FOSSIL CRANIID BRACHIOPODS (CRANIATA) OF AUSTRALIA AND NEW ZEALAND

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ABSTRACT: Three fossil craniid species from Australia are synonymised. Two species are transferred to two different genera, one to *Danocrania* and one to *Novocrania*; these species are described, figured and their geographic ranges illustrated. Five fossil craniid species from New Zealand, four of *Novocrania* and one of *Valdiviathyris*, are described, figured and their geographic ranges illustrated. The species described range in age from middle Paleocene to Recent. The paleoecology is summarised.

Keywords: fossil, craniid, brachiopod, Australia, New Zealand

Inarticulated craniid brachiopods have a very long history, ranging from the early Ordovician to Recent (~450 million years), with 19 fossil and extant genera known (Bassett 2000, 2007). Bassett (2000) noted that interior placement of muscle scars and mantle canals of craniids have hardly changed throughout their history. However, recent observations reported here and in Robinson (2017a) show that the shell morphology within extant and fossil *Novocrania* Lee & Brunton, 2001 species may vary significantly. The amount of morphological variation that may occur within a single craniid species, and the wide geographical range of individual craniid taxa, have not been previously appreciated. These two factors have led to an over-abundance of species names in extant *Novocrania* (Robinson 2017a), in Australian fossil species of *Craniscus* Dall, 1871 and *Westralicrania* Cockbain, 1966 (discussed below) and probably in other fossil craniid genera.

Cohen et al. (2014) completed molecular analyses on extant craniid brachiopod specimens (of *Novocrania* and *Neoancistrocrania* Laurin, 1992)

Figure 1: Australian localities where fossil craniids have been collected.

from around the world and found that there were five clades of *Novocrania* and one clade of *Neoancistrocrania*, each with one extant species. Robinson (2017a) reviewed the shell morphology of the fourteen extant species of *Novocrania* (including examination of the type material or new digital images of five species known from only one

or a few specimens) and proposed that, of the fourteen species names, five are synonynms and one type specimen is not a craniid. This leaves eight valid extant *Novocrania* species based on morphology, although three of these are known only from one or a few dorsal valves or a few whole specimens and may also be synonymous.
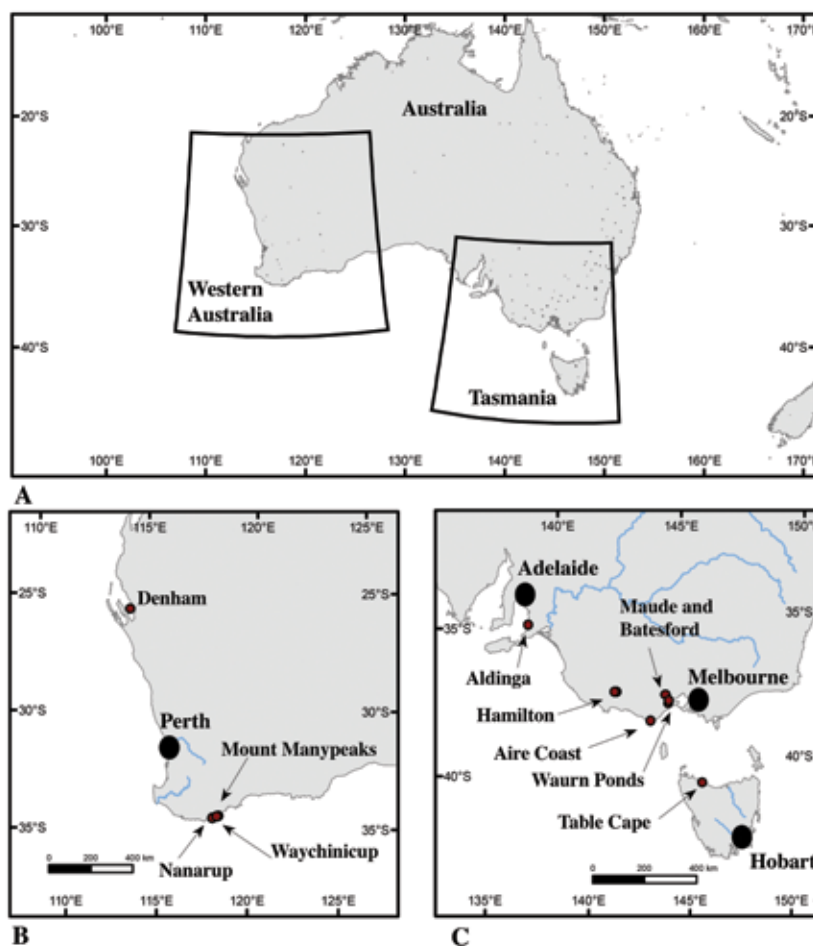
This taxonomic revision of fossil craniids from Australia and New Zealand synonymises three Australian species and transfers two Australian species to different genera. Altogether, five species of *Novocrania* and one species each of *Danocrania* Rosenkrantz, 1964 and *Valdiviathyris* Helmcke, 1940 are described and figured. The fossil localities yielding the collected material are shown in Figures 1 (Australia) and 2 (New Zealand). This revision, and Robinson (2017a), attempt to create a baseline for future craniid taxonomic studies by figuring
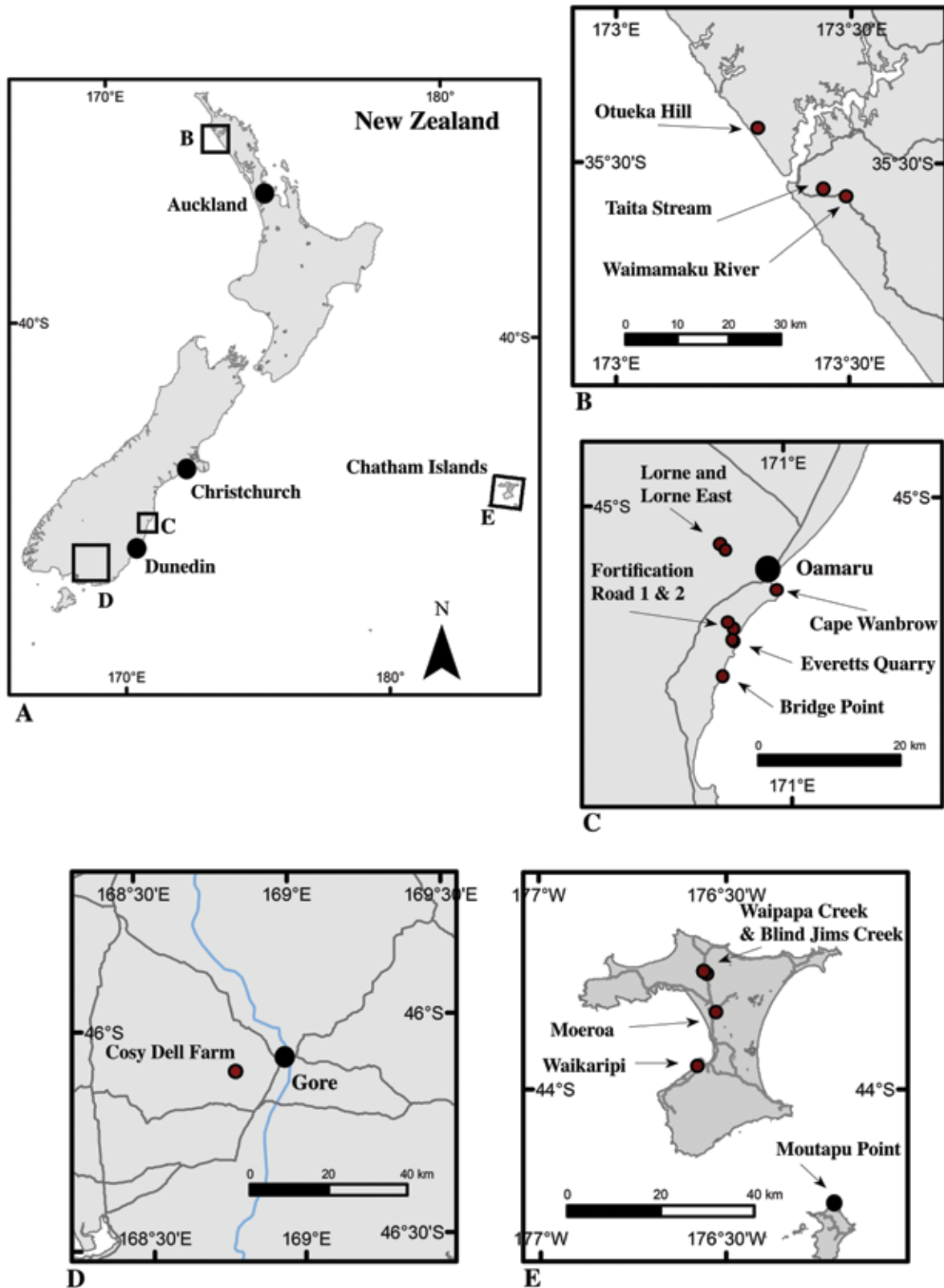

Figure 2: New Zealand localities where fossil craniids have been collected.

the large amount of morphological variation possible within the concept of individual craniid species, at the same time demonstrating the large geographic and stratigraphic ranges of individual craniid taxa. This work confirms that the stratigraphic ranges of some extant craniid species are surprisingly long, including four New Zealand species that extend through more than 20 million years.

New terminology

New terminology for some craniid muscles, based on dissections of specimens of six extant species, was introduced by the author (Robinson 2014). New terms include *small anterior muscles* (previously known as the brachial protractor muscles, Blochmann [1892]) and *support structure* (previously known as the brachial retractor muscles). It was also proposed that the so-called 'brachial elevator muscles' are the quick-muscle portion of the anterior adductor muscles. Robinson also showed that the rostella and ventral posterior adductor muscle attachment surfaces of *N. anomala* and *N. lecointei* are made of organic tissue. In further studies, the author proposed that, in most cases, so-called 'sunken muscle scars' in extant and fossil craniids originally held organic tissue where the muscles attached (and are thus not muscle scars at all) (Robinson 2017b). New terminology includes *organic pads* for the organic rostella and muscle attachment surfaces, *muscle attachment tissue* for the tissue that *organic pads* are composed of, and *latent* muscle scars for the shallow to deep depressions and holes through the ventral valve left behind when the *muscle attachment tissue pads* have decayed away (Robinson 2017b).

Robinson (2014) also introduced the term *ventral mound* for the central raised structure where muscles attach on the ventral valve. However, there is an older term for this structure introduced by Höninghaus (1828), the *rostellum*, that has priority and the term ventral mound is therefore discarded.

MATERIALS AND METHODS

Bulk samples were collected in eastern North Otago, New Zealand, from both well-known and new fossil localities, and from Cosy Dell farm in Southland, New Zealand. Several bulk samples that were collected in the Chatham Islands, New Zealand, by D.E. Lee in 1997 were included in this study. Bulk samples were processed to allow the fossil contents to be examined. All samples were oven-dried at 100° C for 48 hours. Clay-rich samples were briefly soaked in white spirits, which was then drained off. Samples were then immersed in boiling water containing dishwash detergent in order to disaggregate the clays (adapted from Haynes 1981). Compacted (but not cemented) clay-poor samples were soaked in melted sodium thiosulthate

(hypo), which expands fractionally when set, thereby disaggregating all the sediment particles. The hypo was then dissolved in boiling water. All processed samples were sieved into fractions (2 mm, 0.5 mm) and picked under a binocular microscope.

Fossil material was examined from the collections of a number of institutions (specimen number prefix in brackets): the Australian Museum, Sydney (C); Museums Victoria, Melbourne (NMV); the Western Australia Museum, Perth (WAM); the Western Australia Geological Survey, Perth (F); the University of Otago, Dunedin (OU); the Canterbury Museum, Christchurch (CM); and the Maastricht Museum, Maastricht, Germany (OU). All fossil material examined is listed in Tables 1 and 2 and the latitudes and longitudes of fossil localities are listed in Table 3 (approximate only for Australian localities). Material examined from extant populations of *Novocrania* species is listed in Robinson (2017a). Images of all fossil shells were produced on Cambridge JEOL and Ziess Sigma scanning electron microscopes and a Nikon D70 digital camera.

