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Zealandia's oldest volutes (Mollusca: Gastropoda: Volutidae) from the early Paleogene of South Island and Chatham Islands: post Gondwana break-up and evolutionary divergence

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Abstract.—The isolation of Zealandia in the latest Cretaceous and early Paleogene following the final break-up of Gondwana fostered significant provincialism in molluscan faunas, concomitant with the segmentation of oceanic circulation patterns and changing climate nearing the end of the greenhouse phase in the Southwest Pacific. The earliest volutes (Gastropoda: Volutidae) from the Zealandian region reflect this isolation after separation from the Marie Byrd Land region of West Antarctica with several endemic groups being recognized for the first time since collecting first started in the Wangaloa Formation at Mitchells Rocks (Wangaloa), South Island, New Zealand in 1869. Five taxa attributed to the Volutidae are described herein from South Island (Wangaloa Formation and Steel Greensand) and also the Chatham Islands (Red Bluff Tuff) from the early (mid-Danian) to late Paleocene (Thanetian?). These comprise a new mid-Danian fulgorariine? genus and species, *Wangaluta henaconstricta* n. gen. n. sp.; a new combination also from the Wangaloa Formation, *Wangaluta? neozelanica* (Finlay and Marwick, 1937); two new zidonine volutes, the mid-Danian *Alcithoe*. s.l. *wangaloaensis* n. sp. from the Wangaloa Formation, and also *Teremelon onoua* n. sp. from the late Paleocene-early Eocene of the Red Bluff Tuff; and a probable volute, Fulgorariine? gen. indet. sp. indet. from the mid-Danian of the Steel Greensand. All of these taxa are endemic in the early Paleogene of New Zealand and represent a significant boost in our knowledge of post-K-Pg boundary diversification of volutid gastropods in the shrinking Weddellian Biotic Province in the southern rim of the Pacific.

Introduction

Paleogene molluscan assemblages of the New Zealand and Chatham Islands region of the Southern Hemisphere provide crucial data on the post-Cretaceous-Paleogene (K-Pg) biotic recovery processes following the mass extinction event worldwide 66 Ma. New Zealand and the Chatham Islands today, along with New Caledonia and Lord Howe Island, comprise the emergent ca. 7% of a mostly submerged continent spanning nearly four million square kilometres extending from 19° south (but north of New Caledonia) to 56° south (south of New Zealand's subantarctic islands)—collectively known as the geographic region of 'Zealandia' (Fig. 1). The separation of New Zealand and the Chatham Islands (i.e., Zealandia) from the Gondwana margin in the Late Cretaceous (as described below) fostered the development of endemic centers of marked faunal provincialism by the Paleocene Epoch (a total of >515 Southern Hemisphere Paleocene taxa recorded), as reflected in the dominance of new species in new genera, ranging in values from 62.5% to 81%, and many groups arising in this region for the first time (Stilwell, 2003; see review therein of entire Paleocene record of molluscs in New Zealand and Chatham Islands in this paper and not repeated here). These early Paleogene molluscan assemblages exhibit distinct (and sometimes dramatic) signatures of composition and biodiversity levels relating to extinction and post-extinction recovery processes, with a much richer record being recognized since the dawn of the new millennium.

The composition of early Paleogene Mollusca reflects the K-Pg boundary extinctions 66 Ma as a major mechanism of change, which was more buffered in the southern high latitudes with increased survivorship relative to the Northern Hemisphere (Stilwell, 2003; Stilwell et al., 2004, Stilwell and Håkansson, 2012), in association with the final break-up of Gondwana and ensuing changes in oceanic circulation, and last, but not least, significant changes in climate at the boundary and shortly thereafter. One of the most important aspects of the changes in molluscan composition is the recognition of a major 'flip-flop' in diversity of Bivalvia and Gastropoda before and after the boundary 66 Ma with gastropods diversifying greatly after the catastrophe in the ecologic vacuum of much vacant ecospace.

The post-K-Pg molluscan record in Zealandia was one of increasing endemism with the isolation of the region from the Gondwanan margin. During the mid- to late Paleocene the endemic component of the fauna was stronger at this time relative to any other during the entire Cenozoic with bivalve and gastropod genera at a level of endemicity of approximately 30%. As such, the paleoaustral component of the fauna was unsurprisingly high at 51% for bivalves and approximatel 68% for gastropods (Stilwell, 2003). Despite being at the tail end of

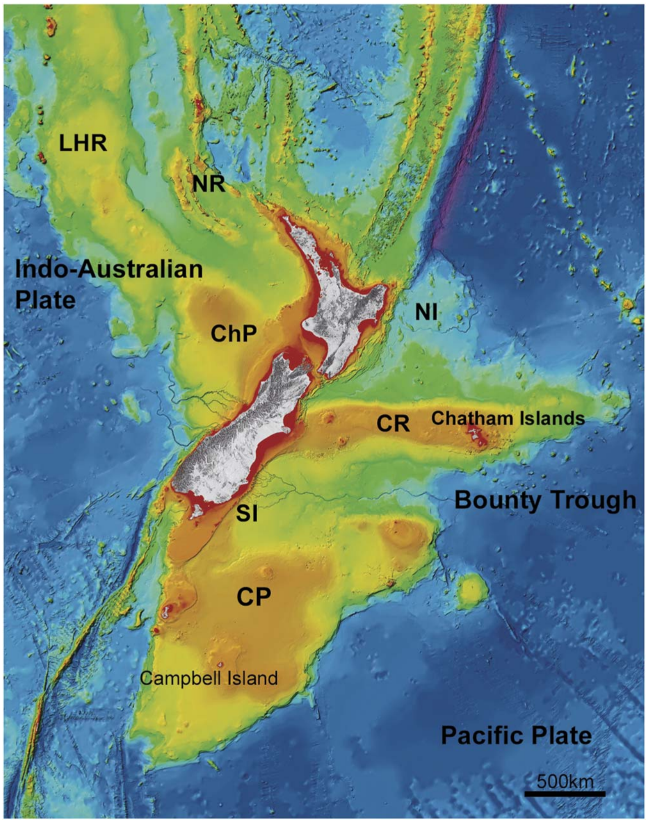

Figure 1. The 'Zealandia' region and location of the mostly submerged Chatham Rise (CR) and Chatham Islands, New Zealand. LHR, Lord Howe Rise; NR, Norfolk Ridge; ChP, Challenger Plateau; NI, North Island (New Zealand); SI, South Island (New Zealand); CP, Campbell Plateau. Adapted from Stilwell and Consoli (2012).

the greenhouse phase during the early Paleogene, there was still a warm-water element to the molluscan composition of 28% for bivalves and 25% for gastropods during this time, and subsequently, lower levels of global distributions of clams and snails, and thus a 23% and 6.5% cosmopolitan component, respectively (Stilwell, 2003). At species level, nearly every recorded invertebrate from the Paleocene of New Zealand is endemic, including the crinoid *Metacrinus* sp. (Stilwell et al., 1994) and the decapod *Glyphea stilwelli* Feldmann, 1993, the latter of which being the only record of this group in the Cenozoic, having survived the K-Pg boundary event. Possible exceptions include the cucullaeid bivalve, *Cucullaea* (*Cucullaea*) *inarata* Finlay and Marwick, 1937, which may be conspecific with the slightly younger Australian species from the Pebble Point Formation, *C.* (*C.*) *psephea* Singleton, 1943, with only minor characters differentiating the two; there is a definite, close relationship. *Taieria allani* Finlay and Marwick, 1937, a rare, early cassid gastropod, is closely allied with a congeneric species in the Chatham Islands from the late Paleocene-early Eocene, but these taxa are probably distinct, given that the 'Wangaloan' species has many more tubercles on the periphery relative to the species from the Red Bluff Tuff.

