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Museum of Comparative Zoology
Harvard University
Cambridge, MA 02138

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Department of Geology
University of California at Davis
Davis, CA 95616

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Deep-sea Gastropods from the New Zealand Region Associated with Recent Whale Bones and an Eocene Turtle

Bruce A. Marshall

Museum of New Zealand Te Papa
Tongarewa
P O Box 467
Wellington, New Zealand

ABSTRACT

Five species of gastropods are newly recorded from decaying whale bone from the deep-sea floor off New Zealand. *Paracocculina cervae* (Fleming, 1948), and new species of *Osteopelta*, Marshall, 1987 (Cocculiniformia), *Brucciella* Warén & Bouchet, 1993 (Vetigastropoda), and *Xylodiscula* Marshall, 1985 (Heterobranchia). Recently discovered material of *Osteopelta mirabilis* is recorded, and this or a closely similar species is recorded associated with turtle bones from the Middle Eocene of New Zealand. The new *Brucciella* and *Xylodiscula* species are the first records of skeneimorph gastropods from bone. Apart from whale bone, *Paracocculina cervae* is associated with sunken wood and algal holdfasts (new record), so it has the most generalised habitat of any known cocculiniform limpet.

Key words: Recent, fossil, Mollusca, Gastropoda, deep-sea, whale bone, turtle bone, New Zealand

INTRODUCTION

Since discovery of the limpet *Osteopelta mirabilis* Marshall, 1987, the first record of a gastropod living in association with decaying whale bones, a second species of *Osteopelta* has been recorded from bone off Iceland (Warén, 1989). More recently McLean (1992) has recorded a new species of *Cocculina* Dall, 1882 (Cocculinidae) and three species of *Pyropelta* McLean & Haszprunar, 1987 (Pyropeltidae) from whale bone from the eastern Pacific. One of these pyropeltid limpets was described as new, while the other two were evidently conspecific with specimens originally obtained from hydrothermal vents (McLean & Haszprunar, 1987). Dell (1987) has reviewed mytilid bivalves associated with whale remains. Additional taxa have been recorded by Smith et al. (1989), who drew attention to similarities between faunas associated with decaying whale bones, hydrothermal vents and hydrocarbon seeps, and suggested that whale skeletons may provide stepping stones for wide dispersal of deep-sea chemosynthetic communities (see also Smith, 1992).

In this paper I introduce a third species of *Osteopelta*, another cocculinid, and species of *Brucciella* Warén & Bouchet, 1993 and *Xylodiscula* Marshall, 1985 new to the fauna of this unusual habitat. *Brucciella* was based on a species from a hydrothermal vent, while previously known *Xylodiscula* species occurred in association with sunken wood, old sea grass (*Posidonia*) fibres, and a hydrothermal vent.

ABBREVIATIONS

- AMS Australian Museum, Sydney
BMNH The Natural History Museum, London
LACM Los Angeles County Museum of Natural History
MNHN Museum National d'Histoire Naturelle, Paris
MNZ Museum of New Zealand, Wellington
NMP Natal Museum, Pietermaritzburg
OU Geology Department, University of Otago, Dunedin
USNM National Museum of Natural History, Washington, DC

Order ARCHAEOGASTROPODA Thiele, 1925
Suborder COCCULINIFORMIA Haszprunar, 1987
Superfamily COCCULINOIDEA Dall, 1882
Family COCCULINIDAE Dall, 1882
Genus *Paracocculina* Haszprunar, 1987

Paracocculina Haszprunar, 1987:321. Type species (by original designation): *Cocculina laevis* Thiele, 1903; Recent, off Nias Island, Sumatra.

Remarks: The genus *Paracocculina* was introduced by Haszprunar (1987) for species that differ from *Cocculina* Dall, 1882 primarily in having a prominent subpallial gland, a pedally innervated copulatory organ on the right side of the foot, and a hypoathroid nervous system with the osphradial ganglion situated at the far left side.

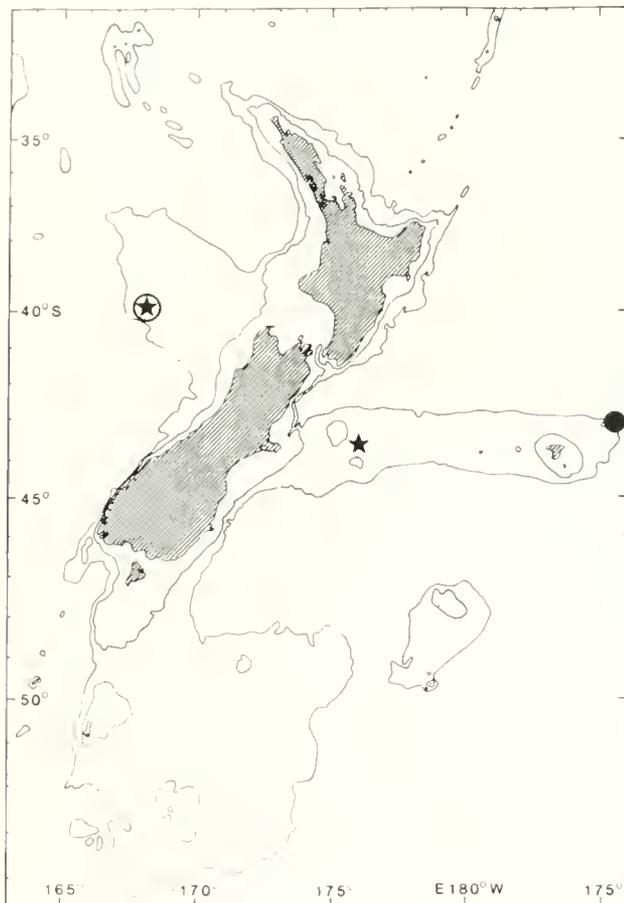


Figure 1. Map of New Zealand region showing localities for *Osteopelta praeceps* n. sp. and *O. mirabilis* (stars), *Bruceiella laevigata* n. sp. (solid circle), and *Bruceiella pruinosa* n. sp. (open circle). 200 and 1,000 meter contours indicated

Paracocculina cervae (Fleming, 1948)

Cocculina cervae Fleming, 1948:88, text fig. 1a-d; Marshall, 1986:508, figs. 2A, 3A-C, 12AB

Tecticerater cervae. Dell, 1956:60; Powell, 1979:81, fig. 10:9.

Paracocculina cervae. Haszprunar, 1987:321.

Material examined: (Additional to that recorded by Marshall, 1986): 39°53.2'S, 168°01.2'E, Challenger Plateau, New Zealand, alive on whale bone, 908–912 m, 3 July 1989, f.v. *Amaltal Explorer* (3 MNZ); 44°40.5'S, 174°01.0'E, off Banks Peninsula, alive on whale skull, 844 m, 11 May 1987, f.v. *Oyang 7* (5 MNZ); 38°38.9'S, 178°38.3'E, off Gable End Foreland, New Zealand, alive on algal holdfast, 529–565 m, 23 September 1985, f.v. *Wanaka* stn WK2/68/85 (1 MNZ); 43°02.5'S, 174°09.0'E, off Kaikoura, New Zealand, alive on algal holdfast, 848–877 m, 24 September 1988, f.v. *James Cook* stn J12/10, S5 (7 MNZ); 50°02.6'S, 169°31'E, east of the Auckland Is., New Zealand, alive on algal holdfast, 614–620 m, 4 December 1992, f.v. *Tangaroa* stn 92011/97 (many MNZ).

Distribution: North Cape to the Auckland Islands, New

Zealand, 18–891 m, on sunken wood, algal holdfasts and whale bone.

Remarks: Specimens from whale bone and deep-sunken algal holdfasts and wood proved to be indistinguishable in shell and radular morphology and in external anatomy.

Superfamily LEPETELLOIDEA Thiele, 1908

Family OSTEOPELTIDAE Marshall, 1987

Genus *Osteopelta* Marshall, 1987

Osteopelta Marshall, 1987:121. Type species (by original designation): *Osteopelta mirabilis* Marshall, 1987; Recent, New Zealand.

Osteopelta mirabilis Marshall, 1987

Osteopelta mirabilis Marshall, 1987:122, figs. 1A, B-D, F-J, 2A, 2B, 3C; Haszprunar, 1988:6, figs. 15–24 (anatomy).

Material examined: (Additional to that recorded by Marshall, 1987): 39°53.2'S, 168°01.2'E, Challenger Plateau, New Zealand, alive on whale bone, 908–912 m, 3 July 1989, f.v. *Amaltal Explorer* (18 MNZ); off Mernoo Bank, Chatham Rise, New Zealand, alive on large whale skull, ca. 900 m, October 1988, f.v. *Amaltal Explorer* (5 MNZ).

Distribution (figure 1): Challenger Plateau and Chatham Rise, New Zealand, on whale bone, 800–955 m.

Remarks: The Challenger Plateau specimens are indistinguishable from type and other material from the Chatham Rise. The protoconch is retained in a specimen 5.00 mm long, and is bilaterally symmetrical and 200 μ m long, with a long tapered apical fold tip on each side. Regrettably the sculpture is unknown, as the outer shell layer has been etched away. The Icelandic species *Osteopelta ceticola* Warén, 1989, also from whale bone, differs in minor details of radular morphology (Warén, 1989).

Osteopelta sp. cf. *mirabilis* Marshall, 1987

Material examined: Isolated concretion of Waihao Greensand on right bank of South Branch of Waihao River, north of Waihao Downs (map ref. J40 45000030), closely associated with bones of fossil leatherback turtle (*Dermochelys* sp.—Reptilia, Chelonia, Dermochelyidae), coll. R. E. Fordyce, A. Grebneff, C. M. Jones and P. A. Maxwell. Age: Bortonian (Middle Eocene) (1 specimen OU41112).

Remarks: The single specimen is embedded apex down in a block of gritty matrix with the fully exposed interior surface showing clearly defined muscle scars. A mould of the exterior where a small piece of the shell margin has broken away shows impressions of weak concentric sculpture. The specimen is indistinguishable from the Recent specimens of *Osteopelta mirabilis* in shape, shell thickness, teleoconch sculpture, muscle scar outline, and size (length est. 7.50 mm, width 6.05 mm). While it is

impossible to be absolutely certain of the relationships of this limpet from the teleoconch alone, particularly the interior, the association with bone suggests that it is probably an osteopeltid.

The Waihao Green sand beds were considered by Maxwell (1992) to have been deposited at 150–250 m depth, which is substantially shallower than the bathymetric range of living *O. mirabilis* (800–955 m).

Osteopelta praeceps n. sp.
(figures 2–6, 18, 19)

Description: Shell up to 6.25 mm long, translucent white, thin and brittle, highly arched, anterior end occupying 48.8–62.5% of shell length in specimens over 4 mm in length. Aperture elliptical, anterior end more narrowly rounded than posterior; apertural plane shallowly concave at ends, weakly convex at sides; broadest slightly behind midlength. Apex tightly rounded, anterior slope flat or weakly concave, posterior slope broadly convex, lateral slopes weakly convex. Periostracum transparent, very thin, smooth.

Protoconch 200 μ m long, bilaterally symmetrical, apical fold producing a small, shallow dimple on each side, sculptured throughout with densely crowded minute punctations arranged in spiral lines.

Teleoconch sculptured with fine collabral growth lines, obscure radial lines, and many minute, randomly distributed, shallow pits.

Animal white. Foot broad and thick. Mantle edge thickened, with weak left anterolateral fold. Snout very large, tapered, longer than broad, deeply concentrically wrinkled, mouth a vertical slit in small, circular, flattened tip. No oral lappets. Cephalic tentacles slender, tapered, tips rounded, minute black eyes sunken in swellings at outer bases. A large secondary gill extending along right mantle groove to above right of head, comprising about 30 anteriorly enlarging leaflets. Seminal groove not detected. Two slender blunt-tipped, dorsoventrally flattened epipodial tentacles at posterior end.

Radula (figures 18, 19) with the formula $\infty + 6 + 1 + 6 + \infty$, indistinguishable from that of *O. mirabilis*.

Type data: Holotype MNZ M 116970 (length 5.50 mm, width 4.20 mm, height 3.40 mm) and 57 paratypes (51 MNZ, others AMS, BMNH, LACM, MNHN, NMP, USNM): 43°34.14'S, 176°18.69'E, E of Mernoo Bank, Chatham Rise, New Zealand, 372–379 m, 29 January 1992, f.r.v. *Tangaroa* stn 9106/168, alive on whale vertebra among crowded individuals of a species of *Idas* Jeffreys, 1876 (Mytilidae).

Other material examined: (Several hundred specimens MNZ): Topotypes (several hundred juveniles, MNZ M.117279); 39°53.2'S, 168°01.2'E, Challenger Plateau, New Zealand, 908–912 m, 3 July 1989, f.v. *Amaltal Explorer* stn 348/129, alive on a piece of whale bone among crowded mytilids (*Idas* sp.) (8 subadult specimens, MNZ M.92453).

Distribution (figure 1): Chatham Rise and Challenger Plateau, New Zealand, on whale bone, 372–912 m.

Remarks: *Osteopelta praeceps* differs from *O. mirabilis* in attaining smaller size and in having a narrower, taller shell with a longer anterior end. Their external anatomies and radulae are extremely similar. *O. praeceps* and *O. mirabilis* occurred living together on the same piece of whale bone from the Challenger Plateau (M 92453 and M.92451, respectively).

Immature specimens of *O. praeceps* are strikingly similar to young of the cocculinid *Paracocculina cervae* that also occurred on the Challenger Plateau bone. *P. cervae*, however, is distinguishable by its larger adult size, lack of shell micropunctations, in having a prominent copulatory organ behind the right cephalic lappet, and in having a snout that is short and broad instead of proboscis-like. Moreover, their radulae and anatomies are entirely different.

The highly arched shell and narrow aperture of *O. praeceps* enable it to live deeply (and inconspicuously) among the associated mytilids, which form densely crowded aggregations at nutrient-rich sites on the bones. By contrast, the larger and broader-shelled species *O. mirabilis* has been observed adjacent to mytilid aggregates (Marshall 1987: fig. 1A), and is probably unable to live as deeply among them.

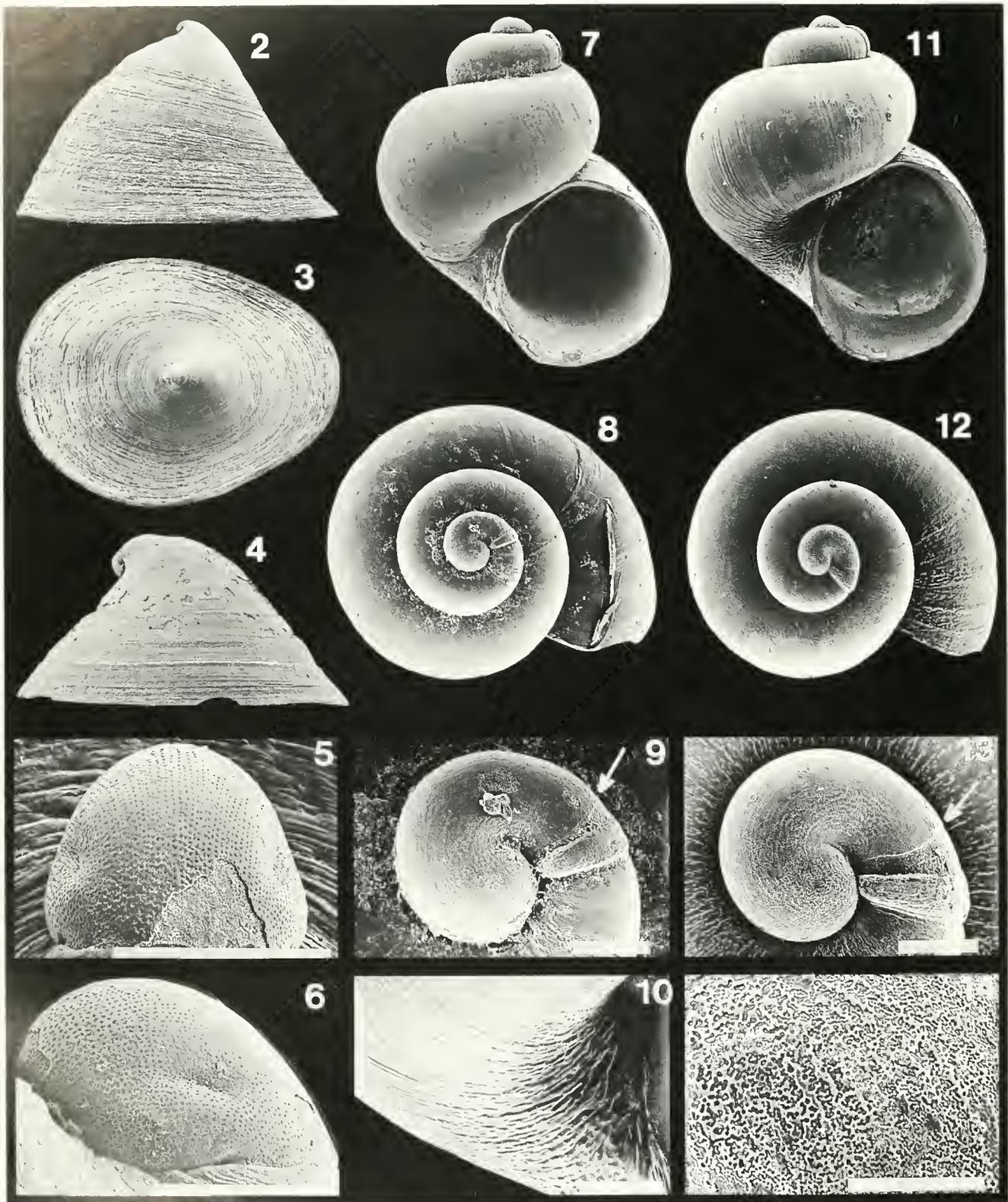
Etymology: Latin *praeceps* (steep).

Suborder VETIGASTROPODA Salvini-Plawen, 1980
Superfamily TROCHOIDEA Rafinesque, 1815
?Family SKENEIDAE Clark, 1851
Genus *Bruceiella* Warén & Bouchet, 1993

Bruceiella Warén & Bouchet, 1993:26. Type species (by original designation): *Bruceiella globulus* Warén & Bouchet, 1993; Recent, North Fiji Basin (hydrothermal vent).

Remarks: In having epipodial tentacles and papillate cephalic tentacles, the animal of *Bruceiella* bears a general resemblance to those of members of the family Skeneidae, the limits of which have been tightly restricted by Warén (1992) and Warén and Bouchet (1993). The lack of a propodial penis and the distally expanded snout, however, led Warén and Bouchet (1993) to suggest that the genus probably does not belong in Skeneidae, but by implication perhaps in a family of its own. The radula bears a striking resemblance to those of a variety of archaeogastropods associated with hydrothermal vents and seeps, especially neomphalids and peltospirids, a similarity that Warén and Bouchet (1993) consider to be the result of convergence.

The otherwise simple shell of *Bruceiella* species is distinctive in having a protoconch sculpture of minute dendritic threads and granules arranged in fine spiral lines, and a pronounced varix almost immediately after the protoconch-teleoconch boundary. Unlike Warén and Bouchet (1993), who interpret the varix as the termination of the protoconch, I consider that the varix is on the teleoconch, and that the actual protoconch-teleo-



Figures 2–14. Shells of *Ostcopelta* and *Brucciella* spp. 2–6. *Ostcopelta praeceps* n. sp. 2, 3. Holotype, length 5.50 mm. 4. Immature specimen, Challenger Plateau, MNZ M.92453, length 2.20 mm. 5, 6. Protoconch of holotype. 7–9. *Brucciella laevigata* n. sp., holotype, height 1.70 mm. 9. Protoconch, with protoconch/teleoconch boundary arrowed. 10–14. *Brucciella pruinosa* n. sp., holotype, height 1.43 mm. 10. Detail of inner part of base. 13. Protoconch, with protoconch/teleoconch boundary arrowed. 11. Detail of protoconch sculpture. Scale bar 14 = 10 μ m, others = 100 μ m.



Figures 15–17. Shell of holotype of *Xylodiscula osteophila* n. sp., width 1.60 mm. 17. Protoconch, note inrolled tip. Scale bar = 100 μ m.

conch boundary is a sharply defined line at a distance behind the varix equivalent to about one varix thickness (figures 9, 13). I also disagree with Warén and Bouchet (1993) that the varix in their genus *Ventsia* is part of the protoconch and instead consider that it is situated at the end of the first quarter teleoconch whorl. Species of the related genus *Xyloskenca* Marshall, 1988 exhibit a change in teleoconch sculpture following a sharply defined growth scar at an equivalent position (Marshall, 1988, figs: 4EJ, 5E; Warén & Bouchet, 1993: fig. 23A). The zone between the varix and the protoconch/teleoconch boundary is analogous to protoconch II of higher gastropods, though not homologous because protoconch enlargement through marginal incrementation is unknown in archaeogastropods other than Neritimorpha. These growth disturbances probably represent a period of crisis, perhaps a change in feeding mode during the earliest stages of postsettlement development.

***Bruceiella laevigata* n. sp.**
(figures 7–9, 20–22)

Description: Shell up to 1.70 mm high, slightly higher than broad, thin, translucent, glossy, with narrow umbilical chink, periostracum smooth.

Protoconch 300 μ m wide, delineated by fine groove, apical fold tip broadly rounded, sculptured with minute anastomosing dendritic threads arranged in fine spiral lines.

Teleoconch of up to 2.20 strongly and rather evenly convex whorls. First sixteenth whorl minutely granulate; next sixteenth whorl occupied by strong, rounded varix, immediately followed by fine groove; elsewhere smooth. Aperture subcircular, lips thin, parietal contact area narrow.

Animal. Snout subquadrate; cephalic tentacles dorsoventrally flattened, tapered, similar, edges ciliated; foot large, anteriorly indented. Small right and large left sub-optic tentacle, 3 small right epipodial tentacles beside operculum, 1 large left epipodial tentacle, 2 small left epipodial tentacles beside operculum. No eyes.

Radula (figures 20–22) with the formula $\infty + 5 + 1$

$+ 5 + \infty$, teeth longer than broad. Central tooth stout; cutting area narrowly angulate, without secondary cusps, prominently hooded; shaft face subtriangular, suddenly narrowed at base. Lateral teeth stout, enlarging outwards, cutting areas large, hooded, roundly angulate, coarsely serrate, terminal cusp largest; shafts outwardly bowed, strongly flanged and convoluted to interlock with adjacent teeth. Marginal teeth slender, outwardly narrowing and with smaller cutting areas and finer cusps, outermost few pairs with spatulate tips and fused shafts.

Type data: Holotype (height 1.70 mm, diameter 1.50 mm, 2.20 teleoconch whorls) MNZ M.116969; paratypes (5 MNZ, 1 AMS, 1 MNHN): 43°00.17'S, 174°05.5'W, NE of Chatham Islands, New Zealand, 1,242 m, 23 August 1989, f.v. *Otago Buccaneer* tow 31; alive amongst crowded mytilids (*Idas* sp.) on a whale skull.

Distribution (figure 1): Northeast of Chatham Islands, New Zealand, on whale bone, 1,242 m.

Remarks: Compared with the type species, *Bruceiella laevigata* is more tightly coiled with a higher spire, but otherwise the two species are similar. Among the host of superficially similar skeneimorph gastropods known from the New Zealand region (MNZ—many undescribed), *B. laevigata* is characterised by the combination of distinctive protoconch sculpture, the strong postlarval varix, and the radular morphology.

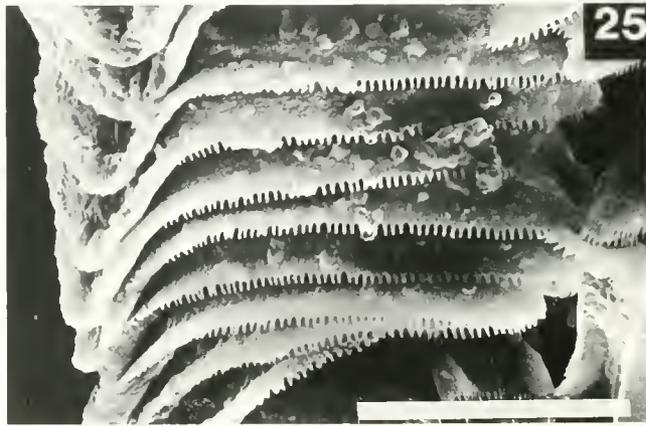
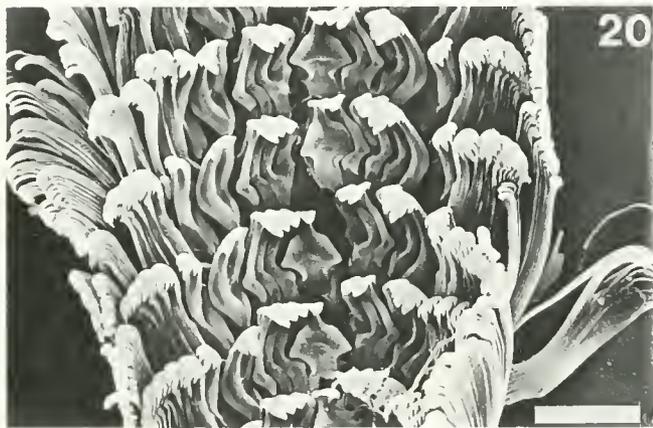
Etymology: Latin *laevigatus* (smooth), alluding to the lack of shell sculpture after the postlarval varix.

***Bruceiella pruinosa* n. sp.**
(figures 10–14, 23)

Description: Shell (holotype) 1.43 mm high, slightly higher than broad, thin, translucent, glossy, with narrow umbilical chink, periostracum smooth.

Protoconch 280 μ m wide, delineated by fine groove, apical fold tip broadly rounded, sculptured with minute anastomosing dendritic threads arranged in fine-spiral lines.

Teleoconch of 2.10 strongly and rather evenly convex



whorls. First sixteenth whorl minutely granulate; next sixteenth whorl occupied by strong, rounded varix, immediately followed by fine groove. Adapical quarter of spire whorls, and inner half of base with minute granules and very fine axial wrinkles, stronger on base. Aperture subcircular, lips thin, parietal contact area narrow.

Animal. Similar to that of *B. laevigata* but with 1 large right and 2 large left epipodial tentacles, instead of 4 right and 3 left epipodial tentacles.

Radula (figure 23) as in *B. laevigata*.

Type data: Holotype MNZ M.116968 (height 1.43 mm, diameter 1.33 mm, 2.10 teleoconch whorls): 39°53.2'S, 168°01.2'E, Challenger Plateau, New Zealand, 908–912 m, 3 July 1989, f.v. *Amaltal Explorer* stn 348/129; alive amongst crowded mytilids (*Idas* sp.) on a piece of whale bone.

Distribution (figure 1): Challenger Plateau, New Zealand, on whale bone, 908–912 m.

Remarks: *Brucciella pruinosa* differs from both *B. globulus* and *B. laevigata* in having a teleoconch sculpture of minute granules and fine axial wrinkles.

Etymology: Latin *pruinosa* (frosty), alluding to the finely granulate surface.

Subclass HETEROBRANCHIA Gray, 1840

Order HETEROSTROPHA Fischer, 1855

Family XYLODISCULIDAE Warén, 1992

Genus *Xylodiscula* Marshall, 1988

Xylodiscula Marshall, 1988:955. Type species (by original designation): *Xylodiscula vitrea* Marshall, 1988, Recent, New South Wales.

Remarks: *Xylodiscula* was originally referred to Orbitestellidae for want of a more appropriate position (Marshall, 1988). Subsequent reevaluation of Orbitestellidae by Ponder (1990), however, suggested that this placement is untenable, and Warén (1992) has segregated *Xylodiscula* in a family of its own.

The new species described below is the first record of a xylodisculid from whale bone. Other *Xylodiscula* species live at 90–1,100 m in association with sunken wood (Marshall, 1988; Warén, 1992) and old sea grass (*Posidonia*) fibres (Warén, 1992). Most recently a *Xylodiscula* species has been recorded from a hydrothermal vent at 2,000 m depth in the North Fiji Basin (Warén & Bouchet, 1993).

***Xylodiscula osteophila* n. sp.**
(figures 15–17, 24, 25)

Description: Shell (holotype) 1.60 mm wide, markedly wider than high, spire weakly elevated, thin, translucent, colorless, umbilicate, periostracum smooth.

Protoconch 270 µm wide, 1.75 whorls; tip infolded, very small, finely granulate; last whorl smooth.

Teleoconch of 2.25 convex whorls, suture shallowly channelled. First 1.25 whorls evenly convex; last whorl with weakly convex side, and strongly rounded periphery. Base convex, evenly rounded into umbilicus, obscure spiral lines throughout. Collabral growth lines gently prosocline on spire, weakly sigmoidal on base. Umbilical diameter 17% of shell diameter. Aperture subcircular. Outer lip thin; inner lip thickened and angled against umbilical rim, thin adapically. Parietal area broad, inductura extremely thin.

Animal unknown (dried). Operculum thin, translucent, chitinous multispiral.

Radula (figures 24, 25) with the formula 2 + 1 + 0 + 1 + 2, extremely small. Lateral teeth small, thin, subquadrate, cutting area almost straight and finely serrate. Marginal teeth similar, large, stout, slender, curved, very long finely serrate cutting area on both edges.

Type data: Holotype (height 1.07 mm, width 1.60 mm, 2.25 teleoconch whorls) MNZ M.116971 off Mernoo Bank, Chatham Rise, New Zealand, ca. 900 m, October 1988, f.v. *Amaltal Explorer*; alive on large whale skull amongst crowded mytilids (*Idas* sp.).

Distribution (figure 1): Off Mernoo Bank, Chatham Rise, New Zealand, on whale bone, ca. 900 m.

Remarks: *Xylodiscula osteophila* differs from other named *Xylodiscula* species in the greater shell height relative to width, the thickened and angled inner lip, and the considerably narrower umbilicus.

Etymology: From the Greek *osteon* (bone) and *philos* (loving).

ACKNOWLEDGEMENTS

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Figures 18–25. Radulae ex holotypes. 18, 19. *Ostcopelta praeceps* n. sp., full width (18) and detail of central and lateral teeth (19). 20–22. *Brucciella laevigata* n. sp., full width (20), central and lateral teeth (21) and marginal teeth (22). 23. *Brucciella pruinosa* n. sp., central (left), lateral and inner marginal teeth. 24, 25. *Xylodiscula osteophila* n. sp., marginal teeth and the small central tooth (left center in 24). Scale bars = 10 µm.

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On the Living Habits of *Acesta bullisi* (Vokes) in Chemosynthetic Bottom Communities, Gulf of Mexico

Barry Kohl

Harold E. Vokes

Geology Department
Tulane University
New Orleans, LA 70118 USA

ABSTRACT

The supposedly pathologic paratype of *Acesta bullisi* (Vokes, 1963) has been re-evaluated based on additional information from the type locality. The specimen is not aberrant, as originally thought, but represents a normal mode of growth in which the shell is attached over the anterior end of chemosynthetic tube worms of the genus *Lamellibrachia* sp., which occur at hydrocarbon seeps in the Gulf of Mexico. It is shown that the paratype is a final stage in the ontogeny of *A. bullisi*, which lives attached to the tube worm *Lamellibrachia*.

Key Words: *Acesta*, Chemosynthetic, *Lamellibrachia*, Gulf of Mexico, tube worms.

INTRODUCTION

Hydrothermal vents and their oases of previously undescribed species were discovered in 1977 on dives of the submersible ALVIN along the Galápagos Rift in the Pacific Ocean. Giant tube worms, large clams, and mussels form an assemblage of invertebrates dependent on hydrogen sulfide-rich waters. These animals contain bacterial symbionts that oxidize the sulfide.

An assemblage of tube worms, clams, and mussels was reported in the Gulf of Mexico near a saline seep at the base of the Florida Escarpment (depth 3,266 meters) by Paull *et al.*, (1984). This was the first record of vent organisms occurring on a passive margin. The following year, Kennicutt *et al.* (1985) described a fauna associated with oil and gas seeps from trawls along the Louisiana continental slope. One trawl contained specimens of *Acesta bullisi* and an entanglement of vestimentiferan tube worms of the genus *Lamellibrachia*, taken near Green Canyon Block 234, (27°45'N, 91°14'W) (Figure 1).

Since the discoveries by Paull *et al.* and Kennicutt *et al.*, there have been many projects designed to document, by manned-submersibles, the occurrences of chemosynthetic communities in the Gulf of Mexico associated with oil and gas seeps. Shore-based research is investigating how these organisms derive their energy from oil, methane, and sulfides, which are toxic to most invertebrates.

In addition to unique chemosynthetic species, there are opportunistic non-chemosynthetic organisms that use either the carbonate substrate surrounding the vents or the chemosynthetic forms for attachment. *Acesta bullisi* is one of these opportunistic organisms found attached to the tube worm *Lamellibrachia* sp. at many sites in the Gulf of Mexico (Carney, 1992; MacDonald & Ambler 1992).

The supposedly "pathologic" hypotype [paratype] of the species described as *Lima (Acesta) bullisi* by Vokes (1963, pl. 2, figs. 1-4), was given to H. E. Vokes in 1962 by H. R. Bullis, Jr. It was alive when retrieved in a trawl from the R/V OREGON Station 3741, at a depth of 548 meters in the Gulf of Mexico (29°10'N, 88°01.5'W).

This location can be equated to a sampling station in Viosca Knoll Block 826 (VK 826, Figure 1), 29°11.0'N, 88°00'W, at a depth of 545 meters (U. S. Dept. of Interior, 1992, vol. 1, table 1) used by the Geochemical and Environmental Research Group (GERG) of Texas A & M University. According to MacDonald and Ambler (1992), this location is the most easterly site within the Gulf of Mexico of chemosynthetic communities associated with hydrocarbon seep activity found to date. The chemosynthetic fauna at the VK 826 site is represented by living tube worms (*Lamellibrachia* sp. and *Escarpia* sp.) and possibly lucinid clams (MacDonald & Ambler, 1992).

The purpose of this paper is to document that the paratype of *Acesta bullisi* described by Vokes in 1963 was a form attached to tube worms from a chemosynthetic community. We hope that this paper will also stimulate an investigation of other "deformed" mollusk species in collections and thereby identify locations of other chemosynthetic communities.

MATERIALS AND METHODS

Specimens of *Acesta bullisi* were collected by personnel from Tulane University and Louisiana State University (LSU) on cruises in the Gulf of Mexico during September 1992 and July 1993. The JOHNSON SEA-LINK (JSL) I & II, manned-submersibles, were used for bottom sampling on a total of 24 dives. Photographs and video were taken

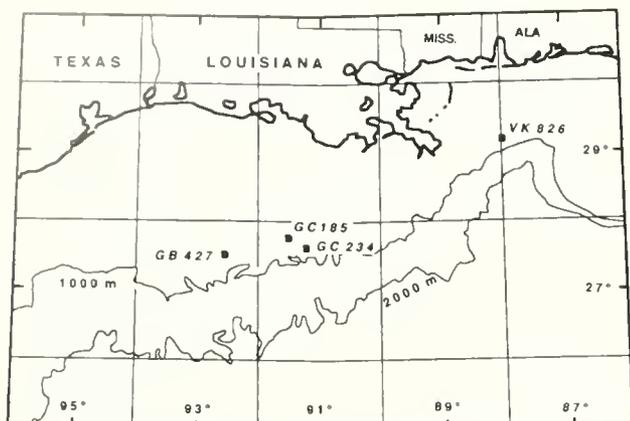


Figure 1. Location map showing Garden Banks Block 427, Green Canyon Blocks 185, 234 and Viosca Knoll Block 826.

of clumps of *Lamellibrachia* and the attached individuals of *Acesta*. Specimens of *Acesta bullisi* used for the present study were collected for research at LSU and were photographed on shipboard by B. Kohl to document the living position of *Acesta* in relationship to the tube worm *Lamellibrachia*. A collection of invertebrates retrieved on the dives is maintained at LSU.

The sites used for this paper are Green Canyon Block 185, 27°46.93'N, 91°30.47'W, dive 3301 (1992), depth 541 meters, and Garden Banks Block 427, 27°33.61'N, 92°25.09'W, dives 3305 (1992) and 3568 (1993), depth 611 meters, (figure 1). Ten specimens of *A. bullisi* attached to *Lamellibrachia* were retrieved by the JSL's mechanical arm by selectively collecting individual tube worms.

RESULTS

BIOLOGY OF TUBE WORMS

Lamellibrachia spp., classified as vestimentiferans, lack a mouth, anus and digestive system. They live in a tough, thick-walled, chitinous tube about one centimeter in diameter and up to two meters in length. The posterior end may either be buried in soft sediments or attached to a rocky substratum. A small red-orange plume, the obturaculum, (approx. one cm in diameter) is extended from the anterior opening and serves as a gas exchange organ. The plume can be withdrawn into the tube at will

(Fisher, 1992; MacDonald *et al.*, 1990). Most of the body volume consists of a trophosome, the organ containing the bacterial symbionts. The animal absorbs H₂S, CO₂ and O₂ through its obturaculum (plume) and, through a complex chemical process, the symbiotic bacteria and enzymes convert CO₂ to organic carbon. See Fisher (1990) for a detailed review of the chemistry involved.

New research has suggested that the O₂ is absorbed through the plume and H₂S is absorbed through the posterior part of the tube, which is located below the sediment/water interface. It has been observed that the living animal extends the entire length of the tube. Absorption of CO₂ possibly takes place along the length of the tube above the sediment/water interface through the porous chitinous wall (R. S. Carney, personal communication).

RELATIONSHIP OF *A. BULLISI* TO *LAMELLIBRACHIA* SP.

Specimens of *A. bullisi* attach to tall individuals of *Lamellibrachia* approximately one-half meter above the sea bottom, near the anterior end of the tube. Specimens collected on the 1992 and 1993 dives show that *A. bullisi* frequently occurs attached to the "bushlike" congregations of the tube worm *Lamellibrachia* sp. This was also reported and illustrated by MacDonald *et al.* (1989) from the Green Canyon Block 184-185 area.

Two attachment positions of *A. bullisi* were observed on our dives. The first is an attachment by a byssus to the side of the tube worm near the upper portion of the tube (figure 3). These individuals do not have the notch or opening and are about half the size of the adult shown in figures 2 and 4.

The second attachment position can be seen in the specimens in figure 2, which completely envelop the anterior region of *Lamellibrachia*. A detail of one of the specimens from figure 2 is shown in figure 4. These specimens are attached by a byssus to the exterior of the tube worm very near the anterior end.

The shape of the growth lines in the valves of the adult *A. bullisi* (figure 9) implies that the opening in the shell developed late in ontogeny.

DISCUSSION

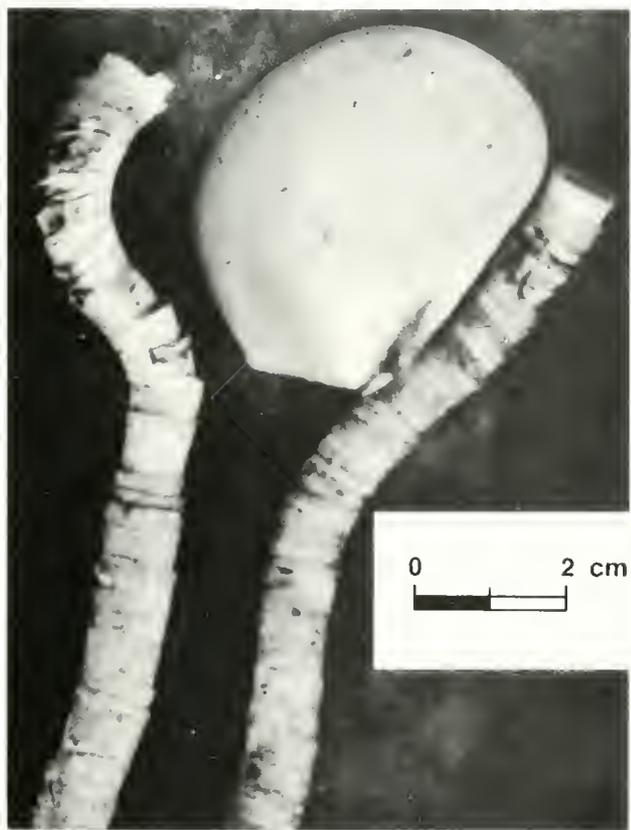
The specimen described by H. E. Vokes was thought to have been damaged at a time when the animal was half grown (Vokes, 1963: 78). Observations of the living an-

Figures 2-4. Living specimens of *Acesta bullisi*. **2.** Live specimens of *A. bullisi* attached to the anterior ends of two *Lamellibrachia* sp., Garden Banks Block 427, dive 3305, depth 611 meters. **3.** A live specimen of *A. bullisi* from Green Canyon Block 185, dive 3301, depth 541 meters. This specimen is attached by a byssus 32 mm below the anterior end of the tube worm and lacks the notch in the anterodorsal margin as seen in figures 4 and 9. It is about 50 mm in height which is half the size of the specimen on left in figure 2. **4.** Detail of the live specimen on the right in figure 2. The specimen is approximately 110 mm in height and surrounds the anterior portion of *Lamellibrachia* sp. Note the position of the tube worm at center of photograph with the plume of the tube worm protruding from the anterior end (arrow) and its relationship to the notch. When the plume is extended, during life position, it is totally contained within the mantle cavity of *A. bullisi*. The byssus holds the *A. bullisi* in a position to envelope the tube worm. Specimen from Garden Banks Block 427, dive 3305, depth 611 meters. Scale in upper left is in centimeters.

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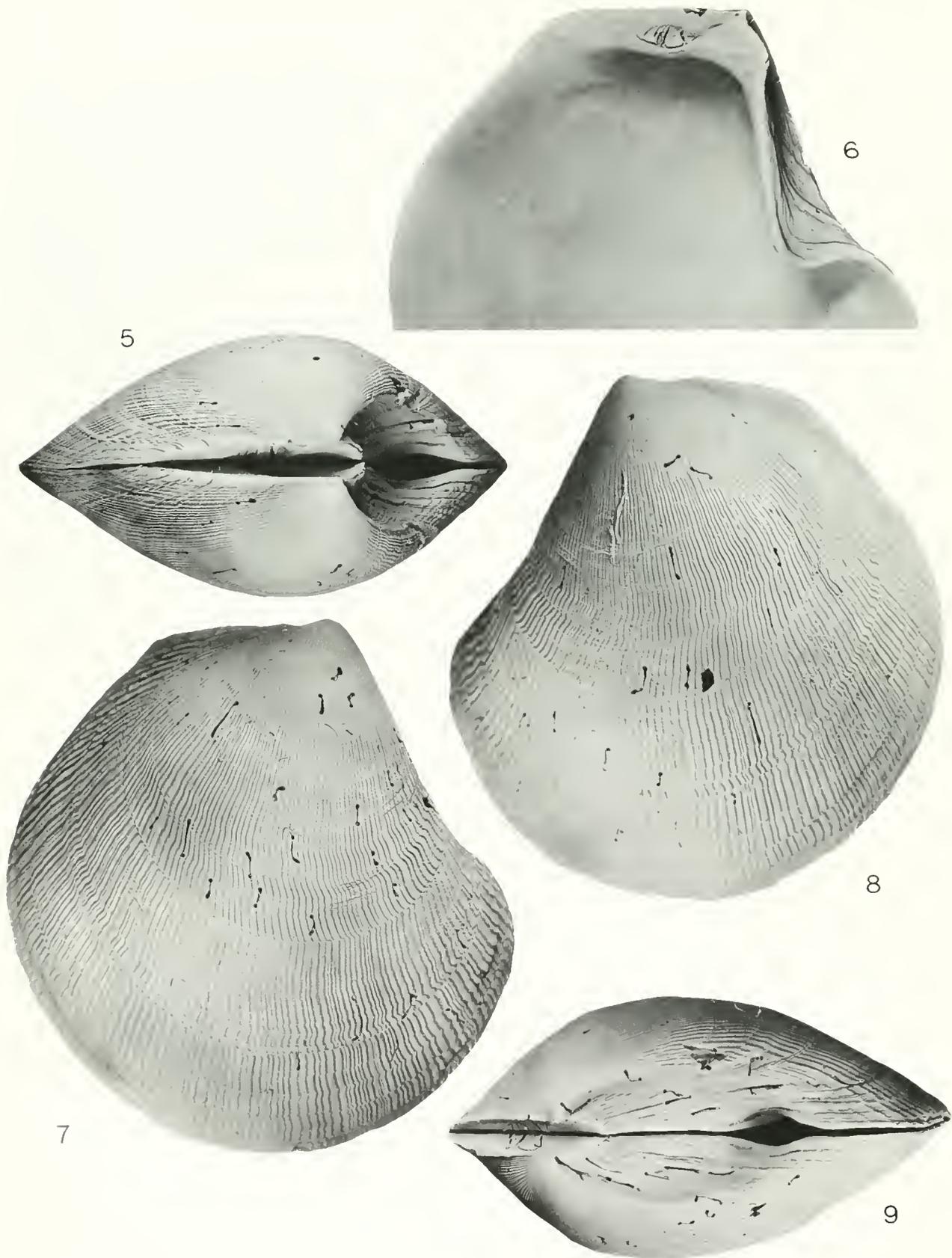


3



4





Figures 5-9. Specimen of *A. bullisi* collected alive from the anterior of a tube worm, Green Canyon Block 185, dive 3301, 541 meters. Magnification (\times 1). This specimen is comparable in size to the one figured by Vokes (1963, pl 2, figs. 1-4). Note the

imals retrieved and photographed (figures 2–4) during recent dives of the JSL (Sept. 1992 and July 1993) have shown that the specimen figured by Vokes was actually an ecophenotypic variant that grows attached to the tube worm *Lamellibrachia* sp. The inbending of the anterodorsal margin of *A. bullisi* and the development of an open gape is the result of its attachment to the anterior end of *Lamellibrachia* sp. This has been reported from specimens collected at Viosca Knoll Block 826 (MacDonald & Ambler, 1992: 46).

Vokes (1963: 78) suggested that "the specimen, which was alive when taken, had suffered serious damage to the shell and mantle in the region of the lunule at a time when the animal was approximately half grown." Without the knowledge that the specimen was originally attached to a tube worm, this was a logical interpretation. We now know that inbending of the anterodorsal margin and open gape is a normal development for specimens growing on the anterior end of *Lamellibrachia* (MacDonald *et al.*, 1989). Carney (1992) reports that specimens of *A. bullisi* with thin shells are either attached to carbonate rocks or swimming freely near the vent communities whereas the forms attached to *Lamellibrachia* have a distinctly thicker shell.

We suggest that smaller specimens of *A. bullisi* may move from an attached position on the side of the tube worm after achieving approximately one-half adult size, and then to an anterior location during the later stages of life where the gape is developed as it closes over the tube worm. Members of the genus *Acesta* can resorb their byssus filaments. Once unattached they can swim to another position, near the anterior end of the tube worm, and re-attach. Since *Lamellibrachia* has neither mouth, gut nor anus and is completely dependent on sulfur-reducing bacteria for its food, it is difficult to understand the ecological relationship between *A. bullisi* and the tube worm. Could there be a symbiotic or commensal association between the two organisms?

Acesta bullisi does not have symbiotic bacteria in its mantle and appears to be a normal filter feeder. Additional research on the biology of *A. bullisi*, being conducted by C. R. Fisher at Pennsylvania State Univ. (R. S. Carney, personal communication), may answer some of these questions.

The description of the "pathologic" specimen of *A. bullisi* by Vokes (1963), collected at Viosca Knoll Block 826, was the first record of a mollusk from an oil seep-chemosynthetic community in the Gulf of Mexico. Careful study of the faunal collections dredged at VK 826 in 1962 by the R/V OREGON would probably reveal the existence of tube worms. Subsequent dives by GERG in 1991 have documented the occurrence of *Lamellibrachia* at VK 826 (MacDonald & Ambler, 1992). Based on our present knowledge of the occurrence of *A. bullisi* in

chemosynthetic communities, there is no doubt that the paratype of *A. bullisi* described by Vokes from VK 826 was a form attached to the anterior end of a specimen of *Lamellibrachia*.

ACKNOWLEDGMENTS

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We also thank Robert S. Carney for the loan of a specimen of *Acesta bullisi* from the LSU collection for photography. Emily H. Vokes, of Tulane University, prepared the plates and reviewed and edited versions of the manuscript. Marco Taviani, Instituto di Geologia Marina, Bologna, Italy, who was on the 1992 cruise, assisted with the shipboard photography. The authors thank two anonymous reviewers for their suggestions to improve the paper.

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position of the notch, (Figs. 5,6,9) which allows *A. bullisi* to close over the tube worm. This is also evident in Vokes (1963, pl. 2, figs. 2–3). Specimen on loan from LSU.

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Shell Alignment for the Morphometric Analysis of High-spired Gastropods.

Paul J. Morris¹

Smithsonian Tropical Research
Institute
Apartado 2072
Balboa, Republica de Panamá

Warren D. Allmon

Paleontological Research Institution
1259 Trumansburg Rd
Ithaca, NY 14850 USA

ABSTRACT

A significant problem often impedes the morphometric analysis of high-spired gastropods. It is usually not possible to obtain large samples of complete specimens. Without the ontogenetic landmarks provided by early whorls it is difficult to align incomplete specimens to compare homologous whorls. We discuss several methods that allow alignment of morphometric data taken from incomplete specimens of high-spired gastropods. We evaluated these methods by treating a set of complete specimens as incomplete. Two methods produce reliable alignments. One of these uses an ontogenetic function of the whorl expansion rate to estimate missing whorls, the other aligns whorls of similar heights. Both produce reasonably precise and accurate alignments, but under different assumptions. Once a set of specimens has been aligned, it can be subjected to conventional statistical analysis using accepted conventions to deal with missing data.

Key words: Morphometrics, Gastropoda, Missing Data, Turritellidae.

INTRODUCTION

Morphometric analyses of very high-spired gastropods (such as members of the families Cerithiidae, Loxonematidae, Murchinsoniidae, Nerineidae, Turritellidae, and Terebridae) are difficult because complete specimens are usually unavailable or rare. This is especially true for fossil taxa. When the juvenile whorls have been broken off of most specimens it is difficult or impossible to specify homologous points (*i.e.*, similar whorl number) among specimens. Therefore, construction of data matrices for morphometric or statistical analyses of a large number of specimens of such incomplete gastropods is usually problematic. This difficulty may account for the paucity of morphometric studies of high spired gastropods in the literature (*e.g.*, Allmon, 1994).

A variety of methods can be used to align the whorls of incomplete specimens with each other. We have implemented three algorithms for use on sets of traditional point-to-point measurements. We assessed the accuracy of these algorithms by their ability to predict true whorl number in a data set of complete specimens that we treated as incomplete. In this data set, we truncated complete specimens at known whorl numbers. Two algorithms produced good alignments of shells of turritellids in this test data set. Both of these align most specimens to within one whorl of their true position. An algorithm that uses iterative comparisons of whorl heights produces slightly more precise alignments. An algorithm that uses an ontogenetic function of the whorl expansion rate to infer numbers of missing whorls is slightly more accurate. There are several tradeoffs between these two algorithms.

SHELL ALIGNMENT

In most gastropods it is possible to identify a homologous point for aligning whorls. Either the end of the protoconch or a varix produced in the adult shell can be used as landmarks from which whorls can be counted. It is therefore easy to align whorls that are of the same distance from this landmark in different specimens. Such aligned specimens are easily compared using traditional point-to-point measures, Raupian parameters, or moving frame parameters. In most high-spired shells, however, whorls differ only in size and shape, and lack discrete landmarks. When specimens have been broken and are incomplete, there are no clear means for inferring how many whorls are missing. Incomplete specimens, which are particularly common as fossils, are therefore difficult to align, homologize, and analyze morphometrically. This problem is depicted in Figure 1.

There are three basic ways of aligning incomplete high spired shells. These are: alignment by homology of ornament, inference of missing whorls from whorl expansion rate (W of Raup, 1966), or alignment by comparisons of whorl heights among specimens. (One can also

¹ Current Address: Paleontological Research Institution, 1259 Trumansburg Rd., Ithaca, NY 14850 USA

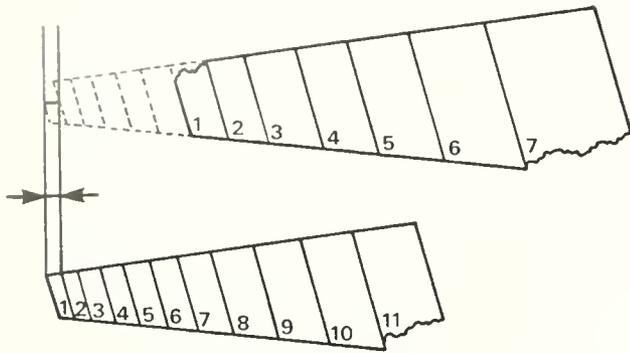


Figure 1. The problem of whorl alignment in two incomplete specimens of high spired gastropods. In the absence of the protoconch, juvenile whorls, or other homologous points, it is necessary to find some means of aligning whorls in order to conduct morphometric analyses. The two principal ways of making alignments are by matching whorls of similar size, or by inferring the number of whorls missing from the small end of each specimen.

use other measures that increase through ontogeny, such as whorl width, but for the remainder of this paper we refer exclusively to whorl height). We have considered five variations of these methods, alignment by: 1) comparison of homologous features of ornament, 2) interpolation of missing whorls using the whorl expansion rate from earliest preserved whorls of each specimen, 3) interpolation of missing whorls using some function of W calculated from a composite average specimen, 4) comparison of whorl heights between each pair of specimens, and 5) iterative correction and comparison of whorl heights with a composite average specimen. A method that uses iterative comparisons of whorl heights appears to be the most generally useful. None of these, however, are entirely perfect ways to infer how many whorls are missing in an incomplete specimen. There is no ideal way to align individual specimens that lack early whorls and homologous end points. Each of these approaches has limitations and makes compromises.

A first approach is alignment using homologous features of spiral ornamentation, such as the points of bifurcation or origination of keels. This approach (because it involves homologous points) would seem most reliable. It is limited, however, by an inability to extend homologies of ornamentation beyond small groups of related species, and by the need for many homologous points spread throughout ontogeny. As a result, it is useful only in a few specific cases. It does not lend itself to implementation as a general algorithm that could apply, for example, to both turritellids and loxonematids. It also must avoid the risk of making arbitrary assignment of homologous points in continuously growing ornament.

A second approach is alignment using whorl expansion rates to infer the number of missing whorls between the protoconch and the first preserved whorl in each specimen. This could be done by first calculating the whorl expansion rate from the first preserved whorls of each specimen. This parameter can then be used to calculate

how many whorls are missing between the first preserved whorl and some smaller first whorl (e.g., the protoconch, or the smallest preserved whorl in the data set). That is, iteratively reducing the height of the smallest preserved whorl of a specimen by its whorl expansion rate. The number of steps required to reduce this height value to below the protoconch size provides an estimate for the number of missing whorls. The advantage of this method is that the estimated number of missing whorls in each specimen is independent of the other specimens in the sample. However, both measurement errors in the smallest whorls and ontogenetic changes in the whorl expansion rate affect these alignments.

These errors can be reduced by using some ontogenetic function of the whorl expansion rate rather than an unchanging W value. This must perforce be calculated from other specimens in the sample. It is not possible to infer from a single specimen how W might have varied in its missing whorls. Ideally, this ontogenetic function of W would be continuously variable, reflecting the real nature of ontogenetic changes in whorl expansion rate. In many of our samples, however, few specimens preserve the smallest whorls in the data set. It is therefore necessary to increase the sample size, and decrease the resolution of ontogenetic changes in W . We feel that three whorl expansion rates, produced by a division of the data set (the composite specimen) into three parts (smallest $\frac{1}{4}$, second $\frac{1}{4}$, largest $\frac{1}{2}$), provide the best compromise between resolution of W and sample size. Thus, a whorl expansion rate is calculated for each pair of whorls in each specimen, and an average W is calculated from the whorls in each part of the specimen. These three W values are then used to infer how many whorls are missing from each specimen.

For example, consider a specimen in which the smallest preserved whorl falls within in the second $\frac{1}{4}$ of the range of whorl sizes in a sample. The number of missing whorls in this specimen are calculated by iteratively reducing the height of its first preserved whorl. While this height value remains within the second $\frac{1}{4}$, the average W value from the second $\frac{1}{4}$ is used to calculate the height of the next smaller whorl. When this value falls into the range of heights of the smallest $\frac{1}{4}$, the average W value from the smallest $\frac{1}{4}$ is likewise used to fill in smaller whorls. In each specimen, the number of steps required to reduce the height of the smallest preserved whorl to less than the height of the smallest whorl in the data set (or a protoconch height) are an estimate of the number of missing whorls.

A third possible approach is the alignment of whorls of similar height. This is the most intuitive approach, and the one we find ourselves naturally taking when physically lining up specimens next to each other. There are two obvious ways to carry out these alignments; each starts by sorting the specimens in order of increasing size of first whorl. Specimens may then be aligned by pairwise comparisons or by constructing a composite average specimen and iteratively locating and moving poorly aligned specimens. Alignment by height, however, offers

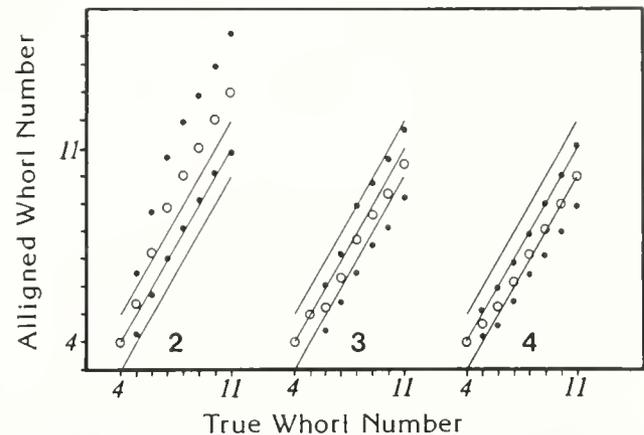
several computational problems. Pairwise comparisons fail unless each pair of specimens overlaps by several whorls. It is therefore necessary to compare all the specimens in the sample to some standard specimen that covers the full range of whorls. If a single specimen is more complete than any other in the sample (having the smallest small whorl and the largest large whorl) all other specimens can be aligned with it. Such specimens are rare. A proxy for such a specimen is easily constructed by averaging across all the specimens in the data set to generate a composite average specimen. This can be used as the reference to which other specimens are aligned. It is a variation of this approach that we have found to be the most generally reliable.

The specific method that we found to be the most precise is the alignment of specimens in the data set through: 1) sorting the specimens in order of increasing size of first preserved whorl, 2) stepping through the data set making pairwise comparisons of first whorl size and moving each larger specimen until its first whorl was aligned with some whorl on each smaller specimen (alignment by smallest whorl size), 3) calculating the average size of each whorl in the data set and the deviation of each specimen from the average composite specimen, 4) moving poorly aligned specimens, and 5) iterating steps 3 and 4 to minimize the total error (total deviation of all specimens from the composite average specimen). The accuracy of these alignments can be improved by removing small whorls represented by only a single specimen.

We have assessed the accuracy and precision of alignment in three of the five methods discussed above. These are: inference of missing whorls using W from the earliest preserved whorls (Juvenile W), inference of missing whorls using a crude function of ontogenetic changes in the whorl expansion rate (Three W Values), and iterative alignment of whorl heights (Height).

SOURCES OF ERROR

There are five principal sources of errors in alignment. These are: 1) ontogenetic changes in coiling parameters or shape, 2) intra-population variability, 3) measurement error, 4) rotation error, and 5) the relationships among size, age, and homology. The effects of some of these sources of error can be avoided or reduced, whereas others are less tractable. Alignment errors introduced by ontogenetic changes in the whorl expansion rate, another coiling parameter, or whorl shape can be reduced by considering some ontogenetic function of W , or by making alignments to a composite average specimen. Effects of measurement error can likewise be reduced by making alignments using information from multiple whorls and specimens. Within-population variability can affect alignments in several ways. Such variability can produce a broad spread of alignments, or it can produce non-intuitive systematic misalignments. It is essential that



Figures 2-4. Accuracy and precision of three methods of whorl alignment discussed in this paper. Whorl heights were measured in ten specimens of *Turritella gonostoma* and used to construct a data set of 50 truncated specimens containing true whorl numbers and whorl height. Open circles are aligned whorl number, filled circles are plus and minus one standard deviation. Lines represent correct whorl alignment and error of plus and minus one whorl. **2.** Alignment from Juvenile W . **3.** Alignment using three W values. **4.** Alignment by Height. Alignment from Juvenile W is neither accurate nor precise. The other two methods are substantially better at correctly aligning specimens in this test.

the user examine aligned samples to understand how this variability may have affected the alignments. Rotation error is the result of taking a set of measurements from one plane in a continuously growing spiral shell. In our test data set it is the principle source of reduced precision for the two best alignment methods. Effects of this source of error can be reduced by either using three dimensional coordinates and moving frame parameters (Ackerly, 1989; 1990; Johnston *et al.*, 1991), or by aligning specimens before measurement (rotating each specimen until a particular whorl width (or height) lies in the plane of measurement).

The relationships among size, age, and homology provide a subtle set of philosophical problems. Age, growth rate, size, and shape are complexly interrelated in gastropods. Environmental factors, such as the availability of food, readily influence the growth rates of gastropods. In time averaged samples it is entirely possible that whorls of the same size (and the same true whorl number) in different individuals represent different points in their ontogenies. In most paleontological studies, however, the primary goal is simply to assess how shape and size vary within and between samples. Patterns in the data can then constrain various taxonomic, evolutionary or paleoecologic hypotheses. The two most common questions for which detailed morphometric studies are undertaken are species discrimination, and trends in variability through time (*i.e.*, tempo and mode of evolution). Lines of evidence beyond morphology, such as taphonomy, are needed to assess the role of ecophenotypic factors in increasing variance or creating clusters in the data.

Table 1. Comparison of advantages and pitfalls of three methods of whorl alignment. These methods are: Alignment by Height using iterative comparison with a composite average specimen, Alignment using three W values computed from composite average specimen, and Alignment using W calculated from smallest three whorls of each specimen. Alignment by Height is the most suitable except for cases where 1) many specimens are being aligned and computing time is a concern, or 2) many specimens consist of just two or three whorls. If the data are three dimensional coordinates suitable for moving frame analysis we expect that a modification of the Height algorithm will probably produce the best alignments. Alignments of a test data set (complete specimens treated as incomplete) suggest Alignment by Height as the best overall technique.

Alignment by	Height HISPIRE 3	Three W values HISPIRE 2	Juvenile W HISPIRE 1
Specimens aligned using	Composite	Composite	Self
Advantages.			
Speed		Fast	Fast
Alignment	Precise	Accurate	
Disadvantages.			
Speed	Slow		
Alignment			Inaccurate
Systematic Missalignment.	Some	None	Much
Dependence on sample composition:	Yes	Yes	No
Recommended for:			
Most applications	+++	+	-
Many specimens	++	++	-
Few whorls	-	+++	-
Principle sources of alignment error:			
Measurement error			+++
Ontogenetic del W			+++
Population del W	++	+++	
Few whorls	+++		
Test data set, <i>Turritella gonostoma</i> :			
Average of SDs:	0.93	1.12	1.73
Relative precision of alignment:			
Small whorls	high	high	low
Middle whorls	high	moderate	low
Large whorls	moderate	moderate	low

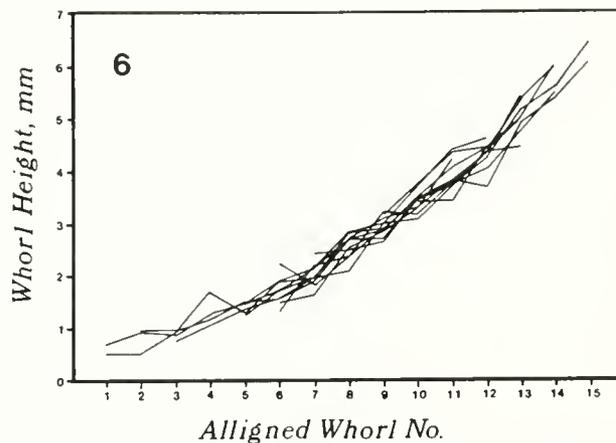
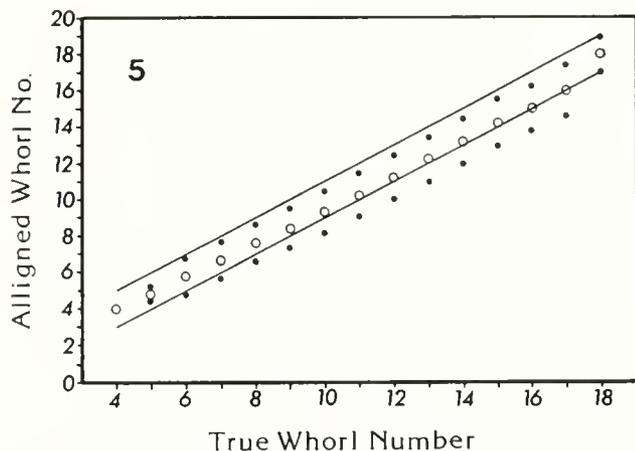
ASSUMPTIONS

A fundamental assumption follows from the previous paragraph: The questions under consideration can be tested with information about size and shape without reference to age (see discussion in James, 1988). Beyond this, each alignment method makes its own set of assumptions about the specimens that are to be aligned. Both the accuracy of alignment and the assumptions behind the methods affect their suitability for particular analytic problems. There are three principal assumptions made by the method of alignment from juvenile W values. It assumes that there is little measurement error in the early whorls. In addition, it assumes that the whorl expansion rate is constant throughout ontogeny. Whorl number is expected to correlate with the height of the first preserved whorl. The method of alignment using three W values allows for ontogenetic variation in the whorl expansion rate. However, it is still sensitive to errors in measurements of the earliest preserved whorl. In addition, this method takes on the assumption that there is little population variability in the whorl expansion rate. Alignment by height assumes that whorls of

similar heights are homologous. It does not directly assume that there is little population variability in the whorl expansion rate, but if this exists, it may produce non-intuitive alignments.

TESTS OF ALIGNMENTS

We have tested the accuracy of these three methods of whorl alignment by evaluating their ability to correctly align whorls in a sample of complete specimens that we treated as incomplete. We used ten complete specimens of *Turritella gonostoma* Valenciennes, 1832, a Recent turritellid that undergoes relatively large ontogenetic changes in whorl expansion rate. We photographed these specimens, enlarged the images, and digitized points at the suture of each whorl using a Numonics digitizing tablet. The heights of successive whorls were calculated from these digitized points. We then truncated the data for each specimen at five different whorls spanning the region of greatest change in whorl profile. This procedure provided us with a data set of 50 incomplete specimens



Figures 5, 6. Assessment of accuracy of whorl alignment by iterative comparisons of whorl height with composite average specimen. **5.** Comparison of true and aligned whorl number. Open circles are aligned whorl number, filled circles are plus and minus one standard deviation. Lines represent error of plus and minus one whorl from correct whorl alignment. **6.** Whorl heights and aligned whorl number. Lines connect the whorls of individual specimens. Note that the accuracy of this method is strongly affected by the alignment of the two smallest specimens in the data set. Elimination of the two smallest aligned whorls will result in substantial improvement in accuracy.

of various numbers of whorls, for which whorl height and true whorl number were known in each whorl. This data set was entered into three conversion programs (HISPIRE, HISPIRE2, HISPIRE3, see Appendix 2) that implement the three whorl alignment algorithms.

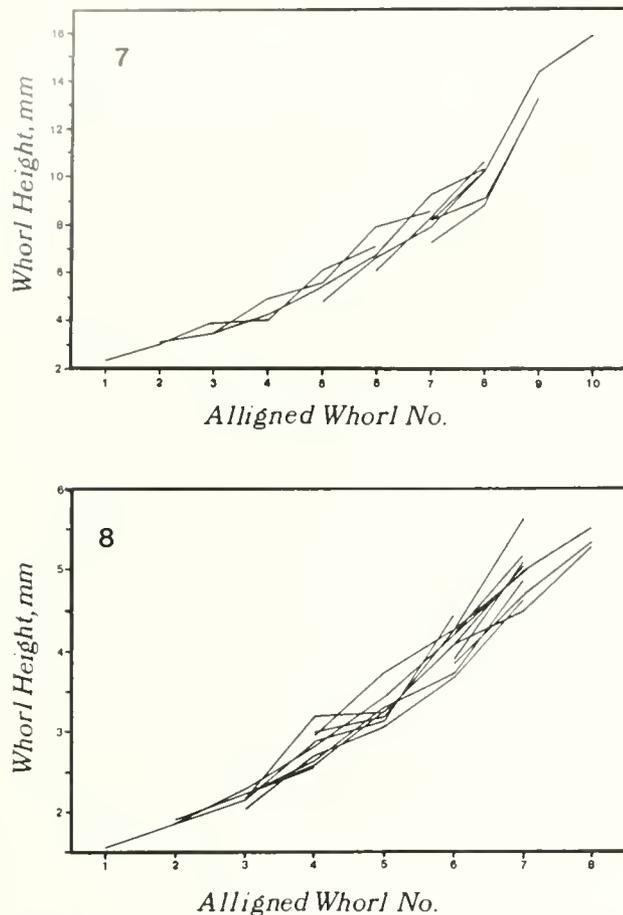
Figures 2-4 illustrate the different alignments of this data set by the three programs. These figures are graphs of true whorl number against aligned whorl number. The mean alignments for these 50 specimens (plus and minus one standard deviation) are compared with a correct alignment (plus and minus one whorl). Clearly alignment by juvenile *W* performs least well in this test. On careful examination of the results, both the ontogenetic changes in whorl expansion rate and measurement error contribute to its failure.