SYSTEMATIC PALEONTOLOGY

Order Craniida Waagen, 1885
Superfamily Cranioidea Menke, 1828
Family Craniidae Menke, 1828
Genus *Danocrania* Rosenkrantz, 1964 (Late Cretaceous – Eocene)
Type species *Danocrania tuberculata* (Nilsson, 1826)

Danocrania allani (Cockbain, 1966)
Stratigraphic range: Paleocene – latest Eocene

Westralicrania allani Cockbain, 1966: p. 75, pl. 35.
Danocrania allani – Lee & Brunton 1986: p. 148.
Westralicrania zenobiae – Craig 1997: p. 312, fig. 1, A–B, fig. 2 A–L.

Cockbain (1966) proposed the new genus *Westralicrania* from Denham, Western Australia, naming the type species *W. allani*. Lee and Brunton (1986) synonymised *Westralicrania* with the genus *Danocrania*. Craig (1997) reinstated *Westralicrania* and proposed a second species, *W. zenobiae* from Albany, Western Australia. Bassett (2000) again synonymised the genus *Westralicrania* with *Danocrania*; however, Craig (2000, 2002) continued to use *Westralicrania*.

Craig (1997) indicated that new species *W. zenobiae* is generally larger with a longer pseudointerarea than *W. allani*; the pseudointerarea is anacline whereas it is apsacline in *W. allani;* and the spines in *W. zenobiae* are shorter and radiate in lines whereas in *W. allani* they are randomly placed. Fourteen ventral valves of *Danocrania*

geulhemensis (Kruytzer & Meijer 1958) from Leige, Belgium (Figure 3A, Table 1) were examined. The ventral pseudointerarea varied from being in the plane of the commissure to being nearly at right angles to the commissure; clearly the angle of the pseudointerarea may be highly variable within a species of *Danocrania*. Spine length is also likely to be variable within a species, and it would be necessary to have many specimens with well-preserved spines in order to use spine length as a taxonomic character. The spines on one specimen of *W. allani* (NMV P313936) are placed both randomly and in radial rows (Figure 3D). These observations suggest that, for the two species *W. allani* and *W. zenobiae*, the variations in the size of valves from different localities, the attitude and size of the pseudointerarea and the size and arrangement of spines are within the range of morphological variation of a single species. The species *W. zenobiae* is therefore placed in synonymy under *W. allani*.

Craig (1997, p. 312) reinstated the genus *Westralicrania* on the grounds that 'the posterior muscle scars in *Westralicrania* are on raised platforms and without pits, in *Danocrania* the muscle scars occur in pits and not on platforms'. Four dorsal valves of Late Cretaceous (Late Maastrictian) species *Danocrania hagenowi* (Davidson 1852) from Eben-Emael, Belgium (Table 1) were examined. These specimens have posterior adductor muscle scars both on raised platforms (Figure 3B) and 'in pits' (these are probably latent muscle scars) (Figure 3C). This morphological variation is within the range of variation of a single species of *Danocrania* and is not sufficient grounds for introduction of a new genus. All morphological features place the species *W. allani* in the genus *Danocrania*. The genus *Westralicrania* is here placed in synonymy under the genus *Danocrania*.

Material examined

Thirty-six ventral valves and eleven dorsal valves, ranging in age from middle Paleocene to Late Eocene (Bartonian) from localities in Western Australia, and a dorsal valve from one latest Eocene (Priabonian) locality in South Australia (Table 1, Figure 1A–C).

Description

Exterior: The dorsal valves are sub-circular, and the apex is placed posteriorly and points posteriorly (Figure 3D–E). The ventral valve is teardrop-shaped with a pseudointerarea of variable size (Figure 3F) that is usually apsacline but occasionally anacline; both valves are robust. The cicatrix (the area of attachment to the substrate) is small, located at posterior tip of the ventral valve (Figure 3G). The largest ventral valve examined is 10.6 mm long and 8.1 mm wide (Figure 3F–G).

Both valves have an ornament of spines and concentric growth lamellae. Specimens may have spines in radial rows (e.g. at localities Nanarup, Waychinicup and Many Peaks, Figure 3G), they may be randomly arranged (e.g. at Denham) (Cockbain 1966), or both arrangements may be present on the same valve. The spines on one specimen from Aldinga are randomly placed on the juvenile part of the valve and on the anterior part of the adult valve, but occur in radial rows on the flanks of the adult valve (Figure 3D). The spines are tubular and they may be hollow or infilled, probably with primary layer calcite (Robinson & Lee 2011), and are broken and/or worn. The longest spine observed is 300 μm.

Interior: In the dorsal valve the strongly convex posterior adductor muscle scars are separated medially by a small posterior mound (Figure 3I). The oblique internal muscle scars are small, oval, flush with the valve surface and located lateral to the posterior adductor muscle scars. The anterior adductor slow-muscle scars are bilobed with a much larger medial lobe. The lateral lobe is close to the support structure scars, which are raised and slope medially, and the anterior adductor quick-muscle scars occur in the dimple between the lobes. The small anterior muscle scars are paired and slope laterally on a short, sub-triangular, anterior mound (Figure 3I–J). The dorsal mantle canals (*vascula media*) form V-shaped branching impressions, one on either side of the anterior mound (Figure 3I). The dorsal valve surface is densely punctate with a flat marginal rim 600 μm wide.

In the ventral valve (Figure 3F, H) the posterior adductor muscle scars are sub-rounded, slightly concave and slightly depressed into the marginal rim. There is a centrally placed conical rostellum, the anterior adductor muscle scars lie on each side of the rostellum (Figure 3H) and the oblique internal muscle scars are placed on the lateral sides of the rounded tip. The ventral mantle canals (*vascula lateralia*) are slightly depressed and emerge from between the posterior adductor muscle scars and the rostellum. The ventral marginal rim is 800 μm wide and smooth (Figure 3F) and the inner surface is densely punctate. The dorsal and ventral valve marginal rims are not tuberculate, unlike the two other species of *Danocrania* figured, which are strongly tuberculate (Figure 3A–C).

Remarks

Lee and Brunton (1986) listed seven species of *Danocrania* from eastern and western Europe ranging in age from the Late Cretaceous (Maastrichtian) to the Paleocene (Danian). *D. allani* is the only non-European species known, and is now recorded from Southern Australia as well as Western Australia; the range of *Danocrania* is extended to the latest Eocene.
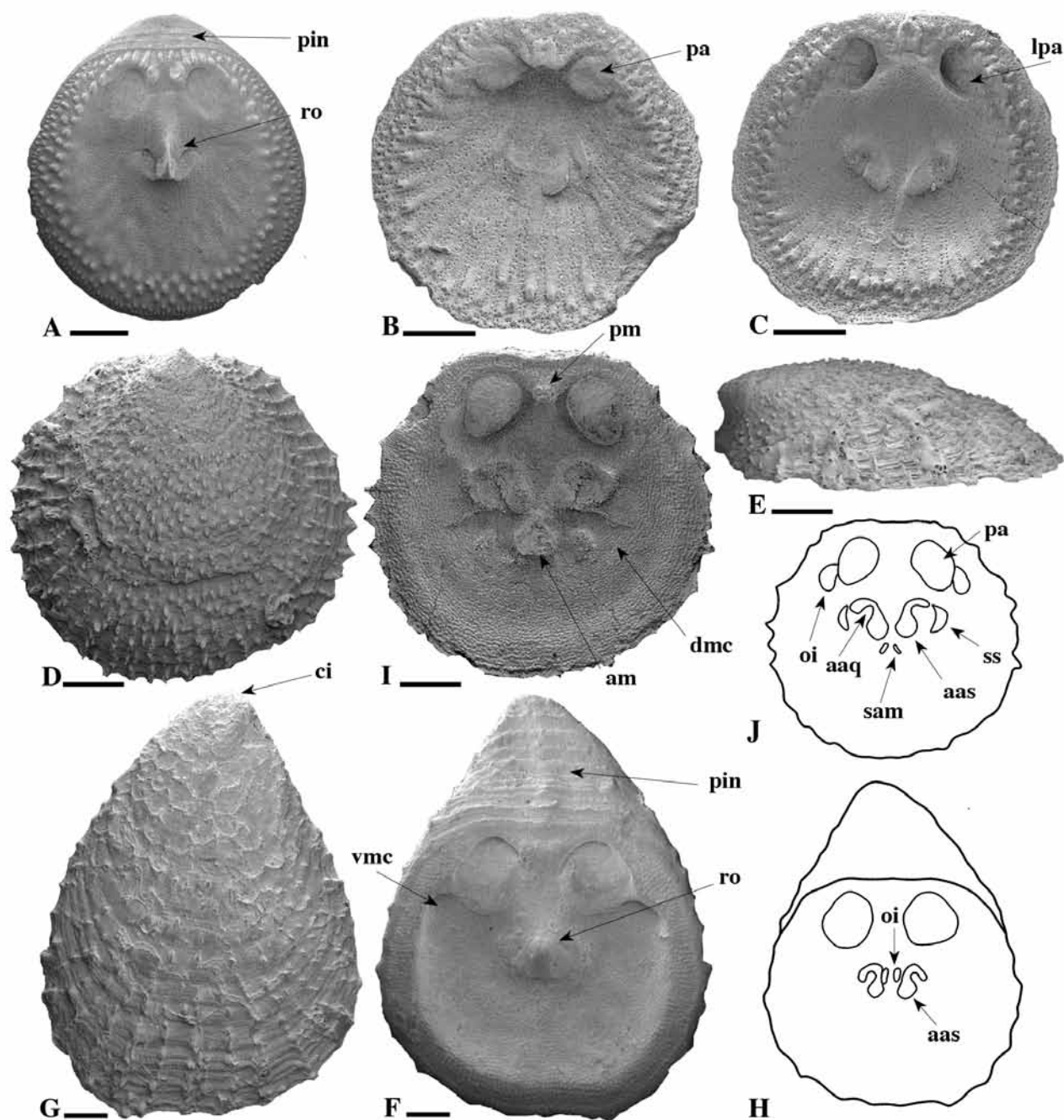
Figure 3: SEM images and line drawings of *Danocrania*. A. OU 44513. *D. geulhemensis*, ventral valve interior. B–C. OU 44514a–b. *D. hagenowi*. B. Dorsal valve interior. C. Dorsal valve interior. D–J. *D. allani*. D–E, I–J. NMV P313936. D. Dorsal valve exterior. E. Dorsal valve lateral exterior. I. Dorsal valve interior. J. Line drawing of interior showing muscle scars. F–H. WAM 94.41. F. Ventral valve exterior. G. Ventral valve interior. H. Line drawing of interior showing muscle scars. All scale bars 1 mm. NMV P – Victoria Museum, Melbourne; OU – Geology Museum, University of Otago, Dunedin; WAM – Western Australia Museum, Perth. Abbreviations: aaq – anterior adductor quick-muscle scar, aas – anterior adductor slow-muscle scar, am – anterior mound, ci – cicatrix, dmc – dorsal mantle canals, lpa – latent posterior adductor scar, oi – oblique internal muscle scar, pa – posterior adductor muscle scar, pin – psuedointerarea, pm – posterior mound, ro – rostellum, sam – small anterior muscle scar, ss – support structure scar, vmc – ventral mantle canals.

Genus *Novocrania* Lee & Brunton, 2001 (Paleocene – Recent)
Type species *Novocrania anomala* (Müller, 1776)

Novocrania turbinata (Poli, 1795)
Stratigraphic range: Early Miocene – Recent

Anomia turbinata Poli, 1795: p. 189, pl. 30.
Crania anomala – Jeffreys 1878: p. 414.
Crania turbinata – Davidson 1888: p. 188, pl. 27, figs 14–23, pl. 28, fig. 8.
Crania anomala – Logan 1979: p. 29.
Neocrania turbinata – Lee & Brunton 1986: p. 152.
Novocrania turbinata – Lee & Brunton 2001: p. 5.
Novocrania cf *turbinata* – Hiller 2011: p. 76, fig. 3A–E.
Novocrania anomala – Emig 2014: p. 159.

