THE NAUTILUS

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Littorina kasatka, a New Species from the Kurile Islands and Okhotsk Sea

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ABSTRACT

A new species, *Littorina* (*Littorina*) *kasatka*, is described from the Kurile Islands and Okhotsk Sea. It is similar in shell characters to a smooth form of *L.* (*Neritrema*) *sitkana*, with which it is sympatric, but is distinguished by the absence of mammilliform glands on the penis of the male and by the small jelly gland of the female. It is predicted that *L. kasatka* produces pelagic egg capsules and has planktotrophic development.

Key words: *Littorina*; Pacific; Larval development.

INTRODUCTION

The generic name *Littorina* has in the past been applied to many littorinids with relatively large, smooth or spirally sculptured shells, that occur in the littoral zone. However, a recent phylogenetic analysis of the Littorinidae, based largely on anatomical rather than shell characters, has defined *Littorina* more narrowly as a monophyletic clade of about 20 species (Reid, 1989). Species of *Littorina sensu stricto* are found only in the northern hemisphere, where they are characteristic inhabitants of the eulittoral and littoral fringe on temperate and cold temperate shores.

During the past two decades close investigation of the reproductive anatomy of European *Littorina* species has revealed the existence of three additional species, previously unrecognized by shell characters (review by Raffaelli, 1982; Johannesson & Johannesson, 1990). The biochemical technique of enzyme electrophoresis has confirmed that these species are genetically distinct (review by Ward, 1990). More recently, a pair of sibling species has been identified in the northeastern Pacific, again using the dual approach of reproductive anatomy and biochemistry (Murray, 1979; Mastro *et al.*, 1982). In contrast, the *Littorina* of the northern and northwestern Pacific are poorly known. This paper describes a new species that was discovered during a genetic study of *Littorina kurila* Middendorff, 1848 from the Kurile Islands and Vostok Bay (Zaslavskaya & Sergievsky, in press). (*Littorina kurila* is a junior synonym of *L. sitkana* Philippi, 1846, see note added in press in Reid, 1990a). Of 11 loci examined, alleles common to the two species were found at only two, and the genetic identity was consequently low (Nei's (1978) genetic identity $I = 0.065$). The new species was recognized independently during anatomical studies of *Littorina* material from the Zoological Institute, Leningrad, as part of a systematic study of all *Littorina* species in the Pacific (Reid, in prep.). Recognition of the new species in the field is difficult, since shell form is similar to that of *L. sitkana* and several other *Littorina* species, but both males and females display unique reproductive anatomy.

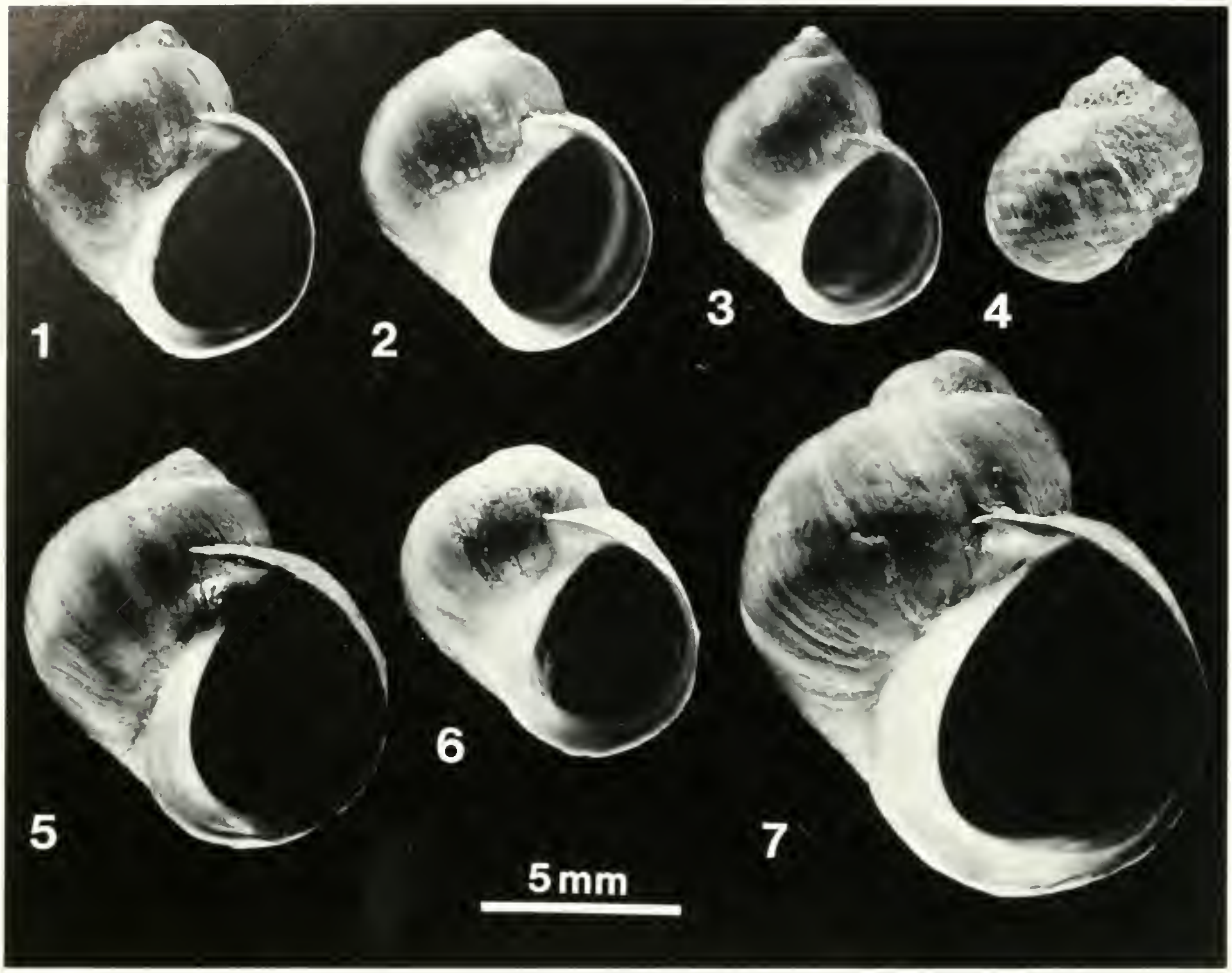
MATERIAL AND METHODS

The new species is described from six lots in the Zoological Institute, Leningrad (ZIL), and one lot in the Zoological Museum, Moscow (ZMM), all of which are duplicated in the Natural History Museum, London (BMNH). That it is indeed undescribed was confirmed by comparison with original descriptions of all available names of *Littorina* species from the Pacific, and with all available type specimens (housed in BMNH, ZIL and National Museum of Natural History, Washington, D.C.); details will appear elsewhere, in a full account of the systematics of *Littorina* (Reid, in prep.). Closely related species are discussed briefly below.

The reproductive anatomy was examined in ten males and nine females. The spiral pattern of the albumen and capsule glands of the pallial oviduct can be seen, without dissection, on the right side of the body adjacent to the columellar muscle, when a female is removed from the shell. Serial histological sections were prepared of the pallial oviduct of two females. Radulae were extracted from six specimens from three localities, and after cleaning in hot concentrated sodium hydroxide solution were examined by scanning electron microscopy. For comparison, 45 specimens of *L. sitkana* were dissected, from localities all around the northern Pacific from Hokkaido to Washington, and four radulae were examined. Details of other *Littorina* species investigated are given in Reid and Golikov (1990).

SYSTEMATIC DESCRIPTION

Littorina (*Littorina*) *kasatka* new species
(figures 1–4, 8–11, 12–20, 23)



Figures 1–4. *Littorina kasatka* new species. **1.** Holotype (BMNH 1990050), Kasatka Point, Iturup I., Kurile Is. **2.** Paratype (BMNH 1990051). **3.** Nataliya Bay, Urup I., Kurile Is. **4.** Paramushir I., Kurile Is. **Figures 5–7.** *Littorina sitkana* smooth form, from localities at which it is sympatric with *L. kasatka*. **5, 7.** Kasatka Point, Iturup I., Kurile Is. **6.** Nataliya Bay, Urup I., Kurile Is. All specimens in BMNH

Types: holotype BMNH 1990050, Kasatka Point, Iturup I., Kurile Is, USSR (figure 1); 9 dry paratypes BMNH 1990051; 38 paratypes in alcohol BMNH 1990052; 10 paratypes in alcohol ZIL.

Etymology: named after type locality.

Shell (figures 1–4): *Dimensions:* Adult size range 6.4–11.0 mm shell height.

Shape: Teleoconch approximately 4 whorls (apices eroded in available specimens), moderately solid. Globular to turbinate, whorls smoothly rounded, sutures distinct. Columella rather narrow, slightly excavated, pillar concave; sometimes a slight chink between edge of inner lip and base of body whorl (not a true umbilicus).

Sculpture: Indistinct axial growth lines only, no spiral grooves; faint spiral striae sometimes visible at high magnification.

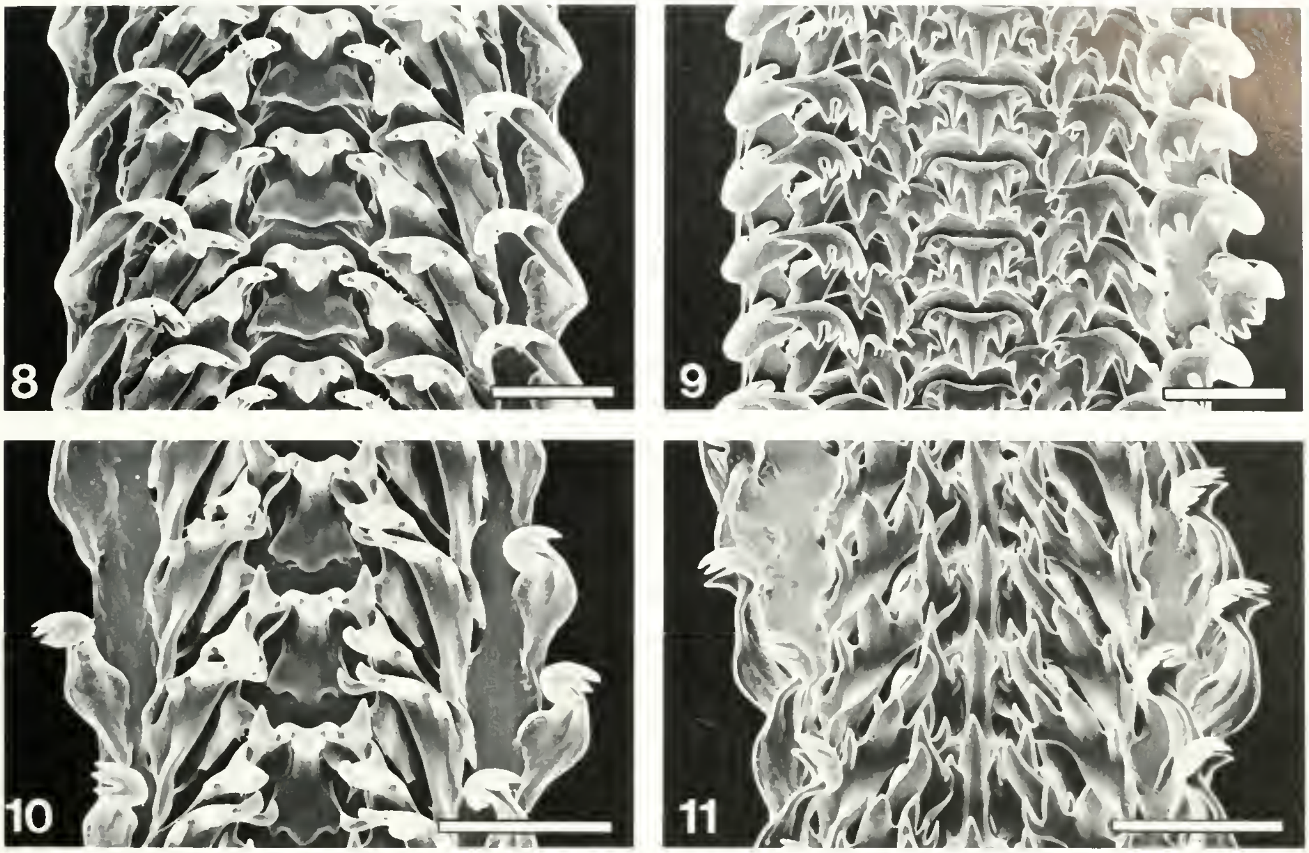
Color: Mid-brown, often with 6–16 rows of smudged whitish dashes, especially at periphery and on base, occasionally forming tessellated pattern (figure 4). Aperture purplish brown. Columella white to pinkish brown.

Animal: *Head-foot (figures 19, 20):* Head black, pale tips to tentacles and snout, unpigmented stripe across tentacle base and eye, or unpigmented patch at inside of tentacle base only. Sides of foot grey to blackish.

Operculum: Normal, paucispiral littorinid (type A of Bandel & Kadolsky, 1982).

Penis (figures 14–18): Wrinkled base lacking mammilliform glands; small, blunt filament not clearly demarcated from base; sperm groove open to tip.

Pallial oviduct (figures 12, 13): Complex spiral of 3 loops of albumen and capsule glands; final straight section



Figures 8–11. Radulae of *Littorina kasatka* new species. Scale bars = 50 μm. **8, 9.** Kasatka Point, Iturup I., Kurile Is. **10, 11.** Paramushir I., Kurile Is. **8, 10.** Viewed flat. **9, 11.** Same radulae as Figures 8, 10, but viewed from angle of 45° to show cusp shape.

(containing jelly gland) short, not swollen or septate. Bursa copulatrix small, opening in anterior position.

Radula (figures 8–11): All cusps moderately pointed. Rachidian with 3 large, 2 small cusps; outline of tooth (viewed flat from above) varies from square to oblong (ratio of length of tooth : width at mid-point 1.00–1.78). Lateral and inner marginal each 4 large cusps. Outer marginal 6–8 cusps.

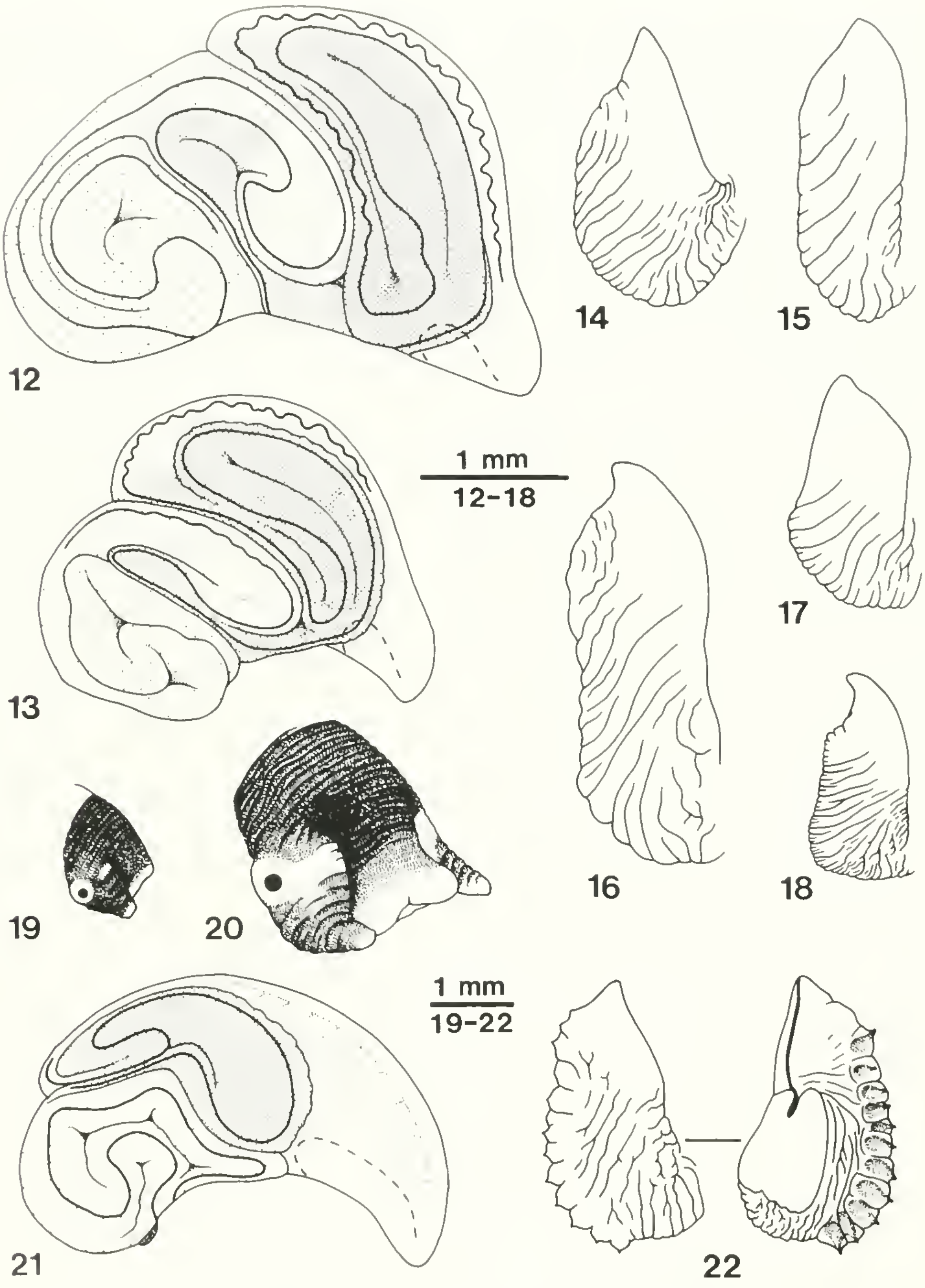
Distribution: *Habitat:* Rocks and boulders in middle and upper littoral zone of sheltered shores.

Range (figure 23): Kurile Islands, Gulf of Shelikov in Okhotsk Sea.

Records: Kasatka Bay and Kasatka Point, Iturup I.; Nataliya Bay, Urup I.; Ryponkich I.; Paramushir I. (all ZIL and BMNH); between Nepropusk and River Gank, W. Kamchatka, Gulf of Shelikov (ZMM, BMNH).

Similar species: Four *Littorina* species are geographically sympatric with *L. kasatka* over its known range: *L.* (*Littorina*) *squalida* Broderip & Sowerby, 1829; *L.* (*Neritrema*) *sitkana*; *L.* (*N.*) *subrotundata* (Carpenter, 1864) and a newly described species (Reid & Golikov, 1990). Of these, no confusion will arise with *L. squalida*, which is a much larger (12–44 mm), spirally-grooved shell (figured by Reid, 1990a). *Littorina subrotundata* and the newly described species are also usually larger (4–14 mm and 6–16 mm respectively), both are a more patulous shape, and both have a color pattern of dark brown spiral lines on a paler brown ground (figured by Reid & Golikov, 1990). Anatomically, these two species both show mammilliform penial glands in the male and a large, swollen, septate jelly gland in the female, unlike *L. kasatka*.

Littorina sitkana is the most similar to *L. kasatka* and is apparently found in the same habitat, since all but one of the seven known collections of *L. kasatka* were separated from mixed lots of the two species. *Littorina sitkana* is highly variable. The form that occurs most commonly in the northeastern Pacific has strong spiral ribs with striae in the grooves between, but in the northwestern Pacific (and especially in the Kurile Islands and Okhotsk Sea) the common form is smooth shelled. This smooth form has been referred to as *L. kurila* (this name is actually a synonym of *L. sitkana*, see Reid, 1990a) in all recent Soviet literature (e.g., Golikov & Kusakin, 1978). Since *L. kasatka* lacks spiral ribs and obvious striations, it is easily distinguished from sculptured shells of *L. sitkana* (figured by Reid, 1990a). However, smooth forms of *L. sitkana* are extremely similar. *Littorina sitkana* is usually larger (commonly 15 mm, up to 23 mm), has a



Figures 12–20. *Littorina kasatka* new species. **12, 13.** Pallial oviducts. **14–18.** Penes. **19, 20.** Heads. **12, 17.** Nataliya Bay, Urup I. **13–15, 20.** Kasatka Point, Iturup I. **16.** Kasatka Bay, Iturup I. **18, 19.** Paramushir I. **Figures 21, 22.** *Littorina sitkana*, Seldovia, Alaska. **21.** Pallial oviduct. **22.** Two views of penis; mammilliform glands shaded. All specimens in BMNH. Key to figures 12, 13, 21: sparse stipple, albumen gland; dense stipple, capsule gland; dotted lines, septa of jelly gland (visible by transparency); dashed lines, bursa copulatrix (visible only by dissection or serial sectioning).

slightly more inflated last whorl, and the columella is relatively wider (figures 5–7). Coloration also differs, *L. sitkana* being purple brown or blackish, sometimes with one or two white or orange spiral bands, and never showing the flecked or tessellated pattern of *L. kasatka*. The only entirely reliable means of distinguishing the two species is by their reproductive anatomy: in females, the pallial oviduct of *L. sitkana* has two loops in the spiral pattern, and a large, swollen, septate jelly gland (figure 21), whereas there are three loops and a small jelly gland in *L. kasatka*; in males, mammilliform penial glands are present in *L. sitkana* (figure 22), but absent in *L. kasatka*.

Shells of the new species do not resemble closely those of any other *Littorina* from the northeastern Pacific or

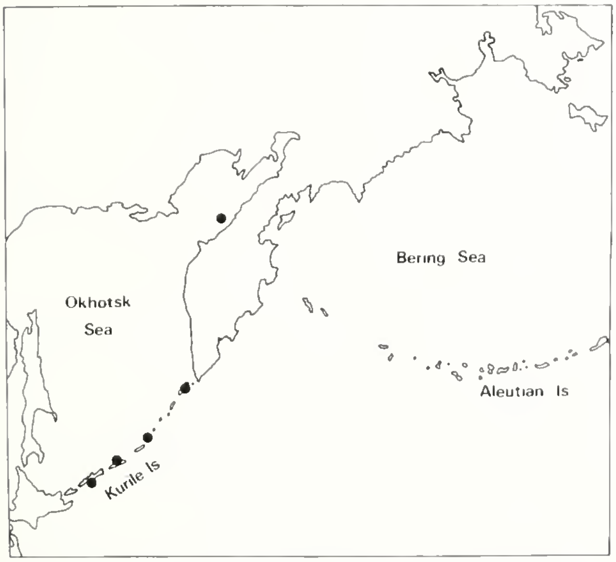


Figure 23. Distribution of *Littorina kasatka* new species. Record from Gulf of Shelikov could not be precisely localized.

Atlantic. No other *Littorina* has a pallial oviduct of the same form (Reid, 1990a), and only in *L. scutulata* Gould, 1849 and *L. striata* King and Broderip, 1832 does the penis also lack mammilliform glands.

DISCUSSION

The diversity of types of spawn and development within the genus *Littorina* have been reviewed by Reid (1989, 1990a), who showed that the type of spawn can be predicted from the relative sizes of the glandular components of the pallial oviduct. From its small jelly gland, lack of brood pouch and presence of a large capsule gland, it is likely that *L. kasatka* produces pelagic egg capsules. In other *Littorina* species that occur at high latitudes and reproduce in this way, the capsules are large (about 1 mm in diameter), biconvex and contain several eggs, and the capsules of *L. kasatka* are probably similar. It has been suggested that large capsules of this type are adaptive in relation to high levels of predation on pelagic propagules in cold seas (Reid, 1990a). The only other Pacific *Littorina* with pelagic capsules that occurs at such a high latitude is *L. squalida*. All known littorinids with pelagic capsules show planktotrophic development, so this can be predicted in *L. kasatka*. In contrast, the other four *Littorina* species in the northern Pacific are non-planktotrophic, developing within benthic gelatinous egg masses (Reid & Golikov, 1990).

A cladistic analysis of the 20 or so species of *Littorina* then known was given by Reid (1990a), and used as a basis for subgeneric classification. With three loops in the spiral of the pallial oviduct, a small jelly gland and probable pelagic egg capsules, *L. kasatka* is clearly a member of the paraphyletic subgenus *Littorina*. Within that area, its relationships cannot yet be resolved by cladistic analysis, because of uncertainty about its spawn. The presence of a bursa copulatrix in an anterior position does, however, suggest that its most likely place on the cladogram is between nodes 9 and 10 (see figure 5 in Reid, 1990a). As a result of the cladistic analysis the subgenus *Neritrema* was defined by the synapomorphies of anterior bursa copulatrix, large jelly gland and non-planktotrophic development (Reid, 1990a). In view of the anterior bursa of *L. kasatka*, this character must now be removed from the list of synapomorphies of *Neritrema*. The cladogram has also been used for a biogeographical analysis, which showed that in general the more derived species of northwestern Pacific *Littorina* occur at higher latitudes (Reid, 1990b). The probable position in the cladogram and known geographical distribution of *L. kasatka* are consistent with this trend.

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Littorina naticoides, New Species, with Notes on the Other Smooth-shelled *Littorina* Species from the Northwestern Pacific

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ABSTRACT

A new species, *Littorina* (*Neritrema*) *naticoides*, is described from the northwestern Bering Sea, Kamchatka and Kurile Islands. It is believed to be the sister species of *L. aleutica* and they can be distinguished by penial and shell characters. The two are allopatric, *L. aleutica* showing an oceanic distribution and *L. naticoides* a more continental one, but their ranges are known to approach to within 250 km of each other. Five *Littorina* species from the northwestern Pacific have smooth-shelled forms, which can be difficult to distinguish. These are *L.* (*N.*) *naticoides*, *L.* (*N.*) *aleutica*, *L.* (*N.*) *sitkana*, *L.* (*N.*) *subrotundata* and *L.* (*Littorina*) *kasatka*. The diagnostic features of their shells and reproductive anatomy are reviewed.

Key words: *Littorina*; Pacific; biogeography.

INTRODUCTION

Systematic studies of the family Littorinidae have been revolutionised by two developments over the past two decades. Firstly, anatomical features have been found to be more reliable than traditional shell characters for identification of species, and, secondly, there has been a growing appreciation of the wide range of shell variation shown by some species, and an understanding of its biological significance. The first use of anatomical characters to discriminate between sibling species (with similar or identical shells) was in the genus *Littorina*. (The generic name is here used in the strict sense, as defined by the cladistic analysis of Reid, 1989a). The most informative of these new characters have proved to be the shape of the penis, type of egg capsules and development (Sacchi & Rastelli, 1966; Heller, 1975; Hannaford Ellis, 1979; Murray, 1979) and also the form of the pallial oviduct (Reid, 1989a, 1990a). In all cases, studies of electrophoretically detectable genetic variation have supported the status of the sibling species initially recognized by anatomical differences (Ward, 1990). Although sometimes only one or other sex can be unequivocally identified by anatomical characters, there are no known cases of morphologically inseparable *Littorina* species.

Extreme intraspecific variation in coloration, sculpture and shape of the shell is a well-known feature of *Littorina*, and contributes to the difficulties of identification. Shell variation is especially marked in those species which show direct development, for here the lack of a widely-dispersed larval phase enhances the potential for adaptation to local environments. Selective factors influencing morphological and color variation between populations are believed to include predation, wave action and damage by mobile boulders (e.g., review by Raffaelli, 1982; Janson, 1982, 1983; Johannesson, 1986; Seeley, 1986). Other factors such as growth rate can also contribute to non-genetic shell variation (Kemp & Bertness, 1984).

The genus *Littorina* is restricted to the northern hemisphere, and most species occur on temperate and cold temperate shores (Reid, 1990b). So far, modern systematic revisions using anatomical details have only been done in Europe and the northeastern Pacific. *Littorina* species are also abundant in the northwestern Pacific, and the most recent review of the littoral molluscs of the Siberian region (Golikov & Kusakin, 1978) recognized six species: *L. squalida* Broderip & Sowerby, 1829; *L. brevicula* (Philippi, 1848); *L. mandshurica* Schrenck, 1861; *L. aleutica* Dall, 1872; *L. sitkana* Philippi, 1846; *L. kurila* Middendorff, 1848. The identifications were based only on characters of the shells. The first anatomical work on northwestern Pacific *Littorina* was done as part of a cladistic analysis of the 20 species then recognized in the genus (Reid, 1990a). This largely supported the classification of Golikov and Kusakin (although *L. kurila* was synonymized with *L. sitkana*), but the anatomical material used did not include any from the Soviet Union.

As part of a wider study of the systematics and distribution of *Littorina* species (Reid, in prep.), it has recently been possible to examine the extensive collection of preserved material from the Siberian coast held in the Zoological Institute, Leningrad. Preliminary results indicate that *L. squalida*, *L. brevicula* and *L. mandshurica* can each be readily identified by shell characters, as described and illustrated by Golikov and Kusakin (1978) and Reid (1990a). The remaining three of the species listed above were distinguished by Golikov and Kusakin (1978) primarily by their shell sculpture: *L. sitkana* having spiral ribs, *L. kurila* being smooth or almost so, and *L. aleutica* having rows of nodules. This division now seems to be an artificial one. Differences in reproductive anatomy define five species in this group: *L. sitkana*, *L. aleutica*, *L. subrotundata* (Carpenter, 1864), *L. kasatka* (recently described by Reid *et al.*, 1990) and *L. naticoides*, which is described herein. The shell characters of all five species are variable, and in particular *L. sitkana*, *L. aleutica* and *L. subrotundata* can show smooth or sculptured shells. "*Littorina kurila*," as defined by Golikov and Kusakin (1978), embraced smooth or slightly sculptured forms of all five species.

The nomenclature of these species is rather complex. During the wider study of *Littorina* systematics all available type specimens (housed in Natural History Museum, London; National Museum of Natural History, Washington, D.C.; Zoological Institute, Leningrad) have been examined and all original descriptions consulted, to ascertain that the new species is indeed undescribed. The available names include 18 synonyms of *L. sitkana* and three of *L. subrotundata*. Complete synonymies and full accounts of the described species will be given elsewhere. Here it need only be noted that preserved syntypes of *L. kurila* Middendorff, 1848 in the Zoological Institute, Leningrad, have shown that this taxon is a synonym of *L. sitkana* (see note added in proof in Reid, 1990a). As discussed below, the name "*L. kurila*" was incorrectly applied by Reid (1989a, 1990a,b) to what is here considered an open-coast form of *L. subrotundata*.

In the present paper the new species will first be described, then the four other similar species which sometimes show smooth shells will be discussed and distinguished.

MATERIALS AND METHODS

This resolution of the smooth-shelled *Littorina* species of the northwestern Pacific is based on examination of all material in the collections of the Natural History Museum, London (BMNH), the Zoological Institute, Leningrad (ZIL) and the National Museum of Natural History, Washington, D.C. (USNM). The new species is described from 21 lots in the ZIL, many of which are duplicated in the BMNH. A total of 27 males and 18 females were dissected, from 8 localities covering the known range of the species. Five radulae were extracted from specimens from three localities, and after cleaning in hot, concentrated sodium hydroxide solution were examined by scanning electron microscopy. For comparison, 32 specimens of *L. aleutica*, 82 of *L. subrotundata*, 45 of *L. sitkana* and 19 of *L. kasatka* were dissected, all from a wide range of localities.

SYSTEMATIC DESCRIPTION

Littorina (*Neritrema*) *naticoides* new species
(figures 1–12, 15–23, 28–35, 37)

Types: holotype BMNH 1990053, Milne Bay, Simushir I., Kurile Is, USSR (figures 1, 16); 2 dry paratypes BMNH 1990054; 6 paratypes in alcohol BMNH 1990055; 2 paratypes in alcohol ZIL.

Etymology: *Natica*-like, a reference to shell shape.

Shell (figures 1–12): *Dimensions:* Adult size range 6.2–15.9 mm shell height.

Shape: Teleoconch approximately 4 whorls, moderately solid. Turbinate, often rather patulous, whorls smoothly rounded, sutures distinct. Columella relatively wide, slightly excavated, pillar concave.

Sculpture: Protoconch 0.73–0.75 mm diameter, 1.8 whorls. Teleoconch: indistinct axial growth lines only, no spiral grooves; faint spiral striae sometimes visible at high magnification, but no strong striations.

Color: Orange brown to dark purple brown, usually 5–12 dark brown or black spiral lines; sometimes a pale spiral band on base. Aperture orange brown to purple brown. Columella white, sometimes tinged purple brown.

Animal: *Head-foot (figures 28–30):* Head grey to black, paler at tips of tentacles and snout; unpigmented patch over eye and usually another at inside of tenacle base. Sides of foot usually pale grey speckles or unpigmented, sometimes blackish.

Operculum: normal, paucispiral littorinid (type A of Bandel & Kadolsky, 1982).

Penis (figures 15–20): Wrinkled base with 4–15 mamilliform penial glands in single row on anterior edge (one specimen with a single gland); filament short, less than half length of base, broadly triangular, with simple subepithelial glandular region (more opaque in preserved specimens); sperm groove open to tip.

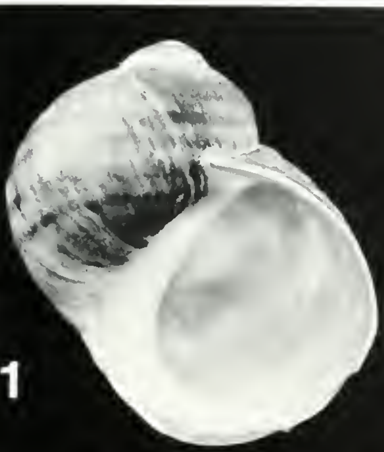
Pallial oviduct (figures 21–23, 37): Complex spiral of 3 loops, first of albumen gland, second and third of capsule gland; final straight section a large, swollen, septate jelly gland. Bursa copulatrix in anterior position.

Spawn: Benthic, gelatinous egg mass up to 6 mm in diameter, containing spherical capsules 0.7–0.8 mm in diameter, each with single egg surrounded by albumen layer 0.5–0.6 mm in diameter.

Radula (figures 31–34): All cusps bluntly rounded. Rachidian with 3 large, 2 small cusps; outline of tooth (viewed flat from above) varies from square to oblong (ratio of length of tooth: width at mid-point 0.77–2.0). Lateral and inner marginal teeth each 4 large cusps. Outer marginal 5–7 cusps.

Distribution: *Habitat:* A range of intertidal habitats are reported: on dead shells in sheltered inlets; *Mytilus*

Figures 1–12. *Littorina naticoides* new species. **1.** Holotype (BMNH 1990053), Milne Bay, Simushir I., Kurile Is. **2, 3.** Ozernovskiy, Kamchatka. **4, 5.** 10 km east of Cape Kamchatskiy, Kamchatka. **6.** Avacha Bay, Kamchatka. **7.** Kronotskiy Gulf, Kamchatka. **8–10.** Egvekinot Inlet, Anadyrskiy Gulf. **11, 12.** Ozerniy River estuary, Kamchatka. **Figure 13.** *Littorina aleutica*, Provideniya. **Figure 14.** *Littorina subrotundata*, Milne Bay, Simushir I., Kurile Is. (All specimens in BMNH).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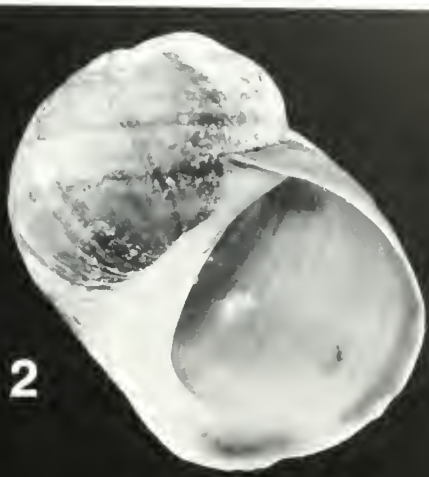
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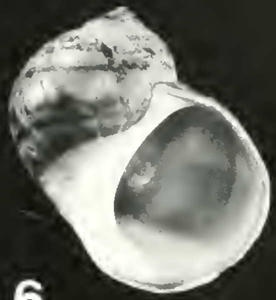
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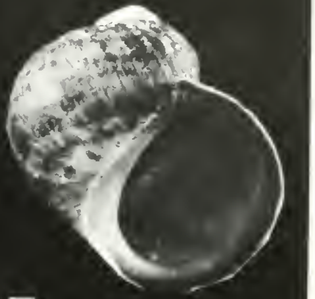
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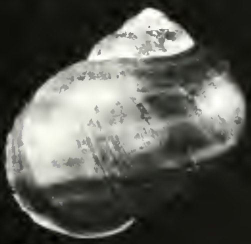
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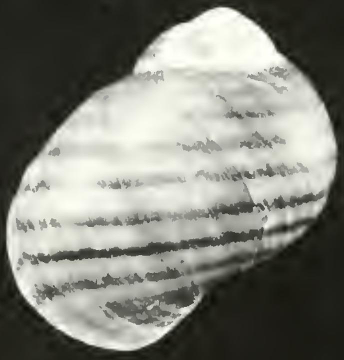
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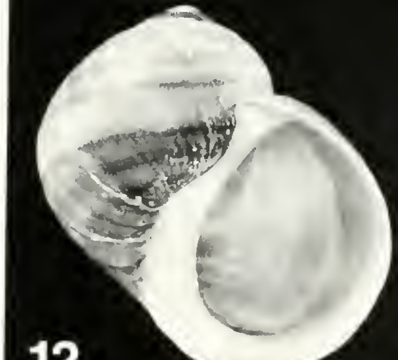
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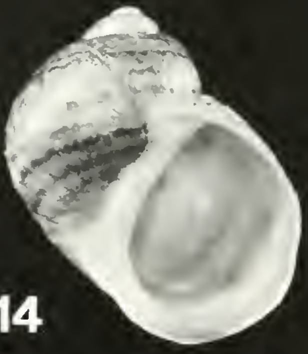
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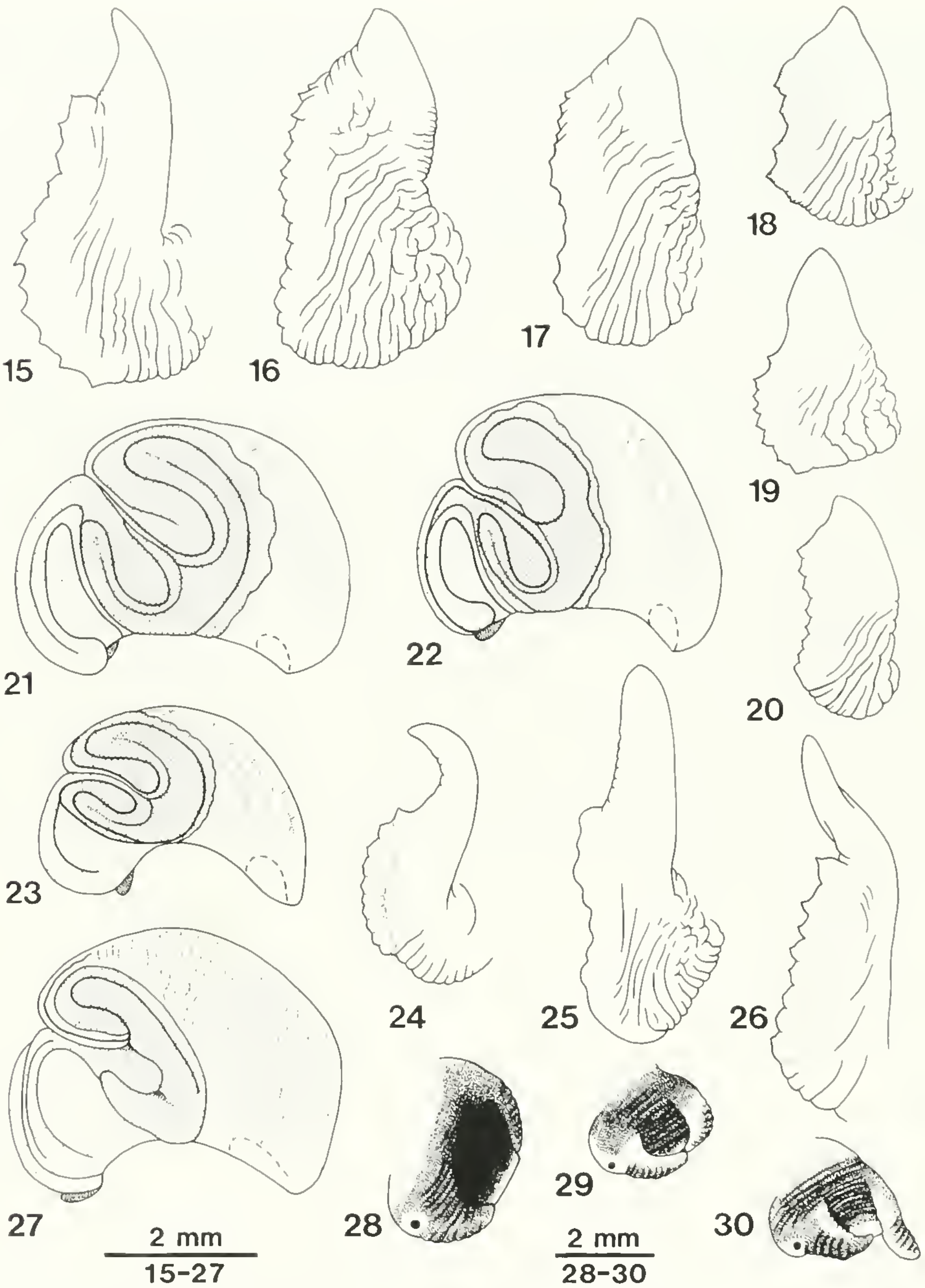
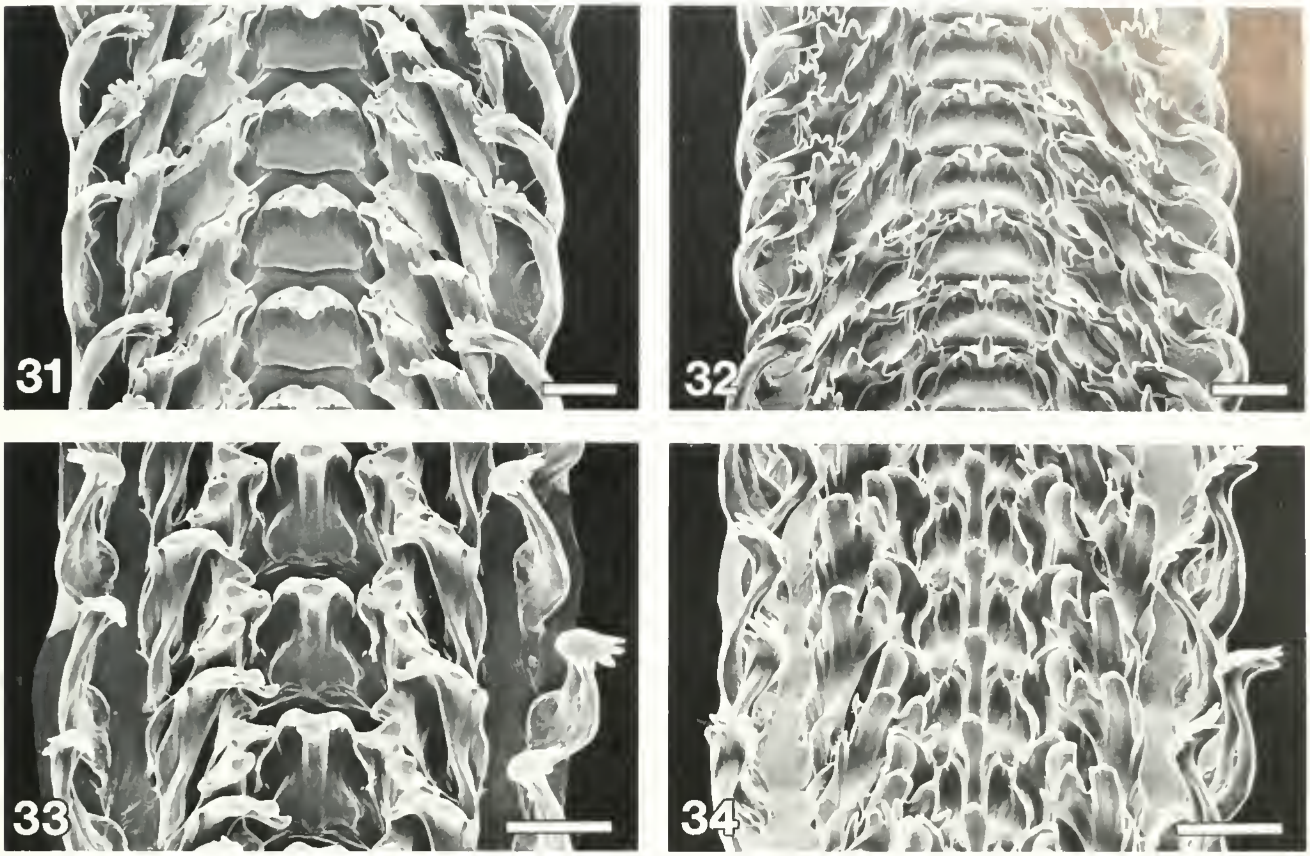


Figures 15–23, 28–30. *Littorina naticoides* new species. **15–20.** Penes: mamilliform glands on left edge, sometimes visible by transparency **21–23.** Pallial oviducts. **28–30.** Heads. **15, 17, 18.** Ozernovskiy, Kamchatka. **16.** Penis of holotype, Milne Bay, Simushir I., Kurile Is. **18, 19, 23, 30.** Krista Gulf, Anadyrskiy Gulf. **20.** Egvekinot Inlet, Anadyrskiy Gulf. **21, 29.** Kronotskiy Bay, Kamchatka. **22.** 10 km east of Cape Kamchatskiy, Kamchatka. **Figures 24–27.** *Littorina aleutica*. **24–26.** Penes. **24, 26.** Lihacheva, Provideniya **25.** Adak I., Aleutian Is. **27.** Pallial oviduct, Nizki I., Aleutian Is. Key to figures 21–23, 27: sparse stipple, albumen gland; dense stipple, capsule gland, dotted lines, septa of jelly gland (visible by transparency); dashed lines, bursa copulatrix (visible only by dissection).

zone on exposed shores; on *Halosaccion* (red alga); in *Alaria* (brown alga) belt.

Range (figure 35): Kurile Islands, south and west Kamchatka, Anadyrskiy Gulf.

Records: Kurile Is: Urup I.; Milne Bay, Simushir I.; Spaseniya, Simushir I.; Diani Bay, Ketoi I., Paramushir I.; Kamchatka: Ozerniy River estuary, Okhotsk Sea; Ozernovskiy; Avachinskaya Bay, near Cape Vilkova; Avacha Bay, near Petropavlovsk; Kronotskiy Gulf; 10 km east of Cape Kamchatskiy; Anadyrskiy Gulf: Egvekinot Inlet, Krista Gulf (all ZIL and BMNH).



Figures 31–34. Radulae of *Littorina naticoides* new species. Scale bars = 50 μm. **31, 32.** 10 km east of Cape Kamchatskiy, Kamchatka. **33, 34.** Egvekinot Inlet, Anadyrskiy Gulf. **31, 33.** Viewed flat. **32, 34.** Same radulae as figures 31, 33, but viewed from an angle of 45° to show cusp shape.

Similar species: As mentioned above, *L. kurila* Middendorff, 1848 is a junior synonym of *L. sitkana* Philippi, 1846, but the name has been widely used in the literature for any of the five *Littorina* species (including *L. naticoides*) in the northwestern Pacific that frequently have smooth shells. The other four members of the group will be considered in turn, and the characters of all five species are summarized in table 1. Radular characters have not proved useful in discriminating between them.

L. (Neritrema) sitkana (figure 39): The typical form of this species has a strongly carinate shell with spiral stri-

Table 1. Summary of characters of five *Littorina* species from the northwestern Pacific.

		aleutica	*kasatka*	*naticoides*	*sitkana*	*subrotundata*
Shell:	adult size (mm)	6–14	6–11	6–16	6–23	4–14
	patulous shape	+	–	+	–	(+)
	nodulose sculpture	(+)	–	–	–	–
	spiral ribs	(+)	–	–	(+)	(+)
	spiral microstriae	+	–	–	(+)	–
	pattern of dark spiral lines	(+)	–	+	(+)	+
	pattern of pale flecks	–	+	–	–	–
Penis:	mamilliform glands	7–12	0	1–15	5–14	5–17
	filament ≥ ½ length of base	+	–	–	–	–
Pallial oviduct	spiral pattern	fig. 38	fig. 36	fig. 37	fig. 39	fig. 40
	swollen, septate jelly gland	+	–	+	+	+
Spawn:	benthic egg mass	+	–	+	+	+
	pelagic capsules	–	+	–	–	–

+ = Present; (+) = sometimes present, – = absent.

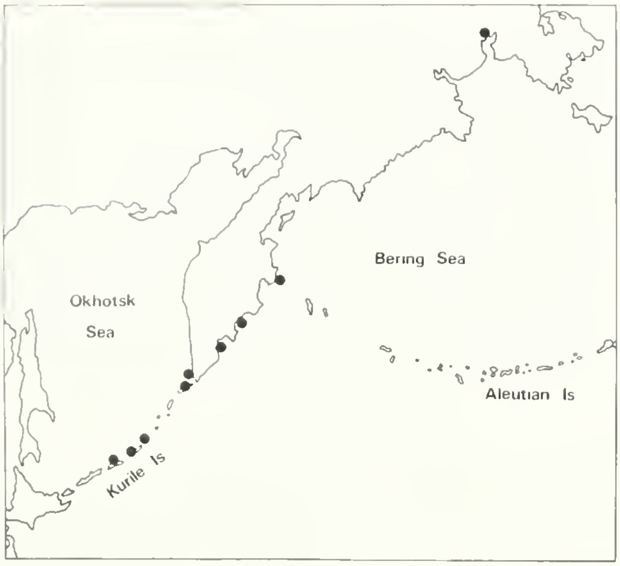


Figure 35. Distribution of *Littorina naticoides* new species.

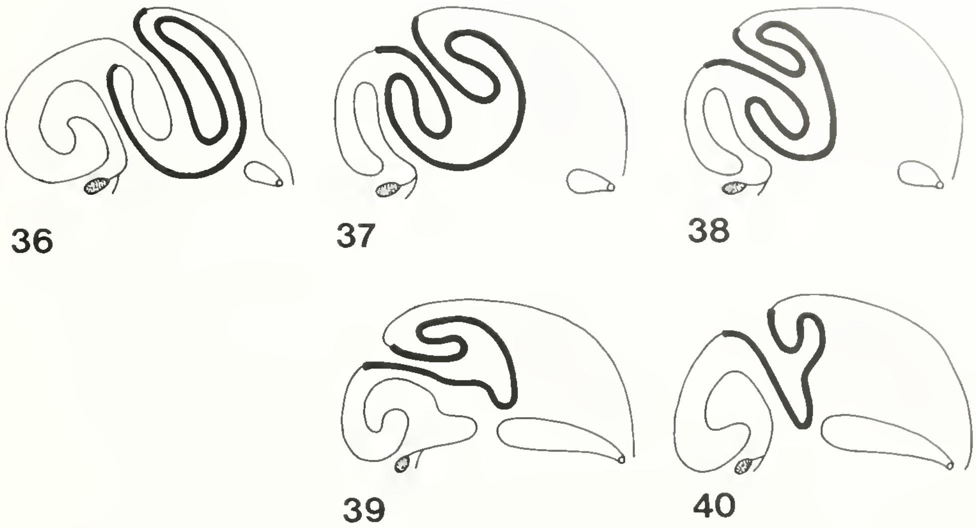
ations between the carinae (e.g., Reid, 1990a: fig. 1l) and is most frequent in the north and northeastern Pacific from Oregon to the Aleutian Islands, while in northern Japan it is usually only the base that bears strong grooves. In either case the shell is thereby distinguished from all others in the group except rare forms of *L. subrotundata*. Problems arise with the smooth forms of this species (Reid *et al.*, 1990: figs 5–7), which predominate in the Kurile Islands and Kamchatka, and also occur in other parts of the range. These shells may be quite large (up to 23 mm), are less patulous than *L. naticoides* and *L. aleutica* and are often uniformly black or brown (except in the Okhotsk Sea, *L. sitkana* commonly lacks the pattern of narrow black lines seen in *L. naticoides* and *L. subrotundata*). Synonyms based on smooth forms of this species include *L. kurila* Middendorff, 1848, *L. subtenebrosa* Middendorff, 1848 and *L. sitkana* var. *atkana* (Dall, 1886). Females of *L. sitkana* can be immediately recognized by the unique spiral pattern of the pallial oviduct (figure 39; Reid *et al.*, 1990: fig. 21) with its long backward loop of capsule gland, but the penis is similar to that of both *L. naticoides* and *L. subrotundata*.

L. (Neritrema) subrotundata (figures 14, 40): There has been confusion about the identity of this species, and the name is here used in a wider sense than by previous authors. As interpreted here, the species has a wide distribution around the northern Pacific, from northern California through the Aleutian Islands to the southern Kurile Islands.

The name has previously been applied only to the thin-shelled, tall-spired form (Reid, 1990a: fig. 1n) initially described by Carpenter (1864) as a doubtful member of the genus *Assiminea*. Synonyms are ?*Paludinella castanea* Carpenter, 1865, and *Paludinella newcombiana* Hemphill, 1877, and the species has sometimes been placed in the genus *Algamorda* Dall, 1918 (a synonym of *Neritrema* Récluz, 1869, regarded as a subgenus of *Littorina*, see Reid, 1989a). The species was poorly known and believed to be restricted to brackish-water salt marshes from northern California to Washington (MacDonald, 1969; Reid, 1990b). The form from this habitat is analogous to the form "*tenebrosa*" of the Atlantic *L. saxatilis* (Olivi, 1792), which is also small, thin-shelled and tall-spired (Muus, 1967; Janson & Ward, 1985), probably as a result of similar selection pressures or ecophenotypic effects in the brackish lagoons in which it occurs. This form of *L. saxatilis* contrasts with the lower-spired and more patulous form on exposed coasts (e.g., Raffaelli, 1979; Janson, 1982).

As a result of the dissection of additional material, it is now believed that, like *L. saxatilis*, *L. subrotundata* also occurs in habitats covering a wide range of wave exposures, and has a similarly wide range of variation in shell morphology. The forms from exposed rocky coasts, here assigned to *L. subrotundata* for the first time, have (like *L. saxatilis* from similar habitats) a lower spire and larger aperture than the salt-marsh form, and were previously incorrectly identified as *L. kurila* (Reid, 1990a, b). A shell of this type from the Aleutian Islands was illustrated by Reid (1990a: fig. 1m), and figure 14 shows a slightly more patulous form. A population from the exposed shores of Tatoosh Island, Washington, has recently been studied by Boulding (1990), who concluded that it was an undescribed subspecies of *L. kurila*. However, examination of specimens from this locality has revealed no significant anatomical differences from either typical *L. subrotundata* collected in salt marshes in Washington, or from specimens of this species from the Aleutian Islands. Furthermore, no diagnostic allelic differences between samples from these three areas have been found by enzyme electrophoresis (E. G. Boulding, personal communication). The available evidence therefore suggests that they are conspecific, but further study would be desirable. Neither the known geographical distribution of *L. subrotundata*, nor its considerable variation in shell morphology throughout its range, support its division into subspecies.

One reason why the name *L. subrotundata* has not previously been used for the exposed-coast form is that, at least in Washington, it appears to be completely ecologically segregated from the typical form in salt marshes, because the species is not known to occur in intermediate habitats. This locally disjunct distribution need not, however, imply genetic isolation of the two forms. It could be maintained, for example, by the action of crab or other predators. It is known that the exposed-coast form is susceptible to attack by crabs because of its thin shell, and that crabs are more abundant in protected rocky habitats than on exposed coasts (Boulding, 1990). It is possible that both exposed coasts and salt marshes are refuges for this species from crab predators. Further north in its range, in Alaska (personal observation), *L. subrotundata* does occur on both exposed and sheltered rocky shores and there is continuous variation in shell shape between the two extremes of habitat. In-



Figures 36–40. Diagrammatic representation of pallial oviducts of *Littorina* species from the northwestern Pacific. **36.** *Littorina (Littorina) kasatka.* **37.** *L. (Neritrema) naticoides.* **38.** *L. (N.) aleutica.* **39.** *L. (N.) sitkana.* **40.** *L. (N.) subrotundata.* Key: continuous line with spiral loops represents path of egg groove through pallial oviduct; thick section, capsule gland; dense stipple, seminal receptacle at posterior end, anterior sac, bursa copulatrix; dotted lines, septa of jelly gland. Shape of loops of capsule gland and its relative size are most important features. Oviducts of *L. aleutica* and *L. naticoides* sometimes indistinguishable; c.f. figures 21–23, 27.

terestingly, there is again a parallel with *L. saxatilis*, which shows a comparable segregation of low-spired and high-spired forms on exposed coasts and in salt marshes respectively, at the southern limit of its European range (Gofas, 1975; personal observation), whereas at more northerly latitudes it occupies the entire spectrum of habitats and morphological intermediates are common (Janson & Ward, 1985; personal observation).

The shell of *L. subrotundata* is often extremely similar to that of *L. naticoides* in size, coloration and shape, although it does not attain such extreme patulous forms as the latter (e.g., figures 3–5). Like *L. naticoides*, it is usually entirely smooth, but occasional forms have spiral ribs; in such cases the lack of strong spiral striations in the grooves distinguishes it from *L. sitkana*. Once again, anatomical characters are more helpful; the form of the pallial oviduct is diagnostic (figure 40) with a relatively smaller capsule gland than that of either *L. sitkana* or *L. naticoides*, but the penis is similar to those of both these species.

L. (Neritrema) aleutica (figures 13, 24–27, 38): Shells of *L. aleutica* from the Aleutian Islands are usually sculptured by four nodulose cords with strong spiral striations in the intervening grooves (Reid, 1990a: fig. 1k). However, in the northwestern Bering Sea the shells are not nodulose; slight spiral ribs may remain, as do the striations (visible at the periphery in figure 13), which help to distinguish the shell from the very similarly shaped, but entirely smooth, *L. naticoides*. In this case it is the male anatomy that is diagnostic, the penis showing a narrower filament at least half as long as the wrinkled base, whereas that of *L. naticoides* is shorter (figures 24–26, c.f. figures 15–20). The pallial oviduct is similar only to that of *L. naticoides*, but the jelly gland is usually relatively larger and the capsule gland a little smaller (figures 22, 38, c.f. figures 21–23, 37).

L. (Littorina) kasatka: This newly-described species (Reid *et al.*, 1990) is the smallest of the five smooth-shelled *Littorina* species (6–11 mm) and has the most restricted distribution, being recorded only from the Kurile Islands and Gulf of Shelikov. The shell is closest to small, smooth specimens of *L. sitkana*, although its shape is subtly different, with a relatively narrower columella and smaller aperture. Coloration also differs, the shell of *L. kasatka* being brown, often with indistinct white flecks or tessellation, unique among the five species discussed here. Despite the superficial similarity of the shell, this species is probably not closely related to the others in the group, since its reproductive anatomy is markedly different. Mamilliform penial glands are absent in the male, while the pallial oviduct lacks a swollen, septate jelly gland and shows a unique spiral pattern of albumen and capsule glands. These characteristics of the oviduct indicate that the spawn consists of pelagic egg capsules, probably with planktotrophic development, and for this reason it is classified in the subgenus *Littorina* (Reid *et al.*, 1990). In contrast, the four other species have a large jelly gland, benthic egg masses and direct development, and are therefore members of the subgenus *Neritrema* (Reid, 1989a, 1990a).

DISCUSSION

An earlier review of living *Littorina* species with a cladistic analysis of their relationships (Reid, 1990a) must be revised in the light of the new information on material from the Siberian coast. At least three changes are necessary. Firstly, "*L. kurila*" (*non* Middendorff, 1848) of the earlier publication is now believed to be the same as *L. subrotundata* (no differentiating characters were found in the earlier analysis). Secondly, *L. kasatka* must be added to the cladogram (Reid 1990a: fig. 5), in a position between nodes 9 and 12 (as yet unclear because of lack of information about egg capsules, but between 9 and 10 most likely, Reid *et al.*, 1990). Thirdly, *L. naticoides* must be added; this is clearly the sister species of *L. aleutica*, since with the exception of shell sculpture, all characters used in the cladistic analysis are the same in both species.

This sister-group relationship is supported by the similar oviducts, egg masses, penial glands and patulous shells. Consistent differences in the relative length of the penial filament and in shell sculpture, and small differences in relative sizes of oviducal glands, are, however, sufficient to separate *L. naticoides* as a new species. So far, the two species have not been found sympatrically. *Littorina aleutica* is recorded from the Aleutian, Komandor and Pribiloff Islands, and from St Lawrence Island and Provideniya in the northern Bering Sea. *Littorina naticoides* occurs from Anadyrskiy Gulf to the Kurile Islands, approaching within 350 km from the closest record of *L. aleutica* in the northern Bering Sea, and within 250 km in eastern Kamchatka. In part this apparent allopatry could be explained by lack of collections from the remote northwestern shores of the Bering Sea. However, the separate distributions in the Aleutian, Komandor and Kurile Islands and in Kamchatka are probably real, because there are extensive collections of *Littorina* from all these areas. Furthermore, the two distributions suggest a possible ecological separation. *Littorina aleutica* has the more "oceanic" distribution, occurring only on islands and at the tip of the Chukotskiy Peninsula, whereas *L. naticoides* is more "continental," occurring on mainland coasts, even in inlets and estuaries, as well as in the Kurile Islands. There are similar examples elsewhere in the Littorinidae of closely related congeners with contrasting "oceanic" and "continental" distributions (*Littoraria*, Reid, 1986; *Peasiella*, Reid, 1989b), but hitherto the phenomenon has been demonstrated only in the tropics.

The biogeography of *Littorina* has been analysed by Reid (1990b). These modifications to the cladogram and distributional data on new species do not alter the earlier conclusion that in general in the northeastern Pacific more apomorphic species occur at higher latitudes, perhaps as a result of climatic cooling which induced speciation. Indeed, recognition of "*L. kurila*" (*sensu* main text of Reid, 1990a and Reid, 1990b) as conspecific with *L. subrotundata* removes the anomaly of the latter's northeastern Pacific distribution. However, *L. naticoides* and *L. aleutica* are the only known example in the genus of sister species that occur in the same ocean and show allopatric distributions; in other cases distributions show broad overlap. This could indicate that a different speciation mechanism has been involved here.

ACKNOWLEDGMENTS

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Activity Patterns and Homing of *Acanthopleura gemmata* (Blainville, 1825) (Mollusca: Polyplacophora) in the Rocky Intertidal of the Jordan Gulf of Aqaba

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ABSTRACT

Acanthopleura gemmata forages and homes irrespective of the time of day. Feeding excursions begin when the water depth of the ebbing tide over the individual is around 10 cm or less and homing occurs prior to the level of the flooding tide reaching about the same depth. The patterns of behavior differ significantly from those of *A. gemmata* previously reported at Heron Island, Australia and in Somalia. Reduced predation pressure is considered to be one of the factors accounting for this difference in behavior.

Key words: Chiton; ecology; predation; Red Sea.

INTRODUCTION

Ferreira (1986) revised the genus *Acanthopleura* Guilding, 1829 to include *Acanthozostera* Iredale and Hall, 1926. The revision also included placement of *Acanthopleura haddoni* Winckworth, 1927 and *A. spiniger* (Sowerby, 1840) into the synonymy of *A. gemmata* (Blainville, 1825). The material examined by Ferreira (1986) included specimens from Israel, Egypt, Djibouti, Oman, Somalia, Heron Island, Australia as well as numerous other localities in the Indo-Pacific region. Of the intertidal chitons, *A. gemmata* has the widest geographic distribution, from 32°E to 140°W and 33′N to 6°48′S (Ferreira, 1986). The synonymy and definition of *A. gemmata* proposed by Ferreira (1986) is followed in the present paper.

Reports on the activity and homing of *Acanthopleura gemmata* include those of Thorne (1967, 1968 as *Acanthozostera gemmata*) at Heron Island, Australia and Chelazzi *et al.* (1983a,b, 1987) and Chelazzi and Parpagnoli (1987) along the coast of Somalia. Of the reports of *A. gemmata* (either as *A. haddoni* or *A. spiniger*) in the Red Sea, including the Gulf of Aqaba (Sykes, 1907; Leloup, 1937, 1960, 1980; Rees & Stuckey, 1952; Safriel & Lipkin, 1964; Eibschütz *et al.*, 1967; Fishelson, 1971; Mergner & Schuhmacher, 1974; Mastaller, 1978, 1979; Pearse, 1978, 1983; Ayal & Safriel, 1980; Soliman & Iskander, 1982; Hulings, 1986, 1987; Al-Hajj, 1987), none contain information on foraging or other patterns of activity, nor on homing behavior.

This paper describes the activity patterns and homing of *Acanthopleura gemmata* (figure 1), the only chiton in the rocky intertidal of Jordan. The vertical distribution of this chiton ranges from the mid-midlittoral to the midlittoral-infralittoral fringe contact. The northern Gulf of Aqaba is the northernmost geographic occurrence of *A. gemmata* according to Ferreira (1986). Voucher specimens of *A. gemmata* have been deposited in the National Museum of Natural History Smithsonian Institution (USNM *858104*) and in the reference collection of the Marine Science Station, Aqaba, Jordan.

STUDY AREA

The characteristics of the rocky intertidal zone along the coast of Jordan have been described by Hulings (1986, 1987). Briefly, the tides are mixed, having a spring range of around 1.0 m and a neap range of 0.5 m. The diurnal inequality of the high tides averages 4.2 cm, that of the low tides 4.7 cm. The tide levels are often influenced by atmospheric pressure (Uziel, 1968; Hulings, 1989). The tide levels also fluctuate with changes in sea level of up to 1 m that occur in the northern Gulf. During the period July through October, sea level is higher while from December through May, it is lower; the intervening periods are transitional (Uziel, 1968; Fishelson, 1973; Hulings, 1989). Although the vertical ranges and variations in the tide are small, the prevailing near horizontal substrata of the midlittoral zone are subjected to extended submergence during the periods of higher sea level and emergence during periods of lower sea level (Hulings, 1986).

The climatic conditions in the northern Gulf of Aqaba are very significantly influenced by the much greater

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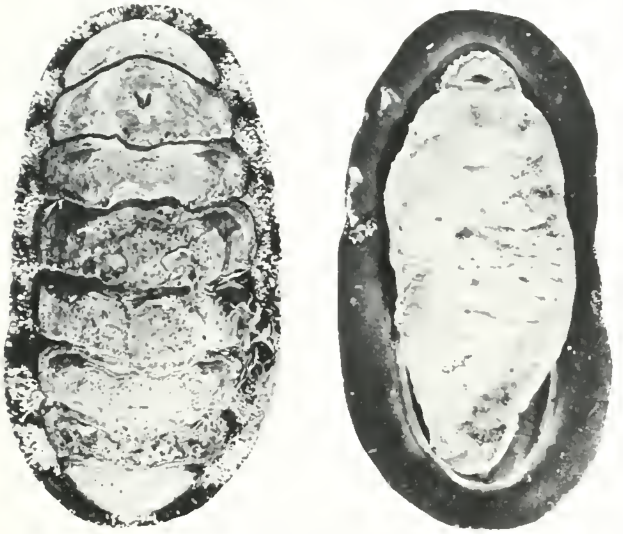

Figure 1. *Acanthopleura gemmata* from the rocky midlittoral zone of Jordan, northern Gulf of Aqaba. (1.0 ×).

Figure 2. A section of the study area during ebbing tide. The arrows indicate: **1.** Approximate supralittoral fringe-midlitorral contact zone; **2.** The *Tetraclita* or mid-midlittoral zone; **3.** lower midlittoral-infralittoral fringe contact; **4.** outer edge of the fringing reef. See text for details.

desert land area surrounding the very limited marine area. The land to sea winds are northerly 93% of the time with Beauforts 3 (7 to 10 kn) and 4 (11 to 16 kn) occurring 63% of the time. Mean air temperatures range from 16 °C in January to 32 °C in July–August; minimum-maximum means ranges are 12 to 20 °C in January and 26 and 37 °C in July–August (Jordan Meteorological Department). Anati (1976, 1980) estimated evaporation in the Gulf to be 4.2 m/yr. The area is further characterized by strong solar insolation (Assaf & Kessler, 1976; Levanon-Spainer *et al.*, 1979).

The locality (figure 2) investigated in detail for the activity of *Acanthopleura gemmata* is located at the Marine Science Station (34°59′20″E, 29°29′30″N), approximately 10 km south of the city of Aqaba. The midlittoral zone is characterized by two types of substrata, landward beachrock and below, a platform of near horizontal calcareous fossil reef matrix. The beachrock area is biologically recognizable by the presence of the giant barnacle *Tetraclita squamosa rufotincta* Pilsbry, 1916, which colonizes the surface of the beachrock. This area is the *Tetraclita* zone of Safriel and Lipkin (1964) and is considered herein as the middle portion of the midlittoral. The zone averages 5 m in width and consists of discontinuous strips of beachrock, underlain by fossil reef, parallel to the shore; between the strips are depressions and tide pools as well as numerous and varied refuges. The surface configuration of the fossil reef in the area of the beachrock is very irregular. In addition, the underlying reef substrate is hard compared to the reef matrix of the platform.

The platform of nearly horizontal, calcareous reef matrix is 10 to 18 m wide, extending from the seaward edge of the beachrock to the midlittoral-infralittoral fringe (Safriel & Lipkin, 1964) contact and is also referred to herein as the lower midlittoral. The surface topography of the platform is mostly even and uniform. In the area of the midlittoral-infralittoral fringe contact, however, the substratum is eroded, providing refuges such as overhangs, crevices and pits. Beyond the contact is a 35 to 85 m wide back reef lagoon of a fringing reef. The lagoon, having a maximum depth of around 2 m depending on the tide and sea level, terminates at the outer edge of the reef. It is here that wind-generated waves break and their energy is further reduced across the lagoon. Thus the intertidal area has minimal exposure to wave action. During high tides, however, wind-induced choppy conditions may prevail, but the wave amplitude is small because of the shallow depth.

At the locality investigated, the mean length of *Acanthopleura gemmata* is 53.0 mm (SD = ±8.6 mm; range, 30 to 75 mm; n = 160) and the mean density is 4.4 individuals/m^2 (SD = ±3.1; n = 80 m^2). According to Hulings (1986), *A. gemmata* becomes sexually mature at a length of between 24 and 27 mm.

METHODS AND MATERIALS

The data on the activity and homing of *Acanthopleura gemmata* were obtained entirely from detailed observations made during the period 14 October through 16 December 1986. Observations were made on groups of *A. gemmata* within a 100 m stretch parallel to the beach and 10 to 18 m wide. The area included the midlittoral range of the vertical distribution of *A. gemmata* as well as its occurrence in beachrock areas, on fossil reef capped by beachrock and on the platform below the beachrock.

The shell plates and the home area or scar of *Acanthopleura gemmata* were color-coded using different colors of enamel paint. Subsequent repainting of the plates was often necessary and there was no detectable negative effect of the painting. Forty-five individuals comprising eight different groups, each with three to eight individuals, were color-coded. One group was on beachrock (six individuals), three on fossil reef capped by beachrock (17 individuals) and four (22 individuals) on the platform. During the study period, one specimen was lost at the beachrock site, two from the beachrock-fossil reef substrata and three from the platform area. Thus 39 individuals, which were present during the entire two month period of investigation, were used in the analyses of activity and behavior. Various combinations of groups and/or individuals were used for the analysis of specific types of activity and behavior.

During the October–December period, daytime observations were made on 46 days. The total number of days included an initial two consecutive days of observations followed by eight weeks of five consecutive days per week and a final four consecutive days. On each day, each individual within the eight groups was observed one or more times (all groups observed each time being a set of observations). The number of observations on each group averaged 5/day (range, 1 to 11/day). Over the 46 days, the number of sets of observations per group ranged from 139 to 161 with the total number being 5,712. Nighttime observations were made on two groups totaling eight individuals during October (2), November (2) and December (1). There were two sets of observations each night, a total of 80 sets or 320 observations. Six additional groups of six to 11 individuals, a total of 53, within the area were checked once a day during each five consecutive days of observations. In addition, periodic observations were made during January, February, June and August 1987 and February and June 1988.

The data recorded during each observation of each color-coded individual included the position in relation to the color-coded home scar. If the individual was in the home scar, it was so noted as well as whether there was a reversal in the orientation. If the individual was away from the scar, the distance in cm from the home scar and the direction was noted. Occasionally, actual movement of an individual was observed. In most cases, however, movement was inferred based on the position of the individual. The depth of water over the individual was measure in approximate cm intervals. If the individual was partially to completely submerged dorsoventrally, it was designated as awash. In the absence of water cover, the substratum was recorded as wet if water was visible or dry if no water was visible.

The number of sets of observations made in relation to the state of the tide during the daytime over the two months were as follows: eight at flood tide, 39 at flooding tide, 27 at ebb tide, 18 at ebbing tide and six at ebbing to ebb tide. During the period, there were 19 days of spring tide, 10 of transitional spring to neap, 10 of neap and seven of transitional neap to spring. During nighttime observations, the tide was at flood on one occasion, at ebb on another, ebbing on a third and flooding on two others. During two of the nights, there were spring tides, during one neap and during two transitional spring to neap.

Two additional groups of *Acanthopleura gemmata* were monitored for vertical migration with changes in sea level from low during October (10 days) to high during December (11 days) with November (22 days) being transitional. One group of 12 individuals was in the *Tetraclita*-beachrock area of the midlittoral and the other group, 11 individuals, was near the midlittoral-infralittoral fringe contact. During the October–December period, a total of 91 observations during 46 days were made on the *Tetraclita*-beachrock group and 24 observations during 16 days on the midlittoral-infralittoral fringe group. Subsequent observations on each group were conducted during January (2 days), February (1), June (1) and August (1) 1987 and February (1), June (1), August (1) and September (1) 1988. These observations included four days of higher sea level and five of lower.

The direction of movement from the home scar during foraging forays was measured in 17 color-coded *Acanthopleura gemmata* in the beachrock area and on the platform over a period of 2 to 29 days. The range of foraging (in cm) was measured among the same individuals over the same period. The range was considered to be the distance from the home scar to the most distant point within the individual grazing area, the latter identifiable by the color being lighter than the surrounding area.

RESULTS

Activity, in terms of movement, of *Acanthopleura gemmata* from mid-October to mid-December 1986 was found to be dependent on the depth of water over the individual (table 1). Based on 19 color-coded individuals in four groups on the platform and five in one group in the beachrock area, when there was movement, it occurred predominantly from when the substratum was wet to when the water depth of the tide over the individual was 10 cm or less irrespective of the time of day. During the day, 88% of the instances of movement occurred within the wet to 10 cm range, while 90% of nocturnal movement occurred within this range. A similar pattern prevailed in relation to the type of tide day and night (table 2). However, movement did not always occur during the wet to 10 cm depth interval (tables 1, 2). Among the same 19 color-coded individuals, day and night movement in relation to the type of tide (table 2) was as follows: 34% of the instances of movement occurred during spring tide, 38% during transitional spring to neap, 16% during neap and 12% during transitional neap to spring.

It is recognized that the number of observations at night was very limited. However, additional evidence for nocturnal activity is derived from comparing the position of an individual at the end of one day with that at the beginning of the next. Among five groups of 24 color-coded individuals, a total of 318 observations revealed 113 (36%) instances of positions different from that of the last observation, usually late afternoon, on the previous day. Among the total different positions, 34 (30%) were in the home scar at the beginning of the second day. By comparison, 193 (94%) of the 205 instances of the position being the same were in the home scar at the beginning of the second day.

Table 1. Movement of *Acanthopleura gemmata* in relation to water depth during day and night (n = number of observations; — = no observation; A = awash).

Water depth (cm)	Movement		No movement	
	Day n	Night n	Day n	Night n
Dry	0	—	26	—
Wet	97	15	264	54
A–5	172	43	171	49
5–10	137	48	128	60
10–15	45	12	104	39
15–20	8	—	102	0
20–25	0	—	48	—
25–30	0	—	32	—
30–35	0	—	10	—
35–40	0	—	5	—
Total	459	118	890	202

Table 3. Home *vs.* away position of *Acanthopleura gemmata* in relation to water depth (n = number of observations).

Water depth (cm)	Home n	Away n
Dry	10	0
Wet	96	46
A–5	42	95
5–10	85	45
10–15	74	21
15–20	75	4
20–25	46	3
25–30	43	3
30–35	25	1
35–40	19	1
50	5	0
Total	520	219

The home *vs.* away position of one group of five individuals with respect to water depth during the day over 41 days is shown in table 3. In 70% of the instances, the individuals were at home over a range of conditions from dry substratum to a water depth of 50 cm, while 85% of the away instances were during the wet to around 10 cm water level period.

The movement of *Acanthopleura gemmata* with the ebbing tide was either rotation within the scar or the initiation of a feeding excursion. The latter generally occurred from when the water depth over the individual was around 10 cm until the time the individual was completely exposed. Following exposure, the animal either returned to the homing scar before complete drying of the substratum or became inactive and remained *in situ*. There was no movement when the substratum was dry (table 1). Movement of the *in situ* individual started upon wetting by the flooding tide and the individual returned to the homing scar immediately before the water depth of the flooding tide reached around 10 cm over the scar. In a few cases, return occurred at a water depth of up to 20 cm (table 1). Fecal pellets similar to those described by Taylor and Way (1976) were released during the period of occupation of the homing scar. The general pattern of activity of *A. gemmata* with the ebbing and flooding tide, based on a total of 4,445 observations of 24 individuals during the October–December period, is summarized in table 4.

Other responses to the flooding tide among 39 chitons based on 2,769 observations were as follows: no movement at all was detected (62%); movement restricted to one or more 180° rotations within the homing scar (15%); short-term excursion, usually not exceeding 5 cm (23%). In addition, 124 observations on 24 individuals during 25 days revealed no long excursions during subsequent tide cycles within the same day in 41 cases (33%).

The direction of movement on long excursions from the homing scar over a period of 2 to 29 days among 17 individuals was within an average angle of 177° (SD = ±98°; n = 179) and ranged from 45 to 360°. The distance of the excursions of the same individuals within the graz-

Table 2. Movement of *Acanthopleura gemmata* in relation to water depth and type type of tide day and night (in parentheses). S = spring tide; SN = transitional spring to neap; N = neap; NS = transitional neap to spring; n = number of observations; — = no observation; A = awash.

Water depth (cm)	Movement				No movement			
	S n	SN n	N n	NS n	S n	SN n	N n	NS n
Dry	0 (—)	0 (—)	0 (—)	0 (—)	26 (—)	0 (—)	0 (—)	0 (—)
Wet	51 (0)	27 (12)	12 (0)	7 (—)	184 (0)	59 (21)	1 (0)	20 (—)
A–5	53 (14)	58 (16)	38 (17)	23 (—)	72 (19)	61 (17)	21 (16)	17 (—)
5–10	39 (20)	60 (14)	7 (20)	31 (—)	48 (14)	42 (19)	17 (14)	21 (—)
10–15	12 (4)	29 (1)	0 (0)	4 (—)	25 (25)	62 (28)	10 (0)	7 (—)
15–20	3 (0)	2 (0)	2 (0)	2 (—)	21 (29)	26 (0)	23 (0)	32 (—)
20–25	0 (—)	0 (—)	0 (—)	0 (—)	2 (—)	13 (—)	14 (—)	19 (—)
25–30	0 (—)	0 (—)	0 (—)	0 (—)	0 (—)	5 (—)	7 (—)	20 (—)
30–35	0 (—)	0 (—)	0 (—)	0 (—)	1 (—)	1 (—)	1 (—)	7 (—)
35–40	0 (—)	0 (—)	0 (—)	0 (—)	1 (—)	1 (—)	2 (—)	1 (—)
Total	158 (38)	176 (43)	58 (37)	67 (—)	380 (87)	270 (85)	96 (30)	144 (—)

ing area averaged 21 cm (SD = ±15 cm; n = 179). On the near horizontal reef matrix, the average angle of the excursions was 149° (SD = ±106°; n = 100) and the mean distance 21 cm (SD = ±13 cm; n = 100) while on beachrock and associated substrata, 233° (SD = ±72°; n = 79) and 23 cm (SD = ±17 cm; n = 79).

Observations on 12 *Acanthopleura gemmata* in the *Tetraclita*-beachrock area and 11 near the midlittoral-infralittoral fringe contact revealed no vertical migration from the period of lower sea level in October through the transitional period during November to higher sea level in December. The absence of vertical migration was subsequently confirmed by four observations during high sea level and five during low sea level in 1987 and 1988. This is contrary to the report of vertical migration of *A. gemmata* in Hulings (1987) which was based on a more limited number of observations.

The investigation of the homing behavior of *Acanthopleura gemmata* during mid-October to mid-December revealed that 79% (SD = ±20%; n = 1,561) of 39 color-coded individuals in eight groups exhibited definite homing behavior, *i.e.*, returning to the same color-coded homing scar following foraging excursions. The observations included day and night as well as during spring, transitional and neap tides. The homing behavior and foraging excursions occurred irrespective of the time of day and the type of tide. The remaining 21% (SD = ±20%; n = 466) occupied new sites for a variable period of one to several days. Observations on other groups totaling 53 individuals as well as periodic observations through June 1988 essentially confirmed these findings.

Within groups in which the individuals were clumped or in close proximity, exchange of home scars was found to be common. The average number of homes occupied by each of 39 individuals over the two month period was 3.2 (SD = ±1.5; n = 2,027). The period of consecutive occupation of a home other than the original among 16 individuals (n = 242) varied from 1 to 19 days and averaged 5.8 days (SD = ±5.0 days). Among 39 individuals, four occupied the original home scar for the entire two month period of observation while seven did not return to the original or new home scar. Among the remaining individuals, there were 20 cases in which there was immediate or eventual return to the original home scar and 49 in which the individual moved to one or more home scars and returned immediately or eventually.

Within one group of five individuals, there was only one case of reciprocal swapping on a daily basis over the two month period (n = 760). In six cases, there was initial reciprosity followed by subsequent continued occupation of up to five days. Within the same group and over the same time span, the total number of sites occupied was 47. There were 27 reoccupations of a site following occupation by another individual.

The most recognizable homing scar of *Acanthopleura gemmata* in the rocky intertidal of Jordan is a distinct depression that is concave in cross and longitudinal sections. The scar is about 1 mm deep with the deepest area coinciding with that region occupied by the foot. The surface of the scar is smooth compared to the surface of the surrounding substratum and has a lighter color than the surrounding substratum, which is covered with epigrowth. Though abandoned scars become overgrown, they remain recognizable. Such readily recognizable homing scars are found on the nearly horizontal, relatively soft, homogenous, fine-grained calcium carbonate fossil reef matrix, a dominant rocky intertidal substratum along the coast of Jordan. The scars are also found on the sides of refuges such as depressions, crevices and small caves. The scars of *A. gemmata* lack the algae occurring in the homing scars of the patellid limpet *Cellana radiata* (Born, 1778) and the pulmonate *Siphonaria laciniosa* (Linnaeus, 1758) reported by Hulings (1985).

Table 4. Activity of *Acanthopleura gemmata* in relation to the tide (n = number of observations).

Activity	n	%
No movement from home during ebbing tide nor during exposure.	1,709	38
Movement from home with the ebbing tide and return home with the subsequent flooding tide.	1,584	36
Movement from home with the ebbing tide and return home prior to the flooding tide.	576	13
Movement of those previously away at ebb tide to home with the flooding tide.	576	13

Other less recognizable scars may be identified on the basis of substrate color. Apart from this difference, the surface configuration of the homing area is not noticably different from that of the surrounding substratum. These scars are also found on calcium carbonate substrata, one type of which underlies beachrock and is harder than the matrix noted above. Another type of substratum with such scars includes fossil coral heads. Recognizable homing scars have not been detected on substrata such as granitic and similar rock and beachrock although homing on these substrata has been observed. Endean *et al.* (1956) noted the absence of excavations by *Acanthopleura gemmata* in hard rock on the coast of Australia.

