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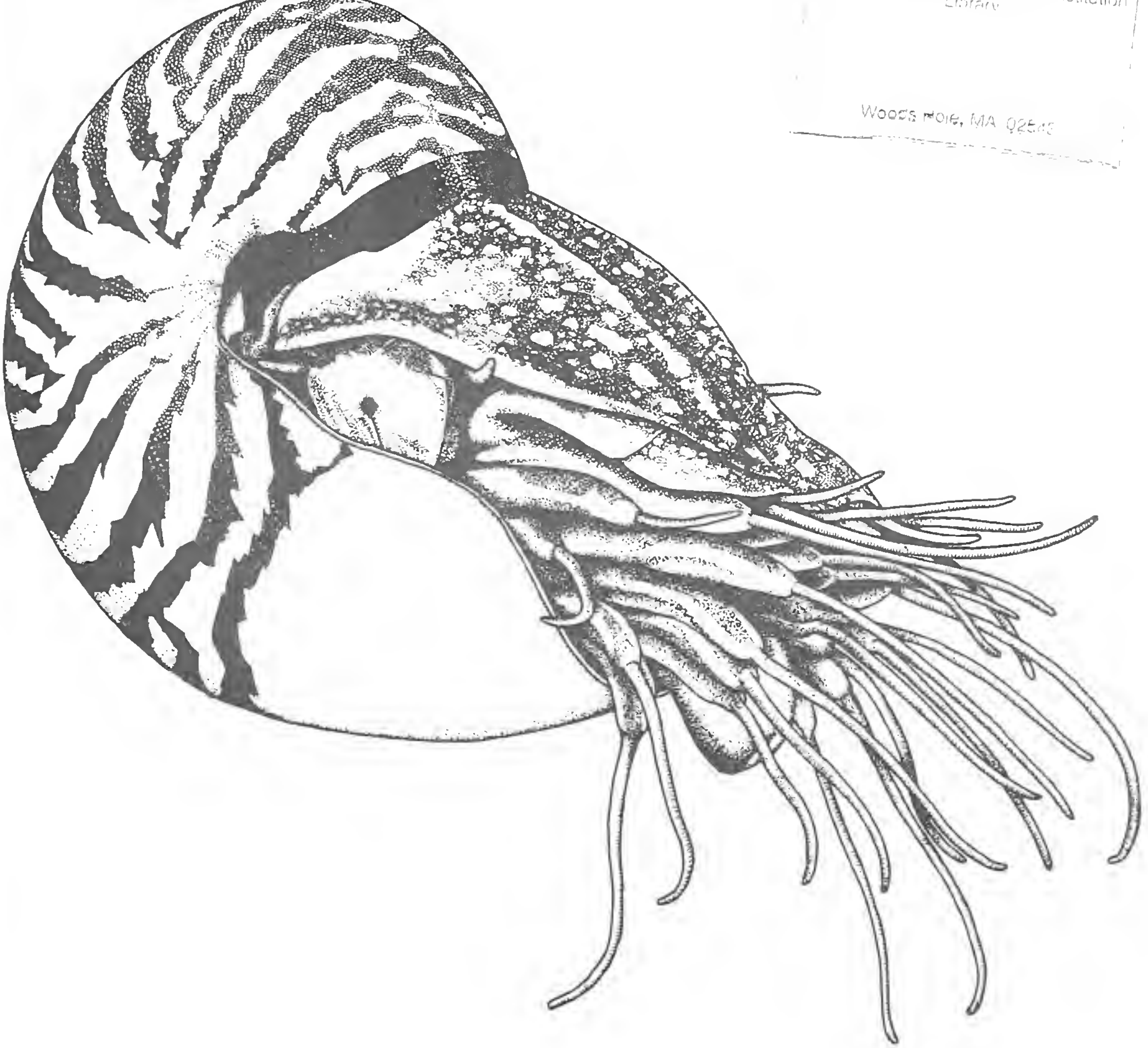

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CONTENTS

Clarification of the Taxonomic Status and Reproductive Anatomy of *Philomycus batchi* Branson, 1968 (Gastropoda: Pulmonata: Philomycidae)

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ABSTRACT

The mantle pattern and reproductive anatomy of specimens of *Philomycus batchi* are compared to specimens of *P. carolinianus*. The results demonstrate that *P. batchi* is distinct from *P. carolinianus* and therefore *P. batchi* is reestablished as a separate species. In the original description of *P. batchi* the reproductive system described is that of a designated paratype from a locality different from that of the holotype. This study demonstrates that the reproductive anatomy of *P. batchi* from the type locality is not the same as that in the original species description. The correct reproductive anatomy is described, it includes a penial pouch, located in the wall of the penis. This pouch is not recorded in any other United States landsnail.

Key Words: Slugs, Philomycidae, *Philomycus*, reproductive anatomy, taxonomy.

INTRODUCTION

The Philomycidae is a family of terrestrial slugs found primarily in the eastern half of the United States. The species in this family are characterized by a mantle that covers the entire body except for the tip of the tail and the anterior portion of the head. The length of an adult slug varies from 25 to 100 mm, depending upon the species. There are three North American genera in this family, *Philomycus*, *Pallifera* and *Megapallifera*. In terms of the reproductive anatomy, the species of *Philomycus* are characterized by the presence of a dart sac and dart; the species of *Pallifera* are small (approximately 30 mm long) and lack the dart sac and dart; the species of *Megapallifera* are large (approximately 80 mm long) and also lack the dart sac and dart but, unlike *Pallifera*, have a bilobed "flap" on the internal surface of the upper atrium. Most of the original species descriptions of these philomycids did not include data describing the internal anatomy, particularly the reproductive anatomy.

The description of *Philomycus batchi* Branson, 1968 did include a figure of a reproductive system and a description of a portion of the terminal genitalia. However, the author utilized the holotype for description of the external morphology only. A designated paratype collected at another locality (approximately 135 km south of the type locality) was used to describe the reproductive anatomy. Later, Hubricht (1974) synonymized, without supporting data, *P. batchi* with *P. carolinianus* (Bosc, 1802).

Fairbanks (1986, 1989, 1990, 1993) examined six of the eight described species of *Philomycus* and all three species of *Megapallifera*. In all of the species examined there were species specific differences in penis shape and/or internal penial anatomy. Because inter-species differences exist, it was decided that the reproductive anatomy of *P. batchi* and *P. carolinianus* should be compared. In particular, it seemed appropriate to compare the reproductive anatomy of specimens of *P. batchi* from the type locality with that of specimens from the paratype locality.

The goals of this study were: (1) to determine whether *Philomycus batchi* was correctly synonymized with *P. carolinianus*, and (2) to determine whether the reproductive anatomy ascribed to *P. batchi* is the same as that of *P. batchi* from the type locality.

MATERIALS AND METHODS

Specimens of *Philomycus batchi* were collected 1.9 km south of Highway 627, on a hillside along the road on the east side of the Kentucky River, elevation 210 m, Clark County, Kentucky, 16 May 1990. This site (site 1 in Fig. 4) is directly across a road from the type locality (the east flood plain of the Kentucky River, opposite Boonesborough State Park, Madison-Clark County line, Kentucky). Other specimens, presumed to be *P. batchi*, were collected from an area along Eagle Knob Branch of Eagle Creek near Cumberland Falls State Park, McCreary County, Kentucky (the paratype locality), elevation 300 m, 6 May 1991 (site 2 in Fig. 4). The holotype of *P. batchi* (FMNH 155478, Field Museum of

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Figure 1. *Philomycus batchi* from the type locality.

Figure 2. *Philomycus batchi* from the paratype locality.

Figure 3. *Philomycus carolinianus* from South Carolina. Scale bars = 10 mm.

Natural History, Chicago) was examined, the paratype used for the description of *P. batchi's* reproductive anatomy has been lost (personal communication, Branley Branson, 6 October 1993). Specimens of *P. carolinianus*, from the author's personal collection, collected from logs alongside a road 5 km north of Huger, Francis Marion National Forest, Berkeley County, South Carolina, 22 June 1988, were used for comparative purposes. This site is 15 km north of the designated (Pilsbry, 1948:754) type locality of Charleston, Charleston County, South Carolina.

All specimens were identified by comparing external morphology with species descriptions. The specimens were drowned in distilled water and immediately dissected. The reproductive systems were removed and pinned out in 70% ethanol for 24 hours prior to preserving them in 70% ethanol. The image of each reproductive system was projected (using an overhead projec-

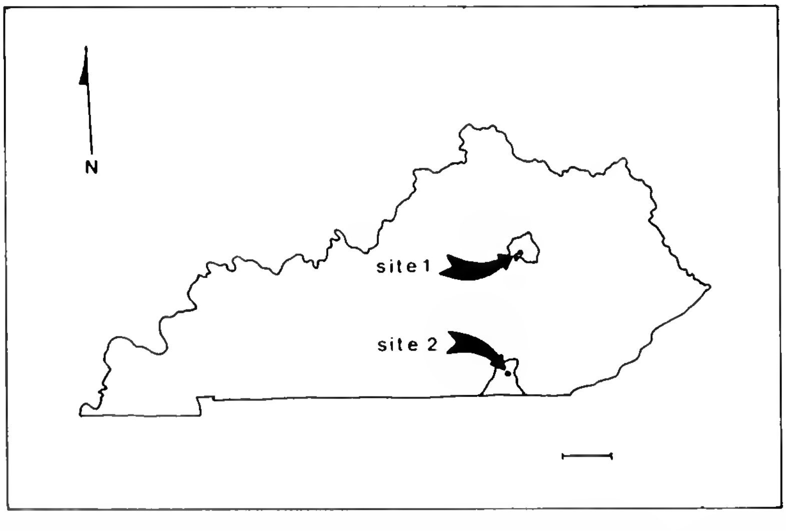


Figure 4. Outline of the state of Kentucky showing the location of the type locality (site 1) and the paratype locality (site 2) of *Philomycus batchi*. Scale bar equals 53 km.

tor) onto paper and traced. The atrium and penis of each specimen were opened and photographed through a dissecting microscope. The slides were then projected onto paper and traced.

Voucher specimens are in the National Museum of Natural History, Smithsonian Institution (USNM 860578, three specimens of *Philomycus batchi* from Clark County, Kentucky, the type locality, and USNM 860579, one specimen of *Philomycus* sp. from McCreary County, Kentucky, the paratype locality), and in the Academy of Natural Sciences, Philadelphia, PA (ANSP A13329 for *P. carolinianus*).

RESULTS

The reproductive systems of four adult specimens of *Philomycus batchi* collected from the type locality (Fig.4, site 1) are as shown in Figure 5. They do not match the reproductive system in the original description of this species. Four specimens matching the description of the external morphology of *P. batchi* were collected from the paratype locality (Fig. 4, site 2). The reproductive system (Fig. 6) of one of these (Fig. 2) matched the characteristics and figure given in the original species description, and will be referred to as *P.* unknown. The reproductive anatomy of the other three specimens was similar to that of the specimens from the type locality and is not figured. The reproductive system of *P. carolinianus* from South Carolina is shown in Fig. 7. The reproductive system *of P. batchi* from the type locality (Fig. 5) had a penis that tapered gradually from its proximal (atrial) end to its junction with the vas deferens. In *P.* unknown from the paratype locality (Fig. 6) the penis tapered rapidly for one-fourth of its length, remained relatively constant in diameter for the next half of its length, and then for the distal one-fourth it rapidly decreased in diameter to merge with the vas deferens (a "two stepped" appearance). The penis of *P. carolinianus* (Fig. 7) was relatively constant in diameter for the first (proximal) half of its length, then the diameter decreased rapidly to match that of the vas deferens (a "one step" appearance).

The internal penial anatomy of *Philomycus batchi* from the type locality is shown in Fig. 9. Figure 8 shows a transverse section through the penial pouch of the penis of a specimen from the type locality. Fig. 10 shows the internal penial anatomy of *P.* unknown whose reproductive anatomy matched that of the original species description. Figure 11 shows the internal penial anatomy of *P. carolinianus*. The internal penial wall of *P. batchi* from the type locality was smooth for the proximal (atrial end) one fourth of its length. The second quarter was covered with very small papillae arranged in longitudinal rows. The third quarter had a large longitudinal ridge, it and the remainder of the internal wall was covered with larger papillae randomly arranged. The distal quarter of the penial wall was covered with narrow folds that led into the opening of the vas deferens. A second ridge extends from near the atrial end of the penis two-thirds of the way to the vas deferens. The internal surface of the penis of *P.* unknown (Fig. 10) was covered with very small randomly placed papillae (not drawn to preserve ridge clarity). A large longitudinal ridge begins at the proximal end of the penis and extends distally approximately two-thirds of the penial length. The ridge has a raised portion at the atrial end. The distal one-third of the internal surface of the penis was covered by thin longitudinal ridges that led into the opening of the vas deferens. The internal penial surface of *P. carolinianus* (Fig. 11) had three to four large folds on the proximal third, a second set of three to four small ridges on the middle third, and the distal third had narrow ridges that led into the vas deferens.

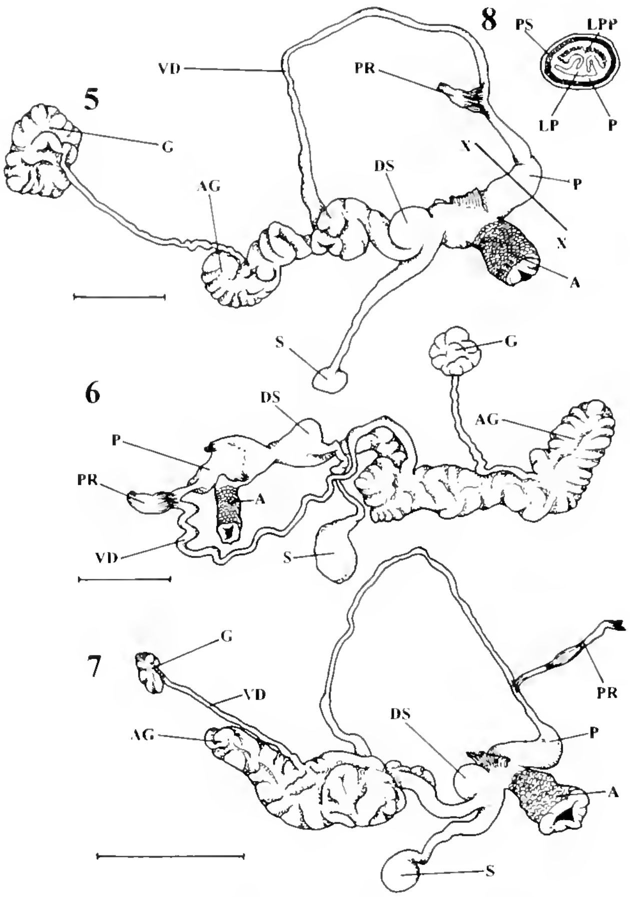
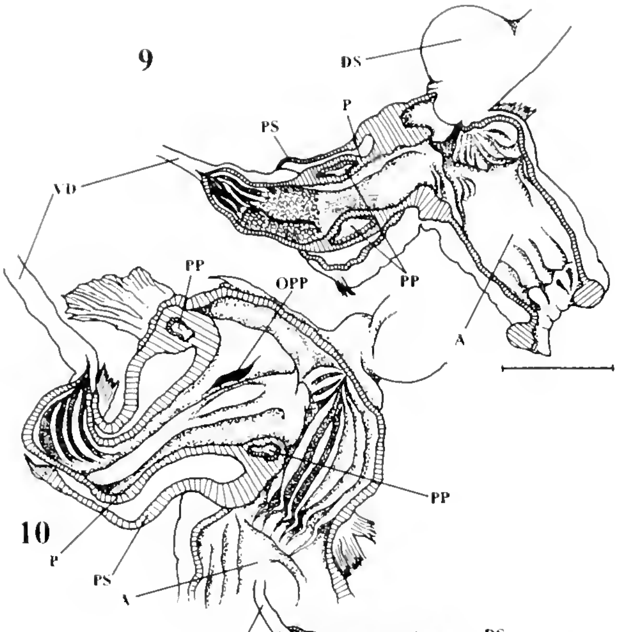


Figure 5. Reproductive system of *Philomycus batchi* from the type locality.

Figure 6. Reproductive system of *Philomycus batchi* from the paratype locality.

Figure 7. Reproductive system of *Philomycus carolinianus* from South Carolina.

Figure 8. Section through the penis along X—X in Fig. 5. Scale bars for Figs. 5, 6 = 10 mm, for Fig. 7, = 5 mm. A, atrium; AG, albumen gland; DS, dart sac; G, ovotestis; LP, lumen of penis; LPP, lumen of penial pouch; P, penis; PR, penial retractor; PS, penial sheath; S, spermatheca; VD, vas deferens.



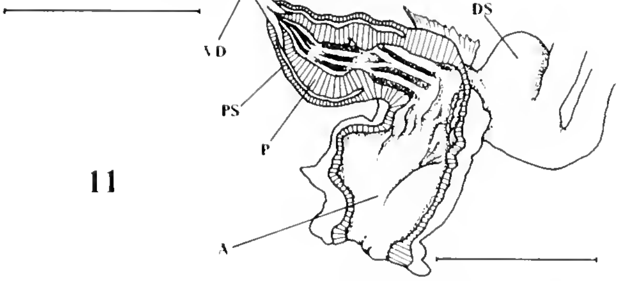


Figure 9. Internal penial anatomy of *Philomycus batchi* from the type locality.

Figure 10. Internal penial anatomy of *Philomycus batchi* from the paratype locality.

Figure 11. Internal penial anatomy of *Philomycus carolinianus* from South Carolina. Scale bars = 10 mm. A, atrium; DS, dart sac; OPP, opening into penial pouch; P, penis; PP, penial pouch; PS, penial sheath. VD, vas deferens.

A small circumferential chamber (the penial pouch) having a slit-like opening into the lumen of the penis (Figs. 9, 10) was present in the penial wall of all specimens from Kentucky used in this study. This chamber extended for nearly two-thirds of the circumference of the penis, and its outer wall was covered with villum-like papillae (Fig. 8). The holotype of *P. batchi* was immature, its reproductive system was one-half to two-thirds fully developed. It was possible to determine the shape of the penis, it was long, narrow with a slight taper from the proximal to the distal end. Two characteristics of the internal penial anatomy were discernible: a penial pouch, which was located approximately one-third of the length of the penis from the proximal (atrial) end, and a single large ridge on the internal wall of the proximal third of the penis.

The correct description of the reproductive anatomy of *Philomycus batchi*, based on material from the type locality is as follows:

Genitalia of *Philomycus batchi* Branson, 1968 (Figs. 5, 8, 9)

Atrium approximately 45% penial length, outer surface glandular, light orange to light pink in color, with finely ridged pad on the inner surface near the opening into the vagina. Vagina approximately 10% penial length. Origin of spermathecal duct approximately 1.7 times the diameter of the oviduct, slight taper to spermatheca. Spermatheca ovoid. Dart sac approximately twice spermathecal diameter. Proximal penis diameter approximately equal to atrial diameter, penis tapers to diameter of vas deferens; penial sheath approximately 70% of penis length. Internal penial surface smooth for proximal 25% of length, tiny papillae in longitudinal lines for next 25%, large papillae for next 25% with one large ridge, thin folds leading into vas deferens for distal 25% of penial length. A second ridge extends from the atrial end of penis two-thirds the distance to the vas deferens; a circumferential pouch in the penial wall with opening into lumen of penis, pouch located in second 25% of penial length, pouch extent approximately 60% of circumference of penis, pouch with villum-like papillae covering outer wall. Vas deferens length approximately 3 times penial length, enters distal end of penis, diameter of vas deferens at distal end 2.5 times that of proximal end. Oviduct length approximately 30% penial length. Penial retractor muscle length approximately 35% penial length, inserted at junction of penis and vas deferens. Accessory retractor muscle robust, located on atrial surface near junction of penis and atrium. Uterus, albumen gland, spermoviduct, and gonad typical of genus.

DISCUSSION

Hubricht (1974) synonymized *Philomycus batchi* with *P. carolinianus* because he saw *P. batchi* as a ". . . melanistic color form of *P. carolinianus.*" However, the usual criteria used to identify *P. carolinianus* are the presence of a double row of black spots along the dorsal surface of the mantle with a brown stripe between them (Fig. 3). *Philomycus batchi* does not have these characteristics (Fig. 1). Furthermore, the internal penial anatomy also is different (Figs. 9, 11). *Philomycus batchi* has two large ridges on the internal surface of the penis and a penial pouch (Figs. 8, 9), whereas *P. carolinianus* has from six to eight much smaller ridges and lacks a pouch (Fig. 11). There are differences in the atrial anatomy as well. *Philomycus batchi* has a large pad, with several small folds in it, in the upper atrium near the opening into the vagina (Fig. 9). *Philomycus carolinianus* has a few small folds that lead into the opening of the vagina, but no pad (Fig. 11). These data demonstrate that *Philomycus batchi* is distinct from *P. carolinianus* and therefore must be reestablished as a species.

The external appearance of *Philomycus batchi* from the type locality was indistinguishable from that of all

Table 1. Comparisons of selected reproductive organs between species of *Philomycus* in this study.

	P. batchi type locality figs. 5 & 9	*P. batchi* paratype locality not figured	*P.* unknown paratype locality figs. 6 & 10	*P. carolinianus* S. Carolina figs. 7 & 11
Internal surface of atrium	ridged; pad near vagina	ridged; pad near vagina	ridged, no pad	ridged, no pad
Shape of penis	gradual taper	gradual taper	"stepped" appearance	gradual taper
Internal surface of penis	part smooth part pustulose	part smooth part pustulose	smooth	part smooth part pustulose
Ridges; internal surface of penis	2, one distal one proximal	2, one distal one proximal	1, extends entire length of penis	2 groups of 3–4, 1 distal 1 proximal
Penial pouch	present	present	present	not present
Size of spermatheca	small	small	large	small

specimens from the paratype locality. However, specific features of the reproductive system of *P. batchi* from the type locality (Fig. 5) were clearly different from those of the original description, as well as from *P.* unknown from the paratype locality (Fig. 6), and did match the original description (see Table 1 for a brief comparison of the reproductive anatomies). Two additional differences between the specimens of *Philomycus batchi* from the type locality and *P.* unknown from the paratype locality, were the position and size of the penial pouch (Figs. 9, 10). That is, the penial pouch is larger in *P. batchi* from the type locality than in *P.* unknown from the paratype locality, and the latter specimen's penial pouch is more proximal than that of the specimens from the type locality.

The data obtained from the immature holotype were consistent with the *Philomycus batchi* specimens collected from the type locality. That is, the general shape of the penis was similar, and the location of the penial pouch and the presence of the ridge on the internal surface near the proximal end of the penis were the same. When Branson (1968) described *Philomycus batchi*, he apparently assumed, based upon external appearance, that slug specimens he had collected in McCreary County, Kentucky were of the same species as the one a colleague had collected in Clark County, Kentucky 135 km to the north. He then described a new species using two specimens. Based upon the data presented in this study, it appears that Branson utilized two different species to describe *P. batchi*. Therefore, a description of the correct reproductive anatomy for *P. batchi* is provided. The specimen that Branson used to describe the reproductive system of *Philomycus batchi* appears to be an undescribed species. Because only one specimen of this species is presently available, its description will appear in a later paper.

An unexpected result of this study was the discovery of a chamber in the penial wall of the specimens of *Philomycus* from Kentucky. The gross structure and position of the chamber is not recorded from any other group of land snails in the United States. Studies are underway to ascertain the number of different species of *Philomycus* that have this chamber, and to try to determine how widely spread these species are geographically. The function or functions of this chamber are unknown at this time.

ACKNOWLEDGMENTS

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Additions and Corrections to the Taxonomy of the genus *Peasiella* Nevill, 1885 (Gastropoda: Littorinidae)

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ABSTRACT

Peasiella is a genus of the Littorinidae with minute, trochoidal shells, found only in the Indo-West Pacific region. A previous monograph recognized six Recent species. As a result of new anatomical information (reproductive anatomy, egg capsules, radulae) two of these are divided into five and two species, respectively, to make a total of 11 species in the genus. Three of these are described as new. Additional notes on distribution, variation and nomenclature are provided on other species. Characters of the radula and pallial oviduct are relatively uniform throughout the genus, but penial shapes are often diagnostic. Shell shape and sculpture show extreme intraspecific variability.

INTRODUCTION

Peasiella is one of the more poorly known genera of the Littorinidae. In common with all members of the subfamily Littorininae, its species occur on hard substrates in the littoral zone. Although easily accessible and often abundant, they are infrequently collected owing to their small size and cryptic habit in rock crevices and among oyster and barnacle shells. All known species occur in the Indo-West Pacific province and most are entirely tropical, although several extend into the temperate zones of southern Africa and the northwestern Pacific. Among littorinids, they are readily recognized by their small (1–7 mm diameter), trochoidal or depressed shells, lacking spines, with open umbilicus and multispiral operculum. These characters are superficially similar to those of trochids (but lacking the nacreous interior of that group), with which they were often confused by early authors (see review of taxonomic history by Reid, 1989a). Other littorinids with trochoidal shells include the genera *Bembicium* and *Risellopsis* from Australia and New Zealand (Reid, 1988), and *Tectarius* and *Cenchritis* from the Indo-West Pacific and western Atlantic (Rosewater, 1972; Reid, 1989b; Reid & Geller, 1997).

For long these small littorinids were neglected taxonomically. The most recent monograph of extant and some fossil *Peasiella* species was that by Reid (1989a); before this the only compilations were a list by Nevill (1885) and a monograph by Tryon (1887). The anatomy (male and female reproductive tracts, paraspermatozoa, egg capsule, alimentary tract, head-foot pigmentation), radula, protoconch and teleoconch were described in detail by Reid (1989a). As a result, the genus was defined not only by shell and opercular characters, but also by the unique combination of the elongate penis with single mamilliform penial gland and closed vas deferens, together with the double-looped form of the pallial oviduct, and other anatomical features. These same characters were included in a phylogenetic analysis of the morphology of the genera and subgenera of the Littorinidae (Reid, 1989b). However, since none of the coded anatomical characters appeared to be apomorphic within the family, the only formal synapomorphies of the genus in this analysis were the trochoidal shell shape and multispiral operculum, and neither of these was unique. Nevertheless, the close morphological similarities among its members leaves little doubt that the genus is a monophyletic one; the arrangement of the loops of the pallial oviduct is one unique character, but owing to difficulties of coding such structures it did not appear as such in the formal analysis. As a result of Reid's (1989b) phylogenetic analysis, it was clear that *Peasiella* was a member of the derived subfamily Littorininae, and probably a relatively basal member, although its precise relationships with such genera as *Mainwaringia*, *Cenchritis* and *Tectarius* were not resolved. A recent molecular study included a species of *Peasiella*, with members of *Tectarius*, *Cenchritis* and *Nodilittorina*, but did not find any close relationships with these other genera (Reid & Geller, 1997).

In the previous systematic account of *Peasiella* species (Reid, 1989a), anatomical details were provided for all the six species then recognized. However, the amount of material available was limited; for example, for *P. 'isseli'* only one preserved male was dissected, and for *P. 'infracostata'* only seven. As a result, it was concluded

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that the genus was anatomically rather uniform, without the striking differentiation in reproductive characters that has proved so useful for the discrimination of species complexes elsewhere in the family (e.g. Reid, 1986a, 1988, 1996). Instead, it was necessary to base species definitions largely on the shape, sculpture and color of the shell (although these characters were evidently variable), and on geographical distributions. Anatomical characters such as head-foot pigmentation, the number of cusps on the outer marginal radular tooth, and presence or absence of a copulatory bursa provided only minor input.

Our attention was once more drawn to the systematics of *Peasiella* as a result of a study by one of us (Y-MM) of the littorinids of Hong Kong.The fauna of Hong Kong was thought to include three *Peasiella* species (Reid, 1992), the highest number then known to occur sympatrically. However, it was found that two distinct shell forms of *P. 'infracostata' sensu* Reid (1989a), both rare in Hong Kong and not yet found syntopically (i.e. on the same shores), produced egg capsules of different shape. This prompted a reexamination of this supposed species throughout its wide range in the Indian and Pacific Oceans. Meanwhile, further collections were made by Y-MM throughout the Far East. During the past decade much new material has also accumulated in the major museums. Using this new material, we found that penial form was, after all, a character showing useful interspecific variation. As a result, we have revised the taxonomy of two species complexes: *Peasiella 'infracostata' sensu* Reid (1989a) is here shown to consist of five species, and *P. 'isseli' sensu* Reid (1989a) of two. These seven species are fully described. We also record additional information on the variability, distribution and nomenclature of other *Peasiella* species. The number of species recognized in the genus is therefore increased from six to eleven.

MATERIALS AND METHODS

The descriptions and records are based on material in the following museums: Natural History Museum, London (BMNH); Muséum National d'Histoire Naturelle, Paris (MNHN); Instituut voor Systematiek en Populatiebiologie, Amsterdam (ZMA); Nationaal Natuurhistorisch Museum, Leiden (NNML); Institut Royal des Sciences Naturelles de Belgique (IRSNB); National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM); Academy of Natural Sciences of Philadelphia (ANSP); Museum of Comparative Zoology, Harvard University (MCZ); Los Angeles County Museum of Natural History (LACM); Natal Museum (NM); National Science Museum, Tokyo (NSMT); Department of Earth and Planetary Science, Kyushu University (KU); Australian Museum, Sydney (AMS) and the private collections of H. Dekker, The Netherlands (HD) and J. Le Renard, Paris (LR). In addition, type specimens have been examined from Oxford University Museum (OUM); Museo Civico di Storia Naturale 'Giacomo Doria', Genoa (MGD) and Zoological Survey of India, Calcutta (ZSI). Unless otherwise indicated, all figured specimens are in BMNH. Lectotypes have been designated from syntypic series only for valid species names.

Shell height (H) was measured parallel to the axis of coiling, and maximum shell diameter (D) perpendicular to this axis. The height/diameter ratio was used as a simple index of shell shape. The number of whorls of the protoconch was counted as described by Reid (1996: 9). Where counts of the number of ribs above the periphery are given, this includes the strong rib at the periphery; this rib is not included in counts of the basal ribs. Living material was preserved in 80% ethanol, and dissected under a binocular microscope. Pallial oviducts were examined by dissection; in very small animals the copulatory bursa can be impossible to find unless filled with recently deposited sperm; to confirm absence of the bursa would require histological preparation, but this was not done in the present study. The loops of the albumen and capsule gland follow a similar path in all species examined, and are therefore not re-described (see Reid, 1989a, for description and figures). Radulae were cleaned of tissue in a cold, dilute solution of hypochlorite bleach, thoroughly rinsed in distilled water, and mounted on a thin layer of polyvinyl acetate glue on glass cover slips. Radulae were examined with a scanning electron microscope. Unworn radular sections were photographed from three orientations: vertically above flat radula (to show shape of teeth), at an angle of 45° from front end of radula (to show shape of tooth cusps), and at an angle of 45° from the side of the radula (to show relief). For three species, egg capsules were obtained from living animals. Females were placed individually in plastic vials (20 × 47 mm) half filled with filtered seawater. Vials were covered and kept at room temperature (24–26° C) with no aeration. The water was renewed daily, and eggs were collected from the bottom of the containers. Eggs were preserved in 5% formalin in seawater, for subsequent examination and measurement using light microscopy.

The lists of material examined are those records used for the distribution maps. Numbers of specimens dissected are indicated by M (male), F (female); R indicates radula preparation, and P protoconch examination. For the seven species described in detail, the material listed includes that examined during the previous study by Reid (1989a), and the descriptions supercede the earlier account. This earlier work should still be consulted for detailed descriptions of the histology of the reproductive system and of the sperm. For those species for which only additional notes and records are given, full descriptions and other records can be found in Reid (1989a).

SYSTEMATIC DESCRIPTIONS OF REDEFINED AND NEW SPECIES OF *PEASIELLA*

Peasiella infracostata (Issel, 1869)

(Figures 1–5, 35–41, 76–79, 108–109, 131)

Trochus sp. Audouin, 1826:42
Risella infracostata Issel, 1869:195–196, 348 [refers to Savigny,

1817: pl. 5, fig. 40.1, 40.2; lectotype (Reid, 1989a; fig.41) + 3 paralectotypes MNHN, seen; Suez (Issel)]. Pallary, 1926:86, pl. 5, fig. 40.1, 40.2. Bouchet & Danrigal, 1982: 13, fig. 64.

Risella (*Peasiella*) *infracostata*.—Nevill, 1885:160. Tryon, 1887: 264, pl. 50, figs. 41, 42.

Peasiella infracostata.—Reid, 1989a:61–64, figs. 106–109,112 [in part; includes *P. fasciata*, *P. fuscopiperata*, *P. habei*, *P. patula*]. Bosch *et al.*, 1995:46, fig. 118.

? *Risella* (*Peasiella*) *tantillus* var. *subinfracostata* Nevill, 1885: 160 [lectotype (Reid, 1989a; fig. 35) + 2 syntypes ZSI; lectotype seen; Nicobar Islands].

Nomenclature: In his description of this species, Issel (1869) referred to Savigny's (1817) unlocalized figures of Egyptian material, and also mentioned three specimens of his own from Suez; the latter were not found by Bouchet & Danrigal (1982) in Issel's collection in MGD. Reid (1989a) therefore designated one of four shells in the Savigny Collection in MNHN as the lectotype.

The identity of *Risella (Peasiella) tantillus* var. *subinfracostata* Nevill, 1885, is uncertain. The lectotype (Figure 35) measures 2.3 mm in diameter by 2.2 mm in height (H/D 0.96), is almost smooth above the periphery, but for fine spiral microsculpture and traces of about four spiral grooves near the periphery; the base bears four subequal ribs around a small umbilicus; the color is cream with a single brown spiral line on the first whorl of the teleoconch, and no other pattern. Of the known species of the genus, this shell can be compared with *P. infracostata* and *P. fasciata*. In outline it resembles *P. infracostata*, for the whorls and aperture are less rounded than in *P. fasciata*; however, it lacks the enlarged midbasal rib that is often present in the former. The sparse color pattern is unlike any known specimens of either of these species. The locality of Nevill's shells, from the Nicobar Islands, is far from the closest known occurrence of *P. infracostata* in Bombay, and from that of *P. fasciata* in Borneo. The only other *Peasiella* species recorded from the Andaman Sea is *P. roepstorffiana* (Reid, 1989a), but that species usually has stronger spiral sculpture, flatter whorls and a strong peripheral keel. Until more information is available, the name is tentatively included in the synonymy of *P. infracostata*.

Reid (1989a) confused five species under the name *P. infracostata* (here distinguished as *P. infracostata s.s.*, *P. fasciata*, *P. fuscopiperata*, *P. habei* and *P. patula*), misled by their similar and confusingly variable shells.

Shell (Figures 1–5, 35–41): Adult size range 1.1–2.6 mm diameter. *Shape:* thickness varies from delicate and translucent, to thick-walled and opaque; equilaterally conical to depressed-globular (H/D 0.7–1.0); outline domed; whorls usually rounded or with rounded shoulder, becoming almost flat-sided on last whorl of largest, thick-walled shells; suture always distinct; periphery occasionally uniformly rounded, but usually marked by sharp angle or rib, rarely developed as a narrow flange; base usually slightly rounded, becoming flat or even slightly concave in largest, thick-walled shells; umbilicus small to large, occasionally closed in thick-walled shells; columella narrow, uniformly rounded. *Sculpture:* protoconch not seen, apex usually eroded; teleoconch whorls always lacking ribs above periphery, microscopically smooth or with fine spiral microstriae (rarely, about 6 striae may be more prominent, but not developed into ribs, Figure 39); 1–4 ribs on base (rarely absent, or 5–6), of which that at mid-point of radius is usually most prominent (producing slight angulation of base). *Color:* translucent yellow-brown, opaque white where shell is thicker at suture and periphery (entirely white in thick-walled shells); pattern of pale or dark brown or black, oblique or zigzag, narrow lines from suture to periphery, numbering 5–19, darkest at periphery and sometimes also at suture; pattern occasionally represented only by peripheral stripes; spire may be brown, or frequently marked only by single spiral brown line; base usually pale with brown line in outermost groove, line sometimes absent, base rarely brownish with paler ribs; columella and parietal area usually not colored, rarely brown.

Animal: *Head-foot:* front of head blackish, with a separate black band across base of snout; tentacles unpigmented; foot may have black pigment around operculum. *Penis (Figures 76–79):* filament long (50–60% total length), tapering; base slightly thicker, with single small mamilliform penial gland. *Pallial oviduct:* bursa not seen. *Radula (Figures 108, 109):* cusps pointed, central cusp of rachidian tooth slightly apiculate; outer marginal tooth with 6–7 long, pointed cusps, outermost more rounded, becoming smaller toward midline.

Distribution: *Habitat:* Among barnacles in upper eulittoral on surf beach (Oman; J. D. Taylor); rock pool on limestone, in upper eulittoral of sheltered shore (Oman; E. Glover); under rocks and stones in intertidal (Oman; R. G. Moolenbeek & H. Dekker); under coral blocks in eulittoral (Egypt; D. G. Reid). Abundant at some localities in Oman and at Karachi, but elsewhere appears to be scarce.

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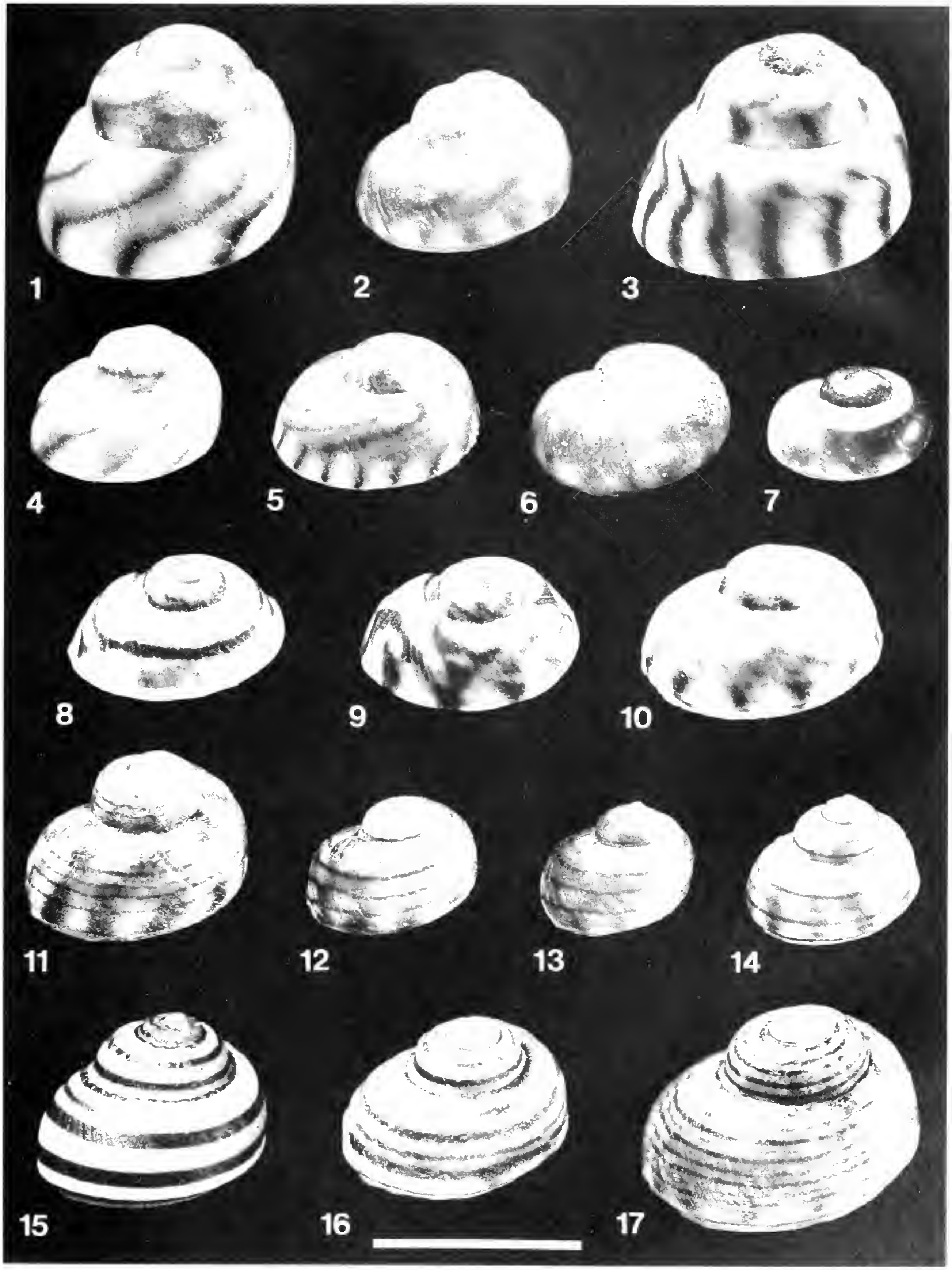
Figures 1–5. *Peasiella infracostata* **1.** Ras al-Hadd, Oman (BMNH 1996381). **2, 4.** Karachi, Pakistan (BMNH 1996383). **3.** Tiwi Beach, 30 km S Mombasa, Kenya (BMNH 1996384). **5.** 4 km S Ras Qudufah, Masirah I., Oman (BMNH 1996385). **6–10.** *Peasiella fuscopiperata* **6.** Lectotype of *Cyclostrema fuscopiperata* Turton, 1932, Port Alfred, South Africa (OUM). **7.** North Bay, Benguera I., Moçambique (NM K7412). **8–10.** Tiwi Beach, 30 km S Mombasa, Kenya (BMNH 1996386). **11–13.** *Peasiella patula*. **11.** Holotype, Changi Point, Singapore (BMNH 1996276). **12, 13.** St. John's I., Singapore (BMNH 1996387). **14–17.** *Peasiella fasciata*. **14.** Uvol Mission, Cape Dampier, New Britain, Papua New Guinea (AMS C163128). **15.** Holotype, Turtle Bay, Cape Ferguson, Queensland, Australia (BMNH 1996272). **16, 17.** Cape d'Aguilar, Hong Kong (BMNH 1996388). Scale bar = 2 mm.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Range (Figure 131): East Africa, Red Sea, Oman, Pakistan, possibly Nicobar Islands.

Records and material examined: Moçambique: Conducia Bay (NM). Tanzania: Zanzibar (BMNH). Kenya: Tiwi Beach, 30 km S Mombasa (BMNH, 2M). Somalia: Mogadiscio (ANSP). Egypt: Hurghada (BMNH; HD); Suez (Issel, 1869). Yemen: Périm Island (MNHN); Aden (MNHN): Hawf, al-Mahrah (HD). Oman: Raysut, Salalah (BMNH; ZMA); Kuria Muria Islands (ZMA); Masirah Island (BMNH, 2M, 1F; ZMA); Ras al-Hadd (BMNH, 1M, 1F, 1R). Pakistan: 7 km W Bulegi Point, Sind (LACM); Karachi (BMNH, 3M, 5F, 2R). India: Mada Island, Salsette Island, Bombay (ANSP); Nicobar Islands (ZSI; uncertain identification, see Nomenclature, above).

Remarks: The shell of this species shows considerable variation in shape, thickness, opacity and coloration. Thin-walled, translucent shells with indistinct pattern, rounded whorls and no peripheral rib (Figures 2, 36, 40) look very different from larger, thick-walled, opaque, strongly domed shells with striking black and white pattern, sharply angled periphery and flat or concave base (Figures 1, 3). Yet these extremes are connected by many intermediates, and even within samples from a single locality there can be great variation (Figures 36, 37, 39, 40). Whether there is a geographical or ecological correlation to this variation is not clear. Shells from Pakistan are mostly of the translucent form with pale pattern, those from East Africa are opaque and strongly marked, whereas those from the Red Sea and Oman span the entire range. A common feature of the shells is the generally small number of basal ribs, often 3 or less, of which that at the mid-point of the radius is usually slightly larger than the rest. The color pattern of narrow oblique or wavy axial lines is also a useful recognition character.

This species is closely similar in shell characters to *P. fuscopiperata*, and some of the translucent, rounded shells are indistinguishable. That they are indeed distinct species is confirmed by the difference of the penis in each (long filament and small mamilliform gland in *P. infracostata*, short filament and large gland in *P. fuscopiperata*), which is maintained in syntopic samples from Tiwi Beach, Kenya (Figures 76, 77, 80, 81). At this locality (as in a dry collection from Conducia Bay, Moçambique) both species are represented by thick-walled forms; the shells of *P. infracostata* have a taller spire, more steeply domed, with flatter final whorl and sharper peripheral angle, the base is flatter with 1–2 or rarely 3 coarser ribs (3–4 in *P. fuscopiperata*) and the umbilicus smaller or closed; the color pattern is sometimes very similar, but in *P. infracostata* the oblique lines are dark and more regular (Figure 3), whereas in *P. fuscopiperata* the coloration is much more variable in intensity and pattern, including irregular markings, spiral bands and fine marbling (Figures 8–10). Thinner-shelled forms of these two species are distinguished by the slightly taller spire of *P. infracostata*, and sometimes by the basal ribs, of which the central one is often enlarged in *P. infracostata*, whereas in *P. fuscopiperata* the ribs become larger toward the periphery.

As a consequence of this similarity, the southern geographical range of *P. infracostata* is uncertain. Available material from southern Moçambique and South Africa consists mainly of dry shells, of the translucent type. All anatomical material seen from this area has been of *P. fuscopiperata*, but more is required to confirm that *P. infracostata* does not occur. No anatomical material has been seen from the Red Sea (including the type locality, Suez), and the association of the name with the specimens from Oman and Pakistan is based on apparently identical shells and geographical proximity. The eastern limit of *P. infracostata* remains unclear; additional material is necessary to confirm the synonymy of Nevill's (1885) *subinfracostata* from the Nicobar Islands (see Nomenclature, above).

Peasiella fuscopiperata (Turton, 1932)
(Figures 6–10, 42–48, 80–83, 110, 111, 132)

Cyclostrema fuscopiperata Turton, 1932:198–199, pl. 51, fig. 1379 [lectotype (here designated, 1.9 mm diam., Figure 6) + paralectotype, OUM, seen; Port Alfred, South Africa].

Peasiella infracostata.—Reid, 1989a:61–64 [in part; includes *P. infracostata*, *P. fasciata*, *P. habei*, *P. patula*; not *P. infracostata* (Issel, 1869)].

Nomenclature: Surprisingly, since this species is not uncommon in southern Africa, it does not appear to have been mentioned in works on mollusks of the region, except in Turton's (1932) original description of shells from the southern extremity of its range.

Shell (Figures 6–10, 42–48): Adult size range 1.3–2.7 mm diameter. *Shape:* thickness varies from delicate and translucent, to more solid and opaque; depressed to flattened (H/D 0.54–0.91); outline domed; whorls rounded, suture impressed; in thin-walled shells periph-

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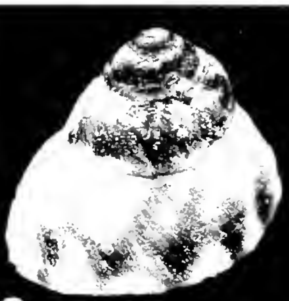
Figures 18–24. *Peasiella habei*. **18, 19.** 4–5 km SW Tsutsu, Tsushima I., Nagasaki Pref., Japan (BMNH 1996389). **20.** Holotype, Esu Cape, Shirahama, Wakayama Pref., Japan (BMNH 1996274). **21.** Tai Ping Bay, Qingdao, China (BMNH 1996390). **22.** Lok Wo Sha, Hong Kong (BMNH 1996391). **23.** Baten, Okinawa, Japan (BMNH 1996392). **24.** Ma Lin Shi, Tolo Harbour, Hong Kong (BMNH 1996393). **25–29.** *Peasiella isseli*. **25, 28.** Dahab, Sinai, Egypt (BMNH 1996394). **26, 27.** Hurghada, Egypt (BMNH 1996395). **29.** Suez, Egypt (BMNH 1882.8.7.316). **30–34.** *Peasiella mauritiana*. **30.** Lectotype of *Risella isseli* var. *mauritiana* Viader, 1951, Grand Bay, Mauritius (BMNH 1989004). **31.** Arabian Gulf (BMNH 1996396). **32.** Inhaca I., Moçambique (NM L3435). **33.** Sadh, Oman (BMNH 1996397). **34.** Zanzibar, Tanzania (BMNH 1904.10.20.97). Scale bar = 2 mm.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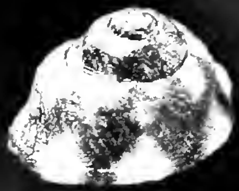
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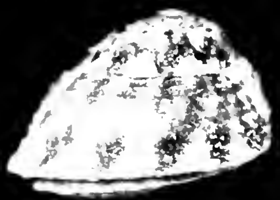
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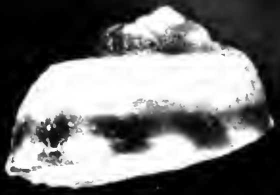
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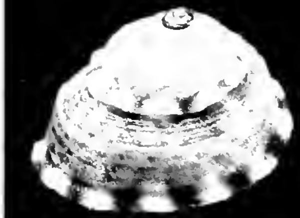
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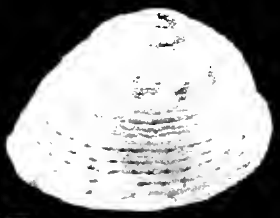
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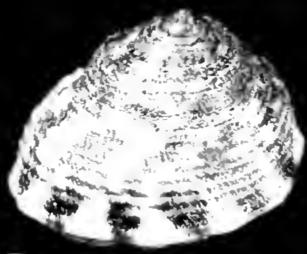
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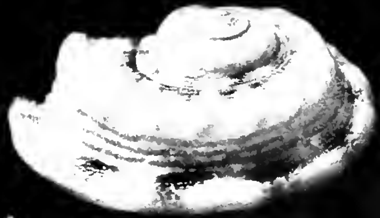
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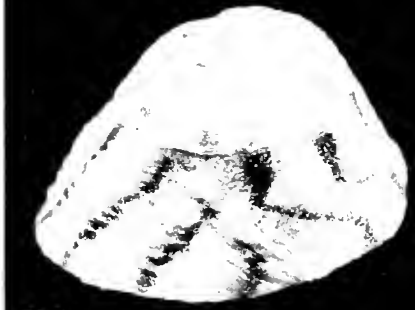
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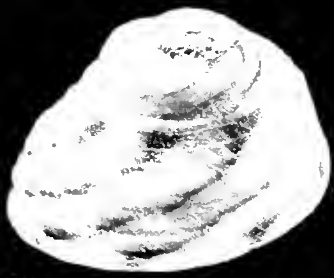
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ery uniformly rounded or marked by slightly thickened rib only, in thicker shells periphery angled and marked by sharp keel or narrow flange; base rounded; umbilicus of moderate size; columella rounded, slightly thickened and angled at base. *Sculpture:* protoconch 240 μm diameter, 2.5 whorls, protoconch II sculptured by scattered granules and narrow raised ridges (as in Figures 106, 107 of *P. fasciata*); teleoconch whorls usually microscopically smooth above periphery, or with fine spiral microstriae, rarely with 2–6 slight or indistinct ribs; 2–6 (rarely 0, 1 or 8) ribs on base, outermost strongest, becoming weaker toward umbilicus; basal ribs fine, indistinct or absent in thin-walled shells; rarely minute periostracal bristles present on basal and dorsal ribs. *Color:* thin-walled shells translucent pale yellow-brown with faint pattern of 6–14 oblique or wavy brown lines (sometimes present only as faint marbling), distinct only at suture and periphery, base unmarked; thicker shells opaque white or beige, with highly variable pattern: red-brown to black coarse, irregular pattern of bands, chevrons and zigzags, usually leaving an unpigmented sutural band; sometimes a continuous broad spiral band on shoulder; sometimes a paler brown pattern of diffuse marbling, with or without 9–12 darker peripheral spots; spire orange-brown, often with dark red-brown spiral band; base sometimes red-brown with 6–10 dark spots on white peripheral keel; lower columella and parietal callus sometimes red-brown.

Animal: *Head-foot:* front of head blackish, with a separate black band across base of snout; tentacles unpigmented; foot with some black pigment on sides or unpigmented. *Penis (Figures 80–83):* filament small (10–20% total length), tapering; base thicker, sometimes wrinkled, with single very large mamilliform penial gland occupying most of its length. *Pallial oviduct:* bursa not seen. *Radula (Figures 110, 111):* cusps pointed, major cusp of lateral and inner marginal tooth sometimes slightly rounded, central cusp of rachidian tooth slightly apiculate; outer marginal tooth with 5–8 long, pointed cusps, outermost more rounded, becoming smaller toward midline; base of rachidian tooth sometimes developing a pair of small posterior denticles.

Distribution: *Habitat:* Eulittoral; low, undercut limestone cliffs with fringing reef platform beyond (Kenya; D.S. Brown); alive in coralline algal debris washed up on strand line (South Africa; D. Herbert).

Range (Figure 132): East coast of South Africa to Kenya.

Records and material examined: South Africa: Port Alfred (NM, OUM); East London (NM); Mbotyi, Pondoland (NM); Port Edward (NM); Umdhloti, Natal (NM); Mapelane, Zululand (NM, 2M); Leven Point, Zululand (NM, 1M). Moçambique: Benguera Island, Bazaruto Archipelago (NM); Conducia Bay (NM). Kenya: Tiwi Beach, 30 km S Mombasa (BMNH, 7M, 4F, 4R, 1P).

Remarks: Reid (1989a) identified smooth-shelled forms of this species as *P. infracostata*, and those rare examples with spiral sculpture above the periphery as *P. isseli* (with which *P. mauritiana* was then included). The form of the penis provided the first evidence that this species is distinct; the short filament is found elsewhere in the genus only in *P. patula*, but there the mamilliform gland is of a different shape. The present species is sympatric with two others, *P. mauritiana* and *P. infracostata*, in East Africa, and penial shape is diagnostic of each. The shell is most similar to that of *P. infracostata*, and separation of the two has been discussed in the Remarks on that species. In both, the shell shows parallel variation in thickness, opacity, spire height, angulation of the margin and intensity of color pattern. Occasional shells with spiral sculpture above the periphery could be confused with those of *P. mauritiana*; *P. fuscopiperata* lacks the shoulder angulation of that species, is usually a more delicate shell and rarely shows the same pattern of strong oblique radial lines.

Peasiella patula new species
(Figures 11–13, 52–56, 84–87, 112, 113, 123, 127, 128, 133)

Peasiella infracostata.—Reid, 1989: 61-64, fig. 110 [in part; includes *P. infracostata*, *P. fuscopiperata*, *P. habei*, *P. fasciata*; not *P. infracostata* (Issel, 1869)].

Etymology: Latin *patulus*, open, in reference to the relatively large aperture.

Types: Holotype BMNH 1996276 (Figure 11); 5 paratypes BMNH 1996277, 49 paratypes in alcohol BMNH 1996278 (Figures 87, 112, 113). Type locality: Changi Point, Singapore.

Shell (Figures 11–13, 52–56): Adult size range 1.2–2.0 mm diameter. *Shape:* depressed to conical (H/D 0.75–0.85); somewhat patulous, last whorl enlarged, aperture relatively large; protoconch (if present) projects as papillose tip to spire; whorls well rounded or inflated, often with rounded shoulder, suture impressed; angled periphery marked by sharp but barely projecting keel; base slightly rounded; umbilicus wide; columella narrow, curved at base; viewed from above or below, apertural

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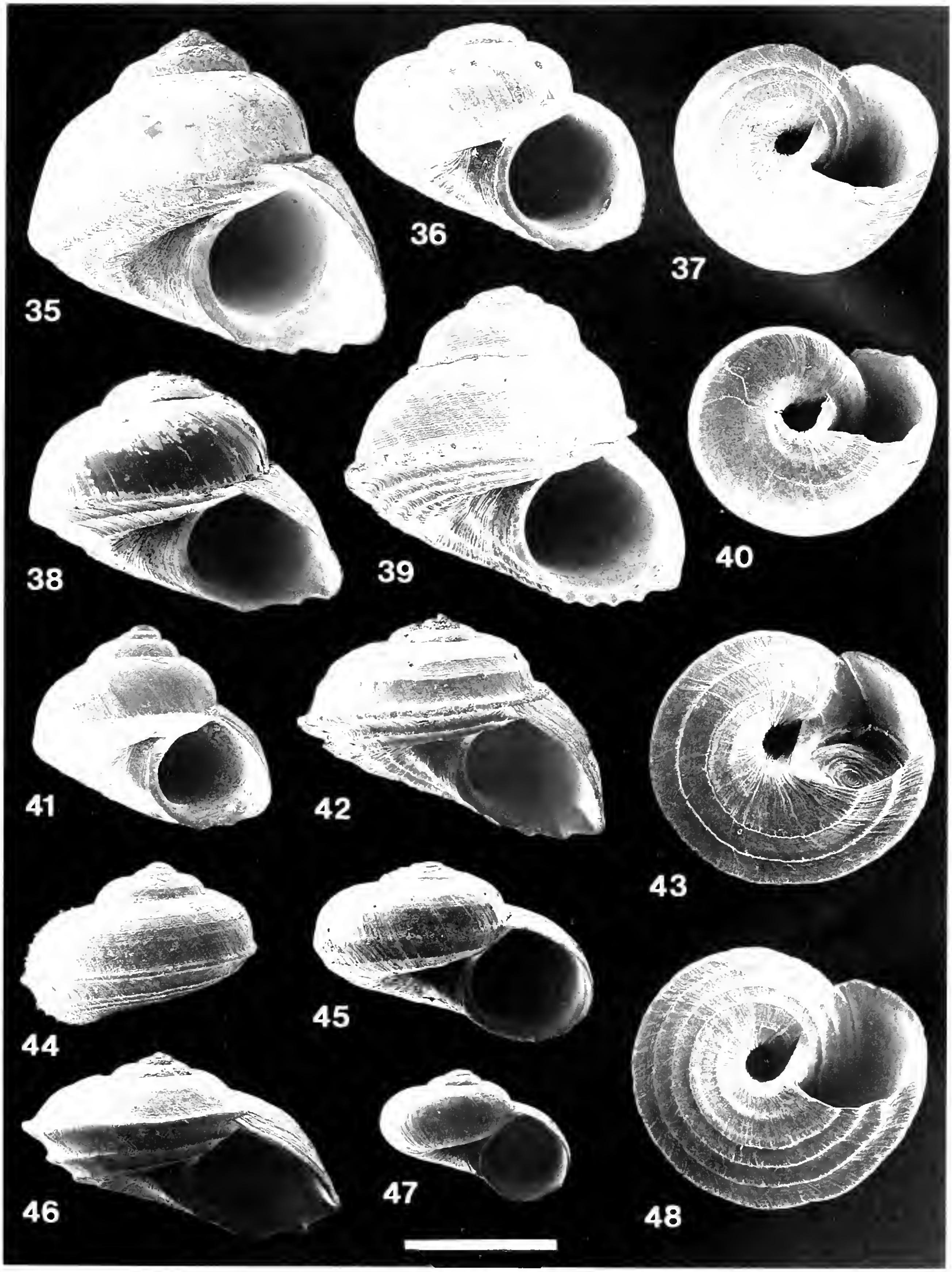
Figures 35–41. *Peasiella infracostata*. **35.** Lectotype of *Risella (Peasiella) tantillus* var. *subinfracostata* Nevill, 1885, Nicobar Is (ZSI). **36, 37, 39, 40.** Karachi, Pakistan (BMNH 1996383). **38.** 4 km S Ras Qudufah, Masirah I., Oman (BMNH 1996385). **41.** Lectotype of *Risella infracostata* Issel, 1869, Red Sea (MNHN). **42–48.** *Peasiella fuscopiperata*. **42, 43, 46, 48.** Tiwi Beach, 30 km S Mombasa, Kenya (BMNH 1996386). **44.** Leven Point, Zululand, South Africa (NM E2745). **45.** Mzamba, Transkei, South Africa (NM 3028). **47.** Mapelane, Zululand, South Africa (NM D2415). Scale bar = 1 mm.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edge is curved (i.e. growing edge is prosocyrt). *Sculpture:* protoconch 260 µm diameter, 2.7 whorls, sculpture not preserved; teleoconch whorls smooth or with 6–7 indistinct to strong spiral ridges; 4–5 fine ribs on base; surface smooth or with fine spiral microstriae; basal ribs occasionally bear minute periostracal bristles. *Color:* cream to yellow ochre, with 4–7 fine brown spiral lines above periphery (including dark line at suture; sometimes increasing to 9 at end of last whorl); 7–12 brown oblique short stripes at periphery and suture, often faint or absent, occasionally continuing indistinctly across dorsal surface; base with 1–2 spiral brown lines at periphery, margin of umbilicus sometimes purplish brown; columella and parietal area purplish brown.

Animal: *Head-foot:* usually entirely unpigmented; sometimes slight blackish pigmentation behind head. *Penis (Figures 84–87):* filament slender, tapering, 30–40% total length; base thick, single large mamilliform penial gland (occupying 60–80% total length) with narrowly elongate reservoir; subepithelial glandular tissue at base of filament and around base of reservoir. *Pallial oviduct:* bursa not seen. *Egg capsule (Figures 123, 127, 128):* diameter 221.7 µm (SD 13.1 µm, n=10; ovum diameter 66.0±1.6 µm; Singapore; this study), of depressed cupola type with 3 concentric rings on upper side and pleated margin (like a thick cogwheel), containing single ovum. *Radula (Figures 112, 113):* all cusps sharply pointed, central cusp of rachidian tooth slightly apiculate; base of rachidian tooth with two sharp posterior denticles; outer marginal tooth with 3–4 pointed cusps, becoming smaller toward midline.

Distribution: *Habitat:* Among barnacles and oysters in upper eulittoral, on rocky shores and sea walls (Singapore).

Range (Figure 133): Singapore, Gulf of Thailand, northern Borneo.

Records and material examined: Singapore: Changi Point (BMNH; 1M,4F, 3R); Changi South (BMNH; 4M, 2F); St. John's Island (BMNH; 2R, 1P).Thailand: Pattaya (Le Renard Colln). Sabah: Berhala Channel, Sandakan (USNM).