Novocrania turbinata was first described as *Anomia turbinata* from Sicily by Poli (1795), but has been given many other names by various nineteenth century authors. Dall (1871) included a synonymy for *Crania turbinata* that listed five genera and five species by eight authors; see partial synonymy lists in Emig (2014) and Robinson (2017a). Lee and Brunton (1986) reviewed the genera in the Family Craniidae and placed some species of *Crania*, including *turbinata*, into a new genus *Neocrania*. Lee and Brunton (2001) reported that the name *Neocrania* was preoccupied, and replaced it with the name *Novocrania*.

There has been much debate about the status of *N. turbinata* in the literature as to whether it is a synonym or subspecies of *N. anomala,* or a separate species. This debate is summarised in Robinson (2017a), with figures showing that the ventral valves of the two species have distinctly different morphology, confirming *N. turbinata* is a separate species. Molecular analysis has placed these two species into separate clades (Cohen et al. 2014). Robinson also figured the very wide geographical range of extant *N. turbinata*, including the Caribbean, the North Atlantic off Portugal and Spain, the Mediterranean Sea, the Indian Ocean and the Western Pacific Ocean from Japan to New Caledonia, Australia, Fiji and Tahiti, and synonymised two species names under *N. turbinata*.

Stratigraphic range

Fossil material from Europe, Japan, New Zealand and Vanuatu identified as, or that may belong in, *N. turbinata*, ranges from the Oligocene to the Pleistocene. Specimens from the Oligocene strata of Malta (Dulai et al. 2015) and the Miocene of France (Bitner et al. 2013, fig. 2B) included ventral valves with radial canals, a morphological feature of both *N. turbinata* (Robinson 2017a) and *Ancistrocrania parisiensis* (Defrance 1818) (well-preserved, diagnostic dorsal valves were absent). Specimens of Middle Miocene age from Bulgaria that were identified as *N. anomala* (Bitner & Motchurova-Dekova 2016, fig. 2C–G) included dorsal valves with pustules on the exterior, raised anterior adductor muscle scars and a median process internally, and a ventral valve with a calcitic rostellum and radial canals on the margins — all features of *N. turbinata.* Additional specimens from the Miocene of France are two worn dorsal valves with anterior pedestals and processes identified as *N. turbinata* by Dulai (2013, figs 37–40). Dorsal valves assigned to *Ancistrocrania abnormis* (Defrance 1818) from the Miocene of Poland (Bitner 1990, figs 3B, 4; Bitner 1993, fig. 1B) may be *N. turbinata,* based on the raised anterior adductor muscle scars. Logan et al. (2004) listed Miocene *N. turbinata* from Italy, but gave no further information.

Hatai (1936) stated that *Craniscus japonicus* (Dall 1920) is found in the Miocene of Japan. Robinson (2017a) transferred extant *C. japonicus* to *N. turbinata*, noted that five extant species of craniid were held in collections in Japan, all under the name of *Craniscus japonicus,* and suggested that (for craniids) the identifications of Hatai are unreliable. Kroh et al. (2008, fig. 2A–F) figured *N. turbinata* from the Early Pliocene of the Azore Islands, North Atlantic. Cooper (1978, pl. 2, figs. 1–8) identified Pleistocene specimens from the New Hebrides (now Vanuatu, South Pacific) as *Craniscus?* cf. *C. japonicus.*

Hiller (2011, fig. 3A–E) described specimens, all dorsal valves, as *Novocrania* cf. *turbinata* from Early Miocene (Otaian) sediments in Northland, New Zealand. The dorsal valves are very similar to extant *N. turbinata* and considered conspecific herein. These are the oldest specimens observed that can be confidently placed into *N. turbinata*, giving this species a provisional stratigraphic range of Early Miocene to Recent. Based on publications listed above, the oldest northern hemisphere specimens that can be placed with confidence into *N. turbinata* are those of Bitner and Motchurova-Dekova (2016) from the Middle Miocene of Bulgaria. This gives *N. turbinata* a provisional geographical range of Bulgaria to New Zealand in the Middle Miocene.

Material examined

Ten dorsal valves (mostly incomplete) of Early Miocene (Otaian) age from Northland (Figure 4A, Table 2), collected by Hiller (2011, fig. 5.3A–E) and held in the Canterbury Museum, Christchurch. Images of specimens referred to, but not figured, in Dulai et al. (2015) were supplied by A. Dulai (pers. comm. 2015).

Description

Exterior: The one complete dorsal valve is 7.5 mm long, 8 mm wide, 1.7 mm high and roughly pentagonal in outline

(Figure 4A). The exterior is worn smooth and the interior is also worn, but some features are visible. There are two sub-oval posterior adductor muscle scars and the marginal rim shows worn tubercles. There are two strongly raised pedestals where the anterior adductor muscles and support structure attach, a small median process where the small anterior muscles attach, a tiny septum running anteriorly from the median process and faint impressions of the dorsal mantle canals. In this specimen, the tuberculate rim, raised pedestals, small median process and tiny anterior septum resemble similar features on an extant specimen of *N. turbinata* from the Kermadec Ridge (Figure 4B). All dorsal valves figured by Hiller (2011, fig. 3A–E) show the raised pedestals bearing the anterior adductor muscle scars, while three have the median process and a tiny anterior septum.

Remarks

On the basis of a personal communication from the author, Hiller (2011) noted that *N. turbinata* had been found in the Late Eocene (Runangan) of New Zealand. The specimen is now considered to be a ventral valve of *Valdiviathyris quenstedti* (see below).

Novocrania lecointei (Joubin, 1901)
Stratigraphic range: late Middle Eocene – Recent

Crania lecointei Joubin, 1901: p. 9–11, pl. 2, figs 13–15.
Crania patagonica – Dall 1902: p. 562.
Crania joubini – Thomson 1918: p. 10, pl. 15, figs 18–19.
Crania valdiviae – Helmcke 1940: p. 234, text fig. 4a–d.
Crania antarcticaensis – Hatai 1965: p. 2, figs 1a–5b.
Neocrania lecointei – Lee & Brunton 1986: p. 152.
Neocrania chathamensis – Lee 1987: p. 61, fig. 7.2–7.8.
Novocrania lecointei – Lee & Brunton 2001: p. 5.

This species was first described from Antarctic waters by Joubin (1901). Foster (1974) synonymised *C. patagonica* Dall, 1902, *C. joubini* Thomson, 1918 and *C. antarcticaensis* Hatai, 1965 with *C. lecointei*; commented on its morphological variability, and noted it was the only craniid species present in Antarctic and South American waters. Lee (1987) and Lee et al. (1997) listed Late Eocene – Early Oligocene fossil specimens from the North Otago and juvenile specimens from the Chatham Island Pliocene locality at Moutapu Point under the name *Neocrania chathamensis* (Allan, 1937). A footnote in Thomson (1927) referred to a 'Miocene' craniid on the New Zealand mainland; Lee indicated that this specimen is from the earliest Oligocene (Whaingaroan) locality Everetts Quarry. These are all synonymised into *Novocrania lecointei*. Robinson and Lee (2011) described the formation of external spines in *N. lecointei*, figured fossil and extant specimens and figured new Recent localities to the north and northwest of New Zealand. Cohen et al. (2014) noted that extant specimens have been recovered from Antarctica, Japan, Chile, the Galapagos Islands and South Africa. Robinson (2017a) synonymised *Novocrania valdiviae* Helmcke, 1940 under *N. lecointei* and figured the extensive known localities of this species. New Zealand and the Chatham Islands are the only places where fossil *N. lecointei* has been found.

Material examined

Several hundred specimens of late Middle Eocene (Kaiatan) to earliest Oligocene (Whaingaroan) age from seven localities in North Otago (Table 2, Figure 2C) and two juvenile dorsal valves from the Pliocene (Waipipian) of the Chatham Islands (Table 2, Figure 2E). The material is
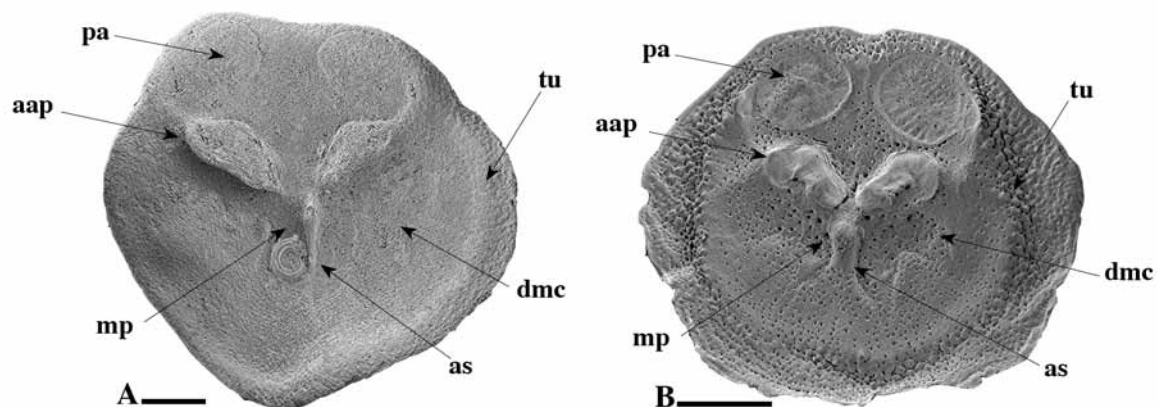

Figure 4: SEM of *Novocrania turbinata*. A. CM 2006.64.87. Fossil dorsal valve interior. B. NIWA 3248. Extant dorsal valve interior. All scale bars 1 mm. CM – Canterbury Museum, Christchurch; NIWA – National Institute of Water and Atmospheric Research, Wellington.
Abbreviations: aap – anterior adductor muscle pedestals, as – anterior septum, mp – median process, dmc – dorsal mantle canals, pa – posterior adductor muscle scar, tu – tubercles.

held in the collections of the Geology Museum, University of Otago, Dunedin.

Description

Exterior: The dorsal valves of fossil *N. lecointei* vary in outline from sub-round to sub-quadrate to sub-hexagonal, and are sub-conical to strongly conical with the apex usually in the posterior third (Figure 5A–D). The largest specimen, from Lorne, is 11.4 mm long, 12.4 mm wide and 3 mm high (Lee 1987, fig. 7.2–7.3). The valves have a variable ornament; they may be spinose (Figure 5A–B, E–F), have strong to weak concentric growth lamellae (Figure 5A–C, E) or may be smooth (Figure 5D).

The number of spines is variable, from more than 100 to a few or none; they occur only sparsely on the valve posterior, are often in radial rows, and may be directed vertically to horizontally to towards the substrate (Figure 5A–B, E–F). The hollow spines are up to 80 μm in diameter at the base, and their length when unbroken may be at least 150 μm. Two juvenile dorsal valves from Moutapu Point, Chatham Islands (Pliocene) have an exterior ornament of concentric growth lamellae and the larger specimen has one small row of spines (Figure 5G).

Interior: The posterior adductor muscle scars are sub-oval, often convex and near to the straight or slightly curved posterior margin, while the oblique internal muscle scars are lateral to the posterior adductor muscle scars and flush with the valve surface. The anterior adductor slow-muscle scars may be reniform (Figure 5H–I) or bi-lobed and variable in shape, including U-shaped (Figure 5J–K, short lobes of equal length) or V-shaped (Figure 5L–M, long lobes of roughly equal length). The anterior adductor quick-muscle scars are placed between the lobes. The support structure scars are crescent-shaped, lateral to the anterior adductor muscle scars, raised, and slope medially (Figure 5H–M). The small anterior muscle scars may be separated (Figure 5H–I) or side by side (Figure 5J–K). Sometimes there is a small anterior septum (Figure 5L). The impressions of the dorsal mantle canals (*vascula media*) are very faint. The valve surface is densely punctate.

