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Marine Mollusca of isotope stages of the last 2 million years in New Zealand. Part 3. Gastropoda (Vetigastropoda - Littorinimorpha).

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Three new species: *Grandicrepidula hemispherica* (Nukumaruan, S Hawke's Bay), *Pelicaria granttaylori* (Mangapanian-early Nukumaruan, Wanganui - Hawke's bay), *Pelicaria arahura* (Waipipian-early Mangapanian, Westland and Hawke's Bay). Drawings of marine species in Smith's (1874) three plates of New Zealand molluscan types are republished. Further Australian molluscs in Wanganui Basin: *Sabia australis* (Lamarck), *Clanculus plebejus* (Philippi), both early Nukumaruan. Further northern New Zealand mollusc in Wanganui Basin: *Stephopoma roseum* (Quoy & Gaimard), OIS 13, 9. Distinctive gastropods extinct at end Nukumaruan: *Struthiolaria frazeri* (Hutton), *Taxonia suteri* (Marwick). *Taniella planisuturalis* (Marwick) (Opoitian-Nukumaruan, southern NZ) and *Trivia (Ellatrivia) zealandica* (Kirk) (Nukumaruan, Hawke's Bay-Wanganui; Castlecliffian, North Canterbury) occur in Castlecliffian (OIS 15?) rocks at Whakatane. *Cantharidella tessellata* (A. Adams) and *Risellopsis varia* (Hutton), formerly Haweran, are recorded from Nukumaruan and Castlecliffian rocks, respectively. New fossil late Nukumaruan-early Castlecliffian records listed from Mikonui-1 offshore well, Westland, include *Malluvium calcareum* (Suter) and 10 other species. Other biostratigraphically useful gastropods: *Calliostoma (Maurea) nukumaruense* (Laws) (Mangapanian-OIS 17); *Argobuccinum pustulosum* (Lightfoot), *Semicassis labiata* (Perry) (both earliest in OIS 7). New synonymy: *Zeacumantus perplexus* (Marshall & Murdoch) = *Z. lutulentus* (Kiener); *Pelicaria vermis* (Martyn) = all named Nukumaruan-Recent forms (other than *P. rugosa* (Marwick) and *P. granttaylori* n. sp.); *Trivia flora* Marwick = *T. zealandica* Kirk. Taxonomy revised: *Zelippistes benhami* (Suter) (OIS 13 & 9 at Wanganui), distinguished from *Lippistes* and *Separatista; Stiracolpus* species, informally; *Maoricrypta profunda* (Hutton), Waipipian-early Castlecliffian (- OIS 19); *M. radiata* (Hutton) (= *incurva* Zittel, = *hochetteriana* Woods, = *wilckensi* Finlay), (Middle Miocene?) Tongaporutuan-Opoitian; *Eunaticina cincta* (Hutton), holotype illustrated.

Keywords: biostratigraphy; Castlecliffian; dispersal; E. A. Smith's illustrations; Haweran; Holocene; Mollusca; new species; New Zealand; Nukumaruan; oxygen isotope stages; Pleistocene; Pliocene; time scale; Wanganui Basin

Introduction

This paper is the third 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. The present report is a reconsideration of the time ranges

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and taxonomy of some 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 in Part 4). A similar paper on "higher" Gastropoda (Ptenoglossa, Neogastropada and Heterobranchia) and a summary paper are in press. 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.

Fleming (1953) listed a number of possibly new taxa in his faunal lists from Wanganui Pliocene–Pleistocene formations, based on material in GNS. Some of Fleming's material is surprising for temperature and migration interpretations, particularly the records (below) of *Sabia* and *Clanculus* from early Nukumaruan rocks in Opawe Stream, Pohangina valley, in eastern Wanganui Basin outside Fleming's (1953) mapped area. However, many of the putative new taxa listed by Fleming (1953) are based on very few specimens, and possibly are undescribed but require confirmation from more material (e.g. species he assigned to *Scissurella*, *Nobolira*, *Scrobs* and *Aupouria*). Other potential new species now seem not to be different from Recent species that are more variable than Fleming realized. A single *Pervicacia* specimen with a much larger protoconch than Recent ones is a typical case of more material being required to confirm the characters of an apparently unnamed species (GS4057, R22/f6388, Kaikokopu Shellbed, OIS 19, Castlecliff coastal section). Still others, such as the several new species of Nuculidae that Fleming intended to name, are well founded but would be better to revise on the basis of the Recent fauna, where all have proved to be common (BA Marshall NMNZ pers. comm.). They have not been included in these papers. The section on Gastropoda has been divided into two papers, and a biostratigraphy section on gastropods, similar to that presented in the earlier Parts 1 and 2 (Beu 2004, 2006), will be included in Part 4, the second gastropod part.

Smith's (1874) illustrations of New Zealand Mollusca

One of the most useful but now hard to obtain of early publications on New Zealand Mollusca is EA Smith's (1874) three plates illustrating type specimens in the Natural History Museum, London (part of the British Museum in 1874) of common New Zealand shallow-water Mollusca. The illustrations seem to have been prepared at an earlier date, apparently for JE Gray before the publication of Gray (1843). Smith's (1874:1) introduction to a brief text of only seven pages stated: 'The four following excellent plates will be very acceptable to Conchologists, as they contain figures of several species (about twenty) which, until the present time, have been known only by descriptions, in some instances very short and insufficient, and also the more interesting as, in thirty-one instances, the actual type specimens are delineated. [New line] Plates 1 to 3 are devoted exclusively to species belonging to the New Zealand fauna. Four of them are new to science, and three, described some years since, are unrecorded in Von Martens' [1873] very useful "Critical list of the Mollusca of New Zealand". [New line] Plate 4 includes, with one exception (*Helix menkeana*), figures of some Australian Land and Freshwater Mollusca of which two appear to be as yet undescribed. [New line] All the species with the exception of *Bulimus antipodum* and *Vermetus cariniferus* are in the British Museum, and those preceded by a * were presented by Sir John Richardson, M.D., F.R.S.'. Nearly all the terrestrial snails are Australian; none of the non-marine taxa illustrated by Smith is included here. The figures of marine molluscs on the first three of Smith's (1874) plates are republished here, scanned from the published originals, approximately as oriented by Smith but rearranged, to make them more widely available. A few small figures on the plates are unnumbered and are not referred to in Smith's text or captions, and are not included here.

Determining which of Smith's illustrations show type specimens is complicated, as only 25 of the captions state 'Type', 'Type figured', or 'Type in the British Museum', rather than the 31 stated by Smith. All types are still present in the Natural History Museum, London. Therefore, it is assumed in the captions presented here that almost all New Zealand species, and certainly Smith's four new species, are illustrated from type material. The status of the specimens labelled 'type' should be treated with care, in view of ICZN Recommendation 73F, 'avoidance of assumption of holotype'. In many cases the figured specimen is known to be one of several syntypes, and in others some original syntypes might now be lost. All are, therefore, considered to be syntypes.

Some comments are necessary on some of the drawings, or on some of the names used by Smith (1874) in his accompanying text.

1. Smith's (1874, pl. 1, fig. 21) illustration (Fig. 1M) is identified as '*Trichotropis clathrata* (A Adams Ms.) Hab. New Zealand (Dr Sinclair, Colonel Bolton and Dr Lyall, RN). The above name is attached to a specimen in the Cumingian collection, without any locality, which agrees in every particular with specimens from New Zealand collected by the gentlemen quoted above. The name appears in Messrs. Adams' list in the "Genera of recent Mollusca" vol. I., p. 280; but as I cannot find a description of any species so designated, I append the following:' [description follows]. Smith (1874:4) noted that 'The figure representing this species is not characteristic, for it is taken from a young example, and the form of the mouth is very different from that of the adult shell'. Smith's illustration evidently is of a different species from the adult syntype, as the illustration shows *Xymene plebeius* (Hutton, 1873) (Muricidae). Suter (1913:296, pl. 44, fig. 9) adopted *T. clathrata* in place of the prior *T. inornata* Hutton, 1873, the common Pliocene–Recent species usually known as *Trichosirius inornatus*, on the grounds that Hutton's species had not been illustrated, an unacceptable criterion even in 1913. He did not mention the *Xymene* illustration. Even Iredale (1915:456), when reinstating Hutton's name, did not mention the misidentified illustration. Suter (1913:296) clarified the situation by attributing the name *T. clathrata* to GB Sowerby II (1874). Sowerby's (1874, pl. 2, fig. 10) illustration is at least of a *Trichotropis* (sensu lato) species, even if not very clearly of *T. inornatus*—the columella is too strongly excavated in Sowerby's drawing. The specimen illustrated by Sowerby (1874, pl. 2, fig. 10) is here designated the lectotype of *Trichotropis clathrata*, to avoid this name being attached to *Xymene plebeius*. This publication (August 1874) is accepted here as earlier than Smith's (1874, undated as to month), and the name is a later synonym of *Trichosirius inornatus*. Smith (1874) or an earlier draughtsman evidently illustrated *Xymene plebeius* in error. Petit (2009:97) confirmed the listing of *Trichotropis clathrata* by H Adams & A Adams (1854:280), 'where it is a nude name'.
2. *Vermetus cariniferus* Gray, 1843 (Smith 1874, pl. 1, fig. 23) (Fig. 1T) is based on a polychaete tube rather than a gastropod, the abundant intertidal zone-forming tubeworm formerly known as *Pomatoceros caeruleus* (Schmarda, 1861), currently

known as *Spirobranchus cariniferus* (Gray, 1843). This illustration presumably shows a syntype.

3. The limpet illustration captions are muddled; both *Patella redimiculum* Reeve, 1854 and *Patella denticulata* Martyn, 1784 are labelled in the text as applying to Smith's (1874, pl. 1, fig. 24) (Fig. 1V). Smith's (1874, pl. 1, fig. 25) (Fig. 1X) illustration is labelled '*Patella antipodum*, sp. n.,' and Smith's (1874, pl. 1, fig. 26) (Fig. 1S) illustration has no caption or text, but clearly shows *Cellana ornata* (Dillwyn, 1817). Pl. 1, fig. 24 (Fig. 1V) shows the southern New Zealand species *Cellana strigilis* (Hombron & Jacquinot, 1841), of which *P. redimiculum* was ranked a subspecies by Powell (1979:45) and Goldstien et al. (2006). Apparently the illustration of *Cellana ornata* (Smith's fig. 26) (Fig. 1S) was misidentified as *P. denticulata*. Suter (1913:79) followed a suggestion by WH Dall in using the name '*Helcioniscus antipodum*' for the eastern Australian species previously known as *Patella tramoserica* Martyn, 1784 (now consistently known as

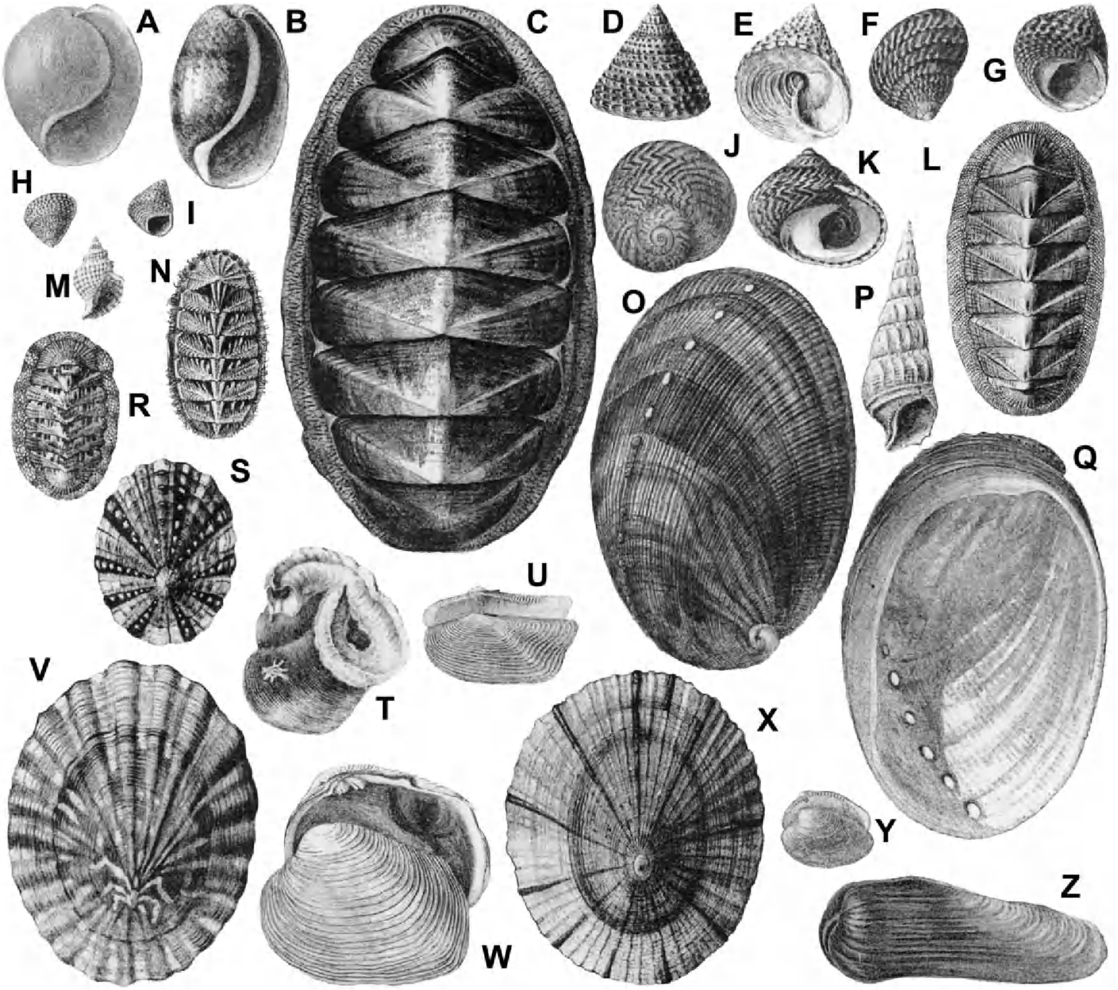

Fig. 1 (*Continued*)

Cellana tramoserica [Holten, 1802]; Wilson 1993:36, pl. 1, fig. 23; Lindberg 1998:647, fig. 15.36C, D; pl. 22 1, 2; Goldstien et al. 2006). However, Smith (1915:78) stated that *H. antipodum* (Smith) is a synonym of *Cellana radians* (Gmelin, 1791).

4. The drawing of *Vanganella taylori* (Smith 1874, pl. 2, fig. 5; Fig. 3B) stated by Smith to be of a 'full-grown' specimen, not the immature 'type specimens presented by the Rev. R. Taylor to the British Museum') shows the species now universally known as *Resania lanceolata* Gray, 1853. J-P Rocroi (MNHN pers. comm. from P Bouchet, 17 April 2008) stated that Gray (1853a), where the name *Resania lanceolata* was established, was published in January 1853, whereas Gray (1853b), where the name *Vanganella taylori* was established, was published on 29 April 1853; *R. lanceolata* has priority.
5. *Venus oblonga* Gray, 1843 is illustrated (Smith 1874, pl. 2, fig. 1) (Fig. 3C), presumably a syntype despite the lack of such a label, whereas the earlier synonym *Dosina zelandica* Gray, 1835 seems at first sight not to be illustrated, despite Smith (1874:6) noting that 'the type' is in the British Museum. However, presumably as a result of a typographical error, an apparently unlabelled figure (Smith 1874, pl. 3, fig. 5) (Fig. 3E) is referred to within the third line of Smith's (1874:6) synonymy as if the reference were within Gray's (1835) publication; this illustration clearly represents a syntype of *Dosina zelandica.* As Smith (1874) noted, it is a short specimen of the same species as *Venus oblonga*, and the earlier name for this species.
6. *Paphies ventricosa* (Gray, 1843): Smith's (1874, pl. 3, fig. 6) illustration (Fig. 2K) shows the remaining syntype, identified as '*Taria ventricosa*', BMNH 1842.5.17.189, 'North shore, Cook's Strait, New Zealand', that is, the Paraparaumu–Waikanae coast of western Wellington Province (where it can still be collected), collected by Dieffenbach. The specimen was illustrated as the 'holotype' by Beu & de Rooij-Schuiling (1982, figs. 22–24) but this does not constitute designation of a lectotype under ICZN Article 74.6, as it has not been

Fig. 1 Reproductions of illustrations of New Zealand marine molluscan type specimens, from Smith (1874), at published size. (A) Smith's pl. 1, fig. 10, *Haminoea zelandiae* (Gray, 1843), "type figured". (B) Smith's pl. 1, fig. 11, *Bulla quoyii* Gray, 1843, "type figured". (C) Smith's pl. 1, fig. 8, *Eudoxochiton nobilis* (Gray, 1843), presumed syntype. (D,E) Smith's pl. 1, fig. 6, *Polydonta tuberculata* Gray, 1843 [= *Coelotrochus viridis* (Gmelin, 1791)], "type figured", that is, syntype of *P. tuberculata*. (F,G) Smith's pl. 1, fig. 14, *Diloma subrostrata* (Gray, 1843), presumed syntype. (H,I) Smith's pl. 1, fig. 12, *Cantharidus sanguineus* (Gray, 1843), "type figured" [see Williams et al. (2010) for adoption of *Coelotrochus* and *Cantharidus*]. (J,K) Smith's pl. 1, fig. 15, *Chlorostoma undulosum* A. Adams, 1853 [= *Diloma subrostrata* (Gray, 1843)], presumed syntype of *C. undulosum*. (L) Smith's pl. 1, fig. 9, *Rhyssoplax aerea* (Reeve, 1847), "type in museum collection". (M) Smith's pl. 1, fig. 21, supposedly *Trichotropis clathrata* Smith, 1874, "young example," not a type [apparently *Xymene plebeius* (Hutton, 1873)]. (N) Smith's pl. 1, fig. 13, *Chiton (Plaxiphora) terminalis* Smith, 1874, syntype [= *Plaxiphora (Maorichiton) caelatus* (Reeve, 1847)]. (O,Q) Smith's pl. 1, fig. 16, "*Haliotis gibba* Philippi?" [actually *Haliotis virginea* Gmelin, 1791], not a type. (P) Smith's pl. 1, fig. 20, *Cerithidea bicarinata* Gray, 1843 [= *Zeacumantus lutulentus* (Kiener, 1841)], "type figured". (R) Smith's pl. 1, fig. 17, *Chiton (Sypharochiton) sinclairi* (Gray, 1843), "the type is figured". (S) Smith's pl. 1, fig. 26, labelled "fig. 24", supposedly *Patella denticulata* Martyn, 1784 [actually *Cellana ornata* (Dillwyn, 1817)], not a type. (T) Smith's pl. 1, fig. 23, *Vermetus cariniferus* Gray, 1843 [that is, *Spirobranchus cariniferus*, Polychaeta], "type figured", despite Smith (1874:1) stating type not in British Museum. (U) Smith's pl. 2, fig. 13, *Neilo australis* (Quoy & Gaimard, 1835), not a type. (V) Smith's pl. 1, fig. 24, *Cellana strigilis redimiculum* (Reeve, 1854), presumed syntype. (W) Smith's pl. 2, fig. 3, *Irus (Notirus) reflexus* (Gray, 1843), "type figured". (X) Smith's pl. 1, fig. 25, *Patella antipodum* Smith, 1874 [= *Cellana radians* (Gmelin, 1791)], a syntype of *P. antipodum,* established in this work. (Y) Smith's pl. 2, fig. 14, *Leionucula strangei* (A. Adams, 1856), syntype BMNH 20040712 (Beu 2006:fig. 3E, F). (Z) Smith's pl. 2, fig. 12, *Zelithophaga truncata* (Gray, 1843), "type figured".

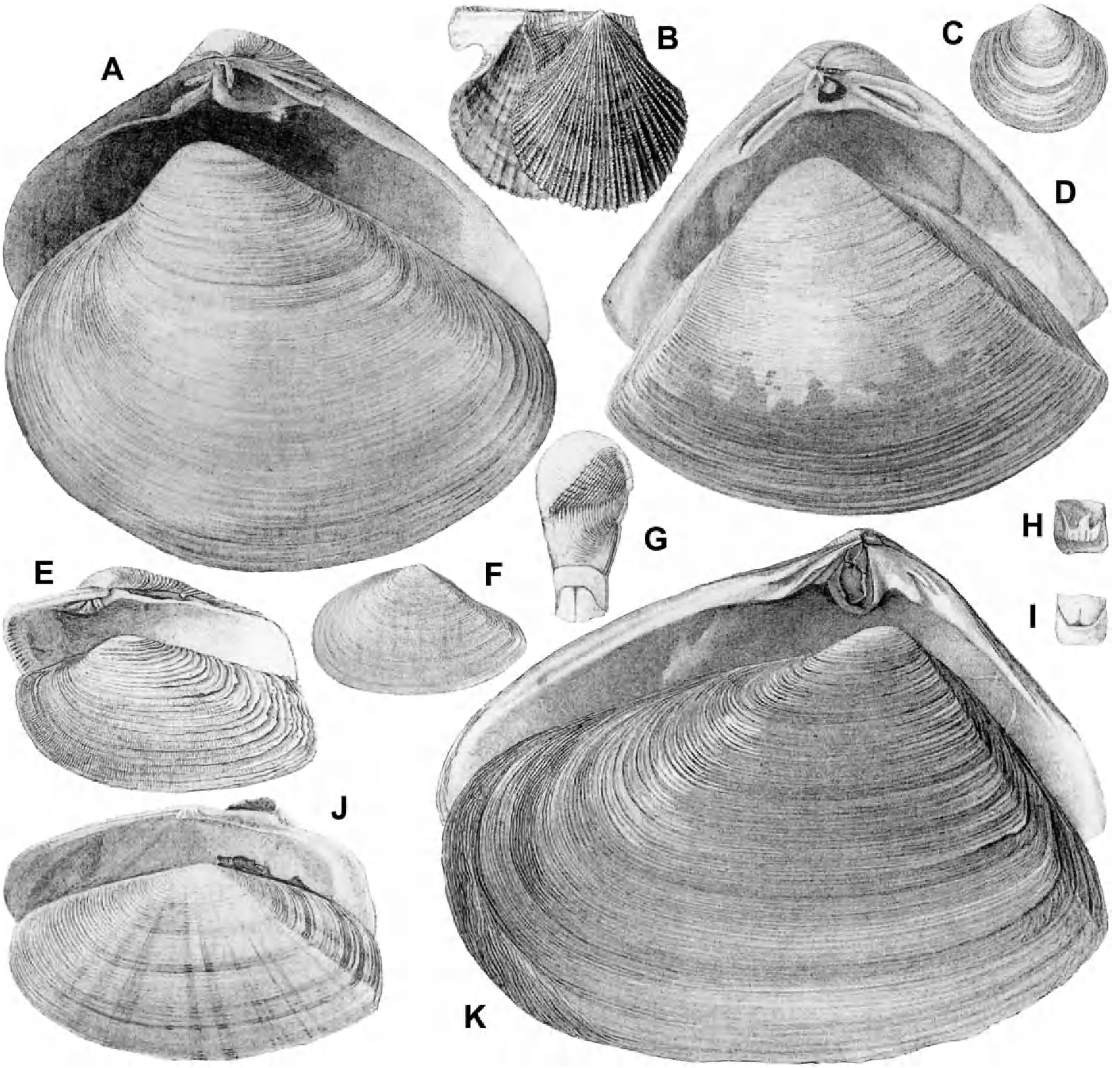

Fig. 2 Reproductions of illustrations of New Zealand marine molluscan type specimens, from Smith (1874), at published size. (A) Smith's pl. 2, fig. 2, *Cyclomactra ovata* (Gray, 1843), "the type is figured" (hinge inaccurate). (B) Smith's pl. 3, fig. 7, *Talochlamys zelandiae* (Gray, 1843), "type figured". (C) Smith's pl. 3, fig. 8, *Felaniella (Zemysia) zelandica* (Gray, 1835), "type figured". (D) Smith's pl. 2, fig. 10, *Crassula aequilatera* (Deshayes in Reeve, 1854) (see Petit 2007:81), "type in Brit. Mus". (E) Smith's pl. 2, fig. 6, *Irus (Notopaphia) elegans* (Deshayes, 1854), "type in Brit. Mus.". (F) Smith's pl. 2, fig. 7, *Tellinota edgari* (Iredale, 1915), "type in Brit. Mus.", that is, syntype of *Tellina glabrella* Deshayes, 1854 (junior primary homonym of *T. glabrella* Delle Chiaje, 1830), renamed *T. edgari*. (G,H,I) Smith's pl. 2, fig. 8, *Pholadidea tridens* (Gray, 1843) and interior and exterior of siphonoplax, "type figured". (J) Smith's pl. 2, fig. 11, *Gari (Psammobia) lineolata* (Gray, 1843), presumed syntype. (K) Smith's pl. 3, fig. 6, *Paphies ventricosa* (Gray, 1843), remaining syntype, BMNH 1842.5.17.189.

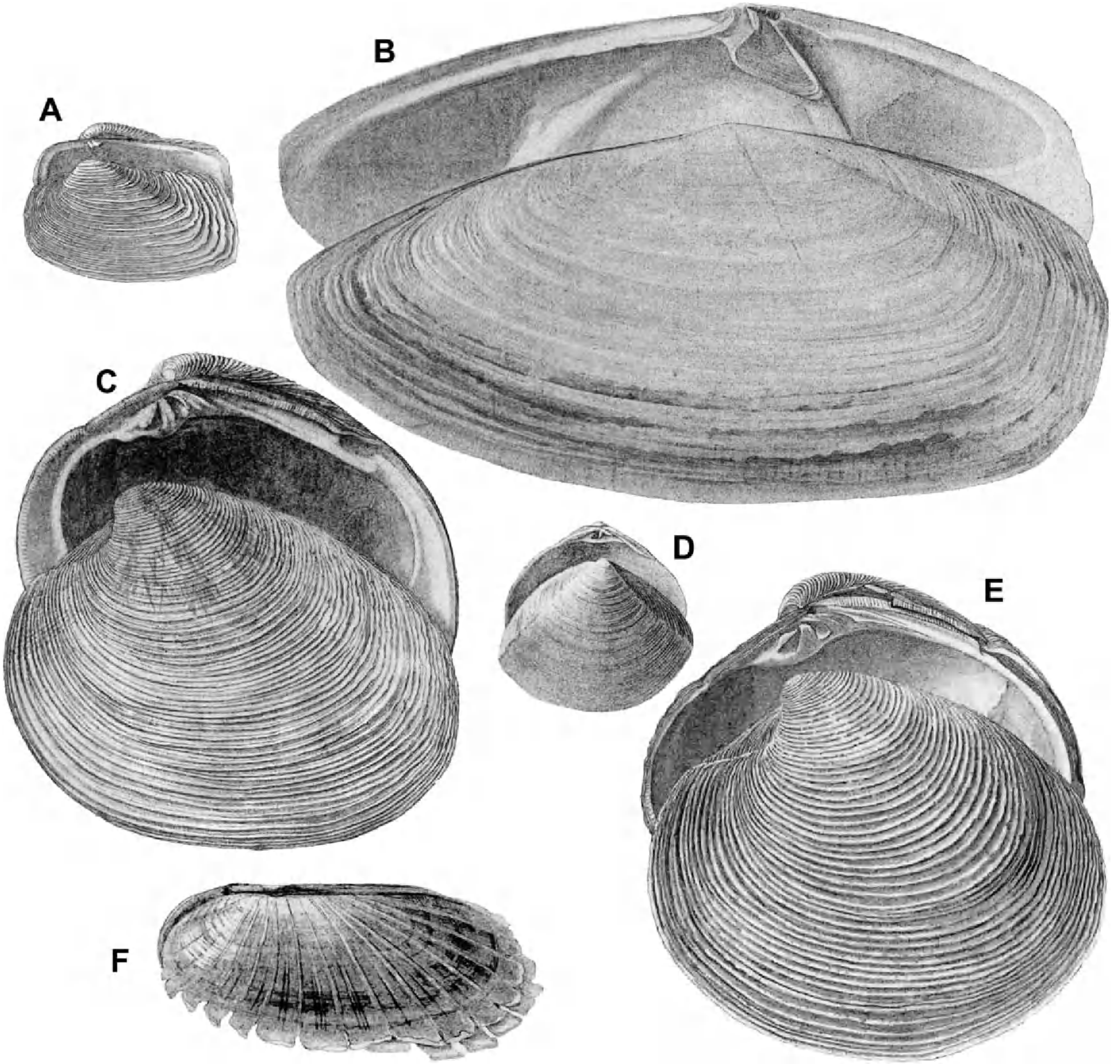

Fig. 3 Reproductions of illustrations of New Zealand marine molluscan type specimens, from Smith (1874), at published size. (A) Smith's pl. 3, fig. 3, *Irus (Notirus) reflexus* (Gray, 1843), not a type, "Fig. 3 on pl. 3 appears to represent a species intermediate between *reflexa* and *V. siliqua* Desh.". (B) Smith's pl. 2, fig. 5, *Vanganella taylori* Gray, April 1853 [= *Resania lanceolata* Gray, Jan. 1853], not a type. (C) Smith's pl. 2, fig.1, *Dosina zelandica* Gray, 1835, presumed syntype of *Venus oblonga* Gray, 1843. (D) Smith's pl. 2, fig. 4, supposedly *Mactra discors* Gray, 1843, not a type ["the … figure is taken from a very young specimen" of *M. murchisoni* Deshayes in Reeve, 1854]. (E) Smith's pl. 3, fig. 5, *Dosina zelandica* Gray, 1835, presumed syntype of *Dosina zelandica*, "the type... is in the British Museum". (F) Smith's pl. 3, fig. 1, *Solemya (Zesolemya) parkinsoni* E. A. Smith, 1874, syntype; established in this work.

accepted that a single type specimen exists. Comparison of this figure with Beu & de Rooij-Schuiling's (1982, figs. 22–24) photographs demonstrated that Smith's drawing is inaccurate, the posterior end being shown shorter and the umbonal-ventral ridge more prominent than they actually are, although other details of the hinge and growth irregularities around the posterior end agree well.

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.
MHNG	Muséum d'Histoire Naturelle de Genève, Geneva.
MNHN	Muséum National d'Histoire Naturelle, Paris.
NHMW	Naturhistorisches Museum Wien, Vienna.
NMNZ	Museum of New Zealand Te Papa Tongarewa, Wellington.
RMNH	Naturalis, Nationaal Museum van Natuurlijke Historie, Leiden (Recent Mollusca collection).
TASM	Tasmanian Museum, Hobart (type Mollusca also prefixed TM).
V311, etc.	Victoria University of Wellington, School of Earth Sciences and Geography, bulk collection locality numbers.
ZMC	University Zoological Museum, Copenhagen.

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.

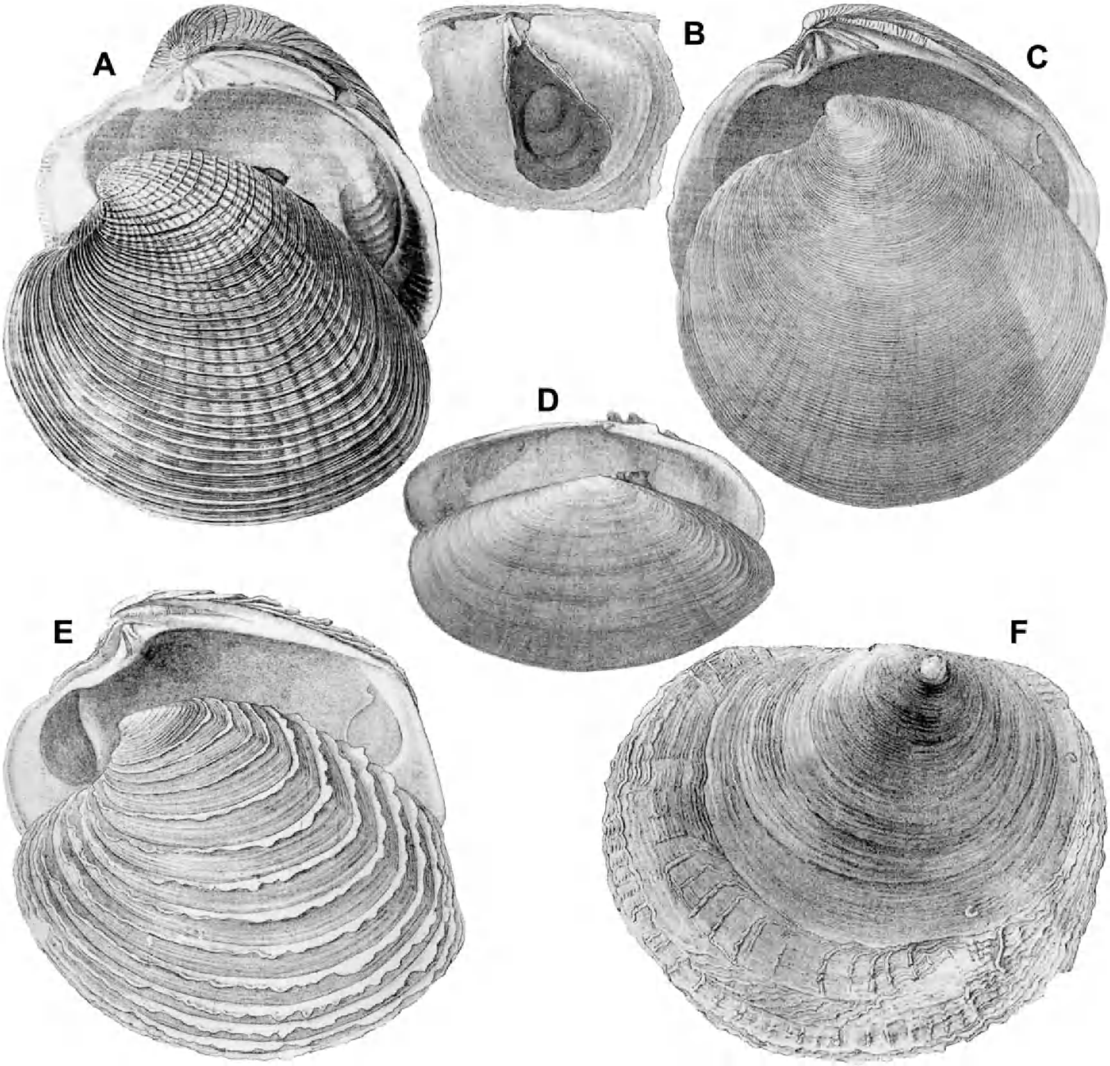

Fig. 4 Reproductions of illustrations of New Zealand marine molluscan type specimens, from Smith (1874), at published size. (A) Smith's pl. 3, fig. 4, *Austrovenus stutchburyi* (Wood, 1828), presumed syntype. (B,F) Smith's pl. 3, fig. 9, 10, *Pododesmus (Monia) zelandica* (Gray, 1843), "type figured" (syntype, Fig. 4F, Smith's fig. 10; and interior of byssal foramen enlarged). (C) Smith's pl. 3, fig. 2, *Dosinia (Phacosoma) subrosea* (Gray, 1835), "the type... is here figured". (D) Smith's pl. 2, fig. 9, *Soletellina nitida* (Gray, 1843), presumed syntype. (E) Smith's pl. 3, fig. 11, *Circomphalus yatei* (Gray, 1835), "The type... is figured".

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.

New records from Mikonui-1 well, off Westland

In an obscure report (Beu in Morgans 1981:12–13, table 1), I recorded Mollusca of

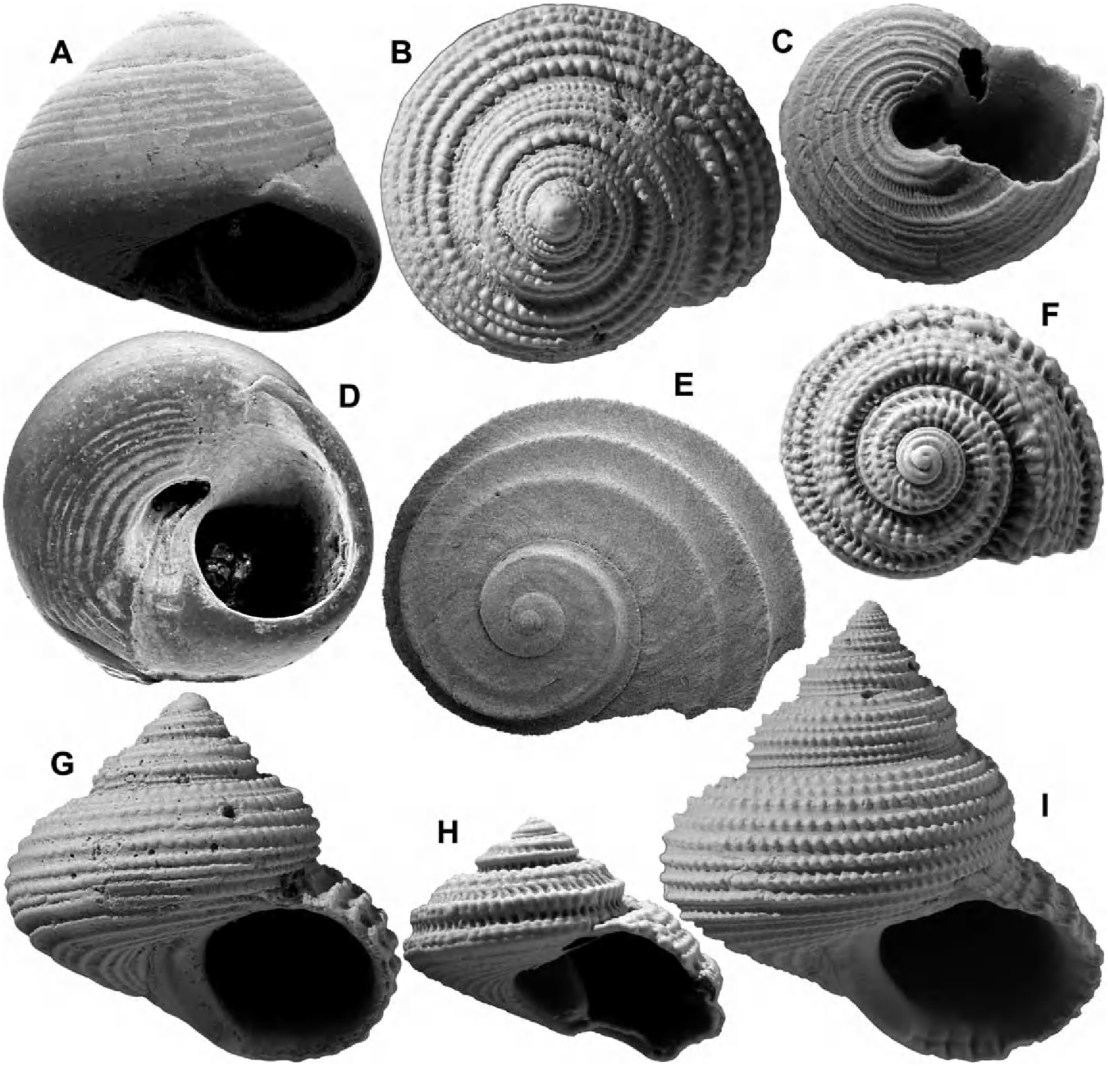

Fig. 5 (A,D) *Cantharidella tessellata* (A. Adams), GS12790, V20/f038, Tangoio Limestone (late Nukumaruan), Petane Pa, Tangoio, Hawke's Bay; SEM, 2 views of abraded specimen, width 6.3 mm. (B,G,I) *Calliostoma (Maurea) nukumaruense* (Laws), 2 specimens, GS4115, R22/f6435, Nukumaru Brown Sand (late Nukumaruan), Nukumaru Beach, Wanganui; B, G, H 16.1, D 17.7 mm; I, height 20.3 mm. (C,F,H) *Clanculus plebejus* (Philippi), GS2784, T23/f6491, 3-10 m above Torlesse greywacke, Opawe Stream, Pohangina Valley, early Nukumaruan; 3 views of 1 shell, width 7.1 mm. (E) *Risellopsis varia* (Hutton), GS15119, R28/f062, 1855 uplifted beach, Cape Turakirae, Wellington; SEM; width 4.7 mm (see also Fig. 6B).

bathyal aspect and late Nukumaruan–early Castlecliffian age from the Mikonui-1 well, a wild-cat oil well drilled off the west coast of the South Island, west of Hokitika, by the '*Sedco 45*' drill ship, at 42°41′15″S, 170°08′45″E. The diverse molluscs were all from well cuttings from the upper part of the core. Depths originally were reported well depths, including 170 m for water depth plus height of the drilling platform above the water; 170 m has therefore been deducted from the depths to arrive at those reported here. Also, the uppermost

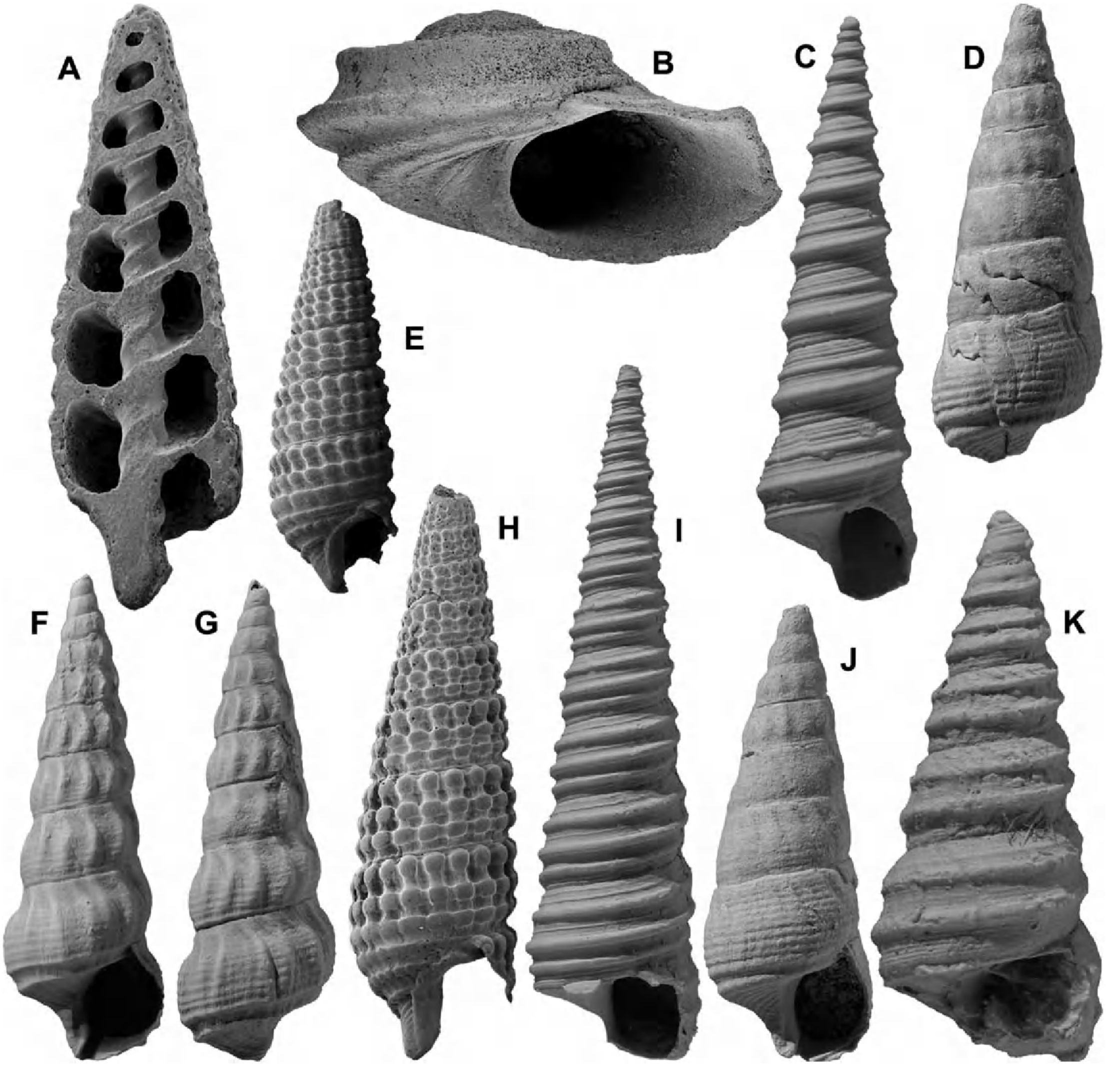

Fig. 6 (A,E,H) *Taxonia suteri* (Marwick), late Nukumaruan, Hawke's Bay, SEM; A, sectioned paratype, GS1063, V21/f8476, roadside 1.6 km NW of Okawa Stream, Matapiro syncline; height 16.0 mm; E,H, GS14833, T24/f062, 2 specimens, table-top hill on Waitio Station, Makuri-Coonoor Road; E, height 10.4 mm; H, height 15.2 mm. (B) *Risellopsis varia* (Hutton), second specimen from same locality as Fig. 5E; width 5.4 mm. (C) *Stiracolpus vigilax* (Marwick), holotype, TM1686, GS4003, R22/f7394, Landguard Sand (Haweran, OIS 9), Landguard Bluff, Wanganui; height 15.3 mm. (D,F,G,J) *Zeacumantus lutulentus* (Kiener); D,J, "*perplexus* form", GS14833, T24/f062, table-top hill on Waitio Station, Makuri-Coonoor Road, Nukumaruan; height 30.6 mm; F,G, RM3289, uncorroded Recent specimen, head of Pauatahanui arm, Porirua Harbour, W Wellington; height 32.0 mm. (I) *Stiracolpus symmetricus* (Hutton), TM5375, paralectotype of *Turritella (Zaria) tricincta* Hutton, 1873 (preoccupied) identified as *Stiracolpus delli murdochi* by Marwick (1957b), Shakespeare Cliff Siltstone (Castlecliffian, OIS 11), "Shakespeare Cliff", Wanganui; height 30.7 mm. (K) *Stiracolpus huttoni* (Cossmann), Marwick's (1957b, pl. 5, fig. 12) illustrated specimen, GS2877, J33/f7076, Lake Kaniere Road, Westland, Opoitian; height 18.3 mm.

170 m drilled in the well was not recovered. Seven samples from near the top of the well (fossil record no. SE42170/f01; extending from 170 to 520 m below the seabed; at 170–180 m, 240–250 m, 270–280 m, 300–310 m, 360–370 m, 450–460 m, and 510–520 m) contained diverse, well-preserved molluscs, including such taxa as *Paracomitas gemmea* (Murdoch, 1900) (see in Part 4) and *Propebela* cf. *abnormis* (Hutton, 1885) (*Propebela* is adopted in Part 4), indicating a probable latest Nukumaruan–early Castlecliffian age. Fragments of other taxa such as *Falsilunatia*, *Splendrillia* and *Scaphander* contribute to the interpretation of this fauna as having lived in the upper bathyal zone, in water depths of 200–400 m, or more. The few fragments present of shelf taxa such as *Austrofusus glans* indicate down-slope transport of some specimens into the deposition site.

Several of the species present in these samples had not previously been recorded as fossils*, but were described in the Recent fauna of New Zealand, and the new records and a few other uncommon species are recorded here:
**Saccella hedleyi* (Fleming, 1951), fragments (240–250 m);
**Austrotindaria benthicola* Dell, 1956 (240–250, 300–310 m);
Poroleda lanceolata (Hutton, 1885) (240–250 m);
**Neilo* cf. *wairoana delli* Marshall, 1978, fragments (all samples);
Neilo cf. *sublaevis* Marwick, 1926, fragments (240–250 m);
**Lissotesta* cf. *errata* Finlay, 1926 (240–250 m);
**Tectisumen clypidellaeformis* (Suter, 1908) (450–460 m);
**Rissoa (Haurakia) subsuturalis* (Dell, 1956) (almost all samples);
**Rissoa (Haurakia) otagoensis* (Dell, 1956) (510–520 m);
**Malluvium calcareum* (Suter) (Suter, 1909) (240–250 m);
Galeodea triganceae Dell, 1953, fragments (240–250, 270–280 m);
Sassia kampyla (Watson, 1885), fragments (170–180, 240–250, 270–280 m);
**Cominella (Eucominia) powelli* (Fleming, 1948) (240–250, 270–280, 360–370 m);
Penion benthicolus Dell, 1956 (240–250, 270–280, 300–310 m);
Paracomitas gemmea (Murdoch, 1900) (240–250 m) (see below);
Taranis nexilis (Hutton, 1885) (170–180, 240–250, 270–280 m);
Aoteadrillia wanganuiensis (Hutton, 1873) (170–180, 240–250 m);
Antimelatona buchanani (Hutton, 1873) (270–280 m);
Propebela cf. *abnormis* (Hutton, 1885) (240–250 m);
**Ringicula* aff. *delecta* Murdoch & Suter, 1906 (240–250 m).

Taxonomy
Phylum Mollusca
Class Gastropoda

Remarks. The taxonomic order here follows that of Bouchet et al. (2005). Authorship and dates of all taxa at subfamily level and above also can be found in Bouchet et al. (2005).

Clade Vetigastropoda

Family Trochidae

Genus *Cantharidella* Pilsbry, 1889

Cantharidella Pilsbry 1889a:197. Type species (by original designation): *Gibbula picturata* A. Adams & Angas, 1864, Recent, SE Australia.

Remarks. Molecular studies of Trochoidea and Turbinoidea are in the process of revitalizing their classification at present, and Williams & Ozawa (2006), Williams (2007) and Williams et al. (2008) have recognized several new families. *Cantharidella* has usually been placed in a subfamily Gibbulinae, but Williams et al. (2008:15) pointed out that the blue-green nacre that characterizes Trochidae Cantharidinae, as compared with the more usual colourless to pearly nacre of other trochoideans, is also present in *Gibbula* and *Cantharidella*. In a wider molecular study, Williams et al. (2010) showed that *Gibbula* and *Cantharidella* belong in the Cantharidinae.

Cantharidella tessellata (A. Adams, 1853) (Fig. 5A,D)

Margarita tessellata A Adams 1853:191.
Gibbula nitida A Adams & Angas 1864:36; Hutton 1880:102.
Chrysostoma inconspicua (sic). Hutton 1873a:36.
Gibbula inconspicua. Hutton 1880:102.
Photinula nitida. Suter 1913:134, pl. 38, fig. 20; Finlay 1926b:358.
Talopena sublaevis Finlay 1924c:520, fig. 3; Cernohorsky 1972:241, fig. 15.
Cantharidella tessellata. Finlay 1926b:358; Powell 1979:57, pl. 18, fig. 25; Spencer & Willan 1996:14; Spencer et al. 2009:203; Maxwell 2009:239.

Type material. Margarita tessellata, three syntypes BMNH 1968107, without locality. *Gibbula nitida*, 18 syntypes BMNH 1870.10.26.144, from 'Hokianga [Harbour, Northland], New Zealand'. All these specimens are conspecific, and are the New Zealand species known by the name *Cantharidella tessellata*, and lectotypes are not needed. *Chrysostoma inconspicuum*, four syntypes NMNZ M.210 (Marshall 1996:13), without locality. *Talopena sublaevis*, holotype, AIM AK70756 (Cernohorsky 1972:241, fig. 15), a juvenile specimen from 'oyster scrapings, Bluff', Foveaux Strait (not seen).

Other material examined. **Nukumaruan:** GS12816, V20/f0147, Darkys Spur Formation, Waipunga Road, central Hawke's Bay (late Nukumaruan, OIS 67–69?; 1); GS12790, V20/f038, Tangoio Limestone, cutting on track 500 m N of Petane Pa, N of Napier, central Hawke's Bay (late Nukumaruan, OIS 65?; one; Fig. 5A,D). **Haweran:** GS12783, R22/f0151, Putiki Shellbed, main highway in Awarua valley, E of Wanganui (early Haweran, OIS 9; 1); also occurs in Brunswick Formation at Mt Jowett (GS4151, R22/f7416, 1) and at Sewell Road, Wanganui (OIS 9); Denby Shellbed at Waihi Beach, Hawera, South Taranaki (OIS 7); Rapanui Terrace, Waitotara, west of Wanganui (OIS 5e); Cape Wanbrow, Oamaru (OIS 5e); and Holocene deposits at Cape Kidnappers and Mahia Peninsula (common in many samples from the transects through Holocene terraces at Table Cape).

Distribution. Cantharidella tessellata occurs now in the intertidal zone of exposed rocky shores throughout the three main islands of New Zealand, but not at the Chatham Islands (Powell 1979:57). Fossils are recorded from late Nukumaruan (OIS 67–69?) rocks to Recent, but are rare other than in a few localities in the Petane Group in Hawke's Bay, in Brunswick Formation (OIS 9) around Wanganui, and in Holocene terrace cover beds.

Dimensions. Margarita tessellata, syntypes H 6.7, D 8.3 mm; H 6.0, D 7.6 mm; H 6.6, D 6.8 mm; RM3443, coast E of Island Bay, Wellington: H 8.2, D 8.8 mm; RM915, Waimarama, E Wairarapa: H 8.3, D 6.9 mm (unusually tall and narrow).

