Fossil vesicomyid bivalves from Miocene hydrocarbon seep sites, North Island, New Zealand

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Two fossil species of vesicomyids are described from Lower to Middle Miocene hydrocarbon seep carbonates in eastern North Island, New Zealand. One elongate species is proposed as a new genus and species: *Notocalyptogena neozelandica*. The other species probably belongs to the genus *Pliocardia*, but due to poor preservation is not identified further. The composition of this Miocene vesicomyid seep fauna differs from that found in modern New Zealand seeps located on the offshore Hikurangi convergent margin, which contain the genera *Calyptogena*, *Archivesica*, and *Isorropodon*. The fossil fauna went extinct locally after the Middle Miocene and has been since replaced by the modern vesicomyid taxa.

Key words: Mollusca, Bivalvia, Vesicomyidae, hydrocarbon seep, Miocene, New Zealand.

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Introduction

The bivalve family Vesicomyidae is a characteristic and species-rich molluscan taxon among the modern chemosynthesis-based fauna from hydrocarbon seeps (e.g., Smith and Baco 2003; Levin 2005; Taylor and Glover 2010; Kiel 2010). For some time the taxonomy of the family has been in a state of flux with, for example, some authors placing all large vesicomyid species in the genus *Calyptogena* (e.g., Boss and Turner 1980; Okutani et al. 2000). However, recent detailed work on shell and soft part morphology, combined with molecular data, has resolved a number of well characterized genera (Krylova and Sahling 2006, 2010; Amano and Kiel 2007; Krylova and Cosel 2011). Moreover, Krylova and Sahling (2010) subdivided Vesicomyidae into two subfamilies: Vesicomyinae and Pliocardiinae. The subfamily Vesicomyinae comprises the small-sized genus *Vesicomya* only; the subfamily Pliocardiinae contains medium to large sized genera with reduced guts and thiotrophic bacterial symbionts in their gills (e.g., Dubilier et al. 2008). The majority of occurrences of modern and fossil vesicomyid species are from the northern hemisphere, with few data points from high southern latitudes, which is likely an artifact of research effort rather than true distributional bias.

One southern high latitude area for which there are records of fossil and modern vesicomyids is New Zealand. Lewis and Marshall (1996) first described and illustrated modern vesicomyids from hydrocarbon seeps of the Hikurangi margin, offshore eastern North Island. They recorded *Calyptogena* spp. A, B, C, and *Vesicomya* sp. While it is evident that *Calyptogena* sp. A should be included in *Calyptogena* sensu stricto, a review of this genus by Krylova and Sahling (2006) did not consider the New Zealand records. Campbell et al. (2010) also illustrated *Calyptogena* sp. and another vesicomyid from the Hikurangi margin deposits. Of these, their *Calyptogena* sp. resembles *Calyptogena* sp. A noted by Lewis and Marshall (1996).

Many inferred chemosynthesis-based fossils also are known from Miocene hydrocarbon seep deposits in eastern North Island. McKay (1877a, b) was the first to describe these geographically isolated carbonates within voluminous mudstones, and noted that they contained coquinas of fossil mussels. The carbonates were recognized in early geological mapping of the region (Adams 1910; Henderson and Ong-