Remarks

At two North Otago localities this species is very common, hundreds of specimens, juvenile to adult, having been collected at each site (Table 2). The range in the number of spines on these specimens is large (from 100+ to few to none). This is an important example of the range of morphological variation that may exist within a single craniid species. Fossil *N. lecointei* occurs with *Valdiviathyris quenstedti* in tuffs and limestones in North Otago, and extant specimens of these two species have been found coexisting on a sandstone boulder dredged from a depth of 400 m, 200 km off the Taranaki coast, New Zealand (Robinson & Lee 2007). The Late Eocene (Runangan) specimen from Bridge Point, Kakanui in Figure 5B–C (OU 43718) was used to calibrate a relative time-tree in Robinson (2017a).

Novocrania huttoni (Thomson, 1916)
Stratigraphic range: Late Oligocene – Recent

Crania sp. indet. Hutton, 1873: p. 87.
Crania huttoni – Thomson 1916: p. 41, pl. 1, figs 1–2.
Neocrania huttoni – Lee & Brunton 1986: p. 152.
Novocrania huttoni – Lee & Brunton 2001: p. 5.

Thomson (1916) described and named this species from extant specimens probably collected in Whangaroa Harbour, Northland (Lee 1987). Robinson (2017a, fig. 4) figured an extended geographical range of extant *N. huttoni*, including New Zealand and Australia. Robinson and Lee (2007) suggested that fossil *N. huttoni* had been found in North Otago; this material is placed in *N. lecointei*.

Material examined

Three partial dorsal valves and many fragments from Late Oligocene (Duntroonian) locality Cosy Dell Farm, Southland (Table 2, Figure 2D). All material is held in the Geology Museum, University of Otago, Dunedin.

Description

Exterior: The three nearly complete dorsal valves are sub-quadrate to sub-pentagonal with a straight posterior margin; the largest specimen is 7.2 mm wide (Figure 6A). The nearly complete valves are conical with the apex near the centre. Some fragments are relatively thick, up to 1.5 mm, suggesting specimens grew large at this locality (extant *N. huttoni* dorsal valves grow up to 22 mm long and 2 mm thick). The valve exteriors are very worn, but one valve and five fragments have a portion of the ornament of radial costae preserved (Figure 6A–C). The valve exteriors and interiors have concentric colour bands that alternate dark-grey and brown or light brown and cream (Figure 6A, D); the colour banding occurs right through the shell. The most complete valve has six alternating bands of each colour, also seen on the radial costae (Figure 6A).

Interior: The posterior adductor muscle scars are sub-oval, close to the posterior margin, flush with the valve surface or very slightly raised. The oblique internal muscle scars are indistinct (Figure 6E–F). The anterior adductor slow-muscle scars are particularly large, U-shaped with wide lobes and flush with the valve floor or slightly raised. The wide lobes sometimes enclose the dimples
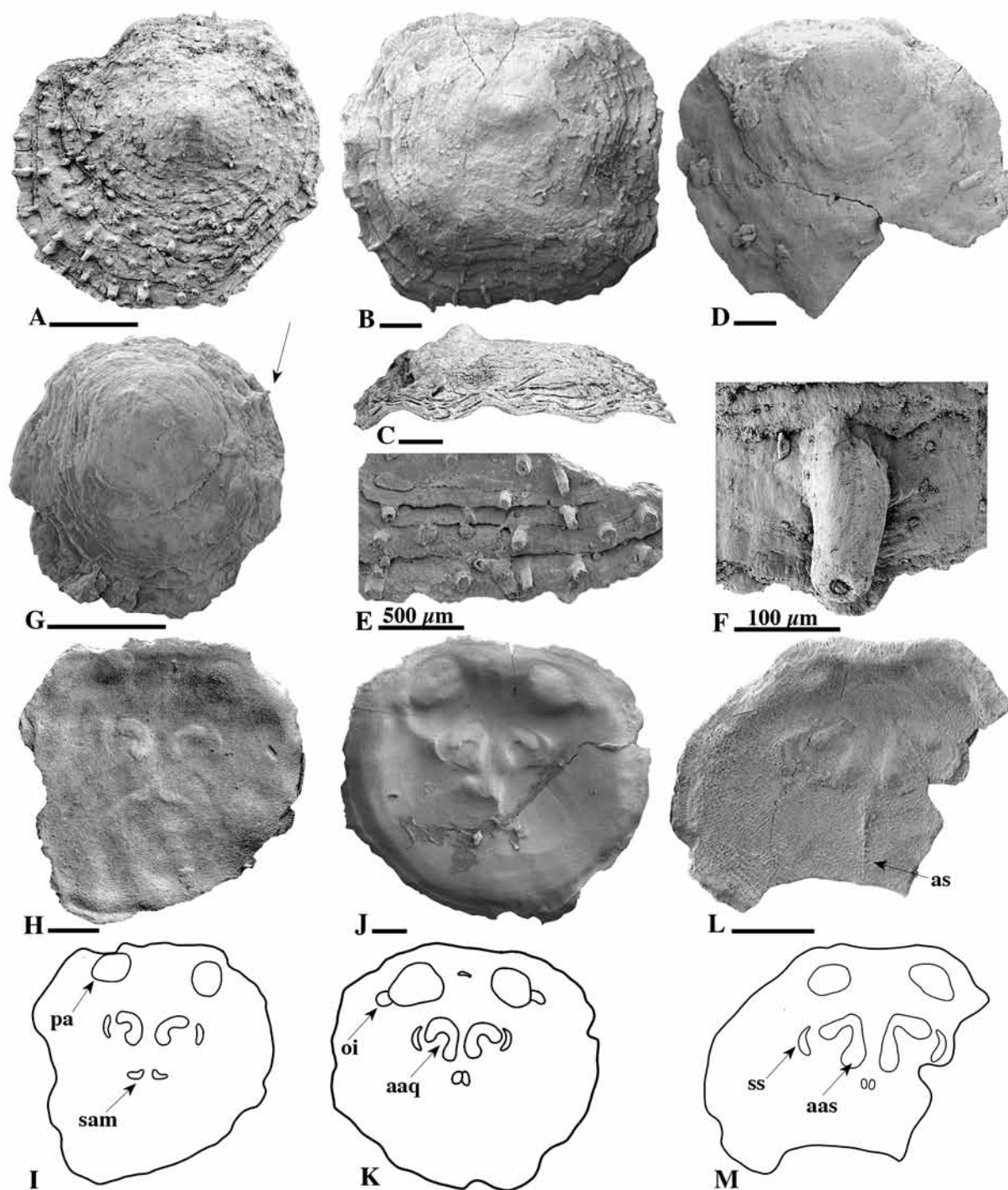
Figure 5: SEM images and line drawings of *Novocrania lecointei*. All fossil dorsal valves. A. OU 45400. Exterior view. B–C. OU 43718. B. Exterior view. C. Lateral view. D. OU 43711. Exterior view. E. OU 46958 Valve fragment with spines. F. OU 45400. Close-up of hollow spine. G. GS 12163. Juvenile valve exterior, single row of spines arrowed. H–I. OU 12001. H. Interior view. I. Line drawing showing muscle scars. J–K. GS 9481. J. Interior view. K. Line drawing showing muscle scars. L–M. OU 44391. L. Interior view. M. Line drawing showing muscle scars. All scale bars 1 mm unless indicated otherwise. GNS Science, Upper Hutt; OU – Geology Museum, University of Otago, Dunedin.

Abbreviations: aaq – anterior adductor quick-muscle scar, aas – anterior adductor slow-muscle scar, as – anterior septum, oi – oblique internal muscle scar, pa – posterior adductor muscle scar, sam – small anterior muscle scar, ss – support structure.

of the anterior adductor quick-muscle scars, while the support structure scars are relatively small and occur at the ends of the lateral lobes of the anterior adductor muscle scars. The small anterior muscle scars form separate indentations in one figured specimen (Figure 6E–F) but are indistinguishable from surface textures in the other specimen (Figure 6G–H). The valve surface is densely punctate.

Remarks

This is the first fossil *N. huttoni* to be described and figured. The Cosy Dell fauna is considered to be from a shallow, rocky shoreline (Lee et al. 2014) and the relatively large anterior adductor slow-muscle scars of *N. huttoni* specimens may reflect the need for large muscles to hold the valves closed in turbulent waters. MacFarlan et al. (2009, p.267) listed "*Novocrania huttoni* E. Pli – Rec." under Cenozoic brachiopods of New Zealand. This refers

to material identified as "*Neocrania chathamensis*?" in Lee (1993, table 4.30) in a list of brachiopods collected from the Plioceneage Whenuataru Tuff, Chatham Islands. This study placed that material into *Novocrania lecointei* (GS 12163, Figure 5G).

***Novocrania chathamensis* (Allan, 1937)**
Stratigraphic range: late Paleocene – Late Eocene

Crania chathamensis Allan, 1937: p. 155, pl. 16, fig. 4.
Neocrania chathamensis – Lee & Brunton 1986: p. 152.
Novocrania chathamensis – Lee & Brunton 2001: p. 5.

Allan (1937) described this species from the Red Bluff Tuff, Waikaripi, of late Paleocene age (Teurian), in the Chatham Islands, New Zealand. Lee (1987) described it in greater detail, noted further localities in the Chatham Islands and on the New Zealand mainland, and extended the stratigraphic range. Lee et al. (1997) noted another locality in North Otago. All specimens of *N. chathamensis*
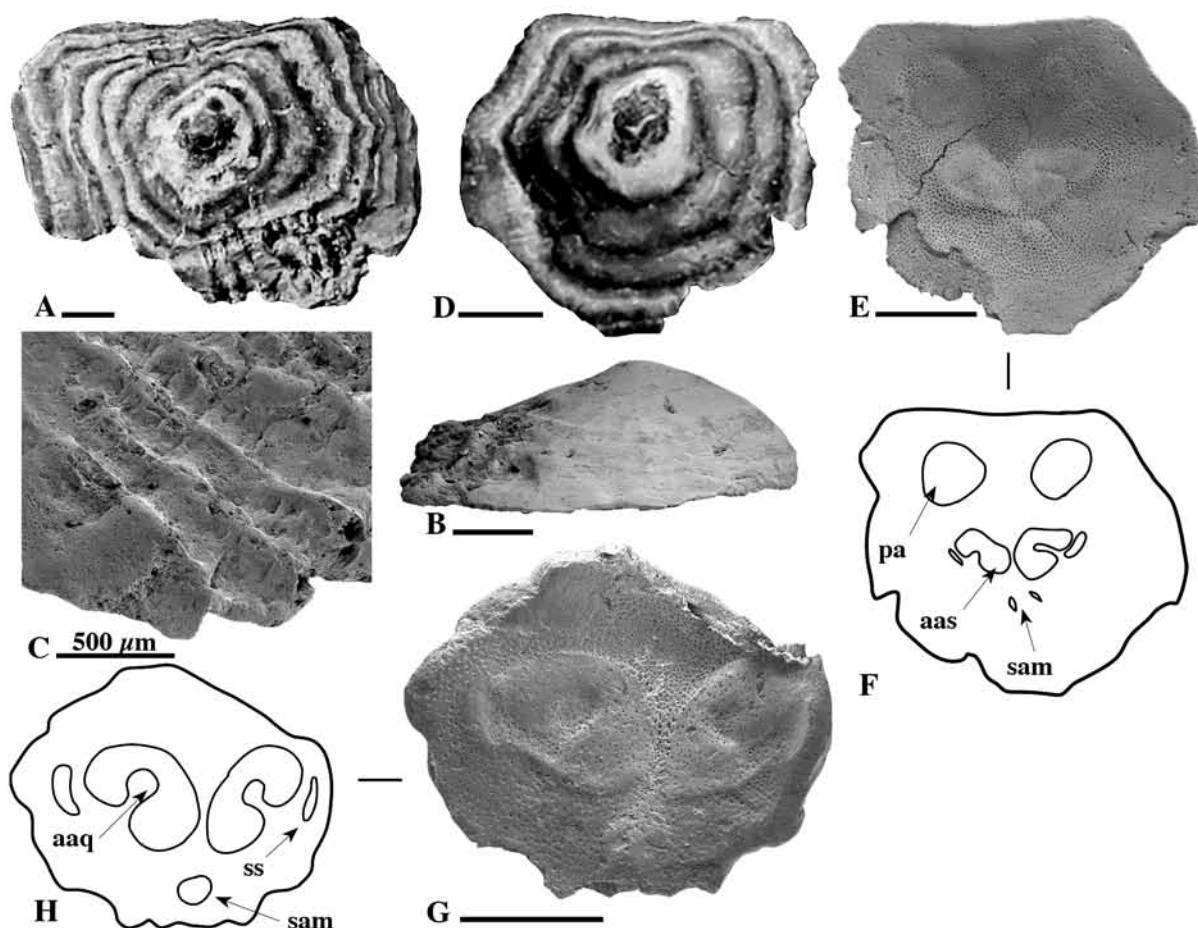

Figure 6: Digital and SEM images and line drawings of *Novocrania huttoni*. All fossil dorsal valves from Cosy Dell farm. A–C. OU 45309. A. Exterior view. B. Lateral view. C. Close-up of radial rib ornament. D–F. OU 45310. D. Exterior view. E. Interior view. F. Line drawing showing muscle scars. G–H. OU 45368. G. Partial valve interior showing anterior adductor muscle scars. H. Line drawing showing muscle scars. All scale bars 1 mm unless indicated otherwise. OU – Geology Museum, University of Otago, Dunedin. Abbreviations: aaq – anterior adductor quick-muscle scar, aas – anterior adductor slow-muscle scar, pa – posterior adductor muscle scar, sam – small anterior muscle scar, ss – support structure muscle scar.

from the North Otago localities of Lee (1987) and Lee et al. (1997) are placed into *N. lecointei*, leaving *N. chathamensis* with a known age range of late Paleocene (Teurian) to Late Eocene (Runangan) and occurring only on the Chatham Islands.