As stated by Maxwell in Campbell et al. (1993), the differences between the coeval latest Paleocene-early eocene Mollusca of the Chatham Islands relate more to distinct lithofacies between eastern Zealandia and the New Zealand mainland than any other factors. The Late Cretaceous and early Paleogene molluscan faunas of the Chatham Islands are essentially tectonically controlled facies faunas relating to the separation of Zealandia from Marie Byrd Land, West Antarctica, with their origins reflecting the divergent plate motions and the resultant deposition of volcaniclastic, transgressive sediments along the Chatham Peninsula/Chatham Rise during this interval (Stilwell, 1997; Consoli and Stilwell, 2011). Links with the early Paleocene 'Wangaloan' assemblages are relatively weak, except for bivalves such as *Nemocardium* (*Pratulum*) and gastropods, such as '*Pyropsis*,' *Taieria*, *Polinices* (*Polinella*), *Amaea*, *Volutomitra*, and *Zemacies*. Most of the Red Bluff Tuff assemblages comprise a dominance of suspension-feeding bivalves at approximately 96% and carnivorous (39%) and browsing-grazing gastropods (34%), including the carnivorous volute described in this paper, *Teremelon onoua* n. sp. In the next section, the new volutes in this paper are placed in their appropriate tectono-stratigraphic context, and also following, their significance in terms of early Paleogene, post K-Pg molluscan composition in the Austral Realm.

Tectono-stratigraphic setting of Zealandia in the Paleogene

The Late Cretaceous interval marked the end of the New Zealand and Chatham Rise region as a Gondwanan margin entity, due to the fragmentation of western and eastern 'Zealandia' (ca. 1.7 million km^2; see Fig. 1) from what is now West Antarctica. Zealandia comprised collectively what is known as New Zealand, Campbell Plateau, Lord Howe Rise, Norfolk Ridge, New Caledonia, and the Chatham Rise, including the Chatham Islands (Luyendyk, 1995). In terms of comparable size, Zealandia as a continental crust entity covered an area approximately half the size of Australia, comprising today 700+ islands and islets. The divergence and opening of the Tasman Sea separating Zealandia from Antarctica occurred 85–80 Ma, and more refined timing recently indicates a separation time of 83.0–82.5 Ma (R. Sutherland in Stilwell et al., 2006; Campbell and Hutching, 2007). This major event in the southern high latitudes created widespread block faulting and uplift, forming a series of mostly east-west trending, half-grabens (20–50 km wide), which extended to the Canterbury region, South Island; the uplifted basement rock and volcanic provinces served as sources for sediment fill many kilometers thick, concurrently with subsidence (see review in Stilwell and Consoli, 2012). During the Campanian to Maastrichtian stages in Zealandia, there was a dominance of a gradual transgression, as reflected in the widespread, fossiliferous, marine deposits of this age, relating to crustal thinning and thermal subsidence of the region and the subsequent erosion of the basement ranges, forming broad floodplains. In the Chathams' region, there is evidence of a significant deepening event, represented by deposition of a widespread limestone ('Unnamed Haumurian Limestone' of Campbell et al. 1993)—a probable response to localized tectonism at a time of global eustatic sea-level fall (see Herzer and Wood, 1988; Wood et al., 1989).

At the Cretaceous-Paleogene (K-Pg) boundary 66.03 Ma, Zealandia had drifted north (Chatham Islands region originally at 75°S–80°S during the Cenomanian-Turonian stages) to latitude ca. 54°S (R. Sutherland in Stilwell et al., 2006), and was totally separated from the Gondwana margin, and both terrestrial and marine fossil assemblages began to diverge concomitant with its isolation (see paleogeographic map, Fig. 5). There is evidence of some land at the K-Pg boundary in Zealandia, despite rising sea-levels, with the discovery of large numbers of fossil birds approximately 66–64 Ma in the Chatham Islands (J.D.S. and J. Clarke, unpublished data). At the boundary global cooling ensued, but by late Paleocene-early Eocene time, the thermal event saw expansion of warm waters during this greenhouse interval and hottest time throughout the entire Cenozoic, with sub-tropical molluscs reaching eastern Zealandia (Beu and Maxwell, 1990; Stilwell, 2014).

Since the dawn of the new millennium, it has been recognized that the Paleocene record is much more widespread in Zealandia than previously reported with fossiliferous assemblages spanning the Castle Hill Basin in Canterbury to Wangaloa, southeastern Otago in South Island and float boulders in the Kaiwhata River, southern North Island to eastern Zealandia in the Chatham Islands (as reviewed by Stilwell, 1994, 2003). The fossils described in this paper were collected from the Wangaloa and Abbotsford ('Steel Greensand') formations in Otago, and the Red Bluff Tuff, exposed on both Chatham and Pitt islands. The Wangaloa Formation (Fig. 2) at Measly Beach and Mitchells Rocks is characterized by highly fossiliferous quartz sandstone and conglomerate of mid-late Danian age (c. 64–62 Ma, age based on foraminiferans, dinoflagellates, and palynomorphs, see review by Stilwell, 1993, 2003, this work), which has been interpreted as being deposited in near-shore environments such as shore-face or during sporadic storm conditions near fair-weather wave base and also tidal channel deposits (Lindqvist, 1986; Lindqvist and Douglas, 1987; Beu and Maxwell, 1990; Stilwell, 1993). Poorly fossiliferous assemblages of Paleocene molluscs and decapods have been collected from the Abbotsford Formation (also of Danian age with conspecific taxa found in the Wangaloa Formation), which also represent quite shallow marine conditions (Stilwell, 1994, 2003). The Red Bluff Tuff spans late Paleocene to early Eocene time, so these rocks are a bit younger than the Danian Wangaloa and Abbotsford formations. The Red Bluff Tuff (Figs. 3, 4) comprises approximately 100 m of marine, calcareous palagonite tuff of basaltic composition with horizons of lapillistone and tuff-breccia and highly fossiliferous assemblages dated as spanning 53–48 Ma based on recent radiometric dating by Németh et al. (2013). The fossils reflect mostly shallow marine, hard-ground substrates on the summits or flanks of volcanic sea-mounts in eastern Zealandia in subtropical waters at the height of the Paleocene-Eocene thermal event (Beu and Maxwell, 1990; Stilwell, 2014).

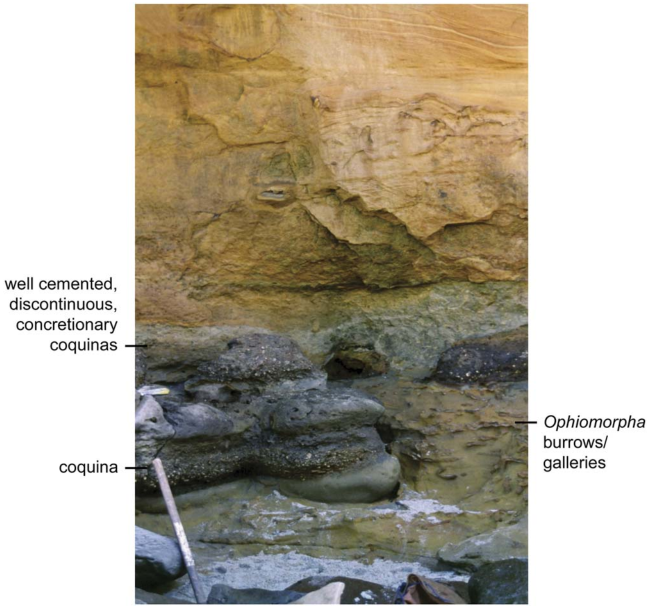

Figure 2. Coastal cliff section of the Wangaloa Formation at Mitchells Rocks, Wangaloa, where the first Paleocene fossils from New Zealand were first collected by Sir James Hector in 1869. Note the shallow, tidal channel deposits, represented by concretionary, highly fossiliferous sandstones and strongly burrowed interval, characterized by anastomosing galleries of the ichnogenus, *Ophiomorpha*, made by a post-K-Pg extinction ghost shrimp (Callianassidae) during a dynamic phase of biotic rebound in the earliest Cenozoic. These deposits host a high diversity of invertebrates and vertebrates with more than 150 taxa recorded (Stilwell, 1993, 1994; Buchanan et al., 2007). The new and revised species of *Wangaluta* n. gen. and *Alcithoe* s.l. were discovered via intense, bulk sampling at this remote SE Otago locality.

