



THE FOSSIL RECORD OF *LIMOPSIS* (BIVALVIA: LIMOPSIDAE) IN ANTARCTICA AND THE SOUTHERN HIGH LATITUDES

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Abstract: *Limopsis* is one of the most speciose and widespread bivalve genera in the Southern Ocean at the present day. However, the fossil record of the genus is poorly known from the southern high latitudes. Here, we review the fossil record in this region to help understand the evolutionary origins of the genus. *Limopsis infericola* sp. nov. and additional specimens of a previously described species are added to the fossil record of Antarctica. The globally distributed limopsid clade had its earliest occurrences in the Early Cretaceous of Europe and New Zealand, then radiated during the

Late Cretaceous (Maastrichtian, 70.6–65.5 Ma). Fossil evidence shows that the genus underwent a second, Cenozoic, radiation related to the isolation of Antarctica and the onset of cooling in the southern hemisphere. The genus has persisted in Antarctica for the last 50 myr, adapting to extreme changes in the environmental conditions, including surviving the last glacial maximum in marine refugia.

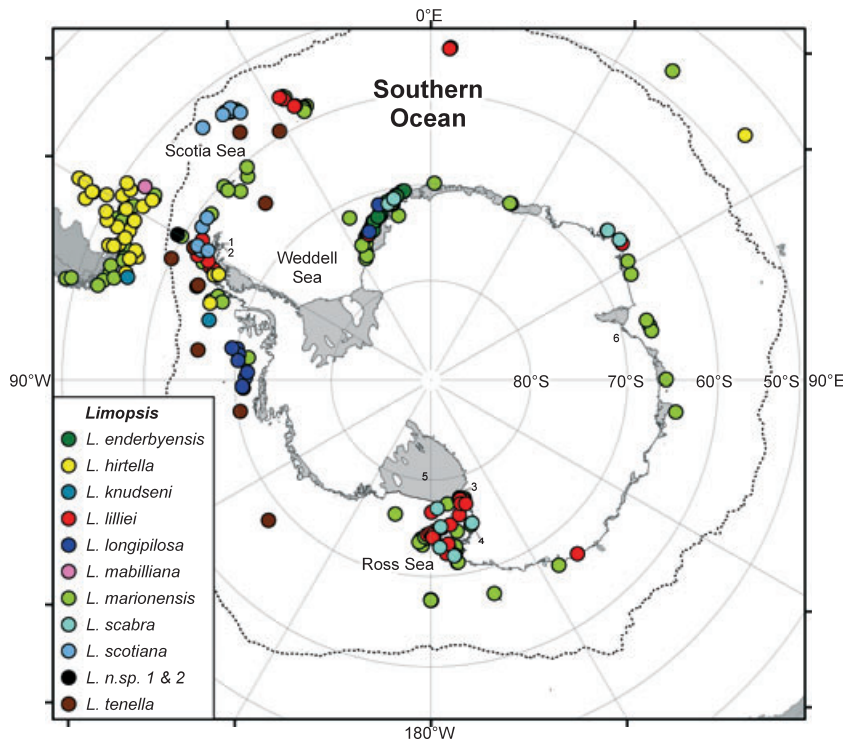
Key words: *Limopsis*, Antarctica, biogeography, systematics, evolutionary origins.

At the present day, the family Limopsidae Dall, 1895 (Arcoidea) contains two genera: *Empleconia* (Dall, 1908) restricted to the North Pacific and Bering Sea with no known fossils, and *Limopsis* Sassi, 1827 with a fossil record from the Mesozoic. At least forty extant and more than thirty extinct species of *Limopsis* are known (Tevesz 1977; Oliver 1981). *Limopsis* is described as having a cosmopolitan distribution, except for the high Arctic Ocean (Oliver 1981; Malchus and Warén 2005). However, *L. minuta* (Philippi, 1836) has been recorded as having a distribution that extends to above 70°N (Gofas *et al.* 2001). Bivalves of the genus *Limopsis* are epibenthic suspension feeders (Oliver and Allen 1980) and are lecithotropic nonbrooders (Malchus and Warén 2005). Species in the genus have a particular affinity to deep-sea habitats and the south polar regions (Nicol 1967; Vermeij 1978; Crame 1996). Members of the genus are characterized by having an orbicular, nearly equilateral shell shape, often with forward obliquity, by possessing strongly anisomyarian muscle scars (the anterior one being much larger than the posterior), a central resilifer and taxodont dentition (Newell 1969; Oliver and Allen 1980).

The global fossil record and evolutionary history of *Limopsis* is still poorly known (Oliver 1981). Tevesz (1977) suggested that the first recorded instance of *Limopsis* in the fossil record was in the Middle Jurassic (around 168 Ma) of Europe. However, the Jurassic species

'*Limopsis*' *minima* (Sowerby, 1825) and '*Limopsis*' *coralinensis* (Buvignier, 1852) have been disregarded by Oliver (1981) and placed in the Grammatodontidae because of the ligament shape. Hallam (1976, 1977) described the radiation of *Limopsis* in the Jurassic, but his records were based on *L. minima* and thus are disregarded. Oliver (1981) believed that the first truly recognizable *Limopsis sensu stricto* specimens, assigned to *L. albiensis* (Woods, 1899), were from the Early Cretaceous (Albian, around 112 Ma) of England (Woods 1899). There is also evidence that *Limopsis* occurred uncommonly in late Early Cretaceous rocks of New Zealand, although species are unnamed (Speden 1975; Moore and Speden 1984). The genus underwent a Late Cretaceous (Maastrichtian) radiation into different life habits (Heinberg 1979; Oliver 1981), reaching a peak in the early Cenozoic (Oliver 1981).

Limopsis is a common element of the modern bivalve fauna in the Antarctic and sub Antarctic (Hain 1990; Linse 1999; Zelaya 2005; Aldea *et al.* 2008), occurring at all water depths of up to 4678 m (Griffiths *et al.* 2003). There are twelve known species from the Southern Ocean and adjacent South American Magellan region (Dell 1990; Linse 2002; <http://www.antarctica.ac.uk/sombase>, K. Linse unpublished data; Text-fig. 1). In the southern high latitudes, seventeen further *Limopsis* species were recorded from waters around Australia in water depths of up to



TEXT-FIG. 1. The distribution of Recent *Limopsis* species in the Southern Ocean and adjacent Magellan Region, with locations of some fossil localities. 1 = Seymour Island, 2 = Snow Hill Island, 3 = McMurdo Sound, 4 = Victoria Land Basin, 5 = Deep Sea Drilling Project Site 270 and 6 = Vestfold Hills.

600 m (Lamprell and Healy 1998), four species were found around South Africa in water depths of up to 550 m (Ocean Biogeographic Information System (2010) <http://www.iobis.org>) and three species from New Zealand in depths from 422 to 1280 m (Beu 2006). The diversity of present-day Southern Ocean limopsids could be explained either by their migration into the region from elsewhere or by origination and diversification *in situ*. Beu (2009) suggests that *Limopsis* has little or no confirmed fossil record in Antarctica. In this study, we have been able to confirm further records in both Antarctica and the southern high latitudes, by studying specimens and published literature, and go on to use these to investigate the origins of the genus.

MATERIALS AND METHODS

SOMBASE (Griffiths *et al.* 2003), SOMBASE-GSCM (the Cenozoic Marine Fauna Database, developed by H. Griffiths) and the Palaeobiology Database (<http://paleodb.org>) were used to access data on the distribution of fossil and Recent limopsids in Antarctica and the southern high latitudes. To confirm the affinity of new Antarctic fossil specimens of *Limopsis*, material was studied at the British Antarctic Survey and the Instituto de Geociências, Universidade de São Paulo, using an optical microscope, measured using vernier callipers, drawn with the aid of a camera lucida and photographed using a digital camera.

