Zootaxa 2744: 1–33 (2011)
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

The Living Columbariinae (Gastropoda: Neogastropoda: Turbinellidae) of New Zealand

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Abstract

The Columbariinae have been represented in the fauna of New Zealand from the Paleocene until the Recent, providing the longest known continuous record for the subfamily. Seven living species, representing the genera *Columbarium*, *Coluzea*, and *Fulgurofusus*, are recognized, and include two species, *Fulgurofusus maxwelli* and *Fulgurofusus marshalli* that are described as new. The New Zealand columbariine fauna is unusually diverse at the generic level, and includes the largest members of the subfamily, as well as the only primarily sublittoral species. The morphology, anatomy, and distribution of the living species are discussed, as are their relationships to living and fossil congeners.

Key words: Neogastropoda, Turbinellidae, Columbariinae, *Columbarium*, *Coluzea*, *Fulgurofusus*, bathyal, new species, biogeography, New Zealand

Introduction

The bathyal to abyssal subfamily Columbariinae Tomlin, 1928, is the most diverse and geographically widespread clade within the family Turbinellidae Swainson, 1835. The remaining subfamilies, the Turbinellinae, and Vasinae H. and A. Adams, 1853, have comparatively few genera and species, are circumtropical, and inhabit depths ranging from the intertidal to the outer continental shelf. Another bathyal clade, the Ptychatractidae Stimpson, 1865, until recently considered a subfamily of Turbinellidae (e.g., Cernohorsky 1973; Harasewych 1998; Kantor *et al*. 2001) has been segregated as a separate family related to the Pseudolividae de Gregorio, 1880 (Bouchet *et al*. 2005: 256). The Tudiclinae Cossmann, 1901, with a single living species endemic to shallow waters of southeastern India, has

Accepted by M. deMaintenon: 21 Dec. 2010; published: 19 Jan. 2011

been included in the Turbinellidae, but is referable to the Buccinidae Rafinesque, 1815, based on the anatomy of its type species (Harasewych in preparation).

Like all turbinellid groups, the Columbariinae have fusiform shells with large protoconchs, tall spires, sculptured peripheries, ovate apertures and long, axial siphonal canals. Opercula are corneous, and have a terminal nucleus. Adaptations of the anterior alimentary system for feeding on tube-dwelling polychaetes [and sipunculans in the case of Vasinae] (Taylor 1984; Taylor & Glover 2003) include: an extremely elongated and narrow proboscis that is withdrawn into a non-evertable proboscis sheath that occupies much of the cephalic hemocoel; a narrow radula with tricuspid rachidian teeth and monocuspid lateral teeth (bicuspid in the case of Vasinae) with expanded basal plates that distribute stresses applied perpendicular to the long axes of the teeth; and large, ascinous salivary glands. Egg capsules and development of Columbariinae remain unstudied, but protoconch morphology indicates direct development, and suggests that the larvae feed on nurse eggs, as do other turbinellids.

Of the 59 described living species of Columbariinae, the vast majority inhabit bathyal depths along the western continental margins of ocean basins. More recent explorations have discovered bathyal columbariines along the eastern margins of the Pacific (McLean & Andrade 1982), and Indian Oceans (Harasewych 1986), as well as species restricted to abyssal depths in the Scotia (Melvill & Standen 1907) and the Bering Seas (Sysoev 2000). Earliest records of the subfamily are from the Late Cretaceous (Maastrichtian) of Europe. Paleocene records are more widespread, ranging from North America to New Zealand. These records as well as those from the Eocene are from shallow water deposits, while younger fossils are usually limited to deep water facies from southeastern Australia and New Zealand (Finlay 1930b; Darragh 1969). The shift of the Columbariinae to deeper water habitats coincided with the development of the psychrosphere, the lower, colder (< 10°C) layer of a two-layer ocean (Benson 1975; Corliss 1979; Benson *et al*. 1984). Table 1 lists the eight genus level taxa that have been included in the Columbariinae. Of these, the genus *Serratifusus* Darragh, 1969, has been transferred to the Buccinidae based on the anatomy of newly discovered living species (Harasewych 1991).

TABLE 1. Genus level taxa attributed to the subfamily Columbariinae.

Columbarium Martens, 1881 (type species: *Pleurotoma* (*Columbarium*) *spinicincta* Martens, 1881, by original designation). Maastrichtian Europe; Paleocene Europe, New Zealand; Lower Eocene SE USA; Upper Eocene-Miocene SE Australia; Recent, SE Africa, Japan, Philippines, South China Sea, eastern Australia, and New Zealand.
Coluzea Finlay *in* Allen, 1926 (type species: *Fusus dentatus* Hutton, 1877, by subsequent designation of Finlay, 1930a:249). Eocene Europe, New Zealand; Recent, southeastern Africa, Madagascar, Thailand, Indonesia, western and northern Australia, New Caledonia, and New Zealand.
Fulgurofusus Grabau, 1904 (type species: *Fusus quercollis* Harris, 1896, by original designation). Paleocene Alabama; Lower Eocene California; Upper Eocene Washington; Recent, Bering Sea, western Atlantic, Caribbean, Scotia Sea, Chile, and New Zealand.
Fustifusus Harasewych, 1991 (type species: *Coluzea pinicola* Darragh, 1987, by original designation). Recent, New Caledonia.
Hispidofusus Darragh, 1969: 67 (type species: *Fusus senticosus* Tate, 1888, by original designation). Lower to Middle Miocene, southeastern Australia.
Histricosceptrum Darragh, 1969: 87 (type species: *Columbarium atlantis* Clench and Aguayo, 1938, by original designation). Recent, Caribbean.
Peristarium Bayer, 1971 (type species: *Columbarium* (*Peristarium*) *electra* Bayer, 1971, by original designation). Recent, Western Atlantic.
Serratifusus Darragh, 1969 (type species: *Fusus craspedotus* Tate, 1888, by original designation). Lower to Middle Miocene, southeastern Australia, Tasmania. Recent, New Caledonia. Transferred to Buccinidae based on anatomy of Recent species by Harasewych 1991.

Most species of Columbariinae are uncommon to rare, known from relatively few specimens, and are generally not well represented in museum collections. The Museum of New Zealand Te Papa Tongarewa, however, houses an exceptionally rich and comprehensive collection of Columbariinae from New Zealand waters that spans many

decades of sampling. This collection serves as the basis for this review of the systematics and biogeography of the living Columbariinae of New Zealand.

Material and methods

The material examined represents all recognized species of Columbariinae living in New Zealand waters, and included preserved or dried animals of all but one of the seven species. Alcohol preserved animals that had previously been removed from their shells often lacked the uppermost whorls. Dried animals were rehydrated and extracted from their shells when alcohol preserved material was not available. Animals were dissected in 70% ethanol. Radulae, protoconchs, and opercula were photographed using a Leica StereoScan 440 Scanning Electron Microscope. The number of protoconch whorls was determined according to the method used by Jablonski and Lutz (1980: fig. 4).

In cases when a depth range was provided with the station data, the bathymetric range for the species is reported as the broadest possible depth range, while the confirmed bathymetric range is the narrowest possible range (e.g. if Specimen A was reported from a depth of 100–200 m, and Specimen B from 400–600 m, the bathymetric range would be 100–600 m, while the confirmed bathymetric range would be 200–400 m). The average, or mid-point of the depth range for each record was used when calculating the average depth for the species, and for plotting bathymetric distributions.

Repositories for examined specimens are indicated by the following abbreviations:

AK	Auckland Museum Tamaki Paenga Hira.
BMNH	The Natural History Museum, London.
DMNH	Delaware Museum of Natural History.
NIWA	National Institute of Water and Atmospheric Research, Wellington
NMNZ	Museum of New Zealand Te Papa Tongarewa
USNM	National Museum of Natural History, Smithsonian Institution.

Systematics

Family TURBINELLIDAE Swainson, 1835

Subfamily Columbariinae Tomlin, 1928

Diagnosis. Shell small to moderate sized (to 127 mm), thin, fusiform, with deviated paucispiral protoconch, sculptured periphery, smooth columella, long, narrow, axial siphonal canal spirally twisted in its distal portion. Opercula strongly ovate, tapering evenly to terminal nucleus, with rounded attachment area, tapered third free. Animal characterized by: extremely long (> shell length), narrow proboscis coiled within a non-evertable proboscis sheath; minute radula; rachidian teeth with 3 simple cusps concentrated along distinctive, central, U-shaped section of basal plate; monocuspid, scythe-like lateral teeth; paired, ascinous salivary glands; absence of accessory glands; small valve of Leiblein; large gland of Leiblein; U-shaped stomach; narrow rectum with small rectal gland. Diet of tubiculous polychaetes. Males with open sperm groove, long, flattened penis with or without terminal papilla. Pallial gonoduct of females consists of: albumen gland, long cylindrical capsule gland, short bursa copulatrix with terminal female opening.

Genus *Columbarium* Martens, 1881

Synonymy:
Pleurotoma (*Columbarium*) Martens, 1881: 105–107, pl.25, figs. 1–4.
Columbarium Piele, 1922: 14, fig. 1; Thiele, 1929: 289, fig. 311; Clench, 1944: 1; Darragh, 1969: 71.

Type species. *Pleurotoma* (*Columbarium*) *spinicinctum* Martens, 1881, by original designation.

Diagnosis. Shell long (to 107 mm), fusiform, with moderately tall spire; shoulder strong, with broad, open, laterally to posteriorly directed spines along periphery; anterior carina strong, usually with scales or open spines; siphonal canal long, stout, axial, with or without spiral bands, scabrous spines along proximal half, smooth, slightly spirally coiled along distal portion. Protoconch bulbous, strongly deviated, first whorl often largest. Suture adpressed onto or slightly above anterior carina of previous whorl. Inner lip of aperture, proximal portion of siphonal canal lined with raised lamina. Shell color white to tan. Pigmentation, when present, darker brown, of axial bands or confined to region between adjacent spines. Rachidian teeth of radula with 3 cusps along U-shaped basal plate lacking significant lateral expansions (Peile 1922: fig. 1; Darragh 1969: fig. 8; Harasewych 1983b: fig. 11).

Remarks. Earliest records attributed to the genus date from the Maastrichtian of Belgium. *Columbarium* has been reported from the Wangaloan (Paleocene) of New Zealand [*Fulgurofusus vulneratus* Finlay & Marwick, 1937 was reassigned to *Columbarium* by Darragh (1969: 73) based on the presence of a columellar lamina that is lacking in *Fulgurofusus*, although Stilwell & Zinsmeister (1992: 117) questioned this reassignment]. *Columbarium pataka* Maxwell, 1978 from the Bortonian (Middle Eocene) Hampden Formation of South Island, was a member of an outer shelf / upper continental slope fauna (Beu *et al*. 1990: 99). Although Maxwell (1978: 38) regarded this species to be more closely related to *Columbarium heberti* Briart & Cornet, 1877, from the Maastrichtian of northern Europe, than to *Columbarium vulneratus*, he questioned its generic assignment (see Remarks under *Coluzea mariae* for a further discussion of this species). *Columbarium maorum* P. Marshall & Murdoch, 1923, from Kaiatan-Runangan (Late Eocene) deposits on South Island, has been reassigned to the turrid genus *Cochlespira* (Beu *et al*. 1990: 125). Several species of *Columbarium* are reported from the Eocene and Upper Miocene of southeastern Australia (Darragh 1969). In the Recent fauna, *Columbarium* is widespread along the western margin of the Pacific Ocean, ranging from central Japan to eastern Australia and New Zealand, with several species occurring off southeastern Africa.

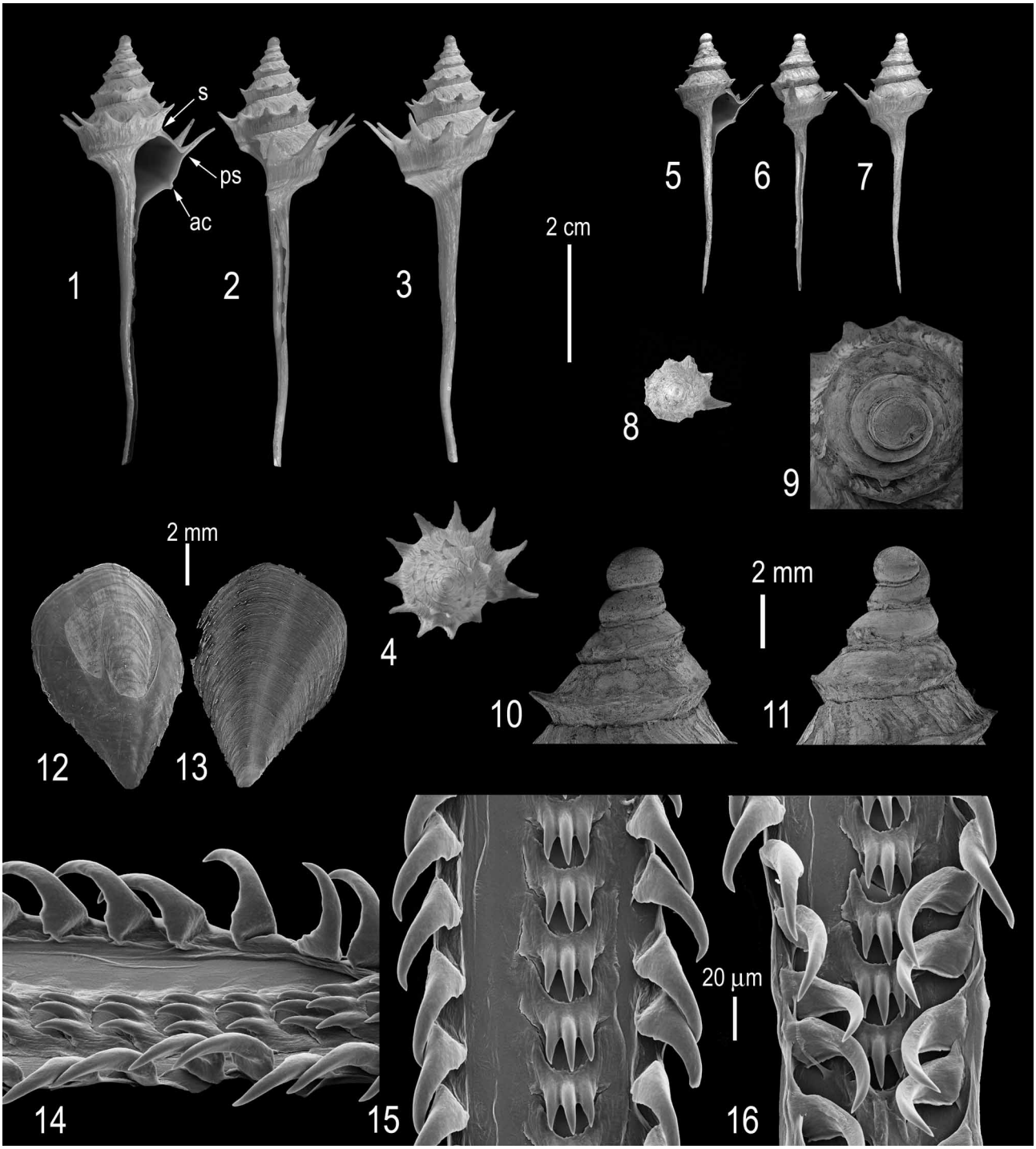
Columbarium veridicum Dell, 1963

(Figures 1–18)

Synonymy:
Columbarium veridicum Dell, 1963: 211–212, fig. 1; Darragh, 1969: 85–86, pl. 4, figs. 62–63; Powell, 1979: 169, pl. 37, fig. 1.

Diagnosis. Shell very large, thin, with relatively short, stepped spire, convex shoulder with long, open spines along periphery angled ~45° to coiling axis, sharply demarcated anterior carina, very long, smooth siphonal canal. Protoconch of 1⅓ whorls, with first whorl nearly spherical, decreasing slightly in diameter prior to transition to teleoconch. Teleoconch with up to 6 whorls. Sculpture limited to row of spines along shell periphery and cord along anterior carina. Siphonal canal smooth.

Description. Shell (Figures 1–8) very large (to 91.4 mm), moderately thin, with obtusely stepped, conical spire (spire angle 48–52˚), small, angular, irregularly pentagonal aperture, extremely long, axial siphonal canal. Protoconch (Figures 9–11) paucispiral, with nearly spherical first whorl deflected from coiling axis by ~53˚. Protoconch diameter increases from ~1.1 mm to 2.6 mm in first whorl, decreases to 2.5 mm after 1⅓ whorls. Transition to teleoconch marked by onset of strong shoulder followed within ¼ whorl by appearance of fine axial growth striae and short, triangular, open spines along shell periphery. Teleoconch of up to 6 inflated, angular whorls. Suture (Figure 1, s) adpressed just above anterior carina of previous whorl. Spiral sculpture limited to open spines (Figure 1, ps) along shell periphery and strong, angular anterior carina (Figure 1, ac) demarcated by strong cord. Axial sculpture of spines along shell periphery increasing in length, prominence, and number from 10 on early whorls to 12 on last whorl, where they form an angle of 45–50˚ to coiling axis. Growth lines weak, sinuous, slightly to moderately opisthocyrt, especially between peripheral keel and anterior carina. Aperture irregularly pentagonal, tapering anteriorly, deflected from shell axis by 27–30˚. Outer lip angular, lined with thin porcelaneous glaze, furrowed beneath peripheral keel and anterior carina, both projecting slightly. Inner lip smooth, with thin glaze along parietal region, flaring slightly at base of columella, along proximal portion of siphonal canal. Siphonal canal very long (61–63% shell length), narrow, axial, proximal half straight, distal half weakly spirally coiled. Shell color light tan to caramel, aperture slightly darker. Periostracum thin, straw colored, very finely lamellose. Operculum (Figures 12, 13) weakly corrugated, broadly ovate, rounded posteriorly, tapered anteriorly, with anterior ⅓ and abaxial edge thickened, free.

