Lucinid bivalves from Miocene hydrocarbon seep sites of eastern North Island, New Zealand, with comments on Miocene New Zealand seep faunas

KAZUTAKA AMANO, CRISPIN T.S. LITTLE, and KATHLEEN A. CAMPBELL


Three new fossil species of lucinids, *Meganodontia haunuiensis*, *Elliptiolucina neozelandica*, and *Lucinoma saetheri*, are described from lower to middle Miocene hydrocarbon seep carbonates from north and south of Hawke Bay, eastern North Island, New Zealand. Of these taxa *Meganodontia haunuiensis* is confined to seep sites south of Hawke Bay, while *Elliptiolucina neozelandica* comes only from the seep sites north of Hawke Bay. Using ecological information from modern bivalve species, we suggest the southern area seep sites formed in shallower waters than the northern sites. Among the lucinids, *Meganodontia haunuiensis* is one of the oldest records of the genus, and its distribution has shrunk from worldwide in the Miocene times to only around Taiwan today. *Elliptiolucina neozelandica* is the second oldest species in the genus. Since the Miocene the distribution of *Elliptiolucina* has narrowed but its habitat range has increased to both seeps and sandy environments, mainly around the Philippines.

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

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Received 22 January 2018, accepted 9 March 2018, available online 28 March 2018.

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Introduction


Until now, only a few modern and fossil lucinid species have been recorded from hydrocarbon seep sites from North Island, New Zealand. Campbell et al. (2010) illustrated *Lucinoma galathea* (Marwick, 1953) from modern seeps off the Hikurangi Margin. Campbell et al. (2008) listed *Lucinoma* aff. *taylori* from the Miocene Rocky Knob seep site in the Gisborne region (Fig. 1). Saether et al. (2016) figured *Meganodontia?* sp. from several seep sites in the Hawke’s Bay region east of Dannevirke (Fig. 1). Kiel et al. (2013) illustrated unidentified species belonging to the genera *Ezolucina?* and *Nipponothracia?* from Cenomanian to Campanian (Cretaceous) North Island seep deposits. Specimens of *Nipponothracia?* from the Cenomanian Port Awani seep site on the Raukumara Peninsula were subsequently described as *Amanocina raukumara?* by Kiel (2013).

The Miocene seep deposits of North Island occur in two main areas north and south of Hawke Bay, respectively, north of Gisborne and east of Dannevirke (Fig. 1). The majority of the molluscan taxa from these seep sites have been described by Saether et al. (2010a, b, 2012, 2016) and Amano et al. (2014, 2015), except for the lucinids. In this paper, we describe and illustrate the Miocene seep lucinids from North Island, and briefly discuss the wider palaeoenvironmental and regional paleobiogeographical context of the Miocene New Zealand seep communities.
Material

In the area east of Dannevirke, lucinids were collected from the Ugly Hill and Haunui seep sites of the lower Miocene Ihungia Limestone. In the area north of Gisborne, lucinid specimens were collected from the Bexhaven, Moonlight North and Rocky Knob seep sites of the middle Miocene Bexhaven Limestone.

All but four of the fossil specimens described and figured herein were collected in February 2012 by the authors, and these are deposited in the paleontology collections of the School of Environment, the University of Auckland (UOA). Additional fossils collected by UOA paleontologists between 1997–2010, also housed in the UOA collections, were examined. All the localities of the illustrated specimens 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. For com-
parative purposes, modern seep lucinids were studied, comprising specimens dredged during the 2007 joint German-New Zealand NEW VENTS Hikurangi margin cruise with the R/V SONNE (stored in the UOA collections), and some *Lucinoma* specimens at the Museum of New Zealand, Te Papa Tongarewa (Wellington). Fig. 2 shows terminology for description.

**Systematic palaeontology**

Class Bivalvia Linnaeus, 1758  
Subclass Heterodonta Neumayr, 1884  
Family Lucinidae Fleming, 1828  
Subfamily Pegophyseminae Taylor and Glover in Taylor et al., 2011

**Remarks.**—Huber (2015) cited the authors of this subfamily name as Taylor, Glover, Smith, Dyal, and Williams, 2011. However, in table 3 of Taylor et al. (2011), the authors were given as Taylor and Glover.

