The deep-sea Buccinoidea (Gastropoda: Neogastropoda) of the Scotia Sea and adjacent abyssal plains and trenches

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ABSTRACT

Four new genera and species of buccinoidean gastropods, *Spikebuccinum stephaniae* new genus, new species; *Drepanodontus tatyanae* new genus, new species; *Muffinbuccinum catherinae* new genus, new species; and *Germonea rachelae* new genus, new species, are described from the Scotia tectonic plate and adjacent abyssal plains. Only *Bathydomus obtectus* Thiele, 1912, *Tromina bella abyssicola* Clarke, 1961 and *T. abyssorum* Lus, 1993, had previously been reported from abyssal depths off Antarctica. The latter two species were proposed in the genus *Tromina,* subsequently shown to belong to the family Muricidae. Therefore, a new genus, *Lusitromina* is proposed for these abyssal and hadal buccinoidean species. Analyses of the taxonomic placement, geographical and bathymetric distribution, and diversity of the 29 buccinoidean genera presently known from Antarctica and the Magellanic Province have shown that the abyssal (>2200 m) buccinoidean fauna of the region shares no genera with the sublittoral or bathyal faunas. None of the six abyssal genera conform readily to the subfamilies represented by the sublittoral or bathyal faunas. Credible sister taxa and likely origins for some abyssal genera occur on the adjacent continental slope. For others, closest relatives may be found on abyssal plains beyond the Antarctic convergence. Generic diversity decreases with increasing depth for both the bathyal and abyssal buccinoidean faunas, while bathymetric range tends to increase. For abyssal buccinoideans, maximum generic diversity occurs between 2600 and 3200 meters. The proportion of monotypic genera in the Antarctic and Magellanic Provinces is extraordinarily high (48.3%), and may be an artefact of low sampling density exacerbated by difficulties in differentiating closely related species. Neither gigantism nor dwarfism is evident in the abyssal buccinoidean fauna. Rather, the range in sizes narrows with increasing depth. Genera inhabiting the base of the continental slope are smaller than those of either the upper slope or continental rise. In the abyssal zone, maximum shell size is reached near the boundary of the continental rise and abyssal plain, and subsequently decreases with increasing depth.

INTRODUCTION

The Buccinoidea are the most geographically widespread and ecologically diverse clade within the Neogastropoda. First appearing during the Early Cretaceous [Valanginian] (Tracey et al., 1993), these predatory snails have radiated to occupy most benthic marine habitats ranging from the tropics to the poles and from the intertidal zone to hadal depths (Clarke, 1962). Several members of the families Nassariidae and Buccinidae have even invaded fresh water (Kantor and Kilburn, 2001; Brandt and Temcharoen, 1971).

Buccinoideans are readily distinguished by their usually weakly sculptured, conical to fusiform shells, their distinctive rachiglossan radula with multicuspid lateral teeth, long to very long proboscis, as well as by the absence of a rectal gland and accessory salivary glands. Their relationships to other Neogastropoda, however, have been variously interpreted, ranging from basal to derived (e.g., Ponder, 1974; Ponder and Warén, 1988; Ponder and Lindberg, 1996; Kantor, 1996; Harasewych et al., 1997). While a number of authors have attributed different taxonomic ranks to Buccinoidea and its component higher taxa (e.g., Powell, 1929; Thiele, 1929; Wenz, 1938; Ponder, 1974; Ponder and Warén, 1988), there is little disagreement as to the monophyly or composition of the group. We had earlier briefly reviewed the history of the higher classification of buccinoideans (Harasewych and Kantor, 1999), which is based primarily on differences in shell, opercular and radular morphologies applied to regional faunas (e.g., Powell, 1929, 1951, Southern Oceans; Habe and Sato, 1973, Northern Pacific; Bouchet and Warén, 1985, Northeastern Atlantic). We continue to retain provisionally the use of Buccinulidae and its subdivisions, as defined by Powell (1951), without necessarily endorsing their taxonomic rank, for the antiboreal members of the Buccinoidea, pending the availability of sufficient anatomical and/or molecular data for a meaningful phylogenetic revision of the higher taxa of Buccinoidea on a global basis. The subfamilial assignments of presently known buccinoidean genera that occur south of the Antarctic Convergence, as well as those from the Magellanic Province are reviewed (Appendix 1) and, in some cases, revised.

Our continuing studies of the Buccinoidea represented in the collections assembled by the United States Antarctic Program (USAP) have revealed a number of

previously undescribed taxa from the abyssal plains and trenches on and adjacent to the Scotia Plate. These taxa are described herein, and their affinities to other Antarctic and abyssal buccinoideans are discussed.

MATERIALS AND METHODS

This report is based primarily on buccinoideans sorted from the abyssal stations sampled by the United States Antarctic Program (USAP) vessels R/V Islas Orcadas and R/V Eltanin and housed in the collections of the National Museum of Natural History (USNM). Additional material, sampled by the German vessel R/V Polarstern and in the collection of the Zoological State Collection, Munich (ZSM) were made available through the kindness of Enrico Schwabe and Michael Schrödl.

In the material examined sections, "specimen" denotes that a preserved animal is present, while "shell" refers to a record based only on an empty shell. Anatomical descriptions are based on gross dissections of preserved specimens. Radulae were removed by gross dissection, cleaned using diluted bleach (NaOCl), coated with carbon and gold, and examined using a LEO 440 Scanning Electron Microscope. Photographs were taken using a Nikon D1 Digital Camera with a AF Micro Nikkor 60 mm lens. Images were processed using Adobe Photoshop 6.0.

The following abbreviations are used in the text: AL—aperture length, D—diameter, FWL—final whorl length, L—length, L/W—length/width, SCL—Siphonal canal length, SL—shell length, SW—shell width, W—width.

SYSTEMATICS

Class Gastropoda Cuvier, 1797
Order Neogastropoda Wenz, 1938
Superfamily Buccinoidea Rafinesque, 1815
Family Buccinulidae Finlay, 1928
Subfamily Buccinulinae Finlay, 1928
Genus *Spikebuccinum* new genus

Type Species: *Spikebuccinum stephaniae* new species, by original designation.

Description: Protoconch large (to 3.5 mm diameter), of 2⅔ smooth, evenly rounded, whorls. Teleoconch small (to 19.9 mm), very thin, translucent, ovate, rounded anteriorly, all but final 2–2½ whorls eroded. Shell sculpture of sharp, closely spaced, spiral cords. Columella weakly concave, shorter than aperture, producing siphonal notch with weak siphonal fasciole, short pseudoumbilicus. Periostracum finely hirsute. Operculum ovate, paucispiral, with subterminal nucleus, spans ~⅓ aperture length. Eyes absent. Buccal mass, odontophoral cartilages longer than retracted proboscis. Rachidian teeth tricuspid, with outer cusps broader, longer than central cusp. Lateral teeth with large outer, shorter inner cusp, with 3–4 denticles between. Salivary glands small, 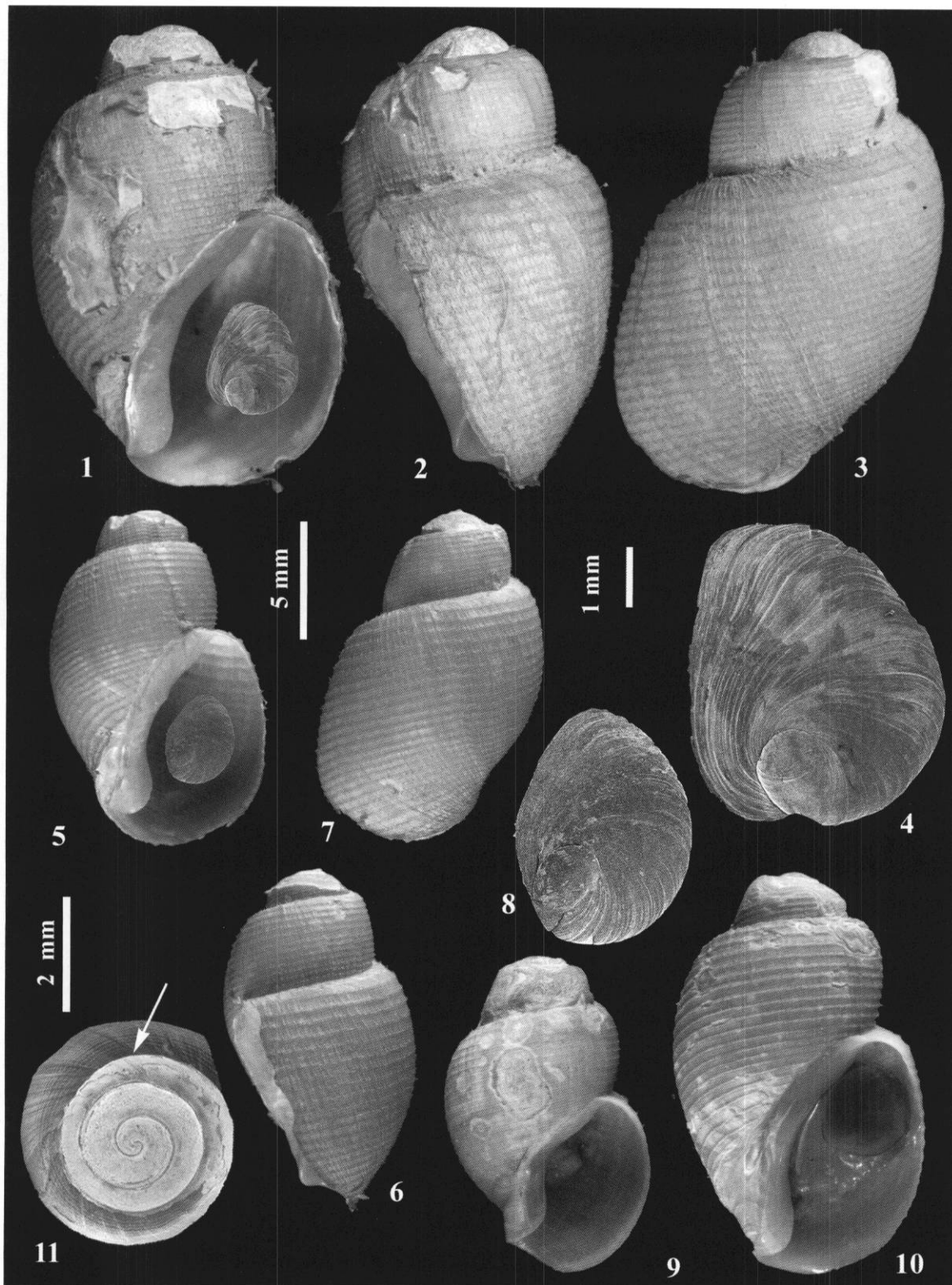unfused. Gland of Leiblein glandular anteriorly, flaccid posteriorly. Posterior oesophagus forms crop before entering simple, U-shaped stomach, which has a well-defined gastric shield.

Etymology: This genus is named after Spike, a Cornish Rex cat that belongs to the senior author's daughter Stephanie.
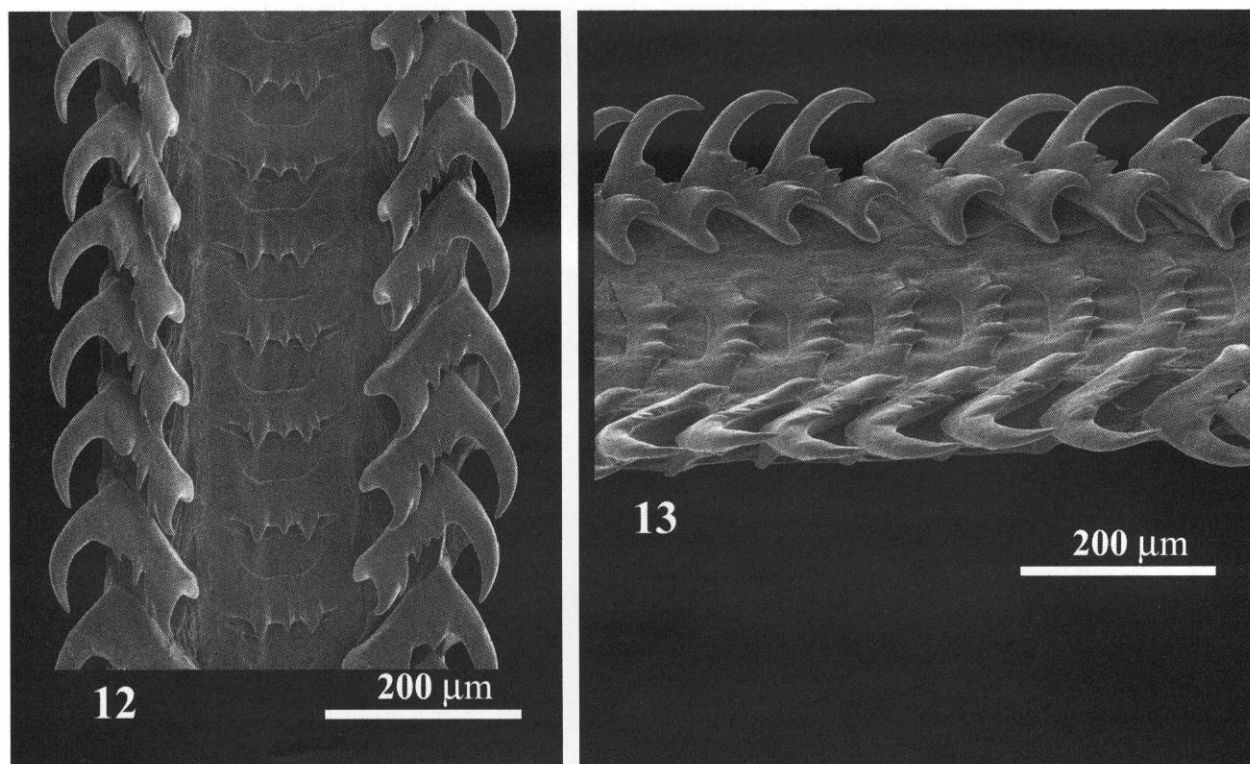
Spikebuccinum stephaniae new species
(Figures 1–23, Table 1)

Description: Shell (Figures 1–3, 5–7, 9, 10) small (to 19.9 mm), very thin, translucent, ovate, with rounded anterior, eroded spire. Protoconch (Figure 11), known from a single juvenile (Paratype 12), increasing in diameter from 0.4 mm to 3.5 mm, in 2⅔ smooth, evenly rounded, pitted whorls. Transition to teleoconch distinguished by slight change in color, from cream to white, and by abrupt transition from coarse, irregular axial growth striae, to finer, regular growth lines. Protoconch and upper whorls eroded on all other specimens. Extrapolation from growth series suggests that teleoconch may reach 5–6 whorls, of which all but last 2–2½ whorls eroded. Whorls evenly rounded, with indistinct shoulder, abutting suture. Axial sculpture limited to very fine, straight, strongly prosocline growth lines. Spiral sculpture of fine, sharp, uniform, evenly spaced cords (21–29 on final whorl, 11–14 on penultimate whorl). Aperture large (AL/SL = 0.60–0.67 when using length of eroded shell; AL/SL = 0.50–0.55, as estimated by linear projections of apex), broadly oval, deflected from shell axis by 22–25°. Outer lip very thin, not reflected, evenly rounded from suture to siphonal notch. Inner lip consists of a long, straight parietal region that meets the shorter, concavely indented axial portion of columella, ending in strong siphonal fold. Columella shorter than aperture, giving rise to a broad siphonal notch. Parietal callus uniformly narrow from suture to siphonal fold. Short, weak, siphonal fasciole and pseudoumbilicus present, often obscured by erosion. Shell color uniformly white. Periostracum very thin, straw yellow in color, with densely spaced axial lamellae, producing short, fine hairs at intersection with spiral cords, giving shell a finely hirsute appearance. Operculum (Figures 4, 8) small, spanning ~0.36 AL, yellowish brown, broadly ovate, paucispiral, with subterminal nucleus rotated relative to opercular axis.

Anatomy (Holotype): Soft tissues (Figures 14–22) comprise approximately 2¼ whorls. Mantle cavity spans just under ⅓ whorl, kidney ¼ whorl, digestive gland and gonad just under 1½ whorl. Columellar muscle short, broad, comprising slightly more than one whorl, attached to shell at rear of mantle cavity. Foot large, broadly rectangular (L/W ≈ 1). Body color yellowish tan, without pigmentation. Head large with long, thin tapering tentacles (Figure 15, tn), without neck. Eyes absent. Nephridium with semi-transparent walls that clearly reveal folds. Nephridial gland (Figure 14, ng) small, very narrow. Pericardium oriented antero-ventrally. Digestive

Figures 1–11. Shells and opercula of *Spikebuccinum stephaniae* new species. **1.** Apertural, **2.** lateral, **3.** and dorsal views of holotype, USNM 896368, off South Georgia Island, 53°02′ S, 37°40′00″ W, in 3056–3102 m [R/V ELTANIN cruise 9, sta. 735]. **4.** Outer view of operculum of holotype. **5.** Apertural, **6.** lateral, and **7.** dorsal views of Paratype 1, USNM 1010626, from the type locality. **8.** Outer view of operculum of Paratype 1. **9.** Apertural view, USNM 1010630, E off South Sandwich Islands, 58°27′ S, 22°22′ W, in 4643–4645 m [R/V ELTANIN sta. 603]. **10.** Apertural view, Paratype 8, USNM 1010629, S off Southern Georgia Island, 58°04′ S, 37°50′ W, in 3255–3166 m [R/V ELTANIN sta. 699]. **11.** Scanning electron micrograph of protoconch of Paratype 12, ZSM (Zoological State Collection, Munich) 20021125, E off South Sandwich Islands, 58°24.98′ S, 25° 1.00′ W, in 2285.5 m, [R/V POLARSTERN cruise ANTXIX, sta. PS61/141-8, 22 Mar 2002] Arrow indicates transition to teleoconch. 5 mm scale bar applies to all shells, 1 mm scale bar applies to opercula, 2 mm scale bar applies to protoconch.

Figures 12–13. Radula of the holotype of *Spikebuccinum stephaniae* new species. **12.** Dorsal, and **13.** Left lateral (30°) views of the central portion of the radular ribbon.

gland lobes (Figure 19, adg, pdg) not fused, separated by ovary (Figure 19, ov).

Mantle Cavity (Figure 20):   Mantle cavity of medium width (L/W ~0.8), mantle edge slightly serrated. Siphon long (0.42 AL), free, muscular, extending substantially beyond mantle edge. Osphradium (Figure 20, os) small (~0.4 mantle cavity length) yellowish, bipectinate, with narrow osphradial nerve. Ctenidium (Figure 20, ct) large, very wide, spans about ¾ of mantle cavity length. The ctenidial lamellae are low. Hypobranchial gland lacks distinct folds, covered by thick layer of mucus.
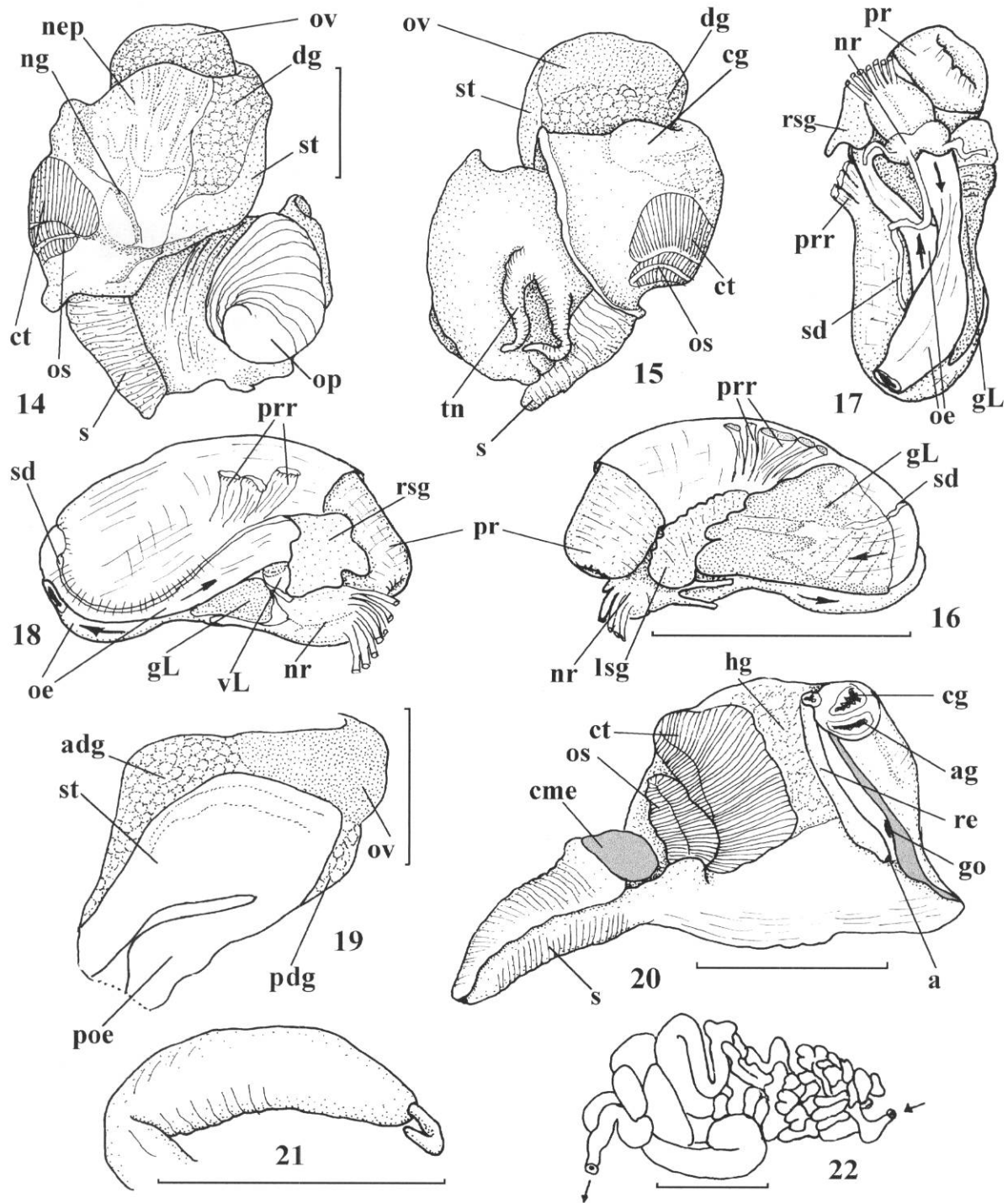
Alimentary System (Figures 14–19):   Proboscis (Figures 16–18, pr) of moderate length when retracted (~0.36 SL, 0.54 AL), thick (L/D ~3.3), smooth, non-pigmented. Proboscis retractor muscles (Figures 16–18, prr) not numerous, but thick, powerful, attached to proboscis sheath at mid-length when proboscis retracted. Proboscis sheath thin-walled, translucent along anterior half, thickened posteriorly, but thinner than proboscis wall. Proboscis wall thick, comprising ~1/10 of retracted proboscis diameter. Mouth opening dorso-ventrally compressed slit. Buccal mass muscular, large, filling retracted proboscis and protruding significantly beyond its rear. Odontophoral cartilages paired, fused anteriorly, slightly longer, than retracted proboscis. Radular ribbon longer than retracted proboscis, 5.4 mm long (0.41 AL), about 480 μm wide (0.037 AL), triserial (Figures 12–13), consisting of 58 rows of teeth, posteriormost 6 rows nascent.

Rachidian teeth with 3 short cusps emanating from central portion of broad, anteriorly deeply arched basal plate. Central cusp slightly shorter, narrower than lateral cusps. Lateral teeth with long basal plate flanked by two main cusps, outermost nearly twice as long as innermost, 3–4 smaller, intermediate denticles vary in size and position from row to row, innermost denticle often abutting inner cusp.

Salivary glands (Figures 16–18, rsg, lsg) small, acinous, yellowish, not fused. Right salivary gland (rsg) dorsal to nerve ring, enveloping most of valve of Leiblein. Left salivary gland (lsg) lateral to, partially covering nerve ring. Salivary ducts (Figures 17–18, sd) thick, attached both to oesophagus and proboscis sheath by numerous connective tissue fibers. Salivary ducts pass along both sides of oesophagus, become "embedded" into oesophagus walls immediately after entering the proboscis. Valve of Leiblein (Figure 18, vL) well defined, large, pyriform, with whitish glandular pad containing ciliary cone visible through walls of valve.

Gland of Leiblein (Figures 16–18, gL) large, massive, glandular anteriorly; flaccid, transparent, lacking glandular tissue posteriorly; opens, via short duct, into oesophagus just posterior to nerve ring. Gland yellowish, only slightly darker than other organs of the cephalic haemocoel.

Oesophagus thick anterior to nerve ring, becoming thin-walled, flattened posterior to nerve ring. Oesopha-

Figures 14–22. Anatomy of *Spikebuccinum stephaniae* new species. **14–20.** Holotype, **21–22.** Paratype 1. **14.** Right, and **15.** Left lateral views of animal removed from shell. **16.** Left, **17.** ventral, and **18.** right lateral views of anterior alimentary system. **19.** Dorsal view of stomach, digestive glands and ovary. **20.** Mantle cavity organs. **21.** Lateral view of penis. **22.** Ventral view of seminal vesicle. Scale bars = 5 mm for **14–21**, 1 mm for **22. a,** anus; **adg,** anterior duct of the digestive gland; **ag,** albumen gland; **cg,** capsule gland; **cme,** cut mantle edge; **ct,** ctenidium; **dg,** digestive gland; **gL,** gland of Leiblein; **go,** female genital opening; **hg,** hypobranchial gland; **lsg,** left salivary gland; **nep,** nephridium; **ng,** nephridial gland; **nr,** circumoesophageal nerve ring; **oe,** oesophagus; **op,** operculum; **os,** osphradium; **ov,** ovary; **pdg,** posterior duct of the digestive gland; **poe,** posterior oesophagus; **pr,** proboscis; **prr,** proboscis retractors; **re,** rectum; **rsg,** right salivary gland; **s,** siphon; **sd,** salivary duct; **st,** stomach; **tn,** cephalic tentacles; **vL,** valve of Leiblein.
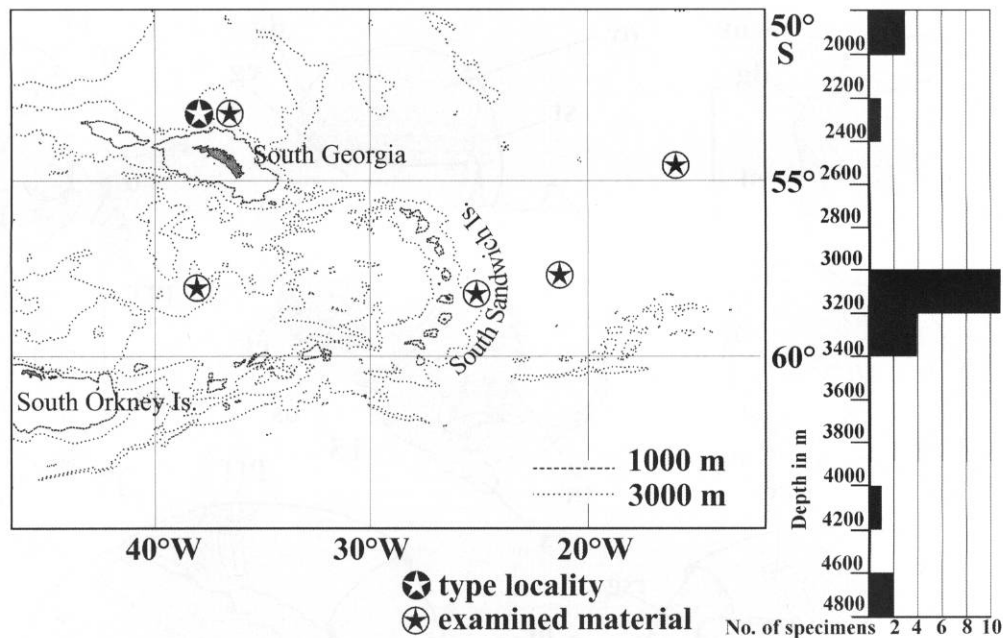
Figure 23. Geographic and bathymetric distribution of *Spikebuccinum stephaniae* new species.

gus widens to form a "crop" (Figure 19, poe) before entering stomach.