Remarks. Cantharidella tessellata is easily recognized by being almost the only one of the common, small, shallow-water New Zealand trochids that is deeply and obviously, if narrowly, umbilicate. Combined with the low, wide, closely spaced spiral cords, the umbilicus is a readily recognized character. Care has to be taken to distinguish *C. tessellata* from umbilicate specimens of *Cantharidus* species, particularly *C. tenebrosus* (A. Adams, 1853), which Marshall (1998:126, fig. 20–23) showed retains an open umbilicus at all sizes in all but the narrowest individuals. However, *C. tenebrosus* is easily distinguished from *C. tessellata* by its larger size, taller spire, and much more prominent, narrow, well-separated spiral cords. In *C. tessellata*, the height is roughly equal to the diameter (slightly taller than the diameter in some specimens), the shape is almost spherical, and the surface is unusually smooth for a New Zealand trochid, with low, closely spaced spiral cords, lightly polished in many specimens. The syntypes of *Margarita tessellata* are all patterned in paler and darker grey, in a checkerboard pattern, whereas the syntypes of *Gibbula nitida* are the more usual multicoloured assortment of checkerboard and spiral patterns.

This is one of several species that Fleming (1953) thought appeared first in Brunswick Terrace cover beds (OIS 9) in Wanganui Basin, at Mt Jowett, Wanganui, and therefore was regarded until recently as a potential Haweran index species. Along with several other such species, it is now clear that there are much earlier records elsewhere (including *Risellopsis varia* (Hutton, 1873) [see below], *Mytilus galloprovincialis* Lamarck, 1819 and *Protothaca crassicosta* (Deshayes, 1835); Beu 2006). These species occupy intertidal rocky shores and therefore have a fossil record that is highly unreliable for biostratigraphy. The common New Zealand shallow offshore to sandy shoreface fossil localities of Castlecliffian–Nukumaruan age rarely contain such taxa. *C. tessellata* now can be recorded from late Nukumaruan (OIS 67–69?) rocks of the Petane Group in Matapiro Syncline, central Hawke's Bay. I am not aware of records earlier than late Nukumaruan, but this apparent first occurrence is most unlikely to be reliable for biostratigraphy. Most fossil specimens are severely abraded, reflecting transport from their intertidal environment.

Genus **Clanculus** Montfort, 1810

Clanculus Montfort 1810:190. Type species (by monotypy): '*Trochus pharaonicus*' (= *Trochus pharaonius*) Linné, 1758, Recent, Indo-West Pacific.

Mesoclanculus Iredale 1924:224. Type species (by original designation, Iredale 1924:182): *Clanculus plebejus* Philippi, 1851, Recent, southern Australia.

Remarks. Wilson (1993:83) pointed out that Cotton & Godfrey's (1934) generic subdivision of *Clanculus* can be applied only to the southern Australian temperate species, and breaks down with the addition of tropical Indo-West Pacific species. *Mesoclanculus* is therefore regarded as a synonym of *Clanculus*, which also has many other synonyms. Jansen (1995b) also used no subgenera in her revision of Australian *Clanculus* species.

Clanculus plebejus (Philippi, 1851) (Fig. 5C,F,H)

Trochus plebejus Philippi 1851:41; Philippi 1855 (in 1846–1855), p. 326, pl. 46, fig. 10; Fischer 1878 (in 1875–1880), p. 243, pl. 83, figs. 2, 2a.
Clanculus nodiliratus A Adams 1853:163; Angas 1865:179; Angas 1871:96; Tenison Woods 1878:40; Tenison Woods 1880:69.
Clanculus angeli Tenison Woods 1877:144 (synonym according to Tenison Woods 1878); Hardy 1915:62.
Clanculus dominicanus Tenison Woods 1877:144 (synonym according to Tenison Woods 1878); Tenison Woods 1878:40; Tenison Woods 1880:69; Hardy 1915:65.
Gibbula multicarinata Tenison Woods 1877:142 (synonym according to Tenison Woods 1878; Iredale 1924:224); Tenison Woods 1878:42; Tenison Woods 1880:70; Petterd 1879:354; Hardy 1915:68.
Trochus muscarius Fischer 1878 (in 1875–1880), pp. 243, 244 (in synonymy of '*Trochus plebejus* var. β'; synonym according to Iredale 1924:224).
Trochus nodoliratus. Whitelegge 1889:271.
Trochus (Clanculus) plebejus. Pilsbry 1889b:79, pl. 10, figs. 19–22; pl. 13, figs. 1, 2.

Clanculus plebejus. Tate & May 1901:401; May 1921:37; May 1923:41, pl. 18, fig. 13; Macpherson & Chapple 1951:113; Macpherson 1958:22, pl. 18, fig. 13; Monger 1984:140, illus.; Wilson 1993:88, unnumbered fig.; Jansen 1995:59, pl. 3, figs. 16–18.
Trochus dominicanus. Pilsbry 1889b:59.
Trochus angeli. Pilsbry 1889b:60.
Clanculus plebeius (sic). Pritchard & Gatliff 1902:122; Verco 1908:6; Verco 1912:202; Hedley 1916a:178; Hedley 1916b:700; Verco 1935:6.
Trochus (Clanculus) takapunaensis Webster 1906:309, pl. 39, Fig. 2, 2a.
Eurytrochus plebejus Hedley 1918:M42.
Mesoclanculus plebeius. Iredale 1924:182, 224.
Clanculus (Mesoclanculus) plebejus. Cotton & Godfrey 1934:89; Singleton 1937:389; Cotton & Godfrey 1938:4; Kershaw 1955:304; Macpherson & Gabriel 1962:73; Macpherson 1966:212; Ludbrook & Gowlett-Holmes 1989:558, fig. 11.16n-p.
Mesoclanculus plebejus. Powell 1958b:89; Cotton 1959:138, fig. 73.
Clanculus (Mesoclanculus) plebeius. Ludbrook 1978:9.

Type material. *Trochus plebejus* Philippi, type material presumably in Philippi's collection, in Museo Nacional de Historia Natural, Santiago, Chile; not available for examination. *Clanculus nodiliratus* A. Adams, no type material present in BMNH (K Way, BMNH pers. comm. 14 Jan 2008), location unknown; without locality. *Gibbula multicarinata* TASM TM5566, one syntype; *Clanculus angeli* TASM TM5564, one syntype; and *C. dominicanus* TASM TM5558, one syntype, all of Tenison Woods (1877) (Hardy 1915:62, 65, 68) (not seen). *Trochus muscarius* Fischer, no type material in MNHN; as this name was proposed in the synonymy of *Trochus plebejus* var. β and has never been used as a valid name, type material presumably was never selected. *Trochus (Clanculus) takapunaensis* Webster, holotype AIM AK70778 (not seen), an empty shell picked up on Takapuna Beach, Auckland; Powell (1958b:89) when synonymizing this name with *Mesoclanculus plebejus* suggested that it was an 'accidentally dropped shell'.

Other material examined. **Nukumaruan:** 3–10 m above Torlesse greywacke, Opawe Stream, Pohangina valley, E Wanganui Basin, with *Glycymeris shrimptoni* Marwick, 1923, *Myadora waitotarana* Powell, 1931, *Sabia australis* (Lamarck, 1819) (see below), *Diloma*, *Micrelenchis*, *Austrolittorina*, and diverse Rissooidea, an unusual shallow-water assemblage that obviously was deposited near an exposed rocky shore (GS2784, T23/f6491, one specimen). **Recent:** 35 m, off Taranga I, Hauraki Gulf, Auckland, C. A. Fleming collection (RM1001, two small, abraded, the larger incomplete).

Distribution. *Clanculus plebejus* is an abundant shallow-water trochid of exposed rocky shores in SE Australia, from Sydney, New South Wales, to Cape Naturaliste, S Western Australia (Wilson 1993:88). Macpherson & Gabriel (1962:73) stated that *C. plebejus* is 'the commonest species of the genus in Victoria obtained in countless numbers on the whole coastline'. A single shell from Takapuna Beach, Auckland, the holotype of *Trochus takapunaensis* Webster, was considered by Powell (1958b) to belong in *C. plebejus*, although it is much more finely sculptured than the specimen illustrated by Wilson (1993:88). Charles Fleming's boyhood collection also contains two small, abraded specimens of '*Clanculus takapunaensis*' from Hauraki Gulf, Auckland. These are typical specimens of *C. plebejus*, with six uniform, rather coarsely nodulose spiral cords on the upper surface of the last whorl. Another New Zealand specimen is recorded here, from early Nukumaruan rocks in Opawe Stream, Pohangina valley, eastern Wanganui Basin, but all new Zealand records presumably result from accidental rafting events (or, for the Recent specimens, might be merely mislocalized Australian shells). Specimens evidently were rafted to New Zealand at least once, and possibly three times.

Dimensions. GS2784, Opawe Stream: H 5.1, D 7.1 mm; normal adults 7 × 10 mm (Cotton 1959:139).

Remarks. The newly recorded Opawe Stream specimen is highly aberrant and does not agree exactly with any southern Australian *Clanculus* species. Firstly, it has an immature aperture, with thin lips, so the final apertural armament is unknown. The umbilical wall also has been perforated by an epibiont, probably a bryozoan formerly attached there. However, it is clear that it is a species of one of the *Clanculus* species groups with a relatively simply sculptured umbilicus and inner lip, and an essentially smooth lining of the umbilicus. It differs from the restricted northeastern New Zealand Recent species *C. peccatus* (Finlay, 1926) (Powell 1979:60, pl. 17, fig. 4) in its much lower spire angle, its strongly convex rather than flat whorl profile, its obviously channelled rather than weakly impressed suture, its fewer, more prominent spiral cords, its more finely sculptured base, and its much less elaborately sculptured aperture and umbilicus. The Opawe Stream specimen has a unique wide, shallow depression occupying the inner half of the base over the last eighth of a whorl, between the umbilicus and a medial angulation along the outer edge of the depression, and it is clear that whatever species it belongs in, it is an aberrant specimen and cannot be expected to agree in all characters with normal specimens. The spiral sculpture on the upper (adapical) surface of early spire whorls consists of three equally prominent, quite coarsely nodulose cords, but on the penultimate whorl the uppermost cord begins to subdivide, producing on the last half-whorl a wide, shallow subsutural channel, followed by a depressed zone with six equally low, closely spaced, finely beaded spiral cords, followed below by two very prominent, widely spaced, coarsely nodulose cords continuing unchanged from the earliest teleoconch whorl; the lowest of these is weakly subdivided by a groove, and the lowest, almost smooth subdivision of this cord forms the periphery. The base bears seven smooth, narrow spiral cords in addition to the peripheral one, with a fine secondary thread between the second and third ones in from the margin. A smooth, low tooth at the base of the columellar margin of the umbilicus is set well back from the aperture; the inner lip is otherwise smooth. The entire surface is crossed by narrow, well-raised axial lamellae, coarse and prominent on the upper surface but thin and low on the base. The general appearance is therefore intermediate between those of Webster's (1906, pl. 39, fig. 2) and Wilson's (1993:88) drawings of *C. plebejus*, with a very similar base apart from the lack of nodules around the outer edge of the umbilicus, but with a protruding lower half of the upper whorl surface, a depressed upper half, and a wide, shallow sutural channel. This very aberrant specimen seems nearest to *C. plebejus*, and perhaps was aberrant as a result of surviving very rare larval transport to New Zealand and finding an unsuitable habitat here. It seems more likely, however, that this specimen was rafted to New Zealand in an algal holdfast or similar floating object. It is interesting that Webster's (1906) specimen was also considered by Powell (1958b:90) to fall within the variation of southern Australian specimens of *C. plebejus*, suggesting the possibility that Webster's specimen was also a rafted shell. As noted above, the two Fleming collection specimens from off Taranga Island, Auckland, are also very small, abraded specimens of *C. plebejus*, so this species that is so abundant in SE Australia evidently is the trochid most commonly rafted from Australia to New Zealand. Jansen (1995:48) recorded that the more westerly species *C. consobrinus* Tate, 1893 (Adelaide to Kalbarri, Western Australia) is similar to *C. plebejus* but has fewer spiral cords, is paler in colour, does not have nodules on all spiral cords, and lacks a columellar tooth, so in some ways the fossil seems closer to *C. consobrinus* than *C. plebejus*. However, the aberrant fossil is difficult to compare, and the further westerly distribution makes *C. consobrinus* an unlikely migrant to New Zealand, so an identification as *C. plebejus* seems more reasonable.

The sole previous fossil record of a southern Australian trochoidean from New Zealand is the specimen of *Bankivia fasciata* recorded by Beu (2004:187). That also was considered likely to have been rafted. *B. fasciata* is also an abundant species in southern Australia. The minute demersal larvae of trochoideans float well and have been identified as a possible means of dispersal by Hadfield & Strathmann (1990) and Hickman (1992). It certainly appears that some trochoidean species have wide distributions in the Indo-West Pacific similar to those of planktotrophic caenogastropods such as *Cypraea* and *Monoplex* species. However, molecular phylogeny has demonstrated that some apparently widespread Indo-West Pacific turbinoideans (recognized as a superfamily separate from Trochoidea by Williams & Ozawa 2006) such as *Astralium rhodostoma* (Lamarck, 1822) (Meyer et al. 2005) are actually diverse species complexes, with restricted species inhabiting each island group, making it obvious that genetic exchange of turbinoideans (and so, by analogy, trochoideans) between island groups has not been as great as shell morphology suggests. This and the fact that not one species of trochoidean is now in common to Australia and New Zealand (BA Marshall NMNZ pers. comm.) makes a rafting origin for southern Australian trochoideans in Wanganui Basin considerably more likely than transport as larvae. The occurrence of another rocky shore intertidal trochoidean, *Diloma nigerrima* (Gmelin, 1791) abundantly in both Chile and New Zealand as well as at Juan Fernandez (Donald et al. 2005) demonstrates another case of rafting of a trochoidean, so their transport on algal holdfasts is possibly more common than has been appreciated previously. Waters (2008) recently argued for a significant role of algal rafting in southern temperate marine biogeography.

Family Calliostomatidae

Genus ***Calliostoma*** Swainson, 1840

Calliostoma Swainson 1840:218, 351. Type species (by subsequent designation, Herrmannsen 1846:154): *Trochus conulus* Linné, 1758, Recent, Mediterranean and northeastern Atlantic.

Remarks. A synonymy of the genus and discussion of its status and synonyms were provided by Marshall (1995a). Calliostomatidae was established firmly as a family of Trochoidea by Williams et al. (2010).

Subgenus ***Maurea*** Oliver, 1926

Maurea Oliver 1926:108. Type species (by original designation): *Trochus tigris* Gmelin, 1791, Pleistocene and Recent, New Zealand [20 December 1926].
Mauriella Oliver 1926:109. Type species (by original designation): *Trochus punctulatus* Martyn, 1784, Pleistocene and Recent, New Zealand [20 December 1926; species name available, ICZN Opinion 479 1957].
Calliotropis Oliver 1926:110. Type species (by original designation): *Trochus cunninghami* Gray, 1834 (= *Trochus selectus* Dillwyn, 1817), Pleistocene and Recent, New Zealand [20 December 1926] (junior homonym of *Calliotropis* Seguenza, 1903).
Mucrinops Finlay 1926b:360. Type species (by original designation): *Ziziphinus spectabilis* A. Adams, 1855, Recent, southern New Zealand [23 December 1926].
Venustas Finlay 1926b:360. Type species (by original designation): *Trochus tigris* Gmelin,

1791, Pleistocene and Recent, New Zealand [23 December 1926; name officially rejected, ICZN Opinion 479 (1957:373); junior homonym of *Venustas* Allan, 7 December 1926].
Calotropis Thiele 1929:49. Replacement name for *Calliotropis* Oliver, 1926, preoccupied.

Calliostoma (Maurea) nukumaruense (Laws, 1930) (Fig. 5B,G,I)

Modelia nukumaruensis Laws 1930:550, pl. 90, fig. 8; Fleming 1966:40.
Calliostoma (sensu lato) *nukumaruense*. Beu & Maxwell 1990:405.
Calliostoma (Maurea) nukumaruense. Maxwell 2009:239.

Type material. Modelia nukumaruensis, holotype AIM AK70483 (not seen), from 'Nukumaru', that is, Nukumaru Brown Sand, Nukumaru Beach, late Nukumaruan (Fleming 1953:143); 'two juvenile paratypes (Kai Iwi)' (early Castlecliffian, horizon unknown).

Other material examined. Fleming (1953:139, 143, 174, 178, 181, 182) recorded '*Modelia nukumaruensis*' from Nukumaru Limestone (GS4183, R22/f6468, Ototoka Stream), Nukumaru Brown Sand (GS4115, R22/f6435, 'member f', Nukumaru Beach), four localities in Butlers Shell Conglomerate, OIS 31 (GS4081, R22/f6412; GS4083, R22/f6413; GS4109, R22/f6432, on the Ototoka coast, and GS4157, R22/f6458, in Kai-Iwi Stream), from the basal conglomerate member of Lower Okehu Siltstone, OIS 29 (Mowhanau Formation; Abbott & Carter 1999) on the Ototoka coast (GS4082, R22/f6532; GS4108, R22/f6431, as '*Maurea* (*Mucrinops*) *nukumaruensis*'), Okehu Shell Grit, OIS 27 (GS4066, R22/f5387; GS4071, R22/f6402), and the basal conglomerate member of Upper Okehu Siltstone, OIS 27 (*Ostrea-Dosina* Bed; Abbott & Carter 1999) (again as '*Maurea (Mucrinops) nukumaruensis*'; from any of five collections, not listed individually). Specimens recorded by Fleming (1953:209) from undifferentiated formations of Kai-Iwi Group (GS4235, R21/f8479, W side Whangaehu Valley; GS4375, S22/f6498, head of Kaukatea valley) are not assignable to a precise formation or age. Material in the GNS reference collection: 'Kai-Iwi', unlocalized to formation, CA Fleming collection (four; abraded, probably from Kaimatira Pumice Sand, OIS 25); Nukumaru Brown Sand, Nukumaru Beach (GS4115, R22/f6435, 18; GS4117, R22/f6437, four; GS4184, R22/f7433, one); GS4066, R22/f6397, Okehu Shell Grit, Okehu Beach (OIS 27; four); Kaimatira Pumice Sand, OIS 25 (GS4139, R22/f6449, one; GS4140, R22/f6450, one; GS4148, R22/f7414, three; GS4064, R22/f6395, nine; GS4163, R22/f6459, one; GS15190, S22/f0155, one abraded); Kaikokopu Shellbed, OIS 19 (GS4134, R22/f7408, four; GS15191, S22/f0156, one fragment); Kupe Formation (OIS 17), Castlecliff coast (GS4047, R22/f6378, two; GS4121, R22/f6521, one, with one *C. punctulatum*; GS14150, R22/f0128, one).

Distribution. Calliostoma nukumaruense is recorded only from late Nukumaruan and early Castlecliffian rocks of Wanganui Basin; the youngest record is from Kupe Formation (OIS 17).

Dimensions. Modelia nukumaruensis, holotype: H 18, D 15 mm (Laws 1930:551); GS4115, Nukumaru Brown Sand, Nukumaru Beach: H 20.3, D 19.3 mm; H 16.4, D 17.0 mm; H 16.9, D 16.9 mm; H incomplete, D 26.9 mm (largest seen, apex missing, identity slightly in doubt); GS4121, Kupe Formation, Castlecliff: H 16.2, D 17.8 mm.

Remarks. Laws (1930) was impressed by the similarity of this species in its turbiniform shape, evenly and strongly convex whorl profile, and relatively coarse, even, nodulose sculpture to *Modelia granosa* (Martyn, 1784) (Turbinidae), and described it under the name *Modelia nukumaruensis*. *M. granosa* was described from the Recent New Zealand fauna but is recorded intermittently from rocks of

Tongaporutuan (late Miocene) to Pleistocene age. Laws compared the new species only with this member of the Turbinidae. CA Fleming published a position in *Calliostoma* in several places in species lists (Fleming 1953), and discussed it with PA Maxwell and me many years ago. Initially this position was based on the observation that no calcareous opercula characteristic of the Turbinidae have been collected anywhere in the formations in which this species occurs, although the shells are common at some horizons within Nukumaru Brown Sand. The teleoconch is much smaller (to ca 27 mm high, although rarely more than 20 mm, compared with to ca 80 mm high in *M. granosa*) and a little more finely sculptured than in *M. granosa*. It also has a general appearance much more nearly like those of New Zealand species of *Calliostoma (Maurea)* with evenly and strongly inflated whorls, a deeply impressed suture, and evenly granulose sculpture, such as the Pliocene–Recent species *C. granti* (Powell, 1931) and the Pleistocene–Recent species *C. punctulatum* (Martyn, 1784) (see Marshall 1995a). There is no doubt that *C. nukumaruense* is closely related to these *Calliostoma* species. It is recognizable by its consistently small size (few specimens > 20 mm high), its thick shell, its strongly and evenly inflated whorls, and its consistently coarse sculpture.

Compared with the development of teleoconch spiral cords on *Calliostoma (Maurea) granti* and *C. punctulatum*, described by Marshall (1995a:89,92, fig. 28, 29), *C. nukumaruense* is distinguished by lacking the strongly convex fifth teleoconch whorl of *C. punctulatum*. All secondary cords appear almost simultaneously (S3 slightly before S1 and S2 on most specimens) on the fourth teleoconch whorl and all enlarge rapidly to be as prominent as the primary cords over the fifth whorl of *C. nukumaruense*. Secondary cords appear on the fifth teleoconch whorl on *C. punctulatum*, leaving an unusually obvious channelled suture on early spire whorls that disappears once the outline is filled in by S3 on the fifth whorl. In contrast, all secondary cords appear earlier and S3 appears particularly early on the fourth whorl, so the suture is filled and a distinctly wider fifth whorl is not developed on *C. granti*. Obvious, narrow axial ridges uniting nodules on neighbouring spiral cords of the first three teleoconch whorls are present on both *C. granti* and *C. nukumaruense*, but not *C. punctulatum*. Some specimens of *C. nukumaruense* have a weakly developed sutural channel on early spire whorls, less obvious (as it extends a shorter way down the teleoconch) than in *C. punctulatum*, but more marked than in *C. granti*. *C. nukumaruense* is therefore more nearly similar to *C. granti* than *C. punctulatum*, but differs from *C. granti* in the later development of S3, all three main secondary cords developing almost simultaneously over the fourth whorl, and the consequent development of a narrow sutural channel on teleoconch whorls 2–3, as well as in its small size, thick shell, and consistently coarse sculpture. Details of the protoconch and first teleoconch whorl are not visible on any material I have seen.

Clade Sorbeoconcha

Superfamily Cerithioidea

Family Cerithiidae

Genus ***Taxonia*** Finlay, 1926

Taxonia Finlay 1926b:384. Type species (by monotypy): *Ataxocerithium suteri* Marwick, 1924, Mangapanian-Nukumaruan (late Pliocene–early Pleistocene), New Zealand.

Taxonia suteri. (Marwick, 1924) (Fig. 6A,E,H)

Ataxocerithium suteri Marwick 1924b:195, pl. 17, fig. 2; Finlay 1924a:474, pl. 51, fig. 9a, b.

Taxonia suteri Finlay 1926b:384; Fleming 1966:48, fig. 929; Beu & Maxwell 1990:318, pl. 41i; Maxwell 2009:240.

Type material. Ataxocerithium suteri, holotype TM6769, GS1063, V21/f8476, Okawa Stream, central Hawke's Bay, late Nukumaruan. (Care is needed to distinguish Okawa Stream, north of the Ngaruroro River in Matapiro Syncline, from Okauawa Stream, in the Kereru district, south of the Ngaruroro River and west of Mason Ridge).

Other material examined. **Mangapanian:** GS6215, M34/f7660, 50 m above Waiauan limestone, Weka Creek, 160 m downstream from junction with Weka Pass Stream, N Canterbury (two; with *Cominella (Eucominia)* aff. *elegantula* (Finlay, 1926), *Polinices waipipiensis* (Marwick, 1924), *Glycymerita (Manaia) manaiaensis* (Marwick, 1923)). **Nukumaruan:** The few records present in the GNS reference collection are: Okawa Stream, central Hawke's Bay (GS1063, V21/f8476, 18 paratypes); 'Petane limestone, Petane', Hawke's Bay (that is, Tangoio Limestone) (GS691, V20/f8476, five); upper band of limestone, Petane, Hawke's Bay (GS720, V20/f8482, six); summit of tabletop hill, Waitio Station, west of Makuri-Coonoor Road, southern Hawke's Bay, in estuarine fauna with *Austrovenus stutchburyi* (Wood, 1828) form *crassitesta* and *Zeacumantus lutulentus* (Kiener, 1842) (GS14833, T24/f062, 22); GS12711, V20/f045, Tangoio Limestone, roadside quarry on Waipunga Road, 1 km N of junction with Turnbull Road, central Hawke's Bay (seven); GS12712, V20/f047, Te Ngaru Mudstone?, Waipunga Road, near top of ascent from Esk valley, thin sand beds with *Paphies* and mud partings (two); GS12790, V20/f038, Tangoio Limestone, cutting on track 500 m N of Petane Pa, N of Napier, central Hawke's Bay (one).

Distribution. All records of *Taxonia suteri* are Nukumaruan, apart from the single Mangapanian record from Weka Pass, N Canterbury. Although there are no records from the youngest Nukumaruan rocks of Wanganui Basin (Fleming 1953) or, indeed, many from Wanganui Basin at all, it is widespread and abundant in late Nukumaruan rocks of central to southern Hawke's Bay. It could be expected to occur in small numbers in Tewkesbury Formation and Pukekiwi Shellbed in Wanganui Basin. I am not aware of records from Wairarapa district and know of only the one Mangapanian one from North Canterbury, suggesting that *T. suteri* was a warm-water species.

Dimensions. Ataxocerithium suteri, holotype: H (incomplete) 19.0, D 6.1 mm; paratypes, GS1063, Okawa Creek, Matapiro syncline: H (incomplete) 18.9, D 5.9 mm; H (incomplete) 16.0, D 5.3 mm (sectioned specimen); GS6215, Weka Creek, N Canterbury: H (incomplete) 17.0, D 6.7 mm.

Remarks. Taxonia suteri is highly distinctive and easily recognized. It is a tall-spired, flat-whorled, narrow shell reaching ca 30 mm in height, with the entire exterior sculptured with three rows per whorl of large, closely spaced, smooth, circular nodules, flattened in the plane of the shell surface. As pointed out by Finlay (1926b:384) and Marwick (1948:28) its most distinctive character is the six unusual, prominent, wide, spiral ridges within the aperture: three inside the outer lip (two high up and one near the base; all formed as enlargements of the internally protruding exterior spiral interspaces), two on the parietal area, and one on the base of the columella. One of the paratypes (Fig. 7A) was sectioned longitudinally by Marwick, apparently in 1924, and confirms that the largest spiral ridge, low on the columella, and the spiral ridge on the top of the columella extend down the entire teleoconch.

Taxonia seems to have been an estuarine genus (as are many of the other warm-water 'mud creepers' in this superfamily at present) and so there are relatively few records before Nukumaruan time, when this facies became better represented in the fossil record than it had been previously. Marwick (1948:28, pl. 7,

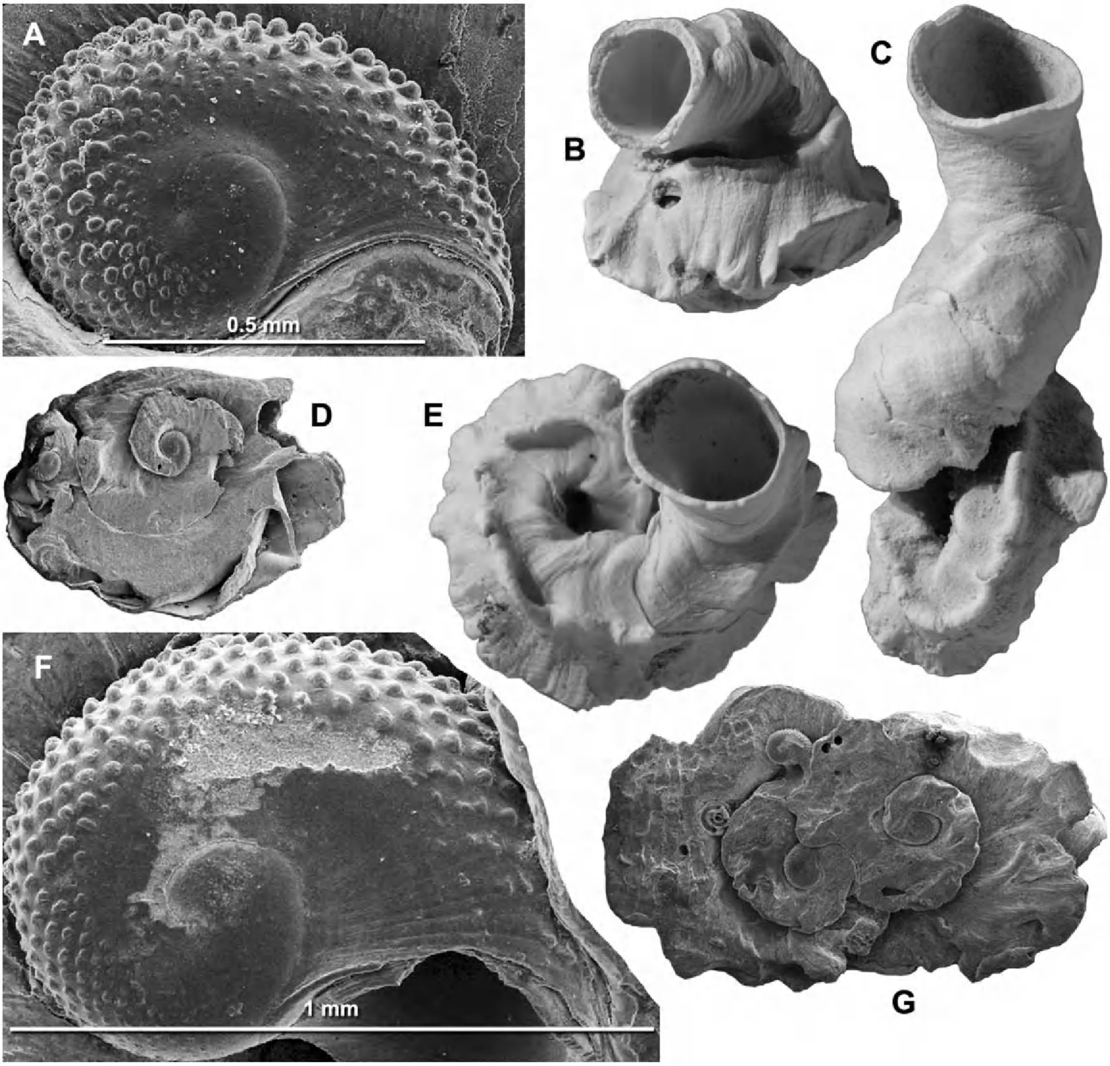

Fig. 7 *Stephopoma roseum* (Quoy & Gaimard). (A,D) GS15443, Y14/f505B, Te Piki, near East Cape, Haweran (OIS 7), SEM; D, basal view of 2 intergrown shells, protoconchs visible, width 7.0 mm; A, protoconch. (B,C,E) GS4013, R22/f6353, Tainui Shellbed (Castlecliffian, OIS 13), "the buttress", Castlecliff, Wanganui, 3 specimens; B,C, lateral views, height 7.9 mm (B) and 17.8 mm (C); E, dorsal view, width 10.8 mm. (F,G) GS4013, R22/f6353, Tainui Shellbed (Castlecliffian, OIS 13), "the buttress", Castlecliff, Wanganui, SEM; G, basal view of group of 3 shells, protoconchs visible, width 10 mm; F, protoconch.

fig. 1) described *T. tesserata* from the Waipipian (Pliocene) estuarine fauna of Otahuhu well, Auckland on the basis of a single specimen with smaller, more spherical nodules and a more deeply impressed suture than in *T. suteri.* The Laws collection material in GNS contains one more specimen. A tubeful of small juvenile cerithioids from Otahuhu well received by GNS in CR Laws' collection is labelled '*Taxonia tesserata* Marwick, paratypes' (TM1984–1988, nine specimens) and these all have almost complete apices and one has a complete protoconch. However, the spire angle and sequence of development of spiral cords agree precisely with other specimens assigned to *Zeacumantus delicatus* Laws, 1950 (that is, *Pyrazus ebeninus* (Bruguière, 1792); Beu 2004:200) and there is no doubt that they have been misidentified. Unfortunately, this means that I have not seen a protoconch of *Taxonia*. Wells (1986:313, fig. 3a–c) described *Taxonia gudrunae* from a Tongaporutuan (late Miocene) deposit in northern Wairarapa. *T. gudrunae* was a member of an estuarine fauna including *Austrovenus stutchburyi*, *Melanopsis trifasciata* Gray, 1843, *Zeacumantus* cf. *tirangiensis* (Marwick, 1926), *Zefallacia ruamahunga* Wells, 1986, and *Cominella (Josepha) graemei* Wells, 1986, which closely resembles the Nukumaruan–Recent estuarine species *C. glandiformis* (Reeve, 1847). Specimens probably representing *Taxonia gudrunae* occur also in mudstone lenses within Tongaporutuan conglomerate underlying Hurupi Formation in Hurupi and Putangirua Streams, South Wairarapa, again associated with *Zeacumantus* cf. *tirangiensis*. Quite similar specimens have also been collected recently from Chatton Formation (Duntroonian, Oligocene) in a pit on Cosy Dell farm, near Waimumu, Southland (in Geology Department, Otago University). The long gaps in this time range indicate that records of *Taxonia* are unreliable for biostratigraphy because of its estuarine habitat and concomitant poor fossil record. However, the genus is one of many whose late Nukumaruan extinction provides a biostratigraphically reliable definition of the Nukumaruan–Castlecliffian boundary.

Family Batillariidae

Genus ***Zeacumantus*** Finlay, 1926

Zeacumantus Finlay 1926b:380. Type species (by original designation): *Cerithidea subcarinata* G. B. Sowerby II, 1855, Pliocene to Recent, New Zealand.

Zeacumantus lutulentus (Kiener, 1842) (Figs. 1P, 6D,F,G,J)

Cerithium lutulentum Kiener 1842:63, pl. 22, fig. 3.
Cerithium bicarinata (sic) Gray 1843:241 (junior primary homonym of *Cerithium bicarinatum* Lamarck, 1804).
Cerithium (Pirenella) bicarinata. A Adams 1855:84.
Cerithium bicarinatum. GB Sowerby II 1855:888, pl. 186, fig. 288.
Cerithidea bicarinata GB Sowerby II 1866, pl. 4, fig. 27; EA Smith 1874:3, pl. 1, fig. 20 (repeated here, Fig. 1P); Tryon 1887:163, pl. 35, fig. 15; Suter 1913:238, pl. 39, fig. 13.
Ataxocerithium perplexum Marshall & Murdoch 1919:254, pl. 20, Fig. 5, 6 (**new synonym**).
Cerithidea perplexa. Marwick 1924b:194; Finlay 1924a:477.
Zeacumantus perplexus. Finlay 1926b:380; Fleming 1966:47; Lozouet 1986:199; Beu & Maxwell 1990:406; Maxwell 2009:240.
Zeacumantus lutulentus. Finlay 1926b:380; Laws 1940b:51; Fleming 1966:47; Morton & Miller 1968:444–445, pl. 17, fig. 3; Powell 1979:131, pl. 31, fig. 10; Lozouet 1986:198–199; Beu & Maxwell 1990:406; Spencer & Willan 1996:17; Spencer et al. 2009:204; Maxwell 2009:240.

Type material. *Cerithium lutulentum*, no type material present in MHNG, presumably lost (Y Finet MHNG pers. comm. 6 November 2007); from 'les côtes de la Nouvelle Zélande'. *Cerithium bicarinatum*, three syntypes BMNH 1842.11.16.53–55, from 'New Zealand', Dr Stanger (not seen) (one syntype illustrated by EA Smith 1874:3, pl. 1, fig. 20, repeated here, Fig. 1P); Gray (1843:241) also cited syntypes from the Bay of Islands (presented by Sinclair) but these have not been recognized if they are present in BMNH. K Way (BMNH pers. comm. 14 January 2008) stated that one of the three syntypes has been segregated from the others (perhaps the specimen illustrated by Smith?) but I am not aware of a published lectotype designation. The clear, if only life-size, illustration of a fresh, young, unworn specimen by Smith (1874, pl. 1, fig. 20; Fig. 1P) leaves no doubt of the identity of this name. The segregated syntype, BMNH 1842.11.16.53, is here designated the lectotype of *Cerithium bicarinatum* Gray, 1843 as well as the neotype of *Cerithium lutulentum* Kiener, 1842. The two types originally were from the same locality, 'New Zealand'. A neotype designation is required to be certain that the name *Cerithium lutulentum* unambiguously is attached to the present species. *Ataxocerithium perplexum*, illustrated syntype TM6762, bearing the original Marshall label: 'Type example with small area of sculpture', is from 'Nukumaru, in blue sandy clay', that is, Tewkesbury Formation, late Nukumaruan; with one illustrated syntype, TM6763. The second syntype has a completely corroded, smooth surface; it was collected with the more complete syntype. These specimens have been labelled holotype (TM6762) and paratype in the GNS type collection, but in my opinion are syntypes; Marshall & Murdoch (1919:254) did not select one as 'the type', or use any other similar term. The specimen with some sculpture remaining, TM6762, is therefore here selected as the lectotype of *Ataxocerithium perplexum* Marshall & Murdoch, 1919, as the other is unidentifiable.

Other material examined. **Nukumaruan:** almost all undoubted specimens of the form known as *Zeacumantus perplexus* Marshall & Murdoch, 1919 are from Nukumaru Brown Sand and Tewkesbury Formation at Wanganui (e.g. GS15348, R22/f6542A, shellbeds above and below Vinegar Hill Tephra (OIS 61), Brunswick Road, Kai-Iwi valley) and from estuarine sands in Hawke's Bay. Specimens in the GNS reference collection are from Nukumaru Beach (Tewkesbury Formation; GS1164, R22/f6348, 5, one without axial ridges down most of the spire) and summit of table-top hill on Waitio Station, west of the Makuri-Coonoor Road, southern Hawke's Bay (GS14833, T24/f062, many; some typical, some more strongly sculptured; with *Taxonia suteri,* see above); GS12712, V20/f047, Te Ngaru Mudstone?, Waipunga Road, near top of ascent from Esk valley, thin sandy beds with *Paphies* and mud partings (14, abraded). However, it is concluded here that *Z. perplexus* is part of the variation of *Z. lutulentus* (Kiener, 1842), which is widespread and abundant throughout New Zealand in Mangapanian to Haweran estuarine rocks and in the Recent fauna.

Fossils of *Zeacumantus lutulentus* in the GNS collection are from Nukumaru Brown Sand, Tewkesbury Formation, Waipuru Shellbed, Butlers Shell Conglomerate, Upper Okehu Siltstone, Kaimatira Pumice Sand, Kaikokopu Shellbed, Kupe Formation, Whangaehu shellbed (OIS 13, underlying Tainui Shellbed on the Whangaehu-Turakina interfluve) and Brunswick Formation at Wanganui, Te Ngaru Mudstone (Nukumaruan, about OIS 65) on Waipunga Road, Hawke's Bay; recorded as *Z. perplexus* at 345 m and 365 m and as *Z. lutulentus* at 314 m and 335 m in Kowai Formation in the Bexley testbore, Page's Road, Christchurch (Beu 1998; M35/f75 and M35/f69, Nukumaruan); GS14418, V15/f024, Manawahe Road, inland from Matata, Bay of Plenty (OIS 13?), and many younger localities such as Te Piki, near East Cape (OIS 7) and Holocene, Tauranga Memorial Park, Tauranga (GS12569, U14/f03).

Distribution. Zeacumantus perplexus has been thought of as a species restricted to late Nukumaruan rocks of Wanganui Basin, but it is a sculptural variant of *Z. lutulentus* (Kiener, 1842) rather than a distinct species of biostratigraphical utility. *Z. lutulentus* is widespread and abundant in estuarine environments throughout the main islands of New Zealand at present, and is a common fossil in Mangapanian to Haweran rocks of this facies.

Dimensions. *Ataxocerithium perplexum*, holotype: H 33.7, D 10.4 mm; paratype, H 35.0, D 11.3 mm; *perplexus* form, GS14833, Waitio Station, Hawke's Bay: H 30.6, D 9.3 mm; H 26.3, D 9.8 mm; GS1102, V21/f8492, Maraekakaho Stream, Ngaruroro River, central Hawke's Bay, Nukumaruan: H 35.9, D 12.2 mm; GS4084 re-collection, R22/f6414, Pukekiwi Shell Sand, Ototoka Stream mouth, Wanganui: H 42.0, D 13.3 mm; Recent, RM3289, excavation for bridge abutments, Pauatahanui, W Wellington: H 32.0, D 10.5 mm (Fig. 7F,G); H 31.3, D 10.9 mm; NMNZ M.17341, Parengarenga Harbour: H 32.1, D 11.5; H 34.2, D 10.6; H 30.7, D 11.0; NMNZ M.39886, Ohiwa Harbour, Whakatane: H 32.8, D 10.8; H 31.2, D 10.7.

Remarks. The lectotype of *Zeacumantus perplexus* is largely corroded, but the last quarter-whorl bears fresh sculpture. It consists of two rather weak peribasal angulations, formed by cords that are slightly more prominent than the others, and fine, close sculpture of low, narrow, closely spaced spiral cords covering the rest of the exterior from the suture to the canal tip. The cords alternate to some extent in prominence and spacing in some areas, particularly in the central part of the upper whorl slope; there are about 18 cords between the suture and the upper peribasal cord, three between the two peribasal cords, and a further 14 on the base. Several narrow, varix-like axial ridges cross the cords at irregular intervals, sinuate in conformity with the outer lip. At face value, this appears to be a very distinctive, restricted late Nukumaruan species, distinguished from the equally large Mangapanian to Recent species *Z. lutulentus* by its finer sculpture, with slightly more numerous, narrow, closely spaced spiral cords, much weaker axial ridges (fading out down the shell, rather than remaining prominent on to the last whorl as in normal specimens of *Z. lutulentus*) and slightly weaker peribasal cords. However, examination of GNS reference material showed that specimens agreeing closely with the holotype occur only at Nukumaru and on the table-top hill on Waitio Station, S Hawke's Bay; almost all were collected from Tewkesbury Formation. Similar specimens from other Nukumaruan localities have slightly more prominent spiral cords, and axial ridges continuing onto the last whorl. They indicate that *Z. perplexus* is based on unusual, weakly sculptured populations of *Z. lutulentus* that occurred only in the Nukumaru area and in southern Hawke's Bay. Comparison with Recent specimens (e.g. NMNZ M.25864, Te Hapua, Parengarenga Harbour, Northland, 11 clean shells) showed that unabraded and uncorroded Recent specimens have the same 18–20 fine spiral cords between the suture and the upper, prominent peribasal cord as on Nukumaruan fossils, and differ from the *perplexus* form only in retaining the axial ridges until the end of the last whorl. *Z. perplexus* is merely a finely sculptured variant of *Z. lutulentus*. Finlay (1924a:477) long ago pointed out that *Ataxocerithium perplexum* Marshall & Murdoch belongs in '*Cerithidea*', is very similar to *C. bicarinata* (that is, *Z. lutulentus*), and suggested that it 'is possibly only this species with the keels rubbed off'. *Zeacumantus perplexus* is here considered to be a finely sculptured variant of *Z. lutulentus* in which the axial costae fade out over the last whorl, and to be of no taxonomic significance or biostratigraphical utility.

'*Zeacumantus*' *delicatus* Laws, 1950 (Otahuhu well, Auckland, Waipipian) was based on juvenile specimens of *Pyrazus ebeninus* (Bruguière, 1792) (Beu 2004). This leaves *Zeacumantus* containing only the lineage of *Z. lutulentus* (including *Z. tirangiensis* (Marwick, 1926) (Tongaporutuan) and the single species *Z. subcarinatus* (G. B. Sowerby II, 1855). Several unnamed Miocene species apparently ancestral to *Z. lutulentus* are represented in GNS collections. *Z. subcarinatus* is one of the many molluscs with an apparent Haweran first appearance in New Zealand, but as it is a high-tidal rocky shore species, its true time range is unknown and it is completely unreliable for biostratigraphy.

Family Siliquariidae

Genus *Stephopoma* Mörch, 1860

Stephopoma Mörch 1860:42. Type species (by subsequent designation, Cossmann 1912:134): *Vermetus roseus* Quoy & Gaimard, 1834, Pleistocene and Recent, New Zealand.
Lilax Finlay 1926b:387. Type species (by original designation): *Stephopoma nucleogranosum* Verco, 1904, Recent, southern Australia.

Stephopoma roseum (Quoy & Gaimard, 1834) (Fig. 7A–G)

Vermetus roseus Quoy & Gaimard 1834:300, pl. 67, figs. 20–23.
Siliquaria rosea. ME Gray 1842, pl. 56, fig. 3 (copy of Quoy & Gaimard 1834, pl. 67, fig. 20); JE Gray 1850:83; JE Gray 1857:128.
Tenagoda rosea. H Adams & A Adams 1854:361 (as *Tenagodus*, p. xxxvii).
Stephopoma roseum. Mörch 1860:42; Mörch 1861:150; Hutton 1880:85; Suter 1913:261, pl. 15, figs. 6, 6a (copy of Quoy & Gaimard 1834, pl. 67, fig. 20); Morton 1951:20,40, figs. 1, 2, pl. 4, figs. 1, 4–6; pl. 5, figs. 7–14; pl. 6, figs. 19–21, 23; Morton 1955:8, fig. 2b; Morton & Keen 1960:27, figs. 8, 12, 16; Powell 1979:129; Beu & Maxwell 1990:407; Bieler 1997:265, figs. 25, 26.
Siliquaria laevigata. Hutton 1873a:31 (not *Siliquaria laevigata* Lamarck, 1818).
Vermetus (Stephopoma) roseus. Martens 1873:28; Tryon 1886:185, pl. 55, fig. 94 (copy of Quoy & Gaimard 1834, pl. 67, fig. 20).
Vermetus (*Stephostoma)* (sic) *roseum*. Clessin 1903:91, pl. 13, fig. 5 (copy of Quoy & Gaimard 1834, pl. 67, fig. 20).
Vermicularia rosea. Suter in Hutton 1904:76.
Vermicularia (Stephopoma) nucleogranosa. Suter 1906:328 (not *Stephopoma nucleogranosum* Verco, 1904).
Stephopoma nucleogranosum. Suter 1913:262, pl. 15, fig. 7–7b (not *S. nucleogranosum* Verco, 1904).
Lilax nucleogranosa. Finlay 1926b:387.
Stephopoma rosea (sic). Fleming 1966:47; Spencer & Willan 1996:18; Spencer et al. 2009:207; Maxwell 2009:241.

Type material. Vermetus roseus seven syntypes (three dry shells in typothèque; four shells and seven animals in ethanol) MNHN moll. 22063 (not seen; Virginie Héros MNHN pers. comm. 14 July 2009); from 'La rivière Tamise... Nouvelle Zélande', 'assez profondeur', that is, Firth of Thames, Hauraki Gulf, New Zealand, at quite a great depth (Morton 1951:21).

Other material examined. **Castlecliffian:** Tainui Shellbed (OIS 13), abundant towards the top of the outcrop at 'the buttress', Castlecliff, some specimens attached to shells or large bryozoan colonies, many loose in the sediment; recorded by Fleming (1953:229) as '*Lilax* n. sp. aff. *nucleogranosum*' from GS 4013, R22/f6353, at 'the buttress' (11 in reference collection, five in later re-collection), and GS 4102, R22/f6516, at 'the pinnacles', both in the coastal outcrop; several early GNS collections from 'Castlecliff', including Suter collection no. 97 (four, one with tall, upright section); NMNZ M.27289, 'Castlecliff' (one), undoubtedly all from Tainui Shellbed. **Haweran**: GS4151, R22/f7416, Brunswick Formation (OIS 9), spur leading SE from summit of Mt Jowett, within Wanganui city (one broken, abraded specimen) (Fleming 1953:261); Te Piki, inland from Whangaparaoa, near East Cape (OIS 7; GS15443, Y14/f505B, 42 specimens, including several attached to *Pecten* shells, & some attached to *Serpulorbis*, in turn attached to *Pecten* shells; NMNZ M.15279, 10; M.40167, many); GS14777, O06/f067, intertidal flats 100 m SE of Waiparera church, NW Hokianga Harbour (OIS 7; 12, one with long, spiral upright section). **Recent**: 51 lots in NMNZ, ranging from the Three Kings Islands to the Bay of Plenty, and one specimen (protoconch only) from Mahia Peninsula (M.20929, no other data); one lot from the Chatham Islands (M.154146, 12–15 m, Ocean Bay, F Brook, four protoconchs). Specimens have been collected in depths from alive just below low tide to 188–228 m (M.113455, Rungapapa Knoll, Bey of Plenty, shell on rock, one specimen; possibly lived during a glacial lowered sea level) but this is the only sample collected in depths greater than 130 m, and few have been collected in more than 80 m. Most are beach shells, or were collected 'under stones at low tide' and on 'rocks near low tide'.

One lot of New Zealand specimens (NMNZ M.94450, 24 km NW of Great I, Three Kings Islands, 710 m; seven protoconchs) has extremely fine granules on the protoconch, obviously finer than in *Stephopoma roseum*, and seems to represent another species, possibly *S. nucleogranosum* Verco, 1904, as illustrated by Bieler (1997, figs. 15–17; Bieler & Simone 2005, figs. 1–8), although *S. tricuspe* Mörch, 1891 (Bieler 1997, figs. 11–14) from eastern Australia is also very similar, differing in details of the opercular bristles (comparison with Australian specimens required). Another lot from the Kermadec Ridge (M.137514, seamount 130 km S of Esperance Rock, 32°28.30′S, 179°15.90′W, 538 m, on longline, one corroded teleoconch and four protoconchs) has markedly coarser and more elongate granules on the protoconch than in *S. roseum*, and represents a third, apparently unnamed species, not described by Bieler (1997).

A further lot of New Zealand Holocene fossils (GS9151, Q07/f9602, Marsden Point oil installation water drillhole no. 3, Whangarei, Northland; 11 specimens; Fig. 8A–C) was assumed at first to belong in *Stephopoma roseum*, but SEM examination (Fig. 9B,C) showed that the protoconchs of these specimens, also, are much more finely granulose than those of *S. roseum*, suggesting they are also either *S. nucleogranosum* or *S. tricuspe*. The granules are not as obviously minute as in the Three Kings Islands specimens (NMNZ M.94450), and these two lots are possibly not conspecific. An adult teleoconch from the Marsden Point collection is also illustrated (Fig. 9A).

Distribution. The molluscan faunal lists by Fleming (1966) and Beu & Maxwell (1990:407) included Altonian (early Miocene) records (queried) of *Stephopoma roseum*, but I do not know what this record was based on; no material is present in GNS. However, Laws (1936:108; 1940a:441) recorded protoconchs of three apparently distinct species at Kaawa Creek, SW Auckland (Opoitian), differing in the size and spacing of the surface granules, indicating that early Miocene specimens are unlikely to be conspecific with *S. roseum*.