The other two alignment methods produce substantially better results. Here, alignment using three *W* values produces more accurate results than alignment by height. Alignment using three *W* values places the mean alignment for each whorl slightly closer to the true whorl value than alignment by height. However, when the standard deviations in alignment in each whorl (excluding the first and last whorls in each case) are averaged, alignment by height is more precise (Table 1). It appears that alignment by height is slightly more precise (tighter clustering) and that alignment using three *W* values is slightly more accurate (closer to true).

In order to understand the quality of alignments, it is important that we consider the reasons for these differences. The sources of these errors are revealed in an examination of plots of true against aligned whorl number, whorl height against true whorl number (e.g., Figures 4,5), and the original data. Alignment using three *W* values is subject to misalignments produced by measurement errors in the early whorls. Such measurement errors, along with slight rotation errors and variation in

W, tend to produce misalignments in steps of one whorl. Using this method, some specimens are well aligned, others suffer quantum misalignment. In contrast, alignment by height produces misalignments that appear to be the result of rotation error. All specimens are tightly aligned with each other (Figure 6) and their spread is some combination of true variation and alignment error. Careful examination of the graph reveals that the lower accuracy of this method is also the result of rotation error. The two specimens that have the smallest whorls in the data set happen to be aligned to the left relative to the others. The alignment of these two specimens is the cause of the reduced accuracy of alignment of the rest of the specimens. A remedy suggests itself at once. Removal of early whorls represented by only a few specimens should make alignment by height the most accurate and precise of the three methods.

To test this contention further, we qualitatively evaluated these programs. We examined the alignments they produce in fifteen samples of four species of Paleocene and Eocene turritellids from the U.S. Gulf coastal plain (*Turritella mortoni* Conrad, 1830, *T. carinata* Lea, 1833, *T. perdita* Conrad, 1865, and *T. praeincta* Conrad, 1864). Almost all the specimens in these samples are incomplete. It is therefore not possible to compare the precision of alignments to true values. Here we assessed the precision of alignments by graphing aligned whorl number against whorl height. In all the samples we examined, alignment by height consistently produced tight clusters. The results shown in Figures 7,8 are typical. In contrast, alignment using three *W* values often placed one or more specimens outside of a cluster of aligned specimens. This again reveals a weakness in this method of alignment. Small errors (in the measurement of the first preserved whorl, or in fit of the specimen to the three *W* values) can easily be magnified to misalignments of one or more whorls.



Figures 7, 8. Whorl alignments in 7, eight specimens of *Turritella mortoni* from the Paleocene Aquia Fm. at Piscataway Creek Prince Georges Co., MD (Appendix 1) and 8, twelve specimens of *Turritella carinata* from the Eocene Gosport Sand at Clayborne Bluff, Monroe Co., Alabama. Aligned whorl number is plotted against whorl height. Lines connect the whorls of individual specimens. These alignments are typical for the samples of fossil turritellids that we examined.

CHECKING ALIGNMENTS

Given the assumptions of these algorithms and the vagaries of real data, the alignment programs cannot be treated as black boxes that produce infallible results. It is essential that the user evaluate the accuracy of the alignments. The programs themselves provide some warnings, but graphs of aligned whorl number against whorl height (as in Figures 7, 8) should be examined for all samples. The programs that implement alignments using whorl expansion rates provide the user with summary statistics. These include the whorl expansion rate at the small end (average of W in first and second preserved whorls of each specimen) and large end (W in largest preserved whorl of each specimen). The mean whorl expansion rate, standard deviation of W , and the coefficient of variation of W [$CV = (SD / \text{Mean}) \times 100\%$], each calculated from the whole data set, are provided for both the large end and the small end. The programs

caution the user if the coefficient of variation of either of these values exceeds 5%, and provide a warning if these CV's exceed 10%. Such large CV's suggest violation of the assumptions of the method. In addition, the program implementing alignment using three W values assesses the variability in whorl expansion rate in each of the three parts of the specimen. Coefficients of variation greater than 10% again suggest violation of the assumption of low between specimen differences in whorl expansion rates. The program that implements alignment by height checks how much variation is present in the heights of each whorl in the composite average specimen. If the average CV for all whorls except the first and the last is less than 7% then alignments are probably reasonable. If this average CV exceeds 8%, then there are probably serious errors in alignment, or considerable variation in the sample. If this average CV exceeds 7%, it is essential that the user evaluate the results by plotting whorl number against whorl height (as in Figure 6).

CHOICE OF METHOD

The choice of alignment method in a particular case involves four factors. These are accuracy, precision, assumptions, and the goal of the analysis. In general, we feel that the goals of a morphometric analysis will best be met by the methods of either three W values or iterative comparison of heights (Table 1). Other methods are preferred in only a few other cases. If many homologous points are available in the ornament of all taxa under consideration then these may prove the best means of alignment. We recommend avoiding use of the whorl expansion rate in the first preserved whorls of each specimen to align whorls unless it can be clearly demonstrated that there is no substantial ontogenetic change in the whorl expansion rate, and that measurement error is not large in small whorls. This method of alignment should not be used if the coefficient of variation of whorl height from a small whorl of a single specimen measured repeatedly ten times is greater than about three percent.

Our examination of the test data set and of alignments in samples of fossil species suggests that the methods of alignment by three W values and alignment by whorl heights both align specimens to within about one whorl of their correct position. Alignment by height is more precise (has less scatter), while alignment by three W values is more accurate (is closer to true whorl number). If comparisons are made between homologous whorls then alignment by height will introduce less error. On the other hand, in comparisons of groups of whole specimens, alignment by three W values will be superior. Population variability in whorl expansion rate will affect both of these methods, but in different ways. If a sample contains specimens from two populations that differ in whorl expansion rate then alignment by height will tend to make good alignments within each cluster. It will, however, systematically misalign one cluster with respect to the other. On the other hand, alignment by three W values will increase the spread of the entire sample.

It will reduce the distinctness of the clusters. Alignment by height is better at preserving differences between individual specimens. In addition, the accuracy of alignment by height can be increased by removing the smallest two whorls from the data set. The smaller sample size of the small (and large) whorls reduces the accuracy of alignment for some specimens. Speed may be an additional concern. At large sample sizes, our algorithm for alignment by height, being iterative, is significantly slower than our algorithm for alignment by three *W* values (17 min. vs. 1 min. for 50 specimens on an 80386 at 20 MHz).

This brings us to the original purpose of this discussion: the morphometric analysis of high-spined gastropods that are missing whorls. The goal of the alignment programs is to place markers in place of measurements in the missing whorls. If the data set is subsequently subjected to multivariate analysis these markers (zeroes in our example, Appendix 1) can be treated as "missing values." Most types of ordination and cluster analysis, however, deal poorly with missing data. It is therefore necessary either to throw out many whorls and reduce the analysis to a set of whorls that are complete in all specimens in the data set, or to apply a technique for estimating missing values. One efficient way to do this is to create a correlation matrix from the data. Multivariate techniques can then be applied to this correlation matrix rather than the incomplete data set (Beale & Little, 1975; Little & Rubin, 1987). For example: an analysis with BMDP (Dixon, 1988) could use program 8D (Correlation with missing data, Engelman, 1988) to create a correlation matrix from the data set. This correlation matrix could then be used as input for program 4M (Factor analysis, which would normally exclude all cases with any missing data from the original data set, Frane *et al.*, 1988). Program 4M could then be used for various sorts of exploratory variable reduction and factor analysis (*e.g.*, Kleinbaum *et al.*, 1988), which could not be performed on the raw data. Holding in mind the caveats of error introduced by rotation error and assumed meaningful similarity between whorls of similar height, the method of alignment by iterative comparisons of whorl heights with a composite average specimen should prove suitable for most cases in which incomplete high-spined gastropods are to be aligned for morphometric analysis.

ACKNOWLEDGEMENTS

R. E. Chapman provided many insightful comments on an earlier version of this paper. He is especially acknowledged for pointing out to us that extant turritellids are often complete, and that it is possible to assess the accuracy of alignment by treating whole specimens as incomplete. These tests have shown us that several of our original assumptions were invalid. S.A. Shellenberg β -tested several versions of HISPIRE and raised many useful questions and suggestions. This manuscript has also benefited from comments by B.A. Robinson and an anonymous reviewer.

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APPENDIX 1

Sample conversion using the method of alignment by iterative comparisons of height (program HISPIRE3, see Appendix 2). Four specimens of *Turritella mortoni* Conrad, 1830 from The Paleocene Aquia Fm. at Piscataway Creed, Prince Georges Co. MD. Variables (see Allmon, 1994) are: SP#, specimen number; WH#, whorl number; Height, whorl height; CH1, carina height; CH2, carina height above suture; SW, width at adapical suture; MW, width at mid-whorl, CW, width at carina; CAN, carina angle.

SP#	WH#	Height	CH1	CH2	SW	MW	CW	CAN
1	1	8.19	6.62	1.56	14.3	16.0	18.9	156
1	2	10.2	8.71	1.56	16.5	18.5	22.4	159
1	3	14.3	10.4	3.90	19.3	22.0	26.1	160
1	4	15.8	11.5	4.28	21.1	24.5	28.6	162
2	1	3.12	2.34	0.779	3.75	4.64	5.39	164
2	2	3.51	2.86	0.650	4.85	6.12	6.94	174
2	3	4.29	3.51	0.779	6.08	7.37	8.54	177
2	4	5.45	4.29	1.16	7.94	8.96	11.3	162

On *Planorbula nebraskensis* Leonard, 1948, and its position in the evolutionary sequence of North American planorbulids

Harold G. Pierce

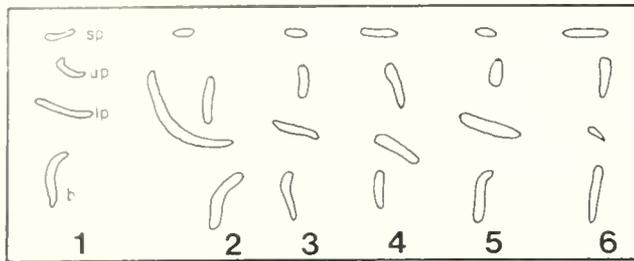
Research Associate
University of Nebraska State Museum
Lincoln, NE 68588-0514, USA

Leonard (1948:62) described *Planorbula nebraskensis* from what he considered to be Yarmouthian sediments in Knox County, extreme northern Nebraska, and later reported this taxon from a second locality in Lyons County, Iowa (Leonard, 1950:18). Leonard commented that "*P. nebraskensis* is apparently related to *P. wheatleyi*" (Lea, 1858) and that the lamellae were "disposed as in *Planorbula wheatleyi*", without further comment on the orientation of specific lamellae of the outer lip. Externally, *P. nebraskensis* is very similar to the modern lamellate species (subspecies?) of *Planorbula*. In fact, without reference to the apertural lamellae, *Planorbula armigera* (Say, 1821) (Figure 1), *P. wheatleyi* (Figure 2), and *P. nebraskensis* can not be separated easily. Subsequent work at Leonard's type locality, near Locality KX-145 of the University of Nebraska State Museum, has shown the age of the fauna to be late Kansan. The fauna is recovered from sediments below a bed of the Pearlette Type O ash, dated at 600 KA, and is associated with a sparse, cool to boreal, mammalian fauna. Topotypes of *P. nebraskensis* were collected for comparison. Examination of these topotypes disclosed a substantial difference in the placement of the upper palatal lamella (Figure 3). With the shell axis vertical and viewed from the axis outward, the upper palatal lamella is oriented vertically, as is the upper palatal lamella of *P. wheatleyi* (Figure 2), not nearly horizontally as with *P. armigera* (Figure 1). However, the lower palatal lamella of *P. nebraskensis* does not have the elongated and very distinctive vertical segment characteristic of *P. wheatleyi*.

Subsequent work on the Albert Ahrens Locality (NO-104) in Nuckols County, extreme southern Nebraska, resulted in collection of another very boreal mammalian fauna of late Kansan (Irvingtonian) age. This locality is not directly associated with an ash, but nearby ash deposits strongly suggest that it is stratigraphically just above the Pearlette Type O ash, and is, therefore, only slightly younger than the KX-145 locality. Mammals were diverse, and of a strongly boreal character (Voorhies & Corner, 1991). Analysis of arboreal pollen confirmed that a boreal, almost taiga-like, environment existed here (Bolick, 1991). The molluscan fauna from this locality is

quite similar to that of Leonard's type locality. Examination of the planorbulids from NO-104 locality showed that they had the unique placement of the labial lamella characteristic of *P. nebraskensis* (Figure 4). This suggested that the *P. nebraskensis* was not an unique aberration of the KX-145 locality, and nearby Lyons County, Iowa only, but a widespread taxa. This also prompted reevaluation of several older (late Pliocene, Blancan, ca. 2 MA) faunas from Nebraska that included planorbulids, especially those reported by Pierce (1990). Careful reevaluation, including break-back of specimens, showed that the planorbids of late Pliocene Localities KX-109, KX-143 and CD-104, had been incorrectly identified as *P. armigera*. These specimens were clearly *P. nebraskensis* (Figure 5), and demonstrated a significant range, both spatially and temporally, for this species.

Fossil planorbulids from strata older than Quaternary are not common, possibly due to the unfortunate past habit of lumping many disparate planispiral taxa under a form genus "*Planorbis*". Taylor (1960:36) lists *P. armigera* as a component of the Sand Draw fauna (Blancan), although I have yet to collect a planorbulid from that locality for comparison. Taylor (1966) refers, with question, several Idaho and Wyoming planorbulids, also of Blancan age, to *Planorbula campestris* (Dawson, 1875). Hannibal (1912:157-158) described *P. mojavensis* from the Miocene Barstow Formation of California. The lamellae of *P. mojavensis* are unique, with only three lamellae on the outer lip (Taylor, 1954:74). Pierce (1993) described *Planorbula powelli* from the late Oligocene (Arikareean) Cabbage Patch beds of southwestern Montana. The lamellae of *Planorbula powelli* (Figure 6) are also of the pattern characteristic of modern *P. wheatleyi*, i.e., with a vertically oriented upper palatal lamella. When compared in series, an evolutionary sequence, beginning with Oligocene *Planorbula powelli*, and extending through *P. nebraskensis* to *P. wheatleyi* is strongly suggested. This also suggests that *P. armigera* may be a late offshoot of the older *P. wheatleyi* lineage. The slight inclination of the upper palatal lamella noted with the otherwise typical *P. nebraskensis* from the Nuckols County locality may represent the beginning of



Figures 1-6. Labial lamellae of planorbilid snails, greatly enlarged. sp=suprapalatal, up=upper palatal; lp=lower palatal; b=basal. **1.** *Planorbula armigera* (Say 1821). **2.** *P. wheatleyi* (Lea 1855). **3.** *P. nebraskensis* Leonard 1948, hypotype. **4.** *P. nebraskensis*, Locality NO-104. **5.** *P. nebraskensis*, Locality KX-109, Blancan. **6.** *Planorbula powelli*, Oligocene (Arikarean) Cabbage Patch beds. Figures 1 and 2 alter Baker 1945, Plate 76.

Figures 7, 8. Apertural lamellae of *P. nebraskensis*, approximately 20 \times , both from lot PPLN 1027, Locality KX-145 (Leonard's type locality). **7.** Lamellae within aperture of small specimen. **8.** Aperture of small specimen broken back to radial of apertural lamellae.

a divergence that led to the lamellar pattern of modern *P. armigera*. *Planorbula vulcanata* Leonard 1948, a fossil of mid-Pleistocene age (ca. 600KA) from southwestern Kansas and adjacent Oklahoma, appears to be the oldest confirmed planorbilid with typical *P. armigera* dentition. This suggested lineage results, however, in a distributional inconsistency. Oligocene *Planorbula powelli* were found to have existed in a climate similar to that preferred by modern *P. wheatleyi*, which is found only in the humid mesothermal climatic zone of the south-

eastern United States. *Planorbula nebraskensis* apparently preferred a cooler, humid, microthermal climate. *Planorbula armigera*, on the other hand, is a very tolerant species, widely distributed from Louisiana to the Northwest Territories of Canada, currently occupying both mesothermal and microthermal climatic zones.

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Effects of Preservatives on Wet-weight Biomass of the Asiatic Clam, *Corbicula fluminea*

Michael E. Smith

Gerry A. Lanfair

Department of Biology
Valdosta State University
Valdosta, GA 31698 USA

The Asiatic clam, *Corbicula fluminea* (Müller, 1774) was first collected in North America from Vancouver Island, Canada in 1924 and in the United States from near the mouth of the Columbia River during 1938 (Counts, 1986; McMahon, 1982). Since its introduction, *C. fluminea* has spread to the east coast of the United States (Counts, 1986) and into South America (Ituarte, 1981) becoming an important component of freshwater ecosystems. The Asiatic clam is often found in high densities creating problems such as biofouling of industrial water intakes and power plant cooling systems (Isom, 1986). *Corbicula fluminea* is also recognized as an important biological monitor in freshwater ecosystems (Doherty, 1990).

When sampling *C. fluminea*, individuals are usually preserved in the field for later laboratory analysis. Preservation can cause changes in wet-weight biomass (Donald & Paterson, 1977; Herke, 1973; Howmiller, 1972; Landahl & Nagell, 1978; Mills *et al.*, 1982; Stanford, 1973; Wiederholm & Eriksson, 1977; Williams & Robins, 1982) that affect estimates of population parameters such as standing crop and production. Thus, the purpose of this study was to determine the effects of two common preservatives, 70% ethanol and 10% neutral buffered formalin, on wet-weight biomass of the Asiatic clam, *Corbicula fluminea*.

Specimens of *Corbicula fluminea* were collected on 6 February 1993 from the confluence of Shellstone Creek and the Ocmulgee River, Bleckley County, Georgia (32°25'35"N, 83°28'50"W). Individuals were removed from their shells and live wet-weights were determined prior to preservation in 70% ethanol (n=18) or 10% neutral buffered formalin (n=18). Formalin and 70% ethanol solutions were prepared by diluting 37% formaldehyde solution and 95% ethanol with distilled water; the 10% formalin solution included 4 g/l sodium phosphate monobasic and 6.5 g/l sodium phosphate dibasic to produce neutral buffering. All specimens were blotted (Donald & Paterson, 1977; Wiederholm & Eriksson, 1977), weighed to the nearest 0.1 mg and placed individually into 100 ml of preservative at room temperature (25 ± 1°C). Preserved specimens were soaked in distilled water for 30 minutes (Howmiller, 1972; Mills *et al.*, 1982), weighed, and returned to their individual containers.

Comparison of live wet-weights between the two groups was by the use of a t-test. Means, 95% confidence intervals and linear regressions were calculated from arcsine transformed data. Homogeneity of regression slopes was tested to determine if there was a difference in weight loss over time between the formalin and ethanol groups (Sokal & Rohlf, 1981).

Live wet-weights were not significantly different ($P > 0.05$) between the formalin and ethanol groups. Mean weight loss proceeded more rapidly in the ethanol preserved specimens and after 163 days, was 41.9% (40.7–43.1%; 95% C.I.) and 21.6% (20.3–22.9%; 95% C.I.) for the ethanol and formalin groups, respectively (Figure 1). Stabilization of mean weight loss occurred at approximately day 77 for the ethanol group with only a 2.9% weight loss over the next two samplings (= 86 days). The formalin group stabilized after day 163; wet-weight biomass was measured at day 385 for the formalin group only and mean weight loss was 22.1%, a loss of 0.5% since day 163. Regression equations were $y = 0.0434 + 0.604x$, $r^2 = 0.961$ for the formalin group and $y = 0.0265 + 0.0690x$, $r^2 = 0.985$ for the ethanol group (Figure 1). Equations are only descriptive for the preservatives and temperature range used in this study. The slopes of the two lines were significantly different ($P < 0.001$) indicating that rate of weight loss was different between the two groups.

Our study demonstrates that the two most commonly used preservatives for freshwater benthic organisms, 70% ethanol and 10% neutral buffered formalin, significantly decrease wet-weight biomass of *Corbicula fluminea*. Use of preserved specimen biomass as an accurate determination of live biomass, therefore is inappropriate. Wet-weight losses for *C. fluminea* fall within the range observed in other studies for freshwater invertebrates (Donald & Paterson, 1977; Howmiller, 1972; Landahl & Nagell, 1978; Stanford, 1973; Wiederholm & Eriksson, 1977). Howmiller (1972) found, as we did, that formalin preservation resulted in less wet-weight loss compared to 70% ethanol.

We recommend that the regression equations be used to convert preserved wet-weight biomass to live wet-weight biomass if 10% neutral buffered formalin or 70% ethanol is used in the temperature range of 25 ± 1°C.

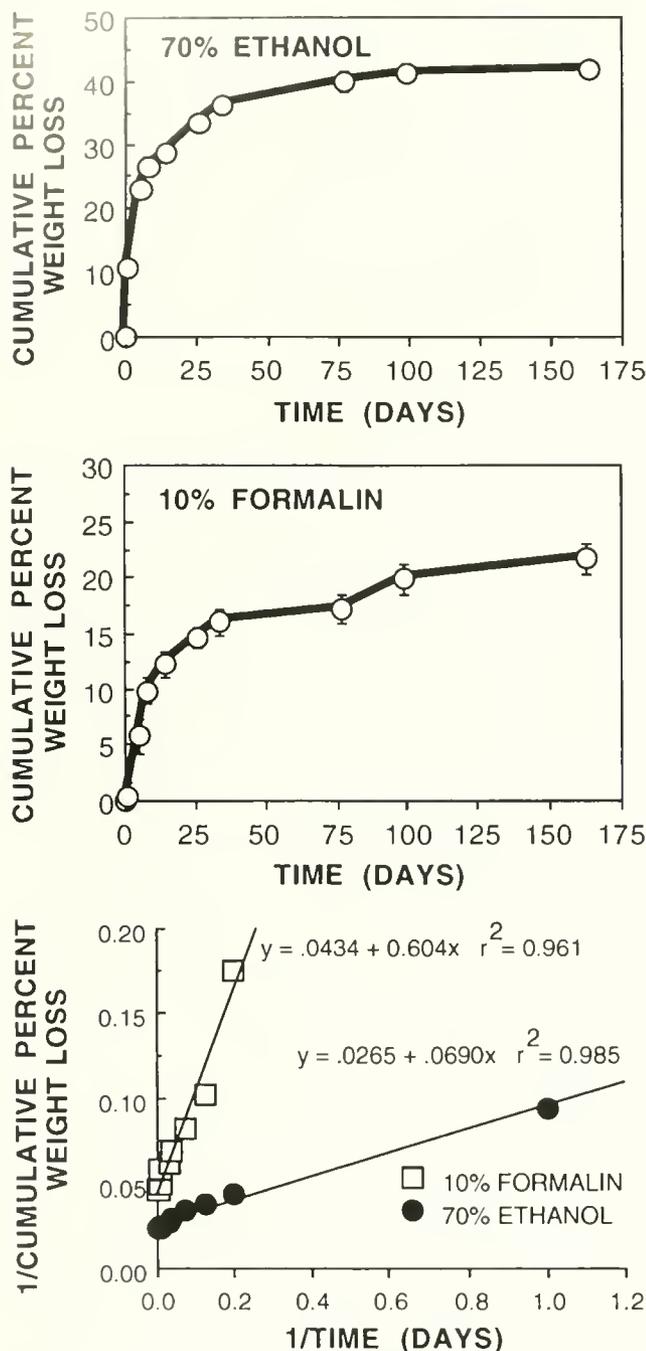


Figure 1. Mean cumulative percent weight loss over time for *Corbicula fluminea* preserved in 70% ethanol and 10% neutral buffered formalin. Error bars represent 95% confidence intervals, $n=15$. Relationship between the reciprocal of time spent in preservative and the reciprocal of mean cumulative weight loss for *Corbicula fluminea* at $25 \pm 1^\circ\text{C}$.

Also, the regression equations are only valid up to 163 days of preservation. Conversion to live wet-weights would be especially beneficial for comparison with other studies where similar equations were generated. If re-

gression equations are not used, we recommend using 10% neutral buffered formalin as the preservative for *Corbicula fluminea* in ecological studies based on lower weight loss.

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A Review of the New Zealand Recent Species of *Poirieria* Jousseume, 1880 (Mollusca: Gastropoda: Muricidae) with Description of a New Species

Bruce A. Marshall

Museum of New Zealand Te Papa
Tongarewa
P.O. Box 467
Wellington, New Zealand

Roland Houart

Research Associate
Institut Royal des Sciences Naturelles
de Belgique
Vautierstraat 29
B-1040 Brussels, Belgium

ABSTRACT

Poirieria syrinx n. sp. is described and compared with *P. zelandica* (Quoy & Gaimard, 1833) and *P. kopua* Dell, 1956. *Poirieria syrinx* is recorded from Early Pleistocene beds at Palliser Bay, and living at 482-786 m off the east coast of the North Island. It is locally sympatric with *P. zelandica*, which is widely distributed off New Zealand at 0-540 m depth. Challenger Expedition specimens of *P. zelandica* reputedly from Tongatabu and the Kermadec Islands are considered to have been translocated from Queen Charlotte Sound, New Zealand. *Poirieria kopua* occurs at 490-1006 m off the east coast of the South Island. Some groups with similar species are commented upon, including *Pagodula* Monterosato, 1884 and *Enixotrophon* Iredale, 1929. The type species of *Enixotrophon* (*Trophon carduelis* Watson, 1883) is newly recorded from New Zealand, and its radula is illustrated for the first time.

Key words: Mollusca, Gastropoda, Muricidae, *Poirieria*, new species.

INTRODUCTION

The present contribution was initiated when we recognized an undescribed species of *Poirieria* from the continental slope of the North Island of New Zealand. The new species differs markedly from the well known species *P. zelandica* (Quoy & Gaimard, 1833) and the rare *P. kopua* Dell, 1956 in having tubular shell spines.

ACRONYMS

AMS The Australian Museum, Sydney
BMNH The Natural History Museum, London
MNHN Muséum National d'Histoire Naturelle, Paris
MNZ Museum of New Zealand, Wellington
NZGS Institute of Geological and Nuclear Sciences, Lower Hutt

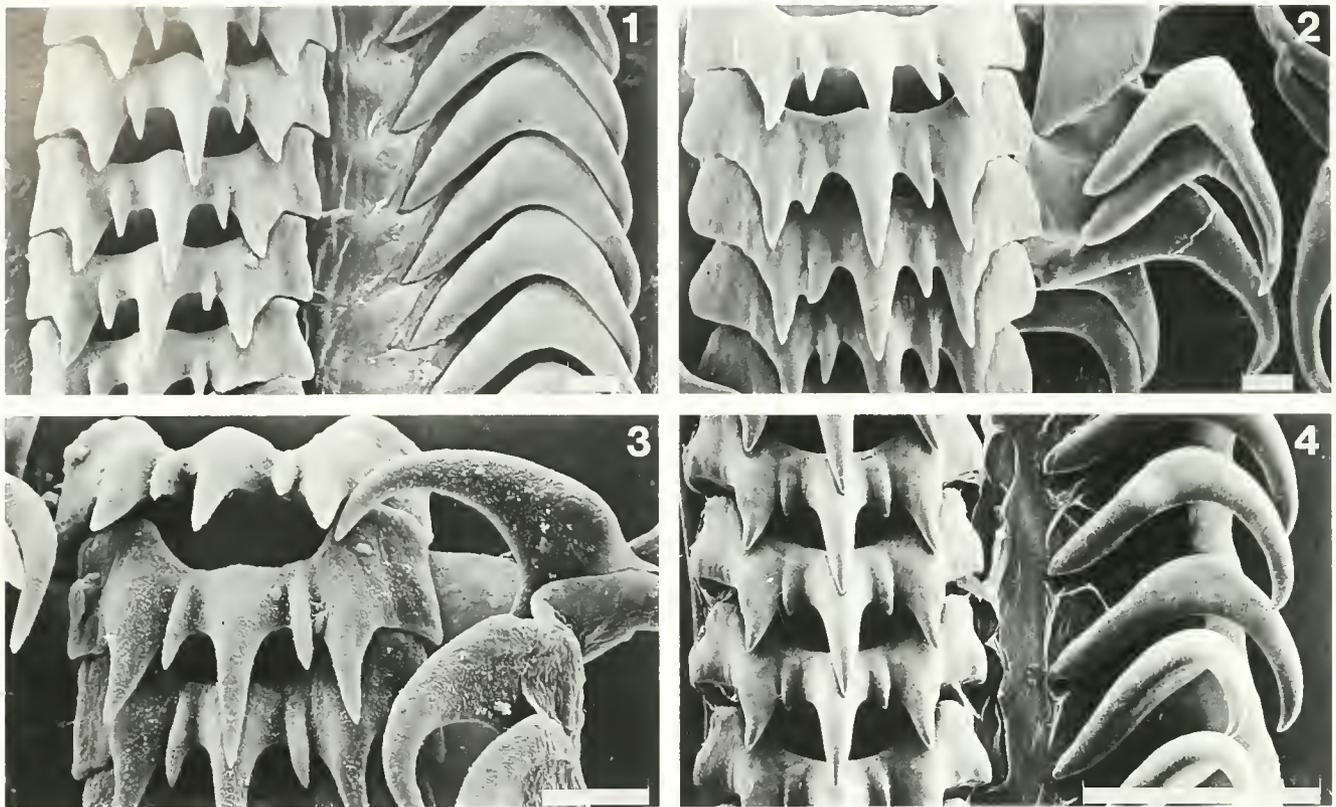
NZOI National Institute of Water and Atmospheric Research, Wellington

SYSTEMATICS

Order Neogastropoda Thiele, 1929
Superfamily Muricoidea Rafinesque, 1815
Family Muricidae Rafinesque, 1815
Subfamily Muricinae Rafinesque, 1815
Genus *Poirieria* Jousseume, 1880

Poirieria Jousseume, 1880:335. Type species (by original designation): *Murex zelandicus* Quoy & Gaimard, 1833; Pliocene-Recent, New Zealand.

Remarks: The radula of *Poirieria* species is morphologically very similar to those of the Recent European muricine *Trophon echinatus* (Kiener, 1840) (Bouchet & Warén, 1985, fig. 333) and a number of bathyal Indo-West Pacific species (mostly undescribed—AMS, MNHN, MNZ), among them *Trophon carduelis* Watson, 1883 (Watson, 1886, pl. 10, fig. 7), the type species of *Enixotrophon* Iredale, 1929 (type locality New South Wales: here newly recorded from off the North Island and the west coast of the South Island, New Zealand, living at 676-1217 m—MNZ, NZOI) (figures 1-4). Some of these have even longer shoulder spines than most *Poirieria* species, though all differ in having the shoulder spines set closer to the rim of each varix, and radular teeth that are larger in shells of comparable size. Neither *Poirieria* species nor *Trophon echinatus* or *T. carduelis* appear to be closely related to *Trophon* Montfort, 1810 (type species *Buccinum geversianum* Pallas, 1774; Recent, southern South America) or to *Boreotrophon* Fischer, 1884 (type species *Murex clathratus* Linnaeus, 1758; Recent, northeastern Atlantic), both of which differ in details of central radular tooth morphology (Harasewych, 1984; personal observation). *Trophon echinatus* is closely similar to *Murex vaginatus* De Cristofori and Jan, 1832



Figures 1–4. Radulae of New Zealand *Poirieria* and *Pagodula* species. 1. *Poirieria zelandica* (Quoy & Gaimard, 1833), subadult, off Matakaoa Point, Hicks Bay, 99–102 m, MNZ M.60498, shell height 30.0 mm. 2. *Poirieria syrinx* new species, holotype (adult). 3. *Poirieria kopua* Dell, 1956, adult paratype, Chatham Rise, 530 m, MNZ M.10506, shell height 14.7 mm. 4. *Pagodula carduelis* (Watson, 1883), adult, off Gisborne, 913–750 m, NZOI sta. E719, shell height 50.5 mm. Scale bars 1–3 = 100 μ m, 4 = 1.0 mm.

(Pliocene, Italy), which is generally interpreted as the type species of *Pagodula* Monterosato, 1884 (Bouchet & Warén, 1985:126). It seems plausible, therefore, that *Pagodula* is the most appropriate genus group name for *T. carduelis*, and thus by implication that *Enixotrophon* is a junior synonym.

The type species of *Paziella* Jousseaume, 1880 (*Murex pazi* Crosse, 1869; Recent, Caribbean), and especially *Actinotrophon* Dall, 1902 (*Trophon actinophorus* Dall, 1889; Recent, Caribbean) (see Bayer, 1971, figs. 30, 35D) are so similar to New Zealand Recent *Poirieria* species in shell and radular morphology that separation on these characters alone seems untenable. Harasewych (1984) and Kool (1993a, b), however, have shown that shell characters (unlike anatomy) in Muricidae are subject to convergence, while Kool (1987) concluded that radular characters are largely unrelated to food-type and are thus a useful clue to phylogenetic relationships. We follow Vokes (1970, 1992) in treating *Paziella* and *Actinotrophon* as subgenera of *Poirieria*.

Incidentally, although *Paziella* was introduced one line before *Poirieria* (Jousseaume, 1880:335), *Poirieria* has consistently been treated as the senior synonym (e.g. Vokes, 1970, 1992) following Cossmann (1903), who was the first reviser according to ICZN Article 24.

Poirieria zelandica (Quoy & Gaimard, 1833)
(Figures 1, 5, 7, 10–15)

Murex zelandicus Quoy & Gaimard, 1833: 529, pl. 36, fig. 5–7.

Poirieria zelandica. Maxwell, 1971:767 (earlier synonymy); Powell, 1979: 170, pl. 35, fig. 2; Beu & Maxwell, 1990: 358, pl. 48K.

Type material: Holotype MNHN: Cook Strait.

Other material examined: About 100 Late Pliocene and Pleistocene specimens (MNZ, NZGS), and about 1500 Recent specimens in 200 lots (MNZ).

Distribution: (figure 5) Early Pliocene (Opoitian) to Recent. Three Kings Islands southward to Stewart Island, Challenger Plateau and Chatham Islands, New Zealand, living at 0–540 m.

Remarks: This well known species is common throughout most of its range at 20–150 m depth. Small (immature) living specimens occur rarely at considerably greater depths, particularly in the Bay of Plenty (deepest record 490–540 m). One of us (B.A.M.) has taken lightly abraded short-spined specimens on numerous occasions alive from sand at low tide at the eastern end of Ohope

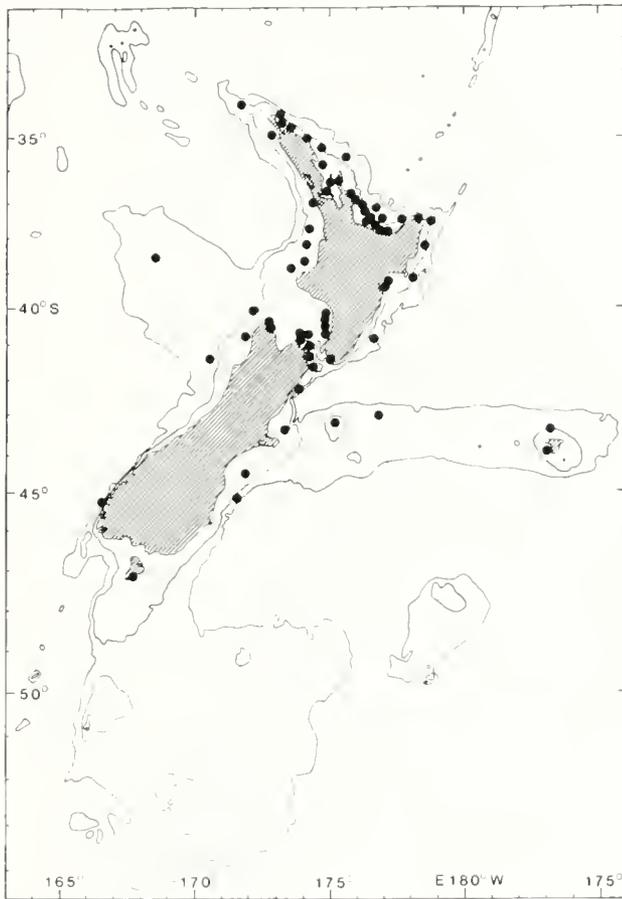


Figure 5. Map of New Zealand showing distribution of *Poirieria zelandica* (Quoy & Gaimard, 1833). 200 and 1000 meter contours indicated.

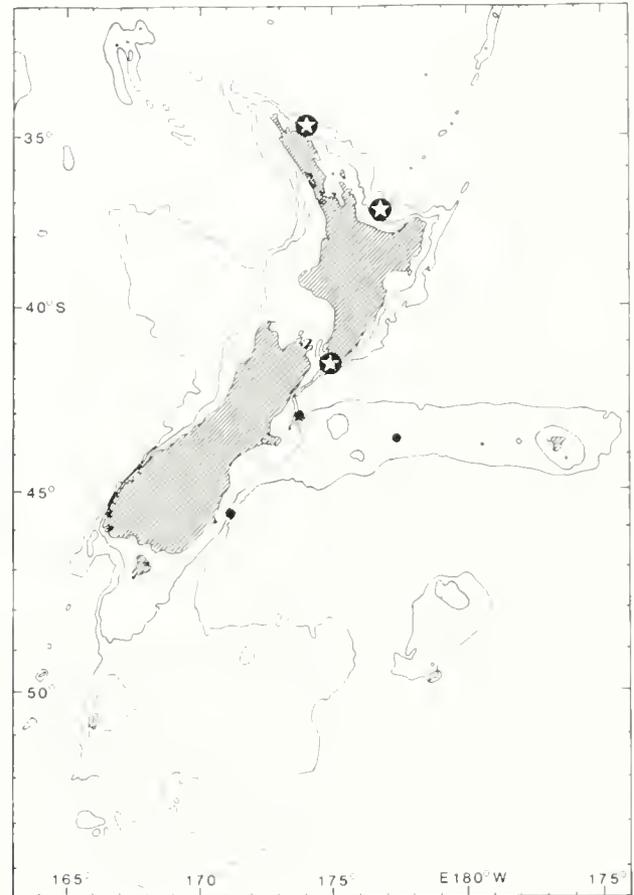
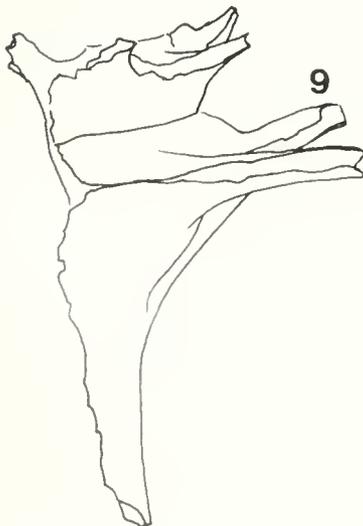
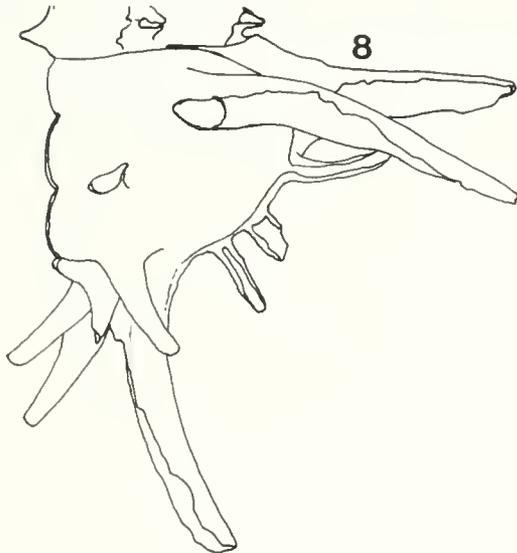


Figure 6. Map of New Zealand showing distribution of *Poirieria syrinx* new species (stars) and *Poirieria kopua* Dell, 1956 (solid circles). 200 and 1000 meter contours indicated.

Beach, but these had probably been transported inshore by storms. There is considerable variation in the length of the spines (figures 10–14), which tend to be longest in specimens from muddy substrata, and shortest in specimens from coarser substrata. Grading southward through intermediate forms, specimens from off the southern South Island and Stewart Island (figure 11) attain about half the size of the largest northern specimens, and are more stoutly built, often with a few low rounded denticles within the outer lip. In their stout build the Recent southern form approaches Late Pliocene (Mangapanian) and Early Pleistocene (Nukumaruan) forms of *P. zelandica* (figure 15), though the fossils are consistently thicker, have more strongly dentate outer lips, and attain the size of Recent northern specimens. It should be appreciated that all of the fossils are from the southern half of the North Island, and since shells of equivalent age are unknown from further north (due to lack of exposures), it is unknown whether northern Late Pliocene–Early Pleistocene shells were more lightly built. Maxwell (1971) concluded that *P. zelandica* evolved gradually from *P. primigena* Finlay, 1930, a species in which the shoulder is set lower on the whorls and that ranges from

Late Oligocene (Duntroonian to Early Pliocene (Opotian)).

Watson's (1886:157) records of *P. zelandica* from CHALLENGER stations 171 (north of Raoul Island, Kermadec Islands, 1097 m) and 172 (off Tongatabu, 18 m.) are highly anomalous since, apart from the Challenger Plateau record, the species has never been obtained from beyond the New Zealand continental shelf. These specimens (BMNH 1887.2.9.546–7, 1887.2.9.548) are perfectly accordant with the specimens from CHALLENGER station 167A (Queen Charlotte Sound, New Zealand, 18 n, BMNH 1887.2.9.544–5) and numerous additional specimens from the vicinity (MNZ). Although it seems clear that the specimens from stations 171 and 172 were introduced through entanglement in the nets or ropes, it is significant that they were not detected at stations 168–170, presumably through oversight or the use of a different trawl. According to the Narrative of the Cruise (Tizard *et al.*, 1885) and the Summary of Results (Murray, 1895), stations 168–171 were sampled by trawl and station 172 by dredge. According to Tizard *et al.* (1885: 1012) station 167A was by dredge alone, but in fact there were also two trawlings at this station (Murray, 1895:



593), which would account for the presence of contaminants in both dredge and trawl stations.

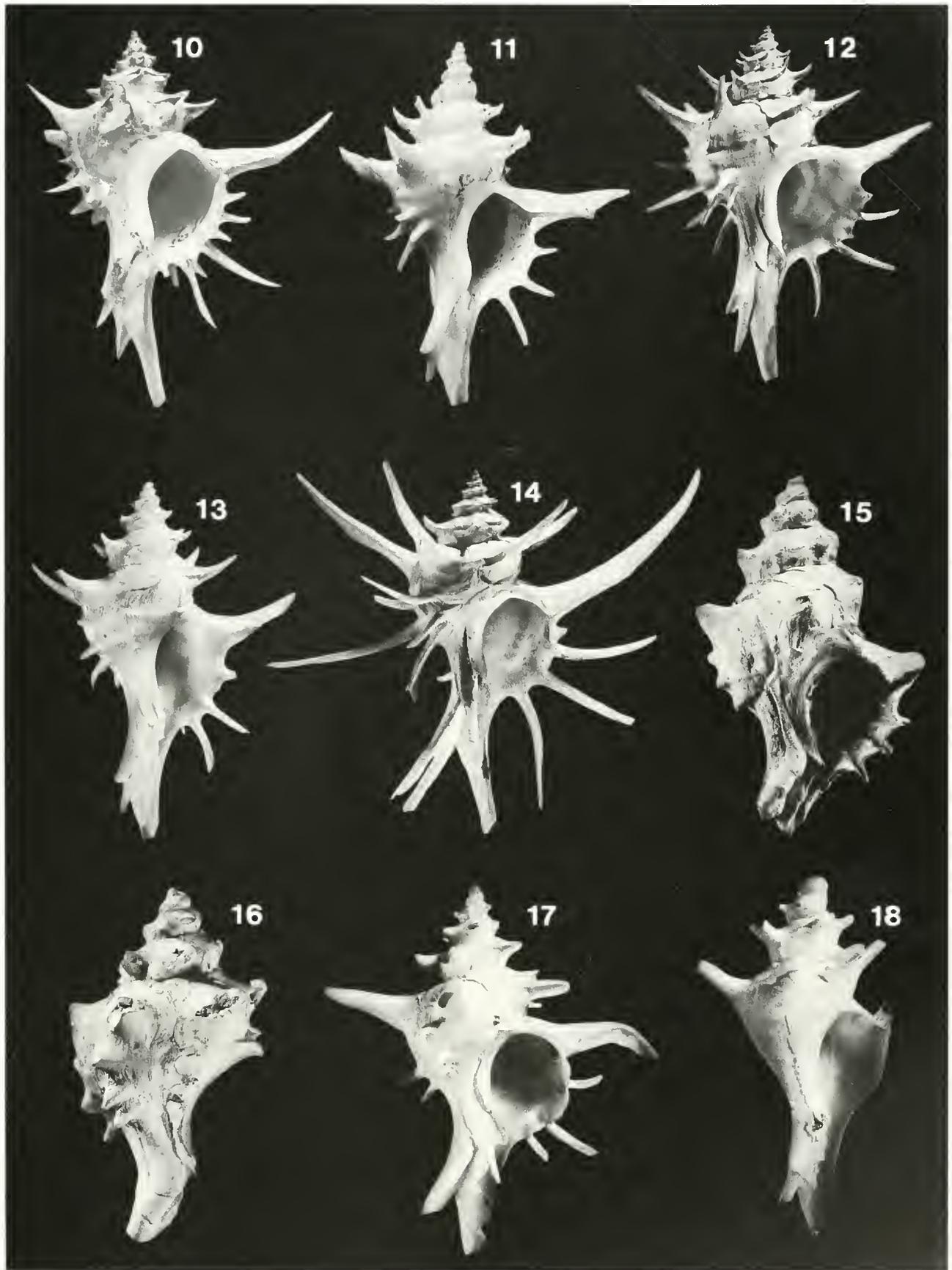
Poirieria syrinx Marshall and Houart, new species
(figures 2, 6, 8, 16, 17)

Poirieria zelandica - Dell, 1962:76 (not Quoy & Gaimard, 1833).
Poirieria kopua - Dell, 1963:212 (not Dell, 1956); Powell, 1979:
170 (text in part).

Description: Shell of medium size for the genus, length up to 45 mm, broadly fusiform, spire slightly higher than aperture, suture well impressed, glossy, white or salmon pink. Protoconch 1.20 mm wide, taller than broad, of $1\frac{1}{4}$ - $1\frac{3}{4}$ convex whorls, smooth, glossy, terminal varix prominent. Teleoconch of up to $5\frac{3}{4}$ convex whorls, suture well impressed. Varices thin, sharp-edged, prominently spinose, numbering 5 on 1st whorl, 5 on 2nd, 5 or 6 on 3rd, 5 or 6 on 4th, and 4 or 5 on 5th whorl. Spines slender, sharp, gently curved, bases set behind varical rim, shoulder spine strongly posterior; leading edge open to varical rim at first, becoming closed after 3rd whorl so that proximal part of each spine is fully tubular. Shoulder spine row the most prominent, situated medially on earliest whorls, then supramedi ally. Secondary spines abapical, 3, relative sizes variable, about equidistant, commencing after 3rd whorl, bases centered well in front of that of shoulder spine, adapical spine row exposed on spire, set about midway between shoulder spine row and suture or abapically, abapical spines of previous whorl in front of aperture. Aperture roundly ovate. Inner lip thin, smooth, fully contacting or free over abapical half.

Figures 7-9. Outer lip profiles of New Zealand *Poirieria* species. 7. *Poirieria zelandica* (Quoy & Gaimard, 1833), Orchard Bay, Marlborough Sounds, 29 m, MNZ M.45110, shell height 28.0 mm. 8. *Poirieria syrinx* new species, holotype, MNZ M.117782, shell height 26.0 mm. 9. *Poirieria kopua* Dell, 1956, paratype, Chatham Rise, 530 m, MNZ M.10506, shell height 14.7 mm. Scale bars = 4.0 mm.

Figures 10-18. Shells of New Zealand *Poirieria* species. 10-15. *Poirieria zelandica* (Quoy & Gaimard, 1833). 10. Holotype, MNHN, shell height 52.0 mm. 11. Port Pegasus, Stewart Island, 40-46 m, MNZ M.26617, shell height 32.7 mm. 12. Off Poor Knights Islands, MNZ M.83858, shell height 54.0 mm. 13. Orchard Bay, Marlborough Sounds, 29 m, MNZ M.45110, shell height 28.0 mm. 14. Off Waiheke Island, 40 m, MNZ M.35635, shell height 57.5 mm. 15. Cliffs west of Whangaimoana, Palliser Bay, Early Pleistocene (Nukumaruan), MNZ M.40361, shell height 32.8 mm. 16, 17. *Poirieria syrinx* new species. 16. Cliffs west of Whangaimoana, Palliser Bay, Early Pleistocene (Nukumaruan), MNZ M.91795, shell height 25.8 mm (incomplete). 17. Holotype, MNZ M.117782, shell height 26.0 mm. 18. *Poirieria kopua* Dell, 1956, paratype, Chatham Rise, 530 m, MNZ M.10506, shell height 14.7 mm.



Outer lip thin at rim, internally slightly thickened, smooth, simple. Siphonal canal long, semitubular, spineless, gently curved, 2 or 3 previous canals retained. Outer shell layer (intritric) hard, dense, weakly or locally obscurely spirally liriate, translucent, glossy, becoming chalky through erosion.

Animal with small subparallel cephalic tentacles, eyes on outer edges at about midlength, subcylindrical behind them, tapered before. Male unknown. Radula (figure 2) similar to that of *Poirieria zelandica*.

Type material: Holotype (M.117782,) and 2 paratypes MNZ: BS761 (R119), 37°22.0'S, 176°40'E, 37 km E of Mayor I., New Zealand, alive, 616–666 m, January 24, 1979, R.V. TANGAROA (type locality). Other paratypes (10): I364, 34°46'S, 174°05.8'E, NE of Cavalli I. alive, 492 m, November 20, 1977, R.V. TANGAROA (1 NZOI); 24 km NE of Plate I., alive, 622–585 m, October 29, 1962, M.V. IKATERE (1 MNZ); BS741 (R99), 37°20.6'S, 176°28.0'E, 17 km E of Mayor I., alive, 482–550 m, January 22, 1979, R.V. TANGAROA (3 MNZ); 37°31.64'S, 176°55.35'E, SW of White I., alive, 500–518 m, January 20, 1993, F.V. KAHAROA (1 MNZ); VUZ97, 41°33'S, 174°57'E, off Palliser Bay, alive, 786 m, August 28, 1957; (3 MNZ, 1 R. Houart collection).

Other material examined: Cliffs west of Whangaimoana, Palliser Bay, New Zealand, 1971–73, B.A. Marshall, Early Pleistocene (Nukumaruan) (1 specimen).

Distribution: (figure 6): Early Pleistocene (Nukumaruan) of Palliser Bay, and Recent off northeastern North Island and Cook Strait, New Zealand, living at 482–786 m on mud.

Remarks: Compared with *Poirieria zelandica*, which it most resembles in shell morphology, *P. syrinx* n. sp. differs in having the bases of the spines set further behind each varical rim, and in that the proximal parts of each spine become fully tubular after the third teleoconch whorl. Other shell differences include the smaller size (maximum length 45 mm vs. 71.5 mm), the larger protoconch (width 1.2 mm vs. of 0.9–1.0 mm), the more prominent spiral microlirae, and the absence or extreme weakness of spiral swellings between the bases of the spines. The animal (preserved material) differs markedly from that of *P. zelandica* in having considerably shorter cephalic tentacles that are almost parallel instead of strongly divergent, with eyes situated closer to the head. Unfortunately the male of *P. syrinx* n. sp. was not available for comparison of the penial morphology. Their radulae are similar (figures 1, 2). *Poirieria syrinx* n. sp. and *P. zelandica* have overlapping geographic and bathymetric ranges, and the two species have been obtained living together (37°20.6'S, 176°28.0'E, off Mayor Island, 482–550 m, MNZ M.60247, 95064).

Poirieria kopua differs from *P. syrinx* n. sp. in attaining a smaller size (to 19.0 mm high), in having a larger protoconch (width 1.5–1.7 mm), in having a fully open shoulder spine on each varix, and in lacking secondary spines. Judging from their protoconchs, both species have

non-planktotrophic larval development (probably direct). They appear to be allopatric, though they could conceivably occur together off Cape Campbell. None of the New Zealand Tertiary species have tubular spine bases (Maxwell, 1971). The Early Pleistocene (Nukumaruan) specimen (figure 16) is indistinguishable from Recent shells. Beu's (1967) conclusion that the Whangaimoana beds were deposited at 400–600 meters depth is accordant with the known bathymetric range of this species.

Etymology: Greek *syrinx* (pipe).

Poirieria kopua Dell, 1956
(figures 3, 6, 9, 18)

Poirieria kopua Dell, 1956:114, pl. 16, figs. 161, 162, 165; Maxwell, 1971:771, figs. 26, 27; Powell, 1979:170 (in part), fig. 42/1.

NOT *Poirieria kopua* Dell, 1962:76; Dell, 1963:212 (= *P. syrinx* n. sp.).

Type material: Holotype MNZ M.9777 and 2 paratypes (MNZ and Canterbury Museum, Christchurch): C.I.E. sta. 59, 43°38'S, 177°19'E, Chatham Rise, alive, 530 m, February 11, 1954, M.V. ALERT.

Other material examined: (11 specimens) BS559, 43°14'S, 173°39'E, wall of Pegasus Canyon, off Kaikoura, New Zealand, dead, 1006–512 m, September 27, 1976, R.V. ACHERON (2 MNZ); BS201, 44°45.6'S, 171°05'E, off Taiaroa Head, dead, c. 549 m, January 23, 1957, M.V. ALERT (3 MNZ); BS582, 45°46'S, 171°03'E, off Taiaroa Head, dead, 660 m, September 1, 1976, R.V. MUNIDA (5 MNZ); Mu 70–45, 45°50'S, 171°01'E, off Taiaroa Head, dead, 540–490 m, October 22, 1970, R.V. MUNIDA (1 NZGS).

Distribution: (figure 6) Chatham Rise and off the east coast of South Island, from Kaikoura to Taiaroa Head, New Zealand, 490–1006 m, taken alive at 530 m.

Remarks: The shell of *P. kopua* differs from that of *P. zelandica* and *P. syrinx* n. sp. in attaining smaller shell size (to 19.0 mm), in having a larger protoconch (width 1.50–1.70 mm), in lacking secondary spines below the peripheral spines, and in that the spines are not fully tubular at their bases. The radula is similar in all three Recent species of *Poirieria* (figures 1–3).

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A New Species of *Charitodoron* (Gastropoda: Mitridae) from Mozambique, with Notes on *C. veneris* (Barnard, 1964)

R. N. Kilburn

Natal Museum

P/Bag 9070

Pietermaritzburg, 3200, South Africa

ABSTRACT

Charitodoron rosadoi n. sp., from off Bazaruto Island, Mozambique, in 200–350 m, is described. This is the first Recent record of the genus *Charitodoron* Tomlin, 1932, from tropical waters. *Mitromorpha veneris*, Barnard, 1964, is referable to *Charitodoron*, and adult examples are described and figured for the first time.

Key words: Mitridae, southern African, continental shelf, *Charitodoron*.

INTRODUCTION

The genus *Charitodoron* Tomlin, 1932, is distinguished from other genera of the Mitridae by the total absence of columellar pleats. Cernohorsky (1976), who revised the described taxa, recognized three species, all of which are endemic to the Agulhas Bank, the temperate-water continental shelf off South Africa. Subsequently, Kilburn (1986:635, fig. 21) pointed out that the holotype of *Mitromorpha veneris* Barnard, 1964, from off Zululand, is actually a worn, juvenile example of a species of *Charitodoron*, but did not discuss its identity further. Most recently Lozouet (1991) recorded the genus for the first time from the Upper Oligocene of France, and illustrated several South African species.

During the Natal Museum Dredging Programme, a number of samples of a distinctive species of *Charitodoron* were collected off Natal and Zululand, confirming that the range of the genus extends into subtropical waters. The early whorls in this material agree with the holotype of the supposed turrid *Mitromorpha veneris* (Barnard, 1964). Subsequently, Mr. José Rosado of Maputo brought to my attention some specimens taken from crayfish traps off Mozambique, which prove to be an undescribed species of *Charitodoron*, and provide the first record of the genus from tropical East Africa.

ABBREVIATIONS

a/h = ratio of aperture length (measured along main axis) to total shell length.

b/h = ratio of maximum protoconch breadth to its height.

l/h = ratio of shell breadth to total length.

MHNM = Museu de Historia Natural, Maputo, Mozambique.

NMSA = Natal Museum, Pietermaritzburg.

NMDP = Natal Museum Dredging Programme.

SAMC = South African Museum, Cape Town.

TAXONOMY

Family MITRIDAE

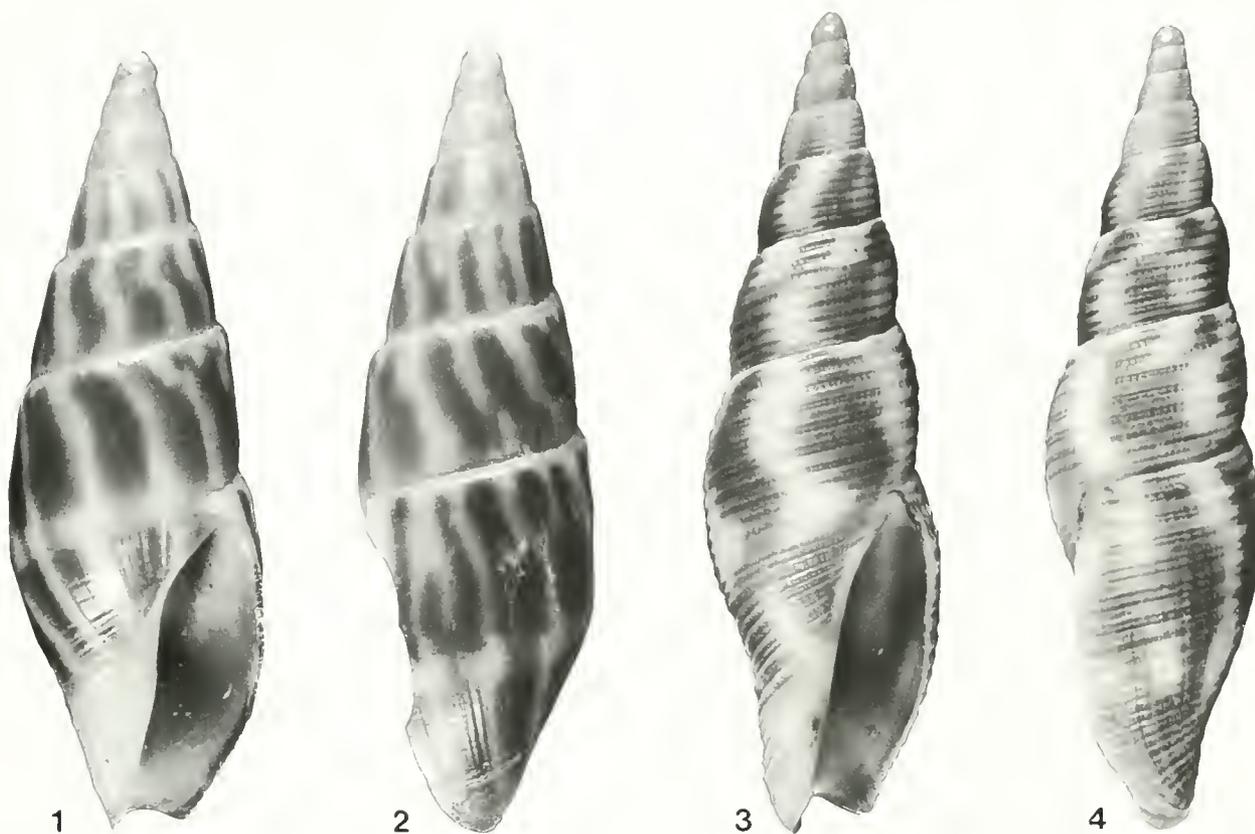
Charitodoron Tomlin, 1932

Charitodoron rosadoi n. sp.

Figures 1, 2

Diagnosis: Whorls almost flat, forming a very narrow shoulder immediately below suture, left side of base of body whorl shallowly concave; aperture with greatest width posterior to middle, columella medially convex, siphonal notch shallow; base of body whorl with 10–12 irregular spiral lirae, sculpture elsewhere weak and inconspicuous, initially of extremely fine axial riblets, becoming somewhat stronger on later whorls (20–30 on penultimate one), but remaining weak and irregular, forming a row of feeble nodules below suture; cream to brownish-white, with axial flames of brownish-orange, interrupted by a pale band at mid-body whorl; base of body whorl white. Protoconch breadth 0.98–1.00 mm. Maximum length 16.9 mm.

Description: Shell fusiform ($l/h = 0.29\text{--}0.35$), aperture narrow, $a/h = 0.39\text{--}0.42$; whorls almost flat, forming a very narrow shoulder immediately below suture, left side of base of body whorl shallowly concave; base slightly oblique, outer lip slightly foreshortened relative to base of columella. Teleoconch whorls approximately 5.4 in number. Aperture with greatest width posterior to middle, gradually tapering anteriorly; parietal region shallowly concave, columella medially convex, without trace of pleats; inner lip with callus deposit only in columellar region, bordered by a longitudinal depression (scarcely a false umbilicus); outer lip thin [edge damaged in all examples examined]; siphonal notch shallowly and obliquely U-shaped.



Figures 1–4. *Charitodoron rosadoi* n. sp. and *C. veneris*, (Barnard, 1964). **1–2.** *Charitodoron rosadoi*, holotype NMSA L1078, 16.9 × 5.5 mm. **3–4.** *C. veneris*, NMSA D4223, off Durban, 130 m, 24.0 × 7.2 mm.

Surface superficially smooth, other than spiral ridging on base of body whorl; under magnification whorls are seen to be axially ribbed, ribs initially extremely fine, indeed little stronger than growth lines, on later whorls strengthening, but remaining weak and irregular; ribs slightly arcuate, moderately prosocline, spacing irregular, forming a row of feeble nodules where they terminate on the subsutural berm; 20–30 ribs on penultimate whorl, becoming obsolete on later part of body whorl. Extremely fine and faint spiral grooves visible on 2nd and 3rd whorls; base of body whorl with 10–12 irregular spiral lirae.

Protoconch somewhat papilliform, limit ill-defined, evidently about 1.7 whorls; smooth, but fine axial riblets developing towards termination, and continuing onto 1st teleoconch whorl; dimensions: breadth 0.98–1.00 mm, height 0.80–0.88 mm (b/h = 1.14–1.23).

Ground color cream to brownish-white, patterned with axial flames of brownish-orange, interrupted by a pale band at mid-body whorl; base of body whorl white.

Dimensions: 16.9 × 5.5 mm (holotype).

Range: Known only from the type locality.

Type material: Holotype NMSA L1078/Tl 168, off Bazaruto Island (21°40'S; 35°25'E), Mozambique, in c. 200–350 m, in a crayfish trap. Paratypes 1 and 2, same data,

in MHNM and private collection J. Rosado respectively. All type specimens appear to have been inhabited by pagurids.

Remarks: Of described species, *Charitodoron rosadoi* shows closest resemblance to *C. agulhasensis*, (Thiele, 1925) of the Agulhas Bank; in particular, the spire whorls of the latter species have a similar profile (although slightly more convex, with a weaker subsutural shoulder) and the color pattern is similar although much more muted; however, in *C. agulhasensis* the early whorls are characterized by much stronger spiral sculpture and the body whorl is much more convex. The ranges of *C. rosadoi* and *C. agulhasensis* are widely separated; the northernmost locality at which the latter species was found during the NMDP was off Mendu Point, Transkei (32°22.6'S; 29°00.4'E, in 250–260 m).

Etymology: Named in honor of its discoverer, Mr. José Rosado.

Charitodoron veneris (Barnard, 1964)

Figures 3–4

Mitromorpha veneris Barnard, 1964:16. Type locality: Off Cape Vidal, Zululand, 80–100 fathoms [≈ 145–180 m].

Charitodoron veneris: Kilburn, 1986:635, fig. 21.

Diagnosis: Whorls convex, suture deep, left side of base of body whorl markedly concave; aperture with greatest width anterior to middle, columella flattened, siphonal notch deep; sculpture of strong, flat-topped spiral lirae, their interstices with coarse collabral threads, feebly indicated on tops of lirae, 8–11 lirae on penultimate whorl, plus a thin thread below suture; white with axial blotches of brownish-orange, markings occasionally very pale. Protoconch breadth 1.08–1.15 mm. Maximum length 24 mm.

Description: Shell fusiform ($b/h = 0.29\text{--}0.30$), with narrow aperture ($a/h = 0.42\text{--}0.49$); whorls convex, with greatest width at basal 0.3 of each whorl, suture deep; left side of base of body whorl markedly concave; base slightly oblique, outer lip slightly foreshortened relative to base of columella. Teleoconch whorls up to 6. Aperture with greatest width anterior to middle; parietal region shallowly concave, columella straight, callus deposit thin; siphonal notch deep and asymmetrically U-shaped; outer lip thin.

Sculptured by flat-topped spiral lirae, their interstices with coarse collabral threads, feebly indicated on tops of lirae. First whorl with 6–9, close-set lirae, becoming more widely-spaced on later whorls (intervals often as wide as lirae); 8–11 lirae on penultimate whorl, plus a thin lira below suture, base of body whorl with 8–11 narrow lirae plus 13–18 somewhat angular and irregular lirae on rostrum.

Protoconch papilliform, 1.7 whorls, smooth with fine axial plicae near termination, termination sharply indicated; breadth 1.08–1.15 mm, height 1.00–1.25 mm ($b/h = 0.92\text{--}1.05$). White with axial blotches of brownish-orange, markings occasionally very pale.

Dimensions: 24.0 × 7.2 mm (largest individual examined).

Type material: Holotype SAMC A8750 (Kilburn, 1986: fig. 21).

Distribution: Continental shelf of Zululand and Natal (Cape Vidal to Amanzimtoti), 98–320 m (fresh shells).

Material examined: (all NM: NMDP unless otherwise stated): ZULULAND: S. E. of Neill Peak (Cunge), 320–340 m, sandy mud (E4023); S. E. of Port Durnford, 310–320 m, glutinous sandy mud (E3190); same locality, 153 m, mud, stones (E4585); off Matigulu River mouth, 300 m, soft mud (E8903); same locality, 145 m, mud, shell rubble (E8791); same locality, 200–220 m, mud, coarse sand (E9024). NATAL: off Tongaat Bluff, 100 m, coarse sand mud (E9817); same locality, 120 m, sandy mud (E9968); off Sheffield Beach, 150 m, muddy sand (E9237); same locality, 110 m, muddy sand (E9303); S. E. of Sheffield Beach, 100–105 m, glutinous gray mud (E5038); N. E. of Umhlanga Rocks, 98 m, fine sand (S256); same locality, 107 m (B6297: A. Connell); off Durban, 130 m,

sandstone gravel, some rocks (D4223); same locality, 95 m, fine, slightly muddy sand (D4059); same locality, 110–120 m, coarse muddy sand (D3816); same locality, 100 m, very fine muddy sand (B5875); same locality, 104 m (B6287: A. Connell); same locality, 104–110 m, muddy sand, broken shells (D4018); same locality, 150 m, sandstone gravel and some sponge, living (D4172); same locality, 100 m, slightly muddy sand (D3898); off Umlaas Canal, 150 m, coarse sand, numerous spatangoids, pebbles (D789); same locality, 150 m, coarse sand (D865); off Amanzimtoti, 260–270 m, medium sand (D1 188); same locality, 115–125 m, medium sand (D1 285).

Remarks: Juveniles of the present taxon were compared (Kilburn, 1986) with the worn and broken holotype of *Mitromorpha veneris*, and found to agree.

Charitodoron veneris is characterized by stronger spiral sculpture than any other Recent member of the genus. There is a distinct but superficial resemblance in shape, sculpture and color pattern to a number of members of the conid genus *Daphnella* Hinds, 1844 (s.l.), but characters of protoconch and outer lip distinguish them at a glance.

Empty shells of *C. veneris* are not rare, although in adults the outer lip is almost always damaged. The foregut anatomy of the only example to be taken alive is presently being examined by Y. Kantor.