Stomach (Figures 14, 15, 19, st) relatively large, broadly U-shaped, without posterior mixing area. Due to poor preservation of holotype it was impossible to examine the internal morphology of the stomach in detail. Digestive gland ducts paired. Arrangement of stomach similar to *Lusitromina abyssorum* (Figure 132) but differs in having well developed, highly cuticularized gastric shield, with crescent-shaped dorsal side that is lifted and significantly protruded into stomach lumen.

Female Reproductive System: Female reproductive system typically buccinoidean, with small albumen gland partially overlapping posterior portion of capsule gland dorsally. Ingesting gland small, opening between albumen and long, broad capsule gland. Small bursa copulatrix situated anterior to capsule gland, tapering anteriorly to form female opening.

Male Reproductive System: Paratype 1, mature

male. Seminal vesicle (Figure 22) of medium size, spans > ½ whorl, formed of numerous loops. Penis (Figure 21) long, narrow, non-pigmented, with slightly folded walls. Penial papilla long, cylindrical, surrounded by circular fold around base.

Type Locality: Off South Georgia Island, 53°02′ S, 37°40′ W, in 3056–3102 m [R/V ELTANIN cruise 9, sta. 735, 13 Sep 1963].

Type Material: Holotype, ♀, USNM 896368; Paratypes 1–4, USNM 1010626, all from the type locality. Paratypes 5–7, USNM 1010628, off South Georgia Island, 53°26.7′ S, 36°32.6′ W, in 1967–2186 m, [R/V ISLAS ORCADAS sta. 28, 12 May 1976]; Paratypes 8–11, USNM 1010629, S of Southern Georgia Island, 58°04′ S, 37°50′ W, in 3255–3166 m, [R/V ELTANIN cruise 9, sta. 699, 30 Aug 1963]; Paratype 12, ZSM 20021125, E of South Sandwich Islands, 58°24.98′ S, 25° 1.00′ W, in 2285.5 m, [R/V POLARSTERN cruise ANTXIX, sta. PS61/141-8, 22 Mar 2002].

Table 1. *Spikebuccinum stephaniae* new species. Measurements of shell characters. Linear measurements in mm. (n = 7, including holotype. Juvenile specimens excluded).

Character	Mean	σ	Range	Holotype
Shell length (SL)	15.6	2.2	13.4–19.9	19.9
Final whorl length (FWL)	13.9	2.2	11.9–18.0	18.0
Aperture length (AL)	10.3	1.7	8.3–13.2	13.2
Shell width (SW)	10.1	1.6	8.6–13.2	13.2
FWL/SL	0.89	0.04	0.81–0.91	0.90
AL/SL	0.65	0.03	0.60–0.68	0.66
SW/SL	0.64	0.02	0.59–0.66	0.66
Number of spiral cords on penultimate whorl	12.4	1.0	11–14	14
Number of spiral cords on final whorl	24.6	2.9	21–29	29

Other Material Examined: USNM 896337, E of South Sandwich Islands, 54°51′ S, 14°54′ W, in 3947–4063 m, [R/V ELTANIN sta. 1571, 28 Feb 1966], 1 specimen; USNM 1010630, E of South Sandwich Islands, 58°27′ S, 22°22′ W, in 4643–4645 m, [R/V ELTANIN cruise 9, sta. 603, 5 May 1963], 1 specimen + 1 shell.

Distribution (Figure 23): The species is found in the Scotia Sea and adjacent abyssal plains at depths of 1967–4645 m.

Etymology: This species is named for the senior author's elder daughter, Stephanie Alexandra Harasewych.

Remarks: The shell morphology of *Spikebuccinum stephaniae* superficially resembles that of several species of *Chlanidota*, especially *C. signeyana* Powell, 1971 and *C. (Pfefferia) invenusta* Harasewych and Kantor, 1999, and, to a lesser extent, an eroded *Neobuccinum eatoni* (Smith, 1875). However, it can readily be distinguished from these taxa by its very short columella, an inconspicuous siphonal fasciole, as well as by having a rachidian tooth in which the central cusp is shorter and narrower, rather than longer and stouter than the outer cusps. The lateral teeth of all species of *Chlanidota* and the monotypic *Neobuccinum* have a strong, single intermediate cusp, rather than the multiple denticles of *Spikebuccinum*. The shell of *Spikebuccinum stephaniae* is also somewhat similar to that of *Antarctodomus okutanii* Numanami, 1996, which has a clearly cominelline radula, with tricuspid rachidian and bicuspid lateral teeth.

The radular morphology of *Spikebuccinum stephaniae* is distinctive, and suffices to distinguish it from all Antarctic and Magellanic buccinoideans. The presence of multiple denticles between the flanking cusps of the lateral teeth would appear to preclude the inclusion of this genus in the subfamily Buccinulinae, which is defined on the basis of having tricuspid rachidian and lateral teeth (Powell, 1951). However, Powell (1951:131) expanded this criterion to include *Bathydomus* Thiele, 1912, within Buccinulinae, citing the conchological affinities of *Bathydomus* to *Chlanidota*. We questionably include *Spikebuccinum* within the subfamily Buccinulinae, noting the possibly pleisiomorphic similarity of its radula to such boreal and temperate taxa as *Neptunea*, some *Buccinum*, *Cantharus* and certain *Busycotypus*.

The strongly paucispiral operculum of *Spikebuccinum stephaniae* is a feature it shares with a number of genera, among them *Neobuccinum*, *Parficulina* Powell, 1958, *Falsitromina* Dell, 1990, *Parabuccinum* Harasewych, Kantor and Linse, 2000, and such boreal genera as *Mohnia* Friele *in* Kobelt, 1878, and *Pararetifusus* Kosuge, 1976. While operculum morphology is undoubtedly useful for distinguishing genera, its utility for discerning phylogenetic relationships among supraspecific taxa is less clear.

Comparative anatomical data is available for only a very few buccinulid taxa, among them *Chlanidota* (Harasewych and Kantor, 1999) and *Parabuccinum* (Harasewych, Kantor and Linse, 2000). Of these, *Spikebuccin-*um appears most similar anatomically to *Chlanidota*, but differs in having proportionally longer odontophoral cartilages, salivary glands that are not fused, a valve of Leiblein with a ciliary cone, a gland of Leiblein that opens to the mid-oesophagus via a narrow rather than broad duct, a broader stomach with a well-defined gastric shield, and a tapering rather than hemispherical bursa copulatrix.
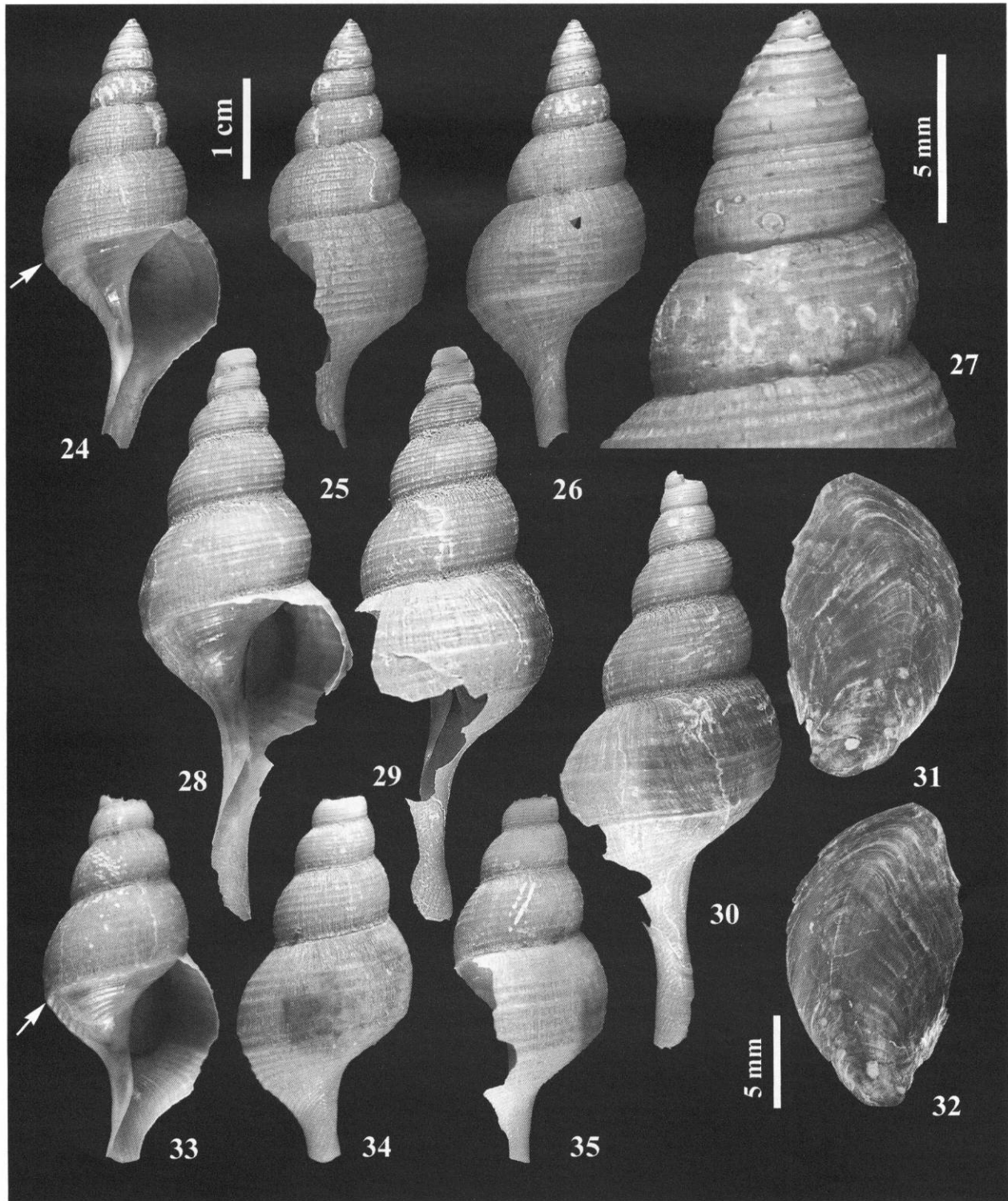
Drepanodontus new genus

Type Species: *Drepanodontus tatyanae* new species, by original designation.

Description: Protoconch eroded. Shell large (to 56 mm), thin, strongly fusiform, with long, broad, open siphonal canal. Early whorls straight to concave, subsequently becoming convex. Whorls lacking shoulder, final whorl evenly convex from suture to distinct peripheral cord, evenly concave from peripheral cord to tip of siphonal canal. Sculpture of axial growth lines, most pronounced on early whorls, and strong, evenly spaced spiral cords. Aperture large, narrow, elliptical. Outer lip not reflected. Parietal region broad posteriorly, columella shorter than siphonal fold. Periostracum lamellose. Operculum large (~0.82 AL), oval, thin, translucent, with terminal nucleus. Head medium-sized, with short, stout tentacles, large eyes. Kidney large. Buccal mass small, odontophoral cartilages short. Rachidian teeth variable, tricuspid, cusps may be fused to appear monocuspid, or supplemental denticles or cusps may be present in some specimens. Lateral teeth with single, large, sickle-shaped cusp that may have one or more denticles. Salivary glands not fused, right gland much larger than left. Gland of Leiblein long, glandular anteriorly, tapering, flaccid posteriorly. Oesophagus broadens to form crop, constricts before entering very large, U-shaped stomach that lacks posterior mixing area.
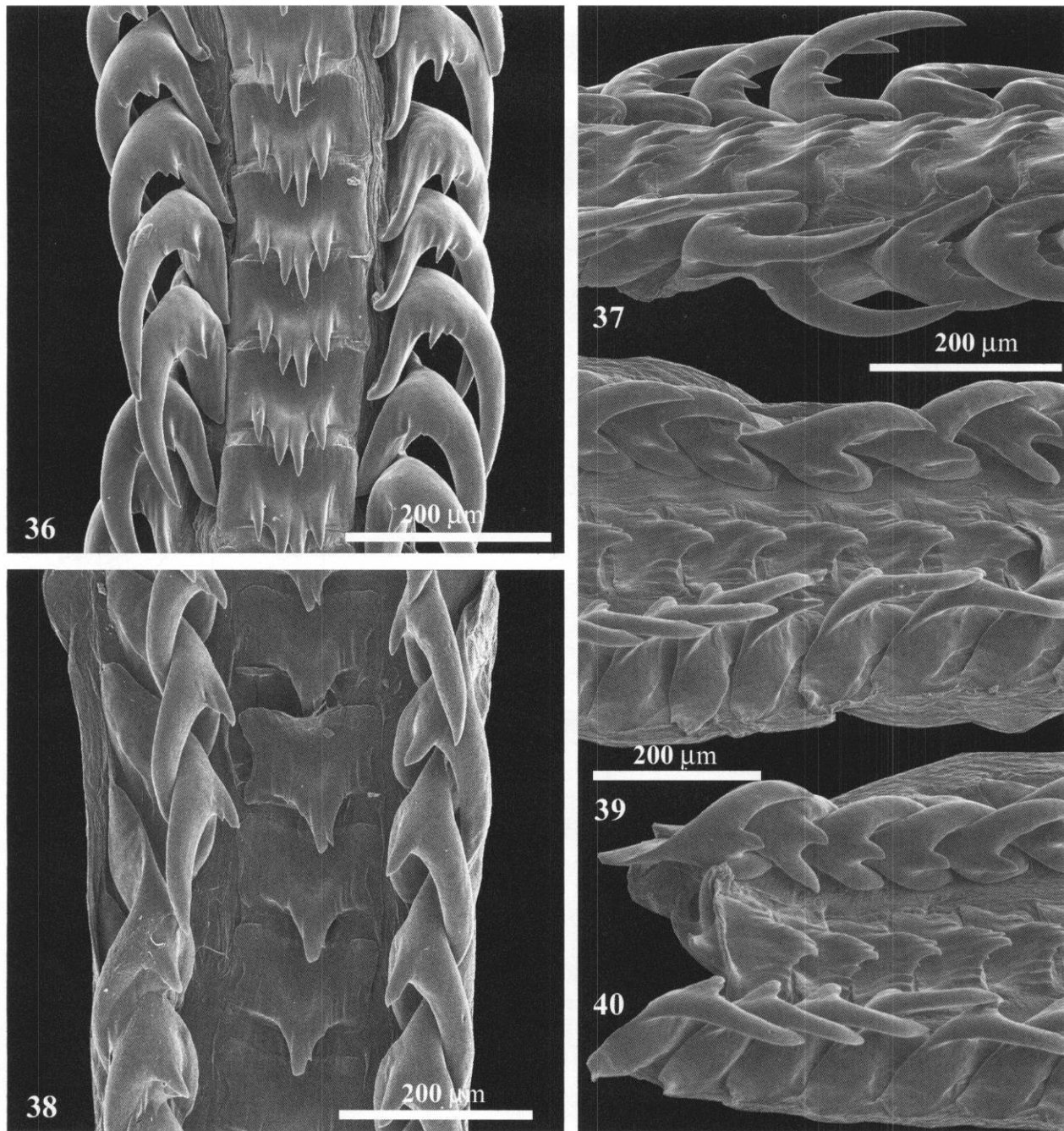
Etymology: *Drepane* (Gr.)—sickle, *odontos* (Gr.)—tooth. The name reflects the very unusual sickle shape of the lateral teeth, consisting of a long, narrow basal plate with a single, long, recurved outer cusp, often with one or more denticles along its inner edge.

Drepanodontus tatyanae new species
(Figures 24–50, Table 2)

Description: Shell (Figures 24–30, 33–35) large (to 43.1 mm), thin, strongly fusiform. Protoconch eroded on all specimens. Early whorls of holotype (Figure 27) indicate that protoconch would likely have been ~2–2½ whorls, < 3 mm in diameter. Transition to teleoconch indistinct in holotype. Teleoconch estimated to consist of up to 7 whorls. Early teleoconch whorls slightly concave in profile, with narrow spiral cords. By third whorl, teleoconch becomes convex, increasingly so in subsequent whorls, forming evenly rounded, oval whorls without distinct shoulder. Suture abutting onto pronounced peripheral cord (Figures 24, 33, arrow). Axial sculpture
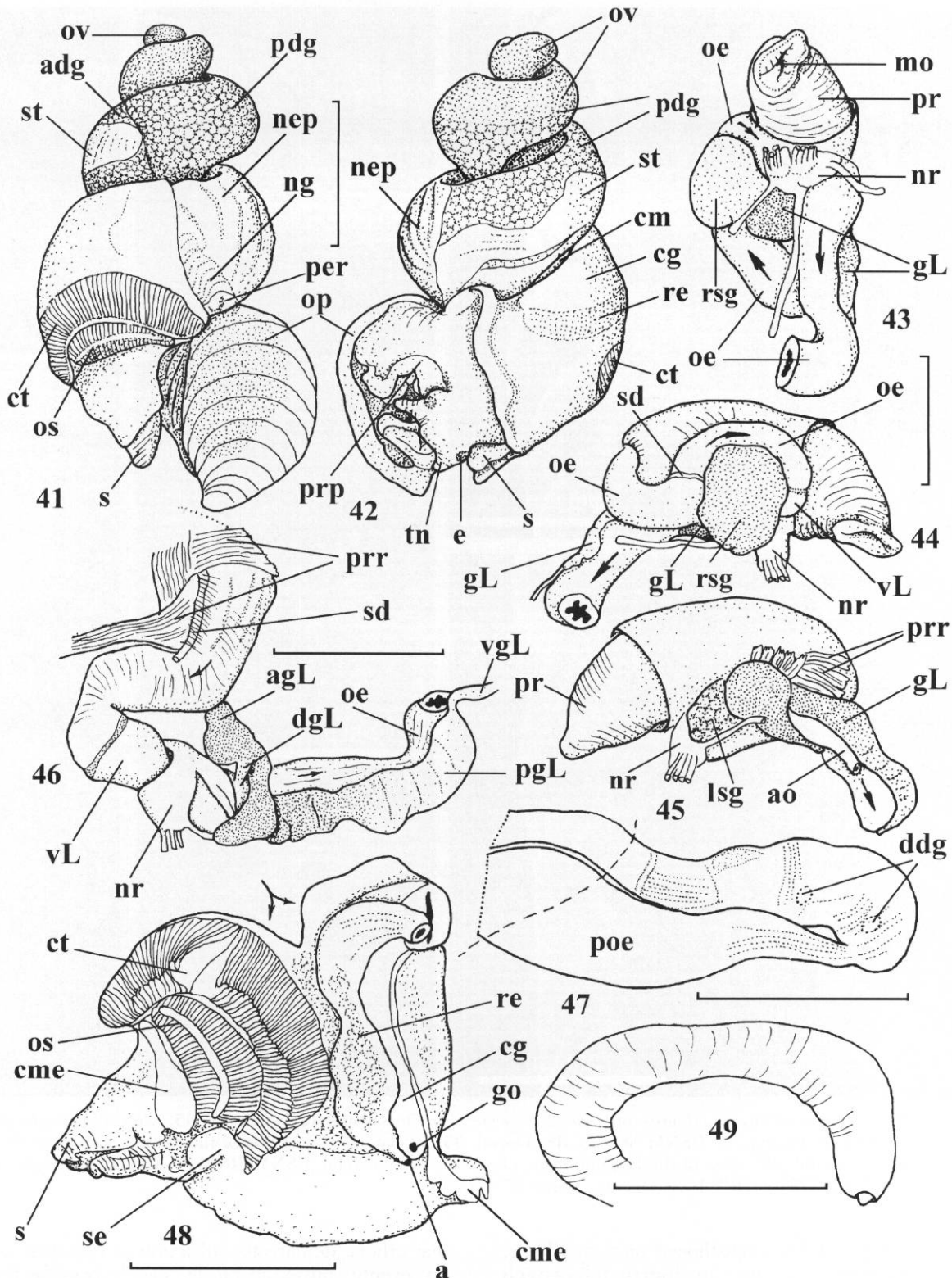
Figures 24–35. Shells and opercula of *Drepanodontus tatyanae* new species. **24.** Apertural, **25.** lateral, and **26.** dorsal views of the holotype, USNM 1010544, NE of South Shetland Islands, 59°01′ S, 52°00′ W, in 3010–3510 m. [R/V ELTANIN cruise 22, Sta. 1511]. **27.** Enlarged upper shell whorls of holotype. **28.** Apertural, **29.** lateral, and **30.** dorsal views of Paratype 1, USNM 881529, E of South Sandwich Islands, 57°00.24′ S, 26°10.06′ W, in 2740–2757 m. [R/V ELTANIN cruise 575, sta. 38]. **31.** Outer, and **32.** inner views of the operculum of Paratype 1. **33.** Apertural, **34.** lateral, and **35.** dorsal views of the shell of paratype 2, USNM 881529. Same locality as Paratype 1.

Figures 36–40. Radulae of *Drepanodontus tatyanae* new species. **36.** Dorsal, and **37.** left lateral (45°) views of the central portion of the radular ribbon of Paratype 1, USNM 881529. **38.** Dorsal, **39.** left lateral (45°) views of the central portion of the radular ribbon, and **40.** left lateral (45°) view of the bending plane of a non-type specimen, USNM 1010545, Argentinean Basin, 47°17.3′ S, 47°45.7′ W, in 5685–5798 m [R/V Islas Orcada, cruise 575, sta. 4].

of pronounced growth lines, opisthocyrt on early whorls, becoming weaker, orthocline by fourth teleoconch whorl. Spiral sculpture of broad, sharp cords (9–12 on penultimate whorl, 10–14 from suture to peripheral cord, 16–24 from peripheral cord to tip of siphon) narrower than intervening spaces, with 0–4 very fine threads between adjacent cords, especially near periphery. Peripheral cord, slightly thicker more pronounced that others, demarcates inflection in curvature of outer lip, evenly convex abapically, evenly concave from peripheral cord to tip of siphonal canal. Aperture large (AL/SL = 0.56), roughly elliptical, deflected from shell axis by 13–17°. Siphonal canal long (~¼ shell length), broad, open, crosses shell axis. Outer lip thin, not reflected. Inner lip of weakly concave parietal region, slightly longer columella, long siphonal fold extending

Figures 41–49. Anatomy of *Drepanodontus tatyanae* new species. (**41–48.** Paratype 1. **49.** Paratype 2, both USNM 881529). **41–42.** Lateral views of animal removed from shell. **43.** Ventral, **44.** right lateral, and **45.** left lateral views of the anterior alimentary system. **46.** Latero-dorsal view of the anterior oesophagus, showing the duct of gland of Leiblein. Oesophagus twisted counterclockwise. **47.** Dorsal view of stomach, dashed line indicates the posterior nephridial border. **48.** Mantle complex of organs. **49.** Lateral view of penis. Scale bars = 1 cm for Figures 41–42, 47–49, 5 mm for Figures 43–46. **a,** anus; **adg,** anterior duct of the digestive gland; **agd,** anterior lobe of digestive gland; **ao,** aorta; **cg,** capsule gland; **cm,** columellar muscle; **cme,** cut mantle edge; **ct,** ctenidium; **dgL,** duct of gland of Leiblein; **e,** eye; **gL,** gland of Leiblein; **go,** female genital opening; **lsg,** left salivary gland; **mo,** mouth opening; **nep,** nephridium; **ng,** nephridial gland; **nr,** circumoesophageal nerve ring; **oe,** oesophagus; **op,** operculum; **os,** osphradium; **ov,** ovary; **pdg,** posterior lobe of digestive gland; **per,** pericardium; **poe,** posterior oesophagus; **pr,** proboscis; **prp,** propodium; **prr,** proboscis retractors; **re,** rectum; **rsg,** right salivary gland; **s,** siphon; **sd,** salivary duct; **st,** stomach; **vL,** valve of Leiblein.
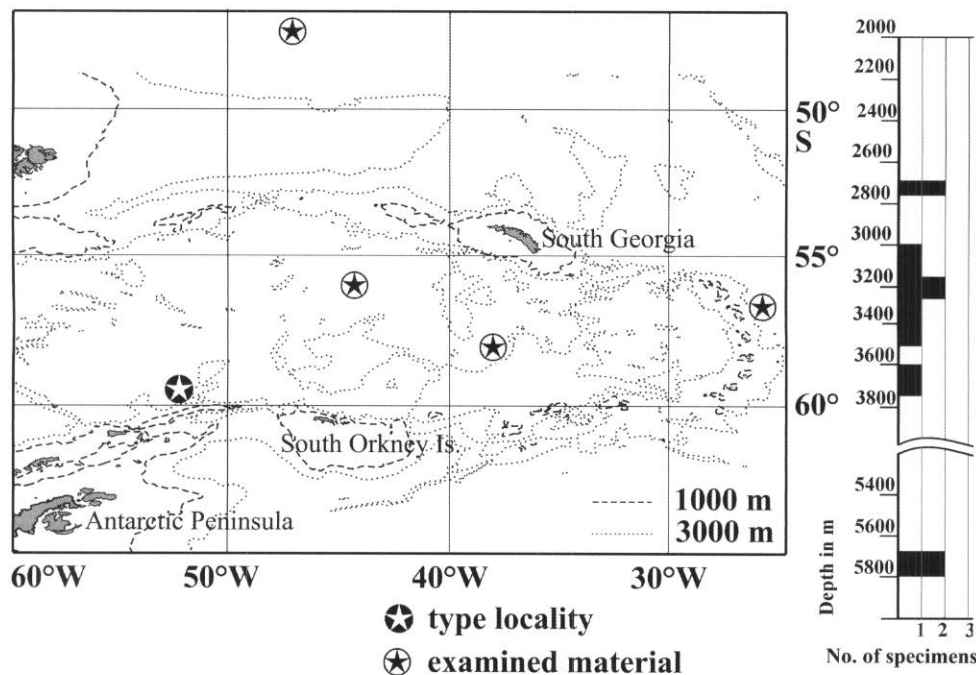
Figure 50. Geographic and bathymetric distribution of *Drepanodontus tatyanae* new species.

beyond glossy, translucent parietal region, broad posteriorly, tapering toward base of siphonal canal. Neither siphonal fasciole nor pseudoumbilicus present. Shell uniformly white, aperture, parietal callus glossy. Periostracum straw-colored, of widely spaced, short axial lamellae. Operculum (Figures 31–32, 41–42, op), large (~0.82 AL), oval, thin, brownish yellow, flexible, with terminal nucleus. Attachment of columellar muscle clearly visible through operculum, oval, spans about ⅔ of operculum surface.

Anatomy (Paratype 1): Soft tissues (Figures 41–42) comprise approximately 3½ whorls. Mantle cavity spans slightly less than ½ whorl. Kidney (Figures 41, 42, nep) broad, spans slightly less than ½ whorl, with 12 transverse folds of unequal width visible through wall. Ne-

phridial gland (Figure 41, ng) narrow, situated anterodorsally to the nephridium. Digestive glands (Figures 41, 42, adg, pdg) of 2½ whorls. Columellar muscle (Figure 42, cm) of 1½ whorls, attached to shell at rear of mantle cavity. Foot medium-sized, short in contracted specimen (L/W ~1.2), with well-developed narrow propodium (Figure 42, prp) separated by narrow propodial cleft. Body color yellowish tan, without pigmentation. Head medium-sized, with short, stout, conical tentacles, with small but distinct lobes at their bases. Eyes present (Figure 42, e), light gray in color and semitransparent, deeply embedded into lobes. Mantle does not cover base of head.

Mantle Cavity (Figure 48): Mantle cavity deep (L/W ~1.2). Mantle edge smooth, slightly thickened. Si-

Table 2. *Drepanodontus tatyanae* new species. Measurements of shell characters. Linear measurements in mm. (n = 3, including holotype).

