.* (1994) noted that the single specimen of this species is poorly preserved. I have not seen it and cannot comment on its taxonomic placement.

DISCUSSION

Rossbach and Carter (1991) and Carter *et al.* (1994) proposed that *Ecphora* arose during the Early Oligocene from a *Tritonopsis*-like ancestor. They pointed to a form of *T. subalveata* (Conrad, 1848) from the Byram Formation of Mississippi with two strong cords on the spire whorls as close to the possible ancestor of *Ecphora*, whose earliest species (*E. wheeleri* Rossbach & Carter, 1991) is known from the approximately coeval River Bend Formation of North Carolina. In support of this hypothesis, these authors noted similarities in spiral sculpture, shell shape, presence of a false umbilicus, and geographical proximity.

Derivation of *Ecphora* from *Tritonopsis* would, however, require the modification of four traits: the loss of the parietal rib, the loss of the central columellar fold, the loss of lirae on the apertural side of the outer lip, and the elimination of the adapical extension of the outer lip. The fact that each of these changes has occurred in one or another rapanine lineage shows that such a derivation is possible, but the alternative that *Ecphora* is unrelated to *Cymia* and *Tritonopsis* seems more parsimonious to me. The reasoning in support of this conclusion is based on the distribution in Muricidae of the four traits enumerated above.

The absence of a parietal rib appears to be plesiomorphic in the Family Muricidae. This is the condition in all Trophoninae and Ocenebrinae, as well as in *Rapana*. The three oldest muricine genera (*Paziella*, *Poirieria*, and *Pterynotus*), all of which existed by Paleocene time, also lack a parietal rib. The rib is present in advanced muricines such as *Bolinus*, *Chicoriscus*, *Hexaplex*, *Murex*, *Phyllonotus*, and *Siratus*, as well as in most rapanines.

The only genera in the Rapaninae other than *Rapana* without a parietal rib are limpet-like taxa. These include *Concholepas*, in which the last whorl completely envelops all preceding whorls, and *Plicopurpura*. In the latter genus, only the limpet-like morphs of the two species, *Plicopurpura columellaris* (Lamarck, 1816) and *P. patula* (Linnaeus, 1758), lack the parietal rib (see Vermeij & Kool, 1994). Within Ocenebrinae, a few species or populations have a parietal knob in the adult shell. This condition exists in Californian thick-shelled morphs of *Nucella emarginata* (Deshayes, 1839), in some individuals of the Californian *Acanthinucella spirata* (Blainville, 1832), and in the Californian *Roperia poulsoni* (Carpenter, 1864) (see Vermeij, 1993). The absence of a parietal rib in *Ecphora* is consistent with assignment to the Ocenebrinae, and probably represents the plesiomorphic condition for the Muricidae rather than the secondary loss of a rib.

The smooth columella is a character state that *Ecphora* has in common with most other muricids. Columellar folds are present in Rapaninae including *Cymia*. The absence of folds in *Ecphora* is probably plesiomorphic in *Ecphora* and other Ocenebrinae, as well as in such rapanines as *Rapana* and *Dicathais* (for further discussion see Vermeij & Kool, 1994). Ponder and Vokes (1985) have similarly argued that rugae on the columella are derived features in several muricine stocks such as *Haus-tellum* and *Bolinus*.

The apertural side of the outer lip of *Ecphora* is smooth. In *Cymia* and many other Rapaninae, however, this surface is adorned with polished spiral ridges, or lirae. Such lirae are never present in Ocenebrinae, although the apertural edge of the outer lip is often thickened and dentate. The plesiomorphic condition of Muricidae is probably a smooth apertural surface of the outer lip. This is the condition seen in Ocenebrinae, Trophoninae, and in the plesiomorphic muricine genera *Paziella*, *Poirieria*, and *Pterynotus*.

The outer lip in *Ecphora* makes a high-angle junction with the preceding whorl, and is neither notched nor extended at its adapical end. In this respect it differs from *Cymia* and all other members of the Rapaninae except the limpet-like *Concholepas*. *Ecphora* shares its outer-lip junction with all other members of the Ocenebrinae and Trophoninae, as well as with plesiomorphic Muricidae.

Detailed anatomical studies by Kool (1993a,b) have revealed that fusiform muricids with a moderately long open siphonal canal and without well-defined varices belong to two distinct clades, the Ocenebrinae Cossmann, 1903, and the Rapaninae Gray, 1853. The Ocenebrinae in addition contains a large group of species with a narrow, sometimes closed, siphonal canal and with predominant axial sculpture. In a subsequent study (Vermeij & Kool, 1994), we identified shell characters by which the two subfamilies can be distinguished. As pointed out above, almost all rapanines have a parietal rib, and the outer lip is either adapically extended or provided with an anal notch. Ocenebrinae lack these traits.

Although a formal cladistic analysis of shell characters must be performed and is in progress to test these arguments, the distribution of characters implies that *Ecphora* shows none of the synapomorphies associated with the Rapaninae (Vermeij & Kool, 1994). I therefore agree with Kool (1993b) that *Ecphora* should be assigned to the Ocenebrinae. The only fact that potentially conflicts with this interpretation is the finding that *Ecphora panlico* Wilson, 1957, and *E. cf. E. quadricostata* (Say, 1824) have a three-whorl (multispiral) protoconch (Ward, 1992; Kool, 1993b). Multispiral protoconchs occur widely among Rapanines and are apparently primitive in the Muricidae (Vokes, 1971; Ponder & Vokes, 1988). The protoconch of *Ecphora* differs from that of rapanines, however, by lacking a sinusigeral notch. Most Ocenebrinae have paucispiral protoconchs, but there are exceptions. Houart (1989) has noted that three West African species of *Ocenebra*, (*O. coscli* Houart, 1989; *O. inermicosta* Vokes, 1964; and *O. isaacsi* Houart, 1984) have a multispiral protoconch. The same may be true of the New Zealand ocenebrine genus *Haustrum* (Kool, 1993b).

Unfortunately, the origins of *Ecphora* within the Ocenebrinae remain obscure. Wilson (1957) and Petuch (1988b) justifiably rejected the idea that the Late Cretaceous species *Ecphora proquadricostata* (Wade, 1917) from the Ripley Formation (Maastrichtian) of Tennessee is related to true *Ecphora*. On the basis of protoconch morphology, Bandel (1993) argues that *E. proquadricostata* is a mesogastropod related to the Trichotropidae. Other Cretaceous genera from the Gulf Coastal Plain assigned to the Muricidae by Sohl (1964a,b) have also been interpreted by Bandel (1993) as belonging to this mesogastropod family. There are no obvious Eocene antecedents of *Ecphora* in North America.

Many ocenebrine genera share with *Ecphora* a sculpture consisting predominantly or exclusively of spiral cords or heavy ribs. These include the South American genus *Chorus* (Miocene to Recent) and the Floridian Pliocene genus *Zulloia* (see Petuch, 1994), as well as members of the so-called *Nucella* group: *Acanthina* in temperate South America, *Acanthinucella* in the north-eastern Pacific, *Lepsiella* and *Lepsithais* in Australia and New Zealand, *Nucella* in the temperate North Pacific and North Atlantic, and *Trochia* in South Africa. None of these genera typically possesses a false umbilicus as does *Ecphora*, and the outer lip of many members of the *Nucella* group is greatly thickened and denticulate on its apertural side. Most species of *Ecphora* have the outer lip thin and smooth on its inner side. This condition also occurs in the South African *Trochia cingulata* (Linnaeus, 1767), the type of *Trochia* Swainson, 1840, which further resembles *Ecphora* in having one to five heavy spiral ribs. None of the genera mentioned above is known from before latest Oligocene time, but a pre-Miocene origin of the *Nucella* group is strongly implied by the Recent distribution of its members (Vermeij, 1993). *Ecphora* is first known in the Early Oligocene of eastern North America and France. Where the group originated cannot be pinpointed with the available evidence.