Other than the possible Altonian and Opoitian records, the fossil record is remarkable, as *Stephopoma roseum* is abundant in Tainui Shellbed (OIS 13) at Wanganui, and one specimen was collected by Charles Fleming from Brunswick Formation (OIS 9) on Mt Jowett, Wanganui, but there are no other records from Wanganui Basin. It is possible that the Brunswick Formation specimen is reworked from Tainui Shellbed, as it is incomplete and highly abraded. The only other fossil occurrences are within its present distribution, in the NE North Island warm province, at Te Piki and Hokianga Harbour. Other than a single record from the Chatham Islands, *S. roseum* is restricted to the NE North Island warm province at present, ranging from the Three Kings Islands to the Bay of Plenty and East Cape, with a single specimen from Mahia Peninsula. Morton & Miller (1968:106–107, Fig. 38; pp. 135, 164, fig. 57; p. 274) described its occurrence in a narrow intertidal zone in shade under boulders, below the zone of the abundant tubicolous polychaete *Spirobranchus cariniferus* in the northern North Island. However, *S. roseum* is not a widespread zone-forming species, but has been found in scattered localities in samples ranging from one shell or a small number of shells to large masses of intertwined shells, up

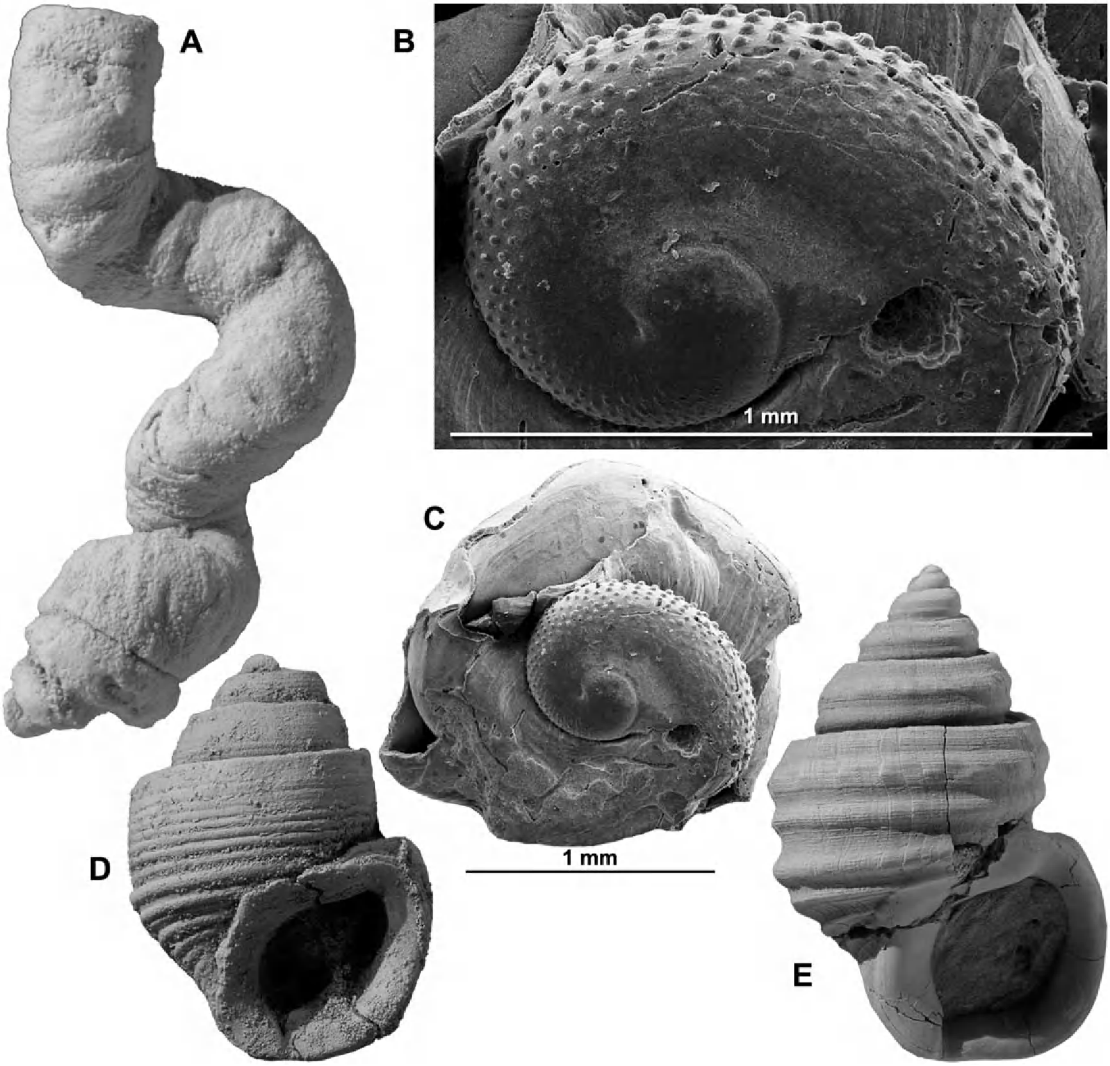

Fig. 8 (A–C) *Stephopoma* cf. *nucleogranosum* (Verco), GS9151, Q07/f9602, Marsden Point water well, Whangarei, Holocene; A, whole tube, height 19.4 mm; B,C, base of a tube, SEM. (D) *Pelicaria zelandiae* (Marshall & Murdoch), Marshall & Murdoch's figured syntype, TM8700, Waipipi, Waverley Beach, W of Wanganui, ex Marshall & Murdoch collection; H 36.4, D 26.8 mm. (E) *Pelicaria arahura* n. sp., paratype, TM8606, GS3046, J32/f9146, cutting S side Kumara-Inchbonnie Road, Big Hohonu River, Westland, Waipipian; height 43.8 mm.

to 50 × 60 × 70 mm, mainly from Northland (Three Kings Islands to the Bay of Islands, Whangarei Heads, and offshore islands of Northland) to the Auckland beaches, including Takapuna reef, with several lots from the Bay of Plenty (e.g. off White Island; Motuhora or Whale Island), and a few localities extending as far south as East Cape (NMNZ M.20909,

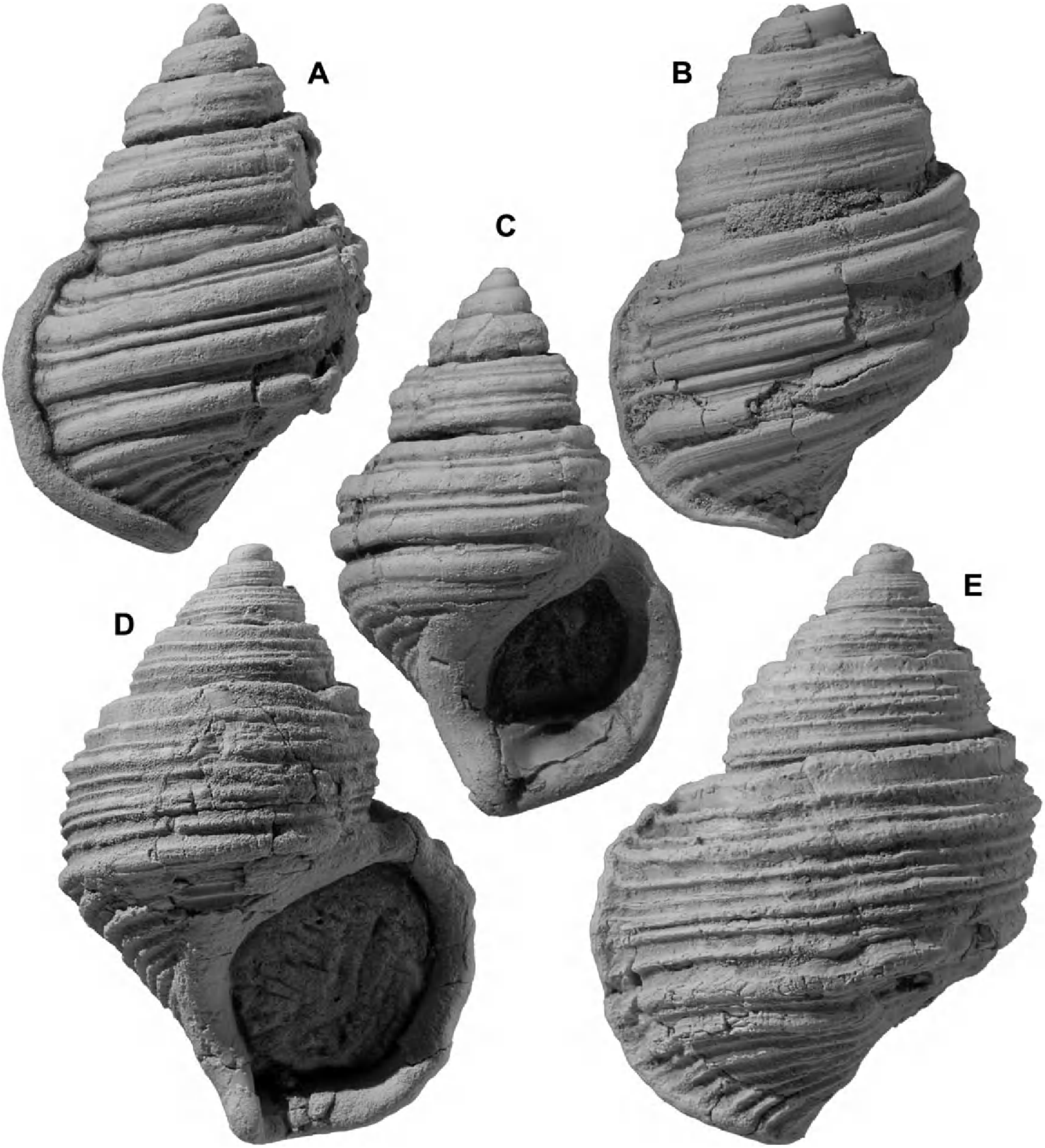

Fig. 9 *Pelicaria granttaylori* n. sp. (A,C) holotype, TM8594, GS11617, T22/f8537A, Hautawa Shellbed (early Nukumaruan), Hautawa Road, between Murimotu Valley, Rangitikei, and Turakina Valley; height 51.1 mm. (B) paratype, TM8701, GS4206, S22/f6444, Hautawa Shellbed (early Nukumaruan), Upokonui Stream, Parihauhau Road, NE of Wanganui; height 50.2 mm. (D,E) paratype, TM8702, GS13076, W19/f027, sandstone upstream from highway, Mohaka River, N Hawke's Bay, Mangapanian; height 56.3 mm.

under boulders at low tide, Lottin Point, E of Cape Runaway, many short, intertwined shells in one mass ca 20 × 30 × 40 mm, with at least 22 brown, granulose protoconchs visible on the underside of the mass; M.154114, 79–83 m, Ranfurly Bank, East Cape, 1).

The Marsden Point drillhole fossils suggest that the fossil record of *Stephopoma* in New Zealand is more complex than has been suspected previously, and will repay fuller study.

Once again, fossils at Wanganui suggest significantly warmer sea temperatures than at present during interglacial periods, and planktotrophic larval transport from the NE North Island allowing range extension down the E North Island and through Cook Strait to Wanganui Basin during OIS 13 and possibly OIS 9 (the same stages as records of *Zelippistes benhami*). BA Marshall (NMNZ pers. comm. July 2009) pointed out that this is an established pattern for several molluscs (e.g. *Micrelenchus rufozona* A. Adams, 1853), Marshall 1998, fig. 63; *Murexsul octogonus* (Quoy & Gaimard, 1833), Marshall & Burch 2000, Fig. 37; *Maoricrypta youngi* Powell, 1940, Marshall 2003, fig. 12) although, in all three of these cases, a relict population remains living in W Cook Strait. Subsequent cooling of the SE North Island by northward extension of the cold Southland Current during glacial periods, which brought the *Zygochlamys delicatula* fauna north to Wanganui Basin early in Nukumaruan time, seems to have reduced the range of some of these species again to the NE North Island warm province. In some cases relict populations have remained in W Cook Strait, whereas in others the species disappeared from the southern North Island altogether. *Stephopoma roseum*, *Maoricrypta costata*, *Zelippistes benhami*, *Prototyphis eos* and possibly *Stiracolpus vigilax* can be viewed as examples of the group that became extinct altogether in the southern North Island.

Stephopoma roseum is abundant in the upper part of Tainui Shellbed at Castlecliff, but this is probably partly an environmental bias, reflecting the sediment-free, mainly shallow subtidal, cemented habit of this filter-feeding species. It is possible that this environment is otherwise not preserved at Wanganui, although the Brunswick Formation record shows than some specimens can be preserved out of their living habitat. *S. roseum* is a useful addition to the short list of species that extended their ranges briefly to Wanganui Basin from the northern North Island during Castlecliffian–Haweran time.

Dimensions. Tallest, 'Wanganui', Suter collection no. 97: H 22.5, D 8.8 mm; GS4013, Tainui Shellbed: H 6.2, D 11.1 mm; H 10.0, D 8.3 mm; H 17.8, D 8.3 mm (with tall, upright tube); H 5.9, D 9.2 mm; H 5.9, D 11.9 mm.

Remarks. The little irregularly coiled gastropod *Stephopoma roseum* has been illustrated only rarely previously; the only diagnostic illustration I am aware of is that by Suter (1915), pl. 15, fig. 7). The shell was not illustrated by Morton (1951). Suter's drawing gives a good idea of the distinctive low-coiled yet irregular shape, with a prominent flange extended ventrally from the whorls of most specimens to cement the shell to its substrate and, on many specimens, a further flange-like ridge around the upper side, facing away from the attachment area, forming a roughly rectangular cross-section. The attachment flange is irregularly but, on most specimens, quite coarsely ridged and puckered, copying the irregular substrate. Some specimens have many fine, low, closely spaced, slightly irregular spiral threads covering the interval between the two spiral flanges, and a few also have transverse ridges crossing the spiral ones, although most are smooth. Many specimens (including the majority of fossils in Tainui Shellbed) are essentially planispiral, with a final short upright section at right angles to the rest of the shell, but some large specimens develop a longer, straighter, cylindrical, upright but irregular section protruding well above the low initial coil. The illustration by Morton & Miller (1968:164, fig. 57.7) shows a specimen in life orientation beneath a boulder, with no upright section and only the unattached side visible, whereas on most specimens the irregular flanges are more conspicuous.

Apart from the obvious, large flanges, the most distinctive character ensuring the identification of *Stephopoma roseum* is the small, almost planispiral protoconch of little more than one evenly rounded whorl, bearing rather closely spaced, large, hemispherical granules all over the exterior. On fresh specimens, including all live-collected ones, the protoconch is pale brown, but it fades to white on many specimens, and on some examined in NMNZ an initial brown protoconch has a white last half-whorl. Examination of the fossil specimens listed above showed that most retain a well-preserved protoconch on the base, surrounded by the attachment flanges. Several of the Tainui Shellbed specimens have two or three protoconchs on the base of one coiled shell, demonstrating that they are actually two or three closely intergrown specimens. All protoconchs examined have identical shape, size, and sculpture of large, hemispherical, closely spaced granules, in GS14777 (Hokianga), Te Piki and GS4013 (Tainui Shellbed). Examination of the large collection at NMNZ showed that all Recent lots from New Zealand have an identical protoconch, other than the one lot of a second species from 710 m off the Three Kings Islands, mentioned above, with a more finely granulose protoconch, and other than this sample and the Marsden Point drillhole specimens, all fossil and Recent specimens are considered to be conspecific. The single specimen from Brunswick Formation at Wanganui (GS4151) seems to be identical to the common form in Tainui Shellbed.

The original illustration of the shell and animal (Quoy & Gaimard 1834, pl. 67, fig. 20; copied by ME Gray 1842, pl. 56, fig. 3, and by Suter 1913 [1915], pl. 15, fig. 6) shows a small, tall shell that is narrowly coiled for its entire length, the loose coil leaving a spiral groove between the whorls. Suter (1913) had difficulties associating this shell with New Zealand material, and identified the more common, nearly planispiral shell form found under low-tidal boulders as the South Australian species *S. nucleogranosum* Verco, 1904. However, Morton (1951:21, 22) matched the multifid opercular bristles of New Zealand material with the illustration by Quoy & Gaimard (1834) and distinguished the bristles and the finer protoconch sculpture of South Australian material of *S. nucleogranosum*, identifying all New Zealand material as *S. roseum*. The group of shells of *S. nucleogranosum* illustrated by Morton (1951, pl. 7, fig. 26) has wider, more upright and less obviously spiral growth than most New Zealand material, with no ridges on the evenly cylindrical upright sections, and more nearly resembles standard vermetids such as *Serpulorbis* than many New Zealand specimens do. Most specimens in the Marsden Point drillhole sample also lack obvious ridges on the exterior of the tube. However, many large lots in NMNZ consist of masses of densely intergrown tubes, twisted to varying degrees, and some are longer and more weakly coiled that the specimens illustrated by Morton (1951;, pl. 7, fig. 26). Some of them resemble Quoy & Gaimard's (1834, pl. 67, fig. 20) drawing quite closely. In particular, NMNZ M.91895 (Doubtless Bay, Northland, from E. Willis of RV '*Ikatere*', so presumably dredged offshore) is a large sample of small masses up to 60 × 40 × 40 mm of intergrown tubes, with many individual tubes up to at least 50 mm long, narrow, smooth, and weakly coiled, without an obvious attachment area or flanges, but with the diagnostic brown, granulose protoconch attached. They are considerably longer and more narrowly tapered than the tubes of *S. nucleogranosum* illustrated by Morton (1951). Other masses of tubes collected subtidally are also quite large, up to ca 50 × 70 × 80 mm, and the degree to which tubes coil together into compact masses or are short and separate clearly depends on the environment; large masses and longer tubes presumably live in sheltered, enclosed habitats, whereas the more common, shorter, tightly coiled, flanged tubes have been collected under boulders low in the intertidal zone, or only slightly deeper. Some of the fossil specimens have a tall, narrowly coiled shell with only a small attachment area, a groove between the irregular whorls, and a weak flange up the entire tube. These also resemble Quoy & Gaimard's (1834, pl. 67, fig. 20) drawing quite closely.

Family Turritellidae

Remarks. The classification of the Turritellidae has always presented problems because of their abundance, their enormous diversity at the species level, and their simple shells with few taxonomic criteria. Authors who have contributed to their classification include Cossmann (1912), Guillaume (1925), Dollfus (1926), Douvillé (1929:54–57), Merriam (1941), Ida (1952), Marwick (1957a, 1957b, 1971), Kotaka (1959), Olsson (1964:185–194), Allison (1965), Adegoke (1967), Allison & Adegoke (1969), Garrard (1972, 1974, 1976), Golikov (1986), Allmon (1996) and DeVries (2007). Kotaka (1959:8–13) reviewed most of the classifications proposed before 1959, and Kantor & Sysoev (2006, pls. 22, 23) illustrated the two new genera proposed by Golikov (1986). However, taxonomists not 'specializing' in turritellids have been reluctant to adopt a finely subdivided classification. Several North American authors have revised numerous taxa and used them for biostratigraphical zonation, but retained them in *Turritella* (including Bowles 1939; Palmer 1947; Saul 1983; extra-American zonations listed by Allmon 1988: 259). The world classification proposed by Marwick (1957a) does little to help resolve phylogenetic relationships within the family, as much because many of the world's species are not classified as because those that are classified are too finely subdivided. Marwick's review was limited to groups 'that have already been named, so it is not at all comprehensive' (Marwick 1957a:149). Also, Marwick (1957a) commented favourably on Iredale's (1924) proposal of Australian genera, and summarized his introduction by noting that 'In a natural classification, [restricted dispersal ability] should be reflected by numerous localized genera' (Marwick 1957a:149). Marwick's resulting assumption that similar turritellid outer lip profiles evolved independently in numerous parts of the world seems based on circular argument, and requires reassessment. It would be fair to say that most taxonomists since 1957 have disagreed with Marwick's conclusion, and continued to use *Turritella* for most or all species (e.g. Allmon 1988, 1992). Yet the type species of *Turritella*, *T. terebra* (Linné, 1758), has a distinctive, large, tall and narrow, strongly sculptured teleoconch with strongly and evenly inflated whorls and an unusually shallow outer lip sinus (although a closely related Pliocene species in Japan, *T. perterebra* Yokoyama, 1923, is much less extreme; Kotaka 1959, pl. 1, figs. 1–7). Clearly, phylogenetic relationships in this family are expressed less than optimally if all species are placed in *Turritella*. I conclude that there are likely to be fewer, more widely distributed genera than Marwick (1957a, 1957b, 1971) assumed, and that some species and genera are likely to have been dispersed widely around the world at various times, as in most other molluscan families, apart from a few extremely 'holobenthic' families such as the Volutidae (Bouchet & Poppe 1988:30). Even in Volutidae some *Athleta* species (especially Paleogene fossils) and some *Calliotectum* and *Lyria* species are exceptions to the 'holobenthic' rule, having dispersive, demersal larvae (Bouchet & Poppe 1995; Maxwell 2003).

Kotaka (1978) pointed out that lineages placed in *Stiracolpus* (in New Zealand), *Haustator* (in Europe), *Neohaustator* (in Japan) and '*Turritella*' (in California) evolved in parallel through a remarkably similar succession of morphological changes during Pliocene and Pleistocene time. Along with the close morphological similarity of all these groups, including a similar outer lip sinus, the closely parallel evolution might well be further evidence of a relationship between them at the generic level, the 'parallelism' resulting from some level of genetic exchange between them. If this is correct, this group, at least, probably belongs in one genus (perhaps with several subgenera), the earliest name for which is *Haustator*

Montfort, 1810. Marwick (1957a:154) pointed out that both Thiele (1931:181) and Wenz (1939:653) regarded *Gazameda* Iredale, 1924 as a synonym of *Haustator*, but Marwick (1957a:154) kept them separate because of the distinct protoconch and early spiral cord development of *Gazameda*. '*Gazameda* is consequently far removed from *Haustator* in development, and is here given generic rank' (Marwick 1957a:154), despite also pointing out that Australian middle Miocene species assigned to *Gazameda* have a turbiniform protoconch with a globose initiation (nucleus), as in most other turritellids including *Haustator*. One of the major themes stressed in the present series of papers is that such developmental differences are no longer regarded as characters distinguishing genera or subgenera; planktotrophy has been lost readily and independently by many gastropod species within originally planktotrophic clades. Marwick (1957a) also pointed out the possibility that *Zeacolpus* Finlay, 1926 had developed from *Haustator* rather than from *Leptocolpus* Finlay & Marwick, 1937 (Paleocene, New Zealand): 'the shallower sinuses of *Leptocolpus*... raises the question whether *Zeacolpus* is not closer to *Haustator* than to *Leptocolpus*' (Marwick 1957a:156). Beu & Maxwell (1990:156, pl. 14f) referred *Zeacolpus grindleyi* Marwick, 1971 (Duntroonian–Waitakian, late Oligocene, New Zealand) to *Gazameda*. *G. grindleyi* closely resembles the weakly sculptured Victorian Miocene species *Gazameda victoriensis* (Cotton & Woods, 1935), indicating that at least some New Zealand taxa are related phylogenetically to Australian *Gazameda* (= *Haustator*?) species.

This discussion suggests the possibility that there have been several separate range extensions to New Zealand by *Haustator* species, or at least by clades descended from *Haustator*: middle to late Eocene, to give rise to the earliest species assigned to *Zeacolpus*; late Oligocene, to give rise to '*Gazameda*' *grindleyi*; and latest Miocene–basal Pliocene, to give rise to the group of species usually included in *Stiracolpus*. Rather than assigning all these species to *Haustator* at present, the traditional New Zealand genera are retained, keeping their probable close relationship to *Haustator* in mind. The family urgently requires a worldwide reassessment, and is another of the poorly understood families with few taxonomic criteria that will benefit greatly from comparion of DNA sequences. Only after a world revision, assessing the possible iterative evolution of lip profiles, will it be appropriate to change the status quo by adopting different genera in New Zealand. However, I have little doubt that the present classification bears little relationship to phylogeny.

A further example of the need to rethink the relationships of New Zealand turritellids is provided by the origin of the most abundant New Zealand Pliocene–Recent species, *Maoricolpus roseus* (Quoy & Gaimard, 1834). The true origins of this species can be seen in Garrard's (1972:324) statement about the relationships of *Maoricolpus murrayanus* (Tate, 1885). *M. murrayanus* is closely similar to *M. roseus* in all characters, although the spiral sculpture is slightly finer in *M. murrayanus*. The similarity is close enough that TA Garrard originally intended to synonymize the two species, and was only persuaded not to by me, because of the different time range (early to middle Miocene) and geographical range (southern Australia) from that of *M. roseus* (Pliocene–Recent, New Zealand). It is ironical, then, that *M. roseus* invaded D'Entrecasteaux Channel in SE Tasmania during the twentieth century, and is now abundant there (Greenhill 1965:67), as well as occurring at many other localities in Tasmania (Greenhill 1965; Bax et al. 2003; Probst & Crawford 2008) and is spreading northwards to inhabit the Furneaux Group islands in Bass Strait (Allmon et al. 1994), with records from Victoria and New South Wales as far north as Sydney (Scott 1997:25; Bax & Gowlett-Holmes 2000). *M. roseus* was not recorded from Tasmania by earlier authors such as May (1921) (Bax et al. 2003). Garrard (1972:322) recorded *M. roseus* also from 110–150 m off Cape Moreton, S Queensland, but Bax et al. (2003) doubted the reliability of this record, and collectors in S Queensland (A Limpus, Bundaburg; T Whitehead, Brisbane; pers. comm. June 2008) have been unable to substantiate it, so *M. roseus* evidently occurs only around Tasmania and in Bass Strait to Sydney, although the lack of natural predators seems to be making it possible for *M. roseus* to spread in Australia (Allmon et al. 1994). If the type species of *Maoricolpus* invaded New Zealand from Australia at the beginning of Pliocene time, what are the real phylogenetic relationships of the other New Zealand taxa referred by Marwick (1971) to *Maoricolpus*? They seem unlikely to belong in the same clade. Marwick obviously realized that not all species assigned to the traditional New Zealand genera belong there, in a phylogenetic sense, and he apparently was aware that his classification was not final. Much remains unknown about the phylogeny of these taxa, and their inclusion by Marwick (1971) in a few restricted New Zealand genera was a matter of practicality. Determining the phylogeny of world turritellids remains a task for molecular phylogeny in the future.

Genus ***Stiracolpus*** Finlay, 1926

Stiracolpus Finlay 1926b:389. Type species (by original designation): *Turritella symmetrica* Hutton, 1873, late Pliocene (Nukumaruan) –Recent, New Zealand.

Remarks. Within New Zealand Turritellidae, Marwick's (1957b, 1971) two monographs display a marked difference in approach, and consequently in biostratigraphical utility. The later monograph, with its careful stratigraphical segregation of species defined within relatively long lineages of *Zeacolpus*, *Maoricolpus* and apparently related larger turritellids (remembering the proviso about *Maoricolpus* pointed out above), resulted in species that are recognizable by subsequent workers, and are useful in biostratigraphy—within limits, because of the inherent similarity of most turritellids. In contrast, Marwick's (1957b) earlier monograph of Pliocene to Recent *Stiracolpus* species was hampered by a bewildering array of variation interpreted with a very narrow species definition, almost an unconsciously typological viewpoint. Re-collection of the *Stiracolpus* species in situ in the Castlecliffian rocks of Wanganui Basin and examination of Marwick's collections in GNS demonstrated that Marwick regarded the coarsely sculptured end-members of the population in each formation as one species, the finely sculptured end-members as another species, and all the intergrading, intermediate specimens as hybrids. The resulting plethora of species has proved impossible for subsequent workers to distinguish, and those familiar with (in particular) Pleistocene and Recent turritellids in New Zealand (RM Carter, James Cook University, Townsville pers. comm.; JA Grant-Mackie, University of Auckland pers. comm.; BA Marshall, NMNZ pers. comm.) agree with my opinion that few of Marwick's taxa are real biological species. The assessment of biostratigraphically useful taxa within Pliocene–Pleistocene turritellids therefore must commence with a new taxonomy of the species. Once again, this is nearly impossible with the characters visible on the shells, and will only be comprehensible after the taxonomy and variation of Recent species have been resolved by molecular techniques.

Nevertheless, some points seem reasonable to conclude, after 50 years' experience with these shells:

1. The great majority of Marwick's (1957b) late Pliocene–Recent 'species', with numerous prominent spiral cords, are part of the variation of either *Stiracolpus symmetricus* (Hutton, 1873) (southern forms) or *S. pagoda* (Hutton, 1873) (all forms living now in central and northern New Zealand). While *S. symmetricus* is most strongly sculptured at present around Foveaux

Strait and Stewart Island, where most specimens have three equally prominent, narrow spiral cords on a strongly convex whorl profile, very similar forms occur in Nukumaruan rocks in Wairarapa district (named *Zeacolpus delli vellai* Marwick, 1957), and an astonishing range of variants on the theme occurs throughout Nukumaruan and Castlecliffian rocks of Wanganui Basin, the East Coast Basin and North Canterbury. The more weakly sculptured Recent central New Zealand forms named (e.g.) *Z. blacki* and *Z. delli* by Marwick (1957b) all intergrade, and are probably variants of the northern New Zealand species *S. pagoda* (Reeve, 1849). Names that apparently were based on trivial variants of *S. symmetricus* are *Z. delli murdochi*, *Z. delli granti*, *Z. delli vellai*, *Z. robinae* and *Z. shepherdi*, all of Marwick (1957b). Names that seem to be based on trivial variants of *S. pagoda* are *Zeacolpus ascencus*, *Z. blacki*, *Z. delli* and presumably *Z. knoxi*, *Z. knoxi tardior*, *Z. uttleyi* and *Z. uttleyi ruahinensis*, all of Marwick (1957b), *Z. pagoda* (Reeve, 1849), *Z. pagoda powelli* Marwick, 1957, *Z. maorius* (Powell, 1940), *Z. mixtus* (Finlay, 1930) and *Z. waikopiroensis* (Suter, 1917). More than one species is possibly hidden in the complex variation of *S. pagoda* (BA Marshall, NMNZ pers. comm. March 2006). Analysis of the ontogeny of development of the spiral cords, with a broader interpretation than Marwick's, could perhaps aid understanding of this group.

2. An exception to the Wanganui Basin 'species' all being synonyms of *S. symmetricus* is provided by *Stiracolpus vigilax* (Landguard Sand, OIS 9, and a few specimens from OIS 11; one specimen from Te Piki, near East Cape, OIS 7), which is smaller and much more strongly unicarinate than any other species at Wanganui. It is very similar to and possibly conspecific with *S. ahiparanus* (Powell, 1927) (Recent, NW North Island), although the Wanganui material reaches only about half the height of Recent material of *S. ahiparanus*. However, *S. ahiparanus* and *S. vigilax* are also both possibly further synonyms of *S. pagoda*.
3. The extremely finely sculptured specimens at Wanganui (most notably in Kupe Formation, OIS 17; a few records from shellbeds deposited during OIS 19 and 15) identified by Marwick (1957b) as '*Zeacolpus (Stiracolpus)* cf. *waikopiroensis*' possibly represent incursions of the northern warm-water *S. pagoda* species group into Wanganui Basin. This needs confirmation, as they might also merely be unusually finely sculptured end-members of *S. symmetricus*. However, it is also possible that *S. waikopiroensis* itself (that is, Hawke's Bay Nukumaruan weakly sculptured forms, assumed here to be finely sculptured end-members of the form identified by Marwick [1957b] as *Z. uttleyi*) is based on a member of the *S. pagoda* species group; these specimens closely resemble the northern North Island Recent form known as *S. maorius*.
4. *Stiracolpus huttoni* (Cossmann, 1912) represents a different species group from the complex of *S. symmetricus* and *S. pagoda*, with only two prominent, widely spaced spiral cords, and no other obvious spiral sculpture. It is remarkably unvaried, implying that it had planktotrophic rather than direct development. I am not aware of records younger than late Nukumaruan.
5. Earlier (Opoitian–Mangapanian) species such as *Stiracolpus kaawaensis* (Laws, 1936), *S. procellosus* (Marwick, 1931), *S. propagoda* (Laws, 1940) and possibly *S. quennelli* (Marwick, 1957) and *S. wiltoni* (Marwick, 1957) seem to be distinct, much less variable species. This implies that (as with *Pelicaria*; see below) the inception of the lecithotrophic (probably direct)

developmental mode that produced the enormously variable 'species complex' of *S. symmetricus* and *S. pagoda* was an early Pleistocene (early Nukumaruan) event. Cooling of the sea seems to have led to similar developmental changes and a marked increase in variation of shell characters during early Nukumaruan time by *S. symmetricus*, *Pelicaria vermis* and *Aoteadrillia wanganuiensis* (see below). *S. huttoni* seems to be an example of the other possibility, stenothermal warm-water taxa that simply became extinct when sea temperatures reached a critical threshold during late Mangapanian–early Nukumaruan glaciations.

This summary results in a group of four or five Pliocene (Opoitian–Mangapanian) species —those listed in the paragraph above plus *Stiracolpus huttoni*—and only a further four or five Nukumaruan–Recent species. One obvious biostratigraphically useful result is the extinction of *S. huttoni* late in (at the end of?) Nukumaruan time. Another is the apparent arrival of *S. symmetricus* (in the broad sense used here) in the southern North Island during early Nukumaruan time, along with the cold-water fauna dominated by *Zygochlamys delicatula* (Fleming 1944). Much further work is required to understand this taxonomically 'difficult' genus in New Zealand, and a detailed taxonomic revision obviously is not appropriate here.

Species I suggest, therefore, should be recognized in *Stiracolpus* are:

Stiracolpus ahiparanus (Powell, 1927), Recent, NW Northland (possibly = *S. pagoda*; possibly = *S. vigilax*).

Stiracolpus huttoni (Cossmann, 1912) (Fig. 7J), Opoitian–Nukumaruan, Westland, Wanganui and Hawke's Bay.

Stiracolpus kaawaensis (Laws, 1936), Opoitian, Kaawa Creek, SW Auckland.

Stiracolpus pagoda (Reeve, 1849), Recent, central and northern North Island (and Pleistocene, Wanganui?) (the species name is an indeclinable noun); probably = *Z. huttoni ohopeus* Marwick, 1957, Castlecliffian (OIS 15?), Ohope, Bay of Plenty.

Stiracolpus procellosus (Marwick, 1931), Opoitian, N Hawke's Bay and N Wairarapa.

Stiracolpus propagoda (Laws, 1940), Mangapanian, Wanganui Basin (possibly = *S. symmetricus*).

Stiracolpus symmetricus (Hutton, 1873) (Fig. 7H), Mangapanian?; Nukumaruan–Recent, central and southern New Zealand (= *S. delli vellai*, etc.).

Stiracolpus vigilax (Marwick, 1957) (possibly = *S. ahiparanus*) (Fig. 7I), OIS 11–9, Wanganui; one specimen in GS10910, Y14/f7505B, Te Piki member, road cut 6 km E of Whangaparaoa, near East Cape, OIS 7 (again suggesting that *S. vigilax* might be just a sculptural variant of *S. pagoda*).

A small list remains of possibly distinct species requiring further study, as their status is unknown:

Stiracolpus hurunuiensis (Marwick, 1957), Waipipian(?) redeposited fauna at Tormore, North Canterbury (this mixed fauna apparently resulted from redeposition of Waipipian fossils during Nukumaruan time; Beu 1977).

Stiracolpus nanulus (Marwick, 1957), Nukumaruan, Kereru, Hawke's Bay (= juvenile *S. symmetricus*?).

Stiracolpus quennelli (Marwick, 1957), Mangapanian, S Hawke's Bay (possibly = *S. symmetricus*).

Stiracolpus wiltoni (Marwick, 1957), Opoitian, N Wairarapa.

Type material. The opportunity is taken to illustrate Hutton's (1873b:13) 'Shakespeare Cliff' paralectotype of *Turritella (Zaria) tricincta* (TM5375; junior primary homonym of *T. tricincta* Borson, 1821, of *T. tricincta* Münster, 1841, and of *T. tricincta* Morris in

Strzelecki, 1845) (almost certainly collected from Shakespeare Cliff Siltstone, where this form is common), as this specimen has never been illustrated previously (Fig. 6I; H 30.7, D 7.7 mm). Marwick (1957b:32) recorded *S. delli murdochi* Marwick, 1957 as the form common in Shakespeare Cliff Siltstone, and Dell et al. (1964:448) identified Hutton's 'Shakespeare Cliff' syntype as *S. delli murdochi*. Hutton (1873b:13) recorded *T. tricincta* also from 'Awatere; Waikari (small variety); Weka Creek; Mount Cookson', and 'var. B' from 'Kanieri; Hatter's Creek; Mount Cookson', so it represents several different genera of Pleistocene to Oligocene age. The illustrated shell is a good example of a Wanganui Castlecliffian specimen of *Stiracolpus symmetricus*. However, it is not a name-bearing type. Although Harris (1897:241) proposed *Turritella kanieriensis* as a replacement name for *T. tricincta* Hutton, because it is a junior primary homonym, he did not mention a type specimen. Dell et al. (1964) described the nomenclatural complications of this case; the International Commission on Zoological Nomenclature (Opinion 810 1967) designated the specimen from 'Kanieri' illustrated by Suter (1914, pl. 16, fig. 5) as the lectotype. This is a specimen of Hutton's (1873b:13) *T. tricincta* var. B. The name *T. kanieriensis* therefore applies to a latest Miocene–early Pliocene (Kapitean–Opoitian) species of *Zeacolpus* rather than to the Castlecliffian *Stiracolpus* species.

I also illustrate the holotype of *Zeacolpus (Stiracolpus) vigilax* Marwick, 1957 (Fig. 6C; TM1686, GS4003, R22/f 7394, Landguard Sand, Landguard Bluff, Wanganui, OIS 9; H 15.3, D 4.75 mm) and one of Marwick's (1957b:35, pl. 5, fig. 12) illustrated specimens of *Stiracolpus huttoni*, from Kaniere (Fig. 6K; TM1665, GS2877, J33/f7076, Lake Kaniere Road, opposite Kaniere powerhouse, Westland; H 18.3, D 7.5 mm; Opoitian; the locality from which *Pelicaria parva* (Suter, 1915) is listed below). It should be noted that Hawke's Bay Nukumaruan specimens of *S. huttoni* have a markedly narrower spire angle than Kaniere specimens, and Marwick (1957b:35) commented on the variable spire angle.

Clade Littorinimorpha

Family Littorinidae

Genus ***Risellopsis*** Kesteven, 1902

Risellopsis Kesteven 1902b:319. Type species (by original designation): *Adeorbis varius* Hutton, 1873, Pleistocene and Recent, New Zealand.

Risellopsis varia (Hutton, 1873) (Fig. 5E, 6B)

Adeorbis varius Hutton 1873a:35.
Risella(?) *varia*. Hutton 1878:27.
Fossarina varius. Hutton 1880:79; Hutton 1882:164.
Risellopsis varia. Kesteven 1902:320, fig. 29–32; Suter 1913:191, pl. 35, fig. 13; Odhner 1924:21; Finlay 1928:241; Powell 1937:67, pl. 9, fig. 11; Fleming 1966:42; Morton & Miller 1968:80,353, fig. 23, 77; Pilkington 1974:411, Fig. 1; Pilkington 1976:338, fig. 1a–c; Powell 1979:88, fig. 13, no. 7; Reid 1988:142, figs. 5, 25–27; Spencer & Willan 1996:18; Spencer et al. 2009:206; Maxwell 2009:240.
Risellopsis varia var. *carinata* Kesteven 1902:321, figs. 33–35; Suter 1913:192, pl. 35, Fig. 14; Bucknill 1924:38, pl. 6, Fig. 21, 21a; Finlay 1928:241.

Type material. *Adeorbis varius*, lectotype (designated by Reid 1988:142) NMNZ M.160, from 'Stewart's Island'; paralectotype NMNZ M.1822, from the Chatham Islands. *Risellopsis varia* var. *carinata* Kesteven, holotype AMS C.11422, from 'New Zealand' (Reid 1988:142) (the last not seen).

Other material examined. **Castlecliffian:** 1 m boulder of Teer Formation (about OIS 25) on beach, ca 1.1 km E of Whiskey Creek and 2 km W of Teer Creek, N coast of Cascade Point, S Westland (GS12293, E38/f13, few specimens; Beu in Sutherland et al. 1995:447). **Haweran:** Brunswick Formation (OIS 9), Mount Jowett, Wanganui (Fleming 1953:260) (GS4151, R22/f7416, one); Brunswick Formation (OIS 9), Sewell Road, N of Brunswick Road, W of Wanganui (GS12425, R22/f10, one); 8.4 m below sea-level in Waikanae Beach test bore, Gisborne, Holocene (Y18/f33, GNS, one); 'paua kill' site on 1855 intertidal slope ca 400 m east of Cape Turakirae, Wellington, Holocene (GS15119, R28/f62, ca 30); 1855 intertidal slope, 100 m north of scientific reserve boundary, Cape Turakirae, Wellington, Holocene (GS15121, R28/f072, one); 'lepadomorph site' beneath large boulder on 1855 intertidal slope, ca 400 m east of Cape Turakirae, Wellington, Holocene (GS15122, R28/f062A, 14). Specimens also occur in several Holocene samples from trenches dug through the cosiesmically uplifted terraces at Table Cape, Mahia Peninsula.

Distribution. Rissellopsis varia is one of several species with an apparent OIS 9 first appearance (around Wanganui, particularly at Mt Jowett, in Brunswick Formation), but which actually occur significantly earlier. Again, though, as it is a high-tidal rocky shore species, its first occurrence is highly unreliable for biostratigraphy. Specimens are now recorded from deposits as old as at least OIS 25 (Teer Formation, Cascade, South Westland).

Dimensions. RM704, Takapuna Beach, Auckland: H 3.1, D 5.0 mm; H 3.3, D 4.9 mm; H 3.6, D 5.1 mm; GS4151, Brunswick Formation, Mount Jowett, Wanganui: H 2.3, D 3.8 mm.

Remarks. Rissellopsis varia is a small (up to ca 6 mm diameter) relative of *Bembicium*, with a strongly depressed, coarsely spirally sculptured shell. Reid (1988) reviewed the characters, range, ecology and variation, and little need be added here. It is limited to exposed high-tidal rocky shores throughout New Zealand. Many specimens shelter under dense sheets of the mussel *Limnoperna pulex* (Lamarck, 1819).

Family Struthiolariidae

Genus *Pelicaria* Gray, 1857

Pelicaria Gray 1857:77. Type species (by monotypy) '*P. vernis*', that is, *Buccinum vermis* Martyn, 1784 (available, ICZN Opinion 479 1957), Pleistocene and Recent, New Zealand.

Pelicaria granttaylori n. sp. (Fig. 9A–E)

Type material. Holotype (TM8594) and three paratypes (TM8595-7) from GS11617, T22/f8537A, Hautawa Shellbed (basal Nukumaruan), disused Hautawa Road, between West Road, Murimotu valley, N of Hunterville, Rangitikei valley, and Otiwhiti Station, Turakina Valley Road.

Other material examined. **Mangapanian:** GS4220, S22/f6450, lower Okiwa Group, Paparangi Road, N of Wanganui (five paratypes; a small form with narrow cords, otherwise resembling *P. arahura* n. sp.); GS4124, R22/f6543, Wilkies Shellbed, Wilkies Bluff, mouth of Waitotara River, W of Wanganui (two fragmentary paratypes, similar to *P. zelandiae* (Marshall & Murdoch, 1920) in sculpture); GS4224, R22/f6467, Wilkies Shellbed, Ohie Stream, W of Wanganui (two fragmentary paratypes, similar to *P. zelandiae* in sculpture); GS13076, W19/f027, brown sandstone upstream from highway in Mohaka River, N Hawke's Bay (one large paratype, TM8702, with many narrow cords, otherwise shaped as in GS4220; Fig. 9D,E). Recorded also by Fleming (1953:120, 124, 129) from Makokako Sand (GS4221, R21/f9504, Kauarapaoa Valley, N of Wanganui); Wilkies Shellbed (GS4209, R21/f8501, Paparangi Road, N of Wanganui), and Te Rama Shellbed

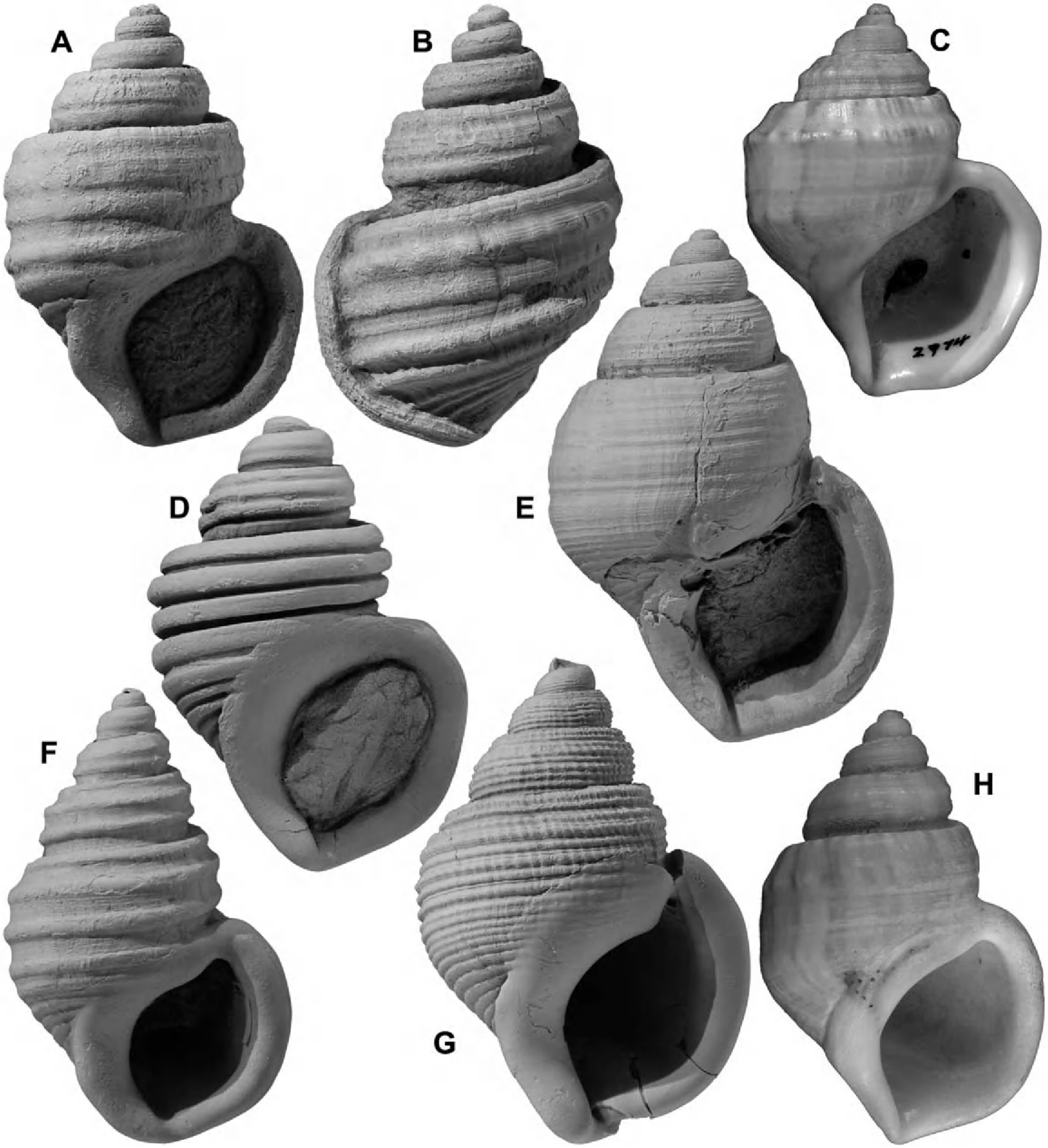

Fig. 10 (*Continued*)

(GS4188, R22/f6471, near Te Rama trig. station, W of Wanganui). **Early Nukumaruan:** GS4206, S22/f6444, Hautawa Shellbed, Upokonui Stream, Parihauhau Road, 5 km NE of junction with Highway 4 (Parapara Road), NE of Wanganui (four paratypes, incomplete to almost complete, distorted; three resemble *P. zelandiae* in shape and cord prominence; one resembles holotype, illustrated, Fig. 9C, TM8701); GS7837, T22/f8504, above Hautawa

Shellbed, Hautawa Road, between Turakina and Rangitikei valleys (one fragmentary paratype). Recorded also by Fleming (1953:131,134) from Hautawa Shellbed (GS3096, T22/f8492, Hautawa Road; GS4204, S22/f6442, near Te Wharau trig. station, Mangamahu Stream, 12 km NE of Mangamahu, NE of Whangaehu valley) and upper Okiwa Group (GS4346, S22/f6471, Turakina River, 1 m above Hautawa Shellbed; GS4359, S22/f6484, Mangawhero Valley, near Klein Trig. Station, 17 m above Hautawa Shellbed; GS4354, S22/f6479, Hales Road, Turakina, 12 m below Ohingaiti Sand).

Distribution. Mangapanian and early Nukumaruan only. *Pelicaria granttaylori* n. sp. is common in Wilkies Shellbed and higher Mangapanian shellbeds in Wanganui Basin, and in Hautawa Shellbed; it tapers off in abundance higher in the succession, and is not known higher than 12 m below Ohingaiti Sand, still quite low in Nukumaruan rocks. I am aware of specimens only from Wanganui Basin (perhaps because of its restriction to near-shore facies), apart from a single large paratype from the Mohaka River, N Hawke's Bay.

Dimensions. Holotype: H 51.1, D (distorted) 33.1 mm; paratype GS4206: H (incomplete) 50.2, D 34.3 mm; paratype GS13076: H 56.3, D 39.7 mm.

Description. Shell characteristic of *Pelicaria* in overall appearance, size, and aperture shape and thickening. Protoconch not seen. Teleoconch of 5–5.5 whorls. Spire moderately tall to rather short for genus; last whorl occupying 2/3 to 3/5 of height. Suture moderately to deeply channelled, channel ranging from narrow, weakly concave, horizontal ramp (in holotype and some other specimens from Hautawa Shellbed) to deeply and narrowly excavated as in *P. zelandiae* (in older specimens, and some from Hautawa Shellbed). Outline below sutural channel straight, vertical in some specimens (which, therefore, resemble *Pelicaria zelandiae* in outline shape), or with weakly defined, outward-sloping sutural ramp, weakly defined but obvious peripheral angulation, and vertical whorl mid-section in other specimens; peribasal angulation weakly defined, rounded in some specimens, more sharply defined by single protruding spiral cord in others. Spiral sculpture of some specimens closely resembling that of *P. zelandiae*, with numerous low, narrow, closely spaced cords not affecting outline shape; in others (including holotype) of relatively few prominent, convex-crested spiral cords, with narrow interspaces each filled by 1–3 narrow, closely spaced secondary cords; three prominent cords on spire whorls and four on last whorl (including subsutural cord) and one secondary cord in each interspace on holotype, slightly more numerous cords on some larger specimens; 6–8 cords on base, slightly lower, narrower and more closely spaced than on whorl sides, decreasing in size anteriorly. Uppermost prominent spiral cord bearing

Fig. 10 (A,B) *Pelicaria arahura* n. sp., holotype, TM8598, GS12289, J33/f066, conglomerate at top of Eight Mile Formation (Waipipian), head of E tributary of Greeks Creek, S side of Arahura Valley, Westland; height 41.4 mm. (C,E,F,H) *Pelicaria vermis* (Martyn); C, RM2974, extreme "*bradleyi* form", Recent, Rabbit Island Beach, Nelson; height 36.6 mm; E, "*convexa* form", GS10748, S28/f6206, Pukenui Limestone (early Nukumaruan), above junction Mangaopari Stream and Makara River, S Wairarapa; height 48.0 mm; F, holotype of *Struthiolaria acuminata* Marwick, TM7682, GS1040, S27/f8448, Pukenui Limestone (early Nukumaruan), White Rock Road, Makara River, S Wairarapa; height 42.9 mm; H, lectotype of *Struthiolaria crenulata* Lamarck and neotype of *Buccinum vermis* Martyn, *Murex australis* Gmelin, *Struthiolaria inermis* G. B. Sowerby I, and *Struthiolaria tricarinata* Lesson, MNHN moll.20522, Recent, New Zealand (Waikanae-Paraparaumu coast, W Wellington?), collected by Péron & Lesueur; height 40.8 mm (MNHN photo by V. Héros). (D) *Pelicaria canaliculata* (Zittel), specimen resembling Zittel's illustration, "Awatere", ex Marshall & Murdoch collection, presumably from Starborough Formation (Waipipian), Seddon; height 42.8mm. (G) *Pelicaria rugosa* (Marwick), Neef's (1970) illustrated specimen, T24/f8049, Marima Sandstone (early Nukumaruan), tributary of Mangahao River E of Marima School, N Wairarapa; height 45.3 mm.