Remarks: The expansion rate of the shell is larger in this species than in other members of the genus, so that it achieves a slightly, but distinctly, patulous shape which is characteristic. The color pattern resembles that of *P. fasciata*, although the lines are usually less pronounced and the sutural and peripheral spots more developed. These two species are distinguished by their penial form, the filament being slender and short in *P. patula*, and the mamilliform gland relatively larger. Their egg capsules differ in shape in samples of *P. patula* from Singapore and *P. fasciata* from Hong Kong. They have not yet been found syntopically, but their known ranges appear to overlap in northern Borneo; additional collecting in the region may well reveal wider sympatry. The radula of *P. patula* is peculiar, showing a pair of sharp posterior denticles on the base of the rachidian tooth (Figures 112, 113). Among other littorinids, similar denticles have been described only in *Melarhaphe neritoides* (Bandel, 1974: figs. 58, 59), but the structures are closer to the posterior edge of the tooth in *P. patula*, and are probably not homologous. Slight development of basal denticles has been found in one example of *P. fuscopiperata* and one of *P. isseli*. One specimen from the type locality showed both a fully formed pallial oviduct and a well developed penis (see remarks on pseudo–hermaphroditism under *P. habei*). This is the rarest of all the *Peasiella* species in museum collections, perhaps because of its limited geographical range; in Singapore it occurs abundantly.

Peasiella fasciata new species
(Figures 14–17, 49–51, 88–91, 106, 107, 117, 122, 125, 126, 134)

Peasiella infracostata.—Reid, 1989a:61–64, fig. 12, fig. 30 (radula), fig. 48 (penis), fig. 112 [in part, includes *P. infracostata*, *P. fuscopiperata*, *P. patula*, *P. habei*; not *P. infracostata* (Issel, 1869)]. Reid, 1992:194, fig. 1c (penis), fig. 2c (oviduct), pl. 1, figs. i, l, m [in part, includes *P. habei*].

Etymology: Latin *fasciatus*, banded, in reference to color pattern.

Types: Holotype BMNH 1996272 (Figure 15); 5 paratypes BMNH 1996273; 1 paratype AMS C203254. Type locality: Turtle Bay, Cape Ferguson, Queensland, Australia.

Shell (Figures 14–17, 49–51, 106, 107): Adult size range 1.3–2.5 mm diameter. *Shape:* turbinate to depressed turbinate (H/D 0.78–1.12); outline domed; whorls well rounded, suture distinct; periphery uniformly rounded, or angled, or marked by a more or less prominent rib; base rounded; umbilicus small or almost closed; columella narrow, uniformly rounded. *Sculpture:* protoconch 240 µm diameter, 2.6 whorls, protoconch I smooth, protoconch II with scattered small granules and narrow wavy or straight ridges, of which 6 are visible above suture (Figures 106, 107); teleoconch whorls

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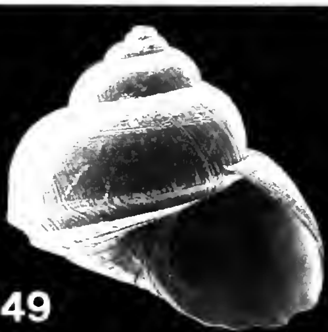
Figures 49–51. *Peasiella fasciata*, Uvol Mission, Cape Dampier, New Britain, Papua New Guinea (AMS C163128). **52–56.** *Peasiella patula* **52.** Changi Point, Singapore (BMNH 1996278). **53–55.** St. John's I., Singapore (BMNH 1996387). **56.** Pataya, Thailand (LR 99012) **57–61.** *Peasiella habei* **57.** 4–5 km SW Tsutsu, Tsushima I., Nagasaki Pref., Japan (BMNH 1996389). **58, 59.** Nejiko, Hirado I., Nagasaki Pref., Japan **60.** Ma Liu Shi, Tolo Harbour, Hong Kong (BMNH 1996393). **61.** Zanpa Point, Okinawa, Japan (AMS C146702). Scale bar = 1 mm



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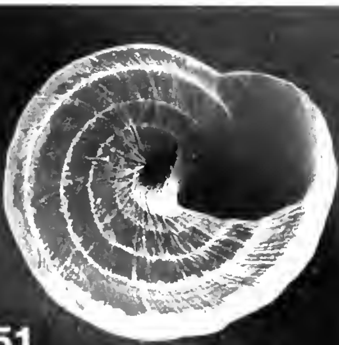

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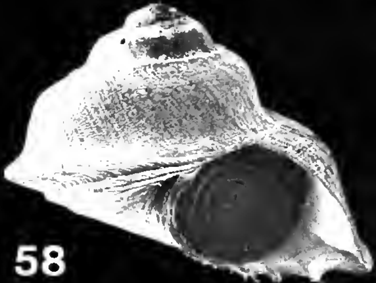

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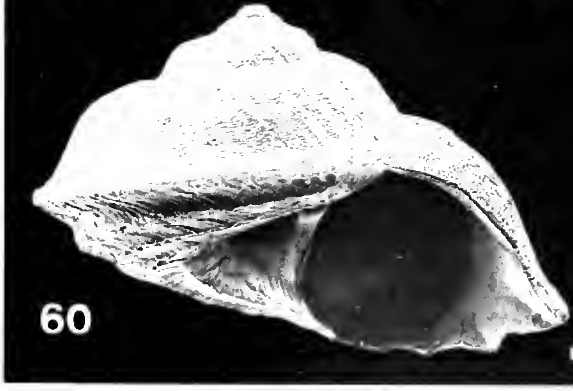

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smooth above periphery, with fine spiral microstriae, rarely with 3–4 faint grooves; 3–4 ribs on base (rarely 1–6), becoming stronger toward periphery. *Color:* translucent cream to opaque grayish white; pattern of brown, dark red-brown or black lines or bands, numbering 2–8 above periphery on last whorl (only 2–4 on spire whorls), bands often alternately thick and thin on last whorl; in addition sometimes 6–13 faint brownish spots at suture and periphery; 2–4 dark lines in grooves at periphery of base; base of columella and umbilical area sometimes dark purplish brown.

Animal: *Head-foot:* front of head blackish, with a separate black band across base of snout; tentacles unpigmented or with single longitudinal black line; foot unpigmented or with blackish sides. *Penis (Figures 88–91):* filament 40–50% total length, cylindrical and rounded at tip; base thicker, with single mamilliform penial gland of moderately large size (30–40% total length). *Pallial oviduct:* bursa present. *Egg capsule (Figures 122, 125, 126):* diameter 215.4 µm (SD 5.8 µm, n=10; ovum diameter 77.8±2.9 µm; Hong Kong; this study), of depressed cupola type with 4 concentric rings on upper side and pleated margin with peripheral keel, containing single ovum. *Radula (Figure 117):* cusps pointed, central cusp of rachidian tooth slightly apiculate; outer marginal tooth with 5–6 long, pointed cusps, outermost more rounded, becoming smaller toward midline.

Distribution: *Habitat:* among algae in rock pools (type locality; A. Mitchell); among short calcareous green algae and *Caulerpa*, on wave-exposed rocky platform (Cape Dampier; P. H. Colman); among eulittoral cobbles, crevices in granite and sedimentary rocks, among *Saccostrea*, on fairly sheltered and wave-exposed coasts (Hong Kong; J. D. Taylor, Y.-M. Mak). Appears to be generally scarce.

Range (Figure 134): Queensland, New Guinea, Borneo, Vietnam, Hong Kong, Taiwan.

Records and material examined: Queensland, Australia: Facing Island, Port Curtis (AMS); Turtle Bay, Cape Ferguson (AMS; 1M, 1R); Halfmoon Bay, Cairns (AMS); Green Island (AMS); Port Douglas (AMS). New Britain, Papua New Guinea: Uvol Mission, near Cape Dampier (AMS; 3M, 2F, 2P); Duke of York Island, Rabaul (AMS). Sabah: Bak-Bak, 9.6 km N Kudat (USNM). Vietnam: La Table Island, Tonkin (MNHN). Hong Kong: Wu Kwai Sha (BMNH; 2M, 2R); Peng Chau (BMNH; 1M); Hoi Ha (BMNH; 2F); Cape d'Aguilar (BMNH). Taiwan: Shi Cheng, Taipei (BMNH).

Remarks: The first evidence that this species was distinct from *P. habei* (both confused under *P. infracostata* by Reid, 1989a, 1992) was provided by their differently shaped egg capsules in Hong Kong (Figures 122, 124). Differences in shell shape and penial form were then recognized, as described in the Remarks on *P. habei*. The shell of *P. fasciata* is easily recognized by its combination of dark spiral lines, turbinate shape with well-rounded whorls, and small umbilicus. Spiral color bands are found in some other *Peasiella* species, especially on the spire whorls, but are only well-developed on the last whorl in one other species, *P. patula*, which is distinguished by its patulous shape. Anatomically, *P. fasciata* is characterized by its penis with long, cylindrical filament and moderately large mamilliform gland. As in *P. infracostata* and *P. fuscopiperata*, the shell can be opaque and solid, or translucent, although it is never as delicate as in some examples of those species. This species is rare in collections.

Peasiella habei new species
(Figures 18–24, 57–61, 92–98, 114–116, 124, 129, 130, 135)

Littorina-capsula habei Tokioka, 1950:151–152, fig. 6.1 (egg capsule) [Ago and Tanabe Bays, Japan; name unavailable, see below]. Habe, 1956:117–121.

Peasiella roepstorffiana.—Habe, 1956:118–121, fig. A (egg capsule). Oyama & Takemura, 1961: *Peasiella* and *Littorinopsis* pl., figs. 1–3. Yamamoto & Habe, 1962:16, pl. 3, figs. 3, 4, figs. 34, 35 (egg capsule). Amio, 1963:303, figs. 22a, b (egg capsule). Habe, 1964:28, pl. 9, fig. 23. Higo, 1973: 46. Habe, 1984:11, fig. 1. Ohtsuka & Yoshioka, 1985:232, fig. 4B. Okutani, 1986:71, unnumbered pl. Fukuda, Mashino & Sugimura, 1992:57, pl. 43, fig. 126. Higo & Goto, 1993:74. [All not *P. roepstorffiana* (Nevill, 1885)].

Peasiella infracostata.—Reid, 1989a:61–64, fig. 10, fig. 29 (radula), fig. 47 (penis), fig. 64 (egg capsule), fig. 111 [in part; includes *P. infracostata*, *P. fuscopiperata*, *P. patula*, *P fasciata*]. Choe, 1992:290, 591, fig. 56. Reid, 1992:194, pl. 1f [in part; includes *P. fasciata*]. Choe & Park, 1993: 19–20, text fig. 2. [All not *P. infracostata* (Issel, 1869)].

Etymology: To honor Prof. T. Habe, who has contributed much to the study of Japanese littorinids.

Types: Holotype BMNH 1996274 (Figure 20); 9 paratypes in alcohol BMNH 1996275. Type locality: Esu Cape, Shirahama, Wakayama Prefecture, Japan.

Nomenclature: Uniquely for a littorinid, the first name for this species was applied to its egg capsules. Tokioka (1950) described two types of littorinid egg capsules in plankton hauls from Ago and Tanabe Bays in southeastern Honshu, to which he gave Latin names. Since the littorinids that produced the capsules were not known, he coined a new genus *Littorina-capsula*. Subsequently, Habe (1956) showed that one of these capsules, *Littorina-capsula habei*, was the egg of the common Japanese species of *Peasiella* (which he misidentified as *P. roepstorffiana*). However, it is debatable whether the specific name given by Tokioka is nomenclaturally available. Habe (1956) apparently considered it so, printing it in italics. Others have not done this, and thus appear to have judged it unavailable (Amio, 1963; Reid, 1989a). In its favour, it can be argued that the name is unambiguous, since the egg capsule is distinctly different from those of other known Japanese littorinids. A name based on only one stage in a life cycle, while undesirable, is not thereby made unavailable (ICZN Art.

17). The generic name *Littorina-capsula* is unavailable (since it is not accompanied by fixation of a type species, ICZN Art. 13b), but this does not affect the standing of a specific name combined with it (ICZN Art. 11h). The inclusion of a hyphen in the generic name is an incorrect spelling (ICZN Art. 32c), and does not indicate that the name is non-binominal. On the other hand, it appears that Tokioka did not intend to introduce new names for littorinid species, for he stated: 'For convenience of recording these capsules met with during our plankton studies, I propose to give them the following provisional names'. This, we believe, debars the names from nomenclatural consideration, since the ICZN Code specifically excludes names proposed 'as means of temporary reference and not for formal taxonomic use as scientific names' (ICZN Art. 1b). This case is a complex and unusual one, and is open to alternative interpretations. If Tokioka's name were to be accepted, the egg capsules studied by him would have the status of type material; inquiries from the Seto Marine Laboratory have shown that no such material exists there (S. Yamato, pers. comm.). In this case, our choice is to re-describe the species as new, based on type material of adult animals collected near the locality of Tokioka's capsules. However, in recognition of Tokioka's discovery of the egg capsules, his intention to honor Prof. T. Habe, and to provide continuity, we use the same specific name.

In the Japanese literature this species has generally been misidentified as *P. roepstorffiana*, while Reid (1989a, 1992) incorrectly included it under *P. infracostata*.

Shell (Figures 18–24, 57–61): Adult size range 1.6–3.8 mm diameter. *Shape:* equilaterally conical or slightly more depressed (H/D 0.60–1.03); outline domed; whorls almost flat-sided or rounded or slightly shouldered, suture inconspicuous or impressed; peripheral keel prominent, often a projecting flange, rarely slightly undulating; base flat to slightly rounded; umbilicus usually narrow; columella narrow, curved at base. *Sculpture:* protoconch 230 μm diameter, 2.5 whorls, sculpture not preserved, apex usually eroded; teleoconch whorls usually smooth, with spiral microstriae, sometimes with 6–11 equidistant spiral grooves above periphery in largest specimens; 3–5 (rarely 6) sharp ribs on base, equidistant or becoming closer around umbilicus; basal ribs (and occasionally dorsal ribs) may bear periostracal bristles. *Color:* variable; fawn, cream or ochre, paler at periphery, with oblique (sometimes axial or zigzag) anastomosing brown stripes (sometimes faint, especially in Hong Kong), always darkening to form single row of 7–12 more or less conspicuous large brown or black spots near periphery (occasionally fusing to give a solid spiral band) which become narrower as they extend over pale peripheral keel; pattern on spire whorls darker, often blackish where eroded (especially in Japan); occasionally 2–4 spiral brown lines on spire whorls (common in Okinawa), usually disappearing on last whorl, but rarely persisting as 5–9 spiral lines; base ochre to brown, darker near umbilicus and in peripheral groove adjacent to keel; sometimes shell more darkly patterned, spire and base black, last whorl with oblique anastomosing black stripes on whitish ground (some from Japan and northern China).

Animal: *Head-foot:* front of head blackish, with separate black band across base of snout, occasionally almost unpigmented; tentacles unpigmented; sides of foot sometimes slightly pigmented. *Penis (Figures 92–98):* filament long (50–60% total length), vermiform; base slightly thicker, 1 (rarely 0 or 2) small mamilliform penial gland. *Pallial oviduct:* bursa present. *Egg capsule (Figures 124, 129, 130):* diameter 261.3 μm (SD 0.5 μm, n=10; ovum diameter 68.3±2.3 μm; Hong Kong; this study), 150–250 μm (Japan; Tokioka, 1950; Amio, 1963; Ohtsuka & Yoshioka, 1985), of cupola type with 4 concentric rings on upperside, containing single ovum. *Radula (Figures 114–116):* cusps pointed, central cusp of rachidian tooth slightly apiculate, major cusp of lateral and inner marginal teeth sometimes slightly rounded; outer marginal tooth with 4–6 (rarely 3) long, pointed cusps, outermost more rounded, becoming smaller toward midline.

Distribution: *Habitat:* In Japan this species is abundant in crevices and among barnacles in the middle and upper eulittoral zone, on sheltered and moderately exposed rocky shores; on exposed shores it shows a preference for surfaces protected from wave action (Mori *et al.*, 1985a, b; Tanaka *et al.*, 1985). In Hong Kong and Taiwan it appears to be rare, and is found among barnacles and oysters in the uppermost eulittoral zone on sheltered shores.

Range (Figure 135): China, Korea, Taiwan, Ryukyu Islands, Japan.

Records and material examined: China: Ma Liu Shi, Tolo Harbour, Hong Kong (BMNH; 1M, 1F, 2R); Lok Wo Sha Bay, Tolo Channel, Hong Kong (BMNH); Paotai, Xiamen (BMNH; 1M, 1F); Gu Leng Yu, Xiamen (BMNH; 1M, 3F,1R, 1P); Tai Ping Bay, Qingdao (BMNH; 2M, 2F, 1R); Hui Quan Bay, Qingdao (BMNH). Korea: Taesori, Sangch'uja I. (Choe, 1992; Choe & Park, 1993). Taiwan: Yehliu, Taipei (BMNH). Japan: 1.5 km WNW Onna, Okinawa (AMS); Bolo Point, Okinawa (AMS, 1F, 1R; USNM, NSMT); Baten, Okinawa (BMNH; 1M, 2F, 3R); Tomioka, Kumamoto Pref. (NSMT, 2R); Nagasaki (USNM); Omura Bay, Nagasaki Pref. (NSMT); Goto, Nagasaki Pref. (AMS); Nejiko, Hirado I., Nagasaki Pref. (BMNH; 1M, 1F); Tsutsu, Tsushima I., Nagasaki Pref. (BMNH); Fukuyoshi, Fukuoka Pref. (KU); Kure, Hiroshima Pref. (KU); Hanazura, Kochi Pref. (MNHN); Tatsukushi, Kochi Pref. (USNM, NSMT); Shirahama, Tanabe Bay, Wakayama Pref. (BMNH; 5M, 2F, 1R; USNM, NSMT); Shionomisaki, Wakayama Pref. (NSMT); Kuchino, Shiznoka Pref. (BMNH, 4M, 2R); Arasaki, Kanagawa Pref. (USNM, NSMT); Oga Peninsula, Akita Pref. (KU); Asamushi, Aomori Pref. (USNM, NSMT); 2.5 km N Tomari, Aomori Pref. (AMS); Kominato, Aomori Pref. (LACM).

Remarks: This species is variable in conspicuous features of the shell including color, spire profile and sculpture, but consistent characteristics are the row of dark spots above the periphery, which extend onto the pale peripheral keel, the darker and often black spire whorls, and the prominent keel at the periphery. There are some recognizable geographical trends in shell characters. In Japan and northern China the shape is taller, with flatter whorls and a sharper peripheral keel; periostracal bristles are present at least on the base of most well-preserved specimens; the spire, usually eroded, is black or darkly patterned (Figures 18–21, 57–59). Shells from the southern parts of the range are distinctly different. Those from Okinawa have a pale pattern; the dark peripheral spots are most conspicuous on the spire whorls, which are also often marked by 2-4 spiral brown lines; the whorls are sometimes rounded at the shoulder, and usually bear strong spiral grooves above the periphery, and the peripheral keel is less pronounced; periostracal bristles have not been seen (Figures 23, 61). Shells from Hong Kong and southern China are similar in shape to those from Okinawa, but are usually smooth above the periphery, sometimes bear periostracal bristles on the base, and the color is ochre with strong peripheral spots and darkly patterned spire (Figures 24, 60). However, these southern populations are also variable, and intermediates apparently connect them with the typical northern forms (Figure 22). Additional material, particularly from the Ryukyu Islands, would be desirable to investigate this variation in more detail, and to confirm our interpretation. The penial shape is similar throughout the range. The egg capsules from Hong Kong (figures 124, 129, 130) are almost identical in shape to those figured from Japan by Tokioka (1950; reproduced by Yamamoto & Habe, 1962; Reid, 1989a), Habe (1956) and Ohtsuka & Yoshioka (1985). However, at a diameter of 261 μm they are slightly larger in size than Japanese capsules, measured as 150–200μm (Tokioka, 1950), 150 μm (Amio, 1963) and 220–250 μm (Ohtsuka & Yoshioka, 1985).

The rounded shells with lined pattern on the spire that can be found in Okinawa bear some similarity to those of *P. fasciata* from Hong Kong. This led Reid (1989a) to consider them conspecific (as *P. infracostata*). However, new material from Hong Kong has shown that both species occur there, although so far they have not been collected syntopically (i.e. on the same shores). In Hong Kong the shells of *P. habei* only occasionally bear 1–2 indistinct spiral brown lines above the periphery on the last whorl, and their conspicuous peripheral spots and darkly patterned spire differ from the 4–8 strong spiral lines of local examples of *P. fasciata*. Anatomically, the mamilliform penial gland of *P. habei* is smaller and the penial filament relatively narrower and slightly more elongate than in *P. fasciata*. The egg capsules of these two species (sampled in Hong Kong) also differ (Figures 122, 124).

Two other species are sometimes sympatric with *P. habei* in the southern part of its range and might be confused with it, *P. lutulenta* in Hong Kong and *P. roepstorffiana* in the southern Ryukyu Islands, Taiwan and Hong Kong. *Peasiella lutulenta* has 5–9 strong spiral ribs above the periphery, usually a gap between inner and outer series of ribs on the base (ribs all equidistant in *P. habei*), the columella has a thickened angulation at the base, and the color pattern is of 7–13 broad and irregular, dark axial stripes (see Reid, 1989a, 1992). Anatomically the two are closely similar; the penial filament of *P. habei* is slightly narrower and more elongate, and there are 4–6 cusps on the outer marginal tooth, but only 3 in *P. lutulenta*. *Peasiella roepstorffiana* (Figures 142–145) has 4–13 strong spiral grooves above the periphery, frequently shows radial plications near the suture and periphery, which give rise to strong crenulations of the peripheral keel; the innermost one third of the basal radius lacks ribs; the color is often bright chrome yellow or orange, with peripheral brown spots or band. Anatomically, *P. roepstorffiana* from Hong Kong lacks the mamilliform penial gland, and the copulatory bursa is absent.

Some abnormalities of the reproductive tract of *P. habei* have been found. A single specimen from Shiznoka Prefecture had no mamilliform penial gland (Figure 98), and one (parasitized by trematodes) from Tanabe Bay had two glands of normal size (Figure 97); in each case normal specimens occurred in the same lots. One other specimen from the latter sample had both a small, fully formed penis and a small oviduct. Genuine hermaphroditism has been described in only one littorinid genus, *Mainwaringia* (Reid, 1986b), but pseudo-hermaphroditism (involving development of a penis and other male characters in females) is known in several littorinid genera (Reid, 1986b, 1996), and is sometimes a response to pollution by organotin compounds (Bauer *et al.*, 1995). *Peasiella* species are not known to be truly hermaphrodite, and this example is probably a case of pseudo-hermaphroditism.

Peasiella isseli (Semper in Issel, 1869)
(Figures 25–29, 62–67, 99–101, 118, 119, 136)

Trochus sp. Audouin, 1826:42
Risella isseli Semper in Issel, 1869:194, 347 [refers to Savigny,

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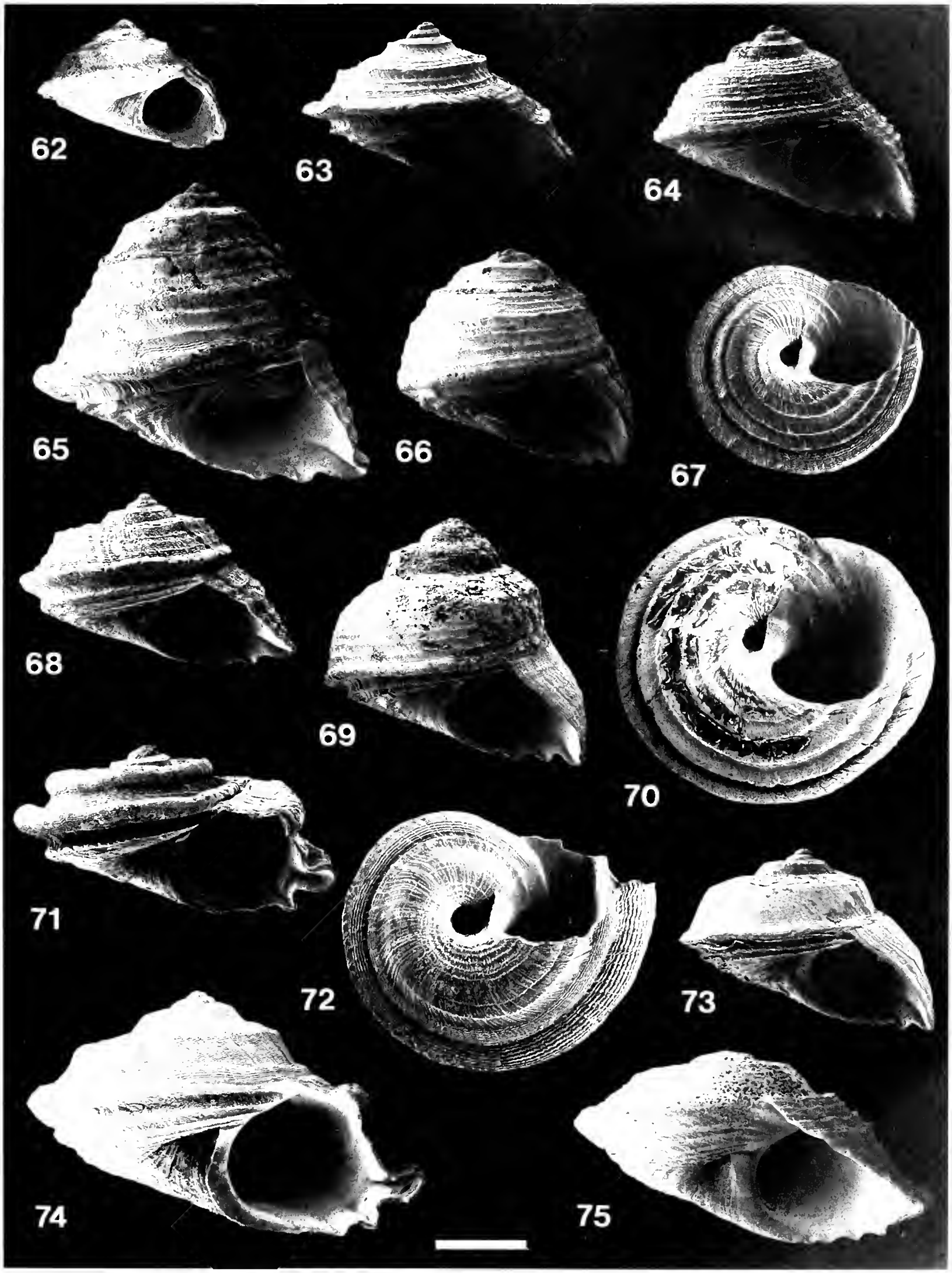
Figures 62–67. *Peasiella isseli* **62.** Lectotype of *Risella isseli* Semper in Issel, 1869, Red Sea (MNHN). **63, 65, 66.** Suez, Egypt (BMNH 1888.10.14). **64, 67.** Hurghada, Egypt (BMNH 1996395). **68–75.** *Peasiella mauritiana*. **68.** Tiwi Beach, 30 km S Mombasa, Kenya. **69, 70, 73.** Sedh, Al Khaysah, Oman. **71.** Kuwait. **72, 74.** Bandar Khayran, Oman. **75.** Baie Ternay, Mahé, Seychelles. Scale bar = 1 mm.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1817: pl. 5, figs. 35.1, 35.2; lectotype (Reid, 1989a: fig. 62) + 2 paralectotypes MNHN, seen; Suez (Reid, 1989a); 2 paralectotypes in MGD ex-Semper Colln, seen, from Zanzibar are *P. mauritiana*]. Pallary, 1926:84, pl. 5, fig. 35.1, 35.2. Lamy, 1938:71. Moazzo, 1939:183. Bouchet & Danrigal, 1982:13, fig. 65.

Risella (*Peasiella*) *isseli*.—Nevill, 1885:160–161 [in part; includes *P. mauritiana*]. Tryon, 1887:263, pl. 50, figs. 39, 40.

Peasiella isseli.—Franc, 1956:25. Mastaller, 1979:40. Reid, 1989a:60–61, fig. 13, fig. 50 (penis), fig. 56 (sperm), figs. 97, 98, 101, 103 [in part, includes *P. mauritiana*].

Trochus sismondae Issel, 1869:225–226, pl. 2, fig. 13 [holotype MGD, seen; Suez].

Risella isseli var. *carinata* Pallary, 1926:84–85, pl. 5, fig. 36 [reproduced from Savigny, 1817; syntype MNHN, seen; Suez].

Risella isseli var. *undata* Pallary, 1926:84, pl. 5, fig. 35.3 [reproduced from Savigny, 1817; types not in MNHN; Suez].

Nomenclature: Throughout its taxonomic history this species, endemic to the Red Sea, has been confused with *P. mauritiana*, and the two taxa have not previously been distinguished at the specific level. In the original description, Issel referred to the figures of Savigny (1817) based on Egyptian specimens. He also mentioned his own material from Suez and Semper's from Zanzibar, of which the latter (in MGD) is *P. mauritiana*. Reid (1989a) designated one of the shells from the Savigny Collection as the lectotype, and restricted the type locality to Suez, thereby fixing the identity of this species.

Shell (Figures 25–29, 62–67): Adult size range 1.7–4.2 mm diameter. *Shape:* conical to depressed conical (H/D 0.55–1.23); outline domed; whorls usually with rounded or angled shoulder, occasionally flat or only gently rounded; suture usually distinct; periphery sharply angled, with prominent rib or flange; dorsal sculpture sometimes slightly rugose, but only rarely does peripheral flange show slight crenulation; base flat or slightly rounded; umbilicus small to moderate; columella rounded, sometimes with a slightly thickened angle at base. *Sculpture:* protoconch 240 µm diameter, 2.3 whorls, protoconch II with scattered small granules and narrow wavy or straight ridges, of which 5 are visible above suture (as in Figures 106, 107, of *P. fasciata*); teleoconch whorls with 6–15 narrow ribs, uniform or unequal in size, above periphery; rib at shoulder sometimes slightly enlarged; surface above periphery covered with fine spiral microstriae; base with 4–6 (rarely 2–7) ribs, larger toward periphery. *Color:* extremely variable; uniform cream, ochre, orange-brown, dark chestnut brown or entirely black; often with darker pattern of fine dots or lines in dorsal grooves; dorsal surface sometimes with fine white and brown marbled pattern; rarely a dark spiral band on dorsal surface; sometimes 7–15 brown spots on white peripheral keel; rarely pale sutural spots in addition to darker peripheral spots, but only very seldom does an indistinct pattern of broad radial bands appear; spire sometimes pink or crimson; apex often lilac or blackish; base lacking color pattern or with small spots in grooves.

Animal: *Head-foot:* head unpigmented or blackish in front, separate black band across base of snout; tentacles usually with 2 longitudinal black lines; sides of foot with some black pigmentation or unpigmented. *Penis (Figures 99–101):* filament long (50% total length), tapering at tip; base thicker, with single mamilliform penial gland of moderate size. *Pallial oviduct:* large anterior bursa present. *Radula (Figures 118, 119):* cusps pointed, major cusp of lateral and inner marginal teeth slightly rounded, central cusp of rachidian tooth sometimes slightly apiculate; base of rachidian tooth occasionally with slight development of pair of posterior denticles; outer marginal tooth with 4 pointed cusps, outermost more rounded, becoming smaller toward midline.

Distribution: *Habitat:* Abundant under coral blocks in upper eulittoral on a moderately sheltered shore (Egypt; D. G. Reid).

Range (Figure 136): Red Sea and Aden.

Records and material examined: Israel: Eilat (BMNH, 1M, 2F; USNM, ANSP). Egypt: Faraun Island, Gulf of Aqaba (HD); Ras el Kura, Dahab, Sinai (HD); Suez (BMNH, 1P, 2R; MNHN); Suez Canal (Tillier & Bavay, 1906; Moazzo, 1939); Hurghada (BMNH, 3M, 2F, 2R; HD). Sudan: Dungunab Bay (BMNH); Port Sudan (BMNH; ANSP). Saudi Arabia: Jeddah (USNM, MNHN). Eritrea: Massawa (BMNH, NM); Dahlak Archipelago (BMNH). Yemen: Périm Island (MNHN); Aden (MNHN).

Remarks: The shells of *P. isseli* and *P. mauritiana* are very similar, and the two have not previously been dis-

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Figures 76–79. Penes of *Peasiella infracostata* **76, 77.** Tiwi Beach, 30 km S Mombasa, Kenya. **78.** Karachi, Pakistan. **79.** Ras al-Hadd, Oman **80–83.** Penes of *Peasiella fuscopiperata*. **80, 81.** Tiwi Beach, 30 km S Mombasa, Kenya. **82, 83.** Mapelane, Zululand, South Africa (NM D5822). **84–87.** Penes of *Peasiella patula*. **84–86.** Changi South, Singapore. **87.** Paratype, Changi Point, Singapore (BMNH 1996278). **88–91.** Penes of *Peasiella fasciata* **88, 89.** Uvol Mission, Cape Dampier, New Britain, Papua New Guinea (AMS C163128). **90.** Wu Kwai Sha, Hong Kong. **91.** Peng Chau, Hong Kong. **92–98.** Penes of *Peasiella habei*. **92.** Tai Ping Bay, Qingdao, China. **93.** Shirahama, Wakayama Pref., Japan. **94.** Baten, Okinawa, Japan. **95–97.** Fujishima, Tanabe Bay, Wakayama Pref., Japan. **98.** Kuchino, Suruga Bay, Shizuoka Pref., Japan **99–101.** Penes of *Peasiella isseli*, Hurghada, Egypt. **102–105.** Penes of *Peasiella mauritiana* **102.** Khor Hajar, Ras al-Hadd, Oman. **103.** Anse La Mouche, Mahé, Seychelles. **104.** Merawwah I., Abu Dhabi. **105.** Tiwi Beach, 30 km S Mombasa, Kenya. Note that structure of mamilliform penial glands is visible by transparency; mucous reservoir is shown by solid line, and extent of subepithelial glandular tissue by dotted line. The penial base is sometimes wrinkled.


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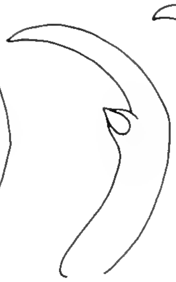
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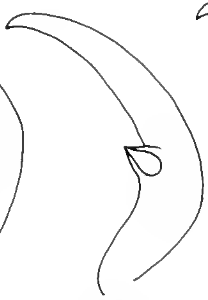
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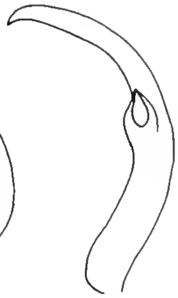
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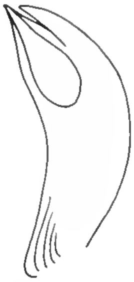
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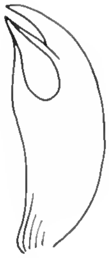
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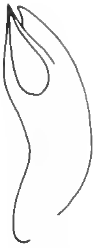
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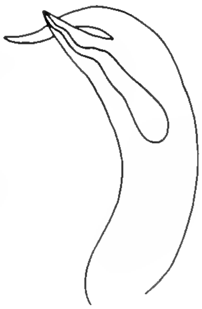
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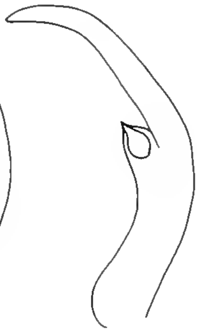
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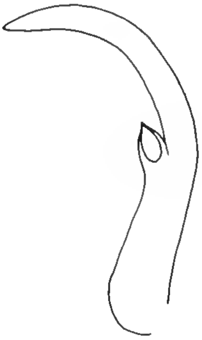
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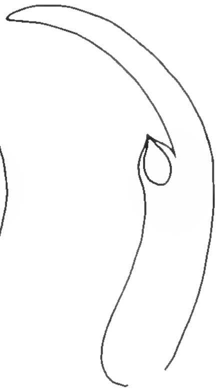
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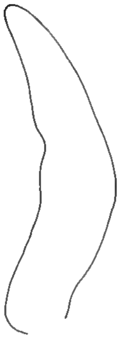
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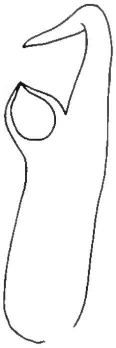
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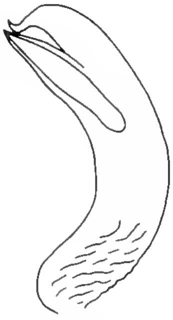
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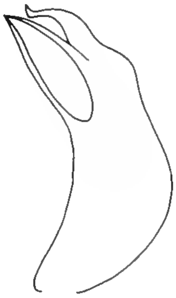
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tinguished as separate species. From the new anatomical material available for each species, it is clear that they can be diagnosed by the form of the penis. This is of the common type for the genus in *P. isseli*, with long filament and small mamilliform gland, whereas in *P. mauritiana* from throughout its large range it has a short filament with mucronate and hooked tip, and a large gland. Having separated the two using this character, correlated differences in shell shape and coloration can be recognized. In both, the development of the shoulder angulation is variable; in *P. isseli* it is often absent or represented only by an angulation of the profile, more rarely by a prominent rib; in *P. mauritiana* the shoulder is usually marked by a sharp angulation, often with an enlarged or even carinate rib.The coloration is also different; in *P. mauritiana* there is usually a pattern of obliquely radial lines or stripes, often darker at the suture and periphery; in *P. isseli* the color is highly variable, but radial stripes rarely appear, and the apex is often pink or blackish. Using these characters, together with knowledge of the regional variation in the shell of *P. mauritiana,* it has been possible to identify shells with confidence. So far, it appears that *P. isseli* is restricted to the Red Sea and Aden, whereas *P. mauritiana* is widespread in the Indian Ocean and Persian Gulf. The two apparently occur sympatrically just at the mouth of the Red Sea. Two dead shells of *P. isseli* have been recorded from Aden (MNHN), from which locality five other samples contained only *P. mauritiana.* Both have been found together in a single lot of dead shells from Périm Island, South Yemen (Jousseaume Colln, MNHN), which contained 50 *P. isseli* and 8 *P. mauritiana,* readily separated by their shell characters.

The only other species to occur sympatrically with *P. isseli* is *P. infracostata.* These two are readily distinguished by the presence of spiral ribs above the periphery in *P. isseli* (absent in *P. infracostata*), and by the color pattern of oblique or zigzag lines in *P. infracostata.* The shape of the penis is, however, similar in both.

Most *Peasiella* species show variation in color pattern, sometimes on a regional or interpopulational scale. This species is unique in the genus in its extreme intrapopulational variation; shells from beneath the same rock may range from cream to patterned to black. Furthermore, occasional specimens can be found in which the color changes from cream on the spire to entirely black on the last whorl (Figure 26).

Peasiella mauritiana (Viader, 1951)
(Figures 30–34, 68–75, 102–105, 120, 121, 137)

Risella isseli —Issel, 1869:194 [in part; includes *P. isseli*].
Risella (*Peasiella*) *isseli.*—Nevill, 1885:160–161 [in part, includes *P. isseli*]. Melvill & Standen, 1901:364 [not Semper in Issel, 1869].
Peasiella isseli.—Reid, 1989a:60–61, figs. 14, 15, fig. 28 (radula), fig. 49 (head), fig. 97, 99, 100, 102, 104, 105 [in part; includes *P. isseli*]. Bosch *et al.*, 1995:46, fig. 119 [not *P. isseli* (Semper in Issel, 1869)].
Risella infracostata.—Dautzenberg, 1929:496 [not Issel, 1869].
Risella isseli var. *mauritiana* Viader, 1951:149, pl. 3, figs 10, 11 [lectotype, here designated, Figure 30, + 2 paralectotypes, seen, BMNH 1989004; Grand Bay, Mauritius; 2 probable paralectotypes Mauritius Institute, not seen].

Nomenclature: Hitherto, this species has always been confused with *P. isseli.* It was first named, as a variety of that species, by Viader (1951). Two specimens of *Risella isseli* var. *mauritiana* were exhibited in the natural history museum of the Mauritius Institute (R. Gajeelee, pers. comm. 1985); these have not been examined, but are likely to have been syntypes. In addition, there are 3 specimens in the Winckworth Collection in BMNH, labeled '*Peasiella isseli* v. *mauritiana* Viader MS' in Winckworth's hand; these are from Grand Bay, one of the two localities mentioned in Viader's (1951) description. It is known that Winckworth received specimens from Viader (see also acknowledgement of Winckworth's assistance in determinations, Viader, 1951:136), and it is likely that this material was sent by Viader before Winckworth's death in 1950. Since Viader (1951) did not designate type specimens, a lectotype is here designated from the BMNH material (ICZN art. 74; recommendation 72B).

Shell (Figures 30–34, 68–75): Adult size range 1.6–5.6 mm diameter. *Shape:* highly variable; depressed conical to flattened (H/D 0.42–1.03); outline domed, straight or spire slightly concave; shoulder usually sharply angled, or with projecting rounded carina (some Persian Gulf and northern Oman specimens), or sometimes becoming rounded or even flattened on last whorl; suture usually distinct; periphery sharply keeled or flanged, or with flaring rounded carina (some Persian Gulf and northern Oman specimens); shoulder occasionally regularly rugose and peripheral flange with 7–8 slight crenulations (some East African specimens); base flat to rounded; umbilicus small to large; columella rounded, sometimes indistinctly thickened and angled at base.

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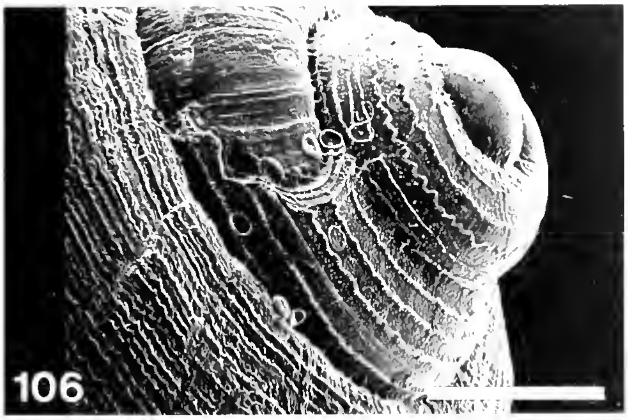
Figures 106, 107. Protoconch of *Peasiella fasciata,* Uvol Mission, Cape Dampier, New Britain, Papua New Guinea (AMS C163128). **Figures 108, 109.** Radulae of *Peasiella infracostata* **108.** Karachi, Pakistan (flat view, shell D=1.5 mm). **109.** Ras al-Hadd, Oman (flat view, shell D=1.9 mm). **110, 111.** Two views (flat and at 45°) of radula of *Peasiella fuscopiperata,* Tiwi Beach, 30 km S Mombasa, Kenya (shell D=1.7 mm). **112, 113.** Two views (flat and at 45° from side) of radula of paratype of *Peasiella patula,* Changi Point, Singapore (BMNH 1996278, shell D=1.7 mm); note posterior denticles on base of rachidian tooth (arrow). Scale bars: **106, 107** = 100 μm, **108–113** = 20 μm.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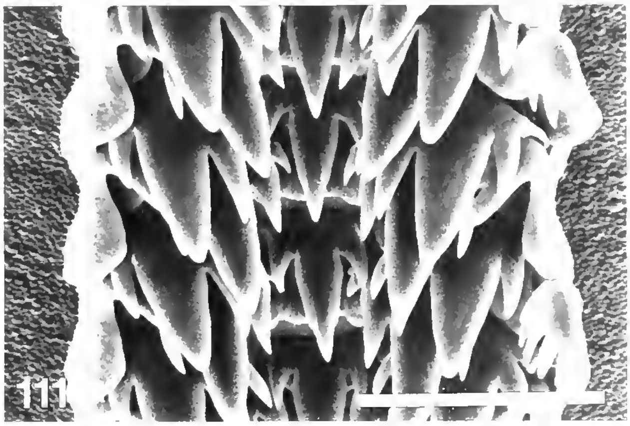
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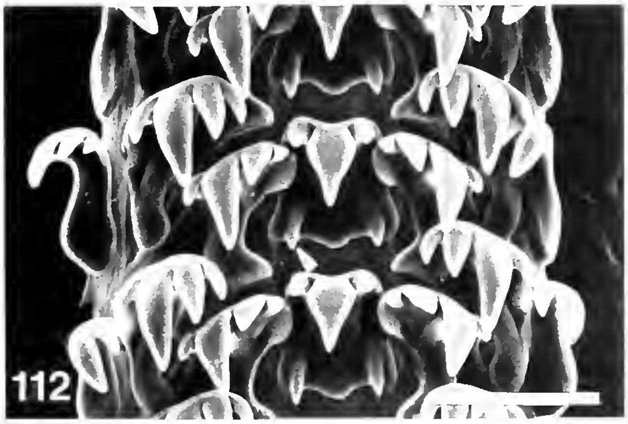
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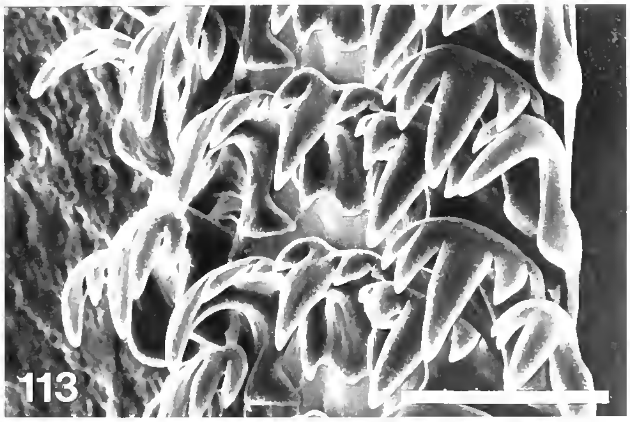
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Sculpture: protoconch 220 μm diameter, 2.2 whorls, protoconch II with scattered small granules and narrow wavy or straight ridges, of which 6 are visible above suture (as in Figures 106, 107, of *P. fasciata*); teleoconch whorls usually with 6–12 fine spiral ribs above periphery, sometimes only single rib at shoulder, or absent; surface above periphery covered with fine spiral microstriae; base with 4–7 (rarely 1–3) ribs, becoming weaker and more closely spaced around umbilicus; periostracum thicker than in other species of the genus, and may flake off from dry shells; ribs on base and rarely on dorsal surface may bear periostracal bristles (some Persian Gulf and northern Oman specimens). *Color:* cream to ochre; usually with dark brown oblique (opisthocline) lines or narrow stripes, numbering 6–11, often darkest or broadest at suture and periphery; in northern Oman and Persian Gulf oblique lines may number up to 23 on last whorl, anastomosing to produce 8–15 spots at suture and periphery; diagonal stripes occasionally present only at suture and periphery (some East African specimens); diagonal pattern only rarely entirely absent or developed only on spire (most specimens from Seychelles); often a single brown spiral line on early spire whorls; base unpatterned or with small brown spots on ribs, occasionally forming radial lines; parietal callus, columella base and umbilical margin sometimes brownish.

Animal: *Head-foot:* front of head blackish or with narrow black band only, separate black band across base of snout; tentacles with 2 longitudinal black lines; sides of foot with some black pigmentation or unpigmented. *Penis (Figures 102–105):* filament short (20–30% total length), with elongate, mucronate tip, distinctly hooked or minutely hammer-shaped at very tip; base thicker, finely wrinkled, with single large mamilliform penial gland (rarely absent) with elongate reservoir. *Pallial oviduct:* bursa present, apparently at posterior end of straight section. *Radula (Figures 121, 122):* cusps pointed, major cusp of lateral and inner marginal teeth slightly rounded, central cusp of rachidian tooth slightly apiculate; outer marginal tooth with 4 pointed cusps, outermost more rounded, becoming smaller toward midline.

Distribution: *Habitat:* intertidal rocks, pools and *Thalassodendron* flats in a sheltered bay (Inhaca Island; R. N. Kilburn); barnacle zone on beach rock (Aldabra; J. D. Taylor); among barnacles in high eulittoral, on surf beach (Masirah Island; J. D. Taylor); crevices in limestone, in upper eulittoral, on sheltered coast and in tidal lagoon (Ras al-Hadd; E. Glover); among barnacles on mangrove pneumatophores (Abu Dhabi; D. George); among *Crassostrea* (Kuwait; D. Jones).

Range (Figure 137): Zululand to Persian Gulf, Mauritius, Madagascar, Seychelles; excluding Red Sea.

Records and material examined: South Africa: Mission Rocks, Zululand (NM). Moçambique: Inhaca Island (NM, 1M); Benguera Island (NM); Moçambique Island (NM). Tanzania: Zanzibar (BMNH). Kenya: Tiwi Beach, 30km S Mombasa (BMNH, 2M, 2F). Madagascar: Tuléar (MNHN); Mahajanga (IRSNB); Nossi-Bé (USNM, ANSP, MNHN, ZMA); Diego-Suarez (IRSNB). Île Mayotte (MNHN, 1M). Mauritius: Grand Bay (BMNH, NM); Pointe Radeau, S of Roches Noires (NM); Pointe d'Azur (NM). Seychelles: Aldabra (BMNH); Baie Ternay, Mahé (BMNH, 2R); Anse la Mouche, Mahé (BMNH, 1M, 1F; USNM); Northwest Bay, Mahé (ANSP). Djibouti (MNHN). Yemen: Périm Island (MNHN); Little Aden (BMNH, 2F); Aden (BMNH, MNHN). Oman: Hamran, Zufar (BMNH); Sudh (BMNH); Sadh (BMNH); Kuria Muria Islands (ZMA); Masirah Island (BMNH, 1F; ZMA, 2F); Sedh, Al Khaysah (BMNH); Khor Hajar, Ras al-Hadd (BMNH, 1M, 2F, 1R); Bandar Khayran (BMNH); Al Bustán, 3.2 km E Muscat (ZMA); Muscat (NM); N of Sharm (BMNH). Abu Dhabi: Merawwah Island (BMNH, 3M, 1F). Qatar: Khor, Doha (BMNH). Kuwait (BMNH).

Remarks: Although shape and coloration are highly variable in this species as a whole, some geographical patterns can be distinguished. In southern Arabia the spire is a little taller, the shoulder more rounded, the peripheral keel less pronounced, and spiral sculpture on the dorsal surface is weaker or even absent (Figures 33, 69, 73). In the Persian Gulf and northern Oman there is a tendency to flattening of the spire, and development of heavy carinae at the shoulder and periphery, while the dark oblique lines become more numerous (Figures 31, 71, 74). Specimens from Kenya and Zanzibar are more rugose, sometimes with regular radial folds and slightly crenulate peripheral flange (Figures 34, 68). In the flattened and weakly shouldered specimens from the Seychelles (Figure 75) the lined color pattern is absent or occasionally present on the spire only. In typical specimens from the Mascarene Islands, Madagascar and Moçambique, the shoulder is scarcely marked and the color pattern is pronounced (Figures 30, 32).

The shell of this species is most likely to be confused with that of *P. isseli* (see Remarks on that species), which

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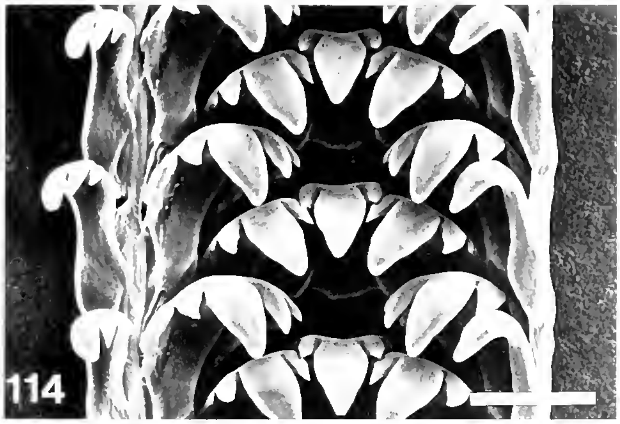
Figures 114–116. Radulae of *Peasiella habei*. **114.** Baten, Okinawa, Japan (flat view, shell D=3.2 mm). **115.** Ma Lin Shi, Hong Kong (view at 45°, shell D=2.2 mm). **116.** Gu Leng Yu, Xiamen, China (view at 45° from side, shell D=1.8 mm). **117.** Radula of paratype of *Peasiella fasciata*, Turtle Bay, Cape Ferguson, Queensland, Australia (BMNH 1996273; view at 45°, shell D=2.1 mm). **118, 119.** Radulae of *Peasiella isseli* **118.** Hurghada, Egypt (flat view, shell D=2.4 mm). **119.** Hurghada, Egypt (view at 45°, shell D= 3.0 mm). **120, 121.** Two views (flat and at 45°) of radula of *Peasiella mauritiana*, Khor Hajar, Ras al-Hadd, Oman (shell D=3.6 mm). Scale bars = 20 μm.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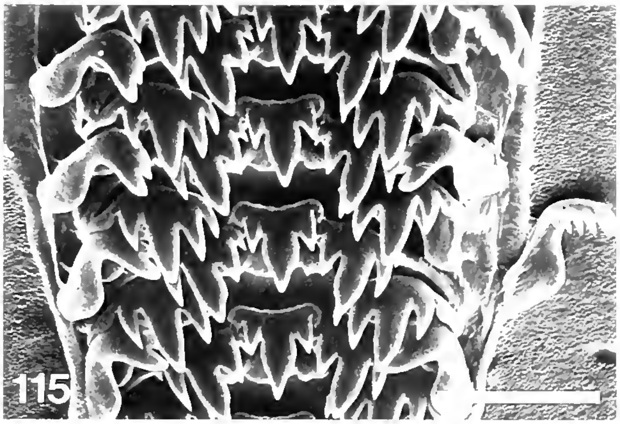
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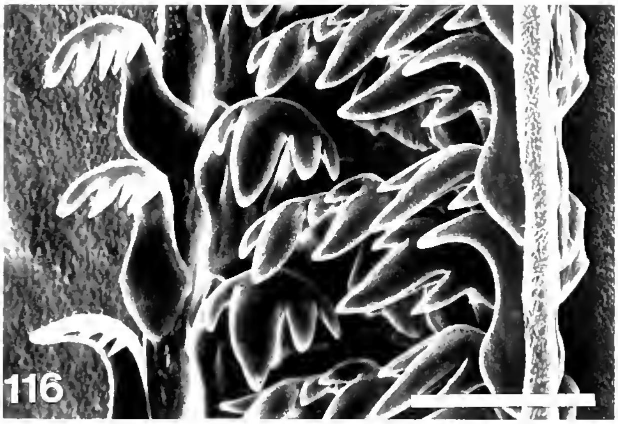
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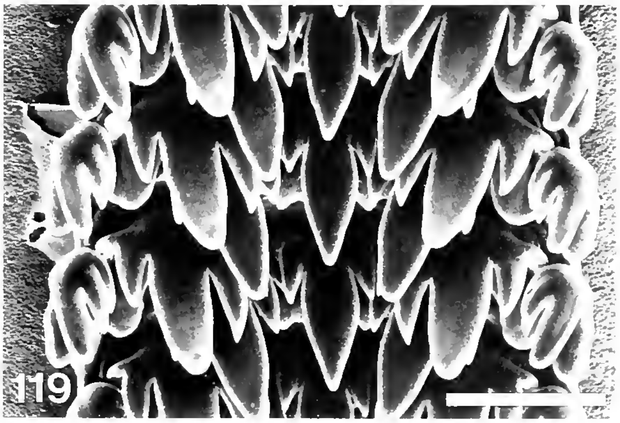
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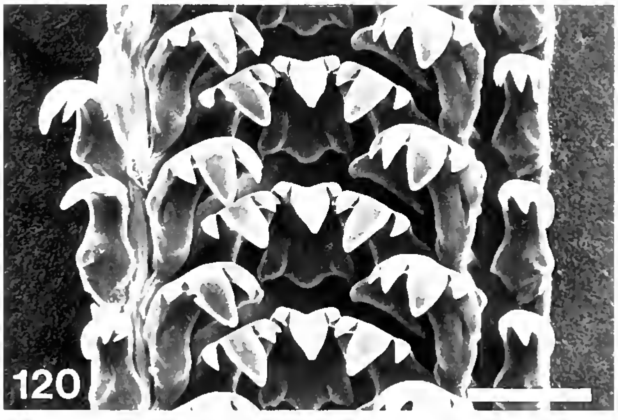
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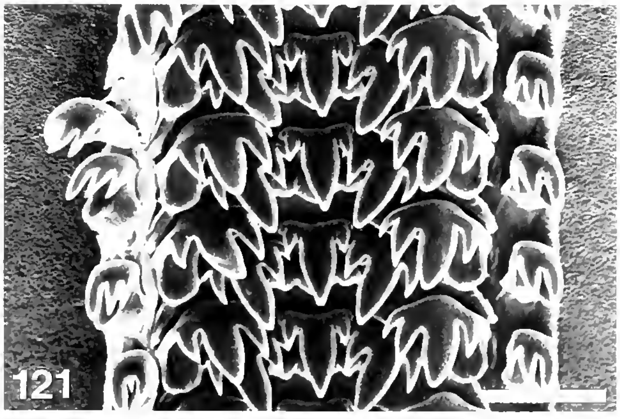
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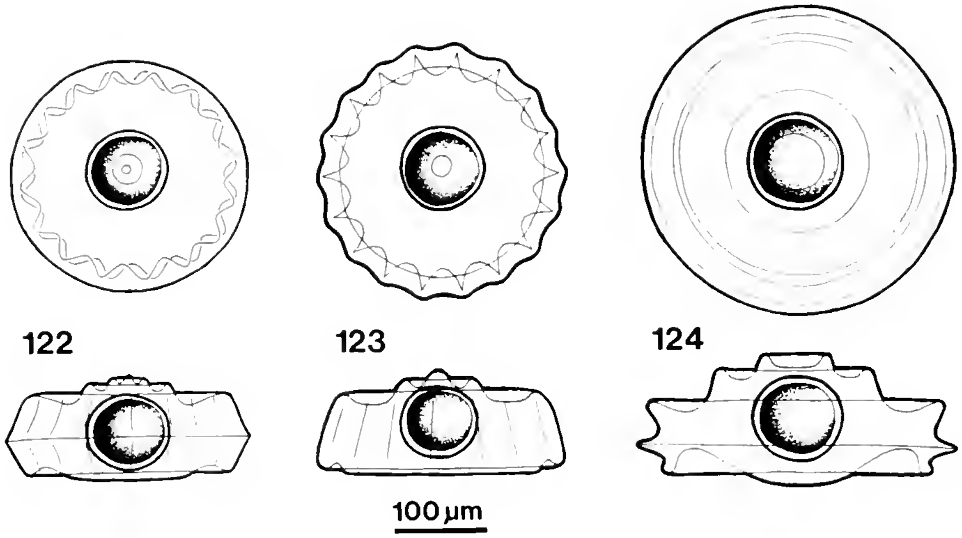


Figures 122–124. Egg capsules of *Peasiella* species. **122.** *Peasiella fasciata*, Cape d'Aguilar, Hong Kong. **123.** *Peasiella patula*, Changi Point, Singapore. **124.** *Peasiella habei*, Ma Liu Shi, Tolo Harbour, Hong Kong.

is endemic to the Red Sea; the two are only known to be sympatric close to the mouth of the Red Sea. Two other species, *P. infracostata* and *P. fuscopiperata*, can be found syntopically with *P. mauritiana*, and all three have diagnostic penial shapes. The shell of *P. infracostata* is always smooth above the periphery, and is thus easily distinguished from all ribbed and shouldered forms of *P. mauritiana*. However, examples of the latter from southern Oman and Yemen may lack ribs above the periphery, and if the shoulder angulation is poorly developed may be confused with *P. infracostata*. The basal ribs may then be useful; in *P. mauritiana* the outermost rib is the largest, but in *P. infracostata* the mid-basal rib is most prominent. Rare examples of *P. fuscopiperata* which have spiral sculpture above the periphery could be confused with this species, but lack the shoulder angulation.

ADDITIONAL NOTES ON OTHER SPECIES OF *PEASIELLA*

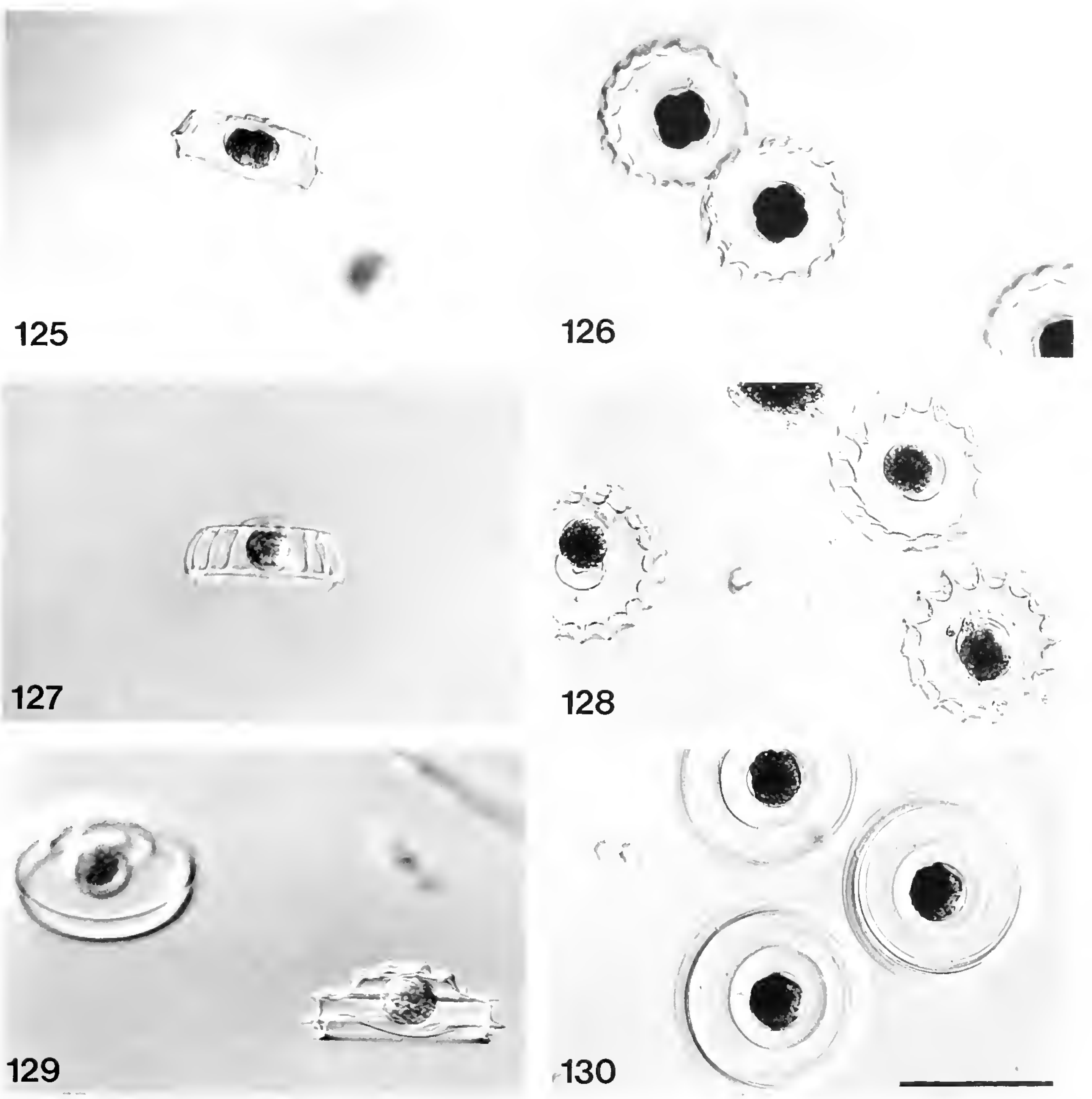
Peasiella roepstorffiana (Nevill, 1885)
(Figures 142–145)

Distribution: *Additional records:* Indonesia: Ambon (NNML). Taiwan: Kending, Kaohsiang (BMNH); Yehliu, Taipei (BMNH). Japan: Kannon Saki, Ishigaki, Ryukyu Islands (BMNH).