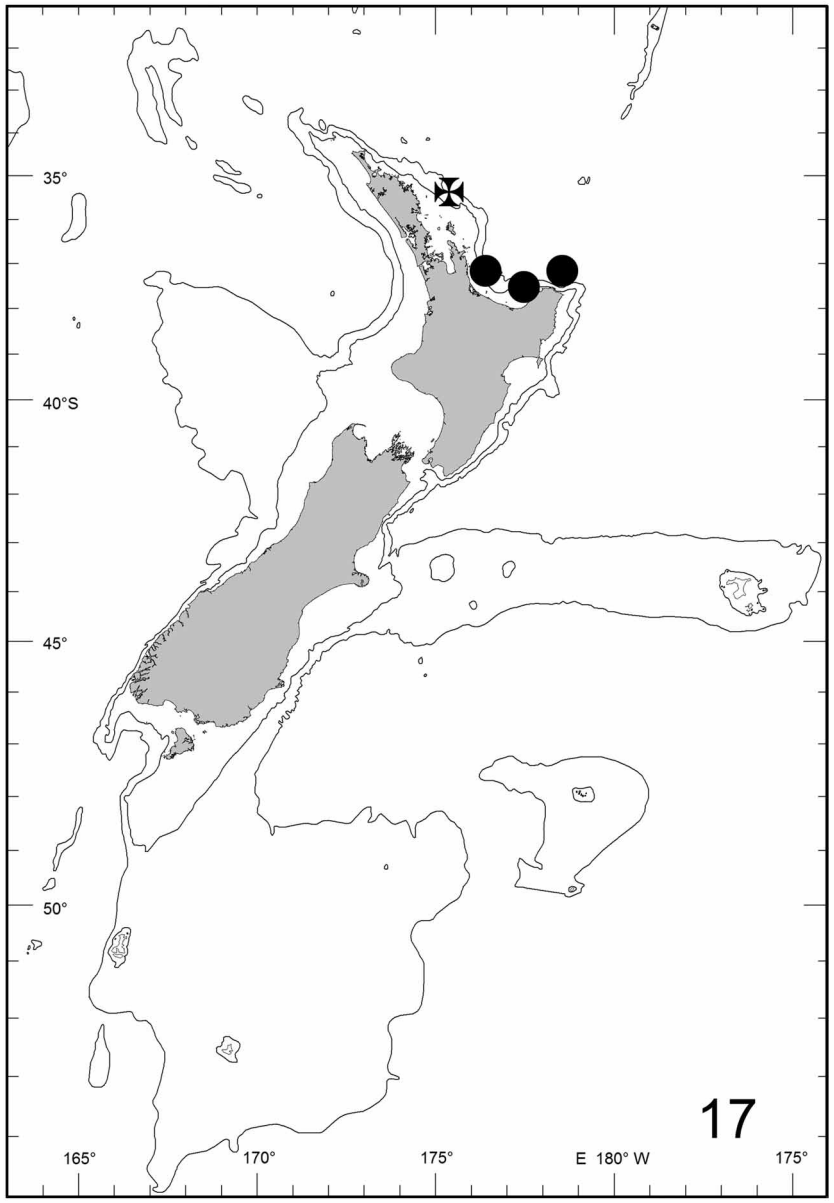


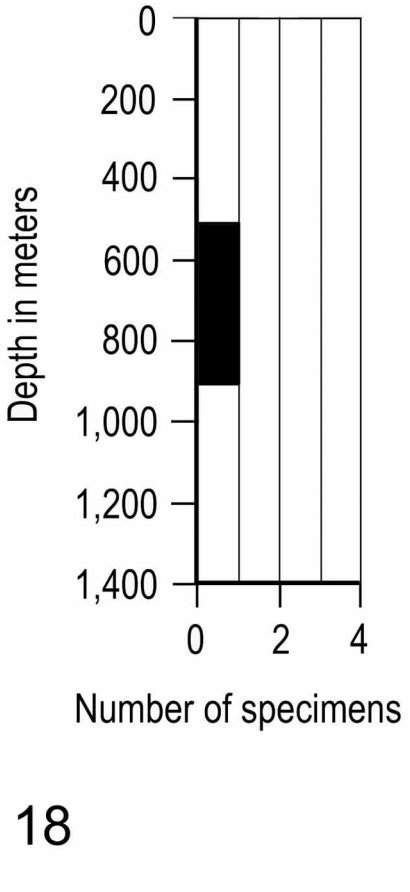
FIGURES 1–16. *Columbarium veridicum* Dell, 1963. **1**, Apertural, **2**, lateral, **3**, dorsal, and **4**, apical views of the holotype, NMNZ M.016274, 28 miles E of Poor Knights Islands, North Island [35°26.0'S, 175°18.0'E], in 558–622 m. **5**, Apertural, **6**, lateral, **7**, dorsal, and **8**, apical views of specimen from NMNZ M.060168, c. 17 km NE of Mayor Island, North Island [37°09.1'S, 176°24.4'E] in 753–826 m, on mud. 2 cm scale bar applies to figures 1–8. **9**, Apical and **10–11**, lateral views of protoconch of specimen in figures 5–8. **12**, Inner and **13**, outer surfaces of operculum of specimen from NMNZ M.074626, W of White Island, North Island [37°10.9'S, 178°38.7'E], in 685–705 m, on mud. **14–16**. Radular ribbon of specimen from NMNZ M.074626. **14**, 45° oblique view of radula, **15**, dorsal view with lateral teeth expanded, **16**, dorsal view with lateral teeth folded. ac, anterior carina; ps, peripheral spine; s, suture.

Single, partially preserved male specimen (NMNZ M.074626, SL = 65.7 mm) examined. Mantle cavity spans ¾ whorl, kidney ¼ whorl, upper whorls not preserved. Foot elongated, rectangular. Tentacles short, blunt, lacking eyes. Mantle edge thickened, with broad papilla corresponding to peripheral keel, and smaller papilla correspond-

ing to anterior carina. Columellar muscle broad, extending ¾ whorl beyond mantle edge. Osphradium bipectinate, long, narrow (L/W ~ 4.2). Ctenidium slightly wider, ~1¼ times as long as osphradium. Hypobranchial gland broad, transversely pleated. Rectum, long, narrow, with small rectal gland. Proboscis extremely long, narrow, coiled within non-evertable proboscis sheath. Radular ribbon (Figures 14–16) 1.64 mm long, with 68 rows of teeth. Rachidian teeth 48 µm wide, with U-shaped basal plate lacking broadly expanded lateral edges. Three long, cylindrical cusps, central cusp longest (25 µm), confined to central 23 µm of rachidian tooth. Lateral teeth with single, long (50µm), scythe-shaped cusp, attaching to radular ribbon along basal plate (20 µm wide). Salivary glands large, right gland slightly larger, valve of Leiblein small, gland of Leiblein large, ventral, to left of proboscis sheath. Male pallial gonoduct forming open, muscular groove running along floor of mantle cavity, inner edge of broad, flattened penis to its rounded, distal end, terminating in very short papilla surrounded by collar.

Type locality. (Figure 17, ✠) E of Poor Knights Islands, North Island [35°26.0'S, 175°18.0'E], 558–622 m, 11 Nov. 1962, RV IKATERE.





FIGURES 17–18. Distribution of *Columbarium veridicum* Dell, 1963. **17**, Geographic distribution. ✠ = type locality. ● = station records. **18**, Bathymetric distribution.

Type material. Holotype, NMNZ M.016274.

Material examined. 1 NMNZ M.060168, c. 17 km NE of Mayor Island, North Island [37°09.1'S,

176°24.4'E], 753–826 m, mud, 23 Jan. 1979, RV TANGAROA; 1 NMNZ M.074626, W of White Island, North Island [37°10.9'S, 178°38.7'E], 685–705 m, mud, 23 Jan. 1981, RV TANGAROA.

Additional material at NMNZ: 1 NMNZ M.059560, c. 17 km NW of Cape Runaway, North Island [37°29.0'S, 177°32.0'E], 818–898 m, 24 Jan. 1979, RV TANGAROA.

Distribution (Figures 17–18): *Columbarium veridicum* is only known from four records, all from off the northern coast of North Island, at depths ranging between 558 and 898 m. The confirmed bathymetric range is 622–818 m, with a mean station depth of 733.1 m.

Remarks. *Columbarium veridicum* is the only living member of the genus *Columbarium* presently known from New Zealand waters. It more closely resembles *Columbarium pagoda pagoda* (Lesson, 1831), from the central Sea of Japan and the South China Sea than any congeners from intervening waters. It may be distinguished from *C. pagoda pagoda* by its slightly larger size, broader, more inflated spire, proportionally longer siphonal canal, and by the absence of spiral cords along the proximal portion of the siphonal canal. The form *C. pagoda stellatum* Habe, 1953, from Tosa Bay, Japan, is similar in having reduced anterior spiral cords, but has fewer, longer, more laterally directed spines along the shoulder. The five species of *Columbarium* [*C. spinicinctum* (Martens, 1881); *C. suzukii* Habe & Kosuge, 1972; *C. pagoda nakayasui* Habe, 1979; *C. sinensis* Zhang, 2003; *C. corollaceous* Zhang, 2003] and one species of *Fulgurofusus* [*F. nanshaensis* Zhang, 2003] reported from the South China Sea by Zhang (2003) as well as the five species of *Columbarium* [*C. spinicinctum* (Martens, 1881); *C. pagodoides* (Watson, 1882); *C. hedleyi* Iredale, 1936; *C. harrisae* Harasewych, 1983a; *C. hystriculum* Darragh, 1987] reported from off eastern Australia by Wilson (1994) all differ from *C. veridicum* in having thicker, heavier shells with prominent spiral cords, often with open scales, below the shell periphery and especially along the proximal portion of the siphonal canal.

Genus *Coluzea* Finlay *in* Allan, 1926

Synonymy:
Coluzea Allan, 1926 (Type species: *Fusus dentatus* Hutton, 1877): Finlay, 1930a: 249; 1930b: 267; Dell, 1956: 47; 1963: 211; Harasewych, 1986: 156; 1991: 245; 2004:93. Harasewych and Fraussen, 2001: 171.
Coluzea Finlay, 1926: (Type species: *Fusus spiralis* A. Adams, 1856). Marwick, 1942: 278.
Coluzea Allan, 1927: Finlay, 1930a: 249; Dell, 1956: 47; Beu *et al*. 1969: 45
Coluzea Finlay, 1927: Powell, 1971: 220; Cernohorsky, 1977: 99: Maxwell, 1978: 38.
Coluzea Finlay *in* Allan, 1926: Beu *et al*., 1990: 196.
Coluzea Finlay *in* Allan, 1927: Darragh, 1969: 104.

Type species. *Fusus dentatus* Hutton, 1877, by subsequent designation, Finlay, 1930a: 249.

Diagnosis. Shell large (to 127.3 mm), fusiform, with tall conical spire, convex whorls, prominent peripheral keel that may be flange-like, bearing tubercles or open spines, weak to very weak anterior carina, long to very long, axial siphonal canal with spiral cords along its stouter, proximal portion and smooth, spirally twisted distal end. Protoconch variable among species, ranging from strongly angular with larger first whorl to cylindrical or evenly conical, consisting of 1⅓ to 2¾ whorls. Suture adpressed onto or slightly below anterior carina of prior whorl. Spiral sculpture generally dominant. Outer lip often furrowed beneath peripheral keel and prominent cords. Inner lip smooth, with outer surface of previous whorl resorbed prior to deposition of thin glaze. Shell color usually white. Pigmentation, when present, brown to tan, generally confined to regions between adjacent spines or tubercles. Rachidian teeth of radula with 3 cusps along U-shaped basal plate with broad, lateral expansions (e.g. Harasewych 1986: pl. 3, figs. 1–6).

Remarks. As is evident from the complex synonymy, the authorship, date, and type species of *Coluzea* have been variously interpreted in the literature due to the appearance of the name *Coluzea* in species lists included in a paper by Allan [1926 (7 December)] that, despite specific instructions to the contrary, was published prior to the to the intended introduction of the genus by Finlay [1926 (23 December)]. Beu *et al*. (1969) clearly and succinctly summarized the complex history of *Coluzea* and other genus level taxa that appeared in both these publications, and requested rulings on these works by the International Commission on Zoological Nomenclature. There has not been a ruling on this matter by the Commission.

As Allan's paper clearly states "issued separately 7th December, 1926" this must be considered the date of publication of *Coluzea* [Article 21.5 (ICZN, 1999: 22)].

The name *Coluzea* had been introduced into Allan's paper by Finlay, who changed the nomenclature at the proof stage (Beu *et al*. 1969: 44). In a footnote to a list of taxa that includes *Coluzea*, Allan (1926: 291) acknowledged "For this and many other name changes and generic placings in this list, refer to Finlay … *antea* this volume." Thus, the authorship of *Coluzea* is Finlay *in* Allan, 1926 [Article 50.1.1 (ICZN, 1999: 52)].

Two species were included in *Coluzea* in separate lists in Allan's publication: *Coluzea climacota* (Suter, 1917) (Allan 1926: 291) and *Coluzea dentata* (Hutton, 1877) (Allan 1926: 304). In an effort to resolve the nomenclatural confusion, Finlay (1930a: 249) reported *Fusus dentatus* to be "the monotype of the genus" *Coluzea*. This fixed *Fusus dentatus* as the type species of *Coluzea* by subsequent designation of Finlay (1930a) [Article 69.1.1 (ICZN, 1999: 72)].

The genus *Coluzea* has an extensive fossil record in New Zealand, ranging from the Early Eocene [Mangaorapan (Ypresian)] to the Recent (Beu *et al*. 1990: 39). Middle to Upper Eocene records are known from the Paris Basin and southern England (Darragh 1969). In the Recent fauna, the genus ranges from southern Africa (Darragh 1969; Harasewych, 2004) to the eastern Indian Ocean (Harasewych 1986), eastern Australia (Darragh 1987), New Caledonia (Harasewych 1991) and New Zealand (Powell 1971).

Although *Coluzea* is readily distinguished from *Columbarium* on the basis of several conchological and anatomical characters (e.g., protoconch morphology, strength of anterior carina, shape of the basal plate of the rachidian), it is far more similar to *Fulgurofusus* Grabau, 1904, a genus with a broader geological (Paleocene to Recent), geographical (western Atlantic, eastern and western Pacific) and bathymetric (bathyal to abyssal) ranges. Several authors (Finlay 1930b: 267–268; Darragh 1969: 99; Harasewych 1983b: 5; 1986: 158; 1991: 245) have noted the similarities between these taxa, yet retained them as separate genera based primarily on minor differences in protoconch morphology and the absence of a columellar lamina in *Fulgurofusus*.

Coluzea spiralis (A. Adams, 1856)

(Figures 19–35, 39)

Synonymy:

Fusus spiralis A. Adams, 1856: 221; Hutton, 1880: 50; Tryon, 1881: 68, 227, pl. 85, fig. 593; Hutton, 1884: 227; Hutton, 1893: 40, pl. 6, fig. 9.

Fusus pensum Hutton, 1873: 8; Dell, 1956: 48; Marshall, 1996: 24.

Fusinus spiralis Suter, 1913: 357–358; Suter, 1915: pl. 41, fig. 4; Bucknill, 1924: 60, pl. 7, fig. 17.

Columbarium suteri E. A. Smith, 1915: 87, pl. 1, fig. 30; Mestayer, 1916: 126, pl. 12, fig. 8.

Coluzea spiralis Finlay, 1926: 407; Powell, 1927: 298, pl. 34, fig. 3; Finlay, 1930b: 268; Powell, 1937: 79, pl. 8, fig. 24; Dell, 1951: 54; Dell, 1956: 47; Cernohorsky, 1977: 99–100, figs. 16–17.

Coluzea espinosa Finlay, 1930b: 268–269.

Columbarium (*Coluzea*) *spiralis* Powell, 1979: 169, pl. 37, fig. 2.

Type locality. *Fusus spiralis*, New Zealand; *Fusus pensum*, Kapiti Island, Cook Strait, New Zealand; *Columbarium suteri*, near North Cape, New Zealand, in 20–37 m; *Coluzea espinosa* Blue clays, Petane, New Zealand [Nukumaruan (Late Pliocene – Early Pleistocene)].

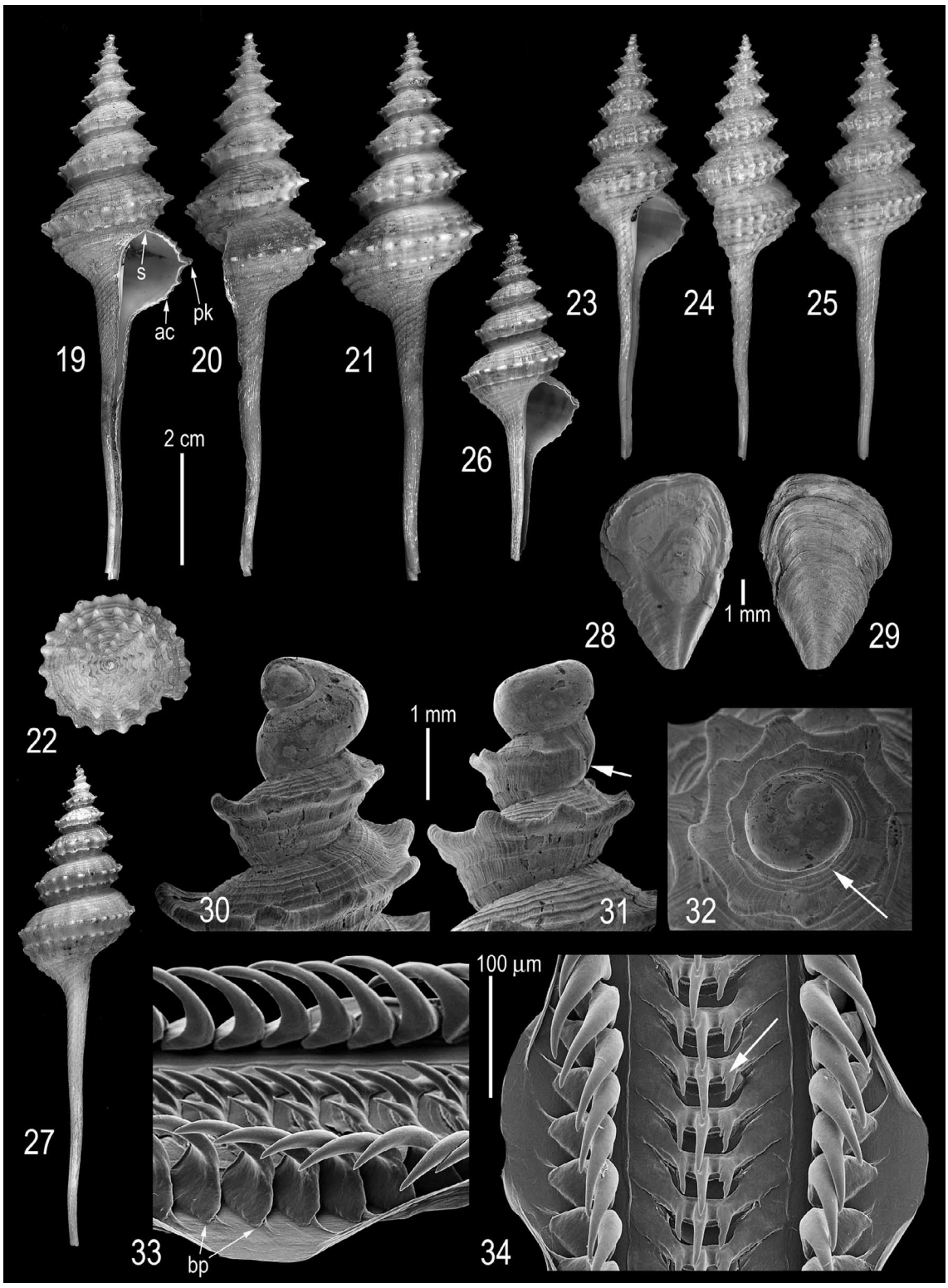
Type material. *Fusus spiralis*, holotype, BMNH 1951.10.16.1. Not illustrated in original publication, subsequently illustrated by Dell (1956, fig. 56) and Cernohorsky (1977: fig. 16).

Fusus pensum, lectotype, NMNZ M.000103. As noted by Marshall (1996: 24), according to Hutton's handwritten type list, a syntype was deposited in the Canterbury Museum, but has been lost or is now unrecognizable. Dell's (1956: fig. 57) illustration of the "Type of *Fusus pensum*" constitutes a lectotype designation [Article 74.4, 5, 6 (ICZN, 1999: 82–83)].

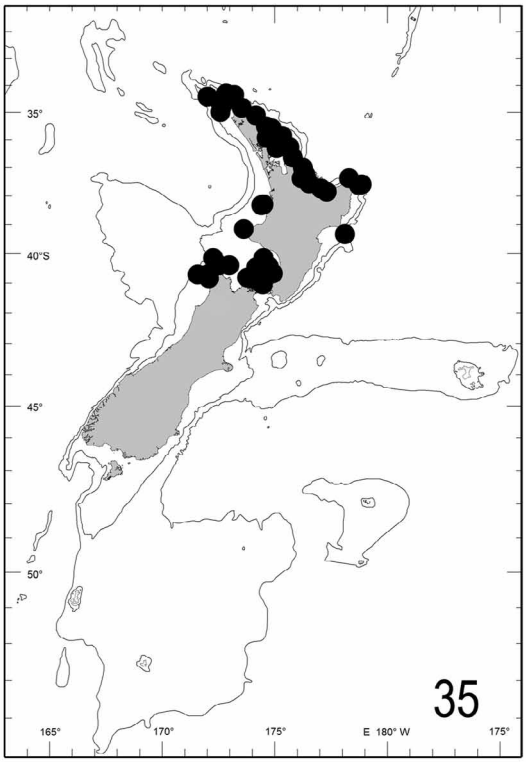
Columbarium suteri, holotype, BMNH 1915.4.18.255. Illustrated by Cernohorsky, 1977: fig. 16.