Character	Mean	σ	Range	Holotype
Shell length (SL)	45.1	10.1	36.2–56.0	43.1
Final whorl length (FWL)	33.8	7.4	28.6–42.2	30.5
Aperture length (AL)	26.7	6.2	22.2–33.7	24.1
Siphonal canal length (SCL)	11.4	4.7	7.5–16.7	10.1
Shell width (SW)	19.1	2.3	17.5–21.8	18.1
FWL/SL	0.75	0.04	0.71–0.79	0.71
AL/SL	0.59	0.03	0.56–0.61	0.56
SCL/SL	0.25	0.05	0.21–0.30	0.23
SW/SL	0.43	0.05	0.39–0.48	0.42
Number of spiral cords on penultimate whorl	10.0	1.5	9–12	10
Number of spiral cords suture to peripheral cord	12.0	2.0	10–14	12
Number of spiral cords peripheral cord to siphon	19.7	4.0	16–24	19

phon (Figure 48, s) short, free, muscular, broad, extending well beyond mantle edge, with thick siphonal edge (Figure 48, se), covering anteriormost part of ctenidium. Osphradium (Figure 48, os) greenish, bipectinate, large, wide, ½ as long, ⅔ as wide as ctenidium. Ctenidium (Figure 48, ct) large, curved, spanning nearly entire mantle cavity length. Ctenidial lamellae broad, triangular, with short recurved edges along posterior part (closer to pericardium), gradually becoming narrower, relatively taller anteriorly. Hypobranchial gland lacks distinct folds, covered by thick layer of mucus. Rectum long, spanning ~4/5 of mantle cavity length.

Alimentary System (Figures 41–47): Proboscis non-pigmented, (Figures 43, 45, pr) short when retracted (~0.2 SL, 0.58 AL), thick (L/D ~3), with slightly folded walls. Proboscis retractor muscles (Figures 45, 46, prr) not numerous, thin, attached to thin-walled, translucent proboscis sheath at middle-posterior region when proboscis retracted. Proboscis wall thin, ~1/10 proboscis diameter. Anterior part of proboscis flattened to form rim surrounding mouth opening (Figure 43, mo) in form of irregular triangular slit. Anterior oesophagus very broad, nearly filling proboscis. Dorsal folds very large, bordering deep groove. Buccal mass small, spans slightly more than ½ of proboscis length. Odontophoral cartilages paired, fused anteriorly, extend nearly entire length of buccal mass, but <½ proboscis length. Radular ribbon (Figures 36–40) equal in length to cartilages, 6.6 mm (0.35 AL), about 380 μm wide (0.020 AL), triserial, consisting of 50 rows of teeth, posteriormost 5 rows nascent. Rachidian teeth of Paratype 1 (Figures 36–37) with 4 cusps, here interpreted as comprising a long central cusp, flanked by shorter, outer cusps, with an additional, asymmetrical cusp on the left side. Rachidian teeth of a second specimen (Figures 38–40) appear monocuspid, but "central cusp" consists of 3 incompletely fused cusps, flanked by additional small denticles (Figure 40). Lateral teeth with distinctive shape, with single large, recurved outer cusp emanating from long, narrow basal plate. Inner surface of cusp with 1 or more, occasionally bifid, posteriorly directed denticles, with number, size of denticles varying from side to side and along radular ribbon.

Right salivary gland medium-sized, rounded, partially covering valve of Leiblein (Figures 43, 44, rsg), laterodorsal to nerve ring. Left salivary gland slightly smaller than right, irregularly shaped, dorsal to nerve ring, ventral to proboscis with its main axis perpendicular to proboscis axis, appears small when viewed from left (Figure 45, lsg). Salivary ducts (Figures 44, 46, sd) short, thick, enter oesophagus wall shortly after leaving gland. Valve of Leiblein (Figure 46, vL) well defined, large, pyriform, with whitish glandular pad visible through walls of valve.

Gland of Leiblein (Figures 43–45, gL) yellowish, slightly darker than other organs of cephalic haemocoel, medium sized, long, tubular, coiled anteriorly. Gland thin-walled, ascinous anteriorly (Figure 46, agL), opens into oesophagus slightly posterior to nerve ring via broad, short duct (Figure 46, dgL), becomes thinner, more transparent posteriorly (Figure 46, pgL), tapering to become flaccid, non-glandular (Figure 46, vgL).

Oesophagus thick, broad anterior to nerve ring, narrowing slightly posterior to the ring. Posterior oesophagus expands greatly to form "crop," (Figure 47, poe) then gradually narrows towards opening into stomach. Stomach (Figure 47) very large, spans ~½ whorl, from the posterior border of nephridium, U-shaped, without posterior mixing area. Preservation inadequate to discern internal morphology. Digestive glands ducts (Figure 47, ddg) large, paired, closely spaced. Posterior duct close to oesophagus entrance, anterior duct at mid-length of stomach. Digestive glands clearly separate. Anterior gland small (Figure 41, adg), spans ~½ whorl, posterior gland ~2 whorls (Figures 41, 42, pdg). Glands meet at the level of the posterior duct to digestive gland. Rectum long, spans ~4/5 of mantle cavity length. Rectum thin-walled, very broad, filled with polychaete spicules, numerous sand grains of different sizes.

Female Reproductive System: Paratype 1, mature female. Pallial gonoduct consists of long, tubular, capsule gland (Figures 42, 48, cg), with a small bursa copulatrix anterior to it. Genital opening (Figure 48, go) below, slightly posterior to anus (Figure 48, a).

Male Reproductive System: Paratype 2, male. Penis (Figure 49) long, very narrow, flattened laterally. Seminal papilla very small, blunt, surrounded by deep circular fold around its base.

Type Locality: NE of South Shetland Islands, 59°01′ S, 52°00′ W, in 3010–3510 m. [R/V ELTANIN cruise 22, Sta. 1511, 26 Jan 1966].

Type Material: Holotype, USNM 1010544, from the type locality. Paratype 1♀, Paratype 2 ♂, USNM 881529, E of South Sandwich Islands, 57°00.24′ S, 26°10.06′ W, in 2740–2757 m. [R/V ELTANIN cruise 575, Sta. 38, 22 May 1975].

Other Material Examined: USNM 1010545, South Atlantic Ocean [Argentine Abyssal Plain], 47°17.3′ S, 47°45.7′ W, in 5685–5798 m. [R/V ISLAS ORCADAS Cruise 575, Sta. 4, 8 May 1975], 2 bodies without shells (radula illustrated, Figures 38–40); USNM 1010546, Scotia Sea, S of South Georgia Island, 58°04′ S, 37°50′ W, 3255–3166 m. [R/V ELTANIN cruise 9, sta. 699, 30 Aug 1963], 1 dead poorly preserved juvenile. USNM 1013084, Scotia Sea, SW of South Georgia Island, 55°56′ S, 44°56′ W, 3742–3614 m. [R/V ELTANIN cruise 575, Sta. 472, 13 Feb 1963], 1 body and fragments of the shell.

Distribution (Figure 50): This species occurs in the Scotia Sea and adjacent Argentine Abyssal Plain, at depths of 2740–5798 m.

Etymology: This species is named in honor of the junior author's wife, Tatyana Steiker, an ichthyologist and illustrator at the P. P. Shirsov Institute of Oceanology.

Remarks: The large, elongate, fusiform, siphonate,

spirally corded shell of *Drepanodontus tatyanae* easily distinguishes this species from most Antarctic buccinoideans. Conchological similarity is limited to relatively few large taxa, notably *Antarctoneptunea aurora* (Hedley, 1912) and *Cavineptunea monstrosa* Powell, 1951, both members of continental shelf and upper slope faunas. *Drepanodontus tatyanae* is most easily distinguished from the former by having a distinctive peripheral spiral cord that demarcates a change in the direction of curvature in the outer lip, while the monotypic *Cavineptunea* is most easily distinguished by its unique, cylindrical, flat-sided, indented protoconch. Both *Antarctoneptunea* (Dell, 1972: fig. 6) and *Cavineptunea* (Powell, 1951: 145) have radulae with tricuspid rachidian teeth and lateral teeth with 3 (or 4) cusps, quite unlike the distinctive radula of *Drepanodontus*.

The radula of *Drepanodontus tatyanae* most closely resembles that of *Kapala bathybius* Bouchet and Warén, 1986 (Bouchet and Warén, 1986: fig. 8), a species inhabiting the Cape Basin off southwestern Africa at depths of 3550 m. Like *Drepanodontus*, *K. bathybius* has rachidian teeth that may appear to be monocuspid in some individuals, with anteriorly indented, squarish basal plates, and lateral teeth characterized by a single, large, sickle-like cusp with secondary denticles that vary in number and prominence from side to side and from tooth to tooth. The shell of *K. bathybius*, and the related *K. bonaespei* (Barnard, 1963), also from the Cape Basin in 2504–3103 m, are comparable in size, and also elongate, fusiform and spirally corded, but broader (Bouchet and Warén, 1986: figs. 42, 43), and lack the distinctive peripheral cord of *Drepanodontus*. Barnard (1963: 432, fig. 6b) illustrates and describes the radula of *K. bonaespei* (which he described as a *Neptunea*) to have rectangular rachidian teeth with a "median cusp, sometimes a minute denticle on one side or on both sides" and lateral teeth "unequally bicuspid, with 2–5 tiny denticles between the two cusps, the denticles not always symmetrical."

Barnard (1963) assigned this species to the genus *Neptunea* Röding, 1798, because of the similarity of its lateral teeth with those of boreal buccinoideans, despite striking differences in the morphology of the shell and rachidian teeth. Bouchet and Warén, (1986: 464) also commented on lateral tooth similarities of *Kapala* (including its type species, the southern Australian bathyal species *K. kengrahami* Ponder, 1982) with the type species of the boreal genera *Volutopsius* Mörch, 1857, *Neoberingius* Habe and Ito, 1965, *Ancistrolepis* Dall, 1895, and certain representatives of *Japelion* Dall, 1918. These boreal taxa have elongated, spatulate lateral teeth with a large outer cusp, a significantly smaller inner cusp, and a variable number of smaller denticles or cusps between them. We interpret the lateral teeth of *Drepanodontus* to be different, in that they have a single, large outer cusp, but lack the shorter inner cusp of the boreal taxa. While some of the denticles that frequently emerge from the inner edge of the cusp of *Drepanodontus* may be large enough to be confused with an inner cusp, the

lateral teeth of the boreal species are fundamentally bicuspid, while those of *Drepanodontus* are fundamentally monocuspid. Interestingly, the radula of *K. bathybius* illustrated by Bouchet and Warén (1986: fig. 8) has monocuspid lateral teeth lacking denticles distally, but developing denticles proximally along the left side of the radula, while the lateral teeth on the right side have 1 large and 1–3 smaller denticles along the inner edge of the single cusp.

The operculum of *Drepanodontus* is large, ovate, and has a terminal nucleus. While all species of *Kapala* share this opercular morphology, it is not distinctive, but widespread throughout Buccinoidea.

Although the presence of large eyes is not surprising in the bathyal type species of *Kapala* (Ponder, 1982: fig. 2), their occurrence in the abyssal taxa *K. bonaespei* (Barnard, 1963: 432) and *Drepanodontus tatyanae* is noteworthy. Other anatomical features that are congruent between *Drepanodontus tatyanae* and *Kapala kengrahami* include a small buccal mass and odontophore, a large kidney, a large, well-developed valve of Leiblein, crop, and a simple stomach.

Drepanodontus tatyanae co-occurs with *Muffinbuccinum catherinae* at the type locality of that species.

Subfamily Prosiphiinae Powell, 1951
Muffinbuccinum new genus

Type Species: *Muffinbuccinum catherinae* new species, by original designation.

Description: Protoconch, early whorls eroded. Teleoconch of moderate size (to ~30 mm) very thin, chalky, with evenly rounded whorls, tapering anterior, short, broad siphonal canal. Sculpture of sharp, narrow axial ribs, crossing uniform, closely spaced spiral cords, occasionally forming finely reticulate surface sculpture. Aperture large, elongate, elliptical. Parietal region broader posteriorly. Columella short, not axial. Periostracum of very fine axial lamellae, not hirsute. Operculum, large (~0.56 aperture length), elongated, claw-like, with terminal nucleus and growth lines nearly perpendicular to long axis. Head large, with tapering tentacles lacking eyes. Columellar muscle short. Nephridium very narrow. Rachidian teeth broadly rectangular, with 3 cusps concentrated near center of tooth, central cusp longest. Lateral teeth as broad as rachidian tooth, roughly rectangular in outline, with 7–8 cusps of nearly equal length, outermost cusp, slightly shorter, stouter, weakly to strongly serrated along outer margin. Salivary glands large, fused ventrally. Gland of Leiblein long, narrowly tubular, highly coiled. Oesophagus muscular, does not widen before opening into stomach. Stomach very small, broadly U-shaped, lacks posterior mixing area. Rectum short, narrow, with terminal papilla.

Etymology: This genus is named after Muffin, a domestic shorthair cat that belongs to the senior author's daughter Catherine.

Muffinbuccinum catherinae new species
(Figures 51–76, Table 3)

Description: Shell (Figures 51–56) of moderate size (to 26.6 mm), very thin, chalky, ovate, with tapering anterior, eroded spire. Protoconch and upper whorls eroded on all available specimens, with no more than last 2½ whorls remaining. Extrapolation suggests that un-eroded specimens might reach 32 mm, with 5–6 teleoconch whorls. Whorls evenly rounded, with indistinct shoulder, abutting suture. Axial sculpture of fine, sigmoidal, weakly prosocline growth lines, narrower than spiral cords, varying in prominence, producing reticulate pattern in some areas of the shell, especially on penultimate whorl (Figures 51, 52, arrows). Spiral sculpture of fine, sharp, uniform, evenly spaced cords (43–50 on final whorl, 18–21 on penultimate whorl), weaker, more broadly spaced between suture and shoulder as well as near siphon. Aperture large (AL/SL = 0.64–0.71 when using length of eroded shell; AL/SL = 0.54–0.60 as estimated by linear projection of apex), elongate, ovate, tapering anteriorly, deflected from shell axis by 17–18°. Outer lip very thin, not reflected, evenly round from suture to siphonal notch. Inner lip of broad parietal region, shorter, non-axial columellar region, long siphonal fold and short, broad, axial siphonal canal. Parietal callus consisting of thin glaze, slightly broader posteriorly, narrower or indented near siphonal fold, may form barely perceptible pseudo-umbilicus-like indentation. Shell color uniformly white. Periostracum of very thin axial blades, straw yellow in color. Operculum (Figures 57–58) large, spanning ~0.56 AL, translucent amber yellow in color, with distinctive, claw-like shape, tapering toward nucleus, which is eroded. Outer surface with numerous growth lines nearly perpendicular to long axis. Inner surface with outer rim slightly thickened, glazed, except for long, narrow, triangular attachment area.
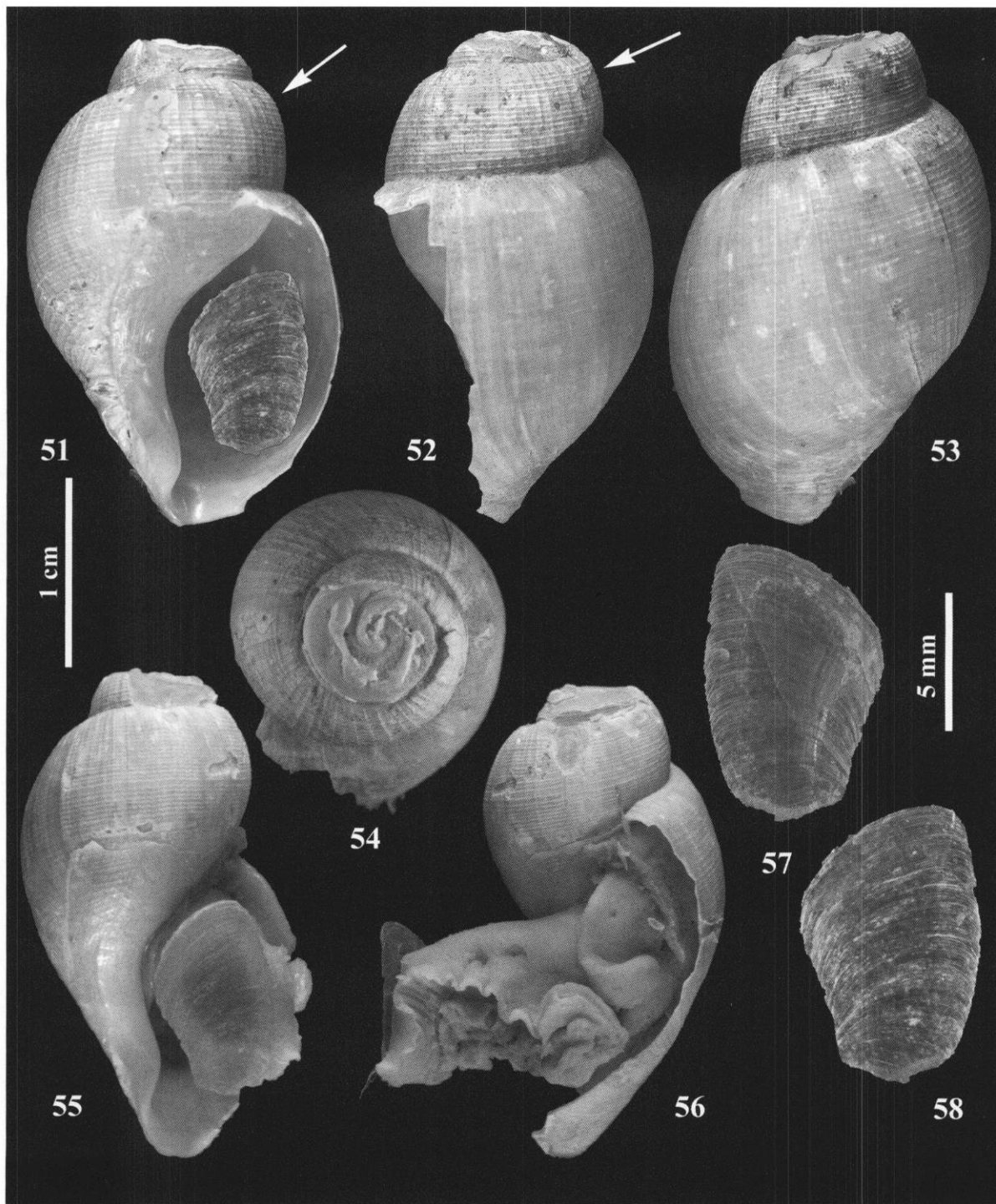
Anatomy (Holotype): Body (Figures 65–66) comprises approximately 2½ whorls. Mantle cavity spans ~⅓ whorl, mantle edge thin, does not cover head or penis base. Nephridium very narrow (Figure 65, nep), spans <1/6 whorl, brown-grey. Border between mantle cavity and nephridium marked by deep cleft. Digestive gland (Figures 65, 66, dg) spans 1½ whorl, overlain by testis. Columellar muscle very short, spanning <1 whorl, broad, attached to shell anterior at rear of mantle cavity. Foot large, narrowly oval (L/W ~2.3 for holotype, up to 2.8 in other specimens), not folded during fixation. Body light yellowish, without pigmentation. Head large, with broad, tapering cylindrical tentacles (Figure 65, 66, tn) lacking eyes.

Mantle Cavity (Figure 67): Mantle cavity short, broad (L/W ~0.63). Siphon very short, thin, weakly muscular, extending slightly beyond mantle edge. Osphradium (Figure 67, os) greenish, bipectinate, with broadly curved axis, spanning < 0.4 mantle cavity length. Ctenidium (Figure 67, ct) large, narrower than osphradium, strongly curved, spanning ⅔ mantle cavity length.
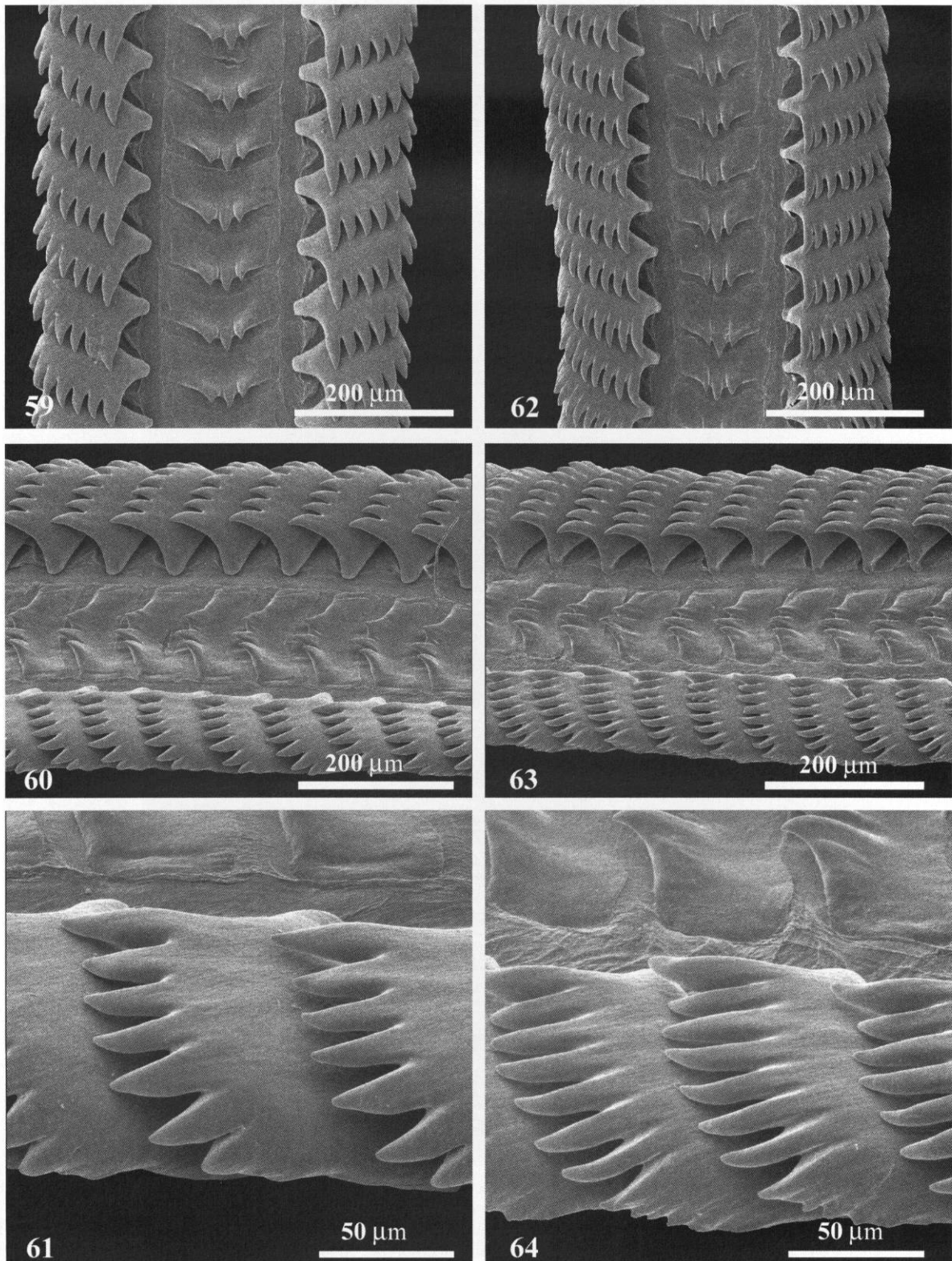
Hypobranchial gland formed of numerous, indistinct, closely spaced oblique folds covered by thick layer of mucus that partly overlays the rectum.

Alimentary System (Figures 70–75): Proboscis (Figure 71, pr) short (~0.46 AL in holotype), thick, smooth-walled, non-pigmented, not coiled, occupies entire cephalic haemocoel. Proboscis sheath extremely thin-walled, anterior half translucent, thicker posteriorly, but <½ thickness of proboscis wall. Mouth opening (Figure 73) rounded, lumen of buccal tube triangular immediately posterior to mouth. Buccal mass muscular, medium-sized, slightly shorter than retracted proboscis. Odontophoral cartilages paired, fused anteriorly, spanning nearly entire length of buccal mass. Radular ribbon slightly longer than cartilages (~0.30 AL in holotype), ~480 μm wide (holotype), triserial (Figures 59–64), consisting of about 70 (holotype) to 85 (paratype 1) rows of teeth, posteriormost 5 teeth nascent. Oldest several rows of teeth with dark brown pigment that faded when radula cleaned with bleach (NaOCl). Rachidian teeth with broad, rectangular, slightly arched base with straight lateral sides, 3 large, robust, closely spaced cusps. Central cusp slightly longer than lateral cusps. Lateral teeth as broad as rachidian teeth, roughly rectangular, with 7–8 cusps nearly equal in length, outermost cusp shortest, stouter than others, weakly (Figure 61) to strongly (Figure 64) serrated along outer margin. Salivary glands (Figures 70–72, sg) large in comparison to proboscis, acinous, yellowish, fused ventrally, dorsal to oesophagus. Right salivary gland covers valve of Leiblein (Figure 70, vL), part of nerve ring and anterior of proboscis. Left salivary gland shifted posteriorly. Salivary glands tightly attached to proboscis sheath by connective tissue. Salivary ducts (Figures 70, 72, sd) thick, free along both sides of oesophagus, becoming embedded in oesophagus walls shortly after entering retracted proboscis. Valve of Leiblein (Figures 70, 72, 74, vL) well defined, large, pyriform, with ciliary cone, yellow, slightly darker than other organs of cephalic haemocoel. Gland of Leiblein (Figures 70–72, 74, gL) long, dark grey, narrowly tubular, glandular, highly coiled, covered by connective tissue sheath, opens into middle oesophagus posterior to nerve ring via short, narrow duct (Figure 74, dgL). Oesophagus muscular, nearly constant in diameter along most of its length, does not widen before opening into stomach. Stomach (Figure 75) very small, broadly U-shaped, lacks posterior mixing area. Preservation was inadequate to document internal morphology of stomach. Rectum (Figure 67, re) short, narrow, thin-walled, with terminal papilla, spans slightly more than half the length of mantle cavity.
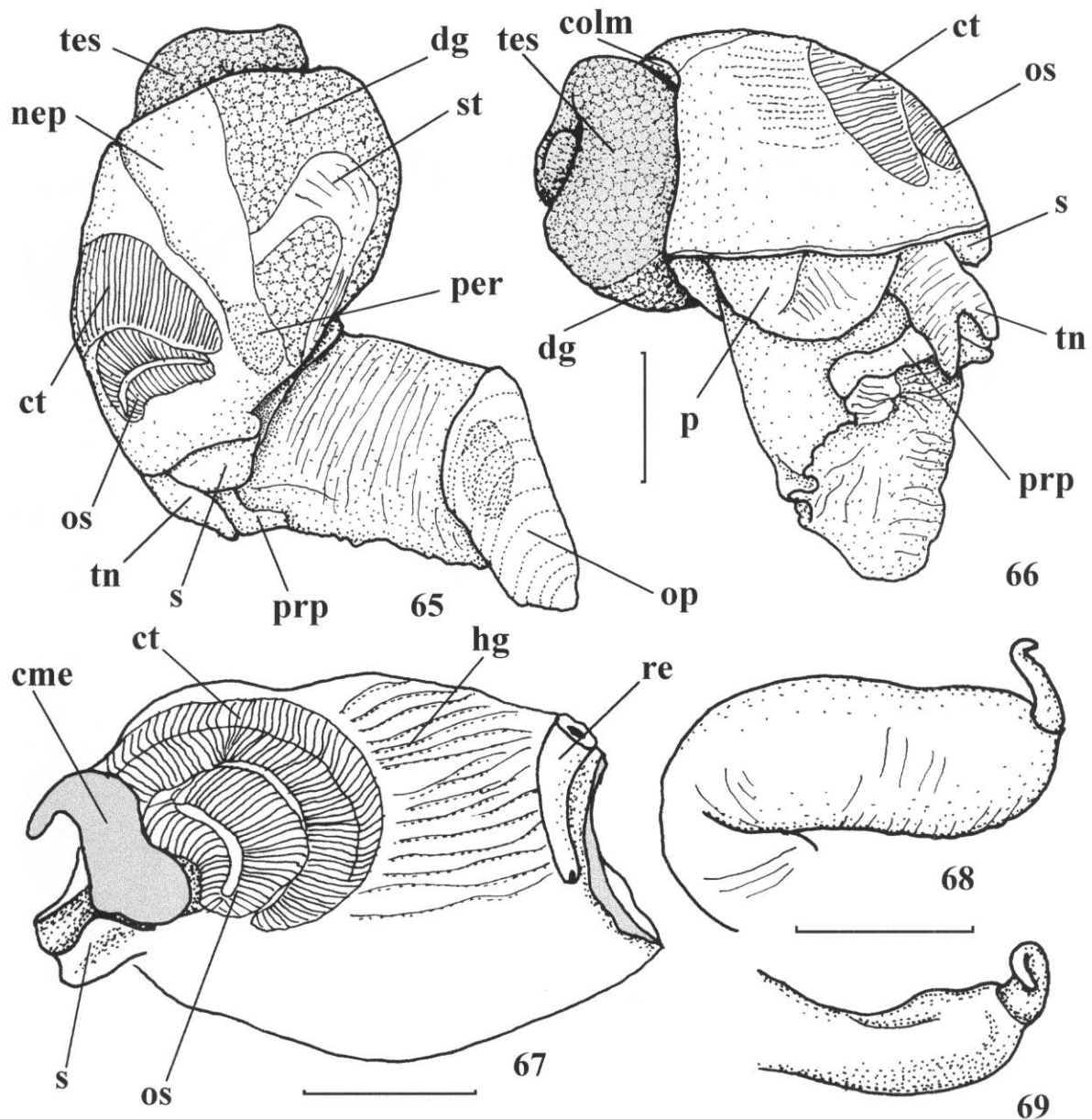
Male Reproductive System: Holotype, Paratypes 1 and 2, males. Testis large, anterior margin at posterior-most part of stomach extends posteriorly along digestive gland for 1½ whorls. Testis similar in color and texture to digestive gland. Seminal vesicle small, formed of very few loops. Penis (Figures 66, p; 68, 69) non-pigmented, spans entire length of mantle cavity, flattened in middle

Figures 51–58. Shells and operculum of *Muffinbuccinum catherinae* new species. **51.** Apertural, **52.** lateral, **53.** dorsal, and **54.** apical views of the holotype, USNM 1010623, South Atlantic Ocean [Argentine Abyssal Plain], 47°17.3′ S, 47°45.7′ W, in 5685–5798 m [R/V ISLAS ORCADAS Cruise 575, Sta. 4]. **55.** Apertural, and **56.** lateral views of the shell of Paratype 1, USNM 1010624, from the type locality. **57.** Inner, and **58.** outer views of operculum of holotype. Arrows indicate regions of finely reticulate surface sculpture.

