Marine Mollusca of isotope stages of the last 2 million years in New Zealand. Part 4. Gastropoda (Ptenoglossa, Neogastropoda, Heterobranchia)

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Marine Mollusca of isotope stages of the last 2 million years in New Zealand. Part 4. Gastropoda (Ptenoglossa, Neogastropoda, Heterobranchia).

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Three new species: *Opalia (Pliciscala) flemingi* (late Nukumaruan-early Castlecliffian, OIS 71-29?, Wanganui); *Kuroshioturris putere* (Opoitian-Waipipian, Westland and Hawke's Bay), *Antimelatoma waimea* (Kapitean-Opoitian, Westland); two new genera: *Cryptofusus* (Turbinellidae) for New Zealand species formerly referred to *Pleia* Finlay (Australian); *Onoketoma* (Conidae, Raphitominae) for "*Insolentia*" *solitaria* King, bathyal Nukumaruan, Palliser Bay. *Xymene* (sensu stricto; separated again from *Axymene, Xymenella* and *Zeatrophon*) is useful biostratigraphically in near-shore facies: *X. drewi* (Hutton) (based on Marwick's lectotype), Mangapanian-late Nukumaruan; *X. expansus* (Hutton), late Nukumaruan-early Castlecliffian (to OIS 19); *X. plebeius* (Hutton), OIS 17-Recent. New fossil records from Pleistocene (OIS 7) deposits at Hokianga Harbour, Northland: *Agnewia tritoniformis* (Blainville), *Hydatina physis* (Linné), *Philine tepikia* Rudman. Other biostratigraphically useful species: *Zeatrophon bonneti* (Cossmann) (Nukumaruan-OIS 9; 7?); *Aeneator delicatulus* Powell, *Buccinulum caudatum* Powell (both OIS 25-19, 17?). New synonymy: *Otahua* Marwick, 1948 = *Bedeva* Iredale, 1936; *Cominella (Eucominia) marlboroughensis* Powell = *C. elegantula* (Finlay), Nukumaruan-Recent; *Antiguraleus* Powell, 1942 = *Propebela* Iredale, 1918; *Antiguraleus depressipirus* (Beu) = *Propebela ula* (Watson); *Oenopota* Mörch, 1853 is possibly an earlier name for *Liracraea* Odhner, 1924, but *Liracraea* is retained; *Antimelatoma ahiparana* and *A. otagoensis* of Powell = *A. buchanani* (Hutton); *Tritonoturris* Dall, 1924 = *Asperdaphne* Hedley, 1922; most Australasian "*Asperdaphne*" species are assigned to *Pleurotomella* Verrill. Taxonomy revised: *Cirsotrema zelebori* (Dunker); *Opalia (Nodiscala) nympha* (Hutton) (Mangapanian-Nukumaruan); *Acirsa cookiana* (Dell, 1956) (OIS 23-Recent); *Cominella (Eucominia) incisa* (Hutton), Nukumaruan, Hawke's Bay; *Euthria pangoides* (Beu), Waipipian; *Iredalula striata* (Hutton), Kapitean(?)-Castlecliffian (-OIS 11) distinguished from *I. alticincta* (Murdoch & Suter), Nukumaruan-Recent; *Ponderia zealandica* (Hutton) (OIS 13-Recent); *Amalda (Baryspira) olsoni* Beu, Nukumaruan; *Kuroshioturris angustata* (Powell), Mangapanian-Recent; *Austrotoma aguayoi* (Carcelles) (Recent, SW Atlantic); *Struthiolariopsis ferrieri* (Philippi), Cretaceous, Quiriquina, Chile (Conoidea); *Mitrellatoma angustata* (Hutton), Nukumaruan; *Gymnobela gypsata* (Watson), Recent, E New Zealand, removed from *Paracomitas*; *Paracomitas protransenna* (Marshall & Murdoch) (Nukumaruan), *P. gemmea* (Murdoch) (Castlecliffian) and *P. augusta* (Murdoch & Suter) (= *P. augusta powelli* Dell; Recent); *Aoteadrillia wanganuiensis* (Hutton) (= *chordata* Suter and many other synonyms; Nukumaruan-Recent), *A. finlayi* (Powell) and *A. apicarinata* (Marshall & Murdoch) (Nukumaruan); *Bulla quoyii* Gray (OIS 7-Recent); *Bulla australis* Férussac, Atlantic, = *B. mabillei* Locard; *Philippia lutea* (Lamarck), Nukumaruan-Recent.

Keywords: biostratigraphy; Castlecliffian; dispersal; Haweran; Holocene; Mollusca; new genus; new species; New Zealand; Nukumaruan; oxygen isotope stages; Pleistocene; Pliocene; time scale; Wanganui Basin.

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Introduction

This paper is the fourth part of a revision of the taxonomy and biostratigraphy of New Zealand fossil Mollusca of the last two million years, with comments on related Recent and earlier Pliocene taxa. The first report (Beu 2004) reconsidered the generic positions or specific determinations of some New Zealand late Neogene to Recent molluscs, including migrants from eastern Australia and the tropical Pacific that appeared only briefly in New Zealand during interglacial periods. The second (Beu 2006) reconsidered time ranges and taxonomy of bivalves over this period, including further warm-water migrants. Part 3 (Beu 2010) commenced reconsideration of the time ranges and taxonomy of some gastropods over the same period.The present report is a reconsideration of the time ranges and taxonomy of the remaining gastropods over the same period, with time ranges recorded in oxygen isotope stages (OIS) where possible. Because of space considerations, a number of further gastropods requiring revision have been deleted from this work (partially listed below). A summary paper will follow. Time ranges have been compiled from the detailed faunal lists provided for the formations of Wanganui Basin by Fleming (1953), assigned to individual oxygen isotope stages in the correlation diagram of cycles in Wanganui Basin compiled by Carter & Naish (1999). The faunas included in this overview, their ages and their oxygen isotope stage correlations were summarized in Part 1 of this series of papers (Beu 2004), modified slightly in the introduction to Part 2 (Beu 2006), and are not repeated here. Once again this work is founded on the seminal works on Wanganui Basin by Fleming (1947,1953), and much of what the present 'Wanganui Basin working group' has published (particularly Beu 2004, 2006; Abbott et al. 2005; Naish et al. 2005; Pillans et al. 2005) is based on Fleming's brilliant foundation.

The obvious new, larger taxa and some previous misidentifications have been revised in these four papers, but there is little doubt that this is merely the beginning of recognising the true relationships of the late Neogene molluscan fauna of New Zealand. Further taxonomic revisions and reidentifications undoubtedly will bring to light an increasing list of molluscs that extended their ranges to Wanganui Basin briefly during the many glacial-interglacial oscillations of late Pliocene-Pleistocene time.

Abbreviations and conventions

Collections and institutions housing specimens listed here are abbreviated:

S22/f123, etc.	Locality numbers in the New Zealand Fossil Record Electronic Database (FRED; http://data.gns.cri.nz/fred/), administered by the Geological Society of New Zealand; map sheet number in NZ Map Series 260 (1: 50,000) followed by the individual fossil locality number within that sheet. (Offshore samples are assigned record numbers based on their latitude and longitude.)
R11/742729, etc.	Grid references to fossil localities on map sheets of NZ Map Series 260 (1: 50,000); map sheet number followed by grid reference on that sheet.
AIM	Auckland War Memorial Museum, Auckland.
AMS	Australian Museum, Sydney.
AUGD	Geology Programme, School of Geology, Geography and Environmental Sciences, University of Auckland
BMNH	Natural History Museum, London.
CMC	Canterbury Museum, Christchurch [New Zealand].

GNS	Institute of Geological & Nuclear Sciences, Lower Hutt; individual collection abbreviations are used throughout the text: GS bulk collection locality numbers; RM New Zealand Recent Mollusca registration numbers; TM type Mollusca registration numbers; WM non-New Zealand Mollusca registration numbers.
MNHN	Muséum National d'Histoire Naturelle, Paris.
NHMW	Naturhistorisches Museum Wien, Vienna.
NMNZ	Museum of New Zealand Te Papa Tongarewa, Wellington.
NMV	Museum Victoria, Melbourne.
SMF	Senckenberg Museum, Frankfurt (Main).
VM	Victoria University of Wellington Geology Department, Mollusca Specimen registration numbers.
V311, etc.	Victoria University of Wellington, School of Earth Sciences and Geography, bulk collection locality numbers.

Other abbreviations and conventions:

MPT	Mid-Pleistocene transition (the change from predominantly 41 ka to roughly 100 ka temperature and sea-level cycles, between 1 and 0.65 Ma).
OIS	Oxygen isotope stage (OIS is preferred here to the alternative, MIS, 'marine isotope stage', as the isotopes involved are exclusively of oxygen and, at least by correlation, the 'stages' can be applied to non-marine as well as marine rocks).

Dimensions of specimens are cited in millimetres, in the consistent order H (= height), D (= diameter).

The standard abbreviations for points of the compass (N = north, S = south, E = east, W = west, NE, SSW, etc.) are used to abbreviate locality details.Unless otherwise stated, I have examined the type material cited below under 'Type material'.

Locality details

Detailed locality records are listed below for the less common species, for which localities help to establish accurate time range. Full locality data are not listed for common, widespread species.

Biostratigraphy

Figure 1 is a time-scale diagram for the last 2 million years in New Zealand, repeated from Beu (2004, fig. 4; 2006, fig. 1), apart from deleting the now out-dated Plio–Pleistocene boundary. Figure 2 shows the time ranges in oxygen isotope stages of most of the gastropods discussed in the present paper and previous papers (Beu 2010). Some taxa with earlier time ranges or no biostratigraphical utility are discussed in the text but not included in Fig. 2. As in Beu (2006), I adopt the time scale of Cooper (2004) and the definitions of local stages adopted by me (Beu in Cooper 2004; Beu 2006:155): Haweran–Castlecliffian boundary at Rangitawa Tephra, 0.34 Ma, in OIS 10 (in Rangitawa Stream, Rangitikei valley); Castlecliffian–Nukumaruan boundary at Ototoka Tephra, 1.63 Ma, in OIS 57 (on the Wanganui coast east of Ototoka Stream mouth); Nukumaruan–Mangapanian boundary at the base of Hautawa Shellbed, 2.4 Ma, in OIS 97 (proposed but not formally defined, on Hautawa Road, between Turakina and Murimoto valleys, north of Hunterville; Beu in Cooper 2004:217); and Mangapanian–Waipipian boundary at the base of Mangapani Shellbed, 3.0 Ma (in Mangapunipuni Stream,

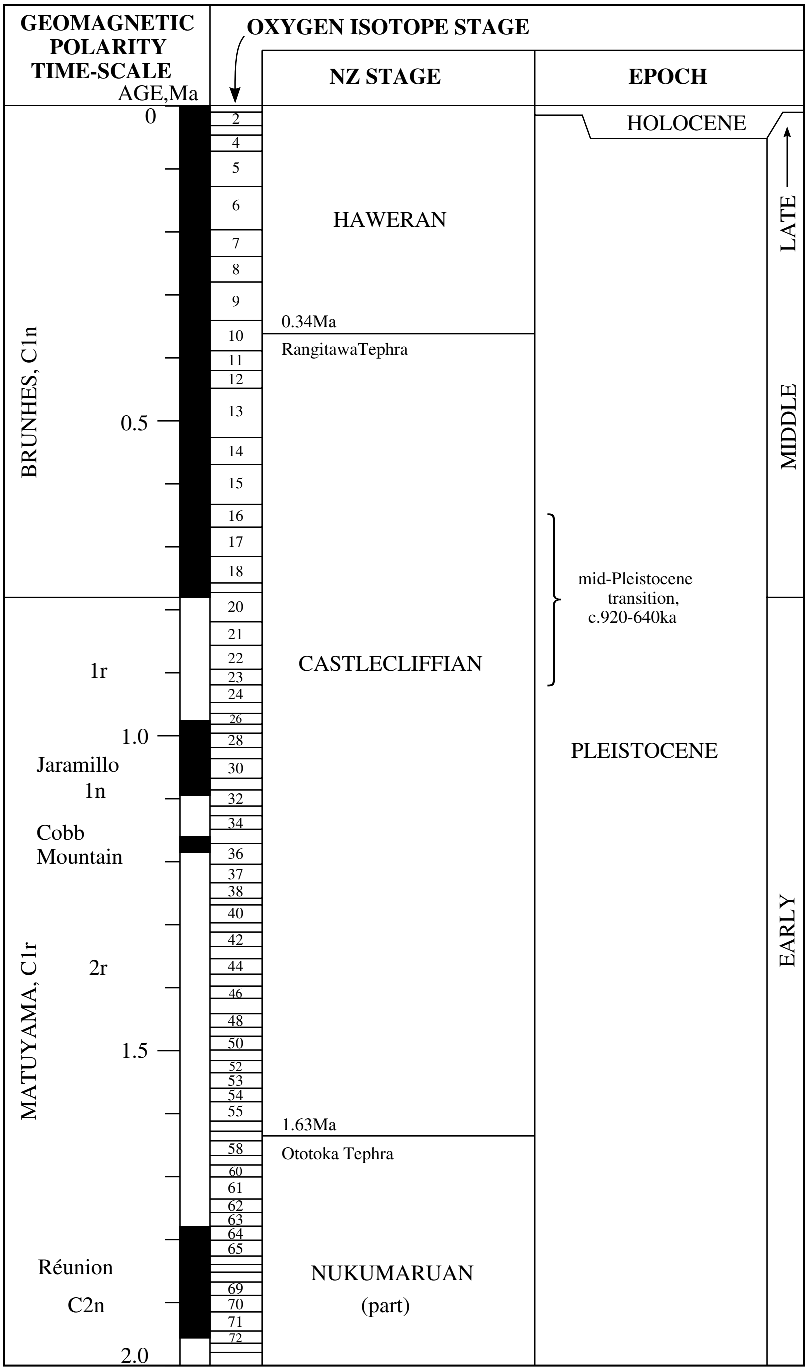

Figure 1 New Zealand Pleistocene-Holocene time scale (Beu 2006, fig. 1). Correlation of oxygen isotope stages with the geomagnetic polarity time-scale modified slightly from Carter & Naish (1999). Pliocene-Pleistocene boundary now at 2.59 Ma, below base of diagram; Late Pleistocene is applied only to the Last Glaciation, OIS 2.

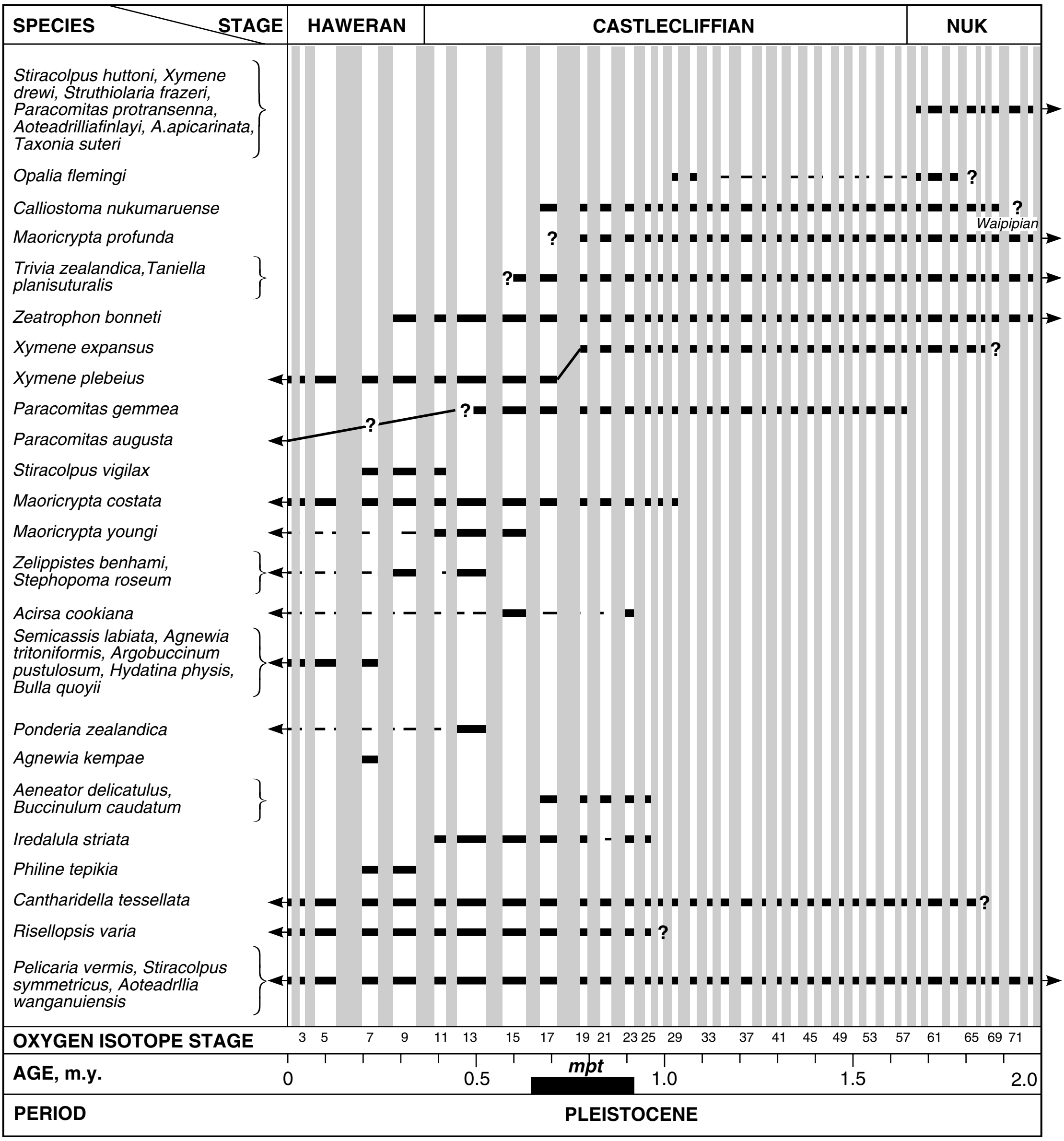

Figure 2 Time ranges of Pleistocene-Recent gastropods discussed in this paper and in Beu (2010), in oxygen isotope stages (additional to Beu 2004, fig. 5; Beu 2006, fig. 2). Time scale as in Fig. 1. Time ranges derived from correlation of Wanganui formations (Fleming 1953; Abbott & Carter 1999; Abbott et al. 2005) with oxygen isotope stages, slightly modified from Carter & Naish (1999) following Pillans et al. (2005). Approximate duration of the Mid-Pleistocene Transition (c. 920-640 ka) from predominantly 41 ka cycles to 100 ka cycles shown by bold bar labelled "MPT". NUK = Nukumaruan Stage; Castlecliffian/Nukumaruan boundary at 1.63 Ma.

Waitotara valley). As I have pointed out before (Beu 2004:155), these New Zealand local stage boundary definitions are critical for allowing the recognition of the stages by the criteria identified in the present paper and in previous papers in this series. The stages would not be identifiable by biostratigraphical proxies if different boundary positions were adopted.

The Plio–Pleistocene boundary, as defined in 1984 in the Vrica section, southern Italy, falls within OIS 65, at 1.81 Ma, but has been removed from the figure, as the International Union of Geological Sciences has recently (July 2009) ratified a new definition of the Pliocene–Pleistocene boundary at the Global Stratotype Section and Point (GSSP) of the Gelasian Stage in the Monte San Nicola section in Sicily, within OIS 103, with a date of 2.588 Ma, only 1 m above the Gauss–Matuyama magnetic reversal in the Monte San Nicola section. The Gelasian Stage is now the lowest stage of the Pleistocene, and the former Pliocene–Pleistocene boundary at Vrica is now defined as the GSSP of the Calabrian Stage. The Pliocene–Pleistocene boundary (as judged by the position of the Gauss–Matuyama reversal) now falls between the Parihauhau and Te Rama Shellbeds of Fleming (1953), as shown in the correlation diagram by Carter & Naish (1999), high in the Mangapanian succession in Wanganui Basin. This position is about 200 ka, or four or five glacial–interglacial cycles, earlier than the first obvious cooling in the New Zealand succession, identified by the appearance of the *Zygochlamys delicatula* (Hutton, 1873) fauna in Wanganui Basin (Fleming 1944), defining the base of the Nukumaruan Stage. It should be noted that this new definition equates the Pliocene–Pleistocene boundary with the Neogene–Quaternary boundary, but the term Neogene is used throughout this paper in the usual sense of Cenozoic stratigraphers working with marine successions (e.g. McGowran et al. 2009), and as usually used in New Zealand, that is, extending from the end of Oligocene time until the present day.

Figure 2 is constructed to demonstrate:

1. A group of species (*Stiracolpus huttoni*, *Struthiolaria frazeri*, *Xymene drewi*, *Paracomitas protransenna*, *Aoteadrillia finlayi*, *A. apicarinata*) and the genus *Taxonia*, all of which became extinct at the end of Nukumaruan time, and so provide reliable criteria for identifying the Nukumaruan–Castlecliffian boundary (with the proviso that a form closely resembling *Aoteadrillia finlayi* still occupies bathyal depths along central eastern New Zealand).
2. Longer-ranging species that became extinct during Castlecliffian–Haweran time: *Calliostoma nukumaruense*, in OIS 17; *Maoricrypta profunda*, in OIS 19 or possibly 17; *Trivia (Ellatrivia) zealandica* and *Taniella planisuturalis*, which both retreated from a Nukumaruan–early Castlecliffian last appearance in central New Zealand to be last known in OIS 15(?) at Ohope Beach, Whakatane; *Iredalula striata* in OIS 11; *Zeatrophon bonneti* in OIS 9.
3. The evolving lineages of *Xymene drewi* (Mangapanian–Nukumaruan), *X. expansus* (late Nukumaruan–OIS 19) and *X. plebeius* (OIS 17–Recent), and of *Paracomitas protransenna* (Nukumaruan), *P. gemmea* (Castlecliffian; OIS 23–14?, limited by its restriction to offshore siltstone facies) and *P. augusta* (Recent).
4. Short-ranging species of biostratigraphical utility during Castlecliffian–Haweran time: *Stephopoma roseum* (OIS 13 and 9 at Wanganui; OIS 7 and Recent in NE North Island); *Stiracolpus vigilax* (OIS 11–9 at Wanganui; OIS 7 at Te Piki, near East Cape), *Maoricrypta costata* (OIS 29–5a at Wanganui, Recent in NE North Island), *M. youngi* (OIS 11–Recent), *Zelippistes benhami* (OIS 13 and 9 at Wanganui; Recent in NE North Island), *Semicassis labiata*, *Argobuccinum pustulosum*, *Agnewia tritoniformis*, *Hydatina physis*, and *Bulla quoyii* (all OIS 7–Recent), *Acirsa cookiana* (OIS 23–Recent), *Opalia*

flemingi (late Nukumaruan–Castlecliffian, OIS 31, 29?), *Ponderia zealandica* (OIS 13 only; Recent in Cook Strait and near East Cape), *Agnewia kempae* (OIS 7 only, at Te Piki), *Aeneator delicatulus* and *Buccinulum caudatum* (both OIS 25–17), and *Philine tepikia* (OIS 9 and 7 only).

5. Species previously thought to have short (Haweran–Recent) time ranges, now known to have appeared earlier and to have unreliable, facies-controlled time ranges: *Cantharidella tessellata* (earliest record late Nukumaruan); *Risellopsis varia* (earliest record OIS 25?, Teer Formation, Cascade, S Westland).
6. Species previously thought to consist of numerous taxa with short ranges of high biostratigraphical utility during this period, but each interpreted in these papers as consisting of one species that ranged right through the period and provides no biostratigraphical utility: *Stiracolpus symmetricus*, *Pelicaria vermis*, and *Aoteadrillia wanganuiensis*.

The biostratigraphically useful taxa in Fig. 5 supplement those shown and discussed previously by me (Beu 2004, fig. 5; 2006, fig. 2), together providing the means of distinguishing Nukumaruan from Castlecliffian faunas, and of identifying a number of the oxygen isotope stages during Castlecliffian–Haweran time.

Mid-Pleistocene transition

As noted previously (Beu 2006:156), one of the aims of this series of papers is to recognize evidence for origination and extinction caused by temperature change during the last 2 m yr and, in particular, to what degree origination and extinction coincided with the mid-Pleistocene transition (MPT) (ca 1.0–0.65 Ma; taken here as occupying OIS 23–17), when glacial-interglacial cycles changed gradually from the 41 ka period of Pliocene–early Pleistocene time to the eccentricity-driven, roughly 100 ka period of the last ~800 ka. Data from Beu (2004, 2006) indicate that only seven events occurred during the MPT. Most obvious origination and extinction events during the last 2 m yr occurred either at the end of Nukumaruan time or since the MPT (23 events), during the period of high-amplitude glacial-interglacial cycles. The end-Nukumaruan extinction apparently resulted from closure of the Manukau seaway and the consequent decrease in larval transport to Wanganui Basin. Data from gastropods (Fig. 2) demonstrate that seven further events occurred during the MPT, whereas a further 20 occurred since then, making totals of 14 MPT and 43 post-MPT events. These numbers confirm that the biota was more drastically affected by the large-scale glacial-interglacial cycles of the late middle and late Pleistocene than by the more gradually changing temperature regime of the MPT.

Other taxa useful in biostratigraphy

Still further molluscan taxa actually or potentially are useful for biostratigraphy in Nukumaruan–Haweran rocks. They have not been investigated in these papers, because of space and time constraints, or because further taxonomic revision is required before they are useful in biostratigraphy (e.g. *Neoguraleus* and *Splendrillia*, Conoidea; *Mesopeplum*, Pectinidae). Some have well-established biostratigraphical utility (e.g. *Aethocola* species). They are listed briefly here, as an indication of further work required; no doubt others remain unrecognized. Several of the listed species (identified with an asterisk*) are small molluscs, under ca 6 mm in greatest dimension, constituting the majority of the Mollusca, but ignored in the present works in favour of taxa identifiable in the field.

Polyplacophora

1. *Cryptoconchus marwicki* Bucknill, 1928 (Beu & Maxwell 1990:333, pl. 43j, l), limited to Castlecliffian rocks (records from OIS 15, 13).

Gastropoda

2. **Scissurona fossilis* Laws, 1940, Mangapanian and Nukumaruan; recorded from Wilkies Shellbed at Wilkies Bluff and Nukumaru Brown Sand at Nukumaru Beach (Laws 1940); occurs also in Waipuru Shellbed.
3. *Haliotis (Sulculus?) powelli* Fleming, 1952 (Beu & Maxwell 1990:347, pl. 47c), occurs in Castlecliffian rocks at Ohope Beach (OIS 15?) and in the Komako area, Pohangina, eastern Wanganui Basin, Nukumaruan (Carter 1972).
4. *Emarginula haweraensis* Powell, 1931, the largest New Zealand *Emarginula* species; occurs in Waipipian to Nukumaruan rocks (Waipipi shellbeds, type; Okauawa Stream and Kaiwaka S Road, Hawke's Bay, late Nukumaruan).
5. **Brookula funiculata* Finlay, 1924, recorded only from late Nukumaruan to Haweran rocks (Waipuru Shellbed to Landguard Sand, OIS 9). Numerous unnamed Recent species of *Brookula* are known from the NZEEZ (Spencer et al. 2009:201) and it is quite feasible that *B. funiculata* is still living.
6. *Zethalia* species (Trochidae, Umboniinae): an excellent example of a long-continued, anagenetic lineage, with arbitrary subdivision into species. Currently accepted species are *Z. russelli* Marwick, 1965 (Opoitian) (Beu & Maxwell 1990:289, pl. 36e, h), a small species (diameter 6–7 mm) with the tallest spire in the genus, a subsutural row of small beads, another periumbilical row of small beads, and the umbilicus not quite filled by a lobe of the inner lip callus forming a spiral plug; *Z. coronata* Marwick, 1948 (Waipipian–early Nukumaruan), intermediate in size (diameter 10–17 mm) and with small beads in a subsutural row, but with a completely filled umbilicus and smooth base; and *Z. zelandica* (Hombron & Jaquinot, 1854) (early Nukumaruan–Recent) (Beu & Maxwell 1990:347, pl. 47l, p), the largest and lowest-spired form (diameter 15–23 mm), almost smooth, with no subsutural row of beads and a smooth base. This genus seems to represent gradual evolution from the strongly sculptured shell of the monileine genus *Antisolarium* to be able more readily to live infaunally and to occupy the mobile sand habitat occupied, convergently, by *Umbonium* in the N Pacific. *Zethalia* was included in tribe Monileini, rather than Umboniini, by Hickman & McLean (1990:126) on anatomical grounds, and although Williams et al. (2010) did not recognize these tribes, they demonstrated that *Umbonium* and *Zethalia* are distinct genera on the basis of molecular phylogeny.
7. *Pliconacca denticulifera* (Marwick, 1924), apparently ranging from early Nukumaruan (Kuripapango, inland Hawke's Bay, GS12687, U20/f10A) to Recent (see Majima [1989:63] for reference to *Pliconacca* Cossmann & Martin in Martin, 1914; Majima specifically mentioned the Miocene species '*Uberella*' *cicatrix* Marwick, 1931, which seems to have been ancestral to *P. denticulifera*).
8. *Galeodea plauta* Beu (2008:313, fig. 17E–G) (Castlecliff, OIS 19, to Recent); living records are from off W Northland only.
9. **Melanella treadwelli* (Hutton, 1885), limited to Castlecliffian rocks at Wanganui; but apparently no specimens have been collected for more than 100 years. However, as with *Brookula* species, numerous unnamed species of Eulimidae are known from the Recent fauna of the NZEEZ (Spencer et al. 2009:205) and one of these could well be *M. treadwelli*.
10. *Margineulima christyi* (Marwick, 1924) (Beu & Maxwell 1990:328, pl. 41h; Maxwell 1992:120), supposedly a Mangapanian–Nukumaruan restricted species, this

large, distinctive species was recorded from Castlecliffian rocks at Wanganui by Fleming (1953:188, 199): Kaimatira Pumice Sand (OIS 25; in GS 4148, R22/f7414) and Kaikokopu Shellbed (OIS 19; in GS4156, R22/f7417).

11. *Murexsul* species: Marshall & Burch (2000) revised *Murexsul* species (as *Muricopsis*) in the modern fauna and some late Pliocene–Pleistocene fossil records. The relatively small species *M. espinosus* (Hutton, 1885) is apparently limited to Mangapanian and Nukumaruan rocks, and the earliest definite record of the larger species *M. octogonus* (Quoy & Gaimard, 1833) (Beu & Maxwell 1990:359, pl. 48 l) is from Castlecliff (Kaikokopu Shellbed, OIS 19; Fleming 1953:199), but Marshall & Burch (2000) recorded specimens similar to both *M. octogonus* and *M. espinosus*, along with a possible third species, from Ashcott Road, W of Waipukurau, Hawke's Bay (GS10858, U22/f 9588, late Nukumaruan). Late Neogene species require further study.
12. *Cominella (Eucominia?) hamiltoni* (Hutton, 1885) (Beu & Maxwell 1990:324, pl. 42g), a distinctive small species limited to Nukumaruan rocks.
13. *Aethocola* species: many species of this genus have highly useful, restricted ranges, most notably the Kapitean index species *A. coerulescens* (Finlay, 1930) (Beu & Maxwell 1990:266, pl. 30e). Several Pliocene species have rather short ranges also: *A. pagoda* Finlay, 1924 (Beu & Maxwell 1990:298, pl. 37g) and *A. (Zelandiella) pliocenica* (Powell, 1931) (Beu & Maxwell 1990:299, pl. 37d), both limited to Opoitian–early Mangapanian rocks; *A. (Zelandiella) propenodosa* (Bartrum, 1919), recorded only from Opoitian rocks at Kaawa Creek, SW Auckland; and *A. (Zelandiella) allani* (King, 1934) (= *conoidea* Zittel, 1864), limited to Opoitian–Waipipian Starborough Formation in the Awatere valley. The superabundant living species *A. glans* (Röding, 1798) (Beu & Maxwell 1990, 364, pl. 49c) is not known fossil earlier than Castlecliffian, but the significance of this is uncertain, as specimens very similar to its supposed 'form' *A. chathamensis* (Finlay, 1928) occur uncommonly in Nukumaruan rocks of Wanganui and Hawke's Bay, in near-shore facies. *A. taitae* Marwick, 1924 (Beu & Maxwell 1990:324, pl. 42k) is limited to late Nukumaruan rocks of Hawke's Bay, *A. cottoni* (King, 1933) is limited to Nukumaruan rocks in S Wairarapa, and *A. clavicula* (King, 1933), an unusual species with a narrowly rounded rather than angulate margin to the sutural ramp, is limited to early Nukumaruan bathyal rocks at Palliser Bay.
14. *Taron dubius* (Hutton, 1878), now limited to the NE North Island warm province; Fleming (1953:188, 199) recorded '*Taron* n. sp.' from Kaimatira Pumice Sand (OIS 25; in GS4163, R22/f6459) and *T. dubius* from Kaikokopu Shellbed (OIS 19; in GS4156, R22/f7417). *Taron* possibly represents another rare warm-water migrant from the N North Island in Wanganui Basin, but *T. dubius* has direct development, so any transport presumably would have been by rafting.
15. *Austromitra planata* (Hutton, 1885), apparently limited to Mangapanian–Castlecliffian rocks. However, the Recent species *A. lawsi* Finlay, 1930 seems to be conspecific (Oaro, Marlborough, Nukumaruan [Beu 1979]; Waipuru Shellbed to Upper Castlecliff Shellbed [OIS 11], as *Proximitra* n. sp., etc., of Fleming's [1953] lists). Taxonomic revision required; again, many unnamed species are recorded from the NZEEZ by Spencer et al. (2009:209) and probably include *A. planata*.
16. *Alcithoe* species: the restricted ranges recorded by Beu & Maxwell (1990) and

Maxwell (2009) for some late Neogene *Alcithoe* species suggest they are useful for biostratigraphy, but in practice they are uncommon and variable, and difficult to use: *A. arabica* (Gmelin, 1791) (Beu & Maxwell 1990:366, pl. 49d), first record Nukumauan; *A. exigua* Marwick, 1926 and *A. nukumaruesis* (Marshall & Murdoch, 1920) (an ecophenotype of *A. arabica*?), both limited to Nukumaruan; *A. fusus* (Quoy & Gaimard, 1833) (Beu & Maxwell 1990:367, pl. 49i), Castlecliffian–Recent.

17. Three large, long, narrow, short-spired, distinctive species of Marginellidae seem to be limited to Nukumaruan rocks of Hawke's Bay: *Serrata hectori* (Kirk, 1882), *S. kirki* (Marwick, 1924), and *S. marwicki* (Finlay, 1927) (Beu & Maxwell 1990:326, pl. 42j; Maxwell 2009:245), but these require revision and comparison with the Recent species renamed by Marshall (2004).
18. *Zeadmete kumeroa* Fleming, 1943, apparently limited to Nukumaruan rocks of S Hawke's Bay, and *Z. pliocenica* (Finlay, 1930), apparently limited to Castlecliffian rocks at Wanganui (recorded by Fleming (1953:226, 230) only from Pinnacle Sand (OIS 14; GS4098, R22/f6425) and Tainui Shellbed (OIS 13; GS4013, R22/f6353, & GS4097, R22/f6516) at Wanganui, but recently collected from Upper Castlecliff Shellbed (OIS 11; GS13590, R22/f0100). Neogene–Recent species require revision.
19. *Bonellitia lacunosa* (Hutton, 1885) (Beu & Maxwell 1990:326, pl. 42 l) is another species apparently limited to late Nukumaruan rocks of Hawke's Bay; collected recently at localities in Petane Group near Napier and at Maharakeke Road SW of Waipukurau. *B. lacunosa* seems to reach a larger size and have coarser sculpture than the Recent species *B. superstes* Finlay, 1930.
20. *Comitas allani* Powell, 1942 (Beu & Maxwell 1990:327, pl. 42p), Opoitian to Nukumaruan; last recorded uncommonly in late Nukumaruan Petane Group in central Hawke's Bay.
21. *Tomopleura subalbula* (Murdoch, 1900), Nukumaruan–Haweran; recorded from Waipuru Shellbed (late Nukumaruan) to Landguard Sand (OIS 9) and at Te Piki, near East Cape (OIS 7); apparently ancestral to the Recent species *T. albula* (Hutton, 1873) but the distinction needs to be verified from more material.
22. **Zenepos lacunosa* (Hutton, 1885); Powell (1942) recorded this from Castlecliff (holotype) only; I am not aware of any other records.
23. **Ringicula uniplicata* Hutton, 1885, recorded only from the late Nukumaruan Petane Group of Hawke's Bay, but again apparently not collected for more than 100 years, and the type material is lost.

Bivalvia

24. **Cosa wanganuica* Finlay, 1930, apparently limited to Castlecliffian rocks of Wanganui (Kaimatira Pumice Sand, OIS 25, to Tainui Shellbed, OIS 13; Fleming 1953).
25. **Hamacuna nukumaruensis* (Laws, 1940), limited to Mangapanian–Nukumaruan rocks (Wilkies Shellbed at Wilkies Bluff and Nukumaru Brown Sand at Nukumaru Beach; Laws 1940).
26. *Talabrica bellula* (A. Adams, 1854) and related species all require investigation. The earliest New Zealand record of the genus seems to be Mangapanian. Fleming (1953:178) recorded *T. bellula* only from Lower Okehu Siltstone (Castlecliffian, OIS 29; Mowhanau Formation of Abbott & Carter 1999). *T. nummaria* Powell, 1931 is recorded only from Nukumaruan and, possibly, Castlecliffian rocks (recorded by Fleming (1953:180) from Okehu Shell Grit (OIS 27), but in brackets, indicating thought reworked from older rocks). *T.*

inornata Wild & King, 1932 apparently is a rare species recorded only from Nukumaruan rocks. *T. senecta* Powell, 1931 (Beu & Maxwell 1990:310, pl. 40b, f) apparently is limited to Nukumaruan rocks at Castlepoint (although both *T. nummaria* and *T. inornata* possibly are synonyms of *T. senecta*). An unnamed species occurs in Castlecliffian (OIS 15) rocks at Matata, Bay of Plenty (NMNZ M.137685), and another is present in the Recent fauna of the Three Kings Islands (NMNZ M.137651; BA Marshall NMNZ pers. comm. October 2009; Spencer et al. 2009:198). Lamprell (2003) treated *Talabrica* Iredale, 1924 as a synonym of *Crassatina* Kobelt, 1881 (West Africa), but judged from illustrations of African species (e.g. Ardovini & Cossignani 2004, figs. pp. 277–278) this synonymy is most unlikely to be correct. The shape and sculpture of *Crassatina* species are both strongly distinct from those of *Talabrica* species.

27. *Marama murdochi* Marwick, 1927 (Beu & Maxwell 1990:316, pl. 41c, d), species and genus last recorded in late Nukumaruan rocks; a distinctive, inflated relative of *Dosina* with a large, pouting lunule and fine commarginal sculpture, limited to offshore, shelf, mudstone facies.
28. '*Parilimya*' *neozelanica* (Suter, 1914) (Boreham 1965:73, pl. 20, figs. 2, 3, as '*Thracia*' *neozelanica*; Beu & Maxwell 1990:346, pl. 46g, i); recorded rarely from Wanganui Castlecliffian rocks and the Recent fauna; collected recently from Upper Castlecliff Shellbed (OIS 11).
29. *Thracia magna* Marshall & Murdoch, 1921 (Beu & Maxwell 1990:288, pl. 34h), limited to Waipipian–Nukumaruan rocks. This distinctive, large species is last recorded from late Nukumaruan rocks (Nukumaru Brown Sand) at Wanganui.
30. Warm-water taxa recorded by Fleming (1953:272–274) from Oturi shellbed, Waipipi (OIS 5a): a final subject that deserves fuller treatment than the cursory glance given it here is the taxa recorded by Fleming from the basal Oturi shellbed of the Hauriri Terrace cover beds (OIS 5a, ca 80 ka) at Waipipi, mouth of Wairoa Stream, W end of Waverley beach, W of Wanganui. Re-collections have shown that this is a 'fossil' boulder beach, with *Barbatia novaezelandiae* (Smith, 1915) abundant among the in situ boulders, infaunal boring bivalves such as *Pholadidea* present in their bore-holes in the boulders, and a few specimens of *Cleidothaerus albidus* (Lamarck, 1819) attached to the boulders. The small amount of shelly sand surrounding the boulders contains the following warm-water species, according to Fleming's (1953) list: *Monodilepas monilifera* (Hutton, 1873), *Maoricrypta costata* (G. B. Sowerby I, 1824), *M.* cf. *youngi* Powell, 1940, *Murexsul mariae* Finlay, 1930, and *Marginella* cf. *mustelina* Angas, 1871 (that is, *Serrata fasciata* (G. B. Sowerby II, 1846); Marshall [2004:8]). These almost all have taxonomic problems or could refer to other, similar species, e.g. Fleming's material identified as *Murexsul mariae* appears to me to be *M. octogonus* (Quoy & Gaimard, 1833), which still lives in W Cook Strait; *Monodilepas* contains a number of similar species with distinct ranges around New Zealand at present; and *Maoricrypta youngi* still lives in W Cook Strait (see below). The only certain warm-water, NE North Island species present is *Maoricrypta costata*, although if Fleming's identification is correct, *Serrata fasciata* is possibly another, as it is not recorded south of Mahia Peninsula (Marshall 2004:9). This fauna deserves further attention, although recent re-collections have not brought any apparently significant species to light.

Taxonomy
Phylum Mollusca
Class Gastropoda
Informal group Ptenoglossa

Family Epitoniidae

Genus ***Acirsa*** Mörch, 1857

Acirsa Mörch 1857:77. Type species (by subsequent designation, Bouchet & Warén 1986:526): *Scalaria eschrichti* Holböll in Möller, 1842, Recent, Arctic & W N Atlantic (N Canada & W Greenland to Massachusetts, USA; Bouchet & Warén 1986:528, fig. 1225).

Acirsella de Boury 1886:xxi. Type species (by original designation): *Scalaria inermis* Deshayes, 1861, Eocene (Lutetian), Paris Basin (Cossmann 1912, pl. 4, figs. 29, 30; synonymy implied by Bouchet & Warén 1986:526).

Hemiacirsa de Boury 1890:268. Type species (by original designation): *Turbo lanceolatus* Brocchi, 1814, Pliocene, Mediterranean (Cossmann 1912, pl. 4, figs. 23, 24; synonym according to Bouchet & Warén 1986:526).

Pseudacirsa Kobelt 1903:26. Type species (by subsequent designation, Nordsieck 1968:75): *Scalaria coarctata* Jeffreys, 1884, Recent, N Norway (Bouchet & Warén 1986:526, fig. 1224; synonym according to Bouchet & Warén 1986:526).

Plesioacirsa de Boury 1909:256. Type species (by original designation): *Scalaria subdecussata* Cantraine, 1835, Recent, S Europe (Bay of Biscay to Madiera and Canaries; W Mediterranean) (Bouchet & Warén 1986:528, fig. 1226; synonym according to Bouchet & Warén 1986:526).

Pseudoacirsa de Boury 1909:256. Type species (by original designation): *Acirsa bezanconi* de Boury, 1909, Eocene (Lutetian), Paris Basin (Cossmann 1912, pl. 4, figs. 33, 34) (**new synonym**).

Tumidiacirsa de Boury 1911:221. Replacement name for *Pseudoacirsa* de Boury, 1909, supposedly a junior homonym of *Pseudacirsa* Kobelt, 1903 (although under the current ICZN Code *Pseudoacirsa* is not a homonym of *Pseudacirsa*, their synonymy with *Acirsa* was implied by Bouchet & Warén (1986:526) so the question is irrelevant) (**new synonym**).

Notacirsa Finlay 1926a: 231. Type species (by original designation): *Turbonilla (Pyrgiscus) oamarutica* Suter, 1917, early Miocene, New Zealand (**new synonym**).

Plastiscala Iredale 1936:302. Type species (by original designation, Iredale 1936:336): *Scala morchi* Angas, 1871, Recent, SE Australia (**new synonym**).

Remarks. Bouchet & Warén (1986:526) regarded all the subgenera of *Acirsa* recognized by Cossmann (1912) based on Recent type species as synonyms of *Acirsa*, and commented that 'Other genera based on fossil type species may be synonyms', implying that they thought the other very similar subgenera listed in the synonymy above are also synonyms. Another synonym may well be *Proacirsa* Cossmann (1912:96; type species *Turritella inornata* Terquiem & Jourdy, 1869, Bathonian, France) but as this almost identical shell is Jurassic in age, whereas all other members of the genus are Cenozoic to Recent, the synonymy deserves more careful evaluation than is possible here. It was discussed in some detail by de Boury (1917:58), who thought the age difference unimportant. In his critique of Cossmann's (1912) classification, de Boury (1917:57) objected to Cossmann's (1912:96) comments on the similarity of these subgenera, pointing out that the protoconch of some of these groups (particularly *Acirsa* sensu stricto) is obtuse and submammillate, whereas that of others (notably

Plesioacirsa) is pointed and elongate. However, this distinction between tall, narrow, planktotrophic protoconchs and shorter, wider, lecithotrophic ones is no longer regarded as a generic character. De Boury (1917:59) also admitted that distinguishing *Acirsella* from *Plesioacirsa* was extremely difficult. Bouchet & Warén's (1986) synonymy is well justified, particularly as the three similar shells they illustrated (Bouchet & Warén 1986, figs. 1224–1226) are the type species of the subgenera *Acirsa* (fig. 1225), *Pseudacirsa* (fig. 1224) and *Plesioacirsa* (fig. 1226). In view of the range of taxa included by Bouchet & Warén (1986) it is accepted here that the New Zealand fossil species assigned to *Notacirsa* by Finlay (1926a) belong in *Acirsa*. One of the few apparently distinctive characters of *Notacirsa*, compared with typical N Atlantic species of *Acirsa*, is the relatively prominent, wide, widely spaced axial ridges (e.g. in *N. oamarutica* (Suter, 1917); Finlay 1926a, pl. 56, fig. 16; *N. vetusta* Maxwell 1992, pl. 14 l), but some other species illustrated by Cossmann have much coarser ridges (e.g. *A. drevermanni* de Boury in Cossmann 1912:196, pl. 6, figs. 4–6; *A. duvergieri* de Boury in Cossmann 1912:197, pl. 6, fig. 21). Other genera proposed for Australian Recent taxa, in particular *Plastiscala* Iredale (1936:302) (type species *Scala morchi* Angas, 1871, Recent, S Australia; Weil et al. 1999:140, fig. 433, holotype illustrated, BMNH 1871.7.5.10) seem highly likely to be further synonyms of this almost cosmopolitan, speciose genus. The holotype of *Scala morchi* (examined, AGB) is very similar to *Acirsa cookiana* (Dell, 1956) in most characters other than its smaller size, its markedly weaker spiral sculpture and its few low varices at irregular, sparse intervals, and generic separation does not seem warranted.

Finlay (1926a:231) gave a very vague type species designation for *Notacirsa*, stating only '*Notacirsa* n. gen./I provide this for *Turbonilla oamarutica* Suter [reference]'. He also included two other named New Zealand species and an Australian fossil, *Scalaria (Hemiacirsa) lampra* Tate, 1888. However, Finlay obviously intended his 'I provide this for' statement to be a type species designation, and this is accepted here.

Acirsa cookiana (Dell, 1956) (Fig. 3F,G)

Mathildona cookiana Dell 1956b:39, fig. 30; Maxwell 1966:447 (position queried); Bieler 1995:632, fig. 92 (holotype; removed from Mathildidae).
Mathildona? *cookiana*. Powell 1979:250.
Acirsa cookiana. Weil et al. 1999:128, fig. 395; Spencer et al. 2009:205.

Type material. Mathildona cookiana, holotype (Bieler 1995, fig. 92; Weil et al. 1999, fig. 395) NMNZ M.8842 (Marshall 1996:23), Recent, Cook Strait, in 137 m, 40°52.6′S, 174°49.5′E; two lots of paratypes in NMNZ, also from Cook Strait, in 113 and 148 m (Dell 1956b:39).

Other material examined. **Opoitian:** A specimen in GS1567, W19/f7516 (Waiau River at junction with Pakihiwi Stream, inland from Wairoa, N Hawke's Bay) is a small spire from a shell very similar to TM8602 (see below). This specimen was identified as '*Aclis* cf. *planostoma* (Hutton, 1885)' by J Marwick in the GNS collection, but is considerably wider and more strongly sculptured than other specimens referred to *A. planostoma*, and appears to be an incomplete spire from a much larger shell similar to *Acirsa cookiana*. **Castlecliffian:** Omapu Shellbed (OIS 23), Castlecliff coastal section E of Mowhanau Beach, coll. C. A. Fleming (TM8601, GS4060, R22/f6391, 1, Fig. 3F, G); Pinnacle Sand (OIS 15/14) at 'the pinnacles' gully, Castlecliff coastal section (one, TM8602), collected and presented by the late Mrs Jean Boswell, a keen collector of fossils from the Castlecliff section, near her home in Wanganui. Jean donated several valuable specimens to GNS's collection over many years. Another specimen of *A. cookiana* from the same locality was present in her collection,

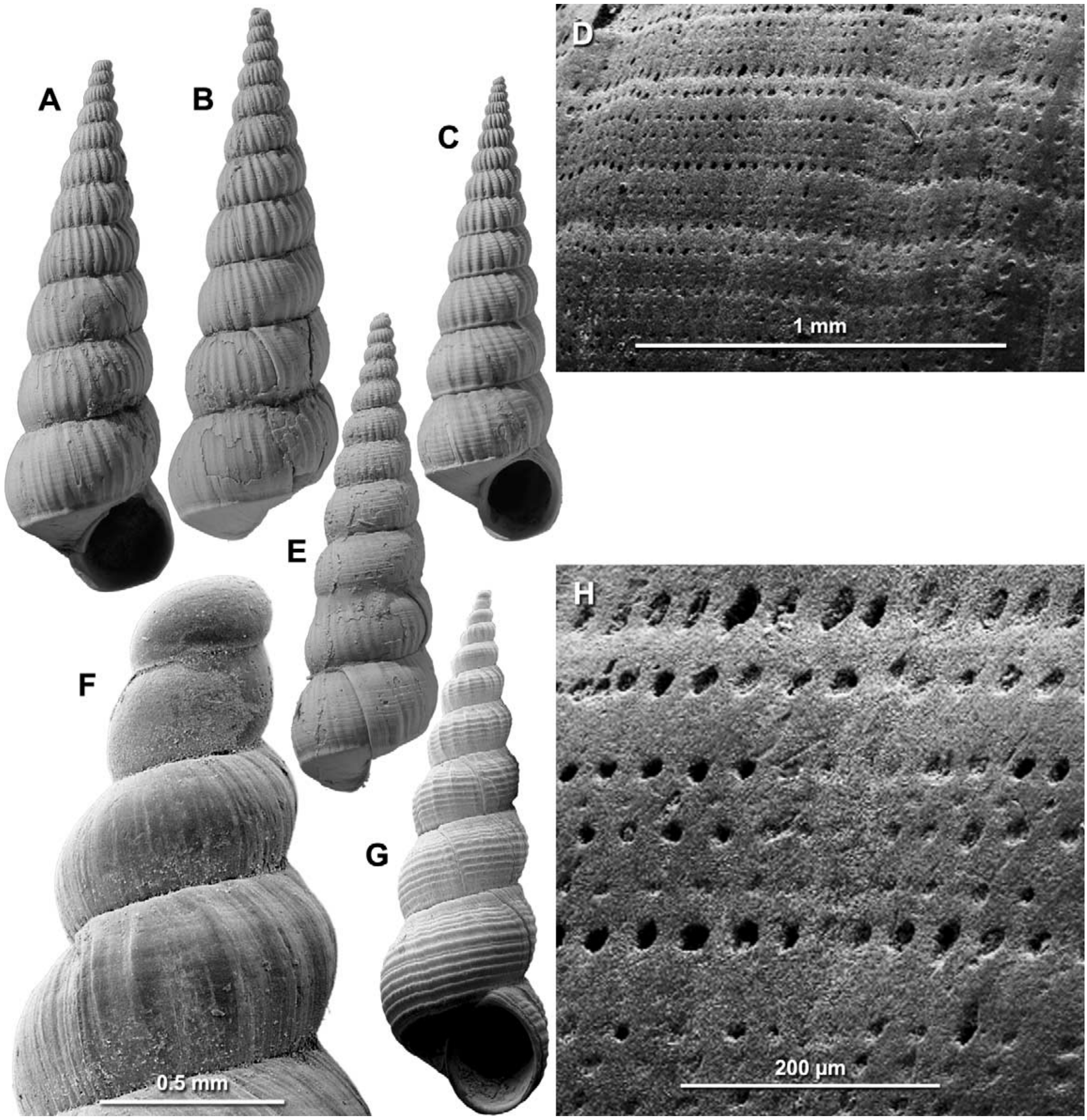

Figure 3 (A–E,H) *Opalia (Pliciscala) flemingi* n. sp.; A, B, holotype, TM8590, GS4107, R22/f6430, Ototoka Siltstone (Castlecliffian, OIS 31), E of Ototoka Beach, Wanganui; height 36.2 mm; C, paratype, TM8593, locality in doubt (stratigraphically higher than Ototoka Siltstone?), illustrated by Beu & Maxwell (1990, pl. 47k); height 31.3 mm; D,E,H, paratype, TM 8591, all data as holotype; D, sculpture of last whorl, SEM; E, whole shell, height 32.3 mm; H, SEM, punctae enlarged. (F,G) *Acirsa cookiana* (Dell), TM8601, GS4060, R22/f6391, Omapu Shellbed (Castlecliffian, OIS 23), E of Mowhanau Beach, Wanganui, SEM; F, protoconch; G, whole specimen, height 14.2 mm.

but I do not know its present location. **Recent:** A specimen in Suter's collection from the famous '110 fathoms [200 m] off Great Barrier Island' sample (Murdoch & Suter 1906) seems likely to be conspecific, and is quite similar to the Omapu Shellbed specimen. It was not mentioned by Murdoch & Suter (1906), but a number of other unrecorded and unidentified taxa from this station are present in Suter's collection. Others: NMNZ M.8839, Cook Strait, 148 m, 40°49.6′S, 174°36.8′E (five, paratypes of *M. cookiana*); NMNZ M.287949, SE slope of Ranfurly Bank, 153–143 m, 37°38.5′S, 178°56.4′E (two); NMNZ M.287 948, N of Alderman Islands, 108–113 m, 36°47.5′S, 176°00.0′E (one); NMNZ M.287950, NZOI Stn P515, 37 km NE of Great Island, Three Kings Islands, 550 m, 33°58.0′S, 172°30.6′E (one).

Distribution. *Acirsa cookiana* is uncommon around northern and central New Zealand at present and a few fossil specimens have now been recognized at Castlecliff, Wanganui. Possibly its uncommonness at Castlecliff results from the deposition of most Nukumaruan–Castlecliffian formations in Wanganui Basin in no more than about 50–70 m of water, that is, significantly shallower than Recent records of *A. cookiana*, which are from ca 100–550 m. The very similar Opoitian specimen from N Hawke's Bay suggests that this is a widespread, if uncommon, species group in New Zealand late Neogene rocks, but its range is poorly known at present.

Dimensions. Holotype: H 9.8, D 3.7 mm (Dell 1956b:39); GS4060, TM8601, Omapu Shellbed: H 14.2, D 4.8 mm; TM8602, 'the pinnacles': H 16.1 (slightly incomplete), D 5.4 mm.

Remarks. *Acirsa cookiana* has more prominent spiral cords than most species assigned to *Acirsa* previously, but relatively weak, uniform spiral sculpture is present over the entire exterior on most *Acirsa* species (Bouchet & Warén 1986, figs. 1224–1226), and some species previously assigned to the synonym *Acirsella* de Boury, 1886 have prominent spiral cords (e.g. Cossmann 1912, pl. 4, figs. 31, 32). The protoconch is present on one of the Castlecliff specimens (Fig. 23I) and is a normal epitoniine lecithotrophic protoconch, closely similar to those illustrated by SEM by Bouchet & Warén (1986, figs. 1165–1181, 1227–1235), lacking the prominent axial costae of planktotrophic protoconchs of Epitoniidae Nystiellinae (Bouchet & Warén 1986, figs. 1131–1138) (Nystiellidae; Nützel 1998). Okutani's (2000, pl. 160, fig. 16) illustration under the name *Plastiscala morchi* (Angas, 1871) shows a specimen closely resembling *Acirsa cookiana*, and much larger than *P. morchi*. However, it has still more prominent, strongly convex, polished spiral cords and weaker axial ridges than New Zealand specimens. Hasegawa & Nakayama (2009) recently confirmed this by recording what is apparently the same species under the name *Acirsa morsei* (Yokoyama, 1926) from off Noto Peninsula, Sea of Japan. Iredale's (1936, pl. 22, figs. 21–23) illustrations of *Plastiscala morchi* show a shell with aligned ventral varices that are absent from New Zealand specimens, and with much weaker spiral cords (*Scala morchi* Angas 1871:15, pl. 1, fig. 7; May 1923:63, pl. 29, fig. 13; Cotton 1956:4, fig. 13; Macpherson 1958:33, pl. 29, fig. 13; Weil et al. 1999:140, fig. 433). Australian specimens are also much smaller (H 7–8 mm for the apparent synonym *Plastiscala verconis* Cotton [1939:172]; H 9.7, D 2.8 mm for the holotype of *P. morchi*, BMNH 1871.7.5.10). New Zealand specimens are also significantly larger and have more numerous, narrower, more closely spaced spiral cords than Australian ones: 12 very closely spaced ones on spire whorls and about 15–16 on the last whorl on TM8601, nine more widely spaced ones on spire whorls and about 12–14 on the last whorl on TM8602 (low, narrow, closely spaced cords on the ramp and base are difficult to count). However, it appears that the relative prominence of secondary cords (all prominent on TM8601, some suppressed over much of the height but strengthening on the last whorl on TM8602) affects the overall shell appearance greatly. New Zealand specimens also lack the true, raised, strongly aligned varices that are present on Australian material of *P. morchi*, although low ridges marking growth pauses are present at irregular intervals on both Castlecliff specimens. Despite the deservedly critical reviews of Weil et al. (1999) by Beechey (2009) and Petit (2009a), I agree with Weil et al. (1999:128) that *A. cookiana* is a prominently sculptured species of *Acirsa*.

Genus *Opalia* H. Adams & A. Adams, 1853

Opalia H. Adams & A. Adams 1853:222. Type species (by subsequent designation, de Boury 1886:xxvi): *Scalaria australis* Lamarck, 1822, Recent, southeastern Australia.

Psychrosoma Tapparone-Canefri 1876:154. Unnecessary new name for *Opalia* Carpenter, 1865, supposedly not of H Adams & A Adams, 1853.

Subgenus *Pliciscala* de Boury, 1887

Pliciscala de Boury 1887:19. Type species (by original designation): *Scalaria gouldi* Deshayes, 1861, Eocene, Paris Basin.

Remarks. Kilburn (1985:271) tentatively referred the only other species I am aware of that resembles *Opalia flemingi* n. sp., *O. aglaia* (Bartsch, 1915), to *Opalia (Pliciscala)*, and is followed here, again tentatively.

Opalia (Pliciscala) flemingi n. sp. (Fig. 3A–E, H).

Acrilloscala n. sp. Fleming 1953:158,174.
Opalia n. sp. Beu & Maxwell 1990:348, pl. 47k.

Type material. Holotype (Fig. 3A, B) TM8590, GS4107, R22/f6430, Ototoka Siltstone (OIS 31), coast E of mouth of Ototoka Stream, W of Wanganui, collected by CA Fleming; with two paratypes, TM8591–2.

Other material examined, all paratypes. GS4107 re-collection, R22/f6430 (one incomplete); GS1198, R22/f6305, 'sandstone immediately above coal [that is, a lignite bed in Maxwell Formation], coast between Ototoka Stream and Okehu Stream' (= upper Tewkesbury Formation; one incomplete); GS1164, R22/f6348, Tewkesbury Formation, Nukumaru Beach, W of Ototoka Stream mouth (one incomplete);?Ototoka Siltstone, poorly localized (TM8593, Fig. 23D, specimen illustrated by Beu & Maxwell (1990:348, pl. 47k); collected by OJ Marston from a locality well to the W of Kai-Iwi). The last paratype was incorrectly stated by Beu & Maxwell (1990:348, pl. 47k) to be from 'the pinnacles' gully, but actually came from well to the west. The collector is unfamiliar with Wanganui stratigraphy, but the specimen is clearly from much lower in the section than Pinnacle Sand. However, its preservation is better than that of the rest of the type material, it bears more prominent axial ridges than the other paratypes, and it is also possible that it is from significantly higher in the section than Ototoka Siltstone. The full stratigraphic range of *O. flemingi* n. sp. is, therefore, unclear at present.

Distribution. Nukumaru–Castlecliff coastal section, only, in Wanganui Basin; early Castlecliffian (OIS 31; possibly later) and latest Nukumaruan; only seven specimens seen. The record of '*Acrillospira*' (sic, = *Acrilloscala*) from Tewkesbury Formation at Nukumaru Beach (Abbott et al. 2005, appendix table, p. 149) was based on Fleming's (1953:158) record of this species (RM Carter, James Cook University pers. comm. 6 October 2005), which in turn was based on Marwick's collections from Nukumaru Beach (Fleming's [1953:158] list for GS1164-1202, R22/f6348, R22/f6309). The only other record by Fleming (1953:174) is from GS4107, R22/f6430, 'Ototoka Siltstone Tongue' of Fleming, in the coastal section E of Ototoka Stream mouth (Ototoka Siltstone; Abbott & Carter 1999:96). Unfortunately, this part of the Wanganui coastal section is heavily overgrown, deeply weathered, and inaccessible at present.

Dimensions. Holotype: H 36.2, D 11.1 mm; paratype TM8591: H (incomplete) 39.9, D 11.2 mm; paratype TM8592: H 32.3, D 9.9 mm.

Description. Shell tall and narrow, large for genus (height 32–40 mm), weakly sculptured with narrow, closely spaced axial and spiral ridges; rather thin and fragile; apparently mostly composed of aragonite (white in most specimens), but with a thin, pinkish to pale brown (presumably calcite) outer layer that detaches rather easily (an intritacalx?). Protoconch not seen. Teleoconch evenly tapered, of 12–13 lightly convex whorls with moderately impressed suture, spire angle 17–18°. Peribasal cord prominent, smooth on most specimens, faintly nodulose on a few, narrowly rounded, issuing from suture on last whorl, continuous with suprasutural cord when that is present, delineating basal disc; termination faintly angling lower right profile of outer lip. Axial sculpture of low, narrow, rather closely spaced, slightly irregular ridges with indistinctly defined edges, weakly curved, inclined slightly forwards towards upper suture; prominent on early spire whorls, weakening down teleoconch; narrower and more closely spaced over upper part of whorl (a weakly defined sutural ramp) than lower down; each axial interspace slightly wider than one ridge; 32 on last whorl and 33 on penultimate whorl of holotype, 26 on last whorl and 28 on penultimate whorl of paratype TM8593. Spiral sculpture of one low suprasutural and one low subsutural fold (subsutural fold formed by closely spaced, weakly nodulose tops of axial ridges) slightly more prominent than remainder of spiral sculpture, rest of whorl (between suture and peribasal cord on last whorl) entirely covered with 12–18 low, weak, closely spaced cords per whorl, crossing axial ridges without forming nodules; relatively few, prominent, uniform and wide on some specimens (e.g. paratype TM8593) but lower, more closely spaced, more varied and more numerous on others, including holotype; with numerous very fine interstitial spiral threads on some specimens, including holotype. Basal disc sculptured much as on whorl sides, but all sculpture much more subdued. Exterior surface bearing microscopic rectangular pits in regular spiral rows; pit rows mostly few and in spiral interspaces on spire whorls, but numerous, closely spaced and covering entire surface including basal disc (but not apertural lips) on last few whorls of well-preserved specimens. Aperture elliptical, with weak posterior sinus, weakly angled at anterior end; lips smooth, thickened, forming continuous peristome and a terminal varix; small, narrow, sharp-edged, weakly ridged fasciole bordering lower half of inner lip on holotype, weakly developed on other specimens. Low, indistinct varices present at irregular intervals of about 2/3 to one whorl on lowest 5–7 whorls.

Remarks. The taxonomic position of this species is a little uncertain. The regular pitting of the whorl surface (Fig. 3D, H) was interpreted by Beu & Maxwell (1990:348) as evidence for a position in *Opalia*, following Kilburn (1985:241,266). The presence of only low, irregular varices also supports a position in *Opalia*. I have searched long and hard for a Recent analogue of this species, with little success; nothing similar was described by Weil et al. (1999), Nakayama (2003) or Garcia (2003, 2004). It is most nearly similar to the South African Recent species *O*. (*Pliciscala) aglaia* (Bartsch, 1915) (Kilburn 1985:271, figs. 51, 52) but the few known specimens of *O. aglaia* are much smaller (reaching 20 × 6.4 mm, but most specimens are half this size) and a little more finely sculptured than *O. flemingi*, with narrower, more numerous (30–40 per whorl), more closely spaced, and slightly more strongly curved axial ridges. Kilburn (1985:272) described *O. aglaia* as having 'micropunctate interstices'. This is the only really similar species I am aware of, and a close phylogenetic relationship with *O. aglaia* appears feasible, implying that this is a further example of transport as planktotrophic larvae in the Antarctic Circumpolar Current.

Two Recent lots in NMNZ (M.171153, off Lord Howe Island, 565–960 m, 31°45.73′S, 159°20.93′E, RV '*Tangaroa*', one large; M.172283, W Norfolk Ridge, W of Cape Reinga, 785–800 m, 34°17.09′S, 168°25.82′E, RV '*Tangaroa*', one large and seven small) are superficially similar to *Opalia flemingi* n. sp., but have more regular, even spiral cords and axial ridges, lack obvious punctae, and belong in the group of epitoniids usually assigned to *Acrilla*. The large specimen in M.171153 is particularly similar in size and shape, but has lightly angled early spire whorls not seen in *O. flemingi* n. sp. A Grebneff (Dunedin pers. comm.) pointed out similarities to *O. leeana* (Verrill, 1883) and *O. (Cylindriscala) andrewsii* (Verrill, 1882) (Abbott 1974, figs. 1211, 1214) from the NE United States. None of the Recent Australian species of *Opalia* is similar; all have much fewer, lower, more widely spaced, less sharply defined axial costae, weaker spiral sculpture, and a more prominent peribasal ridge. The regularly pitted surface of *Opalia flemingi* n. sp. cannot be a preservational artefact, so the new species is not related to such taxa as *Acrilla acuminata* (G. B. Sowerby II, 1844) (Wilson 1993, fig. p. 274; Indo-West Pacific to Keppell Bay, Queensland). Another Australian Recent species that resembles *O. flemingi* n. sp. quite closely is *Propescala valida* (Verco, 1906) (Verco 1906a:147, pl. 4, fig. 7; Cotton 1956:1, fig. 19), which, however, is much smaller (H 7 mm). A final Australian(?) species resembling the new species is '*Scalaria*' *distincta* E. A. Smith (1891:441, pl. 35, fig. 15; Iredale 1936:305, pl. 22, fig. 29), which Iredale included in the 'not rediscovered' list of possible Atlantic species from the muddled HMS '*Challenger*' Station 164B, supposedly dredged off Sydney, New South Wales, in 750 m. '*Scalaria*' *distincta* is particularly similar to *O. flemingi*, but has regular varices in the centre of the venter of each whorl that are not present on *O. flemingi* n. sp., and appears to be related to *Acrilla acuminata*. Whatever its relationships, *Opalia flemingi* n. sp. is a very distinctive addition to the New Zealand epitoniid fauna.