Material examined

Twenty-four dorsal valves (whole and partial), ranging in age from the late Paleocene (Teurian) to the Late Eocene (Runangan), from four Chatham Island localities (Table 2, Figure 2E). The material is held by the Geology Museum, University of Otago, Dunedin, and by GNS Science, Upper Hutt.

Description

Exterior: The dorsal valve is sub-circular, sub-oval or irregular in outline, strongly inflated and robust, with an ornament of strong radial ribs intersecting strong concentric growth lamellae (Figure 7A–B); the valve apex is generally worn (Figure 7A, C–D). The largest valve is the type specimen, 9.4 mm long (Lee 1987).

Interior: The posterior adductor muscle scars are large, sub-oval, and slightly raised above the valve surface. The oblique internal muscle scars are indistinct. The anterior adductor slow-muscle scars are raised, bi-lobed and J-shaped (Figure 7E–F, the medial lobe is longer). The anterior adductor quick-muscle scars form dimples

between the lobes. The crescent-shaped support structure scars are lateral to the anterior adductor muscle scars and flush with the valve surface. The small anterior muscle scars are indistinct but probably attached to a raised mound anterior to the anterior adductor scars, and on either side of the raised mound are two shallow depressions formed by the dorsal mantle canals (*vascula media*) (Figure 7E).

Remarks

Basset (2000) indicated the range of *Novocrania* as Eocene to Recent; however, as *N. chathamensis* is found in late Paleocene strata, the known range of *Novocrania* is extended back to the late Paleocene (~60–56 Ma).

Novocrania skeatsi (Allan, 1940)
Stratigraphic range: Late Oligocene – early Middle Miocene

Crania quadrangularis Tate, 1893: p. 191, pl. 11, figs 12–12a.
[?]*Crania quadrangularis* – Thomson 1927: p. 137.
Ancistrocrania skeatsi – Allan 1940: p. 277, pl. 35, fig.1.
Craniscus skeatsi – Lee & Brunton 1986: p. 146.
Craniscus tasmaniensis – Archbold 1991: p. 427, fig. 3D–J.
Craniscus singletoni – Archbold 1991: p. 427, fig. 3A–C.
Craniscus sp. 1 – Archbold 1991: p. 427, fig. 3O–P.
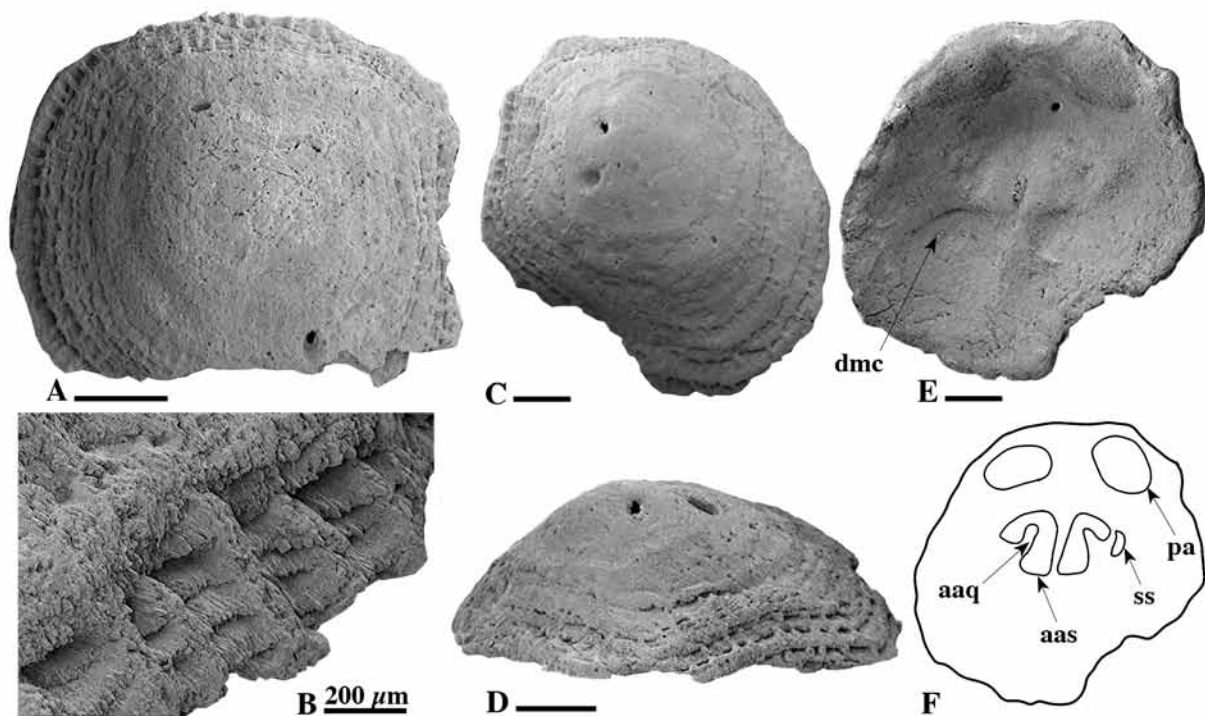*Craniscus* sp. 2 – Archbold 1991: p. 427, fig. 3K–L.

Figure 7: SEM images and line drawing of *Novocrania chathamensis*. All dorsal valves. A–B. GS 12789a. A. Valve exterior. B. Close-up of ornament. C–F. GS 12789b. C. Valve exterior. D. Lateral view. E. Valve interior. F. Line drawing showing muscle scars. All scale bars 1 mm unless indicated otherwise. GS – GNS Science, Upper Hutt.
Abbreviations: aaq – anterior adductor quick-muscle scar, aas – anterior adductor slow-muscle scar, dmc – dorsal mantle canal, pa – posterior adductor muscle scar, ss – support structure scar.

This species was first described as *Crania quadrangularis* from Waurn Ponds, Victoria, Australia, by Tate (1893). It was subsequently discovered in other localities by Tate (1899), Hall and Pritchard (1899), Dennant and Kitson (1903), May (1919) and Crespin and Chapman (1927). Thomson (1927) synonymised this species under the genus *Craniscus* but indicated his uncertainty with question mark. Allan (1940, p. 278) renamed the species *skeatsi*, as the name *quadrangularis* was preoccupied, and noted that 'the Australian fossil does not possess the marked tripartite structure of the genotype of *Craniscus* and is therefore not applicable to it'. He placed it into *Ancistrocrania* Dall, 1877. Lee and Brunton (1986) returned it to the genus *Craniscus,* based on a literature review. Archbold (1991) examined all fifteen known specimens from south-eastern Australia, proposed two new species of *Craniscus*, and designated three individual specimens as *Craniscus* sp. 1, *Craniscus* sp. 2 and Craniacean indeterminate.

Archbold (1991, p. 426) proposed the new species *Craniscus tasmaniensis*, based on two dorsal valves from near Table Cape, Tasmania (Figure 8A–C)*,* distinguished from *C. skeatsi* by having 'comparably thinner shells with generally wider posterior margins, more quadrate to elongate outlines and narrower and weakly defined marginal rims'. However, these specimens have the same distinctive features as *C. skeatsi*, namely the valve ornament, the anterior median septum and the process for attachment of the small anterior muscles; the differences cited by Archbold (1991) fall within the range of species variation.

Archbold (1991, p. 426) proposed the new species *C. singletoni* based on a single valve from the Batesford Limestone (Figure 8D–E). The valve is very wide (25.2 mm) and the dorsal mantle canals are strongly developed (Figure 8D). Williams et al. (1997) noted that, for brachiopods in general, mantle canals are best shown in gerontic individuals; the size of this specimen suggests it was long lived. Archbold (1991, p. 428) noted of this specimen that 'two small septa extend laterally from the small anterior muscles scar' (Figure 8D, arrowed as gmc). These appear to be part of the gerontic mantle canal system. This valve has the same exterior ornament (largely obscured by overgrowth), the same process for attachment of the small anterior muscles and the same anterior median septum as other specimens assigned to *C. skeatsi*.

Archbold (1991, p. 428) designated a partial dorsal valve (SM T882D) as *Craniscus* sp. 1 because the apex is set well to the posterior and the posterior adductors are elongate and unequal in size. This specimen was only observed from Archbold's figures (3O–P); however, the posterior adductor muscle scars may vary markedly in size

and shape within a single craniid species. The radial valve ornament and the anterior adductor muscle scars of this specimen are the same as those in specimens identified as *C. skeatsi*.

Archbold (1991, p. 428) designated specimen MV P121455 as *Craniscus* sp. 2, noted similarities between this specimen and *C. tasmaniensis* on valve outline and exterior appearance, but stated the interior was encrusted with worm tubes preventing assignment at species level. After cleaning of the valve interior, this specimen revealed the same features seen in other specimens of *C. tasmaniensis*. The two species names introduced by Archbold (1991), *C. tasmaniensis* and *C. singletoni*, are here placed in synonymy under *C. skeatsi* as are the specimens designated *Craniscus* sp. 1 and *Craniscus* sp. 2.

Archbold (1991, p. 428) described a single incomplete dorsal valve (MV P121457) as 'Craniacean indet'. This specimen is not a craniid, but probably a mollusc. The inner surface is partially obscured but is smooth rather than worn and there is no sign of punctae or muscle scars.

Specimens of Jurassic *Craniscus* from four European institutions have been examined by the author as part of an unpublished review of the genus *Craniscus*. European Jurassic *Craniscus* specimens have a number of distinctive features (including septa-like partitioning of the dorsal valve interior and placement of the anterior adductor muscle scars on the posterior side of the partitions) not seen in these Australian specimens, and the latter do not belong in the Jurassic genus (as previously stated by Allan). The species *skeatsi* is here transferred to the genus *Novocrania*.

Material examined

Twelve complete dorsal valves (the ventral valve is unknown), ranging in age from the Late Oligocene (Janjukian) to the Early Miocene (Longfordian), from locations in Tasmania and Victoria (Table 1, Figure 1C). The material is held in the collections of the Australia Museum, Sydney and Museums Victoria, Melbourne.