Figures 59–64. Radulae of *Muffinbuccinum catherinae* new species. **59–61.** Paratype 1. **62–64.** Holotype. **59, 62.** Dorsal, and **60, 63.** right lateral (45°) views of the central portion of the radular ribbon. **61, 64.** Enlarged right lateral views of lateral teeth showing the denticles along the outer cusp.

Figures 65–69. Anatomy of *Muffinbuccinum catherinae* new species, holotype. **65.** Left, and **66.** right lateral views of animal removed from shell. **67.** Mantle cavity organs. **68.** Dorsal, and **69.** right lateral views of the penis. Scale bars = 5 mm. **cme,** cut mantle edge; **colm,** columellar muscle; **ct,** ctenidium; **dg,** digestive gland; **hg,** hypobranchial gland; **nep,** nephridium; **op,** operculum; **os,** osphradium; **p,** penis; **per,** pericardium; **prp,** propodium; **re,** rectum; **s,** siphon; **st,** stomach; **tes,** testis; **tn,** cephalic tentacles.

part, widens anteriorly. Long, cylindrical papilla at distal end of penis surrounded by circular fold around its base.

Type Locality: South Atlantic Ocean [Argentine Abyssal Plain], 47°17.3′ S, 47°45.7′ W, in 5685–5798 m. [R/V ISLAS ORCADAS Cruise 575, Sta. 4, 8 May 1975].

Type Material: Holotype, ♂, USNM 1010623; Paratype 1, ♂, shell partially broken, Paratype 2, ♂, shell fragmented, USNM 1010624, all from the type locality.
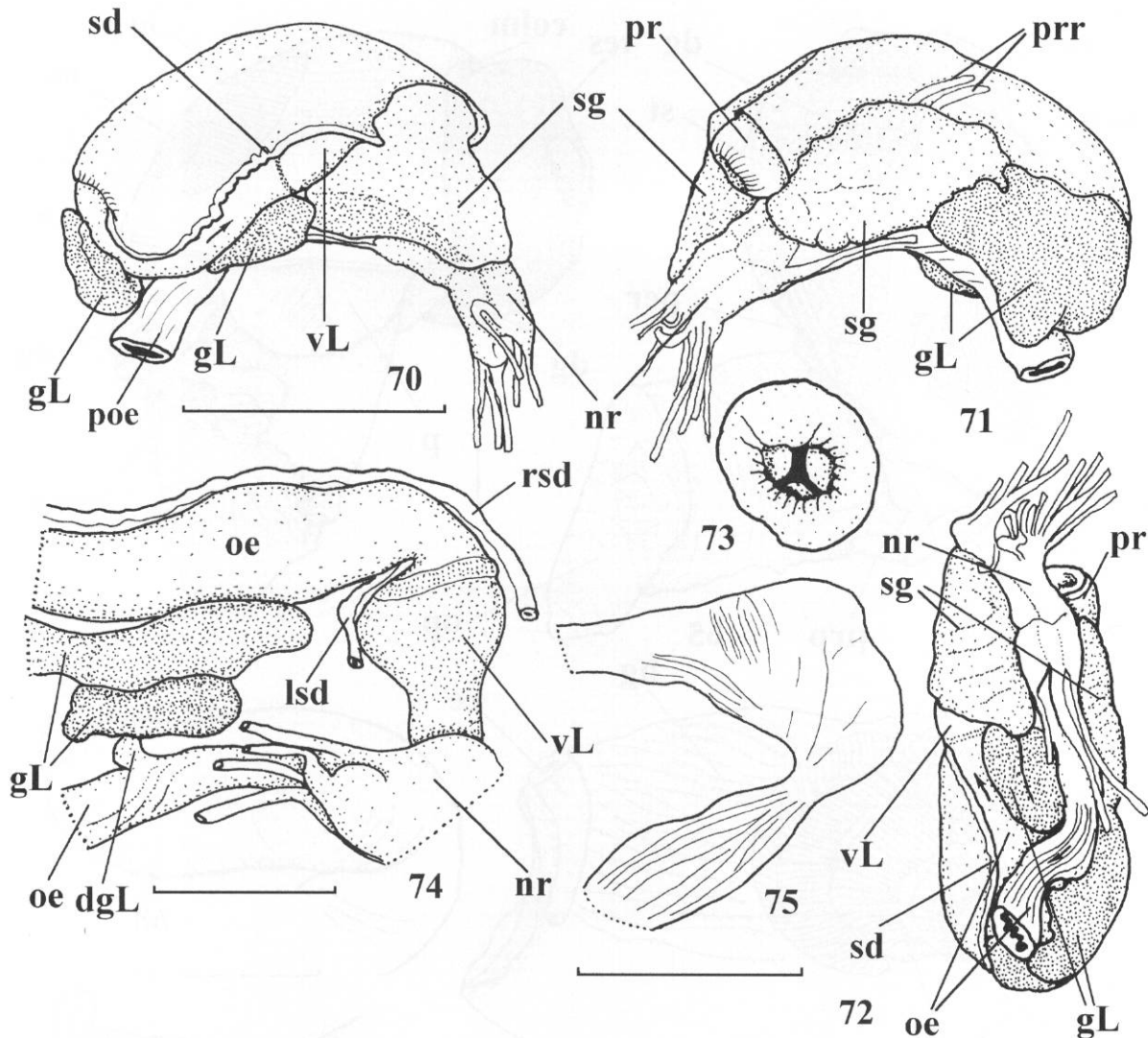
Other Material Examined: USNM 1010625, fragments and soft tissues of 3 specimens from the type

locality. One was dissected to illustrate the anatomy of the anterior foregut.

Distribution (Figure 76): This species is known only from the type locality, the Argentine Abyssal Plain, off the northern slope of the Falkland Plateau, at depths of 5685–5798 m.

Etymology: This species is named for the senior author's younger daughter, Catherine Laura Harasewych.

Remarks: Of the Antarctic buccinoideans, this new species appears conchologically most similar to *Spike-*

Figures 70–75. Digestive system of *Muffinbuccinum catherinae* new species. **70–74.** Female specimen without a shell, USNM 1010625. **75.** Holotype. **70.** Left lateral, **71.** right lateral, and **72.** ventral views of anterior alimentary system. **73.** Anterior view of the proboscis tip. **74.** Right lateral view of the anterior oesophagus showing the opening of the duct of gland of Leiblein and valve of Leiblein. Salivary glands removed. **75.** Dorsal view of stomach. Scale bars = 5 mm for Figures 70–73, 75, and 2 mm for Figure 74. **dgL,** duct of gland of Leiblein; **gL,** gland of Leiblein; **lsd,** duct of left salivary gland; **nr,** circumoesophageal nerve ring; **oe,** oesophagus; **poe,** posterior oesophagus; **pr,** proboscis; **prr,** proboscis retractors; **rsd,** duct of right salivary gland; **sd,** salivary duct; **sg,** salivary gland; **vL,** valve of Leiblein.

buccinum stephaniae and, to a lesser extent, to *Chlanidota (Pfefferia) invenusta.* It differs from both in having a more elongated shell, with a long siphonal fold and a short, broad, anteriorly rounded siphonal canal. The surface sculpture of *Muffinbuccinum catherinae* is finer, and the occasional, weak reticulate sculpture of *Muffinbuccinum* is absent in *Spikebuccinum* and *Chlanidota.*

The distinctive radular morphology of *Muffinbuccinum catherinae,* with its broad, tricuspid rachidian and pectinate lateral teeth, readily distinguishes this species from other buccinoidean taxa. Based on the morphology of the radula, *Muffinbuccinum catherinae* appears to be related to *Proneptunea* Thiele, 1912 (Thiele, 1904, pl. 9, fig. 58; Powell, 1951, fig. K 66–67), a circumantarctic

genus that occurs from sublittoral (*Proneptunea fenestrata* Powell, 1951, 17–27 m) to bathyal (*Proneptunea rossiana* Dell, 1990, 369–870 m) depths. *Muffinbuccinum* and *Proneptunea* both have tricuspid rachidian teeth and multicuspid lateral teeth that may bear serrations along their outer edge. However, the rachidian teeth of *Muffinbuccinum* are as broad as the lateral teeth, shorter than wide, and have the cusps concentrated in the middle portion of the tooth, while the rachidian teeth of species of *Proneptunea* are narrower, with the three cusps spanning much or their width. The longest and most prominent of the 7–8 cusps on the lateral teeth of *Muffinbuccinum* is the innermost cusp, while the largest and most prominent of the 5 cusps on the lateral teeth
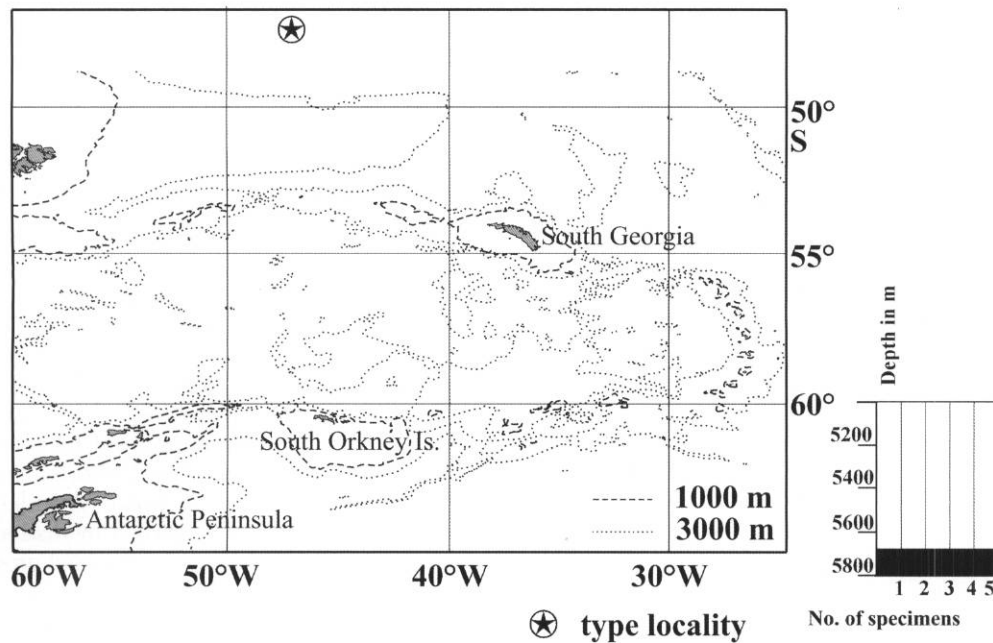
Figure 76. Geographic and bathymetric distribution of *Muffinbuccinum catherinae* new species.

of the 3 (of 6) species of *Proneptunea* for which the radular morphology is known, is invariably the outermost cusp. Based on the presence of a tricuspid rachidian and multicuspid lateral teeth serrated along their outer edge in *Muffinbuccinum*, and their overall resemblance to the radulae of *Proneptunea*, we include *Muffinbuccinum* in the subfamily Prosiphiinae.

Similarities also exist between *Muffinbuccinum catherinae* and several bathyal, abyssal, and hadal buccinoideans of uncertain affinities, notably *Calliloncha* Lus, 1978, *Costaria* Golikov, 1977, *Thalassoplanes* Dall, 1908, and *Troschelia* Mörch, 1876. The radula of *Calliloncha* [as *Calliloconcha*] *knudseni* Bouchet and Warén, 1986 (Bouchet and Warén, 1986: fig. 1), a species from the Kermadec Trench (in 5480 m) resembles that of *Muffinbuccinum catherinae* in having a tricuspid rachidian tooth that is nearly as broad as the lateral teeth, and lateral teeth with 5 cusps of equal length, but lacking

serrations along their outer margin. Bouchet and Warén (1986:484) noted similarities in the radulae of *Bayerius* Olsson, 1971 [Olsson, 1971: fig. 101 for *B. fragilissimus* (Dall, 1908) (type species), and Warén and Bouchet, 2001: figs. 39b,c) for *B. arnoldi* (Lus, 1981) and *B. peruvianus* Warén and Bouchet, 2001, respectively] and *Calliloncha* Lus, 1978 [Lus, 1978: figs. 2 (7–10) for *C. solida* Lus, 1978 (type species), and Lus, 1989: figs. 5 (1–2) for *C. iturupi* Lus, 1989], and speculated that these genera may prove to be synonyms. However, the type species of *Calliloncha*, which dwells in the Izu-Bonin Trench (6770 m), *C. iturupi*, from the Kurile-Kamchatka Trench (8240 m), *Bayerius fragillisimus* (Dall, 1908), known from off Panama and Ecuador (2877–3200 m), *B. arnoldi*, from the Japan, Kuril, and Aleutian Trenches (4800–6135 m), and *B. peruvianus* from 5385–5996 m off Peru all share tricuspid lateral teeth that differ in dentition and proportion from those of *Calli-*

Table 3. *Muffinbuccinum catherinae* new species. Measurements of shell characters of Holotype and Paratype 1. Paratype 2, fragmented. Linear measurements in mm.

Character	Holotype	Paratype 1
Shell length (SL)	26.4	26.6
Final whorl length (FWL)	24.6	23.7
Aperture length (AL)	19.1	20.8
Siphonal canal length (SCL)	2.4	3.6
Shell width (SW)	16.3	15.6
FWL/SL	0.93	0.89
AL/SL	0.72	0.78
SCL/SL	0.09	0.14
SW/SL	0.62	0.59
Number of spiral cords on penultimate whorl	18	21
Number of spiral cords on final whorl	43	50

loncha knudseni. While *Calliloncha* may prove to be a synonym of *Bayerius*, it seems unlikely that *C. knudseni* is referable to this genus. The radulae of *Costaria* (Bouchet and Warén, 1986: fig. 6), *Thalassoplanes* (Bouchet and Warén, 1986: fig. 5) and *Troschelia* (Bouchet and Warén, 1985: figs. 484–485) all have lateral teeth that are roughly rectangular and multicuspid. However, these three genera have rachidian teeth that are very narrow. In *Costaria* and *Thalassoplanes* the central of three cusps may be reduced or absent, while in *Troschelia* the flanking cusps are absent, resulting in monocuspid rachidian teeth.

The operculum of *Muffinbuccinum catherinae* is rather distinctive in being claw-shaped, with growth lines nearly perpendicular to the long axis, and a long, narrow, triangular attachment area along its inner surface. A survey of the literature shows that this operculum type also occurs in *Proneptunea fenestrata* (Powell, 1951: fig. N124), as well as in *Thalassoplanes moerchi* (Bouchet and Warén, 1986: fig. 25), *Calliloncha knudseni* (Bouchet and Warén, 1986: fig. 32), but not *C. solida,* the type of the genus, (Lus, 1978: fig. 2, 4–5) both from the abyssal to hadal zones of the Pacific Ocean, and in *Liomesus ovum* (Turton, 1825) (Bouchet and Warén, 1985: fig. 440) a North Atlantic species inhabiting outer continental shelf depths. *Muffinbuccinum catherinae* co-occurs with *Drepanodontus tatyanae* new genus, new species (see above).

Germonea new genus

Type Species: *Germonea rachelae* new species, by original designation.

Description: Protoconch large (to 4.4 mm), of ~2⅓ whorls, first 2 whorls smooth, rounded, followed by onset broad, rounded spiral cords. Transition to teleoconch distinct, marked by axial indentation, change in shell color. Teleoconch large (to 67.8 mm), of up to 5 smooth, evenly ovate whorls, with indistinct shoulder, abutting suture. Axial sculpture of fine growth lines, irregular rugae near suture. Spiral sculpture of closely spaced cords. Aperture large, narrowly elliptical, with short, broad, siphonal canal. Outer lip may be slightly reflected, thickened along margin. Inner lip with glossy parietal callus, long columella, siphonal fold. Neither siphonal fasciole, nor pseudoumbilicus present. Periostracum thin, tightly adherent. Operculum large (~0.65 AL), long, narrow, with terminal nucleus at end of strongly curved anterior margin. Columellar muscle very short (~½ whorl). Foot with deep propodial cleft. Head large, with short neck, large black eyes at base of broad, tapering tentacles. Buccal mass large, filling proboscis. Odontophore shorter, radula longer than buccal mass. Rachidian teeth long, narrow (L/W ~2.5), Y-shaped, with 3 stout, radially oriented cusps, central cusp longest. Lateral teeth with 3–4 cusps of similar length along innermost ⅔ of basal plate. Salivary glands large, right larger than left. Gland
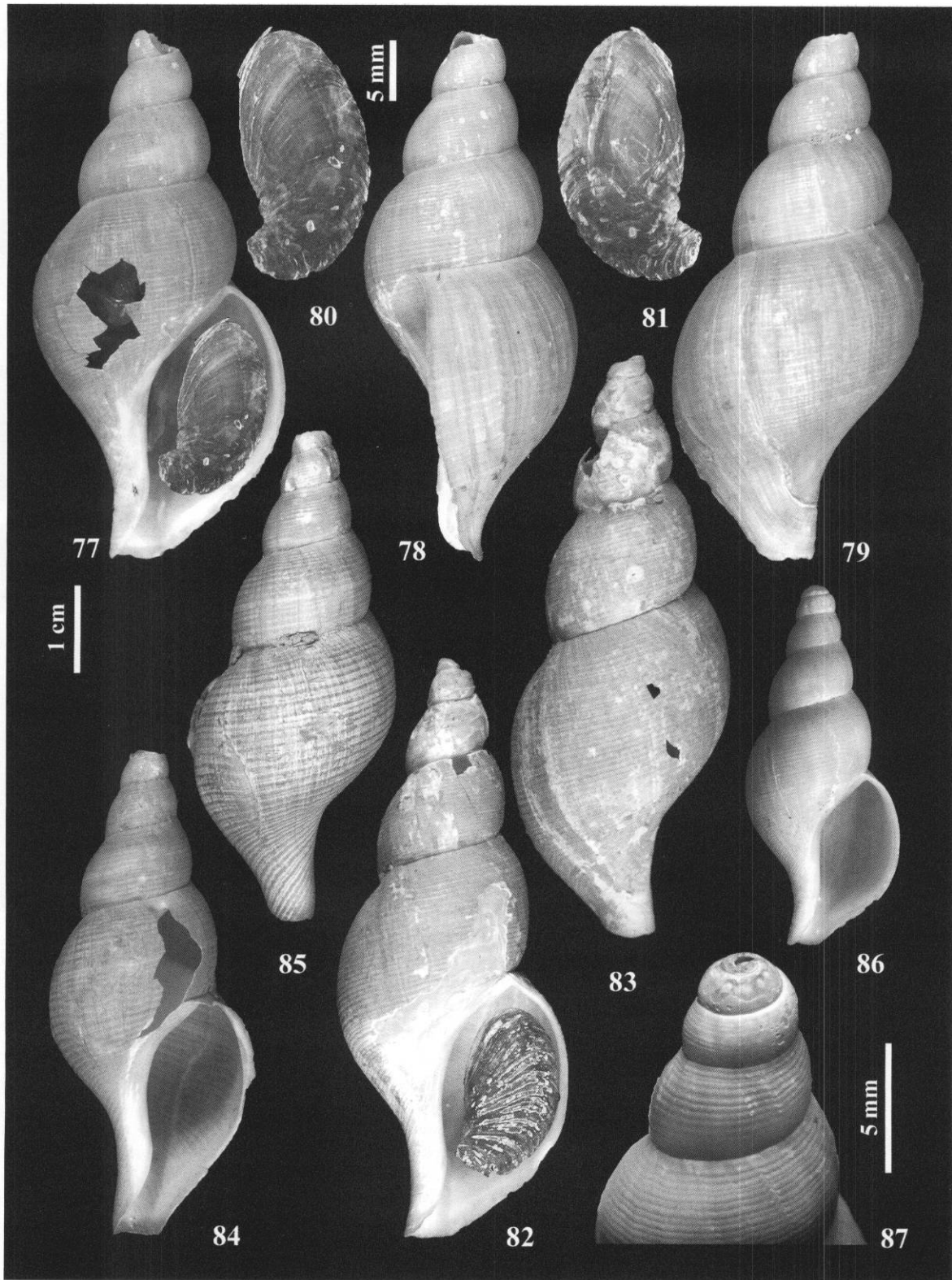
of Leiblein large, ascinous. Oesophagus thick, broad. Stomach U-shaped, lacking posterior mixing area.

Etymology: The genus is named after Mrs. Rachel (Raye) N. Germon, in recognition of her years of work in managing the collections of Antarctic Mollusca at the National Museum of Natural History, Smithsonian Institution.
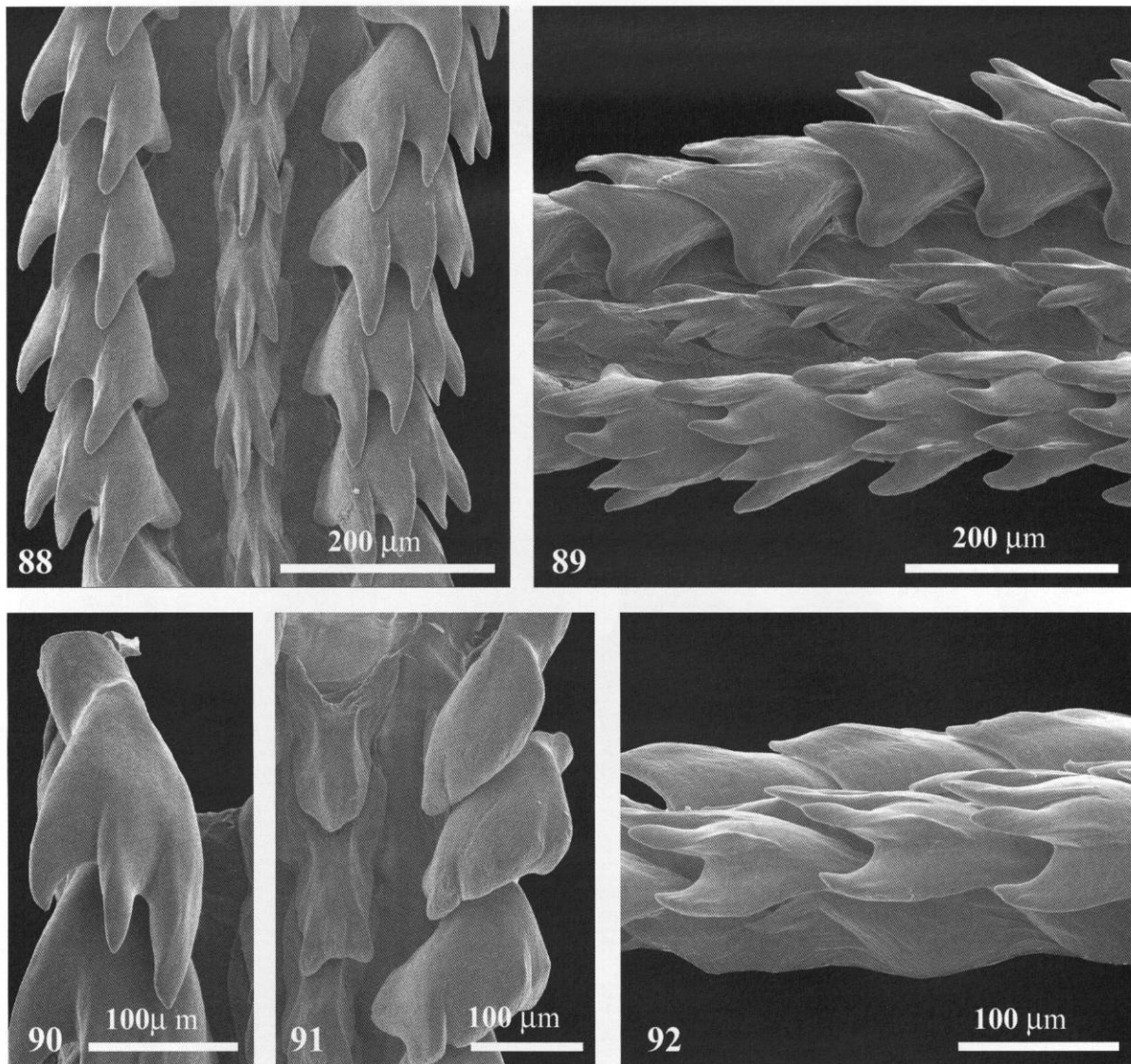
Germonea rachelae new species
(Figures 77–98, Table 4)

Description: Shell (Figures 77–79, 82–86) large (to 67.8 mm), thin to moderately thick, fusiform. Protoconch (Figure 87) increasing from 1.1 mm to 4.4 mm in diameter in ~2⅓ whorls, first 2 whorls smooth, rounded, followed by onset of weak, broad, rounded spiral cords. Transition to teleoconch marked by distinct axial indentation, change in shell color, with axial growth lines, spiral cords markedly more prominent. Teleoconch of up to 5 smooth, evenly ovate whorls, with indistinct shoulder, abutting suture. Axial sculpture limited to fine, straight, weakly prosocline growth lines, some more pronounced, giving rise to irregularly spaced, weak surface rugae near suture. Spiral sculpture of numerous (18–30 on penultimate whorl; 48–81 on last whorl), closely spaced cords, broader than intervening spaces. Finer threads may occur between adjacent cords, especially along anterior portion of final whorl. Aperture large (AL/SL = 0.49–0.57), narrowly elliptical, deflected from shell axis by 14–17°. Siphonal canal short (~¼ aperture length), broad, open, crosses shell axis. Outer lip may be slightly reflected, weakly thickened along margin, evenly rounded from suture to base of siphonal canal. Inner lip of short, weakly convex parietal region, long, slightly concave columella, long siphonal fold extending beyond narrow glossy parietal callus. Neither siphonal fasciole, nor pseudoumbilicus present. Protoconch ivory colored, teleoconch uniformly white, aperture, parietal callus glossy. Periostracum amber yellow to brown, tightly adherent to shell. Operculum (Figures 80, 81) large (~0.65 AL), translucent yellow to amber in color, long, narrow, with terminal nucleus at end of strongly curved anterior margin. Outer surface of operculum with fine, regular growth lines. Inner surface with small, oval attachment area along posterior, adaxial region, broad, strongly thickened, heavily glazed free outer and anterior margins.

Anatomy (Holotype): Based on rehydrated animal, soft tissues (lacking upper part of kidney, digestive gland) comprise approximately 1½ whorl. Mantle cavity spans <⅓ whorl, mantle edge thick, does not cover head or base of penis. Columellar muscle very short, comprising ~½ whorl. Foot of medium size, strongly contracted, broadly oval (L/W ~1.4), with narrow propodium separated by deep propodial cleft. Body yellowish tan, non-pigmented. Head large, with short neck, broad, tapering tentacles, large black eyes at base of tentacles.