**Genus Meganodontia** Bouchet and Cosel, 2004  
*Type species:* *Meganodontia acetabulum* Bouchet and Cosel, 2004; Recent, Tashi fishing ground, off Tashi, NE coast of Taiwan.

**Remarks.**—*Meganodontia acetabulum* Bouchet and Cosel, 2004 has a very large shell (up to 150 mm in length). Bouchet and Cosel (2004) listed the generic characters: edentulous hinge, thick-shelled, large anterior adductor muscle scar broadening ventrally, less prominent umbo and maximum height located behind the umbo. However, based on our observations of published photographs of the Italian fossil species *Meganodontia hoernea* (Des Moulins, 1868), this latter character seems to be absent, so it may be a species rather than generic-level character.

Within the subfamily Pegophyseminae, *Pegophysema* Stewart, 1930 differs from *Meganodontia* by having a smaller and thinner anterior adductor muscle scar, a more swollen umbo, a straighter hinge and some secondary pallial attachment scars (Bouchet and Cosel 2004; Taylor and Glover 2005). In addition, most Recent species of *Pegophysema* come from very shallow water sites, whereas fossil and Recent *Meganodontia* species come from deep-sea vent and seep sites (Bouchet and Cosel 2004; Taylor and Glover 2005, 2016; Kiel and Hansen 2015; Kiel and Taviani 2017).

**Meganodontia haunuiensis** sp. nov.  
Fig. 3.


**Etymology:** Named for the type locality (Haunui) in North Island, New Zealand.

**Type material:** Holotype, UOA L4781 (Fig. 3B) from locality U23/f270 (Haunui), collection AU19880. Paratypes: UOA L4777 (Fig. 3A) from locality U23/f280 (Ugly Hill), collection AU 21299; UOA L4782 (Fig. 3E), UOA L4791 (Fig. 3C), UOA L4792 (Fig. 3F) from locality U23/f270, collection AU 21298.

**Type locality:** Haunui seep site, North Island, New Zealand.

**Type horizon:** Ihungia Limestone, lower Miocene.

**Dimensions.**—See Table 1.

**Diagnosis.**—Moderate-size, subcircular and strongly inflated *Meganodontia* with narrow lunule demarcated by sharp ridge in both valves and deeply sunken posterior lenticular dorsal gape. Hinge rather broad and edentulous.

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<td>0.38</td>
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Description. — Shell moderately thick, moderate size up to 84.6 mm in length, subcircular but slightly longer than high (H/L = 0.87–1.00), strongly inflated (W/L = 0.43–0.68), equivalve, inequilateral. Postero-dorsal margin straight making obtuse angle with subtruncated posterior margin; ventral margin well rounded, graduating subcircular poste-

Fig. 3. Lucinid bivalve Meganodontia haunuiensis sp. nov. from the lower Miocene Ihungia Limestone at Haunui (B–G, U23/270) and Ugly Hill (A, U23/280), North Island, New Zealand. A. UOA L4777 (paratype), edentulous hinge plate of left valve (A1,), left valve (A2). B. UOA L4581 (holotype), dorsal view (B1,) and frontal view (B2) of right valve. C. UOA L4791 (paratype), edentulous hinge plate of right valve. D. UOA L4790, right valve of small specimen. E. UOA L4782 (paratype), dorsal view of slightly compressed specimen (E1), left valve (E2). F. UOA L4792 (paratype), dorsal view showing symmetric lunule in both valves (F1), right valve showing internal mould (F2), enlargement of the anterior adductor muscle scar of F2 (F3). G. UOA L 4789, right valve, showing internal mould of small specimen. Scale bars 10 mm.
rior margin into nearly straight dorsal margin. Umbo rather prominent but not swollen, situated at anterior one-fourth to two-fifths of shell length (AL/L = 0.26–0.44). Maximum height slightly behind umbo in holotype but located at umbo in paratype specimens. Surface sculptured by fine commarginal growth lines and some irregular commarginal undulations. Very weak groove running from umbo to postero-ventral corner. Lunule narrow, demarcated by sharp ridge in both valves and occupying postero-dorsal margin observed in right valve; posterior lanceolate dorsal gape deeply sunken and probably once occupied by ligament. Scar trace of pallial blood vessel observed in one specimen. Hinge rather broad for genus and edentulous, except for nymph separating ligament and subumbonal flat area. Anterior adductor scar rather large, elongate and stout; posterior adductor scar indistinct and subquadrate. Pallial line entire with no secondary pallial attachment scars. Inner surface of shell covered by fine radial grooves.