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Taxonomic Notes on *Kenyonia* Brazier and *Conopleura* Hinds (Gastropoda: Conoidea)

Donn L. Tippett

10281 Gainsborough Road
Potomac, Maryland 20854, USA

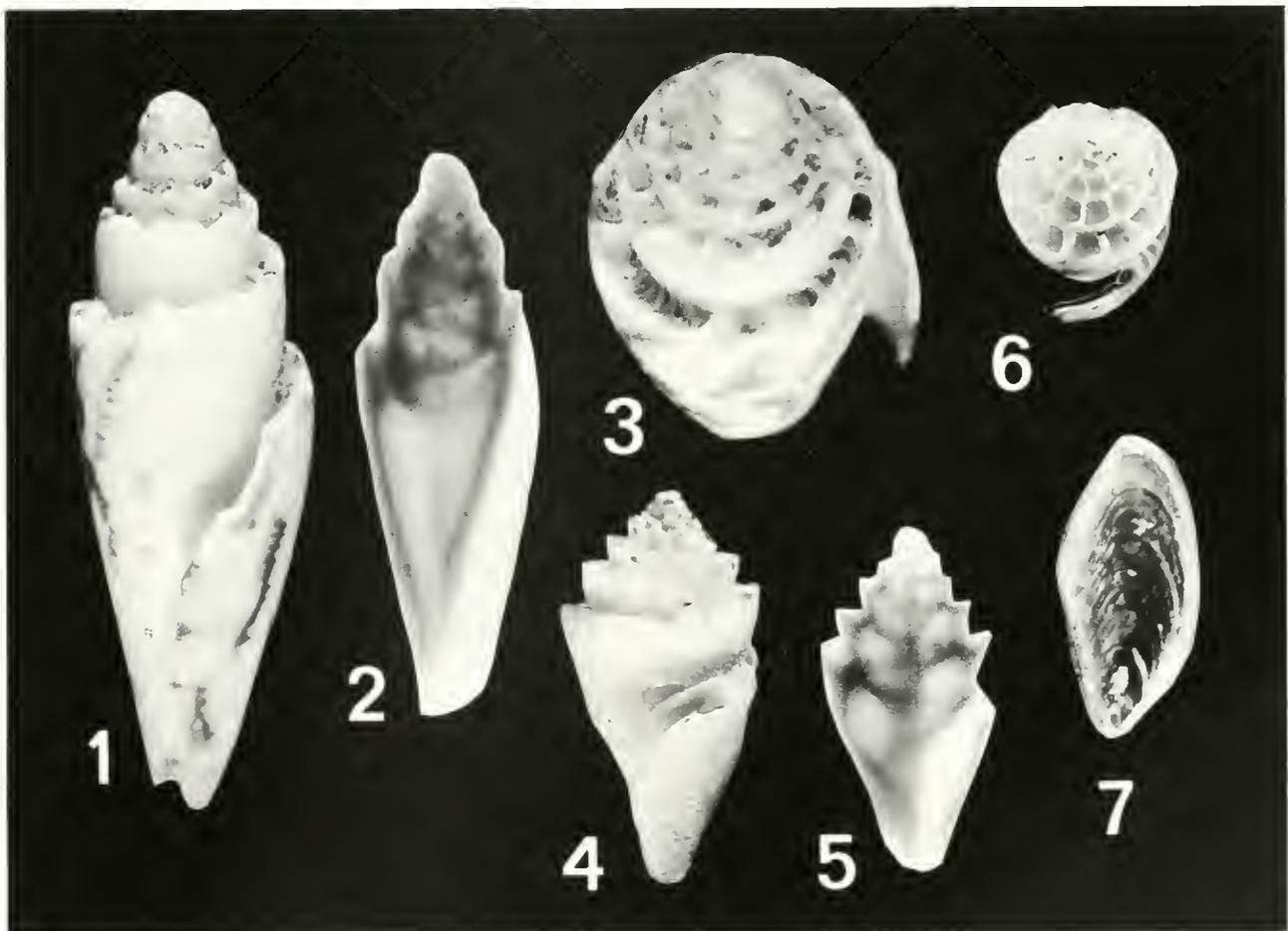
John K. Tucker

Illinois Natural History Survey
Long Term Resource Monitoring
Program-Pool 26
1005 Edwardsville Road
Wood River, Illinois 62095, USA

INTRODUCTION

Kenyonia Brazier, 1896 is a monotypic genus that has been assigned to the families Conidae or Turridae by various authors. Brazier's description of the type species, *Kenyonia pulcherrima*, based on a single, unfigured,

specimen, suggested a morphology so unique that he only tentatively placed the genus as a relative of *Conus*. He stated "This is connected with *Conus* and *Pleurotoma* and may be placed under the former genus for the present until the animal is known." Thought for some time to be lost, the holotype and only known specimen of *K.*



Figures 1-3. *Kenyonia pulcherrima* Brazier, 1896. **1.** Holotype (SAM D6181), New Hebrides, shell length = 27.8 mm. **2.** Radiograph of holotype showing resorption of internal shell structure. **3.** Apical view of holotype showing pitting of shoulder sulcus. **Figures 4-7.** *Conopleura striata* Hinds, 1844. **4.** USNM 869535, Panglao, Bohol Islands, Philippines, shell length = 14.7 mm. **5.** Radiograph showing absence of internal shell resorption. **6.** Apical view showing honeycomb pitting on shoulder sulcus. **7.** Operculum, length = 3 mm.

pulcherrima was located and figured by Zeidler (1985: 71, fig. 2b), who considered its family allocation uncertain. Powell (1966, with query) included *Kenyonia* in the synonymy of *Conopleura*, also a monotypic genus, because he presumed the pits on the shoulder slope reported in the description of *Kenyonia* to be similar to those of *Conopleura* (see figures 3,6.)

Regarded as a turrid unequivocally, the relationships of *Conopleura* within the family have been uncertain. This genus had been grouped with the drilliine genera by older authors such as Fischer (1883) and Tryon (1884). However, Thiele (1929) removed it to Cytharinae (= Mangeliinae), commenting that this assignment was uncertain. Powell (1966) referred *Conopleura* to the subfamily Mangeliinae. A specimen of *C. striata* Hinds, 1844, originally in the junior author's collection (USNM 869535), was discovered to contain an operculum. This finding together with a reevaluation of the shell morphology of this species suggests a different subfamilial affinity. Radiographic examination of the holotype of *Kenyonia* indicates a reclassification of that genus is required. The purpose of this paper is to report the results of these findings.

RESULTS

An X-ray of the holotype of *Kenyonia pulcherrima* (figure 2) clearly demonstrates that it has undergone extensive interior shell remodeling (*sensu* Kohn *et al.*, 1979). Its columella is exceedingly thin. In contrast, a similar X-ray reveals the columella of *Conopleura striata* to be thick and stout (figure 5). The internal portions of body wall in *K. pulcherrima* are also resorbed and thin, while those of *C. striata* are thick. The operculum of *Conopleura striata* (figure 7) is leaf-shaped, with a terminal nucleus.

DISCUSSION

Among the toxoglossate mollusks, extensive interior remodeling of the shell is a derived character state (Kohn, 1990) found in the Conidae (*sensu* Cossmann, 1896 = Conorbinae/Coninae of Taylor *et al.*, 1993). Therefore, *K. pulcherrima* and the genus, *Kenyonia*, belong in the family Conidae since they share this state. The presence of an operculum in *Conopleura striata* supports removal of the genus from Mangeliinae since members of that

subfamily lack opercula. The characteristics of the operculum of *C. striata* are similar to opercula in members of the subfamily Drilliinae. Furthermore, the general shape of the shell and the presence of a subtubular sinus with parietal tubercle are typical of that subfamily. Based on these characters, we transfer the genus *Conopleura* to the subfamily Drilliinae.

ACKNOWLEDGEMENTS

We thank Karen Gowlett-Holmes of the South Australian Museum for loan of the holotype of *Kenyonia pulcherrima*. Marc Moore of the Armed Forces Radiobiology Research Institute, provided the radiographs. Photographic prints were made by Richard Harris.

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Four New Genera for Northeastern Pacific Prosobranch Gastropods

James H. McLean

Los Angeles County Museum of
Natural History
900 Exposition Blvd.
Los Angeles, CA 90007 USA

ABSTRACT

In order to make the names available for use in a faunistic revision of the northeastern Pacific gastropod fauna, four new genera are proposed. Naticidae: new genus *Benthobulbus*, type species *Choristes carpenteri* Dall, 1896. Eulimidae: new genus *Pseudosabinella*, type species *Sabinella bakeri* Bartsch, 1917. Muricidae, Trophoninae: new genus *Ocenotrophon*, type species *Murex (Ocenebra?) painei* Dall, 1903. Buccinidae: new genus *Retimohnia*, type species *Mohnia frielei* Dall, 1891.

Key words: Northeastern Pacific Gastropoda; systematics; new genera.

INTRODUCTION

In the course of preparing a checklist of the northeastern Pacific gastropod fauna, in which all generic assignments are being re-evaluated, I have been unable to reconcile the allocation of a number of species to the genera in which they have previously been placed. The following new genera have been recognized and are here introduced in advance of that work.

Family NATICIDAE Forbes, 1838

Benthobulbus McLean, new genus

Type species: *Choristes carpenteri* Dall, 1896.

Included species: Type species and *Choristes coani* Marinovich, 1975. Marinovich (1977) treated both species in detail and illustrated their radulae; both were further discussed by McLean (1992).

Diagnosis (modified from that of Marinovich, 1977:338, for "*Choristes*" Carpenter): Shell small to medium in size, globose, thin; whorl moderately inflated, spiral sculpture of weak lirae, suture narrowly channeled. Umbilicus narrow to broad, simple. Inner lip slightly thickened, simple, lacking umbilical callus. Parietal callus thin. Operculum chitinous, entirely filling aperture. Radula with monocuspate rachidian, one monocuspate lateral tooth and two monocuspate marginal teeth per half row.

Remarks: McLean (1992:291) assigned the type species of *Choristes* Carpenter in Dawson, 1872, to the synonymy of *Amauropsis islandica* (Gmelin, 1791), leaving two living eastern Pacific species treated by Marinovich without a genus. Marinovich placed *Choristes* next to *Bulbus* Brown in J. Smith, 1839 (type species *Bulbus smithii* Brown in J. Smith, 1839; = *Natica fragilis* Leach, 1819), noting that only *Bulbus* and the two deep-water eastern Pacific "*Choristes*" species had the monocuspate rachidian tooth. Further remarks on the naticid radula are given by Bouchet and Warén (1993:753), who noted that the first marginal of *Bulbus* has three terminal denticles. The unsatisfactory alternatives to placement of these two species in a new genus would be to place them in *Bulbus*, in which the umbilicus is narrow and filled with callus, or in *Euspira* Agassiz, 1838, in which the rachidian is tricuspsate and shells may be larger and thicker.

Family EULIMIDAE Troschel, 1853

Pseudosabinella McLean, new genus

Type and only known species: *Sabinella bakeri* Bartsch, 1917 (synonyms: *Alaba catalinensis* Bartsch, 1920; *Alaba serrana* Smith & Gordon, 1948). See Abbott (1974:126, fig. 1382).

Diagnosis: Shell thin, whorls rounded, with faintly angulate shoulder; suture deep; final lip inflated and produced anteriorly; umbilical chink present; lip scars slightly raised, variable in position; early whorls dark brown, surface of teleoconch tan.

Remarks: Regarding "*Sabinella*" *bakeri*, Warén (1992:189) commented: "This species probably is an eulimid despite having a rather fragile and irregular shell. I have examined a specimen with dried soft parts and it has a ptenoglossate radula, similar to species of *Eulima*. It can provisionally be placed in *Eulima*." *Pseudosabinella bakeri* differs from typical *Eulima* in having rounded whorls, a projecting and flared final whorl and a brown cast to the shell. In contrast, typical species of *Eulima*, as defined by Warén (1984:43; 1992:179), have straight-sided shells, often with color banding. Warén elected not

to provide a genus for this species until the echinoderm host becomes known, but now endorses the need for a genus (pers. comm.). The species is a fairly common and characteristic member of the Californian faunal province, for which the provision of a genus may perhaps provide impetus toward the eventual discovery of its host.

Family MURICIDAE Rafinesque, 1815

Subfamily TROPHONINAE Cossmann, 1903

Ocenotrophon McLean, new genus

Type and only known species: *Murex (Ocinebra?) painei* Dall, 1903. See Radwin & D'Attilio (1976:123, pl. 20, pl. 20, fig. 8).

Diagnosis: Shell small (length about 15 mm), sculpture of numerous lamellar cords of unequal prominence, crossed by sharply raised ribs, forming nodes at intersections; canal short, closed.

Remarks: The generic allocation of the type species has been uncertain, starting with Dall's original assertion that "it resembles one of the austral trophons in miniature." Dall (1921:159, pl. 6, fig. 1) retained it in *Tritonalia* (ICZN rejected name for what is now *Ocinebra* Gray, 1847), evidently because of the sealed canal, which is characteristic of *Ocinebra* but not of trophonine genera. Radwin & D'Attilio (1976:123) followed Dall and retained it in *Ocinebra* but noted that: "The lamellose shell sculpture and short, stout form suggest affinity with the southern trophons (e.g. *T. geversianus* Pallas, 1774); the fused canal implies an ocenebrine relationship; and the radula favors neither of these possibilities." D'Attilio (1980:6) again treated the species and illustrated the radula, concluding that the radula is in fact close to that of *Trophon geversianus*, and reallocated the species in *Trophon*. That allocation is less than satisfactory because *T. geversianus*, type species of *Trophon*, is large, has a dark colored interior, has an open canal and occurs in the intertidal zone of Argentina in the southern hemisphere. Kool (1993) treated the radula and anatomy of *Trophon geversianus*. *Ocenotrophon* differs from species of *Boreotrophon* Fischer, 1884, (in which spiral sculpture is lacking or does not override the axial lamellae) and from species of *Trophonopsis* Bucquoy & Dautzenberg, 1882 (in which spiral sculpture overrides the axial lamellae) in having a thick final lip and in having a shorter, sealed canal rather than a relatively long open canal. Species of *Boreotrophon* and *Trophonopsis* tend to merge at the subgeneric level, whereas *Ocenotrophon painei* stands well apart from all other boreal trophonine species.

Family BUCCINIDAE Rafinesque, 1815

Retimohnia McLean, new genus

Type species: *Mohnia frielei* Dall, 1891. The holotype has been well figured by Kosuge (1972, pl. 13, fig. 3), showing also the characteristic pattern of the operculum.

Included species: *Urosalpinx carolinensis* Verrill, 1884; *Neptunea caelata* Verrill & Smith, 1880; *Sipho glyptus*

Verrill, 1882; *Mohnia clarki* Dall, 1907; *Mohnia micra* Dall, 1907; *Mohnia hondoensis* Dall, 1913; *Mohnia japonica* Dall, 1913; *Mohnia robusta* Dall, 1913; *Mohnia vernalis* Dall, 1913; *Colus (Latisipho) clementinus* Dall, 1919.

Diagnosis: Shell small, fusiform; whorls rounded, canal short, twisted to left; periostracum thick, adherent; dominant sculpture of strong to faint axial ribs on upper half of whorl, becoming obsolete in some species at later growth stages; spiral sculpture of fine to moderate spiral incisions. Initial whorl of protoconch small, not projecting; operculum subspiral, nucleus away from anterior edge.

Remarks: Species grouped in *Retimohnia* have previously been assigned to *Mohnia* Friele in Kobelt, 1878, by Dall (1913), Radwin (1972), and Tiba & Kosuge (1992). Bouchet & Warén (1985:205) only tentatively included in *Mohnia* three northeastern Atlantic species "for which we could not find a better genus, although we are not satisfied with their position here." The latter three species (*Urosalpinx carolinensis* Verrill, 1884, *Neptunea caelata* Verrill & Smith, 1880, *Sipho glyptus* Verrill, 1882) were treated in detail by Bouchet and Warén and are here allocated *Retimohnia*.

The type species of *Mohnia*, *Fusus mohni* Friele, 1877, has been illustrated by Bouchet & Warén (1985:205, figs. 435, 482, 530-531) and by Tiba & Kosuge (1992:1). In species of *Mohnia* (and the subgenus *Tacita* Lus, 1971, as treated by Bouchet & Warén, 1985:210), the whorls are rounded and the suture deep; spiral sculpture predominates, whereas axial sculpture is limited to fine axial riblets that produce a fine clathrate effect in early stages. The characteristic low protoconch was illustrated by Bouchet & Warén (1985).

Axial sculpture of projecting ribs is the principal sculpture in *Retimohnia*, although in *R. clementinus* it may be weak. The protoconch of Pacific species of *Retimohnia* is eroded in specimens I have examined, but is known from the three Atlantic species illustrated by Bouchet & Warén. The operculum is similar in both genera and the genera are evidently related. As is true of the Atlantic species treated by Bouchet & Warén, the Pacific species of both genera occur in deep water, at abyssal depths or the lower continental slope.

Tiba and Kosuge (1992) placed three species in *Mohnia* that are assignable neither to *Mohnia* or *Retimohnia*: "*Chrysodomus*" *brunneus* Dall, 1877, "*C.*" *virens* Dall, 1877, and "*Mohnia*" *siphonoides* Dall, 1913. I retain the first two in the genus *Retifusus* Dall, 1916 (type species *Tritonium jessoense* Schrenck, 1867, Japan), in which they were retained by Dall (as a subgenus of *Plicifusus* Dall, 1902). These two species are not restricted to deep water and have stronger spiral sculpture than species of *Retimohnia*. The operculum of *Retifusus brunneus*, as figured by Tiba & Kosuge (1992, fig. 10) does not have the nucleus sufficiently distant from the margin to be considered comparable to that of *Retimohnia*. Dall (1913: 502) remarked that the species he then described as

Mohnia siphonoides from 987 fathoms off the Pribilof Islands "would certainly be referred to *Tritonofusus*" [now *Colus* Röding, 1798] if it were not for the operculum. I assign the latter species to *Colus*, and assume that Dall mixed the operculum with that of a different species. With the exceptions above and the type species of *Mohnia*, all other species illustrated by Tiba & Kosuge (1992) as *Mohnia*, are here considered typical species of *Retimohnia*. Bouchet & Warén (1985) described and illustrated several typical species of *Mohnia*. New species of *Mohnia* that I have recognized from the northeastern Pacific will be described separately.

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Population Structure, Growth and Fecundity of *Melampus bidentatus* (Say) from Two Regions of a Tidal Marsh Complex in Connecticut

Jessica A. Spelke
Paul E. Fell¹
Lucille L. Helvenston

Department of Zoology
Connecticut College
New London, CT 06320, USA

ABSTRACT

We examined populations of the tidal marsh snail, *Melampus bidentatus* Say, within two regions of the Barn Island Wildlife Management Area in Stonington, Connecticut: a *Spartina patens*-dominated bayfront marsh and a restored impounded valley marsh covered by *Spartina alterniflora* and forbs. On the bayfront marsh, 87% of the snails collected from late May through early November were less than 8 mm in shell length, whereas 99% of the snails on the restored impounded marsh exceeded 8 mm in shell length. Snails from both marsh regions reared in the laboratory on *Spartina alterniflora*/forb turf from the restored impounded marsh grew more rapidly than snails reared on *Spartina patens* turf from the bayfront marsh. In laboratory culture, *Melampus* exhibited a regular lunar (4-week) egg-laying periodicity with cycles of egg-laying occurring in late May, late June and late July. Not only did large snails (9.1–10.0 mm) from the restored impounded marsh deposit nearly twice as many egg masses as small snails (6.1–7.0 mm) from the bayfront marsh, but the egg masses produced by the large snails were significantly larger than those laid by the small snails.

Key words: *Melampus bidentatus*, tidal marsh snail, population structure, growth, fecundity.

INTRODUCTION

Melampus bidentatus Say, 1822, is a pulmonate snail that inhabits the higher elevations of tidal salt marshes along the Atlantic and Gulf of Mexico coasts of North America (Hausman, 1932; Holle & Dincen, 1957; Russell-Hunter *et al.*, 1972). This snail often occurs in large numbers in regions of high marsh covered by *Spartina patens* (Ait) Muhl, 1817 (saltmeadow hay), *Distichlis spicata* (L.) Greene, 1887 (spikegrass) and *Juncus* spp.,

as well as in well-drained regions dominated by stunted *Spartina alterniflora* Loisel., 1807 (saltwater cordgrass). It is frequently a dominant member of the high marsh community (Russell-Hunter *et al.*, 1972; Price, 1980; Hilbish, 1981; Fell *et al.*, 1982; Joyce & Weisberg, 1986).

It has been shown that on a restored impounded tidal marsh dominated by stunted *Spartina alterniflora*, the size of *Melampus bidentatus* is substantially larger than on bayfront, *Spartina patens*-dominated marshes in the same system. On the restored impounded marsh, 83% of the snails exceeded 8 mm in shell length and the modal size was 9.1–10.0 mm. In contrast, on the undisturbed *Spartina patens*-dominated marshes, 95% of the snails were 8 mm in length with a modal size of 6.1–7.0 mm (Fell *et al.*, 1991). Considering specific areas within these marshes, the same difference in the sizes of snails was observed. During the summer of 1990 and the late spring/early summer of 1991, the most abundant size class of *Melampus* within the *Spartina patens* meadows of an undisturbed bayfront marsh was 6.1–7.0 mm, whereas the most abundant size class of this snail in well-drained areas of the restored impounded marsh covered by stunted *Spartina alterniflora* and forbs (herbaceous plants other than grasses, rushes and sedges) was 9.1–10.0 mm. Because of this size difference, the shell-free biomass of *Melampus* in the first area was only about half that in the second, even though snail density was somewhat higher (Peck *et al.*, 1993). Such size differences could be due in large part to quantitative and/or qualitative differences in the food resources available in the two marsh regions (Rietsma *et al.*, 1988; Peck *et al.*, 1993). However, the size differences could also result to some extent from greater size specific predation (Vince *et al.*, 1976; Joyce & Weisberg, 1986) and/or factors that promote greater longevity of snails (Crowe & Covich, 1990) on the restored impounded marsh. *Melampus* feeds extensively on detritus derived from the marsh grasses but also consumes algae and animal tissues (Rietsma *et al.*, 1982; Thompson, 1984). One objective of the present study was to examine growth of *Melampus* from the

¹ To whom correspondence should be addressed.

Spartina patens meadows of an undisturbed bayfront marsh and from stunted *Spartina alterniflora*-dominated regions of the restored impounded marsh when samples from both groups of snails were maintained in the laboratory on marsh turf from these two areas. *Melampus* is a simultaneous hermaphrodite with an ovotestis. It deposits egg masses on the surface of the marsh peat, as well as on the stems and leaves of grasses and on the shells of other *Melampus*. These egg masses are flattened hemispheres about 1 to 2 mm in diameter and approximately 0.5 mm high. Each egg mass may contain from about 500 to more than 1200 eggs (Hausman, 1932; Apley, 1970; Russell-Hunter *et al.*, 1972). A preliminary study (Balboni-Tashiro *et al.*, 1985) indicates that *Melampus* exhibits age (size) specific fecundity. Older snails produce more egg masses containing more eggs. A second objective of this study was to compare egg mass deposition by large *Melampus* from stunted *Spartina alterniflora*-dominated regions of the restored impounded marsh and by smaller snails from the *Spartina patens* meadows of an undisturbed bayfront marsh.

MATERIALS AND METHODS

The study areas are part of the Barn Island Wildlife Management Area in Stonington, Connecticut, which is located in the southeastern corner of the state (figure 1). The marsh complex consists of a series of valley marshes that border Little Narragansett Bay. One study area was the westernmost valley marsh which was impounded in 1946–1947 in an attempt to create waterfowl habitat. This marsh (figure 1, IP) subsequently converted to a *Typha angustifolia* L., 1753 (narrow-leaved cattail)-dominated brackish marsh. In 1978 a 5 ft.-diameter culvert was placed in the impoundment dike, and in 1982 a 7 ft.-diameter culvert was added. As a result of the re-established tidal exchange, typical tidal salt marsh angiosperms have recolonized much of the area, with stunted *Spartina alterniflora* and forbs providing most of the plant cover (Sinicrope *et al.*, 1990). The other study area was an undisturbed *Spartina patens*-dominated bayfront marsh situated below the westernmost impoundment (Wequetequooc Cove marsh, figure 1, WC).

In order to examine the size structure of *Melampus* populations in the *Spartina patens* meadows of the bayfront marsh and stunted *Spartina alterniflora*-dominated areas of the restored impounded marsh, all of the snails contained within two randomly placed 0.25m² quadrats were collected from each marsh area at about 30-day intervals from late May until early November. Shell lengths were measured to the nearest 0.1 mm with vernier calipers.

For experimental studies, small (6.1–7.0 mm) *Melampus* were collected from *Spartina patens*-dominated regions of the bayfront marsh and large (9.1–10.0 mm) snails were gathered from an area of the restored impounded marsh covered by stunted *Spartina alterniflora* and forbs. The snails were maintained in the laboratory on clipped marsh turf. They were placed in covered 11

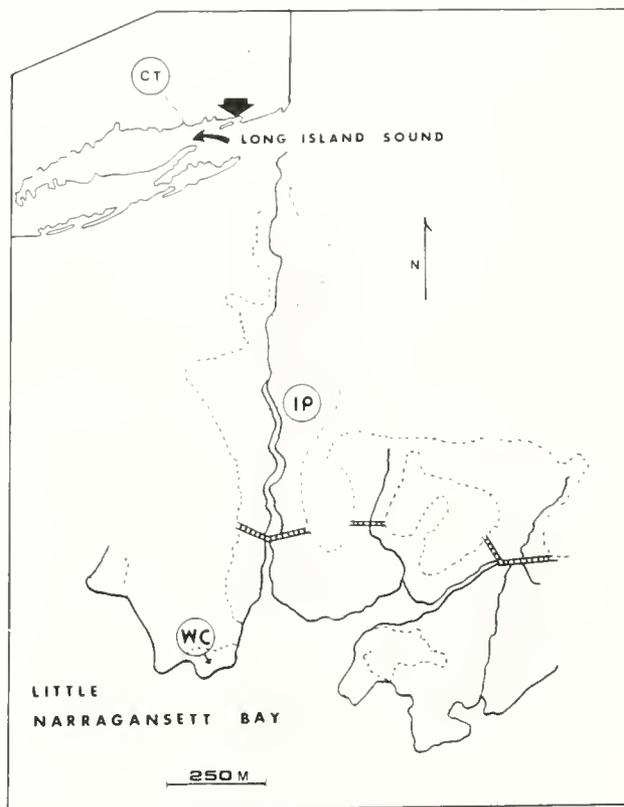


Figure 1. Map of the western portion of the tidal marsh complex within the Barn Island Wildlife Management Area in Stonington, Connecticut (short vertical arrow on inset at upper left). IP marks the collecting site on the restored impounded marsh and WC indicates the location of the Wequetequooc Cove Marsh.

cm-diameter finger bowls containing a piece of turf approximately 6 × 4 × 1.5 cm situated on a 9 cm disc of Whatman No. 1 filter paper moistened with 15 ppt sea water. In most cases, 8 snails were placed in each bowl. The cultures were kept at about 21°C and exposed to natural photoperiod. The filter paper and bowls were changed every 2 days and the marsh turf was replaced every 6 days.

For growth experiments, some of the snails from each marsh region were placed on *Spartina patens* turf taken from the bayfront marsh and others were cultured on *Spartina alterniflora*/forb turf from the restored impounded marsh. Each treatment was replicated 5 times (a total of 40 snails per treatment). The snails were measured to the nearest 0.1 mm with vernier calipers at monthly intervals. The experiments were begun 8 June 1992 and continued until 1 November 1992.

In order to quantify egg mass deposition, snails from each of the two marsh regions were cultured separately on *Spartina patens* turf from the bayfront marsh (15 snails per bowl in 1991 and 8 snails per bowl in 1992). Cultures were initiated 23 May 1991 and 20 May, 10 June and 25 June 1992. Each set of cultures was repli-

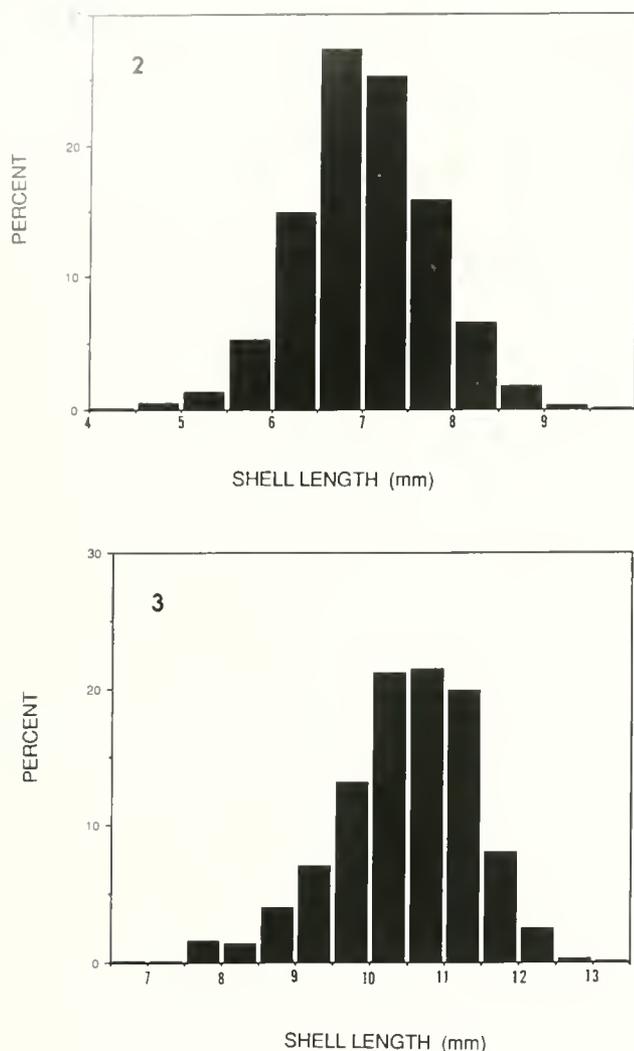


Figure 2-3. Size-frequency distribution of *Melampus bidentatus*. 2. In *Spartina patens* meadows of the bayfront marsh during the reproductive period (20 May to 3 August 1992). N = 1024. 3. In regions of the restored impounded marsh covered by stunted *Spartina alterniflora* and forbs during the reproductive period (20 May to 3 August 1992). N = 702.

cated 3 times. Newly deposited egg masses were removed and counted each day through 31 July.

RESULTS

On the bayfront marsh, 87% of the snails collected throughout the study were less than 8 mm in shell length, and the most abundant size class was 6.6-7.5 mm. In contrast, 99% of the snails on the restored impounded marsh exceeded 8 mm in shell length, and 10.6-11.5 mm was the most abundant size class. During the reproductive period, the minimum length of *Melampus* on the bayfront marsh was 4.1-4.5 mm and the most abundant size class was 6.6-7.5 mm (figure 2). Minimum length of snails from the restored impounded marsh during the reproductive period was 6.6-7.0 mm, and less than 1%

of the snails were of this size. The majority of snails (61%) were 10.1-11.5 mm in shell length (figure 3). Young-of-the-year snails were not observed on either marsh region during the study.

Snails from both marsh regions reared in the laboratory on *Spartina alterniflora*/forb turf from the restored impounded marsh grew more rapidly than snails reared on *Spartina patens* turf from the bayfront marsh (Table 1). Mann Whitney tests with values of tied rank (Zar, 1974) indicated that the difference in growth of *Melampus* from the bayfront marsh on turf from the two marsh regions was statistically significant ($U = 0$, $df = 2$, $p = 0.01$) as was the difference in growth of snails from the restored impounded marsh on these substrata ($U = 23.5$, $df = 2$, $0.05 > p > 0.02$).

In laboratory culture, *Melampus* exhibited a regular lunar egg-laying periodicity with cycles of egg-laying occurring in late May, late June and late July (figure 4). Egg-laying was usually initiated at the time of the full moon and continued for about 9 to 14 days. Deposition of egg masses ceased shortly before the new moon, and little or no egg-laying was observed between the new moon and subsequent full moon. Aggregation of snails was noted 2-3 days before egg-laying began. Egg masses were deposited most commonly on the surface of the peat, but they were also attached to the stems of *Spartina patens* and occasionally to the shells of other *Melampus*.

Egg-laying by *Melampus* collected from the bayfront marsh on 20 May 1992 was not in synchrony with that of other snails gathered from the two marsh regions. For this group, egg-laying began 9 June, six days before the full moon, and continued at a low rate until 25 June, ten days past the full moon. A second cycle of egg-laying was initiated 6 July, eight days before the full moon, and lasted until 15 July.

The snails from the restored impounded marsh deposited nearly twice as many egg masses as those from the bayfront marsh (Table 2). During the summer of 1992, large snails (9.1-10.0 mm) from the restored impounded marsh maintained under laboratory conditions produced an average of 128 egg masses per animal during the reproductive season, whereas small snails (6.1-7.0 mm) from the bayfront marsh deposited an average of 63 egg masses per animal over the same span of time. Analysis of the data from the third spawning period, for which there were three different sets of snails from each marsh region, indicated that the difference in the number of egg masses deposited by the larger snails of the restored impounded marsh and the smaller snails of the bayfront marsh is statistically significant (two-sample t-test: $t = 2.9$, $df = 15$, $p = 0.012$).

The mean size of egg masses produced by snails from the restored impounded marsh was $3.3 \text{ mm} \pm 0.42 \text{ mm SD}$ ($N = 31$) and that of snails from the bayfront marsh was $2.5 \text{ mm} \pm 0.39 \text{ mm SD}$ ($N = 28$). Using a two-sample t-test, the difference was found to be highly significant ($t = 7.58$, $df = 56$, $p < 0.0001$).

During 1991, large snails from the restored impounded marsh, maintained at a density of 15 snails per bowl,

Table 1. Growth (increase in shell length) of *Melampus bidentatus* (Say) from a restored impounded marsh (IP) and an undisturbed bayfront marsh (Wequetequock Cove Marsh, WC) on turf from these two marshes in the laboratory. The experiment extended from 8 June to 1 November 1992.

Origin of snails	Type of marsh turf	Mean initial size (mm) ± SD	Mean size		% increase
			(mm) ± SD at end of experiment	Mean growth (mm)	
WC	<i>S. patens</i> (WC)	6.6 ± 0.27	7.7 ± 0.35	1.1	17
	<i>S. alterniflora</i> /forbs (IP)	6.6 ± 0.28	8.2 ± 0.54	1.6	24
IP	<i>S. patens</i> (WC)	9.6 ± 0.20	10.2 ± 0.37	0.6	6
	<i>S. alterniflora</i> /forbs (IP)	9.7 ± 0.29	10.5 ± 0.46	0.8	8

deposited an average of 96 egg masses per animal during the first cycle of egg-laying and the study was terminated before the cycle was completed. In contrast, during 1992, large snails cultured 8 per bowl produced an average of no more than 71 egg masses per animal for any cycle. The relationship between snail density and egg-laying should be systematically investigated.

DISCUSSION

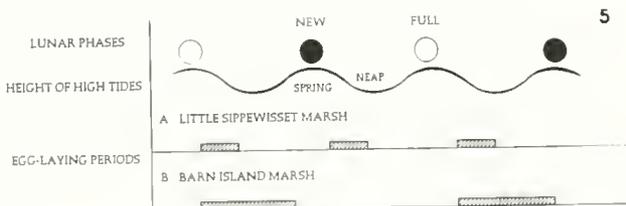
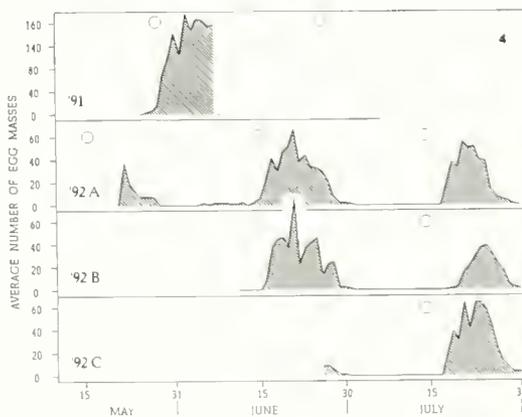
On the Barn Island marshes in southeastern Connecticut, *Melampus* exhibits a clear lunar periodicity in egg-laying. Egg mass deposition begins at about the time of the full moon and continues until shortly before the time of the following new moon. This pattern of egg-laying differs from that described for snails at the Little Sippewisset Marsh in Falmouth, Massachusetts (Cape Cod). Several studies conducted over a 10-yr. period at that location have demonstrated a semilunar pattern of egg-laying by *Melampus* (Apley, 1970; Russell-Hunter *et al.*, 1972;

Price, 1979). The semilunar periodicity is well defined with egg-laying normally taking place for about 4 days beginning on about the second day following a new or full moon (figure 5). Spring tides that occur at these times often immerse the newly deposited egg masses and cover them with a layer of fine detritus that keeps the eggs/embryos moist during the period of neap tides (Russell-Hunter *et al.*, 1972).

The pattern of egg-laying described here does not appear to be an artifact resulting from laboratory con-

Table 2. Production of egg masses by *Melampus bidentatus* (Say) in the laboratory. Small snails were collected from an undisturbed bayfront marsh (Wequetequock Cove Marsh, WC) and large snails were gathered from a restored impounded marsh (IP).

Date of collection	Spawning period	Mean number of egg masses/snail ± SD		Ratio
		9.1-10.0 mm (IP)	6.1-7.0 mm (WC)	
23 May 1991	1	96 ± 6.0	44 ± 1.7	2.2
20 May 1992	1	10 ± 6.1	0	
	2	69 ± 9.3	18 ± 7.0	
	3	50 ± 7.4	41 ± 7.1	
	all	129 ± 22.7	58 ± 14.0	2.2
10 June 1992	2	70 ± 6.6	39 ± 3.1	
	3	37 ± 11.0	32 ± 2.7	
	all	107 ± 17.4	71 ± 4.0	1.5
25 June 1992	3	56 ± 2.7	31 ± 13.5	1.8
All cultures		388	204	1.9



Figures 4-5. Egg-laying by *Melampus bidentatus*. **4.** Snails from the restored impounded marsh in relation to the occurrence of full moons. Each point represents the average number of egg masses produced by three bowls of snails. Cultures were initiated 23 May 1991 and 20 May, 10 June and 25 June 1992. **5.** Snails on the Little Sippewisset Marsh in Falmouth, Massachusetts (after Russell-Hunter *et al.*, 1972) and on the Barn Island marshes in Stonington, Connecticut in relation to phases of the moon and the relative height of high tides (marsh submergence).

ditions. First, egg-laying by *Melampus* maintained in the laboratory follows the same rhythm as that of field populations of this snail (Russell-Hunter *et al.*, 1972 and our unpublished observations). Second, cultures of *Melampus* were initiated a few days before both new and full moon phases, and the pattern of egg-laying was the same in both cases: egg-laying began at the time of the full moon but not at the time of the new moon. It would be interesting to simultaneously compare egg-laying by *Melampus* from Barn Island and Cape Cod under identical laboratory conditions.

How the timing of reproduction by these animals is set is unknown. When *Melampus* spawns with a lunar periodicity, each spawning cycle is about 2–3 times longer than when it spawns with a semilunar rhythm and the period between spawning cycles is nearly doubled. Evidently more eggs are produced per spawning cycle and more time may be required to recover before commencing another cycle of egg-laying.

Melampus is a largely terrestrial snail; its marsh habitat may be unsubmerged for more than 95% of the time. However, this snail possesses an aquatic veliger larva (Russell-Hunter *et al.*, 1972). Although egg-laying is usually initiated during spring tides both on the Little Sippewisset and Barn Island marshes, flooding of the marsh surface is not required for egg-laying to occur. On the other hand, the hatching of veligers and their subsequent settlement back on to the marsh depend upon inundation of the marsh during spring tides (Russell-Hunter *et al.*, 1972). The observed differences in the patterns of egg-laying by the two populations of *Melampus* do not appear to necessarily affect later stages in the life cycle of the snail. For example, larval hatching may occur from about 10 days to 24 or more days after egg mass deposition, depending upon tidal submergence (Russell-Hunter, 1972).

The minimal reproductive size of *Melampus* is from about 5 mm shell length (Apley, 1970) to 5.8 mm shell length (Balboni-Tashiro *et al.*, 1985). However, not all snails of this minimal size reproduce (Balboni-Tashiro *et al.*, 1985). Most of the *Melampus* collected from both marsh regions at Barn Island were greater than 6 mm in shell length.

In the present study, *Melampus* maintained in laboratory culture produced an average of from 63 to 128 egg masses per animal during the reproductive season, depending upon snail size. On the other hand, Russell-Hunter *et al.*, (1972) reported that under their laboratory conditions, snails taken from the Little Sippewisset Marsh produced on average only 39 egg masses during the reproductive period. This is consistent with the observation that egg-laying by the Cape Cod population of *Melampus* is typically restricted to fewer days compared to the populations of this snail at Barn Island. On Cape Cod, there are about 12 to 16 days of egg-laying by *Melampus* each year (Russell-Hunter *et al.*, 1972), whereas at Barn Island snails deposit egg masses during about 20 to 30 days within the reproductive period. However, the snails normally aggregate prior to mating and

egg-laying (Apley, 1970; Russell-Hunter *et al.*, 1972); and the number of egg masses produced may also be influenced by snail density in laboratory cultures and under field conditions.

Not only did the large snails from the restored impounded marsh at Barn Island deposit more egg masses than the smaller snails from the nearby bayfront marsh, but the egg masses were significantly larger. In gastropods for which size specific fecundity has been well documented, the larger egg capsules/masses produced by large individuals contain more eggs than the smaller egg capsules/masses produced by small individuals (Hendler & Franz, 1971; Spight & Emlen, 1976). In addition, a preliminary study by Balboni-Tashiro *et al.* (1985) has shown that older (larger) *Melampus* deposit more eggs per mass than younger (smaller) snails. Therefore even though egg numbers were not determined in the present study, it seems highly probable that large *Melampus* from the restored impounded marsh produced more eggs than smaller ones from the bayfront marsh, indicating that fecundity is size specific for this species. However, interpretation of the data is complicated by the fact that the different sized snails were taken from different marshes. Although snails from the two marshes were maintained on the same substratum (food resources) in the laboratory, an influence of prior nutrition on reproduction beyond a larger size, resulting from a more rapid growth rate, cannot be ruled out (Spight & Emlen, 1976).

Differences in growth rates of snails in the laboratory on turf from the two marsh regions were significant. *Melampus* from both marsh regions grew more rapidly on *Spartina alterniflora*/forb turf from the restored impounded marsh than on *Spartina patens* turf from the bayfront marsh. These results are consistent with the hypothesis that the snails on the restored impounded marsh grow more rapidly than the snails on the undisturbed bayfront marsh because of a larger/better food resource. It would be interesting to determine which potential foods are being used by *Melampus* on the two marshes by examination of gut and fecal pellet contents (Thompson, 1984). It is well documented that *Melampus* prefers old detritus with a low phenolic content and grows more rapidly on this type of diet (Rietsma *et al.*, 1988). However, other factors, such as the structural characteristics (toughness and texture) of the food and/or its moisture content, may also importantly affect palatability. Finally, large microbial populations are often found on detritus particles and they constitute a rich energy source for organisms capable of removing them (Odum & De La Cruz, 1967).

In conclusion, snails inhabiting a restored impounded tidal marsh in southeastern Connecticut are larger, grow more rapidly and produce more eggs than snails occupying an undisturbed bayfront marsh within the same marsh complex. The rapid growth and high fecundity of *Melampus* on the restored impounded marsh indicate that the marsh has become a highly favorable habitat for this snail and provide additional evidence that restoration efforts have been successful.

ACKNOWLEDGMENTS

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News and Notices

SMITHSONIAN FUNDS FOR MALACOLOGY STUDENTS

The Division of Mollusks, Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution announces the availability of the Houbrick-Rosewater Fellowship (up to \$750) to be awarded to graduate students of systematic malacology. This award provides support for students conducting systematic studies of Mollusca (leading to publication) who require access to collections and libraries of the Division of Mollusks, National Museum of Natural History. Funds can be used for travel, subsistence, and research costs. Inter-

ested students should submit a succinct proposal (1–2 pages), including budget, with indication of any matching funds, and a support letter from faculty advisor(s). The application deadline is March 15, 1995. Award(s) will be announced on April 15, 1995. Applications should be sent to:

Dr. Clyde F. E. Roper
Division of Mollusks/NHB stop 118
National Museum of Natural History
Smithsonian Institution
Washington, DC 20560 USA

THE AMERICAN MALACOLOGICAL UNION ANNUAL MEETING

The 1995 meeting of the American Malacological Union will be held at the University of Hawaii at Hilo, in Hilo, Hawaii, June 8–12, 1995 (arrive Hilo June 7—leave June 13). The meeting is a celebration of islands, beginning with a keynote address by Hawaii's well known naturalist and photographer Bill Mull, who will describe with tales and slides some of the wonders of Hawaiian animals and plants, and especially land shells. Three symposia are scheduled: biogeography convened by Gustav Paulay, cephalopods convened by Richard Young, and conservation convened by Elaine Hoagland. Plan to contribute a paper and/or poster for other sessions. The annual auction of books and shells will be exciting. Social events include the President's Welcome, a sunset reception at Lyman House Museum, a barbecue, and final banquet.

Field trips on June 11 include tidepools and snorkeling, lava tubes, rainforest, kipukas (oases with snails on Mauna Kea), and the volcano.

Accommodation will be in University of Hawaii at Hilo

dormitories on campus with a meal plan. Accommodation will run \$25 per night per bed in a four room suite, and the meal plan, covering most meals and coffee breaks from arrival June 7 to leaving June 13 will be about \$150. If you prefer a hotel, you may make reservations from a list with rates to be included with registration forms. Van service to and from the airport will be provided. Special day trips for accompanying guests and family are scheduled.

Please indicate on a postcard, by FAX or e-mail if you wish to receive a registration form and plan to attend:

E. Allison Kay
President, AMU
Department of Zoology
University of Hawaii
2538 The Mall
Honolulu, Hawaii 96822
Phone (808) 956-8620
FAX (808) 956-8612
E-Mail: eakay@zoogate.zoo.hawaii.edu

SYMPOSIUM ON CONSERVATION AND MANAGEMENT OF FRESHWATER MUSSELS

October 16–18, 1995. Symposium on *The Conservation and Management of Freshwater Mussels II: Initiatives for the Future*. Embassy Suites Hotel, St. Louis, Missouri. Sessions devoted to endangered and at-risk species, re-

location and refugia, reproduction and propagation, sampling methods, the mussel industry, and developing partnerships in preservation. For information, contact: Kurt Welke, Wisconsin Department of Natural Resources, 111 West Dunn St., Prairie du Chien, WI 53821, USA. Phone (608) 326-0233.

INSTRUCTIONS TO AUTHORS

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

Manuscripts: Each original manuscript and accompanying illustrations should be submitted in triplicate. Text must be typed on one side of 8½ × 11 inch white paper, double spaced throughout (including literature cited, tables and figure captions), with at least 1 inch of margin on all sides. All pages must be numbered consecutively. If printed on a word processor, the right margin should be ragged rather than justified. Authors should follow the recommendations of the *Council of Biology Editors Style Manual*, which is available from the Council of Biology Editors, Inc., 9650 Rockville Pike, Bethesda, MD 20814, U.S.A. The first mention of a scientific name in the text should be accompanied by the taxonomic authority, including year. Latin names and words to be printed in italics must be underlined; leave other indications to the editor. Metric and Celsius units are to be used.

The sequence of sections should be: title page, abstract page, introduction, materials and methods, results, discussion, acknowledgments, literature cited, tables, figure captions, figures. The title page should include the title, author's name(s) and address(es). The abstract page should contain the title and abstract, which should summarize in 250 words or less the scope, main results and conclusions of the paper. The abstract may be followed by a maximum of 5 key words. All references cited in the text must appear in the literature cited section and vice versa. In the literature cited section, all authors must be fully identified and listed alphabetically. Follow a recent issue of THE NAUTILUS for bibliographic style, noting that journal titles must be unabbreviated. Information on plates and figures should be cited only if not included in the pagination. Tables must be numbered and each placed on a separate sheet. A brief legend must accompany each table. Captions for each group of illustrations should be typed on a separate sheet and include a key to all lettered labeling appearing in that group of illustrations.

All line drawings must be in black, high quality ink, clearly detailed and completely labeled. Photographs must be on glossy, high contrast paper. All figures are to be consecutively numbered (figs. 1, 2, 3, NOT figs. 1a, 1b, 1c, NOR plate 1, fig. 1 . . .). Illustrations must be arranged in proportions that will conform with the width of a page (6¼ inches or 171 mm) or a column (3¼ inches or 82 mm). The maximum size of a printed figure is 6¼ by 9 inches or 171 by 228 mm. All illustrations must be fully cropped, mounted on a firm, white backing, numbered, labeled and camera ready. The author's name, paper title and figure number(s) should appear on the back. Original illustrations must be between one and two times the desired final size. It is the author's responsibility that the line weight and lettering are appropriate for the desired reduction. Original illustrations will be returned to the author if requested. Color illustrations can be included at extra cost to the author.

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Museum of Comparative Zoology
Harvard University
Cambridge, MA 02135

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

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News and Notices

WESTERN SOCIETY OF MALACOLOGISTS ANNUAL MEETING

The twenty-eighth Annual Meeting of the Western Society of Malacologists will be held at the Resort at Chena Hot Springs, near Fairbanks, Alaska, from June 2 to June 6, 1995. The agenda will include contributed papers on all areas of molluscan studies, freshwater, marine, terrestrial, living and fossil. Symposia on ecology and paleoecology are being organized with the help of Howard Feder and David Hopkins. Also in the planning stages

are an auction, reprint sale, and banquet. The University of Alaska Museum Aquatic Collection will be available for visitors before and after the meeting. For more information contact WSM President, Nora R. Foster, University of Alaska Museum, 907 Yukon Drive, Fairbanks, Alaska 99775 USA. Phone: (907) 474-9557. E-Mail: FYA-QUA@aurora.alaska.edu. Or contact Conference and Special Events, 117 Eielson Building, University of Alaska Fairbanks, Fairbanks, Alaska 99775.

INDO-PACIFIC MALACOLOGICAL MEETING PRELIMINARY NOTICE

The Council of the Malacological Society of Australasia has agreed to hold an international meeting on mollusks of the Indo-Pacific region in Perth, Western Australia, in January or February 1997. This notice is intended to alert malacologists worldwide of the upcoming meeting and to solicit suggestions for possible symposia; all suggestions of possible topics are welcome. The meeting will

include all aspects of malacology, including mollusks of marine, freshwater and terrestrial habitats. If sufficient interest develops a post-conference field trip to the southwest of Western Australia can be arranged. As plans develop the conference will be advertised in malacological journals. To be placed on the list for direct receipt of future notices please write: Dr. F. E. Wells, Western Australian Museum, Perth 6000, Western Australia (Fax: 61-9-328-8686).

NEW MOLLUSK JOURNAL LAUNCHED

The Malacological Society of Australia has a history of over forty years of service to the study of mollusks in Australia, and has published the *Journal of the Malacological Society of Australia* since 1957. Like most scientific societies, including AMSA, the Malacological Society has been continuously evolving. In recent years there has been increased emphasis and membership of the Society in New Zealand and countries to the north of Australia. In recognition of its changing role the Society changed its name to the Malacological Society of Australasia at the annual general meeting held in Sydney in November 1993.

With the change in name and emphasis of the Society a re-examination of the role of the *Journal of the Malacological Society of Australia* was appropriate. After extensive discussion within the MSA Council it was decided to broaden the content of the *Journal* and change its name to *Molluscan Research* to reflect the modifications. The cover and pages have been redesigned. To

ensure continuity, the volume numbering remains the same.

Theoretical papers considering any molluscan topic are welcome for consideration for publication in *Molluscan Research*. Papers considering specific geographical areas or new taxa should be restricted to the Indo-West Pacific region, which includes all of Australia. The Journal has previously been an annual publication, but if sufficient quality papers are available, *Molluscan Research* will appear twice a year.

The first issue of *Molluscan Research* has been published in early November, 1994.

For further information about *Molluscan Research* please contact the editor, Dr. F. E. Wells, Western Australian Museum, Perth, WA 6000, Australia. For information about the Malacological Society of Australasia contact the Department of Malacology, Australian Museum, P.O. Box A285, Sydney south, NSW 2000, Australia

Florida as a Biogeographic Boundary: Evidence from the Population Genetics of *Littorina irrorata*¹

Nathan S. Dayan

Graduate Program in Marine Biology
Grice Marine Biological Laboratory
205 Ft. Johnson, Charleston, SC 29412
USA

Robert T. Dillon, Jr.²

Department of Biology
College of Charleston
Charleston, SC 29424 USA

ABSTRACT

The marsh periwinkle, *Littorina irrorata* (Say, 1822), ranges from New York to Texas with an apparently large disjunction around southern Florida. We examined gene frequencies at eight polymorphic enzyme loci in populations from Virginia, South Carolina, Atlantic Florida, Gulf Florida, and Louisiana. The within-population deviation from Hardy-Weinberg expectation was small at all loci examined ($F_{is}=0.049$). Small but significant gene frequency differences among populations were detected at four loci, indicating some isolation by distance. Hierarchical gene diversity analysis suggested, however, that very little of the population divergence present ($F_{ST}=0.033$) is attributable to a division between coasts ($F_{CB}=0.004$). Nei genetic distances calculated between pairs of sites sharing the same coast were comparable to such distances between Atlantic and Gulf pairs. Thus we find no evidence that the Florida peninsula constitutes a significant barrier to *L. irrorata*, in spite of the apparently extensive gap in its range. We offer three hypotheses, not mutually exclusive: that the barrier is not real, that it was breached in the not-too-distant past, or that balancing selection may be ongoing to hold polymorphisms constant at multiple enzyme-encoding loci simultaneously.

Key words: Gastropoda, electrophoresis, allozymes, range disjunction, balancing selection

INTRODUCTION

Shallow, protected regions along the southern Atlantic coast of the United States and the northern coast of the Gulf of Mexico are characterized by temperate climate, depositional environment, and the dominant salt marsh cordgrass, *Spartina*. The molluscan faunas of these two regions are described as "Carolinian" (Rehder, 1954; Coomans, 1962), sharing over 60% of their shallow water gastropod species (query to database of Rosenberg, 1993). However, striking climatic and geological variation along

the Florida peninsula seems to impose a biogeographic boundary between these regions (Briggs, 1974). Due to tropical conditions, mangroves replace salt marshes in protected bays and estuaries around 27°–29° N latitude (Kangas & Lugo, 1990). This transition occurs between Cedar Key and Tampa Bay on the Gulf coast of Florida, and between St. Augustine and Cape Canaveral on the Atlantic coast. Coralline sands become the dominant sediment type along south Florida coasts, replacing terrigenous silt and mud.

Scheltema (1989) surveyed the ranges of 88 mesogastropod and neogastropod species, dividing the western Atlantic coast into eight regions from Arctic Canada to Brazil. He reported that 58 of 72 species inhabiting his "region IV" (Beaufort, North Carolina to Miami, Florida) also occurred in his "region V" (Gulf of Mexico). However, 18 of the 58 shared species did not occur in Scheltema's "region VI", encompassing the southern tip of Florida and the Greater Antilles. For at least these 18 species (including such common species as *Fasciolaria hunteria*, *Polinices duplicatus*, and *Littorina irrorata*) Florida would seem to constitute a potential barrier. This general distributional pattern extends beyond the near-shore molluscan fauna to include many other elements of the flora and fauna of the southeastern United States.

Recent molecular techniques have commonly detected substantial genetic differentiation between animal populations of the southern Atlantic coast and those of the northern Gulf of Mexico. Most of the 19 such species for which mtDNA surveys have been completed, including horseshoe crabs, toadfish, black sea bass, diamondback terrapins, and seaside sparrows, show distinct differentiation associated with the Florida peninsula (Avisé, 1992). To this list could be added the coastal North American tiger beetle, *Cicindela dorsalis*, where mitochondrial DNA sequence data were used to assign four subspecies to either an Atlantic coastline lineage or a Gulf of Mexico coastline lineage (Vogler & DeSalle, 1993). Significant divergence at enzyme-encoding loci has been detected between Atlantic and Gulf populations of such diverse taxa as the sea anemone, *Bunodosoma cavernata* (McCommas, 1982), and the marsh crab *Sesarma reticulatum* (Felder & Staton, 1994).

¹ Contribution number 120 from the Grice Marine Biological Laboratory

² Address for Correspondence



Figure 1. The range of *Littorina irrorata* (shaded), showing sample sites for the present study.

No Florida disjunction is apparent in the range of the American oyster, *Crassostrea virginica*, nor was any divergence in allozyme frequencies detected by Buroker (1983) in his survey of 19 populations from Massachusetts to Texas. Thus the report of substantial mtDNA divergence between Atlantic and Gulf oyster populations by Reeb and Avise (1990) was greeted with unusual interest. Karl and Avise's (1992) re-examination of the issue using restriction fragment length polymorphisms in anonymous single-copy nuclear genes confirmed the mtDNA results, suggesting that Florida does, in fact, constitute a barrier to the dispersal of oysters. Karl and Avise went on to propose that the similarity in allozyme frequencies reported by Buroker might result from balancing selection at multiple enzyme-encoding loci. The importance of natural selection to the preservation of enzyme polymorphism has been a central question in evolutionary biology for over 25 years (Lewontin, 1991). Thus if the findings of Karl and Avise can be generalized beyond oysters, there will be implications for our understanding of evolution as a whole.

The purpose of this study is to document divergence in allozyme frequency between Atlantic and Gulf populations of an heretofore genetically unsurveyed inter-

tidal mollusk, the marsh periwinkle *Littorina* (or *Littoraria*) *irrorata* (Say, 1822). The snail is primarily an inhabitant of salt marshes dominated by the cord grass *Spartina alterniflora*, leaving the marsh surface with the incoming tide to climb the vegetation. It ranges from Jamaica Bay, Long Island, New York (Jacobson, 1965) to Port Isabel, Texas (Bequaert, 1943), with a disjunction around southern Florida (Figure 1). As such it would seem an excellent candidate for an attempt to confirm the Karl and Avise phenomenon.

Littorina has been the object of considerable population genetics research worldwide, with much effort directed toward questions of systematics (Ward & Warwick, 1980; Maestro *et al.*, 1991; Boulding *et al.*, 1993; Zaslavskaya *et al.*, 1992). Other workers have prospected for environmental clines (Newkirk & Doyle, 1979; Janson & Ward, 1984; Johannesson *et al.*, 1993), founder effects (Janson, 1987), or correlates of heterozygosity (Noy *et al.*, 1987; Foltz *et al.*, 1993). However, the only previous examination of *L. irrorata* allozymes, prior to this report, was that of Berliner (1981) in a Virginia salt marsh. He found no significant difference in heterozygosity between young and old size classes, but noted a lower value of heterozygosity in snails of median age. Berliner's study did not extend beyond his single population.

MATERIALS AND METHODS

Approximately 50–60 *L. irrorata* per site were collected from three sites on the Atlantic coast of the southeast United States and two from the Gulf of Mexico: the Virginia Institute of Marine Science Laboratory (VIMS) at Wachapreague, Virginia, the Greece Marine Biological Laboratory (GMBL) at Charleston, South Carolina, Crescent Beach, Florida (CBFL), Tampa Bay, Florida (TBAY), and the Louisiana University Marine Consortium Laboratory (LUMC) at Cocodrie, Louisiana (Figure 1). All sites except TBAY were typical salt marshes dominated by the salt marsh cord grass, *S. alterniflora*. The Tampa Bay site was a small patchy area of *S. alterniflora* growing on sand, rather than mud. At all sites, the snails were found on the stalks of the salt marsh cord grass or on the substrate at the base of the stalks, generally in the mid-marsh to high marsh areas. The snails were transported to Charleston alive, where tissues were frozen at -60°C in 150–300 μl of 0.05 M Tris Tissue buffer pH 7.5 (Dayan, 1994).

Horizontal protein electrophoresis was conducted using methods and equipment previously described (Dillon, 1985; 1992; Dayan, 1994). The 12% starch gels were a 1:1 mixture (by volume) of Electrostarch (Otto Hillar, Madison, WI) and Sigma starch (Sigma Chemical, St. Louis, MO). We initially compared the zymograms of individuals from GMBL and LUMC using 19 enzyme stains and 9 buffer systems. Results were poor or uninterpretable for six enzymes and appeared invariable for seven others. Ultimately we were able to resolve allozymes interpretable as the products of codominant Mendelian alleles at eight loci (encoding six enzymes) using

Table 1. Allele frequencies at eight enzyme-encoding loci in five populations of *Littorina irrorata*. (n) = Sample size.

Locus	Allele	Population				
		VIMS	GMBL	CBFL	TBAY	LUMC
<i>Est1</i>	A	0.571	0.689	0.635	0.556	0.507
	B	0.429	0.292	0.362	0.444	0.485
	C	0.000	0.019	0.000	0.000	0.007
(n)		56	53	58	62	67
<i>Est2</i>	A	0.984	0.989	0.992	0.965	1.000
	B	0.016	0.011	0.008	0.032	0.000
	(n)	61	44	62	62	63
<i>Pgm</i>	A	0.648	0.441	0.490	0.411	0.490
	B	0.270	0.480	0.288	0.218	0.127
	C	0.082	0.078	0.202	0.371	0.343
	D	0.000	0.000	0.019	0.000	0.039
(n)		61	51	52	62	51
<i>Mpi</i>	A	0.992	0.952	0.992	0.968	0.971
	B	0.008	0.048	0.008	0.032	0.029
(n)		63	83	62	62	70
<i>Isdh1</i>	A	0.934	0.965	0.877	0.966	0.918
	B	0.057	0.035	0.098	0.017	0.061
	C	0.008	0.000	0.025	0.017	0.020
(n)		61	57	61	59	49
<i>Isdh2</i>	A	0.992	0.990	1.000	1.000	0.990
	B	0.008	0.010	0.000	0.000	0.010
(n)		60	50	62	62	49
<i>Sdh</i>	A	0.814	0.788	0.856	0.805	0.698
	B	0.161	0.205	0.136	0.161	0.250
	C	0.025	0.008	0.008	0.034	0.052
(n)		59	66	59	59	48
<i>Lap</i>	A	0.917	0.700	0.900	0.860	0.862
	B	0.075	0.255	0.067	0.061	0.078
	C	0.008	0.036	0.025	0.061	0.043
	D	0.000	0.009	0.008	0.018	0.017
(n)		60	55	60	57	58

three buffer systems. The AP6 buffer (Clayton & Tretiak, 1972) was used to resolve esterases (*Est*, two loci), and phosphoglucosyltransferase (*Pgm*). The WW1 (Ward & Warwick, 1980) buffer was also used to resolve *Pgm*, as well as isocitrate dehydrogenase (*Isdh*, two loci), and sorbitol dehydrogenase (*Sdh*). The TC6 buffer (Dillon, 1985) was used to resolve leucine aminopeptidase (*Lap*) and mannose-phosphate isomerase (*Mpi*). Working with *L. saxatilis*, Ward *et al.* (1986, 1991) have confirmed Mendelian inheritance at all these loci except *Est* and *Sdh*.

Data analysis was by Biosys-1 (Release 1.7, Swofford & Selander, 1981) unless otherwise specified. We tested the fits to Hardy-Weinberg expectation for each locus at each population using goodness of fit χ^2 statistics, combining rare genotypic classes as necessary. We then performed two separate gene diversity analyses using Wright's (1978) F-statistics. In the more conventional analysis, the total deviation from Hardy-Weinberg expectation over all loci (F_{IT}) was divided into a component

Table 2. Wright's (1978) F-statistics, averaged over eight loci, measuring gene diversity attributable to individuals (*I*), populations (*S*), and coast (*C*). Values from the hierarchical analysis of coastal variance are set under F_{ST} , the variance attributable to population structure.

Comparison	Coefficient
F_{IS}	0.049
F_{ST}	0.033
F_{SC}	0.020
F_{CB}	0.004
F_{SB}	0.024
F_{IT}	0.080

within populations (F_{IS}) and a component between the five populations (F_{ST}). We also performed a hierarchical analysis (Dillon & Manzi, 1992; Dillon & Wethington, 1995), grouping the three Atlantic and two Gulf populations to determine the proportion of gene diversity attributable to coast. Mean F-statistics calculated in this way we labeled F_{SC} (between populations within coasts), F_{CB} (between coasts) and F_{SB} . Note that F_{SB} is expected to be less than F_{ST} , since that proportion of the variance between populations between coasts remains unattributed in the hierarchical analysis.

For each locus at which *n* alleles were identified, divergence among populations was tested with a $5 \times n$ χ^2 contingency test. To avoid the necessity of combining or eliminating rare alleles for this analysis, we estimated the significance of our values of χ^2 using the Monte Carlo approach of Roff and Bentzen (1989). Unbiased genetic identity and distance between all pairs of populations was calculated using the method of Nei (1978).

RESULTS

Gene frequencies at eight enzyme-encoding loci from five populations of *Littorina irrorata* are shown in Table 1. The fits to Hardy-Weinberg expectation within populations were very close in most cases. Goodness-of-fit values of χ^2 nominally significant at the 0.05 level were obtained only at *Pgm* in VIMS, and at *Isdh* in TBAY, well within expectation for type I error. The mean value of F_{IS} over all loci, measuring deviation from Hardy-Weinberg within-sites over the entire study, was small ($F_{IS}=0.049$, Table 2).

The mean value of $F_{ST} = 0.033$, measuring deviation from Hardy-Weinberg expectation between sites, was lower than the deviation within-sites. However, the data of Table 1 reflect significant divergence among the five populations at four loci. The value of χ^2 testing homogeneity in *Pgm* allele frequencies was 103.6 ($p < 0.001$), with notably high frequencies of *Pgm-A* in VIMS, *Pgm-B* in GMBL, and *Pgm-C* in the three most southern populations. The GMBL population was distinguished by a significantly high frequency of *Lap-B* (overall $\chi^2=46.4$, $p < 0.001$), the LUMC population by high *Sdh-B* (overall $\chi^2=21.7$, $p=0.034$), and the CBFL population

Table 3. Nei's (1978) unbiased genetic identity (above diagonal) and distance (below diagonal) between all pairs of five *L. irrorata* populations.

Populations	VIMS	GMBL	CBFL	TBAY	LUMC
VIMS	—	0.986	0.998	0.990	0.991
GMBL	0.014	—	0.990	0.981	0.974
CBFL	0.002	0.011	—	0.996	0.993
TBAY	0.010	0.019	0.004	—	0.999
LUMC	0.009	0.026	0.007	0.001	—

by high *Isdh1-B* (overall $\chi^2=19.6$, $p=0.047$). Differences at the remaining four loci were not significant.

The contribution of the coastal level to the hierarchical gene diversity analysis was negligible. Table 2 shows that F_{CB} , the deviation from Hardy-Weinberg expectation between coasts, was 0.004. This was lower than the variance between populations within coasts. The values of Nei's unbiased similarity and distance among all pairs of sites are shown in Table 3. The four within-coast values of Nei's distance ranged from 0.001 to 0.014, only slightly less than the range for the six values between coasts (0.004 to 0.026).

DISCUSSION

The data of Table 1 constitute substantial evidence of low-level genetic divergence among populations of *Littorina irrorata* separated by distances on the order of hundreds of kilometers. A general relationship between interpopulation divergence, mode of embryonic development, and dispersal capability has often been noted in marine mollusks (Burton & Feldman, 1981; Scheltema, 1989; Yamada, 1989). *Littorina irrorata* spawn at high tide, females releasing eggs just beneath the water level (Gallagher & Reid, 1974). Egg capsules are planktonic, but slightly negatively buoyant in calm seawater (Bingham, 1972). They hatch into swimming veliger larvae after one to two days of further development, but the time to settlement is unknown. Settlement occurs on *Spartina* shoots (Boothe, 1969), where juveniles remain hidden in curled blades until they reach about 5 mm (Stiven & Hunter, 1976; Crist & Banta, 1983). Berger (1973) compared population divergence in three North American *Littorina* species, *L. littorea* (pelagic larval development), *L. obtusata* (juveniles hatch from gelatinous egg masses), and *L. saxatilis* (ovoviviparous). The levels of genetic differentiation we report here in *L. irrorata* are, as might be expected, comparable to those of *L. littorea* and much less than those of *L. obtusata* or *L. saxatilis*.

Such interpopulation genetic divergence as we have identified does not, however, seem to reflect a barrier to dispersal around the Florida peninsula. Table 1 shows no allele unique to either coast, even the five rarest alleles (*Est2-B*, *Isdh2-B*, *Lap-C*, *Lap-D*, and *Mpi-B*) were found in both Atlantic and Gulf populations. Nor did our hi-

erarchical gene diversity analysis or our inspection of interpopulation genetic distances suggest any evidence of a barrier to gene flow corresponding to the Florida peninsula. The divergence between Atlantic and Gulf populations of *L. irrorata* is indistinguishable from differences among populations sharing the same coast. We offer three (not mutually-exclusive) hypotheses for this unexpected result: no-barrier, past-dispersal, and balancing selection.

It is possible that, in spite of the climate shift in southern Florida and the disappearance of salt marsh habitat, no barrier currently exists between Atlantic and Gulf populations of *L. irrorata*. We are unaware of any collections of adult snails south of Ft. Pierce, Florida. But it is possible that sparse populations do exist on mangroves or concrete bulkheads along the remainder of the southern Florida coast. Long distance dispersal of larvae or juveniles (perhaps on dead *Spartina* rack) is also possible. Only a few days might be required to transport larvae on the Gulf Stream from the west coast of Florida into the eastern Atlantic, although onshore currents would still be necessary to carry larvae back into estuaries. It is difficult, however, to imagine how such a passive dispersal mechanism might be effective for *Littorina* larvae and not for toadfish, black sea bass, horseshoe crabs, sea anemones, or oyster larvae, all of which do exhibit genetic divergence between coasts.