Significance of Paleocene Mollusca and new volutes from Zealandia

Collections of fossils made by the author from Mitchells Rocks, Wangaloa (Fig. 2), have resulted in the discovery of the oldest recorded volutes from the New Zealand region's geologic record (Fig. 6). Collecting at Wangaloa since 1869 and commencing with a small collection by 19th century Scottish geologist James Hector (1834–1907) has not, until this report, produced volutid gastropods. Many large, in situ blocks of fossiliferous sandstone were collected by Pionjär rock drill/hammer and subsequently winched from the beach at Mitchells Rocks up and over a cliff, and taken originally to the laboratory at the University of Otago for analyses and subsequently to James Cook University and Monash University in Australia. Two new species, represented by two specimens collected from the same block, are present in 'Wangaloan'

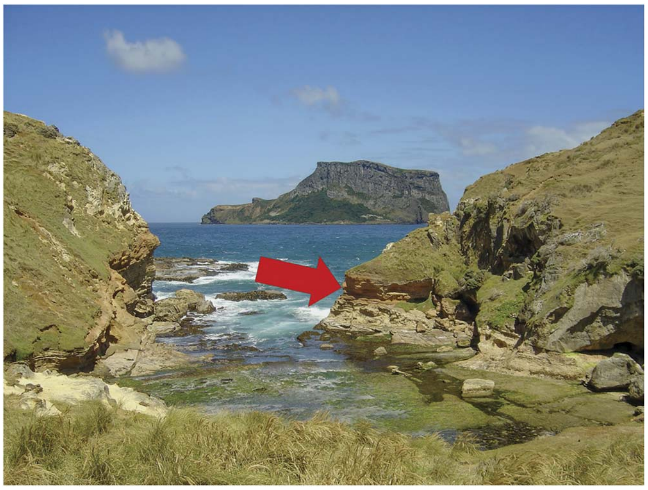

Figure 3. Rocky Side, northwestern Pitt Island, Chatham Islands, where the new volute, *Teremelon onoua* n. sp., was collected in the Red Bluff Tuff (RBT); a view of the bay with red arrow pointing to the RBT in a slump section, where it rests disconformably upon the Upper Cretaceous (Campanian-Maastrichtian) Kahuitara Tuff.

(Danian, early Paleocene) rocks; these are *Wangaluta henaconstricta* n. gen. n. sp. and *Alcithoe* s.l. *wangaloaensis* n. sp., and are described below. These new records are of apparently endemic, short-lived taxa with little in common compared with Paleogene volutes within and outside the Zealandian region in the Gondwana realm, further attesting to New Zealand geographic and genetic isolation during the Paleocene. In addition, a possible 'Wangaloan' volute here referred to Volutidae? n. sp., attributed tentatively to an early Fulgorariine, is recorded form the Steel Greensand of East Taieri, Dunedin. *Paleopsephaea neozelanica* Finlay and Marwick, 1937, is reassigned questionably to *Wangaluta* n. gen.

More than 40 years after the initial discovery of fossils at Wangaloa, the first papers on these significant earliest Cenozoic fossils were published by Henry Suter (1911) and Patrick Marshall (1916, 1917) on a few characteristic, common elements in the Wangaloa Formation, but it would not be until Finlay and Marwick's (1937) epic monograph on the 'Wangaloan fauna' that the assemblages preserved at Wangaloa and Boulder Hill would receive the taxonomic treatment they deserved. The very hard, concretionary sandstone renders any fossil preparation difficult with specimens being notoriously hard to extract without breakage. Amongst the best preservation of the Wangaloan assemblages are to be found at Boulder Hill, and as Finlay and Marwick relayed, they collected 'out' a small lens of loose specimens, which were beautifully preserved. Few works have been published since on the 'Wangaloan' molluscan faunas, except for a checklist of coeval taxa in localities other than Wangaloa and Boulder Hill in Fleming in Harrington (1958), a review of the Paleocene assemblages in Beu and Maxwell (1990), a paper on three new taxa from the Wangaloa Formation by Stilwell (1993), and a PhD thesis by Stilwell (1994), monographing the entire fauna with new taxa.

A further volutid, *Teremelon onoua* n. sp. (Fig. 6), is represented in upper Paleocene rocks of Chatham Islands, south-western Pacific (Figs. 3, 4; Campbell et al., 1993, table 4.11; Stilwell, 2003, appendix, p. 346), collected in 1977 on Pitt Island, and is not closely allied with the 'Wangaloan' forms recorded from the Sobral Formation of Seymour Island, Antarctic Peninsula; this species is probably an early undescribed *Alcithoe* (W.J. Zinsmeister, unpublished data, 1990; J.D.S., personal observation). As far as I am aware, no Paleocene volutes have been recorded from either Australia or South America (oldest in Patagonia are middle? Eocene, del Río and Martínez, 2006; however, new research indicates the possibility of volutes in the Patagonian record, but they remain undescribed, see del Río and Martínez, 2015) and few Cretaceous volutes have been reported from the Southern Hemisphere apart from probable early records from the Late Cretaceous of India by Stoliczka (1867) and Late Cretaceous of Pondoland, South Africa by Woods (1906), who identified species belong to *Fulgoraria*, *Athleta*, *Volutilithes*, and *Lyria*. The early Paleogene volutid gastropod record is poor in the Southern Hemisphere in contrast to coeval taxa in the north. The presence of perhaps as many as four volute species in the 'Wangaloan' significantly extends the stratigraphic range from the late early Paleocene to early? -middle Eocene and significantly expands our knowledge of the early evolution of the Volutidae in the Zealandia region (Fig. 5). Significantly, these new volute taxa, along with the large number of Paleocene invertebrates now recorded from the Zealandian Paleocene, belonged to the shrinking Weddellian Biotic Province of W. J. Zinsmeister (see Zinsmeister, 1982; Stilwell, 2003), which had all but disappeared by the mid-Paleogene.

Figure 4. Southern cliff section of the RBT denoted by the red arrow, which is non-slumped and in situ. The only access to the fossiliferous outcrops is in the slumped section and at low tide along the wave-cut platform.

Systematic paleontology

Phylum Mollusca Linnaeus, 1758
Class Gastropoda Cuvier, 1797
Superfamily Muricoidea Rafinesque, 1815
Family Volutidae Rafinesque, 1815
?Subfamily Fulgorariinae Pilsbry and Olsson, 1954
Wangaluta new genus

Type species.—*Wangaluta henaconstricta* new species (by original designation).