The longer persistence of *Ecphora* in the Western Atlantic than in the European sector of the eastern Atlantic is an example of a common biogeographical pattern in Neogene mollusks. Europe lost many genera after the Middle Miocene that survived in tropical America, the western Atlantic, of the Indo-West Pacific region. Possibly the extinctions of the Middle Miocene were more severe in the eastern Atlantic than elsewhere. Further discussion of this pattern will be deferred to a later paper.

Petuch (1988a) proposed the new subfamily Ecphorinae to encompass *Ecphora* and several other genera that have here been synonymized with *Ecphora*. He considered it to be a parallel development to the Old World Rapaninae, narrowly defined around the genus *Rapana*. Here I consider the Ecphorinae to be a genus in the Ocenebrinae. Whether the morphological resemblance between Rapaninae and spirally sculptured Ocenebrinae (including the *Nucella* group) is the result of convergence or of the retention of plesiomorphic features common to both groups remains an open question.

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Taxonomic Notes on the Western Atlantic Turridae (Gastropoda: Conoidea)

Donn L. Tippett

10281 Gainsborough Road
Potomac, MD 20854, USA

ABSTRACT

This paper presents results of research on the systematics of the western Atlantic Turridae. The following new species are described: *Drillia (Drillia) wolfei*, *Drillia (Clathrodrillia) petuchi*, *Fenimorea kathyae*, *F. petiti*, *Sedihopsis riosi*, and *Clathurella eversoni*. The new name *Drillia (Clathrodrillia) dautzenbergi* is proposed, as are the new generic combinations *Fenimorea pagodula* and *Pilsbryspira (Nymphuspira) auberti*. Lectotypes are designated for *Drillia (Clathrodrillia) dautzenbergi* and *Fenimorea pagodula*. Radulae are figured for *Drillia (Drillia) wolfei*, *Lioglyphostoma hendersoni*, *Viridrillia williami*, *V. hendersoni*, *Inodrillia nucleata*, *Pilsbryspira albocincta*, *Pyrgocythara filosa*, *P. plicosa* and *P. danae* (U. S. west coast). Opercula are figured for: *Drillia (Drillia) wolfei*, *Fenimorea kathyae*, *F. sunderlandi* var., *F. petiti* and *Lioglyphostoma hendersoni*. The animal of *Pilsbryspira albocincta* is figured.

Key Words: Turridae, Taxonomy, Western Atlantic.

INTRODUCTION

Although the family Turridae in the western Atlantic has been extensively studied and documented, there remain many gaps in our knowledge of its systematics and a major review is needed. New species are discovered not infrequently. In the absence of a definitive revision, such as provided for the tropical eastern Pacific by McLean (1971) and currently being carried out by Kilburn (1983, 1985, 1986, 1989, 1991, 1992, 1993, 1994) for the South African fauna, scattered information is at least of some value. This paper presents findings obtained during research on the family conducted over a number of years. Included are descriptions of new species, a new name, lectotype designations, animal and radular details, range data, and other information. It is hoped that these findings will provide clarification of some issues and represent a contribution to our knowledge of the family.

MATERIAL AND METHODS

Specimens, both of empty shells and shells containing either preserved or dried animals, were obtained from various sources. Dried animal material was dissolved in KOH. Radulae were mounted on microscope slides and

stained with Prontosil + CMCP-10. Type specimens, slides, and voucher specimens were deposited at the USNM and other institutions. The conventional classification of the family Turridae is used rather than that proposed by Taylor *et al.*, 1993. This proposed classification is too recent to have gained general acceptance and does not consider the fossil record of the family as noted in a review of the classification by Kohn and McLean (1994).

Abbreviations used:

a = ratio of length of aperture plus canal to shell length;
N = number, (of adult specimens);

S.D. = standard deviation;

w = ratio of maximum shell width to length;

AMNH = American Museum of Natural History, New York;

ANSP = Academy of Natural Sciences, Philadelphia;

DMNH = Delaware Museum of Natural History, Wilmington;

IRSNB = Institut Royal des Sciences Naturelles de Belgique, Brussels;

LACM = Los Angeles County Museum of Natural History, Los Angeles;

MCZ = Museum of Comparative Zoology, Harvard University, Cambridge;

MNHN = Muséum National d'Histoire Naturelle, Paris;

MORG = Museu Oceanografico "Prof. Eliézer de C. Rios", Rio Grande;

NHM = The Natural History Museum, London;

NM = Natal Museum, Pietermaritzburg;

USNM = National Museum of Natural History, Smithsonian Institution, Washington, D.C.