Figures 77–87. Shells and opercula of *Germonea rachelae* new species. **77.** Apertural, **78.** Lateral, and **79.** dorsal views of the holotype, USNM 896594, off South Georgia Island, 58°02′ S, 37°57′ W, in 3197–3239 m [R/V ELTANIN cruise 9, sta. 698]. **80.** Outer and **81.** Inner views of the operculum of the holotype. **82.** Apertural and **83.** Dorsal views of paratype 1, USNM 1010620, N of South Orkney Islands, 58°06′ S, 44°56′ W, in 2800 m [R/V ELTANIN, cruise 7, sta. 480]. **84.** Apertural and **85.** dorsal views of paratype 2, USNM 898828, off South Georgia Island, 55°02′ S, 44°21′ W, in 3623–3714 m [R/V ELTANIN cruise 7, sta. 469]. **86.** Apertural and **87.** apical views of paratype 3, USNM 1010621, off South Georgia Island, 54°59′ S, 38°13′ W, in 2379–2196 m [R/V ELTANIN, cruise 9, sta. 686].
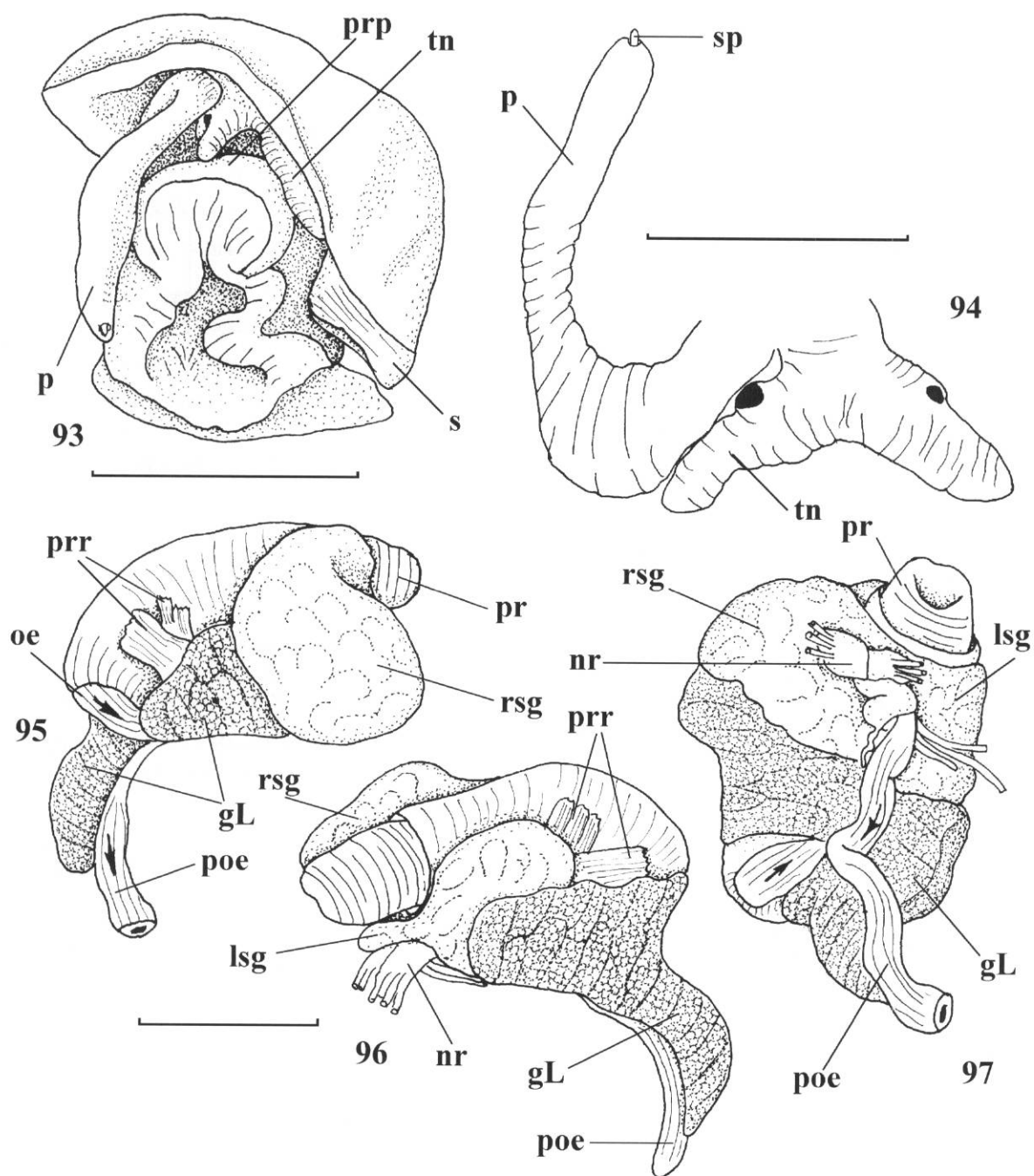
Figures 88–92. Radula of holotype of *Germonea rachelae* new species. **88.** Dorsal, and **89.** right lateral (45°) views of the central portion of the radular ribbon. **90.** Single lateral tooth (partially broken) to show concentration of cusps along inner portion of basal plate. **91.** Dorsal view of the bending plane, showing worn teeth. **92.** Right lateral (75°) view of the central portion of the radular ribbon.

Siphon very short, free, muscular, extends slightly beyond mantle edge.

Mantle Cavity: Mantle of female specimen, although damaged, was partially present. Mantle of moderate width (L/W ~0.8), very thin, mantle edge evenly thickened. Osphradium yellowish, bipectinate, symmetrical, narrow, spanning ~0.7 mantle cavity length. Ctenidium equal in width to osphradium, slightly longer, curved. Lamellae uniform in shape along entire ctenidium length, tall, triangular, with short curved tip, similar to that in posterior part of *Lusitromina abyssorum* (Lus, 1993) (Figure 129). Hypobranchial gland poorly developed, lacks distinct folds. Rectum spans ~⅔ mantle cavity length, with terminal anus, distinct anal papilla.

Alimentary System (Figures 95–97): Proboscis (Figures 95, 97, pr) short when retracted (~0.30 AL), narrow (L/D ~4.0), with folded walls, non-pigmented. Proboscis retractors (Figures 95, 96, prr) powerful, arranged in symmetrical bundles attached to posterior part of proboscis sheath when proboscis retracted. Anterior ⅔ of proboscis sheath very thin-walled, translucent, thickening posteriorly until as thick as proboscis wall, which comprises ~0.1 proboscis diameter. Mouth opening triangular slit. Buccal mass muscular, large, filling, but not extending beyond retracted proboscis. Odontophoral cartilages paired, fused anteriorly, ~¾ of buccal mass length. Radular ribbon of holotype (Figures 88–92) longer than proboscis (14 mm, 0.42 AL), narrow, (~420 μm), triserial, consisting of 110 rows, anteriormost 28

Figures 93–97. Anatomy of *Germonea rachelae* new species. **93–94.** Holotype, male. **95–97.** Female, [R/V ELTANIN, sta. 695]. **93.** Anterior view of animal. **94.** Head and penis. **95.** Right lateral, **96.** left lateral, and **97.** ventral views of anterior alimentary system. Scale bars = 5 mm. **gL,** gland of Leiblein; **lsg,** left salivary gland; **nr,** circumoesophageal nerve ring; **oe,** oesophagus; **p,** penis; **poe,** posterior oesophagus; **pr,** proboscis; **prp,** propodium; **prr,** proboscis retractors; **rsg,** right salivary gland; **s,** siphon; **sp,** seminal papilla; **tn,** cephalic tentacles.

rows below bending plane in sublingual pouch, posteriormost 7 rows nascent. Radula strongly sclerotized, dark yellow. Rachidian teeth (Figures 88, 89) long (~185 μm), very narrow (~75 μm), with anteriorly arched, laterally indented basal plate, 3 stout, radially oriented cusps, central cusp longest. Lateral teeth (Figures 90–92) with long, stout basal plates attached at acute angle

(~22–28°) to axis of radular ribbon, with 3–4 robust, roughly parallel cusps of similar length emanating from innermost ~⅔ of basal plate, outermost ~⅓ of basal plate beneath cusps of adjacent lateral tooth. Teeth along bending plane (Figure 91) badly worn. Salivary glands (Figures 95–97, rsg, lsg) large, seemingly fused, acinous. Right salivary gland (Figures 95, 97, rsg) completely cov-
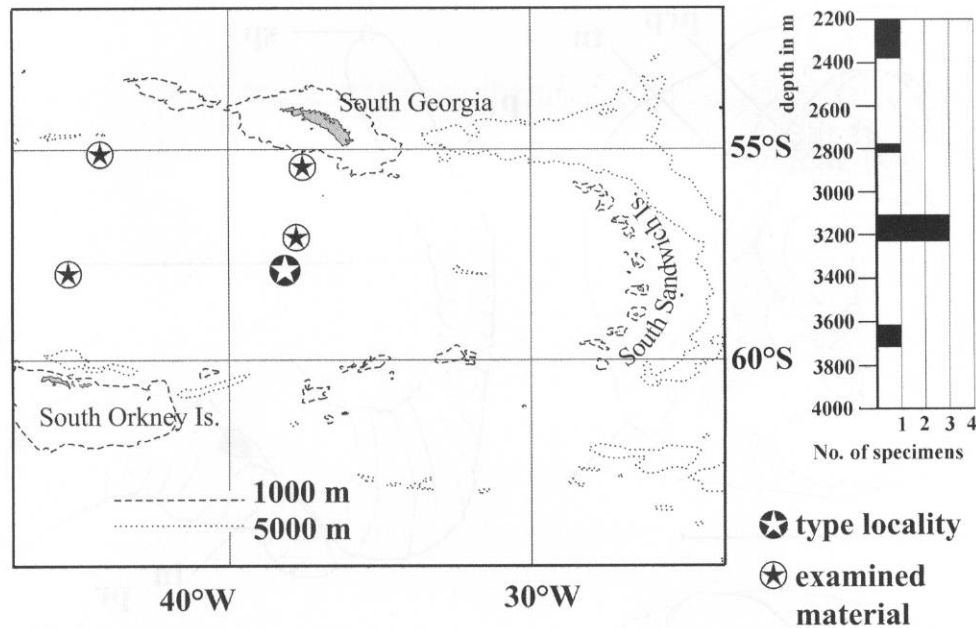
Figure 98. Geographic and bathymetric distributions of *Germonea rachelae* new species.

ers valve of Leiblein, lies dorsal to nerve ring, flanks right, ventral, anterior part of proboscis sheath. Left salivary gland (Figures 96, 97, lsg) smaller than right. Salivary ducts short, thick, become embedded in esophageal wall shortly after leaving salivary glands. Valve of Leiblein large, well defined, pyriform, brownish in preserved specimens, with ciliary cone, whitish glandular pad visible through walls of valve. Gland of Leiblein (Figures 95, 96, gL) large, bulky, brownish, envelopes proboscis ventro-laterally, extends posteriorly along oesophagus, opens into oesophagus via narrow duct well posterior to small circumoesophageal nerve ring (Figures 96, 97, nr). Anterior, mid-, and posterior oesophagus thick, broad, narrowing slightly when passing through nerve ring. Stomach unknown for holotype. Non-type specimen (♀) had portion of stomach preserved, indicating stomach U-shaped, lacking posterior mixing area.

Male Reproductive System (Figures 93–94): Sperm duct runs anteriorly along right side of body to enter base of long, narrow, nearly cylindrical penis (Figure 94) that extends length of mantle cavity. Seminal papilla (Figure 94, sp) very short, surrounded by circular fold.

Type Locality: Off South Georgia Island, 58°02′ S, 37°57′ W, in 3197–3239 m. [R/V ELTANIN cruise 9, sta. 698, 30 Aug, 1963].

Type Material: Holotype, ♂, USNM 896594, from the type locality; Paratype 1, ♂, USNM 1010620, N of South Orkney Islands, 58°06′ S, 44°56′ W, in 2800 m. [R/V ELTANIN, cruise 7, sta. 480, 15 Feb 1963]; Paratype 2, USNM 898828, off South Georgia Island, 55°02′ S, 44°21′ W, in 3623–3714 m. [R/V ELTANIN cruise 7, sta. 469, 12 Feb 1963]; Paratype 3, USNM 1010621, off South Georgia Island, 54°59′ S, 38°13′ W, in 2379–2196 m. [R/V ELTANIN cruise 9, sta. 686, 25 Aug 1963].

Other Material Examined: USNM 1013061, off South Georgia Island, 56°53′ S, 37°33′ W, 3144–3138 m. [R/V ELTANIN cruise 9, sta. 695, 28 Aug 1963], 2 frag-

Table 4. *Germonea rachelae* new species. Measurements of shell characters. Linear measurements in mm. (n = 4, including holotype).

Character	Mean	σ	Range	Holotype
Shell length (SL)	57.0	11.1	41.7–67.8	61.8
Final whorl length (FWL)	41.5	8.0	30.2–47.9	46.1
Aperture length (AL)	30.4	5.8	22.2–35.5	35.5
Shell width (SW)	24.7	5.3	18.2–30.3	30.3
FWL/SL	0.73	0.02	0.71–0.75	0.75
AL/SL	0.54	0.03	0.49–0.57	0.57
SW/SL	0.43	0.04	0.40–0.49	0.49
Number of spiral cords on penultimate whorl	24.5	5.2	18–30	30
Number of spiral cords on final whorl	58.0	14.4	48–81	81

mentary bodies (1♀ + 1♂) without shells (anatomy examined).

Distribution (Figure 98): This species is known only from the abyssal plain of the Scotia Sea, at depths of 2196–3714 m.

Etymology: The species is named after Mrs. Rachel (Raye) N. Germon, in recognition of her years of work in managing the collections of Antarctic Mollusca at the National Museum of Natural History, Smithsonian Institution.

Remarks: *Germonea rachelae* may be easily identified by its large, fusiform shell, with short siphonal canal and deep amber periostracum. Of the few Antarctic species that reach comparable size, only *Cavineptunea monstrosa* Powell, 1951, from outer continental shelf depths off South Georgia Island, is superficially similar, but differs in having a unique, cylindrical protoconch with indented apex, a broader aperture, and in lacking the axial rugae of *Germonea* near the suture.

The radula of *Germonea rachelae*, with its narrow, tricuspid rachidian teeth, and lateral teeth in which the 3–4 cusps are concentrated along the inner half of the basal plate, has clear affinities with several genera assigned to the subfamily Prosiphiinae (Appendix 1). It is most similar to the radula of several species of *Prosipho* [i.e., *Prosipho spiralis* Thiele, 1912, Numanami, 1996: figs. 116D–E; *Prosipho crassicostatus* (Melvill and Standen, 1907), see Hain, 1989: pl. 24, fig. 1] and *Anomacme smithi* Strebel, 1905 (Powell, 1951: fig. K57). The shells of these sublittoral to bathyal genera, while similar in general shape and proportion to those of *Gemonea*, rarely exceed 10 mm in length. The rachidian teeth of *Germonea rachelae* are far narrower, more elongated, and deeply indented anteriorly (producing a tooth with a Y-shaped outline) than any species of Prosiphiinae. While the opercula of relatively few Prosiphiinae are illustrated, Numanami (1996: fig. 110) shows the operculum of *Prosipho hunteri* Hedley, 1916 to be elongated, slightly smaller than the aperture, with a round attachment area and a terminal nucleus. The distal, free portion of the operculum, containing the terminal nucleus, is not as strongly curved as it is in *Germonea rachelae*.

Subfamily Cominellinae Gray, 1857
Lusitromina new genus

Type Species: *Tromina abyssorum* Lus, 1993, by original designation.

Description: Protoconch increasing in diameter from 470 μm to 2.2 mm in 2 whorls. First whorl smooth, followed by onset of fine, sharp axial lamellae, then, ½ whorl later, by broad, shallow spiral cords. Transition to teleoconch distinct, marked by onset of coarser sculpture. Teleoconch of moderate size (to 29.2 mm), up to 3½ whorls, with strong shoulder on first 2 whorls, increasingly rounded thereafter. Axial sculpture prominent on protoconch, reduced on first teleoconch whorl, lim-

ited to fine growth lines on subsequent whorls. Spiral sculpture of broad cords that increase in number, but decrease in prominence with increasing shell size. Aperture large, ovate, columella long, axial, with short siphonal fold. Neither siphonal fasciole nor pseudoumbilicus present. Periostracum of fine axial lamellae. Operculum D-shaped, paucispiral, large. Eyes absent. Kidney narrow. Foot with pronounced propodium. Buccal mass larger than retracted proboscis. Radula with tricuspid rachidian teeth, with central cusp longer, wider that flanking cusps, basal plate broadly rectangular. Lateral teeth with two long, sharp, curved cusps that join above basal plate. Stomach small, U-shaped, without posterior mixing area. Penis with long, cylindrical papilla surrounded by fold around base.

Etymology: The genus is named after the late Dr. Valentina Lus of the P.P. Shirsov Institute of Oceanology, Russian Academy of Sciences, Moscow, for her work on abyssal and hadal Buccinoidea.

Remarks: Dall (1918) proposed the genus *Tromina* without discussion, designating as type species *Fusus unicarinatus* Philippi, 1868, (from subtidal depths of the Magellanic Province), a taxon that he had previously (Dall, 1902: 536) questionably included in the genus "?*Trophon*". Later, Dall (1919: 336) commented that this genus "has the nucleus [protoconch] of a *Trophon* and is probably related to the austral Trophons, but the soft parts are not known." Later still, Dall (1925: 28, plate 21, fig. 7) illustrated the type species.

Several species from the South Atlantic have since been attributed to the genus *Tromina*, including the sublittoral to bathyal Magellanic species: *T. fenestrata* Powell, 1951, *T. simplex* Powell, 1951, *T. tricarinata* Powell, 1951, and *T. bella* Powell, 1951; the abyssal *T. bella abyssicola* Clarke, 1961, from the Cape Basin off SW Africa, and *T. traversiensis* Clarke, 1961, from off the South Sandwich Islands, and the hadal *T. abyssorum* Lus, 1993, from the Orkney Trench. Clarke (1961, 1962) also recognized, but did not name three additional abyssal taxa, referring to them as *Tromina* a, b, c.

Cernohorsky (1977: 110) was the first to note that *Fusus unicarinatus* Philippi, 1868 was preoccupied by *Fusus unicarinatus* Deshayes, 1835. He considered *Tromina tricarinata* to be conspecific with *F. unicarinatus* Philippi, and suggested that it might serve as a replacement name for the type species. Bouchet and Warén (1985: fig. 328, 330) subsequently illustrated the shell (fig. 328) and radula (fig. 330) of *T. unicarinatus*, confirming Dall's (1919) belief that this taxon was a muricid closely "related to the Austral Trophons." Since the original description of *Tromina tricarinata* includes an illustration of its radula that clearly shows this taxon to be a buccinoidean, it could not serve as a replacement name for a species of muricid.

Dell (1990: 208) reviewed the nomenclatural history of *Tromina* and its type species, and proposed *Tromina dispectata* as a new name for *Fusus unicarinatus* Philippi, 1868, *non* Deshayes, 1835. Recognizing that several

buccinoidean taxa previously described in *Tromina* required a new generic allocation, he proposed the new genus *Falsitromina* (type species: *Tromina bella* Powell, 1951), characterized by a distinctive, complex protoconch morphology, small (to 15 mm) shell, paucispiral operculum, and radula with tricuspid rachidian teeth and lateral teeth with two cusps set close together. In addition to the type species, he included *F. simplex, F. tricarinata, F. fenestrata,* and proposed an additional species *F. powelli,* all from bathyal depths of the Magellanic Province, but did not include or mention Clarke's (1961) abyssal species.

The bathyal genus *Antarctodomus* Dell, 1972 (type species: *Bathydomus thielei* Powell, 1958) shares the unusual protoconch morphology (Numanami, 1996: fig. 96C) and obesely fusiform shell shape (Numanami, 1996: fig. 96A–B) of *Falsitromina,* but differs in reaching a much larger size (to 35 mm, Dell, 1990: 169), in having a triangular, sharply tapering operculum (Arnaud, 1972: fig. 20B), and in having a radula with tricuspid rachidian teeth that have a more narrowly rectangular basal plate with a broadly indented anterior edge, and bicuspid lateral teeth with both cusps appearing blunt and nearly cylindrical (Arnaud, 1972: fig. 20C; Numanami, 1996: fig. 96D).

The new genus *Lusitromina* is proposed to contain the abyssal and hadal taxa that were originally described in *Tromina,* namely *T. abyssicola* Clarke, 1961 (as *T. bella abyssicola*), and *T. abyssorum* Lus, 1993. *Tromina traversiensis* Clarke, 1961, was shown to be a cancellariid of the genus *Iphinopsis* Dall, 1924, by Bouchet and Warén (1985: 261).

Lusitromina shares many of the distinctive features characteristic of both *Falsitromina* and *Antarctodomus,* including the complex protoconch morphology, obesely fusiform shell shape, and radulae with tricuspid rachidian teeth and bicuspid lateral teeth. However, the rounded paucispiral operculum of *Lusitromina* serves to distinguish it from *Antarctodomus,* which has a tapering, triangular operculum. The rachidian teeth of *Lusitromina,* while tricuspid, differ from those of both *Falsitromina* and *Antarctodomus* in have a central cusp that is larger than, rather than equal in size to the flanking cusps. The basal plate of the rachidian tooth is broadly rectangular, intermediate between the squarish basal plate of *Falsitromina,* and the very narrow and deeply indented basal plate of *Antarctodomus.* The lateral teeth of *Lusitromina* have two sharp, curved cusps of equal size that fuse above the basal plate, while the cusps of both *Falsitromina* and *Antarctodomus* are not equal in length or width.

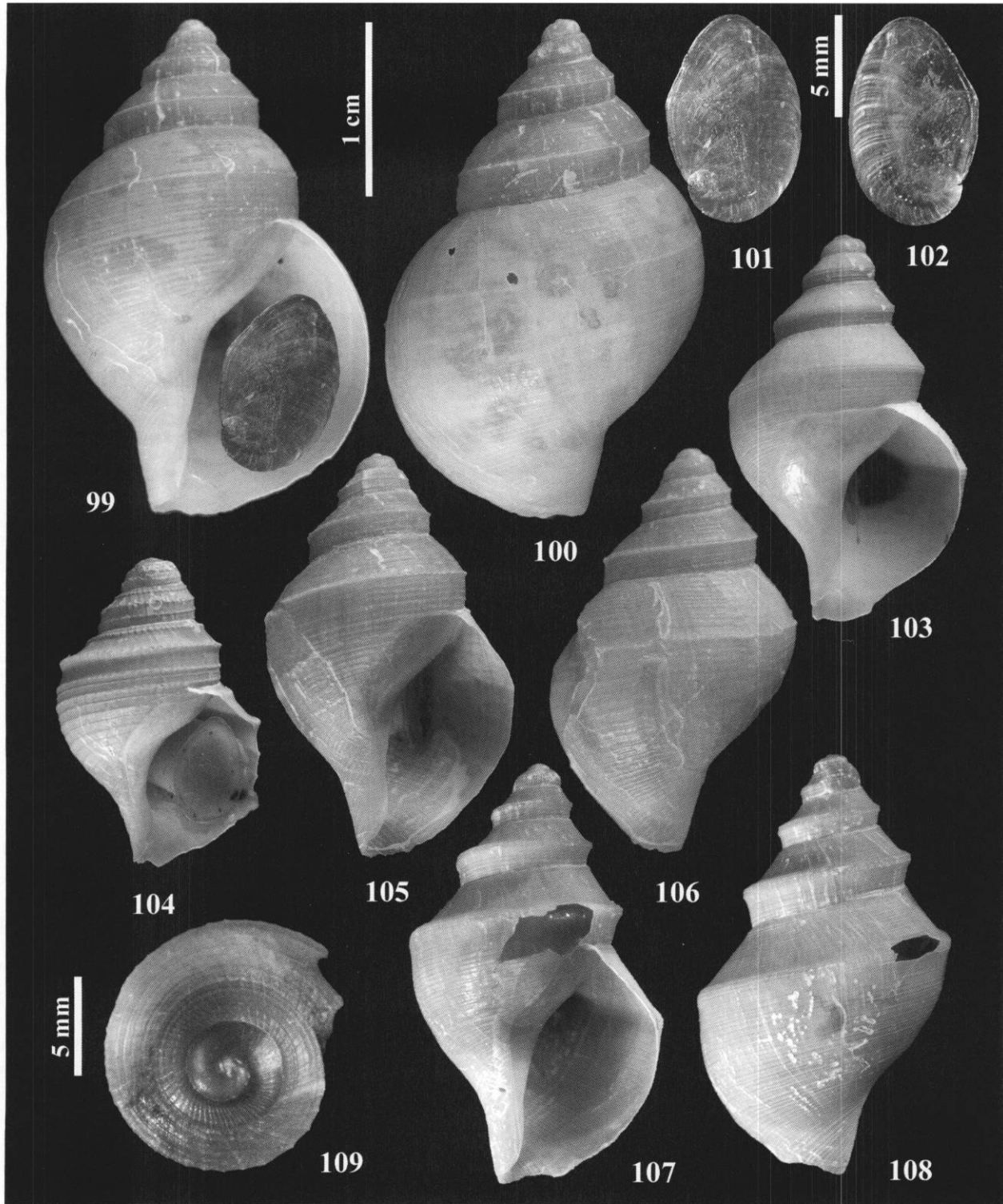*Lusitromina abyssorum* (Lus, 1993)
(Figures 99–137, Table 5)

Synonymy—*Tromina abyssorum* Lus, 1993:178

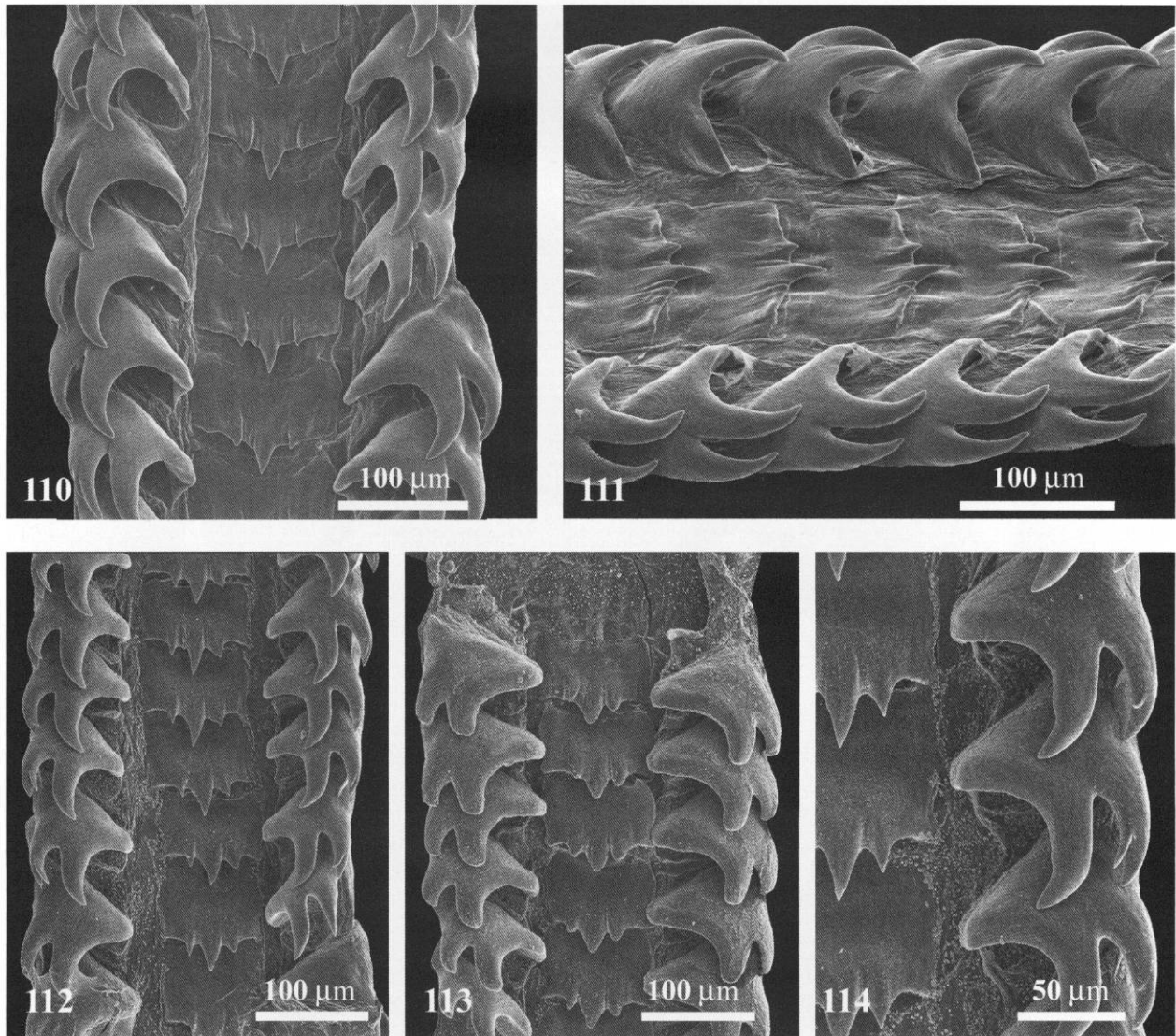**Description:** Shell (Figures 99–100, 103–109) of moderate size (to 29.2 mm), thin, small specimens translucent, largest specimens opaque along last whorl. Shell shouldered, biconical when small, ovate when large. Protoconch well preserved, especially in small specimens (Figures 115–117). Protoconch increasing from 470 μm to 2.2 mm in diameter in 2 whorls, first 0.9 whorl smooth, slightly pitted, followed by onset of fine, sharp axial threads, and ½ later, by broader spiral cords. Transition to teleoconch distinct (Figures 116, 117 arrows), followed by onset of coarser axial sculpture. Teleoconch of up to 3½ whorls. Shoulder pronounced on first 2 whorls, marked by thick spiral cord, producing a stepped spire, becoming progressively less conspicuous in subsequent whorls, entirely rounded following third whorl (Figures 99–100). Axial sculpture of strong, evenly spaced cords dominant on protoconch, becoming more widely spaced, less prominent following transition to teleoconch, disappearing entirely after first ½ teleoconch whorl. Subsequent axial sculpture confined to very fine, weakly prosocline growth lines. Spiral sculpture of broad cords that usually increase in number, but decrease in prominence with increasing shell size, 4–20 on penultimate whorl, 2–20 between suture and shoulder, 19–53 on last whorl. Aperture large (AL/SL = 0.62–0.66), broadly oval, deflected from shell axis by 24–27°. Outer lip very thin, not reflected, evenly rounded from shoulder to base of short, broad, axial siphonal canal. Shell composed of three layers (Figure 121), outermost layer (~2 μm) of columnar calcitic crystals, middle layer, thickest (~26 μm) of collabrally oriented crossed-lamellar crystals, innermost layer (~4 μm) of crossed lamellar crystals oriented perpendicular to middle layer. Inner lip of wide, weakly convex parietal region, straight, weakly indented axial columellar region of equal length, with long siphonal fold defining abaxial portion of siphonal canal. Neither siphonal fasciole nor pseudoumbilicus present. Shell color uniformly white. Periostracum (Figure 120) very thin, straw yellow in color, with extremely fine axial lamellae. Operculum (Figures 101–102, 118–119) D-shaped, large, spanning ~0.61 AL, thin, yellowish, broadly ovate, paucispiral, with nucleus near adaxial, abapical edge (Figures 118–119).