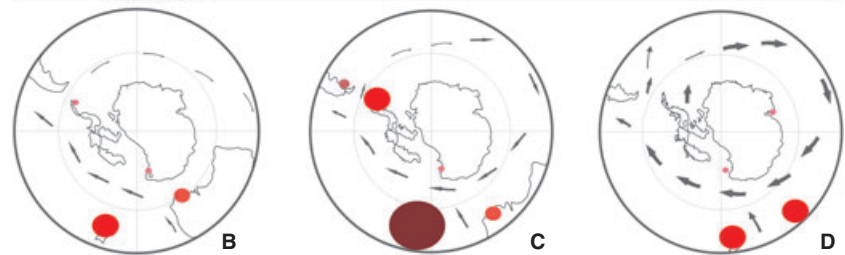
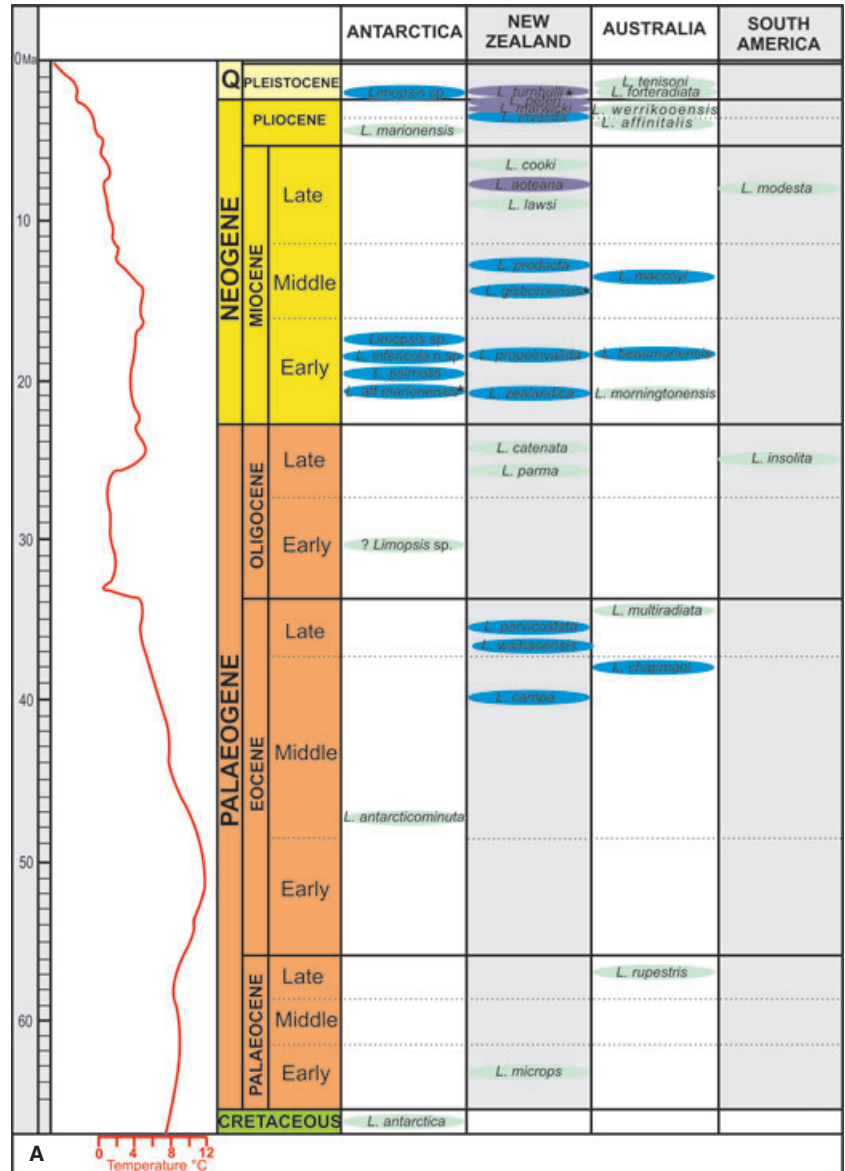
Modern Antarctic specimens from the Scotia Arc region, the Antarctic Peninsula and the Weddell Sea are held in the British Antarctic Survey marine collections, and this material was also examined. Fossil specimens were also studied at the Natural History Museum in London. Published occurrences and systematic descriptions of *Limopsis* were consulted to ascertain the extent of the fossil record in the southern high latitudes, and fossil mollusc experts in the Southern Hemisphere were consulted for information on any unpublished material. Comparative drawings were made from specimens and from published photographs and line drawings.

THE FOSSIL RECORD OF *LIMOPSIS* IN THE SOUTHERN HIGH LATITUDES

Published literature has shown that *Limopsis* occurred in New Zealand from the Cretaceous to the Pleistocene (Text-fig. 2). Although the shallower water species became extinct during the Quaternary, Beu (2006) claimed that species previously assigned to the genus *Pectunculina* should be reassigned to *Limopsis* and therefore there are records of Recent *Limopsis* in New Zealand. A study of new material and published literature has shown that fossil specimens of at least five different species of *Limopsis* have been found in Antarctica, ranging in age from the Maastrichtian (Cretaceous) to the Pleistocene (Text-fig. 2). Published fossil evidence of the genus in southern

TEXT-FIG. 2. A, The fossil record of *Limopsis* in Antarctica and first occurrences in the fossil record of named *Limopsis* species (not subspecies) from the published literature in other southern high latitudes areas from the Maastrichtian (Late Cretaceous) to the Pleistocene. The water depths for the deposits in which the fossils were found are also given (see text for references).

— = Bathyal;
 — = Outer Shelf;
 — = Shallow/Inner shelf; *the fauna may have been transported from shallower depths to the site of deposition. Cenozoic temperature curve from Zachos *et al.* (2001). B, C, Continental reconstructions with palaeocirculation for key time periods are shown (from Lawver and Gahagan 2003) and new occurrences of fossil limopsids are plotted on these. B, Maastrichtian–Eocene. C, Oligocene–Miocene. D, Pliocene–Pleistocene. Coloured dots represent the number of first occurrences of limopsid taxa. • = 1; • = 2; • = 3; • = 4; • = 5; • = over 5.



South America appears to have been restricted to the presence of just two species, found from the Late Oligocene to the Late Miocene in several localities (Sowerby 1846; Ihering 1899; Doello Jurado, 1915; Zinsmeister 1981; Del Río and Martínez 1998; Frassinetti and Covacevich 1999; Del Río 2004; Griffin and Nielsen 2008; Casadio and Griffin 2009; Parras and Griffin 2009). *Limopsis* first appeared in the published fossil record of

Australia from the Late Paleocene and continues to the present day (Chapman 1911).

Cretaceous–Eocene

The oldest named New Zealand species is the Early Paleocene (Danian) age (Text-fig. 2) *L. (Limopsis) microps*

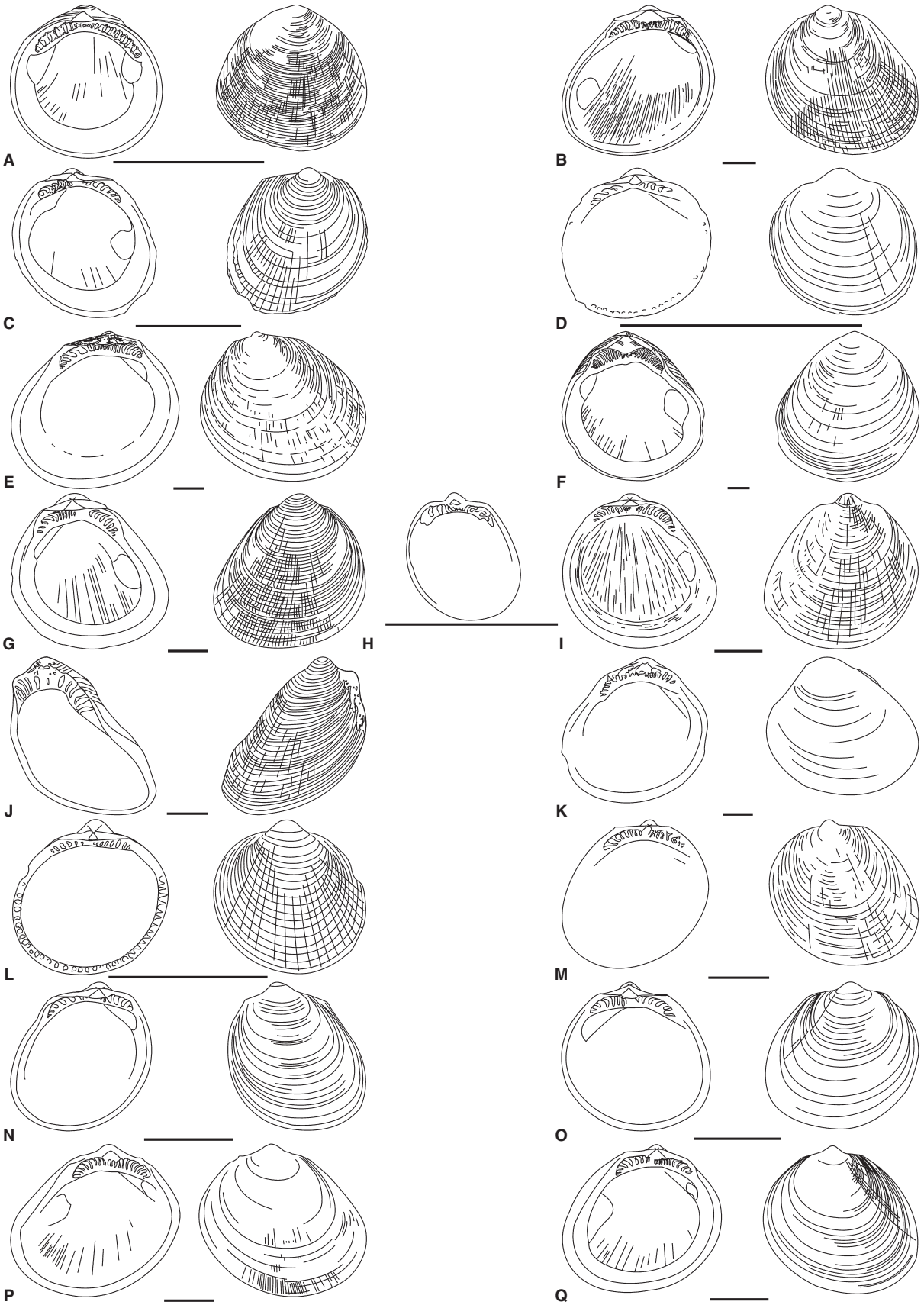
Finlay and Marwick, 1937 from the Wangaloa Formation at Wangaloa and Boulder Hill, South Island, which was a shallow water deposit (Finlay and Marwick 1937; Beu and Maxwell 1990). The species is now referred to *L. microps* (Text-fig. 3A) as Beu (2006) did not consider the subgenus *Limopsista* to be valid. However, there are several records of unpublished and unnamed specimens of *Limopsis* recorded in New Zealand, from the Piripauan–Haumurian local stages (Santonian–Maastrichtian; FRED – The Fossil Record Electronic Database – <http://www.fred.org.nz/index.jsp>) and also some unnamed older occurrences in the Early Cretaceous (Speden 1975; Moore and Speden 1984), so it is clear that *Limopsis* had a much longer and more extensive fossil record in New Zealand than the published literature of described species shows. The Maastrichtian species *L. antarctica* Wilckens, 1910 (Text-figs 2, 4A) from the shallow-water López de Bertodano Formation of Seymour and Snow Hill islands (Text-fig. 1), is the oldest species of *Limopsis* to have been identified in Antarctica (Wilckens 1910; Zinsmeister and Macellari 1988). The oldest Australian species, of Late Paleocene age, is *L. rupestris* Darragh, 1994 (Text-figs 2, 5A) from the Pebble Point Formation, Otway Basin, Victoria, which was interpreted as a high-energy, shallow water deposit (Darragh 1994).