Remarks.—Despite having comparatively smaller shell size compared to other species in the genus, we placed these specimens into Meganodontia Bouchet and Cosel, 2004 because they have a large anterior adductor scar, a less swollen umbo than Pegophysema, a curved hinge area and no secondary pallial attachment scar. However, the broad hinge plate with a distinct posterior ridge has not been observed in other species of Maganodontia. Meganodontia hoernea (Des Moulins, 1868) from the middle to upper Miocene seep deposits of Italy is the most similar species to M. haunuiensis sp. nov. in that it also has a large shell and similar inflation (W/L = 0.31–0.71), but differs from the New Zealand species by being even larger (up to 180 mm in length) and possessing a narrower hinge plate.

Meganodontia sp. was illustrated from the Cuban early Miocene Cantera Portugalete seep site in Kiel and Hansen (2015). These specimens have similar outlines (especially their fig. 7C) to M. haunuiensis sp. nov. However, the Cuban specimens are larger (up to 120 mm in length) than M. haunuiensis sp. nov. A lack of information on the hinge area of the Cuban specimens prevents us from comparing these features.

Meganodontia haunuiensis sp. nov. can be easily distinguished from the type species of the genus, M. acetabulum, by its smaller shell (up to 84.6 mm in M. haunuiensis; up to 150 mm in M. acetabulum), more prominent umbo and much broader hinge plate.

“Anodontia (Anodontia) waharoensis” Eagle, 1992 from Motutara, North Island, New Zealand, does not belong to Anodontia owing to its large size (L = 123 mm), but rather to the Pegophyseminea (genus uncertain). This species differs from M. haunuiensis sp. nov. by having a larger (L = 123 mm), thinner shell that is more elongated (H/L = 0.82; H/L = 0.87–1.00 in M. haunuiensis), with a narrowly rounded anterior margin.

Meganodontia haunuiensis sp. nov. resembles the Recent Indo-Pacific species, Pegophysema philippiana (Reeve, 1850) in its shell outline (H/L = 0.85–0.94 in P. philippiana from the Kawamura Collection and NSMT-Mo 84906 stored at the National Science Museum, Tsukuba, Japan), size (max L = 71.0; Taylor and Glover 2005) and inflation (W/L = 0.52–0.74 from the Kawamura Collection and NSMT-Mo 84906 stored at the National Science Museum, Tsukuba). However, the broader hinge and larger, but narrower lunule of M. haunuiensis sp. nov. are very different from the same shell characters in P. philippiana.

Meretrix sphericula Basedow, 1902 (= Anodontia sphericula by Darragh, 1970) was described from the Miocene crystalline limestone around Edithburg, Australia. Ludbrook (1978) also described a well-preserved specimen from the Pliocene Roe Formation, Australia. This species is large in size (up to 105 mm) and has a strongly inflated shell (W/L = 0.75). However, the Australian species differs from M. haunuiensis sp. nov. in possessing a thinner shell with narrow hinge plate, a more horizontal postero-dorsal margin and a more protruding umbo.

Loripes goliath Yokoyama, 1928, from the Miocene of Taiwan has a very large shell (up to 150 mm in length) and was questionably allocated to Anodontia by Taylor and Glover (2009). This species differs from M. haunuiensis sp. nov. by having a more inflated shell and steeply sloping and straight postero-dorsal margin. Nonetheless, poor preservation and a lack of information about the internal structure of L. goliath prevent us from comparing the species further.

Stratigraphic and geographic range.—Haunui, Ugly Hill, Ngakawa, and Wanstead; Lower Miocene Ihungia Limestone, North Island, New Zealand.

Subfamily Myrteinae Chavan, 1969

Genus Elliptiolucina Cosel and Bouchet, 2008

Type species: Elliptiolucina magnifica Cosel and Bouchet, 2008; Recent, central Philippines.