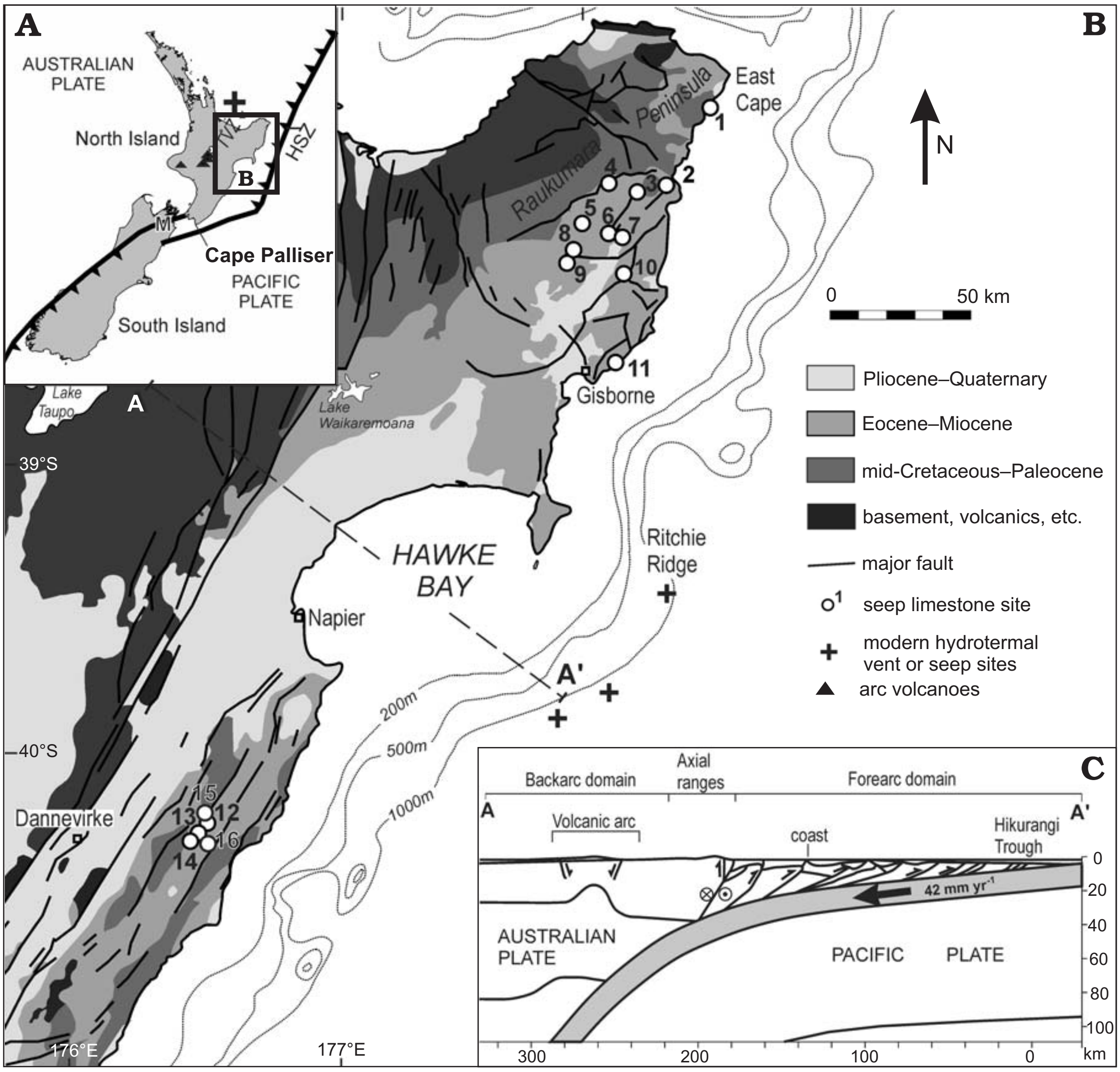

Fig. 1. Geological setting of the Miocene seep sites and fossil localities. **A**. Boundary between the Australian and Pacific Plates, position of the Hikurangi subduction zone (HSZ) and arc volcanoes of the Taupo Volcanic Zone (TVZ); M, Marlborough. **B**. Overview of the geology of the East Coast centered around Hawke's Bay, North Island, New Zealand, showing locations of known Miocene hydrocarbon seep sites (numbered circles). 1–11 = northern sites: 1, Waiapu; 2, Waipiro; 3, Karikarihuata; 4, Bexhaven; 5, Tauwharepare; 6, Puketawa; 7, Totaranui; 8, Moonlight North; 9, Rocky Knob; 10, Waikairo; 11, Turihaua. 12–16 = southern sites: 12, Wanstead; 13, Ugly Hill; 14, Haunui; 15, Ngawaka; 16, Wilder. The fossil vesicomyids described in this study are from fossil seep locations 4, 6, 8, 9, 12, 13, and 14. C. Cross-section (modified from Barnes 2010) showing transpressive subduction of the Pacific Plate beneath the Australian Plate, and relationships of tectonic elements of the northern New Zealand plate margin (see Campbell et al. 2008 and Barnes et al. 2010 for further details on geologic context).

ley 1920), and termed "*Modiolus* limestone" by Ongley and MacPherson (1928). The first stratigraphic grouping of these deep-water carbonates was made by Kamp and Nelson (1988) in a compendium of limestone occurrences from the Neogene plate margin of New Zealand, in which they were informally dubbed the "Moonlight limestone" after a nearby sheep station. Beu and Maxwell (1990) noted that the Moonlight deposits occur widely in the Miocene East Coast Basin (cf. Field et al. 1997) of eastern North Island, as isolated pods from 10–100 m across. They recorded a mytilid resembling *Idasola*, *Lucinoma* aff. *taylori*, trochid and lepetellid gastropods. However, they did not comment on any other taxa, including vesicomyids, from these sites. Mazengarb et al. (1991) formally elevated the scattered Moonlight/*Modiolus* limestone occurrences to formation status, describing them collectively as the Bexhaven Limestone. These limestone lenses occur in deep-water massive mudstone deposits of the Tolaga Group (Early to Late Miocene; Mazengarb and Speden 2000) north of Gisborne. Similar limestones also have been reported from the southern Hawke's Bay area, which were mapped as the Ihungia Limestone by Lillie (1953).