A second possible explanation for the absence of divergence between Atlantic and Gulf *L. littorina* populations would invoke higher levels of gene flow in the not-too-distant past. The Suwannee Straits (or Okefenokee Trough) most recently connected the two coasts of northern Florida during the Pliocene epoch (Avice, 1992). Fossil *L. irrorata* found in North Carolina, South Carolina, and Florida have been dated from the upper Miocene and Pliocene, while fossils found in Louisiana and Texas are Pleistocene in age (Bequaert, 1943). Faunal exchange between Atlantic and Gulf may also have occurred in the Pleistocene epoch, although it is difficult to predict under what environmental conditions. *L. irrorata* could certainly have extended its range southward during glacial periods, but lowering sea levels would have elongated the Florida peninsula. The distance between Atlantic and Gulf shortened as interglacial seas rose, but the snail may have been driven north by the advance of tropical conditions. It would appear, however, that the past-dispersal hypothesis is no better than the no-barrier hypothesis in accounting for the difference between *Littorina* and those (many) species that do show intercoastal divergence.

The third hypothesis would recall Karl and Avice's (1992) work with oysters. Although allozyme frequencies were homogeneous, Karl and Avice were able to establish that a barrier has existed between Atlantic and Gulf oyster populations using mtDNA and anonymous nuclear DNA markers. They concluded that balancing selection may be holding Atlantic and Gulf oyster populations undifferentiated in their enzyme polymorphism in the absence of gene flow, and that caution should be used

regarding the assumption of neutrality for allozyme markers.

The present data are insufficient to distinguish among these three hypotheses. Further, more detailed surveys of *L. irrorata*'s range in south Florida would be helpful, along with an expansion of isozyme studies if necessary. Some examination of the larval behavior and development time of *L. irrorata* would clarify the likelihood of long distance gene flow. And further surveys of genetic divergence among Atlantic and Gulf samples of *L. irrorata* using mtDNA or nuclear DNA markers are strongly indicated.

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Venustaconcha sima (Lea), an Overlooked Freshwater Mussel (Bivalvia: Unionoidea) from the Cumberland River Basin of Central Tennessee

Mark E. Gordon

Zoology Section
Campus Box 315
University of Colorado Museum
Boulder, CO 80309 USA

ABSTRACT

Unio simus Lea, 1838, generally has been considered to be a junior synonym of *Villosa nebulosa* (Conrad, 1834). Examination of recently collected specimens indicates that it is a valid species of *Venustaconcha* restricted to the upper Caney Fork River system in central Tennessee. *Venustaconcha sima* may represent the Cumberlandian counterpart of *V. pleasii* (Marsh, 1891) of the southern Ozark Plateaus.

Key words: Bivalvia, Unionoidea, *Venustaconcha*

INTRODUCTION

During recent studies of the mussel fauna of the Caney Fork River basin (e.g., Farzaad, 1991; Layzer *et al.*, 1993), a major tributary system of the Cumberland River, a diminutive purplish-nacred mussel was found, which possessed a posteroventral emargination with an associated radial sulcus in female shells and relatively heavy hinge dentition. Stansbery (personal communication) considered it to be an undescribed species of *Villosa*; however, the above morphological characters match diagnostic criteria in Haas (1969) for *Venustaconcha*. A review of the multitudinous species descriptions of Isaac Lea and subsequent examination of type specimens in the National Museum of Natural History, Smithsonian Institution, resulted in the identification of this mussel as *Venustaconcha sima* (Lea, 1838).

SYSTEMATICS

Tribe Lampsilini

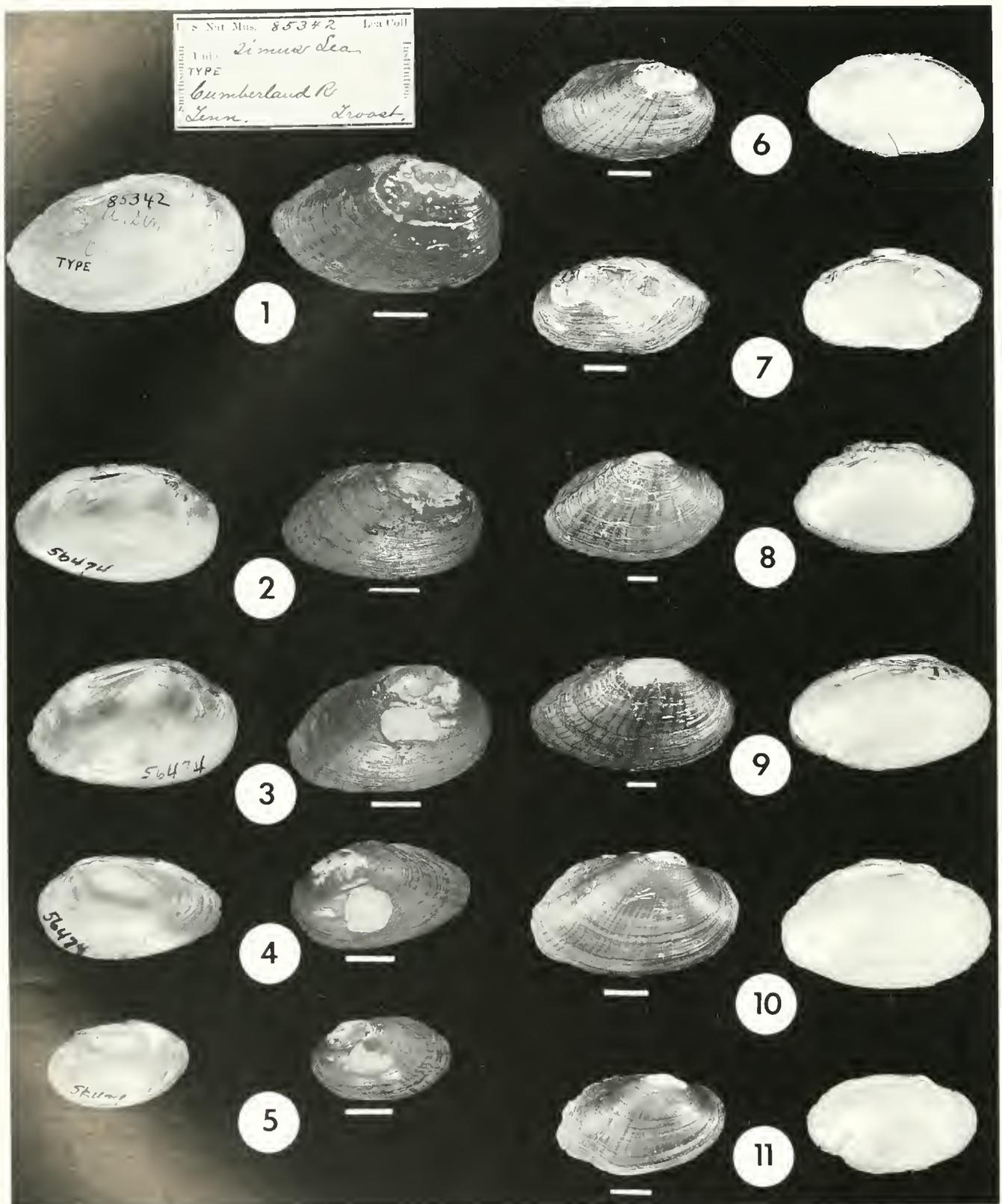
Venustaconcha sima (Lea, 1838)
(Figures 1-7; Table 1)

Margarita (Unio) simus Lea (1836:29) *nomen nudum*
Unio simus Lea (1838:26, figure 20 on plate VIII).
Margaron (Unio) simus Lea (1852:31).
Lampsilis simus Simpson (1900:556).
Lampsilis sima Simpson (1914:123).

Eurynia (Micromya) nebulosa (in part) Ortmann (1918:577).
Micromya nebulosa (in part) Ortmann (1924:102).
Lampsilis (Ligumia) nebulosa (in part) Frierson (1927:78).
Villosa nebulosa (in part) Burch (1975:173).

Description: Shell small, broadly elliptical (males) to somewhat ovate (females), barely inflated ($W/H \cong 0.63$; for interpretation of shell proportions, see Wu, 1978); solid, thinner posteriorly; anterior rounded; dorsal margin slightly convex, oblique, consequently shell may appear humped or somewhat winged, juncture with anterior margin sometimes angular; ventral margin slightly convex to virtually straight; posterior bluntly pointed to biangulate; postero-ventral region of female shells may be swollen with some distention of the extreme posterior of the ventral margin, an emargination and associated radial sulcus may develop posteriorly to the distention; posterior ridge low, vaguely double, somewhat flattened between ridges but may appear rounded; posterior slope slightly concave with a shallow radial furrow, furrow may cause an indentation of the postero-dorsal margin; ligament low, short; umbo compressed, low, barely elevated above dorsal margin; umbonal sculpture "...irregular, somewhat doubly-looped ridges..." (Simpson, 1914); periostracum rather smooth and somewhat shiny in younger specimens, may be dull and rough in older shells, annual growth lines well-marked, yellowish to dark brown or black with narrow dark green rays, raying most prevalent on posterior half of shell and may be wavy and clustered closely together.

Pseudocardinals thick, heavy, serrated, double in left valve, single in right valve but often with small anterior and posterior denticles opposite adjacent sulci; interdentum moderately wide, relatively short; lateral teeth short, straight, lamellar, may be slightly serrate, double in left valve, single in right valve; anterior adductor and retractor muscle scars confluent, rather small, deeply impressed; protractor muscle scar distinct, straight to crescent-shaped; posterior muscle scars typically confluent, impressed, adductor large, retractor small and positioned under distal base of lateral tooth; dorsal muscle scars



Figures 1-11. Shells of *Venustaconcha*. 1-5. Type specimens of *Venustaconcha sima*. 1. Holotype (male, USNM 85342). 2-4. Male paratypes (ANSP 56474). 5. Female paratype (ANSP 56474). 6-7. *Venustaconcha sima* from Collins River, Mt. Olive, Grundy County, Tennessee, collected 15 July 1989. 6. Male. 7. Female. 8-9. *Venustaconcha ellipsiformis* from Osage Fork of Gasconade River, Dryknob, Laclede County, Missouri, collected 3 October 1983. 8. Male. 9. Female. 10-11. *Venustaconcha pleasii* from James River, east of Springfield, Greene County, Missouri, collected 4 October 1983. 10. Male. 11. Female. Scale bars = 1 cm.

Table 1. Shell dimensions of type specimens and representative shells of *Venustaconcha sima* (L = length, H = height, W = width, M = male, F = female; specimens other than types were collected from the Collins River, Tennessee, Grundy County, Mt. Olive, 15 July, 1989).

Specimen	Sex	L	H	W	H/L	W/H
Holotype	M	43.9	25.4	15.2	0.57	0.60
Paratype	M	43.4	26.7	15.6	0.62	0.58
Paratype	M	42.0	24.3	15.2	0.58	0.63
Paratype	M	37.8	21.8	14.1	0.58	0.65
Collins River	M	47.3	27.1	17.5	0.57	0.65
Collins River	M	42.2	24.7	15.7	0.59	0.64
Collins River	M	46.5	27.5	15.8	0.59	0.58
Collins River	M	45.0	25.5	16.6	0.57	0.65
Collins River	M	42.3	24.0	14.9	0.57	0.62
Collins River	M	41.1	23.4	13.4	0.57	0.57
	M				$\bar{x} = 0.58$	$\bar{x} = 0.62$
Paratype	F	29.5	17.7	10.3	0.60	0.58
Collins River	F	42.8	23.4	14.5	0.55	0.64
Collins River	F	36.4	21.7	14.2	0.60	0.65
Collins River	F	33.0	19.6	13.4	0.59	0.68
Collins River	F	31.3	18.4	11.2	0.59	0.61
Collins River	F	34.7	20.7	12.2	0.60	0.59
Collins River	F	36.7	21.4	14.8	0.58	0.69
Collins River	F	30.5	18.3	11.8	0.60	0.65
Collins River	F	32.9	19.9	12.3	0.61	0.62
Collins River	F	30.6	18.3	12.3	0.60	0.67
	F				$\bar{x} \pm 0.59$	$\bar{x} = 0.64$
	Overall				$\bar{x} = 0.59$	$\bar{x} = 0.63$

deeply impressed on underside of interdentum, occasionally causing a notch in interdentum, extend from just posterior of the umbo to base of pseudocardinals; pallial line impressed, lighter posteriorly; beak cavity moderately developed; naere variable, tends to be purple in living individuals but may be lighter, pinkish or whitish, and blotched with brown, color fades rapidly in dead shells.

Type locality: "Cumberland River, Tennessee . . . This shell was procured by Professor Troost from the Cumberland River, but whether near Nashville or not, I am not informed" (Lea, 1838).

Type specimens: Holotype, National Museum of Natural History, Smithsonian Institution (USNM) 85342 (male). Paratypes, Academy of Natural Sciences of Philadelphia (ANSP) 56474 (three males, one female). All type specimens have whitish naere as noted by Lea (1838)¹, evidently reflecting the tendency for the purple coloration to fade in dead shells. Only one additional lot of this species was located at the USNM (782358) labelled "*Villosa trahalis perpurpurca* (Lea, 1861)", but contain-

ing a mixed collection of *Venustaconcha sima* and *Pleurobema gibberum* (Lea, 1838) from the Collins River, Grundy County, Tennessee. Additional lots are located at the Carnegie Museum, Museum of Comparative Zoology, and Ohio State University Museum. Voucher specimens from the present study have been deposited in the USNM, University of Michigan Museum of Zoology, Museum of Comparative Zoology, Carnegie Museum, and University of Colorado Museum.

Distribution: The distribution of this species is difficult to delineate due to the lack of historical records; however, recent collecting indicates that it is restricted to the Caney Fork River basin above Great Falls. Much of its presumed former habitat is inundated by Great Falls Reservoir.

Habitat: *Venustaconcha sima* appears to be associated with riffle systems in small to medium-sized streams, including headwaters. It is most abundant in sandy substrate between cobbles and boulders with slow to moderate current, although it also occurs in courser substrate and faster currents (see Farzaad, 1991).

Etymology: *Venustaconcha*- L. *venusta* [adj.] + *concha* [n., feminine], pretty shell; *sima*-L. [adj.], snub-nosed.

DISCUSSION

Following its original description, *Venustaconcha sima* was known only by its inclusion in synoptic lists of fresh-

¹ Lea (1862:62) stated that *V. sima* had a salmon colored naere. Since examination of available specimens at USNM and ANSP indicated that Lea only had access to specimens in the type lots (all with white naere), he may have confused this particular attribute of the similarly-shaped *Unio notatus* Lea, 1838 (*incertae sedis*) with *sima*.

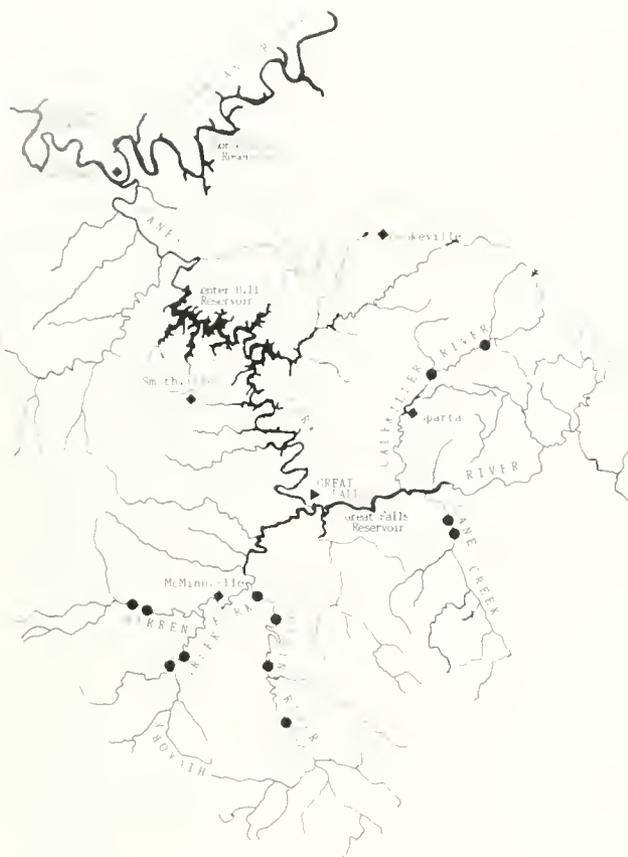


Figure 12. Distribution of *Venustaconcha sima* within the Caney Fork River system, Tennessee.

water mussels (e.g., Troschel, 1839; Conrad, 1853; Lea, 1870). Call (1885) alluded to an affinity with "*Unio iris*, Lea," 1829, which Simpson (1900, 1914) subsequently followed. Simpson (1914) did note its resemblance to "*Lampsilis*" *nebulosa* (Conrad, 1834) and "*L.*" *ellipsiformis* (Conrad, 1836). Ortmann (1918) relegated *sima* as a junior subjective synonym under "*Eurynia* (*Micromya*)" *nebulosa*. *Venustaconcha sima* is a heavier shell than *Villosa iris* or *V. nebulosa*. It tends to be relatively shorter and broader than either of the latter and, particularly in the case of females, more closely resembles *Venustaconcha ellipsiformis* by virtue of its posterior-ventral swelling with associated emargination and radial sulcus, heavy pseudocardinal teeth, wide interdentum, and fine, wavy, closely-spaced rays (Figs. 8-9). These characteristics were among those employed by Haas (1969) to distinguish *Venustaconcha* Frierson, 1927², from *Villosa* Frierson, 1927.

² On several occasions (e.g., Vokes, 1980; Oesch, 1984; Stansbery, *xeroxed ephemera*), authorship of *Venustaconcha* has been attributed to Thiele, 1934 or 1935. *Venustaconcha* was proposed as a replacement name by Frierson (1927) in the "errata et corrigenda" for *Venusta* Frierson, 1927 (*non* Boettger, 1877, *nec* Barrande, 1881).

Within the Cumberland River basin, *Venustaconcha sima* is similar in appearance to and occasionally may be confused with species in the *Villosa iris* / *nebulosa* complex (see above) and *V. trabalis* (Conrad, 1834) (e.g., (USNM 782358). Compared to *Venustaconcha sima*, the latter species is a relatively heavier, larger and more elongate shell. Its periostracum tends to be darker, the posterior-ventral emargination of the female is not as acute, pseudocardinal teeth are relatively larger, and the nacre tends not to be blotched. These two species also appear to be distributed allopatrically. Interestingly, the shells of *V. trabalis* and *V. ellipsiformis* are more similar to each other than either is to *V. sima*, and Frierson (1927) included *trabalis* in his original list of species under *Venustaconcha*. Although further investigation into generic relationships of advanced lampsilines is required (Hoeh and Frazer, personal communications), classification of *trabalis* under *Venustaconcha* may be more representative of actual relationships than an association with *Villosa*.

The distribution of *Venustaconcha sima* appears to be restricted to the portion of the Caney Fork River basin draining the Highland Rim upstream from Great Falls, the cataract at the escarpment between the Highland Rim and Nashville Basin (Fig. 12). Call (1885) listed its range as the "Cumberland river, Tennessee, and Swamp Creek, Whitfield County, Georgia." To this, Simpson (1900, 1914) added "...Tennessee river system(s); Othcalooga Creek, northwest Georgia." As noted above, only two lots of *V. sima* were observed at the USNM. It is unclear upon which specimens Simpson based this range. Call (1885) and Simpson (1900, 1914) possibly may have confused *V. sima* with species of *Villosa* (e.g., *V. iris* complex; *V. vanuxemii* [Lea, 1838]³, particularly the *umbrans* Lea, 1857, morph).

Lea (1838) noted the Cumberland River, Tennessee, as the type locality for *U. simus*, but commented that he did not know the exact collection site. Lea's locality information often was incredibly vague (e.g., *Unio grayanus* Lea, 1834: type locality - China) or reflected the address of the collector (e.g., *Lampsilis reveiana* Lea, 1852: see Gordon & Kraemer, 1984). The latter may be the case with *Venustaconcha sima*. Since the type specimens were sent by Prof. Troost from Nashville, Lea may have assumed that they had been collected from the Cumberland River. With respect to its known distribution (Fig. 12), the type specimens may have originated from the Collins River or possibly its principle

³ Lea (1838) stated that he named this species after Prof. Lardner Vanuxem, yet the original spelling ended with the suffix for a locality name rather than the masculine genitive. The spelling of *vanuxemensis* was corrected to *vanuxemii* by Lea (1858). This change is in accordance with Articles 19a (i), 32c (ii), 32d, 33b (ii) and Appendix D of the International Code of Zoological Nomenclature (third edition). Johnson (1974) previously noted this correction of the *lapsus calami*.

tributary, Barren Fork, in the vicinity of McMinnville, Warren County, Tennessee (the largest town in that area in 1838).

Venustaconcha sima does not appear to have a counterpart in the Tennessee River or drainages northward into Kentucky. As previously observed, Simpson (1914) noted similarities between *V. sima* and *V. ellipsiformis*. However, in both shell morphology and habitat preference, *V. sima* seems to be allied more closely to *V. pleasii* (Marsh, 1891), a small mussel endemic to the Ozark Plateau drainages of the White River system, Arkansas and Missouri (Figs. 10-11) (personal observations; Gordon, 1980). This hypothetical association would be consistent with previously observed molluscan affinities between the fauna of the Cumberlandian and Interior Highlands regions (e.g., Ortmann, 1917; van der Schalie & van der Schalie, 1950).

Although major surveys of the Cumberland River have been conducted (Wilson & Clark, 1914; Neel & Allen, 1964), its mussel fauna has received relatively little attention in comparison with that of the Tennessee River system. Starnes and Bogan (1988) listed 85 species from the Cumberland River drainage, while Gordon and Layzer (1989) reported 94 species. Previous faunal compilations for the Caney Fork included 27 species (Miller, 1984) and 14 species (Starnes & Bogan, 1988); however, Layzer *et al.* (1993) have found that the historical fauna was considerably more diverse than the former accounts indicate. It is apparent that the species richness of the Cumberland River mussel fauna is greater than previously considered.

Ortmann (1924) concluded that the Cumberland River system lacked an endemic mussel fauna. Starnes and Bogan (1988) similarly stated that "all of the mussel species recorded from the Cumberland River occur in the Tennessee River system" despite the inclusion in their synoptic table of two mussels (*Alasmidonta atropurpurea* [Rafinesque, 1831]⁴ and *Pleurobema gibberum*) that are restricted to portions of the Cumberland River drainage. A distinct endemic mussel fauna did evolve in the upper Cumberland River system. Despite massive habitat destruction within the basin (e.g., reservoir construction, acid coal mine run-off), a fragment of this fauna persists, as represented by *A. atropurpurea*, *Quadrula tuberosa* (Lea, 1840: possibly extinct), *P. gibberum*, and *Venustaconcha sima*.

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Richard S. Houbrick (1937–1993): Biographical Sketch and Malacological Contributions

M.G. Harasewych

Alan R. Kabat

Department of Invertebrate Zoology
National Museum of Natural History
Smithsonian Institution
Washington, D.C. 20560 USA

I. BIOGRAPHY

The malacological community lost one of its most eminent and respected members and prolific authors with the death of Richard S. Houbrick on August 26, 1993 at the age of 56, after a long and valiant struggle with leukemia and hepatitis.

Richard Steven Houbrick was born on March 16, 1937 in Trenton, New Jersey to Stephen J. and Barbara A. Houbrick. The family moved to Hollywood, Florida when Joe was 12. As a young student, Joe was an avid field biologist, shell collector, and occasional shell show exhibitor. After completing Broward High School, he entered St. John's Seminary in Little Rock, Arkansas, then transferred to St. Bernard College, Cullman, Alabama, where he graduated with a Bachelor of Arts degree in 1959.

He then entered St. Leo Theological School, St. Leo, Florida, and was ordained to the priesthood in March, 1963. As a member of St. Leo Abbey (Benedictine Order) he took the name Joseph, and has since been known as "Joe" to his many friends and colleagues. He was an Instructor in general biology, zoology, invertebrate zoology, embryology and botany at St. Leo College. He began attending summer sessions of the University of Miami and the University of Florida, taking courses in Biology and Chemistry. In 1964, Joe entered the Graduate School of the University of Miami. He earned a M.S. degree from the Rosenstiel School of Marine and Atmospheric Science, University of Miami in 1967, having completed his thesis on "A survey of the littoral marine mollusks of eastern Costa Rica."

In the summer of 1968, he attended the Biology of Mollusks Training Program, in Hawaii, where he studied molluscan anatomy with Vera Fretter and others. This course had a profound influence on his future research, as shown by his extensive use of anatomy and reproductive biology in his systematic publications.

Joe enrolled in the newly established University of South Florida in 1968, and received the first Ph.D. to be awarded by this University in 1971, for his dissertation on "Taxonomy, anatomy, and life history studies on the genus *Cerithium* (Gastropoda: Prosobranchia) in the western Atlantic." His thesis advisor was Dr. Joseph L. Simon, a marine ecologist. Upon completing his doctorate, Joe joined the staff of the Smithsonian Oceanograph-



Richard S. Houbrick at the Smithsonian Marine Station at Link Port, Florida, February, 1983.

ic Sorting Center, and was subsequently appointed Supervisor of the Benthic Section, and later Acting Director.

In 1977, Joe was appointed Associate Curator in the Division of Mollusks at the National Museum of Natural History, where he became Curator in 1981, a position in which he remained active until shortly before his death.

Noted primarily for his expertise in the systematics, comparative anatomy, functional morphology and reproductive biology of the Cerithioidea, he contributed significantly to the body of descriptive and synthetic literature on this group. Since his work emphasized the

study of living animals and their life-histories, he traveled widely, conducting field work in many parts of the world, including the tropical western Atlantic, the tropical Pacific and Australia. He was a frequent invited participant in symposia and workshops.

Since joining the Division of Mollusks, Joe spent an extremely productive portion of each year working with live animals at the Smithsonian Marine Station at Link Port, Florida. The many colleagues who had an opportunity to work with Joe at the Marine Station soon discovered his special interest in and enormous knowledge of the flora and fauna of Florida that he had accumulated since childhood. Joe was an active supporter of the Marine Station, serving on its Task Force and Advisory Group.

All who knew Joe recognized that he was above all an educator. He was an Adjunct Professor at George Washington University, and served on thesis committees of graduate students at this and other universities. He also served as Advisor to several Smithsonian Post-doctoral Fellows, who have since risen to prominent positions in the field of systematic malacology. Whether student, post-doc or professional colleague, his own or someone else's, Joe would always take the time to show an interest in their work, to learn from them as well as to make helpful comments and offer his own insights.

Joe was active in numerous professional organizations, among them the American Malacological Union (of which he was president in 1980–81), the American Society of Zoologists, the California Malacozoological Society, the Malacological Society of London, Unitas Malacologia, the Biological Society of Washington, and the Smithsonian Senate of Scientists.

Joe will be remembered as a quiet scholar whose research and publications stand as a lasting monument to his scientific dedication and insight. As a person, he was known for his sense of humor, for his enjoyment of the fine arts along with music, and he was invariably most congenial to all. He is survived by his parents, and by his brother James and his family.

ACKNOWLEDGMENTS

We thank James Houbrick, Robert Hershler, and Clyde Roper for their helpful comments on this manuscript.

H. MALACOLOGICAL TAXA

Of R.S. Houbrick's fifty-six publications from 1967 to 1993 (not counting meeting abstracts or notes), twelve included descriptions of twenty-two new taxa. These comprise two family-level taxa, three genus-level taxa (two in the Cerithiidae and one in the Planaxidae) and seventeen species-level taxa (twelve in the Cerithiidae and the remainder in other prosobranch gastropod families). Two of the species-level taxa are replacement names for junior homonyms.

Abbreviations

AMS Australian Museum, Sydney

ANSP Academy of Natural Sciences of Philadelphia
LACM Los Angeles County Museum of Natural History
MNHNP Muséum National d'Histoire Naturelle, Paris
NM Natal Museum, Pietermaritzburg
NMFS National Marine Fisheries Service [USA]
USBF U.S. Bureau of Fisheries
USNM U.S. National Museum [= National Museum of Natural History, Smithsonian Institution]
WAM Western Australian Museum, Perth

Family-level taxa

CERITHIDEIDAE Houbrick 1988, Malacological Review, Supplement 4:88 ff. (diagnosis on page 118). For (by implication) *Cerithidea* Swainson 1840. Subsequently synonymized with the Potamididae H. & A. Adams 1854 by Houbrick (1991, Malacologia, 33(1–2):333). Cerithioidea.

PLESIOTROCHIDAE Houbrick 1990, Proceedings of the Third International Marine Biological Workshop: The Marine Flora and Fauna of Albany, Western Australia, pages 237 ff. (diagnosis on page 248). For *Plesiotrochus* Fischer 1878. Originally placed in the Cerithioidea. Subsequently transferred to the Campaniloidea by Healy (1993).

Genus-level taxa

Ittibittium Houbrick 1993, Malacologia, 35(2):283. Type species *Bittium parvum* Gould 1861; monotypy. Cerithiidae.

Longicerithium Houbrick 1978, Monographs of Marine Mollusca, 1:85. Type species *Cerithium longicaudata* A. Adams and Reeve 1850; original designation. As a subgenus of *Rhinoclavis* Swainson 1840. Cerithiidae.

Simulathena Houbrick 1992, The Veliger, 35(1):64–65. Type species *Simulathena papuensis* Houbrick 1992; monotypy. Planaxidae.

Species-level taxa

abditum, *Cerithium* Houbrick 1992, Smithsonian Contributions to Zoology, 510:18–20, figures 6–8. Holotype USNM 286404; five paratypes USNM 860482. USBF Albatross Station 5569, 554 meters, off Simaluc Island, Tawitawi, Philippines. Cerithiidae.

admirabilis, *Clypeomorus* Houbrick 1985, Smithsonian Contributions to Zoology, 403:99–104, figures 47–49. Holotype WAM 3346–83; seven paratypes USNM 784652; thirty-eight paratypes ANSP 233431; three paratypes AMS 139779. False Cape Creek (near mouth), 100 miles (161 kilometers) S of Broome, Western Australia, Australia. Cerithiidae.

africanum, *Cerithium* Houbrick 1992, Smithsonian Contributions to Zoology, 510:20–23, figures 9–11. Holotype NM H1861; five paratypes USNM 629034. Southwestern Conducia Bay, NW of Choeca, Mozambique. Cerithiidae.

argentea, *Strombina* (*Cotonopsis*) Houbriek 1983, Proceedings of the Biological Society of Washington, 96(3): 349–352, figures 1–2. Holotype USNM 810345; nine paratypes USNM 821851. NMFS R/V *Oregon*, Station 5432, 384–430 meters, 20°48'N, 70°46'W, near Silver Bank, 60 miles NE of Luperon, Dominican Republic. Columbellidae.

diadema, *Rhinoclavis* (*Rhinoclavis*) Houbriek 1978, Monographs of Marine Mollusca, 1:64–66, figures 33–35. Replacement name for *Cerithium nitidum* Hombron and Jacquinot 1854 *non* MacAndrew and Forbes 1847 *et al.*. Lectotype and one paralectotype (of *Cerithium nitidum*), MNHNP (not numbered); selected by Houbriek (1978: 66). Mangareva, Gambier Islands. Cerithiidae.

eximium, *Ataxocerithium* Houbriek 1987, The Nautilus, 101(4):157–159, figures 1–16. Holotype AMS C142394; five paratypes AMS C153005; two paratypes USNM 862328. 421 meters, 34°21'–16'S, 151°24'–28'E, SE of Botany Bay, New South Wales, Australia. Cerithiopsidae.

garciai, *Cerithioclava* Houbriek 1986, Proceedings of the Biological Society of Washington, 99(2):257–260, figure 1. Holotype USNM 849023; two paratypes USNM 849024. 24 meters, off Great Corn Island, Nicaragua [Caribbean Sea]. Cerithiidae.

gloriosum, *Cerithium* Houbriek 1992, Smithsonian Contributions to Zoology, 510:94–97, figures 61–63. Holotype, MNHNP (not numbered); 200 paratypes MNHNP (not numbered); seventy-nine paratypes USNM 862327. Benthedi Station DR-06, 500–600 meters, 11°28'S, 47°12'E, Iles des Glorieuses, Indian Ocean. Cerithiidae.

inflatus, *Acamptochetus* Houbriek 1984, Proceedings of the Biological Society of Washington, 97(2):421–423, figure 1. Holotype USNM 229183; one paratype USNM 820185. USBF *Albatross* Station 5419, 320 meters, 9°58'30"N, 123°46'E, off Lubigon, Bohol, Philippines. Buccinidae.

nympha, *Clypeomorus* Houbriek 1985, Smithsonian Contributions to Zoology, 403:113–120, figures 56–59. Replacement name for *Cerithium variegatum* Quoy and Gaimard 1834 *non* Fischer 1807 *et al.*. Lectotype and one paralectotype (of *Cerithium variegatum*), MNHNP [not numbered]; selected by Houbriek (1985: 113). Tongatapu [Tonga Islands]. Cerithiidae.

pacificum *Cerithium* Houbriek 1992, Smithsonian Contributions to Zoology, 510:143–146, figures 103–104. Holotype USNM 584662; four paratypes USNM 862491. 55–61 meters, Bikini lagoon, Bikini Atoll, Marshall Islands. Cerithiidae.

papuensis, *Simulathena* Houbriek 1992, The Veliger, 35(1):65–67, figures 1–13. Holotype AMS C166326; two paratypes USNM 559456. 8°50'S, 146°32'E, Kairuku, Yule Island, Central District, Papua New Guinea. Planaxidae.

persica, *Clypeomorus bifasciata* (Sowerby 1855) *new subspecies* Houbriek 1985, Smithsonian Contributions to

Zoology, 403:41–43, figures 17–18. Holotype, ANSP 263194; eight paratypes USNM 838028. Ras Tanura, Persian Gulf, Saudi Arabia. Cerithiidae.

purpurastoma, *Clypeomorus* Houbriek 1985, Smithsonian Contributions to Zoology, 403:83–89, figures 38–40. Holotype USNM 774749; sixteen paratypes USNM 784650. Napot Point, Morong, Bataan, Luzon, Philippines. Cerithiidae.

rehderi, *Cerithium* Houbriek 1992, Smithsonian Contributions to Zoology, 510:156–158, figures 112–113. Holotype USNM 859954; five paratypes USNM 798574. 56–72 meters, Haava Straits, between Tahuata and Hiva Oa, Marquesas. Cerithiidae.

reidi, *Cerithidea* Houbriek 1986, The Veliger, 28(3):280 *ff.*, figures 1–16. Holotype WAM 3380-84; one paratype AMS C144144; ten paratypes USNM 828823. Willies Creek, N of Broome, Western Australia, Australia. Potamididae.

scobiniforme, *Cerithium* Houbriek 1992, Smithsonian Contributions to Zoology, 510:177–179, figures 129–130. Holotype USNM 859930; two paratypes USNM 859931; six paratypes LACM 76–702. 1.5 miles S of Estango Island, Port Dimalosan, Cagayan Province, Luzon, Philippines. Cerithiidae.

III. PUBLICATIONS

R.S. Houbriek authored or co-authored a total of fifty-six research papers and notes, along with eighteen abstracts, two "President's Messages" (AMU) and two graduate theses over a twenty-seven year period (1967–1993). Of the research papers, thirty-eight (68%) treated members of the Cerithioidea (twenty-five specifically on the Cerithiidae), thirteen (23%) were on other prosobranch gastropod families, and five (9%) were on general topics.

As for publication venue, the following statistics were obtained. Thirty-one (55%) of his research papers were published in malacological serials, twenty (36%) were published in non-malacological serials (primarily the Proceedings of the Biological Society of Washington and the Smithsonian Contributions to Zoology), and the remaining five (9%) were published as book chapters.

Note: his papers for 1967–1971 were authored as "J.R. Houbriek"; those for 1972–1974b as either "R.S. Houbriek" or "R.S. (J.R.) Houbriek", and the remainder as "R.S. Houbriek".

Abbreviations

AMU American Malacological Union

WSM Western Society of Malacologists

1967 [24 April]. Notes on *Cyclostremiscus schrammii* The Nautilus 80(4):131–133.

1968a [1 Jan]. New record of *Conus ebraeus* in Costa Rica The Veliger 10(3):292.

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NOTE: Dr. Winston F. Ponder (Australian Museum) is editing and revising several uncompleted manuscripts left by R.S. Houbrick for eventual publication.

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New Data on the Distribution and Morphology of some Western Indian Ocean Sepiid Cuttlefishes (Cephalopoda: Sepiida)

Yu. A. Filippova
D. N. Khromov

Russian Research Institute of Marine
Fisheries & Oceanography (VNIRO)
107140 Moscow RUSSIA

K. N. Nesis
I. V. Nikitina

P. P. Shirshov Institute of Oceanology
Russian Academy of Sciences
117218 Moscow RUSSIA

ABSTRACT

New data are presented on the distribution and/or morphology of 21 species of the family Sepiidae, based on the collections of various expeditions during 1956-1989 in the Western Indian Ocean from the Northern Arabian Sea to Southern Mozambique, Agulhas Bank and Cargados-Carajos Islands. Previously neglected or inadequately described characters are provided for *Sepia joubini*, *S. confusa*, *S. typica* and others. New distribution records are provided for *S. omani* off Pakistan, *S. acuminata* off Somalia, Kenya and Madagascar, *S. hieronis* and *S. simoniana* off Kenya, *S. joubini*, *S. incerta*, *S. confusa*, *S. burnupi*, *S. hieronis*, *S. simoniana*, *S. officinalis vermiculata* and *S. zanzibarica* on Saya-de-Malha Bank. The Eastern Atlantic species *S. elegans* was recorded from the SW Indian Ocean on the Agulhas Bank. Four species were found at shallower depths and seven at greater depths than recorded previously. Five species are recorded at depths greater than 300 m.

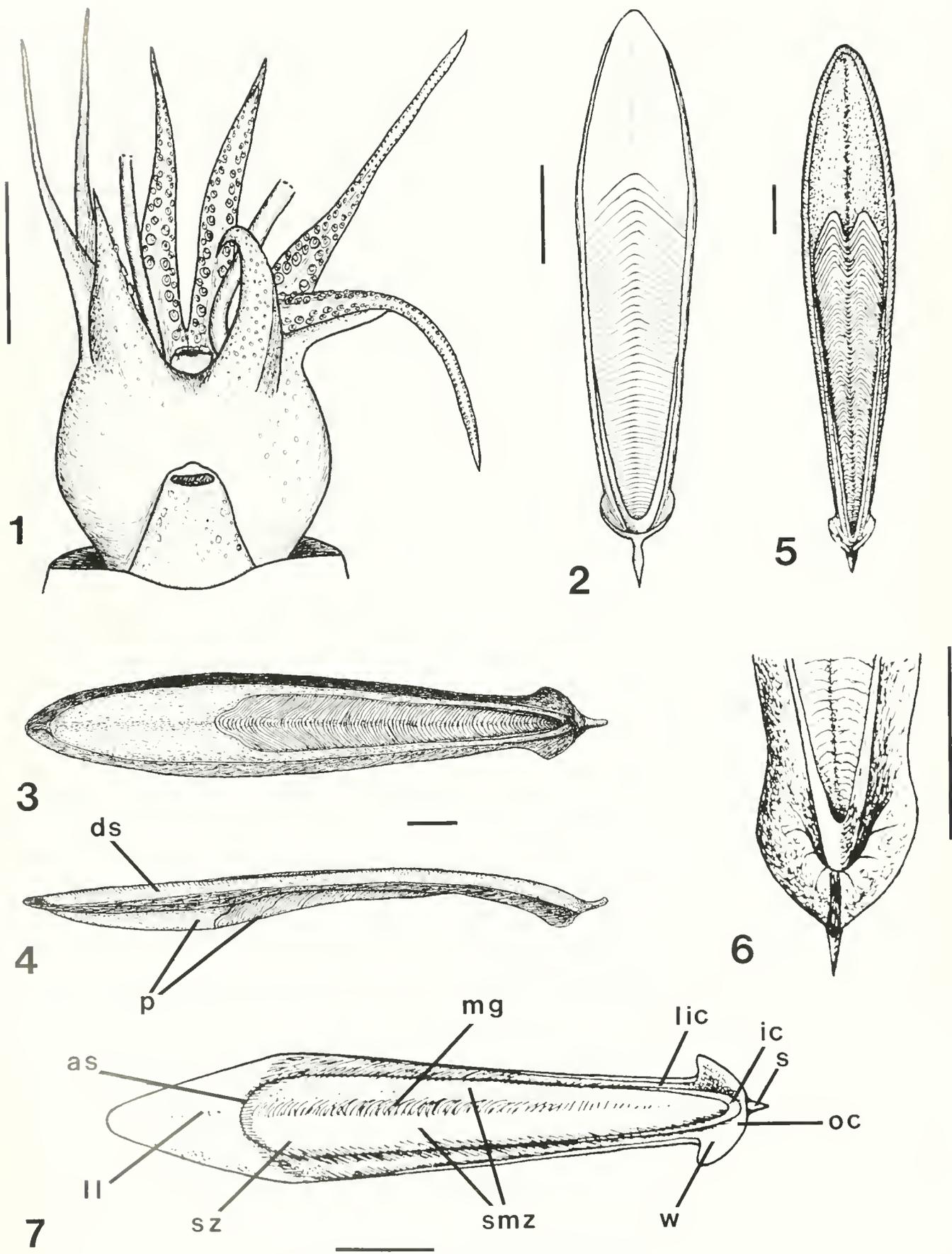
Key words: Sepiida, *Scpia*, cuttlefish, species, morphology, distribution, new records.

INTRODUCTION

The cuttlefish (Sepiidae) fauna of the Indian Ocean is incompletely known. The area has been relatively well studied in the northern part of the ocean (Adam, 1959; Adam & Rees, 1966; Silas *et al.*, 1986), in the southwestern part off South Africa (Voss, 1962; Roeleveld, 1972) and to some extent in the southeastern part off Western Australia (Adam, 1979). However, the Western Indian Ocean between the Gulf of Aden and Southern Mozambique, including many islands, archipelagoes and shallow banks (Socotra, Seychelles, Madagascar, Saya-de-Malha, Cargados-Carajos) remain almost unexplored. This broad area was studied during the last several years by various Soviet expeditions organized by many USSR institutions: All-Union (now Russian) Research Institute of Marine Fisheries and Oceanography (Moscow), Southern Research Institute of Fisheries and Oceanography (Kerch), Institute of Oceanology of the USSR (now Russian) Academy of Sciences (Moscow), Institute of the Biology of the Southern Seas, Ukrainian Academy of

Sciences (Sevastopol), Moscow State University, "Hydronaut" Base (Sevastopol), etc. As a result of these expeditions large amounts of data were gathered, particularly on the taxonomy, distribution and biology of cuttlefishes (Zuev *et al.*, 1968; Zuev, 1971; Druzhinin & Filippova, 1974; Homenko, 1976, 1983, 1989; Nesis, 1980, 1993; Homenko & Khromov, 1984; Khromov, 1982, 1987, 1988a; Filippova & Khromov, 1991; Khromov *et al.*, 1991). As a result of these expeditions, the sepiid fauna of the Western Indian Ocean was found to be richer and more diverse than was previously supposed. Ten new species have been described to date, and others are awaiting description. Some species are common and may have commercial potential. The data gathered permit a fresh examination of the composition, distribution and relationships of the sepiid fauna of the Indian Ocean as a whole. We present new data on the distribution of several known species, and on the morphology of some species described incompletely or inadequately. All but one are inhabitants of the Indian Ocean—*Sepia elegans* is an Atlantic species recorded for the first time in the Indian Ocean off South Africa.

This work is based primarily on the catches made in 1976 by the R/V "Professor Mesyatzev" off East Africa between 2°S and 25°S, off the Cargados-Carajos Islands and on Saya-de-Malha Bank, and by the R/V "Vityaz" in 1988-89 off Socotra, Madagascar, Mozambique and on Saya-de-Malha Bank. We have also studied collections of many other expeditions, and are grateful to the collectors of the following material: G. M. Belyaev ("Ob", 1956), V. N. Semenov ("Akademik Knipovich", 1965-66), the late V. I. Chekunova ("Akademik Knipovich", 1967), the late S. V. Mikhailin ("Gizhiga", 1975), B. G. Ivanov ("Professor Mesyatzev", 1975-76), L. S. Homenko ("Nauka", 1976, "Zheleznyakov", 1977, "Yelsk", 1977-78), N. S. Khromov ("Fiolet", 1976, "Sabah", 1979), V. A. Spiridonov ("Odyssey", 1980), M. G. Karpinsky ("Professor Mesyatzev", 1983), D. L. Ivanov ("Akademik Petrovsky", 1984), Yu. S. Korzun ("Skif", 1986), V. A. Bizikov and D. O. Alekseyev ("Akademik Knipovich", 1984, "Odyssey", 1985, "Gidrobiolog", 1987). All specimens are either in the Russian Research Institute



of Marine Fisheries and Oceanography (VNIRO), the Zoological Museum of Moscow University (ZMMU), or in the Institute of Oceanology of the Russian Academy of Sciences (IOAS), Moscow.

SYSTEMATICS

Family Sepiidae

1. *Sepia (Doratosepion) joubini* Massy, 1927 (Figs. 1, 2, 20)

Material examined: "Vityaz", 25/11/1988, sta. 2634a, bottom trawl, 90–92 m, 25°05'S, 34°50'–34°44'E: 1 female ML 42 mm, IOAS; "Professor Mesyatzev", 24/01/1976, sta. 64, bottom trawl, 167–170 m, 24°23'S, 35°29'E: 1 female ML 64 mm, ZMMU 327.

Description and remarks: This species was described by Massy (1927), redescribed (syntypes) by Adam and Rees (1966), and again redescribed (topotypes) by Roeleveld (1972). In spite of the large number of described specimens of both sexes, the sepions of *S. joubini* remain nearly unknown because they were damaged and decalcified in both the syntypes and the topotypes.

Adam and Rees (1966) doubted the validity of *S. joubini*. According to Roeleveld (1972) the cuttlebones of the topotypes were narrow and elongated, pointed anteriorly, with a median longitudinal ridge dorsally and groove ventrally. The striated zone is convex on both sides of the median groove, angular anteriorly, becoming flattened posteriorly, with convex and wavy striae posteriorly. The inner cone has narrow limbs that form a ledge posteriorly. The outer cone has posterior wings. Roeleveld (1972) also mentioned a peculiar structure at the base of the spine, but it is not known whether it occurs in all specimens. Roeleveld's figure of *S. joubini* illustrates an expansion of the posterior part of the inner cone that is not described in the text. With this discrepancy and her description of a decalcified sepion, unambiguous identification of this species is difficult.

There are two females of *S. joubini* in our material, one (sta. 2634a) properly fixed and in good condition. Therefore we are able to add several important details to the description of this species.

The dorsal surface of the mantle of the living animal has small red spots and interrupted light-colored stripes along the fins that form a series of elongate, raised bolsters as in *S. (D.) peterseni* Appelloef, 1886, and *S. (D.) vietnamica* Khromov, 1987. The fins are narrow and slightly expanded posteriorly. The characteristic arms of the fe-

male differ in length (lateral arms longer than the dorsal and ventral), have attenuated tips and well developed protective membranes (Fig. 1), and correspond to Roeleveld's (1972) description. Longitudinal red stripes are found on the dorsal side of the head and on dorsal and lateral arms of living animals, but are not evident on fixed specimens. The sepion is dark-cream colored, narrowly elongate, width 24%, thickness 9% of length. A median rib, not limited by grooves, lies on the dorsal surface of the sepion. Only the median third of the dorsal shield is calcified and bordered by wide, chitinous margins. The sepion is semi-rounded in cross-section, with a flattened middle part of phragmocone. The median groove, shallow on the striated zone and deep on the last loculus, is clearly marked along the whole length of the phragmocone. The striated zone occupies the entire width on the ventral side, and is bordered by smooth marginal zones. Anterior striae are reversed V-shaped. The inner cone forms a ledge that is slightly expanded posteriorly, but without any blade-like structure, as in Roeleveld's figure. Inner cone limbs are close to the chitinous margins. The outer cone forms a regular, cup-like, decalcified structure posteriorly. The spine is long, narrow at its base, slightly expanded in the middle part, and spindle-like in lateral view.

We confirm Roeleveld's opinion on the validity of *S. joubini* and consider this species to be fully described now.

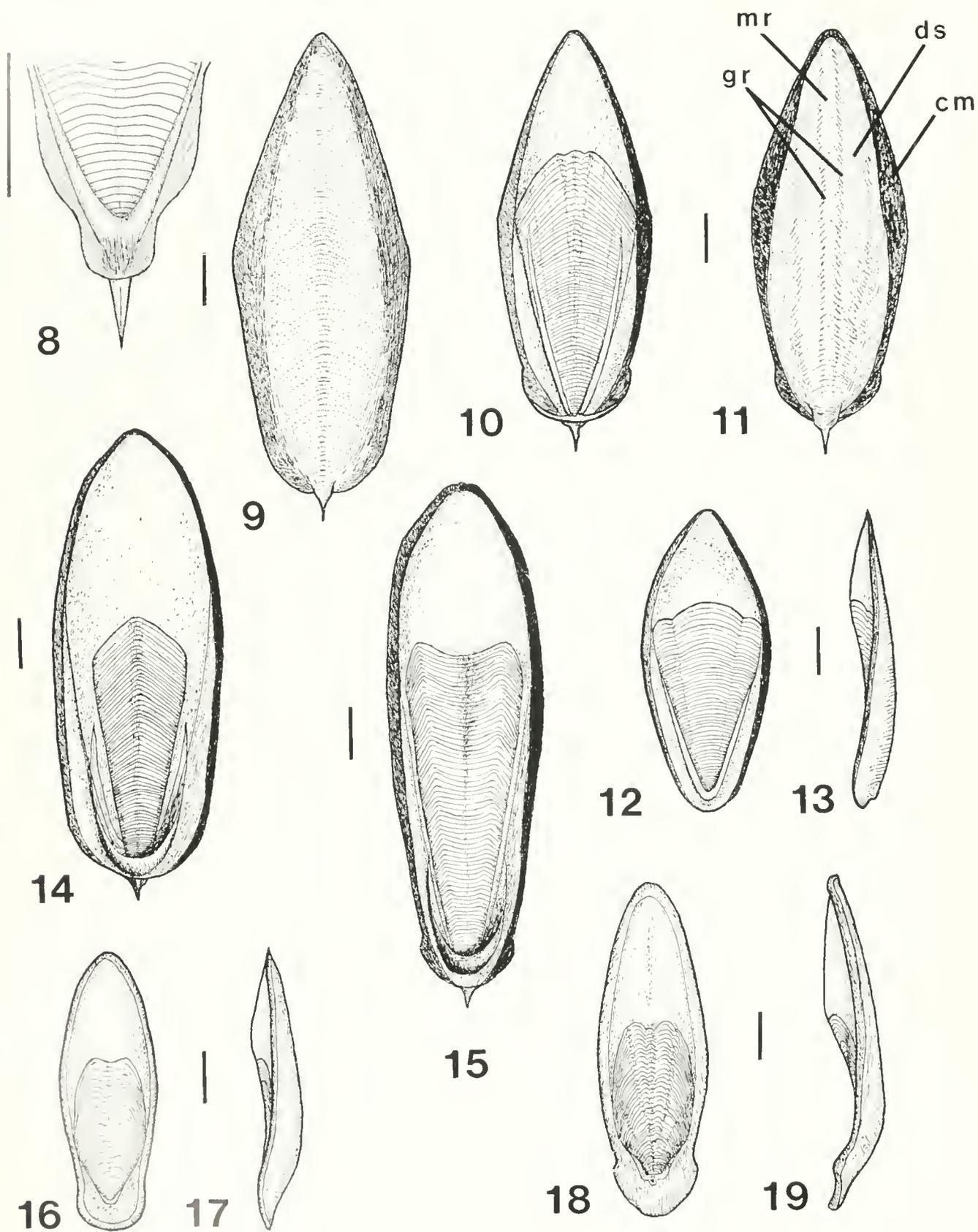
A female (ML 64 mm) in these collections (ZMMU) is the largest known specimen.

Distribution: *Sepia joubini* was recorded off South-eastern Africa, from the Tugela River to Cape Natal (Roeleveld, 1972). We found this species off Southern Mozambique, 24–25°S. The depth range of 66–134 m (Roeleveld, 1972), is expanded to 66–170 m.

2. *Sepia (Doratosepion) incerta* Smith, 1916 (Figs. 3, 4, 20)

Material examined: "Professor Mesyatzev", 18/01/1976, sta. 41, bottom trawl, 100 m, 18°29'S, 37°17'E: 3 males, ML 44, 115, 118 mm, 2 females, ML 82, 88 mm; "Professor Mesyatzev", 19/01/1976, sta. 44, bottom trawl, 152–172 m, 19°07'S, 36°59'E: 1 male, ML 123 mm; "Professor Mesyatzev", 24/01/1976, sta. 64, bottom trawl, 167–170 m, 24°23'S, 35°29'E: 2 males, ML 53, 111 mm, all specimens are in the collections of ZMMU, No 185, 212, 230, 232, 334. "Professor Mesyatzev", 31/01/1976, sta. 77, bottom trawl, 330–345 m, 25°21'S, 34°19'E: 1 female, ML 82 mm, VNIRO. "Vityaz", 25/11/1988, sta.

Figures 1, 2. *Sepia (Doratosepion) joubini* Massy, 1927. ML 42 mm, 25°05'S, 34°50'–34°44'E, 90–92 m, IOAS, uncatalogued. 1. Head of female. 2. Sepion of female. **Figures 3, 4.** *Sepia (Doratosepion) incerta* Smith, 1916 ML 115 mm, 18°29'S, 37°17'E, 100 m, ZMMU No. 212. 3. Dorsal and 4. lateral views of sepion of male. **Figures 5, 6.** *Sepia (Doratosepion) confusa* Smith, 1916 ML 103 mm, 24°23'S, 35°29'E, 167–170 m, VNIRO, uncatalogued. 5. Sepion of male 6. Posterior part of male sepion. **Figure 7.** *Sepia (Doratosepion) trygonina* Rochebrune, 1884 ML 65 mm, Saya-de-Malha Bank, VNIRO, uncatalogued. Sepion of male. All scale bars = 1 cm. as, anterior striae; ds, dorsal shield; ic, inner cone; lic, limbs of inner cone; ll, last loculus; mg, median groove (or furrow); oc, outer cone; p, phragmocone; s, spine; smz, smooth marginal zone; sz, striated zone; sp, spine; w, wings of outer cone.



2634a, bottom trawl, 90–92 m, 25°05'S, 34°50'–34°44'E: 1 male ML 45 mm, 1 female, ML 91 mm, IOAS.

Description and remarks: All our specimens are quite typical and agree completely with the descriptions of Adam and Rees (1966) and Roeleveld (1972). Large males are characterized by a peculiar transformation of the dorsal arms. Males and females differ from all other species in having a furrow on the posterior ventral part of the sepion inner cone. In the largest female (ML 91 mm) the eggs from the ovary are very elongate (8.9 × 3.2 mm).

Distribution: *Sepia incerta* was recorded off eastern Cape Province and Natal, East London to Durban (Massy, 1925). Sepions were also found from Port Elizabeth to Southern Mozambique (Roeleveld, 1972). We found the animals from North to South Mozambique, 18°29' to 25°21'S, at depths of 90–345 m, significantly deeper than previous records for this species (70–79 m; Roeleveld, 1972).

3. *Sepia (Doratossepion) confusa* Smith, 1916 (Figs. 5, 6, 20)

Material examined: "Professor Mesyatzev", 06/01/1976, sta. 25, bottom trawl, 335 m, 05°19'S, 39°09'E: 3 females, ML 64, 69, 69 mm; "Professor Mesyatzev", 22/01/1976, sta. 57, bottom trawl, 150–170 m, 21°27'S, 35°32'E: 1 male, ML 70 mm; "Professor Mesyatzev", 24/01/1976, sta. 64, bottom trawl, 167–170 m, 24°23'S, 35°29'E: 5 males, ML 91–148 mm; "Professor Mesyatzev", 25/01/1976, sta. 65, bottom trawl, 256–258 m, 24°43'S, 35°26'E: 5 males, ML 62–117 mm; "Professor Mesyatzev", 25/01/1976, sta. 66, bottom trawl, 200–210 m, 24°57'S, 35°07'E: 90 males, ML 48–135 mm; "Professor Mesyatzev", 25/01/1976, sta. 67, bottom trawl, 56–53 m, 24°51'S, 35°05'E: 1 male, ML 120 mm, some of the specimens are in the collection of ZMMU, Nos. 206, 215. "Vityaz", 25/11/1988, sta. 2635, bottom trawl, 225–228 m, 25°05'–25°06'S, 35°15'E: 5 females ML 63–68 mm, 30 males 75–115 mm; some of the specimens are in the collection of IOAS, (there were nearly 600 specimens of both sexes of this species in this catch, but males greatly outnumbered females).

Description and remarks: *Sepia confusa* males differ from all other species in having a long "tail" (Adam & Rees, 1966; Roeleveld, 1972). The length of this structure,

formed by fins fused or not fused posteriorly, depends on the stage of maturity. Mature males have long tails that are absent in immature males and in females. The tail first appears at the 2nd maturity stage, and begins to grow exponentially at ML about 90 mm, at which size males change from the 3rd to the 4th maturity stage. In females, the dorsal arms have expanded membranes and two rows of suckers distally as in *S. joubini*. The lateral arms have the same two rows of suckers distally, but the protective membranes do not expand. Dorsolateral arms are not attenuated and are subequal in length. The sepion differs from other species in having a dorsal posterior keel and a ventral margin of the outer cone that is inverted to the outer side, triangular and thickened medially.

Egg size in a female (ML 72 mm) was 5.0–5.1 × 2.6–2.7 mm.

Distribution: *Sepia confusa* occurs off eastern and southeastern Africa (5° to 30°S). The northernmost records are off Zanzibar (Adam & Rees, 1966) and Pemba (our data). We found it to be very common along the coast of Mozambique, 21°30'–25°S. The record of this species from the Arabian Sea (Zuev, 1971), is erroneous, while a record from Saya-de-Malha Bank (Nesis, 1982) was not confirmed by more recent expeditions (Nesis, 1993). This species was recorded at depths of 53–352 m (Roeleveld, 1972; our data).

4. *Sepia (Doratossepion) burnupi* Hoyle, 1904 (= *Sepia exsignata* Barnard, 1962) (Fig. 20)

Material examined: "Professor Mesyatzev", 23/01/1976, sta. 62, bottom trawl, 235–240 m, 23°29'S, 35°33'E: 2 males, ML 54, 56 mm, ZMMU 221.

Description and remarks: This species was hitherto known from three sepions and three specimens taken off Natal (Massy, 1925; Barnard, 1962; Roeleveld, 1972). The two males of *S. burnupi* in our collection are practically identical with Roeleveld's (1972) description and figures of this species.

Distribution: *Sepia burnupi* is a very rare species. Our collections enlarge its known range to Southern Mozambique, and known depth distribution from 40–48 m to 235–240 m.

Figure 8. *Sepia (Anomalosepia) omani* Adam, 1939. Posterior part of female sepion. Redrawn from Adam & Rees, 1966, pl. 22, fig. 144 **Figures 9–11.** *Sepia (Rhombosepion) acuminata* Smith, 1916. **9.** ML 84 mm, 05°19'S, 39°09'E, 335 m, ZMMU No. 204. Atypical sepion of female with furrow. **10–11.** ML 87 mm, 24°25'S, 35°29'E, 170 m, VNIRO uncatalogued. **10.** Ventral and **11.** dorsal view of typical sepion of female with rib. **Figures 12, 13.** *Sepia (Rhombosepion) hieronis* Robson, 1924. ML 62 mm, 04°47'S, 39°24'E, 180–185 m, ZMMU No. 227. **12.** Ventral and **13.** lateral views of sepion of a male. **Figure 14.** *Sepia (Acanthosepion) zanzibarica* Pfeffer, 1884. ML 92 mm, 12°22'S, 54°28'E, 50 m, ZMMU No. 317. Sepion of male. **Figure 15.** *Sepia (Acanthosepion) prashadi* Winckworth, 1936. ML 90 mm, 04°47'S, 39°24'E, 180–185 m, ZMMU No. 249. Sepion of male. **Figures 16, 17.** *Sepiella cyanea* Robson, 1924. ML 60 mm, 17°13'S, 38°39'E, 14 m, ZMMU No. 207. **16.** Ventral and **17.** lateral views of sepion of male. **Figures 18, 19.** *Sepiella inermis* (Férussac & d'Orbigny, 1835). ML 66 mm, Kuwait territorial waters, 0–20 m, ZMMU No. 198. **18.** Ventral and **19.** lateral views of sepion of male. Scale bars = 1 cm. cm, chitinous margin of sepion; ds, dorsal shield; gr, grooves beside median ridge; mr, median ridge (or rib).

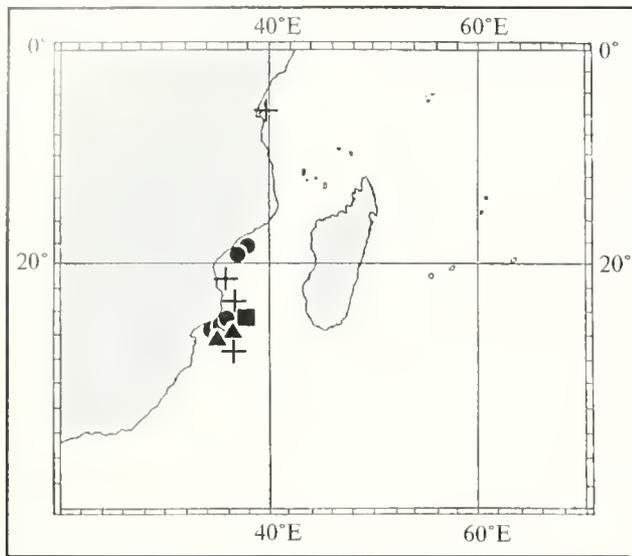


Figure 20. Distribution of *Sepia (Doratossepion)* in the western Indian Ocean. Triangles = *Sepia (Doratossepion) joubini*, circles = *S. (D.) incerta*, crosses = *S. (D.) confusa*, square = *S. (D.) burnupi*.

5. *Sepia (Doratossepion) trygonina* Rochebrune, 1884 (Figs. 7, 21)

Material examined: "Ob", 08/06/1956, sta. 150, bottom trawl, 50 m, 11°50'N, 51°10'E: 8 females, ML 53–85 mm; "Ob", 10/06/1956, sta. 152, bottom trawl, 30 m, 12°05'N, 44°12'E: 1 male, ML 48 mm, 1 female, ML 36 mm; "Professor Mesyatzev", 19/12/1975, sta. 2, bottom trawl, 67–77 m, 2°24'S, 40°56'E: 2 males, ML 110, 41 mm; "Yelsk", December 1977 – January 1978, Saya-de-Malha Bank, 205 m, some sepions; "Professor Mesyatzev", 27/03/1983, sta. 14, bottom trawl, 200 m, 11°30'S, 60°49'E: 2 females, ML 46, 53 mm; "Akademik Petrovsky", 20/01/1984, sta. 67, Sigsbee trawl, 55 m, 15°07'N, 41°41'E: 1 female, ML 28 mm; "Odyssey", 27/05/1984, sta. 9, bottom trawl, 28 m, 12°19'N, 53°22'E: 2 males, ML 51, 59 mm, 8 females, ML 51–74 mm; "Odyssey", 27/05/1984, sta. 10, bottom trawl, 27 m, 12°14'N, 53°46'E: 1 female, ML 31 mm; "Odyssey", 19/04/1985, sta. 95, Sigsbee trawl, 80 m, 12°21'N, 54°28'E: 1 male, ML 30 mm; "Odyssey", 19/04/1985, sta. 96, bottom trawl, 100 m, 12°19'N, 54°25'E: 2 males, ML 47–60 mm; "Skif", 01/11/1986, sta. 140, bottom trawl, 20 m, 15°35'N, 52°32'E: 1 male, ML 47 mm, 1 female, ML 45 mm, 1 juv., ML 25 mm; "Gidrobiolog", 01/05/1987, sta. 2, bottom trawl, 50 m, 13°37'N, 47°23'E: 3 females, ML 47, 49, 61 mm, 5 juv., ML 30–20 mm; "Gidrobiolog", 16/05/1987, sta. 6, bottom trawl, 33 m, 14°47'N, 50°01'E: 2 females, ML 52, 62 mm; "Gidrobiolog", 29/05/1987, sta. 10, bottom trawl, 50 m, 13°55'N, 48°29'E: 5 females, ML 52–64 mm; "Gidrobiolog", 10/05/1987, sta. 18, bottom trawl, 37–40 m, 11°56'N, 53°44'E: 2 females, ML 71, 74 mm; "Gidrobiolog", 28/05/1987, sta. 18, bottom trawl, 40 m, 13°59'N, 47°57'E: 6 females, ML 37–63

mm, collections of VNIRO and ZMMU, Nos. 184, 197, 304, 310, 314, 316, 319, 324, 331.

Remarks: Sepions of *S. trygonina* are very similar to those of *S. burnupi*, but the soft bodies of these species are distinctly different. In *S. trygonina*, the arms of males are not transformed as in *S. burnupi* and the lateral arms of females have two widely spaced rows of suckers in the distal portions.

Distribution: *Sepia trygonina* was first described from the Red Sea and later reported from different areas of the northwestern Indian Ocean: from the Gulf of Aden and Kuria-Muria Islands to the Gulf of Mannar (Adam & Rees, 1966; Druzhinin & Filippova, 1971; Sarvesan, 1976). We found this species south of the equator on the Saya-de-Malha Bank, at 15°35'N to 11°30'S, at depths of 20 to 205 m. Mantle length reaches 110 mm in males, 85 mm in females, and is much larger than reported previously.

6. *Sepia (Doratossepion) mascarensis* Filippova and Khromov, 1991 (Fig. 21)

Material examined: "Professor Mesyatzev", 04/04/1976, sta. 128, bottom trawl, Kargados-Karajos Islands: 1 male, ML 105 mm; "Professor Mesyatzev" 05/04/1976, sta. 129, bottom trawl, 316–325 m, 15°45'S, 61°15'E: 1 male, ML 90 mm; "Professor Mesyatzev", 27/03/1983, sta. 14, bottom trawl, 200 m, 11°30'S, 60°49'E: 20 males ML ? (in poor state); "Professor Mesyatzev", 27/03/1983, sta. 15, bottom trawl, 195 m, 11°31'S, 61°00'E: 15 males, ML 67–124 mm; "Yunaya smena", 1985, Saya-de-Malha Bank: dry and broken sepions, collections of VNIRO and ZMMU, Nos. 233, 234, 349, 350. "Vityaz", 07/01/1989, sta. 2803, bottom trawl, 87–110 m, 11°21'–11°22'S, 61°47'E: 7 females, ML 50–63 mm, IOAS.

Description and remarks: This species is fully described from males (Filippova & Khromov, 1991) and females (Khromov *et al.*, 1991). Our specimens agree completely with these descriptions. The males of *S. mascarensis* are characterized by their untransformed arms, the absence of a hectocotylus, and a narrow and relatively thick sepion that has a rib on its ventral side and reversed, W-shaped, ventral striae. The females of this species have long second arms with two rows of suckers distally and narrow sepions with reversed, W-shaped ventral striae as well as a furrow (not a rib) on the ventral side.

Distribution: *Sepia mascarensis* is reported from the Mascarene Ridge, the Saya-de-Malha Bank and shoals around the Kargados-Karajos Islands, at depths of 87–325 m.

7. *Sepia (Doratossepion) arabica* Massy, 1916 (Fig. 21)

Material examined: "Skif", 01/11/1986, sta. 10, bottom

trawl, 20 m, 15°35'N, 52°32'E: 1 male, ML 88 mm, collection of VNIRO.

Description and remarks: This specimen agrees with the description and illustrations of Adam and Rees (1966). This mature male with a developed hectocotylus is the largest recorded specimen of this species.

Distribution: Red Sea, Gulf of Aden to southern India.

8. *Sepia (Doratossepion) sp.*
(Fig. 21)

Material examined: "Vityaz", 07/01/1989, sta. 2804, bottom trawl, 230–235 m, 11°06'–11°09'S, 62°14'–62°13'E: 1 female ML 65 mm, IOAS.

Description and remarks: Mantle elongate oval, anterior margin somewhat produced dorsally, emarginate ventrally. Arms subequal in length, lateral arms slightly longer. Arms pairs I, II, and III with well developed, spade-like protective membranes covering the suckers on the distal third of arms. The suckers are quadriserial proximally, becoming biserial and widely spaced distally. The fourth arms have quadriserial suckers. Tentacular club with 5 rows of suckers, differing slightly in size, with the suckers of the central row the largest. Sepion is cream colored, narrow, elongate, with a rib, delimited by furrows dorsally and a median groove ventrally, and slightly W-shaped in cross-section. The striated zone occupies the entire width of the ventral side, with the anterior striae semi-rounded, slightly emarginated in the ventral groove. The inner cone forms a ledge that is slightly raised posteriorly, but not expanded. The outer cone is cup-like and calcified, forming a toothed structure on the ventral margin similar to that of *S. incerta* (Roeleveld, 1972, Fig.6,d). The spine is long, lacks a base and spindle-like laterally.