Diagnosis.—Medium-sized, moderately robust volute with subtrapezoid and medially concave whorls; spire angle approximately 43°; sutures moderately clasping, wrapped around axials of succeeding whorls, partially concealing axials; last whorl with adapical, subsutural, convex, swollen band or welt about 5.0 mm broad, bordered abapically by moderately strong constriction; basal constriction moderately rapid to rapid; sculpture of 14 widely spaced, strong, axially extending ribs that fade adapically at constriction and weak spiral threads; axials on spire whorls strongest at abapical third;

growth lines moderately strong, prosocline adapically, broadly sinued below with apex at inception of pronounced axials at periphery; neck moderately long, slightly twisted to the left with poorly developed or obsolete notch; inductura moderately broad, but mostly thin; columella with three medially situated oblique plaits.

Paleobiogeographic element.—Endemic and Paleoaustral.

Discussion.—The enigmatic *Wangaluta* n. gen. is proposed as an apparently endemic group of volutes characterized by a medium-sized shell, fusiform to volutiform outline, strong subsutural adapical welt and constriction on the last whorl interrupting well-developed axially extending ribs, weak spiral sculpture, pronounced basal constriction producing a moderately long neck with a poorly developed siphonal notch, and columella with three plaits. *Wangaluta* n. gen. does not appear to be closely allied with any particular volutid genus, but combines characters present in several groups. In terms of sculpture (e.g., long axially extending ribs on the last whorl and shortened extreme abapical sutural ribs on spire whorls that are mostly concealed by succeeding whorls), suture and excavated spire whorls with medial concavity adjacent to axial ribs and sutural swellings, *Wangaluta henaconstricta* n. gen. n. sp. is consistent with described zidonine species within *Alcithoe* H. and A. Adams, 1858, and *A.* (*Leporemax*) Iredale, 1937. On the other hand, the strong basal constriction, followed by an extended neck and ill-defined siphonal notch in *W. henaconstricta*, is atypical of species of *Alchithoe* s.s. and *Alchithoe* s.l. *Wangaluta* is doubtfully allied with Zidoninae. The similarity of sculpture in *Wangaluta* n. gen. and that of Zidoninae are herein considered to be homeomorphic.

Wangaluta is possibly allied with the fulgorariine genus and subgenera *Fulgoraria* Schumacher, 1817, s.s., *Fulgoraria* (*Psephaea* Crosse, 1871) and *F.* (*Musashia* Hayashi, 1960). Sculpture, coupled with the variably constricted basal part of the last whorl in these groups, is consistent with *Wangaluta* n. gen., but the neck of *Wangaluta* is generally longer and narrower, the basal constriction is much more rapid, the last whorl has an adapical subsutural swollen band and adjacent constriction, and the spire whorls are subtrapezoid with a medial concavity interrupting the strong axial ribs, very much distinct from the previously described fulgorariines. *Wangaluta* seems more akin to fulgorariine volutes than to zidonine taxa, but as with Zidoninae these similarities may be superficial and homeomorphic.

A further possibility is that *Wangaluta* may be allied with ptychatractine genera in Turbinellidae such as *Benthovoluta* Kuroa and Habe, 1950, which includes species with long necks and slightly to moderately constricted bases (see species figured in Harasewych, 1987), but the sculpture of *Wangaluta* is distinct compared with these taxa and there is no subsutural swelling or band, subdued axial sculpture, and no clasping sutures in species of *Benthovoluta*. *Wangaluta* is, thus, placed tentatively in Fulgorariinae.

Etymology.—Genus named for its discovery at Wangaloa, southeastern Otago, and for its inferred relationship to Volutidae.

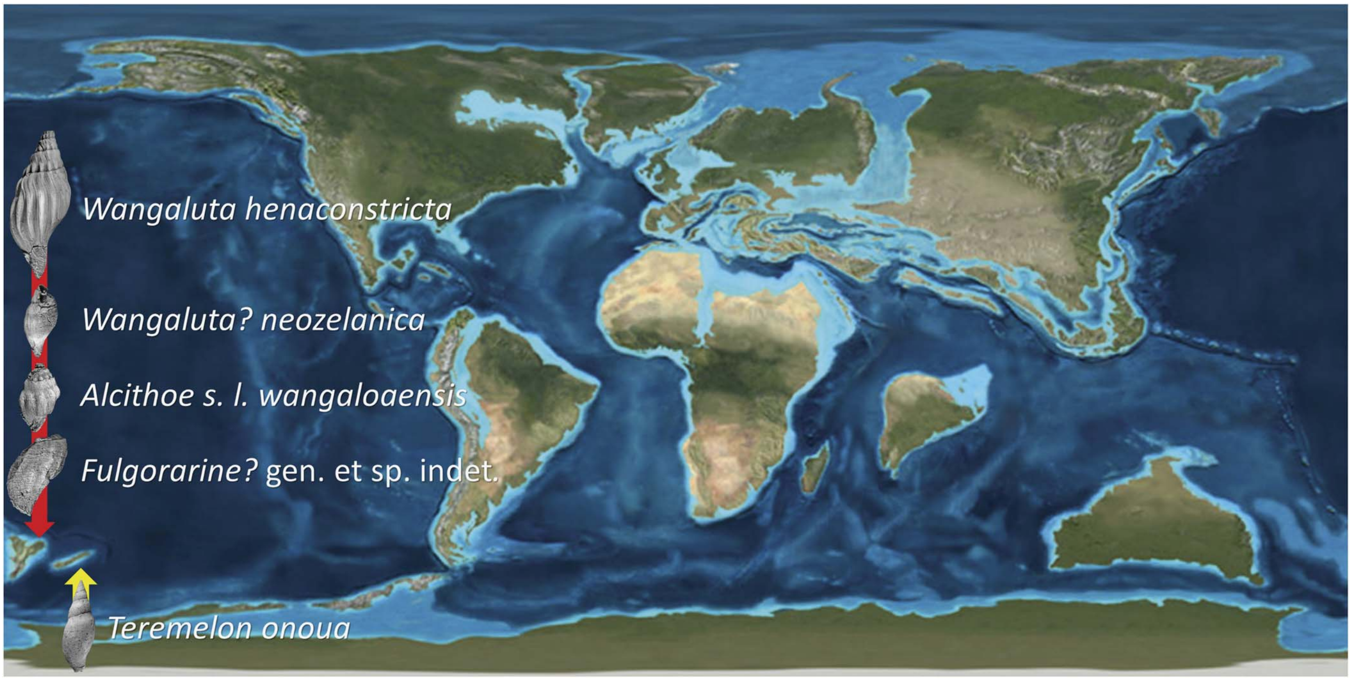

Figure 5. Global paleogeography of the Earth at the Cretaceous-Paleogene boundary ca. 66 Ma with distribution of the Paleocene volutes figured and described in this paper: *Wangaluta henaconstricta* n. gen. n. sp., *W.? neozelanica* (Finlay and Marwick, 1937), *Alcithoe* s.l. *wangaloaensis* n. sp., Fulgorariine? gen. indet. sp. indet. (all from the Wangaloa Formation and latter from the Steel Greensand), and *Teremelon onoua* n. sp. from the Red Bluff Tuff of Chatham Islands. Red bar indicates volute species described in this paper from South Island, New Zealand, and not evolutionary relationships. Yellow bar points to Chatham Islands; note the position of the Chathams in the late Paleocene, which was between 50°S and 55°S, and some 10° further south, compared to their present location. Palaeogeographic base map after Ron Blakey (Colorado Plateau Geosystems, Inc http://cpgeosystems.com/index.html).

Wangaluta henaconstricta new genus new species
Figure 6A–6C, 6G

Diagnosis.—Same as for genus.