Campbell et al. (2008) established that the Bexhaven and Ihungia limestone deposits, from north and south of Hawke's Bay, respectively, are hydrocarbon seep-related. The 14 reported fossil seep carbonate deposits developed during the Early to Late Miocene, when the modern convergent plate boundary was initiated offshore eastern North Island, and are preserved today in deformed and uplifted deep-marine forearc strata for 300 km along the continental margin, from East Cape to Dannevirke (Fig. 1). Subsequent study of the Miocene seep limestone localities from New Zealand has recognized 16 sites, and described the petrographic, stable isotopic and paleontological character of several of the deposits (Ewen 2009; Troup 2010; Saether et al. 2010a, b, 2012; Saether 2011).

Campbell et al. (2008) and Saether (2011) illustrated fossil vesicomyids from seven locations in the Hawke's Bay area (Fig. 1), and briefly compared them with the modern vesicomyids offshore. However, these fossil vesicomyids have never been formally studied. In this paper, we describe the vesicomyids from Lower to Middle Miocene seep sites in the Hawke's Bay area. We also discuss the biogeographic significance of these species by comparing them with the undescribed modern seep fauna offshore.

Institutional abbreviations.—AU, Paleontology Collection, School of Environment, UOA; UOA L, bivalve specimen number, Paleontology Collection, School of Environment, UOA; GNS, GNS Science, Lower Hutt, New Zealand; NMNZ, Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand; UOA, University of Auckland, Auckland, New Zealand.

Other abbreviations.—AL, anterior length; H, height; L, length; W, width; Y and U, map codes in New Zealand.

Material

The vesicomyid specimens described herein were collected from the geographically isolated Lower to Middle Miocene deep-water seep limestone deposits to the north of Gisborne and east of Dannevirke, East Coast Basin, North Island, New Zealand (Fig. 1, Table 1). In the east of Dannevirke area, vesicomyids were collected from the Lower Miocene Ihungia Limestone at the Ugly Hill, Wanstead, and Haunui seep fossil localities; north of Gisborne, vesicomyid specimens were collected from the Lower to Middle Miocene Bexhaven Limestone seep sites at Bexhaven, Puketawa, Moonlight North, and Rocky Knob localities. Foraminiferal data (e.g., Hayward 1986) and lithological comparison to dredgings from modern NZ seeps (Saether et al. 2010b) suggest that these vesicomyids likely occupied seep environments at roughly 500–2000 m depth in the Miocene. The lithological, stable isotopic and faunal character of these fossil seep deposits have been described in detail elsewhere (Campbell et al. 2008; Saether et al. 2010a, b, 2012; Saether 2011).

All fossil localities of the illustrated Miocene specimens (e.g., Y16/f1059, U23/f267) are registered in the New Zealand Fossil Record File database (http://www.fred.org.nz) jointly administered by GNS Science and the New Zealand Geoscience Society. Details of comparative modern vesicomyid specimens from New Zealand are shown in Table 1.

Table 1. Collection and storage details of material discussed herein.

Specimens	Collection and storage institution
Fossils	by the authors in February 2012, UOA
Fossils	by the geology program, School of Environment, UOA
Fossils	by UOA paleontologists between 1997–2010; UOA
Fossils	by GNS Science
Modern	by 2007 joint German-New Zealand NEW VENTS Hikurangi margin cruise with the R/V SONNE; UOA
Modern	NMNZ

Systematic paleontology

Class Bivalvia Linnaeus, 1758

Subclass Heterodonta Neumayr, 1884

Family Vesicomyidae Dall and Simpson, 1901

Subfamily Pliocardiinae Woodring, 1925

?Genus *Pliocardia* Woodring, 1925

Type species: *Anomalocardia bowdeniana* Dall, 1903; Bowden Formation, Late Pliocene, Bowden, Jamaica.

Pliocardia? sp.

Fig. 2A–C.

Material.—Four specimens from Moonlight North (locality Y16/f1059, collection AU19982, specimen numbers UOA L4587, UOA L4588, UOA L4589, UOA L4590); Lower to Middle Miocene, Bexhaven Limestone.