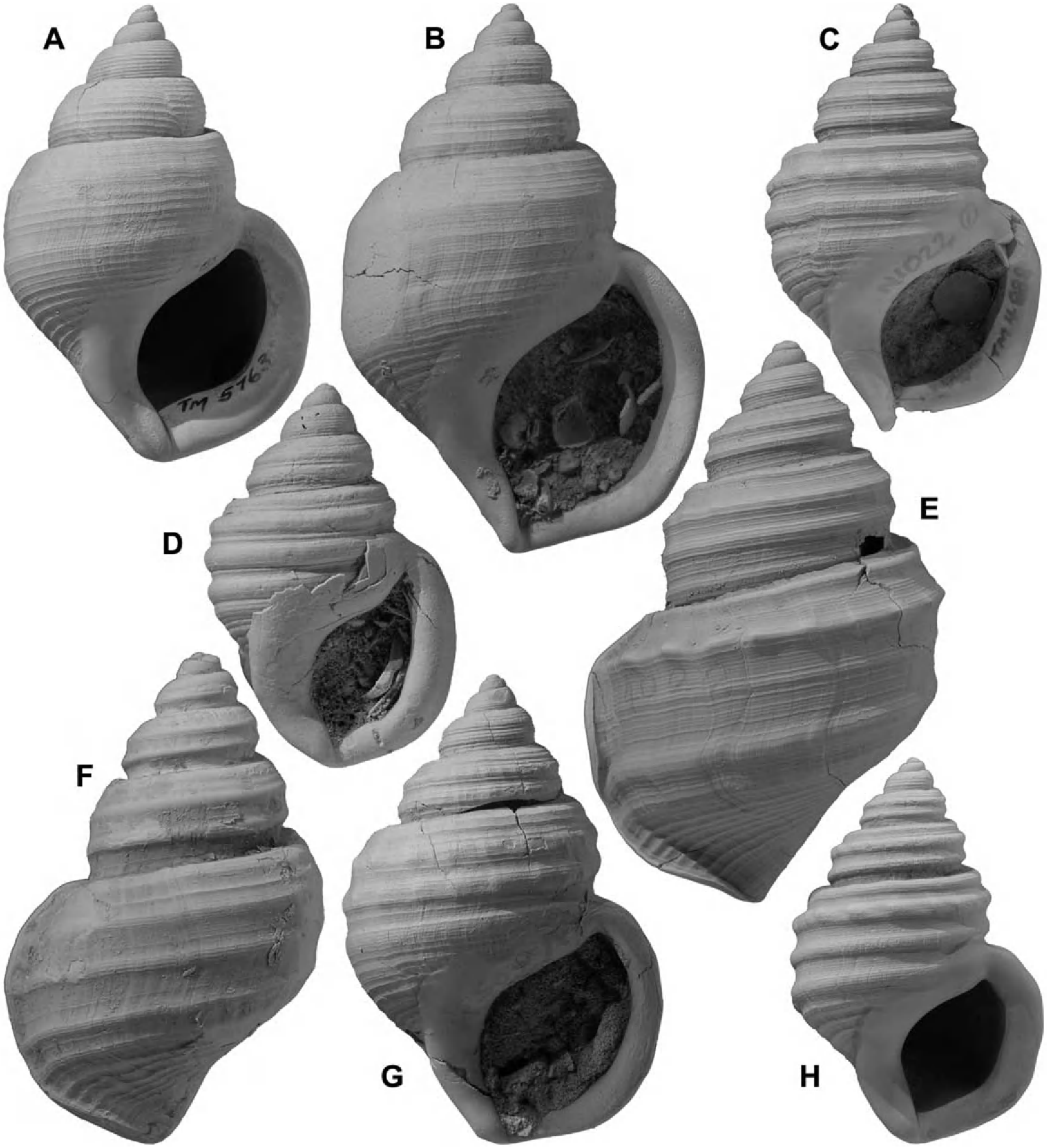

Fig. 11 (*Continued*)

weakly defined, low, irregular nodules in a few specimens. Exterior of well-preserved specimens closely covered with very fine spiral threads. Aperture large, relatively wide as in all *Pelicaria* species, with relatively narrow, evenly rounded terminal varix and smoothly thickened, narrow inner lip (similar in width to outer lip), weakly extended to left over previous whorl in some specimens; outer lip sinuous as in all *Pelicaria* species, deflected abaperturally below suture, followed by obvious, evenly convex adapertural flexure at mid-lip, followed again below by abapertural flexure leaving shallow, evenly concave anterior sinus below junction with columella. Inner lip of uniform thickness in many specimens, that is, without obvious parietal thickening; slight parietal thickening in a few specimens (including holotype) producing shallow, weakly defined posterior sinus.

Remarks. *Pelicaria arahura* n. sp. and *Pelicaria granttaylori* n. sp. share a similarity in shape to *P. zelandiae* (Fig. 8D; Beu & Maxwell 1990:294, pl. 36p) brought about by the shallow but consistent spiral depression above the peribasal spiral cord, the obvious sutural channel, and the adapically inward-sloping sutural ramp below the sutural channel. Most specimens of *P. granttaylori* n. sp. are taller and narrower than *P. arahura* n. sp., and *P. arahura* n. sp. lacks the narrow secondary spiral cords present on nearly all specimens of *P. granttaylori* n. sp. The inward-sloping sutural ramp and the consistent presence of the spiral depressed area between the second and third main spiral cords also distinguish both *P. arahura* n. sp. and *P. granttaylori* n. sp. from all younger species, particularly the early *acuminata* form of *P. vermis* (Martyn, 1784) (see below). *P. arahura* n. sp. also is shorter-spired and has more nearly parallel whorl sides, producing a more rectangular shell shape and a more stepped spire than in younger forms of *P. vermis* and most specimens of *P. granttaylori* n. sp., except for some specimens of the *bradleyi* form of *P. vermis* (Recent, N coast of the South Island) which are similar to *P. arahura* n. sp. in all characters except the much fewer, more prominent spiral cords of *P. arahura* n. sp.

Pelicaria zelandiae differs from *P. granttaylori* n. sp. in its straighter whorl sides and much finer and closer spiral sculpture. Most specimens also have a much more obvious, deeper and wider sutural channel than *P. granttaylori* n. sp., with a narrow rim, and a less obvious sutural ramp and almost straight whorl outlines between the margin of the sutural channel and the prominent, narrow, consistent peribasal angulation. Most specimens of *P. zelandiae* also have sculpture of many narrow, even, closely spaced spiral cords covering the sides and base of the last whorl, although it is a little coarser on a few specimens. In other words, *P. granttaylori* n. sp. is much more variable than *P. zelandiae*. *P. zelandiae* consistently has a wide sutural channel and vertical whorl sides, and varies mainly in the prominence of the spiral cords—weak, numerous, and closely spaced on most specimens, but fewer and more prominent on others—whereas *P. granttaylori* n. sp. is much more variable in outline shape, in the prominence of the sutural channel, and in the prominence of the spiral cords. *P. zelandiae* is particularly well-known from the Waipipi Shellbeds at Waverley Beach, Wanganui, but also occurs at Waihi Beach, Hawera (Waipipian), and at Whakino, South Taranaki (from P. Marshall's collection; Waipipian). Poorly preserved Opoitian specimens of a similar form occur in GS7193, N34/f6789, Omihi Creek, N Canterbury (two moulds with

Fig. 11 *Pelicaria vermis* (Martyn). (A) holotype of *Struthiolaria convexa* Marwick, TM5763, GS1089, V21/f8482, Olrig Station, Okauawa Stream, Kereru Road, central Hawke's Bay, late Nukumaruan; height 42.9 mm. (B) "*vermis/convexa* form", GS13709, S22/f023, Kupe Formation (Castlecliffian, OIS 17), Whangaehu Valley Road, E of Wanganui; height 51.1 mm. (C) holotype of *Pelicaria wellmani* Neef, TM4888, T24/f8022, Marima Sandstone (early Nukumaruan), Mangahao River upstream from Mangahao bridge, N Wairarapa; height 40.3 mm. (D) holotype of *Struthiolaria media* Marwick, TM7884, GS81, U26/f6446, Castlepoint, E Wairarapa, early Nukumaruan; height 35.8 mm. (E) nodulose Tainui Shellbed form, GS4022, R22/f6360, Tainui Shellbed (Castlecliffian, OIS 13), head of "the pinnacles" gully, Castlecliff; height 52.7 mm. (F) RM5559, Recent, deep-water "*tricarinata* form", trawled off Castlepoint, E Wairarapa, 300–350 m; height 45.8 mm. (G) holotype of *Pelicaria rotunda* Vella, TM8587, S27/f7519, Whakarua Stream, Whangaehu River, S Wairarapa, early Nukumaruan; height 44.1 mm. (H) holotype of *Pelicaria mangaoparia* Vella, TM8584, GS2626, S27/f8465, Mangaopari Mudstone (early Nukumaruan), Mangaopari Stream, upstream from junction with Makara River, S Wairarapa; height 35.9 mm.

fine spiral sculpture, and with slightly more convex whorls than Waipipian specimens of *P. zelandiae*).

The other main Pliocene species that needs to be distinguished from *Pelicaria granttaylori* n. sp. is *P. canaliculata* (Zittel, 1864) (Fig. 10D; Beu & Maxwell 1990:293, pl. 36q), which differs in its more evenly convex whorl shape, with a less obvious peribasal angulation, sutural channel and sutural ramp than in *P. zelandiae* and *P. granttaylori* n. sp., and in having four more even, prominent, high, vertical-sided to undercut spiral cords on the sides of the last whorl. Specimens are best known from Starborough Formation in the Awatere district (Starborough Creek; lower Awatere River; coast 2 km N of Cable Station Road, at mouth of Blind River), but also occur less commonly in Greenwood Formation in the lower Waipara Gorge, Canterbury (GS4997, N34/f6192, one fragment); near Taueru, central Wairarapa (GS94, R27/f8495, three poor moulds); in the Mangahao district in N Wairarapa (Neef 1970); and rarely in the Waipipi Shellbeds, Waverley Beach, Wanganui (GNS: one collected by P Marshall, one collected by FD Chambers); all of Waipipian age. *P. procanalis* (Beu, 1970) from Opoitian rocks in the Awatere Valley seems likely to have been ancestral to *P. canaliculata*, and differs from it in its much lower spiral cords. *P. arahura* n. sp. also is similar to *P. procanalis*, again differing in its more prominent spiral cords, and in the presence of the obvious, inward-sloping sutural ramp.

The final named Pliocene species requiring comparison is *Pelicaria cestata* Marwick (1965:32, pl. 7, fig. 21). The holotype (TM3730), from GS1586, X19/f7480, sandstone above Tahaenui Limestone, Makeretu Stream, Mangapoike, N Hawke's Bay (Waipipian), with two paratypes, has prominent, evenly convex spiral cords closely resembling those of the much younger *acuminata* form of *P. vermis* (see below), but a little narrower, more widely spaced and smoother-surfaced than in any specimens of *P. vermis*, and with a more obvious sutural channel, a secondary spiral cord below the channel on most specimens, and distinctive, more prominent spiral cords on the base. It seems to result from an independent evolution of an *acuminata*-like form, although its origin is not obvious. Other specimens in GNS are from GS4887, V22/f8511A, Hickey's Stream, off Argyll Road, Te Aute, S Hawke's Bay, Waipipian (one, smaller than others); GS1541, X18/f9477, sandstone above Tahaenui Limestone, Te Reinga Falls, Wairoa River, N Hawke's Bay, Waipipian (one incomplete); and GS8000, X19/f7642, sandstone overlying Tahaenui Limestone, Mangapoike River below mouth of Haupatanga Gorge, N Hawke's Bay, Waipipian (one incomplete).

Comparison of the range of variation of *Pelicaria granttaylori* n. sp. with that of the highly variable *P. vermis*, as interpreted broadly here (see below), suggests that like *P. vermis*, *P. granttaylori* n. sp. was much more variable in most characters than other *Pelicaria* species are. Therefore, it probably had direct development. Direct development, apparently an adaptation to cooling marine temperatures, evolved separately in both the *P. zelandiae-granttaylori* and *P. canaliculata-vermis* lineages, but in the *P. zelandiae* lineage it was adopted earlier (during early Mangapanian time) than in the *P. canaliculata-vermis* lineage (during earliest Nukumaruan time). Nevertheless, the *P. zelandiae* lineage apparently was unable to adapt to the continued cooling of marine temperatures and became extinct quite early in Nukumaruan time (the youngest record of *P. granttaylori* n. sp. is in GS4354, S22/f6479, 12 m below Ohingaiti Sand, early Nukumaruan). In contrast, *P. vermis* is still a common, widespread species around New Zealand at present. The much greater range of variation than in *P. zelandiae*, indicating direct development, and the rarity of specimens closely resembling typical Waipipian specimens of *P. zelandiae* justify the recognition of *P. granttaylori* n. sp. as a separate species.

Etymology. It gives me great pleasure to honour, with the name for this species, the memory of that great character and 'ideas man', Thomas Ludovic Grant-Taylor (18 October 1923–9 May 1982; New Zealand Geological Survey 1950–1982) (Hornibrook 1982). Tom was a frequent collecting companion, along with Norcott Hornibrook, during my early years in North Island east coast stratigraphy, and helped collect many of the fossil localities where *Pelicaria* species are found.

Pelicaria arahura n. sp. (Fig. 8E, 10A,B)

Type material. Holotype (TM8598) and two incomplete paratypes (TM8599-8600) from GS12289, J33/f066, uppermost concretionary, blue-grey, shelly conglomerate at top of Eight Mile Formation, Blue Bottom Group, head of E tributary of Greeks Creek, S side of Arahura Valley, Westland, Waipipian; one paratype (TM8606) from GS3046, J32/f9146, S side Kumara-Inchbonnie Road, E of former Westbrook Hotel, 2.8 km W of Three Mile Creek bridge and 1.0 km E of Cape Terrace Road, Big Hohonu River, Westland, Waipipian; one paratype (TM8607) from GS11557, J32/f9809, re-collection of GS3046, Kumara-Inchbonnie Road, Westland, Waipipian.

Other material examined. **Waipipian:** GS2875, J33/f7075, top of Eight Mile Formation, Greeks Creek, Arahura valley (two incomplete); GS12354, J33/f063, locality as holotype, from soft sandstone underlying conglomerate (three incomplete); GS3049, J32/f9149, roadside E of former Westbrook Hotel, Kumara-Inchbonnie Road, Westland, 2.8 km W of Three Mile Creek bridge and 1.0 km E of Cape Terrace Road, overlying GS3046 (see above) (one fragmentary); GS12368, J32/f0167, third of three outcrops on Kumara-Inchbonnie Road near former Westbrook Hotel, 2.8 km W of Three Mile Creek bridge and 1.0 km E of Cape Terrace Road, Westland (one incomplete). A few specimens from Hawke's Bay Pliocene rocks apparently are conspecific: GS8164, V20/f8608, Napier-Taupo Highway 1.6 km S of Te Pohue (one incomplete). Almond (1980):198, pl. 6, fig. 1, 2) also recorded and illustrated this species from eight localities in Eight Mile Formation in the Kaniere-Arahura area, E of Hokitika in Westland (J33/f13, head of Foley Creek, off Blue Spur Road, between Arahura and Kaniere valleys; J33/f36A, lower part of E branch, Greek's Creek, Arahura; J33/f40, f41A, f42, f43, all from head of E branch, Greeks Creek; J33/f48, halfway up W branch, Greek's Creek; J33/f51A, small creek between Greeks Creek and Humphreys Gully, S side Arahura valley; material in Geology Department, University of Otago). **Early Mangapanian?:** GS12512, V19/f014, Waihua Valley, Wairoa (one small, with slightly narrower and more prominent spiral cords than all other specimens referred here).

Distribution. *Pelicaria arahura* n. sp. is widespread and not uncommon in Waipipian rocks of the Hokitika district, Westland, and rare in Waipipian and possibly early Mangapanian rocks of northern Hawke's Bay.

Dimensions. Holotype: H 41.4, D 28.0 mm; paratype TM8606: H 43.8, D 29.1 mm; paratype TM8607: H 41.7, D 30.3 mm.

Description. Shell characteristic of *Pelicaria* in overall appearance and aperture shape and thickening; moderate-sized for genus. Protoconch not seen. Teleoconch of 5.5–6.5 whorls. Spire moderately short for genus; last whorl occupying 2/3 to 3/5 of height. Suture deeply and widely channelled; outer border similar in width to major spiral cords lower on whorl sides. Outline below sutural channel with weakly defined, narrow, outward-sloping, weakly concave sutural ramp, bordered below by obvious peripheral angulation formed by single prominent spiral cord; peribasal angulation defined clearly by single prominent spiral cord in all specimens; vertical area between two angulations weakly concave on specimens with weak median spiral cord, almost straight and sloping slightly inward anteriorly in specimens with prominent median spiral cord (most specimens, including holotype). Spiral sculpture of few, prominent, wide, convex-crested spiral cords, with interspaces each equal in width to one cord; two prominent cords on spire whorls, three on main, vertical side of last whorl (the central one varying in prominence on different specimens, prominent on many but weakly developed on a few specimens), one prominent cord on base below peribasal angulation, followed below by 3–4 narrower cords decreasing in size anteriorly. Major spiral cords, particularly at peripheral angulation, bearing low, gently rounded, widely spaced nodules on most specimens; peribasal angulation bearing smaller, more numerous, more closely spaced nodules on some specimens. Spiral sulcus above peribasal cord well-developed on all specimens, forming posterior area of sutural channel on spire. Exterior of well-preserved specimens closely covered with very fine spiral threads. Aperture large, relatively wide as in all *Pelicaria* species, with relatively narrow, evenly rounded terminal varix and smoothly thickened, narrow inner lip, similar in width to outer lip; outer lip sinuous as in all *Pelicaria* species, shallowly deflected abaperturally below suture, followed by obvious, evenly convex but shallow adapertural flexure at mid-lip, followed again below by shallow abapertural flexure leaving evenly concave anterior sinus below junction with columella. Inner lip consistently narrow, not spreading over previous whorl; with slight parietal thickening in most specimens (including holotype) producing shallow, weakly defined posterior sinus.

Remarks. Specimens of *Pelicaria arahura* n. sp. from Waipipian localities in Westland and northern Hawke's Bay are similar to *Pelicaria granttaylori* n. sp. in many characters. However, as noted above, they differ in their consistently slightly smaller size, their shorter spire, and their much more consistent prominence and arrangement of the spiral cords, all lacking the narrow intermediate cords that are present on almost all specimens of *P. granttaylori* n. sp. *P. arahura* n. sp. is similar to *P. zelandiae* in consistently having a spiral depression between the median and lowest main spiral cords on the last whorl, although less obvious than that of *P. zelandiae*, and in many specimens having a weakly developed, inward-sloping sutural ramp above the uppermost main spiral cords, but it differs obviously from both *P. zelandiae* and *P. granttaylori* n. sp. in its much fewer, wider, more prominent spiral cords. Differences from other species are as for *P. granttaylori* n. sp. *P. arahura* n. sp. is relatively unvaried, certainly much less so than either *P. granttaylori* n. sp. or *P. vermis*, implying that it had good genetic exchange between distant populations, as it retained the brief demersal larval life of earlier *Pelicaria* species and *Struthiolaria papulosa*.

Etymology. Name based on the Arahura River, Westland, near the type locality of the species; a noun in apposition.

Pelicaria vermis (Martyn, 1784) (Figs. 10C,E, F,H, 11A–H, 12A–E)

Buccinum vermis Martyn 1784, vol. 2, pl. 53 (available, ICZN Opinion 479 1957).
Murex australis Gmelin 1791:3542; Dillwyn 1817:712; Martens 1872:20.
Struthiolaria inermis GB Sowerby I 1821, pl. 222, figs. 3, 4; GB Sowerby II 1842:23, pl. 5, figs. 12, 13, 19; Hutton 1880:68.
Struthiolaria crenulata Lamarck 1822b:148; Gray 1835:308; Quoy & Gaimard 1835:430, pl. 31, figs. 7–9; Kiener 1838–1839a:5, pl. 2,

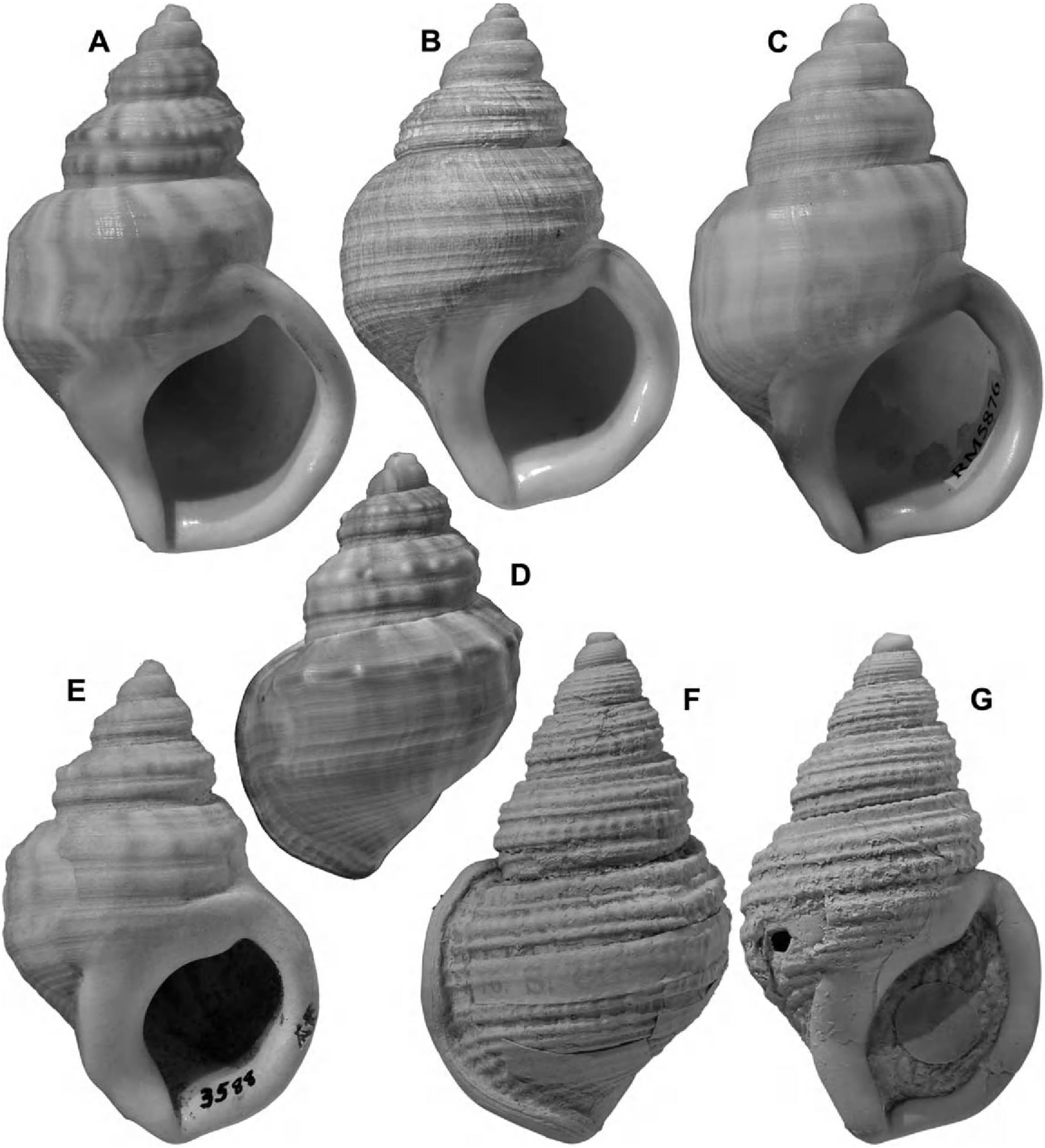

Fig. 12 (A–E) *Pelicaria vermis* (Martyn), Recent; A, RM4425, Te Arai Beach, Northland, height 51.1 mm; B, RM5302, "*grahami* form" with many weak spiral cords, trawled, 18-37 m, off East Cape; height 47.5 mm; C, RM5876, typical Wellington W coast "*powelli* form", Waikanae Beach; height 51.6 mm; D, E, RM3588, 2 specimens, Tokerau Beach, Doubtless Bay, Northland; D, height 40.3 mm; E, height 45.5 mm. (F,G) *Pelicaria monilifera* (Suter), holotype, TM8699, "Awatere" (wrong), locality unknown, North Canterbury?, Opoitian-Waipipian?; height 48.3 mm.

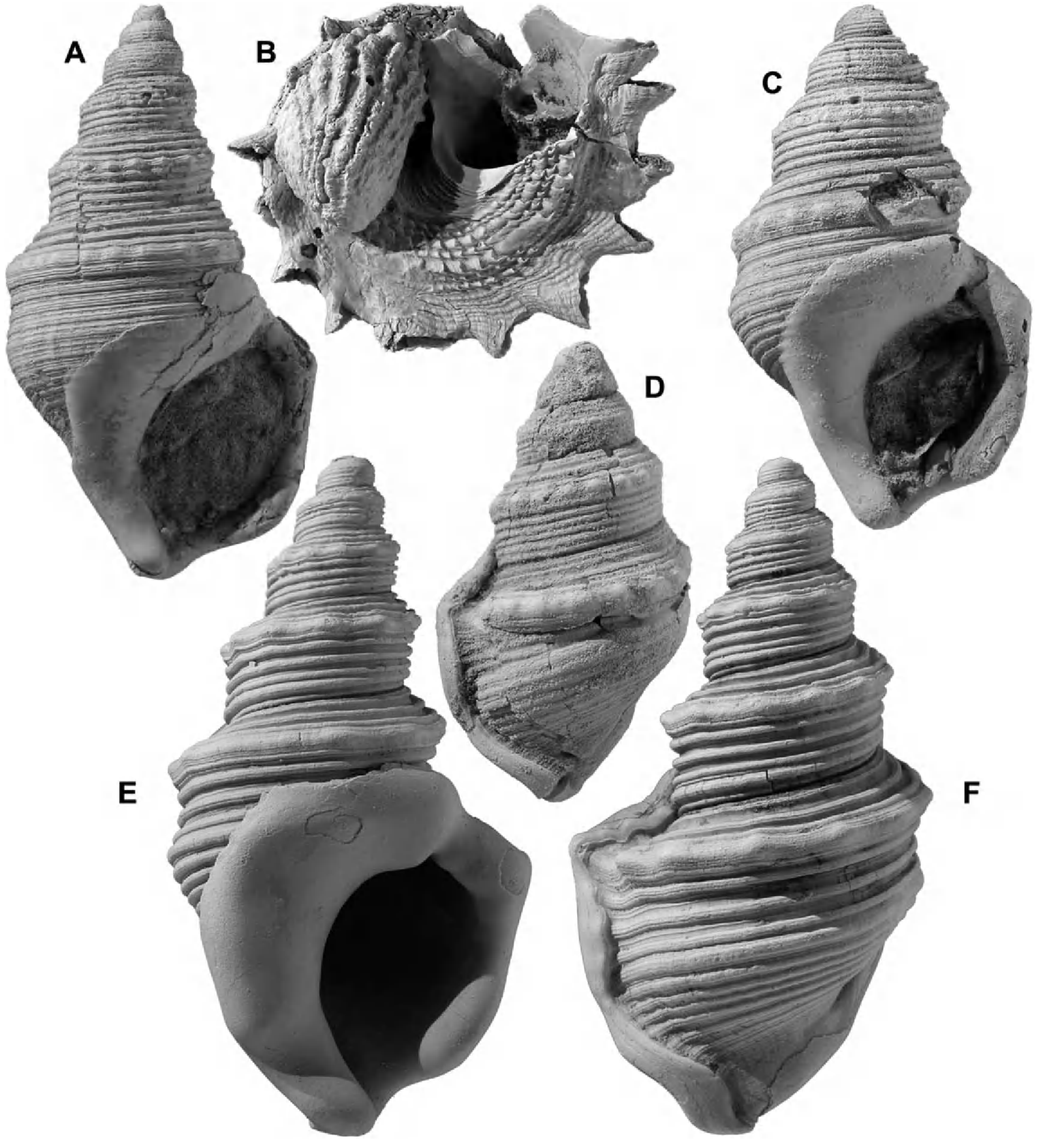

Fig. 13 (A,C–F) *Struthiolaria frazeri* Hutton; A, GS12865, V21/f095, early Nukumaruan sandstone underlying Flag Range Limestone, Napier-Taihape Road W of Sherenden, Hawke's Bay; height 81.2 mm; C,D, GS13079, W19/f027, Mangapanian sandstone, Mohaka River, N Hawke's Bay; C, height 74.9 mm; D, height 64.5 mm; E,F, shallow-water Nukumaruan form, GS11225, V20/f8002, Darkys Spur Formation (late Nukumaruan), Darkys Spur, W of Devils Elbow, central Hawke's Bay; height 95.8 mm. (B) *Maoricrypta costata* (G. B. Sowerby I) attached to underside of *Astraea heliotropium* (Martyn), GS4014, R22/f6513, basal shellbed member of Shakespeare Cliff Sand (Castlecliffian, OIS 11), Castlecliff; width of *Astraea* 64 mm.

figs. 3, 3a; Reeve 1842 (in 1841–1842):201, pl. 245, figs. 3, 4 (as *S. inermis* in plate caption; repeat of G. B. Sowerby I, 1821, pl. 222, figs. 3, 4); ME Gray 1842 (in 1842–1859), pl. 5, figs. 3; 1850 (in 1842–1859), pl. 91, fig. 6; Deshayes 1843:535; JE Gray 1850:2,19,66; Paulucci 1877:225.

Struthiolaria tricarinata Lesson 1841:256; Hutton 1880:68; Suter in Hutton 1904:75; Marwick 1924a:186, pl. 15, figs. 6, 7.

Struthiolaria australis. Reeve 1842:200, pl. 245, figs. 3, 4; Reeve 1851, pl. 1, figs. 1, 2; Martens 187326.

Struthiolaria scutulata Gray 1843:232; Hutton 1873a:24; Hutton 1873b:10 (incorrect use of the name *Tylospira scutulata* (Gmelin, 1791), Australian).

Struthiolaria vermis. Deshayes 1843:535, footnote; H Adams & A Adams 1854:282, pl. 27, fig. 6; Chenu 1859:263, fig. 1653; Tryon 1885:133, pl. 12, figs. 35, 36; Hutton 1873a:24; Hutton 1873b:10; Paulucci 1877:229; Hutton 1893:61; Harris 1897:219; Suter in Hutton 1904:75; Cossmann 1904, pl. 8, fig. 2; Moss 1908:20, pl. 4, fig. 5; Suter 1913:276, pl. 40, fig. 2; Marwick 1924a:187, pl. 15, figs. 1, 2; Bucknill 1924:44, pl. 4, fig. 16; Dell 1955:21, fig. 32.

Struthiolaria vernis (sic). JE Gray 1850:66.

Pelicaria vernis (sic). JE Gray 1857:77.

Struthiolaria sulcata Hector 1886:50, fig. 6 (in part; junior primary homonym of *S. sulcata* Jonas, 1829).

Struthiolaria vermis tricarinata. Suter 1913:276.

Struthiolaria acuminata Marwick 1924a:185, pl. 15, figs. 11, 12 (**new synonym**).

Struthiolaria media Marwick 1924a:187, pl. 15, figs. 13, 14 (**new synonym**).

Struthiolaria convexa Marwick 1924a:188, pl. 15, figs. 3, 4 (**new synonym**).

Struthiolaria fossa Marwick, 1924a:189, pl. 15, figs. 8, 9 (**new synonym**).

Struthiolaria vermis var. *tricarinata*. Bucknill 1924:45, pl. 4, fig. 17.

Pelicaria vermis. Finlay 1926b:391; Morton 1950:456, figs. 4–6, 8; Penniket & Moon 1970:28, pl. 11, fig. 3; Morley 2004:92, upper fig.; Maxwell 2009:241.

Pelicaria acuminata. King 1933:340, pl. 39, fig. 28; Vella 1953:44, pl. 4, fig. 11; Beu & Maxwell 1990:320, pl. 42e; Beu 1995:131, fig. 68i,j; Maxwell 2009:241.

Struthiolaria (Pelicaria) vermis. Powell 1937:73, pl. 14, fig. 25; Powell 1946a:75, pl. 14, fig. 25; Powell 1958a:100, pl. 14, fig. 25; Powell 1962:92, pl. 14, fig. 25; Morton & Miller 1968:491, fig. 182.4; p. 587, fig. 219.5.

Struthiolaria (Pelicaria) tricarinata. Powell 1937:73; Powell 1946a:75; Powell 1958a:100; Powell 1962:92.

Pelicaria mangaoparia Vella 1953:40, pl. 4, figs. 8–10 (**new synonym**).

Pelicaria rotunda Vella 1953:41, pl. 4, figs. 5, 7 (**new synonym**).

Pelicaria media. Vella 1953:44, pl. 4, fig. 4.

Pelicaria aff. *media*. Vella 1953:45, pl. 4, figs. 1–3.

Pelicaria convexa. Vella 1953:45; Beu & Maxwell 1990:320, pl. 42b; Beu 1995:131, fig. 68a–h,k,l; Maxwell 2009:241.

Struthiolaria (Pelicaria) convexa fossa Beu 1965:143, pl. 2, figs. 15–17.

Struthiolaria (Pelicaria) acuminata. Fleming 1966:52, pl. 89, figs. 1054, 1056.

Struthiolaria (Pelicaria) convexa. Fleming 1966:52, pl. 90, figs. 1063, 1064.

Struthiolaria (Pelicaria) fossa. Fleming 1966:52, pl. 90, figs. 1061, 1062.

Struthiolaria (Pelicaria) mangaoparia. Fleming 1966:52.

Struthiolaria (Pelicaria) media. Fleming 1966:52, pl. 90, figs. 1059, 1060.

Struthiolaria (Pelicaria) rotunda. Fleming 1966:52.

Struthiolaria (Pelicaria) vermis vermis. Fleming 1966:52, pl. 90, figs. 1067, 1068; Neef 1970:459, figs. 10, 11, 24, 24a; Powell 1976b:94, pl. 21, fig. 25; Powell 1979:143, pl. 7, fig. 4; pl. 30, fig. 3; Spencer & Willan 1996:21.

Struthiolaria (Pelicaria) vermis tricarinata. Fleming 1966:52, pl. 90, figs. 1065, 1066.
Struthiolaria (Pelicaria) vermis flemingi Neef 1970:462, figs. 12, 13; Powell 1976b:94; Powell 1979:143, pl. 30, fig. 4; Spencer & Willan 1996:21 (**new synonym**).
Struthiolaria (Pelicaria) vermis convexa. Neef 1970:463.
Struthiolaria (Pelicaria) vermis cf. *convexa.* Neef 1970:463, figs. 16, 17.
Struthiolaria (Pelicaria) vermis grahami Neef 1970:465, figs. 20, 21; Spencer & Willan 1996:21 (**new synonym**).
Struthiolaria (Pelicaria) vermis powelli Neef 1970:465, figs. 14, 15; Spencer & Willan 1996:21 (**new synonym**).
Struthiolaria (Pelicaria) vermis bradleyi Neef 1970:467, figs. 18, 19; Spencer & Willan 1996:21 (**new synonym**).
Struthiolaria (Pelicaria) vermis vellai Neef 1970:468, figs. 22, 23 (**new synonym**).
Struthiolaria (Pelicaria) wellmani Neef 1970:472, figs. 35, 36 (**new synonym**).
Pelicaria fossa. Beu & Maxwell 1990:321,407, pl. 42a; Maxwell 2009:241.
Pelicaria vermis vermis. Beu & Maxwell 1990:351,407, pl. 47u; Spencer et al. 2009:207.
Pelicaria vermis flemingi. Beu & Maxwell 1990:407; Spencer et al. 2009:207.
Pelicaria vermis grahami. Beu & Maxwell 1990:407; Spencer et al. 2009:207.
Pelicaria vermis bradleyi. Spencer et al. 2009:207.
Pelicaria vermis powelli. Spencer et al. 2009:207.
Pelicaria flemingi. Maxwell 2009:241.

Type material. As with all of Martyn's illustrated specimens, the type material of *Buccinum vermis* Martyn has long been lost. Neef (1970, figs. 24, 24a) repeated Martyn's original illustrations, which shows the common form of *Pelicaria vermis* (Martyn, 1784) occurring around Auckland and in Northland, with relatively prominent nodules around the periphery. Neef (1970:462) thought a locality near Queen Charlotte Sound likely for the holotype, because the type originated from Cook's voyages to New Zealand, and this was the place where Cook stayed longest and most frequently. However, *Pelicaria vermis* is rare in or, in most areas, absent from the Marlborough sounds, the illustrated shell is clearly an Auckland or Northland specimen, and a type locality in the Bay of Islands is much more likely.

Gmelin (1791:3542) cited as illustrations for *Murex australis* only Spengler's (1782) drawings in 'Spengl. Naturf. 17. t. 2. f. C. D.' (see below), so Spengler's specimen would be the holotype of *Murex australis* if it still existed; unfortunately, it does not. A complication with this name is the usage of the same binomen for the large conoidean species now consistently known as *Nihonia australis* (e.g., Powell 1969:331, pl. 192, figs. 16, 17; pl. 254, figs. 1, 2). Tucker (2004:101) attributed this name to Gmelin (1791:3542), stating incorrectly that Gmelin referred only to Chemnitz (1795, pl. 190, fig. 1827, 1828). Obviously it is impossible for Gmelin (1791) to have referred to a work published in 1795, so it not surprising that Powell (1969:331) attributed this name to a later author, Roissy (1805:72), where it was published as *Pleurotoma australis.* Roissy in turn referred to Chemnitz's (1795, pl. 190, figs. 1827, 1828) figures, among others. Powell (1969:331) made the situation clear by stating under *Nihonia australis*: 'This is not *Murex australis* Gmelin, 1791, which refers to the New Zealand species *Struthiolaria (Pelicaria) vermis* (Martyn, 1784)'. The misunderstanding over this name probably arose because Roissy (1805:72) incorrectly included a reference to 'Spengler, Naturf. 17, tab. 2, fig. C, D' (=*Pelicaria vermis*) in the synonymy of *Pleurotoma australis.* There is no doubt that Gmelin (1791:3542) was referring to *Pelicaria vermis*, as his remarks include '*Habitat in* Oceano australi, *stramineo affinis, testa quoque straminea*…'; *Murex stramineus* Gmelin, 1791 (=*Struthiolaria papulosa* (Martyn, 1784)) is the preceding species on the same page.

Struthiolaria inermis G. B. Sowerby I, 1821, no type material present in BMNH, and no material in the general collection is identified as *S. inermis* (K Way, BMNH pers. comm. 14 January 2008); location of type material unknown. This name has usually been credited to GB Sowerby II (1842), but it was referred to by Lesson (1841), and both Deshayes (1843) and Paulucci (1877) pointed out its earlier publication by GB Sowerby I (1821). None of Lesson's type material of *Struthiolaria tricarinata* is present in MNHN and its location is not known, although a photograph in GNS, sent from MNHN during the 1960s when Neef (1970) was carrying out his research, purports to be of 'the type', and is labelled on the back 'type de *Struthiolaria tricarinata* Lesson, Muséum Paris'. Lesson (1841:256) stated that it was obtained by the frigate '*la Vénus*' (not, as was assumed by Neef [1970:468], Bay of Islands material collected by the '*Coquille*'), Lesson had seen 'about 20 perfectly similar' specimens from New Zealand (that is, there were originally ca 20 syntypes), 'but it appears to be found solely on the beaches of the South Island [l'île Méridionale]'. The described specimen was 22 mm high and 14 mm wide, unusually small for an adult specimen of *P. vermis*. The locality, the size, and Lesson's description of the suture as 'simple et peu profonde' suggest that he was describing the '*bradleyi* form' with a narrow sutural channel, named by Neef (1970:467, figs. 18, 19) from beaches near Nelson, northern South Island—common on Rabbit Island Beach after storms (Fig. 10C), but also seen from Marahau, Kaiteriteri Beach, and Golden Bay. No other form around New Zealand at present has a deep sutural channel, and *Pelicaria* is not cast ashore on any other beaches in the South Island. Specimens from Mahurangi estuary, southern Northland (GNS RM4420, many, collected by JR Penniket) are very similar to the '*bradleyi* form' in their short, squat shape, with an obvious peripheral angulation and a prominent, flat, outward-inclined sutural ramp, but have a much shallower, narrower sutural channel than N South Island specimens. The specimen of *P. vermis* illustrated under the name *S. crenulata* by Kiener (1838–1839a, pl. 2, fig. 3) was also said to 'Habite les plages de la nouvelle baie Tasman, dans le détroit de Cook, à la Nouvelle-Zélande' [found on the beaches of the new Tasman Bay, in Cook Strait, at New Zealand], and clearly has a narrow sutural channel, and so is a specimen of the same form. The 'variety' illustrated by Kiener (1838–1839a, pl. 2, fig. 3a) is shorter, lacks a sutural channel and has nodules around the periphery, and appears to be an Auckland-Northland specimen. Lesson (1841) discussed a species *Struthiolaria oblita* of Kiener, in relation to *S. crenulata*, that is, *Pelicaria vermis*, but this name does not appear in Kiener (1838–1839a). I conclude that no type material exists for any of the four early names *Buccinum vermis*, *Murex australis*, *Struthiolaria inermis* or *Struthiolaria tricarinata*, and at least two names listed by early cataloguers are *nomina nuda* (*S. oblita* 'Kiener' Lesson, 1841; *S. canaliculata* 'Spengl.' H Adams & A Adams 1854:282).

Struthiolaria crenulata, one syntype MNHN moll. 20522, H 40.8 mm, without locality, stated by Lamarck to be from 'Nouvelle Zélande', collected by Péron & Lesueur in 1803; labelled 'Individu nommé par Lamk', although it is considered to be a syntype under ICZN Recommendation 73F, as Lamarck (1822b:148) stated merely 'coll. du Muséum', without stating how many specimens he had before him. Photographs (Fig. 10H) kindly supplied by Virginie Héros (Malacologie, MNHN) show that this, too, possibly is a specimen of *Pelicaria vermis* of the '*bradleyi* form', from northern beaches of the South Island, with a steep but clearly defined sutural ramp and an obvious but shallow sutural channel, although this specimen has a less prominently protruding peripheral cord than most other specimens of the '*bradleyi* form', and is not the specimen of which photographs were supplied earlier as 'the type' of *S. tricarinata* Lesson, which is smaller and has a more prominent, nodulose peripheral cord. It might also possibly be from the beaches of western Wellington (Paekakariki to Otaki), where the taller form with a less obviously channelled suture (Fig. 12C) is cast ashore that was named *S. vermis powelli* by Neef (1970:465, figs. 14, 15). This form appears to be intermediate between the '*bradleyi* form' and forms in the northern North Island. These intermediates and the Mahurangi estuary intermediates in Northland show that there is little justification for treating these forms as geographical subspecies. The syntype, MNHN moll. 20522, is here designated the lectotype of *Struthiolaria crenulata* Lamarck, 1822, in case other syntypes should come to light and are not conspecific with the remaining syntype. In order to attach all other early names permanently and unambiguously to this species rather than to *S. papulosa* (Martyn, 1784), the lectotype of *Struthiolaria crenulata* Lamarck, MNHN moll. 20522, is here designated also the neotype of *Buccinum vermis* Martyn, 1784, the neotype of *Murex australis* Gmelin, 1791, the neotype of *Struthiolaria inermis* G. B. Sowerby I, 1821, and the neotype of *Struthiolaria tricarinata* Lesson, 1841. These species were all stated to come from 'New Zealand', the locality of the neotype, and use of this specimen as the neotype renders all these names objective synonyms of *Pelicaria vermis* (Martyn, 1784).

Struthiolaria acuminata holotype TM7682 (Fig. 10F), GS1040, S27/f8448, sandstone member of Pukenui Limestone, Te Awaite cutting, Awhea Road, 8 km SE of Martinborough, S Wairarapa, with two paratypes, TM7683-4; early Nukumaruan, occurring with *Zygochlamys delicatula*. (The early locality 'Te Awaite cutting' [also written 'Twaite's cutting'] was well-known; it was on an outer curve of White Rock [or Awhea, Te Awaite] Road overlooking Makara River about 1.3 km SW of the present 'banana bridge' over Huangarua River and 1.5 km N of the junction of Makara River and Mangaopari Stream, but was by-passed by road straightening many years ago.) *Struthiolaria media* holotype TM7884 (Fig. 11D), GS81, U26/f6446, Castlepoint, E Wairarapa; early Nukumaruan, with *Z. delicatula*. *Struthiolaria convexa* holotype TM5736 (Fig. 11A), GS1089, V21/f8482, Okauawa Formation (late Nukumaruan) (Erdman & Kelsey 1992), Okauawa Stream, Kereru Road, inland central Hawke's Bay. *Struthiolaria fossa* holotype TM8583, GS191, V21/f8463, 'Shrimpton's', that is, Kikowhero Stream, Matapiro Station, N of Ngaruroro River, central Hawke's Bay; late Nukumaruan, near the axis of Matapiro syncline. *Pelicaria mangaoparia* holotype TM8584 (Fig. 11H), V300, = GS2626, S27/f8465, with two paratypes, TM8585-6, Mangaopari Stream, 1.2 km upstream from Makara River, Awhea Road, SE of Martinborough, S Wairarapa; early Nukumaruan, underlying *Z. delicatula* (which, however, appears late in this succession because of the deep-water facies of the lower part of the section; Gammon 1997; Orpin et al. 1998, fig. 7); other paratypes from V34, V301. *Pelicaria rotunda* holotype TM8587 (Fig. 11G), V205, S27/f7519, junction Whakarua Stream and first tributary from S, upstream from junction of Whakarua Stream and Whangaehu River, S Wairarapa, early Nukumaruan; with paratypes from V7, V25, V59, V204, V216, V272, V274 and V278 (localities and fossil record numbers listed by Vella 1953:46–47); one paratype TM8588, GS5452, T27/f6529, Oreka Stream, W slope of Maungaraki Range, E of junction of Millars Road with Martinborough-Gladstone Road, S Wairarapa; early Nukumaruan. *Pelicaria wellmani* holotype TM4888 (Fig. 11C), with one figured paratype TM4889, G Neef's locality 1022, T24/f8022, listed by Neef (1967, appendix 1) as Marima Sandstone, with three persistent beds of concretions, left bank Mangahao River 350 m NE of bridge at Marima, N Wairarapa, grid ref. T24/401743; age listed by Neef (1970:472) as 'lower Hautawan', that is, early Nukumaruan.

Other material examined. Not listed; *Pelicaria vermis* is widespread and abundant in early Nukumaruan–Haweran rocks throughout most of New Zealand.

Distribution. *Pelicaria vermis* is interpreted here as a single highly variable species (as a result of its direct development) occurring widely in earliest Nukumaruan to Haweran rocks and in the Recent fauna. The many named forms all intergrade, and any evolutionary change during the time range of *P. vermis* apparently was anagenetic. In the Recent fauna it occurs in shallow water (allowing living specimens to be cast ashore after storms) throughout the eastern North Island, rarely on Ninety Mile Beach, NW Northland, and on both sides of Cook Strait, and occurs also on the continental shelf in slightly deeper water (ca 20–80 m) along the east coast of both islands from East Cape to Otago Peninsula (Graham 1962:57; dead specimens rare in Graham's zone 2, 9–55 m). A few specimens have also been collected in much deeper water off eastern New Zealand (e.g. RM5559, 300–350 m, trawled off Castlepoint, E Wairarapa; Fig. 11F) and some of them have relatively prominent spiral cords similar to the Nukumaruan *P. acuminata* form (also known as *P. tricarinata*). It is absent from the rest of New Zealand.

Dimensions. Lectotype of *Struthiolaria crenulata* Lamarck and neotype of *Buccinum vermis* Martyn, *Murex australis* Gmelin, *Struthiolaria inermis* G. B. Sowerby I and *Struthiolaria tricarinata* Lesson: H 40.8 mm, D 26.8 mm; holotype of *P. acuminata*: H 42.9, D 26.7 mm; holotype of *P. media*: H 35.8, D 23.6 mm; holotype of *P. convexa*: H 42.9, D 28.8 mm; holotype of *P. rotunda*: H 44.1, D 30.0 mm; paratype, GS5452: H 47.5, D 32.5 mm; holotype of *P. mangaoparia*: H 35.9, D 23.2 mm; holotype of *P. wellmani*: H 40.3, D 26.5 mm; large, elongate specimens of *acuminata* form, GS3111, T26/f6462, Taueru bridge, N of Masterton, Wairarapa: H 57.5, D 34.5 mm; H 53.5, D 33.6 mm; *acuminata* form, GS2611, S27/f8450, Makara River, 800 m upstream from Ruakokopatuna River junction, S Wairarapa: H 53.1, D 31.0 mm; *convexa* form, GS10748, hillside above Makara River–Mangaopari Stream junction: H 48.0, D 32.4 mm; large specimen of *convexa* form, Waikopiro, S Hawke's Bay, Suter collection: H 56.0, D 38.2 mm; large Recent specimens: RM5244, beach, N side Ayres Point, Te Arai Beach, N of Leigh, Northland: H 56.5, D 35.1 mm; RM5302, trawled in 18–37 m, off East Cape: H 55.4, D 35.2 mm; short '*bradleyi* form', RM2974, Rabbit Island Beach, Nelson: H 36.6, D 28.3 mm.

Remarks. A few authors (Gmelin 1791:3542; Deshayes 1843:535; Martens 1872:20; 1873:26; Paulucci 1877) have recognized that *Pelicaria vermis* was first illustrated by Spengler (1782:31, pl. 2, figs. C, D), who, however, did not propose a name for this species. As mentioned by Iredale (1956:83), Spengler was among the first to illustrate and describe shells brought to Europe by Cook. Spengler (1782) described and illustrated both Recent *Struthiolaria* species, using only the English vernacular names proposed by George Humphrey. The year 1782 is well before any publications by Humphrey, so the names were presumably suggested orally. Spengler stated that he obtained his specimens through Humphrey, who obtained them in turn from Sir Joseph Banks and Daniel Solander; that is, as seems necessary this early, they were collected during Captain James Cook's first visit to New Zealand. H Adams & A Adams (1854:282) listed *Struthiolaria canaliculata* 'Spengl.' in their catalogue of *Struthiolaria* species, but this name was not proposed in Spengler's (1782) paper, and was not listed by Sherborn (1902). It seems to be a *nomen nudum* appearing only in H Adams & A Adams' list. If this name were available, it would be a senior primary homonym of the well-known New Zealand fossil species *Pelicaria canaliculata* (Zittel) (1864:34, pl. 15, fig. 1), originally proposed in *Struthiolaria*; the varietal name *S. canaliculata becki* proposed by Neef (1970:469, figs. 25, 29) would take its place if Zittel's name is a junior homonym. However, *P. canaliculata* (Zittel) appears to be valid. As noted above, Spengler's illustrated specimen is also the holotype of

Murex australis Gmelin (1791:3542). Kathe Jensen (ZMC pers. comm. August 2006) reported that no *Pelicaria* material illustrated by Spengler (1782) remains in Spengler's collection in ZMC. *Pelicaria vermis* is one of several New Zealand species named in Martyn's non-binominal work that were conserved in ICZN Opinion 479 (1957).

The great range of variation of forms of what is here identified as the single species *Pelicaria vermis* has long troubled paleontologists and neontologists alike, and a certain amount of 'art' has always been involved in distinguishing the intergrading forms traditionally recognized as fossil species. I previously (Beu 1995:119–121, fig. 68) discussed their occurrence in central Hawke's Bay, where they at first seemed to offer a similar biostratigraphically useful zonation to that proposed by Vella (1953) in SE Wairarapa. However, I concluded that their arbitrary-looking occurrences resulted from ecological differences between the deposition sites, combined with a temperature control on the prominence of spiral cords, rather than being an evolutionary series. Local populations greatly dominated by the *P. acuminata* form, with a relatively tall (but highly variable) spire and very prominent spiral cords, are encountered in S Wairarapa and at Castlepoint. Only rare specimens of the *P. convexa* form, with a slightly shorter spire and no prominent spiral cords at all, have been found in S Wairarapa. I am aware of only two: one incomplete specimen was reported by Vella (1953:45) from V311 (S27/f7520, sandstone downstream from junction Ruakokopatuna and Makara Rivers [that is, Hautotara Formation], SE of Martinborough, late Nukumaruan) and I collected one specimen (Fig. 10E; GS10748, S28/f6206, sandstone beneath Pukenui Limestone member B, above White Rock Road at the junction of Mangaopari Stream and Makara River, SE of Martinborough; early Nukumaruan, with *Zygochlamys delicatula*). In contrast, local populations dominated by the *P. convexa* form, and only uncommonly and early in the succession varying towards the *P. acuminata* form (Beu 1995, fig. 68c–f,i), occur throughout central and southern Hawke's Bay, as far south as the Totara Road area, near Kumeroa, E of Woodville. Unfortunately, this species group is not known from the geographically intermediate area of central and northern Wairarapa. Suitable facies in this area apparently do not extend this young. I (Beu 1965, 1995:121) described a 'pseudoevolutionary' succession of forms intergrading between *P. convexa* and *P. fossa* in the Devil's Elbow hill section, on Highway 2 N of Napier, in which the degree of expression of the sutural channel characteristic of the *P. fossa* form increases in succeeding siltstone formations up-section. However, alternating sandier units (with *P. convexa* and common *Tawera*) and muddier units (with *P. fossa* and more offshore taxa such as *Amalda mucronata* (G. B. Sowerby I, 1830)) in the succession exposed along Kereru Road, inland central Hawke's Bay, show that the *P. fossa* form occurred in more offshore units contemporaneously with the shallower-water *P. convexa* form. The Devil's Elbow succession evidently reflects water depth increasing gradually up-section during the deposition of siltstone units, rather than the gradual evolution of a distinct species. Despite deposition being affected by rhythmical glacio-eustatic sea-level change, the entire basin sank more rapidly than accommodation was filled with sediment. This confusion between evolutionary and ecophenotypic change is frequent and normal in fossils of the *Pelicaria vermis* species complex, and describes the succession in S Wairarapa (Vella 1953) as well as in Hawke's Bay. Neef (1970) also described a number of local variants (interpreted by him as geographical subspecies) of *P. vermis* living at present in areas around the North Island, northern South Island, and off E Canterbury–N Otago, demonstrating that a similar range of ecological and geographical variation occurs in the Recent fauna.