This female is similar to one of *S. confusa*, but the sepion differs distinctly by the semi-rounded anterior striae, the absence of an inverted, triangle-shaped ventral margin on the inner cone, and a posterior dorsal keel on the sepion. It also resembles *S. joubini*, but the arms of the latter species are markedly longer and attenuated at their ends. Moreover, the striae of *S. joubini* are reversed V-shaped, its sepion is semi-rounded in cross-section, its inner cone is slightly expanded posteriorly, and its outer cone is decalcified. The sepion of *Sepia sp.* can be easily confused with that of *S. incerta*, but it has no groove on the posterior portion of the inner cone.

We could not identify *Sepia sp.* in spite of the good condition of the specimen. Possibly it is a new species, but the description of a new species in so complex a subgenus as *Doratossepion* would not be appropriate in the absence of a male specimen.

9. *Sepia (Anomalosepia) omani* Adam and Rees, 1966
(Figs. 8, 22)

Material examined: "Akademik Knipovich", 19/01/1966, sta. 310, bottom trawl, 210 m, 23°42'N, 66°14'E: 2 males, ML 78, 80 mm, 1 female, ML 85 mm, 3 juv., ML 30, 31, 35 mm, ZMMU 214.

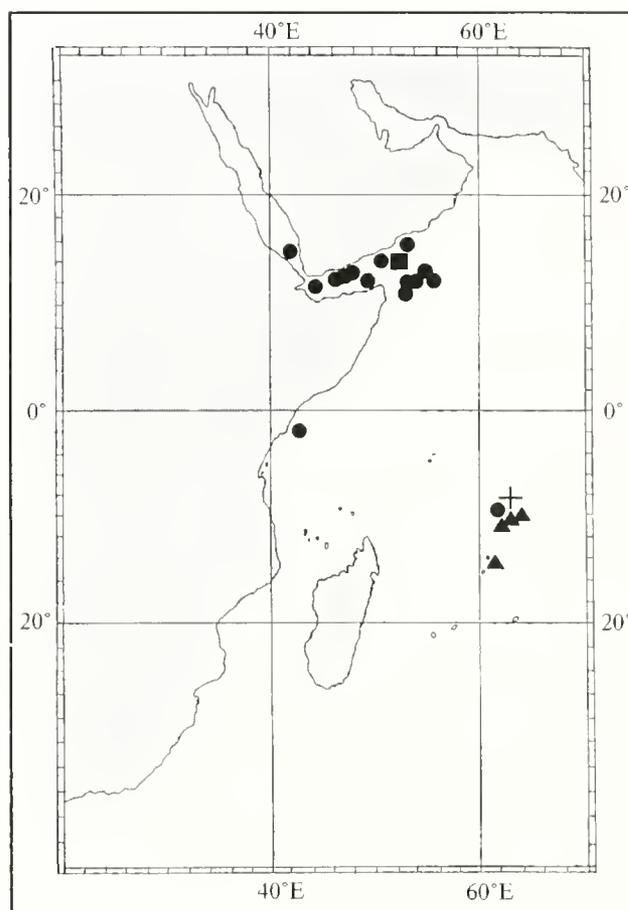


Figure 21. Distribution of *Sepia (Doratossepion)* in the western Indian Ocean. Circles = *S. (D.) trygonina*, triangles = *S. (D.) mascarensis*, square = *S. (D.) arabica*, cross = *S. (D.) sp.*

Description and remarks: *Sepia omani* is the only species with two pairs of outer cone wings on the sepion. Thus, the specimens referred to *S. omani* by Voss and Williamson, 1971 are certainly not correctly identified. The opinion (Klromov, 1988b) that these animals are *S. rex* is also erroneous. The Hong Kong specimens probably belong to a new species.

Distribution: *Sepia omani* was known only from the Gulf of Oman, at a depth of 201 m. We found it in the northern part of the Arabian Sea, off Pakistan, at nearly the same depth, 210 m.

10. *Sepia (Rhombosepia) acuminata* Smith, 1916
(Figs. 9-11, 22)

Material examined: "Professor Mesyatzev", 19/12/1975, sta. 1, bottom trawl, off North Kenya: 1 male, ML 93 mm, 1 female, ML 75 mm; "Professor Mesyatzev", 21/12/1975, sta. 3, bottom trawl, 290–295 m, 3°02'S, 40°26'E: 1 male, ML 84 mm, 1 broken sepion; "Professor Mesyatzev", 04/01/1976, sta. 23, bottom trawl, 44 m, 04°03'S, 40°00'E: 1 male, ML 73 mm, 1 female, ML 75 mm; "Professor Mesyatzev", 06/01/1976, sta. 25, bottom trawl,

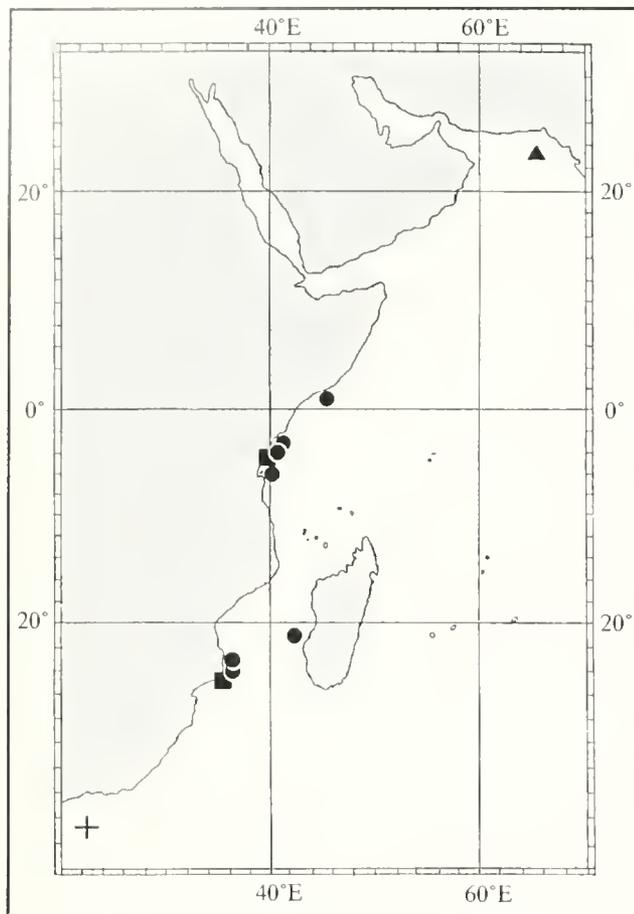


Figure 22. Distribution of *Sepia (Anomalosepia)* and *Sepia (Rhombosepia)* in the western Indian Ocean. Triangle = *Sepia (Anomalosepia) omani*, circles = *Sepia (Rhombosepia) acuminata*, squares = *S. (R.) hieronis*, cross = *S. (R.) elegans*.

335 m, 05°19'S, 39°09'E: 1 male, ML 102 mm, 3 females, ML 56, 100, 111 mm; "Professor Mesyatzev", 24/01/1976, sta. 64, bottom trawl, 170 m, 24°25'S, 35°29'E: 1 sepiion 84 mm; "Zheleznyakov", 07/03/1977, bottom trawl, 230–235 m, 01°31'N, 44°39'E: 1 male, ML 55 mm, 2 broken sepiions, collections of VNIRO and ZMMU, Nos. 191, 192, 204, 225, 242. "Vityaz", sta. 2635, 25/11/1988, bottom trawl, 225–228 m, 25°05'–25°06'S, 35°15'E: 11 females, ML 84–119 mm, 14 males, ML 52–91 mm, 1 juv ML 31 mm, collection of IOAS, 66 unsexed and unmeasured specimens of the same species; "Vityaz", sta. 2644, 02/12/1988, bottom trawl, 325–332 m, 22°19'–22°23'S, 43°06'E: 4 females ML 89–115 mm, 1 sepiion 110 mm, collection of IOAS.

Description and remarks: We note an interesting variability of sepiions in this species. Typical sepiions of *S. acuminata* caught in South African waters (Port Elizabeth) show a distinct median rib and a faint indication of two lateral ribs on the dorsal surface (Adam & Rees, 1966). These authors also reported on three additional sepiions from Mombasa that had a deep, narrow groove instead of a rib. Roeleveld (1972) described specimens

from Mozambique that had a median ridge sometimes sunken below the level of rest of dorsal surface.

Having examined our material, we noted a clear rib on the sepiions of specimens from southern Mozambique, a flat dorsal side or one slightly sunken below the rib on sepiions from northern Mozambique and Tanzania, and a groove on the sepiions of animals from Kenya and southern Somalia. Females of *S. acuminata* from southern Madagascar have a flat dorsal surface on the sepiion. Small males look alike, but the largest male has a sepiion with a slightly marked groove. We therefore suggest that the presence of a rib or groove may be a geographical variation that is more evident in large animals.

Distribution: *Sepia acuminata* has not been previously reported from off Madagascar, northern Kenya, or Somalia. This species has a wide range along all eastern Africa, from 01°30'N to 30°S, including Madagascar. It was recorded at depths of 44–369 m (Roeleveld, 1972; our data). Maximum size is presently a mantle length of up to 100 mm in males and 120 mm in females. Egg size in a female of 110 mm ML was 5.0–5.2 × 4.5–4.7 mm, while in smaller females it ranged between 4.2–4.9 × 3.3–4.5 mm. Females mature at about 85–90 mm ML.

11. *Sepia (Rhombosepia) hieronis* Robson, 1924 (Fig. 12, 13, 22)

Material examined: "Professor Mesyatzev", 05/01/1976, sta. 24, bottom trawl, 180–185 m, 04°47'S, 39°24'E: 1 male, ML 62 mm; "Professor Mesyatzev", 27/01/1976, sta. 73, bottom trawl, 430–440 m, 25°28'S, 33°32'E: 2 males, ML 42, 48 mm, ZMMU 227, 228.

Description and remarks: Our specimens agree completely with the descriptions of Adam and Rees (1966) and Roeleveld (1972).

Distribution: *Sepia hieronis* has been reported in the south-eastern Atlantic, from northern Namibia to Slangkop and in the western Indian Ocean off southern Mozambique and on the Agulhas Bank (Voss, 1962, 1967; Roeleveld, 1972; Okutani & Hasegawa, 1979; Sánchez & Molí, 1984; Sánchez, 1988; Sánchez & Villanueva, 1988). We collected it off Mozambique and Kenya, so *S. hieronis* is quite widely distributed south of Angola and Zanzibar, but is not reported off South Africa between the Cape of Good Hope and St. Francis Bay. The depth range is 43–457 m (Roeleveld, 1972).

12. *Sepia (Rhombosepia) elegans* d'Orbigny, 1826 (Fig. 22)

Material examined: "Ob", 18/03/1957, sta. 263, bottom trawl, 110 m, 37°12'S, 22°30'E: 4 males, ML 39–45 mm; "Gizhiga", 15/02/1975, sta. 266, bottom trawl, 180–200 m, 21°10'S, 13°20'E: 1 female, ML 59 mm; "Fiolent", sta. 136, 12/03/1976, 250 m, 06°26'S, 11°36'E: 4 females, ML 73–89 mm; "Odyssey", 06/12/1980, bottom trawl, 200 m, 31°25'N, 21°10'W: 1 male, ML 55 mm; "Akademik Kuipovich", sta. 8, 05/01/1967, 180–210 m, West Africa: 1 male, ML 50 mm; "Akademik Kuipovich", 07/

06/1969, 80–95 m, 21°50'N, 17°20'W: 1 male, ML 50, 1 female, ML 53 mm; "Akademik Knipovich", sta. 1, 30/01/1984, 140–200 m, 23°46'N, 16°51'W: 3 females, ML 36, 39, 46 mm, collections of VNIRO and ZMMU, Nos. 186, 193 222, 226, 307.

Description and remarks: Our specimens agree completely with the description of Adam and Rees (1966).

Distribution: *Sepia elegans* is a widely distributed eastern Atlantic species, reported along the coasts of Europe and West Africa from Ireland to Namibia (Adam & Rees, 1966; Sánchez & Molí, 1984; Sánchez, 1988). We recorded mature specimens from the Agulhas Bank, so the range of *S. elegans* extends into the southwestern Indian Ocean.

13. *Sepia (Sepia) papillata* Quoy and Gaimard, 1832 (Fig. 23)

Material examined: "Professor Mesyatzev", 06/04/1976, sta. 131, bottom trawl, 180–210 m, 15°48'S, 59°58'E: 1 male, ML 123 mm, 1 female, ML 107 mm; "Odissey", 12/06/1984, sta. 14, bottom trawl, 35 m, 09°42'S, 61°08'E: 2 males, ML 50, 64 mm, ZMMU 254, 330; "Vityaz", 08/01/1988, sta. 2808, bottom trawl, 58–61 m, 11°05'S, 62°02'–62°04'E: 5 males ML 37–58 mm, 10 females ML 28–51 mm; "Vityaz", 08/01/1988, sta. 2810, bottom trawl, 57–70 m, 10°15'–10°16'S, 61°09'E: 2 males, ML 63, 65 mm, 1 female, ML 75 mm, IOAS.

Description and remarks: This species differs from the previous ones in having a broadly oval sepion with a deep and wide median ventral groove and a considerably narrowed and flat inner cone. According to Adam and Rees (1966), there is no spine, but only a blunt knob on the sepion posterior. Roeleveld (1972) described a short spine not exceeding the posterior margins of the shell. Our specimens from Saya-de-Malha Bank are not typical, as some have a short spine visible from the ventral side of the sepion. Thus, the length of spine of *S. papillata* is variable.

Living animals of *S. papillata* from "Vityaz" station 2808 were very brightly colored, scarlet and gold, without stripes or spots, while specimens from station 2810 were brown with zebra-like stripes and red spots. The color of the animals probably reflects the color of the substrate (crustose red algae at sta. 2808). Fixed animals are not brightly colored and can be easily confused with *S. o. vermiculata* and *S. simoniana*. Females mature at about 50 mm ML.

Distribution: This species was previously reported along the coast of South Africa from Luederitz Bay (Atlantic) to the Tugela River (Indian Ocean), and especially near Cape Town (Roeleveld, 1972; Okutani & Hasegawa, 1979). As we have caught it far from this region, on the Mascarene Ridge, the range of *S. papillata* is greatly extended. The depth range for our samples is 35–210 m, somewhat deeper than 26–127 m range recorded previously by Roeleveld (1972).

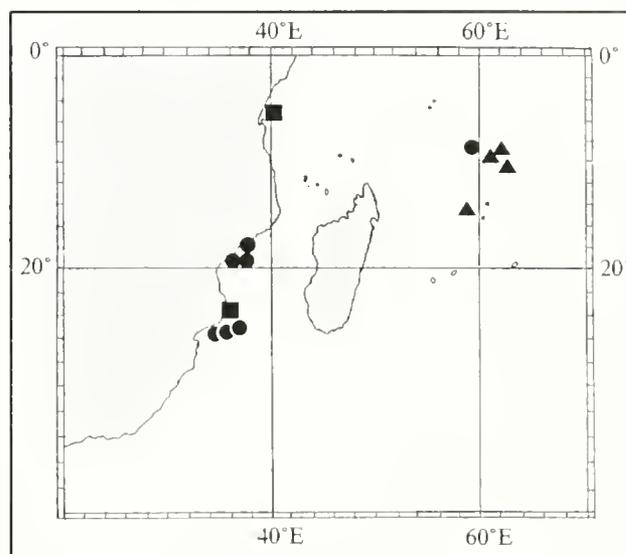


Figure 23. Distribution of *Sepia (Sepia)* in the western Indian Ocean. Triangles = *Sepia (Sepia) papillata*, squares = *S. (S) simoniana*, circles = *S. (S) officinalis vermiculata*.

14. *Sepia (Sepia) simoniana* Thiele, 1921 (Fig. 23)

Material examined: "Professor Mesyatzev", 05/01/1976, sta. 24, bottom trawl, 180–185 m, 04°47'S, 39°24'E: 1 male, ML 91 mm, 1 female, ML 95 mm; "Professor Mesyatzev", 24/01/1976, sta. 64, bottom trawl, 170 m, 24°23'S, 35°29'E: 5 females, ML 58–99 mm, ZMMU 200, 250.

Description and remarks: *Sepia simoniana* is closely related to *S. papillata*, but differs in having equal-sized suckers on the long club, and a long spine on the sepion.

Distribution: This species was first described from Simons Bay, South Africa, and repeatedly reported from the same region, near Cape Town and along the east coast of South Africa to the Tugela River (Roeleveld, 1972). Two specimens were caught on the Agulhas Bank (Adam, 1983). Our material extends the range of *S. simoniana* to the area from northern Kenya to southern Mozambique, at depths 170–185 m (14–134 m reported by Roeleveld, 1972).

15. *Sepia (Sepia) officinalis vermiculata* Quoy and Gaimard, 1832 (Fig. 23)

Material examined: "Professor Mesyatzev", 19/01/1976, sta. 46, bottom trawl, 30–40 m, 19°17'S, 36°22'E: 2 males, ML 82, 87 mm, 1 female, ML 82 mm; "Professor Mesyatzev", 20/01/1976, sta. 47, bottom trawl, 70–75 m, 19°45'S, 36°22'E: 1 male, ML 98 mm; "Professor Mesyatzev", 20/01/1976, sta. 50, bottom trawl, 30 m, 19°37'S, 35°43'E: 4 females, ML 87–133 mm; "Professor Mesyatzev", 26/01/1976, sta. 68, bottom trawl, 44–50 m, 24°54'S, 34°53'E: 1 sepion 93 mm; "Professor Mesy-

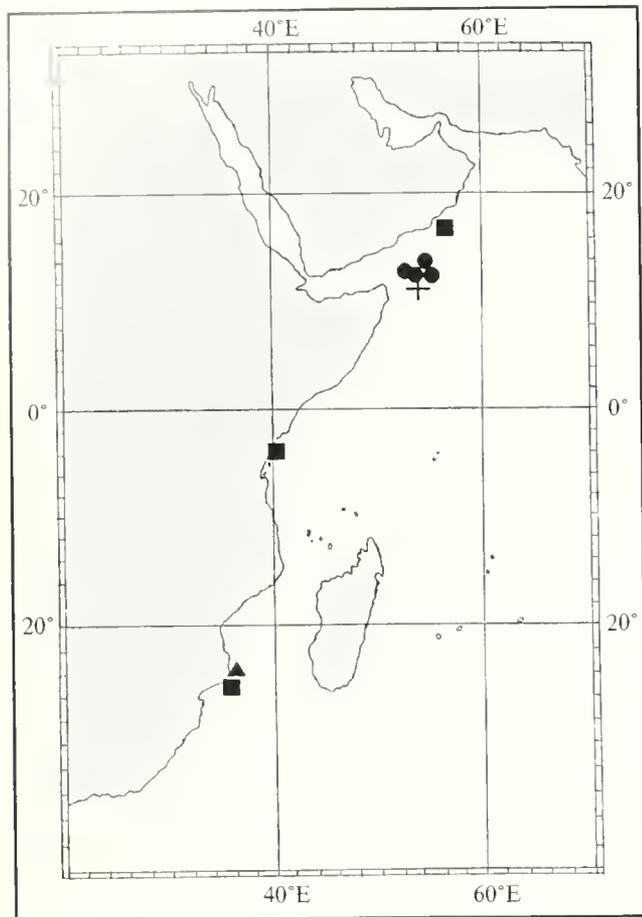


Figure 24. Distribution of *Sepia (Acanthosepion)* and *Sepia (Hemisepion)* in the western Indian Ocean. Circles = *Sepia (Acanthosepion) zanzibarica*, squares = *S. (A.) prashadi*, cross = *S. (A.) savignyi*, triangle = *S. (H.) typica*.

atzev", 13/04/1976, sta. 148, bottom trawl, 25 m, 09°52'S, 60°57'E: 2 males, ML 64, 69 mm, collections of VNIRO and ZMMU, Nos. 224, 251, 252, 253. "Vityaz", 25/11/1988, sta. 2634a, bottom trawl, 90–92 m, 25°05'S, 34°50'–34°44'E: 1 male, ML 100 mm, 1 female, ML 135 mm; "Vityaz", 25/11/1988, sta. 2634b, bottom trawl, 95–102 m, 25°05'–25°06'S, 34°45'E: 1 female, ML 118, collection of IOAS.

Description and remarks: Our specimens agree completely with the description of Adam and Rees (1966).

Distribution: *Sepia officinalis vermiculata* has been found along southern Africa from 30°S in the southeastern Atlantic Ocean to southern Mozambique in the southwestern Indian Ocean (Voss, 1962; Adam & Rees, 1966; Roeleveld, 1972) and reported off Namibia (Sánchez & Molí, 1984; Sánchez, 1985). According to our data, *S. o. vermiculata* ranges northward to central Mozambique, 19°S and on the Saya-de-Malha Bank at depths of 25–102 m. The largest of our specimens are immature (male 100 mm ML and females 118 and 135 mm ML were in the second stage of maturity).

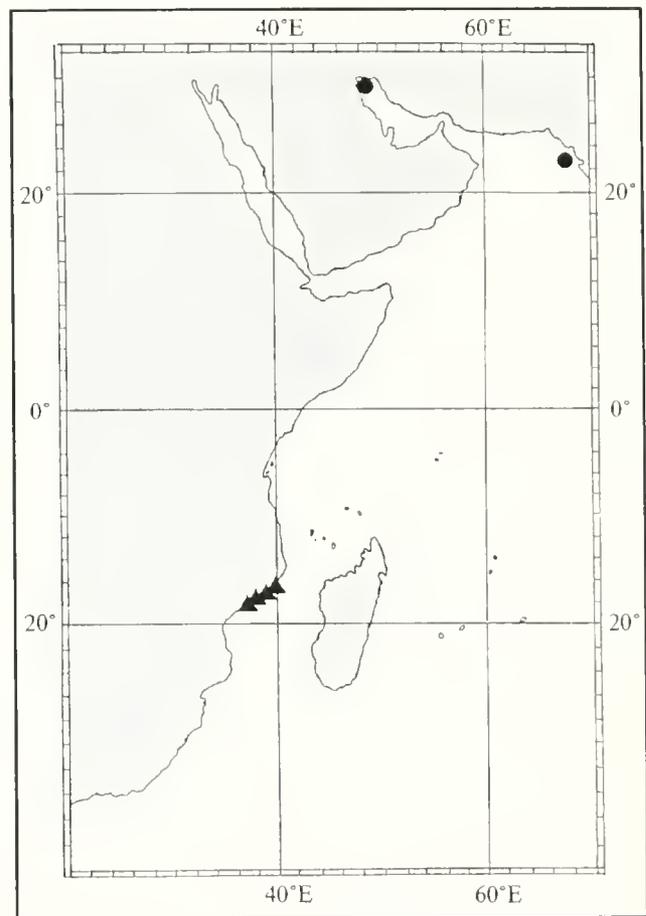


Figure 25. Distribution of *Sepiella* in the western Indian Ocean. Triangles = *Sepiella cyanea*, circles = *S. inermis*.

16. *Sepia (Acanthosepion) zanzibarica* Pfeffer, 1884 (Fig. 14, 24)

Material examined: "Odyssey", 27/05/1984, sta. 9, bottom trawl, 28 m, 12°19'N, 53°22'E: 1 female, ML 104 mm; "Odyssey", 12/06/1984, sta. 14, bottom trawl, 35 m, 09°42'S, 61°08'E: 1 female, ML 58 mm; "Odyssey", 17/04/1985, sta. 95, bottom trawl, 50 m, 12°22'N, 54°28'E: 9 males, ML 71–139 mm, 4 females, ML 88–115 mm; "Odyssey", 19/04/1985, sta. 95, bottom trawl, 40 m, 12°16'N, 53°59'E: 1 male, ML 172 mm; "Odyssey", 17/04/1985, sta. 94, bottom trawl, 40 m, 12°22'N, 54°21'E: 1 female, ML 73 mm, collections of VNIRO and ZMMU, Nos. 317, 326. "Vityaz", 04/12/1988, sta. 2657, bottom trawl, 40 m, 22°10'–22°15'S, 43°09'–43°10'E: 1 female, ML 204 mm; "Vityaz", 08/01/1988, sta. 2810, shrimp trawl, 57–70 m, 10°16'–10°15'S, 61°09'E: 6 males, ML 57–122 mm, 2 females, ML 108, 178 mm, 1 juv ML 41 mm; Toliara (Madagascar), beach: 1 sepion 118 mm, collection of IOAS.

Description and remarks: Our specimens agree with the description of Adam and Rees (1966).

Distribution: *Sepia zanzibarica* was formerly known

from sepions found from Natal to Kenya and Madagascar and by two specimens with soft parts (Adam & Rees, 1966). According to L. S. Homenko (personal communication), *S. zanzibarica* is one of the common cuttlefishes of the northwestern Indian Ocean and Saya-de-Malha Bank, at depths of about 20–125 m. Our data confirm this communication, *Sepia zanzibarica* is common in the open regions of the Indian Ocean, near islands (Socotra, Madagascar) and banks (Saya-de-Malha).

17. *Sepia (Acanthosepion) prashadi* Winckworth, 1936 (Fig. 15, 24)

Material examined: "Professor Mesyatzev", 05/01/1976, sta. 24, bottom trawl, 180–185 m, 04°47'S, 39°24'E: 1 male, ML 90 mm, 2 females, ML 80, 65 mm; "Akademik Knipovich", 13/01/1966, sta. 305, bottom trawl, 55 m, 17°41'N, 56°47'E: 3 males, ML 33, 35, 40 mm, collection of VNIRO and ZMMU, No. 249. "Vityaz", 25/11/1988, sta. 2634a, bottom trawl, 90–92 m, 25°05'S, 34°50'–34°44'E: 2 males, ML 50, 53 mm, collection of IOAS.

Description and remarks: Our specimens agree with the description of Adam and Rees (1966).

Distribution: *Sepia prashadi* is a common northern and western Indian Ocean species, recorded from the Gulf of Suez to the Bay of Bengal and southward to southern Mozambique, Madagascar and the Mauritius. Depth records span the entire continental shelf.

18. *Sepia (Acanthosepion) savignyi* Blainville, 1827 (Fig. 24)

Material examined: "Odyssey", 27/05/1984, sta. 10, bottom trawl, 27 m, 12°14'N, 53°46'E: 3 males, ML 94, 104, 108 mm, 2 females, ML 83, 90 mm, collection of VNIRO.

Description and remarks: *Sepia savignyi* can be confused with *S. plathyconchalis* Filippova and Khromov, 1991, from which it differs in having a ventral median groove on the sepion and a normal striated zone, which is very narrow in *S. plathyconchalis*.

Distribution: *Sepia savignyi* is known from the Red Sea, the Gulf of Aden and the Persian Gulf, but was never recorded south of Socotra Island. This species is replaced by *S. plathyconchalis* off the coast of East Africa.

19. *Sepia (Hemisepius) typica* Steenstrup, 1875 (Fig. 24)

Material examined: "Vityaz", 22/11/1988, sta. 2626, Sigsbee trawl, 290 m, 24°39'S, 35°31'E: 3 males, ML 9, 11, 12 mm, 6 females, ML 5–8 mm, collection of IOAS.

Description and remarks: *Sepia typica* is the type species of the subgenus *Hemisepius*, and distinctly differs from the other species of *Hemisepius* in having ventral mantle pores (12 on each side) (Khromov, 1987). *Sepia typica* is a rather rare species, known from several specimens caught from Saldanha Bay to Cape Natal (Roeleveld, 1972). It was suggested that there is a difference

between western (Atlantic) and eastern (Indian Ocean) forms of the species, and the latter was named *S. (H.) typica* var. *chuni* (Thore, 1945). Roeleveld (1972:264) questioned the validity of these forms and wrote: "A decision must await the collection of further specimens from the eastern coast of South Africa". We think such a decision cannot be final in the absence of a special population study of *S. typica*.

We confirm Thore's report of the differences in size between western and eastern forms. The latter (Massy, 1927 and our material) are much smaller (males at 5th stage of maturity are only 11–12 mm); in fact, our specimens are the smallest mature *Hemisepius* ever reported. We cannot distinguish any morphological differences other than size. Our specimens have a variable number of enlarged suckers in the 7–10th rows of suckers on the dorso-lateral arms. Usually two pairs of suckers occur on the first-second arms and one pair on the third arms. The suckers of the right ventral arm decrease in size distally except for the suckers in approximately the 12th row, which are enlarged. On the hectocotylus there are 8–9 pairs of widely spaced reduced biserial suckers (starting from the proximal pair) and about 10–14 minute suckers distally. These characters are the same as in the Atlantic form as described by Roeleveld (1972).

It is interesting that the eyelids of our specimens look very similar to those of *S. (D.) bathyalis* (Khromov et al., 1991) with two narrow triangular outgrowths on the upper margins. The fins of our specimens extend forward from the anterior margin of the mantle. They are widest in the middle part of the mantle, not in the posterior area as in other species of *Sepia*. The sepion occupies only the anterior half of the mantle, as is characteristic of the subgenus *Hemisepius*. On the other hand, the sepions of our specimens though very thin and fragile, are calcified, which has not previously been reported. We believe that the decalcification of sepions in previously reported specimens of this species (Adam & Rees, 1966; Roeleveld, 1972; etc.) is an artifact due to improper fixation. This supports our opinion that *S. (H.) robsoni*, *S. (H.) faurei*, *S. (H.) dubia* and *S. (H.) pulchra* belong to the subgenus *Hemisepius* of the genus *Sepia* because the decalcification of the sepion *per se* cannot be considered as a character of the subgenus (Khromov, 1987). The phragmocone, inner and outer cones are present but strongly reduced in our specimens.

Distribution: *Sepia (H.) typica* was not previously recorded north of Cape Natal in the Indian Ocean. We found this species off southern Mozambique far north of the known range and at a much greater depth (290 m versus 2–156 m) (Roeleveld, 1972). The other four species of this subgenus are known only from the area off the Cape of Good Hope at depths of 15–168 m.

20. *Sepiella cyanea* Robson, 1924 (Figs. 16, 17, 25)

Material examined: "Professor Mesyatzev", 16/01/1976, sta. 33, bottom trawl, 14 m, 17°13'S, 38°39'E: 2 males, ML 36, 60 mm, 2 females, ML 30, 42 mm; "Akademik

Knipovich", 29/09/1977, sta. 375, bottom trawl, 20–25 m, 18°33'S, 36°48'E: 2 males, ML 54, 67 mm, 1 female, ML 68 mm, ZMMU 187, 207. *Sepiella*, which can be only *S. cyanea* were also noted by B. G. Ivanov (log book) off Mozambique between 17°37' and 18°17' S at the depths of 17–40 m. "Vityaz", 19/11/1988, sta. 2620, bottom trawl, 13–14 m, 17°11'–17°12'S, 38°34'–38°30'E: 14 males, ML 23–50 mm, 16 females, ML 40–65 mm, IOAS.

Description and remarks: Our specimens agree with the descriptions of Adam and Rees (1966), and Roeleveld (1972). Egg size in a female of 65 mm ML ("Vityaz") was 3–5 mm.

Distribution: *Sepiella cyanea* has been reported in South African waters from Durban to Port Elizabeth and off Madagascar (Roeleveld, 1972). We found it near the coast of Central Mozambique at depths of 13–40 m, shallower than previously reported (51–73 m) (Roeleveld, 1972).

21. *Sepiella inermis* (Férussac and d'Orbigny, 1835) (Figs. 18, 19, 25)

Material examined: "Nauka", 30/03/1976, sta. 61, Hindustan: 3 females, ML 54, 55, 56 mm; "Nauka", 06/04/1976, sta. 98, Gulf of Kutch: 3 males, ML 27, 33, 42 mm, 1 female, ML 51 mm, 1 juv ML 23 mm; "Akademik Knipovich", 21/01/1966, sta. 317, bottom trawl, 20–25 m, 22°55'N, 68°22'E: 2 juv, ML 22, 35 mm; "Akademik Knipovich", 09/03/1966, sta. 436, bottom trawl, 40 m, 14°42'N, 97°26'E: 2 females, ML 57, 60 mm; "Sabah", March 1979, 0–20 m, Kuwait territorial waters: 8 males, ML 51–78 mm, 22 females, ML 51–105 mm, collections of VNIRO and ZMMU, Nos. 198, 201, 311.

Description and remarks: According to Adam and Rees (1966), the number of sucker rows on the tentacular club of *S. inermis* is very variable, ranging from 13 to 24 depending on sex and geographical area. Moreover, we must consider the possibility of changes in sucker number during club regeneration. For example, one of our specimens (female, ML 83 mm) has one normal club with about 18 rows of suckers and another (regenerated?) with only 9 rows of suckers. In this case *S. inermis* can hardly be separated from *S. cyanea*, because the latter species is characterized by a similar sepioid and 12 rows of club suckers.

Distribution: *Sepiella inermis* is a wide ranging species inhabiting the northern Indian Ocean and adjacent western Pacific from the Persian Gulf and Red Sea to the Gulf of Tonkin and Indonesia.

DISCUSSION

The analysis of material gathered by the Soviet research vessels in African waters and the Mascarene Ridge region between 24°N and 37°S significantly broadens our knowledge of the sepioid fauna of this poorly known area. Several species, *S. (A.) zanzibarica*, *S. (D.) trygonina*, *S. (S.) officinalis vermiculata*, *S. (S.) papillata*, were caught for the first time in the open waters of the Mascarene Ridge,

which are separated from Africa and Madagascar by a large area of deep water, the Amirante Trench and the Mascarene Basin. Three new species of *Sepia*, *S. (D.) mascarensis*, *S. (S.) plathyeconchalis*, and *S. (D.) saya*, described in previous papers (Filippova & Khromov, 1991; Khromov *et al.*, 1991) are present in this area. The species list of this region may expand further, because we have in our collections several poorly preserved specimens, including at least two more new species.

This survey also revealed the occurrence of several species near the coast of Madagascar: *S. (R.) acuminata* in this paper and *S. (D.) tala* and *S. (D.) bathyalis* reported in Khromov *et al.*, (1991).

The distribution ranges of many South African sepiids are broader than previously believed. *Sepia (D.) joubini* and *S. (D.) burnupi*, known previously from Natal, are recorded from southern Mozambique and *S. (D.) incerta* from northern Mozambique. *Sepia (S.) simoniana*, which was considered endemic to Cape Province, as well as *S. (R.) hieronis* occur along the East African coast to northern Kenya, while *S. (R.) acuminata* ranges to Somalia (and off Madagascar). The Cape-Natal species *S. (H.) typica* was found off northern Mozambique. Thus the endemism of the South African fauna was hitherto greatly exaggerated (Roeleveld, 1972) because of a poor knowledge of the East African offshore and open sea faunas.

It is very significant that the southern and eastern African sepioid faunas, as well as the entire fauna of the Western Indian Ocean, are represented mainly by the species of subgenus *Doratosepion*. It was noted (Nesis, 1980; Khromov, 1987) that the subtropical waters off South Africa were one of the centers of species diversification of *Doratosepion*. In summarizing the data presented in this paper and in previous ones (Khromov, 1982, 1988; Filippova & Khromov, 1991; Khromov *et al.*, 1991), there are 14–16 species of *Doratosepion* in the Western Indian Ocean. This subgenus comprises more than half of the *Sepia* species in this area. *Sepia s. str.* is the second, and *Acanthocepion* the third most diverse subgenus in the region.

An intriguing and puzzling fact is that, despite the large number of trawls, no cuttlefish were recorded from the Seychelles Islands or the Seychelles Plateau, an ancient granitic microcontinent. This is in striking contrast with the great richness and diversity of the cuttlefish fauna of Saya-de-Mallia Bank and Madagascar, two other ancient areas with continental type crust (Nur & Ben-Avraham, 1982), which have not been in contact with the African continent or Indian subcontinent since at least the Late Cretaceous (Kennett, 1982). The geological history of the Seychelles Islands and the Mascarene Ridge is obviously very different (Kennett, 1982). We believe that the distribution of sepioids was governed by dispersal rather than by vicariant events.

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Three Additional New Genera and two Replacement Names for Northeastern Pacific Prosobranch Gastropods

James H. McLean

Los Angeles County Museum of
Natural History
900 Exposition Blvd
Los Angeles, CA 90007 USA

ABSTRACT

Three new genera or subgenera and two replacement names for species homonyms are proposed. New genus level taxa: Trochidae: *Costomargarites*, new subgenus of *Margarites*; type species *Trochus costalis* Gould, 1841. Calyptraeidae: *Grandicrepidula*, new subgenus of *Crepidula*; type species *Crepidula grandis* Middendorff, 1849. Turridae, Crassispirinae: *Pseudotaranis* new genus; type species *Mangelia (Taranis) strongi* Arnold, 1903. New names for homonyms: Trochidae: *Margarites (Costomargarites) baxteri*, new name for *Margarites (Pupillaria) rudis* Dall, 1919, not *Margarita groenlandica* var. *rudis* Mörch, 1869. Turridae: *Leucosyrinx kantori*, new name for *Antiplanes amyceus* Dall, 1919, not *Leucosyrinx amyceus* Dall, 1919.

Key words: Mollusca; Prosobranch gastropods; Trochidae; Calyptraeidae; Turridae; new species; new names.

INTRODUCTION

This paper follows a previous paper (McLean, 1995) with the same objective—to make some generic level names available for other work in progress. Additionally, the opportunity is taken to provide replacement names for two homonyms.

NEW GENUS LEVEL TAXA

Family TROCHIDAE Rafinesque, 1815

Subfamily MARGARITINAE Stoliczka, 1868
Costomargarites McLean, new subgenus

Type species: *Trochus costalis* Gould, 1841.

Included species: Type species [Arctic, North Atlantic and North Pacific] and *Trochus ochotensis* Philippi, 1846 [Northwestern Pacific]. The complex synonymy for the type species was outlined by Abbott (1974:36). The juvenile shell was illustrated by Pilsbry (1889, pl. 60, figs. 27, 28).

Diagnosis: Subgenus of *Margarites* in which early teleoconch sculpture is axial rather than spiral.

Remarks: Sculpture of typical species of *Margarites* and species of other available subgenera of *Margarites* is spiral, to the exclusion of axial sculpture altogether except for growth increments. The strong axial sculpture of juvenile shells of *Margarites (Costomargarites) costalis* suggests a closer resemblance to *Solariella obscure* (Couthouy, 1838) than to other species of *Margarites*. The species in which axial sculpture dominates the morphology of the early teleoconch (and may or may not be expressed in the mature shell) need to be distinguished at least at the subgeneric level. For many years I have been surprised that this common Arctic species has not been made the type species of a subgenus, a gap that I hereby fill.

Family CALYPTRAEIDAE Lamarck, 1809

Grandicrepidula McLean, new subgenus

Type species: *Crepidula grandis* Middendorff, 1849.

Included species: Type species [Boreal Pacific]; *Crepidula princeps* Conrad, 1856 [early Miocene through middle Pliocene of southern California]; *C. excavate* (Broderip, 1834) [Panamic]; *C. maculosa* Conrad, 1846 [Western Atlantic]; *C. convexa* Say, 1822 [Western Atlantic].

Diagnosis: Beak excavated, projecting posteriorly on right side; septal margin nearly straight, extending farther forward on left side; single muscle scar on right side, rectangular or chevron-shaped

Remarks: Hoagland (1977) reviewed the Recent and fossil species of *Crepidula*, treating them in alphabetical order, while not using the available subgenera. Surprisingly, none of the 14 available taxa (see Hoagland, 1977: 399) has a type species in which the septum projects on the right side. It is evident that this condition is not ambiguous—all species illustrated by Hoagland can be assigned on the basis of this character. These diagnostic characters were mentioned and show clearly in Hoagland's drawings of septal configuration (figure 2B, *C. excavate*; figure 2F, *C. grandis*). Moreover, the five species assigned above key out together in Hoagland's key

to the species (page 363, couplets 16-18). Contrary to Hoagland's assertion that the division of *Crepidula* into subgenera is not warranted, I find it useful to base subspecific distinctions on the morphology of the septum, particularly when considering fossil species. In my opinion the remaining species can also be assigned to the available taxa on shell characters.

Family TURRIDAE Swainson, 1840

Subfamily CRASSISPIRINAE Morrison, 1966

Pseudotaranis McLean, new genus

Type species: *Mangelia (Taranis) strongi* Arnold, 1903.

Included species: Type species and the more slender *Antiplanes hyperia* Dall, 1919a (p. 35, pl. 9, fig. 6). The type species was described from the Lower Pleistocene of San Pedro, California; it was also illustrated by Grant & Gale (1931:572, pl. 26, fig. 37); *Borsonia inculta* Moody, 1919 (p. 54, pl. 1, figs. 2a, 2b) is a synonym. The two species (*Pseudotaranis strongi* and *P. hyperia*) live offshore in moderately deep water (100-400 m).

Diagnosis: Shell small (length to 17 mm), spire high, anterior canal short, whorls 6. Axial sculpture lacking, spiral sculpture of two cords emerging on teleoconch and three cords on base; anal sinus shallow, at periphery and coinciding with uppermost cord; lip not projecting. Protoconch paucispiral, of 1.2 low, rounded whorls. Radula of marginal teeth attached to membrane; teeth of long, flat type.

Remarks: Authors prior to 1971 used *Taranis* Jeffreys, 1870 for the type species, but the presence of a radula precludes placement in that genus, in which the radula is lacking (see Powell, 1966:55). Earlier (McLean, 1971: 120, fig. 40), I illustrated the radula of *strongi* and assigned it to *Antiplanes (Rectisulcus)*, a genus now in the subfamily Cochlespirinae, according to Taylor *et al.* (1993). *Pseudotaranis* differs in having the sinus more shallow, the lip less protracted, the anterior canal shorter, and the protoconch more compressed. The radula lacks the vestigial rachidian tooth and the marginals are not of the bifurcated type indicated for *Antiplanes* by Kantor and Sysoev (1991:122). The flat morphology of the lateral teeth agrees with the subfamily Crassispirinae, as defined by Taylor *et al.* (1993). Thus, the radular differences place *Antiplanes* and *Pseudotaranis* in different turrid subfamilies. However, on shell characters, *Pseudotaranis* is atypical of Crassispirinae in not having pronounced callus developed near the anal notch.

NEW NAMES FOR SPECIES LEVEL HOMONYMS

Family TROCHIDAE Rafinesque, 1815

Subfamily MARGARITINAE Stoliczka, 1868

Margarites (Costomargarites) baxteri McLean, new name for *Margarites (Pupillaria) rudis* Dall, 1919b:364, not *Margarita groenlandica* var. *rudis* Mörch, 1869:23.

Remarks: *Margarites (Costomargarites) baxteri* was figured by Dall (1921:179, pl. 18, fig. 13, 14) and by Kosuge (1972, pl. 2, fig. 5), but has otherwise been ignored in the literature. It will be treated by me in work in preparation as a geographic subspecies (in the Gulf of Alaska) of the boreal *M. (Costomargarites) costalis* (Gould, 1841). The new name honors the late Rae Baxter for his efforts at reviewing Alaskan mollusks, cut short by his untimely death in 1991.

Family TURRIDAE Swainson, 1840

Subfamily COCHLESPIRINAE Powell, 1942

Leucosyrinx kantori McLean, new name for *Antiplanes amycus* Dall, 1919a (p. 36, pl. 11, fig. 5), not *Leucosyrinx amycus* Dall, 1919a (p. 5, pl. 3, fig. 7).

Remarks: The proposal of *Leucosyrinx kantori* remedies a problem of secondary homonymy that was initiated when Dall (1919a) described a species in *Antiplanes* that I now consider to be a true member of *Leucosyrinx* Dall, 1889. Dall (1919a) also proposed a species with the name *Leucosyrinx amycus*. Note that both species were described in the same paper. Previously (McLean *in* Keen, 1971:713), I placed *Leucosyrinx amycus* Dall, 1919 in the synonymy of *Aforia goodei* (Dall, 1890). The new name honors Yuri Kantor for his recent work on turritiform gastropods.

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Florida Atlantic University
Boca Raton, FL 33431

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

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

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

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A Revision of the Recent *Calliostoma* Species of New Zealand (Mollusca: Gastropoda: Trochoidea)

Bruce A. Marshall

Museum of New Zealand Te Papa
Tongarewa
P.O. Box 467
Wellington, New Zealand

ABSTRACT

Thirty-three Recent calliostomatids are recorded from New Zealand, ten of which are described as new *Calliostoma* (*Otukaia*) *blacki* (Dell, 1956) is renamed due to homonymy, and the following taxa are newly synonymized *Vcnustas tigris chathamensis* Dell, 1950 with *Calliostoma* (*Mureca*) *tigris* (Gmelin, 1791); *Mureca punctulata ampla* Powell, 1939 and *V. punctulata multigenmata* Powell, 1952 with *C. granti* (Powell, 1931); *V. couperi* Vella, 1954 and *Thoristella chathamensis profunda* Dell, 1956 with *C. blacki* (Powell, 1950), which is resurrected from synonymy under *C. foveauxanum* (Dell, 1950); *Zizyphinus hodgei* Hutton, 1875, *Z. ponderosus* Hutton, 1885, and *C. carnicolor* Preston, 1907 with *C. selectum* (Dillwyn, 1817); *C. undulatum* Finlay, 1923 and *C. pellucidum spiratum* Oliver, 1926 with *C. pellucidum* (Valenciennes, 1846). Lectotypes are designated for *Trochus selectus* Dillwyn, 1817, *T. pellucidus* Valenciennes, 1846, and *Calliostoma onustum* Odhner, 1924

Key words: Mollusca; prosobranch gastropods; Trochoidea; Calliostomatidae; *Calliostoma*; systematics

INTRODUCTION

The family Calliostomatidae comprises about 250 living species. They occur in all oceans from the intertidal zone to about 3000 meters depth, mostly on rocky ground. All known species are carnivores, most feeding on cnidaria, and sometimes carion, though a few feed exclusively on sponges. The group is particularly well represented in the New Zealand region, with 33 living endemic species, including some of the world's largest, notably *Calliostoma* (*Mureca*) *tigris* (Gmelin, 1791), which may exceed 100mm in shell height.

Besides the 33 Recent species recorded herein, at least double this number are known from the New Zealand Cenozoic (Early Eocene—Early Pleistocene), of which more than half are undescribed. Several of the living species have excellent fossil records in the extensive Pliocene-Pleistocene deposits of the southern North Island, and fossil material is recorded and discussed where appropriate.

Two of the recorded Recent species, both of which

are type species of new genera, together with a new genus for *Calliostoma onustum* Odhner, 1924 are named elsewhere (Marshall, 1995). Five additional species are known from off the Kermadec Islands (Appendix).

Attention is drawn to the fact that calliostomatid shell morphology tends to become more variable with increasing size/age, so that species with dissimilar early teleoconchs can be superficially similar at maturity and vice versa. For accurate discrimination of species (and for objective descriptions), it is thus essential to trace and compare the development of individual sculptural elements from the earliest teleoconch whorls following the system used by Icke (1942) and Marshall (1988, 1995) (Figure 28).

ABBREVIATIONS AND TEXT CONVENTIONS

AUG	Geology Department, Auckland University
BMNH	The Natural History Museum, London
MNHN	Muséum National d'Histoire Naturelle, Paris
MNZ	Museum of New Zealand, Wellington
NZGS	Institute of Geological and Nuclear Sciences, Lower Hutt
NZOI	National Institute of Water and Atmospheric Research, Wellington
sa	spire angle (see below)
ZMA	Zoological Museum, Amsterdam

Spire angle measurements for individual shells were averaged (mean spire angle) to reduce bias induced by cyrtocoid spire profile and expanded or narrowed last adult whorl. In other words, for a shell with a cyrtocoid spire outline, which becomes more narrowly conical with increasing shell size, the given spire angle is the mean of the maximum and minimum spire angles measured from that specimen. Vice versa for a shell with an evenly conical or coeloconoid contour in which the last adult whorl expands more rapidly than the previous ones. In illustrations of shells, height dimension precedes diameter.

Readers requiring more detailed information on New Zealand stratigraphy should refer to Fleming (1953), Beu and Maxwell (1990), and Abbott and Carter (1994).

SYSTEMATICS

Order *Vetigastropoda* Salvini-Plawen, 1980

Superfamily *Trochoidea* Rafinesque, 1815

Family *Calliostomatidae* Thiele, 1924

Genus *Calliostoma* Swainson, 1840

Calliostoma Swainson, 1840:218, 351. Type species (by subsequent designation of Herrmannsen, 1846:154): *Trochus conulus* Linnaeus, 1758; Recent, north-eastern Atlantic and Mediterranean. For further discussion and synonymy, see Marshall (1995).

Subgenus *Maurea* Oliver, 1926

Maurea Oliver, 1926:108. Type species (by original designation): *Trochus tigris* Gmelin, 1791; Recent, New Zealand [20th December 1926—see below].

Mauriella Oliver, 1926:109. Type species (by original designation): *Trochus punctulatus* Martyn, 1784; Recent, New Zealand [20th December 1926].

Calliotropis Oliver, 1926:110. Type species (by original designation): *Trochus cunninghami* Gray, 1834 = *Trochus selectus* Dillwyn, 1817; Recent, New Zealand Not *Calliotropis* Seguenza, 1903 [20th December 1926].

Mucrinops Finlay, 1926:360. Type species (by original designation): *Ziziphinus spectabilis* A. Adams, 1855; Recent, New Zealand [23 December 1926].

Venustas Finlay, 1927:360. Type species (by original designation): *Trochus tigris* Gmelin, 1791; Recent, New Zealand [10 March 1927]. Officially rejected name (ICZN Opinion 479). Not *Venustas* Allan, 1926.

Calotropis Thiele, 1929:49. Replacement name for *Calliotropis* Oliver not Seguenza.

Remarks: As indicated by Beu *et al.* (1969), *Venustas* Allan, 1926 (Allan, 1926) was published on 7th December 1926 (ICZN opinion 479) and has priority over *Maurea* Oliver, 1926 (and the officially rejected name *Venustas* Finlay, 1927). Fortunately the type species of *Venustas* Allan (*Calliostoma fragile* Finlay, 1923; Early Miocene, New Zealand) seems unlikely to be consubgeneric with *Calliostoma* (*Maurea*) *tigris* (Gmelin, 1791), the type species of *Maurea*. The paper in which Oliver (1926) introduced *Maurea* was published in Parts II / III of Volume 17 of the Proceedings of the Malacological Society of London, the date of publication of which was interpreted as 20th December 1926 by Dell (ICZN Opinion 479) on the basis of a letter from L. R. Cox to M. K. Mestayer bound into the MNZ volume of the journal. This letter is dated 19th April 1927. The title page to Volume 17, issued on 30th December 1927, states that Parts II and III were issued on 30th December 1926. Whereas I have been unable to trace any firmer evidence that Parts II and III were published prior to 30th December, for the sake of nomenclatural stability it is appropriate to follow ICZN acceptance (right or wrong) of 20th December 1926, otherwise *Maurea* would fall as a junior synonym of *Mucrinops* Finlay, 1926 (23 December). *Maurea* is not endangered by *Venustas* Finlay, which has been deemed to have been published on 10th March 1927 and officially rejected (ICZN Opinion 479).

The type species of *Maurea*, *Calotropis*, *Mauriella*,

and *Mucrinops* are similar to the type species of *Calliostoma* in radular morphology and external anatomy. Although I am unable to justify genus-level status for *Maurea*, it would be inappropriate to treat it as a synonym of *Calliostoma* because all of the New Zealand species are strongly dissimilar to the type species of *Calliostoma* in shell morphology. On the other hand, there is strong mosaic overlap between the type species of *Maurea*, *Calotropis*, *Mauriella*, and *Mucrinops* via the other Recent species herein referred to *Maurea*, and I am unable to justify segregation of these genus-group taxa from each other. Accordingly, they are all interpreted as synonyms of *Maurea*, which in turn is interpreted as a subgenus of *Calliostoma*. Although the origins and relationships of the Recent species are obscure, it is nevertheless clear that *Maurea* as here limited is polyphyletic. In whatever way the Recent species are arranged in groups, most or all contain species of exceptionally large size for the family. With the exception of "*Trochus*" *mutus* Finlay, 1924 and "*Benthastelena*" *susanae* Maxwell, 1992 (Late Eocene—Early Miocene), which are not closely related to any taxa living in the New Zealand region, none of the numerous pre-Pliocene species from New Zealand exceeds much more than about 20 mm in maximum shell dimension, so it would seem that gigantism occurred independently in several species groups after the Miocene. Many of the pre-Pliocene species are similar to the type species of *Fautor* Iredale, 1924 (*Ziziphinus comptus* A. Adams, 1854; Recent, southern Australia) and other species referred there (as a subgenus of *Calliostoma*) by Marshall (1995) from the New Caledonia area. *Calliostoma regale* new species and *C. aupourianum* new species from northern New Zealand are similar to these small-shelled New Caledonian *Fautor* species and to many of the New Zealand pre-Pliocene taxa, and because (independently derived) gigantism alone is no criterion for genus-group discrimination, it is thus difficult to justify segregation of *Maurea* even from the prior *Fautor*. Evidently highly conservative external anatomy and gross shell and radular morphology are inadequate to construct objectively definable supraspecific groupings, or rather, real phylogenetic groups are rendered nebulous and are obfuscated due to conservatism, convergence, gigantism, and uncertain character-state polarity. Molecular cladistic techniques would seem to be a promising source of data for resolution of these problems. For more detailed discussion see Marshall (1995).

Calliostoma (*Maurea*) *tigris* (Gmelin, 1791)
(Figures 1-9, 110, 127)

Chemnitz, 1781:100, pl. 170, figs. 1654, 1655.

Trochus tigris Martyn, 1784, fig. 75. (Officially rejected name—ICZN Opinion 479).

Trochus granatum Gmelin, 1791:3584 (refers to Chemnitz, 1781, pl. 170, figs. 1654, 1655); Lamarck, 1822:26; Fischer, 1875:69, pl. 15, fig. 1.

Trochus tigris Gmelin, 1791:3585 (refers to Martyn, 1784, fig.

- 75) (Officially accepted name—ICZN Opinion 479); Philippi, 1848:50, pl. 10, figs. 16, 17.
- Turbo granatum*—Röding, 1798:88.
- Zizyphinus tigris*—Gray, 1843:237.
- Zizyphinus tigris*—Reeve, 1863, fig. 4, Hutton, 1873:35.
- Zizyphinus granatum*—Hutton, 1880:98; Hutton, 1884:359.
- Calliostoma granatum*—Pilsbry, 1888:313, pl. 41, fig. 30.
- Calliostoma tigris*—Pilsbry, 1889:333; Suter, 1897:280, Suter, 1913:148, pl. 40, fig. 6.
- Calliostoma (Maurea) tigris*—Oliver, 1926:108; Wenz, 1938:282, fig. 600; Shikama, 1964:106, fig. 185.
- Venustas (Venustas) tigris*—Finlay, 1926:360, 371.
- Maurea tigris*—Powell, 1937:64, pl. 1, fig. 12; Matsukuma, Okutani & Habe, 1991, pl. 17, fig. 11.
- Venustas tigris tigris*—Dell, 1950:41, figs. 22, 23, 24.
- Venustas tigris chathamensis*—Dell, 1950:43, figs. 26, 27. **New synonym.**
- Maurea tigris tigris*—Powell, 1957:88, pl. 1, fig. 12; Powell, 1979:60, pl. 10, fig. 1.
- Maurea tigris chathamensis*—Powell, 1957:88; Powell, 1979:61, pl. 19, fig. 3.
- NOT *Zizyphinus granatum*—Reeve, 1863:pl. 1, fig. 2 (*C. pellucidum*).

Type Data: *Trochus tigris*: Martyn, 1784, fig. 75, "New Zealand"; *Trochus granatum*: Chemnitz, 1781, pl. 170, figs. 1654, 1655, "Neuseeland"; *Venustas tigris chathamensis*: Holotype MNZ M.2128, Mangare Island, Chatham Islands.

Other Material Examined: *Fossil*—Boulder at head of largest bend in Wainui Stock Road, Ohope (map ref. W15/638502), B.A. Marshall, 1965 (late Castlecliffian, Late Pleistocene) (1 MNZ); Banks of Ohinekoao Stream, coastal cliffs, Matata, B.A. Marshall, 1969 (late Castlecliffian, Late Pleistocene) (1 MNZ). *Recent*—478 specimens in 198 lots MNZ, 13 specimens in 8 lots NZOI.

Distribution (figure 9): Mid-Pleistocene (late Castlecliffian) to Recent, off Three Kings, North, South, Stewart and Chatham Islands, living at 0-211 m on rocky substrata.

Diet: All guts examined contained thecate hydroids (Cnidaria) and indeterminate tissue.

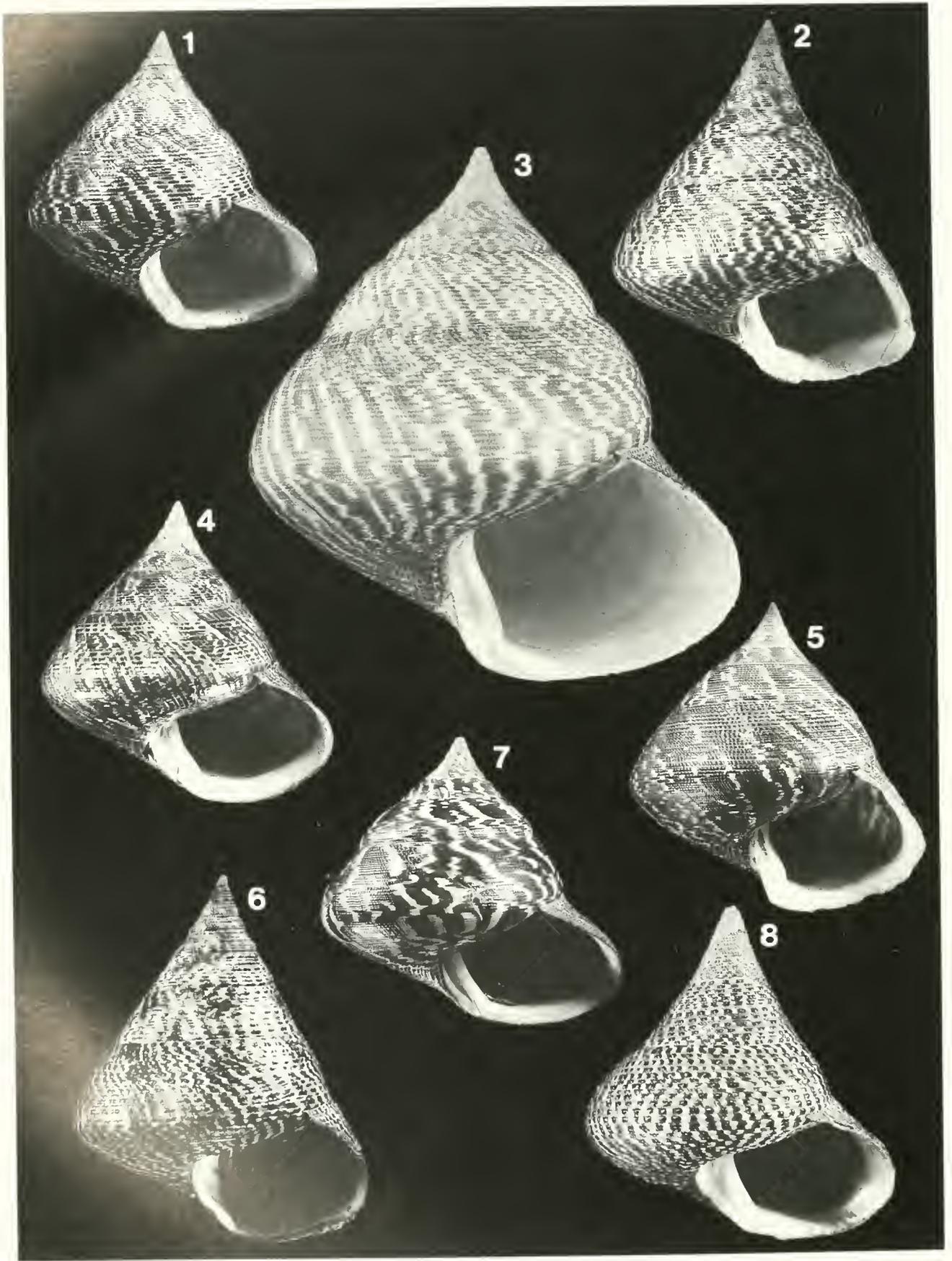
Remarks: This well-known species, the largest known calliostomatid, is characterised by its large size, relatively thin shell, eoelocoid spire, very narrowly conical and distinctively sculptured early teleoconch (figure 108), and by the (usual) colour pattern of yellowish or reddish brown wavy axial bands. Sculptural development in normal specimens (see below) proceeds through a distinctive intermediate stage in which the spiral cords become weakly nodular or smooth and much broader than the interspaces, then reverts to strongly nodular with wider interspaces on the last adult whorl. Mature specimens have a gently sloping shoulder on the last part of the last whorl, a pronounced thickening within the outer lip, and typically a slight abapical descent of the apertural rim. Shells having adult characteristics may be as small as 27.5 mm in height (MNZ M.84227, Cape Runaway), although most are about twice this size. The species at-

tains exceptional size off the Three Kings Islands (height up to 100 mm, figure 3).

Most specimens from Parengarenga Harbour (figure 6) and many specimens from off eastern Northland (figure 2), including Whangamata and the Aldermen Islands in the northern Bay of Plenty, have appreciably narrower spire angles than specimens from north of Cape Reinga, from Hauraki Gulf, and from south of Mayor Island, Bay of Plenty ($sa = 61-72^\circ$, mean 66° , S.D. 3.26, $n = 20$ as against $sa = 68-87^\circ$, mean 77° , S.D. 3.91, $n = 58$). There is complete intergradation between narrowly and broadly conical forms, however, both within and between populations, and there are no other differences between them. Because narrowly conical forms occur only in the warm waters off the north-eastern North Island, it would seem that differences in spire angle are linked in some way to sea temperature (see *C. blacki* below). The occurrence of broadly conical specimens from further north, off the Three Kings Islands, presumably reflects local cooling due to upwelling (Marshall, 1981).

Most specimens seen from off the Chatham Islands, including the holotype of *Venustas tigris chathamensis* Dell, 1950, differ from mainland specimens in lacking discrete axial bands and are instead predominantly reddish or yellowish brown with scattered, irregular white spots and streaks (figure 5). Some Chatham Islands shells (e.g., NZOI Q23), however, have axial bands and are essentially similar to specimens from off the South Island and Stewart Island, which commonly have broader bands than northern shells (figure 7). One specimen from the Three Kings Islands (figure 4) is indistinguishable from typical Chatham Islands shells in colour and in density of colour pattern. Although Dell (1950) considered that Chatham Islands specimens differed from mainland shells in having stronger, more persistent nodules, examination of much additional material reveals that sculpture is variable and that the Chatham Islands form cannot be distinguished using this criterion. Accordingly I am unable to justify continued recognition of *V. tigris chathamensis* as a geographic subspecies. Unless *C. tigris* intermittently reaches the Chatham Islands as drifting eggs or larvae from the mainland, it may have reached there along the summit of the Chatham Rise during periods of low sea level, presumably during Pleistocene glaciations.

Three specimens are known from the north-eastern North Island on which the spiral cords remain strong, widely spaced, and nodular throughout (figures 6, 8). The two from Paua, Parengarenga Harbour (figure 6) are also more deeply pigmented and more densely patterned than others living beside them. The third example, from off Cape Karikari (figure 8), differs from all other material examined in that the spiral cords are alternately spotted yellowish brown and white. To some extent the Parengarenga Harbour shells resemble *C. pellucidum* (Valenciennes) in adult facies, whereas that of the Cape Karikari specimen approaches those of both *C. punctulatum* (Martyn) and *C. osbornei* Powell, with all of which they respectively occurred. Although we cannot entirely preclude the possibility, they seem unlikely to be hybrids



because all have the characteristic and highly stable early teleoconch morphology of *C. tigris* (figure 110).

The epithet *tigris* is from the Latin *tigris* ("tiger", third declension feminine) and is a noun in apposition to the generic name *Calliostoma*, hence it is not declinable.

Calliostoma (Maurea) punctulatum (Martyn, 1784)
(Figures 10-18, 28, 32, 128)

Spengler, 1776: 152, pl. 5, figs. 2a, b.

Chemnitz, 1781:26, pl. 161, figs. 1520, 1521.

Trochus punctulatus Martyn, 1784, fig. 36; Philippi, 1855, pl. 15, fig. 7; Reeve, 1862, pl. 16, figs. 95a-d.

Trochus diaphanus Gmelin, 1791:3580 (refers to Spengler, 1776: 152, pl. 5, figs. 2a, b; and Chemnitz, 1781, pl. 161, figs. 1520, 1521); Wood, 1825, pl. 29, fig. 99; Quoy & Gaimard, 1834:254, pl. 64, figs. 1-5; Gray, 1842, pl. 40*, figs. 1, 1a; Philippi, 1846:8, pl. 2, figs. 5, 6; Fischer, 1873:43, *Turbo* pl. 10, fig. 2.

Turbo diaphanus—Lamarck, 1822:45.

Ziziphinus punctulatus—Gray 1843:237.

Turbo grandineus Valenciennes, 1846, pl. 4, figs. 4, 4ab; Kiener, 1847, *Turbo* pl. 10, fig. 2.

Ziziphinus punctulatus—Hutton, 1873:39; Hutton, 1880:98 (in part = *C. granti*); Hutton, 1882:165, pl. 7, fig. H, Hutton, 1884:360.

Calliostoma punctulatum—Pilsbry, 1889:334, pl. 65, fig. 75, Suter 1897:280; Suter, 1913:146, pl. 8, fig. 11 (in part = *C. granti*); Bucknill, 1924:32, pl. 3, fig. 4 (in part = *C. granti*).

Calliostoma (Mauriella) punctulatum punctulatum—Oliver, 1926:109.

Calliostoma (Mauriella) punctulatum stewartianum Oliver, 1926:109, pl. 10, fig. 1.

Calliostoma (Mauriella) wanganuicum Oliver, 1926:109, pl. 10, fig. 2. **New synonym.**

Venustas (Mucrinops) punctulata punctulata—Finlay, 1926:361, 371.

Venustas (Mucrinops) punctulata urbanior Finlay, 1926:361, pl. 18, fig. 27; Cernohorsky, 1972:243, fig. 17.

Maurea (Mucrinops) punctulata punctulata—Powell, 1937:64, pl. 13, fig. 3 (in part = *C. granti*).

Calliostoma (Mauriella) punctulatum—Wenz, 1938:282, fig. 601.

Maurea (Mucrinops) punctulata urbanior—Powell, 1937:64.

Venustas punctulata punctulata—Dell, 1950:46, fig. 19, 20.

Venustas punctulata urbanior—Dell, 1950:47.

Maurea punctulata punctulata—Powell, 1957:88, pl. 13, fig. 3 (in part = *C. granti*).

Maurea punctulata stewartiana—Powell, 1957:88.

Calliostoma (Maurea) punctulata stewartiana—Shikama, 1964, pl. 59, fig. 6.

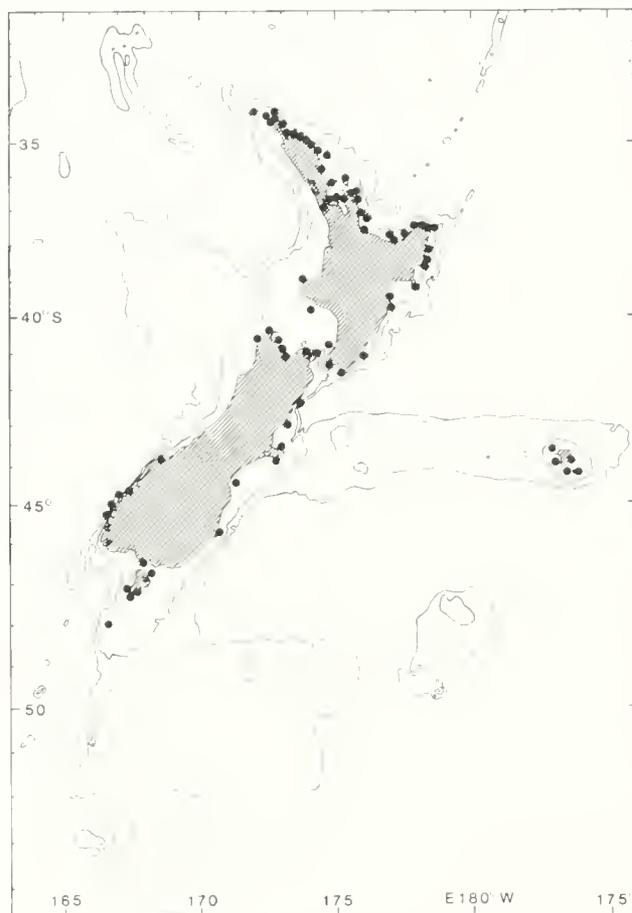


Figure 9. Map of New Zealand region showing distribution of *Calliostoma (Maurea) tigris*. 200 and 1000 meter contours indicated.

Maurea (Mauriella) punctulata punctulata—Fleming, 1966:38.