Remarks.—This genus is characterized by having a subquadrate-ovate and weakly inflated shell, an edentulous hinge except for small cardinal and anterior lateral teeth in E. williamsae Glover and Taylor, 2016, and a short anterior adductor scar. Other edentulous lucinids with a weakly inflated, elongate shell include Nipponothracia Kanie and Sakai, 1997, Elongatolucina Gill and Little, 2013, and Amanocina Kiel, 2013. According to Okutani (2011), Elliptiolucina can be separated from Nipponothracia by its smaller and thicker shell and possession of a characteristic dorsal concavity in the posterior adductor muscle scar. Elongatolucina has an elongate shell with straight ventral margin, which is not seen in Elliptiolucina (see Kiel 2013). Amanocina can be easily distinguished from the other genera as it lacks a subumbonal triangular excavation and has a longer adductor muscle scar detached at a narrower angle from the pallial line (Kiel 2013).

Elliptiolucina neozeelandica sp. nov.

Fig. 4.

Etymology: Named for New Zealand, the country of the type locality.

Type material: Holotype, UOA L4771(Fig. 4A) from locality Y16/
f1174 (Moonlight North), collection AU19923. Paratypes: UOA L4783 (Fig. 4B); UOA L4775 (Fig. 4C); UOA L4774 (Fig. 4D); from locality Y16/f1059 (Moonlight North), collection AU 19982. One silicone rubber cast of the internal shell features made from UOA L4775.

**Type locality:** Moonlight North seep site, North Island, New Zealand.

**Type horizon:** Bexhaven Limestone, middle Miocene.

**Dimensions.**—See Table 2.

**Diagnosis.**—Small and compressed *Elliptiolucina* having a thin shell without a sulcus. Antero-dorsal margin gently sloping to subtruncated anterior margin. Lunule narrow and escutcheon deeply sunken, demarcated by sharp ridge. Hinge of right valve shallowly sunken and edentulous with nymph.

**Description.**—Shell size rather small for genus, up 34.9 mm in length; rather thin-shelled, elongate ovate (H/L = 0.75), compressed, equivale and inequilateral. Antero-dorsal margin gently sloping, making right angle with subtruncated anterior margin; ventral margin broadly arched and subparallel with dorsal margin; postero-dorsal margin nearly straight, leading into subtruncated posterior margin. Distinct but shallow sulcus present from beak to antero-ventral corner; shallow depression from beak running in postero-ventral direction. Surface largely smooth, sculptured by growth lines and about four very low and dense commarginal threads between growth lines. These growth lines turning into lamellated ribs near anterior and posterior dorsal margins. Umbo not prominent, prosogyrate and located at anterior one-third of shell length in one small entire specimen. Lunule narrow, lanceolate, shallowly sunken. Escutcheon lanceolate, deeply sunken and demarcated by sharp ridge. Hinge of right valve shallowly excavated and edentulous with nymph. Pallial line entire. Anterior adductor muscle scar elongate, long and slightly detached from pallial line; posterior adductor muscle scar large, subquadrate and rather deeply depressed on dorsal side.

**Remarks.**—The outlines, hinge characters, and shape of the posterior adductor scar show that the specimens belong to the genus *Elliptiolucina*, except for having rather thin shells. This is the first record of fossil *Elliptiolucina* in New Zealand.

*Elliptiolucina neozelandica* sp. nov. is most similar to the Recent Philippines Sea species, *E. labeyriei* Cosel and Bouchet, 2008 in having a relatively small, rather thin shell, a narrow lunule and a similar outline. However, *E. labeyriei* has a distinct and wide sulcus from the beak to the postero-ventral corner, which is not seen in *E. neozelandica* sp. nov.

*Elliptiolucina williamsae* Glover and Taylor, 2016 from the central Philippines lives in rather shallow water (280–679 m depth) compared to other species in the genus. This
species also has a small, thin shell (up to 44.1 mm), as in *E. neozelandica* sp. nov. However, the Recent species has a well-rounded ventral margin with a cardinal tooth and an anterior lateral tooth.

*Elliptiolucina washingtonia* Kiel, 2013 from the upper Oligocene Lincoln Creek Formation in Washington State (Kiel 2013) is up to 140 mm long, larger than any of the extant species, and larger than *E. neozelandica* sp. nov.

*Elliptiolucina hetzeli* (Martin, 1933) from the upper Miocene formation of Buton Island, Indonesia, redescribed by Kiel (2013), can be separated from *E. neozelandica* sp. nov. by its larger shell (more than 48 mm) and acutely rounded posterior margin.