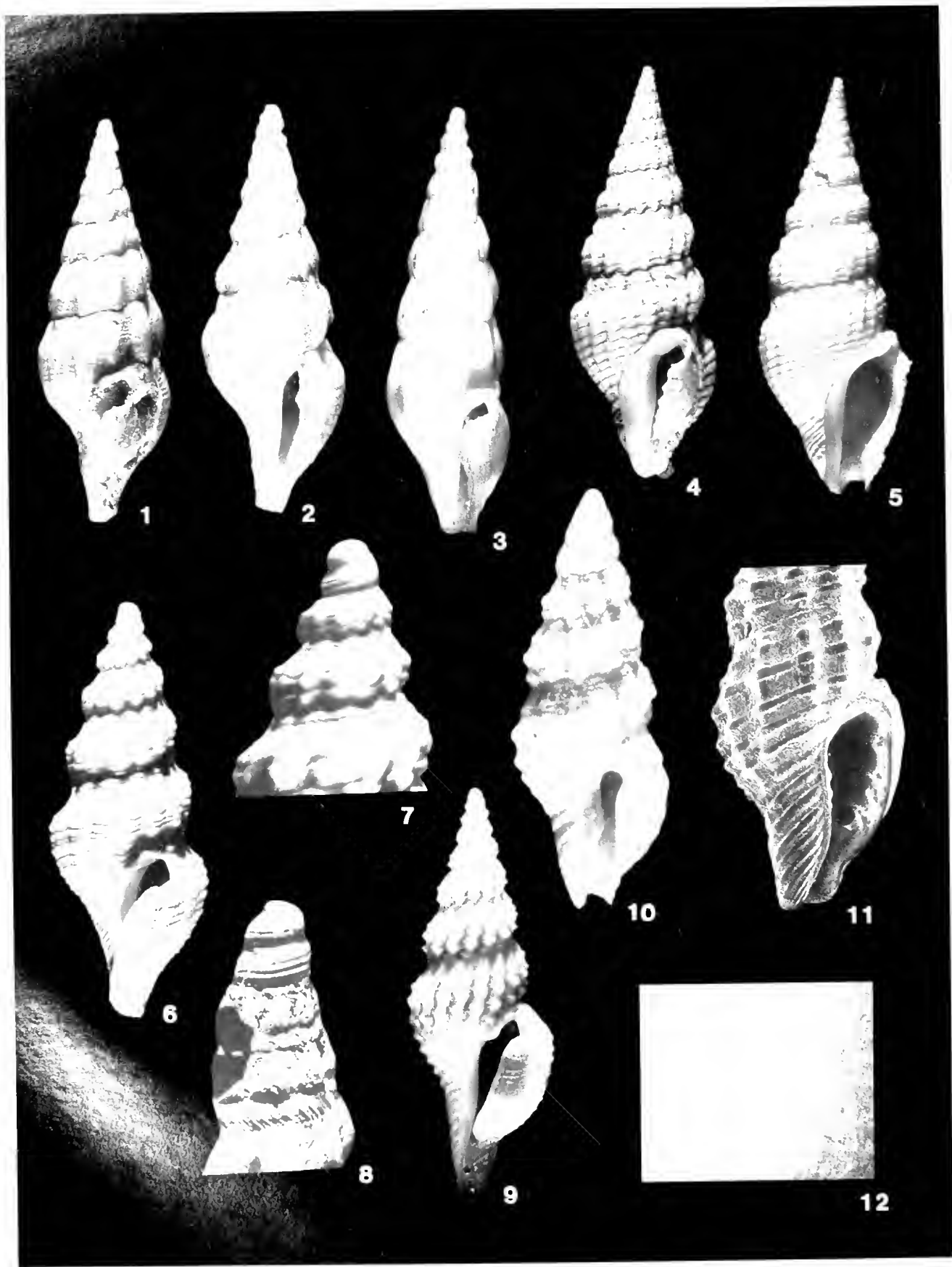
SYSTEMATICS

Subfamily **Drilliinae** Olsson, 1964

Genus *Drillia* Gray, 1838

Type species: *Drillia umbilicata* Gray, 1838; by subsequent designation (Gray, 1847).

Drillia (Drillia) wolfei Tippett, new species
(Figures 1, 28, 31)



? Sp "L" Rice & Kornicker, 1965: 129, pl. 5, fig. 6

Description: Shell small (14.1–19 mm, mean = 15.7, S.D. \pm 1.4, N = 12), elongate-fusiform with tall spire, anterior canal of moderate length, emarginated parietally by strong callus but lacking umbilical chink ($w = 0.33$ – 0.38 , $a = 0.34$ – 0.38). Protoconch of two smooth whorls, nuclear tip laterally placed. Teleoconch whorls initially flat-sided, with slightly concave shoulder slope on last whorl. Axial sculpture of widely spaced, rounded ribs, about 10 per whorl, extending from suture to suture on early whorls, sinuous, reduced in strength on shoulder slope of later whorls. Spiral sculpture of slightly wavy, evenly spaced striae. Sinus on shoulder slope, deep, U-shaped, rather narrow, bordered medially by a parietal tubercle that does not constrict opening. Outer lip thin, sharp, with small but distinct stromboid notch at lower extremity. Varix-like enlarged axial rib about 1/4 whorl behind outer lip. Color uniform light brown. Operculum (figure 31) leaf-shaped with terminal nucleus. Radula (figure 28) drilline, with numerous rows of teeth, each consisting of small, unicuspid rachidian tooth, two comb-like lateral teeth, and two long, sharp-pointed marginal teeth. Dried animal, as viewed during treatment with KOH, with prominent eyes on short eye stalks, mantle with strong anterior siphonal extension and distinct, curved indentation on the right for anal sinus.

Types: Holotype, USNM 880070. Paratypes (donated by Dr. Wolfe), one each at AMNH, MCZ, DMNH, ANSP, LACM, NM, MORG, NHM, MNHN, IRSNB, author's collection, others in the Wolfe collection.

Type locality: 15 km east of Cape Lookout, North Carolina at 20 fm (36 m), from the Elmer Dewey Willis scallop plant, Williston, North Carolina. Leg. Dr. Douglas Wolfe, March–May 1971.

The North Carolina scallop fishery at the time of collection of the present material was concentrating on an area approximately 15 km east of Cape Lookout in about 20 fathoms according to Schwartz and Porter (1977). This is therefore selected as the type locality. Subsequently this scallop plant began to shuck scallops imported from off central to northern Florida. Despite numerous collecting excursions at various scallop shucking houses in Carteret County, North Carolina, both before and after the above dates, this species was not found again.

Range: Off North Carolina, ? Campeche Bank, Yucatan.

Remarks: *Drillia wolfei* superficially resembles *Fenimorea pagodula* Dall, 1889 (figure 3). It differs in having narrower, fewer, and more widely spaced ribs that do not run from suture to suture, stronger and more widely separated spiral threads that are not of the "butterfly wing" type (see below), a weaker varix, and in lacking a spiral color band on the whorl periphery. Despite the geographic separation, Rice and Kornicker's (1965) Sp. "L" (figure 2), from the Campeche Bank off Yucatan, appears to be this species. There is a high percentage (about 1/3) of shells with repaired damage, probably indicating attempts at predation by crabs. Named for Dr. Wolfe for his contribution of the material and assistance in developing important data on collection locality.

Drillia (Clathrodrillia) Dall, 1918

Type species (of subgenus): *Pleurotoma gibbosa* Reeve, 1843 (= *Murex gibbosus* Born, 1778).

Remarks: *Clathrodrillia* is conventionally regarded as a subgenus of *Drillia* (e.g., McLean, 1971, Abbott, 1974, Kilburn, 1988, Sysoev in Taylor *et al.*, 1993). Members of the subgenus have stronger spiral sculpture and a more pronounced terminal varix blotched with color than the nominal genus.

Drillia (Clathrodrillia) dautzenbergi Tippett, new name (Figures 4, 5)

Drillia gibbosa var. *minor* Dautzenberg, 1900: 20, pl. 9, fig. 2 (anterior & posterior views), non *Drillia minor* Seguenza, 1880.

Clathrodrillia minor (Dautzenberg, 1900) Rios, 1975: 130, #580, pl. 39; Altena, 1975: 7, pl. 7, figs. 1, 2.

Description: Shell medium sized (to 27 mm), elongate-ovate, with tall spire, moderately-sized body whorl terminating in barely differentiated, notched, recurved anterior canal ($w = 0.35$, $a = 0.33$). Protoconch of two smooth whorls, with laterally placed, immersed tip, bearing two or three brephic axial ribs at termination of protoconch. Teleoconch of about 9 moderately rounded whorls, with strong sulcus on upper third. Sculpture of numerous, regularly spaced, narrow, rounded axial ribs separated by equal interspaces and decussating, crowded spiral cords separated by deep grooves. Axial ribs reduced in strength, curved on sulcus, spirals cords finer, more on sulcus. Varix low, broad, about 1/4 whorl back from