Maurea (Mauriella) punctulata stewartiana—Fleming, 1966:38.

Maurea punctulata—Powell, 1976:84, pl. 20, fig. 3; Powell, 1979:62, pl. 10, fig. 4 (both in part = *C. granti*).

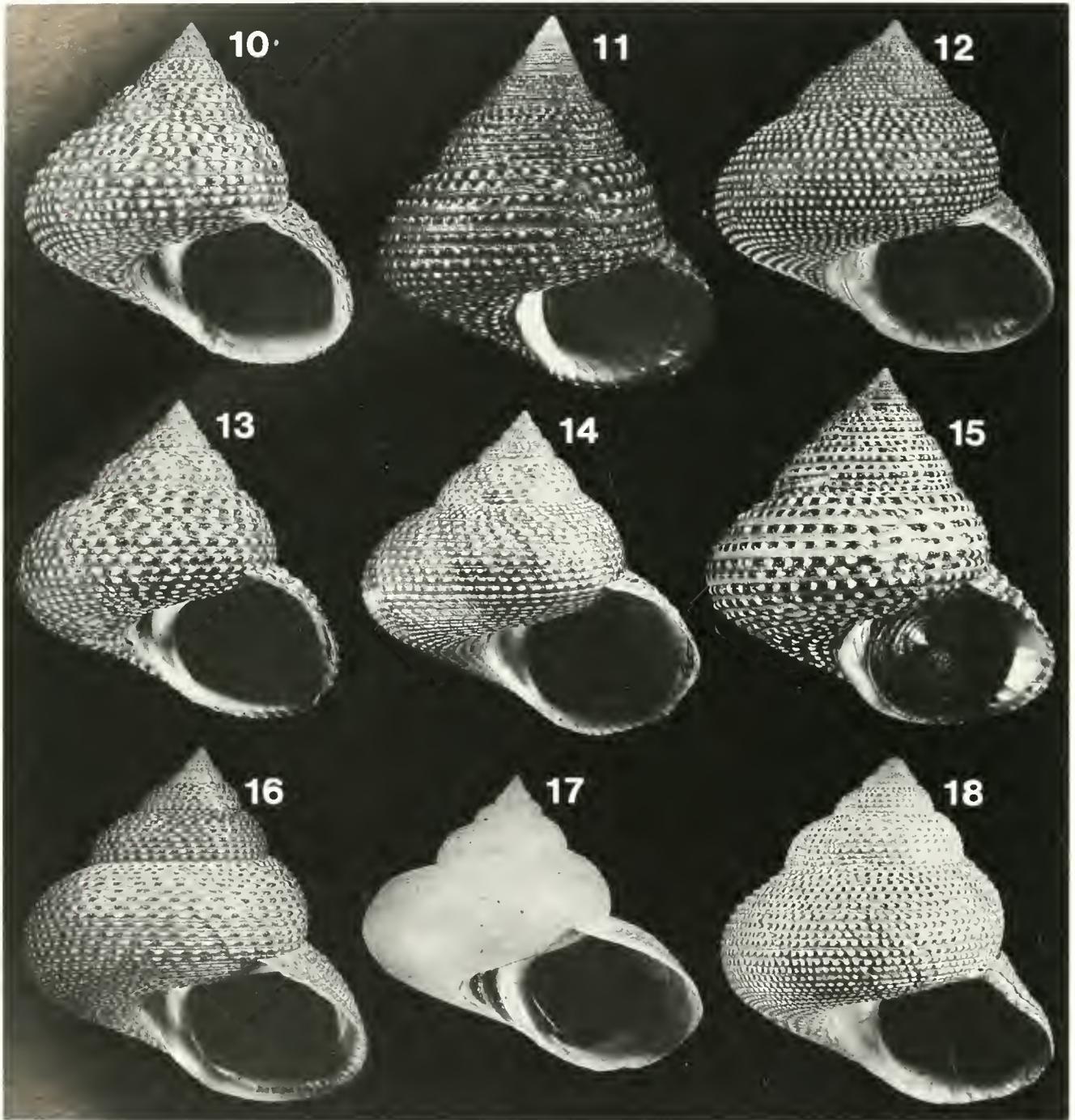
Calliostoma (sensu lato) punctulatum—Beu & Maxwell, 1990:404.

Calliostoma (sensu lato) wanganuicum—Beu & Maxwell, 1990:404.

NOT *Venustas punctulata urbanior*—Powell, 1955:55 (*C. granti*).

NOT *Maurea punctulata*—Dell, 1956:46 (*C. granti*).

Figures 1-8. *Calliostoma (Maurea) tigris* (Gmelin, 1791). 1. Off Southwest Island, Three Kings Islands, 22-23 m, MNZ M.75143 (65.5 × 65.0 mm). 2. Off Poor Knights Islands, 20-30 m, MNZ M 75150 (56.2 × 45.7 mm). 3. Off Three Kings Islands, craypot, MNZ M.75191, natural size (96.0 × 85.3 mm). 4. Reef between Great Island and Farmer Rocks, Three Kings Islands, 33 m, MNZ M.84239 (54.0 × 52.3 mm). 5. Off Southeast Island, Chatham Islands, MNZ M 118120 (54.0 × 51.7 mm). 6. Paua wharf, Parengarenga Harbour, low tide, possibly hybridized with *C. (M.) pellucidum* (Valenciennes, 1846), MNZ M 118337 (57.0 × 45.0 mm). 7. Off Ruggedy Island, Stewart Island, 37 m, MNZ M.18996 (70.0 × 65.0 mm). 8. Off Cape Karikari, 80-120 m, possibly hybridised with *C. (M.) punctulatum* (Martyn, 1784) or *C. (M.) osbornei* Powell, 1926, MNZ M 87026 (36.6 × 32.8 mm).



Figures 10-18. *Calliostoma (Maurea) punctulatum* (Martyn, 1784). 10. Houhora Heads, low tide, MNZ M.2133 (34.6 × 33.6 mm). 11. Paua, Parengarenga Harbour, low tide, MNZ M.80482 (32.8 × 29.0 mm). 12. Northern Pania Reef, Napier, 20m, MNZ M.86724 (34.0 × 35.3 mm). 13, 14. Barrett's Reef, Wellington Harbour, MNZ M. 45062 (29.0 × 30.4 mm, and 29.0 × 31.2 mm). 15. Simpson's Rock, Hauraki Gulf, 15-18 m, MNZ M.89971 (31.0 × 29.0 mm). 16. Timaru breakwater, low tide, MNZ M.5324 (42.4 × 40.8 mm). 17. Cook Strait, 256-274 m, MNZ M.54911 (32.6 × 38.6 mm). 18. Mason's Bay, Stewart Island, beach, MNZ M.7200 (51.5 × 47.3 mm).

Type Data: *Trochus punctulatus*: Martyn, 1784: fig. 36, "New Zealand"; *Trochus diaphanus*: Spengler, 1776: pl. 5, figs. 2a, b, "Südsee"; *Turbo grandineus*: Lectotype (here selected) and 1 paralectotype MNHN, New Zea-

land; *Calliostoma (Mauriella) punctulatum stewartianum*: Holotype MNZ M.879, Stewart Island; *Calliostoma (Mauriella) wanganuicum*: Holotype NZGS TM 4999, mouth of Okehu Stream, Nukumaru Beach, near Wang-

anui (Castlecliffian, Middle Pleistocene); *Venustas (Mucrinops) punctulata urbanior*: Holotype AIM 70824, Foveaux Strait, 37 m.

Other Material Examined: *Fossil*—56 Early-Middle Pleistocene (Castlecliffian) specimens in 22 lots AUG, MNZ, NZGS; *Recent*—1169 specimens in 268 lots MNZ.

Distribution (figure 32): Early Pleistocene to Recent. North, South, and Stewart Islands, living intertidally to 274 m on hard substrata.

Diet: The intestinal tracts of most of the 22 specimens examined (10 localities) contained thecate hydroids (Cnidaria), sand, and sometimes soft tissue of unknown origin (cnidarian?). Two of three specimens examined from Cornwallis, Manukau Harbour contained thecate hydroids, soft tissue, and sand, whereas the intestinal tract of the third animal was packed with calcareous octocoral spicules.

Remarks: This well known, common species is extremely variable in shape, size, thickness, colour, colour pattern, and sculpture (figures 10-18). Recent specimens, however, are readily distinguishable from closely related taxa (see below) by features of the early teleoconch, notably the pronounced whorl angulation at P2, the relatively weak axial costae, and the slow enlargement of S3 (figure 28). Shells range in shape from narrowly to broadly conical (height/diameter ratio 0.87-1.13; sa 65-96°, mean 84.7°, SD 5.83, $n = 74$). Specimens from Parengarenga Harbour are the most narrowly conical, with spire angles ranging from 65° to 72° (figure 11). Specimens taken alive from Cook Strait at 256-274 m (figure 17), the deepest record for the species, are the most broadly conical (sa 86-96°). The latter specimens, and some from off East Otago, Stewart Island, and Foveaux Strait, are unusual in having a callous-filled umbilical depression, the umbilicus being completely invaded by the inner lip in other Recent material. Mature specimens are usually characterised by contraction and descent of the last part of the last whorl and range from 18 to 51 (est.) mm in height, the smallest adult specimens examined occurring off Cape Maria van Diemen, and the largest at Stewart Island in shallow depths, mainly as beach shells (figure 18). Shell thickness varies by a factor of 2 or more. Thicker specimens tend to predominate in exposed situations, and most are more darkly pigmented with fewer and coarser spiral cords than shells from deeper water. Colour ranges from dark reddish to pale yellowish brown, the spirals darker, the nodules either predominantly white or roughly alternating brown and white. Specimens from the northern North Island tend to be more darkly pigmented than material from the southern South Island. Spiral cords are multiplied by repeated intercalation of secondaries and tertiaries at variable stages of growth and range in number from 6 to 25 on the second-to-last whorl of mature specimens. There is a strong correlation between the strength of sculpture and the number of spiral cords on later whorls. Coarsely sculptured specimens with strong primary and secondary spirals tend to

develop fewer secondary spirals, whereas more finely sculptured specimens tend to develop more numerous tertiary spirals that enlarge more rapidly to resemble the adjacent spirals. Coarsely sculptured specimens tend to predominate in the northern North Island, finely sculptured forms in the southern South Island and in deep-living populations. A notable exception is the occurrence of a pale, thin, finely sculptured form at low tide in Manukau Harbour, presumably in response to some local environmental factor. In most specimens from north of Cape Egmont and north of East Cape, including Manukau Harbour, S3 commences about midway between P3 and P4, whereas in most specimens from the south, especially the southern South Island and Stewart Island, S3 commences close beside P4. Although samples from the southern North Island and northern South Island often comprise one form or the other, both forms frequently occur together and completely intergrade in several large samples (e.g., MNZ M.32569, M.44051, M.45062, M.54911). Southern forms have been treated as geographic subspecies (*stewartiana* Oliver, *urbanior* Finlay) of the coarser nominate northern forms, but in fact there is complete mosaic intergradation in all extremes of shell morphology both within and between populations, and it is quite impossible to define regional subspecies.

In the Wanganui basin, *C. punctulatum* first appears in the Butlers Shell Conglomerate (early Castlecliffian, Early Pleistocene) (AU1047, AUG; GS4109, NZGS) (Turner & Kamp, 1990). An imperfectly preserved shell (MNZ M.95387) from an Early Pleistocene (late Nukumaruan) horizon exposed in a cutting on White Rock Road, south of Hautotara Bridge, Martinborough appears to represent this species. A worn, incomplete specimen from a Middle Pliocene (Waipipian) horizon in the Waipara Gorge (GS4946, NZGS) is also similar but cannot be identified with certainty. All specimens from the Butlers Shell Conglomerate and from between it and the younger Kaikokopu Shell Grit (GS4064, 4075, 4134, 4163, 4168, NZGS) (late Castlecliffian, Early Pleistocene), including the holotype of *C. wanganuicum*, differ from Recent specimens in having stronger axial costae on the early teleoconch and in the earlier appearance and more rapid enlargement of S3 (appearing at shell diameter of 1.9-3.4 mm, mean 2.6 mm, $n = 11$ as against 3.1-8.0 mm, mean 4.72 mm, $n = 24$), which is highly conspicuous on early whorls as a suprasutural cord close beside P4. In this character, these specimens bear some resemblance to the Waipipian-Recent species *C. granti* (Powell) but differ in being more broadly conical and by having more strongly convex whorls as in Recent specimens of *C. punctulatum*. S3 appears midway between P3 and P4 in most Recent specimens of *C. punctulatum*, though as already stated, its origination position may vary from median to submedian in some populations. Specimens from the Kupe Formation (late Castlecliffian, Middle Pleistocene) and overlying formations (GS4041, 4052, 4120, 4121, 4122, 4175, 4186, NZGS) are morphologically intermediate between earlier and Recent forms.

Moreover, the fossils are as variable in shape, thickness, nodule size, and strength and number of spiral cords as in Recent material, and there is intergradation between extremes within horizons. Accordingly it seems impossible to justify recognition of *C. wanganuicum* as a distinct species or chronosubspecies. Three specimens from the Butlers Shell Conglomerate (GS4109, NZGS; AU1047, AUG) are unusual in having the umbilicus wide open instead of fully closed through invasion by the inner lip. One of the two umbilicate specimens from GS4109 has the umbilicus considerably narrower than in the other and is thus intermediate between umbilicate and an-omphalous forms from the same sample, which are otherwise indistinguishable.

Calliostoma punctulatum is notable for its absence from the Chatham Islands and the subantarctic islands, including The Snares, and all specimens hitherto so identified from there are *C. granti* (see below). Of yet greater interest is its absence from the Three Kings Islands, some 60 km north of Cape Maria van Diemen, where there are two superficially similar species with closer relationship to *C. granti* (see below). Its absence from this island group may be due to a locally unfavourable environment, either at present or when sea levels were low enough for the species potentially to have reached them, for example during Pleistocene glaciations. As with other local calliostomatids that show pronounced clinal variation, it is likely that *C. punctulatum* has a drifting larval stage of short duration.

***Calliostoma (Maurea) granti* (Powell, 1931)**
(Figures 19-27, 29, 33, 129)

- Zizyphinus punctulatus*—Hutton, 1880:98 (in part not Martyn, 1784).
Calliostoma punctulatum—Suter, 1913:146 (in part).
Maurea (Mucrinops) granti Powell, 1931:97, pl. 13, figs. 34,35.
Maurea (Mucrinops) punctulata punctulata—Powell, 1937:64 (in part).
Maurea (Mucrinops) punctulata ampla Powell, 1939:229, pl. 50, fig. 6. **New synonym**
Venustus punctulata ampla—Dell, 1950:47.
Venustus punctulata (?) n.subsp. Dell, 1950:47.
Venustus punctulata multigemmata Powell, 1952:173, pl. 35, figs. 2,3. **New synonym**.
Venustus punctulata urbanior—Powell, 1955:55 (not Finlay, 1926).
Maurea punctulata—Dell, 1956:46 (not Martyn, 1784).
Maurea punctulata punctulata—Powell, 1957:58 (in part).
Maurea punctulata ampla—Powell, 1957:88.
Maurea punctulata multigemmata—Powell, 1957:88.
Maurea (Mauriella) granti—Fleming, 1966:38.
Maurea (Mauriella) osbornei—Fleming, 1966:38 (not Powell, 1926).
Maurea punctulata—Powell, 1976:84, Powell, 1979:62 (in part).
Maurea multigemmata—Powell, 1976:84; Powell, 1979:62, pl. 10, fig. 6, pl. 19, fig. 8.
Maurea blackii [sic]—Horikoshi, 1959, pl. 4, fig. 12 (not Powell, 1950).
Calliostoma (sensu lato) granti—Ben & Maxwell, 1990:404.

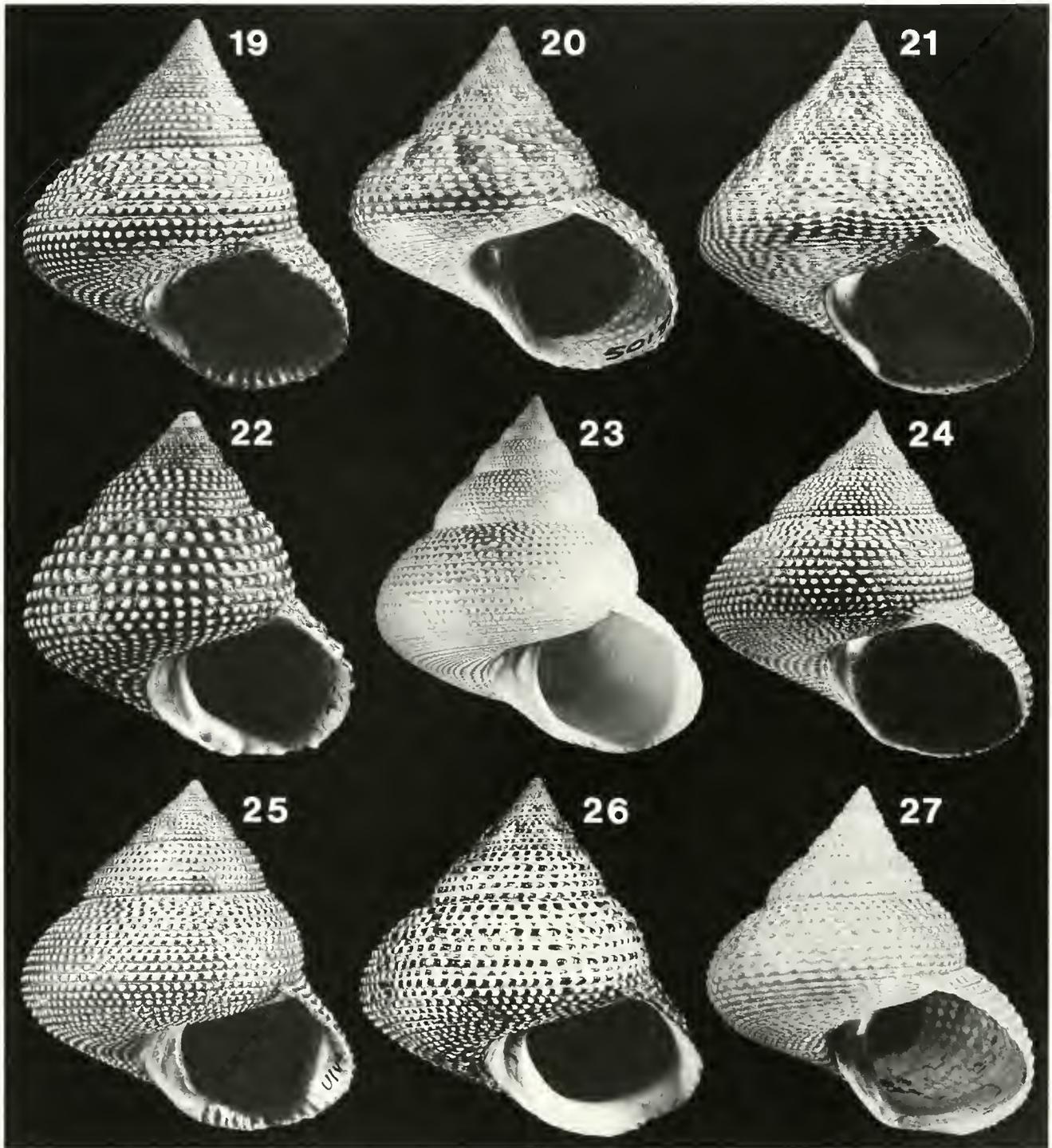
Type Data: *Maurea granti*: Holotype AIM 70449, Waihi Beach, Hawera (Waipipian, Middle Pliocene); *Maurea punctulata ampla*: Holotype AIM 70450, Masons Bay, Stewart Island; *Venustus punctulata multigemmata*: Holotype AIM 71185, off East Otago, 91-128 m.

Other Material Examined: *Fossil*—GS4253, Upper Waipipi Shellbed, Waverley Beach, S. Taranaki (Waipipian, Middle Pliocene) (3 NZGS); GS4949, c. 200 m SE of north end of Greenwood's Bridge, left bank, lower Waipara Gorge, map ref. N34/922867 (f6180) (Waipipian) (1 NZGS); GS5237, 724 m N of Trig Turangatairoa, on main Taihape/Waiouru Road, map ref. T21/429771 (f8503) (probably Waipipian; A.G. Ben, per.comm.); GS4013, Tainui Shellbed, Wanganui (late Castlecliffian, Late Pleistocene) (1 AUG); GS4025, Pinnacle Sand, Wanganui (late Castlecliffian) (1 NZGS). *Recent*—508 specimens in 124 lots MNZ, and 4 specimens in 2 lots NZOI.

Distribution (figure 33): Middle Pliocene (Waipipian) to Recent. North Island south of East Cape and Cape Egmont, and South, Stewart, Snares, Auckland, Campbell, and Chatham islands, living from low-tide level to 220 m on hard substrata.

Diet: From gut contents (pers.obs.) and field observations (M.H.B. O'Neill, pers. comm.), *C. granti* feeds principally on Cnidaria, including thecate hydroids and anemones, as well as ascidians.

Remarks: I am unable to detect any constant differences between Waipipian (Middle Pliocene) specimens of *Calliostoma granti* and the Recent forms named *Maurea punctulata ampla* and *Venustus punctulata multigemmata*. *Maurea punctulata ampla* was originally separated from the sympatric(!) "subspecies" *M. punctulata urbanior* Finlay, 1926 (i.e., *C. punctulatum* Martyn, 1784) on the basis of the larger, more elevated shell, that has 9-12 instead of 12 equally developed spiral cords. *Venustus punctulata multigemmata* was separated from *M. punctulata ampla* because of its more lightly built shell and finer, more numerous spiral cords. Study of many times the number of specimens available when these taxa were proposed, however, reveals that *M. punctulata ampla* and *V. punctulata multigemmata* are based on forms of a single polymorphic species (i.e., *C. granti*) that occurs sympatrically with *C. punctulatum* from East Cape southward to Stewart Island. It transpires that neither *M. punctulata ampla* nor *V. punctulata multigemmata* can be distinguished from *C. punctulatum* using the characters cited in the original descriptions. Like *C. punctulatum*, *C. granti* has considerable variation in shell size and shape, both within populations and clinally, and in the strongly correlated number and relative sizes of the spiral cords on the last two adult whorls. Beach shells and specimens collected intertidally (figure 22) tend to be thick and darkly pigmented with few, strong, strongly nodular spiral cords, whereas specimens from deeper water (figures 20,23) tend to be thin and



Figures 19-27. *Calliostoma (Maurea) granti* (Powell, 1931). **19.** Boil Reef, Napier, 10-20 m, MNZ M 84224 (32.0 × 28.5 mm). **20.** Off Wanganui, 82 m, MNZ M.50181 (21.4 × 22.0 mm). **21.** Westhaven Inlet, low tide, MNZ M.81531 (38.4 × 35.1 mm). **22.** Kahurangi Point, north-west Nelson, beach, MNZ M 23101 (28.0 × 27.4 mm). **23.** Off Oamaru, c. 100 m, MNZ M.102602 (44.6 × 41.4 mm). **24.** Off Seymour Island, Dusky Sound, 24 m, MNZ M.80476 (36.0 × 34.8 mm). **25.** Paterson Inlet, Stewart Island, beach, MNZ M 19119 (45.6 × 42.0 mm). **26.** Point Munning, Chatham Islands, 12 m, MNZ M 111927 (41.0 × 38.1 mm). **27.** Off Auckland Islands, 104 m, NZOI D80 (24.0 × 23.8 mm).

tightly pigmented (or white), with finer, more finely nodular, more numerous spiral cords: the former include the type material of *M. punctulata ampla*, the latter *V. punctulata multigemmata* and *C. granti*. There is complete mosaic intergradation between these extremes in the Recent material.

Although *C. granti* and *C. punctulatum* are similar in gross facies, there are nevertheless marked and constant differences in the shape and sculpture of the early teleoconch whorls (figures 28, 29). *Calliostoma granti* differs from *C. punctulatum* in the following features: (1) the more rapid development of S3, which enlarges to resemble the adjacent primaries at least a full whorl earlier; (2) the stronger axial riblets, which persist over one or two additional whorls; (3) the more weakly convex and more slowly expanding early teleoconch whorls (*i.e.*, narrower early spire angle); and (4) by comparison with *C. punctulata* from within its range, the early teleoconch is evenly conical in shape instead of coeloconoid, although in allopatric *C. punctulatum* from the far north of its range, the spire is typically evenly but yet more broadly conical. Adult teleoconch whorls are typically more weakly convex than in *C. punctulatum*, although they tend to become as strongly convex in deep-living populations (figures 20, 23). The sides of the foot are considerably more finely pustulose in *C. granti* than in *C. punctulatum*.

The holotype of *C. granti* (Powell, 1931, pl.13, figs. 34, 35) is more narrowly and evenly conical than any known Recent specimen (sa 67°, instead of 70-87°, mean 78°, $n = 31$), though all other fossils resemble Recent shells in shape. A coeval specimen (GS4949, NZGS) is substantially larger than the largest known Recent shell (diameter 61 mm, as against 49 mm). All of the fossils are indistinguishable from Recent specimens in sculpture. Because I am unable to detect any character or character state, single or combined, that would enable separation of Recent and fossil specimens, they are all interpreted as forms of a single polymorphic species. Should the Recent form prove to be specifically distinct when additional, better-preserved Waipipian material is available, Powell's *amplum* will be available for the Recent form.

All specimens seen from the Chatham Islands (figure 26) and beach shells from the Auckland Islands and Campbell Island are particularly thick and heavily sculptured. Two specimens from 104 m depth off the Auckland Islands (NZOI D80, figure 27) are thin and finely sculptured and resemble topotypes of the *multigemmata* form. Unless the species has a planktonic larval stage of sufficient duration for transportation to these islands from the mainland by ocean currents, it probably had a more or less continuous distribution between them during periods of lowered sea level, presumably during the Pliocene or Pleistocene. That sea temperature may be a factor restricting its northernmost limit to East Cape is suggested by the occurrence of two closely related species (*C. jamiesoni* new species and *C. gibbsorum* new species) off the Three Kings Islands where sea temperature is

cooler than off adjacent Northland due to local upwelling (see *C. tigris*).

Calliostoma granti resembles *C. osbornei* Powell, 1926 in the rapid enlargement of S3 relative to S1 and S2, but the latter two spirals enlarge more slowly in *C. osbornei*, and *C. granti* has a weak but distinct angulation at P2 on the early teleoconch (figures 29, 31). By comparison with specimens of *C. osbornei* from north of Cape Egmont, the spiral cords on the early teleoconch whorls in *C. granti* are yellowish brown with white nodules instead of being predominantly uniform white, whereas the spiral interspaces are pale buff instead of orange or yellowish to reddish brown. *Calliostoma granti* differs further from *C. osbornei* by having stronger, more numerous axial costae on the early teleoconch whorls, especially on the 4th and early 5th whorls, which are also more strongly convex.

Specimens of *C. osbornei* from off the south-western North Island (figure 41) differ from most northern shells in being as broadly conical as *C. granti* (sa 75-82°, mean 78°), and in that the spiral cords on the early teleoconch whorls are reddish brown between white nodules. Specimens of *C. osbornei* from these southern populations differ from coexisting *C. granti* by having more weakly convex 4th and 5th teleoconch whorls and by having much more deeply and evenly pigmented spiral cords on the early teleoconch whorls.

Calliostoma (Maurea) benthicola (Dell, 1950)
(Figures 33, 34)

Venustas benthicola Dell, 1950:47, fig. 21.

Maurea benthicola—Powell, 1957:88; Powell, 1979:62.

Type Data: Holotype MNZ M.4728, 41°21'S, 175°00'E, Mernoo Bank, western Chatham Rise, 95 m.

Other Material Examined: 22 specimens in 5 lots MNZ.

Distribution (figure 33): Endemic to Mernoo Bank, western Chatham Rise, 75-129 m, taken alive at 95-129 m on shell substratum.

Remarks: *Calliostoma benthicola* differs from *C. granti* by having weaker nodules, and by being white with broad, reddish brown bands on the spiral cords after the fifth teleoconch whorl. It is otherwise extremely similar, particularly to specimens from equivalent depths off Otago, and there can be little doubt that the two forms are very closely related.

Calliostoma benthicola appears to be endemic to the Mernoo Bank and is absent from hundreds of dredge and trawl stations from the adjacent Chatham Rise and off Banks Peninsula and Kaikoura. Mernoo Bank rises from depths exceeding 450 m, which are considerably greater than the known lower limit for living *C. granti* (220 m). It seems likely that *C. benthicola* diverged from *C. granti* stock that was isolated on the Mernoo Bank (and the Chatham Islands), perhaps following a period of lowered sea level during the Pleistocene when Mernoo Bank was an island and the Chatham Rise was sufficiently

close to the surface for icebergs to strand on its summit (Cullen, 1962). *Calliostoma benthicola* appears to be an example of a species that arose from a small, isolated population that carried only a fraction of the total genetic material of the parent population (founder effect of Mayr, 1963). This explanation probably accounts for the origin of the distinctive buccinid *Cominella olsoni* (Dell, 1956), which is also endemic to the Mernoo Bank and is probably derived from *Cominella nassoides* (Reeve, 1846), forms of which occur to the east off Kaikoura and to the west off the Chatham Islands.

***Calliostoma (Maurea) jamiesoni* Marshall, new species** (Figures 30, 33, 36)

Description: Shell up to 33 mm high, higher than broad, spire gently cyrtocoid, spire angle 69-78° (mean 73°, $n = 20$), stout, glossy, anomphalous. Colour of protoconch and 1st 4 teleoconch whorls uniform yellowish to orange brown. Subsequent whorls yellowish to orange brown, spiral cords reddish brown, nodules white or buff white. Protoconch 400 μm wide, sculptured with fine threads that enclose hexagonal spaces. Teleoconch of up to 8 whorls, last adult whorl contracted at maturity. Spire whorls convex, periphery rounded, base weakly convex. First 0.25 whorl delineated by a growth scar, with 2 axial riblets and fine spiral threads. Subsequent whorls sculptured with spiral cords, rounded nodules, and axial riblets; axials strong on 1st 3 whorls, weakening on 4th whorl, becoming obsolete on 5th whorl. Spiral cords rounded, narrow, with broad interspaces on 1st 3 whorls, cords broadening and interspaces narrowing on 4th whorl. Spiral cords numbering 7 or 8 on penultimate whorl and 8 or 9 on last adult whorl. P1-4 commencing immediately, P4 partly covered by succeeding whorls, becoming fully exposed on penultimate whorl by descent of last adult whorl. S1-3 appearing late on 2nd or on 3rd whorl, gradually enlarging to resemble adjacent primaries (S3 absent in 1 specimen). A subsutural spiral appears on penultimate or last whorl in most mature specimens and gradually enlarges to resemble primaries; 1 or more additional spirals intercalate on last adult whorl. Spiral interspaces with collabral growth lines, most interspaces on later spire whorls with up to 4 fine spiral threads. Columella thick. Aperture subcircular. Outer lip thin at rim, thickened within, inner lip spreading onto columella, parietal glaze very thin.

Type Data: Holotype MNZ M.75141 (height 28.5 mm, width 26.0 mm), off Prince's Rocks, Three Kings Is., alive, 15 m, 2 December 1983, scuba, G.S. Hardy and A.L. Stewart. Paratypes (26 MNZ), all from off Three Kings Is.: Off Three Kings Is., alive, craypot, A.D. Howell (1); Three Kings Is., alive, 5 m, March 1982, scuba, K. Burch (2); Tasman Bay, Great King I., alive, 9 m, 19 February 1974, scuba, A.N. Baker & J. Moreland (1); South West I., alive, 22-23 m, 2 December 1983, scuba, G.S. Hardy & A.L. Stewart (3); S side South West I., alive, 27 m, 12 February 1986, scuba, G.S. Hardy (1); reef between Great

King I. and Farmer Rocks, dead, 33 m, 17 February 1986, scuba, G.S. Hardy (15); North West Bay, Great King I., alive, 30 m, 14 February 1986, scuba, G.S. Hardy (1); N. face Hinemoa I., 24 m, 11 February 1986, alive, 3-5 m, 12 February 1986, scuba, G.S. Hardy (2).

Other Material Examined: 129 specimens from 6 stations off Three Kings Is., MNZ, mostly immature.

Distribution (figure 33): Endemic to Three Kings Islands, 5-128 m, taken alive at 5-55 m on rock.

Diet: Intestinal tracts contained thecate hydroids (Cnidaria) and much indeterminate organic matter.

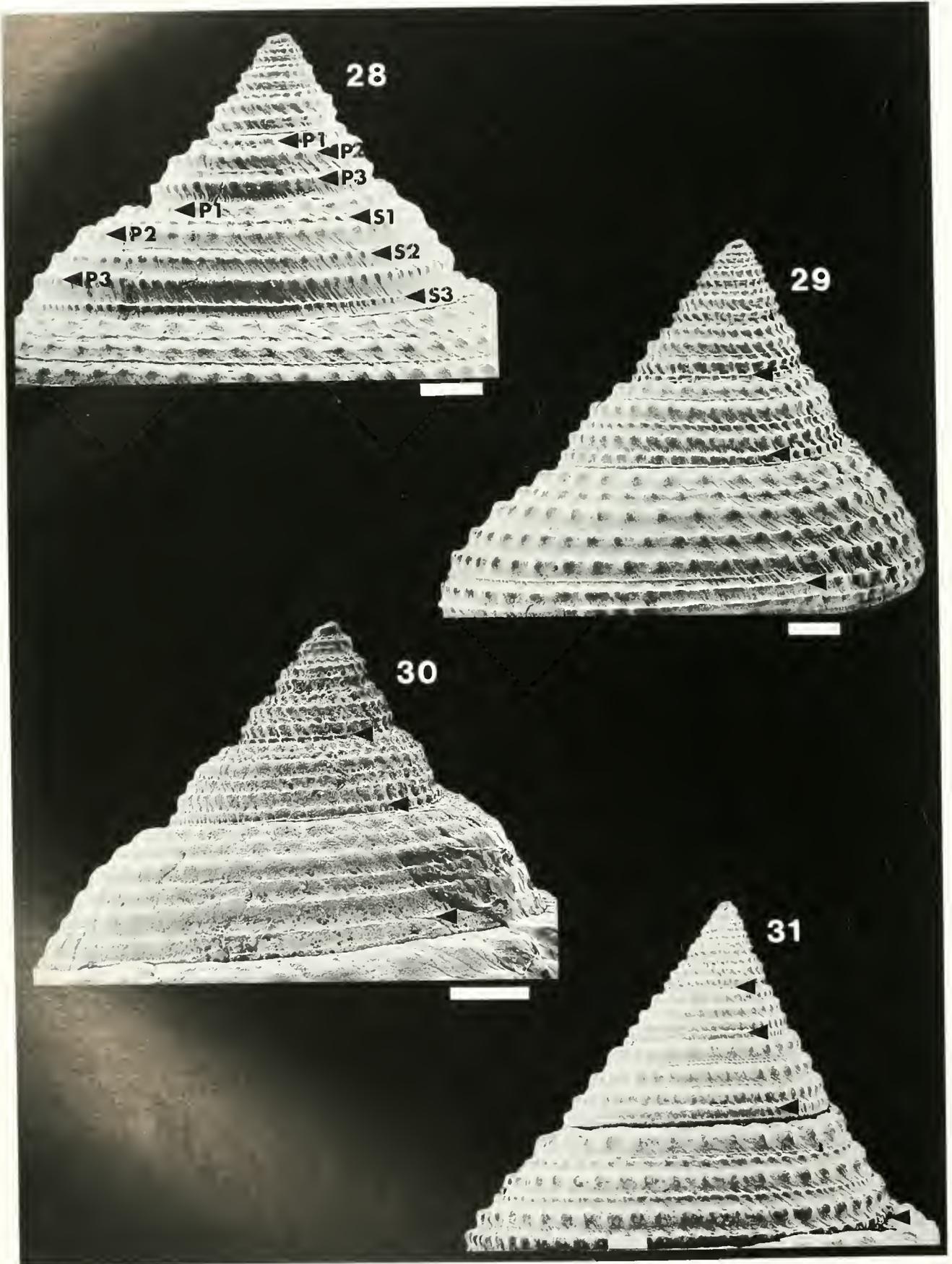
Remarks: *Calliostoma jamiesoni* is superficially similar to *C. punctulatum*, *C. granti*, *C. benthicola*, and broad forms of *C. osbornei*, but most closely resembles *C. granti* and *C. benthicola* in development of the teleoconch sculpture. It differs from all of them, however, in the uniform coloration of the protoconch and early teleoconch whorls and in the low relief of the spiral cords and nodules on the fourth to sixth teleoconch whorls (figures 28-31). The spire tends to be more strongly cyrtocoid and the body whorl more contracted at maturity. It differs further from *C. punctulatum*, *C. granti*, and *C. benthicola* in the early appearance and more rapid enlargement of the secondary spirals, especially S3, and from *C. osbornei* in the roughly simultaneous appearance and rather even rate of enlargement of S2 and S3 and the more strongly convex whorls.

Judging from development of the teleoconch sculpture, *C. jamiesoni* is more closely related to *C. granti*, *C. benthicola*, and *C. gibbsorum* new species (see below) than to the superficially similar species *C. punctulatum* and *C. osbornei*.

Etymology: After Peter Jamieson (Wellington), who sought and provided much material for this revision, and as an appreciation for his fostering of New Zealand malacology in general, both amateur and professional.

***Calliostoma (Maurea) gibbsorum* Marshall, new species** (Figures 33, 35, 109, 130)

Description: Shell up to 28.5 mm (est.) high, higher than broad, spire angle 53-76°, stout, glossy, anomphalous. Colour of protoconch and 1st teleoconch whorl buff or white. Next 2 whorls buff with yellowish brown spirals and white nodules and axials. Subsequent whorls yellowish to orange brown, nodules more lightly pigmented or white, spirals more darkly pigmented. Protoconch 370-400 μm wide, sculptured with fine threads that enclose hexagonal spaces. Teleoconch of up to 8.2 whorls. Spire whorls weakly convex or almost flat, periphery rounded or subangulate, base weakly convex. First 0.25 whorl delineated by a growth scar, with 2 axial riblets and fine spiral threads. Subsequent whorls sculptured with spiral cords, rounded nodules, and axial riblets, the axials strong on 1st 4 whorls, weakening and becoming obsolete on 5th whorl. Spiral cords rounded, narrow with broader



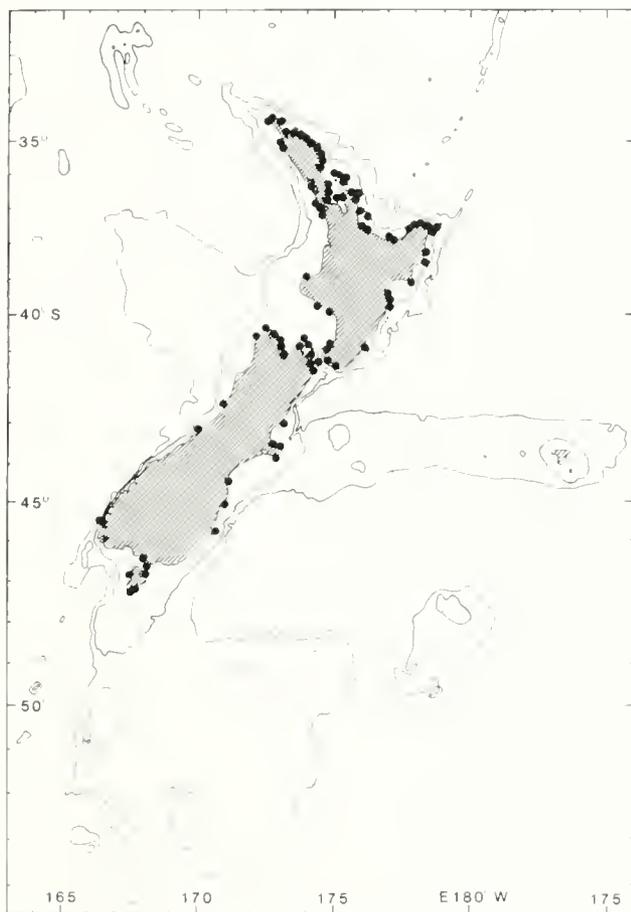


Figure 32. Map of New Zealand region showing distribution of *Calliostoma (Maurea) punctulatum*. 200 and 1000 meter contours indicated.

interspaces on 1st 4 whorls, spirals broadening and interspaces narrowing on 5th whorl. Spiral cords numbering 7 on adult penultimate whorl and 11 on base. P1-4 commencing immediately, P4 almost or entirely covered by succeeding whorls throughout or (as in holotype) becoming entirely exposed at suture from as early as 5th whorl. S1-S3 gradually enlarging to resemble adjacent primaries. Additional spirals intercalated on penultimate and last adult whorls of an exceptionally large specimen. Spiral interspaces with collabral growth lines, a few spiral threads in some specimens. Aperture subquadrate to sub-

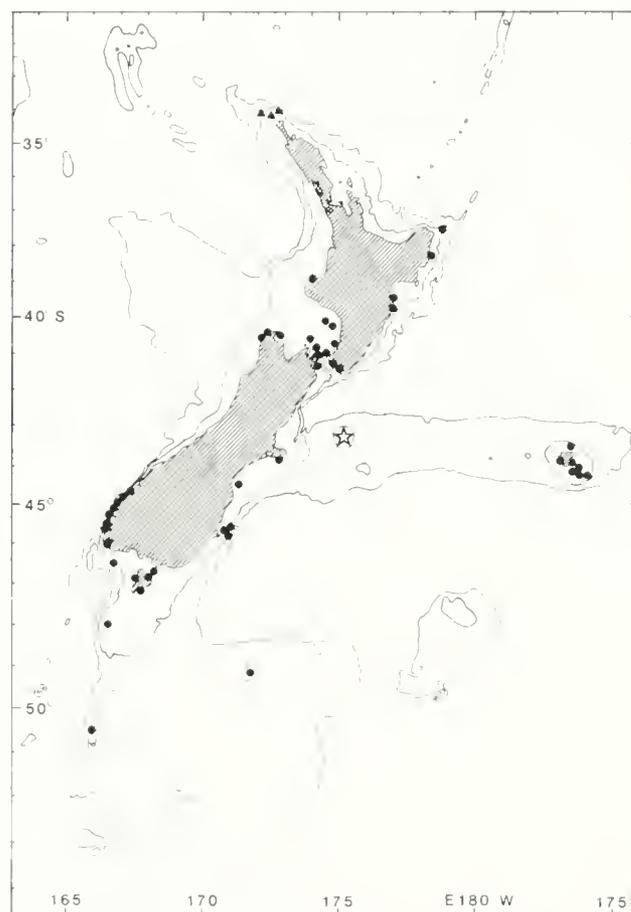


Figure 33. Map of New Zealand region showing distribution of *Calliostoma (Maurea) granti* (circle), *C. (M.) benthicola* (star), and collectively *C. (M.) gibbsorum*, *C. (M.) jamiesoni*, and *C. (M.) regale* (triangle). 200 and 1000 meter contours indicated.

circular. Outer lip thin at rim, thickened within, inner lip spreading onto thick columella, parietal glaze thin.

Type Data: Holotype MNZ M.35456 (height 16.8 mm, width 12.5 mm), BS 389, between Palmer Rocks and South East I., Three Kings Is., dead, 82 m, 18 February 1974, r.v. *Acheron*. Paratypes (3 MNZ): BS 893 (0639), 33°59.9'S, 171°45.3'E, Middlesex Bank, NW of Three Kings Is., dead, 186-196 m, 31 January 1981, r.v. *Tan-*

Figures 28-31. Early teleoconch whorls. Primary (P) and secondary (S) spiral cords indicated. **Figure 28.** *Calliostoma (Maurea) punctulatum* (Martyn, 1784). Cook Strait, 256-274 m, MNZ M.54911. Note late appearance and slow enlargement of S3, weak axial sculpture, and broad, strongly convex 5th teleoconch whorl. **Figure 29.** *Calliostoma (Maurea) granti* (Powell, 1931). Off Stephens Island, Cook Strait, 183-187 m, MNZ M.50266. Note early appearance and rapid enlargement of S3 (arrowed), strong axial sculpture, and narrow, weakly convex 5th teleoconch whorl. **Figure 30.** *Calliostoma (Maurea) jamiesoni* Marshall, new species. Off West Island, Three Kings Islands, 37 m, MNZ M.80656. Note closer similarity of sculpture to that of *C. (M.) granti* (29) than to *C. (M.) punctulatum* (28), S3 arrowed. **Figure 31.** *Calliostoma (Maurea) osbornei* Powell, 1926. Off Cape Maria Van Diemen, 38-43 m, MNZ M.74665. Note late appearance of S1 and S2, early appearance and very rapid enlargement of S3 (arrowed), evenly conical outline, and flattened whorls. Scale bars = 1 mm.

garoa (1) BS 921, *Elingamite* wreck, off West Island, Three Kings Is., dead, 37 m, 16 March 1981, suction dredge, K. Tarlton (1); off Three Kings Is., alive, craypot, A.D. Howell (1).

Other Material Examined: 60 specimens from 13 stations off Three Kings Islands, MNZ, mostly juveniles.

Distribution (figure 33): Off Three Kings Islands, 33-805 m, taken alive at 102 m and probably living as shallow as about 30 m on rugged bryozoan/shell substratum with corals, sponges, and gorgonians. Probably endemic.

Diet: Unknown.

Remarks: *Calliostoma gibbsorum* is superficially similar to *C. jamiesoni*, *C. granti*, *C. benthicola*, and to a lesser degree, *C. punctulatum*, and *C. osbornei*. It closely resembles *C. jamiesoni*, *C. granti*, and *C. benthicola* in development of the spiral teleoconch sculpture, specifically in the more or less simultaneous origin and even rate of development of S1-3. Compared with the sympatric species *C. jamiesoni*, it differs constantly in colour and colour pattern (especially when immature—see descriptions); in having stronger, more crisply defined spirals and nodules after the third teleoconch whorl; in having narrower, more numerous spiral cords on the base (I1 instead of 8 or 9); and in the shape of teleoconch whorls, which expand more slowly and are more weakly convex after the fourth whorl. Compared with the allopatric species *C. granti* and *C. benthicola*, development of teleoconch sculpture is entirely more rapid, S2 and S3 appearing and enlarging to resemble the primaries a half to a full whorl earlier. Moreover, the nodules are more rounded, and the axial sculpture persists for longer and is stronger, especially on the fourth and early fifth whorls. It differs from the allopatric species *C. punctulatum* in the earlier appearance and more rapid enlargement of the secondary spirals (especially S3), the stronger, more persistent axial costae, and the more weakly convex whorls. From the sympatric species *C. osbornei* it differs in numerous details of colour, colour pattern, and sculpture, most obviously in the more or less simultaneous appearance of S2 and S3. For further remarks see *C. jamiesoni* (above).

Etymology: After David and Sharon Gibbs (Auckland) who provided much valuable material and as an appreciation for their fostering of amateur and professional malacology in New Zealand.

Calliostoma (Maurea) osbornei Powell, 1926
(Figures 31, 37-39, 41, 43, 131)

Calliostoma osbornei Powell, 1926:591, pl. 102, fig. 1, 2.

Calliostoma (Mauriella) osbornei—Oliver, 1926:110.

Venustus (Mucrinops) osbornei—Finlay, 1926:361, 371.

Maurea (Mucrinops) osbornei—Powell, 1937:64, pl. 13, fig. 4.

Venustus osbornei—Dell, 1950:47.

Maurea osbornei—Powell, 1957:88, pl. 13, fig. 4, Powell, 1979:62, pl. 10, fig. 5.

Maurea (Mauriella) osbornei—Fleming, 1966:38.

Type Data: Holotype AIM 72037, off Cape Barrier, Great Barrier I., c. 49 m, from fish stomach.

Other Material Examined: *Fossil*—GS4253, Upper Waipipi Shellbed, Waverley Beach, south Taranaki (Waipipian, Middle Pliocene) (1 NZGS). *Recent*—167 specimens in 45 lots MNZ.

Distribution (figure 43): Middle Pliocene (Waipipian) to Recent, Three Kings Islands southward to off Kapiti Island, southern North Island (34°08.5'S-40°50'S), 0-102 m, living at 12-93 m on the sponge *Ancorina alata* Dendy, 1924 on rocky ground.

Diet: *Ancorina alata* Dendy, 1924 (Porifera : Stellettidae).

Remarks: *Calliostoma osbornei* bears a strong superficial resemblance to *C. punctulatum* and *C. granti*. From *C. punctulatum* it differs in numerous details, most notably the rapid enlargement of S3 and the relatively slow enlargement of S1 and S2 (figure 31). Other differences include the more weakly convex whorls, stronger nodules on the early teleoconch, and the lack of a prominent angulation at P2 on the third-fifth teleoconch whorls. Among differences in colour and colour pattern, the most notable are on the first four whorls, which are typically orange with white spiral cords and nodules instead of being predominantly white with reddish or yellowish brown spiral cords and white or alternately spotted nodules. The only known exceptions are specimens from off New Plymouth (figure 41), Wanganui and Kapiti Island at the extreme southern limit of its range, which resemble *C. punctulatum* in colour pattern. Most specimens of *C. osbornei* are more narrowly conical than *C. punctulatum*, though some shells may be as broadly conical, especially those from the extreme south of its range (sa in southern material 50-82°, mean 66°, S.D. 7.29, $n = 52$, as against 65-96°, mean 85°, S.D. 5.83, $n = 64$). Despite the similarity in shape, broad specimens of *C. osbornei* are readily separable from *C. punctulatum* by the characteristic teleoconch sculpture. The Middle Pliocene (Waipipian) specimen lacks the early spire whorls but is otherwise well preserved and indistinguishable from Recent material. Judging from its present restricted northern distribution (figure 43) and rarity south of Cape Egmont, the lack of fossils from overlying horizons in the Wanganui section may be related to sea temperatures, which were cooler after the Waipipian (Beu, 1966). The present distribution of *C. osbornei* is not entirely determined by that of its food, the grey sponge, *Ancorina alata*, which ranges at least as far south as Banks Peninsula (M.H.B. O'Neill, pers. comm.).

Calliostoma (Maurea) regale Marshall, new species
(Figures 33, 40, 111, 132)

Description: Shell up to 12.6 mm high, glossy, of moderate thickness; spire narrowly and rather evenly conical, 1.50-1.87 × higher than aperture in adults; spire angle 54-63°, anomphalous. Colour of tip of apical fold yellow.

lowish brown, rest of protoconch white. Most fresh specimens pale yellowish brown between nodules on P2 and P3 on 2nd and 3rd teleoconch whorls, some specimens with addition of a sub- and/or suprasutural band of dull olive that persists onto 4th whorl. First 2 whorls typically with a pinkish flush. Fresh juveniles with pale yellowish brown spots on spiral cords on innermost third of base. Shell elsewhere rather uniform pale buff white. Protoconch 370 μm wide, sculptured with a network of fine threads that enclose hexagonal spaces, terminal varix strong, rounded. Teleoconch of up to 7.25 whorls. First few whorls rather strongly convex, angulated at P2 and P3, subsequent whorls very weakly convex. Periphery rounded at maturity, base more or less flat. First quarter whorl delineated by a growth scar, with a strong, rounded axial varix and fine spiral threads. Subsequent spire whorls encircled by prominent spiral cords with rounded nodules, the spirals multiplying by intercalation of secondaries and tertiaries that enlarge to resemble primaries. Nodules evenly developed on each spiral, occasionally becoming very weak after 5th whorl on spirals other than P1. P1 commencing late on 2nd or early on 3rd whorl, gradually enlarging to resemble P2 and P3, which commence immediately after growth scar on 1st whorl. P4 covered by succeeding whorls, becoming fully exposed on penultimate whorl by descent of last adult whorl, nodular on last adult whorl, smooth before it. S1 commencing from early on 3rd whorl to start of 6th whorl, S2 commencing from late on 2nd whorl to midway through 3rd whorl, S3 commencing from late on 3rd whorl to midway through 4th whorl. In adults a tertiary spiral intercalates on penultimate whorl, where the total of 8 spirals includes emergent P4. Additional tertiaries intercalate on last adult whorl. Axial riblets strong on 1st 3 whorls, weakening on 4th and becoming obsolete on 5th whorl. Interspace of P3 and P4 on 1st 4 whorls with numerous fine, close, crisp, secondary axial riblets that become obsolete on succeeding whorl. Basal spirals multiplying by intercalation of a few secondaries to number about 10 in adults; interspaces about as wide as each spiral or narrower, sculptured with fine collabral growth lines; spirals weak and smooth in immature specimens, becoming stronger and nodular with increasing size, rarely more or less smooth in adults. Outer basal spirals resembling spire spirals, inner spirals stronger and more strongly nodular. Aperture subquadrate, strongly thickened within and immediately behind apertural rim in adults, especially at base and columella.

Type Data: Holotype M.86730 (height 12.5 mm, width 9.30 mm) and paratype MNZ, BS 902 (0648), 34°10.5'S, 172°11.4'E, off Three Kings Is., dead, 153 m, 1 February 1981, r.v. *Tangaroa*. Paratypes (14, all from off Three Kings Is.): BS 900 (0646), 33°57.0'S, 171°45.4'E, alive, 98-103 m, 31 January 1981, r.v. *Tangaroa* (3 MNZ); BS 905 (0651), 33°57.4'S, 172°19.4'E, alive, 128-123 m, 1 February 1981, r.v. *Tangaroa* (1 MNZ); BS 894 (0640), 34°00.9'S, 171°44.7'E, alive, 201-216 m, 31 January 1981, r.v. *Tangaroa* (1 MNZ); BS 898 (0644), 34°01.2'S,

171°45.8'E, alive, 221-206 m, 31 January 1981, r.v. *Tangaroa* (4 MNZ); E 846, 34°07.5'S, 171°57.5'E, dead, 417 m, 16 March 1968, m.v. *Viti* (1 NZOI); BS 902 (0648), 34°10.5'S, 172°11.4'E, dead, 153 m, 1 February 1981, r.v. *Tangaroa* (2 MNZ); BS 906 (0652), 34°14.8'S, 172°13.6'E, dead, 173-178 m, 2 February 1981, r.v. *Tangaroa* (1 MNZ).

Other Material Examined: 189 specimens from 21 stations off Three Kings Is., 53-805 m, MNZ, mostly immature.

Distribution (figure 33): Off Three Kings Islands (33°57.0'S-34°22.8'S), 53-805 m, taken alive at 98-221 m on rugged, comminuted bryozoan/shell substratum with sponges, hydroids, gorgonians, corals, etc.

Diet: Unknown.

Remarks: *Calliostoma regale* resembles the sympatric species *C. osbornei* in shape but differs in details of colour and colour pattern and in development of teleoconch sculpture, including appearance of S2 before S3 and slow enlargement of P1 on the first two whorls. Among previously described New Zealand Recent calliostomatids, it is rendered highly distinctive by the presence of fine axial riblets between P3 and P4 on the early teleoconch whorls, which facilitates recognition of even very immature specimens (figure 109). *Calliostoma regale* seems to be closely related to *C. simplex* Schepman, 1908 from the Banda Sea, from which it differs principally in having more markedly convex spire whorls and stronger nodules on the base. Moreover, P1 develops later, and P2 and P3 are relatively larger on the early teleoconch whorls. Although the protoconch and first teleoconch whorl of the holotype of *C. simplex* (ZMA) are eroded, enough remains to show that P1 is present almost immediately after the protoconch and that it is as large as P2 midway through the second whorl. In *C. regale*, P1 commences late on the second or early on the third whorl and does not rival P2 in size until midway through the third or fourth whorl. *Calliostoma simplex* is otherwise similar in the order of appearance of the secondary spirals and in having axial riblets between P3 and P4.

Etymology: Royal (Latin). Alluding to the Three Kings Islands.

Calliostoma (Maurea) aupaourianum Marshall, new species
(Figures 42, 50, 112, 133)

Description: Shell up to 8.60 mm high, glossy, of moderate thickness; spire narrowly and rather evenly conical, up to 1.65 \times higher than aperture; mean spire angle 58-65°, anomphalous. Colour of extreme tip of protoconch yellowish brown, elsewhere white. Subsequent whorls yellowish or pale yellowish brown, spire irregularly axially mottled in a darker shade, each dark band followed by a narrow white band, base in adults irregularly axially mottled in yet darker shades. Protoconch 370-380 μm

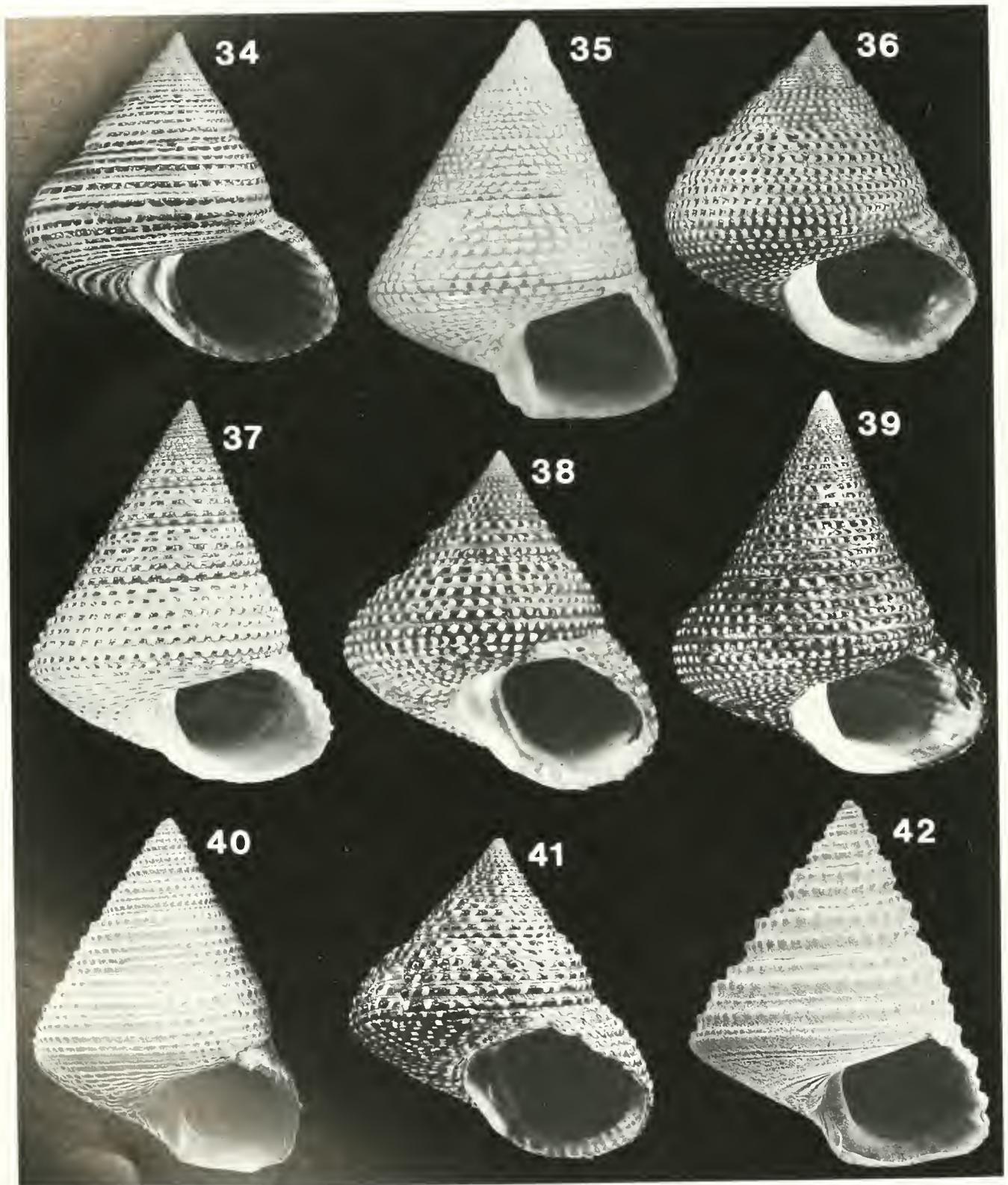


Figure 34. *Calliostoma (Mureca) benthicola* (Dell, 1956). Mernoo Bank, Chatham Rise, 95 m, MNZ M.23626 (30.5 × 29.0 mm).
 Figure 35. *Calliostoma (Mureca) gibbsorum* Marshall, new species. Holotype, off Three Kings Islands, 82 m, MNZ M.35456 (16.8 × 12.5 mm). Figure 36. *Calliostoma (Mureca) jamiesoni* Marshall, new species. Holotype, off Three Kings Islands, 15 m, MNZ M.75141 (28.5 × 26.0 mm). Figures 37-39. 41. *Calliostoma (Mureca) osbornei* Powell, 1926. 37. North Ahipara Bank, western Northland, 53-56 m, MNZ M 74590 (25.0 × 19.5 mm). 38. Between Pandora Bank and Cape Maria Van Diemen, 38-43 m, MNZ M 70955 (22.7 × 20.8 mm). 39. Astrolabe Reef, off Motiti Island, 20-23 m, MNZ M 117841 (32.7 × 26.0 mm). 41. Seal Rock,

wide, sculptured with network of fine threads that enclose roughly hexagonal spaces, terminal varix strong, rounded. Teleoconch of up to 6.4 whorls. First few whorls rather strongly convex, later whorls weakly convex, early or all whorls distinctly angulated at P2, periphery subangulate at maturity, base more or less flat. First quarter whorl delineated by a fine growth scar, sculptured with 2 rounded axial varices and fine spiral threads. Subsequent whorls encircled by prominent spiral cords with conical nodules, spirals multiplying by intercalation from 3 (P2-P4) to 7 (P1-P4, S1-S3), secondaries enlarging to resemble primaries. P4 smooth throughout, S3 finely nodular or smooth, other spire spirals nodular. On 3rd and 4th whorls, or all whorls other than last adult whorl, a single nodule on P2 is considerably enlarged and white immediately following each dark mottling; interval at about each 3rd nodule on early whorls, intervals variable and up to 7 nodules apart on later whorls. P1 commencing early on or midway through 2nd whorl, gradually enlarging to resemble P3; P2 and P3 commencing immediately after growth scar on 1st whorl. P4 almost or entirely covered by succeeding whorls, becoming fully exposed on penultimate whorl by descent of last adult whorl, smooth throughout. S1 commencing late on 5th or 6th whorl or entirely absent in adults, S2 commencing late on 3rd to midway through 4th whorl, S3 commencing early on 4th or 5th whorl. Up to 3 tertiary spirals may intercalate on last adult whorl. Axial riblets strong on 1st 3 whorls, weakening and becoming obsolete on 4th whorl. Interspace of P3 and P4 on 3rd-5th whorls with numerous fine, close, crisp, secondary axial riblets that become obsolete on succeeding whorl. Basal spirals smooth throughout, numbering 11 or 12. Fine collabral growth lines throughout, stronger on base. Aperture subquadrate, strongly thickened immediately within in adults, especially at base and columella.

Type Data: Holotype M.86731 (height 7.15 mm, width 6.00 mm) and paratype MNZ: BS 395, 34°10'S, 172°12'E, off Three Kings Is., dead, 252 m, 19 February 1974, r.v. *Acheron*. Paratypes (5 MNZ): BS 905 (0651), 33°57.4'S, 172°19.4'E, off Three Kings Is., alive, 128-123 m, 1 February 1981, r.v. *Tangaroa* (1); BS 901 (0647), 34°14.1'S, 172°09.0'E, off Three Kings Is., dead, 192-202 m, 1 February 1981, r.v. *Tangaroa* (1); BS 833 (0578), 37°38.5'S, 178°56.4'E, SE slope of Ranfurly Bank, East Cape, dead, 153-143 m, 22 January 1981, r.v. *Tangaroa* (3).

Other Material Examined: 38 specimens from 13 stations off Three Kings Is., dead, 102-805 m, MNZ, mostly immature; BS 747 (R105), 37°16.7'S, 176°17.5'E, off E side Mayor I., dead, 104-109 m, 22 January 1979, r.v. *Tangaroa* (2 immature).

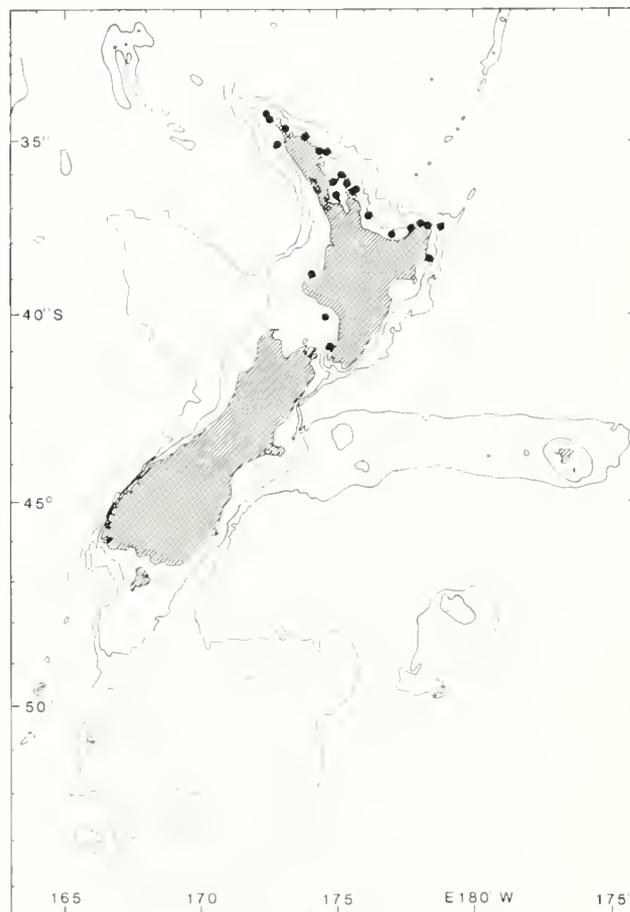


Figure 43. Map of New Zealand region showing distribution of *Calliostoma (Maurea) osbornei*. 200 and 1000 meter contours indicated.

Distribution (figure 50): Off Three Kings Islands, Mayor Island, and East Cape, 102-805 m, taken alive at 123-128 m on rugged comminuted bryozoan/shell substratum with sponges, hydroids, gorgonians, corals, etc.

Diet: Unknown.

Remarks: Compared with the sympatric species *Calliostoma regale*, which it most closely resembles, *C. auppourianum* differs in the later appearance and slower enlargement of the secondary spirals, in having more sharply pointed nodules, in the irregular size of the nodules on P2, and in details of colour pattern as described above.

Etymology: Alluding to the distribution within the boundaries of the former Auppourian marine province.

New Plymouth, 12 m, MNZ M.80156 (28.0 × 27.0 mm). **Figure 40.** *Calliostoma (Maurea) regale* Marshall, new species. Holotype, off Three Kings Islands, 153 m, MNZ M.86730 (12.5 × 9.30 mm). **Figure 42.** *Calliostoma (Maurea) auppourianum* Marshall, new species. Holotype, off Three Kings Islands, 252 m, MNZ M.86731 (7.15 × 6.00 mm).

Calliostoma (Maurea) spectabile (A. Adams, 1855)
(Figures 44-47, 50, 113, 134)

Zizyphinus spectabilis A. Adams, 1855:37, pl. 27, fig. 7; Reeve, 1863, pl. 1, fig. 5a,b; Hutton, 1873:38, Hutton, 1880:98; Hutton, 1884:360.

Calliostoma spectabilis—Pilsbry, 1889:332, pl. 16, fig. 12.

Calliostoma spectabile—Suter, 1897:280; Suter, 1913:147, pl. 40, fig. 5.

Calliostoma (Mauriella) spectabile—Oliver, 1926:110.

Venustus (Mucrinops) spectabilis—Finlay, 1926:360.

Venustus (Mucrinops) spectabilis—Finlay, 1926:360, 371.

Maurea (Mucrinops) spectabilis—Powell, 1937:64.

Venustus spectabile—Dell, 1950:45, figs. 16-18; Powell, 1955:55.

Maurea spectabile—Powell, 1957:88.

Calliostoma (Maurea) spectabilis—Cernohorsky, 1977:93, fig. 9.

Maurea spectabilis—Powell, 1979:63, pl. 19, fig. 1.

NOT *Venustus (Mucrinops) spectabilis*—Finlay, 1926:362, pl. 18, fig. 26 (*C. foveauxanum*).

Type Data: Holotype BMNH 1968150 (Cernohorsky, 1977, fig. 9).

Other Material Examined: 55 specimens in 27 lots MNZ, 4 specimens in 2 lots NZOI.

Distribution (figure 50): Off Auckland and Campbell islands, 0-146 m, taken alive at 9-146 m from hard substrata.

Diet: Guts examined contained thecate hydroids (Cnidaria) and much indeterminate organic matter.