Another Indonesian species, the living *E. virginiae* Cosel and Bouchet, 2008, can be easily separated from *E. neozelandica* sp. nov. by its larger size (up to 78 mm long), truncated posterior margin and narrow hinge plate.

The Recent species, *Elliptiolucina ingens* (Okutani, 2011) from off Amami-Oshima, southwestern Japan, differs from *E. neozelandica* sp. nov. in having a larger (up to 98.4 mm in length; Kuhara et al. 2014) and thick shell with a rounded posterior margin.

Stratigraphic and geographic range.—Moonlight North seep site; middle Miocene Bexhaven Limestone, North Stratigraphic and geographic range.

Subfamily Codakiinae Iredale, 1937

**Genus Lucinoma** Dall, 1901

*Type species:* *Lucina filosa* Stimpson, 1851; Recent, east coast of North America.

*Lucinoma saetheri* sp. nov.

Fig. 5.


*Etymology:* Named for Kristian P. Saether who studied the hydrocarbon seep fauna of New Zealand for his PhD at the University of Auckland.

*Type material:* Holotype, UOA L4780 (Fig. 5D) from locality U23/I266 (Ugly Hill), collection AU19963. Paratypes: UOA L4772 (Fig. 5B) from locality Y16/f1174 (Moonlight North), collection AU 19923; UOA L4773 (Fig. 5A) from locality Y16/f1059 (Moonlight North), collection AU 19982; UOA L4779 (Fig. 5F) from locality U23/I266, collection 19663.

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

*Type horizon:* Ihungia Limestone, lower Miocene.

*Dimensions.*—See Table 3.

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**Table 3.** Measurements (in mm) of *Lucinoma saetheri* sp. nov. Abbreviations: AL, anterior length; H, height; L, length; W, width.

**Diagnosis.**—Large, subcircular and moderately inflated *Lucinoma* with weak commarginal lamellate ribs, rather straight and gently oblique antero-dorsal margin, rounded anterior margin and weak posterior sulcus. Right valve hinge with very weakly bifid posterior cardinal tooth (3b) and relatively thick anterior cardinal tooth (3a). Ligament strong.

**Description.**—Shell large, up to 67.4 mm in length, rather thick, subcircular (*H/L = 0.91–0.99*), moderately inflated (*W/L = 0.52–0.61*), equivalve and slightly inequilateral. Antero-dorsal margin rather straight and gently oblique, making a near right angle turn at anterior margin end, and well-rounded ventral margin; postero-dorsal margin broadly curved, moving into posterior margin at oblique angle; ventral margin semi-circular. Very weak sulcus present from umbo to postero-ventral corner in large specimens, including holo-type and one paratype (UOA L4779). Surface sculptured with regular and widely spaced, thin commarginal lamellae; inter-spaces with two or three dense commarginal threads. In large specimens, these lamellae becoming low and nearly equal in strength with interstitial threads. Umbon prominent above dorsal line, prosogyrate and located at anterior one-third to two-fifths of shell length (*AL/L = 0.31–0.48*). Lunule lanceolate, sunken; demarcated by sharp ridge. Ligament strong, occupying about 70–80% of postero-dorsal length. Hinge of right valve with two cardinal teeth and one anterior lateral tooth; anterior tooth (3a) small, but relatively thick, oblique anteriorly; posterior tooth (3b) stout, very weakly bifid, oblique posteriorly; anterior lateral tooth (AI) very weak. Pallial line entire. Anterior adductor muscle scar elongate and long; posterior adductor muscle scar rather large and pyriform.

**Remarks.**—The shell size of specimens in the seep deposits south of Hawke Bay (such as at the type locality) is often larger than those in the seeps north of Hawke Bay, up to 67.4 mm in length in the former and up to 45.0 mm in length in the latter.

Campbell et al. (2008) listed *Lucinoma* aff. *taylori* from the Rocky Knob seep deposit. However, lucinid specimens from this site are not *Lucinoma taylori* (Powell, 1935), instead belonging to *L. saetheri* sp. nov.