The orientation of both homing scar and chiton varies irrespective of the substratum. The scar may be near to horizontal on such substrata or on the sides of refuges. In the refuges, the anterior-posterior axis of the chiton may be parallel to the horizontal or inclined to vertical with the anterior end up. Semi-quantitative data (Hulings, in preparation) indicates that the density of *Acanthopleura gemmata* in areas with refuges is $4.1/\text{m}^2$ (SD = $\pm 3.2/\text{m}^2$; n = 183) while that in areas without refuges is $5.5/\text{m}^2$ (SD = $\pm 5.4/\text{m}^2$; n = 79).

Among 37 chitons and based on 2,027 observations, the mean percent homing of 22 individuals on relatively soft, nearly horizontal reef matrix where the majority of the readily recognizable homing scars occur was 85% (SD = ±14%). By comparison, the mean homing of 15 individuals on hard substrata such as beachrock and the underlying substrata was 69% (SD = ±24%). The difference between the means is statistically significant at $P = 0.01$ ($n - 2 = 35$). While the mean number of homes occupied by the individuals on soft and hard substrata was almost the same, 3.4 (SD = ±1.4) *vs.* 3.1 (SD = ±1.6), there were eight instances among the individuals on soft substrata of return to the original home *vs.* 12 among those on hard substrata. In the case of movement to a different home and return, there were 34 instances on soft substrata *vs.* 10 on hard.

DISCUSSION

There are limitations that must be imposed on the interpretation of the data obtained during the investigation of the activity patterns and homing of *Acanthopleura gemmata*. First, the data are based entirely on observations; no experimental manipulations were conducted although the value of such is recognized. Second, statistical treatment is limited, of a general nature and is used for indicative purposes only. Finally, the data apply only to adult individuals. Other limitations are indicated below.

The homing behavior of *Acanthopleura gemmata* in the northern Gulf of Aqaba is similar to that reported for this species by Thorne (1967, 1968) at Heron Island, Australia, and by Chelazzi *et al.* (1983a,b, 1987) and Chelazzi and Parpagnoli (1987) on the coast of Somalia. The homing of 79% of the individuals recorded herein is the same as reported by Thorne (1967) while Chelazzi *et al.* (1983b:17) reported a 91% return to the home of the "previous owner." In addition, the same percentage was found for individuals occupying new homes at Heron Island and on the coast of Jordan. Chelazzi *et al.* (1983a) found periodic movement to a new home a common behavioral pattern as did Throne (1967) and found herein. In terms of reciprocal swapping of homes, the low incidence found herein is in agreement with that found by Thorne (1967). The 57% reoccupation of a home following occupation by another individual is higher than the 42% reported by Chelazzi *et al.* (1983b).

The orientation in the homing scar, including 180° rotation, is essentially the same in the three geographic areas. There is also considerable similarity in the morphology and appearance of the homing scar. The occupation of scars in exposed (platform) sites as well as in refuges (pits, crevices, overhangs) is a common behavior (Thorne, 1967; Chelazzi *et al.*, 1983b).

Chelazzi *et al.* (1983b) reported aggressive behavior between a chiton returning to its home scar and an intruder occupying the same homing scar. The returning chiton attempts to oust the intruder, but, if unsuccessful, the owner either moves elsewhere or the two individuals occupy the same scar. In the present study, aggressive behavior was not observed, but the co-occupation of a single scar by two individuals, side by side, was observed on several occasions.

Only a few periods of observations during one day included a combination of a long enough time span, suitable water level conditions and movement by *Acanthopleura gemmata* to indicate the return to the home scar following grazing. During such a combination, 43 observations on eight individuals suggests return by the same route as that of the excursion. This is consistent with the reports of Thorne (1967) and Chelazzi *et al.* (1983b, 1987).

Thorne (1967) suggested chemosensitivity and topographic memory as potential mechanisms whereby *Acanthopleura gemmata* returns to the homing scar. This author (Thorne, 1968) later added celestial navigation, sight, random movements, olfactory clues, topographic memory and detection of previous trails as possible mechanisms. For a variety of reasons, he ruled out the first three and, after subjecting the last three to experimental treatment, considered only topographic memory and detection of trails as possible homing mechanisms in *A. gemmata*. Eibschütz *et al.* (1967) discounted the magnetic properties of the radula of *A. gemmata* at Eilat as a factor in navigation because of the low level of residual magnetism.

Of note is the occurrence of homing even when the scar and the surrounding area was completely covered with sand during periods of sedimentation, or with shell debris following a storm. The frequency of homing by individuals with well-developed scars was significantly higher, suggesting that a chemical trail may be involved in the homing of *A. gemmata*, as indicated by Chelazzi and Parpagnoli (1987). However, reciprocal swapping of scars and the reoccupation of sites following occupation by one or more individuals suggests that there is not a trail specific for each individual but one common to all individuals of the species.

The mean length of the feeding excursions of *Acanthopleura gemmata* in this study was 21 cm. By comparison, Chelazzi *et al.* (1983b) reported 30 cm and Thorne (1967, 1968) 47 cm. Thorne (1967, 1968) found that not all individuals forage every night and Chelazzi *et al.* (1983b:16) noted that nocturnal activity depended "on the position in the spring-neap cycle." In the present study, not all individuals were found to be active during the conditions under which foraging occurs (tables 1, 4) nor during consecutive tide cycles.

Chelazzi *et al.* (1983a) found the feeding excursions of *Acanthopleura gemmata* to be the longest between neap and spring tides and minimal around neap tides. In the present study, the length of feeding excursions in relation to the type of tide was not determined. However, the number of instances of movement in relation to the type of tide was highest during transitional spring to neap tides followed by spring, neap and transitional neap to spring tides (table 2). Based on the assumption that movements during ebbing conditions represent foraging excursions, an analysis of one group of five individuals on 26 days (n = 157) revealed 41% of the instances of movement occurred during ebbing tides. Of this percentage, 43% of the instances occurred during transitional spring to neap tides, 32% during spring, 13% during neap and 5% during transitional neap to spring.

Movement of *Acanthopleura gemmata* in the northern Gulf of Aqaba is more directly related to water depth over the individual than to the type of tide. During periods of higher sea level or portions of the neap tide cycle, the water level over an individual may not drop to 10 cm or less, especially in the lower midlittoral zone. Thus feeding excursions may not occur during one or more consecutive days. The fewer instances of movement during neap and neap to spring tides over that of spring and spring to neap (table 2) may also be indicative of reduced activity.

Many *Acanthopleura gemmata* in the northern Gulf have a well-defined grazing area, recognizable by differences in color from that of the surrounding area. This area is used repeatedly (Chelazzi *et al.*, 1983a,b, 1987), but appears to be exclusive, unlike that reported by Chelazzi *et al.* (1983b). The feeding areas are more dispersed among groups of individuals than the homing scars as also found by Chelazzi *et al.* (1983a). Grazing appears to be most common at the outer limits of the area, as also reported by Thorne (1967).

On the coast of Jordan, the range of the feeding excursions of *Acanthopleura gemmata* was found to differ with the surface topology of the substratum. On the more regular surface of the near horizontal platform of calcareous reef matrix, the range averaged 149° while on the very irregular surface of the beachrock and underlying substrata, the average range was 233°. The difference in the range may reflect the amount of colonization, distribution and abundance of algae as well as recolonization following grazing on the two different substrata. It would appear that the conditions for recolonization are more favorable on the soft, porous reef matrix due to the nature of the substratum and decreased tidal exposure than on the more exposed hard, impervious beachrock and associated substrata. As a result, more algae are more evenly distributed more of the time on the platform. Accordingly, a greater range of foraging would be necessary on the beachrock and associated substrata in order to obtain the necessary food requirements. The mean length of *A. gemmata* along an exposure gradient within the vertical distribution may also reflect food availability as well as a response to exposure (Hulings, in preparation). In the mid-midlittoral beachrock area, the most tidally exposed within the range, the mean length was found to be 47.0 mm (SD = ±7.6 mm; n = 60) while in the area of the midlittoral-infralittoral fringe contact of the platform, the most benign, the mean was 59.8 mm (SD = ±9.8 mm; n = 50). On the platform just below the beachrock, an area intermediate in exposure, the chitons had a mean length of 53.3 mm (SD = ±6.2 mm; n = 50). The difference between the means is statistically significant at $P = 0.001$.

No aggressive behavior within the feeding area of *Acanthopleura gemmata* has been observed. This is consistent with the report of Chelazzi *et al.* (1983b). Among the chitons on the Jordanian coast, there was no prevailing up- or downslope nor lateral direction of the feeding excursions. As a result of orientation and length excursion analyses of *A. gemmata* and the sympatric *A. brevispinosa* (Sowerby, 1840), Chelazzi *et al.* (1983a) and Chelazzi and Parpagnoli (1987) found the prevailing direction of movement during the feeding excursions of *A. gemmata* to be downward and that of *A. brevispinosa* upward. They considered this behavior to be an example of minimizing food competition and maximizing the utilization of algae in the midlittoral.

There is a possible example of minimizing competition in the rocky intertidal of Jordan. Based on density and presence-absence data, the correlation between the spatial distribution of the limpet *Cellana radiata* and *Acanthopleura gemmata* was found to be negative (Hulings, in preparation). The limpet is considered to be the major grazing competitor of the chiton, especially in the lower midlittoral, where the two are the numerically dominant intertidal grazers. However, the conditions under which each forages differs. *Cellana radiata* forages only when submerged, becoming active soon after submergence by the flooding tide to just before or just after emergence (Hulings, 1985). *Acanthopleura gemmata* forages with the ebbing tide.

The timing and the conditions under which feeding excursions of *Acanthopleura gemmata* occur at Heron Island, Australia and on the coast of Somalia differ very significantly from those in the northern Gulf of Aqaba. Thorne (1967, 1968), Chelazzi *et al.* (1983a,b, 1987) and Chelazzi and Parpagnoli (1987) found *A. gemmata* to be active only during nocturnal low tides and not during the day, whether exposed by the tides or not. Chelazzi *et al.* (1983b) reported that *A. gemmata* remains in the homing scar during the following high tide and diurnal low tide.

By comparison, *Acanthopleura gemmata* in the northern Gulf has been found to be active during day and night. Foraging excursions commence when the water depth of the ebbing tide over the individual is around 10 cm or less. Return to the homing scar occurs prior to or with the flooding tide; in the latter case, before the water level is around 10 cm over the individual (table 4).

The mechanism(s) triggering the initiation of feeding excursions and homing in *Acanthopleura gemmata* in the northern Gulf is not known. Other investigators have suggested various mechanisms, including a biological clock (Thorne, 1967) and the release of chemical information during high tide (Chelazzi & Parpagnoli, 1987). Though not investigated, the presence of photoreceptors such as aesthetes and ocelli in the shell plates and the possibility of the girdle being photosensitive (Boyle, 1977) does not appear to be involved in the triggering of movement in *A. gemmata* as it occurred day and night. Of particular interest is the finding of Moulton (1962) of the initiation of movement away from clusters of the cerithiid *Clypeomorus moniliferum* Kiener, 1841 at Heron Island when the water depth reaches 10 cm (the same species occurs in the rocky intertidal of Jordan according to Hulings, 1989). Moulton (1962) suggested a hydrostatic mechanism and, behaviorally, positive barokinesis and thigmotaxis as being involved in clustering and dispersion of the cerithiid. Based on laboratory experiments, Rohde and Sandland (1975) discounted a hydrostatic mechanism as the only factor in dispersion and clustering of *C. moniliferum*.

It is suggested that a difference in predation pressure on *Acanthopleura gemmata* between the Heron Island-Somalia region and the northern Gulf of Aqaba may account, in part, for the nocturnal behavior in the former region *vs.* the diurnal-nocturnal behavior in the latter area. Both Thorne (1967) and Chelazzi *et al.* (1983a,b) considered homing in *A. gemmata* to be of significance in the reduction of and protection against predation.

Among the predators listed by Thorne (1967, 1968) are the grapsoid *Grapsus strigosus* (Herbst, 1799) which is synonymous with *G. albolineatus* Lamarck, 1818 according to Banerjee (1960); the xanthids *Eriphia leavimana* Latrielle, 1817 and *Leptodius exaratus* (H. Milne Edwards, 1834); the anomuran *Clibanarius virescens* (Krauss, 1834); birds including herons, waders and gulls and elasmobranchs. Chelazzi *et al.* (1983b) reported the xanthid crabs *Eriphia smithi* McLeary, 1838 and *Ozius guttatus* H. Milne Edwards, 1834 as less important predators and the tetradontid fish *Arothron immaculatus* (Block and Schneider, 1801) as the most important predator (also see Chelazzi *et al.*, 1987; Chelazzi & Parpagnoli 1987).

In the northern Gulf of Aqaba, the grapsoid *Grapsus granulosus* H. Milne Edwards, 1853 is a common mid-midlittoral slab occupant while *G. albolineatus* most commonly inhabits boulders (Hulings, 1989). Of the above xanthid crabs, only *Leptodius exaratus* has been recorded in the Jordanian Gulf (D. Guinot, personal communication). Other xanthids including *Lybia leptochilis* (Zehntner, 1894) and *Polydectus cupulifer* (Latrielle, 1825) have been found in the rocky "eulittoral" by Mastaller (1979). The anomuran *Clibanarius signatus* Heller, 1861 is a mid-midlittoral species on slab along the coast of Jordan (Hulings, 1989).

Among the fishes, *Arothron immaculatus* has not been reported from the Gulf of Aqaba (Dor, 1984). However, other tetradontids have been reported in the Gulf at Eilat, including *Arothron hispidus* (Linnaeus, 1758) by Ben-Tuvia and Steinitz (1952) and Tortonese (1968) and a questionable *Tetradon* aff. *diademata* Rüppell, 1829 by Steinitz and Ben-Tuvia (1955). There is, however, no information on the habitat occurrences of these tetradontids. Among the species of fish invading the rocky intertidal during high tide according to Fishelson (1977), potential predators on *Acanthopleura gemmata* include the labrid *Cheilio inermis* (Forsskål, 1775) and the balistid *Sufflamen albicaudatus* (Rüppell, 1829) (R. Ormond, personal communication). As for marine birds, there is not a resident population of species in the northern Gulf. However, the area is on the migratory route of gulls, herons and waders (Safriel, 1968).

It is inferred that the predation pressure on *Acanthopleura gemmata* in the northern Gulf of Aqaba is considerably less than at Heron Island and in Somalia. The absence of a resident marine bird population as well as rare occurrences during migratory periods indicates the absence of a diurnal predator that would feed while *A. gemmata* is exposed and active at low tide. The stomach contents of the grapsoids *Grapsus albolineatus* and *G. granulosus* include macerated fragments of algae, hydroids and detrital particles but no chitons (Hulings, unpublished data). In addition, the structure of the chelae of the two grapsoids (Schäfer, 1954) is not suitable for dislodging or preying upon *A. gemmata*. The hermit crab *Clibanarius signatus* in the rocky intertidal of Jordan is small (maximum length around 2 cm) as are the xanthid crabs and are thus considered to be of minor, if any, importance as predators. Evidence for fishes as predators is lacking, including the absence of "scars" on the plates of *A. gemmata* similar to those caused by *Arothron immaculatus* in Somalia as reported by Chelazzi *et al.* (1983b).

The homing scars of *Acanthopleura gemmata* along the coast of Jordan are only a mm or so deep as opposed to those on the coast of Somalia being 1 to 10 cm deep (Chelazzi *et al.*, 1983b). The shallow scars may, in turn, reflect the absence of one or more significant predators during high tide when compared to the situation in Somalia. In the latter case, Chelazzi *et al.* (1983b) considered that the homing behavior of *A. gemmata* protects it from the most important predator, *Arothron immaculatus*, during high tide when predation pressure is the highest.

It is concluded, therefore, that the diurnal-nocturnal pattern of behavior in *Acanthopleura gemmata* in the northern Gulf of Aqaba is a result of the reduced terrestrial and submarine predation pressure.

That periodicity of activity can change with predation pressure has been demonstrated by Fricke (1974), who found that locomotor and feeding activity of the sea urchin *Diadema setosum* (Leske, 1778) in the northern Gulf of Aqaba was nocturnal in the presence of predatory fishes. In another area, where the predators were absent, the urchins were active irrespective of the time of day. Fricke (1974) hypothesized the evolution of the day-night activity as an adaptation in a habitat free of predators.

The timing of the activity patterns in relation to water depth over *Acanthopleura gemmata* in the northern Gulf does, however, suggest a response to predation. The beginning of the feeding excursions at around the 10 cm water depth of the ebbing tide, and homing when the depth of the flooding tide reaches 10 cm, as well as the lack of movement during periods when water depth exceeds 10 cm (table 1) indicates an adaptation whereby movement is minimal at times when it might attract submarine predators. In most of the cases where the water depth over the individual exceeded 10 cm, the chiton was in the home scar (table 3).

By occupying a concave scar on the exposed, soft, horizontal slab, the chiton blends in with the surface topography and coloration of the surrounding substratum. Additional camouflage results from the spreading of the girdle around the internal periphery of the scar. The latter contrasts to the form of the body during exposure at the low tide. During exposure, the body is raised and arched longitudinally as a result of what appears to be contraction of the girdle. Chitons homing in the hard substrata of the beachrock areas most commonly occur under overhangs or in crevices or caves rather than on the surface of the substrata.

The response to submarine predation among other intertidal homing species in the northern Gulf, *Cellana radiata* and *Siphonaria laciniosa*, is different. Both forage and home only when submerged and the activity may continue through maximum flood tide. However, *C. radiata* is active day and night whereas *S. laciniosa* is nocturnal and neither is active when exposed during low tide (Hulings, 1985). These patterns may also be a response to predation pressure.

In addition to protection against predation, homing in *Acanthopleura gemmata* has been attributed to protection against environmental stresses (Chelazzi *et al.*, 1983a,b, 1987). Certainly, the nocturnal foraging and homing of *A. gemmata* at Heron Island (Thorne, 1967, 1968) and on the coast of Somalia (Chelazzi *et al.*, 1983a,b, 1987; Chelazzi and Parpagnoli, 1987) reduces exposure to environmental extremes. However, in the case of the rocky intertidal in the northern Gulf of Aqaba, which is subjected to severe climatic and environmental extremes, the foraging and homing activity of *A. gemmata* is tide-dependent and independent of the time of day or year. And while other intertidal species migrate vertically with changes in sea level in the northern Gulf, a behavior considered, in part, to be an avoidance of environmental extremes (Hulings, 1987), *A. gemmata* does not. As a result, the chiton is active during periods of environmental extremes, including the combined warmer-lower sea level period, as well as during benign periods. As noted above, homing following feeding excursions during periods of maximum exposure to climatic extremes does not always occur. Thus the homing of *A. gemmata* in the northern Gulf as a response to protection against environmental stresses appears to be of less significance than elsewhere.

It is recognized that differences in the behavior patterns of *Acanthopleura gemmata* between the northern Gulf of Aqaba and Somalia-Heron Island may be due to differences in physical conditions. The tides are of the same type in all three areas, although the range is greater than in Aqaba. Other conditions, especially the geomorphology, appears to be similar, based on information given in Endean *et al.* (1956), Vannini *et al.* (1977) and Chelazzi and Vannini (1980). Geographic differences in activity patterns and behavior among the same rocky intertidal species occurring in the northern Gulf of Aqaba and in other geographic areas outside the Red Sea, including Heron Island, have been noted by Hulings (1989). Differences exist even within the Red Sea. The reproductive periodicity of *Acanthopleura gemmata* in the northern Gulf of Aqaba (Hulings, 1986) is similar to that in the Gulf of Suez (Pearse, 1978; Soliman & Iskander, 1982), while both differ from that in the Red Sea proper (Pearse, 1978).

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The Southeastern Brazilian Muricidae Collected by RV *Marion-Dusfresne* in 1987, with the Description of Three New Species

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ABSTRACT

Twenty-five species of Muricidae are recorded from southeastern Brazil, including eight species of Muricinae, nine of Muricopsinae, one of Ergalataxinae, one of Ocenebrinae, four of Trophoninae, and two of Typhinae. A short discussion is given for each species. Three new species are described: *Dermomurex leali* n.sp. differs from related taxa by the presence of 5 varices on its last teleoconch whorl and by its different intritacalx; *Favartia varimutabilis* n.sp. is compared with *F. alveata*, from which it differs by the erratic placement of the varices and by its multispiral protoconch; *Trophon mucrone* n.sp. differs from *T. lacunellus*, *T. dabneyi*, and *T. limicola* by its spiral sculpture, rounded teleoconch whorls, paucispiral protoconch, and number of axial lamellae. Two species remain unidentified and are listed as *Muricopsis* (*?Murexsul*) sp. and *Favartia* (*Favartia*) sp. *Drupa didyma* Schwengel, 1943 is synonymized with *Trachypollia turricula* (von Maltzan, 1884).

Key words: Muricidae; Brazil; *Dermomurex*; *Favartia*; *Trophon*; new species.

INTRODUCTION

The material examined was dredged or trawled off the southeastern coast of Brazil during the Expedition MD55 carried out by the R.V. *Marion-Dufresne* in May 1987, as a joint project of Muséum National d'Histoire Naturelle (MNHN), Paris, and Universidade Santa Ursula, Rio de Janeiro. Drs. A. Guille and F. Roumos were cruise leaders. Drs. P. Bouchet, J. Leal and B. Métivier sorted the gastropod material on board. Muricidae were collected from 34 to 1,575 m, mostly along a series of seamounts running perpendicular to the Brazilian coast, between 18°50′ and 23°47′S. Most of species collected are already known to occur off the Brazilian coast; *Chicoreus* (*Siratus*) *consuelae* (Verrill, 1950), *Poirieria* (*Pazinotus*) *stimpsonii* (Dall, 1889), *Pygmaepterys germainae* Vokes and D'Attilio, 1980, and *Trophon verrillii* Bush, 1893, however, represent new Brazilian records.

A report on the deep-water Volutidae collected during the same cruise has been already published (Leal & Bouchet, 1989).

For references to original descriptions not indicated here, the reader is referred to Radwin and D'Attilio (1976).

The number of dead collected specimens is followed by "dd"; the number of live collected specimens is identified by "lv".

The following institutional abbreviations are used: MCZ, Museum of Comparative Zoology, Cambridge; MNHN, Muséum d'Histoire Naturelle, Paris; MORG, Museu Oceanografico de Rio Grande; USNM, National Museum of Natural History, Smithsonian Institution. Prefixes for station data denote collecting equipment: CB, Blake trawl; CP, beam trawl; DC, dredge.

SYSTEMATICS

Family MURICIDAE Rafinesque, 1815
Subfamily MURICINAE Rafinesque, 1815
Chicoreus (*Siratus*) *coltrorum* Vokes, 1990

Type locality: Ilha de Itaparica, Bahia, Brazil.

Chicoreus (*Siratus*) *coltrorum* Vokes, 1990:127, figs. 7–13 (figure 3)

Material examined: Southeastern Brazil, stn. DC26, Vitoria Bank, 20°21′S, 36°59′W, 97 m (2 dd); stn. DC27, Montague Bank, 20°26′S, 36°42′W, 81 m (1 dd); stn. DC40, Davis Bank, 20°40′S, 34°41W, 60 m (5 dd); stn. DC43, Dogaressa Bank, 20°51′S, 33°45′W, 63 m (2 dd); stn. DC47, Columbia Bank, 20°42′S, 32°13′W, 94–105 m (5 dd); stn. DC48, Columbia Bank, 20°44′S, 32°08′W, 250–300 m (1 dd); stn. DC50, Columbia Bank, 20°44′S, 31°50′W, 95–120 m (3 dd); stn. DC82, 18°56′S, 37°52′W, 85–105 m (1 dd).

A recently described and often misidentified species, *C. coltrorum* is superficially similar to *C. consuelae* (Verrill, 1950) and may be distinguished mainly by the different protoconch (figures 3, 4). The protoconch of *C. coltrorum* has 1½ rounded whorls while *C. consuelae* has a conical protoconch consisting of 2¼ whorls; other differences are minimal. Only empty shells were collected. Rios (1985:82) reports this species from Brazil (as

Siratus consuelae), from Atol das Rocas, Fernando de Noronha; Rio Grande do Norte to Espirito Santo.

Chicoreus (*Siratus*) *consuelae* (Verril, 1950)
(figure 4)

Material examined: Southeastern Brazil, stn. DC52, Martin Vaz Island, 20°29'S, 28°51'W, 64–80 m (3 dd); stn. DC59, Trindade Island, 20°30'S, 29°19'W, 52–60 m (1 dd).

Similar to *C. coltrorum* (see above), the species is reported from off the coast of Texas to Curaçao and in the Lesser Antilles (Vokes, 1990:129).

Chicoreus (*Siratus*) *tenuivaricosus*
(Dautzenberg, 1927)
(figures 18, 19)

Material examined: Southeastern Brazil, stn. CB90, 19°34'S, 39°34'W, 34 m (33dd) (6 lv); stn. CB92, 19°34'S, 38°55'W, 340–360 m (1 dd) (1 lv).

Many specimens, mostly juveniles, were collected from station CB90 in dead and live condition. Two specimens, of which one was alive, were taken from station CB92, in 340–360 m; this record is probably based on specimens that had remained entangled in the net of a previous haul (stn. CB90), and this bathymetrical range requires confirmation.

The radula is muricine, with a lateral sickle-shaped tooth, and a central tooth with 3 major and 2 minor cusps (figures 18–19).

Aspella morchi Radwin and D'Attilio, 1976
(figures 9, 10, 29)

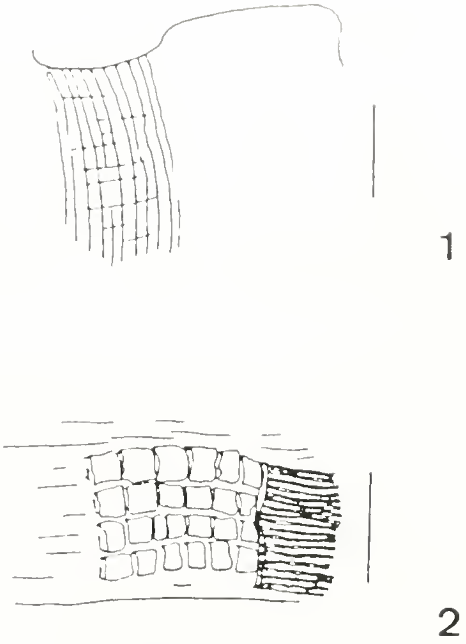
Material examined: Southeastern Brazil, stn. DC22, Vitoria Bank, 20°32'S, 38°11'W, 52 m (4 lv); stn. DC40, Davis Bank, 20°40'S, 34°41'W, 60 m (1 lv); stn. DC41, Davis Bank, 20°39'S, 34°43'W, 58–70 m (2 lv).

The paucispiral protoconch (figures 9, 10) had not previously been figured. The cancellate intritacalx is well illustrated by Radwin and D'Attilio (1976:223, fig. 167). A specimen with 6 teleoconch whorls, and broken protoconch, (MNHN, station DC40) (figure 29) is 10 mm long, while the maximum length given by Radwin and D'Attilio is of 6.6 mm. Previously known from Natal Bay (type locality), Fortaleza (Cerea) (Radwin & D'Attilio, 1976) and Kapmoan (Bahia) (coll. R. Houart).

Aspella senex Dall, 1903

Material examined: Southern Brazil, stn. DC22, Vitoria Bank, 20°32'S, 38°11'W, 52 m (1 dd).

The geographical range reported by Radwin and D'Attilio (1976:25) includes North Carolina and the Gulf of Mexico. Rios (1985:87) reported this species from the Abrolhos Islands. The present record extends the geographical range further southward.



Figures 1, 2. Intritacalx on last teleoconch whorl (scale bars: 0.5 mm). **1.** *Dermomurex* (*Trialatella*) *oxum* Petuch. **2.** *Dermomurex* (*Trialatella*) *leali* n.sp.

Dermomurex (*Trialatella*) *oxum* Petuch, 1979
(figures 1, 26)

Dermomurex (*Trialatella*) *oxum* Petuch, 1979:517, fig. 1E, F.

Type locality: 2 km east of Santa Barbara Island, Abrolhos Archipelago, Bahia State, Brazil, 17°57'S, 38°41'W, in 25 m.

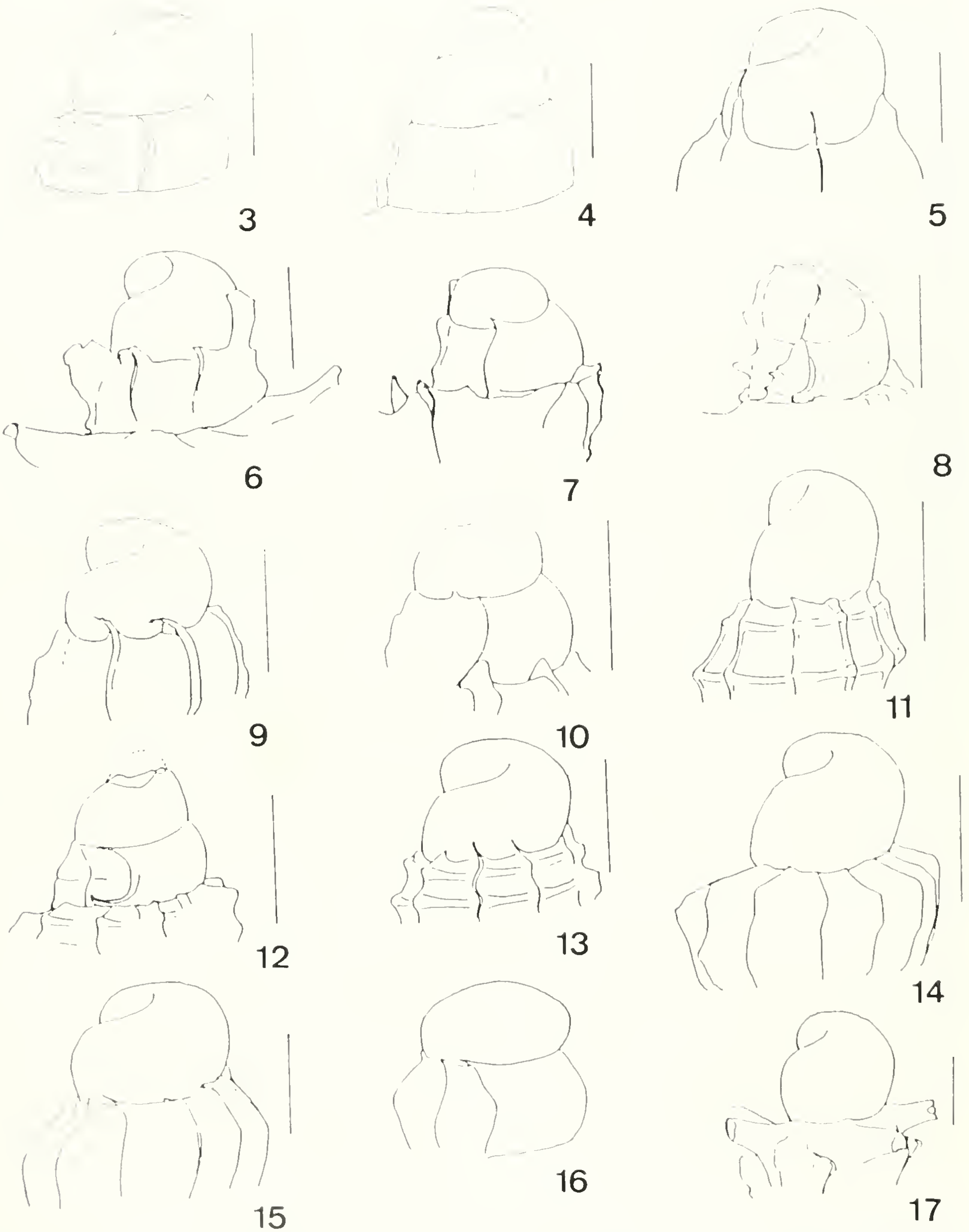
Material examined: Southeastern Brazil, stn. DC22, Vitoria Bank, 20°32'S, 38°11'W, 52 m (1 dd); stn. DC40, Davis Bank, 20°40'S, 34°41'W, 60 m (2 lv); stn. DC82, 18°56'S, 37°52'W, 85–105 m (1 lv).

The largest shell is 15.5 mm long (figure 26), while Petuch mentions 13 mm for his largest specimen (holotype).

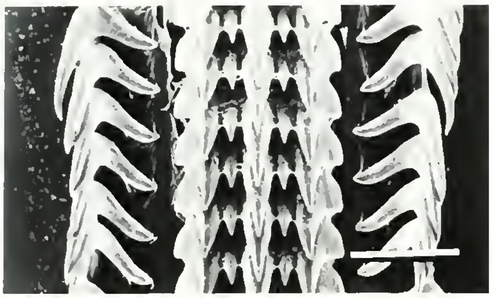
Dermomurex (*Trialatella*) *leali* n.sp.
(figures 2, 5, 27, 28)

Type material: Holotype MOBG 26457, 9.5 × 5.6 mm, southeastern Brazil, stn. DC22, Vitoria Bank, 20°32'S, 38°11'W, 52 m (dd).

Description: Shell 9.5 mm in length, roundly-fusiform. Spire moderately high, with 1.5 protoconch whorls and 4 convex teleoconch whorls (subadult). Suture deeply impressed. Protoconch whorls rounded. Axial ornamentation of first teleoconch whorl consisting of 5 ribs, second whorl of 6 ribs, third whorl of 7 ribs. Last teleoconch whorl with 4 weak, lightly rounded varices. No other



Figures 3–17. Protoconchs (scale bars. 0.5 mm). **3.** *Chicoreus* (*Siratus*) *coltrorum* Vokes, stn. DC26. **4.** *Chicoreus* (*Siratus*) *consuelae* (Verrill), stn DC52. **5.** *Dermomurex* (*Trialatella*) *leali* n.sp., holotype MORG 26457, stn. DC22. **6, 7.** *Poirieria* (*Pazinotus*) *stimpsonii* (Dall), stn. DC82. **8.** *Muricopsis* (?*Murexsul*) sp., stn DC35. **9, 10.** *Aspella morchi* Radwin & D'Attilio, stn. DC40. **11.** *Muricopsis* (*Risomurex*) *necocheana* (Pilsbry), stn. DC22. **12.** *Favartia* (*Caribiella*) *varimutabilis* n.sp., holotype MORG 26458, stn. DC15 **13.** *Favartia* (*Favartia*) sp., stn DC35. **14.** *Trophon aculeatus* Watson, stn. CB104. **15, 16.** *Trophon mucrone* n.sp., paratype MORG 26459, stn DC70 **17.** *Siphonochelus* (*Siphonochelus*) *riosi* (Bertsch & D'Attilio), stn. CB104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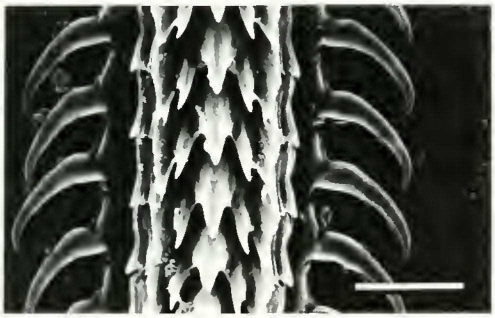
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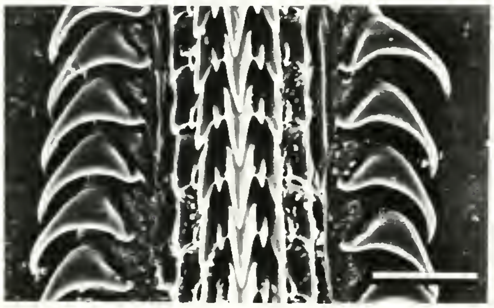
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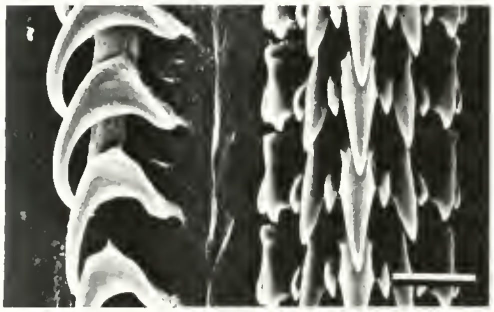
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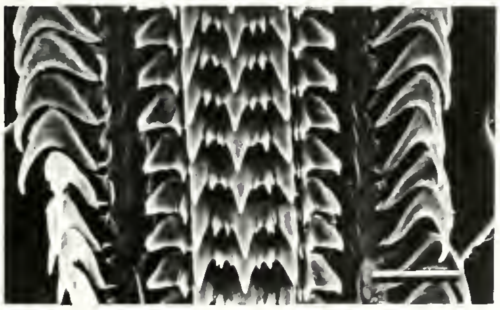
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Figures 18–25. Radulae (scale bars figures 20, 22, 24 20 μm; figures 21, 23, 25: 10 μm; figure 18: 100 μm; figure 19: 50 μm). **18, 19.** *Chicoreus* (*Siratus*) *tenuivaricosus* (Dautzenberg), stn. CP90. **20, 21.** *Favartia* (*Caribiella*) *varimutabilis* n.sp., paratype MNHN. **22, 23.** *Trachypollia turricula* (von Matzan), stn. DC34 **24, 25.** *Siphonochelus* (*Siphonochelus*) *riosi* (Bertsch & D'Attilio), stn. CB104

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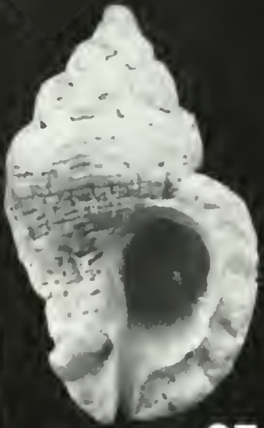

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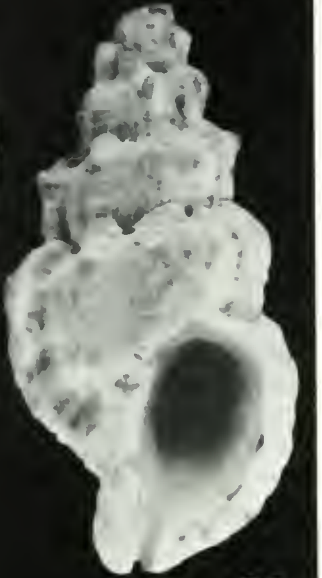

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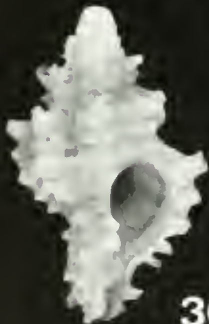

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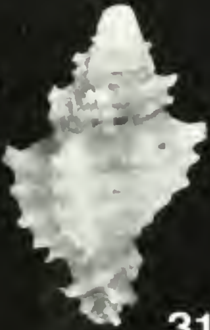

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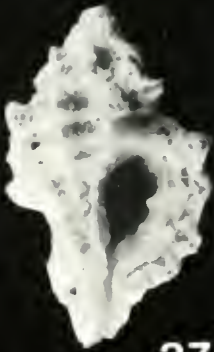

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axial sculpture. No apparent spiral sculpture except thick, whitish intritacalx, strongly reticulate when thin surface layer partially removed, otherwise minutely sculptured with sharp axial striae (figure 2).

Aperture broad, roundly-ovate. Columellar lip smooth, adherent. Anal notch broad, shallow. Outer lip weakly erect, with 4 low denticles within. Siphonal canal short, open, bent adaperturally at tip. Shell whitish.

Etymology: Named after J. H. Leal, School of Marine and Atmospheric Science, Miami, Florida, member of the scientific staff on board of the *Marion-Dufresne* during the MD55 cruise.

Discussion: The *Dermomurex* of the Western Atlantic region have been revised by Vokes (1975, 1976, and 1985) and include the following Recent species: *Dermomurex* (*Dermomurex*) *pauperculus* (C. B. Adams, 1850); *Dermomurex* (*Dermomurex*) *alabastrum* (A. Adams, 1864); *Dermomurex* (*Dermomurex*) *pacei* Petuch, 1988; *Dermomurex* (*Gracilimurex*) *elizabethae* (McGinty, 1940); *Dermomurex* (*Trialatella*) *abyssicola* (Crosse, 1865); *Dermomurex* (*Trialatella*) *oxum* Petuch, 1979; *Dermomurex* (*Trialatella*) *glicksteini* Petuch, 1987; *Dermomurex* (*Trialatella*) *kaicherae* Petuch, 1987; *Dermomurex* (*Trialatella*) *cuna* Petuch, 1990.

In addition there are several fossil species, discussed and illustrated in Vokes (1975).

The holotype of *D. abyssicola* has not been located (Vokes, 1975:148) but the original illustration shows a shell with 3 strong varices and intervaricial ridges, while *D. leali* has 5 varices on the last teleoconch whorl. *Dermomurex abyssicola* has a brown band at the base of its last whorl and a longer siphonal canal.

Dermomurex leali differs from *D. oxum* in having 5 varices on its last whorl instead of 3 strong varices and intervaricial ridge between pairs of varices as in *D. oxum*. *Dermomurex leali* has more rounded whorls, covered by a more finely sculptured intritacalx (figure 2), its aperture is relatively larger, the siphonal canal is shorter and the spire is lower.

Dermomurex leali differs from *D. glicksteini* and *D. kaicherae* by its more globose shell, its more numerous varices on last teleoconch whorl, its absence of intervaricial axial ridges, and shorter siphonal canal.

In addition, *D. oxum*, *D. glicksteini* and *D. kaicherae* have more or less obvious spiral sculpture when the intritacalx is removed, whereas it is absent in *D. leali*.

Dermomurex leali differs from *D. cuna* by its more rounded varices, shorter siphonal canal, comparatively larger aperture and by its different and more sharply striate intritacalx.

Poirieria (*Pazinotus*) *stimpsonii* (Dall, 1889)
(figures 6, 7, 32)

Material examined: Southeastern Brazil, stn. DC22, Vitoria Bank, 20°32′S, 38°11′W, 52 m (2 dd); stn. CB79, 19°02′S, 37°48′W, 1,500–1,575 (1 dd); stn. DC82, 18°56′S, 37°52′W, 85–105 m (1 lv).

Four juveniles, easily recognizable shells. The illustrated specimen (figure 32) is pinkish. The species is known from western Florida to Barbados (Radwin & D'Attilio, 1976:87), but has not previously been recorded south of Barbados.

Subfamily MURICOPSINAE Radwin & D'Attilio, 1971

Muricopsis (?*Murexsul*) sp.
(figures 8, 30, 31)

Material examined: Southeastern Brazil, stn. DC35, Jaseur Bank, 20°42′S, 35°22′W, 82–105 m, (1 lv) (juvenile); stn. DC43, Dogaressa Bank, 20°51′S, 33°45′W, 63 m (1 dd, 3 lv) (juveniles).

The largest of the Brazilian specimens is 5.2 mm long. All are pinkish. Examination of adult specimens is necessary for positive identification.

Muricopsis (*Risomurex*) *necocheanus* (Pilsbry, 1990)
(figure 11)

Material examined: Southeastern Brazil, stn. DC15, 21°37′S, 40°18′W, 37 m (1 dd) (damaged); stn. DC22, Vitoria Bank, 20°32′S, 38°11′W, 52 m (3 lv); stn. CP25, Vitoria Bank, 20°36′S, 37°27′W, 65 m (1 dd).

Recorded by Rios (1985:84) from Espirito Santo, Brazil, to Bahaia Blanca, Argentina. Vokes and Houart (1986: 84) did not observe a complete protoconch, but, from the material then available, they presumed the protoconch to be rounded instead of keeled as in most *Muricopsis*. The protoconch here illustrated (figure 11) confirms their assumption.

Favartia (*Favartia*) *cellulosa* (Conrad, 1846)

Material examined: Southeastern Brazil, stn. DC29, Montague Bank, 20°27′S, 36°41′W, 310–350 m (1 dd).

Recorded by Rios (1985:85). The only specimen collected during the expedition is an empty, juvenile, damaged shell, obviously carried downslope from shallow water.

←

Figures 26–33. **26.** *Dermomurex* (*Trialatella*) *oxum* Petuch, stn. DC22, 15.5 × 8 mm. **27, 28.** *Dermomurex* (*Trialatella*) *leali* n.sp., holotype MORG 26457, 9.5 × 5.6 mm. **29.** *Aspella morchi* Radwin & D'Attilio, stn. DC40, 10 × 5 mm. **30, 31.** *Muricopsis* (?*Murexsul*) sp., stn. DC35, 5.2 × 3.2 mm. **32.** *Poirieria* (*Pazinotus*) *stimpsonii* (Dall), stn. DC82, 6.5 × 4.2 mm. **33.** *Favartia* (*Favartia*) sp., stn. DC22, 8.2 × 5 mm. **Figures 34–36.** *Favartia* (*Caribiella*) *varimutabilis* n.sp. **34, 35.** Holotype MORG 26458, 9 × 5 mm. **36.** Paratype MNHN, stn. DC22, 9 × 5.1 mm. **Figure 37.** *Pygmaepterys germainae* Vokes & D'Attilio, stn. DC34, 5.5 × 3.4 mm.

Favartia (*Favartia*) *nucea* (Mörch, 1850)

Material examined: Southeastern Brazil, stn. DC15, 21°37′S, 40°18′W, 37 m (1 dd); stn. DC40, Davis Bank, 20°40′S, 34°41′W, 60 m (1 lv) (juvenile).

A species that has previously been recorded from Brazil by Rios (1985:85).

Favartia (*Favartia*) sp.

(figures 13, 33)

Material examined: Southeastern Brazil, stn. DC22, Vitoria Bank, 20°32′S, 38°11′W, 52 m (1 dd); stn. DC35, Jaseur Bank, 20°42′S, 35°22′W, 82–105 m (3 lv) (juveniles).

The shell is apparently different from any known western Atlantic *Favartia* species. The shell and the protoconch of a juvenile specimen are here illustrated. The colour is light pink to light brown.

The material collected during the expedition consists only of an adult but damaged shell (figure 33) and of 3 juveniles. There is presently insufficient material to compare in more detail with other *Favartia*.

Favartia (*Favartia*) *varimutabilis* n.sp.

(figures 12, 20, 21, 34, 35, 36)

Type material: Holotype MORG 26458, 9 × 5 mm, southeastern Brazil, stn. DC15, 21°37′S, 40°18′W, 37 m (dd); 3 paratypes MNHN: stn. DC22, Vitoria Bank, 20°32′S, 38°11′W, 52 m (1 dd); stn. DC27, Montague Bank, 20°26′S, 36°42′W, 81 m (1 lv); stn. DC40, Davis Bank, 20°40′S, 34°41′W, 60 m (1 dd).

Other material examined: Stn. DC24, Vitoria Bank, 20°42′S, 37°50′W, 48–52 m, coll. R. Houart (1 dd).

Description: Shell 8.5–9 mm in length, stout, fusiform. Spire high, with 2.5 protoconch whorls and 5 weakly convex, teleoconch whorls. Suture impressed. Protoconch whorls rounded, ending with a deeply indented varix. Last whorl with 3–5 irregular, rounded, erratically placed, squamous varices. Penultimate whorl bearing 8 or 9 varices. No intervaricial axial sculpture. Spiral sculpture of 7 cords, occasionally with 1 thread between each pair of cords, 2 or 3 adapical cords sometimes extending as small spinelets on varices.

Aperture roundly-ovate, outer lip erect and smooth, weakly lirate within. Columellar lip rim erect, with 2 or more small and narrow folds. Anal notch broad, shallow. Siphonal canal short, narrowly open, weakly bent adaperturally, ornamented with 2 small open spines. Shell pale orange to pale brown, with darker spiral cords.

Radula typically muricopsine with a prominent central cusp (figures 20, 21).

Etymology: *Vari*: from varix; *mutabilis*: variable. Named for its variable shape of shell and varices.

Discussion: It seems doubtful that the shells illustrated in figures 34, 35 and 36 are conspecific. In fact, the last teleoconch whorl of *F. varimutabilis* may be weakly convex or rounded, with erratical placement and variable form of the varices. Early teleoconch whorls are identical in all specimens examined.

Favartia (*Caribiella*) *alveata* (Kiener, 1842), known from Florida to Brazil has a shell with fewer, larger, scabrous cords, regularly placed varices and a paucispiral protoconch of 1.5 whorls, denoting nonplanktotrophic larval development. *Favartia varimutabilis* is also related to the Pacific species *F. jeanae* Emerson and D'Attilio, 1979, known from the Philippine Islands.

Favartia (*Murexiella*) *hidalgoi* (Crosse, 1868)

Material examined: Southeastern Brazil, stn. DC55, Martin Vaz Island, 20°32′S, 28°52′W, 780–795 m (1 dd) (fragment); stn. DC81, 19°00′S, 37°48′W, 120–135 m (1 dd).

Known from the Gulf of Mexico to Brazil. In Brazil recorded from Rio Grande do Sul by Rios (1985:85). Only 2 damaged and dead specimens were collected during this expedition.

Favartia (*Murexiella*) *glypta* (M. Smith, 1938)

Material examined: Southeastern Brazil, stn. DC15, 21°37′S, 40°18′W, 37 m (1 dd, 1 lv); stn. DC22, Vitoria Bank, 20°32′S, 38°11′W, 52 m (3 dd) (juveniles); stn. DC73, 19°00′S, 37°48′W, 607–620 m (1 dd) (juvenile).

Comparison of the photograph of the holotype of *Murex glypta* Smith, 1938 illustrated in Vokes (1968:117), of a very similar shell from Ilha do Pai, Brazil (coll. R. Houart), and of the type material of *Murexiella iemanja* Petuch, 1979 (holotype USNM 780652 and paratype USNM 780653) confirms the conclusion of Rios (1985: 85) who synonymised *Murexiella iemanja* Petuch, 1979 with *Murex glypta* Smith, 1938.

The other shell illustrated as *Favartia glypta* in Vokes (1968: pl. 7, fig. 5) from the post-Caloosahatchee Formation, Florida (specimen USNM 645895) is *Favartia cellulosa* (Conrad, 1846).

Rios (1985:85) records *F. glypta* from Amapa to Rio de Janeiro and Abrolhos Islands.

Pygmaepterys germainae Vokes and D'Attilio, 1980

(figure 37)

?*Pygmaepterys germainae* Vokes and D'Attilio, 1980:50, pl. 1, figs. 1–4.

Type locality: Off Punta Higuero, northwestern Puerto Rico, 90 m.

Material examined: Southeastern Brazil, stn. DC24, Vitoria Bank, 20°42′S, 37°50′W, 48–52 m (1 dd); stn. DC27, Montague Bank, 20°26′S, 36°42′W, 81 m (1 dd); stn. DC34, Jaseur Bank, 20°28′S, 35°54′W, 54 m (1 dd).

Described from fossil specimens (Miocene and early Pleistocene) from the Dominican Republic and Costa

Rica and from Recent specimens from the Caribbean Sea (Puerto Rico to Panama, in 12–90 m). The presence of this species off southeastern Brazil extends considerably its geographical range.

Subfamily ERGALATAXINAE Kuroda and Habe, 1971

Cytharomorula grayi (Dall, 1889)

Material examined: Southeastern Brazil, stn. DC28, Montague Bank, 20°27′S, 36°42′W, 525–600 m (1 dd); stn. DC48, Columbia Bank, 20°44′S, 32°08′W, 250–300 m (2 dd); stn. DC55, Martin Vaz Island, 20°32′S, 28°52′W, 780–795 m (14 dd); stn. DC73, 19°00′S, 37°48′W, 607–620 m (3 dd); stn. CB77, 19°41′S, 37°48′W, 790–940 m (2 dd); stn. DC81, 19°00′S, 37°48′W, 120–135 m (2 dd); stn. DC82, 18°56′S, 37°52′W, 85–105 m (3 dd); stn. CB92, 19°34′S, 38°55′W, 340–360 m (1 dd); stn. CB103; 23°36′S, 42°02′W, 200–217 m (1 lv).

Mentioned by Radwin and D'Attilio (1976:44) from Barbados and by Rios (1985:86) from Rio de Janeiro to Rio Grande do Sul in 80–175 m.

The species probably lives throughout the Caribbean to Brazil. Also known in the Eastern Atlantic in the Canary Islands, Madeira and St. Helena (Bouchet & Warén, 1985).

Subfamily OCENEBRINAE Cossmann, 1903

Trachypollia turricula (von Maltzan, 1884)
(figures 22, 23)

Cantharus (Pollia) turricula von Maltzan, 1884:67.

Type locality: Gorée, Sénégal, West Africa.

Material examined: Southeastern Brazil, stn. DC15, 21°37′S, 40°18′W, 37 m (1 dd); stn. DC22, Vitoria Bank, 20°32′S, 38°11′W, 52 m (4 dd, 1 lv); stn. DC27, Montague Bank, 20°26′S, 36°42′W, 81 m (1 dd, 2 lv); stn. DC28, Montague Bank, 20°27′S, 36°42′W, 525–600 m (1 dd); stn. DC30, Jaseur Bank, 20°27′S, 36°17′W, 60 m (1 lv); stn. DC34, Jaseur Bank, 20°28′S, 35°54′W, 54 m (2 lv); stn. DC35, Jaseur Bank, 20°42′S, 35°22′W, 82–105 m (9 dd); stn. DC40, Davis Bank, 20°40′S, 34°41′W, 60 m (1 dd); stn. DC42, Dogaressa Bank, 20°55′S, 34°01′W, 60 m (6 dd); stn. DC43, Dogaressa Bank, 20°51′S, 33°45′W, 63 m (1 dd, 3 lv); stn. DC47, Columbia Bank, 20°42′S, 32°13′W, 94–105 m (1 dd); stn. DC61, Trindade Island, 20°29′S, 29°18′W, 63 m (1 dd); stn. DC82, 18°56′S, 37°52′W, 85–105 m (3 dd); stn. DC83, 18°50′S, 37°57′W, 60 m (1 dd).

The shell dredged at station DC28 (525–600 m) was empty and damaged, and most likely carried downslope.

Drupa didyma Schwengel, 1943 described from off Palm Beach, Florida, is similar; comparison with the original diagnosis and with specimens from West Africa, Florida (coll. R. Houart), and Brazil (MNHN) confirms this synonymy. The multispiral protoconch indicates planktotrophic development, which accounts for the broad distribution of this species in the western and eastern Atlantic.

Subfamily TROPHONINAE Cossmann, 1903

Trophon aculeatus Watson, 1883
(figures 14, 40)

Trophon aculeatus Watson, 1882:390.

Type locality: Off Pernambuco, 09°05′S, 34°50′W, 640 m.

Material examined: Southeastern Brazil, stn. CB77, 19°41′S, 37°48′W, 790–940 m; stn. CB104, 23°42′S, 42°07′W, 430–450 m; stn. CB105, 23°47′S, 42°10′W, 610 m (many live and dead collected specimens).

Rios (1985:88) reported this species to occur off Brazil (off Pernambuco) and Guadeloupe and included the type-locality of *T. lacunellus* (Dall, 1889), a different species that Rios synonymised with *T. aculeatus*. Live-taken specimens were collected by R.V. *Marion-Dufresne* in 430–450 m. All specimens collected in 610–940 m were empty shells.

Trophon pelseneeri E. A. Smith, 1915

Trophon pelseneeri E. A. Smith, 1915:92, pl. 2, figs. 6–7.

Type locality: West of Falkland Islands, 229 m.

Material examined: Southeastern Brazil, stn. CB101, 22°58′S, 42°06′W, 50 m (1 dd); stn. CB102, 23°07′S, 42°04′W, 100 m (1 dd) (damaged).

Recorded by Rios (1985:88), from the state of Rio de Janeiro, Brazil, to the Falkland Islands, Argentina. *Trophon orbignyi* Carcelles, 1946 is a synonym (Rios, 1985: 88). *Trophon pelecetus* Dall, 1902 is probably an earlier name, but study of more specimens is required to confirm this.

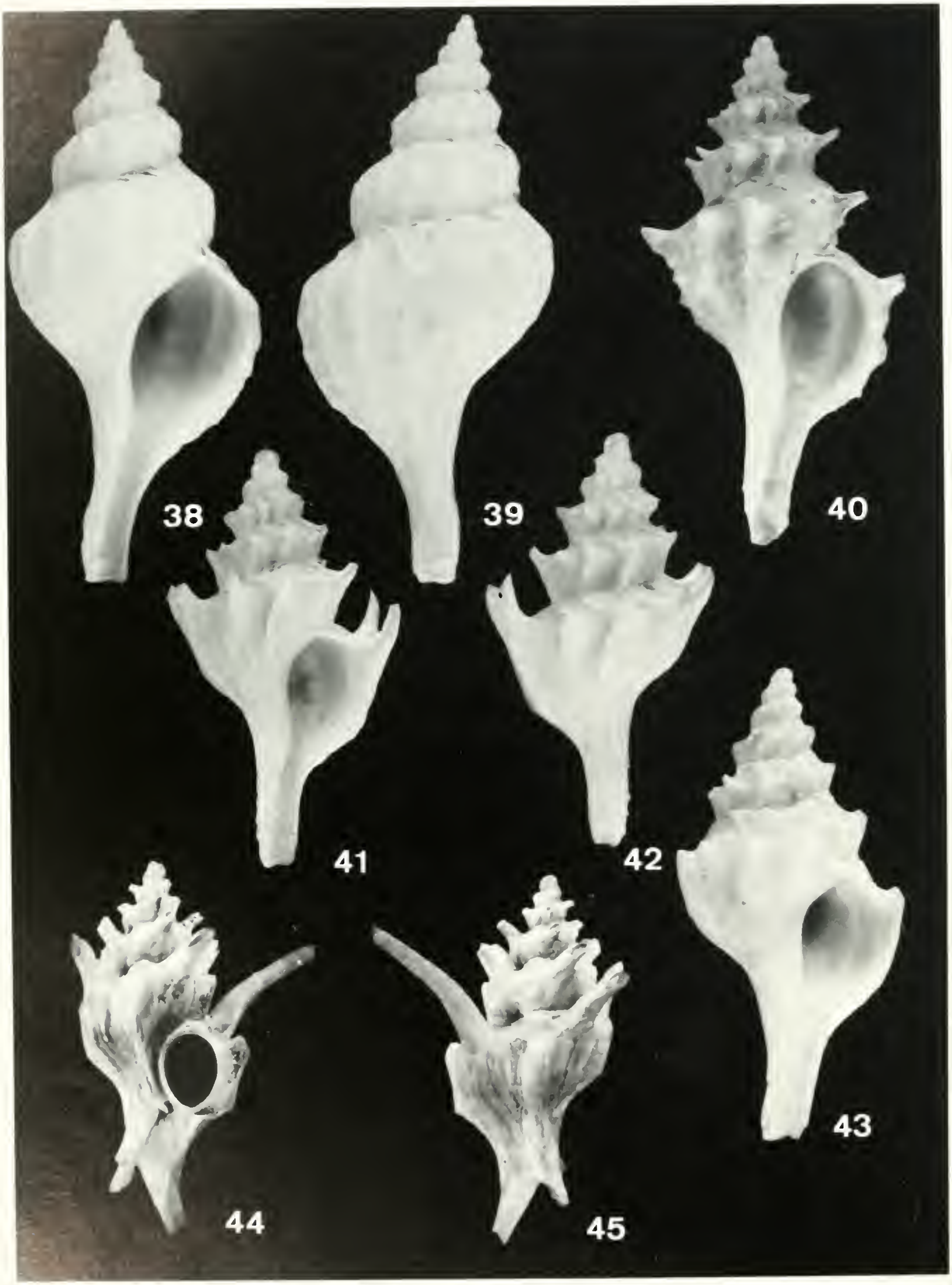
Trophon verrillii Bush, 1893
(figures 41–43)

Trophon verrillii Bush, 1893:214, pl. 1, fig. 16.

Type locality: Off Cape Fear, North Carolina, 1,183 m.

Material examined: Southeastern Brazil, stn. CB76, 18°59′S, 37°50′W, 637 m (3 dd, 4 lv).

Trophon verrillii differs from *T. aculeatus* in having a larger protoconch and totally lacking spiral ornamentation. The illustrated specimen (figures 41, 42) is very similar to the holotype (figure 43). To my knowledge *T. verrillii* was previously known only from the type locality.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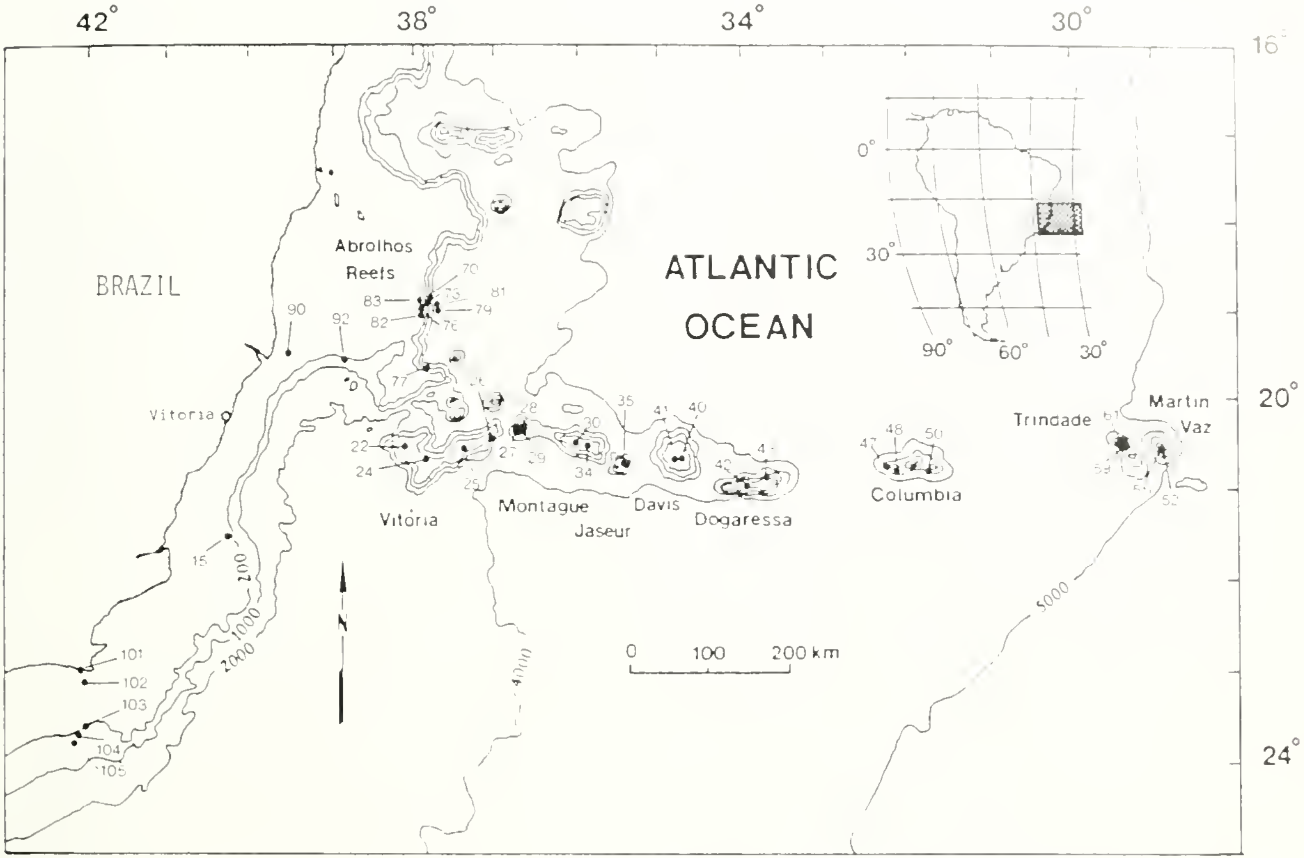

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Figure 46. Map of investigated area with location of cited stations. Reproduced, with permission, from Leal and Bouchet (1991), with some additions.

Trophon mucrone n.sp.
(figures 15, 16, 38, 39)

Type material: Holotype MNHN, 26.5 × 11 mm, southeastern Brazil, stn. CB79, 19°02′S, 37°48′W, 1,500–1,575 m (lv); 7 paratypes MORG 26459; stn. DC70, 18°59′S, 37°48′W, 1,540–1,550 m (4 dd) (juveniles); stn. CB77, 19°41′S, 37°48′W, 790–940 m (1 dd) (damaged); stn. CB79, (2 dd).

Other material examined: Stn. CB78, 18°59′S, 37°48′W, 1,200 m, coll. R. Houart (1) (damaged).

Distribution: Known only from the material examined.

Description: Shell 26.5–28.0 mm in length, roundly-elongate. Spire high with 1.5–1.75 protoconch whorls and 6 or 7 teleoconch whorls. Suture impressed. Protoconch whorls rounded. Axial ornamentation on last teleoconch whorl consisting of 12 sharp, low lamellae and numerous growth striae. Spiral sculpture of 4 or 5 low, weak cords; shoulder smooth, except for axial lamellae.

Aperture broadly ovate. Columellar lip smooth. Anal notch obsolete. Outer lip thin, smooth, glossy within. Siphonal canal moderately long, straight, broadly open. Shell whitish.

Etymology: *Mucrone*-from mucro (tip, sharp end). Named for its arrow or javelin tip shape.

Discussion: Three species, *Trophon lacunellus* (Dall, 1889), described from off Guadeloupe, in 1,406 m, *T. dabneyi* Dautzenberg, 1889, described from the Azores, in 1,287 m, and *T. limicola* Verrill, 1885, described from the New England Coast, in 1,542–3,718 m may be compared.

Trophon lacunellus differs from *T. mucrone* by its higher spired and smaller shell without spiral sculpture, narrower teleoconch whorls, and more rounded protoconch whorls.

Trophon dabneyi has more rounded teleoconch whorls than *T. mucrone*, spiral cords that are absent or very weak, and a multispiral protoconch of 2.5 whorls (prob-

←

Figures 38–40. 38, 39. *Trophon mucrone* n.sp., holotype MNHN, 26.5 × 11 mm **40.** *Trophon aculeatus* Watson, stn. CB104, 13.9 × 7 mm. **Figures 41–43.** *Trophon verrillii* Bush. **41, 42.** Stn. CB76, 10 × 5.5 mm. **43.** Holotype, MCZ119157, 13.9 × 6.8 mm. **Figures 44, 45.** *Siphonochelus* (*Siphonochelus*) *riosi* Bertsch & D'Attilio, stn. CB103, 11.5 × 5.2 mm.

able planktotrophic development) (Houart, 1981: pl. 3, fig. 14; Bouchet & Warén, 1985: fig. 305).

The holotype of *T. limicola* Verrill, 1885, a 10.5 mm high shell, was also compared with a 9.7 mm high juvenile specimen of *T. mucrone*. *Trophon limicola* has 20 axial lamellae on its last teleoconch whorl (only 9 in *T. mucrone*), a longer siphonal canal, more rounded protoconch whorls, and lacks spiral sculpture.

Additional notes on West Atlantic *Trophon* species: *Trophon aculeatus* Watson, 1883 and *T. verrillii* Bush, 1893 differ in many features such as spiral sculpture, number of axial lamellae, shape of whorls and protoconch. *Trophon abyssorum* Verrill, 1885, described from a juvenile specimen of 8 mm, is more closely related to *T. verrillii*, and has angulate and smooth teleoconch whorls, prominent spines at the shoulder and relatively longer siphonal canal.

Subfamily TYPHINAE Cossmann, 1903

Typhis (*Typhina*) *belcheri* Broderip, 1833

Material examined: Southeastern Brazil, stn. CB102, 23°07'S, 42°04'W, 100 m (1 dd).

The holotype of *Typhis belcheri* was illustrated by Kaicher (1980: card 2514). Comparison with the holotype of *Typhis cleryi* Petit, 1842 (MNHN), and with many specimens from Brazil (coll. R. Houart) and from West Africa (MNHN and coll. R. Houart) lead to the conclusion that these taxa are conspecific. The species is recorded by Rios (1985:89) as *Rugotyphis cleryi* (Petit, 1842), from Rio de Janeiro to Torres, Rio Grande do Sul. It lives usually in shallow water.

Typhis belcheri is also known from the Cape Verde Archipelago and Senegal (West Africa) (MNHN).

Siphonochelus (*Siphonochelus*) *riosi*
(Bertsch & D'Attilio, 1980)
(figures 17, 24, 25, 44, 45)

Typhis (*Typhina*) *riosi* Bertsch & D'Attilio, 1980:135, figs. 6, 7.

Type locality: Off Tramandai, southern Brazil, 30°04'S, 47°55'W, 280 m.

Material examined: Southeastern Brazil, stn. CB92, 19°34'S, 38°55'W, 340–360 m; stn. CB102, 23°07'S, 42°04'W, 100 m; stn. CB103, 23°36'S, 42°02'W, 200–217 m; stn. CB104, 23°42'S, 42°07'W, 430–450 m; stn. CB105, 23°47'S, 42°10'W, 610 m (many live and dead specimens).

The specimens collected in 100–217 m are larger than those dredged in 430–450 m, but no other differences are apparent between the two samples. As already mentioned by Vokes (1984:215), the specimen illustrated as *Typhis longicornis* Dall in Bayer (1971: fig. 31) is *S. riosi*.

The radula (figures 24, 25) consists of rachidian teeth and a pair of curved lateral teeth. Rachidian teeth with 3 main cusps and asymmetrical lateral denticles.

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I am very grateful to Dr. P. Bouchet (Muséum National d'Histoire Naturelle, Paris) and to Dr. J. H. Leal (Rosenstiel School of Marine and Atmospheric Science, Miami) for giving me the opportunity to examine this material and for their much appreciated suggestions, to Dr. R. S. Houbrick, D. M. Tyler, S. S. Greenhouse and F. J. Collier (National Museum of Natural History, Smithsonian Institution, Washington, DC) and to Dr. S. P. Kool (Museum of Comparative Zoology, Cambridge) for the loan of type material, to Dr. P. Bouchet and Dr. A. Warén (Swedish Museum of Natural History, Stockholm) for preparation and SEM work of the radulae, and to Dr. P. Bouchet and Prof. E. H. Vokes (Tulane University, New Orleans) for critical review of the manuscript.

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CONTENTS

Malacological Journals and Newsletters, 1773–1990

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ABSTRACT

This compilation lists the 286 malacological journals and newsletters (representing 374 titles), arranged by continent and country. The place, duration, and status of each publication is given and changes in titles are cross-referenced. Of these serials, 157 are still published. It is determined that about 25% of current malacological publications are published in these journals devoted solely to mollusks. The geographical distribution (31 countries represented) and the usage of malacological journals are analyzed in terms of the broader context of the scientific journal literature field.

Key words: Bibliography; journals; malacology; serials.

INTRODUCTION

Malacologists all over the world are often overwhelmed by the enormous diversity of journals and newsletters in our field. It is virtually impossible for any one library to possess all these journals, let alone keep up with the new serials arising every year. The purpose of this paper is to introduce some order to this chaos by providing complete bibliographical data on the corpus of malacological serials. It has been over three decades since the useful, albeit cursory, compilation of Jutting and Altena (1958) who listed only 36 titles. More recently, Bürk and Jungbluth (1985) provided a detailed index to most of the German malacological publications; this valuable reference essentially supersedes previous German efforts such as Buschmeyer's (1938). A brief treatment of malacological serials as part of the history of conchology was presented by Dance (1986:145).

Scientific journals began in 1665 with the appearance of the *Philosophical Transactions* [London] and the *Journal des Sçavans* [Paris]. It would take another century for the start of the first malacological journals: the late 1700's German serials of J. S. Schröter who published four short-lived serials dealing primarily with fossil mollusks (Friess, 1982:93–95). However, "modern" malacological journals did not come into full bloom until the mid 1800's, with several European titles (all now defunct). The oldest currently published malacological journal is the *Archiv für Molluskenkunde* [1868, under an earlier title]. *The Zoological Record, Mollusca Section* [1864] is an abstracting source and not a contributed journal.

As the historian Derek Price (1986:5–6, 18–19) has noted, the total number of scientific journals has doubled every fifteen years, for a 5% increase per year. Yet, obviously this exponential rate of increase cannot continue infinitely; eventually a saturation point representing logistic growth will be reached. The proliferation of new journals in the last decade does not seem to indicate that the field of malacology has reached its carrying capacity, although the recent demise of certain journals may initiate this trend.

Equally important is the usage of scientific articles: how widely they are read and cited by others. Price (1986:118) used Lotka's law and the Pareto distribution to determine that ". . . about 10 percent of all published papers have never been cited, about 10 percent have been cited once, about 9 percent twice, and so on, the percentages slowly decreasing . . .". This widely quoted statement [usually paraphrased as "10 percent of all published papers never subsequently cited" (Wheeler, 1989: 11)] is the inevitable consequence of what the sociologist Robert Merton (1968:61) diagnosed as "insanabile scribendi cacoethes" [= the itch to publish].

MATERIALS AND METHODS

We undertook this project over a two year period, entailing considerable bibliographic research and correspondence. We compiled a master list based on the serial holdings of seven major malacological libraries: Academy of Natural Sciences, Philadelphia; Delaware Museum of Natural History; Field Museum of Natural History; Muséum National d'Histoire Naturelle, Paris; Museum of Comparative Zoölogy; The Natural History Museum, London; and National Museum of Natural His-

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tory, Smithsonian Institution. Then, this list was augmented by extensive correspondence with various colleagues who checked certain geographical sections, as well as with the editors of shell club newsletters (addresses obtained from the American Malacological Union membership list and various other sources); these individuals are listed in the acknowledgements. Unfortunately, no replies were received from some shell clubs and certain other clubs are no longer extant and we were unable to find any complete sets of their newsletters.

While most of the major malacological research libraries have complete sets of the principal journals in the field, the same is certainly not true for the numerous shell club newsletters. It is to be regretted that some museums extend little effort to keep even the newsletter of their own national malacological society. We are aware of the difficulties in treating this "grey" literature and we strongly recommend that malacological libraries endeavor to maintain holdings of these newsletters (especially those published in their country) to the greatest extent possible. The development of online computerized catalogues of library holdings will allow researchers to readily locate these serials.

SCOPE

Herein we have attempted as complete a compilation as is possible of all the malacological serials (journals and newsletters) that have come to our attention. As the reader may be aware, it is not always easy to differentiate between malacological journals and newsletters. Generally, scientific journals publish original research articles and are intended as part of the permanent scientific record. They typically have an editorial review board to maintain scientific standards, and they are often published by a scientific institution or scholarly society. Newsletters usually serve as a vehicle for news and information within the respective organization, and in the case of shell club newsletters they disseminate knowledge in layman's terms, offer advice for beginners in the field and are often simply meant to entertain.

Shell club newsletters are not only of interest to the scientific community because they occasionally provide such original data as biogeographical or habitat information, but also they become permanent scientific record once they (sometimes unintentionally) publish taxonomic statements, especially new species names and type designations. There is obviously no distinct line between journals and newsletters, seeing that some of today's journals started in newsletter format, while some self-proclaimed "journals" hardly deserve that label. We made no attempt to sort the malacological serials into these two categories. We have usually excluded those shell club newsletters which are completely restricted to internal communications, such as membership lists and announcements of upcoming events.

We do *not* include multi-volume malacological treatises that were issued "in parts" over long time periods but represent a single encyclopedic compilation and not a diverse journal. For example, Kiener's *Iconographie des Coquilles Vivantes*; the Martini-Chemnitz and Küster editions of the *Systematisches Conchylien-Cabinet*; Philippi's *Abbildungen und Beschreibungen . . .* ; Reeve's *Conchologia Iconica*; the Rossmässler-Kobelt *Iconographie der Land- und Süsswasser-Mollusken*; Sowerby's *Thesaurus Conchyliorum*; and the Tryon-Pilsbry *Manual of Conchology* are all excluded from this paper. We also do not include symposia volumes, including those of regular meetings, unless specifically issued in serial format.

Several of the French titles in this list actually represent compiled reprints, by one author, of malacological articles from various journals. We have included them since they are obscure and are sometimes cited as if they were serials themselves.

We noted several interesting aspects regarding the etymology of the titles of these various serials. Obviously, most are based on "mollusk", "malaco-", "conch-", or "shell"; others from generic names or famous malacologists. One should note several titles that have been used more than once: *Argonauta, The Conchologist, Journal of Malacology* and *Tide Lines*.

For completeness, and in appreciation of the fact that there is also some intended humor in our field of science, we have included five satirical "serials" in our listings. Three of them, titled *Conchologica Nonsensica, The Double Helix* and *Slug Newsletter*, are easily spotted, but *The Slug* and especially the cleverly produced *Journal of Molluscan Behaviour* are less obvious. These parodies were not included in our statistics.

In compiling this list, we also noted several journals with "malacological" titles, although they do not qualify for inclusion herein as they are not about mollusks at all, or are not exclusively about mollusks. We list them here to avoid future confusion: *Nautilus: A monthly miscellany . . .* [1845–1846; Sag Harbor, New York]; *Astarte, A Journal of Arctic Biology* [1951–1983; Tromso]; *The Conch Shell* [1953–1966; Bishop Museum, Honolulu]; *The Conch: A Biafran Journal of Literary and Cultural Analysis* [1969–current; Paris]. An exception is made for the larger shellfisheries journals (which also cover crustaceans). Here we draw an arbitrary line between those that are included (*e.g., Journal of Shellfish Research*), and others that are not (*e.g., Proceedings of the . . . th National Shellfish Sanitation Workshop*). Coche (1983) lists numerous serial publications in shellfisheries and aquaculture.

We would greatly appreciate information regarding any additions or emendations to this list, since it is our intention to publish future "Addenda". There are several shell club newsletters for which we were unable to obtain full data, despite repeated enquiries. In some cases, the shell clubs themselves do not know the full history of their own newsletter(s). These titles are indicated by an asterisk; the information needed is noted. It is imperative that the *Zoological Record* also be informed of new publications; editors should send copies (or announcements) of their publications to: Mollusca Section, The

Natural History Museum, Cromwell Road, London SW7 5BD, England. The authors will gladly provide editors with a list of the major malacological research museums that should also be informed of new malacological publications.

DISCUSSION

It is worthwhile to consider the role of malacological journals, not only within the field of malacology, but more broadly within the biological sciences. We have found that there are 157 currently published malacological serials. According to *The Serials Directory, 3rd Edition, 1988–89*, there are over 118,000 current serial titles in all fields of knowledge (excluding newspapers). More specifically, according to the *1988/89 Zoological Record Serial Sources* (1990:vi), there are 5,540 current journals in the zoological sciences that are recorded for the *Zoological Record*. Obviously, the malacological journals are a very small part of the whole of scientific literature. Yet, their importance in the field of malacology is far greater than might have been suspected. In order to evaluate this, we have analyzed the titles recorded in the *Zoological Record, Mollusca Section*, to determine the proportion of malacological articles published in malacological serials. The results are as follows:

Year	Number of titles	% published in malac. serials	Number of malac. serials
1880	181	23.2%	12
1930	1,023	24.7%	8
1980	3,904	26.0%	120

[The results for 1880 are based on the entire sample; those for 1930 and 1980 are each based on the average of three subsamples of 100 entries].

It is a remarkable consistency that over the last century, about 25% of all malacological titles covered by the *Zoological Record* have been published in malacological journals. The malacologist is (or should be) cognizant that malacological journals are rarely read by non-malacologists, while non-malacological journals usually reach a wider audience. Hence it is not surprising that the bulk of malacological journals are devoted to papers on systematics, evolution, and organismic-level studies; more reductionist malacological studies (*e.g.*, biochemistry, molecular and cell biology) are invariably found in the appropriate non-malacological journals.

It is also worthwhile to consider the geographic distribution of malacological serials in relation to the distribution of malacologists and more broadly in terms of the overall scientific literature. It is obvious that most journals are published in Europe and the United States; a more detailed analysis reveals several interesting aspects. Altogether, thirty-one countries are represented by malacological serials. We have counted 286 serials (374 including changes in titles) of which 157 (54.9%) are still published. Of the 157 current serials, we informally consider 45 (28.7%) to be professional journals and the remainder as newsletters. The countries with the most serials (and the numbers of serials—not counting changes in titles) are: USA (117); Great Britain (22); France (19); Japan (19); Australia (17); Italy (14); and Germany (13). The distribution by world region is as follows:

Region	Total number of titles	Number of serials*	Number currently published
Europe (12)	121	94	51
Africa (1)	6	5	3
Asia (5)	29	25	14
Oceania (4)	39	29	20
North America (3)	171	125	65
Central and South America (6)	8	8	4
[world totals] (31)	374	286	157

Numbers in parentheses indicate the number of countries.
* Not counting changes in titles.

More specifically, it is obvious that no one malacologist can read, let alone make reference to, all these malacological serials. In his scientometric analyses, Price (1986: 67 *ff.*) noted that the usage of the scientific literature is a function of the inverse square law. That is, given the total number of serials in a field, half the reading will be done from the square root of that total number. Applying this valuable heuristic concept to the field of malacology, we note that there are 157 currently published malacological serials. The square root of 157 is 12.5. Therefore, one can conclude that despite the overabundant diversity of current titles, only about 11–12 will account for half the total usage of malacological serials by malacologists.

An informal poll ["Of the following malacological journals, which eleven do you consider to be the most important?"] of nine professional malacologists revealed a remarkable consensus of opinion: (a) 5 journals were listed by all 9 respondents; (b) 5 journals got 6, 7 or 8 votes; (c) 3 journals got 3, 4 or 5 votes; and (d) 5 journals got only 1 or 2 votes. Altogether, a total of thirteen [13] journals received at least 3 votes; this represents only 8.2% of the total number of current malacological serials.

It does not seem to be essential for a malacological research library to subscribe to every current malacological publication. Indeed, a compilation of the subscription prices for these 13 journals comes to almost $350 (at individual or member rates), which is reasonable when compared to other fields of science. No malacological journals are issued by commercial (for-profit) publishing houses, which are often much more expensive than institution or society journals (Feldmann, 1989). In the field of systematics, it is obviously important to have complete runs of the major journals, including those that are now defunct. It is difficult to estimate the current cost of obtaining a "complete" malacological journal library; certainly in excess of $50,000 as one rarely sees these items in book dealer catalogues and there are relatively few comprehensive private malacological libraries that are potentially available.

Another element of interest is the overall numerical abundance and growth of the malacological literature, including all publication sources. Solem (1974:7–8) has estimated the size of this literature and his results are comparable to ours; Schopf (1967) provided similar calculations for the Ectoprocta [= Bryozoa]. Based on direct counts and estimates from the *Zoological Record* and Ruhoff (1980), we have compiled data on the total number of malacological publications, on an annual basis. As of 1990, we have determined that approximately 167,000 such publications have appeared. The cumulative totals from antiquity to the following years are: 1875 (9,000); 1900 (19,330); 1925 (34,965); 1950 (57,115); 1975 (106,060); and 2000 (estimate 210,000). This literature is doubling every 25 years which seems rather dramatic; however, Price (1986:5–6) documented that the overall scientific literature is doubling every 15 years and certain fields even faster, thus malacology is actually increasing at a slower rate than the overall scientific literature field.

A matter of considerable nomenclatural importance is the description of new species and higher taxa in newsletters or non-professional journals. All too often, these non-refereed papers are not widely available, and the type specimens are commonly not deposited into recognized museums (for further discussion, see Lillico, 1990 and Loch, 1990). We hope that the forthcoming revision of the *International Code of Zoological Nomenclature* will resolve these problems.

In conclusion, these analyses reveal several interesting aspects of the field of malacological journals and newsletters, including their importance in the field of malacology and their geographic distribution. It seems that the quantity (if not quality) of malacological journals will continue to increase arithmetically (if not exponentially), especially as new computer desk-top publishing techniques tempt private individuals to start up their own journals.

For each entry, we have included the full title along with the place(s), duration and status of the publication. For the journals and the newsletters of general interest, we have included the subscription or membership address (which is not always the same as the place of publication). For shell club newsletters of only local interest, we have not included their mailing address; these are listed in Rice (1990). We also list supplements or special editions. References to cumulative indexes or other external sources of information about the journals are included. The periodicals have been arranged alphabetically within each country, according to the first word that is not an article. Major changes in title are listed separately; minor changes in wording of the subtitle are indicated by brackets, with alternate versions separated by a slash (/).