Description.—Shell medium size (L up to 36.2 mm), quadrate-ovate (H/L = 0.71–0.81), moderately inflated (W/L = 0.50–0.59), shell material partly to wholly absent in all specimens; surface sculpture unknown except for faint growth lines. Blunt ridge running from beak to postero-ventral corner. Beak prominent, prosogyrate, situated anteriorly at

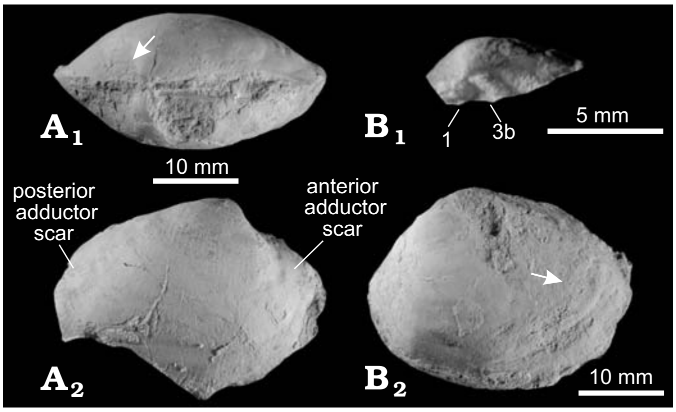

Fig. 2. Vesicomyid bivalve *Pliocardia*? sp. from Moonlight North (Y16/f1059), Early to Middle Miocene. **A**. UOA L4587. Dorsal view of articulated internal mould (A_1), arrow shows lunular incision. Internal mould of right valve (A_2), showing anterior adductor scar and posterior adductor scar. **B**. UOA L4588. Right valve of hinge plate (B_1), anterior tooth is not preserved. Left valve (B_2), internal mould, arrow shows pallial sinus.

24–27% along shell length from anterior margin. Antero-dorsal margin short and broadly arcuate; postero-dorsal margin straight to gently convex, continuing to subtruncated posterior margin; ventral margin usually moderately convex. Lunular incision weakly visible in dorsal view; large, deep grooves flanking central ligamental area along postero-dorsal margin, suggesting ligament external. Hinge plate of right valve narrow, with very thin ventral tooth (1); rather strong posterior tooth (3b); anterior cardinal tooth (3a?) obscure. Anterior adductor muscle scar ovate; posterior muscle scar subquadrate. Pallial sinus indistinct and shallow.

Dimensions.—See Table 2.

Table 2. Measurements of *Pliocardia*? sp. Abbreviations: AL, anterior length (* distance of umbo from anteior margin); H, height; L, length; W, width (** width of articulated shell).

UOA specimen	L (mm)	H (mm)	AL (mm)*	W (mm)**	H/L	L/H	AL/L	Valve
L4587	29.2	21.8	6.9	14.6	0.75	1.34	0.24	both
L4588	28.8	21.7	7.8	–	0.74	1.33	0.27	left
L4589	36.2	29.4	8.7	–	0.81	1.23	0.24	right
L4590	11.2	9.0	3.0	6.2	0.80	1.24	0.27	both

Discussion.—From its size, blunt ridge, lunular incision, right valve hinge dentition and pallial sinus, this species probably represents a new species in the genus *Pliocardia* Woodring, 1925, which was redefined by Krylova and Janssen (2006). However, until more details are known about the external shell and the left valve dentition we refrain from naming a new species.

Our species resembles *Pliocardia kawadai* (Aoki, 1954) from the Lower to Middle Miocene in Japan (see Amano and Kiel 2012) in having a similar size and outline. However, *P. kawadai* has more inflated valves, a radial depression, and a V-shaped pallial sinus.

Genus *Notocalyptogena* nov.

Etymology: A combination of Greek *notos*, south and the genus *Calyptogena*.

Type species: *Notocalyptogena neozelandica* sp. nov.; see below.

Species included: Only type species.

Diagnosis.—Shell medium size, moderately inflated, elongate; sculpture smooth except for growth lines; blunt external ridge running from beak to posterior corner. Radial internal ridge distinct, running from beak to postero-ventral corner and in contact with posterior adductor scar. Hinge plate narrow. Subumbonal pit absent. Hinge of right valve with three cardinal teeth; anterior tooth (3a) along postero-dorsal margin; middle tooth (1) strong, oblique anteriorly; posterior tooth (3b) vertical or slightly anteriorly inclined; deeply depressed or flat area behind posterior cardinal tooth. Hinge of left valve with three cardinal teeth; anterior tooth (2a) long, connecting with middle stout tooth (2b); posterior tooth (4b) also rather stout. Pallial line entire.