Etymology. It is a pleasure to name this finest of the new Wanganui Plio–Pleistocene molluscs in honour of Charles Fleming KBE FRS, the leading New Zealand paleontologist of the late twentieth century. Fleming's seminal work on the stratigraphy and paleontology of Wanganui Basin underpins all later research on this magnificent succession.

Subgenus **Nodiscala** de Boury, 1890

Nodiscala de Boury 1890:12. Type species (by original designation): *Scalaria bicarinata* G. B. Sowerby II, 1844, Recent, tropical Indo-West Pacific (Hawaii and the Red Sea to South Africa; Weil et al. 1999:106, fig. 339, as *Opalia (Nodiscala) bicarinata*).

Remarks. The taxonomy of this group of Epitoniidae is complex and undecided even at the generic level, and I use *Nodiscala* here as a subgenus of *Opalia* (1) to underscore the need for a reassessment of these epitoniid genera, (2) because the genera and subgenera in this group, discussed below, all have punctate teleoconchs resembling that of *Opalia*, and (3) because the *Nodiscala* species illustrated by Cossmann (1912, pl. 4, figs. 5, 6; pl. 5, figs. 23, 25–27; pl. 6, figs. 9, 15, 20, 24) most closely resemble the New Zealand species under consideration here, *O. (Nodiscala) nympha* (Hutton, 1885), *O. (Nodiscala) ahiparana* (Powell, 1930), *O. (Nodiscala) zelandica* (Finlay, 1930) and *O. (Nodiscala) maxwelli* (Finlay, 1930).

These species (at least *Opalia nympha* and *O. maxwelli*, in most previous classifications) have been placed by most previous authors in *Funiscala* de Boury (1891:205; type species [as reidentified by de Boury 1911:219]: *Scalaria speyeriana* Sacco, 1891, Oligocene, Italy). The type species originally designated for *Funiscala* by de Boury (1891:205) was *Scalaria pusilla* Philippi, 1844 (Oligocene or Miocene, N Germany) but Cossmann (1912:86, footnote 2) stated that the type species was misidentified. Cossmann's treatment followed that of de Boury (1911:219), who discussed the problem of *Funiscala* in more detail. He concluded that in at least two earlier publications he had misidentified the shell he now called *Scalaria speyeriana* Sacco as *S. pusilla*. *S. speyeriana* then, in his opinion, became the true type species of *Funiscala*, whereas he now regarded *S. pusilla* as a species of *Bifidoscala*. The situation is that covered by ICZN Article 70.3. As de Boury's (1911) identification of the type species of *Funiscala* has been accepted by subsequent authors, the type species is here fixed (under Article 70.3) as *Scalaria speyeriana* Sacco, 1891, misidentified as *Scalaria pusilla* Philippi, 1841 in the original designation by de Boury (1891:205). De Boury (1917:50) made this case still more complex: 'unfortunately, *Funiscala* must be called *Rugatiscala*'. He repeated the type-species problem and considered that the type species of *Rugatiscala* is *Scala levesquei* de Boury, 1887 (Cossmann 1912, pl. 3, fig. 43). He also stated (de Boury 1917:51) that the main distinguishing character of *Bifidoscala* is the presence of a single row of punctae in the [spiral] furrows, whereas *Nodiscala* species illustrated by Cossmann (1912, pl. 5, figs. 23, 25–27; pl. 6, figs. 9, 15, 20, 24) are more prominently and coarsely punctuate, and species assigned to *Funiscala* by Cossmann (1912:5, figs. 8, 9, 24) lack punctae altogether. The presence or absence and degree of punctation in various species of *Opalia* (sensu lato) varies greatly, and it is as difficult to use this character as all others in Epitoniidae. At present the name *Funiscala* (and possibly also *Bifidoscala* Cossmann, 1888, *Rugatiscala* de Boury, 1913, and several others) is regarded as a probable synonym of *Nodiscala*, although it is unclear whether *Nodiscala* really can be maintained as separate from *Opalia* and/or *Pliciscala* in the long run.

Opalia (Nodiscala) nympha (Hutton, 1885)
(Fig. 4A, B, D–F)

Scalaria nympha Hutton 1885a:321; Hutton 1893:67, pl. 8, fig. 71.
Epitonium nympha. Suter 1915:13.
Funiscala nympha. Finlay 1930b:233; Laws 1940:53; Fleming 1966:49; Beu & Maxwell 1990:411.
Funiscala (?) *nympha*. Maxwell 2009:244.
Not *Epitonium (Confusiscala) nympha*. Suter 1917:85 (Miocene).

Type material. *Scalaria nympha*, two syntypes Canterbury Museum M-3098, M-3099 (Bradshaw et al. 1992:33), from Petane, Hawke's Bay, Nukumaruan, that is, Tangoio Limestone or Mairau Mudstone, high in Petane Group, hillside N of Esk River and junction of Highways 3 and 5, 30 km N of Napier.

Other material examined. **Waipipian:** a record in FRED of '*Epitonium* aff. *nympha*' from GS876, Q21/f6493, Tangahoe Formation, mouth of Waihi Stream, Waihi Beach, Hawera, S Taranaki (identification published by Suter 1921:25; as '*Epitonium* aff. *(Confusiscala) nympha* (Hutt)') is not matched by a specimen in the GNS collection. **Mangapanian:** Mangapani Shell Conglomerate, Mangapani Bluff, Mangapunipuni Stream, Waitotara valley, Mangapanian (late Pliocene) (Laws 1940:53; Fleming 1953:119; recorded from GS4227, R21/f8478; but again specimen not found in GNS). **Nukumaruan:** otherwise recorded only from Nukumaruan rocks, although not recorded from Wanganui Basin Nukumaruan rocks by Fleming (1953). The single specimen attributed to this species in the GNS reference collection is from GS6985 (T24/f6489, shelly conglomerate at Ashhurst Domain, cliff 600 m W of railway bridge over Manawatu River, E of Palmerston North; Fig. 4E, F).

Distribution. (Waipipian?); Mangapanian–Nukumaruan, Wanganui Basin and Hawke's Bay.

Dimensions. Syntypes, M-3098: H (incomplete) 6.1, D 2.6 mm; M-3099: H (incomplete) 6.2, D 2.9 mm; GS6985: H 7.9, D 2.8 mm.

Remarks. *Opalia (Nodiscala) nympha* is a small species (H 6–8 mm) with a teleoconch of at least seven whorls (the teleoconch spire apex and protoconch are not preserved on the material examined; naturally decollate?) with

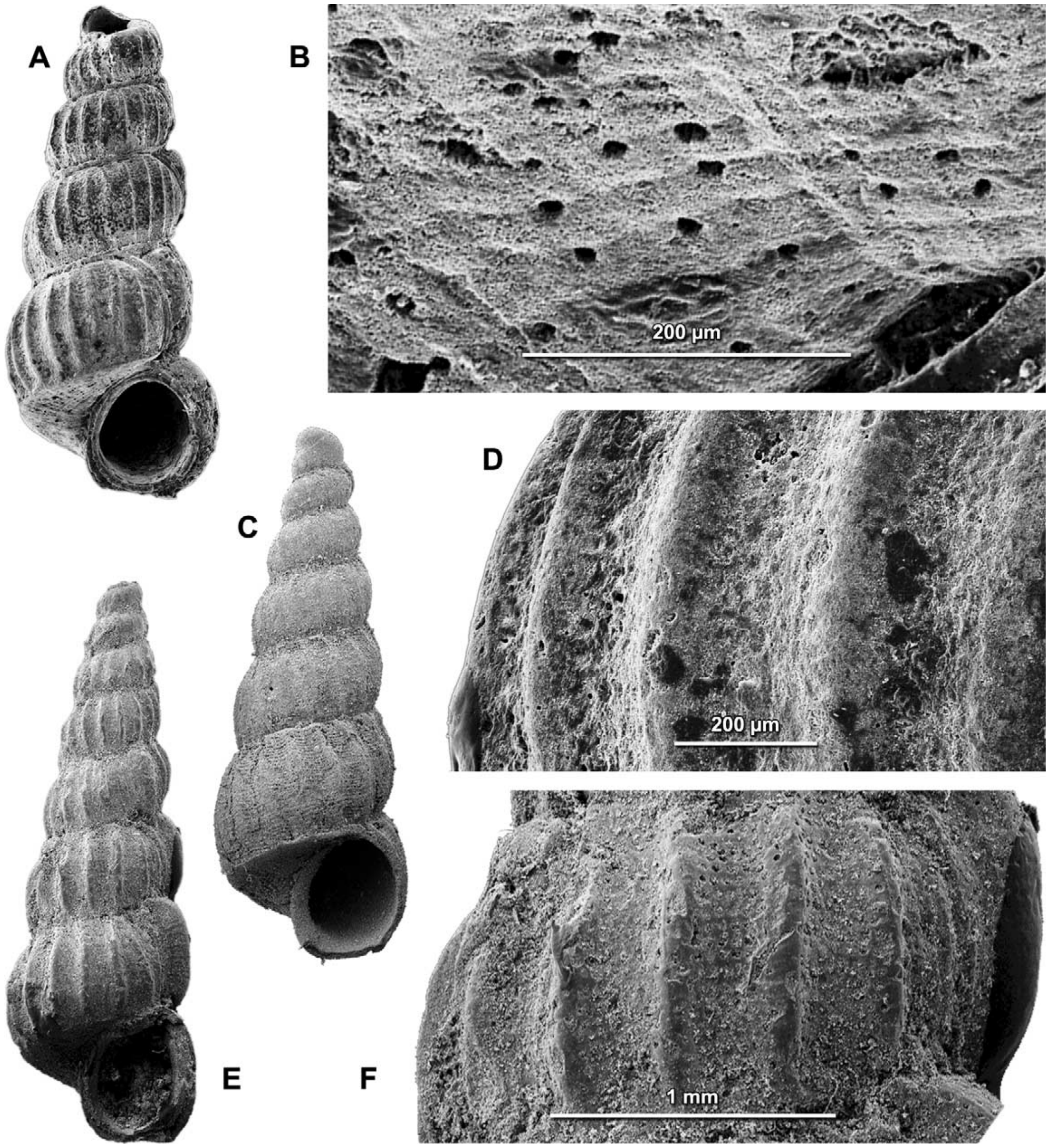

Figure 4 (A,B,D–F) *Opalia (Nodiscala) nympha* (Hutton), Nukumaruan, SEM; A,B,D, syntype, CMC M3098, "Petane", Hawke's Bay; A, incomplete specimen, height 5.8 mm; B, punctae on base of A; D, surface of penultimate whorl; E,F, GS6895, T24/f6489, Ashurst Domain, E of Palmerston North; E, whole specimen, height 7.9 mm; F, surface of penultimate whorl. (C) *Opalia (Nodiscala) maxwelli* (Finlay), RM4020, Recent, Portobello sta. Mu68–45, c. 130–200 m, near head of Papanui Canyon, off Otago Peninsula, RV "*Munida*"; SEM, height 5.0 mm.

14–15 wide, prominent, essentially smooth axial costae per whorl. The costae have narrow crests, concave sides and wide edges, merging imperceptibly into the intercostal intervals, which are each about twice the width of one costa. The intercostal intervals appear under the light microscope to be crossed by many even, fine, low, closely spaced spiral lirae, but under SEM examination these are seen to be vague, partially obliterated, irregular ridges, possibly resulting from partial abrasion of a former intriticalx. A prominent peribasal spiral rib marks off the apparently smooth, flat basal disc, and high, weakly spirally lirate varices are present at roughly one whorl intervals down the entire spire. The apertural lips are wide, double (that is, grooved), smooth on the inner edge, but raised into a prominent, spirally lirate varix on the exterior, and the inner lip is margined by a narrow fasciole. SEM examination showed that the surface between the axial ridges bears irregular, small, subcircular pits, and the basal surface inside the peribasal cord is coarsely and regularly pitted.

The most nearly similar of Recent species is *Opalia maxwelli* (Powell 1979:252, fig. 58.3), which has very similar axial sculpture but has a more obviously concave base and less prominent varices than *O. nympha* (Fig. 4C). Its surface also bears pits in the base, inside the peribasal ridge, as in *O. nympha*. SEM examination also showed that Recent specimens bear a finely reticulate intritacalx, and the unusual, irregularly ridged surface of both fossil specimens of *O. nympha* examined possibly results from the abrasion of an intritacalx. *O. ahiparana* (Powell 1979:262, fig. 58.1) has less prominent axial costae, two more prominent peribasal cords (one in the usual peripheral position, the other below it on the base) bearing large, rounded nodules that are not present on any other New Zealand Epitoniidae, and lacks obvious varices before the terminal one, which is more prominent than in *O. nympha*. The final species needing comparison, *O. zelandica* (Powell 1979:252, fig. 58.2) is more *Epitonium*-like than *O. nympha*, with lower, narrower and more numerous axial costae, and no peribasal spiral cord; 'the labial varix is heavy, and previous varices are prominent on the spire at ¾ whorl intervals' (Powell 1979:252).

Opalia (Nodiscala) nympha has remained little-known since it was described, and is illustrated here with the aim of allowing wider recognition of the species, and so assessment of its possible utility as a Mangapanian–Nukumaruan index species. As noted above, its generic position also is unclear. *O. nympha* resembles the specimen illustrated as *Funiscala levesquei* (de Boury, 1887) (middle Eocene [Cuisian], Paris Basin) by Cossmann (1912, pl. 3, fig. 43). The two species have similarly prominent axial sculpture, interrupted at irregular intervals by more prominent varices, a correspondingly thickened, varicate outer lip, a similar rather restricted basal disc, and similar weak spiral sculpture. If *F. levesquei* were a typical *Funiscala* species, the generic position of *O. nympha* would be clear. However, in their catalogue of Paris Basin Paleogene molluscs, Le Renard & Pacaud (1995:93) referred *F. levesquei* to *Opalia (Rugatiscala)* de Boury, 1913, proposed after Cossmann (1912) was published. This suggests that *Rugatiscala* de Boury (1913:176–177; type species *Scalaria levesquei*) might be a more suitable position. However, the better illustration of a complete specimen of *R. levesquei* by de Boury (1913, pl. 8, fig. 6) demonstrates that this is a more typically *Opalia*-like shell than the incomplete, more finely sculptured (evidently distinct) one illustrated by Cossmann (1912, pl. 3, fig. 43), having coarser axial and spiral sculpture than in the earlier illustration and a series of regular varices almost aligned down the ventral face of the teleoconch. The situation is further confused by the characters of the Recent species *O. maxwelli*, which lacks the finely reticulate surface sculpture (an intritacalx?) of species referred to *Funiscala* by Cossmann (1912), and is much closer in appearance to species Cossmann referred to *Nodiscala* de Boury, 1890. Finlay (1930b:232, pl. 44, fig. 35) proposed *Nodiscala zelandica* at the same time as *Funiscala maxwelli*, and evidently thought them not to be congeneric because of the more prominent axial ridges of *O. maxwelli*. As noted above, a position in *O. (Nodiscala)* is adopted for all the New Zealand species discussed here, but this group is urgently in need of major revision. The major generic overhaul of all epitoniids suggested by the excellent new research by Gittenberger & Gittenberger (2005) and Gittenberger et al. (2006) indicates that none of the species considered here is likely to be placed in its phylogenetically correct genus at present, but a huge amount of further research is required before the genera are resolved.

Genus ***Cirsotrema*** Mörch, 1853

Cirsotrema Mörch 1853:49. Type species (by monotypy): *Scalaria varicosa* Lamarck, 1822, Recent, Indo-West Pacific (Wilson 1993:274, pl. 44, fig. 1a,b).

Caloscala Tate 1885:3. Type species (by subsequent designation, Tate 1890:230): *Caloscala mariae* Tate, 1885, late Eocene, Tortachilla Limestone, Aldinga, South Australia (synonym of *Cirsotrema* according to de Boury [1887:40] and Tate [1890:230]).

Pseudostenorhytis Sacco 1891:72. Type species (by monotypy): *Cirsotrema (Pseudostenorhytis) stenorhytoides* Sacco, 1891, late Miocene, Italy (synonym according to Cossmann 1912:51).

Elegantiscala de Boury 1911:216. Type species (by original designation): *Scalaria elegantissma* Deshayes, 1861, Eocene, Paris Basin (synonym according to Cossmann [1912:51], but not according to de Boury [1917:39]).

Cirsotremopsis Thiele 1928:92. Type species (by monotypy): *Scalaria cochlea* G. B. Sowerby II, 1844, Recent, Mediterranean Sea to Angola (Weil et al. 1999:32, fig. 790) (synonym according to Clench & Turner 1950:226).

Dannevigena Iredale 1936:303. Type species (by original designation): *Dannevigena martyr* Iredale, 1936, Recent, southeastern Australia (**new synonym**).

Remarks. The New Zealand Pliocene–Recent species *Scalaria zelebori* Dunker, 1866 has usually been assigned to *Cirsotrema*, but its generic position has been debated recently. Weil et al. (1999:128, figs. 399, 400) placed *C. zelebori* in *Boreoscala* Kobelt, 1902 (type species: *Scalaria greenlandica* Perry, 1811, Recent, North Atlantic–North Pacific), and this has been followed by a few New Zealand authors (Morley 2004:101). The New Zealand fossil and Recent species are definitely less elaborately sculptured than the more extreme Recent tropical species of *Cirsotrema*. However, the rather different nature of the wide, simple, closely spaced spiral cords, lack of a basal disc, and wide, low, smooth, convex-crested axial ridges of *Boreoscala greenlandica* (see Bouchet & Warén 1986:518, figs. 1210–1213), compared with the complex orders of spiral cords and threads and complex, multilamellate varices in New Zealand species assigned to *Cirsotrema*, makes a position in *Boreoscala* unlikely to be correct. The original assignment of Australasian fossil species to *Cirsotrema* was made by the well-known epitoniid specialist de Boury (1887:40), who regarded Tate's Adelaide Eocene species *Caloscala mariae* Tate, 1885 and the other species included in *Caloscala* by Tate, *Scalaria lyrata* Zittel, 1864 (Oligocene–Miocene, New Zealand) as species of *Cirsotrema*. As de Boury's (1887) work is not widely available, his brief statement is quoted in full here: 'The subgenus *Caloscala* has been established by M. Ralph Tate for *C. lyrata* (Zittel) and *C. mariae*, Ralph Tate. The author has had the generosity to send us a very beautiful example of this latter species, which has many similarities ["beaucoup de rapports"] with *S. acuta*, Sow. We have demonstrated that this species cannot be separated from the true *Cirsotrema*' (free translation from de Boury 1887:40). Later, de Boury (1911:215) restated this case: 'I persist in thinking that there is no place to conserve this subgenus [*Caloscala*], which appears to include shells belonging to *Cirsotrema* Mörch. These forms cannot be, as I had thought for a while, confounded with our subgenus *Coroniscala*, which differs completely from *Cirsotrema* by its ribs, which are not at all crisped and frilled like those of the last subgenus' [*Cirsotrema*]. The illustration of *C. mariae* by Tate (1893, pl. 12, fig. 2) shows a shell very similar to such large, prominently sculptured New Zealand fossil species as *C. lyratum* (Zittel, 1864) and the Argentinean fossil species *C. rugulosum* (G. B. Sowerby I, 1846) (Griffin & Nielsen 2008:305, pl. 23, figs. 8, 9). Cossmann (1912:52) and de Boury (1913:170) also expressly included *C. zelebori* in *Cirsotrema*. The Nukumaruan–Castlecliffian specimens reported below, with thicker varices than *C. zelebori*, are intermediate in many characters between *C. zelebori* and the large Oligocene–Miocene species such as *C. lyratum* and *C. caelicola* Finlay, 1926, helping confirm a position in *Cirsotrema* for *C. zelebori*. On the other hand, it should be noted that Cossmann, 'avec la collaboration de M. de Boury' (1912, pl. 3, figs. 5, 6), placed the large Patagonian Oligocene–early Miocene species here identified as *Cirsotrema rugulosum* (G. B. Sowerby I, 1846) in genus *Boreoscala*, significantly confusing the generic position, as these South American shells are exceedingly similar to the large New Zealand fossils of the same age. The large Recent southern Australian species *Dannevigena martyr* Iredale (1936:303, pl. 22, fig. 25; Wilson 1993:275, pl. 44, fig. 4; named for the drowned captain of FIS '*Endeavour*', HC Dannevig; Verco 1935, pl. 16) is particularly closely similar to the large New Zealand and South American Oligocene–Miocene species assigned to *Cirsotrema*, although its spiral sculpture ('faintly…striate'; Wilson 1993:275) is weaker than on most fossil species, other than *C. gagei* Maxwell (1978:36, fig. 44). There is little doubt that *C. martyr* is a Recent species of the same clade as the Australian, New Zealand and South American fossil species, that is, *Dannevigena* is a further synonym of *Caloscala* and *Cirsotrema*. It seems likely that more of the greatly over-split subgenera proposed in Epitoniidae by de Boury should be regarded as synonyms of *Cirsotrema*. If the very similar New Zealand, Australian and South American fossil species usually assigned to *Cirsotrema* should require a distinct genus or subgenus, *Caloscala* Tate, 1885 is available for them. Like Recent tropical *Cirsotrema* species, but few other epitoniids, the fossils have a calcitic teleoconch and preserve well in limestone faunas from which the aragonitic molluscs have been dissolved. Epitoniidae is perhaps the most obvious group crying out for resolution by molecular techniques, because of its poorly understood phylogeny, staggering diversity and few, intergrading taxonomic characters, and a position in *Cirsotrema* should be maintained for *C. zelebori* and similar species until molecular studies can be carried out to confirm or deny this position.

Tate (1885:3) included two species in *Caloscala*, but did not designate a type species. I am grateful to TA Darragh (Museum Victoria pers. comm. September 2005) for pointing out that Tate (1890:230) subsequently designated the type species himself, with the statement (under the heading *Scalaria (Cirsotrema) mariae* Tate) that 'This species is the type of my subgenus *Caloscala*…'.

Cirsotrema zelebori (Dunker, 1866) (Fig. 5A–E)

Scalaria zelebori Dunker in Dunker & Zelebor 1866:912; Hutton 1873a:21; Hutton 1880:69; Tryon 1887:78, pl. 15, fig. 75; Hutton 1893:66; Clessin 1897:50, pl. 13, fig. 5; Suter in Hutton 1904:80; Suter 1905a:72; Moss 1908:30, pl. 7, fig. 17.

Scala (Opalia?) zelebori. Frauenfeld 1867:7, pl. 1, fig. 6.

Scalaria (Opalia) zelebori. Martens 1873:29.

Scalaria intermedia Hutton 1873b:10.

Scalaria reevei Clessin 1897:63, pl. 15, fig. 9; Suter 1899a:54.

Scalaria (Opalia) zelebori. Suter 1899a:54.

Scala zelebori. Verco 1906a:145 (South Australian record dismissed).

Scala (Cirsotrema) huttoni de Boury in Cossmann 1912:52 (unnecessary new name for

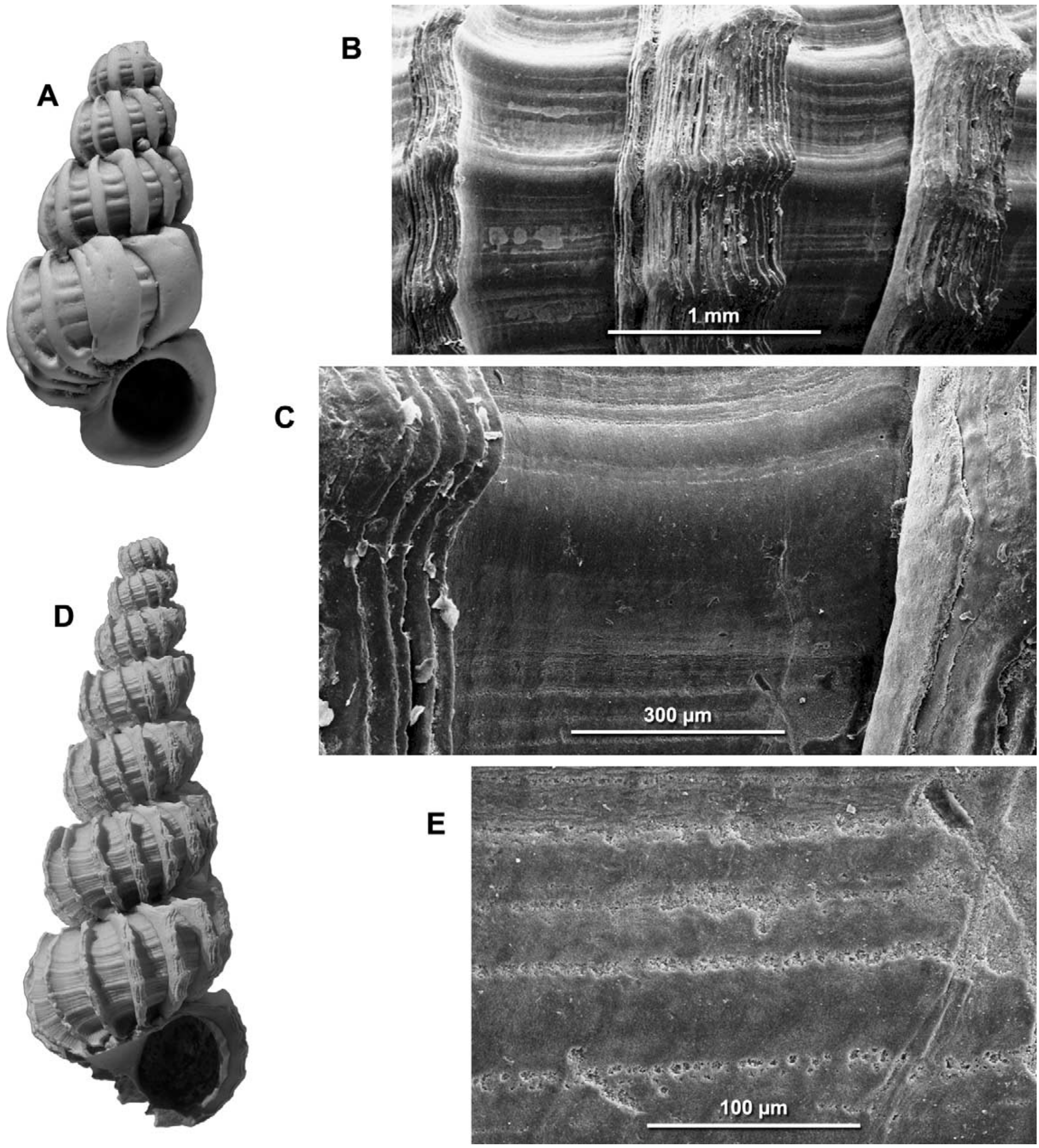

Figure 5 *Cirsotrema zelebori* (Dunker), Wanganui fossils. (A) GS15338, S22/f0164, *Maoricrypta*-dominated shellbed, Turakina Valley Road, E of Wanganui; early Castlecliffian, c. OIS 43–41; short, coarsely sculptured, abraded specimen, possibly an unnamed species; height 14.9 mm. (B,C,E) *C. zelebori*, GS4003, R22/f7394, Landguard Sand (Haweran, OIS 9), Landguard Bluff, Wanganui, SEM; B, surface of penultimate whorl, with multilamellate varices; C, centre right area of B enlarged; E, lower right area of C enlarged, showing micropunctae. (D) *C. zelebori*, holotype of *Scalaria intermedia* Hutton, TM8285, Tainui Shellbed (Castlecliffian, OIS 13), ''Shakespeare Cliff'', Wanganui; height 33.2 mm.

Scalaria intermedia Hutton, 1873, not a junior homonym).

Scala (Cirsotrema) zelebori. de Boury 1913:170, pl. 8, fig. 2.

Epitonium (Opalia) zelebori. Suter 1913:322, pl. 46, fig. 8 (emended to *Epitonium (Cirsotrema)* in corrigenda).

Epitonium zelebori. Bucknill 1924:58, pl. 7, fig. 12.

Cirsotrema zelebori. Finlay 1928:246; Laws 1936:111; Powell 1937:75, pl. 8, fig. 25; Powell 1946a:77, pl. 8, fig. 25; Powell 1958a:98, pl. 8, fig. 25; Powell 1962:90, pl. 8, fig. 25; Fleming 1966:49; Powell 1976a:107, pl. 15, fig. 15; Powell 1979:252, pl. 48, fig. 17; Beu & Maxwell 1990:411; Spencer & Willan 1996:24; Nützel 1998:93, pl. 13I–K, O–Q (showing punctate sculpture, pl. 13Q).

Cirsotrema (Cirsotrema) zelebori. Spencer et al. 2009:205; Maxwell 2009:244.

Boreoscala zelebori. Weil et al. 1999:128, fig. 399, 400; Morley 2004:101.

Type material. The type material of *Scalaria zelebori* was stated by Suter (1913:322) to be in NHMW. Anita Eschner (NHMW pers. comm. 5 October 2007) reported that 11 syntypes of *Scalaria zelebori* are present: NHMW 89781 (one syntype, labelled as 'Dunker's original'), NHMW 89782 (nine syntypes), and NHMW 89783 (one syntype, from J Zelebor's collection), all from 'New Zealand' (not seen). The type material of *Scalaria reevei* was stated by Clessin (1897:63) to be in 'Mus. Stuttgt.' [Stuttgart], not seen. *Scalaria intermedia*, holotype TM8285 (Fig. 5D), from Shakespeare Cliff, Wanganui; almost certainly from Tainui Shellbed (OIS 13).

Cossmann (1912:52) listed the name '*Scalaria huttoni* de B. (=*Sc. intermedia* Hutton)', so presumably Cossmann and de Boury thought that *S. intermedia* is a junior homonym, but did not state the earlier usage, and I have been unable to find one. De Boury (1913) returned to the name *Scalaria intermedia* Hutton, so apparently it is not preoccupied. This is unimportant, as *S. intermedia* is clearly a synonym of *C. zelebori*.

Other material examined. Not listed; widespread and not uncommon. The earliest record of *Cirsotrema zelebori* seems to be from Kaawa Creek, SW Auckland, Opoitian (Laws 1936:111). It occurs at most younger fossil localities throughout New Zealand, including almost all formations in Wanganui Basin. I have seen the apparently distinct Turakina valley species (OIS 43–41?; see below) only from the one early Castlecliffian shellbed. Recent specimens of *C. zelebori* occur throughout New Zealand, usually found washing ashore on sandy beaches; particularly common on Orewa Beach, Northland. Its host cnidarian(s) have not been identified.

Distribution. Opoitian (early Pliocene) to Recent, throughout New Zealand.

Dimensions. 'Type' of *Scalaria zelebori*: H 24, D 8 mm (Suter 1913:322); *Scalaria intermedia*, holotype: H 33.2 (incomplete, originally ca 36), D 12.4 mm; Recent, RM4759, Waihi Beach, Bay of Plenty: H 27.2, D 9.6 mm; H 26.3, D 9.6 mm; RM319, Mount Maunganui, Bay of Plenty: H (incomplete) 27.0, D 10.2 mm; H 26.2, D 9.5 mm; NMNZ M.18724, Waihi Beach, Bay of Plenty: H 30.4, D 11.5 mm; NMNZ M.277711, beach, Maioro, SW of Waiuku, SW Auckland: H 29.8, D 10.6 mm; H 28.3, D 11.1 mm.

Remarks. Suter (1899a:54) and de Boury (1913:170) attributed the name *Scalaria zelebori* to Frauenfeld, as Frauenfeld (1867:7) seems to have considered that he described the species first. However, the name was first published by Dunker (in Dunker & Zelebor 1866:912), as Suter (1905a:72) later pointed out.

Fleming (1953:144) listed '*Cirsotrema* n. sp. aff. *zelebori* (Dunk.)' in the fauna from Nukumaru Brown Sand in the Nukumaru Beach coastal section, from GS4117, R22/f6437, 'unlocalised as to member'. Reconsideration of this record, among the many other 'n. sp.' records of molluscs by Fleming (1953), raised the question of the status of *Scalaria intermedia* Hutton, 1873, and more generally the taxonomy of New Zealand late Neogene species of *Cirsotrema*.

The holotype of *Scalaria intermedia* has not been illustrated previously, and an illustration therefore is provided here (Fig. 5D) as an example of a typical, large specimen of *C. zelebori*. The question of its status was considered by de Boury (1913:170–171), who examined a 'magnifique' specimen identified as *C. intermedia*, 27 mm high, which MNHN acquired from M Bonnet (a fossil, and so presumably from Castlecliff, Wanganui; de Boury did not state a locality, but Cossmann [1912:52] cited Wanganui). De Boury thought *C. intermedia* distinct from *C. zelebori*, although he admitted that he had compared *Scala intermedia* with only a few abraded Recent specimens of *C. zelebori*, and that comparison with better specimens was desirable. The holotype is merely a large specimen of *C. zelebori*. The spiral sculpture, the number and position of the complex axial lamellae and the ridges and nodules formed on them by the spiral cords, the peribasal cord, and the aperture, including the fasciolar ridge alongside the inner lip, all agree exactly. The only slight difference, also pointed out by de Boury (apart from the slightly larger size of *C. intermedia* at the same number of whorls—27 vs 24 mm), is the slightly higher and thinner axial lamellae of the fossil. However, the varices are compound axial ridges as in Recent material, and the holotype is closely comparable with many Recent specimens. The specimen identified by Fleming (1953:144) as '*C.* n. sp. aff. *zelebori*' (GS4117, R22/f6437) also agrees in almost all characters with Recent specimens, and again has slightly higher and thinner axial lamellae than most Recent specimens. There is little doubt that this difference is trivial.

Nützel (1998:93, pl. 13I–K,O–Q) illustrated specimens of *Cirsotrema zelebori*, including SEM enlargements showing the micropunctate sculpture. The very small punctae occur in spiral rows in the interspaces of the spiral cords (Fig. 5C,E), although Nützel (1998:93) noted that the punctae are not visible on all specimens. SEM examination showed that the punctae are much smaller and sparser than those of *Opalia* species, seem to be at least partially revealed by corrosion of the shell surface, and vary in visibility over the surface of one specimen. This newly revealed character requires comparison in a range of other New Zealand material to determine whether it is present, but is likely to be present on all *Cirsotrema* species.

Two specimens from a *Maoricrypta*-dominated shellbed exposed on Turakina Valley Road, east of Wanganui (Fig. 5A; GS15338, S22/f0164, S22/096385, ca 600 m S of Mangara Stream bridge and ca 200 m N of Glenroy Station; early Castlecliffian, ca OIS 43–41) belong in a species distinct from *Cirsotrema zelebori*. They are similar in appearance to a moderate-sized specimen of *C. zelebori*, but have a slightly wider spire angle, very wide, almost smooth axial ridges (heavy varices), up to five times as thick as on any specimens of *C. zelebori* I have seen, and a very wide, prominent fasciolar ridge alongside the inner lip. However, it is unclear to what extent the smoothness of the outer surfaces of the lamellae is due to abrasion. If it is naturally smooth, these specimens conform to the description provided by A Grebneff (Otago Uuniversity pers. comm. May 2008) of *Cirsotrema forresti* Dell (1956b:40, figs. 33, 47, 48), originally proposed in *C. (Tioria)* Marwick, 1928. Grebneff has concluded that the *Cirsotrema* species in deep, cool water in southern New Zealand is *C. forresti*, with a slightly lower spire than in *C. zelebori*, smooth rather than spirally ridged variceal surfaces, a more prominent basal cord and fasciole than in *C. zelebori*, and in many specimens a nodule or spine on the shoulder (adapical extremity) of each axial ridge. It seems possible that this species occurs at Wanganui. However, it is likely that the Turakina Valley Road specimens are smooth because they have been abraded during reworking from Nukumaruan or older rocks, and the wider varices suggest that they are a species distinct from both *C. zelebori* and *C. forresti*. A few other, relatively large specimens of *C. zelebori* from Nukumaruan localities (GS4259, R22/f6489, muddy sandstone below Kuranui Limestone, Waitotara desert [Fleming 1953:130]; Nukumaru Limestone, bluff alongside Nukumaru Stream on New Plymouth-Wanganui highway, in GNS) include specimens with much thicker axial ridges than any Recent specimens seen, but are not as extreme as the Turakina Valley Road early Castlecliffian ones. The latter probably represent an unnamed species, but better material is required to confirm their distinctive characters. An attempt at re-collection of this material did not reveal any further specimens.

Cirsotrema zelebori is also similar to *Epitonium (Boreoscala) blainei* Clench & Turner (1953:361, pl. 180), from Florida (A Grebneff pers. comm. May 2008). The illustrations by Clench & Turner (1953) show a specimen with thicker, slightly more fluted axial ridges and coarser spiral cords than *C. zelebori*, although otherwise similar in size, shape and the presence of a peribasal spiral cord. Clench & Turner (1953:362) mentioned the similarity of *E. blainei* to '*E. magellanicum* Philippi [1845] from Patagonia'. *C. magellanicum* is another species of the same group as *C. zelebori*, but has weaker spiral sculpture and a slightly lower spire than *C. zelebori*, and is possibly descended from the Patagonian fossil species related to *C. rugulosum*.

Clade Neogastropoda

Family Buccinulidae

Remarks. I follow Harasewych & Kantor (2004) in recognizing on anatomical grounds several of the Southern Hemisphere families proposed by Powell (1929). In particular, most New Zealand 'buccinids' probably belong in Buccinulidae Powell, 1929 whereas, if '*Buccinulum*' *pangoides* Beu, 1973 is correctly referred to *Euthria* (as is suggested below), it seems likely to be a member of the mostly Northern Hemisphere family Buccinidae. It should be noted, however, that Hayashi (2005) did not distinguish Buccinulidae from a monophyletic Buccinidae on the grounds of molecular phylogeny (determined from complete 16S rRNA gene sequences). The family position of *Iredalula* has long been in doubt, and in recent years it has usually been referred to the Buccinidae (sensu lato), but following Ponder (1968b) and Beu & Maxwell (1987), it seems likely to be a member of the Colubrariidae, which was recognized as a family by Bouchet et al. (2005).

Genus ***Aeneator*** Finlay, 1926

Aeneator Finlay 1926b:414. Type species (by original designation): *Verconella marshalli* Murdoch, 1924, Pleistocene and Recent, New Zealand.

?Ellicea Finlay in Marwick 1928:432. Type species (by monotypy): *Siphonalia orbita* Hutton, 1873, Pliocene (and Recent?), New Zealand.

?*Pittella* Marwick 1928:486. Type species (by original designation): *Ellicea (Pittella) valida* Marwick, 1928, Pliocene, Pitt Island, Chatham Islands.

Remarks. Although it has been customary in recent years to treat *Ellicea* Finlay, 1928 as a synonym of *Aeneator* Finlay, 1926 (e.g. Powell 1979:201; Spencer & Willan, 1996:26; Spencer et al. 2009:208), their fossil records seem to indicate that they had distinct times of origin in New Zealand and, therefore, possibly different ancestors. *Ellicea* has the earlier first record (Tongaporutuan, early late Miocene; three bathyal species described) whereas *Aeneator huttoni* Finlay, 1930 (Kapitean, latest Miocene) is the earliest species recorded in *Aeneator* (sensu stricto) in New Zealand. Both are otherwise Pliocene to Recent (sub?)genera, at least in New Zealand. *Trophon succinctus*

Tenison Woods (1897:16, pl. 4, fig. 6, 6a) was referred to *Ellicea* by Darragh (1970:198) and Goudey (2006:32, figs. 6, 6a; 49, fig.1) and superficially resembles *Ellicea* species closely, especially *E. valida* (Marwick) (1928:486, fig. 130) from Waipipian (Pliocene) Whenuataru Tuff, Pitt Island, Chatham islands. However, TA Darragh (Museum Victoria pers. comm. 6 August 2010) informed me that *T. succinctus* belongs in *Dennantia* Tate, 1888. This removes an apparently anomalously shallow-water record of what is an entirely bathyal (sub)genus in New Zealand. At least three species living along the Chilean coast at present have been assigned to *Aeneator* (McLean & Andrade 1982:12-15; Osorio & Romajo 2007) and one referred to *A. (Ellicea)* (*A. loisae* Rehder 1971:593, figs. 7, 8). Most of these species would be better referred to another (unnamed?) genus, but *A. loisae* does seem to be a species of *Ellicea*, suggesting the possibility that *Ellicea* was a Neogene migrant to New Zealand. The Seymour Island Eocene species referred to *Aeneator* by Stilwell & Zinsmeister (1990) seem more likely to belong in the Antarctic genus *Prosipho* Thiele, 1912 (Beu 2009). *Ellicea* and *Aeneator* also possibly had an earlier, unrecorded history in New Zealand. Further research is needed on these obviously similar generic groups, but it seems likely that they are not as closely related, in a phylogenetic sense, as the similar teleoconchs and radulae of Recent species seem to indicate. Once again, this is a question that will be resolved by DNA studies.

Aeneator (Aeneator) delicatulus Powell, 1929 (Fig. 6E, J)

Aeneator delicatula Powell 1929:91, pl. 4, fig. 75.

Aeneator delicatulus. Fleming 1966:59; Beu & Maxwell 1990:361, pl. 48o.

Aeneator (Aeneator) delicatulus. Maxwell 2009:244.

Type material. Aeneator delicatulus holotype AIM AK72003, from between Kai-Iwi and Okehu Streams, Castlecliff coastal section, Wanganui. Powell (1929:92) also recorded a 'large specimen' (here regarded as a paratype) in GS1163, R22/f6498, between Ototoka and Okehu Streams, Wanganui coastal section, but this specimen cannot be located in GNS.

Other material examined. **Castlecliffian:** the stratigraphically lowest record of *Aeneator delicatulus* is in Kaimatira Pumice Sand (OIS 25; Fleming 1953:188) in the Castlecliff coastal section. Other records are from Lower Kai-Iwi Siltstone (OIS 23), particularly common (Fleming 1953:192), Omapu Shellbed (OIS 23; Fleming 1953:194) and Lower Westmere Siltstone (OIS 21; Fleming 1953:196). Records from Kaikokopu Shell Grit (OIS 19; Fleming 1953:199, '*Aeneator* aff. *delicatula*') and Kupe Formation (OIS 17) in at least two collections (Fleming 1953:203, gastropod shellbed and *Mactra tristis* layer, '*A.* aff. *delicatula*') are based on small, abraded, equivocal specimens, possibly all reworked from older units. *A. delicatula* therefore essentially is limited to Kaimatira Pumice Sand and the siltstone beds of OIS 27–21 in cycles exposed in the cliffs NW and SE of Mowhanau Beach, Castlecliff. Specimens in the GNS reference collection are: Kai-Iwi, Castlecliff, CA Fleming collection (three); basal conglomerate member, Upper Okehu Siltstone (OIS 27), coast W of Kai-Iwi, Wanganui (GS4075, R22/f6406, one, slightly coarser spiral sculpture than others); upper part of Lower Kai-Iwi Siltstone (OIS 23), Castlecliff section (GS4061, R22/f6392, six); Omapu Shellbed (OIS 23), coast E of Omapu Stream, E of Mowhanau, Wanganui (GS4060, R22/f6391, and GS10909, R22/f6391A, eight); fossiliferous silt member, Lower Westmere Siltstone (Lower Westmere Shellbed; Abbott & Carter 1999; OIS 21), coast E of Mowhanau, Castlecliff (GS4058, R22/f6389, one).

Distribution. Early Castlecliffian, OIS 25–21; 19–17?, Wanganui Basin only; there are no

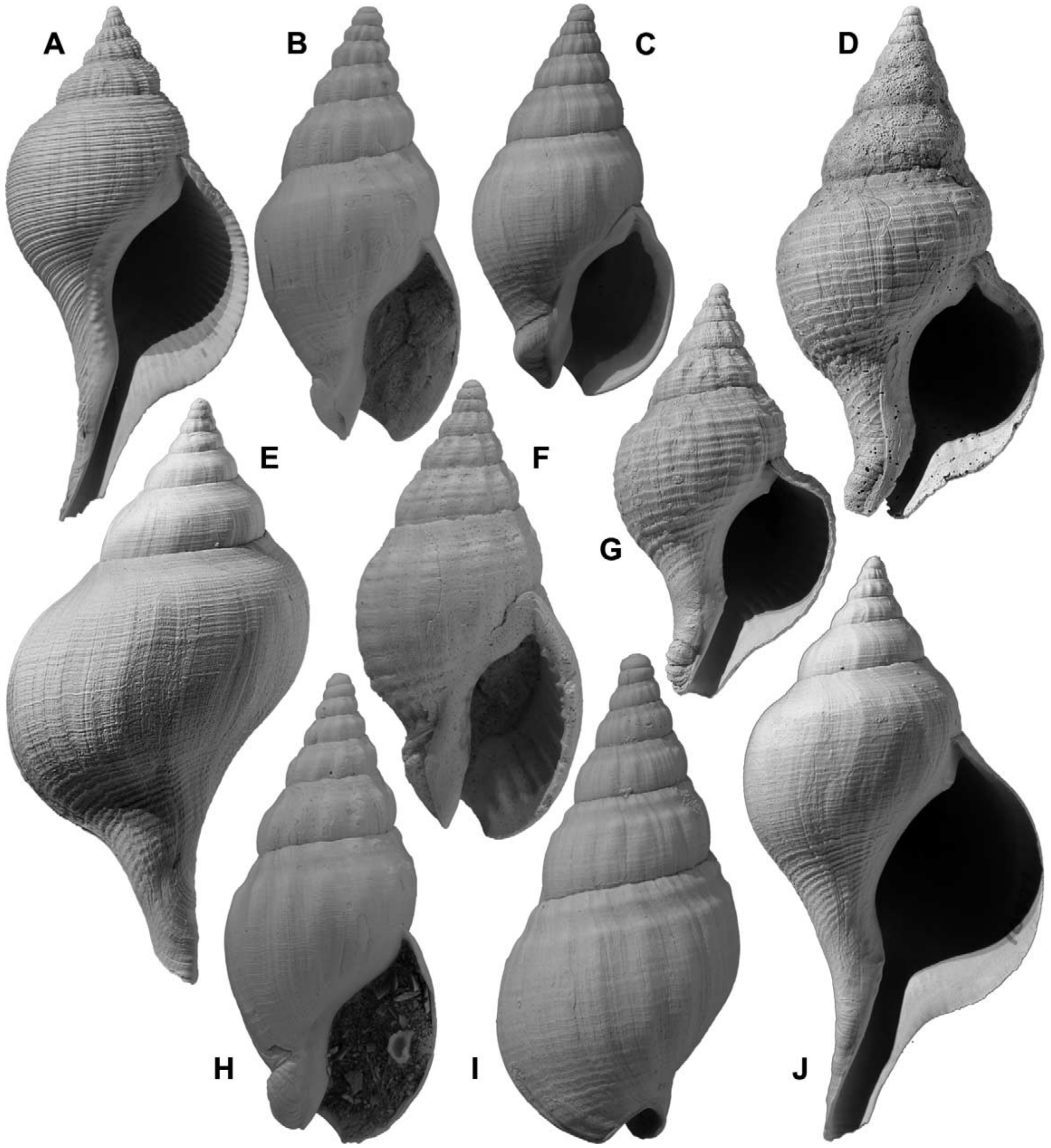

Figure 6 (A) *Aeneator (Aeneator) marshalli* (Murdoch), type species of *Aeneator* Finlay, 1926, lectotype, TM6837, "Castlecliff, blue sandy clays", Castlecliffian; height 71.7 mm. (B,C,F,H,I) *Cominella (Eucominia) elegantula* (Finlay); B, GS4013, R22/f6353, Tainui Shellbed (Castlecliffian, OIS 13), "the buttress", Castlecliff; height 30.5 mm; C,I, Recent, 2 specimens of "*marlboroughensis* form", NMNZ M.50340, RV "*Acheron*" stn. 76481, W of Makara, Cook Strait, 119–132 m; C, height 31.4 mm; I, height 34.5 mm; F, GS11465, V21/f6015A, Mairau Mudstone (late Nukumaruan), "the Watchman" hill, Napier; height 31.8 mm; H, GS4140, R22/f6450, Lower Castlecliff Shellbed (Castlecliffian, OIS 15), Castlecliff coast; height 33.1 mm. (D, G) *Buccinulum caudatum* Powell, 2 specimens, GS4060, R22/f6391, Omapu Shellbed (Castlecliffian, OIS 23), E of Mowhanau beach, Wanganui; D, height 48.1 mm; G, height 38.8 mm. (E,J) *Aeneator (Aeneator) delicatulus* Powell, GS10909, R22/f6319A, Omapu Shellbed (Castlecliffian, OIS 23), E of Mowhanau Beach, Wanganui; height 64.4 mm.

records from localities away from the excellent exposures in the coastal section.

Dimensions. *Aeneator delicatulus*, holotype: H 42, D 21.5 mm; large specimen in GS1163: H 68, D 31 mm (Powell 1929:92); GS10909, R22/f6319A, Omapu Shellbed: H 54.4, D 27.5 mm (Fig. 26A,B; specimen illustrated by Beu & Maxwell 1990, pl. 48o).

Remarks. *Aeneator delicatulus* is a very distinctive, small *Aeneator* species with a short spire, a long, very straight, left-inclined anterior siphonal canal, and consistently very fine, closely spaced, silky-looking spiral sculpture. The maximum size achieved is smaller and the sculpture of *A. delicatulus* is quite obviously much finer than that of the much more common and widespread, more long-ranging type species of the genus, *A. marshalli* (Murdoch, 1924) (Nukumaruan–Recent) and there is no doubt that these are distinct species. *A. marshalli* also is not found in siltstone beds, and seems essentially limited to Type B shellbeds (high-stand systems tract shellbeds) in the Wanganui succession. As Recent specimens occasionally wash ashore on ocean beaches (e.g. Ohope Beach, Whakatane), at least part of the range of *A. marshalli* is evidently further inshore than that formerly inhabited by *A. delicatulus*.

The type material of *Aeneator marshalli* includes four syntypes representing two possible species; two are the relatively large, short-spired species usually known by this name, whereas two are the smaller, more elongate, possibly distinct species *A. attenuatus* Powell, 1927. These all seem best regarded as syntypes despite Murdoch's (1924:159,160) statements 'Type in the Wanganui Museum' and 'A fossil specimen is chosen for the type...', as the illustrated specimen is not identified as 'type' in the caption, and no syntype is now labelled as 'type' or any other qualifying word or phrase. To ensure that this name is maintained in its accustomed usage, Murdoch's (1924) larger illustrated syntype is here designated the lectotype of *Verconella marshalli* Murdoch, 1924 (Fig. 6A; GNS TM6837, 'Castlecliff, blue sandy clays'). One of the other, taller syntypes was also illustrated by Murdoch (1924, pl. 10, figs. 2, 3) as '*Verconella marshalli* (juv.)'. Dimensions of lectotype: H 71.7, D 33.5 mm.

Genus ***Buccinulum*** Deshayes, 1830

Buccinulum Deshayes 1830:143. Type species (by subsequent designation, Iredale 1921:208): *Murex lineatus* Gmelin, 1791 (=*Buccinum linea* Martyn, 1784; valid, ICZN Opinion 479 1957), Pleistocene and Recent, New Zealand.

Evarne H Adams & A Adams 1853:79. Type species (by monotypy): *Buccinum linea* Martyn, 1784.

Euthrena Iredale 1918:34. Type species (by original designation): *Fusus vittatus* Quoy & Gaimard, 1833, Pleistocene and Recent, New Zealand.

Tasmeuthria Iredale 1925:262. Type species (by original designation): *Siphonalia clarkei* Tenison Woods, 1875, Recent, southeastern Australia.

Evarnula Finlay 1926b:415. Type species (by original designation): *Cominella striata* Hutton, 1875 (=*Buccinum linea* Martyn, 1784).

Chathamina Finlay 1928:252. Type species (by original designation): *Tritonidea fuscozonata* Suter, 1908, Recent, New Zealand.

Buccinulum caudatum Powell, 1929 (Fig. 6D, G)

Buccinulum (Evarnula) caudatum Powell 1929:75, pl. 2, fig. 50; Fleming 1966:60.
Buccinulum lineum caudatum. Ponder 1971:243, fig. 5, nos. 1–3.
Buccinulum caudatum. Beu & Maxwell 1990:362, pl. 49b; Maxwell 2009:244.

Type material. Buccinulum (Evarnula) caudatum, holotype AIM AK72018, from 'between Kai Iwi and Okehu, Wanganui, Upper Pliocene' (Powell 1929:76), that is, early Castlecliffian beds of the Wanganui coastal section (not seen).

Other material examined. **Castlecliffian:** *Buccinulum caudatum* was recorded by Fleming (1953:188, 192, 194, 196, 199, 203) from Kaimatira Pumice Sand ('*B.* aff. *caudatum*'; OIS 25), Lower Kai-Iwi Siltstone and Omapu Shellbed (OIS 23), fossiliferous silt member of Lower Westmere Siltstone (Lower Westmere Shellbed; Abbott & Carter 1999; OIS 21), Kaikokopu Shell Grit (OIS 19), and Kupe Formation ('derived'; OIS 17). As with *Aeneator delicatulus*, the youngest records are based on equivocal, abraded specimens, possibly derived from older formations, and the true time range seems to be OIS 25–19. Specimens in the GNS reference collection are: Kai-Iwi, Castlecliff, CA Fleming collection, labelled 'topotypes' (15); fossiliferous silt member, Lower Westmere Siltstone, Castlecliff coast (GS4058, R22/f6389, two); Omapu Shellbed, coast E of Omapu Stream, E of Mowhanau, Wanganui (GS4060 re-collection, R22/f6391, 30).

Distribution. Early Castlecliffian, OIS 25–19 (–17?), in the Wanganui coastal section only.

Dimensions. Buccinulum caudatum, holotype: H 57.5, D 27 mm; paratype: H 61, D 27.5 mm (Powell 1929:76); GS4060, R22/f6391, Omapu Shellbed: H 48.1, D 23.2 mm; H 38.8, D 18.9 mm; 'Kai-Iwi, topotypes', CA Fleming collection: H 52.0, D 27.3 mm; H 47.6, D 25.3 mm.

Remarks. As with *Aeneator delicatulus*, *Buccinulum caudatum* is limited to early Castlecliffian rocks (OIS 25–19; 17?) and as it is a very large, highly distinctive species, the largest species referred to *Buccinulum* (the still larger *B. pangoides* Beu, 1973 is transferred below to *Euthria* Gray, 1850), it is useful for biostratigraphy within Wanganui Basin. Ponder (1971:243) treated *B. caudatum* as a subspecies of *B. linea* (Martyn, 1784). However, the species status of *B. caudatum* is demonstrated by both the strongly marked morphological differences and the partial syntopy of the two forms. Specimens of *B. caudatum* differ from those of *B. linea* in their much larger size, in their strongly concave rather than straight or weakly concave sutural ramp, in their much more prominent axial ridges, in their longer and more prominent transverse (spiral) ridges inside the outer lip, and in their more flared outer margin of the outer lip, outside the transverse ridges. The protoconch also is correspondingly larger than that of *B. linea*. The stratigraphic range of *B. caudatum* is virtually identical to that of *Aeneator delicatulus*, and specimens of the two species occur syntopically. However, specimens of *B. caudatum* are more common in Kaikokopu Shellbed than is *A. delicatulus*, and it seems likely that at least some of these are in situ, that is, its time range more certainly extends up to include OIS 19.

Genus ***Cominella*** Gray, 1850

Cominella Gray 1850:72. Type species (by subsequent designation, Iredale 1918:34; confirmed by ICZN Opinion 479 1957): *Buccinum testudineum* Bruguière, 1798 (= *Buccinum maculosum* Martyn, 1784; valid, ICZN Opinion 479 1957), Pleistocene and Recent, New Zealand.

Acominia Finlay 1926a:240. Type species (by original designation): *Buccinum adspersum* Bruguière, 1789, Pleistocene and Recent, New Zealand.

Subgenus ***Eucominia*** Finlay, 1926

Eucominia Finlay 1926a:239. Type species (by original designation): *Buccinum nassoides* Reeve, 1846, Pliocene–Recent, southern New Zealand.

Zephos Finlay 1926a:239. Type species (by original designation): *Nassa cingulata* Hutton, 1885, Pliocene, New Zealand. Synonym of *Eucominia* according to Ponder (1968a:35).

Cominella (Eucominia) elegantula (Finlay, 1926) (Fig. 6B, C, F–I)

Eucominia elegantula Finlay 1926a:240, pl. 57, figs. 14, 15.
Eucominia elegantula subspecies *verrucosa* Finlay 1926a:241, pl. 57, fig. 16.
Cominella (Eucominia) elegantula. Powell 1929:95; Fleming 1966:62; Ponder 1968a:35; Beu & Maxwell 1990:364, 412, pl. 49e; Maxwell 2009:244.
Cominella (Eucominia) elegantula verrucosa. Powell 1929:95.
Cominella (Eucominia) marlboroughensis Powell 1946b:143, pl. 12. fig. 10 (**new synonym**).
Eucominia marlboroughensis. Dell 1956b:52, fig. 60.
Eucominia cf. *elegantula*. Dell 1956b:53, fig. 62.
Cominella (Eucominia) verrucosa. Fleming 1966:62.
Cominella (Eucominia) elegantula marlboroughensis. Ponder 1968a:35; Powell 1979:195, pl. 40, fig. 5; Spencer & Willan 1996:27; Spencer et al. 2009:208.

Type material. *Eucominia elegantula*, holotype AIM AK70218, from Castlecliff, Wanganui, horizon unknown, possibly from Tainui Shellbed (OIS 13); with one paratype AK71669, same data as holotype. *Eucominia elegantula verrucosa*, holotype AIM AK70282 (O Lee, AIM, pers. comm. 11 March 2008); Finlay (1926a:241) stated the locality only as 'same as last, with the species itself, but rarer', that is, he used 'subspecies' in the sense of a sculptural variant rather than the modern usage of a geographically isolated form. *Cominella (Eucominia) marlboroughensis*, holotype AIM AK71453, Recent, from 150 m, 41°16′S, 173°17′E, ca 40 km E of Cape Campbell, Cook Strait (all not seen).

Other material examined. **Mangapanian:** a single specimen from Weka Pass, N Canterbury (GS6215, M34/f7660, 50 m above Waiauan limestone, Weka Creek, 160 m downstream from junction with Weka Pass Stream; with *Taxonia suteri*, *Polinices waipipiensis* (Marwick, 1924), and *Glycymerita (Manaia) manaiaensis* (Marwick, 1923)) resembles *Cominella elegantula* and *C. virgata* closely in most characters, but is a little larger than any specimens from Wanganui or Hawke's Bay and has rather more prominent spiral cords. It possibly represents an unnamed species. **Nukumaruan:** 30 m above Torlesse basement, Makohine Stream, Pohangina, E Wanganui Basin, early Nukumaruan (GS2763, T23/f6486; one); Tangoio Limestone, roadside quarry on Waipunga Road, 1 km N of junction with Turnbull Road, central Hawke's Bay (GS12711, V20/f045; 12 incomplete); Mairau Mudstone, 'the watchman' hill, Ahuriri lagoon, Napier (GS11465, V21/f6015A; eight); Okawa Stream, Matapiro syncline (GS1063, V21/f8476; four); limestone underlying shellbed on Trig. Y, 1 km NW of Paeroa Road, 2 km SW of Whetukura on Ormondville–Te Uri Road, ca 15 km ENE of Dannevirke (GS2365, U23/f6410; two); Mairau Mudstone, walkway W side of Roro-o-kuri, Ahuriri, Napier (GS12386, V21/f05; two); Maharakeke Mudstone, Maharakeke Road, W of Waipukurau, Hawke's Bay (GS10857, U23/f7049; one); Tirohia Station, opposite Maraekakaho, Matapiro syncline (GS12424, V21/f013; 10); Darkys Spur Formation?, lowest limestone bed in sequence, Waipunga Road, N side of hairpin bend on ascent from Esk Valley towards Kaiwaka Road, N of Napier, central Hawke's Bay (GS12816, V20/f147; three, almost smooth); Tangoio Limestone, cutting on track 500 m N of Petane Pa, N of Napier, central Hawke's Bay (GS12790, V20/f038; five, most incomplete and abraded, almost smooth); Mairau Mudstone, 'Petane corner', junction of Highways 3 and 5, opposite Esk River bridge, N of Napier (GS12501, V20/f017; one, smooth, more inflated than all others, referred uncertainly). Recorded also by Fleming (1953:151) from GS3093, S22/f9489, Waipuru Shellbed (?), Hunterville-Turakina Valley Road 5 km W of Hunterville, Rangitikei valley. **Castlecliffian:** common in most later Castlecliffian highstand systems tract shellbeds at Wanganui, not listed; recorded by Fleming (1953:203–204, 209, 218, 230, 239) from gastropod shellbed, *Cyclomactra tristis*, and bivalve shellbed members of Kupe Formation (OIS 17), undifferentiated Kai-Iwi Group, W side Whangaehu valley (GS4235, S22/f6457, 'cf. *verrucosa*'), Lower Castlecliff Shellbed (OIS 15), Tainui Shellbed (OIS 13), and Upper Castlecliff Shellbed (OIS 11). **Recent:** the holotype of *Cominella marlboroughensis* and the material reported by Dell (1956b:52, 53) as '*Eucominia marlboroughensis*' and '*Eucominia* cf. *elegantula*' are from Cook Strait (150 m, 40 km E of Cape Campbell, Cook Strait, holotype; 275 m, 41°28.5′S, 174°50′E, & 110 m, between Island Bay Bank and East Bank [Dell 1956b:52], and 137 m, 40°52.6′S, 174°49.5′E [Dell 1956a:53]); 15 other lots in NMNZ, ranging from Kahurangi Shoals, N Westland, 91 m (M.59050, four small) and off Westhaven Inlet, to off Kapiti Island (M.7681, two), throughout Cook Strait, to Port Gore, Marlborough, 139–144 m (M.53717, one small) and to Palliser Bay, E Cook Strait, in 274 m (M.11543, one). The largest lot is M.135047, Nicholson Canyon, off Turakirae Head, 640 m (24 stained, dead specimens).

Distribution. Mangapanian, N Canterbury?; early (rarely) and late Nukumaruan in Hawke's Bay and (rarely) Wanganui Basin; common in later Castlecliffian rocks of Wanganui Basin; still living offshore in Cook Strait in about 110–280 m. Available records suggest that in Hawke's Bay, *Cominella elegantula* is limited to upper beds of Petane Group (Darkys Spur Formation to Te Ngaru Mudstone, and possibly a few units above and below these), of late Nukumaruan age. However, I have not seen specimens from the highest, richly fossiliferous unit, Devils Elbow Mudstone, where *Cominella (Cominella) excoriata* (Finlay, 1926) is common. Most specimens of *C. elegantula* are abraded, whereas *C. excoriata* is not abraded when collected from offshore siltstone units, so apparently *C. elegantula* lived in relatively shallow water, and *C. excoriata* lived significantly further offshore in Hawke's Bay. This probably reflects a facies limitation rather than the real time range, reducing any possible biostratigraphical utility.

Dimensions. Holotype of *Cominella marlboroughensis*: H 29.3, D 13.4 (Powell 1946b:143); Cook Strait: H 26.8, D 12.7 mm; H 25.4, D 12.3 mm; H 32.7, D 17.7 mm (Dell 1956a); GS4013, R22/f6353, Tainui Shellbed at 'the buttress', Castlecliff: H 30.5, D 14.6 mm; GS4140, R22/f6450, Lower Castlecliff Shellbed, Castlecliff: H 33.1, D 15.0; GS2763, Makohine Stream, Pohangina, Nukumaruan: H 32.2, D 16.5 mm; GS10857, Maharakeke Road, Waipukurau, Nukumaruan: H 33.8, D 18.5 (unusually wide specimen); GS12424, Tirohia Station, central Hawke's Bay: H 35.0, D 17.6 mm; H 28.2, D 15.1 mm; H 28.4, D 14.5 mm; GS11465, 'the watchman', Napier: H 31.8, D 16.3 mm; Recent, NMNZ M.50340, W of Makara, W Cook Strait, 119–132 m, 41°11.00′S, 174°39.00′E, RV Acheron sta. 76481 (Fig. 26I,K): H 34.5, D 16.8 mm (dorsal view); H 31.4, D 16.2 mm (ventral view).

Remarks. Ponder (1968a:37) described the new Recent 'subspecies' *Cominella (Cominella) excoriata tolagaensis* on the basis of a large number of specimens from Tolaga Bay and nearby areas in the eastern North Island, north of Gisborne, where it occurs as far N as the point E of Te Araroa on the N coast of East Cape. It was stated expressly to be a 'chronosubspecies' of *C. (Cominella) excoriata*, a highly distinctive species occurring in high Nukumaruan formations of the Petane Group in central Hawke's Bay. One of the themes of this series of papers is that chronosubspecies do not exist; speciation (or origination) produces discrete species and, if no speciation event occurred, members of a gradual anagenetic series are conspecific. In some ways *C. elegantula* more nearly resembles *C. tolagaensis* than does *C. excoriata*. It is clear, though, that these actually are three distinct species.

Cominella excoriata is distinguished readily from all other New Zealand species by its prominent, narrow, almost smooth, widely separated, obviously sinuous axial costae and its low, weakly defined spiral cords. Its outer lip is sinuous in conformity with the axial costae. It has no clearly defined sutural ramp, but the area below the suture is slightly flattened through the posterior (adapical) weakening of the axial costae. *C. tolagaensis* has wider but less prominent, more closely spaced, and much less sinuous axial ridges than *C. excoriata*, but has much more prominent, wide, closely spaced spiral cords than any other New Zealand *Cominella* species, with each spiral interspace filled with 1–2 much narrower, closely spaced cords. The prominent, wide, closely spaced axial ridges and outer lip are nearly straight, as in almost all other *Cominella* species, but in stark contrast with their obvious, strong sinuosity in *C. excoriata*. It also differs markedly from *C. excoriata* in its taller, more obvious, more deeply concave sutural ramp. Its pattern of 'chequerboard' colour maculations also is unique for a New Zealand *Cominella* species, other than the still more 'square-patterned', essentially smooth species *C. maculosa* (Martyn, 1784), although it is not unlike that of Australian species such as *C. lineolata* (Lamarck, 1809) (Wilson 1994, pl. 9, fig. 5A–C) and *C. acutinodosa* (Reeve, 1846) (Wilson 1994, pl. 9, fig. 8A–B). Some specimens in Hawke's Bay shallow-water late Nukumaruan rocks differ from both *C. tolagaensis* and *C. excoriata* in their slightly smaller size, lower spire, weaker spiral sculpture, weakly developed sutural ramp, and in most specimens almost completely lacking axial sculpture. However, careful comparison has demonstrated that these are merely abraded specimens of *C. (Eucominia) elegantula*, and more coarsely sculptured specimens of *C. elegantula* also occur at nearby, coeval localities in Hawke's Bay (Fig. 26J). *C. elegantula* occurs fairly commonly in shellbeds in the Castlecliff section, Wanganui, and not uncommonly in Nukumaruan siltstone units in central Hawke's Bay. *C. elegantula* is a small, weakly sculptured northern end-member of *C. nassoides* (Reeve, 1846), with a less prominent sutural ramp than other forms and only weak or, in some specimens, no peripheral nodules on its regular, even, axially elongate ridges. Specimens recorded from the Recent fauna in Cook Strait by Powell (1946b) and Dell (1956b) as *C. (Eucominia) marlboroughensis* and further material examined in NMNZ demonstrate that closely similar, small, weakly sculptured specimens intergrading with *C. elegantula* still live in the Cook Strait area. The main point for the present paper is that *C. elegantula* is a single, rather variable species (or geographical subspecies of *C. nassoides*; BA Marshall NMNZ pers. comm.) of Nukumaruan and possibly Mangapanian to Recent age, offering no biostratigraphical criteria through the distinction between a fossil species *C. elegantula* and a Recent species *C. marlboroughensis*. Also, *C. (Eucominia) elegantula*, *C. (Cominella) tolagaensis* and *C. (Cominella) excoriata* definitely are three distinct species.