Three *Limopsis* species have been documented from the Eocene in New Zealand. The Bortonian (Lutetian–Bartonian: Middle Eocene) species *L. campa* Allan, 1926 (Text-figs 2, 3B) was found in the Waihao Greensand, Waihao Downs, South Island, a unit deposited in a deeper water, shelf environment (Beu and Maxwell 1990). The Kaiatan (Priabonian: Late Eocene) species *L. waihaensis* Allan, 1926 (Text-figs 2, 3C; which ranged to the Runangan) and *L. parvicostata* (Maxwell, 1992; Text-fig. 2) were both found towards the top of the Waihao Greensand in the Tahu Member at McCulloch's Bridge, South Island (Beu and Maxwell 1990), which was deposited in outer shelf to the uppermost bathyal waters (Maxwell 1992). The species *L. parvicostata* was originally assigned to the genus *Pectunculina* because of the presence of marginal crenulations (Text-fig. 3D). Maxwell (1992) considered that these crenulations made the species distinct from the smooth margined genus *Limopsis*. *Pectunculina* is a taxon which has a contentious tax-

onomic history. Although considered as a subgenus of *Limopsis* at the time, Vella (1954) also believed *Pectunculina* should be regarded as a separate genus because of its crenulated margin. However, Beu (2006) stated that the significance of a crenulate margin as a distinguishing character is unclear as the degree of crenulations can vary, meaning that there are intermediate species that cannot be placed in *Pectunculina* or *Limopsis* (Beu 2006; A. G. Beu, pers. comm. 2010). He also placed several New Zealand species previously assigned to *Pectunculina* into the genus *Limopsis*. Also, Lamprell and Healy (1998) placed *Pectunculina* as a subgenus of *Limopsis*, and Oliver (1981) referred all species previously named as *Pectunculina* to *Limopsis* (*s.l.*), but suggested that cladistics need to be employed to resolve this matter (Oliver, pers. comm. 2010).

The Eocene species *L. antarcticominuta* Stilwell, 2000 (Text-figs 2, 4B) was restricted to erratics at McMurdo Sound in East Antarctica (Text-fig. 1), which were considered by Stilwell (2000) to be from shallow water facies. The age of the erratics was not accurately constrained, but the fauna present in the unit placed it around the late Early Eocene to Late Eocene (Stilwell 2000). The species *L. chapmani* Singleton, 1932 (Text-figs 2, 5B) first occurred in an unnamed Middle–Late Eocene sandstone unit in the Carnarvon Basin of Western Australia (Darragh and Kendrick 2008). The unit was thought to have been deposited in a middle-shelf environment, although the fossils appeared broken, so transport may have occurred (Darragh and Kendrick 2008). The species also has other records from the Late Eocene, Oligocene and Early Miocene (Darragh and Kendrick 1980; Darragh 1985; Darragh and Kendrick 2008). The subspecies *L. chapmani valida* Singleton, 1932 was described from Birregurra, Victoria. Singleton (1932) stated that they differed slightly from *L. chapmani* in morphology, such as being more tumid; the specimens were tentatively dated as Miocene, but no geological information was given about the locality. The Aldingan (Bartonian–Priabonian: Late Eocene) species *L. multiradiata* Tate, 1886 (Text-figs 2, 5C) was found in the shallow-water Blanche Point Formation of the St Vincent Basin at Kent Town and Aldinga Bay, South Australia (Ludbrook 1973).

TEXT-FIG. 3. A–Q, Fossil *Limopsis* species found in New Zealand in order of first appearance in the fossil record, oldest to youngest. Unless otherwise stated, images were taken from the original descriptions. A, *L. microps* Finlay and Marwick, 1937. B, *L. campa* Allan, 1926. C, *L. waihaensis* Allan, 1926, picture from Beu and Maxwell (1990). D, *L. parvicostata* (Maxwell, 1992). E, *L. parva* Marwick, 1929. F, *L. catenata* Suter, 1917; picture from Beu and Maxwell (1990). G, *L. zealandica* Hutton, 1873; picture from Beu and Maxwell (1990). H, *L. propeinvalida* Laws, 1939. I, *L. gisbornensis* (Maxwell, 1978) originally described and illustrated as *L. retifera* by Marwick (1931). J, *L. producta* Finlay and McDowall, 1923. K, *L. lawsi* King, 1933. L, *L. aoteana* (Vella, 1954). M, *L. cooki* Marwick, 1931. N, *L. invalida* Marwick, 1928. O, *L. marwicki* Powell, 1938, picture from Beu (2006). P, *L. peteri* Beu, 1969; picture from Beu (2006). Q, *L. turnbulli* Beu, 2006. Scale bars represent 5 mm.



Oligocene–Miocene

Early Oligocene specimens tentatively identified as ?*Limopsis* sp. (Text-fig. 2) were found in the CRP-3 drillhole in the Victoria Land Basin, Antarctica (Taviani and Beu 2001; Text-fig. 1). The stratigraphic units on either side of the unit in which the fossils were found were interpreted as having been deposited in inner- to middle-shelf environments (Taviani and Beu 2001). The identification was based on two fragments of a single valve of a specimen on which some shell sculpture and a small area of the hinge were preserved; the shell had a symmetrical, sub-circular shape, and the shell material was thick (Taviani and Beu 2001).

Four new species of *Limopsis* first appeared in the Early Miocene of Antarctica (Text-fig. 2). Several specimens identified as *Limopsis* aff. *marionensis* by Dell and Fleming (1975) were collected from mudstone and diamictite sediments from Deep Sea Drilling Project site 270 in the Ross Sea (Dell and Fleming 1975; Text-fig. 1). The identification was based on shell morphology, which was thought to resemble that of the Recent species *L. marionensis* Smith, 1885 (Dell and Fleming 1975). It was suggested that they had been transported to the deeper water depositional setting, without the separation of valves, by gravity slide or turbidity current (Dell and Fleming 1975). This assessment was based on the Recent distribution of *L. marionensis*; the possibility that the fossil specimens inhabited this depth was not considered. The oldest specimen from the drilling site, a broken juvenile, occurred just above the Oligocene/Miocene boundary (identified from microfossils in the core). Younger Miocene specimens included a left valve and fragments of an articulated pair of valves (Dell and Fleming 1975). Dell and Fleming (1975) suggested that the continuous occurrence of sea ice was unlikely, but the presence of diamictites in the samples indicated at least periodic glacial conditions.