Coluzea espinosa, holotype, AK 70179. Not illustrated in original publication, subsequently illustrated by Dell (1956, fig. 59).

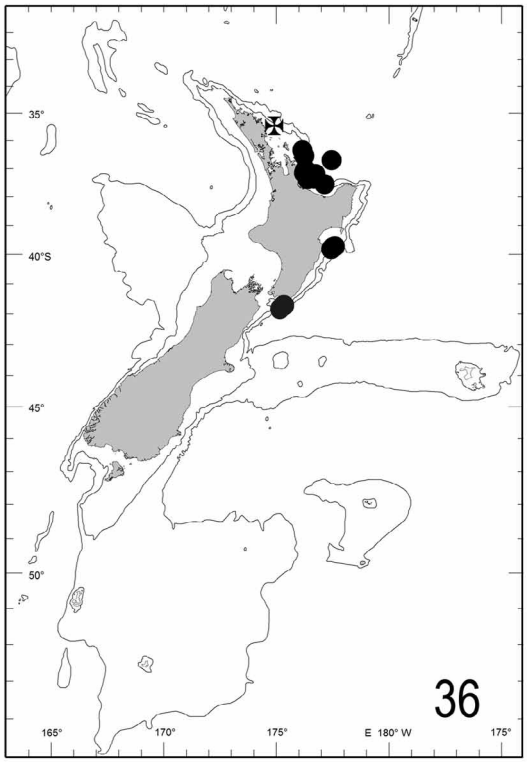
Diagnosis. Shell moderately large, narrow, fusiform, tan-colored, with tall, acutely stepped, conical spire (spire angle 33–37°), rounded shoulder with multiple spiral threads or cords, nodulose periphery, strong cord anterior to periphery, weak anterior carina, and long, axial siphonal canal. Protoconch of ~1⅓ whorls, first whorl broad, angular, deviated. Teleoconch with up to 8 strongly convex whorls. Axial sculpture of 20–25 weak ribs most evident near periphery, with weak, irregular, brown axial bands present between adjacent ribs.



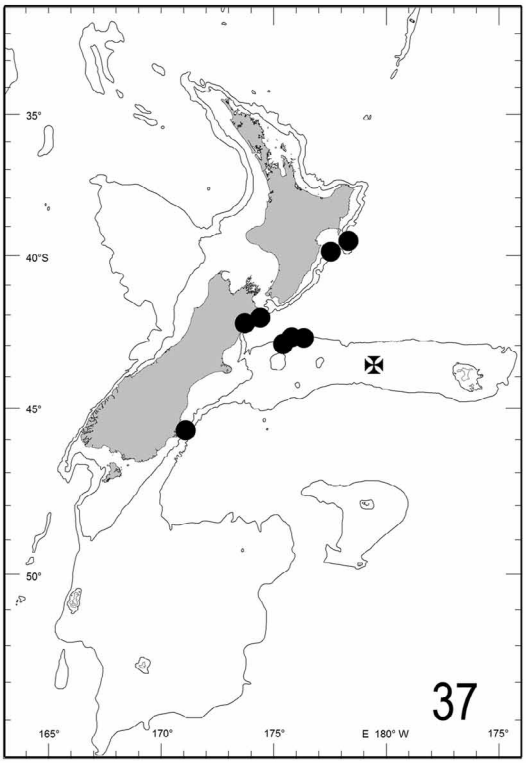
FIGURES 19–34. *Coluzea spiralis* (A. Adams, 1856). **19**, Apertural **20**, lateral, **21**, dorsal, and **22**, apical views of specimen from NMNZ M.074903, off Parengarenga Harbour North Island [34°32.0'S, 173°06.0'E], in 102–93 m, on foraminiferal ooze. **23**, Apertural, **24**, lateral and **25**, dorsal views of specimen from NMNZ M.059528, off Ninety Mile Beach, North Island [34°59.4'S, 172°35.5'E], in 156–160 m. **26**, Apertural view of a male specimen from NMNZ M.297523, off Opotiki, North Island [37°53'S, 177°17'E], in 37 m. **27**, Dorsal view of shell from NMNZ M.060132, E of Mahia Peninsula, North Island [39°17.2'S, 178°12.7'E], in 258–306 m, on mud. 2 cm scale bar applies to figures 19–27. **28,** Inner and **29**, outer surfaces of operculum of specimen in figure 26. **30**–**31**, Lateral and **32**, apical views of protoconch of specimen from NMNZ M.035884, W of Poor Knights Islands, North Island [35°32.0'S, 174°41.0'E], in 121–113 m, on mud. Arrows indicate transition to teleoconch. **33–34**. Radular ribbon of specimen in figure 26. **33**, oblique view of radula, **34**, dorsal view with lateral teeth expanded. 100 mm scale bar applies to figures 33–34. Arrow indicates atypical denticles on cusp or rachidian tooth. ac, anterior carina; bp, basal plate of lateral tooth; pk, peripheral keel; s, suture.



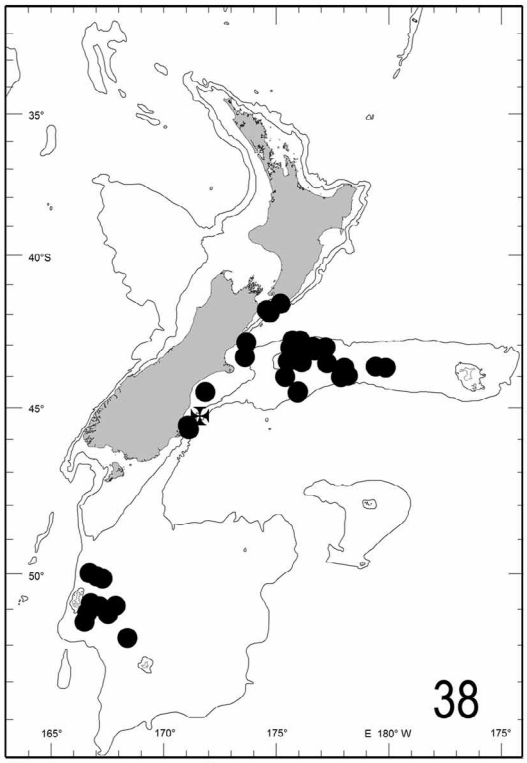
Coluzea spiralis



Coluzea wormaldi



Coluzea altocanalis



Coluzea mariae

FIGURES 35–38. Geographic distributions of species of New Zealand *Coluzea*. **35**, *Coluzea spiralis* (A. Adams, 1856). The type locality is New Zealand. **36**, *Coluzea wormaldi* Powell, 1971. **37**, *Coluzea altocanalis* Dell, 1956. **38**, *Coluzea mariae* Powell, 1952. ✠ = type locality. ● = station records.

Description. Shell (Figures 19–27) large (to 107.2 mm), moderately thin, with very tall, acutely stepped, conical spire (spire angle 33–37˚), small, ovate aperture, and long, stout, axial siphonal canal. Protoconch (Figures 30–32) with broad, angular, tilted first whorl initially increasing in diameter from 410 μm to 1.53 mm, then decreasing slightly to 1.48 mm after 1⅓ whorls. First whorl deviated from coiling axis of shell by ~60˚. Transition to teleoconch marked by abrupt onset of strong shoulder (Figures 31, 32 arrows) followed within ¼ whorl by formation of fine spiral threads between suture and shoulder, and of short, broad spines along shell periphery. Spines angled posteriorly on early whorls, becoming laterally directed elements of peripheral keel by third postnuclear whorl. Teleoconch of up to 8 convex whorls. Suture (Figure 19, s) adpressed against anterior carina (Figure 19, ac) of previous whorl. Spiral sculpture of: 3–5 cords between suture and nodulose peripheral keel (Figure 19, pk) increasing in prominence toward periphery; 1 strong cord, which may be flanked by a weaker cord on each side, situated between periphery and weak anterior carina; 3–5 weaker cords between carina and siphonal canal; 9–14 weak cords along proximal third of siphonal canal. Fine to very fine threads on or between adjacent spiral cords. Axial sculpture of weak ribs (8 on first teleoconch whorl, 22–25 on last whorl) most conspicuous along periphery and adjacent spiral cords, especially those anterior to periphery. Growth striae weak, orthocline to slightly sinuous. Aperture broadly ovate, tapering anteriorly. Aperture narrower in juveniles, becoming more rounded with increasing shell size (Figures 26→23→19), deflected from shell axis by 24–28˚. Outer lip with porcelaneous glaze furrowed beneath spiral cords, most deeply beneath peripheral keel. Inner lip smooth, with thin glaze adhering tightly along parietal region, but flaring slightly at base of columella and proximal portion of siphonal canal, producing a slightly raised lamina. Siphonal canal very long (~½ shell length), narrow, axial, with stout, straight proximal half, weakly spiral distal half. Base color of shell white to cream, with irregular axial bands of light tan most conspicuous between axial ribs near periphery and along siphonal canal. Nodes along periphery, adjacent spiral cords white, internodal areas darker tan. Periostracum moderately thin, brownish yellow, lamellose. Operculum (Figures 28, 29) thin, ovate, broadly rounded posteriorly, tapering anteriorly, with broadly ovate attachment area, anterior ⅓ free. Operculum weakly corrugated, with lateral edges thickened, nucleus and free edges worn, abraded.

External anatomy. Preserved, male specimen (NMNZ M.297523, Figure 26, SL = 61.5 mm) comprised > 2½ whorls, with mantle cavity spanning ⅞ whorl, kidney ¼ whorl, and digestive gland and gonad 1+ whorls. Columellar muscle long, broad, attached to shell ⅔ whorl beyond mantle edge. Contracted foot broadly rectangular (L/W ≈ 2) with deep propodial groove along its anterior edge. Body color yellowish, without discernable pattern. Tentacles short, blunt, with large, round black eyes at their bases. Mantle edge thickened, papillated, siphonal canal long, narrow, muscular, with papillae along its proximal half.

Mantle cavity. Mantle cavity broad, deep, with organs situated as in most neogastropods. Osphradium, bipectinate, long (8 mm), narrow (L/W ≈ 2.4), with ~75 leaflets above broad osphradial nerve, ~65 leaflets below. Ctenidium 1¼ times as long, ⅔ as wide as osphradium, with ~120 thin, triangular leaflets. Ctenidium extending from just behind thickened mantle edge to rear of mantle cavity, its posterior edge adjacent to broad pericardium. Pericardium containing small auricle, large ventricle, lined by narrow nephridial gland. Hypobranchial gland transversely pleated, spanning roof of mantle cavity, thicker along right side, which partially covers rectum. Renal organ fairly short, with primary and secondary lamellae not interdigitated [termed Meronephridiens (Perrier 1889)], forming right rear wall of mantle cavity.

Alimentary system. Proboscis extremely long (95 mm, ~1½ shell length), narrow (<1 mm in diameter), greatly convoluted when retracted into thin-walled, non-evertable proboscis sheath broadest near rear of cephalic haemocoel. Mouth small, situated at tip of rounded distal end of proboscis, opening into small buccal cavity. Buccal mass narrow, slightly shorter that radula. Radular ribbon (Figures 33, 34) 5.25 mm long, comprised of 135 rows of teeth. Rachidian teeth 134.6 μm wide, with a basal plate with U-shaped central section flanked by broad, rectangular lateral edges. Central of 3 cusps (54.1 μm), 1¼ times as long as flanking cusps, its distal end resting in dimple in base of corresponding cusp of posteriorly adjacent tooth. Inner edge of right cusp with serrated edge (Figure 34, arrow), an anomalous feature not previously seen in radulae of *Coluzea spiralis* (see Harasewych, 1991:fig. 21) or any other species of Columbariinae. Lateral teeth, each with a single, long (98 μm), recurved, scythe-shaped cusp, attached to radular ribbon by thin band along widest portion (54 μm) of basal plate (Figure 33, bp). Anterior esophagus narrow, extending length of proboscis, then anteriorly from rear of proboscis sheath, expanding slightly to form small valve of Leiblein just prior to passing through nerve ring. Esophagus runs posteriorly beneath broad, flattened, posteriorly tapered gland of Leiblein, leaving cephalic hemocoel to enter U-shaped stomach lining anterior portion of digestive gland. Intestine enters mantle cavity, running anteriorly along its right side to form a nar-

row, tubular rectum, terminating in simple anus and small anal gland. Two ascinous salivary glands, the right gland larger, compacted in anterior end of cephalic hemocoel, emptying laterally into the buccal mass via long, narrow ducts passing beneath dorsal folds of esophagus.

Male reproductive system. Testes line inner wall of digestive gland, forming a thick- walled, highly convoluted seminal vesicle, embedded within anterior wall of digestive gland. Testicular duct runs from its anterior end, along pericardium, entering mantle cavity along its right wall, running ventral and parallel to the rectum before descending to floor of mantle cavity. Duct joins muscular, open groove lined with prostatic tissue that leads to base of broad, dorsoventrally flattened penis, along its outer edge to tip of a long, narrow, tapering papilla.

Female reproductive system. Partially preserved female specimen (NMNZ M.061102, SL = 79.3 mm) with oviduct extending anteriorly from ovary, embedded in right wall of digestive gland, running along kidney and pericardium before entering rear of mantle cavity. Pallial oviduct linear, consisting of a thin-walled albumen gland, a cylindrical, glandular capsule gland, and an anterior, muscular bursa copulatrix with a terminal female opening. Ingesting gland not found, possibly due to poor preservation.

Material examined. NORTH ISLAND: 1 NMNZ M.086706, N of North Cape [34°20.0'S, 173°06.6'E], 163–168 m, 27 Jan. 1981, RV TANGAROA; 1 NMNZ M.074903, off Parengarenga Harbour [34°32.0'S, 173°06.0'E], 102–93 m, foraminiferal ooze, 27 Jan. 1981, RV TANGAROA; 2NMNZ M.076035, NW of Ahipara [34°50.0'S, 172°46.1'E], 90 m, sandy mud, 10 Jan. 1981, RV TANGAROA; 1 NMNZ M.059528, off Ninety Mile Beach [34°59.4'S, 172°35.5'E], 156–160 m, 19 Nov. 1978, RV JAMES COOK; 2 NMNZ M.043632, Off Takou Bay, N of Kerikeri [35°10'S, 174°11'E], 80 m, mud, sand and sponge bottom, 16 Feb. 1974, RV ACHERON; 3 NMNZ M.035884, W of Poor Knights Islands [35°32.0'S, 174°41.0'E], 121–113 m, mud,15 Feb. 1974, RV ACHERON; 2 NMNZ M.066727, SE of Alderman Islands [37°00.8'S, 176°12.3'E], 178–248 m, mud, 23 Jan. 1979, RV TANGAROA; 7 NMNZ M.060111 and 5 NMNZ M.066561, NW of Mayor Island [37°11.5'S, 176°10.0'E], 198–273 m, mud, 22 Jan. 1979, RV TANGAROA; 1 NMNZ M.060104, c. 11 km NW of Mayor Island [37°13.1'S, 176°07.8'E], 119–169 m, mud, 22 Jan. 1979, RV TANGAROA; 2 USNM 896320 [37°35'S, 178°46'E], 128–146 m, 28 May 1966; 4 NMNZ M.060581, c. 9 km N of Motuhora Island [37°45.8'S, 177°00.8'E], 72–84 m, mud, 20 Jan. 1979, RV TANGAROA; 4 NMNZ M.297523, off Opotiki [37°53'S, 177°17'E], 37 m, 1967, RV IKATERE; 2 NMNZ M.060132, E of Mahia Peninsula [39°17.2'S, 178°12.7'E], 258–306 m, mud, 27 Jan. 1979, RV TANGAROA; 4 NMNZ M.061102, E of Mahia Peninsula [39°18.7'S, 178°04.6'E], 127–134 m, mud, 27 Jan. 1979, RV TANGAROA; 2 NMNZ M.053738, off Foxton [40°30.5'S, 174°53.5'E], 101 m, 1 Mar. 1976, RV ACHERON; 4 NMNZ M.052731, off Foxton [40°33.5'S, 174°59.5'E], 86–88 m, mud, 2 Mar. 1976, RV ACHERON; 1 DNMH 73077, Whale Island, 137 m; 1 DMNH 48393, Off Kawau Id.; 1 USNM 681696, off Plate Island, Bay of Plenty, 73 m, 1968; 1 USNM 22859, New Zealand. COOK STRAIT: 1 NMNZ M.049935, Midway between Cape Jackson and Mana Island, Cook Strait narrows [41°02'S, 174°33'E], 256–186 m, rock bottom, 6 Mar. 1976, RV ACHERON. SOUTH ISLAND: 7 NMNZ M.053084, c. 24 miles NE of Stephens Island [40°24'S, 174°17'E], 110 m, mud, 4 Mar. 1976, RV ACHERON; 1 NMNZ M.053490, N of base of Farewell Spit [40°28'S, 172°48'E] in 51 m, on sand. 10 Mar 1976, RV ACHERON; 6 NMNZ M.053432, N tip of Farewell Spit [40°31.5'S, 173°03'E], 44 m, 10 Mar. 1976, RV ACHERON; 3 NMNZ M.059020, off Kahurangi Shoals, NW of Kahurangi Point [40°42.5'S, 172°07'E], 91 m, stones and subfossil shells, 10 Mar. 1976, RV ACHERON; 1 NMNZ M. 297041, between Titi Island and Alligator Head [40°57'S, 174°08'E], 84–88 m, mud and shell bottom, 30 Aug. 1975, RV ACHERON; 1 USNM 877100, off Canterbury, in 366 m.