EUROPE/NEAR EAST

Belgium

Achatina. A Newsletter of African non-marine malacology. [Tervuren; Leiden (The Netherlands)]. 1 [1970]–13 [1985].

Annales de la Société Malacologique de Belgique. [Bruxelles]. 1 [1863]–15 [1880]. (Comprising "Mémoires" and "Bulletin [des Séances]".) Continued as Annales de la Société Royale Malacologique de Belgique. See Backhuys (1985); Dhondt (1989).

Annales de la Société Royale Malacologique de Belgique. [Bruxelles]. 16 [1881]–37 [1902]. Continuation of Annales de la Société Malacologique de Belgique. Continued as Annales de la Société Royale Zoologique et Malacologique de Belgique.

Annales de la Société Royale Zoologique et Malacologique de Belgique. [Bruxelles]. 38 [1903]–52 [1921]. Continuation of Annales de la Société Royale Malacologique de Belgique.

Apex. [Bruxelles]. 1 [Feb. 1986]–current. Continuation of Informations de la Société Belge de Malacologie. {M. J. Buyle, Av. Maurice Maeterlinck 56, B-1030 Bruxelles, Belgium}

Arion. Bulletin de contact [trimestriel] de la Société Belge de Malacologie. [Bruxelles]. 1 [Jan. 1977]–current, {address: see Apex}

Bulletin Mensuel d'Information de Malacologie Les Naturalistes Belges [variously titled]. [Bruxelles]. 1 [1966]–4 [1971]. Continued as Informations de la Société Belge de Malacologie.

Bulletin Périodique, Fondation Conchyliologique de Belgique/Belgische Concholiologische Vereniging/Conchological Foundation of Belgium [Rhode-Saint-Genèse]. 1 [1961]. [Single number: English, Flemish and French editions].

La Conchioline. Bulletin mensuel du Groupement Belge d'étude des Coquilles et Mollusques. [Bruxelles]. 1 [1976]–15 [1977].

Gloria Maris. Tijdschrift uitgegeven door de Belgische Vereniging voor Conchyliologie [, Malacologie en Paleontologie]. [Antwerpen]. 1 [1967]–current. Also, "Mededelingenblad": local members' newsletter and meeting announcements, 1 [1986]–current. Miscellaneous supplements, "Bijvoegsel", loose pages. {Ferd. Verbieststr. 9/6, B-2030 Antwerpen, Belgium}

Informations de la Société Belge de Malacologie. [Bruxelles]. 1 [Jan. 1972]–13 [Nov. 1985]. Continuation of Bulletin Mensuel d'Information de Malacologie Les Naturalistes Belges. Continued as Apex. New taxa listed by Duchamps (1986).

Procès-Verbaux des Séances de la Société Malacologique de Belgique. [Bruxelles]. 1 [1872]–9 [1880]. Continued as Procès-Verbaux des Séances de la Société Royale Malacologique de Belgique. Largely overlaps with the "Bulletin" of the Annales de la Société Royale Malacologique de Belgique; see that entry.

Procès-Verbaux des Séances de la Société Royale Malacologique de Belgique. [Bruxelles]. 10 [1881]–27 [1898]. Continuation of Procès-Verbaux des Séances de la Société Malacologique de Belgique.

France

[for French Polynesia and New Caledonia, see under Oceania]

Aménités Malacologiques par M. J. R. Bourguignat. [Paris]. 1 [1853–1856]–2 [1856–1860]. Collected reprints from Révue et Magasin de Zoologie.

Annales de Malacologie. Société Malacologique de France. [Paris]. 1 [1870–1884]–2 [1884–1886].

Archives Malacologiques par M. Jules Mabille. [Paris]. 1 [1867]–5 [1869].

Bibliothèque Conchyliologique (J. C. Chenu). [Paris]. (série 1) 1 [1845]–4 [1846]; (série 2) 1 [1845]. The first series is a translation of seven English-language malacological monographs; the second series is a translation of the malacological articles from the Transactions of the Linnean Society (London), volumes 1–17, 1791–1835.

Bulletins de la Société Malacologique de France. [Paris]. 1 [Jan. 1884]–7 [1890].

Contributions à la faune malacologique française (A. Locard). [Paris]. 1 [1889]–16 [1891]. [Some are reprinted from several French journals].

Elona. Bulletin de liaison de Malacologie continentale fondamentale et appliquée. A Newsletter of French nonmarine Malacology. Société Française de Malacologie. [Paris]. 1 [1974]–6 [1980].

Haliotis. Société Française de Malacologie. [Paris]. 1 [1971]–current. {Lab. Biol. Invertébrés Marins et Malacologie, Muséum National d'Histoire Naturelle, 55 rue de Buffon, F-75005 Paris 05, France}

Journal de Conchyliologie. Comprenant l'Etude des [Animaux, des Coquilles vivantes et des Coquilles fossiles/Mollusques vivants et fossiles]. [Paris; Mosman (Australia)]. 1(1) [Feb. 1850]–115(4) [Dec. 1979]. For dates of early issues, see Fischer-Piette (1937) and Winckworth (1936, 1937). History: Fischer (1978). Index issues: 1850–1872 (1878); 1873–1892 (1897); 1893–1936 (1940). Dance (1986:145) erroneously stated that this journal "has continued publication to this day".

Magasin de Conchyliologie. [Paris]. 1 [1830]–2 [1845]. Reprints of molluscan sections of the Magasin de Zoologie, d'Anatomie Comparée et de Paléontologie, Deuxième Section, Mollusques et Zoophytes.

Mappa. Club français des collectionneurs de coquillages. [Paris]. 1 [1974]–9 [1980]. Continued as Xenophora.

Miscellanées Malacologiques, par A. de Saint-Simon. [Toulouse]. 1 [1848]–2 [1856].

Le Nouveau Pes-Pelicani. [Nice]. 1 [1973]–8 [1974]. Continuation of Pes-Pelicani.

Nouvelles Miscellanées Malacologiques par M. le Docteur Paladilhe. [Paris]. 1 [1866]–4 [1869]. [Compiled reprints from Révue et Magasin de Zoologie].

Pes-Pelicani. [Nice]. 1 [1968]–17 [1972]. Continued as Le Nouveau Pes-Pelicani.

***Pyrum.** Bulletin de liaison et d'études des collectionneurs de coquillages Région Provence Côte d'Azur. [Toulon]. 1 [1975/76?]–7 [post 1977?]. [Issues 1–3 and 6–7 were undated; 4 and 5 dated 1977].

Revue Biographique de la Société Malacologique de France. [Paris]. 1 [1870]–2 [1886].

Séries Conchyliologiques comprenant l'Énumération de Mollusques terrestres et fluviatiles recueillis pendant le cours de différents voyages, ainsi que la description de plusieurs espèces nouvelles (A. Morelet). [Paris]. 1 [1858]–4 [1875].

Les Spiciléges Malacologiques par M. J. R. Bourguignat. [Paris]. 1 [1860]–15 [1862]. [Mostly collected reprints, from Révue et Magasin de Zoologie].

Vertigo. Association Française pour l'Etude des Mollusques continentaux. [Chartres]. 1 [1990]–current. {12 rue Saint-Michel, F-28000 Chartres, France}

Xenophora. Bulletin du Club Français des Collectionneurs de Coquillages/Bulletin de l'Association Française de Conchyliologie. [Paris]. 1 [Jan. 1981]–current. Continuation of Mappa. {1 impasse Guéménée, F-75004 Paris, France}

Germany

[See Bürk and Jungbluth (1985) for an overall review and index of most of these journals.]

Abhandlungen des Archiv für Molluskenkunde. See entry under Archiv für Molluskenkunde.

Acta Conchyliorum. Club Conchylia e.V. [Darmstadt; Stuttgart]. 1 [1981]–current. Number 2 [May 1990] was also sold as a book, "News on Conidae . . .". {Neckaranlage 6, W-6930 Eberbach am Neckar, Germany}

Archiv für Molluskenkunde. [Frankfurt am Main]. 52(1) [Jan. 1920]–current. A supplement series, Abhandlungen des Archiv für Molluskenkunde, 1(1) [Jan. 1922]–2(2) [July 1929]. Continuation of Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft. {Forschungsinstitut Senckenberg, Senckenberganlage 25, W-6000 Frankfurt-am-Main 1, Germany}

Beilage zum Nachrichtsblatt. See entry under Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft.

***Club Conchylia Informationen.** [Eberbach]. 1 [19 ?]–current. Continuation of the Concha.

Concha. Informationen des e[ingetragenen] V[ereins] Club Conchylia. [Wilnsdorf-Obersdorf]. 1 [1969]. Continued as Club Conchylia Informationen.

Conchologische Mittheilungen. [Kassel]. 1 [1881]–3 [1894]. Continuation of Novitates Conchologicae.

Für die Litteratur und Kenntniß der Naturgeschichte, sonderlich der Conchylien und der Steine. [Weimar]. 1 [1781]–2 [1782]. Continuation of Journal für die Liebhaber des Steinreichs und der Konchyliologie. Continued as Neue Litteratur und Beyträge zur Kenntniß der Naturgeschichte, vorzüglich der Conchylien und Foßilien.

Heldia. Münchner Malakologische Mitteilungen. [München]. 1(1) [May 1984]–current. Sonderheft 1 [1987] "Land- und Süßwassermollusken der Maltesischen Inseln", K.-H. Beckmann. {Postfach 26-01-23, W-8000 München 26, Germany}

Jahrbücher der Deutschen Malakozoologischen Gesellschaft. [Frankfurt am Main]. 1 [1874]–14 [1887].

Journal für die Liebhaber des Steinreichs und der Konchyliologie. [Weimar]. 1 [1773]–6 [1780]. Continued as Für die Litteratur und Kenntniß der Naturgeschichte, sonderlich der Conchylien und der Steine.

Malakologische Abhandlungen. Staatliches Museum für Tierkunde in Dresden. [Dresden]. 1 [1964]–current. {Augustusstraße 2, O-8010 Dresden, Germany}

Malakozoologische Blätter. [Kassel]. 1 [1854]–25 [1878]; new series 1 [1879]–11 [1891] (reprinted, 1969, Otto Koeltz, Koenigstein-Taunus). Continuation of Zeitschrift für Malakozoologie.

Mitteilungen der Berliner Malakologen. [Berlin]. 1 [1953]–19 [1967].

Mitteilungen der Deutschen Malakozoologischen Gesellschaft. [Frankfurt am Main]. 1(1) [June 1962]–current. [Volume numbers discontinued after 3(36); only as issues thereafter.] Supplement 1 [1982] "Bericht über den ersten Workshop Malakozoologie in der Bundesrepublik Deutschland vom 09. bis 11. Oktober 1981 in Münster i.W.". {address: see Archiv für Molluskenkunde}

Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft. [Frankfurt am Main]. 1 [Dec. 1868]–51(4) [Oct.–Dec. 1919]. A supplement series, Beilage zum Nachrichtsblatt, Beiträge zur Kenntniss der mitteleuropäischen Najadeen, 1 [1908]–4 [1910]. Continued as the Archiv für Molluskenkunde. Index to volumes 1–45: Kobelt (1914).

Neue Litteratur und Beyträge zur Kenntniß der Naturgeschichte, vorzüglich der Conchylien und Foßilien. [Leipzig]. 1 [1784]–4 [1787]. Continuation of Für die Litteratur und Kenntniß der Naturgeschichte, sonderlich der Conchylien und der Steine. Continued as Unterhaltungen für Conchylienfreunde und für Sammler der Mineralien.

Novitates Conchologicae. Series prima. Mollusca extramarina. Beschreibung und Abbildung neuer oder kritischer Land- und Süsswasser Mollusken . . . (ed. L. Pfeiffer). [subtitles varied]. [Kassel]. 1 [1854–1860]–5 [1876–1879]. Collation: Johnson (1969).

Novitates Conchologicae. Abtheilung II; Meeres-Conchylien. Abbildung und Beschreibung neuer Conchylien . . . (ed. W. Dunker). [subtitles varied]. [Kassel]. 1 [1858]–16 [1878]. Supplement 1 [1862] "Monographie der Molluskengattung *Dosinia*, Scopoli (*Artemis*, Poli)", E. Römer. Supplement 2 [1853] "Index Molluscorum quae in itinere ad Guineam inferiorem collegit Georgius Tams", G. Dunker. Supplement 3 [1864–1862] "Monographie der Molluskengattung *Venus* Linné", E. Römer. Supplement 4 [1869–1874] "Japanische Meeres-Conchilien", C. E. Lischke. Supplement 5 [1874] "Ueber Vorderasiatische Conchylien nach den Sammlungen des Prof. Hausknecht", E. von Martens. Supplement 6 [1877]. "Clausilienstudien", O. Boettger. Supplement 7 [1882] "Index Molluscorum Maris Japonici", G. Dunker. Collation: Johnson (1969).

Schriften zur Malakozoologie aus dem Haus der Natur. [Cismar]. 1 [1989]–current. {Haus der Natur-Cismar, Hinter dem Kloster 42, W-2433 Cismar, Germany}

UNITAS Malacologica Newsletter. [Tübingen]. 1 [1987]–current. {Tropenmed. Inst., Univ. Tübingen, Wilhelmstraße 31, W-7400 Tübingen, Germany}

Unterhaltungen für Conchylienfreunde und für Sammler der Mineralien. [Erlangen]. 1 [1789]. Continuation of Neue Litteratur und Beyträge zur Kenntniß der Naturgeschichte, vorzüglich der Conchylien und Foßilien.

Zeitschrift für Malakozoologie. [Hannover; Kassel]. 1 [Jan. 1844]–10(12) [Dec. 1853]. Continued as Malakozoologische Blätter.

Great Britain

The British Shell Collectors' Club Newsletter. [Nottingham]. 1 [1972]–14 [1983]. Continued as Pallidula. Index, 1982, numbers 1–50 (D. Feld).

Bulletin of the Malacological Society of London. [London]. 1 [Sept. 1983]–current. Continuation of the Malacological Society of London Newsletter. {address: see Journal of Molluscan Studies}

The Cephalopod Newsletter. [London]. 1 [1977]–current. {Dept. of Geological Sciences, University College, Gower Street, London WC1E 6BT, England}

CIAC [Cephalopod International Advisory Council] Newsletter—Cephalopod International Advisory Board. [London; Cambridge]. 1 [1985]–current. {British Antarctic Survey, NERC, High Cross, Madingley Road, Cambridge CB3 0ET, England}

[Conchological Leaflets] (F. P. Marrat). [Liverpool]. (1) [1876]–11 [1880/1883]. See McMillan (1961).

The Conchological Society of Great Britain and Ireland. Papers for Students. [London]. 1 [1964]–18 [1981].

Conchological Society of Great Britain and Ireland Special Publication. [London]. 1 [Feb. 1980] "Marine Mollusca described by John Gwyn Jeffreys, with the location of the type material", A. Warén.

The Conchologist: A quarterly Magazine for Conchologists. [London]. 1(1) [March 1891]–1(4) [Dec. 1891]. Continued as The Conchologist: A Journal of Malacology.

Originally printed as a quarto in 58 pages; reprinted in 1903 in octavo, and repaginated with 88 pages; see Tomlin & Fisher (1935). Index: McClelland (1923).

The Conchologist: A [quarterly] Journal of Malacology. [London]. 2(1) [March 1892]–2(8) [Oct. 1893]. Continuation of The Conchologist: A quarterly Magazine for Conchologists. Continued as The Journal of Malacology. Index: McClelland (1923).

The Conchologists' Newsletter. The Conchological Society of Great Britain and Ireland. [London]. 1 [1961]–current. {address: see Journal of Conchology}

The Cowry. [St. Austell, Cornwall; Port Macquarie (Australia)]. 1 [1960]–2(1) [1968]. [Vol. 1 nos. 1–3 reprinted by Philip L. Hano, New York].

Digesta Malacologia. [London]. 1 [1901]–2 [1903]. Number 1 is an index to the American Journal of Conchology (*q.v.*); number 2 is an index to the malacological articles in the Annals and Magazine of Natural History (a journal not exclusively about mollusks).

Handlists of the Molluscan Collections in the Department of Zoology, National Museum of Wales. Series 1, The Melvill-Tomlin Collection. [Cardiff]. 1 [1981]–current. {National Museum of Wales, Cathays Park, Cardiff CF1 3NP, Wales}

Helix. Land Shell Studies Group. [Nottingham]. 1 [1981].

The Journal of Conchology. Conchological Society of Britain and Ireland. [London]. 2(1) [Jan. 1879]–current. Continuation of The Quarterly Journal of Conchology. Index [1879–1922, vols. 2–16]: McClelland (1923). {A. Seccombe, 36a Selbourne Road, Ilford, Essex IG1 3AJ, England}

The Journal of Malacology. [London]. 3(1) [March 1894]–12(4) [Dec. 1905]. Continuation of The Conchologist. Index: McClelland (1923).

Journal of Molluscan Behaviour, The International Journal devoted to the Behaviour of Molluscs. [East Orkney]. 12(6):48 [1966]; only issue (a parody).

The Journal of Molluscan Studies. Malacological Society of London. [London]. 42(1) [April 1976]–current. Continuation of Proceedings of the Malacological Society of London. Supplements 1 [1976], 3 [1977], 5 [1978], 6 [1978; reprinted 1988], 7 [1980], 9 [1981], 11 [1982], 15 [1985], 16 [1986], 17 [1990]: "The Prosobranch Molluscs of Britain and Denmark, Parts 1–10", V. Fretter & A. Graham. Supplement 2 [1977] "On the genus *Tornatina* and related forms", E. Marcus. Supplement 4 [1977] "An annotated checklist of the western Atlantic warm water opisthobranchs", E. Marcus. Supplement 8 [1980] "Revision of the North-East Atlantic bathyal and abyssal Turridae (Mollusca, Gastropoda)", P. Bouchet & A. Warén [see Bollettino Malacologico Supplemento 2, 3 for continuation]. Supplement 10 [1982] "Systematics of the genera of the Order Ascoglossa (Gastropoda)", E. Marcus. Supplement 12 [1983] "Catalogue of Recent and fossil *Lithophaga* (Bivalvia)", K. H. Kleeman. Supplement 12A [1983; reprinted 1988] "Proceedings of the Second Franco-British Symposium on Molluscs", ed. A. Bebbington. Supplement 13 ["1983" 27 February 1984 *fide* Bollettino Malacologico (1986) Supplemento 2: 561; reprinted 1988] "A generic revision of the family Eulimidae (Gastropoda, Prosobranchia)", A. Warén. There was no Supplement 14. {D. Roberts, Dept. of Biology, Queen's Univ. of Belfast, Belfast BT7 1NN, Northern Ireland}

The Littorinid Tidings. Occasional Newsletter of the Littorinidae Research Group. [Manchester]. 1 [April 1974]–8 [June 1979].

The Malacological and Conchological Magazine. [London]. 1 [1838]–2 [1839].

Malacological Society of London Newsletter. [London]. 1 [1976]–16 [April 1983]. Issues 3–7 not numbered; issues 3–4 not dated [both 1977]. Continued by the Bulletin of the Malacological Society of London.

***[Newsletter].** Northamptonshire Natural History Society (Conchology Section). [Northampton]. ?–current. {The Humfrey Rooms, Castilian Terrance, Northampton NN1 1LD, England}

Pallidula. The Magazine of the British Shell Collectors' Club. [Carlisle]. 15 [1984]–current. Continuation of The British Shell Collectors' Club Newsletter. {12 Grainger Road, Isleworth, Middlesex TW7 6PQ, England}

Proceedings of the Malacological Society of London. [London]. 1(1) [Oct. 1893]–41(6) [Dec. 1975]. Continued as The Journal of Molluscan Studies. Index [1893–1923, vols. 1–15]: McClelland (1923).

The Quarterly Journal of Conchology. [London]. 1(1) [Feb. 1874]–1(17) [Nov. 1878]. Continued as The Journal of Conchology. Index: McClelland (1923).

Species Conchyliorum. [London]. 1(1) [Nov. 1830]. [Although intended as an multivolume treatise, only one number was ever published].

***Subscriber's Bulletin.** The Snail Centre. [Colwyn Bay]. 1 [198 ?]–current.

Tentacle. IUCN/SSC Mollusc Specialist Group. [Glasgow]. 1 [1989]–current. {Natural History Dept., Art Gallery and Museum, Kelvingrove, Glasgrow G3 8AG, Scotland}

The Zoological Record. Mollusca Section. [London]. 1 [1864]–current. {Biosis, 2100 Arch Street, Philadelphia, PA 19103-1399}

Hungary

Malakológiai Tájékoztató. Mátra Múzeum. [Gyöngyös]. 1 [1980]–current. {Kossuth Lajos utca 40, H-3200 Gyöngyös, Hungary}

Soosiana. [Budapest]. 1 [1973]–current. Supplement 1 ["1977" 1979] "A Magyarországi Recens Puhatestüek Elterjedése" [= "Distribution of the Recent Mollusca of Hungary"], L. Pintér. {Természettudományi Múzeum, Baross utca 13, H-1088 Budapest, Hungary}

Israel

Argamanit. The Hebrew Newsletter. [Haifa; Jerusalem; Kibbutz Netzer Sereni]. [1970]–[1976]. Continued as Levantina.

Argamon. Journal of the Israel Malacological Society [and the (Municipal) Malacological Museum, Nahariya]. [Haifa; Jerusalem; Kibbutz Netzer Sereni]. 1 [1970]–7(5) [1981]. Continued as Argamon, Israel Journal of Malacology.

Argamon. Israel Journal of Malacology. [Kibbutz Netzer Sereni]. 7(6) [1988]–current. Continuation of Argamon, Journal of the Israel Malacological Society. {Kibbutz Netzer Sereni, 70-395 Israel}

Levantina. A Malacological Newsletter. [Kibbutz Netzer Sereni]. 1 [1976]–53 [1984]. Continuation of Argamanit. Continued as Levantina, A Journal of Malacology.

Levantina. A Journal of Malacology. [Kibbutz Netzer Sereni]. 54 [1984]–current. Continuation of Levantina, A Malacological Newsletter. [address: see Argamon]

Italy

Argonauta, Journal of Malacology. Associazione Malacologica Internazionale (A.M.I.). [Roma]. 1 [May 1985]–current. Supplementos [1987–current] "Notiziario A. M. I." [reviews and announcements of malacological serials and books]. {Casella Postale, P.O. Box 45, 00125 Acilia, Roma, Italy}

Bollettino Malacologico. Società Italiana di Malacologia. [Milano]. 15(1–2) [Jan.–Feb. 1979]–current. Continuation of Conchiglie, Notiziario Mensile della Unione Malacologica Italiana. Indice specifico generale (1965–1986), 1986. Supplemento 1 [1985] "Revision of the Northeast Atlantic bathyal and abyssal Mollusca, Part 2: Neogastropoda excluding Turridae", P. Bouchet & A. Warén. Supplemento 2 [1986] "Revision of the Northeast Atlantic bathyal and abyssal Mollusca, Part 3: Aclididae, Eulimidae, Epitoniidae", P. Bouchet & A. Warén [continuation of Journal of Molluscan Studies, Supplement 8]. Supplemento 14 [1979]–22 [1986] "Guida illustrata all'identificazione delle Conchiglie del Mediterraneo", B. Sabelli & G. Spada. Continued from the supplements in Conchiglie. Additional miscellaneous supplements, such as membership lists. {Acquario Civico, Viale Gadio 2, 20121 Milano, Italy}

Bulletino della Società Malacologica Italiana. [Pisa]. 1 [1875]–20 [1897]. Continuation of Bulletino Malacologico Italiano. Both reprinted by Antiquariaat Junk, Lochem, Netherlands (1973). Index for both by Lamme (1974) Antiquariaat Junk, Lochem, Netherlands, 53 pages.

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Chicago Shell Club Newsletter. [Chicago, Illinois]. 1 [1966]–19 [1984]. Continued as Thatcheria.

Clam Chatter. [Orlando, Florida]. 1(2) [1980]. A temporary variant title of Central Florida Shell News.

The Collector. A Publication of the Sacramento Valley Conchological Society. [Sacramento, California]. 1(1) [Jan. 1955]–8(4) [Dec. 1962].

*__Conch Courier.__ North Texas Conchological Society. [Plano, Texas]. ?–current. [Earliest issue seen: January 1985].

Las Conchas. Meeting Notice and Newsletter of Pacific Shell Club, Inc. [Downey, California]. 1 [1969]–current. Continuation, in part, of News of the Western Association of Shell Clubs.

*__Conchological Memoranda.__ [San Francisco?]. 1 [1866]–4 [1868/9?]; 6 [1871]–13 [1875]; number 5 was not published. Reprinted, in part, by Smith (1976) [but note that page 2 of number 7 was accidentally reprinted as page 2 of number 8].

Conchological Notes for [month, year]. Conchological Club of Southern California. [Los Angeles]. [April, 1939]–[June 1941]. Issued monthly; not numbered. Continued as Minutes of the Conchological Club of Southern California.

The Conchologist. Isaac Lea Chapter of Conchology (No. 119) of the Agassiz Association. [Alameda, California]. 1(1–3) [January–March, 1901]. Continuation of the Transactions of the Isaac Lea Conchological Chapter of the Agassiz Association. See Roth & Carlton (1970).

Conchologist. [Houston, Texas]. 1(2) [Oct. 1964]–1(3) [Nov. 1964]. Continuation of the Publication of the Conchology Group of the Outdoor Nature Club, Houston, Texas. Continued as the Texas Conchologist.

The Conchologist's Exchange. [Philadelphia, Pennsylvania]. 1(1) [1886]–2(9) [March–April 1988]. Continued as The Nautilus [for index, see that entry].

Conchologists of America Bulletin. 1 [1974]–15(1) [1987]. [Various places of publication]. Continued as American Conchologist. [Note: in volume 1, there were two different issues of "Number 7"; one "Number 8" and no "Number 9"; *fide* American Conchologist (June 1989) 17(2): 11].

Cone Shell Alert (John K. Tucker). [Effingham, Illinois]. 1(1) [Oct. 1980]–1(2) [Nov. 1980].

Contributions to Conchology (C. B. Adams; E. Chitty). [New York; Kingston, Jamaica]. 1 [1849]–13 [1853].

Convention Papers, National Shellfisheries Association. [Washington, D.C.]. (23) [1931 "1930"]–(44) [1953]. Continued as Proceedings of the National Shellfisheries Association. The numbers of 1931–1950 were printed on "micro cards"; 1950–1953 were issued in mimeographed form. "Volumes 1 (1909)–22 (1929)" do not exist, except as meeting handouts. See Malacological Review (1970 "1969"), 2:153, footnote 4 regarding these complexities.

Corbicula Communications. [Cincinnati, Ohio]. 1 [1970]–2 [1971].

Corbicula Newsletter. [Oak Ridge, Tennessee; Fort Worth, Texas]. 1(1) [August 1975]–9(1) [May 1985].

Crown Crier. St. Petersburg Shell Club. [St. Petersburg, Florida]. [1983]–[1988]. [Bimonthly report]. Combined with the Tidelines in 1988.

The Double Helix (A Guide to the Konks of A.M.U.). Unofficial Organ of the American Mal-ecological Unionidae. Published under the auspices of the [New Orleans/Deep South] Shell Club, New Orleans [La./Louisiana]. [New Orleans, Louisiana]. 1(1) [July 1968]; 2(1) [July 1969]; 7(1) [July 1971]; possibly there were other issues. [A parody, by D. Dundee].

Dredgings. Pacific Northwest Shell Club, Inc. [Seattle, Washington]. 14(1) [Feb. 1974]–current. Continuation of Pacific Northwest Shell News.

The Echo. Abstracts and Proceedings of the __ Annual Meeting of the Western Society of Malacologists. [San Francisco]. 1 [1968]–6 [1974]. Continued as Western Society of Malacologists Annual Report.

The Epitonium. Newsletter of the Boston Malacological Club, Inc. [Newton, Massachusetts]. 1987–current. Continuation of Boston Malacological Club, Inc., Newsletter.

The Festivus. [A publication of the] San Diego Shell Club. [San Diego, California]. 1(1) [Jan. 1969]–current. Supplement [1984] "Illustration of the types named by S. Stillman Berry in his 'Leaflets in Malacology'", C. M. Hertz. Supplement [1987] "A faunal study of the bivalves of San Felipe and environs, Gulf of California . . .", J. Gemmell *et al.* Supplement [1988] "An illustrated catalogue of the family Typhidae Cossmann, 1903", A. D'Attilio & C. M. Hertz. Author Index, volumes 1–18 (1987), 10 pp., by T. H. Fulsby. Continuation, in part, of News of the Western Association of Shell Clubs. {3883 Mt. Blackburn Avenue, San Diego, CA 92111, USA}

***Florida Keys Shell Club.** [Key West, Florida]. 1(1) [1980]–current?

***Fort Myers Shell Club Newsletter.** [Fort Myers, Florida]. ?–? [Seen: 4, 1968; 12, 1977].

Friends of the Gastropods [Club] Newsletter. See Amici Gastropodorum.

***Galveston Shell Club [Newsletter/Quarterly].** [Galveston, Texas]. ?–? [Issues seen: no. 58, May 1971; no. 87, Dec. 1973; vol. 9 no. 1, Jan. 1974; vol. 9 no. 12, Dec. 1974; Winter 1976].

Gastropodia (Glenn Webb). [Everman, Texas; Kutztown, Pennsylvania; Fleetwood, Pennsylvania]. 1(1) [Oct. 1952]–current. [Page 21 issue 2(3) "reprinted" 22 May 1984; but the original not published until 12 March 1990]. {Route 1, Box 158, Fleetwood, PA 19522, USA}

Grand Strand Shell Club Newsletter. [Surfside Beach, South Carolina]. 1(1) [March 1990]–2(1) [August 1990]. Continued as Grand Strand Shell News.

Grand Strand Shell News. Grand Strand Shell Club. [Surfside Beach, South Carolina]. 2(2) [October, 1990]–current. Continuation of Grand Strand Shell Club Newsletter.

***The Greater Tampa Shell Club, Newsletter.** [Tampa, Florida]. 1 [1976]–? [Last seen April 1979]. Continued, in part, as Tampa Drill.

Guam Shell News. [Agana, Guam]. 1(1) [Jan.–Feb. 1979]–1(4) [Dec. 1979].

Hawaiian Marine Mollusks. Recent [and New] Species (C. S. Weaver). [Honolulu, Hawaii] 1 [1960]–2 [1966].

The Hawaiian Malacological Society [newsletter]. [Honolulu, Hawaii]. 1(1) [March 1952]–1(8) [Oct. 1952]. Continued as Hawaiian Shell News.

Hawaiian Shell News. Hawaiian Malacological Society. [Honolulu, Hawaii]. 2(1) [Nov. 1953]–current. In addition to volume/number, the issues are numbered consecutively from number 1 of the "new series" [= 8(1)]. Supplement 1 [1990] "Hawaiian Epitoniidae", H. DuShane. Indexes, 1976–1981 (vols. 24–29), 1975–1984 (vols. 23–32), 1985–1987 (vol.s 33–35), and 1985–1989 (vols. 33-37), by Stuart Lillico, Hawaiian Malacological Society. Continuation of The Hawaiian Malacological Society [newsletter]. {P.O. Box 22130, Honolulu, HI 96823–2130, USA}

Indo-Pacific Mollusca. [Philadelphia, Pennsylvania; Greenville, Delaware]. 1(1) [March 1959]–3(17) [Sept. 1976]. Dual pagination scheme utilized.

Irradians. [Baldwin, New York]. 7 [1980]–current. Continuation of Long Island Shell Club News.

The Jersey Sheller. Garden State Shell Club. [Newark, New Jersey]. 1 [1966]–2 [1967].

Johnsonia. Monographs of the marine Mollusks of the Western Atlantic. [Cambridge, Massachusetts]. 1(1) [Oct. 1941]–5(50) [July 1974]. The issues of volume 1 were individually paginated. Volume 1 reprinted 1968; volume 2 reprinted 1975.

Journal for Medical and Applied Malacology/Revista de Malacología Médica y Aplicada. International Society for Medical and Applied Malacology/Sociedad Internacional de Malacología Médica y Aplicada. [Ann Arbor, Michigan]. 1 [1989]–current. Supplement/Suplemento 1 [1989], "Proceedings of the First International Congress on Medical and Applied Malacology/Actas del Primer Congreso Internacional de Malacología Médica y Aplicada", ed. J. B. Burch *et al.* Also a biannual newsletter. {P.O. Box 2715, Ann Arbor, MI 48106, USA}

Journal of Shellfish Research. National Shellfisheries Association. [Various places; now at West Boothbay Harbor, Maine]. 1 [1981]–current. Continuation of Proceedings of the National Shellfisheries Association. {Dr. Tom Soniat, Dept. of Biology, Univ. of New Orleans, New Orleans, LA 70148, USA}

***Junonia.** Sanibel-Captiva Shell Club. [Sanibel, Florida]. ?–current. Continuation of Sanibel-Captiva Shell Club Newsletter.

The Laddergram. Palmetto Shell Club, Inc. [Columbia, South Carolina]. 1 [Sept. 1987]–current.

Leaflets in Malacology. [Redlands, California]. 1(1) [Nov. 1946]–1(26) [Dec. 1969]. Illustrations of type specimens, Hertz (1984); see Petit (1988) regarding two versions of number 13 [printings of 7 and 9 July, 1956 of which the former was suppressed].

The Littorina. The Louisville Conchological Society. [Louisville, Kentucky]. 1 [1975]–11(1) [Jan.–March 1986].

Long Island Shell Club News. [Flushing, New York; Baldwin, New York]. 1 [1975]–6 [1980]. Continued as Irradians.

Louisiana Malacological Society Occasional Papers. [Baton Rouge, Louisiana]. 1 [1988].

Low Country Shell Club Newsletter. [Charleston, South Carolina]. 1(1) [May, 1979]–2(7) [Sept. 1980]. [Volume 1 comprised numbers 1–9 and 12; there were no numbers 10 or 11].

Malacologia. [Ann Arbor, Michigan; Philadelphia, Pennsylvania]. 1(1) [Nov. 1962]–current. Dates of publication given on the inside back cover of 11(2) and with the index of later volumes. History: Burch & Huber (1968), Burch (1973). {Malacology Department, The Academy of Natural Sciences, 19th & The Parkway, Philadelphia, PA 19103, USA}

Malacological Review. [Ann Arbor, Michigan; Boulder, Colorado]. 1 [June 1969 "1968"]–current. Dates of publication are given on page ii of the latest volume. Supplement 1 [1973] "The freshwater snails of Taiwan (Formosa)", G. L. Pace. 2 [1980] "The Meking Schistosome", ed. J. I. Bruce *et al.* Supplement 3 [1982] "A dissection guide, field and laboratory manual for the introduced bivalve *Corbicula fluminea*", J. C. Britton & B. Morton. 4 [1988] "Prosobranch Phylogeny", ed. W. F. Ponder *et al.* History: Burch (1974 "1973"). {P.O. Box 637, Niwot, CO 80544, USA}

Malacology Data Net [Ecosearch Series]. [Portland, Texas]. 1(1) [April 1986]–current. [The cover of issue 2(1/2) was erroneously labelled as "Vol. 2 No. 1"]. {325 E. Bayview, Portland, TX 78374, USA}

Marginella Marginalia. [Dayton, Ohio]. 1(1) [March 1986]–current. {Dayton Museum of Natural History, 2629 Ridge Avenue, Dayton, OH 45414, USA}

Members of the American Malacological Union. [Philadelphia, Pennsylvania]. (1) [1932]. Continued as Mrs. Imogene C. Robertson's rambling notes. [An account of the first meeting appeared in the Nautilus, 45(1):1–5 (1931).]

Miami Malacological Society Quarterly. [Miami, Florida]. 1(2) [1967]–5(4) [1972]. Continuation of Quarterly Report Miami Malacological Society.

Minutes [number, date] Conchological Club of Southern California. [Los Angeles]. 1 [July, 1941]–200 [June, 1960]. Continuation of Conchological Notes for . . . . See Coan (1976) regarding status of the new taxa proposed in this serial.

The Mitchelli. Coastal Bend Shell Club. [Corpus Christi, Texas]. 1(1) [Dec. 1980]–current. Continuation of the Beachcomber Report.

Mollusca. [Tavares, Florida]. 1(1) [Sept. 1944]–2(6) [Aug. 1949].

The Mollusca. Off the Beach Notes. Shell Club of the Ryukyu Islands. [Ryukyu/APO San Francisco]. 1(1) [1960]–2(8) [Dec. 1961]. [Although from Japan, this English-language newsletter was published by U.S. Armed Services personnel and their families stationed in Ryukyu].

Molluscan Digest. The International Publication for Malacological Research. [Pismo Beach, California; Oxnard, California]. 1(1) [Jan. 1971]–4(1–2) [Sept. 1976].

The Mollusk. Greater Miami Shell Club [previously as: South Florida Shell Club]. [Miami, Florida]. 14(7) [1976]–current. Continuation of South Florida Shell Club Mollusk Chaser.

Mollusk-Chaser South Florida Shell Club. [Miami, Florida]. 5(4) [April 1967]–7(7) [July 1969]. Continuation of The South Florida Shell Club's Newsletter Mollusk-Chaser. Continued as the South Florida Shell Club Mollusk Chaser.

Monographs of Marine Mollusca. [Greenville, Delaware; Melbourne, Florida; Silver Springs, Maryland]. 1 [Dec. 1978]–current. [Early numbers (1–3) followed the dual pagination scheme of the Indo-Pacific Mollusca and the Standard Catalogue of Shells]. {P.O. Box 7279, Silver Spring, MD 20907-7279, USA}

Mrs. Imogene C. Robertson's Rambling Notes on the Second Annual Meeting of the American Malacological Union in Washington, D.C. May 26–28, 1932. [Buffalo, New York]. (2) [1932]. Continuation of Members of the American Malacological Union. Continued as Report, __ Annual Meeting and Membership, The American Malacological Union. [See also the Nautilus, 46(1):1–3 (1932); an account of the third meeting appeared in the Nautilus, 47(1):37–44 (1933)].

Naples Shell News. Naples Shell Club, Inc. [Naples, Florida]. 1 [1966]–current. [Sporadic numbering of volumes and issues; "The Shell Case" a temporary variant title, *q.v.*].

***National Shellfisheries Association Quarterly Newsletter.** [Port Norris, New Jersey]. ? [October 1989]–current.

The Nautilus. [Philadelphia, Pennsylvania; Greenville, Delaware; Melbourne, Florida; Silver Spring, Maryland]. 3(1) [May 1889]–current. [Volumes 3–30 with 12 numbers each; subsequent volumes with four numbers each]. Supplement 1 [1990] "Catalogue of the Superfamily Cancellarioidea Forbes and Hanley, 1851 (Gastropoda: Prosobranchia", R. E. Petit & M. G. Harasewych. Continuation of the Conchologist's Exchange. Indexes: (1) "Index to The Nautilus, vols. 3 to 34, 1889–1921 and to its predecessor, The Conchologist's Exchange, vols. 1, 2, 1886–1888" by J. B. Henderson *et al.*, 1927, 434 p. (published by G. M. Clapp & B. Walker). (2) "Index to The Nautilus, volumes 35 to 60, 1921–1947" by A. LaRocque *et al.*, 1951, 332 p. (published by Univ. of Michigan Press, Ann Arbor). (3) "Author Index to The Nautilus, vols. 3–75 . . ." by A. LaRocque, 1963, 279 p. (Columbus, Ohio). (4) "Author Index to The Nautilus, vols. 76–85" by A. LaRocque, 1972, Sterkiana 47:21–38. (5) Indexes to The Nautilus: Geographical (vols. 1–90) and scientific names (vols. 61–90)" by R. T. Abbott *et al.*, 1979, iv + 238 p. (American Malacologists, Inc., Melbourne, Florida). An anthology: Abbott (1976). Dating of the first 75 volumes best accomplished by reference to Clench & Turner (1962). {P.O. Box 7279, Silver Spring, MD 20907-7279, USA}

NCMC Newsletter. Northern California Malacozoological Club. [Novato]. 1 [1988]–current. Continuation of the Northern California Shell Club News.

[Newsletter]. National Capital Shell Club. [Washington, D.C.]. 1 [1974]–current

[Newsletter]. New Jersey Shell Club. [Maywood, New Jersey; Park Ridge, New Jersey]. 1973 [October]–1977 [May/June].

Newsletter, Marco Island Shell Club, Inc. [Marco Island, Florida]. 1 [1982]–current.

The [month] Newsletter of the Jersey Cape Shell Club [Stone Harbor, New Jersey]. [May, 1982]–current.

News of the Associated Shell Clubs of California. [Northern California Malacozoological Club, Berkeley; Pacific Shell Club, Los Angeles; Conchological Club of Southern California, Los Angeles]. 1(1) [May 1960]–2(1) [July 1961]. Continuation, in part, of the Proceedings [Minutes] of the Pacific Shell Club. Continued as News of the Western Association of Shell Clubs.

News of the Western Association of Shell Clubs. [As above, with the San Diego Shell Club, San Diego]. 2(2) [Oct. 1961]–10(4) [1969]. [Issue 7(1) (1966) erroneously labelled as "Vol. 6 No. 7"]. Continuation of News of the Associated Shell Clubs of California. Continued, in part, by The Festivus and Las Conchas.

New York Shell Club Notes. [New York]. 1 [1950]–current. {Department of Invertebrates, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, USA}

The Noble Pen. Newsletter of the Cen.[tral] Penn.[sylvania] Beachcombers. [Elizabethtown, Pennsylvania; Lancaster, Pennsylvania]. 1(1) [Nov. 1983]–current. [The first two issues were untitled].

North Carolina Shell Club Bulletin. [Morehead City, North Carolina]. 1 [1963]–9 [1978].

Northern California Shell Club News. Northern California Malacozoological Club. [Novato]. 1 [1978]–10 [1987]. Continued as NCMC Newsletter. Note: The Veliger, volumes 1–6 [1958–1963], was originally published as the newsletter of this club.

Northwest Shell News. [Poulsbo, Washington]. 1(1) [Jan. 1961]–1(5) [Oct. 1961]. Continued as Pacific Northwest Shell News.

Notes and Quotes. Rochester Shell and Shore Club. [Rochester, New York]. 1 [August 1967]–66 [November 1980].

Occasional Papers on Mollusks. Department of Mollusks, Museum of Comparative Zoology, Harvard University. [Cambridge, Massachusetts]. 1(1) [Feb. 1945]–current. {Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138, USA}

Of Sea and Shore. [Port Gamble, Washington]. 1 [1970]–current. Supplements, [1971] "Dictionary of English–French/French–English shell terms", C. Geerts; [1971] "Identification Guide: Cowries of the Red Sea Area", J. O'Malley. {P.O. Box 219, Port Gamble, WA 98364, USA}

Opisthobranch. A monthly publication on mollusks and marine life. [Phoenix, Arizona]. 16(1–4) [Jan.–April 1984]. Continuation of Opisthobranch Newsletter. Continued as Shells and Sea Life.

Opisthobranch Newsletter. [Pismo Beach, California]. 1 [1969]–15 [1983]. Continued as Opisthobranch.

Oregon Shell News. Oregon Society of Conchologists. [Portland, Oregon]. 1(1) [1970]–current. [1(1) labelled as "new series"].

The Original Tide-ings. Indiana's first shell club. [Crown Point, Indiana]. 3(7) [July 1973]–6(1) [Jan.–March 1976]. See discussion under Tide-ings.

Pacific Northwest Shell News. [Poulsbo, Washington]. 1(6) [1961]–13(5) [Oct. 1973]. Continuation of Northwest Shell News. Continued as Dredgings.

Palm Beach County Shell Club News. [Lake Worth, Florida]. [1961]–[1961]. Continued as Seafari.

The Pariah. [Highstown, New Jersey]. 1[1977]–8[1980].

Pittsburgh Shell Club Bulletin. [Pittsburgh, Pennsylvania]. (1) [1966]–(12) [1977] [most issues not numbered].

Proceedings of the National Shellfisheries Association. [Duxbury, Massachusetts]. 45 [1955 "1954"]–70 [1980]. Continuation of Convention papers, National Shellfisheries Association. Continued as Journal of Shellfish Research. Index, "Titles of papers presented at annual meetings, 1930–1973", ii + 37 pages.

Proceedings of the Pacific Shell Club. [Los Angeles]. 1 [1955]. Also issued as irregular "Minutes" and "Annual Report" of the Pacific Shell Club; these publications were only distributed at meetings and not mailed. Continued, in part, by the News of the Associated Shell Clubs of California.

Proceedings of the Philadelphia Shell Club. [Philadelphia, Pennsylvania]. 1(1) [1955]–1(9) [1964].

Proceedings of the Society for Experimental and Descriptive Malacology. Earlier reports published in Malacological Review 2(1), 5(1), 6(1), 7(1) and 8(1–2). Later reports published in Walkerana (*q.v.*).

Publication of the Conchology Group of the Outdoor Nature Club, Houston, Texas. [Houston, Texas]. 1(1) [Sept. 1964]. Continued as the Conchologist.

Quarterly Report Miami Malacological Society. [Miami, Florida]. 1(1) [1967]. Continued as Miami Malacological Society Quarterly.

Report. — Annual Meeting and Membership. The American Malacological Union. [Philadelphia, Pennsylvania]. (3) [1934]–(4) [1935]. Continuation of Mrs. Imogene C. Robertson's Rambling Notes . . . . Continued as The American Malacological Union. — Annual Meeting —, Membership List . . . .

***A Review of the Broward Shell Club.** [Pompano Beach, Florida]. 1(1) [1963]–? [last issue seen: 1(3), 1965].

Revista de Malacología Médica y Aplicada: see entry under Journal for Medical and Applied Malacology.

***Sanibel-Captiva Shell Club Newsletter.** [Sanibel Island, Florida]. ?–? [seen: 8 (Nov. 1965); 9 (June 1966)]. Continued as the Junonia.

***San Marcos Shell Club Quarterly Newsletter.** [San Marcos, Texas]. 1 [1972]–? [last issue seen: 5(4), 1976].

Sarasota Shell Club Newsletter. [Sarasota, Florida]. [1982]–current.

The Sayana. South Carolina Shell Club Newsletter. [Charleston, South Carolina]. [April 1989]–current [1989 issues not numbered].

Seafari. Palm Beach County Shell Club. [Lake Worth/West Palm Beach, Florida]. [1961]–current. Continuation of Palm Beach County Shell Club News. First numbered issue is "6(12)" [Dec. 1964]; issues 9(3–8) [1967], erroneously labelled as volume 8.

The Searcher. Newsletter of the Sea Shell Searchers of Brazoria County. [Lake Jackson, Texas]. [1977]–current.

***Shell and Tell.** Newsletter of the Gulf Coast Shell Club. [Beaumont, Texas]. ?–current? [only two issues seen: 4(1), 1984; 5(1) 1985]. Continuation of Between the Tides?

***The Shell Case.** Naples Shell Club. [Naples, Florida]. [1971]–[1977?]. [Seen: 1971, 2(1), 3(1), 4(1); a temporary variant title of the Naples Shell News, *q.v.*].

Shell Collector. [Fort Lauderdale, Florida]. Premieré [1978]; 1 [1978]–2 [1979].

The Shelletter of Shells and their Neighbors. [Redlands, California]. 1 [1960]–24 [1964].

Shell Museum & [Research/Educational] Foundation, Inc., Newsletter. [Sanibel, Florida]. 1 [1988]–current.

Shell Notes (Frank Lyman). [Lantana, Florida]. 1(1) [1942]–2(13–15) [June 1951].

[The] Shell-O-Gram. Jacksonville Shell Club, Inc. [Jacksonville, Florida]. 1 [1966]–current. [Various issues have erroneous volume and number labels].

Shells and Sea Life. [Phoenix, Arizona; Bayside, California]. 16(5) [May 1984]–current. Continuation of Opisthobranch. [Various changes in format and subtitles; vol. 18(3), 1986, announced a change to three separate series: (1) a monthly "Shells and Sea Life News"; (2) a "Shells and Sea Life Quarterly"; and (3) a new technical journal "Acta Mollusca". This plan was apparently abandoned]. Supplement [1986] "Directory of Clubs & Services". (1701 Hyland Street, Bayside, CA 95524, USA)

***The Shell Sheet.** Reef Roamers Shell Club [formerly, The Anderson Reef Roamers]. [Yigo, Guam]. 1 [19 ?]–current.

The Slit Shell. [Newsletter of the] Indianapolis Shell Club. [Indianapolis, Indiana]. [1977]–current. [Some issues numbered].

The Slug. Perrine Muckulogical Society. [Miami, Florida]. 1(1) [1 April 1989]. [A parody].

South Florida Shell Club [incorporated/Inc.] Mollusk Chaser. [Miami, Florida]. 7(8) [August 1969]–14(6) [1976]. Continuation of the Mollusk-Chaser South Florida Shell Club. Continued as The Mollusk. [Various changes in format and style; some issues of volume 9 (1971) labelled as "new series"; December issue of volume 10 (1972) labelled as "Supplement"].

South Florida Shell Club Newsletter. [Miami, Florida]. 1 [1963]–2(5) [1964]. Continued as The South Florida Shell Club's Newsletter Mollusk-Chaser.

The South Florida Shell Club's Newsletter Mollusk-

Chaser. [Miami, Florida]. 2(6) [1964]–5(3) [March 1967]. Continuation of the South Florida Shell Club Newsletter. Continued as Mollusk-Chaser South Florida Shell Club.

***South Padre Island Shell Club [Newsletter].** [South Padre Island, Texas]. ?–? [seen; issues from 1962–Oct. 1980].

***Southwest Florida Shell News.** Journal of the Southwest Florida Conchologist Society, Inc. [Fort Myers, Florida]. ?–current.

Southwestern Malacological Society, Monthly Meeting Notice and Newsletter. [Phoenix, Arizona]. [1966]–current.

Special Occasional Publication. Department of Mollusks, Museum of Comparative Zoology, Harvard University. [Cambridge, Massachusetts]. 1 [1973]–current. {Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138, USA}

Sterkiana. [Columbus, Ohio; Shawsville, Virginia]. 1 [Nov. 1959]–71 [1981].

Suncoast Shorelines. Suncoast Conchologists. [Palm Harbor, Florida]. 1 [1984]–current.

Tabulata. [Santa Barbara, California]. 1(1) [July 1967]–7(4) [Oct. 1974]. Index (1974), 14 p.

***Tampa Drill.** The Greater Tampa Shell Club. [Tampa, Florida]. ?–? [earliest issue seen: 1(3), 1972; latest issue seen: May 1977 labelled as "volume 11 first issue"]. Continuation, in part, of The Greater Tampa Shell Club, Newsletter.

Texas Conchologist. Houston Conchology Society. [Houston, Texas]. 1(4–6) ["Dec. 1964–Jan./Feb. 1965"]–current. [Also a newsletter for meeting announcements]. Continuation of Conchologist. {3706 Rice Boulevard, Houston, TX 77005, USA}

Texas Shell News of the San Antonio Shell Club. [San Antonio, Texas]. 1 [1958]–15 [1972]. ["Vol. VII" (1964) erroneously also used for 1965 and 1966].

Thatcheria. [Chicago]. 19 [1984]–current. Continuation of Chicago Shell Club Newsletter.

***Tibia Trumpet.** Broward North Shell Club. [?, Florida]. 1 [1973]–2 [1974]. [No further issues?].

Tide-ings. The Newsletter of the Crown Point Shell Collectors' Study Group, Inc. [Crown Point, Indiana]. 1 [1971]–current. See also The Original Tide-ings; the latter was started due to an editorial dispute within this shell club.

Tide Lines. St. Petersburg Shell Club [, Inc.]. [St. Petersburg, Florida]. [1970]–current. Continuation of an annual (unnamed) St. Petersburg Shell Club show souvenir booklet [1965–1969]. Combined with the Crown Crier in 1988.

Tide Lines. Treasure Coast Shell Club, Inc. [Palm City, Florida]. 1(3) [1987]–2(2) [1988]. Continued as Treasure Coast Shell News. Note: this newsletter started in March 1986, but 1(1) and 1(2) were unnamed.

The Tidewater Triton. The Tidewater Shell and Fossil Club. [Tidewater, Virginia]. 1 [1969]–4 (1973) [some issues of volumes 3 (1972) and 4 (1973) erroneously labelled as "IV" or "VI", respectively].

***Transactions of the Isaac Lea [Conchological] Chapter of the Agassiz Association.** 1 [1889?]–10? [1899?]. This "serial" actually comprised members' reports, which were annually compiled into a single (?) bound manuscript volume, and circulated from one member to the next during the following year. Extracts were published in various journals, including The Nautilus, usually titled as the "Isaac Lea Department". We have not been able to locate any extant set(s) or issues of the Transactions (including the copy mentioned by Keen, 1954). See Coan (1989) for further discussion. Continued as The Conchologist.

Transactions of the POETS Society. See Walkerana.

Treasure Coast Shell News. Treasure Coast Shell Club, Inc. [Palm City, Florida]. 2(3) [1988]–current. Continuation of Tide Lines (*q.v.*) [the St. Petersburg Shell Club complained of the theft of their title, so 2(3) was given the current name].

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First Records For *Cymatium mundum* (Gould) in the Eastern Pacific Ocean, with Comments on the Zoogeography of the Tropical Trans-Pacific Tonnacean and Non-Tonnacean Prosobranch Gastropods with Indo-Pacific Faunal Affinities in West American Waters

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ABSTRACT

Cymatium (*Monoplex*) *mundum* (Gould, 1849), a wide-ranging Indo-West Pacific species, is recorded from the Galapagos Islands. This taxon has yet to be recognized elsewhere in the eastern Pacific Ocean, but is here reported from the western Atlantic for the first time. A lectotype is selected for *Cymatium gemmatum* (Reeve, 1844), which was previously confused with *C. mundum*. The occurrences are documented in west American waters for other trans-Pacific Tonnacean species of the following genera: *Tonna* in the Tonnidae, *Charonia*, *Cymatium*, *Linatella* in the Ranellidae, *Distorsio* in the Personidae, and *Bursa* in the Bursidae.

The modern Tonnacean faunal element in the eastern Pacific apparently reflects survivors of a previously widespread, post-Tethyan biota modified by factors resulting from the closure of the Central American Seaways about three million years ago, together with post-Pliocene supplementation from the central Pacific. The present non-Tonnacean prosobranchs in the eastern Pacific with Indo-Pacific faunal affinities appear to represent largely post-Pliocene additions to the eastern Pacific that were derived from western Pacific communities.

Key words: Tonnacea; systematics; new records; Ranellidae; Personidae; Bursidae; zoogeography; Indo-Pacific Prosobranchia in eastern Pacific Ocean; marine snails.

INTRODUCTION

This paper records the presence in the eastern Pacific Ocean of the Indo-West Pacific ranellid gastropod, *Cymatium mundum* (Gould, 1849). The occurrences of this wide-ranging species in the New World are based on specimens collected by Jacqueline DeRoy and Carmen Angermeyer in the Galapagos Islands, some 15 to 35 years ago. This taxon is differentiated from *Cymatium gemmatum* (Reeve, 1844), with which it was commonly confused. The first records of *C. mundum* in the western Atlantic are here reported, based on specimens collected by Frank and Vera Lyman off Florida some 50 years ago. Additional specimens of *Cymatium muricinum* (Röding, 1798), a tropical cosmopolitan species known elsewhere in the eastern Pacific from Panama (Emerson, 1983:119, figs. 15, 16) are reported from the Galapagos Islands confirming a previous record which was based on a specimen in the DeRoy Collection (Emerson, *in* Radwin, 1969:235).

A zoogeographical survey was undertaken of the tropical trans-Pacific Tonnacean species and non-Tonnacean prosobranchs with Indo-Pacific faunal affinities known to occur in the western and eastern Pacific. On the basis of the available data, the origins of these faunal elements in the eastern Pacific Ocean are discussed in terms of their distribution in time and space.

ABBREVIATIONS

AHF = Allen Hancock Foundation Collection; see Fraser (1943) and McCulloch (1977) for station data (deposited in the LACMNH)
AMNH = American Museum of Natural History, New York
BM(NH) = The Natural History Museum, London [formerly the British Museum (Natural History)]
CASIZ = California Academy of Natural Sciences, San Francisco, CA
LACMNH = Los Angeles County Museum of Natural History, CA
MCZ = Museum of Comparative Zoology, Harvard University, Cambridge, MA
MNHN-Paris = Muséum National d'Histoire Naturelle, Paris

NMNH = National Museum of Natural History, U.S. National Museum Collection (USNM), Smithsonian Institution, Washington, D.C.

NZGS = New Zealand Department of Scientific and Industrial Research, Geology and Geophysics Division [formerly the New Zealand Geological Survey], Lower Hutt

SBMNH = Santa Barbara Museum of Natural History, Santa Barbara, CA

SYSTEMATIC TREATMENT

For many years, the identity of *Cymatium mundum* (Gould, 1849) has been misunderstood by most workers, who erroneously considered Gould's taxon to be a junior subjective synonym of *C. gemmatum* (Reeve, 1844). This confusion dates from Reeve's (1844a) original description and illustrations in which specimens of what are now recognized as *C. mundum* (Gould, 1849) were considered by him to be a variety of *C. gemmatum* (A. Beu, *in litt.*, November 13, 1989). As indicated by Springsteen and Leobrera (1986:116), *C. mundum* differs from *C. gemmatum* in the shell being "... shorter and wider and more coarsely sculptured; [with] the varices ... thicker and [with] the intervarical cords ... more pronounced especially on the spire whorls. ..." The slender, more delicate *Cymatium gemmatum* is rarely white and is commonly orange-brown in basal color, with darker brown and white varical bands as shown in color by Springsteen and Leobrera (1986:115, pl. 31, figs. 12a, 12b). The more massive *C. mundum* is yellowish to white in basal color and specimens commonly exceed 30 mm in length (Abbott and Dance, 1982:120, as *C. gemmatum* Reeve). In contrast, specimens of *C. gemmatum* rarely attain 30 mm in length and they lack, in maturity, the heavy outer lip characteristic of *C. mundum* on which the apertural lip projects above the labral surface (cf. figure 8 with figure 24).

Cymatium gemmatum appears to be largely confined in distribution to the western Pacific, where in the central Philippine Islands specimens are found in depths to 100 meters. Verified records of this taxon from localities on the Pacific Plate, however, are scarce. In the case of *C. mundum*, the range is spread throughout the Indo-Pacific faunal province. Moreover, specimens of this taxon are commonly found at localities on the Pacific Plate, from the intertidal zone to moderate depths. See range data given below.

In the following section, the taxonomic status of these two taxa is reevaluated and the two nominal species are recognized as separate and distinct taxa.

Family Ranellidae Gray, 1854

(= Cymatiidae Iredale, 1913; see Beu and Cernohorsky, 1986:242)

Subfamily Cymatiinae Iredale, 1913; see Jansson and Beu, 1990a, proposal to conserve Cymatiinae under ICZN article 49b, in place of Neptunellininae Gray, 1854 as used by Warén and Bouchet, 1990:58.

Genus *Cymatium* Röding, 1798

Type species: *Murex femorale* Linné, 1758, by subsequent designation of Dall (1904:133). Synonyms: *Lotorium* Montfort, 1810; *Tritocurris* Lesson, 1842; *Nyctilochus* Gistel, 1848.

Subgenus *Monoplex* Perry, 1811

Type species: *Monoplex australasiae* Perry, 1811 [= *Cymatium parthenopeum* (von Salis, 1793)], by subsequent designation of Dall (1904:138), *fide* Beu and Kay (1988:197).

Synonyms: *Lampusia* Schumacher, 1817; *Cymatriton* Clench and Turner, 1957.

Cymatium (*Monoplex*) *gemmatum*
(Reeve, 1844)
(figures 1–8)

Triton gemmatus Reeve, 1844a, *Triton* text, pl. 15, figs. 60a,b; figs. 1, 2 herein.

Type locality: Island of Ticao, Philippines (12°30′N, 123°42′E), "Found on stones at low water); Cuming". Reeve, 1844b:117.

Cymatium (*Monoplex*) *gemmatum*, Beu, 1985:58, "West Pacific".

Cymatium (*Septa*) *gemmatum*, Springsteen and Leobrera, 1986 114, 116, pl. 31, figs. 12a,b, "Camotes Sea and Sulu Sea", Philippines.

Triton (*Simpulum*) *gemmatus*, Tryon, 1880:13, in part, pl. 7, fig. 41 only [copy of Reeve, 1844a, pl. 15, fig. 60a].

Range: western Pacific: Philippine Islands (Bohol Straits, AMNH 232143; Punta Engaño, Mactan Island, Cebu, ex.—F. J. Springsteen, AMNH 232142); Palau Islands (Kror Island, AMNH 92774), Indonesia (Ambon Island, USNM 746407); Solomon Islands (AMNH 93092; NZGS); Fiji Islands (Vanua Levu, USNM 695079); New Caledonia (MNHN-Paris; *teste* Beu); Coral Sea (Chesterfield–Bellona Plateau, MNHN-Paris; *teste* Beu), Austral Islands (Tubuai Island, USNM 705501).

Remarks: The probable syntypes of *Triton gemmatus* Reeve in the BM(NH) [lot #198055] consist of 4 specimens, which range from 16.2 mm to 28.9 mm in height. One of these specimens appears to be the specimen used to illustrate *Triton gemmatus* (Reeve, 1844, pl. 15, figs. 60a,b) and is here selected as the lectotype (cf. figures 1, 2 with 3, 4 herein). The lectotype (28.9 mm in height) is slightly larger than Reeve's figure (28.1 mm). The early whorls are missing owing to breakage, as is the case in Reeve's figure, but the lectotype possesses a varix on the third postnuclear whorl which is not shown on Reeve's illustration. Otherwise, the lectotype compares favorably with the figure. Three paralectotypes of *C. gemmatum*


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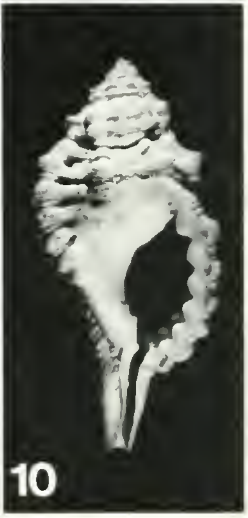
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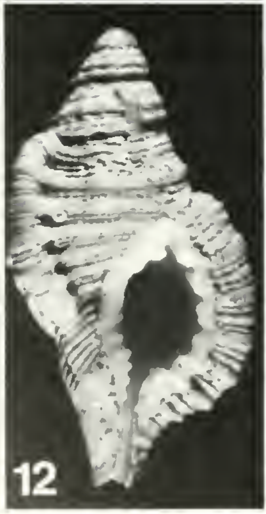
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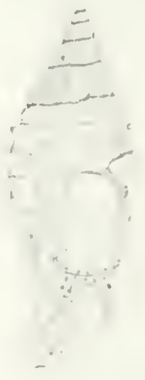
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Figures 1–8. *Cymatium gemmatum* (Reeve); ×2. **1, 2.** Copy of *Triton gemmatus* Reeve, 1844a, pl. 15, figs. 60a,b. **3, 4.** Lectotype BM(NH) 198055. **5, 6.** Paralectotype BM(NH) 198055a. **7, 8.** AMNH 232142, off Mactan Island, Cebu, Philippines, ex-F. J. Springstein. **Figures 9, 10.** *Cymatium muricinum* (Röding). Crabbed specimen, Santa Cruz Island, Galapagos Ids., Oct. 1969, AMNH 232144, ex-J. DeRoy; ×1. **Figures 11–15.** *Cymatium mundum* (Gould); ×2. **11.** Copy of *Triton mundum* Gould, 1849, after Gould, 1856, pl. 17, fig. 297. **12, 13.** Lectotype USNM 5695. **14, 15.** Copies of *Triton mundum* Gould, 1849, after Gould, 1856, pl. figs. 297a,b.

are here recognized in the type lot [BM(NH) 198055]. The largest of the three paralectotypes is illustrated herein (figures 5, 6).

The old locality label accompaning the type lot reads, "*T. gemmatus*, var., I. Masbate [12°11′N, 123°30′E] on the reefs, under stones. H. [ugh] C. [uming]". Whereas the "Hab. [itat]" given by Reeve (1844a); for *T. gemmatus* is "Island of Ticao, Philippines" [12°13′N, 123°42′E], (found under stones at low water; Cuming)." These islands are in close proximity, being separated by the Masbate Pass. Inasmuch as the existing label accompanying this lot refers to a variety of *T. gemmatus*, the original locality stated by Reeve (1844a); for this taxon is here retained as the type locality.

At the time *Triton gemmatus* was proposed, Reeve (1844a, pl. 15, fig. 60c) briefly described and illustrated a specimen of what is now recognized as *Cymatium mundum* under the appellation of "*Triton gemmatus* variety B." There are three specimens in the type lot [BM(NH) #196736]. The largest specimen most closely resembles Reeve's figure (see figure 20, herein), but this specimen measures 40.9 mm in height *vs.* the figure which is 38 mm in height. The other two specimens are, respectively, 38.9 and 33.5 mm in height. Although these specimens are typical of examples of *Cymatium mundum* (Gould, 1849), they retain the status of paralectotypes of *Cymatium gemmatum* (Reeve). The old label accompanying the type lot cites only the "Philippines" as the locality.

Cymatium (*Monoplex*) *mundum*
(Gould, 1849)
(figures 11–24)

Triton gemmatus variety B, Reeve, 1844a, *Triton* text, pl. 15, fig. 60c [figure 20 herein], "Island of Annaa (Chain island), South Pacific Ocean, and island of Burias, Philippines (found under stones in both localities at low water); Cuming". Reeve, 1844b:117. Not *T. gemmatus* Reeve.

Triton mundum Gould, 1849:143; Gould, 1856:506, pl. 17, figs. 297, 297a–b [figures 11, 14, 15 herein]; Gould, 1862:66; Johnson, 1964:112. Type locality: "Tutuilla [*sic*; Tutuila] Samoa Islands" (American Samoa, 14°18′S, 170°42′W).

Cymatium (*Monoplex*) *mundum*, Beu 1985:58, "Indo-West Pacific".

Cymatium (*Septa*) *mundum*, Springsteen and Leobrera, 1986:116, pl. 31, fig. 13, "Camotes Sea and Sulu Sea", Philippines.

Triton (*Simpulum*) *gemmatus*, Tryon, 1880:13, in part, pl. 7, figs. 43, 44 [copy of Gould, 1856, figs. 279, 279a] only. Not *T. gemmatus* Reeve.

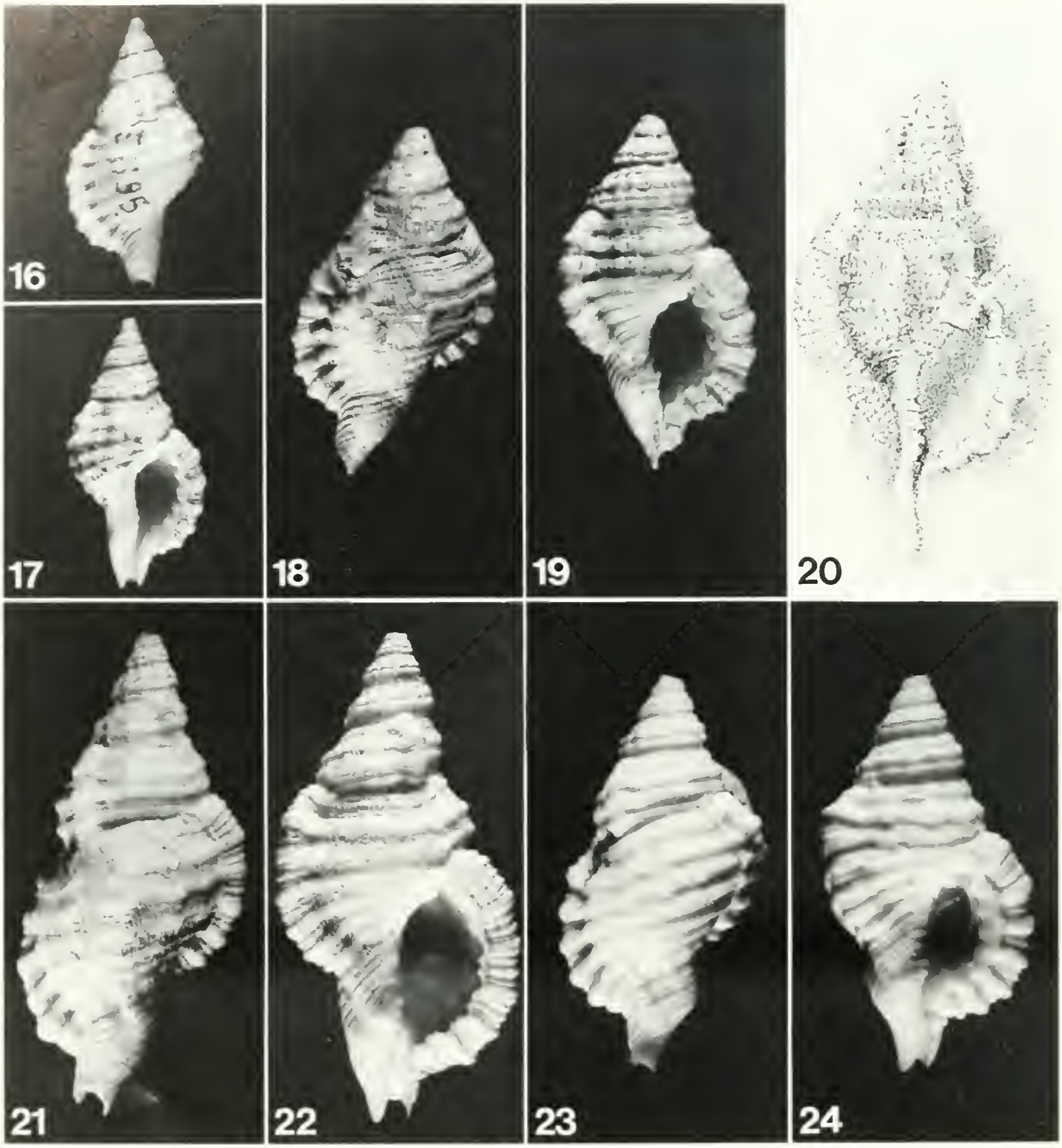
Cymatium (*Septa*) *gemmatum*, Clench and Turner, 1957:222, in part, reference in synonymy to *Triton mundum* Gould only. Not *T. gemmatus* Reeve. [Clench and Turner mistakenly referred their western Atlantic records of the Indo-west Pacific species, *C. vespaceum* (Lamarck, 1822), to *C. gemmatum*. Beu (1985:60) now considers these east American populations to be a distinct species, namely: *C. comptum* (A. Adams, 1854)]. Finet, 1985:19, "Galapagos Islands", based on AMNH 139535. Not *T. gemmatus* Reeve.

Cymatium gemmatum, Salvat and Rives, 1980:306, fig. 173, "îles de la Société aux Tuamotu à Raevavae (Australes) et aux Marquises"; Abbott and Dance, 1982: 120, "Indo-Pacific; West Indies, under coral, on sand, shallow water; uncommon". Not *C. gemmatum* Reeve.

Range (Selected localities from 50 AMNH lots): Western Indian Ocean (Durban Bay, South Africa, AMNH 196938); (off Gedi, Kenya AMNH 96528); (off Kizimkazi, Zanzibar, AMNH 101032); off Somalia (Mogadiscio, AMNH 142680); (Mauritus, AMNH 113606); eastward into the Pacific Ocean, northward to southern Japan (Okinawa, AMNH 169800) and southward to the Fiji Islands (Suva Reef, AMNH 214467), Solomon Islands (Malaita Island, AMNH 118330) and New Caledonia (Touho, AMNH 104266), northeastward to the Hawaiian Islands (Oahu Island, AMNH 152284; Maui Island, AMNH 147510) and southeastward to the Society Islands (Huahine Island, AMNH 231972; 239056); French Austral Islands (Tubuai, AMNH 84641) and Marquesas Islands (Salvat and Rives, 1980:305). NEW RECORDS For The Eastern Pacific Ocean: Galapagos Islands, Academy Bay, Isla Santa Cruz, 1 fresh specimen, found on beach, June, 1966, ex-J. DeRoy (AMNH 139535); 1 crabbed specimen, found at low tide, December, 1965, ex-J. DeRoy (AMNH 232145), see figures 21, 22. Galapagos Islands, 1 crabbed specimen, South Channel (Isla Santa Cruz–Isla Baltra) collected about 1975, C. Angermeyer collection. NEW RECORDS For The Western Atlantic: 1 specimen, south end of Lake Worth, Palm Beach County, Florida, Vera Lyman!, ex-A. D'Attilio collection (NZGS WM15228, *teste* A. Beu). 1 specimen dredged from Gulf Stream, off Palm Beach County, Florida, Frank Lyman! 1940, ex-AHF (LACM 115537, *teste* A. Beu).

Remarks: In a review of the taxa described by Augustus A. Gould, Johnson (1964:112) selected for *Triton mundum* Gould (1849:506, pl. 17, fig. 297, a–b) the lectotype (USNM 5695, cf. figures 12, 13 with Figure 11, herein) and a "paratype" [= paralectotype] (USNM 612311, cf. figures 14, 15 with figures 16, 17 herein). These specimens, which measure 29.9 and 21.9 mm in height, respectively, compare favorably with Gould's somewhat stylized drawings. As Johnson (1964:112) noted, an additional specimen, which is labeled a paratype [= paralectotype] from the A. A. Gould Type Collection, No. A427, is present in the Museum of Comparative Zoology (#169249). The MCZ specimen (figures 18, 19), which had been obtained from the New York State Museum, measures 28.8 mm in height.

The two type specimens (lectotype and paralectotype) in the USNM collection are presumably from the type locality, "Tutuilla, Samoa Islands" (Gould, 1849), but the existing labels only identify the source of the two lots, namely: the U.S. Exploring Expedition (1838–42). There



Figures 16–24. *Cymatium mundum* (Gould); ×2. **16, 17.** Paralectotype USNM 612311. **18, 19.** Paralectotype MCZ 169249. **20.** Copy of *Triton gemmatus* var. B. Reeve, 1844a, pl. 15, fig. 60c [= *C. mundum*]. **21, 22.** Crabbed specimen, Santa Cruz Island, Galapagos Ids., AMNH 232145, ex-J. DeRoy. **23, 24.** Huahine Island, Society Ids., AMNH 239056, note fully developed outer lip.

are no additional data in the USNM catalogue for either lot (*teste* M. G. Harasewych).

ZOOGEOGRAPHIC IMPLICATIONS

Tables 1 and 4 enumerate and document the trans-Pacific Tonnacean species known to occur in the tropical eastern Pacific, including records for the oceanic islands (Clipperton Island, Revillagigedo Islands, Cocos Island, and Galapagos Islands) as well as those from the continental borderland. Some of the records are based on limited samples of one to three individuals that are known only from dead-collected specimens. These include *Tonna perdix perdix*, *Cymatium aquatile*, *C. mundum*, and

Linatella succincta. The rarity of these and other records may reflect, in part, the lack of extensive collecting by means of SCUBA diving and dredging operations. The marine mollusks of Cocos Island (about 9 km in circumference) are now reasonably well known owing largely to the intensive collecting activities during the past decade of Drs. Donald R. Shasky and Michel Montoya with the cooperation of their numerous field associates (Shasky, 1989c; Montoya, 1983, 1988). Whereas the molluscan faunas of most of the other oceanic islands may have received attention for a longer period of time, much of this collecting predates the use of SCUBA diving, and the insular faunas of these widely isolated and not easily accessible islands still remain poorly known. This is also largely true of the Galapagos Islands because of the geographical extent of this archipelago and the long-standing restrictive regulations pertaining to the collection of specimens (cf. Wellington, 1984). On the mainland, for most of the tropical zone (Mexico to Ecuador), much of the subtidal coastal waters and those of the near-shore islands have not been extensively explored by collectors. This is especially true of the communities associated with the coral-reef biotope (Emerson, 1967:91). A possible exception are the coral reefs of Panama where James Ernest, Royce Hubert and others have concentrated their collecting efforts for mollusks in recent years (Emerson, 1983). Nevertheless, the majority of the Tonnacean records are based on live-collected or well-preserved dead specimens from numerous sources over a considerable period of time, commencing with explorations early in the nineteenth century by Alexander von Humboldt and Aimé Bonpland (Valenciennes, 1833).

Students of zoogeography have long noted the presence of marine mollusks with Indo-Pacific faunal affinities in the subtropical and tropical waters of the eastern Pacific (Carpenter, 1857:346; Darwin, 1860:391 and others). Hertlein (1937) was the first, however, to discuss specifically this subject and detail the shallow-water molluscan species then known to be common to Polynesian and western American waters. He concluded that these Indo-Pacific species had likely dispersed the 5,000-km-wide body of open ocean (Ekman's East Pacific Barrier) separating the most eastern situated Polynesian Islands and the New World by means of long-lasting larval stages transported by ocean currents, and/or by attachment to drifting objects, to pelagic fishes, to mammals, or on the feet of wide-ranging oceanic birds. He also noted that nearly all of these mollusks were gastropods, many in the Conidae, Cymatiidae [= Ranellidae and Personidae] and Cypraeidae, and most of them were known in the eastern Pacific only from the oceanic islands, far from the West American Continental Borderland.

Our present knowledge largely serves to support Hertlein's conclusions. In the tropical Tonnacea, several species of *Cymatium* including *C. pileare martinianum*, and *C. muricinum*, have been shown to have teleplanic larvae (Scheltema, 1989:439). Additionally, a larval stage lasting nearly a year in the water column is known for the cosmopolitan species *Cymatium parthenopeum* and *C. nicobaricum* (Scheltema, 1971: table 1). Furthermore, *C. parthenopeum* and others are known to feed in the plankton and to be able to delay metamorphosis until a shallow-water substrate is reached (Pechenik *et al.*, 1984).

Oceanic currents appear to be the primary vehicle for the passive dispersal of mollusks with hemipelagic larvae (Scheltema, 1986, 1989; Zinsmeister & Emerson, 1979; Emerson, 1990) and for the distribution of species that attach to, or burrow into floating objects. Rafting may be the means of dispersal for some epifaunal bivalves (Turner, 1966:52, 1971; Scheltema, 1977;93; Emerson, 1978:92) and gastropods (Jokiel, 1990:71). The major current circulation in the tropical Pacific apparently has favored east to west dispersal pathways since the late Neogene, or perhaps much earlier (cf. Grigg, 1988; Newton, 1988; Scheltema, 1988; Skelton, 1988). On the other hand, the paucity of mollusks with Panamic faunal affinities in Polynesian waters suggests that recruitment of tropical Panamic species into the central Pacific via dispersal by the westward flowing current patterns has been largely unsuccessful (cf. Briggs, 1970:134; Zinsmeister & Emerson, 1979:36; Scheltema, 1988:149). This mostly one-way trans-Pacific distribution exists even though the westward transport of organisms across the East Pacific Barrier would presumably be facilitated by the acceleration of westward flowing currents during pre–El Niño/Southern Oscillation events (Jokiel, 1990:69).

As noted previously, Hertlein (1937:309) pointed out that many of the Indo-Pacific species recorded by him occurred only on the oceanic islands in the eastern Pacific and were not known to have spread eastward to the continental borderland of the Americas. This observation remains largely true for the non-Tonnacean prosobranch species, of which only 20 of the 48 taxa (41%) compiled herein are known from the mainland (tables 2, 3, Appendix). In contrast, 42 (87%) of these 48 taxa are reported from the oceanic islands in the tropical eastern Pacific, with 33 (68%) at Clipperton Island, 16 (33%) at Cocos Island, 10 (20%) in the Galapagos Islands, 7 (14%) in the Revillagigedo Islands, and 1 (2%) at Guadalupe Island (table 4). These species represent an attenuated Indo-Pacific element that has reached the oceanic islands in the eastern Pacific, but the majority of these taxa (59%) have not been reported from the west American mainland (table 4). Furthermore, none of the 48 species is known from the western Atlantic, although one survives in the eastern Atlantic and the Mediterranean, presumably as a post-Tethyan faunal relict (table 4).

The only fossil evidence for the temporal existence of the non-Tonnacean Indo-Pacific faunal element in west America is the presence of *Cypraea cernica* Sowerby in the Pleistocene of Guadalupe Island (Lindberg *et al.*, 1980:52) and *Hastula albula* (Menke) in the Miocene of California, a species living at the present time in the Revillagigedo Islands (Bratcher & Burch, 1971; table 3, herein). Nor have any representatives of this faunal element been recovered from Mesoamerican archaeological sites (Emerson, 1983:120). If large and colorful gastropods such as *Mitra mitra* (Linné) had been commonly

Table 1. Wide-ranging tropical Tonnacean species known from the western Pacific that occur in the eastern Pacific on the continental mainland (Mexico to Peru) and offshore on the Oceanic Islands, with their occurrences in the Atlantic Ocean and the Mediterranean Sea based on Beu (1985) unless otherwise indicated

	Eastern Pacific							
	Clipperton Island	Revillagigedo Islands	Cocos Island	Galapagos Islands	Mainland	Western Atlantic	Eastern Atlantic	Mediterranean Sea
Tonnacea								
Tonnidae								
1. *Tonna p. perdix* (Linné)*+#	—	—	—	X[19,24]	—	X[36]	—	—
Ranellidae								
Cymatiinae								
2. *Charonia t. tritonis* (Linné)*+#	—	—	X[5,13]	X[5]	—	X[37]	X[37]	X[37]
3 *Cymatium aquatile* (Reeve)+#	—	—	X[2,7]	—	X[2,28]	X	X	—
4 *Cymatium corrugatum amictum* (Reeve)[31]	—	X[20]	X[21]	X[1]	X[9]	X[38]	X[39,43]	X[39]
5 *Cymatium mundum* (Gould)+#	—	—	—	X[17]	—	X[40]	—	—
6. *Cymatium muricinum* (Röding)*	—	—	—	X[3,10,17]	X[4]	X	X	X
7 *Cymatium pileare macrodon* (Valenciennes)*+#[32]	X[2,6,26]	X[6]	X[2,6]	X[2,6]	X[2,6]	X[41]	X[41]	—
8. *Cymatium nicobaricum* (Röding)*+#	X[8,11,16]	—	X[14]	—	—	X	X	X
9. *Cymatium parthenopeum keenae* Beu+#[33]	—	—	—	X[2]	X[9]	X[42]	X[42]	X[42]
10 *Linatella succincta* (Linné)+#	—	—	—	X[15]	—	—	X[43]	—
Personidae								
11. *Distorsio c. constricta* (Broderip)[34]	—	—	X[22]	X[18]	X[9]	X[44]	—	—
[*Distorsio perdistorta* Fulton[35]	—	—	—	—	X[(?),30]	X	X	—]
Bursidae								
12 *Bursa asperrima* (Dunker)*#	X[1,29]	—	—	X[27]	—	—	—	—
13. *Bursa g. granularis* (Röding)*+#	X[8,11,12,16]	X[25]	X[13]	—	X[23]	X[45]	—	—
Total N of taxa = 13	4 (30%)	3 (23%)	7 (53%)	10 (76%)	7 (53%)	11 (84%)	8 (61%)	5 (38%)

Records based on: 1, Beu, 1985; 2, Beu and Kay, 1988; 3, Emerson, 1978; 4, Emerson, 1983; 5, Emerson, 1989, 6, Emerson and Old, 1963; 7, Emerson and Old, 1964, 8, Hertlein and Allison, 1960; 9, Keen, 1971; 10, Radwin, 1969; 11, Sachet, 1962; 12, Salvat and Ehrhardt, 1970; 13, Shasky, 1983a; 14, Shasky, 1984a; 15, Shasky, 1989a; 16, Shasky, 1989c; 17, herein; 18, Finet, 1985, "verified record", based on 3 lots in LACMNH (AHF 324-35; 788-38; 816-38) *teste* Finet, *in litt.* 2-28-90, 19, Finet, 1987; 20, LACMNH (AHF 141-34); 21, LACMNH (AHF 772-38; 780A-38); 22, LACMNH (AHF 780A-38); 23, LACMNH 38-6, Bahía Chamelo, Jalisco, Mexico; 24, LACMNH 84-27, Isla Marchena (Bindloe Id.); 25, SBMNH 55151, Socorro Island, crabbed specimen, 1987; 26, CASIZ 069681, 4 specimens, 1956, 1958; 27, CASIZ 069683, 1 specimen Jervis Id., 1964 and CASIZ 069684, 1 beach specimen, James Id., 1969; 28, CASIZ 069686, 1 specimen, "Gulf of California, Mexico, Capt. Porter", Hemphill coll., CASIZ 069685, 1 specimen, "Central America west coast", W. S. Raymond coll.", W. S. Raymond coll. 29, LACMNH C-99, 1 specimen, C. Limbaugh, May 5, 1959; records of *B. cruentata* (Sowerby) of Hertlein and Allison, 1960, are referable to this species (4 specimens, Clipperton Id., E. C. Allison, 1956, 1958, CASIZ 069682). 30, 1 specimen questionably from "near Oaxaca, w. Mexico, 1987, ex-M. Parth coll., *teste* A. Beu (*in litt.*) June 5, 1990. 31, not known from the central Pacific. 32, *C. p. pileare* (Linné) in the Indo-Pacific. 33, nominate subspecies and *C. p. echo* Kuroda and Habe in the Indo-Pacific. 34, *D. c. habei* Lewis in the western Pacific. 35, Populations in the Indo-Pacific and western Atlantic. 36, as *T. p. maculosa* (Dillwyn). 37, as *C. t. variegata* (Lamarck). 38, as *C. c. krebsii* (Mörch). 39, as *C. c. corrugatum* (Lamarck). 40, 2 specimens off Palm Beach Co., Florida (teste Beu). 41, as *C. p. martinianum* (d'Orbigny). 42, as *C. p. parthenopeum* (von Salis). 43, known from west Africa. 44, as *D. c. macgintyi* Emerson and Puffer. 45, as *B. g. cubaniana* (d'Orbigny).