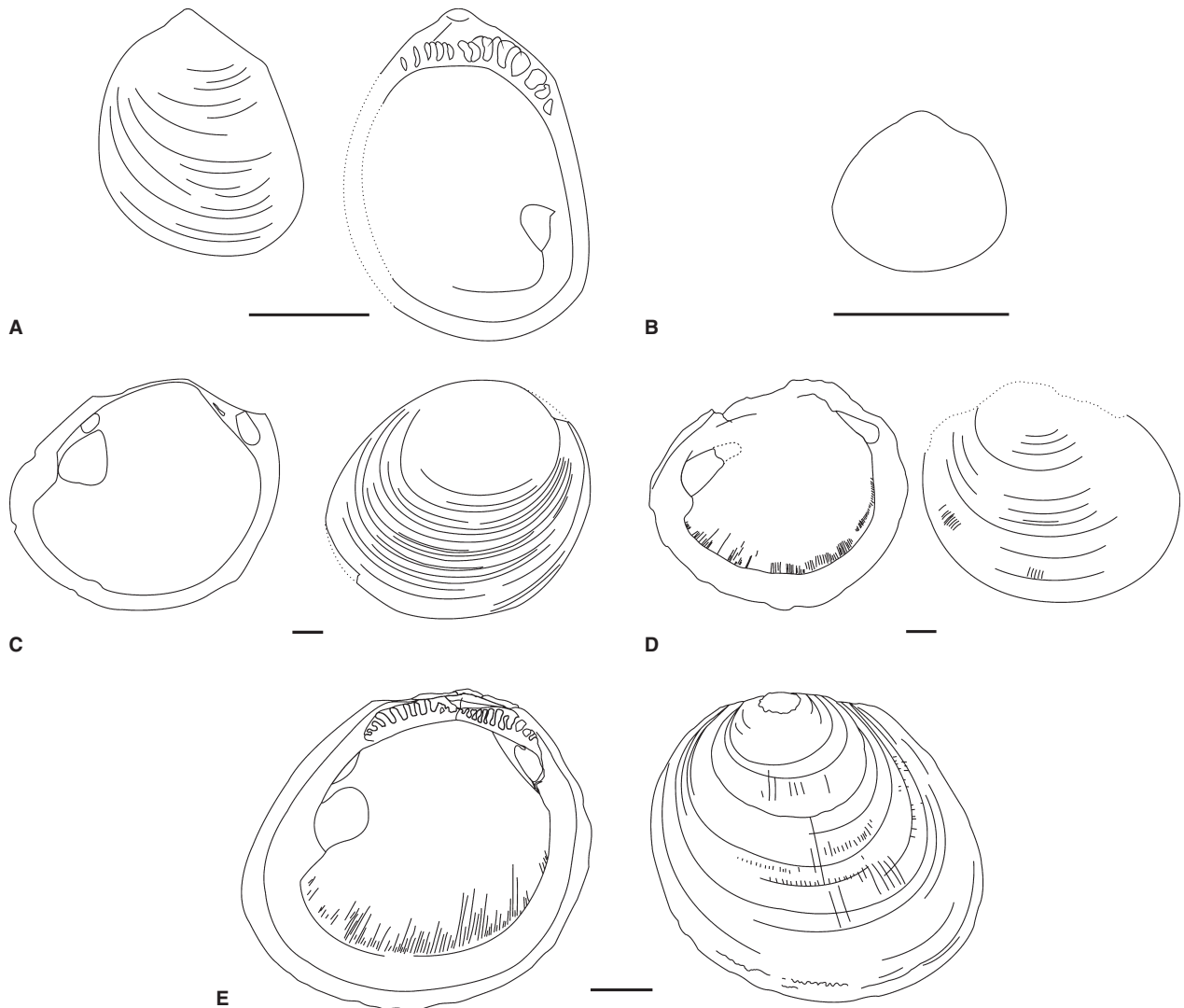
Early Miocene limopsids also occurred in the Cape Melville Formation, King George Island (South Shetland Islands; Text-fig. 6). This outer shelf to upper slope glacial unit was dated using Sr isotopes from bivalve specimens at 22.6 ± 0.4 Ma (Early Miocene; Dingle and Lavelle 1998). Five specimens of *Limopsis psimolis* Anelli, Rocha-Campos, Dos Santos, Perinotto and Quaglio, 2006 were identified; this species was characterized by large, thick shells and strongly anisomyarian muscle scars (Text-figs 4C, 7A). Two additional specimens from the BAS collections (P. 2702.696 right and left valve preserved and P. 2702.25, internal mould of both valves, hinge region missing) have been assigned to *L. psimolis* based on shell shape, shell thickness and shape of the muscle scars (Text-figs 4D, 7B). Three specimens from the BAS collections have been identified as *Limopsis* sp. (P. 2702.226, P. 2702.170 and P. 2702.735); species designation is not pos-

sible because of abrasion and preservation as internal moulds. Finally, four specimens have been assigned to a new species of *Limopsis* (*L. infericola* sp. nov. see systematic palaeontology below; Text-figs 4E, 7C).

Limopsis insolita (Sowerby, 1846; Text-figs 2, 8) was a long-ranging species known from Patagonia. It was common throughout the tertiary shallow marine molluscan assemblages of Argentina, which ranged from the Oligocene to Middle Miocene (Del Río 2004). The species was found at several localities, in three geological units – the San Julian, Monte León and Chenque Formations (Zinsmeister 1981; Griffin and Nielsen 2008; Casadío and Griffin 2009; Parras and Griffin 2009). *L. insolita* was also identified from the Late Oligocene to Early Miocene Guadal Formation, Pampa Castillo, Región de Aisén in Chile (Frassinetti and Covacevich 1999). Two specimens of an undescribed Miocene species of *Limopsis* were found in the Navidad Formation of Chile (see GSA Data Repository item 2010262 of Kiel and Nielsen 2010); however, they have not yet been described or figured. The species *L. modesta* Doello Jurado, 1915 (Text-figs 2, 8B) was found in rocks deposited in shallow water from the Late Miocene Arroyo Pescado borehole in the Buenos Aires Province (Del Río and Martínez 1998).

There are several early references to *L. insolita* occurring in New Zealand in the Oligocene–Miocene (Zittel 1864; Hutton 1873). However, these records have not been substantiated. Shells originally assigned to *L. insolita* by Zittel (1864) and Hutton (1873) were then referred to *L. zitteli*, Ihering, 1907 (*in* Ihering 1905–1907). This name was considered to be a *nomen dubium* by Beu and Maxwell (1990), who assigned the specimens to *L. catenata* Suter, 1917. Also, material recorded by Hutton (1873) as *L. insolita* could not be traced (Beu and Maxwell 1990). There were poorly illustrated Australian specimens assigned to *L. insolita* by Chapman (1911), who stated that Dennant and Kitson (1903) synonymized the specimens with *L. morningtonensis* Pritchard, 1901. Tate (1886) also referred several specimens to *L. insolita*. These occurrences of *L. insolita* in Australia were disputed by Singleton (1932), who placed them all in the species *L. chapmani*.

Several Early Miocene *Limopsis* species have been recorded from Australia (Text-fig. 2). *L. morningtonensis* Pritchard, 1901 (Text-fig. 5D) first occurred in the Fishing Point Marl, Horden Vale, Victoria, which was a shallow water deposit (Darragh 1985). *L. beaumariensis* Chapman, 1911 (Text-fig. 5E) (Ludbrook 1955) is associated with the Gellibrand Marl Formation at Lake Bullenmerri in the Otway Basin, Victoria (Chapman 1911; Bock and Cook 2001); this was thought to be a cool, deep water deposit (Nicolaidis 1995). Chapman (1911) also stated that the variant *L. beaumariensis* var. *depressa* Chapman, 1911 could be distinguished from *L. beaumariensis* by its thin,