Cominella (Eucominia) incisa (Hutton, 1885)
(Fig. 7A–G)

Clathurella incisa Hutton 1885a:328.
Nassa incisa. Hutton 1887:210.
Phos incisus. Suter 1915:26, pl. 4, fig. 13.
Zephos incisa. Finlay 1926a:240; Fleming 1966:62.
Cominella (Eucominia) incisa. Beu & Maxwell 1990:412; Maxwell 2009:244.

Type material. *Clathurella incisa* holotype CMC M3259 (again, not included in the catalogue by Bradshaw et al. 1992), from 'Te Aute, Hawke's Bay. Collected by Mr. A. Hamilton' (Hutton 1885a:328; the collector is stated only in the original publication). Age stated by Suter (1915:26) as 'Miocene'.

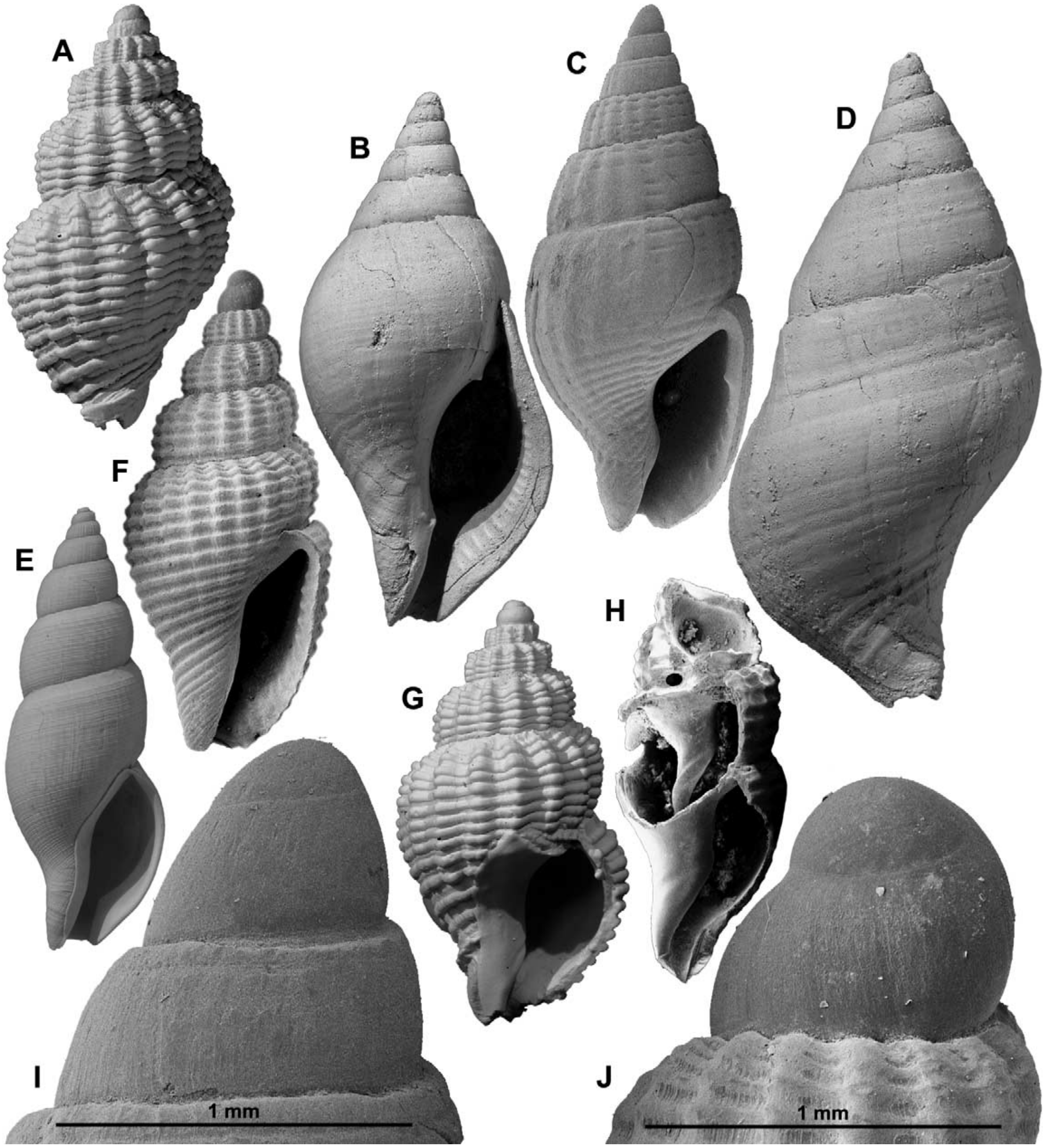

Figure 7 (A,G) *Cominella (Eucominia) incisa* (Hutton), holotype, CMC M3259, "Te Aute, Hawke's Bay", between Raukawa Range and Mason Ridge?, early Nukumaruan?; height 20.0 mm. (B,D) *Euthria pangoides* (Beu), GS4253, Q22/f7544, Upper Waipipi Shellbed (Waipipian), Waverley Beach, W of Wanganui; A, holotype, TM5092, height 50.5 mm; D, paratype, TM5093, height 61.5 mm. (C,I) *Antizafra speighti* Marwick, GS10858, U22/f9588, Ashcott Road, W of Pukeora hill, W of Waipukurau, Hawke's Bay, Nukumaruan; H, whole specimen, height 10.6 mm; I, protoconch of H. (E) *Iredalula striata* (Hutton), "Wanganui, Pliocene", Suter collection no. 50; height 30.8 mm. (F,H,J) *Antizafra pisanopsis* (Hutton), type species of *Antizafra* Finlay, 1926, all data as for Figs. C,I; SEM, 2 specimens; F, whole specimen, height 9.7 mm; H, broken specimen showing columellar plait, height 8.1 mm; J, protoconch of F.

Other material examined. Road cut E side of Raukawa Road, on curve ca 300 m S of junction with Burma Road, W of Raukawa Range, ca 4 km NW of Te Hauke and Te Aute College, Hawke's Bay; in early Nukumaruan siltstone between Te Onepu Limestone (Mangapanian) and Mason Ridge Limestone (early Nukumaruan) (GS12694, V22/f351; one incomplete).

Distribution. Recorded only from the two listed specimens. Too rare to have any biostratigraphical utility.

Dimensions. Holotype: H 20.0, D 11.1 mm.

Remarks. *Cominella (Eucominia) incisa* is almost as little-known and poorly understood as *Mitrellatoma angustata* (Hutton, 1886) (see below). However, the taxonomic position of *C. incisa* is much clearer than that of *M. angustata*. Suter's (1915, pl. 4, fig. 13) illustration (the only previous one) and examination of the holotype (Fig. 7A, G) make it clear that it is a small *Cominella (Eucominia)* species in the group typified by *C. onokeana* (King) (1933:345, pl. 37, fig. 14) and *C. otagoensis* (Finlay, 1926). Finlay (1926a:240) included all these in his genus *Zephos*, now regarded as a synonym of *Cominella (Eucominia)*. As the specimen is turned slightly to the left in Suter's illustration, it is not clear that it actually has a narrow columella and moderately contracted base of the last whorl, and a very prominent, ridge-margined siphonal fasciole. With its prominent sculpture of narrow, well raised, closely spaced spiral cords (nine on the penultimate and 13 on the last whorl, becoming markedly coarser and more widely spaced over the base) crossing high, relatively narrow, evenly rounded axial folds (14 on the penultimate and 16 on the last whorl), it resembles *C. powelli* (Fleming, 1948) and *C. cantuariensis* (Dell, 1956), although it differs from this species group in its more rounded axial ridges; they are narrowly angular and more widely spaced in the *C. powelli* group. The protoconch is well-preserved on the holotype and, as in *C. onokeana*, it is large (1.75 mm in diameter) and consists of two smooth, upright, evenly inflated whorls with a flattened apex and a minute planorboid initiation. The protoconch terminates in a short section bearing six narrow, closely spaced, smooth but shouldered axial ridges, after which the normal spiral sculpture and more widely spaced axial ridges commence. An identical protoconch is present on the specimen in GS12694. The closest similarity is with *C. onokeana*, which differs from *C. incisa* in its slightly taller spire, its taller, more steeply sloping and less well-defined sutural ramp, and in the spiral cords around the peripheral, maximally inflated area of the last whorl being slightly but obviously more widely spaced.

Hutton's original 'Te Aute' locality for *Cominella incisa* initially seemed unlikely to be correct, as there are few localities with fossil molluscs, other than Pectinidae in Pliocene Te Aute facies limestone, where this species might have been collected close to Te Aute College (alongside Highway 2, near Te Hauke in south-central Hawke's Bay). Some years ago I collected a single incomplete spire of this species from siltstone cropping out along Raukawa Road, between the Raukawa Range and the E side of Mason Ridge, NW of Te Aute College, apparently explaining the previously enigmatic provenance of Hutton's holotype. If this is indeed near the type locality of *C. incisa*, it is about the same age (earliest Nukumaruan) as *C. onokeana*.

Most material assigned to *Cominella (Eucominia) onokeana* is from the Palliser Bay cliffs between Lake Ferry (on Lake Onoke) and the mouth of Whangaimoana Stream, South Wairarapa, and further east along the same cliffs. A specimen from Okawa Stream, Matapiro syncline, Hawke's Bay (GS1063, V21/f8476) labelled '*Zephos onokeana*' by J Marwick is severely abraded, and may well be a poor specimen of *C. incisa*. However, I have also previously recorded specimens of *C. onokeana* from bathyal mudstone in the Ohara depression, east of the Ruahine Range in inland Central Hawke's Bay

(Beu et al. 1977, table 1) (GS11464, U21/f8558, overlying Sentrybox Limestone (with *Zygochlamys delicatula*) in small outcrop on Mangleton Road; GS11781, U21/f02, Jumped-up Stream downstream from Mangleton Road), so these species are probably distinct. *Cominella (Eucominia) cingulata* (Hutton, 1885) (*Nassa (Tritiaria) cingulata* Hutton 1885a:327, 'Greta, Canterbury', 'perhaps a *Cominella*'), a similar species common in bathyal mudstone (Greta Formation) near Waikari, North Canterbury (early Nukumaruan), differs from *C. incisa* and *C. onokeana* in its much wider, lower spiral cords, separated only by linear grooves (GS3297, N33/f9112, Greta Creek at main north road, 5 km S of Hurunui River, N Canterbury; 14 specimens, labelled by J Marwick and CA Fleming 'topotypes of *cingulata*' and 'also topotypes of *purchasi*'). An almost equally poorly known species is *Cominella (Eucominia) purchasi* Suter (1917:34, pl. 4, fig. 20), also from 'Waikari Valley, near the Greta Railway-station, right on the bank of the stream' (Suter 1917:34), that is, possibly from the same locality as *C. cingulata*. Suter's illustration shows a shell with slightly narrower spiral cords than most material of *C. cingulata*, but agreeing in all other characters, and *C. purchasi* is taken here to be a synonym of *C. cingulata*. The relationships of all these similar species, *C. incisa*, *C. onokeana* and *C. cingulata*, require clarification from further, well-localized material.

Family Buccinidae?

Genus ***Euthria*** Gray, 1850

Euthria Gray 1850:67. Type species (by monotypy): *Fusus lignarius* 'Chiaje' (= *Fusus lignarius* Lamarck, 1816, = *Murex corneus* Linné, 1758), Pliocene to Recent, Mediterranean–S Portugal.

Remarks. Several colleagues have expressed an opinion to me that '*Buccinulum*' *pangoides* Beu (1973:323) is not correctly placed in *Buccinulum* and, indeed, it was placed there 'with some hesitation' originally, mainly because *Buccinulum* is the traditional New Zealand genus in which to include relatively small, elongate, weakly sculptured buccinoideans. *B. pangoides* differs from species of *Buccinulum* in its larger size (H 50–61.5, D 24.8–32.3 mm), its wider shape, its much weaker sculpture (little sculpture other than low, smooth, widely spaced spiral cords around the neck of the last whorl), its unusually weakly impressed suture producing an almost straight spire outline, its tall, steep, concave sutural ramp riding up to the periphery of the previous whorl, its short, widely open anterior siphonal canal with little constriction on the right (outer) side, its tall, narrow posterior canal produced by the posteriorly elongate sutural ramp, its row of short but prominent spiral lirae inside the outer lip and, above all, the obvious, sharp, but relatively weak angulating ridge on the base of the columella, forming a low columellar fold that is not present in any *Buccinulum* species or, indeed, in any similar New Zealand Buccinidae. The columellar fold is accompanied by a few small, narrow nodules nearby on the inner lip, and the parietal ridge is unusually small, short, narrowly pointed and prominent. These characters are distinctive, and produce a shell with an overall appearance that is much heavier, thicker, wider and smoother than any *Buccinulum* species.

The most similar genus I am aware of is *Euthria*, which is very similar to *Buccinulum pangoides* in shape, general appearance, and relatively weak sculpture. Most European and, in particular, West African *Euthria* species (Cosel 1982; Cosel & Burnay 1983; Rolán 1985; Rolán et al. 2003, 11 Cape Verde Islands species discussed; most illustrated by Ardovini & Cossignani 2004:162–163; Robin 2008:185) as well as South African *Euthria* species (*E. ponsonbyi* GB Sowerby III 1889:149, pl. 3, fig. 3; *E. queckettii* EA Smith 1901:110, pl. 1, fig. 1; Barnard 1959:169–172; but *E. filmerae* G. B. Sowerby III, 1900 was transferred to *Latirus* (sensu lato) by Kilburn 1970:41) and a species from Indonesia (*E. effendyi* Fraussen & Dharma [2002]; Bali Strait, in 30–40 m) have a slightly to markedly longer anterior siphonal canal, and most lack the parietal nodule of *Buccinulum pangoides* and have only a low, weak ridge on the base of the columella. The two Philippine Islands species referred to *Euthria* by Fraussen (2003) were transferred to *Fusolatirus* (Fasciolariidae) by Snyder & Bouchet (2006). Most *Euthria* species also have a prominent to low but obvious siphonal fasciole, which is lacking in *Buccinulum pangoides*. However, the range of characters of the 17 or more Recent species now referred to *Euthria* is very wide, and *E. quecketti* and some of the species named recently from the New Caledonian region have a small, narrow parietal nodule, a nodule on the base of the columella, and almost no siphonal fasciole, and despite their longer anterior siphonal canals they resemble *Buccinulum pangoides* more than other *Euthria* species do. Particularly similar New Caledonian species are *Euthria philpoppei* Fraussen (2002) and *E. solifer* Fraussen & Hadorn (2003); the latter resembles *E. quecketti* closely. Most *Euthria* species also have a relatively large, wide, essentially smooth, paucispiral (lecithotrophic) protoconch, and that of the holotype of *B. pangoides* seems to have been similar, although with a smaller initiation than most other named *Euthria* species. *E. philpoppei* is similar to *B. pangoides* in overall shape as well, but differs in its more strongly concave sutural ramp, its low, rounded but obvious nodules on the subsutural fold and on the periphery of all but the last whorl, and its slightly longer anterior siphonal canal. It has similar apertural armature, a similarly weak siphonal fasciole and, in particular, similar short transverse lirae inside the outer lip to those of *B. pangoides*. '*Buccinulum*' *pangoides* seems to be the first authentic New Zealand species of *Euthria*.

The resemblance of *Euthria pangoides* to *Pangoa* Marwick (1931:119, pl. 12, figs. 232, 233) is entirely superficial, and is produced largely by the weak sculpture (perhaps entirely due to abrasion) and the tall, narrow posterior canal. The exceedingly battered holotype of *Pangoa mira* Marwick, 1931 cannot be placed in a family with any confidence. Attempts to recollect further material from the type locality have been unsuccessful ('Tutamoe conglomerate', that is, basal, coarse-grained, fossiliferous beds of turbidite sequences, in 'James creek' (informal local name), a tributary of Pangopango Stream, north of Gisborne). The fauna at this site (GS13955, Y16/f564, grid ref. Y16/558152; 1 km E of Te Rimu station, Tauwhareparae, inland between Tolaga and Tokomaru Bays) consists of poorly preserved, calcite neomorphs of a Lillburnian (middle Miocene) bathyal fauna. It includes a common large, apparently unnamed, angular *Neilo* species, and probably includes the specimens of unidentified *Zemacies*, *Gemmula* and *Comitas* species. It is admixed with battered fragments of a shallow-water fauna (*Crassostrea*, *Eucrassatella*, *Struthiolaria (Callusaria) callosa* Marwick, 1924, *Cypraea*, *Zeacolpus*, *Cominella hendersoni* Marwick, 1926) transported downslope into the deposition site. The holotype of *Pangoa mira* apparently has been severely abraded by this transport, and would have been better left unnamed. It has been placed in Muricidae by convention in recent catalogues, but seems just as likely to be a fasciolariid.

Ironically, numerous authors in the past referred many other New Zealand buccinoideans to *Euthria* (e.g. see comments by Finlay 1928:250) as well as such muricids as *Axymene aucklandicus* (Smith, 1902) (see below), but all proved to belong in other genera. In particular, many early authors referred species to *Euthria* that are now included in *Buccinulum*. However, *Buccinulum* differs from *Euthria* in its smaller size, smaller protoconch, relatively larger parietal ridge, more elongate shape, and consistent spiral sculpture and colour pattern. *Buccinulum* is limited to New Zealand and southern Australia. The resemblance is probably, again, superficial, as *Euthria* presumably is a genus of the mostly Northern Hemisphere family Buccinidae, whereas *Buccinulum* was recognized by Harasewych & Kantor (2004) as belonging in a distinct southern subfamily (or family?) Buccinulinae/idae. The recognition that *Euthria* occurs in South Africa and extends at present as far east as Indonesia and New Caledonia suggests that this is another of the groups that entered the Pacific from the Atlantic via South Africa, and leaves no great surprise that a species of *Euthria* extended down the Norfolk Ridge to New Zealand during the warm middle Pliocene.

Euthria pangoides (Beu, 1973) (Fig. 7B, D)

Buccinulum pangoides Beu 1973:323, figs. 27, 30–33; Beu & Maxwell 1990:298, pl. 37s.
Buccinulum (?) *pangoides*. Maxwell 2009:244.

Type material. Holotype TM5092, GS4253 recollection, Q22/f7544, lower part of Upper Waipipi Shellbed, 200 m E of mouth of Wairoa Stream, Waipipi Beach, that is, W end of Waverley Beach, W of Wanganui; with five paratypes, TM5093-5097, from the same locality.

Other material examined. A few other specimens from the same locality and shellbed in the collection of FD Chambers.

Distribution. *Euthria pangoides* is still recorded only from the lowest, soft, matrix-supported part of Upper Waipipi Shellbed, with a fauna dominated by relatively small gastropods (unlike the upper, specimen-supported part of the shellbed with its fauna dominated by large bivalves), at Waipipi, Waverley Beach.

Dimensions. Holotype: H 50.5, D 24.8 mm; tallest paratype, TM5093: H 61.5, D 28.9 mm; widest paratype, TM5094: H 60.2, D 32.3 mm (Beu 1973:324).

Remarks. Little can be added to the description of *Euthria pangoides* given under the generic heading above. The protoconch remains largely unknown. I (Beu 1973:323) described the protoconch as 'perhaps only slightly damaged on holotype where it appears to consist of one and a half whorls, the initial half-whorl tightly coiled and planorbid and the later whorl inflated', significantly different from the smaller, paucispiral, mammillate protoconch with a large initiation (evidently reflecting lecithotrophic development) present in *Buccinulum*, and similar to that of some species of *Euthria*.

Family Colubrariidae

Genus ***Iredalula*** Finlay, 1926

Iredalula Finlay 1926a:231. Type species (by original designation): *Bela striata* Hutton, 1873, early Pliocene–Pleistocene (–OIS 11), New Zealand.

Remarks. The family position of *Iredalula* has long been in doubt as, although Hutton (1873b:5) and several later workers referred the type species to various genera of Conoidea, traditionally it has been referred to the Buccinidae in recent years. Ponder (1968b) placed it in family Colubrariidae based on its close similarity to genera such as *Colubraria* Schumacher, 1817 and, in particular, *Metula* H. Adams & A. Adams, 1853, and described some anatomical characters. Beu & Maxwell (1987:62) followed a verbal suggestion by WF Ponder in placing the group in Family Buccinidae, Subfamily Pisaniinae. *Iredalula* species differ from *Metula* species mainly by their finer sculpture dominated by spiral cords, with no axial elements other than faint growth lines, their larger, wider and more obviously shouldered protoconchs, and their almost complete lack of varices. The outer lip is sinuous as in *Metula*, but only lightly thickened inside in *I. striata*, although a slight terminal varix is formed by the Recent species *I. alticincta* (Murdoch & Suter, 1906). Oliverio & Modica (2010) demonstrated on molecular phylogenetic grounds that *Colubraria* and *Metula* belong in a separate family Colubrariidae, and are followed here. A position for *Iredalula* near *Metula* in the Colubrariidae seems likely, bur requires DNA confirmation.

Iredalula striata (Hutton, 1873) (Fig. 7E)

Bela striata Hutton 1873b:5.
Siphonalia(?) *cingulata* Hutton 1885a:315; Hutton 1893:41.
Daphnella striata. Hutton 1887:214; Hutton 1893:52, pl. 7, fig. 33; Harris 1897:63; Suter 1913, appendix p. 1084 (in part not *Bela striata* Hutton, 1873); Suter 1915:42.
Mitromorpha striata. Suter 1907:265; Suter 1910:11; Suter 1913:488, pl. 46, fig. 27 (in part not *Bela striata* Hutton, 1873).
Iredalula striata. Finlay 1926a:231; Fleming 1966:60; Beu & Maxwell 1987:62; Beu & Maxwell 1990:364, 412, pl. 49f.
Not *Iredalula striata*. Ponder 1968b:221, figs. 9, 10; Powell 1979:204; Spencer & Willan 1996:27; Spencer et al. 2009:208 (= *I. alticincta* Murdoch & Suter, 1906).

Type material. *Bela striata*, type material missing according to Suter (1915:42), but two syntypes are present in GNS, TM8686-7, from 'Wanganui (U), Shakespeare Cliff', Castlecliffian (almost certainly from Shakespeare Cliff Siltstone, OIS 13). The syntypes are labelled '*Daphnella striata*' and '*Acamptochetus striatus*', 'the larger sp. of 23 mm is the lectotype', both by J Marwick and on an earlier label, but I am not aware of a published lectotype designation. They also have a very early hand-written label (by FW Hutton?) reading '*Bela striata*', and bear the old dark brown insoluble glue characteristic of specimens that have been removed from Hutton's wooden type-specimen tablets. The two specimens are conspecific, and a lectotype is not required. *Siphonalia*(?) *cingulata* four syntypes CMC M-3206 (not seen) (Suter 1915:42; Bradshaw et al. 1992:36; but note that Bradshaw et al. listed them under *Bela striata*, whereas these are definitely syntypes of *Siphonalia*(?) *cingulata*, and not of *Bela striata*), from 'Wanganui', that is, siltstone beds of the Castlecliff coastal section. Suter (1915:42) examined the syntypes and confirmed that *Siphonalia*(?) *cingulata* was based on immature 'undoubted examples' of '*Daphnella*' *striata*.

Other material examined. Finely sculptured specimens attributed to *Iredalula striata*: **Opoitian**: GS2891, J32/f9089, Shamrock Creek, near Kapitea Creek, ca 1 km upstream from Goldsborough, Westland (one incomplete); GS12521, X19/f033, mudstone just below Opoiti Limestone, 100 m N of prominent limestone outcrop on Mangapoike Valley Road, N Hawke's Bay (one small). **Waipipian**: GS1586, X19/f7480, sandstone above Tahaenui Limestone, Makeretu Stream, tributary of Mangapoike River above Haupatanga Gorge, N Hawke's Bay (one fragmentary). **Castlecliffian**: recorded by Fleming (1953:188, 192, 194, 200, 203–204, 207, 209, 226, 230, 232, 239) from Kaimatira Pumice Sand (OIS 25), Lower Kai-Iwi Siltstone and Omapu Shellbed (OIS 23), Upper Westmere Siltstone (Upper Westmere Shellbed, OIS 19), Kupe Formation and Upper Kai-Iwi Siltstone (OIS 17), undifferentiated Kai-Iwi Group, Pinnacle Sand (OIS 15-14), Tainui Shellbed and Shakespeare Cliff Siltstone (OIS 13) and Upper Castlecliff Shellbed (OIS 11). I have not seen specimens from higher in the section at Wanganui.

More coarsely sculptured specimens attributed to *Iredalula alticincta*: **Nukumaruan**: GS5216, V20/f8517, road cutting NE of Puketapu, inland from Napier, central Hawke's Bay, late Nukumaruan (one spire, moderately finely sculptured); GS12386, V21/f05, Mairau Mudstone (late Nukumaruan), N end of Roro-o-kuri, N end of Ahuriri lagoon, Napier (one moderately finely sculptured + two apices); GS10612, T27/f6021, mudstone beneath Pukenui Limestone (early Nukumaruan), E of summit of Admiral Road, Maungaraki Range, SE Wairarapa (one large, coarsely sculptured); NMNZ M.40402, *Lophelia* coral thicket (early Nukumaruan) in cliffs E of Lake Ferry, Palliser Bay (two coarse apices); M.59368, mudstone beneath Pukenui Limestone (Mangapanian/early Nukumaruan), cutting on Tupurupuru-Te Wharau Road, E of Gladstone, S Wairarapa (six, coarsely sculptured); M.117614, large gully between Lake Ferry and Whangaimona, Palliser Bay, early Nukumaruan (one coarse apex). **Castlecliffian**: GS13707, W15/f9583A, one; GS14551, W15/f9583B, many; NMNZ M.40277, many; all from cutting on Wainui Road, W side Ohiwa Harbour, Whakatane (OIS 15?). **Recent**: 53 lots examined in NMNZ, ranging from off Ahipara, around the E North Island to off Palliser Bay, in 10–550 m.

Distribution. Finely sculptured specimens of *Iredalula striata* are rare in Opoitian and Waipipian rocks of Westland and N Hawke's Bay, and common in Kaimatira Pumice Sand (OIS 25) and siltstone formations of OIS 23–11 at Castlecliff, Wanganui, particularly in Shakespeare Cliff Siltstone (OIS 13), although there are no records from OIS 21. No Recent specimens are now identified as *I. striata*. The Recent species *I. alticincta* lives from the NW North Island (off Ahipara) to Palliser Bay, Cape Campbell and into E Cook Strait; the few specimens from the W North Island are shorter and possibly distinct. Fossils of *I. alticincta* are recorded only from Castlecliffian rocks at Whakatane and from Nukumaruan rocks of Hawke's Bay and Wairarapa where, as in the Recent fauna, specimens in shallow-water formations tend to be finely sculptured whereas those in bathyal deposits are all very coarsely sculptured.

Dimensions. Syntypes of *Bela striata*: H 22.5, D 9.3 mm (H:D = 2.42) (marked 'T' inside outer lip); H 21.0, D 8.2 mm (H:D = 2.56); large, relatively narrow specimen of *Iredalula striata* (Fig. 27J), 'Wanganui, Pliocene', Suter collection no. 50: H 30.3, D 11.3 mm (H:D = 2.68); largest in NMNZ: M.26767, Castlecliff: H 30.8, D 12.4 mm (H:D = 2.48); H 27.4, D 12.1 mm (H:D = 2.26); largest specimen of *I. alticincta*, M.61081, ENE of Castlepoint, 278 m: H 35.3, D 11.2 mm (H:D = 3.15); figured syntype of *I. alticincta*: H 15.7, D 5.75 mm (H:D = 2.73) (Murdoch & Suter 1906:286); largest syntype remaining in Suter's collection (GNS TM943): H 18.8, D 7.75 mm (H:D = 2.43) (accompanied by three small syntypes, TM944-945); holotype of *I. venusta*: H 23.75, D 8.0 mm (H:D = 2.97) (Powell 1934b:158); large specimen of *I. alticincta*, GS10612, Admiral Road, S Wairarapa: H 25.9, D 8.9 mm (H:D = 2.91).

Remarks. Comparison of fossils and the Recent specimens in NMNZ revealed a surprising taxonomy of *Iredalula*. No Recent specimens are as finely and evenly sculptured as Castlecliff specimens of *I. striata*, which have about 50–60 very narrow, low, closely spaced (almost uncountably fine) spiral threads on the penultimate whorl. Recent specimens have 6–20 wider and more widely spaced spiral cords on the penultimate whorl. The sculpture of Recent specimens is exceedingly variable and, although coarsely sculptured specimens similar to the syntypes of *I. alticincta* (Murdoch & Suter 1906:285, pl. 22, figs. 12, 13) tend to occur most commonly towards the southern limit of its range (from Gisborne to Palliser Bay and into E Cook Strait) and in deeper water (in ca 100–550 m), even northern shallow-water specimens can be very coarsely sculptured, and most specimens are intermediate in sculptural coarseness between the types of *I. venusta* Powell (1934b:157, pl. 22, fig. 9) (with eight spiral cords on the penultimate whorl) and *I. alticincta* (with five cords). Others, particularly in the north of its range from E Northland to the Bay of Plenty, are intermediate in coarseness between the holotype of *I. venusta* and Castlecliff specimens of *I. striata*, but none is anywhere near as finely sculptured as Castlecliff specimens. Some samples include a range of sculpture within one collection (e.g. NMNZ M.67634, W of Plate Island, 59–64 m, six relatively finely sculptured *I. venusta* form, one *I. alticincta* form). The holotype of *I. venusta* is from off Cape Campbell, Marlborough, the southernmost record of the genus. Very coarsely sculptured fossils do occur, but they are all in either Hawke's Bay Nukumaruan rocks of shallow facies (all relatively finely sculptured specimens resembling the holotype of *I. venusta*, with 8–15 spiral cords on the penultimate whorl), or in S Wairarapa bathyal localities (coarsely sculptured specimens resembling the syntypes of *I. alticincta*, with 5–6 spiral cords on the penultimate whorl). Other differences between Castlecliff specimens and all others also seem constant. Castlecliff shells are slightly wider (height: diameter = 2.2–2.5, rarely as great as 2.7, compared with Recent specimens: 2.8–3.2, rarely as little as 2.4), consistently more evenly inflated (particularly the area between the outer margin of the sutural ramp and the neck; the lateral outline is almost flat on most Recent shells), the sutural ramp is not defined by the obvious margining ridge of Recent specimens, fine axial ridges on the first teleoconch whorl are weak on *I. striata* but well-developed on Recent shells, and the outer lip is significantly thinner on Castlecliff specimens than on Recent shells, most large ones of which have a lightly thickened but obvious, slightly developed external varix that is scarcely discernible on Castlecliff fossils. In my opinion Castlecliff fossils, and probably the few Opoitian–Waipipian fossils from Westland and N Hawke's Bay, are the extinct species *I. striata*, whereas Recent specimens, Ohope Beach Castlecliffian fossils, and Hawke's Bay–S Wairarapa Nukumaruan fossils are another species, for which the earlier name is *I. alticincta*. There is certainly no doubt that *I. venusta* intergrades completely with *I. alticincta* in sculptural prominence, the one character that distinguishes these two forms.

The only Recent specimens I have seen that diverge from this pattern are from the W North Island (NMNZ M. 52642, W of Rangitikei River mouth, 82 m, three specimens; M.153427, WNW of Cape Egmont, 146 m, one; M.153431, SW of Manukau Harbour, 502 m, one). These specimens are smaller, shorter and wider than E North Island specimens and have fewer, lower, wider, more widely spaced spiral cords that fade out over the last half-whorl. They also have 3–5 fine spiral threads on each wide, low spiral cord, and could have evolved from *I. striata* after OIS 11 by suppression of groups of spiral threads. They are also all old, chalky shells with a corroded surface, and more material is required to determine whether they constitute a third species.

The abundant specimens of *Iredalula striata* at Wanganui (Castlecliffian, OIS 25–11) seemed at first sight to provide a further example of a northern species or form that extended its range southwards to Wanganui during interglacial periods (e.g. Beu 2004). Some aspects of its range at Wanganui, such as the absence from OIS 21, probably result from its preference for offshore siltstone habitats rather than a true absence from the basin. However, it now seems likely that the history of *Iredalula* is more complex. The finely sculptured species *I. striata* seems to have occurred widely in New Zealand early in Pliocene time, but then retreated to become an endemic Cook Strait species by Pleistocene time—although the very small amount of Opoitian–Waipipian material makes identification uncertain, and the older specimens have a slightly more obvious terminal varix than Castlecliff shells. *I. striata* became extinct at some time during or after OIS 11 (there are no records from Wanganui Basin younger than OIS 11). Concurrently, the more coarsely sculptured and more flat-sided species *I. alticincta* occupied the E North Island, including in deeper environments than *I. striata* is known from, and remains living there. The many Castlecliffian specimens from Ohope Beach, Whakatane (OIS 15?) reach a smaller maximum size, are narrower and flatter-sided, and have fewer, slightly more prominent spiral cords than Castlecliff shells, and seem best identified as *I. alticincta*.

Therefore, three species seem to be recognizable in *Iredalula*: *I striata* (Opoitian–Castlecliffian; Castlecliffian at Wanganui only, last recorded in OIS 11), *I. alticincta* (Nukumaruan–Recent, E North Island), and an apparently unnamed species living off the W North Island. This is a very preliminary conclusion, requiring at least the examination of radulae and anatomy of many Recent specimens from E and W North Island to tell whether they are indeed all conspecific, as their sculptural variation seems haphazard.

Family Columbellidae

Genus ***Antizafra*** Finlay, 1926

Antizafra Finlay 1926b:421. Type species (by original designation): *Columbella pisanopsis* Hutton, 1885 (Fig. 7H), Pliocene, New Zealand.

Remarks. *Antizafra* is a distinctive genus, with one or two wide, low plaits on the base of the columella (Fig. 7H). Both *A. pisanopsis* (Hutton, 1885) (Fig. 7F, H, J) (originally spelled '*pisaniopsis*', but corrected in the volume's corrigenda sheet to '*pisanopsis*' [Beu & Maxwell 1990:325], although Hutton himself [1893:45] later spelled it '*pisaniopsis*' again) and the markedly taller and narrower species *A. cancellaria* (Hutton, 1885) have two low plaits occupying the lower two-thirds of the columella, with a weak groove between them, whereas *A. speighti* (Marwick, 1924) (Fig. 27H, I) has only a single relatively narrow plait on the base of the columella. However, only the lower plait seems to extend down the whole columella in *A. pisanopsis* and *A. cancellaria*. All three also have unusually graceful shapes and narrow, cancellate spiral and axial sculpture, although the sculpture is much weaker on *A. speighti* than on the others. *A. pisanopsis* and *A. cancellaria* also differ from *A. speighti* in having a shorter and more mammillate protoconch (Fig. 7I, J), although it is equally smooth in all three species. Only the Nukumaruan and possibly Mangapanian species *A. pisanopsis*, *A. cancellaria* and possibly *A. speighti* belong in this genus; the other species previously referred here are transferred tentatively to *Macrozafra* Finlay, 1926, and this might well be a better position than *Antizafra* for *A. speighti*.

Fleming (1953:131, 140, 144, 146, 148,151, 158, 174) recorded specimens of *Antizafra pisanopsis* from Wanganui Nukumaruan rocks (Hautawa Shellbed, Nukumaru Limestone, Nukumaru Brown Sand, Mangamako Shellbed, undifferentiated Nukumaru group, Waipuru Shellbed, and Tewkesbury Formation). He also recorded *A. speighti* from Nukumaru Limestone (Fleming 1953:140) and from Okehu Shell Grit (p. 181; Castlecliffian, OIS 27; as '*A.* aff. *speighti*', possibly reworked?). As far as I am aware, all three species of *Antizafra* are limited to Nukumaruan and possibly Mangapanian rocks, and the extinction of the genus occurred at about the end of Nukumaruan time. There are no records of *A. cancellaria* and only the two of *A. speighti* listed here from localities outside Hawke's Bay.

Family Muricidae

Subfamily Tripterotyphinae

Genus ***Ponderia*** Houart, 1986

Ponderia Houart 1986:88. Type species (by original designation): *Typhis zealandica* Hutton, 1873, Pleistocene and Recent, New Zealand.

Remarks. Houart (1986) demonstrated that '*Typis*' *zealandica* Hutton, 1873, usually placed in *Pterynotus* or *Prototyphis* in recent years, belongs in a distinctive genus otherwise occurring in the subtropical to tropical Southwest Pacific, designating *T. zealandica* as the type species of the new genus *Ponderia*. He included *Ponderia abies* Houart, 1986 (off New South Wales, in 154–164 m) and *Ponderia canalifera* (G. B. Sowerby II, 1841), an earlier name for the restricted Norfolk Island species later named *Pterynotus zealandicus iredalei* by Fleming (1962a). Houart (1988, 1990) has since added the species *P. caledonica*, *P. magna* and *P. elephantina*, all from New Caledonia and the Coral Sea. Houart & Héros (2008:471) included *Ponderia* in the subfamily

Tripterotyphinae, along with *Tripterotyphis* Pilsbry & Lowe, 1932, *Pterotyphis* Jousseaume, 1880, *Prototyphis* Ponder, 1972 and possibly *Semityphis* Martin, 1931. Whether this group really deserves separation from subfamily Typhinae was not resolved by Barco et al.'s (2010) phylogeny, as they did not include any purported genera of Tripterotyphinae.

Ponderia zealandica (Hutton, 1873) (Fig. 8A–C)

Typhis zealandica Hutton 1873b:2.
Murex zealandica. Hector 1886:50, fig. 7, no. 4 (not *Murex zelandica* Quoy & Gaimard, 1833, type species of *Poirieria*).
Murex (Alipurpura) angasi. Suter 1913:404; Suter 1914:2 (not *Murex angasi* Crosse, 1863).
Pterynotus (Poropteron) zealandicus. Finlay 1926b:419, fig. 56; Fleming 1961:13–15.
Pterynotus (Pterochelus) zealandicus zealandicus. Fleming 1962a:115, pl. 1, figs. 15, 16; Dell & Fleming 1964:1, 2, fig.; Fleming 1966:57, figs. 1262, 1263.
Ponderia zealandica. Houart 1986:88, figs. 1, 1a; Maxwell 2009:245.
Pterotyphis (Ponderia) zealandicus. Beu & Maxwell 1990:358, pl. 48i; Spencer & Willan 1996:26; Spencer et al. 2009:211.

Type material. Typhis zealandica, holotype TM8294 (Fig. 8C), from Shakespeare Cliff, Wanganui; undoubtedly from Tainui Shellbed, the only formation this species occurs in.

Other material examined. **Castlecliffian:** limited to Tainui Shellbed (OIS 13) at Wanganui; moderately common throughout Wanganui Basin. **Recent:** 10 lots in NMNZ: M.17977, due N of Cape Farewell, 82–95 m (one good, closely similar to Wanganui fossils); M.90254, NE of Cape Farewell, 95–102 m (one); M.50593, S of Waverley, Wanganui, 77–82 m (two); M.50080, SW of Wanganui, 58–64 m (two); M.50113, SW of Turakina River mouth, 55–57 m, on bryozoa and shells (10 small dead); M.53311, W of Rangitikei River mouth, 75 m (one small dead); M.70662, Ranfurly Bank, off East Cape, 103–106 m (three); M.60467, Ranfurly Saddle, off East Cape, 126–128 m (one fragment); M.60026, Rangatira Knoll, NW of White Island, 166–169 m (one small dead); M.64788, Rangatira Knoll, NW of White Island, Bay of Plenty, 164 m (one small dead).

Distribution. Castlecliffian to Recent; OIS 13 (Tainui Shellbed), only, at Wanganui; living in the Cook Strait region from Cape Farewell to offshore from Wanganui to the Rangitikei River, and on Ranfurly Bank, East Cape. The two small dead specimens from Rangatira Knoll, Bay of Plenty, are possibly late Pleistocene fossils, as have been reported from a nearby locality previously (37,000–40,000 yrs, at Rungapapa Knoll; Beu 2004:155).

Dimensions. Typhis zealandica, holotype: H 27.3, D 18.7 mm (spines slightly incomplete); GS4013, R22/f6353, Tainui Shellbed at 'the buttress', Castlecliff: H 31.8, D 17.9 (spines incomplete); H 30.0, D 21.1 mm; Recent, M.17977, N of Cape Farewell: H 22.7, D 18.9 m; M.50080, SW of Wanganui: H 23.4, D 15.5 mm (spines slightly incomplete).

Remarks. The very distinctive little muricid *Ponderia zealandica* is entirely restricted to Tainui Shellbed (OIS 13) in the Wanganui succession, and therefore is useful for identifying this shellbed in isolated outcrops. It has a completely closed siphonal canal and shoulder (anal) spine, and three wing-like varices similar to those of *Pterynotus*. It also has a classic muriciform aperture, smooth and evenly oval with a continuous peristome and a well-raised rim, a prominent shoulder angulation delimiting a narrow, strongly concave sutural ramp, a narrow peribasal angulation formed by a relatively prominent spiral cord, and sculpture of a few other weak spiral cords crossing several low, narrow axial ridges in each intervariceal interval, forming low nodules at their intersections with the peripheral cord. The terminal varix closely resembles that of the similar-sized, less common but more widely

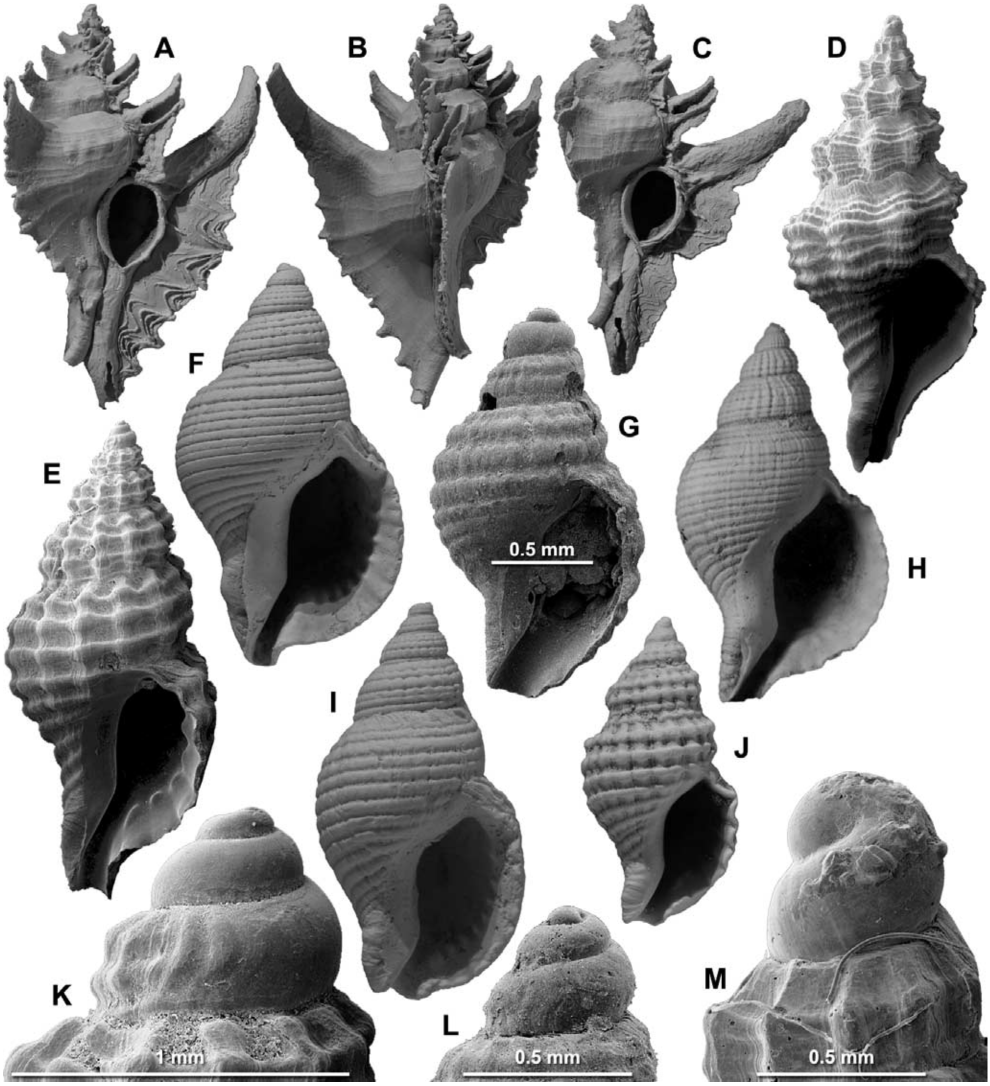

Figure 8 (A–C) *Ponderia zealandica* (Hutton), type species of *Ponderia* Houart, 1986, Tainui Shellbed (Castlecliffian, OIS 13), Wanganui; A,B, GS4013, R22/f6353, "the buttress", Castlecliff; height 30.0 mm; C, holotype, TM8294, "Shakespeare Cliff", Wanganui; height 27.3 mm. (D,M) *Axymene aucklandicus* (Smith), type species of *Axymene* Finlay, 1926, coarsely sculptured form, GS10963, R22/f6619A, Tainui Shellbed (Castlecliffian, OIS 13), "the buttress", Castlecliff, SEM; D, whole specimen, height 13.6 mm; M, protoconch of D. (E,K) *Xymenella pusilla* (Suter), type species of *Xymenella* Finlay, 1926, RM4389, Recent, MV "*Wahine*" wreckage, Taranaki Street wharf, Wellington, SEM; E, whole specimen, height 8.9 mm; K, protoconch of E. (F,H) *Xymene expansus* (Hutton); F, GS15338, S22/f0164, *Maoricrypta*-dominated shellbed, Turakina Valley Road, early Castlecliffian, c. OIS 43–41; height 24.1 mm; H, Hutton's figured syntype, CMC M3301, "Wanganui", ex Drew collection; height 22.8 mm. (G,J,L) *Xymene plebeius* (Hutton), type species of *Xymene* Iredale, 1915; G, juvenile, SEM, GS14698, Q31/f0431, Kaikoura Peninsula high terrace (last interglacial, OIS 5e-5c?); L, protoconch of G; J, RM1950, Recent, Laingholme, Manukau Harbour, Auckland; height 11.5 mm. (I) *Xymene drewi* (Hutton), GS12711, V20/f045, Kaiwaka Limestone (late Nukumaruan), quarry near junction Turnbull and Waipunga Roads, above Esk Valley, N of Napier; height 14.7 mm.

stratigraphically distributed species *Prototyphis eos* (Hutton, 1873) in being thin, flange-like and almost flat, bearing low, wavy lamellae in conformity with three low radial frills that are not well preserved on most specimens. However, the long shoulder spine and closed canals make *Ponderia zealandica* readily recognized.

Dell & Fleming (1964) recorded a specimen of *Ponderia zealandica* dredged in Cook Strait, on a rough bryozoan bottom (M.17977, listed above). Nearby areas in Cook Strait have since yielded 17 further specimens. It appears that this species has occupied bryozoan-dominated substrates in the same area for at least the last half-million years. Fleming (1962a) surmised that the Norfolk Island endemic species he called '*Pterynotus' zealandicus iredalei* (= *Ponderia canalifera*) indicated that the similar form *P. zealandica* was among the warm-water migrants that appeared briefly in New Zealand from the north during interglacial periods, but actually it is a temperate Cook Strait and East Cape species in an otherwise subtropical to tropical SW Pacific genus. The limitation of this species to Tainui Shellbed in the Wanganui succession presumably results from a narrow ecological tolerance, and the rare preservation of the offshore bryozoan-oyster community in the Wanganui succession. The other tripterotyphine in the Wanganui fauna, *Prototyphis eos* (= *P. angasi powelli* Fleming, 1962) occurs more widely in Waipuru Shellbed, Kaikokopu Shellbed (two collections), Kupe Formation, and Lower Castlecliff Shellbed (Fleming 1953:151, 199, 203, 218), and was collected from Pinnacle Sand by Mrs Jean Boswell, reflecting its wider tolerance of a variety of rocky shallow-water and offshore environments at present. Houart & Héros (2008:473) listed the species referred to *Prototyphis*, nearly all of which are limited to New Zealand. The exceptions are *P. angasi* (Crosse, 1863), which occurs in southeastern Australia, and *P. gracilis* Houart & Héros, 2008 from Fiji.

Three fragmentary specimens from Devils Elbow Mudstone at the top of Devils Elbow hill, Highway 2 ca 35 km N of Napier, Hawke's Bay (late Nukumaruan; GS10849, V20/f8572) are much larger than *Ponderia zealandica*, but otherwise similar (H 40.0, D [incomplete] 21.4 mm; H [incomplete] 34.2, D 20.4 mm).They possibly represent a large, unnamed species of *Ponderia* reaching about 50 mm in height. However, more prominent spiral cords around the base and secondary spines on the face of the terminal varix suggest a closer relationship with *Prototyphis eos*. As usual, only more material can resolve the status of this form.

Subfamily Ocenebrinae

Genus ***Xymene*** Iredale, 1915

Kalydon Hutton 1883b:576; Hutton 1884:222 (Marshall 1995:495). Type species (by monotypy): *Fusus plebeius* Hutton, 1873, Pleistocene and Recent, New Zealand (suppressed, ICZN Opinion 911 1970). Iredale (1915:471) pointed out that *Kalydon* is a junior homonym of *Calydon* Thomson, 1864; this is still the case under ICZN Article 58.5.

Xymene Iredale 1915:471. Type species (by original designation): *Fusus plebeius* Hutton, 1873, Pleistocene and Recent, New Zealand. (Although essentially a replacement name for *Kalydon* Hutton, 1883, *Xymene* was proposed specifically as a new genus, with a type species designation.)

Remarks. *Xymene* was used by Ponder (1972) as an all-encompassing genus for most New Zealand Ocenebrinae, including several taxa that, considering the level of genera currently recognized in the Muricidae, are clearly not congeneric. The complex is being revised by BA Marshall and R Houart (pers. comm.), and most taxonomic revision will be covered by them, but as an initial step the genera *Axymene*, *Xymenella* and *Zeatrophon* of Finlay (1926b) are separated again here from *Xymene*. *Xymene plebeius* (Fig. 8G, J, L) and other species of *Xymene* (sensu stricto) have a distinctive, very short, smooth, conical, paucispiral protoconch of ca 2.2 whorls, with a low, wide, hemispherical initiation with an in-rolled, slightly heterostrophic appearance. The junction with the teleoconch is rather obscure, suggesting that this is a lecithotrophic protoconch. In combination with the distinctive, wide spiral cords on the teleoconch, the weak axial ridges producing low nodules at sculptural intersections, and the simple aperture with a lightly flared outer lip, this protoconch allows recognition of a separate genus *Xymene*. *Axymene aucklandicus* (Fig. 8D,M), type species of *Axymene* Finlay, 1926, also has a paucispiral, smooth protoconch, but it consists of little more than one whorl, and is much more upright and dome-shaped than that of *Xymene* (sensu stricto), with a large, swollen initiation and a deeply impressed suture, similar to protoconchs of many Cancellariidae. The junction with the teleoconch is abrupt, as the shell acquires normal teleoconch axial ridges. This is more certainly a lecithotrophic protoconch than that of *Xymene*, and indicates possible direct development. Combined with the more elongate teleoconch shape, the more strongly shouldered whorls, the more prominent, sparser teleoconch sculpture, foliose on some specimens, and the less flared aperture with nodules inside the outer lip, the much more paucispiral protoconch allows distinction of the genus *Axymene* from *Xymene*. In contrast, the other similar genera, *Zeatrophon* and *Xymenella*, have taller protoconchs with more numerous whorls. *Zeatrophon bonneti* (Fig. 9D) has a tall, conical, multiwhorled protoconch of ca 3.2 whorls, sculptured entirely with fine, widely spaced granules, more obvious on the first whorl than lower down, and with a distinctive spiral keel around the last whorl. The junction with the teleoconch is abrupt and obvious, and development clearly is planktotrophic. *Z. ambiguus* (Fig. 9J has a similar tall, conical protoconch, but smooth and a little shorter, of only ca two whorls, with a larger initiation; the junction with the teleoconch is much less abrupt than that of *Z. bonneti*. The protoconch developes a keel on the last half-whorl, but less obvious than that of *Z. bonneti*, and this passes gradually into the first teleoconch spiral cord, and gradually acquires teleoconch axial sculpture. This, therefore, seems to be a lecithotrophic protoconch, and the distinction from that of *Z. bonneti* probably once again merely reflects the developmental difference. Combined with the prominently lamellate, clathrate teleoconch sculpture of species assigned to *Zeatrophon*, the genus is easily recognized within the New Zealand context. However, its relationships to such genera as *Trophon*, *Trophonopsis* and *Boreotrophon* need to be defined. *Xymenella pusilla* (Suter, 1907) (Fig. 8E, K), type species of *Xymenella* Finlay, 1926, has a similar protoconch to that of *Xymene* species, but a little taller and more obviously conical, of ca 2.5 whorls, joining the teleoconch abruptly after 2–3 prominent, curved axial ridges. The teleoconch is distinctive because of its prominent, convex-crested spiral cords, small size but relatively tall shape, and very prominent nodules inside the outer lip. Not all the small New Zealand ‘trophonine’ taxa fit neatly into these genera, however, and e.g. the generic position of ‘*Zeatrophon*’ *huttoni* (Murdoch, 1900) is not obvious (although this is a reasonably common fossil at Castlecliff). These genera require clarification and confirmation, including radular study.

Some of the younger fossil species of *Xymene* (sensu stricto) are reviewed here, as they are useful in Nukumaruan–Castlecliffian biostratigraphy, as pointed out by Fleming (1955:521) when correlating the Castlecliffian rocks at Ohope Beach, Whakatane. Because of its intertidal environment, *Xymene* appears to have a mostly late Neogene time range, but this is a classic case of the poor preservation of the near-shore environment in the fossil record.

Named species included in *Xymene* (sensu stricto):

Xymene coctor Marwick, 1948, Waipipian, Otahuhu well, Auckland (based on abundant, very small, apparently immature specimens with fewer spiral cords and wider spiral interspaces than *X. drewi*; status unclear).

Xymene drewi (Hutton, 1882) (Fig. 8I), Mangapanian–late Nukumaruan (to ca OIS 73-71?).

Xymene expansus (Hutton, 1882) (Fig. 8F, H), late Nukumaruan–early Castlecliffian (ca OIS 73–19).

Xymene moniliferus (Hutton, 1885), Opoitian?, 'Shepherd's hut, Waipara', N Canterbury (Waiauan–Waipipian according to Ponder's (1972:478) synonymy; early forms of *Xymene* require further study, based on better material; they are more coarsely sculptured than *X. drewi*).

Xymene plebeius (Hutton, 1873) (Fig. 8G, J, L), Castlecliffian (OIS19/17)–Recent.

Xymene pulcherrimus (Suter, 1917), Waipipian, Starborough Creek, Awatere (possibly = *X. moniliferus* and/or *X. coctor*). This name is a senior secondary homonym of '*Xymene*' *pulcherrimus* (Finlay, 1930), proposed in *Zeatrophon*, but listed in *Xymene* by Ponder (1972:468), Powell (1979:174) and Spencer & Willan (1996:26). Returning to a position in *Zeatrophon* would remove the necessity for a replacement name, so one is not proposed here, although it should have been proposed by Ponder (1972).

Xymene drewi (Hutton, 1882) (Fig. 8F)

Cominella drewi Hutton 1882:278 (Marshall 1995:497); Hutton 1883a:410.

Pisania drewei (sic). Hutton 1893:42, pl. 6, fig. 13.

Euthria drewi. Suter 1915:23 (in part).

Xymene drewi. Marwick 1924b:198, pl. 17, fig. 8; Finlay 1926b:424; Fleming 1966:232, fig. 1240.

Xymene plebeius expansus. Ponder 1972:477, fig. 3.6, 7 only; Beu & Maxwell 1990:415 (in part not *Xymene expansus* Hutton, 1882).

Xymene expansus. Maxwell 2009:246 (in part not *Xymene expansus* Hutton, 1882).

Type material. *Cominella drewi*, 'holotype' (invalid lectotype of Suter 1915:23) CMC M3222, from 'Wanganui'; this specimen (a specimen of *Buccinulum*) is concluded here to be the paralectotype; 'paratype' (valid lectotype of Marwick 1924b:198) CMC M3223, also from 'Wanganui' (Bradshaw et al. 1992:63). Both are probably from Nukumaru Brown Sand at Nukumaru Beach, although the horizon of CMC M3222 is uncertain.

The status of the type material of *Cominella drewi* is confusing. Suter (1915:23) treated one of the two syntypes present in CMC as the 'holotype' and the other as the 'paratype' (that is, inadvertently designating them as lectotype and paralectotype under ICZN Article 74.6), although he did not illustrate them, it is not known what evidence he used to make this choice, and it is not possible to tell from Suter's text which specimen was designated as which; Suter's (1915) text is a bald description, with no qualifying statements, and there is no definite evidence that Suter's 'holotype' was among Hutton's type specimens. Indeed, there is no way of demonstrating that the labels are not now associated with the wrong specimens. Marwick (1924b:198), possibly on the basis of Suter's now missing labels, stated that Suter, apparently not realizing that the 'holotype' and 'paratype' represent two distinct genera and species, had chosen the larger specimen as 'lectotype and wrongly called "holotype" by him', although the 'holotype' does not agree with Hutton's description, Hutton's stated dimensions, or Hutton's (1893, pl. 6, fig. 13) illustration, which is a drawing of the specimen regarded by Suter as the 'paratype'. Marwick (1924b:198) noted that 'the smaller one is what has generally been considered as *Euthria drewi*, and is the specimen figured in the *Macleay Memorial Volume* [Hutton 1893]. It has therefore a better claim to be considered the type of *E. drewi* than does the shell chosen by Suter'. The problem is that Suter's lectotype is a poor, abraded specimen of *Buccinulum* cf. *littorinoides* (Reeve, 1846), family Buccinidae (illustrated by Fleming 1966, pl. 106, figs. 1289, 1290, from a sketch by J Marwick; Fleming (1966) identified it as 'paralectotype of *Cominella drewi* Hutton, wrongly called "Holotype" by Suter'), whereas the specimen identified as the paralectotype by Suter is the *Xymene* species that was illustrated by Hutton (1893, pl. 6, fig. 13) and consequently has borne this name consistently up until the revision by Ponder (1972) (who evidently did not realize the complications underlying this name). Marwick's solution was to regard Suter's lectotype selection as invalid, although he did not state so explicitly. He did, however, illustrate the *Xymene* specimen (CMC M3223) and identified it as the lectotype (Marwick 1924b, pl. 17, fig. 8). Acceptance of Suter's lectotype designation would necessitate adopting a different (possibly new) name for this well-known species, and consigning the accepted name to the synonymy of one or other of several *Buccinulum* species (the specimen is so abraded that it is not clear which species it belongs in). I therefore follow Marwick (1924b) in treating Suter's (1915) inadvertent lectotype designation as invalid, as it did not select the specimen and species illustrated by Hutton (1893) and does not agree with the species described by Hutton (1882, 1883a), and I regard the lectotype designation by Marwick (1924b, pl. 17, fig. 8) as the valid one. This case seems to be covered by ICZN Article 74.2: 'If it is demonstrated that a specimen designated as a lectotype was not a syntype, it loses its status as a lectotype'. Suter's inadvertently designated lectotype is not conspecific with the species described and illustrated by Hutton, and so seems unlikely to have been a syntype, and under Article 74.2 cannot be considered to be the lectotype.

Other material examined. Not listed; abundant. *Xymenedrewi* was recorded by Fleming (1953:119, 140, 144, 146, 148, 151, 158, 163, 174) from Mangapani Shellbed, Nukumaru Limestone, Nukumaru Brown Sand (along with '*Xymene* cf. *expansus*'), Mangamako Shellbed, undifferentiated shellbeds of Nukumaru Group, Waipuru Shellbed, Tewkesbury Formation (along with '*Xymene* aff. *expansus*'), Pukekiwi Shell Sand ('*Xymene* aff. *drewi*', along with '*Xymene expansus*, derived') and Butler's Shell Conglomerate (in square brackets, indicating that he thought it reworked from older rocks) in Wanganui Basin. It also occurs widely and commonly in Nukumaruan rocks of Hawke's Bay, Wairarapa and North Canterbury, in shallow-water sandstone units with common *Zethalia* and other shoreface taxa.

Distribution. The earliest occurrence is unclear, but *Xymene drewi* certainly occurs in early Mangapanian rocks; it presumably evolved from still more coarsely sculptured species such as *X. pulcherrimus* (=*X. coctor*?) in Waipipian rocks. It extends as young as Nukumaru Brown Sand and Tewkesbury Formation in the Wanganui succession, that is, latest Nukumaruan, early Pliocene. It is common in shoreface rocks throughout Wanganui Basin, Hawke's Bay, Wairarapa and North Canterbury. *X. pulcherrimus* (Suter 1917:38, pl. 12, fig. 8), from Starborough Formation (Waipipian), Starborough Creek, Awatere valley, differs little from *X. drewi* in most characters other than its coarser spiral sculpture and may well intergrade gradually—that is, this might well be an anagenetic series—and would then indicate a range from at least Waipipian to Nukumaruan.

Dimensions. Hutton (1893:42) stated the dimensions as 'length 20 mm; breadth 11 mm'. Suter (1915:23) stated the dimensions as H 17, D 8 mm, probably referring to the *Buccinulum* specimen he wrongly selected as the 'holotype'. Marwick (1924b:199) stated the dimensions of the lectotype as H 13, D 7 mm, and pointed out that Hutton usually seems to have provided the dimensions of the largest specimen available, regardless of the dimensions of his type material; GS12711, V20/f045, Kaiwaka Limestone (Nukumaruan), Kaiwaka South Road, Hawke's Bay: H 13.7, D 8.1 mm; H 14.7, D 7.6 mm; H 17.1, D 8.9 mm; H 13.5, D 7.4 mm; GS1984, V22/f6496, Maraekakaho Creek, S side Ngaruroro River, central Hawke's Bay, Nukumaruan: H 17.2, D 9.2 mm; H 16.9, D 9.2 mm.

Remarks. *Xymene drewi* is the common, widespread, typical *Xymene* species of Nukumaruan rocks. As pointed out by Marwick (1924b:199), 'Generically this shell cannot be separated form *Xymene plebeius* (Hutton), from which it differs in the non-carination of the whorls', that is, *X. drewi* lacks the shoulder angulation, demarcating the obvious sutural ramp, that is so prominent on *X. plebeius* and *X. expansus*. Although it is similar in size to *X. plebeius*, *X. drewi* also differs from *X. plebeius* in its wider and shorter shape, thicker shell, and wider, more closely spaced spiral cords. From *X. expansus*, apparently the immediate descendent of *X. drewi*, it differs in its smaller size, thicker shell, narrower shape, coarser spiral sculpture and lack of the characteristic expanded last whorl mid-section developed by adult *X. expansus*. *X. expansus* also has a markedly thinner outer lip, with less obvious internal ridges than *X. drewi*, has a more markedly left-directed anterior siphonal canal, and develops a shallow sinus in the outer lip, corresponding to the low carina at the shoulder angle, that is absent from *X. drewi*. *X. plebeius* also differs from *X. drewi* in having the more markedly left-directed anterior siphonal canal of *X. expansus*, but has narrower, more clearly separated spiral cords than either similar species.

Ponder (1972) was impressed by the apparent intergradation between *Xymene drewi* and *X. expansus*, and synonymized these names. However, the collection he examined was an early, mixed one, from both Nukumaru Brown Sand and Tewkesbury Formation, and more careful localization of specimens has demonstrated that these are separate species, stratigraphically segregated to some extent (*X. drewi* in Nukumaru Brown Sand, *X. expansus* in Tewkesbury Formation), and apparently occupying slightly different environments. *X. expansus* seems to have inhabited more strongly estuarine environments than *X. drewi*, presumably part of a gradual adoption of a more estuarine environment through the lineage, as *X. plebeius* occurs only on hard substrates in estuaries at present. Ponder's (1972, fig. 3, nos. 6–8) illustrations show two specimens of *X. drewi* (nos. 6, 7) and one of *X. expansus* (no. 8). This, then, is a biostratigraphically useful lineage in shallow-water rocks, *X. drewi* occurring in Mangapanian to late Nukumaruan rocks, *X. expansus* occurring in late Nukumaruan and early Castlecliffian rocks (Nukumaru Brown Sand to about Kupe Formation [OIS 17] at Wanganui), and *X. plebeius* occurring in late Castlecliffian to Recent faunas. The evolution from *X. drewi* to *X. expansus* was not a simple one, and if these species had an ancestor-descendent relationship, *X. drewi* survived for a short period after the evolution of *X. expansus*. The evolutionary change from *X. expansus* to *X. plebeius* also seems to have been gradual over a short but appreciable period (OIS 19–17), although it is possible that specimens reworked from older units confuse this picture.

Xymene expansus (Hutton, 1882) (Fig. 8F, G)

Trophon expansos (sic) Hutton 1882:278 (Marshall 1995:497).
Trophon expansus. Hutton 1883a:410; Hutton 1893:39, pl. 6, fig. 5.
Trophon (Xanthochorus) expansus. Cossmann 1903:52, pl. 3, fig. 6; Suter 1915:27.
Xymene expansus. Finlay 1926b:424; Fleming 1966:57; Beu & Maxwell 1990:359, pl. 48e; Maxwell 2009:246 (in part not *Xymene expansus* Hutton, 1882).
Xymene plebeius expansus. Ponder 1972:427, fig. 3, no. 8 only (in part not *Trophon expansus* Hutton, 1882).

Type material. *Trophon expansus*, holotype CMC M-3301 (Fig. 8H), with two paratypes, M-3302, from 'Wanganui', ex Drew collection (Bradshaw et al. 1992:64) (these are probably better considered as three syntypes). The type horizon is unknown, but seems likely to be Tewkesbury Formation. Marshall (1995:497) pointed out that the original spelling '*expansos*' (a typographical error?) is an incorrect Latin termination, and adoption of '*expansus*' is mandatory.

Other material examined. *Xymene expansus* was recorded by Fleming (1953:144, 158, 163, 174, 178, 181, 182, 188, 199, 203–204) from Nukumaru Brown Sand (as *X.* cf. *expansus*), Tewkesbury Formation (as *X.* aff. *expansus*), Pukekiwi Shell Sand ('derived'), Butler's Shell Conglomerate (OIS 31), basal conglomerate member of Lower Okehu Siltstone (OIS 29; Mowhanau Formation of Abbott & Carter 1999), Okehu Shell Grit (OIS 27), basal conglomerate member of Upper Okehu Siltstone (OIS 27; *Ostrea-Dosinia* bed of Abbott & Carter 1999), Kaimatira Pumice Sand (OIS 25), Kaikokopu Shell Grit (along with '*Xymene* aff. *expansus* aff. *plebeius*'; OIS 19) and Kupe Formation (OIS 17; in square brackets, 'derived', along with *X.* cf. *plebeius*). It also occurs widely in late Nukumaruan shoreface sands in central and southern Hawke's Bay. Fleming & Marwick (in Lillie 1953, table 22) recorded *X. expansus* from GS2324, U23/f6376 and GS2457, U23/f8355, in Nukumaruan Upper Kumeroa Formation in Dannevirke district, southern Hawke's Bay, and commented: '… *Xymene expansus* (Hutt.), a common lower Castlecliffian fossil which ranges down into the uppermost Nukumaruan rocks' (Fleming & Marwick in Lillie 1953:139).

Distribution. Late Nukumaruan–early Castlecliffian (ca OIS 71 to ca OIS 19/17), in Wanganui Basin and Hawke's Bay.