Description

Exterior: The valves are sub-conical, sub-quadrate to six-sided; the posterior margin is straight and nearly the full valve width; the posterior corners are often close to right angles. The posterior lateral margins are straight to slightly curved; the anterior lateral margins are curved; the anterior margin is straight and parallel to the posterior margin. The ornament may occur right to the valve apex but is often completely worn away. The apex position varies from being central to being at the posterior third. The valves from Tasmania (Figure 8A–C) are relatively thin, up to 0.5 mm, with a fine ornament of concentric growth lamellae

and radial ribs. The valves from Victoria have a coarser ornament and are more robust, up to 1.3 mm thick (Figure 8D–I). The largest valve is 21.3 mm long, 25.2 mm wide and 3 mm high (Figure 8D) but some of the smaller valves are higher.

Interior: The posterior adductor muscle scars are widely spaced and range from flush with the valve floor to being moderately convex (Figure 8B, D, H). The oblique internal muscle scars are lateral to the posterior adductor muscle scars (Figure 8E). In some specimens there is a low transverse platform that slopes posteriorly where the anterior muscles attach (Figure 8D, H). The

anterior adductor slow-muscle scars are variable in shape, from broadly and evenly U-shaped (Figure 8B–C) to elongated (Figure 8D–E). The anterior adductor quick-muscle scars form deep dimples between the lobes. The support structure scars are crescent-shaped, raised laterally and slope medially (Figure 8C, E, I). The small anterior muscle scars occur on raised mounds or stumpy processes. The anterior median septum is attached to the posterior side of the mound/process and is highly variable, ranging from being completely absent to being short (Figure 8B), to reaching two-thirds of the way to the posterior margin, or to reaching the posterior margin (Figure 8D, H). The
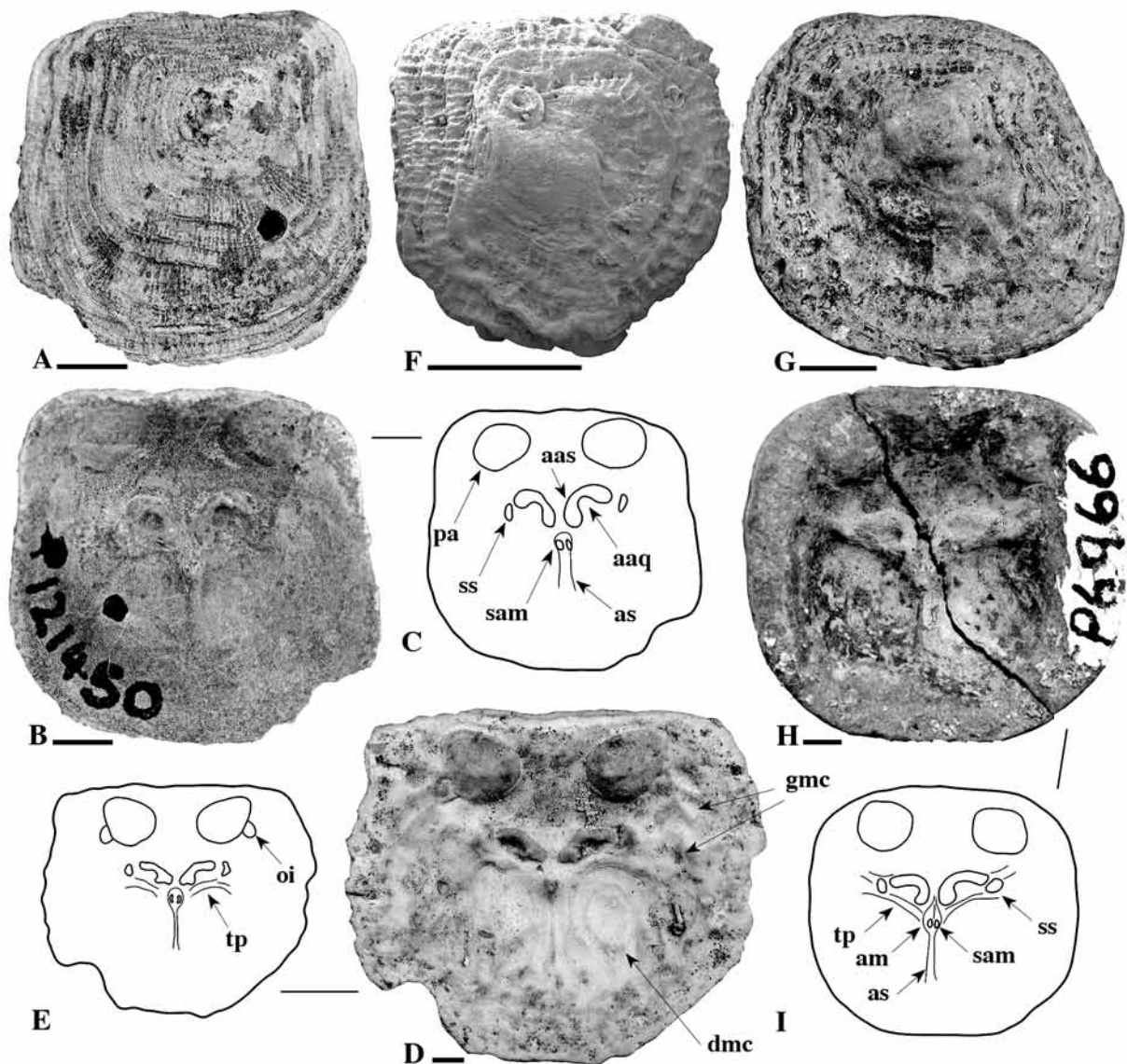

Figure 8: Digital and SEM images and line drawings of *Novocrania skeatsi*. All fossil dorsal valves. A–C. NMV P121450. A. Valve exterior. B. Valve interior. C. Line drawing of internal features. D–E. NMV P120315. D. Valve interior. E. Line drawing of internal features. F. C142688. Juvenile exterior (SEM). G. C142689. Valve exterior. H–I. NMV P6966. H. Valve interior. I. Line drawing of internal features. All scale bars 2 mm. C – Museum Australia, Sydney; NMV – Victoria Museum, Melbourne.
Abbreviations: aaq – anterior adductor quick-muscle scar, aas – anterior adductor slow-muscle scar, am – anterior mound, as – anterior septum, dmc – dorsal mantle canals, gmc – gerontic mantle canals, oi – oblique internal muscle scar, pa – posterior adductor muscle scar, sam – small anterior muscle scar, ss – support structure scar, tp – transverse platform.

valves have a smooth, flat marginal rim, 2–4 mm wide in the specimens from Victoria (Figure 8D, H); the valve surface is densely punctate.

Remarks

The very wide, flat marginal rim in some specimens suggests this species may have had a thin organic ventral valve like extant *Novocrania huttoni* and *N. lecointei*. The marginal rims of extant *Novocrania* species with a calcified ventral valve are often concave (to fit onto a convex ventral valve rim) and tuberculate.

Genus *Valdiviathyris* Helmcke, 1940 (late Middle Eocene – Recent)
Type species *Valdiviathyris quenstedti* Helmcke, 1940

Valdiviathyris quenstedti Helmcke, 1940
Stratigraphic range: late Middle Eocene – Recent

Valdiviathyris quenstedti Helmcke, 1940: p. 237, text fig. 5.

Helmcke (1940) described this species from a single type specimen from Saint Pauls Island in the Indian Ocean (Robinson & Lee 2007, fig. 2). Robinson and Lee described and figured extant specimens from several localities to the west and north of New Zealand and from Fiordland,

New Zealand, and fossil specimens (dorsal valves only) from three Late Eocene (Runangan) – earliest Oligocene (Whaingaroan) localities in coastal North Otago, New Zealand.

Material

Twelve whole dorsal valves, more than 100 partial dorsal valves and a single partial ventral valve from six localities, five in eastern North Otago and one in the Chatham Islands, ranging in age from late Middle Eocene (Kaiatan) to earliest Oligocene (Whaingaroan) (Table 2). Many of the dorsal valves lack the valve margins but retain all or part of the diagnostic twin median processes. All material is held in the Geology Museum, University of Otago, Dunedin.

Description

Exterior: The dorsal valves are smooth and delicate with a very thin shell; most specimens are incomplete, with the thinnest lateral and anterior margins broken. The valve outline is sub-quadrate to sub-transverse-oval (Figure 9A; Robinson & Lee 2007, figs 21–23).

Interior: The dorsal valve interior has sub-oval posterior adductor scars (Robinson & Lee 2007, figs 22–23). The small anterior muscle scars occur on a pair of median processes that may be directed ventrally or anteriorly. The
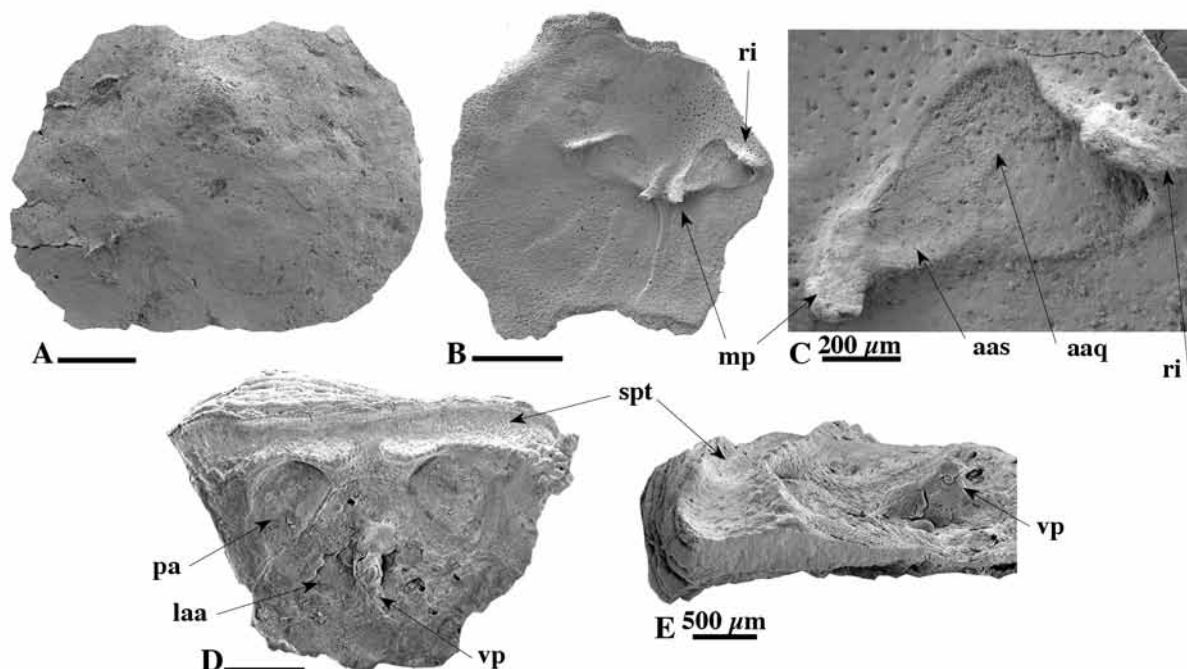

Figure 9: SEM of *Valdiviathyris quenstedti*. A. OU 45402a. Valve exterior. B–C. OU 45402b. B. Partial valve interior. C. Close-up of median process, anterior adductor scar and ridgelet where support structure attaches. D–E. OU 43723. Partial ventral valve. D. ventral view. E. Lateral view. All scale bars 1 mm unless indicated otherwise. OU – Geology Museum, University of Otago, Dunedin. Abbreviations: aaq – anterior adductor quick-muscle scar, aas – anterior adductor slow-muscle scar, laa – latent anterior adductor muscle scars, mp – median process, pa – posterior adductor muscle scar, ri – ridgelet, spt – straight posterior trough, vp – ventral process.

support structure scars are placed on the anterior side of small triangular ridgelets, the anterior adductor muscle scars lie between the processes and ridgelets (Figure 9B–C). The partial ventral valve has sub-oval posterior adductor muscle scars, a slim process rather than a full rostellum and the ventral anterior adductor muscle scars are probably latent. There is a straight posterior trough (Figure 9D–E) that is also found in extant *Valdiviathyris* (Robinson & Lee 2007, figs 8–10).