Description.—Shell medium-sized for family (49.5 mm high), moderately robust, fusiform; spire moderately high, of at least four subtrapezoid, medially concave whorls; length of aperture slightly longer than height of spire; whorl inflation moderately rapid from penultimate to last whorl; spire angle approximately 43°; protoconch unknown, but probably large and bulbous; sutures moderately clasping, wrapped around succeeding whorls mostly concealing axially extending ribs; last whorl slightly to moderately inflated, elongate; last whorl with adapical, subsutural, convex, swollen band or welt (5.0 mm wide), bordered abapically by moderately strong constriction; last whorl with steep convex slope; basal constriction moderately rapid to very rapid, drawn abapically to moderately strong neck; sculpture on last whorl of moderately strong growth lines, faint spiral threads, adapically near future and disappearing abapically, and 14 strong, raised, broad, rounded, axially extending ribs that originate at suture where they are slightly more subdued, fade at adapical constriction, reappear at last whorl periphery where they are robust and fade and disappear midway down basal constriction; axials widely separated at approximately 2.0 mm intervals, interspaces smooth; penultimate and older whorls also with 14 axial ribs confined mostly to abapical third of whorl where they are strongest and adapical third where they are weakest subsuturally, fading centrally at whorl constriction; on teleoconch whorls axials are parallel to subparallel to each other; spire whorls with approximately 25 wavy spiral threads; growth lines broadly sinused with apex located centrally on last whorl at onset of pronounced axials, more subprosocline subsuturally and adapically and slightly sinused abapically at onset of basal constriction; growth lines cross axials obliquely on adapical portion of last whorl and then follow axials on central and abapical portion; aperture elongate, narrow, siphonostomatous; siphonal canal moderately long to long for family, slightly twisted to the left with feebly developed or obsolete notch; fasciole poorly developed; labium with moderately broad, relatively thin inductura, broadening slightly in the parietal region; columella slightly concave bearing three spaced, oblique plaits centrally, medial plait strongest of the three; outer lip moderately thin.

Dimensions.—Holotype OU 41227 height 49.5 mm, probably approximately 55.0 mm if complete, diameter of last whorl 21.0 mm.

Type.—Holotype OU 41227.

Type locality.—Mitchells Rocks, Wangaloa, southeastern Otago, South Island, H46/f166A.

Figured specimen.—OU 41227.

Material.—Holotype.

Stratigraphic range.—Wangaloa Formation, 'Wangaloan' Stage = lower part of the Teurian Stage, mid-Danian, early Paleocene, *P. golzowense* Zone, Wilson (1992b), approximately 64–62 Ma.

Geographic distribution.—Wangaloa, Southeastern Otago.

Discussion.—*Wangaluta henaconstricta* n. gen. n. sp. is known from the beautifully preserved holotype from Mitchells Rocks, Wangaloa. Affinities of *W. henaconstricta* n. gen. n. sp. are unclear, but a close relationship with *Paleopsephaea neozealanica* Finlay and Marwick, 1937 (pp. 80–81, pl. 11, fig. 6–7; Fleming, 1966, p. 328, pl. 115, figs. 1409–1411), seems probable. Disparity of the number of columellar plaits, growth lines and sculpture of *W. henaconstricta* and *P. neozelanica* hinders comparisons of this species with other forms. *Wangaluta henaconstricta* n. gen. n. sp. has very strong axially extended ribs, smaller abapical ribs on the penultimate whorl, spiral sculpture of threads, stronger more prosocline growth lines on the swollen subsutural band and three developed columellar plaits, compared to *P. neozelanica*, which has no to feebly developed axial sculpture on the last whorl, large broad axial ribs on the abapical third of the penultimate whorl, more orthocline growth lines and a well-developed oblique fold on the columella and a second, slightly higher and feebly developed fold.

Voluta elongata d'Orbigny, 1842 (pp. 323–324, pl. 220, fig. 3 (not fig. 2 as stated in the text by d'Orbigny); Stoliczka, 1867, pp. 87–89, pl. 7, figs. 1–9, especially fig. 3 (reassigned to *Fulgararia pro Fulgoraria)*, an inferred variable species from the Late Cretaceous of France and southern India, is reminiscent of the Danian Wangaloa Formation species in outline and sculpture, but has a slower and more constant basal constriction, a less swollen subsutural welt, more axially extending ribs and a much stronger spiral sculpture. Probably not all of the figures of shells on plate 7, attributed to *Fulguraria elongata* by Stoliczka, are conspecific, as considered by him.

Other superficially similar, but probably unrelated species, include the Neogene New Zealand species *Alcithoe (Leporemax) gatesi* Marwick, 1926a (p. 302, pl. 70, fig. 7; Fleming, 1966, p. 356, pl. 129, fig. 1504; Beu and Maxwell, 1990, pp. 300–301, pl. 37, fig. o) and the Recent rare Chinese species *Fulgoraria* s.s. *leviscula* Rehder, 1969 (see discussion and figures by Weaver and du Pont, 1970, p. 35, pl. 10, figs. C–D), but these species compared to *W. henaconstricta* n. gen. n. sp. lack the distinctive subsutural band, have more columellar plaits, display differences in sculpture, have distinct siphonal canals and have a slower basal constriction.

Authoritative works on Volutidae such as Marwick (1926a), Smith (1942), Wenz (1943), Sohl (1964), Weaver and du Pont (1970), Darragh (1988), and Oleinick (1993), and on ptychatrachine turbinellid gastropods including Harasewych (1987), assist little in identifying the affinities of *Wangaluta henaconstricta* n. gen. n. sp., which appears to have been a short-lived and very rare taxon. It is quite probable that *W. henaconstricta* n. gen. n. sp., along with *Alcithoe* s.l. *wangaloaensis* n. sp., described below, may have been brought into shallower shelf setting from a slightly deeper environment as reflected by both species' rarity either by storm even or by Decapoda and the like. This scenario is speculative as the excellent preservation of both volutes suggests minimal transport. The holotype of *W. henaconstricta* reveals an oblique repaired break quite similar to other 'Wangaloan' gastropods on its antepenultimate whorl that seemingly little affected its sculpture on later teleoconch whorls. The break was probably caused by a lip-peeler such as a decapod that either used the gastropod as a meal and/or abode.

Etymology.—Species named from the Greek *henos* (= old) and Latin *constrictus* (drawn together, contracted) for its early occurrence in the New Zealand Paleocene and for its adapical constriction.

Wangaluta? *neozelanica* (Finlay and Marwick, 1937)
Figure 6I, 6J

1937 *Paleopsephaea neozelanica* Finlay and Marwick, p. 80, pl. 11, figs. 6–7.

1966 *Paleopsephaea neozelanica* Finlay and Marwick; Fleming, p. 328, pl. 115, figs. 1409, 1411;

1990 *Paleophsephaea* (err. pro. *Paleopsephaea*) *neozelanica* Finlay and Marwick; Beu and Maxwell, pp. 88, 205, 414.

2003 *Paleopsephaea neozelanica* Finlay and Marwick; Snyder, p. 239 (error, not a Cretaceous species).

Supplementary description.—Shell medium-sized, moderately robust to robust, fusiform; spire unknown except for small fragment, probably about the same height as aperture, seemingly concave adapically and convex abapically reflected strong axial ribs; penultimate whorl slightly constricted centrally; suture apparently abutting, wrapped around axial ornament of succeeding whorl; growth lines suborthocline; last whorl elongate, rather narrow, constricted abapically and drawn out to a moderately long neck with out a fasciole; last whorl with gentle subsutural adapical constriction and subsutural swelling; ornamentation of approximately 15 pronounced rounded axially extending ribs, slightly narrower than the interspaces and becoming obsolete on last half of last whorl; axials extend from suture below to medial position marked by slight constriction on penultimate whorl and fade on last whorl at onset of basal constriction; no spiral sculpture; aperture long, narrow, not notched abapically, siphonostomatous; inner lip with moderately thick broad callus; columella long, straight bearing a single strong oblique plait centrally and an extremely poorly developed obsolete one slightly above; outer lip moderately thick.