Dimensions. *Trophon expansus*, Hutton's figured syntype: H 22.8, D 13.3 mm; GS15338, S22/f0164, *Maoricrypta*-dominated shellbed, Turakina Valley Road, near Mangara Stream, early Castlecliffian: H 24.9, D 14.5 mm; H 22.0, D 13.2 mm; H 23.5, D 13.7 mm; H 21.2, D 11.4 mm.

Remarks. *Xymene expansus* is characterized by its larger, wider teleoconch than either *X. drewi* or *X. plebeius*, and by its thinner-shelled, lighter-weight appearance produced by the lower, wider spiral cords and thinner outer lip than in either similar species. The outer lip is also angled sharply outwards at the base of the sutural ramp more obviously than in either *X. drewi* or *X. plebeius*, and in most larger specimens of *X. expansus* the last whorl is expanded markedly more widely than in either similar species (presumably inspiring the species name) and the outer lip is flared weakly. The low, closely spaced spiral cords and weak axial ridges are also obviously less prominent than in either *X. drewi* or *X. plebeius*. This is therefore quite a distinctive species, resembling an unusually large, wide, weakly sculptured specimen of *X. plebeius* with a more sharply angled outer lip profile. Very large specimens of the '*inferus* form' of *X. plebeius* are as tall as normal specimens of *X. expansus*, but differ from *X. expansus* in their narrower shape and narrower sutural ramp. Most large specimens of *X. plebeius* are corroded so severely that their spiral cords are not visible.

Xymene plebeius (Hutton, 1873) (Fig. 8G, J, L)

Fusus plebeius Hutton 1873a:9; Hutton 1873b:3.
Fusus inferus Hutton 1873a:9.
Trichotropis clathrata. EA Smith 1874:3, pl. 1, fig. 21 (Beu 2010, Fig. 1N) (in part not *Trichotropis clathrata* GB Sowerby II August 1874, pl. 2, fig. 10).
Kalydon plebeius. Hutton 1884:220.
Kalydon inferus. Hutton 1884:220.
Trophon (Kalydon) inferus. Suter 1913:414, pl. 46, fig. 17.
Trophon (Kalydon) plebejus (sic). Suter 1913:416, pl. 46, fig. 19.
Xymene plebeius. Iredale 1915:471; Fleming 1966:57; Powell 1979:173, pl. 37, fig. 16; Spencer & Willan 1996:26; Spencer et al. 2009:210; Maxwell 2009:246.
Xymene inferus. Iredale 1915:471; Finlay 1926b:424.
Xymene plebejus. Finlay 1926b:424.
Xymene plebeius plebeius. Ponder 1972:475, fig. 1, no. 1; fig. 2, no. 1; fig. 3, nos. 1–5; Beu & Maxwell 1990:415.

Type material. *Fusus plebeius*, lectotype (of Ponder 1972, fig. 3) NMNZ M.80, with two paralectotypes M.1820 (Marshall 1996:24), from 'New Zealand'; no locality was stated by Hutton (1873a:9). According to Ponder (1972:475) the type material of *Fusus inferus* is lost; Hutton (1973a:10) stated the locality as 'Stewart's Island', southern New Zealand, and similar unusually large, severely corroded specimens have been collected recently on tidal flats near the head of Patterson Inlet. In order to associate the name unambiguously with a species, so that it cannot threaten the stability of other names, the lectotype of *Fusus plebeius* Hutton, 1873, NMNZ M.80, is here designated the neotype of *Fusus inferus* Hutton, 1873. The synonymy list by Ponder (1972:475) provided the first reviser's action selecting the name *Fusus plebeius* as the valid one of the two names proposed by Hutton (1873a), *Fusus plebeius* and *Fusus inferus*.

Other material examined. *Xymene plebeius* was recorded by Fleming (1953:199, 203–204, 207, 214, 218, 226, 230, 242, 245, 261, 273) from Kaikokopu Shell Grit (as '*Xymene* aff. *expansus* aff. *plebeius*'; OIS 19), Kupe Formation (as '*X*. cf. *plebeius*') and Upper Kai-Iwi Siltstone (OIS 17), Seafield Sand and Lower Castlecliff Shellbed (as '*X*. cf. *plebeius*'; OIS 15), Pinnacle Sand and Tainui Shellbed (OIS 13), Mosstown Sand (OIS 11?), Landguard Sand and Brunswick Formation (OIS 9), Denby Shellbed, at Hawera, and Waipuna Conglomerate (OIS 7) in Wanganui Basin. It is not a common fossil elsewhere, but occurs in some young Pleistocene terrace cover beds throughout New Zealand; Holocene, 1 m below surface, 150 m N of Henley railway station, Taieri Plains, Otago (GS3513, H45/f9479, abundant), and other Holocene fossils throughout New Zealand.

Distribution. Mid-Castlecliffian (ca OIS 19–17) to Recent; most fossil records are from Wanganui Basin. Recent specimens live throughout New Zealand on stones and shells—that is, any available hard substrate—lying on soft substrates in estuaries.

Dimensions. GS3513, Henley, Taieri Plains, Holocene: H 16.4, D 9.1 mm; H 16.5, D 9.3 mm; H 12.7, D 6.9 mm; H 10.8, D 5.7 mm; H 10.9, D 5.8 mm; RM1950, Recent, Langholme, Manukau Harbour, Auckland: H 14.9, D 6.9 mm; H 11.2, D 5.5 mm; H 11.6, D 5.9 mm; '*inferus*' form, Stewart I., Suter collection no. 4021: H 26.6, D 12.7 mm.

Remarks. Comparisons with *Xymene drewi* and *X. expansus* are provided above. *Xymene plebeius* is easily distinguished from all earlier species by its narrower shape and the more prominent appearance of its sculpture, produced by the narrower, more widely separated spiral cords. It also has a sutural ramp defined clearly by an obvious shoulder angulation, as in the larger and thinner-shelled species *X. expansus*, but the angulation is absent from or much weaker on all earlier species.

Genus ***Axymene*** Finlay, 1926

Axymene Finlay 1926b:424. Type species (by original designation): *Axymene turbator* Finlay, 1926 (= *Euthria aucklandica* E. A. Smith, 1902), central and southern New Zealand, Mangapanian–Recent (Ponder 1972:494–495, fig. 8).

Axymene aucklandicus (E. A. Smith, 1902) (Fig. 8D, M)

Euthria aucklandica E. A. Smith 1902:203, pl. 24, figs. 12, 13.
Trophon (Kalydon) columnaris Suter 1908:178, pl. 7, fig. 1 (?junior primary homonym of *Trophon columnarius* Hedley & May, Sept. 1908).
Trophon (Kalydon) erectus Suter 1909a:27 (replacement name for *T. columnaris* Suter, 1908); Suter 1913:414, pl. 19, fig. 7.
Trophon (Kalydon) aucklandicus Suter 1909a:27; Suter 1909b:254; Suter 1913:411, pl. 46, fig. 18.
?*Buccinulum pertinax*. Finlay 1926b:422 (not *Euthria lineata pertinax* von Martens, 1878).
Axymene erectus. Finlay 1926b:424.

Axymene turbator Finlay 1926b:426, pl. 23, figs. 127, 128.
Axymene traversi aucklandica. Fleming 1951:137, pl. 18, fig. 4; Powell 1955:105.
Axymene traversi erectus. Fleming 1951:137; Powell 1955:104.
Xymene aucklandicus. Ponder 1972:494, figs. 1.7, 2.16, 17, 8.1–8; Powell 1979:175; Beu & Maxwell 1990:415; Spencer & Willan 1996:26; Spencer et al. 2009:210; Maxwell 2009:246.

Type material. Euthria aucklandica, lectotype designated by Fleming (1951:137, caption to pl. 18, fig. 4), BMNH 1902.5.16.18, with three paralectotypes BMNH 1902.5.16.19-21, all from Auckland Islands, 20 m. *Trophon columnaris* Suter, lectotype TM957, with 10 paralectotypes, TM958-967, designated by Boreham (1959:47), from near the Bounty Islands, 100 m. Boreham expressly designated the lectotype for *Axymene traversi erectus* (Suter, 1909), but as *Trophon erectus* was a replacement name for the preoccupied *Trophon columnaris* Suter, 1908, Suter's type material was identified only as '*Trophon erectus*' by Suter (the original label evidently having been discarded), Boreham did not mention the replaced name, and there is no separate type material for *T. columnaris*, Boreham's designation applies equally to the replaced and replacement names, in the spirit of ICZN Article 72.7. *Axymene turbator*, holotype AIM AK70088, with two paratypes AK72906, AK72907 (not seen). Finlay (1926b:426) published the type locality as 'Dunedin Harbour, under stones at low tide', but the type material is labelled 'Taieri Beach, 8 km S of Taieri River', S Otago coast (Owen Lee, AIM pers. comm. Nov. 2007).

Other material examined. Tainui Shellbed strongly sculptured form: GS10963, R22/f6619A, re-collection of GS4013, Tainui Shellbed (OIS 13) at 'the buttress', Castlecliff coastal section, Wanganui (nine, including TM5523, specimen illustrated by Ponder [1972, fig. 8.7]); GS4013, R22/f6353, Tainui Shellbed at 'the buttress' (35); GS4022 re-collection, R22/f6360, head of 'the pinnacles' gully (one). Recorded also by Fleming (1953:230) from Tainui Shellbed in GS4031, R22/f6369; GS4097 and GS4102, both allocated R22/f6516; all from the Castlecliff coastal section.

Fleming (1953:203–204, 207, 218, 226, 239) also recorded '*Aymene* n. sp.' from two members of Kupe Formation at Castlecliff, and from Upper Kai-Iwi Siltstone, Lower Castlecliff Shellbed, Pinnacle Sand, and Upper Castlecliff Shellbed, but examination of these specimens has shown that his identifications were based on more normal specimens of either *A. aucklandicus* or *A. traversi* (Hutton, 1873). Fleming (1953) also listed '*Xymenella* n. sp.' from several units, but again these are based on only slightly unusually sculptured specimens of *X. pusilla* (Suter, 1907). A range of other Mangapanian–Haweran localities for *A. aucklandicus* was listed by Ponder (1972:495).

Distribution. *Axymene aucklandicus* occurs widely in New Zealand in rocks of Mangapanian to Castlecliffian age, at a few Haweran localities, and in the Recent fauna throughout central and southern New Zealand. The more strongly spirally sculptured, axially foliate form described here is restricted to Tainui Shellbed (OIS 13), as far as I am aware. Most material is from the Castlecliff coastal section, because of its excellent exposure.

Dimensions. Lectotype of *Euthria aucklandica*: H 8.6, D 4.1 mm; paralectotypes: H 9.3, D 4.2 mm; H 8.8, D 4.0 mm; H 7.4, D 3.2 mm; GS4013, Tainui Shellbed at 'the buttress', Castlecliff: H 14.2, D 6.5 mm (TM5523); H 18.0, D 7.5 mm; H 15.6, D 6.7 mm; H 14.8, D 6.2 mm.

Remarks. Ponder (1972:494, figs. 1.7, 2.16, 17, 8.1–8) described the variation and range of *Axymene aucklandicus* (under *Xymene*). His description of the large range of variation exhibited by both *A. aucklandicus* and the other common, widespread species, *A. traversi*, allows recognition that the many forms identified by Fleming (1953) as '*Axymene* n. sp.' are part of the variation of one or the other of these species. Ponder also commented that 'A fossil population from the Tainui Shellbed at Castlecliff, Wanganui, has a stronger shoulder and more distinct secondary axial foliation than most Recent shells (fig. 8:7). Other Castlecliffian shells resemble Recent specimens so that the Tainui form is here regarded as merely an aberrant population of *aucklandicus*. Somewhat similar shells are found in deep water off the Otago coast' (Ponder 1972:495). As this distinctive form is limited to Tainui Shellbed, I examined it to assess its utility in biostratigraphy. The prominent, narrow, well-separated spiral cords distinguish Tainui Shellbed specimens from most other specimens of *A. aucklandicus*. However, they are not as distinctive as the more clearly defined, wider, almost smooth sutural ramp having only weak spiral sculpture, the narrowly rounded peripheral angulation, and the well-defined axial foliation, which separate the Tainui Shellbed form from all other specimens of *A. aucklandicus*. The most extremely coarsely sculptured specimens of *A. aucklandicus* I have examined from other localities (RM19, Lyall Bay, Wellington, one; GS12290, E38/f015, boulders in Whiskey Creek, N coast of Cascade Point, S Westland; Castlecliffian, ca OIS 25; three) differ from Tainui Shellbed specimens in their smooth, lightly polished surface, without any axial foliation, and in having a consistently narrower sutural ramp and less obvious peripheral angulation, despite their prominent, narrow, widely spaced spiral cords, similar to those of Tainui Shellbed specimens. The smooth, paucispiral, dome-shaped protoconch of Tainui Shellbed specimens is also indistinguishable from that of other specimens of *A. aucklandicus*. Also, a few large specimens in the Tainui Shellbed population develop a more rounded periphery, less sharply defined sutural ramp and weaker spiral cords over the last half-whorl, and closely resemble the more coarsely sculptured end-members of other populations. I therefore conclude that Ponder (1972:495) was correct to rank this form as part of the variation of *A. aucklandicus* rather than as a distinct species. Although this form seems to be limited to Tainui Shellbed, and will have some minor utility in biostratigraphy, its reliability is very low.

Typical specimens of *Axymene traversi* occur in small numbers in Tainui Shellbed syntopically with *A. aucklandicus*, and are immediately separable by retaining their coralline algal encrustation, as well as by their much weaker spiral sculpture, sharper peripheral nodules, and taller protoconch with more numerous whorls than in *A. aucklandicus*. They also bear a prominent spiral carina on the last protoconch whorl that is absent from *A. aucklandicus*. Similar-sized specimens of '*Zeatrophon*'(?) *huttoni* (Murdoch, 1900) also occur in small numbers syntopically with both *A. traversi* and *A. aucklandicus*.

Genus ***Zeatrophon*** Finlay, 1926

Zeatrophon Finlay 1926b:424. Type species (by original designation): *Fusus ambiguus* Philippi, 1844).

Remarks. The genus *Zeatrophon* is used here without prejudice, as a group to contain the following species deserving comment in this paper, and requiring removal from *Xymene*. The correct generic position must await the revision by Marshall & Houart (pers. comm.). *Zeatrophon bonneti* (Cossmann, 1903) has a distinctive, tall and relatively narrow, granulose protoconch of ca 3.2 whorls with a prominent spiral keel on the last whorl (Fig. 29F), whereas the type species, *Z. ambiguus* (Philippi, 1844), has shorter, smooth protoconch of ca 2.5 whorls (Fig. 29E,G) with a less obvious keel. However, it appears that the protoconch of *Z. bonneti* reflects planktotrophic development, whereas that of *Z. ambiguus* reflects lecithotrophic development, probably with at least a brief demersal larval life.

Zeatrophon bonneti (Cossmann, 1903) (Fig. 9A–D, H)

Trophon stangeri. Hutton 1893:38 (not *Trophon stangeri* Gray, 1843).
Trophon (Trophonopsis) bonneti Cossmann 1903:200, pl. 3, fig. 7.
Zeatrophon bonneti. Finlay 1926b:424; Fleming 1966:57.
Xymene bonneti bonneti. Ponder 1972:486, fig. 6: 1–4; Beu & Maxwell 1990:359, pl. 48m.
Xymene bonneti. Maxwell 2009:246.
Not *Trophon (Trophonopsis) bonneti*. Suter 1913:417, pl. 45, fig. 23 (incorrectly synonymized with *T. ambiguus pumila* Suter, 1899, Recent).

Type material. The holotype of *Trophon (Trophonopsis) bonneti* (Cossmann 1903:200, pl. 3, fig. 7) has been recognized recently in MNHN, Département Sciences de la Terre, and registered as J09323 (Fig. 9A,B; photos kindly sent by Didier Merle MNHN pers. comm. 29 June 2009). It is clear that this is indeed the specimen illustrated by Cossmann (1903, pl. 3, fig. 7), although the sculptural details have not been appreciated from Cossmann's small figure. It is from the collection of Bonnet, and is from 'Wanganui', New Zealand, presumably originally sent by a New Zealand collector such as R Murdoch. There is no doubt that Cossmann originally had only one specimen, so two others remaining in the Cossmann collection, Département Sciences de la Terre, MNHN (J08923) (Jean-Michel Pacaud MNHN pers. comm. August 2007) presumably were added from Bonnet's collection at a later date, and have no type status. The holotype raises a slight problem, as it is not a typical coarsely cancellate, grey-stained specimen from Castlecliff, but has a brownish yellow stain, a weaker peripheral spiral cord than typical specimens, and narrow, secondary spiral cords are present in all spiral interspaces. The sculpture is similar to that of specimens of the *lassus* and *murrayi* forms of *Z. bonneti*. The yellow stain and excellent preservation, completely free of matrix, suggest it is possibly from Landguard Sand (OIS 9) at Landguard Bluff, but the sculpture suggests it is more probably a Nukumaruan specimen from a locality such as Nukumaru Beach, or from Waipuru Shellbed or a similar stratigraphic horizon in the Rangitikei valley. The two non-type specimens bear Cossmann's label reading: '9670 N. Z. Wanganui *Trophon bonneti* Cossm. dedit. M. Bonnet'. They are more typical grey-stained, coarsely cancellate specimens, almost certainly from Castlecliffian rocks of the Wanganui coastal section, and probably from Tainui Shellbed, but it is impossible to be sure of the provenance of any of Bonnet's specimens. Recognition (below) that *Z. lassus* Marwick, 1928 and *Z. murrayi* Fleming, 1943 intergrade with *Z. bonneti* removes some of the difficulties presented by the holotype of *Z. bonneti*, but it is unfortunate that the holotype is so unlike the usual Castlecliff specimens.

Other material examined. **Nukumaruan**: 'Waikopiro', Suter collection (two); hillside above Glenstrae Station, Oaro, Marlborough (GS10337, O32/f8843; four); Devils Elbow Mudstone, top of Devils Elbow hill, Highway 2, N of Napier (GS10849, V20/f8572; 60+; GS2220, V20/f8462, two); Kaiwaka Limestone, Kaiwaka South Road, ascent from Esk Valley, N of Napier (GS12712, V20/f047A, five); Mairau Mudstone, walkway W of Roro-o-kuri, Bayview, Napier (GS12386, V21/f05, one); Mairau Mudstone, 'the watchman' hill, Ahuriri lagoon, Napier (GS11465, V21/f6015, two); Waipunga Road, 1.5 km S of junction with Kaiwaka Road, W of Devils Elbow (GS1983, V20/f8459, one); Maharekeke Mudstone, Maharakeke Road, W foot of Pukeora Hill, Waipukurau (GS10857, U23/f7049, four); Waipuru Shellbed, Mangawhero valley (GS4360, S22/f6485, two); shellbed 150 m above Waipuru Shellbed, upstream from Livingstone Bridge, Rangitikei River (GS3098, T22/f8494, two). **Castlecliffian**: Ototoka Siltstone (OIS 31), Ototoka beach, Wanganui

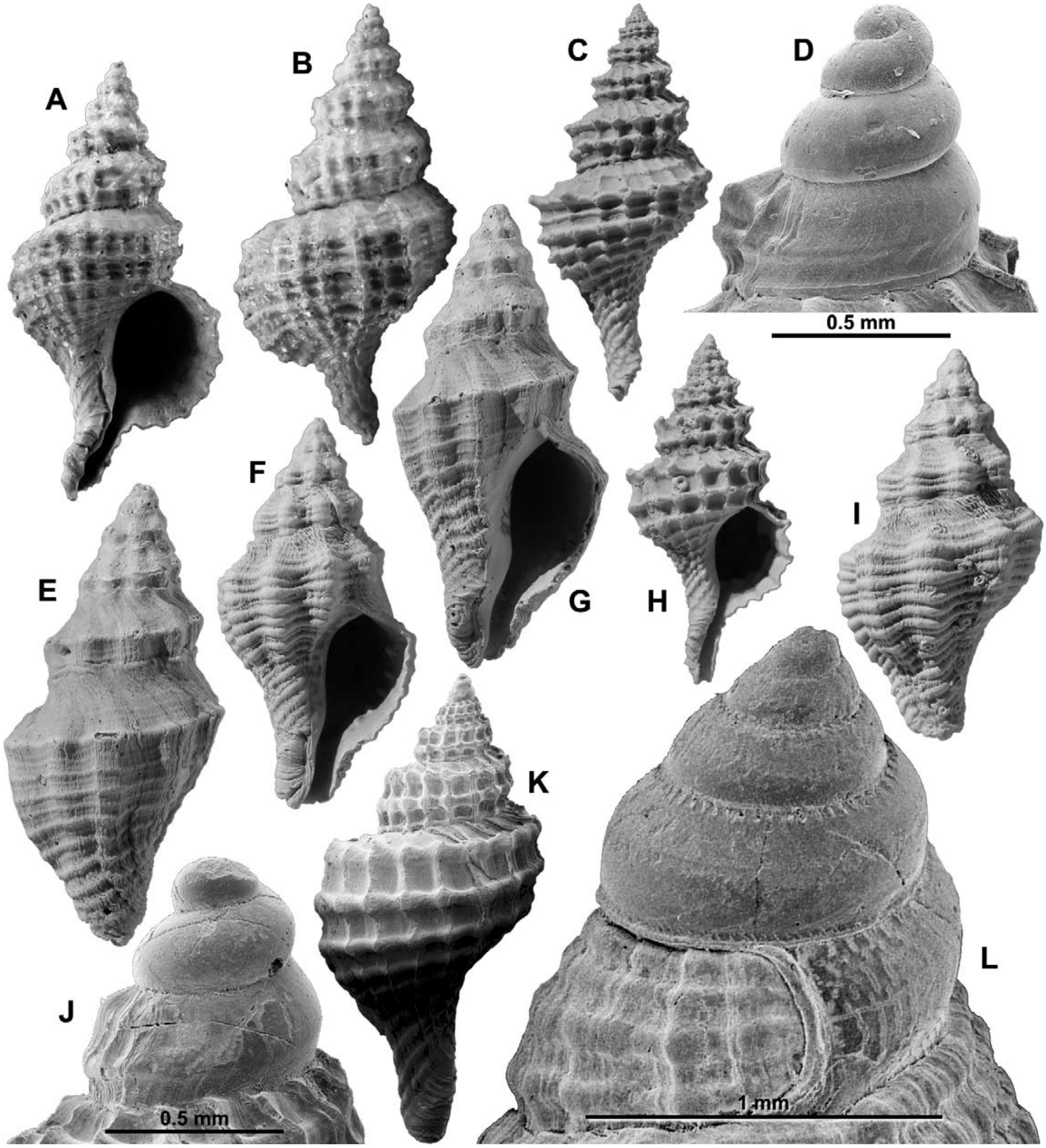

Figure 9 (A–D,H) *Zeatrophon bonneti* (Cossmann), Castlecliff, Wanganui; A, B, Cossmann's illustrated syntype, MNHN Dépt Science de la Terre, J09323, "Wanganui, dedit. M. Bonnet"; height 25 mm; D. Merle photo, MNHN; C, D, H, GS4102, R22/f6516, 3 specimens, Tainui Shellbed (Castlecliffian, OIS 13), "the buttress", Castlecliff; C, height 22.5 mm; D, protoconch, SEM; H, height 19.6 mm. (E,G) *Bedeva bartrumi* (Marwick), type species of *Otahua* Marwick, 1948, paratype, TM8301, Otahuhu well, Auckland, Waipipian, ex Laws collection; height 43.2 mm. (F,I) *Bedeva paivae* (Crosse), WM12047, Dunwich, Stradbroke Island, Queensland, Australia; height 22.2 mm. (J,K) *Zeatrophon ambiguus* (Philippi), type species of *Zeatrophon* Finlay, 1926, GS4121, R22/f6521, Kupe Formation (OIS 17), Castlecliff coast, SEM; J, protoconch of K; K, small specimen, height 13.2 mm. (L) *Agnewia kempae* Powell, protoconch of specimen in Fig. 10J, GS10911, Y14/f7505C, Te Piki Member (Haweran, OIS 7), Te Piki, near East Cape; SEM.

(GS4107, R22/f6430, one); Kaimatira Pumice Sand (OIS 25), mouth of Kai-Iwi Stream, Castlecliff (GS4068, R22/f6399, two); as last, Mowhanau Stream between bridge and mouth, Kai-Iwi (GS4163, R22/f6459, four); as last, Kai-Iwi Beach Road, Wanganui (GS4064, R22/f6395, three); as last, Tuckers pumice workings, Brunswick Road, W of Wanganui (GS4148, R22/f7414, one); Lower Kai-Iwi Siltstone (OIS 23), Castlecliff (GS4061, R22/f6392, 25); Omapu Shellbed (OIS 23), Castlecliff (GS4060, R22/f6391, 14); gastropod shellbed, Kupe Formation (OIS 17), Castlecliff (GS4121, R22/f6521, five); Kupe Fm, Castlecliff (GS4041, R22/f6373, one); Kupe Formation, Castlecliff (GS4050, R22/f6381, one); bivalve shellbed, Kupe Formation, Castlecliff (GS4045, R22/f6376, one); gastropod shellbed, Kupe Formation, Castlecliff (GS4047, R22/f6378, one; GS4121, R22/f6521, one); undifferentiated Kai-Iwi Group, ridge off end of No. 3 Line, E of Wanganui (GS4361, S22/f6486, three); uppermost sand member, Seafield Sand (OIS 15), Castlecliff (GS4027, R22/f6365, two); Lower Castlecliff Shellbed (OIS 15), 'the pinnacles', Castlecliff (GS4104 re-collection, R22/f6518, three); Lower Castlecliff Shellbed, Castlecliff (GS4140, R22/f6450, two); Tainui Shellbed (OIS 13) at 'the buttress', Castlecliff (GS4102, R22/f6516, eight); Tainui Shellbed, N side Waimutu Road, Turakina valley (GS15140, S23/f084, one). **Haweran**: GS4003, R22/f7394, Landguard Sand (OIS 9), Landguard Bluff, Wanganui (one). A particularly large, fine specimen and three smaller ones from Te Piki, 6 km E of Whangaparaoa, near East Cape (OIS 7) are similar to *Z. bonneti*, but have intermediate, secondary spiral cords and seem to intergrade with *Z. caudatinus*, although they have a prominent shoulder angle (GS5833, Y14/f505A, two; GS15443, Y14/f505B, two).

Distribution. The first occurrence of typical specimens of *Zeatrophon bonneti* is relatively late in Nukumaruan time (approximately OIS 86?) and the last occurrence I am aware of is in OIS 9 (Landguard Sand), with a probable occurrence at Te Piki, near East Cape (OIS 7). Specimens are rare other than at Castlecliff, Wanganui, but it is common in Devils Elbow Mudstone at Devils Elbow, Napier-Wairoa Highway, and a few specimens occur in other Nukumaruan rocks in central Hawke's Bay. However, this form intergrades with specimens identified as *Z. lassus*, and it appears that this is another single, anagenetically evolving species (see below). The earlier time range is, therefore, poorly known, but *Z. bonneti* in the broad sense probably extends from Opoitian to OIS 7.

Dimensions. Holotype, MNHN J09323, approximate dimensions (determined from photo scale): H 25, D 12.5 mm; non-types, MNHN J08923: H 19.4, D 8.9 mm; H 15.8, D 7.4 mm; GS4027, Seafield Sand, Castlecliff: H 29.0, D 15.1 mm; H 21.3, D 10.0 mm; GS4102, Tainui Shellbed, Castlecliff: H 21.4, D 10.9 mm; H 22.4, D 9.8 mm; GS5833, Te Piki, East Cape: H 35.7, D 19.3 mm.

Remarks. The small, beautifully and elaborately sculptured species *Zeatrophon bonneti*, with high, narrow, fenestrate axial and spiral ridges, is particularly distinctive, and has a biostratigraphically useful extinction time. Typical Castlecliff specimens have narrow, well-raised spiral cords with few interstitial cords, crossed by narrow axial ridges. Most specimens have no interstitial cords at all, but some specimens have one interstitial cord in one or a few interspaces. The upper of the two spiral cords on spire whorls is as prominent as or even more prominent than the lower cord, whereas on the Recent apparently descendent species *X. caudatinus* (Finlay, 1930) the upper spiral cord is less prominent than the lower one, producing a more 'rounded' effect to the margin of the sutural ramp, and interstitial spiral cords are more numerous (Ponder 1972).

Comparison of a range of specimens demonstrated that Ponder (1972) correctly described the gradual development of the extreme late Nukumaruan–Castlecliffian form of *Zeatrophon bonneti* from *Z. lassus* (Marwick

1928:487, fig. 143) throughout middle to late Pliocene time, encompassing the type material of *Z. murrayae* (Fleming 1943:205, pl. 31, fig. 30) (Nukumaruan, GS3093, S22/f9489, Hunterville-Turakina Valley Road, Wanganui; recorded also by Fleming from several localities in Dannevirke Subdivision, S Hawke's Bay; holotype TM8611, with four paratypes, TM8612-15; eight paratypes from GS2312, U22/f9488, Ashcott Road, W of Waipukurau, TM8616-23). Most Nukumaruan populations from Hawke's Bay (common at Ashcott Road and in Devils Elbow Mudstone at the top of Devils Elbow hill) have numerous interstitial secondary spiral cords, particularly on the last whorl, that are reduced on or absent from Castlecliff shells, and a more flared outer lip than typical Castlecliff shells, and are indistinguishable from the holotype and the few other specimens seen from the type formation of *Z. lassus*, Whenuataru Tuff (Waipipian–Mangapanian), Pitt Island, Chatham Islands (holotype TM8624, Whenuataru Tuff, Taruwhenua Peninsula, Pitt I). The protoconch differences described by Fleming (1943:205) are slight and seem to result from damage; protoconchs are essentially identical on specimens I have examined that were assigned to *Z. bonneti*, *Z. lassus* and *Z. murrayae*. *Z. murrayae* is here regarded as a synonym of *Z. lassus*. However, *Z. lassus* and *Z. bonneti* intergrade very gradually with time, that is, they are part of an anagenetically changing series, and it is probably best to regard them as conspecific. However, further study of pre-Nukumaruan specimens is warranted before this synonymy is accepted and the time range is clear.

Comparison of specimens of *Zeatrophon ambiguus* (Fig. 9J, K) and *Z. elegans* Fleming (1943:205, pl. 31, fig. 32; Nukumaruan, holotype TM8625, GS2687, T24/f7415, Kumeroa, E of Woodville, S Hawke's Bay) demonstrated that Ponder (1972) also was correct to regard *Z. elegans* as falling within the range of variation of *Z. ambiguus*. Specimens from Mangapani Shellbed (GS4227, R21/f8478, Mangapunipuni Stream, Waitotara Valley; Mangapanian) illustrated by Ponder (1972, figs. 5.4, 5.5) clearly are intermediate between these named forms. In this case, the *elegans* form seems merely to be an uncommon sculptural variant of *Z. ambiguus*. The nominal taxa *Z. elegans* and *Z. murrayi* clearly are not restricted Nukumaruan species of biostratigraphical utility, and a distinction between an earlier species *Z. lassus* (Opoitian–Nukumaruan) and a later species *Z. bonneti* (late Nukumaruan–Castlecliffian) is of very low reliability.

In contrast, another synonymy proposed by Ponder (1972) that I cannot support is of *Zeatrophon mutabilis* Marwick (1928:488, figs. 144, 146, 148) with *Z. ambiguus*. The many specimens of *Z. mutabilis* now available from the type locality, Titirangi Sand at Titirangi Point, Te Whanga Lagoon, Chatham Island (early Nukumaruan), differ from all mainland New Zealand specimens in their consistently more predominant sculpture of wide, flat spiral cords and their consistent short, wide shape, with a shorter siphonal canal than in *Z. ambiguus*. Contrary to Ponder's (1972:486) statement, they are separable at all ages. There is no doubt that *Z. mutabilis* is a distinctive species restricted to Titirangi Sand (early Nukumaruan). It also formerly occurred commonly in the disused Moutapu quarry at the E end of Karewa Peninsula (GS12170, CH/f11; GS13190, CH/f261; listed as '*Xymene mutabilis*' in Campbell et al. 1994:158). More significantly, abraded, brown-stained specimens of *Z. mutabilis* occur also in small numbers on the beach N of Owenga, SE Chatham Island, demonstrating that one reason for the distinctive nature of the 'Owenga shell bed' fauna (Dell 1960:154), that is, the fauna cast ashore on the beach north of Owenga, is that it includes a contribution from Titirangi Sand. Although no outcrops of Titirangi Sand have been observed along this coast, the formation is now known to be widespread, occurring as far W as in the cliff-face above the beach N of Red Bluff, Petre Bay, N of Waitangi, where it contains an ocean beach fauna dominated by *Paphies subtriangulata* (Wood, 1828), and on the shore of Lake Te Wapu, S of Kaingaroa

Harbour, NE Chatham Island (discovered in 2009 by Dr Kat Holt, Massey University). Erosion of former Titirangi Sand outcrops (apparently now overgrown) along the coast N of Owenga would explain the occurrence of this and other taxa at Owenga that have not been found elsewhere in the modern beach fauna, such as *Cominella ellisoni consobrina* Powell (1933:206, pl. 36, fig. 8), a probable synonym of the Titirangi Sand species *C. ellisoni* Marwick, 1928.

Subfamily Haustrinae Tan, 2003

Genus ***Bedeva*** Iredale, 1924

Bedeva Iredale 1924:273. Type species (by original designation): *Trophon hanleyi* Angas, 1867, Recent, southeastern Australia.

Otahua Marwick 1948:32. Type species (by original designation): *Otahua bartrumi* Marwick, 1948, Pliocene (and Pleistocene?), New Zealand (**new synonym**).

Remarks. Tan (2003) provided a detailed comparison of the anatomical, radular and opercular characters of Australian and New Zealand species previously classified in *Bedeva*, *Haustrum* Perry, 1811, *Lepsiella* Iredale, 1912, and *Lepsithais* Finlay, 1928 and, in view of their close similarity, proposed that they be placed together in a new Subfamily Haustrinae—apart from '*Lepsiella' reticulata* (Quoy & Gaimard, 1832) and '*L*'. *botanica* (Hedley, 1918), which Tan transferred to *Phycothais* Tan, 2003 in Subfamily Rapaninae. In contrast, I pointed out (Beu 2004:214–216) that species referred to *Lepsiella* and *Lepsithais* (other than *L. botanica* and *L. reticulata*) are indistinguishable from *Haustrum* in most characters, and are better transferred there. *Bedeva* differs strongly from *Haustrum* in teleoconch characters, with a markedly taller spire, a smaller aperture and a markedly longer anterior siphonal canal, as well as in its distinctive foliose axial sculpture, and seems better regarded as a genus distinct from *Haustrum*. I also preferred to follow Kool (1993) and retained *Bedeva* and *Haustrum* in Subfamily Ocenebrinae. A further recent contribution to the molecular phylogeny of the Muricidae (Claremont et al. 2008) retained the same genera in the Rapaninae and Ocenebrinae as were recognized by Kool (1993) and, more recently, Barco et al. (2010) established Haustrinae firmly as a muricid subfamily, on the basis of molecular phylogeny, and showed that *Lepsiella* and *Lepseithais* can be accepted as synonyms of *Haustrum* (although, unfortunately, they did not include *Bedeva* in their analysis). Its highly distinctive shell characters demonstrate that *Bedeva* should be retained as a genus separate from *Haustrum* at present.

Bedeva bartrumi (Marwick, 1948) (Fig. 9E, G)

Otahua bartrumi Marwick 1948:32, pl. 7, figs. 5, 6, 12, 13; Fleming 1966:57.
Bedeva bartrumi. Beu & Maxwell 1990:295, pl. 37h; Maxwell 2009:245.

Type material. *Otahua bartrumi* holotype AIM AK71074 (not seen), five paratypes TM8297-TM8301, all from GS3528, R11/f7014, Otahuhu well, Auckland, Waipipian (Pliocene).

Other material examined. **Waipipian:** Otahuhu well, Auckland, Waipipian (GS3528, R11/f7014, six specimens); Greenwood Formation (Waipipian), Lower Waipara Gorge, North Canterbury (GS4997, N34/f6192, two abraded). **Nukumaruan:** shellbeds above and below Vinegar Hill Tephra (OIS 61; Pillans et al. 2005:79, figs. 5A, 11), Tewkesbury Formation (late Nukumaruan), Brunswick Road, E side Kai Iwi Valley, Wanganui (GS15348, R22/f6542A, one, severely abraded). **Castlecliffian:** shellbed low in Maraetotara Formation, NW of high terraces of Maraetotara River, south of Cape Kidnappers, Castlecliffian (OIS 29-31?; GS5315, W21/f8522, one, severely abraded).

Distribution. Waipipian–early Castlecliffian (–OIS 29–31?), in Auckland, Wanganui Basin, North Canterbury, and Hawke's Bay (Cape Kidnappers). *Bedeva bartrumi* is a rare fossil, presumably reflecting its exposed intertidal rocky shore habitat (to judge from that of Recent *Bedeva* species in Australia) and the poor preservation of this environment in the fossil record. It is unlikely to have any biostratigraphical utility.

Dimensions. *Otahua bartrumi*, figured paratype: H 45.7, D (incomplete) 20.3 mm; largest paratype: H 46.8 (incomplete, originally ca 55 mm), D (incomplete) 22.8 mm; almost complete paratype (TM8301, ex CR Laws collection; Fig. 9E,G): H 43.2, D 20.2 mm.

Remarks. When proposing the genus *Otahua*, Marwick (1948) remarked that it was probably closest to the eastern Australian genus *Bedeva* Iredale, 1924, and the differences are in my opinion of specific rather than generic rank. New Zealand specimens are particularly similar to *Bedeva paivae* (Crosse, 1864) (Fig. 9F,I) as illustrated by Wilson (1994, pl. 5, fig. 28A–C), having similar proportions and sculpture, a similar sutural ramp without spiral cords and a similar sharp peripheral angulation, and a very similar aperture, anterior sculpture and siphonal fasciole. The only obvious differences are the larger size, thicker shell, slightly weaker sculpture and more weakly armed aperture of Otahuhu specimens. Wilson (1994:21) pointed out the difficulty of distinguishing *B. hanleyi* from *B. paivae* 'in field samples', and stated that *B. hanleyi* reaches 40 mm in height. Marwick (1948, pl. 7, figs. 5, 6) illustrated the low, dome-shaped, lecithotrophic protoconch of about 1.5 whorls in *B. bartrumi*, possibly one of the reasons for his assuming that *Otahua* must be a genus distinct from *Bedeva*, as the protoconch makes it unlikely that *Bedeva* can have dispersed as larvae from Australia to New Zealand. Anderson (1966:243–244, figs. 3–6) described the brooding of veligers within a brood pouch and their feeding on the yolks of nurse eggs by *B. hanleyi* in New South Wales. *B. hanleyi* produces crawl-away miniatures of the adult, that is, it has direct development, and the protoconch of the initial hatched juvenile (Anderson 1966, fig. 6) consists only of a half-whorl hemispherical 'cap' and an initial half-whorl of teleoconch. The New Zealand species *B. bartrumi* therefore had similar development to *B. hanleyi*, despite the larger (slightly more multispiral) protoconch of *B. bartrumi* and, assuming it was a Pliocene arrival from SE Australia, the genus can have arrived in New Zealand only by rafting. The distinct protoconchs demonstrate that *B. bartrumi* is a species distinct from *B. paivae*. Dr Emily Vokes (formerly of Tulane University pers. comm.) several years ago pointed out the similarity of *B. bartrumi* to *B. blosvillei* (Deshayes, 1832). That larger and more strictly tropical species has slightly more elaborate sculpture and has been referred to *Lataxiena* Jousseaume, 1883 (Wilson 1994:22, pl. 5, fig. 27A,B). However, the latest classification returned *B. blosvillei* to *Bedeva*; the 46-mm-high specimen illustrated (Houart in Poppe 2008:198, pl. 394, fig. 10) is similar to *B. bartrumi*. The Otahuhu specimens are particularly similar to a specimen labelled '*Bedeva vapida* Woolacott, 1957' in GNS (WM9323, Yeppoon, Queensland, ex W. J. Paul collection; H 34.1 mm) as it lacks the foliose axial sculpture on the sutural ramp of *B. paivae*; this name is listed by Wilson (1994:22) as a synonym of *B. blosvillei*.

Specimens from Lower Waipara Gorge (Waipipian), shellbeds on Brunswick Road, Kai-Iwi, Wanganui (late Nukumaruan) and the early Castlecliffian succession (OIS 29–31?) at Cape Kidnappers are all severely abraded and not certainly referred to this species, but they show no differences to distinguish them from *B. bartrumi*, and have a distinctive yellowish, calcitic outer shell layer. It appears that the 'Australian' genus *Bedeva* became extinct in New Zealand only recently, during early Castlecliffian time, but was never common as a fossil, because of its intertidal rocky shore habitat.

Hutton (1880:49) and Suter (1913:415, pl. 45, fig. 22) mistakenly recorded the abundant southern Australian species *Bedeva paivae* from the New Zealand present-day fauna. Suter (1913:416) cited its range as 'North and South Islands, but not common, between tide-marks to about [40 m]; Chatham Islands'. However, Finlay (1926b:421) stated unequivocally of *Bedeva* that 'this genus does not occur in New Zealand'. The two lots of specimens in Suter's collection identified as '*Trophon (Kalydon) hanleyi*' (none is identified as *T. paivae*) are from Titahi Bay, Wellington (Suter's no. 3101, one; collected by MK Mestayer) and 'Chatham Is.' (Suter's no. 2534, 13; no source stated); all are beach-abraded specimens of *Axymene traversi*. The entire record of *Bedeva* as a member of the Recent fauna of New Zealand was based on misidentifications. The present fossils therefore represent the only authentic records of the genus in New Zealand.

Subfamily Rapaninae

Genus ***Agnewia*** Tenison Woods, 1878

Cheletropis Forbes 1852:385. Type species (by monotypy): *Cheletropis huxleyi* Forbes, 1852, Recent, SE Australia (larva of *Agnewia tritoniformis* (Blainville, 1832) (*nomen oblitum*).

Adamsia Dunker 1857:357. Type species (by original designation): *Thais (Adamsia) typica* Dunker, 1857 (= *Purpura tritoniformis* Blainville, 1832), Pleistocene and Recent, southeastern Australia and northern New Zealand (junior homonym of *Adamsia* Forbes, 1840, Tunicata).

Agnewia Tenison Woods 1878:29. Replacement name for *Adamsia* Dunker, 1857, junior homonym (*nomen protectum*).

Remarks. The earliest name for this genus seems to be *Cheletropis* Forbes (1852:385, pl. 3, fig. 9a,b), based on a '*Sinusigera* larva', *Cheletropis huxleyi* Forbes, 1852, collected in a towing net off Cape Howe, SE Australia, during the voyage of the '*Rattlesnake*'. The same or a very similar larva apparently had earlier been named *Struthiolaria microscopica* by Gray (1839:108; attributed to Blainville, 'Indian Ocean, Paris Museum', but never published by Blainville), and was identified again as *Sinusigera microscopica* by Brazier (1878:144) from '360 miles [580 km] north-east of Sydney'. This synonymy is stated unequivocally in Charles Hedley's unpublished, loose-leaf bibliographic catalogue in AMS. H Adams & A Adams (1854, vol. 2:89) also suggested that *Struthiolaria microscopica* Gray was the same species as *Macgillivrayia* (sic, = *Macgillivraya*) *pelagica* Forbes, 1852 (type species of *Macgillivraya* Forbes, 1852; 'taken in the towing-net by Mr. Macgillivray off the East coast of Australia, fifteen miles [24 km] from the shore'; H Adams & A Adams 1854, vol. 2:89). However, illustrations of *M. pelagica* (Forbes 1852, pl. 3, fig. 8a,b; H Adams & A Adams 1854, pl. 69, fig. 3a–c) show a very simplified, smooth-shelled veliger with four long, narrow velar lobes and a triangular operculum, clearly a larva of *Tonna* rather than a muricid, whereas *Cheletropis huxleyi* in Forbes' (1852, pl. 3, fig. 9a,b) illustration is a strongly bicarinate, taller-spired shell with a typical 'sinusigera claw' on the outer lip; H Adams & A Adams's suggested synonymy is incorrect. *Sinusigera cancellata* d'Orbigny (H Adams & A Adams 1858, pl. 137, fig. 4) is much more like *C. huxleyi* and the larva of *A. tritoniformis*. H Adams & A Adams (1858:613–614) also noted that *Cheletropis huxleyi* Forbes was a synonym of *Sinusigera microscopica* (Gray), and that *Cheletropis* is a synonym of *Sinusigera*. Although the identity of *Sinusigera cancellata* Orbigny, 1841 (named in Orbigny's [1841] work on Cuba) seems not to have been established, it will have been based on the larva of quite a different muricid species from the Caribbean Sea, not congeneric with *A. tritoniformis*. To my knowledge, *Cheletropis* has not been used as the valid name for a genus since 1899, and as

Agnewia tritoniformis is a well-known name satisfying the requirements of ICZN Code Article 23.9.1, *Agnewia* is declared a *nomen protectum* here, and *Cheletropis* is declared a *nomen oblitum*. The requisite list of names to justify this status (at least 25 usages of *Agnewia* as the valid name for this genus by at least 10 authors during the last 50 years) is provided in the following synonymy.

Agnewia tritoniformis (Blainville, 1832) (Fig. 10D, F, G, H)

Purpura tritoniformis Blainville 1832:221, pl. 10, fig. 10; Kiener 1836, *Purpura*, p. 37, pl. 8, fig. 8; Kesteven 1902:533, pl. 29, figs. 2, 3, 5, 7; Hedley 1903:384; Suter in Hutton 1904:72; Pritchard & Gatliff 1906:44; Lamy 1918:357; Fischer-Piette & Beigbeder 1943:433.

Struthiolaria microscopica. Gray 1839:108 (larval shell).

Cheletropis huxleyi Forbes 1852:385, pl. 3, fig. 9a,b (larval shell).

Adamsia typica Dunker 1857:357; Angas 1867:192; Kobelt 1878:236; Gillies 1882:171.

Sinusigera microscopica Brazier 1878:144 (larval shell).

Agnewia typica. Tenison Woods 1878:29.

Urosalpinx tritoniformis. Tryon 1880a:156, pl. 39, fig. 491 (not including figs. 488, 496).

Cominella (Adamsia) typica. Watson 1886:214.

Cominella (Agnewia) tritoniformis. Brazier 1888:995; Whitelegge 1889:248; Brazier 1894:167; Pritchard & Gatliff 1898:275.

Agnewia tritoniformis. Tate & May 1901:353; Iredale 1915:475; Hedley 1918:M93; Cooke 1919:100, fig. 26 (radula); May 1921:87; Gatliff & Gabriel 1922:131; May 1923:85, pl. 40, fig. 16; Finlay 1926b:427, pl. 21, fig. 82; Powell 1937:80; Powell 1940:214; Powell 1946a:83; Dell 1950:26; Macpherson & Chapple 1951:130; Richardson 1953:39, figs. 3–5; Bennett & Pope 1953:131; Kershaw 1955:316; Powell 1958a:103; Allan 1959:147, text-fig. 33.2; McMichael 1960:112, fig. 252; Bennett & Pope in Dakin 1960:257, pl. 65, fig. 2; Powell 1962:95; Fleming 1962b:86, 98, fig.; p. 102, fig.; Macpherson & Gabriel 1962:179, fig. 216; Iredale & McMichael 1962:73; Hodgkin et al. 1966:45, pl. 17, fig. 5; Macpherson 1966:254; Grant-Mackie & Chapman-Smith 1971:675; Fleming 1975:52, 74, fig.; p. 78, fig.; Powell 1976b:99; Fleming 1978:723; Fleming 1979:76, 97, 108, fig.; p. 112, fig.; Powell 1979:181, pl. 36, fig. 8; Rehder 1980:71, pl. 3, fig. 2 (radula); Trew & Oliver 1981:33; Monger 1984:50, unnumbered fig.; Richmond 1992:47, fig. 67; Wilson 1994:40, pl. 5, fig. 19; Jansen 1995:57, fig. 218; Spencer & Willan 1996:26; Richardson 1997:9; Jansen 2000:46, fig. 175; Hayward et al. 2001:61, fig. 8; Spencer et al. 2002, on-line list; Tan 2003:967, figs. 3E,F, 5U,V, 18A–K, 19; Herbert et al. 2007:21, fig. 4C,D; Spencer et al. 2009:210; Maxwell 2009:246.

Purpura tritoniformis levidensis Kesteven 1902:534, pl. 29, figs. 2, 5, 7.

Thais (Stramonita) tritoniformis. Suter 1913:424, pl. 45, fig. 19.

Thais (Agnewia) tritoniformis. Thiele 1929:298; Wenz 1941:1122, fig. 3188.

Agnewia nautica Thornley 1952:43, fig. 2.

Type material. *Purpura tritoniformis* Blainville, 'probable holotype' in MNHN, as noted by Lamy (1918:357); without locality; severely abraded and evidently a beach shell, but certainly conspecific with the species usually known by this name; illustrated by Tan (2003:967, fig. 18A,B). The type locality is here designated as Sydney Harbour (Port Jackson), New South Wales. *Cheletropis huxleyi*, holotype not found in BMNH, location unknown (K Way, BMNH pers. comm. 14 January 2008); probably such a minute, largely conchiolin shell (a larval shell of *A. tritoniformis*) has not survived storage in ethanol since it was collected during the cruise of the '*Rattlesnake*' in 1846–1850. *Adamsia typica*, four syntypes BMNH 1991575, labelled 'Philippinen. Adelaide?' in Dunker's handwriting (Tan 2003:965) (not seen), almost certainly from SE Australia (although records from as far west as Adelaide are not confirmed by modern collections; probably from near Sydney, New South

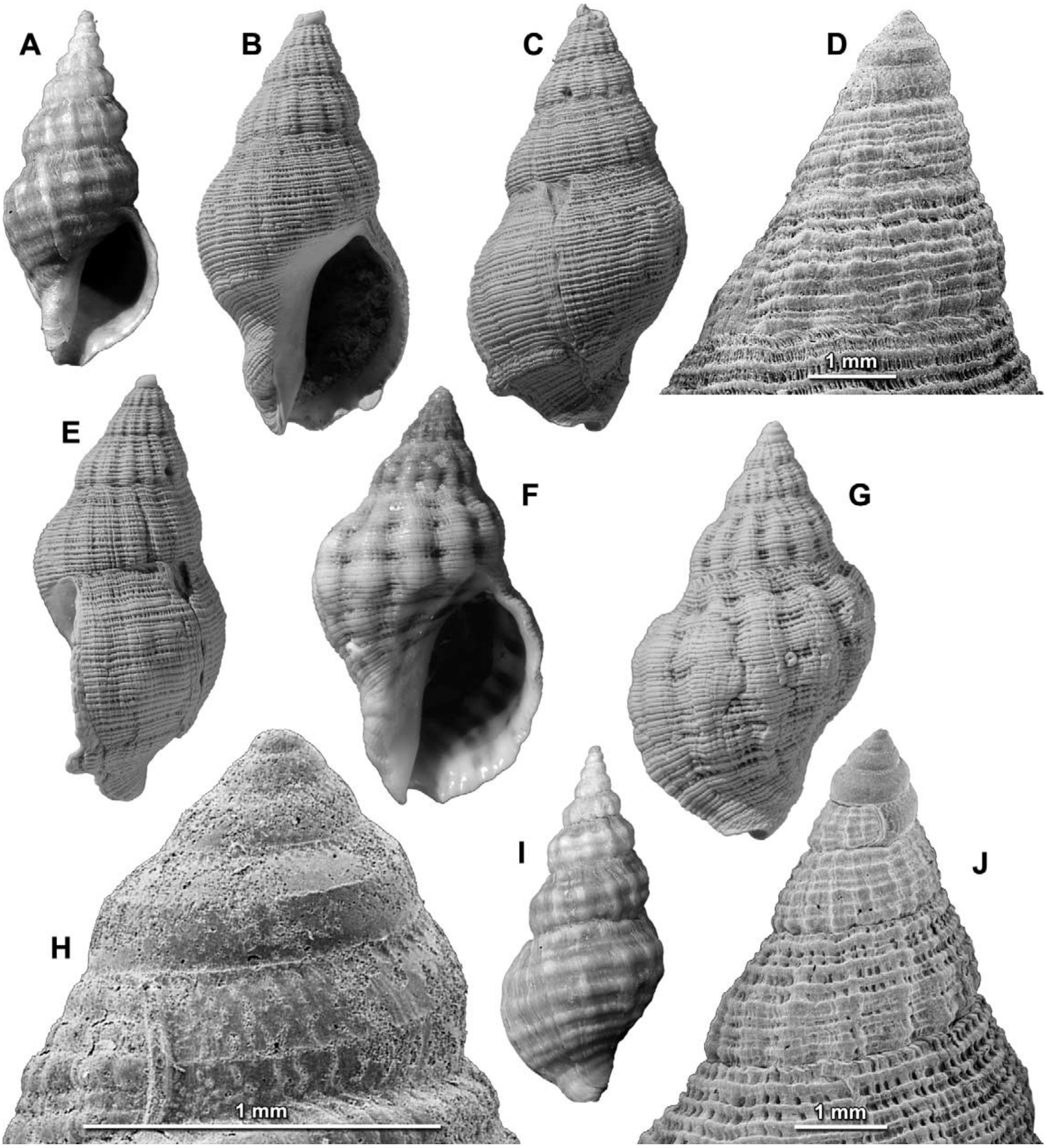

Figure 10 (A,I) "*Adamsia*" *adelaidae* A. Adams & Angas, holotype, BMNH 1870.10.26.76, Recent, "Adelaide", South Australia; H 16.7, D 7.5 mm. (B,C,E,J) *Agnewia kempae* Powell, GS10911, Y14/f7505C, Te Piki Member (Haweran, OIS 7), Te Piki, near East Cape; B,C,E, specimen lacking protoconch, all data as for Fig. 10J; 3 views of one specimen, with prominent nodule on outer lip, height 20.0 mm; J, apex of specimen in Fig. 9L. (D,F,G,H) *Agnewia tritoniformis* (Blainville), type species of *Agnewia* Tenison Woods, 1878, Recent; D,H, WM6364, Sydney, New South Wales, Australia; D, spire apex; H, protoconch of D; F,G, RM4784, dived, 5 m, Cape Karikari, Northland, New Zealand; height 19.7 mm; F, unwhitened; G, whitened with MgO.

Wales). *Purpura tritoniformis levidensis* Kesteven, holotype AMS C.13179 (Tan 2003, fig. 18C,D), said by Kesteven to be from 'New South Wales and Lord Howe Island', but the holotype is labelled 'Port Jackson, Sydney', a strongly axially ridged specimen of *A. tritoniformis*. *Agnewia nautica* Thornley, holotype AMS C.103331, with 14 paratypes, C.305363 (nine), C.346697-8 (five), all from Port Stephens, New South Wales (holotype: Tan 2003, fig. 18E,F), a rather short and weakly sculptured form of *A. tritoniformis*. I am not aware of the repository of any type material of *Struthiolaria microscopica*.

Other material examined. **Haweran:** *Akera-Diala-Anadara* locality, bank behind tidal flats between Te Rewa Point and Waiparera, Hokianga Harbour, Northland, OIS 7 (GS14778, O06/f064, one). **Recent:** RM2018, Whangaparapara, Great Barrier Island, CA Fleming collection (one); RM4784, SCUBA, 5 m, Cape Karikari, Northland (seven); 19 lots in NMNZ, from Cape Maria van Diemen to as far SE as Cape Runaway, and to Koakanui Point, Tokomaru Bay, N of Gisborne (NMNZ M.21639) (listed by Tan 2003:968).

Distribution. OIS 7 and Recent in New Zealand; living in the northeastern North Island warm province only. Although Gillies (1882:171) recorded *Agnewia tritoniformis* from New Zealand in his comments on Hutton's (1880) catalogue with the bald statement '*Adamsia typica*—Add', Finlay (1926b:427) was the first to provide accurate locality records from New Zealand (two specimens in the collection of W La Roche). Powell (1940:214) recorded specimens from Cape Maria van Diemen and Tom Bowling Bay, N Northland, and Dell (1950:26) recorded further specimens from four localities. Richardson (1953) added 17 further records, as far south as Oruaiti Bay, Whangaparaoa, E Bay of Plenty. In Australia, it lives from New South Wales (where it is common) to Bass Strait and Tasmania (Wilson 1994:40), and at Lord Howe and Norfolk Islands; in Victoria, recorded from Port Phillip and Westernport to Lorne and Apollo Bay (Macpherson & Gabriel 1962:179). I am not aware of authentic records from South Australia.

Dimensions. *Purpura tritoniformis*, 'probable' holotype: H 21.4, D 12.4 mm; *Purpura tritoniformis levidensis* holotype: H 28.3, D 14.9 mm; *Agnewia nautica* holotype: H 24.6, D 14.0 mm; GS14778, Hokianga, OIS 7: H 22.1 (incomplete; originally ca 27 mm), D (incomplete) 12.4 mm; RM4784, Cape Karikari: H 21.0, D 11.3 mm; H 19.7, D 11.8 mm; H 18.8, D 10.0 mm; NMNZ M.212303, Lord Howe Island: H 35.3, D 18.9 mm; NMNZ M.39766, intertidal, Otarawairere Bay, Ohope Beach, Bay of Plenty: H 29.5, D 15.7 mm; H 24.0, D 15.1 mm.

Remarks. The restricted New Zealand species *Agnewia kempae* Powell, 1933 occurs uncommonly at Te Piki, inland from Whangaparaoa, near East Cape (OIS 7) (see below). It seems likely that *A. kempae* evolved through genetic drift from a founder population of the very similar species *A. tritoniformis* that appeared in New Zealand as planktonic larvae from eastern Australia (Grant-Mackie & Chapman-Smith 1971:675; Beu & Maxwell 1990:360). *A. tritoniformis* is common on SE Australian shores at present, and is well known for its classical '*Sinusigera*' protoconch (Fig. 10D, H) (Kesteven 1902; Powell 1979:181), implying a long planktotrophic larval life. *A. tritoniformis* now lives uncommonly in several remote localities, subtidally on extremely exposed rocky shores, in northeastern New Zealand, from Cape Maria van Diemen to Tokomaru Bay, N of Gisborne (Richardson 1953; Tan 2003). A single poorly preserved fossil specimen of *A. tritoniformis* collected from the *Anadara-Diala-Akera* locality at Te Rewa Point, northern Hokianga Harbour, indicates that this species appeared in New Zealand at least as early as OIS 7, approximately coeval with the Te Piki records of *A. kempae*. It seems likely that *Agnewia* arrived in New Zealand at some time earlier than OIS 7 (presumably during OIS 11–9) and evolved into the endemic

A. kempae, and that OIS 7 and later records of *A. tritoniformis* are pseudopopulations recruited as planktotrophic larvae from eastern Australia.

Agnewia kempae Powell, 1934 (Figs. 9L, 10B, C, E, J)

Agnewia kempae Powell 1934a:273, pl. 59, figs. 19, 20; Richardson 1953:41, figs. 1, 2; Fleming 1966:58; Grant-Mackie & Chapman-Smith 1971:675; Beu & Maxwell 1990:360, pl. 48h; Richardson 1997:9; Maxwell 2009:246.

Type material. Agnewia kempae, holotype AIM AK70011, with one paratype AK72423 (neither seen), from Te Piki, near Whangaparaoa, East Cape, Haweran (penultimate interglacial, OIS 7).

Other material examined. GS10911, Y14/f7505C, Te Piki Member (OIS 7), Te Piki road cutting, ca 6 km E of Whangaparaoa, near East Cape (one); same locality, CA Fleming collection (presented by AWB Powell?) (five); same locality, NMNZ M.26395 (one); M.40126 (two).

Dimensions. GS10911, Te Piki: H 20.0 (protoconch incomplete), D 9.8 mm (Fig. 10B, C, E); H 19.7, D 10.3 m; H 18.2, D 10.0 mm; H 16.9, D 8.8 mm; H 15.5, D (slightly incomplete) 7.9 mm; M.26395: H 20.1, D 9.8 mm.

Distribution. Agnewia kempae is recorded only from the Te Piki Member (OIS 7) at Te Piki, inland from Whangaparaoa, near East Cape. Most of the more unusual fossils at Te Piki (that is, other than *Maoricolpus roseus*, *Dosina zelandica* Gray, 1835, *Dosinia (Kereia) greyi* Zittel, 1864, and *D. (Fallartemis) lambata* (Gould, 1850), which are common throughout the member) occur in small but exceedingly diverse, closely packed fossil concentrations (ca 1 × 2 × 2 m) greatly dominated by *Pecten novaezelandiae* (Reeve, 1853). The concentrations are scattered sparsely through the member, separated from each other by some tens of metres. A concentration I excavated recently had an uppermost layer ca 50–80 mm thick of concentrated, broken *Atrina* shells, with moderately common specimens of the ranellid *Linatella caudata* (Gmelin, 1791), whereas *L. caudata* was not collected further inside the shell concentration. This indicates that a pinnid-dependent community was developed across the estuarine flat, where Ranellidae fed on Pinnidae, as has been observed at several localities in estuaries in the tropical Pacific, along the South African coast, and at Whangarei Heads in Northland at present. The concentrations evidently represent tidally excavated 'pot-holes' in the estuarine flats that trapped shells washed into the small Te Piki embayment from the present Waihau Bay and the open coast outside it. The commonness of some species, including *Agnewia kempae*, varies from concentration to concentration, and *A. kempae* has not been collected during recent visits.

Remarks. Agnewia kempae is compared here with *A. tritoniformis*, as *A. kempae* seems to be a restricted New Zealand species. As pointed out by Beu & Maxwell (1990:360), the two species are very similar. However, *A. kempae* is slightly smaller (H 20 rather than up to at least 35 mm) and most specimens are slightly narrower than *A. tritoniformis*. Also, *A. kempae* is consistently more thin-shelled than *A. tritoniformis*, and also differs in consistently having weaker axial folds and primary spiral cords, fading out before the last whorl, revealing a relatively narrow, prominent peribasal spiral cord, sculptured with several narrower, closely spaced spiral cords, and bearing a shallow groove along its crest. The surface is otherwise sculptured with single, fine, moderately widely spaced, sharply raised, slightly wavy spiral cords and fine axial ridgelets in *A. kempae*. The cords are single over most of the surface and rather evenly spaced over the entire exterior, with a few narrow secondary threads on the centre of the last whorl, whereas they are significantly more closely spaced into groups that form the major spiral cords in *A. tritoniformis*, with many secondary and finer cords; the major spiral interspaces bear more widely spaced spiral cords and otherwise weaker sculpture. One of the Te Piki specimens in M.40126 retains wide, evenly rounded axial folds to the end of the last whorl, but its much finer spiral cords than in *A. tritoniformis* and its peribasal cord are readily distinguished. The raised peribasal cord ends at an anteriorly protruding nodule on the outer lip, quite prominent in some specimens (Fig. 30C,F,G), although it is not well preserved on all specimens. Freshly collected specimens of *A. kempae* are rather a bright reddish brown, reflecting their calcitic outer shell layer (Tan 2003:969) and possibly in part the original exterior colour. Comparison of the nine specimens of *A. kempae* listed above directly with the seven of *A. tritoniformis* in RM4784, from Cape Karikari, and with numerous specimens from Sydney Harbour showed that they can be distinguished consistently by relative sculptural prominence (much weaker in *A. kempae* than in *A. tritoniformis*), spire height (taller in most specimens of *A. tritoniformis* than in *A. kempae*), the peribasal spiral swelling of *A. kempae* and the anteriorly protruding nodule on the outer lip of *A. kempae*, contrasting strongly with the finely and narrowly sinuous lip edge in all specimens of *A. tritoniformis*. Most specimens of *A. kempae* that lack the nodule on the outer lip have a thickened, rough area on the anterior edge of the lip, apparently the base of the former nodule, now broken off. Microscopic examination showed that the axial growth ridges are curved around a formerly protruding lip extension over the peribasal cord of all specimens, even when the nodule is not preserved on the lip itself. Evidently *A. kempae* fed by opening (edge-chipping?—as described for the muricid *Hexaplex trunculus* (Linné, 1758) by Morton et al. 2007) other molluscan shells with its lip nodule in a manner not adopted by *A. tritoniformis*, so the nodule presumably was broken and regrown during life by some specimens. The protoconch also is slightly taller and narrower and is well preserved on most specimens of *A. kempae*, whereas that of *A. tritoniformis* is slightly shorter and in most specimens is more abraded, suggesting that *A. kempae* occupied a more sheltered habitat than the rocky subtidal one of *A. tritoniformis*. It seems feasible that *Agnewia kempae* occupied the shallow, sheltered, subtidal *Atrina* beds described under 'Distribution', above.

Consideration was given to the possibility that *Agnewia kempae* might be another species previously known from Australia, rather than a restricted New Zealand species. The only other Recent Australian species that has been assigned to *Agnewia* in recent years is *Adamsia adelaidae* A Adams & Angas (1864:421, pl. 37, fig. 2) (not to be confused with *Ricinula adelaidensis* Crosse & Fischer [1865:50, pl. 2, fig. 1], which was listed as a synonym of *Haustrum vinosum* (Lamarck, 1822) by Tan [2003:998]). The poorly known species *Adamsia adelaidae* tentatively was assigned to *Agnewia* by Tan (2003:965), but definitely is not congeneric with *A. tritoniformis* and is unlike any other Australian muricid I know of (holotype BMNH 1870.10.26.76; Fig. 10A, I). It is a small (H 16.7, D 7.5 mm), tall and narrow, tall-spired shell with 12–14 moderately prominent, widely spaced, narrow axial ridges per whorl, two wide, prominent spiral cords around the periphery, a further narrower one on the ramp and four on the neck of the last whorl, a thin outer lip, and a very short, widely open anterior siphonal canal. The entire exterior is sculptured with many low, thin, widely spaced, irregular axial lamellae, and the pale brown exterior, with paler spiral cords, indicates the presence of a calcite outer shell layer. The protoconch is blunt and paucispiral, smooth, of about 1–1.5 whorls; that is, similar to those of *Bedeva paivae* and *Haustrum vinosum* (Tan 2003, fig. 2A,B) although not clearly differentiated from the teleoconch, very different from the planktotrophic 'sinusigera' of *A. tritoniformis*. A relationship with *Bedeva* and *Haustrum* (subfamily Rapaninae; Claremont et al. 2008:218) seems likely, but only examination of the radula and anatomy will confirm the generic position of *Adamsia adelaidae*. No similar species have been illustrated in any recent identification guides to Australian gastropods.

The type material (holotype and 14 paratypes) of *Agnewia nautica* Thornley, 1952 also was compared carefully with *A. kempae*, as this rather small, short-spired, weakly sculptured form is most similar to *A. kempae* of Australian material I have examined. However, all material assigned to *A. nautica* has the same spiral sculpture as *A. tritoniformis* and lacks the protruding small rounded nodule on the outer lip, formed by a peribasal spiral cord, that characterizes *A. kempae*. *A. nautica* is correctly assigned to the synonymy of *A. tritoniformis*. Apparently *A. kempae* evolved from *A. tritoniformis* in New Zealand, rather than being a migrant from Australia.

Family Turbinellidae

Genus ***Cryptofusus*** n. gen.

Type species. *Pleia cryptocarinata* Dell, 1956, Nukumaruan–Recent, bathyal, southern and central New Zealand.