Remarks

Two partial specimens from the Early–Middle Eocene (Waipawan–Bortonian) of the Chatham Islands (Table 1) may be *Valdiviathyris* but the poor preservation negates a definite identification. Robinson and Lee (2007) noted that extant *Valdiviathyris* has a central cavity in the ventral valve. Robinson (2017b) stated that in the ventral valves of extant *V. quenstedti* the rostellum is usually latent but may be partly calcitic, partly latent. The rostellum in the single fossil ventral valve (Figure 9D–E) appears to be partly calcitic, partly latent. Robinson and Lee (2007, p. 129) suggested that 'by having the brachial protractor muscles attachment point situated more ventrally, on the processes, *V. quenstedti* may be able to manipulate its lophophore more effectively as the muscles are not all contracting dorsally'. Robinson (2014) found that the so-called brachial protractor muscles do not attach to the lophophore and renamed them the small anterior muscles. The function of these very small muscles, and how this function is (presumably) enhanced by the development of the processes they attach to in *Valdiviathyris*, remains unknown.

PALEOECOLOGY

The fossil craniid species of Australia and New Zealand occur in biofacies ranging in depth from shallow-shelf to very shallow water, in tropical to subtropical to temperate water temperatures and in limestones, calcarenites, tuffs, sandstones/conglomerates and mudstones (Table 4).

Danocrania allani is known from three calcarenite formations and two limestone formations in Western Australia (WA). The Wadera, Cashin and Pirie calcarenites of northern WA are rich in bryozoans and have ten, six and five species of brachiopod respectively (Cockbain 1966; Craig 2002). The Nanarup Limestone of southern WA is also dominated by bryozoa but includes brachiopods (nine species), bivalve and gastropod molluscs, echinoids, nautiloids, crabs and crinoids (Craig 1997). The Wilson Bluff Limestone of southern WA is fine-grained to chalky, dominated by bryozoa and echinoids and locally rich in molluscs and brachiopods (Clarke et al. 2003). A single

dorsal valve of *D. allani* was collected from the Blanche Point Formation, Aldinga, South Australia, which ranges in lithology from limestone through marl to biosiliceous clay, and contains a wide range of invertebrate fauna together with penguin bones (James & Bone 2000). *D. allani* lived in water depths varying from < 50 m to 100 m and sea temperatures from cool to warm.

Novocrania skeatsi has been collected from five localities in Victoria, Australia. Four localities are shallow-shelf, bioclastic bryozoal calcarenites— the Waurn Ponds Limestone, Calder River Limestone, upper Maude Limestone and Batesford Limestone. The fifth locality is the Muddy Creek Marl, a 'richly fossiliferous grey silty marl' (Fitzgerald 2004). Specimens have also been collected at a single locality in Tasmania, the shallow-water, mollusc-rich Freestone Cove Sandstone (Quilty 1972). *N. skeatsi* lived in water depths varying from < 20 m to < 70 m in subtropical sea temperatures.

Novocrania turbinata specimens were collected from deep-water mudstones and muddy sandstones in Northland, New Zealand; however, they were probably transported by mass debris flows from shallow-shelf depths (Hiller 2011) and thus the associated fauna may be mixed. *N. turbinata* probably lived in sea temperatures that were subtropical to marginally tropical (Hornibrook 1992).

Novocrania lecointei and *Valdiviathyris quenstedti* are known from two formations in eastern North Otago, New Zealand. The Ototara Limestone interfingers with the discontinuous Waiareka–Deborah Volcanics, which includes one large, stacked volcano (Moorhouse et al. 2015), and many small short-lived volcanoes (Coombs et al. 1986) that erupted pillow lavas and coarse to fine volcaniclastics into shallow-shelf, warm-water conditions. *N. lecointei* is the most abundant brachiopod at two Waiareka–Deborah Volcanics localities, at Bridge Point and Cape Wanbrow, both on the post-eruptive flanks of volcanoes. Both craniids are rare in the Ototara Limestone. The Waiareka–Deborah Volcanics have widely varying faunas at different localities, with bryozoa, brachiopods, echinoderms, bivalve molluscs, crinoids, barnacles and formanifera being locally abundant. The Ototara Limestone is dominated by bryozoa, while brachiopods are very abundant in some localities, with bivalve molluscs, echinoids, crinoids, barnacles and foraminifera varying in abundance. *N. lecointei* and *V. quenstedti* lived in water depths varying from 10 m to 100 m and the surface temperature was 18–20° C.

Novocrania huttoni is found in the Chatton Formation at Cosy Dell farm, Southland. This species lived in a turbulent, shallow-water, rocky shoreline environment; the preserved highly diverse, shallow-water molluscan fauna is exceptional (Lee et al. 2014). The thick dorsal valve of

N. huttoni, made thicker by radial costae, may be a defence against predatory drilling gastropods; many Cosy Dell mollusca and brachiopods have drilled valves. At Cosy Dell, *N. huttoni* lived at water depths of probably < 30 m and the water temperature was subtropical.

DISCUSSION

A southern hemisphere clade

The molecular analyses of Cohen et al. (2014, p. 145) found there were five clades of extant *Novocrania*, each with a single extant species, including a New Zealand clade (with *N. huttoni*) and a Southern clade (with *N. lecointei*). Cohen et al. (2014) stated that '*N. huttoni* is the sister-group of *N. lecointei*'. New analyses of the same data by Cohen et al. (Appendix 1, Robinson 2017a) place *N. huttoni* into the Southern clade with *N. lecointei*.

Four fossil species from Australia and New Zealand figured herein (*N. chathamensis*, *N. lecointei*, *N. huttoni*, *N. skeatsi*) have a strong radial element in their ornament that is not seen in other Recent and fossil *Novocrania* species. These four species may be part of the Southern clade of Cohen et al. (Appendix 1, Robinson 2017a). The calibrated time-tree in Robinson (2017a) suggested that *N. lecointei* and *N. huttoni* split from an ancestral species in the Late Eocene. *N. chathamensis* is the oldest species currently placed in *Novocrania* and may be the ancestor of the other Southern clade species (Figure 10).

Morphological stasis

There are many examples of long-lived taxa. Lee et al. (1997) described bryozoans encrusting pebbles from two North Otago Late Eocene localities and stated that two of these bryozoan species are extant and present in New Zealand waters. An extant tadpole shrimp, *Triops cancriformis* (Bosc et al. 1801), is indistinguishable from specimens known from the Permian (Gall & Grauvogel-Stamm 2005). Late Eocene specimens of *Novocrania lecointei* and *Valdiviathyris quenstedti* from North Otago are morphologically indistinguishable from extant specimens.

Cohen et al. (2014) stated that evolution of craniid rDNA is 'exceptionally slow', suggesting that craniid species may exist for a long time. The work presented here suggests that four fossil craniid species from New Zealand have very long stratigraphic ranges: *V. quenstedti* and *N. lecointei*
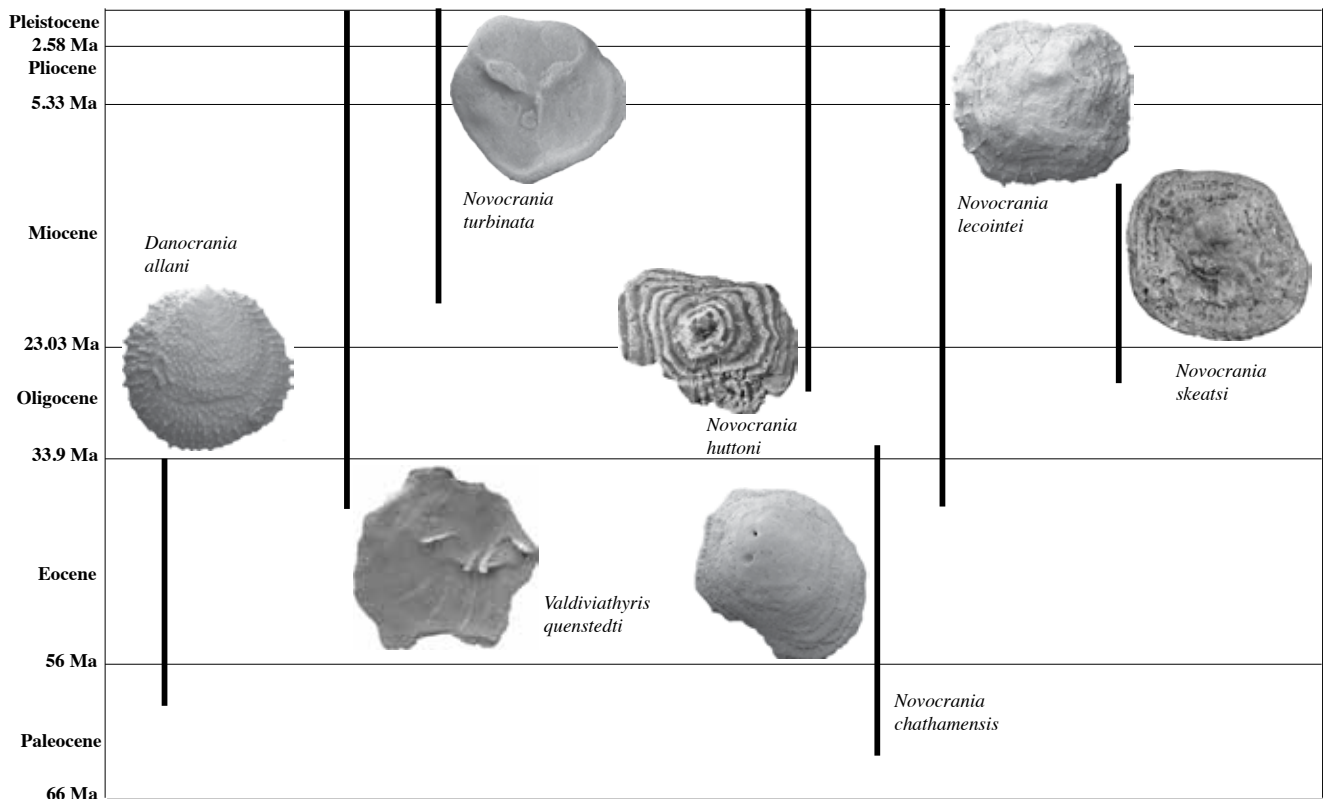

Figure 10: Known stratigraphic ranges of New Zealand and Australian craniid brachiopods. Timescale approximately to scale. The four species with a strong radial ornament (*N. chathamensis*, *N. lecointei*, *N. huttoni* and *N. skeatsi*) may all be part of a southern hemisphere clade, ie, having a single common ancestor.

(late Middle Eocene, Kaiatan, 39.1–36.7 Ma – Recent), *N. huttoni* (Late Oligocene, Duntroonian, 27.3–25.2 Ma – Recent) and *N. turbinata* (Early Miocene, Otaian, 21.7–18.7 Ma – Recent) (ages of stage boundaries from Raine et al. 2015). These long-lived species are regarded as a case of morphological stasis where 'morphologically delimited species persist without appreciable change for millions of years' (Futuyma 2010, p. 1867).

CONCLUSIONS

Westralicrania zenobiae is synonymised with *W. allani* and this species is transferred to the genus *Danocrania*. The stratigraphic range of *D. allani* is extended to the latest Eocene. *Craniscus tasmaniensis* and *C. singletoni* are synonymised under *C. skeatsi* and this species is transferred to the genus *Novocrania*. Fossil material previously identified as *Novocrania* cf. *turbinata* is confirmed as *N. turbinata*. Fossil *N. huttoni* is described and figured for the first time, and the stratigraphic ranges of *N. lecointei* and *N. huttoni* are extended back to the the late Middle Eocene and the Late Oligocene respectively. Four fossil craniid species with a strong radial ornament from Australia and New Zealand may be part of a southern hemisphere clade. Four fossil craniid species in New Zealand might be considered examples of morphological stasis with stratigraphic ranges longer than 20 million years.

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Table 1: Australian and European fossil *Danocrania* and Australian fossil *Novocrania* examined in this study.
C = Australian Museum, Sydney, New South Wales; F = Geological Survey of Western Australia, Perth; NMV P = Museum Victoria, Melbourne; OU = Geology Museum, University of Otago, Dunedin; SM = South Australian Museum, Adelaide; WAM = Western Australian Museum, Perth.