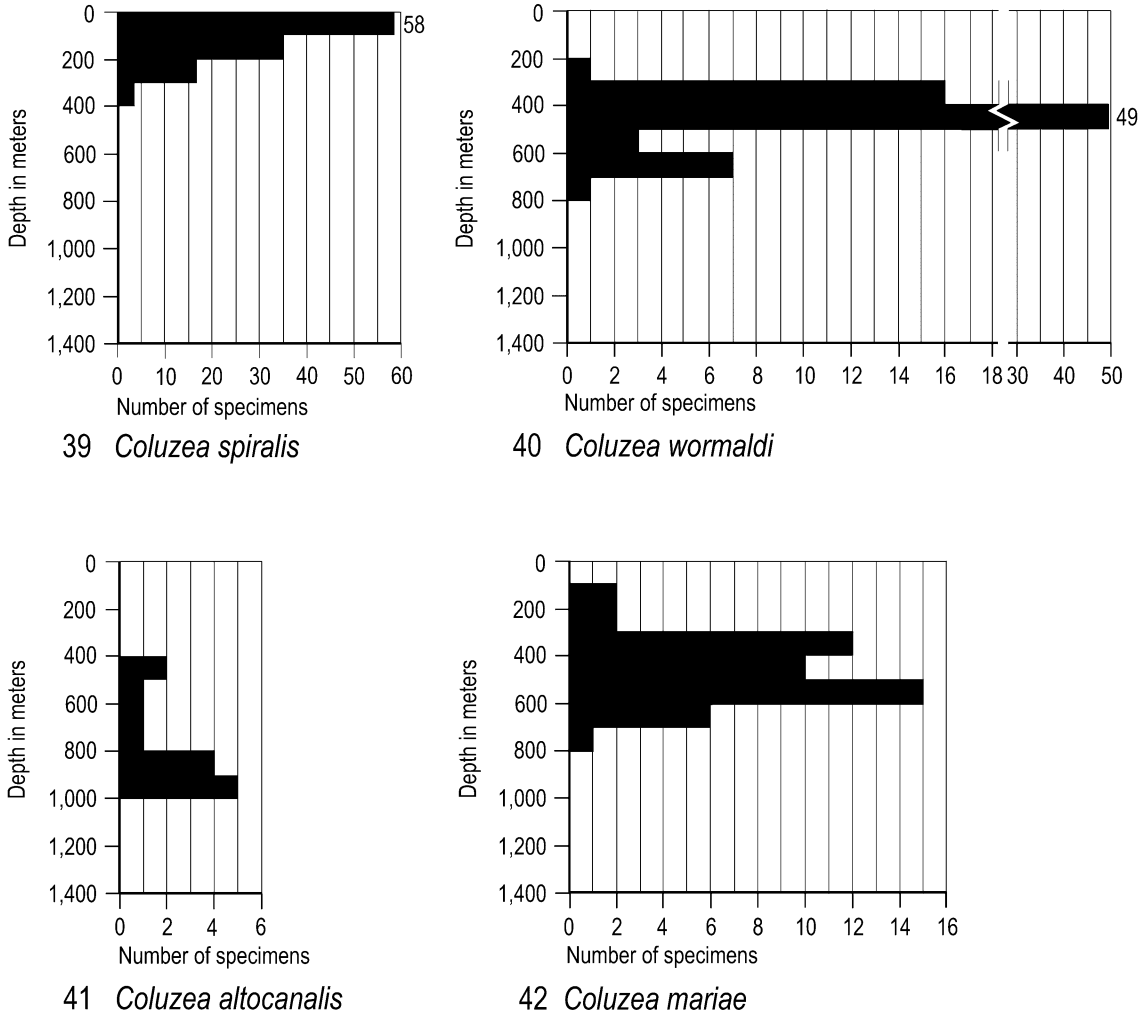
Additional material at NMNZ. NORTH ISLAND: 1 NMNZ M.148196, off Tom Bowling Bay [34º19.43'S, 172º54.57'E], 94 m, 26 Jan. 1999, RV KAHAROA; 1 NMNZ M.153113, off Cape Reinga [34º22.80'S, 172º24.60'E], 121 m, bryozoa and shell bottom, 2 Feb. 1981, RV TANGAROA; 4 NMNZ M.297040, E of North Cape [34º 25.00' S, 173º 13.10' E], 257–327 m, foraminiferal sand, 27 Jan. 1981, RV TANGAROA; 1 NMNZ M.002522, 15'S of Great Island, Three Kings Islands [34°25.1'S, 172°09.0'E], 179 m, 29 May 1914, SS HINEMOA; 1 NMNZ M.153114, Great Exhibition Bay [34º33.60'S, 173º 04.90'E], 66 m, 27 Jan. 1981, RV TANGAROA; 1 NMNZ M.153115, NW of Ahipara [34º50.00'S, 172º46.10' E], 90 m, sandy mud, 10 Jan. 1981, RV TANGAROA; 2 NMNZ M.083862, off Ninety Mile Beach [34º53.00'S, 172º55.00'E]; 1 NMNZ M.025800, off Doubtless Bay [34º55.00'S, 173º30.00'E], 47 m, 18 Sep. 1971; 1 NMNZ M.035741, off Cape Brett [35º08.00'S, 174º12.50'E], 80 m, mud, 16 Feb. 1974, RV ACHERON; 8 NMNZ M.028457, NE of Ninepin Rock, Bay of Islands [35º08.80'S, 174º10.90'E], 79 m, 01 Dec. 1971, MV KOKINGA; 2 NMNZ M.030757, NE of Ninepin Rock, Bay of Islands [35º08.80'S, 174º10.30'E], 75 m, 1 Dec. 1971, MV KOKINGA; 1 NMNZ M.112109, off Deep Water Cove, Bay of Islands [35º11.70'S, 174º17.40'E], 55

m, Mar. 1973; 4 NMNZ M.035093, N of Poor Knights Islands [35º22.00'S, 174º43.00'E], 146 m, sandy mud, 15 Feb. 1974, RV ACHERON; 1 NMNZ M.016233, SE of Poor Knights Islands [35º38.00'S, 174º56.00'E], 165 m, 20 Nov. 1962, RV IKATERE; 1 NMNZ M.297068, off Peach Cove, Bream Bay [35º 53.367'S, 174º 33.00' E], 77 m, 26 Feb. 1998; 1 NMNZ M.021045, off Miner's Head, Great Barrier Island [35º55.00'S, 175º20.50'E], 73–82 m; 1 NMNZ M.153116, Centre Reef, N of Little Barrier Island, Hauraki Gulf [36º00.00'S, 175º07.50'E], 73 m, May 1967; 3 NMNZ M.083865, off Hauraki Gulf; 1 NMNZ M.090206, Hauraki Gulf, 50–60 m, 1986; 1 NMNZ M.083864, off Miner's Head, Great Barrier Island [36º04.00'S, 175º21.00'E], 1950; 6 NMNZ M.130835, SE of Te Arai Point, Mangawhai, N of Warkworth [36º10.50'S, 174º42.00'E], 35–40 m, sand and shell suction dredged for beach replenishment at Mission Bay, Auckland, 3 Mar. 1996; 1 NMNZ M.083863, off Horn Rock, Great Barrier Island [36º15.00'S, 175º11.00'E]; 1 NMNZ M.016220, N of Cuvier Island [36º17.00'S, 175º46.00'E], 110 m, 25 Nov. 1962, RV IKATERE; 1 NMNZ M.136053, Omaha Bay, N of Auckland [36º20.48'S, 174º49.98'E], 32 m, mud, 30 Nov. 1995; 1 NMNZ M.136133, Omaha Bay, N of Auckland [36º20.87'S, 174º50.98'E], 34 m, mud, 30 Nov. 1995; 1 NMNZ M.021048, off Whale Rock, Mercury Islands, Whitianga [36º42.00'S, 175º54.50'E], 73–91 m, 1967; 1 NMNZ M.021049, off Mercury Bay, Whitianga [36º47.00'S, 175º50.00'E], 73 m, 11 Apr.1967; 1 NMNZ M.153111, N of the Aldermen Islands [36º47.50'S, 176º 0.00'E], 108–113 m, mud, 24 Jan. 1981 RV TANGAROA; 1 NMNZ M.044393, off the Aldermen Islands [36º59.00'S, 176º12.00'E], 165 m, 10 Jun. 1970, RV IKATERE; 1 NMNZ M.039421, off Slipper Island [37º01.00'S, 175º57.00'E], 37 m, 8 Apr. 1970, RV IKATERE; 1 NMNZ M.039453, off Slipper Island [37º03.00'S, 175º59.00'E], 55 m, 2 Dec. 1969, RV IKATERE; 3 NMNZ M.083861, off Mayor Island, 91 m; 1 NMNZ M.119093, off Lottin Point [37º26.10'S, 178º13.10'E], 255 m, 29 Jan. 1995, RV KAHAROA; 1 NMNZ M.039528, off Plate Island [37º35.00'S, 176º36.00'E], 146 m, 9 Jun. 1970, RV IKATERE; 1 NMNZ M.039537, off Plate Island [37º35.00' S, 176º36.00'E], 155 m, 7 Apr. 1970, RV IKATERE; 1 NMNZ M.083866, off Plate Island; 5 NMNZ M.153112, off East Cape, southeastern slope of Ranfurly Bank [37º38.50'S, 178º56.40'E], 153 m, mixed Recent and fossil fauna, 22 Jan. 1981, RV TANGAROA; 3 NMNZ M.112411, Between Motuhora and White Islands [37º40.20'S, 178º53.60'E], 117 m, mud, shell and pumice, 2 May 1990, RV AKADEMIK ALEXANDER NESMEYANOV; 3 NMNZ M.039988, off Whale Island (Motuhora) [37º51.00'S, 176º58.00'E],18–55 m, 1967; 2NMNZ M.083709, off Whale (Motuhora) Island; 3 NMNZ M.088299, SW of Kawhia Harbour [38º21.50'S, 174º17.80'E], 83 m, 13 Jan. 1981, RV TANGAROA; 1 NMNZ M.028428, off New Plymouth [39º07.00'S, 173º48.00'E], 97 m, 21 May 1964; 1 NMNZ M.050583, S of Waverley [40º10.00'S, 174º40.00'E], 82 m, bryozoa and shell bottom, 1 Mar. 1976, RV ACHERON; 2 NMNZ M.053335, W of Rangitikei River mouth [40º16.00'S, 174º58.50'E],75 m, 2 Mar. 1976, RV ACHERON; 1 NMNZ M.052615, W of Rangitikei River mouth [40º18.00'S,174º59.00'E], 82 m, mud, 2 Mar. 1976, RV ACHERON; 2 NMNZ M.053811, NW of Manawatu River mouth [40º22.50'S, 174º59.50'E], 86 m, mud, 2 Mar. 1976, RV ACHERON; 2 NMNZ M.052912, N of Kapiti Island [40º38.00'S, 174º54.50'E], 91 m, 1 Mar. 1976, RV ACHERON; 1 NMNZ M.000103, Kapiti Island; 1 NMNZ M.048946, off Whakatane, 1966; 1 NMNZ M.083867, off Cape Runaway. COOK STRAIT: 1 NMNZ M.013779, Nicholson Canyon, off Turakirae Head [41º28.50'S, 174º 50.00'E], 274 m, mud, gravel and shell bottom, 21 Mar. 1954, MV ALERT. SOUTH ISLAND: 2 NMNZ M.090257, NE of Cape Farewell [40º06.00'S, 172º12.00'E], 102–137 m, 11 Nov. 1987, FV UNZEN MARU; 1 NMNZ M.053752, NE of Stephens Island [40º31.00'S, 174º15.00'E], 117–119 m, mud, 4 Mar. 1976, RV ACHERON; 1 NMNZ M.053040, NE of Stephens Island [40º33.00'S, 174º07.00'E], 132 m, mud, 4 Mar. 1976, RV ACHERON; 1 NMNZ M.032979, W of Cape Farewell [40º40.00'S, 171º33.00'E], 265 m, 15 Jan. 1971, RV JAMES COOK; 4 NMNZ M.053599, off Seal Bay, S of Kahurangi Point [40º52.00'S, 172º04.00'E], 64 m, 10 Mar. 1976, RV ACHERON; 2 NMNZ M.055072, Admiralty Bay [40º54.00'S, 173º56.00'E], 44 m, mud, 5 Mar. 1976, RV ACHERON; 1 NMNZ M.050558, NW of Wekakura Point, between Kahurangi Point and Heaphy River [40º54.00'S, 172º04.00'E], 55 m, sandy mud,10 Mar. 1976, RV ACHERON.

Fossil specimens at NMNZ. NORTH ISLAND: 4 NMNZ M.001418, Castlecliff, Wanganui, Lower Beds, Pleistocene (Castlecliffian), 1924; 2 NMNZ M.017770, Castlecliff, Wanganui, Blue mudstone. Pleistocene (Castlecliffian) 26 Jan 1909; 13 NMNZ M.026406, Castlecliff, Wanganui, Pleistocene (Castlecliffian); 1 NMNZ M.026407, Shakespeare Cliff, Wanganui (GS206), Pleistocene (Castlecliffian); 2 NMNZ M.026408, Castlecliff, Wanganui, Blue mudstone. Pleistocene (Castlecliffian). 29 Jul 1909; 1 NMNZ M.028184, Castlecliff, Wanganui, Pleistocene (Castlecliffian); 4 NMNZ M.071116, Buttress, Tainui Shellbed, Wanganui, Pleistocene (Castlecliffian) 17 Jul 1974.

Distribution (Figures 35, 39). *Coluzea spiralis* inhabits mud, sand and rubble bottoms on the mid- to outer continental shelf and uppermost continental slope along the northern, western, and northeastern coasts of North Island, the Cook Strait, and off Cape Farewell, South Island. Excluding one questionable 366 m ["200 fm"] record

originating from a private collection, the species has been reported from depths ranging between 32 and 327 m, with a mean station depth [n = 74] of 111.9 m, and a confirmed bathymetric range of 32–274 m. The distribution of *Coluzea spiralis* is confined to the area north of the biogeographic disjunction south of the Cook Strait at 42°S latitude that has been documented for several shallow water species (see Apte & Gardner 2002: fig. 1; Ayers & Waters 2005: fig. 1).



FIGURES 39–42. Bathymetric distributions of species of New Zealand *Coluzea*. **39**, *Coluzea spiralis* (A. Adams, 1856). **40**, *Coluzea wormaldi* Powell, 1971. **41**, *Coluzea altocanalis* Dell, 1956. **42**, *Coluzea mariae* Powell, 1952.

Remarks. *Coluzea spiralis* is the shallowest dwelling member of the subfamily Columbariinae, with the majority of records sampled from mid to outer continental shelf depths. Nearly all of the shallowest records (< 50 m) are from the northern coast of North Island, an area with coastal upwelling and bottom water temperatures approaching 15°C (Longdill & Healy 2008: figs. 5, 6). Deepest records (>200 m) are from steep slopes near the various capes at the corners of North Island, the Mahia Peninsula and Cape Farewell on South Island. The fossil record of *Coluzea spiralis* extends to the Nukumaruan (Pliocene / Pleistocene) and Castlecliffian (Pleistocene) deposits on North Island (Beu *et al*. 1990: 356).

Dell (1956: 48) commented on the occurrence of northern and southern forms of *Coluzea spiralis*. The northern form, which he considered to be exemplified by the holotype of *Fusus spiralis*, has a single, prominent keel on the last whorl. A southern form, occurring from Kapiti Island southward and exemplified by Suter's (1913: pl. 41, fig. 4) illustration (based on a photograph of the holotype of *F. pensum*), is distinguished by the presence of two keels on the antepenultimate and penultimate whorls. Finlay (1930b: 269) speculated that perhaps Suter's drawing was based on a fossil (Nukumaruan) specimen, and went on to describe that phenotype as *C. espinosa*. Dell (1956: 48) reported that Castlecliff (Castlecliffian) fossils have a single keel and are indistinguishable from the northern

form, and went on to note that specimens from the northern portion of the range may also develop two keels (see Figures 19, 23, 27), but do so at a larger size than southern specimens.

Coluzea spiralis may be discerned from other Recent New Zealand species of *Coluzea* by its stout shell, tall spire with stepped, angular whorls, its strongly angular protoconch, nodular peripheral keel, weak anterior carina, and the presence of a strong, often nodular spiral cord between the peripheral keel and anterior carina. Brownish pigment is often present in areas between nodules along the periphery and the subperipheral spiral cord, especially in larger specimens. The peripheral keel is more posteriorly situated along the whorls than in other living species of New Zealand *Coluzea*. The aperture is more ovate and less rounded than in *C. wormaldi* or *C. altocanalis*. The radula of *C. spiralis* differs from that of other Recent species of New Zealand *Coluzea* in having the three cusps span a proportionally narrower section of a broader basal plate.

Although *Coluzea spiralis* is the only species of Columbariinae inhabiting the western coast of New Zealand, its geographic range overlaps with that of *Columbarium viridicum* and *Coluzea wormaldi* along the northern shore of North Island, and with *Coluzea wormaldi* and *Coluzea altocanalis* along the eastern shore of North Island. However, the confirmed bathymetric range of *C. spiralis* [32–274 m] does not overlap with the ranges of *Columbarium veridicum* [622–818 m], *Coluzea wormaldi* [337–685 m]; or *C. altocanalis* [403–984 m].

Coluzea wormaldi Powell, 1971

(Figures 36, 40, 43–61)

Synonymy:
Coluzea mariae (*non* Powell, 1952) Dell, 1963: 211, pl. 1, fig. 4.
Coluzea wormaldi Powell, 1971: 221–222, fig. 17.
Columbarium (*Coluzea*) *wormaldi* Powell, 1979: 170, pl. 37, fig. 3.

Diagnosis. Shell large, broad, fusiform, with a very long, distally twisted siphonal canal. Spire short, broadly conical (spire angle 44–48˚), with low, compressed whorls. Cord adjacent to periphery most pronounced of spiral cords between suture and periphery. Peripheral keel nodulose, with prominent spiral cord between periphery and weak anterior carina. Protoconch broadly conical, of ~1⅓ whorls. Teleoconch with up to 8 whorls. Axial sculpture of 12–20 low ribs with prominent nodular tubercles along periphery and, in some specimens, on immediately adjacent spiral cords. Shell color uniformly white.

Description. Shell (Figures 43–55) large (to 110.1 mm), thin, with short, conical spire (spire angle 44–48˚), small, rounded aperture, very long axial, siphonal canal. Protoconch (Figures 58, 59), tall, conical, of weakly inflated, heavily eroded whorls increasing in diameter from 400 μm to 1.75 mm in ~1⅓ whorls. First whorl deflected from shell coiling axis by ~32˚. Transition to teleoconch marked by strong shoulder followed by onset of weak spiral threads, and, within ¼ whorl, by peripheral keel with 11–12 broadly rounded tubercles per whorl. Teleoconch of 7½–8 roundly convex, broadly ovate whorls. Suture (Figure 49, s) adpressed onto or just beneath spiral cord along weak anterior carina (Figure 49, ac) of previous whorl. Spiral sculpture of: smooth area adjacent to suture, 1 strong and 0–4 weaker spiral cords nearer periphery, short, laterally directed peripheral keel (figure 49, pk), 1 prominent cord between periphery and anterior carina (may be stronger than carina), 3–4 strong cords between carina and siphonal canal, 5–11 progressively weaker cords along proximal ⅓ of siphonal canal. Fine to very fine spiral threads between major cords. Axial sculpture of weak to moderately strong axial ribs producing tubercles or nodes along peripheral keel (10–12 broad, undulating tubercles on early whorls, 17–20 strong to weak, bead-like nodes on last whorl of larger specimens), occasionally on adjacent spiral cords (e.g., Figures 43–45, on spiral cords anterior to peripheral keel, Figures 49–52, on spiral cord posterior to peripheral keel). Orthocline growth striae most pronounced between adjacent spiral cords. Aperture ovate, tapering anteriorly, narrower in juveniles, more rounded with increasing shell size (Figures 47→49→53→43), deflected from shell axis by 24–28˚. Outer lip thinly glazed, furrowed beneath peripheral keel, adjacent spiral cords. Inner lip smooth. Portions of outer shell layer comprising surface sculpture resorbed along parietal region, columella and siphonal canal prior to deposition of thin porcellaneous glaze. Siphonal canal very long (52–56% shell length), narrow, axial, thin, with proximal ⅓ straight, distal ⅔ spirally coiled. Shell color uniformly white. Periostracum thin, straw colored, finely lamellose. Operculum (Figures 56, 57) broadly rounded posteriorly, sharply tapered anteriorly, attached to columellar muscle along broadly ovate area confined to posterior 2/3 of operculum. Operculum weakly corrugated, its lateral edges thickened, its nucleus and free edges worn, abraded.

Single, preserved, male specimen examined (Figures 53–55, SL = 78.0 mm). General anatomical organization same as that of *Coluzea spiralis*. Conspicuous differences include: lack of pigmented eyes, presence of a shorter penial papilla. Radular ribbon (Figures 60, 61) 4.95 mm long, with 118 rows of teeth. Rachidian teeth 118.9 µm wide, basal plate with U-shaped central section (49.2 µm wide), flanked by broad, rectangular, anteriorly skewed edges. Of 3 cusps, central cusp longest (56.0 µm), broadest, with tip reaching dimple in next posterior tooth. Lateral teeth with single, long (113.2 µm), scythe-shaped cusp, attached to radular ribbon along narrow, posterior edge of broadly triangular basal plate (49.2 µm wide).

Type locality. (Figure 36, ✠) E of Poor Knights Islands, North Island, in 549 m.

Type material. Holotype, Auckland Museum, AK71334. The original publication identified 2 paratypes, also from the type locality, but did not specify where they were deposited. They are not in the collections of the Auckland Museum.