Remarks: The range of this species is now extended from Hong Kong (Reid, 1989a, 1992) to Taiwan and the southernmost Ryukyu Islands (Figures 142, 144, 145), and also includes Ambon in Indonesia. A curious feature of this species is the apparent dimorphism of penial form; a mamilliform gland is present in material from Queensland, but not in specimens from Asia (Reid, 1989a). The absence of a penial gland has been confirmed in material from Ishigaki and Ambon. Additional anatomical material has also been seen from Lautoka, Viti Levu, Fiji (BMNH); penial glands were found to be absent in two specimens, but in a third a rudimentary gland was present, with a cluster of subepithelial tissue but no reservoir or papilla. This supports the earlier suggestion that the penial dimorphism is indeed intraspecific. A similar case of geographical variation in presence or absence of a single penial gland has since been recorded in *Littorina kasatka* (Reid, 1996). The new Fijian material also supports the identification of the distinctive darkly tessellated shell from the eastern part of the range as merely a color variant of this species. Six additional radulae examined (Hong Kong, Singapore, Taiwan, Japan) each have 3 cusps on the outer marginal tooth, as recorded by Reid (1989a). The egg capsule of this species was described by Mak (1995) from Hong Kong; it is much larger than those capsules described here, 360–390 µm in diameter, and similar in shape to that of *P. habei*, although without the two inner concentric rings on the upper surface.

Peasiella conoidalis (Pease, 1868)
(Figures 138–141)

Remarks: Additional anatomical material of this species has been seen from Taiwan and Ishigaki, Ryukyu Islands (BMNH). The penial shape is the same as that illustrated by Reid (1989a), with a small and slender penial gland. Shells from these localities are often darker in color than those found elsewhere, with brown dots (or occasionally fine lines) in the spiral grooves above the periphery and strong brown marks in the folds between the peripheral crenulations (Figure 138). In some shells the pattern consists of 10–17 dark brown axial stripes (Figure 140). *Peasiella roepstorffiana* also occurs at these localities, and shells of the two are easily confused since both are yellow,



Figures 125–130. Egg capsules of *Peasiella* species. **125, 126.** *Peasiella fasciata*, Cape d'Aguilar, Hong Kong. **127, 128.** *Peasiella patula*, Changi Point, Singapore. **129, 130.** *Peasiella habei*, Ma Liu Shi, Tolo Harbour, Hong Kong. Scale bar = 200 µm.

have radially plicate sculpture and peripheral crenulations (Figures 138, 141, 142, 145). They are separated by the following characters: in *P. conoidalis* the spiral grooves above the periphery usually contain small brown dots rather than continuous lines and the peripheral brown marks are weaker; the middle of the base of *P. conoidalis* shows 1–2 rows of small brown spots, whereas that of *P. roepstorffiana* is unmarked but for dark blotches on the underside of the peripheral keel and purple-tinged columella; the wide unsculptured area surrounding the umbilicus is characteristic of *P. roepstorffiana*; anatomically, the single mamilliform penial gland of *P. conoidalis* is lacking in *P. roepstorffiana* (note that these characters do not necessarily apply to the two species in other parts of their ranges, see Reid, 1989a). These two species are only occasionally found sympatrically elsewhere (e.g. Lizard Island, Australia; southeastern Papua New Guinea; Ambon, Indonesia; some islands in Fiji and the Philippines), since *P. conoidalis* has an oceanic distribution while that of *P. roepstorffiana* is more continental in character. An unidentified *Peasiella* species from Chichijima, in the Ogasawara (Bonin) Islands, illustrated by Fukuda (1993), is a small, worn example of this species (specimen now in BMNH). *Peasiella conoidalis* has also now been recorded on the African mainland for the first time, from Tiwi Beach, Kenya (BMNH), where it occurred with *P. infracostata*, *P. fuscopiperata* and *P. mauritiana*. Another new record is from Ambon, Indonesia (NNML).

Peasiella lutulenta Reid, 1989

Remarks: This species is now recorded from Singapore (BMNH), where it appears to be rare. One of the five specimens found was a female with a mature pallial oviduct as well as a small penis (see Remarks on *P. habei* and *P. patula*). Two additional radulae examined each have 4 cusps on the outer marginal teeth, whereas Reid (1989a) found 3 cusps.

Peasiella petiti Le Renard, 1994

Remarks: This species from the Eocene of France was described and figured as *P. minuta* (Deshayes, 1824) by Reid (1989a); this name is preoccupied, and the species was renamed by Le Renard (1994).

DISCUSSION

SHELL VARIATION

Our reassessment of the taxonomy of *Peasiella* has not altered the earlier conclusion (Reid, 1989a) that the shell characters of these littorinids are unusually variable. Elsewhere in the family, species with likewise planktotrophic development do not normally show such conspicuous variation (e.g. Reid, 1986a, 1996). The variations in whorl outline and sculpture are most striking, since these characters are traditionally used to diagnose littorinid species. For example, in *P. infracostata* and *P. fuscopiperata* the periphery may be strongly keeled or smoothly rounded. In *P. isseli* and *P. mauritiana* the whorl profile may be almost flat or may develop a prominent carina at the shoulder. In *P. fuscopiperata*, *P. patula*, *P. habei* and *P. mauritiana* the surface above the periphery may be smooth or bear spiral ribs. Shell thickness is also variable, ranging from solid and opaque to thin and translucent in both *P. infracostata* and *P. fuscopiperata*. One sculptural character that is more useful for identification is the number and size of the ribs on the base. Many littorinids are conspicuously variable in shell color and pattern, and this is also the case in some *Peasiella* species, notably *P. isseli*. Nevertheless, we have found the number and arrangement of the oblique or spiral color bands to be one of the more useful characters for their identification. The cause and adaptive significance of shell variation in non-planktotrophic littorinids has been the subject of much research, but that of the planktotrophic species is less well understood (reviews by McQuaid, 1996; Reid, 1996).

ANATOMY

Throughout the family Littorinidae the shape of the penis is known to be one of the most useful taxonomic characters, and probably plays a role in species recognition in nature (e.g. taxonomic accounts and reviews by Reid, 1986a, 1989b, 1996). It was therefore surprising that the previous account of *Peasiella* (Reid, 1989a) concluded that penial shape was similar throughout the genus. All the six species for which anatomical material was then available showed a penis with a long filament and a single mamilliform penial gland (although in *P. roepstorffiana* the gland was found to be absent over much of the geographical range). The new material available to us in the present study has revealed that sympatric species do in fact frequently show diagnostic differences in penial form, particularly in the relative sizes of filament and penial gland.

The gross morphology of the female reproductive system does not, however, show useful diagnostic characters. The arrangement of the loops of the egg groove through the glands of the pallial oviduct is the same in all 11 species of *Peasiella* (as illustrated by Reid, 1989a: figs. 57, 58, 65, 66). The copulatory bursa is apparently absent in six species, but this character is not useful for identification since it can be difficult to trace without histological preparation. Furthermore, in at least one littorinid, *Littorina saxatilis*, there is intraspecific variation in this feature, for the bursa is sometimes vestigial or absent in small, but mature, adults (Reid, 1996: 312).

The egg capsules of four *Peasiella* species have now been described (*P. habei*, *P. patula*, *P. fasciata*, herein; *P. roepstorffiana* in Mak, 1995). At least in *P. habei* the form of the capsule is constant over a wide geographical range, although there is some variation in size (see description of this species). These four species each show a unique capsule shape, and there is an almost twofold range of diameters among them. Similar interspecific variation is present in the genera *Nodilittorina* and *Littoraria* (reviews by Bandel & Kadolsky, 1982; Reid, 1986a, 1989b; Mak, 1995), although in most cases intraspecific variation is poorly known. The radial plication of the capsules of *P. patula* and *P. fasciata* has hitherto been described only in *Nodilittorina* species.

In general, the radula of littorinids is taxonomically useful for the diagnosis of generic groups (Reid, 1989b), but not at the species level (e.g. Reid, 1986a, 1996). As in the earlier study, we have found the radula of *Peasiella* species to be relatively uniform in the genus, showing interspecific variation only in the number of cusps on

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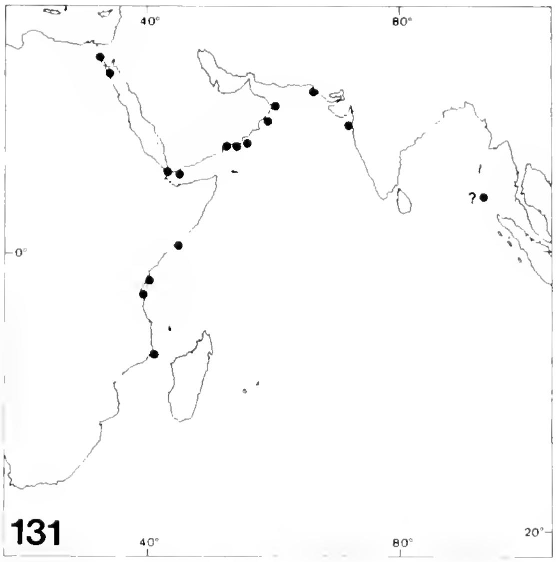
Figures 131–135. Distribution maps of *Peasiella* species, compiled from records listed in text. **131.** *Peasiella infracostata* **132.** *Peasiella fuscopiperata* **133.** *Peasiella patula*. **134.** *Peasiella fasciata*. **135.** *Peasiella habei*



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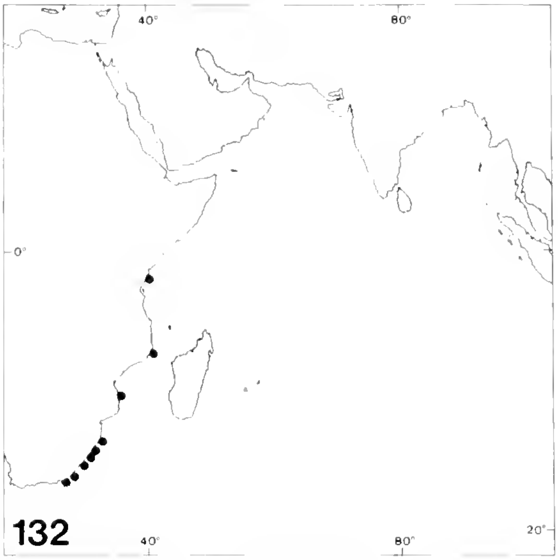
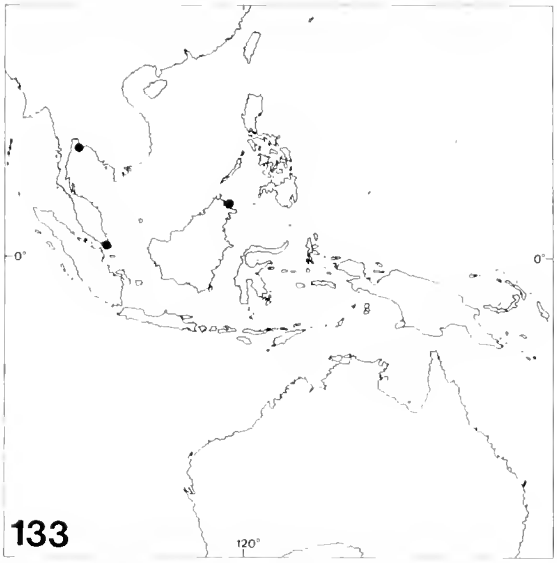
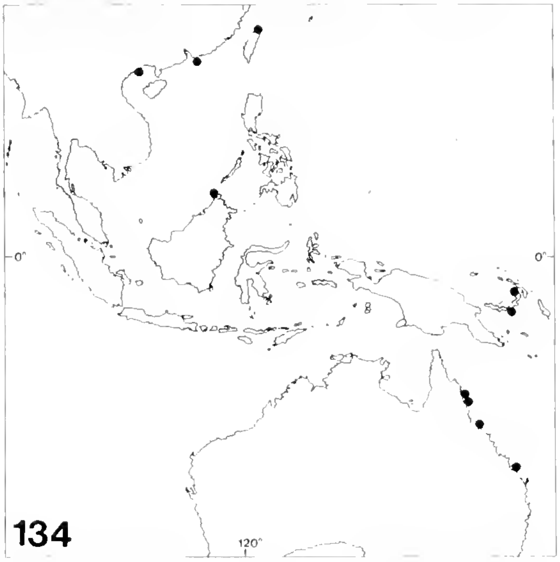


132



133



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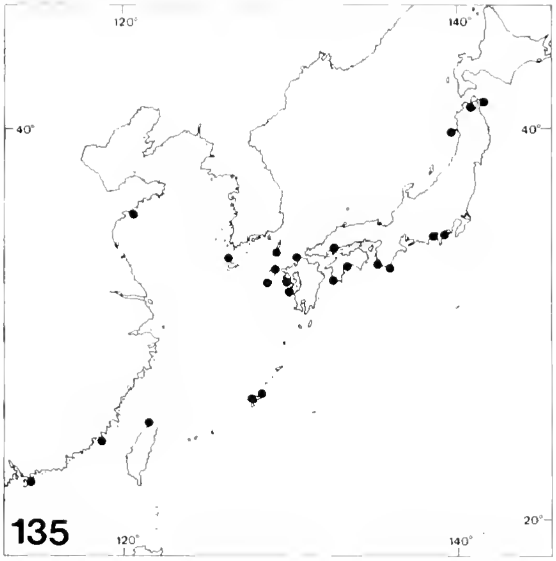

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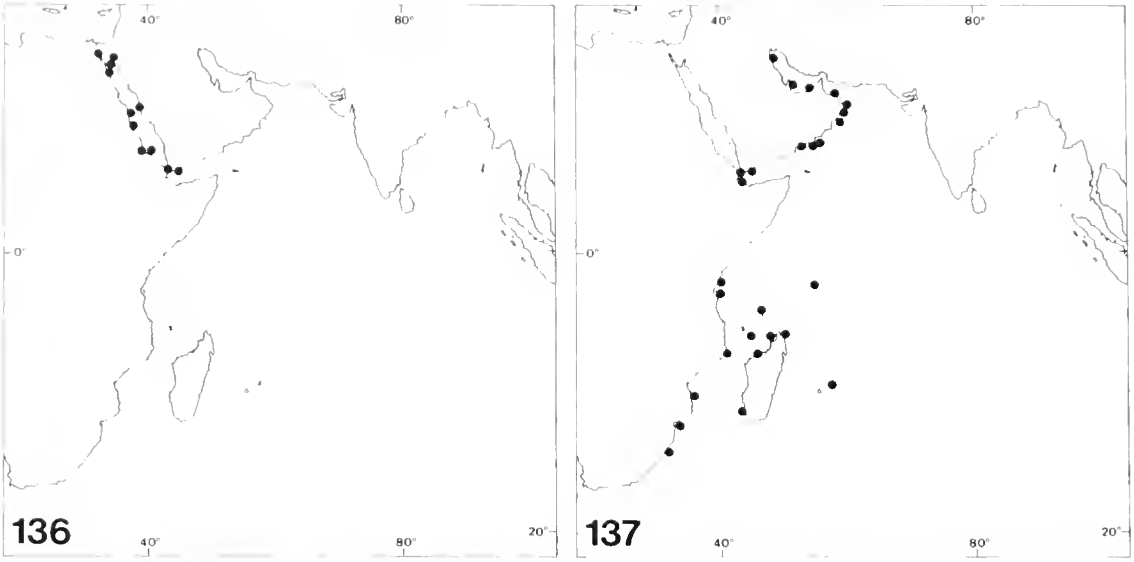
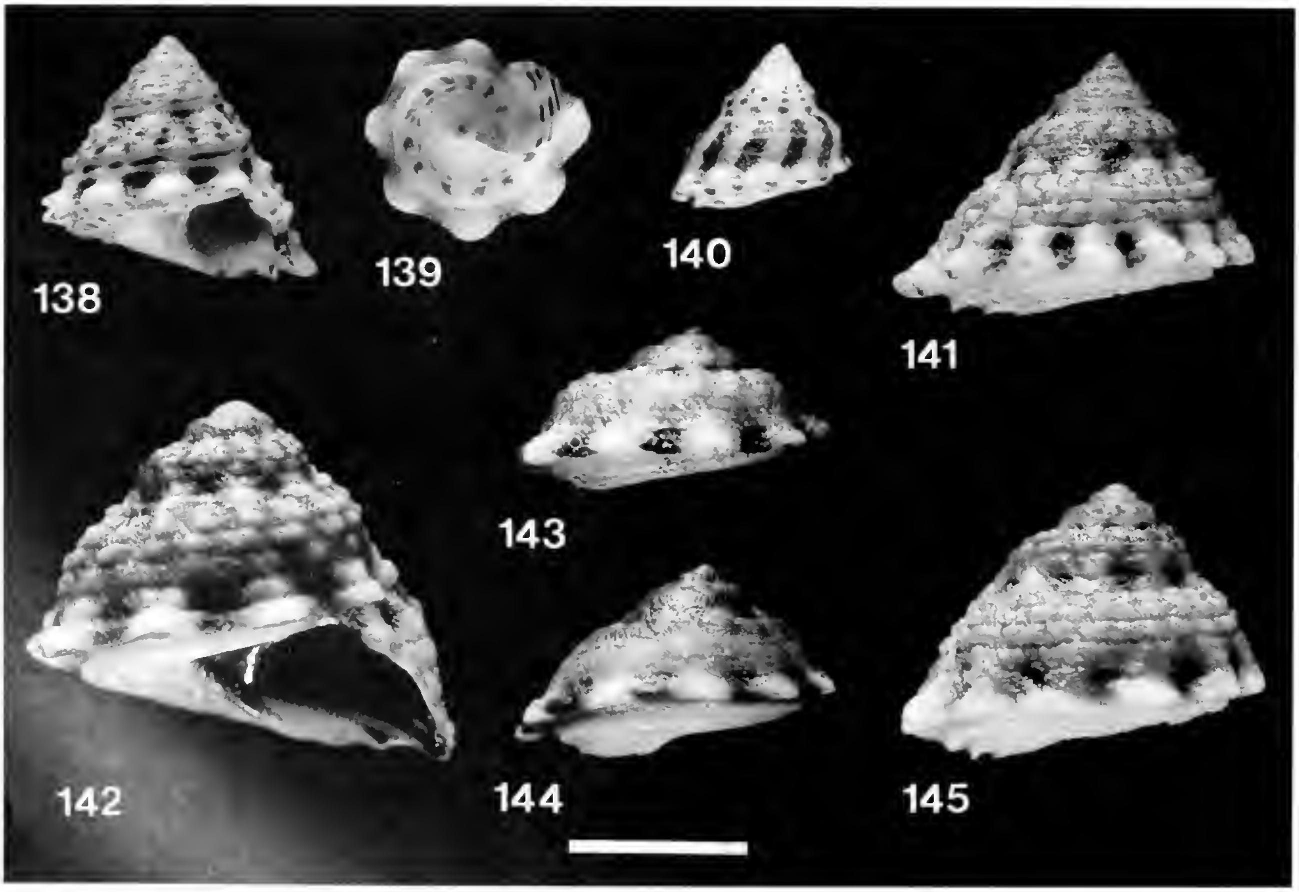


Figures 136, 137. Distribution maps of *Peasiella* species, compiled from records listed in text. **136.** *Peasiella isseli* **137.** *Peasiella mauritiana*.



Figures 138–141. *Peasiella conoidalis*, Kending, Kaohsiang, Taiwan (BMNH 1996398). **142–145.** *Peasiella roepstorffiana* **142.** Kannon Saki, Ishigaki, Japan (BMNH 1996399) **143.** Ma Liu Shi, Hong Kong (BMNH 1996400). **144.** Yehliu, Taipei, Taiwan (BMNH 1996401). **145.** Kending, Kaohsiang, Taiwan (BMNH 1996402). Scale bar = 2 mm.

the outer marginal tooth, and in the development of basal denticles on the rachidian tooth.

Phylogeny and Biogeography

The phylogenetic relationships of *Peasiella* within the Littorinidae remain uncertain. In the morphological phylogenetic analysis of Reid (1989b), the genus appeared as the sister-taxon of *Mainwaringia* in the consensus of all equally parsimonious trees; however, no unique synapomorphy for these two taxa was found. Anatomically, they are similar in their penial form (single mamilliform gland and closed sperm duct), pallial oviduct loops (although these are slightly more complex in *Mainwaringia*, Reid, 1986b) and egg capsule shape (compare Reid, 1990:fig. 3j with Mak, 1995: fig. 2d), but some of these resemblances may be plesiomorphic. They are so different in their shell and opercular shape, radular teeth and in the unique hermaphroditism of *Mainwaringia*, that a close relationship might seem unlikely. Nevertheless, preliminary molecular data offers some support for their sister-group relationship, and is currently under investigation (R. H. Thomas, pers. comm.).

Morphological features do not provide sufficient information for a cladistic analysis at the species level, and in the absence of an unequivocal sister-group the polarities of the few available characters are doubtful. The five species confused by Reid (1989a) under the name *P. infracostata* (*P. infracostata*, *P. fuscopiperata*, *P. patula*, *P. habei*, *P. fasciata*) are a possible clade, showing some similarity in shell form (tendency to reduction of peripheral keel and spiral ribs, presence of spiral color bands), and in radular cusps (4–8 cusps on outer marginal tooth, except 3–4 in *P. patula*; cf. 3–4 in all remaining species).

Four probable pairs of sister-species can be suggested. *Peasiella infracostata* and *P. fuscopiperata* are closely similar in shell characters; both lack a copulatory bursa, and radular cusps are similar. Their geographical distributions are known to overlap only between Moçambique and Kenya, which might suggest an allopatric mode of speciation followed by limited secondary contact. These two have strikingly dissimilar penial shapes, as would be predicted if this were either an isolating or species-recognition mechanism (Reid, 1996). A second likely sister-species pair is *P. isseli* and *P. mauritiana*. Again these are similar in shell characters, but differ in penial shape. These are almost completely allopatric; *P. isseli* is restricted to the Red Sea, while *P. mauritiana* occurs widely in the Indian Ocean and Persian Gulf, and they overlap only in the vicinity of Aden and at the mouth of the Red Sea. While endemism in the Red Sea fauna is high in some groups, among mollusks it is generally low (Sheppard *et al.*, 1992). During the substantial falls in sea level produced by Pleistocene glaciation, the Red Sea became hypersaline, and recolonization from the Arabian Sea has occurred only since the Holocene transgression. Speciation in the Red Sea may therefore be a recent phenomenon. At present, the currents at the mouth of the Red Sea do not appear to prevent passage of planktonic larvae, but the cold upwelling on the southern Arabian coast during the summer months may cause a partial isolation of the Red Sea from the Arabian Sea and Indian Ocean (Sheppard *et al.*, 1992). The third likely pair is *P. habei* and *P. fasciata*, which both belong in the '*infracostata* group'. These are known to overlap only between Hong Kong and Taiwan, and show a slight but consistent difference in penial shape. Finally, *P. conoidalis* and *P. tantilla* may be sister-species. Their radula, oviduct and penis are identical, shells are similar in sculpture, and both occur only on oceanic islands (Reid, 1989a). The former is widespread throughout the Indo-West Pacific, whereas the latter is restricted to the Hawaiian Islands, suggesting a case of speciation by peripheral isolation. The species status of *P. tantilla* is based only on its distinct shell. The two are not known to occur sympatrically and, assuming that penial shape is an isolating mechanism, there has presumably been no selection for its divergence.

ACKNOWLEDGMENTS

This work was carried out while Y-MM was in receipt of a post-doctoral fellowship from the Croucher Foundation, Hong Kong. We thank E. Glover and J. D. Taylor (BMNH), S-Y. Chan (Singapore), H.L. Strack (Dordrecht, The Netherlands), Y. Shikano, (Tokyo) and E. Platts (Winchester, U.K.) for providing specimens. For assisting Y-MM with field collecting we thank K. S. Tan (National University of Singapore), Fu-xue Li (Xiamen University), C. K. Tseng (Institute of Oceanography, Qingdao), Huang Shong (National Taiwan Normal University), Michael Hin-kin Mok (National Sun Yat-sen University, Taiwan), S. Yamato and S. Ohgaki (Kyoto University, Shirahama), Y. Takada (Ishigaki Tropical Station) and all their colleagues. For providing loans of material we are grateful to P. Bouchet (MNHN), H. Dekker (The Netherlands), H. Fukuda (Tokyo Metropolitan University), R. N. Kilburn (NM), I. Loch (AMS), R. Moolenbeek (ZMA) and J. Pickering (OUM). For their expert photography of shells we thank H. Taylor and N. Hayes (BMNH). P. York (BMNH) kindly assisted with the photomicroscopy of egg capsules. We appreciate the helpful comments of two anonymous referees.

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Donald Richard Moore (February 16, 1921–October 19, 1997): Biographical Sketch, Zoological Taxa, and Bibliography

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Donald R. Moore was born in West Palm Beach, Florida, son of Walter R. and Estelle K. Moore. He attended elementary school in Venice, California and Hobe Sound, Florida, and high school in Stuart, Florida. Growing up in Florida provided Don with, in his words, "plenty of sea, swamp, lagoon, and woods to roam in". He joined the U.S. Marine Corps in September 1941. Don's love for shells and marine life consolidated after his stay in the Central and Southwest Pacific, something that happened with so many young naturalists who fought the Second World War in that part of the world. Don took his dive mask with him to the Pacific, and dived as much as events would permit, at Midway, New Hebrides, and the Solomon Islands.

After receiving an honorable discharge in October 1945, Don entered the undergraduate program at the University of Miami in June 1948, and graduated in February 1954 with a Bachelor of Science degree in Zoology. He joined the Graduate School of the University of Miami shortly thereafter, aiming for a M.S. degree in Marine Science. In the summer of 1954 Don traveled to Houston, Texas, taking on a temporary assignment with the Exploration and Product Research Division of Shell Oil Company as field biologist. A job offer as Research Scientist at the Institute of Marine Science, University of Texas, caused Don to put his academic efforts temporarily on hold. From Texas he moved to Ocean Springs, Mississippi, to join the staff at the Gulf Coast Research Laboratory, working on oyster culture with Gordon Gunter as an Assistant Marine Biologist. It was there that he published his first scientific article (Moore, 1956). Taking advantage of his proximity to the University of Southern Mississippi campus in Hattiesburg, he enrolled in the graduate program at that institution with Gordon Gunter as his advisor, earning the Master of Science degree in June 1960.

In September of 1960, he again entered the Graduate School at the Institute of Marine Science (now the Rosenstiel School of Marine and Atmospheric Science, RSMAS), University of Miami, graduating under the guidance of Gilbert L. Voss on June 7, 1964, with a Ph.D. degree in Marine Science. His Ph.D. dissertation revised the systematics of western Atlantic vitrinellid gastropods. Don once told me of his first meeting with the great Henry Pilsbry. In the early stages of his dissertation work, Don visited Pilsbry at the Academy of Natural Sciences in Philadelphia. In Pilsbry's office, he briefly introduced himself and his research goals. After hearing Don's desire to revise the western Atlantic Vitrinellidae, Pilsbry offered his hand, saying, "Here, I salute a hero!". His unpublished dissertation remains the best source of information about this difficult family of gastropods.

From the historic perspective of the end of the twentieth century, the timing of Don's Ph.D. defense could not have been better: the "golden age" of tropical western Atlantic marine science, centered at the lab in Miami was under full sail in the mid-1960s. Don was hired in 1964 as an Assistant Professor of Marine Science at that institution. There he shared an extremely productive academic environment with marine biologists such as Gilbert Voss, Raymond Manning, Frederick Bayer, C. Richard Robins, and Hillary B. Moore, as well as with geologists of the caliber of Robert Ginsburg and Cesare Emiliani. During the sixties, Don cruised extensively on the Institute's research vessels in the Caribbean Basin, northern South America, Brazil, Straits of Florida and the Bahamas, and the eastern seaboard of the U.S. In 1971 Don was promoted to Associate Professor of Marine Geology, remaining in that position until he retired to become Professor Emeritus in 1984. Don continued working and participating in students' committees until the day of his death.

Don showed great appreciation of other cultures and was proud of his travels and ability to read and speak several foreign languages. Among his many travels and professional visiting appointments, he was a visiting scientist at the Instituto de Investigaciones de Punta Betín in Santa Marta and taught for Sea Grant in Cartagena, both in Colombia. In 1980, Don worked at the Natural History Museum in Basel, Switzerland, by invitation of the Swiss National Science Foundation. An active participant in the American Malacological Union, he served as Councillor-at-Large of that organization in 1968–69, Vice-President in 1973–74, and President in 1974–75. Following an invitation by then-editor R. Tucker Abbott, Don joined the first group of consulting editors of *The Nautilus* in July 1972, a position he retained for the rest of his life (Don's first three peer-reviewed articles were published in *The Nautilus*). He was also a member and strong supporter of the Miami Geological Society, serving as their Vice-President in 1967, President in 1968–

Young Donald R. Moore in 1954, surveying Gulf of Mexico mollusks on the coast of Texas for Shell Oil Co., as featured on the cover of Shell News Magazine (Anonymous, 1955).

Dr Donald R. Moore in 1989, Coral Gables, Florida. Photo courtesy RSMAS Archives.

69, and Secretary in 1977–78. He was a strong supporter of Unitas Malacologica as a global organization, and played a key role, as a Scientific Committee member, in the formation of the Committee for Latin American Congresses in 1990.

Don Moore served on more than one hundred University of Miami graduate student committees, mainly at RSMAS, but also at the University of Miami's Department of Biology and Department of Geological Sciences, on the Coral Gables Campus. He was committee chair or co-chair for the students: Richard S. Houbrick (M.S.), José H. Leal (Ph.D.), John Meeder (Ph.D.), James Quinn, Jr. (Ph.D.), Nidia Romer (M.S.). Don also was a committee member for the following malacologists: George Darcy (M.S.), Thomas Brackoniecki (M.S. and Ph.D.), Charles D'Asaro (Ph.D.), Steven Hess (Ph.D.), Edward J. Petuch (M.S. and Ph.D.), James Quinn, Jr. (M.S.), Ronald Toll (Ph.D.).

Both as my personal friend and academic advisor, Don was always present and supportive, in good and bad times. A large portion of my personal library comprises used books and reprints that were gifts from Don (and I know the same to be true for many of his students). An avid reader and staunch bookworm, Don used to spend a great deal of his time in bookstores and book fairs. He also used to gauge the merit of small towns by the presence or absence of good second-hand bookstores. Although most of his scientific productivity took place in the 1960s and 1970s, Don was allowed to retain for life his office in the North Grosvenor Building at RSMAS. His office doors were always open, a symbolic depiction of his view of the world and of the special affection and warmth he had for students, no matter how inexperienced, or how distant their homelands.

Don's immediate family survive him: his wife Cynthia is Research Associate with the Division of Marine and Atmospheric Chemistry at RSMAS, and son Walter is Systems Administrator with Eckerd College at St. Petersburg, Florida.

ZOOLOGICAL TAXA

Abbreviations for repositories of type material:

AMNH	American Museum of Natural History, New York
ANSP	The Academy of Natural Sciences, Philadelphia
BMNH	The Natural History Museum, former British Museum (Natural History), London, England
CNMS	Colombian National Museum of Science, Bogotá, Colombia
DMNH	Delaware Museum of Natural History, Wilmington
FMNH	Field Museum of Natural History, Chicago
FSBC	Florida Marine Research Laboratory, St. Petersburg

MNHN	Muséum national d'Histoire naturelle, Paris, France
MNRJ	Museu Nacional, Rio de Janeiro, Brazil (also MNHSL)
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge
MORG	Museu Oceanográfico, Fundação Universidade do Rio Grande, Rio Grande, Brazil
NNM	Nationaal Natuurhistorisch Museum, Leiden, The Netherlands (formerly Rijksmuseum van Natuurlijke)
UF	Florida Museum of Natural History, University of Florida, Gainesville
UMML	Marine Invertebrate Museum, Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami
USNM	National Museum of Natural History, Smithsonian Institution, Washington, DC

Family-Level Taxon

CYCLOSTREMELLIDAE Moore, 1966, Bulletin of Marine Science, 16(3):480–484 (diagnosis on page 481). For *Cyclostremella* Bush, 1897. Robertson (1973) indicated that this genus belongs to the Pyramidellidae. Ponder & Warén (1988) included the Cyclostremellinae as as a subfamily of Pyramidellidae.

Genus-Level Taxon

Dimyella Moore, 1969, Journal de Conchyliologie 107(4):137–141 (diagnosis on page 137). Type-species: *Dimyella starcki* Moore, 1969, by monotypy. Dimyidae.

Species-level Taxa

All type-specimens collected by D. R. Moore except where otherwise indicated.

bullisi, *Linckia* Moore, 1960, Bulletin of Marine Science of the Gulf and Caribbean 10(4):414–416, fig. 1. Holotype: USNM E-8120, off Guiana, South America, 8°15'N, 58°17'W, 72 to 91 m. (=*Linckia nodosa* Perrier, 1875, *fide* Downey, 1968) (Echinodermata, Asteroidea, Ophidiasteridae).

calcicola, *Nucula* Moore, 1977, The Nautilus 91(4):120–121, figures 1–3. Holotype: USNM 758535, Chancanab [Chankanaab] Lagoon, Cozumel, Quintana Roo, Mexico, 2 m; All paratypes from type locality: USNM 758537, 7 paired specimens + 3 single valves; MCZ 288445, 3 paired specimens + 4 single valves, from type locality; UMML 28.2812, 3 paired specimens + 4 single valves, from type locality; AMNH 183857, 10 single valves; ANSP 344387, 5 paired specimens + 4 single valves; MNHN unnumbered, 5 paired specimens, 2 left valves, 1 right valve; DMNH 120581, 6 paired specimens + 1 single valve; BMNH 1977089, 3 paired specimens + 3 single valves; NNM 55302, 4 paired specimens + 4 single valves, all dry. Nuculidae.

colombiana, *Alvania* (*Alvania*) Romer and Moore, 1988, The Nautilus 102(4):131–133, figures 1–5. Holotype USNM 859339, off west Florida, 29°35′N, 87°20′06″W, 107.3 m; Paratypes: USNM 859340, 1 paratype, type locality; FSBC 33113–114, 2 paratypes, off west Florida, 28°24′N, 85°15′06″W, 164.6 m; MCZ 297220, 1 paratype, off Puerto Rico, 17°53′24″N, 66°35′10″W, 221 m; MCZ 297219 and UMML 30.8349, 2 paratypes, off Miami, Florida, 25°47′N, 80°01′30″W, 137 m; UMML 30.8350 and CNMS ICN-MHN(MO) 523, 2 paratypes, off Miami, Florida, 25°46′30″N, 80°00′08″W, 76.81 m; CNMS ICN-MHN(MO) 522, 1 paratype, off Caribbean coast of Colombia, 09°52′35″N, 75°47′25″W, 72 m. Rissoidae.

condylum, *Caecum* Moore, 1969, Bulletin of Marine Science 83(1):26–28, figure 1. Holotype: USNM 679348, Payardi Island, near Colón, Atlantic coast of Panamá. Paratypes: USNM 679348, 1 paratype, East Flower Garden Bank, Gulf of Mexico, 27°54′30″N, 93°35′45″W, coral debris, 18.3–23.8 m. Caecidae.

cynthiae, *Condylonucula* Moore, 1977, The Nautilus 91(4):123–124, figures 6–7. Holotype: USNM 758534, about 800 m west of outer reef (lagoon), Courtown Cays (Cayos del E.S.E.), off Nicaragua, western Caribbean Sea, 7.5 m. Paratypes: USNM 758538, 5 paired specimens + 1 broken right valve + 1 fragment, Courtown Cays, off Nicaragua, 1.5 m; ANSP 344388, 1 paired specimen + 1 right valve, Courtown Cays, off Nicaragua, 1.5 m; DMNH 120580, 1 paired specimen + 1 left valve; MCZ 288444, 1 paired specimen + 2 left valves, Courtown Cays, north end, 2 m; UMML 28.2811, 1 paired specimen + 1 left valve, Courtown Cays, outer reef, 1 m. Nuculidae.

esperanza, *Thala* Leal and Moore, 1993, The Nautilus 107(2):58–62, figures 1–6. Holotype: USNM 860280, Playa Esperanza, 40 km west of San Juan, Municipality of Manatí, northern Puerto Rico. All paratypes from type locality: USNM 860281, paratypes 1–4; UF 193382–383, paratypes 5–6; ANSP 391938, paratype 7; AMNH 232313, paratype 8; MCZ 302588, paratype 9; MNHN unnumbered, paratype 10; FMNH 223388, paratype 11; UMML 30.8375, paratype 12; USNM 860262, paratypes 13–16. Costellariidae.

floridana, *Macromphalina* Moore, 1965, The Nautilus 78(3):75–76, plate 7, figure 1–3. Holotype: USNM 636610, Madeira Beach at 150th Avenue, Saint Petersburg, Florida; paratypes: ANSP 295621, 1 shell, type locality; UMML 302773, 1 shell, east of Soldier Key, Biscayne Bay, Florida, 1 m. Vitrinellidae.

indiscreta, *Rissoina* Leal and Moore, 1989, Bulletin of Marine Science 45(1):139–147, figures 1–12. Holotype: MNRJ 5760, Ponta Verde Beach, Maceió, Alagoas State, Brazil, 09°38′S, 35°44′W, beach at low tide. Paratypes: MNHSL 6025, paratypes 1–4, type locality; MORG 4164, paratypes 5–7, type locality; MNHN unnumbered, paratypes 8–11, type locality; USNM 859335–338, paratypes 12–15, type locality; MNRJ 5761, paratypes 16–18, type locality; BMNH 1988.043, paratypes 19–22, type locality; MORG 25463, paratypes 23–24, Atol das Rocas, Brazil, 03°52′S, 33°49′W; MORG 25464, paratypes 25–28, Abrolhos Reef Complex, Bahia, Brazil, 17°58′S, 38°42′W; UMML 8347–48, paratypes 29–30, Jaraguá Beach, Maceió, Alagoas State, Brazil, 09°38′S, 35°44′W. Rissoidae.

insularum, Caecum Moore, 1970, Bulletin of Marine Science 20(2):368–373, figures 1A-B. Holotype: USNM 679178, open sandy bottom at head of Lesser Lameshur Bay, St. John, Virgin Islands, 1.5 m. All paratypes from type locality: USNM 679179, 12 paratypes; ANSP 315477, 10 paratypes; MCZ 271305, 11 paratypes; AMNH 147965, 10 paratypes; UMML 30.3203, 14 paratypes; "more than a hundred paratypes ... kept by the author". Caecidae.

maya, Condylonucula Moore, 1977, The Nautilus 91(4): 124–126, figures 4–5. Holotype: USNM 758536, Chancanab [Chankanaab] Lagoon, Cozumel, Quintana Roo, Mexico, 2m. All paratypes from type locality: USNM 758536, 7 paired specimens + 1 right valve, type locality; MCZ 288443, 2 paired specimens + 1 right valve; ANSP 344389, 3 paired specimens + 1 left valve; AMNH 183858, 2 paired specimens + 1 left valve; DMNH 120579, 3 paired specimens + 2 single valves; FMNH 198080, 1 paired specimen. Nuculidae.

semipunctus, Solariorbis Moore, 1965, The Nautilus 78(3):77–78, figures 1–3. Holotype: USNM 636309, northwest Campeche Bank, Mexico, 18 m, muddy bottom. Paratype: UMML 30.2774, 1 paratype, Baie de Aquin, Haiti, beach drift. Vitrinellidae.

starcki, Dimyiella Moore, 1969, Journal de Conchyliologie 107(4):138–139, one plate with two figures. Holotype: USNM 678363, complete shell with two larval specimens in brood chamber, Cozumel Island, México. All paratypes from type locality: USNM 678364, 1 paired specimen + 1 detached upper valve; ANSP 312218, 1 paired specimen + detached upper valve; BMNH 1967.6171, 1 paired specimen + another with broken lower valve; MNHN 1967.226, 1 paired specimen + detached upper valve; MCZ 257727–257726, 1 paired specimen with brood chamber in upper valve + detached upper valve; UMML 28.784, 1 paired specimen + another with both valves broken + three small detached upper valves. Dimyidae.

texana, Vitrinella Moore, 1965, The Nautilus 78(3):76–77, plate 7, figures 4–6. Holotype: USNM 636311, Mustang Island, near Port Aransas, Texas. Paratypes: ANSP 295622, 1 paratype, type locality; USNM 636312, 1 paratype, type locality; UT 1015, two shells, Cline's Point, Port Aransas, Texas; UT 1016, 1 paratype, Ferry Landing, Port Aransas, Texas; UMML 30.2775, 1 paratype, Port Aransas, Texas; UMML 30.2776, 1 paratype, Port Aransas, Texas. Vitrinellidae.

GRADUATE THESES

Moore, D. R. **1960.** The marine and brackish water Mollusca of the Mississippi Gulf Coast. Master of Science, University of Southern Mississippi. 116 pages.

Moore, D. R. **1964.** The family Vitrinellidae in South Florida and the Gulf of Mexico. Doctor of Philosophy, University of Miami. xi + 235 pages, 35 figures, + vitae. [7 June]

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This listing includes peer-reviewed articles as well as Don's reports and contributions to several scientific organizations. Also included are the extended meeting abstracts published up to 1980 by the American Malacological Union (AMU) in its Annual Reports and Bulletin. References are listed in chronological order.

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Notices

THE R. T. ABBOTT VISITING CURATORSHIP

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The curatorship, established originally in accordance with the wishes of the late Dr. R. T. Abbott, Founding Director of the Shell Museum, is awarded annually to enable mollusk systematists to visit the museum for a period of one to two weeks. Abbott Fellows will be expected, by performing collection-based research, to assist with the curation of the portions of the museum's Mollusk Collection and to provide one evening talk for the general public. The museum collection consists of marine, freshwater, and land shells, with emphasis on SW Florida. A large percentage of the records has been catalogued through a computerized database management system. A substantial portion of the time will be available for research in the museum collection, but field work in SW Florida can be arranged. The R. T. Abbott Visiting Curatorship is accompanied by a stipend of $1,500.

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Send materials to:

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

Applications for the 1999 Visiting Curatorship should be sent no later than January 31, 1999. The award will be announced by February 28, 1999. Questions about the R. T. Abbott Visiting Curatorship should be directed to Dr. Leal at:

(941) 395-2233; fax (941) 395-6706, or e-mail: leal@water.net

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In Memoriam

Harold ("Hal") Lewis

1927–1998

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Thecosome Pteropod (Gastropoda) Assemblages of the Mexican Caribbean Sea (1991)

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ABSTRACT

The composition, distribution, and abundance of the thecosome pteropods collected off the Mexican coast of the Caribbean Sea were analyzed. Samples were collected during four months (February, March, May, and August) of 1991. Highest mean thecosome pteropod density was recorded in May (329 org./10^3 m^3), while lowest mean density occurred in March (71 organisms/10^3 m^3). Seventeen species and subspecific forms were identified. *Creseis acicula acicula*, *Limacina trochiformis*, *L. inflata*, *Clio pyramidata pyramidata* and *Cavolinia longirostris longirostris* were the more abundant species, accounting for 84% of the overall thecosome pteropod counts. The first two species represent the influence of Caribbean surface waters in the surveyed area. The local thecosome pteropod fauna also shows some affinity with that from the southern Gulf of Mexico. Cluster analysis of the stations revealed two types of assemblages of low and high densities, with distributions that showed month-to-month variations. Circadian variations were well defined for two of the more abundant species; the other two species were nearly equally abundant in day and night samples. The thecosome pteropod community along this oceanic area seems to be represented by a homogeneous complex dominated by neritic-oceanic species with a strong influence of *C. acicula acicula* even in fully oceanic areas. Intermixing of these assemblages and the co-occurrence of neritic and oceanic species near the coast could be attributed to the narrow width of the continental shelf and to local circulation patterns.

INTRODUCTION

Thecosome pteropod molluscs are one of the most abundant holoplanktonic groups in neritic and oceanic environments. As a group, they show an adaptive trend toward shell reduction that results in less density and increased ability for vertical displacement in the water column (Van der Spoel, 1996). The Thecosomata is one of the two holoplanktonic orders of Opisthobranchia (the other one is Gymnosomata) that were formerly united under the name Pteropoda. Today we know that these two orders are not closely related (Lalli and Gilmer, 1989). The term "pteropod" is used herein mainly as an easy reference name based on widespread, common practice. Thecosome pteropods are mainly herbivorous, and feed upon microplankton and diatoms using drifting mucous webs to capture food (Lalli and Gilmer, 1989). Most species inhabit surface waters, but some exhibit large migration patterns from depths of 1000–2000 m. Some species are useful as hydrological, geological and ecological indicators (Biekart, 1989).

In the northwestern Atlantic Ocean thecosome pteropods have been surveyed mainly in the Gulf of Mexico and along the East Coast of the United States (Wormelle, 1962; Chen and Hillman, 1970; Matsubara, 1975; Michel and Michel, 1991; Suárez-Morales and Gasca, 1992). Some studies have been made in the Caribbean Sea about general aspects of their abundance and their horizontal and vertical distribution (Wells, 1975, 1976; Haagensen, 1976; Gasca and Suárez-Morales, 1992). A general review of the thecosome pteropod records in the Gulf of Mexico and adjacent areas is presented by Suárez-Morales (1994). However, knowledge of the composition, distribution and abundance of the thecosome pteropod fauna in the Caribbean Sea off Mexico, the westernmost portion of the Caribbean Sea, is practically limited to the innermost reaches of the coast (Gasca and Suárez-Morales, 1990). In the present work, the composition, distribution and abundance of thecosomes pteropods collected in the oceanic area off the Mexican coast of the Caribbean during four oceanographic cruises are analyzed.

STUDY AREA

The surveyed area lies between 18° and 21°30′N and 86°20′ and 87°40′W off the eastern coast of the Yucatan Peninsula, Mexico (Figure 1). The area is under the influence of the northward flow of Caribbean surface water on its way into the Gulf of Mexico through the Yucatan Channel. The continental shelf is narrow along this section of the coast and depth drops very quickly offshore (Merino and Otero, 1991). Hydrographic condi-

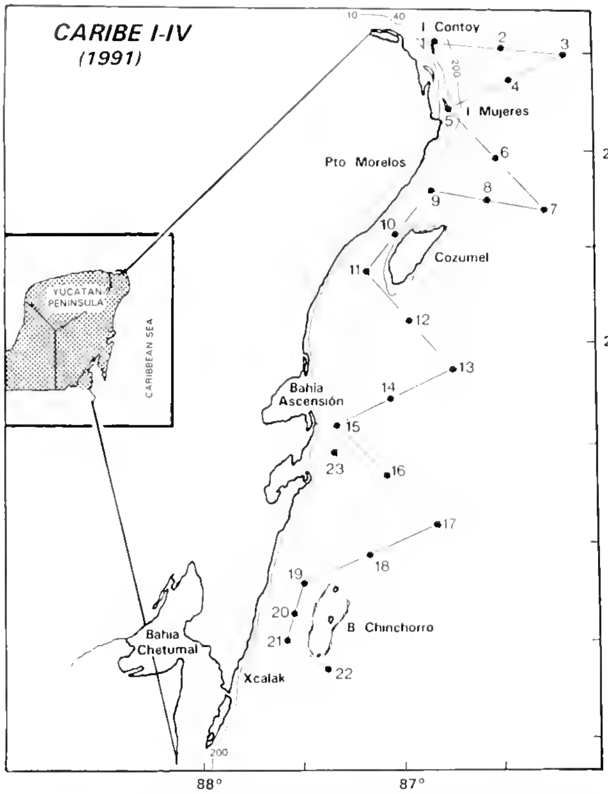

Figure 1. Surveyed area with zooplankton sampling stations off the Mexican coast of the Caribbean Sea (1991).

tions along the Caribbean coast of Mexico are determined by the main northward flow of the Yucatan Current and by a southward-flowing coastal countercurrent (Merino, 1986). The Yucatan Current shows seasonal variation in strength; its maximum and minimum intensities occur respectively during spring and winter (Merino 1992). Three main climatic periods can be distinguished: dry (March–June), rainy (July–October), and the "nortes" period, with northern dominant winds, from November to February.

MATERIALS AND METHODS

Four oceanographic cruises were carried out during February, March, May, and August 1991, on board different "Draguminas" (minesweeper) ships of the Mexican Secretaría de Marina (February: *D-12*; March: *D-04*; May and August: *D-05*). The sampling plan included 22 stations (Figure 1).

Zooplankton was collected by surface oblique hauls (0–10 m) using a square-mouth (0.45 m side) standard plankton net (0.3 mm mesh size). A digital flowmeter was attached to the net mouth to estimate the amount of water filtered by the net (mean volume: 160 m^3 per haul). Zooplankton samples were fixed and preserved in a buffered 4% formalin solution (Smith and Richardson, 1979). Thecosome pteropods were sorted from the entire samples, identified (Van der Spoel, 1981), and counted. Voucher material of the Mexican Caribbean thecosome pteropods is deposited in the zooplankton collection of El Colegio de la Frontera Sur (ECOSUR) under catalog numbers ECO-CH-Z0073 through ECO-CH-Z0090. Density data were integrated into four data sets, one for each cruise. Shannon's Index of Diversity was calculated (in bits/individual, which expresses the average degree of uncertainty in predicting what species an individual chosen at random will belong to; Ludwig and Reynolds, 1988). The Index of Importance Value (IIV) was used as a dominance measurement. The IIV accounts for relative (percentual) density and frequency of the species. In one standard data matrix, IIV would have a maximum value of 200 (100% of density plus 100% of frequency) (Brower and Zar, 1977). The IIV has been used more often by botanists, but the index can also be used in faunal studies (De la Cruz, 1994). The Bray-Curtis Similarity Index was used to identify station clusters and analyze the thecosome pteropod community structure within individual cruises.

RESULTS

Mean temperature during the four-month period was 28°C, with a minimum of 23°C in February and maximum of 29°C in August. Salinity averaged 35.2 ‰, with a maximum of 35.6 ‰ in May, and a minimum of 34.5 ‰ in February.

Space distribution of thecosome pteropod densities in the surveyed area showed monthly variations (Table 1). Highest total mean densities were recorded during May (296.25 organisms/10^{3}m^3), followed by February (158 org./10^{3}m^3), August (141.79 org./10^{3}m^3), and March (71 org./10^{3}m^3). During February, thecosome pteropods showed two high-density zones, one in the northern portion of the area, and the other in the central zone. No high-density zones were detected during March. In May, thecosome pteropods showed high densities along the entire coast, and in August two groups of stations with high densities were observed, one in the north and the other in the central portion. Most high-density stations were sampled at night (Figure 2).

A total of 17 species and subspecific forms were collected in the surveyed area (Table 1). Four species, *Creseis acicula acicula* (Rang, 1828), *Limacina inflata* (d'Orbigny, 1836), *L. trochiformis* (d'Orbigny, 1836), and *Clio pyramidata pyramidata* Linnaeus, 1767 were recorded as the dominant thecosome pteropods in the area throughout the surveyed period. Together they constituted 86.6% of the total overall pteropod catch (83% in February, 81% in March; 95.6% during May; 74.6% in August). The relative abundance (%) and mean density (org./10^{3}m^3) of each species during the four cruises is shown in Table 1.

Overall thecosome pteropod densities were 2.2 times higher during the night (mean density 298.75 org./10^{3}m^3) than during daytime (mean density 133 org./10^{3}m^3). During the night samplings, thecosome pteropods were most abundant during May (499 org./10^{3}m^3),

Table 1. Mean density (org./10) and relative abundance (%) of pteropod species during each of four CARIBE cruises in the Mexican Caribbean Sea (1991)

	CARIBE I February		CARIBE II March		CARIBE III May		CARIBE IV August		Total Mean Density
	Density	%	Density	%	Density	%	Density	%	
Creseis acicula acicula (Rang, 1828)	38.00	24.13	4.44	6.23	160.30	54.11	55.28	38.90	64.50
Creseis acicula clava (Rang, 1828)	4.31	2.74			8.10	2.73	2.52	1.77	3.73
Creseis virgula conica Eschscholtz, 1829	2.75	1.75	12.96	18.11	0.35	0.12	2.77	1.95	4.70
Clio pyramidata pyramidata Linnaeus, 1767	14.63	9.29	19.18	26.93	20.40	6.90	3.31	2.33	14.37
Clio pyramidata lanceolata (Lesueur, 1813)			0.44	0.62					0.11
Diacria quadridentata (de Blainville, 1821)					0.70	0.24			0.17
Cavolinia longirostris longirostris (de Blainville, 1821)	18.69	11.87			1.55	0.52			5.06
C. longirostris limbata (d'Orbigny, 1836)	0.44	0.28					27.39	19.30	6.95
C. longirostris f ?					0.35	0.12			0.08
C. uncinata uncinata (Rang, 1829)	0.5	0.32	0.31	0.44	0.60	0.20	0.75	0.53	0.54
C. inflexa inflexa (Lesueur, 1813)					1.05	0.35	0.29	0.20	0.33
C. inflexa imitans (Pfeffer, 1880)					0.25	0.08	0.39	0.27	0.16
Cymbulia peroni de Blainville, 1818							0.22	0.15	0.05
Limacina lesueuri (d'Orbigny, 1836)							1.24	0.87	0.31
Limacina inflata (d'Orbigny, 1836)	65.75	41.72	8.06	11.42	89.45	30.22	23.98	16.90	46.81
Limacina trochiformis (d'Orbigny, 1836)	12.44	7.90	25.37	35.63	13.15	4.44	23.22	16.30	18.54
Limacina bulimoides (d'Orbigny, 1836)					0.61	0.43			0.15
Total mean density	157.51		71.08		296.25		141.79		
Number of species and formae	9		7		13		12		
Day/Night relative density	47.3/52.7		66.9/33.1		57.97/42.03		94.66/5.34		

followed by February (332), August (295), and March (69). Daytime densities were highest during May (264 org./10^{3}m^3), followed by February and August (97), and by March (76).

Overall mean density of *C. acicula acicula* at night (59.5 org./10^{3}m^3) was similar to that of daytime samples (61.9). The same was recorded for *Limacina trochiformis* (20.8 (day) *vs.* 14.5 (night) org./10^{3}m^3). *Limacina inflata* was clearly most abundant at night (137.2 *vs.* 9.8 org./10^{3}m^3), as was *C. pyramidata pyramidata* (23 *vs.* 9.4 org./10^{3}m^3).

In February the most abundant species was *Limacina inflata*. This species represented 41.7% of the total thecosome pteropods, and was mostly captured at night on the central portion of the surveyed area (Figure 3e). *Limacina inflata* was followed by *Creseis acicula acicula* (24.1%), which shows a broader distribution (Figure 3a), and by *Cavolinia longirostris longirostris* (11.8%). *Creseis acicula acicula* occurred in 80% of the stations, while the other two species occurred in less than 50%. *Limacina trochiformis* and *Clio pyramidata pyramidata* occurred only at a few stations (Figure 4 a, e). About 77% of the total thecosome pteropod density was collected in nighttime samples (daytime mean density: 97 (day) *vs.* 332 org./10^{3}m^3 at night). The Index of Importance Value (IIV) showed a shared dominance of *L. inflata* and *C. acicula acicula* (IIV > 53), followed by *C. pyramidata pyramidata* (IIV = 24). Although diversity was variable (0.6–1.4), on average it was moderately high (1.22 bits/ind.). Clustering revealed two station groups (Figure 5e). The first one included stations with less than 45 org./10^{3}m^3, and contained only 11.7% of the thecosome pteropod numbers in this month. In most of these stations *Creseis acicula acicula* was the only spe-

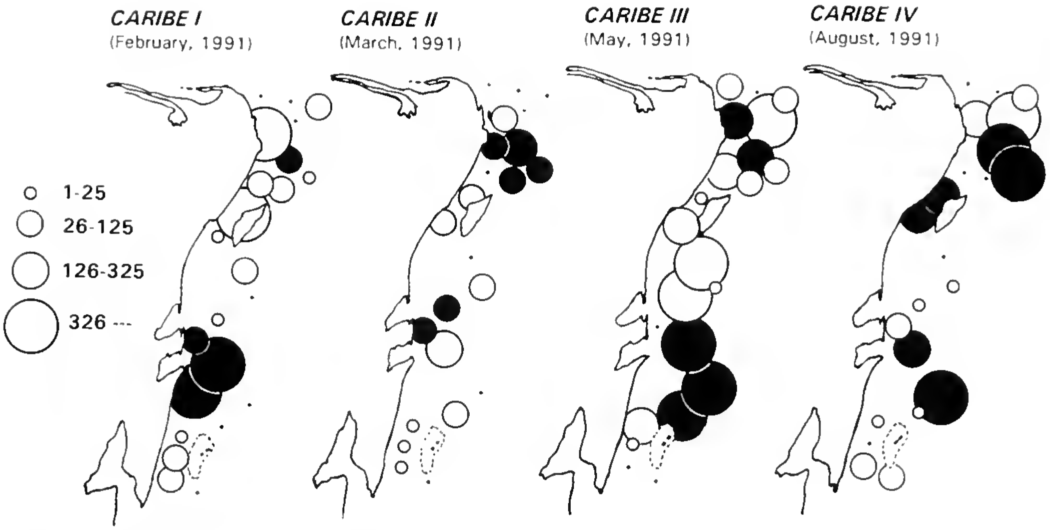

Figure 2. Monthly densities (org./10^3m^3) of thecosome pteropods for each sampling station during the surveyed period in the Mexican Caribbean Sea. Black circles indicate night samples.

cies present, but with densities below 30 org./10^3m^3. The group was distributed in the fully oceanic zone and in the shelf border area. The second assemblage showed the same general distribution as the first one; it included stations with the highest density values (most over 100 org./10^3m^3) (Figure 5a). *Limacina inflata* was characteristic of this group, which comprised 100% of the occurrence of the species.

In March, *Limacina trochiformis* represented up to 35.6% of the total thecosome pteropod numbers, followed by *C. pyramidata pyramidata* (27%) and by *C. virgula conica* (18%). *Clio pyramidata pyramidata* and *Creseis acicula acicula* occurred in more than 80% of the stations, the former with higher densities (Figures 3b, 4f). Both species of *Limacina* showed a limited distribution, and were more frequent in night samples (Figures 3f, 4b). Nighttime density represented 47% of the total catch (mean density: 76 (day) *vs.* 69 (night) org./10^3m^3). *Clio pyramidata pyramidata* was dominant (IIV = 56.3), followed by *L. trochiformis* (49) and *C. virgula conica* (36). Diversity was moderate (mean 1.14), slightly lower than in February. Two station clusters were revealed (Figure 5f), with a distribution similar to that of February (Figure 5b). The first group was characterized by low to moderate thecosome pteropod densities (28–128 org./10^3m^3), and included only 38% of the total thecosome pteropod density. Up to 75% of *C. pyramidata pyramidata* and 96% of *L. inflata* numbers were included in this group. A second group showed low and high densities (5–344 org./10^3m^3), and was characterized by the highest densities of *L. trochiformis*; this group included up to 84% of the total number of *C. virgula conica*

In May the most abundant species was *Creseis acicula acicula*, representing about 54% of the total thecosome pteropod catch; it was followed by *L. inflata* (30%) and by *L. trochiformis* (4.4%). Only *C. acicula acicula* occurred at all stations, with medium and high densities (Figure 3c); *C. pyramidata pyramidata* was collected at most stations with medium densities (Figure 4g), and *L. trochiformis* was collected at a few stations (Figure 4c). *Limacina inflata* was abundant in nighttime samples on the southern portion of the area (Figure 3g). Nighttime overall density represented 65% of the total catch and was 1.8 times higher than daytime density (499 *vs.* 264 org./10^3m^3). The IIV showed the dominance of *C. acicula acicula* (80) and of *L. inflata* (42.1) in this month. Mean diversity was moderate (1.10 bits/ind.), but slightly lower than in the two previous months. Two clusters were defined (Figure 5 g). The first one included only four stations with the lowest densities (9–29 org./10^3m^3). Only 0.1% of the thecosome pteropod numbers occurred in this cluster; these stations were made in the oceanic area and near the coast (Figure 5c). *Creseis acicula acicula* and *Clio pyramidata pyramidata* were present in this group. The second cluster showed the highest total densities (over 98 and up to 1578 org./10^3m^3), with more than 98% of *C. acicula acicula* and 100% of *L. inflata* numbers. This group showed a variable diversity.