Diagnosis. A genus of Turbinellidae containing small, tall, narrow shells (20–35 mm high) with a tall, narrow spire, a long, straight, narrow, anterior siphonal canal without a siphonal fasciole (at least, in later, Miocene–Recent species), the spire about equal in height to the aperture and canal; a small, oval, weakly armed aperture with a single low, narrow columellar plait terminating at the base of the columella, and two much weaker plaits decreasing in prominence above in some species (*Cryptofusus otaioensis* (Finlay, 1930)), the outer lip moderately thin and crenulated by the exterior spiral cords (in *C. cryptocarinatus*), or slightly thickened and bearing low transverse ridges, and with 5–6 low, short lirae well within the aperture (in *C. otaioensis*); and with sculpture dominated by prominent, well-rounded axial ridges with evenly concave interspaces each equal in width to one ridge, extending from just below the upper suture (forming a narrow, concave sutural ramp above the axial ridges) to the lower suture on spire whorls and fading out over the base on the last whorl, crossed by prominent, sharply defined, widely spaced, convex-crested spiral cords over the entire teleoconch surface, with narrow secondary threads in some interspaces, forming only low nodules at sculptural intersections. The protoconch is low, dome-shaped, of about two whorls, with its termination indistinct; the initial tip is minute, sharp, and followed by a rather wide, flattened upper surface; the second whorl is taller, bearing low axial ridges; incomplete or corroded on all material seen.

Remarks. Finlay (1930a:60) proposed the genus *Pleia* for shells resembling a small species of *Pleuroploca* but having one low, narrow rather than three conspicuous columellar plaits, and selected the Australian middle Miocene species *Fasciolaria decipiens* Tate (1888:150, pl. 8, fig. 1; a synonym of *P. tenisoni* (Tenison Woods, 1879); TA Darragh Museum Victoria pers. comm. October 2007) as the type species. He referred his new species *Pleia otaioensis* (from Bluecliffs, Otaio River, New Zealand; Otaian, early Miocene) to *Pleia*, but it seems likely that Finlay misinterpreted the scale of Tate's (1888) illustration, as he somehow failed to realize the size difference between the New Zealand and Australian species. *Pleia tenisoni* (Balcombian, Middle Miocene; Muddy Creek, Victoria and River Murray cliffs, South Australia; Darragh 1970:165, 200; Fig. 11E, H) is a much larger, more coarsely sculptured species than the New Zealand fossil and Recent species assigned to *Pleia* (illustrated specimen, Fig. 11E,H; NMV P.314675, Muddy Creek Formation [Balcombian, early middle Miocene], Muddy Creek, near Hamilton, western Victoria: H 70.8, D 25.4 mm, rather than 20–35 mm as in *Cryptofusus* species). It also has markedly wider whorls,

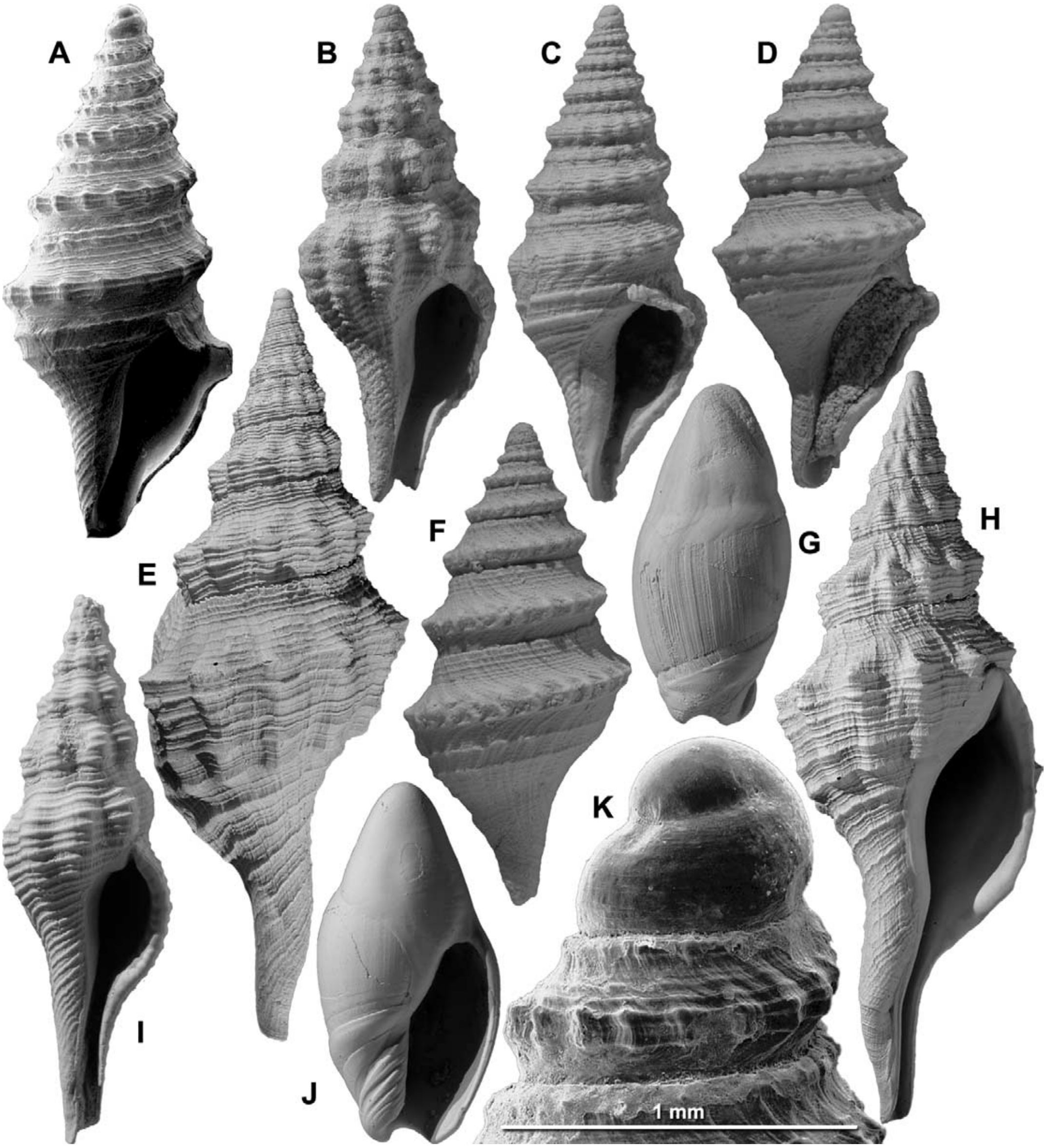

Figure 11 (A,K) *Kuroshioturris angustata* (Powell), RM4033, Recent, 90 m, Doubtless Bay, Northland, SEM; A, whole specimen, height 9.4 mm; K, protoconch in A. (B) *Cryptofusus cryptocarinatus* (Dell), type species of *Cryptofusus* n. gen., GS10844, U26/f6037, Castlepoint, E Wairarapa, early Nukumaruan; height 23.3 mm. (C,D,F) *Kuroshioturris putere* n. sp., GS1567, W19/f7516, right bank Waiau River at junction Pakihiwi Stream, inland from Wairoa, N Hawke's Bay, Opoitian; C, paratype, TM8673, height 14.0 mm; D,F, holotype, TM8672, height 13.7 mm. (E,H) *Pleia tenisoni* (Tenison Woods), type species of *Pleia* Finlay, 1930, NMV P.314675, Muddy Creek Formation (Balcombian, Middle Miocene), Muddy Creek, near Hamilton, W Victoria, Australia; height 70.8 mm. (G,J) *Amalda (Baryspira) olsoni* Beu, GS11225, V20/f8002, Darkys Spur Formation (late Nukumaruan), Darkys Spur, W of Devils Elbow, Hawke's Bay; G, height 31.9 mm; J, height 34.3 mm (see also Fig. 17E). (I) *Cryptofusus otaioensis* (Finlay), GS9569, I38/f7748, Mount Harris Formation (Waitakian), upper Tengawai River, Canterbury; height 25.8 mm.

more prominent peripheral nodules defining a much more obvious, strongly concave sutural ramp, a second row of peribasal nodules defining a lower angulation, a sharply contracted neck, a very long, narrow, twisted siphonal canal, an unusually widely flared outer lip, and a single very low, narrow columellar plait stopping well inside the aperture but placed significantly higher up than in *Cryptofusus* n. gen. The new genus *Cryptofusus*, in contrast, contains much smaller shells with rounded axial ridges having only weak nodules, a more weakly defined sutural ramp, a rather more gently contracted base, and a shorter siphonal canal. The protoconch of *P. tenisoni* is relatively large (1.8 mm wide) and blunt, of little over one whorl, smooth and polished, with a large, rounded but low initiation, merging gradually into the teleoconch over a quarter of a whorl. It is clearly a lecithotrophic one, so the larva of *Pleia* is unlikely to have been dispersed from Australia to New Zealand. The large Australian species of *Pleia* clearly are more nearly related to *Pleuroploca* Fischer, 1884 (particularly some of the smaller Australian Recent species such as *P. bakeri* (Gatliff & Gabriel, 1912); Wilson 1994, pl. 12, fig. 2a,c) and, in particular, *Latirus* Montfort, 1810 and *Hemipolygona* Rovereto, 1899 (Wilson 1994, pl. 11; Vermeij & Snyder 2006, figs. 1, 2) than to the small, elongate, axially ridged but otherwise weakly sculptured New Zealand species included by Finlay (1930a) in *Pleia*. Indeed, *Pleia tenisoni* seems closely related to *Latirus*, differing mainly in its much weaker columellar plait and much longer, narrower siphonal canal. Darragh (1970) referred to *Pleia* the three Australian middle Miocene species *Fasciolaria concinna* Tate, 1888, *F. decipiens* and *F. tenisoni*, although in his opinion *P. tenisoni* and *P. decipiens* are conspecific. Iredale & McMichael (1962:68) also referred the two Recent New South Wales species '*Pleia coronata* (Lamarck, 1822)' and '*P.*' *bakeri* (Gatliff & Gabriel, 1912) to *Pleia*, but these are typical species of *Pleuroploca* Fischer, 1884, with 2–3 much more prominent columellar plaits ('*Pleia*' *coronata* is a synonym of *Pleuroploca australasiae* (Perry, 1811); Wilson 1994:74, pl. 12, fig. 2a,b; *P. bakeri*: Wilson 1994:74 [as a form of *P. australasiae*], pl. 12, fig. 2c). The new genus *Cryptofusus* is proposed for the New Zealand species previously referred to *Pleia*, with *Pleia cryptocarinata* Dell, 1956 selected as type species so that Recent specimens can be used to determine phylogenetically important characters.

In most characters *Cryptofusus* n. gen. is more similar to *Dolicholatirus* Bellardi, 1884 (type species: *Murex lancea* Gmelin, 1791, Recent, Indo-West Pacific) (Wilson 1994:67, pl. 11, figs. 6–9, 15) than to *Pleia tenisoni*, but differs in its shorter shape, its weaker sculpture and its much less obvious columellar plait, terminating inside the aperture and only just visible at the columellar base of most species. *Latirogona ornata* (Marshall, 1918) (Otaian–Altonian, Pakaurangi Point, Kaipara Harbour, Northland; Beu & Maxwell 1990:230, pl. 25s), type and only species of *Latirogona* Laws, 1944, is similar to *Dolicholatirus* and *Cryptofusus* in size (height 20–30 mm) and general appearance, but is a little wider, with more inflated whorls, more prominent axial folds, a more complex series of fine, closely spaced spiral cords, and a much more complexly and prominently armoured aperture: 'columella with two or three definite plaits, and 3–6 additional short ridges and tubercles; parietal region with 2–4 short ridges. Outer lip with 9–11 narrow lirae within' (Beu & Maxwell 1990:230). The European Cenozoic genera *Latirulus* Cossmann, 1899 (= *Lathyrulus* Cossmann, 1901) (type species: *L. subaffinis* (Orbigny, 1850), Eocene, Paris Basin) and *Dertonia* Bellardi, 1884 (type species: *D. iriae* Bellardi, 1884, Pliocene, Italy) are similar in shape and size to *Cryptofusus*, but differ in sculpture, have a shorter anterior siphonal canal, and have three prominent columellar plaits (Wenz 1943:1242–1243). Maxwell (1992:123, pl. 16m–q) assigned his new species *Latirulus*(?) *fraudator* (Kaiatan, late Eocene, McCulloch's Bridge, South Canterbury) to *Latirulus* quite hesitantly, and it is certainly much smaller than European species, with a still shorter siphonal canal, and possibly represents a further unnamed genus.

Vermeij & Snyder (2006:419) also doubted that *L. fraudator* is correctly assigned to *Latirulus*, which they considered to be limited to Eocene rocks of Europe. Still further genera probably will be required for New Zealand Turbinellidae.

Maxwell (1992:124, fig. 9g, pl. 18m) referred *Latirofusus optatus* Marshall & Murdoch, with some hesitation, to *Fractolatirus* Iredale, 1936 (type species: *F. normalis* Iredale, 1936, Recent, Sydney Harbour) but *F. normalis* has two equal (if weak) plaits, is prominently lirate deep within the outer lip, and is a shorter, more solid shell resembling a small species of *Latirus* (H 26 mm). Judging from Maxwell's (1992:124) comparisons a position in *Streptochetus* Cossmann, 1899 seems more reasonable, as the protoconch differences pointed out by Maxwell are not now considered to be a generic character (paucispiral, that is, lecithotrophic in *Streptochetus*; of four whorls, conical, that is, planktotrophic in '*L*'. *optatus*). However, *Streptochetus intortus* (Lamarck, 1803) has a very prominent, flared siphonal fasciole on a shell otherwise quite like *Cryptofusus* new genus, although with weaker spiral cords and axial ridges and less strongly convex whorls (Wenz 1943:1264, fig. 3598). *Streptochetus incertus* (Deshayes, 1835) in the coloured illustration by Merle et al. (2008, pl. 27, fig. 3) lacks the widely flared fasciole, but is significantly larger and more finely sculptured than *L. optatus* and *Cryptofusus* species. *L. optatus* is possibly an early species of *Cryptofusus*, in a genus that later lost planktotrophy, although its spiral sculpture is finer than in all other species assigned here. The weak siphonal fasciole also could have been lost by later species. Better material will help resolve the position of *C.* (?) *optatus*. Darragh (1970) referred *Fusus aciformis* Tate (1888:139, pl. 7, fig. 5a,b) to *Fractolatirus* also, but it is a typical species of *Dolicholatirus*.

A final question is the family position. Vermeij & Snyder (2006) revised the genera related to *Latirus*, with excellent coloured figures, and concluded that '*Dolicholatirus* likely belongs in the Turbinellidae and is not a fasciolariid' (Vermeij & Snyder 2006:414). On this basis, it appears likely that *Pleia* belongs in the Fasciolariidae, subfamily Peristerniinae, near *Latirus*, whereas *Cryptofusus* belongs in the Turbinellidae near *Dolicholatirus*. A position in Turbinellidae tentatively is accepted here, for both *Cryptofusus* n. gen. and *Latirogona* Laws, 1944. Similar small, elongate tubinellids were referred to Subfamily Ptychatractinae by Beu & Maxwell (1990:414) but Family Ptychatractidae Stimpson, 1865 was referred to Superfamily Pseudolivoidea de Gregorio, 1880 by Bouchet et al. (2005:256). *Dolicholatirus*, *Cryptofusus*, *Latirogona* and the New Zealand 'ptychatractines' *Egestas* Finlay, 1926, *Exilia* Conrad, 1860 (referred to Turbinellidae by Kantor et al. 2001), *Latiromitra* Locard, 1897 (see Bouchet & Kantor 2000) and *Paleopsephea* Wade, 1926 are referred here to Turbinellidae Turbinellinae Swainson, 1835.

Species referred to *Cryptofusus* n. gen. are:

Cryptofusus cryptocarinatus (Dell) (1956b:89, pl. 14, fig. 137) (Fig. 11B), bathyal, Nukumaruan–Recent. Fossils in bathyal fauna at Palliser Bay (Beu 1967:111, pl. 2, fig. 17), and at Castlepoint, E Wairarapa coast (GS10844, U26/f6037, one specimen, Fig. 11B, collected and presented by Trevor Ritsema).

Cryptofusus otaiaoensis (Finlay) (1930a:60, pl. 3, fig. 30) (Fig. 11I), Waitakian–Altonian, Mount Harris Formation, South Canterbury–North Otago (GS9569, I38/f7748, upper Tengawai River, Waitakian, Fig. 11I; GS458, J39/f7476, Pareora River, Otaian; GS11154, J39/f026, Pareora River below Mt Horrible, Otaian; GS11149, X16/f8050, 'The Peaks', Waihao Downs, Altonian).

Cryptofusus n. sp., axial ridges obsolete on last two whorls, columellar plaits as in *O. otaioensis*; one specimen from Pukeuri road cutting, Oamaru, Altonian (GS1912, J41/f9499); = 'N. gen. of Fasciolariidae' in list by Olson in Gage (1957:125) (possibly an aberrant specimen of *C. otaioensis*).

Cryptofusus(?) n. sp., small (height 13–14 mm), with two equal, weak columellar plaits, siphonal canal relatively short; several specimens from Target Gully Shellbed, Oamaru, Altonian (labelled '*Lathyrulus*' in early GNS collections). *Cryptofusus*(?) *optatus* (Marshall & Murdoch) (1923:123, pl. 12, fig. 2), Kaiatan (late Eocene), McCulloch's Bridge, South Canterbury.

Etymology. Composed from *kryptos* (Greek, secret, hidden) and from the name of the type species, *Pleia cryptocarinata*, and from *fusus* (Latin, a spindle), used in the names of many slender, siphonostomatous gastropods. Gender masculine.

Family Olividae
Subfamily Ancillariinae

Genus ***Amalda*** H. Adams & A. Adams, 1853

Amalda H Adams & A Adams 1853:148. Type species (by subsequent designation, Vokes 1939:131): *Ancillaria tankervillii* Swainson, 1825, Recent, tropical western Atlantic (Venezuela to N Brazil).

Subgenus ***Baryspira*** Fischer, 1883

Baryspira Fischer 1883:600. Type species (by subsequent designation, Cossmann 1889:64): *Ancillaria australis* G. B. Sowerby I, 1830, Pliocene–Recent, New Zealand.

Pinguispira Finlay 1926b:433. type species (by original designation): *Ancilla (Baryspira) opima* Marwick, 1924, Pleistocene (Nukumaruan), New Zealand.

Gemaspira Olson 1956:14. Type species (by original designation): *Ancilla (Baryspira) robusta* Marwick, 1924, Oligocene–early Miocene (Duntroonian–Altonian), New Zealand.

Spinaspira Olson 1956:17. Type species (by original designation): *Baryspira (Spinaspira) stortha* Olson, 1956, early and middle Miocene (Altonian–Waiauan), New Zealand.

Remarks. The distinction between such taxa as *Amalda (Spinaspira)*, with a narrow apex apparently reflecting a narrow, multispiral protoconch, and *Amalda (Baryspira)*, with a broader apex, seems to be based solely on a developmental difference, and is not recognized here. The 'subgenera' (listed above) proposed by Olson (1956) intergrade in shell shape and have very similar radular and anatomical characters, and are synonyms in my opinion. In contrast, the distinctive radula demonstrates that *Gracilispira* Olson, 1956 is probably a separate genus.

Amalda (Baryspira) olsoni Beu, 1970 (Figs. 11G,J, 17E)

Amalda (Gracilispira) olsoni Beu 1970a:132, pl. 5, figs. 39–41.
Amalda (Baryspira) olsoni. Beu & Maxwell 1990:416; Maxwell 2009:246.

Type material. Holotype VM316, with five paratypes VM317–321, in Geology Department, Victoria University of Wellington; VM316–320 from Devils Elbow Mudstone, top of Devils Elbow hill, Highway 2, ca 35 km N of Napier; VM321 from Te Ngaru Mudstone (the mudstone formation underlying Devils Elbow Mudstone) at the same locality; all late Nukumaruan.

Other material examined. GS11225, V20/f8002, Darkys Spur Formation, long N–S horizontal cutting on Darkys Spur road, between Waipunga and Kaiwaka, 5 km WNW of Devils Elbow, late Nukumaruan (abundant; 86 collected).

Distribution. I (Beu 1970a:133) originally knew of *Amalda olsoni* only from the two uppermost siltstone units exposed on Devils Elbow hill road. However, it has since proven to be very much more common and to attain a much larger size in shallow-water sandy mudstone of Darkys Spur Formation (Haywick et al. 1991:219) exposed on Darkys Spur road, on the steep face above Waipunga, 5 km (straight line) WNW of the exposure at the top of Devils Elbow hill. I have still seen specimens from only these two localities, so it apparently is limited to late Nukumaruan rocks of central Hawke's Bay. The uncommon specimens at Devils Elbow evidently represent the fringe of the population of a species that preferred shallower water nearer to shore.

Dimensions. Holotype: H 20.5, D 9.2 mm; largest paratype, VM317: H 27.7, D 12.3 mm (Beu 1970a:133); GS11225, Darkys Spur: H 42.8, D (incomplete) 18.4 mm; H 38.0, D 18.2 mm; H 35.6, D (incomplete) 16.8 mm; H 34.4, D 17.8 mm; H 32.1, D 15.5 mm; H 30.0, D 14.8 mm; H 27.7, D 14.6 mm.

Remarks. Because of its unusually tall, relatively narrow spire, with straight outlines apart from the distinctive spire callus protruding to the left (in conventional apertural, spire-upward view), and because the type specimens were relatively small and narrow, I (Beu 1970a:132) placed *Amalda olsoni* in the subgenus *A. (Gracilispira)* Olson, 1956 (type species: *Ancillaria novaezelandiae* G. B. Sowerby II, 1859, Pliocene–Recent, New Zealand). Collection of the much larger specimens (30–42 mm rather than 20–27 mm high) that are abundant at Darkys Spur immediately made it obvious that *A. olsoni* is actually a species of *A. (Baryspira)* resembling the Pliocene to Recent shallow-water species *A. australis* (G. B. Sowerby I, 1830) in most characters, particularly the size and shape of the last whorl, and a change of subgenus was adopted by Beu & Maxwell (1990:416). *A. olsoni* differs from *A. australis* in its narrower shape, caused by the taller and narrower spire, its evenly hemispherical spire apex heavily coated with successive layers of spire callus, the right edge of the spire callus (in conventional ventral view) enveloping the uppermost part of the outer lip and curving slightly backwards from the outer lip to extend up in an almost straight line to cross the spire apex, and the left edge of the spire callus curving around to the left to the suture, and then back to the right to merge with the parietal callus. The prominent, well raised, semicircular pad thus produced on the left side of the spire is unique and renders *A. olsoni* easily recognized, as it contrasts strongly with the slightly but evenly convex outlines and narrowly pointed apex of the spire of *A. australis* and *A. mucronata*. The top fasciolar band around the base also protrudes more obviously (to the left in standard apertural view) than in all other species I have compared it with. *A. olsoni* is, therefore, a distinctive species limited to Hawke's Bay late Nukumaruan rocks, although apparently common only at Darkys Spur.

Superfamily Conoidea

Remarks. As noted by Bouchet (1990), some earlier taxonomists (particularly Powell 1942, 1944, 1966; Laseron 1954; Shuto 1969, 1971, 1983, and in several other papers) subdividing the huge 'family' Turridae recognized 'pairs' of genera with distinct protoconchs but identical teleoconch characters in several groups, originally based on Finlay's (1931) outdated concept that one genus could not contain more than one protoconch type. Turridae is now recognized as Superfamily Conoidea, composed of several families (Taylor et al. 1993; Puillandre et al. 2007, 2008), containing more than 11,000 named species (Tucker 2004; Bouchet et al. 2009). One genus in each of these 'pairs' of genera has a blunt, paucispiral, relatively simply sculptured protoconch, reflecting lecithotrophic development, whereas the other has a narrower, pointed, multiwhorled, more elaborately sculptured protoconch, reflecting planktotrophic development. The various types of lecithotrophic development are not distinguishable from protoconch characters alone, so all non-planktotrophs are referred to here as lecithotrophs, whether development is direct (spending their whole larval life protected within the parent's brood pouch, as in *Pelicaria*, or within an egg capsule as in volutes such as *Alicithoe*, in either case emerging as a small, crawling adult), demersal, or short-lived planktonic (in either case with a brief free-living larva, feeding on yolk as in direct developers, rather than feeding in the plankton). The point of Bouchet's (1990) comment is that planktotrophy is easily lost within one genus, and developmental mode alone is not a character distinguishing genera. Marshall (1978:50; 1983:3) discussed the same question for the generic classification of Cerithiopsidae and Triphoridae, in which the same range of protoconch types is encountered but, luckily, generic splitting has not occurred. He noted of Triphoridae that 'planktotrophic and lecithotrophic larval development occur throughout the family, often in the same genus or species pair'. In some genera, such as New Zealand species traditionally referred to *Tomopleura*, it has been realized for at least 20 years (initially pointed out to me by the late Phillip Maxwell) that species with lecithotrophic protoconchs ('subgenus *Maoritomella*' Powell, 1942) evolved by a number of different species losing planktotrophy independently. That is, *Maoritomella* is not a clade, but a grade, a group of unrelated species of *Tomopleura* with short, blunt protoconchs. Maxwell (2009:247) has also convincingly transferred some species previously placed in this grade, along with some placed by Powell (1942) in *Turridrupa*, to *Drilliola* Cossmann, 1903. However, both he (Maxwell 2009:247–8) and Spencer et al. (2009:209) catalogued both *Tomopleura (Maoritomella)* and *Bathytoma (Micantapex)* as subgenera, when recognition of the solely developmental difference these 'subgenera' were based on indicates their synonymy. Much rationalization of conoidean genera is required to delete 'genera' based solely on developmental differences. Medinskaya & Sysoev (2001) and Kantor et al. (2008) have also demonstrated that teleoconch characters do not always reflect radular differences in Conoidea, so the molecular phylogeny of the subfamily Turrinae (Heralde et al. 2007) and of the superfamily begun by Puillandre et al. (2008) and Bandyopadhyay et al. (2008) is desperately in need of expansion with many further taxa.

Many New Zealand Conoidea need to be reclassified to delete meaningless 'genera' based only on developmental type. Some obvious cases are *Lirasyrinx* Powell, 1942 = *Parasyrinx* Finlay, 1924; *Austroclavus* Powell, 1942 = *Splendrillia* Hedley, 1922; *Micantapex* Iredale, 1936 = *Bathytoma* Harris & Burrows, 1891 (a long-accepted synonymy); and as noted above, *Maoritomella* Powell, 1942 = *Tomopleura* Casey, 1904, if indeed *Tomopleura* is appropriate for New Zealand species. (The type species of *Tomopleura*, *T. nivea* (Philippi, 1851) [Kilburn 1986, figs. 62–65; Sysoev in Poppe 2008:754, pl. 627, figs. 8, 9; height 26–29 mm] is larger and has a much less well-defined sutural ramp and mid-whorl angulation than are so obvious on species referred to *Tomopleura*. *Cryptomella* Finlay, 1924 [type species: *Leucosyrinx transenna* Suter, 1917, early Miocene, New Zealand] may be required for New Zealand taxa previously included in *Tomopleura* and *Maoritomella*, other than those transferred to *Drilliola* by Maxwell [2009]. This is one of many conoidean questions that will only be resolved by molecular studies.) Some other synonymous generic 'pairs' were pointed out by Bouchet (1990), and many others recognized by Powell (1966) require synonymy. Some new generic placements are suggested here for New Zealand Neogene–Recent Conoidea, although many other New Zealand Conoidea still require re-evaluation. In particular, taxonomic clarification of *Neoguraleus* sensu lato, the most speciose and taxonomically 'difficult' of New Zealand conoidean genera, is a large task beyond the scope of this paper.

Family Turridae
Subfamily Turrinae

Genus ***Kuroshioturris*** Shuto, 1961

Kuroshioturris Shuto 1961:83. Type species (by original designation): *Gemmula (Kuroshioturris) hyugaensis* Shuto, 1961, Pliocene to Recent, Japan (Hasegawa, Okutani & Tsuchida in Okutani 2000:627, pl. 312, fig. 40).

Kuroshioturris angustata (Powell, 1940) (Fig. 11A, K)

Pleurotoma (Hemipleurotoma) nodilirata Murdoch & Suter 1906:284, pl. 22, fig. 11 only (in part, Castlecliff specimen only; junior primary homonym of *Pleurotoma nodilirata* E. A. Smith, 1878).
Micantapex angustatus Powell 1940:245, pl. 31, fig. 7; Powell 1942:56; Dell 1956a:130, pl. 19, fig. 194; Fleming 1966:70.
Lucerapex angustatus. Powell 1966:50, text-fig. C49; Powell, 1979:228, fig. 53.1; Beu & Maxwell 1990:418; Spencer & Willan 1996:29; Tucker 2004:72; Spencer et al. 2009:211.
'*Lucerapex*' *angustatus*. Maxwell 2009:249.

Type material. Micantapex angustatus holotype AIM AK70470, Recent, from 48 m, off Waikuku Beach, North Cape (not seen).

Other material examined. **Mangapanian or earliest Nukumaruan:** beneath Pukenui Limestone in large cutting on Tupurupuru Road, E of Gladstone, S Wairarapa (NMNZ M.42870, one typical), probably late Mangapanian rather than early Nukumaruan; Waihua River, 2.5 km up Waihua Valley Road from Highway 2, 200 m N of sharp horseshoe bend in road, N Hawke's Bay, early Nukumaruan (GS1409, W19/f8477, one). **Nukumaruan:** Petane, Hawke's Bay, ex Suter collection (GNS, one); 'Petane, cliffs opposite Eskdale Bridge', that is, Mairau Mudstone, cliff at Esk River bridge, junction of Highways 3 and 5 (GNS, one); Petane (NMNZ M.27004, one); road cut, Puketapu, inland from Napier (GS5216, V20/f8517, six); Castlepoint Fm, Castlepoint, E Wairarapa (GS10844, U26/f6037, one). **Castlecliffian:** several early GNS lots labelled 'Castlecliff, Wanganui'; Lower Castlecliff Shellbed (OIS 15) (GS4104, R22/f6518, re-collection, two); Upper Castlecliff Shellbed (OIS 11), Castlecliff (GS4185, R22/f6502, three); recorded also by Fleming (1953:199, 218, 226, 230) from Kaikokopu Shell Grit (OIS 19; GS4134, R22/f7408, Kaikokopu Road, and GS4156, R22/f7417); Lower Castlecliff Shellbed (OIS 15; GS4104, R22/f6518), Pinnacle Sand (OIS 13; in four collections on the coast), and Tainui Shellbed (OIS 13; in three collections; GS10963, R22/f6619A, re-collection of GS4013, two); NMNZ M.40275, cutting on Wainui Road, SW shore of Ohiwa Harbour, Ohope, Bay of Plenty, OIS 15? (13); M.158073, Herepuru Road, Matata, Bay of Plenty, OIS 15? (14). **Haweran:** Landguard Sand (OIS 9), Landguard Bluff, opposite Wanganui City (GS4003, R22/f7394, re-collection, three; WRB Oliver collection, NMNZ, M.15715, one); also recorded by Fleming (1953:273) from Waipuna Conglomerate (OIS 7) at Landguard Bluff, opposite Wanganui City (GS4001, R22/f7392). **Recent:** RM72, 68 m, NW of Cuvier I, Coromandel (one); RM78, 200 m, off Great Barrier Island, from the sample reported by Murdoch & Suter (1906) (two); RM4033, 90 m, off Doubtless Bay, Northland (four); 87 lots in NMNZ, ranging from (southernmost) off Oamaru, 55–120 m (M.110910, one) and the Chatham Rise, through Cook Strait as far W as Kapiti Island and Stephens Island, and up the east coast of the North Island as far N as North Cape (M.158067, E of North Cape, 357–447 m, one; M.158067, E of North Cape, 257–327 m, one) and around as far W as Ahipara; most material is from the warm-water province between East Cape and North Cape.

Distribution. *Kuroshioturris angustata* lives in a wide range of depths (ca 30–>300 m) all around northern and eastern New Zealand. There are no records from the southern South Island, around the Chatham Islands, around the Three Kings Islands, or from the W coast of either main island, other than in W Cook Strait and off Ahipara. It is most common on offshore, soft, fine-grained substrates, so its apparent scarcity in early Nukumaruan and early Castlecliffian rocks probably reflects this facies preference. As a fossil, *K. angustata* has been collected mainly from Castlecliffian–Haweran rocks in Wanganui Basin and Nukumaruan rocks in central Hawke's Bay, although there are records also from late Mangapanian–early Nukumaruan rocks in Wairarapa and Castlecliffian rocks in the Bay of Plenty.

Dimensions. GS5216, Puketapu, Hawke's Bay: H (incomplete) 14.8, D 6.3 mm; H 15.6, D 6.2 mm; GS4185, Upper Castlecliff Shellbed, Castlecliff: H 12.8, D 4.6 mm; Castlecliff, early collection: H 16.5, D 5.6 mm; Recent, NMNZ M.112114, Deepwater Cove, Bay of Islands, 55 m: H 13.3, D 4.8 mm; H 13.4, D 4.6 mm; NMNZ M.67615, W of Plate I, Bay of Plenty, 59–64 m: H 15.8, D 5.3 mm; H 13.2, D 5.1 mm.

Remarks. The generic position of '*Micantapex*' *angustatus* has long been in doubt. It differs from species of *Bathytoma* (= *Micantapex*) in its small size and much narrower shape, and so resembles several other genera, including *Gemmula*, at least superficially. Powell (1966) transferred it to *Lucerapex* Iredale, 1936, but the type species (*Pleurotoma casearia* Hedley & Petterd, 1906, Recent, deep water off New South Wales) lacks all spiral sculpture other than the peripheral nodulose carina formed by the trace of the sinus apex, and instead has the surface crossed by wavy axial lines (low, thin axial lamellae). Species of *Lucerapex* recognized in the New Caledonian fauna by the MNHN informal 'Turridae group' (P Bouchet, Y Kantor, RN Kilburn, A Sysoev; CD of unpublished colour catalogue examined) are taller and narrower than the species considered here, with either a completely smooth, polished teleoconch surface apart from the peripheral nodule row, or the rest of the teleoconch sculptured with thin, closely spaced axial lamellae. The New Zealand fossil and living species are not congeneric with these.

The illustration of a representative species of *Kuroshioturris* Shuto, 1961 by Powell (1966:48, pl. 6, figs. 7, 8) has only weak nodules at the periphery, and does not appear to be related to '*Micantapex*' *angustatus*. However, the Japanese Recent species illustrated by Hasegawa et al. in Okutani (2000) have a single row of prominent peripheral nodules, and closely resemble *M. angustatus*: *K. hyugaensis* (Shuto, 1961), that is, the type species (Hasegawa et al. in Okutani 2000:627, pl. 312, fig. 40); *K. albogemmata* Kuroda & Oyama in Kuroda, Habe & Oyama (1971:221, pl. 57, fig. 8; pl. 111, fig. 3; Hasegawa et al. in Okutani 2000, pl. 312, fig. 38); *K. nipponica* (Shuto, 1961) (Hasegawa et al. in Okutani 2000, pl. 312, fig. 39); and *K. kurodai* (Makiyama, 1927) (Hasegawa et al. in Okutani 2000, pl. 312, fig. 41). *K. albogemmata* and *K. nipponica* resemble *M. angustatus* particularly closely. The apex of the sinus trace forms the peripheral nodule row, as in *Bathytoma*, *Gemmula* and *M. angustatus*. The protoconch was described by Powell (1966:48) as 'rather large and composed of a depressed, rounded and smooth first volution and a convex and inflated second one, which is smooth except for the last quarter whorl, with brephic axials'. However, this is clearly a lecithotrophic protoconch; at least *K. albogemmata* and *K. kurodai* have a smaller, narrower apex and are possibly planktotrophic. The teleoconch shape, with a weak peribasal angulation, the presence or absence of a weak subsutural cord, the spiral sculpture of several narrow cords, and the presence of one peripheral nodule row in *K. albogemmata* and *K. nipponica* agree exactly with *M. angustatus*. *Kuroshioturris* appears to be the appropriate genus for *M. angustatus*.

The Opoitian–Waipipian specimens assigned below to *Kuroshioturris putere* n. sp. differ from *Gemmula* species in their much smaller size, shorter shape, much shorter anterior siphonal canal, lack of a stromboid notch in the lower margin of the outer lip, and shallower posterior sinus at the peripheral keel. It also has a simpler, low protoconch, which is quite unlike the protoconch of *Gemmula*, described by Powell (1966:47) as 'tall, conical, polygyrate, and axially costate', although that of *Gemmula* is probably planktotrophic. *K. angustata* has a low, rounded, smooth, mammillate protoconch of little more than 1.5 whorls (Fig. 11K), reflecting lecithotrophic development, and *K. putere* n. sp. apparently has an identical one. Powell (1966:48) ranked *Kuroshioturris* as a subgenus of *Ptychosyrinx* Thiele, 1925 (Turrinae), but the shells illustrated by Hasegawa et al. in Okutani (2000) show that it is a distinct genus, smaller and more weakly sculptured than *Ptychosyrinx*. Powell also placed *Lucerapex* nearby, and illustrated the radula of '*L.*' *angustatus* as representing the genus *Lucerapex*, commenting that 'If *angustatus*... is correctly assigned to *Lucerapex*, then the radula... is very similar to that of *Lophiotoma acuta* [(Perry, 1811)], consisting of a pair of marginals, with the base spread like a pair of calipers' (Powell 1966:50, text-fig. C49). The turrine radula indicates a position in Turrinae (and in *Kuroshioturris*) for '*M.*' *angustatus*, as compared with the clathurelline radula described for *Bathytoma* by Powell (1966:64, as *Micantapex*). Neither *Kuroshioturris* nor *Lucerapex* were studied but *Bathytoma* is included in 'Clathurellinae' clade 20 by Puillandre et al. (2008). The radula, and preferably the DNA, of *Lucerapex* should be examined from a more typical species, to re-evaluate its subfamilial position, which is completely unknown at present. Some relatively small Recent Australian species that traditionally have been placed in *Bathytoma* or *Epidirona* also possibly belong in *Kuroshioturris*, such as '*Micantapex*' *hecatorguia* (Verco, 1907) (Cotton 1947, pl. 3, unnumbered fig.) and *Epidirona nodulosa* Laseron (1954:9, pl. 1, figs. 21–23). The same is also true of some of the small, narrow New Zealand fossil species traditionally included in *Bathytoma*, such as *B. filaris* (Marwick) (1931:134, pl. 15, fig. 279). Some of the smaller, more finely sculptured species referred by Marwick (1931) to *Gemmula*, such as *G. peraspera* (Marwick 1931:133, pl. 15, figs. 276, 277), are also similar to *Kuroshioturris putere* n. sp. in their paucispiral protoconch, narrowly triangular peripheral keel, and few prominent spiral cords on the base of an otherwise finely sculptured shell, and their taxonomic position deserves reassessment. There may well be still earlier occurrences of this poorly known genus in New Zealand.

I (Beu 1970b:232) followed Powell's placement of '*Micantapex*' *angustatus* in *Lucerapex* when I suggested that '*Micantapex*' *pulcherrimus* Vella, 1954 also belongs in *Lucerapex* (Tongaporutuan, Bell's Creek bathyal fauna, near White Rock Road, S Wairarapa). '*M.*' *pulcherrimus*, with its numerous similar rows of large, sharp nodules, also resembles species of *Gemmuloborsonia* Shuto, 1989. Sysoev & Bouchet (1996) revised the Pacific Recent species of *Gemmuloborsonia*, showing that it is a widespread Miocene to Recent bathyal turrine genus, although it was included in a clade separate from Turrinae (sensu stricto) by Puillandre et al. (2008). However, all species referred to *Gemmuloborsonia* have a low, wide columellar plait in at least some specimens, and this has not been observed in '*M.*' *pulcherrimus*. Species of *Gemmuloborsonia* also are much larger than '*M*'. *pulcherrimus*. These characters, therefore, suggest that '*M.*' *pulcherrimus* should be referred to *Kuroshioturris* rather than *Gemmuloborsonia*. *Gemmuloborsonia* species have a turrine radula (Sysoev & Bouchet 1996, fig. 1A) not unlike that of *Kuroshioturris angustata*, rather than the clathurelline one that would have been expected from the *Borsonia*-like teleoconch. More typical, unnamed species of *Gemmuloborsonia* are represented by material in GNS from middle Miocene deep-water siltstone in Westland—a large, typical, robustly sculptured species from Marsden-Kumara Road, Clifdenian (GS4784, J32/f9586) and Eight-Mile Creek, Waiauan (GS4277, K32/f8521) and a smaller species from Alexander Street, Greymouth, Clifdenian (GS3159, J32/f7559).

Kuroshioturris putere n. sp. (Fig. 11D, C, F)

Type material. Holotype TM8672, with three paratypes TM8673–5, GS1567, W19/f7516, right bank Waiau River at junction with Pakihiwi Stream (small side-stream to W), 600 m N of end of Steed forestry road and 1.3 km S of Ruapapa dam powerhouse, ca 5 km WNW of Cricklewood, ca 25 km straight-line distance WNW of Wairoa, N Hawke's Bay; grid reference W19/708424; Opoitian, with *Stiracolpus procellosus* (Marwick, 1931), etc.

Other material examined. **Opoitian:** stream in headwaters of Waihua River, 200 m N of Trig. O no. 2, 800 m S of junction of Putere and Cricklewood Roads, ca 10 km straight-line distance W of type locality (GS1567), Wairoa district, N Hawke's Bay; grid reference W19/619401; with *Pelicaria parva*, *Zeatoma decens* (Marwick, 1931), *Kaweka fulta* Marwick, 1931, in a large fauna (one paratype, TM8676, GS1576, W19/f7483). **Waipipian:** second-to-top shellbed, with abundant *Polinices waipipiensis* (Marwick, 1924), near head of E branch, Greek's Creek, S side of Arahura valley, Westland; grid reference J33/547283; with *Austrofusus pagoda* (Finlay, 1924), *Lamprodomina*, *Clavatoma* (one paratype, TM8677, GS12356, J33/f065).

Distribution. Recorded at present only from Opoitian rocks of N Hawke's Bay and Waipipian rocks of Greek's Creek, Arahura valley, Westland.

Dimensions. Holotype: H 13.7, D 6.3 mm; paratype TM8673: H 14.0, D 6.6 mm; paratype, TM8676: H (incomplete) 12.7, D 5.9 mm.

Description. Shell small (H 14 mm), tall and moderately slender, with tall spire and relatively short last whorl (siphonal canal apex and outer lip slightly incomplete). Protoconch low, rounded, smooth, mammillate, of little more than 1.5 whorls, with a large, subspherical initiation, apparently as in *Kuroshioturris angustata*, but somewhat abraded on all specimens. Teleoconch of ca 6.5 whorls, spire relatively wide, rendered prominently gradate by strongly protruding peripheral keel at base of sutural ramp, keel just above suture on most spire whorls; suture descending on last whorl on some specimens, raising position of keel to mid-whorl height on paratype TM8673; base weakly convex below keel, tapering evenly and strongly into weakly concave neck and moderately long, gently tapered, incomplete but apparently unnotched anterior canal. Sutural ramp moderately wide, upper two-thirds steeply sloping, almost flat; lower third deeply concave, curving out to form protruding peripheral keel. Sculpture visually dominated by one peripheral row of prominent, narrow, sharply pointed, triangular nodules formed by apex of trace of posterior sinus, otherwise predominantly of fine spiral cords; 20 nodules on last whorl and 19 on penultimate whorl of holotype, 23 on last whorl and 22 on penultimate whorl of paratype TM8673. Spiral sculpture commencing on first teleoconch whorl as one prominent subsutural row of moderately large triangular nodules and one prominent peripheral row of larger triangular nodules, together occupying most of whorl surface, all weakening down spire; subsutural row gradually weakens to form 2–3 moderately prominent spiral cords (the lowest finely nodulose) over mid-spire, then weakens further to form wide zone of 3–4 low, narrow, closely spaced spiral cords slightly elevated above rest of ramp, with scarcely any nodules, on last two whorls of holotype, fading out altogether on some paratypes; 4–5 fine, closely spaced spiral threads develop on upper part of wide, strongly concave sutural ramp, lower third almost smooth; three very narrow, closely spaced spiral cords develop around peripheral nodule row on last 2–3 teleoconch whorls, uppermost very faint, central most prominent; two prominent, narrow spiral cords on upper part of base, upper cord margining suture and lower appearing from suture on holotype, upper cord appearing from suture on some paratypes; 1–3 lower, narrower, closely spaced, very fine spiral threads above and between two prominent cords on base, 12–15 further fine threads below, fading out over siphonal canal. Axial sculpture of growth lines only, apart from peripheral nodules. Aperture unthickened, without parietal callus, inner lip slightly excavated into previous whorl; outer lip thin and simple, without stromboid notch; profile of outer edge of outer lip biarcuate, moderately convex over sutural ramp, forming narrowly rounded posterior sinus at peripheral nodule row, curving forwards again moderately below ramp.

Remarks. *Kuroshioturris angustata* has been thought of as a late Pliocene (Nukumaruan) to Recent species only (Beu & Maxwell 1990:418) and so, potentially, *Kuroshioturris* is a group that arrived in New Zealand late in Pliocene time. However, a similar form, *K. putere* n. sp., a little wider, more prominently and sharply nodulose at the periphery than *K. angustata* and with only two prominent basal spiral cords, is now recorded from Opoitian–Waipipian rocks. The specimens from N Hawke's Bay were included in the faunas reviewed by Marwick (1965), but were not described by him, and labels on some of the specimens show that he was undecided whether they belonged in *Gemmula* or '*Micantapex*', although some are clearly labelled as related to '*Micantapex*' cf. *angustatus*. *K. putere* n. sp. has a slightly narrower and more strongly protruding peripheral keel than in *K. angustata*, producing a slightly wider and more strongly concave sutural ramp. The peripheral nodule row also bears three narrow spiral cords more obviously in *K. putere* n. sp. than in *K. angustata*, and as the central cord protrudes the most, the keel is raised into a row of pointed, spine-like nodules rather than the lower, subquadrate nodules of *K. angustata*. Also, the subsutural fold of *K. putere* n. sp. is considerably lower and less well defined over the last few whorls than in *K. angustata*, scarcely raised at all in some specimens. The base also has only two moderately prominent spiral cords, narrow and quite closely spaced, high up below the peripheral angulation, and the remainder of the base and the sutural ramp bear fine, closely spaced spiral threads in *K. putere* n. sp., whereas there are three prominent, rather more widely spaced cords in *K. angustata*. The result is an overall appearance that is more finely sculptured, although with a slightly shorter spire, and with a sharper and more narrowly defined peripheral keel in *K. putere* n. sp. than in *K. angustata*. Paratype TM8676 (GS1576, Waihua River, 800 m S of junction of Putere and Cricklewood Roads, Wairoa district) has a complete outer lip, including the sinus apex flared outwards at the peripheral keel as is seen in many Recent specimens of *K. angustata*, and provided the lip description included above. The similarity in size, shape, sculpture, sinus shape and protoconch leave little doubt that *K. putere* n. sp. is closely related to *K. angustata*, and possibly was its direct ancestor; the change seems to have been an abrupt speciation event. However, the specimen of *K. angustata* listed above from Waihua River, N Hawke's Bay (GS1409, W19/f8477, Mangapanian or early Nukumaruan) has a slightly shorter spire and more triangular peripheral nodules than in most other specimens of *K. angustata*, although it agrees with *K. angustata* in having the subsutural fold prominent and nodulose down onto the last whorl, and in having more numerous spiral cords on the base than in *K. putere* n. sp. The late Miocene (Tongaporutuan) bathyal species *K. pulcherrima* differs from *K. putere* n. sp. in having three prominently nodulose spiral cords below the peripheral keel and in retaining a prominently nodulose subsutural fold onto the last whorl, so that its obvious sculpture consists of five rows of similar, triangular nodules, whereas other species suggested above to be potential members of *Kuroshioturris*, such as *Bathytoma filaris*, are more similar to *K. putere* n. sp., differing in their more even, fine spiral sculpture and less prominent peripheral nodules.

Etymology. The species name is from the type locality, near Putere-Cricklewood Road in N Hawke's Bay; a noun in apposition.

Subfamily Crassispirinae

Genus ***Aoteadrillia*** Powell, 1942

Aoteadrillia Powell 1942:87. Type species (by original designation): *Pleurotoma wanganuiensis* Hutton, 1873, (Mangapanian?) Nukumaruan–Recent, New Zealand.

Aoteadrillia wanganuiensis (Hutton, 1873) (Figs. 12A–G, J, Fig. 13A–G, J)

Pleurotoma wanganuiensis Hutton 1873b:4; Hutton 1893:50, pl. 6, fig. 28; Harris 1897:46.
Drillia chordata Suter 1908:184, pl. 7, fig. 16; Suter 1913:475, pl. 21, figs. 5, 5a (**new synonym**).
Drillia wanganuiensis. Suter 1914:29, pl. 2, fig. 13.
Austrodrillia alpha King 1933:349, pl. 36, fig. 6; Beu 1967:114.
Austrodrillia beta King 1933:349, pl. 36, fig. 7.
Austrodrillia gamma King 1933:350, pl. 36, fig. 8.
Inquisitor wanganuiensis. Powell 1934a:264.
Aoteadrillia gamma. Powell 1942:90; Fleming 1966:73.
Aoteadrillia beta. Powell 1942:90; Fleming 1966:73.
Aoteadrillia alpha. Powell 1942:90; Fleming 1966:73; Beu 1979:88; Beu & Maxwell 1990:418.
Aoteadrillia thomsoni Powell 1942:90, pl. 2, fig. 7; Fleming 1966:73; Beu & Maxwell 1990:419; Maxwell 2009:249 (**new synonym**).
Aoteadrillia trifida Powell 1942:91, pl. 12, fig. 13; Fleming 1966:73; Beu & Maxwell 1990:419, Maxwell 2009:249 (**new synonym**).
Aoteadrillia wanganuiensis. Powell 1942:91; Fleming 1966:73; Beu & Maxwell 1990:367, pl. 49p; Powell 1979:231; Spencer & Willan 1996:29; Tucker 2004:1072; Spencer et al. 2009:211; Maxwell 2009:249.
Aoteadrillia wanganuiensis chordata. Powell 1942:92; Boreham 1959:59; Powell 1966:86, pl. 13, fig. 7; Fleming 1966:73; Tucker 2004:199.
Aoteadrillia bisecta Powell 1942:92, pl. 1, fig. 6; Fleming 1966:73.
Aoteadrillia chordata. Beu & Maxwell 1990:419; Spencer et al. 2009:211; Maxwell 2009:249.

Type material. *Pleurotoma wanganuiensis*, two syntypes TM8306–7, from 'Shakespeare Cliff', Wanganui; almost certainly from Tainui Shellbed (OIS 13), which formerly cropped out at Shakespeare Cliff, within Wanganui City. The slightly larger syntype (TM8306) was labelled 'lectotype' when received from NMNZ many years ago, but this unpublished designation has no status; the two syntypes are conspecific and both are well preserved. *Drillia chordata*, lectotype (designated by Boreham 1959:59, as 'paratype' in error) TM1109, with three paralectotypes, TM1110–TM1112, ex Suter collection, Recent, dredged off Otago Heads. *Austrodrillia alpha*, holotype TM8308 (Fig. 12F), from Onoke Formation (early Nukumaruan), cliffs E of Lake Ferry, Palliser Bay, S Wairarapa. *Austrodrillia beta*, holotype TM8309 (Fig. 12D), from the same locality. *Austrodrillia gamma*, holotype TM8310 (Fig. 12B), from the same locality. *Aoteadrillia thomsoni*, holotype AIM AK70914, with one paratype AK71790, from E shore of Lake Grassmere, Marlborough (Nukumaruan?); two paratypes TM8315–TM8317 (Fig. 13A, C), from type locality, collected by JA Thomson; four paratypes TM8318-TM8321, from GS2329, U23/f6381, W-facing hillside 0.5 km N of Whetukura, 4 km SE of Ormondville, Dannevirke district, S Hawke's Bay, probably Mangapanian (below uppermost Te Aute limestone, that is, Te Onepu Limestone; Beu 1995). *Aoteadrillia trifida*, holotype TM8311 (Fig. 12G), from GS2624, S27/f8463, Makara-Mangaopari River junction, White Rock Road, S Wairarapa; Pukenui Limestone, early

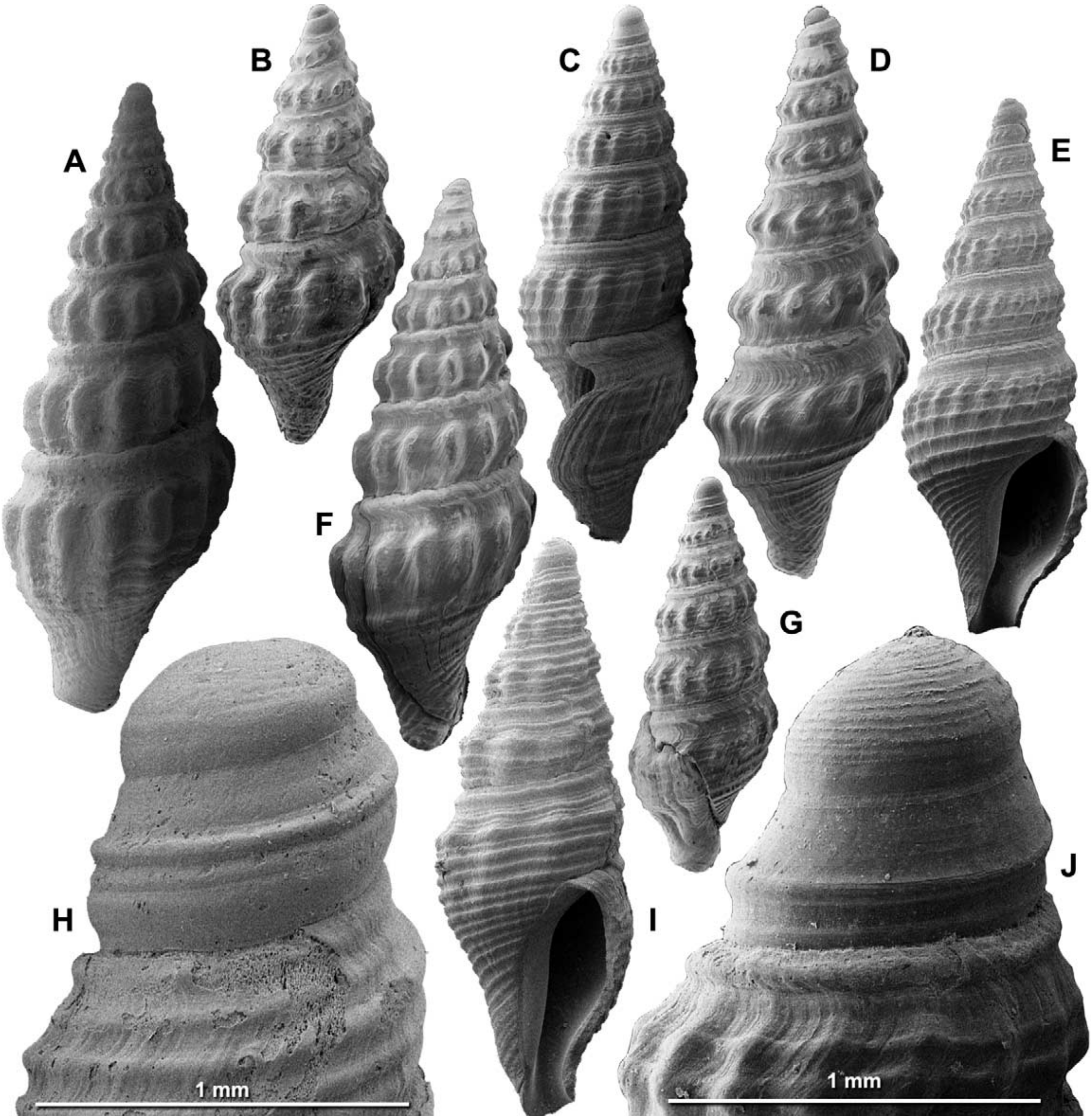

Figure 12 (A–G,J) *Aoteadrillia wanganuiensis* (Hutton), type species of *Aoteadrillia* Powell, 1942; SEM; A, paratype of *Aoteadrillia bisecta* Powell, TM8312, GS2610, S27/f8449, Makara River, S Wairarapa, early Nukumaruan; height 14.2 mm; B, holotype of *Austrodrillia gamma* King, TM8310, Onoke Formation (early Nukumaruan), cliffs E of Lake Ferry, Palliser Bay; height 9.8 mm; C,E,J, GS10963, R22/f6619A, 2 specimens, probable topotypes of *A. wanganuiensis*, Tainui Shellbed (Castlecliffian, OIS 13), "the buttress", Castlecliff; C, height 12.2 mm; E, height 12.2 mm; J, protoconch of C; D, holotype of *Austrodrillia beta* King, TM8309, Onoke Formation (early Nukumaruan), cliffs E of Lake Ferry, Palliser Bay; height 12.8 mm; F, holotype of *Austrodrillia alpha* King, TM8308, Onoke Formation (early Nukumaruan), cliffs E of Lake Ferry, Palliser Bay; height 12.8 mm; G, holotype of *Aoteadrillia trifida* Powell, TM8311, GS2624, S27/f8463, junction Mangaopari Stream and Makara River, S Wairarapa, early Nukumaruan; height 8.8 mm. (H,I) *Aoteadrillia apicarinata* (Murdoch & Suter), GS10858, U22/f09, Ashcott Road, NW of Pukeora hill, W of Waipukurau, Hawke's Bay, Nukumaruan, SEM; H, whole specimen, height 11.1 mm; I, protoconch of H.

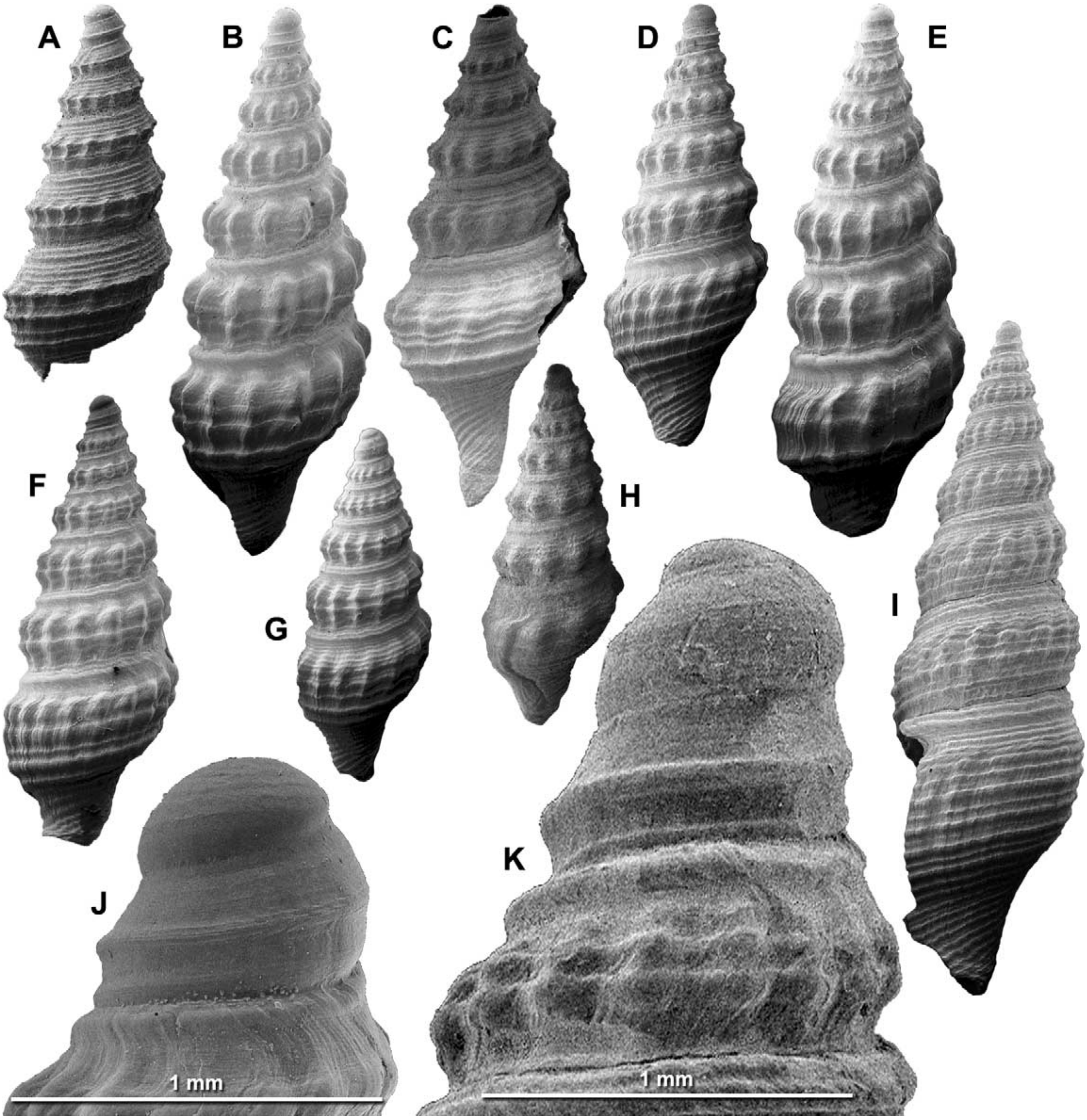

Figure 13 (A–G,J) *Aoteadrillia wanganuiensis* (Hutton), SEM; A, C, 2 paratypes of *Aoteadrillia thomsoni* Powell, GS2329, U23/f6381, Takapau Survey District, Dannevirke, early Nukumaruan; A, TM8318, height (incomplete) 8.5 mm; C, TM8319, height 11.4 mm; B,E,G, 3 specimens, GS10337, Q32/f8843, bathyal early Nukumaruan fauna, hill above Glenstrae woolshed, Oaro, Marlborough; B, height 12.3 mm; E, height 12.0 mm; G, height 8.0 mm; D,F,J, "*chordata* form", 2 specimens, Recent, RM5589, Portobello sta. Mu70–45, 540–490 m, Papanui Canyon, off Otago Peninsula; D, height 10.0 mm; F, height 10.2 mm; J, protoconch of F. (H) *Aoteadrillia waihuaensis* Powell, holotype, GS1560, W19/f8480, TM8698, Waihua River upstream from Ngamahanga Stream, N Hawke's Bay, Waipipian-Mangapanian; H 8.1, D 3.1 mm. (I,K) *Aoteadrillia finlayi* Powell, GS11465, V21/f6015, Mairau Mudstone (late Nukumaruan), "the Watchman" hill, Napier; I, height 18.3 mm; K, protoconch of I.

Nukumaruan. *Aoteadrillia bisecta*, holotype AIM AK70911, from Petane, central Hawke's Bay, late Nukumaruan; three paratypes TM8 312–TM8314 (Fig. 12A), from GS2610, S27/f8449, Makara River, 1 km upstream from junction with Ruakokopatuna River, S Wairarapa; Pukenui Limestone, early Nukumaruan.

Other material examined. Not listed; abundant and widespread.

Distribution. *Aoteadrillia wanganuiensis* is common and widespread in Nukumaruan and Castlecliffian rocks wherever they occur in New Zealand, in North Canterbury, Marlborough, Wairarapa district, Hawke's Bay and Wanganui Basin, as well as Castlecliffian and Haweran rocks in the Bay of Plenty (Matata, Ohope, Te Piki) and Castlecliffian rocks at Cape Kidnappers (Fleming in Kingma 1971:98). At most localities where faunas are preserved that lived in shallow shelf environments on soft substrates it is much the most common conoidean found, although in still shallower water *Neoguraleus* species are more common. Coarsely sculptured forms living in cooler water than more finely sculptured specimens at present indicates that the various intergrading named forms are of little biostratigraphical utility, except for the dominance of coarsely sculptured forms resembling *Drillia chordata* in early Nukumaruan rocks of Wairarapa and North Canterbury. Recent specimens in NMNZ occur from the Otago fiords (Dusky Sound, Thomson Sound, Doubtful Sound) and the Otago shelf and canyons north to New Plymouth on the west coast and to the Bay of Plenty on the east coast. There are no records in NMNZ from the southernmost South Island, Stewart Island, the Chatham Islands, or the northern North Island north of the central Bay of Plenty. However, a single empty shell is present among BW Hayward's dredged molluscs from Port Pegasus, Stewart Island (GNS RM6061), suggesting that it is rare near the extremities of its range rather than completely absent.

Dimensions. GS2610, S27/f8449, TM8312, paratype of *Austrodrillia bisecta*, Makara River, S Wairarapa: H 14.1, D 5.1 mm; GS2329, U23/f6381, TM8318, paratype of *Aoteadrillia thomsoni*, Whetukura, S Hawke's Bay: H 12.7, D (slightly incomplete) 4.9 mm; GS11465, V21/f6015, Mairau Mudstone, 'the watchman' hill, Ahuriri, Napier, Nukumaruan (occurring with *A. finlayi*): H 11.7, D 4.3 mm; H 11.5, D 4.3 mm; GS10337, O32/f8843, hill above Glenstrae Station, Oaro, Marlborough, Nukumaruan: H 14.8, D 4.9 mm; H 12.5, D 4.3 mm; H 11.9, D 4.3 mm; GS5833, Y14/f7505A, Te Piki, near East Cape, OIS 7: H 10.8, D 3.9 mm; H 10.1, D 3.8 mm; Recent, RM5589, 540–490 m, Papanui Canyon, E Otago: H 9.7, D 3.6 mm; H 10.5, D 3.7 mm; H 11.1, D 3.7 mm; *Austrodrillia alpha* King, holotype: H 12.8, D 4.5 mm; *Austrodrillia beta* King, holotype: H 12.9, D (incomplete) 4.5 mm; *Austrodrillia gamma* King, holotype: H 9.3, D 4.0 mm; *Aoteadrillia trifida* Powell, holotype: H 9.0, D 3.3 mm.

Remarks. My experience of biostratigraphy of Mangapanian–Nukumaruan rocks in Wairarapa and North Canterbury suggests that gradually changing forms of *Aoteadrillia wanganuiensis* have a low-level utility for biostratigraphy. Extremely coarse variants are characteristic of early Nukumaruan time. However, this apparently is ecologically (probably temperature-) controlled variation, and all the named forms listed in the synonymy are part of the variation of one species. I have suggested most of the synonymy previously (Beu 1967:114).

The first point is to separate *Aoteadrillia finlayi* from this complex. I wrongly included it in the synonymy of *A. wanganuiensis* previously (Beu 1967). *A. finlayi* is easily separated from all other similar forms by its markedly larger size and narrow shape, as though it added another 1–2 whorls to its height compared with all other *Aoteadrillia* species without increasing its diameter, by its consistently very fine sculpture of two or more closely spaced, low, narrow spiral cords around the periphery crossing 20–24 fine, close axial ridges, by its finer spiral sculpture on the base, with narrow secondary threads between the primary cords, and by its slightly taller protoconch with a slightly more prominent keel on the second whorl. The keeled protoconch led Marwick (1965:43, pl. 11, fig. 18) to assign an apical fragment of *A. finlayi* from GS2818 (W19/f8494, highway above Waihua rail tunnel, northern Hawke's Bay; Nukumaruan, with rare *Struthiolaria frazeri* and the *convexa* form of *Pelicaria vermis*) to *Paracomitas*, but the two fine, closely spaced, peripheral spiral cords on the teleoconch spire whorl fragment demonstrate that his specimen is *A. finlayi*. *A. finlayi* apparently is limited to Nukumaruan rocks, and I have seen specimens definitely assigned here only from late Nukumaruan (Petane Group) rocks of central and northern Hawke's Bay. However, specimens from the Recent bathyal fauna and bathyal rocks in S Wairarapa also are very similar to *A. finlayi* (see below).