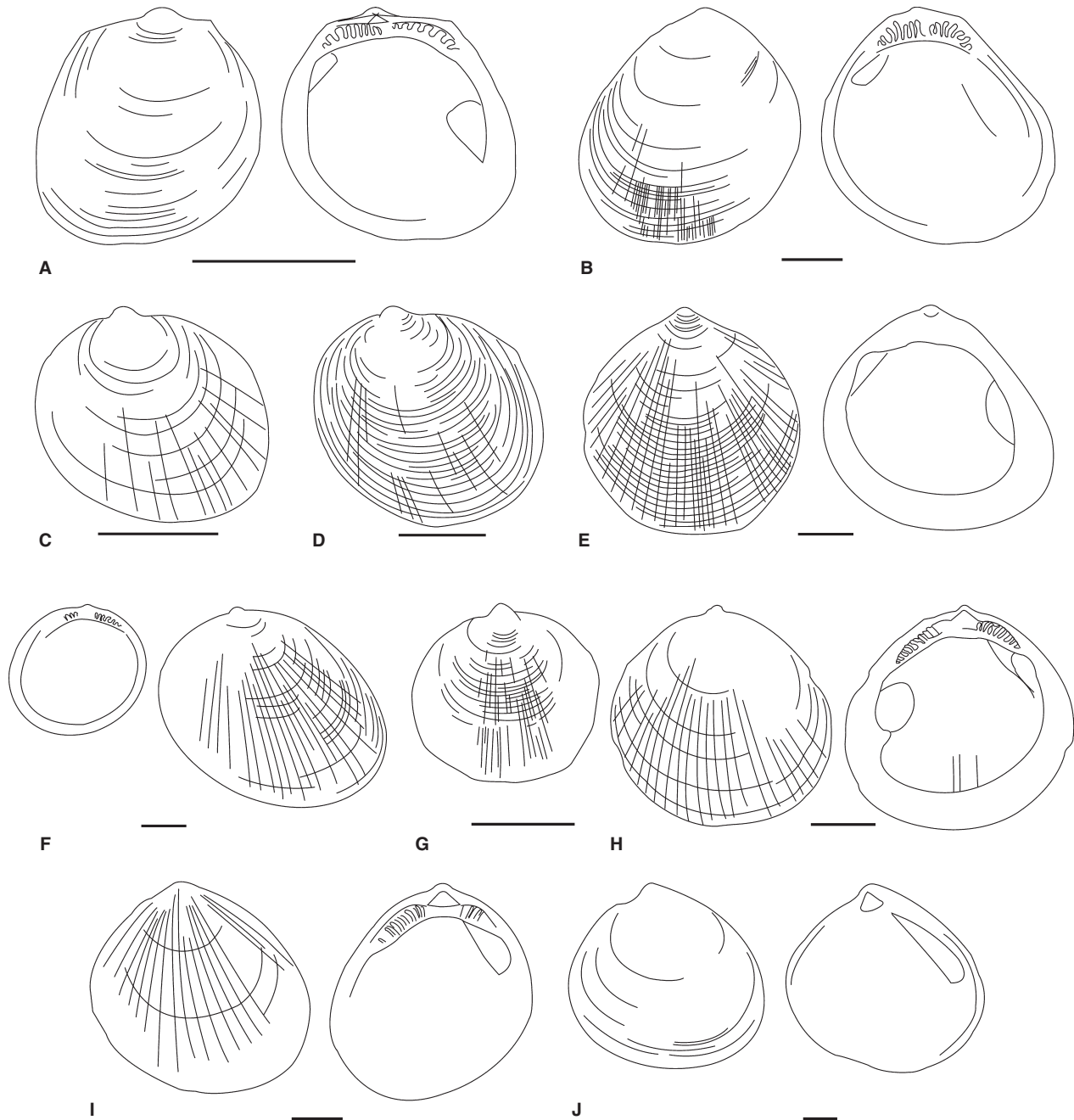


TEXT-FIG. 4. A–D, Fossil *Limopsis* species found in Antarctica. A, *L. antarctica* Wilckens, 1910. B, *L. antarcticominuta* Stilwell, 2000. C, *L. psimolis* Anelli et al., 2006. D, *L. infericola* sp. nov. DSDP and ODP specimens ?*Limopsis* sp., *L. aff. marionensis* and *Limopsis* sp. are not illustrated in the original literature and thus could not be included in this figure. The Cape Melville specimens assigned to *Limopsis* sp. are not illustrated because of the poor preservation of the material. Scale bars represent 5 mm.

depressed form, apiculate umbo and stronger concentric striae. Finally, *L. maccoyi* Chapman, 1911 (Text-fig. 5F) also occurred in the Gellibrand Marl Formation from Brown's Creek, Victoria (Nicolaidis 1995).

Limopsis species were common throughout the Oligocene and Miocene (Text-fig. 2) in New Zealand in a variety of different environments. The Duntroonian (Chattian: Late Oligocene) species *L. parma* Marwick, 1929 from the Chatton Formation, Shell Gully, Chatton, South Island was preserved in a shallow water assemblage (Beu and Maxwell 1990; Text-fig. 3E). During the Duntroonian (Chattian: Late Oligocene), the first specimens of *L. catenata* Suter, 1917 (Text-fig. 3F) were found from the upper part of the Wharekuri Greensand, Lake Waitaki,

South Island in a mid-shelf depth assemblage. The species also occurred in shallow water assemblages until the Waiauan (Serravallian: Middle Miocene; Beu and Maxwell 1990). Waitakian (Aquitanian: Early Miocene) aged examples of *L. zealandica* Hutton, 1873 (Text-fig. 3G) were identified from two localities on South Island: first, from the Mount Harris Formation in the Tengawai River near Trap Creek and second, in the Otekaie Limestone Formation at Trig Z, Otiake. At both of these localities, deeper water assemblages were preserved (Beu and Maxwell 1990). *L. zealandica* was a long-ranging species, with records until the Altonian (Burdigalian–Langhian: Early–Middle Miocene) and possibly younger (Burdigalian–Serravallian; A. G. Beu, pers. comm. 2010). The

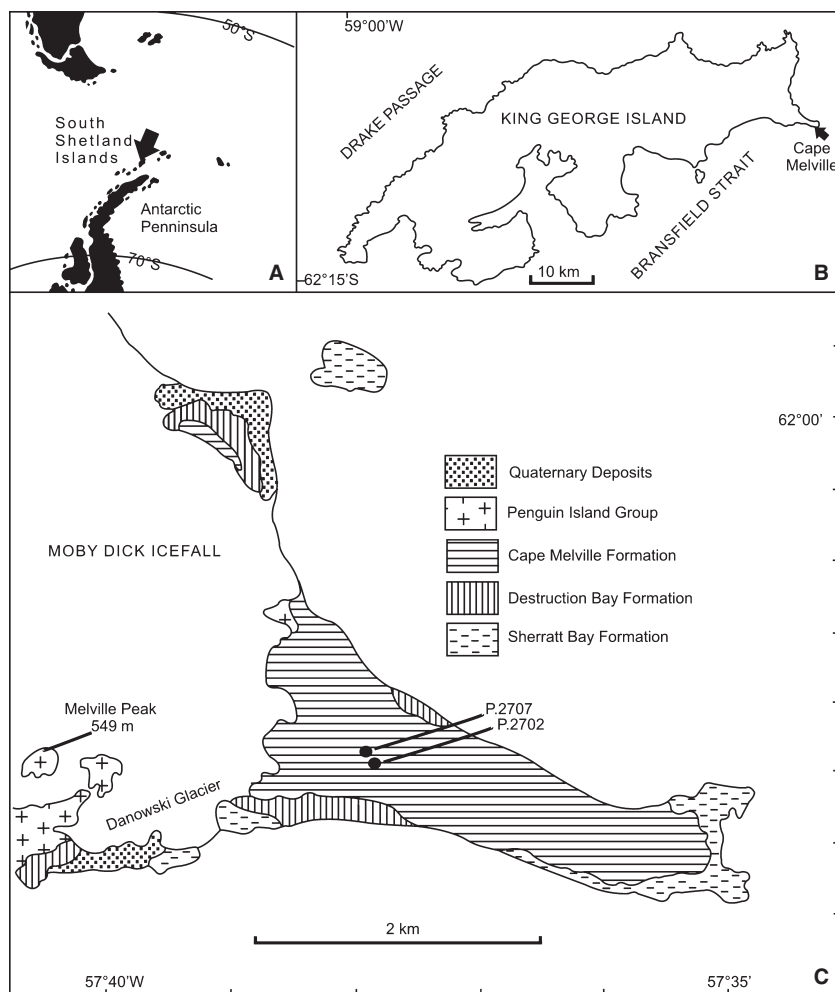


TEXT-FIG. 5. A–F, Fossil *Limopsis* species (not subspecies) found in Australia in order of first appearance in the fossil record, oldest to youngest. Unless otherwise stated, images were taken from the original descriptions. A, *L. rupestris* Darragh, 1994. B, *L. chapmani* Singleton, 1932. C, *L. multiradiata* Tate, 1886. D, *L. morningtonensis* Pritchard, 1901. E, *L. beaumariensis* Chapman, 1911, external view from Ludbrook (1955). F, *L. maccoyi* Chapman, 1911. G, *L. affinitalis* Chapman and Crespin, 1928. H, *L. werrikoensis* Singleton, 1941. I, *L. forteradiata* Cotton, 1930 picture from Lamprell and Healy (1998). J, *L. tensioni* (Tenison-Woods, 1878) picture from Lamprell and Healy (1998). Scale bars represent 5 mm.

Otaian (Aquitanian: Early Miocene) *L. propeinvalida* Laws, 1939 (Text-fig. 3H), from the Pakaurangi Formation, Pakaurangi Point, Kaipara Harbour, North Island was preserved within an outer shelf assemblage (Laws 1939; Beu and Maxwell 1990). This species ranged until

the Altonian (Burdigalian–Langhian: Early–Middle Miocene; Beu and Maxwell 1990). The Lillburnian (Serravalian: Middle Miocene) species *L. gisbornensis* Maxwell, 1978 (Text-fig. 3I) occurred in the Tutamoe Conglomerate, Pangopango Stream, Gisborne District, North Island

TEXT-FIG. 6. A, Location of the South Shetland Islands in relation to the Antarctic Peninsula. B, King George Island, showing the location of Cape Melville. A, B, from: Birkenmajer (1987). C, Cape Melville geology and site localities (P. 2702 and P. 2707) for *Limopsis infericola* n. sp. specimens. (From Feldmann and Crame 1998).