Figure 1 *Drillia (Drillia) wolfei* Tippett, new species. Holotype, USNM 880070, 16.6 × 6.1 mm. **Figure 2** Sp. "L" Rice & Kornicker, 1965. USNM 667703, 12.1 × 4.2 mm. **Figure 3** *Fenimorea pagodula* (Dall, 1889). Lectotype, USNM 87471, 17.7 × 5.8 mm. **Figure 4–5.** *Drillia (Clathrodrillia) dautzenbergi* Tippett, new name. **4.** Lectotype, IRSNB, 24.2 × 9.3 mm. **5.** USNM 880076, 27.1 × 10.2 mm. **Figures 6–7.** *Sediliopsis riosi* Tippett, new species. **6.** Holotype, MORG 31.775, 14.6 × 5.4 mm. **7.** Apex, 12 ×. **Paratype,** MORG 31.776. **Figure 8** *Sediliopsis gracilis* (Conrad, 1830) Apex, after Gibson, 1962, pl. 41, fig. 11. **Figure 9** *Lioglyphostoma hendersoni* (Bartsch, 1934). USNM 880078, 13.7 × 5.4 mm. **Figures 10–11.** *Clathurella eversoni* Tippett, new species. Holotype, USNM 880074, 4.5 × 1.7 mm. **10.** Anterior view. **11.** SEM of aperture showing teeth, 22 ×. **Figure 12.** *Fenimorea janetae* (Bartsch, 1934). Holotype, USNM 430249, SEM showing "butterfly wing" microsculpture, 22 ×.

outer lip. Lip fluted by spirals cords. Siphonal fasciole moderately developed. Sinus deep, U-shaped, occupying entire sulcus, with reflected rim terminating in parietal tubercle continuous with marginated columellar callus bearing weak false umbilicus below. Outer lip with broad, shallow stromboid notch just above anterior end. Color pure white.

Type: Institut Royal des Sciences Naturelles de Belgique, one specimen, no catalog number, here selected as lectotype.

Type locality: Isla Margarita, Venezuela.

Range: Widespread in the lower Caribbean and north Brazil.

Remarks: Both Rios (1975) and Altena (1975) recognized that this species is not a form of *D. (C.) gibbosa* as thought by Dautzenberg. It differs in being much smaller and in having more delicate sculpture, including finer spiral cords, and a weaker varix, siphonal fasciole and parietal tubercle. It is all white in color and lacks the color blotch on the varix that is present in *D. (C.) gibbosa*. *Drillia dautzenbergi* has spirals on the sulcus, which are lacking in *D. (C.) gibbosa*. Both Rios (1975) and Altena (1975) not only distinguished this species from *D. (C.) gibbosa*, but also raised *Clathrodrillia* to full generic rank, a step not taken in the classification herein. As a consequence of being retained in the genus *Drillia*, this species name is preoccupied by *Drillia minor* Seguenza, 1880 (Seguenza, 1880:103, pl. 11, fig. 8), a species from the Miocene of Italy. A new name thus becomes necessary and is supplied here. The species is named after the original author.

The specimen from IRSNB (figure 4) is housed in a circular box containing an old identification slip stating "*Drillia gibbosa* Born var. *minor* Dautz. Type. pl. A, f. 2.2, I. Margarita, 24 I 96." The same is written on the bottom of the container. A label of Glibert's states the specimen to be the holotype. Comparison of the shell with Dautzenberg's original figures shows that it was undoubtedly used for these illustrations. They are identical including repaired breakage preceding the lip and a somewhat short anterior canal. There is a second healed break about halfway through development of the body whorl that alters the continuity of the canal, making it shorter than normal. Altena's (1975) figures and the specimen shown here (figure 5) demonstrate the full development of the canal. The specimen illustrated in figure 5 has slightly finer axial and spiral sculpture and more and finer spirals on the sulcus than the IRSNB specimen,

but otherwise shows the same characters. Dautzenberg did not designate a holotype. The species was originally reported as being from various South Caribbean localities. Altena (1975) mentions having seen syntypes. As Glibert's assignment was not published, it cannot be considered a lectotype designation. As designation of a lectotype is appropriate, this specimen [IRSNB (figure 4)] is here designated as the lectotype.

Drillia (Clathrodrillia) petuchi Tippett, new species (Figure 18)

? *Crassispira* sp. Sully, 1986:96, photo.

Splendrilla sp. Petuch, 1988:160, pl. 38, figs. 3,4

Description: Shell moderately large (to 53 mm), fusiform, turreted, with tall spire. Body whorl somewhat truncated, ending in short, open, slightly notched, recurved anterior canal ($w = 0.39$, $a = 0.43$). Whorls ca. 13 including 2 smooth nuclear whorls with immersed tip. Teleoconch whorls rounded, with deeply concave shoulder slope. Periphery angulated along upper ends of axial ribs, situated $1/3$ whorl below suture. Sculpture of strong, rounded axial ribs (about 14 on penultimate whorl) with equal interspaces, with fine spiral striae that are absent on sulcus. Massive varix $1/4-1/3$ whorl behind flaring, fluted outer lip, bearing small but strong stromboid notch just above end of anterior canal. Axial ribbing reduced or absent following varix. Sinus deep, U-shaped, margined by recurved callus, bearing parietal tubercle, its entrance narrowed by upward extension of outer lip edge. Siphonal fasciole present. Large specimens with small umbilical chink. Color white, with 3 brownish spiral bands, adapical band spotted, on rear surface of ribs. Varix shows a blotch of same color.

Type: Holotype, USNM 880071.

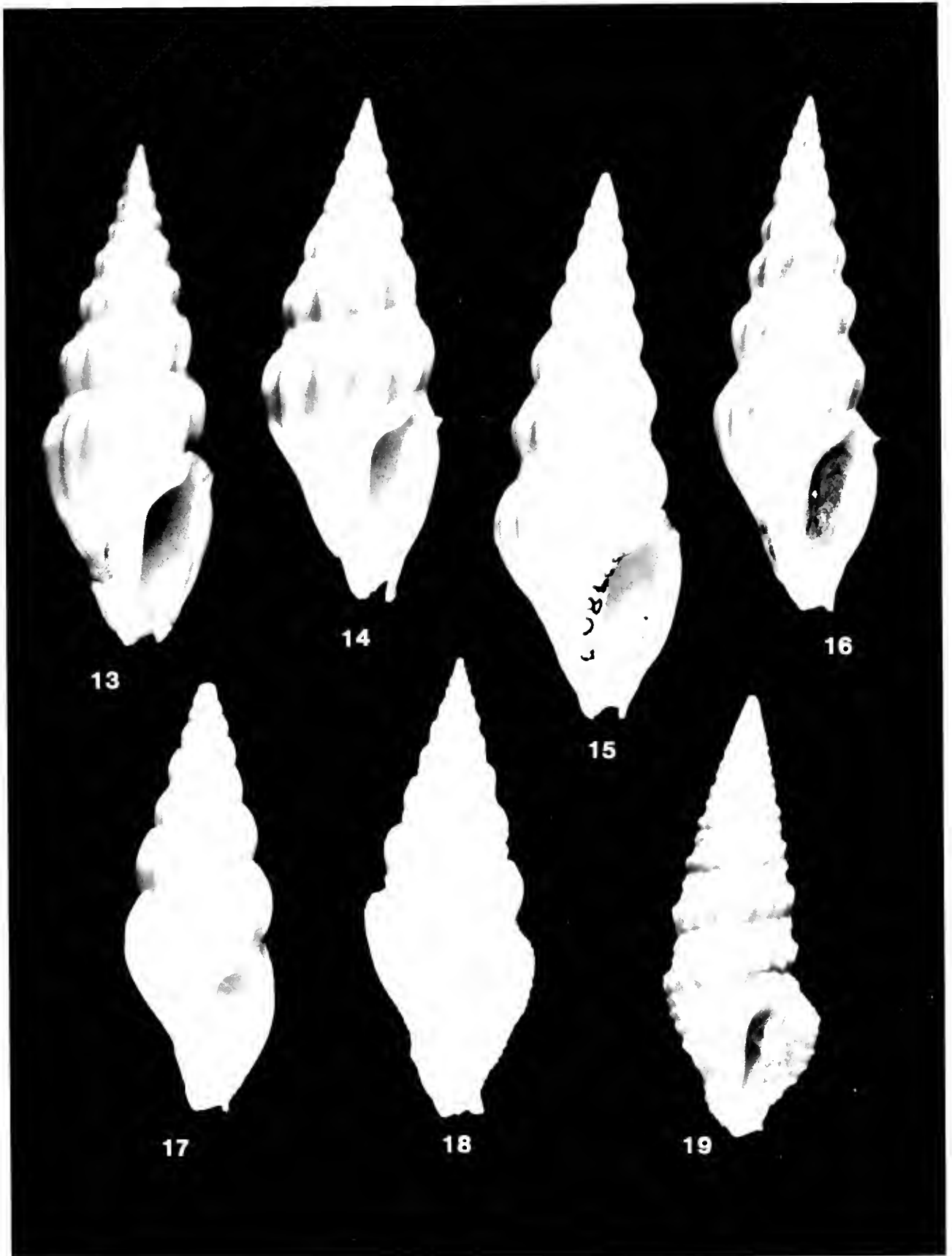
Type locality: Off Barbados, 470 ft (142 m), crabbed, Dec. 1986, D. Hunt!