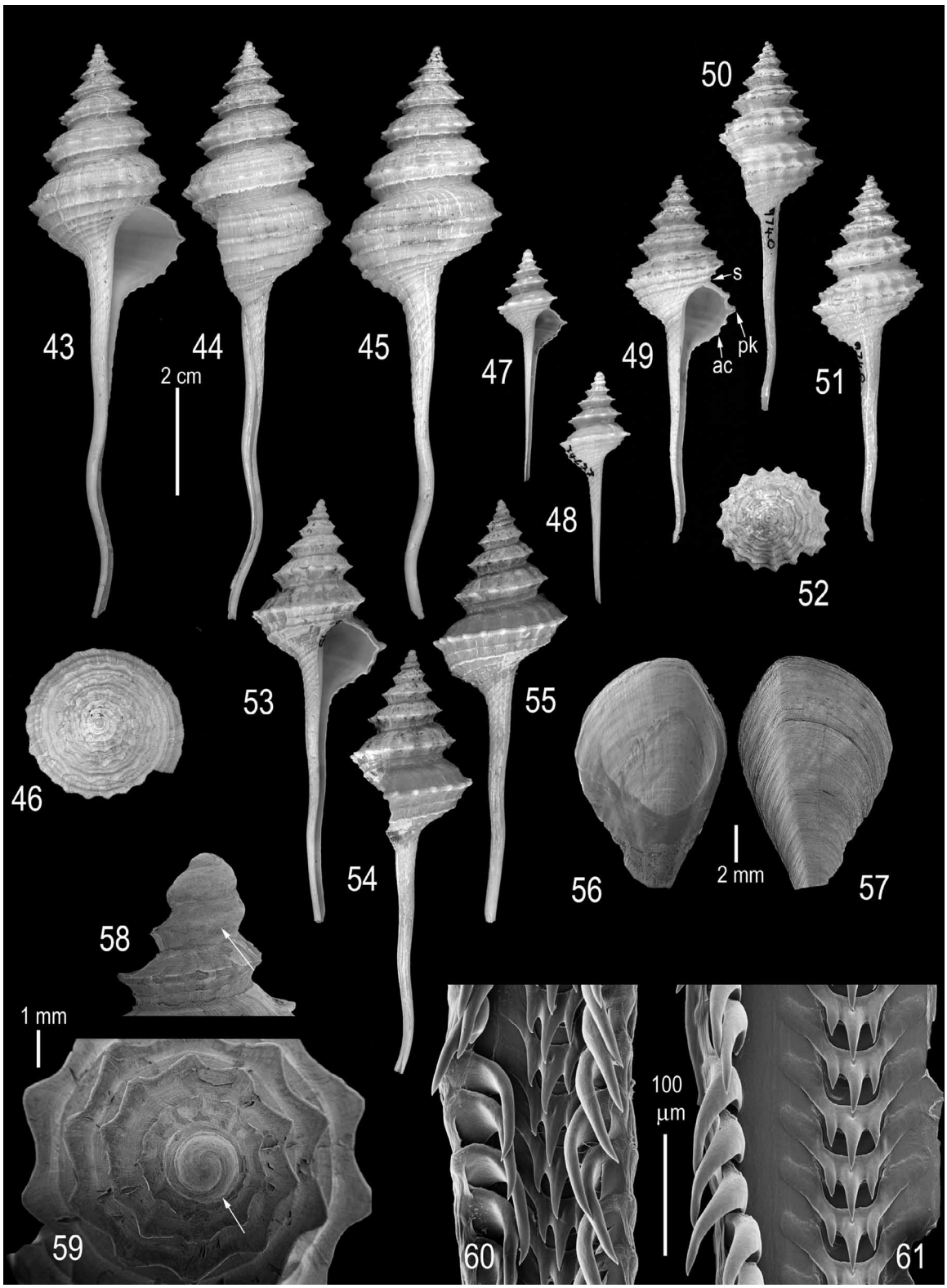
Material examined. NORTH ISLAND: 1 NMNZ M.016272, 23 miles NE of Cuvier Island [36°20.0'S, 176°12.0'E], 476–494 m, 8 Nov. 1962. RV IKATERE; 18 NMNZ M.090102, E of Aldermen Islands [37°00.0'S, 176°16.0'E], 380–420 m, Oct. 1987, FV TRINITY; 1 NMNZ M.081465, SE of Aldermen Islands [37°01.0'S, 176°14.8'E], 357–312 m, mud, 24 Jan. 1981, RV TANGAROA; 3 USNM 702121, off Alderman Islands, in 640 m, Jun. 1969; 4 NMNZ M.061039, c. 15 km NNW of Mayor Island [37°08.7'S, 176°14.2'E], 356–380 m, mud and pumice, 23 Jan. 1979, RV TANGAROA; 1 NMNZ M.060064, c. 15 km NNW of Mayor Island [37°08.8'S, 176°21.8'E], 512–632 m, mud, 23 Jan. 1979, RV TANGAROA; 2 NMNZ M.060997, c. 13 km NW of Mayor Island [37°09.6'S, 176°12.2'E], 293–348 m, mud and pumice, 22–23 Jan. 1979, RV TANGAROA; 3 NMNZ M.074627, W of White Island [37°10.9'S, 176°38.7'E], 685–705 m, mud, 23 Jan. 1981, RV TANGAROA; 2 NMNZ M.060195, c. 37 km E of Mayor Island [37°22.0'S, 176°40.0'E], 616–666 m, mud, 24 Jan. 1979, RV TANGAROA; 1 NMNZ M.060184, c. 43 km E of Mayor Island [37°23.5'S, 176°45.0'E], 631–666 m, mud, 21 Jan. 1979, RV TANGAROA; 1 NMNZ M.009740, Off Cape Palliser [41°39.5'S, 175°17'E], 91–366 m, 23 Feb. 1956; 1 NMNZ M.059653, Slope off Cape Palliser [41°42.0'S, 175°15'E], 461 m, mud, 9 Jan. 1979, RV TANGAROA.

Additional material at NMNZ. NORTH ISLAND: 1 NMNZ M.183923, E of Great Barrier Island [36°18.0'S, 176°10.0'E], 430 m. 15 Oct. 2006, FV CHRISTMAS; 1 NMNZ M.131874, off Great Barrier Island, North Island, in 400 m. 1996; 1 NMNZ M.183810, ENE of Red Mercury Island [36°34.7'S, 176°10.7'E], 371–410 m, 2 Jun. 2006, FV CHRISTMAS; 2 NMNZ M.088350, E of Aldermen Islands [36°54.2'S, 176°17.4'E], 400 m, 22 Jun. 1987, FV TRINITY; 2 NMNZ M.088369, E of Aldermen Islands [36°59.0'S, 176°16.6'E], 430 m, 23 Jun. 1987, FV TRINITY; 22 NMNZ M.090001, E of Aldermen Islands [37°00.0'S, 176°16.0'E], 410–415 m, Jul. 1987, FV TRINITY; 1 NMNZ M.090202, E of Aldermen Islands [37°07.0'S, 176°15.0'E], 380–420 m, Dec. 1987, FV TRINITY; 1 NMNZ M.083868, off the Aldermen Islands, 549 m; 5 NMNZ M.278401, off Aldermen Islands, 475–550 m, Apr. 1969; 9 NMNZ M.090158, SE of Mayor Island [37°21.0'S, 176°26.0'E], 390–420 m, Nov. 1987, FV TRINITY; 2 NMNZ M.278400, between Mayor Island and Poor Knights Island, 365–550 m, Jan 1969, FV VALYRIE; 1 NMNZ M.0119038, S of White Island [37°36.3'S, 177°10.2'E], 337 m, 15 Jan. 1995, RV KAHAROA; 1 NMNZ M.0118397, off Cape Kidnappers [39°43.0'S, 177°35.3'E], 360 m, 4 Jun. 1994; 1 NMNZ M.0119058, off Cape Kidnappers [39°44.2'S, 177°33.3'E], 354 m, 17 Jan. 1995, RV KAHAROA; 3 NMNZ M.153117, off Cape Kidnappers [39°49.0'S, 177°28.0'E], 400 m; 2 NMNZ M.134566/1, off Waimarama [39°51.2'S, 177°20.9'E], 325 m, 5 Dec. 1996, FV BILYARA.

Fossil specimens at NMNZ. NORTH ISLAND: 1 NMNZ M.0117612, cliffs W of Whangaimoana, Palliser Bay, Late Pliocene (Mangapanian), 1971.

Distribution (Figures 36, 40**).** *Coluzea wormaldi* inhabits the waters off the northern and eastern coasts of North Island. Records from the northern coast [n = 25] range in depth from 293 to 705 m, with a confirmed bathymetric range of 337–685 m, and a mean station depth of 459.3 m. Records from the eastern coast are fewer [n = 4] and have a range of 91 to 461 m, with a confirmed bathymetric range of 366–461 m, and a mean station depth of 353.6 m.

Remarks. *Coluzea wormaldi* is most similar to *C. spiralis*, from which it can be readily distinguished on the basis of its shorter, broader spire (greater spire angle), with more compressed whorls (suture closer to periphery of preceding whorl), a protoconch that is conical and rounded rather than angular, and a proportionally longer siphonal canal. The shell of *C. wormaldi* is white. Anatomical differences include the lack of pigmented eyes in *C. wormaldi*, and a penial papilla that is shorter than that of *C. spiralis*.



FIGURES 43–61. *Coluzea wormaldi* Powell, 1971. **43**, Apertural, **44**, lateral, **45**, dorsal, and **46**, apical views of specimen from NMNZ M.016272, NE of Cuvier Island, North Island, [36°20.0'S, 176°12.0'E], in 476–494 m. **47**, Apertural and **48**, dorsal views of specimen from NMNZ M.074627, W of White Island, North Island [37°10.9'S, 176°38.7'E], in 685–705 m, in mud. **49**, Apertural, **50**, lateral, **51**, dorsal, and **52**, apical views of specimen from NMNZ M.009740, off Cape Palliser, North Island [41°39.5'S, 175°17'E], in 91–366 m. **53**, Apertural, **54**, lateral and **55**, dorsal views of specimen from NMNZ M.060195, c. 37 km E of Mayor Island, North Island [37°22.0'S, 176°40.0'E], in 616–666 m, in mud. 2 cm scale bar applies to figures 19–27. **56**, Inner and **57**, outer surfaces of operculum of specimen in figures 53–55. **58**, Lateral and **59,** apical views of protoconch of specimen in figures 47, 48. Arrows indicate transition to teleoconch. **60**–**61**, Radular ribbon of specimen in figures 53–55. **60**, Dorsal view with lateral teeth folded. **61**, Dorsal view with lateral teeth expanded. ac, anterior carina; pk, peripheral keel; s, suture.

The geographic range of *Coluzea wormaldi* overlaps with those of *Columbarium veridicum* and *Coluzea spiralis* along the northern coast of North Island, and with *Coluzea spiralis* and *C. altocanalis* along the eastern coast of North Island. *Coluzea spiralis* is a species that dwells in shallower water, and its confirmed bathymetric range does not overlap with that of *C. wormaldi*.

The type localities of *Coluzea wormaldi* and *Columbarium veridicum* are both off Poor Knights Island, the former from 549 m, the latter from 558–622 m. Live specimens of both species have been collected together from a single RV TANGAROA station west of White Island, in 685–705 m (*Columbarium veridicum*, NMNZ M.074626; *Coluzea wormaldi*, NMNZ M.074627). Records of *Coluzea wormaldi* from along the eastern coast of North Island are fewer, and from somewhat shallower waters. Its confirmed bathymetric range [366–461 m] does not overlap with that of *C. spiralis* [32–274 m], nor with *Coluzea altocanalis*, which inhabits considerably greater depths [785–880 m] off North Island.

Coluzea altocanalis Dell, 1956

(Figures 37, 41, 62–76)

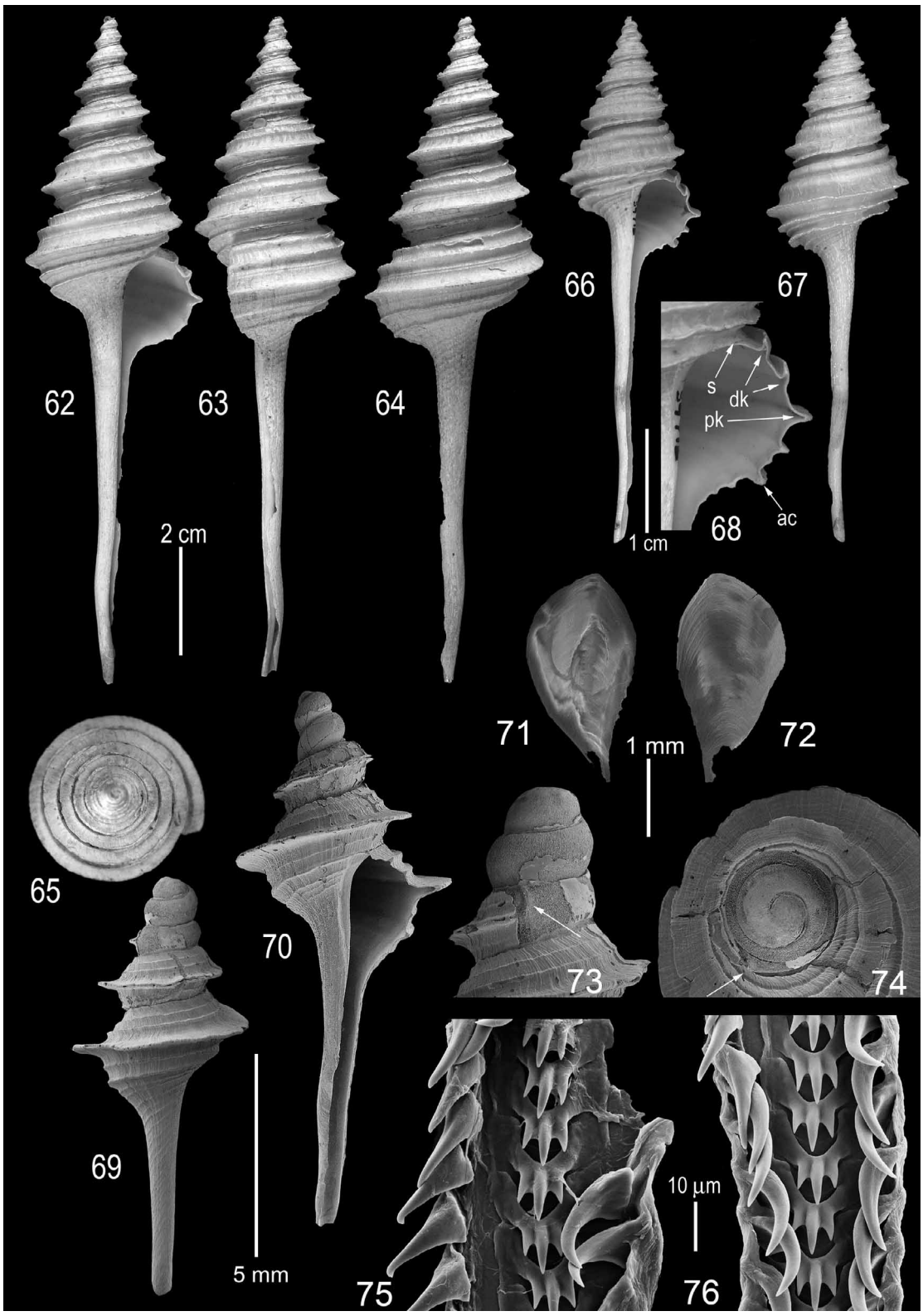
Synonymy:
Coluzea altocanalis Dell, 1956: 50, figs. 53, 54.
Columbarium (*Coluzea*) *altocanalis* Powell, 1979: 169.
? *Fulgurofusus* sp. cf. *benthocallis* Darragh, 1969: 104, pl. 6, fig. 114.

Diagnosis. Very large species with narrow, fusiform, white shell with tall, conical spire (spire angle 30–36˚), laterally oriented, flange-like keel along shell periphery, long (~½ shell length) axial siphonal canal. Protoconch cylindrical, of ~2¼ whorls. Teleoconch with two strong, posteriorly deflected cords between suture and periphery. Axial sculpture limited to growth lines, irregular undulations in spiral sculpture.

Description. Shell (Figures 62–70) largest in subfamily (to 127.3 mm), moderately thin, with very tall, conical spire (spire angle 30–36˚), small aperture, long, axial siphonal canal. Protoconch (Figures 73–74) tall, narrow, nearly cylindrical, with weakly inflated, heavily eroded whorls increasing in diameter from 520 µm to 1.7 mm in ~2¼ whorls. First whorl deflected from coiling axis of shell by ~58˚. Transition to teleoconch marked by development of strong shoulder followed within ¼ whorl by onset of spiral cords and laterally directed peripheral keel. Teleoconch extrapolated to consist of up to 8 strongly convex, broadly ovate whorls. Suture (Figure 68, s) abutted to or subducted beneath keel of anterior carina (Figure 68, ac) of previous whorl. Sculpture limited to two prominent spiral cords between suture and periphery, a strong, flange-like peripheral keel (Figure 68, pk), a prominent cord between keel and anterior carina, 2–4 weaker cords between carina and siphonal canal, and 6–12 weak cords along proximal ⅓ of siphonal canal. Spiral cords between suture and shoulder pronounced, developing into posteriorly deflected minor keels (Figure 68, dk) with increasing shell size. Fine to very fine spiral threads on keels and between major cords. Axial sculpture lacking, apart from weak growth striae and occasional undulations along spiral sculptural elements. Aperture ovate, tapered anteriorly, narrower in juveniles, more rounded with increasing shell size (Figures 70→66→62), deflected from shell axis by 14–24˚. Outer lip glazed, furrowed beneath spiral cords and keels, most deeply beneath peripheral keel. Inner lip smooth. Outer shell layer comprising surface sculpture resorbed along parietal region, columella and proximal siphonal canal prior to deposition of a thin porcellaneous glaze. Siphonal canal long (~½ shell length), narrow, axial, stout, proximal ½ straight, distal ½ weakly spiral. Shell color uniformly white. Periostracum very thin, yellowish, finely lamellose. Operculum (Figures 71, 72) thin, elongated, broadly rounded posteriorly, sharply tapering anteriorly, attached to columellar muscle along broadly ovate area limited to posterior ⅔ of operculum. Operculum weakly corrugated, with thickened lateral edges. Nucleus anterior, free edges are usually worn, abraded.

Dried tissues of single juvenile specimen (Figure 70, SL = 13.2 mm) rehydrated. General anatomical organization typical of *Coluzea*. Radular ribbon (Figures 75, 76) short, of ~42 rows of teeth. Rachidian teeth 25.7 µm wide, basal plate with U-shaped central section flanked by broad, rectangular, laterally expanded edges. Three long, cylindrical cusps, central cusp longest (12.5 µm), confined to central 9.5 µm of rachidian tooth. Lateral teeth, each with a single, long (20.7µm), scythe-shaped cusp, attached to radular ribbon along a basal plate 14 µm wide.

Type locality. (Figure 37, ✠) Chatham Rise [43°40.0’S, 179°28.0’E], 403 m. 24 Jan. 1954, MV ALERT.



FIGURES 62–76. *Coluzea altocanalis* Dell, 1956. **62**, Apertural, **63**, lateral, **64**, dorsal, and **65**, apical views of specimen from NMNZ M.074636, E of Cape Kidnappers, North Island [39°52.8'S, 177°36.5'E], in 785–882 m, on mud. **66**, Apertural, **67**, dorsal views, **68**, detail of outer lip of specimen from NMNZ M.059715, northern Mernoo slope, [42°38.2'S, 176°10.5'E], in 999–984 m, on mud. 2 cm scale bar applies to figures 62–67. **69,** Dorsal view of specimen from NMNZ M.074636, E of Cape Kidnappers, North Island [39°52.8'S, 177°36.5'E], in 785–882 m, on mud. **70**, Apertural view of specimen from NMNZ M.059715, northern Mernoo slope, Chatham Rise [42°38.2'S, 176°10.5'E], in 999–984 m, on mud. 5 mm scale bar applies to figures 69–70. **71,** Inner and **72**, outer surfaces of operculum of specimen in figure 70. **73**, Lateral and **74** , apical views of protoconch of specimen in figure 69. Arrows indicate transition to teleoconch. **75–76**, Radular ribbon of juvenile specimen in figure 70. **75**, Dorsal view with lateral teeth expanded. **76**, Dorsal view with lateral teeth folded. ac, anterior carina; dk, deflected keels; pk, peripheral keel; s, suture.