Classification follows Beu (1985) with the exception that *Cymatium macrodon* and *C. martinianum* are considered subspecies of *C. pileare*. Explanation of symbols: asterisk (*) = taxa known from Line Islands (Jewell, 1962; Kay, 1971; Kay and Switzer, 1974); plus sign (+) = known from French Polynesia (Dautzenberg and Bouge, 1933; Rehder, 1968; Salvat and Rives, 1980; Richard, 1985); and number sign (#) = known from Hawaiian Archipelago (Gage, 1962; Schmeltz, 1978, 1979; Kay, 1979).

Table 2. Shallow-water Indo-Pacific prosobranch gastropods (excluding the Tonnacea) recorded from the West American Continental Borderland (Appendix) and their distribution on the eastern Pacific islands (records from Emerson, 1978, 1983, Everson, 1988; Robertson, 1979; Shasky, 1983–1989, and herein). None of these species is known from the Atlantic Ocean, except *Quoyula madreporarum* which was reported from the Cape Verde Islands (Emerson, 1983:122).

	Clipperton Island	Revil-lagigedo Islands	Cocos Island	Galapagos Islands	Guadalupe Island
Neritacea					
Titiscaniidae					
1. *Titiscania limacina* (Bergh)	—	—	—	—	—
Architectonicacea[1]					
Architectonicidae					
2. *Heliacus trochoides* (Deshayes)+#	—	—	—	—	—
3. *Philippia radiata* (Röding)+#	—	—	X	—	—
Littorinidae					
4. *Littorina pintado* (Wood)#	X	—	—	—	—
Cypraeacea					
Cypraeidea					
5. *Cypraea caputserpentis* Linné*+#	X	—	X	—	—
6. *Cypraea talpa* Linné*+#	—	—	X	—	—
7. *Cypraea teres* Gmelin [= ?*alisonae* Burgess]*#	X	—	X	X	—
Ovulidae					
8. *Pseudocypraea adamsonii* (Sowerby)+	—	—	X	X	—
Muricacea					
Muricidae					
9. *Quoyula madreporarum* (Sowerby)*+#	X	X	—	—	—
10. *Reliquiaecava robillardi* (Lienard)*	X	—	—	—	—
11. *Rhizochilus antipathicus* (Steenstrup)#	—	—	—	—	—
Mitracea					
Mitridae					
12. *Mitra mitra* (Linné)*+#	—	—	X	X	—
Conacea					
Conidae					
13. *Conus chaldeus* (Röding)*+#	X	—	X	X	—
14. *Conus ebraeus* Linné*+#	X	—	X	X	—
15. *Conus tessulatus* Born*+	X	X	X	—	—
Terebridae					
16. *Terebra affinis* Gray*+#	—	—	—	—	—
17. *Terebra laevigata* Gray+#	—	—	—	—	—
18. *Terebra maculata* (Linné)*+#	X	X	X	—	—
Turridae					
19. *Kermia felina* (Hinds)+	—	—	—	—	—
20. *Microdaphne trichodes* (Dall)*+	—	—	—	X	—
Total N taxa on mainland = 20	9 (45%)	3 (15%)	10 (50%)	6 (31%)	0

Explanation of symbols: asterisk (*) = taxa also known from Line Islands (Jewell, 1962; Kay, 1971; Kay and Switzer, 1974); plus sign (+) = known from French Polynesia (Dautzenberg and Bouge, 1933; Rehder, 1968; Salvat and Rives, 1980; Richard, 1985); and number sign (#) = known from Hawaiian Archipelago (Gage, 1962; Schmeltz, 1978, 1979; Kay, 1979).

[1] For the purposes of this tabulation, Architectonicacea is retained in the subclass Prosobranchia and not transferred to the subclass Heterobranchia (see classification of Ponder and Warén, 1988:308).

available in west American waters, one would expect specimens to have been reported in the kitchen middens and burial sites of the Native Americans. On the other hand, the tropical shallow-water Tertiary record is poorly preserved on the northwest American borderland. Until recently, no fossiliferous marine Tertiary onshore deposits were recognized regionally, from southern Nicaragua northward (Woodring, 1966, 1978; Perrilliat, 1978), except for the long-known exposures on the Tres Marias Islands, off San Blas, Mexico, onshore and on the islands in the Gulf of California and in southeastern California (Durham & Allison, 1960; Powell, 1988; Smith, 1989). In the mid-1970's however, reconnaissance exploration along the Pacific coast of Mexico, northwest of Tehuantepec (Durham *et al.*, 1981) determined the presence of seven onshore Tertiary sedimentary basins on the North America Plate, negating the belief previously held that most of these sediments had been lost to subduction or continental-margin truncation into the Middle American Trench system (Karig *et al.*, 1978; Beck & Plumley, 1979). Four of these onshore west Mexican basins have yielded fossiliferous marine sediments of Miocene and younger

Table 3. Shallow-water Indo-Pacific prosobranch gastropods (excluding the Tonnacea) recorded from the eastern Pacific Oceanic Islands that are not known from the West American Continental Borderland (records from Bakus, 1975, Cate, 1969, Emerson, 1978, 1983, Everson, 1988, Finet, 1987a,b; Kay, 1979, Shasky, 1983–89, and herein). None of these species is known from the Atlantic Ocean.

	Clipperton Island	Revillagigedo Islands	Cocos Island	Galapagos Islands	Guadalupe Island
Fissurellacea					
Fissurellidae					
1. *Diodora granifera* (Pease)*+#	X	—	—	—	—
Trochacea					
Phasianellidae					
2. *Tricolia variabilis* (Pease)*+#	—	—	X	—	—
Neritacea					
Neritidae					
3. *Nerita plicata* Linné*+#	X	—	—	—	—
Cerithiacea					
Cerithiidae					
4. *Cerithium nesioticum* Pilsbry & Vanatta*+#	X	—	—	—	—
Cypraeacea					
Cypraeidae					
5. *Cypraea depressa* Gray*+	X	—	—	—	—
6. *Cypraea helvola* Linné*+#	X	—	—	—	—
7. *Cypraea maculifera* (Schilder)*+#	X	—	—	—	—
8. *Cypraea moneta* Linné*+#	X	—	X	X	—
9. *Cypraea rashleighana* Melvill+*	X	—	?	—	—
10. *Cypraea schilderorum* (Iredale)*+#	X	—	—	—	—
11. *Cypraea scurra* Gmelin*+#	X	—	—	—	—
12. *Cypraea vitellus* Linné*+#	X	—	—	—	—
Muricacea					
Muricidae					
13. *Drupa morum* Röding*+#	X	—	—	—	—
14. *Drupa ricinus* (Linné)*+#	X	—	—	X	—
15. *Morula uva* (Röding)*+#	X	—	X	—	X
16. *Nassa serta* (Bruguière)*+#	X	—	—	—	—
17. *Coralliobia fimbriata* (A. Adams)*#	X	—	—	—	—
18. *Coralliophila violacea* (Kiener)*+#	X	X	X	X	—
Buccinacea					
Buccinidae					
19. *Clivipollia costata* (Pease)+#	X	—	—	—	—
20. *Clivipollia fragaria* (Wood)+#	—	—	X	—	—
21. *Cantharus fumosus* (Dillwyn)+#	—	—	—	X	—
Mitracea					
Mitridae					
22. *Mitra edentula* Swainson+#	X	—	—	—	—
23. *Mitra ferruginea* Lamarck*+#	X	—	X	—	—
24. *Mitra papalis* (Linné)+#	X	—	X	—	—
25. *Strigatella litterata* (Lamarck)*+#	X	—	—	—	—
Volutacea					
Harpidae					
26. *Harpa gracilis* Broderip & Sowerby+	X	—	—	—	—
Conacea					
27. *Terebra crenulata* (Linné)*+#	X	X	X	—	—
28. *Hastula albula* (Menke)+#	—	X	—	—	—
Total N of insular taxa = 28[1]	24 (85%)	3 (10%)	8 (32%)	4 (14%)	1 (3%)

Explanation of symbols: asterisk (*) = taxon also known from Line Islands (Jewell, 1962; Kay, 1971; Kay and Switzer, 1974); plus sign (+) = known from French Polynesia (Dautzenberg and Bouge, 1933; Rehder, 1968; Salvat and Rives, 1980, Richard, 1985); and number sign (#) = known from Hawaiian Archipelago (Schmeltz, 1978, 1979; Kay, 1979).

[1] Additional unverified records: 1, *Vanikoro acuta* (Récluz) from Cocos Island (Shasky, 1987:49) and *Triphora triticea* Pease from the Galapagos Islands (Shasky, 1989a:8)

ages (Durham *et al.*, 1981; Perrilliat, 1981). Indo-Pacific molluscan elements have yet to be reported from these basins (Perrilliat, 1987). Furthermore, no mollusks of the non-Tonnacean Indo-Pacific faunal element have been recorded from the numerous fossiliferous terrace deposits of Pleistocene age along the west American mainland, from Mexico to Peru. Thus, the paucity of tropical Tertiary fossils from much of the middle West American Continental Borderland has largely limited paleogeographic interpretations of the faunistic history of the modern molluscan Panamic Province to the regional Pleistocene fossil record and to comparisons with the Tertiary faunal records of the adjoining Californian and Caribbean regions.

The non-Tonnacean element (tables 2, 3) is present only at the genus-group level in the Tertiary faunas of the Caribbean region. A small Indo-Pacific relict element (conid subgenera, etc.) is recognized by Petuch (1988: 94, 96) as regionally extinct species in the West Indian Gurabo Formation (Pliocene). However, none of the non-Tonnacean Indo-Pacific species now living in the eastern Pacific is known to inhabit the western Atlantic (table 4) and none of these species has been recognized in the fossil record of the east American tropics. The modern and fossil occurrences of the species of the non-Tonnacean Indo-Pacific faunal element in the eastern Pacific, therefore suggest that these taxa largely represent post-Pliocene colonizers derived by trans-Pacific dispersal from populations in the central Pacific.

This distributional pattern is in sharp contrast to that for the 13 trans-Pacific Tonnacean species cited in table 1. Eleven of the 13 species (84%) also occur in the western Atlantic, 7 (53%) of which are recognized as subspecifically divergent taxa. The vast majority (8 of the 13 taxa) are represented in the eastern Atlantic and several (5 of the 10 taxa) also have populations in the Mediterranean Sea (see table 1). Only eight (61%) of these trans-American taxa, however, can be termed truly circumtropical in distribution as the others are not known from the eastern Atlantic (table 4).

The fossil record of the Tonnacean species in the New World tropics, although sparse, is somewhat better documented at the species-group level than that of the non-Tonnacean trans-Pacific prosobranch species cited herein (tables 2, 3, Appendix). In the Tertiary, species of *Cymatium* (*sensu lato*) are recognized in Oligocene deposits of Panama and Mississippi (MacNeil and Dockery, 1984; Schmelz, 1989). Other cymatiid taxa are known from the Neogene period and Pleistocene epoch of the eastern Pacific and western Atlantic tropics. Beu and Kay (1988:196) recorded the presence of "... both *C. pileare* and *C. aquatile* ... in the Pacific [Basin] since Miocene time", and they noted "... that *C. aquatile* lived in northwestern Ecuador at some time [Pliocene] during the Neogene [Olsson (1964; pl. 30, fig. 3, as *C.* cf. *pileare*)], and that unnamed taxa close to, but different from, both *C. aquatile* and *C. martinianum* lived in the Caribbean during Miocene to mid-Pliocene time." The genus *Distorsio* is also known from the Oligocene of Mississippi (MacNeil, 1984) and elsewhere in Neogene and Pleistocene deposits of the east Americas, from Florida to Brazil (Pilsbry, 1922; Emerson & Puffer 1953; Woodring, 1959). In west America, *Distorsio* is reported from the Mio-Pliocene of southeastern California (Powell, 1988:17, as *D. constricta*), of Costa Rica (Aguilar & Fischer (1986:223) and of northwestern Ecuador (Pilsbry and Olsson, 1941:40; Olsson, 1964:174). *Distorsio* first appears in the Cretaceous of Madagascar (Beu, 1988:89), *Cymatium* (*sensu lato*) is known from the Paleogene and Neogene of the Old World (*e.g.*, Oligocene onwards in the Aquitaine Basin), and *Charonia* occurs in the Oligocene of Europe and the Neogene of both southern Europe and the Caribbean area (Beu, 1970; Gibson-Smith, 1971) suggesting that the New World representatives of these taxa form part of a post-Tethyan distributional pattern.

All 13 of the Tonnacean species listed in table 1 are known to occur on the oceanic islands within the eastern Pacific. Ten (76%) of the species are recorded from the Galapagos Islands, with 7 (53%) at Cocos Island, 4 (30%) at Clipperton Island and 3 (23%) in the Revillagigedo Islands. Seven species (58%) are reported from the mainland, including *Cymatium corrugatum amictum*, a non-trans-Pacific species with divergent subspecies in the western and eastern Atlantic Ocean (west Africa) and the Mediterranean Sea (table 1). Only 4 of the 13 taxa are commonly found on the west American mainland (*Cymatium corrugatum amictum*, *C. pileare macrodon*, *C. parthenopeum keenae*, and *Distorsio c. constricta*). One of these taxa (*C. p. macrodon*) is recognized by Beu and Kay (1988:211) as a full species on the basis of shell morphology, although they note the close resemblance of the eastern Pacific specimens to specimens of "typical" *C. pileare* in the western Pacific. Moreover, a faunal antiquity for the east American Tonnacea is further supported by the recognition in the western Atlantic of 7 of the 11 Pan-Panamian species divergent at the subspecies level.

The presence of 10 of the 13 eastern Pacific Tonnacean species living in the Galapagos Islands, with only 7 species on the west American mainland, may identify this archipelago as a post-Pliocene refuge for some of these Tonnaceans. This hypothesis is supported by the low numbers of Tonnacean species known from the other oceanic islands, especially Clipperton Island (4 species) and Cocos Island (7 species). Adverse post-Pliocene conditions in the tropical eastern Pacific may have caused the extinction of some elements of the insular and mainland Tonnacean populations. If this is the case, some of the present trans-Pacific Tonnacean fauna in the eastern Pacific must represent elements derived by dispersal from central Pacific populations commencing with the emergence of the Panamanian isthmus. Dana (1975) made a similar case for the decline of the Indo-Pacific hermatypic corals in the west American tropics during the Pliocene and their subsequent trans-Pacific replacement in the Pleistocene–Holocene. These factors (fossil record and the modern distributional pattern in the New World tropics) suggest

Table 1. A compilation comparing the distribution of the Indo-Pacific non-Tonnacean and Tonnacean prosobranchs in the eastern Pacific Ocean, with their occurrences in the Atlantic Ocean and Mediterranean Sea (based on tables 1–3, Appendix).

	Eastern Pacific Ocean		Atlantic Ocean		
	Oceanic Islands	Mainland	Western Atlantic	Eastern Atlantic	Mediterranean Sea
Non-Tonnacean species					
1. *Diodora granifera*	X[1]	—	—	—	—
2. *Tricolia variabilis*	X[3]	—	—	—	—
3. *Nerita plicata*	X[1]	—	—	—	—
4. *Titiscania limacina*	—	X	—	—	—
5. *Littorina pintado*	X[1]	X	—	—	—
6. *Cerithium nesioticum*	X[1]	—	—	—	—
7. *Heliacus trochoides*	—	X	—	—	—
8. *Philippia radiata*	X[3]	X	—	—	—
9. *Cypraea caputserpentis*	X[1,3]	X	—	—	—
10. *Cypraea depressa*	X[1]	—	—	—	—
11. *Cypraea helvola*	X[1]	—	—	—	—
12. *Cypraea maculifera*	X[1]	—	—	—	—
13. *Cypraea moneta*	X[1,3,4]	—	—	—	—
14. *Cypraea rashleighana*	X[1,?3]	—	—	—	—
15. *Cypraea schilderorum*	X[1]	—	—	—	—
16. *Cypraea scurra*	X[1]	—	—	—	—
17. *Cypraea talpa*	X[3]	X	—	—	—
18. *Cypraea teres*	X[1,3,4]	X	—	—	—
19. *Cypraea vitellus*	X[1]	—	—	—	—
20. *Pseudocypraea adamsonii*	X[3,4]	X	—	—	—
21. *Drupa morum*	X[1]	—	—	—	—
22. *Drupa ricinus*	X[1,4]	—	—	—	—
23. *Morum uva*	X[1,3,5]	—	—	—	—
24. *Nassa serta*	X[1]	—	—	—	—
25. *Quoyula madreporarum*	X[1,2]	X	—	X	X[14]
26. *Reliquiaecava robillardi*	X[1]	X	—	—	—
27. *Rhizochilus antipathicus*	—	X	—	—	—
28. *Coralliobia fimbriata*	X[1]	—	—	—	—
29. *Coralliophila violacea*	X[1,2,3,4]	—	—	—	—
30. *Clivipollia costata*	X[1]	—	—	—	—
31. *Clivipollia fragaria*	X[3]	—	—	—	—
32. *Cantharus fumosus*	X[4]	—	—	—	—
33. *Mitra edentula*	X[1]	—	—	—	—
34. *Mitra ferruginea*	X[1,3]	—	—	—	—
35. *Mitra mitra*	X[3,4]	X	—	—	—
36. *Mitra papalis*	X[1,3]	—	—	—	—
37. *Strigatella litterata*	X[1]	—	—	—	—
38. *Harpa gracilis*	X[1]	—	—	—	—
39. *Conus chaldeus*	X[1,3,4]	X	—	—	—
40. *Conus ebraeus*	X[1,3,4]	X	—	—	—
41. *Conus tessulatus*	X[1,2,3]	X	—	—	—
42. *Terebra affinis*	—	X	—	—	—
43. *Terebra crenulata*	X[1,2,3]	—	—	—	—
44. *Terebra laevigata*	—	X	—	—	—
45. *Terebra maculata*	X[1,2,3]	X	—	—	—
46. *Hastula albula*	X[2]	—	—	—	—
47. *Kermia felina*	—	X	—	—	—
48. *Microdaphne trichodes*	X[4]	X	—	—	—
Total N of taxa = 48	42 (87%)	20 (41%)	0	1 (1%)	1 (1%)
Tonnacean species					
1. *Tonna p. perdix*	X[4]	—	X[6]	—	—
2. *Charonia t. tritonis*	X[3,4]	—	X[7]	X[7]	X[7]
3. *Cymatium aquatile*	X[3]	X	X	X	—
4. *Cymatium corrugatum amictum*	X[2,3,4]	X	X[8]	X[9]	X[9]
5. *Cymatium mundum*	X[4]	—	X	—	—

Table 1. Continued

	Eastern Pacific Ocean		Atlantic Ocean		
	Oceanic islands	Mainland	Western Atlantic	Eastern Atlantic	Mediterranean Sea
6. *Cymatium muricinum*	X^{4}	X	X	X	X
7. *Cymatium pileare macrodon*	$X^{1,2,3,4}$	X	X^{10}	X^{10}	—
8. *Cymatium nicobaricum*	$X^{1,3}$	—	X	X	X
9. *Cymatium parthenopeum keenae*	X^{4}	X	X^{11}	X^{11}	X^{11}
10. *Linatella succincta*	X^{4}	—	—	X	—
11. *Distorsio c. constricta*	$X^{3,4}$	X	X^{12}	—	—
12. *Bursa asperrima*	$X^{1,4}$	—	—	—	—
13. *Bursa g. granularis*	$X^{1,2,3}$	X	X^{13}	—	—
Total N of taxa = 13	13 (100%)	7 (53%)	11 (84%)	8 (61%)	5 (38%)
Non-Tonnacean and Tonnacean species Total N of taxa = 61	55 (90%)	27 (44%)	11 (18%)	9 (14%)	6 (9%)

Known from: 1 = Clipperton Island, 2 = Revillagigedo Islands, 3 = Cocos Island, 4 = Galapagos Islands, and 5 = Guadalupe Island. Recognized as subspecies: 6 as *T. p. maculosa*, 7 as *C. t. varicgata*, 8 as *C. c. krebsii*, 9 as *C. c. corrugatum*, 10 as *C. p. martinianum*, 11 as *C. p. parthenopeum*, 12 as *D. c. macgintyi*, 13 as *B. g. cubaniana*, 14 described as *Q. m.* var *mediterranea* Parenzan (1970).

a dual origin for elements of the Tonnacean species now living in the eastern Pacific: 1, Survivors of a previously widespread Pan-Panamian post-Tethyan biota and 2, New arrivals of trans-Pacific species from the Central Pacific after the closure of the Central American Seaways.

The apparently rare occurrences of many of the taxa of both the Tonnacean and non-Tonnacean constituents found on the islands and/or the mainland may reflect in part records of species that cannot maintain viable populations for any significant duration without frequent replacement by larval recruitment or by other means of dispersal from established populations in the mid-Pacific. One of the major causes of temporal instability of these populations may result from the harsh environmental changes caused by major El Niño events in the eastern Pacific. Shasky (1985:4) reported a definite decline in numbers of some of the more common non-Tonnacean Indo-Pacific species and in the condition of the reef-coral at Cocos Island following the warming of the local waters as a result of the severe 1982–83 El Niño episode. He noted in 1984 the mortality of *Pocillopora* and found no living *Coralliophila violacea* until 1989, when a single living specimen was taken (Shasky, *in litt.*, August 19, 1990). Unfortunately the collection database for the mollusks provided herein (tables 1–3, Appendix) is not sufficient to determine the long-term influence of the El Niño induced changes on the survival of the Indo-Pacific faunal elements in the tropical eastern Pacific. The El Niño disturbances may temporarily benefit some faunal elements and harm others, *e.g.*, cause adverse effects on the communities associated with the coral-reef biotope (Glynn, 1988; Richmond, 1990; Robinson, 1985, 1987). For an excellent review of the many factors affecting the biotic composition of eastern Pacific stony corals and other tropical marine organisms in time and space, see Glynn and Wellington (1983:167–207).

The establishment at Clipperton and Cocos Islands of reproductively viable populations of the Indo-Pacific faunal element during "normal" conditions (non El Niño periods) would appear to be the key to the post-Pliocene dispersal of these faunal consituents to other areas in the tropical eastern Pacific. The large number of the non-Tonnacean Indo-Pacific taxa known from Clipperton and Cocos Islands serves to support this thesis (tables 2, 3). Twenty-four (85%) of the 28 taxa that are not known from the mainland have been reported from Clipperton Island, whereas 8 (28%) occur on Cocos Island. Of the 20 species known from the mainland, 9 (45%) have been recorded from Clipperton Island, and 10 (50%) occur on Cocos Island. In contrast, 10 of the 13 (76%) Tonnacean species occur in the Galapagos Islands, 7 (53%) on Cocos Island, and 4 (30%) on Clipperton Island. If all the Indo-Pacific prosobranch gastropods (Tonnacean and non-Tonnacean) in the eastern Pacific are considered, 55 (90%) of the 61 taxa are known from the oceanic islands and 27 (44%) are reported from the mainland (table 4). Thirty-seven of the 61 taxa (60%) are recorded from Clipperton Island, 25 (40%) from Cocos Island, 18 (29%) from the Galapagos Islands, 9 (14%) from the Revillagigedo Islands, and 1 (<1%) from Guadalupe Island (table 4). The presence at these stepping-stone islands of several species of hermatypic corals, mostly with western Pacific faunal affinities (Glynn & Wellington, 1983:176), affords a habitat for Indo-Pacific molluscan species associated with the coral reef biotope.

If the established populations of the Indo-Pacific element at Cocos and Clipperton Islands serve as a major source for larval dispersal to the Galapagos Islands and the west American mainland via the North Pacific Equatorial Countercurrent (Abbott, 1966:109; Emerson, 1967: 89; Wellington, 1984:256; Glynn & Wellington, 1983: 167), any prolonged disruption of the reproductive viability of the populations at these insular sites would affect the gene replenishment required to reestablish declining or defunct populations on the mainland and in the Galapagos Islands. The subsurface Equatorial Undercurrent (Cromwell Current), however, is a possible source for larval transport directly to the Galapagos Islands from the central Pacific. This subsurface current passes eastward through the Line Islands and could presumably disperse to the Galapagos Islands tropical organisms tolerant of temperate/subtropical temperatures (20–25°C at its core of maximum velocity, between 50 and 100 m depth, *teste* R. S. Scheltema; cf. Glynn & Wellington, 1983:168). Furthermore, with the commencement of El Niño conditions, the surface flow eastward from the Line Islands extends to the Galapagos Islands and onward toward the mainland (Richmond, 1990). Glynn (1985) estimated the period of uninterrupted growth of living *Pocillopora* in the Gulf of Panama at about 190 years, based on the death of the protective coral barriers as a result of warming during the El Niño event of 1982–83. In terms of geological time, if only one such El Niño-related dispersal event occurred every 200 years, this would result in 5,000 disruptive episodes per million years and have a significant influence on the composition of the biota, past and present, in the eastern Pacific (Richmond, 1990).

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APPENDIX

Geographic records of the 20 shallow-water Indo-Pacific prosobranch gastropods (other than Tonnacea) known from the West American Continental Borderland, from Mexico to Peru including the Near-shore Islands. None of these taxa is known from the Atlantic Ocean except *Quoyula madreporarum* reported from the Cape Verde Islands (Saunders, 1976:14).

Not cited in this list are unverified records of west American taxa that are poorly understood taxonomically, but may have populations in Indo-Pacific waters. These records include 1. *Phenacovolva ? brevirostris* (Schumacher) Isla Los Zurrones, Panama, 1 specimen, AMNH 198612, R. E. Hubert, 1979 (see Bertsch and Bibbey, 1982:430 [= ?*P. lenoreae* Cardin and Walls (1980:1), Isla Gobernadora, Panama, 32 specimens]. 2. *Bizetiella shaskyi* Radwin and D'Attilio (1972:347), known from the Gulf of California, Islas las Tres Marias, Jalisco, Mexico, and the Galapagos Islands, with a single specimen cited from Moorea, French Polynesia (Shasky, 1983b). This may be a west American species that has extended into the central Pacific. 3. *Tripterotyphis lowei* (Pilsbry), known from the Gulf of California to Panama (Keen, 1971), is recognized at the subspecies level from Australia, Norfolk Island, and the Solomon Islands by D'Attilio and Hertz (1984), who also report the nominate form from the Galapagos Islands. 3. *Amphithalamus inclusus* Carpenter, known from California to the Gulf of California (Keen, 1971) [= ?*A. trosti* Strong and Hertlein, type locality: Panama], was reported on the basis of 2 specimens from Midway Island by Shasky (1987:49).

I. MEXICO

Conus tessulatus Born. "west Mexican coast, especially on the offshore islands." (Keen, 1971:667). Los Frailes, Baja California Sur, living specimen dredged in 23 m, IX-1975, ex-S. Bennett coll., AMNH 232136; Small island off La Paz, 1 fresh specimen, 1950, ex-A. Barlow coll., AMNH 239982.

Littorina pintado (Wood). "Southern Baja California to Panama" (Keen, 1971:366, as *L. pullata* Carpenter; see Reid, 1989:96).

Microdaphne trichodes (Dall). "Puertecitos, head of the Gulf of California, to Gorgona Island, Colombia." (Keen, 1971:762, fig. 1848). Cedros Island, west coast of Baja California, to Puertecitos, Baja California Norte in the Gulf of California, southward to Punta Ancon, Santa Elena Peninsula, Peru, intertidal to 146 meters (83 lots in the LACMNH, *teste* J. H. McLean).

Quoyula madreporarum (Sowerby). "The southern part of the Gulf of California and Tres Marias Islands, Mexico, to Panama." (Keen, 1971:546). Bahía Balandra, Baja California Sur, 1 dead specimen, IX-1960, Ariel Exped., ex-H. DuShane coll., AMNH 242842; Cabo Pulmo, 8 living specimens on coral (*Pocillopora*), IV-1966, H. DuShane leg., AMNH 242843; Pulmo Reef, in 2–3 meters, 1965, D. R. Shasky, leg. and coll. Bahía Jaltemba, Nayarit, 7 living specimens, ex-C. Skoglund coll., AMNH 200776. Isla María Madre, Nayarit, in 1–5 meters, XII-1961, D. R. Shasky, leg. and coll. Barra de Navidad, Jalisco, in 2–3 meters, VII-1965, D. R. Shasky leg. and coll.

Rhizochilus aff. *R. antipathus* Steenstrup, off Sonoran coast, on antipatharian coral, in 20–60 meters (Poorman, 1981:165).

Terebra affinis Gray. "Gulf of California, Mexico" (Bratcher and Cernohorsky, 1986:80). Bahía San Luis Gonzaga, Baja California Norte, 1 living specimen (Bratcher, 1970:6; Keen, 1971:672, fig. 1519).

Titiscania limacina (Bergh). west of Puerto Peñasco, Sonora, sandy beach, C. Skoglund coll. Puerto Lobos, Sonora (Marcus and Marcus, 1967b:145).

II. GUATEMALA

Conus ebraeus Linné. San Jose, Escuintla Department, 1 specimen, tidal flats, 1947, G. Farris leg. (Emerson, 1968:33; AMNH 114575, ex-J. Zager coll.).

III. COSTA RICA

Conus chaldeus (Röding). Isla de Caño, Puntarenas Province, 1 specimen, IV-1977 (Anders, 1978:17, fig. 1); 1 living specimen, III-18, 1972, intertidal, J. H. McLean leg., LACMNH loc. 72-68. Playas del Coco, Guanacaste Province, 1 living specimen, IV-24, 1972, intertidal, R. Koch leg. & coll.

Conus ebraeus Linné. Playas de Jaco, 1 living specimen, IV-25, 1975 (Sutton, 1975:79; AMNH 187658, ex-B. Sutton coll.). Guanacaste Province, 1 living specimen, T. Dranga leg. (Hertlein and Emerson, 1953:351). Playas del Coco, Guanacaste Province, 2 living specimens, III-18, 1965 (Houbrick, 1968:292, MCZ 256447, ex-Houbrick coll., *fide* Emerson, 1968:33). Isla de Caño, Puntarenas Province, 1 fragment, intertidal, III-18, 1972, J. H. McLean leg., LACMNH loc. 72-68. 1 hermit crab specimen, on rock pinnacle, near Isla de Caño, Puntarenas Province, 21 to 41 meters, III-18, 1972, J. H. McLean leg., LACMNH loc. 72-65. Isla de Caño, Puntarenas Province, 9 specimens, IV-8-1977 (Anders, 1978:17, fig. 2).

Microdaphne trichodes (Dall). 10 localities, from Bahía Salinas to Isla de Caño, in 2.4 to 73 meters, LACMNH coll., 1935 to 1972, *teste* J. McLean. Bahía Bullena, Golfo de Nicoya, in 14 meters, III-1984, D. R. Shasky leg. and coll.

Mitra mitra (Linné). Isla de Caño, Puntarenas Province, 1 living specimen, on sand near coral patches, 7 to 12 meters, III-1972, McLean and Wheeler leg., LACMNH loc. 72-63 (*teste* J. H. McLean; Sphon, 1976:63). Playas del Coco, Guanacaste Province, Golfo de Papagayo, 1 living specimen, intertidal on sand, 1968, Houbrick leg.

IV. PANAMA

Conus chaldeus (Röding). Isla Gobernadora, Golfo de Montijo, 2 living specimens on rocks, extreme low tide, V-1979, ex-R. E. Hubert, AMNH 203815 (Emerson, 1983:122, figs. 7, 8). Isla Canal de Afuera, Golfo de Veraguas, 1 living specimen, on dead coral, snorkling, V-79, 1982, ex-J. Ernest, AMNH 206683.

Conus ebraeus Linné. Isla Gobernadora, Golfo de Montijo, 1 fresh specimen, low tide under rock, VII-1979, J. Ernest leg., AMNH 242839, ex-H. DuShane coll.

Conus tessulatus Born. Isla Pedro Gonzales, Golfo de Panama, 1 fresh specimen, II-1981, ex-R. E. Hubert; AMNH 203266 (Emerson, 1983:122, figs. 1, 2). Isla Membrillos, Archipielago de las Perlas, Golfo de Panamá, 1 fresh specimen, III-1975, ex-R. E. Hubert, AMNH 183218 (Emerson, 1983:122, figs. 3, 4). Isla Boyarena, Archipielago de las Perlas, 1 living specimen, 1982, ex-J. Ernest, AMNH 206080 (Emerson, 1983:122, figs. 5, 6); Bahía Anton Viejo, Isla Los Pajaros, 2 living specimens, IV-6, 1981, H. DuShane leg., AMNH 242837, specimens, crawling at night on sand exposed at low tide (several other specimens collected by field party). Isla Canal de Afuera, Golfo de Veraguas, 1 living juvenile, dredged 15–24 m, 1983, ex-J. Ernest, AMNH 242133.

Cypraea teres Gmelin [= ?*alisonae* Burgess]. Islas Secas, Golfo de Chiriqui, 1 specimen, II-4, 1935 (Bakus, 1968:94; Emerson and Old, 1968:99, pl. 12, figs. 1–3). Bahía Honda, Golfo de Chiriqui, 1 specimen II-21, 1934 (Bakus, 1968:94). Isla Pedro Gonzales, Archipielago de las Perlas, 2 lots, ex-R. E. Hubert, II-75, 1 living specimen under a rock near sand, AMNH 183217; II-1981, 2 living specimens, shallow water in coral, AMNH 203809 (Emerson, 1983:122, figs. 9, 10); 1 living specimen, low tide, exposed in coral, 1984, ex-H. DuShane coll., AMNH 242836. Isla Taboga, Bahía de Panama, VI-1979, 1 living specimen in coral, ex-R. E. Hubert, AMNH 203812. Isla Los Zurrones, Golfo de Montijo, 2 living specimens, shallow water, in coral, VIII-1979, ex-R. E. Hubert, AMNH 208750. Isla Gobernadora, Golfo de Montijo, 2 living specimens under rocks around coral, IV-1980, ex-R. E. Hubert, AMNH 203810; 1 living specimen in 2–3 m, II-1985, J. Ernest leg., AMNH 219982. 1 living specimen coral heads, 1984, J. E. Ernest leg., ex-H. DuShane coll., AMNH 242835. Isla Canal de Afuera, Golfo de Veraguas. 3 specimens, under coral in 1.8 to 3.6 meters, 1982, J. Ernest leg., AMNH 206081, and elsewhere in the Golfo de Panamá and off Isla Cebaco (*teste* J. Ernest, *in litt.* 1983).

Cypraea talpa Linné. Isla Canal de Afuera, Golfo de Veraguas, 1 living specimen, on dead coral, 1981, ex-J. Ernest, AMNH 206760 (Emerson, 1983:122, figs. 13, 14); 1 fresh specimen, under coral, I-1984, ex-H. DuShane coll., AMNH 242832; Isla Gobernadora, Golfo de Montijo, 1 living specimen from coral head, V-1984, J. Ernest leg., AMNH 242831, ex-H. DuShane coll.

Kermia felina (Hinds). Isla Taboga, in 5 meters (Shasky, 1983b:28 as *K. maculosa* Pease); see Richard (1985: 432).

Microdaphne trichodes (Dall). 9 localities from off Isla Secas to off Bahía Honda, in 9 to 91 meters, LACMNH coll., 1934 to 1965, *teste* J. H. McLean.

Mitra mitra (Linné). Los Zurrones, off Isla Cebaco, 1 living specimen, on sandy bottom, 1979, J. Ernest leg., AMNH 198611 (Emerson, 1983:122, figs. 11, 12). Isla Canal de Afuera, Golfo de Veraquas, 1 living specimen (129 mm by 36 mm) on white sand, near coral, X-1981, J. Ernest leg., AMNH 206082. Isla Contadora, Golfo de Panamá, 2 living specimens, coral-sand VIII-1982, P. Piantino leg. (Anonymous, 1983:15). Isla Mogo Mogo, Archipielago de las Perlas, 1 living specimen (120 mm by 34.5 mm) on sand in 1.8 to 3 meters, 1982, snorkling, J. Ernest leg., AMNH 206083; 1 dead specimen, on beach, IV-1981, H. DuShane leg., AMNH 242841.

Quoyula madreporarum (Sowerby). "Panama" (Keen, 1971:546). Isla de Boyarena, Archipielago de las Perlas, intertidally, III-1977, D. R. Shasky, leg. and coll.

Terebra laevigata Gray. "Panama Bay" (Keen, 1971: 680). Based on type specimen of *T. stylus* Dall from "Panama", but west American record questioned by Bratcher and Cernohorsky (1986:54).

Terebra maculata (Linné). Isla Gobernadora, 1 specimen dredged, 1987, J. Ernest leg., T. Bratcher coll.

Titiscania limacina (Bergh). "Pacific Coast of Panama" (Marcus and Marcus, 1967a:124).

V. COLOMBIA

Conus chaldeus Röding. Isla de Gorgona, 1 beach shell. ". . . gathered by the prisoners for shellcraft" (von Cosel, 1977:423).

Cypraea caputserpentis (Linné) Isla de Gorgona, 1 dead specimen, XII-1988 (J. R. Cantera K., 1991).

Cypraea teres Gmelin [= ?*alisonae* Burgess]. Isla de Gorgona, "present" (von Cosel, 1977:424; 3 specimens III-30, 1980, 2 specimens XI-4, 1984, near coral (Cantera, 1986:23). Isla del Malpelo, III-1972 (Birkeland *et al.*, 1975:67).

Microdaphne trichodes (Dall). Isla de Gorgona (Keen, 1971:762; 3 localities, AHF-LACMNH, I-1935.

Mitra mitra (Linné). Isla de Gorgona, 1 living specimen, II-1972 (von Cosel, 1977:422, figs. 5a, 5b).

Philippia radiata (Röding). Isla de Gorgona, 1 dead-collected specimen, IX-1979 (Robertson, 1979:191, figs. 1-3; ANSP 348879).

Quoyula madreporarum (Sowerby). Isla de Gorgona, "present" (von Cosel, 1977:424).

Reliquiaecava robillardi (Lienard). Isla de Gorgona, 1 specimen on coral (*Pavona*), LACMNH loc. 35-51 (AHF 412-35), I-1935, *fide* Massin (1987:81). "Gorgona Island", as *Coralliobia cumingii* (H. and A. Adams), based on above specimen (Keen, 1971:546, fig. 1070). Earlier names for this taxon may be *Campulotus cumingii* H. and A. Adams, 1864, and *Concholepas* (*Coralliobia*) *fimbriata* A. Adams, which has priority and dates from 1854.

VI. ECUADOR

Heliacus trochoides (Deshayes). Ayangue, 30 km northeast of Punta Santa Elena, 1 living specimen, II-27, 1971 (Robertson, 1976:13; figs. 1–3; ANSP A6572).

Microdaphne trichodes (Dall). Punta Ancon, Santa Elena Peninsula, intertidal, J. H. McLean, LACMNH loc. 70-11, III-1970. Manabi Province (Isla de la Plata; Isla de Salango; and Punta Mala); 1978–1980 (Shasky 1984b:30).

Pseudocypraea adamsonii (Sowerby). Isla de la Plata, VI-21, 1979, 1 living specimen, under a rock in 17 meters, D. Shasky leg. and coll. (Emerson, 1982:13; Shasky, 1983b: 28).

Quoyula madreporarum (Sowerby). Isla de la Plata, in 1–3 meters, on coral, V-1979, D. R. Shasky, leg. and coll.

Rhizochilus aff. *R. antipathus* Steenstrup. Isla de la Plata, Manabi Province, on antipatharian coral, in 30 meters, V-1979, D. R. Shasky, leg. and coll.

VII. PERU

Microdaphne trichodes (Dall). Isla Lobos de Afuera, 1.5 to 9 meters, J. H. McLean *et al.*, LACMNH loc. 74-6, XII-1976.

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CONTENTS

Lamellitrochus, a New Genus of Solariellinae (Gastropoda: Trochidae), with Descriptions of Six New Species from the Western Atlantic Ocean

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ABSTRACT

Lamellitrochus new genus is erected for eight western Atlantic species of Solariellinae. The genus is distinguished by having conicoturbinate shells with angular whorls; strong, usually lamelliform axial riblets that usually become obscure or are absent on last whorls; strong subsutural angulation bearing rounded, conical, or lamellate tubercles; strong, smooth to tuberculate peripheral carina; strong, circumbasal carina; intritacalx-like outer shell layer; usually micropustules on early whorls; and radula lacking a lateromarginal plate. Included in *Lamellitrochus* are the type species, *Margarita lamellosa* Verrill & Smith, 1880; *Solariella pourtalesi* Clench & Aguayo, 1939; and six new species: *L. inceratus*, *L. carinatus*, *L. suavis*, *L. filosus*, *L. fenestratus*, and *L. bicoronatus*.

Key words: Gastropoda; Trochidae; Solariellinae; *Lamellitrochus*; systematics, new species.

INTRODUCTION

The Solariellinae Powell, 1951, was erected for trochid genera having short radulae with reduced numbers of marginal teeth (usually 10 or fewer pairs per row). More recent work has shown that features of the external anatomy (a broad, fringed snout; propodium with lateral horns; reduced epipodium) are also characteristic of the subfamily (Fretter & Graham, 1977; Herbert, 1987; Hickman & McLean, 1990). Although the subfamily is well defined, Herbert (1987) has shown that animals with similar shell characters can have different radulae, and that assignment of these species to genera based solely on shell characters is sometimes inadvisable. Indeed, this is reflected in the low number of extant genera (10) recognized at present (Hickman and McLean, 1990). Despite the obvious convergence of shell characters of many species, some species defy ready assignment to existing genera. Eight such species occur in the western Atlantic Ocean, and the genus *Lamellitrochus* is proposed to include those taxa.

Institutional abbreviations used in this paper are as follows: DMNH (Delaware Museum of Natural History, Wilmington, Delaware); FSBC I (Florida Marine Research Institute, St. Petersburg, Florida); MNHN (Museum National d'Histoire Naturelle, Paris); MORG (Museu Oceanográfico da Fundacão Universidade do Rio Grande, Rio Grande, RS, Brazil); UF (Florida Museum of Natural History, University of Florida, Gainesville, Florida); UMML (Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, Florida); and USNM (National Museum of Natural History, Smithsonian Institution, Washington, DC).

SYSTEMATICS

Family Trochidae Rafinesque, 1815
Subfamily Solariellinae Powell, 1951
Genus *Lamellitrochus* Quinn new genus

Margarita: Verrill & Smith *in* Verrill, 1880:392 (*partim*); Verrill, 1880:378 (*in* 1880–1881); 1881:406; 1882:530, 531 (*partim*); 1885:527; Dall, 1881:40 (*partim*).

Margarita (*Solariella*)*:* Dall, 1889a:378–382 (*partim*); 1889b:164 (*partim*); 1903:164 (*partim*); Pilsbry, 1890:307–330 (*partim*).

Solariella: Dall, 1927:128–130 (*partim*); Johnson, 1934:71 (*partim*); Clench & Aguayo, 1939:190, 191; Rice & Kornicker, 1965:117 (*partim*); Porter, 1974:21 (*partim*); Abbott, 1974:41 (*partim*); Treece, 1980:559

Solariella (*Machaeroplax*)*:* Abbott, 1974:40 (*partim*).

Solariella (*Solariella*)*:* Quinn, 1979:37–42 (*partim*).

Diagnosis: Shell small (usually <10 mm); subsutural angulation tuberculate; peripheral carina prominent, smooth to tuberculate; umbilicus broad; sharp, usually lamellate axial riblets on early teleoconch whorls; microsculpture usually of irregular pustules; intritacalx-like outer shell layer; and oblique, circular to ovate aperture.

Description: Shell small, largest attaining height of about 10 mm but usually less than 5 mm, conicoturbinate, umbilicate, nacreous under thin intritacalx and white porcelaneous layers. Whorls tubular, shouldered, peripherally carinate, with prominent axial and spiral sculpture. Axial sculpture of strong, sharp lamellate riblets on first 2–4 teleoconch whorls; later whorls (when present) with discontinuous remnants of riblets, most prominent on spiral carinae, and weak to strong axial rugae; generally axially oriented micropustules on adapical surface of teleoconch whorls. Spiral sculpture above suture of strong cords or angulations, often tuberculate, and usually fine threads between angulations; peripheral carina strongest, tuberculate, undulate, or smooth. Base weakly convex to flat, bounded by strong, smooth carina, and with weak to strong, smooth or finely beaded spiral cords. Umbilicus broadly open, funnel-shaped, bounded by one (rarely two) strong, tuberculate spiral cord; walls usually with spiral cords and axial rugae. Aperture oblique, circular to ovate.

External anatomy typically solarielline, with broad snout having numerous, finger-like projections at tip; long, micropapillate cephalic tentacles; lateral extensions of the propodium; cephalic lappets lacking. Eyestalks small, slender, with terminal eye; right postoptic tentacle lacking. Epipodium reduced; left neck lobe represented by pair of short tentacles, anterior one near base of left cephalic tentacle, posterior one near base of anterior epipodial tentacle; right neck lobe simple or with small triangular extension, and may be partially fused to basal half of right eyestalk. Epipodium with 3 pairs of micropapillate tentacles; anterior pair long, about midway between cephalic tentacle and second pair; second pair long or short, near anterior edge of opercular lobe; posterior pair long, near posterior edge of opercular lobe; small, thin, triangular flap may be present between anterior 2 pairs.

Radula short, broad, with about 20–30 transverse rows of teeth; formula 6–8.4.1.4.6–8. Rachidian tooth cusp triangular, denticulate, excavated dorsally to accommodate next anterior rachidian tooth cusp; base triangular, articulating with inner lateral tooth base. Lateral teeth 4 pairs, similar to those of *Ilanga* (Herbert, 1987). Marginal teeth 6–8 pairs, denticulate on outer edge near tip. Lateromarginal plate lacking.

Type species (here designated): *Margarita lamellosa* Verrill & Smith, 1880.

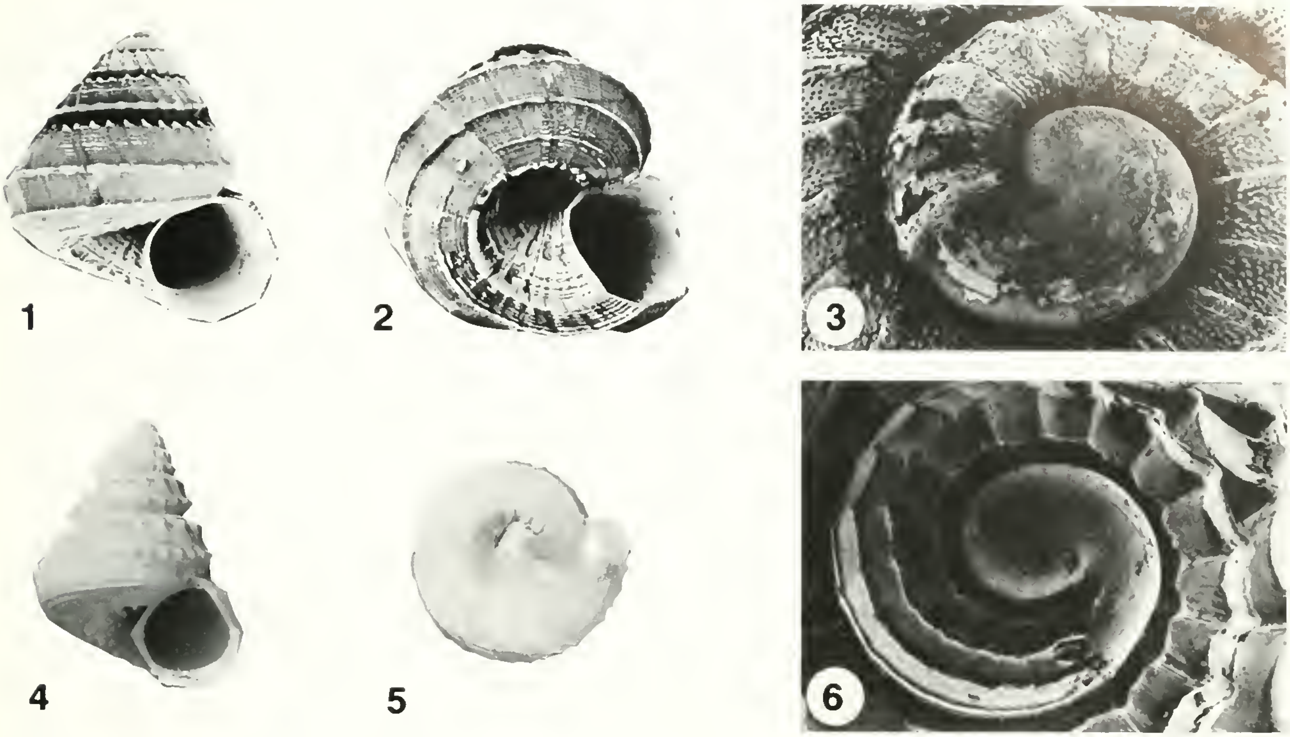
Etymology: From the Latin *lamella*, a little blade, and *trochus*, a child's hoop; gender masculine.

Included species: *Margarita lamellosa* Verrill & Smith, 1880; *Solariella pourtalesi* Clench & Aguayo, 1939; *Lamellitrochus carinatus* Quinn new species; *L. inceratus* Quinn new species; *L. suavis* Quinn new species; *L. filosus* Quinn new species; *L. fenestratus* Quinn new species; and *L. bicoronatus* Quinn new species.

Remarks: The shells of species assigned to *Lamellitrochus* are distinguished from all other solarielline genera by their strongly angular whorl profiles and distinctive macro- and microsculpture. The angular whorl profile is caused by the development of a strong subsutural angulation set with rounded, conical, or lamellate tubercles; a strong peripheral carina that is smooth, undulate, or tuberculate; a strong basal carina that is usually smooth, but may be finely rugose; and a strong, tuberculate circumumbilical cord. The whorl surfaces between these angulations are almost flat, and usually have a varying number of fine spiral lirae. Several species currently assigned to *Solariella* Wood, 1842, also have shells with angulate whorl profiles: *S. triplostephanus* Dall, 1910; *S. patriae* Carcelles, 1953; and some forms of *S. cinctus* (Philippi, 1836) and *S. intermissa* Thiele, 1925. I have not examined specimens of the first two species, and illustrations and descriptions (Carcelles, 1953; McLean, 1971) are not detailed enough for me to determine the species' generic assignment; however, I doubt that these two species are congeneric with the *Lamellitrochus* species. Scanning electron micrographs of shells of *S. cinctus* (Fretter & Graham, 1977: fig. 32) and *S. intermissa* (Herbert, 1987: figs. 111, 112) reveal that neither species has micropustules on the early whorls.

An extremely thin, calcified shell layer, which may be chalky or polished, overlies the outer porcelaneous shell layer of the last one or two teleoconch whorls. This thin outer layer may be the calcified periostracum, or intritacalx, described by D'Attilio and Radwin (1971). Neither an intritacalx nor a periostracum have been reported for species of other solarielline genera, but they may have been overlooked; the systematic significance of the presence or absence of intritacalx in the Solariellinae is unknown at present. The surface of the first 2–3 whorls usually has a covering of micropustules, although the pustules may be restricted to the sutural area. In addition to those for *Solariella cinctus* and *S. intermissa*, SEM micrographs of the apical whorls of shells of *Ilanga* Herbert, 1987, *Spectamen* Iredale, 1924, *Minolops* Iredale, 1929, and *Zeminolia* Finlay, 1927 (Herbert, 1987), and *Minolia* Adams, 1860 (Hickman & McLean, 1990) have been published. Of the species illustrated, only the South African species *Spectamen adarticulatum* (Barnard, 1963) (see Herbert, 1987: fig. 124) has discernible micropustules. Conversely, *Lamellitrochus pourtalesi* seemingly lacks micropustules (figure 6). Micropustules also do not occur on shells of western Atlantic *Solariella*, *Microgaza* Dall, 1881, or *Suavotrochus* Dall, 1924 (personal observations), but are present in *Pagodatrochus* Herbert, 1989 (Herbert, 1989: fig. 4a,b).

Six of the eight species discussed in this paper have well-developed, usually lamellate axial riblets that appear on the first half-whorl, usually immediately following the terminal rim of the protoconch. Shells of a ninth species from Argentina (off Rio de la Plata, USNM 330860) also have this characteristic, but, because the two specimens are juveniles, this species is not described here. The illustrations of the first whorls of the genera cited above (Fretter & Graham, 1977; Herbert, 1987; Hickman & McLean, 1990) show that shells of other solarielline genera lack strong axial riblets on the first whorl, and that the riblets, present on later whorls are generally weaker, more rounded, and more closely spaced than those of *Lamellitrochus*.



Figures 1–6. **1–3.** *Lamellitrochus lamellosus* (Verrill & Smith, 1880) from *Eolis* Station 351, SE of Fowey Light, Florida, 165 m (USNM 438440). **1.** Apertural view, 11.6 ×. 2. Basal view (oblique), 12.7 ×. 3. Protoconch, 118 ×. **4–6.** *Lamellitrochus pourtalesi* (Clench & Aguayo, 1939). **4, 5.** Shell from *John Elliott Pillsbury* Station P-747, 11°46′N, 67°05.7′W, 1,175–1,098 m (UMML 30.6832). **4.** Apertural view, shell height 9.1 mm. **5.** Basal view, shell diameter 7.6 mm **6.** Protoconch of shell from *Alaminos* Station 69A11-86, 21°41′N, 96°51′W, 969–1,079 m, FSBC I 40300, 53 ×.

The radula of *Lamellitrochus* lacks any trace of a lateromarginal plate (figures 28–36) and resembles *Ilanga* Herbert, 1987, "some North Atlantic taxa" (Herbert, 1987:287), and possibly *Zetela* Finlay, 1927 (Herbert, 1987) in lacking this structure. Herbert (1987) used the presence or absence of a lateromarginal plate to assign species with similar shell morphologies to different genera, but he did not speculate on the broader systematic implications of the character because of the lack of detailed knowledge of many genus-level groups.

The presence of an intritacalx is the only character that seems to be unique to this species group, but in combination with presence of strong axial riblets and distinct micropustules on the early whorls of most species; presence of strong, usually tuberculate, subsutural and peripheral carinae; and lack of a lateromarginal plate of the radula, it supports establishment of a new genus-group taxon. Until more detailed analyses of shell and radular characters of more solarielline species groups are made, I prefer to treat *Lamellitrochus* as a genus rather than a subgenus of *Solariella*.

Lamellitrochus pourtalesi is illustrated here for comparison with the other species, but a complete species account is found in Quinn (1979).

Key to species of *Lamellitrochus*:

1. Protoconch diameter greater than 350 μm 2
1. Protoconch diameter less than 350 μm 3
2. Protoconch diameter 350–375 μm; axial riblets present on first half-whorl . . *inceratus* new species
2. Protoconch diameter 525–550 μm; axial riblets absent on first half-whorl . . . . *pourtalesi* (Clench & Aguayo, 1939)
3. Tubercles on subsutural angulation lamellate 4
3. Tubercles on subsutural angulation conical or rounded 5
4. Axial riblets continuous between suture and periphery; shell wider than high; height less than 3 mm . . . . *carinatus* new species
4. Axial riblets not continuous from suture to periphery; shell higher than wide; height greater than 3 mm 5
5. Peripheral carina smooth to weakly undulate . . . . *lamellosus* (Verrill & Smith, 1880)
5. Peripheral carina with strong, conical tubercles . . . . *filosus* new species
6. Subsutural angulation and circumumbilical cord formed by double rows of rounded tubercles . . . . *bicoronatus* new species

6. Subsutural angulation and circumumbilical cord formed by single rows of conical tubercles 7
7. Axial riblets present on first half-whorl; peripheral carina tuberculate .... *suavis* new species
7. Axial riblets absent on first half-whorl; peripheral carina undulate .... *fenestratus* new species

Lamellitrochus lamellosus (Verrill & Smith, 1880)
(figures 1–3, 28–30)

Margarita lamellosa Verrill & Smith *in* Verrill, 1880:392, 397, 398.
Solariella (*Solariella*) *lamellosa:* Quinn, 1979:40, 42 (*partim*).

Description: Shell small, attaining 4.2 mm height, 3.55 mm width, conicoturbinate, peripherally carinate, broadly umbilicate, white, nacreous under thin outer porcelaneous layer. Protoconch 280–310 μm maximum diameter. Teleoconch whorls about 5, tubular, shouldered, carinate; first two whorls with strong, sharp, axial lamellae extending from suture to suture; axials becoming discontinuous or obsolete on subsequent whorls; micropustules rather strong, covering entire surface of first 1.5–2 whorls; subsutural angulation and peripheral carina appear on second whorl; subsutural angulation becoming strong, tuberculate, tubercles lamellate and closely set; peripheral carina becoming strong, tuberculate, but usually becoming smooth or irregularly undulate on last 1–2 whorls; as many as 13 weak spiral threads present between subsutural angulation and peripheral carina; as many as 12 weak spiral threads present between peripheral and basal carinae. Base flat, circumscribed by strong, smooth spiral carina; as many as 20 weak, smooth spiral cords present between basal carina and strong, tuberculate circumumbilical cord; umbilicus broadly open, 35–45% maximum shell diameter, funnel-shaped, walls with about 10 fine, weak spiral threads and weak axial rugae. Aperture oblique, circular, lips thin; peristome complete. Animal and radula as for genus.

Holotype: USNM 44738, height 3.0 mm, width 3.0 mm.

Type locality: Off Martha's Vineyard, Massachusetts, *Fish Hawk* Station 871, 40°02′54″N, 70°23′40″W, 210 m.

Other material examined: More than 100 lots in USNM, DMNH, FSBC I; see Quinn (in press) for listing.

Remarks: Shells of *Lamellitrochus lamellosus* are most similar to those of *L. filosus* in shape and in having lamellate tubercules on the subsutural angulation; however, the former species is absolutely and relatively larger (4.2 mm *vs.* 3.15 mm with about 5 whorls) but has a smaller protoconch (280–310 μm *vs.* 315–325 μm). The tubercles on the peripheral carina of shells of *L. filosus* are stronger, conical, and more widely spaced than those of *L. lamellosus*, and the spiral threads in the intercarinal spaces are weaker and the axial threads are stronger in *L. filosus* than in *L. lamellosus*. The shell of *L. suavis* is also very similar in shape and general sculpture, but the subsutural tubercles are rounded, the periphery has rather strong tubercles, the micropustules are not as prominent and are concentrated near the suture, and the intercarinal spiral sculpture is weaker than in *L. lamellosus*. *Lamellitrochus lamellosus* is distributed along the United States east coast from Massachusetts southward through the Florida Keys, and in the Gulf of Mexico off western Florida, Texas, and the Campeche Bank in depths of 50–250 m (usually in 100–200 m).

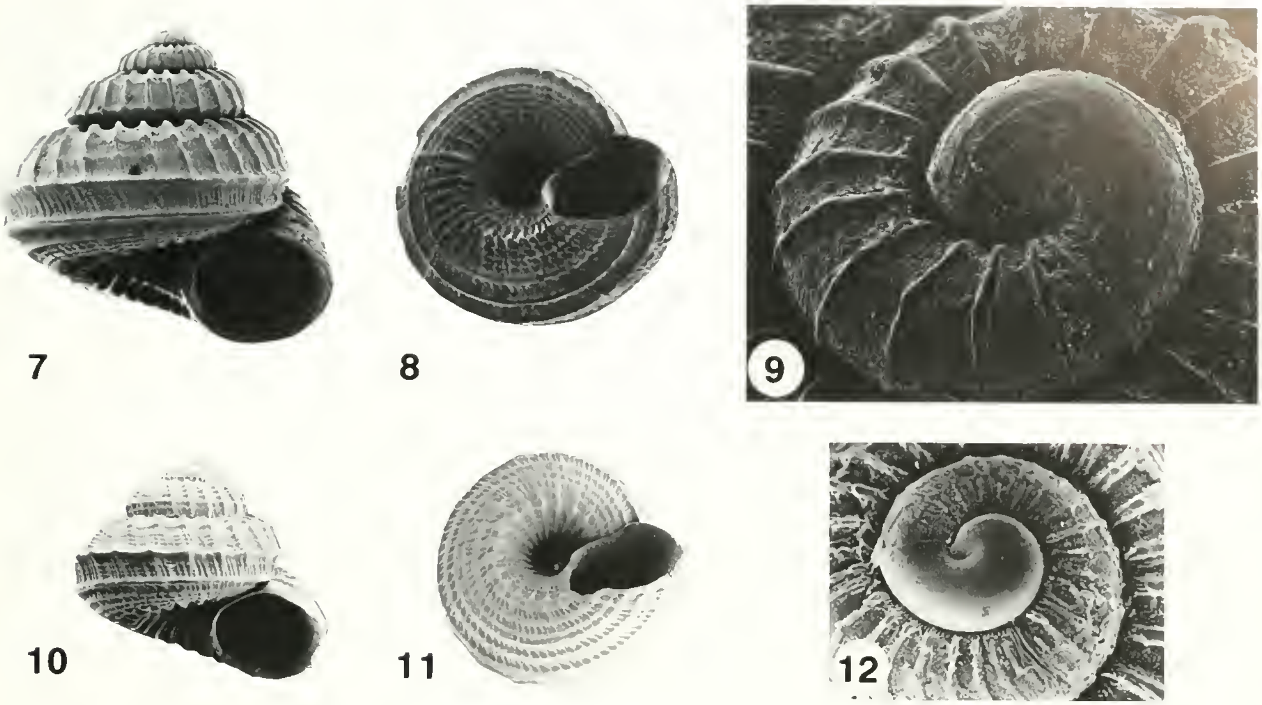
Lamellitrochus carinatus new species
(figures 7–12, 34, 35)

Description: Shell very small, attaining 2.75 mm height, 2.90 mm width, depressed conicoturbinate, peripherally carinate, broadly umbilicate, white, nacreous under thin outer porcelaneous layer. Protoconch 275–300 μm maximum diameter. Teleoconch whorls about 4, tubular, shouldered, carinate; first two whorls with strong, sharp, axial lamellae extending from suture to suture, but ending at or just above peripheral carina on subsequent whorls; micropustules rather strong, covering entire surface of first 2 whorls; subsutural angulation and peripheral carina appear on second whorl, peripheral carina becoming strong, smooth to weakly undulate; 1–7 weak spiral threads present between subsutural angulation and peripheral carina; 0–4 weak to strong spiral threads may be present between peripheral and basal carinae; whorl surface with microscopic pustules. Base weakly convex, circumscribed by strong, smooth spiral carina; 1–8 (usually 3–6) weak to strong, smooth to weakly undulate spiral cords present between basal carina and strong, tuberculate circumumbilical cord; umbilicus broadly open, 35–45% maximum shell diameter, funnel-shaped; walls with 1–7 weak spiral cords and strong axial rugae that radiate onto inner part of base, forming strong, radially elongate tubercles on circumumbilical cord. Aperture oblique, circular, lips thin, peristome complete.

Holotype: DMNH 179393, height 2.50 mm, width 2.70 mm.

Type locality: SW of Egmont Key, Florida, 366–421 m; J. Moore, collector.

Paratypes: DMNH 186768, 22 specimens; USNM 859408, 1 specimen; FSBC I 37633, 1 specimen; UF 161754, 1 specimen; all from same lot as holotype.—USNM 859431, 13 specimens; *Eolis* Station 360, off Fowey Light, Miami, Florida, 146 m.—USNM 438401, 3 specimens; *Eolis* Station 321, off Western Dry Rocks, Florida, 119 m.—31, DMNH 179392; 100 mi SW of Egmont Key, Florida; D. Steger, collector.—FSBC I 24259, 5 specimens; MAFLA Station 2746-41, 27°07′N, 84°13′W, 122 m; 23 August 1977; box corer.—USNM 500245, 37 specimens; State University of Iowa Barbados Station 29, off Lazaretto, 165–183 m.—USNM 500266, State University of Iowa Barbados Station 77, off Cable Station, 73–137 m.—MORG 26529, 1 specimen; *Marion-Dufresne* Cruise MD-55, Station DC-61, 20°29′S, 29°18′W, 63 m; May 1987; dredge.—MNHN uncatalogued, 1 specimen; *Marion-Dufresne* Cruise MD-55,



Figures 7–12. *Lamellitrochus carinatus* new species. **7–9.** Paratypes from SW of Egmont Key, Florida, 366–421 m (DMNH 186768). **7.** Apertural view, 15 ×. **8.** Basal view, 17 ×. **9.** Protoconch, 134 ×. **10–12.** Paratype from *Marion-Dufresne* Cruise MD-55, Station DC-61, 20°29′S, 29°18′W, 63 m (MORG 26529). **10.** Apertural view, 15.3 ×. **11.** Basal view, 14.9 ×. **12.** Protoconch, 82 ×.

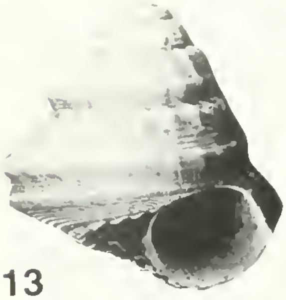
Station DC-59, 20°30′S, 29°19′W, 52–60 m; May 1987; dredge.

Other material examined: More than 50 lots in USNM and FSBC I; see Quinn (in press) for listing.

Remarks: Shells of *Lamellitrochus carinatus* are distinguished from those of all other *Lamellitrochus* species principally in being distinctly wider than high and usually having strong and continuous axial riblets on all whorls. This species also has the smallest shells, with heights of 2.50–2.75 mm and widths of 2.75–2.90 mm; adult shells of all other species exceed 3 mm in height. Variation in shell morphology occurs between northern and southern populations, but this is a reflection of the frequency of individual character states because the same variations also occur within individual populations. Shells of the northern (Florida) populations tend to have smooth to weakly undulate peripheral carinae; 2–4 strong, often unequally sized basal spiral cords; fewer, usually weaker spiral threads in the spaces between the subsutural angulation and peripheral carina (usually 1–3), and the peripheral and basal carinae (0–1); and narrower spaces between the axial riblets (about 0.15–0.20 mm apart on the third whorl). Shells from Barbados and Brazil usually have distinctly undulate peripheral carinae, the crests of the undulations often sharp; the basal spiral cords tend to be more numerous (usually 3–6, sometimes 7 or 8) and often equally sized and spaced; spiral threads in the intercarinal spaces are relatively numerous (usually 3–4 in each) and distinct; and the axial riblets are more widely spaced (about 0.25 mm apart on third whorl). This species is the most widely distributed of all *Lamellitrochus* species, ranging from off North Carolina southward to both sides of Florida; off Cuba, Puerto Rico, Antigua, and Barbados; and Trinidade Island off eastern Brazil, usually in depths of 100–200 m.

Lamellitrochus fenestratus new species
(figures 13–15)

Description: Shell small, attaining 3.35 mm height, 2.95 mm width, conicoturbinate, peripherally carinate, broadly umbilicate, white, nacreous under thin outer porcelaneous layer. Protoconch 275–300 μm maximum diameter. Teleoconch whorls 4.6, tubular, shouldered, carinate; first 0.5 whorl with 4 spiral cords, increasing to 6 on second whorl; whorls 0.5–2 with initially weak, progressively stronger, rounded, axial riblets extending from suture to suture; axials becoming discontinuous or obsolete on subsequent whorls; micropustules weak, restricted to sutural area of first 2 whorls; subsutural angulation and peripheral carina appear on third whorl, peripheral carina becoming strong, undulate; 5–7 spiral threads present between subsutural angulation and peripheral carina; 2–5 weak spiral threads and distinct axial rugae present between peripheral and basal carinae. Base flat, circumscribed by strong, smooth spiral carina; 6–9 weak, smooth spiral cords present between basal carina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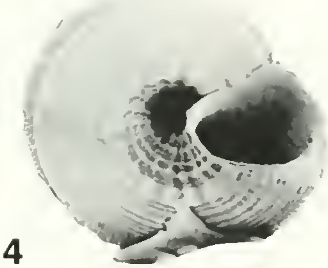
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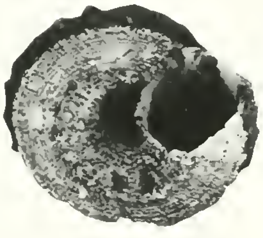
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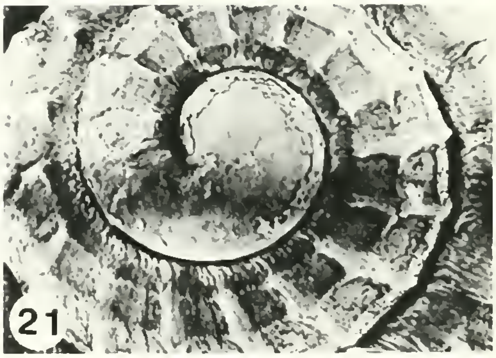
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Figures 13–21. **13–15.** *Lamellitrochus fenestratus* new species, paratype from off Barbados, 183 m (USNM 859429). **13.** Apertural view, 14 ×. **14.** Basal view, 14 ×. **15.** Protoconch, 84 ×. **16–18.** *Lamellitrochus filosus* new species, holotype from off English Harbor, Antigua (USNM 500230). **16.** Apertural view, 14.3 ×. **17.** Basal view, 14.2 ×. **18.** Protoconch, 91 ×. **19–21.** *Lamellitrochus suavis* new species, holotype from off Barbados (USNM 500224). **19.** Apertural view, 13.7 ×. **20.** Basal view, 13.1 ×. **21.** Protoconch, 92 ×.

and strong, tuberculate circumumbilical cord; umbilicus broadly open, 30–35% maximum shell diameter, funnel-shaped, walls with about 4 spiral cords and strong axial rugae. Aperture oblique, circular, lips thin; peristome complete.

Holotype: USNM 859428, height 3.15 mm, width 3.00 mm.

Type locality: Off Barbados, *Blake* Station (data unrecorded), 183 m.

Paratypes: USNM 859429, 4 specimens; from same lot as holotype.—USNM 500202, 1 specimen; State University of Iowa Barbados Station 62, off Pelican Island, 229 m.—USNM 859430, 1 specimen; State University of Iowa Barbados Station (data unrecorded), "deep".

Remarks: Shells of *L. fenestratus* are most similar to those of *L. bicoronatus* but differ in having only a single row of conical tubercles forming the subsutural angulation rather than a double row of rounded tubercles, in having a stronger peripheral carina with stronger tubercles, and in having a single rather than double circumumbilical cord. Shells of *L. fenestratus* are also similar to those of *L. filosus* and *L. suavis* in size, protoconch width, and general shape, but differ from both in lacking axial riblets on the first half-whorl; in having conical tubercles in the subsutural angulation as in *L. filosus*, but a more undulate peripheral carina rather than that of *L. suavis*; and the spiral threads between the subsutural and peripheral carinae are stronger in *L. fenestratus* than in either *L. filosus* or *L. suavis*.

Lamellitrochus filosus new species
(figures 16–18)

Description: Shell small, attaining 3.15 mm height, 2.85 mm width, conicoturbinate, peripherally carinate, broadly umbilicate, white, nacreous under thin outer porcelaneous layer. Protoconch 315–325 μm maximum diameter. Teleoconch whorls about 5, tubular, shouldered, carinate; first two whorls with strong, sharp, lamellate axial riblets extending from suture to suture; axials becoming discontinuous or obsolete on subsequent whorls; micropustules weak, restricted to sutural area on first 2 whorls; subsutural angulation and peripheral carina appear on second whorl; subsutural angulation becoming strong, tuberculate, tubercles lamellate; peripheral carina becoming strong, tuberculate; 13–15 very weak spiral threads present between subsutural angulation and peripheral carina; as many as 11 very weak spiral threads present between peripheral and basal carinae; spiral threads intersecting equally sized axial threads forming file-like surface sculpture. Base flat, circumscribed by strong, smooth spiral carina; as many as 20 weak, smooth spiral cords present between basal carina and strong, tuberculate circumumbilical cord; umbilicus broadly open, 40–45% maximum shell diameter, funnel-shaped, walls with 6–8 or more very weak spiral cords and weak, lamellate axial rugae. Aperture oblique, circular, lips thin; peristome complete.

Holotype: USNM 500230, height 2.75 mm, width 2.50 mm.

Type locality: State University of Iowa Antigua Station 116, off English Harbor, "deep".

Paratypes: USNM 859425, 4 specimens; from same lot as holotype.

Remarks: Shells of *L. filosus* are most similar to those of *L. lamellosus*, particularly in having lamellate tubercles on the subsutural angulation, but differ in being smaller (3.15 mm *vs.* 4.20 mm, respectively, at whorl 4.9), in having strong, conical tubercles on the peripheral carina, and in having much weaker spiral threads between the subsutural carination and peripheral carina. Shells of *L. filosus* are also similar to the holotype of *L. suavis*, but have lamellate rather than conical tubercles on the subsutural angulation, and a fine, file-like sculpture on the surface of the last whorl.

Lamellitrochus suavis new species
(figures 19–21)

Description: Shell small, attaining 3.35 mm height, 2.90 mm width, conicoturbinate, peripherally carinate, broadly umbilicate, white, nacreous under thin outer porcelaneous layer. Protoconch 325 μm maximum diameter. Teleoconch whorls 4.6, tubular, shouldered, carinate; first two whorls with strong, sharp, lamellate, axial riblets extending from suture to suture; axials becoming obsolete on subsequent whorls; micropustules weak, scattered over entire surface of first 2.5 whorls; subsutural angulation and peripheral carina appear on second whorl; subsutural angulation becoming strong, tuberculate, tubercles bluntly conical; peripheral carina becoming strong, tuberculate; 5 weak spiral threads present between subsutural angulation and peripheral carina; 3 or 4 extremely weak spiral threads present between peripheral and basal carinae on last whorl. Base flat, circumscribed by strong, smooth spiral carina; 10 weak, smooth spiral cords present between basal carina and strong, tuberculate circumumbilical cord; umbilicus broadly open, 35% maximum shell diameter, funnel-shaped, walls with weak axial rugae. Aperture oblique, circular, lips thin; peristome complete.

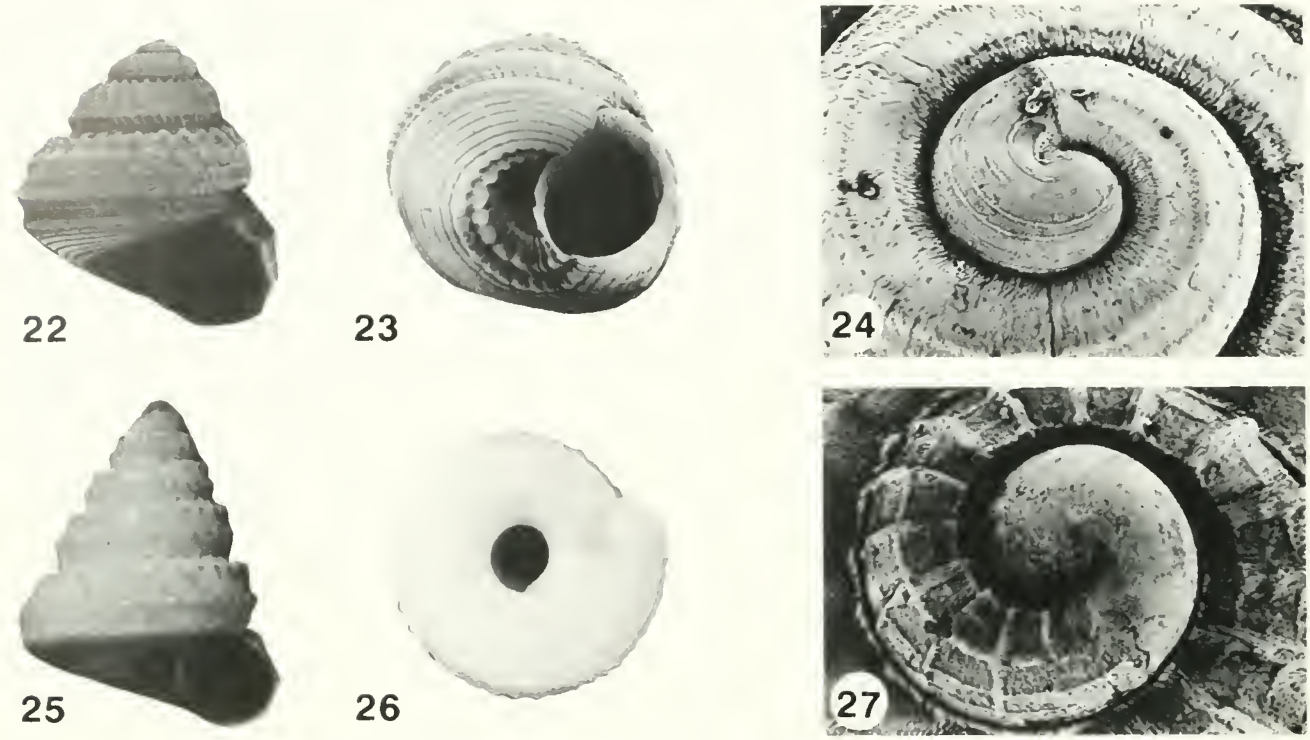
Holotype: USNM 500224, height 3.35 mm, width 2.90 mm.

Type locality: State University of Iowa Barbados Station (data unrecorded), "deep".

Remarks: The shell of *L. suavis* resembles a miniature *L. inceratus* in shell shape and sculpture, but is smaller and has a smaller protoconch (325 μm *vs.* 350–375 μm, respectively). Shells of *L. filosus* are similar to that of *L. suavis* in size, protoconch width, and tuberculate peripheral carina, but differ in having lamellate rather than conical tubercles on the subsutural angulation, and in having fine, crowded axial threads that interact with equally fine spiral threads to produce a fine, file-like sculpture on the whorl surface.

Lamellitrochus bicoronatus new species
(figures 22–24)

Description: Shell small, attaining 3.55 mm height, 3.20 mm width, conicoturbinate, peripherally carinate, broadly umbilicate, white, nacreous under thin outer porcelaneous layer. Protoconch 290–300 μm maximum diameter. Teleoconch whorls 4.3, tubular, shouldered, carinate; first whorl with 5 strong spiral cords with additional threads appearing on second whorl and increasing in number on subsequent whorls; 3 cords, 1 just below suture, 1 above midwhorl, and 1 below midwhorl strengthening on second whorl, forming tuberculate subsutural and undulate shoulder angulations, and weakly undulate peripheral carina, respectively; low, rounded axial riblets appear at end of first whorl, becoming stronger and more lamellate on whorls 2–3, and becoming low, broad folds between suture and shoulder angulation on last whorl; micropustules weak, scattered over entire surface of first 2 whorls, but most concentrated near suture; last whorl with 3–4 spiral threads between subsutural and shoulder angulations, 5–7 spiral threads between shoulder angulation and peripheral carina, and 4–5 spiral threads and distinct axial rugae between pe-



Figures 22–27. 22–24. *Lamellitrochus bicoronatus* new species, paratype from off Barbados, 183 m (USNM 859436). **22.** Apertural view, 13.1 ×. **23.** Basal view, 14.3 ×. **24.** Protoconch, 119 ×. **25–27.** *Lamellitrochus inceratus* new species. **25, 26.** Paratype from *Gerda* Station G-967, 24°15′N, 82°26′W, 499–503 m (UMML 30.8062). **25.** Apertural view, shell height 8.3 mm. **26.** Basal view, shell diameter 7.0 mm. **27.** Protoconch of paratype from *Albatross* Station 2644, 25°40′N, 80°00′W, 353 m (USNM 859432), 81 ×.

ripheral and basal carinae. Base flat, circumscribed by strong, smooth spiral carina; 6–8 weak to strong, smooth spiral cords present between basal carina and 2 strong, tuberculate circumumbilical cords; umbilicus broadly open, about 40% maximum shell diameter, funnel-shaped, walls with 2–4 weak spiral cords and weak axial rugae. Aperture oblique, circular, lips thin; peristome complete.

Holotype: USNM 859435, height 3.55 mm, 3.20 mm.

Type locality: Off Barbados, *Blake* Station (data unrecorded), 183 m.

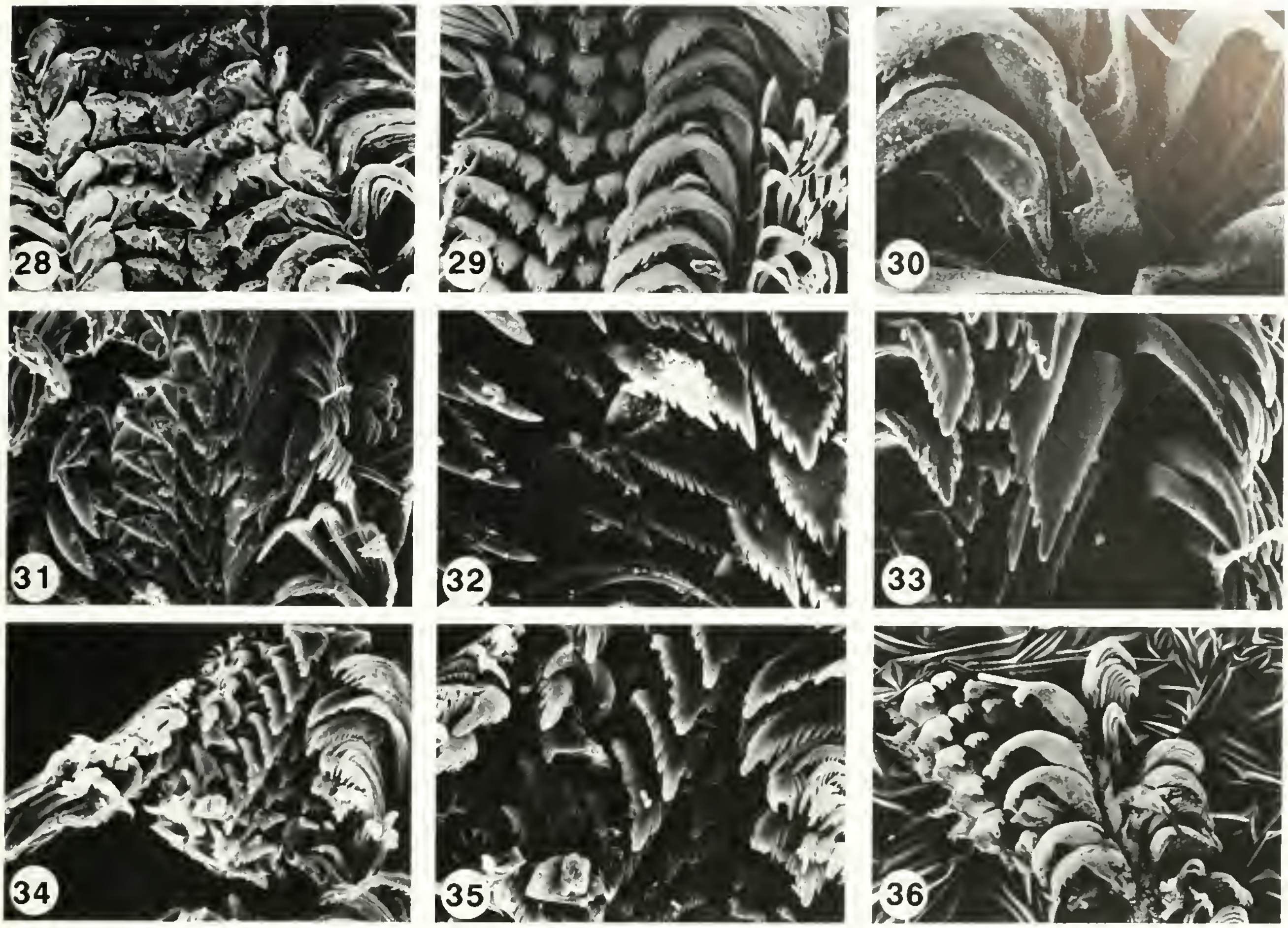
Paratypes: 4 specimens, USNM 859436; from same lot as holotype.