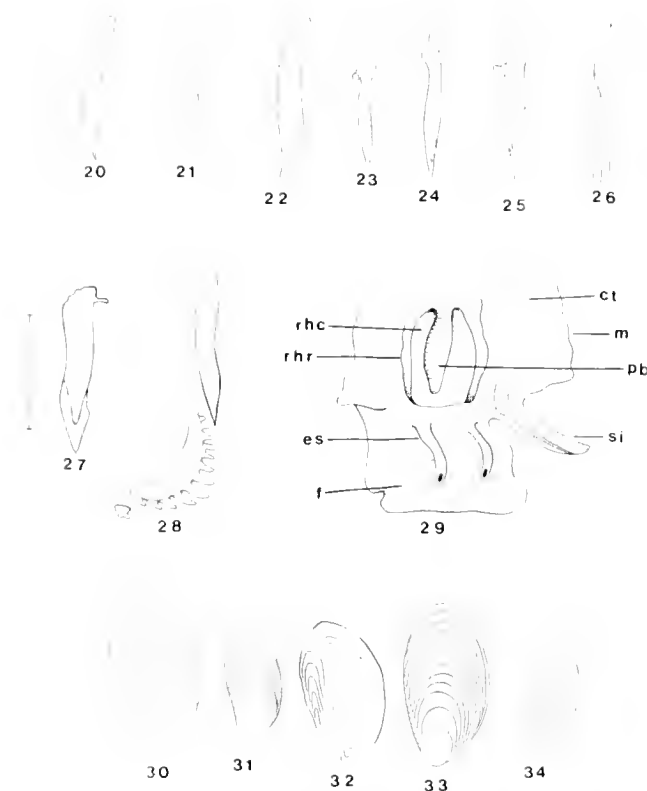
Additional material examined: AMNH 186435, 1 spec.; author's collection, 1 spec.

Range: Known only from Barbados.

Remarks: *Drillia petuchi* is similar to *Drillia (Clathrodrillia) gibbosa*, but differs in being more tumid and robust, having fewer and broader ribs, having a less recurved but more strongly notched anterior canal, and in having a base color that is white rather than pale brown. The varix is much more strongly colored in *D. (C.) gibbosa*, which lacks the spiral banding.

Figure 13. *Fenimorea janctae* (Bartsch, 1934). Holotype, USNM 430249, 37.8 × 14.3 mm. **Figure 14.** *Fenimorea kathyae* Tippett, new species. Holotype, USNM 880072, 36.1 × 14 mm. **Figure 15.** *Fenimorea sauderlandi* (Petuch, 1987). Holotype, USNM 859800, 40 × 14 mm. **Figure 16.** *Fenimorea sauderlandi* (Petuch, 1987) var. USNM 880077, 52 × 17.9 mm. **Figure 17.** *Fenimorea petiti* Tippett, new species. Holotype, USNM 880073, 13.2 × 5.2 mm. **Figure 18.** *Drillia (Clathrodrillia) petuchi* Tippett, new species. Holotype, USNM 880071, 39.4 × 15.4 mm. **Figure 19.** *Pilsbryspira (Nymphispira) auberti* (Lamy, 1934), new combination. USNM 880079, 34.7 × 12.5 mm.





Figures 20–28. Radular teeth. Scale bars = 100 μ m. **20.** *Inodrililla nucleata*. USNM 87454. **21.** *Viridrillia williamsi*. USNM 319167. **22.** *Viridrillia hendersoni*. USNM 354327. **23.** *Pyrgocythara plicosa*. USNM 880083 (specimen sacrificed). **24.** *Pyrgocythara danae*. USNM 266350. **25.** *Pyrgocythara filosa*. USNM 880082 (specimen sacrificed). **26.** *Lioglyphostoma hendersoni*. USNM 880050 (specimen sacrificed). **27.** *Pilsbryspira albocincta*. USNM 880081 (specimen sacrificed). **28.** *Drillia wolfei*. USNM 880084 (specimen sacrificed). **Figure 29.** *Pilsbryspira albocincta*. USNM 880081. Schematic drawing of animal, anterior area opened. **Figures 30–34.** Opercula. **30.** *Fenimorea sunderlandi* var. USNM 880077, 10.0 \times 5.5 mm. **31.** *Drillia wolfei*. USNM 880070, 3.4 \times 1.7 mm. **32.** *Fenimorea kathya*. USNM 880072, 4.5 \times 2.6 mm. **33.** *Fenimorea petiti*. USNM 880073, 2.4 \times 1.3 mm. **34.** *Lioglyphostoma hendersoni*. USNM 880078, 3.0 \times 1.5 mm.

ct, ctenidium; es, eye stalk; f, foot; m, mantle edge; pb, proboscis; rhc, rhynchodeal cavity; rhr, rhynchodeal roof, reflected; si, siphon

Petuch (1988:160) considered this species to be an example of his Barbadian Secondary Relict Pocket forms and a possible relative of the *Splendrillia scala* (= *Drillia scala* Pilsbry & Jolimon, 1917:155) complex of his Guranian subprovince. However *Splendrillia scala* is not a *Clathrodrillia*, whereas the present form is a typical member of the group having the characteristic hump-backed form blotched with color, as well as distinct, relatively coarse, spiral threading. Barbados, the type locality of *D. (C.) petuchi*, is near the Venezuelan subprovince, where *D. (C.) gibbosa* occurs. A more similar form is Jung's (1965:567) *Clathrodrillia* ?n. sp. aff. *C. isalindae* (Maury, 1917) from the Miocene of the Parag-

uana Peninsula, Venezuela. That species is a typical clathrodrilline, has the same number of axial ribs as *D. (C.) petuchi*, but is narrower and the axials tend to extend sinusoidally over the sulcus to the suture above. It is possible that Maury's species is an ancestor of both *D. (C.) gibbosa* and *D. (C.) petuchi*. The present species is named for Dr. Edward J. Petuch, who first noted the species, and who has made significant contributions to the Caribbean molluscan fauna.