Discussion.—*Notocalyptogena* gen. et sp. nov. closely resembles *Calyptogena* Dall, 1891 in its size, elongate outline, lack of subumbonal pit, and integripalliate condition. However, this new genus differs from *Calyptogena* by having a narrow hinge plate without a U-shaped tooth overhanging a ventral tooth, and by having a depressed or flat area behind the 3b tooth in the right valve. Moreover, the strong internal ridge from the beak to posterior ventral corner of this new genus is not seen in *Calyptogena*. *Notocalyptogena* gen. nov. shares a narrow hinge plate, elongate shell shape, lack of subumbonal pit and an entire pallial line with *Christineconcha* Krylova and Cosel, 2011. However, the right valve hinge of *Christineconcha* has a much shorter 3a tooth and teeth that radiate less around the umbo. *Elenaconcha* Cosel and Olu, 2009 can be easily distinguished from *Notocalyptogena* gen. nov. by having a lunule, a subumbonal pit and multiple "posterior nymphal ridges". Although *Hubertschenckia* Takeda, 1953 has a similar arrangement of cardinal teeth to *Notocalyptogena* gen. nov., the former genus also has a subumbonal pit and pallial sinus, which are never seen in the new genus. *Adulomya* Kuroda, 1931 shares an elongate shell and a lack of a subumbonal pit with *Notocalyptogena* gen. nov. However, *Adulomya* differs from the new genus by having two radiating cardinal teeth in the right valve.

Stratigraphic and geographic range.—Lower Miocene Ihungia Limestone and Lower to Middle Miocene, Bexhaven Limestone, North Island, New Zealand.

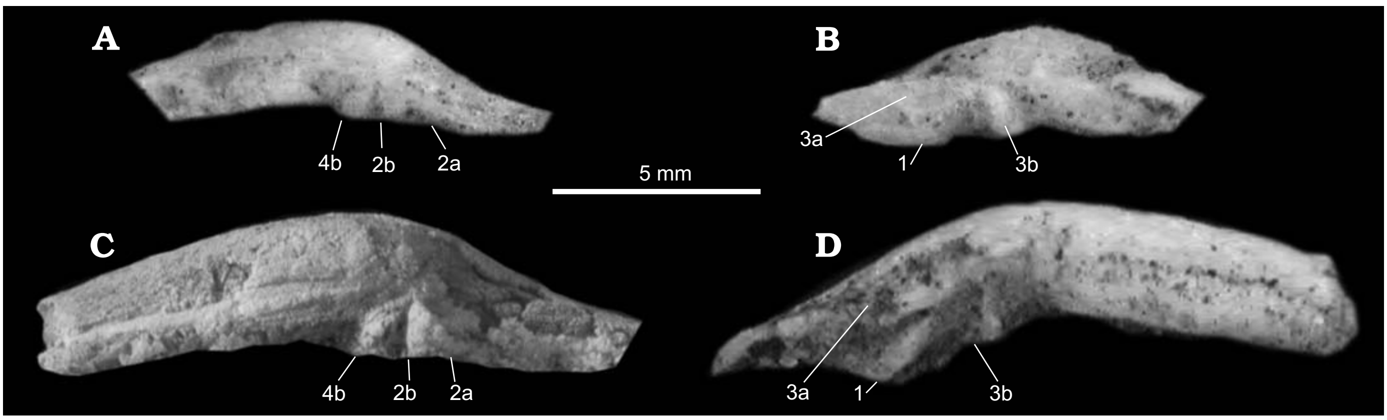

Fig. 3. Hinge of vesicomyid bivalve *Notocalyptogena neozelandica* gen. et sp. nov. from Ugly Hill (U23/f267 for A, B, D; U23/f266 for C), Early Miocene. Left (**A**, **C**) and right (**B**, **D**) valve hinge. **A**. UOA L4606. **B**. UOA L4605. **C**. UOA L4596, paratype. **D**. UOA L4593, paratype.

Notocalyptogena neozelandica sp. nov.

Figs. 3A–D, 4A–G.

Etymology: Named for the country of origin.

Type material: Holotype UOA L4591 (Fig. 4D). Paratypes: UOA L4592 (Fig. 4G), UOA L4593 (Fig. 3D), UOA L4594 (Fig. 4F), UOA L4595 (Fig. 4C) from locality U23/f267, collection AU19983; UOA L4596 (Fig. 3C) from locality U23/f266, collection AU19664.

Type horizon: Ihungia Limestone, Lower Miocene.

Type locality: Ugly Hill, North Island, New Zealand.

Material.—11 poorly to well preserved specimens from Ugly Hill: U23/f267, AU19983. Among them, the specimens catalogued as UOA L4606 (Fig. 3A), UOA L4605 (Fig. 3B), UOA L4607 (Fig. 4A), UOA L4600 (Fig. 4E) show the internal structure of shell. The specimen as UOA L4603 (Fig. 4B) shows the surface of left valve.

Dimensions.—See Table 3.

Diagnosis.—As for the genus.