Anatomy (Figures 122–124): Soft tissues comprise approximately 3¼ whorls. Mantle cavity spans just under ½ whorl, kidney narrow, spans about 1/7 whorl. Columellar muscle short, comprising slightly less than 1 whorl, attaching to shell at rear of mantle cavity. Foot large, long (L/W ~2.2), with well developed, crescent-shaped propodium. Propodial cleft very wide, containing conspicuous propodial gland with rounded opening (Figures 123, 124, pg). Body color yellowish tan, without pigmentation pattern. Kidney, digestive system, testis all greenish. Head large, with long, conical tentacles (Figure 123, tn), without discernable neck. Eyes absent. Nephridium brown, folds lighter in color, visible through wall. Mantle covers base of head and most of penis. Pericardium (Figure 122, per) ventral to narrow nephridial gland.

Mantle Cavity (Figure 128): Mantle cavity short,

Figures 99–109. Shells and opercula of *Lusitromina abyssorum* (Lus, 1993). **99–102.** USNM 1010536, off Saunders Island, South Sandwich Islands, 57°39′00″ S, 26°00′24″ W, in 2380–2609 m [R/V ISLAS ORCADAS, sta. 54]. **99.** Apertural, and **100.** dorsal views of shell. **101.** Outer, and **102.** inner views of operculum. **103.** Apertural view, USNM 896533, off South Georgia Island, 56°04′ S, 33°59′ W, in 3138–3239 m [R/V ELTANIN, sta. 722]. **104.** Apertural view, USNM 896785, N of South Orkney Islands, 60°06′ S, 45°26′ W, depth not recorded (estimated > 5000 m), [R/V ELTANIN, sta. 488]. **105.** Apertural and **106.** Dorsal views, USNM 1010535, E of Candlemas Island, South Sandwich Islands, 57°00′24″ S, 26°10′06″ W, in 2740–2757 m [R/V ISLAS ORCADAS, sta. 38]. **107.** Apertural, **108.** dorsal, and **109.** apical views, USNM 896525, N of South Georgia Island, 53°02′ S, 37°40′ W, in 3056–3102 m [R/V ELTANIN, sta. 735].
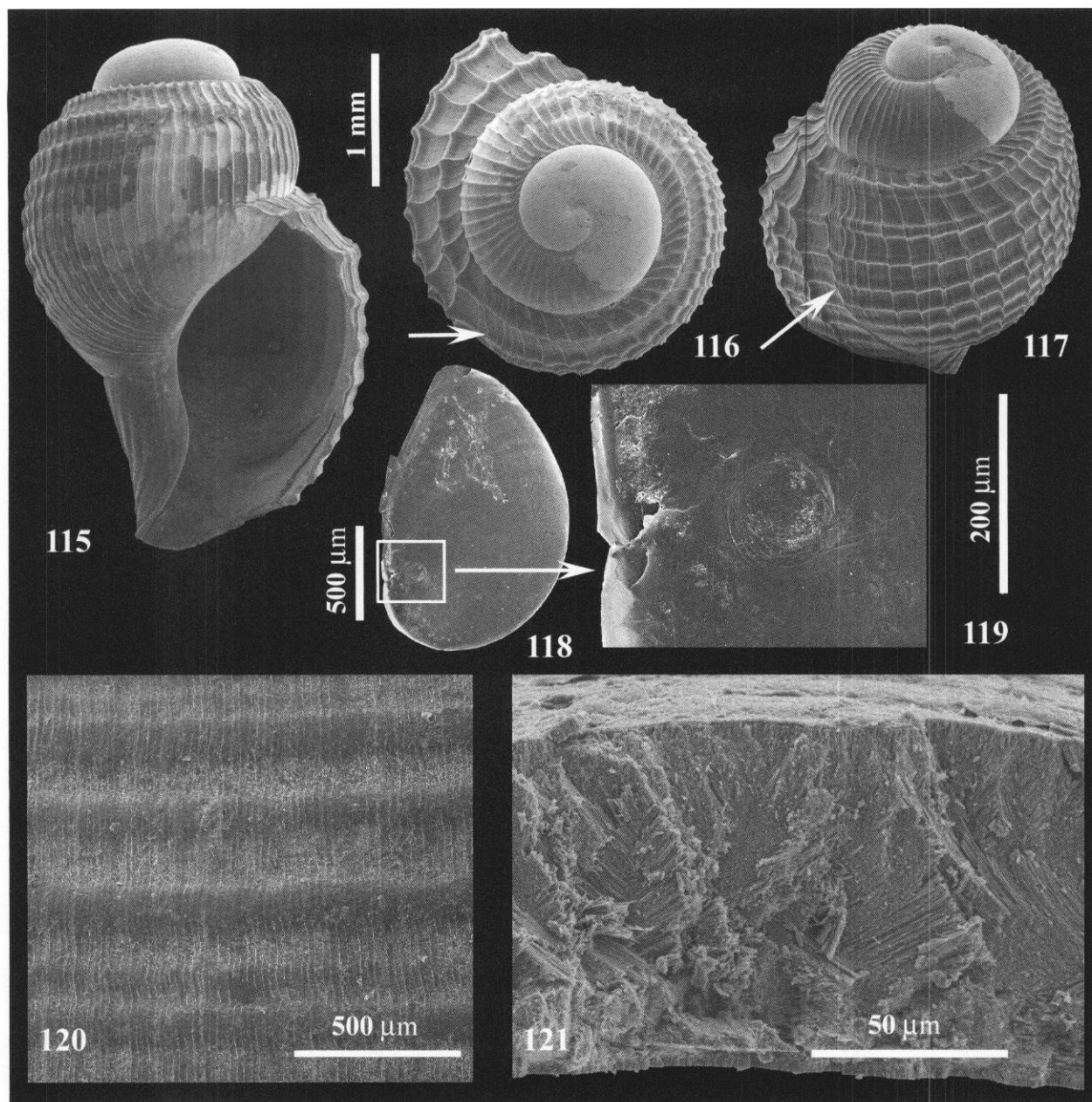
Figures 110–114. Radulae of *Lusitromina abyssorum* (Lus, 1993). **110.** Dorsal, and **111.** Right lateral (30°) views of the central portion of the radular ribbon of specimen in Figures 99–100, USNM 1010536. **112–113.** Dorsal views of the radular ribbon of specimen in Figures 107–109, USNM 896525. **112.** Dorsal view of central portion of radula. **113.** Anteriormost part of radular ribbon, showing worn teeth. **114.** Enlarged right lateral teeth, showing bifurcation of outer cusp.

broad (L/W ~0.6). Mantle edge smooth. Siphon very short, broad, muscular, extending slightly beyond mantle edge. Osphradium (Figure 128, os) yellowish, bipectinate, large (~½ mantle cavity length), very wide, with wide, curved osphradial nerve. Ctenidium (Figure 128, ct) large, narrower than osphradium, strongly curved, spanning nearly entire mantle cavity length. Shape of ctenidium lamellae varies with position along organ. Lamellae tall, triangular posteriorly (Figure 129), gradually becoming narrower anteriorly (Figure 130). Hypobranchial gland without distinct folds, covered by thick layer of mucus. Rectum short, spans <½ mantle cavity length. Anus terminal, without papilla.

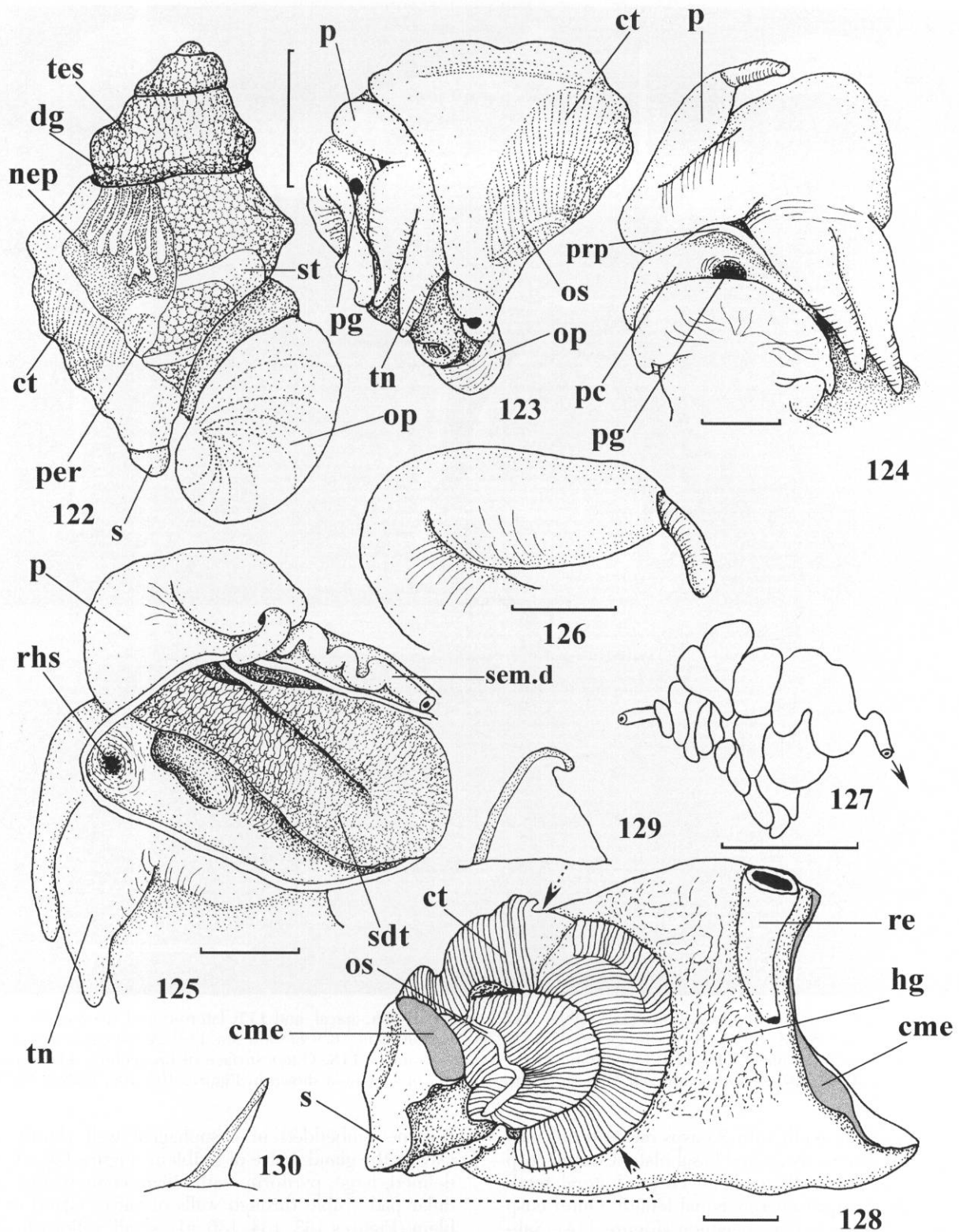**Alimentary System (Figures 131–136):** Proboscis (133, pr) short when retracted (~0.36 AL), not thick (L/ D ~3.3), smooth, non-pigmented. Proboscis retractors (Figures 133, 134, prr) not numerous, but thick, powerful, attached to proboscis sheath at mid-length, when proboscis retracted. Proboscis sheath very thin-walled, anterior half translucent, thickened posteriorly to become as thick as proboscis wall. Proboscis wall thin ~1/10 proboscis diameter. Mouth opening triangular slit. Buccal mass muscular, large, filling retracted proboscis, slightly protruding from its posterior end (Figure 136, bm). Odontophoral cartilages paired, fused anteriorly, but connected only by very thin layer of tissue, comprise ~¾ of buccal mass length. Radular ribbon equal in length to retracted proboscis (4.3–5.0 mm, 0.26–0.28 AL), 300–330 μm wide, triserial (Figures 110–114), with 65–76 rows of teeth, posteriormost 5–6 rows
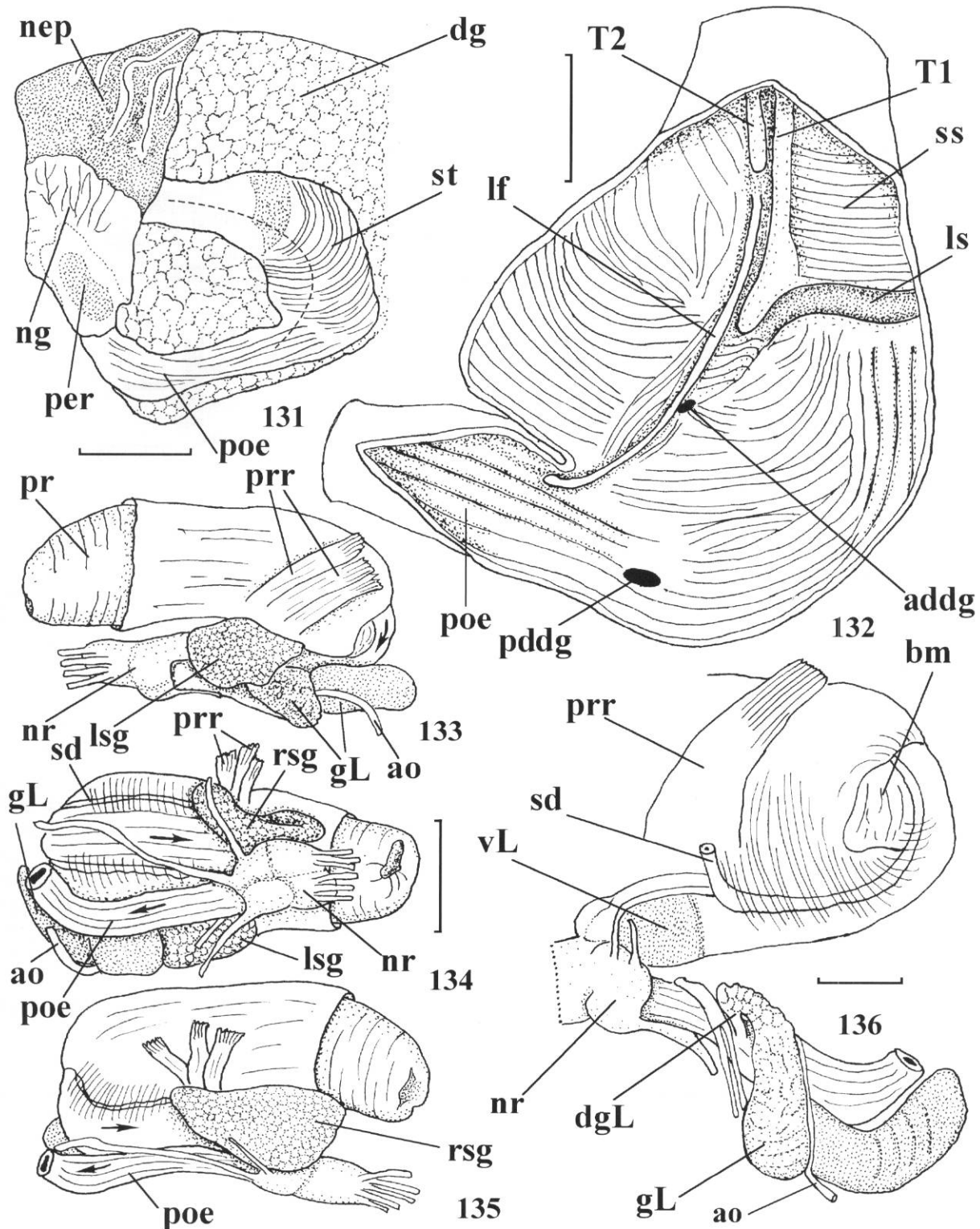
Figures 115–121. *Lusitromina abyssorum* (Lus, 1993). **115.** Apertural, **116.** apical, and **117.** latero-dorsal views of the shell of a juvenile specimen, USNM 896800, Scotia Ridge, 56°02′ S, 61°56′ W, in 4008 m, [R/V *Eltanin*, sta. 112]. Arrows indicate transition from protoconch to teleoconch. **118–119.** Operculum of the same specimen. **118.** Outer surface of operculum. **119.** Enlarged nucleus of operculum. **120.** Periostracum, and **121.** shell ultrastructure of specimen shown in Figures 107–109, USNM 896525.

nascent. Rachidian teeth with 3 cusps on posterior portion of broad, anteriorly arched basal plate. Central cusp slightly longer, wider than lateral cusps. Lateral teeth with 2 cusps of approximately equal length. Outer cusp with bifurcated tip in one specimen (Figure 114). Salivary glands (Figures 133–135, lsg, rsg) small, not fused, acinous. Right salivary gland completely covers valve of Leiblein, lies dorsally to the nervous ring (Figures 134, 135, rsg). Left salivary gland more rounded, situated laterally, just posterior to the nerve ring (Figure 133, 134, lsg). Salivary ducts (Figure 134, 136, sd) short, thick,

become embedded in oesophageal wall shortly after leaving the gland. Valve of Leiblein (Figure 136, vL) well defined, large, pyriform, with ciliary cone, whitish glandular pad visible through walls of valve. Gland of Leiblein (Figures 133, 134, 136, gL) small, yellowish, short, tubular, not coiled, opening into oesophagus via short duct (Figure 136, dgL) slightly posterior to the nerve ring. Oesophagus thick, broad anterior to nerve ring, narrower posterior to nerve ring (Figures 134, 135, poe), does not widen before entering stomach (Figures 131, 132, poe). Stomach (Figures 131, st; 132) small, U-

Figures 122–130. Anatomy of *Lusitromina abyssorum* (Lus, 1993), specimen shown in Figures 107–109, USNM 896525. **122–123.** Lateral views of the animal removed from shell. **124.** Anterior view of the foot showing the pedal gland. **125.** Cephalic haemocoel, with organs of the digestive system removed to show the enlarged seminal duct. **126.** Dorsal view of penis. **127.** Seminal vesicle. **128.** Mantle cavity organs. **129–130.** Shape of ctenidium lamellae in different regions of ctenidium. Scale bars = 2 mm. **cme,** cut mantle edge; **ct,** ctenidium; **dg,** digestive gland; **hg,** hypobranchial gland; **nep,** nephridium; **op,** operculum; **os,** osphradium; **p,** penis; **pc,** propodium; **per,** pericardium; **pg,** propodial gland; **re,** rectum; **rhs,** rhynchostome; **s,** siphon; **sdt,** glandular seminal duct (prostate gland); **sem.d,** seminal duct; **st,** stomach; **tes,** testis; **tn,** cephalic tentacles.

Figures 131–136. Anatomy of digestive system of *Lusitromina abyssorum* (Lus, 1993). **131–132.** Specimen shown in Figures 107–109, USNM 896525. **131.** Dorsal view of stomach, embedded in digestive gland. **132.** Stomach, opened dorsally along incision shown by dashed line in Figure 131. **133–136.** Specimen shown in Figures 99–100, USNM 1010536. **133.** Left lateral, **134.** ventral, and **135.** right lateral views of anterior alimentary system. **136.** Latero-dorsal view of the anterior oesophagus to show the opening of the duct of gland of Leiblein. Scale bars = 2 mm for Figures 131, 133–135, 1 mm for Figures 132, 136. **a,** anus; **addg,** anterior duct of the digestive gland; **ao,** anterior aorta; **bm,** buccal mass; **dg,** digestive gland; **dgL,** duct of gland of Leiblein; **gL,** gland of Leiblein; **lf,** longitudinal fold; **ls,** lateral sulcus; **lsg,** left salivary gland; **nep,** nephridium; **ng,** nephridial gland; **nr,** circumoesophageal nerve ring; **pddg,** posterior duct of digestive gland; **per,** pericardium; **poe,** posterior oesophagus; **pr,** proboscis; **prr,** proboscis retractors; **rsg,** right salivary gland; **sd,** salivary duct; **ss,** style sac; **st,** stomach; **T1, T2,** major and minor typhlosoles; **vL,** valve of Leiblein.
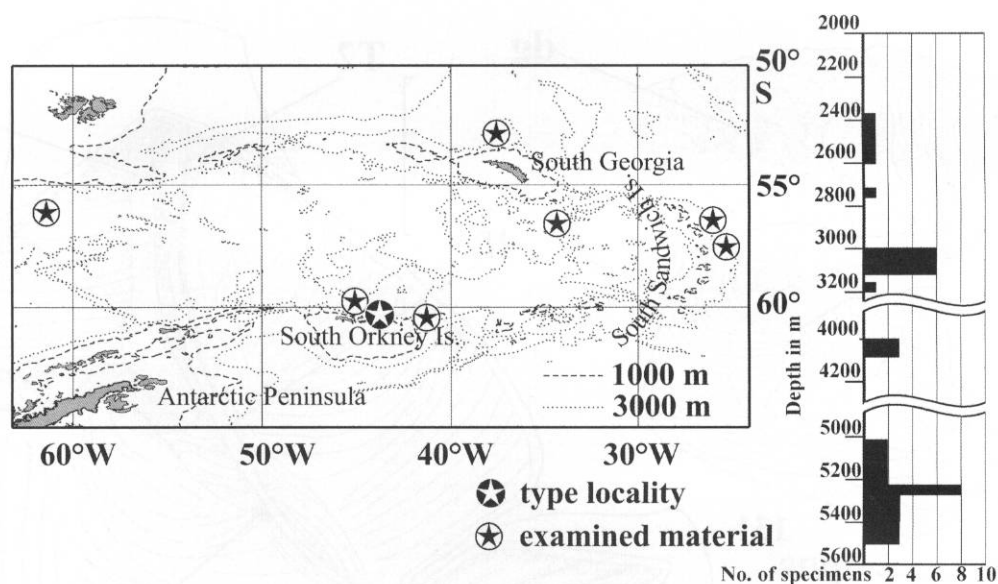
Figure 137. Geographic and bathymetric distribution of *Lusitromina abyssorum* (Lus, 1993).

shaped, without posterior mixing area, with numerous, fine, semicircular dorso-ventral folds. Transition from oesophagus to stomach marked by change from tall longitudinal folds to much finer, curved folds that line stomach. Posterior duct of digestive gland (Figure 132, pddg) large, situated near entrance of oesophagus. Longitudinal fold (Figure 132, lf) narrow, distinct, originates at entrance of oesophagus, runs length of stomach, becomes obsolete near intestine. Anterior duct of digestive gland (Figure 132, addg) small. Lateral sulcus (Figure 132, ls) shallow. Typhlosoles (Figure 132, T1, T2) more prominent in intestine, bordering, deep, narrow intestinal groove. Posterior part of style sac (Figure 132, ss) lined with transverse folds. Folds lining stomach very low, ventral channel of gastric chamber poorly separated from dorsal chamber.

Male Reproductive System: Seminal vesicle of medium size (Figure 127), spans less than ⅓ of whorl, formed of few large loops. Seminal duct descends to floor of mantle cavity at its rear, becomes thickened, sin-

uous, running to base of penis, where it enters cephalic haemocoel (Figure 125) expands greatly, makes a long loop posteriorly, before entering penis. Penis shorter than mantle cavity, flattened, non-pigmented, with long, cylindrical terminal papilla surrounded by circular fold at its base (Figure 126).

Type Locality: Lorie Trench, off South Orkney Islands, 60°12'9" S, 43°59'0" W, in 5450–5480 m. [R/V AKADEMIK KURCHATOV, sta. 909, 10 Dec 1971].

Type Material: Holotype and 2 paratypes, from the type locality; 2 paratypes, Orkney Trench, 60°50'5" S, 41°11'7" W, in 5063–5470 m, [R/V DMITRIY MENDELEEV, sta. 4089, 4 Mar, 1989]. Type material could not be located in the collections of the Institute of Oceanology of Russian Academy of Sciences, Moscow. The type series consists entirely of juvenile specimens. The shell of the holotype (the only intact shell) measured 7.4 mm in length, 5.5 mm in width.

Other Material Examined: SOUTH GEORGIA IS-

Table 5. *Lusitromina abyssorum* (Lus, 1993). Measurements of shell characters. Linear measurements in mm. (n = 5).