Genus *Fenimorea* Bartsch, 1934

Type species: *Fenimorea janetae* Bartsch, 1934.

Remarks: Bartsch created the genus *Fenimorea* for his new species *F. janetae* on the basis of its odd micro-sculpture of fine axial and spiral striae that produces a characteristic wavy pattern that "resembles the scales on some butterfly wings" (Bartsch, 1934:3. See figure 12). He was aware that there are other species with the same characteristic, including Dall's *F. moseri* (Dall, 1889) and *F. fucata* Reeve, 1845, but did not assign them to his new genus.

Fenimorea kathya Tippett, new species
(Figures 14, 32)

Splendrillia sp. Petuch, 1985, pl. 35, figs. 5,6.

Description: Shell medium sized (to 36 mm), fusiform-biconic with moderately tall spire. Body whorl gradually narrowing, terminating in scarcely differentiated, short, notched siphonal canal ($w = 0.39$, $a = 0.37$). Whorls ca. 11 including protoconch of two smooth whorls. Teleoconch whorls moderately rounded, with concave sulcus on upper 1/3, roundly angulated below by upper ends of axial ribs. Sculpture of strong, rounded axial ribs (about 10 on penultimate whorl) with narrower interspaces. Spiral striae fine, wavy, forming "butterfly wing" pattern in later whorls. Sinus deep, U-shaped, with parietal tubercle, entrance narrowed by an upward extension of outer lip. Constriction varies from slight to almost complete closure. Large varix 1–3 whorl behind lip. Stromboid notch shallow. Columellar callus variably emarginate. Color white, typically with three red spiral bands, the most prominent peripheral and visible on spire just above suture. Varix slightly blotched with red on forward surface. Operculum (figure 32) leaf-shaped with terminal nucleus.

Type: Holotype, USNM 880072.

Type locality: West coast Barbados, dredged, 500 ft (152 m), Oct. 1986, D. Hunt!

Additional material examined: 1 specimen, dredged at 300 ft (91 m), off Egmont Key, FL; 1 specimen, Hypoluxo, FL, 190 ft. (58 m), both in author's collection.

Range: Barbados, peninsular Florida.

Remarks: The present species is another example of the *F. janetae* complex of attractive shells. When fresh the shells are shiny and colorful, having bright spiral

banding in various shades of orange, red-brown or red. *Fenimorea kathyae* is most similar to *F. janetae* (figure 13), ($w = 0.35$, $a = 0.36$), having shouldered whorls and a sulcus but with a shorter spire, longer base, as well as fewer and broader ribs. The spiral banding in *F. janetae* is orange and broad but is bright red and narrow in *F. kathyae*. *F. sunderlandi* (Petuch, 1987) (figure 15), ($w = 0.35$, $a = 0.34$), another member of this group, lacks a sulcus, has non-angulate whorls, and narrower, more numerous ribs that are opisthocline, rather than orthocline, as in *F. janetae* and *F. kathyae*. As noted by Petuch (1987:19), *F. sunderlandi* has been misidentified as *F. janetae*. The shells so misidentified (figure 16, figure 30 for operculum), ($w = 0.34$, $a = 0.35$), coming principally from the well-known "bushels," dredgings, of Jim Moore and Riley Black in the 1960s and 1970s, are a variety of *F. sunderlandi* that is larger and narrower. This form has a facies suggestive of *F. janetae*, but shows the whorl-outline and rib characteristics of *F. sunderlandi*. All members of the group have the "butterfly wing" spiral sculpture although it differs in strength from specimen to specimen. The species is named for another beauty, and fine field collector, the author's wife.

Fenimorea petiti Tippett, new species
(Figures 17, 33)

? *Drillia albicoma* Dall, 1889, Sunderland & Sunderland, 1993:
14 (figured).

Description: Shell small (10–17.7 mm), fusiform, with tall spire and moderately elongate body whorl gradually tapering to short, unnotched anterior canal ($w = 0.34$ – 0.45 , $a = 0.31$ – 0.47). Whorls rounded, lacking sulcal region. Sculpture of axial ribs, 10–12 on penultimate whorl, extending suture to suture, tending to be only slightly curved below the suture at area usually occupied by sulcus, and fine spiral striae of "butterfly wing" type overall. Sinus moderately deep, U-shaped, occupying most of shoulder slope, with parietal callus. Varix 1/4 whorl behind thin lip with shallow stromboid notch. Color white, with variable banding of orange shades. Operculum leaf-shaped, with terminal nucleus (figure 33).

Type material: Holotype, USNM 880073. Paratypes, one each at NMNH, AMNH, MCZ, DMNH, ANSP, LACM, NM, MORG, NHM, MNHN, IRSNB; others in author's collection.

Type locality: Gulf of Mexico west of Crystal River, Florida, 30 fm (59 m), dredged, Jim Moore!, May, 1963.

Range: Known only from the Gulf of Mexico from the Cedar Keys to the Florida Keys. The shell figured by the Sunderlands appears to be this species but would need verification as to identification and locality. A number of specimens have lost the precise locality data but are from the Gulf. All material is from the Jim Moore dredgings.

Remarks: The author initially considered *F. petiti* a possible dwarf form of *F. janetae* on the basis of general

appearance. However examination of additional material showed the resemblance to be superficial. The taxon is nearer a species that, on cursory scrutiny, does not even appear to be of the group, *Fenimorea pagodula*. (See below.) The major differences between the two species are that *F. petiti* is more tumescent, although quite variable, and has fewer, wider, and straighter axials. *Fenimorea petiti* shows variation of color pattern, the spiral band being pale and perhaps interrupted in some examples, but this is nearly always stronger and more colorful than the bland and unremarkable banding of *F. pagodula*. The species is named for Mr. Richard E. Petit for his kind donation of the material and in recognition of his many contributions to malacology.

Fenimorea pagodula (Dall, 1889) new combination
(Figure 3)

Drillia pagodula Dall, 1889:90, pl. 13, fig. 6.

Remarks: Identification of *F. pagodula* has been on uncertain grounds because Dall did not designate a holotype and a number of syntype lots with shells of somewhat disparate nature, located both at the USNM and MCZ, exist. These have been examined and the shell illustrated in figure 3 (USNM 87471, off Havana, 119–175 fm (217–320 m)) is a good representation of Dall's description and figure despite being two mm shorter than the measurement given by Dall in the plate caption. The width of the specimen illustrated in figure 3 is 5.8 mm, as is stated in Dall's description. It is here designated lectotype of the species. Although not bright in general appearance, as typical of the *Fenimoreas*, this species has the microsculpture characteristic of *Fenimorea*. Paralectotypes: USNM 887466 (separated from USNM 87471); USNM 87472, 3 specimens, Dominica, 118 fm (216 m), sand, 65°F, Blake St. 177; MCZ 7068, off Barbados, 154 fm (282 m), Blake St. 282; MCZ 7069, 11 specimens (a mixed lot and only 5 specimens are true *F. pagodula*), off Barbados, 103 fm (188 m), Blake St. 273; MCZ 7070, off Barbados, 73 fm (133 m), Blake St. 290; MCZ 7071, W. of Fla., 50 fm.