Species	Formation and Locality	Age	Catalogue Number
Danocrania allani			
3 whole ventral valves, 15 partial ventral valves, 5 partial dorsal valves	'Denham2 drillcore', Pirie Calcarenite, Denham, Western Australia	Middle Paleocene	F610215
1 ventral valve	'Waychinicup Limestone', Waychinicup, Western Australia	Middle Eocene	WAM 07.132
14 ventral valves and 5 dorsal valves	Nanarup Limestone, Nanarup, Western Australia	Late Eocene (Bartonian)	WAM 07.226
1 ventral valve	Nanarup Limestone, Mt Many Peaks, WA	Late Eocene	WAM 94.41
1 ventral valve	Nanarup Limestone, Mt Many Peaks, WA	Late Eocene	WAM 94.806
1 dorsal and 1 ventral valve	?Nanarup Limestone Mt Many Peaks, WA	Late Eocene	WAM 94.807
1 dorsal valve	Blanche Point Formation, Aldinga, South Australia	Late Eocene (Priabonian)	NMV P313936
Danocrania hagenowi			
4 dorsal and 4 ventral valves	Eben-Emael, Gulpen Formation, Leige, Belgium	Cretaceous (Late Maastrichian)	OU 44514 - 15
Danocrania geulhemensis			
5 dorsal valves and 14 ventral valves	Houthem Formation, Vroenhoven, Belgium	Paleocene (Early Middle Danian)	OU 44513
Novocrania skeatsi			
5 dorsal valves	Waurn Ponds Limestone, Waurn Ponds, Victoria	Late Oliocene (Janjukian)	C 142689, NMV P3836, P3834, P3835, P6966
2 dorsal valves	Calder River Limestone, Aire Coast, Victoria	Late Oligocene (Janjukian)	NMV P79448
1 dorsal valve	Upper Maude Limestone, Maude, Victoria	Early Miocene (Longfordian)	NMV P121455
2 dorsal valves	Freestone Cove Sandstone, Table Cape, Tasmania	Early Miocene (Longfordian)	NMV P121450, P121451
1 dorsal valve	Batesford Limestone, Batesford, Victoria	Early Miocene (Longford. – Batesford.)	NMV P120315
1 dorsal valve, 1 partial dorsal valve	Muddy Creek Marl, Hamilton, Western Victoria	Middle Miocene (Balcom. – Bairnsdal.)	C 142688, SM T882D

Table 2: New Zealand fossil *Novocrania* and *Valdiviathyris* specimens examined in this study.
CM = Canterbury Museum, Christchurch; GS = GNS Science, Upper Hutt; OU = Geology Museum, University of Otago, Dunedin.

Genus species	FRF Number	Formation and Locality	Age	Catalogue Number
Novocrania turbinata				
1 whole, 4 partial	O06/f0115	Waitiiti Formation, Waimamaku River	Otaian	CM 2006.64.87, 88, 91
4 partial valves	O06/f0117 O06/f0119	Waitiiti Formation, Taita Stream	Otaian	CM 2006.64.90
1 partial valve	O05/f0144 O05/f0145	Waitiiti Formation, Otueka Hill	Otaian	CM 2006.64.89
Novocrania lecointei				
4 whole, 7 partial dorsal valves	J41/f8025	Waiareka-Deborah Volcanics, Lorne	Kaiatan	OU 41306
55 partial valves	J41/f137	Waiareka-Deb. V. Lorne East	Kaiatan	OU 45400
Several hundred whole and partial dorsal valves	J41/f148	Waiareka-Deborah Volcanics Cape Wanbrow, Oamaru	Runangan	OU 44382, 44384, 44395
Several hundred whole and partial dorsal valves	J42/f036	Waiareka-Deborah Volcanics, Bridge Point, Kakanui	Runangan	OU 43718, 44381, 45374, 45399
1 whole dorsal valve		Waiareka-Deborah Volcanics Fortification Rd.	Runangan	OU 41306
8 partial dorsal valves		Ototara Limestone, Gees Road	Runangan	OU 45393
3 whole dorsal valves	J42/f435	Ototara Limestone, Everett's Quarry	Whaingaraoan	OU 12001
2 juvenile dorsal valves	CH/f13B	Whenuataru Tuff, Moutapu Pt	Pliocene	GS 12163
Novocrania huttoni				
3 partial dorsal valves, 100+ fragments	F45/f396	Chatton Formation, Cosy Dell farm, Waimumu, Southland	Duntroonian	OU 45309–10, 45391
Novocrania chathamensis				
1 partial valve	CH/f104	Red Bluff Tuff, Waikaripi,	Teurian – Waipawan	OU 45612
1 whole, 1 partial dorsal valve	CH/f475	Matanginui Limestone, Waipapa Creek	Waipawan – Bortonian	GS 12167
2 partial valves		Matanginui Limestone, Blind Jims Creek, Chatham Islands	Waipawan – Bortonian	OU 45593
11 whole, 8 partial dorsal valves	CH/f512	Te One Limestone, Moeroa, Chatham Islands	Kaiatan – Whaingaraoan	GS 12789
Valdiviathyris quenstedti				
1 partial dorsal valve	CH/f475	Matanganui Lst, Waipapa Creek, Chatham Islands	Waipawan – Bortonian	OU 45389
1 dorsal valve		Matanginui Limestone, Blind Jims Creek, Chatham Islands	Waipawan – Bortonian	OU45594
2 partial dorsal valves	J41/f137	Waiareka-Deborah Volcanics Lorne East	Kaiatan	OU 45401
6 whole, 65 partial dorsal valves, 1 partial ventral valve	J41/f148	Waiareka-Deborah Volcanics, Cape Wanbrow, Oamaru	Runangan	OU 44395-96, 43719, 45390. 45396, 45402a–b
3 whole, 45 partial dorsal valves	J42/f036	Waiareka-Deborah Volcanics, Bridge Point, Kakanui	Runangan	OU 43998, 45397
1 partial dorsal valve		Ototara Lst, Fortification Rd 2	Runangan	OU 45392
2 whole dorsal valves	J42/f435	Ototara Lst, Everett's Quarry	Whaingaraoan	OU 43184–85

Table 3: Latitude and longitude of localities of fossil craniids of Australia and New Zealand. Latitude-longitude with a ~ is approximate.

Species and locality	Author/ Material examined	Latitude	Longitude
Danocrania allani			
Denham, Western Australia	F610215	~25.91°S	~114.04°E
Aldinga, South Australia	NMV P313936	~35.22°S	~138.46°E
Waychinicup, Western Australia	WAM 07.132	~34.88°S	~118.35°E
Waychinicup, Western Australia	WAM 07.226	~34.88°S	~118.35°E
Nanarup, Western Australia	WAM 94.41	~34.97°S	~118.04°E
Nanarup, Western Australia	WAM 94.806	~34.89°S	~118.26°E
Nanarup, Western Australia	WAM 94.807	~34.89°S	~118.26°E
Novocrania skeatsi			
Hamilton, Victoria	C 142688	~37.74°S	~142.02°E
Waurn Ponds, Victoria	C 142689	~38.22°S	~144.27°E
Waurn Ponds, Victoria	NMV P3834	~38.22°S	~144.27°E
Waurn Ponds, Victoria	NMV P3835	~38.22°S	~144.27°E
Waurn Ponds, Victoria	NMV P3836	~38.22°S	~144.27°E
Waurn Ponds, Victoria	NMV P6966	~38.22°S	~144.27°E
Aire Coast, Victoria	NMV P79448	~38.8°S	~143.46°E
Batesford, Victoria	NMV P120315	~38.1°S	~144.29°E
Table Cape, Tasmania	NMV P121450	~40.98°S	~145.72°E
Table Cape, Tasmania	NMV P121451	~40.98°S	~145.72°E
Maude, Victoria	NMV P121455	~37.92°S	~144.16°E
Hamilton, Victoria	SM T882D	~37.74°S	~142.02°E
Novocrania chathamensis			
Blind Jims Creek, Chatham Islands	OU 45593	43.78°S	176.55°W
Waikaripi, Chatham Islands	OU 45612	43.958°S	176.576°W
Waipapa Creek, Chatham Islands	GS 12167	43.774°S	176.56°W
Moeroa, Chatham Islands	GS 12789	43.854°S	176.525°W
Novocrania lecointei			
Moutapu Point, Chatham Islands	GS 12163	44.227°S	-176.222°W
McDonalds Quarry, Kakanui	OU 45393	45.16°S	170.904°E
Everett's Quarry, Kakanui	OU 12001	45.176°S	170.903°E
Cape Wanbrow, Oamaru	OU 44382	45.113°S	170.982°E
Bridge Point, Kakanui	OU 43718	45.220°S	170.882°E
Lorne, Weston	OU 12000	45.053°S	170.883°E
Lorne East, Weston	OU 45400	45.061°S	170.893°E
Fortification Rd, Kakanui	OU 41306	45.174°S	170.901°E
Fortification Road 2, Kakanui	OU 45393	45.152°S	170.893°E
Novocrania turbinata			
Waimamaku River, Hokianga	CM 2006.64.87	35.559°S	173.49°E
Taita Stream, Hokianga	CM 2006.64.90	35.545°S	173.486°E
Otueka Hill, Hokianga	CM 2006.64.89	35.441°S	173.302°E
Novocrania huttoni			
Cosy Dell Farm, Southland	OU 45309–10, 91	46.111°S	168.8001°E
Valdiviathyris quenstedti			
Everetts Quarry, Kakanui	OU 43185	45.176°S	170.903°E
Bridge Point, Kakanui	OU 43998, 45397	45.220°S	170.882°E
Waipapa Creek, Chatham Islands	OU 45389	43.774°S	-176.56°W
Fortification Road 2, Kakanui	OU 45392	45.152°S	170.893°E
Lorne East, Weston	OU 45401	45.061°S	170.893°E
Cape Wanbrow, Oamaru	OU 45396, 45402	45.113°S	170.982°E
Blind Jims Creek, Chatham Islands	OU 45594	43.78°S	-176.55°W

Table 4: Paleoecology of Australian and New Zealand craniid species in this study.

Species	Depth	Temp.	Lithology	Fauna	Author
Danocrania allani Western Australia	< 50–100 m		calcarenite	bryozoa, brachiopods, echinoids, crinoids	Craig (2000); Milner (1989)
southern Western Australia	< 100 m	warm water	calcarenite/ limestone	bryozoa, echinoids, brachiopods, molluscs, foramifera	Craig (1997); Li *et al*. (2003)
South Australia	50–100 m	15° C	glauconitic marl	bivalves, brachiopods, bryozoan, echinoids, nautiloids	James & Bone (2000)
Novocrania turbinata	shallow shelf	warm temperate	mudstone – sandstone	brachiopods, molluscs	Hiller (2011)
Novocrania lecointei	10–100 m	18–20° C	limestone, volcanic tuff	brachiopods, molluscs, bryozoa, foraminiferids, ostracods, corals, barnacles	Lee *et al*. (1997) Robinson & Lee (2007) Edwards *et al*. (1991)
Novocrania huttoni	< 30 m	sub-tropical	sandstone conglomerate	molluscs, brachiopods, barnacles, bryozoa, corals, plants, seeds	Lee *et al*. (2014)
Novocrania chathamensis	10–100 m	+20° C	limestone	brachiopods, molluscs, bryozoa, foraminiferids, ostracods, corals, barnacles	Lee *in* Campbell et al. (1993) Robinson & Lee (2007) Edwards *et al*. (1991)
Novocrania skeatsi Victoria		sub-tropical	calcarenite limestone	bryozoa, brachiopods, echinoids, foraminifera	Gourley & Gallagher (2004)
Tasmania	< 70 m < 20 m	sub-tropical	sandstone	gastropods, brachiopods, sharks teeth, calcareous algae	Gill *et al*. (1962), Quilty 1972
Valdiviathyris quenstedti	10–100 m	18–20° C	limestone volcanic tuff	bryozoa, brachiopods, molluscs, foraminiferids, ostracods, corals, barnacles	Lee *et al*. (1997) Robinson & Lee (2007) Edwards *et al*. (1991)