Dimensions.—Holotype TM 7343 (GNS) height 44.0 mm incomplete, diameter of last whorl 22.0 mm.

Type.—Holotype TM 7343 (GNS; Finlay and Marwick, 1937, pl. 11, fig. 6–7; Fleming, 1966, pl. 115, figs. 1409, 1411).

Figured specimen.—TM 7343 (GNS).

Material.—Holotype.

Locality.—Boulder Hill, Dunedin, Otago, South Island, I44/f8486 (type).

Stratigraphic range.—Wangaloa Formation ('Wangaloan' Stage = lower part of Teurian Stage, Danian, early Paleocene, probably *G. golzowense* Zone, ca. 64–62 Ma).

Geographic distribution.—Boulder Hill, Otago.

Discussion.—*Paleopsephaea* Wade, type species *P. mutabilis* Wade, 1926, from the Late Cretaceous of North America, is characterized by its fusiform outline, whorls with an adapical constriction, abapically constricting last whorl that extends to a moderately long siphonal canal, dominant sculpture of strong collabral transverse ribs, slightly curved siphonal canal (inclined to the left) and usually three oblique plaits on the columella (Sohl, 1964, p. 209). *Paleopsephaea* is a long ranging and widespread Late Cretaceous genus that is similar to both *Drilluta* Wade, 1926, and *Bellifusus* Stephenson, but 'differs from the former primarily by its lack of a strong collar and from the latter by its less inflated and rounded whorls, its more subdued ornament, and loess strongly constricted whorls' (Sohl. 1964, p. 209). *Paleopsephaea* was placed in Volutidae by Finlay and Marwick (1937, p. 80) and Wenz (1943, p. 80) and later in Fasciolariidae by Sohl (1964, p. 209). Fleming (1966, p. 328) questionably placed *P. neozelanica* Finlay and Marwick, 1937, in the Volutidae: Athletinae. Beu and Maxwell (1990, pp. 88, 205) regarded the 'Wangaloan' species as 'almost certainly a turbinellid' and assigned this species to the subfamily Ptychatractinae. In a review of the fossil genera of the Ptychatractinae, Harasewych (1987) excluded *Paleopsephaea* from the subfamily. However, the shell morphology of *Paleopsephaea* is similar to taxa within the Ptychatractinae; 'recent work on the higher classification of Volutidae suggests that many of the 'volutid' genera and subfamilies that diversified in the Mesozoic may not be related to our modern concept of Volutidae.' (M.G. Harasewych, personal communication). Most recently, Snyder (2003) retained this species in *Paleosephaea*, but did so without comment; he apparently consulted Finlay and Marwick (1937), as Snyder stated the species is from the New Zealand Cretaceous, but today the assemblages are dated as Danian (early Paleocene).

Paleopsephaea neozelanica is doubtfully regarded herein as a member of this genus as it differs greatly from other described members of the group. Finlay and Marwick (1937, p. 81) remarked that his species seems to be closely allied with the type species of *Paleopsephaea*, *P. mutabilis* Wade, 1926 (p. 123, pl. 40, figs. 4–5; see also Wenz, 1943, p. 1328, fig. 3772; Sohl, 1964m p. 209–210, pl. 28, figs. 1–6), from the latest Cretaceous of North America differing in having constricted and apparently subtrapezoid whorls, no spiral sculpture and only one strong and a second feeble columellar fold opposed to several in *P. mutabilis*. These differences are significant and should be considered to be interspecific variation, especially when other species assigned to *Paleopsephaea* are compared. The affinity of *Paleopsephaea neozelanica* most certainly lies with *Wangaluta* n. gen., although its allocation to Ptychatractinae, as suggested by Beu and Maxwell (1990), is arguable and not necessarily appropriate. Beu and

Maxwell did not present any evidence for their inclusion and movement of *P. neozelanica* in Ptychatractinae, the mostly poorly known subfamily in the Turbinellidae (Harasewych, 1987, p. 167). The poorly preserved nature of the 'Wangaloan' species, represented by a single incomplete and eroded specimen, hinders any in-depth treatment of its identify and affinities. As stated earlier in the discussion of *Wangaluta henaconstricta* n. gen. n. sp., *P. neozelanica* is probably a *Wangaluta*, but it is distinct from the newly described species. Additional collecting at Boulder Hill and Wangaloa has yielded no further examples of this enigmatic species.

Subfamily Zidoninae H. and A. Adams, 1853 (= Alcithoinae Pilsbry and Olsson, 1954)

Genus *Alcithoe* H. and A. Adams, 1853

Type species.—(by subsequent designation, Cossmann, 1899) *Voluta pacifica* (Solander MS) Perry, 1811.

Paleobiogeographic element.—Paleoaustral (possibly endemic) as interpreted herein.

Alcithoe s.l. *wangaloaensis* new species

Figure 6F

Diagnosis.—Small- to moderately sized volute with a robust, low fusiform, stumpy shell; sutures clasping, mostly concealing axials of succeeding whorls; spire angle 67°; last whorl capacious, obtusely angulate with nearly vertical sutural ramp; sculpture of about nine inflated, broad, separated, axially extending ribs strongest at angulation and fading abapically along slow to moderately rapid basal constriction; columella with at least four oblique plaits; differs from *A.* (*Leporamax*) *consisa* Marwick, 1926a, and *A.* (*Alcithoe*) *cylindrica* Marwick, 1926a, in having a more squat shell, low fusiform profile, smaller shell, more capacious last whorl, more clasping suture and more concealed axials on spire whorls.

Description.—Shell small- to medium-sized for family (32.0 mm high nearly complete), robust, low fusiform, stumpy or squat; spire low of at least four small, gently concave, nearly flush, subtrapezoid whorls; whorl inflation very rapid from penultimate to last whorl; spire angle approximately 67°; protoconch unknown; sutures clasping, wrapping around succeeding whorls, nearly concealing axially extending ribs apart from adapical ends of ribs creating a sutural noded effect; last whorl capacious, obtusely angulate, moderately broad, and elongate, adapical sutural ramp of last whorl very steep, nearly vertical, smooth without sculpture, moderately long and concave; basal constriction slow to moderately rapid; sculpture of about nine inflated, broad (c. 3.5 mm), rounded, widely separated, axially extending ribs, strongest at shell periphery and fading abapically towards siphonal canal; axials originated abruptly at angulation and are concave inbetween; no spiral sculpture discernable; growth lines feeble, weakly prosocline on ramp becoming more orthocline abapically; siphonal canal details unknown due to being fragmentary, but probably short; columella slightly concave to mostly straight, bearing at least four oblique, spaced plaits centrally; outer lip probably moderately thin, if complete.

Dimensions.—Holotype OU 41228 height 32.0 mm nearly complete, diameter of last whorl 18.5 mm nearly complete.

Type.—Holotype OU 41228.

Type locality.—Mitchells Rocks, Wangaloa, southeastern Otago, South Island, H46/f166*A*.

Figured specimen.—OU 41228.

Material.—Holotype.

Stratigraphic range.—Wangaloa Formation, 'Wangaloan' Stage = lower part of Teurian Stage, Danian, early Paleocene, probably *G. golzowense* Zone, Wilson, 1992b, ca. 64–62 Ma.

Geographic distribution.—Wangaloa, southeastern Otago.