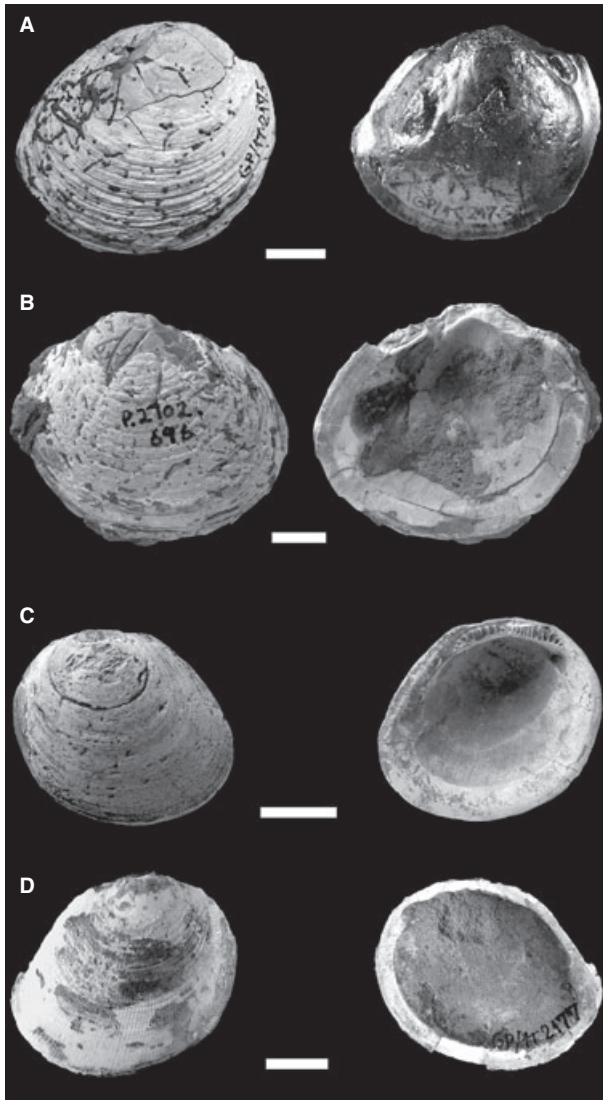


(Maxwell 1978). The Tutamoe Conglomerate was a deeper water unit that also contained shallow water molluscs, suggesting a degree of transport for some aspects of the fauna (Beu and Maxwell 1990). *L. gisbornensis* was previously designated as *L. retifera* Marwick, 1931; however, the name *L. retifera* had already been assigned to another specimen (Maxwell 1978; Beu and Maxwell 1990). The Waiuan (Serravallian: Middle Miocene) *L. producta* Finlay and McDowall, 1923 (Text-fig. 3J) was found in the Dowling Bay Limestone, Dowling Bay, Dunedin, South Island (Beu and Maxwell 1990); the unit was thought to represent an outer shelf depositional setting (Finlay and McDowall 1923). However, this specimen came from a highly tectonised locality and was possibly a distorted specimen of other common species at the locality such as *L. zealandica* or *L. gisbornensis* (Beu, pers. comm. 2010). The early Tongaporutuan (Tortonian: Late Miocene) *L. lawsi* King, 1933 (Text-fig. 3K), from the Hurupi Series, Hurupi Creek, Palliser Bay, Southern Wairarapa, North Island and Blind River, Marlborough, north South Island, was described as a shelf dwelling species (Beu 2006). The Middle Tongaporutuan (Tortonian: Late Mio-

cene) species *L. aoteana* (Vella, 1954) (Text-fig. 3L) from bathyal mudstones at Bell's Creek, Southern Wairarapa, North Island (Vella 1954; Beu and Maxwell 1990) was originally assigned to the genus *Pectunculina*. Late Miocene specimens of *L. cooki* Marwick, 1931 (Text-fig. 3M) were described from the Ormond Formation, Gisborne District, North Island, which has been interpreted as a shallow water deposit (Marwick 1931). Beu (pers. comm. 2010) suggested that there are probably many unidentified specimens of *Limopsis* in New Zealand fossil collections, including several unnamed new species in the richly diverse, shelf depth successions at Clifden, Southland from the Altonian–Waiuan (Burdigalian–early Tortonian: Early–Late Miocene).

Pliocene–Pleistocene

Several species first appeared in the Late Pliocene to Early Pleistocene fossil record of New Zealand (Text-fig. 2). The Waipipian–Mangapanian (Piacenzian–Gelasian: Late Pliocene) species *L. invalida* Marwick, 1928 (Text-fig. 3N)



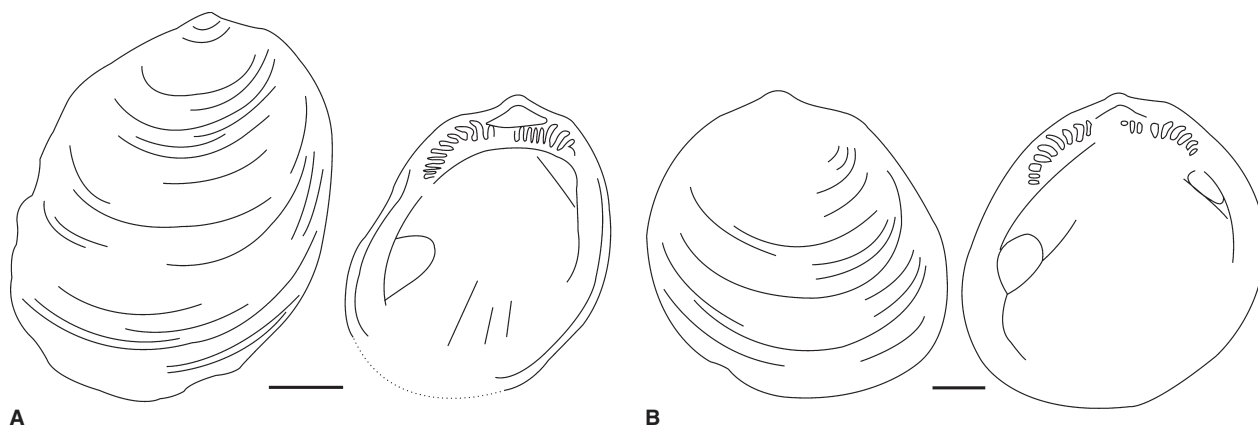
TEXT-FIG. 7. A–D. *Limopsis* specimens from the Cape Melville Formation, King George Island, South Shetland Islands, Antarctica. A, *L. psimolis* Anelli *et al.*, 2006. B, *L. psimolis* P. 2702.696 from British Antarctic Survey collection. C, *L. infericola* sp. nov., holotype P. 2702.736. D, Specimen GP/1T 2177, previously identified as a paratype of *L. psimolis* by Anelli *et al.* (2006), is re-assigned to *L. infericola* sp. nov. Scale bars represent 10 mm.

from the Whenuataru Tuff, Pitt Island, Chatham Islands probably inhabited deep, cold waters (Marwick 1928; Beu and Maxwell 1990). The Nukumaruan (Gelasian: Late Pliocene) *L. marwicki* Powell, 1938 (Text-fig. 3O) occurred in the Castlepoint Formation, Castlepoint, East Wairarapa, North Island, which was originally considered to be a mixed shelf and upper bathyal fauna, but Beu (2006) considered it to be entirely bathyal. Another Nukumaruan (Gelasian: Late Pliocene) species was *L. peteri* Beu, 1969 (Text-fig. 3P), from a mudstone stratigraphically lower

than the Pukenui Limestone, from Palliser Bay as well as from the Ruakokopatuna and Mangaopari valleys in South Wairarapa, North Island; this was deposited in deep, cold waters (Beu 2006). Finally, the Castlecliffian (Pleistocene) species *L. turnbulli* Beu, 2006 (Text-fig. 3Q) occurred in a Pleistocene mudstone, Wilson River, SW Fiordland, South Island, which was also interpreted as a deep, cold water deposit (Beu 2006; Turnbull *et al.* 2007). The shallower water *Limopsis* species were absent in New Zealand from the Late Pleistocene (Beu 2006); Beu stated that bathyal species (assigned to *Pectunculina*, which he placed in *Limopsis*) are present in waters around New Zealand at the present day and suggested that the genus retreated to deep water around New Zealand as temperatures fell during the late Neogene (Beu 2006).