Character	Mean	σ	Range
Shell length (SL)	20.9	6.5	12.3–29.2
Final whorl length (FWL)	16.7	4.9	10.3–23.2
Aperture length (AL)	13.4	4.1	8.6–18.9
Siphonal canal length (SCL)	2.5	0.4	1.9–3.3
Shell width (SW)	13.4	4.2	7.9–19.4
FWL/SL	0.80	0.02	0.78–0.84
AL/SL	0.65	0.03	0.61–0.70
SCL/SL	0.12	0.02	0.10–0.16
SW/SL	0.64	0.04	0.60–0.70
Number of spiral cords on penultimate whorl	12.8	6.4	4–20
Number of spiral cords suture to peripheral cord	9.6	7.4	2–20
Number of spiral cords peripheral cord to siphon	35.0	13.1	19–53

LAND: USNM 896525, 53°02′ S, 37°40′ W, in 3056–3102 m. [R/V ELTANIN, sta. 735, 13 Sep 1963], 6 specimens (1 adult + 5 juveniles), (anatomy examined); USNM 896533, 56°04′ S, 33°59′ W, in 3138–3239 m, [R/V ELTANIN, sta. 722, 8 Sep 1963], 1 specimen. SOUTH SANDWICH ISLANDS: USNM 1010535, E of Candlemas Island, 57°00′24″ S, 26°10′06″ W, in 2740–2757 m. [R/V ISLAS ORCADAS, sta. 38, 22 May 1975], 1 specimen; USNM 1010536, Saunders Island, 57°39′00″ S, 26°00′24″ W, in 2380–2609 m. [R/V ISLAS ORCADAS, sta. 54, 27 May 1975] 1 specimen (radula and anterior foregut anatomy studied). SCOTIA RIDGE: USNM 896800, 56°02′ S, 61°56′ W, in 4008 m. [sta. 112, 20 Jul 1962], 4 specimens (juveniles). SOUTH ORKNEY ISLANDS: USNM 896785, 60°06′ S, 45°26′ W, depth not recorded, but > 5000 m according to the bathymetric Atlas GEBSCO97], [R/V ELTANIN, sta. 488, 18 Feb 1963] 1 specimen; USNM 1010537, 60°07′ S, 45°14′ W, 5285 m. [R/V ELTANIN, sta. 485, 18 Feb 1963] 8 specimens (juveniles).

Distribution (Figure 137): Within and around the margins of the Scotia Sea, in 2380–5480 m.

Remarks: Lus's (1993) original description of *Tromina abyssorum* is undoubtedly the most extensive of any Antarctic or abyssal buccinoidean in terms of conchological and anatomical detail. She was familiar with Clarke's (1961) work on the abyssal mollusks from the South Atlantic Ocean, and regarded *T. abyssorum* to be closely related to *T. bella abyssicola* Clarke, 1961. She was apparently unfamiliar with Dell's (1990) clarification of the taxonomic affinities of *Tromina*, as discussed in the remarks under *Lusitromina* (above).

DISCUSSION

While exploration of Antarctic Seas began during the second half of the eighteenth century (Conrad, 1999 for chronology), significant additions to our knowledge of their molluscan fauna originated with the cruises of the H.M.S. CHALLENGER (Numanami, 1996: Table 1) and continue to this day. Several of the research cruises during the late 19th and early 20th centuries sampled at least some stations at abyssal depths, yet only a single buccinoidean genus (*Bathydomus* Thiele, 1912) had been described from these depths off Antarctica. Clarke (1961) reported on the abyssal mollusks collected during the cruises of the R/V VEMA in the South Atlantic (1957–1958). He recognized five buccinoidean taxa, but attributed them all to the subtidal genus *Tromina*. Following his example, Lus (1993) described a related abyssal to hadal species in the genus *Tromina*, trawled by the Russian vessels R/V AKADEMIK KURCHATOV (1971) and R/V DMITRIY MENDELEEV (1989) during their explorations of the abyssal benthic faunas of the Weddell and Scotia Seas. The present study, based on material collected by the United States Antarctic Program (USAP) vessels R/V ISLAS ORCADAS, R/V ELTANIN and supplemented by samples from the German vessel R/V POLARSTERN, has

increased the number of abyssal buccinoidean genera from the seas surrounding Antarctica to six.

In the course of our study, we have reviewed the taxonomic placement, geographic and bathymetric distribution, diagnostic characters, and diversity of each of the 29 genera that have thus far been proposed for Antarctic and Magellanic Buccinoidea (Appendix 1). The bathymetric ranges of these genera are plotted in Figure 138. We analysed the bathymetric distribution of these taxa by subdividing depth into 200 meter increments, and scoring each genus as present or absent within each increment. Employing the Correlation Distance Measure and Ward's Method for Group Linkage, PC-ORD (McCune and Mifford, 1999) was used to cluster the depth increments based on similarities of their buccinoidean fauna. The resulting dendrogram (Figure 138, Ward's Method) reveals a primary and profound dichotomy in generic composition of the faunas at depths above and below 2200 m, roughly corresponding to the transition from the bathyal to the abyssal zone (Gage and Tyler, 1991). This differentiation of slope and abyssal faunas is absolute, with the two faunas having no genera in common. The apparent minor overlap in the ranges of *Parabuccinum* and *Spikebuccinum* shown in Figure 138 is spurious, as all records for *Parabuccinum* from depths greater than 866 m are based on dead shells (Harasewych, Kantor and Linse, 2000). On a finer scale, the continental shelf (0–200 m; Figure 138: A) and upper continental slope (200–1,000 m; Figure 138: B) faunas are differentiated from the lower slope fauna (1000–2200 m; Figure 138: C), while the abyssal fauna is partitioned into continental rise (2200–3800 m; Figure 138: D), abyssal plain (3800–4800 m; Figure 138: E), and hadal (>4800 m: Figure 138: F) faunas. The pattern of clustering agrees generally with that obtained by Rex (1977: fig. 1) for the deep-sea gastropod fauna of the western North Atlantic, except that, for Antarctic and Magellanic Buccinoidea, the upper continental slope fauna is more similar to the continental shelf fauna than to the lower continental slope fauna.

When assessing the taxonomic placement of genera, we observed that those genera occurring at continental shelf and slope depths conform readily to Powell's (1951) criteria for the subfamilies Buccinulinae, Prosiphiinae and Cominellinae. However, taxa from abyssal and hadal depths do not. It is interesting to note that Powell (1951: 131) had to modify his criteria for Buccinulinae to accommodate *Bathydomus*, the only abyssal genus previously included in his classification. We admit to having similarly modified or expanded subfamilial criteria in order to fit our newly described abyssal taxa into an existing classification for the sake of taxonomic expediency. While the sublittoral and bathyal buccinoideans of Antarctica and the Magellanic Province are likely the product of one, or very few *in situ* evolutionary radiations, the origins and relationships of the abyssal fauna are more complex. For some abyssal genera (e.g., *Spikebuccinum, Germonea, Lusitromina*), credible sister taxa inhabit adjacent continental slopes. For others (e.g., *Dre-*
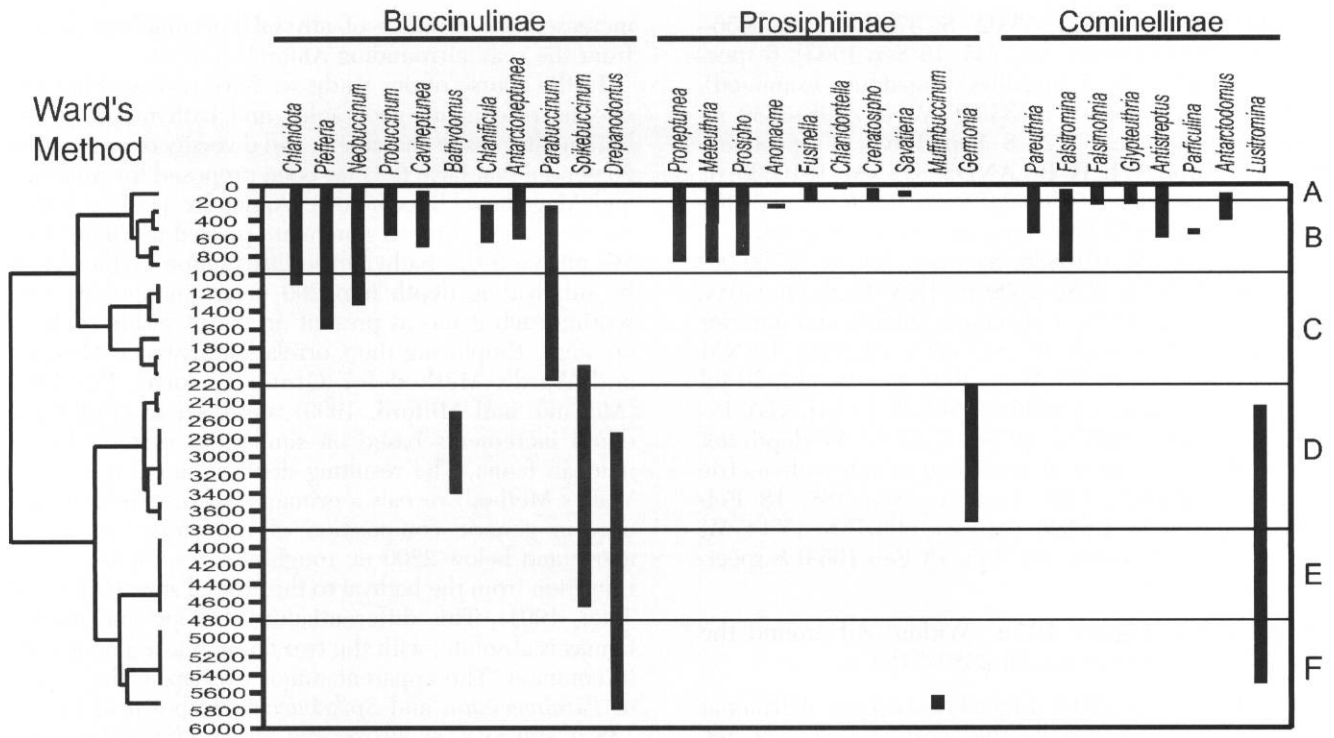
Figure 138. Bathymetric distributions of buccinoidean genera occurring in the Magellanic Province and south of the Antarctic convergence. The dendrogram clusters 200 m increments of depth on the basis of shared buccinoidean genera. A, continental shelf; B, upper continental slope; C, lower continental slope; D, continental rise; E, abyssal plain, F; hadal depths.
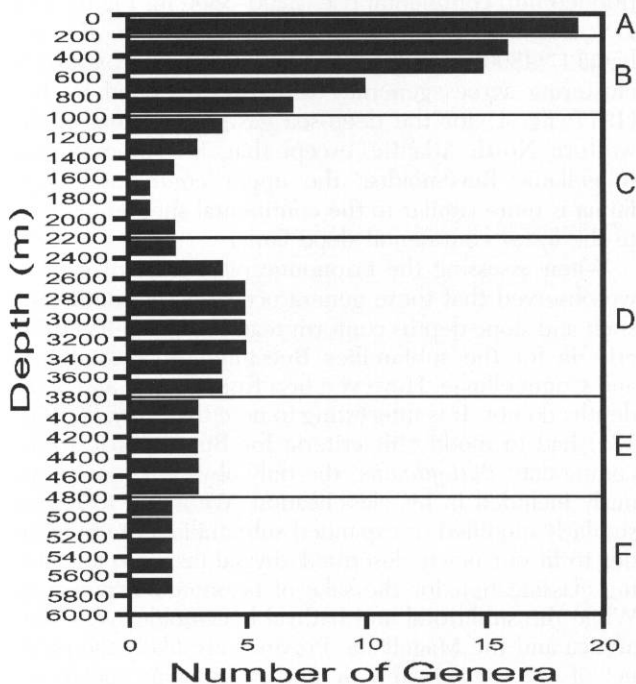

Figure 139. Diversity of buccinoidean genera vs. depth. A, continental shelf; B, upper continental slope; C lower continental slope; D, continental rise; E, abyssal plain; F, hadal depths.

panodontus, Muffinbuccinum), we have noted closer affinities with abyssal or hadal taxa from austral seas beyond the Antarctic convergence. Lipps and Hickman (1982) reviewed various hypotheses regarding origin and age of deep-sea and Antarctic faunas. They concluded that both faunas have evolved primarily in place since at least the Mesozoic, but were supplemented by subsequent minor immigration. Our findings are qualitatively consistant with this hypothesis, indicating that, at least for the Buccinoidea, which have origins in the late Mesozoic, the abyssal Antarctic fauna consists of a combination of taxa, some with nearest relatives, and presumably origins, on the adjacent continental slope, and others with nearest relatives in neighboring ocean basins.

The diversities of both the slope and the abyssal buccinoidean faunas decrease with increasing depth (Figure 139). While the shallower components of each fauna tend to have narrow bathymetric ranges and the deeper dwelling genera tend to have broader bathymetric ranges, most genera span two or three bathymetric regions. Only 4 of 19 sublittoral genera (21.1%) are confined to the continental shelf, while 3 of 16 (18.8%) upper slope genera and 0 of 4 lower slope genera (0%) are limited to a single region. Within the abyssal zone, 2 of 5 genera (40.0%) are known only from the continental rise, while none of the 3 genera that occur on the abyssal plain are restricted to it. Of the 3 hadal genera, only one (33.3%), *Muffinbuccinum*, is restricted to this zone. The genus *Muffinbuccinum* is presently known from a single sta-
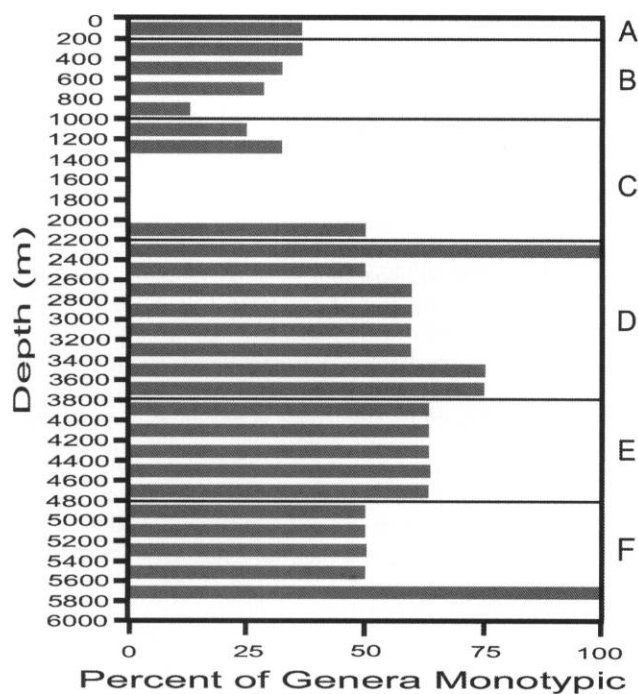
Figure 140. Proportion of monotypic genera vs. depth. A, continental shelf; B, upper continental slope; C, lower continental slope; D, continental rise; E, abyssal plain; F, hadal depths.

Figure 141. The range and mean of maximum shell size within a genus vs. depth. A, continental shelf; B, upper continental slope; C, lower continental slope; D, continental rise; E, abyssal plain; F, hadal depths.

tion. *Drepanodontus,* which co-occurs with *Muffinbuccinum* at this station, has a much broader bathymetric range. For the abyssal buccinoideans, the maximum generic diversity occurs from 2600 to 3200 m, which closely corresponds to the depths for peak of gastropod species richness reported by Rex (1981: fig. 1).

The buccinoidean fauna of the Antarctic and Magellanic Provinces contains an extraordinarily high proportion (14 out of 29, 48.3%) of genera known only from their type species. In comparison, of 33 genera of boreal Buccinidae, only 5 (15.2%) are monotypic. When plotted by depth (Figure 140), it is evident that the abyssal fauna has a much higher fraction of such genera. The bathymetric distribution of monotypic genera at abyssal depths in the Southern Ocean appears to be the inverse of that predicted by a plot of species per genus ratios against depth (Rex, 1983: fig. 4). Based on samples from the NW Atlantic Ocean, the number of species per genus actually peaks between 2000 and 3000 m. Data are insufficient to determine if this pattern represents a real biological phenomenon (true monotypy as the result of an early adaptive radiation into the deep-sea around Antarctica without subsequent diversification), or is an artefact of low sampling density exacerbated by difficulties in differentiating closely related species. As noted by Gage and Tyler (1991: 204), the few large data sets that are available for deep-sea faunas have produced rarefaction curves that do not even approach their asymptote, the point at which additional sampling will no longer discover new taxa. While buccinoidean genera have his-
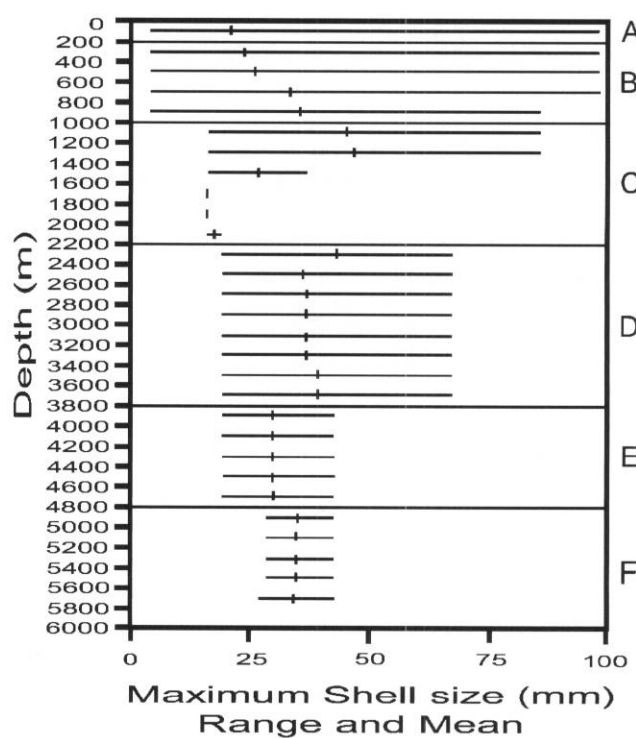
torically been based on features of the shell, operculum and radula, species within genera tend to have very similar opercula and radulae, and are usually differentiated primarily on shell morphology. Increases in latitude and depth each contribute to a reduction in the amount of calcium carbonate in seawater, which, in turn, has profound effects on shell thickness, geometry and the presence of sculpture (Graus, 1974). High latitude and deepwater gastropods often have shells that are thin, roughly spherical (minimizing the ratio of surface area to volume), and lack pronounced surface sculpture. There are numerous examples in the Antarctic fauna of such convergent ecophenotypic similarities in shell form obscuring phylogenetic relationships, even at the level of families and superfamilies (e.g., discussions of *Tromina* and *Notoficula* in Appendix 1; Kantor and Harasewych, 1999, 2000). Some of the genera now regarded as monotypic will likely be discovered to contain additional cryptic or sibling species with similar shell and/or radular morphologies when investigated using molecular or multivariate morphometric techniques.

A number of authors (e.g., Lipps and Hickman, 1982; Gage and Tyler, 1999) have noted the prevalence of both gigantism and small body size in organisms from the Antarctic and the deep-sea. Rex et al. (1999) reported that size increases significantly with depth from upper bathyal region to the abyssal plain for the related neogastropod family Turridae. They suggested that larger size may be favored at greater depths because of its met-

abolic and competitive advantages, and noted that the density of polychaete worms, a major food source for Turridae as well as buccinoideans (Taylor, 1978), decreases exponentially with depth.

We plotted the range and mean of maximum shell sizes of all genera occurring within each 200 m bathymetric increment (Figure 141). The continental shelf and upper continental slope support the largest as well as the smallest buccinoidean genera, with the range in size narrowing as depth increases. The mean of the maximum sizes of genera increases from the continental shelf to the lower slope, before decreasing abruptly at the base of the continental slope. The trend of decreasing size range with increasing depth is repeated in the abyssal fauna, with the largest genera and the broadest range in size occurring along the continental rise. Despite the differences in taxa, ocean basins, and sample sizes between the work of Rex et al. (1999: fig. 2) and the present study, both indicate that taxa inhabiting the base of the continental slope are smaller than those of either the upper slope or continental rise, and that maximum shell size is reached near the boundary of the continental rise and abyssal plain, and subsequently decreases with increasing depth.

ACKNOWLEDGMENTS

LITERATURE CITED

Arnaud, P. M. 1972. Invertébrés marins des XIIème et XVème expéditions antarctiques françaises en Terre Adélie 8.—Gastéropodes Prosobranches. Téthys Supplement 4: 105–134.

Barnard, K. H. 1963. Deep sea Mollusca from west of Cape Point, South Africa. Annals of the South African Museum 46: 407–452.

Bouchet, P. and A. Warén. 1985. Revision of the Northeast Atlantic Bathyal and Abyssal Neogastropoda, excluding Turridae (Mollusca, Gastropoda). Bolletino Malacologico, Supplement 1: 121–196.

Bouchet, P. and A. Warén. 1986. Mollusca: Gastropoda: Taxonomical notes on tropical deep water Buccinidae with descriptions of new taxa. Mémoires Muséum national d'Histoire naturelle, Sér A, Zool. 133: 457–499, pls. 1–18.

Brandt, R. A. M. and P. Temcharoen. 1971. The molluscan fauna of the Mekong at the foci of Schistosomiasis in South Laos and Cambodia. Archiv für Molluskenkunde 101: 111–140.

Cernohorsky, W. O. 1977. The taxonomy of some Southern Ocean Mollusca (Gastropoda) mainly Antarctic and subantarctic. Records of the Auckland Institute and Museum 14: 105–119.

Clarke, A. H. 1961. Abyssal mollusks from the South Atlantic Ocean. Bulletin of the Museum of Comparative Zoology 125(12): 345–387, pls. 1–4.

Clarke, A. H. 1962. Annotated List and Bibliography of the Abyssal Marine Molluscs of the World. National Museum of Canada Bulletin No. 181, pp. vi + 114.

Conrad, L. J. 1999. Bibliography of Antarctic Exploration. Expedition Accounts from 1768–1960. L. J. Conrad, Washougal, Washington, xv + 424 pp.

Cossmann, M. 1906. Essais de paléontologie comparée. Livraison 4. Chez L'Auteur, Paris. 293 pp., 10 pls.

Dall, W. H. 1902. Illustrations and descriptions of new, unfigured, or imperfectly known shells, chiefly American, in the U. S. National Museum. Proceedings of the United States National Museum 24: 499–566, pls. 27–40.

Dall, W. H. 1918. Changes in and additions to molluscan nomenclature. Proceedings of the Biological Society of Washington 31: 137–138.

Dall, W. H. 1919. Descriptions of new species of Mollusca from the North Pacific Ocean in the collection of the United States National Museum. Proceedings of the United States National Museum 56(2295): 293–371.

Dall, W. H. 1925. Illustrations of unfigured types of shells in the collection of the United States National Museum. Proceedings of the United States National Museum 66(2554): 1–41, pls. 1–36.

Dell, R. K. 1972. A new genus of Antarctic buccinid gastropod. Records of the Dominion Museum 8(7): 115–119.

Dell, R. K. 1990. Antarctic Mollusca, with special reference to the fauna of the Ross Sea. Royal Society of New Zealand, Bulletin 27, 311 pp.

Finlay, H. J. 1928. The Recent Mollusca of the Chatham Islands. Transactions of the New Zealand Institute 59: 232–286.

Gage, J. D. and P. A. Tyler. 1991. Deep-sea biology, a natural history of organisms at the deep-sea floor. Cambridge University Press, Cambridge, xvi + 504 pp.

GEBSCO97. 1997. Digital Bathymetric Atlas. British Oceanographic Data Centre, Birkeenhead. CD-ROM.

Graus, R. R. 1974. Latitudinal trends in the shell characteristics of marine gastropods. Lethaia 7: 303–314.

Habe, T. and J. Sato. 1973. A classification of the family Buccinidae from the North Pacific. Proceeding of the Japanese Society of Systematic Zoology 8: 1–8, pls. 1, 2.

Hain, S. G. 1990. Beiträge zur Biologie der beschalten Mollusken (Kl. Gastropoda und Bivalvia) des Weddellmeeres, Antarktis. Berichte zur Polarforschung 70: 1–181.

Harasewych, M. G., S. L. Adamkewicz, J. A. Blake, D. Saudek, T. Spriggs and C. J. Bult. 1997. Neogastropod Phylogeny: A Molecular Perspective. Journal of Molluscan Studies 63: 327–351.

Harasewych, M. G. and Yu. I. Kantor. 1999. A revision of the Antarctic genus *Chlanidota* (Gastropoda: Neogastropoda: Buccinulidae). Proceedings of the Biological Society of Washington 112: 253–302.

Harasewych, M. G., Yu. I. Kantor and K. Linse. 2000. *Parabuccinum*, a new genus of Magellanic Buccinulid (Gastropoda: Neogastropoda), with a description of a new species. Proceedings of the Biological Society of Washington 113: 542–560.

Hutton, F. W. 1880. Manual of the New Zealand Mollusca, a systematic and descriptive catalogue of the marine and land shells, and of the soft mollusks and polyzoa of New Zealand and the adjacent islands. James Hughes, Wellington, pp. xvi + iv + 224.

Kantor, Yu. I. 1996. Phylogeny and relationships of Neogastropoda. *In:* J. D. Taylor (ed.): Origin and evolutionary radiation of Mollusca. Oxford University Press, Oxford, pp. 221–230.

Kantor, Y. I. and M. G. Harasewych. 1999. Rediscovery of the Antarctic species *Sipho gaini* Lamy, 1910 (Gastropoda: Neogastropoda) with remarks on its taxonomic position. Antarctic Research 11: 431–436.

Kantor, Yu. I. and M. G. Harasewych. 2000. *Obscuranella papyrodes,* a new genus and species of abyssal Tonnoidean Gastropod from Antarctica. The Nautilus 114: 103–111.

Kantor, Yu. I. and R. N. Kilburn. 2001. Rediscovery of *Canidia dorri* Wattlebed, 1886, with a discussion of its systematic position (Gastropoda: Neogastropoda: Nassariidae: *Nassodonta*). The Nautilus 115: 99–104.

Linse, K. 2002. The Shelled Magellanic Mollusca: with special reference to biogeographic relations in the Southern Ocean. Theses Zoologicae 34: vii + 252 pp.

Lipps, J. H. and C. S. Hickman. 1982. Origin, age, and evolution of Antarctic and deep-sea faunas. *In:* W. G. Ernst and J. G. Morin (eds). The Environment of the Deep Sea. Prentice-Hall, Englewood Cliffs, pp. 324–356.

Lus, V. Ya. 1978. New genus and species of Buccinidae (Mollusca: Prosobranchia, Buccinidae) from the lower abyssal zone of Idzu-Bonin Trench in the Pacific Ocean. Proceedings of the P. P. Shirsov Institute of Oceanology 113: 147–156. [In Russian, English summary].

Lus, V. Ya. 1989. The deepest gastropods Buccinacea (Neogastropoda: Buccinacea). Proceedings of the P. P. Shirsov Institute of Oceanology 123: 151–164. [In Russian, English summary].

Lus, V. Ya. 1993. New species of *Tromina* (Neogastropoda, Buccinulidae, *Tromina*) from low abyssal of Antarctic trenches, Lorie and Orkney. Proceedings of the P. P. Shirsov Institute of Oceanology 127: 176–197. [In Russian, English summary].

McCune, B. and M. J. Mefford. 1999. PC-ORD. Multivariate Analysis of Ecological Data, Version 4. MjM Software Design, Gleneden Beach, Oregon.

Numanami, H. 1996. Taxonomic study on Antarctic gastropods collected by Japanese Antarctic Research Expeditions. Memoirs of National Institute of Polar Research Series E (Biology and Medical Science) 39: 1–244.

Oliver, P. G. 1983. *Notoficula* Thiele, a neotenous genus of Eratoid gastropod from Antarctica. British Antarctic Survey Bulletin 61: 1–6.

Olsson, A. A. 1971. Mollusks from the Gulf of Panama collected by the R/V John Elliott Pillsbury, 1967. Bulletin of Marine Science 21: 35–92.

Ponder, W. F. 1973. A review of the Australian species of *Penion* Fischer (Neogastropoda: Buccinidae). Journal of the Malacological Society of Australia 2: 401–428.

Ponder, W. F. 1974. The origin and evolution of the Neogastropoda. Malacologia 12: 295–338.

Ponder, W. F. 1982. A new genus and species of Buccinidae (Mollusca: Gastropoda) from the continental slope of eastern and southern Australia. Journal of the Malacological Society of Australia 5: 201–207.

Ponder, W. F. and D. L. Lindberg. 1996. Gastropod Phylogeny—Challenges for the 90's. *In:* J. Taylor (ed). Origin and Evolutionary Radiation of the Mollusca. Oxford University Press, Oxford, pp. 135–154.

Ponder, W. F. and A. Warén. 1988. Classification of the Caenogastropoda and Heterostropha—a list of the family group names and higher taxa. Malacological Review Supplement 4: 288–326.

Powell, A. W. B. 1929. The Recent and Tertiary species of the Genus *Buccinulum* in New Zealand, with a review of related genera and families. Transactions of the New Zealand Institute 60: 57–98.