In August, *Creseis acicula acicula* was again the most abundant species (39% relative abundance), followed by *Cavolinia longirostris limbata* (19.3%), by *L. inflata* (16.9%) and by *L. trochiformis* (16.3%). *Creseis acicula acicula* occurred at all stations with medium and high densities (Figure 3 d), only both species of *Limacina* occurred at more than 50% with medium density values (Figures 3 h, 4 d), while the remaining species each occurred at less than 20% of the sampling sites. *Clio pyramidata pyramidata* was scarce in this cruise (Figure 4 h). Nearly 75% of the total density was collected in nighttime samples; mean density was about 3 times higher during night collections (295 *vs.* 97 org./10^3m^3). *Creseis acicula acicula* showed the highest dominance

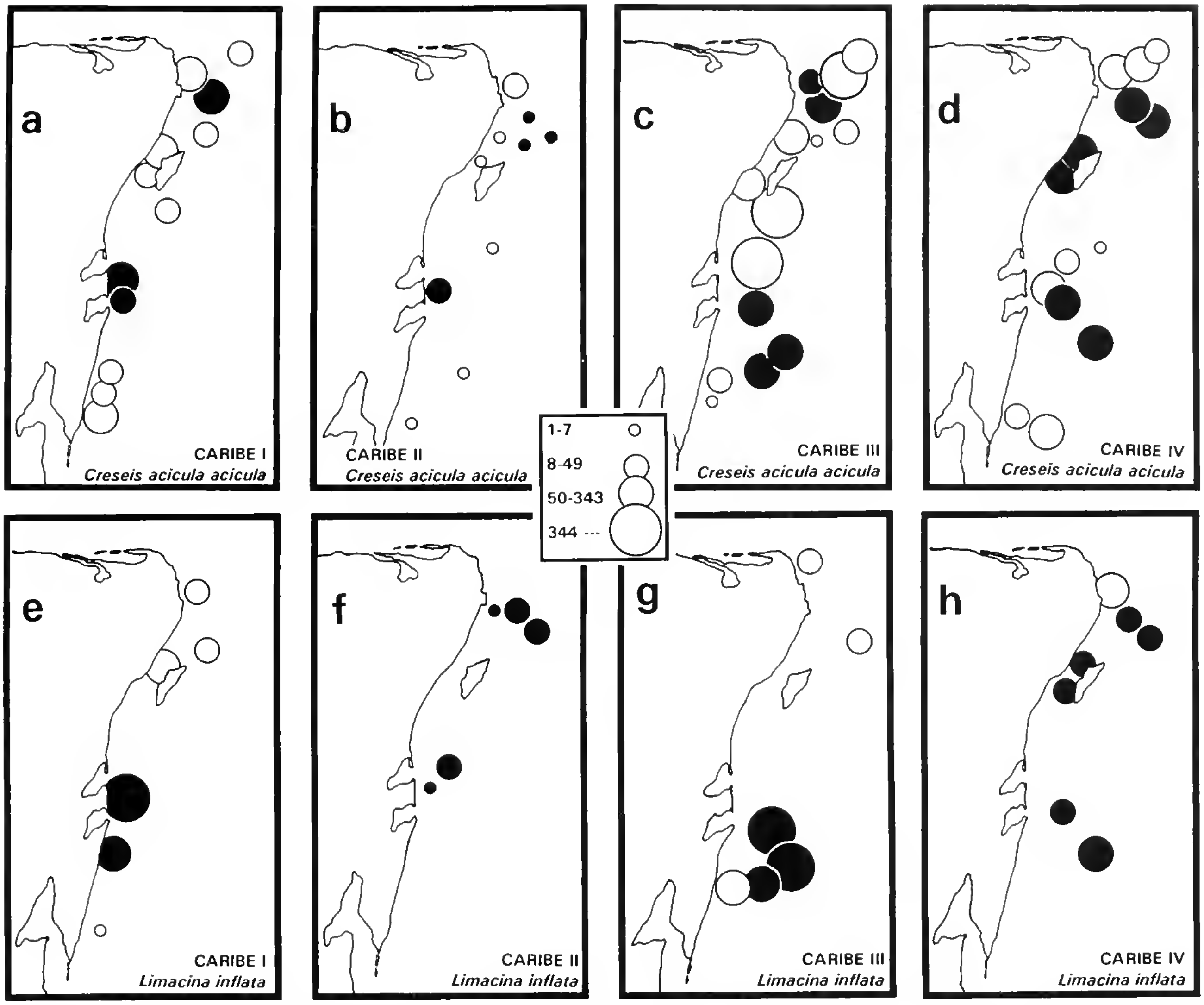

Figure 3. Distribution and density of the most abundant species during the surveyed period. **a-d.** *Creseis acicula acicula*; **e-h.** *Limacina inflata*. Black circles indicate night samples.

(IIV = 61.6), while *L. inflata*, *C. longirostris limbata* were less dominant. Diversity fluctuated (0.67–1.28) and was in average (1.16 bits/ind.) the second highest in the survey. Again, two clusters were defined, as shown in Figure 5h. The first assemblage, with stations distributed at the middle and southern portions of the area, was characterized by the lowest total thecosome pteropod densities (below 20 org./10^3m^{-3}) and contained only 1.4% of the total thecosome pteropod counts. In this four-station cluster, *C. acicula acicula* was either absent or showed its lowest densities. Diversity was low. The second assemblage was distributed all along the surveyed area and showed the highest total densities (40–450 org./10^3m^{-3}) (Figure 5d). More than 98% of *C. acicula acicula*, 100% of *L. trochiformis* and of *L. inflata* occurred in this assemblage. Diversity was variable.

DISCUSSION

Previous records of thecosome pteropods from the tropical northwestern Atlantic report 51 species and subspecific forms (Wells, 1975, 1976; Haagensen, 1976; Suárez-Morales and Gasca, 1990; Michel and Michel, 1991; Suárez-Morales, 1994). Most of these records are from the Gulf of Mexico and the central and eastern portions of the Caribbean Sea. All the species identified here have been reported previously from adjacent areas of the Northwestern Atlantic (Suárez-Morales, 1994). In a coastal system adjacent to the surveyed area, only 6 species have been recorded (Gasca and Suárez-Morales, 1990). However, the present study shows for the first time faunal records of thecosome pteropods in the oceanic area of the Caribbean Sea off Mexico. Moreover, occurrence of *Limacina lesueuri*, *Creseis acicula*

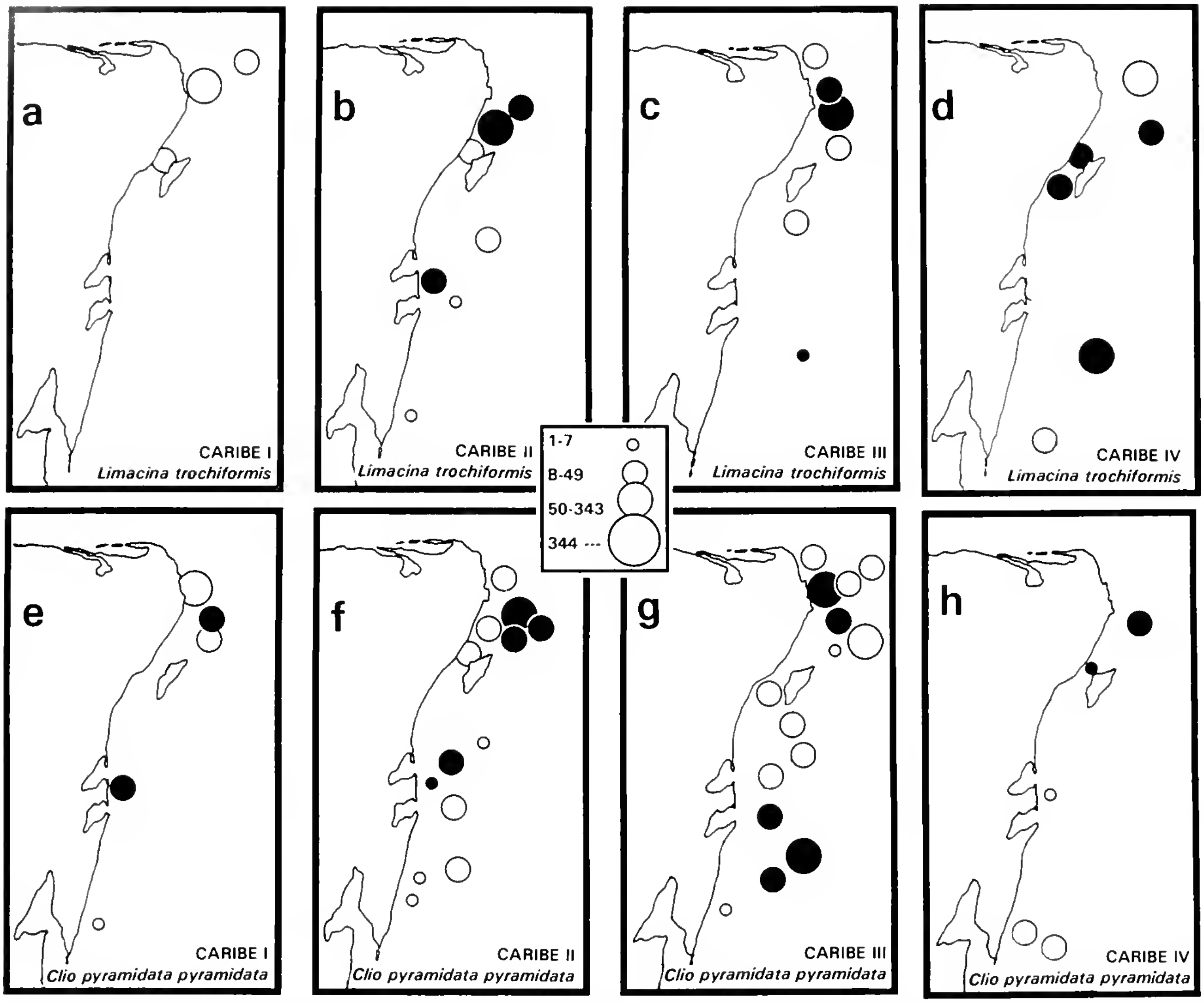

Figure 4. Distribution and density of the most abundant species during the surveyed period. **a-d.** *Limacina trochiformis*; **e-h.** *Clio pyramidata pyramidata*. Black circles indicate night samples.

clava and *Cymbulia peroni* in the Caribbean Sea is herein recorded for the first time. These species were previously known only from the central and southern portions of the Gulf of Mexico (Suárez-Morales, 1994).

The main branch of the Yucatan Current, which transports Caribbean surface waters northward, affects offshore conditions in the Mexican Caribbean. The current represents an important factor that influences the faunal distributions and the dynamics of the entire ecosystem. The pteropod fauna of tropical surface waters of the Caribbean is dominated by a group of several species (Haagensen, 1976), which include *Creseis acicula*, *Limacina trochiformis*, *Creseis virgula* and *Carolinia longirostris*. Only part of this group of species was found to be dominant in the surface layer of the Caribbean Sea off Mexico during the present study. The former two species indicate the primary influence of the Caribbean surface water on the study area. The low abundance of *C. virgula conica* and *C. longirostris* might result from specific, unknown local conditions. The main species group of the Mexican Caribbean is similar to that reported by Suárez-Morales (1992) for the southern Gulf of Mexico (*C. acicula acicula*, *L. inflata*, *L. trochiformis*, *C. longirostris longirostris*).

The near-shore and continental shelf oceanographic dynamics along the Caribbean coast of Mexico are related to the strength of a coastal countercurrent moving southwards (Merino, 1986) from the northernmost edge of the Caribbean coast, which is also the easternmost portion of the Campeche Bank. Its influence would explain, at least partially, a certain affinity of the local thecosome pteropod fauna with that of the southern Gulf of Mexico, with at least 60% of species in common between the 2 areas (Leal, 1965; Matsubara, 1975; Suárez-Morales and Gasca, 1992). The species composition of the local thecosome pteropod fauna seems to represent a mixed faunal complex of Caribbean and Gulf of Mexico affinities.

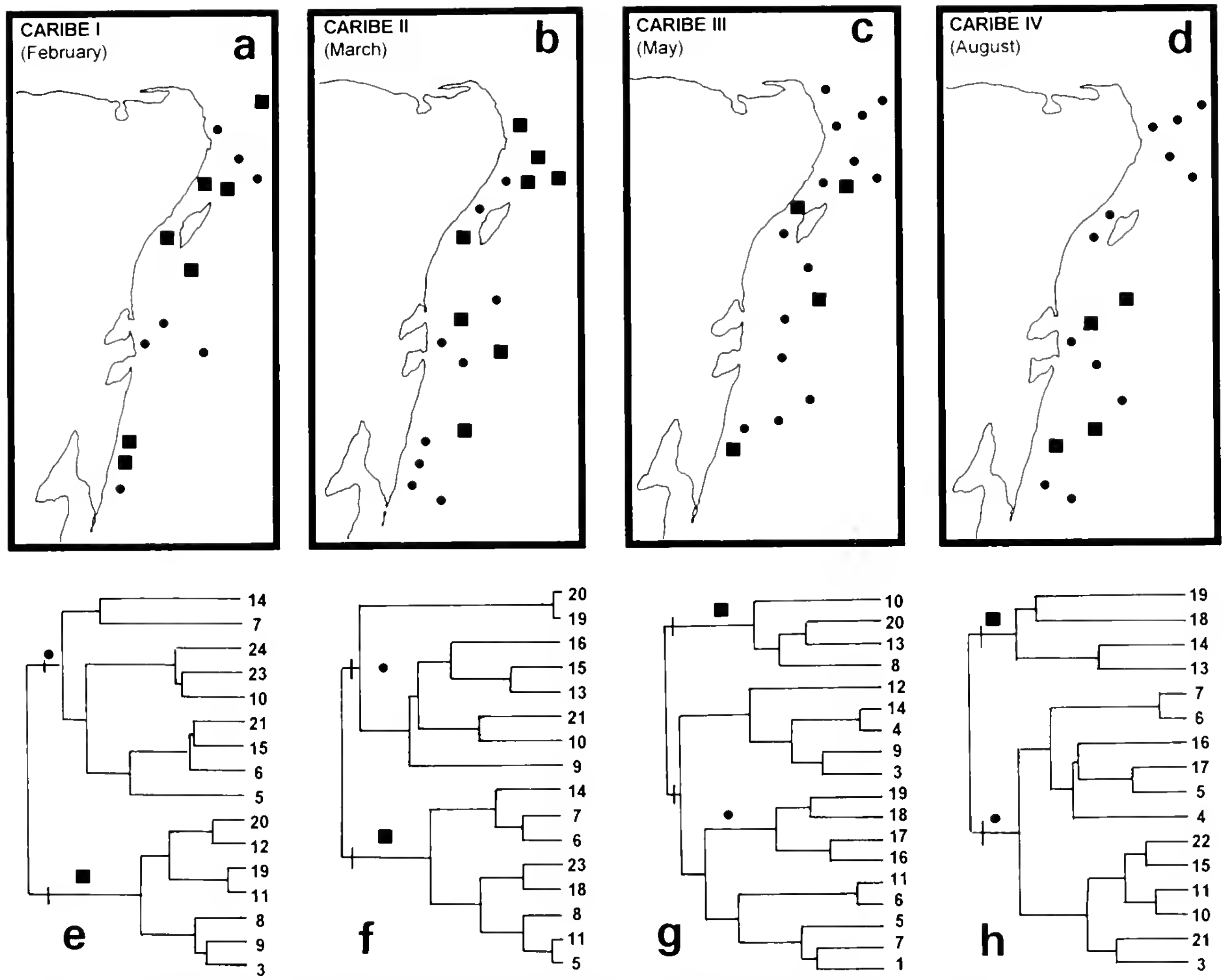

Figure 5. Distribution of pteropod assemblages. **a-d.** Obtained from the Bray-Curtis Index during the four months. **e-h.** Dendrograms resulting from the Bray-Curtis Index during the four months surveyed.

In the surveyed area, the oceanic thecosome pteropod *Limacina bulimoides* was collected quite close to the coast, as most of the species (either neritic-oceanic or neritic) recorded here. In Bahia de Ascensión, a coastal-estuarine system on the central coast of the Mexican Caribbean (Figure 1), species such as *C. acicula acicula*, *L. trochiformis* and *C. longirostris longirostris* have been recorded well inside this system (Suárez-Morales and Gasca, 1990). The occurrence of neritic/oceanic zooplankton within the estuarine systems on this coast has been studied by Zamponi and Suárez-Morales (1991) and by Suárez-Morales and Gasca (1996). According to local studies of coastal surface currents (Merino, 1986), the plankton carried northward by the western edge of the Yucatan Current tend to drift inshore. This might explain the presence of oceanic species very near the coast, over the narrow shelf, and in the estuarine systems. The inshore drift might also promote the hydrographic homogeneity represented by the salinity and temperature values recorded during the survey period. It is generally accepted that the low variability of these factors does not have a pronounced effect on the zooplankton distribution in the Caribbean (Hubbard et al., 1991). Another possible consequence of the narrow shelf present in this area is the presence of deep-sea species near the shelf break (Segura-Puertas and Ordóñez-López, 1994). However, no deep-sea thecosome pteropods were recorded during this survey.

Most species have been reported as common in neritic and oceanic waters, and represent more than 85% of the recorded species; *C. acicula acicula*, the most abundant thecosome in the area, has been considered to be the most abundant thecosome in Caribbean neritic-coastal waters. (Haagensen, 1976). The influence of neritic waters on these otherwise mainly oceanic assemblages is represented by the occurrence of high densities of *C. acicula acicula*. The study area clearly shows a strong oceanic affinity with a variable neritic influence. Neritic-oceanic species were numerically dominant or subdominant during the four-month survey and can be regarded as the main group of representative local pteropods. This is probably a result of local mixing processes within the boundaries of the main current and the coastal countercurrent. In a survey of fish larvae, Sánchez-Velasco and Flores-Coto (1994) found that the Caribbean Sea off Mexico is characterized mainly by oceanic species intermixed with neritic-coastal species.

The Bray-Curtis Index clusters show a similar pattern throughout the area during the four surveyed periods, with overlapping distributions and irregular zonation patterns. Clusters were sorted mainly by whether stations showed low or high densities. However, day-night results were partially affected by the migratory, circadian behavior of the most abundant species. This was evident for *Limacina inflata* and *C. pyramidata pyramidata*, known to be present during the day below the 100–200 m, moving up to the surface layer at night (Haagensen, 1976; Wormuth, 1981; Gilmer and Harbison, 1986). In the surveyed area, up to 85% of the local density of *L. inflata* and over 70% of *C. pyramidata pyramidata* density was recorded in night trawls.

Clearly, the high-density assemblages were determined mostly by the night samples; two (*C. acicula acicula* and *L. trochiformis*) out of four dominant species were represented by similar densities during both day and night samples, as recorded by Haagensen (1976) in the Caribbean. This, and the fact that overall day-night differences were not significant, would buffer the effect of circadian variations in our cluster patterns. It appears that, even with the migration effect, the species composition did not vary significantly, which suggests that the local thecosome pteropod community is more or less homogeneous throughout the surveyed area. High and low density assemblages overlapped in several areas during the four cruises, probably as a result of strong and continuous mixing processes between the oceanic and the neritic environments. Monthly variations in thecosome pteropod density and distribution may be related to the influence of the Yucatan Current, which increases in the northern portion of the survey area during late spring upwelling (May). During winter and early spring (March-February), the current is weak and the environment becomes oligotrophic (Merino, 1992). This could cause a slight decrease in density (as observed during March), but the community structure remains otherwise relatively stable throughout the four-month period.

The studied area represents a nearly homogeneous mixing zone in which oceanic and neritic-oceanic species were represented during the survey periods by variable and mixed distributional patterns of distribution. This could be related to the presence of different environments (coastal, neritic, oceanic) within a relatively small area, and to the dispersal and transport caused the local hydrologic dynamics (mixing processes, eddies).

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A New Deep-sea Limpet of the Genus *Pectinodonta* Dall, 1882 from New Zealand, and New Distribution Records for *P. aupouria* and *P. morioria* Marshall, 1985 (Gastropoda: Acmaeidae)

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ABSTRACT

Pectinodonta marinovichi n. sp. is described and illustrated, and new distribution data are provided for *P. aupouria* Marshall, 1985 and *P. morioria* Marshall, 1985.

Key words: Mollusca, Acmaeidae, *Pectinodonta*, deep-sea, new species, New Zealand

INTRODUCTION

Since the discovery of two Recent *Pectinodonta* species in the New Zealand region (Marshall, 1985), a third species has been recognized, and considerable additional material of the other two species has come to hand. The opportunity is taken to record this additional material and to plot the distributions. Note that New Zealand *Pectinodonta* species have only been found in areas that have been extensively worked by commercial trawlers, so their true distributions are likely to be more extensive than implied by the distribution maps presented here (Figures 6–8). Acronyms: NMNZ, Museum of New Zealand, Wellington; NZOI, National Institute of Water and Atmospheric Research, Wellington.

SYSTEMATICS

Superfamily Acmaeoidea Forbes, 1850
Family Acmaeidae Forbes, 1850
Subfamily Pectinodontinae Pilsbry, 1891
Genus *Pectinodonta* Dall, 1882

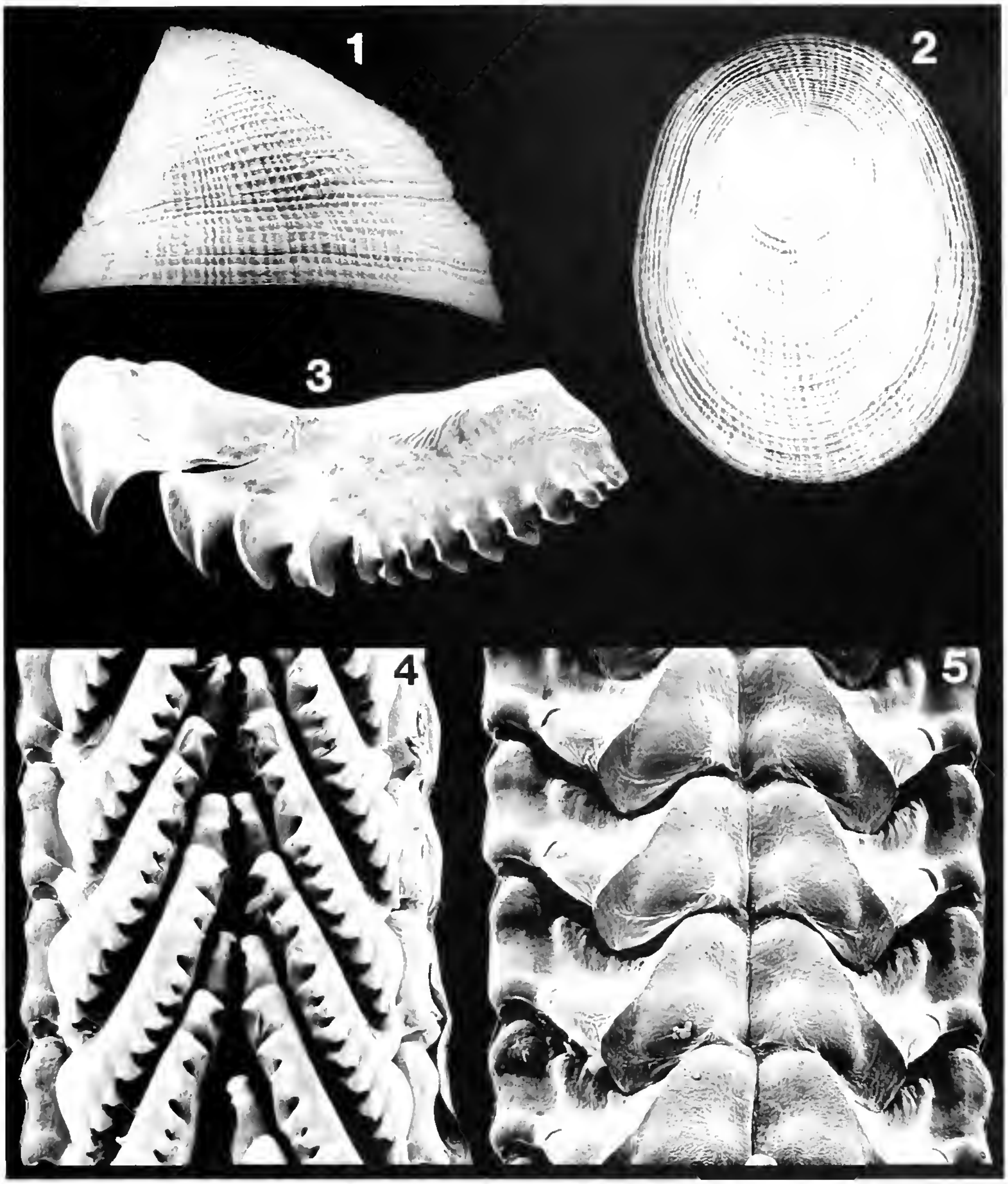
Pectinodonta Dall, 1882: 409 Type species (by original designation): *Pectinodonta arcuata* Dall, 1882; Recent, Caribbean

Remarks: Lindberg (1986) redefined Acmaeidae, restricted it to include *Acmaea mitra* Rathke, 1833 (Acmaeinae) and *Pectinodonta* species (Pectinodontinae) alone, and referred most other taxa hitherto referred there to Lottiidae. More recently Okutani *et al.* (1992) have introduced two new genera (*Serradonta* and *Bathyacmaea*) for pectinodontines with highly distinctive radulae that live on vestimentiferan tubes and *Calyptogena* valves from a bathyal cold seep in Sagami Bay, Japan. Worldwide Recent and Tertiary *Pectinodonta* species were listed by Marshall (1985). Lindberg and Hedegaard (1996) discussed pectinodontine shell structure, recruitment patterns and phylogenetic relationships.

Pectinodonta marinovichi new species
(Figures 1–6)

Pectinodonta aupouria Marshall, 1985: 277 (in part; largest measured paratype).

Description: Shell (Figures 1, 2) up to 25.4 mm long, strongly arched, of moderate thickness, white, exterior dull, interior porcellanous. Anterior end occupying 20–31 % of shell length; anterior slope weakly concave in most specimens, in others almost flat or weakly convex; posterior slope rather strongly convex; lateral slopes weakly convex. Aperture elliptical, shallowly or very shallowly concave from side to side, sides broadly rounded, anterior end more broadly rounded than posterior. With growth, shell gradually twisting clockwise about 10° between juvenile and adult. Teleoconch at 1.6–1.8 mm length translucent and glossy, smooth apart from very fine growth lines; fine radial lines show through outer shell layer but do not resolve as surface features. Subsequent teleoconch chalky white, with low, rounded radial ribs, interspaces wider than each rib; and stronger, rounded or roundly angulate concentric ridges. Fine, crowded, concentric growth lines throughout. Myostracum clearly defined. Animal with eyes lacking. Foot and mantle edge cream white. Large, tapered ctenidium extending antero-laterally from left to right behind head. Mantle edge weakly and irregularly serrate. Muzzle lap-



Figures 1–5. *Pectinodonta marinovichi* new species **1, 2.** Holotype, off Cape Kidnappers, 1100 m, length 25.4 mm. **3–5.** Radula of holotype **3.** Inner side of single tooth (length 370 µm). **4.** Part of radular ribbon showing teeth *in situ* attached to basal plates (width 330 µm). **5.** Part of radular ribbon showing basal plates from which teeth have been removed (shrinkage is minimal) (width 370 µm).

pets thin, broad. Cephalic tentacles small, circular in section, tapered, tips rounded. Radular ribbon about 40% longer than shell. Radular formula 0+3+0+3+0, each tooth (as defined here) comprising 3 fused laterals, individual units of which are defined by fine grooves (Figures 3–5). Teeth arranged in a posteriorly diverging V-shape; each with 13 or 14 conical cusps, innermost cusp largest, next 3 cusps smaller, outer cusps yet smaller and similar.

Type data: Holotype, NMNZ M.127085 (length 25.4 mm, width 19.4 mm, height 15.0 mm) and 3 paratypes, NMNZ M.127023: Off Cape Kidnappers, 39° 50′ S, 177° 39′ E, alive on wood with *P. aupouria*, 1100 m, 10 August 1995, F.V. *Petersen*, coll. M. Marinovich.

Other material examined: Off White Island, Bay of Plenty, New Zealand, 37° 23.7′ S, 177° 39.5′ E, alive on wood together with *P. aupouria*, 1075–1100 m, 23 November 1981, coll. O.M. Moore and P.J. McMillan, F.V. *Kalinovo* (stn. KO1/19/81) (3, NMNZ M.126299); off East Cape, 37° 32.6′ S, 179° 19.3′ E, alive on wood with

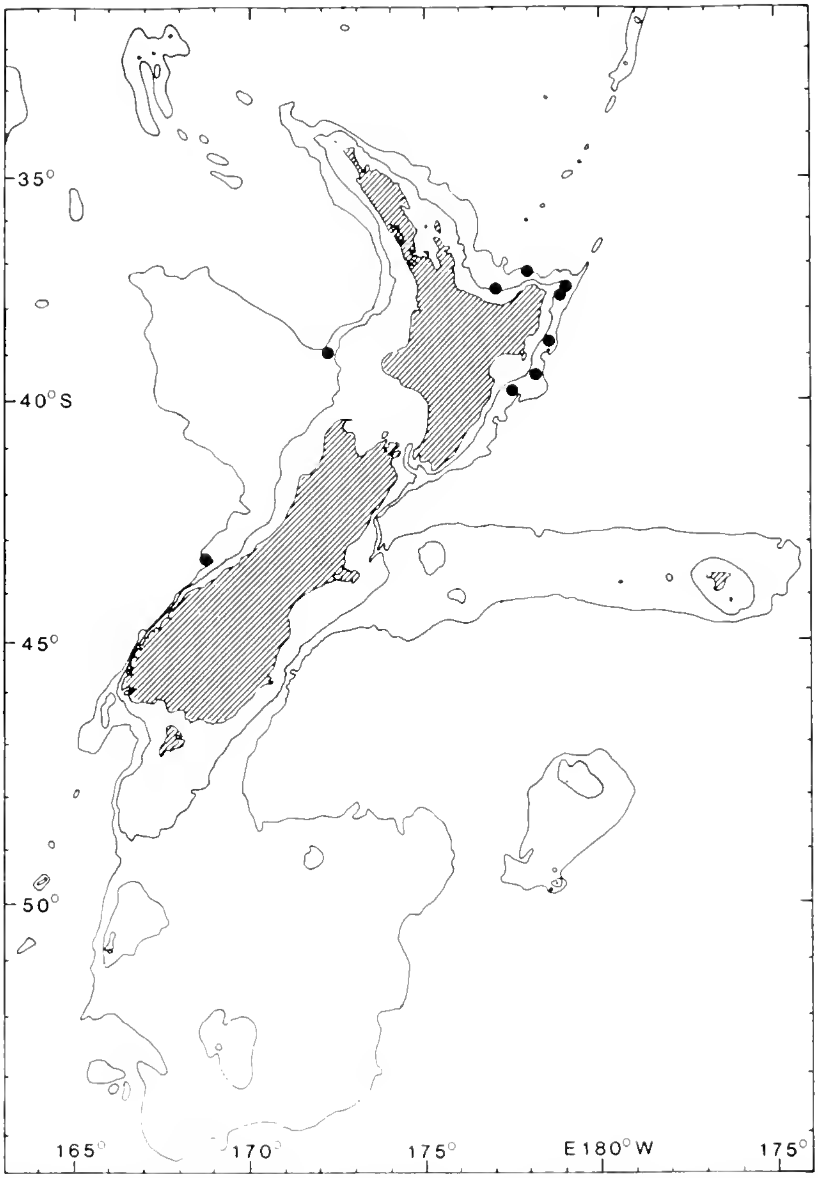


Figure 6. Map of New Zealand showing distribution of *Pectinodonta marinovichi* new species; 200 and 1000 m isobaths indicated

P. aupouria, 1280–1215 m, 4 August 1974, R.V. *Tangaroa* (2, NZOI, stn. K873/2); N of Cape Runaway, 37° 19.46′ S, 178° 04.16′ E, alive on wood with *P. aupouria*, 1124–1169 m, 14 May 1995, F.R.V. *Tangaroa* (stn. 9506/12) (1, NMNZ M.126152); off East Cape, 37° 47.95′ S, 179° 04.35′ E, alive on wood, 1289–1364 m, 23 March 1993, F.R.V. *Tangaroa* (stn. 9303/57) (33, NMNZ M.118799); off Gisborne, 38° 49.14′ S, 178° 34.81′ E, alive on wood, 736–760 m, 25 March 1993, F.R.V. *Tangaroa* (stn. 9303/69) (6, NMNZ M.117958); off Cape Egmont, 38° 58.5′ S, 172° 10.2′ E, alive on wood, 1045–1055 m, 3 June 1986, F.V. *Wanaka* (stn. WK5/17/86) (1, NMNZ M.86819); off Mahia Peninsula, 39° 25.7′ S, 178° 25.3′ E, alive on wood, 921–939 m, 24 June 1986, F.V. *Otago Galliard* (stn. OG2/31/86) (20 NMNZ M.126569); off Hokitika, 43° 27′ S, 168° 47′ E, alive on wood, 910–987 m, 17 May 1985 (3, NMNZ M.118017).

Distribution (figure 6): Off White Island to off Hokitika, New Zealand, living and feeding on wood, 736–1364 m.

Remarks: *Pectinodonta marinovichi* attains larger size than *P. aupouria* and smaller size than *P. morioria* (length up to 25.4 mm against 18.2 mm and 14.7 mm respectively). It differs further from both these species in that the radial ribs are much narrower, and the interspaces are broader than each rib instead of much narrower. The anterior slope is weakly concave in most of specimens of *P. marinovichi*, but convex in most specimens of *P. aupouria*. The mantle edge is more weakly

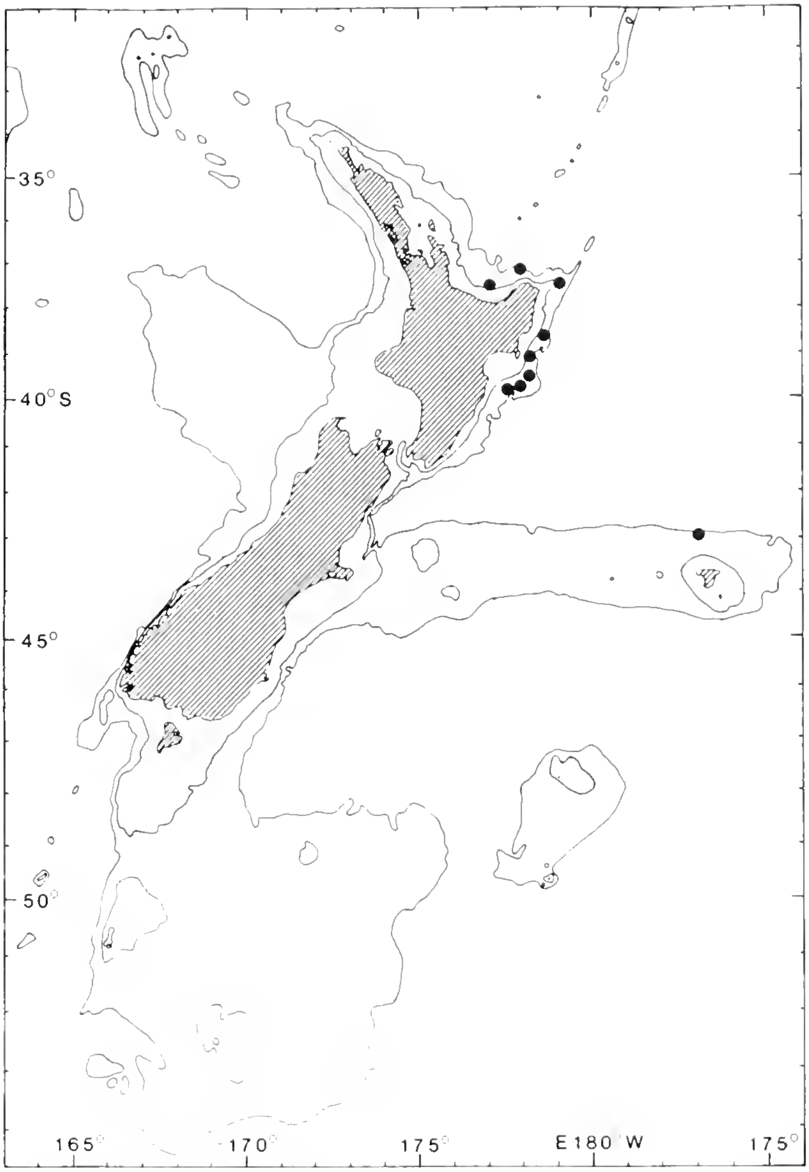


Figure 7. Map of New Zealand showing distribution of *Pectinodonta aupouria* Marshall, 1985. 200 and 1000 m isobaths indicated.

serrate than in *P. aupouria*. The radula resembles that of *P. aupouria* and has more numerous cusps than that of *P. morioria*. *P. marinovichi* has been taken twice living together on the same piece of wood as *P. aupouria*. Three specimens of *P. marinovichi* were found among the 1232 paratypes of *P. aupouria* Marshall, 1985, the largest of which (length 20.2 mm) was unfortunately included in a table of shell measurements for that species (Marshall, 1985, Table 1).

Etymology: After Miro Marinovich, F.V. *Petersen* (Simunovich Fisheries, Auckland), who collected the holotype and who has acquired tremendous quantities of bycatch for the Museum of New Zealand.

Pectinodonta aupouria Marshall, 1985
(Figure 7)

Pectinodonta aupouria Marshall, 1985: 277, fig. 1, 3F–I, 4A, D (in part, largest paratype = *P. marinovichi* n. sp.; specimen identified by Powell (1979) as *Maoricrater explorata* = *P. morioria*).

Type data: Holotype, M.76089 and 1229 paratypes, NMNZ; Off White Island, Bay of Plenty, New Zealand, 37° 23.7′ S, 177° 39.5′ E, alive on wood together with *P. marinovichi* n. sp., 1075–1100 m, 23 November 1981, coll. O.M. Moore and P.J. McMillan, F.V. *Kalinovo* (stn. KO1/19/81).

Other material examined: N of Cape Runaway, 37°

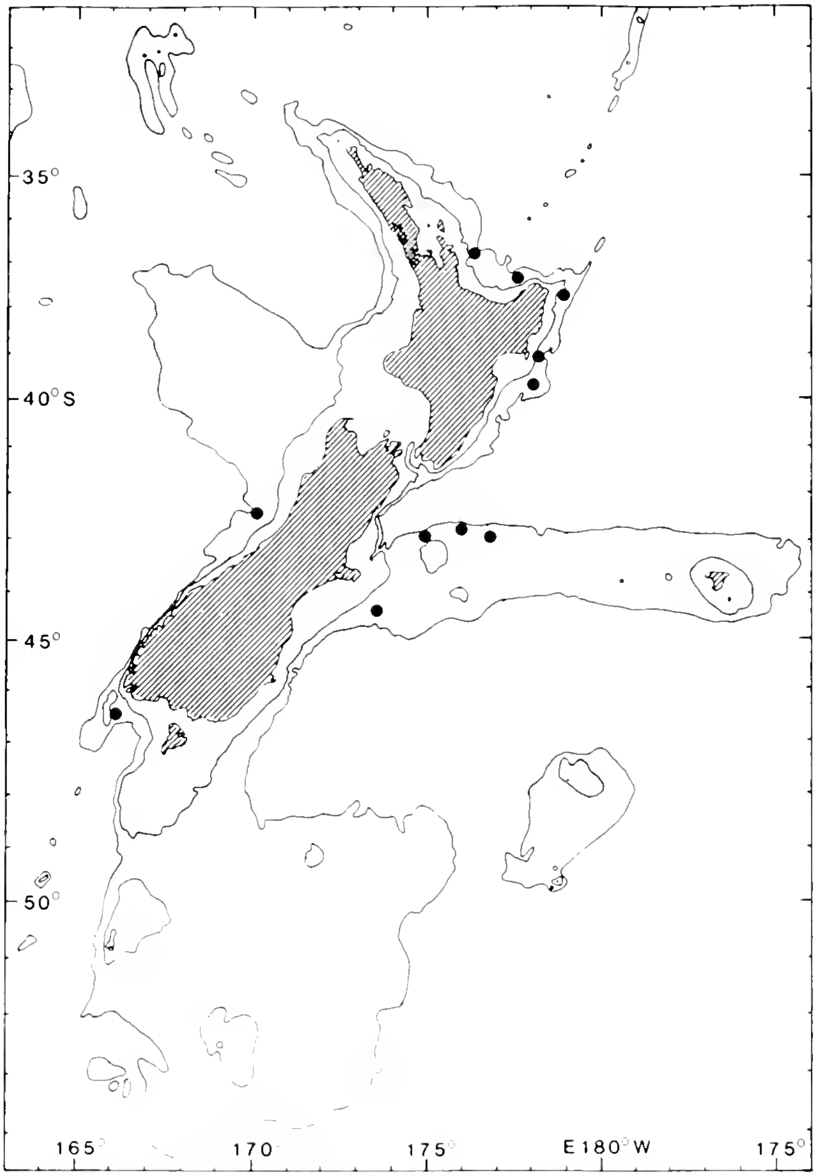


Figure 8. Map of New Zealand showing distribution of *Pectinodonta morioria* Marshall, 1985: 200 and 1000 m isobaths indicated

19.46′ S, 178° 04.16′ E, alive on wood with *P. marinovichi*, 1124–1169 m, 14 May 1995, F.R.V. *Tangaroa* (stn. 9506/42) (1, NMNZ M.126151); off East Cape, 37° 32.6′ S, 179° 19.3′ E, alive on wood with *P. miranovichi* n. sp., 1280–1215 m, 4 August 1974, R.V. *Tangaroa* (9, NZOI, stn. K873/2); off Gisborne, 38° 39.00′ S, 178° 43.5′ E, alive on wood, 885–1000 m, 17 October 1988, F.R.V. *James Cook* (stn. J12/45/88) (14, NMNZ M.92452); off Mahia Peninsula, 39° 05′ S, 178° 10′ E, alive on wood with *P. morioria*, 900–1000 m, June 1994, coll. M. Marinovich, F.V. *Petersen* (28, NMNZ M.118319); E of Mahia Peninsula, 39° 24.64′ S, 178° 27.68′ E, alive on wood, 1271–1352 m, 25 March 1993, F.R.V. *Tangaroa* (stn. 9303/73) (30, NMNZ M.117964); off Cape Kidnappers, 39° 42.91′ S, 178° 10.15′ E, alive on wood with *P. morioria*, 818–952 m, 8 June 1993, coll. M. Clark, F.R.V. *Tangaroa* (stn. 9306/210) (4, NMNZ M.117997); off Cape Kidnappers, 39° 50′ S, 177° 39′ E, alive on wood with *P. marinovichi*, 1100 m, 10 August 1995, F.V. Petersen, coll. M. Marinovich (18, NMNZ M.127022); N of Chatham Islands, 42° 45.37′ S, 177° 09.74′ W, alive on wood, 1064–1067 m, 23 July 1994, F.R.V. *Tangaroa* (stn. 9406/383) (16, NMNZ M.118817).

Distribution (figure 7): White Island to off Cape Kidnappers, north-eastern North Island, and off Chatham Islands, New Zealand, living and feeding on wood, 818–1280 m.

Remarks: In the original description of *Pectinodonta aupouria* I stated that the shell attains a length of 20.2 mm. This measurement, however, refers to a specimen of *P. marinovichi*, which was included with the type material, and the largest specimen of *P. aupouria* seen (a paratype) is 18.2 mm long. I was also mistaken in concluding that the *Pectinodonta* species misidentified by Powell (1979) as "*Notocrater explorata* Dell, 1953" (a lepetid) was *P. aupouria*, for examination of the actual specimen reveals that it is *P. morioria*. *P. aupouria* has been taken alive on two occasions with *P. morioria* and on four occasions with *P. marinovichi*.

Pectinodonta morioria Marshall, 1985
(Figure 8)

Maoricrater explorata —Powell, 1979: 50, fig. 5: 1, 2 (not *Notoacmea explorata* Dell, 1953).
Pectinodonta aupouria Marshall, 1985: 277 (in part, Powell's (1979) record as *Maoricrater explorata* only).
Pectinodonta morioria Marshall, 1985: 279, fig. 3J, K, 4B, E.

Type data: Holotype, NMNZ M.76090 and many paratypes, NMNZ M.75107: NE of Mernoo Bank, Chatham Rise, New Zealand, 42° 43.9′ S, 176° 08′ E, alive on wood, 800–810 m, 28 September 1982, F.V. *Kaltan* (KTN/152/82). Paratypes (4, NMNZ M.75242): Off Timaru, 44° 33.2′ S, 173° 42.3′ E, alive on wood, 750–738 m, 8 June 1984, F.R.V. *James Cook* (stn. J10/4/84).

Other material examined: Off Aldermen Islands, 366–476 m, on wood (1, Auckland Institute and Museum AK131610); off Aldermen Islands, alive on wood, 400 m, April 1988, pres. D. Gibbs (2, NMNZ M.95302); off Cape Runaway, 37° 29.9′ S, 177° 47′ E, alive on wood, 450–481 m, 8 December 1985, F.V. *Wanaka* (stn. WK3/19/85) (ca. 1000, NMNZ M.84252); off East Cape, 37° 47.64′ S, 179° 04.45′ E, alive on wood, 1289–1342 m, 24 March 1992, F.R.V. *Tangaroa* (stn. 9203/133) (27, NMNZ M.117898); off Mahia Peninsula, 39° 05′ S, 178° 10′ E, alive on wood with *P. aupouria*, 900–1000 m, June 1994, coll. M. Marinovich, F.V. *Petersen* (18, NMNZ M.118321); off Cape Kidnappers, 39° 42.91′ S, 178° 10.15′ E, alive on wood with *P. aupouria*, 818–952 m, 8 June 1993, coll. M. Clark, F.R.V. *Tangaroa* (stn. 9306/210) (several hundred, NMNZ M.117996); off Hokitika, 42° 37.6′ S, 170° 02.8′ E, alive on wood, 490–439 m, 13 October 1988, F.V. *Diashin Maru* 22 (stn. 269/24) (several hundred, NMNZ M.92467); slope of Mernoo Bank, Chatham Rise, 42° 58.06′ S, 175° 01.03′ E, N alive on wood, 545 m, 15 January 1992, F.R.V. *Tangaroa* (stn. 9106/91) (many hundreds, NMNZ M.126570); E of Mernoo Bank, Chatham Rise, 42° 53′– 43° 08′ S, 176° 04′–177° 00′ E, alive on wood, 370–420 m, December 1994, coll. M. Marinovich, F.V. *Petersen* (50, NMNZ M.119153); off Puysegur Point, 46° 29′ S, 166° 14′ E, alive on wood, 560 m, 20 October 1987, F.V. *Chiyo Maru* 5 (52, NMNZ M.90196).

Distribution (figure 8): Aldermen Islands to off Puysegur Point, New Zealand, living and feeding on wood, 366–1342 m.

Remarks: *Pectinodonta morioria* proves to attain a shell length of 14.7 mm, which is considerably larger than the type material (length of largest paratype 8.30 mm). Apart from smaller size, *P. morioria* differs from *P. aupouria* in having more numerous radial ribs, rounded instead of adapically shelved concentric ribs, finer, more numerous cusps on the radular teeth, and a smooth instead of serrate mantle edge. *P. morioria* and *P. aupouria* have been taken living together on the same piece of wood on two occasions.

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Rediscovery of *Discus brunsoni* Berry, 1955 and *Oreohelix alpina* (Elrod, 1901) in the Mission Mountains, Montana, with Comments on *Oreohelix elrodi* (Pilsbry, 1900)

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ABSTRACT

During summer 1997, extant populations of the endemic land snails *Discus brunsoni* and *Oreohelix alpina* were rediscovered near the type localities in the Mission Mountains, Montana, last known collections were made 33 and 48 years ago, respectively. *Discus brunsoni* and *Oreohelix elrodi* (also endemic to the Mission Mountains and nearby Swan Range) were previously reported to be sympatric in subalpine limestone talus. Both species were found in 1997 in diorite talus, the latter species also occupied argillite talus with little, if any, limestone present at any site. Live *D. brunsoni* ($n = 8$) were found near the talus surface only on bare rock or foliose lichen on rock during cool, wet conditions. Live *O. elrodi* were found near the talus surface on rock ($n = 9$) or organic litter accumulations ($n = 55$) under all conditions, although in reduced number during warmer and drier weather. Above treeline, live *O. alpina* were found exclusively in exposed locations under limestone talus, sometimes attached to rock surfaces ($n = 7$) but more often present in organic detritus ($n = 10$). Lack of collecting records of *D. brunsoni* and *O. alpina* in recent decades probably resulted from 1) extremely restricted distributions, 2) limited knowledge of habitat requirements, and 3) scarcity of active collectors in the region.

Key words: *Discus brunsoni*, *Oreohelix alpina*, *Oreohelix elrodi*, Montana, distribution, ecology.

INTRODUCTION

The Mission Mountains of northwestern Montana are recognized as an area of significant snail endemicity in the Interior Columbia River Basin (Frest and Johannes, 1995). The mountains extend about 80 km north to south and 19 km east to west, rising abruptly from a base at 1036 m in the Swan and Flathead valleys to a crest of nearly 3018 m. The range is composed of Precambrian Belt rocks (mostly limestone and argillite) that were deeply dissected by alpine glaciers during the Pleistocene (Alden, 1953). The Mission Mountains still support small cirque glaciers and permanent ice patches. The portion of the mountain range within Lake County contains the type localities for three narrowly endemic terrestrial snail species, none of which has yet been documented at more than two sites.

Oreohelix elrodi (Pilsbry, 1900) was discovered in 1899 in talus slopes between 1067–1524 m above the north side of McDonald Lake (Pilsbry, 1900; Elrod, 1903a), where it was most common, and also found rarely along the south side of the lake. The amphitheater around McDonald Lake remains the only known locality for *O. elrodi* in the Mission Mountains, but the species has been found more recently above Lion Creek in the nearby Swan Range (Fairbanks, 1984). *Oreohelix alpina* (Elrod, 1901) was first found in 1900 on "Sinyaleamin Mountain" (Elrod, 1901; 1902; 1903b) and again later that year on the west ridge of McDonald Peak; both localities were above treeline between 2377–2743 m and remain the only sites where this species has been located. A single shell of *Discus brunsoni* Berry, 1955, was first encountered in 1948 in talus slopes above the north side of McDonald Lake, at an estimated elevation of 1067 m. Additional material was collected there in 1950 (Berry, 1955; Brunson, 1956). The type locality remains the only known occurrence site for *D. brunsoni*. Interestingly, this talus slope is also the type locality for *O. elrodi*, which had been collected several times between 1899 and 1948 (Brunson, 1956); *D. brunsoni*, however, was not discovered there until almost half a century later. Known localities for the three snail species in the Mission Mountains are within the Mission Mountains Tribal Wilderness of the Confederated Salish and Kootenai Tribes and are relatively secure from human disturbance. None of the snail species has any special federal designation but all three are on the state list of Animal Species of Special Concern maintained by the Montana Natural Heritage Program.

Live *Oreohelix elrodi* were reported at the type locality as recently as 1993 (Frest and Johannes, 1995). There are no known records in recent years, however, for *O. alpina* and *Discus brunsoni* (Frest and Johannes, 1995). Apparently, *O. alpina* was last collected on 2 August 1949 on McDonald Peak, and *D. brunsoni* was last collected on 29 May 1964 at McDonald Lake (R. B. Brunson, pers. comm. for both records). Primary objectives of this study are to 1) revisit the type localities of *Oreohelix alpina* and *Discus brunsoni* and, if possible, locate extant populations of each species, and 2) supplement previous descriptions of the habitats associated with each species.

MATERIAL AND METHODS

I used a variety of sources to obtain relatively precise descriptions of type localities and habitat use by *Oreohelix alpina* and *Discus brunsoni*, including published literature, conversations with Dr. R. B. Brunson (who made the last known collections of each species), and examination of Brunson's specimen catalog. The type locality of *D. brunsoni* was easily identified. Berry (1955) provided a photograph of the site and Brunson (1956) added considerable detail of its conditions and physical setting. The site (Site 1) is an extensive talus slope on the north side of McDonald Lake (T19N R19W S11) that is accessible by trail. Trips to Site 1 were made on 10 June, 1 July, 4 July and 10 July 1997. Rock at Site 1 was composed predominantly of blocks of diorite about 1 m^3 in size, intermixed with less than 5% of argillite fragments. Neither rock material reacted with acid, which indicates the absence of calcium carbonate. Canopy cover was 0% in the search area, slope = 36° facing SSE. Forest at the margins of the talus slope was composed of Douglas fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*). Pockets of water birch (*Betula occidentalis*), quaking aspen (*Populus tremuloides*) and mock orange (*Philadelphus lewisii*) were scattered in and near the margins of the talus. Their leaves comprised much of the organic litter among the talus fragments. Talus was inspected to a maximum depth of 1 m in an area of 25 × 40 m. Additional searches during other visits to Site 1 were focused in this area. Site 2 (about 100 m east of Site 1) was composed of about equal amounts of smaller-sized diorite and argillite; average talus fragment size was about 30 × 30 cm. Canopy cover (surrounding species composition as at Site 1) was 0%, slope = 32° facing SSE, search area was 15 × 20 m. Site 3 was about 500 m east of Site 2. Search area at Site 3 was 10 × 25 m, rock was 100% argillite with average fragment size about 10 × 20 cm. Slope, aspect, cover and surrounding vegetation at Site 3 were similar to the other two sites.

Access to the historical sites of *Oreohelix alpina* was not so straightforward. Neither location can be reached by trail. The McDonald Peak site is in the Grizzly Bear Conservation Zone of the Mission Mountains Tribal Wilderness and is closed to all recreational use from 15 July–1 October. Snowpack often precludes trips into the alpine areas before mid-July, so the McDonald Peak site was not visited in 1997. Elrod (1901; 1902; 1903b), Pilsbry (1939) and Frest and Johannes (1995) describe the type locality as above treeline on "Sinyaleamin Mountain". There is no Sinyaleamin Mountain on current U.S.G.S. topographic maps. Details of the 1900 trip during which the species was discovered (Elrod, 1902) indicate, however, that Sinyaleamin Mountain is now known as East St. Marys Peak; *O. alpina* was collected by Elrod on the southwest ridge of that mountain (T18N R18W S20).

I climbed East St. Marys Peak on 27 August 1997 and searched for *Oreohelix alpina* at two sites (Sites 1 and 2) along the southeast ridge (T18N R18W S21) and also along the top of the southwest ridge (Site 3), which included the summit. Site 1 was a broad level area atop the southeast ridge at approximately 2637 m; the ground was covered with a variety of alpine forbs and grasses (vegetation cover = 60–70%) in which were open patches of limestone scree (fragment diameter about 2–4 cm). Site 2 was farther north about 1 km, where the ridge narrowed between 2713–2774 m. Exposure at this site was to the southwest but near the ridge crest. Shallow limestone talus became predominant with only scattered patches of alpine vegetation present (cover = 85–95% rock). Plants in the area included snow cinquefoil (*Potentilla nivea*), mountain avens (*Dryas octopetala*), alpine sorrel (*Oxyria digyna*) and moss campion (*Silene acaulis*). Site 3 included the summit (2873 m) and top of the southwest ridge. Plant composition and percent-cover at this site were similar to Site 2.

Time spent searching for each species was recorded as a measure of search effort (Ausden, 1996); time of day refers to Mountain Daylight Time. The substrate on which each live snail was found ("rock" or "organic litter") was noted, and shell diameter of live individuals was measured with a dial caliper. Photographs of live snails and habitats for each species were taken and are available from the Montana Natural Heritage Program, Helena, Montana. Voucher specimens of *Discus brunsoni* (MTHP 4069) and *Oreohelix alpina* (MTHP 4071) were verified by R. B. Brunson and will be deposited at the U.S. National Museum following anatomical study by H. L. Fairbanks. Only empty shells of *O. elrodi* were collected for reference material, as the species is very distinctive and readily recognized from photographs. *G*-tests (Sokal and Rohlf, 1981) were used to analyze frequency distributions of substrate use; statistical significance was assumed when $P<0.05$.

RESULTS

DISCUS BRUNSONI AND *OREOHELIX ELRODI*

Presence at different sites: Three talus sites within the general type locality of both species were examined during four different visits (Table 1). All sites were at 1128 m along the trail paralleling McDonald Lake on its north side. On 10 June and 4 July, weather was sunny and warm (21–23°C) at the time of the searches (10:15–12:00); no precipitation had fallen in the previous 48 hours. On both dates only Site 1 was checked. Four live estivating *Oreohelix elrodi* and no *Discus brunsoni* were found during 75 min of searching by two persons on 10

Table 1. Maximum diameter (mean ± SD) of live *Oreohelix elrodi* and *Discus brunsoni* in three talus sites on 1 and 10 July 1997, Mission Mountains, Montana. All measurements are in mm. Sample sizes (n) are in parentheses.

	Site 1	Site 2	Site 3
Rock type	diorite	diorite, argillite	argillite
Average fragment size m^3	1.0 m^3	0.09 m^3	0.02
O. elrodi			
mean	16.2 ± 4.5 (39)	14.0 ± 4.7 (18)	12.0 ± 4.2 (7)
range	4.1–22.6	7.5–22.3	6.5–17.7
D. brunsoni			
mean	9.5 ± 1.4 (8)	—	—
range	6.7–10.5	—	—

June. The 4 July visit was devoted to study of the rocks and no live snails of either species were noted.

On 1 July weather was wet and cool (10°C) during the search period (10:00–13:00); the area had received steady precipitation during the previous 48 h. At Site 1 I found 20 live *Oreohelix elrodi* and 5 live *Discus brunsoni* in 120 min. At Site 2 I found 11 *O. elrodi* and no *D. brunsoni* during 60 min. Under similar conditions on 10 July (wet, 14–17°C) I found 19 live *O. elrodi* and 3 live *D. brunsoni* at Site 1 during 120 min (11:00–13:00). At Site 2 I found 7 live *O. elrodi* and no *D. brunsoni* in 30 min (13:30–14:00). At Site 3 I found 7 live *O. elrodi* and no *D. brunsoni* in 15 min (15:35–15:50).

Substrate selection within talus: Substrate of occurrence (rock, organic litter) for live snails found at all three sites was documented on 1 and 10 July. All live *Discus brunsoni* (n = 8) were found on bare or lichen-covered rock. Nine of 64 live *Oreohelix elrodi* were found on similar substrate, 55 were found on organic litter accumulations (bark, twigs, leaf fragments, needles) or live moss among the talus. The difference in substrate selection between the two is statistically significant ($G = 26.724$, $df = 1$, $P < 0.001$).

Shell diameter: *Discus brunsoni* measured in average 9.5 mm diameter and ranged from 6.7–10.5 mm (Table 1). For *Oreohelix elrodi* at Site 1, 28 (71.8%) of 39 live individuals were > 15 mm diameter. At Sites 2 and 3 the respective numbers of live snails in this category were 6 (33.3%) of 18, and 2 (28.6%) of 7. Samples undoubtedly contained members of more than one cohort. The presence of individuals ≤ 7.5 mm diameter in each sample suggests reproduction is occurring at each site.

OREOHELIX ALPINA

Presence at different sites and substrate selection: Weather on East St. Marys Peak was clear and cool (12.5°C at the summit) on 27 August. I found no snails in 30 min (12:15–12:45) at Site 1 on the southeast ridge.

At Site 2 I found 16 live *O. alpina* in 45 min (13:30–14:15) in three areas searched along 300 m of ridge. All live snails were under limestone blocks about 20 × 30 cm square and 4–8 cm thick. Six snails were attached to the undersides of limestone fragments or atop bare rock beneath overlying blocks, one group of 10 live snails was found in leaf litter (area = 9 cm^2) accumulated near the base of snow cinquefoil. Some soil development was present at each site where live snails were found. Dead shells were found with little effort on open ground.

I searched the summit area (Site 3) for 15 min (14:30–14:45) and found one live snail at 2865 m near the top of the southwest ridge. This individual was on bare rock under a limestone block near a patch of snow cinquefoil.

Shell diameter: Diameter of live shells (mean ± SD, $n = 16$) was 5.7 ± 1.9 mm; range was 2.5–8.5 mm. The smaller individuals indicate that reproduction is probably occurring at this location. Mean diameter of dead shells ($n = 9$) was 8.9 ± 0.5 mm; range was 8.0–9.6 mm.

DISCUSSION

Extant populations of *Discus brunsoni* and *Oreohelix alpina* were located in 1997 at or near the type localities 33 and 48 years, respectively, after the last documented collections (R. B. Brunson, pers. comm.; T. J. Frest, pers. comm.). The range in shell size of live individuals at each site (including *O. elrodi* sites) indicates the presence of multiple cohorts and likelihood of continuing reproduction. The sites where *O. alpina* was found on the southeast ridge of East St. Marys Peak represent a slight range expansion. (The type locality is on the southwest ridge.) I have found no evidence that *O. alpina* has been collected on East St. Marys Peak since 1900, when Elrod discovered the species. The last documented collection of *O. alpina* (Brunson specimen catalog) was made on McDonald Peak on 2 August 1949. Correspondence from Stillman Berry (21 August 1951; Brunson pers. comm.) indicates that another collection may have been made on McDonald Peak in 1950 or 1951, but there is no evidence of this in Brunson's catalog.

Several interacting factors probably contributed to the failure to find *Discus brunsoni* and *Oreohelix alpina* during the last several decades. First, I know of no active resident collectors of terrestrial mollusks. Non-resident collectors passing through the area may have visited sites when conditions were not especially favorable for finding these species (*D. brunsoni* in particular) near the surface of talus slopes. The nearly half-century span between first discoveries of *O. elrodi* and *D. brunsoni* at the same site supports this contention. Differences in habitat selection may have contributed to this lapse, as will be discussed below. Furthermore, it seems unlikely that very many non-resident collectors would attempt to visit the relatively inaccessible localities of *O. alpina*. Second, the known distributions of both species are quite restricted. It would be easy for a collector to overlook them without knowledge of the geographical area. For example, one cannot identify "Sinyaleamin Mountain" or find the exact location of *O. alpina* on this mountain or on McDonald Peak without a copy of Elrod's (1902) description of his collecting trip. Third, habitat requirements, especially for *D. brunsoni*, may be narrower than previously appreciated. Information gleaned from Berry (1955) and Brunson (1956) suggests that *D. brunsoni* and *O. elrodi* are sympatric in talus slopes on the north side of McDonald Lake. However, it may be that both species co-occur in only a very restricted zone defined by the narrower habitat preference of *D. brunsoni*. Evidence to date indicates that *O. elrodi* is significantly more widespread, even in the McDonald Lake cirque.

All three snail species favor exposed talus habitats. The type of talus in which each species is found, however, appears to differ among species. *Oreohelix alpina* is found exclusively above treeline in shallow limestone talus on mountain ridges. The descriptions provided by Elrod (1901; 1902; 1903b) and Frest and Johannes (1995) generally coincide with my 1997 findings. Elrod (1902) commented that the snails were found among and under rocks with little vegetation nearby. All live individuals I located were under the protection of stones in areas of scant vegetation cover, but usually with some soil and litter accumulation nearby. Ten (62.5%) of 16 live individuals that I could measure (one shell was broken during handling) were smaller than the minimum diameter (7 mm) described for this species (Elrod, 1903b; Pilsbry, 1939). However, size range of empty shells found mostly on open ground closely matched the published range and mean. Perhaps adults are more likely to be caught away from refuges in adverse conditions, with dead adult shells washing onto open ground.

Discus brunsoni and *O. elrodi* are found well below the treeline in talus slopes surrounded by closed- and open-canopy forest (Brunson, 1956), but the rock types comprising the talus inhabited by the snails are infrequently mentioned in published reports. Berry (1955) and Frest and Johannes (1995) identified the talus as limestone; Elrod (1901; 1902; 1903a) and Brunson (1956) failed to mention rock composition. I did not detect limestone at the three sites where I found one or both species. *Discus brunsoni* was found exclusively in talus where diorite boulders predominate. *Oreohelix elrodi* was found at this site as well as in smaller-sized talus of argillite (Table 1). *Discus brunsoni* may have narrower habitat requirements than expected, associating only with a particular subset of available rock types.