As noted above, *Lucinoma saetheri* sp. nov. does somewhat resemble *L. taylori* (Powell, 1935) from the lower Miocene Trikohua Formation of the Motutara area, west coast of Auckland, New Zealand. However, *L. taylori* is not as large as *Lucinoma saetheri* sp. nov. and has a shorter antero-dorsal margin, a broadly arched ventral margin, a
more distinct posterior sulcus, and a less inflated shell (W/L = 0.46 in holotype; W/L = 0.52–0.61 in *L. saetheri* sp. nov.).

*Lucinoma galathea* (Marwick, 1953) is a Recent species living in and around New Zealand, and differs from *L. saetheri* sp. nov. by having a distinctly bifid and more oblique posterior tooth (3b), a strong anterior lateral tooth, a subtruncated anterior margin, and being smaller (maximum size up to 51.5 mm; up to 67.4 mm in *L. saetheri* sp. nov.).

Another large, living *Lucinoma* species, *L. taiwanensis* Cosel and Bouchet, 2008, can be easily separated from *L. saetheri* sp. nov. by having a distinct ridge from the beak to the anterior ventral corner.

*Lucinoma perusinum* (Sacco, 1901) from the middle to upper Miocene seep carbonates of northern Italy was described as *L. perucina* by Kiel and Taviani (2017) who allocated this species to the genus *Lucinoma* rather than
the original designation as *Dentilucina perusina* by Sacco (1901). We agree with their allocation, but as *Lucinoma* is a neutral noun, the species name should be changed to *perusinum*. This Italian species is similar to *L. saetheri* sp. nov. in having a similar condition of the umbo and outline. However, the Italian species has a straight postero-dorsal margin and a more elongate lunule than *L. saetheri* sp. nov.

*Lucinoma acutilineatum* (Conrad, 1849) is a common species of *Lucinoma* from the lower Miocene seep sites of Japan. Specimens from the Kokozura Formation have a large shell (up to 58.5 mm in length; Kamada 1962). However, *L. acutilineatum* (Conrad, 1849) has some regularly lamellate commarginal ribs, even in large specimens, and a distinctly truncated posterior margin, so differs from *L. saetheri* sp. nov.

**Stratigraphic and geographic range.**—Ugly Hill and Hanui; lower Miocene Ihungia Limestone. Bexhaven, Moonlight North and Rocky Knob; middle Miocene Bexhaven Limestone. North Island, New Zealand.

**Discussion**

**Characteristics of the Miocene New Zealand seep faunas.**—Table 4 shows the molluscan taxa described so far from the Miocene seep sites in eastern North Island of New Zealand, based on this study and data from Saether et al. (2010a, b, 2012, 2016) and Amano et al. (2014, 2015). The species composition differs to the north and south of Hawke Bay. *Bathymodiolus heretaunga*, *Gigantidas coseli*, and *Provanna marshalli* are shared by both areas, but are predominant in the northern area. Some of the taxa intimately linked to seepage are confined to the northern seep sites; solemyids, *Elliptiolucina neozelandica*, *Thyasira beui*, *Pliocardia?* sp., and “*Serradonta* kimberleyae”, together with vagrant species: the taxodont bivalves *Lamellinucula* and *Nuculana*, the limid *Acesta*, the mud pecten *Parvamussium* and the cardiid *Pratulum*. In contrast, lucinids are predominant members of the southern seep sites. Of these, *Maganodontia haunuiensis* has been found only from the southern sites; whereas *Lucinoma saetheri* is common to both areas.

The distribution pattern of the lucinids suggest that there was likely a palaeobathymetric difference between the northern and southern areas of Miocene seepage in eastern North Island. *Elliptiolucina* and some vagrant specimens occur only at the northern Moonlight North locality. Most modern *Elliptiolucina* species live in the deep sea (520–2570 m) around the Philippines, Indonesia, and southern Japan (Cosel and Bouchet 2008; Okutani 2011; Kuhara et al. 2014). Of the vagrant species, *Lamellinucula* and *Pratulum* now live in shallow water around New Zealand, 5–46 m and 15–180 m, respectively (Powell 1979). However, the former lives in deeper seas of Japan (50–3000 m; Higo et al. 1999). The living depth of *Nuculana* ranges from 0–980 m around New Zealand (Powell 1979). *Acesta saginata* and *Parvamussium maorinum* are confined to the deep sea 1000–1400 m and 168–1300 m, respectively (Powell 1979).