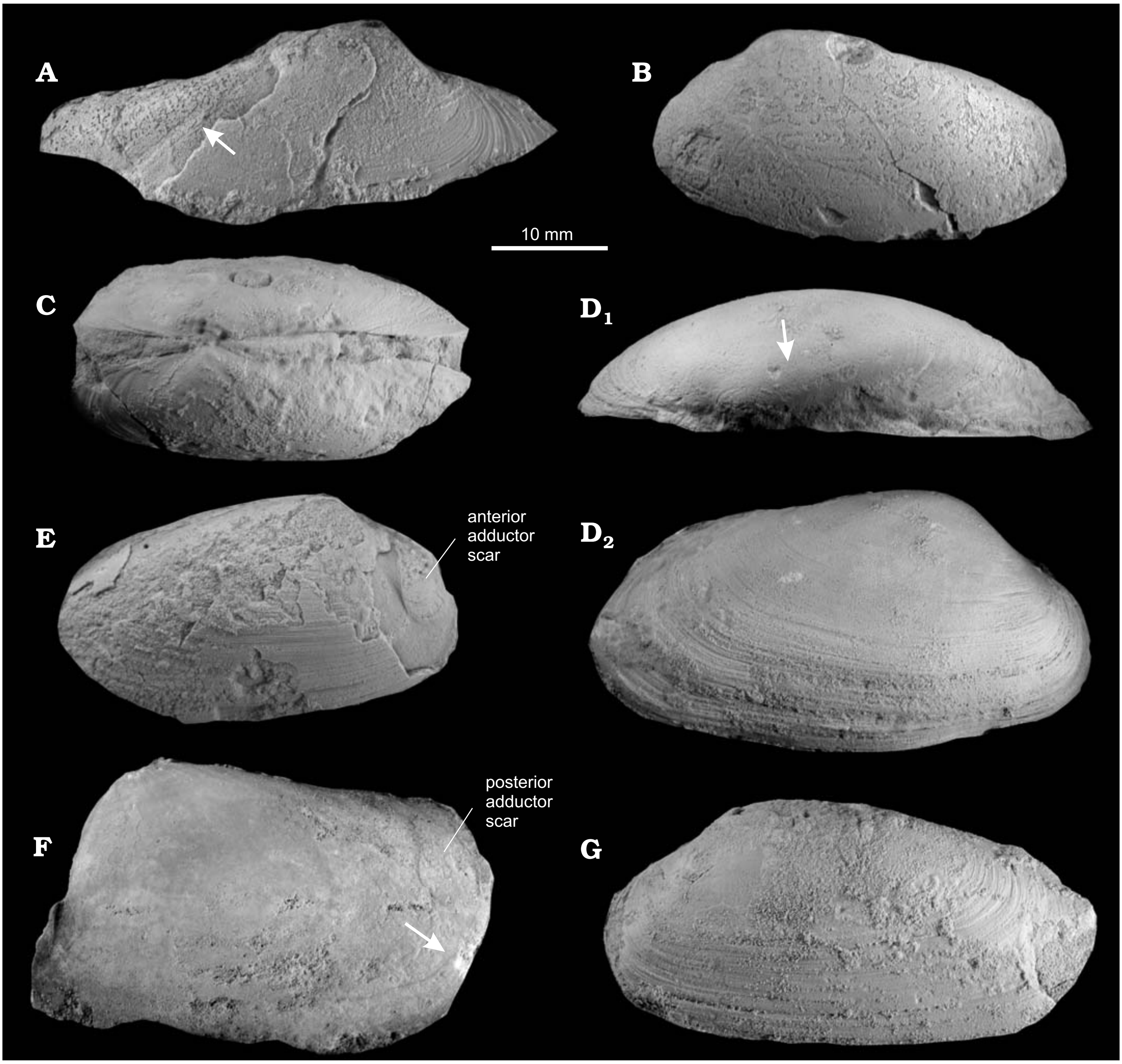

Fig. 4. Vesicomyid bivalve *Notocalyptogena neozelandica* gen. et sp. nov. from Ugly Hill (U23/f267), Early Miocene. **A**. UOA L4607; right valve showing internal ridge from beak to posterior corner (arrow). **B**. UOA L4603; external surface of left valve. **C**. UOA L4595, paratype; dorsal view showing strong ligament. **D**. UOA L4591, holotype; dorsal view (D_1). Note blunt external ridge from beak to posterior ventral corner (arrow). External right valve view (D_2). **E**. UOA L4599; right valve showing anterior adductor scar. **F**. UOA L4594, paratype; left valve internal mould showing pallial line without sinus (arrow) and posterior adductor scar. **G**. UOA L4592, paratype; left valve.