The biology and ecological requirements of *Discus brunsoni* and *Oreohelix elrodi* remain largely unknown, and the following explanations for patterns of presence or absence near the surface of talus slopes are speculative. *Oreohelix elrodi* was more abundant (4–6 fold during my searches) than *D. brunsoni* near the surface of talus in wet and cool conditions, and a few individuals could still be found when it was warmer and drier. Several factors could contribute to this pattern. First, absolute population size of *O. elrodi* at Site 1 may be greater than that of *D. brunsoni*. Ratios of each species near the talus surface could be representative for all depths in talus. Second, I found significant differences in substrate selection between the two species. Some *D. brunsoni* were found on foliose lichen (tentatively identified as *Arctoparmelia subcentrifuga*) that grows on the diorite, but most individuals were found on bare rock. In contrast, *O. elrodi* were most often found on organic litter and vegetation. Preference by *O. elrodi* for organic litter may keep them nearer the surface of talus slopes where litter accumulations are larger and apparently more numerous. Third, larger shell size of *O. elrodi* might reduce its rate of desiccation by decreasing the surface area/volume ratio (see Goodfriend, 1986), allowing larger individuals to remain nearer the drier talus surface for longer periods than *D. brunsoni* and small *O. elrodi*. The four live *O. elrodi* found on 10 June in warm and dry conditions measured 18–21 mm diameter and were estivating at that time. Fourth, timing of my searches did not allow for detection of this pattern, but *D. brunsoni* may tend to be nocturnal or crepuscular and make vertical migrations to the talus surface during periods of activity (Brunson, 1956).

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Epitonium fabrizioi (Gastropoda: Epitoniidae), a New Species from Patagonia, Argentina

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ABSTRACT

Epitonium fabrizioi, a new species of gastropod mollusk belonging to the family Epitoniidae, is described from shallow waters of Puerto Pirámides, Chubut Province, Argentina. This new species is similar to *E. georgettinum* from the same area, which was known only from its shell. It can be distinguished from *E. georgettinum* by its smaller size, more straight profile and, by its sharper, most numerous ribs. In addition, the protoconch of the new species consists of 4.25 whorls. Its radula has only marginal teeth, each with three cusps. The outermost cusp is larger and hook-like, the central and inner cusps are shorter and similar in size. An additional, obsolete, cusp is present near the base of the teeth. The egg capsules have a mean diameter of 76 μm. The new species is compared with *E. georgettinum*, the species with which it co-occurs, and *E. albidum*

INTRODUCTION

Most recent papers about the family Epitoniidae deal with species from the northern hemisphere (Caribbean: Robertson, 1983a, 1983b, 1994a, 1994b; northeastern Pacific: DuShane, 1974, 1979; northeastern Atlantic: Bouchet and Warén, 1986). An exception is the work of Kilburn (1985) who studied representatives of the family from South Africa and Mozambique, and provided a good account of the subgenera living in that area. In their classic and comprehensive work, Clench and Turner (1951, 1952) reported most of the known western Atlantic species. Rios (1994) included a complete list of the approximately 30 species of Epitoniidae known from northern South America, together with illustrations and distribution ranges. However, the material examined in his work was primarily from Brazil, and only marginally included representative species from Uruguay and northern Argentina.

The Magellanic area is poorly represented in molluscan faunal reports, and almost never represented in published revisions of Epitoniidae. Strebel (1905) was the last author to publish a systematic account of the Magellanic epitoniid fauna. He described one species and one variety from the Strait of Magellan.

In this paper we describe a new species of *Epitonium*, and include illustrations of its radula, operculum and protoconch. Data on eggs and egg capsules are also included.

MATERIALS AND METHODS

Specimens of *Epitonium fabrizioi* were collected from tidepools near Puerto Pirámide, Chubut, Argentina (42°34′S, 64°17′W) in November, 1995, during spring (lower low water) tides, and near Punta Loma (42°49′S, 64°53′W) in February, 1996 (see Map 1). This species was found only in the intertidal zone around the pedal discs of sea-anemones (genus *Bunodactis*?) on which they probably feed. In several cases, more than one specimen was found on the same sea-anemone. Several animals were dissected and the radulae were prepared for the SEM observation. The protoconch whorls were counted following the method of Jung (1986). Institutional abbreviations used are: ANSP, Academy of Natural Sciences of Philadelphia; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; MHNG, Muséum d'Histoire naturelle de Genève, Switzerland; MLP, Departamento Zoología Invertebrados, Museo de La Plata, La Plata, Argentina; USNM, National Museum of Natural History, Smithsonian Institution.

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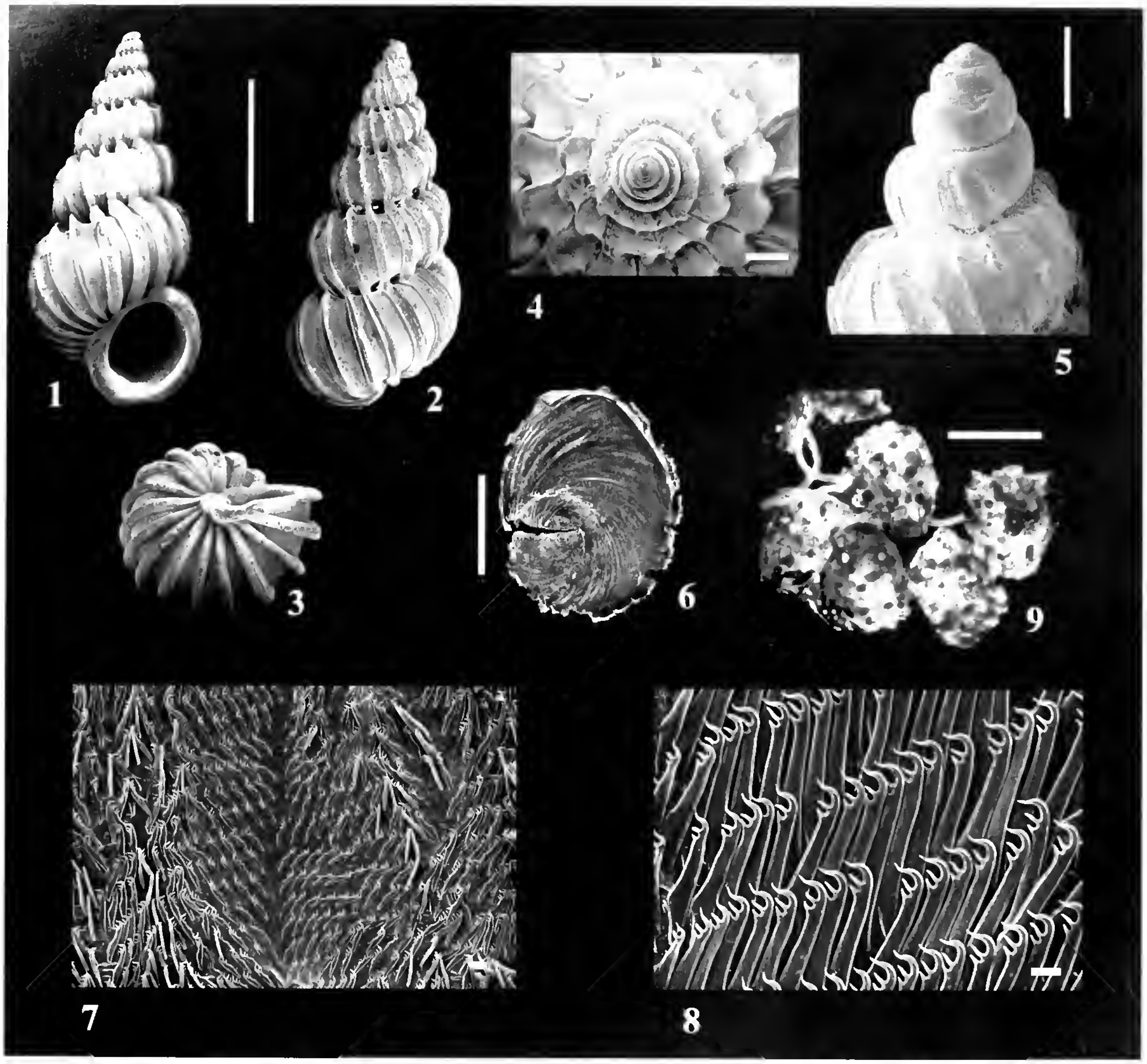


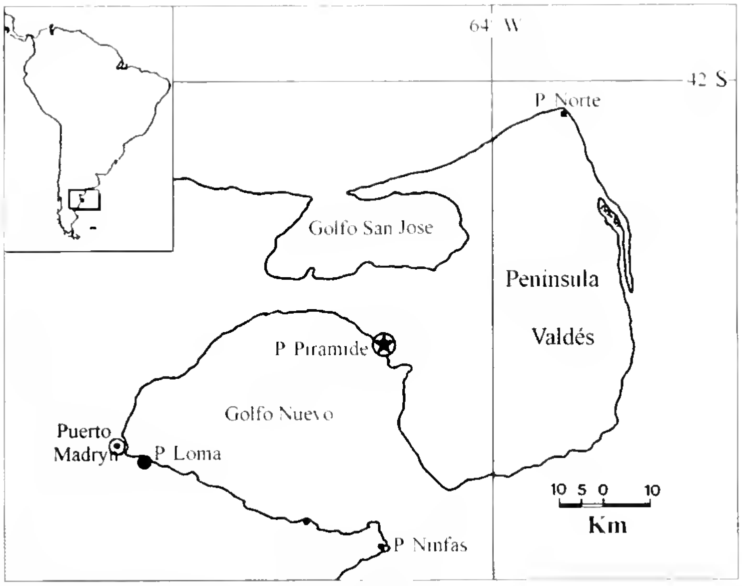
Figures 1–9. *Epitonium fabrizioi* new species. **1–3.** Holotype, MLP 5402. Scale bar = 5 mm. **4.** Apical view, MLP 5333. Scale bar = 200 µm. **5.** Protoconch, MLP 5333. Scale bar = 250 µm. **6.** Operculum of holotype. Scale bar = 5 mm. **7.** Radula of holotype in general view. Scale bar = 20 µm. **8.** Detail of marginal teeth. Scale bar = 10 µm. **9.** Egg capsules. Scale bar = 1 mm.

SYSTEMATICS

Family Epitoniidae Berry, 1910
Genus *Epitonium* Röding, 1798
Epitonium fabrizioi new species
(Figures 1–9)

Epitonium albidum (d'Orbigny, 1842). — Clench and Turner, 1951: pl. 114, fig. 3 only.
Epitonium georgettina (Kiener, 1839). — Scarabino, 1977:183, pl. 2, fig. 8.
Epitonium georgettinum (Kiener, 1839). — Pastorino, 1995:8, pl. 2, fig. 10.

Description: Shell small (up to 13 mm length), chalky, thin, opaque. Protoconch (worn in all but one specimen) consisting of 1.25 whorls and measuring 485 length × 390 µm width. Protoconch whorls smooth under SEM, transition to teleoconch not very sharp. Teleoconch with 8 gently convex, smooth whorls. Spire angle 40°, profile straight. Suture crossed by termination of axial ribs (fenestrate). Axial ornamentation consisting of very sharp ribs, up to 18 on last whorl, but usually 13–14 (Table 1). Axial ribs slightly oblique in relation to shell axis, with irregularly defined edges near suture, and remnants from breakage in the rest. Axial ribs gently reflected on last whorl. All ribs perfectly aligned with overlapping ribs from preceding whorl, attachment erect. Aperture oval, peristome with one layer, forming a gentle basal expansion (auriculate). Columellar callus weakly developed. Umbilicus closed.



Map 1. Records of *Epitonium fabrizioi* (★ = type locality).

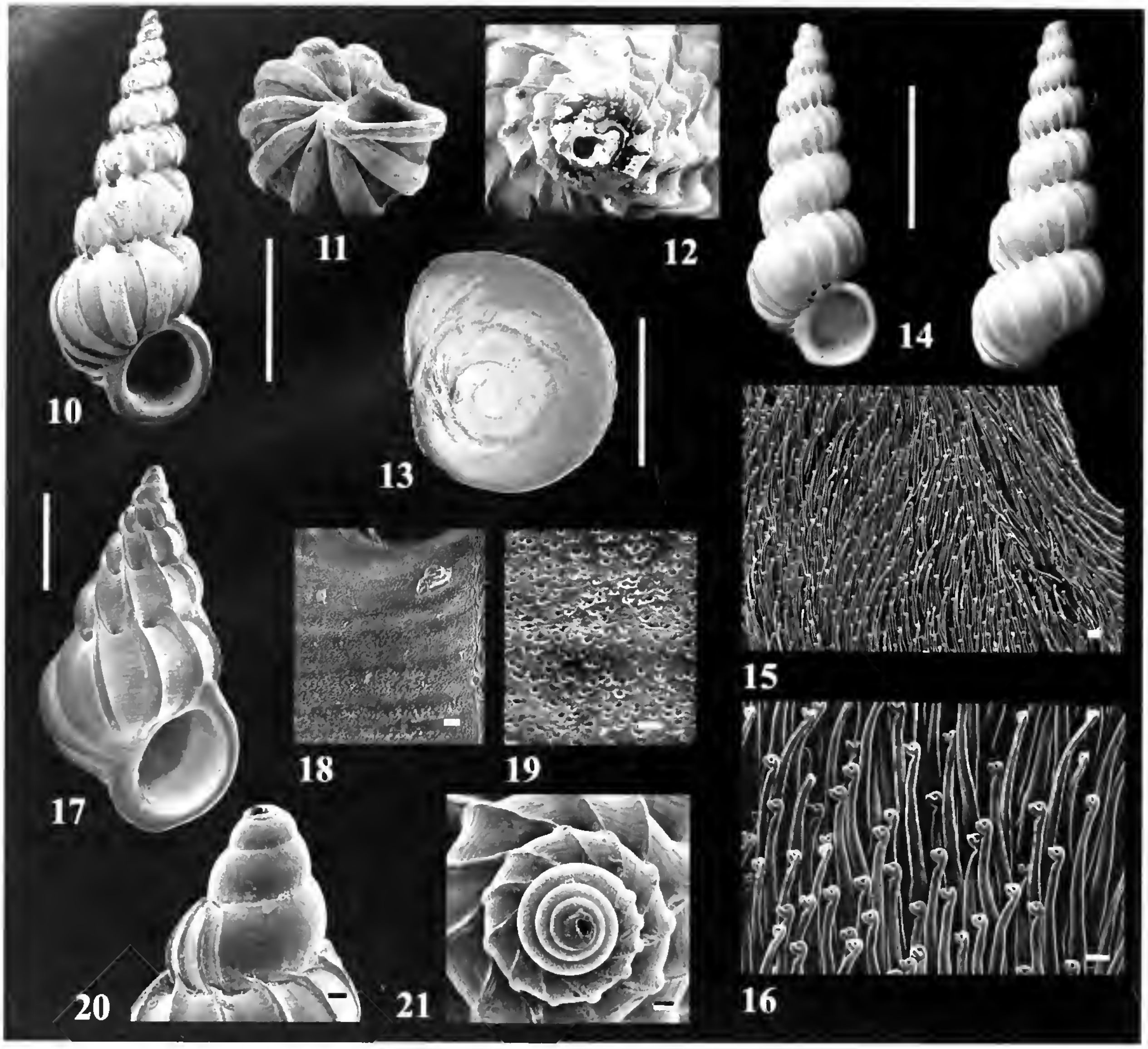
Operculum oval, paucispiral, thin, translucent, brownish, entire surface covered by growth lines.

Radula lacking central and lateral teeth, but with numerous tricuspid marginal teeth, identical in shape. Outermost cusps large and hook-like, central and inner cusps similar in size and shorter. Secondary cusp present centrally on teeth near base.

Egg masses always found near (but not attached to) adults. Egg masses composed of 180–320 egg capsules attached to each other by tough elastic string as in other

Table 1. *Epitonium fabrizioi*. Shell measurements and number of axial ribs per whorl. Numbered column headings refer to whorl number. Dashes indicate worn ribs on that whorl.

Shell No	Length	Width	Teleoconch whorls	1	2	3	4	5	6	7
1	10.92	5.30	5.5	—	—	16	15	15		
2	11.7	5.9	6.5	—	13	13	13	13	14	
3	15.01	6.92	6.5	—	—	14	14	14	15	
4	6.89	3.32	5.5	—	13	13	13	14		
5	13.22	6.07	6.5	—	13	13	13	13	15	
6	12.10	5.85	6.5	—	13	13	13	13	14	
7	8.68	4.45	6	—	—	14	14	14	14	
8	13.05	6.54	6.5	—	—	12	12	13	15	
9	7.89	4.1	6	—	—	12	12	13	14	
10	12.91	6.14	6	—	—	14	14	13	15	
11	12.27	5.56	6	—	13	13	13	13	14	
12	12.57	6.15	6.5	—	14	12	14	14	15	
13	9.18	4.49	6.5	—	13	12	13	13	14	
14	10.66	5.30	7	—	—	—	15	15	15	16
15	9.72	4.92	6.5	—	13	14	14	14	15	
16	11.78	5.76	5.5	—	—	14	13	14		
17	10.94	5.14	5.5	—	—	14	14	15		
18	6.37	3.20	6.5	—	—	—	14	13	14	
19	9.10	4.77	5.5	—	14	14	14	15		
20	10.52	5.01	6.5	—	—	14	14	14	16	
21	10.17	4.95	6.5	—	—	—	14	14	16	
22	9.23	4.54	6.5	—	13	13	13	13	14	
23	8.48	4.57	5.5	—	—	15	15	16		
24	11.50	5.36	6.5	—	—	—	15	15	16	
25	9.96	5.08	7	—	—	—	14	14	17	18



Figures 10–16, 17–21. *Epitonium georgettinum* (Kiener, 1839). **10–12.** Apertural, basal, and apical views. MLP 5404. Puerto Pirámides. Scale bar = 5 mm. **13.** Operculum of a 24.72 mm length specimen. Scale bar = 10 mm. **14.** *Scalaria georgettina*, paralectotype, MHNG 983/111/2, "Ocean Atlantique". Scale bar = 10 mm. **15.** Radula of the specimen shown in Figures 10–12. Scale bar = 20 µm. **16.** Detail of the radula. Scale bar = 10 µm. **17–21.** *Epitonium albidum* (d'Orbigny, 1842). **17, 18.** USNM 439556, Baie Anglaise, Haiti. **17.** Apertural view. Scale bar = 1 mm. **18.** Detail of the shell surface. Scale bar = 10 µm. **19.** Detail of the same area under higher magnification. Scale bar = 2 µm. **20.** Protoconch. Scale bar = 40 µm. **21.** Apical view. Scale bar = 40 µm.

species of same genus. Largest egg capsules examined measured 1.35 × 1.1 mm (n=20; $\bar{x}$ = 1.19 × 0.94; SD = 0.080 × 0.069). Egg capsules pyramidal or polyhedral in shape and covered with sand grains. Number of eggs per capsule ranged 69–141 (n=10, $\bar{x}$=123.9; SD=20.12). Uncleaved eggs measured 76 µm in diameter.

Type locality: Puerto Pirámides, Chubut Province, Argentina (42°34'S, 64°17'W).

Type material: Holotype MLP 5402; 10 paratypes, USNM 880252; 1 paratype, MLP 5333; 4 paratypes, ANSP A18860; 10 paratypes MLP 5403; all from the type locality, G. Pastorino coll., November 1995; MLP 5333, 1 specimen (protoconch), from near Punta Loma, Chubut Province, Argentina, 42°49′S, 64°53′W, J. Mermoz coll., February 1996.

Other material examined: Five specimens, MACN unnumbered, from near Punta Loma, Chubut Province, Argentina, 42°49′S, 64°53′W, J. Mermoz coll., Feb. 1996.

Etymology: Dedicated to Fabrizio Scarabino, young malacologist and friend, who called our attention to the new species.

Table 2. *Epitonium georgettinum* (Kiener). Shell measurements and number of axial ribs per whorl. Numbered column headings refer to whorl number. Dashes indicate worn ribs on that whorl.

Shell No	Length	Width	Teleoconch whorls	1	2	3	4	5	6	7	8	9
1	31.13	10.64	9	—	—	16	16	16	14	13	13	14
2	24.75	8.90	8.5	—	14	13	12	13	12	13	14	
1	26.73	9.72	9.5	—	—	13	15	13	13	12	12	13
4	20.81	8.33	9	—	13	13	12	13	12	12	11	12
5	18.02	6.73	9	—	—	12	12	12	11	10	11	11
6	14.79	5.86	8	—	—	13	12	13	12	12	12	

DISCUSSION

Epitonium georgettinum (Kiener, 1839) is the most similar species to *E. fabrizioi.* It also occurs in the littoral zone in the Puerto Pirámides area, where it lives near sea anemones on hard substrate, but, unlike *E. fabrizioi*, it can also be found on sandy bottom.

The type specimens of *Epitonium georgettinum* (MNHG 983/111/1–3) were illustrated by Clench and Turner (1951, Pl. 117, fig. 1). Figure 14 herein represents one of the paralectotypes (MHNG 983/111/2). The main conchological differences between *E. georgettinum* and the new species is the profile of the shell, which is straighter in *E. georgettinum*, and the whorls, which are more convex and detached in this latter species. The ribs in *E. fabrizioi* are sharper, thinner, and increase in number with growth (Tables 1, 2). *Epitonium georgettinum* has a multispiral, thick, and opaque operculum (Figure 13), whereas that of *E. fabrizioi* is paucispiral, thin, and translucent (Figure 6). The radula of *E. georgettinum* is also distinct. It has one sharp terminal cusp per marginal tooth, and two blunt cusps, one almost obsolete (Figures 15–16).

The eggs and egg capsules of these two species are quite similar (Pastorino and Penchaszadeh, in press). However, based on the material available, *E. fabrizioi* has smaller egg capsules, each containing fewer eggs although egg diameter is nearly identical to that in *E. georgettinum.* Bell (1985) has indicated the larval lifespan and size in *E. ulu* Pilsbry, 1921 (26 days; 3 whorls, 390 µm). The larger number of protoconch whorls and size of *Epitonium fabrizioi* (4.25 whorls, 485×390 µm) suggests that *E. fabrizioi* spends more time than *E. ulu* in the planktotrophic larval stage. In comparison with other known species of *Epitonium*, the new species has the largest protoconch (Table 3).

Epitonium albidum (d'Orbigny, 1842) is similar in shell shape, but its protoconch shows a delicate (visible under SEM) ornamentation that contrasts with that in the new species (Figure 20). In addition, the entire surface of the teleoconch in *E. albidum* shows a characteristic pitted microsculpture (visible under SEM; Figures 18, 19). This character is not typical of the genus *Epitonium* and may support a new generic allocation for *E. georgettinum*, as suggested by Bouchet and Warén (1986) for *E. albidum.* In contrast, *E. fabrizioi* lacks this type of microsculpture. Robertson (1983b) pointed out that Clench and Turner's (1951) Argentinean record of *E. albidum* from Bahia San Blas was zoogeographically anomalous. Their illustration (Clench and Turner, 1951; Plate 114, fig.3) represents a specimen of *E. fabrizioi.*

Kilburn (1985) proposed a subgeneric arrangement for the South African species of Epitoniidae. He did not consider, however, that radular morphology could provide reliable taxonomic characters to his arrangement. If we followed Kilburn's classification, *E. fabrizioi* could be allocated in the subgenus *Hirtoscala* Monterosato, 1890. However, *E. fabrizioi* does not have coronate lamellae and a duplicate peristome that are characteristic of that subgenus.

Including *E. fabrizioi*, there are 5 named species of Epitoniidae living in the Magellanic province. Keen (1971) illustrated 76 Epitoniidae from the tropical eastern Pacific; Kilburn (1985) cited 80 species from southern Africa and Mozambique; Rios (1994) recorded 30

Table 3. Measurements of protoconchs of *Epitonium* species in relation to the adult size (in mm).

Epitonium species	Protoconch Whorls	Adult size	Protoconch size length-width	Source
E. millecostatum	2.7	9.7	0.5	Robertson, 1981
E. equinaticosta	3.5–5	9.5	0.9–0.3	Robertson, 1983a & 1994b
E. albidum	4	8–15	0.4	Robertson, 1983b
E. phymanthi	3.2–3.4	16.9	0.42–0.5	Robertson, 1993
E. worsfoldi	4.1–4.2	25.3	0.52–0.54	Robertson, 1993
E. ulu	3	13	0.39 × 0.30	Bell, 1985
E. fabrizioi	4.25	13	0.48 × 0.39	this paper

from Brazil, while Díaz-Merlano and Puyana-Hegedüs (1994) listed 22 from the Colombian Caribbean. Based on published records of the known distribution of Epitoniidae this family is more speciose in tropical than in temperate and cold regions.

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Special thanks are due to J. Mermoz, who provided specimens of *Epitonium* from Punta Loma. Yves Finet, Muséum d'Histoire naturelle de Genève, Switzerland, kindly sent photographs of the paralectotype of *Epitonium georgettinum*. M. G. Harasewych, National Museum of Natural History, Smithsonian Institution, gave good advice on early stages of the manuscript. Two reviewers improved considerably the original manuscript. This work was made possible by an external fellowship granted by the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina, to G. P. and a grant from Fundación Antorchas, Argentina to P. P.

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Two New Species of *Periploma* (Bivalvia: Anomalodesmata: Periplomatidae) from the Southern Caribbean

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ABSTRACT

Periploma coseli new species and *P. sanctamarthaensis* new species are described from near Santa Marta, Caribbean coast of Colombia. The overall shape of the shell, the outline of the pallial sinus and the shape and/or orientation of the resilifer are the main features distinguishing the two new taxa from each other, and from other congeneric species from the western Atlantic, eastern Atlantic, or eastern Pacific regions.

Key words: Santa Marta, Colombia, Caribbean Sea, western Atlantic, eastern Pacific, eastern Atlantic, Thracioidea.

INTRODUCTION

The family Periplomatidae (Anomalodesmata: Thracioidea) is a relatively small taxon consisting of about 30 living recognized species arranged in 7 genera (see Rosewater, 1968; Bernard, 1989). The group is best represented in the eastern Pacific and the western Atlantic regions. Notwithstanding, only 2 species were found so far in the Caribbean Sea, both belonging to the genus *Periploma* (*s.s.*) Schumacher, 1817: *P. margaritaceum* (Lamarck, 1801) and *P. coquettae* Altena, 1968. In addition to these 2 taxa, 2 other unnamed species of the genus have been collected along the Caribbean coast of Colombia. Cosel (1978, 1986) and Díaz (1985, 1990), who studied the molluscan fauna from different localities of the Colombian coast, first noticed the occurrence of these unnamed *Periploma*. Further material of one of these species has become available to the authors in recent years through intensive collecting near Santa Marta. They are herewith described as new species. Institutional abbreviations are: BMSM, The Bailey-Matthews Shell Museum, Sanibel, Florida; INVEMAR MOL, Collection of Mollusks, Instituto de Investigaciones Marinas y Costeras, Santa Marta, Colombia; SMF, Senckenberg Museum Frankfurt, Germany.

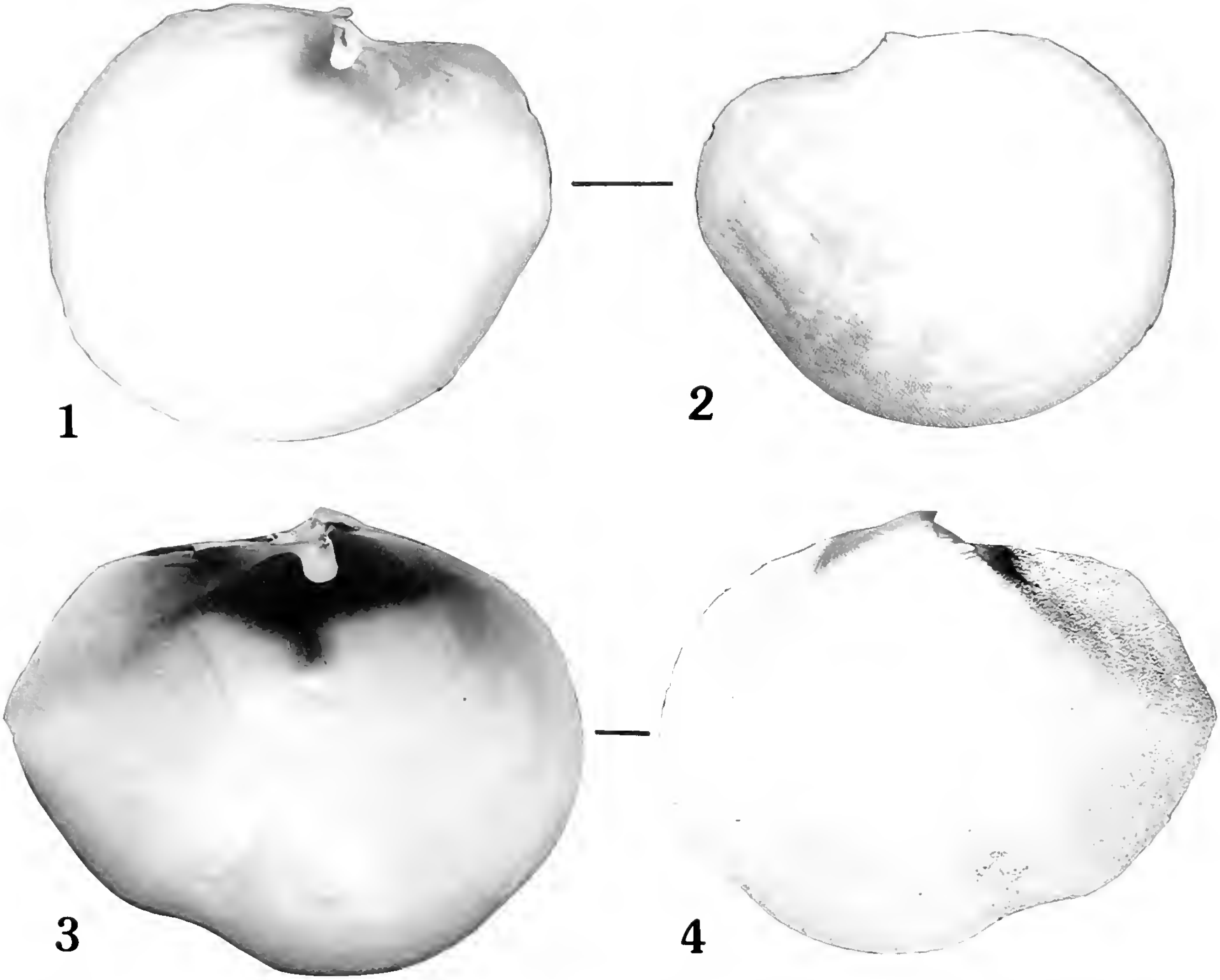
SYSTEMATICS

Class Bivalvia Linnaeus, 1758
Subclass Anomalodesmata Dall, 1889
Superfamily Thracioidea E.A. Smith, 1885
Family Periplomatidae Dall, 1895
Genus *Periploma* Schumacher, 1817
Periploma (*Periploma*) *coseli* new species
(Figures 1, 2, 5)

Periploma spec.—Cosel, 1978:161, pl. 4, figs. 12,13.
Periploma spec. II.—Díaz, 1985:84, erroneously figured in pl.12, fig.1
Periploma sp.—Cosel, 1986: 199, fig. 113.
Periploma sp. 1.—Díaz & Puyana, 1994:104, pl.31, fig. 303

Description: Shell medium-sized (length up to 29.3 mm), subcircular-oval, very thin and fragile, moderately convex, antero-ventral margin evenly circular, posterior margin somewhat projected upward and subtruncate. Subequilateral, anterior end slightly larger, beaks with characteristic transversal slit. Outer surface white, with irregular growth lines and numerous, extremely fine, irregular radial striae more apparent in the central area. Periostracum dirty gray, with comarginal rows of microscopic granules. Inner surface weakly nacreous, smooth but with weak impressions of growth lines. Pallial sinus broad and short, reaching to about 1/3 of shell length. Ligament internal; resilifer conspicuous, spoon-shaped, directed vertically toward center of valve and weakly reinforced at its basis by curved buttress pointing to posterior muscle scar.

Type material: Holotype, SMF 311857, complete shell (left valve slightly broken), 29.3×25.2 mm (length×height), trawled by R/V *Ancón* at type locality, C.P. Arango coll. September 1995. Paratypes: INVEMAR MOL-1151, 1 complete shell (left valve fractured near midline), 24.8×20.0 mm, Golfo de Salamanca, Colombia, 11°07′N, 74°20′W, trawled by R/V *Ancón*, 59 m, muddy sand, C.P. Arango coll. September 1995; INVEMAR MOL 1152, 1 complete shell (left valve damaged), 10.5×8.5 mm and BMSM 2361, 10.9×8.8 mm, 1 complete shell (left valve damaged), off mouth of Toribio



Figures 1–4. **1–2,** *Periploma coseli.* Holotype, right valve, 29.3 mm length, 25.2 mm height. **3–4,** *Periploma sanctamarthaensis.* Holotype, left valve, 21.9 mm length, 17.5 mm height.

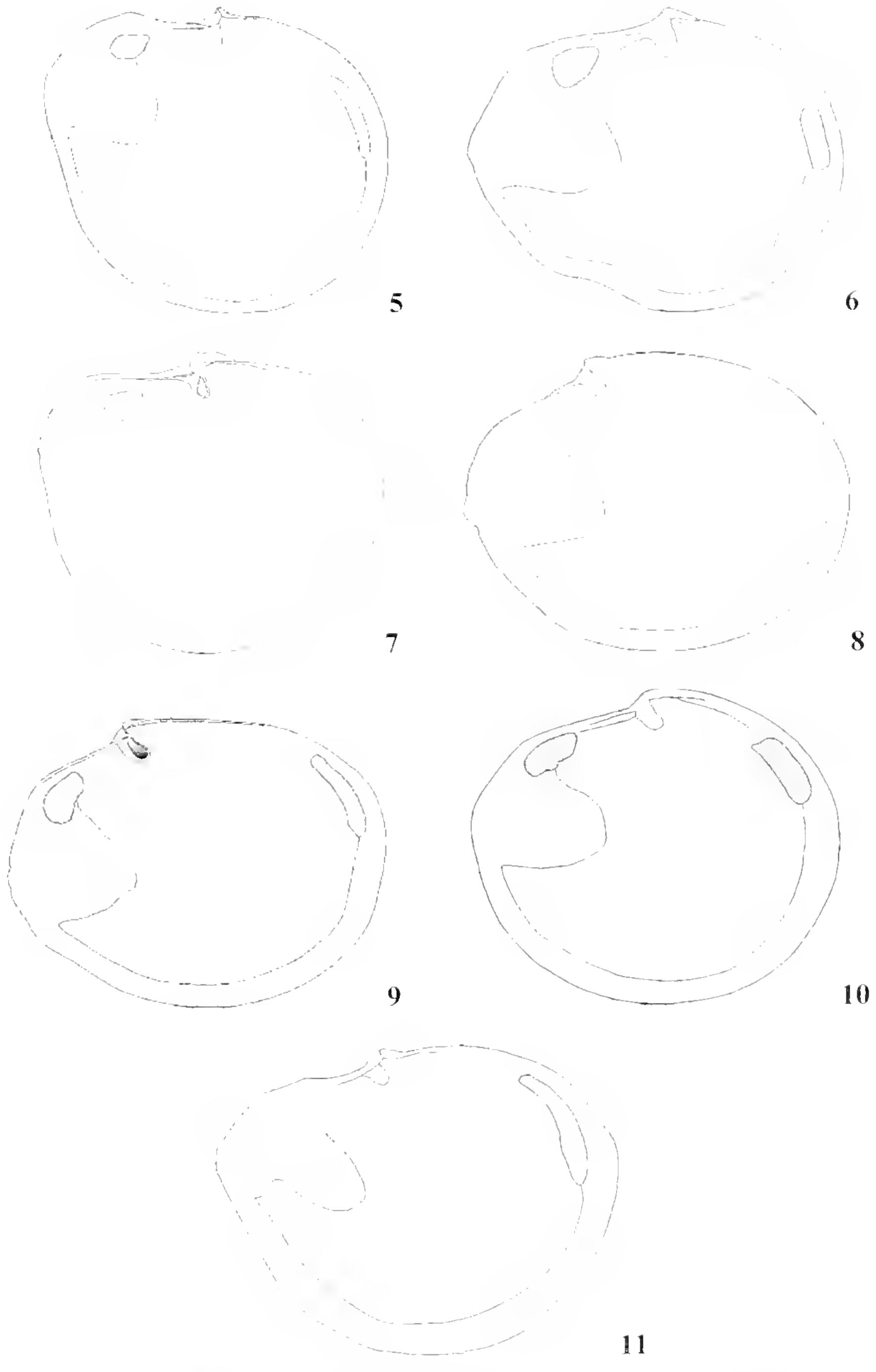
river, 11°04′N, 74°15′W, taken by bottom grab, 6 m, mud, N. Ardila coll. October 1996; BMSM 2360, 1 complete shell, 16.8×14.2 mm, off mouth of Toribio River, 11°04′N, 74°15′W, bottom grab, 6 m, mud, N. Ardila coll. January 1998.

Type locality: Golfo de Salamanca, Colombia, 11°11′N, 74°15′W, 59 m, muddy sand.

Etymology: Named after Rudo von Cosel, who first noticed the existence of this species in his comprehensive study of the molluscan fauna of the Caribbean coast of Colombia.

Remarks: *Periploma coseli* new species is similar to *P. discus* Stearns, 1890, from the eastern Pacific, and to *P. camerunensis* Cosel, 1995, from off west Africa. The postero-dorsal margin of *P. discus* is almost straight (somewhat projected dorsally in *P. coseli*), and its posterior margin more angulate (broadly rounded in the new species) (compare figures 5 and 7). *Periploma camerunensis* exhibits a somewhat more elongated shell, with the umbones situated posteriorly to the vertical midline. In addition, the resilifer in *P. camerunensis* is projected obliquely, in relation to the hinge line and toward the antero-ventral margin, whereas it is almost perpendicular in relation to the hinge line in *P. coseli* (compare Figures 5 and 8). These 3 species may be regarded as members of a group of similar taxa that show Recent disjunct distribution. Isolation of eastern Pacific and eastern Atlantic ancestral populations could have occurred respectively after establishment of a continuous Isthmus of Panama and a full-fledged mid-Atlantic oceanic barrier. Absence of planktotrophic development in the genus *Periploma* (see Goodsell *et al.* 1983) may have facilitated isolation and subsequent speciation.

P. coquettae Altena, 1968 from the northern and



Figures 5–11. Diagrams of the inner surfaces of left valves of several species of *Periploma*. **5.** *P. coseli* Holotype. **6.** *P. sanctamarthaensis* Holotype. **7.** *P. discus* Stearns, 1890, redrawn from Keen (1971 fig. 750). **8.** *P. camerunensis* Cosel, 1995. Holotype redrawn from Cosel (1995 fig. 144). **9.** *P. coquettae* Altena, 1967. Holotype redrawn from Altena (1967 fig.147a). **10.** *P. planiusculum* Sowerby, 1834, redrawn from Keen (1971 fig. 752). **11.** *P. lagartilla* Olsson, 1961. Holotype redrawn from Olsson (1961 pl. 82, fig. 5b).

northeastern coasts of South America (off Suriname and Colombia), is another vaguely similar species, but it has definitely a more elongated and inequilateral shell (compare Figures 5 and 9).

P. coseli seems to be widely distributed along the Caribbean coast of Colombia. Cosel (1986) recorded this species as "*Periploma* spec." from off Punta Broqueles (approximately 9°20′N, 76°15′W) and the Santa Marta Bay, and Díaz (1990) found it also as north as Portete Bay (12°18′N, 71°55′W).

Periploma (Periploma) sanctamarthaensis new species (Figures 3, 4, 6)

Periploma spec. 1.—Díaz, 1985:84, pl. 12, fig. 2.
Periploma sp. 2.—Díaz & Puyana, 1994:104, pl.32, fig. 304

Description: Shell medium-sized (length to 22 mm), semicircular-oval, equilateral, convex, very fragile; antero-ventral margin semicircular; posterior margin subtruncate, postero-dorsal margin straight. Beaks with a characteristic transversal slit. Outer surface milky white, with irregular growth lines, some of which appear as shallow grooves under magnification. Radial ridge runs from beaks to postero-ventral margin. Periostracum yellowish-gray, with numerous microscopic granules which are arranged comarginally and are more abundant within growth lines and posterior slope. Inner surface dirty-white and weakly nacreous, showing impressions of irregularities on outer surface. Pallial sinus broadly triangular in outline and rather deep, reaching to about ½ of shell length. Ligament internal, in well-defined, squarish resilifer. Resilifer oblique in relation to hinge line, oriented toward ventral margin.

Type material: Holotype, SMF 311858, 21.9×17.5 mm (length×height), 1 left valve, from type locality, SCUBA, J.M. Diaz coll. February1983; Paratype, INVEMAR MOL 1153, 13.4×11.3 mm, 1 right valve (broken in two pieces after measurements), from type locality, SCUBA, J.M. Diaz coll. February 1983.

Type locality: Bahia Nenguange, Tayrona Natural National Park, Colombia, 11°20′N, 74°05′W, 7 m, coarse coralline sand with broken shells.

Etymology: The species is named after the city of Santa Marta, near which the Tayrona National Natural Park, the type locality, is located.

Remarks: The shell of *Periploma sanctamarthaensis* differs from that of *P. coseli* in being smaller and more inflated. In addition, the outline of the antero-ventral margin is gently rounded, has a straight postero-dorsal margin that does is not projected dorsally, and a radial ridge running obliquely along the postero-ventral slope. Additional differences between these species do exist in the outline of the pallial sinus and the shape of the resilifer (compare Figures 5 and 6).

Periploma planiusculum Sowerby, 1834, from the eastern Pacific, has a larger and more elongated shell with a short, rounded pallial sinus (broadly triangular in *P. sanctamarthaensis*) (compare Figures 6 and 10). *Periploma lagartilla* Olsson, 1961, from the Pacific coast of Panama, is also more elongated, and exhibits a rather pointed posterior margin and a short and narrow pallial sinus (compare Figures 6 and 11).

P. sanctamarthaensis new species is so far known only from the type locality.

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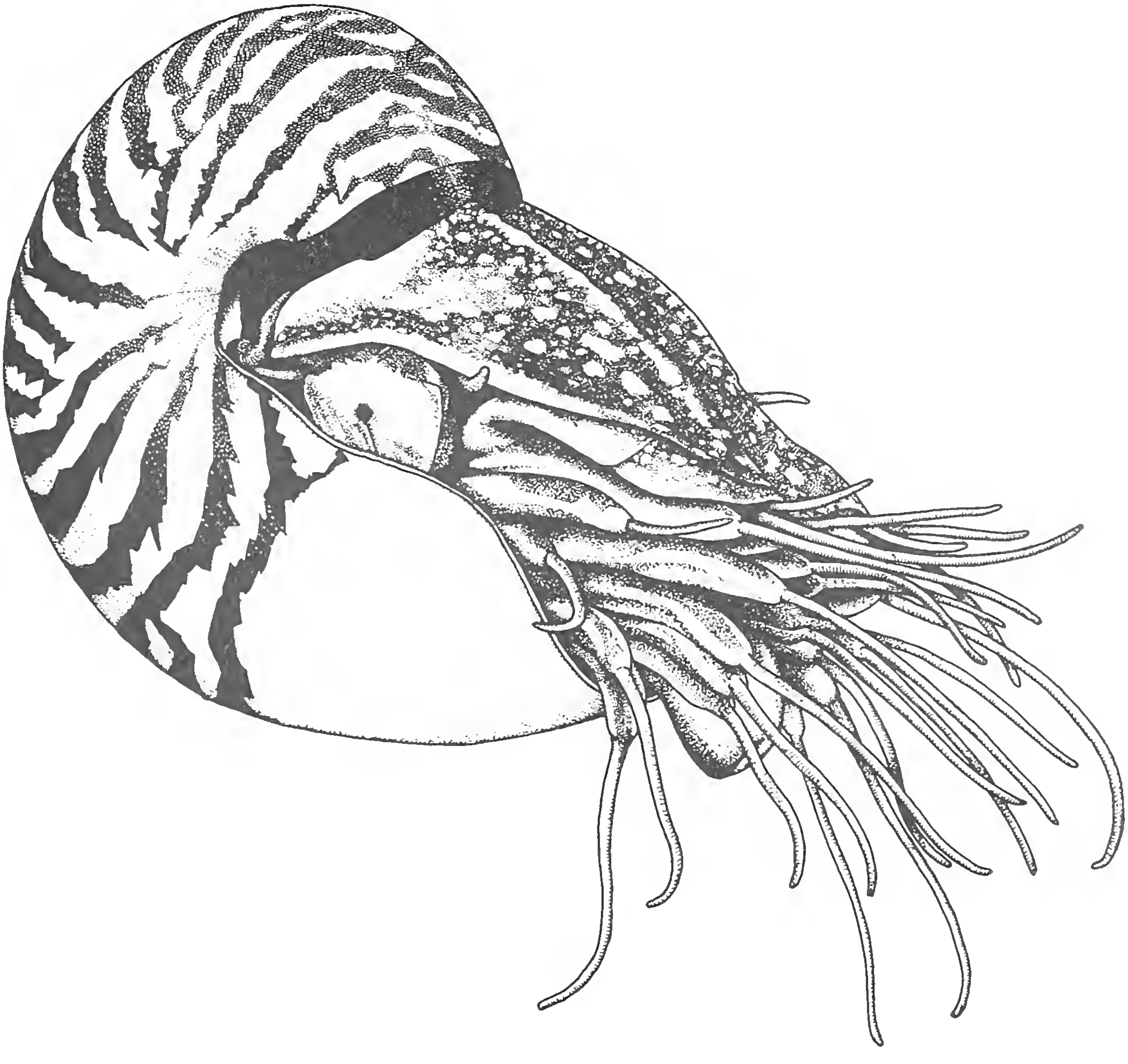

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Learning from the Collector: A Survey of Azooxanthellate Corals Affixed by *Xenophora* (Gastropoda: Xenophoridae), with an Analysis and Discussion of Attachment Patterns

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ABSTRACT

All species of the gastropod family Xenophoridae affix foreign objects to the upper shell surface. Affixed objects may include bivalve shells, smaller gastropod shells, shell fragments, and coral skeletons, as well as a wide array of inorganic material. In deep water, *Xenophora* may serve as useful proxy collectors of benthic organisms. Since 1842, coral skeletons have been noted among the attached objects, but this association has never been studied in detail. This paper surveys 227 *Xenophora* shells, comprising 8 species from 69 stations, for affixed azooxanthellate corals. Five hundred and eighty-one coralla were found, representing 74 coral species, 2 of which remain undescribed. Twenty-four of the affixed coralla were alive at the time the *Xenophora* hosts were collected; *Xenophora* not only collect live corals, but corals can remain alive long after being affixed. Corals were found at 6 sites where they had previously been unknown, and the geographic ranges of 29 species of coral were expanded as a result of specimens found on *Xenophora*.

This paper has two sections. In the first, quantitative observations were made on the orientation of affixed corals; statistical analysis of these observations revealed non-random patterns of attachment, based on orientation of both the long axis of the coral and the coral calice. Qualitative observations suggest that species of *Xenophora* favor corals of particular shapes. In the second section, the speculations of previous authors regarding the ecological basis for attachment behavior are summarized and new theories are discussed. Four of these explanations suggest defensive adaptations, and the remaining 3 are functional support adaptations. Three of these hypotheses (armor, tactile camouflage, and snowshoeing) are proposed for the first time in this paper.

Key words: Carrier shells, Mollusca, gastropods, ahermatypic corals.

INTRODUCTION

According to Ponder (1983), the monotypic gastropod family Xenophoridae contains 25 Recent species of *Xenophora*, marine gastropods that inhabit the continental shelf and slope regions of tropical and temperate oceans. *Xenophora* have drawn the attention of naturalists and systematists since the early 1800s. This was caused primarily because of a peculiar behavioral pattern: all species affix objects to the upper surface of the shell throughout some or all of its growth (see Shank, 1969 for a detailed description of the affixing procedure in *X. conchyliophora* (Born, 1780)). Although objects are only affixed at the growing edge of the whorl, older attachments remain on the perimeter of earlier whorls as the shell increases in size. Older attachments often become secondarily affixed to the younger whorl that is formed beneath them. One of the traits used to distinguish species of *Xenophora* is the degree to which the shell surface is obscured by attachments (Ponder, 1983).

A great diversity of material has been found affixed to *Xenophora*: among the objects we observed in the course of this study were coral skeletons, bivalve and other mollusk shells, brachiopod shells, echinoderm spines and skeletal fragments, bryozoans, sponges, sharks' teeth, and a wide assortment of inorganic fragments.

Although corals typically comprise less than 10% of the affixed objects, their presence on *Xenophora* shells was first recorded a century and a half ago (Reeve, 1842). Pourtalès (1871) was the first to report a deep-sea (azooxanthellate) coral, *Caryophyllia cornuformis* Pourtalès, affixed to a *Xenophora* shell, collected from the Straits of Florida at 433–454 m. In this case, the coral remained alive after attachment. Morton (1958) listed living, solitary flabellid corals affixed to *X. corrugata* (Reeve, 1843) from New Zealand, and Kawase (1996) identified 4 species of azooxanthellate corals on *X. pallidula* (Reeve, 1842) from Japanese waters. Cairns (in press) reported 19 azooxanthellate species affixed to xenophorid shells collected from the slope region of

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Vanuatu (=New Hebrides) (Figure 6), prompting the research presented here. In summary, there have been several published observations of deep-water corals affixed to *Xenophora*, but no comprehensive review of the association.

Xenophora are not highly mobile (Berg, 1975). It is therefore possible for one to learn something about the benthic fauna of a particular region by examining the local *Xenophora*. Although some species are found only in shallow water, most *Xenophora* inhabit regions well below the penetration depth of photosynthetically active radiation, and specimens have been dredged from depths exceeding 1000 m (Ponder, 1983). Because relatively little is known about the deep-water benthos, deep-dwelling *Xenophora* are potentially useful as proxy collectors.

In the process of examining *Xenophora* shells for affixed corals, we noticed that there appeared to be some regularity in orientation of affixed objects with respect to the shell. These apparent trends, in the context of the previously documented observation that *Xenophora* attach lamellibranch valves with the concave side up (Ponder, 1983; Morton, 1958; Linsley and Yochelson, 1973; Shank, 1969), led us to look for statistical patterns in the manner and orientation of coral attachment. The results of that analysis are presented in this report.

MATERIAL AND METHODS

Two hundred and twenty-seven coral-bearing *Xenophora* shells were examined: 145 of these are from the collections of the National Museum of Natural History (USNM), Washington, DC; 42 from the Muséum national d'Histoire naturelle (MNHN), Paris; 38 from the Delaware Museum of Natural History (DMNH), Wilmington; and 2 from the Museum of Comparative Zoology (MCZ), Cambridge. Appendix I lists the stations at which coral-bearing *Xenophora* were collected, the station data, and the coral species collected at those stations. The study material includes shells collected throughout the Indo-West Pacific, Hawaiian Islands, and the Gulf of Guinea. Eight coral-bearing species of *Xenophora* were examined, a large majority of the specimens (166/227, including all shells borrowed from the MNHN and DMNH) belonging to the species *X. pallidula*. The other 7 species, in order of abundance were: *X. japonica* Kuroda and Habe, 1971, *X. peroniana kondoi* Ponder, 1983, *X. corrugata*, *X. cerea* (Reeve, 1845), *X. neozealanica* Suter, *X. crispa* (König, 1831), and *X. granulosa* Ponder, 1983. The 145 USNM specimens included all coral-bearing shells in the USNM collections, with the exception of those belonging to *X. conchyliophora*, which is typically found in shallow water (Ponder, 1983), and certain lots of *X. peroniana* and *X. japonica*, which preliminary examination showed to be redundant in terms of sites sampled and corals collected.

When possible, corals were identified to the species level; when only a coral fragment or badly eroded or damaged corallum was present, it was identified to the lowest possible taxonomic level (typically genus). Undescribed species were designated by a letter. If a well-preserved but unidentifiable phenotype appeared repeatedly, it was given the designation n. sp. Any corallum that contained remnants of dried coral tissue or was exceptionally well preserved was considered to have been alive when the *Xenophora* was collected.

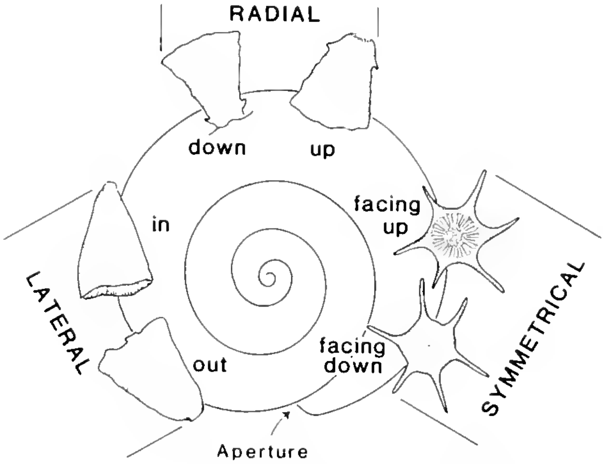


Figure 1. Diagram of the apical view of a *Xenophora* shell, illustrating the various types of orientations in which a solitary coral may be affixed: radial (up, down), lateral (out, in), and symmetrical (facing up, facing down). Note: Number of apical whorls underrepresented in figure.

Every coral found was classified as a primary or secondary attachment. Primary attachments were those that were embedded in the shell and had clearly been affixed by the *Xenophora*; secondary attachments included those corals growing on a substrate which was subsequently affixed to the *Xenophora* and those that settled upon the surface through no action of the *Xenophora*. The length of the long axis (maximum dimension, regardless of the orientation of morphological features) of each coral skeleton was recorded. The orientation of the long axis was classified as radial, meaning roughly perpendicular to the arc of the whorl; lateral, meaning roughly parallel to the arc of the whorl; or symmetrical, meaning that all axes of the coral were equal. The orientation of the calice (Figure 1) was also noted as being: up or down (a subset of radial orientation), in or out (a subset of lateral orientation) or facing up or facing down (a subset of symmetrical orientation). We applied statistical hypothesis testing (chi-square test) to the orientation data, using as our null hypothesis the assumption that each type of orientation would have the same chance of occurring.

We measured each *Xenophora* shell across the shell base, and took the maximum diameter as a proxy for shell size. For selected *X. pallidula*, we measured the diameter of each whorl, both with and without attachments. Using a circular approximation for area, we calculated the ratio of shell basal area (radius measured, not including attachments) to expanded shell basal area

Table 1. Numerical distribution of azooxanthellate scleractinian genera, species, and individuals per families of coral-bearing *Xenophora*.

Family	Genera	Species	Individuals
Pocilloporidae	1	0	1
Fungiacyathidae	1	2	3
Micrabaciidae	1	1	3
Oculinidae	1	1	3
Anthemiphylliidae	1	3	9
Caryophylliidae	8	34	181
Turbinoliidae	5	5	6
Flabellidae	5	21	241
Gardineriidae	1	1	7
Guyniidae	2	2	4
Dendrophylliidae	3	4	56
Unidentifiable to genus	—	—	67
TOTALS:	29	74	581

(radius measured, including attachments) for each shell whorl. These ratios were analyzed for statistical trends; Pearson product-moment correlation coefficients and the respective tests of significance were computed with the aid of Statview SE statistical software. For selected *Xenophora solaris* (Linnaeus), we counted the number of spines per whorl and analyzed these data for any trends, again using Statview SE.

Lists of coral species previously reported were available for 2 series of stations (*Albatross* Expedition, Cairns and Zibrowius (1997); MUSORSTOM 8 Expedition (Cairns, in press)). We compared the list for each station with the corals that we found affixed to the *Xenophora* at that site, and noted any instances of affixed corals not previously known from that location, as well as which corals were potentially available for fixation but were not affixed.

RESULTS

A total of 581 azooxanthellate coralla were found affixed to *Xenophora* shells, 511 of which were identifiable to genus, and 411 to species. The affixed coral fauna represents a diverse taxonomic distribution, including species from all 5 suborders in 11 families, 29 genera, and 74 species. The only zooxanthellate coral species encountered was *Fungia (Cycloseris) vaughani*, found on *X. peroniana* from the Hawaiian Islands. Table 1 shows the numerical distribution of genera, species, and individuals among families of corals and the *Xenophora* species that affixed them. A taxonomic list of all azooxanthellate coral species is included in Appendix 2.

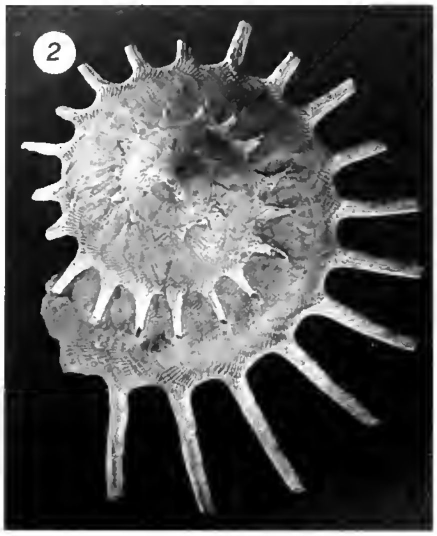
Sixty-seven of the 74 species were recognizable as described species of Scleractinia. Of the remaining 7, 5 (designated as sp. A or sp. B) are represented by single specimens and may be aberrant examples of described species. The remaining 2 are considered undescribed species. One of the undescribed species had previously been observed in dredged samples from the same region, and illustrated by Stolarski (1996) as "Gardineriidae gen. n." Seven well-preserved specimens of this taxon were found on 3 *X. pallidula* shells from MUSORSTOM stations 1008 (Figures 8–9), 1087, and 1088 off the coast of Vanuatu (=New Hebrides). The second undescribed species belongs to the genus *Placotrochides* and is represented by 4 specimens affixed to 2 *X. peroniana* shells from 2 stations in the Hawaiian Islands. The genus *Placotrochides* had not previously been collected near the Hawaiian Islands, and no other truncate flabellids (transversely dividing members of the family Flabellidae) are known from the area. Even though none of the specimens of *Placotrochides* n. sp. is particularly well preserved (Figure 10), they are clearly not members of other described *Placotrochides* species.

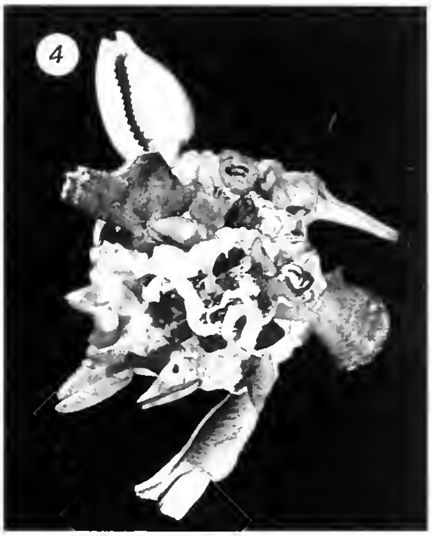
Large specimens of *Truncatoflabellum gardineri* Cairns and Keller proved to be new size records for that species. The previously listed maximum length for *T. gardineri* was 18.7 mm. We discovered 8 specimens larger than that, the largest (USNM M818232) measuring 27.5 mm from base to calice (Figure 7).

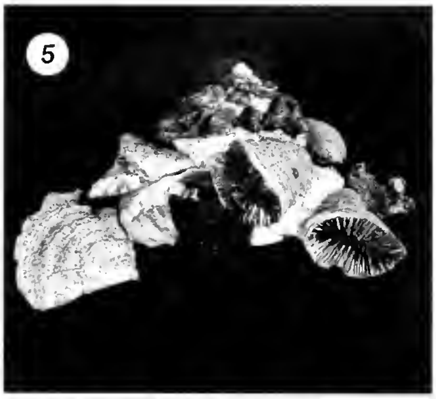
Xenophora frequently collected corals that were not previously known from their source station: in 74 instances, a coral species found affixed to *Xenophora* from a given site had not previously been found at that site. These discoveries expanded the known geographic ranges of 29 coral species. Coral-bearing *Xenophora* were also found at 6 sites (*Albatross* 5121, 5394, 5395, 5416, 5661; MUSORSTOM 8–1008) where dredging had not previously produced any corals at all.

There are definite patterns in the orientation of affixed corals. Seventy-two percent, 359 of 498 non-symmetric coralla, were positioned with the long axis radial rather than lateral (Figure 1); occurrence of such a high percentage of radially oriented coralla is extremely unlikely ($p \ll 0.01$) if *Xenophora* affix corals at random, without regard to orientation of the long axis. Calice orientation was also distinctly non-random. The down and out orientations were encountered significantly more times than it would have been if *Xenophora* ignored calice orientation ($p \ll 0.01$), whereas the up and in orientations were encountered significantly fewer times. Certain shape classes were attached in a specific manner: conical corals were typically oriented radially with the calice in the down position (Figures 1, 4), whereas flabellids were typically oriented laterally with the calice in the out position (Figures 1, 3, 5). Symmetrical flat corals were found (with only 1 exception among 92 flat corals) with the calice facing up (i.e., with the base cemented to the shell).