Genus *Sediliopsis* Petuch, 1985

Type species: *Pleurotoma graecilis* Conrad, 1830.

Sediliopsis riosi Tippett, new species
(Figures 6, 7)

Description: Shell small (12–15 mm), claviform, turreted, with moderately tall spire, short, unnotched siphonal canal ($w = 0.37$, $a = 0.41$). Whorls about 7 including protoconch of two whorls, the first smooth, the second bearing 3–4 spiral cords. Adult whorls rounded, somewhat tumid, with distinct suture followed by subsutural cord, deep shoulder sulcus, whorls angulated by upper ends of axial ribs. Sculpture of dominant axial ribs crossed by incised spiral striae producing wider, somewhat flattened cords most evident as laterally elongate

beading on ribs. Ribs broad, well rounded, about 16 on body whorl, with a tendency to bifurcate basally. Sinus moderately deep, U-shaped, occupying most of sulcus, apex at mid-point. No stromboid notch or varix. Color uniform milky white.

Types: Holotype, MORG 31.775. Paratypes, MORG 31.776 -one specimen, MORG 31.777 - five specimens; USNM 880075 - one specimen; one specimen in author's collection.

Type Locality: Off Sao Paulo, Brasil, 24°31'S, 44°28'W, in 250 m. This species and *Lioglyphostoma hendersoni*, below, were dredged using a beam trawl by the "W. Besnard" on Dec. 9, 1988. Bottom temp. 13.2°C. Ana Maria Vanin!

Range: Known by only the type material.

Remarks: This species represents the discovery of a living member of what has hitherto been known solely as a fossil genus. The distinguishing feature of the genus is the characteristic protoconch (figure 8), which bears three or four spiral cords on the second and, if present, third whorl(s), a state unique for the family in the western Atlantic. Gibson (1962:238), discussing Conrad's *Pleurotoma gracilis*, recognized this and identified several (fossil) species with the same type of protoconch, but only suggested that the group may deserve ranking as a separate genus or subgenus. Petuch (1988) erected the genus, feeling that the closest relative was *Sedilia* Fargo (1953:370), a Pliocene genus from southwestern Florida having a different type of protoconch. He stated, based on the available knowledge, that *Sediliopsis* became extinct after the time of the Saint Mary's formation (late Miocene of the Maryland coastal plain). The present species apparently represents an instance of relict-pocket occurrence, as discussed by Petuch. Further study of forms with this type of protoconch shows that others outside the restricted geotemporal range of *S. gracilis* (middle western Atlantic coastal plain Miocene) exist: *S. chowanensis* (Gardner, 1948), from the upper Pliocene of North Carolina and *S. aphanitoma* (Dall, 1892) and *S. ondulum* (Fargo, 1953), both from the Pliocene of Florida. This broader geographic and temporal range of members of the genus makes it reasonable that *Sediliopsis* could also occur in the Recent fauna of Brasil. This species is named in honor of Professor Eliézer de C. Rios for his contributions to Brazilian malacology and for providing the material for study.

Subfamily Crassispirinae Morrison, 1966, emended McLean, 1971

Genus *Lioglyphostoma* Woodring, 1928

Type species: *Lioglyphostoma adematum* Woodring, 1928.

Lioglyphostoma hendersoni (Bartsch, 1934)
(Figures 9, 26, 34)

Glyphostoma (Glyphostomops) hendersoni Bartsch, 1934 17,
pl. 5, figures 2.5.8.
Sp."E" Rice & Kornicker, 1965:125, pl. 7, fig. 15.

Material examined: See with *Sediliopsis riosi* above: 34 specimens. Voucher specimen, USNM 880078, 2 specimens in author's collection; remainder at MORG.

Remarks: Described from Puerto Rico, this species has also been recorded from off North Carolina (Porter, 1975: 35). The present report of *L. hendersoni* from off Brazil and a specimen from the Campeche Bank, Yucatan (Rice & Kornicker, 1965) indicate that it is widespread. The shells were compared with both the holotype and approximately 65 other lots in the USNM from the Miami and Florida Keys areas. Although the present material shows stronger beading at the intersections of the axial and spiral sculpture than does the holotype, there is complete intergrading of forms. Bartsch (1934) selected a specimen with weaker sculpture as the type. Unknown previously, the operculum (figure 34) is leaf shaped with a terminal nucleus, and the radula (figure 26) shows about 40 pairs of duplex teeth with a presumably detached accessory limb (detachment can not be determined conclusively using light microscopy).

Genus *Inodrillia* Bartsch, 1943

Type species: *Pleurotoma (Drillia) nucleata* Dall, 1881.

Inodrillia nucleata (Dall, 1881)
(Figure 20)

Pleurotoma (Drilha) nucleata Dall, 1881:9.
Drillia nucleata Dall, 1889 92, pl. 11, fig. 1.
Inodrillia (Inodrillia) nucleata Bartsch, 1943 102, pl. 8, fig. 6;
pl. 10, fig. 4; pl. 13, fig. 1.

Genus *Viridrillia* Bartsch, 1943

Type species: *Viridrillia williamsi* Bartsch, 1943.

Viridrillia williamsi Bartsch, 1943
(Figure 21)

Viridrillia (Viridrillia) williamsi Bartsch, 1943:92, pl. 8, fig. 2,
pl. 10, fig. 2.

Viridrillia hendersoni Bartsch, 1943
(Figure 22)

Viridrillia (Viridrillina) hendersoni Bartsch, 1943:99, pl. 7, fig. 3;
pl. 10, fig. 1, pl. 15, fig. 5.

Remarks: Bartsch's genera and the species from them are noted to ensure placement in the subfamily Crassispirinae and to illustrate the radulae of *Viridrillia williamsi* and *V. hendersoni*. Powell (1966, text figs. E 109-111) had figured J.P.E. Morrison's drawings of radulae, from the USNM, of *Inodrillia nucleata*, *I. miamia*, and *I. ino* Bartsch, but not those of *Viridrillia*, although they were

available to him. Powell commented about *Viridrillia* (1966:74, with the genus *Cerodrillia*): "... a very different radula, which consists only of a pair of elongate, foliated marginals." He placed the genera in his subfamily Clavinae, as he interpreted it at that time, principally on the basis of shell characters. Subsequently, McLean (1971:119) separated this grouping, largely on the basis of radular form, into the subfamilies Clavinae [subsequently Drillinae, Clavinae being preoccupied (Cernohorsky, 1985:60)] and Crassispirinae. The teeth of *Inodrillia* and *Viridrillia*, although not typical, are most similar to those of Crassispirinae, certainly not to those of the Drillinae. Sysoev, in Taylor *et al.* (1993:164), recognized this and listed *Inodrillia* as a crassispirine genus. Morrison's illustrations are somewhat unclear so I reviewed his slides and the figures presented here were made. The teeth of both genera are essentially the same, consisting of simple, elongate, solid, pointed marginals. They are not clearly duplex but show a lengthwise thickening suggestive of an accessory limb, perhaps a step in the evolution towards accessory limbs. Bartsch's subgenera *Viridrillina*, *Inodrillina*, *Inodrillara* now are synonymized with their respective parent genera *Viridrillia* and *Inodrillia*.