Remarks: Shells of *L. bicoronatus* differ from those of all other *Lamellitrochus* species in having most of the first teleoconch whorl devoid of axial riblets, and having a double spiral row of strong, rounded tubercles forming the subsutural angulation, and a similar double spiral row of tubercles circumscribing the umbilicus.

Lamellitrochus inceratus new species
(figures 25–27, 36)

Calliostoma tiara: Dall, 1889a:365 (*partim*).
Solariella amabilis: Dall, 1889a:378, 379 (*partim*)
Solariella (*Solariella*) *lamellosa:* Quinn, 1979:40–42, figs. 61, 62 (*partim*).

Description: Shell small, attaining 8.2 mm height, 7.3 mm width, conicoturbinate, peripherally carinate, broadly umbilicate, white, nacreous under thin outer porcelaneous layer. Protoconch 350–375 μm maximum diameter. Teleoconch whorls 6.0, tubular, shouldered, carinate; first whorl with strong, sharp, axial lamellae extending from suture to suture, rapidly becoming restricted to subsutural angulation and peripheral carina on subsequent whorls; micropustules rather weak, covering entire surface of first 2 whorls; first whorl with 2–4 weak spiral threads, two of which later interact with axial lamellae to form tuberculate subsutural angulation and peripheral carina; 0–5 very weak spiral threads present between subsutural angulation and peripheral carina; spiral threads absent between peripheral and basal carinae. Base flat, circumscribed by strong, smooth spiral carina; 5–11 weak, flat, smooth spiral cords present between basal carina and strong, tuberculate circumumbilical cord; center part of base often smooth; umbilicus broadly open, 45–50% maximum shell diameter, funnel-shaped, walls with 0–4 weak spiral cords and weak axial rugae. Aperture oblique, circular, lips thin; peristome complete.



Figures 28–36. Radulae of *Lamellitrochus* species. **28–30.** *Lamellitrochus lamellosus* (Verill & Smith, 1880) from specimen in Figure 1. **28.** Anterior segment, 339 ×. **29.** Middle segment, 339 ×. **30.** Anterolateral area, 690 ×. **31–33.** *Lamellitrochus pourtalesi* (Clench & Aguayo, 1939) from specimen in Figure 6. **31.** Middle segment, 240 ×. **32.** Rhachidian and laterals, 600 ×. **33.** Anterolateral area, 600 ×. **34, 35.** *Lamellitrochus carinatus* new species, from paratype from *Eolis* Station 360, off Fowey Rocks, Florida, 183 m (USNM 859431). **34.** Anterior segment, 600 ×., **35.** Same, 1,200 ×. **36.** *Lamellitrochus inceratus* new species, from paratype in Figure 27, right anterior fragment, 169 ×.

Holotype: USNM 94946, height 7.05 mm, width 6.90 mm.

Type locality: Off Cape Florida, Key Biscayne, Florida, *Albatross* Station 2644, 25°40′N, 80°00′W, 353 m.

Paratypes: USNM 108141, 1 specimen; USNM 754272, 1 specimen; *Albatross* Station 2668, 30°58′30″N, 79°38′30″W, 538 m.—UMML 30.8051, 2 specimens; *Gerda* Station G-300, 26°16′N, 79°30′W, 640 m.—UMML 30.8025, 1 specimen; *Gerda* Station G-4, 25°49′N, 79°59.5′W, 256 m.—UMML 30.8338, 2 specimens; *John Elliott Pillsbury* Station P-1309, 25°44.5′N, 79°50.0′W, 311 m.—UMML 30.7565, 1 specimen; *Gerda* Station G-830, 25°40′N, 79°59′W, 342 m.—USNM 859432, 6 specimens; USNM 330559, 4 specimens; same locality as holotype.—UMML 30.8099, 2 specimens; *Gerda* Station G-23, 25°32′N, 79°44′W, 768 m.—UMML 30.8042, 2 specimens; *Gerda* Station G-857, 25°22′N, 80°03′W, 194–186 m.—UMML 30.7538, 1 specimen; *Gerda* Station G-834, 25°15′N, 80°10′W, 86–79 m.—UMML 30.7914, 1 specimen; *Gerda* Station G-1035, 24°34.7′N, 80°58.6′W, 254–358 m.—UMML 30.7770, 8 specimens; *Gerda* Station G-970, 24°24′N, 82°08′W, 512 m.—UMML 30.8063, 1 specimen; *Gerda* Station G-969, 24°18′N, 82°33′W, 269–402 m.—UMML 30.7644, 1 specimen; *Gerda* Station G-968, 24°17′N, 82°34′W, 499–503 m.—UMML 30.8062, 6 specimens; *Gerda* Station G-967, 24°15′N, 82°26′W, 499–503 m.—UMML 30.8065, 1 specimen; *Gerda* Station G-1099, 24°12.5′N, 82°50′W, 622 m.—UMML 30.8058, 1 specimen; *Gerda* Station G-861, 24°08′N, 81°36′W, 514–558 m.—USNM 421840, 5 specimens; Waldo Schmitt Station 69, off Dry Tortugas, 455–655 m.—USNM 94947, 4 specimens; *Blake* Station 2, 23°14′N, 82°25′W, 1,472 m.—USNM 94948, 4 specimens; *Blake* Station 21, 23°02′N, 83°13′W, 525 m.—USNM 859433, 1 specimen; *Blake* Station (data unrecorded), Yucatan Channel, 1,170 m.—USNM 94058, 3 specimens; *Albatross* Station 2150, 13°34′45″N, 81°21′10″W, 699 m.—

USNM 94106, 1 specimen; *Albatross* Station 2135, 19°55′58″N, 75°47′07″W, 457 m.—USNM 429872, 5 specimens; USNM 429873, 2 specimens; USNM 429895, 2 specimens; Johnson-Smithsonian Deep-Sea Expedition Station 94, 18°37′45″N, 65°05′00″W, 549–860 m.—UMML 30.8339, 1 specimen; *John Elliott Pillsbury* Station P-929, 15°29.5′N, 61°11.5′W, 457–503 m.—USNM 94949, 2 specimens; *Blake* Station 211, 14°28′40″N, 61°06′08″W, 653 m.—UMML 30.8340, 8 specimens; *John Elliott Pillsbury* Station P-905, 13°46.3′N, 61°05.4′W, 384–963 m.—UMML 30.8341, 13 specimens; *John Elliott Pillsbury* Station P-904, 13°45.5′N, 61°05.7′W, 201–589 m.—UMML 30.8342, 1 specimen; *John Elliott Pillsbury* Station P-903, 13°44′N, 61°03.1′W, 231–430 m.

Remarks: Shells of *Lamellitrochus inceratus* are similar in shape and sculpture to that of *L. suavis*, but are much larger (up to 8.2 mm *vs.* 3.35 mm, respectively) and have larger protoconchs (350–375 μm *vs.* 325 μm, respectively). Shells of *L. pourtalesi* (figures 4–6) are most similar to those of *L. inceratus*, but are somewhat larger (to 10.3 mm), have much larger protoconchs (525–550 μm), have a narrower umbilicus (about 35% *vs.* 45–50% of shell width, respectively), lack axial riblets on the first 0.5 whorl, the aperture is ovate rather than circular, and the tubercles on the subsutural angulation and peripheral carina are sharply conical and axially elongate rather than rounded and spirally elongate as in *L. inceratus*. *Lamellitrochus inceratus* occurs off southern Georgia; in the Straits of Florida from off Cape Florida to the Dry Tortugas, and off Havana and Bahia Honda, Cuba; in the Yucatan Channel; off Old Providence Island; off southeastern Cuba; off northern Puerto Rico; and the Lesser Antilles from Dominica to St. Lucia. This species is usually collected in depths of about 250–550 m.

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Tridacna tevoroa Lucas, Ledua and Braley: A Recently-described Species of Giant Clam (Bivalvia; Tridacnidae) from Fiji and Tonga

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ABSTRACT

Tridacna tevoroa Lucas, Ledua and Braley is the eighth extant species of giant clam. It has only been found in the eastern Lau Islands of Fiji and the northern Vava'u and Ha'apai islands of Tonga. It inhabits relatively deep water (20+ m) compared to other giant clam species and is apparently intolerant of shallow conditions. *Tridacna tevoroa* occurs sympatrically with *T. derasa* (Roding) and appears to be most closely related to it, both belonging in the subgenus *Persikima* Iredale. The two species are readily separated by the presence in *T. tevoroa* of a rugose mantle, prominent guard tentacles on the incurrent aperture, thinner valves, and colored patches on the shell ribbing near the umbonal area. *Tridacna tevoroa* has some *Hippopus*-like characters: shell pigmentation, absence of byssal gape, lack of lateral mantle projection, and absence of hyaline organs in the mantle. These necessitate modification of Rosewater's diagnostic features distinguishing the two genera of extant giant clams, *Tridacna* Bruguiere and *Hippopus* Lamarck.

Key words: Giant clam, Tridacnidae, *Tridacna*, taxonomy, key, *Hippopus*.

INTRODUCTION

Rosewater (1965) reviewed the confused taxonomy of giant clams (Order Veneroida, Superfamily Tridacnacea, Family Tridacnidae), recognizing six extant species in two genera, *Hippopus* Lamarck, 1799 and *Tridacna* Bruguiere, 1797. He subsequently described a further *Hippopus* species (Rosewater 1982). Thus, after Rosewater's pivotal work, the family consisted of seven extant species, *H. hippopus* (Linnaeus, 1758), *H. porcellanus* Rosewater, 1982, *T. gigas* (Linnaeus, 1758), *T. derasa* (Röding, 1798), *T. squamosa* Lamarck, 1819, *T. maxima* (Röding, 1798) and *T. crocea* Lamarck, 1819.

This taxonomic revision of the family Tridacnidae was very timely, as it preceded the period of intense interest in giant clams in recent years. Before 1970, there was little research interest in giant clams, despite it being known that giant clams are unique among bivalve mollusks in having hypertrophied siphonal tissues packed with symbiotic algae (zooxanthellae) (Lucas, 1988). Then, in the 1970's, there was a surge of research. This resulted partly from academic interest in their unique features, but mainly from interest in farming giant clams. It was recognized that giant clam stocks were being heavily over-exploited through most of their geographic ranges and that some species had been fished to extinction in particular regions. Furthermore, it was found that giant clams grow more rapidly than previously envisaged (Munro & Gwyther, 1981). Farming them as a means of supplying the demands for giant clam meat and other products, and thus taking pressure off natural populations, became a desirable and feasible proposition.

Rosewater's taxonomy of giant clams has been widely accepted and validated through use in species' identifications in numerous studies. However, at an international meeting on giant clams in 1988, the possibility of a rare, new species in Fiji was raised (Lewis & Ledua, 1988). This new taxon was subsequently found also in Tonga and recently described as *Tridacna tevoroa* by Lucas *et al.* (1990).

This paper provides further description of *T. tevoroa*, including morphometric comparison with *T. derasa*. It also considers the affinities of the new species within the family Tridacnidae.

GENERA AND SUBGENERA OF TRIDACNIDAE

In order to consider the affinities of *T. tevoroa* within the family Tridacnidae, it is necessary to review Rosewater's diagnoses of *Hippopus* and *Tridacna*, and subgenera of the latter. Rosewater (1965) recognized three subgenera of *Tridacna*: *Tridacna s.s.* Bruguiere, 1797 (containing *T. gigas*), *Persikima* Iredale, 1937 (containing *T. derasa*), and *Chametrachea* Mörch, 1853 (containing *T. squamosa*, *T. maxima*, and *T. crocea*). As the diagnostic features for the various taxa are not clearly

Table 1. Diagnostic features of *Tridacna* and *Hippopus* from Rosewater (1965), with additions and modifications.

Feature	*Tridacna*	*Hippopus*
Hyaline organs in mantle surface	present (usually present)[1]	absent
Byssal orifice	well defined (poorly–well defined)[1]	poorly defined
Tightly fitting teeth along byssal orifice	absent	present
Posterior adductor muscle scar location	sl. behind mid-line	central
Outer demibranch of ctenidia	complete–incomplete	complete (?)[2]
Elongate-triangular shape[3]	no	yes (in large specimens)[3]
Strawberry blotches on early portion of shell	not present (usually not present)[1]	present
Mantle projects laterally over shell margins[4]	yes (usually)[1]	no
Distinct ventral region of shells[5]	not present	present

[1] Modification required to accommodate *T. tevoroa*.

[2] It is presumed that Rosewater was referring to the presence or absence of a distal food groove in describing the outer demibranch as "complete" or "incomplete"; however, J. Norton (personal communication) has found that the two *Hippopus* species have no food groove on the outer demibranch and are thus "incomplete".

[3] Small *H. porcellanus* are semicircular.

[4] From Lucas (1988).

[5] From this paper.

set out in Rosewater (1965), the features he considered to be diagnostic are compiled in tables 1 and 2.

One feature of the *Hippopus* species was not emphasized by Rosewater. This is the well-defined ventral region of the valves, distinctly angled to the adjacent shell curvature and almost parallel to the lateral body axis. This region includes the byssal orifice and is outlined by the ventral-most pair of rib-like radial folds. It is approximately ovate and flat in small specimens. In large specimens it is heart-shaped and concave. This feature is recognized in the common name for *H. hippopus*, "horse's hoof" clam. The ventral region is closely applied to the substrate in small juveniles attached by their byssus. Thus, the long body axis of *Hippopus* juveniles is strongly angled to the substrate in a characteristic fashion.

While *T. squamosa* is included in the subgenus *Chametrachea*, it shows little if any tendency to bore into hard substrates in our experience. Furthermore, some large specimens of *T. squamosa* lose their byssal attachment, in accordance with the general pattern of large size and loss of byssal attachment in tridacnids. All tridacnid species are attached to their substrate with byssal threads as juveniles; however, as they grow, the byssus is apparently insufficiently strong to maintain the clam in its vertical orientation (mantle uppermost, prominently exposed to sunlight) against strong wave forces. Instead, the clam greatly thickens the umbonal regions of the valves. This basal weight, together with strongly convex curvature of the valves near the umbos, provides a strong righting force when the large clam is displaced onto its side.

The features by which the other two members of *Chametrachea* (*T. crocea* and *T. maxima*) differ from other tridacnids, *i.e.*, small size, permanent byssal attachment, wide byssal orifice (which must be concealed or predators will penetrate it), substrate erosion and numerous shell scutes (for wedging and eroding), are a suite of functionally interrelated features.

TERMINOLOGY

The terminology used in various publications to describe the anatomical orientation of giant clams is inconsistent. This arises from alternative interpretations of the clam's unusual body form, with its greatly expanded siphonal region. Yonge (1936, 1980) followed some earlier authors

Table 2. Diagnostic features of the three subgenera of *Tridacna*, derived from Rosewater (1965).

Feature	*Tridacna s.s.*	*Persikima*	*Chametrachea*
Outer demibranch	with food groove	w/o food groove	w/o food groove
Adult shell length	large (to 1+ m)	medium (to 500+ mm)	small–med. (150–400 mm)
Byssal orifice	small	small	med.–large
Adult attached to substrate	no	no	yes[1]
Coral boring	no	no	yes/no[2]
Lateral shape of valves	equilateral	umbo displaced backward	ca. equil.—umbo displaced forward
Deep radial folds on shell	yes	no	no
Shell scutes	only in small juveniles	only in small juveniles	yes
Guard tentacles on incurrent aperture	no	yes	yes
Ctenidia extend dorsally	no	yes	no

[1] Not always for large *T. squamosa*.

[2] Not for *T. squamosa*.

in considering that the expansion of the giant clam's siphonal region had occurred through the mantle/shell rotating 180° about the viscero-pedal mass. In this view, the relationship between the body and shell of giant clams is the reverse of other bivalves. Stasek (1962, 1963) concluded that there was no evidence for an altered functional relationship between the body and the mantle/shell in giant clams; their unusual morphology results from growth largely in a posterior direction, in contrast to typical growth that is largely in a ventral direction.

In this paper we follow the anatomical orientation terminology of Stasek (1962, 1963), and this is illustrated in figure 1. In this terminology, ventral, posterior, etc., relate to the equivalent regions in typical bivalve mollusks, not to the orientation of the adult tridacnid. This terminology poses problems in referring to the relative positions of structures within the body, *e.g.*, to say that one structure is posterior to another is quite imprecise as the posterior region of the tridacnid occupies almost 70% of its total circumference (Stasek, 1962; figure 2). Terms such as "above", "below", "before" and "behind", or equivalents, are suggested for the four directions in sagittal plane, which would otherwise be "mid-posterior", "anterior", "postero-dorsal" and "postero-ventral", respectively. Stasek (1962) used terms such as "foremost" and "upward".

The anatomical orientation terminology used by Yonge (1936, 1980) and Rosewater (1965, 1982), and in Lucas *et al.* (1990), is illustrated in figure 2. It reflects the orientation of the adult tridacnid, but has no relationship to the equivalent regions of typical bivalve mollusks.

Shell dimensions measured in this study are illustrated in figures 3–5.

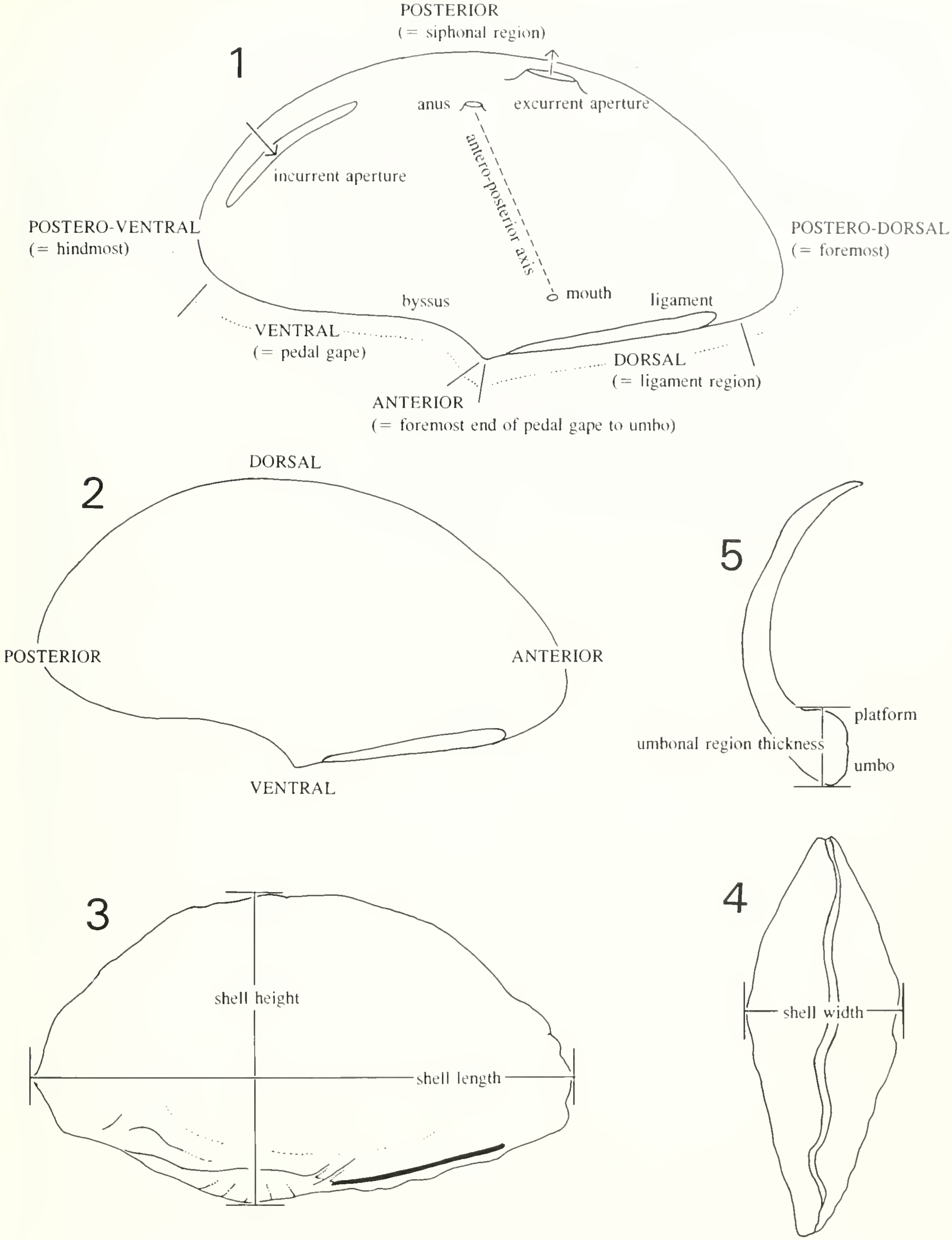
Tridacna (*Persikima*) *tevoroa*
Lucas, Ledua and Braley 1990
(figures 6–11, 16)

Tridacna sp. (cf. *T. derasa*), Lewis and Ledua 1988:82.
Tridacna tevoroa Lucas, Ledua and Bradley 1990:1.

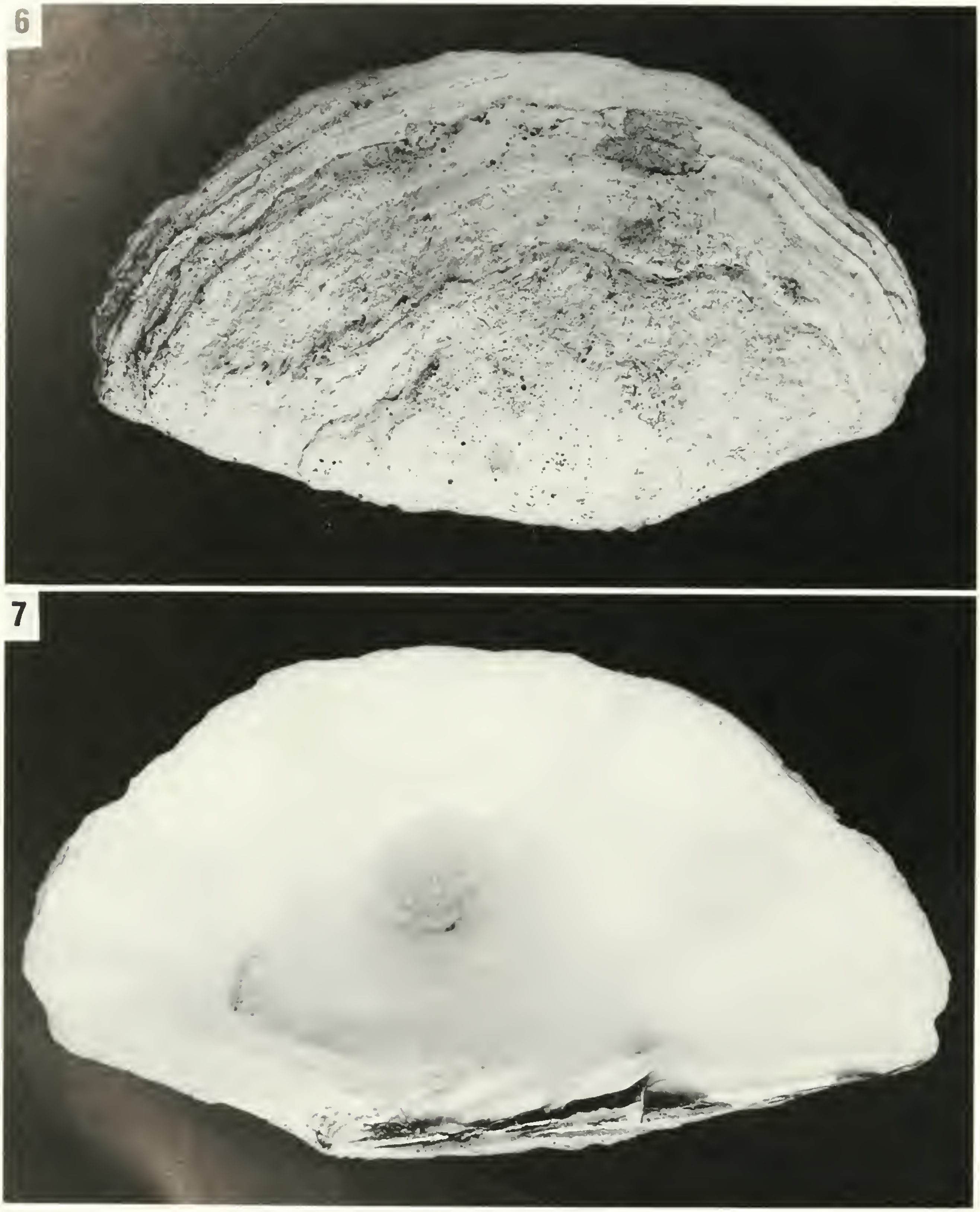
Diagnosis: Lateral shell outline asymmetrical, with long hinge line and short ventral margin. Byssal orifice poorly defined, but without interlocking teeth. Shell with 6 or 7 rib-like radial folds usually having strawberry colored patches near umbonal region, producing a striped appearance. Mantle surface rugose, with numerous protuberant lobes. Long, broad and prominent guard tentacles on incurrent aperture.

Description: *Shell:* Reaching 550 mm length; suboval in lateral outline, but strongly asymmetrical, with dorsal region much longer than ventral region; shell height : length ratio *ca.* 0.6:1 in large (>300 mm) specimens. Umbo angle >150°; umbo slightly opisthogyrous. Valves moderately inflated, thin at margins but distinctly thickened in umbonal region in large specimens. Shell colored gray-white externally, usually with strawberry colored patches on rib-like radial folds in umbonal area (extending up *ca.* 100 mm from umbo), giving ribs a striped appearance. Strawberry patches are not evident in some old specimens (including holotype), apparently lost through erosion or obscured by calcareous overgrowths of umbonal region (*cf.* figure 11). Primary radial sculpture consisting of 6 or 7 prominent folds, plus 3 short thin ridges near ligament. Prominent rib-like folds grading into undulating folds near shell edge in large specimens. Secondary radial sculpture consisting of fine ribs, much stronger in fold interstices than on radial folds; fine ribs not evident in distal shell region of large specimens. Apparent remains of eroded scutes often present on rib-like folds (figure 11) from umbo to extent of strawberry colored striping; occurring on white regions between colored patches. Other concentric sculpture limited to fine growth lines. Upper shell margins weakly undulating, with 5 rounded medially-projecting processes, representing extremities of rib interstices; upper shell margins often thin and sharp (figure 8). Length of hinge line *ca.* 0.6 × shell length. Umbo strongly backward of mid-point of shell length. Cardinal tooth and cardinal socket (figure 7) not strongly developed, even in large specimens. Lateral hinge tooth little more than a ridge. Ventral shell margin somewhat irregular and slightly convex. Byssal orifice poorly defined; without teeth; with *ca.* 5 rows of small plicae in byssal orifice region. Interior of shell white; glossy distal to pallial line, dull medial to pallial line. Hinge plate with pale brown tinge. Pallial line strongly indented in ventral region. Posterior adductor muscle scar large and strongly indicated with lines and ridges; *ca.* 70 mm high and 55 mm wide in 435 mm shell length specimen; sited behind midpoint of shell length but in front of umbo on long shell axis. Posterior pedal retractor muscle scar adjacent to foremost border of posterior adductor scar and much smaller, <0.2× area of posterior adductor scar. *Soft parts:* Mantle of subdued color, brown, gray-brown or green-brown, uniform in color or mottled; without striations, but sometimes with pale lines following mantle surface contours (figure 10). Mantle surface rugose, with numerous protuberant lobes (figure 10). Mantle tissue with few iridophores, without hyaline organs, and with most zooxanthellae situated close to mantle surface (figure 16). Mantle not or barely extending laterally over shell edges. Expanded mantle broad and exposed by wide gaping of valves. Incurrent aperture with long, broad guard tentacles, usually white, but sometimes brown (presumably through presence of zooxanthellae), often projecting prominently out from aperture. Byssus absent and foot vestigial in all large specimens (300+ mm shell length). Ctenidia demibranchs extending forwards beyond proximal oral grooves for ⅕–¼ of their length. Outer demibranch of similar size or slightly less than depth of inner demibranch; outer demibranch may be upwardly reflected in some regions and the ctenidial axis is exposed in some regions. Inner demibranch with food groove and outer demibranch without. Long distal oral grooves lead from ctenidia to labial palp bases.

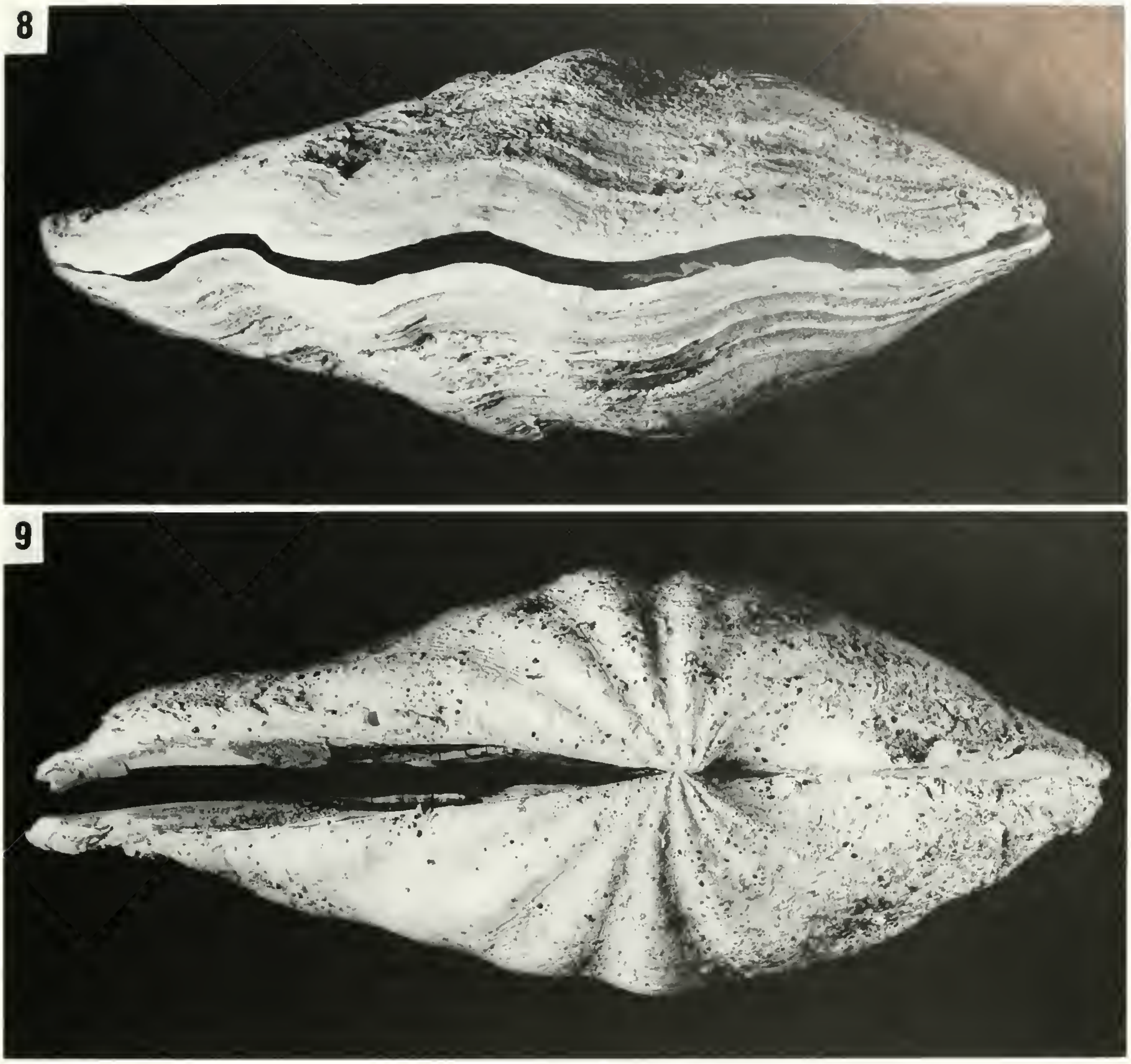
Morphometrics: In comparing the morphometrics of *T. tevoroa* and *T. derasa*, seven parameters were mea-



Figures 1–5. Diagrams of anatomical terminology for giant clams and shell dimensions measured. **1.** Orientation terminology used in this paper (following Stasek, 1962). **2.** Alternative orientation terminology (after Rosewater, 1965, 1982; Yonge, 1936, 1980). **3.** Lateral view of valve. **4.** Upper view of valves. **5.** Cross-section of valve.



Figures 6, 7. Lateral views of *T. tevoroa* holotype left valve. **6.** External surface. **7.** Internal surface.



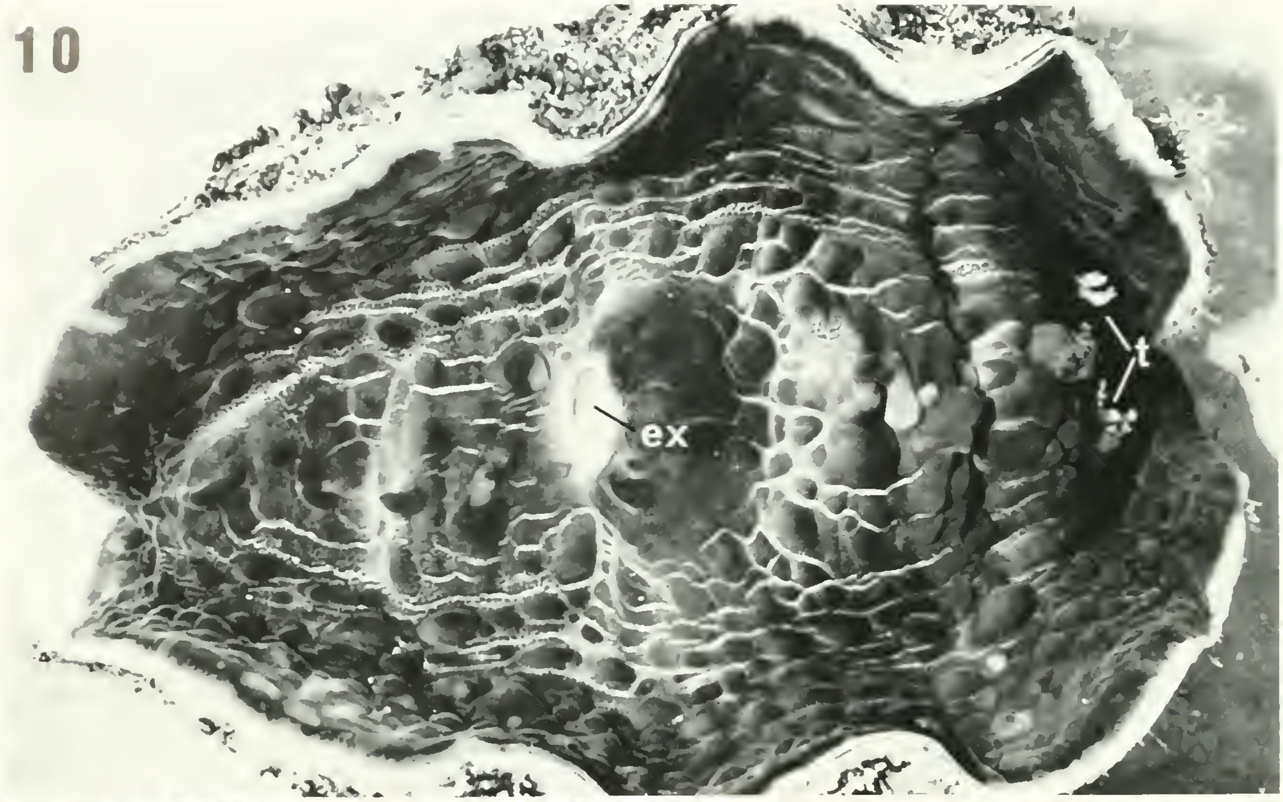
Figures 8, 9. *T. tevoroa* holotype. **8.** Upper view. **9.** Umbonal view.

sured: 1. shell length (figure 3); 2. shell height (figure 3); 3. shell width of conjoined valves (figure 4); 4. shell weight; 5. underwater shell weight; 6. umbonal region thickness (maximum distance through the umbonal region) (figure 5); 7. distal shell thickness (measured 25 mm in from the margin of the medial radial fold). Only measurements 1, 2 and 3, and sometimes 7 could be made on living specimens. The shell weight (4) in living specimens was estimated from the underwater weight of the whole animal, which was assumed to be entirely due to shell (=5), the soft tissues having approximately neutral buoyancy.

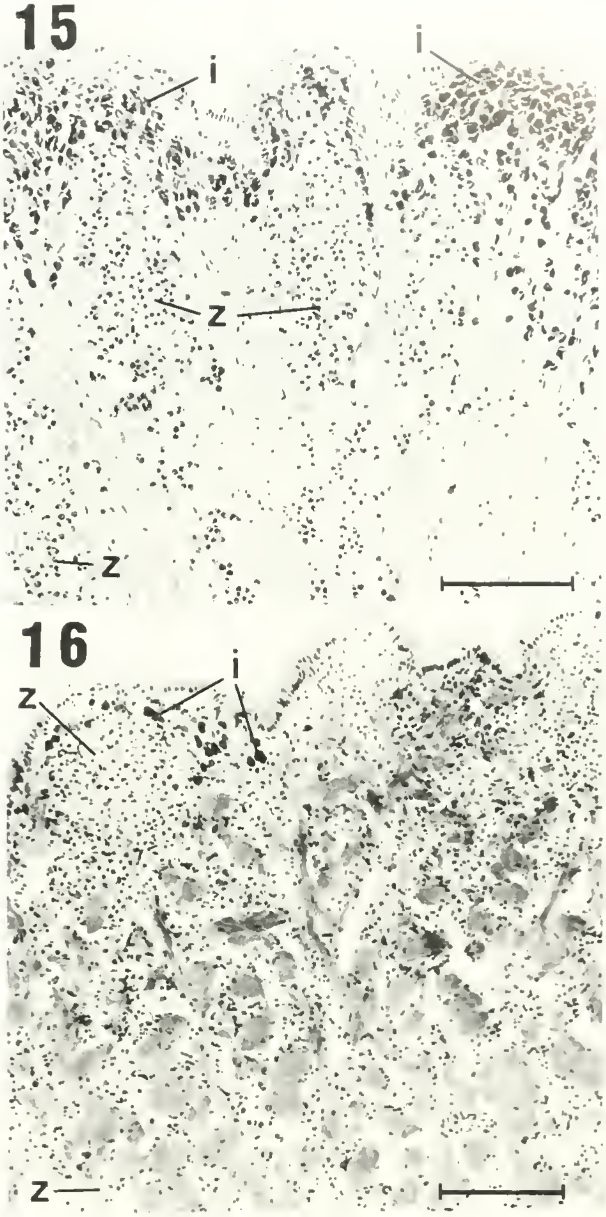
$$\text{shell weight} = 1.611 \times \text{underwater weight}$$

This relationship between shell weight and underwater shell weight was found to be very regular (1.611 ± 0.008 s.d.) in *T. derasa* and *T. tevoroa*.

Parameters 2–7 were related to shell length (1), which was used as the general measure of size. Least squares regressions were calculated for each of parameters against shell length for each species (table 3). The slopes and intercepts for each pair of regressions, and their standard errors, were compared by t-tests (2-tail) for statistically significant differences. There were no significant differences between the intercepts for each pair of regressions. Slopes were significantly different ($P < 0.05$) between species for three of the regressions: shell width, umbo



Figures 10, 11. Live *T. tevoroa* specimens. **10.** Rugose mantle; ex, excurrent aperture; t, conspicuous guard tentacles on incurrent aperture. **11.** Umbonal regions. Note that the umbonal region of the specimen in the foreground is heavily eroded and encrusted, showing little striping of the radial ribs, but striping and apparent eroded scutes are clear on the rear-left specimen (arrowed); striping is clear on the rear-right specimen (arrowed).



Figures 15, 16. Cross-sections of surface layers of mantle tissues. **15.** *T. derasa.* **16.** *T. tevoroa.* i, iridophores; z, zooxanthellae. Scale bars = 100 micrometers.

thickness and shell weight versus shell length (table 3). These data are figured in figures 12–14.

Types: *Holotype:* Australian Museum, Sydney, Reg. No. C164071. Whole specimen with soft tissue preserved

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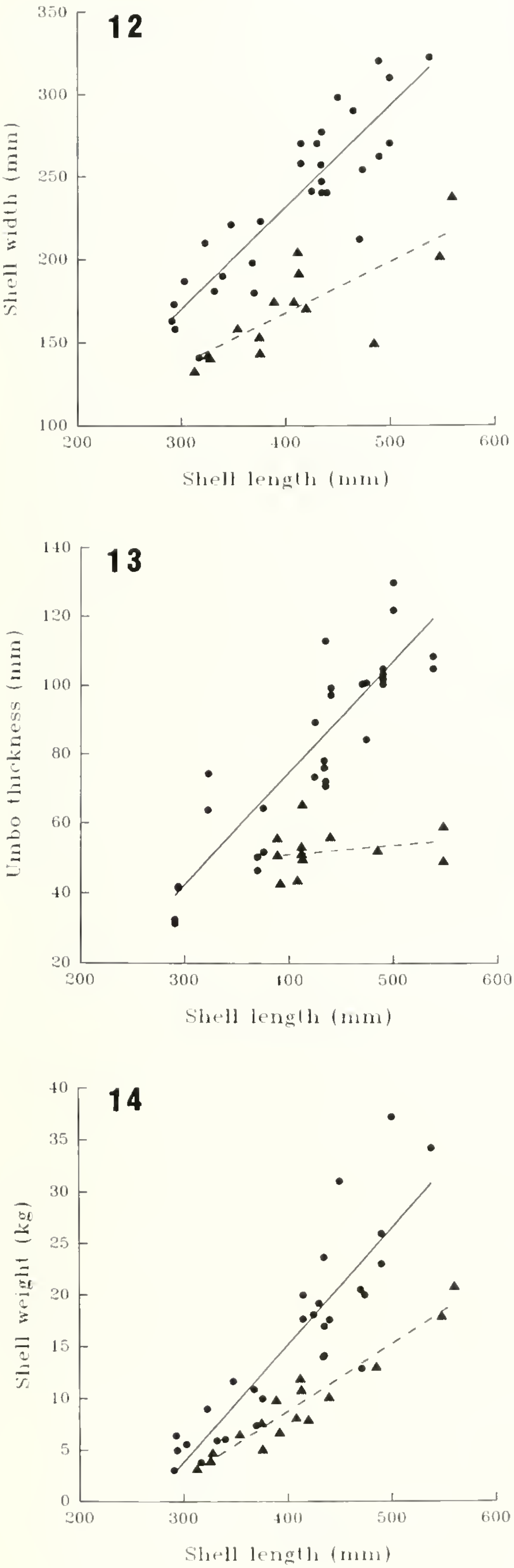

Figures 12–14. Morphometric comparisons of *T. tevoroa* (triangles and dashed regression line) and *T. derasa* (circles and continuous regression line). **12.** Shell width versus shell length. **13.** Umbo thickness versus shell length. **14.** Shell weight versus shell length

Table 3. Morphometrics of *T. tevoroa* and *T. derasa*. Coefficients and standard errors (SE) for 'a' (slope) and 'b' (Y axis intercept) for least squares regressions of $Y = aX + b$, where X is shell length (mm). Sample numbers (n) for *T. tevoroa* and *T. derasa* ranged from 18–35 and 9–16, respectively. P, significance level of correlation; vs, very significant ($P \ll 0.01$); *, slope coefficients differ significantly between species at $P < 0.05$ level

		Tridacna tevoroa			*Tridacna derasa*		
Y	a/b	Coeff.	SE	P	Coeff.	SE	P
Shell width (mm)	a	0.307*	0.071	vs	0.613*	0.061	vs
	b	45.0	29.4	0.2	−13.77	25.34	0.6
Shell height (mm)	a	0.548	0.075	vs	0.657	0.058	vs
	b	23.05	31.20	0.5	−11.42	24.57	0.6
Umbo thickness (mm)	a	0.026*	0.034	0.5	0.324*	0.034	vs
	b	40.8	14.8	0.02	−54.93	14.49	vs
Shell margin thickness (mm)	a	0.0072	0.0145	0.6	0.031	0.008	vs
	b	5.52	6.26	0.4	1.46	3.41	0.7
Shell weight (kg)	a	0.0649*	0.0053	vs	0.114*	0.012	vs
	b	−17.17	2.19	vs	−30.29	4.78	vs
Underwater weight (kg)	a	0.0418	0.0040	vs	0.0716	0.0115	vs
	b	−11.33	1.59	vs	−18.95	4.71	vs

in formalin (figures 6–9). Shell length 485 mm. Collected at Cakau Tabu Reef, Southern Lau islands, eastern Fiji, 17°40′S, 178°32′W, A. Lewis and Filipe Viala, 26 January 1986. *Paratypes:* 1. Fiji Museum, Suva, Reg. No. C-001. Whole specimen with soft tissue preserved in formalin. Shell length 328 mm. Collected at Vatoa Island, Southern Lau islands, eastern Fiji, 19°49′S, 178°13′W, E. Ledua and M. Tavisa, 23 November 1989. Habitat details: at 24 m depth on gentle slope outside the reef on the southern side of the island; only low, hard corals were present and scattered in low numbers; very clear water. 2. National Museum of Natural History, Smithsonian Institution, Washington, DC, USA, Reg. No. USNM 859439. Specimen consisting of valves only. Shell length 389 mm. Collection and habitat details as for paratype 1. 3. Museum of Tropical Queensland, Townsville, Australia, Reg. No. MO 17791. Specimen consisting of valves only. Shell length 413 mm. Collection and habitat details as for paratype 1.

Type locality: Cakau Tabu Reef, Lau Islands, Fiji.

Distribution: Lau Islands, Fiji (known from Cakau Tabu, Komo Island, Namuka Island, Vatoa Island and Vuata Vatoa, 17°40′S–19°56′S, 178°13′W–178°32′W; Lewis & Ledua, 1988). Islands within the Ha'apai and Vava'u groups, Tonga.

Habitat: From the limited collection details, the habitat of *T. tevoroa* appears to be along outer slopes of leeward reefs, in very clear, oceanic water at 20–30 m. *Tridacna derasa* is also found in this kind of habitat, and some specimens may occur down to these depths in very clear water.

Material examined for morphometrics: *T. tevoroa:* Fiji, Lau Island group: 440 mm, single valve; 392 mm, single valve; 413 mm, valves only; 548 mm, valves only; 389 mm, valves only; 375 mm, live specimen; 354 mm, live specimen. Tonga, Vava'u Islands: 560 mm, live specimen; 326 mm, live specimen; 420 mm, live specimen; 376 mm, live specimen; 313 mm, live specimen. Tonga, Ha'apai Islands: 408 mm, valves only; 412 mm, valves only. *T. derasa:* Fiji, Makogai Island: 538 mm, valves only; 425 mm, valves only; 370 mm, valves only; 368 mm, live specimen; 348 mm, live specimen; 317 mm, live specimen. Tonga, Tongatapu: 490 mm, valves only; 376 mm, valves only; 434 mm, valves only; 435 mm, valves only; 323 mm, valves only; 294 mm, valves only; 291 mm, valves only; 474 mm, valves only. Tonga, Falevai, Vava'u group: 415 mm, live specimen; 293 mm, live specimen; 332 mm, live specimen; 471 mm, live specimen. Australia, Great Barrier Reef, Bramble Reef: 435 mm, valves only; 500 mm, valves only; 490 mm, valves only; 440 mm, valves only; 470 mm, single valve; 303 mm, live specimen; 415 mm, live specimen; 435 mm, live specimen; 340 mm, live specimen; 430 mm, live specimen; 450 mm, live specimen; 465 mm, live specimen; 500 mm, live specimen.

Etymology: The species name is derived from the clam's Fijian name, "tevoro" (devil), with a latin termination (nominative, feminine).

Comparison: *Tridacna tevoroa* is most like *T. derasa* in general appearance, with the latter species occurring in shallower reef areas at all the localities where *T. tevoroa* has been collected. The similarity of these species goes beyond superficial appearance: in those features by which the subgenus *Persikima* is distinguished from other subgenera of *Tridacna* (table 2), *T. tevoroa* belongs with *T. derasa* in *Persikima*. It is, however, readily distinguished from *T. derasa* by a number of features relating to both hard and soft anatomy (table 4). Among these distinguishing features, the most conspicuous are the rugose mantle, prominent guard tentacles on the

Table 4. Features which distinguish *T. tevoroa* from *T. derasa*. (These features apply to specimens ca 250 mm shell length and greater.)

Feature	*T. tevoroa*	*T. derasa*
Byssal orifice	poorly defined	small, but clearly defined
Umbonal region of rib-like primary folds	striped with color, apparently with eroded scutes	uncolored, without scutes
Mantle	rugose, with protuberances	smooth, plain
Iridophores in mantle tissue	low density (mantle dull colors)	high density (mantle often bright colors)
Hyaline organs	absent	present
Mantle projecting beyond shells	not or barely	yes
Guard tentacles on incurr. apert.	long, broad, prominent	short, thin, not prominent
Demibranchs of ctenidia	similar size	outer smaller
Cardinal tooth	not prominent	very prominent

incurrent aperture, thinner valves, and colored patches on the shell ribbing of *T. tevoroa*.

The three shell parameters versus shell length for which regression slopes differ significantly between *T. tevoroa* and *T. derasa* (table 3) are interrelated, *i.e.*, they reflect the thinner shell of *T. tevoroa* compared to *T. derasa*. There is, however, little difference in shell thickness between medium-sized specimens of the two species, ca. 300 mm shell length; interspecific differences become pronounced in the largest (and probably oldest) specimens, 450+ mm (figures 12–14). The sharpness and thinness of the shell margins of *T. tevoroa*, noted by Lewis and Ledua (1988), are certainly evident in some specimens (figure 8), but its shells soon thicken behind the margin and there is no significant difference in regression slopes between the species for distal shell thickness, 25 mm behind the margin, versus shell length.

Stasek (1962) described the ctenidia of some tridacnid species from Eniwetok Atoll in detail, distinguishing *T. derasa* and *H. hippopus* from other species in having food grooves on both inner and outer demibranchs. *Tridacna derasa* was further distinguished from other species in having similar-sized demibranchs, with the outer demibranch upwardly reflected, exposing the ctenidial axis. In view of this reported distinctiveness of the ctenidia of *T. derasa*, it would seem to be appropriate to compare these structures in *T. tevoroa* and *T. derasa*. However, Rosewater (1965) described *T. derasa* as having an "incomplete" outer demibranch, and recent studies of tridacnid morphology by J. Norton (personal communication) have revealed that *T. derasa* specimens from Fiji and Tonga, at least, have short outer demibranchs without food grooves. The degree of upward reflection of the outer demibranch and exposure of the ctenidial axis vary between specimens; they may partly reflect handling during dissection. Thus, the distinctiveness of ctenidial morphology in *T. derasa* observed by Stasek is questionable, and comparisons with *T. tevoroa* are made on the basis of Rosewater's and Norton's observations.

Tridacna tevoroa has some features typical of *Hippopus* in the *Hippopus*/*Tridacna* separation based on Rosewater (1965) (table 1). Its byssal aperture is indistinct and it has reddish markings on the external surfaces of the shells. Its dull mantle color, lack of hyaline organs and mantle posture (only reaching the shell margins but offset by wide gaping of the valves) are also like *Hippopus* but unlike *Tridacna*, *sensu lato*. However, these features of *T. tevoroa* are never completely like those of *Hippopus*. Its byssal aperture differs from the *Hippopus* species in not having interlocking teeth, nor does it have the distinctive "horse-shoe" ventral surface of the valves. It is unlikely that attached juveniles of *T. tevoroa* orient to the substrate in the characteristic manner of *Hippopus* juveniles. While *T. tevoroa* shares shell color patches with the *Hippopus* species, its colored stripes on the radial ribbing are unlike the irregular color patches of *Hippopus* species. The mantle of *T. tevoroa* is distinct from that of all other tridacnids.

It is conceivable that *T. tevoroa* represents a transitional stage between these two genera, the divergence of which goes back in the fossil record at least to the lower Miocene (Rosewater, 1965). However, it comfortably fits with *T. derasa* in the subgenus *Persikima* and we do not propose to give it separate subgeneric or generic status.

One consequence of the discovery of *T. tevoroa* is the need to make some modifications to the characters distinguishing *Hippopus* and *Tridacna* (table 1).

Small juveniles of *T. tevoroa* are unknown, but they are likely to be distinctly unlike *T. derasa* and any other tridacnid. This is because of the colored stripes on the valve ribs and also the probable presence of scutes on the ribs; these characters being present up to about 150 mm shell length. The distinctive appearance is lost in larger specimens.

Remarks: Lewis and Ledua (1988) hypothesized that the localized distribution of the "tevoro" clam in eastern Fiji may represent a "relict population on the eastern edge of both its own former range and that of the apparently more abundant and successful *T. derasa*". Their prediction, that other populations might be found, was soon confirmed by collections in Tonga. The known distribution of *T. tevoroa* is still, however, limited to several island groups over about 300 km distance in the southwestern Pacific. At none of these localities is it abundant: in the Vatoa area, Fiji, Lewis and Ledua (1988) estimated its relative abundance compared to *T. derasa* was on the order of 1:50. It thus must be regarded as the giant clam species most vulnerable to extinction. The previous bearer of this unfortunate distinction was *H. porcellanus*, with a relatively restricted distribution centered on the southern Philippines (Lucas, 1988), and a high demand within the international shell trade despite CITES (Convention on International Trade in Endangered Species) protection. Fortunately, the deep habitat of *T. tevoroa* partially protects it from human predation, but there is still some exploitation. This is evident from the fact that there are local names for *T. tevoroa* in the three island groups where it occurs (Lucas *et al.*, 1990) and there are anecdotal reports of its consumption, *i.e.*, one diver on Vava'u Island, Tonga, reported having collected and eaten about 20 specimens. Fortunately, there is no major trade in giant clam shells in Fiji or Tonga.

Tridacna tevoroa has only been collected from relatively deep-water habitats for giant clams (20–30 m depth). Their mantle tissue contains symbiotic zooxanthellae like other tridacnids, and presumably photosynthetic products from these symbionts are used in their nutrition. However, there are low light levels and a shifted light spectrum at the depths they inhabit, and probably the extent to which autotrophy supports the clam's nutrition will be reduced. Thus, *T. tevoroa* is expected to have morphological adaptations to facilitate using the low light intensities at these depths. Extending the mantle laterally over the shell margins to increase its exposed surface, as in other *Tridacna* species, is surprisingly not shown by *T. tevoroa*. However, it achieves a large mantle surface area through the mantle protuberances and wide gaping of its valves. The dull mantle color is due to low densities of iridophores (iridocytes) (*cf.* figures 15 and 16), with the brown coloration of zooxanthellae showing through. Iridophores in giant clams contain thin reflecting platelets (Kamishima, 1990). They are particularly common near the mantle tissue surface in brightly colored tridacnids, including some *T. derasa* (figure 15). Most zooxanthellae are situated below the iridophore layer in *T. derasa*. In *T. tevoroa* the zooxanthellae also occur close to the mantle surface (figure 16); clusters of zooxanthellae may occur in small elevations of the mantle surface. The paucity of iridophores and shallow distribution of zooxanthellae in the mantle of *T. tevoroa* clearly reflect the need to maximize light reaching the zooxanthellae. It has been shown that zooxanthellae photo-adapt to low light levels (Mingoa, 1988) and this may be important for *T. tevoroa*.

It seems that *T. tevoroa* are not only adapted to relatively deep conditions, but they are intolerant of shallow habitats. In early collections by Fiji Fisheries staff, these clams were transported on the decks of Fisheries vessels and kept in shallow conditions (*ca.* 3 m) at Makogai Island. Rapid mortality occurred until the clams were moved into deeper water (*ca.* 14 m). Solar UV radiation penetrates clear tropical waters sufficiently to have significant biological effects down to 20 m and it is possible that *T. tevoroa* lacks or has insufficient of the UV screening agents that protect organisms inhabiting the shallow regions of coral reefs, *e.g.*, Dunlap *et al.* (1988). Also, it may have insufficient enzymes that deal with the toxic oxygen levels generated by photosynthesis at high light levels (*e.g.*, Shick & Dykens, 1985).

KEY TO THE TRIDACNID SPECIES

There are now eight extant species of giant clams and the key to species given by Lucas (1988) needs to be expanded and modified to incorporate *T. tevoroa*.

1 Byssal orifice region of opposed valves with interlocking teeth; distinct region of shell around byssal orifice, outlined by ventral-most pair of prominent radial ribs; mantle, when fully extended, not projecting laterally beyond shell margins . . . . *Hippopus* . . . 2
Byssal orifice of opposed valves without interlocking teeth; no distinct ventral region of shell outlined by prominent radial ribs; mantle, when fully extended, usually projecting laterally beyond shell margins . . . . *Tridacna* . . . 3
2(1) Shells thick and strongly ribbed, with reddish blotches in irregular bands; incurrent apertures without guard tentacles . . . . *H. hippopus*
Shells in specimens less than about 200 mm shell length not thick nor strongly ribbed and with only faint reddish blotches; incurrent apertures with guard tentacles . . . . *H. porcellanus*
3(1) Shell length of large specimens >550 mm, sometimes greater than 1 m; with about four elongate, interdigitating projections of each distal shell margin, being most elongate and acute in large specimens; shell without scutes, except for some tubular projections near umbo in very small juveniles; mantle brownish, with numerous iridescent blue-green circles . . . . *T. gigas*
Shell length rarely >550 mm; without elongate, interdigitating projections on each distal shell margin; mantle variably colored, without iridescent blue-green circles 4
4(3) Shell length up to 550 mm, occasionally larger; upper region of large shells plain, without scutes or strong ribs; hinge usually longer than half shell length 5
Shell length usually <400 mm; upper shell region with scutes or eroded scutes; hinge equal to or less than half shell length 6
5(4) Rib-like radial folds on shell without colored patches; mantle without protuberances; incurrent aperture with inconspicuous guard tentacles . . . . *T. derasa*
Rib-like radial folds on shell usually striped with colored patches near umbo; mantle with protuberances; incurrent aperture with conspicuous guard tentacles . . . . *T. tevoroa*
6(4) Shell approximately symmetrical about umbo in lateral view, with hinge about half shell length; scutes large and well-spaced both within and between the radial rows; lateral distance between scutes in adjacent rows usually about the same as scute width; byssal aperture narrow to moderately wide; not embedded into substrate; mantle usually of subdued and mottled color;

incurrent aperture with distinct guard tentacles . . . . *T. squamosa*

Shells usually asymmetrical about umbo in lateral view, with hinge less than half shell length; scutes usually low and often eroded, set close together both within radial rows and between rows; byssal aperture moderately wide to wide; embedded or partly embedded into substrate; mantle brightly colored; incurrent aperture with indistinct guard tentacles .7

7(6) Shell length <150 mm; shells not strongly asymmetrical about umbo in lateral view; byssal aperture wide; scutes eroded away except near shell margin; occurs deeply embedded in reef substrate . . . . *T. crocea*

Shell length of large specimens often >150 mm; shell often strongly asymmetrical about umbo in lateral view; byssal aperture moderately wide to wide; scutes present in substantial part of upper shell region; occurs partially embedded in reef substrate . . . . *T. maxima*

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Dates of Publication and Supraspecific Taxa of Bellardi and Sacco's (1873–1904) "I molluschi dei terreni terziarii del Piemonte e della Liguria" and Sacco's (1890) "Catalogo paleontologico del bacino terziario del Piemonte"

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ABSTRACT

Dates of publication are determined for the serial parts of Bellardi and Sacco's "I molluschi dei terreni terziarii del Piemonte e della Liguria" and its largely overlooked companion series, the latter containing the earliest valid introductions of many taxa. Genus group taxa introduced by Sacco (1890) in the rare work "Catalogo paleontologico del bacino terziario del Piemonte" have been hitherto ignored or treated as *nomina nuda*, although most meet criteria for availability and predate introductions in Bellardi and Sacco's 1873–1904 work. Supraspecific taxa introduced in these works are listed with bibliographic references. Attention is drawn to some taxonomic problems that result from recognition of hitherto overlooked valid introductions of names.

Key words: Bellardi; Sacco; compilation; dates; supraspecific taxa; Tertiary fossils; Mollusca; *Mastodon*.

INTRODUCTION

Bellardi and Sacco's monumental work "I molluschi dei terreni terziarii del Piemonte e della Liguria" is one of the most comprehensive treatments of a regional Tertiary fauna ever published. Issued between 1873 and 1904 in 30 numbered quarto parts, it contains descriptions of thousands of species and infraspecific taxa, numerous genus group taxa, and several families and subfamilies. The Bellardi and Sacco collection is now in the care of the Museo Regionale di Scienze Naturali, Turin (Ferrero Mortara et al., 1982, 1984).

The primary objective of this contribution is to draw attention to the fact that many names generally considered to date from this work were validly introduced earlier by Sacco in a little-known companion series and in the rare "Catalogo paleontologico del bacino terziario del Piemonte".

Parts 1–8, 11 and 13a of "I molluschi dei terreni terziarii del Piemonte e della Liguria" were published in "Memorie della Reale Accademia delle Scienze di Torino". It has been seldom appreciated that reprints of these parts were actually published *earlier* than the parent volumes (table 1). The remainder of the series (parts 9, 10, 12, 13b, 14–30) was published independently by Carlo Clausen, Turin. In all assembled sets of the work that I have seen (including the reprint by Atlante Malacologico, Rome, 1987–89), parts 1–8, 11 and 13a are represented by reprints. Although identical in content, the reprints differ from corresponding parts in the parent journal in being independently paginated and in having wrappers and title pages that were specially printed for each part. Determination of even the pagination of each part of the work was a laborious exercise, since there is considerable inconsistency in pagination from part to part in the parent journal, the reprints, the independently published parts, and in Sacco's (1904:vii) compilation (table 2). To avoid confusion with the companion series (see below), reprints, parent journal and independently published parts are referred to collectively as the "Memorie/Clausen" series. Page reference to the Memorie/Clausen series in the following discussions and in table 3 refer only to the reprints, though both paginations are indicated in table 2 and in the compilation of the work.

The companion series (hereafter referred to as the "Bollettino" series) has the same title as the Memorie/Clausen series and was issued serially in association with parts 7–29. It was published in "Bollettino dei Musei di Zoologia ed Anatomia Comparata della Reale Universita di Torino". The first two parts of the Bollettino series (Sacco 1890c,e) are subtitled "nota preventiva" (introductory note), so the parts of this series were clearly intended to precede corresponding parts of the Memorie/Clausen series (see Sacco 1891a:1, footnote). Of the 22 issued parts of the Bollettino series, 17 were evidently published prior to the corresponding Memorie/Clausen parts, and 12 of these contain nomenclaturally valid introductions of new taxa (see below). There are few references to the Bollettino series in the Memorie/Clausen series (Sacco 1891a:1 footnote, 1891d, synonymies). Sub-

Table 1. Dates of Publication and receipt of "I molluschi dei terreni terziarii del Piemonte e della Liguria." (BMNH—The Natural History Museum, London; KVA—University Library, Stockholm; LSL—Linnean Society, London; MCZ—Museum of Comparative Zoology, Harvard).

Part	Memorie della Reale Accademia di Torino (series 2)	Reprint	Bollettino dei Musei di Zoologia ed Anatomia comparata della Reale Universita di Torino
1	Vol. 27 1873[1] (November[2])–April 15 1874 (KVA)	June 10 1873 (p. 264)—Receipt date unknown	—
2	Vol. 29 1878[1] (November 1 1877[2])–December 1878 (KVA)	June [30] 1877 (p. 364)—Receipt date unknown	—
3	Vol. 34 1883[1] (January 1[2])–September 1883 (KVA)	December 10 1882 (p. 253)—Receipt date unknown	—
4	Vol. 37 1886[1] (May 1[2])–June 29 1886 (BMNH)	December 1 1884 (p. 62)–April 4 1885 (MCZ)	—
5a	Vol. 38 1888[1] (March 1[2])–June 2 1888 (BMNH)	January 15 1887 (p. 85)–April 18 1887 (MCZ)	—
5b	Vol. 38 1888[1] (March 1[2])–June 2 1888 (BMNH)	June 1 1887 (p. 67)–October 8 1887 (MCZ)	—
5c	Vol. 39 1889[1] (June 1[2])–September 25 1889 (BMNH)	September 20 1888 (p. 25)–December 12 1888 (BMNH)	—
6	Vol. 40 October 15 1890[3]–December 5 1890 (BMNH)	April 6 1890 (p. 2)–July 3 1890 (BMNH)	—
7	Vol. 40 October 15 1890[3]–December 5 1890 (BMNH)	June 18 1890 (p. 2)–September 1 1890 (BMNH)	Vol. 5 (82) June 13 1890–August 22 1890 (LSL)
8	Vol. 41 August 1 1891[4]–November 5 1891 (BMNH)	March 25 1891[4]–May 26 1891 (BMNH)	Vol. 5 (86) August 12 1890–August 22 1890 (LSL)
9	—	May [31] 1891 (p. 1)–February 12 1892 (MCZ)	Vol. 6 (103) May 29 1891–June 18 1891 (LSL)
10	—	September [30] 1891 (p. 1)–April 2 1892 (BMNH)	Vol. 6 (103) May 29 1891–June 18 1891 (LSL)
11	Vol. 42 September 16 1892[4]–January 13 1893 (BMNH)	June 30 1892 (p. 2)–November 7 1892 (BMNH)	Vol. 7 (121) April 30 1892–June 23 1892 (LSL)
12	—	June [30] 1892 (p. 1)–February 20 1893 (BMNH)	Vol. 7 (121) April 30 1892–June 23 1892 (LSL)
13a	Vol. 44 1894[1] (October 1[2])–December 15 1894 (BMNH)	April [30] 1893[5]–August 14 1893 (BMNH)	Vol. 8 (153) May 31 1893–October 4 1893 (BMNH)
13b	—	September [30] 1893 (p. 55)–April 24 1894 (BMNH)	Vol. 8 (153) May 31 1893–October 4 1893 (BMNH)
14	—	December [30] 1893 (p. 1)–July 14 1894 (BMNH)	Vol. 8 (165) December 11, 1893–January 1 1894 (LSL)

Table 1. *Continued*

Part	Memorie della Reale Accademia di Torino (series 2)	Reprint	Bollettino dei Musei di Zoologia ed Anatomia comparata della Reale Universita di Torino
15	—	April [29] 1894 (p. 1)—Receipt date unknown	Vol. 9 (171) April 27 1894—Receipt date unknown
16	—	August [31] 1894 (p. 1)—March 20 1895 (BMNH)	Vol. 9 (171) April 27 1894—Receipt date unknown
17	—	June [30] 1895 (p. 1)—Receipt date unknown	Vol. 10 (197) February 25 1895—Receipt date unknown
18	—	September [30] 1895 (p. 1)–April 11 1896 (BMNH)	Vol. 10 (206) May 30 1895—Receipt date unknown
19	—	December [30] 1895 (p. 1)–April 20 1896 (BMNH)	Vol. 11 (267) December 14 1896–May 1897 (BMNH)
20	—	May [31] 1896 (p. 1)–September 16 1896 (BMNH)	Vol. 11 (267) December 14 1896–May 1897 (BMNH)
21	—	September [30] 1896 (p. 1)—Receipt date unknown	Vol. 11 (267) December 14 1896–May 1897 (BMNH)
22	—	March [31] 1897 (p. 1)—Receipt date unknown	Vol. 11 (267) December 14 1896–May 1897 (BMNH)
23	—	June [30] 1897 (p. 1)—Receipt date unknown	Vol. 12 (298) June 11 1897–December 10 1897 (LSL)
24	—	December [30] 1897 (p. 1)—Receipt date unknown	Vol. 12 (298) June 11 1897–December 10 1897 (LSL)
25	—	August [31] 1898 (p. 1)–November 8 1898 (BMNH)	Vol. 13 (332) December 14 1898–February 14 1899 (LSL)
26	—	December [30] 1898 (p. 1)–June 17 1899 (BMNH)	Vol. 13 (332) December 14 1898–February 14 1899 (LSL)
27	—	September [30] 1899 (p. 1)–December 28 1899 (BMNH)	Vol. 14 (349) May 23 1899—Receipt date unknown
28	—	April [29] 1900 (p. 1)–August 31 1900 (KVA)	Vol. 16 (409) November 25 1901–October 7 1902 (BMNH)
29	—	June [30] 1901 (p. 1)–December 3 1901 (BMNH)	—
30	—	August [31] 1904[1]—Receipt date unknown	—

[1] Title page.
[2] List of members of the Academy.
[3] End wrapper.
[4] Title page verso.
[5] See discussion.

Table 2. Pagination of "I molluschi dei terreni terziarii del Piemonte e della Liguria." T/V—title/verso pages; pag'd—paginated

	Memorie			Reprint			
Part	Implied[1]	Paginated	Remarks	Paginated	Remarks (plates unpag'd)	Sacco 1904	Plates
1	33–324(292)	33–294(262)	Plates unpag'd	1–264(264)	T/V pag'd, captions unpag'd	279	15
2	1–364(364)	1–364(364)	Plates unpag'd	1–364(364)	T/V + captions unpag'd	373	9
3	219–469(251)[2]	219–469(251)	Plates unpag'd	1–253(253)	T/V pag'd, captions unpag'd	265	12
4	3–66(64)	3–62(60)	Plates unpag'd	1–62(62)	T/V pag'd, captions unpag'd	64	2
5a	79–166(88)	79–166(88)	Plates pag'd	1–85(85)	T/V pag'd, captions unpag'd		2
5b	257–328(72)	257–327(71)	Plates pag'd	1–72(72)	T/V + captions pag'd	209	2
5c	145–194(50)	145–194(50)	Plates pag'd	1–52(52)	T/V + captions pag'd		2
6	295–368(74)	295–368(74)	Plates pag'd	1–76(76)	T/V + captions pag'd	76	2
7	469–560(92)	469–560(92)	Plates pag'd	1–96(96)	T/V + 2 extra pp + captions pag'd	96	2
8	225–338(114)	225–338(114)	Plates pag'd	1–114(114)	T/V unpag'd, captions pag'd	114	2
9	—	—	—	1–103(103)	T/V pag'd. Pl. 2 caption here counted	104	2
10	—	—	—	1–68(68)	T/V pag'd, 2 captions here counted	69	2
11	585–682 (98)	585–682(98)	Plates pag'd	1–100(100)	T/V + captions pag'd	100	2
12	—	—	—	1–88(88)	T/V pag'd, 2 captions here counted	88	2
13a	1–56(56)	1–54(54)	Plates unpag'd	1–54(54)	T/V + captions unpag'd	56	2
13b	—	—	—	55–143(89)	T/V + captions pag'd	"143" (error)	9
14	—	—	—	1–40(40)	T/V + captions pag'd	40	2
15	—	—	—	1–74(74)	T/V + captions pag'd	74	3
16	—	—	—	1–82(82)	T/V + captions pag'd	82	3
17	—	—	—	1–86(86)	T/V + captions pag'd	86	3
18	—	—	—	1–52(52)	T/V + captions pag'd, 1 caption here counted	52	1
19	—	—	—	1–46(46)	T/V + captions pag'd	46	3
20	—	—	—	1–65(65)	T/V + captions pag'd	65	5
21	—	—	—	1–64(64)	T/V + captions pag'd	65	4
22	—	—	—	1–148(148)	T/V + captions pag'd	148	10
23	—	—	—	1–66(66)	T/V + captions pag'd	66	11
24	—	—	—	1–116(116)	T/V + captions pag'd	116	21
25	—	—	—	1–76(76)	T/V + captions pag'd	76	12
26	—	—	—	1–92(92)	T/V + captions pag'd	92	12
27	—	—	—	1–102(102)	T/V + captions pag'd	102	14
28	—	—	—	1–98(98)	T/V + captions pag'd	98	11
29	—	—	—	1–216(216)	T/V + captions pag'd	216	29
30				1–203,I–XXXVI(270)	T/V unpag'd, 31 unpag'd captions here counted	300	31
			Total	3633			247

In parts 9, 10, 12, 13b—21 blank pages (or plates) are not counted as pages because they are not so counted in completely paginated parts. However, they are (and were) counted as pages in parts 22–29.

[1] Total number of pages to first page of following article in volume.

[2] Last paper in volume.

sequent references to the Bollettino series by other authors are rare, and the few that I have been able to trace (*e.g.*, Wenz, 1938–44, Ferrero Mortara et al., 1984) refer only to parts 7 and 8 (Sacco 1890c,e). Moreover, the series has been overlooked in a compilation of his published works (Anonymous, 1948).

While the Memorie/Clausen series was in progress, Sacco (1890a) also published "Catalogo paleontologico del bacino terziario de Piemonte". This is essentially a tabular listing of the 5,472 species of Tertiary fossils known from Piedmont. Although Sacco (1904:40, 74) dated his new subgenera *Simplicotaurasia* and *Miocenia* from this work, the fact that other genus group names are potentially available there has been entirely overlooked.

DATES OF PUBLICATION

All reprints of parts 1–8, 11, and 13a of the Memorie/Clausen series were clearly published *before* corresponding parts in the parent journal (table 1).

Reprints of parts 1–5[a–c] bear year dates on the title pages and wrappers and are secondarily dated in the text with a year, month and, with the exception of part 2, a day. With the exception of part 1, the imprinted year dates on the title page and in the text are accordant. Although it is possible that the textual dates actually represent dates of completion of the manuscripts, they are interpreted as dates of publication in the absence of evidence to the contrary (ICZN, 1985, Art. 21).

Part 1 (Bellardi, 1873) is almost invariably dated from 1872 (*e.g.*, Sacco, 1889:155, 1904:vii; Wenz, 1944:1513) in accordance with the date on the title page and wrapper. The text (p. 264), however, is dated June 10 1873 and there are references to a publication dated 1873 in some synonymies (*e.g.*, p. 130), so the 1872 date is clearly an error.

Dates imprinted on the backs of the title pages of reprints of parts 6, 7, 8 and 11 are unequivocally dates of *printing*, as are dates on their parent volumes (table 1). Curiously, Sacco (1904:vii) dated part 6 from February 1890, part 8 from August 1890, and part 11 from February 1892, but these are surely errors since they predate the printing dates. That Sacco's dating of August 1890 for part 7 is almost certainly incorrect is suggested by the fact that the Natural History Museum, London (BMNH) copy of the reprint was accessioned on September 1, 1890 yet all other parts were accessioned by that library 2–8 months later than the imprinted dates.

The reprint of part 13a bears only the year of publication (1893), although from the statement on the title page verso it must have been published after February 1893 and presumably before September 1893, the publication date of part 13b. In the absence of conflicting evidence, it is appropriate to accept Sacco's (1904:vii) indication that it was published in April 1893 (received BMNH August 14 1893).

For bibliographic and priority purposes, the day of publication is interpreted as the last day of the stated month (ICZN, 1985, Art. 21i). Days of publication of reprints so interpreted (table 1) are shown in square parentheses. Year dates associated with new supraspecific taxa in the body of the text in both the Memorie/Clausen and Bollettino series frequently do not correspond with the actual year of publication and evidently represent merely *anticipated* years of publication.

All parts of the Bollettino series bear imprinted dates (day, month and year), and library accession date stamps are accordant with their interpretation as dates of publication (table 1).

Sacco's "Catalogo paleontologico del bacino terziario del Piemonte" was submitted to the general assembly of the Società Geologica Italiana on September 23 1889 for publication in Bollettino della Società Geologica Italiana (BSGI—vol. 8(3), p. 545, 565). Presumably because of its length it was decided to split the work into two parts, which were published in BSGI volumes 8(3) and 9(2). The work also exists reprinted in its entirety as part 3 of Sacco's "Il bacino terziario e quaternario del Piemonte" (1889–90). Despite extensive enquiries with numerous libraries, including the publishers and Società Geologica Italiana, I have been unable to determine the exact dates of publication of the two forms of the Catalogo.

References to Sacco's article in BSGI vol. 8(3) have been consistantly dated from 1889, but although parts 1–3 of this volume bear the date 1889 beside the volume number, part 3 is dated 1890 at the foot of the page (parts 1 and 2 are dated 1889). The latest date mentioned in the text of part 3 (p. 582) is in a report on an excursion that took place on September 26 1889, so it cannot have been published before then. Strong evidence that part 3 was published early in 1890 is provided by the list of new publications on the back wrapper (National Museum of New Zealand, Wellington) of series 3, volume 1, numbers 3 and 4 ("Marzo e Aprile 1890") of the Bollettino del Reale Comitato Geologico d'Italia (BRCGI) in which papers from BSGI volume 8(3) are dated 1890. The latest date shown in BRCGI 1(3,4) and thus the earliest date that it can be demonstrated to have been published (ICZN Art. 21c) is April 30 1890 (p. [159]) (interpretation accordant with dates of publication of journals mentioned on pp. 151, 153, 156, 157). That BSGI 8(3) was probably published no later than early March 1890 is suggested by the fact that the BMNH copy was received on May 3 1890, yet other Italian works of the period (table 1) were accessioned by this library 2 or more months after publication (see below).

BSGI 9(2) is dated 1890 on the title page and was evidently published mid-late 1890. Unfortunately, the earliest references to it that I have located all date from early 1891 and are thus of little assistance (received BMNH February 21).

The reprint was printed from the same plates as the BSGI parts and is identical apart from being independently paginated and in that page 78 was split for division of the BSGI parts. It is dated 1889 on the title page and 1890 on the front wrapper (University Library, Stockholm), and bears the statement (p. [ii]) "Estratto dal Bol-

Table 3. List of molluscan supraspecific taxa introduced by Bellardi & Sacco (1873–1904) in "I molluschi dei terreni terziarii del Piemonte e della Liguria," and by Sacco (1890) in "Catalogo paleontologico del bacino terziario del Piemonte"

Acrilloscala Sacco, 1890a 214(321) (1891b:[iv]; 1891d:86).
Adiscoacrilla Sacco, 1890a:214(321) (1891b:[iii]; 1891d:67).
Alectryonella Sacco, 1897b:100 (1897d 19).
Alvaniella Monterosato *in* Sacco, 1895b:76 (1895d:25).
Amathinoides Sacco, 1896a:41.
Ampullonatica Sacco, 1890a:208(315) (1890e:40, 1891a:105).
Amussiopecten Sacco, 1897c:102 (1897e:53).
Ancillarina Bellardi, 1882:217.
Ancillina Bellardi, 1882:220.
Angulatomitrella Sacco, 1890b:36.
Anura Bellardi, 1873:201.
Archimediella Sacco, 1895e:12.
Arcuatomitrella Sacco, 1890b:37.
Ascolatirus Bellardi, 1884:41.
Asperarca Sacco, 1898d:10.
Aulachalia Sacco, 1893e:33
Bivoniopsis Sacco, 1896a:15
Brachelixella Sacco, 1890a:115(222) (1890b:34).
Callistotapes Sacco, 1900:52.
Cardiolucina Sacco, 1901a:89.
Centrocardita Sacco, 1899b:14.
Ceromyella Sacco, 1901a:133.
Clanculella Sacco, 1896b:22.
Clinomitra Bellardi, 1888:10.
Clinurella Sacco, 1890a:117(224) (1890b:44).
Coccodentalium Sacco, 1896f:98 (1897a:110).
Conocerithium Sacco, 1895a:72 (*nom.nud.*); 1895c:22
Contortia Sacco, 1894b:69 (1894d:48).
Costatoscala Sacco, 1891d:72.
Costoanachis Sacco, 1890b:57
Crassostrea Sacco, 1897b:99 (1897d 15).
Cubitostrea Sacco, 1897b:99 (1897d 12).
Cyclodostomia Sacco, 1892a:53 (*nom.nud.*); 1892c:46.
Cyllenina Bellardi, 1882:161.
CYLLENINAE Bellardi, 1882:159.
Cymbulostrea Sacco, 1897d:12.
Cyrsocrassiscala Sacco, 1891e:66.
Cytherocardia Sacco, 1900:5.
Denticuloglabella Sacco, 1890b:25.
Dertonia Bellardi, 1884:51.
Diptychomitra Bellardi, 1888:10.
DIPTYCHOMITRINAE Bellardi, 1888:10
Discoscala Sacco, 1890a:213(320) (1891b:[iii]; 1891d:57).
Ditoma Bellardi, 1877:295.
Dizoniopsis Sacco, 1895a:74 (1895c:67).
Dolicholatirus Bellardi, 1884:38.
Echinophoria Sacco, 1890a.88(195) (1890c:9; 1890d:39).
Ecostoanachis Sacco, 1890b:59
Eolatirus Bellardi, 1884:15.
Eratotrivia Sacco, 1894c:62.
Euspirocrommium Sacco, 1890a:208(315) (Sacco, 1890e:42, 1891b:[i]; 1891d:10).
Fimbriatella Sacco, 1895e:36.
Flabellipecten Sacco, 1897c:102 (1897e:55).
Flabellulum Bellardi, 1873:32
Flexopecten Sacco, 1897c:102 (1897e:39).
Fulguroficus Sacco, 1890a:97(204) (1890e:27; 1891a:41).
Fusimorio Sacco, 1896f:90 (1897a:25).
Fusoficula Sacco, 1890a:97(204) (*nom. nud.*); 1890e:26 (1891a:38).
Fusoterebra Sacco, 1891c:[vi] (1891e:59).
Galeodinopsis Sacco, 1895b:77 (1895d:28).
Galeodocassis Sacco, 1890a:85(192) (*nom. nud.*); 1890c:5 (1890d:18).
GALEODOLIIDAE Sacco, 1890e:21 (invalid—no type genus); 1891a:1
Galeodolium Sacco, 1891a:4
Galeodosconsia Sacco, 1890a.93(200) (1890c:17; 1890d 69).
Gamopleura Bellardi, 1873:28.
Genea Bellardi, 1873:205.
Gibbomodiola Sacco, 1898a:41.
Gibborissoia Cossmann *in* Sacco, 1895d:34.
Gibbuloidea Sacco, 1896b:32
Gibbuloidella Sacco, 1896b:38
Giganteotrochus Sacco, 1897a:4.
Gigantostrea Sacco, 1897b:99 (1897d 14).
Glabrondina Sacco, 1892c:49.
Glabropecten Sacco, 1897e:39, 73 (error for *Flexopecten*).
Granosolarium Sacco, 1892b:56 (1892d:59).
HALIIDAE Sacco, 1893d 64 (1893e:32) (=Halliidae Sismonda, 1842).
Hordeulima Sacco, 1892a:52 (1892c:17).
Jania Bellardi, 1873:147.
Jousseaumia Sacco, 1894c:8.
Kleistopyrazus Sacco, 1895c:56.
LACHESINAE Bellardi, 1877:150.
Lazariella Sacco, 1899a:112 (1899b:21).
Ledina Sacco, 1898c:107 (1898d:53).
Limatulella Sacco, 1898a:16
Lissochlamis Sacco, 1897c:102 (1897e:46).
Luponovula Sacco, 1894a:66 (*nom. nud.*); 1894c:44
Macomopsis Sacco, 1901a:107.
Macrochlamis Sacco, 1897c:101 (1897e:32).
Macrodostomia Sacco, 1892a:53 (*nom. nud.*); 1892c:43
Macrurella Sacco, 1890a:117(224) (1890b:46).
Mantellina Sacco, 1904:148.
Margovoluta Sacco, 1890a:94(201) (*nom. nud.*); 1890c:20, (1890d:82).
MATHILDIDAE Sacco, 1892c:27 (=Mathildidae Dall, 1889).
Mayeria Bellardi, 1873:156.
Megacardita Sacco, 1899a:111 (1899b:9).
Micromitra Bellardi, 1888:5
Miocardiella Sacco, 1904:161
Miocenia Sacco, 1890a 100(207) (1904:40).
Mioporomya Sacco, 1901a:140
Mitraefusus Bellardi, 1873:204
MITROLUMNIDAE Sacco, 1904 88.
Modiolula Sacco, 1898a:41.
Monodontella Sacco, 1896b:23.
Morionassa Sacco, 1890a:93(200) (*nom. nud.*); 1890c:18 (1890d:74).
Myrsopsis Sacco, 1900:57.
Myrteopsis Sacco, 1901a:96.
Neoathleta Sacco, 1890a:152(259) (1890b:12).
Neolatirus Bellardi, 1884:40.
Nodosolarium Sacco, 1892d:63.
Obliquarca Sacco, 1898c:106 (1898d:16).
Oombolma Sacco, 1896b:15.
Oopecten Sacco, 1897c:102 (1897e:54).
Oostrombus Sacco, 1893d:63 (1893e:13).
Ooterebralia Sacco, 1895c:51.
Ornastralium Sacco, 1896b:15
ORTHOMITRINAE Bellardi, 1887a:3.