Early observations led us to hypothesize that *Xenophora* select objects preferentially based on shape. The shells from MNHN frequently collected *Bourneotrochus stellulatus* Cairns, a small, coin-shaped, spinose coral, but none of these morphological traits appeared in significant numbers at other regions or in other collections. By contrast, we noted a high frequency of attachment for both flabellate and cornute coralla at widely distributed sites. It is difficult, however, to test these frequen-







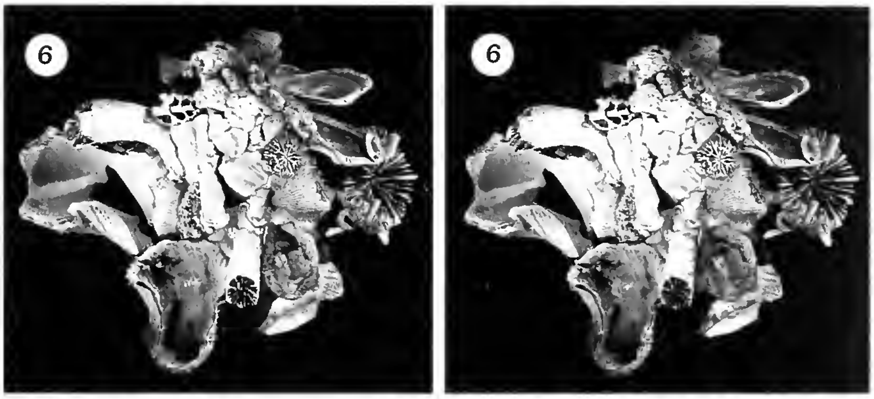


Figure 2. *Xenophora solaris* from Maqueda Bay, Philippines (DMNH 5173), apical view, × 0.82. **Figures 3, 5.** *X. pallidula* from off Zululand (DMNH 20120), apical and lateral views showing live *Truncatoflabellum gardineri* affixed in the in and out lateral positions, × 0.75, × 0.58, respectively. **Figure 4.** *X. pallidula* from Sulu Sea (W498; USNM M807763), showing two live coralla of *Trochocyathus cooperi* affixed in the radial (down) position. **Figure 6.** Stereo apical view of *X. pallidula* from MUSORSTOM 8-963 (MNHN), illustrating a heavily (encrusted) shell with 6 species of solitary coral. **Figure 7.** Largest known (length 27.5 mm) corallum of *Truncatoflabellum gardineri* affixed to *X. pallidula* from off Durban (W320) (USNM M818232), × 1.4. **Figures 8–9.** Coralla of the family Gardineriidae n. gen. n. sp. affixed to *X. pallidula* from MUSORSTOM 8-1008 (MNHN), figure 9 showing rejuvenescence (from presumed growth trauma scar) following fixation, × 2.8, × 6.5, respectively. **Figure 10.** Corallum of *Placotrochides* n. sp. affixed to *X. peroniana* from *David Starr Jordan* TC32-2 (USNM M807659), × 7.1.

cies for statistical significance, as each *Xenophora* has a different range of shapes available, and it would be necessary to know if the frequencies of attachment were significantly different from the frequencies at which the various shapes occur unattached. The latter figures are not available due to lack of data.

A small number of affixed corals (24 specimens, approximately 4%) were alive at the time their *Xenophora* hosts were collected. Only 3 of these were secondary attachments, allowing us to confirm that *Xenophora* actively affix living corals, if only at a low frequency. Living corals were often affixed to earlier whorls, and typically bore a visible growth-trauma scar on the theca (outer surface). The presence of live-at-collection corals on earlier whorls indicates that corals may survive after attachment, and a growth-trauma scar (Figure 9) suggests that they also continue to grow. Relative frequencies of "live" and "dead" corals on *Xenophora* shells cannot, unfortunately, be compared with relative frequencies of living corals and coral skeletons *in situ* because the latter figures are unknown. It is therefore impossible at this time to state whether *Xenophora* preferentially selects or avoids living corals, although the small number of living corals suggests that it is unlikely that live specimens are preferred.

DISCUSSION

DESCRIPTIVE DATA

The examination of 227 *Xenophora* shells brought to light 2 undescribed species of coral, increased the size range for one described species, and extended the geographic ranges for 29. Had the shells been examined immediately upon collection, the results would have been even more impressive: 215 of the 581 coralla were found on *Xenophora* collected by the *Albatross* cruises before 1910, at which time 24 of the collected species (32%) were undescribed.

Admittedly, *Xenophora*-based sampling has limitations. There was not a single case in which we found every coral known to exist at a given site (i.e., at a station where coral was previously recorded) affixed to *Xenophora* shells. Altogether, 41 species of coral known to co-occur with *Xenophora* were not affixed by the gastropod. This may be an artifact of the small number of *Xenophora* typically known from each site, but, given the broad expanse of the benthic plain and the unknown population densities of *Xenophora*, samples are likely to remain small. Many of the non-collected coral species were only passed over 1 time (i.e., were only present at 1 *Xenophora* source station where they were not affixed). This single occurrence makes their omission statistically negligible, but others were conspicuously absent from *Xenophora* shells, suggesting that there are groups within azooxanthellate Scleractinia which *Xenophora* does not affix. The reasons behind this are often clear: for example, *Xenophora* is unlikely to affix any coral that settles and anchors firmly onto hard substrate. Similarly, colonial corals are typically too bulky and irregular to be affixed. There is a strong possibility of a selection mechanism in *Xenophora* that causes them to choose certain more suitably shaped corals over others.

Still, it is difficult to dispute the usefulness of *Xenophora* as proxy-collectors. Examination of any *Xenophora* collected in a dredge sample may reveal attached species that were not otherwise collected in that sample. Because blind dredging is still the most common method for sampling the benthos, any method that complements or makes more complete use of the dredged sample should not be overlooked.

ATTACHMENT BEHAVIOR

Introduction: Arthur Adams (1848:248), the naturalist and assistant-surgeon on board the H.M.S. *Samarang*, observed *Xenophora* (species unknown) during an 1842 voyage from Singapore to Java. Adams remarked: "In order for them to escape from their enemies, nature has instructed them to cover their shells with the same material as those of the banks which they inhabit." Adams' rationale is understandable. Many people, both shell-collectors and scientists, have made the same assumption about *Xenophora*. In the modern era of deep-sea exploration, however, it is unreasonable to accept the visual camouflage hypothesis for those species of *Xenophora* that live below the depth of light penetration.

Although many of the frequently attaching species can be found in relatively shallow water, 2 of the most spectacularly encrusted species (*X. pallidula* and *X. japonica*) range deeper than their congeners (Ponder, 1983). Object attachment is an energetically expensive behavior (Shank, 1969). For *Xenophora* to attach an object to the growing edge of the shell it must first select and properly position the object (see Shank, 1969), and then affix it by secreting shell material around it, using more calcium carbonate than would be required to secrete an equivalent section of shell. Given that members of the family Xenophoridae are found in the fossil record as far back as the Cretaceous, it is unlikely that such an energetically expensive behavior would persist if it was purely non-adaptive.

A number of hypotheses have been suggested to explain attachment behavior. These fall into 2 broad, mechanistic categories: defense and functional support. Table 2 lists the various hypotheses and the authors that have supported them in the past. It is rare for any author to cite just one hypothesis, but no recent efforts have been made to collect and review all the hypotheses, although Linsley and Yochelson (1973) and St. Jean (1977, 1983) provided the most comprehensive review previous to this report.

Defense Theories: Most authors still regard camouflage as the most likely explanation for object fixation by *Xenophora*. Camouflage usually implies *visual concealment*, but in the case of deep-water *Xenophora*, it must be expanded to include *olfactory concealment* as well. Shank (1969: 5), one of the few people to maintain *Xen*-

Table 2. Outline of possible adaptive advantages of attachment behavior in *Xenophora*, and those authors who have discussed those views.

I. Defensive
  A. Camouflage
    1 Visual (Adams, 1848; Morton, 1958; Shank, 1969; Linsley and Yochelson, 1973; Berg, 1975; St. Jean, 1977, and 1983; Das, et al., 1981; Ponder, 1983)
    2. Olfactory (Shank, 1969, Linsley and Yochelson, 1973; St. Jean, 1977, 1983; Ponder, 1983)
    3. Tactile
  B. Armor Hypothesis
II. Functional Support
  A. Snowshoeing
  B. Increased Shell Stability (Berg, 1975; St. Jean, 1983)
  C. Feeding Cone Hypothesis (Shank, 1969; Linsley and Yochelson, 1973; Berg, 1975; St. Jean, 1977, 1983)

ophora alive in aquaria for any length of time, remarked that "everything [*Xenophora*] do points to a means of eluding detection." While observing captive specimens of *Xenophora conchyliophora*, a species typically found in shallower water, Shank witnessed the animals burying their feces, a behavioral trait generally associated with predator evasion (Shank, 1969; Linsley and Yochelson, 1973). Shank and others have also observed that the peculiar and discontinuous motion of *Xenophora* would be less likely to attract the attention of a predator, and might create less of a chemical trail than the "crawling" movement of many gastropods (Shank, 1969; Linsley and Yochelson, 1973; St. Jean, 1977, 1983).

These observations are of value for understanding the ecology of a shallow-water species of *Xenophora*, but may not be generalizable to all species in the family. Linsley and Yochelson (1973) observed (Linsley's observations) live *X. neozealanica* for several months and did not witness the feces-burying behavior recorded by Shank. Additionally, they noted that, despite the characteristically discontinuous motion of *X. neozealanica*, the animal's foot was in contact with the sediment frequently, implying that the discontinuous trail hypothesis is less likely for that species.

Tactile camouflage is also a possible advantage of affixing objects. If animals that find prey by touch encounter *Xenophora*, the peculiar assortment of attachments might confuse them. We consider this hypothesis unlikely due to the lack of complete shell-coverage in many species. Although *X. conchyliophora* and *X. japonica* are often completely covered, other species that frequently show attachments (e.g., *X. pallidula*, *X. peroniana*, and *X. crispa*) do not coat their entire shells with affixed objects. The attachment pattern of this latter group would probably only deter a cursory chemo-tactile search, and, in the case of shallow-water specimens, would be unlikely to deceive a visually orienting predator.

To our knowledge, the suggestion that objects are attached as a means of *armoring shells* against predators has not previously been made. Ponder (1983), however, noted that the shells of some *Xenophora* species are quite thin. Considering the extent to which some species, such as *X. conchyliophora*, are encrusted, one may theorize that objects are affixed to enhance the protective value of the shell. There are a number of arguments that can be made against this hypothesis. Whereas it is not known what type of animal preys upon *Xenophora*, both Berg (1975) and Linsley and Yochelson (1973) attempted to elicit an escape response from *Xenophora* (*X. conchyliophora* and *X. neozealanica*, respectively) by confronting them with starfish and predatory gastropods. Linsley and Yochelson (1973: 5) reported that "the general reaction to these predators was one of apparent unconcern." Berg (1975) lists several species of fish as principle predators. Affixed objects may have made *Xenophora* immune to predation from drilling gastropods; however, armor of this type would provide little defense against predation by malacophagous fish, which routinely crush far more durable shells (Berg, 1975). As noted above, few *Xenophora* are as thoroughly covered as *X. conchyliophora*. The mechanism of attachment is arguably inefficient for producing armor: any object affixed in such a way that it projects out from the shell margin is largely useless as armor until the next whorl is formed under it. Finally, the species of *Xenophora* that do not frequently affix foreign objects produce either a projecting, unbroken flange, or a fringe of radial spines or digitations (Figure 2), which suggests a function analogous to that of the projecting fringe of attachments, but lack any armoring potential. It has been argued that other gastropods, such as the genus *Murex*, produce spines to expand their effective size and make themselves less vulnerable to predators (oral pers. comm., M. G. Harasewych). Berg (1975) has observed that the affixed objects quadruple the basal area of *X. conchyliophora*, so *Xenophora* may also be employing this mechanism.

Functional Support Theories: The gross morphological similarity between frequently attaching and spine/flange-producing species of *Xenophora* (Figure 2) is the source of several structural theories. That certain structural features appear to be present in all species argues powerfully for a common functional basis. Ponder (1983: 43) has noted this similarity remarking for *X. pallidula* that "this species habitually attaches large, often elongate shells in a radial fashion, so that they presumably function in the same way as digitations on some other species." We believe that the analogy can be expanded in some respects to all known species of *Xenophora*.

As mentioned above, the flange or spines produced by some *Xenophora* expand the effective radius of the shell in much the same way as the projecting fringe of attachments. One possible purpose for this projecting "skirt" is suggested by the material nature of the benthic plain: if *Xenophora* commonly inhabit soft (i.e., high water content) substrates, they run the risk of sinking and suffocation. Thayer (1975:185) has assembled a list of the various methods used by invertebrates to confront this danger, among which is the so-called *"snowshoe" effect*: "The potential value of a broad, flat form to distribute the weight of an organism has long been recognized. In 1909, Hornell (p. 92) suggested that the windowpane oyster, *Placuna placenta*, was able to live on soft mud by employing 'the same principle as is embodied in the use of snowshoe'". Although snowshoeing has not been mentioned in the literature on *Xenophora*, both attachments and flanges seems to have the structural potential to serve that purpose.

More careful scrutiny reveals significant problems with this hypothesis. In order to snowshoe effectively, *Xenophora* would be expected to select for broad, lightweight objects that expand the contact profile as much as possible while minimizing the addition of weight. But *Xenophora* from certain regions manufacture an attachment fringe entirely from elongate gastropod shells, which would penetrate the surface of soft substrate with little resistance. Also, several species of *Xenophora* often bear more than their own weight in attachments (Shank, 1969; Linsley and Yochelson, 1973). Our own observations suggest that *Xenophora* attach objects with little regard to weight.

Because mass increases in proportion to volume, with the cube of length, we expected that the expanded basal area produced by the attachments would increase relative to the basal area of the shell as the animal grew to mature size. We found the opposite to be true for *X. pallidula*: the ratio of expanded shell basal area with attachments to shell basal area without attachments decreased significantly ($p<0.01$) in the larger whorls. In other words, as *Xenophora pallidula* grow larger, their hypothetical snowshoe becomes relatively smaller. Though the same test could not be performed on the spines of *X. solaris* due to the large number of broken spines, we found that the number of spines per whorl increased statistically ($p<0.01$). Thus, *X. solaris* is increasing the area of contact with the substrate by decreasing the angular interval between spine production (Figure 2). Although this itself is not convincing evidence of snowshoeing, it suggests that more thorough morphometric analysis of *X. solaris* is needed.

Multiple authors have noted that the expanded base provides added *stability* to the shell (Shank, 1969; Berg, 1975; St. Jean, 1983). Although Shank (1969) and Berg (1975) observed that *Xenophora* is capable of righting itself even if overturned in soft sediment, both also noted that the righting procedure is time-consuming. *Xenophora* may be in greater danger of predation when overturned, either due to lack of camouflage or to exposure of the apertural surface. If this is the case, reducing the amount of time spent overturned and in the righting process would give attaching and flange/spine-producing *Xenophora* an advantage over less derived forms. We consider this stability hypothesis to be relatively unimportant: although it is empirically true that *Xenophora* are more stable than they would be without the spines, flange, or attachments, without further ecological knowledge it is impossible to say whether this provides a selective advantage. Some potential predators of *Xenophora*, such as fish, would certainly be capable of flipping the shell, even assuming that an upright shell would be less vulnerable than an overturned shell.

One significant structural feature is conserved among all species of *Xenophora*: the apertural surface of the shell is raised off the substrate, although different species may achieve that using different structures (e.g., spines, flange, attachments). This has been observed by Shank (1969), Linsley and Yochelson (1973), and St. Jean (1977, 1983). Linsley and Yochelson place particular emphasis on this trait, suggesting that the "stilt" effect provides a means of olfactory camouflage by allowing the *Xenophora*'s body to remain suspended above the substrate and thus leaving a discontinuous scent trail. We believe that the "stilts" may also aid in the feeding process by providing a broad-based *feeding cone* under which the animal is able to graze. This hypothesis is supported by its sedentary lifestyle. As Shank (1969:5) has commented, "when there is plenty of food it never reaches beyond its shell, but feeds entirely on the material beneath . . .". Whether or not this "feeding cone" provides *Xenophora* with some safety while feeding is subject to debate.

A number of more or less convincing theories have been presented as to the function and origin of the attachment behavior in *Xenophora* Our observations of coral-bearing specimens have led us to conclude that there is some measure of truth in several of the various theories. We also suggest that different species of *Xenophora*, subject to different predation pressure and different environmental conditions, may have adapted the basic attachment behavior to serve different purposes. For example, it seems likely that shallow-dwelling, highly encrusted species, such as *X. conchyliophora*, camouflages itself against visually orienting predators, whereas the deep-water, spinose *X. solaris* may use the snowshoe effect to prevent suffocation. We conjecture that visual camouflage was the original function. The degree to which the other functions are derived presents an interesting evolutionary puzzle, but the attachment and flange/spine-producing behaviors can certainly be used to help clarify the phylogenetic relationships between the various species of *Xenophora*

To achieve a more satisfactory understanding of the attachment behavior detailed morphometric analysis should be performed on the size, shape, spatial density, and orientation of attached objects. Ultimately, however, we need to known more about the life history of *Xenophora*. The differences and similarities in the biology, ecology, and behavior of the various species should provide important clues, and perhaps eventually answer the riddles posed by the remarkable carrier shells.

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Appendix 1. Names and localities of azooxanthellate coral species affixed to *Xenophora* shells.

MNHN

MUSORSTOM 8–963 (20°20′S, 169°49′E, 400–440 m), on *X. pallidula*, MNHN: *F. variegatus* (1), *S. complicata* (1), *Caryophyllia* sp. A (1), *C. abrupta* (1), *T. brevispina* (1), *B. stellulatus* (2), *D. corrugatus* (1), *H. sulcatus* (2), *H.* sp. (1); *T. labidus* (1), *Flabellum* sp. (2), *F. aotearoa* (1), *T. kermadecensis* (1).

MUSORSTOM 8–1008 (18°53′S, 168°53′E, 919–1000 m), on *X. pallidula*, MNHN: *Truncatoflabellum* sp. (1), gardinerid, n. gen. n. sp. (3).

MUSORSTOM 8–1016 (17°53′S, 168°28′E, 291–300 m), on *X. pallidula*, MNHN: *C. abrupta* (1), *Conotrochus* sp. (1), *C. asymmetros* (1), *T. dens* (1).

MUSORSTOM 8–1017 (17°53′S, 168°26′E, 294–295 m), on *X. pallidula*, MNHN: *Caryophyllia* sp. (1), *C. asymmetros* (1), *Conotrochus* sp. (1), *E. grayi* (1).

MUSORSTOM 8–1018 (17°53′S, 168°25′E, 300–301 m), on *X. pallidula*, MNHN: *B. stellulatus* (1), *N. conicus* (1).

MUSORSTOM 8–1023 (17°48′S, 168°49′E, 321 m), on *X. pallidula*, MNHN: *Caryophyllia* sp. (1), *Caryophyllia* sp. B (1), *B. stellulatus* (1), *Deltocyathus* sp. (1), *Conotrochus* sp. (2), *H. sulcatus* (1), *Truncatoflabellum* sp. (1), *Flabellum* sp. (1), *T. kermadecensis* (2).

MUSORSTOM 8–1087 (15°10′S, 167°14′E, 394–421 m), on *X. pallidula*, MNHN: *Caryophyllia* sp. (1), *C. abrupta* (1), *C. decamera* (1), *Trochocyathus* sp. (1), *T. rhombocolumna* (1), *T. vasiformis* (1), *T.* sp. (1), *B. stellulatus* (2), gardinerid, n. gen. n. sp. (2).

MUSORSTOM 8–1088 (15°09′S, 167°15′E, 425–455 m), on *X. pallidula*, MNHN: *C. abrupta* (2), *P. folliculus* (1), *T. discus* (2), *T.* sp. (1), *Truncatoflabellum* sp. (1), gardinerid, n. gen. n. sp. (2).

MUSORSTOM 8–1091 (15°10′S, 167°13′E, 344–350 m), on *X. pallidula*, MNHN: *S. complicata* (1), *C. abrupta* (3), *C. lamellifera* (1), *Heterocyathus* sp. (1), *F. paronimum* (1).

MUSORSTOM 8–1092 (15°10′S, 167°12′E, 314–321 m), on *X. pallidula*, MNHN: *C. ambrosia* (1), *C. funicolumna* (3), *Truncatoflabellum* sp. (2).

MUSORSTOM 8–1097 (15°05′S, 167°10′E, 281–288 m), on *X. pallidula*, MNHN: *S. complicata* (1), *B. stellulatus* (11), *Deltocyathus* sp. (1), *D. stella* (1), *H. sulcatus* (1), *C. asymmetros* (1), *C. bruneus* (1), *C.* sp. (1), *Flabellum* sp. (1), *T. pusillum* (1), *T.* sp A (1), *G. annulata* (1).

MUSORSTOM 8–1106 (15°05′S, 167°11′E, 305–314 m), on *X. pallidula*, MNHN: *C. abrupta* (1), *B. stellulatus* (9), *D. heteroclitus* (2), *D.* sp. (1), *H. sulcatus* (1), *T. dens* (1), *T. pusillum* (3), *T.* sp. (2), dendrophylliid (2).

DMNH

Marinduque, Philippines, 124–126 m, on *X. pallidula*, DMNH 188571: *Caryophyllia* sp. A (2), *Flabellum* sp. (1), *Truncatoflabellum* sp. (1).

Marinduque, Philippines, depth not known, on *X. pallidula*, DMNH 189002 and 188943: *A. frustum* (1), *C. spinacarens* (4), *H. sulcatus* (1), *F. deludens* (1), *Truncatoflabellum* sp. (1), *B. cornu* (2).

Batangas, Philippines, 152–163 m, on *X. pallidula*, DMNH 189854: *T. formosum* (3).

Batangas, Philippines, depth unknown, on *X. pallidula*, DMNH 190007: *C. spinacarens* (1), *H. sulcatus* (1).

Philippines, depth unknown, on *X. pallidula*, DMNH 188572: *C. spinacarens* (7), *C.. transversalis* (1).

Philippines, depth unknown, on *X. pallidula*, DMNH 188944: *C. spinacarens* (1), *T. pusillum* (1), *B. cornu* (1), *B. imperialis* (1).

Quezon, Philippines, 596 m, on *X. pallidula*, DMNH 189043: *Truncatoflabellum* sp. (1).

Off Zululand, 293 m, on *X. pallidula*, DMNH 11505–7, 11499, 17902: *Madracis* sp. (1), *Caryophyllia* sp. (2), *Flabellum* sp. (1), *F. pavoninum* (5), *Truncatoflabellum* sp. (6), *T. gardineri* (6), dendrophylliid (1).

Off Zululand, 220–293 m, on *X. pallidula*, DMNH 20120: *F. pavoninum* (4), *F.* sp. (1), *T.* sp. (1), *T.* cf. *formosum* (1), *T. gardineri* (10).

Off Natal, South Africa, 293–329 m, on *X. pallidula*, DMNH 186438: *Flabellum* sp. (1), *F. pavoninum* (1), *T. gardineri* (2).

off Japan, 110 m, on *X. pallidula*, DMNH 6180: *C. quadragenaria* (1), *P. dentiformis* (2), *F. pavoninum* (1), *Endopachys grayi* (1).

Sagami Bay, Japan, depth unknown, on *X. pallidula*, DMNH 55071: *F. paliferus* (1), *H. sulcatus* (1), *Truncatoflabellum* sp. (1).

off Kii, Japan, 183 m, on *X. pallidula*, DMNH 55070: *E. grayi* (1), P. dentiformis (2).

MCZ

Auckland, New Zealand, depth unknown, on *X. neozealandica*, MCZ 160266–67: *M. rubrum* (4).

USNM

Albatross 3810 (southeast of Oahu, Hawaiian Islands, 386–463 m), on *X. peroniana*, USNM M749844: *A. pacifica* (1), *E. grayi* (1).

Albatross 3838 (southeast coast of Molokai, Hawaiian Islands, 168–388 m), on *X. peroniana*, USNM M335067: *E. grayi* (5).

Albatross 4079 (Puniawa Point, Maui, Hawaiian Islands, 262–326 m), on *X. peroniana*, USNM M335063: *A. macrolobata* (3).

Albatross 5117 (13°52′22″N, 120°46′22″E, 216 m), on *X. pallidula*, USNM M243416: *C. spiniger* (1), *Flabellum* sp. (1).

Albatross 5131 (off Panabutan Point, Philippines, 49 m), on *X. pallidula*, USNM M243391: *C. secta* (1), *H. sulcatus* (1).

Albatross 5212 (12°04′15″N, 124°04′36″E, 198 m), on *X. pallidula*, USNM M277576: *F. lamellulosum* (2), *T.* cf. *gardineri* (1), *B. cornu* (3), *B. imperialis* (1).

Albatross 5213 (12°15′00″N, 123°57′30″E, 146 m), on *X. pallidula*, USNM M243398: *Truncatoflabellum* sp. (1).

Albatross 5265 (13°41′15″N, 120°00′50″E, 247 m), on *X. pallidula*, USNM M243347–9, −353, −356–357, −361–2, −366, −368, −370, −372, −373, −375, −376, −426, −881: *Anthemiphyllia* sp. (1), *C. spinacarens* (1), *C. secta* (2), *C. grayi* (1), *T. virgatus* (1), *H. sulcatus* (1), *D. philippinensis* (1), *C. pileus* (1), *Flabellum* sp. (3), *F. pavoninum* (1), *F. lamellulosum* (1), *T. formosum* (12), *T. dens* (1), *T. pusillum* (1), *T.* sp. (1), *B. cornu* (1), *B. imperialis* (2), *E. grayi* (1), *H. cochlea* (1).

Albatross 5273 (13°58′45″N, 120°21′35″E, 209 m), on *X. pallidula*, USNM M237519: *Balanophyllia* sp. (1).

Albatross 5278 (14°00′10″N, 120°17′15″E, 187 m), on *X. pallidula*, USNM M 243411: *C. octonaria* (1), *H. sulcatus* (3), *H. alternatus* (1), *A. rubescens* (1), *Tropidocyathus* sp. (1).

Albatross 5289 (13°41′50″N, 120°58′30″E, 315 m), on *X. pallidula*, USNM M237585: *T. formosum* (1), *T. incrustatum* (1).

Albatross 5312 (21°30′00″N, 116°32′00″E, 256 m), on *X. japonica*, USNM M243420: *T.* cf. *gardineri* (1).

Albatross 5391 (12°13′15″N, 124°05′03″E, 216 m), on *X. japonica*, USNM M238138: *H. sulcata* (1), *F. politum* (14), *T. candeanum* (1), *Balanophyllia* sp. (2).

Albatross 5392 (12°13′35″N, 124°02′48″E, 247 m), on *X. pallidula*, USNM M238192, 243394: *F. pavoninum* (2), *F. politum* (7), *F.* sp. (10), *B. cornu* (4),

Albatross 5392 (see above) on *X. japonica*, USNM M238192: *F. politum* (50), *F. pavoninum* (1), *F.* sp. (13), *B. cornu* (6), *B.* sp. (5).

Albatross 5394 (12°00′30″N, 124°05′36″E, 280 m), on *X. pallidula*, USNM M243415: *T. candeanum* (1).

Albatross 5395 (11°56′40″N, 124°14′E, 256 m), on *X. pallidula*, USNM M240513: *B. cornu* (1).

Albatross 5405 (10°49′20″N, 124°24′23″E, 479 m), on *X. pallidula*, USNM M238257: *Conotrochus* sp. (2).

Albatross 5408 (10°40′15″N, 124°15′00″E, 291 m), on *X. pallidula*, USNM M238277: *Fungiacyathus* sp. (1), *Madrepora oculata* (2), *H. sulcatus* (4).

Albatross 5416 (10°11′30″N, 123°53′30″E, 274 m), on *X. pallidula*, USNM M238372: *A. frustum* (2), *H. sulcatus* (5), *Flabellum* sp. (3), *T. angustum* (1).

Albatross 5417 (10°10′00″N, 123°53′15″E, 302 m), on *X. pallidula*, USNM M243381: *Deltocyathus* sp. (1), *Flabellum* sp. (2), *F. pavoninum* (2).

Albatross 5418 (10°08′50″N, 123°52′30″E, 291 m), on *X. pallidula*, USNM M243377: *M. oculata* (1), *D. andamanicus* (1), *Flabellum* sp. (1), *T. angustum* (1).

Albatross 5592 (4°12′44″N, 118°27′44″E, 558 m), on *X. pallidula*, USNM M229317: *H. alternatus* (1).

Albatross 5661 (5°49′40″S, 120°24′30″E, 329 m), on *X. pallidula*, USNM M239497: *Caryophyllia* sp. (1).

David Starr Jordan, stn TC32–2 (21°21′54″N, 158°12′24″W, 119–291 m), on *X. peroniana*, USNM M807659: *Anthemiphyllia* sp. (1), *E. grayi* (2), *Placotrochides* n. sp. (1).

David Starr Jordan, stn TC33–9 (21°00′06″N, 156°45′42″W, 227–234 m), on *X. peroniana*, USNM M807662: *A. pacifica* (1), *Flabellum* sp. (2), *F. pavoninum* (1), *Placotrochides* n. sp. (3).

David Starr Jordan, stn TC40–8 (21°09′42″N, 157°24′42″W, 183 m), on *X. peroniana*, USNM M807631: *Balanophyllia* sp. (1), *E. grayi* (2).
David Starr Jordan, stn TC52–99 (21°02′06″N, 156°47′15″W, 223 m), on *X. peroniana*, USNM M807652: *E. grayi* (3).
Off Kisamaya, Somalia, depth unknown, on *X. pallidula*, USNM M819755: *F. pavoninum* (6).
16–32 km off southern Zululand, 293–329 m, on *X. pallidula*, USNM M635312–313: *H. sulcatus* (1), *F. pavoninum* (1), *T. gardineri* (1), *T. multispinosum* (2), *T.* sp. (2).
W-320, off Natal, S. Africa, 37 m, on *X. pallidula*, USNM M818232: *H. sulcatus* (1), *Flabellum* sp. (1), *T. gardineri* (2).
W-253, off Durban, S. Africa, 366 m, on *X. pallidula*, USNM M818231: *T. multispinosum* (1).
Sagami Bay, Japan, depth unknown, on *X. pallidula*, USNM M346151: *C. dentata* (1), *P. dentiformis* (1), *T. candeanum* (1), *H. cochlea* (3).
Kanabe, Kii, Japan, depth unknown, on *X. pallidula*, USNM M273680: *P. dentiformis* (9), *Heterocyathus* sp. (1), *Truncatoflabellum* sp. (1).
Off Kii, Japan, depth unknown, on *X. pallidula*, USNM M605915: *P. dentiformis* (1), dendrophylliid (1).
Minabe, Wakayama, Japan, 64 m, on *X. pallidula*, USNM M605785: *P. dentiformis* (1), *H. sulcatus* (1), dendrophylliid (1).
Off Tosa, Japan, depth unknown, on *X. cerea*, USNM M346150: *C. jogashimaensis* (1), *Truncatoflabellum* sp. B (2).
Off Japan (W-976), on *X. japonica*, USNM M348868: *Truncatoflabellum* sp. (2).
Sulu Sea, Philippines (W-498), on *X. pallidula*, USNM M807763: *T. cooperi* (3), *H. sulcatus* (1), *P. laevis* (1), *H. cochlea* (2).
Tayabas Bay, Philippines, 15–30 m, on *X. pallidula*, USNM M 876993: *H. sulcatus* (4).
Stn CPI/S (3°15′S, 128°08′E, 26–55 m), on *X. corrugata*, USNM M746695: *H. cochlea* (1).
Stn KRVI (5°32′S, 132°41′E, 37 m), on *X. corrugata*, USNM M746948: *H. cochlea* (1).
22°19′S, 167°11′E, 290–310 m, on paratype of *X. granulosa*, USNM M842996: *D. heteroclitus* (1).
LaRafalo, stn 7 (5°18′N, 9°54′30″W, 200 m), on *X. crispa*, USNM M762004: *C. smithii* (23).

Appendix 2. Taxonomic list of azooxanthellate Scleractinia affixed to *Xenophora* shells, and frequency of occurrence on those shells (in parentheses). See Appendix 1 for locality data of corals and shells.

- Order Scleractinia
  - Suborder Astrocoeniina
    - Family Pocilloporidae
      - *Madracis* sp. (1)
  - Suborder Fungiina
    - Family Fungiacyathidae
      - *Fungiacyathus paliferus* (Alcock, 1902) (1)
      - *F. variegatus* Cairns, 1989 (1)
      - *F.* sp. (1)
    - Family Micrabaciidae
      - *Stephanophyllia complicata* Moseley, 1876 (3)
  - Suborder Faviina
    - Family Oculinidae
      - *Madrepora oculata* Linnaeus, 1758 (3)
    - Family Anthemiphylliidae
      - *Anthemiphyllia frustum* Cairns, 1994 (3)
      - *A. pacifica* Vaughan, 1907 (2)
      - *A. macrolobata* Cairns, in press (3)
      - *A.* sp. (1)
  - Suborder Caryophylliina
    - Family Caryophylliidae
      - *Caryophyllia (C.) smithii* Stokes and Broderip, 1828 (23)
      - *C. (C.) abrupta* Cairns, ms (9)
      - *C. (C.) secta* Cairns and Zibrowius, 1997 (3)
      - *C. (C.) ambrosia* Alcock, 1898 (1)
      - *C. (C.) jogashimaensis* Eguchi, 1968 (1)
      - *C. (C.) lamellifera* Moseley, 1881 (1)
      - *C. (C.) octonaria* Cairns and Zibrowius, 1997 (1)
      - *C. (C.) quadragenaria* Alcock, 1902 (1)
      - *C. (C.) transversalis* Moseley, 1881 (1)
      - *C. (C.)* sp. A (3)
      - *C. (C.)* sp. B (1)
      - *C. (C.)* sp. (7)
      - *C. (A.) spinicarens* (Moseley, 1881) (14)
      - *C. (A.) decamera* Cairns, in press (1)
      - *C. (A.) dentata* Moseley, 1876 (1)
      - *C. (A.) grayi* (Milne Edwards and Haime, 1848) (1)
      - *C. (A.) spinigera* Saville Kent, 1871 (1)
      - *Premocyathus dentiformis* (Alcock, 1902) (16)
      - *Trochocyathus (T.) cooperi* (Gardiner, 1905) (3)
      - *T. (T.) discus* Cairns and Zibrowius, 1997 (2)
      - *T. (T.) rhombocolumna* Alcock, 1902 (1)
      - *T. (T.) vasiformis* Bourne, 1903 (1)
      - *T. (T.)* sp. (2)
      - *T. (A.) brevispina* Cairns and Zibrowius, 1997 (1)
      - *Tethocyathus virgatus* (Alcock, 1902) (1)
      - *Bourneotrochus stellulatus* (Cairns, 1984) (25)
      - *Deltocyathus heteroclitus* Wells, 1984 (3)
      - *D. andamanicus* Alcock, 1898 (1)
      - *D. corrugatus* Cairns, in press (1)
      - *D. philippinensis* Cairns and Zibrowius, 1997 (1)
      - *D. stella* Cairns and Zibrowius, 1997 (1)
      - *D.* sp. (4)
      - *Heterocyathus sulcatus* (Verrill, 1866) (31)
      - *H. alternatus* Verrill, 1865 (2)
      - *H.* sp. (3)
      - *Conotrochus asymmetros* Cairns, in press (3)
      - *C. funicolumna* (Alcock, 1902) (3)
      - *C. brunneus* (Moseley, 1881) (1)
      - *C.* sp. (6)
    - Family Turbinoliidae
      - *Alatotrochus rubescens* (Moseley, 1876) (1)
      - *Tropidocyathus labidus* Cairns and Zibrowius, 1997 (1)
      - *T.* sp. (1)
      - *Cyathotrochus pileus* (Alcock, 1902) (1)
      - *Notocyathus conicus* (Alcock, 1902) (1)
      - *Peponocyathus folliculus* (Pourtalès, 1868) (1)
    - Family Flabellidae
      - *Flabellum (F.) politum* Cairns, 1989 (71)
      - *F. (F.) pavoninum* Lesson, 1831 (26)
      - *F. (F.) lamellulosum* Alcock, 1902 (3)
      - *F. (F.)* sp. A (1)
      - *F. (F.)* sp. (43)
      - *F. (U.) aotearoa* Squires, 1964 (1)
      - *F. (U.) deludens* Marenzeller, 1904 (1)

         - *Truncatoflabellum gardineri* Cairns, 1993 (20)
         - *T.* sp. cf. *T. gardineri* (3)
         - *T. formosum* Cairns, 1989 (16)
         - *T.* sp. cf. *T. formosum* (1)
         - *T. pusillum* Cairns, 1989 (6)
         - *T. angustum* Cairns and Zibrowius, 1997 (2)
         - *T. candeanum* (Milne Edwards and Haime, 1848) (3)
         - *T. dens* (Alcock, 1902) (3)
         - *T. incrustatum* Cairns, 1989 (1)
         - *T. multispinosum* Cairns, 1993 (3)
         - *T.* sp. A (1)
         - *T.* sp. B (2)
         - *T.* sp. (25)
         - *Placotrochides* n. sp. (4)
         - *Placotrochus laevis* Milne Edwards and Haime, 1848 (1)
         - *Monomyces rubrum* (Quoy and Gaimard, 1833) (4)
      - Family Gardineriidae
         - Gardineriid n. gen. sensu Stolarski (1996) (7)
      - Family Guyniidae
         - *Guynia annulata* Duncan, 1872 (1)
         - *Temnotrochus kermadecensis* Cairns, 1995 (3)
   - Suborder Dendrophylliina
      - Family Dendrophylliidae
         - Dendrophylliid (5)
         - *Balanophyllia cornu* Moseley, 1881 (18)
         - *B. imperialis* Kent, 1871 (4)
         - *B.* sp. (9)
         - *Endopachys grayi* Milne Edwards and Haime, 1848 (17)
         - *Heteropsammia cochlea* (Spengler, 1781) (8)
- Solitary corals unidentified to genus (67)

Shell Microstructure of Mytilids (Bivalvia) from Deep-Sea Hydrothermal Vent and Cold-Water Sulfide/Methane Seep Environments

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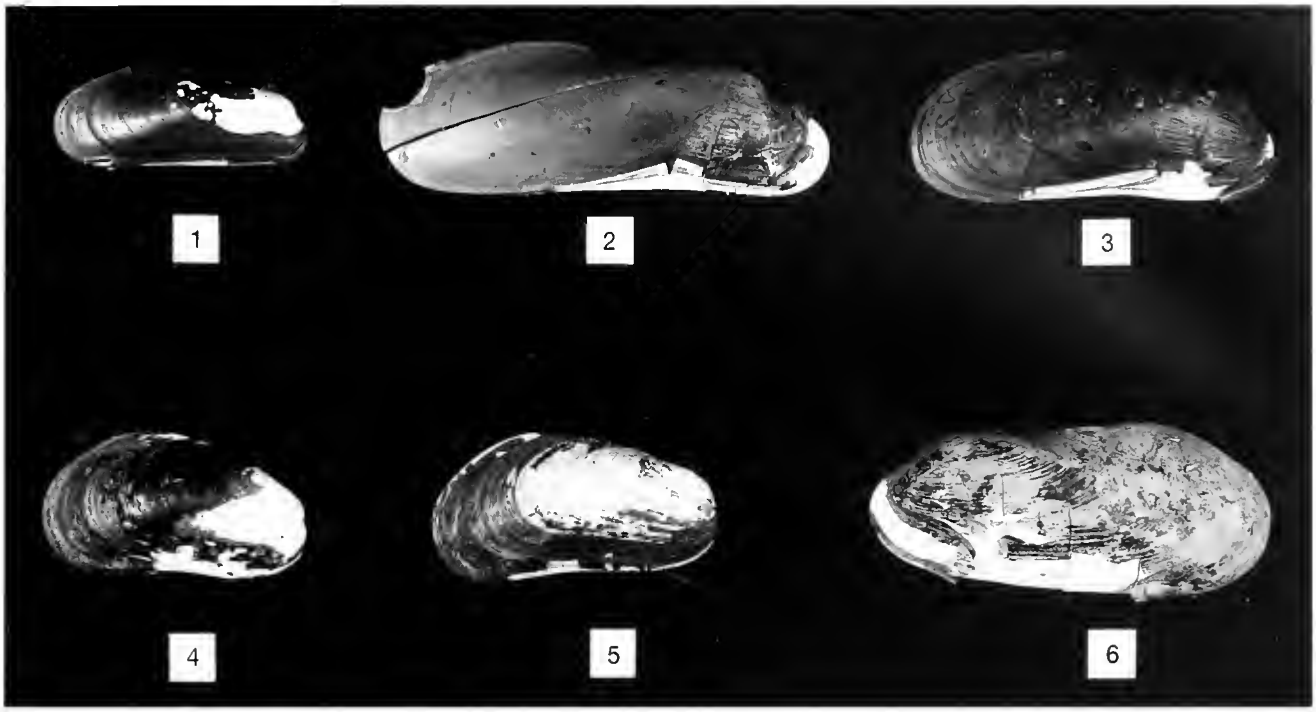
ABSTRACT

The shell microstructures of 6 mytilid species from deep-sea hydrothermal vent and cold-water sulfide/methane seep sites is characterized by scanning electron microscopy. Examination of fractured and sectioned specimens reveals similar shell microstructures in distinct arrangements. The shell microstructures of the mytilids investigated in this study consist of outer fibrous prismatic and inner nacreous structures, which underlie a periostracal layer. Simple prismatic structure, comprising the adductor and pallial myostraca, is also present. The shell microstructures of these species exhibit similar complexity as microstructures of the previously described vent mussel *Bathymodiolus thermophilus* Kenk and Wilson, 1985.

Table 1. Deep-sea mytilid specimens examined in this study.

Date	Sampling site	Depth (m)	Species	Collection number	Specimen number	Length (cm)
Cold-water Sulfide/Methane Seeps						
6/3/92	Florida Escarpment 26°01.8′N 84°54.6′W	3313	Species A	ANSP400787	1	8.0
10/16/86	Florida Escarpment 26°01.5′N 84°55.3′W	3300	Species B	ANSP400788	1	14.1
4/13/90	Alaminos Canyon 26°21.3′N 94°29.7′W	2222	Species C	ANSP400789	1 2	11.4 13.0
9/15/91	Louisiana Slope (Bush Hill) 27°46.9′N 91°30.4′W	546	Species D	ANSP400790	1 2	8.3 8.7
9/29/91	Louisiana Slope 27°50′N 92°10′W	650	Species E	ANSP400791	1 2	3.3 8.9
Hydrothermal Vents						
6/21/93	Mid-Atlantic Ridge (Snake Pit) 23°22.1′N 44°57.1′W	3521	Species F	ANSP400792	1 2 3	11.0 11.1 12.5
5/28/90	Galápagos Rift (Mussel Bed) 00°47.9′N 86°09.2′W	2515	*Bathymodiolus thermophilus*		1 2	13.0 14.5
6/7/90	East Pacific Rise (Mussel Bed) 12°48.6′N 103°56.5′W	2630	*Bathymodiolus thermophilus*		1 2	10.7 14.9



Figures 1–6. External shell surface of the deep-sea mytilid specimens examined. **1.** Species A, ANSP 400787, right valve. Length = 8.0 cm. **2.** Species B, ANSP 400788, right valve. Length = 14.1 cm. **3.** Species C, ANSP 400789, right valve. Length = 11.4 cm. **4.** Species D, ANSP 400790, right valve. Length = 8.3 cm. **5.** Species E, ANSP 400791, right valve. Length = 8.9 cm. **6.** Species F, ANSP 400792, left valve. Length = 12.5 cm.

INTRODUCTION

Among unique faunal assemblages discovered at cold-water sulfide/methane seep sites in the Gulf of Mexico as well as at deep-sea hydrothermal vent sites in the north Atlantic are a number of unnamed mytilids. Efforts are underway to describe both the soft and calcified tissues of these mytilids with the primary purpose of providing new information for taxonomic differentiation of members of the group. Here we report for the first time on the shell microstructures observed within the shells of 5 mytilid species collected at cold-water sulfide/methane seep sites in the Gulf of Mexico and 1 species from deep-sea hydrothermal vent sites on the Mid-Atlantic Ridge (23°22.1′N, 44°57.1′W). The shell microstructures of these specimens are also compared with those of the previously described, deep-sea hydrothermal vent mussel *Bathymodiolus thermophilus* Kenk and Wilson, 1985 collected at sites on the Galápagos Rift and East Pacific Rise.

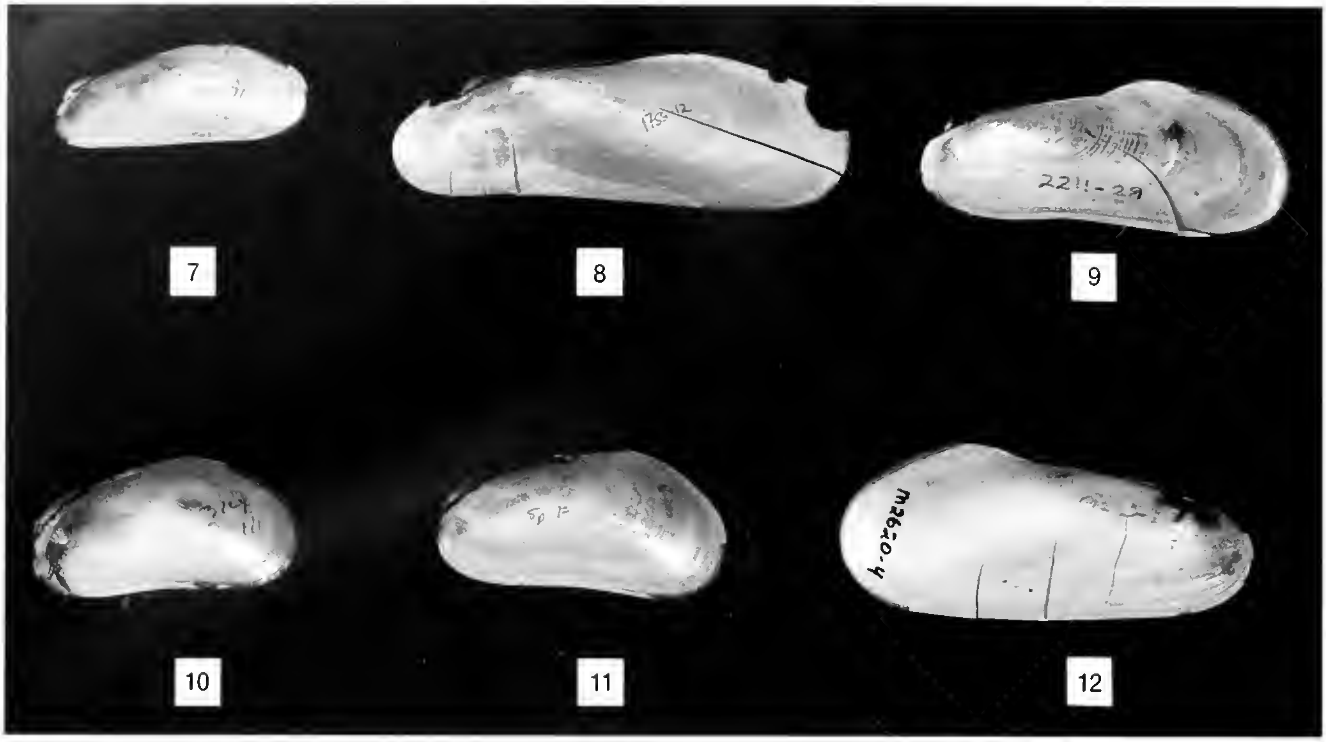
MATERIALS AND METHODS

Mytilid specimens ranging in length from 3.3–14.9 cm were collected alive via submersible sampling from hydrothermal vent sites at Snake Pit (23°22.1′N, 44°57.1′W) on the Mid-Atlantic Ridge (3 specimens), at Mussel Bed (00°47.9′N, 86°09.2′W) on the Galápagos Rift (2 specimens), and on the East Pacific Rise (12°48.6′N, 103°56.5′W) (2 specimens), as well as from cold-water sulfide/methane seep sites on the Florida Escarpment (26°01.8′N, 84°54.6′W; 26°01.5′N, 84°55.3′W) (2 specimens), Alaminos Canyon (26°21.3′N, 94°29.7′W) (2 specimens), and Louisiana Slope (27°46.9′N, 91°30.4′W; 27°50′N, 92°10′W) (5 specimens). The depth of the sampling sites varied from 546 to 3521 m (Table 1). The soft tissues of the mussels were excised and frozen at −70°C. However, they were not examined histologically, and the sex and stage of development of the mussels were not determined. The shells were air-dried, carefully packaged, and sent to the laboratory for analysis. The taxonomy and systematic relationships of these taxa have not been studied. Voucher specimens of the 6 unnamed species (Table 1) were deposited in the collection at the Department of Malacology, Academy of Natural Sciences of Philadelphia (ANSP).

Seventeen specimens were prepared for scanning electron microscopy (SEM) following the 2 methods outlined by Kennish et al. (1996, 1998):

Preparation 1. Shells were fractured, sonicated in distilled water, dehydrated in 95% ethanol, air-dried, and coated with gold/palladium.

Preparation 2. Shells were embedded in resin, sectioned, polished, treated with sodium hypochloride, rinsed with water, dehydrated in 95% ethanol, air dried, and coated with gold/palladium.



Figures 7–12. Internal shell surface of the deep-sea mytilid specimens examined. **7.** Species A, ANSP 400787, same specimen shown in Figure 1. Length = 8.0 cm. **8.** Species B, ANSP 400788, same specimen shown in Figure 2. Length = 14.1 cm. **9.** Species C, ANSP 400789, same specimen shown in Figure 3. Length = 11.4 cm. **10.** Species D, ANSP 400790, same specimen shown in Figure 4. Length = 8.3 cm. **11.** Species E, ANSP 400791, same specimen shown in Figure 5. Length = 8.9 cm. **12.** Species F, ANSP 400792, same specimen shown in Figure 6. Length = 12.5 cm.

After preparation, the specimens were observed and photographed in an Amray 1830 SEM.

SHELL MICROSTRUCTURE

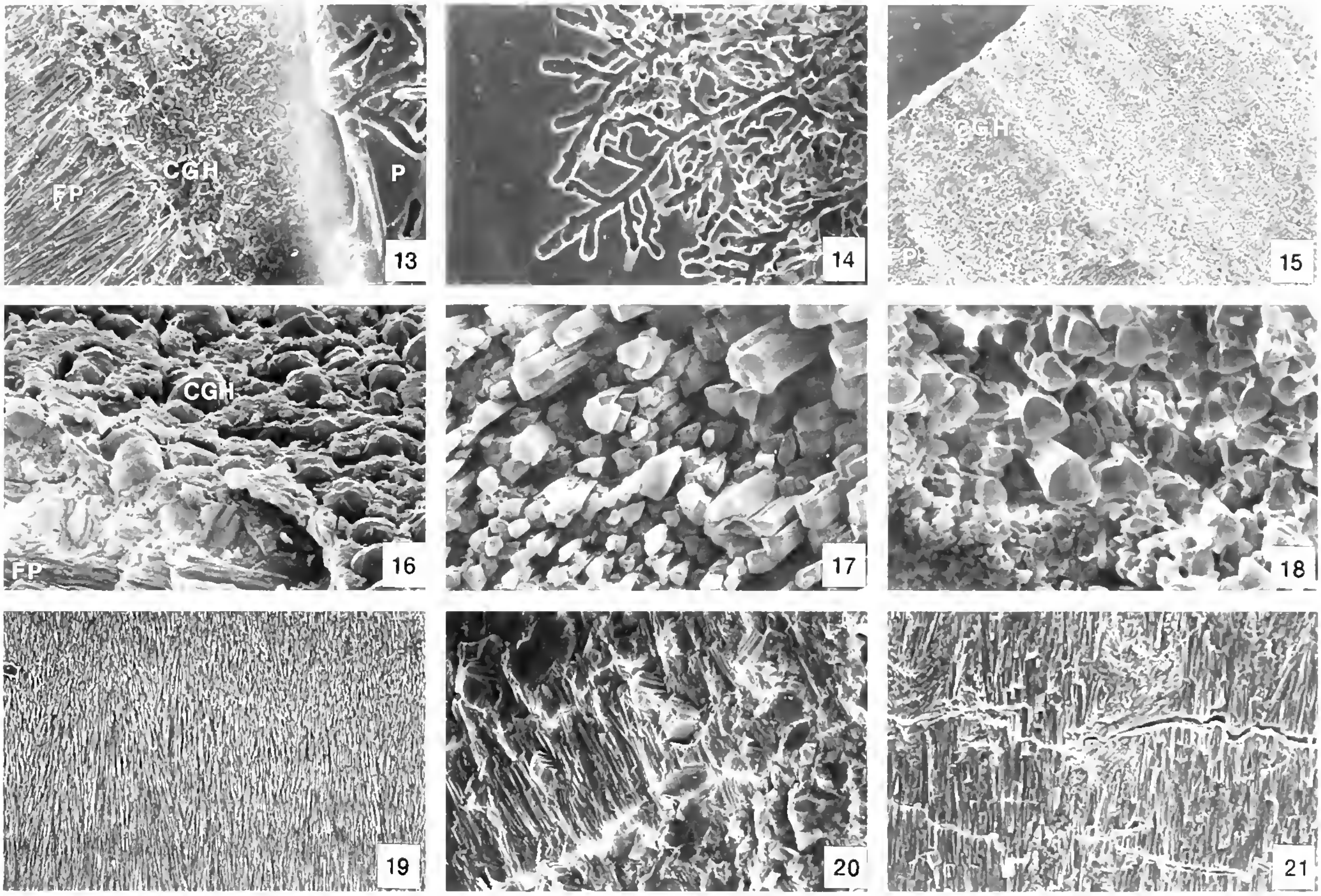
Cold-Seep Mytilids

The shells of the cold-seep mytilids consist of 4 shell layers. They are basically composed of outer fibrous prismatic and inner nacreous structures which underlie a periostracal layer that may be infected with branching filamentous organisms (Figures 1, 2). Simple prismatic (aragonite) structure is also present, constituting the adductor and pallial myostraca. A thin layer of coarse-grained homogeneous structure may be present between the periostracum and the outer fibrous prismatic layer (Figures 1, 3, 4). The first-order prisms comprising the outer fibrous prismatic layer are composed of laths or rods of calcite (Figures 1, 5, 6), and they have a much greater length/width ratio than is typically observed in simple prismatic structure. In the fibrous prismatic structure of the cold-seep mytilids the prisms are usually arranged parallel to each other with the long axis inclined toward the hinge. However, near the periostracum or at growth bands, the prisms assume either a conical or crossed configuration. The conical arrangement of the prisms resembles planar spherulitic prismatic structure (Figure 7), and the crossed arrangement, crossed lamellar or complex crossed lamellar structure (Figures 8, 9).

The underlying nacreous layer may or may not be separated from the fibrous prismatic layer by blocky prismatic structure (Figures 10, 11). At the boundary between the fibrous prismatic and nacreous layers, the nacreous tablets are arranged as stacks or sheets (Figure 12, 13). Sheet or row-stack nacre occurs away from the shell margin (Figure 14–16). The adductor and pallial myostraca exhibit first-order prisms that are well defined and generally non-interdigitating (Figure 17, 18). They have relatively low to moderate length/width ratios in contrast to those comprising the fibrous prismatic layer.

Hydrothermal-Vent Mytilids

The microstructures encountered within the shells of the hydrothermal-vent mytilids examined in this study are typical of calcified structures previously described in other members of the family Mytilidae, including the vent mussel *Bathymodiolus thermophilus*. From the vacuolated periostracum inwards, the calcified layers of *B. thermophilus* consist of: (1) fibrous prismatic calcite; (2) nacre (aragonite); (3) irregular prismatic aragonite (pallial myostracum); and (4) nacre (aragonite) (Lutz and Rhoads, 1980). A relatively thick organic periostracum appears to effectively prevent substantial dissolution of



Figures 13–21. Microstructures of deep-sea mytilids. **13–15.** Species A, ANSP 400787. **13.** Angular view of periostracum (P) (ventral margin), coarse grained homogeneous (CGH) (comarginal fracture), and fibrous prismatic (FP) structures. Antero-posterior shell axis from top to bottom of micrograph. Horizontal field width (HFW) = 240 μm. Preparation 1. **14.** Exterior view of periostracum infested with branching filamentous organisms. Same orientation as Figure 1. HFW = 320 μm. Preparation 1. **15.** Exterior view of an oblique fracture of the coarse grained homogeneous (CGH) and fibrous prismatic (FP) structures. Antero-posterior shell axis from top left to bottom right of micrograph. Ventral shell margin to right. HFW = 405 μm. Preparation 1. **16–17.** Species B, ANSP 400788. **16.** Coarse grained homogeneous (CGH) and fibrous prismatic (FP) structures. Double fracture: (1) radial fracture towards bottom left of micrograph; (2) horizontal (tangential) fracture towards top right. Antero-posterior shell axis perpendicular to plane of micrograph. HFW = 70 μm. Preparation 1. **17.** Transverse fracture of predominantly lath-type fibrous prismatic structure. Outer shell surface towards bottom of micrograph. Antero-posterior shell axis from left to right of micrograph. HFW = 35 μm. Preparation 1. **18.** Species C, ANSP 400789, transverse fracture of predominantly rod-type fibrous prismatic structure. Outer shell surface towards bottom of micrograph. Antero-posterior shell axis from left to right of micrograph. HFW = 35 μm. Preparation 1. **19.** Species D, ANSP 400790. Radial fracture showing conical arrangement of rod-type fibrous prismatic structure. Outer shell surface towards top of micrograph. Outer shell surface towards bottom of micrograph. Antero-posterior shell axis from left to right of micrograph. HFW = 305 μm. Preparation 2. **20–21.** Species E, ANSP 400791. **20.** Radial fracture showing crossed lamellar arrangement of lath-type fibrous prismatic structure. Antero-posterior shell axis from bottom left to top right of micrograph. HFW = 70 μm. Preparation 1 (Same orientation as Figure 7). **21.** Radial fracture showing complex crossed lamellar arrangement of lath-type fibrous prismatic structure. Antero-posterior shell axis from bottom left to top right of micrograph. HFW = 170 μm. Preparation 1 (Same orientation as Figure 7).

the relatively thin and fragile shell of *B. thermophilus* throughout its life (Lutz, 1982).

The calcitic fibrous prismatic layer, a specialized layer observed in the mytilids, is characterized by prisms with high length/width ratios. As reported by Carter (1990), first-order prisms in fibrous prismatic structures have a non-spherulitic prismatic and non-composite prismatic substructure, but unlike simple prisms, appear as long fibers. Several investigators have classified fibrous prismatic structure as an independent entity because of its unique structure (MacClintock, 1967; Carter, 1980a, b; Carter and Clark, 1985; Watabe, 1988; Carter, 1990).

Nacreous structures in hydrothermal-vent mytilids are composed of tabular aragonitic crystals deposited on an organic matrix. The calcareous tablets, identical to the sheet nacre described by Carter and Clark (1985) and Carter (1990), are arranged in broadly continuous, regular, and mutually parallel sheets. They exhibit similar

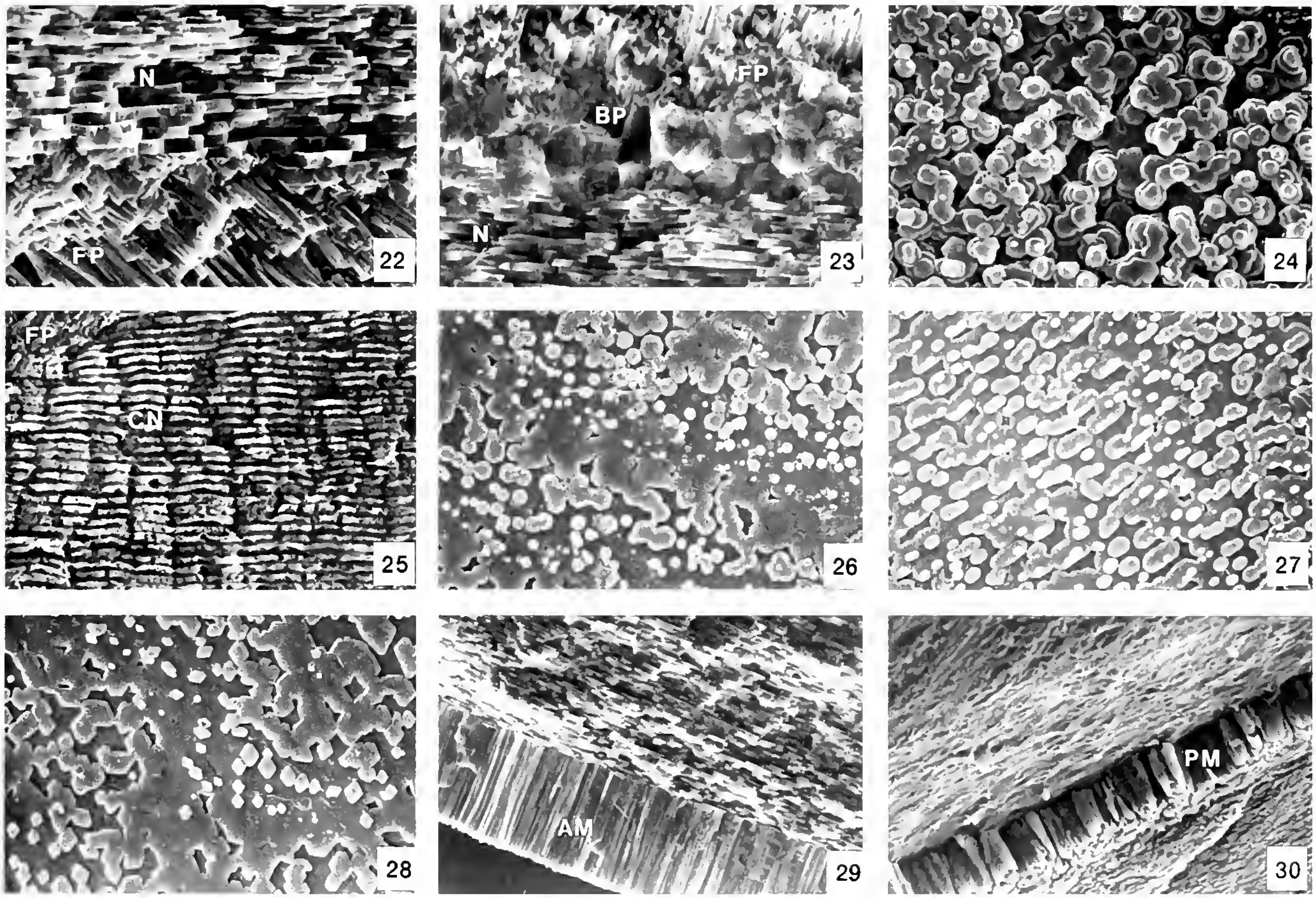


Figure 22–30. Microstructures of deep-sea mytilids. **22.** Species C, ANSP 400789. Radial fracture of the boundary between fibrous prismatic (FP) and nacreous (N) structures. Dorsal shell surface towards bottom of micrograph. Antero-posterior shell axis from bottom left to top right of micrograph. HFW = 35 µm. Preparation 1. **23.** Species A, ANSP 400787. Transverse fracture of the blocky prismatic (BP) sandwiched between the fibrous prismatic (FP) and nacreous (N) structures. Dorsal shell surface towards top of micrograph. Antero-posterior shell axis from left to right of micrograph. HFW = 35 µm. Preparation 1. **24.** Species B, ANSP 400788. Inner surface view of the nacreous structure, near the boundary between fibrous prismatic and nacreous structures. Ventral shell surface towards left of micrograph. Antero-posterior shell axis from top to bottom of micrograph. HFW = 70 µm. Preparation 1. **25–27.** Species D, ANSP 400790. **25.** Radial section of columnar nacre (CN) underlying the fibrous prismatic (FP) structure. Ventral shell surface towards bottom of micrograph. Antero-posterior shell axis from left to right of micrograph. HFW = 45 µm. Preparation 2. **26.** Inner surface view of hexagonal tablets of sheet nacre. Shell margin towards bottom left of micrograph. HFW = 70 µm. Preparation 1. **27.** Inner surface view of oval tablets of sheet nacre. Shell margin towards bottom left of micrograph. HFW = 70 µm. Preparation 1. **28.** Species D, ANSP 400790. Inner surface view of rhomboidal tablets of stack nacre. Shell margin towards bottom left of micrograph. HFW = 70 µm. Preparation 1. **29.** Species C, ANSP 400789. Radial fracture of adductor myostracum (AM) consisting of simple prismatic structure underneath the nacreous layer. Inner shell surface towards bottom left of micrograph. HFW = 70 µm. Preparation 1. **30.** Species B, ANSP 400788. Angular view of pallial myostracum (PM) consisting of simple prismatic structure underneath the nacreous layer. Inner shell surface towards bottom right of micrograph. HFW = 70 µm. Preparation 1

complexity and form as those comprising the inner or middle shell layer of other mytilid species (Carter, 1990).