A Pliocene occurrence of *L. marionensis* (Text-fig. 2) was recorded from an unnamed sandstone horizon at Marine Plain in the Vestfold Hills, East Antarctica (Pickard *et al.* 1988; Text-fig. 1). The depositional setting was thought to have been shallow water, less than 50 m deep, in an interglacial period, warmer than at present (Pickard *et al.* 1988). Unfortunately, there was no description or illustrations of the specimens. In Australia, the Pliocene species *L. affinitalis* Chapman and Crespin, 1928 (Text-figs 2, 5G) was recorded from a borehole on the Mornington Peninsula, Victoria, in sandy sediments thought to have been deposited in shallow waters (Chapman 1928). The Late Pliocene species *L. werrikooensis* Singleton, 1941 (Text-figs 2, 5H) occurred in the Werrikoo Limestone, Glenelg River, Victoria, Australia, a unit that was deposited in very shallow water (Singleton 1941; Darragh 1985). In Australia, two of the species that arose during the Miocene, *L. beaumariensis* and *L. maccoyi*, had a continuing record into the Pliocene (Chapman 1911; Ludbrook 1955). Chapman (1911) also stated that in the Pliocene, *L. maccoyi* was ‘moderately rare; passing into *L. tenisoni* (living)’ suggesting that there was a continuous record of some species of *Limopsis* in Australia. This is also shown by *L. forteradiata* Cotton, 1930 (Text-figs 2, 5I) and *L. tensioni* (Tenison-Woods, 1878; Text-figs 2, 5J), which were both recorded in the Early Pleistocene in the east of Western Australia, in the shallow water Roe Calcarenite (Ludbrook 1978). These two species both range until the present (Lamprell and Healy 1998).

A Middle Pleistocene record of *Limopsis* (Text-fig. 2) was found in an unnamed carbonate-rich unit in the CRP-1 drillhole, Cape Roberts, Victoria Land Basin, Antarctica (Taviani *et al.* 1998; Text-fig. 1). However, the age of this unit was not precise, and there was no description or image of the *Limopsis* specimen. Taviani *et al.* (1998) estimated water depth at the time of deposition to have been approximately within the range of 100–200 m. There are currently no published records of *Limopsis* from southern South America in the Pliocene–Pleistocene.



TEXT-FIG. 8. A, B, Fossil *Limopsis* from South America. A, *L. insolita* (Sowerby, 1846) from South America (From Griffin and Nielsen 2008). B, *L. modesta* Doello Jurado, 1915 (From Del Río and Martínez 1998). Scale bars represent 5 mm.

Recent

Oliver (1981) divided Recent *Limopsis* species into three major groups (limopsiform, glycymeriform and abyssate) and thirteen morphological classes based on shell characters and anatomical features. In Antarctica, there is a diversity of *Limopsis* species at the present day in comparison with other genera (Text-fig. 9), with current circum-Antarctic and Magellan Region species belonging to three of the morphological classes (I, V and XIII) described by Oliver (1981). Classes I and V belong in Oliver's limopsiform group and class XIII belongs to the abyssate group. There are no members of glycymeriform group in Antarctica, this class being present in the Indo-Pacific and Australia (Oliver 1981). Oliver (1981) stated that class I limopsids are cosmopolitan, except for the Arctic Ocean, and are typically ploughing forms living semi-infaunally in soft sediments. They are represented by *L. marionensis* (Text-fig. 9A) and *L. tenella dalli* Lamy, 1912 (Text-fig. 9B), which are found in Antarctic waters and the Magellan Region, and *L. tenella tenella* Jeffreys, 1879 (Text-fig. 9C) from Antarctic waters (Text-fig. 1). Class V limopsids are cosmopolitan, except for the Arctic Ocean; they are more sedentary and have an infaunal habit. Representatives from Antarctic waters are *L. longipilosa* Pelseener, 1903 (Text-fig. 9D) and *L. scabra* Thiele, 1912 (Text-fig. 9E); *L. mabilliana* Dall, 1908 (Text-fig. 9F) is found both in Antarctic waters and in the Magellan Region (Text-fig. 1). Class XIII limopsids are only found in the Antarctic Ocean and are thought to have a shallow burrowing mode of life (Oliver 1981). The Antarctic species *L. enderbyensis* Powell, 1958 (Text-fig. 9G), *L. lilliei* Smith, 1915 (Text-fig. 9H), and *L. scotiana* Dell, 1964 (Text-fig. 9I) belong to this group, and Oliver (1981) also included *L. hirtella* Mabile and Rochebrune, 1911 (*in* Rochebrune and Mabile 1889; Text-fig. 9J), which is

found in Antarctic waters and the Magellan Region (Text-fig. 1). Finally, Recent Southern Ocean species that have not been assigned to a morphological group include *Limopsis* sp. 1 (Text-fig. 9K) and *Limopsis* sp. 2 (Text-fig. 9L), which have been identified by K. Linse from Antarctic waters (unpublished data) and *L. knudseni* Dell, 1990 (Text-fig. 9M), known from the Antarctic and Magellan Region (Text-fig. 1).

Modern *Limopsis* species are also found in South African and Australian waters in depths of up to 600 m (Oliver 1981; Lamprell and Healy 1998). Several species have been described from bathyal depths around New Zealand; however, they were originally assigned to *Pectunculina* as they possess crenulate inner ventral margins. Beu (2006) included *L. lata* (Smith, 1885; placed in morphological class VII, limopsiform group by Oliver, 1981), *L. proceritas* (Crozier, 1966) and *L. tasmani* (Dell, 1956; placed in morphological class V, limopsiform group by Oliver (1981)) in *Limopsis*. Therefore, several deep-water *Limopsis* species are present in New Zealand waters.

SYSTEMATIC PALAEOLOGY

Order ARCOIDA Stoliczka, 1871

Superfamily LIMOPSOIDEA Dall, 1895

Family LIMOPSIDAE Dall, 1895

Genus LIMOPSIS Sassi, 1827

Type species. *Arca aurita* Brocchi, 1814 by original designation.

Remarks. Specimens have been assigned to *Limopsis* based on their shell shape, strongly anisomyarian muscle scars (the anterior one being much larger than the

posterior), central resilifer and taxodont dentition (Newell 1969; Oliver and Allen 1980). Extensive study of literature and material has confirmed these morphological characters, and new specimens agree with this description.

Limopsis infericola sp. nov.

Text-figures 4E, 7C–D

Derivation of name. Latin *inferus* – southern; *cola* – dweller.

Holotype. P. 2702.736 (Text-fig. 7c) is designated as the holotype. The specimen consists of the left valve only.

Paratype. P. 2702.225 internal mould; preserves both the right and left valves.

Material. P. 2702.35: a partial internal mould of the right valve, P. 2707.20: both the right and left valves are preserved, the posterior of the shell is missing and specimen GP/1T 2177 (Fig. 7D) described as *L. psimolis* by Anelli *et al.* (2006), but unfigured in their original description.

Diagnosis. Fossil *Limopsis* species with a long straight hinge margin, oblique shell shape and large lenticular resilifer.

Description. Thin-shelled species, orbicular, obliquely elongate towards the posterior. Height 27.4 mm (P. 2702.736), length 26.9 mm (P. 2702.736) and inflation 14 mm (P. 2702.225). The dorsal margin is straight and the ventral margin is well rounded. The postero-dorsal margin is long, over twice the length of the anterior dorsal margin. The antero-ventral margin is almost twice the length of the postero-ventral margin. The postero-ventral and antero-ventral margins are curved and the antero- and postero-dorsal margins are slightly curved. The umbones are abraded but appear to be small on P. 2702.736; they cannot be seen on additional specimens as they are missing on GP/1T 2177 and the other material consists of internal moulds.

The species possesses strongly anisomyarian muscle scars; the posterior muscle scar is over twice the width of the anterior muscle scar. There is a very prominent anterior ridge and within this is located the ovate anterior muscle scar, which is positioned more dorsally than the posterior muscle scar. There are commarginal growth ridges on the external surface of the shell and fine radial linear striations indenting the shell at a density of 2–3/mm. Internally, the ventral margin of the shell

shows very clear striations immediately dorsal to the pallial line, at a density of about 3–4/mm. The species exhibits taxodont dentition, with 12 anterior teeth and 11 posterior teeth (P. 2702.736). The anterior teeth are more closely spaced than the posterior teeth on P. 2702.736. P. 2702.225 has 12 posterior teeth and 12 anterior teeth. P. 2702.35 is incomplete and abraded, so not all of the teeth were visible, but 7 teeth can be seen posteriorly and 10 can be seen anteriorly. The resilifer is large and lenticular.

Remarks. *Limopsis infericola* sp. nov. differs from the holotype of the other Cape Melville Formation species, *L. psimolis*, as it is smaller, more elongate, has a thinner shell, and in the shape and position of the posterior muscle scars (Text-fig. 7). Unfortunately, the hinge line is incomplete in all specimens of *L. psimolis*, so a direct comparison of this feature cannot be made. The new species is very similar to GP/1T 2177, which was designated as a paratype of *L. psimolis* by Anelli *et al.* (2006). This paratype differs significantly from the holotype of *L. psimolis*. GP/1T 2177 and *L. infericola* are both thin shelled, with fine ornament and posterior elongation. Therefore, specimen GP/1T 2177 should be re-assigned from *L. psimolis* to *L. infericola* sp. nov.