Table 3. *Continued*

Orthurella Sacco, 1890a:117(224) (1890b:51).
Panthernaria Sacco, 1894a:65 (1894c:10,67).
Papillicardium Monterosato *in* Sacco, 1899a:143 (1899b:44).
Parvamussium Sacco, 1897c:102 (1897e:48).
Parvivenus Sacco, 1900:45
Parvochlamys Sacco, 1904:145.
Pectinatarca Sacco, 1898c:106 (1898d:26).
Phorculellus Sacco, 1896b:35.
Pithocerithium Sacco, 1895a:72 (1895c:28).
Plesiolatirus Bellardi, 1884:32.
PLESIOMITRINAE Bellardi, 1887b:23
Plicostonia Monterosato *in* Sacco, 1892c:46.
Poculina Bellardi, 1873:33
Polygirculima Sacco, 1892c:10.
Proadusta Sacco, 1894a:66 (1894c:33).
Pseudavena Sacco, 1896f:92 (*nom. nud.*); 1897a:39.
Pseudemarginula Sacco, 1897a:17.
Pseudolatirus Bellardi, 1884:46.
Pseudonina Sacco, 1896b:9.
Pseudoninella Sacco, 1896b:51.
Pseudosthenorytis Sacco, 1891d:43.
Pseudotorinia Sacco, 1892d.66.
Pseudoxyperas Sacco, 1901a:26.
Ptycheulimella Sacco, 1892a:53 (1892c:59).
Ptychocerithium Sacco, 1895a:72 (1895c:23).
Ptychomelania Sacco, 1895b:75 (1895d:7).
Ptychopotamides Sacco, 1895a:73 (1895c:44).
Purpurella Bellardi, 1882:193.
PURPURELLINAE Bellardi, 1882.193.
PURPURINAE Bellardi, 1882:174 (=Purpurinae Lamarck, 1809).
Pyrogolampros Sacco, 1892b:54 (*nom. nud.*); 1892c:85.
Rhombomya Sacco, 1901a:133.
Ringiculella Sacco, 1892b:55 (1892d: 16).
Ringiculocosta Sacco, 1892b:56 (1892d:33).
Ringiculospongia Sacco, 1892b:55 (1892d:15).
Rouaultia Bellardi, 1877:223.
Saintiopsis Sacco, 1898a:11.
Sassia Bellardi, 1873:219
Scabrella Sacco, 1890a:118(225) (*nom. nud.*); 1890b:54.
Scalaricardita Sacco, 1899b:23.
Scaptorrhynchus Bellardi, 1873:12
Seguenziella Sacco, 1904:123.
Sigaretotrema Sacco, 1890a:207(314) (1890e:38, 1891a:97).
Simplicodolium Sacco, 1891a:13.
Simplicoglabella Sacco, 1890b:21.
Simplicotaurasia Sacco, 1890a:124(231) (1904:74).
Spica Monterosato *in* Sacco, 1892a:53 (*nom. nud.*); 1892c:63.
Spineoterebra Sacco, 1891c:[vi] (1891e:58).
Stazzania Sacco, 1890a:138(245) (1890b:26).
Steirotuba Sacco, 1895e:40.
Strigosella Sacco, 1896b:49
Striolucina Sacco, 1901a:83
Strioterebrum Sacco, 1891c:[vi] (1891e:33).
Strioturbonilla Sacco, 1892b:55 (1892c:94).
Sulcogladius Sacco, 1893d:63 (1893e:15).
Sulcomarinula Sacco, 1896f:95 (*nom. nud.*); 1897a:80.
Sulcosubularia Sacco, 1892a:52 (*nom. nud.*); 1892c:17.
Sulcoturbonilla Sacco, 1892b:55 (1892c:92).
Syndesmyella Sacco, 1901a:122.
Taurasia Bellardi, 1882:194.
TAURASINAE Sacco, 1904:74.
Tauraxinus Sacco, 1901a:61
Tauremarginula Sacco, 1897a:13.
Tauroforis Sacco, 1895c:62.
Taurotapes Sacco, 1900:58.
Tectonatica Sacco, 1890a:205(312) (1890e:33; 1891a:81).
TEREBELLIDAE Sacco, 1893d:64 (=Terebellinae H. & A. Adams, 1854).
Tetrastomella Sacco, 1890a:116(223) (1890b:41).
Thiarella Sacco, 1890a:117(224) (1890b:52).
Thiarinella Sacco, 1890a:118(225) (1890b:56).
Tiaracerithium Sacco, 1895a:72 (1895c:35).
Tiarapirenella Sacco, 1895a:73 (1895c:60).
Tomochiton Sacco, 1877a:90 (*nom. nud.*).
Torculoidella Sacco, 1895e:28.
TORNIDAE Sacco, 1896b:55.
Trochocerithium Cossmann & Sacco *in* Sacco, 1896b:60.
Trochotugurium Sacco, 1896a:27.
Tuberculodolium Sacco, 1891a:9
Turritodostomia Sacco, 1892a:53 (1892c:41).
Tylastralium Sacco, 1896b:19.
Uromitra Bellardi, 1887b:23.
Variamussium Sacco, 1897c:102 (1897e:49).
Ventricoloidea Sacco, 1900:31.
Vulgocerithium Sacco, 1895c:7.

lettino della Società geologica italiana Vol. 8(3)". This strongly suggests that the reprint was printed when it was still assumed that the work was to be published entire in BSGI 8(3) and thus before that part was published. The date "1889" on the title page could indicate that it was printed late in that year and that the wrapper was dated 1890 when it was realised that the work would not be circulated until 1890, or that BSGI 8(3) was to be published in 1890. It seems more plausible, however, that the reprint was printed in 1890, and that the 1889 date was added to the manuscript by Sacco and/or simply represents the *nominal* year for BSGI volume 8. The earliest reference to the work (Sacco, 1890d:7, footnote—"Boll. Soc. geol. it., 1889–90") appears in an introduction dated February 5 1890. Since the work cannot be proven to have been published in 1889, in the absence of evidence to the contrary the date of publication is interpreted as February 5 1890 (ICZN, 1985, Art. 21c). This conclusion is accordant with C. D. Sherborn's, who noted "issued before the Bollettino" on the title page of the BMNH copy of the reprint.

STATUS OF TAXA

Apart from supraspecific names (see below), parts 7 and 8 of the Bollettino series (Sacco 1890c,e) contain brief Latin diagnoses of hundreds of species group taxa accompanied by specimen dimensions and type localities.

Although these descriptions are brief and unaccompanied by illustrations, many meet criteria for availability (ICZN, 1985: Art. 11, 12), so that approximately half the total number of species group taxa more fully described and illustrated in the corresponding parts of the Memorie/Clausen series actually date from the prior Bollettino parts (taxa in part 8 so dated by Ferrero Mortara et al., 1984). The remainder of the species group names first introduced in parts 7 and 8 of the Bollettino series and all of those in subsequent parts are *nomina nuda*, since they are mentioned by name only.

Most supraspecific names first introduced in the Bollettino series meet criteria for availability since they are accompanied by one or more valid species names that were introduced by earlier authors. Some of the generic and subgeneric names, however, are *nomina nuda*, since they are accompanied only by specific names (*i.e.*, Sacco's) that are themselves *nomina nuda*. Two subfamily names (Orthomitrinae and Plesiomitrinae) introduced by Bellardi (1887a,b) are unavailable since they are not based on a type genus, while Galeodoliidae is unavailable at its first introduction (Sacco, 1890e:21) because it is unaccompanied by a type genus (*Galeodolium* Sacco, 1891a: 4). Genus group names first introduced by Sacco (1890c,e, 1891b) in parts 7–9 of the Bollettino series lack type species designations, while type species are designated unequivocally in all of the following parts. Type species for many genus group names introduced by prior authors are indicated in parts 17–29 of the Bollettino series and are thus potentially available as first subsequent designations.

All molluscan species group names introduced by Sacco in "Catalogo paleontologico del bacino terziario del Piemonte" are *nomina nuda*. Of the 26 genus group names first introduced there, however, 21 meet criteria for availability because they are accompanied by valid specific names that were introduced in prior publications (ICZN, 1985: Art. 12b(5)). The only species group name that is validly introduced in this work (reprint p. 192) is *Mastodon arvernensis* var. *cantamessae* Sacco, 1890 (Mammalia).

Attention is drawn to the fact that dating of genus group taxa from the Bollettino series and the "Catalogo" affects some currently accepted type species designations. For example, in cases where Sacco did not designate a type species in the Memorie/Clausen series, authors have selected type species by subsequent designation, but some of these designations are invalid because the species were not among those included when the genus was first introduced. These problems should preferably be treated individually by specialists, and to avoid influencing future decisions they are not considered here.

All molluscan supraspecific names introduced by Bellardi (1873–1888) and Sacco (1890–1904) that I have been able to trace are listed (table 3). For convenience, page references are provided for all names in the Memorie/Clausen series (reprints) and in "Catalogo paleontologico del bacino terziario del Piemonte", but only to prior introductions (valid and invalid) in the Bollettino series. Page references to the "Catalogo" include both the reprint and (in parentheses) Bollettino della Società Geologica Italiana 9(2). Unless indicated as *nomen nudum* or otherwise invalid, the first citation is interpreted as the earliest nomenclaturally valid introduction of the name.

SPELLING OF *LISSOCHLAMIS*, *MACROCHLAMIS* AND *VARIAMUSSIUM*

In part 24 of the Memorie/Clausen series, Sacco (1897e) altered the original spellings (Sacco, 1897c) of *Lissochlamis*, *Macrochlamis*, and *Variamussum* to *Lissochlamys*, *Macrochlamys* and *Variamussium*. Although "chlamis" is an incorrect transliteration of the Greek "chlamys" (a garment), incorrect transliterations are not to be considered inadvertent errors (ICZN, 1985: Art. 32c), so *Lissochlamys* and *Macrochlamys* are unjustified emendations (ICZN, 1985: Art. 33). That Sacco's (1897c) original spellings of *Lissochlamis* and *Macrochlamis* were perhaps intentional is suggested by the consistent usage (twice each), as subgenera of *Chlamys* (sic.—three times). Accordingly, I follow Hertlein (1969) and Vokes (1980) and interpret *Lissochlamis* and *Macrochlamis* as correct spellings, despite the fact that *Lissochlamys* and *Macrochlamys* have been widely used.

The original spelling *Variamussum* has been entirely overlooked, and Sacco's subsequent spelling has been universally accepted. Although *Variamussum* is consistently so-spelt (twice) in the original reference, it is obviously a lapsus, so from the standpoint of nomenclatural stability it is appropriate in this instance to accept *Variamussium* as a justified emendation.

COMPILATION OF "I MOLLUSCHI DEI TERRENI TERZIARII DEL PIEMONTE E DELLA LIGURIA", AND "CATALOGO PALEONTOLOGICO DEL BACINO TERZIARIO DEL PIEMONTE"

It should be noted that the sections entitled "Catalogo generale dei molluschi dei terreni terziarii del Piemonte e della Liguria" occurring in each part of the Memorie/Clausen series (*i.e.*, in both parent journal and reprints) were reprinted independently with independent paginations and title pages. Identical to the originals, these reprints were prepared for separate binding and are not included here.

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Bellardi, L. 1877. I molluschi dei terreni terziarii del Piemonte e della Liguria. Parte 2: Gasteropoda (Pleurotomidae). Memorie della Reale Accademia delle Scienze di Torino (2) 29, 1878:1–364 (reprint 364 p.), 9 plates (June 30 1877).

Bellardi, L. 1882. I molluschi dei terreni terziarii del Piemonte e della liguria. Parte 3: Gasteropoda (Buccinidae, Cyclopsidae, Purpuridae, Coralliophilidae, Olividae). Memorie della Reale Accademia delle Scienze di Torino (2) 34, 1883:219–469 (reprint 253 p.), 12 plates (December 10 1882).

Bellardi, L. 1884. I molluschi dei terreni terziarii del Piemonte e della Liguria. Parte 4: Fasciolariidae e Turbinellidae. Memorie della Reale Accademia delle Scienze di Torino (2) 37, 1886:3–62 (reprint 62 p.), 2 plates (December 1 1884).

Bellardi, L. 1887a. I molluschi dei terreni terziarii del Piemonte e della Liguria. Parte 5[a]: Mitridae. Memorie della Reale Accademia delle Scienze di Torino (2) 38, 1888:79–166 (reprint 85 p.), 2 plates (January 15 1887).

Bellardi, L. 1887b. I molluschi dei terreni terziarii del Piemonte e della Liguria. Parte 5[b]: Mitridae (continuazione). Memorie della Reale Accademia delle Scienze di Torino (2) 38, 1888:257–327 (reprint 72 p.), 2 plates (June 1 1887).

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Sacco, F. 1890b. I molluschi dei terreni terziarii del Piemonte e della Liguria. Parte 6: (Volutidae, Marginellidae, Columbellidae). Memorie della Reale Accademia delle Scienze di Torino (2) 40, 1890: 295–368 (reprint 76 p.), 2 plates (April 6 1890).

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Sacco, F. 1890d. I molluschi dei terreni terziarii del Piemonte e della Liguria. Parte 7: (Harpidae e Cassididae). Memorie della Reale Accademia delle Scienze di Torino (2) 40, 1890:469–560 (reprint 96 p.), 2 plates (June 18 1890).

Sacco, F. 1890e. I molluschi dei terreni terziarii del Piemonte e della Liguria. Parte 8: Galeodoliidae, Doliidae, Ficulidae e Naticidae. Bollettino dei Musei di Zoologia ed Anatomia comparata della Reale Universita di Torino 5(86):21–43 (August 12 1890).

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A Note on Supposed Homonyms of *Octopus australis* Hoyle, 1885, with Comments on *Octopus campbelli* Smith, 1902 (Cephalopoda: Octopodinae)

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ABSTRACT

"*Octopus australis* (Massy, 1916)" and "*O. australis* (Benham, 1942)", both from New Zealand, are determined not to be homonyms of *O. australis* Hoyle, 1885, from Australia, as previously suggested. Examination of new material attributable to *Octopus campbelli* Smith, 1902, from New Zealand, supports the taxonomic distinction between *O. campbelli* and *O. australis*. Massy's, Benham's and Dell's material is probably referable to *O. campelli*.

Key words: Octopus australis; Octopus campbelli; Octopodinae.

Tait (1982) redescribed and reviewed the taxonomic position of *Octopus australis* Hoyle, 1885, originally described from Port Jackson, New South Wales, Australia. In his review of related taxa 'described' from New Zealand, Tait (1982:20) indicated that two nominal taxa, "*Polypus australis* Massy [not Massey], 1916" and "*Robsonella australis* Benham, 1942," are junior homonyms of *Octopus australis* Hoyle, following the placement of *Polypus* and *Robsonella* into the synonymy of *Octopus s. s.* by Robson (1929) and Pickford (1955), respectively. Tait (1982:20) concluded that these two species require renaming. Massy's (1916) account, however, clearly indicated that she did not describe *Polypus australis* as a new species, but actually attributed her specimens to Hoyle's *australis*, and indeed cited Hoyle as the author. Therefore, *Polypus australis* is simply a new combination proposed by Massy, with Hoyle retained as the author of the species [see ICZN, 1985: Art. 50(c)(ii)]. The same is true for *Robsonella australis*, a new combination, not a new species, proposed by Benham (1942) based on his examination of new material.

Tait (1982:19) suggested, and I agree, that based on characters of the hectocotylus, it is highly unlikely that *Octopus australis* from Australia and *O. campbelli* Smith, 1902, from Campbell Island, New Zealand are conspecific, as proposed by Robson (1929:115). Tait further stated (pg. 20) that "all the New Zealand species previously considered to be synonyms of *O. australis* Hoyle appear to be separate and distinct". The available data, however, do not support this assertion. The type of *O. campbelli* and the specimens attributed to Hoyle's *australis* by Massy (1916), Benham (1942), and Dell (1952) are all characterized by W-shaped funnel organs. Robson (1929:190) gave the value 8.5 as the ligula length index (LLI) of the type of *O. campbelli*. Benham's specimens, remeasured by Tait, have a LLI of 6 to 10. Massy's specimen has a LLI of 10.9; however, the proximal starting point along the hectocotylus used to obtain this measurement is unclear. Dell's specimens have a LLI of 5–7. These overlapping data sets certainly cannot be used to distinguish among taxa. In comparison, Tait (1982) reported the LLI for *O. australis* as 12–18. Massy's (1916) figure of the radula showed a symmetrical, pentacuspid rachidian. Dell (1952) reported that the rachidian tooth is asymmetrical (however, he gave the formula as "A_4", probably an error due to the confusing situation created by Robson's original designation of the letter A for symmetrical rachidian teeth, see Robson, 1925). This variation of the radula is within the range observed from new material of *O. campbelli* examined here (see below). Therefore, based on these accounts there appears to be no clear taxonomic separation among New Zealand specimens.

For comparison to published accounts, I examined six specimens of *Octopus campbelli* (4 males, ML 22–30 mm, all with spermatophores; 2 mature females, ML 25–27 mm) from Portobello, New Zealand, deposited in the collections of the Invertebrate Museum, Rosenstiel School of Marine and Atmospheric Sciences, University of Miami, Florida (UMML 31.2447). The range of LLI is 6.5–11.1 (mean = 8.48). Two inconsistencies exist between the original description of the type of *O. campbelli* and the specimens I have examined. The Portobello specimens have gill lamellae counts of 7–8 (including terminal lamella). Smith (1902) gave no data on the gills from the holotype of *O. campbelli*. Robson (1929:190) stated that the gill count of the holotype is "probably ten", based on his reexamination. Robson's 1929 monograph contains certain factual inconsistencies (Voss, 1973). Indeed, Tait

(1982:20) found that Robson, despite his assertion that he had examined the radula from one of the syntypes of *O. australis*, could not have done so because the buccal mass had not been removed from either specimen at the time Tait acquired them for examination. Therefore, Robson's gill lamellae data, given with some degree of uncertainty, should be discounted.

The second discrepancy concerns the greatly enlarged and elevated suckers (seventh pair only) on the lateral arm pairs of the type of *O. campbelli* (SnI ~ 8.5; SeI ~ 14.3). Three Portobello male specimens have moderately enlarged suckers (SnI 8.2–10.4; SeI 10.7–12.2) which are not distinctly elevated. In these specimens about three pairs of suckers, beginning with the fifth pair, are enlarged on the lateral arm pairs. Specially enlarged suckers are not mentioned specifically in the accounts of Massy, Benham, or Dell. While this disparity is curious, it could be the result of differences in reproductive maturity. In light of the other numerous similarities in morphology, dermal texture, and absolute size, I do not consider this difference to be substantiative.

The radulae of three of the Portobello specimens were examined and showed considerable variation. The rachidian tooth is strongly asymmetrical in one specimen, weakly asymmetrical in the second, and varies from symmetrical in one region to asymmetrical along another region in the third example. Intraspecific (including intra-radular) variation is known to occur in Octopoda (Robson, 1925, 1929; Adam, 1933, 1941; Voss, 1973; Toll, 1981, unpublished); therefore, differences in the symmetry of the radula can be unreliable in distinguishing among related species.

Based on examination of all pertinent accounts, I find that no homonyms of *Octopus australis* Hoyle, 1885 exist; therefore, no renaming needs to be take place. *Octopus australis* Hoyle and *Octopus campbelli* Smith, 1902 appear to be distinct allopatric taxa, most easily differentiated on the basis of hectocotylus and penial apparatus morphology, dermal texture and absolute size. Furthermore, the specimens described by Massy, Benham and Dell from New Zealand are consistent with the characters of *O. campbelli* and I consider them to be referable to it.

ACKNOWLEDGEMENTS

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Mollusks of the Genus *Antiplanes* (Gastropoda: Turridae) of the Northwestern Pacific Ocean

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ABSTRACT

Mollusks of the genus *Antiplanes* are represented in the fauna of the northwestern Pacific Ocean by 11 Recent species and one subspecies. Only *Antiplanes vinosa* (Dall) is sinistral, the remaining members of the genus are dextrally coiled. The new name *Antiplanes gabbi* is proposed for *Pleurotoma perversa* Gabb, 1865, the type species of *Antiplanes* and a junior homonym of *Pleurotoma perversa* Philippi, 1847. Six species: *Antiplanes abyssalis*, *A. dendritoplicata*, *A. obliquiplicata*, *A. kurilensis*, *A. spirinae*, and *A. habei* are described as new, as is the subspecies *A. motojimai aquilonalis*. The paucity of diagnostic features together with the high degree of intraspecific and ontogenetic variability in shell characters requires the use of statistical analyses for delineation of species. Three groups of species can be distinguished on the basis of shell sculpture and the rates of growth of radular teeth. *Antiplanes* does not occur in the Gulf of Alaska. Thus, there are no species in common between the Asian (including Bering Sea) and the western American (south of the Gulf of Alaska) faunas.

Key words: *Antiplanes*, Turridae, northwestern Pacific; sublittoral, bathyal, radular growth.

INTRODUCTION

Gastropods of the genus *Antiplanes* are among the largest and most abundant representatives of the family Turridae in the sublittoral and bathyal zones of the northern Pacific Ocean. Although many Recent and fossil species have been described, the validity of many of these taxa is questionable. The present revision of this genus is limited to the fauna of the northwestern Pacific Ocean from northern Japan to the Bering Sea, and is based on the considerable material from this region that was available to us.

MATERIALS AND METHODS

This study was based primarily on the collections of the P. Shirshov Institute of Oceanology of the U.S.S.R. Academy of Sciences (Moscow), the Zoological Museum of the Moscow State University, and the Zoological Institute of the U.S.S.R. Academy of Sciences (Leningrad). These samples, containing about 280 lots and over 900 specimens, were collected in the northwestern Pacific over a period of 90 years. Comparative material from British Columbia was kindly provided by Dr. R. Shimek (Monroe, Washington). The syntypes of *Antiplanes beringi* (Aurivillius) were made available by Dr. A. Warén (Naturhistoriska Riksmuseet, Stockholm). Photographs of the types of W. H. Dall's, E. A. Smith's and T. Habe's taxa were provided by Dr. J. H. McLean (Los Angeles County Museum of Natural History), Mrs. A. Thompson (British Museum (Natural History)) and Dr. A. Matsukuma (National Science Museum, Tokyo), respectively.

When studying shell variability we counted the number of spiral cords on the body whorl. Since the number and degree of cord development on the anal fasciole were quite variable, only cords below the fasciole were counted. In some cases the relative height of the body whorl was an important taxonomic character. In a few cases in which the upper whorls were lost, ratios of the body whorl height to the height of the last three whorls were used. Ratios of the length of the marginal teeth of the radula to shell height were calculated using the mean length of at least ten marginal teeth, measured with an ocular micrometer calibrated to 0.001 mm.

The following abbreviations for scientific research institutes are used:

BM(NH)—British Museum (Natural History), London
CAS—California Academy of Sciences, San Francisco
NRS—Naturhistoriska Riksmuseet, Stockholm
NSMT—National Science Museum, Tokyo
SBMNH—Santa Barbara Museum of Natural History
SDNHM—San Diego Natural History Museum
UCMP—Museum of Paleontology, University of California, Berkeley
USNM—National Museum of Natural History, Smithsonian Institution, Washington, D.C.

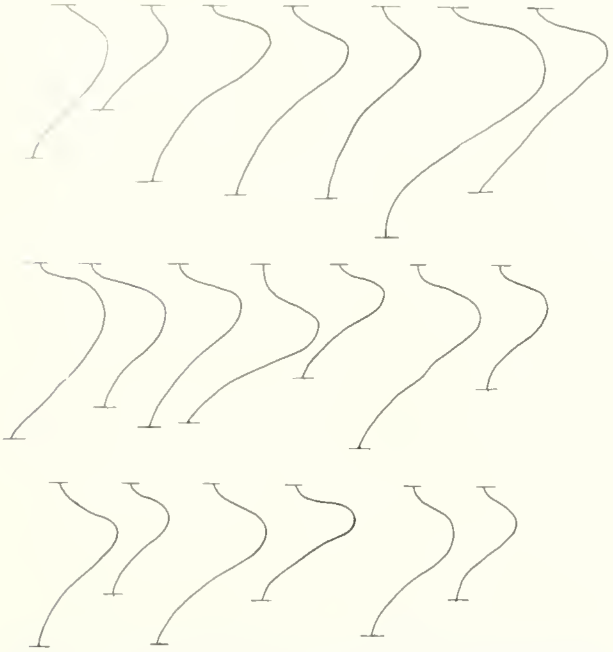

Figure 1. Variability of anal sulcus form in *Antiplanes sanctiioannis* (Smith, 1875). Growth lines along different whorls of the same specimen are connected by dotted lines.

ZIN—Zoological Institute of the U.S.S.R. Academy of Sciences, Leningrad
ZM—Zoological Museum of the Moscow State University

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We want to thank Dr. M. G. Harasewych, Editor, for his help in checking the manuscript and making it more clear for the readers.

HISTORICAL REVIEW OF THE GENUS *ANTIPLANES*

The first species presently referred to *Antiplanes* to be described was *Pleurotoma perversa* Gabb, 1865. Dall (1902) proposed the genus *Antiplanes* and described 17 Recent and fossil species from American and Asian waters (Dall, 1874, 1902, 1919, 1925). Bartsch (1944a,b) described three additional American species and isolated the dextral species of *Antiplanes* as a separate genus *Rectiplanes*. Bartsch began a revision of these groups, but this was never completed or published. Three Japanese species were later described by Habe (1958) who also established the subgenus *Rectisulcus* to include those dextral species with well-developed spiral sculpture.

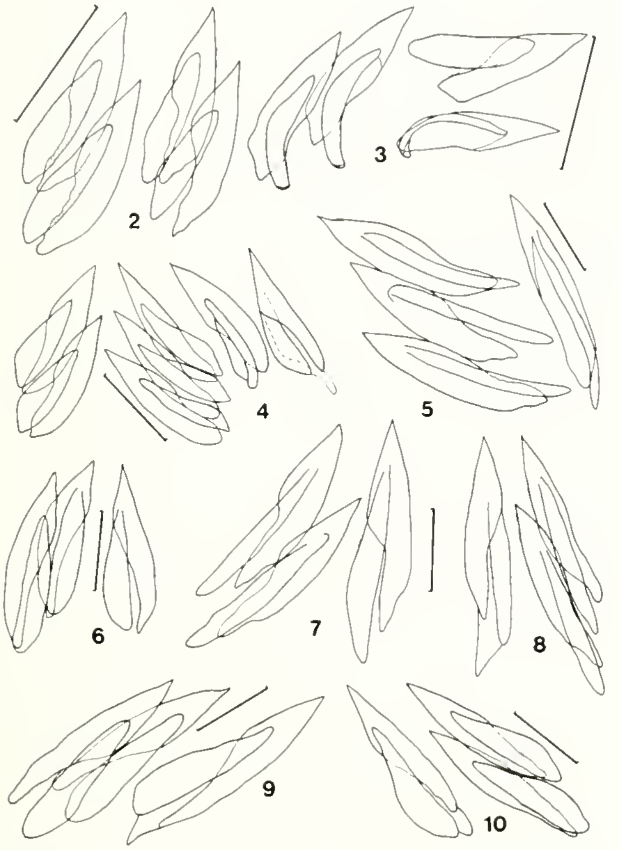
Antiplanes differs from most other members of the family Turridae in containing sinistral forms. The taxonomic status of these sinistral forms has been variously interpreted by recent workers. Based on the study of extensive collections of fossils and Recent specimens from California, Grant and Gale (1931) concluded that the direction of shell coiling was subject to intraspecific variability and synonymized almost all species known at that time with *A. perversa*. This view was shared by Golikov and Gulbin (1977) and by Golikov and Scarlato (1985). Bartsch (194a,b), however, considered sinistrality to be of generic significance.

It was shown in recent malacological literature that most sinistral forms, including those of Turridae, are separate species (Tippett, 1983; Kantor, 1990). However, sinistral individuals and even isolated sinistral populations lacking taxonomic status have been reported (e.g., the sinistral population of *Conus mediterraneus*, see Donati *et. al*, 1984). Analysis of the available material showed that sinistral *Antiplanes* from the northwestern Pacific belong to a single separate species. We have not found any examples of sinistral individuals or populations within normally dextral species of *Antiplanes*.

SPECIES VARIABILITY AND CRITERIA FOR SPECIES DIAGNOSES

In our revision of this genus, we encountered an unusually high degree of variability in many conchological features, along with a general paucity of shell diagnostic characters. Thus, characters of shell form and proportions of its parts appeared to be taxonomically insignificant in most cases. Hickman (1976) documented the taxonomic importance of anal sinus shape in Turridae. Our analysis of intraspecific and ontogenetic variation of this feature in nearly 100 individuals of *A. sanctiioannis* as well as in other species showed a very high degree of variability overlapping between species (figure 1).

Although we considered a great many potential conchological characters, the most taxonomically significant feature was determined to be the number of spiral ribs below the anal fasciole. Based on this character, two large groups of species can be distinguished; one is characterized by complete or nearly complete absence of spiral sculpture (*A. abyssalis* n. sp., *A. obliquiplicata* n. sp., *A. dendritoplicata* n. sp. and *A. kawamurai*), the other, containing the remaining species treated herein, by the presence of variably developed spiral sculpture. It should be emphasized that the number of spiral ribs on the body whorl, being an ontogenetically and geographically variable feature, allows only statistical differentiation of species (figures 117, 118, 138).

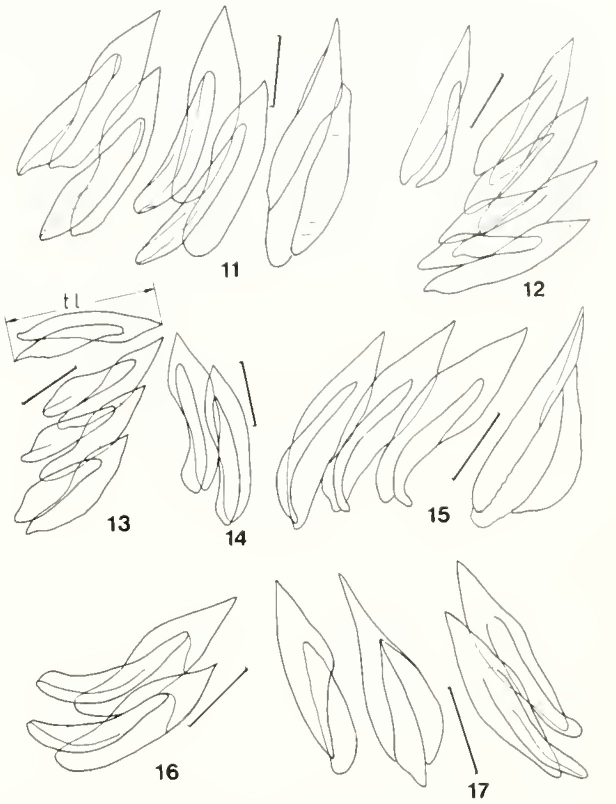


Figures 2–10. Radulae of *Antiplanes* spp. Shell lengths and catalog numbers are given in parentheses. **2.** *Antiplanes dendritoplicata* n. sp., paratype (28.3 mm, ZIN N 6/54581); **3.** *A. obliquiplicata* n. sp., paratype (40.3 mm, ZM N Lc 6899); **4.** *A. spirinae* n. sp., paratype (22.4 mm, ZM N Lc 6905); **5.** *A. isaotakii* (Habe, 1958) (30.8 mm); **6.** *A. kurilensis* n. sp., paratype (28.8 mm, ZIN N 1/54583); **7, 8.** *A. habei* n. sp. **7.** holotype (38.0 mm, ZM N Lc 6909); **8.** paratype (23.1 mm, ZM N Lc 6910); **9, 10.** *A. vinosa* (Dall, 1874). **9.** (36.3 mm), **10.** (28.6 mm). Scale bars all 100 μm.

It is interesting to note that similar patterns of morphological variation occur in different species. Specimens of *A. sanctiioannis* from Sakhalin Bay have fewer ribs on their body whorl than individuals from the Kurile Islands. The same pattern is seen in *A. vinosa*, a sister species of *A. sanctiioannis*.

The morphology of the radula offers additional characters of taxonomic importance. Though the form of the marginal teeth was similar in all species (figures 2–17), rates of radular growth permitted species to be segregated into three groups: those with rapidly, moderately and slowly growing marginal teeth (figure 18). A geographical component to the variability of this character was observed. However, comparisons of specimens of the same size from the same locality showed distinct differences between species. In figure 18, points representing different species from the same locality are connected by dotted lines.

The groups of species isolated on the basis of radular



Figures 11–17. Radulae of *Antiplanes sanctiioannis* (Smith, 1875). The collection locality and shell length of individual specimens follow. **11.** Sakhalin Bay, 45.0 mm. **12.** Sakhalin Bay, 41.9 mm; **13.** Tatar Strait, 38.0 mm; **14.** Sakhalin Bay, 36.0 mm, **15.** Southern Kurile Islands, 34.5 mm; **16.** Eastern Kamchatka, 42.0 mm; **17.** Tatar Strait, 25.0 mm. Scale bars all 100 μm.

growth pattern also differed in the degree of spiral sculpture. Species with the most slowly growing marginal teeth (*A. dendritoplicata* n. sp. and *A. obliquiplicata* n. sp.) generally lack spiral sculpture. Species with moderate marginal tooth growth rates (*A. sanctiioannis*, *A. vinosa*, *A. spirinae* n. sp., and *A. kurilensis* n. sp.) are characterized by more numerous and less developed spiral cords than the group of species with rapid marginal tooth growth (*A. habei* n. sp. and *A. isaotakii*). As with the variation in marginal tooth growth rates, species and species groups based on shell sculpture can only be distinguished statistically.

In some cases, the relative height of the body whorl was also useful for distinguishing similar species. Pairs of species such as *A. sanctiioannis* and *A. kurilensis* n. sp. as well as *A. dendritoplicata* n. sp. and *A. obliquiplicata* n. sp. (figure 46) were readily distinguished by this character.

The systematics of the genus *Antiplanes* were difficult to discern using traditional techniques due to high ontogenetic and geographical variability of nearly all generally accepted diagnostic characters. We have been able to distinguish close but distinct species by using graphs

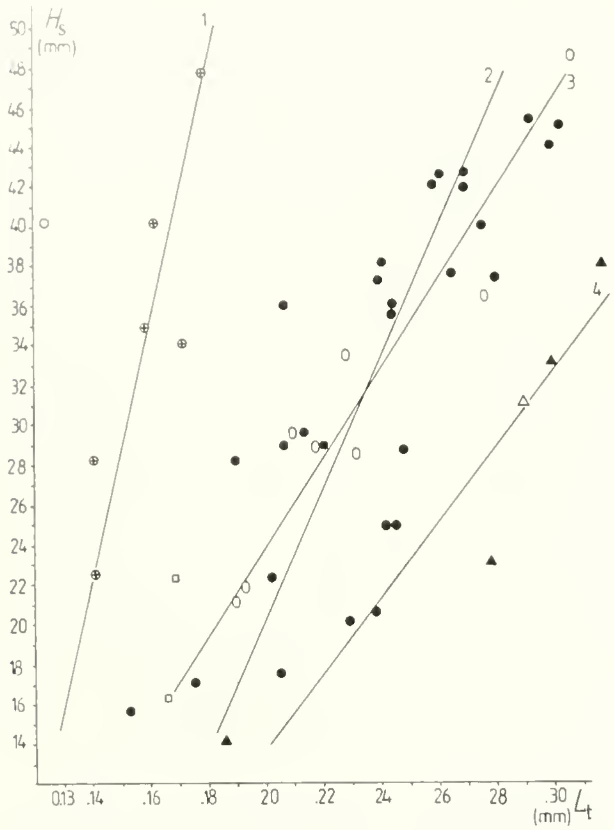


Figure 18. Rates of radular growth in species of *Antiplanes*. Crossed circles—*A. dendritoplicata* n. sp.; open squares—*A. spirinae* n. sp.; open circles—*A. obliquiplicata* n. sp.; solid circles—*A. sanctiioannis* (Smith); open ovals—*A. vinosa* (Dall); open triangles—*A. isaotakii* (Habe); solid triangles—*A. habei* n. sp. The lines of regression: 1. *A. dendritoplicata* n. sp.; 2. *A. sanctiioannis* (Smith); 3. *A. vinosa* (Dall); 4. *A. habei* n. sp. Lt—mean length of marginal tooth, Hs—shell length.

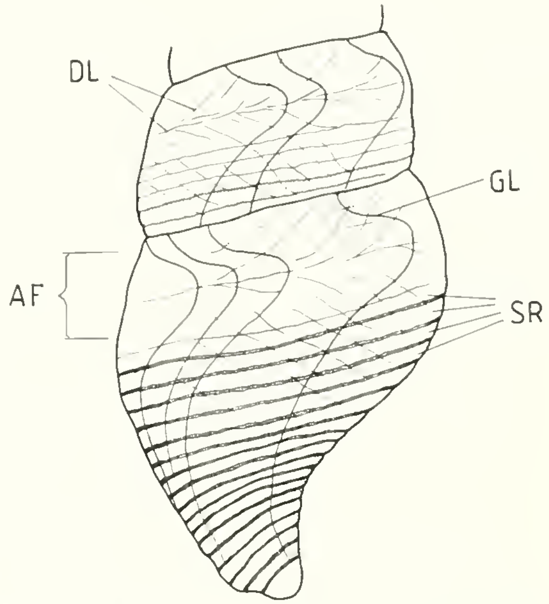


Figure 19. Diagrammatic representation of the shell base of *Antiplanes habei* n. sp. AF—anal fasciole, DL—dendritic ribs, GL—growth lines, SR—spiral ribs.

and regression analyses of various characters relative to shell height. This approach forms the basis of the following systematic treatment of this genus.

SYSTEMATICS

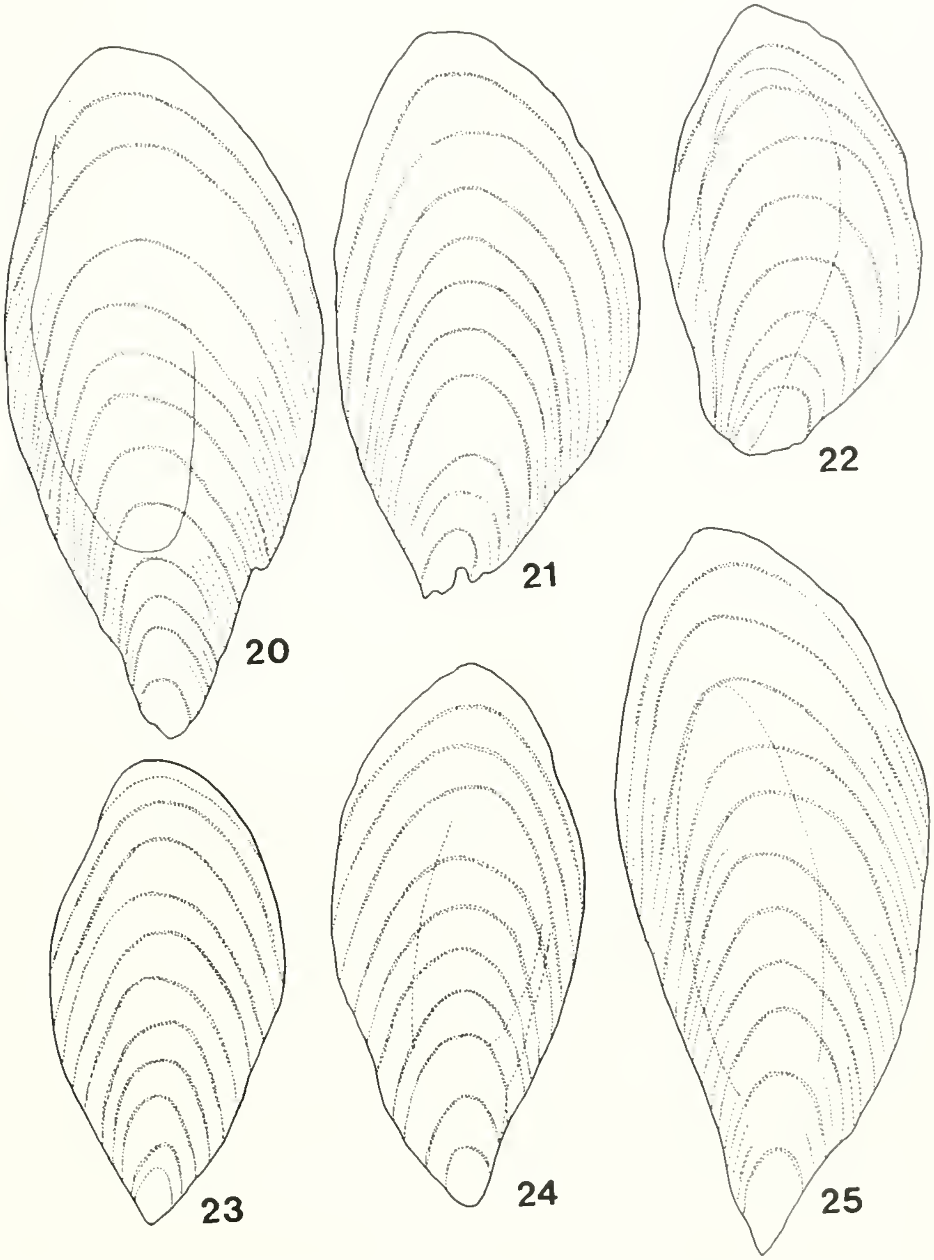
Family TURRIDAE Swainson, 1840
Subfamily Turriculinae Powell, 1942
Genus *Antiplanes* Dall, 1902

Dall, 1902:513 (type species, by original designation—*Pleurotoma* (*Surcula*) *perversa* Gabb, 1865).
Rectiplanes Bartsch, 1944b:59 (type species, by original designation—*Pleurotoma* (*Antiplanes*) *santarosana* Dall, 1902)
Rectiplanes (*Rectisulcus*) Habe, 1958:184 (type species, by original designation—*Rectiplanes* (*Rectisulcus*) *motojimai* Habe, 1958)

Diagnosis of the genus: Shell large (to 72 mm), dextral or sinistral fusiform, covered by smooth, thick periostracum. Axial sculpture absent. Spiral sculpture may be absent or composed of ribs and dendritic threads (figure 19, DL) that may be obliquely and irregularly disposed, with ramifying small threads radiating from extremities of anal sinus growth lines. Anal sinus deep, located on shoulder or near periphery. Siphonal canal long, occasionally slightly curved. Operculum (figures 20–25) large, drop-shaped, terminally nucleated, filling the aperture. Radula "nontoxoglossate", consisting of proximally bifurcated marginal teeth and of vestigial rachidian teeth.

Type species: *Pleurotoma* (*Surcula*) *perversa* Gabb, 1865, the originally designated type species of *Antiplanes*, is a primary homonym of *Pleurotoma perversa* Philippi, 1846. Grant and Gale (1931) considered *P. perversa* Gabb to be a synonym of *P. voyi* Gabb, 1869. However, the original descriptions and illustrations demonstrate that these are different species. Indeed, one of them (*P. perversa*) is sinistral while the other (*P. voyi*) is dextral. As no available name exists for *Pleurotoma perversa* Gabb, 1865, we here propose *Antiplanes gabbi*, ***nomen novum***, as a replacement name. Syntypes (UCMP 15929 and 31547) Catalina Island, California (Recent); (UCMP 15930), Pleistocene of San Pedro, California (Coan & Bogan, 1988).

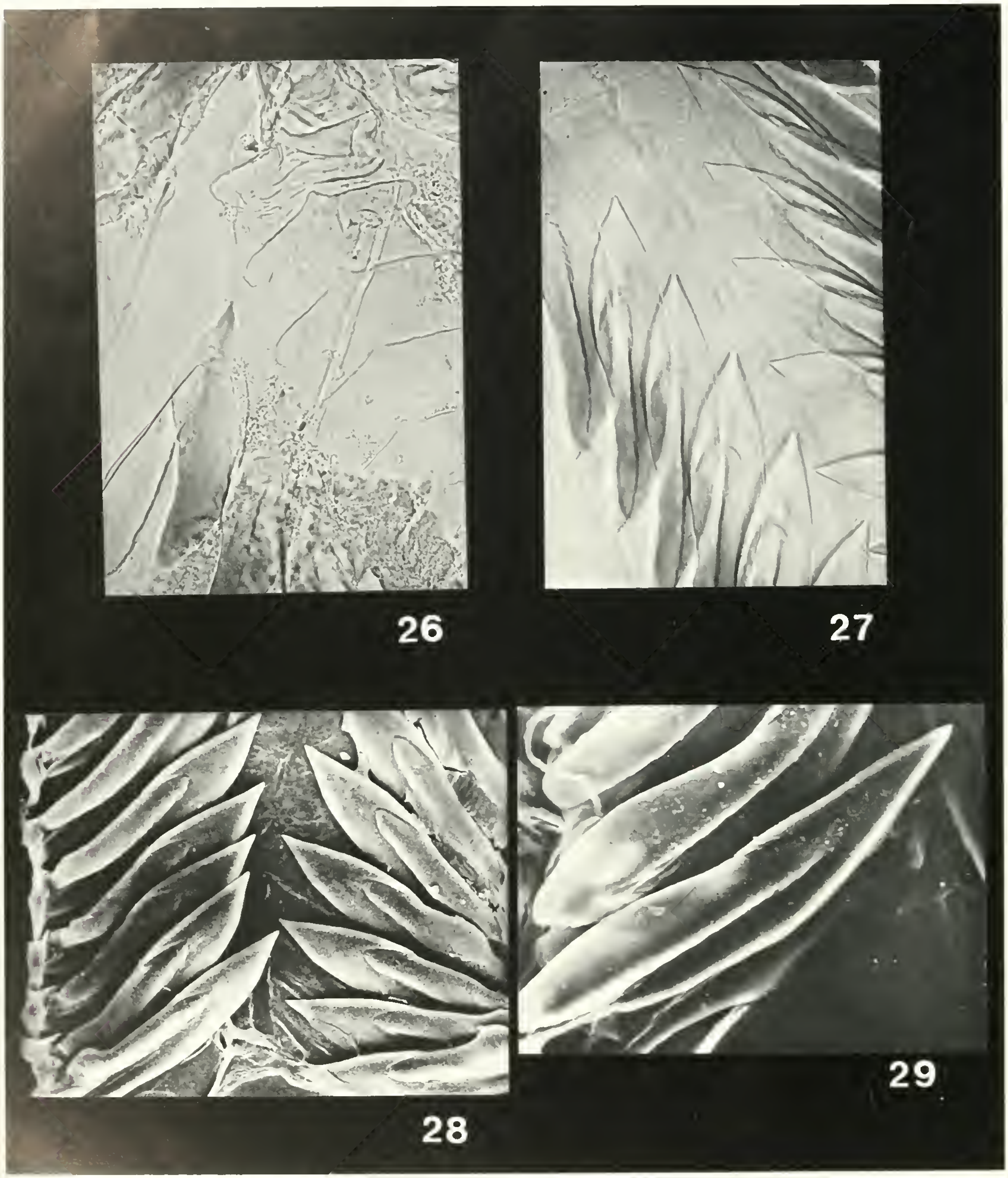
Distribution: Species of *Antiplanes* live in the northern part of the Pacific Ocean from California to British Columbia, along the American coast and from Honshu, Japan to the Gulf of Anadyr, Bering Sea, along the Asian coast, at sublittoral to upper abyssal depths. In the Bering Sea, *Antiplanes* were found in western, eastern and central parts. Neither the literature nor samples at our disposal contain records of *Antiplanes* from the Gulf of Alaska. According to our data, western American (southward of the Gulf of Alaska) and Asian (including the Bering Sea) faunas have no species in common.



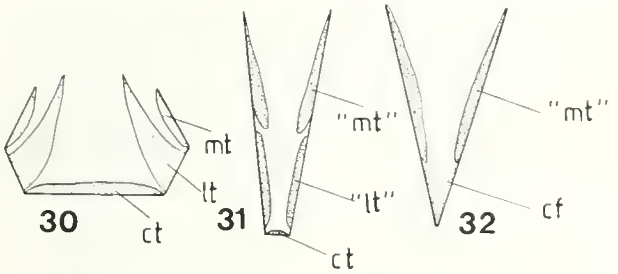
Figures 20–25. Opercula of *Antiplanes* spp. **20.** *A. obliquiplicata* n. sp., holotype, ZM N Lc 6898, 40.3 mm **21.** *A. dendritoplicata* n. sp., paratype, ZIN N 6/54581, 28.3 mm. **22.** *A. spirinae* n. sp., paratype, ZM N Lc 6905, 16.3 mm. **23.** *A habei* n. sp., paratype, ZIN N 1/54627, 33.3 mm. **24.** *A. vinosa* (Dall), 36.3 mm. **25.** *A. sanctiioannis* (Smith), 42.7 mm

Fossil species of *Antiplanes* are known from the Eocene of North America (*Drillia cooperi* Dickerson, according to Grant and Gale, 1931). In the eastern Pacific, the genus was frequently found in Pliocene deposits of Oregon and Washington (Grant & Gale, 1931; Addicott, 1976) and in Pliocene and Pleistocene of California (Grant & Gale, 1931). In the western Pacific, earliest occurrences of the genus were recorded from the Middle Miocene of Japan (*A. sadoensis* (Yokoyama)—Chinzei, 1959, and *A. sanctiioannis* (Smith)—Amano, 1983). Species of *Antiplanes* are abundant in Pliocene deposits of Honshu and Hokkaido, Japan (Masuda & Noda, 1976). *Antiplanes voyi* and a dextral *Antiplanes* sp. were found in the upper Pliocene to lower Pleistocene of eastern Kamchatka (Petrov, 1982).

Remarks: The genus *Rectiplanes* was erected by Bartsch (1944b) to contain dextral species only. No other characters distinguishing *Rectiplanes* and *Antiplanes* can be identified. Since we do not consider direction of shell coiling to be of more than a species level character, *Rectiplanes* is regarded as a synonym of *Antiplanes*.



Figures 26–29. Light (26, 27) and SEM (28, 29) micrographs of radulae. **26–28.** *Antiplanes sanctiioannis* (Smith). **29.** *A. vinosa* (Dall).



Figures 30–32. Diagrammatic representations of transverse sections of the radula in the radular sac. **30.** *Olivella borealis* Golikov, 1967. **31.** *Splendrillia chatamensis* Sysoev and Kantor, 1989. **32.** *Antiplanes sanctiioannis* (Smith, 1875). cf—"central formation", ct—central tooth, lt—true lateral tooth, "lt"—the so called "lateral" tooth of Turridae, mt—true marginal tooth, "mt"—the so called "marginal" tooth of Turridae.

Habe (1958) established the subgenus *Rectisulcus* for dextral species with well developed spiral ribs. As there is a continuum in the degree of spiral rib development, we follow Powell (1966), in synonymizing *Rectisulcus* with *Antiplanes*.

Varying opinions exist as to the composition of the transverse rows of teeth in the *Antiplanes* radula. A reduced central tooth having the form of a narrow plate pointed at both ends occurs in the eastern Pacific species *A. santarosana* and *A. thalaea* (Powell, 1966, figures 57, 58). However, McLean (1971) indicated that eastern Pacific species of *Antiplanes* lacked central teeth. Structures superficially resembling the central teeth of other Turriculinae were seen in *Antiplanes* by means of light microscopy (figures 26, 27). Only the anterior and parts of the lateral borders of these optically transparent structures were clearly seen in unstained preparations (figure 26). When the radula was stained with Orange G and Aniline Blue, these structures appeared to be paired and symmetrical (figure 27). However, scanning electron microscopy showed that there were no distinct tooth plates on the central part of the radular membrane (figures 28, 29). The membrane had only indistinct folds that are similar to those of some other Turriculinae.

The manner in which the radular membrane is folded within the radular sheath is significant for evaluating the nature of these central structures. The radular membrane of prosobranch mollusks is folded within the radular sheath. These folds occur between groups of teeth, or between separate teeth if the radulae are greatly oligomerized. Taenioglossate radulae, for example, have two pairs of folds, one between the central and lateral teeth, the other between the lateral and marginal teeth. The same pattern occurs in those Neogastropoda that have five teeth per transverse row (*Olivella*, figure 30). However, in turrids with five teeth per transverse row (subfamily Clavinae) there is only one pair of folds, placed between the central and lateral teeth. We have also observed this pattern in two species of *Splendrillia* (figure 31).

Study of the radula of *Antiplanes* shows that the radular membrane has but a singular fold situated exactly along the middle of the "central structure." Moreover, the membrane can be easily torn along this bend. In our opinion this suggests that the "central formation" is a rudiment of a pair of lateral teeth but not of the central tooth. We propose that the central tooth was completely reduced during evolution, and that the paired folds of the membrane have then grown nearer and fused into a single bend. Maes (1983) proposed a similar evolutionary pathway for *Crassispira* (*Crassiclava*) *apicata* (Reeve) (figures 31, 32), and referred to these structures as "soft lateral teeth". Although studies of the embryonic development of the radula of *Antiplanes* would shed further light on this question, such data is presently not available.

The competing hypotheses, one of weakening of the central tooth and complete reduction of lateral teeth, the other of loss of the central tooth along with regaining of the weakened lateral teeth, cannot be fully resolved at this time.

WESTERN PACIFIC SPECIES ERRONEOUSLY ATTRIBUTED TO *ANTIPLANES*

Rectiplanes (?) *yukiae* Shikama, 1962. Shikama, 1962: 50, pl. 3, figs. 3a,b, 4a,b.

Type locality: Off Choshi, eastern Honshu—Japan, 250–300 fms. The species was subsequently reassigned to the genus *Benthodaphne* Oyama, 1962 (Okutani, 1964, 1968).

Rectiplanes (*Rectisulcus*) *hayashii* Shikama, 1977. Shikama, 1977:19, pl. 3, fig. 12a,b.

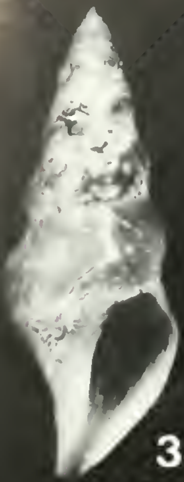
Type locality: Ensyu-nada, south-western Japan. This species has well developed axial sculpture and is here referred to the genus *Comitas* Finlay, 1926.

RECOGNIZED SPECIES OF *ANTIPLANES*

Antiplanes abyssalis new species
(figures 33–35, 45)

Material examined: Holotype: R/V 'Vityaz', 39th cruise, sta. 5603, south-east of Simushir, Kurile Islands, 46°22′N, 153°03′E, depth 3,175–3,250 m, 15.VII.1966 (ZM N Lc 6889); paratype R/V 'Vityaz', 14th cruise, sta. 2210, south-east of southern Kamchatka, 50°01.8′N, 157°39.2′E, depth 2,430–2,670 m, 24.VI.1953 (ZM N Lc 6890).

Description of holotype: Shell slender, with slightly curved axis, consisting of 6.5 teleoconch whorls and at least 1.5 heavily eroded protoconch whorls. Whorl profile angulated at periphery, whorl shoulder concave. Sutures deep. Body whorl high, comprises about 0.6 of shell height. Shell base weakly convex, passing gradually and without bending into a moderately elongate siphonal canal. Growth lines distinct. Spiral sculpture nearly absent, represented by single somewhat wavy riblet on anal fasciole and by marked dendritic ribs that reach upper and lower sutures of spire whorls but disappear on shell base. Anal sinus wide, rounded. Aperture wide, elongate-oval, poor-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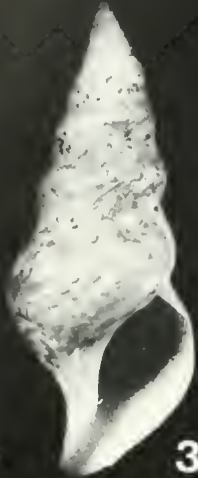
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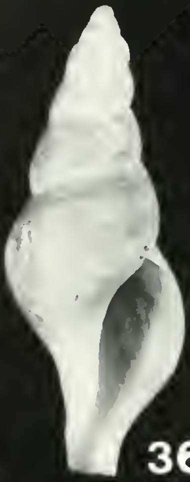
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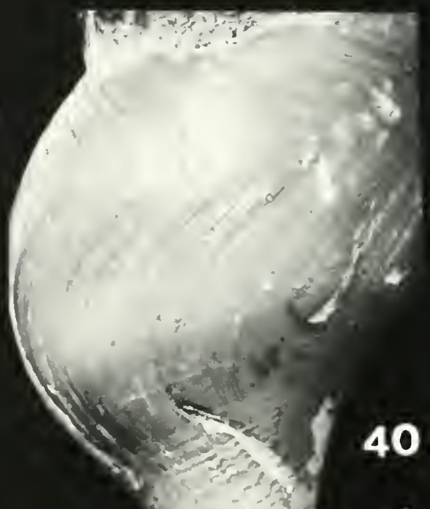
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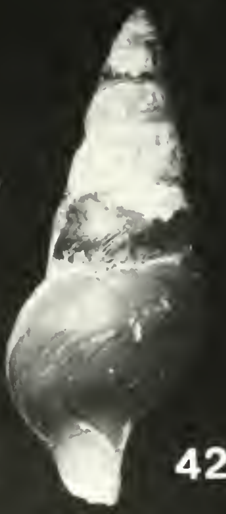
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ly differentiated from siphonal canal, outer lip attached to columella at acute angle. Columella straight, covered with narrow, white, glossy callus. Color light-yellow. Periostracum thin, smooth, glossy, fitting closely to hypostracum.

Dimensions of holotype: Shell height 31.0 mm, body whorl height 18.7 mm, aperture height 14.2 mm, shell diameter 12.0 mm.

Remarks: The paratype differs from the holotype in having a somewhat darker periostracum, a less concave profile of the shoulder, and a wider siphonal canal. The spiral riblet on the anal fasciole is weaker in the paratype.

This species differs from *Antiplanes dendritoplicata* n. sp., its nearest relative, in lacking spiral ribs on the shell base and siphonal canal, and from *A. obliquiplicata* n. sp. in having a higher body whorl as well as in whorl profile.

Distribution: This species was found along the Kurile-Kamchatka trench at depths of 2430–3250 m (figure 45).

Antiplanes dendritoplicata new species
(figures 2, 21, 36–44, 45)

Material examined: Holotype (ZM N Lc 6891) and 3 paratypes (ZM N Lc 6892): R/V 'Vityaz', 39th cruise, sta. 5641, east of Iturup, southern Kurile Islands, 44°46′N, 148°45′E, depth 472–479 m, Sigsbee trawl, 10.IX.1966; paratypes: R/V 'Vityaz', 12th cruise, sta.1779, northeastern Okhotsk Sea, depth 464 m, Sigsbee trawl, 13.X.1952 (2 specimens—ZM N Lc 6893); 12th cruise, sta. 1831, northwestern Okhotsk Sea, 56°57.5′N, 145°57.0′E, depth 196 m, Sigsbee trawl, mud, 15.X.1952 (2 specimens—ZM N Lc 6894); 24th cruise, sta. 3578, east of Honshu, 38°35.0′N, 142°53.3′E, depth 1,641 m, Sigsbee trawl, clay, 11.V.1957 (1 specimen—ZM N Lc 6895); 39th cruise, sta. 5638, east of Iturup, 44°36′N, 149°07′E, depth 1,675–1,845 m, Galathea trawl, 10.IX.1966 (1 specimen—ZM N Lc 6896); 52th cruise, sta. 6671, east of Honshu, 40°12.0′N, 143°35.8′E, depth 2,400–2,720 m, Sigsbee trawl, 23.VI.1972 (1 specimen—ZM N Lc 6897); Okhotsk Sea, sta. 139/20, 55°45′N, 145°50′E, depth 218 m, sandy mud, 1.VIII.1930, coll. P. V. Ushakov (3 specimens—ZIN N 1/54576); R/V 'Toporok', sta. 63, southeastern Sakhalin, 46°49.5′N, 143°52.3′E, depth 187 m, 4.IX.1947 (1 specimen—ZIN N 2/54577); sta. 70, southeastern Sakhalin, 46°26.2′N, 143°22.0′E, depth 103 m, mud with gravel, 6.IX.1947 (1 specimen—ZIN N 3/54578); sta. 13-a, northwest of Hokkaido, 44°47.6′N, 144°29.8′E, depth 700 m, 26.VIII.1948 (3 specimens—ZIN N 4/54579); sta. 17, off Shikotan, 43°37.1′N, 147°02.8′E, depth 1,450–1,530 m, Sigsbee trawl, mud, 28.VIII.1948 (2 specimens—ZIN N 5/54580); sta. 100, off Iturup, 44°42.0′N, 147°56.7′E, depth 299 m, 14.IX.1949 (1 specimen—ZIN N 6/54581); sta. 101, off Iturup, 44°20.8′N, 148°24.0′E, depth 414 m, 14.IX.1949 (1 specimen—ZIN N 7/54582).

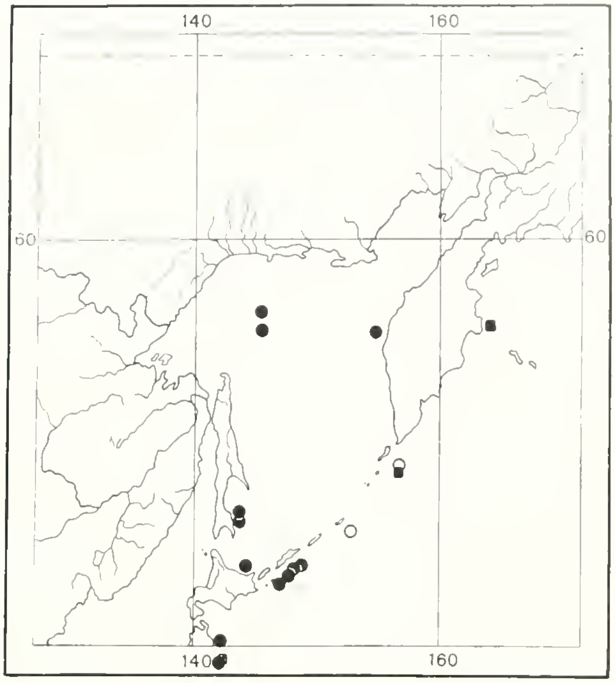

Figure 45. Geographic distribution of *Antiplanes abyssalis* n. sp. (open circles), *A. dendritoplicata* n. sp. (solid circles), *A obliquiplicata* n. sp. (solid squares).

Description of holotype: Shell slender, fusiform, composed of 5 teleoconch whorls and 1.5 heavily eroded protoconch whorls. Surface of upper 2.5 teleoconch whorls heavily eroded, rose-colored. Coiling axis slightly curved. Body whorl high, convex, comprising 0.64 of shell height. Teleoconch whorls convex, evenly rounded, divided by deep sutures. Shell base weakly convex, almost flat, passing into long siphonal canal without pronounced bend. Growth lines distinct. Spiral sculpture of indistinct, interrupted riblets on anal fasciole (3–4 on body whorl, 2–3 on penultimate whorl) and of moderately developed dendritic ribs that reach sutures on spire whorls but become smooth on shell base. Siphonal canal with 8 indistinct spiral ribs separated by shallow grooves. Aperture

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Figures 33–44. Shells of *Antiplanes* spp. **33–35.** *Antiplanes abyssalis* n. sp. **33.** holotype, ZM N Lc 6889, 31.0 mm. **34, 35.** paratype, ZM N Lc 6890, 36.2 mm. **36–44.** *Antiplanes dendritoplicata* sp. nov. **36, 37.** Holotype, ZM N Lc 6891, 41.4 mm **38.** Paratype, off Shikotan, Kurile Islands, ZIN N 5/54580, 35.2 mm. **39.** Paratype, eastward off Iturup, southern Kurile Islands, ZM N Lc 6892, 32.6 mm. **40.** The shell base of 42, note the spiral ribs on the canals. **41, 42.** Paratype, northwest of Hokkaido, ZIN N 4/54579, 37.0 mm. **43.** Paratype, east of Chonshu, ZM N Lc 6897, 27 0 mm **44.** Paratype, northwestern Okhotsk Sea, ZM N Lc 6894, 47.7 mm

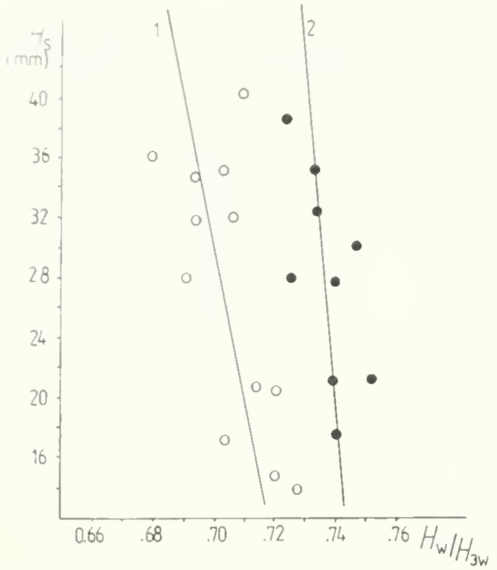

Figure 16. Comparison of the relative height of the body whorl of *A. dendritoplicata* n. sp. (open circles, 1—line of regression) and *A. obliquiplicata* n. sp. (solid circles, 2—line of regression). The shell height is plotted along the abscissa. the ratio between the body whorl height to the height of the last 3 whorls is plotted along the ordinate.

high, elongate, oval. Columella slightly thickened by white, glossy callus. Siphonal canal differentiated from aperture by its parallel margins. Shell color light-olive. Periostracum thin, glossy.

Dimensions of holotype: Shell height 41.4 mm, body whorl height 26.6 mm, aperture height 20.7 mm, shell diameter 16.0 mm.

Remarks: Paratypes have less convex whorls, more distinct and closely set riblets on the anal fasciole (up to 4 on spire whorls), a more weakly developed bend at juncture of the body whorl periphery and the shell base, and a shorter siphonal canal that is better differentiated from the shell base. Ribs on the siphonal canal of paratypes may be more numerous (up to 15) and extend onto the shell base.

Radulae of 6 paratypes were examined (figure 2). Radular teeth are small, the shell height/mean marginal tooth length ratio ranges from 159.6 (shell height 22.5 mm) to 266.5 (shell height 47.7 mm). Mean length of marginal teeth increases slowly. The linear regression equation is:

$$Y = 0.1052 + 0.0016\ X,$$

where Y is the mean length of marginal teeth and X the shell height.

Antiplanes dendritoplicata n. sp. is most similar to *A. obliquiplicata* n. sp., and the variable shell forms of both species overlap. However, *A. dendritoplicata* always has ribs on the siphonal canal (figure 40). These ribs are invariably absent in *A. obliquiplicata* (figure 52). These two species can also be distinguished by significant differences in the relative height of the body whorl (body whorl height/height of last three last whorls—figure 46). The relative height of the body whorl decreases linearly during growth. In young individuals (shell height <30 mm), differences between species are less clearly discerned, but these two species differ significantly in mean values. The regression equations are:

A. dendritoplicata

$$Y = 0.7344 - 0.0011\ X$$

A. obliquiplicata

$$Y = 0.7485 - 0.0004\ X,$$

where Y is the relative height of the body whorl and X is the height of 3 last whorls.

Distribution: This species was recorded from eastern Honshu to the northern part of the Okhotsk Sea at depths from 103 m (south-eastern Sakhalin) to 2,720 m (east of Honshu) (figure 45).

Antiplanes obliquiplicata new species
(figures 3, 20, 45, 47–52)

Material examined: Holotype (ZM N Lc 6898) and 6 paratypes (ZM N Lc 6899): R/V 'Vityaz', 24th cruise, sta. 3577, E of Honshu, 38°40.1′N, 143°29.3′E, depth 3042 m, mud, 10.V.1957; paratypes: R/V 'Vityaz', 5th cruise, sta. 618, western Bering Sea, 57°03.5′N, 168°30.5′E, depth 3,875 m, Sigsbee trawl, mud, 25.IX.1950 (1 specimen—ZM N Lc 6900); 14th cruise, sta. 2209, E of southern Kamchatka, 49°46′N, 157°48′E, depth 3,660 m, Sigsbee trawl, 23.V.1953 (4 specimens—ZM N Lc 6901); 24th cruise, sta. 3578, E of Honshu, 38°35.0′N, 142°53.3′E, depth 1641 m, Sigsbee trawl, clay, 11.V.1957 (1 specimen—ZM N Lc 6902).

Description of holotype: Shell slender, fusiform, composed of 8 whorls. Three upper whorls heavily eroded. Two upper whorls considerably smaller in diameter, probably representing protoconch. Body whorl convex, comprising 0.56 of shell height. Shell covered by thin, olivaceous, somewhat glossy, non-exfoliating periostra-

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Figures 17–58. Shells of *Antiplanes* spp. **47–52.** *Antiplanes obliquiplicata* n. sp. **47. 48.** Holotype, ZM N LC 6898, 40.3 mm. **49.** Paratype. east of Chonshu. ZM N Lc 6899, 36.2 mm. **50.** Paratype, east of Chonshu. ZM N Lc 6902, 32.0 mm. **51.** Paratype, the same sample as 49, ZM N Lc 6899, 20.8 mm. **52.** The shell base of the holotype, note the absence of spiral ribs on the canal. **53–58.** *Antiplanes kawamurai* (Habe, 1958). **53, 54.** Holotype, NSMT N 38598, 35.8 mm. **55.** Off Shikotan, Kurile Islands, ZIN N 56322, 52.1 mm. **56, 57.** East of Chonshu, 30.6 mm. **58.** The same sample as 56, 57, 11.7 mm.


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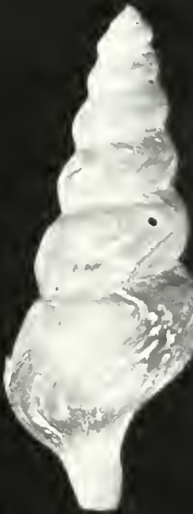
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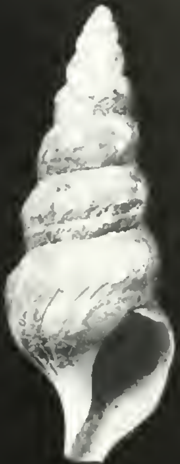
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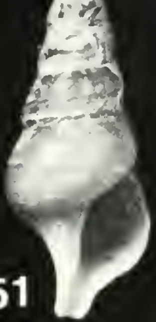
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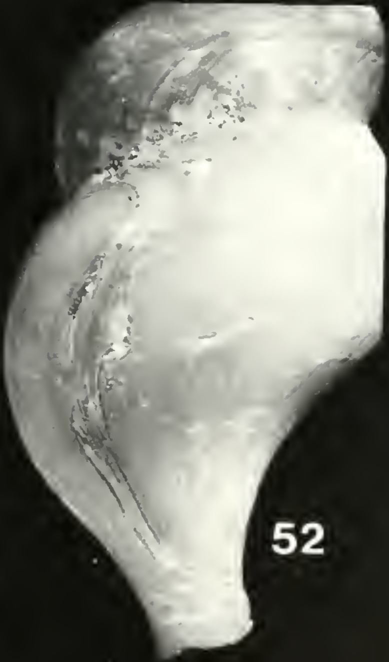
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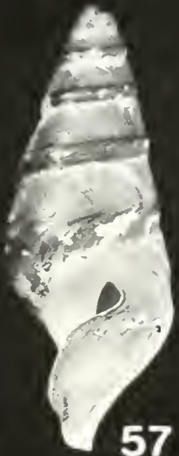
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cum. Teleoconch whorls highly convex, evenly rounded, separated by deeply impressed suture. Shell base extremely convex, giving rise to long, broad, curved siphonal canal. Growth lines thin, indistinct. Axial folds oriented parallel to growth lines below anal fasciole on upper whorls, absent on body whorl. Anal sinus deep, wide, rounded. Spiral sculpture of well-developed dendritic threads that reach sutures on spire whorls and siphonal canal on body whorl. Spiral riblets (2–3) can be traced on anal fasciole of upper whorls. Spiral sculpture absent on shell base and siphonal canal. Aperture elongate-oval, well differentiated from siphonal canal. Columella concave, covered by white, glossy callus.

Dimensions of holotype: Shell height 40.3 mm, body whorl height 22.7 mm, aperture height 18.0 mm, shell diameter 15.5 mm.

Remarks: Radular teeth of the paratype (figure 3) are small. Mean length of marginal teeth is 0.124 mm (shell height/tooth length = 325). The shoulders and shell bases of the paratypes are weakly angular; their whorls may be more flattened. The anal fasciole and the part of the whorl nearest to the upper suture may be covered with thin spiral cords. The canal may be straighter and more differentiated from the aperture.

This species is most similar to *A. dendritoplicata*, and may be differentiated from that species as discussed in the remarks for that species.

Distribution: *Antiplanes obliquiplicata* ranges from Honshu to eastern Kamchatka at depths of 1,641 to 3,875 m (figure 45).

Antiplanes kawamurai (Habe, 1958)
(figures 53–58)

Rectiplanes kawamurai—Habe, 1958:181–184, text-fig. 1; Shikama, 1962:50–51, pl. 3, figs. 1a,b, 2a; Okutani, 1964:423, pl. 14, fig. 6; 1968:37, pl. 3, fig. 7.

Type specimens: Holotype (NSMT N 38598), shell height 35.8 mm; paratype (NSMT N 52671), shell height 34.8 mm.

Type locality: Off Choshi, Chiba Pref., Honshu, Japan, in 183–274 m.

Material examined: Off Shikotan, Kurile Islands, 43°35.5′N, 147°20.5′E, depth 1,450–1,530 m, mud, 28.VII.1948 (1 specimen ZIN N 56322); E of Honshu, Japan (4 specimens).

Description: Shell light greenish or brownish, broadly fusiform, with flat-sided spire outline. Body whorl moderately convex, tapering rapidly to join broad, short siphonal canal. Whorls weakly convex, angulated below anal fasciole, nearly turreted in young specimens. Anal fasciole usually concave, with spiral sculpture absent or of indistinct threads. Dendritic cords well developed, reaching suture on spire whorls, occasionally reaching shell base. Aperture oval, broad, outer lip joining columella at right or obtuse angle. Shell height reaching 56 mm (Shikama, 1962).

Remarks: This species is easily distinguished from other species of *Antiplanes* with weakly developed spiral sculpture (*A. dendritoplicata*, *A. obliquiplicata*, *A. abyssalis*) by its broad shell and angulated whorls.

Distribution: *Antiplanes kawamurai* inhabits the eastern coast of Japan from Sagami Bay to the southern Kurile Islands (Shikotan Island), at depths of 1,520 m (Sagami Bay—Okutani, 1968) to 183 m (type locality).

Antiplanes sanctiioannis (Smith, 1875)
(figures 1, 11–17, 25, 26–28, 59–88, 100–103)

Pleurotoma (?*) *Sancti-Ioannis* Smith, 1875:416–417.
Pleurotoma Beringi Aurivillius, 1887:377, Taf. 13, fig. 3.
Pleurotoma (*Antiplanes*) *piona* Dall, 1902:514
Antiplanes piona Dall, 1925:4, pl. 21, fig. 5.

→

Figures 59–69. Shells of *Antiplanes* spp. **59–62.** *Pleurotoma sanctiioannis* Smith, 1875. **59, 60.** Lectotype, BM(NH) N 1873.8.6.16, 39.2 mm. **61, 62.** Paralectotypes, BM(NH) N 1873.8.6.16, 39.9, 23.2 mm. **63–66.** *Pleurotoma beringi* Aurivillius, 1887. **63, 64.** Lectotype, NSR N 1557, 38.3 mm. **65, 66.** Paralectotypes, NSR N 1557, 37.7, 16.6 mm. **67.** *Pleurotoma* (*Antiplanes*) *piona* Dall, 1902. holotype, USNM 109179, 42.0 mm **68.** *Antiplanes yessoensis* Dall, 1925, holotype, USNM 111053, 39 mm. **69.** *Antiplanes willetti* Berry, 1953, holotype, 18.4 mm.

Figures 70–82. Shells of *Antiplanes sanctiioannis* (Smith, 1875). **70–73.** Tatar Strait, Okhotsk Sea (70, 71—39.3 mm, 72—35.1 mm. 73—33.8 mm). **74.** Sakhalin Bay, Northern Sakhalin, Okhotsk Sea (41.3 mm). **75.** Off Paramushir, northern Kurile Islands (38.2 mm). **76.** Off Onekotan, central Kurile Islands (37.2 mm). **77.** Tatar Strait, Okhotsk Sea (32.0 mm). **78.** Off Iona Island, northwestern Okhotsk Sea (30.4 mm). **79.** Off Iturup, southern Kurile Islands (32.1 mm). **80.** Off eastern Sakhalin, (38.9 mm). **81–82.** Northern part of Okhotsk Sea (81—34.3 mm, 82—40.6 mm).

Figures 83–99. Shells of *Antiplanes* spp. **83–88.** *Antiplanes sanctiioannis* (Smith, 1875). **83.** Tatar Strait, Okhotsk Sea (32.0 mm). **84.** Bristol Bay, eastern Bering Sea (34.0 mm). **85–88.** Bering Sea (85—31.7 m, 86, 87—29.6 mm, 88—39.9 mm). **89–93.** *Antiplanes kurilensis* n. sp. **89, 90.** Holotype, ZM N Lc 6903, 54.6 mm. **91.** Paratype, Kurile Islands, ZM N Lc 6904, 52.3 mm. **92.** Paratype, east off Shumshu, northern Kurile Islands, ZIN N 1/54583, 28.8 mm **93.** Off Moneron Island, Tatar Strait, subfossil specimen, ZIN N 2/54584, 35.4 mm. **94–99.** *Antiplanes spirinae* n. sp. **94, 95.** Holotype, ZIN N 1/54585, 36.5 mm. **96–98.** Paratypes, of Simushir, central Kurile Islands, ZM N Lc 6905 (96—22.4 mm, 97—14.2 mm, 98—16.3 mm). **99.** The shell base of the holotype.