Irregular simple prismatic structure occurs under the areas of muscle attachment: the pallial and adductor myostraca. The prism cross sections are highly variable along their lengths (Carter, 1980a; 1990). This irregularity of the prism cross sections results in a lens-like or wedge-like prism shape (Carter and Clark, 1985).

DISCUSSION

SEM examination of fractured and sectioned shells of deep-sea mussels targeted in this study reveals similar microstructures in distinct arrangements. The shells of mytilids inhabiting both cold-water sulfide/methane seep and deep-sea hydrothermal vent environments are consistently composed of outer fibrous prismatic and inner nacreous structures, which underlie a periostracal layer. Simple prismatic structure forming the adductor and pallial myostraca are also present. The microstructures in these specimens exhibit similar complexity to those of the previously described vent mussel *Bathymodiolus thermophilus*.

Based on shell microstructure, Taylor et al. (1969) identified 2 groups of species belonging to the Mytilacea:

(1) a two-layered, wholly nacreous, wholly aragonitic warm-water group (e.g., *Perna viridis* (Linnaeus, 1758), *Choromytilus palliopunctatus* (Carpenter, 1857), and *Perumytilus purpuratus* (Larmarck, 1819); and (2) a two- or three-layered aragonitic and calcitic, temperate group (e.g., *Mytilus edulis* (Linnaeus, 1758) and *Mytilus californianus* (Conrad, 1837)). In the latter group, the prismatic layers consist of calcite, whereas the nacreous layers are composed of aragonite. Between the outer calcitic prismatic and the inner nacreous layers, a middle aragonitic prismatic layer is present in some mytilid shells (Blackwell et al., 1977; Carter, 1980a). Lutz and Rhoads (1980) and Lutz (1982) recognized 4 distinct layers in the vent mussel *Bathymodiolus thermophilus*, including (1) fibrous prismatic calcite, (2) nacre (aragonite), (3) irregular prismatic aragonite (pallial myostracum), and (4) nacre (aragonite).

The shell microstructures in *Bathymodiolus thermophilus* are most similar to those in species of *Mytilus*, *Idasola*, and *Modiolus* (Carter, 1990). According to Carter (1990), the outer shell layer of *B. thermophilus* is calcitic with outer homogeneous and inner, predominantly fibrous prismatic sublayers. The middle and inner shell layers are largely comprised of nacre, with minor irregular simple prismatic structure. Hence, the findings of Carter (1990) corroborate those of Lutz and Rhoads (1980) and Lutz (1982).

Carter (1990) noted that the outer shell layer of mytilids in general shows considerable mineralogical and microstructural variability. In studies of mytilids from the Carboniferous to Recent, some species exhibit a calcitic fibrous outer shell layer, whereas other species have various, different calcitic and/or aragonitic prismatic, homogeneous, and even minor crossed structures in this layer. Waller (1978) generalized that a calcitic outer shell layer in the Mytiloida, where present, consists of regular fibrous prismatic structure. Carter (1990), however, identified various combinations of aragonitic and/or calcitic irregular simple prismatic, irregular spherulitic prismatic, irregular fibrous prismatic, regular fibrous prismatic, and homogeneous structures in the outer shell layers of this order.

The shell microstructures of the 6 undescribed mytilid species investigated in this study contain 4 calcified shell layers composed of aragonite and calcite, although differences in the layers can be significant owing to various combinations of aragonitic and/or calcitic structures present within the shell layers. The arrangement of shell layers can also vary appreciably from one part of a mytilid shell to another, because of alternating adductor myostraca, dissolution, or other effects. Thus, in the assessment of shell microstructure patterns, careful examination of the entire shell is necessary, as conducted in this study. These differences in shell microstructure appear to be of great potential value in systematic studies of mytilids from deep-sea hydrothermal-vent and cold-water sulfide/methane seep environments.

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Molluscan Taxa and Bibliography of Henry van der Schalie

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Henry van der Schalie was born in Amsterdam, The Netherlands, on January 8, 1907. His family immigrated to the United States in 1909, following the death of his father, and settled in Paterson, New Jersey. Van left New Jersey in 1925 to enroll in Calvin College, Grand Rapids, Michigan. During his undergraduate studies, he developed an interest in parasitology. After receiving his A.B. in 1929, Van began graduate studies in parasitology at the University of Michigan (UM) under George R. LaRue, Chair of the Department of Zoology. But before long he accepted an assistantship in and transferred to the Mollusk Division of the Museum of Zoology at UM. He received an M.S. in 1931 and Ph.D. in 1934. Thus began a career in malacology at the Museum of Zoology that extended from his initial appointment as a museum assistant in 1929 to his retirement as curator of mollusks and professor of zoology in 1977. A review of activities in the Division of Mollusks during this period is presented in van der Schalie (1981).

Van became assistant curator of mollusks in 1934 and was promoted to curator of mollusks in 1944 following the retirement of Calvin Goodrich. Initially appointed as an instructor of zoology (1937–1944), he later held assistant (1944–1950), associate (1950–1956), and full professorships (1957–1977) in the Department of Zoology, UM, and served in visiting or adjunct capacities at other institutions. With the onset of World War II, his research returned to parasitology. He studied mollusks as vectors for various diseases, particularly schistosomiasis. Subsequently, he served on numerous national and international committees and as a consultant to various international organizations involved in medical malacology. Van was widely known as a researcher, educator, and advocate in malacology, parasitology, environmental conservation, and general education. He received many research grants and was member of numerous professional societies. In recognition for his early contributions to malacology, the fossil alasmidontine (Bivalvia: Unionoidea) taxon, *Vanderschalica* Modell (1943: 112; type-species: *Unio kolasii* Modell, 1931), was named after him. Although retiring as curator emeritus from the University of Michigan in 1977, he did not cease his professional interests and continued his research and advocacy until his death on 15 April, 1986.

In addition to data in van der Schalie (1981), biographic information has appeared in Kraemer and Berry (1986) and Abbott (1987); however, none of these references listed or reviewed his publications or the taxa that he described. Van der Schalie published 142 manuscripts during the period of 1932–1986. Several of these works were published initially as a summary or an abstract, with the complete version of the paper published later in a different journal. A few papers were reprinted in other journals; in the following bibliography, the subsequent printing is noted in parentheses after the original reference. Between 1934 and 1939, Van co-authored 3 new species of prosobranch (Hydrobiidae) and 4 pulmonate (1 Ancylidae, 2 Oleacinidae, 1 Sagdidae) gastropods from Guatemala with his mentor, Calvin Goodrich, and described 3 new species of unionoid bivalves (2 from the United States, 1 from Canada).

MOLLUSCAN TAXA

Abbreviations: CM = Carnegie Museum, Pittsburg, Pennsylvania; UF = Florida Museum of Natural History, University of Florida, Gainesville; UMMZ = Museum of Zoology, University of Michigan, Ann Arbor.

aguadae, Ferrissia (*Laevapex*) Goodrich and van der Schalie, 1937 (15 March), Miscellaneous Publications, Museum of Zoology, University of Michigan 34:23, pl. 1, fig. 7–7a ; type locality: Aguada de Copó, one mile south of La Libertad, Petén, Guatemala. Holotype: UMMZ 65583. The generic allocation of this species is uncertain.

alvaradoi, Spiraxis Goodrich and van der Schalie, 1937 (15 March), Miscellaneous Publications, Museum of Zoology, University of Michigan 34:23, pl. 1, fig. 1; type locality: limestone knoll five miles north of El Paso de los Caballos, Petén, Guatemala. Holotype: UMMZ 65165.

brooksiana, Anodonta van der Schalie, 1938 (4 June), Annals of the Carnegie Museum 27:167, pl. 16; type locality: Spout Pond Arm, Ferryland District, Southern Shore, Newfoundland. Holotype: CM 61.13137. The taxonomic status of this species is not clear. (W. R Hoeh, personal communication).

clenchi, Somatogyrus Goodrich and van der Schalie, 1937 (15 March), Miscellaneous Publications, Museum of Zoology, University of Michigan 34:37, pl. 1, fig. 6; type locality: Río de la Pasión, Sayaxché, Petén, Guatemala. Holotype:

UMMZ 65371. *Aroapyrgus clenchi* (*fide* Hershler and Thompson, 1992).

francesae, *Cochliopa* Goodrich and van der Schalie, 1937 (15 March), Miscellaneous Publications, Museum of Zoology, University of Michigan 34:38, pl. 1, fig. 3; type locality: Río de la Pasión, at the mouth of Arroyo Chajchinic, northwest of Porvenir, Alta Vera Paz, Guatemala. Holotype: UMMZ 65338. *Cochliopina francesae* (*fide* Hershler and Thompson, 1992).

funibus, *Spiraxis* Goodrich and van der Schalie, 1937 (15 March), Miscellaneous Publications, Museum of Zoology, University of Michigan 34:23, pl. 1, fig. 2; type locality: limestone knoll five miles north of El Paso de los Caballos, Petén, Guatemala. Holotype: UMMZ 65166.

jonesi, *Lampsilis* van der Schalie, 1934 (4 May), The Nautilus 47(4):125, pl. 15, fig. 1a-b, 2, 3a-b; type locality: Pea River, Preston's Mill, Dale County, Alabama. Type material originally was deposited in the Alabama Museum of Natural History; however, the malacological collection of that museum was given to the Florida Museum of Natural History with several lots subsequently transferred to the Museum of Comparative Zoology, Harvard University (F.G. Thompson, personal communication). Lectotype: UF 65558, designated by Johnson (1967; the specimen selected was the male figured in van der Schalie, 1934). *Ptychobranchus jonesi* (*fide* Athearn, 1964).

mcglameriae, *Medionidus* van der Schalie, 1939 (24 June), Occasional Papers, Museum of Zoology, University of Michigan 407:1, pl. 1; type locality: Tombigbee River, Epes, Sumpter County, Alabama. Holotype: UMMZ 130460.

pasionensis, *Amnicola* Goodrich and van der Schalie, 1937 (15 March), Miscellaneous Publications, Museum of Zoology, University of Michigan 34:36, pl. 1, fig. 4; type locality: Arroyo Subín, tributary of the Río de la Pasión, about two miles above Santa Teresa, Petén, Guatemala. Holotype: UMMZ 65357. *Aroapyrgus pasionensis* (*fide* Hershler and Thompson, 1992).

taintori, *Xenodiscula* Goodrich and van der Schalie, 1937 (15 March), Miscellaneous Publications, Museum of Zoology, University of Michigan 34:26, pl. 1, fig. 5, 5a-b; type locality: woodland just east of El Paso de los Caballos, Petèn, Guatemala. Holotype: UMMZ 65177.

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A New *Favartia (Murexiella)* from the Panamic Province (Gastropoda: Muricidae) and Designation of a Lectotype for *F. (M.) exigua* (Broderip, 1833)

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ABSTRACT

A new species of *Favartia* (*Murexiella*) is described from the eastern Pacific Ocean and compared with similar species *F* (*M*) *exigua* (Broderip, 1833) and *F.* (*M.*) *lappa* (Broderip, 1833). *Favartia venustula* Poorman, 1983, is found to be a junior synonym of *F.* (*M.*) *exigua*, and a lectotype is designated for *F.* (*M.*) *exigua*

Key words: eastern Pacific, new species, Costa Rica, Ecuador, México, Panamá.

INTRODUCTION

Over ten years ago, Carol Skoglund of Phoenix, Arizona, brought to the Marine Invertebrate Department of the San Diego Natural History Museum several specimens of a species of *Favartia* for identification. Anthony D'Attilio, then Acting Curator, and the authors examined the specimens, noting that they were similar to *F. exigua* (Broderip, 1833). But, at the time, no type or comparative material was available to us.

Since then, we have examined twenty-two specimens of this species from the Hertz, Kaiser, Koch, Shasky and Skoglund collections. We studied the type material of the three more similar species, *F.*(*M.*) *exigua*, *F.*(*M.*) *radicata* (Hinds, 1844), junior synonym of *F.* (*M.*) *lappa* (Broderip, 1833), and *F.* (*M.*) *venustula* Poorman, 1983, as well as comparative material of other eastern Pacific *Favartia* (*Murexiella*). As a result, we determined that the specimens belong to an undescribed species.

The following abbreviations for institutions are used in the text: AMNH, American Museum of Natural History; BMNH, The Natural History Museum, London; SBMNH, Santa Barbara Museum of Natural History; SDNHM, San Diego Natural History Museum; USNM, National Museum of Natural History, Smithsonian Institution.

SYSTEMATICS

Family Muricidae Rafinesque, 1815
Subfamily Muricopsinae Radwin and D'Attilio, 1971
Genus *Favartia* Jousseaume, 1880
Subgenus *Murexiella* Clench and Pérez-Farfante, 1945
Favartia (Murexiella) paulskoglundi new species
(Figures 1–5)

Description: Shell small, up to 17.1 mm length × 11.2 mm width, biconic, spire elongate. Protoconch of three pale tan, pustulose turbinate whorls, buttressed on last whorl. Teleoconch of five whorls; suture indistinct; shoulder sloping; six or seven thickened varices on body whorl, eight or nine on penultimate whorl. Leading edge of varix foliate forming short, straight, open spines at periphery, spines occasionally slightly recurved. Aperture ovate, lip edge crenulate, lirate within reflecting spiral cords. Inner lip erect along entire length, smooth within; anal sulcus weakly defined. Siphonal canal of moderate length, straight, narrowly open to right, weakly recurved distally with two to four well-preserved canal terminations. Spiral sculpture of two strong cords on first three teleoconch whorls; penultimate whorl with two strong cords and a minor cord between, anterior to these are two additional, minor cords; shoulder with two or three minor cords. Body whorl with five strong major cords, interspaces each with a minor cord; gap between major cords and canal; two or three major cords on canal. Shoulder of body whorl with two to four minor cords. Entire shell surface lamellose, forming webbing between cord terminations. All major cords divided along their length by four incised lines. Operculum muricopsine, unguiculate, annulate centrally with basal nucleus. Shell color cream. Orange-brown flush on varices, spine terminations, and occasionally in intervarical area.

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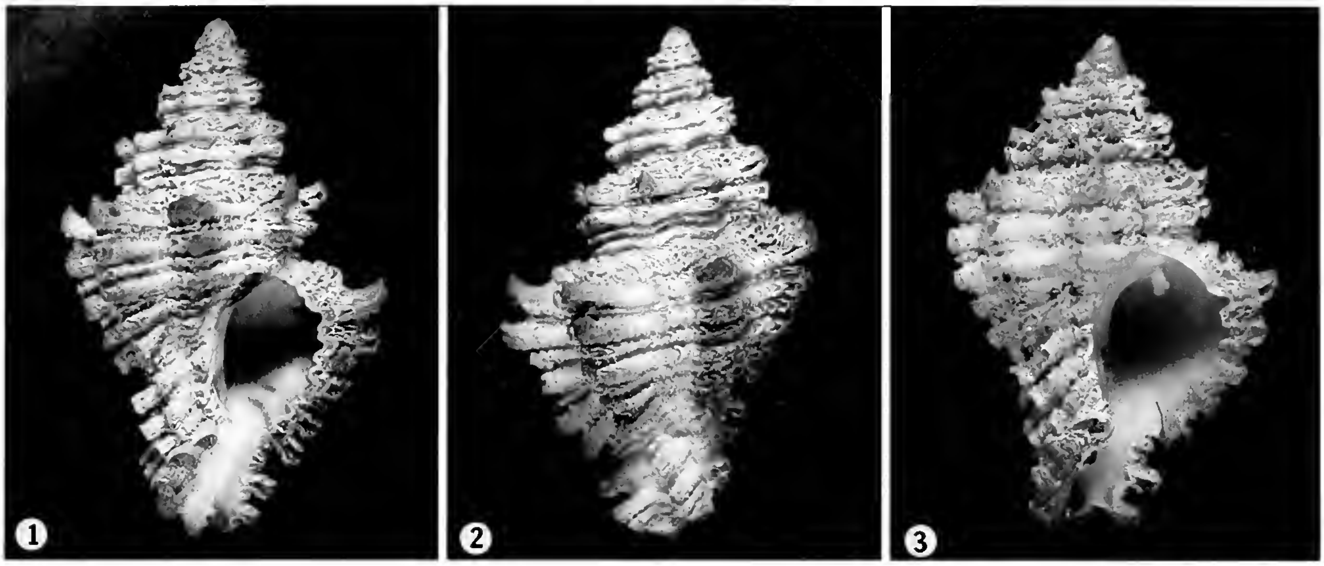


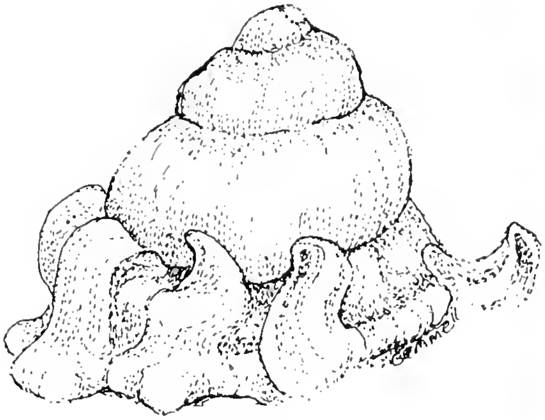
Figures 1–3. *Favartia (Murexiella) paulskoglundi* new species. Holotype, SDNHM 78066, 17.1×11.2 mm, Pedro Gonzales, Islas Las Perlas, Panamá, in 5.5 m. **1.** Apertural view; **2.** Dorsal view; **3.** Paratype A, USNM 880267, 8.5×5.1 mm, Isla la Plata, Ecuador.

Type material: Holotype: SDNHM 78066, 17.1×11.2 mm, type locality, R. Hubert coll., *ex* D'Attilio Collection, October 1971; Paratypes: Paratype A, USNM 8800267, 8.0×5.1 mm, Isla la Plata, Ecuador, 1°16′S, 81°05′10″W, D. R. Shasky coll., June 1979; Paratype B, Shasky Collection, 15.5×9.6 mm, same as Paratype A; Paratype C, SBMNH 144458, 10.4×5.9 mm, off Isla Viradores, Playas del Coco, Guanacaste, Costa Rica, 10°34′N, 85°34′W, dredged 9–15 m, R. Koch coll., 2–4 April 1986; Paratype D, Koch Collection, 10.2×6.0, same as Paratype C; Paratype E, AMNH 290728, 11.5×7.3 mm, S of Isla Chitre, Islas las Perlas, Panamá, 8°36′N, 79°4′W, dredged 15–18 m, C. and P. Skoglund and R. and W. Koch coll., 15 April 1984; Paratype F, Skoglund Collection, 13.4×7.9 mm, same as Paratype E; Paratype G, Skoglund Collection, 12.2×7.8 mm, same as Paratype E; Paratype H, Skoglund Collection, 11.6×7.8 mm, same as Paratype E; Paratype I, Shasky Collection, 16.2×10.5 mm, Isla Venado, Panamá, 8°52′30″N, 79°39′30″W, J. McDaniel coll., 8 September 1979; Paratype J, Shasky Collection, 12.9×7.8 mm, N side of Isla Salango, Ecuador, 1°35′15″S, 80°52′52″W, D. R. Shasky coll., 15 September 1978; Paratype K, Koch Collection, 11.5×7.2 mm, Isla Negritos Adentro, Golfo de Nicoya, Costa Rica, 9°57′N, 84°52′W, dredged 12–27 m, C. and P. Skoglund and R. and W. Koch coll., 8 May 1982; Paratype L, Koch Collection, 11.6×7.0 mm, Bahías de Huatulco, Oaxaca, México, 15°40′N, 96°08′W, dredged 9–30 m, R. and W. Koch , 2–4 June 1991; Paratype M, Koch Collection, 15.5×9.6 mm, same as Paratype E, 16 April 1984; Paratypes N-P: N, 14.6×9.0 mm; Paratype O, 12.7×8.2 mm; P, 12.5×7.3 mm, data for all same as Paratype E; Paratype Q, Skoglund Collection 10.1×6.9 mm, off Isla Viradores Sur, Playas del Coco, Guanacaste, Costa Rica, 10°34′N, 85°34′W, dredged 9–18 m, C. and P. Skoglund coll., April 1986; Paratype R, Skoglund Collection 12.1×8.2 mm, off Isla Ranchería, Golfo de Chiriquí, Panamá, 7°35′N, 81°40′W, dredged 24–36 m, C. and P. Skoglund coll., March 1986; Paratype S, Hertz Collection, 10.5×7.3 mm, Islas Tres Marietas, Nayarit, México, 21°41′N, 105°36′W, diving in 13.7 m, K. L. Kaiser coll., 22 February 1995; Paratypes T-U, K. L. Kaiser Collection: T, 12.6×7.9 mm; U, 10.9×7.4 mm, Bahía John Huston, Bahía Banderas, Jalisco, México, 20°30.55′N, 105°21.11′W, 9 m, in sand under rocks, 2 January 1995, K. L. Kaiser coll.

Type locality: Pedro Gonzales, Islas las Perlas, Panamá, 8°25′N, 79°05′W, 5.5 m depth.

Distribution: *Favartia (Murexiella) paulskoglundi* is known to occur from Islas Tres Marietas, Nayarit, México, its most northern locality, with an intermittent distribution south to Isla Salango, Ecuador, in 5.5–36.0 m depth.

Discussion: The new species was compared with the three syntypes of *Favartia (Murexiella) exigua* (BMNH 19841227, Figures 6, 7). Vokes (1988) considered *F. (M) exigua* to be a valid species and referred to the illustration of the largest syntype figured in Vokes (1984, pl. 2, fig. 3), although she erroneously considered *F. (M.) radicata* as a synonym of *F. (M.) exigua* in the 1984 paper. We have selected the largest specimen (16.2×9.4 mm) of the syntype series of *F. (M.) exigua* as the lectotype. Two smaller specimens (12.6×7.5 mm and 10.8×6.8 mm) are chosen as paralectotypes. *Favartia (M.) paulskoglundi* differs from *F. (M.) exigua* in having an indistinct suture and sloping shoulder with thickened varices, whereas *F. (M.) exigua* has an impressed suture and somewhat excavated shoulder with sharply elevated varices. The new species has five strong major cords with one minor cord in each interspace, whereas *F. (M.) ex-*



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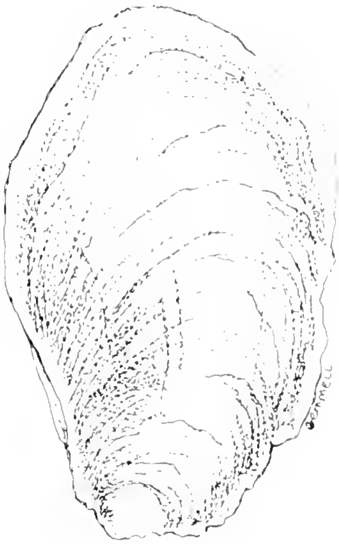

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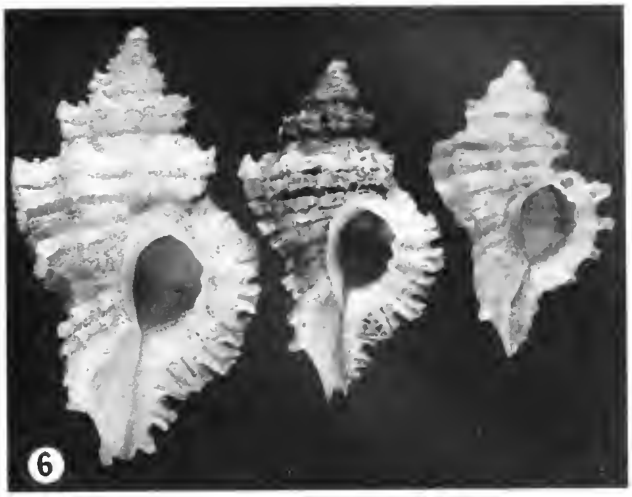
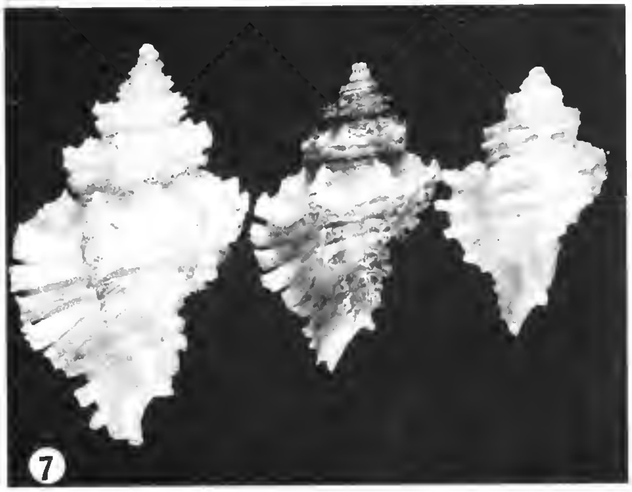
Figure 4, 5. *Favartia (Murexiella) paulskoglundi* new species. **4.** Paratype A, camera lucida drawing of protoconch (1.1 mm diameter). **5.** Paratype A, camera lucida drawing of operculum (3.5 mm length).

igua has five strong cords with no minor cords in the deeply-cut interspaces, the edges of the cords somewhat overlapping the interspaces.

Since Vokes (1970) stated that "the type of *M. lappa* is no longer to be found," the new species was compared with the holotype of *F. (M.) radicata* (Hinds, 1844) (BMNH 1907.10.28.136, Figure 8), a junior synonym of *F. (M.) lappa* (Broderip, 1833) (Radwin and D'Attilio, 1976; Fair, 1976) and comparative material of *F. (M.)*





Figures 6, 7. *Favartia (Murexiella) exigua* (Broderip, 1833), BMNH 1984122, syntype lot. Locality: "?Salango". **6.** Apertural view. **7.** Dorsal view. Largest specimen, 16.2×9.4 mm, selected as lectotype. Two smaller specimens, 12.6×7.5 mm and 10.8×6.8 mm, selected as paralectotypes. Specimens photographed with kind permission of the trustees of The Natural History Museum, London.

lappa in private collections. *Favartia (M.) paulskoglundi* differs from *F. (M.) lappa* in the number of spiral cords on the body whorl, five major cords with strong minor cords between on the new species, and five major cords with two strong minor cords on the shoulder and no minor cords on the body whorl on *F. (M.) lappa*. In *F. (M.) paulskoglundi* there are six to seven varices which do not obscure the indistinct suture, whereas in *F. (M.) lappa* the five varices project above and obscure the suture. The type species of *F. (M.) radicata* had no remaining protoconch.

Comparisons between the new species and *F. (M.) venustula* (holotype, SDNHM 81610), show that *F. (M.) venustula* and *F. (M.) exigua* are conspecific. Both species are of comparable size with similar protoconchs (*F. (M.) exigua* with slightly more than 2.5 smooth, convex whorls and *F. (M.) venustula* with 3 smooth, convex

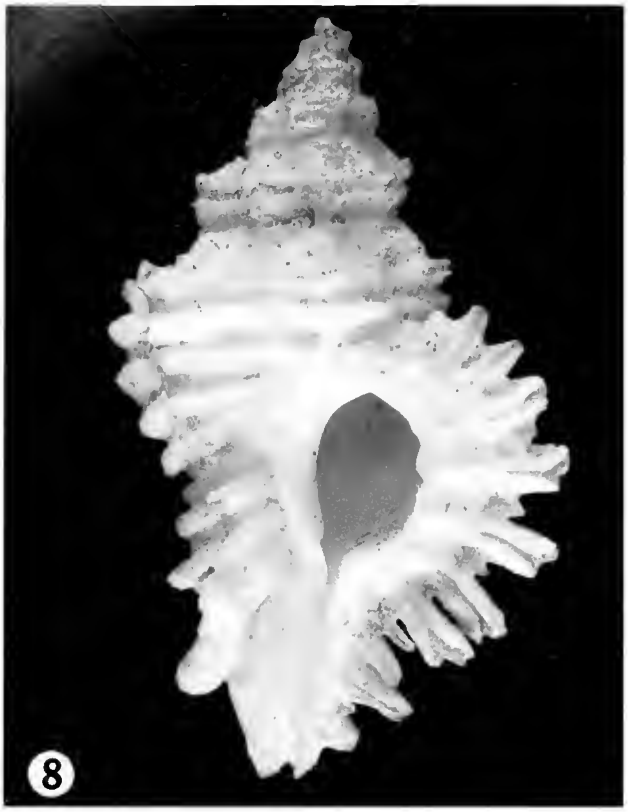


Figure 8. *Favartia (Murexiella) radicata* (Hinds, 1844). Holotype, BMNH 1907.10.28.136, 19.8×11.7 mm. Apertural view. From: "...San Blas, west coast of Mexico. From 11 fms." Junior synonym of *Favartia (Murexiella) lappa* (Broderip, 1833). Specimen photographed with kind permission of the Trustees of The Natural History Museum, London.

whorls); both have teleoconchs with 5 whorls and 7 sharp varices crossing the suture to the preceding whorl. Both species have 2 spiral cords on the spire, 5 flattened spiral cords on the body whorl with incised threads along their length and deep interspaces lacking minor cords. The oval aperture with shallow anal sulcus and moderately long canal narrowly opened distally are characters of both species. Therefore *F. (M.) venustula* is considered to be a junior synonym of *F. (M.) exigua.*

Etymology: The species is named for the late Paul Skoglund of Phoenix, Arizona, who actively participated in the collection of deep-water Panamic species and designed a tube-pulley arrangement for small boat dredging.

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Robert Koch, Donald R. Shasky and Carol Skoglund made specimens available for study and each donated paratypes. Kirstie Kaiser also lent specimens for study. The Natural History Museum, London, sent type material on loan. Henry W. Chaney (SBMNH) was helpful in providing coordinate information, David K. Mulliner photographed all the type specimens and Joyce Gemmell made camera lucida drawings of details of the new species. The San Diego Natural History Museum made their facilities available to us. Emily H. Vokes reviewed a draft of the manuscript and made helpful suggestions. To all of them we express our gratitude.

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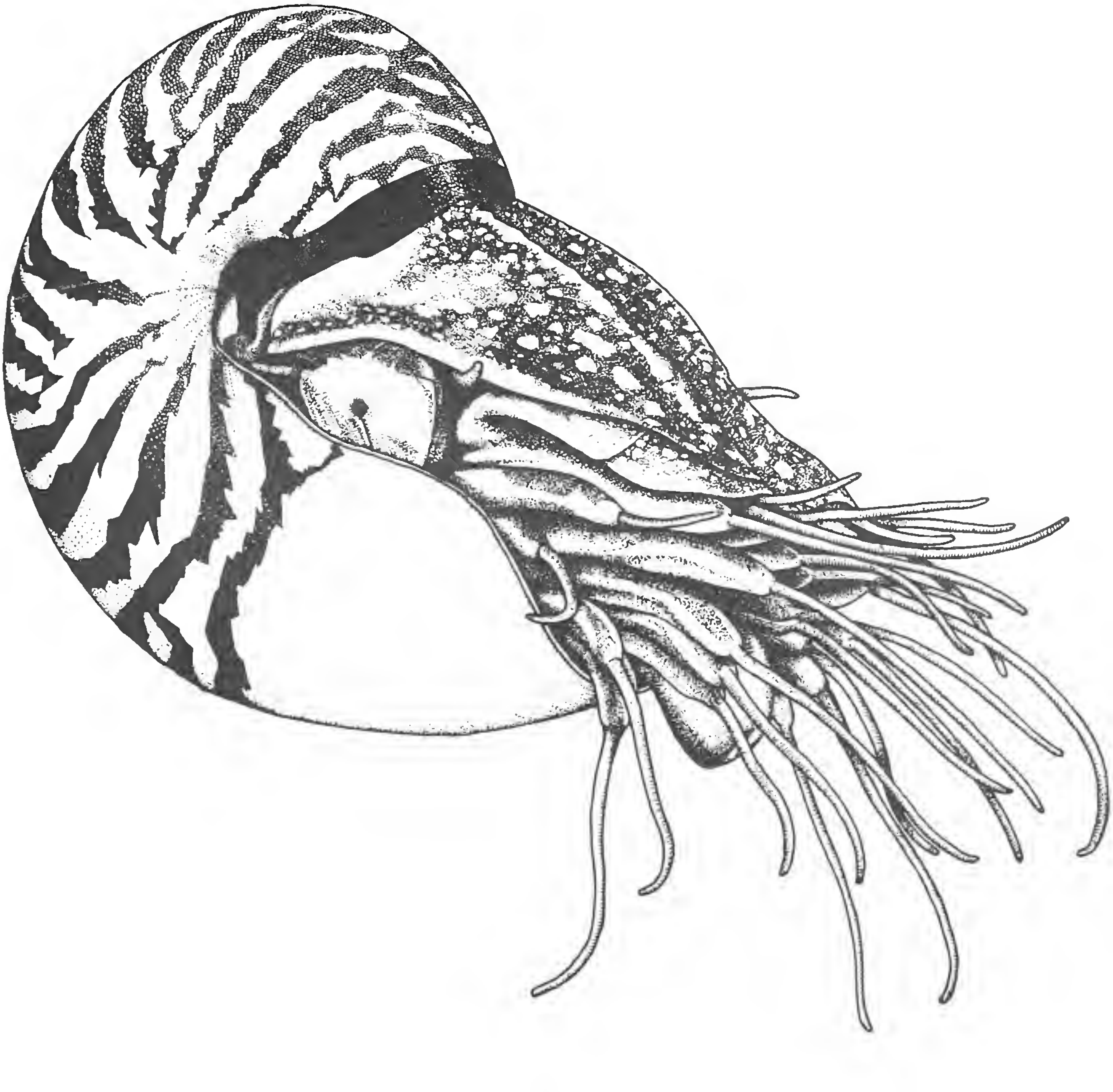

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Pulvinites exempla (Hedley, 1914) from the New Zealand Region (Bivalvia: Pulvinitidae)

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ABSTRACT

Pulvinites exempla (Hedley, 1914), hitherto known only from New South Wales and Victoria, Australia, is newly recorded from Fiordland, southwestern South Island, New Zealand, off Curtis Island, Kermadec Islands, and Tasmania. *Pulvinites exempla* is the only known living member of the Pulvinitidae, a family known otherwise only from the Mesozoic era and Paleocene epoch.

Key words: Pulvinitidae, *Pulvinites exempla*, new records, New Zealand

INTRODUCTION

During a recent search for certain bivalves in collections from Fiordland at the National Institute of Water and Atmospheric Research, Wellington, I was astonished to find 3 specimens of a large pulvinitid in a sample dredged from Dusky Sound, New Zealand. Steve O'Shea, the curator of this collection, subsequently located 2 additional valves from the Kermadec Ridge. During a recent sampling program in Fiordland, at my request, Paul Brewin and associates (Otago University) sought and successfully videotaped animals *in situ* on fiord walls at 269–285 meters depth. New Zealand and Kermadec Islands specimens are very similar to the holotype and other Australian specimens of *Pulvinites exempla* (Hedley, 1914). This is the only known living member of the Pulvinitidae, a family known otherwise only from the Mesozoic of Europe, North America and Antarctica, and the Paleocene of California (Zinsmeister, 1978; Palmer, 1984).

Pulvinitids resemble isognomonids in gross shell morphology, but differ in that the byssus passes through a foramen in the right valve instead of a marginal byssal notch. Abbreviations and text conventions are: AMS, Australian Museum, Sydney; BMNH, The Natural History Museum, London; NZOI, National Institute of Water and Atmospheric Research, Wellington; ROV, remotely operated vehicle; TM, Tasmanian Museum, Hobart.

SYSTEMATICS

Class Bivalvia Linnaeus, 1758
Superfamily Pterioidea Gray, 1847
Family Pulvinitidae Stephenson, 1941
Genus *Pulvinites* Blainville, 1824

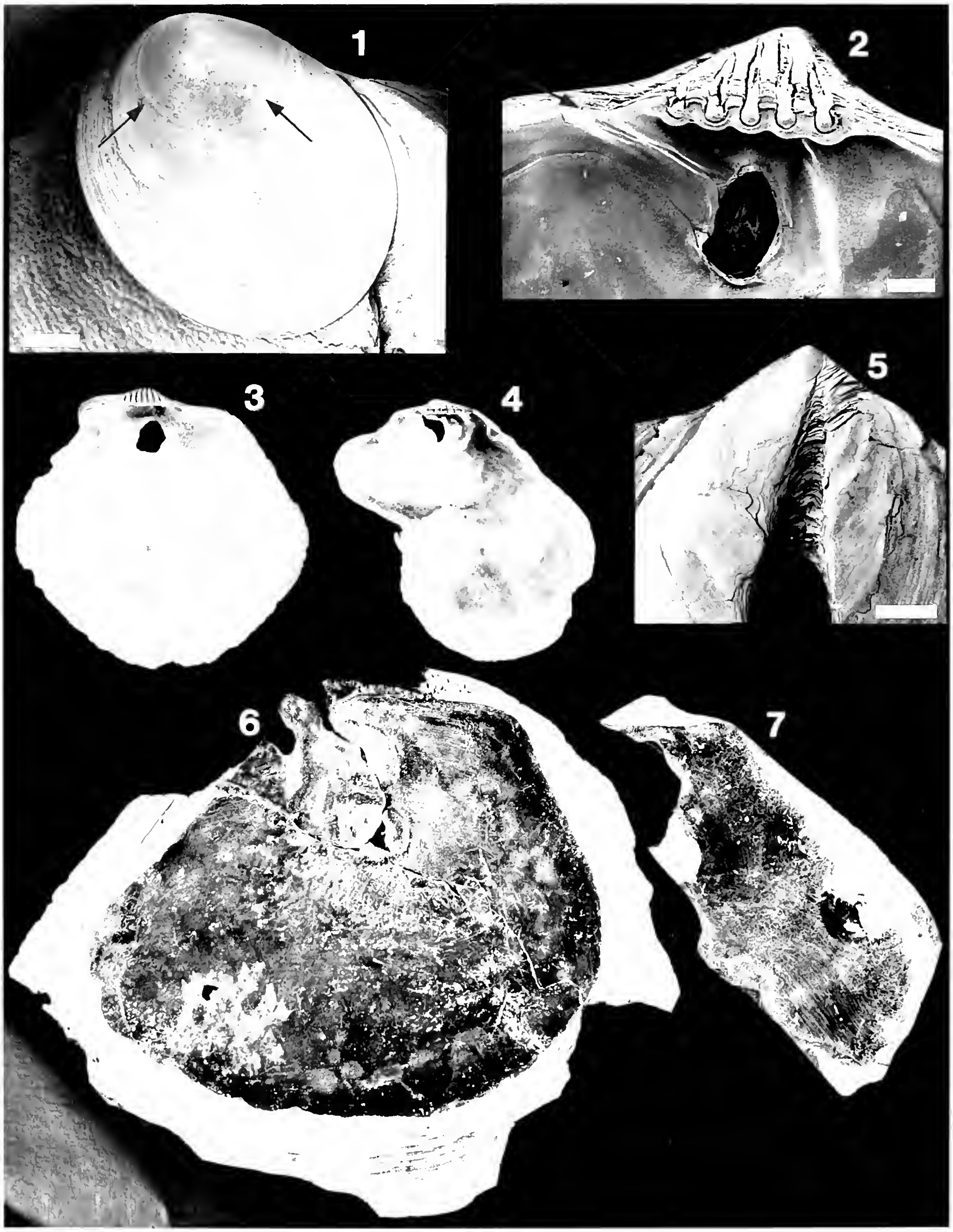
Pulvinites Blainville, 1824: 316. Type species (monotypy): *Pulvinites adansonii* Blainville, 1824; Late Cretaceous, France.

Hypotrema d'Orbigny, 1853: 435. Type species (by subsequent designation of Cox, 1969): *Pulvinites rupellensis* d'Orbigny, 1850, Late Jurassic, France.

Foramelina Hedley, 1914: 70. Type species (by original designation): *Foramelina exempla* Hedley, 1914, Recent, southeastern Australia.

Remarks: Pulvinitids are considered to be a group derived from Isognomonidae, in which the byssal sinus in the right valve has become enclosed to form a foramen by fusion of the dorsal and ventral margins (Cox, 1969; Palmer, 1984). Ventral displacement and enlargement of the foramen is marked on the exterior of the valve (only) by a concave groove extending dorsoventrally from the anteroventral margin of the prodissoconch (Figure 5). On the interior surface (only), extending posteriorly from the anterior corner of the ligamental platform to the foramen, is a narrow suture that is formed whole and incrementally throughout ontogeny, earlier suture lines being covered by subsequent deposition of shell material (Figure 2). In other words, the posterior extremity of the sinus (the foramen) remains at a more or less central position relative to the umbones, and both the foramen and the whole internal suture line migrate ventrally as the shell enlarges. The suture line is formed throughout life by secretion from the sides of the byssal embayment, and therefore does not mark the course followed by the byssus during ontogeny as implied by Conrad (1867), Hedley (1914) and Palmer (1984).

Cox (1969) suggested that formation of a foramen may have occurred independently in *Foramelina* because of the absence of a byssal suture in fossil species, though the latter have them too, and Recent and fossil species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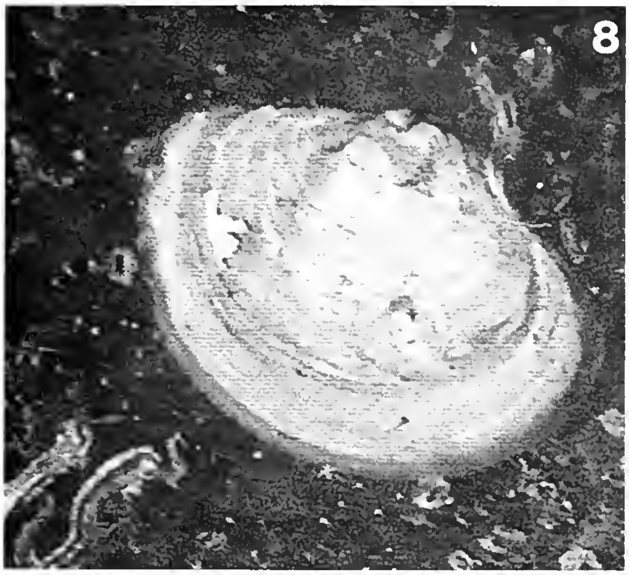

Figures 8, 9. *Pulvinites exempla* (Hedley). *In situ* individuals on wall of Bradshaw Basin, Bradshaw Sound, Fiordland, New Zealand, 285 m (digitized images ex-ROV videotape). Judging from tubeworms each is about 70 mm in maximum dimension. The small bivalve attached to the individual in Figure 8 is probably a juvenile *Pododesmus zelandicus* (Gray, 1843).

are closely similar (Palmer, 1984). If pulvinitids are derived from Isognomonidae, as suggested by Palmer (1984), it may be more appropriate to group Pulvinitidae as a subfamily of Isognomonidae; comparative anatomical data are, however, wanting.

Pulvinites exempla (Hedley, 1914)
(Figures 1–9)

Foramelina exempla Hedley, 1914: 71, pl. 11, fig. 6, pl. 12, fig. 7, 8. Cox, 1969: 326, fig. 3a, b; Tenner, 1981: 3.
Pulvinites exempla.—Palmer, 1984: 823, pl. 72, fig. 6.

Description: Shell large (width up to 130 mm), flattened, brittle, ostreiform, irregularly shaped though generally subcircular or subtrapezoidal, attached to substratum by bundle of strong, chitinous, byssal threads that pass through a foramen in right valve below ligamental plate. Right valve more or less flat, internally with a subcircular adductor scar at about dorsal third, and a narrow suture line extending from anterior end of ligamental plate to byssal foramen; left valve weakly convex, internally with a subcircular byssal pedal retractor muscle scar opposite foramen in right valve, below which, at about dorsal third, is a smaller, subcircular adductor muscle scar. Shape of the muscle scars and the distance between them variable in material examined. Hinge edentulous, wide trigonal ligamental plate with series of narrow, elongate, subparallel, transverse ligament grooves. Prodissoconch (AMS C.129659) globular, subcircular, smooth apart from collabral growth lines, prodissoconchs I and II clearly separated (widths 230 µm and 630 µm). Periostracum rather thick, yellowish brown, readily exfoliating and very brittle when dry. Interior nacreous-bronze.

Type material: Holotype (AMS C.170923) and paratype (AMS C.37004), both collected alive.

Type locality: South of Gabo Island, Victoria, 183–457 m.

Other material examined: Off Passage Point, Bowen Channel, Dusky Sound, Fiordland, New Zealand, 45°44.3′S, 166°44.8′E, 148 m, collected alive, 8 June 1961 (2 large valves from 2 individuals, and 1 live subadult, NZOI stn B490); off Curtis Island, Kermadec Islands, 30°31′S, 178°39′W, 710–725 m, 27 March 1982, R/V *Tangaroa* (2 valves from 2 individuals, NZOI stn T256); E of Sydney, New South Wales, ca 400m, March 1980 (1 pair, AMS C.122000); off Sydney, ca 457 m, August 1980 (AMS C.126893);

←

Figures 1–7. *Pulvinites exempla* (Hedley). **1, 2, 5.** Right valve of live-taken juvenile, NNE of Sydney, New South Wales, ca 400 m, AMS C.129659. **1.** Prodissoconch, boundary between PI and PII indicated by arrows. **2.** Interior showing hinge plate, foramen and suture line (arrow). **5.** Exterior showing prodissoconch, and channel with growth lines formed by ventrally migrated foramen. **3.** Interior of right valve, off Curtis Island, Kermadec Islands, 710–725 m, NZOI stn T256. **4, 6, 7.** Interiors of left (6) and right (4, 7) valves, off Passage Point, Bowen Channel, Dusky Sound, Fiordland, New Zealand, 148 m, NZOI stn B490. Scale bar for figure 1 = 100 µm, figures 2, 5 = 1 mm, figures 3, 4, 6, 7 approximately natural size.

NNE of Sydney, alive, 406 m, 16 July 1981 (many from wing of sunken aircraft, AMS C.129659); Mackas Hill, SE Tasmania, 44°13′S, 147°03′E, 750–900 m, 29 January 1997, R/V *Southern Surveyor* stn SS01/97–52 (2 valves, TM E21041).

Other records: Wall of Bradshaw Basin, Bradshaw Sound, Fiordland, New Zealand, 45°17.43′S, 167°01.31′E, 285 m, 20 May 1997, videotaped *in situ* by ROV (2 individuals recognised; Figures 8, 9); Kellard Basin, Doubtful Sound, Fiordland, New Zealand, 45°21.70′S, 167°03.84′E, 269 m, 22 May 1997, videotaped *in situ* by ROV (2 individuals recognized).

Distribution: Southeastern Australia, Fiordland, New Zealand, and Kermadec Islands, 148–ca. 900 m, taken alive at 148–ca. 400 m. Living attached by byssus to rock and other solid surfaces.

Remarks: The large prodissoconch II indicates planktotrophic larval development (Figure 1). Judging from the large sample from off New South Wales (AMS C.129659), and the 2 specimens from Fiordland, adult shell morphology is very variable, and confirmation of conspecificity must await comparison of additional specimens and anatomy. Accordingly, it is at the moment impossible to tell whether Australian and New Zealand populations represent a single species whose conspecificity is maintained through periodic recruitment of larvae from Australia (via the East Australian Current), or if they are allopatric descendants of a common ancestor whose distribution became disjunct, perhaps as a result of seafloor spreading in the Tasman Basin (Late Cretaceous to Early Eocene). Unfortunately, the Fiordland specimens lack prodissoconchs, but the prodissoconch on a Kermadec Islands valve, though worn, is similar to Australian ones in shape and size. Unless additional material indicates otherwise, it seems appropriate to interpret specimens from Australia, New Zealand, and the Kermadec Islands as a single, widely distributed species with a planktonic larval stage of exceptionally long duration.

In Fiordland, *Pulvinites exempla* occurs in shallower water than elsewhere (148–285 m versus ca. 400–900 m), so it would seem to be another example of deep-water emergence associated with unusual hydrological conditions in Fiordland (Grange *et al.* 1981; Ryan and Paulin, 1998).

In videotape footage from Fiordland, individuals of *Pulvinites exempla* were detected on clean, more or less vertical rock faces, and were easily discernible due to their shape and yellowish coloration contrasting against the darker rock (Figures 8, 9). They could not be detected (obscured?) on extensive areas of near-vertical wall covered with a thin sediment film. *Pulvinites exempla* was by far the largest bivalve visible in any of the images, and was very thinly and patchily distributed.

ACKNOWLEDGMENTS

I am grateful to Paul Brewin and associates (Otago University, Dunedin) for videotape footage of Fiordland, Karen Gowlett-Holmes (Commonwealth Scientific and Industrial Research Organisation, Tasmania) and Ian Loch (Australian Museum, Sydney) for loan of Australian material and access to collections, Steve O'Shea (National Institute of Water and Atmospheric Research, Wellington) for access to New Zealand specimens, and to Norman Heke (Museum of New Zealand, Wellington) for the photography.

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Acrorbis petricola Odhner, 1937 (Gastropoda: Pulmonata: Planorbidae) at Iguazú, Misiones, Argentina, and the Rediscovery of the Type Series of *Acrorbis odhneri* Hylton-Scott, 1960

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ABSTRACT

The presence of *Acrorbis petricola* Odhner, 1937, a rare planorbid species, at Iguazú Falls, Misiones, Argentina is here reported. Upon the analysis of these specimens and of types of *Acrorbis odhneri* Hylton Scott, 1960 (=*A. petricola*) (rediscovered at the Museo de La Plata malacological collection), details of shell morphology and data on intraspecific shell variation are given. Differences in shell anatomy of the specimens from Iguazú (e.g., less developed whorl, depressed spire, shell aperture not oblique) in relation to previous descriptions are here analyzed and regarded as a possible response to dislodgement by the strong water current, which is one of the relevant environmental characteristics at the collection site. A detailed scanning electron microscope study of the radulae, and comments on the anatomy of the terminal male genital system, are also given.

INTRODUCTION

The genus *Acrorbis* Odhner, 1937, is atypical of the Planorbidae, and has attracted the interest of several authors (Pilsbry, 1938; Baker, 1945; Hubendick, 1955; Paraense & Deslandes, 1959). Paraense (1986) regarded the genus to be monotypic. However, Rumi (1986) recognized 2 nominal species: *Acrorbis petricola* Odhner, 1937, and *Acrorbis odhneri* Hylton-Scott, 1960.

At present, the genus is known only from a restricted geographical area in northeastern Argentina and southern Brazil (Paraense, 1975; Rumi, 1991; Ageitos de Castellanos & Miquel, 1991), where the species inhabit rocky substrates covered by moss and algae close to rapids and waterfalls.

Odhner (1937) described *A. petricola* from specimens collected at Nova Teutonia (27°16′S, 52°20′W), Santa Catarina, Brazil. Paraense and Deslandes (1959), based on radular morphology and anatomy of the male genital system, treated *A. petricola* as a member of the genus *Drepanotrema*, as previously suggested by Pilsbry (1938). Hylton-Scott (1960) described a second species, *Acrorbis odhneri*, from specimens collected at Salto Encantado (27°03′S, 54°50′W), located on the headwaters of Cuñapirú Brook, near Aristóbulo del Valle, Department of Cainguas, central Misiones, Argentina, a site close to the type locality of *A. petricola*. Moreover, Hylton-Scott (1960) excluded *Acrorbis* from the family Planorbidae and proposed a new family, Acrorbidae, to include the 2 known species, based on a misinterpretation of radular morphology, especially that of the marginal teeth.

After an analysis of shell and radular morphology of 23 specimens from Salto Encantado, the type-locality of *Acrorbis odhneri*, Paraense (1986) concluded that *A. odhneri* is a junior synonym of *A. petricola*, and provided evidence to support the inclusion of the genus *Acrorbis* in the family Planorbidae.

Rumi (1986) reported the presence of the genus *Acrorbis* from Saltos de Apipé, Corrientes, Argentina (27°27′S, 56°42′W), based on the collection of several dead shells, and noted a number of differences in shell morphology between the known species. The lack of soft parts did not allow her to determine the specific identity of the reported specimens. This collection site, which is now under water and inaccessible due to the filling of the Yacyretá Dam empoundment, had environmental characteristics similar to those of previously known localities for the genus. In a review of Argentinean Planorbidae, Rumi (1991) considered *A. odhneri* to be a valid species, making no reference to the specimens from Saltos de Apipé. The known geographical range for the genus *Acrorbis* had been limited to 1 locality in southern Brazil (Nova Teutonia, Santa Catarina State), and 2 localities in northeastern Argentina (Salto Encantado, Misiones Province, and Saltos de Apipé, Corrientes Province). This paper reports a new record of *Acrorbis petricola* from Salto Dos Hermanas, Iguazú Falls, Misiones, Argentina (25°35′S, 54°35′W), and includes data on radular morphology and variability in shell shape. Shell measurements and scanning electron micrographs of the type specimens of *Acrorbis odhneri* from the collection of M. I. Hylton-Scott, recently deposited in the Department of Invertebrates of Museo de La Plata (MLP), are also given.

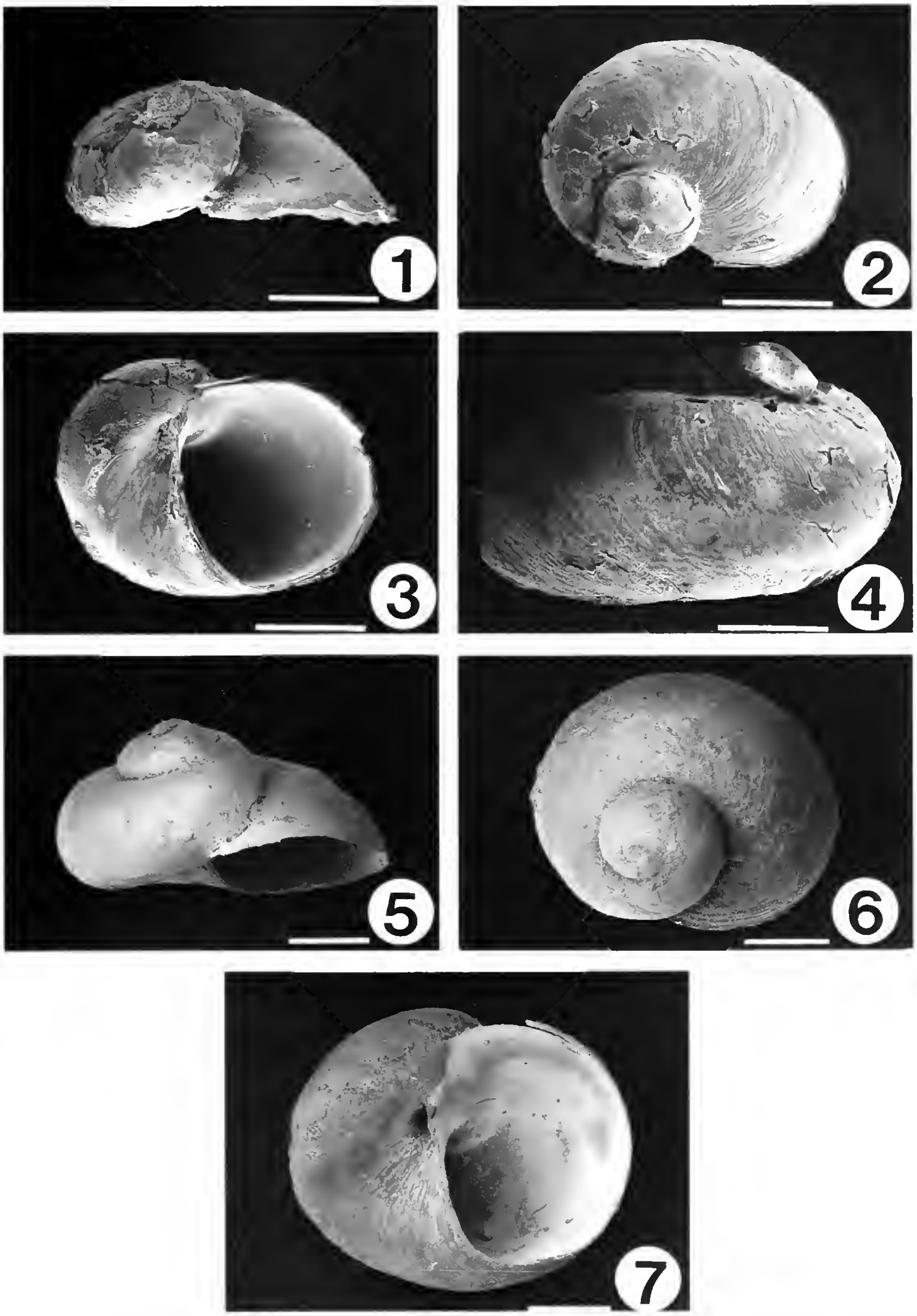
MATERIAL AND METHODS

Several specimens of *Acrorbis petricola* (MLP 5090) were collected on a basaltic cliff behind the waterfall known as Salto Dos Hermanas at the Iguazú National Park, Misiones, Argentina. The rocky wall was densely covered by mosses and epilithic algae, whose rapid growth is favored by the permanent, localized spray of water. The specimens were fixed *in toto* in a 10% formalin solution immediately after being relaxed by brief immersion in warm water (50°C for 2–3 minutes). The specimens of *Acrorbis* were collected together with other gastropod mollusks such as *Chilina megastoma* Hylton-Scott, 1958 and *Potamolithus* sp.; the samples were analyzed 3 years later. For this reason, the shells were seriously damaged by the corrosive action of the formalin. However, 2 shells were preserved intact. Prior to dissection, specimens were rinsed for 24 hours in an aqueous solution of 5% formalin and 2% acetic acid. The radulae were extracted from the bucal mass under a stereoscopic microscope, treated for 2 hrs in a 10% potassium hydroxide solution, rinsed in distilled water and mounted on stubs for observation under scanning electron microscope (SEM). Shell measurements were taken following the criteria: shell length and shell width as the maximum and minimum diameters respectively, taken along the basal shell plane; shell height as the maximum perpendicular distance between the basal shell plane and the apex (or the most distant point on the shell surface); aperture length as the maximum distance across the aperture and parallel to the maximum diameter axis. Shells of 7 syntypes of *A. odhneri* (MLP 5089) from Salto Encantado, Cainguas, central Misiones were measured and photographed under the SEM for comparative purposes.

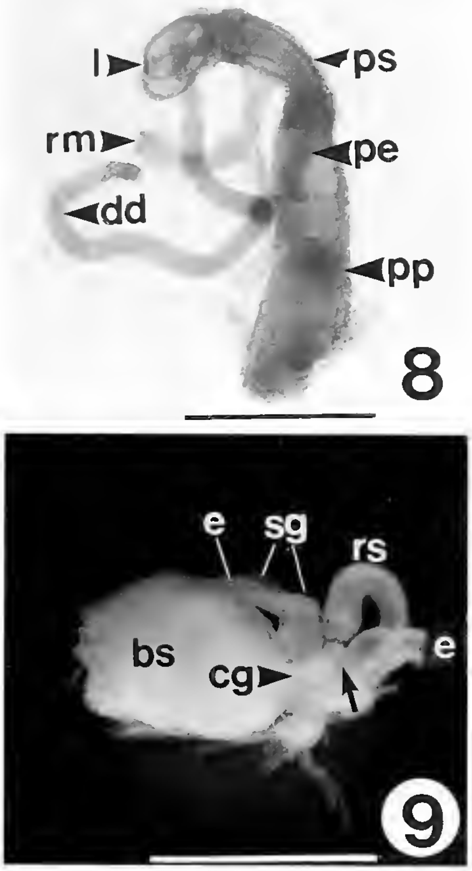
RESULTS

Description of specimens from Iguazú, Misiones (Figures 1–4): Shell small, very low, depressed, not strictly turbinate or helicoidal (Figures 1–3), with up to 2.5 rapidly expanding whorls. Two well-preserved shells measured: 2.65 and 2.6 mm in length; 2.15 and 2.2 mm in width; 1.2 and 1.1 mm in height. Apex laterally displaced due to ontogenetic change in coiling angle, apex not highest point on spire. Shell wide, flat at base, with rapid expansion of body whorl, which occupies ≈ ¾ of spire. Aperture wide, D-shaped, with inner margin slightly curved. Aperture length exceeds half shell length (65 and 69% of shell length). Inner and outer lips sharp. Umbilicus only partially covered by small basal reflection of inner lip. Shell wall thin, with olive-brown to yellowish periostracum. Shell-surface sculptured, with oblique striae and smooth spiral lines (Figure 4). External anatomy: Foot with quadrangular base, rectangular or subrectangular anteriorly, widely rounded posteriorly, diffusely pigmented. Head uniform gray, pigmentation darker between tentacles. Mantle unpigmented over lung, darkly pigmented over albumen gland and distal end of visceral mass. Genital ducts: Due to poor fixation and preservation, only male terminal genitalia is described. Penis, unarmed, with sharply pointed tip. Prepuce about twice as long as penis sheath. Flagella paired, short, wide, somewhat rounded, attached to base of vergic sac. Flagella half as long as vergic sac. Retractor and protractor muscles fused together before insertion into lateral wall of vergic sac (Figure 8). Alimentary system: Salivary glands arise dorsally from buccal sac, run posteriorly, passing through nerve ring. Pair of salivary glands join to form small loop behind cerebral comissure (Figure 9). Esophagus arises from dorsal wall of buccal sac, runs posteriorly, passing under cerebral commissure. Intestine passes over albumen gland. Jaw single, horseshoe-shaped, somewhat enlarged at free ends (Figure 10), consisting of numerous, small, cylindrical segments, highest (≈ 50 μm) at central part of organ, lower highest (≈ 35 μm) at ends. Radula folded along most of its length, radular sack tubular, very long, extending beyond posterior end of buccal mass, reflected dorsally (Figure 9). Each row of teeth composed of 1 central tooth, 13–14 teeth on each side (Figure 11). Central tooth bicuspid, left cusp longer than right, with 1 spine-shaped denticle between cusps, 1 denticle along each outer edge of tooth (Figures 12, 13). Lateral teeth (5–7) each with 3 cusps (Figures 14, 15): mesocone, rhomboidal in shape, with major axis elongated, longer than entocone, ectocone, forwardly displaced with respect to their bases. Ectocone, entocone robust, prong-like, with outer margin more curved than inner margin. Margin straight in ectocone. Entocone generally slightly longer than ectocone. Mesocone firmly attached to center of tooth plate by means of wide, median base (Figure 15). Mesocone tapering markedly towards base (Figure 15), entocone, ectocone with relatively wide bases. Small but robust accessory cusps develop on either side of mesocone, outside of ectocone and entocone. Other minor cusps are added to mesocone and ectocone, entocone in 2–3 intermediate teeth that follow (Figure 16). Robustness of cusps decreases progressively from first lateral to marginal teeth. The marginal teeth (generally 4), with multiple accessory cusps (usually 9–10) added to mesocone, ectocone, and entocone (Figures 16–17). Ectocone and entocone fade toward radular row margin, becoming nearly indistinguishable from accessory cusps.