Morton (1950) described the development of *Pelicaria vermis*, in which 'the embryos are completely incubated within the [brood] pouch, and are liberated as tiny replicas of the adult which at once take on a benthic existence', an excellent example of direct development. In a popular account (Morton 1997a b) he compared the anatomy, ecology, life history and phylogeny of *Pelicaria* with *Struthiolaria, Perissodonta, Tylospira, Aporrhais* and other stromboideans, emphasizing the different developmental modes of *Struthiolaria papulosa* and *Pelicaria vermis*. Direct development and the consequent lack of genetic exchange between local populations by a significant, although relatively brief, demersal larval stage (as occurs in *Struthiolaria papulosa*) explains the maintenance of distinct forms in discrete areas by *P. vermis*, as well as the intergradation of the long series of subtly different forms of *P. vermis* recognized previously as species and subspecies by paleontologists. In contrast, *S. papulosa* exhibits simple clinal variation in spire height and peripheral nodule size over New Zealand, with smaller, shorter, prominently nodulose specimens in the far north of the North Island, much larger, taller, narrower specimens lacking nodules altogether at Stewart Island, and a complete morphological and geographical intregradation between these extremes. *Pelicaria vermis* is therefore interpreted here as a classic example of a single long-ranging, anagenetically changing, direct-developing species, highly plastic in its phenotypic expression. Although forms within it might be useful for biostratigraphy in local areas (one sub-basin or smaller area) over short time scales, my experience in Hawke's Bay and SE Wairarapa indicates that the ecological and temperature controls on the variation of *P. vermis* have produced a fossil record that confuses rather than aids the biostratigrapher. It has also always been impossible to distinguish some Castlecliffian forms that traditionally would have been identified as *P. vermis* (e.g. in Kupe Formation in Wanganui Basin; Fig. 12E) from the Nukumaruan form in Hawke's Bay traditionally identified as *P. convexa*. In my opinion this is one variable species, and it is time to study its interesting genetics and ecology rather than attempt to force it into apparent biostratigraphical utility that produces conflicting or simply incorrect results.

Neef (1970) described an evolutionary series preserved in Waipipian–Mangapanian rocks in the Marima area, SW of Woodville in N Wairarapa, in which *Pelicaria vermis* (as interpreted broadly here) evolved gradually from *P. canaliculata* in a series of forms with progressively lower spiral cords with progressively less strongly undercut edges (Neef 1970, fig. 6; 'period of co-existence', '*clarki* probably grades into *marima*', etc.). This, then, poses the question of where the boundary should be drawn of what is included in *P. vermis*. Neef's (1970) study is detailed enough to show that the succession of forms at Marima represents an evolving unidirectional series of species rather than the arbitrary-looking series of random walks (ecophenotypic adaptation to local environmental variation) adopted in different geographical areas by *P. vermis*. The early Nukumaruan form named *P. wellmani* by Neef (1970:472, figs. 35, 36) is closely similar to specimens identified as *P. acuminata* elsewhere in Wairarapa and Hawke's Bay, and is assumed here to represent the first specimens of the direct-developing species *P. vermis*. As the enormous range of variation of *P. vermis* commences with the *P. acuminata* form, and populations of what Neef (1970) called *P. canaliculata, P. clarki* and *P. marima* are remarkably unvaried (even though apparently evolving gradually, that is, anagenetically), it seems likely that a demersal larval stage was abandoned and direct development adopted on evolving the *P. acuminata* form, at the beginning of Nukumaruan time. The forms intermediate between typical, early *P. canaliculata* (Waipipian) and *P. acuminata* deserve further study, and perhaps would be best recognized as the single species *P. canaliculata*, but are here segregated from *P. vermis*, which is limited here to the direct-developing, final species of the genus.

A further form that seems to fall within the range of variation of *Pelicaria vermis* is early Nukumaruan specimens in GNS identified as related to *P. lacera* (Marwick 1931:96, figs. 133, 134). This species with a few prominent, very narrow, widely spaced spiral carinae was named from poor, distorted, mouldic material from GS1244 (Z17/f6464, Mangatuna Quarry, main highway N of Tolaga Bay, N of Gisborne; Kapitean, late Miocene) and represents a small, wide, very early, latest Miocene species that is almost unknown elsewhere. The large early Nukumaruan specimens with narrow cords that have been thought related to *P. lacera* are essentially tall-spired specimens of the *acuminata* form with unusually narrow, widely spaced spiral cords, and are included here in *P. vermis*: GS2481, T24/f6408, Lower Kumeroa Formation, Tahoraite SD, Dannevirke, one large, incomplete; GS2651, T24/f7389, all data as last, one; GS11959, T24/f8797, gully 900 m ESE of Pahiatua trig. station, N Wairarapa, G Neef, two; GS11991, T24/f8051, left bank Mangahao River, N Wairarapa, G Neef, one incomplete; TM4896, T24/f8041, Neef's locality 1041, slip W side of Mangaramarama Stream, 2 km E of Totaranui Station, between Konini and Pahiatua, N Wairarapa; specimen illustrated by Neef (1970, fig. 37).

Pelicaria vermis provides an example of the type of highly variable complex of forms that commenced in early Nukumaruan time, and is also exemplified by *Stiracolpus symmetricus* and *Aoteadrillia wanganuiensis*.

Pelicaria rugosa (Marwick, 1924) (Fig. 11G)

Struthiolaria cingulata. Hutton 1873b:11 (in part, 'Patea' shell only, not *S. cingulata* Zittel, 1864); Suter 1914:18, pl. 1, fig. 9 (not *S. cingulata* Zittel, 1864).
Struthiolaria rugosa. Marwick 1924a:189, pl. 13, fig. 2.
Struthiolaria (Pelicaria) rugosa. Fleming 1966:52, pl. 89, fig. 1058; Neef 1970:472, fig. 38.
Pelicaria rugosa Beu & Maxwell 1990:321, pl. 42c; Maxwell 2009:241.

Type material. Struthiolaria rugosa, holotype TM4898, supposedly from 'Patea', S Taranaki (early NZ Geological Survey type-set label glued onto specimen), but this Waipipian locality is obviously an error; early Nukumaruan, apparently from North Canterbury (Beu & Maxwell 1990:321), possibly from Motunau Beach. The holotype of *P. rugosa* is the specimen that Hutton (1873b:11) recorded as *S. cingulata* from 'Patea', and that Suter (1914:18, pl. 1, fig. 9) illustrated as *S. cingulata*. The printed label attached to the shell reflects this early confusion; both the locality and the identification were incorrect. Suter (1914:18) followed Hutton's error and described Hutton's (1873b:11) 'var. B. – Ribs sub-moniliform' as the subspecies *S. cingulata monilifera*, that is, *Pelicaria monilifera* (Fig. 12F,G). *Struthiolaria cingulata* is a more prominently spirally ridged, typical *Struthiolaria* species limited to Kapitean–Opoitian rocks of the Awatere valley.

Other material examined. **Nukumaruan:** GS2855, U24/f6440, Waitahora Road, Mangaotoro, S Hawke's Bay (one; Beu & Maxwell 1990, pl. 42c); GS2419 (U24/f6337, Mangapuku Stream, 2 km E of Waitahora Valley Road and 2.5 km S of Dannevrke-Weber Road; few); GS2472 (U24/f6368, tributary of Mangamaire Stream, 2 km NE of Dannevirke-Weber Road and 5 km SE of Mangatoro; few); GS2483 (T24/f7375, hill slope above Highway 2, 1 km W of Waiaruhe, between Woodville & Dannevirke; few); and GS2758 (U24/f6436, Mangatoro Stream, 1 km SW of Mangatoro; few), all in Lower Kumeroa Formation of Dannevirke Subdivision (Fleming & Marwick in Lillie 1953, table 21); G Neef's fossil locality 1049, T24/f8049, 1 km SW of Marima, N Wairarapa (30 cm-thick *P. rugosa* shellbed in Marima Sandstone, tributary of Mangahao River 0.5 km SE of Naenae Road, grid ref. T24/391735; Neef 1967, appendix 1, table following p. 359; 'a [30 cm] shell bed largely composed of *P. rugosa*...is unique.... Scattered *P. rugosa* shells occur up to [1.6 m] above the *P. rugosa* bed in otherwise unfossiliferous sandstone'; Neef 1967:183; 1970:472, fig. 38); GS5490, S27/f8593, low in Pukenui Limestone (presumably the same horizon as the following one), stream beside Te Muna Road, W side Huangarua River, 2.2 km upstream from Martinborough-Masterton Road, 4 km SE of Martinborough, SE Wairarapa (one); common in a thin bryozoan-rich zone in Mangaopari Stream ca 10 m upstream from Birch Hill Station access bridge, ca 200 m upstream from junction with Makara River, 100 m S of White Rock Road, S Wairarapa; GS10965, S28/f6202A and re-collections, common in sandstone with abundant *Zygochlamys delicatula* where Whangaimoana Stream flows into beach sands at its mouth, E end of Whangaimoana Beach, between Lake Ferry and Hurupi Stream, Palliser Bay, S Wairarapa; abundant (with *Z. delicatula*) in the matrix of the enormous debris flows (Lewis 1976:539) at Motunau Beach, North Canterbury; common (with *Z. delicatula*) in the Gower River and nearby areas, Cheviot district, North Canterbury.

Distribution. *Pelicaria rugosa* occurs only in a brief basal Nukumaruan zone in S Hawke's Bay, N and S Wairarapa, and in the Cheviot district and at Motunau Beach in North Canterbury. It provides a very useful biostratigraphical index of earliest Nukumaruan time; all these localities seem to correlate closely in age. It occurs with *Zygochlamys delicatula* at all localities other than in S Hawke's Bay and N Wairarapa, where the facies seems to have been too shallow for *Z. delicatula* to occur (*Z. delicatula* lives now below 70 m, and almost all records are from water deeper than 200 m). This highlights an unusual aspect of the occurrences of *P. rugosa*: it occurs in moderately deep-water (outer shelf to upper bathyal) facies, deeper than most or all other *Pelicaria* species, and I am not aware of syntopic occurrences with *P. vermis*. Among other things, *P. rugosa* is helpful for identifying the age of most of the fossil penguins in concretions at Motunau Beach, North Canterbury (Marples 1960; Simpson 1972) as early Nukumaruan. I am not aware of any authentic records of *P. rugosa* from Wanganui Basin, again probably because depositional facies there were too shallow.

Dimensions. Holotype: H 40.9, D 28.0 mm; GS5490, Te Muna Road, S Wairarapa: H 44.8, D 31.5 mm; GS2855, Mangaotoro, S Hawke's Bay: H 45.3, D 32.0 mm; GS10965, Whangaimoana Stream mouth, Palliser Bay: H 34.2, D 22.9 mm.

Remarks. *Pelicaria rugosa* is the one *Pelicaria* species I am aware of in post-Mangapanian rocks that is distinct from *P. vermis*, apart from the early Nukumaruan records (above) of *P. granttaylori* n. sp. *P. rugosa* is rendered highly distinctive by its exterior sculpture, as it lacks the prominent, wide spiral cords (often labelled cinguli in this genus) so characteristic of *P. arahura* n. sp., *P. granttaylori* n. sp., *P. canaliculata*, and several early forms of *P. vermis*. Instead it bears numerous low, narrow, closely spaced, convex-crested spiral ridges, about 10 on spire whorls and 25 on the last whorl, with interspaces each about equal in width to one cord, crossed by numerous low, narrow axial ridges with the same prominence and spacing as the spiral cords, forming small, narrowly rounded nodules at the intersections and so producing the finely nodulose surface reflected in the species name. The shape is similar to that of the *convexa* form of *P. vermis*, with no clearly defined sutural ramp, with rounded shoulders and a gradually rounded base, and the smoothly rounded lips are very similar to those of all other *Pelicaria* species. *P. rugosa* is almost completely constant in its characters, implying again that it retained a demersal larval life that allowed genetic exchange throughout its range, as in earlier *Pelicaria* species and *Struthiolaria papulosa*. A little-known, more coarsely sculptured species, *P. monilifera* (Suter) (1914:18, pl. 1, fig. 10)

(Opoitian–Waipipian, rare in N Canterbury –Marlborough; holotype Fig. 13F,G), is similar apart from its fewer, larger nodules (caused by its fewer, wider spiral cords) and markedly taller spire, and possibly was the ancestor of *P. rugosa*.

Recognized Pelicaria species. This part of the present paper essentially is a revision of the Pliocene to Recent species of *Pelicaria*, so a list is provided of the taxa now recognized in the genus. The status of a few named species remains unclear. '*Pelicaria*' *incrassata* (Powell) (1931:101, pl. 13, figs. 30–33) (Waipipian, Tangahoe Formation, Waihi Beach, Hawera) does not belong in any obvious lineage of *Pelicaria*, and the late PA Maxwell suggested to me that it is a small species of *Struthiolaria*. The relatively tall, narrow shape, the presence of only two spiral cords bordering an otherwise wide, concave, last whorl mid-section, the small aperture, the heavily thickened, weakly sinuous lips, and the unusual, large parietal tubercle all agree with this position, and I consider *S. incrassata* to be a species of *Struthiolaria*. *P. pseudovermis* (Bartrum & Powell) (1928:142, pl. 30, figs. 63, 64) (Opoitian, Kaawa Creek, SW Auckland) also has some similarities with *Struthiolaria*, particularly the unusually deep, prominent anterior sinus in the outer lip. However, Bartrum & Powell (1928:142, pl. 30, figs. 63, 64) argued for a relationship with *P. nana* (Marwick, 1926), the earliest species of *Pelicaria* (Beu & Maxwell 1990:262, pl. 29g), and although the last whorl lacks the characteristic *Pelicaria* median spiral cord, it is present on spire whorls. A relationship with *P. nana* appears feasible, and this species is retained in *Pelicaria*. The status of *P. clarki* and *P. marima*, N Wairarapa species recognized by Neef (1970), remains to be clarified, and they are listed here despite apparently intergrading anagenetically with *P. canaliculata*. So although two new species are named here, the 19 species and subspecies listed by Beu & Maxwell (1990:407) are reduced to 15, and probably in the long run will be reduced to 13.

Recognized species are:

Pelicaria arahura n. sp., Figs. 8E, 10A,B, Waipipian (–Mangapanian?), Westland, N Hawke's Bay.

Pelicaria canaliculata (Zittel, 1864), Fig. 10D, Opoitian?, Waipipian, Hawke's Bay–N Canterbury; rare in Waipipi shellbeds, Waverley Beach, W of Wanganui.

Pelicaria cestata Marwick, 1965, Waipipian, N Hawke's Bay.

Pelicaria clarki (Neef, 1970), Mangapanian, N Wairarapa (probably intergrades with *P. canaliculata*).

Pelicaria granttaylori n. sp., Fig. 9A–E, Mangapanian–early Nukumaruan, Wanganui & N Hawke's Bay.

Pelicaria lacera (Marwick, 1931), Kapitean, Gisborne district.

Pelicaria marima (Neef, 1970), Mangapanian, N Wairarapa (probably intergrades with *P. canaliculata*).

Pelicaria monilifera (Suter, 1914), Fig. 12F,G, (Opoitian?), Waipipian, N Canterbury.

Pelicaria nana (Marwick, 1926), Tongaporutuan, N Taranaki and S Wairarapa.

Pelicaria parva (Suter, 1915), Opoitian, holotype from unknown locality (others in GNS: GS1574, W19/f7481; GS1576, W19/f7483, both Wahanui Road, N Hawke's Bay, one at each locality; GS4936, W21/f8555, between shelter huts and Black Reef, Cape Kidnappers, three; GS2230, T25/f6521, Kaitawa Road, Makuri, E of Woodville, S Hawke's Bay, one unusually tall and narrow, possibly a distinct species; GS11519, J33/f088, outcrop west of McKay Creek mouth, opposite lower power house, Lake Kaniere Road, Westland, in a diverse fauna including *Veprichlamys scandula* (Hutton, 1873), *Mesopeplum* cf. *waikohuense* (Marwick, 1931), *Marama murdochi* (Marwick, 1927), *Zeacolpus kanieriensis* (Harris, 1897), *Galeodea flemingi* Beu & Maxwell, 1990, *Aeneator* n. sp., *Polinices* (*Polinella*) *obstructus* (Marwick, 1924); two specimens).

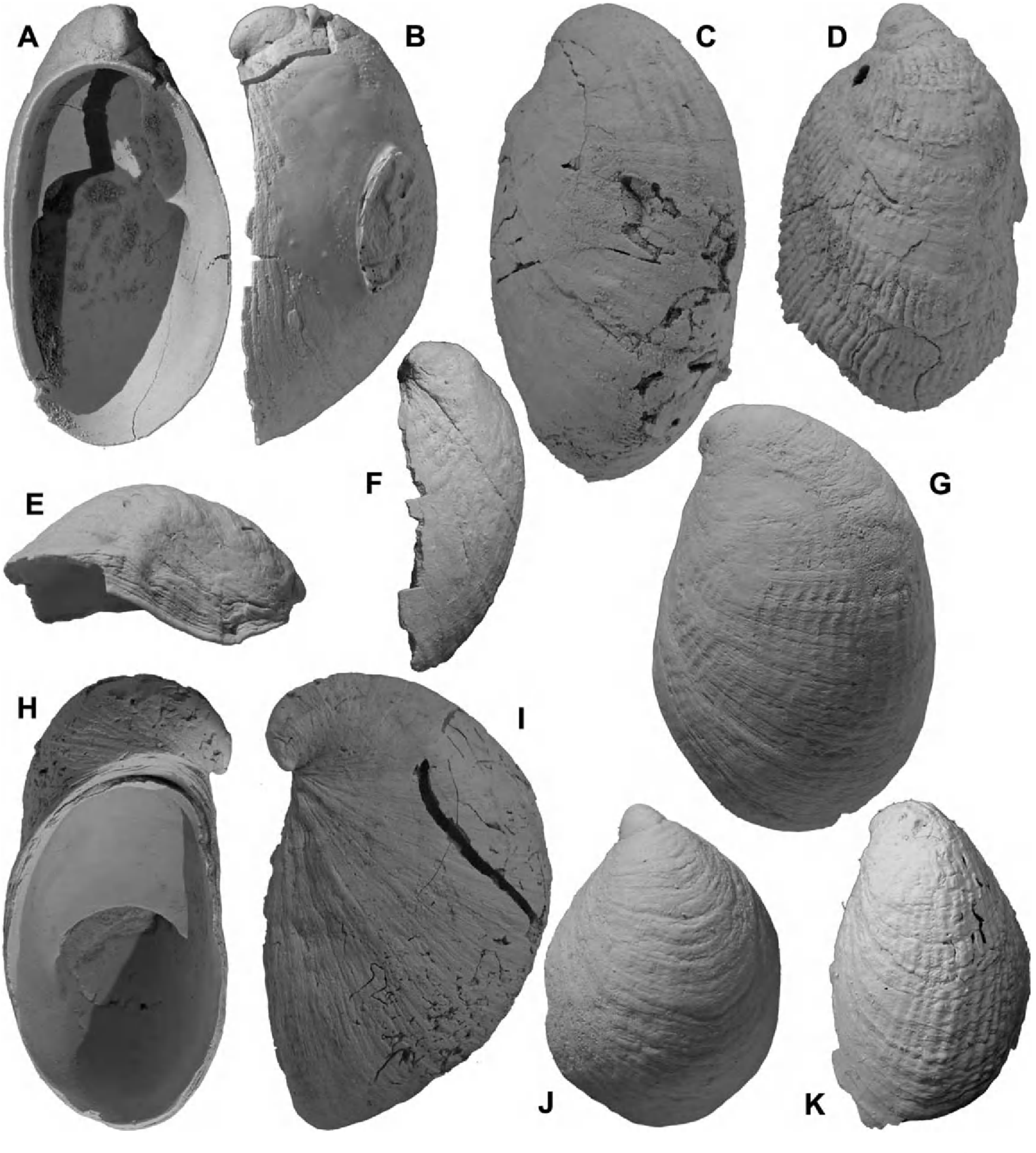

Fig. 14 (A–D, G–I) *Maoricrypta profunda* (Hutton); A,B, lectotype, TM8223, "Shakespeare Cliff" (wrong; Tangahoe Formation (Waipipian), Waihi Beach, Hawera); height 31.5 mm; C,D, 2 specimens, GS4253, Q22/f7544, Upper Waipipi Shellbed (Waipipian), Waverley Beach, W of Wanganui; C, height 45.1 mm (radial costae on early part only); D, height 38.5 mm (narrow radial costae all over); G, GS4356, S22/f6481, Nukumaru Brown Sand (late Nukumaruan), Mangawhero Road, W of Wanganui; height 40.4 mm; H, I, GS14094, Q21/f6501A, Tangahoe Formation (Waipipian), Waihi Beach, Hawera; large smooth specimen, height 64.6 mm. (E,J) *Maoricrypta youngi* Powell, Castlecliff fossils; E, GS4014, R22/f6513, basal shellbed member of Shakespeare Cliff Sand; left side view, height 14.4 mm; J, GS4022, R22/f6360, Pinnacle Sand (OIS 14), head of "the pinnacles" gully; dorsal view, height 15.2 mm. (F,K) *Maoricrypta radiata* (Hutton), holotype of *Crypta opuraensis* Bartrum & Powell, AUGD G5739, Kaawa Creek, SW Auckland, Opoitian; height 23.5 mm.

Pelicaria procanalis Beu, 1970, Opoitian, Awatere valley.
Pelicaria pseudovermis (Bartrum & Powell, 1928), Opoitian, Kaawa Creek.
Pelicaria rugosa (Marwick, 1924), Fig. 10G, early Nukumaruan, Hawke's Bay–N Canterbury.
Pelicaria vermis (Martyn, 1784), Fig. 10C,E,F,H, 11A–H, 12A–E, early Nukumaruan–Recent, widespread.
Pelicaria zelandiae (Marshall & Murdoch, 1920), Fig. 10A, Opoitian, N Canterbury?; Waipipian, S Taranaki–W Wanganui.

Genus ***Struthiolaria*** Lamarck, 1816

Struthiolaria Lamarck 1816, pl. 431, fig. 1a,b; 'Liste des objets représentés dans les planches de cette livraison' p. 7. Type species (by monotypy): *Struthiolaria nodulosa* Lamarck, 1816 (=*Buccinum papulosum* Martyn, 1784; available, ICZN Opinion 479 1957), Pliocene–Recent, New Zealand.

Struthiolaria frazeri Hutton, 1885 (Figs. 13A,C–F)

Struthiolaria frazeri (*ex* Hector MS) Hutton 1885:329; Harris 1897:220, pl. 6, fig. 10a, b; Speight 1913:31; Suter 1921:19; Marwick 1924a:181, pl. 13, figs. 8, 10; Fleming 1966:51, figs. 1020, 1022; Beu & Maxwell 1990:318, pl. 42f; Maxwell 2009: 241.
Struthiolaria fraseri. Hector 1886:48, fig. 5.1; Hutton 1893:61.
Struthiolaria papulosa. Marwick 1924a:180, pl. 12, fig. 4 only (in part not *S. papulosa* Martyn, 1784).
Struthiolaria tasmani King 1933:340 (in part, not pl. 39, fig. 30); Fleming 1966:51, fig. 1029.

Type material. Marwick (1924a:181) discussed the possible type material of *Struthiolaria frazeri*, and concluded that the holotype is the specimen then in the 'Geological Survey collection at the Dominion Museum'. These type specimens were transferred to the New Zealand Geological Survey in the 1950s. The holotype (an unusually small specimen) is TM8284, GS231, V21/f8466, from 'McLean's', that is, Donald McLean's station at Maraekakaho, opposite 'Shrimpton's' on the S side of the Ngaruroro River, central Hawke's Bay; from fine-grained interbeds in Scinde Island Limestone of Mason Ridge. Specimens of *S. frazeri* in BMNH recorded by Harris (1897:221) are from the same collection, made by Hector in 1871. *Struthiolaria tasmani* King, 1933, holotype TM8703, the specimen illustrated by Marwick (1924a, pl. 12, fig. 4), a severely abraded specimen from GS1094, U21/f8494, Mangatahi River, Kereru Road, central Hawke's Bay (late Nukumaruan), apparently a weakly sculptured form of *S. frazeri*.

Other material examined. **Mangapanian:** an ancestral Mangapanian–early Nukumaruan form of *Struthiolaria frazeri* occurs in shallow-water facies rocks of northern Hawke's Bay: GS12508, V19/f012, brown sand beneath three obvious major conglomerate beds, Matahorua Road, W of Tutira, N of Napier, Hawke's Bay (seven); GS13076, W19/f027, brown sands underlying Nukumaruan siltstone in Mohaka River, upstream from Highway 2 bridge, N Hawke's Bay (five); GS13079, W19/f031, as last, at small side waterfall 20 m further downstream (two). **Early Nukumaruan:** GS12865, V21/f095, roadside, Napier-Taihape Road, 2 km W of Sherenden hall, low in Nukumaruan rocks of Matapiro syncline (one); definitely Nukumaruan in age, underlying by about 30 m the Nukumaruan limestone-conglomerate succession of the Flag Range (Flag Range Limestone; Beu 1995:130). **Late Nukumaruan:** almost the only previous record of *Struthiolaria frazeri* from Wanganui Basin is that by Marshall & Murdoch (1920:123) 'over a distance of [1.6 km] south [actually ESE] from the Nukumaru boat-landing'. Fleming (1953:158) assigned this specimen to Tewkesbury Formation. Marwick (1924a:182) recorded the specimen as 'broken to pieces in transmission from Mr. Suter', and a fragmentary but reglued specimen labelled '12 m below moa bed, Nukumaru' in GNS is evidently this shell. The only complete Wanganui Basin specimen I am aware of is an unusually large specimen from the Suter collection in GNS labelled 'Wanganui, Pliocene'. It has a yellow stain suggesting that it came from sands or Nukumaru Limestone facies high in the succession (e.g. from a horizon such as Waipuru Shellbed, or higher), rather than the grey stain of specimens from Tewkesbury Formation. Therefore, it is interesting that RM Carter (James Cook University, Townsville pers. comm. August 2003) reported an incomplete spire of *S. frazeri* in 'shellbed f' (of Abbott et al. [2005, fig. 3], in the second cycle up from the base of Tewkesbury Formation, 18 m above the base of the section, deposited during OIS 71) on the Nukumaru coast, seen during a visit in August 2003. The only other Wanganui Basin record I am aware of is that by Fleming (1953:148) from GS4341, S22/f6466, a 'sub-Waipuru' shellbed in the Turakina valley, E of Wanganui.

All other records are from central and northern Hawke's Bay. *Struthiolaria frazeri* is abundant in two shellbeds high in Okauawa Formation, cropping out in Okauawa Stream, Whanakino Stream, Poporangi Stream and nearby streams in the Kereru district, inland central Hawke's Bay, high in the Nukumaruan succession in this area (stratigraphy described by Erdman & Kelsey 1992): GS5439, V21/f8575, Okauawa Stream (six); GS10943, V21/f8575A, lower 200 m of Okauawa Stream (two); GS12868, U21/f028, road cutting W side Whanakino Stream (two); GS12866, U21/f033, Okauawa Stream (15); GS14584, V21/f096, Racham Station (one). Specimens also occur as scattered individuals at a range of other localities in Hawke's Bay, from 'not far below the Scinde Island limestone at Maraekakaho, Ngaruroro River', that is, in interbeds within Mason Ridge limestone, very near the type locality (Marwick 1924a:182); in several limestone beds in the Waipunga Road section, ascending from Esk Valley towards Devils Elbow; underlying the Devil's Elbow succession at the Aropaoanui Stream bridge on the Napier-Wairoa Highway; in Mairau Mudstone at 'the watchman' hill, Ahuriri, Napier (GS11465, V21/f8015A, two fragmentary); and in Darkys Spur Formation on Darkys Spur road, 5 km WNW of Devils Elbow (GS11225, V20/f8002, two; common but difficult to remove) to pockets in sandstone high in the Nukumaruan succession in Matahorua Gorge, on the Napier-Wairoa Highway, and scarce specimens in mudstone near the Mohaka River highway bridge, also in northern Hawke's Bay. It extends into late Nukumaruan rocks, in Tewkesbury and Okauawa Formations, although I am not aware of a record from the highest Nukumaruan fossiliferous unit in Wanganui Basin, Pukekiwi Shell Sand.

Distribution. Struthiolaria frazeri is a valuable, highly distinctive, Mangapanian–Nukumaruan index fossil. Most records are from late Nukumaruan rocks of central and northern Hawke's Bay, but four specimens are recorded from Wanganui Basin. I am not aware of any specimens from Wairarapa district or anywhere further south, so evidently it was a warm-water species. Intergrading ancestral specimens are also recorded here from Mangapanian–early Nukumaruan rocks of central and northern Hawke's Bay.

Dimensions. Struthiolaria frazeri, holotype, H 73.9, D 42.2 mm; large specimen, GS14584, Racham Station, Kereru Road: H 93.4, D 48.8 mm; Suter's 'Wanganui Pliocene' specimen: H 96.8 (apex incomplete; estimated originally 100 mm), D 52.9 mm; GS12865, Sherenden, Hawke's Bay, early Nukumaruan: H 81.2, D 43.6 mm; GS13076, Mohaka River, Mangapanian: H 69.6, D (slightly incomplete) 38.5 mm.

Remarks. Hector (1886:48) and Hutton (1893:61) spelled the species name '*fraseri*', rather than the original and more usual spelling '*frazeri*'. The only likely source of the name is Charles Fraser (1823?–1886) (Breward 1990), who, as one of the founders of both the

Philosophical Institute of Canterbury (secretary 1868–1869) and the Canterbury Museum, would have been well known to both Hector and Hutton. However, I know of no published evidence that the name was intended to honour Charles Fraser, so the original spelling *frazeri* should be retained.

Struthiolaria frazeri is a highly distinctive Nukumaruan index fossil. Firstly, it is the largest struthiolariid, reaching 100 mm in height. Also, it has much coarser and more prominent spiral cords than any other struthiolariid, and among the most prominent of all New Zealand gastropods. Its spire also is unusually tall, with a strongly stepped outline, and with a rather narrow but almost horizontal sutural ramp. The rounded shoulder angle protrudes a little beyond the weakly to quite strongly concave lateral shell outline anterior to the periphery, and on some specimens the shoulder is weakly or, in a few specimens, quite strongly nodulose. The few, very wide, strongly raised, flat-topped spiral cords are closely spaced around the shoulder angle and on the peribasal angle, but more widely spaced both above and below both angulations, becoming low and narrow over the central area of the base. The aperture is very prominently but rather narrowly callused for a *Struthiolaria* species. The varix is flat but unusually wide in the spiral plane, and corrugated at the back where it meets the spiral cords.

Specimens occurring in Mangapanian and early Nukumaruan rocks of central and northern Hawke's Bay (Fig. 14A–C) are interpreted as ancestral, intergrading specimens. They are similar to younger specimens of *Struthiolaria frazeri* in their tall, narrow shape, with a strongly stepped spire and relatively small last whorl with weakly concave outlines below the peripheral angle, in having more prominent spiral sculpture than other *Struthiolaria* species, and in their prominently but rather narrowly callused aperture. They differ from middle to late Nukumauan specimens of *S. frazeri* in their smaller size, and in particular, in their narrower, more numerous and more closely spaced spiral cords. While the cords are very clearly defined, with vertical sides and a flat crest as in later specimens of *S. frazeri*, there are 6–7 cords on the sutural ramp (three on late Nukumaruan *S. frazeri*), 5–7 cords between the peripheral and peribasal angles, with many fine interstitial cords on some specimens (3–4, without interstitial cords, on late Nukumaruan *S. frazeri*), and 20–30 fine, narrow, closely spaced cords, including many interstitial ones, on the base (six plus several faint, narrow ones in late Nukumaruan *S. frazeri*). These characters suggest that Mangapanian–early Nukumaruan specimens are intermediate between a more typical *Struthiolaria* species resembling *S. papulosa* (Martyn, 1784) and late Nukumaruan specimens of *S. frazeri*. However, the characters of late Nukumaruan specimens of *S. frazeri* also vary ecophenotypically and specimens from more offshore environments, e.g. Mairau Mudstone at 'the watchman' hill, Ahuriri, Napier, closely resemble Mangapanian–early Nukumaruan ones. The holotype of *S. tasmani* King seems to be a relatively short, weakly sculptured ecomorph of *S. frazeri* of this type; such specimens are common in a second shellbed near Kereru Road overlying the one with abundant *S. frazeri*, whereas the specimens from S Wairarapa identified by King (1933:34, pl. 39, fig. 30) as *S. tasmani* definitely are strongly sculptured specimens of *S. papulosa*. Beu & Maxwell (1990:350) included *S. tasmani* in the synonymy of *S. papulosa* but, strictly speaking, following King's (1933) designation, the holotype is Marwick's illustrated specimen from near Kereru Road, inland Hawke's Bay. Pliocene species of *Struthiolaria* (sensu stricto) are poorly understood, and the ancestor of *S. frazeri* is not obvious. Assuming the early form is not simply ecophenotypic, *S. frazeri* seems to provide yet another example of an anagenetically evolving succession. As there is no point in this succession at which a subdivision into more than one species would be anything other than arbitrary, in my opinion the Mangapanian–Nukumaruan form is part of the variation of one species, *S. frazeri*. The earlier form possibly can be used to identify rocks of Mangapanian–early Nukumaruan age in shallow-water facies in Hawke's Bay, but must be used with care in view of the phenotypic variation observed in late Nukumaruan specimens.

Family Calyptraeidae

Genus ***Maoricrypta*** Finlay, 1926

Maoricrypta Finlay 1926b:393. Type species (by original designation): *Crepidula costata* G. B. Sowerby I, 1824, Pleistocene and Recent, New Zealand.
Zeacrypta Finlay 1926b:393. Type species (by original designation): *Calyptraea monoxyla* Lesson, 1831, Pleistocene and Recent, New Zealand.

Remarks. Marshall (2003) recognized *Maoricrypta* as a valid genus for most New Zealand species that recently have been referred to *Crepidula*, on the basis of its two muscle scars; no muscle scars are visible in most species of *Crepidula* (but see Simone [2006, fig. 122]; a single scar is present in some South American species of the *C. plana* Say, 1822 species complex). The generic distinction was confirmed by Collin (2003) on the basis of molecular phylogeny. Marshall (2003:118) also recognized that although most of the younger species in New Zealand have two muscle scars, one on each side of the columellar septal insertion, and belong in *Maoricrypta* (*M. costata* [see below], Castlecliffian–Recent; *M. haliotoidea* Marwick, 1926, Tongaporutuan, N Taranaki; *M. kopua* Marshall, 2003, Recent; *M. monoxyla* (Lesson, 1830), Recent; *M. profunda* (Hutton, 1873) [see below]; *M. sodalis* Marshall, 2003, Haweran [Landguard Bluff, OIS 9]–Recent; *M. radiata* (Hutton, 1873) [see below], the Tongaporutuan-Opoitian stacking species, and *M. youngi* Powell, 1940 [see below]). A few other species have only one muscle scar, on the right side, and belong in *Grandicrepidula* McLean, 1995 (see below).

McLean (2009) recognized that still further genera of Calyptraeidae can be defined in the '*Crepidula*-group' based on the number of muscle scars. He pointed out that they are separately evolved conditions. One scar (the presumed basal condition) is present in *Bostrycapulus*, *Crepipatella*, *Grandicrepidula* and an unnamed genus, two scars are present in *Garnotia* and *Maoricrypta*, and no scars are present in *Crepidula* (sensu stricto), *Verticumbo* and *Siphopatella*.

Dimensions. For dimensions of specimens of *Maoricrypta* and *Grandicrepidula* special abbreviations are required because of their atypical shape; H is used for greatest dimension (overall height of the specimen, parallel to the apertural plane), W for width, and D for depth (height normal to the apertural plane).

Maoricrypta costata (G. B. Sowerby I, 1824) (Fig. 13B)

Crepidula costata GB Sowerby I 1824, part 23, pl. 152, fig. 3; Quoy & Gaimard 1835:414, pl. 72, figs. 10, 12; Gray 1843:242; Reeve 1842, in 1841–1842:29, pl. 143, fig. 3; Reeve 1859, pl. 4, fig. 21a,b; Martens 1873:28; GB Sowerby III 1883:67, pl. 452, figs. 113, 114; Suter 1913:287, pl. 44, figs. 6, 6a; Iredale 1915:456; Hoagland 1977:370; Beu & Maxwell 1990:408; Bandel & Reidel 1994:341; Spencer & Willan 1996:21.
Crepidula costata Deshayes 1830:26 (synonymous junior primary homonym of *Crepidula costata* G. B. Sowerby I, 1824; junior primary

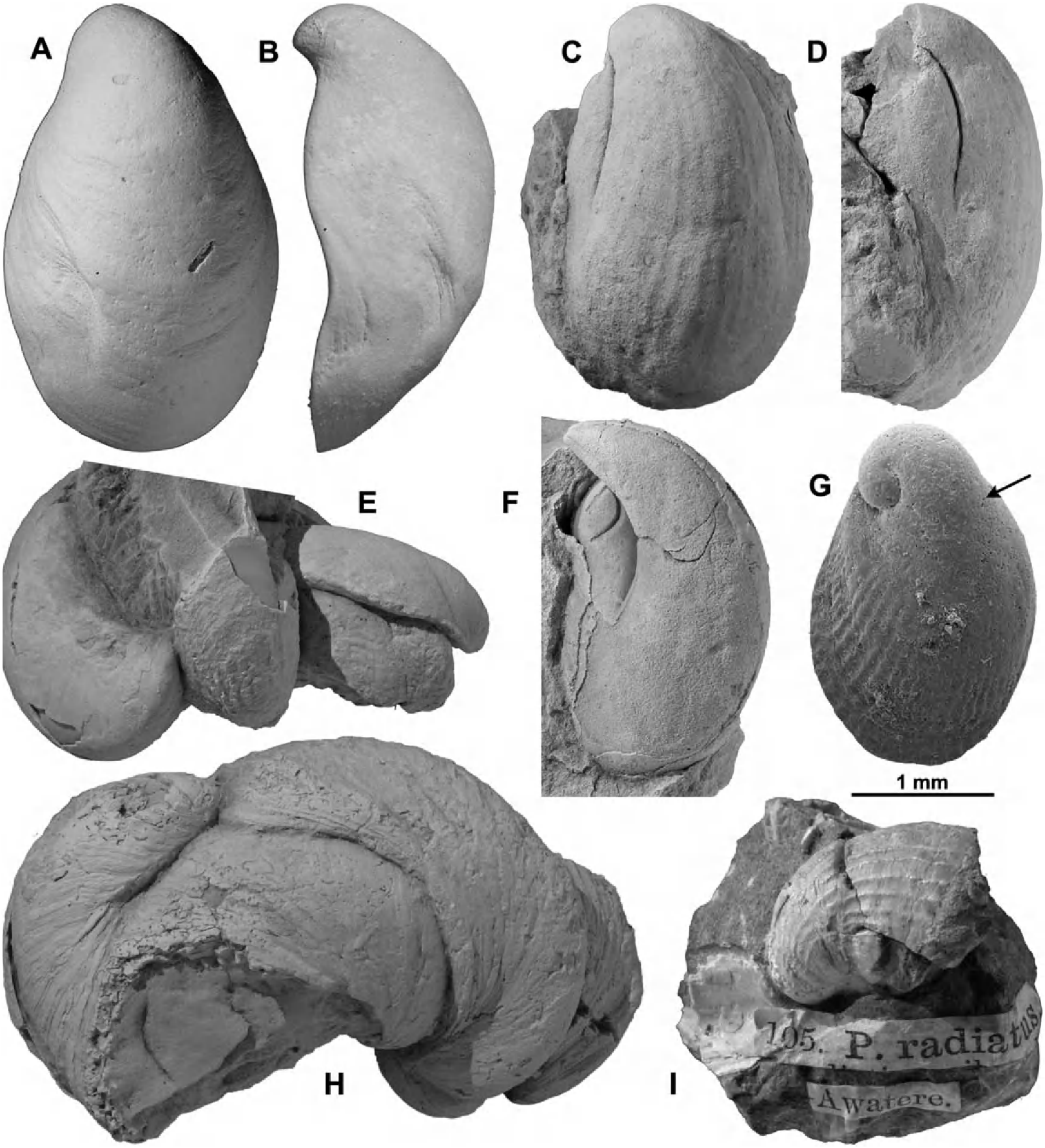

Fig. 15 *Maoricrypta radiata* (Hutton). (A,B) holotype of *Crypta turnialis* Bartrum & Powell, AUGD G5737, Kaawa Creek, SW Auckland, Opoitian; height 31.6 mm. (C,D) dorsal and lateral views, specimen formerly identified as holotype of *Pilaeopsis radiata* (not a type), TM8580, "Awatere", Kapitean-Opoitian; height 57 mm. (E) GS14892, P29/f0395, Upton Brook, Awatere Valley, Kapitean; 2 smooth and 2 sculptured specimens attached to each other, width 69 mm. (F) lectotype of *Crepidula hochstetteriana* Wilckens (tentatively synonymised with *M. radiata*), TM2608, GS13, O32/f8025, Haumuri Bluff, Marlborough, "Late Cretaceous" (Middle Miocene); dorsal view of partial slab with lectotype mould, height 50 mm. (G) AUGD G7130, Kaawa Creek, SW Auckland, Opoitian; juvenile specimen showing protoconch (terminating at line at arrow tip); SEM, height 2.4 mm. (H) GS10616, S28/f6169, Hurupi Formation (Tongaporutuan), Whatarangi cliffs, E Palliser Bay; 4 specimens attached to each other, width 90 mm. (I) holotype of *Pilaeopsis radiata* Hutton, TM8581, Awatere Valley, Kapitean?; whole block 34 mm wide, unwhitened to show original labels.

homonym of *Crepidula costata* Morton, 1829); Hoagland 1983:2.
Crypta costata. Deshayes 1838 [in 1835–1845], p. 644; Hutton 1873a:32; Hutton 1873b: 14; Hutton 1880:87; Hutton 1883:122, pl. 14, fig. A.
Crepidula (Crypta) aculeata. Tryon 1886:129, pl. 39, fig. 65 only (in part not *Crepidula aculeata* Gmelin, 1791).
Crepidula aculeata. Suter in Hutton 1904:79 (not *Crepidula aculeata* Gmelin, 1791).
Maoricrypta costata. Finlay 1926b:393; Fleming 1966:50; Pilkington 1974:419; Powell 1979:149, pl. 30, fig. 13; Marshall 2003:118, figs. 1, 2, 11, 25, 26, 66; Spencer et al. 2009:204; Maxwell 2009:242.
Crepidula (Maoricrypta) costata. Wenz 1940: 904, fig. 2661.

Type material. *Crepidula costata* G. B. Sowerby I, three 'probable syntypes' BMNH 1993118, from 'New Zealand', from the collection of H Cuming. The largest syntype appears to be that illustrated by Sowerby (1824, pl. 152, fig. 3) (as also was commented by Marshall 2003:119), demonstrating that at least this specimen is an authentic syntype, and by Reeve (1842:29, pl. 143, fig. 3; Reeve 1859, pl. 4, fig. 21a,b); Reeve's illustrations are both reprintings of Sowerby's (1824) plate (Petit 2006, appendix 2). *Crepidula costata* Deshayes, six syntypes in MNHN (recorded, but not illustrated, by Hoagland 1983:2), from 'Baie des Iles' (Bay of Islands), northern North Island; all are normal, coarsely ribbed specimens of *C. costata*, with a muscle scar clearly visible on each side of the front margin of the columellar septum.

Other material examined. **Castlecliffian:** recorded in GNS files from: Kaimatira Pumice Sand (OIS 25), Castlecliff (GS4064, R22/f6395), Kaikokopu Shellbed (OIS 19), Turakina valley (GS15194, S22/f0159); Lower Castlecliff Shellbed (OIS 15), Turakina valley (GS15141, S23/f085); 'Otapatu' shellbed (OIS 13), between Kakariki and Onepuhi, E bank Rangitikei River (GS13720, S23/f022); Shakespeare Cliff Sand (OIS 11), Turakina valley (GS15182, S22/f0161). **Haweran:** Te Piki, near East Cape, OIS 7; Waipuna Conglomerate (OIS 7), coast E of Wanganui (GS14151, R22/f0129); Hauriri Terrace shellbed (OIS 5a), Waverley Beach (GS4174, Q22/f7464; Fleming 1953:273); Holocene, Mahia Peninsula, and Cape Kidnappers (GS13796, W21/f057, terrace at shelter hut, one fragment). Recorded also by Fleming (1953:188,203,226,229,236,261) from Kaimatira Pumice Sand (OIS 25), Kupe Formation (OIS 17), Pinnacle Sand (OIS 15–14), Tainui Shellbed (OIS 13), Shakespeare Cliff Sand (OIS 11) and Brunswick Pebbly Sand (OIS 9; as '*Maoricrypta* aff. *radiata*') at Wanganui, and Oturi shellbed, mouth of Wairoa Stream, Waverley Beach (OIS 5a; GS4174, Q22/f7464; Fleming 1953:273).

Distribution. OIS 25 to OIS 5a, Wanganui; Ohope Beach, Whakatane, OIS 15? (NMNZ M.43129, shellbed below old reservoir in stream at foot of Ohope-Whakatane road, four specimens; Marshall 2003:119); Te Piki, Whangaparaoa, near East Cape, OIS 7; Holocene; that is, a range of mid-Castlecliffian to Recent; Recent in the northeastern North Island only, as far south as Mahia Peninsula, living intertidally down to 47 m (Marshall 2003:119). Richardson (2002) recorded *M. costata* from Hawke's Bay Nukumaruan rocks, but this record is presumably based on relatively prominently ribbed specimens of *M. profunda* (see below). Boreham (in Kingma 1971, table p. 91, and table 10A) also recorded *M. costata* from at least 21 localities in early to late Nukumaruan rocks of central Hawke's Bay, but only *M. profunda* is present (along with what is apparently *M. monoxyla* (Lesson, 1830)) in all GNS collections from Nukumaruan rocks of Hawke's Bay, except for the record of *Grandicrepidula hemispherica* n. sp. (below) at Maharakeke Road, W of Waipukurau.

Dimensions. *Crepidula costata* G. B. Sowerby I, largest (figured) syntype: H 42.6, W 31.1, D 15.5 mm; *Crepidula costata* Deshayes, largest syntype: H 37.0, W 26.4, D 12.8 mm; RM2523, Takapuna Beach: H 46.6, W 34.9, D 18.4 mm; NMNZ M.16454, dredged off Takapuna, Auckland: H 55.8, W 32.4, D 19.8 mm; H 42.5, W 32.7, D 18.8 mm.

Remarks. Hoagland (1977:371) suggested that *Crepidula lineolata* Deshayes (1830:26) might be a further synonym of *C. costata* Sowerby, but later (Hoagland 1983:4) she showed that the three syntypes (in MNHN) include one specimen of *C. excavata* (Broderip, 1834) (Chile) and two specimens of the widespread North Atlantic species *C. fornicata* (Linné, 1758). Hoagland (1977) also pointed out that the New Zealand species was named *Crepidula costata* independently twice, first by GB Sowerby I (1824) and later by Deshayes (1830).

Maoricrypta costata is the large, abundant, consistently prominently costate, externally convex *Maoricrypta* species of northern New Zealand at present. It lives only in the north-eastern North Island warm-water province, from Cape Maria van Diemen to East Cape, and sparsely as far south as Mahia Peninsula. The only recorded fossils are from Castlecliff, Wanganui (OIS 25, and a continuous record from OIS 19 to 5a), from the Castlecliffian of Ohope Beach, Whakatane (Marshall 2003:119) and the late middle Pleistocene of Te Piki, Whangaparaoa, near East Cape (OIS 7; Marshall 2003:119). This is therefore another warm-water immigrant at Wanganui from the northern North Island. The record of *M. costata* from upper Okiwa Group (early Nukumaruan) at Wanganui by Fleming (1953:134) is presumably based on a strongly sculptured specimen of *M. profunda* (Hutton, 1873) (GS4346, S22/f6471, siltstone 1 m above Hautawa Shellbed, Turakina River), but I have not been able to find this specimen in GNS collections. Specimens in Fleming's collections from nearby localities definitely are relatively coarsely sculptured specimens of *C. profunda.* A few specimens in GNS from Target Gully Shellbed, Oamaru (Altonian, early Miocene) represent an unnamed species resembling *C. costata,* but with thinner, sharper radial ridges. The protoconch of Recent specimens was illustrated by Marshall (2003, figs. 25, 26) and consists of about one smooth whorl, with a large, rounded, inflated initiation and an obvious spiral suture.

Maoricrypta profunda (Hutton, 1873) (Fig. 14A–D, G–I)

Crypta profunda Hutton 1873b:14.
Crepidula monoxyla Hutton 1893:62 (in part not *Calyptraea (Crepidula) monoxyla* Lesson, 1830).
Crepidula crepidula. Suter 1914:5 (in part; not *Patella crepidula* Linné, 1767).
Maoricrypta radiata. Marwick 1948:30; Fleming 1953:109–209; Fleming 1966:50 (in part not *Pilaeopsis radiatus* Hutton, 1873).
Crepidula radiata. Beu & Maxwell 1990:259,408, pl. 29j (in part not *Pilaeopsis radiatus* Hutton, 1873).
Crepidula youngi. Beu & Maxwell 1990:259 (in part not *Maoricrypta youngi* Powell, 1940).
Maoricrypta profunda. Marshall 2003:122, figs. 5, 6; Maxwell 2009:242.

Type material. Crypta profunda, lectotype (Fig. 14A,B; designated by Beu & Maxwell 1990:259) TM8223, supposedly from 'Shakespeare Cliff', Wanganui; suggested by Marshall (2003:122) to actually be from Tangahoe Formation at Waihi Beach, Hawera (Waipipian), a provenance confirmed by the soft grey sandstone inside the shell.

Other material examined. Not listed, abundant in all Waipipian–early Castlecliffian (to OIS 19, perhaps younger) rocks throughout New Zealand. Exceedingly abundant in the Otahuhu well, Auckland (Waipipian). Recorded by Fleming (1953:109–113, 118, 124, 131, 134, 139, 144, 146, 148, 151, 158, 174, 178, 181, 182, 188, 198, 209) as *Maoricrypta radiata,* from Pepper Shell Sand, Rangikura Sandstone, Wapipi Formation (Waipipi shellbeds), Waverley Formation, Mangapani Shell

Conglomerate, Wilkies Shellbed, Hautawa Shellbed, upper Okiwa Group (recorded as *M. costata*, p. 134), Nukumaru Limestone, Nukumaru Brown Sand, Mangamako Shellbed, undifferentiated Nukumaru Group, Waipuru Shellbed, Tewkesbury Formation, Butlers Shell Conglomerate (OIS 31; listed in parentheses, indicating 'known or suspected to be derived from older sediments'; Fleming 1953:175), basal conglomerate member of Lower Okehu Siltstone (OIS 29; recorded as '*Maoricrypta* aff. *radiata*'), Okehu Shell Grit (OIS 27; listed in parentheses), basal conglomerate member of Upper Okehu Siltstone (OIS 27; not listed in parentheses), Kaimatira Pumice Sand (OIS 25; not listed in parentheses), Kaikokopu Shellbed (OIS 19; listed as '[*Maoricrypta* aff. *radiata*]'; indicating that this record was 'known or suspected to be derived from older sediments'), and undifferentiated Kai-Iwi Group (not listed in parentheses, that is, thought to be in situ). This includes almost all formations in Wanganui Basin of Waipipian to early Castlecliffian age, up to OIS 19. Also recorded by Fleming (in Kingma 1971:98) from Maraetotara Sand (early Castlecliffian) at Cape Kidnappers, Hawke's Bay (GS5378, V22/f8768, as *Maoricrypta radiata*).