Powell (1942:92) discussed 'the species grouped around [*Aoteadrillia*] *wanganuiensis*', describing 'the lengthening of the spire' with increasing age, and recognizing several of the more extreme sculptural variants as 'divergent Nukumaruan forms'. Unfortunately, he allowed little variation within one species. In particular, the significance of the form named *Drillia chordata* by Suter (1908:184, pl. 7, fig. 16) has troubled taxonomists since it was proposed. Although Powell (1942:92) ranked this as a subspecies of *A. wanganuiensis* applying only to Recent specimens collected off Otago, he noted that 'two forms of *wanganuiensis* occur throughout its [time] range, the typical species having long axials crossed by three to four spiral cords, and the second form *chordata*, with shorter and stronger axials forming a double peripheral series of strong rounded nodules'. Specimens from deeper water off Otago (bathyal material, from the heads of the Otago canyons) also consist mostly of the *chordata* form, although a few specimens of the 'typical' finely sculptured form occur also. Despite limiting the name to Recent Otago specimens, Powell (1942) also recorded specimens as *A. wanganuiensis chordata* from Petane, Hawke's Bay (late Nukumaruan) and from GS1590, O32/f8039, near Leader River bridge, Hawkeswood, North Canterbury (early Nukumaruan). Evidently he was unable to distinguish between Nukumaruan and Recent coarsely sculptured variants, as I also conclude here. Powell (1979:231) later considered the *chordata* form to be part of the variation of *A. wanganuiensis*. The variation of extremes of the *chordata* form led to the recognition of the 'species' *A. alpha* (King, 1933) (Fig. 12F), *A. beta* (King, 1933) (Fig. 12D), *A. gamma* (King, 1933) (Fig. 12B), *A. thomsoni* Powell, 1942 (Fig. 13A, C), *A. trifida* Powell, 1942 (Fig. 12G) and *A. bisecta* Powell, 1942 (Fig. 12A). Specimens resembling the holotype of *Drillia chordata*, from off Otago (Fig. 13D, F), are in fact among the more weakly sculptured of the variants of *A. wanganuiensis*, and can be matched in most large collections of Nukumaruan and Castlecliffian age from Wanganui and central Hawke's Bay, particularly by specimens of the form Powell (1942) called *A. bisecta*. I have no doubt that the *chordata* form intergrades completely with *A. wanganuiensis*. Forms such as that named *Austrodrillia beta* by King (1933) (Fig. 12D) are considerably more extreme, almost resembling a *Paracomitas* species in their prominent peripheral row of smooth, narrowly rounded, obliquely angled nodules, but again intergrade completely with 'typical' *A. wanganuiensis* through many of the Hawke's Bay–Wairarapa early Nukumaruan specimens. The immediate ancestor of this complex seems likely to have been the Waipipian (–Mangapanian?) species *A. waihuaensis* Powell (1942:91, pl. 12, fig. 14; Fig. 13H), which is smaller and more finely sculptured than all the Nukumaruan–Recent forms, with narrow peripheral nodules similar to those of the holotype of *Austrodrillia beta* and some paratypes of *A. thomsoni* and *A. trifida*. *A. consequens* (Laws 1936:121, pl. 17, figs. 76, 78) from Kaawa Creek, SW Auckland (Opoitian, early Pliocene) is still narrower and more strongly monocarinate, resembling *Kuroshioturris angustata*, and makes a plausible link between the Pliocene–Recent species related to *A. wanganuiensis* and the early Miocene (Altonian) species *A. callimorpha* (Suter, 1917), the earliest species of *Aoteadrillia* named at present. Powell (1942) named still further sculptural variants of *A. wanganuiensis* as *A. thomsoni* and *A. trifida*, both of which have several narrow peripheral spiral cords. The form he named *A. bisecta* has a row of massive axial folds around the periphery, subdivided to varying degrees by a median spiral groove, but intergrades through decreasing nodule strength with the *chordata* form.

Late Nukumaruan specimens in Hawke's Bay are mostly typical, finely sculptured *Aoteadrillia wanganuiensis*, although they occur with the confusingly similar but markedly taller and slightly more finely sculptured species *A. finlayi.* At Castlecliff, Wanganui, in siltstone formations of the Castlecliffian coastal section, only the typical form of *A. wanganuiensis* occurs (Fig. 12C, E). The *A. alpha*-*beta*-*gamma*-*bisecta*-*trifida* range of variants, with markedly coarser sculpture, seems to represent an early Nukumaruan excursion by *A. wanganuiensis* into greater sculptural variation that was later reversed. The complete intergradation between the finer and coarser sculptural extremes makes it impossible to recognize separate species, but the recognition of coarsely sculptured forms limited to early Nukumaruan rocks has definite biostratigraphical utility.

The most significant connotation of the Recent distribution of the '*chordata* form' coarse variants recognized by Powell (1942)—limited to eastern Otago, among the most southern of present-day records of the species—is that fossils of similar but even more coarsely sculptured forms of *Aoteadrillia wanganuiensis* in early Nukumaruan rocks of Wairarapa to North Canterbury reflect cool sea temperatures at the deposition site. The spread of the cool-water *Zygochlamys delicatula* community northwards to form a major element of the early Nukumaruan fauna of Wairarapa and North Canterbury has long been a helpful concept for understanding late Pliocene sea-temperature change in New Zealand (Fleming 1944; Beu et al. 1977; Beu 1985, 1995). As well as *Z. delicatula*, other southern cool-water molluscs such as *Cominella nassoides* and the subantarctic spider crab *Jacquinotia edwardsii* (Jacquinot in Jaquinot & Lucas, 1853) (Yaldwyn & Beu, appendix in Beu et al. 1977) were dispersed as larvae in the proto-Southland Current to the central and southern North Island at 2.4 Ma, in the first strongly marked evidence of Pleistocene cooling in New Zealand marine faunas. The abrupt appearance of this cool fauna in Wanganui Basin is used to identify the base of the Nukumaruan Stage (Beu in Cooper 2004). I suggested (Beu 2010: 102–112) that a similar pattern was followed by *Pelicaria vermis*, in which the variation became extreme from early Nukumaruan time on, indicating that this species evolved direct development—and, consequently, now has a paucispiral protoconch—at about 2.4 Ma, at the beginning of Nukumaruan time. A similar interpretation was also suggested (Beu 2010: 91–92) for the highly variable species *Stiracolpus symmetricus*. *Aoteadrillia wanganuiensis* followed a similar pattern. However, the protoconch type remained constant in *Aoteadrillia* throughout its history, so apparently it did not undergo any fundamental change of developmental type. A reasonable explanation seems to be that *Aoteadrillia* was lecithotrophic, with a relatively brief demersal larval life, and merely shortened the period before metamorphosis during earliest Nukumaruan time. I conclude that the coarsely sculptured forms of *Aoteadrillia wanganuiensis* are cool-water variants of no taxonomic significance, and I regard the many trivial forms recognized by Powell (1942) as part of the variation of *A. wanganuiensis.*

Aoteadrillia finlayi Powell, 1942 (Fig. 13I,K)

Aoteadrillia finlayi Powell 1942:93, pl. 1, fig. 5; Fleming 1966:73; Beu & Maxwell 1990:419; Tucker 2004:378; Maxwell 2009:249.

Paracomitas n. sp. Marwick 1965:43, pl. 11, fig. 18.

Aoteadrillia alpha. Beu 1967:114 (in part not *A. alpha* King, 1933).

Type material. Aoteadrillia finlayi, holotype AIM AK70912, with one paratype AK71786, from 'Petane corner', cliff at junction of Highways 3 and 5, S of Esk River bridge, 20 km N of Napier, central Hawke's Bay; Mairau Mudstone, late Nukumaruan (not seen).

Other material examined. **Nukumaruan:** highway above Waihua rail tunnel, between Waihua and Wairoa valleys, N Hawke's Bay (GS2818, W19/f8494, one spire apex; the basis of Marwick's [1965:43, pl. 11, fig. 18] record of '*Paracomitas* n. sp.'); 'Petane corner', junction Highways 3 and 5, Esk River bridge, N of Napier, CR Laws collection (GNS, one); locality as last (GS10937, V20/f8500A, three); Maharakeke Mudstone (of Thomson 1926), Maharakeke Road, W foot of Pukeora Hill, Waipukurau (GS10857, U23/f7049, three); Makaretu Mudstone (of Thomson 1926), Ashcott Road, N foot of Pukeora Hill, Waipukurau (GS10858, U22/f09, 12); Devils Elbow Mudstone, top of Devils Elbow hill, Highway 2, N of Napier (GS10849 = GS10936, V20/f8555, 46); Darkys Spur Formation, Darkys Spur road, between Waikawau and Devils Elbow (GS11225, V20/f8019, one); Mairau Mudstone, 'the watchman' hill, Ahuriri lagoon, Napier (GS11465, V21/f6015A, 21); Mairau Mudstone, walkway W side of Roro-o-kuri, Onehunga Road, N end of Ahuriri 'lagoon', Napier (GS12386, V21/f05, 74 specimens).

Bathyal form referred tentatively to *Aoteadrillia finlayi*: **Mangapanian:** NMNZ M.42867, road cut 1 km NW of Tupurupuru-Westmere Road junction, S Wairarapa, Mangapanian (underlying Pukenui Limestone) (14). **Nukumaruan:** NMNZ M.147776, cliffs E of Lake Ferry, Palliser Bay (one). **Recent:** NMNZ M. 12901, 494 m, off Mayor Island (three); M.60246, 482–550 m, 17 km E of Mayor Island (one); M. 118497, 357–312 m, SE of Alderman Islands (one; closely similar to Hawke's Bay Nukumaruan fossils); M.61150, 443–527 m, 17 km E of Alderman Islands (two); M.60222, 660–765 m, 35 km WNW Orete Point, Cape Runaway (one; large peripheral nodules, doubtfully referred); M. 61112, 127–134 m, 17 km E of Portland Island, Mahia Peninsula (one); M.60343, 434–446 m, 41 km SE of Cape Campbell (two).

Distribution. I am aware of specimens definitely referred to *Aoteadrillia finlayi* only from late Nukumaruan rocks of central and north-central Hawke's Bay. However, the list above also includes a form that seems indistinguishable from *A. finlayi* (pointed out to me by BA Marshall, NMNZ) occurring in bathyal Mangapanian and Nukumaruan rocks, and in bathyal depths in the Recent fauna from Mayor Island, N Bay of Plenty, to Cape Campbell, Marlborough (it is not strictly bathyal; M.61112 is from 127–134 m). Some specimens seem indistinguishable from Hawke's Bay Nukumaruan ones, and this form tentatively is referred to *A. finlayi*. This species apparently is still living along eastern New Zealand, so the variation and time range of *A. finlayi* require further study as more material becomes available.

Dimensions. GS10849, Devil's Elbow: H 20.4, D 6.5 mm; H 19.3, D 6.0 mm; H 19.0, D 6.3 mm; H 18.7, D 6.1 mm; H (slightly incomplete) 18.9, D 6.2 mm; H 18.3, D 6.5 mm; GS11465, Mairau Mudstone, 'the watchman' hill, Ahuriri, Napier (occurring with *A. wanganuiensis*): H 18.6, D 6.0 mm; H 15.9, D 5.8 mm; H 14.6, D 5.6 mm; H (slightly incomplete) 14.2, D 5.4 mm.

Remarks. Aoteadrillia finlayi is distinguished above from *A. wanganuiensis*. Specimens recognized by BA Marshall in bathyal faunas (S Wairarapa, and in the Recent bathyal fauna from N Bay of Plenty to Cape Campbell) apparently are conspecific with *A. finlayi*. This indicates the possibility that *A. finlayi* had a wide bathymetric range (as *A. wanganuiensis* does), still lives around New Zealand in the bathyal zone, and possibly retreated there after Nukumaruan time.

Aoteadrillia apicarinata (Marshall & Murdoch, 1923) (Fig. 12H,I)

Drillia apicarinata Marshall & Murdoch 1923:125, pl. 17, figs. 76, 78.
Aoteadrillia apicarinata. Powell 1942:90; Fleming 1966:73; Powell 1966:87; Beu & Maxwell 1990:418; Richardson 2002:12; Tucker 2004:80; Maxwell 2009:249.

Type material. Drillia apicarinata, holotype TM8302, from Waikopiro, near Ormondville, southern Hawke's Bay, late Nukumaruan, ex H Suter collection. The illustration of *Drillia apicarinata* by Marshall & Murdoch (1923, pl. 12, fig. 5) shows an almost complete specimen, and the height is stated to be 10 mm. The specimen in GNS identified as the holotype has the anterior end (siphonal canal and anterior half of the last whorl) broken away, and a note on the label by CA Fleming states 'canal noted broken' on 10 February 1947 (when the Marshall & Murdoch collection was incorporated in the NZGS collection by CA Fleming). As Marshall & Murdoch (1923) stated that they had only one specimen, the GNS specimen labelled 'type' is the holotype.

Other material examined. **Nukumaruan:** the distinctive species *Aoteadrillia apicarinata* is reasonably common at only one locality I am aware of, the former road cutting on Ashcott Road (abandoned by the 1980s deviation of Highway 2) immediately NW of Pukeora Hill, SW of Waipukurau, Hawke's Bay (GS10858, U22/f09, four). The type locality, 'Waikopiro', E of Ormondville in S Hawke's Bay, seems not to have been re-collected during the last 80–100 yr. Powell (1942:90) also recorded material from 'inner harbour, Napier', that is, cliffs of the former Ahuriri Lagoon, in Mairau Mudstone, high in the Petane Group (late Nukumaruan), presumably based on specimens in the Finlay collection, as I have seen no material of *A. apicarinata* from this area. Richardson (2002:12) also listed specimens from his localities 1–3 in Nukumaruan rocks of Hawke's Bay (1: walkway W side of Roro-o-kuri, Onehunga Road, Bay View, N of Napier; Mairau Mudstone, late Nukumaruan; 2: 'the watchman' hill, in the former Ahuriri Lagoon, W of Napier airport, also in Mairau Mudstone; 3: Ashcott Road, that is, the locality where *A. apicarinata* is recorded here as moderately common).

Distribution. Limited to late Nukumaruan rocks of Hawke's Bay.

Dimensions. Drillia apicarinata, holotype: H (incomplete) 8.6, D 3.3 mm; GS10858, Ashcott Road: H 11.1, D 4.0 mm (Fig. 32A,B).

Remarks. Aoteadrillia apicarinata is a very distinctive small species, with even, narrow, prominent, closely spaced spiral cords over the entire surface below the sutural ramp, and a few fine spiral cords on the ramp, as well as a prominent subsutural spiral ridge (as in all other *Aoteadrillia* species) composed of one or two spiral cords. Moderately prominent, rounded axial ridges begin abruptly at the border of the ramp (the shoulder angle), and extend well down the last whorl, without forming nodules at the intersections with the spiral cords; they are much fewer and more widely spaced than those of *A. wanganuiensis*. The protoconch is unusual, as it blends gradually into the teleoconch, and the spiral sculpture begins early on the first protoconch whorl and passes onto the teleoconch unchanged. The initial protoconch half-whorl is low, superficially smooth and rounded, but actually bearing numerous fine spiral threads (Fig. 12H) as in *A. wanganuiensis* (Figs. 12J, 13J), and the prominent, median, sharply defined keel commences gradually over the next quarter-whorl; one or two spiral threads develop gradually below the keel over the succeeding half-whorl, so after one whorl all specimens display some spiral sculpture, and it simply continues to strengthen and to develop more cords as the shell grows. It is impossible to identify the protoconch-teleoconch junction, indicating that *A. apicarinata* had lecithotrophic development. Its restriction to a few localities in Hawke's Bay suggests the possibility that development was direct. *A. apicarinata* does not resemble *A. wanganuiensis* (type species of *Aoteadrillia*) very closely but, as pointed out by Powell (1942:90), it is quite similar to the early Pliocene (Opoitian) species *A. consequens*. Evidently the genus *Aoteadrillia* consists of at least two discrete lineages that evolved from the early Miocene species *A. callimorpha*, culminating respectively in *A. apicarinata* and *A. wanganuiensis*.

Genus ***Antimelatoma*** Powell, 1942

Antimelatoma Powell 1942:97. Type species (by original designation): *Drillia maorum* E. A. Smith, 1877 (= *Pleurotoma buchanani* Hutton, 1873), late Pliocene–Recent, New Zealand.

Antimelatoma buchanani (Hutton, 1873) (Fig. 14B–F, H)

Pleurotoma buchanani Hutton 1873b:4; Hutton 1880:42; Hutton 1893:50, pl. 6, fig. 26; Harris 1897:47.
Pleurotoma (Drillia?) maorum EA Smith 1877:497 (**new synonym**).
Drillia buchanani. Hutton 1878:16; Suter 1914:29.
Drillia maorum. Hutton 1880:44; Hutton 1885b:116.
*Surcula traill*i. Suter 1899b:68; Suter 1902b:211; Suter in Hutton 1904:71 (not *Pleurotoma trailli* Hutton, 1873; Suter 1913:474).
Drillia buchanani maorum. Suter 1905a:73; Murdoch & Suter 1906:282; Suter 1913:474, pl. 46, fig. 22.
Surcula buchanani maorum. Suter 1905b:200.
Melatoma buchanani. Hedley 1922:250.
Melatoma buchanani maorum. Powell 1927:296.
Antimelatoma buchanani. Powell 1942:97; Fleming 1966:73; Powell 1966:30; Tucker 2004:159; Maxwell 2009:249.
Antimelatoma buchanani maorum. Powell 1942:97; Dell 1963a:176, pl. 2, fig. 7; Powell 1966:30, pl. 2, figs. 2, 3; Fleming 1966:73; Powell 1969:298, pl. 234, figs. 2, 3; Grant-Mackie & Chapman-Smith 1971:680; Powell 1979:231; Spencer & Willan 1996:29; Tucker 2004:596; Spencer et al. 2009:211.
Antimelatoma ahiparana Powell 1942:98, pl. 2, fig. 11; Powell 1966:30; Powell 1979:231, pl. 45, fig. 14; Spencer & Willan 1996:29; Tucker 2004:40; Spencer et al. 2009:211 (**new synonym**).
Antimelatoma benthicola Powell 1942:98, pl. 2, fig. 10; Powell 1966:30; Powell 1979:232, pl. 45, fig. 12; Spencer & Willan 1996:29; Tucker 2004:120; Spencer et al. 2009:211 (**new synonym**).
Antimelatoma n. sp. Fleming 1953:245.
Antimelatoma maorum. Maxwell 2009:249.

Type material. *Pleurotoma buchanani* type material consists of two syntypes (TM8628–9) formerly glued to one wooden tablet, which is labelled '*Drillia buchanani* (Hutton) Type. (Suter, 1912). (Type of *Pleurotoma buchanani* Hutton, 1873). Shakespeare Cliff, Wang.'. The specimens are labelled lectotype and paralectotype, but I am not aware of any publication of this designation. Hutton (1873b:4) cited specimens from 'Shakespeare Cliff' and 'Awamoa', but of course only the former two syntypes belong in this species. Hutton's Awamoa specimen is no longer identifiable. The Wanganui specimen (TM8628; Fig. 14B) that was formerly glued by its dorsum (so the aperture does not bear glue) is here designated the lectotype, to be certain that this name continues to be applied in its accustomed sense rather than to a Miocene species from Oamaru. It presumably came originally from Shakespeare Cliff within Wanganui City and almost certainly from Tainui Shellbed (OIS 13). The paralectotype is TM8629. *Pleurotoma* (*Drillia?*) *maorum*, holotype BMNH 1852.3.19.52 (Fig. 14F; Dell 1963a, pl. 2, fig. 7), from 'New Zealand, leg. Lieut. Col. Bolton'. *Antimelatoma ahiparana*, holotype AIM AK72181 (Fig. 14E), with 13 paratypes AK71791 (Fig. 14C, H), Recent, dredged in 42 m off Ahipara, NW Northland,

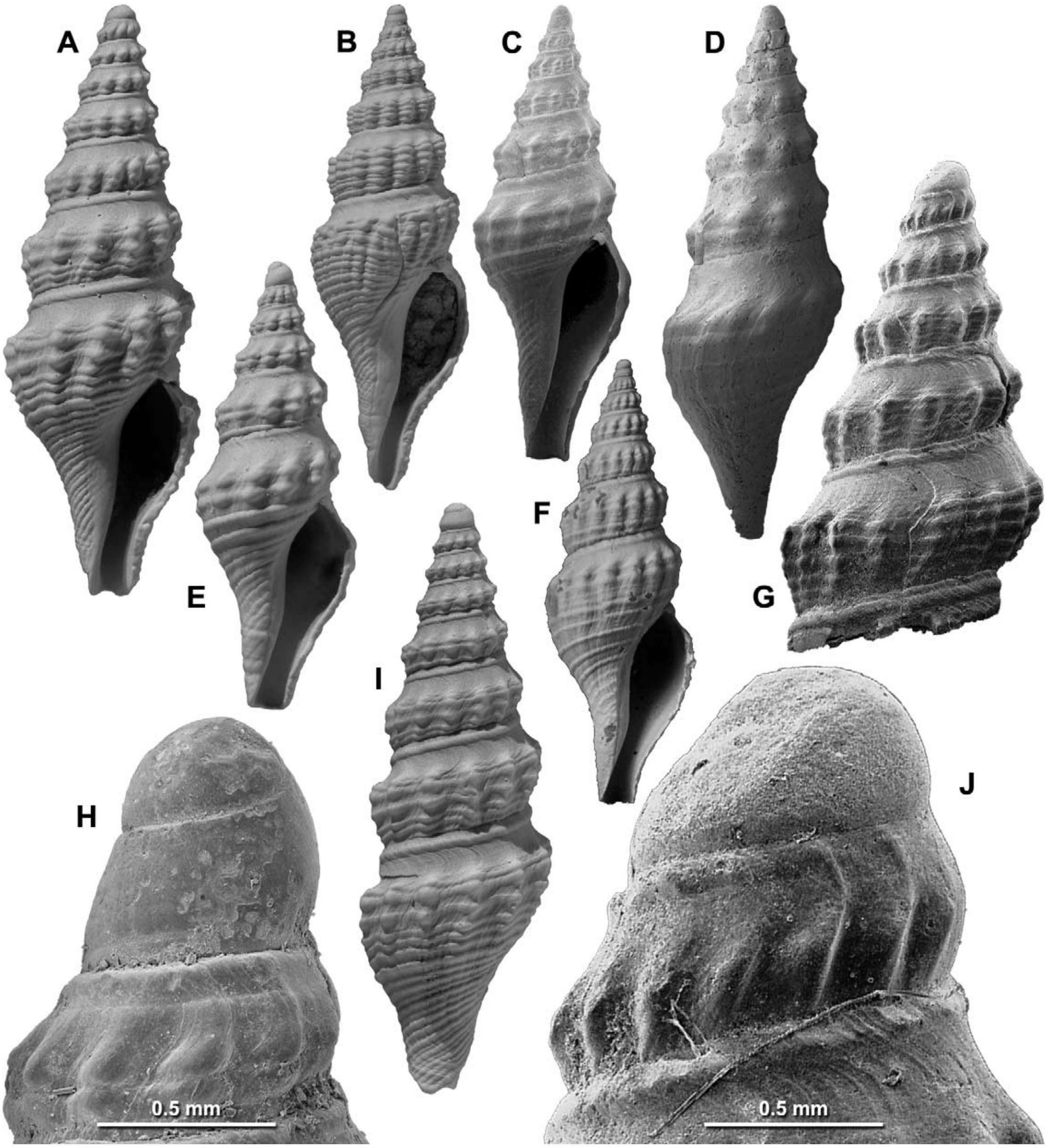

Figure 14 (A,G,I,J) *Antimelatoma waimea* n. sp.; A,I, holotype, TM8670, GS3013, J32/f9113, upper Waimea Creek, between Taramakau and Arahura Rivers, Westland, Kapitean; height 16.5 mm; G,J, paratype, TM8671, GS3030, J32/f9130, lower Waimea Creek, Westland, Opoitian; G, incomplete shell, height 13.4 mm; J, protoconch of G. (B–F,H) *Antimelatoma buchanani* (Hutton); B, lectotype of *Pleurotoma buchanani*, TM8628, Tainui Shellbed, Castlecliffian (OIS 13), "Shakespeare Cliff", Wanganui; H 21.0, D 6.8 mm; C,H, paratype of *Antimelatoma ahiparana* Powell, AIM AK71791, dredged, 42 m, off Ahipara, Northland, ex Finlay collection; C, height 12.8 mm; H, protoconch of C; D, GS4003, R22/f8002, Landguard Sand (Haweran, OIS 9), Landguard Bluff, Wanganui; height 15.1 mm; E, holotype of *A. ahiparana*, AIM AK72181, same data as paratype; H 12.5, D 4.6 mm; F, holotype of *Pleurotoma (Drillia?) maorum* Smith, BMNH 1852.3.19.52, Recent, "New Zealand"; H 20.4, D 7.0 mm.

ex HJ Finlay collection. *Antimelatoma benthicola*, holotype AIM AK70910, ex HJ Finlay collection, from 160–225 m, off Otago Heads (not seen).

Other material examined, A. ahiparana *form.* **Haweran:** Landguard Sand (OIS 9), Landguard Bluff, E of Wanganui River (GS4003, R22/f7394, six; including re-collections); recorded also by Fleming (1953:245) from Landguard Sand, as '*Antimelatoma* n. sp.'; NMNZ M.15713, Landguard Bluff (one). **Recent:** RM2090, dredged, 42 m, off Ahipara (five; two presented to J Marwick by W La Roche; three ex CA Fleming collection); NMNZ M.4229, off Reef Point, Ahipara (three); M.90601, Ahipara Bay (45, consistently *A. ahiparana* form); M.118479, 103 m, NW of Ahipara, 34°41.90′S, 172°33.50′E (eight, spiral cords as in *A. ahiparana* form, axial ridges more prominent); M.118483, 90 m, NW of Ahipara, 34°50.00′S, 172°46.10′E (four fragmentary); M.54961, 24 m, off Pakawau Beach, Golden Bay, Nelson, 40°37.00′S, 172°48.00′E (one small, coarse nodules); M.50033, 24–26 m, off flats inside Farewell Spit, Golden Bay (three large, more prominent peripheral nodules than most *A. buchanani*, spiral sculpture more like the normal form of *A. buchanani*).

Fleming (1953:131, 146, 151, 188, 203–204, 215, 218, 226, 230, 232, 239, 240, 245) recorded *Antimelatoma buchanani* from many Nukumaruan–Castlecliffian formations in Wanganui Basin (Hautawa Shellbed, Mangamako Shellbed, Waipuru Shellbed, Kaimatira Pumice Sand, Kupe Formation, Seafield Sand, Lower Castlecliff Shellbed, Pinnacle Sand, Tainui Shellbed, Shakespeare Cliff Siltstone, Upper Castlecliff Shellbed, Karaka Siltstone and Landguard Sand). It also occurs commonly throughout mudstone formations in Hawke's Bay, Wairarapa and N Canterbury-Marlborough, and in Castlecliffian–Haweran rocks at Cape Kidnappers and at Ohope Beach and Te Piki, Bay of Plenty.

Distribution. The *Antimelatoma buchanani* '*ahiparana* form' is known fossil in Landguard Sand (OIS 9) in Wanganui Basin only, and occurs in the Recent fauna off W North Island and in W Cook Strait (taken in 24–103 m). Specimens from further south (NMNZ M.59044, 91 m, off Kahurangi Shoals, NW of Kahurangi Point, NW Nelson; four chalky; substrate labelled as 'subfossil shells') are normal, relatively finely sculptured *Antimelatoma buchanani*. The specimens from flats inside Farewell Spit (NMNZ M.50033) are intermediate in most characters between the *buchanani* and *ahiparana* forms. This is therefore interpreted as an ecophenotypic form intergrading with *A. buchanani*, the typical form of which occurs throughout N and E New Zealand (and presumably along the W South Island), and is an abundant fossil in Nukumaruan to Haweran rocks throughout New Zealand. Upwelling N of the northernmost North Island possibly restricts gene flow there between the *buchanani* and *ahiparana* forms. *A. buchanani* occurs widely, syntopically with *Aoteadrillia wanganuiensis*, at most Nukumaruan and younger fossil localities in Wanganui Basin, the Bay of Plenty, Hawke's Bay, Wairarapa and Marlborough-North Canterbury, but consistently is less abundant than *A. wanganuiensis*.

Dimensions. Lectotype of *Pleurotoma buchanani*: H 21.0, D 6.8 mm; paralectotype: H 17.5, D 6.6 mm; holotype of *Pleurotoma (Drillia?) maorum*: H 20.4, D 7.0 mm; holotype of *Antimelatoma ahiparana*: H 12.5, D 4.8 mm; paratypes AK71791: H 13.8, D 4.9 mm; H 13.1, D 4.7 mm; H 12.8, D 4.6 mm; GS4003, Landguard Bluff: H 14.8, D 5.2 mm; H (incomplete) 13.3, D 5.0 mm; H 11.3, D 4.2 mm; NMNZ M.50033, 24–26 m, inside Farewell Spit: H 19.2, D 6.3 mm.

Remarks. Specimens of *Antimelatoma* from Landguard Sand, Landguard Bluff, Wanganui, differ from the common, widespread form of *Antimelatoma buchanani* in having a longer, more steeply sloping sutural ramp, only two prominent spiral cords around the periphery down the entire teleoconch, and prominent, widely spaced, clearly defined spiral cords on the base. It has three prominent, widely spaced spiral cords over the convex area of the base below the peripheral two, and above the concave area of the neck. Well-preserved specimens also have a glossy exterior. These characters are shared with the Recent form named *A. ahiparana* by Powell (1942:98, pl. 2, fig. 11) and comparing the Landguard specimens directly with the holotype and 13 paratypes of *A. ahiparana* showed that they are closely similar in size, shape and sculpture. The protoconchs also are identical. As Landguard Sand at Landguard Bluff is the horizon and locality with the greatest number of warm-water migrants recorded at Wanganui (*Capulus danieli*, *Eunaticina papilla*, *Pupa affinis* (A. Adams, 1855), *Zelippistes benhami*, *Philine tepikia* Rudman, 1970 [see below] and possibly *Stiracolpus vigilax*), this seemed to be another record at Wanganui of a species now limited to northern New Zealand. However, the distribution of *Antimelatoma* forms along the west coast of New Zealand seems better interpreted as a more coarsely sculptured ecophenotypic form occurring from the Ahipara region southwards, intergrading with more finely sculptured specimens of the common form of *A. buchanani* south of western Cook Strait. The common finely sculptured form occurs from N of Cape Reinga to the Three Kings Islands and throughout eastern New Zealand. The Landguard Bluff specimens then probably are merely standard western New Zealand specimens of *A. buchanani*, possibly reflecting the cutting off (possibly by closure of the Manawatu Strait) of the dispersal of larvae from eastern New Zealand after about OIS 11–10. Specimens from lower in the Castlecliff section are all typical 'eastern New Zealand' specimens of *A. buchanani*, with more even, fine sculpture, a shorter sutural ramp, and the two peripheral cords not distinguished from their neighbours.

Landguard Sand specimens are also similar to the form long known as *Antimelatoma buchanani maorum* (E. A. Smith, 1877). Dell (1963a:176, pl. 2, fig. 7) pointed out that this form had never been illustrated previously, apart from Suter's (1913, pl. 46, fig. 22) featureless little drawing, and supplied a photograph of the holotype, in BMNH. Dell's illustration and examination of the holotype (Fig. 14F) show that this form differs from the common Nukumaruan–Castlecliffian form of *Antimelatoma buchanani*, as noted by Powell (1942:97), by the slightly more prominent uppermost two spiral cords, at the periphery, in *A. buchanani maorum*, and their more even strength in *A. buchanani buchanani*, although Powell admitted that 'This does not always apply, however'. Powell claimed a further slight but constant difference in the lengths of the anterior canals, but I cannot see any difference between fossil and Recent specimens in this character, despite this later (Powell 1979:231) being maintained as the major difference between the two forms. *A. buchanani* is highly variable in Recent material in NMNZ, some specimens in a few lots from other areas resembling the Ahipara specimens (e.g. NMNZ M.71413, 89–94 m, Ranfurly Bank, off East Cape; one specimen of *A. ahiparana* form with 13 coarsely sculptured but otherwise typical *A. buchanani*). A few specimens almost completely lack axial ridges, nodules and prominent spiral cords on the last few whorls (particularly NMNZ M.58826, 139 m, ENE of Tolaga Bay, E North Island, 38°15.20′S, 178°38.60′E; two large). Most Recent specimens from eastern New Zealand are inseparable from Nukumaruan–Castlecliffian fossils, and the variation is all part of the single species *A. buchanani*. The range of variation now accepted for *A. buchanani* also includes the form named *A. benthicola* by Powell (1942:98, pl. 2, fig. 10), based on a single only slightly more coarsely sculptured specimen from shallow water off E Otago; Otago specimens in NMNZ are typical *A. buchanani*.

Powell (1942, 1966) referred only the New Zealand Nukumaruan to Recent species to *Antimelatoma*, but Cotton (1947:11) included eight Recent Australian species in *Antimelatoma*, although he later reduced this to three species (Cotton 1959:393): *A. gratiosa* (G. B. Sowerby III, 1896), *A. harpularia* (Desmoulins, 1842) and *A. agasma* Cotton, 1947. Cotton was followed by Macpherson & Gabriel (1962:232), who referred two Victorian Recent species here, *A. harpularia* and *A. subviridis* (May, 1910). GNS material of '*Antimelatoma*' *harpularia* (WM19103, Portland, Victoria; four) has prominent, long, narrow, closely spaced axial ridges and weak spiral cords and is more nearly similar to species of *Splendrillia* Hedley, 1922 than to *A. buchanani*, and *Pleurotoma harpularia* was placed in *Splendrillia* by Powell (1966:83), although the other species in Cotton's (1959:393) list and '*A.*' *subviridis* were not included in Powell's (1966) monograph. Wells (1990:87, pl. 4, figs. 1, 2) and Tucker (2004:965) also included *Drillia subviridis* in *Splendrillia*, Wells (1990:77) synonymized *Antimelatoma agasma* with *Splendrillia woodsi* (Beddome, 1883), and Wells (1991:65, pl. 1, fig. 3) included *Drillia gratiosa* in *Splendrillia* (Tucker 2004:439). Therefore, none of the Australian Recent species listed in *Antimelatoma* by Cotton (1947, 1959) was correctly assigned there.

Antimelatoma waimea n. sp. (Fig. 14A, G, I, J)

Type material. Holotype (Fig. 14A,I) TM8670, GS3013, J32/f9113, grid reference J32/557353, Kapitean (late Miocene), occurring with *Aethocola coerulescens* (Finlay, 1930); main course of Waimea Creek, 200 m N of Stafford Loop Road and 400 m WNW of Goldsborough, 4 km upstream from Stafford and ca 9 km upstream from mouth of Waimea Creek, between Taramakau and Arahura Rivers, Westland; one incomplete paratype (Fig. 14G, J) TM8671, GS3030, J32/f9130, grid reference (estimated) J32/546359, Opoitian (early Pliocene), with *Marama murdochi* (Marwick, 1927) and *Amalda (Baryspira)* cf. *tholiculus* (Marwick, 1931), ca 1.25 km downstream from type locality, main course of Waimea Creek, Westland.

Distribution. Known only by the type material.

Dimensions. Holotype: H 16.5, D 5.3 mm.

Description. Shell small for genus, tall and gracefully slender, with tall, narrow spire and relatively short last whorl (siphonal canal apex and outer lip slightly incomplete). Protoconch of 1.5 whorls, with low, wide, blunt apex followed by one taller, evenly inflated whorl, all smooth; passing into teleoconch gradually by development of progressively more prominent brephic axial ridges, towards end of ridges gradually developing low, smooth subsutural cord and medial angulation defining sutural ramp; brephic axial ridges curved, with apex abapertural; similar to that illustrated by Powell (1942, text-fig. C10) for *A. buchanani*, but with more prominent brephic axial ridges and lacking spiral cords. Teleoconch of seven whorls, spire rendered prominently gradate by peripheral angulation at base of sutural ramp, at about upper third on spire whorls; base weakly convex below angulation, passing gradually into weakly concave neck and moderately long, gently tapered, unnotched anterior canal. Sculpture visually dominated by prominent, narrow, long axial ridges, moderately strongly opisthocline in conformity with outer lip, each interspace slightly wider than one ridge, commencing abruptly and forming small rounded nodules at lower margin of sutural ramp, producing a much more deeply concave ramp than on *A. buchanani*; 12 axial ridges on last whorl and 13 on penultimate whorl of holotype. Spiral sculpture of one prominent, smooth, rather narrow subsutural cord, an almost smooth sutural ramp (crossed only by weak growth ridges defining posterior sinus), one narrow and two much more prominent spiral cords around periphery, the uppermost two closely spaced and the next two below more distantly spaced, with lower, narrower, more closely spaced cords below, gradually becoming revealed down spire as ramp descends; cords are weakly convex-crested and sharply defined; two further cords on sides of antepenultimate and three on penultimate whorl below more prominent cords; followed below by ca eight similar cords on base of last whorl, passing into ca 10 further weak, low, closely spaced cords on siphonal canal; small, narrowly rounded nodules (much more obvious than any seen on *A. buchanani*) formed at sculptural intersections on uppermost two prominent spiral cords on last two whorls, weaker higher up spire; cords scarcely raised over axial ridges lower down last whorl. Aperture unthickened, without parietal callus, outer lip slightly incomplete but evidently thin and simple, without stromboid notch; profile moderately concave over sutural ramp, forming posterior sinus; curving forwards moderately below ramp to form standard *Antimelatoma* convex outer lip profile.

Remarks. *Antimelatoma waimea* n. sp. from late Miocene–early Pliocene rocks of Westland has more prominent axial and spiral sculpture than *A. buchanani*, and also has a slightly shorter, more strongly nodulose teleoconch (particularly with a shorter anterior siphonal canal, although it is slightly to highly incomplete on both specimens) with a more strongly concave sutural ramp and more prominent, narrow, widely spaced, more strongly oblique axial ridges than any forms of *A. buchanani*. The protoconch (Fig. 14J) is very well preserved on both holotype and paratype, and differs significantly in its larger size and in having more prominent brephic axial ridges (where the sculpture gradually passes from that of the protoconch to the telcoconch) and in lacking the spiral cords on the last whorl of the protoconch of *A. buchanani*. The differences seem unexpectedly marked from *A. buchanani*, particularly in the protoconch, suggesting that this species may not have had a direct ancestor-descendent relationship with *A. buchanani*. The forms named by Powell (1942) now all being considered part of the variation of the single species *A. buchanani*, *A. waimea* n. sp. is only the second species of *Antimelatoma* recognized in New Zealand.

Antimelatoma quemadensis (Ihering) (1907:195, pl. 6, fig. 39; proposed in *Fusus*) (Oligocene–early Miocene, Yegua Quemada, near Santa Cruz, Argentina; Monte Leon Formation), was referred to this genus by Beu et al. (1997:95). It differs from the New Zealand species in having a less prominent angulation around the base of the sutural ramp, and the axial ridges (although also said by Ihering [1907:196] to be 12 per whorl) are less prominent than in both *A. buchanani* and *A. waimea* n. sp. Comparison is still required to be certain that this species belongs in *Antimelatoma*. The age of *Antimelatoma waimea* n. sp. moves the time of Neogene immigration of *Antimelatoma* to New Zealand from South America, as postulated by Beu et al. (1997:95), to during late Miocene time, much earlier than the Nukumaruan date envisaged previously. I am not aware of any other possible origin for the New Zealand species of this genus.

Etymology. The species name is that of the type locality; a noun in apposition.

Family Conidae

Subfamily Pseudotominae?

Genus ***Austrotoma*** Finlay, 1924

Austrotoma Finlay 1924:515. Type species (by original designation): *Bathytoma sulcata excavata* Suter, 1917, Otaian (early Miocene), Kaipara Harbour, Northland, New Zealand

Remarks. A position for this subfamily(?) in Conidae is provisional. A cladogram of Brazilian conoideans (Simone 2007, fig. 11), based on Simone's research on caenogastropod comparative anatomy, shows '*Pleurotomella*' *aguayoi* (referred below to *Austrotoma*) as the nearest relative of *Conus* of the taxa Simone studied, so a position in Conidae seems likely. This group is not recognized in the preliminary molecular phylogeny of Conoidea by

Puillandre et al. (2008), but none of its possible members was studied by them. Recognition that *Austrotoma* is still living in the SW Atlantic provides an opportunity to examine the anatomical characters and familial position of the potential subfamily Pseudotominae, recognized by Beu & Maxwell (1990:417) and Maxwell (1992:153; 2009:249) as a useful subfamily of distinctive, large, wide taxa, most of which have an unusually short, widely open anterior siphonal canal and an only weakly contracted last whorl. Of course, this subfamily name was used by many earlier workers, such as Finlay (1924:516) and as 'the *Acamptogenotia* group' by Hickman (1976:47). The subfamily name usually has been attributed to L Bellardi (1877:209). However, Bouchet et al. (2005:145) attributed the subfamily name to A Bellardi (1875:19) and pointed out that *Pseudotoma* Gray is an incorrect spelling of *Pseudostoma*, leaving *Pseudotoma* A. Bellardi available.

Few Recent species seem correctly referred to this group, apart from the several Indo-West Pacific Recent bathyal species of *Marshallena* Allan, 1927 (Powell 1969:365–372; *M. philippinarum* (Watson, 1882)—Sysoev in Poppe 2008:784, pl. 687, fig. 8). Another is *Megasurcula carpenteriana* (Gabb, 1865) from California, USA (Powell 1966:32, pl. 2, fig. 18), type species of *Megasurcula* Casey, 1904 (by subsequent designation, Grant & Gale 1931:495). Grant & Gale (1931:497–500, pl. 25, figs. 3–4b) compared *M. carpenteriana* with *Pseudotoma intorta* (Brocchi, 1814) (Grant & Gale 1931, pl. 25, fig. 1a,b; Hickman 1976, pl. 4, figs. 12, 15; Fig. 16C), type species of *Pseudotoma* A. Bellardi, 1875. Hickman (1976), Beu & Maxwell (1990:417) and Maxwell (1992) included the following genera in subfamily Pseudotominae: *Belophos* Cossmann, 1901, *Austrotoma* Finlay, 1924, *Liratomina* Powell, 1942, *Belatomina* Powell, 1942, *Marshallaria* Finlay & Marwick, 1937, *Marshallena* Finlay, 1926, *Megasurcula* Casey, 1904, *Pseudotoma* A. Bellardi, 1875 (= *Acamptogenotia* Rovereto, 1899; = *Pseudotomina* Finlay, 1924, unnecessary replacement names), *Surculites* Conrad, 1865 and its subgenus or synonym *Notogenota* Powell, 1942, *Nekewis* Stewart, 1926, *Tahuia* Maxwell, 1992, and *Zeatoma* Maxwell, 1992. *Marshallena* and *Megasurcula* were included in Family Turridae, Subfamily Cochlespirinae by Taylor et al. (1993:165), but any close phylogenetic relationship seems unlikely with the small, slender genus *Cochlespira* Conrad, 1865, with its long, narrowly contracted siphonal canal, and *Cochlespira* is the furthest removed from *A. aguayoi* of all Conoidea in Simone's (2007, fig. 11) cladogram. Pseudotominae was listed as a synonym of Family Conidae, Subfamily Clathurellinae by Bouchet et al. (2005:256) and this seems a phylogenetically more likely association. However, anatomical and molecular evaluation of this group is still required, based expressly on *Megasurcula carpenteriana* and/or *Austrotoma aguayoi* and other living Brazilian species of *Austrotoma*. Hickman (1976) threw new light on the characters of supposedly geographically restricted genera in this group when she described Oligocene species of both *Pseudotoma* and *Austrotoma* from the Keasey Formation of NW Washington State, USA. She reconsidered the relatively minor differences between these and *Megasurcula*, ranking all these groups as subgenera of *Pseudotoma*. She also illustrated the Italian Pliocene species *Pseudotoma bonellii* Bellardi, 1877 (Hickman 1976, pl. 4, figs. 13, 14), which bears the prominent subsutural ridge that supposedly differentiates *Austrotoma* from *Pseudotoma*, and *Pseudotoma morreni* (de Koninck, 1838) (Hickman 1976, pl. 4, figs. 6, 7), Rupelian (Oligocene), Germany, which closely resembles *Austrotoma* and *Megasurcula* species. Species of *Nekewis* and *Surculites* occur with those of *Pseudotoma* and *Austrotoma*, so the Keasey Formation has an unusually diverse pseudotomine fauna. Hickman (1976) also suggested that *Belophos* Cossmann, 1901 might be the earliest name for the genus or subgenus usually known as *Austrotoma*, and her evidence certainly suggests that groups such as *Pseudotoma* and *Austrotoma* are very similar and are possibly congeneric rather than merely consubfamilial. Molecular comparison of *M. carpenteriana* and *A. aguayoi* would be an excellent beginning to understanding relationships in this group; it would not be surprising if they fall into one clade, that is, constitute a single genus.

Marwick (1924a:161, fig. 1a) suggested that the poorly known genus *Struthiolariopsis* Wilckens (1904:208; type species by monotypy: *Fusus ferrieri* Philippi, 1887; Maastrichtian [late Cretaceous], Quiriquina Island, Chile) also was based on a relatively large conoidean resembling *Austrotoma*. Both Wilckens' (1904, pl. 18, fig. 5) drawing and Marwick's (1924a, fig. 1a) copy of it resemble *Austrotoma* in their single row of peripheral nodules, prominent spiral cords around the gently tapering base, and tall, almost smooth, weakly concave sutural ramp occupied by a shallow anal sinus. However, Philippi's (1887:43, pl. 2, fig. 6) original drawing seems to show a different, more coarsely sculptured, buccinoidean shell. Bandel & Stinnesbeck (2000) did not refer to *Fusus ferrieri*, but Klaus Bandel (Universität Hamburg, pers. comm. June 2008) stated that it is among the species they referred to *Pyrifusus* Conrad, 1858 (Bandel & Stinnesbeck 2000, list p. 784, '*Pyrifusus* several species'). Sven Nielsen and Steffen Kiel (Institut für Geowissenschaften, Christian-Albrechts-Universität Kiel pers. comm.) consider that Quiriquina material of *Struthiolariopsis ferrieri* is similar to species of the conoidean genus *Beisselia* Holzapfel, 1889 (type species: *Koenenia speciosa* Holzapfel, 1888, late Cretaceous, Europe; Wenz 1943:1316, fig. 3746). They provided digital images of the remaining syntype of *Fusus ferrieri* (SGO.PI.567) sent to them by Dr Daniel Frassinetti (Paleontología Invertebrados, Museo Nacional de Historia Natural, Santiago, Chile), showing that it is conspecific with the material illustrated here. They also lent Quiriquina material of *S. ferrieri* (Fig. 15I, J) (in collection S. Kiel, Institut für Geowissenschaften, Christian-Albrechts-Universität Kiel, five incomplete specimens, all calcite neomorphs, including Q3020: H [very incomplete] 30.0 [originally ca 37], D 27.8 mm; Q2186: H [incomplete] 21.6, D 14.2 mm). This demonstrates that *Struthiolariopsis* is indeed a conoidean, with an obvious, moderately deep anal sinus occupying the concave sutural ramp. However, it is more coarsely sculptured than most *Austrotoma* species and has a prominent subsutural fold and a more strongly tapered last whorl with a narrower siphonal canal, so that it resembles a nodulose species of *Marshallena* or *Nekewis* more closely than *Austrotoma*. Both Philippi's and Wilckens' drawings are inaccurate. *Struthiolariopsis ferrieri* is not closely similar to *Austrotoma*, but is possibly an early member of the 'group' or subfamily Pseudotominae.

Belophos, *Austrotoma*, *Lirotomina* and *Belatomina*, recognized as separate genera by Powell (1942, 1944, 1966), are among the many groups requiring reassessment in Conoidea, as Hickman (1976) pointed out. *Belophos woodsii* (Tate) (1888:147, 173, pl. 4, fig. 3) (Fig. 15E, H, K) has usually been considered to be the valid name for the type species of *Belophos* Cossmann (1901:162; type species (by original designation): *Bela woodsii* Tate, 1888, Fossil Bluff, near Wynyard, N Tasmania; gender neuter). However, there is apparently no reason not to use the original name, *B. cancellatum* (Tenison Woods, 1877). Tate's species name apparently is an unnecessary replacement name for *Cominella cancellata* Tenison Woods (1877:107); I have been unable to find any earlier usage of *Cominella cancellata*. The combination *Belophos cancellatum* was reintroduced for this species by Goudey (2006:46, figs. 21, 22; p. 48, fig. 2) and is followed here. Illustrations of *Belophos cancellatum* by Cossmann (1901, pl. 6, figs. 9, 10), Powell (1966, pl. 4, figs. 2, 3) and Goudey (2006) show a shell closely resembling *Tahuia formosa* (Allan, 1926) (Maxwell 1992, pl. 22g,n) and *Marshallaria decipiens* Maxwell (1992, pl. 22d,f,j,k), that is, it has more prominent axial ridges and peripheral nodules than New Zealand species assigned to *Austrotoma* (although not more so than in Recent Brazilian species discussed below). Specimens examined (WM18996, Fossil Bluff, near Wynyard, N Tasmania, type locality; Longfordian, early Miocene; three specimens; NMV P315217-P315224, eight specimens lent by Dr TA. Darragh; Fig. 15E, H, K) show that, as described by Powell (1966), *B. cancellatum* has a relatively blunt, low-conical protoconch of about 3.5–4 whorls, with a small, blunt apex, convex outlines, and raised, flat-crested spiral cords on the last whorl, similar to that of *T. formosa* (shown accurately in the drawing by Cossmann 1901:163, fig. 42). It is also very similar to those of *Marshallaria* and *Zeatoma* species. Comparison of specimens showed that *Tahuia formosa* is smaller, has a more rounded peripheral angulation, and has a slightly shorter, blunter protoconch than *B. cancellatum*. However, *B. cancellatum* is quite variable in axial fold development (Fig. 15E, H, K) and some specimens have very weak axial sculpture over the last half-whorl; the specimens illustrated by Cossmann (1901, pl. 6, figs. 9, 10) have a slightly more rounded periphery than those I have examined, and closely resemble *Tahuia formosa* in all characters. Some undescribed species of *Marshallaria* (e.g. GS9723, NO2/f7594, Paratoetoe, opposite Te Hapua, N shore Parengarenga Harbour, N Northland; Altonian, early Miocene; three specimens) have a sharper, more prominent peripheral angulation than species illustrated by Maxwell (1992), and resemble *Tahuia* and *Belophos* species in all characters. Both *Belophos cancellatum* and *Tahuia formosa* have a sharply ridge-margined siphonal fasciole formed by their shallowly notched anterior canals, and bear highly distinctive, fine, closely spaced, axial and spiral threads over the entire teleoconch, rendering them particularly closely similar. The sculpture of some *Marshallaria* species is little different, although wider spiral cords predominate on most species. In contrast, *Zeatoma* species are characterized by their exceedingly fine, closely spaced spiral threads between the primary spiral cords, not crossed by any obvious fine axial sculpture. *Austrotoma* species have fewer, slightly coarser spiral threads between the primary spiral cords, and again lack the obvious, fine, close axial threads present in *Tahuia*, *Marshallaria* and *Belophos*. *B. cancellatum* also closely resembles the shorter and more robustly sculptured of the South American and Antarctic Paleogene fossil species previously assigned to *Austrotoma* (Stilwell & Zinsmeister 1992; Nielsen 2003; Griffin & Nielsen 2008:297, pl. 20, figs. 24–27) although, again, these species lack the fine axial threads characteristic of *Belophos* and *Tahuia*. The range of sculpture and shape exhibited by *Austrotoma* species in New Zealand also includes most shell shapes of species assigned by Powell (1942, 1944) to *Belophos*, *Liratomina* and *Belatomina*. Few Australian or New Zealand *Austrotoma* species have as deeply concave a sutural ramp or as prominent a peripheral keel as *Belophos cancellatum*, but again the SW Atlantic Recent species discussed below and a few extreme New Zealand species such as *A. clifdenica* Powell, 1942 (Fig. 15M) are similar to *B. cancellatum* in this respect. In view of the range of sculpture shown by the material illustrated by Hickman (1976) and the South American and Antarctic species, it seems likely that the differences between *Belophos*, *Tahuia*, *Marshallaria*, *Austrotoma* and *Lirotomina* are trivial, that is, these names possibly are synonyms. All of them (along with *Megasurcula*) are also possibly simply synonyms of *Pseudotoma*. Even Powell (1944:27), when describing *Liratomina adelaidensis*, commented that 'this species has a strong superficial resemblance to *Austrotoma*'. His new species *Austrotoma inexpectata* and *L. adelaidensis* are very similar in all characters; it appears that his sole reason for placing *L. adelaidensis* in *Liratomina* was the absence of the subsutural fold that he considered diagnostic of *Austrotoma*. Large Conoidea of this 'group' or subfamily are widespread and their differences are much less marked than Powell supposed, so the occurrence of species of this group living in the SW Atlantic is not really surprising, and *A. aguayoi* is possibly not very closely related, phylogenetically, to New Zealand *Austrotoma* species.

This discussion suggests that in a relatively conservative, but still finely subdivided classification, *Tahuia* is best ranked as a synonym of *Belophos*, *Belatomina* is best ranked as a synonym of *Marshallaria*, and *Liratomina* is best ranked as a synonym of *Austrotoma*. It also seems possible that *Pseudotoma* is the earliest name for a genus that has also been named *Marshallaria* and *Belatomina*. However, in my opinion *Belophos* (=*Tahuia*), *Marshallaria* (=*Belatomina*), *Austrotoma* (=*Liratomina*), *Megasurcula* and *Pseudotoma* all should be retained as genera at present, until at least DNA sequences of *M. carpenteriana* and *A. aguayoi* can be compared. *Marshallena* seems well separated from these other genera by its slightly longer, narrower and more constricted anterior siphonal canal. The relatively fine axial and spiral sculpture present on *A. aguayoi*, only slightly coarser than that of *Belophos cancellatum*, and its relatively weak subsutural spiral ridge suggest that a position in *Pseudotoma* might be just as suitable as one in *Austrotoma*. However, a few New Zealand species of *Austrotoma* lack a prominent subsutural ridge (e.g. the undescribed species in Fig. 15F), it is absent from the species Powell (1944) referred to *Liratomina*, and it is present or absent in various European Neogene species assigned to *Pseudotoma* (Hickman 1976, pl. 4, figs. 12–15); its taxonomic significance seems low. Further research is obviously required on this group.

Austrotoma aguayoi (Carcelles, 1953) (Fig. 15A–D)

Clathurella aguayoi Carcelles 1953:12, pl. 4, fig. 20a–d.
Pleurotomella aguayoi. Rios 1994:178, pl. 59, fig. 823; Núñes Cortés & Narosky 1997:61, illus.; Forcelli, 2000:109, fig. 321; Tucker 2004:39; Absalão et al. 2005:34, fig. 95, 112; Simone 2007:198, fig. 11.

Type material. Carcelles (1953:12) listed the type material, in Museo de Historia Natural de Montevideo (not seen).

Other material examined. **Brazil**: trawled by fishermen, 25–35 m, off Vitoria, Espirito Santo State, S Brazil (WM19004, two); trawled by shrimpers at 100–120 m, off Niterói, Rio de Janeiro State, S Brazil, August 2004 (WM19012, ex Museu de Zoologia da Universidade de São Paulo, MZSP 70943; two; Fig. 15C,D); dredged, 100–120 m, off Arraial de Cabo, Rio de Janeiro State, Brazil, Sept. 2008 (WM19015, four; Fig. 15A, B). **Argentina**: dredged, 'old mussel bed', 38°26′S, 57°40'W, 40–50 m, off SE Argentina, presented by Laura Schejter, Lab. de Bentos, Inst. Nacional de Investgación y Desarrollo Pesquero, Mar del Plata, Argentina, 2009 (WM19053, one). In January 1998 I also examined 20 lots dredged off the coast of northern Argentina in Museo Nacional de Ciencias Natural (MACN), Buenos Aires. Most lots were dredged on the inner continental shelf, but one is labelled 'banco de mejillones [mussel bank], Necochea', ca 100 km S of Mar del Plata (MACN 31127, four specimens), that is, it occurs as shallow as the low-water spring tide line, where *Trophon geversianus* (Pallas, 1774) and banks of *Aulacomya atra* (Molina, 1782) are abundant along the very wide, gently shelving, sandy Argentinean shore. Presumably *Austrotoma* predates *Aulacomya*, among other prey.

Distribution. Núñes Cortés & Narosky (1997:61) and Forcelli (2000:109, fig. 321) recorded *Austrotoma aguayoi* as ranging from Rio de Janeiro State, Brazil, to Chubut Province, Argentina, in 35–70 m. Absalão et al. (2005:34) recorded specimens from three stations (D2, 22°53′S, 41°09′W, 82 m; D3, 22°52′S, 41°09′W, 80 m; R1#1, 21°38'57″S, 40°10'47″W, 100–180 m) off south-central Brazil, between Salvador (Bahia State) and Cabo de São Tomé (Rio de Janeiro State), so it occurs further north and in slightly deeper water than recorded previously, although all records are in temperate waters.

Dimensions. WM19015, dredged, 100–120 m, off Arraial de Cabo, Rio de Janeiro State: H

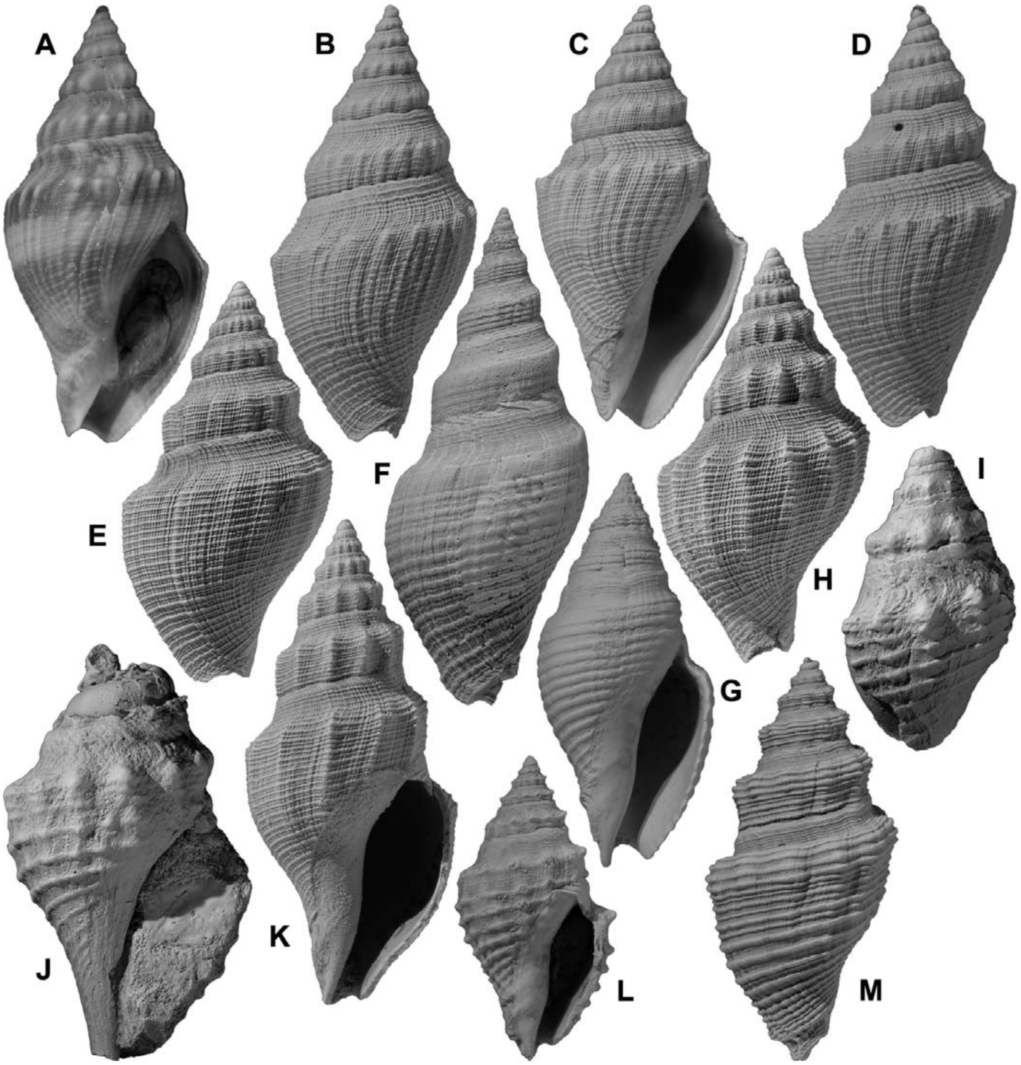

Figure 15 Conidae, subfamily Pseudotominae? (A–D) *Austrotoma aguayoi* (Carcelles), Recent, dredged off Rio de Janeiro State, S Brazil; A,B, WM19015, 100–120 m, off Arraial de Cabo; H 25.0, D 12.0 mm; A, unwhitened, note operculum; B, whitened with MgO; C,D, WM19012, 100–120 m, off Niterói, H 24.3, D 12.4 mm. (E,H,K) *Belophos cancellatum* (Tenison Woods), type species of *Belophos* Cossmann, 1901, Freestone Cove Sandstone (Longfordian, Early Miocene), Fossil Bluff, N Tasmania, NMV; E, P.315222, H 29.2, D 15.2 mm; H, P.315218, H 30.2, D 15.1 mm; K, P.315217, H35.1, D 15.3 mm. (F) *Austrotoma* n. sp., weak subsutural fold, GS8101, Y14/f7618A, Oweka Creek, between Whangaparaoa and Hicks Bay, East Cape, Opoitian (Early Pliocene); H 48.2, D 19.5 mm. (G) *Austrotoma* cf. *nervosa* Powell, GS9700, J38/f9681, Southburn Sand (Altonian, Early Miocene), 1.5 km SW of Sutherlands, Tengawai River, S Canterbury; H 37.7, D 17.4 mm. (I,J) *Struthiolariopsis ferrieri* (Philippi), type species of *Struthiolariopsis* Wilckens, 1904, Quiriquina I., Chile, Maastrichtian (Late Cretaceous), in collection S. Kiel; I, Q2186, H 21.6, D 14.2 mm; J, Q3020, H 30.0, D 27.8 mm. (L) *Austrotoma echinata* Powell, GS2155, D45/f8428, left bank Waiau River 400 m above bridge, Clifden, Southland, Lillburnian (Middle Miocene); H 29.0, D 15.1 mm. (M) *Austrotoma clifdenica* Powell, GS11213, D45/f002, Slip Point Siltstone (Clifdenian, early Middle Miocene), between Long Beach and Slip Point, Clifden, Southland; H 38.8, D 19.3 mm.

25.0, D 12.0 mm; H 23.5, D 10.2 mm; WM19012, trawled by shrimpers, 100–120 m, off Niteroi, Rio de Janeiro State: H 24.3, D 12.4 mm; H 23.2, D 11.2 mm; WM19053, 40–50 m, dredged, 'old mussel bed', off SE Argentina: H 20.3, D 10.6 mm.

Remarks. This Recent species is included to point out that *Austrotoma* (as used traditionally, that is, ignoring the possibility that this genus should be known as *Belophos* or even *Pseudotoma*) is not the 'restricted Australian and New Zealand' genus it has still usually been thought to be, despite comments to the contrary by Hickman (1976), but is still living in shallow water in the SW Atlantic Ocean. Several fossil species of *Austrotoma* occur in Oligocene–Miocene rocks of South America (Chile: Nielsen 2003:190, pl. 39, figs. 7–15, *A. echinulata* (Hupé, 1854) = *Pleurotoma turbinelloides* G. B. Sowerby II, 1846, junior primary homonym of *P. turbinelloides* Reeve, 1846; = *Fusus modestus* Philippi, 1887); undescribed ones observed near Santa Cruz in S Argentinean Patagonia (M Griffin pers. comm.); Oligocene/Early Miocene, King George Island, Scotia Arc: Karczewski (1987, pl. 35, fig. 4; as *Perissodonta* cf. *exilis*); and in Eocene rocks of Seymour Island, Antarctic Peninsula (Stilwell & Zinsmeister 1992, pl. 23a–d,f–i). A Recent occurrence in the SW Atlantic is therefore not surprising, but provides an example of the opposite theme to much of this series of papers: a supposedly 'restricted Australian and New Zealand' genus that is extinct in Australia and New Zealand but survives in the temperate South Atlantic. Coloured photographs were published by Núñes Cortés & Narosky (1997:61) and Forcelli (2000:109, fig. 321) and illustrations of Brazilian specimens of this *Austrotoma* species and two other, apparently unnamed species are published on a recent web page among 1960 colour photos of Conoidea (http://www.femorale.com.br/shellphotos/thumbpage.asp?family = TURRIDAE&nav = 102). These demonstrate that *A. aguayoi* is a reasonably typical *Austrotoma* species resembling *A. excavata* (Suter, 1917) (Beu & Maxwell 1990, pl. 26h), *A. clifdenica* Powell, 1942 (Fig. 15M; Beu & Maxwell 1990, pl. 26e), *A. nervosa* Powell, 1942 (Fig. 15G; *A.* cf. *nervosa*) and *A. lawsi* Powell, 1942 (Beu & Maxwell 1990, pl. 22 l), with a slightly wider anterior end, smaller nodules at the periphery, and a markedly weaker subsutural fold than *A. lawsi.* The peripheral nodules are more prominent in the photograph by Rios (1994, fig. 823) than in most New Zealand fossils, and are also very prominent in some of the Femorale web page illustrations. However, other New Zealand fossil species such as *A. echinata* Powell, 1942 (Fig. 15L) have much more prominent peripheral nodules than the Recent shells. The specimens illustrated by Núñes Cortés & Narosky (1997:61) and Forcelli (2000:109, fig. 321) are orange-brown, with faintly paler spiral bands. Specimens illustrated on the Femorale web page are darker red-brown to purplish brown banded with white, whereas other illustrated Atlantic species are almost plain white.

Recent Atlantic specimens of *Austrotoma aguayoi* are particularly similar to *Belophos cancellatum* (Fig. 15E, H, K) in their fine, closely spaced axial and spiral sculpture, but have a slightly better-developed subsutural fold and coarser axial ridges than *B. cancellatum.* In view of the great range of characters displayed by *Belophos*, *Austrotoma*, *Pseudotoma*, *Marshallaria* and *Megasurcula* species, the generic position of *A. aguayoi* is undecided at present, but I tentatively place it in *Austrotoma* until DNA sequences can be compared with *Megasurcula carpenteriana* and *Marshallena* species.

Absalão et al. (2005, fig. 112) illustrated the smooth, polished, bulbous protoconch of one whorl present on *Austrotoma aguayoi.* This lecithotrophic protoconch passes gradually into the teleoconch and so is significantly different from the sharply demarcated, narrowly pointed one of 4–5 whorls on New Zealand *Austrotoma* species. Powell (1942: 71, text-fig. B6) described the protoconch of

New Zealand species as 'polygyrate of 4–5 whorls with a minute globular tip, the first three whorls being smooth and the remainder bearing strong flat-topped spiral cords and thin axials towards its close' (similar to the descriptions and illustrations by Maxwell [1992:154–158] of the protoconchs of *Zeatoma*, *Marshallaria* and *Tahuia*, and to Cossmann's [1901:163, fig. 42] illustration of that of *Belophos cancellatum*). This again seems likely to be a distinction between a direct-developing (Brazilian) and either a demersal lecithotrophic or a planktotrophic protoconch type (New Zealand), of no significance in phylogeny. Two of the specimens in WM19015 (off Arraial de Cabo) have the operculum placed in the aperture (Fig. 15A); its width fills the aperture and it is long and narrowly leaf-shaped with an anterior terminal nucleus, although not as long as the aperture, and similar to that illustrated by Powell (1966:14, text-fig. F, opercula, fig. 176) for *Benthofascis biconica* (Hedley, 1903).