Type material. Holotype NMNZ M.008219, paratype 1, NMNZ M.008220, both from the type locality. A second paratype was deposited at the Canterbury Museum (Dell, 1956: 50).

Material examined. NORTH ISLAND: 2 NMNZ M.074636, E of Cape Kidnappers [39°52.8'S, 177°36.5'E], 785–882 m, mud, 21 Jan. 1981, RV TANGAROA. CHATHAM RISE: 1 NMNZ M.059580, Northern Mernoo slope [42°38.1'S, 176°16.3'E], 980–1,000 m, mud, 11 Jan. 1979, RV TANGAROA; 6 NMNZ M.059715, Northern Mernoo slope [42°38.2'S, 176°10.5'E], 999–984 m, mud, 11 Jan. 1979, RV TANGAROA. SOUTH ISLAND: 1 NMNZ M.058503, Papanui Canyon, NE of Taiaroa Heads [45°46'S, 171°03'E], 660 m, 1 Sep. 1976, RV MUNIDA.

Additional material at NMNZ. NORTH ISLAND: 1NMNZ M.100332, SE of Mahia Peninsula [39°32.8'S, 178°16.5'E], 857–880 m, 29 Sep. 1989, RV JAMES COOK. CHATHAM RISE: 1 NMNZ M.059755, northern slope of Mernoo Bank [42°57.9'S, 175°27.8'E], 500–518 m, mud, 12 Jan. 1979, RV TANGAROA. SOUTH ISLAND: 1 NMNZ M.059621, ridge c 35 km off Clarence River mouth [42°16.3'S, 174°20.8'E], 790–860 m, 14 Jan. 1979, RV TANGAROA; 1 NMNZ M.050976, off Kaikoura Peninsula [42°28.5'S, 173°47.5'E], 786 m, mud, 18 Mar. 1976, RV ACHERON.

Distribution (Figures 37, 41**).** *Coluzea altocanalis* inhabits the upper continental slope off the eastern coast of North Island, South Island, and along the Chatham Rise at depths ranging from 403–1,000 m. This species has a confirmed bathymetric range of 403–984 m, and a mean station depth [n = 9] of 675.6 m. There appears to be an inverse relationship between the depth at which this species occurs and latitude, with southern records occurring at shallower depths than northern records.

Remarks. *Coluzea altocanalis* is easily distinguished from the other living New Zealand species of Columbariinae on the basis of its large size, narrow spire angle, lack of axial sculpture, even on the early whorls, cylindrical protoconch, and prominent, keel-like spiral sculpture. Young specimens resemble *Coluzea kiosk* Finlay, 1930, a fossil species from the Hutchinsonian Stage (Burdigalian – Aquitanian Miocene) of Clifden, South Island, which differs in having a much taller, narrower spire, axial sculpture that is evident on early whorls and along the peripheral keel, and a thicker, more heavily sculptured siphonal canal. The type of *C. kiosk* is small (47 mm), but Finlay (1930b: 270) extrapolated that, based on fragments, this species reached about 120 mm in length. In the Recent fauna, *Coluzea altocanalis* resembles *Coluzea kallistropha* Harasewych, 2004, from deeper waters (1,335–1,600 m) off Mozambique. *Coluzea kallistropha* is distinguished by having a smaller shell (to 52 mm) with a more conical protoconch, a shorter, broader spire, a flatter shoulder, and a peripheral keel that is much wider and situated higher on the aperture.

Darragh (1969: 104, pl. 6, fig. 114) illustrated a dead and damaged specimen taken in 912–997 m off Castle Point, North Island that he provisionally identified as *Fulgurofusus* sp. cf. *benthocallis* (Melvill & Standen, 1907). This record falls within both the geographic and bathymetric ranges of *Coluzea altocanalis*, and the illustration closely resembles the juvenile specimen shown in figure 69, herein. With the re-identification of this specimen as *C. altocanalis*, *F. benthocalis* remains endemic to the Scotia Sea in the southern Atlantic.

Coluzea altocanalis has a broad range in New Zealand waters. Off the eastern coast of North Island, it overlaps geographically with both *C. spiralis* and *C. wormaldi*. However, it inhabits considerably greater depths [785–880 m] than either *C. spiralis* [172–306 m] or *C. wormaldi* [91–461 m] in this region. Although the distribution of *C. altocanalis* overlaps with that of *C. mariae* off South Island and on the Chatham Rise, the two species have been collected in a single station only once, off Papanui Canyon, at a depth of 660 m [RV MUNIDA]. All of the specimens of *C. mariae* collected at this station were dead and worn. In other areas of geographic overlap, *C. altocanalis* occurred at depths 200–300 m greater that records for *C. mariae*.

Coluzea mariae Powell, 1952

(Figures, 38, 42, 77–96)

Synonymy:
Coluzea mariae Powell, 1952: 180, pl. 35, fig. 8; Dell, 1956: 49, pl. 45, fig. 49.
Columbarium (*Coluzea*) *mariae* Powell, 1979: 169–170, pl. 37, fig. 4.

Diagnosis. Large species with broad, fusiform, uniformly white shell, very long, distally twisted siphonal canal. Spire short, broadly conical (spire angle 48–53˚), with very low, compressed whorls. Spiral sculpture limited to numerous moderately strong cords, a weak peripheral keel and anterior carina. Axial sculpture of 20–23 weak to

moderately strong ribs most prominent near periphery, producing minor nodules along peripheral keel and carina. Protoconch short, nearly cylindrical, of 1⅓– 1¾ whorls. Teleoconch with up to 8 strongly convex whorls.

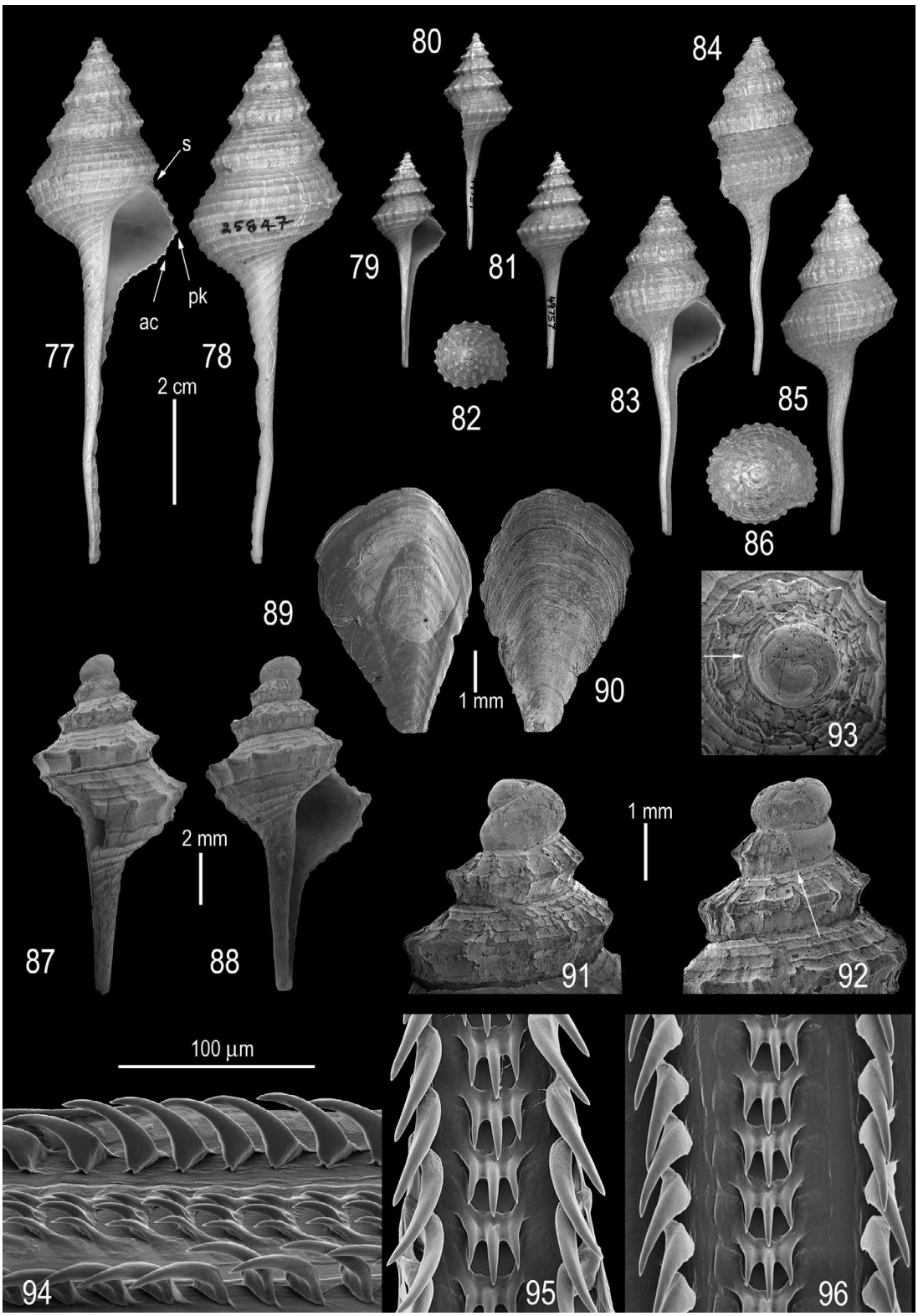
Description. Shell (Figures 77–88) large (to 100.1 mm), stout, with short, conical spire (spire angle 48–53˚), ovate aperture, and long axial siphonal canal. Protoconch (Figures 91–93) short, broad, nearly cylindrical, with weakly inflated, heavily eroded whorls increasing in diameter from ~520 µm to 1.7 mm in 1⅓– 1¾ whorls. First whorl deflected from coiling axis of shell by ~71˚. Transition to teleoconch distinct, marked by sharp transition from smooth, rounded shell of protoconch to shouldered shell of teleoconch, followed by spiral cords and laterally directed nodular peripheral keel. Teleoconch extrapolated to span up to 8 strongly convex, broadly inflated, ovate whorls. Suture (Figure 77, s) adpressed onto anterior carina (Figure 77, ac) of previous whorl. Spiral sculpture of: 3–4 spiral cords between suture and periphery, increasing in prominence toward periphery; peripheral keel (Figure 77, pk) consisting of strong nodulose cord; two weaker cords between periphery and weak anterior carina; 3–4 cords between carina and siphonal canal; 6–12 progressively weakening cords along proximal ⅓ of siphonal canal. Spiral threads may develop between adjacent major cords with increasing shell size. Axial sculpture of low, rounded ribs, 12–14 on early whorls, 20–23 less prominent ribs on last whorl of adults. Axial ribs extending from suture to siphonal canal, strongest from just above periphery to just below anterior carina, producing nodules at intersections with spiral cords. Aperture ovate, deflected from shell axis by 14–24˚, tapering anteriorly, narrower in juveniles, becoming more rounded with increasing shell size (Figures 88→79→83→77). Outer lip glazed, weakly furrowed beneath major spiral cords and keel. Inner lip smooth, with portion of outer shell layer resorbed along parietal region, columella and siphonal canal prior to deposition of thin porcellaneous glaze. Siphonal canal very long (50–54% shell length), stout, narrow, axial, proximal ½ straight, distal ½ straight to very weakly spiral. Shell color uniformly white. Periostracum thin, yellowish, finely lamellose, lamellae broadest between adjacent spiral cords. Operculum (Figures 89, 90) thin, elongated, with thickened lateral edges, weakly corrugated along long axis. Columellar muscle attached along broadly ovate posterior area.

Two juvenile female specimens resemble *Coluzea spiralis* in gross anatomy, except for absence of pigmented eyes. Pallial gonoduct not developed in these specimens. Radular ribbon of specimen in Figures 79–82 (SL = 41.4 mm) 2.66 mm long, consisting of 93 rows of teeth. Rachidian teeth 60.0 µm wide, U-shaped basal plate with central section flanked by broad, expanded lateral edges. Three long, cylindrical cusps, central cusp longest (29.2 µm), confined to central 25.2 µm of tooth. Lateral teeth, each with single, long (64.3 µm), irregularly triangular, scythe-shaped cusp, attached to radular ribbon along a basal plate 24 µm wide.

Type locality. (Figure 38, ✠) Off eastern Otago, New Zealand, 60–70 fathoms. [110–128 m].

Type material. Holotype, Auckland Museum, AK711190.

Material examined. SOUTH ISLAND: 1 NMNZ M.059701, c. 43 km SE of Cape Campbell [41°55.9’S, 174°43.2’E], 454–424 m, coral and mud bottom, 14 Jan. 1979, RV TANGAROA; 5 NMNZ M.050874, c. 24 miles off Waiau River mouth, S of Kaikoura [42°55’S, 173°43’E], 549–586 m, mud, 18 Mar. 1976, RV ACHERON; 2 NMNZ M.049757, 16–20 miles off Waiau River [42°55’S, 173°43’E], 640–512 m, on mud, 21 Feb. 1976, RV ACHERON; 3 NMNZ M.052790, wall of Pegasus Canyon, Pegasus Bay, NE of Banks Peninsula [43°14’S, 173°39’E], 1,006–512 m, coral bottom, 27 Sep. 1976, RV ACHERON; 1 NMNZ M.011337, off Timaru, in 146–164 m; 1 USNM 824522, off Canterbury, trawled in 366 m; 1 NMNZ M.051067, head of Karitane Canyon, NE of Taiaroa Head [45°38.5’S, 171°05’E], 585–530 m, shell and mud, 19 Mar. 1976, RV ACHERON; 2 NMNZ M.009052, Tairoa Canyon, off east Otago Peninsula [45°45.4’S, 171°05’E], 549 m, coarse medium sand with shell fragments, 16 Aug. 1955, MV ALERT; 7 NMNZ M.058466, Papanui Canyon, off Otago Peninsula [45°46’S, 171°03’E], 660 m, 1 Sep. 1976, RV MUNIDA. CHATHAM RISE: 1 NMNZ M.060313, NE of Mernoo Bank [42°50.8’S, 175°43.8’E], 683–703 m, mud, 11 Jan. 1979, RV TANGAROA; 1 USNM 898588, off Chatham Islands [43°31.0’S, 176°10.0’E], 143–183 m, 24 May 1966, USNS ELTANIN sta. 1709; 2 NMNZ M.008214 [43°38’S, 177°19’E], 531 m, fine green mud and sand, 11 Feb. 1954, MV ALERT; 1 USNM 870658, off Chatham Islands [44°00.0’S, 178°06’E], 430 m, 29 Nov. 1964; 2 NMNZ M.025847 [44°03’S, 177°55.8’E], 475 m, 30 Aug. 1971, RV JAMES COOK; 1 NMNZ M.008218, SE of Pitt Island [44°32’S, 176°05’E], 302 m, fine green sand, 3 Feb. 1954, MV ALERT; 3 NMNZ M.008212, SE of Pitt Island [44°35.5’S, 176°04’E], 604 m, 3 Feb. 1954, MV ALERT. CAMPBELL PLATEAU: 2 NMNZ M.058384 [51°47’S, 168°19’E], 687–695 m, 19 Jan. 1977, RV JAMES COOK. AUCKLAND ISLANDS : 1 NMNZ M.032965 [51°10’S, 167°14’E], 540 m, 22 Feb. 1972, RV JAMES COOK; 1 NMNZ M.032966 [51°11’S, 167°08’E], 558 m, 21 Feb. 1972, RV JAMES COOK.



FIGURES 77–96. *Coluzea mariae* Powell, 1952. **77**, Apertural and **78**, dorsal views of specimen from NMNZ M.025847, Chatham Rise [44°03'S, 177°55.8'E], in 475 m. **79**, Apertural, **80**, lateral, **81**, dorsal, and **82**, apical views of specimen from NMNZ M.049757, 16–20 miles off Waiau River, South Island [42°55'S, 173°43'E], in 640–512 m, on mud. **83**, Apertural, **84**, lateral, **85**, dorsal, and **86**, apical views of specimen from NMNZ M.032966, off Auckland Islands [51°11'S, 167°08'E], in 558 m. 2 cm scale bar applies to figures 77–86. **87**, Lateral and **88**, apertural views of two specimens from NMNZ M.009052, Tairoa Canyon, off east Otago Peninsula, South Island [45°45.4'S, 171°05'E], in 549 m, on coarse medium sand with shell fragments. **89**, Inner and **90**, outer surfaces of operculum of the specimen in figures 79–82. **91–92**, lateral and **93**, apical views of protoconch of specimen in figure 88. Arrows indicate transition to teleoconch. **94–96**, Radular ribbon of specimen in figures 79–82. **94**, 45° oblique view of radula, **95**, dorsal view with lateral teeth folded. **96**, Dorsal view with lateral teeth expanded. ac, anterior carina; pk, peripheral keel; s, suture.

Additional material at NMNZ: SOUTH ISLAND: 2 NMNZ M.060400, SE of Cape Campbell [41°55.8'S, 174°40.7'E], 434 m, coral and mud, 14 Jan. 1979, RV TANGAROA; 3 NMNZ M.008919, Taiaroa Canyon, off Otago Peninsula [45°45.4'S, 171°05.0'E], 549 m, on coarse to medium sand with shell fragments, 16 Aug. 1955, MV ALERT; 4 NMNZ M.011274, Taiaroa Canyon, NE of Otago Peninsula [45°45.6'S, 171°05.0'E], 549 m, fine sandy mud, 23 Jan. 1957, MV ALERT; 2 NMNZ M.137640, Papanui Canyon, off Otago Peninsula [45°46.1'S, 171°05.0'E], 530–720 m, on mud, 15 Apr. 1997, RV MUNIDA; 3 NMNZ M.130747, off Otago Peninsula [45°51.05'S, 171°00.9'E], 550–589 m, 4 Jun. 1992, RV MUNIDA; 1 NMNZ M.008209, S of Timaru; 1 NMNZ M.011327, Off Timaru; 2 NMNZ M.110669, off Oamaru, 1959. CHATHAM RISE: 12 NMNZ M.118860, E of Mernoo Bank [42°53.0'S, 176°04.0'E], 370–420 m, Dec 1994, FV PETERSON; 30 NMNZ M.118998, E of Mernoo Bank [43°01.0'S, 176°45.5'E],368–411 m, 27 Dec. 1994, FV PETERSON; 1 NMNZ M.116990, E of Mernoo Bank [43°02.1'S, 176°39.0'E], 400 m, Jun. 1992, FV VENTURE K; 1 NMNZ M.117025, E of Mernoo Bank [43°05.5'S, 176°50.8'E], 340 m, Jun. 1992, FV VENTURE K; 1 NMNZ M.283962 [43°07.75'S, 177°10.015'E], 270–271 m, 25 Apr. 2007, RV TANGAROA; 18 NMNZ M.127028, NE slope of Mernoo Bank [43°10.0'S, 175°44.0'E], 450 m, Oct. 1995, FV PETERSON; 4 NMNZ M.008217 [43°14.0'S, 176°11.0'E], 366 m, 23 Jan. 1954, MV ALERT; 1 NMNZ M.284038, off Chatham Islands [43°30.67'S, 176°10.567'W], 194–218 m, 14 Apr. 2007, RV TANGAROA; 1 NMNZ M.131185, off Chatham Islands [43°31.0'S, 176°10.0'E],143–183 m, 24 May 1966, USNS ELTANIN; 2 NMNZ M.008215 [43°36.0'S, 175°31.0'E], 375 m, 12 Feb. 1954, MV ALERT; 1 NMNZ M.008556 [43°38.0'S, 177°19.0'E], 531 m, fine green mud and sand, 11 Feb. 1954, MV ALERT; 5 NMNZ M.008213 [43°40.0'S, 179°28.0'E], 403 m,24 Jan. 1954, MV ALERT; 2 NMNZ M.008221 [43°40.0'S, 177°59.0'E] in 585 m, 11 Feb. 1954, MV ALERT; 1 NMNZ M.008211[43°42.0'S, 179°55.0'E], 512 m, fine grey sand and mud, 24 Jan. 1954, MV ALERT; 1 NMNZ M.009225, E of Forty-Fours, Chatham Islands [44°04.0'S, 175°23.5'E], 238 m, 1 Feb. 1954, MV ALERT. AUCKLAND ISLANDS: 1 NMNZ M.147018 [50°00.1'S, 166°38.2'E], 415 m, 26 Mar. 1998, FV ALBATROSS II; 2 NMNZ M.118758, E of Auckland Islands [50°50.0'S, 166°52.0'E], 390–400 m, 11 Nov. 1994, FV PETERSON; 1 NMNZ M.147032 [50°53.0'S, 166°46.0'E], 390 m,12 Mar. 1998, FV ALBATROSS II; 3 NMNZ M.147014 [50°57.0'S, 167°12.0'E], 485 m. 18 Mar. 1998, FV ALBATROSS II; 2 NMNZ M.147003 [50°58.0'S, 167°57.0'E],485 m, 17 Mar. 1998, FV ALBATROSS II; 26 NMNZ M.117116 & 117116/1 [51°10.0'S, 166°40.0'E], 360–390 m, 1992, FV VENTURE K; 17 NMNZ M.119008 [51°10.0'S, 167°37.0'E], 490–510 m, 31 Oct. 1994, FV PETERSON; 1 NMNZ M.058401, Cathedral Banks [51°20'S, 166°34'E], 646–670 m, 19 Jan. 1977, RV JAMES COOK.