Distribution. *Maoricrypta profunda* is now adopted as the name for the large, abundant, widespread *Maoricrypta* species in New Zealand mid-Pliocene–early Pleistocene rocks, succeeding *M. radiata* (Hutton, 1873), the common Tongaporutuan–Opoitian species that formed tall, irregular to spiral stacks of specimens living on top of each other. Stacks were not formed by Waipipian–early Castlecliffian specimens. The known time range is Waipipian to early Castlecliffian (OIS 19), but it is difficult to evaluate whether some of the Opoitian records here assigned to *M. radiata* might actually be specimens of *M. profunda*; collection and examination of further juvenile specimens with protoconchs will be needed to clarify the taxonomy of this genus further. Protoconchs as described by Marshall (2003:119, figs. 28, 29) for the 'smaller' species aff. *M. costata*, with a clearly visible protoconch suture, have been confirmed on material assigned to *M. profunda* from: GS3528, R11/f7014, Otahuhu well, Auckland (Waipipian); GS11465, V21/f6015A, Mairau Mudstone, 'the watchman' hill, Ahuriri, Napier (Nukumaruan); GS10858, U22/f09, Makateru Mudstone (Thomson 1926), Ashcott Road, W of Waipukurau (Nukumaruan); and GS4084 re-collection, R22/f6414, Pukekiwi Shell Sand, Ototoka Beach, Wanganui (latest Nukumaruan). Specimens assigned to *M. radiata* from GS8101, Y14/f7618A, Oweka Creek, between Whangaparaoa and Hicks Bay, East Cape (Opoitian) and Kaawa Creek, SW Auckland (AUGD G5739, holotype of *Crypta opuraensis* Bartrum & Powell) have a markedly longer spiral suture visible on the protoconch, similar to that of *M. costata* (Marshall 2003, figs. 25, 26) but still more strongly spiral (Fig. 15G).

Dimensions. Lectotype, TM8223: H 31.5, W 17.5, D 16.7 mm; GS14094, Q21/f6501A, Tangahoe Formation (Waipipian), Waihi Beach, Hawera: H 65.7, W 41.6, D 29.1 mm; GS4124, R22/f6543, Wilkies Shellbed (Mangapanian), Wilkies Bluff, W of Wanganui: H 63.2, W 34.0, D 24.6 mm; GS4117 re-collection, R22/f6437, Nukumaru Brown Sand (Nukumaruan), Nukumaru Beach, Wanganui: H 50.0, W 32.3, D 24.5 mm.

Remarks. The taxonomy of Cenozoic fossil *Maoricrypta* species in New Zealand is complex and as yet very poorly understood (Beu & Maxwell 1990:259; Marshall 2003). Marshall (2003) pointed out that Beu & Maxwell (1990:259) were wrong to suggest that *M. profunda* was an earlier name for *M. youngi* Powell, 1940, as they have different protoconchs—narrower at the end, joining the teleoconch (130 µm in *M. profunda*, 330–430 µm in *M. youngi*)—and the matrix in the lectotype of *M. profunda* is not that of any Castlecliff formation, but is a soft grey sandstone closely resembling Tangahoe Formation at Waihi Beach, Hawera (Waipipian). Waihi Beach is here taken to be the type locality, implying (as noted by Marshall 2003) that this is the earliest name for the abundant, widespread *Maoricrypta* species in New Zealand Pliocene–early Pleistocene rocks. Most specimens are relatively long and narrow ('boat-shaped') with a weakly recurved apex, and the lectotype agrees with this common form. Specimens are almost as strongly variable in the prominence of the spiral sculpture as is *M. radiata* (see below), from completely smooth to prominently ribbed, but none is as prominently ribbed and spinose as are normal specimens of *M. costata.* A range of variants is illustrated here. Marshall (2003:119, fig. 28, 29) described and illustrated two late Pliocene species of *Maoricrypta* from Mangahao, N Wairarapa, one with and one without a protoconch suture visible, but lacked comparative material to decide which species they were—although it should be noted that at least *Grandicrepidula hemispherica* n. sp. (below) is quite variable in the extent to which the suture is visible. Examination of juvenile specimens from many localities has demonstrated that the species with the protoconch suture clearly visible is *M. profunda*, although most protoconchs of pre-Pliocene *Maoricrypta* specimens from New Zealand have proved to be similar to this. A second species without the suture visible has proven to be much more elusive, although it is possibly *Grandicrepidula hemispherica* n. sp. (below).

A few large specimens from Tangahoe Formation (Waipipian) at Waihi Beach, Hawera (NMNZ M.276921, three specimens) bear obvious scars on the dorsum formed by the anterior end of other specimens that formerly lived attached to them, demonstrating that some early specimens of *M. profunda* formed short stacks of 2–3 similar-sized specimens, but I have not seen any specimens that were collected attached to each other in stacks, so this was evidently not their normal mode of life.

The significant point about *Maoricrypta profunda* for molluscan biostratigraphy is the age of its youngest occurrence. Following long-accepted time ranges (e.g. Fleming 1966:50), I have previously assumed that *M. profunda* (that is, the Pliocene–early Pleistocene non-stacking species previously known as *M. radiata*, with the protoconch suture clearly visible on juveniles) occurred last in late Nukumaruan rocks. The explanation usually assumed for the common early Castlecliffian specimens has been that they have been reworked from Nukumaruan or older rocks. However, it is now clear that specimens of *M. profunda* in early Castlecliffian shellbeds in Wanganui Basin are too abundant and too little-abraded to be reworked Nukumaruan specimens (particularly abundant in GS15338, S22/f0164, S22/096385, shellbed, Turakina Valley Road, east of Wanganui, ca 600 m S of Mangara Stream bridge and ca 200 m N of Glenroy Station; early Castlecliffian, OIS 43–41?). They indicate that *M. profunda* definitely survived into early Castlecliffian rocks. Its upper age limit is uncertain at present, as the reality of Castlecliffian occurrences has only recently been accepted, but seems likely to be above OIS 25 (Kaimatira Pumice Sand) and probably as young as Kaikokopu Shellbed (OIS 19). As usual, so many of the molluscs in Kaikokopu Shellbed are abraded and evidently reworked from older rocks as to make the reality of unreworked Kaikokopu occurrences likely but uncertain.

The later specimens (Nukumaruan–Castlecliffian) of *Maoricrypta profunda* are significantly shorter, wider and more inflated than Waipipian–Mangapanian specimens, and most are not prominently sculptured, but dimensions overlap greatly, and the change (if indeed it represents anagenetic evolution

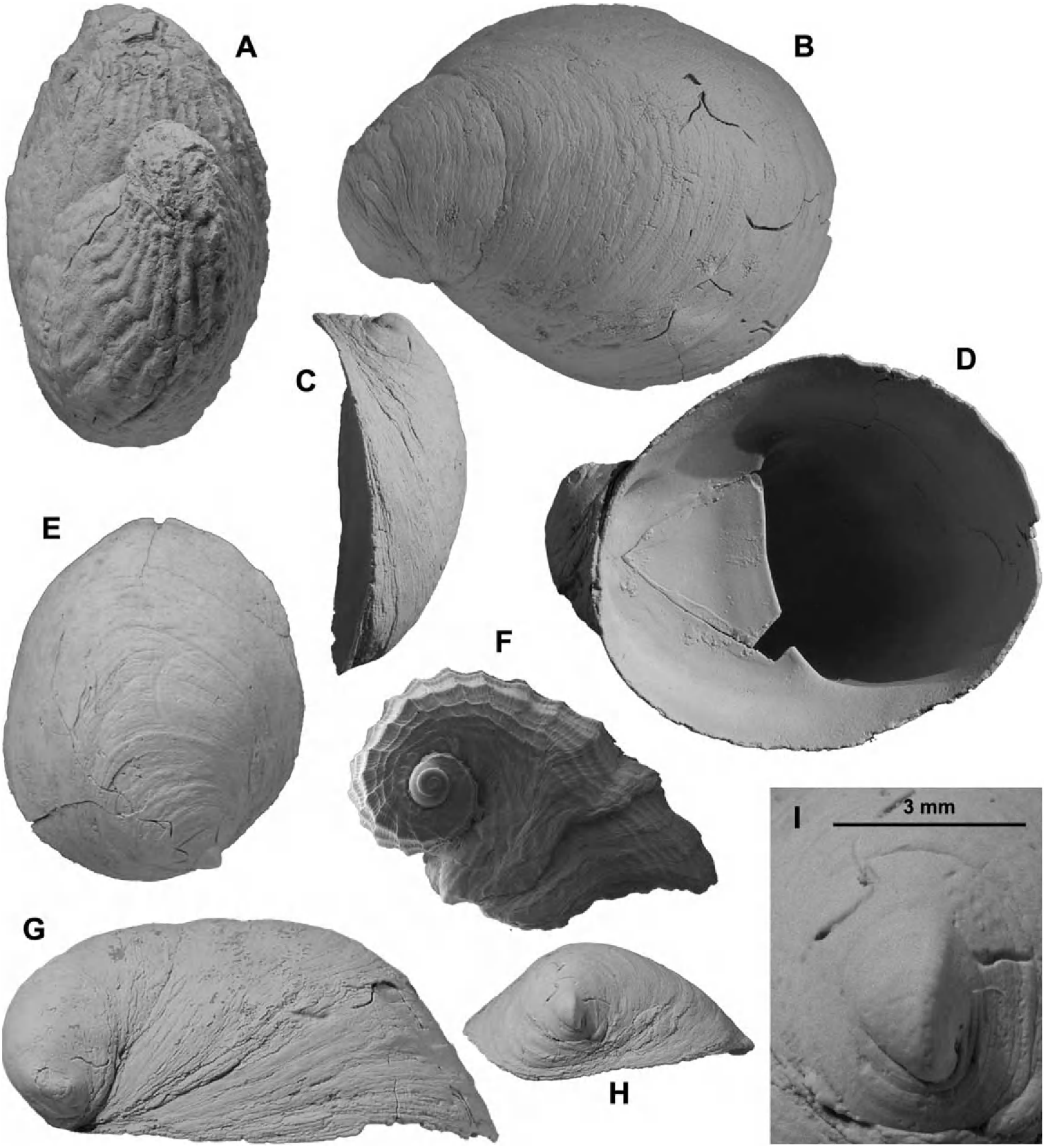

Fig. 16 (A) *Maoricrypta radiata* (Hutton), GS10950, P29/f6581, Upton Brook, Awatere Valley, Kapitean; 2 stacked, coarsely sculptured specimens, height 41 mm. (B-E, G-I) *Grandicrepidula hemispherica* n. sp., GS10857, U23/f7049, Maharakeke Mudstone (Nukumaruan), Maharakeke Road, W side Pukeora Hill, W of Waipukurau, Hawke's Bay; B,D,G, largest paratype, TM8689; height 35.0 mm, dorsal, ventral and lateral views; C,E,H,I, holotype, TM8688, height 24.3 mm; C,E,H, lateral, dorsal and posterior views; I, protoconch in H enlarged. (F) *Zelippistes benhami* (Suter), type species of *Zelippistes* Finlay, 1926, NMNZ M.100507, Recent, King Bank, Three Kings Islands, 123-128 m, 32°57.40'S, 172°19.40'E; dorsal view, SEM, diameter 10.8 mm.

rather than just phenotypic variation) is very gradual. All Waipipian–early Castlecliffian specimens are interpreted as one species here but, as usual, more research is required to clarify this genus. It seems likely that younger specimens merely inhabited a different substrate from the earlier ones, but the fossil history could also be interpreted as a gradual withdrawal from the stacking habit to living individually on flat surfaces through early Pliocene (Opoitian–Waipipian) time.

Maoricrypta radiata (Hutton, 1873) (Figs. 14F,K, 15A–I, 16A)

Crepidula incurva Zittel 1864:44, pl. 15, fig. 9; Harris 1897:248 (junior primary homonym of *Crepidula incurva* Orbigny, 1841).
Crepidula sp. Zittel 1864:44, pl. 15, fig. 10.
Pilaeopsis radiatus Hutton, 1873b:14.
Crypta striata Hutton 1873b:14 (proposed for specimen illustrated by Zittel 1864:44, pl. 15, fig. 10).
Hipponyx radiatus. Hutton 1887:218.
Hipponix radiatus. Suter 1914:20, pl. 1, fig. 14.
Crepidula gregaria. Ortmann 1902:184 (in part not *C. gregaria* G. B. Sowerby II, 1846, South American); Suter 1914:20, pl. 2, fig. 15a,b.
Crepidula crepidula. Suter 1914:5 (in part; not *Patella crepidula* Linné, 1767).
Crepidula hochstetteriana Wilckens 1922:5, pl. 1, fig. 9a,b (**new synonym**).
Crepidula wilckensi Finlay 1924d:101 (replacement name for *C. incurva* Zittel, 1864, not *C. incurva* Orbigny, 1841).
Crepidula radiatus. Finlay 1924d:100.
Crepidula radiata. Powell 1924:283; Beu & Maxwell 1990:259,408, pl. 29j (in part not *Pilaeopsis radiatus* Hutton, 1873).
Crypta turnialis Bartrum & Powell 1928:144, pl. 27, figs. 23, 24 (**new synonym**).
Crypta opuraensis Bartrum & Powell 1928:145, pl. 27, fig. 25 (**new synonym**).
Maoricrypta radiata. Finlay 1926b:394; Marwick 1948:30; Fleming & Marwick in Lillie 1953, tables 21, 22; Fleming 1966:50 (in part not *Pilaeopsis radiatus* Hutton, 1873); Maxwell 2009:242.
Maoricrypta striata. King 1934:23.
Maoricrypta wilckenseni (sic). Dell 1952:74, fig. 6.
Maoricrypta wilkinsi (sic). Fleming & Marwick in Lillie 1953, table 21.
Maoricrypta opuraensis. Fleming 1966:50; Maxwell 2009:242.
Maoricrypta turnialis. Fleming 1966:50; Maxwell 2009:242.
Crepidula turnialis. Grant-Mackie 1990:399, figs 330–333; Beu & Maxwell 1990:408.
Crepidula opuraensis. Beu & Maxwell 1990:408.
Maoricrypta wilckensi. Maxwell 2009:242.

Type material. Crepidula incurva Zittel (not of Orbigny), holotype NHMW 1959/335/29, labelled ‘Awatere-Thal’, probably from the Kapitean–Opoitian succession in Upton Brook, Awatere valley, where stacked specimens of *Maoricrypta radiata* are common, particularly in Kapitean rocks. Zittel’s (1864:44, pl. 15, fig. 10) other illustrated but unlabelled specimen, the holotype of *Crypta striata* Hutton, is NHMW 1959/335/30, also from ‘Awatere-Thal’, that is, the same locality as *C. incurva*.

Pilaeopsis radiatus, supposed holotype TM8580 (Fig. 15C,D), ‘Awatere’, apparently also from the Kapitean–Opoitian succession of Upton Brook (Marwick 1948:30). This specimen bears a label in J Marwick’s handwriting, pointing out that there are areas of glue on the original wooden tablet that do not match those formerly attaching the supposed holotype, and ‘it may be that this specimen was wrongly glued to the label after Suter had handled it’. On the back of the label Marwick has also written: ‘Hutton gave the dimensions of his *Pilaeopsis radiatus* as 0.65 × 0.65 [inches]. Obviously this is not his specimen [the supposed holotype is 56.8 mm long and 45.5 mm wide, or about 2.2 × 1.8 inches]. Equally obviously it is a *Crepidula* with the platform showing. Hutton could not have missed that’. I can add that the original wooden tablet is not large enough to accommodate the specimen without it extending beyond the edges of the tablet, whereas all other original Hutton wooden tablets remaining in GNS are about 20–40% larger than the attached specimen. Therefore, there is little doubt that TM8580 is not Hutton's holotype, and it has been wrongly attached to the original labelled type tablet. It appears that TM8580 was not an original type specimen.

Another original Hutton specimen in GNS, TM8581 (Fig. 15I), is much smaller (an incomplete, strongly ribbed *Maoricrypta* shell about 23 mm long and 15 mm high, or about 0.8 × 0.6 inches, in a block of concretionary sandstone 34 × 33 mm, the same size as the glue patches on the type tablet for *Pilaeopsis radiatus*) bearing an original type-set label, glued onto the shell, reading '105. *P. radiatus* Awatere'. It seems likely that this specimen is the holotype. The number '105' is the species' number in Hutton (1873b:14); the type face precisely matches the style, size and letter thickness of that in Hutton (1873b:14), and the glued label clearly was cut from an original printed copy of Hutton's text, as was also done for several other Hutton types still in GNS (but no other material I am aware of), strengthening the interpretation that this is the holotype. The shell is present on the remaining fragment so that the septum is not visible, and anyone not familiar with the sculpture of *M. radiata* would not immediately recognize this specimen as belonging in *Maoricrypta*, so it is possible that Hutton considered it to be a patellogastropod limpet. Hutton's (1973b:14) description reads 'High, curved, with about twenty-four radiating ribs, which are much narrower than the intermediate spaces', and this applies well to TM8581, except that it has only about 18 radial ribs (which, however, are narrow, closely spaced and difficult to count near the margins). Hutton cited only 'Awatere' as a locality. The block also contains fragments of *Struthiolaria* sp. similar to *S. cincta* Hutton, 1873, confirming the locality as likely to be late Miocene rocks of the Awatere valley. Apparently Marwick (1948:30) did not notice that confirmation that this specimen is indeed the holotype is provided by Suter's (1914, pl. 1, fig. 14) illustration of this specimen, TM8581, as '*Hipponix radiatus* (Hutton). Holotype. Awatere'. Another clean, complete, smooth specimen of the same species was illustrated by Suter (1914), pl. 1, fig. 15a,b) as '*Crepidula gregaria* Sowerby. Plesiotype. Awatere', so it is certain that Suter did not realize that these specimens are conspecific. TM8581 is accepted here as the holotype of *Pilaeopsis radiatus*.

Crepidula hochstetteriana, lectotype (selected here, Wilckens' figured syntype, TM2608; Fig. 15F) and undiagnostic, fragmentary paralectotype from GS13, O32/f8025, Haumuri Bluff, Marlborough, internal moulds in beach concretions from the Miocene succession overlying the Cretaceous rocks (see below). *Crypta turnialis* Bartrum & Powell, holotype AUGD G5737 (Fig. 14F,K), with one paratype G5738, from Kaawa Creek, coast S of Waikato Heads, SW Auckland, Opoitian. *Crypta opuraensis* Bartrum & Powell, holotype AUGD G5739 (Fig. 15B,C), with one paratype G5740, from Kaawa Creek, coast S of Waikato Heads, SW Auckland, Opoitian. *Maoricrypta haliotoidea* Marwick, 1926, holotype TM8582, from GS1135, R19/f8007, Tirangi Stream, N Taranaki, Tongaporutuan; smooth and low, possibly an unusually shaped specimen of *M. radiata*, but probably distinct.

Distribution. Extremely abundant and widespread in all middle Miocene–early Pliocene (Tongaporutuan–Opoitian, and probably earlier) shallow-water rocks throughout New Zealand; usually found as piles or stacks of large specimens attached to each other. The taxonomy and phylogeny of early Miocene and older species in New Zealand is almost completely unstudied, but none of them formed obvious, large stacks.

Dimensions. Supposed 'holotype' of *Pilaeopsis radiatus*, TM8580: H 56.8, W not measurable, D 14.0 mm; true holotype of *P. radiatus*, TM8581: H (highly incomplete) 22.8, D 14.4 mm; lectotype of *C. hochstetteriana*: H 49.9, D 20.5 mm; holotype of *C. incurva* Zittel: H 42.5, W 25.5 mm; holotype of *C. striata* Hutton, NHMW 1959/335/30: H 25.6, W 18.3, D 8.1 mm (a very low specimen); holotype of *C. haliotoidea*, TM8582: H 39.0, W 25.3, D 14.7 mm; holotype of *Crypta turnialis*: H 31.6, W 19.8, D 11.6; holotype of *Crypta opuraensis*: H 23.5, W 15.0, D 9.1 mm; 'Waipara', N Canterbury, Suter Collection no. 558 (yellow sandy matrix; apparently from Double Corner Shellbeds, Lower Waipara Gorge, Waiauan): H (incomplete) 76.4, W 49.2, D 33.0 mm; GS1037, S28/f6446, Hurupi Stream, Palliser Bay, Tongaporutuan: H 52.5, W 30.2, D 20.7 mm; GS5485, S28/f6568B, Putangirua Stream, Palliser Bay: H 53.3, W 35.1, D 18.8 mm.

Remarks. Hutton's (1873b) decalcified supposed holotype of *Pilaeopsis radiatus* has a groove (a mould of the former septum) across the centre and clearly belongs in *Maoricrypta*, rather than being the patellogastropod limpet suggested by the generic name *Pilaeopsis*. This was first pointed out by Powell (1924:283; quoting correspondence from J Marwick) although, as noted above, this is not the holotype selected by Hutton. The true holotype also clearly is a very incomplete specimen of a strongly sculptured specimen of *Maoricrypta*. Hutton (1973b:14) named *Crypta striata* at the same time, based on Zittel's (1864:44, pl. 15, fig. 10) illustrated specimen of '*Crepidula* sp.', from rocks of the same age in the same area as *Pilaeopsis radiatus* (late Miocene, Upton Brook, Awatere valley). Smooth and radially ribbed specimens occur in the same stacks of specimens in Upton Brook (Fig. 15E) and these names are certainly synonyms. *Crepidula incurva* Zittel (1864:44, pl. 15, fig. 9a,b) also was described from late Miocene rocks of the Awatere valley, and is again conspecific, but thinking that this name is a junior primary homonym of *C. incurva* Broderip, 1834, Finlay (1924d:101) provided the replacement name *Crepidula wilckensi* for it. This was unnecessary, as *Pilaeopsis radiatus* Hutton is available for the same species. Marwick (1948:30) provided a synonymy for *M. radiata* (although he did not include Suter's usage and illustration of *Hipponix radiatus*) and pointed out that '*C. incurva* Broderip' was proposed in *Calyptraea*, but that *Crepidula incurva* Orbigny, 1841 is a senior primary homonym of *C. incurva* Zittel, 1864. King (1934:23) thought *M. striata* a species separate from *M. radiata*, but Marwick (1948:30) pointed out that this species is highly variable in sculpture, and *M. striata* is part of the variation of *M. radiata*. As first reviser, I select the name *Pilaeopsis radiatus* Hutton, 1873 as the valid name to be used for the species named both *Pilaeopsis radiatus* and *Crypta striata* by Hutton (1873b:14). This abundant Tongaporutuan–Opoitian (and earlier?—apparently at least Waiauan, possibly all middle Miocene) stack-forming species therefore should be known as *Maoricrypta radiata*, with synonyms *C. incurva* Zittel, 1864 (not *C. incurva* Orbigny, 1841), *C. striata* Hutton, 1873, *C. wilckensi* Finlay, 1924, and probably *C. hochstetteriana* Wilckens, 1922. *M. haliotoidea* Marwick (1926:318, pl. 73, fig. 10) possibly is a further synonym, based on a low, wide specimen with its apex curled laterally more than usual. A specimen in GS1037, S28/f6446, from Hurupi Stream, Palliser Bay (Tongaporutuan) is shaped very similarly to the holotype of *M. haliotoidea*, and occurs with abundant specimens of normal *M. radiata*; it appears possibly to be merely a specimen of *M. radiata* that lived on a smooth, flat substrate rather than in a stack of other specimens. However, another specimen (GS11014, R19/f8059, stream 3.2 km N of Pohokura Saddle, 16 km W of Whangamomona, inland Taranaki; Tongaporutuan) is more complete, with a relatively tall, spirally coiled spire of one whorl and the septum commencing unusually well back in the shell, demonstrating that *M. haliotoidea* probably is a distinct, uncommon species. This has been deleted from the synonymy above, therefore. More complete specimens (again, with protoconch) are required to be certain of the status of *M. haliotoidea*. The protoconch of *M. radiata* is, as noted above, similar to that of *M. costata* (Marshall 2003, figs. 25, 26) but has a markedly longer spiral suture visible on the protoconch, with a longer coiled spire.

Crypta turnialis and *Crypta opuraensis* of Bartrum & Powell (1928:144–145, pl. 27, figs. 23–25) from Kaawa Creek were considered by Laws (1936:110) and Grant-Mackie (1990) to be conspecific, and Grant-Mackie (1990), as first reviser, selected *C. turnialis* as the senior synonym. The holotypes are similar in size and shape, but that of *C. opuraensis* (Bartrum & Powell 1928, pl. 27, fig. 25; Fig. 14F,K) bears uneroded sculpture of low, narrow, closely spaced radial (that is, spiral) ridges, whereas that of *C. turnialis* (Bartrum & Powell 1928, pl. 27, figs. 23, 24; Fig. 15A,B) is smooth because it is a severely abraded specimen, perhaps picked up after eroding out of the outcrop and being abraded on the beach; the paratype is very similar but narrower. The holotype of *C. turnialis* clearly bears a muscle scar on each side, interior to the end of the septum, confirming a position in *Maoricrypta*. Grant-Mackie (1990, figs. 330–333) described and illustrated quite high stacks of specimens attached in life position to *Glycymerita (Manaia) kaawaensis* (Marwick, 1923) and a smaller stack attached to *Austrofusus (Zelandiella) propenodosa* (Bartrum & Powell, 1928). As Grant-Mackie (1990) also described the very variable, relatively fine radial sculpture present on many Kaawa specimens, and all other Opoitian material I have seen from New Zealand includes specimens in life position in tall stacks, it seems likely that the Kaawa Creek specimens fall within the range of variation of *M. radiata*. Therefore, both *Crypta opuraensis* and *C. turnialis* are taken here to be further synonyms of *M. radiata*. A juvenile specimen from Kaawa Creek (Fig. 15G; AUGD G7130) examined by SEM has a large, inflated protoconch for a *Maoricrypta* species, 1.40 mm wide in total and 1.19 mm wide at the junction with the teleoconch, similar to that of *M. costata* (Marshall 2003, figs. 25, 26) and the species illustrated by Marshall (2003, fig. 28), but with a larger initiation and longer and more evenly coiled suture than in those Recent species, and with no straight section after the coiled apex.

As noted previously by Saul & Squires (2008:133), a palynoflora was examined from the matrix of *Crepidula hochstetteriana* Wilckens (1922:5, pl. 1, fig. 9a,b; Fig. 15F) recently by G Wilson (formerly of GNS pers. comm.), in a sample sawn off the slab bearing the lectotype of *C. hochstetteriana* designated here. He reported that it contains a middle to late Miocene dinoflagellate assemblage and palynoflora, including pollen of *Acacia*, a genus with an early Miocene to middle Pleistocene time range in New Zealand (Mildenhall & Pocknall 1989:61). The identification as *Acacia* was confirmed by JI Raine (GNS). This supposedly late Cretaceous species was based on material in pale grey concretions (rather than the dark grey to brown Cretaceous lithologies) from the late Oligocene to middle Miocene (Waitakian–Lillburnian) Waima Formation siltstone (Warren 1995:15–16) overlying the Cretaceous rocks at Haumuri Bluff (Warren & Speden 1977, map 1). *M. hochstetteriana* is, therefore, probably another synonym of *M. radiata*, which is not surprising as the lectotype and the fragmentary paralectotype are large internal moulds of an uncoiled *Maoricrypta* species resembling some Awatere specimens of *M. radiata*. However, checking of muscle scars is required on better specimens from middle Miocene rocks, as the type material does not rule out a position in *Grandicrepidula*, and there is some suggestion on the poor, partly recrystallized holotype mould that only the right muscle scar is present. Other late Cretaceous calyptraeids elsewhere in the world have not reached the evolutionary stage of *Crepidula* (Louella Saul, Los Angeles County Museum of Natural History pers. comm. 2006) so it is also not surprising from a phylogenetic viewpoint that *C. hochstetteriana* turns out to have been based on a Miocene specimen. A Miocene origin was pointed out earlier by me (Beu 1966) for *Zenatia cretacea* (Wilckens, 1922), another species supposedly from Cretaceous rocks at

Haumuri Bluff. The middle Miocene Waima Formation at Haumuri Bluff must be kept in mind as the likely provenance of other supposedly late Cretaceous species described from Haumuri Bluff by Wilckens (1922), but not subsequently re-collected from Cretaceous rocks.

Maoricrypta species, like all other calyptraeids, are sedentary filter-feeders living attached to hard objects, which in some cases include other *Maoricrypta* shells. *Maoricrypta radiata* is the middle Miocene (and earlier?) to Opoitian species that lived in large, narrow, irregular to evenly spiral stacks, with many large females at the base and making up much of the stack, males at the top, and individuals progressing through their sexual cycle as they become older through the upper part of the stack. It is the only New Zealand species I am aware of that formed high, obvious stacks in the same manner as the abundant North Atlantic species *Crepidula fornicata* (Linné, 1758) (Collin 2006). One stack of specimens (pointed out to me by JK Williams and VE Neall, Massey University) in *Maoricrypta-Struthiolaria* shellbeds in Matemateaonga Formation (Opoitian) east of Waiouru military camp, central North Island, formed a complete circle about 20 cm in diameter, and in cross-section resembled the nautiloid cephalopod *Aturia*. In contrast, all other New Zealand fossil species lived (and the Recent ones described by Marshall [2003] all live) as isolated large females with one or a few much smaller males closely associated, males living on the shell of the female in many cases.

Maoricrypta youngi Powell, 1940 (Fig. 14E,J)

Crypta contorta. Hutton 1873b:14 (in part not *C. contorta* Quoy & Gaimard, 1835; Wanganui record only).
Maoricrypta youngi Powell 1940:232, pl. 33, figs. 12, 13; Powell 1946a:75; Powell 1979:149, pl. 30, figs. 11, 12; Marshall 2003:121, figs. 3, 4, 7–9, 12, 27, 30, 70; Spencer et al. 2009:204; Maxwell 2009:242.
Crepidula youngi. Hoagland 1977:394.
Crepidula profunda. Beu & Maxwell 1990:259 (in part not *Crypta profunda* Hutton, 1873).

Type material. Maoricrypta youngi holotype AIM AK70473, from beach, Cape Maria van Diemen, N North Island (not seen).

Other material examined. Marshall (2003: 121) stated that Hutton's (1873b:14) specimen identified as '*Crypta contorta*' from 'Wanganui (U)' is a specimen of *Maoricrypta youngi.* Other specimens occur in Upper Castlecliff Shellbed (OIS 11) on the Castlecliff coast. They are presumably among the specimens recorded as '*Zeacrypta monoxyla* (Less.)' by Fleming (1953:239) from GS4008, R22/f7396, and GS4185, R22/f6502, both on the Castlecliff coast, where I have observed them not uncommonly. Others are present in the GNS collection from GS4022 re-collection, R22/f6360, Pinnacle Sand (OIS 14) at head of 'the pinnacles' gully, Castlecliff (1; Fig. 15J) and GS4014 re-collection, R22/f6513, basal shellbed member of Shakespeare Cliff Sand, Castlecliff (one; Fig. 15G). Similar specimens from a few other units (e.g. GS4013, R22/f6353, Tainui Shellbed, OIS 13, at 'the buttress', Castlecliff, one specimen) appear to be *M. youngi*, but are not certainly distinguishable from weakly sculptured specimens of *M. costata* when their protoconch characters cannot be observed. Fleming (1953:203, 218, 245) recorded specimens as '*Zeacrypta monoxyla*' from a range of other late Castlecliffian units at Wanganui (Kupe Formation, OIS 17, two members; Lower Castlecliff Shellbed, OIS 15, GS4028, R22/f6366, coastal section; GS4104, R22/f6518, coastal section; GS4231, S22/f6454, Waikupa Road, off Fordell-Whangaehu highway, E of Wanganui; Pinnacle Sand, OIS 15–14, GS4098, R22/f6425, uppermost 23 cm in 'the pinnacles' gully, Castlecliff; Landguard Sand, GS4003, R22/f7394) and any or all of these might have been based on specimens of either *M. youngi* or *M. sodalis* Marshall, 2003. The stratigraphic ranges of both these species are poorly constrained at present.

Distribution. *Maoricrypta youngi* was recorded from Wanganui (Castlecliffian) by Marshall (2003:121), so the small, wide, almost smooth, strongly inflated specimens occurring moderately commonly in Upper Castlecliff Shellbed (OIS 11) and confused with *M. profunda* by Beu & Maxwell (1990:259) belong in *M. youngi.* As *M. youngi* now occurs as far south as western Cook Strait (Marshall 2003:121), Castlecliff fossils are within the Recent range of the species. Castlecliff fossils I have seen are all small, strongly inflated and with deeply curved and embayed apertural planes, and apparently lived attached to the ubiquitous gastropod *Maoricolpus roseus*, cited by Marshall (2003:122) as a common substrate for *M. youngi.*

Dimensions. NMNZ M.134496, 50 m, off Bream Tail, Northland: H 28.3, W 17.1, D 10.8 mm; NMNZ M.117767, 55 m, off Mahia Peninsula, attached to *Charonia*: H 22.5, W 16.8, D 9.3 mm; NMNZ M.15633, Falcon Shoal, Wellington Harbour, attached to *Maoricolpus*, closely resembling Wanganui fossils: H 25.4, W 15.0, D 9.1 mm; H 22.8, W 15.5, D 11.5mm; H 18.0, W 12.7, D 8.6 mm; GS4022, Pinnacle Sand: H 15.2, W 11.2, D 7.4 mm; GS4014, basal shellbed of Shakespeare Cliff Sand; H 14.4, W 8.9, D 7.1 mm.

Remarks. Marshall (2003:122) pointed out that *Maoricrypta youngi* differs from the superficially similar *M. monoxyla* in its brownish rather than white shell, its whitish rather than yellow animal, and its more strongly convex protoconch. It also differs from weakly sculptured specimens of *M. costata* (living specimens of which can occur alongside *M. youngi*) in its more paucispiral protoconch, and in the considerably broader start of the first whorl of the protoconch (width of exposed part 330–430 µm, compared with 230–270 µm in *M. costata*). The protoconch also is completely smooth, apart from commarginal growth lines, in *M. costata* (Marshall 2003, figs. 25, 26), whereas it is initially smooth but then abruptly adopts crisp radial (spiral) sculpture in *M. youngi* (Marshall 2003, figs. 27, 30). Their modern ranges and, to some extent, habitats are also distinct, as *M. costata* occurs at present only in the northeastern North Island, with one record as far south as NE Mahia Peninsula (Marshall 2003, fig. 11) whereas *M. youngi* occurs all around the eastern North Island, and through Cook Strait up the west coast as far north as Wanganui (Marshall 2003, fig. 12). *M. costata* also occurs attached to the undersides of rocks and to *Perna canaliculus* (Gmelin, 1791), and a few specimens occur alongside *M. youngi* on the undersides of *Xenophora neozelanica* Suter, 1908, whereas *M. youngi* has been found attached only to other gastropod shells. Marshall (2003) listed as hosts for *M. youngi* living specimens of *Astraea heliotropium* (Martyn, 1784), *Penion sulcatus* (Lamarck, 1816), *Maoricolpus roseus*, *Turbo smaragdus* (Gmelin, 1791), *Calliostoma (Maurea) granti* (Powell, 1931) and *X. neozelanica*, and empty shells of *Charonia lampas* (Linné, 1758). A fossil specimen of *M. costata* from Wanganui (GS4014 re-collection, R22/f6513, basal shellbed of Shakespeare Cliff Sand, Castlecliff coast) is still in situ attached to the base of a specimen of *Astraea heliotropium* (Fig. 13B), showing that these two species can occur on the same substrate fairly frequently.

Genus **Grandicrepidula** McLean, 1995

Grandicrepidula McLean 1995:80. Type species (by original designation): *Crepidula grandis* Middendorf, 1849, Recent, boreal Pacific.

Remarks. Marshall (2003:129) adopted *Grandicrepidula* for New Zealand species resembling *Crepidula* but with a single muscle scar visible, under the right edge of the columellar septum (as viewed in standard apertural view, with apex directed dorsally; this is also anatomically the right side of the living animal). No scar is present in most species of *Crepidula*, and two are present (one on each side) in *Maoricrypta*. Marshall also stated as a character of the genus 'septal rim oblique relative to longitudinal axis of shell', but this character does not hold for all New Zealand fossil species (as judged by the single muscle scar), as in the new species described below the edge of the septum is at right angles to the long axis of the shell. The teleoconch apex is weakly coiled to the right in all species I am aware of. Marshall (2003:118) pointed out that *Crepidula densistria* Suter, 1917 (early Miocene, Oamaru area), *Maoricrypta salebrosa* Marwick, 1929 (Duntroonian, late Oligocene, Southland) and the Recent species *G. collinae* Marshall, 2003 should be referred to *Grandicrepidula*. The Oligocene and Miocene species have regular radial sculpture, unlike the smooth Pliocene and Recent species. Examination of GNS collections demonstrated that several other, unnamed species of Oligocene and Miocene age also belong here.

Grandicrepidula hemispherica n. sp. (Fig. 16B–E,G–I)

Type material. Holotype (TM8688; Fig. 15C, D,G,K) and four paratypes (TM8689 –TM8692), GS10857, U23/f7049 (=GS10944, U23/f7498A), Maharakeke Mudstone (of Thomson 1926), 200–300 m along Maharakeke Road from Highway 2, at the E edge of the Takapau plain 1.5 km SW of Pukeora Hill, W of Waipukurau, S Hawke's Bay; occurring with the *Pelicaria convexa* form of *P. vermis* (Martyn, 1784), *Austrofusus taitae* (Marwick, 1924), *Bonellitia lacunosa* (Hutton, 1885) and *Paracomitas protransenna* (Marshall & Murdoch, 1923), in a diverse, typical Hawke's Bay late Nukumaruan fauna. The type material was collected syntopically with specimens of *Maoricrypta profunda*.

Distribution. So far known only from the type locality.

Dimensions. Holotype: H 25.3, W 20.6, D 10.0 mm; largest paratype (Fig. 16B,E,H), TM8689: H 35.0, W 27.0, D 14.7 mm; paratype TM8690: H 26.0 (incomplete), W 24.5, D 10.2 mm.

Description. Shell moderately small for genus, smooth, highly inflated, wide (width 77–81% of length), with low, evenly inflated dorsum in small adults (height 40% of length, 49% of width in holotype) but slightly taller in large specimens (height 42% of length, 54% of width in largest specimen). Protoconch large (2.75 mm long on holotype), clearly demarcated from teleoconch by shallow groove on most specimens, rounded-triangular, with apex weakly inclined to left and curled under teleoconch; with low median external ridge in most specimens, nearer left than right edge of protoconch, providing triangular shape to whole protoconch; initial whorl coiled under, with initial protoconch suture located at edge of teleoconch and not visible in some specimens, scarcely visible above teleoconch edge in others, or located well above teleoconch edge and clearly visible in still other specimens; a few specimens with 1–3 very low, obscure, accessory ridges parallel to main central one. Teleoconch strongly and evenly inflated, with apex directed weakly towards right in small specimens but increasingly strongly towards right in larger ones, situated well above and slightly anterior to posterior margin in small, evenly oval specimens (3.7 mm above margin in holotype) but overhanging posterior margin slightly in largest specimen. Exterior smooth on smaller specimens, but with irregular, slightly scaly growth ridges on larger specimens. Aperture subcircular to evenly oval, apertural plane flat in largest specimen but weakly arcuate in smaller ones, indicating that small specimens live attached to dorsum of similar shells. Columellar septum occupying a little under half shell height, flat, with lightly and evenly curved anterior margin normal to long axis of teleoconch, curved around more strongly at margins to join side walls of shell; one obvious, small, moderately deeply impressed muscle scar beneath septum edge on right side, but none on left.

Remarks. Grandicrepidula hemispherica n. sp. is provided for nearly circular (when relatively young) to highly inflated, oval, smooth specimens of a previously unnamed species of *Grandicrepidula* from Maharakeke Road, W of Waipukurau, with the apex an unusually long way from the posterior end of the shell and a weakly triangular protoconch with a few unusual, low radial ridges and, in many specimens, no suture visible at all. The anterior edge of the columellar septum is aligned approximately at right angles to the long axis of the teleoconch. Most specimens with well-preserved protoconchs have a single prominent radial ridge extending from the visible apex to fade out at the end of the protoconch, producing a prominent, rounded-triangular shape for the protoconch as a whole, although a few specimens have weak subsidiary ridges parallel to the prominent one. The holotype has been chosen as a specimen that displays a single relatively prominent ridge and triangular protoconch shape. In some specimens the protoconch suture is aligned with the edge of the subsequent, enveloping teleoconch whorl, and scarcely visible or not visible at all, as in illustrations of the protoconch of *Grandicrepidula collinae* by Marshall (2003, figs. 23, 24), whereas in others the initial spiral section is slightly smaller, and a short but obvious suture is revealed on the side of the protoconch above the teleoconch margin, establishing that the extent to which the protoconch suture is revealed is quite variable in (at least some) *Grandicrepidula* species. Specimens of *G. hemispherica* n. sp. with the internal muscle scar visible under the anterior end of the columellar shelf display an obvious but relatively small, moderately deeply impressed, semicircular scar on the right side but none on the left, whereas one markedly larger but more shallowly impressed one is obvious on each side in specimens of *M. profunda* collected at the same locality (identified by their smaller, narrower protoconchs, straight shell apex, and narrower, 'boat-shaped' form, and the presence of weak to moderately prominent radial ribs on the exterior of the teleoconch). I have not seen the new species from elsewhere, but it is possibly the second species mentioned under *Maoricrypta* by Marshall (2003) occurring at Mangahao, N Wairarapa, lacking a protoconch suture. However, it also seems feasible that several other Pliocene–early Pleistocene species of *Maoricrypta* and *Grandicrepidula* remain unrecognized in New Zealand, and certainly there are several unnamed Miocene and Oligocene taxa.

A few small specimens of *Grandicrepidula hemispherica* n. sp. have been collected attached to each other in small piles of 2–3 specimens, but tall stacks have not been seen at the one locality where it has been collected. Most smaller specimens (to about 25–28 mm long) have a weakly curved apertural plane, arched upwards across the central area and down at the anterior and posterior ends, suggesting that they have been attached to other specimens of *G. hemispherica* n. sp. In contrast, the largest specimen (H 35 mm) has a flat apertural plane and apparently lived attached to a flat surface, such as a rock or an oyster. Possibly this species changes it habitat as it grows. Of New Zealand calyptraeids, the protoconch of *Grandicrepidula hemispherica* n. sp. most nearly resembles that of *G. collinae* Marshall, 2003 in its lack of obvious fine sculpture, its subtriangular shape (much more marked in *G. hemispherica* than in *G. collinae*), weak radial ridge(s), and lack of a visible suture on many specimens. *G. hemispherica* n. sp. also differs obviously from *G. collinae* in its smaller size, more evenly inflated shape with a higher dorsum, more evenly subcircular to oval rather than subtriangular apertural outline, and the anterior margin of the columellar septum being normal to the long axis of the teleoconch rather than oblique. One of the most distinctive characters of *G. hemispherica* n. sp. is the position of the apex, which is well above and a short distance in front of the posterior margin in most

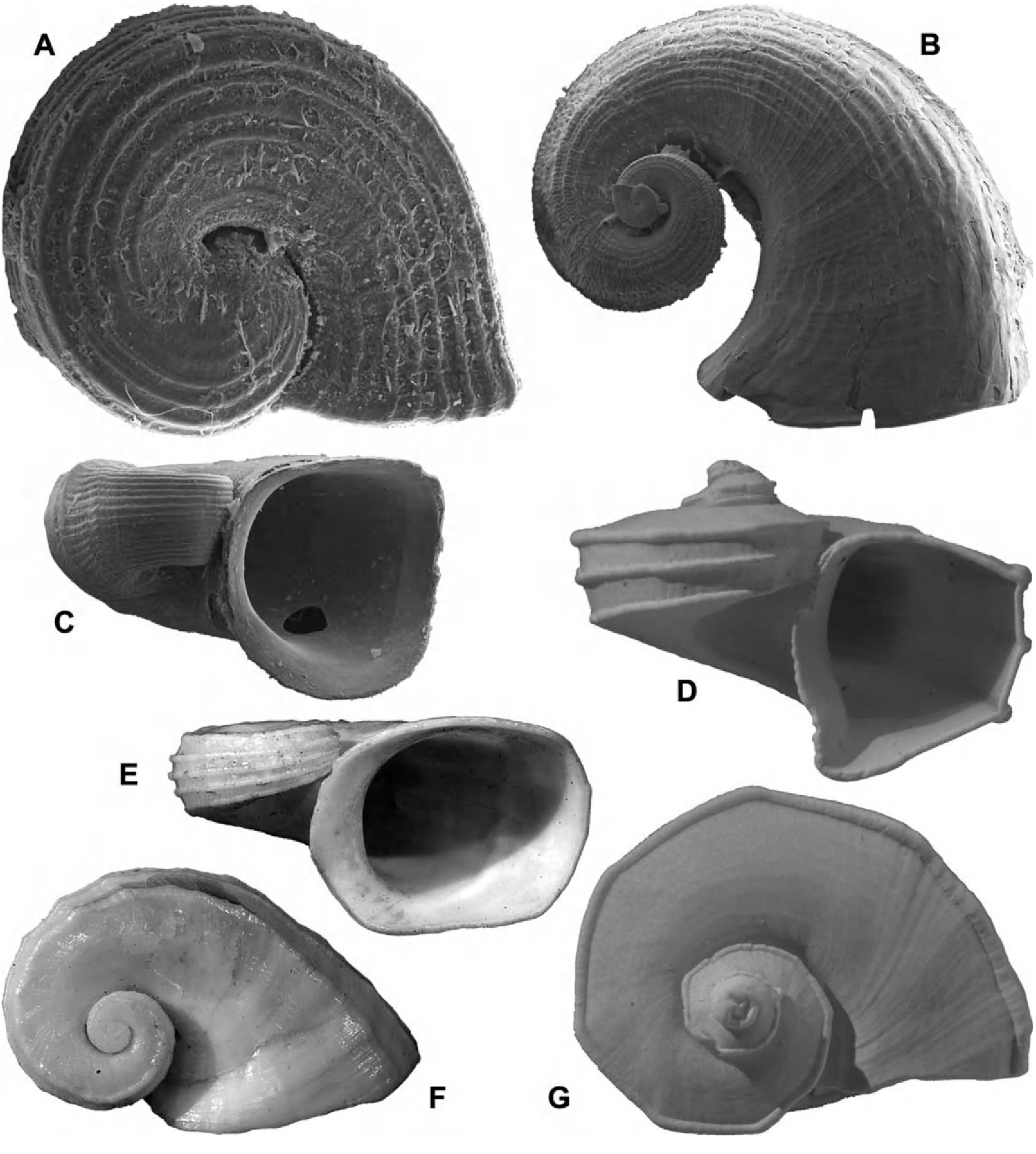

Fig. 17 (A–C,E,F) *Lippistes cornu* (Gmelin), type species of *Lippistes* Montfort, 1810, South Africa; A,B, NMP E1147, De Hoop, E of Cape Agulhas, 50 m; A, protoconch, diameter 0.79 mm; B, whole shell of same specimen, partially uncoiled form, diameter 7.7 mm; C, NMP S8243, Aliwal Shoal, off Scottsburg, Natal, 10 m; juvenile, protoconch plus 0.5 teleoconch whorl; width 1.50 mm; E,F, largest syntype of *Separatista grayi* A. Adams, BMNH 198352, "South Africa", the western tightly coiled form of *L. cornu*; H 7.4, D 14.8 mm. (D,G) *Separatista helicoides* (Gmelin), type species of *Separatista* Gray, 1847, NMNZ M.246409, Onslow, Western Australia; small specimen, H 6.4, D 10.9 mm.

specimens, and only overhangs the margin in the largest paratype.

It seems possible that *Grandicrepidula hemispherica* n. sp. occurs also in eastern Australia, in view of Marshall's (2003:118) statement that 'all Australian crepiduliform species' he had examined, other than *Maoricrypta immersa* (Angas, 1865), belong in *Grandicrepidula*. However, the possibility this provides of recognizing another warm-water migrant to New Zealand during late Pliocene–early Pleistocene time must await a taxonomic study of Australian calyptraeids, an almost completely unstudied group.

Etymology. Latin, hemispherical, half a sphere; intended to refer to the almost circular to evenly oval shape and high dorsum of this species.

Family Capulidae

Genus ***Zelippistes*** Finlay, 1926

Zelippistes Finlay 1926b:396. Type species (by original designation): *Separatista benhami* Suter, 1902, Pleistocene and Recent, New Zealand.

Remarks. There has been much confusion in the literature about the status of the superficially similar genera *Lippistes* Montfort, 1810 and *Separatista* Gray, 1847. To evaluate these genera and *Zelippistes* Finlay, 1926, I compared material of *Lippistes cornu* (Gmelin,1791) from South Africa, *Separatista helicoides* (Gmelin, 1791) from the tropical Pacific, and *Zelippistes benhami* (Suter, 1902) from northern New Zealand. The results are summarized here.

1. *Lippistes cornu* (Fig. 17A–C,E,F) and a second South African species (not *L. grayi* [A. Adams, 1850]; holotype examined [Fig. 17E,F], BMNH 198352, = *L. cornu*) are highly distinctive, planispirally coiled species (included by Bouchet et al. [2005] in Hipponicidae) with distinctive, cap-shaped, paucispiral, planispiral protoconchs, reflecting lecithotrophic development. The whorl section on spire whorls is almost square, with numerous weak to prominent spiral cords around the outer surface. Specimens of *L. cornu* from eastern South Africa are evenly but loosely coiled, that is, all whorls are separated from each other evenly and regularly but narrowly, whereas specimens from western South Africa have all whorls closely attached to each other and have a more laterally expanded aperture; the two forms intergrade clinally around the coast. *Lippistes* is a narrow-whorled, planispiral genus restricted to South Africa.
2. *Separatista* contains two species of widespread tropical Pacific to southern Australian species of Capulidae resembling *Trichotropis* Broderip & Sowerby, 1829 and, in particular, *Turritropis* Habe, 1961 (Kantor & Sysoev 2006, pl. 27) in most characters, including its aperture shape, its low to moderately tall spire and its heavily hirsute periostracum, but consistently having three smooth spiral cords around the wide, flat, vertical periphery, and on many (but by no means all) specimens the last quarter to half of the last whorl tends to separate slightly to markedly from the previous whorl. A few specimens (such as the holotype of *Zelippistes eccentricus* Petuch, 1979) have the entire last whorl widely separated, so that it resembles that of *Lippistes cornu*, but all specimens intergrade. The protoconch is low-spired and paucispiral, with four raised spiral cords, significantly different from those of *Lippistes* and *Zelippistes*. The two species are *S. helicoides* (Gmelin, 1791) (Fig. 17D,H) (= *Turbo separatista* Dillwyn [1817:867; Wilson 1993:166, pl. 22, fig. 2], = *Separatista chemnitzii* A. Adams [1850b:

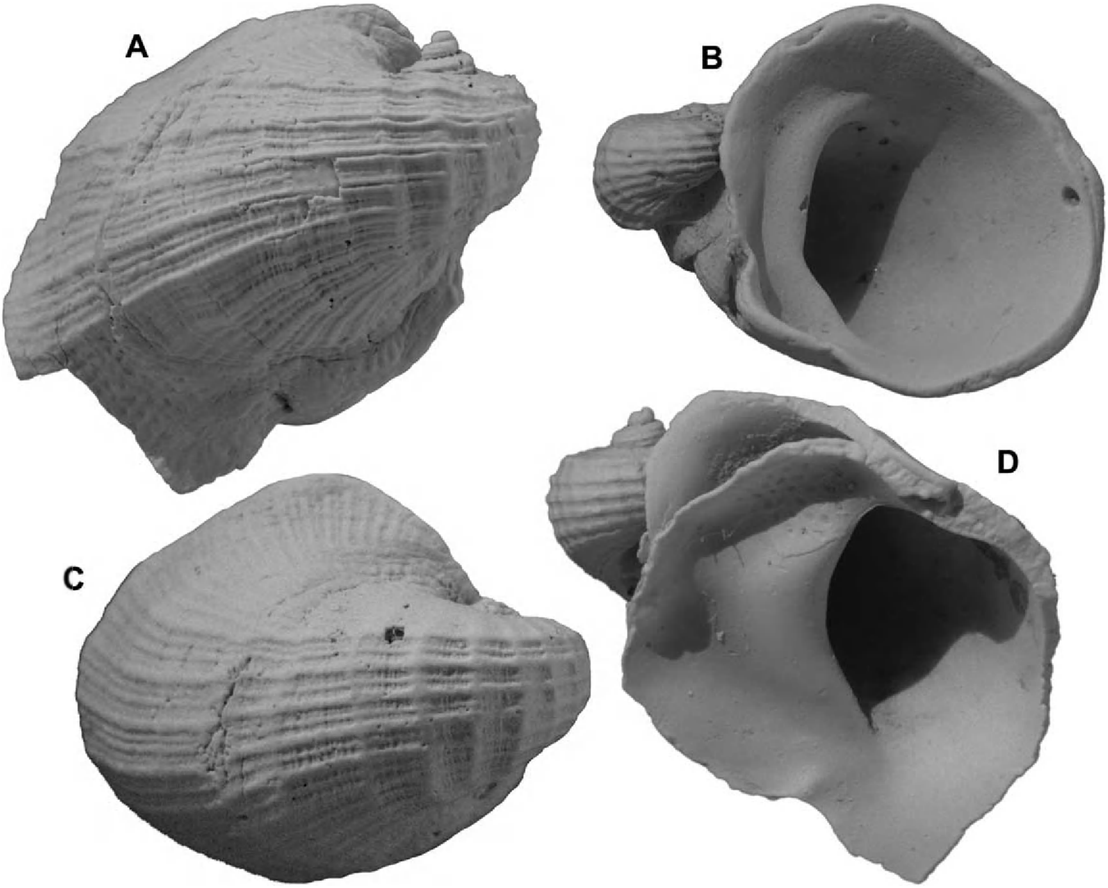

Fig. 18 *Zelippistes benhami* (Suter). (A,D) GS4019, R22/f6358, Tainui Shellbed (Castlecliffian, OIS 13), Castlecliff coastal section, Wanganui; H 13.5, D 12.2 mm. (B,C) NMNZ M.84120, Recent, Hole in the Rock, Whangaroa, Northland; H 10.0, D 13.6 mm.