Description of syntypes of *A. odhneri* Hylton-Scott, 1960 (MLP 5089) (Figures 5–7): Type-series of *A. odhneri* composed of 7 well-preserved shells, 4 adults, 3 juveniles. Shells pale brown or amber, very thin, nearly translucent. Surface sculptured in several specimens, with weak spiral lines superimposed onto transverse,



Figures 1–7. Shells of *Acrorbis petricola* Odhner, 1937. **1–4.** specimens from Iguazú Falls, Misiones, Argentina (MLP 5090). **5–7.** Syntypes of *Acrorbis odhneri* Hylton-Scott, 1960 (Aristóbulo del Valle, Misiones, Argentina) (MLP 5089). Scale bars for all figures = 1 mm.



Figures 8–9. Some aspects of the soft part anatomy of *Acrorbis petricola*. **8.** Penial complex. Scale bar = 0.5 mm. **9.** Buccal sac. Scale bar = 1 mm. Abbreviations: bs, buccal sac; cg, cerebral ganglion; dd, deferent duct; e, esophagus; fl, flagella; pe, penis; pp, prepuce; ps, penis sheath; rs, radular sac; sg, salivary glands (the arrow indicates the small loop behind the nerve ring).

oblique striae that are present in all shells. Shell is typically helicoid. Spire relatively elevated, with up to 3½ whorls separated by deep suture. Aperture nearly circular in shape, very oblique, with inner margin straight. Umbilicus covered by weakly developed lip reflection. Measurements of 4 adult shells shown in Table 1.

DISCUSSION

The specimens of *Acrorbis petricola* collected at Iguazú Falls show several differences in shell morphology and radular tooth shape from those of published descriptions for this species. The shell of *A. petricola* from Iguazú is low and depressed, its apex laterally displaced and not prominent. The plane of the aperture is coincident with the base of the shell (Figures 1, 3). These characters differ from the typical, helicoidal shell-shape of *A. petricola* described and figured from Nova Teutonia, Brazil and Aristóbulo del Valle, Argentina (Figures 5, 6). In specimens from Iguazú, the spire is less developed than in specimens from the type locality, the shell does consist of more than 2.5 whorls, and the aperture is markedly D-shaped (Figure 3) rather than circular or subcircular as in other localities. The Iguazú Falls specimens also have a wide umbilicus that is covered by a small reflection of the inner lip.

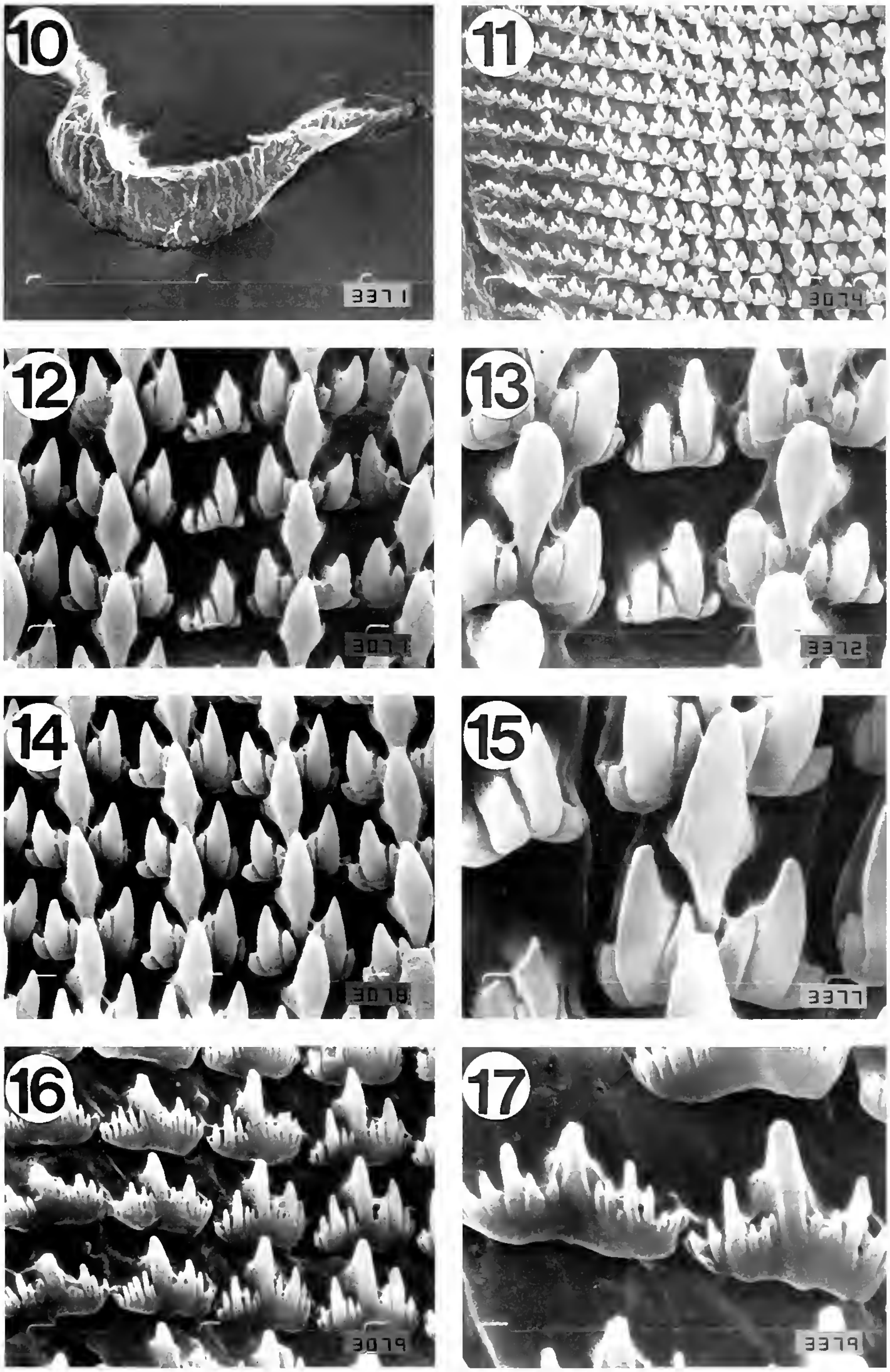
With respect to the shell shape, the specimens from Iguazú are similar to those described by Rumi (1986) from Saltos de Apipé, Corrientes, which were diagnosed as having: a shell that was helicoidal in shape but with a flattened base; a teleoconch of not more than 2.5 whorls; a rapid whorl expansion rate; an umbilicus not covered by a reflected lip; a shell surface sculptured with weak spiral lines; small adult size (1.12 mm length × 0.91 mm height).

The variability in shell morphology observed in *A. petricola* seems correlated with habitat characteristics. The 4 localities at which this species was recorded are all associated with high-energy water courses (Hylton-Scott, 1960; Paraense, 1986; Rumi, 1986).

The spray and or flow of water from waterfalls or high energy streams onto rocky banks contributes to the rapid growth of moss and algae on which *A. petricola* feeds. However, these hydrodynamic forces may also be capable of dislodging specimens. This is particularly evident in the case of the specimens collected at Salto Dos Hermanas, Iguazú Falls. Here, the population of *A. petricola* is exposed to powerful water forces that intermitently sweep the vertical rocky cliff behind the water fall (> 20 m high). Trussell *et al.* (1993) studied a population of *Littorina obtusata* living on a wave exposed intertidal rocky shore, and found that exposure to high wave action may induce intraspecific variation in the shell and foot morphology so as to reduce the shells coefficient of drag. Similarly, there seems to be selection in *A. petricola* for flat shells and increased basal area (apertural plane tangential to the outer edge of the shell) to decrease hydrodynamic resistance in response to the force of the water flow. This is likely to occur in specimens of *A. petricola* from Iguazú Falls (and Saltos de Apipé, Corrientes) were water flow is very swift.

The radular morphology of *A. petricola* from Iguazú is similar to that previously described (Paraense & Deslandes, 1959; Paraense, 1986). However, the shape of the teeth differs slightly but constantly, particularly along the mesocone of the lateral teeth, which is rhomboidal rather than having long dagger-like cusps, as described and figured by Paraense (1986). The cusps tend to be shorter and more robust in the Iguazú Falls specimens.

The gross anatomical features of the Iguazú Falls specimens generally agree with the detailed decriptions given by Paraense & Deslandes (1959) and Paraense (1975). However, several minor differences were observed in the Iguazú Falls material. The posterior ends of the salivary glands, which pass through the nerve ring, fuse together to form a small loop, which seems to be significantly shorter than previously figured. The flagella appear to be shorter and more rounded than previously described. These differences, as well as those reported



Figures 10–17. Scanning electron micrographs of the jaw and radula of *Acrorbis petricola* from Iguazú Falls, Misiones Argentina (MLP 5090). **10.** Jaw. Scale bar = 100 μm **11.** Dorsal view of half radula. **12–13.** Central and first lateral teeth The central teeth in figure 12 are somewhat abnormal **14–15.** Lateral teeth **16.** Intermediate (right) and marginal (left) teeth. **17.** marginal teeth Scale bars for figures 11–17 = 10 μm

Table 1. Measurements of adult shells in the type-series of *Acrorbis odhneri* Hylton Scott, 1960 (MLP 5089) (=*Acrorbis petricola*) (all measurements are given in millimeters).

Shell-length	Shell-width	Shell-height	Aperture length
3.6	3.0	2.0	2.0
3.65	3.0	1.9	2.0
3.7	3.1	1.9	1.95
3.8	3.3	2.1	2.1

for the length ratios calculated for the vergic sac and prepuce, may be due to *post mortem* changes during fixation of muscular organs and structures without skeletal support. It is the author's opinion, given the evidence here presented and reviewed, that *Acrorbis petricola* and *A. odhneri* are conspecific taxa.

As previously reported, *A. petricola* is known only specific habitats always associated with high-energy water courses such as rapids and water falls (Paraense & Deslandes, 1959; Hylton-Scott, 1960; Rumi, 1986). Such particular environmental requirements may be the factor responsible for the limited geographical distribution of this species. Given the abundance of rapids and small waterfalls in Misiones Province, a survey of the malacological fauna of the region would most likely result in the extension of the known geographical range of *A. petricola*.

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A New Species of Land Snail of the Genus *Georissa* (Gastropoda: Hydrocenidae) from the Philippine Islands

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ABSTRACT

Georissa cavini new species is described from an isolated limestone outcrop in the northeastern extremity of Panay Island, Philippine Islands. The new species is characterized by its relatively large size and shell sculpture of weak spiral threads which become increasingly oblique below the periphery. It is most similar to *Georissa coccinea* Quadras and Moellendorff, 1895 from Masbate Island, Philippine Islands. *Georissa everetti* E. A. Smith, 1895 from Sarawak has a similar shell, but much stronger shell sculpture.

Key Words: Hydrocenidae, *Georissa*, new species, Philippine Islands, Panay Island, Masbate Island.

INTRODUCTION

The author conducted a survey of the terrestrial mollusks of Panay Island, Visayan Islands, in the central Philippines, during April-May, 1992. Fifty-five sites were sampled, with emphasis on the small species found in the widespread limestone areas of Panay and its satellite islands.

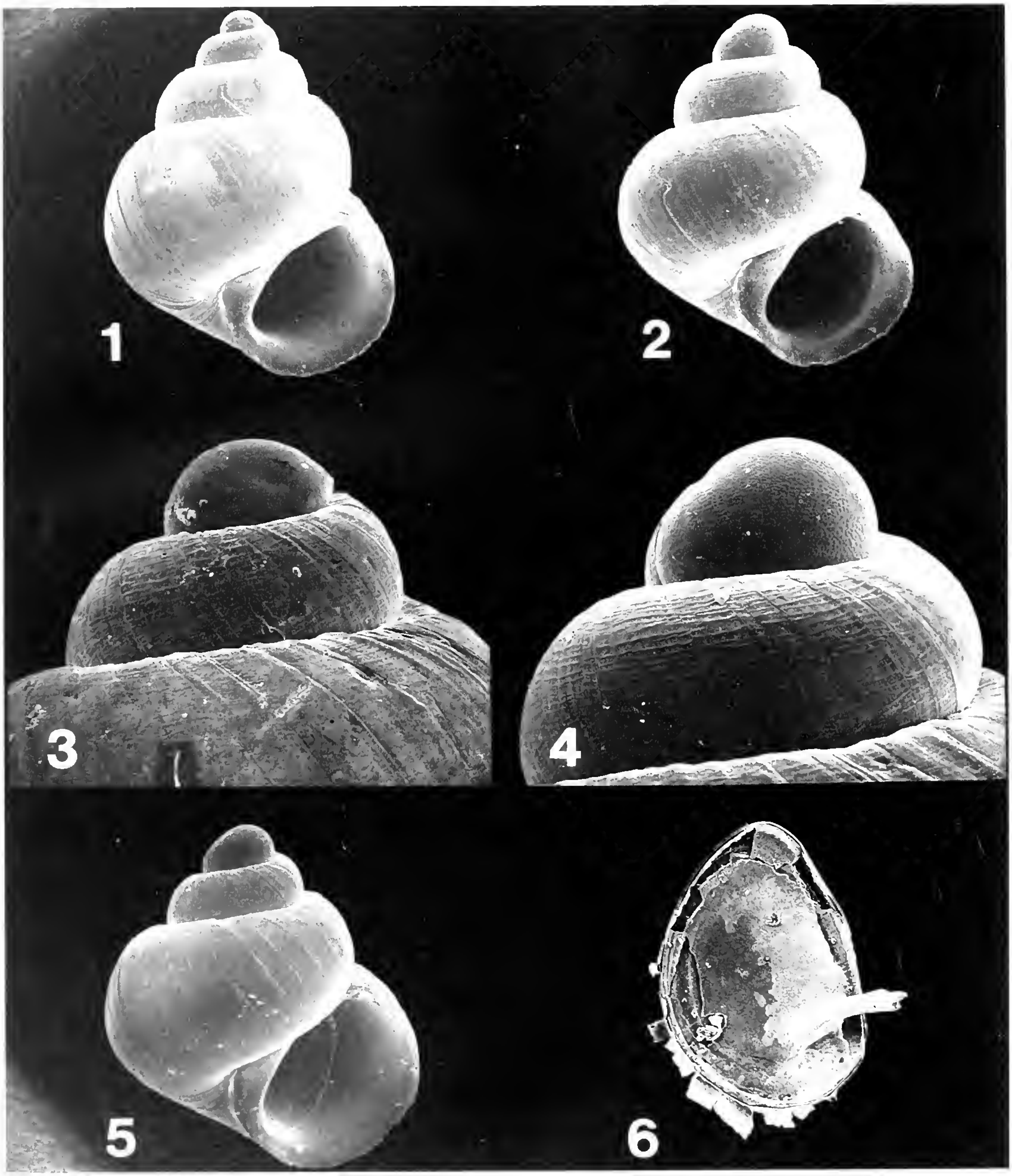
Only about 52 species and subspecies of terrestrial mollusks have been recorded from Panay (Bartsch, 1919, 1938, 1939, 1942; Moellendorff, 1898; Smith, 1932a, b). This is a small number, when compared to landmasses of similar size in the Philippines. However, much of the island consists of low, rolling hills (now mostly converted to agriculture), which do not provide the varied habitats of other areas of the Philippines. Substantial elevations and a greater diversity of habitats favorable to terrestrial mollusks occur only in the extreme western portion of the island. Most taxa previously recorded from Panay are still extant, but their distributions are now restricted to small plots of remnant forest, except those of the comparatively pristine higher elevations (> 800m) in the west. Few undescribed species were encountered. *Georissa* is a common faunal component throughout the Philippines, yet all specimens of this genus found in Panay belong to a single, undescribed species. This new species is here named and described.

The type-series and other specimens examined are deposited in the Philippine National Museum (PNM) and Florida Museum of Natural History, University of Florida (UF).

SYSTEMATICS

Class Gastropoda Cuvier, 1797
Superfamily Neritoidea Rafinesque, 1815
Family Hydrocenidae Troschel, 1856
Genus *Georissa* Blanford, 1864
Georissa cavini new species
(Figures 1, 3, 5, 6)

Description: Shell (Figure 1) medium-sized for genus (mean = 2.4 mm length, 1.8 mm width), turbiniform, ratio length/width about 1.33. Shell with 3.6 whorls. Embryonic whorl bulbous; subsequent whorls convex. Sutures deeply impressed; sutural channel distinct on early whorls, occasionally becoming very shallow on last half whorl. Sculpture of embryonic whorls a fine mesh of pits. Teleoconch glossy, with growth threads of variable strength, crossed by extremely fine oblique spiral threads that become increasingly oblique below periphery. Growth striations more distinct on body whorl; spiral threads stronger on upper whorls (Figure 3). Aperture subovate, ratio aperture length/shell length about 0.42. Parietal wall lying at an angle of about 27–38° (mean = 34°) to axis of shell; plane of aperture in lateral profile at about 28–34° (mean = 31°) to shell axis. Umbilical area indented; basal area with wide concave columellar shield; edge of basal lip extending to left in an arc, forming thin, but prominent ridge terminating in umbilical region, bordering columellar shield on left. Umbilical callus concave to very slightly convex. Peristome thickened internally, usually more so near base of columella and upper insertion (Figure 1). Outer lip slightly sinuose in lateral profile. Shell color brick-red to orange, usually more intense on spire; inner edge of lip and insertion area with rose red border in live-collected specimens. Operculum (Figure 6) calcareous, concentric with subcentral nucleus. Inner surface with relatively long, slen-



Figures 1–6. *Georissa catum* new species and *G. coccinea* Quadras and Moellendorff, 1895. **1, 3.** *G. catum* holotype, 2.3 mm [illegible] 2481. **2, 4.** *G. coccinea*, 1.8 mm length, UF 87296. **5.** *G. catum*, paratype juvenile, 1.5 mm length, UF 250000. **6.** Surface of operculum, paratype, 0.9 mm operculum length, UF 267482.

Table 1. Adult shell measurements (mm, converted from ocular micrometer units) of selected specimens of *Georissa cavini* new species (holotype in parentheses) and *Georissa coccinea* (UF 87296). L = length, W = width, Ap = aperture.

	G. cavini	*G. coccinea*
Number of specimens	7	3
L	2.2–2.8 (2.3)	1.7–1.8
W	1.8–2.0 (1.8)	1.4
W/L	0.70–0.82 (0.77)	0.77–0.84
ApL	0.9–1.0 (1.0)	0.7
ApW	0.8–0.9 (0.8)	0.6
ApW/ApL	0.76–0.84 (0.76)	0.83–0.91
ApL/L	0.37–0.47 (0.44)	0.37–0.44
Number of Whorls	3.2–3.9 (3.8)	3.2

der peg along columellar margin. Peg lying at low angle to plane of operculum; laterally compressed, interior surface of peg narrower than base; base extending to columellar edge of operculum. Inner surface of operculum flat with slightly raised callus along edge. Outer surface covered with thin chitinous sheet extending well beyond edge of operculum.

Type material: Holotype, PNM-CO 39481, 2.3 mm length × 1.8 mm width, (coated for scanning electron microscopy); Paratypes: UF 250000, 12 paratypes; UF 267482, 2 paratypes (shells and opercula coated for scanning electron microscopy). The holotype and paratypes were collected alive.

Type locality: Philippine Islands, Panay Island, Iloilo Province, ca. 10 km NE of Balasan, shaded limestone cliff face, limestone outcrop about 5 m above sea level on east side of the road between Balasan and Carles (GPS: 11°29′15″N, 123°00′27″E).

Other material examined: UF 267481, 53 shells, collected dead at type locality, in soil sample taken at the base of the limestone outcrop.

Etymology: I take great pleasure in naming this species in honor of Mr. Edward W. Cavin of Jacksonville, Florida. Mr. Cavin not only assisted in the collection of the type series, but has shared with me the rigors of fieldwork on several occasions, usually under spartan living conditions and with far less than adequate means of transportation.

Comparative remarks: The shell sculpture of *Georissa cavini* new species is most similar to *G. coccinea* Quadras and Moellendorff, 1895 (Figures 2, 4), only reported from Palanoc, Masbate (Quadras and Moellendorff, 1895:88), probably currently known as Palanog, a village located in the lowlands about 8 kilometers SSE Masbate City. *Georissa coccinea* has a smaller, broadly conical shell with a proportionately shorter spire than *G. cavini* (Figure 2, Table 1). The former usually has about 0.4 fewer whorls (Table 1), which are decidedly more convex in outline (Figure 2). The prominent ridge bordering the columellar shield in *G. cavini* is very thin and erect. When present in *G. coccinea* this ridge is weak and low. Juvenile *G. cavini* and adult *G. coccinea* of equivalent shell size are superficially similar, but the former are more globose, have a simple, unthickened peristome and a proportionately larger aperture (Figure 5). Opercular characters of *G. coccinea* are unknown. *Georissa everetti* E. A. Smith, 1895 of Sarawak has a similar, but much stronger shell sculpture. The shell of *G. everetti* is smaller (1.95–2.20 mm length), with deeply impressed sutures and a more broadly conical shell shape (Thompson and Dance, 1983:120–121, figs. 55–57).

Large (> 2.4 mm length) individuals of *G. cavini* have more protruding protoconchs and whorls which descend more rapidly than those of typical adult shells, developing a longer spire and a more elongate shell. A continuum is presented in the type series and, besides these differences, the shells are identical to the other examined material.

DISCUSSION

The Hydrocenidae are widely distributed in southeastern Europe, Africa, Madagascar, much of southern Asia, northern Australia, New Zealand, and some Pacific Islands. Some taxonomic confusion exists at the genus level, but most Asian species have been assigned traditionally to *Georissa*. Most hydrocenids are obligatory inhabitants of limestone rockfaces and many have extremely limited distributions. Collectors, because of the small size of hydrocenids, may easily overlook these snails. Specimens can be most successfully found through close inspection of limestone rock faces and soil samples. Undoubtedly, many undescribed species exist throughout the vast range of the group. Available information indicates that the highest diversity of *Georissa* occurs in the Philippines (11 species; this paper and Moellendorff, 1898, but 3 of these species are better assigned to the Assimineidae, see below) and Borneo (14 species; Thompson and Dance, 1983).

Georissa cavini was the only hydrocenid collected during the survey of Panay, despite thorough searches in many limestone areas throughout the island. Dead shells were not found even though soil samples were taken at most collecting sites. Several series of *Georissa subglabrata* Moellendorff, 1887, which has been recorded from numerous localities throughout the Philippines (Moellendorff, 1898), were collected. However, this species and probably two other very similar taxa, *G. regularis* Quadras and Moellendorff, 1895, and *G. turritella* Moellendorff, 1893, are properly assigned to the Assimineidae (Auffenberg, pers. obs.) Surprisingly, *Georissa denselirata* Moellendorff, 1894, which is known from other Visayan Islands, including Negros, Cebu and Romblon (Zilch, 1973), was not encountered on Panay.

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Cancellaria (Euclia) laurettae, a New Species of Cancellariidae (Mollusca: Neogastropoda) from Western Panama

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ABSTRACT

Cancellaria (Euclia) laurettae new species, is described from eleven specimens dredged in the Golfo de Chiriqui, Panama at depths of 270–360 meters. This species is assigned to the subgenus *Euclia* based on the morphology of its columellar plications, spiral sculpture, and overall shell shape. It is readily distinguished from the other Recent members of the subgenus by its lack of a distinct shoulder with spines or nodes and finer spiral sculpture.

Key words: Cancellariidae, Panamic Province, eastern Pacific, Neogene, bathyal.

INTRODUCTION

This paper describes a new species of cancellariid that was recently trawled from bathyal depths in the Golfo de Chiriqui, Panama. Based on conchological features, it is assigned to the genus *Cancellaria* Lamarck, 1799, subgenus *Euclia* H. & A. Adams, 1854, which, in its Recent geographical range, is endemic to the tropical eastern Pacific. While similar to the Recent species *Cancellaria (Euclia) cassidiformis* Sowerby, 1832, and *C. (E.) balboae* Pilsbry, 1931, this new species is more similar to the Miocene *C. (E.) dinota* Woodring, 1970, from the Gatún Formation of Panama and especially the Late Miocene/Early Pliocene *C. (E.) maldonadoi* Olsson, 1964 of the Angostura Formation of Ecuador than to either of the Recent species. The taxonomic history of the subgenus *Euclia* is briefly reviewed, and a table of included species provided.

ABBREVIATIONS USED

AMNH	American Museum of Natural History, New York
ANSP	Academy of Natural Sciences, Philadelphia
LACM	Natural History Museum of Los Angeles County, Los Angeles
USNM	National Museum of Natural History, Smithsonian Institution, Washington, DC.

SYSTEMATICS

Family Cancellariidae Forbes & Hanley, 1851
Subfamily Cancellariinae Forbes & Hanley, 1851
Genus *Cancellaria* Lamarck, 1799

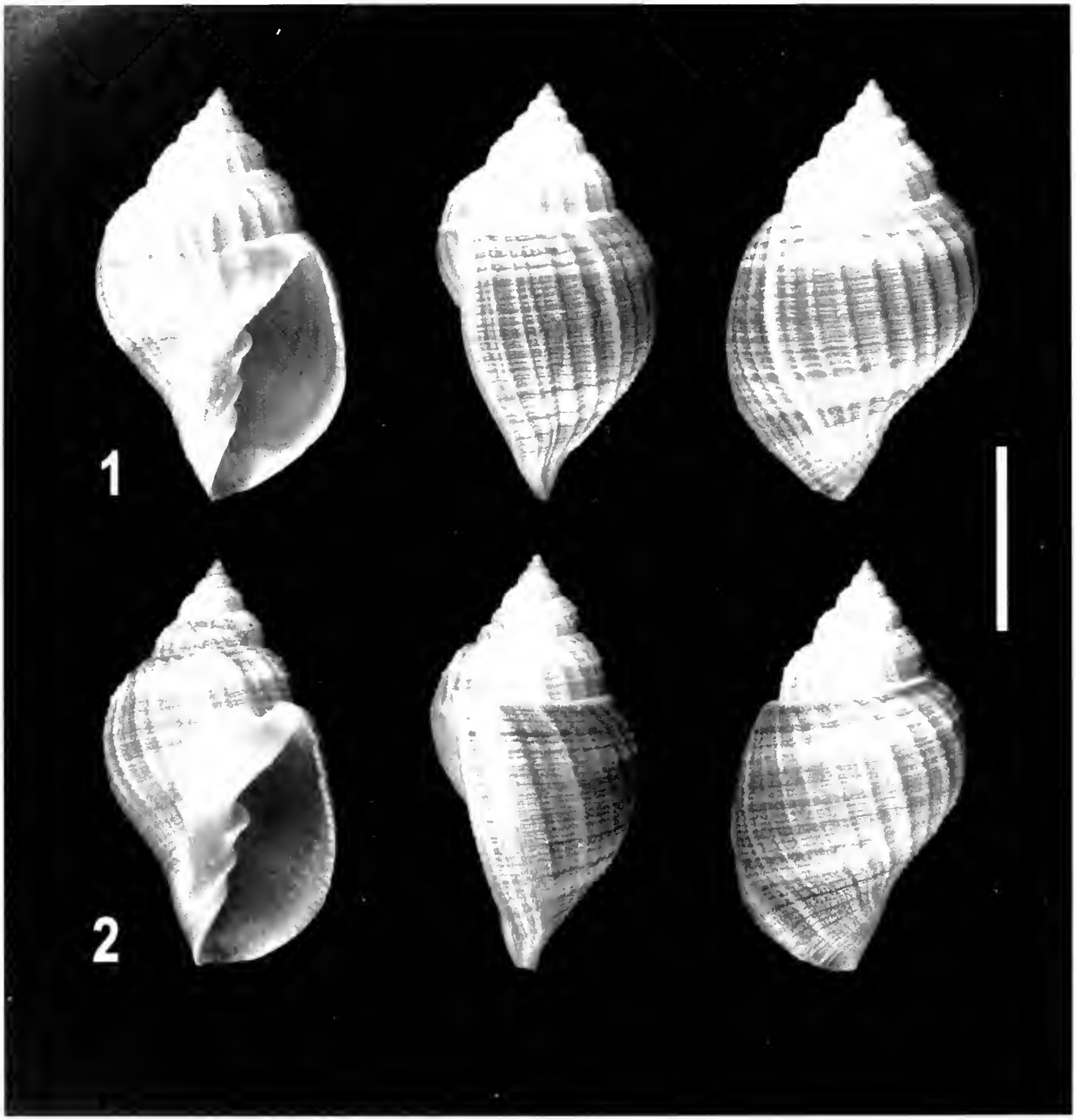
Cancellaria Lamarck, 1799 Type species: *Voluta reticulata* Linné, 1767, by monotypy.

Subgenus *Euclia* H. & A. Adams, 1854

Euclia H. & A. Adams, 1854: 277. Type species: *Cancellaria cassidiformis* Sowerby, 1832, by subsequent designation of Cossmann, 1899).

Table 1. Species assigned to the subgenus *Euclia*, together with their geographical and geological ranges.

Panamic
Cancellaria (Euclia) cassidiformis Sowerby, 1832—Gulf of California to Peru, RECENT
C. (E.) balboae Pilsbry, 1931—Mexico to Panama, RECENT
C. (E.) laurettae, new species—Gulf of Panama, RECENT
C. (E.) harpiformis Pilsbry & Olsson, 1941—Ecuador, Canoa Formation, PLIOCENE
C. (E.) larkinii Nelson, 1870—Peru, Tumbes Formation, LATE MIOCENE
C. (E.) triangularis Nelson, 1870—Peru, Tumbes Formation, LATE MIOCENE
C. (E.) dinota Woodring, 1970—Panama, Gatún Formation, LATE MIOCENE
C. (E.) maldonadoi Olsson, 1964—Ecuador, Angostura Formation, LATE MIOCENE
Caribbean
C. (E.) codazzii Anderson, 1929—Northern Colombia, Tubará Group, LATE MIOCENE–EARLY PLIOCENE
C. (E.) venezuelana Hodson, 1931—Falcón, Venezuela, UPPER MIDDLE MIOCENE
C. (E.) montserratensis Maury, 1925—Trinidad, Springvale Formation, EARLY PLIOCENE
C. (E.) werenfelsi Jung, 1965—Venezuela, Cantaure Formation, LATE EARLY MIOCENE

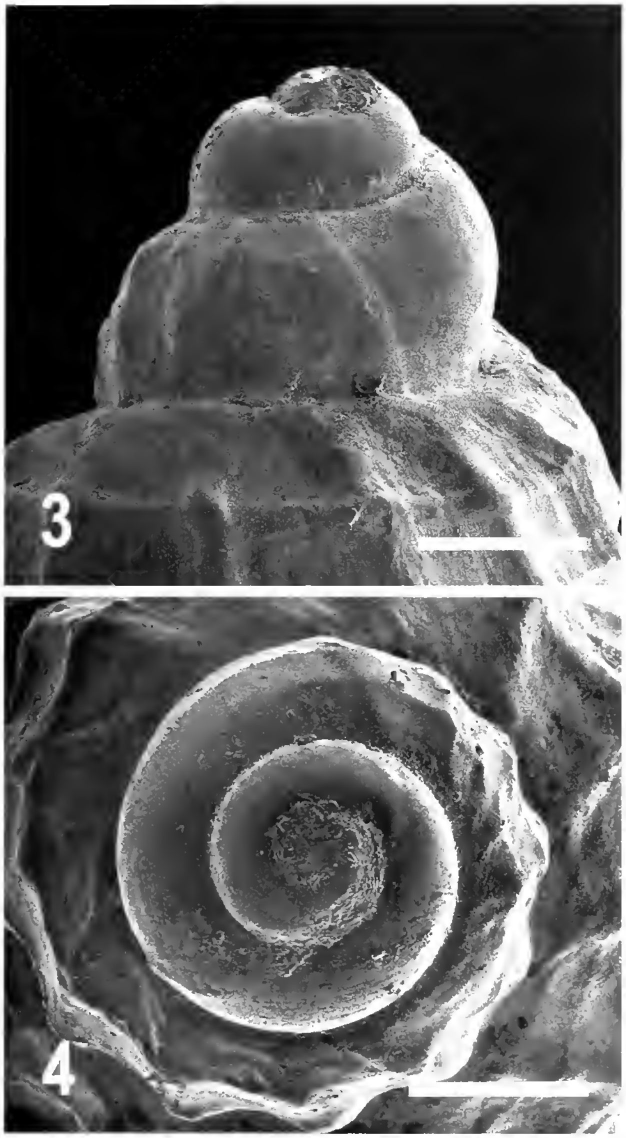


Figures 1–2. *Cancellaria (Euclia) laurettae* new species. **1.** Holotype, USNM 880277. **2.** Paratype 1, USNM 880278. Off Isla Montuosa, Golfo de Chiriqui, Panama, trawled in 270–360 meters. Scale bar = 2 cm.

Cancellaria (Euclia) Olsson, 1932:157; Olsson, 1964:122; Keen, 1971:651.

Diagnosis: Shell with a conical spire and large body whorl, contracted at the base as in *Cancellaria* s.s. Shoulder of body whorl may be smooth, tuberculate or spinose. Sculpture of sharply defined cords or threads that are narrower than intervening spaces. Columella lacking an umbilicus to weakly pseudo-umbilicate, with 2 sharply keeled columellar folds (posterior fold not bifid) and a siphonal fold. Parietal callus generally present.

Remarks: The taxonomic history of *Euclia* was summarized by Olsson (1932), who noted that Jousseaume (1887) and Cossmann (1899) considered it to be synonymous with *Cancellaria*. Olsson (1932:158) regarded Cossmann's (1899) designation of *Cancellaria cassidifor-*



Figures 3–4. *Cancellaria* (*Euclia*) *laurettae* new species **3.** Lateral and **4.** apical views of protoconch of holotype. Scale bars = 500 μm.

mis as type species of *Euclia* to be an unfortunate misinterpretation of H. & A Adam's intent, because, of the 4 species originally included in *Euclia* by these authors, it differs most from their description. Although *Euclia* is restricted to the Panamic Province in the Recent fauna, its range extended into the Caribbean during the Neogene. Species presently included in this subgenus are listed in Table 1.

Table 2. Shell measurements of *Cancellaria* (*Euclia*) *laurettae* new species. All linear measurements in mm The measurements are based on the entire type series, consisting on the holotype and 10 paratypes (N = 11)

Character	Mean	Range	σ
Shell length	43.0	38.6–46.2	2.2
Aperture length	30.6	28.0–31.8	1.5
No of whorls, protoconch[1]	2.5	2.2–2.6	0.1
No of whorls, teleoconch	5.6	4.6–6.0	0.4
No of axial ribs, body whorl	24.6	20–30	3.0
No apertural lirae	13.1	0, 12–14[2]	0.9

[1] N = 9 for this character

[2] Apertural lirae were not yet developed in 2 specimens and thus scored at 0 When present, apertural lirae numbered 12–14 The mean and standard deviation for this character is based on 9 specimens.

Cancellaria (*Euclia*) *laurettae* new species
(Figures 1–4, Table 2)

Description: Shell (figures 1–2) to 46 mm, thin, biconic, lacking umbilicus or weakly pseudoumbilicate. Spire high (spire angle 68–71°) conical, comprising about 1/3 shell length. Protoconch (figures 3–4) coaxial with teleoconch, paucispiral, of approximately 2½ low, evenly inflated, glassy whorls, separated from teleoconch by flaring lip. Teleoconch of up to 6 evenly convex whorls. Shoulder inconspicuous. Suture deeply impressed. Axial sculpture of 20–30 ribs, triangular in profile, narrower than intervening spaces. Ribs prosocline on body whorl, less so on siphonal canal, with conspicuous inflection at stromboid notch. Spiral sculpture of fine, evenly spaced primary cords (3 on early whorls, 6–9 on penultimate whorl, 56–62 on body whorl and siphonal canal) that form weakly cancellate sculpture at intersections with axial ribs. Weaker, secondary cords appear between adjacent primary cords on body whorl. Fine threads (0–1) present between primary and secondary cords in most specimens. Aperture deflected from coiling axis by 20–22°, large, broad and evenly rounded or with outer edge straight and nearly parallel to coiling axis. Specimens with ovate apertures lighter in weight, with thinner parietal calluses that specimens with straight-sided outer lips. Outer lip finely crenulated, weakly outwardly flared, with broad, shallow "stromboid notch". Inner surface may be smooth or bear 12–14 recessed spiral lirae, diminishing 1/6th whorl into the aperture. Inner lip with 2 columellar and 1 siphonal fold, each with single, sharp keel. Most posterior fold largest, overlaying weak siphonal fasciole, anterior siphonal fold weaker, strongly deflected anteriorly. Pustules (3–4) may be present on inductura in region between columellar folds. Siphonal canal narrow, nearly axial. Base color white to light beige, with 3 broad, spiral bands of ginger to dark brown (darkest along suture, 1 at mid-whorl, 1 anterior to stromboid notch). Aperture with light tan overglaze, with darker band along outer lip of specimens with strong denticles.

Type locality: Off Isla Montuosa, W of Punta Hermosa, Isla de Coiba, Golfo de Chiriqui, Panama, trawled in 270–360 meters.

Type material: Holotype, USNM 880277 , 44.9 mm; Paratype 1, USNM 880278, Paratype 2, LACM 2815; Paratype 3, ANSP 401180; Paratype 4, AMNH 292527;

Paratypes 5-6, R. Petit Collection; Paratypes 7–8, E. Garcia Collection; Paratypes 9-10, J. Ernest Collection. All from type locality.

Etymology: This species honors Mrs. Lauretta Marr of Midland, Texas, for her contributions to the collection and study of Panamic mollusks.

Comparative remarks: *Cancellaria laurettae* occurs in 2 forms as indicated in the above description. The ovate form (figure 1) is much lighter in weight and slightly larger than the squarer form (figure 2). As no anatomical material is available, it is not clear if these differences represent sexual dimorphism. This new species differs from the 2 previously known Recent species included in the subgenus *Euclia* by Keen, 1971, by its lack of a well-defined tuberculate shoulder and by its more delicate sculpture. *Cancellaria laurettae* is closest in overall appearance to the Late Miocene *C. (E.) maldonadoi* Olsson, 1964 (which Woodring, 1970, incorrectly synonymized with *C. (E.) codazzii* Anderson, 1929) than to the other Recent or fossil species. However, it differs from *C. maldonadoi* in lacking a peripheral cord on the shoulder, in having more numerous and finer spiral sculpture and in lacking folds along the inductural region of the parietal shield.

ACKNOWLEDGMENTS

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Leucozonia ponderosa, a New Fasciolariid Gastropod from Brazil

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ABSTRACT

A new species of fasciolariid gastropod, *Leucozonia ponderosa*, is described. The new species is apparently endemic to Trindade Island, which is located 1140 km east of the Brazilian mainland. This large, thick-shelled species is characterized by three spiral rows of tubercles, three basal cords on the last whorl, and a distinct labral tooth. Like other described and undescribed Trindade endemics, *L. ponderosa* appears to be derived from a western Atlantic ancestor.

INTRODUCTION

The fasciolariid genus *Leucozonia* is a tropical American and eastern Atlantic group of shallow-water predators. In the course of a review of the species of this genus, we have discovered a distinct, unnamed species that appears to be endemic to Trindade Island, Brazil. Here we introduce this new species as *Leucozonia ponderosa*, and comment briefly on the western Atlantic affinities of this and other Trindade endemics. Abbreviations used are: MNHN, Muséum national d'Histoire naturelle, Paris, France; MORG, Museu Oceanográfico, Fundação Universidade do Rio Grande, Rio Grande, Brazil.

SYSTEMATICS

Family Fasciolariidae Gray, 1853
Genus *Leucozonia* Gray, 1847

Type species: *Murex nassa* Gmelin, 1791, by original designation.

Leucozonia ponderosa new species
(Figures 1–4)

Leucozonia nassa (Gmelin, 1791).—Leal, 1991, p. 157, pl. 20, figs. B, C (in part).

Diagnosis: A *Leucozonia* with five or six primary spiral cords on the last whorl, the adapical three rows being sculptured by low, rounded tubercles; distinct labral tooth present at end of third cord.

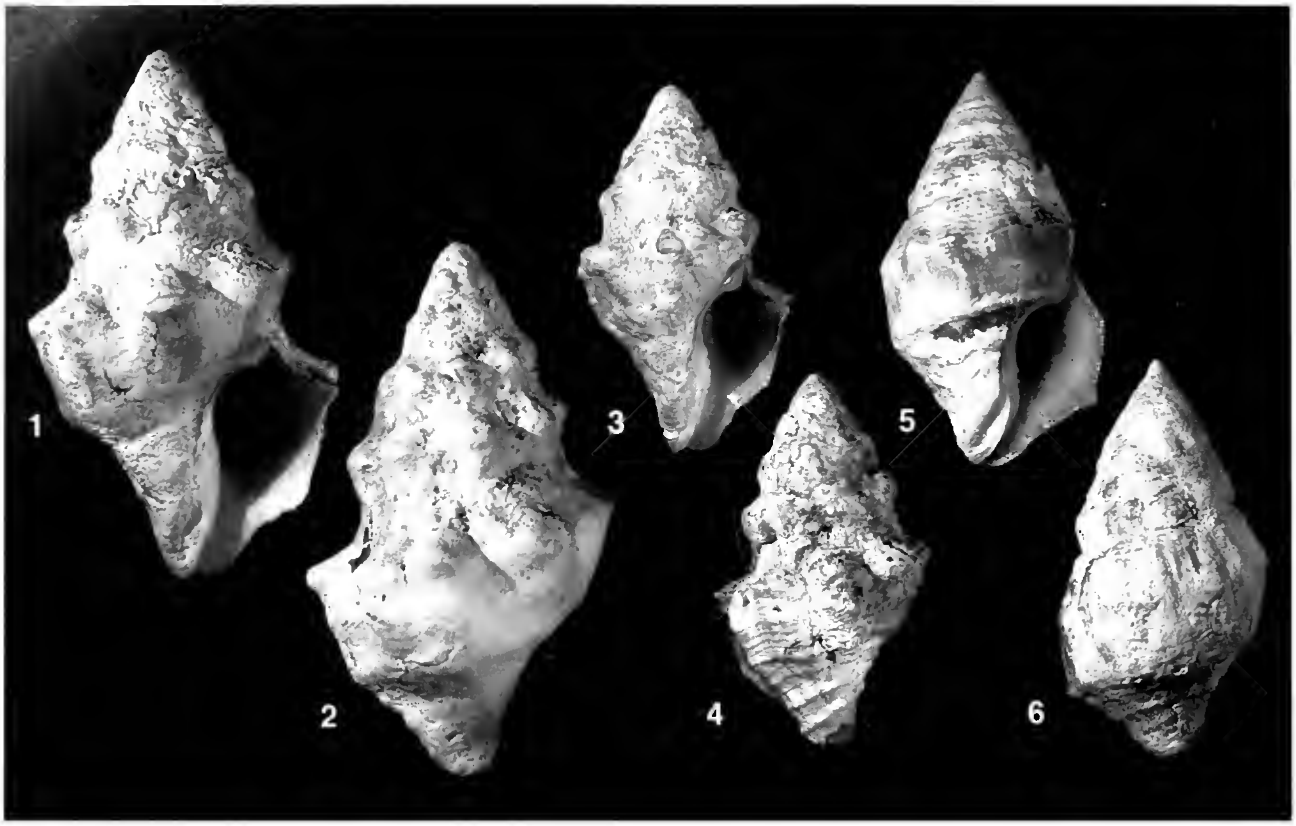
Description: Shell large (maximum length 67 mm), moderately squat (length:width 1.56–1.72), moderately high-spired (last whorl length:length 0.53–0.59), heavy and solid. Color light-brown. Spiral sculpture of last whorl consisting of six (sometimes five) cords, one at shoulder, a second below the shoulder, and a third central, and three (sometimes two) basal cords, all separated by fine threads. Axial sculpture of last whorl consisting of eight strong, rounded ribs, forming low, rounded nodes where they are crossed by each of the three adapical spiral cords. Outer lip with distinct adapical sinus, convex medial sector, and weakly concave abapical sinus. Third spiral cord ending in well-developed labral tooth. Adaxial side of outer lip with 11–12 strong, beaded lirae. Aperture relatively broad (aperture length:aperture width 2.4–2.7), color light-peach. Siphonal fasciole well developed; umbilical slit absent. Siphonal canal relatively long (siphonal canal length:aperture length 0.38–0.42).

Type locality: Enseada dos Portugueses, Trindade Island, Brazil, 20°30′S, 29°20′W, depth 10 m, rocky bottom.

Type material: Holotype, MORG 39298, length 47.3 mm, width 28.8 mm, aperture length 28.0 mm, aperture width 10.5 mm, siphonal canal length 11 mm; Paratype 1, MORG 39299, length 66.8 mm, width 40.0 mm, aperture length 35.5 mm, aperture width 14.2 mm, siphonal canal length 15 mm; Paratype 2, MNHN, length 62.8 mm, width 36.6 mm, aperture length 35.7 mm, aperture width 15.1 mm, siphonal canal length 15 mm, collected by J. H. Leal and P. Bouchet, SCUBA, 10 m, 22 May 1987 (all from type locality).

DISCUSSION

Two species of *Leucozonia* occur on Trindade Island. One of these is a thick-shelled, obsoletely spirally sculptured form of the widespread western Atlantic species *Leucozonia nassa* (Gmelin, 1791) (figures 5–6). This form, which also occurs at Fernando de Noronha Ar-



Figures 1–2. *Leucozonia ponderosa* new species, Trindade Island, Brazil, length 66.8 mm, paratype 1, MORG 39299 **Figures 3–4.** *Leucozonia ponderosa*, Trindade Island, Brazil, length 47.3 mm, holotype, MORG 39298. **Figures 5–6.** *Leucozonia nassa*, Trindade Island, Brazil, length 52.1 mm, MNHN unnumbered, Enseada dos Portugueses, Trindade Island, Brazil, J. H. Leal and P. Bouchet, SCUBA, 10 m depth, 22 May 1987.

chipelago, Atol das Rocas, and Bahia (all in Brazil), is characterized by spiral sculpture consisting of weak threads or sometimes very weak spiral cords. If cords are present, they number six or seven from the shoulder to the central, tooth-bearing cord. The single specimen we have seen from Trindade has a dark-peach colored aperture and strongly granulated lirae on the adaxial side of the outer lip. The second species from Trindade, which we distinguish as the new species *L. ponderosa*, is characterized by three distinct, nodose adapical spiral cords, one at the shoulder, a central cord that bears the labral tooth, and a cord between these two. In addition to these adapical cords, there are three (sometimes two) major cords below the tooth-bearing cord. The aperture is of a light-peach color, and the lirae on the adaxial side of the outer lip are weakly beaded.

Some specimens of *L. nassa* from Curaçao and elsewhere in the southern and eastern Caribbean superficially resemble *L. ponderosa* in having three nodose adapical cords, but they differ from *L. ponderosa* in having the two adapical cords so close together that the shoulder appears to have a double keel. In *L. ponderosa*, the second row of nodes lies farther from the shoulder. Moreover, the aperture of Caribbean specimens of *L. nassa* is white instead of peach-colored.

Two other species of *Leucozonia* have three adapical cords sculptured by nodes or tubercles. *L. triserialis* (Lamarck, 1822) from the Cape Verde Islands differs from *L. ponderosa* in having a much more tuberculate shell, one basal cord instead of three, and a white instead of a peach-colored aperture. *L. tuberculata* (Broderip, 1833) from the Galápagos and Cocos Islands in the eastern Pacific differs from *L. ponderosa* by having two instead of the usual three basal cords, by being smaller in size, and by having a white aperture. Moreover, the third (tooth-bearing) cord of *L. tuberculata* is not nodose, whereas that of *L. ponderosa* bears nodes.

BIOGEOGRAPHY OF TRINDADE

Trindade Island, located 1140 km east of the Brazilian mainland at 20°30′ S, 29°20′ W, is a small (4.8 km in length), high island in the South Atlantic. Its gastropod fauna was first systematically studied by Leal (1991). Species in the island's fauna that are not endemic are widely distributed in the tropical western Atlantic. Leal (1991) reported that about 16% of the gastropod species in the fauna of Trindade are endemics. Thus far, only two of these, the lottiid *Patelloida marcusi* (Righi, 1966) and the neritid *Nerita ascensionis trindadensis* Vermeij, 1970, have been described. Both species also occur at Martin Vaz, a tiny archipelago 48 km east of Trindade (Leal, 1991). In addition, Leal (1991) reports unnamed species endemic to Trindade in the genera *Diodora, Calliostoma, Solariella, Arene, Melanella, Nassarius, Anachis, Vexillum, Granulina, Fenimorea,* and *Kurtziella.*

As Leal (1991) pointed out, the endemic species all belong to western Atlantic clades. We may surmise that they arose as isolated propagules from populations occupying the seamounts and banks extending from Trindade westward to Vitória on the Brazilian mainland. In the case of *Leucozonia,* the initial dispersal event would probably not have involved transport by ocean currents, because eggs in this genus hatch into crawling benthic juveniles (Bandel, 1976; Leal, 1991). *Leucozonia ponderosa* does not appear to occur at Martin Vaz. Whether this absence is the consequence of inadequate sampling or of a failure to disperse remains unclear.

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Book Review

The Pearly Mussels of New York State

by David L. Strayer and Kurt J. Jirka, 1997. New York State Museum Memoir 25, the University of the State of New York, The State Education Dept., xiii, 1–113, 27 color plates.

This is the first comprehensive volume on the freshwater mussels (Unionoidea) for New York since William B. Marshall (1895) summarized the knowledge of the state's unionoid fauna. There have been several papers dealing with restricted portions of the New York State mussel fauna, such as those by Imogene Robertson and C.L. Blakeslee (1943) [the Niagara Frontier] and Arthur Clarke and Clifford Berg (1959) [central New York]. Interestingly, Henry A. Pilsbry prepared a manuscript for a monograph entitled "Land and fresh water Mollusca of New York" in 1925. This impressive manuscript of 1200 pages was never published. Strayer and Jirka publish here for the first time the magnificent color illustrations prepared by three illustrators for Pilsbry's monograph. Ms. Helen D. Winchester, an illustrator with the Academy of Natural Sciences of Philadelphia, produced the majority of the illustrations.

This volume is divided into four major sections including Introduction, Identification Keys, Species Accounts, and References. The Introduction covers the basic biology of pearly mussels, the geography and environmental setting of the State of New York, information on the history of the study of unionoids in New York, an overview of the unionoid fauna of the state and what the authors view as the factors controlling unionoid distribution. Strayer and Jirka recognize 14 drainage basins within the state including tributaries to the Ohio River, St. Lawrence River, and Atlantic Slope drainages. The diversity of the fauna draws upon the historical differences of these major drainages. The authors list the historical literature on the state and discuss the problems with erroneous and questionable records. The next subsection, Collecting and Identifying Unionoids, provides definitions of terms and shell landmarks used in identification. The notes in the Identification Key section are prefaced with a very important comment, "Users should know that if they rely solely on this key, they will misidentify many shells." A total of 63 species are treated as having occurred at least historically in the state of New York. The Species Account section lists the species alphabetically by genus and species, accompanied by the common name. Each species account consists of a short shell description, a comparison with closely related species or with species with which this species might be confused, total distribution range, followed by comments on the population status and if host fish are known, they are listed. A map of the known distribution in New York accompanies each species account. Distribution information is plotted using three different symbols, filled dot for records of living or recently dead animals found since 1970; open circles, pre-1970 records; and an open triangle for imprecise records. The combined historic and modern collection coverage appears to be quite complete based on the coverage illustrated in Figure 6. No map of the total distribution of each species is given. Three subsections follow the accounts of species known to occur in New York: Hypothetical Species, Species Erroneously Recorded from New York and Synonymy. The Hypothetical Species subsection includes four species presumed to have occurred in the State of New York in historic times but for which no solid evidence exists to support their suspected occurrence in the state. The species erroneously reported from New York section includes 10 species reported from the state that are either mis-localized specimens or mis-identifications. The subsection Synonymy is based on Burch (1975) and Letson (1905). This informal synonymy of 109 *nomina* is provided to help readers with some of the other names encountered in the literature on New York unionoid bivalves. The References format includes complete citations and none of those annoying cryptic abbreviations.

The book is printed on recycled, acid-free paper. The text is printed on a light greenish paper while the beautiful plates are printed on a white stock. I was not very happy with the text printed on green paper. Another organizational item I found disturbing was that all of the figures were placed together at the end of the volume instead of with the species account. The plates were published as set up by Pilsbry for his manuscript.

This volume basically uses the common and scientific names from Turgeon et al. (1988) with some minor subsequent revisions. Some readers will have some discomfort with Strayer and Jirka's concept of the *Lampsilis ovata* (Say, 1817) complex. The very clear figures are of shells that have been identified by many malacologists as *Lampsilis cardium* Rafinesque, 1820 (+ *Lampsilis ventricosa* (Barnes, 1823)) and they may jump to the conclusion that this figure is erroneously labeled. However, if they read the discussion under *Lampsilis ovata*, it will be clear the authors have chosen a conservative approach and have chosen to use the earliest name for this group. Strayer and Jirka carefully point out there have been no published diagnoses to separate the shells or animals of *L. ovata* and *L. cardium*. Another point of discomfort or confusion with the taxonomy used in this volume is their decision to use the name *Pleurobema cordatum* for the representative of this species complex in New York. Strayer and Jirka recognize that *Pleurobema coccineum* occurs in New York and is today *Pleurobema sintoxia* (Rafinesque, 1820). However, they have chosen to take the conservative approach and use *Pleu-*

robema cordatum for the whole complex until the taxonomy of this complex has been resolved.

Several additional criticisms I have of this fine volume include a very short discussion of the role of the zebra mussel (*Dreissena polymorpha*) in the decline of native unionoids. There is no species account, information on the biology and impact of this species on the native unionoid fauna. No mention is made of the quagga mussel (*Dreissena bugensis*), another dreissenid introduced into the Great Lakes and competing with the native fauna. No mention is made of the earlier introduction of the Asiatic clam (*Corbicula fluminea*) and its distribution within the state. One other shortcoming of this very fine volume is the lack of an index.

Notwithstanding the several problems discussed, this is one of the finest state handbooks on unionoid bivalves published to date. The beautiful illustrations are the best I have seen in any of the unionoid handbooks. This volume is well worth the cost just for the illustrations and should be a standard reference in any freshwater molluscan library.

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Notices

THE R. T. ABBOTT VISITING CURATORSHIP

The Bailey-Matthews Shell Museum is pleased to invite applications for the 1999 R. T. Abbott Visiting Curatorship.

The curatorship, established originally in accordance with the wishes of the late Dr. R. T. Abbott, Founding Director of the Shell Museum, is awarded annually to enable mollusk systematists to visit the museum for a period of one to two weeks. Abbott Fellows will be expected, by performing collection-based research, to assist with the curation of the portions of the museum's Mollusk Collection and to provide one evening talk for the general public. The museum collection consists of marine, freshwater, and land shells, with emphasis on SW Florida. A large percentage of the records has been catalogued through a computerized database management system. A substantial portion of the time will be available for research in the museum collection, but field work in SW Florida can be arranged. The R. T. Abbott Visiting Curatorship is accompanied by a stipend of $1,500.

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

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

Applications for the 1999 Visiting Curatorship should be sent no later than January 31, 1999. The award will be announced by February 28, 1999. Questions about the R. T. Abbott Visiting Curatorship should be directed to Dr. Leal at:

(941) 395-2233; fax (941) 395-6706, or e-mail: leal@water.net

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In Memoriam

Harold E. Vokes

1908–1998

THE NAUTILUS

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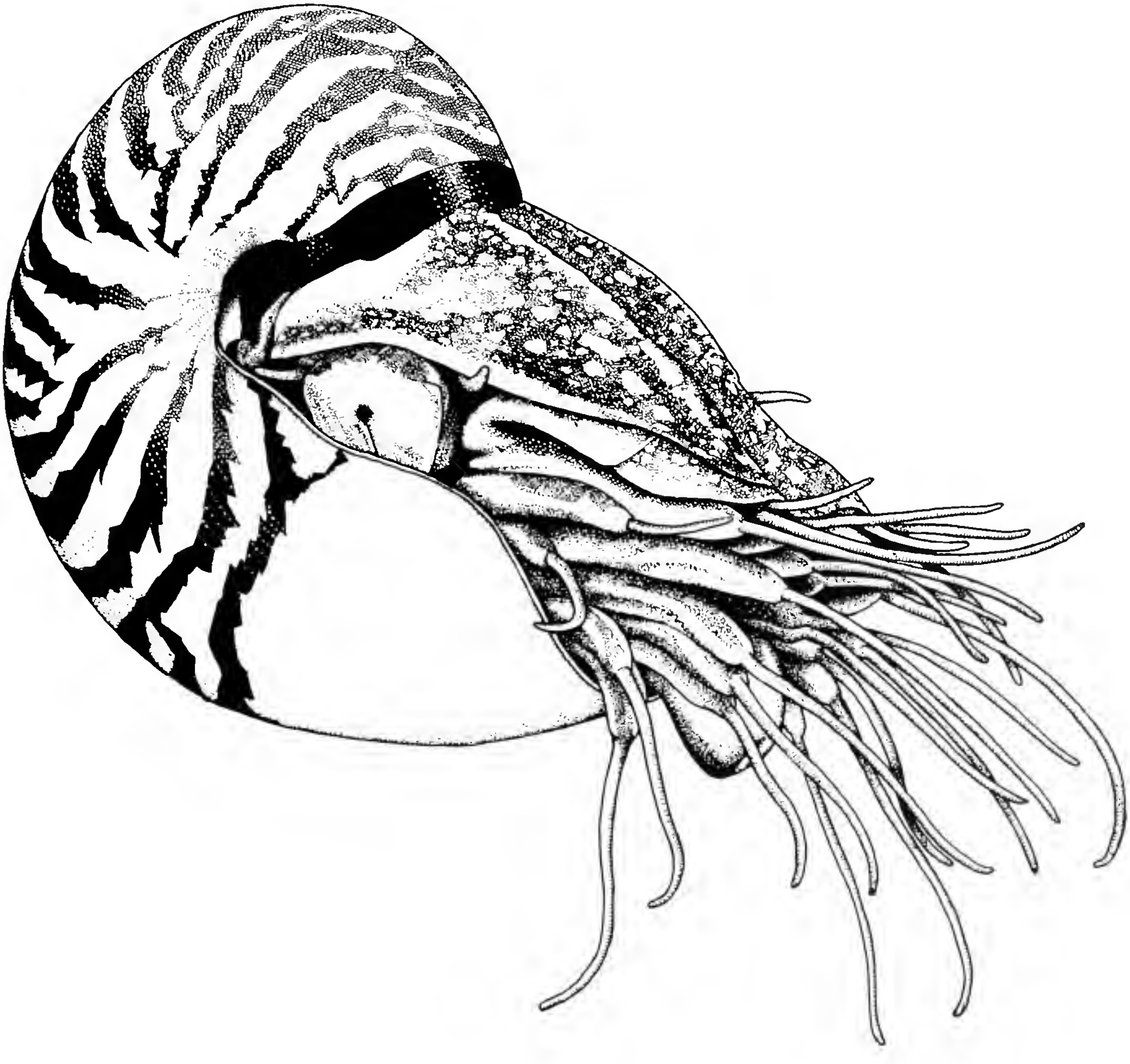

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THE NAUTILUS publishes papers on all aspects of the biology and systematics of mollusks. Manuscripts describing original, unpublished research as well as review articles will be considered. Brief articles, not exceeding 1000 words, will be published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

Manuscripts: Each original manuscript and accompanying illustrations should be submitted in triplicate. Text must be typed on one side of 8½ × 11 inch white paper, double spaced throughout (including literature cited, tables and figure captions), with at least 1 inch of margin on all sides. All pages must be numbered consecutively. If printed on a word processor, the right margin should be ragged rather than justified. Authors should follow the recommendations of the *Scientific Style and Format—The CBE Manual for Authors, Editors, and Publishers*, which is available from the Council of Biology Editors, Inc., 11250 Roger Bacon Drive, Suite 8, Reston, VA 20190, USA (http://www.cbe.org/cbe). The first mention of a scientific name in the text should be accompanied by the taxonomic authority, including year. Latin names and words to be printed in italics must be underlined; leave other indications to the editor. Metric and Celsius units are to be used.

The sequence of sections should be: title page, abstract page, introduction, materials and methods, results, discussion, acknowledgments, literature cited, tables, figure captions, figures. The title page should include the title, author's name(s) and address(es). The abstract page should contain the title and abstract, which should summarize in 250 words or less the scope, main results and conclusions of the paper. The abstract may be followed by a maximum of 8 key words. All references cited in the text must appear in the literature cited section and vice versa. In the literature cited section, all authors must be fully identified and listed alphabetically. Follow a recent issue of THE NAUTILUS for bibliographic style, noting that journal titles must be unabbreviated. Information on plates and figures should be cited only if not included in the pagination. Tables must be numbered and each placed on a separate sheet. A brief legend must accompany each table. Captions for each group of illustrations should be typed on a separate sheet and include a key to all lettered labeling appearing in that group of illustrations.

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

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

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