Pleurotomella esmeralda Olsson (1964:104, pl. 17, figs. 4–4b) is a further superficially similar species from the Early Pliocene Onzole Formation at Punta Gorda, Esmeraldas Province, Ecuador. Olsson did not provide a comparison with any other species, but his illustrations show a species with a slightly more narrowly contracted base and less protruding peripheral nodules than in *A. aguayoi*. Although the Ecuadorean species appears to be shorter than *Megasurcul*a species and more similar to *Austrotoma*, like many of the other species discussed here it is intermediate in many characters between these two supposed genera.

Subfamily Clathurellinae

Remarks. Puillandre et al. (2008) recognized that a large number of subfamily-level clades (seven in the relatively small number of taxa they examined) is subsumed within 'subfamily Clathurellinae'. It will be many years before the real relationships of New Zealand taxa are revealed, and the present classification is retained in the meantime.

Genus ***Mitrellatoma*** Powell, 1942

Mitrellatoma Powell 1942:109. Type species (by original designation): *Columbella angustata* Hutton, 1886, Nukumaruan (late Pliocene), central Hawke's Bay, New Zealand.

Remarks. Glibert (1954:40, pl. 1, fig. 16; pl. 5, fig. 13) assigned *Pleurotoma ligata* Defrance, 1826 to '*Asthenotoma (Mitrellatoma)*', and it was also placed in *Mitrellatoma* by Powell (1966:88). However, *P. ligata* is certain to be a homologue rather than a member of clade *Mitrellatoma* (if there is one). *P. ligata* has a taller, narrower spire than *M. angustata* (Hutton, 1886), the type species of *Mitrellatoma*, and also differs in having a weakly concave rather than almost flat sutural ramp and more prominent spiral sculpture. Glibert (1954) and Powell (1966) pointed out similarities to *Asthenotoma* species, and *P. ligata* should be referred to *Asthenotoma* provisionally. Kilburn (1986: 682, figs. 97, 101) referred a third species to *Mitrellatoma*, the Recent species *M. mitra* Kilburn, 1986, from southern Mozambique, East Africa. This little shell (height 6.4 mm) has a much deeper anal sinus than *M. angustata*, and its sculpture of even, wide, low spiral cords is distinctive. Again this seems highly likely to be a convergent form rather than a species of clade *Mitrellatoma*, particularly as I question below whether *Mitrellatoma* is a recognizable clade even in New Zealand. Such small, simple, featureless shells will not be classifiable until the radula is known, at least, and their DNA sequences require comparison for their relationships to be resolved finally.

Mitrellatoma angustata (Hutton, 1886) (Fig. 16H, K)

Columbella angustata Hutton 1886:333; Hutton 1893:45; Pace 1902:54.
Alcira angustata. Suter 1915:29, pl. 8, fig. 9.
Mitrellatoma angustata. Powell 1942:110, pl. 12, fig. 7; Powell 1966:88, pl. 13, fig. 15;

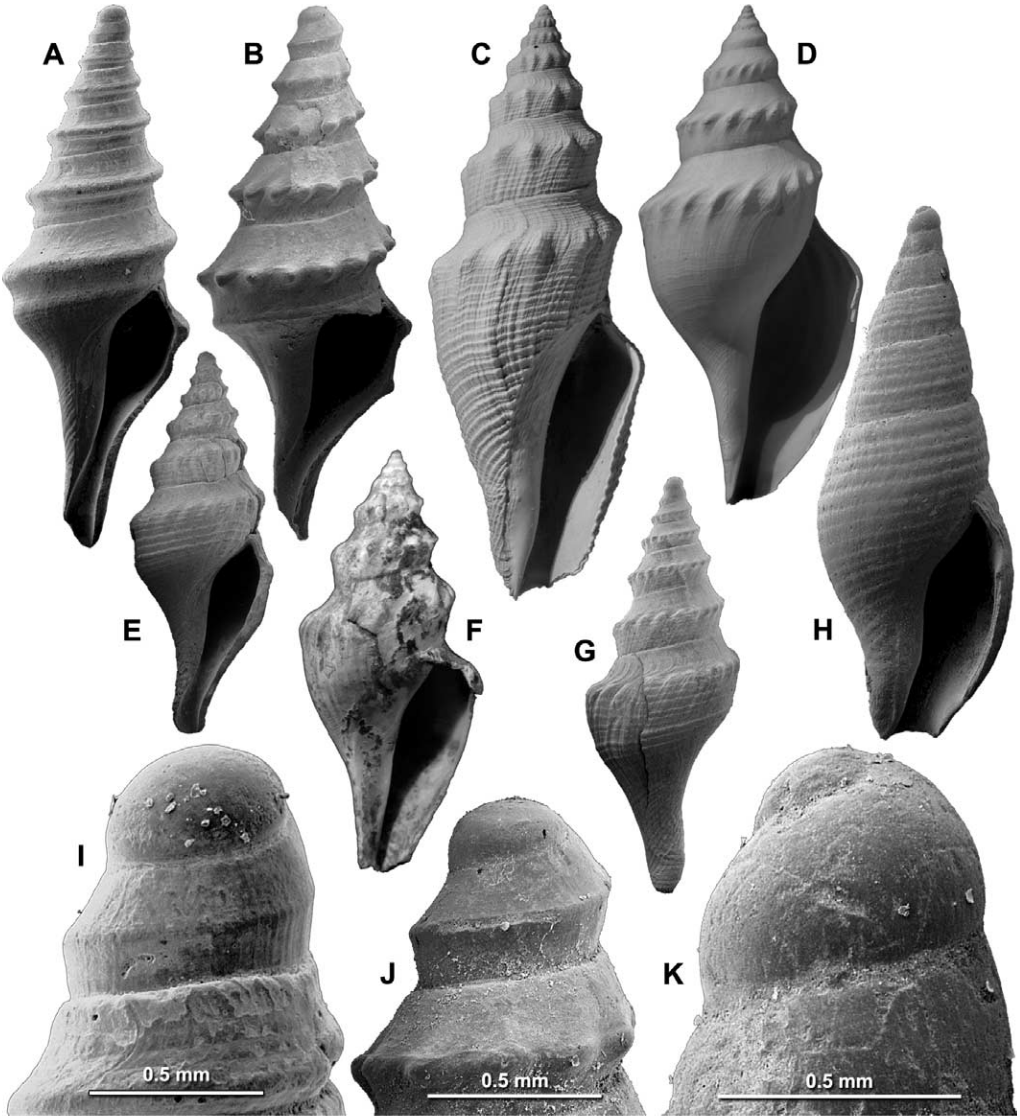

Figure 16 (A,I) *Paracomitas protransenna* (Marshall & Murdoch), GS10857, U23/f7049, Maharakeke Mudstone (Nukumaruan), Maharakeke Road, W of Waipukurau, Hawke's Bay; A, height 11.2 mm; I, protoconch of A. (B,J) *Paracomitas augusta* (Murdoch & Suter), TM1107, paralectotype, ex Suter collection, Recent, 200 m, off Great Barrier Island, E of Auckland; B, height 6.4 mm; J, protoconch of B. (C) *Pseudotoma intorta* (Brocchi), type species of *Pseudotoma* A. Bellardi, 1875, WM7025, Castelnuovo don Bosco, near Asti, NW Italy, Piacenzian (Pliocene); H 57.5, D 21.4 mm. (D,F) *Gymnobela gypsata* (Watson); D, NMNZ M.59541, 1723–1549 m, head of Hikurangi Trench, E of South Island, H 47.9, D 21.3 mm; F, 1 of 2 syntypes, BMNH 1887.2.9.979–980, HMS "*Challenger*" Sta. 169, 1280 m, off East Cape, New Zealand; H 36.8, D 15.8 mm. (E,G) *Paracomitas gemmea* (Murdoch), type species of *Paracomitas* Powell, 1942, 2 specimens; GS4061, R22/f6392, Lower Kai-Iwi Siltstone (Castlecliffian, OIS 23), Castlecliff coast; E, H 13.8, D 5.4 mm; G, H 14.9, D 5.7 mm. (H,K) *Mitrellatoma angustata* (Hutton), type species of *Mitrellatoma* Powell, 1942, specimen resembling holotype, SEM, GS2220, V20/f8462, Devils Elbow Mudstone (late Nukumaruan), top of Devils Elbow hill, Hawke's Bay; H, height 10.5 mm; K, protoconch of H.

Fleming 1966:74; Beu & Maxwell 1990:419; Tucker 2004:72; Maxwell 2009:248.

Type material. Columbella angustata, holotype in CMC according to Powell (1942:110), but not included in the catalogue of CMC fossil types by Bradshaw et al. (1992); from Petane, 30 km N of Napier, central Hawke's Bay, precise locality unknown; Tangoio Limestone or Mairau Mudstone, Petane Group, late Nukumaruan; collected by Augustus Hamilton. Norton Hiller (CMC pers. comm. 11 December 2007) reported that the holotype (M3361) is still present in CMC, and was merely missed out of the catalogue by Bradshaw et al. (1992), and I have now examined it.

Other material examined. The one specimen of *Mitrellatoma angustata* I am aware of other than the holotype is that illustrated by Powell (1942, pl. 12, fig. 7), from Devils Elbow Mudstone at the top of Devils Elbow hill, Napier-Wairoa Highway (Highway 2) ca 35 km N of Napier, late Nukumaruan (TM8589, GS2220, V20/f8462; Fig. 16H, K). Despite extensive re-collection at this highly diverse locality over 50 yr, I have not collected another specimen.

A specimen in GNS ('middle marls', Newton Range, E of Lake Tutira, Hawke's Bay, that is, high in Petane Group in the block NE of Arapaoanui River, N of Devil's Elbow; among the many Conoidea presented to GNS by HJ Finlay) was labelled '*Phenatoma angustata*' by Finlay. It is a relatively large (H 14.7 mm) but poorly preserved specimen of the *Phenatoma* species now usually known as *P. precursor* Powell, 1942, a species that occurs uncommonly in Petane Group mudstone units throughout Hawke's Bay. The anal sinus of this specimen is very weak and faint, indicating that the sinus can be suppressed through injury. The one other lot of four specimens in GNS assigned to this species was received from an early collector at Wanganui (R Murdoch?) and bears an early label reading '*Alcira angustata* Hutton', and a more recent one reading '*Mitrellatoma angustata*, Kai Iwi', but these specimens from the lower part of the Castlecliff coastal section represent a small (H 4.4 mm) columbellid with even, narrow, closely spaced spiral grooves and no sinus in the outer lip, closely resembling *Zemitrella choava* (Reeve, 1859). None of these is conspecific with the holotype of *M. angustata*.

Dimensions. Holotype, CMC M3361: H 9.8, D (slightly incomplete) 3.8 mm; GS2220, TM8589: H 10.5, D 4.0 mm.

Remarks. This virtually unknown species is included to point out its apparently distinctive characters and the lack of knowledge of its relationships, in the hope that more specimens might come to light so its status is clarified. *Mitrellatoma angustata* is one of the rarest and least well understood of Hawke's Bay Nukumaruan molluscs, being recorded only as the holotype (as stated by Powell [1942:109], the holotype is a rather poor, severely abraded specimen) and the single specimen illustrated by Powell (1942, pl. 12, fig. 7) (also significantly abraded). Powell (1942:109) stressed its great similarity to a small specimen of a *Phenatoma* species, and it appears feasible to me that this species is based on a highly aberrant individual of a *Phenatoma* species, such as the weakly sculptured Nukumaruan species *P. precursor* Powell (1942:109, pl. 10, fig. 8). *P. precursor* occurs uncommonly in Devils Elbow Mudstone on Devils Elbow hill, where the illustrated specimen of *M. angustata* was collected. *P. precursor* also occurs commonly in shallower-water facies such as shoreface sands in central Hawke's Bay (e.g. GS11225, V20/f8002, Darkys Spur Formation, long N–S horizontal cutting on Darkys Spur road, between Waipunga and Kaiwaka, 5 km WNW of Devils Elbow, late Nukumaruan; 10 specimens). However, it must be stressed that the two known specimens of *M. angustata* are very similar, and at present it seems just as likely that this is a distinct but very rare species. *M. angustata* apparently differs from *Phenatoma* in its much smaller size (the larger is 10.5 mm high, compared with up to ca 25 mm in *P. precursor* and up to 35 mm in Recent specimens of *P. rosea* (Quoy & Gaimard, 1833)), its smoother and more evenly, consistently sculptured surface with very even, wide, low, closely spaced spiral cords, with obscurely defined edges, and only faint axial sculpture of growth lines in the spiral interspaces (although both specimens assigned here are abraded, and the apparently distinctive sculpture might merely result from abrasion), its shallower anal sinus, and its more evenly inflated protoconch of fewer whorls than in *Phenatoma* (*M. angustata*: Fig. 16H, K; Powell 1942, text-fig. B15, p. 38; *P. rosea*: Powell 1942, text-fig. C21, p. 39). However, on the basis of the two known specimens, even the protoconch characters possibly could be based on aberrant or severely abraded individuals, as the protoconch (Fig. 16K) is obviously abraded. In the circumstances, assignment to Subfamily Clathurellinae (alongside *Phenatoma*) is provisional. Assignment of extra-New Zealand taxa to a 'genus' *Mitrellatoma* clearly is unjustified, and further, better-preserved specimens are required to clarify the status of *M. angustata* and the genus *Mitrellatoma*.

Subfamily Cochlespirinae

Remarks. The subfamily Cochlespirinae (sensu stricto) was revealed as a distinct clade by Puillandre et al. (2008, fig. 1), although some of the taxa formerly included in it on anatomical grounds, such as *Leucosyrinx* and *Comitas*, belong in other, unnamed clades, and even the species included in *Comitas* are polyphyletic. Powell (1942) originally suggested a relationship between *Paracomitas* and *Comitas* Finlay, 1926, although admitting that *Paracomitas* was 'puzzling'. However, a relationship with *Cochlespira* Conrad, 1865 and similar genera seems much more likely. The relatively early, rather generalized species *Cochlepira maora* (Marshall & Murdoch, 1923) (= *Tahusyrinx finlayi* Powell, 1942; Maxwell 1992:152, pl. 21q,r; Kaiatan [late Eocene], McCulloch's Bridge, S Canterbury) has more complex spiral sculpture and a much more strongly protruding peripheral keel, but is otherwise similar to *Paracomitas* species in most characters, and a similar cochlespirine taxon could well have given rise to *P. protransenna*. The smooth peribasal cord, a prominent peripheral carina and a very similar shoulder sinus to that of *Paracomitas* are present on all the close relatives of *Cochlepira* (listed by Powell 1966:20). A further helpful character of *C. maora* is the tall, clearly carinate protoconch, quite different from the bulbous, paucispiral, smooth (lecithotrophic) protoconch of most *Cochlepira* species. This demonstrates that the keeled protoconch of *Paracomitas* is not greatly discordant with other cochlepirine protoconchs although, of course, the great reliance placed on protoconch characters by Powell (1942, 1966) is not followed here. In view of the strong teleoconch similarity, *Paracomitas* is here referred to subfamily Cochlespirinae (sensu stricto).

Genus ***Paracomitas*** Powell, 1942

Paracomitas Powell 1942:61. Type species (by original designation): *Surcula castlecliffensis* Marshall & Murdoch, 1919 (= *Pleurotoma gemmea* Murdoch, 1900), Castlecliffian (Pleistocene), New Zealand.

Remarks. Species of *Paracomitas* are characterized by their small size, their prominent peripheral carina, a rather weak peribasal angulation consisting of a smooth spiral cord extending from the suture, a relatively long, narrow anterior siphonal canal, a broad, relatively shallow anal sinus occupying the width of the almost smooth, concave sutural ramp, a forward-extended outer lip below the sinus, and a protoconch with a low, dome-shaped first whorl and a prominent, narrow, median carina on the succeeding whorl. The earliest species in an apparently simple evolutionary lineage is *P. protransenna* (Marshall & Murdoch, 1923), limited to Nukumaruan rocks. This species is unusual in having the peripheral carina smooth, whereas later species bear gemmae on the carina where it is crossed by low axial ridges. I (Beu 1970b) proposed a subgenus *Paracomitas (Macrosinus)* for species with a deeper anal sinus, more uniformly present spiral sculpture and a less protruding periphery. It is conceivable that this group was ancestral to *Paracomitas*, but the differences are great enough to suggest that the similarity is superficial, and *Macrosinus* is regarded here as a distinct genus. The species revised here are those previously assigned to *Paracomitas* (sensu stricto).

Paracomitas protransenna (Marshall & Murdoch, 1923) (Fig. 16A, I)

Surcula protransenna Marshall & Murdoch 1923:126, pl. 12, fig. 6.
Parasyrinx protransenna. Finlay 1924:514.
Paracomitas protransenna. Powell 1942:62; Fleming 1966:71; Tucker 2004:796.
Paracomitas (Paracomitas) protransenna. Beu & Maxwell 1990:327, pl. 42r; Maxwell 2009:249.

Type material. *Surcula protransenna*, holotype TM8287, with six paratypes TM8288–8293, from Waikopiro, near Ormondville, southern Hawke's Bay, Nukumaruan; ex Marshall & Murdoch Collection; stated by Marshall & Murdoch (1923:127) as 'Waikopiro. (Seven specimens, Suter collection)', that is, the types are from Suter's collection from Waikopiro. The tube of specimens received from the Wanganui Museum remained in its original condition when I examined it; five specimens were separated from the two in the entrance to the tube, which were identified by a small paper label in P Marshall's handwriting reading 'type'. These are assumed to be the two specimens whose dimensions were provided by Marshall & Murdoch (1923:127): 'Length 13 mm; width, 5 mm. Another example: Length, 10 mm, width, 4 mm' (see actual measurements below). This indicates that the larger of the specimens labelled 'type' is the figured one. Marshall & Murdoch (1923:127) also made the clear statement 'Type and paratypes in Wanganui Museum', so the illustrated specimen is considered to be the holotype.

Other material examined. **Nukumaruan:** none was reported from Wanganui Basin by Fleming (1953); Devils Elbow Mudstone, top of Devils Elbow hill, Highway 2, ca 35 km N of Napier (GS2220, V20/f8462, one; GS10849, V20/f8572, three); above Te Onepu Limestone, tributary of Porangahau Stream, 3 km S of Takapau, S Hawke's Bay (GS2330, U23/f6382, one); headwaters of tributary of Waikoukou Stream, 3 km NNE of Ormondville, S Hawke's Bay (GS2369, U23/f6414, one); Maharakeke Road, W foot of Pukeroa Hill, Waipukurau (GS10857, U23/f7049, one); Ashcott Road, NW foot of Pukeora Hill, Waipukurau (GS10858, U22/f09, nine); Mairau Mudstone, Seafield Road, Bayview, N of Napier (GS10875, V21/f6575, one); Mairau Mudstone, walkway W side of Roro-o-kuri, Onehunga Road, N end of Ahuriri 'lagoon', Napier (GS12386, V20/f05, six); Paulsen Road, 2.5 km N of Rangitoto trig. station, SE of Takapau, S Hawke's Bay (GS11479, U23/f6528, one).

Distribution. Restricted to Nukumaruan rocks; all records are from the upper siltstone formations of Petane Group in central Hawke's Bay, and laterally equivalent units in S Hawke's Bay and S Wairarapa, of Nukumaruan age. Specimens are never abundant, but are more widespread in Hawke's Bay Nukumaruan rocks than above records suggest.

Dimensions. *Surcula protransenna*, holotype: H 12.3, D 4.6 mm; Marshall & Murdoch's measured paratype, TM8288: H 9.7, D 3.5 mm; GS10858, Ashcott Road: H 13.0, D 4.5 mm; H 13.1, D 5.1 mm; H 13.2, D 4.6 mm; GS10849, Devils Elbow Mudstone, top of Devils Elbow hill: H 16.8, D 5.8 mm; GS2220, locality as last: H 12.6, D 4.4 mm.

Remarks. *Paracomitas protransenna* is one of the most distinctive of New Zealand conoideans, easily recognized by its small size (H 12–17 mm), its very prominent, smooth, narrowly convex peripheral carina, its obvious, smooth peribasal angulation, its elongate, graceful shape, its moderately deep, wide anal sinus, and its prominently keeled protoconch. Therefore, despite its small size, it is useful as a Nukumaruan index fossil, although it is only moderately common, and seems to be recorded only from Hawke's Bay and Wairarapa; most records are from siltstone and sandy siltstone beds of Petane Group, particularly the more offshore units of highstand systems tracts. The sutural ramp and the whorl surface between the two carinae are more strongly concave than in later species of *Paracomitas*, although it seems likely that *P. gemmea* (Murdoch, 1900) is simply its direct descendent. A few specimens of *P. protransenna* have small nodules on the peripheral carina on early spire whorls, fading out down the spire, and these more closely resemble *P. gemmea* than completely smooth specimens do.

Paracomitas gemmea (Murdoch, 1900) (Fig. 16E, G)

Pleurotoma gemmea Murdoch 1900:217, pl. 20, fig. 9.
Surcula castlecliffensis Marshall & Murdoch 1919:255.
Paracomitas gemmea. Powell 1942:62; Powell 1966:29; Fleming 1966:71; Tucker 2004:412.
Paracomitas castlecliffensis. Powell 1942:62, pl. 10, fig. 1; Powell 1966:29, pl. 2, fig. 1; Fleming 1966:71.
Paracomitas (Paracomitas) gemmea. Maxwell 1988:60; Beu & Maxwell 1990:368, pl. 49q; Maxwell 2009:249.

Type material. Pleurotoma gemmea, holotype TM6842 (Beu & Maxwell 1990, pl. 49q), from Castlecliff, Wanganui, 'blue-clay cliffs, west of Wanganui Heads', Castlecliffian, from Marshall & Murdoch collection. *Surcula castlecliffensis*, holotype TM8286, from 'Castlecliff, in blue sandy clay', Wanganui, Castlecliffian, also from Marshall & Murdoch collection.

Other material examined. **Castlecliffian:** reported by Fleming (1953:192, 184, 199, 200, 207) from Lower Kai-Iwi Siltstone and Omapu Shellbed (OIS 23), Kaikokopu Shellbed and Upper Westmere Shellbed (OIS 19) and Upper Kai-Iwi Siltstone (OIS 17) in Wanganui Basin; specimens in reference collection: coast between Kai-Iwi & Okehu streams, Castlecliff (GS1163, R22/f6498, six); Lower Kai-Iwi Siltstone (OIS 23), Castlecliff (GS4069, R22/f6400, seven); data as last (GS4061, R22/f8392, six); Pinnacle Sand (OIS 14), 'the pinnacles' gully, Castlecliff (GS4022 re-collection, R22/f6360, three); also two good specimens with slightly more prominent peripheral nodules and a more prominent peribasal cord from 240–250 m in the Mikonui-1 well, off Hokitika (?early Castlecliffian) and fragments of what is probably this species from almost all other samples in the top 170–520 m of the well (see Beu 2010: 70).

Distribution. Records range from OIS 23-14, and it probably occurs in Tainui Shellbed (OIS 13), as well as in the Mikonui-1 well (?latest Nukumaruan–early Castlecliffian). However, almost all are from siltstone units (the more offshore parts of highstand systems tracts), and the offshore habitat of *Paracomitas* suggests that its occurrences are likely to be limited to fine-grained, offshore depositional facies. The real time range is likely to have been earliest Castlecliffian to Haweran, when it gave rise to *P. augusta*, and this species is of low reliability for biostratigraphy.

Dimensions. Pleurotoma gemmea, holotype: H 12.7 (incomplete), D 5.3 mm; *Surcula castlecliffensis*, holotype: H 12.2 (incomplete), D 4.2 mm; GS4061, Lower Kai-Iwi Siltstone, Castlecliff: H 16.5, D 6.7 mm; H 15.0, D 5.7 mm; GS4069, as last: H 17.4, D 7.3 mm; H 17.8, D (slightly incomplete) 6.7 mm.

Remarks. Powell (1942:62) maintained *Paracomitas castlecliffensis* and *P. gemmea* as distinct species, claiming that *P. gemmea* has fewer, more prominent nodules on the peripheral carina than *P. castlecliffensis*. However, Maxwell (1988:60) and Beu & Maxwell (1990:368) pointed out that the two forms intergrade completely, and represent a single species. *P. gemmea* differs from *P. protransenna* in having a less prominent peripheral carina, which bears gemmae (short axial costae), in its taller and flatter interval between the two carinae, and in having numerous fine, closely spaced spiral cords over the entire surface below the peripheral carina, rather than being entirely smooth over at least the last 3–4 whorls as in *P. protransenna*. *P. gemmea* also is larger and wider and has a less prominent peripheral carina, smaller peripheral nodules, and more prominent spiral cords below the carina than in *P. augusta*.

Paracomitas augusta (Murdoch & Suter, 1906) (Fig. 16B, J)

Pleurotoma (Leucosyrinx) augusta Murdoch & Suter 1906:286, pl. 22, figs. 14–17.

Turris (Leucosyrinx) augusta. Suter 1913:472, pl. 21, fig. 3.

Paracomitas augusta. Powell 1942:62; Dell 1956b:176; Boreham 1959:59; Powell 1966:29; Tucker 2004:99.

Paracomitas augusta powelli Dell 1956b:56, fig. 25; Powell 1979:229; Spencer & Willan 1996:29; Tucker 2004:785.

Paracomitas augusta augusta. Powell 1979:229; Spencer & Willan 1996:29.

Paracomitas (Paracomitas) augusta augusta. Spencer et al. 2009:211.

Paracomitas (Paracomitas) augusta powelli. Spencer et al. 2009:211.

Type material. *Pleurotoma augusta*, lectotype NMNZ M.1715 (Marshall 1996:28), two paralectotypes TM1107–8 (Boreham 1959:59; Figs. 16B, J), Recent, dredged in 200 m off Great Barrier Island, E of Auckland. Suter's specimens (TM1107–8) are labelled 'syntypes' in Suter's handwriting, so it is not clear that the NMNZ specimen (M.1715) was originally selected as the holotype, and it is here designated as the lectotype. *Paracomitas augusta powelli*, holotype NMNZ M.8840 (Marshall 1996), from 106 m, E of Stephens Island, Cook Strait, 40°42′S, 174°10.6′E; two paratypes M.8841, from the same locality.

Other material examined. Recent, typical *Paracomitas augusta*, 15 lots in NMNZ, all from NE North Island: M.147932, 357–447 m, E of North Cape (four small); M.42261, 124 m, off Poor Knights Islands, Northland (one); M.35840, 113–121 m, W of Poor Knights Islands (seven); M.35744, 80 m, off Cape Brett (four); M.11068, 207–220 m, off Mayor Island (two); M.66590, 198–273 m, NW of Mayor Island (11); M.61018, 293–348 m, NW of Mayor Island (three); M. 11059, 494 m, off Mayor Island (one); M.60242, 482–550 m, E of Mayor Island (two); M. 61326, 203–248 m, SE of Mayor Island (one); M.147933, 108–113 m, N of Aldermen Islands (two); M.44432, 145 m, off Aldermen Islands (one); M.66723, 178–248 m, SE of Aldermen Islands (one); M.59831, 139 m, ENE of Tolaga Bay (one); M.7960, 366 m, off Cape Kidnappers (one). *P. augusta powelli* form: 24 lots in NMNZ, all from W New Zealand, ranging from NW of Ahipara, Northland (M.15803, 90 m; three) to Bradshaw Sound, Thompson Sound and Doubtful Sound in the W Southland Fiords; most material is from W Cook Strait.

Distribution. Typical *Paracomitas augusta*, with a single prominent peribasal spiral cord, seems to be limited to the E North Island, NMNZ material ranging from off Cape Kidnappers to North Cape. The '*powelli* form', with two prominent peribasal spiral cords and several other obvious basal spiral cords, occurs along the W coast of New Zealand from Ahipara, N Northland, to W Otago. This is interpreted here as one species, although the geographical separation suggests that further study is justified. Records range from 80–550 m, but the deepest ones are transported chalky shells, and the normal depth range of living specimens seems to be about 100–300 m.

Dimensions. *Pleurotoma augusta* lectotype: H 10.32, D 3.9 mm (Murdoch & Suter 1906:286); paralectotypes: TM1107–8: H 6.4, D 2.6 mm; H 5.6, D 2.5 mm; NMNZ M.42261, off Poor Knights Islands: H 11.6, D 4.1 mm; M.61018, NW of Mayor Island: H 11.0, D 4.0 mm; M.59831, ENE of Tolaga Bay: H 9.8, D 4.1 mm.

Remarks. The type material of *Paracomitas augusta* has a single row of very prominent, laterally protruding, slightly obliquely set gemmae around a much narrower peripheral keel than in *P. gemmea*, and a prominent, narrow, smooth peribasal keel issuing from the suture. The gemmae are larger and the peribasal cord is considerably more prominent than in *P. gemmea*, giving the shell a different, narrower, more finely sculptured appearance than either fossil species. Other than a few weak spiral threads on the area between the two keels, the teleoconch is almost smooth, apart from faint growth ridges. The protoconch also is even more strongly carinate than in either fossil species, but this possibly results from better preservation.

Dell (1956b:56, fig. 25) named a subspecies *Paracomitas augusta powelli*, from depths of 106 and 137 m in Cook Strait. This form differs from *P. augusta* in having two (rather than one) prominent, well separated peribasal keels, slightly more prominent peripheral nodules, the peripheral nodules subdivided into two rows by a deep groove, and more prominent secondary spiral cords. Examination of the 24 lots of specimens in NMNZ (see above) showed that the size, shape and sculpture are little different from those of *P. augusta*, apart from the consistent presence of two peribasal cords that are more prominent than the others, rather than one on the E North Island form of *P. augusta*. Subdivision or not of the peripheral nodules by a median groove occurs along both coasts, and most specimens have a weak groove around the nodules. This form therefore seems likely to be part of the variation of *P. augusta*. Certainly, all Recent material in NMNZ is significantly smaller, narrower and with a markedly narrower peripheral spiral ridge than in the Castlecliffian *P. gemmea*, and *P. gemmea* and *P. augusta* clearly are distinct species. The distinction between *P. gemmea* (Castlecliffian) and *P. augusta* (Recent) offers some possibility of biostratigraphical utility in offshore facies (such as oil wells), but the precise age is unknown of the speciation event when *P. augusta* presumably evolved.

Subfamily Raphitominae

Genus ***Gymnobela*** Verrill, 1884

Gymnobela Verrill 1884:157. Type species (by subsequent designation, Cossmann, 1896:63): *Gymnobela engonia* Verrill, 1896, Recent, deep water, North Atlantic.

Spergo Dall 1895:680. Type species (by subsequent designation, Dall 1918:331): *Spergo gladiniformis* Dall, 1895, Recent, off Hawaii.

Theta Clarke 1959:234. Type species (by original designation): *Pleurotomella (Theta) lyronuclea* Clarke, 1959, Recent, abyssal, North Atlantic.

Speoides Kuroda & Habe in Habe 1961:77; appendix, p. 29 Type species (by monotypy): *Speoides yoshidai* Kuroda & Habe, 1961, Recent, deep water, Japan to New Caledonia and N New Zealand.

Remarks. Sysoev & Bouchet (2001:305) regarded *Theta* and *Speoides* as synonyms of *Gymnobela* Verrill, 1884, pointing out that *Spergo* Dall, 1895 is probably a further synonym, as had already been suggested by Powell (1966:137). Bouchet & Warén (1980:61, figs. 128, 252) illustrated the diagonally reticulate protoconch of *Gymnobela* characteristic of the Raphitominae. *Pleurotoma gypsata* Watson, 1881 from deep water around central E New Zealand has been referred to *Paracomitas* previously (Powell 1942, 1979) but is similar to *Gymnobela yoshidai* and is illustrated here to show that it is not correctly referred to *Paracomitas* (*Speoides yoshidai* Kuroda & Habe in Habe 1961:77, pl. 38, fig. 17, appendix p. 29; Habe 1964:120, pl. 38, fig. 17; *Spergo (Speoides) yoshidai*: Powell 1966:137, pl. 22, figs. 11, 12; Hasegawa et al. in Okutani 2000:667, pl. 332, fig. 237; *Gymnobela yoshidai*: Sysoev & Bouchet 2001:308, figs. 134–144, 173).

Gymnobela gypsata (Watson, 1881) (Fig. 16D, F)

Pleurotoma gypsata Watson 1881:413; Watson 1886:297, pl. 25, fig. 1.
Surcula gypsata. Suter 1899b:69; Suter 1913:486, pl. 21, fig. 13.
Paracomitas gypsata. Powell 1942:62; Dell 1963a:176, pl. 2, figs. 10, 11; Powell 1966:29; Powell 1979:230; Spencer et al. 1996:29; Tucker 2004:444.
Paracomitas (Paracomitas) gypsata. Spencer et al. 2009:211.

Type material. *Pleurotoma gypsata* Watson, two syntypes BMNH 1887.2.9.979–980, from HMS '*Challenger*' Sta. 169, off East Cape, New Zealand, in 1280 m. Watson (1886:298) clearly listed 'two dead and broken specimens' (Fig. 16F). Therefore, although the larger syntype was illustrated by Dell (1963a, pl. 2, figs. 10, 11) and identified as a 'type', under ICZN Article 74.6 this usage of 'type' does not constitute designation of a lectotype.

Other material examined. NMNZ M.151262, 865–741 m, Calyptogena Bank, Ritchie Ridge, off Mahia Peninsula (two); M.118135, 900 m, SE of Cape Kidnappers (one); M.74976, 1125–1150 m, off Castlepoint (one); M.59718, 999–984 m, N Mernoo Slope, Chatham Rise (one); M.59541, 1723–1549 m, 42°41.70′S, 174°28.00′E, head of Hikurangi Trench between Kaikoura and Mernoo bank (one, largest; Fig. 16D).

Distribution. Material of *Gymnobela gypsata* has been collected so far from off East Cape to the N Chatham Rise, in 740–1723 m.

Dimensions. *Pleurotoma gypsata*, syntypes: H 40.8, D (incomplete) 17.7 mm; H 36.8, D (incomplete) 15.8 mm; large illustrated specimen (Fig. 36D), NMNZ M.59541, NW Mernoo Slope: H 47.9, D 21.3 mm.

Remarks. *Pleurotoma gypsata* is a large (H 40–50 mm) *Gymnobela* species that has been collected in small numbers in recent years in deep water (>700 m) off central E New Zealand. This species has no bearing on relationships within the lineage of small *Paracomitas* species discussed above.

The material of *Gymnobela yoshidai* illustrated by Sysoev & Bouchet (2001, figs. 134–144, 173) is quite variable in relative teleoconch width and nodule prominence, but *G. yoshidai* differs from *G. gypsata* in its narrower shape, taller spire, markedly narrower and more steeply inclined sutural ramp, and smaller and less obviously oblique peripheral nodules. As much of the material of *G. yoshidai* recorded by Sysoev & Bouchet (2001:308) is from New Caledonia and the Norfolk Ridge, as far south as 24°57′S, it is not surprising to find that this or a similar species extends its range further south down the Norfolk and Kermedec Ridges to encompass northern New Zealand (NMNZ five lots, from 514–540 m, S Norfolk Ridge, NW of Cape Reinga, to 924–712 m, Rumble V volcano, S Kermadec Ridge, off Bay of Plenty).

Genus ***Pleurotomella*** Verrill, 1873

Pleurotomella Verrill 1873:15. Type species (by monotypy): *Pleurotomella packardi* Verrill, 1873, Recent, bathyal, North Atlantic (Bouchet & Warén 1980:38, figs. 96, 97, 216; Fig. 17B, C, D, G, H).

Systenope Cossmann 1889:289. Type species (by original designation): *Raphitoma (Systenope) polycolpa* Cossmann, 1889, Eocene, Paris Basin.

Tasmadaphne Laseron 1954:45. Type species (by original designation): *Tasmadaphne spicula* Laseron, 1954, Recent, New South Wales (Powell 1966:124, pl. 19, fig. 19) **(new synonym)**.

Fusidaphne Laseron 1954:47. Type species (by original designation): *Fusidaphne bullata* Laseron, 1954, Recent, New South Wales (Powell 1966:124, pl. 20, fig. 1) **(new synonym)**.

Anomalotomella Powell 1966:132. Type species (by original designation): *Pleurotomella anomalapex* Powell, 1951, Recent, Antarctica **(new synonym)**.

Remarks. The characters of the type species of *Pleurotomella*, *P. packardi* Verrill, 1873 (Fig. 17B, C, D, G, H; dimensions of illustrated specimen: H 9.2, D 4.9 mm) were clarified by Bouchet & Warén (1980, figs. 96, 97, 216), who commented that they included a far less diverse group of species in the genus than the large, heterogeneous assemblage included by Powell (1966). Powell's (1966) lack of recognition of the 'Australasian' genus *Asperdaphne* in this assemblage implies that he was not aware of the characters of *P. packardi*. Four Atlantic species included in *Pleurotomella* by Bouchet & Warén do not belong here (*P. anceyi* (Dautzenberg & Fischer, 1897), *P. sandersoni* Verrill, 1884, *P. lottae* Verrill, 1885 and *P. megalembryon* Dautzenberg & Fischer, 1896; the genus *Azorilla* Nordsieck, 1968 is available for *P. lottae* and *P. megalembryon*; Bouchet & Warén [1980:49]; Morassi & Bonfitto [2006:231] referred *Pleurotomella anceyi* to *Cryptodaphne* Powell, 1942). The other North Atlantic *Pleurotomella* species form a uniform group with strongly inflated, evenly rounded whorls, apart from the concave sutural ramp, and with a strongly and rapidly contracted base and prominent, narrow, and in most species obviously curved axial ridges. This is the genus for which Hedley (1922) and Powell (1944, 1966, 1979) used the name *Asperdaphne* in Australia and New Zealand. As usual, Powell (1966:132) proposed a distinct subgenus, *Anomalotomella*, for species with a dome-shaped, paucispiral protoconch, as distinct from the 'typical' species with a conical, diagonally cancellate raphitomine one, but these are developmental types within one genus (see Numanami [1996:214–222] for discussion and illustration of Antarctic species assigned to *Anomalotomella*). *Tasmadaphne spicula* Laseron (1954:46, pl. 11, figs. 242, 243) appears to be a further species of *Pleurotomella* with a lecithotrophic protoconch, and *Fusidaphne bullata* Laseron (1954:46, pl. 12, figs. 246, 247; Powell 1966:124, pl. 20, fig.1) is probably another. *Neopleurotomoides* Shuto (1971:5; type species [by original designation]: *Clathurella rufoapicata* Schepman, 1913, Recent, bathyal, Indonesia) was distinguished from *Pleurotomella* by Bouchet & Warén (1980:43) because of its different protoconch sculpture, of medially keeled whorls with vertical (axial) riblets, unlike the usual raphitomine diagonally reticulate, evenly convex whorls of planktotrophic species of *Pleurotomella*. In this light, the generic synonymy proposed here is tentative, and the protoconch characters of type species of genera will need to be compared before the synonymy is accepted. The New Zealand Recent species referred to *Asperdaphne*, other than *A. ula* (Watson, 1881) (referred below to *Propebela* Iredale, 1918), that is, *A. expeditionis* Dell (1956a:137, figs. 204, 205; Powell 1979, fig. 56.4; Fig. 17A, F) and *A. aculeata* (Webster, 1906) (Suter 1913, pl. 22, fig. 10) and several unnamed species in NMNZ, have inflated, evenly rounded whorls without a peripheral carina, and with

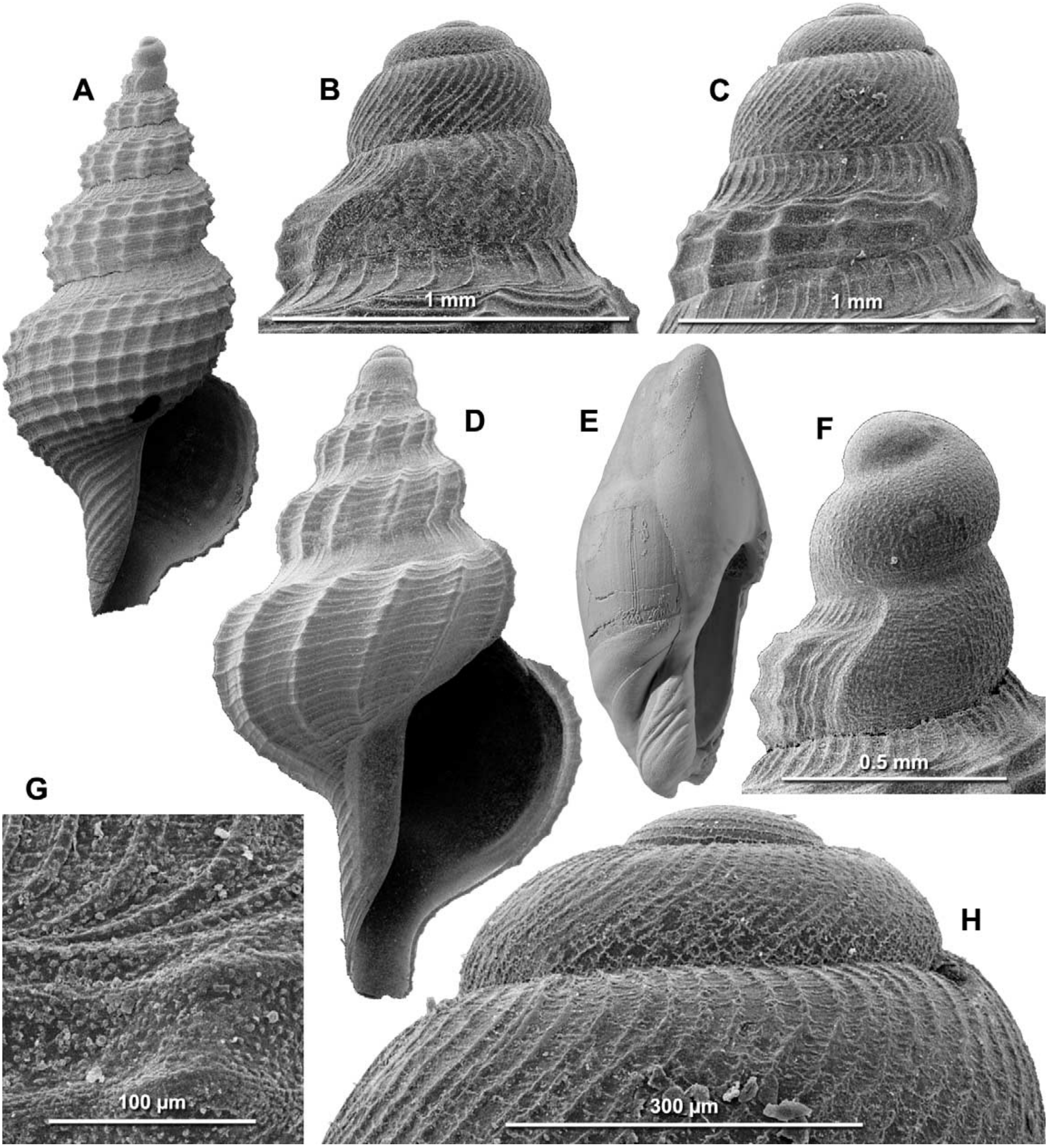

Figure 17 (A,F) *Pleurotomella expeditionis* (Dell), SEM, RM5590, Portobello sta. Mu70–45, 540–490 m, Papanui Canyon, off Otago Peninsula, RV "*Munida*"; A, height 8.2 mm; F, protoconch of A. (B,C,D,G,H) *Pleurotomella packardi* Verrill, type species of *Pleurotomella* Verrill, 1872; SEM, 2 specimens, MNHN, Biogas Sta. CP37, Golfe de Gascoigne, E Atlantic, 2175 m, 47°34'N, 08°39'W; B, protoconch; C,D,G,H, second specimen, height 9.2 mm; C, protoconch of D; G, granulose sculpture on teleoconch sutural ramp; H, sculpture of protoconch in C. (E) *Amalda (Baryspira) olsoni* Beu, GS11225, V20/f8002, Darkys Spur Formation (late Nukumaruan), Darkys Spur, W of Devils Elbow, Hawke's Bay; largest specimen seen, height 42.8 mm.

a reversed-L-shaped raphitomine anal sinus, and are congeneric with most of the Australian species referred to *Asperdaphne* by Hedley (1922, pl. 54, figs. 170–173; pl. 55, figs. 174–176), Powell (1942, pl. 6, figs. 7, 8) and Cotton (1947:22), and with *Pleurotomella packardi*. However, these species clearly are not congeneric with *Daphnella versivestita* Hedley, 1912, the Australian Recent type species of *Asperdaphne* Hedley, 1922 (Hedley 1912:148, pl. 63, fig. 12; Laseron 1954:45, pl. 11, fig. 230; Powell 1966, pl. 20, fig. 16). *A. versivestita* closely resembles *Tritonoturris robillardi* (H. Adams, 1869) (Recent, Mauritius; Powell 1966, pl. 20, fig. 23), type species of *Tritonoturris* Dall, 1924, in all characters. The only obvious difference between them is that *T. robillardi* has a typical raphitomine cancellate protoconch, whereas that of *A. versivestita* is 'paucispiral, blunt tipped, closely packed with minute spiral threads and developing two spiral keels on the last whorl' (Powell 1966:127), that is, it has lecithotrophic development. *A. versivestita* also resembles *Tritonoturris* species in its relatively large size (H 23, D 9 mm; Hedley 1912:148) compared with most other species assigned to *Asperdaphne* by Hedley and Powell. *Asperdaphne* appears to be an earlier name for *Tritonoturris*. *Asperdaphne versivestita* resembles *Tritonoharpa macandrewi* (EA Smith, 1882) very closely (Li et al. 2010:198, figs. 5–8,11), apparently differing only in protoconch shape (tall and multispiral in *T. macandrewi*, short and paucispiral in *A. versivestita*).

Sysoev (in Poppe 2008:750, pl. 670, fig. 1) used *Asperdaphne* for a species from the Philippines, *A. peradmirabilis* (E. A. Smith, 1879), but this also seems to be a relatively weakly sculptured species of *Tritonoturris*. The other Australian and New Zealand species referred to *Asperdaphne* are smaller than *Tritonoturris versivestita* and lack the prominent axial ridges, effuse outer lip, short last whorl and short, widely open anterior siphonal canal that characterise *Tritonoturris*; most are typical species of *Pleurotomella*.

The one obvious difference between Australasian species and the North Atlantic species included in *Pleurotomella* by Bouchet & Warén (1980:34–41) is that, once again, most Atlantic species have a tall, diagonally cancellate raphitomine protoconch, whereas most Australasian species have a blunt, paucispiral, spirally ridged to finely and irregularly nodulose protoconch (Fig. 17F). However, the type species, *P. packardi*, has a blunt, short protoconch with fine, rather irregular spiral threads over the uppermost third and short, diagonally arcuate ridges over the lowest two-thirds of each whorl (Fig. 17B, C, H) and apparently has lecithotrophic development. Greater enlargement showed that the protoconch is quite coarsely granulose and the teleoconch more finely so (Fig. 17G). Again this protoconch difference is solely a developmental difference, and *Pleurotomella* is adopted here for the Australian and New Zealand species previously assigned to *Asperdaphne*.

Several genera are represented among the species included in *Asperdaphne* by Hedley (1922), but at least some Australian species are correctly referred to *Pleurotomella* (see below), although protoconchs will need to be checked to be sure that some do not belong in *Neopleurotomoides*. Some other species included by Hedley (1922) or Cotton (1947) in *Asperdaphne* may well belong in *Pleurotomella*, but require further research.

Fenestrodaphne pulchra Powell (1944:61, pl. 6, fig. 10), type and only species referred to *Fenestrodaphne* Powell, 1944, is very similar to '*Asperdaphne*' *tasmanica* (Tenison Woods, 1877) (Hedley 1922, fig. 12, p. 343), but neither can be referred to *Pleurotomella*. Rather, they seem to be species of *Taranis* Jeffreys, 1870. '*Asperdaphne*' *vestalis* Hedley (1922:344, fig. 13; Laseron 1954:46, pl. 11, figs. 240, 241) is also a species of *Taranis* (WM8381, 120 m, off Port Jackson; two specimens examined). Hedley (1922:341) noted of '*Asperdaphne*' *esperanza* (May, 1910) that it is closely related to *Bathytoma gratiosa* Suter, 1908, from southern New Zealand, and as *B. gratiosa* is a typical species of *Taranis*, *A. esperanza* evidently belongs in *Taranis* also. The late PA Maxwell (pers. comm.) recognized a New Zealand early Cenozoic species of *Taranis* with a tall, diagonally reticulate, planktotrophic raphitomine protoconch. Bouchet & Warén (1980, figs. 272–273) also illustrated a similar, if slightly shorter protoconch for the Atlantic species *Taranis malmii* (Dall, 1889). *Taranis* therefore belongs in Subfamily Raphitominae, being simply a raphitomine that has lost its radula (Taylor et al. 1993), and the Subfamily Taraninae of Kantor & Sysoev (1989) and Taylor et al. (1993) was synonymized with Raphitominae by Bouchet et al. (2005:256) and other authors. *Taranis* therefore is closely related phylogenetically to *Pleurotomella*, which explains Powell's (1944) association of *T. pulchra* with '*Asperdaphne*'. Material illustrated in the New Caledonian fauna (MNHN 'Turridae group', in preparation) also suggests that many extra-New Zealand species assigned to *Mioawateria* Vella, 1954 are actually species of *Taranis* with a tall, diagonally cancellate, planktotrophic raphitomine protoconch and a wide sutural ramp, and *Mioawateria* is possibly simply a synonym of *Taranis*. Bonfitto & Morassi (2006) proposed the new genus *Acanthodaphne* for *A. sabellii* Bonfitto & Morassi, 2006 (Recent, Gulf of Aden; type species), *A. abbreviata* (Schepman, 1913) (Recent, Indonesia) and *A. pusula* (Laws, 1947) (Early Miocene, Northland, New Zealand), and commented that some species of *Mioawateria* are similar to *Acanthodaphne* species, so the relationships of *Acanthodaphne*, *Mioawateria* and *Taranis* need reconsideration.

In summary, (1) the type species of *Asperdaphne* is a lecithotrophic species of *Tritonoturris*; (2) most other Australian and New Zealand species that have been referred to *Asperdaphne* belong in *Pleurotomella*; (3) some of the other species previously referred to *Asperdaphne* belong in *Taranis*; and (4) many of the other genera previously proposed for Raphitominae similar to *Pleurotomella* (particularly by Powell, Laseron and Shuto) are probably synonyms of *Pleurotomella*, *Neopleurotomoides* or *Taranis*, but require reassessment.

Fleming (1953:226) included a record in his list of molluscs from Pinnacle Sand (OIS 15–14) of 'New genus aff. *Asperdaphne* n. sp.', but examination of the single specimen showed that it belongs in *Neoguraleus* (GS4098, R22/f6425, uppermost 23 cm of Pinnacle Sand in the Castlecliff coastal section, in 'the pinnacles' gully, the only locality where this interval is accessible).

Australian and New Zealand species tentatively referred here to *Pleurotomella* (pending assessment of a possible position in *Neopleurotomoides*) are:

Pleurotomella aculeata (Webster, 1906), Recent, New Zealand.

Pleurotomella aculeola (Hedley, 1915) (Laseron 1954:47, pl. 11, figs. 244, 245), Recent, New South Wales.

Pleurotomella amplecta (Hedley 1922, pl. 54, figs. 171, 172), Recent, Australia.

Pleurotomella balcombensis (Powell 1944, pl. 6, fig. 7), Fyansford Formation, Balcombe Bay, Melbourne, middle Miocene.

Pleurotomella brenchleyi (Angas, 1877) (Laseron 1954:45, pl. 11, figs. 231, 232), Recent, New South Wales.

Pleurotomella buccinoides (Shuto 1983:18, pl. 2, figs. 12, 13, text-fig. 4; proposed in *Tritonoturris*), Recent, Sydney Harbour.

Pleurotomella bullata (Laseron 1954:47, pl. 12, figs. 246, 247), Recent, New South Wales.

Pleurotomella capricornea (Hedley 1922, pl. 54, fig. 173), Recent, E Australia.

Pleurotomella chapplei (Powell 1944:59, pl. 6, fig. 6), Muddy Creek, western Victoria, middle Miocene.

Pleurotomella compacta (Hedley 1922, pl. 55, fig. 174), Recent, Australia.

Pleurotomella contigua (Powell 1944, pl. 6, fig. 8), Fyansford Formation, Altona Bay, Melbourne, middle Miocene.

Pleurotomella cuspidata (Chapple, 1934), Fyansford Formation, Balcombe Bay, Melbourne, middle Miocene.

Pleurotomella expeditionis (Dell, 1956), Recent, New Zealand (Fig. 17A, F).

Pleurotomella hayesiana (Angas, 1877) (Laseron 1954:45, pl. 11, figs. 233, 234), Recent, New South Wales.

Pleurotomella rugosa (Laseron, 1954) (Laseron 1954:46, pl. 11, figs. 235–237), Recent, New South Wales.

Pleurotomella sepulta (Laseron, 1954) (Laseron 1954:46, pl. 11, figs. 238, 239), Recent, New South Wales.

Pleurotomella spicula (Laseron 1954:47, pl. 11, figs. 242, 243), Recent, New South Wales.

Pleurotomella vercoi (G.B. Sowerby III, 1896) (Hedley 1922, pl. 55, figs. 175–176), Recent, Australia.

Pleurotomella n. sp. A and B of Long (1981:46, pl. 7, figs. 8, 9; as *Asperdaphne*), Aldingan (late Eocene), Brown's Creek Clay and Glen Aire Clay, SE Victoria.

Genus ***Onoketoma*** n. gen.

Type species. *Insolentia solitaria* King, 1933, early Nukumaruan Late Pliocene bathyal fauna in Onoke Formation, Palliser Bay, S Wairarapa.

Diagnosis. A genus assigned to the Raphitominae on the basis of its deep, reversed-L-shaped posterior sinus and only very short adapical limb to the sinus, but readily distinguished from all previously named genera of Raphitominae by its low, dome-shaped protoconch of 1.5 smooth, rounded whorls, passing gradually into the teleoconch by the acquisition of axial sculpture; a few distinctive, curved axial ridges are present on the last half-whorl of the protoconch. The spire is moderately tall, gradate, with a relatively narrow, flat, steeply sloping sutural ramp equal in width to the vertical whorl side above the ramp, followed below by a narrowly rounded, smooth peripheral angulation lacking prominent nodules. The posterior (anal) sinus is deeply and evenly concave, widely open, occupying the full width of the sutural ramp, swinging forward only a little adapically to the narrow subsutural cord, but followed below by a long, forward-swinging outer lip, with obvious, fine, steeply oblique growth ridges parallel to the lip. The spiral sculpture consists of many narrow, closely spaced, smooth, convex-crested cords over the entire teleoconch, other than a weakly sculptured sutural ramp; a rounded, smooth subsutural fold is prominent initially, but fades out down the spire to be little more prominent than the other fine spiral cords on the last few whorls. The axial sculpture consists of moderately prominent, evenly rounded, strongly opisthocline folds, inclined forwards at ca 45° to the horizontal, with interspaces each equal in width to one fold, forming low, spirally elongate nodules on the spiral cords where they cross the axial folds. The aperture is simple, unthickened, without a parietal callus or stromboid notch; the anterior end is incomplete on all material, but has a weak, rounded peribasal angulation and contracts only weakly below that, over the neck; the siphonal canal evidently is relatively short.

Remarks. *Onoketoma* n. gen. seems most similar to species of *Pleurotomella* with a lecithotrophic protoconch, but the protoconch is still simpler and smoother than in any similar, previously named Raphitominae. On the teleoconch, its initially prominent subsutural cord, fading out down the spire, its smooth, weakly carinate periphery, its only weakly contracted base, its flat sutural ramp, its almost straight whorl profile between the peripheral and peribasal angulations, and its sculpture dominated by even, closely spaced spiral cords are characters distinguishing *Onoketoma* from *Pleurotomella*. The spiral sculpture is finer and more closely spaced, the axial threads are much less obvious, the teleoconch shape is taller and narrower with a taller spire and a more steeply inclined, flatter sutural ramp, and the axial ribs are more prominent than in *Taranis*.

King (1933:350) had only the incomplete holotype when he proposed '*Insolentia*' *solitaria*. Powell (1942:69) reassigned it to *Comitas* 'without prejudice', as more appropriate than a position in *Insolentia* on the basis of the protoconch. Beu & Maxwell (1990) suggested a position in *Austroturris* Laseron, 1950 because of a general resemblance to the Australian Recent species *Austroturris steira* (Hedley, 1922) (Laseron 1954, pl. 1, figs. 3, 4) and, in particular, *Austrocarina recta* (Hedley, 1903) (Laseron 1954, pl. 4, fig. 88) but I have since examined these species (material in GNS); they are very much smaller and have a much shallower anal sinus than *Onoketoma solitaria*, and any resemblance is superficial. Further material from Palliser Bay has enabled the taxonomic position of *O. solitaria* to be reassessed, although all specimens are a little incomplete. King (1933:350) noted that the folds are inclined to the shoulder angulation at a prominent angle, and it is about 45°in the available material (Fig. 18B, C, G), indicating an unusually long, forward-swinging anterior lip. The deep reversed-L-shaped sinus, with almost no adapical limb but a long anterior limb, seems to indicate a position in subfamily Raphitominae. The entire surface is covered with fine, low, closely spaced, convex-crested spiral cords or threads. All specimens examined have a simple aperture with thin lips, and no columellar or parietal callus, although none has a complete aperture or anterior siphonal canal.

One of the few other conoideans I am aware of that resembles *Onoketoma solitaria* closely is *Plicisyrinx binicostata* Sysoev & Kantor, 1986 (Kantor & Sysoev 2006:217, pl. 109C) but this has a shallower sinus and lacks obvious spiral cords, and was placed in subfamily Cochlespirinae by its authors. The similarity is evidently superficial. It is likely that *Onoketoma solitaria* will be found living in bathyal depths around New Zealand. Recent specimens will allow the subfamilial position to be reassessed using radular characters. Of genera referred previously to the Raphitominae, the nearest in teleoconch characters to *Onoketoma solitaria* is *Fenestrodaphne* Powell, 1944, but I suggest above that this is a synonym of *Taranis* Jeffreys, 1870. *Taranis pulchra* (Powell, 1944) and the similar Recent species *T. tasmanica* differ from *Onoketoma solitaria* in having much weaker axial sculpture, without any axial costae, in their shorter spire, in their shallower posterior sinus, in their more prominent and more widely spaced spiral cords, and in their shorter protoconch, which is 'closely axially costate' all over, with 'two weak spiral keels' (Powell 1944:60), and is distinguished from the teleoconch only by the addition of further spiral cords. This contrasts strongly with the smooth protoconch with a few brephic axial ridges where it joins the teleoconch in *Onoketoma solitaria*, but it is helpful in suggesting a relationship between *Onoketoma* and *Taranis*.

Etymology. From the name of the formation and locality where the type species occurs, Onoke Formation at Lake Onoke, Palliser Bay; combined with 'toma' (abbreviation of *Pleurotoma*), used in the names of many genera of Conoidea. Gender feminine.

Onoketoma solitaria (King, 1933) (Fig. 18B, C, G, H)

Insolentia solitaria King 1933:350, pl. 36, fig. 11.
?*Comitas solitaria*. Powell 1942:60; Fleming 1966:71; Powell 1966:29.
Austroturris(?) *solitaria*. Beu & Maxwell 1990. p. 419; Tucker 2004:918.
'*Insolentia*' *solitaria*. Maxwell 2009:249.

Type material. *Insolentia solitaria*, holotype (Fig. 18B) TM8322, from Onoke Formation, cliffs east of Lake Ferry, which is on Lake Onoke, Palliser Bay, S Wairarapa. The age of the Palliser Bay Pliocene bathyal fauna is accepted as early Nukumaruan because of the occurrence of occasional specimens of *Zygochlamys delicatula*. I am still not aware of any confirmed records of *Z. delicatula* older than Nukumaruan.

Other material examined. **Nukumaruan:** GS15629, R28/f078, cliffs between Lake Ferry and Whangaimoana, Palliser Bay (seven specimens).

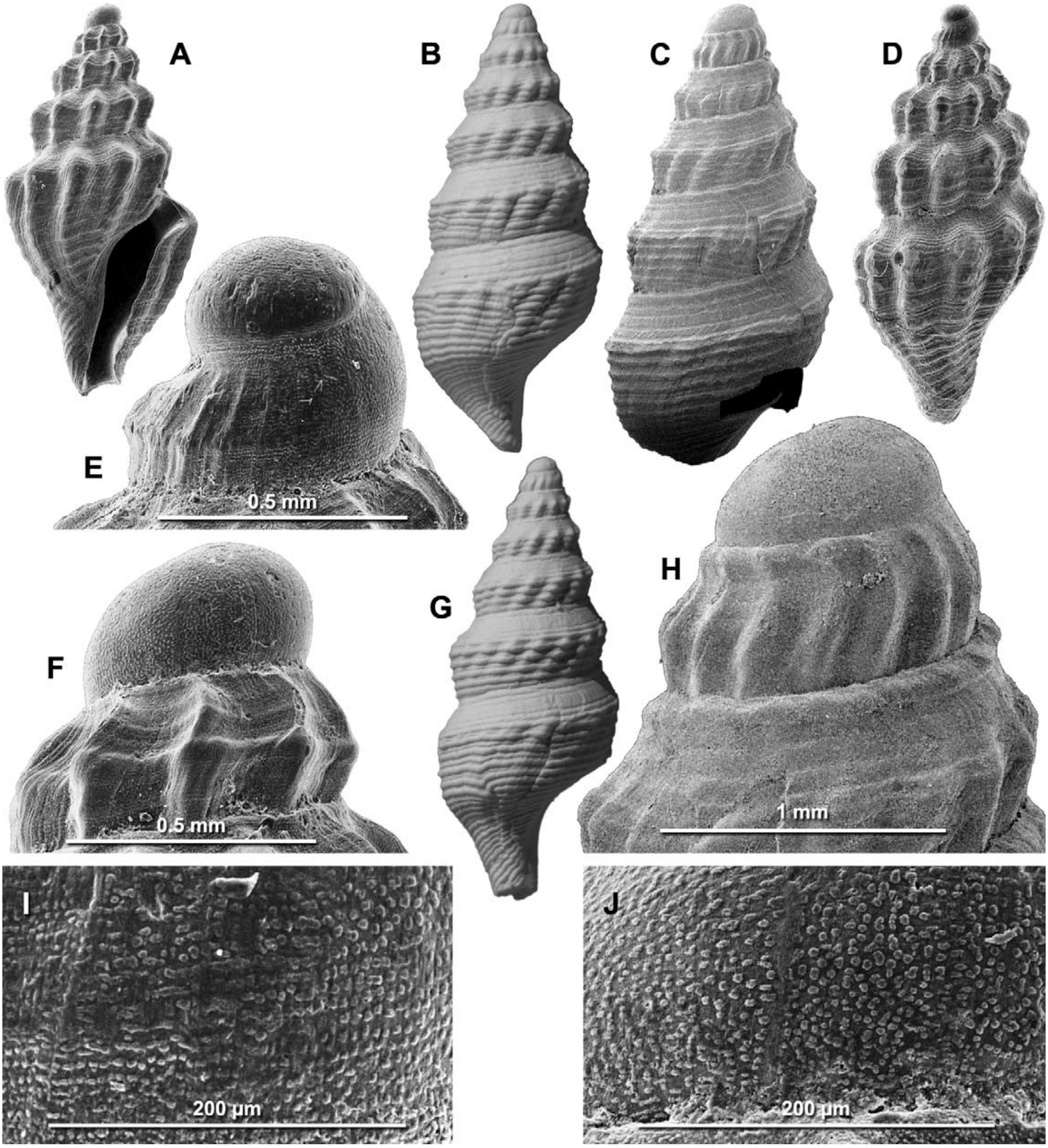

Figure 18 (A,D–F,I,J) *Propebela abnormis* (Hutton), GS10849, V20/f8572, 2 specimens, Devils Elbow Mudstone (late Nukumaruan), top of Devils Elbow hill, Hawke's Bay; A, F, J, height 5.5 mm; F, protoconch of A; J, granules on protoconch in F; D, E, I, height 5.9 mm; E, protoconch of D; I, granules at protoconch termination. (B,C,G,H) *Onoketoma solitaria* (King), type species of *Onoketoma* n. gen., Onoke Formation (early Nukumaruan), cliffs E of Lake Ferry, Palliser Bay; B, holotype, TM8322, H 12.5, D 5.1 mm; C,G,H, GS15629, R28/f078; C, SEM, height 8.1 mm; G, H 12.4, D 4.9 mm; H, protoconch of C.

Distribution. *Onoketoma solitaria* is known so far only from the bathyal Nukumaruan fauna in Onoke Formation at Palliser Bay. However, it seems likely that it eventually will be found in the Recent bathyal fauna of New Zealand, where a large number of conoidean taxa remains unnamed (Spencer et al. 2009:211); few of the Onoke Formation taxa have proven to be distinct from living ones.

Dimensions. Holotype, TM8322: H 12.5, D 5.1 mm; GS15629, cliffs E of Lake Ferry, almost complete specimen: H 12.4, D 4.9 mm; most complete specimen: H 10.9, D 4.1 mm; H (incomplete) 11.0, D 4.5 mm.

Remarks. Little can be added to the comparison under the generic heading above. On a few specimens the axial folds fade out before the last whorl, rendering the teleoconch unusually narrow, but other equally large specimens have axial folds continuing to the end of the last whorl. The fine spiral cords vary from close and even to more widely spaced; those with widely spaced cords appear as if every second one were suppressed, but they intergrade completely with the more common, evenly and finely sculptured shells.

Subfamily Oenopotinae

Genus ***Propebela*** Iredale, 1918

Propebela Iredale 1918:32. Type species (by original designation): *Murex turricula* Montagu, 1803, Pliocene–Recent, NE Atlantic.

Antiguraleus Powell 1942:146. Type species (by original designation): *Antiguraleus otagoensis* Powell, 1942, Pleistocene(?) and Recent, New Zealand (**new synonym**).

Paraguraleus Powell 1944:49. Type species (by original designation): *Guraleus (Paraguraleus) balcombensis* Powell, 1944, middle Miocene, Victoria, Australia. Synonymized with *Antiguraleus* by Powell (1966:106) (**new synonym**).

Lorabela Powell 1951:171. Type species (by original designation): *Bela theilei* Powell, 1951, Recent, Antarctica.

Belalora Powell 1951:171. Type species (by original designation): *Bela pelseneeri* Strebel, 1908, Recent, Antarctica.

Paramarshallena Long 1981:27. Type species (by original designation): *Paramarshallena propebeloides* Long, 1981, late Eocene (Aldingan), Brown's Creek Clay, Johanna coast, S Victoria, Australia (**new synonym**).

Remarks. Beu & Maxwell (1990:328) suggested that *Antiguraleus* Powell, 1942, with a New Zealand type species, is a synonym of *Oenopota* Mörch (1853:37; type species: *Fusus pleurotomarius* Couthouy, 1838 [= *Buccinum pyramidale* Ström, 1788], Recent, Norway to Iceland and Spitzbergen) (Bogdanov 1990, fig. 447; Kantor & Sysoev 2006, pl. 116J). This was based on the similarity in both teleoconch and protoconch characters between New Zealand and Australian species referred to *Antiguraleus* by Powell (1942) and to *Paraguraleus* by Powell (1944), and the North Atlantic species referred to *Oenopota* by Bouchet & Warén (1980:66–75). In particular, the characteristic low, dome-shaped protoconch sculptured with many closely spaced microscopic granules is identical in some species placed in the two genera (Bouchet & Warén 1980, figs. 258–269). Bouchet & Warén (1980:66–67) listed 12 generic names as synonyms of *Oenopota*, including two of Powell's (1951) apparently 'restricted Antarctic' genera: *Propebela* Iredale, 1918; *Turritomella*, *Nodotoma*, *Funitoma*, *Cestoma*, *Granotoma*, *Nematoma*, *Curtitoma*, *Venustoma* and *Canetoma*, all of Bartsch (1941a,b), and *Belalora* and *Lorabela* of Powell (1951). Since then, Bogdanov (1987) has proposed Subfamily Oenopotinae, and (Bogdanov 1990) revised the boreal taxa of this group in detail. Hasegawa et al. in Okutani (2000, pls. 325–327) and Kantor & Sysoev (2006, pls. 112–120) also have illustrated many of the boreal species assigned to these genera, with clear colour photographs. Bogdanov (1990) treated *Oenopota*, *O. (Nodotoma)* Bartsch, 1941, *Curtitoma* Bartsch, 1941, *Granotoma* Bartsch, 1941, *Obesotoma* Bartsch, 1941 and *Propebela* and *P. (Canetoma)* Bartsch, 1941 as distinct generic groups, while listing several of Bartsch's (1941a) genera as synonyms of these. His generic classification was followed by both Hasegawa et al. in Okutani (2000) and Kantor & Sysoev (2006).