45], = *Trichotropis blainvilleanus* Petit de la Saussaye [1851:22, pl. 1, fig. 5; Macpherson & Gabriel, 1962:129, fig. 153; holotype examined in MNHN], = *Trichotropis tricarinata* Brazier [1878:313; Hedley 1901:126, pl. 17, figs. 22, 23; holotype examined in AMS], = *T. gabrieli* Pritchard & Gatliff [1899:183, pl. 20, fig. 7; Wilson 1993:166, pl. 22, fig. 1a,b], = *Lippistes meridionalis* Verco [1906b]:221, pl. 9, figs. 1, 2] [note that Verco [1906b]:220, pl. 9, figs. 6–9] also recorded *'Lippistes' separatista* [that is, *Separatista helicoides*] from nearby localities in South Australia, illustrating the radula and operculum, apparently not realizing that these forms intergrade], = *Separatista fraterna* Iredale [1936: 293; holotype examined in AMS], = *Zelippistes eccentricus* Petuch [1979]:5, figs. 7–9; Poppe 2008a, pl. 98, fig. 5]; synonymy based on examination of most of the type material), occurring throughout the Indo-West Pacific to southern Australia; and *S. gracilenta* (Brazier) (1878:313; holotype examined in AMS), a much smaller, narrower, taller-spired species with closely attached whorls, occurring in Queensland. The specimen identified as *Trichotropis flavida* Hinds, 1843 by Poppe (2008a, pl. 98, fig. 1) appears to be conspecific with Australian specimens identified as *S. gracilenta*, indicating an earlier name and a wide tropical Indo-West Pacific distribution for *S. flavida*. *Separatista* is a tall-spired genus with a weakly uncoiled last whorl, closely resembling *Trichotropis* and *Turritropis*, that occurs throughout the tropical Indo-West Pacific as far south as southern Australia. It is strongly distinct from *Lippistes* in size, shape, sculpture, protoconch characters and degree of uncoiling, although the small specimen illustrated here has a lower spire than most other specimens and does not appear as strongly distinct from *L. cornu* as larger, tall-spired specimens do (Fig. 17D,G; NMNZ M.246409, Onslow, Western Australia; H 6.9, D 10.9 mm).

3. *Zelippistes benhami* (Figs. 16F, 18A–D, 19A,C,E) is a further distinctive capulid that has evolved a laxly coiled last teleoconch whorl from *Trichosirius* independently in New Zealand. The last whorl is separated from the others similarly to that of some *Separatista* specimens and large western South African specimens of *L. cornu*, but this produces a more limpet-like adult. The moderately tall, smooth protoconch, with strongly inflated whorls, and tall early spire whorls are virtually indistinguishable from those of the type species of *Trichosirius*, *T. inornatus* (Hutton, 1873), and only the last whorl of *Z. benhami* adopts a wide, low, weakly uncoiled growth form. Most large specimens have the gap between the spire and last whorl filled by a flange, complex in many specimens, formed by folding the inner lip strongly back on itself, and the aperture and outer lip become irregular on most large specimens. *Zelippistes benhami* evidently is a *Trichosirius* relative that lives permanently attached to a hard substrate, and is more strictly sedentary than *Trichosirius* species. *Zelippistes* is an initially tall-spired but later weakly uncoiled, monotypic genus restricted to New Zealand. Its distinction from *Trichosirius* is a little tentative, requiring confirmation from anatomical and molecular studies.

These three taxa have developed a shell form with a partly to completely uncoiled last whorl, reflecting a sedentary life habit, quite independently of each other, from distinct ancestors. This taxonomy will be reviewed elsewhere, and is merely summarized here to substantiate *Zelippistes* as a distinct genus.

Zelippistes benhami (Suter, 1902) (Figs. 16F, 18A–D, 19A,C,E)

Separatista benhami Suter 1902a:65, text fig.
Lippistes benhami. Suter 1913:297, pl. 15, fig. 19.
Lippistes benhami var. *perornatus* Marshall & Murdoch 1923:121, pl. 15, figs. 6, 7 (**new synonym**).
Zelippistes benhami. Finlay 1926b:396; Dell & Ponder 1964:64, figs. 1–7, 11, 14; Powell 1979:148, fig. 37, nos. 1, 2; Morley 1996:22–23, figs. 2, 3; Spencer et al. 2009:204.
Zelippistes benhami perornatus. Dell & Ponder 1964:69, figs. 9, 10, 12, 13; Fleming 1966:50; Beu & Maxwell 1990:408.
Zelippistes perornatus. Maxwell 2009:242.

Type material. *Separatista benhami*, holotype said by Suter (1902a) to be in 'Otago University Museum, Dunedin', now in Otago Museum, Dunedin, IV7917 (Ilka Söhle, Otago Museum pers. comm. 3 March 2005), from beach, Cape Maria van Diemen, 'found by Mr. Rayner, formerly lighthouse keeper at Cape Maria' (Suter 1902a) (not seen). *Lippistes benhami* var. *perornatus*, holotype TM8295, from 'blue clay, Castlecliff', almost certainly from Tainui Shellbed, Castlecliff coastal section (OIS 13); with one paratype, TM8296. Marshall & Murdoch (1923) mentioned that 'there are two specimens, one in perfect condition, the other somewhat worn and the aperture imperfect'. They also illustrated the perfect one, referred to here as the holotype, and stated 'Type to be

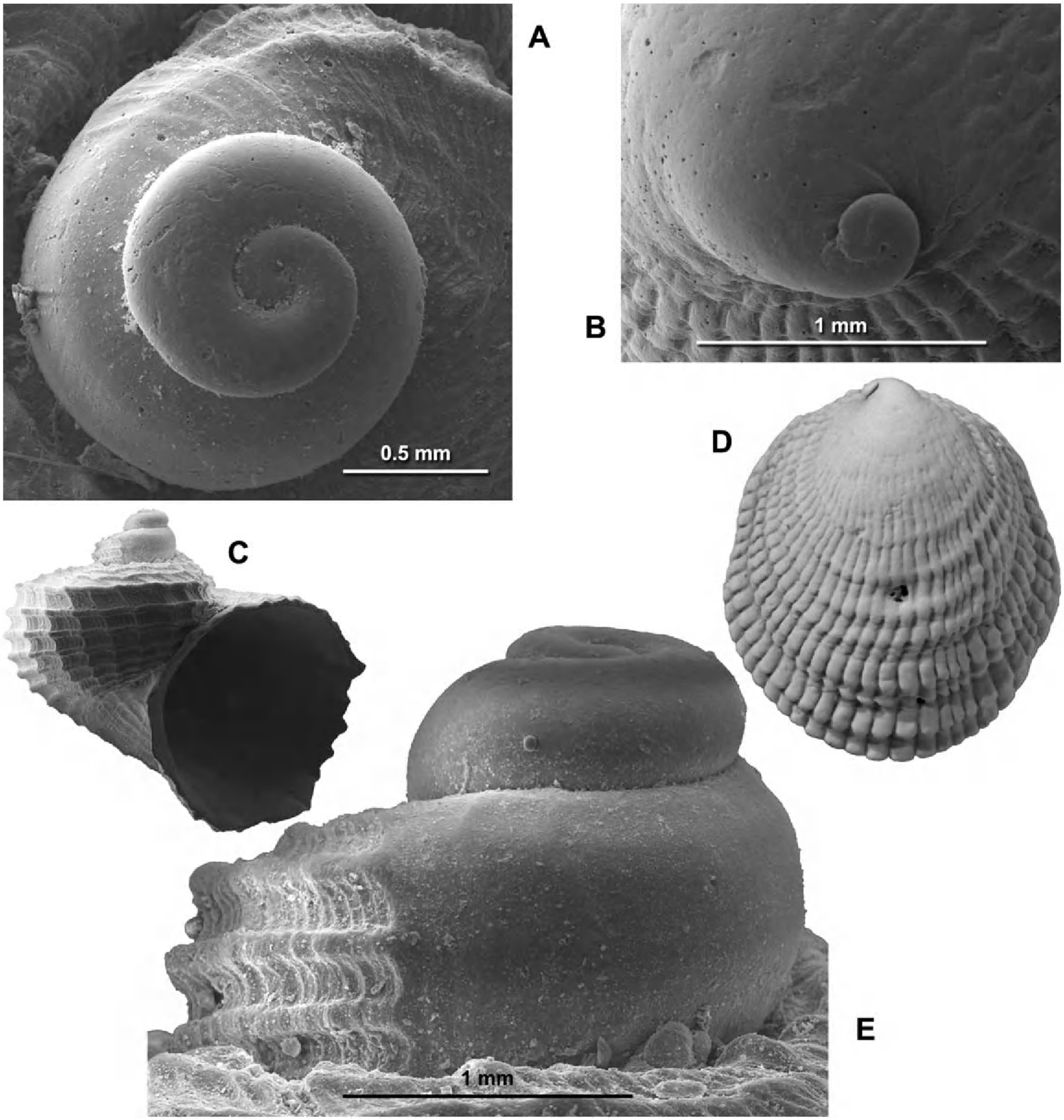

Fig. 19 (A,C,E) *Zelippistes benhami* (Suter); A, protoconch of specimen in Fig. 16F, SEM, dorsal view; C,E, NMNZ M.112179, Recent, 27-37 m, NE of Urupukapuka I., Bay of Islands, Northland, 34°14.10'S, 172°9.00'E, SEM; C, whole shell, diameter 8.4 mm; E, protoconch of C, lateral view. (B,D) *Sabia australis* (Lamarck), GS2784, T23/f6491, 3-10 m above Torlesse greywacke, Opawe Stream, Pohangina Valley, W Wanganui Basin, early Nukumaruan; B, abraded protoconch, SEM; D, whole shell, height 7.6 mm.

presented to the Wanganui Museum'. (The combined collection of P Marshall and R Murdoch was purchased by the New Zealand Geological Survey from the Wanganui Museum in 1946, along with H Suter's collection.) The illustrated specimen is considered to be the holotype, because of Marshall & Murdoch's 'type' statement.

Other material examined. **Castlecliffian:** Tainui Shellbed (OIS 13), basal portion of Shakespeare Cliff, Wanganui City (GS4026, R22/f6364, one); Tainui Shellbed, Castlecliff coastal section (GS4097, R22/f6516, one); also three unlocalized 'Castlecliff' specimens in GNS, in a fine muddy matrix, probably from Tainui Shellbed; 'Castlecliff, blue mud W. R. B. Oliver' (NMNZ M.27300, one large, in a fine sandy mudstone matrix, formation uncertain, but apparently not from Tainui Shellbed; Pinnacle Sand?). **Haweran:** Landguard Sand (OIS 9), Landguard Bluff, east of Wanganui River (GS4003 re-collection, R22/f7394, one). **Recent:** 37 lots in NMNZ, ranging from King Bank, N of Three Kings Islands, to beach, Boulder Bay, Motuhora Island, off Whakatane, Bay of Plenty (NMNZ M.33073, three), from cast ashore on beaches to a depth of 710 m. Morley (1996) also recorded specimens from the Three Kings Islands, Spirits Bay, the Bay of Islands and Goat Island Beach, Leigh.

Distribution. Apparently in OIS 13 and 9 only, at Wanganui (the same stages as *Stephopoma roseum*), but possibly more widespread stratigraphically, as several specimens lack detailed localities; Recent, N Northland to the Bay of Plenty; most Recent material is from the Three Kings Islands, the Bay of Islands and W Bay of Plenty.

Dimensions. Separatista benhami, holotype H 6.5, D 7 mm (Suter 1902a); *Lippistes benhami perornatus*, holotype H 9.6, D 13.4 mm; largest in GNS (unlocalized, 'Castlecliff'): H (incomplete) 12.3, D 17.5 mm; GS4003 re-collection, Landguard Bluff: H 7.1, D 7.0 mm; large Recent shells: NMNZ M.84120, Hole in the Rock, Whangaroa, Northland: H 10.0, D 13.6 mm; M.21500, beach, Smugglers Bay, Whangarei Heads: H 9.5, D 18.5 mm; M.12134, fish stomach, Bay of Plenty: H 8.7, D 14.3 mm; M.75170, 25 m, outside entrance to Whangaroa Harbour: H 8.5, D 14.8 mm. Recent shells reach up to 21.5 mm in maximum dimension (Powell 1979:148).

Remarks. Dell & Ponder (1964) maintained a subspecific distinction between Castlecliff fossils and Northland Recent specimens of *Zelippistes benhami* on the basis of the fossils having five spiral cords raised more than the others, whereas in Recent specimens they were all said to be subequal. Recent specimens in the large collection in NMNZ (37 lots) are highly variable in shape, coiling irregularity, and sculptural prominence, and there is no doubt that the trivial 'forms' *Z. benhami* and *Z. benhami perornatus* intergrade; several of the Recent specimens have spiral sculpture identical to that of fossils. Large specimens develop a strongly concave, shelf-like flange on the inner lip, where it bends back strongly over the columella to reach the previous whorl. Dell & Ponder (1964) described the external appearance of the animal, the mantle cavity organs and the foregut of *Z. benhami*, including the style gland and stomach, and the conspicuous food groove extending from the ctenidium up the mantle cavity roof, to meet another groove running around the right cephalic tentacle, taking food to the proboscis. They also illustrated the short, disc-shaped, sucker-like foot, and commented that it 'is probably little used for locomotion' and 'is almost certainly a sedentary animal' (Dell & Ponder 1964:68), reflecting its filter-feeding habit and its sedentary habitat on cylindrical substrates. However, these aspects of the anatomy and ecology of *Trichosirius inornatus* have not been described, and need to be compared with those of *Z. benhami.*

One moderately large specimen of *Zelippistes benhami* in NMNZ (M.84119, trawled off Great Barrier Island, E of Auckland) was living attached to a black coral tree (*Antipathes* sp.) when collected. However, Morley (1996:22) recorded a specimen collected living attached to the exterior of the tube of the polychaete worm *Galeolaria hystrix*, with its aperture near the tubeworm's aperture. *Zelippistes*, therefore, is the kleptoparasitic species it might be expected to be from its irregular shape and, in particular, irregular aperture, feeding by gathering food particles that escape the tubeworm's feeding. The specimen collected on *Antipathes* presumably was actually attached to a tubeworm growing on the *Antipathes* tree. The similarities between the teleoconchs of species of *Lippistes*, *Separatista* and *Zelippistes* no doubt result from them all independently adopting a kleptoparasitic habit on cylindrical hosts, probably tubeworms in all cases.

Zelippistes benhami clearly is another warm-water element in the Castlecliff fauna, a migrant (as planktotrophic larvae) from the northern North Island. Recent records are only from the northeastern North Island warm province. It is of interest, then, that fossil specimens have been collected recently only from Tainui Shellbed (OIS 13) at Castlecliff and from Landguard Sand (OIS 9) at Landguard Bluff, the two formations in Wanganui Basin from which the highest numbers of warm-water species are recorded (Beu 2004, 2006).

Family Hipponicidae

Genus ***Sabia*** Gray, 1841

Amalthea Schumacher 1817:56, 181 Type species (by subsequent designation, Gray 1847:157): *Amalthea conica* Schumacher, 1817, Recent, Indo-West Pacific (junior homonym of *Amalthea* Rafinesque, 1815).

Sabia Gray 1841:94 (no included species). Type species (by subsequent designation, Gray 1847:157, in synonymy of *Amalthea*): *Amalthea conica* Schumacher, 1817.

Saptadanta Prashad & Rao 1934:2. Type species (by original designation): *Saptadanta nasika* Prashad & Rao, 1934, Recent, Andaman Islands (= *Sabia conica* (Schumacher, 1817); see illustrations by Rajagopal 1977, pl. 9, figs. 1–6).

Remarks. Higo et al. (1999:112) stated that *Sabia* was first established by Gray (1839), but I have been unable to find the name *Sabia* in Gray's (1839) work. A reference by Agassiz to its establishment by Gray (1839) was also mentioned by Sherborn (1930:5708), who commented '*sed non comp.*', that is, he also could not find the name in Gray's work. The first publication of the name, therefore, was by Gray (1841:94). Iredale (1937:251) concluded that *Sabia* Gray (1841) is a *nomen nudum*, and that a description was first provided by Reeve (1842). However, Gray (1841:94) gave the following description: 'In *Capulus* the foot is flat, with a plaited front edge; in *Hipponyx* and *Sabia* it is, as it were, folded on itself, and is unfit for walking upon; the back of the foot of the former of these animals secretes a shelly plate, marked with a horse-shoe shaped muscular impression, like an operculum; and of the latter forms a depression by corroding a space on the surface of the shell to which it is attached of the size of its own shell, and marked with a crescent-shaped ridge, shewing the place where the muscles were affixed;...'. This is an available description of the new genus *Sabia*, distinguishing it from *Hipponix* Defrance, 1819, and the genus name *Sabia* clearly was made available by Gray (1841). Species were first included by Gray (1847), and there is nothing to indicate that *Sabia* Reeve (1842:34) was any more than a mention of the name established by Gray (1841); Reeve (1842) did not describe the genus or include any species in it. Iredale (1937:251) also pointed out that Gray (1847:157) provided two type species selections for *Amalthea*, as he also did for *Hipponix*. Gray selected *Amalthea conica* Schumacher, 1817, the sole included species, as type species of Schumacher's (1817) '*Amalthea* α', and *A. ungaricus* (Linné, 1758) as type species of '*Amalthea* β'. Ludbrook (1957:49, pl. 4, figs. 1, 2) and Knudsen (1991, fig. 1c) both described and illustrated the holotype of *Amalthea conica* (ZMC 181, no. 1071), showing it to be essentially identical to the southern Australian species usually known as *Sabia australis*, although with a taller apex and correspondingly longer posterior slope than most Recent Australian specimens. Ludbrook (1957:49) clarified the synonymy of this species and its confusion with *Capulus danieli* (Crosse, 1858) in South Australia (see Beu 2004:192). However, she assumed that *Sabia australis* is conspecific with *Sabia conica*, whereas I follow Knudsen's (1991) suggestion and keep these species separate at present.

Sabia australis (Lamarck, 1819) (Fig. 19B,D)
Patella australis Lamarck 1819, part 1, p. 335; Delessert 1841, pl. 23, fig. 11a–c; Deshayes 1843:541 (transferred to '*Pileopsis* de la section des Hipponices' in footnote).
Hipponix listeri Gray 1827:491.
Hipponyx australis. Deshayes 1832:274; Menke 1843:33; Menke 1844:61; Crosse 1862:21; Tryon 1886:136, pl. 41, figs. 9–15; Tate 1893:330; Pritchard & Gatliff, 1900:198; Tate & May 1901:377; Odhner 1917:46.
Hipponix australis. Quoy & Gaimard 1835:434, pl. 72, figs. 25–34; Knudsen 1991:642, figs. 1a,b, 2–11 (with further synonymy, table 1); Wilson 1993:161, pl. 22, figs. 11a–c.
Amalthea australis. H Adams & A Adams 1858:374, pl. 41, fig. 4; Watson 1886:457.
Capulus danieli. Angas 1865:175 (not *Capulus danieli* Crosse, 1858; Hedley 1902b:601).
Amalthea conica. Angas 1865:175; Tenison Woods 1877:38; Thiele 1930:580 (not *A. conica* Schumacher, 1817).
Pileopsis conica. Maplestone 1872:51, pl. 26, fig. 28.
Capulus australis Hedley 1902b:600; Iredale 1924:245; Singleton 1937:392.
Capulus conica. Verco 1908:8; Verco 1935:8.
Hipponix conicus. Hedley 1916a:40 (in part); May 1921:57; May 1923:57, pl. 26, fig. 15; Macpherson 1958:30, pl. 26, fig. 15; Hartley 1958:37, pl. 8, figs. 1–4; Laws 1970:115, figs. 1–6; Spencer et al. 2009:205.
Sabia conica. Cotton & Godfrey 1938:18; Ludbrook 1941:100; Kershaw 1955:313; Cotton 1959:365; Monger 1984:50, illus; Simone 2002:85, figs. 36–38, 83, 83, 329–342.
Sabia australis. Macpherson & Chapple 1951:126; Ponder 1998:770, fig. 15.123C,D.
Hipponix (Sabia) conicus. Ludbrook 1957:49, pl. 4, figs. 1–4; Ludbrook 1978:123, pl. 13, figs. 1, 2; Ludbrook 1984:82,234,268, figs. 20o,p; 57t; 64l; pl. 5h.
Sabia wyattae Powell 1958b:90, pl. 12, figs. 3, 4 (**new synonym**).
Capulonix australis. Iredale & McMichael 1962:44.
Hipponyx conicus. Macpherson & Gabriel 1962:127, fig. 152; Macpherson 1966:217.
Hipponix conicus wyattae. Powell 1979:145, pl. 30, figs. 15, 16; Spencer & Willan, 1996:21.

Type material. *Patella australis* Lamarck, no type material present in MHNG, although a specimen (presumably a syntype) was illustrated by Delessert (1841, pl. 23, fig. 11a–c), and Rosalie de Lamarck's annotations of Lamarck's copy of '*Animaux sans vertèbres*' in MHNG indicate that Lamarck owned three specimens; the type material has been missing for many years (Y Finet MHNG pers. comm. 6 November 2007). The specimen illustrated by Delessert (1841, pl. 23, fig. 11a–c) is apparently not conspecific or even congeneric with the interpretation adopted here, as (although clearly a hipponicid) it has prominent, extremely narrow radial ribs and very wide, flat interspaces, and so is not appropriate for lectotype designation. Further research is required on a possible neotype. *Sabia wyattae*, holotype AIM AK71238, with one paratype, AK71471, from beach at Tutukaka, Northland, living attached to *Penion sulcatus* (Lamarck, 1816) (not seen).

Other material examined. **Nukumaruan:** 3–10 m above Torlesse greywacke, Opawe Stream, Pohangina valley, E Wanganui Basin; early Nukumaruan, with *Glycymeris shrimptoni*, *Myadora waitotarana*, *Clanculus plebejus*, *Diloma*, *Cantharidus*, *Austrolittorina* and diverse Rissooidea (GS2784, T23/f6491, one specimen). **Recent:** NMNZ M.35225, off Poor Knights Islands, 110 m, 35°29′S, 174°43.5′E, RV '*Acheron*' (one); M.34817, N of Three Kings Islands, 620 m, 34°01′S, 172°07′E, RV '*Acheron*' (six); M.33748, off Three Kings Islands, 91 m, 34°11′S, 172°10′E, RV '*Acheron*' (one); NMNZ M.287803, off Great Mercury I, 24 m (one).

Distribution. As interpreted by Knudsen (1991), *Sabia australis* is a species living along the coast of southern Australia, from southern Western Australia to southern New South Wales and around Tasmania. A few records (above) are known of empty Recent shells from NE New Zealand, besides the live-collected type material of *S. wyattae*, and a single fossil is recorded here from late Pliocene (early Nukumaruan) rocks of Wanganui Basin. Fossils were also recorded from the Pleistocene Ellen Point and Glanville Formations in South Australia by Ludbrook (1984). Specimens on which Maxwell (in Campbell et al. 1994, table 4.30, p. 143) based his records of *Hipponix* from Whenuataru Tuff, Pitt Island, Chatham Islands, and that Laws (1936:109) identified as Kaawa Creek specimens of *Hipponix centrifugalis* Marwick, 1931 are more nearly similar to tropical Pacific and eastern Australian material of *Pilosabia trigona* (Gmelin, 1791), and will be considered in a later paper. *Pilosabia centrifugalis* (Marwick 1931:97, pl. 8, figs. 139, 140), from Lillburnian (middle Miocene) rocks of the Gisborne district, has an unusual combination of relatively coarse radial sculpture over much of the shell, broken up by commarginal ridges towards the margin, and also seems more nearly similar to *Pilosabia trigona* than to *S. australis*. Hipponicidae are sedentary filter-feeders living attached to hard substrates, and in view of its severe facies restrictions, the time range in New Zealand of this shallow-water species may well have been much longer and more continuous than the Nukumaruan–Recent records suggest.

Dimensions. GS2784, Opawe Stream: H 2.8, D 7.6 mm.

Remarks. Usages of the name *Hipponix* (or *Sabia*) *conica* or *Sabia australis* for tropical Pacific records have not been included in the above synonymy, but the synonymy is still remarkably complex, reflecting long-continued doubts about the classification of and name for this species. It should be noted, though, that it would not be surprising if the correct name is eventually determined as *Sabia conica*; only molecular studies will resolve the taxonomy. It is important to note that this, rather than tropical material of *S. conica*, is the species identified by Simone (2002:85, figs. 36–38, 83, 83, 329–342) as *Sabia conica* in his anatomical evaluation of the Hipponicidae, in which he substantiated *Sabia* as a distinct genus (he examined material from Cockburn Sound, S Western Australia, and Green Cape, Maria Island, Tasmania). Laws (1970) pointed out several differences in animal coloration, number of egg capsules, and number of larvae per capsule between South Australian specimens and the tropical Pacific specimens reported by Cernohorsky (1968), supporting the distinction of *S. australis* from *S. conica*. This led Knudsen (1991) to suggest that *S. australis* should be maintained as a species separate from *S. conica*. However, whether this is correct is unknown, as the variation of these characters and whether there is any discontinuity or areas of syntopy in the distribution of *Sabia* species around the coast of Australia have not been studied; it is quite feasible that the distinguishing characters vary clinally, and all specimens are conspecific.

The specimen now recorded from early Nukumaruan rocks in eastern Wanganui Basin (from the same locality as the new record of *Clanculus plebejus*, above) is almost identical to the one illustrated by Ponder (1998, fig. 15.123C,D). Although the apical area has been abraded smooth, a protoconch closely similar to that illustrated by Knudsen (1991), fig. 6b) is present. The exterior bears about 58 radial costae around the margin, including behind the apex, all relatively flat, wide and closely spaced, and separated by deep, linear grooves. This appears to be a typical specimen of the form identified by Knudsen (1991) as *Sabia australis*.

Powell (1958b:90, pl. 12, figs. 3, 4) proposed the name *Sabia wyattae* for Recent specimens found living on an empty shell of *Penion sulcatus* cast up on the beach at Tutukaka, NE North Island. Powell distinguished this form from *S. australis* only by its fewer radial costae, an exceedingly variable character in both *S. australis* and *S. conica*. Although no further records have been published, four lots from off northern New Zealand are present in NMNZ (listed above). The specimens illustrated by Powell and the NMNZ specimens are within the range of variation of *S. australis* as illustrated and described by Knudsen (1991), and indicate that *S. australis* occurs uncommonly in NE New Zealand. The New Zealand occurrences possibly are pseudopopulations recruited as planktotrophic larvae from southern Australia. If this is so, the single record of *Sabia australis* in Wanganui Basin early Nukumaruan rocks represents another case of a warm-water mollusc transported as larvae from southern Australia into Wanganui Basin, and it has certainly extended its range to Wanganui briefly from at least the northern North Island.

Family Triviidae

Genus ***Trivia*** Broderip, 1837

Trivia Broderip 1837:256. Type species (by subsequent designation, Gray 1847:142): *Cypraea europaea* Montagu, 1808 (= *C. monacha* Da Costa, 1778), Pliocene–Recent, NE Atlantic & Mediterranean (Iredale [1912:34] showed that *Trivia* was first made available, along with Gray's other manuscript names for Cypraeidae [sensu lato], by Broderip [1837] in his article on Cypraeidae in the 'Penny cyclopedia').

Subgenus ***Ellatrivia*** Iredale, 1931

Ellatrivia Iredale 1931:221. Type species (by original designation, Iredale 1931:233): *Trivia merces* Iredale, 1924, late Pliocene–Recent, central and N New Zealand and SE Australia.

Remarks. Several genera have been proposed in Triviidae, but their distinction is very subtle. Cernohorsky (1971:111) referred all New Zealand Triviidae to *Ellatrivia* Iredale, 1931. Maxwell (1992:97) followed Beu & Maxwell (1990:118) in referring all New Zealand Triviidae to *Trivia*, remarking that there do not seem to be any taxonomically important differences between *Trivia monacha* (Da Costa, 1778), the type species of *Trivia* Broderip, 1837, and *T. pinguior* Marwick, 1926 (late Eocene, S Canterbury–N Otago). He maintained this position recently (Maxwell 2009:242). In contrast, Dolin (2001) recognized *Trivia (Trivia)*, *T. (Decoratitrivia)*, *Dolichupis*, *Trivellona*, *Niveria*, *N. (Ellatrivia)*, *Trivirostra*, *Cleotrivia* and *Semitrivia* as generic groups within Indo-Pacific Triviidae. They are separated by subtle differences in the shape of the basal callus, apertural canals and dorsum, in the prominence of the dorsal sulcus, and in the shape and sculpture of the fossula, a concave columellar area inside the aperture, parallel to the inner lip. Dolin (2001:218) referred the New Zealand and SE Australian shallow-water triviids to *Niveria* Jousseaume (1884:100) (type species: *Cypraea nivea* Gray in GB Sowerby I 1832 (junior primary homonym of *Cypraea nivea* Wood, 1828; = *Niveria nix* Schilder, 1922), Recent, western Atlantic), subgenus *Niveria (Ellatrivia)*, expressly including *Trivia kaiparaensis* Laws, 1939 (early Miocene, Pakaurangi Point, Kaipara Harbour, Northland). However, Fehse (in Poppe 2008a:668–681) used only *Trivia*, *Cleotrivia*, *Dolichupis*, *Trivellona* and *Trivirostra* for Philippine Islands Triviidae, most of which were assigned to either *Trivirostra* or *Trivellona*. Several of the species proposed by Dolin (2001) were assigned to *Trivellona* by Fehse (in Poppe 2008a). All taxa illustrated by

Fehse (in Poppe 2008a) have either more protruding anterior and posterior extremities or more prominent exterior ribs than in the New Zealand–SE Australian species considered here. The classification of triviids is obviously undecided, differing between authorities. In the circumstances, it seems best to follow Spencer et al. (2009) and retain the usage of the subgenus *Trivia (Ellatrivia)* for New Zealand species. *Trivia zealandica* Kirk, 1882, discussed below, differs from all other New Zealand triviids in lacking transverse ridges over the dorsum—the very short ridges stop at the dorsal edges of the narrow lateral callus—but the taxonomic significance of this character also is unclear. Illustrations of *Trivellona suiduirauti* (Lorenz, 1996) by Fehse (in Poppe 2008a, pl. 282, figs. 4a,b, 6a,b) show that the ribs are reduced to faint angulations on the dorsal surface of this species, but do not fade out completely as in *T. zealandica*. The aperture is also considerably wider and the spire protrudes more in *T. suiduirauti* than in *T. zealandica*. The position of the dorsal sulcus (an antero-posterior groove between the dorsal ends of the transverse ridges on some of the more strongly sculptured species) is clearly shown by a smooth area between the surface granules in well-preserved specimens of *T. zealandica*, and it seems to be a normal *Trivia (Ellatrivia)* species in all characters other than the length of the ridges. It is assumed here that the loss of dorsal ribs is merely a continuation of the trend towards weakening of the dorsal ribs already seen in such Recent species as *T. (Ellatrivia) merces* (Iredale, 1924), and *Trivia zealandica* also is referred to *Trivia (Ellatrivia)*.

Trivia (Ellatrivia) zealandica (Kirk, 1882) (Fig. 20A–C)

Trivia zealandica Kirk 1882:409; Suter 1915:11, pl. 8, fig. 3a,b; Beu & Maxwell 1990:351, pl. 47m, q; Maxwell 2009:242.
Trivia neozelanica (sic). Hutton 1893:58 (error for *T. zealandica* Kirk).
Trivia flora Marwick 1928:182, figs. 118, 119; Fleming 1966:52, figs. 1071, 1072; Beu & Maxwell 1990:408; Maxwell 2009:242 (**new synonym**).
Niveria (Ellatrivia) flora. Schilder 1941:75.
Ellatrivia zealandica. Fleming 1966:52; Cernohorsky 1971:113, fig. 9.
Ellatrivia flora. Cernohorsky 1971:113.

Type material. Trivia zealandica, lectotype (of Suter 1915:11, pl. 8, fig. 3a,b) NMNZ M.1815, an incomplete shell, with one paralectotype NMNZ M.1816 (Marshall 1996:21), from 'Petane', that is, Tangoio Limestone or Mairau Mudstone, formations high in Petane Group (late Nukumaruan) in Matapiro Syncline, 30 km N of Napier, central Hawke's Bay. Marshall (1996:21) discussed the complex history of the type material, and concluded that Cernohorsky (1971:113) was incorrect to regard Suter's (1915) selection as designating a neotype. *Trivia flora*, holotype TM8575, from Whenuataru Tuff (Waipipian, and perhaps in part Mangapanian), Flowerpot Harbour, Pitt Island, Chatham Islands.

Other material examined. **Waipipian:** GS12162, CH/f20A, Whenuataru Tuff, E side Flowerpot Bay, Pitt Island (four); GS12163, CH/f13B, Whenuataru Tuff, Motutapu Point, Pitt Island (one fragment); GS12164, CH/f25, Whenuataru Tuff, tip of Taruwhenua Peninsula, Pitt Island (one). **Nukumaruan:** specimens of *Trivia (Ellatrivia) zealandica* occur uncommonly in the 'Petane beds' (late Nukumaruan formations of Petane Group in Matapiro Syncline, central Hawke's Bay; Beu 1995:117–135) in eastern North Island (Okawa Stream, GS1063, V21/f8476, two specimens; Puketapu, Matapiro Syncline, NW of Napier, GS5216, V20/f8517, one; walkway on W side of Roro-o-kuri, Onehunga Road, Ahuriri 'lagoon', Napier, Mairau Mudstone, GS12386, V21/f05, three; 'the watchman' hill, Ahuriri Lagoon, Napier, Mairau Mudstone, GS11465, V21/f8015A, one; Flat Rock, Tangoio, calcite neomorph fauna in Tangoio Limestone, GS12392, V20/f07, one).

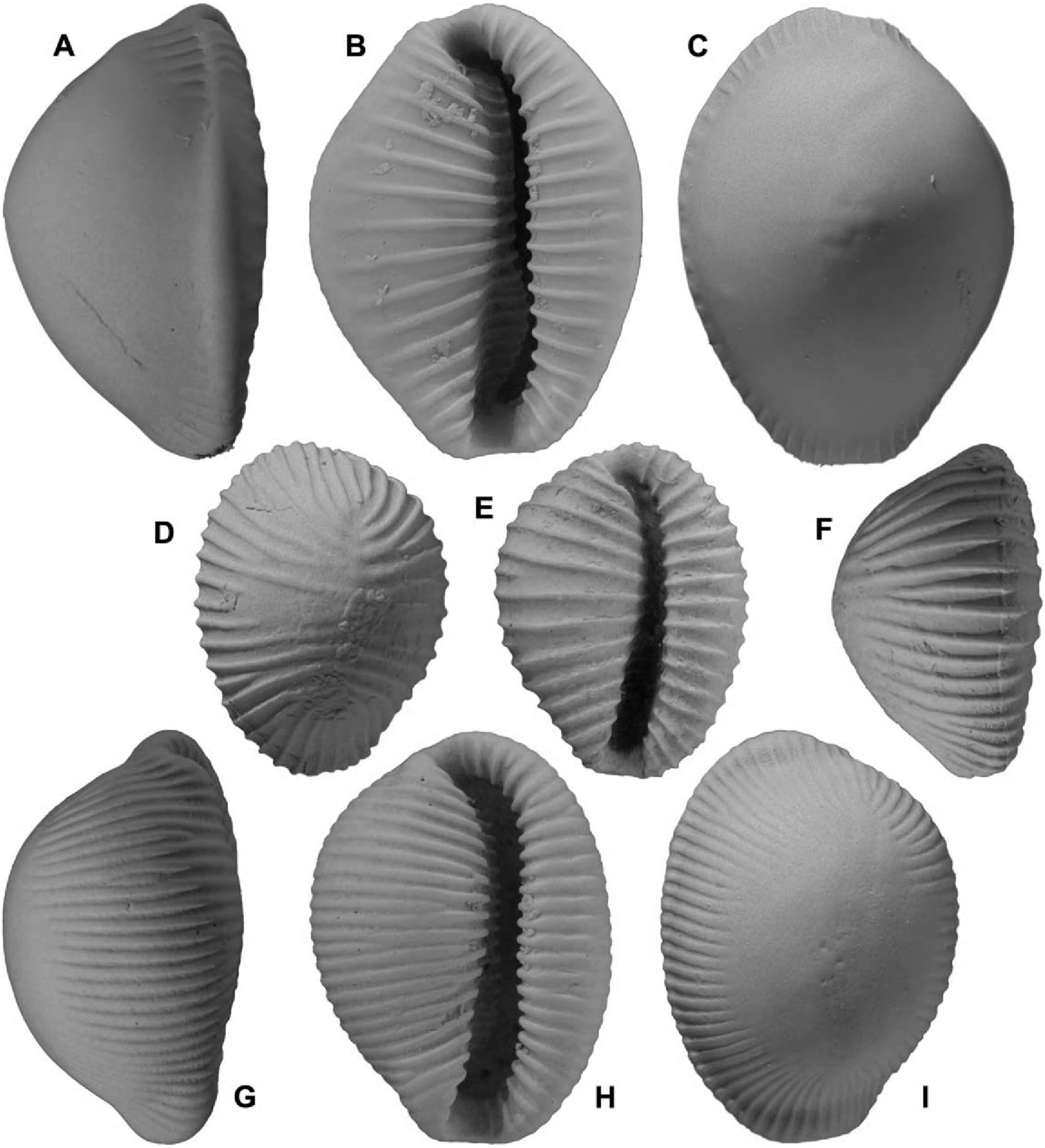

Fig. 20 (A–C) *Trivia (Ellatrivia) zealandica* (Kirk), O32/f8875, Leader siltstone lithofacies (early Castlecliffian, OIS 31 or earlier), Leader River, Parnassus, N Canterbury; height 12.8 mm. (D–F) *Trivia* (sensu lato) sp., cf. *Trivellona paucicostata valeriae* (Hart), GS15629, R28/f078, Onoke Formation (early Nukumaruan), bathyal fauna E of Lake Ferry, Palliser Bay; height 9.4 mm. (G–I) *Trivia (Ellatrivia) merces* (Iredale), abraded specimen, GS689, Y19/f9491, uplifted Holocene terrace, N shore Mahia Peninsula; height 11.6 mm.

Trivia (Ellatrivia) zealandica also occurs rarely in early Nukumaruan limestone at Castlepoint, eastern Wairarapa, in rudstone beds (Van der Lingen et al. 1985) with common *Chama ruderalis* (Lamarck, 1819) (= *C. huttoni* Hector, 1886, type locality; Beu 2006), alternating with floatstone beds containing the cold-water scallop *Zygochlamys delicatula* (Beu 1995:156) (GS10844, U26/f6037). Van der Lingen et al. (1985) described and illustrated complex liquefaction deformation structures in the floatstone component and low-angle cross-stratification in the interbedded rudstone, in a sequence of two or three sedimentary cycles (stratigraphic column: van der Lingen et al. 1985, fig. 3). Beu & Kitamura (1998:146) suggested that deposition of Castlepoint Formation occurred as deep-water, canyon-head debris flows in response to cyclic sea-level changes on the adjacent shelf. It seems likely that the floatstone component was deposited as near-in situ sediment in the canyon head, and the rudstone beds represent coarser material slumped into the site as a result of sediment accumulation on the shelf around the canyon head. Loading of floatstone by the rudstone component and slumping of the entire mass further into the canyon head as a result of sea-level lowering, and perhaps coseismic shaking, would then have produced the liquefaction structures.

In Wanganui Basin, *Trivia (Ellatrivia) zealandica* has been collected only from early Nukumaruan mudstone a short distance above Hautawa Shellbed, at the disused Hautawa Road, off West Road, north of Hunterville, Rangitikei valley, and from Tewkesbury Formation ca 200 m W of the mouth of Ototoka Stream, Nukumaru Beach, in the Wanganui coastal section (specimen in the collection of Mrs Julie Loveridge, Waitotara). The only other record I am aware of from outside Hawke's Bay is in NMNZ: M.287951, head of gully 800 m S of Pahiatua Trig., Konini, Pahiatua, N Wairarapa (four). **Castlecliffian:** Castlecliffian specimens are recorded only from eastern New Zealand: Leader River, 'Mendip Hills' Station, Parnassus, North Canterbury, where it underlies Potaka Tephra (Warren 1995, fig. 20, 21), and so is older than 1.0 Ma (Shane 1994; Shane et al. 1996), that is, approximately OIS 29–31 or older (O32/f8875; Beu & Maxwell 1990:352, pl. 47m, q; Fig. 20A–C); and Matata and Ohope Beach, Whakatane, Bay of Plenty (OIS 15?): NMNZ M.96442, large bend on Wainui Stock Road, south of Ohope Beach (one); NMNZ M.42960, shellbeds below old reservoir in stream at foot of Whakatane-Ohope Road (one + five fragments); NMNZ, locality F518, Ohinekeao Stream, W of Matata (one fragment).

Distribution. Waipipian (–Mangapanian?), Whenuataru Tuff, Pitt island; Early Nukumaruan, just above Hautawa Shellbed, Wanganui Basin (one specimen), at Castlepoint, East Wairarapa, and near Pahiatua Trig., Konini, N Wairarapa; late Nukumaruan, Wanganui Basin (rare) and Hawke's Bay (uncommon); early Castlecliffian, Mendip Hills station, Leader River, North Canterbury (OIS 29–31 or older), one specimen (Fig. 20A–C); later Castlecliffian at Matata and Ohope Beach, Whakatane (OIS 15?).

Dimensions. O32/f8875, Leader River, Parnassus, early Castlecliffian: H 12.8, D 9.4, H (normal to aperture) 7.4 mm; GS5216, Puketapu, Hawke's Bay: H 11.5, D 8.0, H (normal to aperture) 6.5 mm; GS12386, Roro-o-kuri, Napier: H (incomplete) 11.4, D 9.8, H (normal to aperture) 7.6 mm; holotype of *T. flora*: H 10.0, D 7.3, H (normal to aperture) 6.0 mm (Marwick 1928:482).

Remarks. Trivia (Ellatrivia) zealandica is rendered very distinctive, compared with all the other New Zealand species of Triviidae, because the narrow ridges on the exterior extend only to the dorsal margin of the lateral callus areas, and the superficially smooth, microscopically granulose dorsum is clearly slightly conical in shape. The lateral callus areas also are narrower and more prominent than in other New Zealand species. It is also one of the larger triviids recorded from New Zealand, reaching 13 mm high (specimens of *E. merces* reach 15.3 mm high: NMNZ M277017, beach, Reef Point, Ahipara, N Northland, H 15.3 mm; NMNZ M277019, beach, Cape Maria van Diemen, Northland, H 15.2 mm; NMNZ M277015, beach, Taupiri Bay, Northland, H 14.9 mm).

It is not quite certain that the relatively small specimen (height 8.4 mm) from 'Petane' illustrated by Cernohorsky (1971, fig. 9) as *Trivia (Ellatrivia) zealandica* is conspecific with the significantly larger specimens that usually bear this name. Cernohorsky's figure shows the narrow ridges extending a significant distance up the sides of the dorsum above the lateral callous ridges, whereas they stop at the dorsal edges of the callous ridges in almost all specimens I have examined (but note the comment below on *Trivia flora* Marwick, 1928). However, the specimen agrees in shape, in its narrow aperture, and in its conical dorsum with *T. zealandica*, and Cernohorsky (1971) described the dorsum as 'distinctly finely granulose', so it evidently is a slightly unusual specimen of *T. zealandica*.

Marwick (1928:428) distinguished *Trivia flora*, from the Pliocene of Pitt Island, Chatham Islands, from *T. zealandica* by the 'bluntly conoid' rather than rounded shape of the dorsum, and by being 'not so attenuated anteriorly'. However, the few specimens collected since and the holotype seem indistinguishable from *T. zealandica*. The shape of the dorsum is identical in specimens from the Chatham Islands and mainland New Zealand, Whenuataru Tuff specimens are only slighty smaller than the largest Hawke's Bay Nukumaruan specimens of *T. zealandica*, and the shape of the anterior seems within the range of variation of one species. One of the Pitt Island specimens has the narrow ridges extending slightly further up the sides than I have seen in Nukumaruan specimens, slightly above the lateral callous ridges, but the holotype and all othe specimens examined agree with the common form of *T. zealandica* in this character, and the specimen of *T. zealandica* illustrated by Cernohorsky (1971, fig. 9) has the ridges extending further dorsally than on any Pitt Island specimens I have seen. In my opinion *T. flora* is simply a synonym of *T. zealandica*. Therefore, *T. zealandica* is a considerably longer-ranging species than has been thought previously.

Cernohorsky (1971:115, figs. 10, 10a) recorded *Trivia (Ellatrivia) merces* also as a fossil at 'Petane' (that is, from a late Nukumaruan formation of Petane Group in the Matapiro Syncline in central Hawke's Bay), on the basis of a single specimen in the Auckland Museum, but I have not seen specimens from Hawke's Bay. The other fossils of *T. merces* I am aware of are from Te Piki, Cape Runaway (OIS 7) (Grant-Mackie & Chapman-Smith 1971: 673; Richardson 1997:8), and Denby Shellbed (OIS 7) at Waihi Beach, Hawera (Thomson 1917:417, as *Trivia zealandica*; Fleming 1953:271). A single specimen (Fig. 20G–I) is also present in GNS collections from a Holocene terrace at Mahia Peninsula (GS689, Y19/f9491, 'raised beach, north shore', collected by Alexander McKay), and a fragment is present in a collection from the highest Holocene terrace at Aramoana Beach, S Hawke's Bay coast SE of Waipukurau (V23/f61, 200 m NE of Gibralter Road, V23/372112). *T. merces* has, therefore, a Nukumaruan–Recent time range, but clearly has a highly unreliable fossil record and is not useful for biostratigraphy, whereas *T. zealandica* is known in post-Nukumaruan rocks only at Parnassus and Ohope Beach, and has some utility in biostratigraphy.

A further, apparently undescribed early Nukumaruan fossil triviid is represented by a single specimen (Fig. 20D–F) from the bathyal fauna (Beu 1967, 1969) in Onoke Formation mudstone (early Nukumaruan) in the cliffs east of Lake Ferry, Palliser Bay, collected and presented by Sashia Wood (GS15629, R28/f078). It resembles *Trivellona paucicostata valeriae* (Hart 1996; Dolin 2001:219, figs. 12, 13, 47) in many characters, having relatively sparse, prominent riblets passing across the dorsum with little interruption, that is, longer than in both *Trivia (Ellatrivia) zealandica* and *Trivia merces*, the two more common species in New Zealand. Dolin (2001) pointed out that

'*Erato*' *tetatua* Hart, 1996 is based on an immature specimen of *Trivellona paucicostata valeriae* Hart. The Palliser Bay shell differs from *Trivellona paucicostata valeriae* in its smaller size, its more elongate shape, and in its fewer, narrower, more widely spaced dorsal ridges, interrupted by a narrow sulcus in the centre of the dorsum. The fossula is scarcely visible, as the specimen was cracked and has been filled with glue. Further specimens are needed to clarify the identity of the Lake Ferry species.

Family Naticidae

Genus ***Taniella*** Finlay & Marwick, 1937

Taniella Finlay & Marwick 1937:48. Type species (by original designation): *Natica notocenica* Finlay, 1924, early Miocene, New Zealand.

Remarks. *Taniella* differs from *Tanea* Marwick, 1931 (type species: *Natica zelandica* Quoy Gaimard, 1835, late Pliocene–Recent, New Zealand) in its significantly smaller size, its markedly lower spire in most specimens, and its straight spire outlines, with a weakly impressed, tangential suture. The apertural characters, including a prominent funicle, are similar in both groups. The relationship between *Tanea* and *Taniella* is unclear because *Taniella* apparently is extinct, and radular characters are critical to understand naticid relationships. The operculum of *Taniella notocenica* (Finlay, 1924) was described by Finlay & Marwick (1937:48) as 'almost flat, exteriorly with a thickened, medial concentric [that is, commarginal] ridge (as in many *Astraea*) the surface inside this smooth, the surface outside finely but conspicuously granulate with traces of numerous subsurface spirals, ending as well-marked granulations on the inner posterior margin; no trace of marginal grooves'. This differs markedly from the operculum of *Tanea zelandica*, with its two conspicuous marginal grooves and margining ridge, and suggests that *Taniella* and *Tanea* are not closely related. Finlay & Marwick (1937) suggested a close relationship between *Taniella* and *Tectonatica* Sacco, 1890 (type species: *Natica tectula* Sacco, 1890, Pliocene, Italy), and the similarity is great enough that generic distinction is uncertain (the distinction was probably based mainly on Finlay's conviction that New Zealand taxa are all restricted endemics). *Tectonatica rizzae* (Philippi, 1844) (Bouchet & Warén 1993:764, figs. 1822, 1823) is very similar to *Taniella* species in size (8.1–10.6 mm high), its shape, its low spire with straight outlines, its tangential, flat suture, and its obvious umbilical callus (funicle) that leaves a surrounding groove. However, the juvenile illustrated by Bouchet & Warén (1993, fig. 1879) has two narrow but obvious marginal opercular grooves around the margin against the outer lip, reduced in the adult to one groove (Bouchet & Warén 1993, fig. 1908). *Tectonatica tecta* (Anton, 1838) (Recent, Namibia to E Cape Province, South Africa; neotype illustrated by Kilburn 1976, figs. 7b, 8b, 9) has an essentially smooth operculum, apart from a weak callus ridge in the nuclear region, and has a weakly sinuous spire outline similar to that of the tall-spired specimens of *Taniella planisuturalis* described below. Having none or one rather than two marginal opercular grooves seems to distinguish *Tectonatica* from *Taniella*. Also, both *T. rizzae* and juvenile specimens of *T. filosa* (Philippi, 1845) (Bouchet & Warén 1993, fig. 1880) have a conspicuously thickened umbilical callus at a very small size, the umbilicus is completely filled with callus at all growth stages in *T. tecta*, and the columellar margins of the opercula of *T. rizzae* and *T. filosa* bear obvious transverse ridges, transformed a little in the adult (Bouchet & Warén 1993, fig. 1906, 1908) into short ridges down the adapical third of the columellar margin. *Taniella* seems best retained as a distinct genus, although

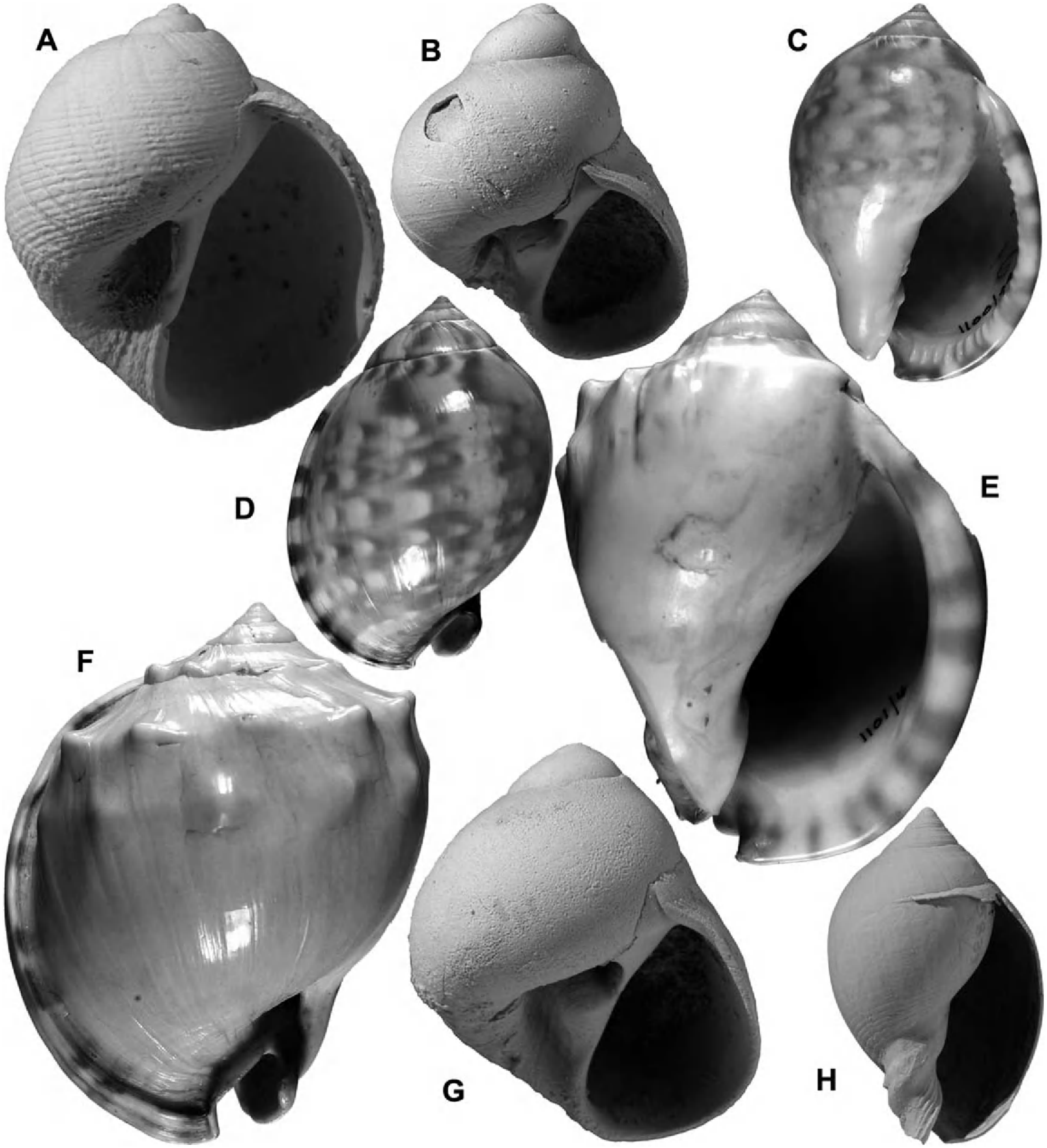

Fig. 21 (A) *Eunaticina papilla* (Gmelin), holotype of *Sigaretus (Naticina) cinctus* Hutton, CMC M3014, Landguard Sand (Haweran, OIS 9), Landguard Bluff, Wanganui; H 14.8, D 12.8 mm. (B,G) *Taniella planisuturalis* (Marwick), 2 large, tall-spired specimens, GS11225, V20/f8002, Darkys Spur Formation (late Nukumaruan), Darkys Spur, W of Devils Elbow, Hawke's Bay; B, H 16.8, D 13.7 mm; G, H 18.2, D 15.3 mm. (C-F,H) *Semicassis labiata* (Perry); C,D, lectotype of *Cassis achatina* Lamarck and neotype of *Cassidea labiata* Perry, 1811, MHNG 1100/99; unlocalised (type locality Port Jackson, Sydney, Australia); height 53 mm; E,F, 2 syntypes of *Cassis zeylanica* Lamarck, unlocalised (South Africa); E, MHNG 1101/4, ventral view, height 81 mm; F, MHNG 1101/3, dorsal view, height 76 mm; H, GS5833, Y14/f7505A, Te Piki Member (Haweran, OIS 7), Te Piki, near East Cape; height 31.3 mm.

probably closely related to *Tectonatica* phylogenetically.