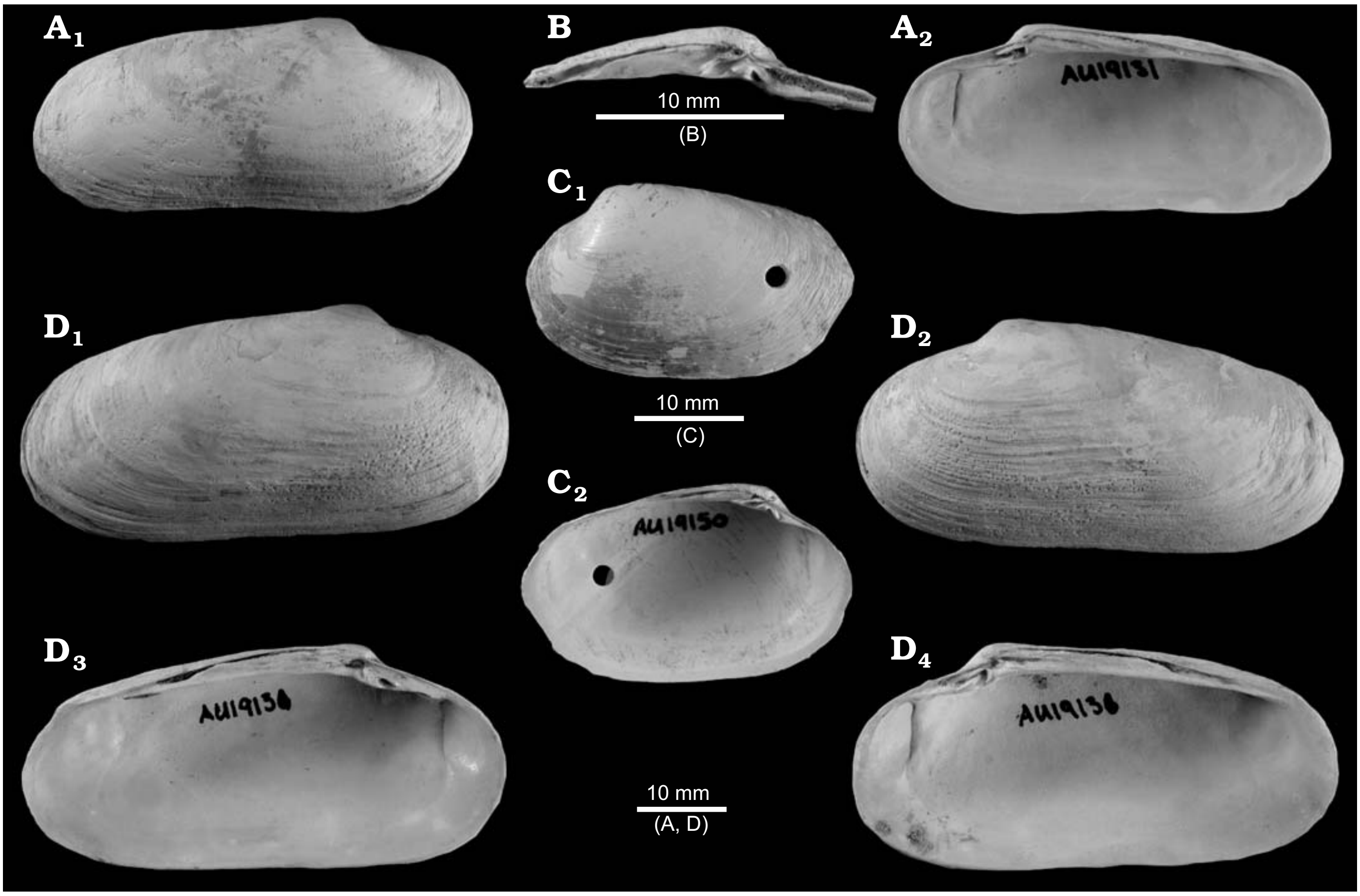

Fig. 5. Modern vesicomyids from the Hikurangi Margin. **A**, **D**. *Calyptogena* sp. **A**. UOA L4610; right valve external (A_1) and internal (A_2) views. **D**. UOA L4611; external views of right (D_1) and left (D_2) valves. **B**, **C**. *Archivesica* sp. **B**. UOA L4608; left valve hinge. **C**. UOA L4609; left valve external (C_1) and internal (C_2) views.

Description.—Shell medium size (L up to 51.7 mm), rather thick, moderately inflated, elongate-ovate (H/L = 0.43–0.59), equivalve and inequilateral. Antero-dorsal margin broadly curved into narrowly rounded anterior margin; postero-dorsal margin nearly straight, steeply sloping into oblique posterior margin at obtuse angle; posterior end acutely rounded; ventral margin slightly convex. Blunt external ridge running from beak to posterior corner. Internal radial ridge also prominent from beak to just behind posterior adductor muscle scar, making deep groove on internal moulds. Beak prominent, swollen, prosogyrate and located at anterior one-fifth to one-third of shell length (at 20–37% of shell length from anterior margin). Nymph long, occupying about half of shell length. Lunule and lunular incision absent. Ligament strong, occupying about 60% of postero-dorsal length. Shell surface with numerous growth lines. Hinge of right valve with three cardinal teeth; anterior tooth (3a) thin, disposed along antero-dorsal margin; middle tooth (1) strong, oblique anteriorly; posterior tooth (3b) thin, vertical or slightly anteriorly inclined; deeply depressed or flat area behind posterior cardinal tooth. Hinge of left valve with three cardinal teeth; anterior tooth (2a) long and thin, connecting with middle stout tooth (2b); posterior tooth (4b) also rather stout. Pallial line entire. Anterior adductor scar ovate; posterior adductor scar pyriform.