Table 4. Occurrence of molluscan fossils from the seep sites in North Island, New Zealand (Amano et al. 2014, 2015; Saether et al. 2016; this study). Localities: BX, Bexhaven; KK, Karikarihuata; MN, Moonlight North; PK, Puketawa; RK, Rocky Knob; TH, Turihaua; TT, Totaranui; TW, Tauwhareparea; HA, Haunui; NG, Ngawaka; UH, Ugly Hill; WA, Wanstead; WP, Waipiro.

<table>
<thead>
<tr>
<th>Species</th>
<th>Localities North of Hawke Bay</th>
<th>South of Hawke Bay</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Species</strong></td>
<td>BX</td>
<td>KK</td>
</tr>
<tr>
<td>Lamellinucula sp.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nuculana sp.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Solemyidae gen. et sp. indet.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bathymodiolus (sensu lato) heretaunga</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gigantidas coseli</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acesta cf. saginata</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Parvamussium cf. maorinum</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leptomya sp.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Meganodontia haunuiensis sp. nov.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Elliptiolucina neozelandica sp. nov.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lucinoma saetheri sp. nov.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Thyasira beui</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pratulum quinariarium</td>
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<td></td>
</tr>
<tr>
<td>Pliocardia? sp.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Notocalyptogena neozelandica</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Semeloidea (sensu lato) bexhavenensis</td>
<td></td>
<td></td>
</tr>
<tr>
<td>“<em>Serradonta</em> kimberleyae”</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Homalopoma? sp.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Provanna marshalli</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Naticidae gen. et sp. indet.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mitrella sp.</td>
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</tbody>
</table>
The large lucinid *Meganodontia* occurs only in the southern seep sites. The sole Recent species, *Meganodontia acetabulum*, has been recorded from 246 m to 472 m water depth as dead shells (Bouchet and Cosel 2004). These shells were plausibly derived from shallower water. In addition, as described above, *Lucinoma saetheri* sp. nov. is larger in the southern sites than the northern ones and, according to Tunberg (1984), off Norway the Recent species *Lucinoma borealis* grows larger in shallower water than deeper sites. Moreover, one vagrant species from the Haunui seep site, *Leptomya*, now lives in shallow water (4–216 m) around New Zealand (Powell 1979).

Using the above depth ranges of living bivalves as a comparative tool, we suggest the seep sites north of Hawke Bay formed in deeper water than the seep deposits to the south of Hawke Bay, the latter inferred to have developed over a depth range of approximately 250–472 m (based on *Meganodontia*). This palaeobathymetric estimation is consistent with the lithological differences between seep deposits in the northern and southern areas previously noted by Campbell et al. (2008). Specifically, the southern seep deposits are sandier than those in northern areas. This lithological difference also reflects the occurrence of the two deposit feeding bivalves taxa *Lamellinucula* and *Nuculana*, which are confined to the finer-grained, northern seep deposits.

**Ancient and Recent distributions of Lucinoma, Meganodontia, and Elliptiolucina.**—*Lucinoma* first appeared in seep sites of early Oligocene age (33.9–27.8 Ma) in western Washington, USA (Goedert and Campbell 1995; Peckmann et al. 2002; Kiel 2010), and today is widely distributed among seep sites at upper bathyal depths on the Louisiana slope, off Chile, West Africa, Taiwan, Japan, and New Zealand, as well as in Mediterranean mud volcanoes and the oxygen minimum zones off California and Oman (e.g., Taylor and Glover 2010; Campbell et al. 2010). Thus, the worldwide distribution of *Lucinoma* indicates its adaptability to different environments, and may be one of the reasons why *L. saetheri* is found regionally, and in different lithologies, in Miocene seeps of New Zealand, unlike the other two lucinid genera in North Island seep deposits.