Discussion.—The affinity of this small, unusual, new volute appears to lie with *Alcithoe* and if it does, indeed, belong to this group, it is then the oldest recorded member, previously reported in rocks no older than the Eocene. The previously described *Wangaluta henaconstricta* n. gen. n. sp. is easily separated from *Alcithoe* s.l. *wangaloensis* n. sp. in having a higher spired fusiform outline and presence of a subsutural band, compared to the latter 'Wangaloan' species that has a low fusiform or more squat profile, a steep adapical sutural ramp without a swelling or axial sculpture, and broader and fewer axial ribs. These two taxa are doubtfully closely related.

The complete shell of *Alcithoe* s.l. *wangaloaensis* n. sp. probably had an outline, suture and sculpture close to *Alcithoe (Leporemax) concise* Marwick, 1931 (p. 127, fig. 271; Fleming, 1966, p. 356, pl. 129, fig. 1500) from the New Zealand Opoitian (lower Pliocene). *Alcithoe* s.l. *wangaloaensis* n. sp. is lower spired with a more squat profile, has a more capacious last whorl, more pouty and clasping sutures and more concealed axials on the spire whorls. The Altonian (upper lower Miocene) species *Alcithoe cylindrica* Marwick, 1926a (p. 290, pl. 65, fig. 3; Fleming, 1966, p. 344, pl. 123, fig. 1471; see discussions of synonyms *A. wekaensis*, *A. compressa*, *A. armigera*, *A. robusta* and *A. sequax* (all Marwick, 1926a) in Beu and Maxwell, 1990 p. 206, especially *A. robusta* Marwick, 1926a, p. 291, pl. 65, fig. 5) is also comparable to *A.* s.l. *wangaloaensis* n. sp., differing mainly in its higher spire, less clasping suture, much larger size and sculptural details.

Alcithoe s.l. *wangaloaensis* n. sp. may represent a new genus or subgenus, but better-preserved material is necessary to secure relationships.

Etymology.—Species named after its discovery at Mitchell Rocks, Wangaloa.

Genus *Teremelon* Marwick, 1926

Type species.—(by original designation) *Scaphella tumidior* Finlay, 1926 (= *Waihaoia (Teremelon) awamoaensis* Marwick, 1926).

Paleobiogeographic element.—Paleoaustral.

Discussion.—*Teremelon* Marwick, 1926, ranges from the late Paleocene-earliest Eocene (this work) to the Recent and, as such, is one of the world's longest ranging volutid gastropods with the acme in its diversity being reached in the mid-Cenozoic in the Altonian Stage (late early Miocene) in New Zealand. In relative terms, *Teremelon* species are small volutes in the Zidoninae, have all but no axial sculpture except sometimes on the early whorls, characteristically have a moderately deep anterior notch, and a poorly developed fasciole (Beu and Maxwell, 1990, p 205). *Teremelon onoua* n. sp. probably lived in shallow waters in the Red Bluff Tuff, but more recent taxa such as *T. knoxi* (Dell, 1956), which is the sole survivor of the *Teremelon* lineage, is restricted to the upper bathyal zone today between 220 and 320 fathoms and some fossil taxa are inferred to have lived in the inner to mid-shelf (Powell, 1979; Beu and Maxwell, 1990), including *T. onoua* n. sp.

Teremelon onoua new species
Figure 6D, 6E

1990 *Teremelon* Beu and Maxwell, p. 205.
1993 *Teremelon* n. sp. Campbell et al., p. 85, tab. 4.11;
1994 *Teremelon* Stilwell, p. 1027;
2009 *Teremelon* Beu and Raine, no page number for Miscellaneous Series No. 27 (web reference).

Diagnosis.—Shell relatively large to moderately so at approximately 70 mm, if complete, and thick fusiform with at least six teleoconch whorls that are slightly angulate on youngest three whorls; spire higher compared to other fossil species; siphonal canal long and slightly twisted; columella with four very well-developed plaits that are more oblique closer to canal and more sub-horizontal toward suture; outer lip moderately thick.

Description.—Shell moderately large to large for subfamily (c. 70 mm with protoconch preserved), modetately thick, high-spired fusiform, spire 0.4 total height; spire moderately high, of at least five teleoconch whorls, becoming weakly angulate to convex by antepenultimate whorl, nearly straight on early teleoconch whorls; whorl inflation rapid in early whorls, becoming very rapid from penultimate to last whorl; spire angle approximately 36°; protoconch unknown, but prominent in other fossil forms of 1.5 squat, mamillate whorls; sutures weakly impressed, somewhat clasping around older whorls and declivous; last whorl moderately inflated, elongate-ovate and convex, smooth with no axial or spiral sculpture, and only very weak growth lines; minor repaired break noted approximately 10 mm from outer lip on last whorl; aperture narrow, constricted both abapically and adapically; shell siphonostomatous with narrow, deep notch, slightly twisted, siphonal canal; columella moderately long, slightly concave to mostly straight, bearing four, very well developed and equally spaced plaits centrally, third and fourth fold becoming more inclined toward siphonal canal, first and second plaits sub-horizontal above; outer lip probably moderately thick, only partially complete

Dimensions.—Holotye TM 8917 height 69.5 mm, diameter of last whorl 25.0 mm; paratypes TM 8918 height 35.0 mm, diameter 15.5 mm (incomplete, partial teleoconch preserved); TM 8919 height 37.5 mm, height 18.0 mm (incomplete, partial last whorl and siphonal canal).

Types.—Holotype TM 8917, paratypes TM 8918 and TM 8919.

Type locality.—Flowerpot Harbour ('Onoua'), north of Bluff Homestead, Pitt Island, Chatham Islands, New Zealand, GS12159, CH/f471, grid reference 713236.

Material.—Three specimens (one nearly complete, holotype), collected 1977.

Stratigraphic range.—Red Bluff Tuff Formation in pebbly, coarse, pale yellow-green brown calcareous, tuffaceous sandstone and lapillistone in Section CI-2/1 at approximately 7.5 m from base of section at sea-level and about 5 m below unconformable contact with Onoua Limestone in same section (see Campbell et al., 1993, p. 228 for section details and stratigraphic log). The Red Bluff Tuff was dated radiometrically recently as approximately 53–48 Ma by Németh et al. (2013).

Discussion.—Protracted, sporadic, volcanic pulses in the Chatham Islands region during the late Paleocene to early Eocene had a dramatic effect on invertebrate assemblages in the eastern Zealandian region, and it may have taken thousands of years between volcanic events to reach an acme in biotic assemblages Sorrentino et al., 2011, 2014). Many invertebrates (including gastropods, bivalves, cnidarians, poriferans, cirripeds, brachiopods, and others) are preserved in volcaniclastic and phreatomagmatic sediments, resulting from Surtseyan-style eruptions in the region; it is surprising that many fossils, including *Teremelon onoua* n. sp. described here, are so well preserved, and some fossils escaped being crushed between tholeiite volcanic flows and eroded boulders of basalt, which eventually resulted in shoaling of marine waters, similar to those fossils preserved the older Upper Cretaceous Kahuitara Tuff of Pitt Island (Stilwell, 1997, 1998, 2014).

Teremelon onoua n. sp. pre-dates the previously oldest recorded member of the genus, *T. striata* (Laws, 1935) from the Bortonian Stage (late middle Eocene), by more than 10 million years. In terms of morphologic similarity, *T. onoua* n. sp. is most closely allied with Neogene members of the genus, especially *T. elegantissima* (Suter, 1917) from the Altonian (Miocene) of Weka Pass (see *Scaphella elegantissima* Suter, 1917, p. 41, pl. 5, fig. 9; Marwick, 1926, p. 280, pl. 72, fig. 1), but *T. elegantissima* is much smaller at 50 mm height with a slightly higher spire and more developed, twisted siphonal canal. The type species, *T. tumidior* (Finlay, 1926) (p. 250, pl. 56, fig. 6; Marwick, 1926, p. 280, pl. 62, fig. 2; Beu and Maxwell, 1990, p. 204–205, pl. 21, fig. r), which spans the Duntroonian to Altonian stages (late Oligocene to late early Miocene), is distinct from *T. onoua* n. sp. in being much smaller at a maximum height of 48 mm and lower spired, relative to the Red Bluff Tuff species. In several decades of collecting in the Red Bluff Tuff on both Chatham and Pitt islands, only three *Teremelon* specimens have become known, all collected in 1977.