Subfamily **Clathurellinae** H. & A. Adams, 1858

Genus *Clathurella* Carpenter, 1857

Type species: *Clavatula rava* Hinds, 1843, by subsequent designation Cossmann, 1896.

Clathurella eversoni Tippett, new species.
(Figures 10, 11)

Description: Shell very small (4.5 mm), biconic-fusiform, with tall spire, short anterior canal ($w = 0.35$, $a = 0.33$). Protoconch of three smooth whorls. Adult whorls four, sculptured by 11-12 rounded axial ribs separated by equal interspaces, crossed by spiral cords forming laterally elongate beading at intersections. Spiral cords extend down over base and canal. Sinus moderately deep, U-shaped, on shoulder slope, with only modest parietal callus. Enlarged axial rib behind lip. Five spirally elongate denticles inside outer lip. Columella with two weak pustules. Color light brown with paler band on peripheral spiral.

Type: Holotype, USNM 880074.

Type locality: Off Dania Beach, Florida, between second and third reefs, 70 ft (21 m), in rubble, SCUBA at night, Gene Everson!

Remarks: Although known only from the holotype, this species is distinctive and warrants description. The holotype is still slightly juvenile and would undoubtedly show a deeper sinus at full maturity; also it is somewhat worn. There is a vestige of carination on the later protoconch whorls and traces of minute granulation on the shell surface, which are characteristic of the genus.

Until the description of *C. fuscobasis* Rehder (1980:87, pl. 11, figs. 3,4) from Easter Island, *Clathurella* in its modern concept was known only from the tropical eastern Pacific. The present species extends the range of the genus to the western Atlantic area. *Clathurella eversoni* is nearest *C. rava* (Hinds, 1843), differing in being smaller, having a broader shoulder slope, stronger spiral cord at the shoulder, and different color pattern. This species is named for its discoverer, Mr. Gene Everson.

Subfamily **Zonulispirinae** McLean, 1971

Genus *Pilsbryspira* Bartsch, 1950

Type species: *Pilsbryspira pilsbryi* Bartsch, 1950 (= *Pleurotoma jayana* C. B. Adams, 1850b).

Pilsbryspira (Pilsbryspira) albocincta (C. B. Adams, 1845)
(Figures 27,29)

Pleurotoma albocincta C. B. Adams, 1845:3 (reprinted Clench & Turner, 1950:253, pl. 29, fig. 5).

Material examined: Two specimens, alcohol preserved, Cabbage Patch, Abaco Island, Bahamas, under rocks in 3 ft water, Colin Redfern!, July 8, 1972.

Remarks: Shells are an exact match to the lectotype (Clench & Turner, 1950, pl. 29, fig. 5). Animal is uniformly grayish pink. Prominent inhalant siphon leads to a large gill. Proboscis is of the intraembolic form. A much convoluted poison gland with a large muscular bulb is present. The oesophagus was empty. Radula (figure 27) consists of numerous pairs of broad marginal teeth, flaring at the distal end and bearing a small barb. The teeth are typical of the subfamily.

Subgenus *Pilsbryspira (Nymphispira)* McLean, 1971

Type species: *Crassispira nymphia* Pilsbry & Lowe, 1932.

Pilsbryspira (Nymphispira) auberti (Lamy, 1934), new combination
(Figure 19)

Drillia auberti Lamy, 1934:435 (description and figure).

Crassispira auberti (Lamy, 1934) Radwin, 1969:232 (list).

Pilsbryspira harfordiana (Reeve, 1843) Vokes & Vokes, 1953
30, pl. 2, fig. 11a

Crassispira harfordiana (Reeve, 1843) Sunderland & Sunderland, 1993:14 (figure).

Material examined: 3 specimens, dredged, 120 ft (36 m), Porto Bello Bay, Caribbean Panama, James Ernest! Voucher specimen, USNM 880079. Others in Everson and Ernest collections.

Remarks: As seen in the synonymy, there has been uncertainty as to the identification and placement of this species. Lamy's type material cannot be found (pers. comm., P. Bouchet) and thus identification must neces-

sarily be based on comparison with Lamy's description and figure. Fortunately, these are reasonably good, and the present material appears to be this species, agreeing in overall form, sculptural detail, and color. Also the current material is from the same geographic area. The material referred to in the cited publications appear to be the same species. It can be assumed that Radwin (1969) was accurate in his identification because his material came from the type locality. A broader geographic range than known previously is suggested. The Vokes' (1983) specimens came from Yucatan, not a surprising range extension, while Sunderland and Sunderland (1993) reported on material from Cuba. Identification of the Cuban specimens as *Crassispira (Glossispira) harfordiana* is in error, despite superficial similarity. This species is from the eastern Pacific and has a more tumescent outline, crassispirine sinus structure, blackish color, and other, finer, differences. Although soft parts of *P. auberti* are not available, the sinus structure, beaded base, and color pattern are consistent with the present assignment.

Subfamily **Mangeliinae** P. Fischer, 1887

Genus *Pyrgocythara* Woodring, 1928

Type species: *Pyrgocythara eminula* Woodring, 1928.

Pyrgocythara filosa Rehder, 1943
(Figure 25)

Pyrgocythara filosa Rehder, 1943:203, pl. 20, fig. 2.

Material examined: Six specimens, alcohol preserved, Pine Island, east Florida, sieved from *Spartina* grass, 24 September 1993, John Wise!

Remarks: Shells of these specimens match the holotype except that the axials are slightly narrower and their shoulder angulation is slightly sharper. Animal white with black eyes located near the ends of short stalks. There is a prominent inhalant siphon. The mantle is speckled black and this coloring extends back over the visceral segment. There is a coiled poison gland and muscular bulb. The radula consists of paired marginal teeth enclosed in a radular sac. Radular tooth (figure 25) elongate, sharply pointed, bearing a small barb 1/3 the distance from the tip, and has a projection at the base from which a triangular extension of tissue protrudes posteriorly. The radular teeth are of the "hilted-dagger" type described by Powell (1966) and are very similar to those of *Pyrgocythara danae* (Dall, 1919) from the eastern Pacific except that the teeth of that species do not have barbs (figure 24).

Pyrgocythara plicosa (C. B. Adams, 1850)
(Figure 23)

Pleurotoma plicosa C. B. Adams, 1850b:54 (new name for *Pleurotoma plicata* C. B. Adams, 1840, non Lamarek, 1804).

Material examined: 2 live specimens, Little Jim Island, Fort Pierce, Florida, grass and mud flats, intertidal, hand sieved, 24 & 25 January 1991, John Wise!

Remarks: The animal has a whitish, semitranslucent foot and head speckled with fine, bright, ivory-white spots, the eyes prominent toward the ends of rather long stalks. No operculum. The mantle is white speckled with sooty-black, and this coloration extends back over the visceral lobe. A long penis with a fingernail-shaped end is attached to the right side of the head and curls back inside the mantle cavity. Large gills, osphradium, and hypobranchial glands are present. The proboscis is intraembolic. The radular teeth (figure 23) are enclosed in a radular sac and number about 35 pairs. They are of the "hilted-dagger" form and resemble those of *P. danae* but lack an angulation toward the tip.

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