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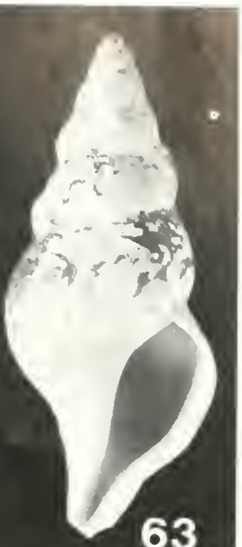
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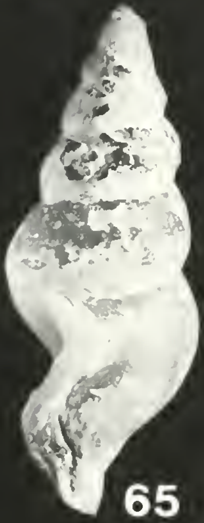
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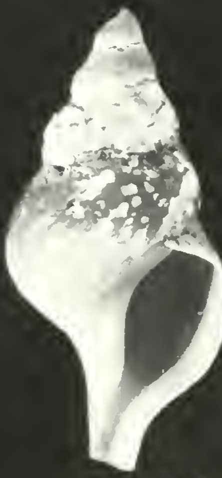
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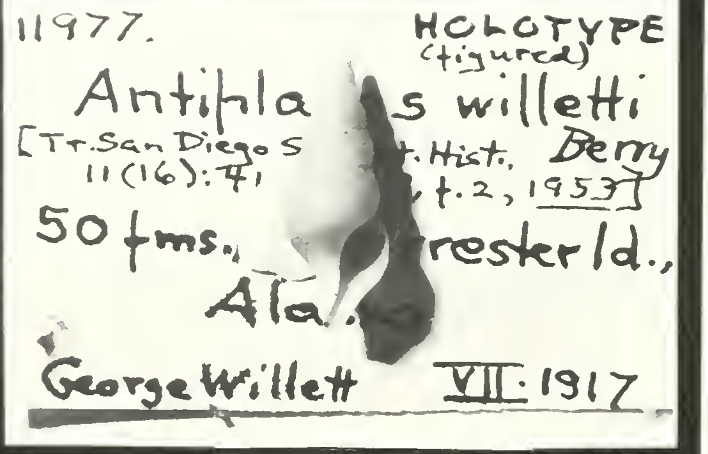

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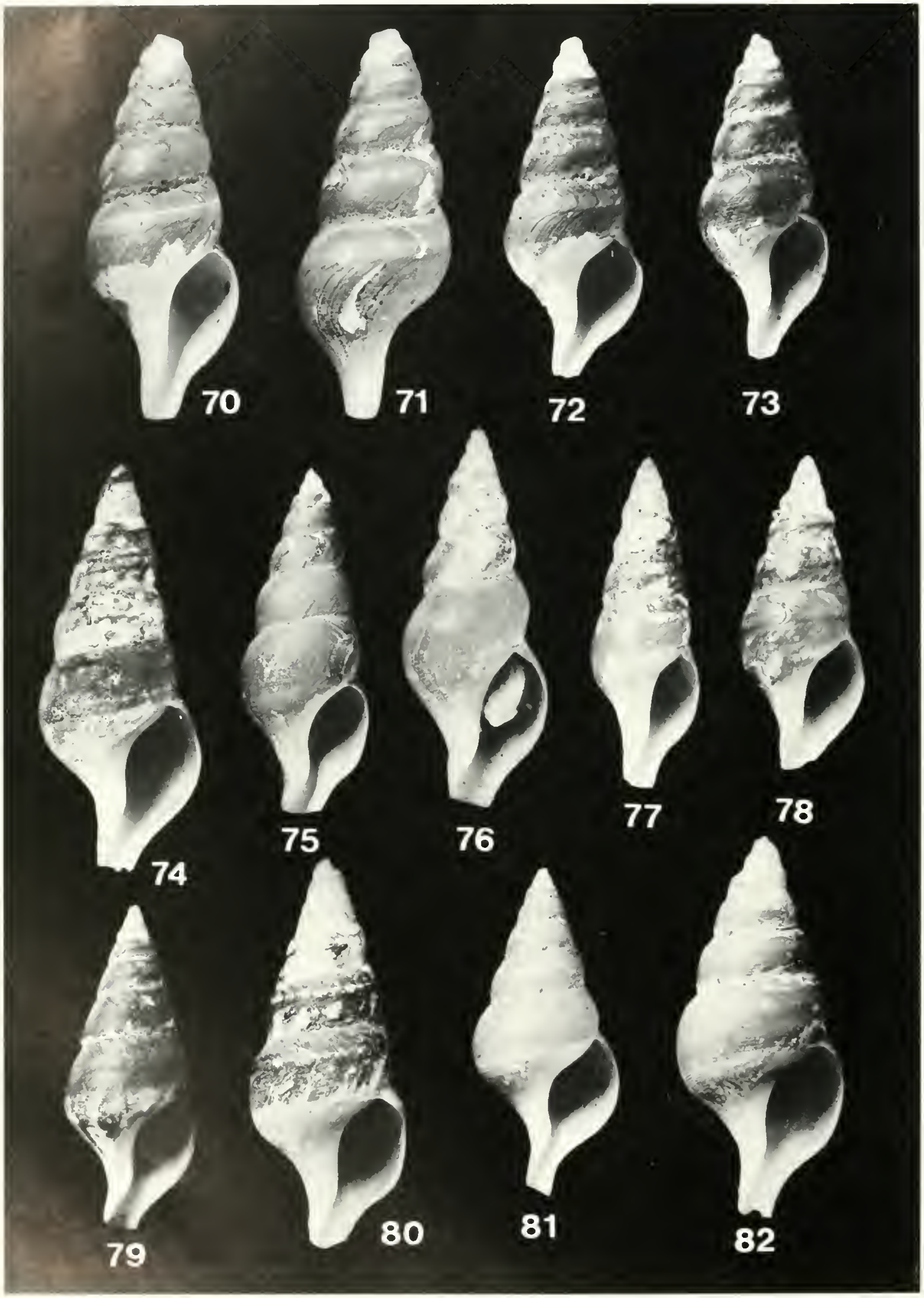
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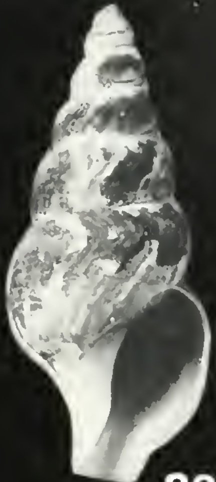
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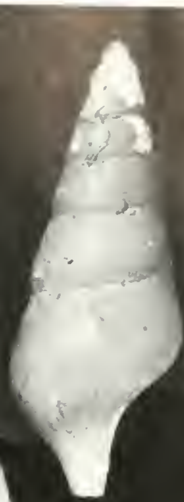
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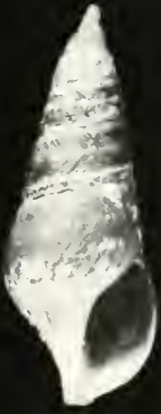
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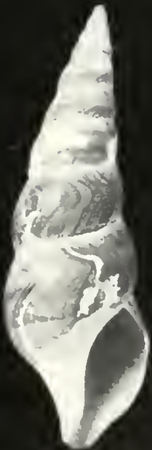
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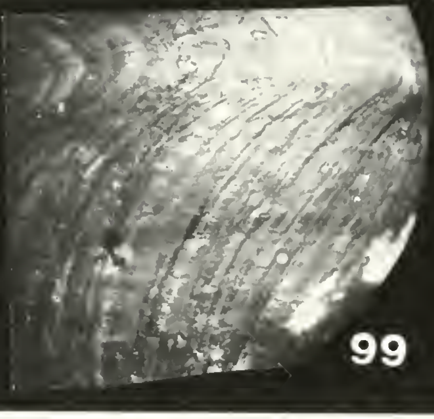
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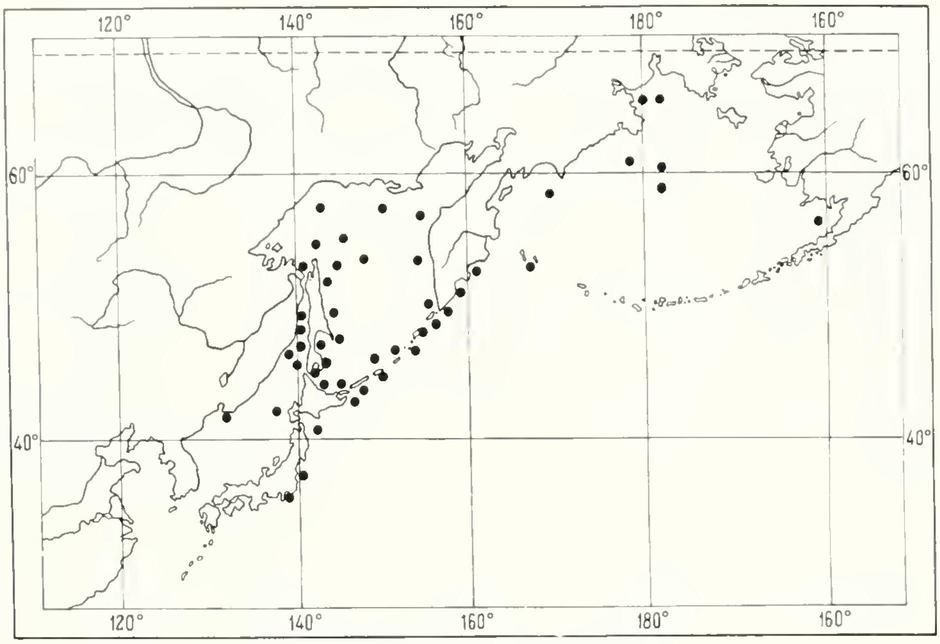

Figure 100. Geographic distribution of *Antiplanes sanctiioannis* (Smith, 1875).

Antiplanes yessoensis Dall, 1925:4, pl. 21, fig. 3.

Antiplanes (*Rectiplanes*) *willetti* Berry, 1953:419–420, pl. 29, fig. 2.

Antiplanes sadoensis Otuka, 1949:pl. 13, fig. 16 (*sensu auct.*, non Yokoyama, 1926).

Antiplanes thalaea Dall, 1919:37, pl. 11, fig. 6 (*sensu auct.*, non Dall, 1902:514).

Type specimens: Lectotype of *P. sanctiioannis* BM(NH) 1873.8.6.16, shell height 39.2 mm; paralectotypes BM(NH) 1873.8.6.16, shell height 39.9 mm, 23.2 mm. Type locality, about 100 miles south-eastward of Yesso [Hokkaido, Japan].

Lectotype of *P. beringi* (here designated), NRS N 1557, shell height 38.3 mm; paralectotypes NRS N 1557, 4 specimens. Type locality, 'Vega' Expedition, Bering Sea, 62°39'N, 177°05'W, 55 fms.

Holotype of *P. piona* USNM 109179, shell height 42 mm. Type locality, off S. coast of Kamchatka, 51°00'00"N, 157°48'00"E, in 96 fms, black sand, 'Albatross', sta. 3644 fms.

Holotype of *A. yessoensis* USNM 111053, shell height 39 mm. Type locality, Japan Sea, S. coast of Hokkaido, 41°58'00"N, 142°30'30"E, in 404 fms, brown mud, 'Albatross', sta. 5036.

Holotype of *A. willetti* CAS 064665, shell height 18.4 mm; paratypes—SBMNH No. 34539, and SDMNH 22856. Type locality, off Forrester Island, SW Alaska, 50 fms.

Material examined: Over 200 lots (about 700 specimens) were studied.

Description: Shell very variable, from elongate fusiform (figures 70, 77) to broadly fusiform (figures 81, 82), white with periostracum from light yellow to dark-brown. Body whorl variously convex. Relative height of body whorl varies within wide range (0.54–0.67). Whorls evenly rounded to angular at the shoulder and shell base, occasionally, below periphery of spire whorls (form described as *A. yessoensis*). Anal fasciole concave, flat, or convex. Anal sulcus form varies considerably, even within same specimen (figure 1). Spiral sculpture of numerous relatively narrow ribs, usually weaker at upper part of the whorl periphery and especially above anal fasciole. Ribs with serrated borders where crossed by growth lines, covered with secondary riblets that are usually inconspicuous or absent. Dendritic ribs moderately to highly developed only on anal fasciole, do not reach sutures on spire whorls. Siphonal canal usually recurved, varies from short, broad (figure 83) to long, narrow (figure 81). Shell height reaches 60 mm.

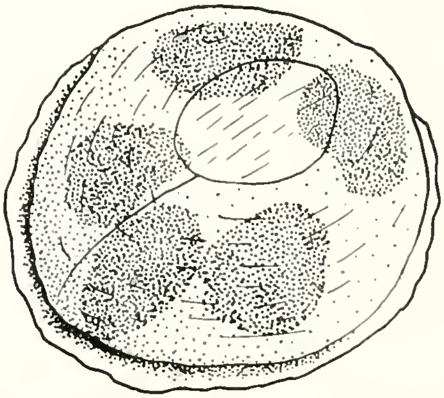

Figure 101. The egg capsule of *Antiplanes sanctiioannis* (Smith, 1875).

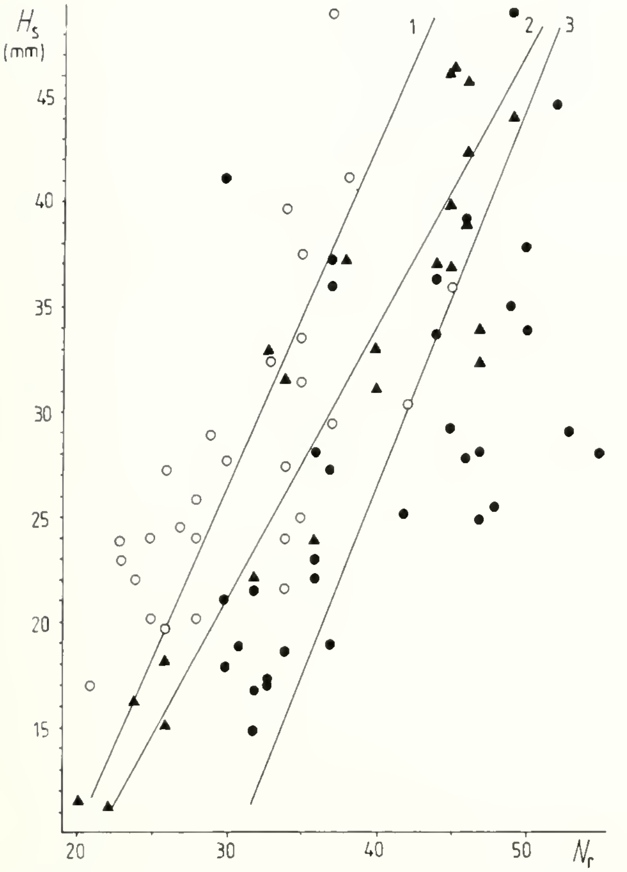

Figure 102. Comparison of the number of spiral ribs on the body whorl below the anal fasciole in populations of *Antiplanes sanctiioannis* (Smith). The shell height along the abscissa, the number of spiral ribs along the ordinate. Sakhalin Bay (open circles, 1—line of regression), east Sakhalin (solid triangles, 2—line of regression), and Tatar Strait (solid circles, 3—line of regression).

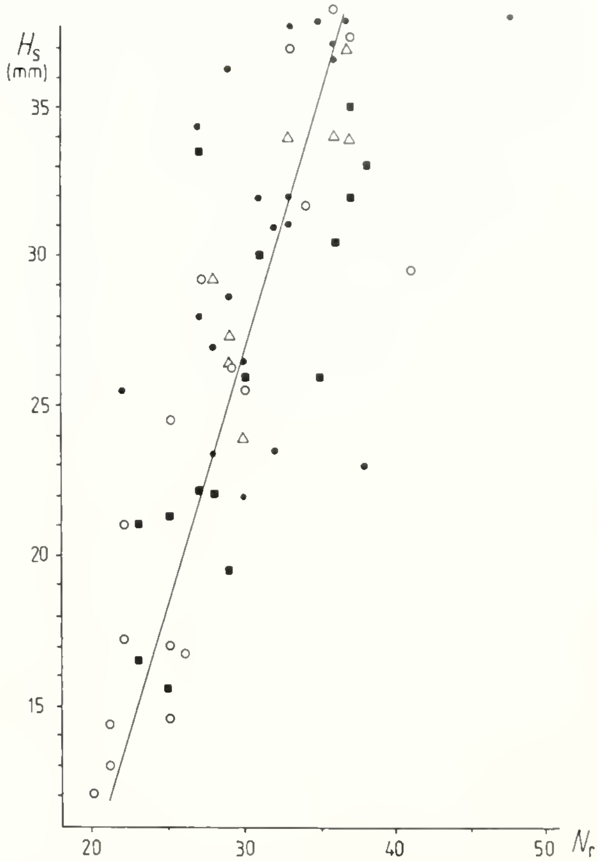

Figure 103. Comparison of the number of spiral ribs on the body whorl below the anal fasciole in populations of *Antiplanes sanctiioannis* (Smith). The shell height along the abscissa, the number of spiral ribs along the ordinate. Southern Kurile Island (solid squares), northern Kurile (solid circles), east Kamchatka (open circles), and Bristol Bay (open triangles).

Radula relatively large, ratio between shell height and mean marginal tooth length ranging from 85.4 (shell height 20.3 mm) to 173.4 (shell height 35.9 mm) (figure 18). Length of marginal teeth increases rapidly during ontogeny. Relationship between marginal tooth length and shell height nearly linear, expressed by regression equation:

$$Y = 0.1401 + 0.0030X$$

Egg capsules, most containing eggs, attached to shells of living *A. sanctiioannis*. Capsules were hemispherical (diameter—3 mm), with narrow flange at base. Surface covered with minute concentric creases, containing translucent, nearly circular apical plug (diameter—1 mm) (figure 101). Three capsules studied each contained up to 6 developing embryos.

Remarks: Shell morphology of this species is highly variable. The spiral ribs above the anal fasciole are usually absent, but may be poorly to well developed. Sculpture on the anal fasciole may consist of broad low ribs or very thin threads that may become obscure when dendritic ribs are well developed. The dendritic ribs are moderately to highly developed only on the anal fasciole and do not reach the sutures of the spire whorls. Spiral ribs become stronger, more widely spaced and usually broader below the anal fasciole. The number of ribs below the fasciole varies (3–12, usually 6–8, on the penultimate whorl) within populations and during ontogeny. When secondary riblets are well developed, the primary ribs tend to be low and uneven. Only a single specimen from the Bering Sea had uniform, equally developed ribs over the entire shell surface (figures 86, 87), and we refer this specimen to *A. sanctiioannis* with some doubt.

Although *A. sanctiioannis* is highly variable, different suites of morphological characters predominate in different portions of the species range. Among populations from the vicinity of Sakhalin Island, those in the Tatar Strait and adjacent waters have shells with dark coloration and distinct spiral sculpture that is more or less uniformly developed over the entire shell surface but that weakens slightly towards the suture (figures 70–73). Dendritic ribs are well-developed in most specimens from this area, but may be weak or limited to certain portions

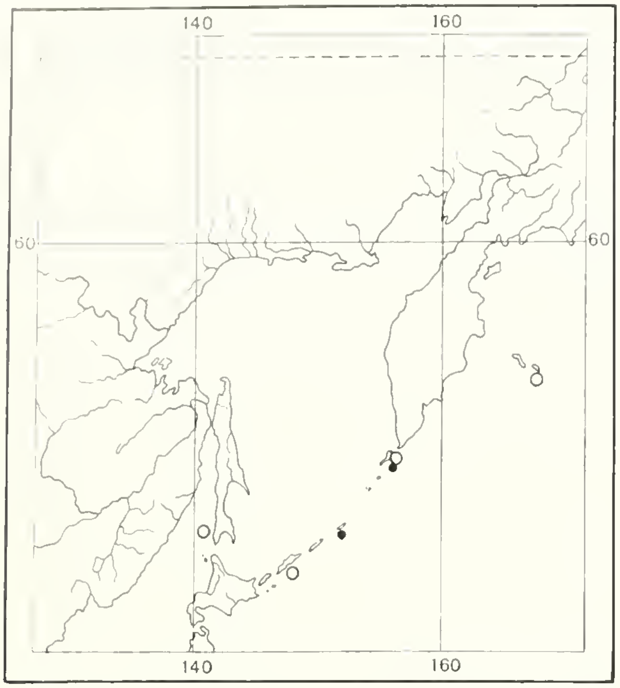

Figure 104. Geographic distribution of *Antiplanes kurilensis* n. sp. (open circles) and *A. spirinae* n. sp. (solid circles).

of the shell. Whorls are evenly rounded. The anal fasciole is flat or rarely concave. Numerous spiral ribs distinguish this population.

Specimens from Sakhalin Bay (northwestern Sakhalin) tend to be relatively light in color, and often have a convex anal fasciole and inconspicuous sculpture of fewer spiral ribs (figure 74). Spiral ribs weaken towards the periphery and dendritic ribs are usually well developed.

Intermediate forms occur along the eastern coast of Sakhalin and in the adjacent waters of the Okhotsk Sea. Specimens with angular shoulders and shell bases (figure 80) appear to be restricted to this region. Only there and, rarely, in the central and northeastern parts of the Okhotsk Sea do broadly fusiform shells with abruptly narrowing siphonal canals occur (figures 81, 82).

When these populations are compared on the basis of a quantitative character (number of spiral ribs below the anal fasciole of the last whorl), the population from the Tatar Strait (figure 102, black dots) overlaps little with the population from Sakhalin Bay. However, specimens from eastern Sakhalin occupy an intermediate position, suggesting clinal variation. Specimens found along the Kurile Islands usually have pronounced spiral sculpture over the entire shell surface, including the anal fasciole. Dendritic ribs are generally absent in these populations. Color is light yellowish to yellowish brown. Specimens with very shallow sinuses were found only near the Kurile Islands (figure 1 top, left). Specimens from the Kurile Islands, Sakhalin Bay, eastern Kamchatka, and the Bering Sea have a similar number of the ribs on the body whorl (figure 103).

Antiplanes sanctiioannis differs from *A. obliquiplicata* n. sp., *A. dendritoplicata* n. sp., *A. abyssalis* n. sp., and *A. kawamurai* in having well developed spiral sculpture that is always present below the anal fasciole of the spire whorls. *Antiplanes kurilensis* n. sp. can be distinguished from *A. sanctiioannis* by its higher spire (body whorl height/shell height ratio in *A. sanctiioannis* ranges from 0.542 to 0.667, mean value = 0.615 ± 0.004, while in *A. kurilensis* it varies from 0.500 to 0.533, mean value = 0.515 ± 0.005) and less elongate shell (shell diameter/shell height ratio for *A. kurilensis* ranges from 0.310 to 0.380, mean value = 0.346 ± 0.008, while in *A. sanctiioannis* it varies between 0.360 and 0.477, with a mean value of 0.420 ± 0.003). Features that distinguish *A. sanctiioannis* from *A. spirinae* n. sp. include the presence of spiral ribs with secondary riblets, as well as proportionally longer marginal teeth, which are evident when comparing equal-sized specimens (figure 18).

Antiplanes sanctiioannis differs from *A. isaotakii*, *A. motojimai*, and *A. habei* n. sp. in having more numerous spiral ribs (figure 138), and ontogenetically more slowly elongating marginal teeth.

Distribution: This widespread boreal species ranges from Sagami Bay (Honshu) to the Gulf of Anadyr in the northwestern Bering Sea, and has also been collected in the Sea of Japan and the Sea of Okhotsk. The bathymetric range of this species extends from 50 m (southern Sakhalin) to 1,530 m (southern Kurile Islands). Most specimens are from depths of 100 to 300 m (figure 100).

Antiplanes kurilensis new species
(figures 6, 89–93, 104)

Material examined: Holotype (ZM N Lc 6903): R/V 'Gydrobiolog' Iturup Island (Kurile Islands), depth 55–125 m, 1982; paratypes: R/V 'Gydrobiolog', Kurile Islands, 1982 (1 shell—ZM N Lc 6904); R/V 'Lebed', sta. 111, E off Shumshu, northern Kurile Islands, 50°46.9′N, 157°13.4′E, depth 103–104 m, muddy sand, 22.VII.1954 (1 specimen—ZIN N 1/54583); R/V 'Vityaz', 5th cruise, sta. 529, off Medny Island, Commander Islands, Bering Sea, 54°25.0′N, 168°16.4′E, depth 110 m, Sigsbee trawl, 14.VIII.1950 (5 specimens—ZM N Lc 6907); Expedition of the Institute of Marine Biology of the USSR Academy of Sciences, sta. 42, off Moneron Island, Tatar Strait, 46°16.7′N, 141°10.6′E, depth 115 m, 30.VIII.1972 (1 subfossil specimen—ZIN N 2/54584).

Description of holotype: Shell elongate-fusiform, with very high spire consisting of 10 whorls. Surface of first 3 whorls eroded. Body whorl moderately convex, comprising 0.51 of shell height. Shell light-brown, covered with thin, smooth, partly eroded periostracum. Teleoconch whorls evenly convex, enlarge slowly. Suture shallowly impressed, nearly canaliculate. Incremental growth lines thin, distinct, producing finely rugose appearance on shell surface. Spiral sculpture of narrow, non-dendritic, slightly wavy cords, 25 between sutures on spire whorls, about 50 on body whorl below anal fasciole. Cords evenly developed over entire shell surface. Surface of cords with pronounced growth lines. Base of shell weakly convex, gradually passing into short, straight, obliquely truncated siphonal canal. Aperture oval, narrow. Inner lip slightly curved, covered with very thin callus. Callus better developed on columella. Aperture comprises 0.35 of shell height.

Dimensions of holotype: Shell height 54.6 mm, body whorl height 27.7 mm, aperture height 19.2 mm, shell diameter 17.6 mm.

Remarks: Paratypes have less conspicuous spiral sculpture, especially on the upper part of the whorls, and less numerous spiral ribs below the anal fasciole of the body whorl (<40 in paratype with shell height of 52.3 mm). Weak dendritic threads may be present on or above the anal fasciole. Only a single specimen from off Shumshu Island had moderately developed dendritic threads on the anal fasciole.

The radula (figure 6) of a paratype (shell height 28.8 mm) was studied. Marginal teeth were 0.221 mm long (shell height/marginal tooth length = 130.3).

Antiplanes kurilensis is most closely related to *A. sanctiioannis*, but differs in having a higher spire (body whorl height/shell height = 0.500–0.533, mean value 0.515 ± 0.005 for *A. kurilensis*, 0.542–0.667, mean value 0.615 ± 0.004 for *A. sanctiioannis*).

Distribution: This species occurs in the northern and southern Kurile Islands and off Medny Island at 55–125 m. One subfossil specimen was found near Moneron Island (figure 104). A specimen resembling this new species conchologically was found in Pliocene deposits of northeastern Honshu, and was referred to *Antiplanes* (*Rectiplanes*) *sadoensis* (Yokoyama) by Chinzei (1959:pl. X, figs. 6–7, not figs. 8–9).

Antiplanes spirinae new species
(figures 4, 22, 94–99, 104)

Material examined: Holotype (ZIN N 1/54585): R/V 'Lebed', sta. 122, off Shumshu Island, northern Kurile Islands, 50°32.5′N, 157°27′E, depth 280 m, sand, gravel I.VIII.1954; paratypes: R/V 'Odyssey', 34th cruise, sta. 47, off Simushir, central Kurile Islands, 46°44.9′N, 155°21.0′E, depth 450–480 m, 30.XII.1984 (3 specimens—ZM N Lc 6905, shell heights 22.4; 16.3; 14.2 mm).

Description of holotype: Shell thin, high spired consisting of 9 preserved whorls. Two earliest whorls lost. Teleoconch whorls evenly rounded, weakly convex, widest below shoulder. Sutures shallow. Body whorl rather convex, comprising about ½ shell height. Coiling axis curved. Shell dark olivaceous; shell base, portions of anal fasciole lighter. Periostracum thin, finely granulated, peeling. Growth lines very thin, often darker than shell surface. Spiral sculpture on anal fasciole of 3–4 wide, unequal spiral cords somewhat broken by growth lines. Spiral cords less conspicuous toward body whorl. Dendritic threads stronger on anal fasciole, but generally much weaker than in other species of *Antiplanes*. Remaining surface of shell whorls covered by wide, flattened cords that become less conspicuous in later whorls, nearly absent on body whorl. Entire shell surface covered by microscopic secondary spiral threads, most conspicuously on shell base (figure 99). Shell base weakly convex, joining short siphonal canal, broken at tip. Aperture short, narrow, oval. Outer lip joining columella at acute angle. Parietal wall, columella covered by narrow, thin, white callus.

Dimensions of holotype: Shell height 36.5 mm, body whorl height 17.9 mm, aperture height 12.2 mm, shell diameter 12.0 mm.

Remarks: The paratypes have flatter whorls and less developed spiral cords on the shell surface and on the anal fasciole. The secondary threads are better developed and dendritic threads are practically absent in the paratypes.

Radulae of two paratypes were studied (figure 4). The mean length of the marginal teeth of the specimen with a shell length of 16.3 mm was 0.166 mm (shell height/marginal tooth length length = 98.2). The corresponding values for the 22.4 mm specimen are 0.169 mm and 132.5.

Antiplanes spirinae is most similar to *A. sanctiioannis*, but differs in having a narrower shell with a higher spire and less convex whorls, as well as spiral sculpture of poorly developed spiral cords and well developed secondary threads. The marginal teeth of *A. spirinae* are generally shorter than in *A. sanctiioannis* (figure 18, specimens from the same localities connected by a dotted line).

Etymology: This species is named in honor of Dr. N. Spirina, who collected the holotype.

Distribution: This species is known from the northern and central Kurile Islands at depths of 280–480 m (figure 104).

Antiplanes vinosa (Dall, 1874)
(figures 9, 10, 24, 29, 105–120)

Pleurotoma vinosa Dall, 1874:553.
Pleurotoma (*Antiplanes*) *vinosa* Dall, 1902:514, pl. 34, fig. 4
Antiplanes kamchatica Dall, 1919:33–34, pl. 10, fig. 1.
Antiplanes contraria Yokoyama, Kira, 1965:100, pl. 36, fig. 2

Type specimens: Holotype of *Pleurotoma vinosa*, USNM 220899, shell height 36 mm. Type locality—Kyska Harbour, Great Kyska Island, Aleutian Islands, 10 fms.

Holotype of *Antiplanes kamchatica*, USNM 225255, shell height 52 mm. Type locality—south-eastern coast of Kamchatka, 100 fms.

Material examined: 40 samples (more than 150 specimens) were studied.

Description: Shell sinistral, variable, usually with high spire. Color dark-brown to light yellow. Body whorl comprises 0.53 to 0.61 of shell height. Shell axis often curved. Whorls weakly to moderately convex, evenly rounded. Growth lines inconspicuous. Spiral sculpture of numerous

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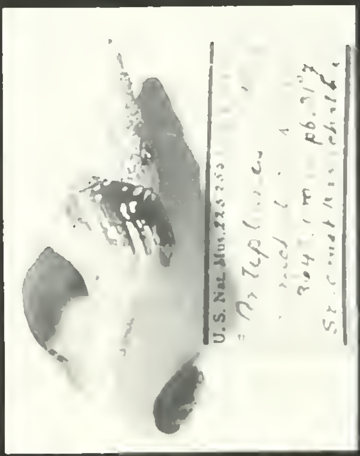

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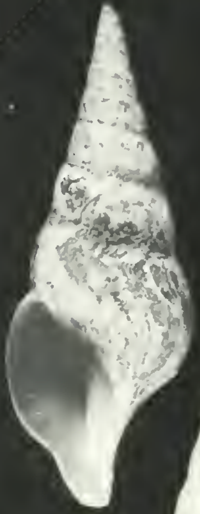

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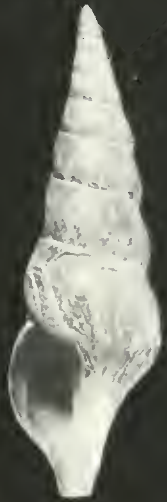

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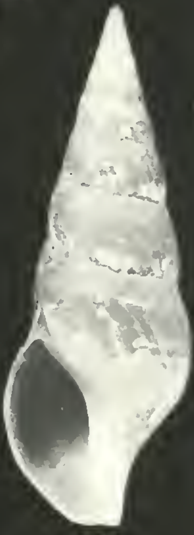

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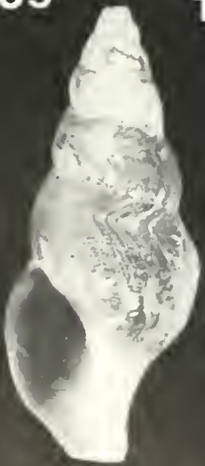

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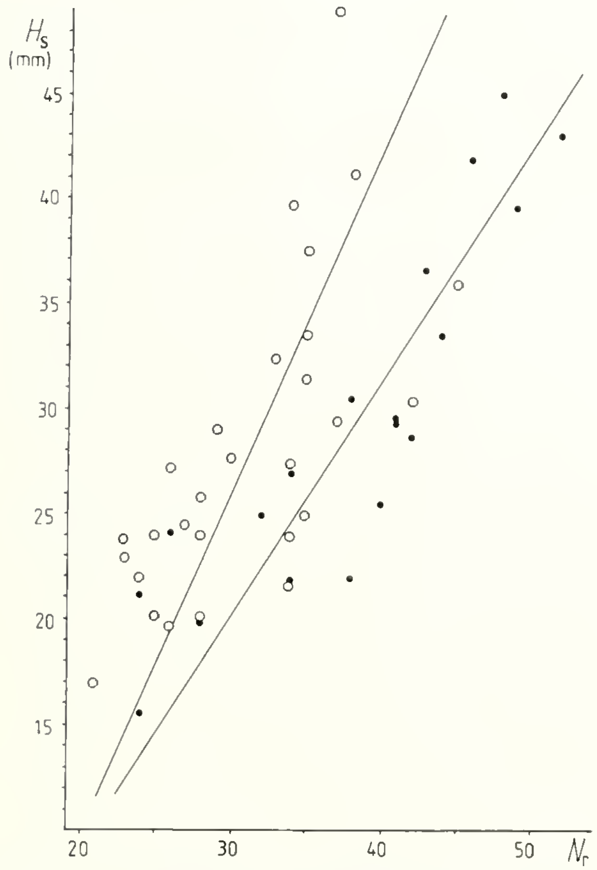

Figure 117. Comparison of the number of spiral ribs on the body whorl below the anal fasciole in Sakhalin Bay populations of *Antiplanes vinosa* (Dall) (solid circles, right regression line) and *A. sanctiioannis* (Smith) (open circles, left regression line). The shell height along the abscissa, the number of spiral ribs along the ordinate.

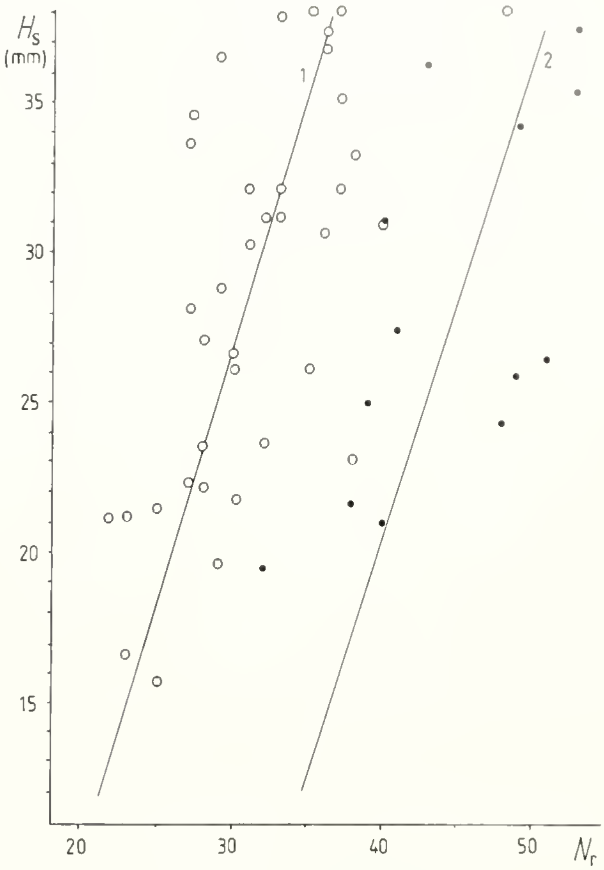

Figure 118. Comparison of the number of spiral ribs on the body whorl below the anal fasciole in the Kurile populations of *Antiplanes vinosa* (Dall) (solid circles, 2—line of regression) and *A. sanctiioannis* (Smith) (open circles, 1—line of regression). The shell height along the abscissa, the number of spiral ribs along the ordinate.

variably developed wavy spiral cords spanning shell surface, most pronounced on siphonal canal. Cords sometimes indistinct on and above anal fasciole. Dendritic threads variable in development, usually present on the anal fasciole, but not reaching suture on spire whorls. Aperture narrow, oval, usually well-differentiated from long, straight siphonal canal.

Radula medium sized for genus, shell height/mean marginal tooth length varies from 111.6 (shell height 21.2 mm) to 158.4 (shell height 48.8 mm). Increase in marginal tooth length with shell growth similar to that of *A. sanctiioannis*; regression equation: Y = 0.0942 + 0.0043X (figure 18).

Remarks: *Antiplanes vinosa* is the only sinistral species of *Antiplanes* in the northwestern Pacific Ocean. *Antiplanes sanctiioannis* is the most closely related dextral species. The number of spiral cords below the anal fasciole on the body whorl of *A. vinosa* is greater than in *A. sanctiioannis* (figure 117). Moreover, the spire of *A. vinosa* is generally higher than that of *A. sanctiioannis*, even in sympatric specimens (figure 119). In Sakhalin Bay, the ratio body whorl height/shell height is 0.57–0.62 (mean 0.589 ± 0.006) for *A. sanctiioannis*, and 0.53–0.57 (mean 0.553 ± 0.006) for *A. vinosa*. Regression equations are Y = 0.5852 − 0.0007X and Y = 0.6346 −

←

Figures 105–116. Shells of *Antiplanes vinosa* (Dall, 1874). **105.** Holotype of *Pleurotoma vinosa* Dall, 1874, USNM 220899, 36 mm. **106.** Holotype of *Antiplanes kamchatica* Dall, 1919, USNM 925255, 52 mm. **107.** Sakhalin Bay, Okhotsk Sea, 45.2 mm. **108.** Tatar Strait, 28.5 mm. **109.** Central Kurile Islands, 51.7 mm. **110.** Off Moneron Island, Tatar Strait, 42.0 mm. **111.** Off Paramushir, northern Kurile Islands, 46.5 mm. **112.** Northern Okhotsk Sea, 53.7 mm. **113.** Off Shikotan, southern Kurile Islands, 40.9 mm. **114.** Eastern Kamchatka, 35.3 mm. **115.** Off Onekotan Island, central Kurile Islands, 29.7 mm. **116.** Southern Kurile Islands, 31.3 mm.

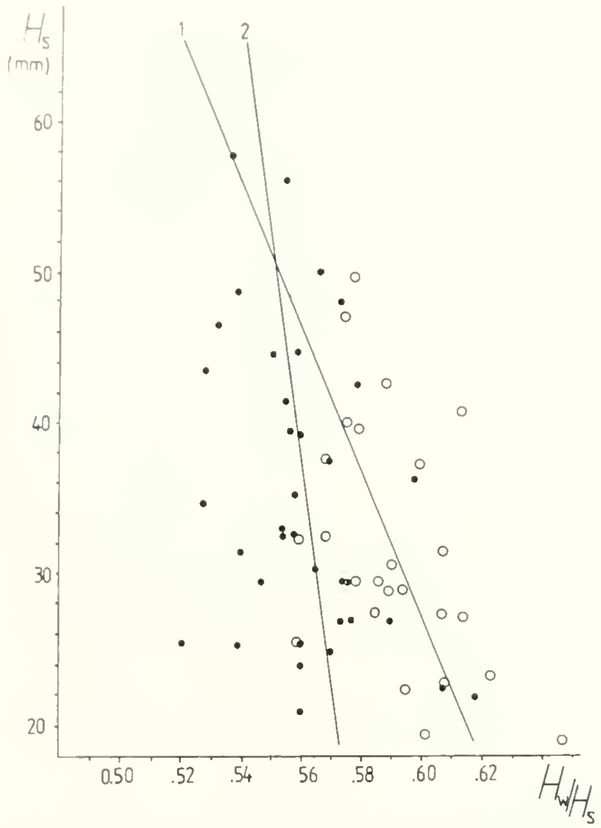

Figure 119. Comparison of the relative height of the body whorl of *Antiplanes vinosa* (Dall) (solid circles, 2—line of regression) and *A. sanctiioannis* (Smith) (open circles, 1—line of regression). The shell height along the abscissa, the ratio between the body whorl height and the shell height along the ordinate.

0.0013X respectively, where Y is the ratio of body whorl height to shell height and X is the shell height.

Distribution: *Antiplanes vinosa* was recorded from the northeastern part of Honshu (Kira, 1965), the northern Japan Sea to the northern Okhotsk Sea, and from the Bering Sea (figure 120).

Antiplanes isaotakii (Habe, 1958)
(figures 5, 121, 123–125, 137, 138)

Rectiplanes (*Rectisulcus*) *isaotakii* Habe, 1958:182, 185–186, text. fig. 2; Okutani 1964:424

Type specimens: Holotype, NSMT 38591, shell height 28.5 mm; paratype, NSMT 52684. Type locality, of Choshi, Chiba Pref., Honshu.

Material examined: Off Kurile Islands (1 specimen); off southern Kurile Islands (1 specimen).

Description: Shell light-olivaceous, elongate, high spired. Body whorl weakly convex, comprising 0.57–0.62 shell height. Spire whorls weakly to moderately convex, slightly angulated at periphery, flattened at anal fasciole. Suture shallow. Siphonal canal long, slightly curved. Aperture narrow, short, comprising 0.44–0.52 of shell height. Outer lip joining columella at nearly right angle. Spiral sculpture well developed, comprised of 2–3 flattened to convex cords between suture and anal fasciole, ≤5 cords on fasciole, sometimes with traces of dendritic threads, 20 wide, rounded cords, uniformly developed over entire body whorl below anal fasciole. Earlier whorls with 4–5 cords below anal fasciole.

Radula of 30.8 mm specimen was studied (figure 5). Marginal teeth were large (mean length = 0.289 mm, shell height/tooth length ratio = 106.6) (figure 18).

Remarks: *Antiplanes isaotakii* is conchologically similar to some forms of *A. sanctiioannis*, but differs in having longer marginal teeth and fewer spiral cords that are more convex, wider, and more evenly spaced. It differs from *A. habei* in having fewer spiral cords and a more acutely angled periphery.

Distribution: *Antiplanes isaotakii* was recorded off Chiosi, Honshu, in Sagami-Bay and off the southern Kurile Islands in 200–780 m (figure 137).

Antiplanes motojimai motojimai (Habe, 1958)
(figures 122, 137)

Rectiplanes (*Rectisulcus*) *motojimai* Habe, 1958:182–185, fig. 3; Okutani, 1964:424, pl. 4, fig. 7.

Type specimens: Holotype, NSMT 30600, shell height 38.2 mm; paratypes, NSMT 30600a–b, shell heights 37.0, 35.5 mm. Type locality—off Chiosi, Chiba Prefecture, Honshu, Japan.

Description: "Shell elongate with about eight whorls which are moderately inflated but deeply constricted at the suture, covered with the olivaceous periostracum; surface sculptured with the spiral cords, two or three of which are contained in the area between the rather broad fasciole and the upper suture and also two or three in the area between the fasciole and the lower suture; body whorl very large and stout, occupying about two-thirds of the shell length, the periphery of which is rounded and the base is marked by the spiral cords all over; aperture wide, the outer margin broadly sinuated in V-shape at a little above the periphery; canal broad and short; columellar margin white." (Habe, 1958:184).

Remarks: This species is most similar to *A. isaotakii*, but differs in having a broader shell and fewer spiral cords (21 cords below the anal fasciole on the body whorl of the holotype) that become narrower towards the siphonal canal.

Distribution: This subspecies occurs from Sagami Bay to the Sea of Kashima Nada (eastern Honshu), in 550–870 m (Okutani, 1964). It is not represented in collections of USSR institutions.

Antiplanes motojimai aquilonalis new subspecies
(figures 126, 127, 137)

Material examined: Holotype (ZM N Le 6906): R/V 'Adler', 18th cruise, sta. 169, eastern Bering Sea, 62°59′N,

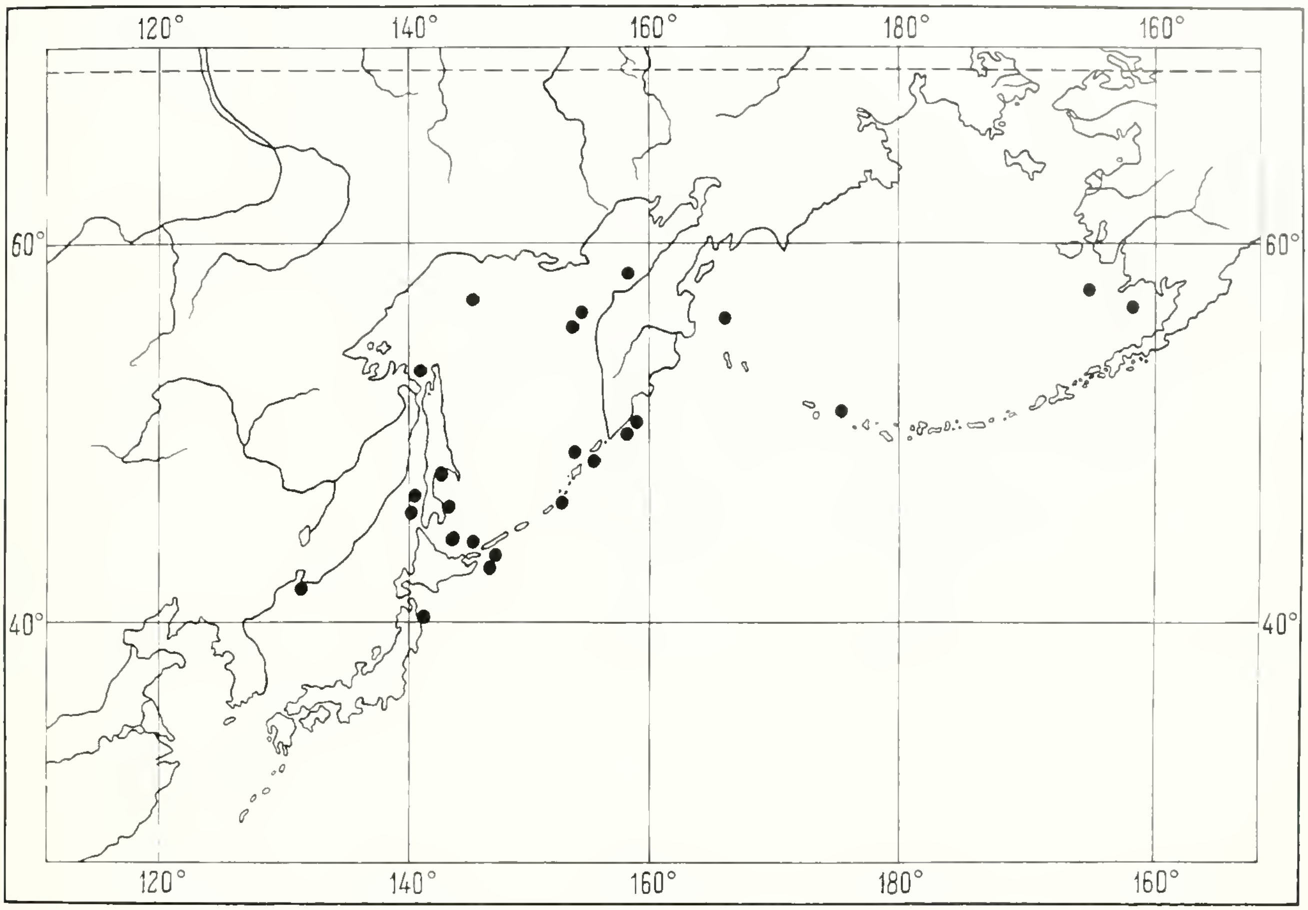

Figure 120. Geographic distribution of *Antiplanes vinosa* (Dall).

171°05′W, depth 46 m, 1983; paratypes: R/V 'Vityaz', 2nd cruise, sta. 20, southern Okhotsk Sea, 45°01.1′N, 144°21.0′E, depth 429–404 m, muddy sand and gravel, 10.VIII.1949 (empty shell—ZM N Lc 6908); R/V 'Akademik Oparin', 7th cruise, sta. 17, north-eastern Okhotsk Sea, 56°00′N, 146°29′E, depth 397 m, 1988 (empty shell—ZIN N 1/54624).

Description of holotype: Shell broad, consisting of 6 whorls, with earliest 1.5 whorls lost, next 3 whorls eroded. Spire whorls evenly convex, with narrow, flattened subsutural band above anal fasciole. Suture deeply impressed. Shell color dark olive. Periostracum thick, glossy. Growth lines numerous, some raised, rough, forming raised flat tubercles along lower parts of whorls. Spiral sculpture well developed, with 4–5 distinct, flattened ribs below anal fasciole on spire whorls. Body whorl with two narrow cords adjacent to anal fasciole, next 4 cords 1.5 times as broad, remaining 10 cords becoming progressively narrower towards siphonal canal. Cords flat, with serrated borders at intersections with growth lines. Anal fasciole with 2–3 thin threads, separated by wide interspaces. Dendritic threads well developed, reaching suture on spire whorls, disappearing on shell base. Anal fasciole with very thin secondary threads, especially on spire whorls. Siphonal canal broken. Shell base eroded. Aperture narrow, oval.

Dimensions of holotype: Shell height 35.5 mm, body whorl height 21.6 mm, aperture height 14.2 mm, shell diameter 16.5 mm.

Remarks: Paratypes are very similar to the holotype, but differ in having three ribs above the anal fasciole. This new subspecies differs from the nominatypical one in spiral sculpture: while *Antiplanes motojimai motojimai* has equally developed cords on the periphery of the whorls and on the anal fasciole, *Antiplanes motojimai aquilonalis* lacks wide ribs on the fasciole. These two subspecies differ in their geographical distributions.

Distribution: This new subspecies was recorded in the Okhotsk and Bering Seas at depths from 46 m (Bering Sea) to 550 m (southern Okhotsk Sea) (Fig. 137).

Etymology: *aquilonalis* Latin—northern, from *Aquilo* Latin—northern wind.

Antiplanes habei new species
(figures 7, 8, 23, 128–135, 137, 138)

Material examined: Holotype (ZM N Lc 6909): R/V 'Vityaz', second cruise, sta. 100, central part of the Okhotsk

Figures 121, 122. Shells of *Antiplanes* spp. **121.** *Rectiplanes isaotakii* Habe, 1958, holotype, NSMT N 52684, 28.5 mm. **122.** *Rectiplanes* (*Rectisulcus*) *motojimai* Habe, 1958, holotype, NSMT N 38600, 38.2 mm.

Sea, 54°35.0′N, 149°49.5′E, depth 543 m; paratypes: R/V 'Vityaz', 12th cruise, sta. 1853, central part of the Okhotsk Sea, 55°38.5′N, 143°01.0′E, depth 389 m, mud (1 specimen—ZM N Lc 6910); R/V 'Adler', 18th cruise, sta. 42, Okhotsk Sea, 49°12.7′N, 144°57.6′E, depth 245–260 m (1 specimen—ZM N Lc 6911); R/V 'Gagara', sta. 217, Okhotsk Sea, 51°35′N, 154°46′E, depth 410 m, (1 specimen—ZIN N 3/54625); R/V 'Gagara', sta. 252, Okhotsk Sea, 55°32.4′N, 149°14′E, depth 335 m (3 specimens—ZIN N 2/54626); R/V 'Toporok', sta. 17, off Shikotan, 43°32.5′N, 147°20.5′E, depth 1,450–1,530 m (2 specimens—ZIN N 1/54627).

Description of holotype: Shell elongate-fusiform, with high spire and high, weakly convex body whorl that comprises 0.57 of shell height. Shell of seven whorls, with at least one upper whorl lost. First preserved whorl eroded. Shell yellowish, with darker spiral band below anal fasciole. Periostracum thin, glossy. Whorls weakly convex, with flattened periphery nearly parallel to shell axis. Sutures impressed, shallow. Incremental growth striae thin, inconspicuous, some marked by color. Spiral sculpture of inconspicuous dendritic thread-like riblets on anal fasciole (4–5 on penultimate whorl, 3 on body whorl) reaching sutures on spire whorls and disappearing at periphery of body whorl. Ribs, 2–3 above fasciole, 4–5 below fasciole on three upper whorls, up to 9 on other spire whorls, 31 below fasciole on body whorl, becoming more distinct toward siphonal canal. Five ribs below anal fasciole flattened and of equal width, subsequent ribs more narrow and raised. Shell base flattened, joining short siphonal canal with distinct bend. Aperture narrow, short, comprising 0.43 of shell height. Outer lip joins columella at obtuse angle. Callus thin, narrow, white, glossy, covers columella and parietal wall. Siphonal canal poorly differentiated from aperture.

Dimensions: Holotype, shell height 38.0 mm, body whorl height 21.6 mm, aperture height is 16.3 mm, diameter 13.6 mm.

Remarks: Paratypes have slightly more convex and rounded whorls, wider apertures, more distinct spiral ribs below the anal fasciole, and wide, flat ribs on the fasciole that are absent on the body whorl. Limited material does not allow an evaluation of the range of intraspecific variability. We provisionally refer to this species two specimens from off Shikotan that differ from other paratypes in having: rounded or angulated, but never flattened whorls, a longer siphonal canal, high anal sinus apex, different geographic (southern Kuriles rather than the Okhotsk Sea) and bathymetric (1,450–1,530 m vs. 335–575 m) distributions.

The radulae of four specimens were studied (figures 7, 8). The marginal teeth are large; the ratio between the shell height and the tooth length varies from 76.3 (the shell height 14.2 mm) to 118.9 (37.8 mm). Their length rapidly increases with shell growth according to the regression equation:

→

Figures 123–136. Shells of *Antiplanes* spp. **123–125.** *Antiplanes isaotakii* (Habe, 1958). **123, 124.** ? Kurile Islands, 31.0 mm. **125.** Southern Kurile Islands, 24.3 mm. **126, 127.** *Antiplanes motojimai aquilonalis* n. subsp. holotype, ZM N Lc 6906, 35.5 mm. **128–135.** *Antiplanes habei* n. sp. **128.** Holotype, ZM N Lc 6909, 38.0 mm. **129, 130.** Paratype, Okhotsk Sea, ZM N Lc 6911, 29.0 mm. **131, 132.** Central part of Okhotsk Sea, ZM N Lc 6910, 23.0 mm. **133–135.** Off Shikotan, Kurile Islands, ZIN N 1/54627 (133—33.5 mm, 134, 135—23.2 mm). **136.** *Antiplanes bulimoides* Dall, 1919 Holotype, 31 mm.


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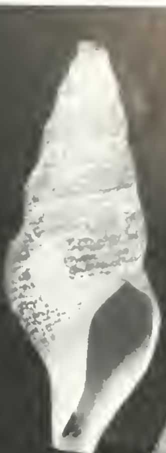
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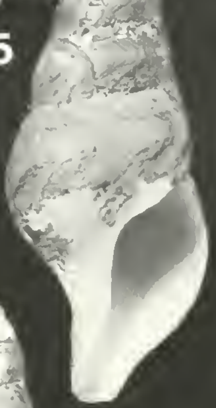
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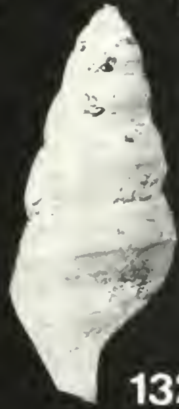
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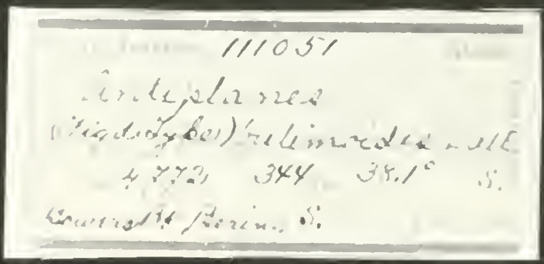
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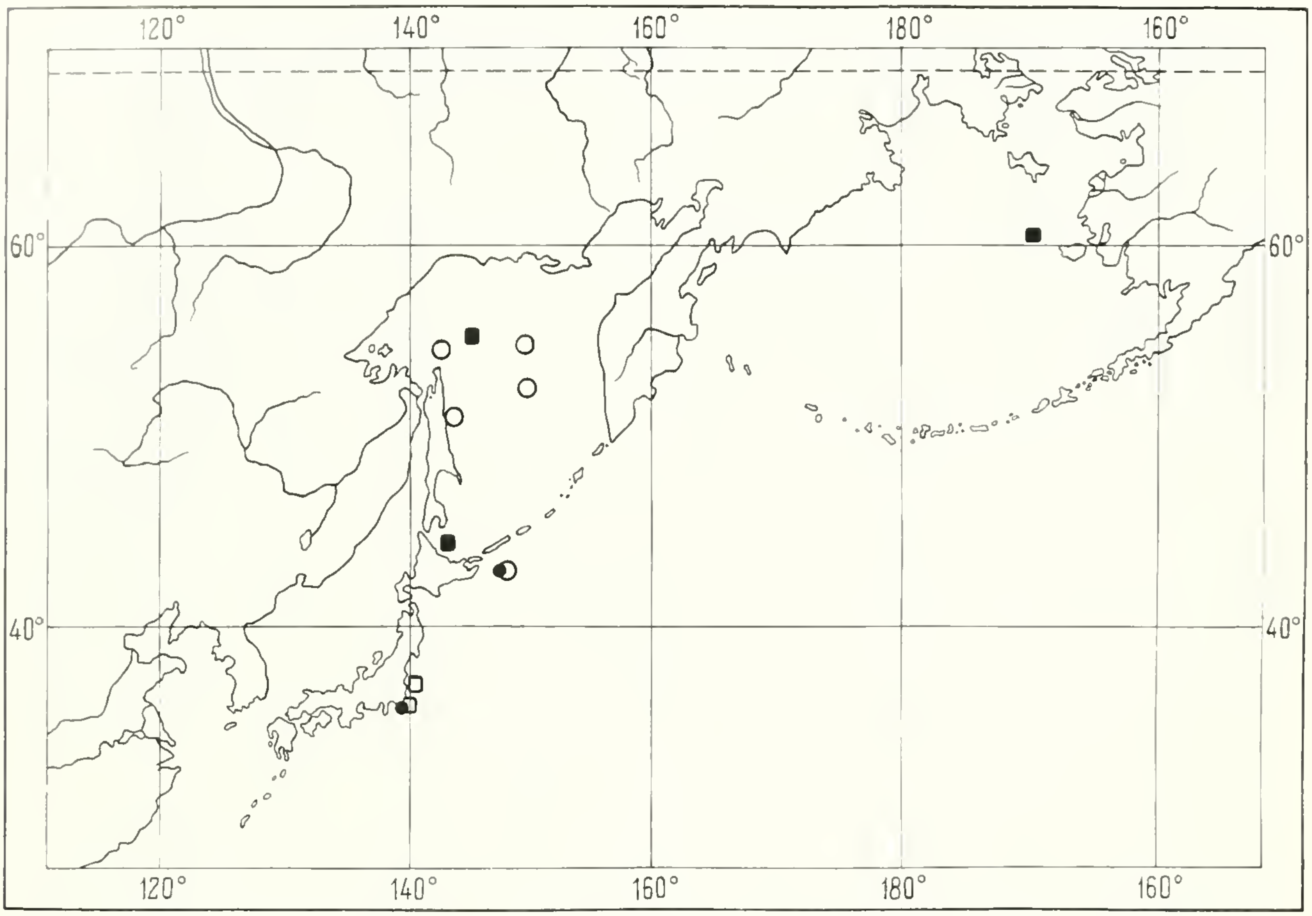

Figure 137. Geographic distribution of *Antiplanes isaotakii* (Habe) (solid circles), *A. motojimai motojimai* (Habe) (open circles), *A. motojimai aquilonalis* n. subsp. (solid squares), and *A. habei* n. sp. (open circles).

$$Y = 0.1290 + 0.0052X.$$

Antiplanes habei is most similar to *A. sanctiioannis*, but differs in having more convex, wider and less numerous ribs (figure 138) that are nearly equal over the body whorl. The ribs of *A. sanctiioannis* are considerably more pronounced on the shell base and the siphonal canal. This new species has large marginal teeth (figure 18), which is most clearly seen when comparing equal-sized specimens from the same locality (the respective points are connected by dotted line in figure 18). *Antiplanes habei* also resembles *A. isaotakii*, but differs from it in having a deeper suture, more convex whorls, more numerous ribs on the body whorl, as well as in lacking the angular periphery.

Distribution: *Antiplanes habei* was recorded in the Okhotsk Sea and the southern Kurile Islands at depths from 335 m (central part of the Okhotsk Sea) to 1,530 m (off Shikotan) (figure 137).

Etymology: This new species is named in honor of Dr. Tadashige Habe, who has considerably widened our knowledge of the north-western Pacific species of *Antiplanes*.

Antiplanes bulimoides Dall, 1919
(figure 136)

Dall, 1919:34, pl. 11, fig. 7; Dall, 1925:4, pl. 31, fig. 2.

Material examined: Holotype (USNM 111051), U.S. Bureau of Fisheries, Station 4772 on Bowers Bank, Bering Sea, 54°30′30″N, 179°13′00″E, in 344 fathoms, green-brown sand, bottom temperature 38.1°F, 6.IV.1906.

Description: "Shell elongate, decollate. Whorls six or more, four remaining. Suture distinct, not appressed. Whorls moderately convex, smooth, with pale polished greenish periostracum, in spots minutely granulose, apparently from some wrinkling of the periostracum. Anal sulcus wide, shallow, barely forming a fasciole. Outer lip thin, sharp, moderately produced. Inner lip with a thin white layer of callus. Columella straight, with an oblique anterior attenuation. Canal wide, hardly differentiated. Length of three complete whorls, 31 mm. Length of last whorl, 23 mm. Diameter at apex, 5 mm. Maximum shell diameter, 15 mm."

Remarks: So far as we know, this species is known only from the holotype, which is figured and described here.

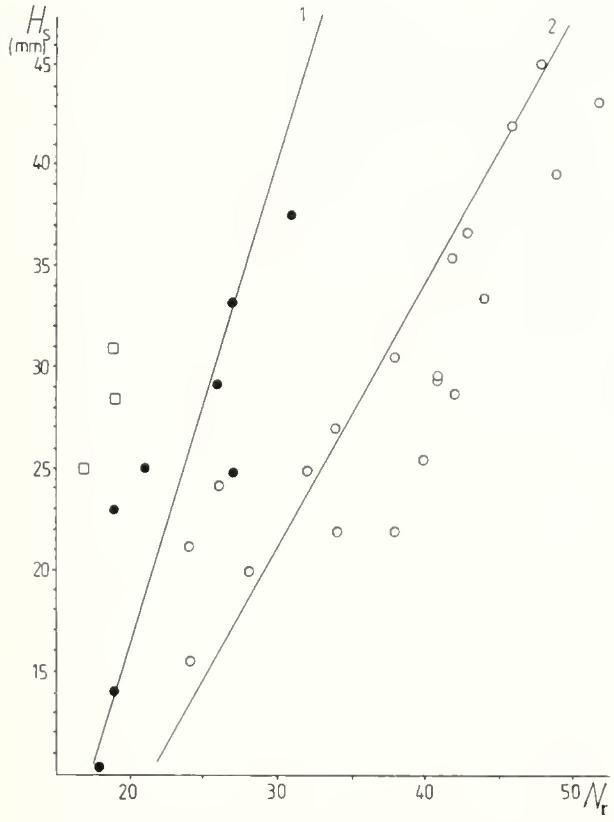

Figure 138. Comparison of the number of spiral ribs on the body whorl below the anal fasciole in populations of *Antiplanes isaotakii* (Habe) (open squares), *A. habei* n. sp. (solid circles, 1—line of regression), and *A. sanctiioannis* (Smith) (open circles, 2—line of regression). The shell height along the abscissa, the number of spiral ribs along the ordinate.

The bulimoid shape and glistening greenish periostracum makes this species quite unique.

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Two New Species of *Vexillum* from the Western Pacific (Gastropoda, Costellariidae)

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ABSTRACT

Vexillum brunneolinea n. sp. is described from the Palau Islands and compared to *Vexillum acuminatum* (Gmelin, 1791) and *V. semisculptum* (Adams & Reeve, 1850). It is the first member of its genus reported in which some individuals lack apertural lirations. *Vexillum elliscrossi* n. sp. is described from Hawaii and central Pacific guyots and compared to *Vexillum daedalum* (Reeve, 1845) and *Vexillum xenium* Pilsbry, 1921.

Key words: Costellariidae; Hawaiian Islands; Palau Islands; *Vexillum.*

INTRODUCTION

We first became aware of the two *Vexillum* species described in this paper more than twelve years ago. Our research in the literature at intervals during those years, involving study of the original descriptions of more than two thousand living and fossil species of miters (mitrids and costellariids), failed to uncover names for these taxa, although during that period both species were illustrated under erroneous names. We have not assigned the species we describe to subgenera because the limits of the subgenera of *Vexillum* are poorly defined and will surely change as anatomical knowledge of the group increases. On the basis of shell characters, it is possible that *Vexillum brunneolinea* n. sp. will be assigned to the subgenus *Costellaria*, and *V. elliscrossi* n. sp. to the subgenus *Pusia.*

SYSTEMATIC DESCRIPTIONS

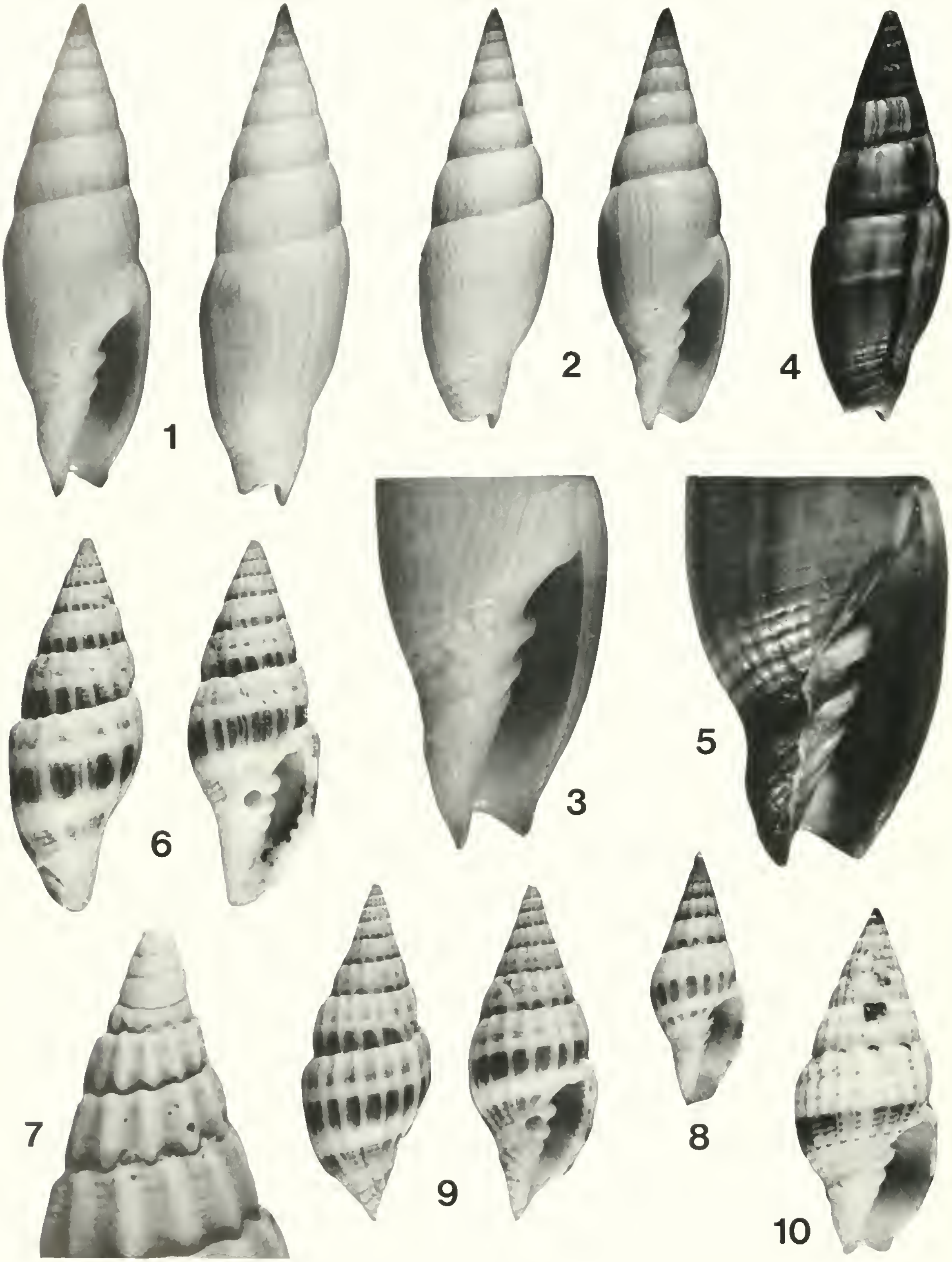
Family Costellariidae MacDonald, 1860
Genus *Vexillum* Röding, 1798
Vexillum brunneolinea new species
(figures 1–3)

Vexillum (*Costellaria*) *acuminatum* f. *politum* "Reeve" Turner, 1989, pp. 12, 28, pl. 5, fig. 21, right hand specimen only; not *Mitra politum* Reeve, 1844.

Description: Adult shell length ranges from 17.4 to 25.5 mm; width ranges from 28 to 33 percent of length, and spire height from 37 to 42 percent of shell length. A summary of measurements is given in table 1. The shell is white with 29 to 57 fine brown axial lines visible through a pale yellow periostracum. In live-collected specimens the periostracum is greenish-yellow and opaque. The green color may be due to the presence of commensal algae, as it rapidly fades after collecting.

The protoconch and first three or four teleoconch whorls are dark rust in color. The protoconch is smooth, about 0.5 mm in diameter and consists of about 2.2 whorls; the teleoconch consists of 8.9 to 10.5 convex whorls. The upper whorls have 12 to 20 axial ribs per whorl, typically 13 to 16. These ribs become obsolete by the penultimate whorl, which is smooth. On the upper three teleoconch whorls, there are 3 or 4 spiral grooves, which in some cases increase to five in number on succeeding whorls. These grooves are visible as pits between the axial ribs, but do not cross the ribs; they usually become obsolete by the penultimate whorl, but are still faintly visible on the body whorl in some specimens. There are three to seven spiral cords above the fasciolar ridge, and four to six below it on the siphonal fasciole. In some specimens the cords on the fasciole are obsolete or absent. The aperture and columella are white. There are four plications on the columella; the strongest is the posteriormost, which ranges up to 0.40 mm in width distally in adult specimens. There are 0–13 apertural lirations. In some specimens the lirations are of normal strength for *Vexillum*, in others they are shortened, reduced in number or in length, or, in seven specimens, are entirely absent. To make sure that lirations were lacking, a high intensity light was shone through the body whorl opposite the aperture. This procedure shows any trace of a liration in high relief, and none were detected in these specimens. The lack of apertural lirations has not been documented in any other *Vexillum* species.

The radula of the holotype is preserved on a slide prepared at the Academy of Natural Sciences (ANSP) between 1955 and 1958 by the late Virginia Orr Maes; it is typical of *Vexillum* species as illustrated by Cernohorsky (1970). The radula is fragmentary, with only 26 rows of teeth represented. Its width is 0.14 mm. The spacing between rows is about 0.025 mm, so there would have been about 40 rows of teeth per millimeter of ribbon length. The rachidian teeth have eight to ten cusps; the



Figures 1–3. *Vexillum brunneolinea* new species. **1.** Holotype, length 25.5 mm, ANSP 217492, with periostracum. **2.** Paratype, length 21 mm, Salisbury collection, periostracum removed. **3.** Apertural detail of holotype, aperture length 11.5 mm. **Figures 4, 5.** *Vexillum acuminatum* (Gmelin, 1791). **4.** Form *politum* (Reeve, 1844), length 20.5 mm, ANSP 28635, Philippines. **5.** Apertural detail of large individual, aperture length 16.3 mm, ANSP 29699, Sri Lanka. **Figures 6–9.** *Vexillum elliscrossi* new species. **6.** Holotype, length 18.5 mm, BPBM 219991. **7.** Paratype, apex, coated with magnesium oxide, IMT Sta. 73-15. **8.** Same specimen

lateral teeth are smooth. The rachidians are 0.08 mm in length, the laterals 0.06 mm; the ratio of their lengths is 1.33. Radular statistics are all within the ranges reported by Cernohorsky (1970:10) for *Vexillum*.

Type material: HOLOTYPE. ANSP 217492 (radula slide 937), 25.5 × 7.5 mm. PARATYPES. ANSP 202887 (1 specimen); ANSP 203082 (3 specimens); ANSP 203341 (2 specimens); ANSP 203787 (2 specimens); ANSP 217471 (2 specimens, bodies in ethanol); ANSP 382159 (1 specimen). Salisbury Collection, 7 specimens. Paratypes total eighteen specimens.

Type locality: Dredged in sand at 9 meters, inside the outer reef 12.9 km WNW of Koror Island, Palau Islands, Western Carolines. 7°24′N, 134°21′E. Collected by A. J. Ostheimer, 3rd; Station 441-6, 21 August 1955.

Distribution: All known specimens have been taken in the Palau Islands. Data for ten paratypes at ANSP that were dredged by A. J. Ostheimer, 3rd in 1955 are as follows:

ANSP 202887—Sta. 452, at 31 meters, 3.2 km NE of Gamudoko Island off Urukthapel Island, 24 August. 7°17.5′N, 134°21.5′E.

ANSP 203082—Sta. 436, in sand at 27 meters, Malakal Harbor, 20 August. 7°19′N, 134°27′E.

ANSP 203341, 217471—Sta. 361, in clean fine sand at 8 to 12 meters, in bay on inner edge of barrier reef 1.6 km south of West Passage, Babelthuap Island, 16 July. 7°31′N, 134°29′E.

ANSP 203787—Sta. 450, at 33 meters, east of Yoo Passage, 4.8 km NE of Eil Malk, 24 August. 7°12′N, 134°25.7′E.

The other paratypes were collected by Dieter Cosman using SCUBA in April 1978 in sand at 5.5 meters in the rock islands around Koror. One of these is ANSP 382159, the other seven are in the Salisbury collection. Turner (1989, pl. 5, fig. 21, right-hand specimen) published a color photograph of a 24 mm specimen in the Ted Baer collection taken at 10–20 meters in sand and fine rubble in Palau.

Etymology: "*Brunneolinea*" is derived from Latin *brunneus* (brown) and *linea* (line) referring to the brown axial lines characteristic of the species. It is a noun in apposition, and so does not change endings to match the gender of the genus.

Table 1. Measurements (mm) and counts of conchological features of *Vexillum brunneolinea* n. sp. Number of specimens varies because in some cases values for juvenile, damaged and worn specimens were omitted or could not be determined.

	Mean	Range	N
Shell length	21.3	17.3–25.5	10
Body whorl length	13.0	10.1–15.6	10
Body whorl width	6.4	5.0–7.6	10
Spire length	8.3	7.1–9.9	10
Aperture length	9.5	7.3–11.5	10
Aperture width	2.3	1.7–2.8	10
Plica 1 width	0.32	0.20–0.40	10
Teleoconch whorls	9.6	8.9–10.5	10
Ribs, whorl 1	12.8	12–14	14
Ribs, whorl 2	13.6	12–16	19
Ribs, whorl 3	14.5	13–17	19
Ribs, whorl 4	14.9	13–18	19
Ribs, whorl 5	16.0	13–19	18
Ribs, whorl 6	15.9	13–20	17
Protoconch width	0.49	0.47–0.52	15
Protoconch whorls	2.2	2.1–2.4	6

Discussion: This species was considered a variant of the *politum* form of *Vexillum acuminatum* (Gmelin, 1791) by Turner (1989, p. 12). *Vexillum brunneolinea* is easily distinguished from typical *Vexillum acuminatum* as the latter is brown in color, has a light band below the suture and has axial ribs on the body and penultimate whorls. *Vexillum acuminatum* form *politum* (Reeve, 1844) (figure 4) is smooth on these whorls, and sometimes develops a pattern of brown axial lines on a grayish-brown background. However, these lines are broader and more widely spaced than those in *V. brunneolinea*. The lines are darkly pigmented areas along growth lines of the shell, whereas the axial lines in *V. brunneolinea* are somewhat flexuous and in some cases bifurcate; they do not follow the growth lines.

Another feature that separates these species is that the posteriormost columellar tooth in fully mature individuals of *V. acuminatum* is broader than that in *V. brunneolinea*, and is often grooved at the top, giving it a biplicate appearance (figure 5). This tooth is convex in outline in *V. brunneolinea*. *Vexillum acuminatum* has been recorded from Palau, so *V. brunneolinea* cannot be considered a geographical variant of it.

Some forms of *Vexillum semisculptum* (Adams & Reeve, 1850) are also morphologically similar to *V. brunneolinea*. The species is usually ribbed, but as in *V. acuminatum*, smooth variants are known. However, the coloration of *V. semisculptum* is a uniform greenish, bluish or grayish brown with a white line below the suture. The aperture is brown except for the white line visible there also. Its color pattern differs strikingly from that seen in *V. brunneolinea*.

Vexillum elliscrossi new species
(figures 6–9)

Pusia daedala "Reeve," Kosuge, 1979, p. 27, pl. 6, fig. 28, not *Mitra daedala* Reeve, 1845.

Pusia sp., Salisbury, 1981, p. 6, figs. 8A–B (in color).

←

as fig. 7, length 12.8 mm. **9.** Paratype, length 17.2 mm, Salisbury collection. **Figure 10.** *Vexillum xenium* Pilsbry, 1921, holotype, length 17.8 mm, ANSP 116983. **Note:** All figures except 3, 5 and 7 are printed at the same magnification.

Table 2. Measurements (mm) and counts of conchological features of *Vexillum elliscrossi* n. sp. Number of specimens (N) varies because in some cases values for juvenile, damaged and worn specimens could not be determined.

	Mean	Range	N
Shell length	17.4	16.9–18.5	3
Body whorl length	10.7	9.8–12.0	4
Body whorl width	6.3	5.8–6.8	4
Spire length	6.3	6.2–6.4	3
Aperture length	8.6	7.7–9.5	4
Aperture width	2.5	2.5–2.7	4
Apertural lirations	9.3	6–13	6
Plica 1 width	0.38	0.30–0.46	4
Teleoconch whorls	7.5	7.0–7.8	3
Ribs, whorl 1	13.7	12–15	3
Ribs, whorl 2	14.6	12–16	5
Ribs, whorl 3	15.0	12–16	5
Ribs, whorl 4	16.2	12–19	5
Ribs, whorl 5	17.4	14–22	5
Ribs, whorl 6	18.4	16–23	5
Ribs, whorl 7	20.0	18–23	3
Protoconch width	0.62	0.60–0.64	3
Protoconch whorls	4.4	4.4–4.5	2

Description: Shell length of adult specimens ranges from 16.9 to 18.5 mm; body whorl width and spire height both range from 35 to 38 percent of shell length. A summary of measurements is given in table 2. The shell is white with four brown bands on the body whorl, two of which are visible on the spire whorls. The band below the suture is sometimes faint and is lightest near the suture; the band below it is the darkest of the four. Fresh specimens are suffused with lavender, which fades rapidly after collecting. The axial ribs are white and cut the brown bands into a series of tightly spaced blotches. The aperture and columella are white. All specimens studied have large, diagonal scars where breaks in the shell were repaired.

The protoconch is amber in color and appears smooth under a light microscope. It is tall (0.90–0.95 mm), consisting of about 4.4 whorls. There are up to eight teleoconch whorls. These are convex and slightly terraced. The number of ribs on the early teleoconch whorls ranges from 12 to 16, and increases to about 20 on the body whorl. Spiral grooves are visible between the ribs. These are faint on the first three teleoconch whorls and increase in strength towards the body whorl. From 7 to 9 grooves are visible on the spire whorls and 24 to 28 are visible on the body whorl. The grooves on the body whorl are stronger and more widely spaced along the siphonal canal. There is no siphonal notch and consequently there is no fasciolar ridge or distinct siphonal fasciole. There are four plications on the columella; the strongest is the posteriormost, which is up to 0.5 mm wide. There are 6 to 13 apertural lirations.

Type material: HOLOTYPE. BPBM 219991, 18.5 × 6.8 mm. PARATYPES. IMT, 3 uncatalogued specimens; Salisbury Collection, 1 specimen; Leonard Hill Collection Cs-173, 1 specimen, figured by Salisbury (1981).

Type locality: Off Waikiki, Oahu, Hawaii, at 180 meters on a sand bottom, collected by the "Pele Expedition" on 21 March 1965.

Distribution: The three paratypes in IMT were cited by Kosuge (1979), from stations 73-3 (29°47.0′N; 179°04.7′E), 73-4 (29°47.4′N; 179°02.9′E), and 73-15 (26°18.9′N; 174°30.9′W) on central Pacific guyots west of Midway Island. We did not examine a fourth specimen, figured by Kosuge (pl. 6, fig. 28), from station 73-25 (29°48.0′N; 179°01.3′E) as it was not included in the material loaned to us. The IMT specimens were dredged in March 1973 at depths from 67 to 267 m. The paratype in the Salisbury collection was dredged off Keehi Lagoon, Oahu by E. R. Cross. The paratype in the Hill collection was taken off Honolulu at about 90 meters in rock and coralline algal rubble.

Etymology: We are pleased to name this species in honor of Ellis R. Cross, editor emeritus of the Hawaiian Shell News, who collected one of the paratypes. His work with deep-dredged shells has contributed greatly to knowledge of the molluscan fauna of the Hawaiian Islands.

Discussion: Kosuge (1979) identified *Vexillum elliscrossi* as *Vexillum daedalum* (Reeve, 1845), but it is easily distinguished from that species. *Vexillum daedalum* has a brown or ashy green shell with a single white peripheral band, whereas *V. elliscrossi* has a white shell with four brown bands. The aperture and columella are brown in *V. daedalum* and white in *V. elliscrossi*. The axial ribs on the body whorl in *V. daedalum* number 10 to 15 (Cernohorsky, 1972), whereas *V. elliscrossi* has 18 to 23 ribs. *V. daedalum* has a siphonal notch and fasciole whereas *V. elliscrossi* lacks the notch and fasciole. The shell that Kay (1979) illustrated from Hawaii as *Vexillum* sp. cf. *rufofilosum* (E. A. Smith, 1876) may be a deep water form of *Vexillum daedalum*. Cernohorsky (1972) and Turner (1989) considered *V. rufofilosum* to be synonymous with *V. daedalum*; Turner illustrated the holotype of *V. rufofilosum*. *Vexillum oniscinum* (Lamarck, 1811) might prove to be an older name for *V. daedalum*.

Another species that occurs in Hawaii that might be confused with *Vexillum elliscrossi* is *V. xenium* Pilsbry, 1921 (figure 10). The holotype of *V. elliscrossi* was originally catalogued at the Bishop Museum as "*V.* (*C.*) *xenium*?" but comparison to the holotype and paratype of *V. xenium* (ANSP 116983) shows that the species are easily distinguished. The apertural lirations in *V. xenium* are interrupted; in *V. elliscrossi* they are continuous. *Vexillum xenium* has a siphonal notch and fasciole; these are lacking in *V. elliscrossi*. The brown peripheral band in *V. xenium* is strongest on top of the spiral cords and lighter in the grooves. There are several narrow bands of brown on top of individual cords elsewhere on the whorl; these are darkest where they cross the ribs and lighter or absent in the interspaces. In contrast, the brown bands in *V. elliscrossi* do not cross the ribs, but cover the spiral cords and grooves uniformly. *Vexillum xenium* also has scattered brown subsutural blotches; these blotches are absent in *V. elliscrossi*.

ACKNOWLEDGEMENTS

We thank Dieter Cosman for sharing his knowledge of *Vexillum brunneolinea* with us. We regret that we could not name the species for him, but there is already a *Vexillum cosmani* Kay, 1979, and the International Commission on Zoological Nomenclature discourages giving species in the same genus or in allied genera names honoring the same person [ICZN Recommendation D(I)6]. We thank Robert H. Cowie of the Bernice P. Bishop Museum (BPBM), Leonard C. Hill (Miami, Florida), and Sadao Kosuge of the Institute of Malacology, Tokyo (IMT) for providing information and loaning specimens.

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Parasitic Mites (Acari: Unionicolidae) of Fresh-water Mussels (Bivalvia: Unionidae) in the Duck and Stones Rivers in Central Tennessee

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ABSTRACT

The Duck and Stones Rivers in central Tennessee were sampled for fresh-water mussels in 1956 and 1962. Twenty-nine species of Stones River mussels were examined for parasitic mite infestations. Twenty mussel species were infested by a total of 14 species of mites (*Unionicola*). Of the 552 mussel specimens examined, 321 (58.2%) were infested with one or more mite species. In the Duck River, 20 species of mussels were examined for parasitic mite infestations. Thirteen mussel species were infested by a total of 11 species of mites (*Unionicola*). Of the 637 mussel specimens examined, 381 (59.8%) were infested with one or more mite species. Mussel-mite associations are listed. These data provide a unique insight into a native fauna that may now be irrecoverably damaged, at least in the impounded areas of Stones River.

Key words: Unionidae; mussels; Unionicolidae; *Unionicola*; mites; Stones River; Duck River; Tennessee.

INTRODUCTION

Fresh-water mussels (Bivalvia: Unionidae) form a major part of the macrobenthos in streams and lakes of North America. Although these mussels are commonly parasitized by aquatic mites (Acari: Unionicolidae), few published studies of geographical co-occurrence of the host and parasite species exist. Classical works, especially those of Wolcott (1899) and Marshall (1933), provide a few host records and no comprehensive mite species incidence records for the stations sampled. In the first concise work on the Tennessee mussel mites, Mitchell and Wilson (1965) describe 5 new species of mites from 5 mussel species in the Duck River. Before the 1980s, the taxonomy of unionicolid mites was very poorly understood; recent works (Vidrine 1980, 1985a, 1986d, 1987, 1988), however, propose 53 new species and a revision of the supraspecific systematics. Vidrine (1989), Vidrine and Vidrine (1987), and Vidrine, Bouchon and Poirrier (1986) discussed incidence of mussel-mite associations in Arkansas, Louisiana, Mississippi, and Texas. Earlier attempts to describe mussel-mite community structure by Dobson (1966), Calnan (1976) and Vidrine (1974) were hampered by the lack of recognition and definitive descriptions of many of the mite species encountered.

This paper describes the mussel-mite associations from collections made by JLW (junior author) in the Stones River (Cumberland River drainage) and the Duck River (lower Tennessee River drainage) in central Tennessee, during 1956 and 1962. These data provide a unique insight into a native fauna of the Stones River (impoundment in 1968: J. Percy Priest Lake) and the Duck River (impoundment in 1976: the Normandy Project).