Distribution (Figures, 38, 42**):** *Coluzea mariae* inhabits fine mud to coarse sand, shell and coral bottoms off Cape Campbell southward along the eastern coast of South Island, the western Campbell Plateau in the vicinity of the Auckland and Campbell Islands, and along the western Chatham Rise. Depth records range from 110 to 1,006 m, with a confirmed bathymetric range of 128–687 m and a mean station depth [n = 47] of 444.6 m. The vast majority of records are from depths greater than 300 m. However, there are several records, including the type locality, from much shallower water (128–238 m) from the Canterbury Bight, and from Mernoo Bank on the Chatham Rise.

Remarks. *Coluzea mariae* is a distinctive species characterized by its short, broad spire, with the shell periphery situated low on the whorl, close to the suture of the succeeding whorl, a roundly ovate aperture, and a very long siphonal canal. Axial ribs are prevalent on early whorls, but become less pronounced with increasing shell size. The protoconch consists of few, rounded whorls and is broadly conical, nearly cylindrical. The geographic range of *Coluzea mariae* overlaps with that of *Coluzea altocanalis* along the eastern coast of South Island as well as on the Chatham Rise, but, as noted under the discussion for *C. altocanalis*, the latter species generally occurs at substantially greater depths.

The holotype of *Columbarium pataka* Maxwell, 1978, a rare species from Middle Eocene (Hampden Formation, Bortonian) near Otago, South Island, is similar to juvenile specimens of *Coluzea mariae*, but differs chiefly in having a more pronounced peripheral keel, anterior carina and axial sculpture, and particularly in having short, stout, but open spines along the peripheral keel. Open spines are lacking in Recent New Zealand *Coluzea*, but occur in *Coluzea* from both the western and eastern Indian Ocean as well as in congeners from Eastern Australia and New Caledonia. Maxwell (1978: 38) noted that *C. pataka* "is clearly rather divorced from other species of *Columbarium*", that it "almost certainly belongs to some other genus group taxon", and that it "possibly belongs to a group that gave rise to *Coluzea*." Based on close morphological similarity, *Columbarium pataka* is here transferred to the genus *Coluzea*.

Genus *Fulgurofusus* Grabau, 1904

Synonymy:
Fulgurofusus Grabau, 1904:86; Wenz, 1941: 1086; Shimer & Shrock, 1944: 507; Darragh, 1969: 99; Harasewych, 1983b: 5.
Columbarium (*Fulgurofusus*) Bayer, 1971: 170.

Type species. *Fusus quercollis* Harris, 1896, by original designation.

Diagnosis. Shell of moderate size (to 86 mm), fusiform, with short or tall, conical spire, rounded whorls, peripheral keel that may be prominent and flange-like or a weakly nodulose cord, weak anterior carina, and stout, axial siphonal canal of moderate length. Protoconch cylindrical to weakly conical, of 1½–3 whorls. First whorl bulbous, deviated. Transition to teleoconch generally indistinct. Suture adpressed onto or slightly above anterior carina. Spiral sculpture of numerous fine threads and weak cords extending from suture to middle of siphonal canal. Early whorls with two closely adjacent cords along periphery, forming an incised furrow between them. Axial sculpture of small nodules along periphery, or low ribs extending from suture to siphonal canal. Outer lip porcellaneous, furrowed beneath periphery. Inner lip smooth, with outermost layers of previous whorls resorbed prior to deposition of a thin glaze that does not produce a raised lamina. Shell color uniformly white. Rachidian teeth of radula with 3 cusps on a U-shaped basal plate with prominent lateral expansions (e.g. Harasewych 1983b: fig. 9).

Remarks. The genus *Fulgurofusus* is based on a Paleocene type species from the Gulf Coast of the United States. Several Eocene species have been reported from western North America and Antarctica. In the Recent fauna, *Fulgurofusus* is the most wide ranging genus within Columbariinae, extending from the Bering Sea to the Bounty Plateau along the western Pacific, and from the Blake Plateau to the Scotia Sea in the western Atlantic. *Columbarium tomicici* McLean & Andrade, 1982, from lower bathyal depths off Chile is likely referrable to *Fulgurofusus* [based on the lack of a raised columellar lamina and the presence of rachidian teeth with a laterally expanded basal plate (McLean & Andrade 1982: figs. 26–30)], further expanding the range of this genus. Unlike other columbariine genera, the bathymetric range of *Fulgurofusus* extends to the lower continental slope and onto the abyssal plain, especially near the poles.

Finlay (1930b: 267–268) considered *Fulgurofusus* to be less advanced than *Coluzea*, and presumed it to be ancestral to *Coluzea*.

Fulgurofusus maxwelli, new species.

(Figures 97–116, 118)

Diagnosis. Small to moderately sized species with fusiform shell, tall, conical, weakly stepped spire, weakly pentagonal aperture, long, axial siphonal canal. Protoconch nearly cylindrical, of 2–3 rounded whorls. Early teleoconch whorls with sharply angled shoulder, prominent peripheral keel, angular anterior carina becoming more rounded, less pronounced with increasing shell size. Teleoconch of up to 8 whorls. Peripheral keel low on whorls, well below midpoint between successive sutures. Spiral sculpture of numerous fine threads, cords, with adjacent cords along periphery forming incised furrow between them. Axial sculpture of low, weak ribs most pronounced at shoulder and anterior carina.

Description. Shell (Figures 97–108) of moderate size (to 86.1 mm), stout, with tall, conical spire (spire angle 39–46˚), ovate aperture, long axial siphonal canal. Early whorls generally eroded. Protoconch (Figures 111–112) tall, conical, nearly cylindrical, with rounded, heavily pitted whorls increasing in diameter from 495 µm to 1.7 mm in 2¾ whorls. First whorl deflected from coiling axis of shell by ~68˚. Transition to teleoconch marked by onset of strong shoulder, thin, spiral threads, sharp peripheral keel. Teleoconch extrapolated to consist of up to 8 angular whorls, becoming more rounded with increasing size. Suture (Figure 102, s) adpressed in smaller specimens, abutting spiral cord along anterior carina of previous whorl (Figure 102, ac) in larger specimens. Spiral sculpture of: fine threads or weak cords, 4–26 between suture and laterally expanded peripheral keel; 4–11 between peripheral keel and anterior carina; 4–6 between anterior carina and base of siphonal canal; up to 22 along proximal ½ of siphonal canal. Peripheral keel pronounced, with incised furrow along perimeter in early whorls, furrow reduced by 6th postnuclear whorl, indistinct by 7th postnuclear whorl. Axial sculpture of 10–14 wide, weak ribs most pronounced between periphery and anterior carina, producing broad undulating nodules along periphery. Aperture angular,

irregularly pentagonal in juvenile specimens (Figure 108), progressively more rounded with increasing size (Figures 108→101→105→97), deflected from shell axis by 24–29˚. Outer lip smooth, evenly glazed, weakly furrowed beneath peripheral keel, anterior carina, especially in early whorls. Spiral sculptural elements of preceding whorl wholly or partially resorbed prior to deposition of thin porcellaneous glaze along parietal region, columella, length of long, axial siphonal canal. Distal ⅓ of siphonal canal may be weakly spirally coiled. Shell surface generally eroded. Periostracum, where preserved, very thin, straw colored, weakly lamellose. Operculum (Figures 109, 110) thin, elongated, weakly corrugated, with thickened edges, ovate attachment area, worn free end.

Gross anatomy of an immature female specimen (Figures 101–104, SL = 40.5 mm) generally similar to that of *Coluzea spiralis*. Radular ribbon of this specimen (Figures 113–115) 2.52 mm long, with 96 rows of teeth. Rachidian teeth 54.5 μm wide, basal plate with U-shaped central section flanked by broad, expanded lateral edges. Three long, cylindrical cusps, central cusp longest (24.6 μm), confined to central 18.9 μm of tooth. Lateral teeth, each with single, long (51.4 μm), irregularly triangular, scythe-shaped cusp, attached to radular ribbon along a basal plate 19.9 μm wide.

Etymology. This new species honors the late Phillip A. Maxwell, for his prolific contributions to our knowledge of the invertebrate paleontology of New Zealand.

Type locality. (Figure 116, ✠) Campbell Plateau [53°30.6'S, 172°24.0'E] in 625 m, 22 Sep 1978, RV TANGAROA (NIWA S48).

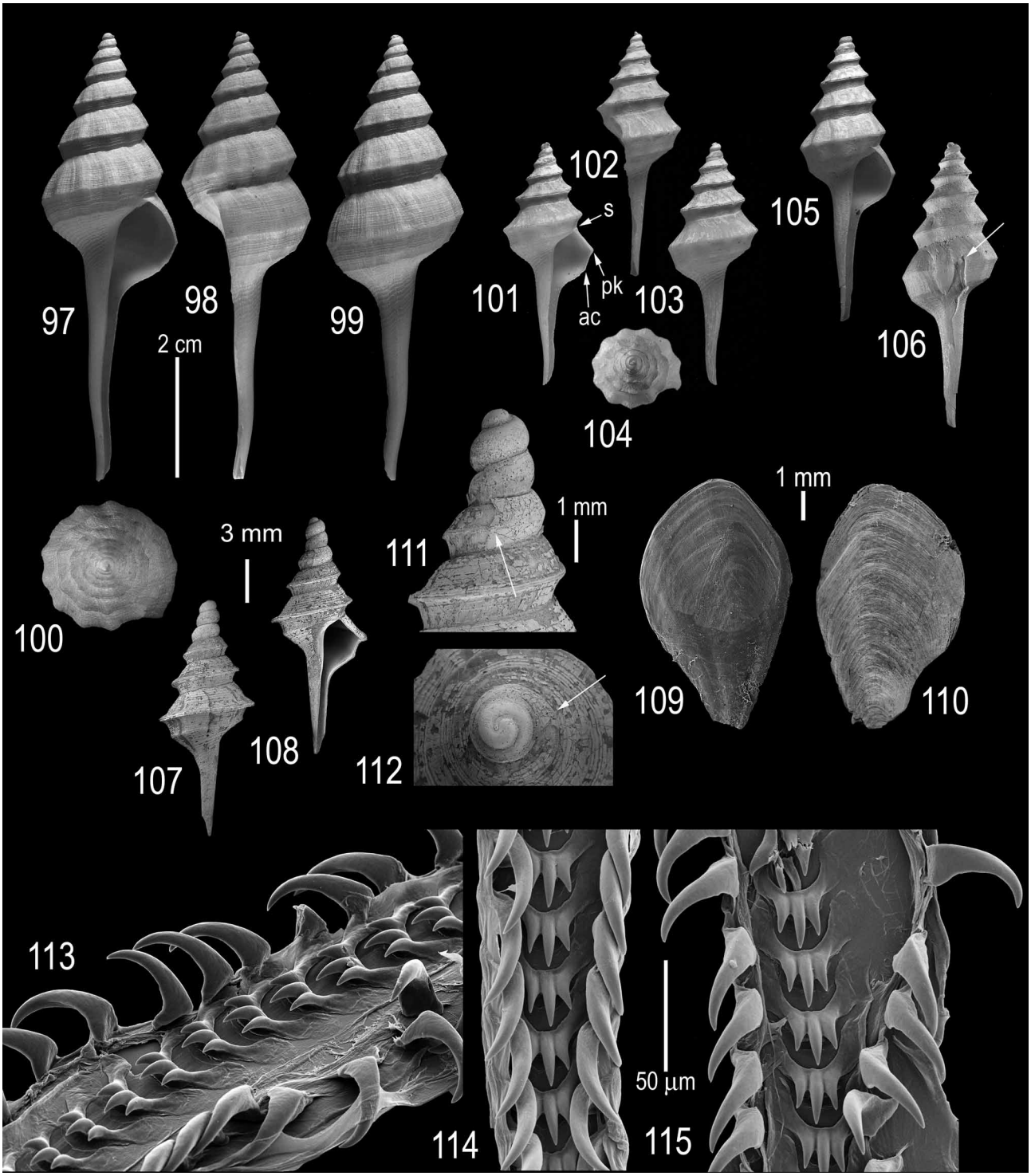
Type material. Holotype, NIWA 67593, 2 paratypes M 297055, USNM 1146128, from the type locality. Additional Paratypes: 2 NMNZ M.297044, 1 NIWA S153, northern Bounty Trough [45°21.2'S, 173°35.8'E], 1,386 m, 27 Nov. 1979, RV TANGAROA; 1 NMNZ M.297043, northern Bounty Trough [45°24.2'S, 173°59.8'E], 1,373 m, 27 Oct. 1979, RV TANGAROA; 2 NMNZ M. 297051, 1 NIWA I703, Bounty Plateau [48°10.9'S, 178°15.9'E], 875 m, 21 Mar. 1979, RV TANGAROA; 6 NMNZ M. 297053, 5 NIWA I683B, Bounty Plateau [48°18.5'S, 179°56.8'W], 516–495 m, 15 Mar. 1979, RV TANGAROA; 17 NMNZ M. 297052, 18 NIWA I698, Bounty Plateau [48°20.0'S, 178°30.0'E], 726 m, 19 Mar. 1979, RV TANGAROA; 2 NMNZ M.297042, 1 NIWA I697, Bounty Plateau [48°29.1'S, 178°16.6'E], 917 m, 19 Mar. 1979, RV TANGAROA; 1 NMNZ M.297046, 1 NIWA I686, Bounty Plateau [48°30.5'S, 179°45.0'W], 710 m, 16 Mar. 1979, RV TANGAROA; 2 NMNZ M. 297049, 2 NIWA I689, Bounty Plateau [48°50.6'S, 178°41.5'E], 808–608 m, 17 Mar. 1979, RV TANGAROA; 1 USNM 870882, off Antipodes Island [49°40'S, 178°53'E], 476–540 m, 3 Jan. 1967, RV ELTANIN, sta. 1851.

Additional material at NMNZ. 1 specimen, NMNZ M.284042, W of Chatham Islands [44°16.5'S, 178°31.6'E], 1148–1165 m, 8 Apr. 2007, RV TANGAROA.

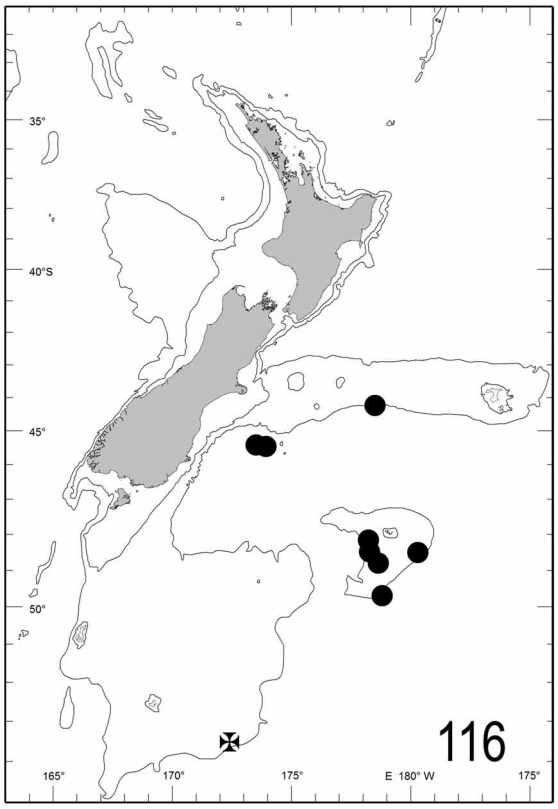
Distribution (Figures 116, 118). *Fulgurofusus maxwelli* inhabits muddy bottoms along the northern Bounty Trough, the Bounty Plateau, and the eastern margins of the Campbell Plateau at depths ranging from 476 to 1,386 m, with a mean station depth [n = 11] of 862.7 m, and a confirmed bathymetric range of 516–1,386 m.

Remarks. The generic assignment of this new species is somewhat provisional. The tall, nearly cylindrical protoconch of nearly three whorls most closely resembles those of several species of *Coluzea*, among them *Coluzea dentata*, the type of the genus. The early teleoconch whorls manifest a prominent peripheral keel with an incised furrow along its perimeter that becomes nodulose as it intersects axial sculpture, a distinct anterior carina, and sculpture of multiple spiral cords, all features more characteristic of *Fulgurofusus*. In larger specimens the peripheral keel becomes reduced or absent, the anterior carina less pronounced, and axial ribs dominate the sculpture, resulting in a phenotype more characteristic of *Peristarium* Bayer, 1971, a subgenus of *Fulgurofusus* previously reported only from the Recent fauna of the tropical and temperate western Atlantic. Adult specimens of *Fulgurofusus maxwelli* more closely resemble *Fulgurofusus* (*Peristarium*) *timor* Harasewych, 1983 (Harasewych 1983b: fig. 46–49) a species from comparable depths off Cape Fear, North Carolina, that any living or fossil New Zealand Columbariinae. *Fulgurofusus maxwelli* differs from *F. timor* in having a 3 whorled protoconch, more inflated whorls, and a weaker peripheral keel situated lower on the whorl. It also lacks the prominent spiral cords along the proximal portion of the siphonal canal and the incised furrow interrupted by axial nodes that are features of *F. timor.*

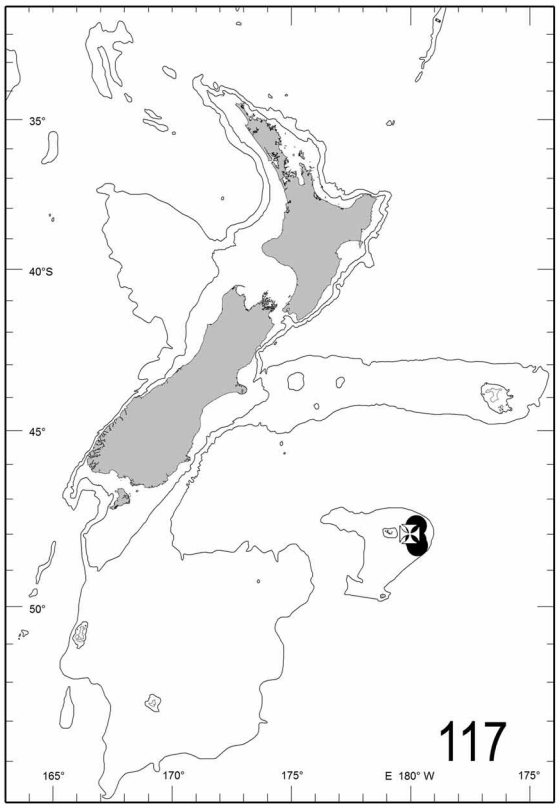
The geographic range of *Fulgurofusus maxwelli* overlaps slightly with that of *Coluzea mariae* along the southern margins of the Chatham Rise. However, the confirmed bathymetric range of *F. maxwelli* in this region is 1,165–1,386 m, compared to 128–687 m for *C. mariae*. These two species also occur on the Campbell Plateau. *Coluzea mariae* is known from the western portions of the plateau at depths of 360–687 m. The type locality of *F. maxwelli* is along the eastern margin of the Campbell Plateau in 625 m.