Powell, A. W. B. 1951. Antarctic and Subantarctic Mollusca: Pelecypoda and Gastropoda. Discovery Reports 26: 47–196, pls. 5–10.

Powell, A. W. B. 1958. Mollusca from the Victoria-Ross Quadrants of Antarctica. B.A.N.Z. Antarctic Research Expedition (1929–1931). Report Series B. (Zoology & Botany) 6(9): 165–215.

Powell, A. W. B. 1960. Antarctic and Subantarctic Mollusca. Records of the Auckland Institute and Museum 5 (3 and 4): 117–193.

Rex, M. A. 1977. Zonation in deep-sea gastropods: the importance of biological interactions to rates of zonation. *In:* B. F. Keegan, P. Ó Céidigh, and P. J. S. Boaden (eds.). Biology of Benthic Organisms. Pergammon Press, New York. pp. 521–530.

Rex, M. A. 1981. Community structure in the deep-sea benthos. Annual Review of Ecology and Systematics 12: 331–353.

Rex, M. A. 1983. Geographical patterns of species diversity in the deep-sea benthos. *In:* The Sea G. T. Rowe (ed). John Wiley, New York. Volume 8, pp. 453–472.

Rex, M. A., R. J. Etter, A. J. Cain and M. S. Hill. 1999. Bathymetric patterns of body size in deep-sea gastropods. Evolution 53: 1298–1301.

Suter, H. 1913. Manual of the New Zealand Mollusca. John Mackay, Wellington. xvi + 1120 pp.

Taylor, J. D. 1978. The diet of *Buccinum undatum* and *Neptunea antiqua* (Gastropoda: Buccinidae). Journal of Conchology 29: 309–318.

Thiele, J. 1904. Die beschalten Gastropoden der deutschen Tiefsee-Expedition 1898–1899. B. Anatomisch-systematische Untersuchungen einiger Gastropoden. Wissenschaftliche Ergebnisse der deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 7: 147–180, pls. 6–9.

Thiele, J. 1912. Die antarktischen Schnecken und Muscheln. Deutschen Sudpolar-Expedition 1901–1903. Vol. 13: 183–285, pls. 11–19.

Thiele, J. 1929. Handbuch der systematischen Weichtierkunde. G. Fischer, Stuttgart, 1–376.

Tomlin, J. R. Le B. 1932. Reports on the marine Mollusca in the collections of the South African Museum. VI–VIII. Annals of the South African Museum 30(2): 157–169.

Tracey, S., J. A. Todd and D. H. Erwin. 1993. Mollusca: Gastropoda. *In:* M. J. Benton (ed), The Fossil Record 2. Chapman and Hall, London, pp. 137–167.

Warén, A. and P. Bouchet. 2001. Gastropoda and Monoplacophora from hydrothermal vents and seeps; new taxa and records. The Veliger 44: 116–231.

Wenz, W. 1938–1943. Gastropoda. Allgemeiner Teil und Prosobranchia. *In:* O. H. Schindewolf (ed). Handbuch der Paläozoologie. Gebrüder Borntraeger, Berlin, pp. 1–1506.

Appendix 1. A review of the taxonomic placement of the genera of Antarctic and Magellanic Buccinulidae.

The family Buccinulidae was proposed by Finlay (1928: 250) to unite a number of genera from the region of New Zealand that had previously been included in Muricidae, Neptuniidae (as Chrysodomidae), and Buccinidae by earlier workers (Hutton, 1880; Cossmann, 1906; Suter, 1913). Shortly thereafter, Powell (1929: 58) expanded and revised Finlay's classification based mainly on the morphology of the radula, sorting primarily austral genera into the families:

Buccinulidae. Recognized by having a radula with 3 cusps on rachidian teeth and 3 cusps on lateral teeth, and an operculum with a terminal nucleus. This family was further subdivided into groups A–E based on morphology of the siphonal canal, parietal tubercle, and protoconch.

Neptuniidae. Recognized by having a radula with 4 cusps on rachidian teeth and 3 cusps on lateral teeth. The operculum also has a terminal nucleus.

Buccinidae. Characterized by having a radula with about 6 cusps on rachidian teeth and 4 cusps on lateral teeth. The operculum has a median, submarginal nucleus.

Cominellidae. Distinguished by having a radula with 3 cusps on rachidian teeth, 2 cusps on lateral teeth, and an operculum with a terminal nucleus.

Published the same year, Thiele's (1929) treatment of the Stenoglossa interpreted the family Buccinidae far more broadly, subsuming all of the families treated by Powell (1929) without recognizing any natural groupings or subdivisions. Powell (1951: 131) proposed a revised classification of the southern whelks, reaffirming his earlier (Powell, 1929) narrower interpretation of Buccinidae (limited to the genera *Buccinum* Linné, 1758 and *Burnupena* Iredale, 1918), and stating that the Buccinulidae were more closely related to the northern Neptuniidae than to the Buccinidae. He subdivided the Buccinulidae into the subfamilies Buccinulinae, Prosiphiinae and Cominellinae. In subsequent works, Powell (1960) again elevated Cominellinae to family status. In the section below, we list chronologically the genera originally assigned to each subfamily by Powell (1951), update the systematics for Antarctic and Magellanic genera, and add genera from this region that were published subsequently.

Family Buccinulidae Finlay, 1928

Subfamily Buccinulinae Finlay, 1928.
Defined on the basis of a radula with three cusps on the rachidian teeth and three cusps on the lateral teeth. Originally included genera:

New Zealand: *Buccinulum* Swainson, 1837; *Aeneator* Finlay, 1926; *Verconella* Iredale, 1915.
Australia: *Austrosipho* Cossmann, 1906; *Berylsma* Iredale, 1924.
California: *Kelletia* Bayle, 1884.

Antarctic and Subantarctic: *Chlanidota* Martens, 1878; *Pfefferia* Strebel, 1908 (reduced to a subgenus of *Chlanidota* by Harasewych and Kantor, 1999); *Neobuccinum* Smith, 1877; *Probuccinum* Thiele, 1912; *Cavineptunea* Powell, 1951; *Bathydomus* Thiele, 1912. [additional genera: *Chlanificula* Powell, 1958; *Antarctoneptunea* Dell, 1972; *Parabuccinum* Harasewych, Kantor and Linse, 2000; *Spikebuccinum* Harasewych and Kantor, herein; *Drepanodontus* Harasewych and Kantor, herein].

Neobuccinum Smith, 1877

Type Species: *Buccinopsis eatoni* Smith, 1875 (by monotypy).
Distribution: Circum-Antarctic, Kerguelen and Heard Islands, in 6–1335 m.
Remarks: Shell large (to 86 mm). Operculum large, occupying nearly entire aperture, oval, paucispiral. Rachidian teeth with 3 strong cusps, broad basal plate. Lateral teeth with 3 cusps, middle cusp small.
Diversity: Currently a monotypic genus. Numanami (1996: 147) noted some geographical differences in shell morphometry.

Chlanidota (*Chlanidota*) Martens, 1878

Type Species: *Cominella* (*Chlanidota*) *vestita* Martens, 1878 (by monotypy).
Distribution: Circum-Antarctic. Kerguelen Island, the Crouzets, Herald Island, South Georgia Island, Antarctica, in 3–1100 m.
Remarks: Shell medium-sized (to 43 mm). Operculum very small (less than 0.4 AL), coiled, with terminal nucleus. Rachidian teeth with 3 strong cusps, broad, anteriorly indented basal plate, lateral teeth with 3 cusps, middle cusp small.
Diversity: 5 species (recent revision—Harasewych and Kantor, 1999).

Chlanidota (*Pfefferia*) Strebel, 1908

Type species: *Pfefferia palliata* Strebel, 1908 (by subsequent designation, Wenz, 1943).
Distribution: South Georgia Island, in 45–1600 m.
Remarks: Shell medium-sized (to 38 mm). Operculum large (0.5–0.8 AL), leaf-shaped, coiled, with terminal nucleus. Posterior edge of operculum with tall ridge of feathered lamellae. Rachidian teeth with 3 strong cusps, broad, anteriorly indented basal plate. Lateral teeth with 3 cusps, middle cusp small.
Diversity: 3 species (recent revision—Harasewych and Kantor, 1999).

Probuccinum Thiele, 1912

Type species: *Neobuccinum tenerum* Smith, 1907 (by subsequent designation, Wenz, 1943).

Distribution: Circum-Antarctic, in 50–590 m.
Remarks: Shell medium-sized (to 30 mm). Operculum large (~⅔ AL), with terminal nucleus. Rachidian teeth with 3 cusps, central cusp largest, may bear denticles (Numanami, 1996: fig. 104H); basal plate broad, rectangular. Lateral teeth with 3 cusps of approximately equal size.
Diversity: 8 species (Powell, 1960).

Bathydomus Thiele, 1912

Type species: *Bathydomus obtectus* Thiele, 1912 (by original designation).
Distribution: Antarctic, Marion Island and Crozets, in 2500–3400 m.
Remarks: Shell medium-sized (to 30 mm). Operculum large (~0.5 AL) long, narrow, wedge-shaped, with terminal nucleus. Rachidian teeth with 3 strong cusps, middle cusp largest, flanked by 1 weak denticles on each side. Basal plate broad, squarish, anteriorly indented. Lateral teeth with 2 large cusps with 2–3 smaller cusps between them (Thiele, 1912: pl. 16, fig. 23).
Diversity: 3 species (Dell, 1990: 198).

Cavineptunea Powell, 1951

Type species: *Cavineptunea monstrosa* Powell, 1951 (by original designation).
Distribution: South Georgia Island, in 90–700 m.
Remarks: Shell large (to 70 mm), with characteristic protoconch, "like a tall, spirally wound collar, and surrounds a deep apical cavity" (Powell, 1951: fig. N105). Operculum large (~⅔ AL), with terminal nucleus. Rachidian teeth with 3 cusps, central cusp largest, broad, anteriorly indented basal plate. Lateral teeth usually with 3, occasionally 4 cusps, outermost cusps largest.
Diversity: A monotypic genus.

Chlanificula Powell, 1958

Type species: *Chlanificula thielei* Powell, 1958 (by original designation).
Distribution: Weddell Sea to off Enderby Land, Antarctica, in 220–660 m.
Remarks: Shell medium-sized (to 30 mm). Operculum large, occupying nearly entire aperture, narrow, wedge-shaped, with terminal nucleus. Rachidian teeth with strong central cusp, flanked by one smaller cusp and one denticle on each side. Basal plate squarish, shallowly indented anteriorly. Lateral teeth with 3 cusps, middle cusp smaller, additional denticles may appear between cusps (Hain, 1990: pl. 23, fig. 2). Powell (1958) regarded this genus to be part of the "*Chlanidota* complex" closest to *Notoficula*. The genus *Notoficula* Thiele, 1917, has been transferred to Eratoidae by Oliver (1983) based on radular morphology.
Diversity: A monotypic genus.

Antarctoneptunea Dell, 1972

Type species: *Fusitriton aurora* Hedley, 1916 (by original designation).
Distribution: Ross Sea to off Enderby Land, Antarctica, 15–603 m.
Remarks: Shell large (to 102 mm). Operculum large (~⅔ AL), with terminal nucleus. Rachidian teeth with three cusps. Basal plate broad, deeply indented anteriorly. Lateral teeth with 3 cusps, middle cusp smaller. This genus is hardly distinguishable from *Penion* Fischer, 1884 in general shell shape, radula and operculum (Ponder, 1973).
Diversity: A monotypic genus.

Parabuccinum Harasewych, Kantor and Linse, 2000

Type species: *Chlanidota bisculpta* Dell, 1990 (by original designation).
Distribution: Magellanic region, in 247–2165 m.
Remarks: Shell small (to 16.5 mm). Operculum large (> 0.5 AL), oval, paucispiral. Rachidian teeth with 3 strong cusps, broad, anteriorly indented basal plate. Lateral teeth with 3 cusps, middle cusp small. Included in Buccinulinae by Harasewych, Kantor and Linse (2000).
Diversity: 4 species (recent revision—Harasewych, Kantor and Linse, 2000).

Spikebuccinum Harasewych and Kantor, herein.

Type species: *Spikebuccinum stephaniae* Harasewych and Kantor, herein (by original designation).
Distribution: Scotia Sea and adjacent abyssal plains, in 1967–4645 m.
Remarks: Shell small (to 19.9 mm). Operculum small (~0.36 AL), broadly ovate, paucispiral, with subterminal nucleus. Rachidian teeth with 3 cusps, central shorter, weaker that outer cusps. Basal plate broad, deeply indented. Lateral teeth with large outer, smaller inner cusp, with 3–4 smaller denticles between them.
Diversity: A monotypic genus.

Drepanodontus Harasewych and Kantor, herein.

Type species: *Drepanodontus tatyanae* Harasewych and Kantor, herein (by original designation).
Distribution: Scotia Sea and adjacent Argentine Abyssal Plain, in 2740–5798 m.
Remarks: Shell large (to 43.1 mm). Operculum large (~0.82 AL), oval, with terminal nucleus. Rachidian teeth usually with 3 cusps, central cusp large, may or may not be flanked by one lateral cusp and additional denticles. Basal plate narrow, rectangular, weakly indented. Lateral teeth with 1 cusp, which may bear 1 or more denticles, near inner edge of basal plate.
Diversity: A monotypic genus.

Subfamily Prosiphiinae Powell, 1951

Defined on the basis of a radula with 3 cusps on the rachidian teeth, and lateral teeth with multiple cusps.

Contains taxa with heterogeneous lateral tooth morphologies, that may be divided into: *Proneptunea* type lateral teeth, with multiple cusps spanning the width of the basal plate, usually fused above the basal plate, may have one or more denticles along the outer edge; *Prosipho* type lateral teeth, with cusps confined to inner portion of basal plate, often rotated to form an acute angle with the basal plate, the outer portion of which is thin and lacks teeth. Prosiphiinae appear to be restricted to Antarctic and subantarctic seas. Originally included genera:

Antarctic and subantarctic: *Proneptunea* Thiele, 1912; *Meteuthria* Thiele, 1912; *Prosipho* Thiele, 1912; *Anomacme* Strebel, 1905; *Fusinella* Thiele, 1917 (replacement name for *Buccinella* Thiele, 1912, non Perry, 1811); *Chlanidotella* Thiele, 1929. [additional genera: *Savatieria* Rochebrune and Mabille, 1885; *Crenatosipho* Linse, 2002; *Muffinbuccinum* Harasewych and Kantor, herein; *Germonea* Harasewych and Kantor, herein].

Savatieria Rochebrune and Mabille, 1885

Type species: *Savatieria frigida* Rochebrune and Mabille, 1885 (by monotypy).
Distribution: Magellanic region, in 100 m.
Remarks: Shell small (usually < 10 mm). Operculum large, oval, with terminal nucleus. Radula *Prosipho* type. Rachidian teeth narrow, with 3 cusps. Lateral teeth with 4 short, broad cusps, basal plate prolonged anteriorly.
Diversity: 7 species (Powell, 1960: 149).

Anomacme Strebel, 1905

Type species: *Anomacme smithi* Strebel, 1905 (by monotypy).
Distribution: Magellanic region, 220–250 m.
Remarks: Shell small (< 10 mm). Operculum not described. Radula *Prosipho* type. Rachidian teeth with 3 cusps, basal plate squarish, broader than long, weakly indented anteriorly. Lateral teeth with long, narrow basal plate, with 6 cusps concentrated toward the inner portion of the radular tooth, 4th cusp longest (Thiele, 1912: pl. 16, fig. 14). This genus was included in Cominellidae by Powell (1960: 149), presumably because of its similarity in shell shape to *Glypteuthria,* despite its different radular morphology.
Diversity: A monotypic genus.

Proneptunea Thiele, 1912

Type species: *Proneptunea amabilis* Thiele, 1912 (by original designation).
Distribution: Kerguelen, South Georgia Island, South Orkney Islands, Ross Sea, Antarctica, in 12–870 m.
Remarks: Shell small (< 15 mm). Operculum medium-sized, oval, with terminal nucleus. Radula *Proneptunea* type. Rachidian teeth with 3 cusps. Basal plate longer than wide, shallowly indented anteriorly. Lateral

teeth broad, spatulate, with 5 long cusps fused above basal plate. Outer edge may have multiple denticles (Powell, 1951: fig. K 66–67).
Diversity: 5 species (Dell, 1990: 199).

Meteuthria Thiele, 1912

Type species: *Euthria martensi* Strebel, 1905 (by original designation).
Distribution: Magellanic region, and Ross Sea, Antarctica, in 57–870 m.
Remarks: Shell very small (< 5 mm). Operculum undescribed. Radula *Prosipho* type, without rachidian teeth. Lateral teeth with multiple (4–5) cusps concentrated toward inner portion of tooth. Outermost cusp may have denticles (Powell, 1951: fig. K62; Dell, 1990: fig. 296). This genus was included in the subfamily Cominellidae by Powell (1960: 149), presumably because of its similarity in shell shape to *Glypteuthria,* despite its different radular morphology.
Diversity: 4 species, 1 subspecies (Powell, 1960: 149; Dell, 1990: 173).

Prosipho Thiele, 1912

Type species: *Prosipho gaussianus* Thiele, 1912 (by subsequent designation, Thiele, 1929).
Distribution: Circum-Antarctic, in 12–800 m.
Remarks: Shell small, rarely > 10 mm. Operculum large (~⅔ AL), oval, with coiled nucleus. Radula *Prosipho* type. Rachidian teeth with 3 cusps, basal plate squarish to longer than broad, weakly indented anteriorly. Lateral teeth with long, narrow basal plate, with 2 or more cusps concentrated toward the inner portion of the radular tooth.
Diversity: About 40 species (Powell, 1951; Dell, 1990; Numanami, 1996).

Fusinella Thiele, 1917 (replacement name for *Buccinella* Thiele, 1912, non Perry, 1811)

Type species: *Buccinella jucunda* Thiele, 1912 (by monotypy).
Distribution: Kerguelen Island, 0–100 m.
Remarks: Shell very small (< 6 mm). Operculum oval, with terminal nucleus. Radula *Prosipho* type. Rachidian teeth with 3 cusps of equal size near center, with an additional cusp at each posterior corner of the squarish basal plate with a deep, V-shaped indentation anteriorly. Lateral teeth with long, narrow basal plate, with multiple (5–6) cusps concentrated along inner half of basal plate and directed parallel to its long axis (Thiele, 1912: pl. 16, fig. 13).
Diversity: A monotypic genus.

Chlanidotella Thiele, 1929

Type species: *Cominella modesta* Martens, 1885 (by monotypy).

Distribution: South Georgia, 0–18 m.
Remarks: Shell medium-sized (< 15 mm). Operculum medium-sized (~0.5 AL), oval, with terminal nucleus. Radula *Proneptunea* type. Rachidian teeth with 3 cusps, central cusp slightly longer than flanking cusps. Basal plate broader than long, deeply indented anteriorly. Lateral teeth with 4 cusps roughly equal in length, spanning the entire width of the basal plate. Thiele's illustration (1912: textfig. 11) of the radula shows a denticle along the outer edge along one side of the radula, while Powell's illustration (1951: fig. L 80) does not.
Diversity: A monotypic genus.

Crenatosipho Linse, 2002

Type species: *Crenatosipho beaglensis* Linse, 2002 (by original designation).
Distribution: Magellanic region, in 67–200 m.
Remarks: Shell small (to 9 mm). Operculum large, oval with eccentric nucleus. Radula *Prosipho* type. Rachidian teeth very narrow, long, without cusps. Lateral teeth with up to 6 cusps long concentrated toward the inner margin of the tooth, with long, cuspless outer portion of the basal plate. (Linse, 2002: fig. 9.1.1–112).
Diversity: A monotypic genus.

Muffinbuccinum Harasewych and Kantor, herein

Type species: *Muffinbuccinum catherinae* Harasewych and Kantor, herein (by original designation).
Distribution: Argentine Abyssal Plain, off the northern slope of the Falkland Plateau, in 5685–5798 m.
Remarks: Shell of moderate size (to 27 mm). Operculum large (~0.56 AL), triangular, tapering toward terminal nucleus. Radula *Proneptunea* type. Rachidian teeth with 3 cusps, central cusp slightly longer than flanking cusps. Basal plate broad, short, shallowly indented anteriorly. Lateral teeth with 7–8 cusps spanning basal plate, innermost cusp longest, outermost shortest, with or without denticles along outer edge.
Diversity: A monotypic genus.

Germonea Harasewych and Kantor, herein

Type species: *Germonea rachelae* Harasewych and Kantor, herein (by original designation).
Distribution: Abyssal plain of the Scotia Sea, in 2196–3714 m.
Remarks: Shell large (to 68 mm). Operculum large (~0.65 AL), narrow, recurved, with terminal nucleus. Radula *Prosipho* type. Rachidian teeth with 3 cusps, very long, narrow, deeply indented anteriorly, appearing Y-shaped. Lateral teeth with 3–4 broad, stout cusps concentrated toward the inner margin of the tooth, with short, cuspless outer portion of the basal plate.
Diversity: A monotypic genus.

Subfamily Cominellinae Gray, 1857

Defined on the basis of a radula with 3 cusps on the rachidian tooth, and lateral teeth with 2 cusps. Originally included genera:
New Zealand and Australia: *Cominella* Gray, 1850; *Fax* Iredale, 1925.
Tropical Pacific: *Phos* Montfort, 1810.
Northwest Pacific: *Searlesia* Harmer, 1914.
Antarctic and Subantarctic: *Pareuthria* Strebel, 1905; *Tromina* Dall, 1918; *Notoficula* Thiele, 1917 [now in Eratoidae]; *Falsimohnia* Powell, 1951; *Glypteuthria* Strebel, 1905. [additional genera: *Antistreptus* Dall, 1902; *Parficulina* Powell, 1958; *Antarctodomus* Dell, 1972; *Lusitromina* Harasewych and Kantor, herein].

Antistreptus Dall, 1902

Type species: *Antistreptus magellanicus* Dall, 1902 (by original designation).
Distribution: Magellanic region, in 30–600 m.
Remarks: Shell very small (< 5 mm), sinistral. Operculum described but not figured by Linse (2002: 100) as "small, horny, brown, thin, eccentric, with a large oval foot muscle scar." The radula is unknown. Apart from being sinistral, shell shape is similar to *Glypteuthria* and *Anomacme*. This genus was described within Muricidae and compared to *Trophon* by Dall (1902). Powell (1951) included it in Buccinulidae, but later placed it in Cominellidae (Powell, 1960).
Diversity: 2 species, *Antistreptus magellanicus* Dall, 1902, *A. rolani* Castellanos, 1985.

Pareuthria Strebel, 1905

Type species: *Fusus plumbeus* Philippi, 1844 (by subsequent designation, Tomlin, 1932).
Distribution: Magellanic region, Circum-Antarctic, in 0–549 m.
Remarks: Shell small (< 10 mm). Operculum ovate, with terminal nucleus. Despite shell similarities between Magellanic and Antarctic species, there are conspicuous differences in radular dentition between species inhabiting these regions. Magellanic species, including the type species of the genus, have broad rachidian teeth with 3 subequal cusps. Antarctic species have rachidian teeth with squarish basal plates and a large triangular central cusp that may or may not be flanked by one or rarely more (Numanami, 1996: fig. 125D), smaller denticles on each side. Lateral teeth with long, stout basal plates that give rise to 2 long, recurved cusps.
Diversity: About 18 species (Powell, 1960; Numanami, 1996).

Glypteuthria Strebel, 1905

Type species: *Euthria meridionalis* Smith, 1881 (by subsequent designation, Tomlin, 1932).

Distribution: Magellanic region, Southern Africa, in 6–250 m.

Remarks: Shell medium-sized (< 29 mm). Operculum ovate, with terminal nucleus. Rachidian teeth with 3 cusps on squarish, posteriorly indented basal plate. Lateral teeth with broad basal plate, 3 cusps, inner and outer cusps long, intermediate cusp short. Powell (1951: 138) regarded *Glypteuthria* to be a strongly sculptured relative of *Pareuthria*, with the intermediate cusp a bifurcation of the inner cusp, and not comparable to the 3rd cusp of *Probuccinum*.

Diversity: 7 species, 4 Magellanic, 3 South African.

Notoficula Thiele, 1917 (New name for *Ficulina* Thiele, 1912, *non* Gray, 1867)

Type species: *Ficulina bouveti* Theile, 1912 (by monotypy). The anatomy, radular morphology, and operculum of the type species remain unknown. Oliver (1983) described an additional species of *Notoficula*, and, based on its radular morphology and anatomy, transferred the genus to Eratoidae. Powell (1958: 192) reconsidered the affinities of the species he originally described as *Notoficula problematica* Powell, 1951, and erected the genus *Parficulina* Powell, 1958 to accommodate it (see below).

Tromina Dall, 1918

Type species: *Fusus unicarinatus* Philippi, 1868 (by original designation). The type species of this genus was shown to belong to the family Muricidae. Dell (1990) proposed the name *Falsitromina* to include the bathyal Magellanic buccinoidean taxa previously included in *Tromina*. The genus *Lusitromina* is proposed herein for the abyssal species that had been assigned to *Tromina*. For a detailed review of the taxonomy of *Tromina*, see the "Remarks" section under the description of *Lusitromina*.

Falsimohnia Powell, 1951

Type species: *Buccinum albozonatum* Watson, 1881 (by original designation).

Distribution: South Georgia, Kerguelen Island, in 18–250 m.

Remarks: Shell small (< 10 mm), operculum small, with blunt, terminal nucleus. Rachidian tooth with single, triangular cusp on squarish basal plate with shallow anterior indentation. Lateral teeth with long basal plate giving rise to 2 teeth, outermost broader, longer. Powell (1951: 137) regarded *Falsimohnia* to be derived from *Pareuthria*.

Diversity: A monotypic genus (see comments under *Antarctodomus* diversity).

Parficulina Powell, 1958

Type species: *Notoficula problematica* Powell, 1951 (by original designation).

Distribution: Magellanic region, in 545 m.

Remarks: Shell small (to 7 mm). Operculum medium sized (~0.50 AL), D-shaped, paucispiral. Rachidian teeth with 3 equal cusps on a squarish basal plate. Lateral teeth with 2 cusps, the inner cusp much broader than the outer cusp. See remarks under *Notoficula* (above).

Diversity: A monotypic genus.

Antarctodomus Dell, 1972

Type species: *Bathydomus thielei* Powell, 1958 (by original designation).

Distribution: Eastern hemisphere, from the Ross Sea to off Queen Maud Land, Antarctica, 110–420 m.

Remarks: Shell medium-sized (to 30 mm). Operculum long, triangular, with terminal nucleus (Dell, 1972). Rachidian tooth with 3 cusps, basal plate broad, short, deeply indented anteriorly. Lateral teeth with 2 long, blunt, cusps, basal plate narrower than rachidian teeth.

Diversity: 2 species (Numanami, 1996: 147. In our view, *Antarctodomus okutanii* Numanami, 1996 differs in opercular and radular morphology from the type species of *Antarctodomus*, and may be referable to *Falsimohnia*).

Falsitromina Dell, 1990

Type species: *Tromina bella* Powell, 1951 (by original designation).

Distribution: Magellanic region, in 81–878 m [Dell (1990: 175) reported but did not illustrate or provide catalog numbers for two specimens he attributed to *F. bella* from the Ross Sea, at depths of 1565–1674 m.]

Remarks: Shell small (to 14 mm). Operculum medium-sized (~0.50 AL), oval, paucispiral. Rachidian teeth with 3 cusps, central cusp may be slightly longer, on a squarish basal plate, shallowly indented anteriorly. Lateral teeth with two broad curved cusps that join above the basal plate.

Diversity: 5 species (Dell, 1990).

Lusitromina Harasewych and Kantor, herein

Type species: *Tromina abyssorum* Lus, 1993 (by original designation).

Distribution: Scotia Sea, and adjacent abyssal plains, Cape Basin, in 2380–5480 m.

Remarks: Shell medium sized (to 29 mm). Operculum D-shaped, large (~0.61 AL), broadly ovate, paucispiral. Rachidian teeth with 3 cusps on posterior portion of broad, anteriorly arched basal plate. Central cusp slightly longer, wider than lateral cusps. Lateral teeth with 2 cusps of approximately equal length.

Diversity: 2 species.