Here I adopt *Propebela* Iredale, 1918 as the genus to contain '*Asperdaphne*' *ula* and other Australian and New Zealand species previously referred to *Antiguraleus* Powell, 1942 and *Paraguraleus* Powell, 1944. Most of the remaining possible synonyms in Bouchet and Warén's (1980) list are clearly considered by workers in the relevant regions to be distinct genera. Bogdanov's (1987) Subfamily Oenopotinae tentatively was ranked as a separate subfamily of Conidae by Taylor et al. (1993:166), with genera listed as recognized by Bogdanov (1990), and well as by Bouchet et al. (2005:256), Kantor & Sysoev (2006:221), and Hasegawa (2009:338–350, figs. 350–412) and so is adopted here.

It is clear from Bogdanov's (1990) monograph that the similarities between *Antiguraleus* and some genera closely related to *Oenopota* are not due to convergence; they are closely related phylogenetically, and some are probably congeneric. However, the species assigned by Powell (1942) to *Antiguraleus* are much more closely similar to species assigned by Bogdanov (1990) to *Propebela* Iredale, 1918 than to *Oenopota*. The type species, *Propebela turricula* (Montagu, 1803) (Bogdanov 1990, figs. 368–370, 404D,E; Kantor & Sysoev 2006, pl. 120E,F) is closely similar in all characters to such New Zealand species as *Antiguraleus subtruncatus* (Powell 1942, pl. 8, fig. 1) and *A. abernethyi*, *A. multistriatus* and *A. fusiformis* of Dell (1956a, pl. 20, figs. 200, 202, 206). The many other boreal species assigned to *Propebela* also are very similar, with a shoulder angulation defining a narrow to moderately wide sutural ramp, weak to moderately prominent axial and spiral sculpture as in species previously assigned to *Antiguraleus*, and a short, paucispiral, granulose protoconch, with a few low spiral cords in some species, but not the loosely coiled, strongly spirally sculptured protoconch of *Oenopota*. The supposedly restricted 'Antarctic genera' *Lorabela* and *Belalora* of Powell (1951) also differ from *Propebela* in only trivial protoconch characters, and seem to be further synonyms of *Propebela*, as suggested previously by Bouchet & Warén (1980). The New Zealand and Australian species previously assigned to *Antiguraleus* and *Paraguraleus* (which was synonymized with *Antiguraleus* by Powell 1966:106) seem to me to belong in *Propebela*. These include *Antiguraleus stellatomoides* Shuto (1983:14, pl. 2, figs. 8, 9, text-fig. 3), from off North Reef, Queensland. Shuto (1983) mentioned several similar species (*Mangilia woodwardiana* Melvill, 1917, Persian Gulf; *Pleurotoma angicostata* Reeve, 1844; and *Mangilia misera* Thiele, 1925, Agulhas Bank, South Africa, a species apparently not treated in Kilburn's revisions of South African Conoidea) that may well be further species of the cosmopolitan genus *Propebela*. The distribution of species assigned to *Propebela* seems bipolar at present, but the addition of Shuto's (1983) tropical species suggests that this is the result of the poor knowledge of small tropical deep-water conoideans, which are enormously diverse.

Long (1981:27) proposed *Paramarshallena* for a single Australian Eocene species, *P. propebeloides*. His description of the protoconch ('paucispiral, dome-shaped, of 1.5–2.0 whorls, tip partly immersed, first whorl smooth, second developing orthocline axial ribs before merging into teleoconch') and the illustration of the standard *Propebela* teleoconch show that this is a species of *Propebela*, in the sense interpreted here, assuming that the protoconch actually bears microscopic granules. The small size (H 8.6–13.5 mm), the weak spiral sculpture, the peripheral nodules and the protoconch characters rule out a relationship with *Marshallena*. In my opinion *Paramarshallena* is a further synonym of *Propebela*. Unnamed Japanese *Propebela* species illustrated by Hasegawa (2009, figs. 406–412) with prominent, sharp peripheral nodules closely resemble *Propebela propebeloides* (Long) in all characters.

Australian species of this group will require reassessment. New Zealand species now assigned to *Propebela* Iredale, 1918 are:

Propebela abernethyi (Dell, 1956), Recent.
Propebela abnormis (Hutton, 1885), Mangapanian–Nukumaruan (late Pliocene–early Pleistocene) (Fig. A, D–F, I, J).
Propebela decepta (Powell, 1942), Nukumaruan–Castlecliffian (Pleistocene) (see below) (Fig. B, F, I).
Propebela fenestrata (Powell, 1942), Recent.
Propebela fusiformis (Dell, 1956), Nukumaruan (Pleistocene)–Recent.
Propebela infanda (Webster, 1906), Recent.
Propebela makaraensis (Vella, 1954), Nukumaruan (Pleistocene).
Propebela multistriata (Dell, 1956), Recent.
Propebela munda (Suter, 1909), Recent.
Propebela murrhea (Webster, 1906), Recent.
Propebela otagoensis (Powell, 1942), Castlecliffian (middle Pleistocene)–Recent.
Propebela pedica (Powell, 1942), Recent.
Propebela pulcherrima (Powell, 1942), Recent.
Propebela rishworthi (Vella, 1954), Tongaporutuan (late Miocene).
Propebela rossiana (Powell, 1942), Nukumaruan (Pleistocene)–Recent.
Propebela subtruncata (Powell, 1942), Nukumaruan (Pleistocene)–Recent.
Propebela taranakiensis (Marwick, 1926), Tongaporutuan (late Miocene).
Propebela ula (Watson, 1881) (=*depressipira* Beu), Nukumaruan (Pleistocene)–Recent (see below).

Wanganui Basin Castlecliffian records of *Propebela* (as *Antiguraleus*) by Fleming (1953:219, 226, 230) and in the GNS reference collection are: *Antiguraleus* n. sp. aff. *abnormis*, Lower Castlecliff Shellbed (OIS 15; GS4104, R22/f6518), *A*. cf. *abnormis*, Pinnacle Sand (OIS 14; GS4023, R22/f6361), *Antiguraleus* n. sp., uppermost Pinnacle Sand (GS4098, R22/f6425), and *Antiguraleus* n. sp., Tainui Shellbed (OIS 13; GS4013, R22/f6353). *Antiguraleus* is not listed in the fauna from Kupe Fm (OIS 17), but a specimen is present in GS4118, R22/f6438, from the bivalve shellbed member. All specimens (only one in each collection) are from the Castlecliff coastal section. They differ from *Propebela abnormis* (Fig. A, D–F, I, J) in their taller and narrower shape and straighter outlines, lacking the strongly outward-inclined outer lip and wide sutural ramp of *P. abnormis*, and are more nearly similar to *P. decepta*. It is clear that although *P. abnormis* is limited to Nukumaruan rocks, species similar to *P. decepta* are not. The common Hawke's Bay Nukumaruan species *P. abnormis* and *P. decepta* are illustrated here (Figs. A, D–F, I, J, B, F, I), although they are shorter and more heavily sculptured than most other New Zealand species referred to *Propebela*.

Propebela ula (Watson, 1881)

Pleurotoma (Drillia) ula Watson 1881:413.
Pleurotoma (Bela) ula. Watson 1886:321, pl. 22, fig. 1.
Mangilia ula. Suter 1899b:71.
Bela ula. Suter 1913:485, pl. 21, fig. 12 (with further synonymy).
Asperdaphne ula. Powell 1942:162; Dell 1956a:136, pl. 20, fig. 207; Dell 1963a:176, pl. 2, fig. 9; Powell 1979:244, fig. 56.5; Spencer et al. 2009:209.
Mioawateria depressispira Beu 1969:494, fig. 7 (**new synonym**).
Antiguraleus(?) *depressispirus*. Maxwell 1988:68; Beu & Maxwell 1990:420; Maxwell 2009:248.

Type material. *Pleurotoma ula*, holotype BMNH 1887.2.9.1004, from HMS '*Challenger*' Sta. 169, off East Cape, New Zealand, in 1280 m (illustrated by Dell, 1963a, fig. 9). *Mioawateria depressispira*, holotype in Geology Department, Victoria University of Wellington, VM349, from locality V1901, S28/f6884, sea cliffs E of mouth of Whangaimoana Stream, Palliser Bay, early Nukumaruan.

Other material examined. **Opoitian:** GS1567, W19/f7516, Waiau River at junction with Pakihiwi Stream, inland from Wairoa, N Hawke's Bay (the locality from where *Acirsa* cf. *cookiana* is recorded, above) (one incomplete, similar to *P. ula* but with less sharply contracted whorls below the sutural ramp). **Nukumaruan:** the only other fossil specimen is from the same locality as the holotype of *M. depressipira*, in the collection of D Cowe, Greytown (Maxwell 1988:67). **Recent**: NMNZ M.12832, 548 m, E of Taiaroa Head, E Otago (three; labelled 'compared with type'); NMNZ M.9149, '*Alert*' stn 54–17, 475–640 m, ENE of Taiaroa Head, E Otago (one).

Distribution. Propebela ula occurs at present along the E coast of New Zealand, where it is recorded only from the E Otago canyons to East Cape, in 475–1280 m. Fossils are recorded only from the Palliser Bay Nukumaruan bathyal fauna, where they suggest a greater depth of deposition (>500 m) than previously thought. A possible Opoitian relative suggests that this group has occupied bathyal environments off New Zealand since early Pliocene time.

Dimensions. Pleurotoma ula, holotype: H 5.5, D 3.0 mm; *Mioawateria depressispira*, holotype: H 4.6, D 3.7 mm (Beu 1969:495); NMNZ M.12832, off Taiaroa Head: H 5.9, D 3.4 mm; H 5.9, D 3.3 mm; M.9149, off Taiaroa Head: H 4.8, D 2.8 mm.

Remarks. '*Asperdaphne*' *ula*, referred to *Asperdaphne* (that is, *Pleurotomella*) by Powell (1942, 1966), seems better referred to *Propebela*. The protoconch agrees with that of *Propebela*. '*Asperdaphne*' *ula* has a shallow but obviously U-shaped sinus with its apex in the centre of the sutural ramp, and clearly does not have the deep reversed-L-shaped sinus of *Pleurotomella*.

The small, short, strongly keeled shell from Palliser Bay named *Mioawateria depressipsira* by me (Beu 1969:494) belongs in *Propebela* and seems likely to be a synonym of *Propebela ula*. Maxwell (1988:67) and Beu & Maxwell (1990:420) recognized that the lack of a raphitomine protoconch and the absence of a prominent moniliform subsutural fold rule out a position in *Mioawateria* for '*M*'. *depressispira*, and assigned it to *Antiguraleus*. The holotype of *P. ula* (Dell 1963a, pl. 2, fig. 9) and other, shorter specimens (Dell 1956b:228, fig. 207) seem to differ from *A. depressispira* only in being slightly taller, and height is obviously variable in this species.

Genus *Liracraea* Odhner, 1924

Liracraea Odhner 1924:44. Type species (by original designation): *Clathurella epentroma* Murdoch, 1904, Recent, southern New Zealand.

Remarks. The type species of *Oenopota*, *O. pyramidale* (Ström, 1788) (Recent, Arctic Ocean), has a loosely coiled, paucispiral protoconch with three or four prominent, angling spiral keels (Bogdanov 1990, figs. 397D,E, 399A,B) and much more closely resembles the New Zealand genus *Liracraea* Odhner, 1924 than it does *Propebela*. New Zealand species assigned to *Liracraea* reach only 7–9 mm in height, whereas the specimens of *O. pyramidalis* illustrated by Bogdanov (1990, figs. 191–208) are 10.3–17.7 mm high. Several of the species assigned to *Liracraea* also are narrower, have a slightly shallower anal sinus, have straighter and more prominent axial ridges, and have a shorter anterior siphonal canal than most *Oenopota* species. However, *O. pingelii* (Möller, 1842) (Arctic Ocean; Bogdanov 1990, figs. 209, 210; Kantor & Sysoev 2006, pl. 116F; Figs. 19A, D, 20A–C) resembles *Liracraea* species more closely in shape, sculpture and protoconch sculpture, and Bogdanov's figured specimens are only 10.4–10.7 mm high (illustrated specimen: H 7.5, D 3.0 mm). SEM comparison of specimens of *Liracraea odhneri* Powell, 1942 (Fig. 19C, G) and *L. subantarctica* Powell, 1942 (Fig. 19E, H, J) with *O. pingelii* (Figs. 19A, D, 20A–C) revealed minor differences. *Liracraea* species have more prominent, regular spiral cords on the protoconch than in

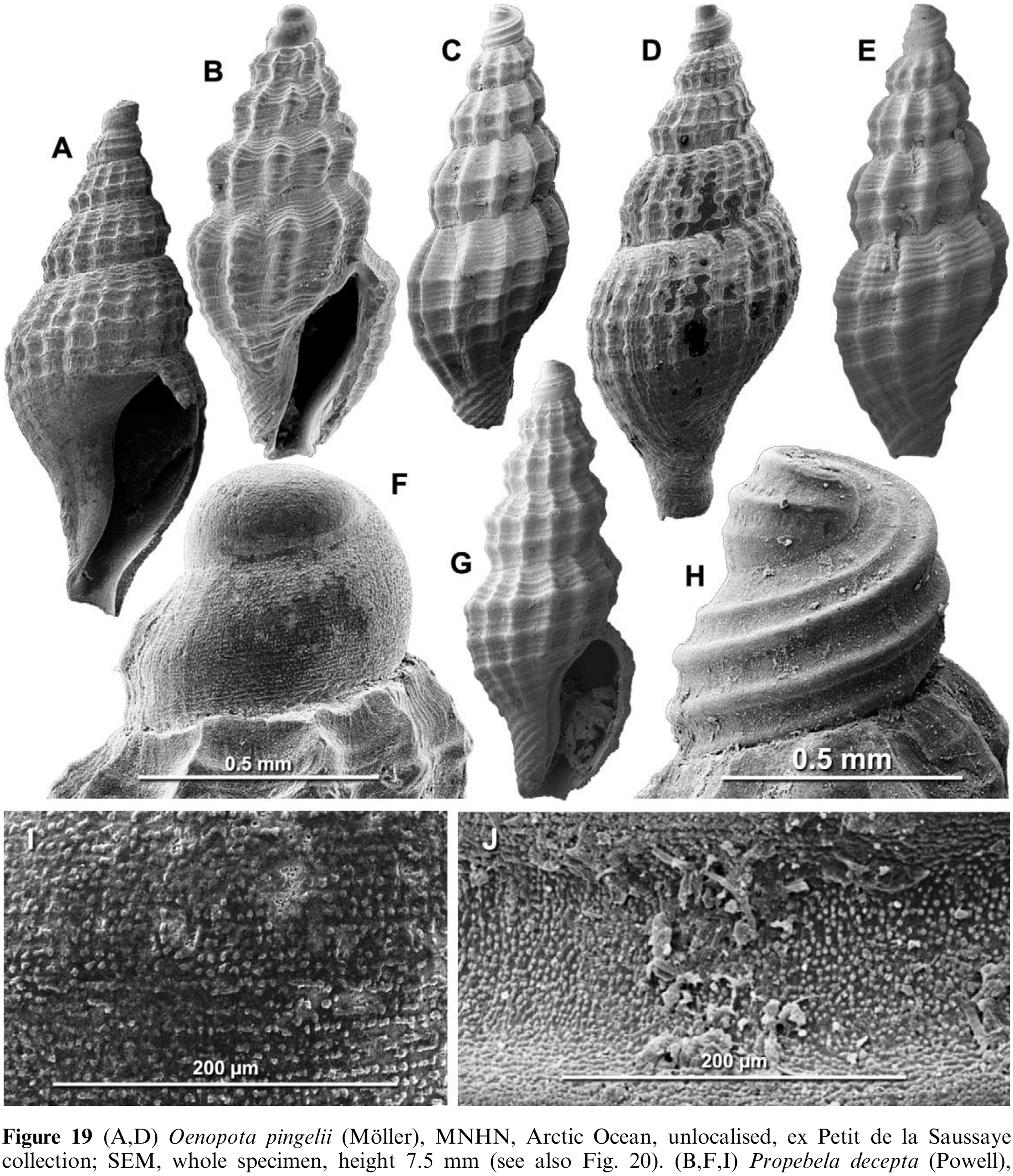

Figure 19 (A,D) *Oenopota pingelii* (Möller), MNHN, Arctic Ocean, unlocalised, ex Petit de la Saussaye collection; SEM, whole specimen, height 7.5 mm (see also Fig. 20). (B,F,I) *Propebela decepta* (Powell), GS10858, U22/f9588, Ashcott Road, W of Waipukurau, Hawke's Bay, Nukumaruan; B, whole specimen, height 6.5 mm; F, protoconch of B; I, granules on protoconch. (C,H,J) *Liracraea subantarctica* Powell, RM2835, Carnley Harbour, Auckland Islands; C, height 6.2 mm; H, protoconch of C; J, granules between 2 spiral cords in H. (E,G) *Liracraea odhneri* Powell, 2 specimens, RM5585, Portobello sta. Mu70–45, 540–490 m, Papanui Canyon, off Otago Peninsula, RV "*Munida*"; E, height 6.6 mm; G, height 6.4 mm.

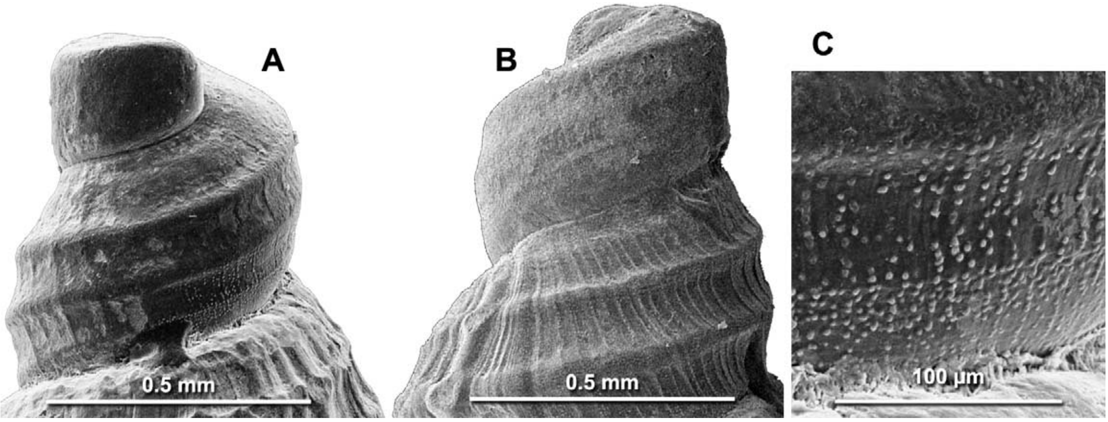

Figure 20 *Oenopota pingelii* (Möller), MNHN, Arctic Ocean, unlocalised, ex Petit de la Saussaye collection, SEM; specimen in Figs. 19A,D; (A,B) protoconch; (C) granules on protoconch in B.

O. pingelii. Also, the protoconch microsculpture of minute granules looks similar on the two at first sight, but the granules of *O. pingelii* are arranged in regular axial lines, whereas those of *Liracraea* species are uniformly and evenly distributed, or have a tendency to form spiral rows. The protoconch is one whorl taller, and so narrower, in *O. pingelii* than in *Liracraea*, and on the last protoconch whorl of *O. pingelii* the lines of granules develop into regular, narrow, relatively widely spaced, granulous axial ridges that are not present on *Liracraea* species. Despite these differences, comparison with the protoconchs of the other species assigned to *Oenopota* by Bogdanov (1990) demonstrated that *Liracraea* probably intergrades with *Oenopota*. Several *Oenopota* species have few, prominent spiral cords on a loosely coiled protoconch closely similar to that of species assigned to *Liracraea* (Bogdanov 1990, figs. 395G–E, *O. declivis* (Lovén, 1846); fig. 396, *O. elegans* (Möller, 1842); fig. 397A,B, *O. harpa* (Dall, 1884); fig. 398, *O. impressa* (Mörch, 1869); fig. 399A,B, *O. pyramidalis*). Several of these have the minute surface granules evenly and uniformly arranged, as in New Zealand species assigned to *Liracraea*, and whether there are axial ridges on the last whorl of the protoconch also differs from species to species. *Liracraea* seems likely to be a synonym of *Oenopota*.

When proposing *Liracraea*, Odhner (1924:44) did not compare it with *Oenopota*, although he must have been familiar with it. Presumably this implies that he did not consider a close phylogenetic relationship between New Zealand and Arctic Ocean species to be possible. The apparently bipolar distribution is still a significant obstacle to the adoption of *Oenopota* in New Zealand, but it is possible that *Oenopota* species remain to be recognized between the Arctic/boreal and New Zealand species. However, it seems best not to adopt *Oenopota* for New Zealand species until their position can be checked by comparison of DNA sequences.

Clade Heterobranchia

Family Aplustridae

Genus ***Hydatina*** Schumacher, 1817

Hydatina Schumacher 1817:55, 186. Type species (by subsequent designation, Gray 1847:162): *Hydatina filosa* Schumacher, 1817 (= *Bulla physis* Linné, 1758), Pleistocene & Recent, world-wide tropics.

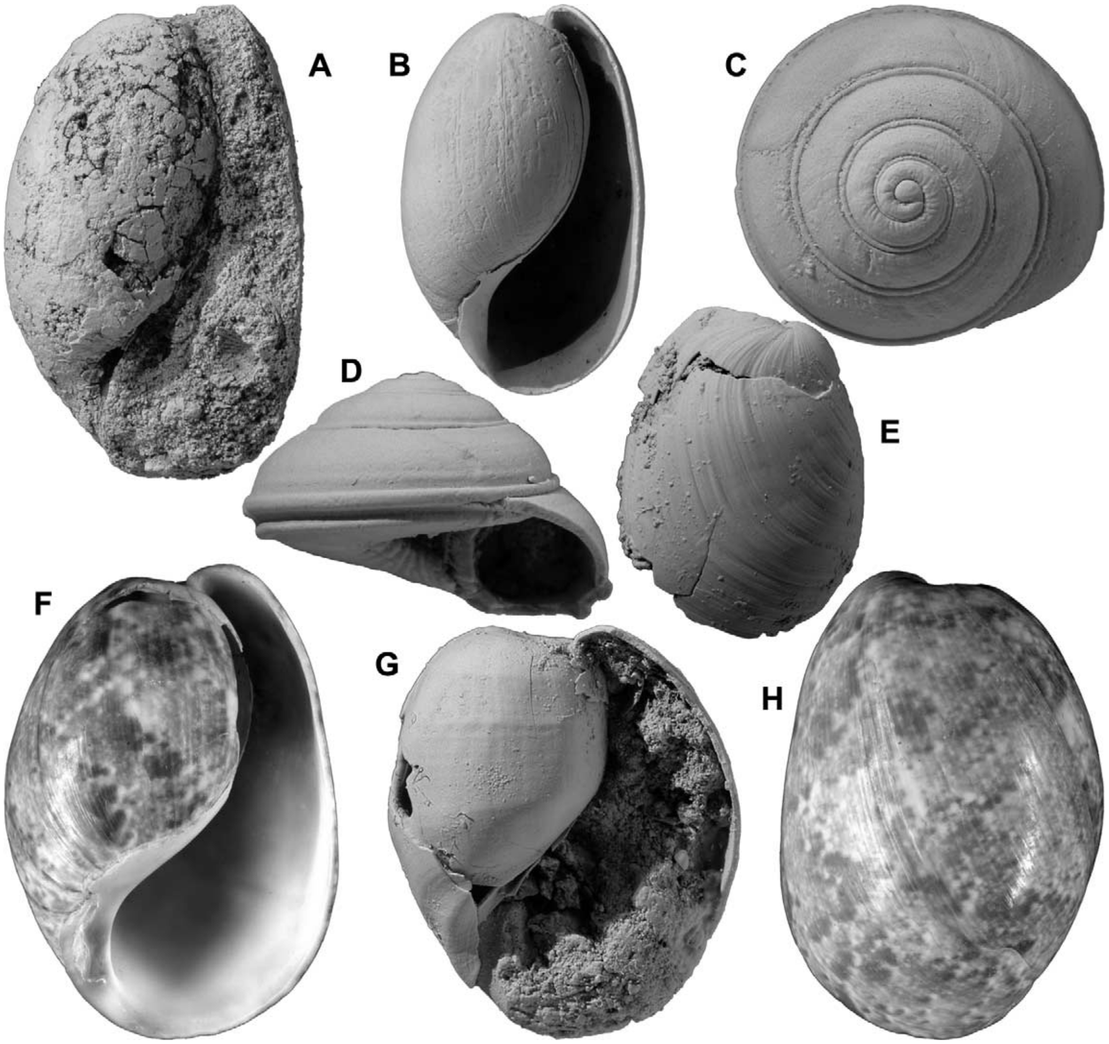

Figure 21 (A,B) *Bulla quoyii* Gray; A, internal mould, GS13743, Y14/f022, farm road cutting at top of Te Piki Member (Haweran, OIS 7), Te Piki, near East Cape; H 41.8, D 26.6 mm; B, RM90, Recent, Mission Bay, Auckland; H 34.5, D 22.1 mm. (C,D) *Philippia lutea* (Lamarck), GS1932 re-collection, U21/f9488, Okauawa Stream bridge, Kereru Road, central Hawke's Bay, late Nukumaruan; dorsal and apertural views, H 8.3, D 12.3 mm. (E) *Philine tepikia* Rudman, GS14777, O06/f087, Waiparera church, NW Hokianga Harbour, Northland, Haweran, OIS 7; H 14.7, D 10.8 mm. (F,H) *Bulla mabillei* Locard, lectotype of *Bulla australis* Férussac, MNHN moll. 20975, "Port Jackson" (unlocalised; France?); H 41.1, D 29.4 mm (MNHN photos). (G) *Hydatina physis* (Linné), GS14778, O06/f064, W side Te Rewa Point, NW shore Hokianga Harbour, Northland, Haweran (OIS 7); H 22.2, D 18.8 mm.

Aplustrum Schumacher 1817:63, 108. Type species (by subsequent designation, Gray 1847:162, as *Amplustrum*): *Bulla amplustre* Linné, 1758, Recent, Indo-West Pacific (synonym according to Rudman 1972b:135).

Hydatoria Iredale 1936:334. Type species (by original designation, Iredale 1936:338): *Bulla cinctoria* Perry, 1811 (= *Hydatina zonata* (Lightfoot, 1886); = *Bulla physis* Linné, 1758), Recent, Indo-West Pacific (synonym according to Rudman 1972b:136) (unavailable, no distinction from related taxa; ICZN Article 13.1).

Remarks. Rudman (1972b) synonymized *Aplustrum* Schumacher, 1817 with *Hydatina* Schumacher, 1817, using *Hydatina* as the senior synonym, a first reviser's action. Bouchet et al. (2005) showed that Aplustridae Gray, 1847 is a senior synonym of Hydatinidae Pilsbry, 1895.

Hydatina physis (Linné, 1758) (Fig. 21G)

Bulla physis Linné 1758:727.
Bulla vesicaria Lightfoot 1786:136.
Bulla velum Gmelin 1791:3433.
Bulla fasciata Bruguière 1792:380 (senior synonym of *H. stroemfelti* Odhner, 1932; Nordsieck & Garcia-Talavera 1979:174); junior secondary homonym of *Bulla fasciata* (Müller, 1776), included in *Bulla* by Gmelin (1791:3433).
Bulla cinctoria Perry 1811, pl. 40.
Hydatina filosa Schumacher 1817:186.
Bulla (Hydatina) straminea Menke 1853:136.
Hydatina physis. Pilsbry 1895:387, pl. 45, figs. 14–17 (with further synonymy); Powell 1924:284; Habe 1950:17, text-fig. 1; Kira 1962:115, pl. 40, fig. 17; Powell 1964:18; Kuroda et al. 1971:284, pl. 64, fig. 17; Rudman 1972b:122, figs. 1–14, pl. 1A,B,H; Powell 1976a:159; Powell 1979:270, pl. 54, fig. 6; Nordsieck & Garcia-Talavera 1979:174, pl. 44, fig. 30; Kay 1979:420, figs. 131A, 135H; Bosch et al. 1995:180, fig. 830; Voskuil 1995:32, pl. 1, figs. 1–4; Spencer & Willan 1996:33; Hasegawa et al. in Okutani 2000:737, pl. 367, fig. 1; Ardovini & Cossignani 2004:243, three figs; Spencer et al. 2009:212; Maxwell 2009:251.
Hydatina stroemfelti Odhner 1932:26, pl. 1, figs. 21–23; Duffus & Johnston 1969:36.
Hydatina vesicaria. Bartsch 1940:192; Abbott 1954:276, pl. 13q; Warmke & Abbott 1961:141, pl. 27a; Rehder 1967:23; Abbott 1974:314, pl. 10, fig. 3938; Voskuil 1995:33, pl. 1, figs. 5, 6.
Hydatina physis forma *fasciata*. Nordsieck & Garcia-Talavera 1979:174, pl. 44, fig. 31.

Type material. Investigating the type material and synonymy of this world-wide tropical opisthobranch is beyond the scope of this paper. A synonymy up until 1895 was provided by Pilsbry (1895:387), and Rudman (1972b, 2004) revised the world-wide synonymy of the genus *Hydatina* and of *H. physis* (Linné, 1758), although he did not provide a detailed chresonymy, and neither he nor any other author has provided information on the type material. Syntype(s) of *Bulla physis* apparently remain in Linné's collection, housed by the Linnean Society of London, as it is not in Dance's (1967:21–22) list of species not represented. The type material of *H. stroemfelti* Odhner is in the Swedish Natural History Museum, Stockholm (SMNHI 4195; Sandberg & Warén 1993:129), and probably no type material exists for any of the other names in the synonymy.

Other material examined. **Haweran:** *Akera-Diala-Anadara* locality, Te Rewa Pt, N Hokianga Harbour, Northland, OIS 7 (GS14778, O06/f064, one; Fig. 21G).

Distribution. OIS 7, Hokianga Harbour; Recent. An uncommon straggler to NE New Zealand harbours during summer months; throughout the tropical Indo-West Pacific and Atlantic.

Dimensions. GS14778, Te Rewa Point, Hokianga: H 22.2, D 18.8 mm; RM2902, Recent, Takou Bay, Northland: H 26.2, D 21.0 mm; NMNZ M.95230, Rangiputa Beach, Northland, August 1988: H 33.2, D 24.3 mm; H 38.4, D 31.1 mm; H 43.1, D 34.3 mm; M.95229, as above, after storm, July 1988: H 56.4, D 47.0 mm; H 54.7, D 46.8 mm.

Remarks. *Hydatina physis* is a large, very thin-shelled bullomorph opisthobranch found 'world-wide ... in warm seas' (Rudman 1972b; Powell

1979:270; although there appear to be no eastern Pacific records). Large adult shells reach at least 57 mm high and 47 mm wide (Powell 1979:270; and above). Living specimens have been collected in northeastern New Zealand sporadically over many years. They were reported first by Powell (1924) and have since been collected in Parengarenga Harbour, in the far north of the North Island, in some numbers (Powell 1964, 1976a, 1979). Specimens have also been found further south, at Houhoura Harbour, Whangaroa Harbour, Takou Bay and Rangiputa Beach, to as far south as Tryphena and Port Fitzroy, Great Barrier Island, east of Auckland. The shell is ovate, simple and virtually smooth, with a simple, pear-shaped aperture and wide, evenly rounded anterior end, no umbilicus, a thin outer lip, and a slightly sunken, narrow spire with the posterior surface of the spire whorls revealed. It is easily distinguished from *Bulla* species by the much thinner and more fragile shell, by the shorter and wider shape with a wider aperture, and by the earlier whorls revealed in the spire apex, with the protoconch visible, rather than the deep, narrow, apical tube of *Bulla*. Recent specimens have a striking colour pattern of narrow, dark brown spiral lines on a whitish background, although Rudman (2004) emphasized the variability of the colour pattern.

Miguel Griffin (Museu de La Plata, Argentina) and I collected a reasonably complete fossil specimen of *Hydatina physis* at Te Rewa Point, northern Hokianga Harbour (OIS 7). The shape is within the range of variation of Recent specimens. The specimen bears several very low, indistinct, widely spaced, spiral angulations. Rudman (2004; W Rudman AMS pers. comm. 16 November 2007) reported that *H. zonata* (Lightfoot, 1786) (Powell 1979:270, pl. 54, fig. 7, as the synonym *H. albocincta* (van der Hoeven, 1839); Spencer et al. 2009:212) (also = *H. velum* (Gmelin, 1791) and *H. cinctoria* (Perry, 1811)), with fewer, wider spiral colour bands, is probably merely a colour form of *H. physis* (see also illustrations in Voskuil 1995:34, pl. 1, figs. 1–10; figs. 7, 8 identified as *H. albocincta*, figs. 9, 10 identified as *H. zonata*, figs. 5, 6 identified as *H. vesicaria*). The exterior animal characters and internal anatomy are indistinguishable, and the pattern of spiral colour bands on the shell is highly variable. The smaller species *H. amplustre* (Linné, 1758) differs in its slightly thicker, stronger shell and fewer colour bands, which include two wide pink bands outlined in black on most specimens (Rudman 1972b), but again the animal characters are very similar. The more widely black-banded form from the Marquesas Islands named *H. exquisita* by Voskuil (1995: 37, pl. 1, figs. 13, 14) is probably a colour form of *H. amplustre*.

Hydatina species have an annual life-cycle and a planktotrophic larval stage, like *Akera soluta* (Gmelin, 1791) (Burn & Thompson 1998; Willan 1998), which also occurs abundantly in the outcrop between Te Rewa Point and Waiparera (Beu 2004). They are able to metamorphose and settle in an area during favourable conditions, breed, and then not necessarily be seen again in that area for some years. Presumably *Hydatina physis* arrived and thrived at several times in sheltered northern North Island harbours during warm interglacial periods, as it still does today. Powell (1964, 1976a, 1979) suggested that the New Zealand occurrences are pseudopopulations recruited from the tropical southwest Pacific, but not breeding in New Zealand. However, the large numbers of large shells reported in New Zealand on some occasions suggest that temporary breeding populations are likely in New Zealand at present, although the two possibilities would be indistinguishable in the fossil record (25 living specimens at Takou Bay, Northland; Powell [1964, 1976a]; 17 from Rangiputa Beach in NMNZ M.95230).

Family Architectonicidae

Genus ***Philippia*** Gray, 1847

Philippia Gray 1847:146. Type species (by monotypy): *Solarium luteum* Lamarck, 1822, Recent, Indo-West Pacific (mainly S Australia and N New Zealand; Bieler 1993:113, fig. 89).

Philippia lutea (Lamarck, 1822) (Fig. 21C, D)

Solarium luteum Lamarck 1822b:5; Deshayes 1830 (in 1830–1832):159; Kiener 1838–1839:9, pl. 4, fig. 9b (in part; not fig. 9a, = *Philippia hybrida* (Linné, 1758); Bieler 1993:110); Delessert 1841, pl. 24, fig. 2a–c; Deshayes 1843:100; Philippi 1853:9, 31, pl. 1, figs. 10, 11 (in part; not pl. 4, fig. 11, = *P. hybrida*; Bieler 1993:110); Reeve 1864, pl. 3, fig. 14; Suter in Hutton 1904:79; Bieler & Petit 2005:48.

Philippia lutea. Gray 1847:146; H Adams & A Adams 1858:243, pl. 25, figs. 8–8b; Angas 1867:201; Hutton 1878:24; Hutton 1880:70; Finlay 1926b:401; Thiele 1929:184, fig. 170; Cotton & Godfrey 1933:72, pl. 1, fig. 1; Powell 1937:75, pl. 9, fig. 35; Wenz 1939:670, fig. 1911; Powell 1946a:77, pl. 9, fig. 35; Powell 1958a:97, pl. 9, fig. 35; Iredale & McMichael 1962:68; Macpherson & Gabriel 1962:100, fig. 126; Powell 1962:89, pl. 9, fig. 35; Beu 1970a:128; Powell 1976b:107, pl. 16, fig. 35; Beu in Suggate et al. 1978:724, fig. 11.13.6; Powell 1979:248, pl. 48, fig. 2; Beu & Maxwell 1990:422; Bieler 1993:110, figs. 86–89; Spencer & Willan 1996:31; Spencer et al. 2009:211; Maxwell 2009:249.

Solarium luteum var. *novaehollandiae* Philippi 1853:41.

Solarium (Philippia) luteum. Chenu 1859:233, fig. 1355; Hanley 1863:237, pl. 253, figs. 53, 54 (in part; not fig. 52, = *P. hybrida*; Bieler 1993:111); Marshall 1887:16, pl. 5, fig. 71, 72; Cooper 1899:137.

Architectonica (Philippia) lutea. Suter 1913:316, pl. 46 (1915), fig. 4.

Architectonica lutea. May 1921:102; May 1923:97, pl. 46, fig. 1; Bucknill, 1924:56, pl. 7, fig. 20.

Philippia (Philippia) lutea. Robertson 1973:37; Garrard 1977:509, 525, fig. 14 (operculum), pl. 5, figs. 13–18; Boss & Merrill 1984:359, pl. 57, fig. 1; Bieler 1985:236, pl. 2, fig. 8 (lectotype).

Philippia hybrida. Hinton 1978, pl. 10, fig. 10 (not *Trochus hybridus* Linné, 1758).

Type material. *Solarium luteum*, lectotype (designated by Bieler 1985:236; Bieler 1993, fig. 86) and five paralectotypes MHNG 1095/41, 'Habite les mers de la Nouvelle Hollande' (Australia); not seen. Iredale & McMichael (1962:3, 68) designated the type locality as 'Sydney, N. S. W.'. Bieler (1993) did not know the location of any type material of *S. luteum* var. *novaehollandiae* Philippi, from 'Neuholland?' (Australia); it is likely to be in Philippi's collection in Museu Nacional de Historia Natural, Santiago, Chile (not accessible for consultation).

Other material examined. **Nukumaruan**: Mangatahi River, on NW side of Okauawa Stream junction, Kereru Road, SW of Maraekakaho, central Hawke's Bay (GS1932 re-collection, U21/f9488; one; Fig. 21C, D); Devils Elbow Mudstone, cutting at top of Devils Elbow hill, Napier-Wairoa Highway, N of Napier (GS10849, V20/f8572; one). **Recent**: rather uncommon throughout northern New Zealand (44 lots examined in NMNZ and eight in GNS), from the Three Kings Islands (northernmost: NMNZ, M.117094, S end of North East Island, 34°8.30′S, 172°10′E, one specimen; M.93986, reef between Great Island and Farmer Rocks, 34°9.00′S, 172°10′E; three) to as far south as Mount Maunganui, Bay of Plenty (GNS RM276, two) and Boulder Bay, Motuhora Island, Bay of Plenty (NMNZ, M.33021, M.33071, 37°51.70′S, 176°57.60′E; two) and East Cape (NMNZ, M.117625; three); NIWA stn B619, 44°42′S, 167°33.25′E, off Four-Mile Point, N of entrance to Sutherland Sound, Fiordland, 19 October 1962 (seven live-collected); NMNZ M.160306, 44°55.50′S, 167°23.50′E, middle of George Sound, Fiordland, 37 m, 14 February 1987 (one fragment).

Distribution. *Philippia lutea* occurs moderately commonly around southern Australia (Western Australia, N to Vansittart Bay, 14°03′S; around southern Australia and Tasmania, to Woolgoolga, northern New South Wales, 30°07′S; Garrard 1977:526) and in the NE North Island warm province of New Zealand, as far south as the E Bay of Plenty. Bieler (1993:110–114) discussed the characters, variation, and distribution of *P. lutea*, and thought records from the Philippines and Howland Island require confirmation. *P. japonica* (Pilsbry & Stearns in Pilsbry, 1895) (Bieler 1993:114, fig. 90) is extremely similar, differing only in having a slightly smaller protoconch (averaging 0.81 mm in diameter, rather than 0.94 mm in *P. lutea*), and it is possible that *P. lutea* is a poorly understood, wide-ranging, western Pacific species occurring from Japan to New Zealand, although rare between the latitudinal extremes, and varying clinally in protoconch size. Such a distribution would be similar to that of the planktotrophic tonnoideans that occur in both Japan and Australia–New Zealand, but are rare in the tropics in between (*Charonia lampas* (Linné, 1758); *Monoplex parthenopeus* (von Salis Marschlins, 1793); *Monoplex exaratus* (Reeve, 1844); Beu 2010).

Dimensions. NIWA stn B619, off entrance to Sutherland Sound, Fiordland: H 15.0, D 18.0 mm (H:D 0.83); H 15.2, D 16.8 mm (H:D 0.90); H 13.3, D 15.8 mm (H:D 0.85); H 12.0, D 15.8 mm (H:D 0.76); H 10.9, D 13.6 mm (H:D 0.80); H 11.9, D 13.4 mm (H:D 0.89); H 9.9, D 13.1 mm (H:D 0.76); GNS WM15278, Collaroy Beach, Narrabeen, Sydney, NSW: H 10.5, D 12.5 mm (H:D 0.84); H 7.6, D 10.8 mm (H:D 0.70); GNS RM3907, Ocean Beach, Whangarei Heads, Northland: H 8.7, D 12.3 mm (H:D 0.71); RM5122, Otahei Bay, Bay of Islands: H 10.3, D 12.5 mm (H:D 0.82); RM5350, north head, Parengarenga Harbour: H 9.0, D 12.1 mm (H:D 0.74); GS1932, Kereru Road: H 8.3, D 12.3 mm (H:D 0.67); GS10846, Devils Elbow: H 9.3, D (incomplete) 13.4 mm (H:D 0.75).

Remarks. A sample of seven specimens of *Philippia lutea* in NIWA stn B619, off Sutherland Sound, Fiordland, is unusual for the large size. Garrard (1977:525) recorded 'fully grown' Australian specimens reaching H 10, D 15 mm, whereas the Fiordland specimens reach H 15.2, D 18.0 mm. They also have tall spires (H:D 0.76–0.90) and very pale coloration. Specimens from northern New Zealand are pale yellow ochre to reddish tan in colour, apart from the prominent, bright, short, closely spaced, alternating yellow and dark brown dashes around the two peripheral spiral cords. The Fiordland specimens also all contain the dried animal, and apparently have been preserved in ethanol for some time, so the shells possibly have faded. They also were collected from an unusually great depth for the species (92 m), as Garrard (1977:526) recorded the greatest depth as 82 m. They have 35–45 narrow colour bands around the peripheral cords of the last whorl, the main character stated by Bieler (1993:113) to distinguish *P. lutea* (with 23–52 colour bands) from the Atlantic–Mediterranean species *P. hybrida* (with 19–26 colour bands; Melone & Taviani 1984:166, fig. 25; Ardovini & Cossignani 2004:232, lower right two figs). Garrard (1977:526) described New South Wales specimens as 'invariably elevated conic and coloured yellow ochre or light buff, a few specimens light grey', with H:D 0.7–0.8. In contrast, Victorian specimens are predominantly pale to dark grey, with H:D 0.6–0.7, South Australian specimens have a reddish tinge and a more depressed spire, and Western Australian specimens are still more depressed (H:D 0.45–0.55) and are predominantly pale to deep blackish red. Recent specimens from northern New Zealand are intermediate in spire height (H:D 0.71–0.82), whereas the two known New Zealand fossils have rather low spires (H:D 0.67–0.75). In view of the range of variation in Australian specimens described by Garrard (1977), it is likely that the Fiordland specimens were recruited as planktotrophic larvae from a New South Wales population.

The specimen recorded by me (Beu 1970a:128; Beu in Suggate et al. 1978:724, figs. 11.13.6; Fig. C, D) as *Philippia lutea* from late Pliocene (late Nukumaruan) rocks of central Hawke's Bay has been compared again with Recent specimens of *P. lutea*, and with the one other incomplete but slightly larger fossil specimen collected since, from

Devils Elbow Mudstone at the top of Devils Elbow hill. These specimens have a rather depressed spire for *P. lutea* and are weakly sculptured, with almost completely smooth upper whorl surfaces, but display the two almost equally prominent, almost smooth peripheral spiral cords characteristic of *Philippia*. They can be matched among Recent Northland specimens of *Philippia lutea*. Their occurrence presumably resulted from the transport of planktotrophic larvae southwards from the present range in Northland during warm Nukumaruan interglacial periods. Although the geographical subdivision of colour and spire height around Australia indicates some restriction of genetic exchange, Architectonicidae are among the most wide-ranging of gastropods, well-known for having long planktotrophic larval lives allowing distributions similar to those of the most wide-ranging tonnoideans (Scheltema 1968, 1971, 1979; Scheltema & Williams 1983; Scheltema et al. 1996). Their larvae easily could be transported from Australia and from northern New Zealand to central and southern New Zealand.

Family Bullidae

Genus ***Bulla*** Linné, 1758

Bulla Linné 1758:725 (placed on the Official List of Generic Names in Zoology in ICZN Opinion 196 1954). Type species (ICZN Opinion 196): *Bulla ampulla* Linné, 1758, Pleistocene and Recent, Indo-West Pacific.

Bullus Montfort 1810:330. Type species (by monotypy): *Bullus ampula* (sic) 'de Lamarck' (=*Bulla ampulla* Linné, 1758).

Bullaria Rafinesque 1815:142. Replacement name for *Bulla* Linné, 1758.

Bullea Blainville 1825:477. Type species (designated here): *Bulla ampulla* Linné, 1758 (three species included; no type species was designated by Gray [1847], Hermannsen [1846–1852], Pilsbry [1895:327] or Malaquias & Reid [2008], and I am not aware of any other designation).

Vesica Swainson 1840:360. Type species (by subsequent designation, Malaquias & Reid 2008:457): *Bulla ampulla* Linné, 1758.

Quibulla Iredale 1929:349. Type species (by original designation): *Bullaria botanica* Hedley, 1918 (=*Bulla quoyii* Gray, 1843), Pleistocene and Recent, southern and eastern Australia and northern New Zealand.

Bulla quoyii Gray, 1843 (Fig. 21A, B)

?*Bulla nebulosa* Schröter 1804:20 (nomen dubium; Pilsbry 1895:350; Malaquias & Reid 2008:524).
Bulla australis Gray 1825:408; Gray 1827:490; Gray 1835:308; Gray 1843:243; Brazier 1885:89; Whitelegge 1889:275; Pilsbry 1895:346, pl. 36, figs. 17, 18; Pritchard & Gatliff 1903:214; Iredale 1929:349, pl. 33, fig. 4 (junior primary homonym of *Bulla australis* Férussac, 1822).
Bulla striata. Quoy & Gaimard 1833:354, pl. 26, figs. 8, 9 (incorrect usage of *Bulla striata* Bruguière, 1792).
Bulla australis Quoy & Gaimard 1833:357, pl. 26, figs. 38, 39; Deshayes 1836:673; H Adams & A Adams 1854:16; Chenu 1859:389, fig. 2938; Martens 1873:38; Watson 1886:638 (junior primary homonym of *B. australis* Férussac, 1822 and of *B. australis* Gray, 1825).
Bulla quoyii Gray 1843:243; EA Smith 1874:5, pl. 1, fig. 11; Pilsbry 1895:348, pl. 39, fig. 71; Willan 1977:11–17, fig. 1, pl. 1a–j, pl. 2a–d, pl. 3a–c; Willan 1978:58, figs. 15–24; Wells 1985:30, pl. 1, figs. 1–7; Spencer & Willan 1996:33; Richardson 1997:11; Burn & Thomson 1998:957, fig. 16.36A,B; Morley 2004:120, fig; Malaquias & Reid 2008:524, figs. 25C, 27D–K,

28F, 29E, 31F, 32E, 34A,B, 36D,E, 37H,I, 39; Spencer et al. 2009:213.

Bulla oblonga A Adams 1850:577, pl. 123, fig. 74; H Adams & A Adams 1854:16; Angas 1867:226; GB Sowerby II 1868, pl. 3, fig. 4a–c; Hutton 1873a:52; Tenison Woods 1878:47; Hutton 1880:121; Pilsbry 1895:346, pl. 35, figs. 12–14.

Bulla castanea A Adams 1850:584, pl. 124, fig. 106a.

Bulla (Bullea) substriata Menke 1853:136 (proposed partly as replacement name for *Bulla striata* of Quoy & Gaimard, 1833, not of Bruguière).

Bulla tenuissima GB Sowerby II 1868, pl. 2, fig. 4; Pilsbry 1895:347, pl. 39, fig. 72 (synonym according to Wells 1985:30, pl. 1, figs. 1–7).

Bulla quoyi. Martens 1873:38; Hutton 1873a:52; Hutton 1880:121; Pilsbry 1895:348, pl. 39, fig. 71; Powell 1979:275, pl. 52, fig. 2; Beu in Yoshikawa et al. 1980:251; Beu & Maxwell 1990:422; Maxwell 2009:251.

Bulla australis var. *oblonga*. Pilsbry 1895:346, pl. 35, figs. 12–14.

Haminea castanea. Pilsbry 1895:374, pl. 41, fig. 14

Bulla dubiosa Mabille 1896:113 (no locality or types; synonym according to Malaquias & Reid 2008:524).

Bullaria australis. Suter 1913:534, pl. 49, fig. 6.

Bullaria australis quoyi. Suter 1913:535.

Bullaria australis. Hedley 1916:72.

Bullaria quoyi. Hedley 1916:72.

Bullaria botanica Hedley 1918:M104 (replacement name for *Bulla australis* Gray, 1825, preoccupied); May 1921:103; Macpherson 1958:50, pl. 46, fig. 14; Macpherson & Gabriel 1962:242, fig. 281.

Quibulla botanica. Iredale 1929:349, pl. 38, fig. 4; Iredale & McMichael 1962:88.

Quibulla quoyi. Dell 1955:31, fig. 61; Morton & Miller 1968:534, fig. 202.5; Rudman 1971:657, figs. 1D,E, 8–12; Penniket & Moon 1970:68, pl. 31, fig. 2.

Bulla (Quibulla) quoyi. Powell 1965:167, pl. 22, fig. 10.

Bulla botanica. Burn 1966:266; Coleman 1975:14, fig. 9.

Type material. Willan (1978:59) reviewed the type material of most of the names in the above synonymy. An expanded synonymy was provided by Malaquias & Reid (2008:524); these are summarized here. As noted by Beu (2010: 62–63), EA Smith (1874:5, pl. 1, fig. 11) illustrated the 'type' (the largest of 10 syntypes, BMNH 1842.11.18.135–142; Willan 1978:59; lectotype selected by Malaquias & Reid [2008:524, fig. 27G] = largest, H 22.5 mm; repeated by Beu [2010, fig. 1B]) of *Bulla quoyii*, in BMNH, collected in New Zealand by Frederick Strange (almost certainly from the Bay of Islands, N North Island). *Bulla oblonga*, three syntypes BMNH 197647 (one figured, Malaquias & Reid 2008, fig. 27D), 'Philippines and Annaa I.', Cuming collection (incorrect; probably from Port Jackson, New South Wales). *Bulla* (not *Haminea*) *castanea*, probable holotype BMNH 1881.5.20.22 (Malaquias & Reid 2008, fig. 27F), from the Lombe-Taylor collection, from 'shores of New Zealand'. *Bulla australis* Gray, three syntypes BMNH 20060585, from 'Australia' (not seen; Malaquias & Reid 2008:524). *Bulla australis* Quoy & Gaimard, 11 syntypes examined in MNHN (one illustrated, Valdés & Héros 1998:708, fig. 3I), from King George Sound ('port de Roy Georges'), Albany, southern Western Australia. When describing *Bulla substriata*, Menke (1853b:136) mentioned *B. striata* of Quoy & Gaimard (1833), although he did not expressly propose it as a replacement name. The type, 'ad Novam Hollandiam', was collected by Preiss, so came from southern Western Australia. Part of Menke's collection was acquired some years ago by SMF in the Bronn collection, but R Janssen (SMF pers. comm. November 2007) reported that most of Menke's collection was dispersed before Bronn acquired it, and no type material of *Bulla substriata* is present in SMF. *Bulla tenuissima*, one syntype BMNH 196750 (Wells 1985, pl. 1, fig. 7; Malaquias & Reid 2008, fig. 27E; not seen), from Swan River, Western Australia.

Willan (1978) included '*Bulla striata* Quoy & Gaimard, 1833:354, pl. 26, fig. 8, 9… (non *Bulla* *striata* Bruguière, 1792)' in the synonymy of *Bulla quoyii*. However, Quoy & Gaimard (1833:354) used a name they attributed to Lamarck for specimens from 'Baie des Iles, à la Nouvelle-Zélande'. Lamarck (1822a:33) attributed the name *Bulla striata* in turn to Bruguière, and this is merely a misidentification. There is no separate type material in MNHN for *Bulla striata* of Quoy & Gaimard's usage.

Other material examined. **Haweran:** Te Piki, road cut 6 km E of Whangaparaoa, near East Cape, OIS 7 (GS13743, Y14/f022, cutting towards top of farm road at west end of outcrop, collected by Y. Ota; one specimen, limonitized internal mould; Fig. 21A).

Distribution. The one fossil record I am aware of in New Zealand is the specimen recorded here from the Te Piki member, inland from Whangaparaoa, near East Cape (OIS 7). Recent specimens occur from Cape Maria van Diemen and Spirits Bay south to Cape Runaway, eastern Bay of Plenty, with one record from Nelson in the northern South Island (Willan 1978:59). In Australia *Bulla quoyii* occurs from central Western Australia (Houtmans Abrolhos Islands) to South Australia, Victoria, Tasmania and northern New South Wales (Malaquias & Reid 2008:526, fig. 39), but seems not to have been reported as a fossil. Malaquias & Reid (2008:526) mentioned that Australian specimens reach a larger size (H 62.2 mm) than New Zealand ones (H 45.0 mm) and, while this might be so on average, the presence of specimens in Parengarenga Harbour, Northland, up to 65.6 mm high (see below) shows that there is no consistent difference in dimensions.

The close phylogenetic relationship of *Bulla quoyii* with E Pacific–Atlantic species of *Bulla*, and a corresponding lack of relationships with W Pacific species, has been pointed out by M Malaquias (BMNH pers. comm. October 2007) based on molecular phylogeny. *B. quoyii* falls within a clade that includes *B. gouldiana* Pilsbry, 1895 (E Pacific), *B. punctulata* A. Adams, 1850 (E Pacific), and *B. mabillei* (Atlantic) (Malaquias & Reid 2008, fig. 40). The spiral grooves on the base of the shell provide a character shared only with the Atlantic species *B. striata* Bruguière, 1792 and *B. occidentalis* A. Adams, 1850 (Malaquias & Reid 2008:526). Therefore, *B. quoyii* is apparently another of the Atlantic taxa that arrived in Australia and New Zealand via South Africa during Pleistocene time as planktotrophic larvae transported in the Antarctic Circumpolar Current. It joins a small group of taxa including *Mytilus galloprovincialis* Lamarck, 1819, *Modiolula phaseolina* (Philippi, 1844) (Beu 2004), *Pecten* (Beu 2006), *Lutraria (Lutraria) grandis* (Hutton, 1873) (Beu 2006), and the tonnoideans *Ranella olearium*, *Charonia lampas*, *Monoplex parthenopeus* (von Salis Marschlins, 1793), possibly other *Monoplex* species such as *M. exaratus* (Reeve, 1844), and *Semicassis labiata* (see above). Other tonnoideans have been transported in the same way from the North Pacific via South America (*Argobuccinum*, *Fusitriton*). More such migrants probably await recognition.

Dimensions. Larger syntypes of *Bulla australis* Quoy & Gaimard: H 58.7, D 35.3 mm; H 57.8, D 33.5 mm; H 52.6, D 32.2 mm; GS13743, farm road above Te Piki outcrop: H 41.8, D 26.6 mm; RM2164, Rangaungu Harbour, Northland: H 48.2, D 29.4 mm; NMNZ largest specimens, M.94074, shell bank, Kauanga Channel, Parengarenga Harbour: H 65.6, D 42.7 mm; H 61.0, D 38.0 mm.

Remarks. *Bulla quoyii* is a tall, narrow species with a weakly 'waisted' outline formed by a weakly concave outer lip, and with a few faint spiral grooves around the base. Malaquias & Reid (2008:426) stated that it is the largest species in the genus. It has been recorded fossil previously only in the 'Otamaroa Terrace' faunal list (Beu in Yoshikawa et al. 1980:251) and in the Te Piki faunal list of Richardson (1997, 1999). The single fossil specimen (an internal mould) I am aware of, the basis of all three previous records, is illustrated here (Fig. 21A). It was collected by Professor Yoko Ota in 1978 as part of her work on the uplifted terraces of the northeastern Bay of Plenty (Yoshikawa et al. 1980). As it was collected from a relatively concentrated, deeply weathered fossiliferous horizon apparently overlying the Te Piki Member on the farm access track at the SW end of the Te Piki outcrop, Yoshikawa et al. (1980) assumed that this fauna represented the marine cover beds of the Otamaroa Terrace (last interglacial terrace, OIS 5e). Also, the inclusion of such estuarine species as *Macomona liliana* (Iredale, 1915) and *Bulla quoyii* that are otherwise rare or unknown in Te Piki Member made assignment to Te Piki Member seem unlikely. However, I have since re-examined this site. The fauna includes abundant specimens of *Pecten novaezelandiae* (Reeve, 1852) of the *tainui* phenotype (Beu 2006) and at least one specimen of *Eunaticina papilla*. They occur with several other species that are common throughout the Te Piki Member, such as *Dosinia (Fallartemis) lambata*, *D. (Kereia) greyi*, *Dosina zelandica* and *Maoricolpus roseus*, but are otherwise unknown (*D. greyi*) or unusual constituents of uplifted terrace faunas. The leached, limonite-cemented nature of the material merely results from its position at the top of the Te Piki exposure. There is no doubt that the fauna reported by Yoshikawa et al. (1980:251) merely is a shell concentration at the top of Te Piki Member. The fauna suggests that the member shallowed and became more estuarine in nature towards the top, as would be expected of the deposits of a single interglacial period in a small enclosed bay. No fossiliferous marine deposits are known associated with the Otamaroa Terrace, and the specimen of *B. quoyii* is assigned to OIS 7 rather than OIS 5e. *Bulla quoyii* is a characteristic member of the northern North Island warm-water fauna, and the fossil locality lies within its living range.

Status of Bulla australis *Férrusac*. Willan (1978) did not resolve the status of *Bulla australis* Férussac, 1822, the senior homonym of *B. australis* Gray, 1825. Malaquias & Reid (2008:524) treated it as an earlier name for *Bulla quoyii*, but a nomen dubium. Férussac (1822:573) stated that his type material of *Bulla australis* came from 'Port Jackson', New South Wales, Australia, but the species was not illustrated and has remained unknown. It was defined only by comparison with the preceding and succeeding species: 'Un peu plus petite que la précédente [a little smaller than the preceding species: *B. pisum* Férussac, no locality], se rapprochant de la suivante par son forme' [approaching the following in form: *B. orbignyana* Férussac, from near La Rochelle, Atlantic coast of France; that is, presumably a specimen of either *Bulla striata* or *B. mabillei*]. The remaining syntype of *Bulla australis* Férussac, MNHN 20975, illustrated here (Fig. 21F, H) and by Valdés & Héros (1998:708, fig. 3H; Fig. 41G,H; H 41.1, D 29.4 mm) resembles *B. vernicosa* Gould, 1859 (Malaquias & Reid 2008:527; = *B. angasi* [not of Pilsbry, 1895; a synonym of *B. mabillei*; Malaquias & Reid 2008:492], the name used by Willan [1978:60, figs. 1, 2, 25–37] for the second *Bulla* species in northern New Zealand and central eastern Australia to New Caledonia and Samoa). It is definitely not a specimen of *B. quoyii*. Because of this similarity and the locality 'Port Jackson', I investigated this name in case it is an earlier name for *B. vernicosa*. The remaining syntype differs from *B. vernicosa* in having a more evenly convex outer lip, not weakly concave in the centre as in *B. vernicosa*, and the colour pattern is a more reddish-purple, diffused, cloudy one with relatively large, variably blended, circular spots, without the many finer dots that make up the pattern of *B. vernicosa*. The syntype is accompanied by a hand-written label stating 'specimen = *Bulla mabillei* Locard [1897], Atlantic. Robert Burn, January 1992'. Comparison of specimens and illustrations (Locard 1897:50, pl. 11, figs. 1, 2; Talisman stn 107, 70 m, St Vincent, Cape Verde Islands; a large specimen, H 60, D 42 mm; Poppe & Goto 1991:195, pl. 37, figs. 23, 24; Ardovini & Cossignani 2004:242, central left two figs) showed that Burn's identification is correct. This was confirmed by Malaquias & Reid (2008:524). *B. australis* Férussac is identifiable only by its remaining syntype, which apparently (like many type specimens of other molluscs) bears an incorrect locality. Because of the confusion over the possible type locality, and the consequent identity of the species, the remaining syntype of *B. australis* Férussac, MNHN 20975 (Fig. 21F,H) is here designated the lectotype of *Bulla australis* Férussac, 1822, which is, therefore, an earlier name for the Atlantic species *B. mabillei* Locard, 1897. As the name *Bulla australis* Férussac has not been used as the valid name for a species after 1899, and *B. mabillei* is a well-established name, it is likely that *B. australis* qualifies as a nomen oblitum. However, Malaquias & Reid (2008:492) pointed out that both *B. cruentata* A. Adams, 1850 and *B. angasi* Pilsbry, 1895 also are earlier names for *B. mabillei.* They retained the name *B. mabillei*, pending an application to the ICZN, so *B. australis* Férussac should be included in the same application.

Family Philinidae

Genus ***Philine*** Ascanius, 1772

Philine Ascanius 1772:331. Type species (by monotypy): *Philine quadripartita* Ascanius, 1772 (=*Bulla aperta* Linné, 1767), Recent, North Atlantic & Mediterranean.

Remarks. The first published synonymy for *Philine* that I am aware of is that by Valdés (2008:713–714), who, however, did not include some of the names concluded here to be synonyms. Pilsbry (1895) provided no synonymy, referring to Fischer's (1883, in 1880–1887:563) treatment. As for *Hydatina*, the details of the synonymy are beyond the scope of this paper, as I am unable to determine the type species of some genera, but following Fischer (1883), Rudman (1970; 1972a: 185–186), Kitao & Habe (1982), Burn & Thomson (1998:951) and Valdés (2008), the following names are concluded to be synonyms of *Philine*: *Lobaria* Müller (1776:28, 260); *Bullaea* Lamarck (1801:63); *Laona* A. Adams (1865:324); *Utriculopsis* M. Sars (1870:177); *Hermania*, *Johania* and *Ossiania* of Monterosato (1884:147); *Yokoyamaia*, *Choshiphiline* and *Philinorbis* of Habe (1950:50, 52); *Globiphiline* Habe (1958:120); *Rhinodiaphana* Lemche (1967:208); *Retusophiline* and *Philingwynea* of Nordsieck (1972:20, 22); and *Pseudophiline* Habe (1976:154).

Philine tepikia Rudman, 1970 (Fig. 21E)

Philine tepikia Rudman 1970:31, fig. 2M, pl. 3C; Maxwell 2009:251.
Philine tepikiensis (sic) Beu & Maxwell 1990:422.

Type material. Philine tepikia, holotype TM4855, from GS4003, R22/f7394, Landguard Sand, Landguard Bluff, east of Wanganui City (Haweran, OIS 9); one paratype AUGD G5868, from Te Piki member, road cut inland from Whangaparaoa, near East Cape (Haweran, OIS 7).

Other material examined. **Haweran:** the only specimen of *Philine tepikia* I am aware of other than the type material is from Hokianga Harbour (GS14777, O06/f67, bank at back of tidal flats in front of Waiparera Church; Haweran, OIS 7).

Distribution. Known only by the three specimens recorded here, from Landguard Bluff, Te Piki, and Waiparera (OIS 9–7). The shell is extremely thin and fragile, and fossils are difficult to collect, so its range is likely to be greater than these specimens suggest, and its biostratigraphical utility is minimal.

Dimensions. *Philine* tepikia, holotype: H 29.5, D 22 mm (Rudman 1970:31); GS14777, Waiparera: H 14.6 (incomplete), D 10.8 mm.

Remarks. *Philine* has a very thin, fragile, translucent shell with a very large, simple aperture, widely open anteriorly, with the small, ovate spire whorls almost completely enveloped by the last whorl, and with a flat or slightly sunken spire apex. Many, but not all, species have spiral sculpture of weak spiral grooves, punctate on some species, and some species have spines or other protrusions from the upper (adapical) part of the outer lip. Fred Brook collected a single specimen of the relatively large species *P. tepikia* from GS14777, NW Hokianga Harbour (OIS 7). The holotype (Rudman 1970:31, fig. 2M, pl. 3, fig. C) is an almost complete specimen 29.5 mm high, collected from Landguard Sand (OIS 9) at Landguard Bluff by CA Fleming. Rudman (1970) also recorded a specimen from Te Piki, Cape Runaway (OIS 7). The Waiparera specimen is 14.3 mm high, and agrees with the holotype of *P. tepikia* in having unusually prominent dorsal growth ridges, and 8–10 quite prominent, narrow, closely spaced, punctate spiral ridges in the apical depression. The Waiparera specimen has only 3–4 faint, shallow spiral grooves across the adapical part of the exterior below the apex, rather than the numerous, slightly more closely spaced ones across the adapical two-thirds of the shell on the holotype. However, this difference seems likely to be part of the variation of one species; the number of grooves presumably increases as the shell grows, and the holotype is twice the size of the Waiparera specimen. Therefore, it appears that a relatively large *Philine* species was endemic to New Zealand during OIS 9–7, and that the similarly large species *P. angasi* (Crosse & Fischer 1865:38, pl. 2, fig. 8), which differs from *P. tepikia* in lacking spiral grooves, reached New Zealand (or possibly evolved from *P. tepikia*) only after OIS 7. The largest specimen of *P. tepikia* recorded so far is not from the warm-water northeastern North Island, where *P. angasi* occurs at present, but from Landguard Sand (OIS 9) at Wanganui.

Landguard Sand has produced the largest number of warm-water migrants at Wanganui. The species now recorded from Landguard Sand, only, at Wanganui and otherwise known fossil or living only in the northern New Zealand warm-water province are *Capulus danieli*, *Stiracolpus vigilax* (= *ahiparanus*?; = *pagoda*?), *Eunaticina papilla*, *Pupa affinis* and *Philine tepikia*. The warm-water, northeastern North Island species *Zelippistes benhami* also is recorded from Landguard Sand, and otherwise apparently is recorded at Wanganui only from Tainui Shellbed (OIS 13). Other northeastern North Island and/or tropical Pacific species occurring in Landguard Sand, with longer time ranges, include *Amygdalum striatum* (Hutton, 1873), *Limaria orientalis* (A. Adams & Reeve, 1850) and *Leucotina casta* (A. Adams, 1853).

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