Remarks: This species is characterised by a large, heavy, strongly sculptured shell; cyrtoconoid early spire whorls; and convex, rapidly expanding early teleoconch whorls. Late teleoconch whorls range from strongly convex to almost flat, and the spire is broadly to narrowly conical (sa 52-80°, mean 61°, SD 7.59, $n = 29$), the most broadly conical specimens tending to have the most strongly convex whorls. Specimens washed ashore and living as deep as 9 m at the Auckland Islands (figure 45) have the most broadly conical spires (sa 60-80°, mean 70°, SD 5.83, $n = 9$). Auckland Islands specimens (figure 47) from greater depths (37-146 m) and all Campbell Island shells (figure 46) are exclusively narrow-spined (sa 52-60°, mean 56°, SD 2.93, $n = 20$), though some beach shells from the Auckland Islands may be as narrowly conical (figure 44). Most specimens from Campbell Island (figure 46) are more weakly nodular than Auckland Islands specimens, and have slower enlargement of the secondary spirals, though similar forms occur in both populations. Whilst Auckland and Campbell islands populations are probably conspecific, the differences suggest that there may be little genetic exchange between them.

Calliostoma (Maurea) foveauxanum (Dell, 1950)
(Figures 48, 50, 114, 135)

Venustus (Mucrinops) spectabilis—Finlay, 1926:362, pl. 18, fig. 26 (not A. Adams, 1855).

Venustus foveauxana Dell, 1950:45, fig. 13-15

Maurea foveauxana—Powell, 1957:88; Powell, 1979:63, pl. 10, fig. 7.

Calliostoma spectabile foveauxanum—Beu, 1976:78.

Maurea blacki—Abbott & Dance, 1982:40 (not Powell, 1950). NOT *Calliostoma (sensu lato) foveauxanum*—Beu & Maxwell, 1990:404 (*C. blacki* Powell, 1950).

Type Data: Holotype MNZ M.4727, Foveaux Strait, 53 m. Paratype (1 MNZ), Stewart Island.

Other Material Examined: 68 specimens in 8 lots MNZ, 5 specimens in 3 lots NZOI.

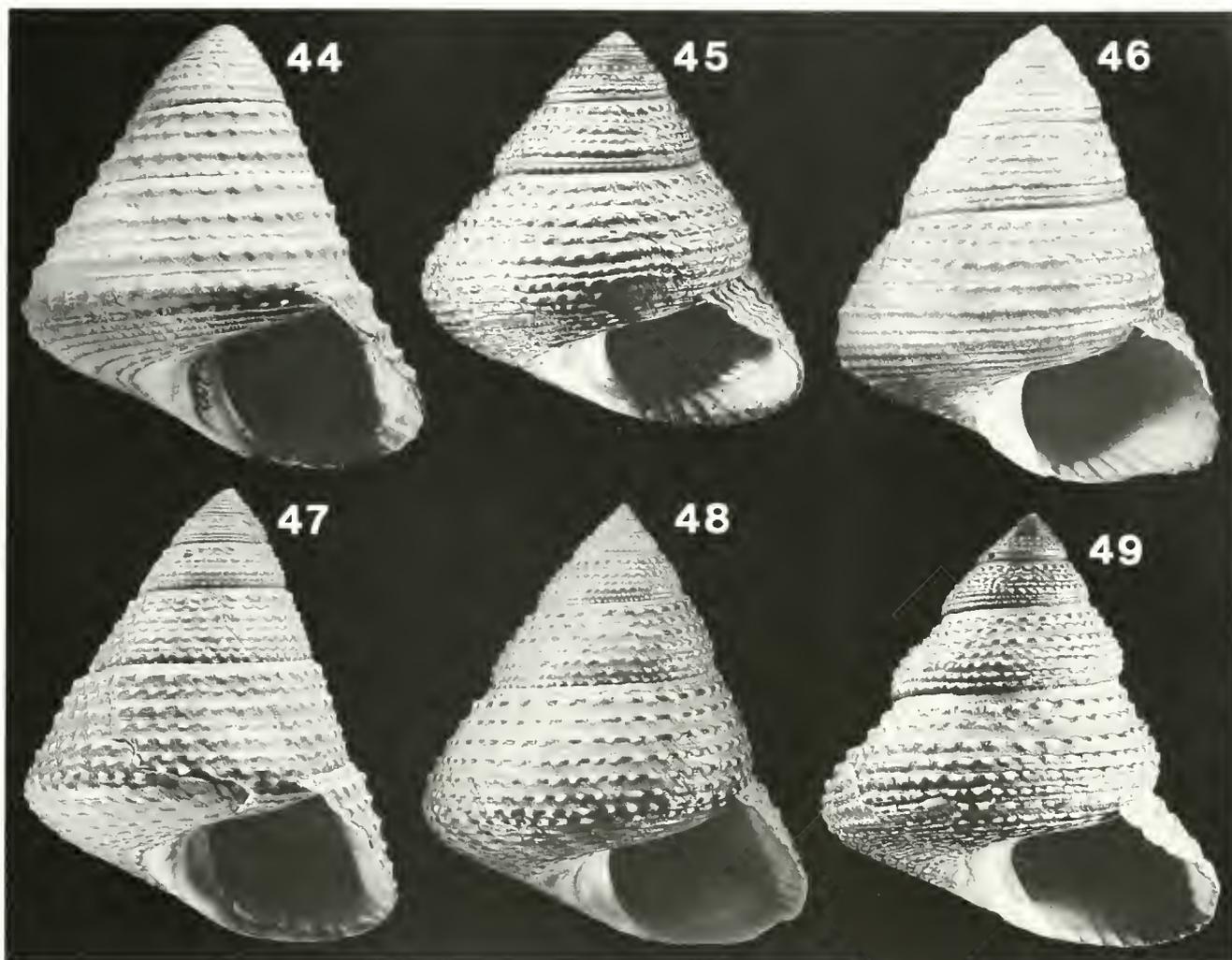
Distribution (figure 50): South-eastern South Island, Stewart Island, and The Snares, 73-549 m, taken alive at 91-220 m from bryozoan/shell substrata.

Diet: Intestinal tracts examined contained mostly thecate hydroids (Cnidaria) with some indeterminate organic matter.

Remarks: From *Calliostoma spectabile*, to which it is most closely related, *C. foveauxanum* differs principally in being more finely sculptured and in that the contour of the early teleoconch is more weakly cyrtoconoid. Although they are allopatric, there is no clinal intergradation within their respective geographic ranges, so it seems likely that they are distinct, closely related species rather than disjunct populations of a single species. Another closely related species from the Antipodes Islands is described below.

Calliostoma (Maurea) eminens Marshall, new species
(Figures 49, 50)

Description: Shell up to 51 mm high, higher than broad, spire up to 1.68 × higher than aperture, stout, weakly cyrtoconoid, spire angle 62-66°, suture deep, anomphalous. Colour yellowish brown, spiral cords reddish brown, nodules white, basal spirals alternately spotted reddish brown and white. Parietal and inner lips porcellaneous white. Protoconch unknown (etched). Teleoconch of up to at least 8.5 convex whorls, earliest whorls unknown (eroded—whorl numbers estimated). First 5 whorls rather evenly convex, subsequent whorls flattened adapically, periphery rounded, base weakly convex. After 5th whorl, zone between suture and P1 steepens until almost vertical, channeling suture. Sculpture consisting of strong, rounded spiral cords and weaker axial costae, axials weakening and vanishing on 4th whorl. Spiral cords numbering 6 or (usually) 7 on adult penultimate whorl, comprising P1-P4 plus intercalating secondaries that commence after 1st 4-4.5 whorls, additional tertiaries intercalate on last adult whorl, 7-10 cords on base. First 3 whorls inserted against P4, subsequent whorls descending and inserted between P4 and outermost basal spiral. Spire spirals with rounded nodules, those on P1 strongest, nodules finer and more numerous on abapical half of each whorl, basal spirals undulant. Fine collabral growth lines throughout, some specimens with fine spiral lirae in some spiral interspaces. Aperture ovate. Outer lip thin at rim,



Figures 44-47. *Calliostoma (Maurea) spectabile* (A. Adams, 1855). 44. Auckland Island, beach, MNZ M.102600 (48.0 × 43.0 mm). 45. West coast, Auckland Island, 9 m, MNZ M.36711 (51.0 × 49.3 mm). 46. Boyaek Point, Campbell Island, 6 m, MNZ M.117480 (47.0 × 39.4 mm). 47. North of Auckland Islands, 113m, NZOI D200 (56.0 × 46.0 mm). Figure 48. *Calliostoma (Maurea) foveauxanum* (Dell, 1950). Off Otago Peninsula, 130-150 m, MNZ M.117268 (53.5 × 46.8 mm). Figure 49. *Calliostoma (Maurea) eminens* Marshall, new species. Holotype, off Archway Island, Antipodes Islands, 13-15 m, MNZ M.84112 (50.8 × 45.0 mm).

thickened within, parietal and inner lips a continuous spreading glaze.

Type Data: Holotype M.84112 (height 50.8 mm, width 45.0 mm, 8 teleoconch whorls) and paratype MNZ, N side of Archway I., Antipodes Is., alive on sloping rock, 13-15 m, 29 November 1978, scuba, D.S. Horning. Paratypes (18): A728, 49°38.4'S, 178°48.7'E, off Antipodes Is., dead, 95 m, 7 November 1962, m.v. *Taranui* (1 NZOI); 49°40'S, 178°53'E, off Antipodes Is., dead, 103 m, USNS *Eltanin* stn 1850 (9 USNM, 3 MNZ); A739, 49°40.19'S, 178°44.3'E, off Antipodes Is., dead, 113 m, 9 November 1962, m.v. *Taranui* (1 NZOI); A723, 49°42'S, 178°50.3'E, off Antipodes Is., dead, 123 m, 7 November 1962, m.v. *Taranui* (4 NZOI); E side Perpendicular Head, Antipodes Is., under large boulder, alive, 19 m, 27 November 1978, scuba, D.S. Horning (1 MNZ); S side Ringdove

Bay, Antipodes Is., on rocks, alive, 18-20 m, 21 November 1978, scuba, D.S. Horning (2 MNZ).

Distribution (figure 50): Off Antipodes Islands, 13-123 m, taken alive at 13-20 m from hard substrata. Probably endemic.

Diet: Guts contain mostly thecate hydroids (Cnidaria) and some indeterminate organic matter.

Remarks: *Calliostoma eminens* differs from its allopatric relatives *C. spectabile* and *C. foveauxanum* in having more strongly convex whorls and in that the suture is set lower on each whorl and is thus correspondingly deeper and the whorls correspondingly more strongly convex. It differs further from *C. spectabile* in being more lightly built and from *C. foveauxanum* in its stronger basal sculpture.

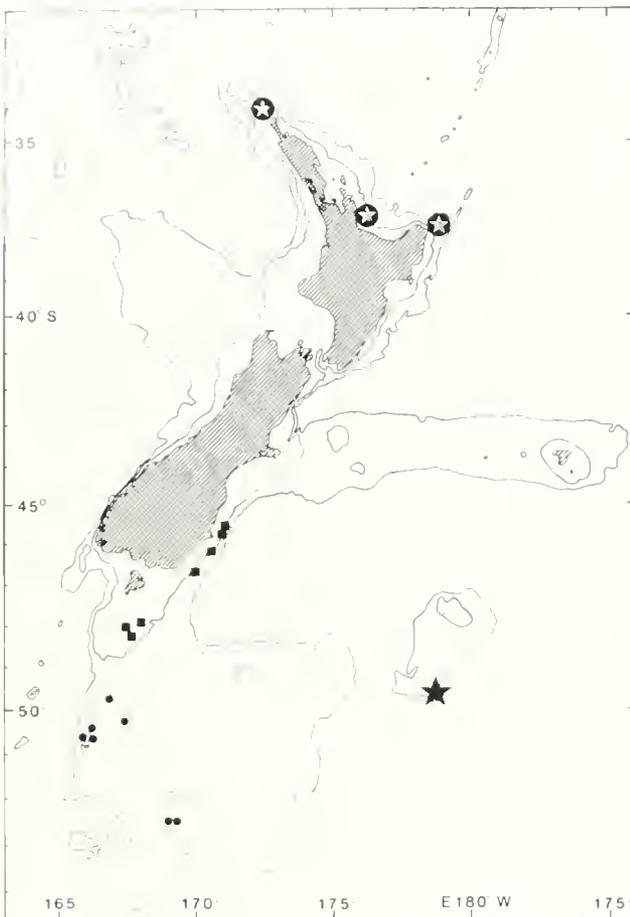


Figure 50. Map of New Zealand region showing distribution of *Calliostoma (Maurea) aupourianum* (hollow star), *C. (M.) spectabile* (circle), *C. (M.) foveauxanum* (square), and *C. (M.) eminentens* (solid star). 200 and 1000 meter contours indicated.

Etymology: High (Latin).

Calliostoma (Maurea) blacki (Powell, 1950)
(Figures 51-63, 115, 136)

- Venustus blacki* Powell, 1950:80, pl. 7, fig. 3, 4.
Venustus couperi Vella, 1954:543, pl. 25, fig. 6, **New synonym**.
Thoristella chathamensis profunda Dell, 1956:44, pl. 6, fig. 57, **New synonym**
Maurea blacki—Powell, 1957:88; Powell, 1979:63, pl. 19, fig. 10, 11
Maurea (Mauriella) couperi—Fleming, 1966:38; Beu, 1978, 724, figs. 11, 13/13
Calliostoma (Maurea) spectabile foveauxana—Beu, 1979:88 (in part not Dell, 1950).
Calliostoma spectabile couperi—Beu, 1981:74, pl. 32, fig. 13.
Calliostoma (sensu lato) couperi—Beu & Maxwell, 1990:404
Calliostoma (sensu lato) foveauxanum—Beu & Maxwell, 1990, 404 (not Dell, 1950).
 NOT *Maurea blacki*—Abbott & Dance, 1986:10 (*C. foveauxanum*).
 NOT *Maurea blackii* [sic]—Horikoshi, 1989, pl. 4, fig. 12 (*C. grantii*).

Type Data: *Venustus blacki*: Holotype AIM 71168, off eastern Otago, c.128 m; *Venustus couperi*: Holotype NZGS TM 4995, east side of Makara Stream, north of Te Awaite cutting, Wairarapa (early Nukumaruan, Late Pliocene).

Other Material Examined: 128 Recent specimens in 30 lots MNZ, 34 specimens in 13 lots NZOI.

Distribution (figure 63): Late Pliocene (early Nukumaruan) to Recent, Chatham Rise, South Island east coast from Kaikoura southwards; Stewart, Snares, Auckland, Campbell, and Bounty islands, 73-549 m, taken alive at 95-549 m from bryozoan/shell substrata.

Diet: Gut contents examined comprised thecate hydroids (Cnidaria) and indeterminate organic matter.

Remarks: This species has great variation in shell morphology and is frequently confused with *C. foveauxanum* (Beu, 1976:79; Powell, 1979:497) and *C. simulans* in collections. The spire angle ranges from 60° to 91° (mean 75°, SD 6.64, $n = 59$), and the whorls may be more or less flat-sided throughout with an angulate periphery, or they may become convex with increasing shell size so that the last whorl is evenly rounded. Shell thickness may vary by up to a factor of three, and there is considerable variation in the strength of the spiral cords and nodules. There is complete integration between all extremes in shell morphology, and it is clear that all of the specimens examined represent a single, highly polymorphic species. Specimens from the Chatham Rise (figures 51, 53) and some from off Kaikoura, at the northernmost limit of its range, tend to be the most lightly built, more finely sculptured, and more broadly conical (sa 78-91°, mean 82°, $n = 17$) than the more southern ones. The whorls tend to become markedly convex-sided towards maturity (figure 51), although they may remain weakly convex in some specimens from the Chatham Rise east of the Mernoo Bank (figure 53). Specimens from the Pegasus Canyon off Banks Peninsula (figure 52) and from southward to off Timaru (figures 55, 56) are slightly heavier-shelled than specimens from the north, and most are more narrowly conical (sa 71-79°, mean 73°, $n = 6$) and more strongly nodular, with more weakly convex whorls. In some specimens from off East Otago (sa 71-83°, mean 76°, SD 3.13, $n = 28$) (figure 57), including the holotype, the whorls become as strongly convex as in most specimens from localities to the north, but most of them are as narrowly conical as shells from Pegasus Canyon southward to off Timaru. Specimens from off Stewart Island and The Snares (figure 58) are indistinguishable from most East Otago specimens. Specimens from off the Auckland Islands (figure 62) and Campbell Island are the thickest and most strongly sculptured and are consistently narrowly conical (sa 62-70°, mean 67°, $n = 4$) with almost flat-sided whorls. Specimens from off the Bounty Islands (figure 60) have the most strongly flattened whorls and the narrowest spires (msa 60-63°, mean 61°, $n = 5$) and are thinner and more finely sculp-

tured than shells from off Auckland and Campbell islands. Thus the shell in *C. blacki* tends to become more narrowly conical towards the south and shows a roughly oscillating cline in whorl convexity between Kaikoura and East Otago.

Evidence that spire angle is at least partly a response to sea temperature is suggested by the occurrence of long-dead (probably Pleistocene), narrowly conical, thick, strongly nodular shells in dredge samples containing living specimens with broadly conical, thin, finely nodular shells from the Mernoo Bank (BS 655, 43°07.2'S, 175°22.9'E, 148-150 m, MNZ M.61184, M. 61185) (figure 61) and off the Chatham Islands (NZOI D876, 43°20'S, 176°50'W, 148 m). A long-dead (probably Pleistocene) specimen has been obtained from off Palliser Bay (41°33'S, 174°50'E, c.274 m, MNZ M.11534), which is north of the northernmost known living specimens (NZOI C703, off Kaikoura, 42°42'S, 173°37.8'E, 180-140 m), and resembles living specimens taken from Pegasus Canyon and southward to off Timaru. This specimen occurred with similarly preserved valves of the stenothermic, cool-water pectinid *Chlamys delicatula* (Hutton, 1873) (MNZ M.11521), which is currently unknown living north of Cook Strait (Pantin, 1963). Past northward range expansions of *C. delicatula* have been interpreted as evidence of lowered sea temperature by Fleming (1944, 1951), Boreham and Fleming (*in* Pantin 1957), Beu (1969, 1974, 1977), and Beu *et al.* (1977). Past northward range extensions of *C. blacki* also appear to be associated with low temperatures, and the narrowly conical, flat-sided, strongly sculptured, subrecent northern shells are considered to have lived when sea temperatures were cooler than at present. This explanation could account for the occurrence of old-looking shells from submarine canyons off East Otago, notably the Papanui Canyon (NZGS RM4721), which have flatter-sided whorls than any known Recent specimens from the vicinity. The holotype of the Late Pliocene (Nukumaruan) *Venustas couperi* Vella, 1954 (figure 59) is essentially similar to Recent specimens of *C. blacki* from off Timaru and East Otago, and it is considered to be conspecific. *Thoristella chathamensis profunda* Dell, 1956 is based on juveniles from the vicinity of the type locality. The Late Pliocene (Nukumaruan) specimen from Oaro recorded by Beu (1979) resembles Recent specimens from the vicinity (off Kaikoura). *Calliostoma blacki* may be distinguished from *C. foveauxanum* by the following characteristics: (1) spiral interspaces translucent white or pinkish white instead of yellowish brown; (2) spiral cords reddish brown with white nodules after first 1.5 whorls instead of uniform reddish brown or at least unicoloured (including nodules) on first 4 teleoconch whorls; (3) P4 on first 5 teleoconch whorls almost entirely covered by succeeding whorls and alternately spotted reddish brown and white instead of almost entirely exposed and uniform reddish brown; (4) 5th and 6th teleoconch whorls more strongly convex in *C. foveauxanum*; and (5) *C. blacki* attains smaller shell size than *C. foveauxanum* within the geographic range of the latter (height up to 50 mm as against 62 mm or

more). Unlike *C. blacki*, shell morphology in *C. foveauxanum* is extremely stable.

Calliostoma (Maurea) megaloprepes (Tomlin, 1948)
(Figures 63, 64)

Maurea (Mucrinops) megaloprepes Tomlin, 1948:225, pl. 2, fig. 1

Venustas megaloprepes—Powell, 1955:55.

Maurea megaloprepes—Powell, 1957:88, Powell, 1979:63, pl. 19:2.

Type Data: Holotype BMNH 1951.6.13.38, BANZARE stn 80, off north-eastern corner of Macquarie Island, 120-80 m.

Other Material Examined: 15 live-taken specimens: 54°24'S, 159°01'E, 79-93 m, 10 February 1965, USNS *Eltanin* stn 1417 (6 USNM, 3 MNZ); C733, 54°25'S, 159°02'E, 104 m, 25 November 1961, m.v. *Viti* (2 NZOI); 54°32'S, 159°02'E, 86-101 m, 10 February 1966, USNS *Eltanin* stn 1418 (1 USNM); D9, 54°52'S, 158°50'E, 113 m, 20 April 1963, m.v. *Viti* (2 NZOI); C730, 54°55'S, 158°47'E, 110 m, 24 November 1961, m.v. *Viti* (1 NZOI).

Distribution (figure 63): Off Macquarie Island, living at 79-113 m on bryozoan/shell substrata. Endemic.

Diet: Gut contents examined comprised mostly foraminiferal sand with fragments of thecate hydroids (Cnidaria) and indeterminate organic matter.

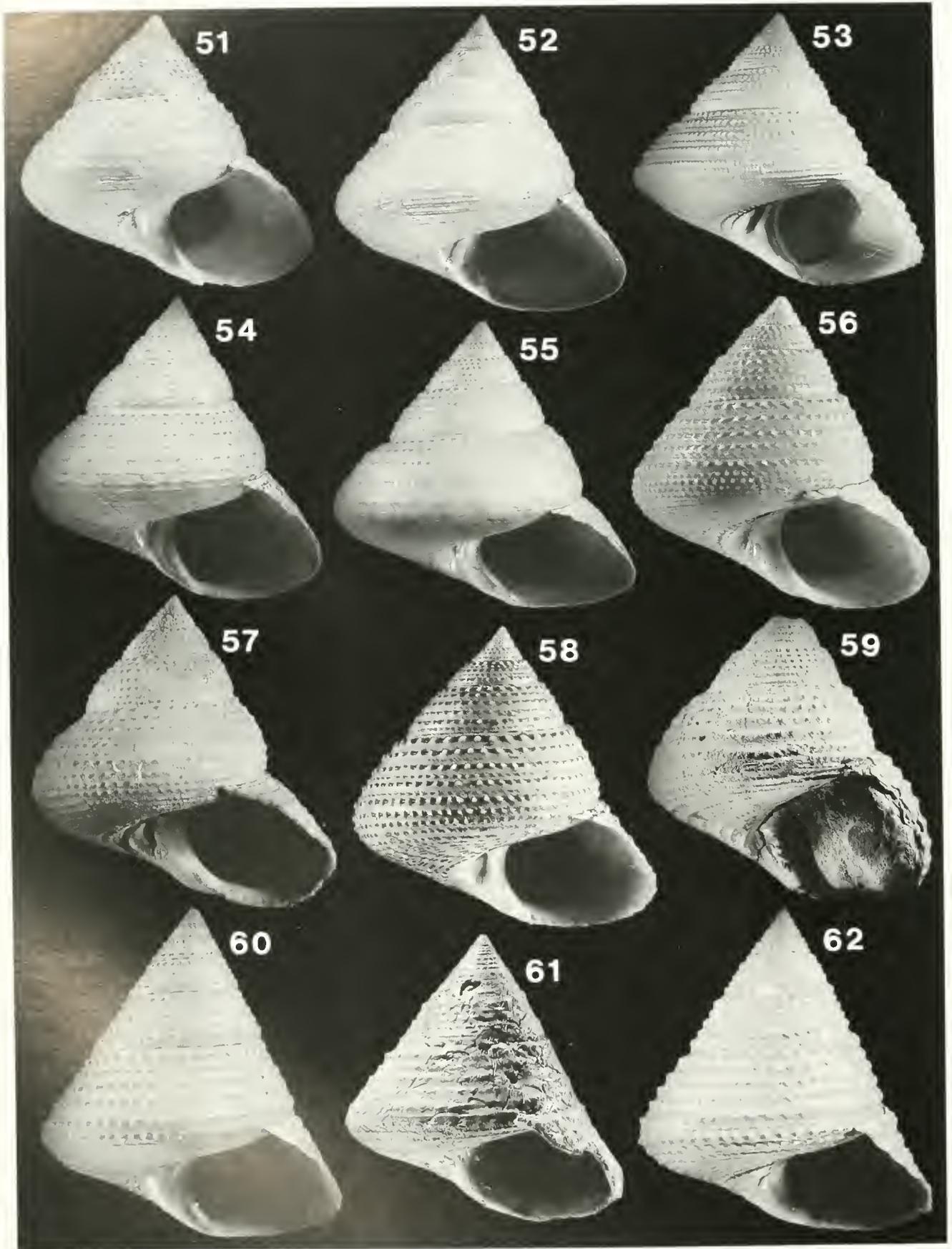
Remarks: This species is rendered highly distinctive by its rich chestnut-brown shell coloration and by the virtual obsolescence of all of the spiral cords other than (rarely including) P1 on the sides and base of the last two adult whorls. *Calliostoma megaloprepes* is otherwise similar to *C. blacki* and the two species are evidently closely related.

Calliostoma (Maurea) simulans Marshall, 1994
(Figures 63, 65-68, 116, 137)

Calliostoma (Maurea) simulans Marshall, 1994. 68, pl.1, figs. 1-3.

Type Data: Holotype MNZ M.87450 (height 30.5 mm, width 29.0 mm, 8.3 teleoconch whorls) and 33 paratypes MNZ: BS 558, 43°30'S 173°31.3'E, head of Pegasus Canyon, NE of Banks Peninsula, alive, 446 m, 27 September 1976, r.v. *Acheron*. Paratypes (158 MNZ): BS 786, 43°25'S, 173°26'E, wall of Pegasus Canyon, alive, 329-183 m, 21 February 1979, r.v. *Acheron* (35); BS 785, 43°25'S, 173°26'E, Pegasus Canyon, alive, 485-476 m, 21 February 1979, r.v. *Acheron* (59); BS 784, 43°29.5'S, 173°30.5'E, Pegasus Canyon, alive, 402-338 m, 21 February 1979, r.v. *Acheron* (12); BS 783, 43°31'S, 173°30.5'E, Pegasus Canyon, alive, 256-293 m, 21 February 1979, r.v. *Acheron* (52).

Other Material Examined: 3 specimens in 3 lots MNZ, 28 specimens in 13 lots NZOI, 3 specimens in 1 lot USNM.



Distribution (figure 63): Recent, Challenger Plateau, off New Plymouth, Cook Strait to SE of Banks Peninsula, Chatham Rise, and off Bounty and Campbell islands, 183-1006 m, taken alive at 256-410 m from soft substrata with shells.

Diet: Intestinal tracts of all specimens examined contained fragmented chitinous polychaete tubes (*Sedentaria*, probably *Chaetopteridae*) and indeterminate organic matter.

Remarks: *Calliostoma simulans* is characterised by a rather large shell with strong spiral cords on the spire and convex, evenly expanding whorls. Shell characters are rather stable throughout the geographic and bathymetric range, though specimens from the west coast (figure 67) and from Cook Strait southward to Banks Peninsula, including the type material (figure 65), are more lightly built and attain smaller size than specimens from elsewhere (figures 66, 68). Occurring throughout most of the range of the highly polymorphic species *C. blacki*, and locally in sympatry, most specimens of *C. simulans* are strongly differentiated from *C. blacki*, but some forms of *C. blacki* from the Chatham Rise and off the southeastern South Island (figures 54, 57) approach *C. simulans* in convexity of the late teleoconch whorls. *Calliostoma simulans* differs from all forms of *C. blacki* in having more strongly convex early teleoconch whorls. It differs further from *C. blacki* from localities other than the eastern Chatham Rise in that S1 becomes as large as P1 or (in most specimens) larger, and the nodules on S1 become correspondingly as large or larger. By contrast, in *C. blacki* from other than the eastern Chatham Rise, S1 only occasionally becomes as large as P1 and the nodules on P1 are consistently larger than those on S1 before the last adult whorl. Although specimens of *C. blacki* from the Chatham Rise east of Veyan Bank (figure 53) have P1 as finely nodular as in *C. simulans*, all pass through a stage on the early teleoconch when P1 is by far the most strongly nodular spiral cord as in other forms of the species. Despite the similarity of some Chatham Rise specimens to *C. blacki*, the two species are strongly differentiated where they occur in strict sympatry, such as off Banks Peninsula (figures 52, 65) and particularly off the Bounty Islands and off the Auckland Islands and Campbell Island (figures 62, 68).

***Calliostoma (Maurea) antipodense* Marshall, new species**
(Figures 63, 69, 117, 138)

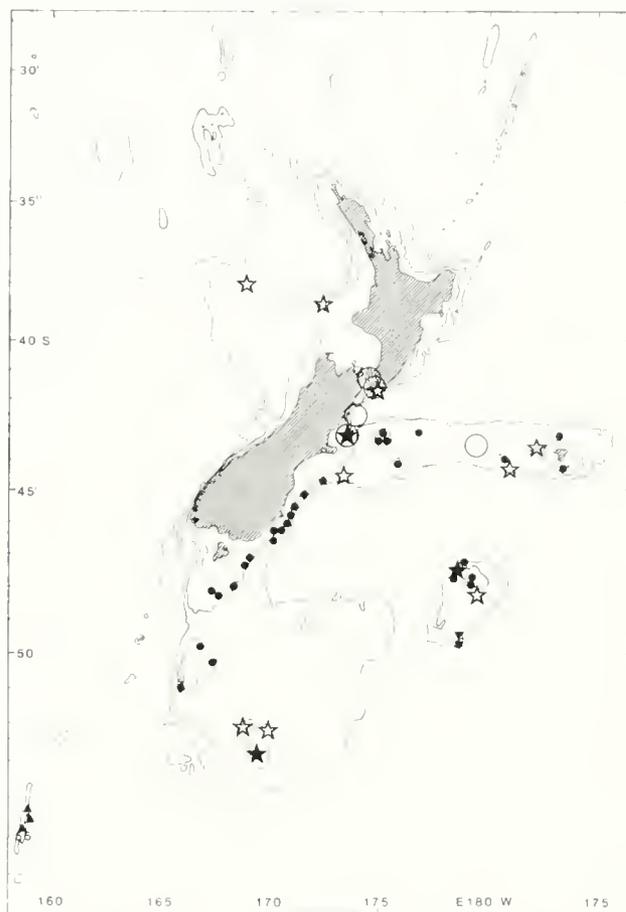


Figure 63. Map of New Zealand region showing distribution of *Calliostoma (Maurea) blacki* (solid circle), *C. (M.) maui* (open circle), *C. (M.) simulans* (star, solid star = sympatric with *C. (M.) blacki*), *C. (M.) antipodense* (inverted triangle), and *C. (M.) megaloprepes* (upright triangle). 200 and 1000 meter contours indicated.

Description: Shell up to 37 mm high, slightly higher than broad, rather thin, anomphalous, glossy; spire up to 1.77 × as high as aperture, rather evenly conical, spire angle 71-74°. Colour orange buff, spiral cords reddish brown between paler nodules. Protoconch 400 μm wide, sculptured with network of fine threads that enclose hexagonal spaces, terminal varix strong. Teleoconch of up to 8.5 strongly convex whorls, suture becoming deeply channelled after 4th whorl, periphery rounded, base

Figures 51-62. *Calliostoma (Maurea) blacki* (Powell, 1950). **51.** Mernoo Bank, Chatham Rise, 95 m, MNZ M.118378 (37.5 × 40.0 mm). **52.** Pegasus Canyon, off Banks Peninsula, 256-293 m, MNZ M.64651 (41.7 × 40.4 mm). **53.** Off Chatham Islands, 315-279 m, MNZ M.90037 (40.3 × 43.4 mm). **54.** Off Oamaru, c. 90 m, MNZ M.102603 (44.3 × 42.8 mm). **55, 56.** Off Timaru, 293 m, NZOI E424 (55.0 × 55.3 mm, and 51.0 × 49.4 mm). **57.** Continental Shelf off Dunedin, MNZ M.7209 (51.0 × 50.0 mm). **58.** Off The Snares, 154-168 m, MNZ M.92443 (42.3 × 41.0 mm). **59.** Holotype of *Venustus couperi* Vella, 1954, Late Pliocene-Early Pleistocene (Nukumaruan), Makara Stream, Wairarapa, NZGS TM4995 (34.2 × 35.8 mm). **60.** Off Bounty Islands, 155 m, NZOI 1708 (42.8 × 37.5 mm). **61.** Subrecent (probably Late Pleistocene), Mernoo Bank, Chatham Rise, 148-150 m, MNZ M.61185 (41.0 × 39.0 mm). **62.** Off Auckland Islands, 113 m, NZOI D200 (45.4 × 40.0 mm).

weakly convex. First 0.2 whorls delineated by a growth scar, with 2 axial costae and 4 spiral threads. Subsequent spire whorls sculptured with spiral cords that multiply by intercalation from 4 (P1-P4) to 9 (P1-P4, S1-S3 + 2 suprasutural spirals); summit of P4 partly covered by succeeding whorls on 1st 4 whorls, after which insertion point progressively descends to fully expose P4 and then 2 additional spirals, the lower of which is either partly covered by succeeding whorls or fully exposed; nodules rounded on P1, P2, P3, S1, and S2, other spirals smooth, spiral interspaces considerably wider than each spiral. P1 at first much weaker than P2 and P3, which are strong and similar throughout, gradually enlarging over 1st 5 whorls then weakening and becoming obsolete. Secondary spirals enlarging to resemble adjacent primaries. S1 and S2 commencing on mid 4th to early 5th whorl, S3 commencing mid 4th to mid 5th whorl. Base with 6 spiral cords of similar size, weaker than spire spirals, inner 3 smooth or with rounded nodules, others smooth. Axial costae strong on 1st 3 whorls, weakening and vanishing on 4th whorl. Fine spiral lirae on 1st 3 or 4 whorls, fine collateral growth lines and obscure spiral lines throughout; fine spiral threads in basal interspaces and intercalating in spiral interspaces on spire on last 1 or 2 adult whorls. Aperture ovate, outer lip simple, inner lip thickened, parietal glaze extremely thin and transparent.

Type Data: Holotype MNZ M.80434 (height 31.8 mm, width 29.2 mm, 8.3 teleoconch whorls) and paratype, off Leeward I., Antipodes Is., alive, 18-73 m, 21 November 1972, r.v. *Acheron*. Paratypes (31): *Eltanin* stn 2141, 49°40'S, 178°52'E, off Antipodes Is., alive, 86-95 m (2 MNZ, 4 USNM); *Eltanin* stn 27/1850, 49°40'S, 178°53'E, off Antipodes Is., alive, 103 m, 3 January 1967 (4 MNZ, 20 USNM).

Distribution (figure 63): Off Antipodes Islands, taken alive at 18-103 m (minimum limit uncertain) from hard substrata. Probably endemic.

Diet: The intestinal tract of the specimen examined contained many calcareous octocoral scales (Cnidaria, Primnoidae), a few thecate hydroid fragments, and sand.

Remarks: Compared with *C. simulans*, to which it is most closely related, *C. antipodense* differs in its deeper shell pigmentation, more strongly convex whorls, deeply channeled suture, and obsolescence of P1 after the fifth teleoconch whorl. Interestingly, *C. eminens*, the other Antipodes Islands endemic, also has an exceptionally deep suture.

Calliostoma (Maurea) maui Marshall, new species (figures 63, 70-72)

Description: Shell up to 4.1 mm high, broader than high, thin, anomphalous or with a shallow umbilical depression, glossy; spire 1.24-1.59 × higher than aperture, evenly conical, spire angle 73-91°. Protoconch and earliest teleoconch whorls translucent white. Subsequent whorls either pale pink through uniform translucent white outer

shell layer or pale buff or pinkish buff with yellowish or reddish brown spiral cords and predominantly white nodules. Protoconch ca. 400 μm wide, surface sculpture worn away in all available specimens. Teleoconch of up to 9 strongly and rather evenly convex whorls, suture well impressed, periphery rounded, base weakly convex. Primary sculpture on spire consisting of spiral cords that multiply by intercalation from 4 (P1-P4) to 7 (P1-P4, S1-S3) or occasionally 6 (S3 absent), up to 3 tertiary spirals occasionally arise on penultimate and last adult whorl, summit of P4 partly covered by succeeding whorls and locally fully exposed. Nodules roundly conical; spiral interspaces considerably broader than each spiral, becoming finely spirally lirate. P1-P4 commencing immediately. P1 at first much weaker than P2 and P3, which are similar throughout, gradually enlarging to resemble them, occasionally weakening and becoming obsolete on last adult whorl. Secondary spirals gradually enlarging to resemble primaries, S1 commencing early to late on 4th whorl, S2 on late 3rd to mid 4th whorl, S3 on mid 4th to early 5th whorl. Base covered with spiral lirae, 2 or 3 nodular spiral cords on innermost part, other basal spiral cords almost or entirely obsolete. Axial costae strong on 1st 3 whorls, obsolete thereafter. Aperture ovate, inner lip thickened, parietal lip very thin, outer lip thin and simple.

Type Data: Holotype MNZ M. 87449 (height 27.3 mm, width 31.3 mm, 7.1 teleoconch whorls); BS 561, 41°24'S, 174°33'E, Cook Strait, alive, 256-274 m, 29 September 1976, r.v. *Acheron*. Paratypes (6): 41°35'S, 175°00'E, off Palliser Bay, alive, 256-490 m, 19-20 December 1966, USNS *Eltanin* stn 1848 (1 USNM); C 703, 42°42'S, 173°37.8'E, off Kaikoura, alive, 180-140 m, 19 June 1961, m.v. *Viti* (1 NZOI); E 759, 42°45'S, 173°40'E, off Kaikoura, alive, 195-213 m, 31 March 1967, m.v. *Viti* (1 NZOI); BS 783, 43°31'S, 173°30.5'E, Pegasus Canyon, NE of Banks Peninsula, alive, 256-293 m, 21 February 1979, r.v. *Acheron* (1 MNZ); 43°56.4'S, 179°25.1'W, W of Chatham Is., alive, 303-296 m, 15 September 1987, f.v. *Chiyo Maru 5* (1 MNZ); off North Canterbury, alive, ca 100 m, J. Sutherland (1 MNZ).

Other Material Examined: 10 specimens MNZ: BS 542, 41°08'S, 174°35.5'E, Cook Strait, subfossil, 282-293 m, 12 March 1976, r.v. *Acheron* (5); BS 561, 41°24'S, 174°33'E, Cook Strait, subfossil, 256-274 m, 29 September 1976, r.v. *Acheron* (4); VUZ 99, 41°34.3'S, 174°43.3'E, old shell, 274 m, 29 August 1957.

Distribution (figure 63): Cook Strait, Chatham Rise, and off north-eastern South Island, living at 140-490 m on rugged substrata.

Diet: The intestinal tract of the holotype contained mostly fragments of thecate hydroids (Cnidaria), with some indeterminate organic matter.

Remarks: *Calliostoma maui* closely resembles lightly built forms of *C. simulans* and depressed forms of *C. blacki* from the eastern Chatham Rise in general facies,

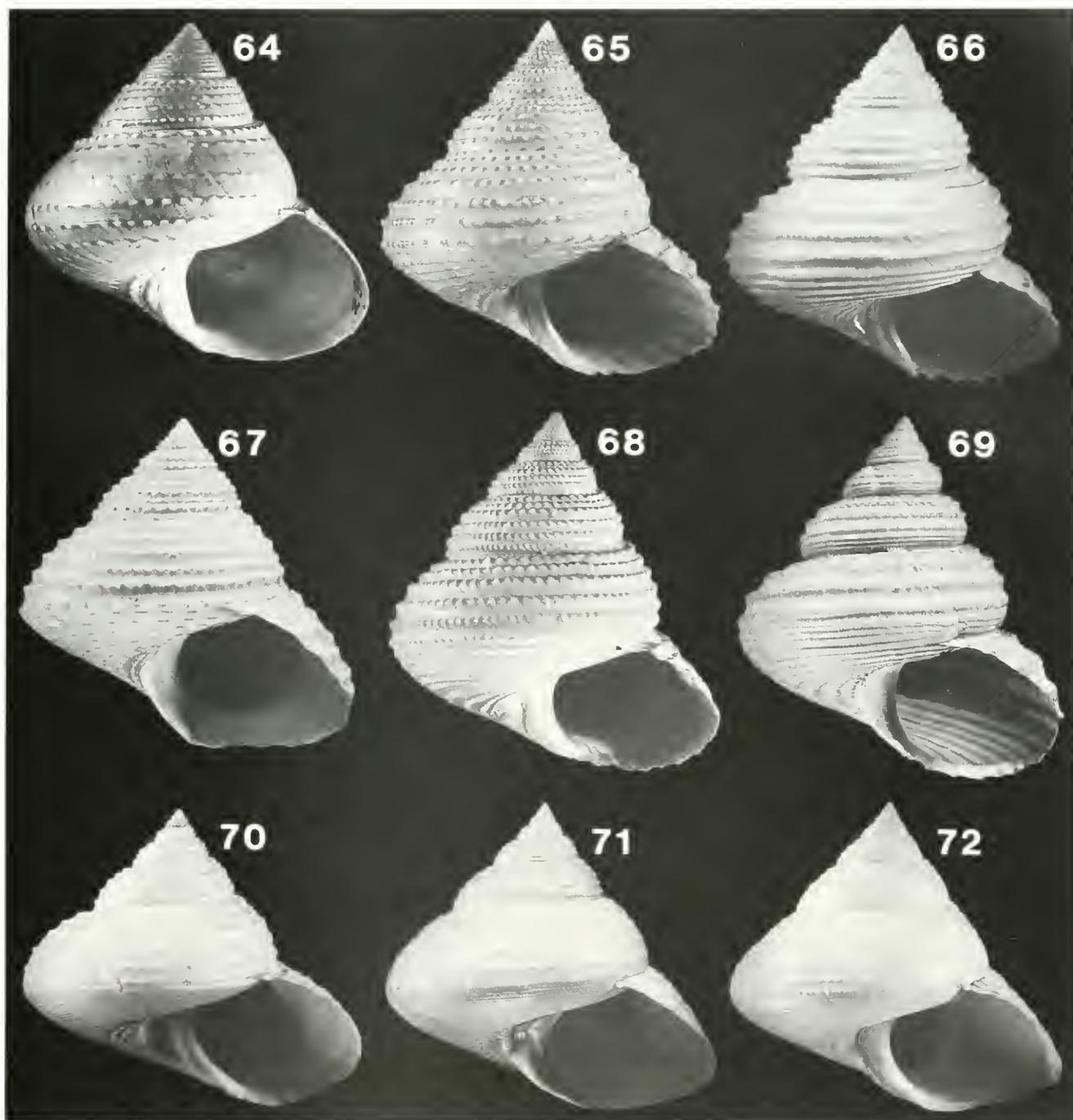


Figure 64. *Calliostoma (Maurea) megaloprepes* (Tomlin, 1948). Off Macquarie Island, 79-93 m, MNZ M.23623 (32.9 × 34.2 mm). **Figures 65-68.** *Calliostoma (Maurea) simulans* Marshall, 1994. **65.** Holotype, Pegasus Canyon, off Banks Peninsula, 446 m, MNZ M.87450 (30.5 × 29.0 mm). **66.** Central Chatham Rise, 410 m, NZOI G259a (51.0 × 48.5 mm). **67.** Challenger Plateau, 337 m, NZOI D242 (27.0 × 27.8 mm). **68.** Off Campbell Island, 188 m, NZOI D35 (52.0 × 48.0 mm). **Figure 69.** *Calliostoma (Maurea) antipodense* Marshall, new species. Holotype, off Leeward Island, Antipodes Islands, 18-73 m, MNZ M.80434 (31.8 × 29.2 mm). **Figures 70-72.** *Calliostoma (Maurea) maui* Marshall, new species. **70.** Holotype, Cook Strait, 256-274 m, MNZ M.87449 (27.3 × 31.3 mm). **71.** Off North Canterbury, ca 100 m, MNZ M 74647 (42.4 × 45.4 mm). **72.** Off Kaikoura, 139 m, MNZ M 102606 (45.0 × 48.7 mm).

all three having similar development of teleoconch sculpture, numerous fine spiral lirae on adult teleoconch whorls, and a tendency toward obsolescence of all but the innermost few spiral cords on the base. *Calliostoma maui* closely resembles *C. simulans* in having all teleoconch whorls markedly convex and in that PI at no stage becomes larger or more heavily nodular than the other primary spire spirals as it does in *C. blacki*. It differs from *C. simulans* in having considerably finer spiral cords on the spire with finer, mostly more sharply pointed nodules, and in being usually more broadly conical (sa 73° - 91° , mean 81° , $n = 7$; instead of 66° - 81° , mean 72° , $n = 54$). During early stages of the present study I suspected that *C. maui* might be an extreme phenotypic variant of either *C. blacki* or *C. simulans*. Subsequent recognition of a specimen living together with *C. blacki* and *C. simulans* in a single sample from off Banks Peninsula (MNZ M.90065, 64651, 64650), however, suggests that another closely related species is involved. Further evidence is suggested by the occurrence in Cook Strait of populations of *C. maui* that are geographically intermediate between populations of *C. simulans* (figure 63). Living specimens from Cook Strait, including the holotype (figure 72), are distinctive in having a shallow umbilical depression. Broken, worn, rust-stained specimens from the floor of the Cook Strait Canyon (MNZ M.52531, 54912) are evidently Pleistocene fossils that have been reworked by current scour of soft sediment following breaching of a Cook Strait land bridge, probably after the last glaciation (Fleming, 1951, 1963; Pantin, 1957; Marshall, 1978). They have considerably thicker shells than Recent specimens from Cook Strait but are otherwise identical.

Etymology: After Maui, the legendary Maori fisherman.

Calliostoma (Maurea) selectum (Dillwyn, 1817)
(Figures 73-77, 85, 118)

Chemnitz, 1795:168, pl. 196, figs 1896-97.

Trochus selectus Dillwyn, 1817:801, refers to Chemnitz, 1795:168, pl. 196, figs. 1896-97; Wood, 1825:140, pl. 29, fig. 101a.

Trochus cunninghami Gray, 1834:600, pl. 1, fig. 7; Fischer, 1876:119, pl. 39, fig. 1.

Zizyphinus cunninghami—Gray, 1843:237;

Trochus cunninghami [sic]—Philippi, 1855:281, pl. 41, fig. 7.

Zizyphinus cunninghamii—Reeve, 1863:pl. 1, fig. 6

Zizyphinus cunninghami—Hutton, 1873:38; Hutton 1880:98.

Zizyphinus hodgei Hutton, 1875:458, pl. 21. **New synonym.**

Zizyphinus decarinatus—Hutton, 1884:359 (not Perry, 1811).

Zizyphinus ponderosus Hutton, 1885:322. **New synonym**

Calliostoma selectum—Pilsbry, 1889:335, pl. 65, figs. 73, 74 (not pl. 65, fig. 78 = *C. pellucidum*); Suter, 1897:281; Suter, 1913:146, pl. 40, fig. 4.

Calliostoma ponderosa—Hutton, 1893:69, pl. 8, fig. 75; Suter, 1915:2.

Calliostoma hodgei—Hutton, 1893:70; Suter, 1915:2.

Calliostoma carnicolor Preston, 1907:140, pl. 8, figs. 6, 7. **New synonym**

Calliostoma (Calliotropis) pagoda Oliver, 1926:112, pl. 10, fig. 4

Calliostoma (Calliotropis) cunninghamii—Oliver, 1926:112.

Calliostoma (Calliotropis) hodgei—Oliver, 1926:114

Venustas (Venustas) cunninghami—Finlay, 1926:360, 371.

Venustas (Venustas) ponderosa—Finlay, 1926:360, 371.

Venustas (Venustas) hodgei—Finlay, 1926:360, 371.

Venustas cunninghami regifica Finlay, 1927:485, pl. 24, figs. 9, 10, Cernohorsky, 1972:244.

Calliostoma (Calotropis) cunninghamii—Thiele, 1929:49.

Maurea (Maurea) cunninghami cunninghami—Powell, 1937:64, pl. 13, fig. 1.

Maurea (Maurea) cunninghami pagoda—Powell, 1937:64.

Calliostoma (Calotropis) cunninghami [sic]—Wenz, 1938:282.

Maurea (Calotropis) cunninghami cunninghami—Powell, 1946:66, pl. 13, fig. 1.

Maurea (Calotropis) cunninghami pagoda—Powell, 1946:66.

Venustas cunninghami cunninghami—Dell, 1950:53.

Venustas cunninghami pagoda—Dell, 1950:53.

Maurea cunninghami cunninghami—Powell, 1957:88, pl. 13, fig. 1.

Maurea cunninghami pagoda—Powell, 1957:88.

Calliostoma (Maurea) cunninghami—Shikama & Horikoshi, 1963, pl. 8, fig. 15.

Maurea (Calotropis) cunninghami—Fleming, 1966:38.

Maurea hodgei—Fleming, 1966:38.

Maurea ponderosa—Fleming, 1966:38.

Calliostoma (Maurea) selectum—Cernohorsky, 1974:149, fig. 7

Maurea selecta—Powell, 1979:61, pl. 10, fig. 2; Abbott & Dance, 1982:40; Matsukuma, Okutani & Habe, 1991, pl. 17, fig. 10.

Maurea pellucida—Abbott & Dance, 1982:40 (not Valenciennes, 1846).

Calliostoma (sensu lato) selectum—Beu & Maxwell, 1990:404 NOT *Trochus selectus*—Philippi, 1855 (*C. pellucidum*).

NOT *Zizyphinus selectus*—Reeve, 1863; Hutton, 1873, 1880, 1884 (*C. pellucidum*).

NOT *Calliostoma selectum*—Pilsbry, 1889: pl. 65, fig. 78 (*C. pellucidum*).

NOT *Calliostoma (Calotropis) selectum*—Wenz, 1938 (*C. pellucidum*).

Type Data: *Trochus selectus*: Lectotype (here selected) University Zoological Museum, Copenhagen (Cernohorsky, 1974, pl. 149, fig. 7), "coasts of New Zealand"; *Trochus cunninghami*: Holotype BMNH 1987047, ex J.E. Gray collection, no locality data, = New Zealand (probably a Wellington west coast beach); *Zizyphinus hodgei*: Holotype Otago Museum, Dunedin C.54.50, "Wanganui, in blue clay", probably Landguard Bluff (Late Pleistocene, early Haweran); *Zizyphinus ponderosa*: Holotype Canterbury Museum, Christchurch M.2766, "Wanganui", horizon unspecified but probably Butlers Shell Conglomerate (Middle Pleistocene, early Castlecliffian); *Calliostoma carnicolor*: Repository unknown, "Celebes(?)" = New Zealand; *Calliostoma (Calliotropis) pagoda*: Holotype MNZ M.1602, off Cape Campbell, c.37 m; *Venustas cunninghami regifica*: Holotype AIM 70823, off Otago Heads, 55m.

Other Material Examined: *Fossil*—20 Late Pliocene—Early Pleistocene (Nukumaruan) specimens in 8 lots AUG, NZGS; 21 Middle Pleistocene (Castlecliffian) specimens in 18 lots AUG, MNZ, NZGS; *Recent*—273 specimens in 86 lots MNZ.

Distribution (figure 85): Late Pliocene (Nukumaruan) to

Recent; North, South, Stewart and Chatham islands, 0-293 m, living at 27-274 m on sandy or muddy substrata with shell or stones.

Diet: Gut contents of all specimens examined contained mostly sand with fragments of either agglutinated polychaete tubes or thecate hydroids (Cnidaria), together with indeterminate organic matter. One specimen contained some crustacean fragments.

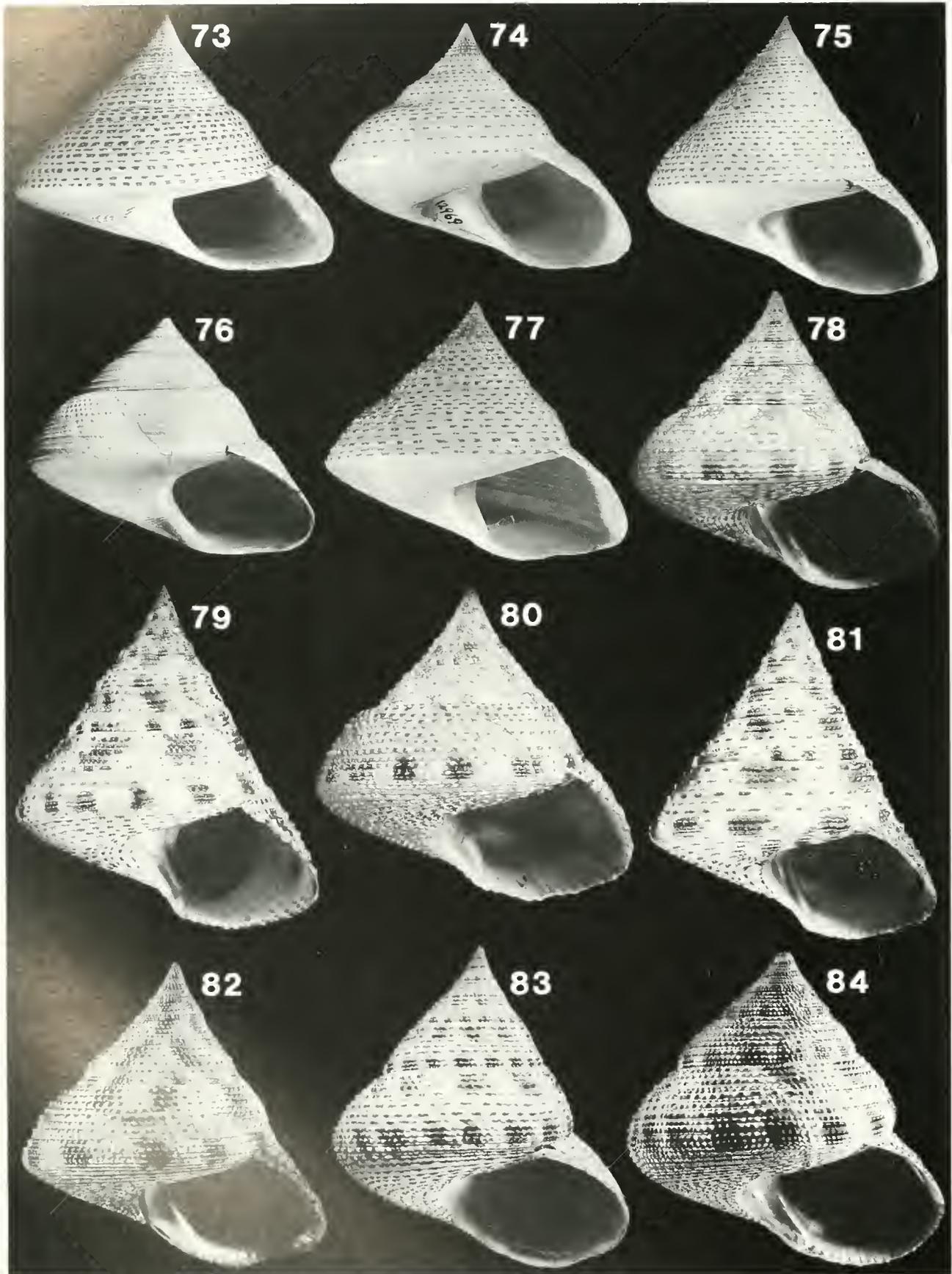
Remarks: Recent specimens of this well-known species are characterised by large size (diameter up to 70 mm); low, broadly conical spire (sa 73-94°); weakly and evenly convex whorls, angulate or narrowly rounded periphery, weakly to rather strongly convex base, weak axial costae on early teleoconch whorls, similarity of P1-P3 throughout, and the late appearance of the secondary spirals, especially S3. Recent specimens from the South Island east coast from Banks Peninsula southwards tend to have more narrowly conical spires (sa 73-80°, mean 76.8°, SD 1.76, $n = 20$) than specimens from the North Island (sa 74-94°, mean 84.2°, SD 4.49, $n = 40$), but there is complete intergradation between high- and low-spired forms off the northern South Island (sa 77-90°, mean 82°, SD 4.22, $n = 20$) and the southern North Island. Two specimens from off Jackson Bay, Westland (MNZ M.17669) are as broadly conical as material from the northern South Island (sa 81° and 85°). North-south clinal gradation in spire height is independent of depth. There is considerable variation in the strength of nodules on the spiral cords, and many specimens from Cook Strait tend to be particularly weakly nodular (figure 74). Specimens from the Chatham Islands (figure 77) are indistinguishable from mainland material (sa 76-81°, mean 79°, SD 1.87, $n = 5$).

The fragmentary holotype of *Zizyphinus hodgci* resembles specimens from Landguard Bluff (early Haweran, Middle Pleistocene) in shell morphology and preservation, suggesting that it may have come from that horizon. Moreover, it is indistinguishable from Recent specimens from off the east coast of the South Island.

The holotype of *Zizyphinus ponderosa* is a heavily abraded adult shell from an unspecified horizon in the Wanganui sequence. The shell morphology and state of preservation closely match specimens from the Butlers Shell Conglomerate (early Castlecliffian, Early Pleistocene) (figure 76), suggesting that it originated from this horizon. All but one of these specimens (see below) and another from the Nukumarū Brown Sand (GS4115, NZGS; Nukumaruan, Late Pliocene) differ from all specimens from later horizons in having distinctly cyrtoconoid instead of shallowly coeloconoid spires. They also have considerably thicker shells than most Recent specimens, as do most adult Middle Pleistocene specimens from the overlying Pinnacle Sand (GS4022, NZGS) and Shakespeare Cliff Sand formations (AUG 989), although the few Recent specimens known from Stewart Island (MNZ) are as heavily built. However, Early Pleistocene specimens from the Lower Kai Iwi Siltstone (AUG 1028, 1034), which underlies the Pinnacle Sand, are as thin as the

most lightly built Recent specimens. Specimens from the Shakespeare Cliff Sand and earlier formations (notably GS4022, NZGS) commonly show much later appearance of some or all of the secondary spirals (especially S3) than any known Recent specimens, often as late as the last or second-to-last adult whorl. Fossils from these early horizons are unlike Recent shells in that the spiral cords frequently become smooth and sometimes very weak after an initial nodular stage, becoming stronger and nodular again on the last or second-to-last whorl or remaining weak and smooth throughout. A single specimen (GS10964, NZGS) collected by A.G. Beu from the Butlers Shell Conglomerate (Early Pleistocene) differs from others from this horizon in being considerably thinner and having a more broadly conical spire that is distinctly coeloconoid rather than cyrtoconoid in outline. As in some other specimens from this horizon, the shell is entirely devoid of nodules on the remaining three whorls, and the spiral cords are almost obsolete on the last adult whorl. It is thus similar to some Middle Pleistocene shells from the Kupe Formation (GS4041, 4121, NZGS) and the thin, weakly sculptured specimens from the Lower Kai Iwi Siltstone (AU1028, 1034, AUG). It is possible that the more lightly built form lived *in situ* in a low-energy environment, whereas the heavier shells may have washed in from a shallower, high-energy environment or were perhaps reworked from a slightly older horizon (presumably late Nukumaruan, Early Pleistocene). This contention is supported by the fact that the heavier shells are all worn to some extent and many are bored, whereas the lightly built (fragile) form was in fresh condition. As discussed by Fleming (1953:175, 176), many shells from the Butlers Shell Conglomerate have undoubtedly been transported, whereas others are clearly reworked from older beds. All of the fossils otherwise resemble Recent specimens in early teleoconch morphology. There is intergradation between specimens with early- and late-developing secondary spirals and between specimens in which the spiral cords are weak or strong and nodular or smooth, both within and between samples from the Shakespeare Cliff Sand and older formations. Accordingly, *Z. ponderosa* and *C. selectum* are interpreted as forms of a single polymorphic species. Great intraspecific variation during the Pleistocene was probably at least partly a response to oscillating glacial-interglacial temperatures and sea levels, with associated variations in sediment type and habitat stability. Interpretation of the fossils is potentially complicated by the likelihood of reworking from older horizons during interglacial marine transgressions.

Calliostoma carnicolor Preston, 1907 was based on a specimen reputedly from the Celebes, though from the description and illustration (Preston, 1907, p.140, pl.8, figs. 6, 7), it appears to be a perfectly typical, northern specimen of *C. selectum*. Nothing similar has been recorded subsequently from the Celebes (or from elsewhere for that matter), and it almost certainly represents a mislocalised specimen of *C. selectum*. The original specimen could not be traced despite extensive enquiries.



Calliostoma (Maurea) pellucidum (Valenciennes, 1846)
(Figures 78-84, 86, 119)

Trochus pellucidus Valenciennes, 1846:pl. 4, fig. 2; Fischer, 1875:70, pl. 15, fig. 2.

Trochus torquatus Anton in Philippi, 1848:126; Philippi, 1855:261, pl. 38, fig. 13 (not H.C. Lea, 1846).

Trochus punctulatus—Kiener, 1847:pl. 15, fig. 2 (not Martyn, 1784).

Trochus selectus—Philippi, 1855:261, pl. 1, figs. 6, 7, pl. 38, fig. 12 (not Dillwyn, 1817).

Zizyphinus selectus—Reeve, 1863:pl. 1, fig. 1; Hutton, 1873:38; Hutton, 1880:98; Hutton, 1884:359 (not Dillwyn, 1817).

Zizyphinus granatus—Reeve, 1863:pl. 1, fig. 2 (not Gmelin, 1791).

Calliostoma selectum—Pilsbry, 1889:pl. 65, fig. 78 only (not Dillwyn, 1817).

Calliostoma pellucidum—Suter, 1897:281; Suter, 1913:145, pl. 40, fig. 3.

Calliostoma undulatum Finlay, 1923:104, pl. 10, figs. 5a, b.
New synonym.

Calliostoma (Calliotropis) pellucidum pellucidum—Oliver, 1926:111.

Calliostoma (Calliotropis) pellucidum spiratum Oliver, 1926:111. **New synonym.**

Calliostoma (Calliotropis) undulatum—Oliver, 1926:111.

Venustas (Venustas) pellucida—Finlay, 1926:360, 371.

Venustas (Venustas) undulata—Finlay, 1926:360, 371.

Maurea (Maurea) pellucida pellucida—Powell, 1937:64, pl. 13, fig. 2.

Maurea (Maurea) pellucida spirata—Powell, 1937:64.

Calliostoma (Calotropis) selectum—Wenz, 1938, fig. 603 (not Dillwyn, 1817).

Venustas pellucida pellucida—Dell, 1950:49, figs. 7, 8, 12.

Venustas pellucida spirata—Dell, 1950:50, fig. 3.

Maurea pellucida pellucida—Powell, 1957:88, pl. 13, fig. 2; Powell, 1979:61, pl. 19, fig. 4.

Maurea pellucida spirata—Powell, 1957:88; Powell, 1979:61, pl. 19, fig. 6.

Maurea (Calotropis) pellucida—Fleming, 1966:38.

Maurea (Calotropis) undulata—Fleming, 1966:38.

Calliostoma (sensu lato) pellucidum—Beu & Maxwell, 1990:404.

Calliostoma (sensu lato) undulatum—Beu & Maxwell, 1990:404.

NOT *Maurea pellucida*—Abbott & Dance, 1982:40 (*C. selectum* Dillwyn, 1817).

Type Data: *Trochus pellucidus*: Lectotype (here selected) and 6 paralectotypes MNHN; *Trochus torquatus*: Repository of type material unknown, "locality un-

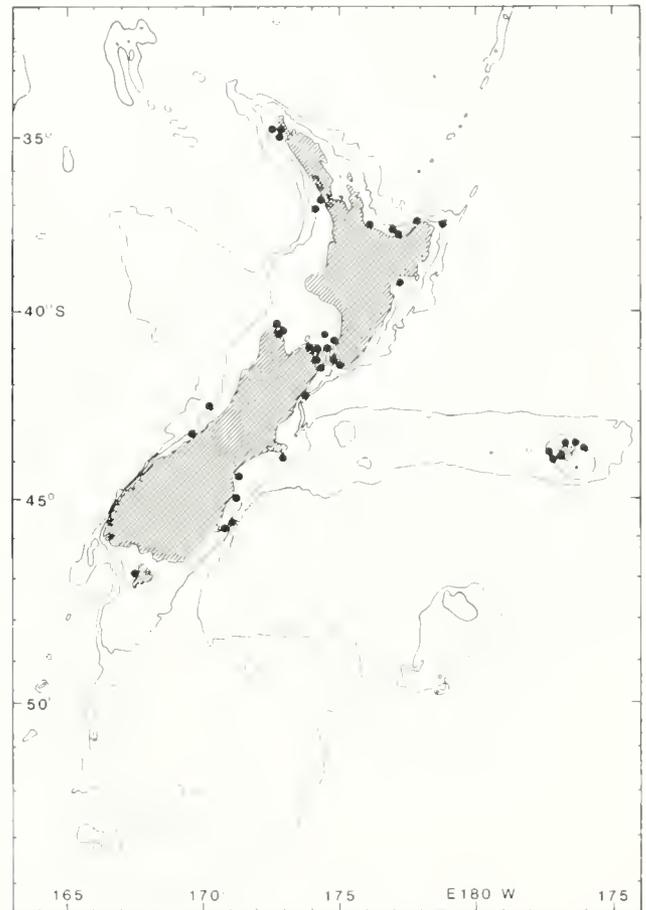


Figure 85. Map of New Zealand region showing distribution of *Calliostoma (Maurea) selectum*. 200 and 1000 meter contours indicated

known". *Calliostoma undulatum*: Holotype NZGS TM 5001, Castlecliff, Wanganui, formation unknown (probably mid-late Castlecliffian or early Haweran, Mid-Late Pleistocene); *Calliostoma pellucidum spiratum*: Holotype MNZ M.11865, Spirits Bay, beach drift.

Other Material Examined: 6 Pleistocene specimens (from unspecified horizons in the Wanganui coastal sequence) in 5 lots MNZ, NZGS, and 235 Recent specimens in 94 lots MNZ.

Figures 73-77. *Calliostoma (Maurea) selectum* (Dillwyn, 1817). **73.** Off Ahipara, 90 m, MNZ M.72032 (40.0 × 47.8 mm). **74.** Off Palliser Bay, 274 m, MNZ M.12969 (42.7 × 51.0 mm). **75.** Off Timaru, 110-128 m, MNZ M.7162 (47.0 × 50.0 mm). **76.** Early Pleistocene (Castlecliffian), Butler's Shell Conglomerate, Wanganui, NZGS (38.5 × 46.0 mm). **77.** Off Chatham Islands, 248-236 m, MNZ M.90061 (44.7 × 50.2 mm). **Figures 78-84.** *Calliostoma (Maurea) pellucidum* (Valenciennes, 1846). **78.** Takapuna, Auckland, low tide, MNZ M.83646 (38.0 × 38.0 mm). **79.** Pua, Parengarenga Harbour, low tide, MNZ M.80536 (37.7 × 34.0 mm). **80.** Between Pandora Bank and Cape Maria Van Diemen, 33 m, MNZ M.74676 (35.3 × 34.5 mm). **81.** Off Rarawa Beach, Northland, 40 m, MNZ M.86657 (35.0 × 29.5 mm). **82.** Reotahi, Whangarei Heads, low tide, MNZ M.83643 (39.5 × 38.0 mm). **83.** Akaroa Harbour entrance, 20 m, MNZ M.75153 (43.1 × 39.9 mm). **84.** Foveaux Strait oyster beds, 31 m, MNZ M.21719 (48.0 × 47.8 mm).

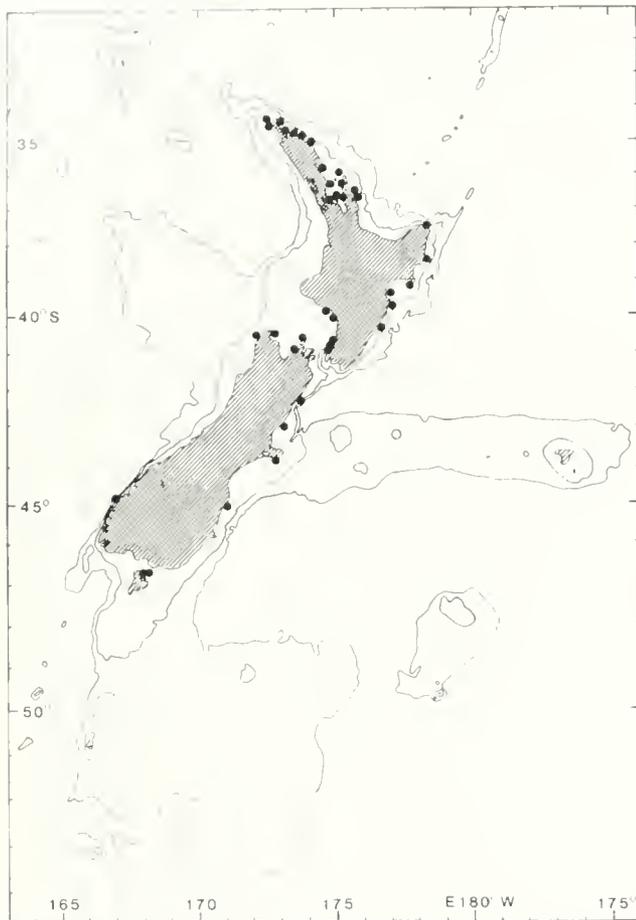


Figure 86. Map of New Zealand region showing distribution of *Calliostoma (Maurea) pellucidum*. 200 and 1000 meter contours indicated.

Distribution (figure 86): Middle Pleistocene to Recent, North, South and Stewart islands, living at 0-187 m on hard substrata.