Generic lucinid compositions are similar between the southern seeps of New Zealand and the middle to late Miocene seep faunas in Italy (Kiel and Taviani 2017), containing both *Meganodontia* and *Lucinoma*. The paleobathymetry was estimated as 200–800 m for the Italian “Calcari a Lucina”, based on benthic foraminifers and oxygen isotopes (Aharon and Sen...
Gupta 1994). Rather shallow settings allowed Meganodontia to live in the seeps of southern New Zealand and Italy. M. haunuiensis is one of the oldest records of the genus, contemporaneous with Meganodontia sp. from the early Miocene (20.44–15.97 Ma) of Cuba. All fossil species of Meganodontia are found in hydrocarbon seep sites, while the sole modern species, M. accetabulum, inhabits waters off Taiwan. The distribution of the genus has shrunk from worldwide in the Miocene to only around Taiwan today (Fig 6).

Until now, all fossil Elliptiolucina species have only been found from hydrocarbon seep sites in the Pacific. The oldest species, E. washingtonia, comes from an upper Oligocene (37.8–33.9 Ma) seep site in Washington State (Kiel 2013). The second oldest species is E. neozelandica from the middle Miocene (15.97–11.63 Ma) in New Zealand. E. hetzelii is from upper Miocene (11.63–5.33 Ma) deposits of Buton Island, Indonesia (Kiel 2013), and probably also from the lower Pliocene cold-seep deposits in Leyte, Philippines (Kase et al. 2007). In comparison, modern species of Elliptiolucina are found mainly in the Philippines, and also occur in Indonesia and Amami-Oshima, southwestern Japan (Cosel and Bouchet 2008; Okutani 2011; Kuhara et al. 2014; Glover and Taylor 2016). Of these, E. magnifica, E. labeyrieri, and E. ingens were collected with vesicomyid bivalves, probably from seep sites (Cosel and Bouchet 2008; Kuhara et al. 2014). The species living in shallowest water is E. williamsae, collected from sandy substrates (Glover and Taylor 2016). The habitat of E. virginiae is unknown. The species of this genus once lived in hydrocarbon seep sites around the Pacific; since then their distribution has narrowed and their habitat has expanded to include both seep sites and also sandy environments, mainly around the Philippines (Fig 6).

Conclusions

This paper presents a study of lucinid bivalves from the lower to middle Miocene hydrocarbon seep carbonates in the north and south of Hawke Bay in North Island of New Zealand. Three new fossil species belonging to each of the genera Meganodontia, Elliptiolucina, and Lucinoma are described. Using modern bivalve depth ranges as a comparison, we suggest the southern area seep sites formed in shallower waters than the northern sites. Among the lucinids, the genera Meganodontia and Elliptiolucina were distributed worldwide or Circum Pacific area in the Miocene but their distribution has since narrowed to around the Philippines, Indonesia and southern Japan.

Acknowledgements

We acknowledge Kristian P. Saether (Nanjing Institute of Geology and Palaeontology, China) for his PhD study of some lucinids of New Zealand, John Taylor (The National History Museum, London, UK) for information about Meganodontia and Pegophysea, Steffen Kiel (Swedish Museum of Natural History, Stockholm, Sweden) for information on Caribbean fossil lucinids, Bruce Marshall (Te Papa Museum, Wellington, New Zealand) for showing us modern lucinid specimens from seeps of the Hikurangi margin, Neville Hudson (University of Auckland, New Zealand) for his help with fossil curation and access to material stored in the University of Auckland paleontological collections, Wilma Blom (Auckland War Memorial Museum, New Zealand) for helping us examine Powell’s and Eagles’ collections, Hiroshi Saito (National Science Museum, Tsukuba, Japan) for showing us Recent species of “Anodontia” and Elliptiolucina, and Robert G. Jenkins (Kanazawa University, Japan) for helping KA to collect some Japanese fossils. We also thank Steffen Kiel, Krzysztof Hryniewicz (Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland), and an anonymous reviewer for their review and useful comments. Iain McInnes (Emslaw One Ltd., Gisborne, New Zealand) kindly allowed access to the Moonlight North site. James and Sue Hewitt (Wanstead, New Zealand) granted access to the Haunui site, and Tim and Maggie Simcox, and Paul and Kate Dearden (Wanstead, New Zealand) gave us permission to work at Ugly Hill. This research was partly supported by a Grant-in-aid for Scientific Research from the Japan Society for the Promotion of Science (C, 23540546, 2011–2013; C, 17K05691, 2017–2019) (to KA). Field work also was supported by the Royal Society of New Zealand’s Marsden Fund (06-UOA-082) (to KAC) and a travel fund from the Royal Society (to CTSL).

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