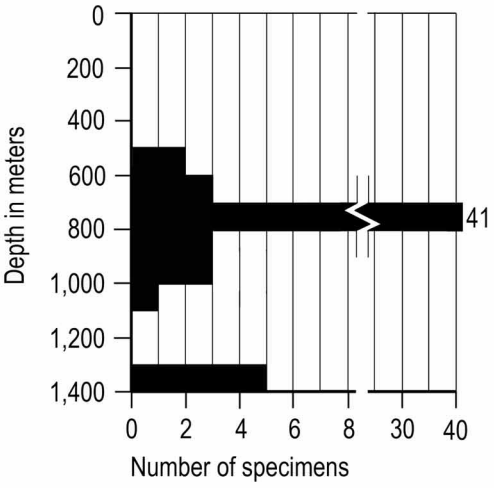
FIGURES 97–115. *Fulgurofusus maxwelli*, new species. **97**, Apertural, **98**, lateral, **99**, dorsal, and **100**, apical views of the holotype, NMNZ M 297055, from the Campbell Plateau [53°30.6'S, 172°24.0'E], in 625 m. **101**, Apertural, **102**, lateral, **103**, dorsal, and **104**, apical views of a paratype from NMNZ M. 297051, Bounty Plateau [48°10.9'S, 178°15.9'E], in 875 m. **105**, Apertural, and **106**, dorsal views of paratype from NMNZ M. 297042, Bounty Plateau [48°29.1'S, 178°16.6'E], in 917 m. Arrow indicates unsuccessful attack by predator (probably a crustacean). **107**, Dorsal and **108**, apertural views of a paratype from NMNZ M. 297052, Bounty Plateau [48°20.0'S, 178°30.0'E], in 726 m. **109**, Inner and **110**, outer surfaces of operculum of the paratype in figures 101–104. **111**, Lateral and **112**, apical views of protoconch of paratype in figures 107–108. Arrows indicate transition to teleoconch. **113–115**, Radular ribbon of paratype in figures 101–104. **113**, 45° oblique view of radula. **114**, Dorsal view with lateral teeth folded. **115**, Dorsal view with lateral teeth expanded. ac, anterior carina; pk, peripheral keel; s, suture.



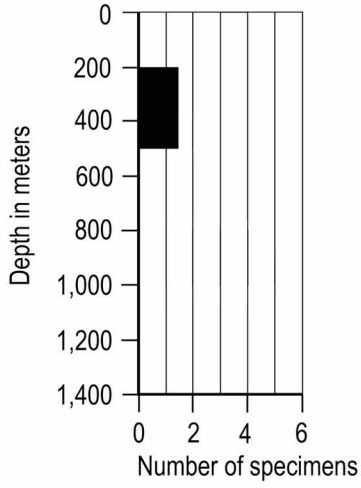
Fulgurofusus maxwelli



Fulgurofusus marshalli



118 *Fulgurofusus maxwelli*



119 *Fulgurofusus marshalli*

FIGURES 116–117. Geographic distributions of species of New Zealand *Fulgurofusus.* **116**, *Fulgurofusus maxwelli*, new species. **117**, *Fulgurofusus marshalli*, new species**. Figures 118–119.** Bathymetric distributions of species of New Zealand *Fulgurofusus.* **118**, *Fulgurofusus maxwelli*, new species. **119**, *Fulgurofusus marshalli*, new species**.** ✠ = type locality. ● = station records.

***Fulgurofusus marshalli* new species.**
(Figures 117, 119–132)

Diagnosis. Small species with strongly fusiform shell, tall, sharply stepped spire, shoulder with weak peripheral keel high on whorl, at or above midpoint between successive sutures. Protoconch conical, with 3 rounded whorls. Spiral sculpture of numerous cords, threads, adjacent cords along periphery producing incised furrow. Axial sculpture of strong, rounded ribs extending from suture to siphonal canal, most prominent along shoulder, forming nodules at intersection with peripheral keel on early whorls, more rounded on later whorls. Anterior carina with strong spiral cord. Aperture weakly angular along outer lip, rounded along parietal region and columella. Siphonal canal comparatively short (< ½ shell length) stout, tapering distally.

Description. Shell (Figures 120–129) of small to moderate size (to 43.3 mm), stout, with tall, stepped, conical spire (spire angle 35–38˚), narrow, ovate aperture, comparatively short, axial siphonal canal. Outer shell layers of early whorls, including protoconch, generally eroded. Protoconch (Figures 131–132) very tall, uniformly conical, with rounded whorls increasing in diameter from 435 µm to 1.8 mm in ~3 whorls. First whorl deflected from coiling axis of shell by ~40˚. Transition to teleoconch marked by onset of a weak shoulder followed almost immediately by thin, spiral threads and later by a weak peripheral keel (Figure 130, pk). Teleoconch of up to 6 whorls. Early whorls angular, later whorls more rounded. Suture (Figure 130, s) adpressed onto spiral cord along anterior carina (Figure 130, ac) of previous whorl. Spiral sculpture of 8–12 strong, narrow, equally spaced cords between suture and peripheral keel. Peripheral keel weak, comprised of two closely opposed cords forming an incised furrow between them. Furrow reduced by 4th postnuclear whorl, disappearing as two cords fuse by 5th postnuclear whorl. Spiral sculpture of: 6–9 cords and threads between peripheral keel and anterior carina; 4–5 between anterior carina and siphonal canal; 9–11 progressively diminishing cords along proximal ⅓ of siphonal canal. Axial sculpture of 9–14 rounded ribs, slightly narrower than intervening spaces, extending from suture to siphonal canal, most pronounced near periphery and anterior carina. Aperture narrowly ovate, slightly more rounded in larger specimens, deflected from shell axis by 21–25˚. Outer lip thin, smooth, evenly glazed, not furrowed beneath peripheral keel or anterior carina (Figure 130). Inner lip with thin, porcellaneous glaze along parietal region, columella, axial portion of siphonal canal. Siphonal canal axial, tapering distally. Shell surface generally worn or eroded. Periostracum, operculum, radula and anatomical features unknown, as all specimens dead collected or crabbed.

Etymology. This new species honors Bruce Marshall for his many contributions to our knowledge and understanding of the molluscan fauna of New Zealand and of the deep sea.

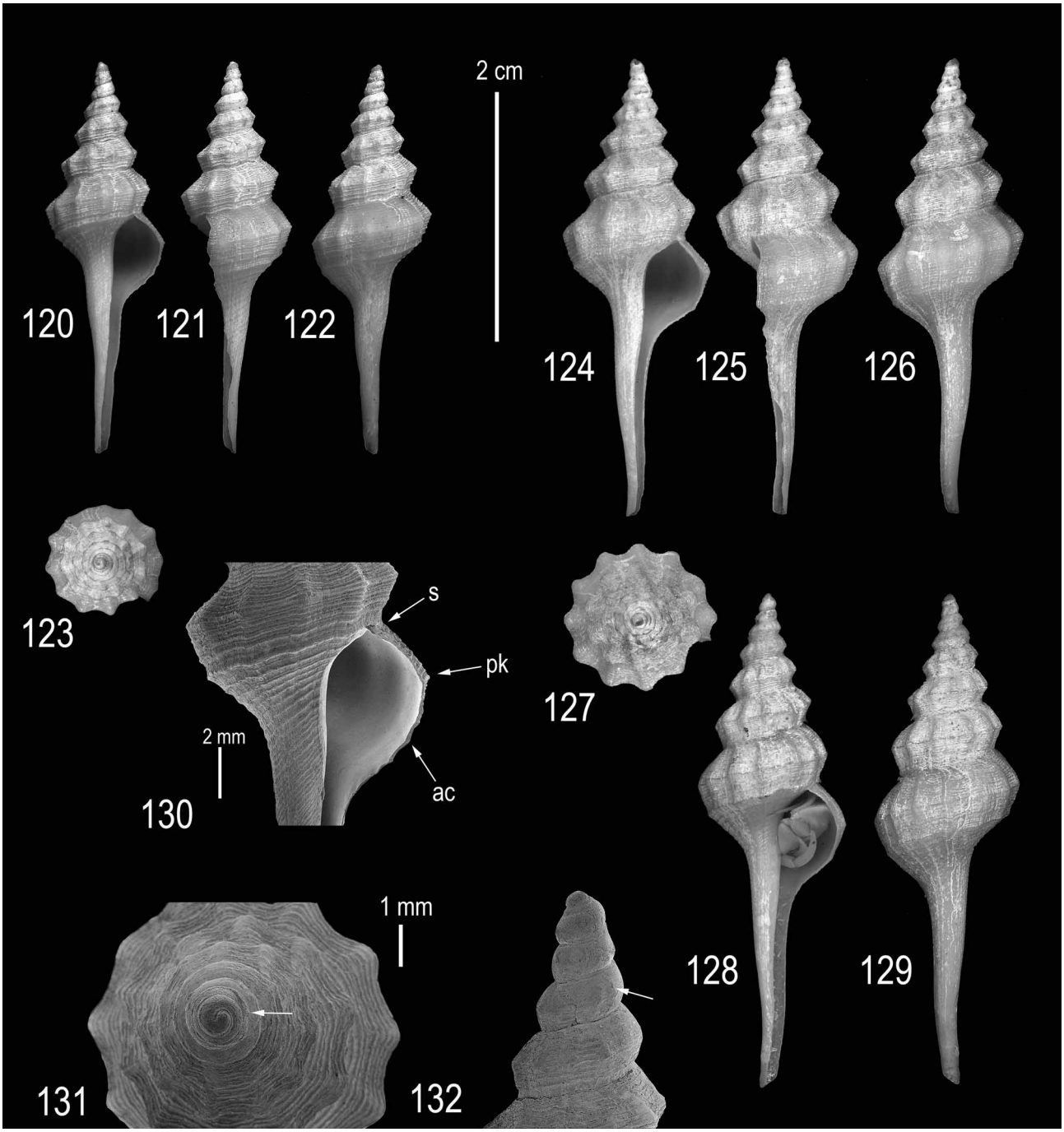
Type locality. (Figure 117, ✠) Bounty Plateau [48°00.0’S, 180°00.0’E], 280 m, 13 Mar 1979, RV TANGAROA (NIWA I671).

Type material. Holotype, NIWA 67594, 2 paratypes, NMNZ M.297047, from the type locality. Additional paratypes: 1 NMNZ M.297048, 1, NIWA I669; 1, USNM 1146129, Bounty Plateau [47°49.0’S, 179°45.7’E], 355 m, 13 Mar. 1979, RV TANGAROA; 1 NMNZ M.297045, Bounty Plateau [48°10.0’S, 179°45.0’E], 457 m, 14 Mar. 1979, RV TANGAROA; 1 NMNZ M.297050, 1, NIWA I682, Bounty Plateau [48°20.0’S, 179°49.5’E], 450 m, 15 Mar. 1979, RV TANGAROA.

Distribution (Figures). *Fulgurofusus marshalli* is known only from the Bounty Plateau. This species has been reported from depths ranging from 280 to 457 m, with a mean station depth [n = 4] of 385.5 m, and a confirmed bathymetric range of 280–457 m.

Remarks. The shell of *Fulgurofusus marshalli* differs from that of comparably sized *F. maxwelli* in having: a more evenly conical protoconch; a less prominent peripheral keel that is obscured by far more prominent axial ribs, which are the dominant sculptural elements; a less pronounced anterior carina; a slightly narrower spire angle; and a more stepped spire, in which the peripheral carina is situated midway between the sutures of successive whorls. The strong axial sculpture of *F. marshalli* is reminiscent of *Fulgurofusus* (*Peristarium*) *aurora*, a species that inhabits roughly comparables depths in the Straights of Florida, and which differs in having stronger, rounder and more numerous axial ribs and stronger spiral cords, a proportionally smaller aperture, and a far stouter siphonal canal. Four species of *Peristarium* have been reported from off the Southeastern United States, yet none overlap in their bathymetric ranges. As in the western Atlantic, the strongest axial sculpture occurs in the shallowest dwelling species.

Fulgurofusus marshalli is known only from the Bounty Plateau at depths ranging from 280 to 457 m. The broader geographic range of *F. maxwelli* includes the Bounty Plateau, where its confirmed bathymetric range extends from 516 to 917 m.



FIGURES 120–132. *Fulgurofusus marshalli*, new species. **120**, Apertural,**121**, lateral, **122**, dorsal, and **123**, apical views of the holotype, NMNZ M.297047, Bounty Plateau [48°00.0'S, 180°00.0'E], in 280 m. **124**, Apertural, **125**, lateral, **126**, dorsal, and **127**, apical views of a paratype from NMNZ M. 297050, Bounty Plateau [48°20.0'S, 179°49.5'E], in 450 m. **128**, Apertural, and **129**, dorsal views of paratype from NMNZ 297045, Bounty Plateau [48°10.0'S, 179°45.0'E], in 457 m. **130**, Detail of the aperture of the holotype. **131**, Apical and **132**, lateral views of the protoconch of the holotype. ac, anterior carina; pk, peripheral keel; s, suture.

Discussion

The subfamily Columbariinae has been a component of the New Zealand molluscan biota since the Paleocene (Wangaloan), and is represented in the modern fauna by seven species assigned to the genera *Columbarium*, *Fulgurofusus* and *Coluzea*. Both living and fossil species have been described in these genera, or in *Fusus* or *Fusinus*,

based on the morphology of type specimens that were often worn, or, in the case of fossils, fragmentary. The attribution of species to these genera has, on some occasions, been equivocal or contested, particularly the assignment of living species to genera based on fossil type species, and vice versa.

The oldest record of the subfamily in New Zealand (Wangaloan /Paleocene) has been attributed to the genus *Columbarium* by Darragh (1969), while Finlay & Marwick (1937) and Stilwell & Zinsmeister (1992) referred this species to *Fulgurofusus*. Of the two Eocene species that had been described in the genus *Columbarium*, one has been reassigned to the turrid genus *Cochlespira* (Beu *et al*. 1990: 125), the other transferred to *Coluzea* (herein). In the Recent fauna, the occurrence of *Columbarium* in New Zealand is confined to a single species that is limited to bathyal depths off the northern shore of North Island and represents the southernmost record for the genus. It is more closely related to a group of species inhabiting the Sea of Japan and South China Sea than to congeners from off the eastern coast of Australia. The several species from southeastern Africa that have been assigned to *Columbarium* differ substantially from the two western Pacific groups.

The genus *Coluzea* dominates the columbariine fauna of New Zealand, both fossil and living. Beu *et al*. (1990: 196; fig. 6g) reported *Coluzea* to occur in New Zealand from the Lower Eocene (Mangaorapan) to the Recent. The Early Eocene record was based on an as yet undescribed species from the upper Waihao Valley, South Canterbury, South Island, on which Maxwell was working at the time of his death [Beu, personal communication]. This is the earliest reported record for *Coluzea* and predates the Middle Eocene records from Europe (Darragh 1969: 104). As Maxwell (1978: 38) noted, the Middle Eocene (Bortonian) *Coluzea pataka* (Maxwell, 1978) differs from the Late Eocene (Kaiatan) *Coluzea climacota* in having open spines along the periphery. While lacking in younger New Zealand species, such open spines commonly occur in species of *Coluzea* inhabiting the eastern and western margins Indian Ocean and New Caledonia (Harasewych 1986, 1991, 2004). The open-spined phenotype is likely ancestral, suggesting that the New Zealand *Coluzea*, which have nodules rather than open spines, may have diverged during the Late Eocene. As presently understood, the genus *Coluzea* is the most diverse within the subfamily Columbariinae. In the Recent fauna, twelve species are known from eastern Africa and Madagascar, six from the eastern Indian Ocean, four from New Zealand, one from Queensland, and one from New Caledonia. In addition to lacking open spines along the periphery, New Zealand *Coluzea* are distinctive in that they are largest known species in the subfamily, and include the only primarily sublittoral species.

Coluzea is widely distributed in New Zealand waters, occurring along the northern and eastern coasts of North Island, the eastern coast of South Island, as well as on the Chatham Rise and Campbell Plateau. The range of *C. spiralis* extends onto the shallow western shores of North Island to Cape Farewell, South Island. Despite the overlap in geographical distributions among species of New Zealand columbariines, there is only a single case of sympatry (*Columbarium veridicum* and *Coluzea wormaldi*). In all other instances, species that overlap geographically have different bathymetric ranges. Similar patterns of bathymetric segregation have been previously reported for western Indian, and eastern Indian Ocean *Coluzea* by Harasewych (1986: 166), who suggested that bathymetric speciation may be a consequence of sea level changes during the Cenozoic.

Apart from a single Paleocene species of disputed generic affinities, the genus *Fulgurofusus* had not previously been reported from New Zealand. Other fossil records are thus far known only from the Paleocene and Eocene of North America and Antarctica. The two species of *Fulgurofusus* described herein extend the known western Pacific range of the genus from the Bering and South China Seas to New Zealand. As was noted by Darragh (1969), *Fulgurofusus* may be readily distinguished from *Columbarium* by a variety of characters. The distinctions and relationships between *Fulgurofusus*, *Coluzea*, *Peristarium* and *Histricosceptrum*, however, are less well understood, and often further obscured by morphological differences between Paleogene and living congeners. Finlay (1930b: 267–268) regarded *Coluzea* to be derived from *Fulgurofusus*. Of the two additional genera proposed within Columbariinae, the Miocene to Recent *Serratifusus* has been transferred to the family Buccinidae based on anatomical characters of living species. The distinctive genus *Hispidofusus* Darragh, 1969, known only from the Lower to Middle Miocene of southeastern Australia, appears to be most closely related to *Columbarium*.

While the Columbariinae are already the most species rich group within Turbinellidae, continuing discoveries of new taxa, primarily from bathyal and abyssal depths, suggest that the diversity, as well as the geographic and bathymetric distribution of this subfamily are likely to be substantially greater than presently known, making the Columbariinae an intriguing group for the study of global bathyal and abyssal biogeography.

Acknowledgements

I am very grateful to Bruce Marshall [Museum of New Zealand Te Papa Tongarewa] for making available much of the material on which this study is based on an extended loan, as well as for numerous contributions of information at many stages during the preparation of this manuscript. Wilma Blom [Auckland Museum Tamaki Paenga Hira] kindly provided information about type specimens at that museum. I thank Alan Beu for supplying information regarding some of the fossil species. The assistance of Yolanda Villacampa [National Museum of Natural History, Smithsonian Institution] in obtaining Scanning Electron Micrographs is gratefully acknowledged.

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