Diet: Intestinal tracts of specimens examined contained thecate hydroids (Cnidaria) together with some indeterminate organic matter.

Remarks: *Calliostoma pellucidum* has long been confused with the superficially similar species *C. waikanae*, with which it is locally sympatric throughout its range. Highly distinctive characters of *C. pellucidum* include reddish brown subsutural and peripheral maculations, strong teleoconch sculpture, consistent appearance of S3 before S1 and S2, and strong P3 on early teleoconch whorls. The spire is shallowly coeloconoid and 1-1.5 times higher than the aperture, and the spire angle ranges from 56° to 86°. The most narrowly conical specimens occur off eastern Northland north of Whangaroa (sa 57-69°, mean 64°, SD 3.35, $n = 22$), especially in Parengarenga Harbour (figures 79, 81). In specimens from the north-western extremity of Northland (figure 80), however, including the holotype of *C. pellucidum spiratum* Oliver, 1926, the mean spire angle is rather constantly about

75°, and these broadly conical shells are closely similar to material from south of Whangaroa (sa 68-81°, mean 75°, SD 3.45, $n = 43$) (figures 78, 82-84). The periphery tends to be broadly rounded in southern specimens (figures 83, 84) and more sharply angulate in northern specimens (figures 79, 81), but there is complete intergradation from north to south. The Pleistocene type material of *C. undulatum* Finlay, 1923 is indistinguishable from Recent specimens of *C. pellucidum*.

***Calliostoma (Maurea) waikanae* Oliver, 1926**
(Figures 87-95, 99, 120, 139)

Calliostoma (Calliotropis) waikanae Oliver, 1926:11, pl. 10, fig. 3.

Maurea (Maurea) waikanae—Powell, 1937:64.

Maurea (Calotropis) waikanae—Powell, 1946:66.

Maurea pellucida morioria Powell, 1946:140, pl. 11, fig. 3; Powell, 1979:61, pl. 19, fig. 5. **New synonym**

Venustus pellucida waikanae—Dell, 1950:50, figs. 4,5,9,11.

Venustus pellucida forsteriana Dell, 1950:51, figs. 1,2,10. **New synonym.**

Venustus pellucida morioria—Dell, 1950:53.

Venustus pellucida haurakiensis Dell, 1950:53, fig. 6. **New synonym.**

Maurea pellucida forsteriana—Powell, 1957:88; Powell, 1979:61, pl. 10, fig. 3.

Maurea pellucida haurakiensis—Powell, 1957:88; Powell, 1979:61.

Maurea pellucida morioria—Powell, 1957:88; Powell, 1979:61, pl. 19, fig. 5.

Maurea waikanae—Powell, 1957:88; Powell, 1979:62, pl. 19, fig. 7.

Type Data: *Calliostoma (Calliotropis) waikanae*: Holotype MNZ M.1603, Waikanae Beach; *Maurea pellucida morioria*: Holotype AIM 71037, Owenga Beach, Chatham Islands; *Venustus pellucida forsteriana*: Holotype MNZ M.2120, Preservation Inlet, Stewart Island. *Venustus pellucida haurakiensis*: Holotype NZGS TM 456, Hauraki Gulf, 46 m.

Other Material Examined: *Fossil*—AU1023, Kaikokopu Shell Grit, coastal section, Wanganui (early Castlecliffian, Middle Pleistocene) (1 AUG); GS4045, 4047, 4049, Kupe Formation, coastal section, Wanganui (late Castlecliffian, Middle Pleistocene) (3 NZGS); GS4187, Shakespeare Cliff Siltstone, coastal section, Wanganui (late Castlecliffian) (2 NZGS). *Recent*—470 specimens in 148 lots MNZ.

Distribution (figure 99): Middle Pleistocene (early Castlecliffian) and possibly Middle Pliocene (Waipipian). Recent off North, South, Stewart, Snares and Chatham islands, and Mernoo Bank, 0-549 m, taken alive at 18-549 m on bryozoan/shell substrata.

Diet: Intestinal tracts of specimens examined contained fragments of thecate hydroids (Cnidaria) together with indeterminate organic matter.

Remarks: *Calliostoma waikanae* occurs throughout the geographic range of *C. pellucidum*, and the two species

have been thoroughly confused taxonomically because of their variability and superficial similarity. *Calliostoma waikanae* was treated as a subspecies of *C. pellucidum* by Dell (1950), whereas forms of *C. waikanae* have been consistently treated as "subspecies" of *C. pellucidum*, namely *Maurea pellucida morioria* Powell, *Venustus pellucida forsteriana* Dell, and *V. pellucida haurakiensis* Dell, all of which are here interpreted as local populations of *C. waikanae*. Although they are similar in shape, size, colour, and colour pattern, *C. waikanae* is easily distinguishable from *C. pellucidum* by the constant appearance of S1 and S2 well before S3 instead of vice versa (figures 119, 120). *C. waikanae* differs further in having finer pustules on the side of the foot and tends to have a more lightly pigmented shell with finer, more finely beaded spiral cords, and the summit of P4 is usually partly or entirely exposed on the spire instead of being almost entirely covered by succeeding whorls. In other words the suture is bordered by P4 in *C. waikanae* and by S3 in *C. pellucidum*. S3 is seldom nodular in *C. waikanae*, but constantly becomes strongly nodular in *C. pellucidum* from an early stage of growth.

Most specimens from off the Three Kings Islands and North Cape (figure 88), the north-western North Island southward to off Kawhia (figure 89), and the north-eastern North Island as far south as East Cape (figure 87) have narrower and correspondingly higher spires than specimens from further south (sa 68-76°, mean 72°, $n = 27$, as against 73-92°, mean 82°, $n = 76$)(figures 90-95). They differ further in that P3 frequently remains considerably stronger than P1 and P2 onto later whorls, often until the second to last adult whorl, and typically surmounts a prominent, narrow suprasutural bulge together with S3 and P4. Such specimens intergrade completely with specimens in which the primaries become similar through progressive enlargement of P1 and P2 and weakening of P3 at an earlier stage of growth and in which the suprasutural bulge is correspondingly weak or absent. Weakness or absence of a suprasutural bulge is a characteristic of type and topotypic material of *V. p. haurakiensis* and most material from southern localities, though some specimens from Fiordland (figure 94) have a well-developed and persistent peripheral bulge. Specimens from north of Cape Reinga attain larger size (diameter up to 52.5 mm) and are more darkly and extensively pigmented than specimens from elsewhere off the northern North Island but are otherwise identical.

Calliostoma waikanae is exceptionally variable in the area off the west coast of the southern North Island and in Cook Strait. In many specimens from this area, including the holotype of *C. waikanae*, the spiral cords and nodules weaken with increasing shell size, and the nodules may become almost obsolete (figure 91). There is, however, complete gradation between weakly and strongly sculptured forms both within and between populations. Moreover, these specimens show exceptionally wide variation in the development of S3, which may fuse with P4, become as large as P3, remain weak throughout, or entirely fail to appear. Again there is complete mosaic

intergradation between the extremes. Pronounced variation in shell morphology in this area is probably at least partly the result of repeated divergence and remixing of populations isolated to the east and west of Cook Strait land bridges that formed during Pleistocene glaciations (Fleming, 1962). This explanation probably also accounts for extreme local variation in direct developers such as buccinids of the genera *Penton* Fischer and *Cominella* Gray.

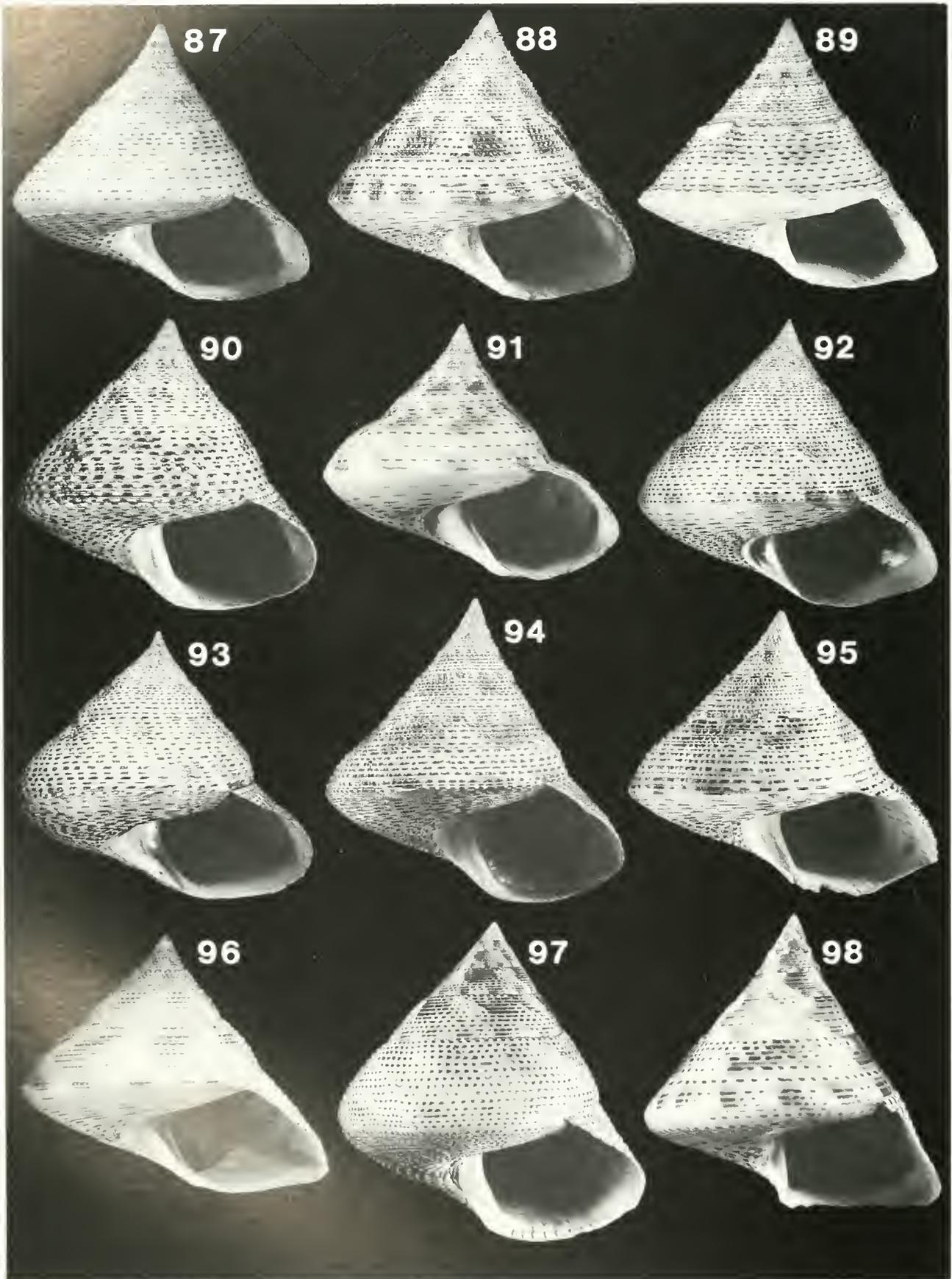
The only significant differences that I am able to detect between specimens from the Cook Strait area and the southern South Island (*forsteriana*) is the more general tendency for the southern form to have a rounded periphery at maturity and a slightly narrower spire angle (73-86°, mean 79°, $n = 23$ as against 75-92°, mean 82°, $n = 53$). Again, however, there is complete intergradation both within samples and clinally between the northern and southern forms.

Specimens from the Chatham Islands (*morioria*) (figure 95) are indistinguishable from mainland specimens.

Existing collections suggest that *C. waikanae* has a rather patchy distribution (figure 99) and the differences between specimens from off north-eastern North Island/Kawhia and the Wanganui/Cook Strait area are certainly greater than between specimens from Cook Strait/Kaikoura area and East Otago, suggesting that the northern population may be more strongly isolated than the other mainland populations are from each other. In view of the tendency for this and other New Zealand calliostomatids to form morphologically discrete local populations and to show pronounced clinal geographic and bathymetric variation, it seems clear that all of the nominate forms should be interpreted as local populations of a single polymorphic species.

Middle Pleistocene specimens from the Kaikokopu Shell Grit (AU1023, AUG) and the Kupe Formation, Wanganui (GS4045, 4047, 4049, NZGS), differ from Recent specimens in being thicker at maturity and in the early appearance and more rapid enlargement of the spiral cord between the suture and P1, which develops to resemble P1. The two subadult specimens from the Shakespeare Cliff Siltstone (GS4187, NZGS) are very lightly built and have sculpture that becomes obsolete on the sixth whorl and gradually reappears on the eighth whorl. All of these fossils are indistinguishable from Recent specimens in early teleoconch morphology, and they are interpreted as *C. waikanae* that is both undergoing genetic drift through time and varying in response to changing sea temperature and bathymetry. A single fragmentary specimen from below the Te Aute Limestone, 2.5km south-east of Takapau, Takapau Survey District, Hawke Bay (GS2320, NZGS)—age either Nukumaruian or (more likely) Waipipian (Middle Pliocene) (A.G. Beu, pers. comm.) — is even more similar to Recent *C. waikanae* than the Pleistocene material, but better material is required to ascertain its status.

Calliostoma (Maurea) turaerarum (Powell, 1964)
(Figures 96, 100, 121)



Maurea turnerarum Powell, 1964:11, pl. 3, fig. 1-3; Powell, 1979:62, pl. 19, fig. 9; Horikoshi, 1989:pl. 4, figs. 8,9

Type Data: Holotype AIM 71239, off Mayor Island, Bay of Plenty, 366 m.

Other Material Examined: 37 specimens in 19 lots MNZ.

Distribution (figure 100): Three Kings Islands, off Ninety Mile Beach, and north-eastern North Island as far south as Cape Runaway, 186-805 m, taken alive at 312-529 m on muddy substrata with shells.

Diet: The intestinal tracts of specimens examined contained numerous fragments of thecate hydroids (Cnidaria) together with some indeterminate organic matter.

Remarks: *Calliostoma turnerarum* resembles *C. waikanae* in gross facies, and the two species are undoubtedly closely related. *Calliostoma turnerarum* differs in having a more lightly built shell with finer sculpture on adult whorls and in having pale, wavy axial bands, within which the strongest spiral cords are streaked deep reddish or yellowish brown. Compared with specimens of *C. waikanae* from within its geographic range, *C. turnerarum* is more broadly conical, the spire angle ranging from 83° to 95° (mean 87°, $n = 5$) instead of 68° to 75° (mean 72°, $n = 27$). Although the early teleoconch sculpture is similar in both species, P3 remains similar to P2 in *C. turnerarum*, whereas P3 becomes markedly stronger and more strongly nodular in *C. waikanae*.

Calliostoma (Maurea) penniketi Marshall, new species (Figures 97, 98, 100, 123, 140)

Description: Shell up to 57 mm high, about as high as broad at maturity, spire 1.19-1.78 × as high as aperture, spire outline evenly conical or shallowly cocloconoid, last whorl slightly contracting at maturity, spire angle 65-78°, rather thin but strong, anomphalous throughout. Protoconch and 1st teleoconch whorl white. Ground colour on subsequent whorls pale yellowish brown or buff white, rich yellowish brown on last adult whorl of a few specimens. Spiral cords spotted and spire whorls typically maculated with yellowish or reddish brown, maculations absent from a few specimens. Spiral cords becoming spotted after 2nd-4th whorl, typically on each alternate spiral on early whorls and on each spiral on later whorls, nodules predominantly white on last 2 adult whorls, most

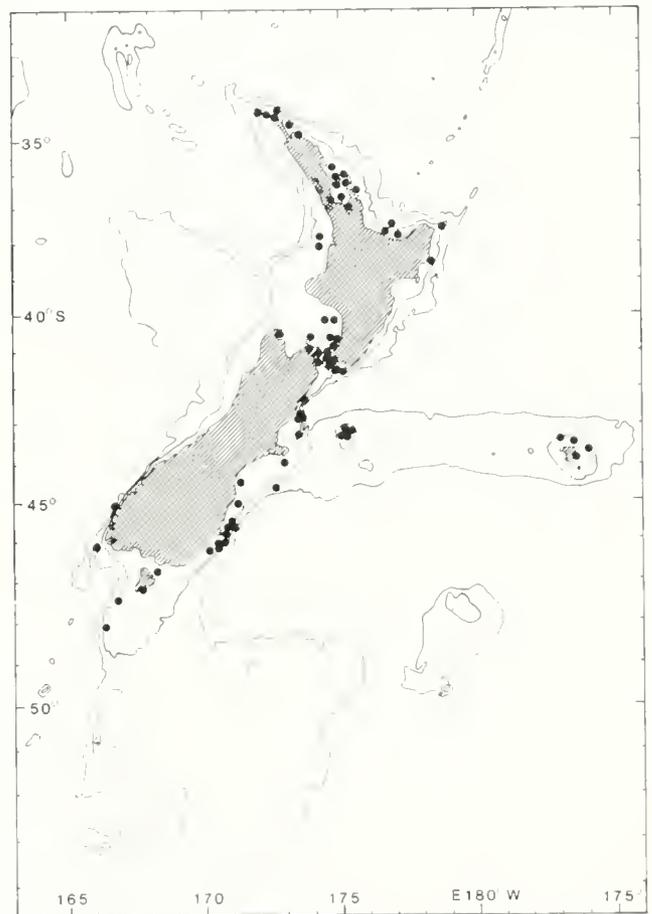


Figure 99. Map of New Zealand region showing distribution of *Calliostoma (Maurea) waikanae*. 200 and 1000 meter contours indicated.

deeply pigmented on maculations. Maculations irregular, subquadrate, occupying rather discrete subsutural and suprasutural zones, becoming obsolete on last whorl. Subsutural maculations typically more darkly pigmented than suprasutural ones, almost entirely traversing early whorls, narrowing to occupy adapical half of later whorls, numbering 7-9 on adult penultimate whorl. Suprasutural maculations small, occupying narrow band throughout, numbering 13 or 14 on adult penultimate whorl. Inner lip white, aperture nacreous. Protoconch 370 μ m wide,

Figures 87-95. *Calliostoma (Maurea) waikanae* Oliver, 1926. 87. Paratype of *Venustus pellucida haurakiensis* Dell, 1950, Hauraki Gulf, 46 m, MNZ M.15910 (36.9 × 35.3 mm). 88. Off North Cape, 178-167 m, MNZ M.74670 (51.0 × 51.3 mm). 89. Off Kawhia, 83 m, MNZ M.74656 (36.5 × 40.0 mm). 90. Erie Bay, Tory Channel, Wellington, c. 20 m, MNZ M.17931 (41.0 × 42.0 mm). 91. Between Mana Island and Cape Jackson, Cook Strait, 256-186 m, MNZ M.49913 (32.0 × 36.0 mm). 92. Off Oamaru, c. 73 m, MNZ M.102589 (50.5 × 51.0 mm). 93. Foveaux Strait oyster beds, 37-46 m, MNZ M.80567 (48.0 × 52.5 mm). 94. Bligh Sound, Fiordland, c. 20 m, D. Gibbs collection (42.5 × 41.2 mm). 95. Off Kaingaroa, Chatham Islands, craypots, MNZ M.92395 (36.2 × 39.0 mm). Figure 96. *Calliostoma (Maurea) turnerarum* (Powell, 1964). North of Three Kings Islands, 348-312 m, MNZ M.71984 (47.5 × 56.7 mm). Figures 97, 98. *Calliostoma (Maurea) penniketi* Marshall, new species. 97. Holotype, off Three Kings Islands, c. 55 m, MNZ M.74817 (57.0 × 53.0 mm). 98. Banfurly Bank, East Cape, 76-71 m, MNZ M.64782 (27.2 × 27.0 mm).

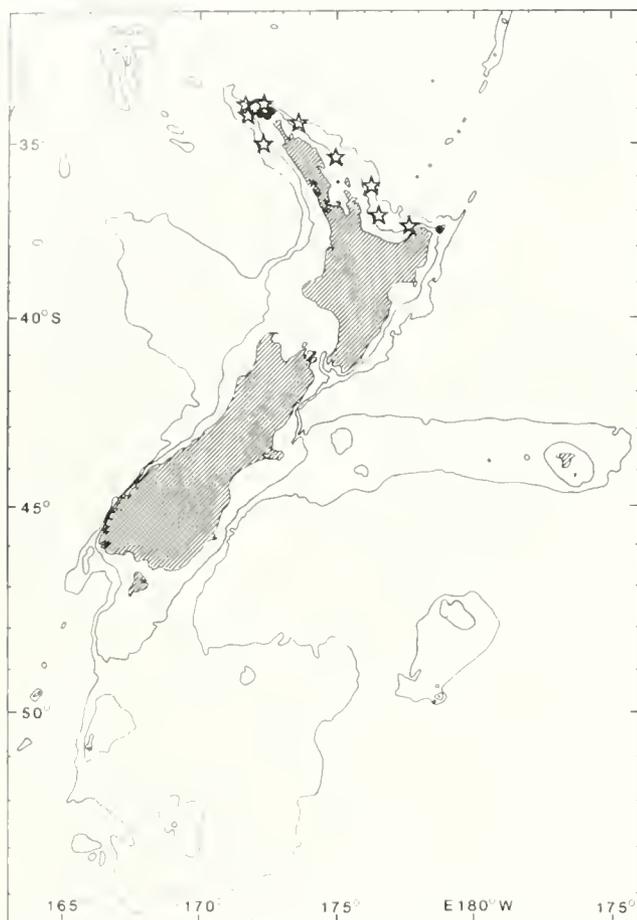


Figure 100. Map of New Zealand region showing distribution of *Calliostoma (Maurea) penniketi* (circle) and *C. (M.) turnerarum* (star). 200 and 1000 meter contours indicated.

sculptured with a network of fine threads that enclose roughly hexagonal spaces, terminal varix strong. Teleoconch of up to 10 whorls, 1st 2.5-3 whorls convex, subsequent whorls more or less flat, last 2 whorls weakly convex. Periphery tightly rounded, becoming rather broadly rounded on last whorl; base almost flat, becoming weakly rounded at maturity. First 3 whorls sculptured with spiral cords, axial riblets, and a few crisp spiral threads, axials and spiral threads weakening and vanishing over next whorl. P1-P4 commencing immediately, P1 thread-like on 1st whorl, gradually enlarging to resemble P2 and P3, which are similar throughout; P4 peripheral, covered by succeeding whorls, becoming exposed by descent of last whorl. S1-S3 commencing on 3rd whorl, enlarging to resemble P1-P3; tertiary spirals commencing on 5th whorl or late on 4th whorl, 1 in each interspace and between P1 and suture, enlarging to resemble secondaries and primaries. Additional finer spirals in each interspace on last few whorls. Spirals about as high as broad with considerably wider interspaces and prominent rounded nodules on 1st 5 whorls, then flattening, becoming smooth, and broadening until separated by shallow grooves; finally becoming strong, crisply

nodular and widely spaced on penultimate or last adult whorl. P3 more strongly nodular than P1 and P2 on 3rd and 4th whorls. Adult base with about 18-20 major, spotted, nodular spiral cords, additional finer threads in most interspaces. Aperture subquadrate to subcircular. Outer lip thin at rim, thickened within, strongly so at base. Inner lip a spreading glaze. Parietal glaze thin, restricted to a narrow outer spiral band.

Type Data: Holotype M.74817 (height 57.0 mm, width 53.0 mm, c.10 teleoconch whorls) and 2 paratypes MNZ, off Three Kings Is., c.55 m, alive in craypots, coll. A.D. Howell, pres. M. Sanson. Paratypes (9) : C763, 33°58'S, 172°17.6'E, off Three Kings Is., dead, 73-99 m, 18 February 1962, m.v. *Viti* (1 NZOI); B93, 34°00'S, 172°30'E, alive, 55-91 m, 22 September 1958, m.v. *Viti* (1 NZOI); BS392, 34°08.5'S, 172°11'E, dead, 102 m, 18 February 1974, r.v. *Acheron* (1 MNZ); BS902 (0648), 34°10.5'S, 172°11.4'E, dead, 153 m, 1 February 1981, r.v. *Tangaroa* (1 MNZ); BS901 (0647), 34°14.1'S, 172°09'E, dead, 192-202 m, 1 February 1981, r.v. *Tangaroa* (1 MNZ); BS910 (0656), 34°18.8'S, 172°18.5'E, dead, 93-88 m, 2 February 1981, r.v. *Tangaroa* (2 MNZ); BS911 (0657), 34°20.2'S, 172°21.8'E, dead, 121 m, 2 February 1981, r.v. *Tangaroa* (1 MNZ); BS769 (R127), 37°33.2'S, 178°50.3'E, Ranfurly Bank, East Cape, alive, 76-71 m, 25 January 1979, r.v. *Tangaroa*; BS678 (R36), 37°36.3'S, 178°53.1'E, dead, 74 m, 17 January 1979, r.v. *Tangaroa* (1 MNZ).

Other Material Examined (mostly juveniles): Off Three Kings Islands—50 specimens in 11 lots MNZ; Ranfurly Bank, East Cape—8 specimens in 4 lots MNZ.

Distribution (figure 100): Three King Islands and Ranfurly Bank, East Cape, 55-622 m; taken alive at 55-76 m on rugged, bryozoan/shell substratum with sponges, corals, gorgonians, etc.

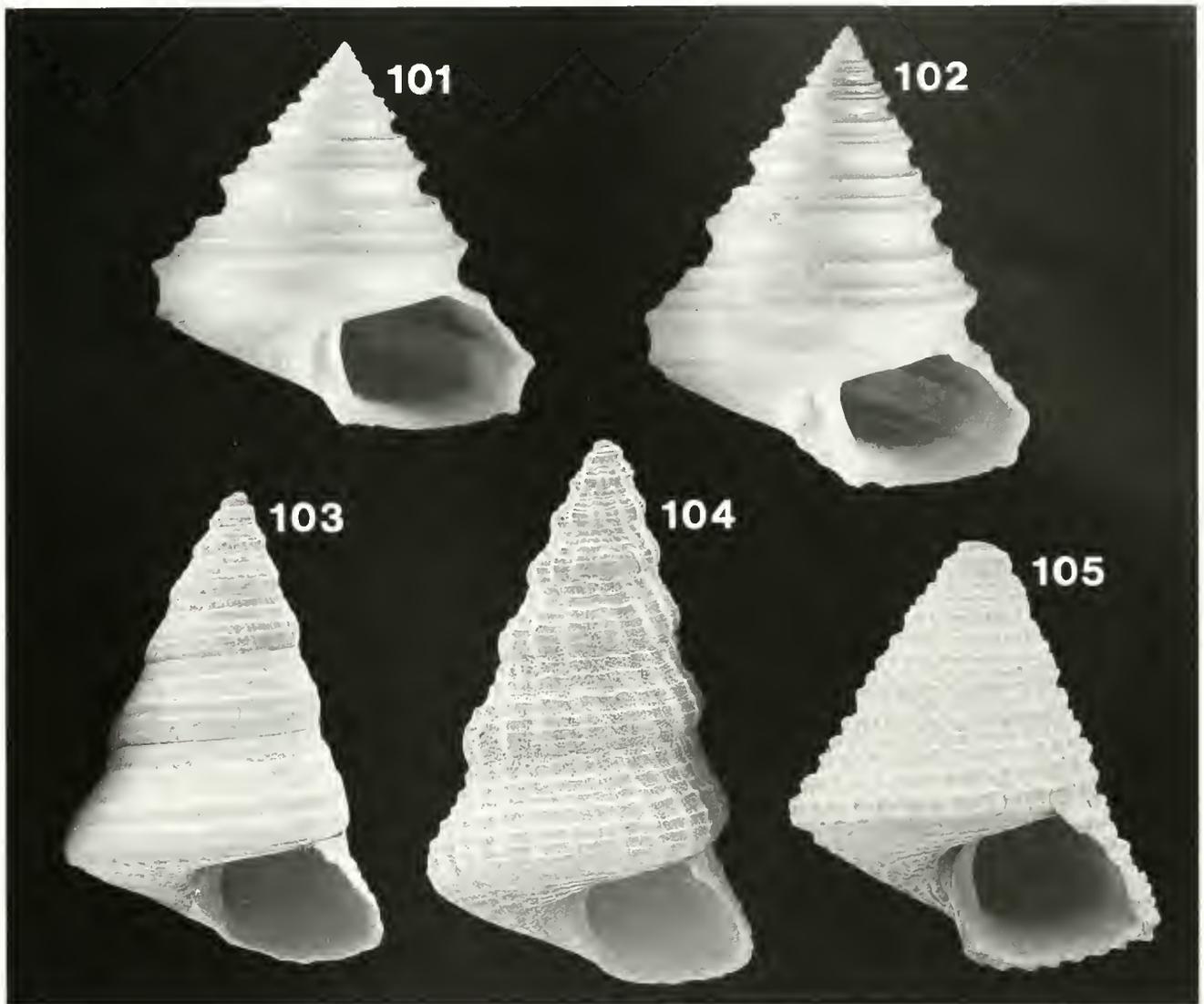
Diet: The alimentary tract of a paratype from off the Three Kings Islands at 55 m contained fragments of thecate hydroids and indeterminate organic material.

Remarks: *Calliostoma penniketi* is closely related to *C. waikanae* and *C. pellucidum*, which it resembles in size, colour, and colour pattern. It is readily separable from them by the finer, more numerous nodules and weaker P3 on the early spire whorls, and in passing through an intermediate growth stage in which the spiral cords become low, broad, and smooth. Specimens from off the Three Kings Islands and East Cape are indistinguishable. *Calliostoma penniketi* may eventually be discovered at intermediate localities, which are as yet inadequately sampled at appropriate depths on hard substrata.

Etymology: Named in honour of the late J.R. (Bob) Penniket, a connoisseur of New Zealand Calliostomatidae, and in recognition for his fostering of New Zealand malacology, both amateur and professional.

Subgenus *Otukaia* Ikebe, 1942

Otukaia Ikebe, 1942:277 Type species (by original designa-



Figures 101, 102. *Calliostoma (Otukaia) alertae* Marshall, new name. **101.** Off Cape Karikari, Northland, 743 m, NZOI F913 (27.0 × 25.7 mm). **102.** Off Bounty Islands, 475 m, NZOI I704 (31.5 × 25.5 mm). **Figure 103.** *Calliostoma (sensu lato) limatulium* Marshall, new species. Holotype, King Bank, north-east of Three Kings Islands, 128 m, MNZ M.90129 (8.05 × 5.50 mm). **Figure 104.** *Calliostoma (sensu lato) onustum* Odhner, 1924 King Bank, north-east of Three Kings Islands, 128 m, MNZ M.50551 (9.85 × 5.50 mm). **Figure 105.** *Calliostoma (sensu lato) kopua* Marshall, new species. Holotype, off Cape Campbell, 454-424 m, MNZ M.59698 (5.35 × 4.95 mm).

tion): *Calliostoma kiheiziebisu* Ootaka, 1939; Recent, Japan.

Alertalex Dell, 1956:46. Type species (by original designation): *Alertalex blacki* Dell, 1956 (*Calliostoma alertae* Marshall, new name); Recent, New Zealand.

Remarks: Most members of this group are characterised by a moderate to large-sized shell (height up to 36 mm); strong, smooth or weakly beaded P2 and P3; and the extreme weakness of P1. All have a highly nacreous shell due to translucency of the colourless outer shell layers, and the group (as currently interpreted) occurs worldwide at bathyal depths. The radula, jaw, external anatomy, and development of sculpture on the early teleconch are essentially similar to those in *Calliostoma (sen-*

su stricto), and I am unable to justify segregation of the group at genus level. Since I am not able to justify placement of *Otukaia* as a synonym of *Calliostoma* either, I follow McLean and Andrade (1982) in interpreting it as a subgenus.

Calliostoma (Otukaia) alertae Marshall, new name (Figures 101, 102, 108, 122, 141)

Alertalex blacki Dell, 1956:46, figs. 61, 120, 260; Dell 1962:75 (secondary homonym of *Venustus blacki* Powell, 1950). *Otukaia blacki*—Dell, 1963:208, Powell, 1979:63, pl. 19, fig. 13.



Figures 106, 107. Radula of holotype of *Calliostoma (sensu lato) kopua* Marshall, new species. **106.** Central and lateral teeth. **107.** Marginal teeth, innermost tooth indicated (x). Scale bars = 10 μ m.

Type Data: Holotype MNZ M.9767 and 1 paratype MNZ: 44°04'S, 178°04'W, Chatham Rise, alive, 476 m, 10 February 1954, m.v. *Alert*. Paratypes (4 MNZ): 43°42'S, 179°55'E, Chatham Rise, alive, 512 m, 24 January 1954, m.v. *Alert*.

Other Material Examined: 17 specimens in 12 lots MNZ, 30 specimens in 20 lots NZOI.

Distribution (figure 108): Off Cape Brett southward to off The Snares, Challenger Plateau, Chatham Rise, Bounty Plateau, and Pukaki Rise (34°43.5'S-49°02'S), living at 280-861 m on muddy substrata with shells.

Diet: Gut contents of the few specimens examined comprise much indeterminate organic matter together with fragments of thecate hydroids (Cnidaria).

Remarks: Since *Otukaia* is here interpreted as a subgenus of *Calliostoma*, *C. (Otukaia) blacki* (Dell, 1956) becomes a homonym of the prior *C. (Maurea) blacki* (Powell, 1950). In the absence of junior synonyms it is here renamed *C. (O.) alertae*. Should *Otukaia* prove to be worthy of genus-group status, the specific name will revert to the original (ICZN Art 59d).

This species is strongly characterised by its iridescent, weakly nodular shell, very strong P2 and P3, the late appearance and extreme weakness of P1, and the strong development of S2, which enlarges to resemble P2.

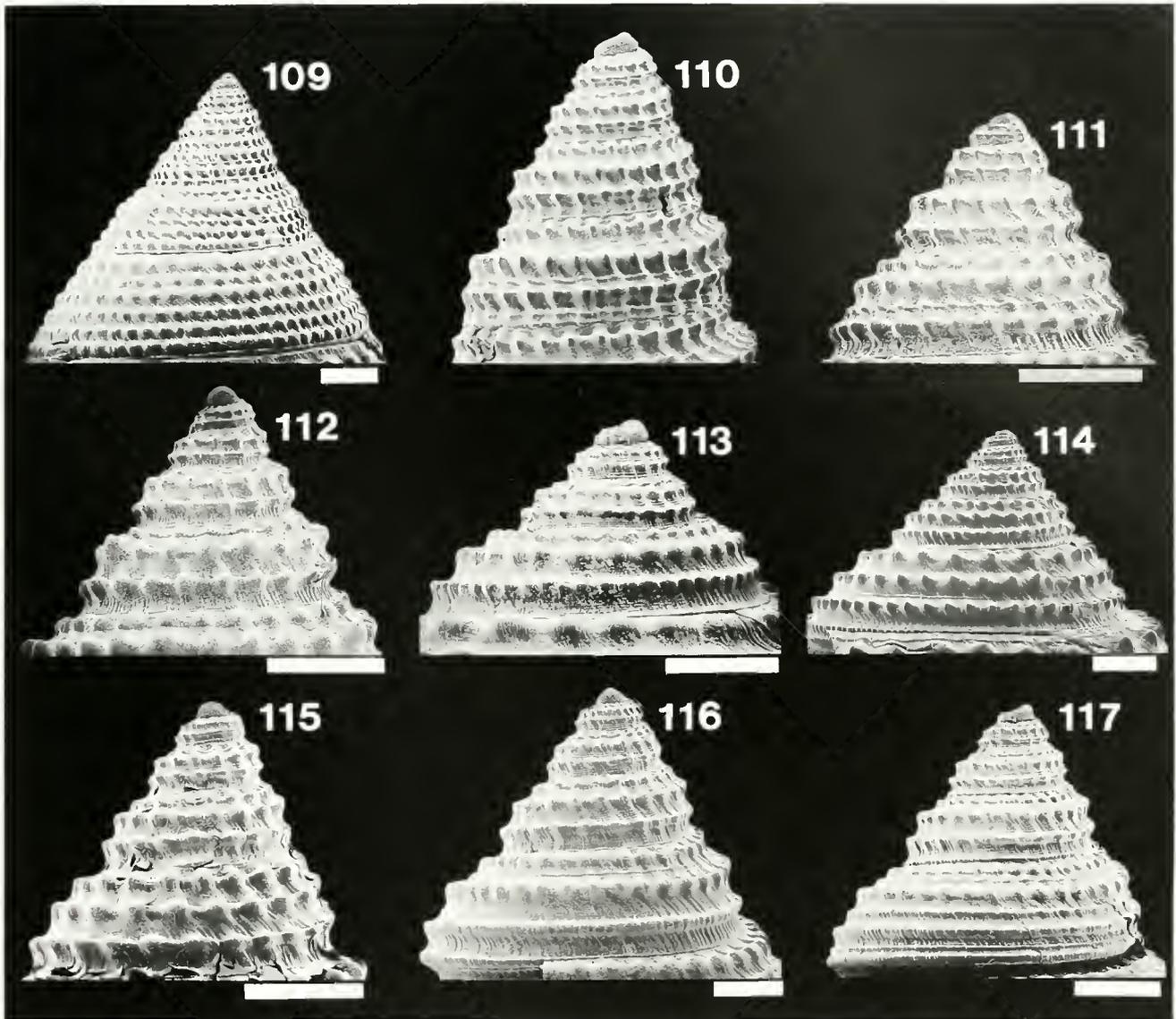
Calliostoma alertae shows slight southward narrowing of the spire angle, which ranges from 61° to 70° (mean 65.7°, $n = 7$) in material from north of East Cape (figure 101) and 55° to 60° (mean 57.8°, $n = 7$) in specimens from the Bounty Platform (figure 102). Specimens from these extreme northern and southern populations also have respectively the most lightly and heavily built shells. Material from geographically intermediate localities are intermediate in spire angle and shell thickness.

Calliostoma (sensu lato) onustum Odhner, 1924
(Figures 104, 108, 124, 142)



←

Figure 108. Map of New Zealand region showing distributions of *Calliostoma (Otukaia) alertae* (dot), both *C. (s.lat.) lima-tulum* and *C. (s. lat.) onustum* (star), and *C. (s. lat.) kopua* (open circle). 200 and 1000 meter contours indicated.



Figures 109-117. Early whorls of *Calliostoma* species. **Figure 109.** *Calliostoma (Maurea) gibbsorum* Marshall, new species. Off Three Kings Islands, craypot, MNZ M 74663. **Figure 110.** *Calliostoma (Maurea) tigris* (Gmelin, 1791). Whangaroa Harbour entrance, 20 m, MNZ M.41060. **Figure 111.** *Calliostoma (Maurea) regale* Marshall, new species. Holotype, off Three Kings Islands, 153 m, MNZ M.86730. **Figure 112.** *Calliostoma (Maurea) aupourianum* Marshall, new species. Holotype, off Three Kings Islands, 252 m, MNZ M.86731. **Figure 113.** *Calliostoma (Maurea) spectabile* (A. Adams, 1855). Off Auckland Islands, 42-44 m, NZOI D71. **Figure 114.** *Calliostoma (Maurea) foveauxanum* (Dell, 1950). Off Otago Peninsula, 220 m, MNZ M.8939. **Figure 115.** *Calliostoma (Maurea) blacki* (Powell, 1950). Off Otago Peninsula, 476-549 m, MNZ M.8891. **Figure 116.** *Calliostoma (Maurea) simulans* Marshall, 1994. Paratype, wall of Pegasus Canyon, off Banks Peninsula, 329-183 m, MNZ M 64654. **Figure 117.** *Calliostoma (Maurea) antipodense* Marshall, new species. Paratype, off Antipodes Islands, 103 m, MNZ M.80469. Scale bars = 1mm.

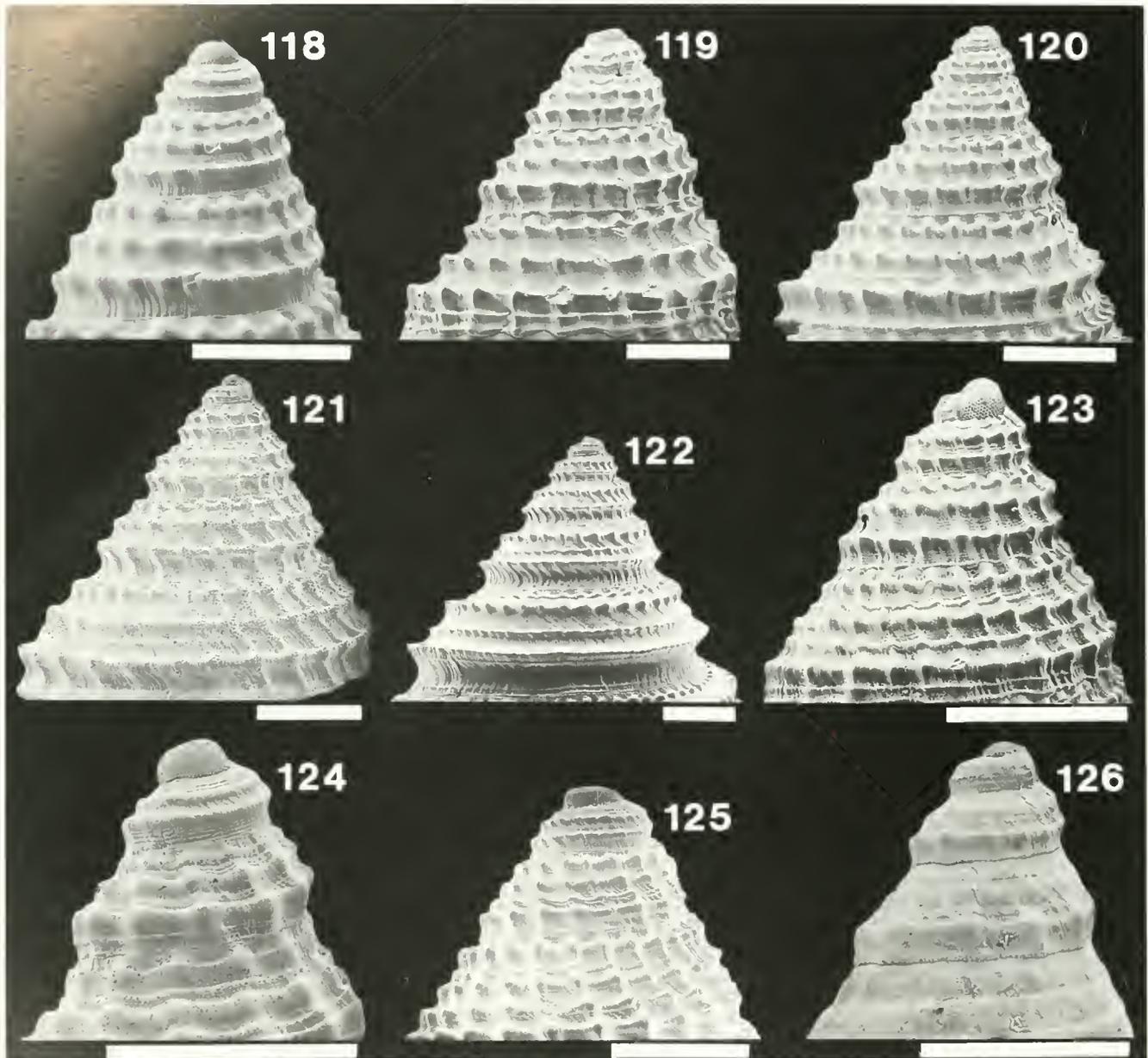
Calliostoma onustum Odhner, 1924:16, pl 1, fig. 4.

Calliostoma (Maurea) onustum—Oliver, 1926:108.

Fautor onustus—Finlay, 1926:360; Powell, 1979:63, pl 19, fig. 12.

Description: Shell up to 6.63 mm high, of moderate thickness, considerably higher than broad; spire narrowly and evenly conical, up to $3.4 \times$ higher than aperture; juveniles with minute umbilical chink, larger specimens anomphalous. Iridescent nacreous through translucent

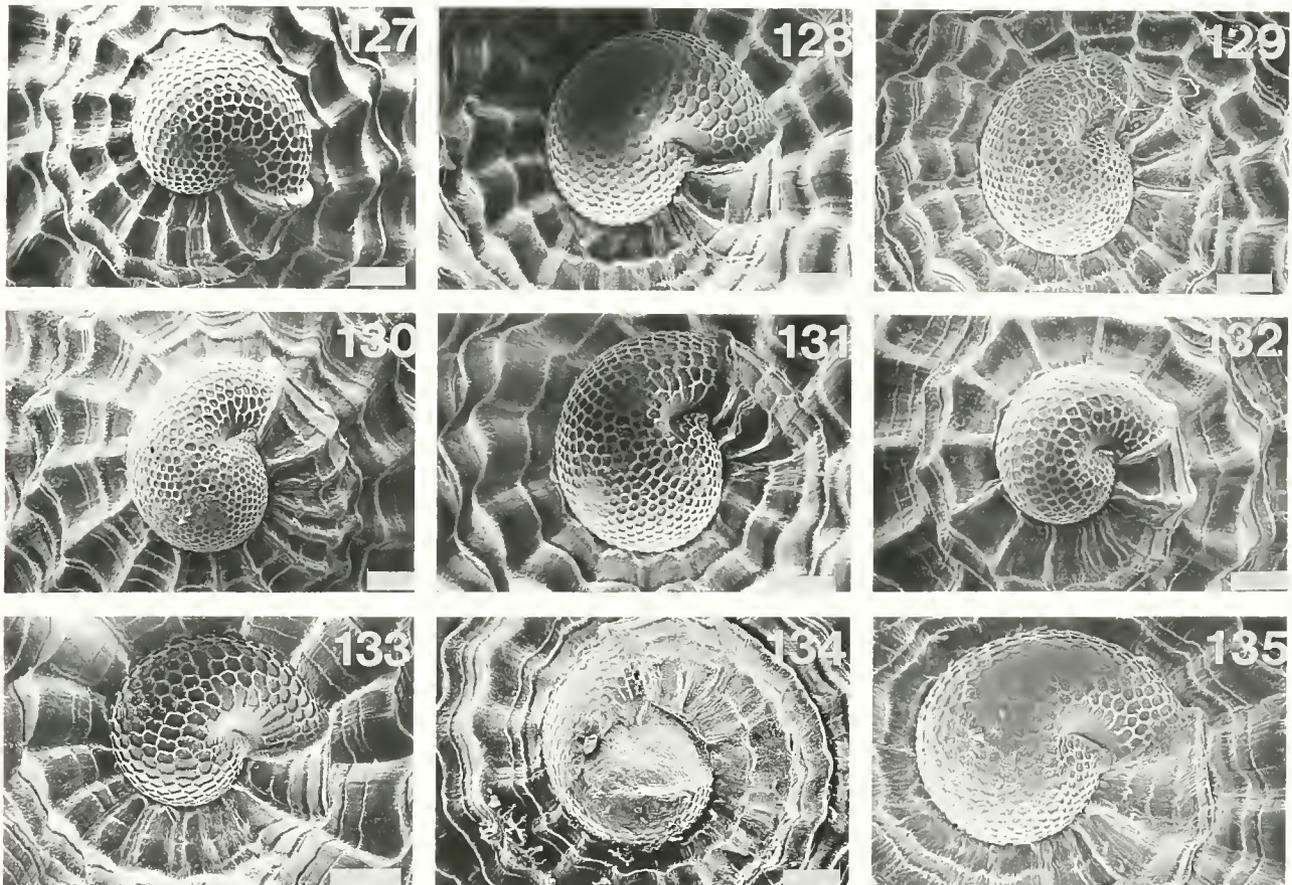
outer shell layer, which is colourless when fresh, dead specimens white, base and P4 pale buff in some specimens, protoconch and 1st teleoconch whorl pink in some specimens. Protoconch $320\text{--}330 \mu\text{m}$ wide, sculptured with fine threads that enclose hexagonal spaces, terminal varix strong, rounded. Teleoconch of up to 6.50 whorls, 1st whorl rounded, next 2 angulated at P3; subsequent whorls rounded over abapical half, weakly concave adapically; periphery narrowly rounded, base more or less flat. First



Figures 118-126. Early whorls of *Calliostoma* species. **Figure 118.** *Calliostoma (Maurea) selectum* (Dillwyn, 1817). Tasman Bank, Golden Bay, 26-24 m, MNZ M.50508 **Figure 119.** *Calliostoma (Maurea) pellucidum* (Valenciennes, 1846). Off Stephens Island, Cook Strait, 183-187 m, MNZ M.50269 **Figure 120.** *Calliostoma (Maurea) waikanac* Oliver, 1926. Pelorus Sound mouth, 29 m, MNZ M.51450 **Figure 121.** *Calliostoma (Maurea) turnerarum* (Powell, 1964). Off Great Island, Three Kings Islands, 440 m, MNZ M.118380 **Figure 122.** *Calliostoma (Otukaia) alertae* Marshall, new name. Wall of Pegasus Canyon, off Banks Peninsula, 1006-512 m, MNZ M.52781 **Figure 123.** *Calliostoma (Maurea) penniketi* Marshall, new species. Off Three Kings Islands, 187 m, MNZ M.34246 **Figure 124.** *Calliostoma (sensu lato) onustum* Odhner, 1924. Off Three Kings Islands, King Bank, north-east of Three Kings Islands, 128 m, MNZ M.50551 **Figure 125.** *Calliostoma (sensu lato) kopua* Marshall, new species. Holotype, off Cape Campbell, 454-424 m, MNZ M.59698 **Figure 126.** *Calliostoma (sensu lato) lmatulum* Marshall, new species. Holotype, King Bank, north-east of Three Kings Islands, 128 m, MNZ M.90129. Scale bars = 1mm.

c. 0.3 whorl demarcated by growth sear, not sculpturally differentiated from succeeding half whorl. First 1.5 whorls with fine, crisply defined spiral threads. Spiral cords rounded, sharply shelved adapically, nodular where traversing axial costae, multiplying by intercalation from 3 (P2-P4) to 7 (P1-P4, S1-S3); interspaces concave, about

as wide as each spiral. Spiral cords enlarging from the spiral threads. P1 commencing later than P2-P4, which are similar throughout, P1 as large as them after 2nd whorl. Summit of P4 exposed on spire throughout. Secondary spirals rapidly enlarging to resemble primaries; S1 commencing on late 2nd to late 3rd whorl, S2 on mid



Figures 127-135. Protoconchs of *Calliostoma* species. **Figure 127.** *Calliostoma (Maurea) tigris* (Gmelin, 1791). Whangaroa Harbour entrance, 20 m, MNZ M.41060. **Figure 128.** *Calliostoma (Maurea) punctulatum* (Martyn, 1784). Cook Strait, 256-254 m, MNZ M.54911. **Figure 129.** *Calliostoma (Maurea) granti* (Powell, 1931). Off Stephens Island, Cook Strait, 183-187 m, MNZ M.50266. **Figure 130.** *Calliostoma (Maurea) gibbsorum* Marshall, new species. Off Three Kings Islands, 102 m, MNZ M.34249. **Figure 131.** *Calliostoma (Maurea) osbornei* Powell, 1924. Off Wanganui, 33-35 m, MNZ M.118381. **Figure 132.** *Calliostoma (Maurea) regale* Marshall, new species. Off Three Kings Islands, 102 m, MNZ M.80699. **Figure 133.** *Calliostoma (Maurea) aupourianum* Marshall, new species. Middlesex Bank, north-west of Three Kings Islands, 246-291 m, MNZ M.80675. **Figure 134.** *Calliostoma (Maurea) spectabile* (A. Adams, 1855). Off Auckland Islands, 42 m, NZOI D71. **Figure 135.** *Calliostoma (Maurea) foveauxanum* (Dell, 1950). Off Otago Peninsula, 220 m, MNZ M.8939. Scale bars = 100 μ m.

2nd to early 3rd whorl, S3 on late 1st to mid 2nd whorl. Axial costae commencing late on 1st whorl, gently prosocline, non-collabral, entirely traversing all subsequent whorls, very strong between P2 and P4, numbering 16-20 on 5th whorl. Base with 7-9 similar, rounded spiral cords, their outer edges beveled, at first smooth, becoming weakly nodular with increasing shell size; interspaces wider than each spiral in most specimens but narrower in a few specimens. Collabral growth lines prosocline on spire, opisthocyrt on base. Aperture subquadrate, inner and outer lips thin and simple, parietal glaze very thin.

Type Data: Lectotype (Odhner's described and illustrated specimen here selected) and 1 paralectotype, Zoological Museum, Copenhagen: 10 miles NW of Cape Maria van Diemen, dead, 91 m, 4 January 1915.

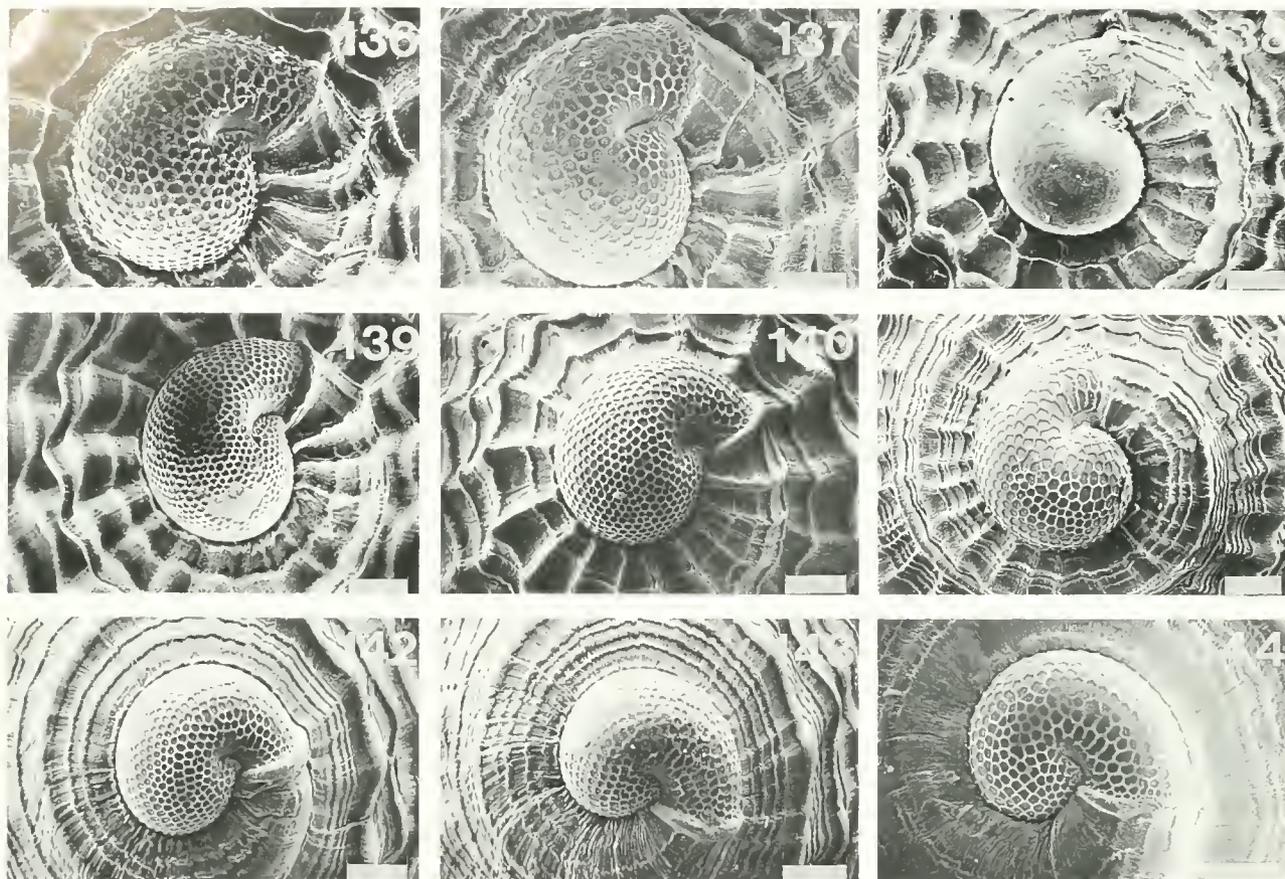
Other Material Examined: 48 specimens in 12 lots MNZ.

Distribution (figure 108): Off Three Kings Islands and off Cape Reinga (33°57.0'S-34°25.0'S), 55-310 m, taken alive at 102-202 m on rugged, bryozoan/shell substratum with sponges, gorgonians, and hydroids.

Diet: Unknown.

Remarks: Among previously described taxa, *Calliostoma onustum* most closely resembles the southern Australian species *C. retiarium* Hedley & May, 1908, from which it differs in having a flattened or concave shoulder on the teleoconch whorls and broader spiral cords. The smaller specimen (paralectotype) recorded by Odhner (1924) is an immature specimen of *Thysanodonta wairua* Marshall, 1988 (Calliostomatidae: Thysanodontinae).

Marshall (1995) will refer this species to a new genus based on the highly distinctive shell morphology and



Figures 136-144. Protoconchs of *Calliostoma* species. **Figure 136.** *Calliostoma (Maurea) blacki* (Powell, 1950). Off Otago Peninsula, 476-549 m, MNZ M.8891. **Figure 137.** *Calliostoma (Maurea) simulans* Marshall, 1994. Paratype, wall of Pegasus Canyon, off Banks Peninsula, 329-183 m, MNZ M.64654. **Figure 138.** *Calliostoma (Maurea) antipodense* Marshall, new species. Paratype, off Antipodes Islands, 103 m, MNZ M.80469. **Figure 139.** *Calliostoma (Maurea) waikanae* Oliver, 1926. Pelorus Sound mouth, 29 m, MNZ M.51450. **Figure 140.** *Calliostoma (Maurea) penniketi* Marshall, new species. Off Three Kings Islands, 187 m, MNZ M.34246. **Figure 141.** *Calliostoma (Otukaia) alertae* Marshall, new name. Wall of Pegasus Canyon, off Banks Peninsula, 1006-512 m, MNZ M.52781. **Figure 142.** *Calliostoma (sensu lato) onustum* Odbner, 1924. Off Three Kings Islands, 102 m, MNZ M.34251. **Figure 143.** *Calliostoma (sensu lato) kopua* Marshall, new species. Holotype, off Cape Campbell, 454-424 m, MNZ M.59698. **Figure 144.** *Calliostoma (sensu lato) limatulium* Marshall, new species. Off Three Kings Islands, 102 m, paratype, MNZ M.118352. Scale bars = 100 μm .

degenerate radula (figures 106, 107). *C. retiarium* and the two new taxa described below are congeneric.

Calliostoma (sensu lato) limatulium Marshall, new species
(Figures 103, 108, 126, 144)

Description: Shell up to 6.60 mm high, of moderate thickness; higher than broad, considerably so at maturity; some juveniles with minute umbilical chink, adults an-omphalous; spire narrowly and evenly conical, up to 2.9 \times higher than aperture. Iridescent naereous through translucent outer shell layer, which is colourless when fresh, dried specimens becoming white; occasionally with a few scattered irregular patches of pale buff; protoconch and 1st 1 or 2 teleoconch whorls sometimes pink. Protoconch 330 μm wide, sculptured with fine threads that enclose hexagonal spaces, terminal varix strong, rounded

Teleoconch of up to 6.10 whorls, 1st whorl rounded, subsequent whorls flattened adapically, angulate at P3 on 2nd and 3rd whorls, rounded thereafter, periphery narrowly rounded, base more or less flat. First c. 0.3 whorl demarcated by growth scar, not sculpturally differentiated from succeeding half whorl. First 1.5 whorls with fine, crisply defined spiral threads. Spiral cords enlarging from fine threads, rounded, sharply shelved adapically, multiplying by intercalation from 3 (P2-P4) to 5 or occasionally 6 (P1-P4, S2 \pm S1), interspaces narrower than each spiral, P3 and P4 becoming most closely spaced. Spiral cords enlarging from fine threads. P1 commencing later than P2 and P3, after mid 2nd-4th whorl as large as P2; P2 and P3 of similar size on 1st whorl, P3 stronger thereafter; summit of P4 exposed on spire throughout. When present, S1 either developing in parallel with P1 and resembling it throughout or commencing as late as mid 4th whorl and enlarging to resemble P1; S2 com-

mencing on late 1st or on 2nd whorl, as large as P1 and P2 after late 3rd whorl. Spirals nodular on early whorls, strongly so on P3 and P4, on 4th or 5th whorl nodules weakening and vanishing from all spirals, which are smooth thereafter. Early spire whorls either entirely traversed by strong axial costae, or costae strong between S2 and P4 and weaker adapically. Axials obsolete after 3rd-5th whorl. Base with 7 or 8 broad, smooth, rounded spiral cords with interspaces considerably narrower than each spiral, occasionally with up to 12 finer cords. Collabral growth lines prosocline on spire, opisthocyrt on base. Aperture subquadrate, inner lip thin.

Type Data: Holotype MNZ M.90129 (height 8.05 mm, diameter 5.50 mm, 7.00 teleoconch whorls), BS 904 (0650), 33°57.0'S, 172°19.0'E, King Bank, NE of Three Kings Is., dead, 128 m, 1 February 1981, r.v. *Tangaroa*. Paratypes (31 MNZ): BS 898 (0644), 34°01.2'S, 171°44.4'E, dead, 206-211 m, 31 January 1981, r.v. *Tangaroa* (2); BS 637 (P485), 34°05.0'S, 172°24.6'E, dead, 200 m, 24 June 1978, r.v. *Tangaroa* (1); BS 392, 34°08.5'S, 172°11.0'E, alive, 102 m, 18 February 1974, r.v. *Acheron* (8); BS 901 (0647), 34°14.1'S, 172°09.0'E, alive, 192-202 m, 1 February 1980, r.v. *Tangaroa* (11); BS 911 (0657), 34°20.2'S, 172°21.8'E, alive, 121 m, 2 February 1981, r.v. *Tangaroa* (6); BS 912 (0658), 34°22.8'S, 172°24.6'E, dead, 121 m, 2 February 1981, r.v. *Tangaroa* (2); BS 631 (P441), 34°24.0'S, 172°16.8'E, dead, 120 m, 20 June 1978, r.v. *Tangaroa* (1).

Other Material Examined: 72 specimens in 10 lots MNZ.

Distribution (figure 108): Off Three Kings Islands and off Cape Reinga, 91-805 m, taken alive at 102-310 m on rugged, bryozoan/shell substratum with sponges, gorgonians, and hydroids.

Diet: Unknown.

Remarks: *Calliostoma limatum* is closely similar to the sympatric species *C. onustum*, differing principally in being more broadly conical, in having axial costae confined to the early spire whorls, in having an extra spiral cord on the spire (S3), and in that the spiral cords on the spire become broader and smooth with increasing shell size. The two species have identical protoconch and first teleoconch whorl morphologies, and they are similar in shell structure and shell size relative to the number of whorls. Their geographic and bathymetric distributions are similar, and they commonly occur together in dredge samples. I have not overlooked the possibility that they may be forms of a single sexually dimorphic species, but without knowledge of the reproductive anatomy it is impossible to tell.

Calliostoma (sensu lato) kopua Marshall, new species (Figures 105, 106, 107, 125, 143)

Description: Shell up to 5.35 mm high, slightly higher than broad, with minute umbilical chink; spire evenly conical, up to 1.78 × higher than aperture. Iridescent nacreous through colourless, translucent outer shell layer.

Protoconch 320 μm wide, sculptured with fine threads that enclose hexagonal spaces, terminal varix strong, rounded. Teleoconch of up to 4.70 whorls, 1st whorl convex, subsequent whorls flat sided, periphery angulate; base almost flat at first, becoming weakly convex. A growth scar almost immediately after protoconch. First 1.5 whorls with fine, crisply defined spiral threads. Spiral cords on spire angulate in section, sharply beveled adapically, with rounded conical nodules where traversing axials, multiplying by intercalation from 3 (P2-P4) to 6 (P1-P4, S1, S2), summit of P4 exposed on spire; interspaces concave, broader than each spiral, P3 and P4 becoming closer than others with increasing shell size. P1 very weak on 1st whorl, by end of 2nd whorl as large as P2 and P3, which are similar throughout, P3 peripheral, summit of P4 exposed on spire throughout. Secondary spirals developing to resemble primaries, S1 commencing on early to late 3rd whorl, S2 commencing on 1st half of 2nd whorl; axial costae commencing at end of 1st whorl, strong, prosocline, entirely traversing all spire whorls to P4. Base with 7 or 8 similar, strong, rounded spiral cords, at first smooth then with small rounded nodules, interspaces about as wide as each spiral or wider. Surface minutely granulate throughout. Collabral growth lines prosocline on spire, opisthocyrt on base. Aperture subquadrate. Radula (figures 106-107) with formula c.6 + 3 + 1 + 3 + c.6, highly degenerate, all teeth other than innermost 2 pairs of marginals flexible, almost gelatinous. Central and lateral teeth slender, narrowly tapered, extremely thin in section, tips finely serrate. Innermost marginal shortest, stoutest, cutting area angulate, strong terminal cusp and 3 or 4 secondary cusps on each side. Outer marginals slender, innermost pair longest, cutting area with long series of stout, narrowly tapered, curved cusps; outer marginals weakly developed.

Type Data: Holotype MNZ M.59698 (height 5.35 mm, width 4.95 mm, 4.70 teleoconch whorls): BS 668 (R26), 41°55.9'S, 174°43.2'E, SE of Cape Campbell, alive, 454-424 m, 14 January 1979, r.v. *Tangaroa*. Paratypes (4 MNZ): BS 969 (R27), 41°55.8'S, 174°40.7'E, SE of Cape Campbell, alive, 434-446 m, 14 January 1979, r.v. *Tangaroa*.

Other Material Examined: 1 incomplete shell MNZ, 45°45'S, 171°02'E, off East Otago, 600-520 m, r.v. *Munida*.

Distribution (figure 108): Off Cape Campbell and off East Otago, 424-600 m, taken alive at 424-454 m from rugged substrata with shells and corals.

Diet: Unknown.

Remarks: Compared with the Australian species *Calliostoma retiarium*, which it most closely resembles, *C. kopua* differs principally in being more strongly nodular, in being larger relative to the number of whorls, and in having a less exert protoconch. The single incomplete shell from off East Otago is 6.55 mm in diameter (estimated height 7 mm), suggesting that the type specimens are immature. As in other members of this group the

radula is degenerate through developmental retardation, *C. kopua* having the most degenerate radula of any known calliostomatid.

Etymology: Deep (Maori).

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APPENDIX

CHECKLIST OF RECENT CALLIOSTOMATIDAE FROM THE NEW ZEALAND REGION WITH NEW SYNONYMS
CALLIOSTOMATINAE

- Calliostoma (Maurea) antipodense* Marshall, new species.
C.(M.) aupourianum Marshall, new species.
C.(M.) benthicola (Dell, 1950).
C.(M.) blacki (Powell, 1950) (= *couperi* Vella, 1954 = *profunda* Dell, 1956).
C.(M.) emmens Marshall, new species.
C.(M.) foveauxanum (Dell, 1950).
C.(M.) gibbsorum Marshall, new species.
C.(M.) granti (Powell, 1931) (= *ampla* Powell, 1939 = *multigemmata* Powell, 1952).
C.(M.) jamiesoni Marshall, new species.
C.(M.) maui Marshall, new species.
C.(M.) megaloprepes (Tomlin, 1948).
C.(M.) osbornei Powell, 1926.
C.(M.) pellucidum (Valenciennes, 1846) (= *undulatum* Finlay, 1923 = *spiratum* Oliver, 1926).
C.(M.) penniketi Marshall, new species.
C.(M.) punctulatum (Martyn, 1784).
C.(M.) regale Marshall, new species.
C.(M.) selectum (Dillwyn, 1817) (= *hodgci* Hutton, 1875 = *ponderosus* Hutton, 1885 = *carnicolor* Preston, 1907).
C.(M.) simulans Marshall, 1994
C.(M.) spectabile (A. Adams, 1855).
C.(M.) tigris (Gmelin, 1791) (*chathamensis* Dell, 1950).
C.(M.) turnerarum (Powell, 1964).
C.(M.) waikanae Oliver, 1926 (= *morioria* Powell, 1946 = *forsteriana* Dell, 1950 = *haurakiensis* Dell, 1950).
C.(Otukaia) alertae Marshall, new name (*blacki* Dell, 1956).
C. (sensu lato) kopua Marshall, new species.
C. (sensu lato) limatulum Marshall, new species.
C. (sensu lato) onustum Odhner, 1924.
New genus A, new species (Marshall, 1995).
New genus B, new species (Marshall, 1995).
THYSANODONTINAE
Thysanodonta aucklandica Marshall, 1988.
T. wairua Marshall, 1988.
Carinastele coronata Marshall, 1988
C. jugosa Marshall, 1988.
C. kristellae Marshall, 1988

Five additional calliostomatines are known from the Kermadec Islands, to the north-east of New Zealand (Marshall, 1979):
Calliostoma new species A = *C. (Tristichotrochus)* sp. cf. *simplex* of Marshall, 1979, figs. C, D, not Schepman, 1908 (Marshall, 1995).

- C.* new species B = *C. (T.)* sp. cf. *simplex* of Marshall, 1979, figs. E, F, not Schepman, 1908 (Marshall, 1995).
C. (Tristichotrochus) gendalli Marshall, 1979.
C. (T.) species cf. *tosaense* (Kuroda & Habe, 1961).
C. (Fautor) consobrinum (Powell, 1958).

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