MATERIALS AND METHODS

During the summers of 1956 and 1962, mussels were collected from the following 8 stations in the Stones River:

1. Stones River at lower end of Charlton Ford off Couchville Pike, Davidson Co., Tennessee. 25 August 1956 (now under backwater of J. Percy Priest Lake).
2. Stones River *ca.* 200 m above Couchville Pike Bridge, Davidson Co., Tennessee. 18 June, 16 and 29 July 1962 (now under backwater of J. Percy Priest Lake).
3. Stones River *ca.* 100 m above bridge on Stewart's Ferry Road, southeast of Donelson, Davidson Co., Tennessee. 14 August 1962 (now under backwater of J. Percy Priest Lake).
4. Stones River *ca.* 1.0 km below "Old Jefferson" Bridge *ca.* 4.5 km east of Smyrna and 1.3 km north of Hwy. 6306, Rutherford Co., Tennessee. 17 August 1962 (now under backwater of J. Percy Priest Lake).
5. Stones River *ca.* 30 m below junction of East Fork and West Fork Stones Rivers and 1.3 km upstream from "Old Jefferson" bridge and *ca.* 4.5 km east of Smyrna and 1.3 km north of Hwy. 6306, Rutherford Co., Tennessee. 20 August 1962 (now under backwater of J. Percy Priest Lake).
6. East Fork Stones River below bridge below dam at Walterhill on Hwy. 231, *ca.* 0.8 km north of Murfreesboro, Rutherford Co., Tennessee. 20 August 1962

(above impoundment and free flowing; near station E3 of Schmidt (1982)).

7. East Fork Stones River below bridge on Hwy. 6189, *ca.* 4.5 km northeast of Readyville (on Hwy. 705), Rutherford Co., Tennessee. 23 August 1962 (above impoundment and free flowing; near station E14 of Schmidt (1982)).
8. East Fork Stones River *ca.* 30 m below mill dam (still operating) and *ca.* 1.3 km east of Lascassas and *ca.* 3.0 km south of Rte. Tenn. 96, Rutherford Co., Tennessee. 23 August 1962 (above impoundment and free flowing; near station E6 of Schmidt (1982)).

Mussels were also collected from the following 10 stations in the Duck River:

1. Duck River below bridge on Hwy. 41 north of Manchester, Coffee Co., Tennessee. 31 July 1962 (above backwater of Normandy Reservoir and free flowing: J. Jenkinson, personal communication, 1990).
2. Duck River below bridge on Hwy. 231 in Shelbyville, Bedford Co., Tennessee. 26 July 1962 (free flowing, *ca.* 45 km below the dam of Normandy Reservoir, and minimally impacted by cold water discharge from the impoundment: J. Jenkinson, personal communication, 1990).
3. Duck River below bridge on Hwy. 31a south of Chapel Hill, Marshall Co., Tennessee. 5 July 1962 and 26 July 1962 (free flowing: J. Jenkinson, personal communication, 1990).
4. Duck River *ca.* 200 m below dam (Lillard Mill—an old hydroelectric dam) and 0.7 km N of Hwy. 4277 at Milltown, Marshall Co., Tennessee. 25 June and July 1962 and 26 August 1956 (free flowing and with a large mussel community: J. Jenkinson, personal communication, 1990).
5. Duck River *ca.* 100 m below old mill dam below bridge on Hwy. 431, Maury–Marshall Co. line, Tennessee. 27 July and 29 August 1962 (free flowing and with a large mussel community, old dam now washed out: J. Jenkinson, personal communication, 1990).
6. Duck River above bridge on Rte. Tenn. 7 at northwestern city limits of Columbia, Maury Co., Tennessee. 2 and 29 August 1962 (free flowing with a large mussel community: J. Jenkinson, personal communication, 1990).
7. Duck River below bridge at Williamsport on Rte. Tenn. 50, Maury Co., Tennessee. 2 August 1962 (free flowing but with few or no mussels: J. Jenkinson, personal communication, 1990).
8. Duck River below Wm. Erwin McEwen Bridge at Rte. Tenn. 50, Maury–Hickman Co. line, Tennessee. 23 July 1962 (free flowing but with few or no mussels: J. Jenkinson, personal communication, 1990).
9. Duck River *ca.* 100 m downstream from bridge at western city limits of Centerville on Rte. Tenn. 50, Hickman Co., Tennessee. 23 July and 6 August 1962. Obviously polluted by sewage in 1962 (still free flowing and polluted by sewage and industrial wastes, with few or no mussels: J. Jenkinson, personal communication, 1990).
10. Duck River below bridge on Rte. Tenn. 50, *ca.* 5 km west of Centerville, Hickman Co., Tennessee. 6 August 1962 (still free flowing but with few or no mussels: J. Jenkinson, personal communication, 1990).

A total of 557 mussels from the Stones River, and 637 mussels from the Duck River was examined by dissection, for adult and nymphal mites by JLW. All but 5 of these mussels were identified by Henry van der Schalie and Ralph Sinclair. The unidentified mussels (all from Stones River) are excluded from consideration here. The mites of each individual mussel were stored in separate, labelled vials of Koenike's fluid. The mites were identified by MFV in 1987. Mussel names have been updated to conform with the concepts of Burch (1975) and Davis and Fuller (1981). The mussels were deposited in the collections of the Museum of Zoology at the University of Michigan, Ann Arbor.

RESULTS

Fourteen species of *Unionicola* were found in 20 of 29 species of fresh-water mussels from the Stones River. Of the 552 mussels examined, 321 (58.2%) were infested with one or more species of *Unionicola*: 268 had one species, 40 had two species, and 13 had three species. Results of these examinations are summarized in table 1. The mussel diversity and abundance conform generally with those reported by Wilson and Clark (1914) and Schmidt (1982).

Eleven species of *Unionicola* were found in 13 of 20 species of fresh-water mussels from the Duck River. Of the 637 mussels examined, 381 (59.8%) were infested with one or more species of *Unionicola*: 372 had one species, 7 had two species, and 2 had three species. Results of these examinations are summarized in table 2. The mussel diversity and abundance conform generally with those reported by Isom and Yokely (1968), H. van der Schalie (1973), Ahlstedt (1986), and Jenkinson (1988).

Mussel-mite associations can be classified as resident, transient, or vagrant (Vidrine 1989), as adapted from Treat's (1975) definitions for Lepidoptera-mite associations. All 15 species of *Unionicola* reported here are naturally resident mites in the encountered mussel hosts, as inferred from associations encountered in other studies (Vidrine 1985b, 1986a,b,c, 1987, 1989). The few vagrant associations encountered here are naturally incidental and/or inevitable artifacts of sample handling.

The following associations were encountered in the Stones River (site of natural infestation within branchial chamber of hosts is provided within parentheses) (% infection of a specific mussel species by a specific mite species is provided in parentheses):

1. *Unionicola dimocki* Vidrine 1986b (gills) (83.1%) and *U. smithae* Vidrine 1986a (mantle and foot) (6.8%) were found in *Lasmigona costata* (Rafinesque

Table 1. Summary of mussel-mite associations in the Stones River, Tennessee, based upon collections in 1956 and 1962

Number of mussels examined (in bold)
Number of mussels infested by parasitic mites

Mussels Mites	Stations 1	2	3	4	5	6	7	8	Total
***Anodonta grandis* Say 1829**	—	—	—	—	—	—	—	**1**	**1**
Unionicola smithae Vidrine 1986a	—	—	—	—	—	—	—	1	1
***Lasmigona costata* (Rafinesque 1820)**	—	**11**	**3**	**2**	**10**	**34**	**3**	**55**	**118**
U. dimocki Vidrine 1986b	—	8	1	2	8	25	3	51	98
U. smithae Vidrine 1986a	—	—	—	—	1	—	—	7	8
***Amblema plicata* Say 1817**	—	**26**	**37**	**35**	**18**	**13**	—	**22**	**151**
U. amandita Mitchell and Wilson 1965	—	—	—	—	—	—	—	15	15
U. tupara Mitchell and Wilson 1965	—	2	18	7	15	11	—	—	53
U. serrata (Wolcott 1898)	—	—	2	1	6	1	—	1	11
***Amblema gigantea* (Barnes 1823)**	—	**17**	**6**	—	—	—	—	—	**23**
U. tupara Mitchell and Wilson 1965	—	12	5	—	—	—	—	—	17
***Fusconaia flava* (Rafinesque 1820)**	—	—	—	—	—	**1**	—	—	**1**
U. parkeri Vidrine 1987	—	—	—	—	—	1	—	—	1
***Elliptio dilatata* Rafinesque 1820**	—	**13**	**7**	**7**	**5**	**1**	—	**2**	**35**
U. serrata (Wolcott 1898)	—	—	—	1	—	—	—	—	1
U. tupara Mitchell and Wilson 1965	—	—	—	—	2	—	—	—	2
***E. crassidens* (Lamarck 1819)**	—	**2**	—	—	—	—	—	—	**2**
***Cyclonaias tuberculata* (Rafinesque 1820)**	—	**7**	**1**	**14**	**4**	—	—	—	**26**
U. sakantaka Mitchell and Wilson 1965	—	6	—	14	4	—	—	—	24
U. abnormipes (Wolcott 1898)	—	2	—	—	—	—	—	—	2
U. causeyae Vidrine 1985b	—	2	—	2	2	—	—	—	6
U. serrata (Wolcott 1898)	—	1	—	1	—	—	—	—	2
U. vamana Mitchell and Wilson 1965	—	—	1	—	—	—	—	—	1
***Quadrula pustulosa* (Lea 1831)**	—	**3**	**19**	—	—	—	—	—	**22**
U. causeyae Vidrine 1985b	—	—	1	—	—	—	—	—	1
***Orthonymus cylindrica* (Say 1817)**	—	—	**1**	—	—	—	—	—	**1**
U. sakantaka Mitchell and Wilson 1965	—	—	1	—	—	—	—	—	1
***Tritogonia verrucosa* (Rafinesque 1820)**	—	—	**1**	—	**3**	**3**	—	—	**7**
U. vamana Mitchell and Wilson 1965	—	—	—	—	3	3	—	—	6
***Actinonaias carinata* (Barnes 1823)**	—	**5**	**6**	**1**	**1**	**3**	—	—	**16**
U. hoesei Vidrine 1986c	—	3	6	1	—	2	—	—	12
U. abnormipes (Wolcott 1898)	—	3	—	1	1	—	—	—	5
U. serrata (Wolcott 1898)	—	1	—	1	1	—	—	—	3
***A. pectorosa* (Conrad 1834)**	**1**	**17**	**13**	**1**	—	**1**	—	—	**33**
U. hoesei Vidrine 1986c	1	10	10	1	—	1	—	—	23
U. serrata (Wolcott 1898)	1	2	5	—	—	—	—	—	8
U. abnormipes (Wolcott 1898)	—	2	2	—	—	—	—	—	4
***Lampsilis orbiculata* (Hildreth 1928)**	—	—	—	—	**1**	**2**	—	**1**	**4**
U. hoesei Vidrine 1986c	—	—	—	—	1	—	—	—	1
U. abnormipes (Wolcott 1898)	—	—	—	—	1	1	—	—	2
***L. ovata* (Say 1817)**	—	**4**	**15**	—	—	**1**	**1**	**5**	**26**
U. hoesei Vidrine 1986c	—	3	13	—	—	—	1	5	22
U. abnormipes (Wolcott 1898)	—	1	1	—	—	—	—	4	6
U. serrata (Wolcott 1898)	—	1	2	—	—	—	—	—	3
***L. fasciola* Rafinesque 1820**	—	—	**3**	—	—	—	**1**	—	**4**
***Obovaria subrotunda* (Rafinesque 1820)**	—	**1**	—	—	—	—	—	—	**1**
***Truncilla truncata* Rafinesque 1820**	—	**1**	—	—	—	—	—	—	**1**
***T. donaciformis* (Lea 1828)**	—	**1**	—	—	—	—	—	—	**1**
***Plagiola lenior* (Lea 1840)**	—	**1**	—	—	—	—	—	—	**1**
***P. interrupta* (Rafinesque 1820)**	—	—	**4**	—	—	—	—	—	**4**
***Potamilus purpuratus* (Lamarck 1819)**	—	—	—	—	—	**1**	—	—	**1**
***P. alatus* (Say 1817)**	—	**1**	**15**	—	—	—	—	—	**16**
U. hoesei Vidrine 1986c	—	1	10	—	—	—	—	—	11
U. fulleri Vidrine 1986c	—	—	4	—	—	—	—	—	4
U. australindistincta Vidrine 1985b	—	1	4	—	—	—	—	—	5
U. serrata (Wolcott 1898)	—	—	1	—	—	—	—	—	1

Table 1. Continued

Number of mussels examined (in bold)
Number of mussels infested by parasitic mites

Mussels Mites	Stations 1	2	3	4	5	6	7	8	Total
***Ligumia recta* (Lamarck 1819)**	**—**	**3**	**3**	**—**	**—**	**—**	**—**	**—**	**6**
U. serrata (Wolcott 1898)	—	1	—	—	—	—	—	—	1
U. abnormipes (Wolcott 1898)	—	—	1	—	—	—	—	—	1
***Villosa taeniata* (Conrad 1834)**	**2**	**2**	**6**	**1**	**—**	**—**	**1**	**—**	**12**
U. hoesei Vidrine 1986c	2	—	1	1	—	—	1	—	2
***Medionidus conradicus* (Lea 1834)**	**3**	**—**	**—**	**—**	**—**	**—**	**—**	**—**	**3**
U. hendrixi Vidrine 1987	3	—	—	—	—	—	—	—	3
***Leptodea fragilis* (Rafinesque 1820)**	**—**	**—**	**2**	**—**	**—**	**—**	**—**	**—**	**2**
U. hoesei Vidrine 1986c	—	—	2	—	—	—	—	—	2
***Ptychobranchus fasciolare* (Rafinesque 1820)**	**—**	**11**	**4**	**9**	**7**	**2**	**—**	**—**	**33**
U. hoesei Vidrine 1986c	—	1	—	3	5	—	—	—	8
U. causeyae Vidrine 1985b	—	—	—	—	1	—	—	—	1
***Obliquaria reflexa* Rafinesque 1820**	**—**	**1**	**—**	**—**	**—**	**—**	**—**	**—**	**1**
Totals of mussels	**6**	**127**	**146**	**70**	**49**	**62**	**6**	**86**	**552**

1820); a single vagrant specimen of *U. smithae* was found in *Anodonta grandis* Say 1829.

2. *Unionicola amandita* Mitchell and Wilson 1965 (gills) was found only in *Amblema plicata* Say 1817 (10.0%).
3. *Unionicola tupara* Mitchell and Wilson 1965 (gills) was found in *A. plicata* (35.1%) and *Amblema gigantea* (Barnes 1823) (73.9%).
4. *Unionicola sakantaka* Mitchell and Wilson 1965 (gills) was found in *Cyclonaias tuberculata* (Rafinesque 1820) (92.3%) and *Orthonymus cylindrica* (Say 1817) (100.0%).
5. *Unionicola vamana* Mitchell and Wilson 1965 (gills) was found in *Tritogonia verrucosa* (Rafinesque 1820) (85.7%); a vagrant specimen was found in *C. tuberculata*.
6. *Unionicola hoesei* Vidrine 1986c (gills), a common parasite of 15 genera in the Lampsilini (Unionidae: Ambleminae) in North America (Vidrine 1986c), was found in *Lampsilis ovata* (Say 1817) (84.6%), *Lampsilis orbiculata* (Hildreth 1828) (25.0%), *Villosa taeniata* (Conrad 1834) (41.7%), *Actinonaias carinata* (Barnes 1823) (75.0%), *Actinonaias pectorosa* (Conrad 1834) (69.7%), *Leptodea fragilis* (Rafinesque 1820) (100.0%), *Ptychobranchus fasciolare* (Rafinesque 1820) (24.2%) and *Potamilus alatus* (Say 1817) (68.8%) (all lampsilinines) in the Stones River.
7. *Unionicola fulleri* Vidrine 1986c (gills) (25.0%) and *Unionicola australindistincta* Vidrine 1985b (mantle and foot) (31.3%) were found only in *P. alatus*.
8. *Unionicola hendrixi* Vidrine 1987 (gills) was found only in *Medionidus conradicus* (Lea 1834) (100.0%).
9. *Unionicola parkeri* Vidrine 1987 (gills) was found only in *Fusconaia flava* (Rafinesque 1820) (100.0%).
10. *Unionicola causeyae* Vidrine 1985b (mantle and foot) was found in *C. tuberculata* (23.1%), *P. fasciolare* (3.0%), and *Quadrula pustulosa* (Lea 1831) (4.5%).
11. *Unionicola abnormipes* (Wolcott 1898) (mantle and foot) was found in *A. carinata* (31.3%), *A. pectorosa* (12.1%), *L. ovata* (23.1%), *L. orbiculata* (50.0%) and *Liqumia recta* (Lamarck 1819) (16.7%); a vagrant specimen was found in *C. tuberculata*.
12. *Unionicola serrata* (Wolcott 1898) (labial palps) was found in *A. carinata* (18.8%), *A. pectorosa* (24.2%), *A. plicata* (7.3%), *C. tuberculata* (7.7%), *Elliptio dilatata* Rafinesque 1820 (2.9%), *L. ovata* (11.5%), *L. recta* (16.7%), and *P. alatus* (6.3%).

The following associations were encountered in the Duck River (site of natural infestation within branchial chamber of hosts is provided within parentheses) (% infection of a specific mussel species by a specific mite species is provided in parentheses):

1. *Unionicola dimocki* (gills) (89.5%) and *U. smithae* (mantle and foot) (12.3%) were found only in *L. costata*.
2. *Unionicola amandita* (gills) was found only in *A. plicata* (48.7%).
3. *Unionicola tupara* (gills) was found in *A. plicata* (0.3%) and *A. gigantea* (84.2%).
4. *Unionicola sakantaka* (gills) was found in *C. tuberculata* (90.7%) and *O. cylindrica* (100.0%); a vagrant specimen was found in *T. verrucosa*.
5. *Unionicola vamana* (gills) was found in *T. verrucosa* (83.0%); vagrant specimens were found in *C. tuberculata* (1) and *Q. quadrula* (Rafinesque 1820) (5).
6. *Unionicola vikitra* Mitchell and Wilson 1965 (gills) was found in *Q. quadrula* (47.6%) and *Q. pustulosa* (100.0%); a vagrant specimen was found in *C. tuberculata*.
7. *Unionicola hoesei* (gills) was found in *Lampsilis fasciola* Rafinesque 1820 (50.0%), *Villosa fabalis* (Lea 1831) (81.3%), *A. pectorosa* (62.5%), *L. fragilis* (8.3%), and *P. alatus* (30.0%) (all lampsilinines).

Table 2. Summary of mussel-mite associations in the Duck River, Tennessee, based upon collections in 1956 and 1962.

Number of mussels examined (in bold)
Number of mussels infested by parasitic mites

Mussels Mites	Stations 1	2	3	4	5	6	7	8	9	10	Total
***Anodonta grandis* Say 1829**	—	—	—	—	—	**1**	—	—	—	—	**1**
***Alasmidonta marginata* Say 1819**	—	—	—	—	**2**	—	—	—	—	—	**2**
***Lasmigona complanata* (Barnes 1823)**	—	—	—	—	—	**5**	—	—	—	—	**5**
***L. costata* (Rafinesque 1820)**	—	**11**	**18**	**14**	**14**	—	—	—	—	—	**57**
Unionicola dimocki Vidrine 1986b	—	8	18	11	14	—	—	—	—	—	51
U. smithae Vidrine 1986a	—	1	4	1	1	—	—	—	—	—	7
***Strophitus undulatus* (Say 1817)**	—	—	—	—	—	—	—	—	**3**	—	**3**
***Amblema plicata* Say 1817**	—	**3**	**29**	**170**	**74**	**42**	—	—	—	—	**318**
U. amandita Mitchell and Wilson 1965	—	2	17	90	45	1	—	—	—	—	155
U. tupara Mitchell and Wilson 1965	—	—	—	—	—	1	—	—	—	—	1
***A. gigantea* (Barnes 1823)**	—	—	—	**5**	**10**	**4**	—	—	—	—	**19**
U. tupara Mitchell and Wilson 1965	—	—	—	4	10	2	—	—	—	—	16
***Cyclonaias tuberculata* (Rafinesque 1820)**	—	**1**	**28**	**13**	**9**	**1**	**2**	—	—	—	**54**
U. sakantaka Mitchell and Wilson 1965	—	1	27	12	9	—	—	—	—	—	49
U. vikitra Mitchell and Wilson 1965	—	—	1	—	—	—	—	—	—	—	1
U. vamana Mitchell and Wilson 1965	—	—	—	—	—	1	—	—	—	—	1
***Tritogonia verrucosa* (Rafinesque 1820)**	—	—	**19**	**20**	**6**	**5**	—	—	**3**	—	**53**
U. vamana Mitchell and Wilson 1965	—	—	19	17	6	2	—	—	—	—	44
U. sakantaka Mitchell and Wilson 1965	—	—	—	1	—	—	—	—	—	—	1
***Orthonymus cylindrica* (Say 1817)**	—	—	**2**	—	—	—	—	—	—	—	**2**
U. sakantaka Mitchell and Wilson 1965	—	—	2	—	—	—	—	—	—	—	2
***Quadrula quadrula* (Rafinesque 1820)**	—	—	—	—	—	**60**	—	**1**	**2**	—	**63**
U. vikitra Mitchell and Wilson 1965	—	—	—	—	—	30	—	—	—	—	30
U. vamana Mitchell and Wilson 1965	—	—	—	—	—	5	—	—	—	—	5
***Q. pustulosa* (Lea 1831)**	—	—	—	**1**	—	**1**	—	—	—	—	**2**
U. vikitra Mitchell and Wilson 1965	—	—	—	1	—	1	—	—	—	—	2
***Elliptio crassidens* (Lamarck 1819)**	—	—	—	—	—	**1**	—	—	**2**	—	**3**
***Lampsilis ovata* (Say 1817)**	—	—	—	—	—	—	—	—	**1**	—	**1**
***L. teres* (Rafinesque 1820)**	—	—	—	—	—	**2**	—	—	—	—	**2**
***L. fasciola* Rafinesque 1820**	**6**	—	—	—	—	—	—	—	—	—	**6**
U. hoesei Vidrine 1986c	3	—	—	—	—	—	—	—	—	—	3
***Villosa fabalis* (Lea 1831)**	**16**	—	—	—	—	—	—	—	—	—	**16**
U. hoesei Vidrine 1986c	13	—	—	—	—	—	—	—	—	—	13
***Actinonaias pectorosa* (Conrad 1834)**	**5**	—	**1**	**1**	**1**	—	—	—	—	—	**8**
U. hoesei Vidrine 1986c	4	—	1	—	—	—	—	—	—	—	5
***Leptodea fragilis* (Rafinesque 1820)**	—	—	—	—	**1**	**2**	—	—	**9**	—	**12**
U. hoesei Vidrine 1986c	—	—	—	—	1	—	—	—	—	—	1
***Potamilus alatus* (Say 1817)**	—	—	—	**3**	**1**	—	—	—	**5**	**1**	**10**
U. hoesei Vidrine 1986c	—	—	—	3	—	—	—	—	—	—	3
U. fulleri Vidrine 1986c	—	—	—	2	1	—	—	—	—	—	3
U. australindistincta Vidrine 1985b	—	—	—	1	—	—	—	—	—	—	1
U. serrata (Wolcott 1898)	—	—	—	1	—	—	—	—	—	—	1
Totals of mussels	**27**	**15**	**97**	**227**	**118**	**124**	**2**	**1**	**25**	**1**	**637**

8. *Unionicola fulleri* (gills) (30.0%), *U. serrata* (labial palps) (10.0%), and *U. australindistincta* (mantle and foot) (10.0%) were found only in *P. alatus*.

The following mussels were not found parasitized by mites in either or both of the rivers studied: *Alasmidonta marginata* Say 1819, *Lasmigona complanata* (Barnes 1823), *Strophitus undulatus* (Say 1817), *Elliptio crassidens* (Lamarck 1819), *Lampsilis teres* (Rafinesque 1820), *Obovaria subrotunda* (Rafinesque 1820), *Truncilla truncata* Rafinesque 1820, *Truncilla donaciformis* (Lea 1828), *Plagiola lenior* (Lea 1840), *Plagiola interrupta* (Rafinesque 1820), *Potamilus purpuratus* (Lamarck 1819), and *Obliquaria reflexa* Rafinesque 1820.

DISCUSSION

Intra-host regulation of a mite-parasite load, perhaps through rivalry of sexual competitors, as described by Mitchell (1965), was apparent in several mite species encountered here. In the Stones River, *Unionicola aman-*

dita, *U. dimocki*, *U. hoesei*, *U. sakantaka*, *U. vamana*, *U. hendrixi* and *U. parkeri* typically occurred in small, characteristically discrete numbers within each host: a single male, and one or two females usually infested the gills of their mussel host. One to four individuals of *U. tupara* and *U. fulleri* (all males, all females, or combinations of both sexes) infested the gills of their hosts. One or two females of *U. smithae* were usually found on the mantle or foot of infested hosts, while males were absent, probably due to seasonal reasons. One to four specimens of the gill mites *U. tupara* and *U. fulleri* were found in each host. One or two individuals of the less host-specific labial palp parasite, *U. serrata*, were found in 7 genera of mussels. One to five individuals of *U. abnormipes*, *U. causeyae* and *U. australindistincta*, which infest the mantle and foot of their hosts, were found in a variety of amblemine hosts. The large number of individuals (range 1–65, but most often 7) of *U. abnormipes* infesting individual hosts may represent an absence of the strict territoriality apparent in the above associations.

In the Duck River, *Unionicola amandita*, *U. dimocki*, *U. hoesei*, *U. sakantaka*, *U. vamana* and *U. vikitra* typically occurred in small numbers within each host: a single male, and one or two females infesting the gills of their individual hosts. One to nineteen, usually 5, individuals of *U. tupara* and *U. fulleri* infested the gills of their hosts. One to five females of *U. smithae* were found on the mantle or foot in each infested host, while males were not found. Only a single male of *U. serrata*, a labial palp mite, was found. A single *Potamilus alatus* had one male and two females of *U. australindistincta*, a mantle and foot parasite.

In both the Stones River and the Duck River, *U. australindistincta* was found in *P. alatus*. These are new host and locality records for *U. australindistincta*, which has been previously known mainly from other species of the genus *Potamilus* and *Leptodea fragilis* in Arkansas, Louisiana, Mississippi, and Texas (Vidrine 1986b). The closely related mite species, *U. indistincta* (Wolcott 1898), is the usual parasite of *P. alatus*, both in the upper Mississippi and upper Tennessee river drainages (Clinch and Powell Rivers) (Vidrine, 1980; Wolcott, 1899). The addition of *P. alatus* to the host list for *U. australindistincta* neither confirms nor refutes Vidrine's (1985b) contention that *U. australindistincta* is a southern form of *U. indistincta*. In this sampling, only a single, unparasitized *P. purpuratus* (a common host of *U. australindistincta* south of Tennessee) was found in the Stones River.

The data in tables 1 and 2 illustrate the incidence of specific mite taxa in specific mussel groups (subfamilies Anodontinae and Ambleminae). The anodontine mussels, for example, are infested by distinctly different mantle and gill mites than are amblemine mussels. This phenomenon was noted by Vidrine and Bereza (1978) and reinforced by Vidrine (1980, 1986a,b,c,d, 1987, 1989).

These data suggest that *Unionicola* tend to be found in the more abundant mussel species in a habitat. A critical threshold of host population size may be an obligatory prerequisite for a population of a specific, extant mite species to be sustained locally. Small and unparasitized populations of certain mussel species may be naturally below a threshold assuring survival of mites capable of parasitizing them, or artificially so as a result of human impact. Although found parasitized elsewhere, the following species were locally *Unionicola*-free in this study: *E. crassidens* was found parasitized in neither the Duck or Stones Rivers; *L. fasciola*, *O. subrotunda*, *T. truncata*, *T. donaciformis*, *P. purpuratus*, and *O. reflexa* were not found parasitized in the Stones River; *A. grandis*, *A. marginata*, *L. complanata*, *S. undulatus*, *L. ovata*, and *L. teres* were not found parasitized in the Duck River. Whether or not this local phenomenon is due to naturally small or to damaged populations of these mussels, is unknown.

Some mussel species may have never achieved critical population sizes that could realize the very evolution of a mite into a parasitic relationship with them. The typically small populations of mussels in the genus *Plagiola* may exemplify this phenomenon, and may be culpable in hastening the extinction of several species of *Plagiola* in the last century, little doubt as a result of human impact. *Plagiola* were never found parasitized by *Unionicola* in the field or in museum holdings thus far by MFV, and no published records are extant.

The data derived from these collections are historically important because all mussels that were *found* were *collected*, providing a rough estimate of the relative species abundance and incidence in these damaged and/or impacted faunas. Also, these data are enriched by a mite-mussel parasitization profile, providing another dimension to the systematics and natural history of these faunas, and an insight into a diverse and differentially specialized host-parasite complex. The Cumberlandian mussel fauna and much of the lower Tennessee River fauna, now largely decimated down to their few remaining refugia, historically represented the most diverse sympatric freshwater mussel fauna known on Earth. Insights into the mite-mussel coevolutionary strategies and into the delicate population control mechanisms that are necessary to maintain such a diverse community are now largely unattainable from these mussel communities, as the necessary sampling of mussels is untenable in the few viable populations, or impossible in those extirpated by impoundment. Recent mussel studies (Ahlstedt 1986; Jenkinson 1988; Schmidt 1982) do indicate that diverse communities still exist in portions of both the Duck and the Stones Rivers. The presented baseline data sets will, we hope, provide some corroborative elements to future studies of the now-relict Cumberlandian and other mussel faunas and their parasites and perhaps engender interest from ecologists who seek to explain the intricacies that drive the complex biotic relationships within benthic invertebrate communities.

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Volutes from Saya de Malha Bank: The Saga of *Lyria surinamensis* and a New Species

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ABSTRACT

The supposedly fulgorariine volute *Dallivoluta surinamensis* Okutani, 1982 is shown to have been described from an erroneous type locality in the Caribbean. It actually originates from Saya de Malha Bank, in the Indian Ocean, where it is probably endemic. *Dallivoluta* Okutani, 1982 is regarded as a synonym of *Lyria* Gray, 1847. It is further suggested that *Murex surinamensis* Okutani, 1982 was also erroneously localized and actually originates from the same submarine Indian Ocean bank. *Lyria doutei* n.sp. is described from Saya de Malha, and compared with other species in the group of *L. lyraeformis*. Endemism on Saya de Malha is discussed in connection with the history and isolation of the bank.

Key words: Indian Ocean; Mascarene Plateau; Caribbean; Volutidae; endemism.

INTRODUCTION

In the last few months, collectors in Western Europe have obtained from Russian sources specimens of two remarkable volute species trawled by Soviet research vessels on Saya de Malha Bank, in the Indian Ocean. Nothing similar had been described from the Indo-Pacific, and the Saya de Malha shells appeared to represent two new species of *Lyria*, when we noticed the identity of one of them with *Dallivoluta surinamensis* Okutani, 1982. We present below the reasons why we believe that *D. surinamensis* was erroneously localized in the original description, we synonymize *Dallivoluta* with *Lyria*, and we describe the second *Lyria* as a new species.

The species *Dallivoluta surinamensis* Okutani, 1982: The volute *Dallivoluta surinamensis* was described as a new genus and species, based on a single dead shell (figure 1) and fragments collected by Japan Marine Fishery Resources Research Center (JAMARC), supposedly off the coast of Surinam in December 1978 (Okutani, 1982:115). The type locality was given as 11°03′N, 61°01′W, depth 128 m. Okutani (in Takeda & Okutani, 1983:290) provided an abridged description and color photographs of the holotype. No further original information on *Dallivoluta surinamensis* has been published since the original description.

Okutani (1982) compared *Dallivoluta* with *Tractolira* Dall, 1869 and especially *Fulgoraria* Schumacher, 1817, which is probably the reason why Poppe (1987:14) placed *Dallivoluta* in the subfamily Fulgorariinae.

The type locality: The type locality indicated by Okutani (1982) is not situated off Surinam, as the specific name would imply. The geographical coordinates indicate a position 700 km to the northwest of Surinam, between the islands of Trinidad and Tobago, off Venezuela. The depth (128 m) is in the range of depths found around these islands. The type locality of *Murex surinamensis* Okutani, 1982, described in the same paper, is 10°46′N, 61°32′W, 94 m. These coordinates indicate a position *on* the island of Trinidad, not in the seas around it.

In fact, neither of these localities falls within the area encompassed by the JAMARC study area off Surinam and French Guiana (Takeda & Okutani, 1983:9, 11), and there are grounds to suspect that they are erroneous. Vokes (1990a:4, footnote; 1990b:6) had expressed doubts on the type locality of *Murex surinamensis*, and suggested that "opportunity for mixed locality data is certainly present" (Vokes, 1990a).

Identity of *Dallivoluta surinamensis* with the Saya de Malha volute: The volutes obtained from Soviet sources belong to two different species of *Lyria*. Of one of these, we have seen two complete shells, empty but very fresh and probably live taken, said to have been collected by Soviet research vessels on Saya de Malha: one is in the Douté collection (Germany); the other is in the second author's collection (figure 2). In addition, we have seen photographs of a third specimen from another private collection. Comparison of this material with Okutani's (1982, 1983) description and figures (this paper figure 1) leaves no doubt as to their identity. The spiral cords are more distinct on the spire whorls of the newly collected specimen, but this is undoubtedly due to the better preservation of this shell.

We therefore conclude that the type locality is erroneous. When the geographical coordinates of the type locality are read with South instead of North, and East instead of West (*i.e.*, 11°03′S, 61°01′E, instead of 11°03′N,

Figure 1. *Lyria surinamensis* (Okutani, 1982). Holotype (from Okutani, in Takeda & Okutani, 1983). Height 105 mm.

Figure 2. *Lyria surinamensis*. Specimen collected on Saya de Malha Bank by Soviet vessels (Bail collection). Height 87 mm.

61°01'W), the position given is precisely correct for Saya de Malha Bank, in the Indian Ocean! We also suggest that the type locality of *Murex surinamensis* is similarly inaccurate, and should be read 10°46'S, 61°32'E, also on Saya de Malha Bank. This would confirm the observation by Ponder and Vokes (1988:12) and Vokes (1990a:4, 1990b:6) that there are no species of *Murex* s.s. in the New World.

It would thus appear that the Surinam material provided to Dr. Okutani by JAMARC had unfortunately been contaminated by specimens trawled from the Indian Ocean.

Dallivoluta surinamensis and *Murex surinamensis* will add to the list of species with unfortunate geographical specific names, such as the Caribbean *Cassis madagascariensis* Lamarck, 1822, originally believed to come from Madagascar, or *Puncturella agulhasae* Clarke, 1961, the type locality of which was erroneously believed to be within the limits of Agulhas Basin (see Barnard, 1963: 296). A similar case of mistaken geographical coordinates concerns the magellanic *Marginella warrenii* Marrat, 1876, described from 50°23'N, 64°04'W (Gulf of St. Lawrence), an error for 50°23'S, 64°04'W (between the Falklands and Cape Horn) (Bavay, 1913).

***Dallivoluta*, a synonym of *Lyria*:** Okutani was struck by the general resemblance of *D. surinamensis* with the NW Pacific genus *Fulgoraria* and regarded the non-tilted protoconch, whitish columellar callus and color pattern to differ from the character states observed in *Fulgoraria*. However, we find *D. surinamensis* most closely related to the E. African *Lyria lyraeformis* (Swainson, 1821) and regard the generic characters enumerated by Okutani to be of specific importance only. The shell characters of *Dallivoluta surinamensis* fall within the range observed in the genus *Lyria*, as restricted by Bouchet (1990), and we regard *Dallivoluta* Okutani, 1982 as a synonym of *Lyria* Gray, 1847.

Description of *Lyria doutei*: The second species of *Lyria* obtained from Soviet sources is known to us from a single shell, originally in the Douté collection. At least one other specimen was collected. It is in a private collection in Europe or North America, and was available for examination.

Lyria doutei n.sp.
(figures 4, 5)

Type material: Holotype in (Muséum national d'Histoire naturelle (MNHN), leg. H. Douté.
Type locality: Saya de Malha Bank, 10°30'S, 62°25'E, 135 m.

Description: Shell (figure 4) large, fusiform, solid, consisting of 1.5 protoconch and 6 teleoconch whorls. Protoconch (figure 5) bulbous, with an indication of a calcarella on the initial part, remaining part with convex smooth whorls. Protoconch/teleoconch transition sharp. Teleoconch whorls convex, with appressed, but very slightly channeled suture. Sculpture consisting of orthocline, gently sigmoid axial ribs; no spiral sculpture. Fourteen axial ribs on first teleoconch whorl, gradually increasing to 24 on body whorl. Last rib forming a thick labial varix behind outer lip. Aperture ovate, outer lip smooth, inner lip with thin glaze over body whorl and two groups of plaits; 8 plaits in columellar region, decreasing in strength from base to apex of shell; after a smooth zone, 3 weaker plaits in parietal region. Siphonal canal short, broad, open. Ground color creamy beige with a more complex pattern of yellowish brown to brown flamules and lines arranged in spiral bands. Spire whorls with two darker bands, adapically and abapically, separated by lighter band on mid part of whorl. Adapical band with 6 brown flamules usually extending over one rib and part of the interspaces adjacent to it; brown flamules on abapical band with more indistinct contour. Medial light band with two interrupted brown spiral lines. Body whorl with one light band, and one dark basal band in addition to pattern described above. Aperture creamy beige.

Dimensions: Height 83.5 mm, breadth 30.0 mm, aperture 39 mm.

Remarks: *Lyria doutei* is named after Mr. Harald Douté (Bad Säckingen, Germany), a keen collector specializing in volutes who first recognized it as a new species. Mr. Douté generously provided the holotype, which he had acquired from Mr. Igor Bondarev (Sebastopol, USSR).

Four Indian Ocean species have a general shell morphology and/or color pattern that resemble that of *L. doutei*. These are: *L. lyraeformis*, *L. leslieboschae* Emerson & Sage, 1986, *L. cloveriana* Weaver, 1963 and *L. surinamensis*.

Lyria lyraeformis differs by having fewer axial ribs on the body whorl: it has 16 ribs in southern populations (Mombasa region, southern Kenya), and 20–23 ribs in northern populations (northern Kenya and Somalia). The color pattern of *L. lyraeformis* is extremely stable over its entire range: there are three uninterrupted brown bands on the body whorl, each lined with a dark brown (sometimes interrupted) thread; these brown bands are separated by two lighter spiral bands, each of them carrying 4–7 brown lines. *Lyria lyraeformis* also has a somewhat larger protoconch (height 4.9–5.4 mm vs 4.0 mm in *doutei*), and when more specimens of *L. doutei* are known it may appear that *L. lyraeformis* reaches a significantly larger adult size: Weaver & DuPont (1970) record specimens of 145 mm, but we have seen adults of 180 mm.

Lyria leslieboschae is known only from the four shells on which the original description was based (Emerson & Sage, 1986). It is recognized by the distinct anal canal formed by its outer lip. Its color is of the *lyraeformis* type, but with a more diffused pattern. This species differs from both *L. lyraeformis* and *L. doutei* by having dark axial flamules interrupting the lighter spiral bands.

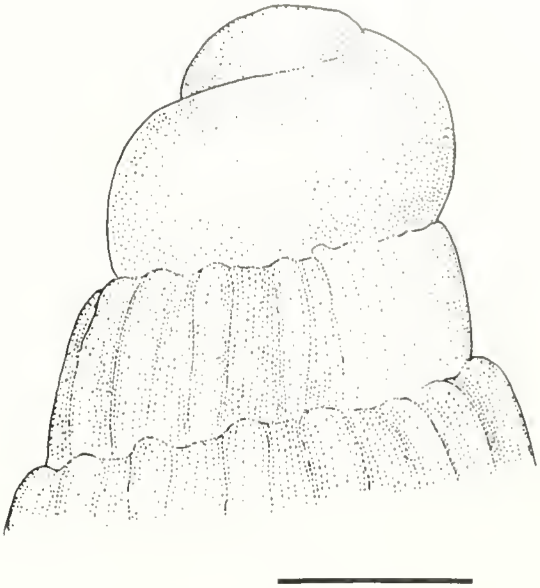

Figure 3. *Lyria surinamensis*. Protoconch of specimen in figure 2. Scale line 2 mm.

Lyria cloveriana is more distantly related. It has an even larger protoconch (height 6.4–7.1 mm); the axial ribs become obsolete on the abapical part of the body whorl; and the color pattern consists of evenly spaced reddish brown spiral lines, without distinct darker spiral bands as in the other species discussed above.

Finally, *L. surinamensis* differs from *L. doutei* by having spiral cords in addition to the axial ribs. *Lyria surinamensis* may also have fewer (19) ribs on body whorl, and the color pattern consists only of poorly defined orange-brown spiral bands on lighter beige background.

Mode of development and biogeographical remarks: The bulbous protoconch of *Lyria surinamensis* (figure 3) and *L. doutei* (figure 5) are comparable in size with those of *L. lyraeformis* and *L. cloveriana* Weaver, 1963. As in all other modern volutes, it indicates non-planctotrophic development, and the large size further suggests intracapsular metamorphosis and hatching as a crawling juvenile (Bouchet & Poppe, 1988). This type of development is incompatible with long distance passive transport of larvae and/or juveniles and, considering the isolation of Saya de Malha Bank (figure 6), suggests that *L. surinamensis* and *L. doutei* are endemic to this bank.

Saya de Malha Bank is a large (*ca.* 4,000 km^2) flat plateau arising abruptly from the Indian Ocean sea-floor, from depths in excess of 4,000 m. Its shallowest parts reach as shallow as 10 m, with the large summital area within the 200 m isobath. Together with the Seychelles

Figure 4. *Lyria doutei* n.sp. Holotype MNHN. Height 83.5 mm.

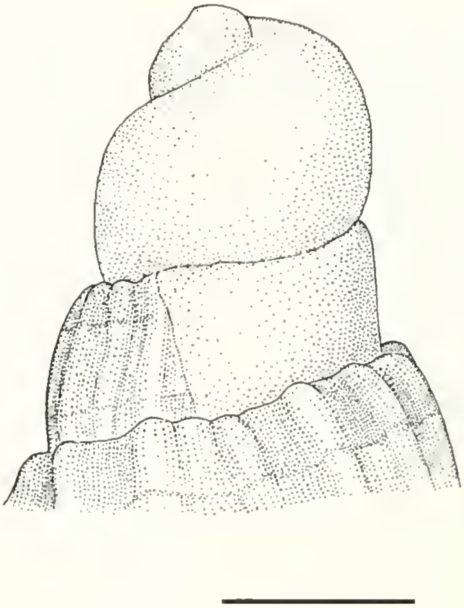

Figure 5. *Lyria doutei* n. sp. Protoconch of holotype. Scale line 2 mm.

Bank to the northwest and Nazareth and Cargados Carajos Banks to the south, it forms the Mascarene Plateau. The Seychelles Bank is composed of late Precambrian granitic rocks and is sometimes called the Seychelles Microcontinent. On the other hand, Saya de Malha, Nazareth and Cargados Carajos Banks have been formed by the Réunion hotspot, Saya de Malha being the oldest in the arc. It dates back to the Paleocene, while the carbonate rocks on Nazareth Bank are not older than Eocene (Backman *et al.*, 1988). Saya de Malha and Nazareth are separated by a sill shallower than 500 m and are only 200–250 km apart. Saya de Malha is separated from the Seychelles Bank by depths greater than 2,000 m and a distance of about 650 km. Distances to other *Lyria*-inhabited continental shelves are: Saya de Malha–Madagascar, 1,200 km; Saya de Malha–Kenya, 2,000 km; Saya de Malha–Sri Lanka, 2,700 km.

For shelf-living volutes with large, crawl-away juveniles, this means that Saya de Malha and Nazareth Banks are very isolated structures that are not easily colonized. However, because they have never been connected to a land mass since *Lyria* appeared in the Eocene, only the dispersal of demersal lecithotrophic larvae can account for colonization of such isolated oceanic banks. It is therefore remarkable that *Lyria surinamensis* has one of the largest protoconchs in the genus, and that its conchological affinities appear to be with species geographically remote: *L. lyraeformis* (Kenya), *L. leslieboschae* Emerson & Sage, 1986 (Arabian Peninsula), *L. cloveriana* Weaver, 1963 (Sri Lanka). We hypothesize that the following scenario may have taken place: 1. Saya de Malha is colonized by an ancestral *Lyria* species with smaller, lecithotrophic, demersal larvae, having a broad Indian Ocean distribution; 2. The species evolves intracapsular metamorphosis with large crawl-away juveniles (this is a general trend in volute evolution and has been noted, *e.g.*, by Hansen (1983) in American Paleogene volutes), demersal dispersal is lost; 3. Geographical isolation enhances genetic isolation, and morphological divergence accumulates through time into different species.

Lyria anna (Lesson, 1835) is another volute endemic to this part of the Indian Ocean. The origin of this species has long remained mysterious (Weaver & Dupont 1970), but there are indications that it probably originates from Mauritius (Richards, 1990), nearby areas NE of Mauritius in 170–230 m (Anonymous, 1984) and/or Cinq Brandons

Figure 6. Simplified bathymetric map of the southwestern Indian Ocean banks, showing the localities mentioned in the text. Stippled area, 0–100 m; thin intermediate line, 200 m isobath; thick line, 500 m isobath. Scale line 500 kilometers.

shoals on the Cargados Carajos Bank of the Mascarene Plateau (unverified information from local Mauritius collectors and dealers). *Lyria anna* is conchologically not closely related to *L. surinamensis* and indicates that the colonization scenario above has occurred several times in the family Volutidae. We predict that more species of Volutidae will be found on banks of the Mascarene Plateau, including the Seychelles Bank.

Finally, it is noteworthy that, beside *Lyria surinamensis* and *Murex surinamensis*, *Conus primus* Röckel & Korn, 1990 was very recently described from Saya de Malha Bank, at depths of 80–98 m. It also has a paucispiral protoconch indicating non-planktotrophic larval development.

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Mistaken Localities for Some Shells "from Surinam"

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Dr. Philippe Bouchet, of the Muséum national d'Histoire naturelle, Paris, and Dr. William K. Emerson, of the American Museum of Natural History, New York, coincidentally alerted me that the type locality reported for *Dallivoluta surinamensis* was incorrect. They had each recently obtained specimens from the Indian Ocean that were identical to *D. surinamensis*. Both suggested that the correct locality was not 11°03′N, 61°01′W but rather 11°03′S, 61°01′E.

In publishing a survey report on shrimp trawl grounds based on samples provided by the Japan Marine Fisheries Research Center (JAMARC) (Okutani, 1983b), I discovered several undescribed species of gastropods and bivalves in the material that had been sent to me for study. A total of ten new species and one new genus were described based on this material (Okutani, 1982, 1983a). After being alerted by Drs. Bouchet and Emerson to the problem with the locality data, I inquired of JAMARC as to the origins of these samples.

JAMARC had conducted a bottom-fish survey on the Saya de Malha Bank in the Indian Ocean in December of 1978, and a survey of shrimp grounds off Surinam and French Guiana from June of 1979 to March of 1983. Although different vessels were used for each of these surveys, the frozen samples were stored in the same refrigerated warehouse when the vessels returned to port. Each frozen block was labeled with precise data as to date, position, depth, haul number, etc. Among the large series of samples, the designations N, S, E, W, were sometimes omitted from the labels, although latitude and longitude were always given. I was not aware of the contamination of the samples as the numerical values of the latitudes and longitudes were so close to each other.

In reviewing the records, I found that species described on the basis of material collected prior to 1979 were all from Indian Ocean samples. These taxa, together with their correct type localities, are:

Murex (Murex) surinamensis Okutani, 1982

Type locality: 10°46′S, 61°32′E, in 94 m.

Dallivoluta surinamensis Okutani, 1982 (now *Lyria surinamensis*, see Bouchet and Bail, 1991)

Type locality: 11°03′S, 61°01′E, in 128 m.

Pteria pictura Okutani, 1983a

Type locality: 10°34′S, 61°35′E, in 97 m.

Spondylus jamarci Okutani, 1983a

Type locality: 11°03′S, 61°01′E, in 128 m.

The following taxa are from the continental shelf or slope off Surinam or French Guiana as originally published:

Plicifusus jamarci Okutani, 1982

Buccinofusus surinamensis Okutani, 1982

Volutomitra bayeri Okutani, 1982

Barbarofusus chocolatus Okutani, 1983a

Sarepta surinamensis Okutani, 1983a

Portlandia nigromaculata Okutani, 1983a

It is hoped that this note will clarify the doubts posed by Ponder and Vokes (1988), Vokes (1990) and Bouchet and Bail (1991).

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New Species of *Gaza, Mirachelus, Calliotropis,* and *Echinogurges* (Gastropoda: Trochidae) from the Northwestern Atlantic Ocean

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ABSTRACT

Five new species of Trochidae from the northwestern Atlantic Ocean are described. *Gaza olivacea*, from the northern coast of South America, is similar to *G. superba* (Dall, 1881) but differs in shell shape and characters of the outer lip and umbilical septum. *Mirachelus acanthus*, known only from Bermuda, most resembles *M. clinocnemus* Quinn, 1979, but differs in shell shape and sculpture. *Calliotropis globosa*, from off the Yucatán Peninsula, Mexico, Jamaica, and the northeastern coast of South America from Venezuela to Suriname, is most similar to *C. actinophora* (Dall, 1890) but differs in relative shell height and umbilical diameter and in sculpture. *Calliotropis dentata*, known only by the holotype from off Venezuela, is most similar to *C. persculpta* (Sowerby, 1903) from off South Africa but has a proportionately higher shell and stronger, coarser sculpture. *Echinogurges tuberculatus*, from off eastern Florida, the Straits of Florida, and the northern Bahamas, is most similar to *E. clavatus* (Watson, 1879) but is distinguished by sculptural details.

Key words: Trochidae; *Gaza*; *Mirachelus*; *Calliotropis*; *Echinogurges*; systematics; new species.

INTRODUCTION

Many undescribed species were discovered during the preparation of two geographically limited monographs of western Atlantic Trochidae (Quinn, 1979, in press a). This paper presents accounts of five new species of the subfamilies Margaritinae and Eucyclinae (following the classification of Hickman & McLean, 1990). New species of the subfamilies Solariellinae and Calliostomatinae are presented elsewhere (Quinn, 1991; in press a,b; in preparation).

Institutional abbreviations used in this paper are as follows: AMNH—American Museum of Natural History; ANSP—Academy of Natural Sciences of Philadelphia; DMNH—Delaware Museum of Natural History, Wilmington; UF—Florida Museum of Natural History, University of Florida, Gainesville; FSBC I—Florida Marine Research Institute, Department of Natural Resources, St. Petersburg; LACM—Natural History Museum of Los Angeles County, Los Angeles; MCZ—Museum of Comparative Zoology, Harvard University, Cambridge; TAMU—Texas A&M University, College Station; UMML—Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami; USNM—National Museum of Natural History, Smithsonian Institution, Washington.

SYSTEMATICS

Family Trochidae Rafinesque, 1815
Subfamily Margaritinae Stoliczka, 1868
Tribe Gazini Hickman and McLean, 1990

Genus *Gaza* Watson, 1879

Type species (monotypy): *Gaza daedala* Watson, 1879.

Gaza olivacea new species
(figures 1–3)

Gaza superba: Okutani, 1983:240.
Gaza sp.: Hickman and McLean, 1990: fig. 51A.

Description: Shell large, attaining 38.1 mm height, 44.9 mm width, broadly conical; whorl profiles weakly convex, with broadly rounded peripheries; umbilicate with umbilical septum; drab-olive to light brown, nacreous under thin outer porcelaneous layer. Protoconch usually missing. Teleoconch whorls about 6, weakly shouldered subsuturally, weakly convex with broadly rounded peripheries, smooth except for microscopic spiral striae. Base almost flat, smooth except for striae like those above. Umbilicus wide, about 25% maximum whorl diameter; wall smooth, parallel to shell axis. Aperture ovate; outer lip oblique and reflected into slightly thickened, nacreous rim, tangential to periphery of previous whorl; inner lip reflected and expanded to form nacreous septum covering umbilicus; columella weakly concave in immature specimens, sigmoid in mature specimens.

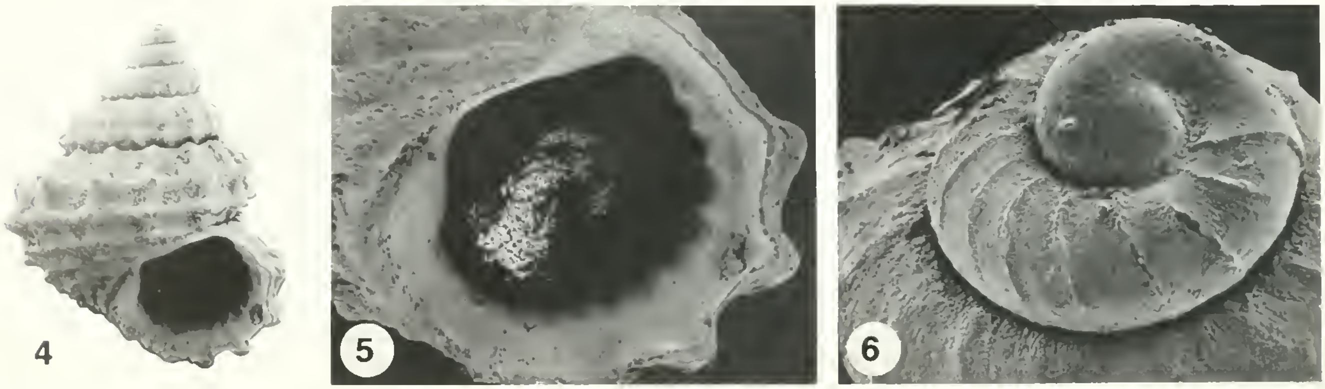
Figures 1–3. *Gaza olivacea* new species. Holotype, USNM 752369, height 32.9 mm, width 39.8 mm, from N of Cabo de la Vela, Peninsula de la Guajira, Colombia, *Oregon* Station 5690, 12°30′N, 72°08′W, 470 m.

Type material: Holotype, USNM 752369; 22 paratypes, USNM 859424; *Oregon* Station 5690, 12°30′N, 72°08′W, 470 m; 40-foot otter trawl; 10 October 1965.—17 paratypes, USNM 752390; 1 paratype, UMML 30.8365; 1 paratype, FSBC I 39513; *Oregon* Station 4301, 7°35′N, 54°13′W, 366 m; 65-foot otter trawl; 24 March 1963.

Type locality: North of Cabo de la Vela, Peninsula de la Guajira, Colombia, *Oregon* Station 5690, 12°30′N, 72°08′W, 470 m.

Other material examined: 14 specimens, USNM 752391 (+ 61 uncatalogued USNM, and duplicates in other museums); *Oregon* Station 2026, 7°10′N, 53°07′W, 366 m; 40-foot otter trawl; 9 November 1957.—15 specimens, USNM 752389 (+ 200–300 uncatalogued USNM, and duplicates in other museums); *Oregon* Station 2005, 7°34′N, 54°50′W, 366 m; 40-foot otter trawl; 6 November 1957.—1 specimen, USNM 752383; *Oregon* Station 1982, 10°00′N, 59°59′W, 457 m; 40-foot otter trawl; 3 November 1957.—8 specimens, USNM 752388; *Oregon* Station 5028, 11°30′N, 60°46′W, 366–439 m; 40-foot otter trawl; 22 September 1964.—2 specimens, USNM 752393; *Oregon* Station 5930, 15°38′N, 61°07′W, 808 m; otter trawl; 5 March 1966.—19 specimens, USNM 752384 (+ 54 uncatalogued USNM, and duplicates in other museums); *Oregon* Station 2351, 11°31′N, 62°24′W, 338–366 m; 40-foot otter trawl; 23 September 1958.—17 specimens, USNM 752377; *Oregon* Station 2780, 11°36′N, 62°52′W, 393–421 m; 40-foot otter trawl; 20 April 1960.—15 specimens, USNM 752366; *Oregon* Station 4420, 11°46′N, 69°17′W, 421 m; 40-foot otter trawl; 4 October 1963.—7 specimens, USNM 752372; *Oregon* Station 5692, 12°31′N, 71°58′W, 375 m; 40-foot otter trawl; 10 October 1965.—4 specimens, TAMU 4-1737; 2 specimens, TAMU 4-0388; *Alaminos* Station 70A10-40, 12°40′N, 72°00′W, 622–658 m; 57-foot trawl; 18 July 1970.—9 specimens, USNM 752373; *Oregon* Station 4923, 12°21′N, 72°40′W, 439–448 m; 40-foot otter trawl; 2 June 1964.—13 specimens, UMML 30.8364; *John Elliott Pillsbury* Station P-781, 11°30.1′N, 73°26.5′W, 567–531 m; 10-foot otter trawl; 30 July 1968.—16 specimens, USNM 752376; *Oregon II* Station 11252, 11°25′N, 73°56′W, 435 m; 71-foot otter trawl; 10 November 1970.—3 specimens, USNM 752374; *Oregon II* Station 11251, 11°23′N, 74°16′W, 457 m; 71-foot otter trawl; 10 November 1970.—7 specimens, USNM 752364; *Oregon II* Station 10266, 11°04′N, 74°25′W, 27 m; 71-foot otter trawl; 2 December 1968.—12 specimens, USNM 752365; *Oregon II* Station 11248, 11°18′N, 74°44′W, 600 m; 71-foot otter trawl; 9 November 1970.—9 specimens, USNM 752363 (+ 100 uncatalogued USNM, and duplicates in other museums); *Oregon II* Station 10260, 11°03′N, 75°18′W, 366 m; 71-foot otter trawl; 2 December 1970.—5 specimens, USNM 752375; *Oregon* Station 5722, 9°36′N, 76°22′W, 512 m; 65-foot otter trawl; 16 October 1965.—1 specimen, USNM 94991; *Albatross* Station 2143, 9°30′45″N, 76°25′30″W, 283 m; small beam trawl; 23 March 1884.—4 specimens, USNM 752392; *Oregon* Station 3584, 9°13′N, 81°30′W, 366 m; 40-foot otter trawl; 25 May 1962.—20 USNM lots with localities within range indicated above.

Remarks: Shells of *Gaza olivacea* are most similar to those of *Gaza superba* (Dall, 1881) but differ in being more broadly conical and in having more flattened whorl profiles and much weaker spiral striae; the outer lip is not angulate at the junction with previous whorl (figures 2, 3); and the nacreous septum covers the entire umbilicus. With the exception of the spiral striae and umbilical septum, shells of *G. olivacea* differ from those of the Galapagan *G. rathbuni* Dall, 1890, by the same characters that differentiate *G. olivacea* and *G. superba*. *Gaza olivacea* is known from Golfo de los Mosquitos, Panamá, eastward along the northern coast of South America to Suriname and French Guiana. Although the depth range for this species is 283–808 m ($\bar{x}$ = 433 m, n = 38), 87% of all collections were made in depths of 350–550 m; these analyses ignored records of 15 fms (27 m; *Oregon II* Station 10266) and 25 fms (46 m; *Oregon II* Station 11275) because they are most likely errors for 150 fms and 250 fms, respectively. These depths are shallower than those for *G. superba* (range = 360–1,006 m; $\bar{x}$ =



Figures 4–6. *Mirachelus acanthus* new species. **4.** Paratype, DMNH 187590, height 3.45 mm, width 2.95 mm, from off Bermuda. **5.** Same specimen, aperture, 27 ×. **6.** Same specimen, oblique view of protoconch and first whorl, 108 ×.

556 m, n = 78), for which 86% of all collections have been made between 440 m and 680 m (Quinn, in press a). The geographic ranges of *G. olivacea* and *G. superba* overlap slightly only in Panamá in the west, and off Grenada and Suriname in the east. A third western Atlantic species, *G. fischeri* Dall, 1889, has a geographic range that encompasses the ranges of both *G. olivacea* and *G. superba*, but occurs in depths deeper than either of those species (80% of lots from 550–825 m; $\bar{x}$ = 692 m; n = 33), although *G. fischeri* and *G. superba* have sometimes been collected together (Quinn, in press a). Like shells of *G. superba*, almost all shells of *G. olivacea* have a small, neat hole replacing the protoconch and leading into the umbilicus, and a narrow channel at the junction of the umbilical rim and outer lip (figure 3), both caused by a commensal polychaete worm that lived in a mud tube within the umbilicus (Quinn, in press a).

Subfamily Eucyclinae Koken, 1897
Tribe Chilodontini Wenz, 1938
Genus *Mirachelus* Woodring, 1928

Type species (original designation): *Calliostoma corbis* Dall, 1889.

Mirachelus acanthus new species
(figures 4–6)

Description: Shell small for genus, attaining 3.70 mm height, 2.95 mm width, conical, nonumbilicate, white, nacreous under thin outer porcelaneous layer. Protoconch about 325 μm maximum diameter, about one whorl. Teleoconch whorls about 5.4; first 1.5–2 whorls with strong axial lamellae, remaining strong but becoming more rounded on subsequent whorls, spaced about 0.5 mm apart on fifth whorl; very fine, oblique threads covering whorl surface; 2 spiral cords appearing near end of second whorl, abapical cord stronger and forming periphery; weak angulation or spiral cord sometimes present at suture; strong, conical tubercles at intersections of axial and spiral sculpture. Base convex, with 4–5 strong spiral cords, spiral cords undulate or weakly beaded abaxially, more distinctly beaded adaxially. Aperture oblique, ovate, thickened within, with 8–9 weak ridges on thickening; columella short, thickened, weakly inflated medially.

Type material: Holotype, DMNH 187589; 3 paratypes, DMNH 187590; 1 paratype, USNM 860246; Lightbourn-Guest *Northstar* Expedition Station 582, off Castle Harbour, Bermuda, 100 m.

Type locality: Off Castle Harbour, Bermuda, in 100 m.

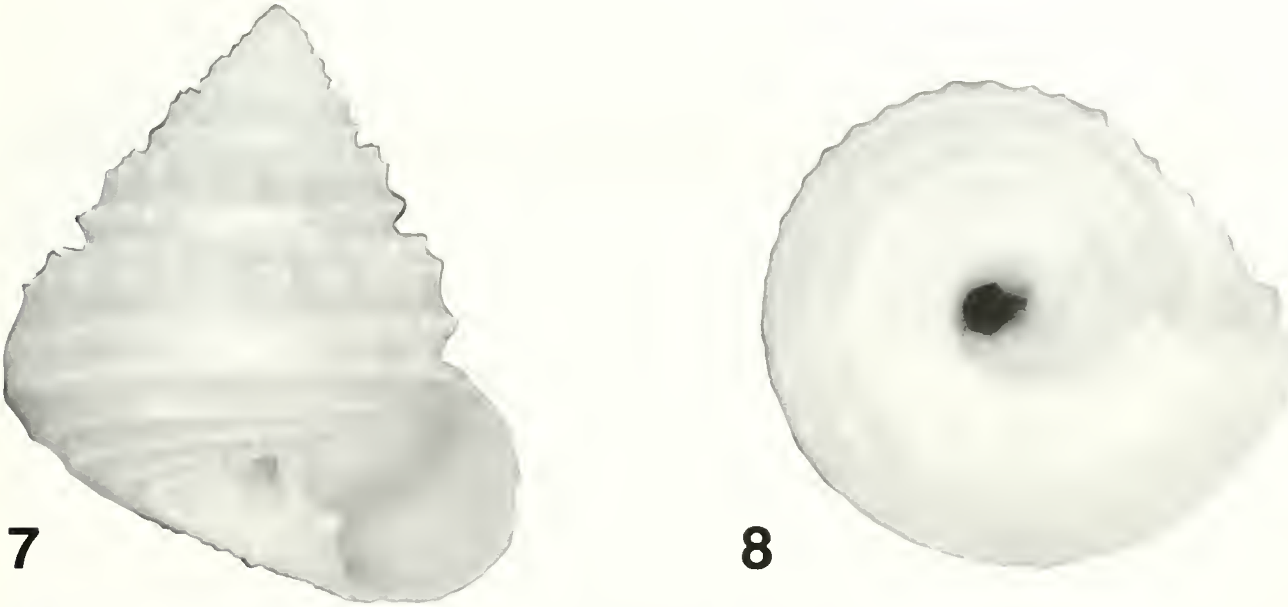
Remarks: Shells of this species are most similar to those of *Mirachelus clinocnemus* Quinn, 1979, but differ in having weaker but sharper spiral cords, the peripheral one stronger and more projecting than the one just adapical; in having the axial lamellae sharper and more widely spaced (0.5 mm apart in *M. acanthus*, 0.25 mm apart in *M. clinocnemus*); and in having more prominent, sharply conical tubercles on the peripheral and supraperipheral spiral cords. The shells of *M. acanthus* are also slightly broader than those of *M. clinocnemus*.

Tribe Calliotropini Hickman and McLean, 1990
Genus *Calliotropis* Seguenza, 1903

Type species (original designation): *Trochus ottoi* Philippi, 1844.

Calliotropis globosa new species
(figures 7, 8)

Description: Shell of medium size for genus, attaining 9.7 mm height, 8.7 mm width, turbinate with inflated whorls, umbilicate, white, nacreous under thin outer porcelaneous layer. Protoconch large, about 525–550 μm maximum diameter, 1 whorl. Teleoconch whorls 6.25; first 1.5 whorls with thin axial riblets, rapidly becoming weaker on next whorl, finally becoming restricted to subsutural area on last whorl; pair of spiral threads appearing on first whorl, one subsutural, one just below midwhorl and forming whorl periphery, both becoming slightly stronger on subsequent whorls; third spiral thread appearing on third whorl between suture and primary subsutural spiral thread, gradually becoming slightly



Figures 7, 8. *Calliotropis globosa* new species. Holotype, USNM 859419, height 9.45 mm, width 8.70 mm, from S of Jamaica, 17°21.4′N, 77°34.8′W, 805–1,089 m.

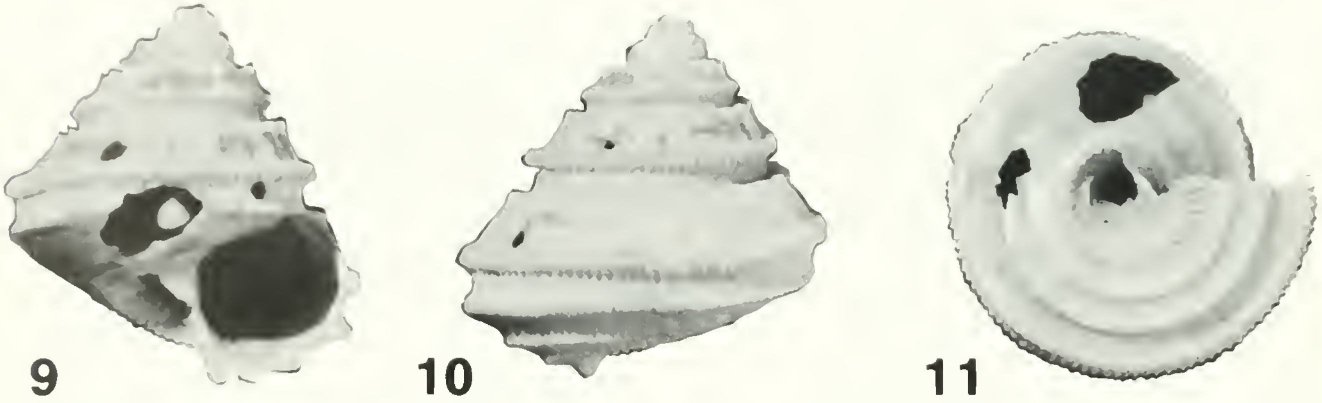
stronger than primary subsutural spiral thread on subsequent whorls; fourth spiral thread similar to peripheral thread, appearing on last whorl, coincident with suture on spire whorls. Base convex, with 4 spiral cords; outermost cord almost smooth, cords becoming progressively more strongly tuberculate adaxially; innermost 2 cords most closely spaced; transverse rugae becoming progressively stronger adaxially. Umbilicus deep, walls axially rugose and almost vertical. Aperture subovate, lips thin; columella sigmoid, thin, with rather strong, rounded tooth medially in some specimens.

Type material: Holotype, USNM 859419; 2 paratypes, USNM 859420; 2 paratypes, ANSP 383289; 2 paratypes, FSBC I 39515; 2 paratypes, UF 169956; 2 paratypes, MCZ 302452; 2 paratypes, AMNH 232160; 21 paratypes, UMML 30.8358; *John Elliott Pillsbury* Station P-1262, 17°21.4′N, 77°34.8′W, 805–1,089 m; 10-foot otter trawl; 15 July 1970.

Type locality: South of Jamaica, *John Elliott Pillsbury* Station P-1262, 17°21.4′N, 77°34.8′W, 805–1,089 m.

Other material examined: 17 specimens, UMML 30.8355; *John Elliott Pillsbury* Station P-604, 18°58′N, 87°28′W, 970–988 m; box dredge; 17 March 1968.—27 specimens, UMML 30.8356; *John Elliott Pillsbury* Station P-605; 18°50.1′N, 87°31.5′W, 695–773 m; 10-foot otter trawl; 17 March 1968.—10 specimens, UMML 30.5703; 11 specimens, UMML 30.8361; *John Elliott Pillsbury* Station P-607, 18°30′N, 87°37′W, 715–787 m; 10-foot otter trawl; 17–18 March 1968.—3 specimens, MCZ 294845; *Blake* Station XVIII, 18°20′30″N, 87°16′40″W, 1,097 m; 1880.—4 specimens, UMML 30.8360; *John Elliott Pillsbury* Station P-1255, 17°18′N, 78°32′W, 622–823 m; 10-foot otter trawl; 14 July 1970.—2 specimens, UMML 30.8359; *John Elliott Pillsbury* Station P-1261, 17°13′N, 77°50′W, 595–824 m; 10-foot otter trawl; 15 July 1970.—1 specimen, MCZ 135174; *Atlantis* Station 3454, 23°24′N, 80°36′W, 1,097 m; 4 May 1939.—4 specimens, MCZ 135175; *Atlantis* Station 3457, 23°23′N, 80°36′W, 1,006 m; 4 May 1939.—3 specimens, MCZ 135179; *Atlantis* Station 3345, 21°08′N, 79°56′30″W, 1,280 m; 8 April 1939.—3 specimens, MCZ 135177; 6 specimens, MCZ 135178; *Atlantis* Station 3366, 20°46′N, 74°59′W, 1,097 m; 19 April 1939.—5 specimens, MCZ 135183; *Atlantis* Station 3359, 20°38′N, 74°32′W, 1,829 m; 18 April 1939.—1 specimen, UMML 30.8357; *John Elliott Pillsbury* Station P-919, 16°05.3′N, 61°19.3′W, 704–732 m; 5-foot Blake trawl; 12 July 1969.—6 specimens, UMML 30.8362; *John Elliott Pillsbury* Station P-850, 11°45.5′N, 61°29.5′W, 896–923 m; 10-foot otter trawl; 3 July 1969.—9 specimens, UMML 30.7337; *John Elliott Pillsbury* Station P-846, 11°37.8′N, 60°37.4′W, 878–942 m; 10-foot otter trawl; 2 July 1969.—1 specimen, UMML 30.7347; *John Elliott Pillsbury* Station P-847, 11°37.3′N, 0°59.4′W, 920–1,244 m; 41-foot otter trawl; 2 July 1969.—13 specimens, UMML 30.6912; *John Elliott Pillsbury* Station P-754, 11°36.0′N, 68°42.0′W, 684–1,574 m; 10-foot otter trawl; 26 July 1968.

Remarks: Shells of this species are most similar to those of *Calliotropis actinophora* (Dall, 1890) in size, general shape, and sculpture but differ in being proportionately narrower; in having narrower umbilici; in having stronger, more widely spaced subsutural axial rugae; in having the adaxial two spiral rows of tubercles more closely spaced; and in having four rather than three basal spiral cords. *Calliotropis globosa* is known from the Yucatán



Figures 9–11. *Calliotropis dentata* new species. Holotype, USNM 859419, height 9.4 mm, width 9.2 mm, from off Isla Orchilla, Venezuela, 11°47.8′N, 66°06.8′W, 1,052–1,067 m.

coast near Banco Chinchorro, from Cay Sal Bank and Cuba, from south of Jamaica, and along the northern South American coast from Venezuela to Suriname, mostly in depths of about 700–1,100 m (range = 595–1,829 m).

Calliotropis dentata new species
(figures 9–11)

Description: Shell of medium size for genus, attaining at least 9.4 mm height, 9.2 mm width, conical with shouldered whorls, peripherally carinate, strongly sculptured, white, nacreous under outer porcelaneous layer. Protoconch and much of first whorl missing. First remaining whorl with narrow axial riblets and weak subsutural and peripheral spiral angulations. Second whorl largely decorticated but showing strengthening angulations. Subsutural angulation becoming spiral row of strong, conical, axially elongate tubercles rising above level of suture; peripheral angulation forming carina set with closely set, cog-like tubercles connected and crossed by fine spiral thread. Final whorl with second carina, similar to peripheral carina but slightly weaker, abapical to peripheral carina and coincident with suture line. Whorl surface between spiral carinae flat, with fine, collabral growth lines. Base convex, with 3 strong, tuberculate spiral cords; whorl surface between innermost 2 spiral cords with weak collabral rugae that generally connect tubercles of cords. Umbilicus about 30% maximum shell diameter, funnel-shaped, walls with axial rugae and single weak spiral thread. Lips of aperture and columella broken.

Type material: Holotype, USNM 859422; *John Elliott Pillsbury* Station P-741, 11°47.8′N, 66°06.8′W, 1,052–1,067 m; 40-foot otter trawl; 23 July 1968.

Type locality: Off Isla Orchilla, Venezuela, *John Elliott Pillsbury* Station P-741, 11°47.8′N, 66°06.8′W, 1,052–1,067 m.

Remarks: The shell of *Calliotropis dentata* is easily distinguished from those of all other western Atlantic *Calliotropis* by having the peripheral and subperipheral spiral cords with closely set, cog-like beads instead of conical tubercles. The shell of *C. dentata* is very similar in sculpture to that of *C. persculpta* (Sowerby, 1903) (see Kaicher, 1990: card 5695) from South Africa but differs in being higher spired and in having stronger basal spiral cords and a narrower umbilicus.

Genus *Echinogurges* Quinn, 1979

Type species (original designation): *Trochus* (*Margarita*) *clavatus* Watson, 1879.

Echinogurges tuberculatus new species
(figures 12–14)

Echinogurges rhysus: Quinn, 1979:21, 22, figs. 39, 40. [Misidentification; not *Trochus* (*Margarita*) *rhysus* Watson, 1879.]

Description: Shell small, attaining 4.6 mm height, 3.9 mm width, conical with shouldered whorls, strongly sculptured, umbilicate, white, nacreous under thin outer porcelaneous layer. Protoconch about 375 μm maximum diameter, bulbous, 1 whorl. Teleoconch whorls 5.5, tubular, carinate, first whorl with strong, thin axial riblets that become weak collabral ridges on subsequent whorls; pair of spiral ridges appearing on second whorl, one subsutural, one at midwhorl forming carinate whorl periphery; third tuberculate spiral ridge present on body whorl, coincident with suture on spire whorls; strong, conical tubercles at intersections of axial and spiral sculpture. Base convex, rounding into umbilicus, with 4 smoothish to finely tuberculate spiral cords. Umbilicus narrow, pore-like, wall with axial rugae. Aperture subcircular, lips thin, inner lip weakly reflected into umbilicus; columella concave, thin, rounding smoothly into outer lip.

Type material: Holotype, USNM 330606; 4 paratypes, USNM 859426; *Albatross* Station 2654, 27°57′30″N, 77°27′30″W, 1,207 m; large beam trawl; 2 May 1886.—13 paratypes, MCZ 302536; *Atlantis* Station 2993,

Figures 12–14. *Echinogurges tuberculatus* new species. **12. 13.** Paratype, UMML 30.8095, height 4.0 mm, width 3.1 mm, from southern Straits of Florida, *Gerda* Station G-1106, 24°02′N, 81°30′W, 1,706–1,723 m. **14.** Protoconch of paratype (USNM 859426) from NE of Little Bahama Bank, *Albatross* Station 2654, 27°57′30″N, 77°27′30″W, 1,207 m, 97 ×.

33°19′N, 80°44′W, 1,061 m; 15 March 1938.—4 paratypes, USNM 859426; *Albatross* Station 2415, 30°44′N, 79°26′W, 805 m; large beam trawl; 1 April 1885.—2 paratypes, UMML 30.8054; *Gerda* Station G-368, 24°03′N, 81°10′W, 961–1,016 m; 16-foot otter trawl; 15 September 1964.—1 paratype, UMML 30.8041; *Gerda* Station G-130, 23°59′N, 81°10′W, 1,021 m; 10-foot otter trawl; 21 June 1963.—1 paratype, UMML 30.8163; *Gerda* Station G-859, 23°54′N, 81°57′W, 1,161–1,200 m; 10-foot otter trawl; 29 August 1967.—2 paratypes, USNM 438284; 10 miles N of Cuba, 1,427 m; J. B. Henderson coll.—2 paratypes, MCZ 7584; *Blake* Station, Yucatan Channel, 1,171 m.

Type locality: Northeast of Little Bahama Bank, *Albatross* Station 2654, 27°57′30″N, 77°27′30″W, 1,207 m.

Other material examined: 1 specimen, UMML 30.8095; *Gerda* Station G-1106, 24°02′N, 81°30′W, 1,706–1,723 m; 10-foot otter trawl; 29 April 1969.—4 specimens, MCZ 135026; *Atlantis* Station 2988, 23°15′N, 79°57′W, 695 m; 14 March 1938.

Remarks: Shells of *Echinogurges tuberculatus* are most similar to those of *E. clavatus* (Watson, 1879) but differ in having only a single peripheral spiral ridge; weaker, more widely spaced axial sculpture; and fewer basal spiral cords. Specimens of *E. tuberculatus* were misidentified as *E. rhysus* (Watson, 1879) by Quinn (1979). Subsequent examination of the types of *Trochus* (*Margarita*) *rhysus* Watson, 1879, revealed that *T.* (*M.*) *rhysus* is actually a species of *Calliotropis* Seguenza, 1903 (Quinn, in press a). *Echinogurges tuberculatus* is known only from off the east coast of Florida, the Bahama Islands, and the Straits of Florida in depths of 805–1,723 m.

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Acroloxus coloradensis (Henderson), a Rare North American Freshwater Limpet

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The freshwater limpet family Acroloxidae (Basommatophora) contains seven species, all in the genus *Acroloxus*. One, *A. lacustris* (Linnaeus), is common in lentic habitats of much of Europe and parts of Asia. Five species, *A. improvisus* (Polinski), *A. macedonicus* (Hadzisce), *A. kobelti* (Dybowski), *A. sibiricum* (Gerstfeldt), and *A. troscheli* (Dybowski), appear to be endemic to a few ancient lakes (e.g., Lake Ochrid and Lake Baikal) of Yugoslavia and U.S.S.R. (Clarke, 1973). Only one species, *A. coloradensis* (Henderson), is found in North America. It is readily distinguished from other freshwater limpets by its spine-like apex, which is directed posteriorly towards the left margin (figure 1). *Acroloxus coloradensis* has hitherto been reported from only seven North American localities. Four of the records are from Rocky Mountain lakes: Colorado (Walker, 1925), Alberta (Mozley, 1930), Montana (Russell and Brunson, 1967), and British Columbia (Clarke, 1981). The other three records are from ponds in Ontario and Quebec (Clarke, 1970).

We recently collected *Acroloxus coloradensis* specimens from one location of the Beaver River in Alberta, Canada. Voucher specimens are deposited in the Canadian Museum of Nature, Ottawa, Ontario, Canada, catalog number #92900. This is the first report of *A. coloradensis* collected from a stream and apparently the first report of any of the seven *Acroloxus* species from a lotic habitat. The Beaver River runs through the southern limit of mixed boreal forest and the northern limit of agricultural activity in northeastern Alberta and is a tributary of the Churchill River, which empties into Hudson Bay.

We sampled various sites of the Beaver River, but *Acroloxus coloradensis* was collected at only one location: where the Beaver River is crossed by a small road bridge south of Highway 55 (54°32′N, 111°52′W). Specimens were collected to a depth of about 0.8 meters. Samples were collected between 30 May and 2 August 1989 by kick samples taken with a dip net (mesh size: 500 μm) and by inspecting substratum taken from the river. The width of the Beaver River at the collecting site was 17.5 m; water temperatures ranged from 17 °C on 30 May 1989 to 25 °C on 20 July 1989. There were no riffle regions in the vicinity, and current velocity was undetectable using a Price AA current meter. Free-floating and submergent macrophytes were common at the sampling site. The river's substratum immediately upstream and downstream of the collecting site (the bridge) consisted of mud and plant detritus with rooted macrophytes near the banks of the river. However, *A. coloradensis* was collected only where the bridge crossed the stream, and here the substratum consisted of gravel, peb-

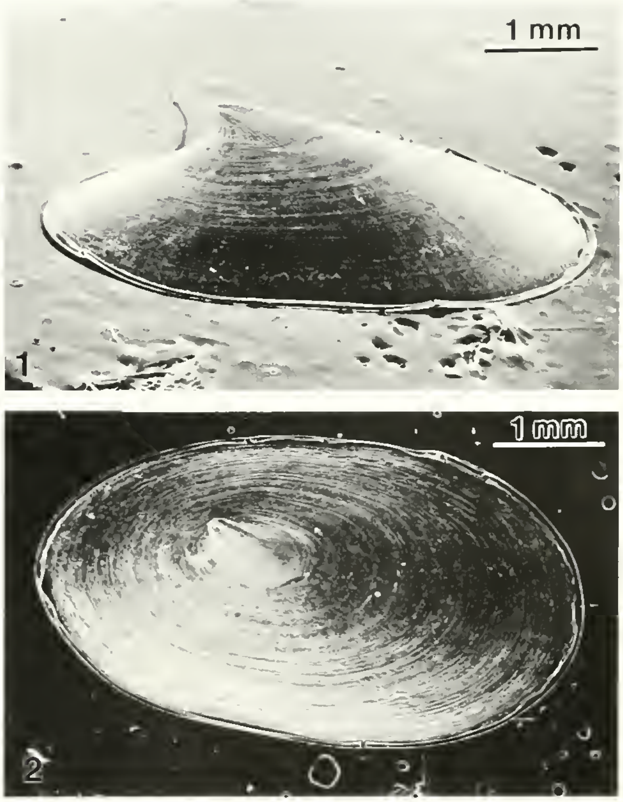

Figure 1. Scanning electron micrographs of *Acroloxus coloradensis* from the Beaver River, Alberta, Canada. **1.** Side view. **2.** Top view.

bles and large cobbles; presumably the large substrata was introduced when the bridge was constructed. Other gastropods collected from this location were *Valvata sincera helicoidea* Dall; *Menetus cooperi* Baker, *Promenetus exacuous exacuous* (Say), *Armiger crista* (Linnaeus), *Lymnaea stagnalis jugularis* (Say), *Stagnicola* spp., *Helisoma* spp., and *Gyraulus* spp.

Bryce (1970) postulated that *Acroloxus coloradensis*, based on its known distribution at that time, was a cold-water stenotherm, limited to Rocky Mountain lakes. More recent records of the limpet in Ontario and Quebec (Clarke, 1970), Colorado (Wu 1989), and our finding indicate that *A. coloradensis* is not restricted to Rocky Mountain lakes. The large temperature variations (17°–25 °C) experienced over the summer by *A. coloradensis* in the Beaver River indicate that it is not a cold-water stenothermal species.

Clarke (1973) and Burch (1982) suggest *A. coloradensis* might be a rare species with a relic distribution. Its discovery in the Beaver River is not inconsistent with this idea, and we can only speculate on its occurrence in the Beaver River of Alberta, Canada. Possibly *A. coloradensis* will eventually be recorded from Saskatchewan and Manitoba, indicating a wide but rare distribution across Canada on both sides of and in the Cordillera. The southerly populations of *A. coloradensis*, e.g., in Montana and Colorado, might now be restricted to in and near the Cordillera.

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