Discussion.—The modern vesicomyid, *Calyptogena* sp. A by Lewis and Marshall (1996) and *Calyptogena* sp. by Campbell et al. (2010), collected from the Hikurangi margin, can be distinguished from the new species by having a broad posterior tooth (3b) connecting with anterior tooth (3a), no depressed area behind 3b tooth, and no distinct inner ridge running from beak to postero-ventral corner.

Stratigraphic and geographic range.—Lower Miocene, Ihungia Limestone, Ugly Hill, Wanstead and Haunui; Lower to Middle Miocene, Bexhaven Limestone, Bexhaven, Moonlight North, and Rocky Knob.

Modern New Zealand vesicomyids and palaeobiogeographic implications

Among the modern shell collections from seeps sites on the Hikurangi margin of New Zealand (Table 1) referred to in

Table 3. Measurements of *Notocalyptogena neozelandica* gen. et sp. nov. Abbreviations: AL, anterior length (* distance of umbo from antrior margin); H, height; L, length; W, width (** width of each valve).

UOA specimen	Type	L (mm)	H (mm)	AL (mm)*	W (mm)**	H/L	L/H	AL/L	Valve
L4591	holotype	37.6	20.0	9.3	7.4	0.53	1.88	0.25	right
L4592	paratype	42.7	21.2	10.0	8.9	0.50	2.01	0.23	left
L4597		34.9	18.5	6.9	–	0.53	1.89	0.20	right
L4598		29.4	14.5	8.1	–	0.49	2.03	0.28	right
L4599		32.5	18.5	9.3	–	0.57	1.76	0.29	right
L4600		31.3	16.9	8.1	–	0.54	1.85	0.26	right
L4601		33.0	17.9	7.3	–	0.54	1.84	0.22	right
L4602		33.6	17.0	6.9	–	0.51	1.98	0.21	left
L4603		30.8	15.3	7.0	–	0.50	2.01	0.23	left
L4604		38.3	17.2	8.2	–	0.45	2.23	0.21	left

Campbell et al. (2010) are three modern vesicomyid species: *Calyptogena* sp., *Archivesica* sp., and *Isorropodon* sp.

Calyptogena sp. (Fig. 5A, D) was described as *C.* sp. A and B by Lewis and Marshall (1996: figs. E–H). This species has an elongate shell and a low posterior cardinal tooth in the right valve. It is similar in appearance to *C. tuerkayi* Krylova and Janssen, 2006 from the Edison Seamount and *C. makranensis* Krylova and Sahling, 2006 from the Makran margin, off Pakistan. *Archivesica* sp. (Fig. 4B, C) was illustrated in Campbell et al. (2010: fig. 6D, E) as a vesicomyid bivalve. A more detailed examination of this specimen shows it has a subumbonal pit, pallial sinus and three cardinal teeth in the right valve. Its outline is very close to that of *Archivesica nanshaensis* (Xu and Shen, 1991) from the South China Sea (see also Lutaenko and Xu 2008). *Isorropodon* sp. was described as *Vesicomya* sp. A, B by Lewis and Marshall (1996: figs. I–L). Judging from its size, the left valve dentition and ill-defined lunular incision, this species belongs to *Isorropodon*. Of these modern vesicomyids from the Hikurangi margin, *Calyptogena* sp. is the dominant species.

A similar dominance of one vesicomyid species, in this case *Notocalyptogena neozelandica*, is seen in the Miocene New Zealand vesicomyid fauna, with *Pliocardia*? sp. being a relatively uncommon element. However, the modern New Zealand vesicomyids have no phylogenetic relationship at genus level with the fossil seep vesicomyid fauna. This indicates that at some point since the Miocene the New Zealand vesicomyid seep fauna suffered a local extinction and has been replaced by genera with probable South China Sea or South Pacific origins.

While *Notocalyptogena* was present in seeps in New Zealand in the Early and Middle Miocene, contemporary Pacific seep sites in Japan and Alaska were dominated by the genera *Adulomya* and *Archivesica* (Kanno 1971; Kiel and Amano 2010; Amano and Kiel 2011), and *Calyptogena* was absent.

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