Etymology.—Species named after the Moriori name for Flowerpot Harbour ('*Onoua*'), Pitt Island, Chatham Islands, where the type material was collected.

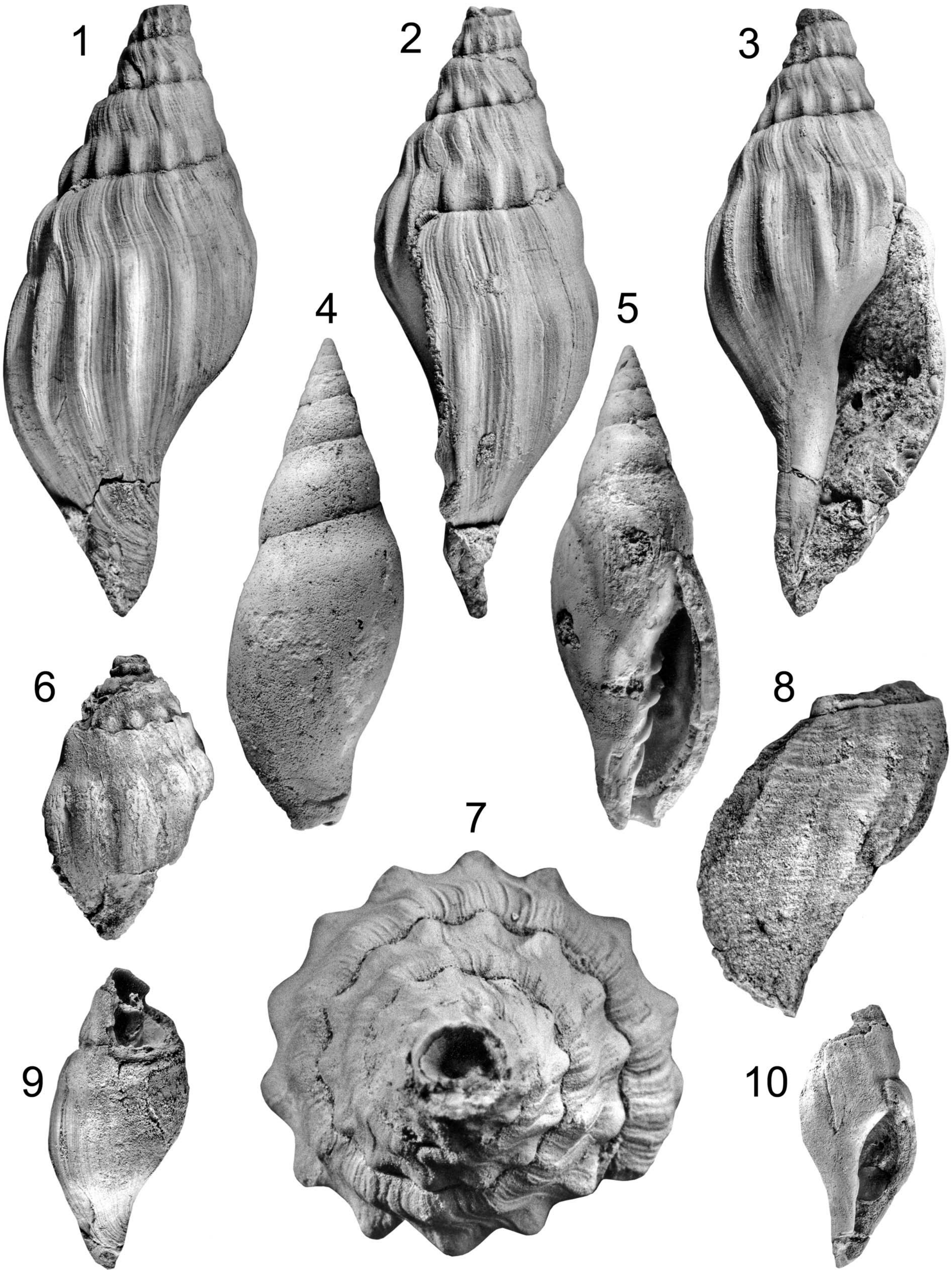

Figure 6. *Wangaluta henaconstricta* n. gen. n. sp. (**1**) abapertural view of nearly complete holotype OU 41227 height 49.5 mm, locality Mitchells Rocks, Wangaloa, southeastern Otago, South Island, New Zealand, H46/f166A, all specimens on plate coated with ammonium chloride for macrophotography; (**2**) lateral view of holotype; (**3**) apertural view of holotype; (**7**) apical view of holotype. *Teremelon onoua* n. sp. (**4**) abapertural view of holotype TM 8917 height 69.5 mm, GS12159, Flowerpot Harbour ('Onoua'), north of Bluff Homestead, Pitt Island, Chatham Islands, New Zealand, CH/f471; (**5**) apertural view of holotype. *Alcithoe* s.l. *wangaloaensis* n. sp. (**6**) holotype OU 41228 height 32.0 mm nearly complete, locality H46/f166A, abapertural view. Volutidae? (Fulgorariinae?) gen. indet. sp. indet. (**8**) Figured specimen, OU 41229, East Taieri, Dunedin, Otago, South Island, I44/f8516. *Wangaluta neozelanica* (Finlay and Marwick, 1937). (**9**) abapertural view of holotype TM 7343 (GNS), height 44.0 mm incomplete, Boulder Hill, Dunedin, Otago, South Island, I44/f8486 (type); (**10**) apertural view of holotype, also Boulder Hill.

Volutidae? (Fulgorariinae?) gen. indet. n. sp.
Figure 6H

Dimensions.—OU 41229 height 21.5 mm incomplete, diameter of last whorl 13.0 mm.

Figured specimens.—OU 41229.

Material.—One specimen.

Locality.—East Taieri, Dunedin, Otago, South Island, I44/f8516.

Stratigraphic range.—Steel Greensand, 'Wangaloan' Stage = lower part of Teurian Stage, Danian, lower Paleocene; probably *P. golzowense*, Wilson (1992a), ca. 64–62 Ma.

Geographic range.—East Taieri, Otago.

Discussion.—This enigmatic shell has been recorded from Wangloa, Boulder Hill or localities in North Otago, but is associated with several 'Wangaloan' taxa found at these localities. Only the last whorl and part of the penultimate whorl are preserved and the shell is slightly distorted due to compaction. Because of this preservational deficiency, a tentative assessment is given here.

The last whorl has an elongate outline, sculpture of approximately 13 spaced, axially extending ribs that extend to the suture and more than 30 coarse spiral threads, simple suture, a moderately rapid basal constriction, and a seemingly short canal. The complete shell was probably moderately to high-spired fusiform. These features are consistent with fulgorariine volutes such as *Fulgoraria* s.s., and various subgenera of *Fulgoraria* (see characteristic extant taxa in Weaver and dupont, 1970, and Paleogene taxa in Oleinik, 1993). A relationship of this inferred, new 'Wangaloan' species with Fasciolariidae cannot be discounted, but an affinity with Volutidae: Fulgorariinae is preferred.

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