Finlay & Marwick (1937:49) referred *Natica subnoae* Tate, 1893 (Janjukian, Oligocene; Bird Rock, Torquay, Victoria) to *Taniella*, 'the only Australian species at present known'. Darragh (1970:197) followed their suggestion. Wilson (1993:218–219) referred several Indo-West Pacific and Australian species to *Tectonatica*, but most have a significantly taller spire than *Taniella notocenica* and *T. planisuturalis*. One Recent species that seems very similar to *T. planisuturalis* is *Natica elkingtoni* Hedley & May (1908:119, pl. 23, fig. 18) from moderately deep water (180 m) off Cape Pillar, S Tasmania. The spire of *N. elkingtoni* is slightly taller than that of most specimens of *T. planisuturalis*, despite all other characters being similar, but that is also true of the New Zealand Miocene fossil species assigned to *Taniella*, and of a few large specimens of *T. planisuturalis* described below from shallow-water environments. A close phylogenetic relationship between New Zealand *Taniella* species and Australian or tropical Pacific species remains possible, but requires further research. If a position in *Taniella* could be confirmed for *N. elkingtoni*, it would allow the radula and DNA of *Taniella* to be assessed, and it would not be surprising if *Taniella* is a synonym of *Tectonatica*.

Taniella planisuturalis (Marwick, 1924) (Figs. 21B, G)

Natica planisuturalis Marwick 1924c:550, pl. 55, figs. 10, 11.
Natica haweraensis Marwick 1924c:551, pl. 55, figs. 6, 7.
Taniella planisuturalis. Finlay & Marwick 1937:49; Fleming 1966:53, fig. 1987, 1988; Beu & Maxwell 1990:321, pl. 41n; Maxwell 2009:242.
Taniella haweraensis. Finlay & Marwick 1937:49; Fleming 1966:53, figs. 1084, 1085.

Type material. *Natica planisuturalis*, holotype TM6888, from GS1089, V21/f8482, 'blue clays' (Okauawa Formation), Okauawa Stream, Kereru Road, inland central Hawke's Bay (late Nukumaruan, early Pleistocene). *Natica haweraensis*, holotype TM6887, from GS1173, Q21/f6495, Tangahoe Formation, Waihi Beach, Hawera, South Taranaki (Waipipian, mid-Pliocene).

Other material examined. **Opoitian:** GS8101, Y14/f7618A, Oweka Creek, halfway between Whangaparaoa and Hicks Bay, East Cape (four); GS5626, C46/f9594, Birch's Mill shell lens, Te Waewae Bay, Southland (five); Kaawa Creek, SW Auckland (recorded by Laws (1936, list p. 99) as '*Tanea notocenica* (Finlay)', the early Miocene type species of *Taniella*). **Waipipian**: occurs at Waihi Beach and Waipipi; recorded by Fleming (1953:112) from Middle Waipipi Shellbed (GS1101, Q22/f7303). **Mangapanian:** recorded from Mangapani and Wilkies Bluff by Laws (1940b: 38); recorded by Fleming (1953:119,120,124) from Mangapani Shellbed (GS4227, R21/f8478), Makokako Sand (GS4221, R21/f9504) and Wilkies Shellbed (GS4124, R22/f6543; GS4224, R22/f6467). **Nukumaruan:** Fleming (1953:131, 139, 144, 151) recorded *Taniella planisuturalis* from Hautawa Shellbed, Nukumaru Limestone, Nukumaru Brown Sand, and Waipuru Shellbed in Wanganui Basin. Scott (in Kingma 1971, table 10A) also recorded it from six localities in Petane Group in Te Aute Subdivision, but it is much more common and ubiquitous in mudstone and sandstone formations of Petane Group than this record suggests. **Castlecliffian:** Fleming (1953:174, 181) recorded *T. planisuturalis* from Butler's Shell Conglomerate (early Castlecliffian, OIS 31; GS4083, R22/f6413, Ototoka coast section, listed in parentheses to indicate thought reworked from older rocks), and Okehu Shell Grit (Castlecliffian, OIS 27; GS4072, R22/f6403, road from Kai-Iwi Station to beach, again in parentheses). Fleming (in Kingma 1971:98) also recorded *T. planisuturalis* from Maraetotara Sand (early Castlecliffian, from shellbeds underlying Potaka Tephra, ca OIS 29–31) at Cape Kidnappers, Hawke's Bay

(GS5313, W21/f8520, bend in tributary of Maraetotara River to NW of high terraces; GS5309, W21/f8516, lowest shellbed, 1.6 m above unconformity, coast W of Black Reef). BA Marshall's collections from Ohope Beach, Whakatane (Castlecliffian, about OIS 15?) in NMNZ include the following records of *Taniella planisuturalis*: M.40267, cutting on Wainui Stock Road, SW shore Ohiwa Harbour (two); M.43035, shellbeds below old reservoir in stream at foot of Whakatane-Ohiwa Road, Ohope (six); M.95323, large bend on Wainui Stock Road, S of Ohope Beach (23).

Distribution. Opoitian, Kaawa Creek, Oweka Creek and Te Waewae Bay, probably more widespread; Waipipian–Nukumaruan and, probably, early Castlecliffian in Wanganui Basin (assuming some OIS 31–27 records are not reworked); up to early Castlecliffian in eastern New Zealand, at Cape Kidnappers (OIS 31–29?) and mid-Castlecliffian at Ohope Beach, Whakatane (OIS 15?). Widespread and common throughout New Zealand Pliocene rocks. *Taniella planisuturalis* evidently retreated gradually from central New Zealand to the north as temperatures fell after Nukumaruan time, surviving in New Zealand until about OIS 15 in the Bay of Plenty, that is, in the northeastern New Zealand warm province. The only other examples with extensive enough fossil records to reveal such a gradual retreat are (1) *Arca cottoni* Waghorn, 1926 which, as noted by me (Beu 2004:133), is also recorded from Castlecliffian (OIS 15?) rocks at Ohope Beach, Whakatane, but at no other post-Nukumaruan localities in New Zealand, and (2) *Trivia (Ellatrivia) zealandica*, which also is recorded above from OIS 15 rocks at Whakatane. *Arca cottoni* might well be a synonym of one of the living tropical western Pacific species (Beu 2004:133).

Dimensions. Marwick (1924c:550, 551) stated the dimensions of the holotypes as: *N. planisuturalis*, H 11, D 11 mm; *N. haweraensis*, H 10, D 10 mm; he also stated that 'an imperfect specimen from Waipipi Beach is 20 mm high'; GS11225, V20/f8002, Darkys Spur, Nukumaruan: H 18.2, D 15.3 mm; H 16.8, D 13.7 mm.

Remarks. This small species (commonly up to 12 mm high, reaching 20 mm) easily is recognized by the combination of the flat, tangential suture, in most small specimens having a rather low spire with straight outlines and a relatively squat shape, and the very prominent, clearly demarcated funicle, which is separated from the last whorl by a deep, narrow groove. Some larger specimens from Hawke's Bay Nukumaruan sandstone units (presumably living in shallower water than most; particularly from Darkys Spur Formation, Darkys Spur, off Kaiwaka Road, 5 km WNW of Devils Elbow, N of Napier, GS11225, V20/f8002, three specimens, Fig. 21B,F) develop a much more excert spire with more sinuous outlines than the common low-spired form. The suture of such specimens gradually descends below the periphery of the previous whorl as the shell grows. These specimens resemble *Tectonatica* species more closely than the usual short-spired form does. Beu & Maxwell (1990:321) suggested that the Waipipian *Taniella haweraensis* is part of the variation of *T. planisuturalis*, and the wide range of variation of Hawke's Bay Nukumaruan specimens makes this synonymy certain. *T. planisuturalis* is widespread in New Zealand in Pliocene and early Pleistocene rocks, of Opoitian to early-mid Castlecliffian age. Their inclusion in the one synonymy list and usage of the name *T. planisuturalis* for the species by Beu & Maxwell (1990:321) constitute the necessary first reviser's action to make *T. planisuturalis* the valid name for the species named both *N. planisuturalis* and *N. haweraensis* by Marwick (1924c). Specimens definitely in situ are not known in Castlecliffian rocks in Wanganui Basin, although it is possible that some early Castlecliffian records are based on specimens in situ, whereas they occur in early Castlecliffian rocks (OIS 31?–29) at Cape Kidnappers, and in rocks deposited during about OIS 15 at Whakatane. Obviously, this species must be used as a Nukumaruan index fossil with caution, although it seems likely to be limited to Nukumaruan and older rocks in Wanganui Basin and further south.

Genus ***Eunaticina*** Fischer, 1885

Naticina Gray 1840:147 (*nomen nudum*); Gray 1847:150. Type species (by original designation): '*Nat. papilla*' (=*Natica papilla* Gmelin, 1791), Recent, Indo-West Pacific; Pleistocene, New Zealand (junior homonym of *Naticina* Guilding, 1834).
Eunaticina Fischer 1885 (in 1880–1887), p. 768; replacement name for *Naticina* Gray, 1847.

Eunaticina papilla (Gmelin, 1791) (Fig. 21A)

Eunaticina papilla. Beu 2004:206, fig. 22D–F,H (with synonymy).
Eunaticina linneana. Maxwell 2009:242.

Type material. Since I (Beu 2004:206) discussed the type material and variation of this species and its synonyms, I enquired at CMC about the possible continued existence of the holotype of *Sigaretus (Naticina) cincta* Hutton (1885: 318). Norton Hiller (CMC pers. comm. 11 December 2007) reported that Hutton's holotype is still present in the Museum (CMC M3014, Fig. 21A), and was simply missed out of the catalogue by Bradshaw et al. (1992). As the holotype still exists, the neotype proposed by Beu (2004:209) (AIM AK102482) was unnecessary, and has no status (ICZN Art. 75.8). It should be noted that the holotypes of *Mitrellatoma angustata* (Hutton, 1886) (see Part 4) and *Cominella incisa* (Hutton, 1885) have the same history; no type material was listed by Bradshaw et al. (1992), but both holotypes are still in CMC. Obviously the catalogue by Bradshaw et al. (1992) must be used with caution.

Dimensions. Holotype of *Sigaretus cinctus*: H 14.8, D 12.8 mm; neotype proposed by Beu (2004:209): H 11.3, D 10.2 mm.

Remarks. The synonymy and the time range in New Zealand of *Eunaticina papilla* were discussed in Part 1 of this series (Beu 2004:206). During the search of Henry Suter's notes and photographs in GNS (for the illustration of a syntype of *Venericardia zelandica* Potiez & Michaux, 1844, = *Austrovenus stutchburyi* (Wood, 1828), sent to Suter by the curator of the Muséum de Douai, France; Beu 2006:280), a set of photographic prints was found. These are evidently duplicate prints of the illustrations in several of Suter's New Zealand Geological Survey Paleontological Bulletins, particularly Suter (1915). One of them shows the holotype of *Sigaretus (Naticina) cinctus* Hutton. This print is considerably larger and clearer than Suter's (1915, pl. 4, fig. 5) published figure and demonstrates that the holotype recognized by Suter (1915) definitely is the specimen of *E. papilla* in CMC (M3014). The dimensions of the holotype were stated by Suter (1915:9) as H 16, D 12.5 mm, substantially agreeing with those of M3014 (H 14.8, D 12.6 mm), indicating that the illustration by Marwick (1924c), pl. 60, figs. 12, 16) is enlarged × 2, not × 1 as stated in the caption; Marwick's illustration is about 31 mm high. The holotype is a white, slightly chalky shell with a pale yellow stain, closely resembling many other shells from Landguard Sand, and Marwick (1924c:573) was incorrect to doubt its provenance. The holotype of *S. cinctus* is actually a rather small, inflated specimen of *E. papilla*, considerably smaller than the several specimens known from Te Piki, near East Cape, although it is larger and a little taller and narrower than the redundant neotype I proposed (Beu 2004:209).

Family Cassidae

Genus ***Semicassis*** Mörch, 1853

Semicassis Mörch 1853:112. Type species (by subsequent designation, Harris, 1897:198): *Cassis japonica* Reeve, 1848 (= *Cassis bisulcata*

Schubert & Wagner, 1829), Miocene to Recent, Indo-West Pacific.

Faurotis Jousseaume 1888:188, Type species (by original designation): *Faurotis faurotis* Jousseaume, 1888, Recent, western Indian Ocean & Red Sea.

Xenophalium Iredale 1927:333. Type species (by original designation): *Xenophalium hedleyi* Iredale, 1927 (= *Cassidea royana* Iredale, 1914), Recent, northern New Zealand, Kermadec Islands and southeastern Australia.

Xenogalea Iredale 1927:339. Type species (by original designation): *Cassis pyrum* Lamarck, 1822, Pleistocene and Recent, New Zealand and southeastern Australia.

Tylocassis Woodring 1928:306. Type species (by original designation): *Buccinum inflatum* Shaw, 1811 (= *Buccinum granulatum* Born, 1778), Pleistocene and Recent, western Atlantic.

Remarks. The synonymy above is taken from Beu (2005:50), and was based on research on tropical American Neogene Tonnoidea (Beu 2010). The minor characters of nodulation and ridges of the inner lip callus separating supposed genus-group taxa such as *Semicassis*, *Tylocassis*, *Xenophalium* and *Xenogalea* are in my opinion only of specific rank, and no characters of the radula, protoconch or internal anatomy separate these species into distinct genera.

Semicassis labiata (Perry, 1811) (Fig. 21C–F,H)

Cassidea labiata Perry 1811, pl. 34, fig. 1.

Cassis achatina Lamarck 1816, pl. 407, fig. 1a, b, 'Liste des objets' p. 3; Lamarck 1822b:226; Kiener 1835:37, pl. 13, fig. 24; Deshayes 1843:33; Reeve 1848, *Cassis*, pl. 10, fig. 28a; Krauss 1848:115; Küster 1857:34, pl. 50, figs. 3, 4; Angas 1867:196; Hutton 1873a:20; Hutton 1880:66; GB Sowerby III 1892:23; Pritchard & Gatliff 1900:189.

Cassis zeylanica Lamarck 1822b:226; Kiener 1835:38, pl. 13, fig. 26; Deshayes 1843:33.

Buccinum achatinum. Wood 1828:105, pl. 22, fig. 22.

Cassidea achatina. Swainson 1840:299.

Cassis pyrum var. Küster 1857:29, pl. 49, figs. 3, 4 (in part; references to *C. zeylanica* Lamarck only).

Cassis (Casmaria) achatina. Tryon 1885:278, pl. 8, fig. 95.

Cassis ceylonica (sic). Tate & May 1901:444.

Cassidea labiata. Hedley 1902a:27.

Cassis pirum var. *intercedens* Martens 1904:54, 56, note 12.

Semicassis labiata. Suter in Hutton 1904:75; Moss 1908:23, pl. 5, fig. 6; Beu 1976:421; Wilson 1993:233, pl. 37, fig. 1a,b; Richardson 1997:9; Spencer at al. 2009:204.

Phalium labiatum. Suter 1913:312, pl. 40, fig. 12; Hedley 1918:M67; Bucknill 1924:55, pl. 4, Fig. 10; Coleman 1975:187, fig. 528.

Phalium n. sp. (*labiatum* auct.) Finlay 1926b:400, pl. 20, figs. 62, 63.

Xenogalea labiata. Iredale 1927:347:31, fig. 1; Cotton 1945:251; Macpherson & Gabriel 1962:149, fig. 178; Iredale & McMichael 1962:56; Anderson 1966:243, pl. 10 (egg mass).

Xenogalea insperata Iredale 1927:349, pl. 31, fig. 8; Iredale & McMichael 1962:56.

Xenogalea collactea Finlay 1928:246.

Xenophalium labiatum. Powell 1928:640, figs. 15–17; Powell 1937:74, pl. 12, fig. 21; Penniket & Moon 1970:32, pl. 13, fig. 3.

Xenophalium insperatum. Powell 1928:640, fig. 19.

Cassis achatina craticulata Turton 1932:112 (not *Cassis craticulata* Euthyme, 1884).

Cassis zealanica (sic). Turton 1932:112.

Phalium (Xenogalea) labiatum. var. *iredalei* Bayer 1935:109 (**new synonym**).

Phalium pyrum var. *zeylanica* Bayer 1935:110.

Xenophalium collactea. Powell 1937:74, pl. 12, fig. 23.

Xenogalea inseparata (sic) Cotton 1945:251.

Xenophalium (Xenogalea) labiatum Powell 1946a:77, pl. 12, fig. 21; Powell 1958a:101, pl. 12, fig. 21; Powell 1962:93, pl. 12, fig. 21.

Xenophalium (Xenogalea) collactea Powell 1946a:77, pl. 12, fig. 23; Powell 1958a:101, pl. 12, fig. 23; Powell 1962:93, pl. 12, fig. 23.

Phalium iheringi Carcelles 1953:5, figs. 7–10 (**new synonym**).
Phalium (Xenophalium) labiatum. Abbott 1968:183, pl. 13, figs. 1–5, 17–21; pl. 173; pl. 175.
Xenophalium labiatum labiatum. Powell 1976b:96, pl. 19, fig. 21; Powell 1979:159, pl. 34, figs. 7, 8.
Xenophalium labiatum insperatum. Powell 1976b:93, pl. 19, fig. 23; Powell 1979:159, pl. 34, figs. 9, 10.
Phalium (Casmaria) decipiens Kilburn 1980:195, figs. 7, 8 (**new synonym**).
Casmaria decipiens. Kreipl 1997:43, pl. 15, fig. 44.
Semicassis (Semicassis) labiata labiata. Kreipl 1997:57, pl. 20, fig. 66.
Semicassis (Semicassis) labiata forma *collactea.* Kreipl 1997:57, pl. 20, fig. 66a.
Semicassis (Semicassis) labiata iheringi. Kreipl 1997:57, pl. 20, figs. 67, 67a.
Semicassis (Semicassis) labiata zeylanica. Kreipl 1997:58, pl. 20, figs. 68, 68a.
Semicassis (Semicassis) labiata forma *iredalei.* Kreipl 1997:58, pl. 20, fig. 68b.
Semicassis (Semicassis) labiata. Maxwell 2009:243.

Type material. No type material is known for the taxa proposed by Perry (1811). The Lamarck collection in Geneva contains two specimens (MHNG 1100/99–100; Fig. 21G–I) identified as *Cassis achatina*, and the annotations by Rosalie de Lamarck on Lamarck's copy of *Animaux sans vertèbres* indicate that Lamarck owned two specimens (Y Finet MHNG pers. comm. June 2004). In the opinion of Y Finet, it is difficult to be certain that these two specimens are the original Lamarck syntypes, but as there are no other possible syntypes in the Delessert collection that might have belonged to Lamarck, these specimens are accepted as syntypes. The difficulty is the size—Lamarck stated the height as '2 pouces 2 lignes', which is about 58.5 mm, whereas the two specimens in MHNG are 54.5 and 53.0 mm high. Not enough detailed characters are visible to be able to match either of the specimens with the illustration by Lamarck (1816, pl. 407, fig. 1a, b). However, there is no doubt that specimen MHNG 1100/99 is that illustrated by Kiener (1835, pl. 13, fig. 24). Abbott (1968:186) designated this specimen as the lectotype of *Cassis achatina* Lamarck, 1816. Both Lamarck and Kiener indicated the type locality as 'Nouvelle-Hollande', and the type locality is here designated as Sydney Harbour, New South Wales. In order to attach the name *Cassidea labiata* Perry, 1811 unambiguously to this species, the same specimen, MHNG 1100/99 (Fig. 21C,D), is here designated the neotype of *Cassidea labiata* Perry, 1811. The type material of *Cassis zeylanica* Lamarck was also said by Abbott (1968:187) to be in MHNG. The Lamarck collection in MHNG contains two specimens identified as *Cassis zeylanica* Lamarck (MHNG 1101/3–4; Fig. 21D,E) and again, Rosalie de Lamarck's annotations on Lamarck's copy of *Animaux sans vertèbres* call for two specimens in Lamarck's collection (Y Finet MHNG pers. comm. June 2004). However, again there is little proof that the two segregated specimens are Lamarck's original syntypes, as this species was not illustrated by Lamarck (1816), but both are from the Delessert collection, and one of them appears to be that illustrated by Kiener (1835, pl. 13, fig. 26). Although they are labelled 'Ceylan', as stated by Lamarck (1822b) (that is, Sri Lanka), they are not accompanied by an original Lamarck label. Nevertheless, in the absence of any other possible Lamarck syntypes, these specimens are accepted as the syntypes of *Cassis zeylanica* Lamarck. Lamarck (1822b:226) stated the dimensions as '2 pouces 10 lignes et demie', or about 77.5 mm; MHNG 1101/3 is 76 mm high, and MHNG 1101/4 is 81 mm high. *Xenogalea insperata*, two syntypes AMS C53270, from Sydney Harbour, New South Wales (illustrated by Abbott 1968, pl. 173). *Xenogalea collactea*, holotype AIM AK70851, from Opotiki, Bay of Plenty, with one paratype, AIM AK72554 (not seen). *Phalium labiatum* var. *iredalei*, holotype

RMNH.MOLL.110052, from 'South Africa'; three paratypes RMNH.MOLL.110053, from Port Elizabeth, South Africa; two paratypes RMNH.MOLL.110054, from Port Elizabeth (photographs sent by J Goud RMNH 5 November 2007). *Phalium iheringi*, holotype in Museu de Historia Natural de Montevideo, Uruguay, no. 13805, with two paratypes, nos. 16764, 17797; holotype and paratype no. 17797 from beach, Mar del Plata, Argentina; paratype no. 16764 from 37°38′S, 56°20′W, 84 m, '*Undine*', October 1926 [off Macedo, northern Argentina N of Mar del Plata] (Carcelles 1953; not seen). *Phalium (Casmaria) decipiens* Kilburn, holotype Natal Museum, Pietermaritzburg, NM5422, T2292, from Melville, Natal south coast, South Africa; 4 paratypes examined in Natal Museum, listed by Kilburn (1980:196–197).

Other material examined. **Haweran:** the earliest New Zealand occurrence of *Semicassis labiata* I am aware of is in the Te Piki fauna, road cutting 6 km E of Whangaparaoa, near East Cape, OIS 7 (GS5833, Y14/f7505A, Fig. 21H, one immature specimen, the basis of the record by Richardson 1997:9). I am not aware of any other fossil record.

Distribution. OIS 7–Recent, largely limited to the NE North Island warm province, although rarely extending as far south as the Kapiti Coast, W Wellington (Bracegirdle 2007); Recent in Australia, from southern Queensland (as far north as Moreton Bay; database maps by I Loch, AMS pers. comm.) to NE Victoria and, uncommonly, across the southern coast of Australia to southern Western Australia (Wilson 1993:234); South Africa and southern South America, that is, circum-Southern Ocean.

Dimensions. GS5833, Te Piki (immature): H 31.3, D 20.5 mm; adult Recent specimens: RM370, Mangapai, Northland: H 63.1, D 39.8 mm; RM4971, Waihau Bay, E Bay of Plenty: H 74.8, D 47.7 mm.

Remarks. As with several other circum-Southern Ocean tonnoideans, it seems likely that *Semicassis labiata* occupies the entire Southern Ocean, and the other named, supposedly geographically restricted forms are part of the variation of one species (*S. labiata iheringi* Carcelles, 1953, southern South America; Rios 1994:86, pl. 28, fig. 334; Kreipl 1997:57, pl. 20, figs. 67, 67a; *S. labiata zeylanica* Lamarck, 1822, South Africa; Kilburn & Rippey 1982:72,212, pl. 16, fig. 12a,b; Kreipl 1997:58, pl. 20, figs. 68–68b). However, this needs further research, including a molecular study, before it is accepted, particularly as some Southern Ocean tonnoideans are now known to comprise several distinct species—notably in *Fusitriton*. Specimens of the *zeylanica* form also have a wider groove between the siphonal fasciole and the previous whorl than in Australian–New Zealand specimens of *S. labiata*. The South African form named *Phalium (Casmaria) decipiens* by Kilburn (1980:195, figs. 7, 8; Kreipl 1997, pl. 15, fig. 44) is coloured and sculptured identically to the usual southern Australian and northern New Zealand smooth form of *S. labiata*, and has a very narrow groove between the siphonal fasciole and the previous whorl. It is possibly a synonym of *S. labiata*, based on the form that is common in Australia and New Zealand, but evidently is uncommon in South Africa, although the specimen illustrated by Kreipl (1997, pl. 15, fig. 44) has a larger protoconch than Australasian specimens. I (Beu 1976) pointed out that *S. labiata* is virtually indistinguishable from European fossil specimens usually identified as *Semicassis laevigata* (Defrance, 1817). Landau et al. (2004:48) showed that *S. laevigata* and *S. saburon* (Bruguière, 1792) are distinct species, the Miocene–Pliocene species lacking the obvious spiral grooves of the Pleistocene and Recent species *S. saburon*. In the Australian and New Zealand fauna, the uncommon species *S. labiata* easily is distinguished from the much more abundant *S. pyrum* (Lamarck, 1822) by its smaller size, its narrower, more ovoid shape with a more convex spire outline, its smoother exterior, its more consistently nodulose interior of the outer lip and, in particular, by the much narrower groove separating the siphonal fasciole from the previous whorl. The variation is quite marked in all populations of *S. labiata*, and includes both smooth ('typical *S. labiata*') and nodulose specimens ('*insperata*', '*collactea*'), and specimens with and without short transverse ridges inside the outer lip. The paralectotype of *Cassis achatina*, MHNG 1100/100 (Fig. 21I), is an unusual specimen combining the characters of the typical *labiata* and '*collactea*' forms, with nodules on the periphery of the pale penultimate whorl up until the aperture, then changing on the last whorl to a smooth, brightly coloured surface. Specimens with obvious nodules around the periphery seem mainly to have been collected on soft substrates near rocks, or to wash ashore on sandy beaches, whereas the more common smooth form lives on rocky shores and subtidal rocks. Communal egg-laying by at least seven smooth specimens on subtidal rocks off Sydney (N Coleman pers. comm.), New South Wales, was illustrated by Coleman (1975:187, fig. 528), and the animal illustrated creeping along with foot, siphon and cephalic tentacles expanded on a sand substrate at Jervis Bay, southern New South Wales, in the photograph above (Coleman 1975:187, fig. 527) is the '*insperata*' form of *S. labiata*, rather than *S. pyrum* as identified in the caption. Anderson (1966:243, pl. 10) also described communal egg-laying in this species and illustrated a large communal egg mass.

Semicassis labiata is recorded earliest in New Zealand in the Te Piki fauna (OIS 7), although a small, nodulose form of *S. pyrum* is much more common at Te Piki than *S. labiata*. The phylogenetic relationship between *S. labiata* and the Atlantic and Mediterranean Miocene–Pliocene species *S. laevigata* is very close, but they appear to be distinct species, as *S. labiata* is narrower and still more smoothly oval than *S. laevigata*. The first appearance of *S. labiata* in New Zealand probably is biostratigraphically meaningful, as it was dispersed around the Southern Ocean in the Antarctic Circumpolar Current as planktotrophic larvae from South Africa. However, in New Zealand this species is uncommon everywhere, and it occurs only rarely outside the warm-water NE North Island province, and so will be of biostratigraphical utility only if it should be found in terrace cover-bed faunas in N New Zealand.

An important implication for dispersal times and routes is provided by *Semicassis labiata* appearing in New Zealand only during OIS 7. This is at least 1 m yr after the more strongly sculptured species *S. saburon* had evolved in the North Atlantic–Mediterranean area, during Pleistocene time, whereas the smooth Southern Hemisphere specimens are scarcely distinguishable from the extinct European species *S. laevigata*, last known in early Pleistocene rocks. This suggests that a complex history of stepping-stone dispersal allowed *S. labiata* to evolve during its migration to the Southern Hemisphere; migration evidently did not take place in a single rapid event during one glacial or interglacial period. Migrations of other tonnoideans to and around the Southern Hemisphere possibly occurred in a similar way. *S. laevigata* probably reached the warm southeastern Atlantic (and probably also South Africa) near the end of Pliocene time, along with other Mediterranean–West African tonnoideans known to occur as far south as Angola and Namibia, such as *Charonia lampas* and *Aspa marginata* (Gmelin, 1791) (Beu 2010), before *S. saburon* had evolved in the Mediterranean. In southern Africa and the South Atlantic, it evolved into the sister species *S. labiata*. At some later time, *S. labiata* was dispersed passively as planktotrophic larvae in the Antarctic Circumpolar Current to Western Australia, as Wells & Kilburn (1986) demonstrated for three other restricted South African molluscs, including the tonnoidean *Cabestana africana* (A. Adams, 1855). It might then have taken a significant further period of time for

S. labiata to disperse to eastern Australia and New Zealand. Other, smaller islands along the way, such as St Paul and Amsterdam Islands in the southern Indian Ocean, have certainly provided stepping stones where larvae have been able to survive and breed, for some tonnoideans such as *Argobuccinum*, *Charonia lampas* and both Recent *Ranella* species (Arnaud & Beurois 1972). The enormously long planktotrophic larval lives that have been evolved by tonnoideans (as well as Architectonicidae) to allow larval dispersal in ocean currents over wide distances are exemplified by *Fustriton oregonensis* (Redfield, 1846), which Strathman & Strathman (2007) have shown can survive as veligers for at least 4.5 yr. This provides plenty of scope for *Semicassis labiata* and *Argobuccinum pustulosum* (Lightfoot, 1786) to be dispersed around the Southern Ocean in the Antarctic Circumpolar Current.

Family Ranellidae

Genus ***Argobuccinum*** Herrmannsen, 1846

Argobuccinum Herrmannsen 1846:77. Type species (by original designation): *Murex argus* Gmelin, 1791 (=*Buccinum pustulosum* Lightfoot, 1786), middle Miocene to Recent, circum-Southern Ocean.
Gondwanula Finlay 1926b:399. Type species (by original designation): *Bursa tumida* Dunker, 1862 (= *Buccinum pustulosum* Lightfoot, 1786).
Mediargo Terry 1968:42. Type species (by original designation): *Gyrineum mediocre* Dall, 1909, middle Miocene–Pliocene, western United Sates of America.

Remarks. *Mediargo* was proposed by Terry (1968:42) for NW American fossil species that are slightly smaller and more weakly sculptured than species previously referred to *Argobuccinum*. However, as species such as '*Mediargo*' *mediocris* (Dall, 1909) are the only known possible ancestors of the Pliocene–Recent species of *Argobuccinum*, this seems to be a single clade, and in my opinion *Mediargo* is a synonym of *Argobuccinum*.

Argobuccinum pustulosum (Lightfoot, 1786) (Fig. 22A–E)

Buccinum pustulosum Lightfoot 1786:88; Dall 1921:125.
Murex argus Gmelin 1791:3547; Dillwyn 1817:694.
Tritonium argo-buccinum Röding 1798:127.
Cassidea tuberculata Fischer von Waldheim, 1807:185; Ivanov & Kantor, 1991:82; Ivanov et al. 1993:77, pl. 7, fig. 4.
Ranella polyzonalis Lamarck 1816, pl. 414, fig. 3a,b; '*Liste des objets*':4.
Ranella argus. Lamarck 1822b:151; Kiener 1841:31, pl. 8, fig. 1; Reeve 1844, pl. 3, fig. 12; Küster & Kobelt 1870:125; 1878:329, pl. 37, figs. 5, 6.
Triton ranelliformis King 1832:347.
Ranella vexillum GB Sowerby II 1835, pl. 84, fig. 3; Menke 1843:24; Reeve 1844, pl. 3, fig. 13.
Ranella kingii Orbigny 1841a:451 (unnecessary new name for *Triton ranelliformis* King, 1832, not a homonym of *Triton ranelloides* Reeve, 1844).
Argobuccinum argus. Herrmannsen 1846:77; Suter 1913:309, pl. 43, fig. 4; Dell 1963b:218, pl. 2, figs. 1, 5; JT Smith 1970:458, pl. 39, figs. 7, 10–12; Arnaud & Beurois 1972:869–870.
Ranella ampullacea Valenciennes 1858:759,762 (synonym according to Kantor & Sysoev 2002:121, figs. 1A,B).
Bursa tumida Dunker 1862:239, Dunker 1863:56, pl. 18, figs. 8, 9.
Bursa zelebori Dunker 1863:57 (*nomen nudum*).
Bursa (Apollon) proditor Frauenfeld 1865:894.
Bursa (Apollon) prodita. Frauenfeld 1867:4, pl. 1, figs. 1a, 1b.
Ranella (Argobuccinum) argus. Tryon 1880b:44, pl. 24, fig. 61; Watson 1886:400.

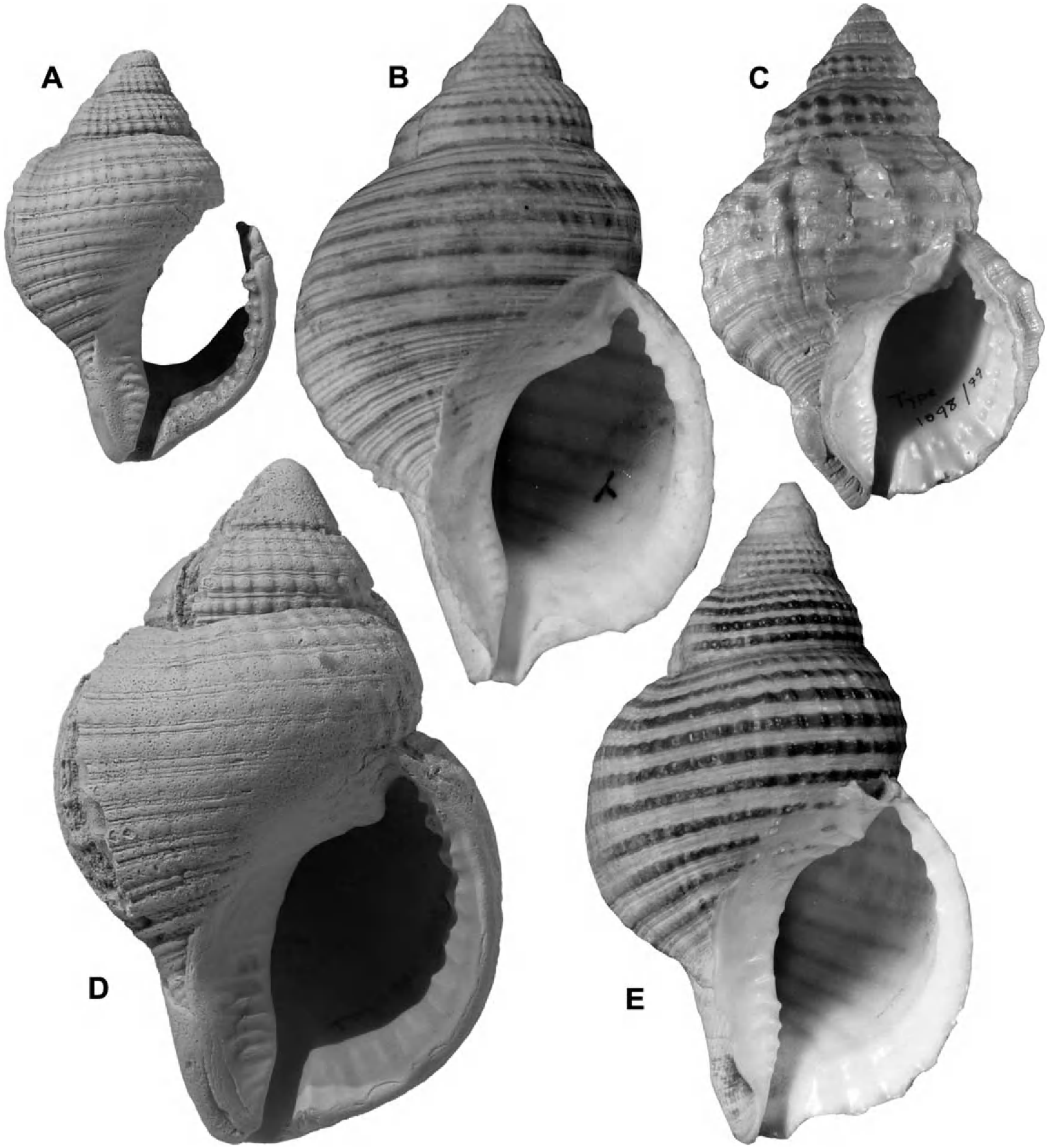

Fig. 22 *Argobuccinum pustulosum* (Lightfoot). (A) GS4175, Q21/f6499, Denby Shellbed (Haweran, OIS 7), Waihi Beach, Hawera, earliest New Zealand record; height 57.7 mm. (B) BMNH 1973113, Dunker's illustrated syntype of *Bursa tumida* Dunker, 1862, "New Zealand", height 92.6 mm. (C) holotype of *Ranella polyzonalis* Lamarck, 1816, MHNG 1098/79, neotype of *Buccinum pustulosum* Lightfoot, 1786, of *Murex argus* Gmelin, 1791, and of *Tritonium argobuccinum* Röding, 1798; type locality Jeffreys Bay, South Africa; height 71 mm. (D) TM3992, GS5674, J41/f8710, Hillgrove Formation (Last Interglacial, OIS 5e), Old Rifle Butts, S of Cape Wanbrow, S Oamaru; height 96.2 mm. (E) BMNH 1950.11.28.17, largest syntype of *Ranella vexillum* G. B. Sowerby I, 1835, "Chiloé, Concepción", Chile; height 94.9 mm.

Ranella tristanensis 'Gray' Paetel 1888:106 (*nomen nudum*).
Argobuccinum tumidum. Hedley 1913:297; Fleming 1952:79,84; JT Smith 1970:469, pl. 39, figs. 1, 3; pl. 41, figs. 1–4, 8, 9; Powell 1979:166, pl. 12, fig. 5; Maxwell 2009:243.
Gondwanula tumida. Finlay 1926b:399.
Argobuccinum (Argobuccinum) ranelliformis ranelliformis (sic). Dell 1963b:219, pl. 2, Fig. 2.
Argobuccinum (Argobuccinum) ranelliformis (sic) *tumidum*. Dell 1963b:220, text-Fig. 1.2, pl. 1, figs. 1–4.
Argobuccinum (Argobuccinum) proditor proditor. Dell 1963b:221, pl. 2, fig. 4; Beu 1985:56.
Argobuccinum (Argobuccinum) proditor tristanensis (sic). Dell 1963b:222, pl. 2, figs. 3, 6.
Argobuccinum pustulosum. Rehder 1967:16; Kilburn & Rippey 1982:75, pl. 17, fig. 1a,b; Kilburn 1984:8, pl. Af, h, g.; Wilson 1993:241, pl. 41, fig. 8.
Argobuccinum ranelliforme. JT Smith 1970:462, pl. 39, figs. 2, 4, 6, 9; pl. 40, figs. 2, 6, 7, 10–12.
Argobuccinum tristanense. JT Smith 1970:466, pl. 39, figs. 5, 8: pl. 40, fig. 1.
Argobuccinum proditor. JT Smith 1970:468, pl. 41, figs. 5–7, 10.
Argobuccinum ranelliforme ranelliforme. Arnaud & Beurois 1972:869–870.
Argobuccinum ranelliforme tumidum. Arnaud & Beurois 1972:869–870.
Argobuccinum ranelliforme proditor. Arnaud & Beurois 1972:866, figs. 1, 4; pl. 1, figs. 1, 4 (=*tristanense* Dell, 1963; not pl. 1, fig. 3a,b, =*Ranella gemmifera* Euthyme, 1886).
Argobuccinum (Argobuccinum) proditor tristanense. Beu 1985a:56.
Argobuccinum (Argobuccinum) pustulosum pustulosum. Beu 1985:56, fig. 4.
Argobuccinum (Argobuccinum) pustulosum ranelliforme. Beu 1985:56.
Agrobuccinum (Argobuccinum) pustulosum tumidum. Beu 1985:56.
Argobuccinum (Argobuccinum) pustulosum. Henning & Hemmen 1993:13, pl. 1, fig. 1.
Argobuccinum (Argobuccinum) ranelliforme. Henning & Hemmen 1993:14, pl. 1, fig. 2.
Argobuccinum (Argobuccinum) tumidum. Henning & Hemmen 1993:15, pl. 1, fig. 3.
Argobuccinum (Argobuccinum) proditor. Henning & Hemmen 1993:15, pl. 1, fig. 4.
Argobuccinum (Argobuccinum) tristanense. Henning & Hemmen 1993:16, pl. 1, fig. 5.
Argobuccinum pustulosum tumidum. Spencer et al. 2009:206.

Type material. No type material is known for taxa proposed by Lightfoot (1786), Gmelin (1791) or Röding (1798). *Cassidea tuberculata*, lectotype designated by Ivanov & Kantor (1991:82–83), Zoological Museum, Moscow University no. ZMUM N L-518, without locality; illustrated by Ivanov *et al.* (1993), pl. 7, fig. 4), a typical if rather tall and narrow specimen of *Argobuccinum pustulosum* (not seen). *Ranella polyzonalis* Lamarck, holotype MHNG 1098/79 (Fig. 22C), now labelled '*Ranella argus* Lamarck', without locality. The specimen closely matches the illustration by Lamarck (1816, pl. 414, fig. 3a,b). The type locality was designated by me (Beu 2010) as Jeffreys Bay, eastern Cape Province, South Africa. To attach all earlier names unambiguously to the present species, I (Beu 2010) designated the holotype of *Ranella polyzonalis* Lamarck as the neotype of *Buccinum pustulosum* Lightfoot, 1786, the neotype of *Murex argus* Gmelin, 1791, and the neotype of *Tritonium argobuccinum* Röding, 1798. *Triton ranelliforme* King, five unregistered presumed syntypes in BMNH, two probable syntypes presented by Captain PP King and three 'possible' syntypes from the Broderip collection (labelled B2115 or B2252 inside the aperture), all unlocalized, stated by King (1832:347) to be from 'Sinum Peñas et oram occidentalum America meridionalis'. *Ranella ampullacea* Valenciennes, one syntype in MNHN (Kantor & Sysoev 2002, fig. 1A,B), supposedly from the 'Straits of Tartary', between Sakhalin and eastern Russia; a wrongly localized specimen of the South American *vexillum* form of *A. pustulosum*, type locality designated by me (Beu 2010) as Chiloé Island, Chile. *Ranella vexillum* G. B. Sowerby II, three syntypes BMNH 1950.11.28.17–19, from 'Chilöe Id., Concepción, rocky places, 3–5 fathoms' [6–10 m]; the medium-sized syntype (Fig. 22E; H 85.0, D 50.0 mm) is the specimen illustrated by both GB Sowerby II (1835, pl. 84, fig. 3) and Reeve (1844, pl. 3, Fig. 13). *Ranella kingii* d'Orbigny, three syntypes BMNH 1854.12.4.533, from Isla Mocha, Chile. *Bursa tumida* Dunker, 1862, three syntypes BMNH 1973113, from 'New Zealand'; the largest specimen (Fig. 22B) is the one illustrated by Dunker (1863, in 1863–1864, pl. 18, figs. 8, 9). *Ranella (Apollon) proditor* Frauenfeld, five syntypes NHMW 689–693, from St Paul Island; the largest syntype (NHMW 689, H 100.9, D 56.6 mm) is the specimen illustrated beautifully by Frauenfeld (1867, pl. 1, fig. 1a,b). *Argobuccinum proditor tristanense* Dell, holotype BMNH 1887.2.9.1221, collected on the shore at Tristan de Cunha Island by the '*Challenger*' Expedition, with four lots of paratypes.

Other material examined. **Haweran:** the oldest New Zealand fossil record is from Denby Shellbed (OIS 7), Waihi Beach, Hawera (GS4175 re-collection, Q21/f6499, two specimens from different collectors; Fig. 22A); thereafter common in OIS 5e shellbeds, particularly in southern New Zealand (specimens in GNS reference collection: GS9727, N33/f7580, terrace above Cranky Toms Creek, Motunau, N Canterbury; GS14842, N34/f094, Motunau terrace, N Canterbury, OIS 5e; common in GS5674, J41/f8710, Hillgrove Formation, Old Rifle Butts, S of Cape Wanbrow, Oamaru, OIS 5e (Fig. 22D; see Worthy & Grant-Mackie 2003); GS158, O32/f9038; GS167, J39/f7477; & GS14697, O32/f0108, Haumuri Bluff high terrace, Marlborough, OIS 5c?) and in many younger deposits (e.g. GS13796, W21/f057; GS13937, W21/f058, terrace at shelter hut, Cape Kidnappers, Hawke's Bay, 2500 yr old; GS12254, CH/f0532, Owenga 'shell bank', Chatham Island, Holocene; and several other Holocene localities). The young radiocarbon ages (22,476 ± 352 – 33,711 ± 1215 ^{14}C yr) for the avifauna of Hillgrove Formation, Oamaru, listed by Worthy & Grant-Mackie (2003) are either minimum ages, or imply that the non-marine, vertebrate-rich upper part of this formation is much younger than the basal part, with marine fossils, as this youngest marine terrace along the Otago coast is likely to have been cut during OIS 5e (ca 125,000–130,000 yr), like all the main uplifted terraces around New Zealand and much of the rest of the world.

Distribution. OIS 7–Recent, in New Zealand. Recent specimens occur around the entire Southern Ocean, in South Africa, including up the west coast north of Capetown, at St Paul and Amsterdam Islands, at Kerguelen, around southern South America from central Chile (Talcahuano, 36°40′S; Dell 1963b:220; but Aldea & Valdovinos [2005] recorded it only as far north as Isla Santa María, 37°00′12″S) south to Cape Horn and north to central Argentina, along the southern coasts of Australia in South Australia, Victoria and Tasmania, and throughout New Zealand (where, however, it is more common in the south) and the Chatham Islands. JT Smith (1970:465) recorded a single fossil specimen in Chile from Navidad Formation (traditionally dated as middle or late Miocene, but concluded by Finger et al. [2007] to be reworked Oligocene to early Miocene fossils in rocks of late Miocene–early Pliocene age). However, as there are no other records from Navidad Formation, particularly in the large collections in the Museo Nacional de Historia Natural, Santiago, the specimen Smith cited possibly bears an incorrect locality. Fossils are common in later Pliocene rocks (at La Cueva and Coquimbo) and are common in Pleistocene terrace cover beds in Chile (Herm 1969:71; JT Smith 1970).

Dimensions. Largest New Zealand Recent specimens, RM5691, 120 m, off Taiaroa Head, E Otago: H 135.1, D 81.2 mm; RM4265, beach, Cape Campbell, Marlborough: H 128.1, D 74.1; NMNZ M.19477, Foveaux Strait: H 136.4 mm; large fossil, GS5674, TM3992, Hillgrove Formation, Old Rifle Butts, South Oamaru: H 96.2, D 62.7 mm; GS4175 re-collection, Q21/f6499, Denby Shellbed, Hawera, OIS 7: H 57.7, D 37.7 mm; *Bursa tumida* Dunker, syntypes: H 92.6, D 56.5 mm; H 91.2, D 55.6 mm; H 81.2, D 53.2 mm; *Ranella vexillum* Sowerby, syntypes: H 94.9, D 58.3 mm; H 85.0, D 50.0 mm; H 67.3, D 38.4 mm; *Argobucinum proditor tristanensis* Dell, holotype: H 53.4, D 29.8 mm; largest paratype: H 74.9, D 36.2 mm.

Remarks. The taxonomy of the Recent Southern Ocean *Argobuccinum* species has long been debated, because of the great similarity of the several named forms around the Southern Ocean and their intergradation in most shell characters. Opinions have ranged from a single variable species (Suter 1913, and several earlier authors; Beu 2010) to various combinations of species and geographical subspecies at each of the separate landmasses and islands (Dell 1963b; JT Smith 1970; Arnaud & Beurois 1972). The overlap of characters seen when a large collection is assembled seems to encompass all named forms, and I tentatively consider them all to be conspecific with *Argobuccinum pustulosum*, awaiting a study of DNA sequences. The only other realistic possibility is that *A. pustulosum* (South Africa), *A.ranelliforme* (King, 1832) (South America), *A. tumidum* (Dunker, 1862) (New Zealand and S Australia), *A. proditor* (Frauenfeld, 1865) (St Paul & Amsterdam Islands) and *A. tristanense* Dell, 1963 (Tristan da Cuñha & Nightingale I.) are distinct species.

Argobuccinum pustulosum is a large, robust shell, which preserves well in terrace cover beds (and is common in places, notably along the SE South Island) even when their fauna consists of few, abraded shells. Among the New Zealand late Neogene and Recent Ranellidae, it is easily recognized by its low spire and short, wide shape, its evenly inflated last whorl, its low varices (wider than they are high) at about each 180–190° around the shell, that is, almost aligned up the opposing sides of the spire, and its large, subcircular, weakly armed aperture. The exterior sculpture consists mainly of many low, narrow, finely nodulose spiral cords, although some specimens have several to many small nodules on one or two cords around the periphery, and in a few specimens quite coarse nodules are present over most of the exterior, so that these closely resemble South African specimens of the typical form of *A. pustulosum*. Fresh shells, including some late Haweran fossils, have a marbled red-brown and blackish colour pattern that becomes speckled with white when the nodules are abraded. Dell (1963b) recorded fossil specimens from a few localities in New Zealand. Subsequent improved dating of these faunas has shown that the sole record older than OIS 5e is that from Denby Shellbed, Hawera (OIS 7). *Argobuccinum pustulosum* is probably useful for segregating terrace faunas older than OIS 5e (lacking *Argobuccinum*) and younger than OIS 7 (with *Argobuccinum*). As with *Semicassis labiata*, this is probably a biostratigraphically useful first appearance, as *Argobuccinum pustulosum* was dispersed around the Southern Ocean (originally from South America; the genus evolved in the North Pacific) as planktotrophic larvae in the Antarctic Circumpolar Current, apparently during glacial OIS 8, but evidently was rare in New Zealand (or occurred mainly in the subantarctic zone to the south?) before OIS 5e.

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