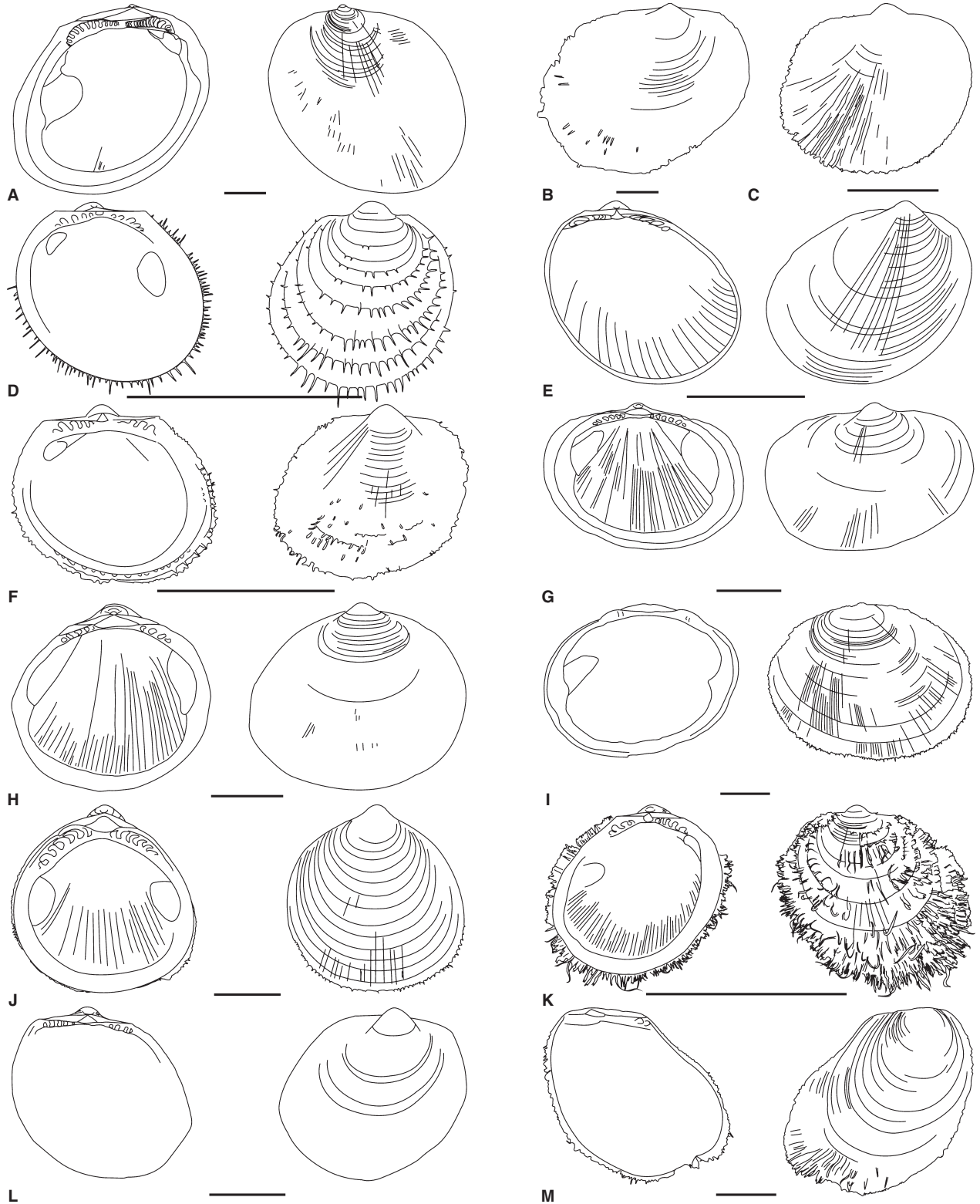
Limopsis infericola sp. nov. resembles several *Limopsis* species from the Cenozoic of New Zealand in general size and shape, including *L. campa* Allan, 1926 and *L. zealandica* Hutton, 1873. However, *L. infericola* differs from these species in having a longer hinge margin, a slightly different shell outline and in the muscle scar shape. The dentition of *L. infericola* is similar to that of *L. parma* Marwick, 1929, but the new species differs as it has a straighter dorsal margin, the umbones are less pronounced, the anterior and posterior margins are different and the resilifer is much larger. *L. catenata* Suter, 1917 has a large resilifer similar in shape to *L. infericola*, but has a shell that is less oblique and a wider hinge line. *L. infericola* also has a much longer and straighter dorsal margin. *L. infericola* differs from *L. turnbulli* Beu, 2006 in having a longer dorsal margin and less pronounced umbones.

The holotype has a very similar hinge line to Recent specimens (MR 597; Text-fig. 9A), identified as *L. marionensis* Smith, 1885. *L. infericola* differs only in the shape of the ventral part of the shell, which is more rounded and less oblique towards the posterior in comparison with

TEXT-FIG. 9. A–M, Recent *Limopsis* species from waters around Antarctica and the Magellan region. Images were used from the original descriptions, unless otherwise stated. A, *L. marionensis* Smith, 1885 (specimen MR 597 from the BAS marine collection). B, *L. tenella dalli* Lamy, 1912 (image from Dell 1990). C, *L. tenella tenella* Jeffreys, 1879 (image from Dell 1990). D, *L. longipilosa* Pelseneer, 1903. E, *L. scabra* Thiele, 1912 (image from Dell 1990). F, *L. mabilliana* Dall, 1908 (image from Dell 1990). G, *L. enderbyensis* Powell, 1958. H, *L. lilliei* Smith, 1915. I, *L. scotiana* Dell, 1964. J, *L. hirtella* Mabile and Rochebrune, 1889 in Rochebrune and Mabile (1889) (image from Lamy 1911). K, *Limopsis* undescribed sp. 1 BAS marine collection. L, *Limopsis* undescribed sp. 2 BAS marine collection. M, *L. knudseni* Dell, 1990. Scale bars represent 5 mm.

MR 597, and in the length of the dorsal margin, which is shorter than in MR 597. It is possible that these two species are related and *L. infericola* may be an ancestral form of this modern Antarctic taxon.

Occurrence. Cape Melville, King George Island, South Shetland Islands, Antarctica in the Early Miocene (Aquitanian) Cape Melville Formation, Moby Dick Group, 62°02'S, 57°38'W (Text-fig. 6).



BIOGEOGRAPHICAL HISTORY OF *LIMOPSIS* IN THE SOUTHERN HIGH LATITUDES

The first published occurrence of a named species of the genus *Limopsis* in the southern high latitudes (Wilckens 1910; Zinsmeister and Macellari 1988) is coincident with the initial Late Cretaceous (Maastrichtian) radiation of the genus documented by Heinberg (1979) and Oliver (1981), although other older unpublished and unnamed occurrences of *Limopsis* are known from New Zealand (Speden 1975; Moore and Speden 1984 FRED – The Fossil Record Electronic Database – <http://www.fred.org.nz/index.jsp>). Subsequently, throughout the Paleocene and Eocene, there were sporadic occurrences of *Limopsis* species in the southern high latitudes (Text-fig. 2). In the Oligocene to Miocene, the genus underwent a second radiation; species numbers increased in Antarctica as well as in temperate New Zealand and Australia (Text-fig. 2). Three new *Limopsis* taxa appeared in the Early Miocene of Antarctica, three in the early to Middle Miocene of Australia, and nine of the seventeen species described from New Zealand appeared from the Late Oligocene and throughout the Miocene (Text-fig. 2). Specimens of *L. insolita* and *L. modesta* first occurred in Chile and Argentina during the Late Oligocene to Late Miocene, and *L. insolita* was common and abundant throughout this time period. The first radiation of the genus in the Late Cretaceous was probably related to habitat differentiation (Oliver 1981), with new species developing both endobysate and epibysate modes of life. The second radiation in the southern high latitudes appears to have been related to environmental changes occurring throughout the southern region at the time, linked to the isolation of the continental shelves following the final breakup of the southern high-latitude continents. This distribution history is not unique to the limopsisid clade, as a similar pattern of Mesozoic ancestry in the northern hemisphere followed by a Cenozoic radiation in the Southern Ocean is shown by marine isopods (Brandt *et al.* 1999).

The onset of deep water associated with the formation of the Antarctic Circumpolar Current (ACC) resulted in cooling temperatures in Antarctica, but the exact dates for these events have not been firmly established (Pfuhl and McCave 2005; Scher and Martin 2006; Livermore *et al.* 2007; Lyle *et al.* 2007). Most studies place the onset of the ACC around Eocene/Oligocene boundary to Early Oligocene (Barker *et al.* 2007). The timing for the onset of a deepwater connection around Antarctica has been a matter of debate, with the oldest date to be given as 31 ± 2 Ma (Early Oligocene; Lawver and Gahagan 2003). However, Pfuhl and McCave (2005) stated that there is little sedimentary evidence for this date and suggest the

younger age range of 29.7–21.8 Ma (Late Oligocene–Early Miocene), as given in Eagles and Livermore (2002) and Livermore *et al.* (2004). More recently, Pfuhl and McCave (2007) stated that sedimentary evidence from the Southern Ocean suggested that the onset of the ACC immediately preceded the Oligocene/Miocene boundary. Ocean Drilling Program and Deep Sea Drilling Project results suggested that the full development of the ACC resulted in faunal turnover, with cool water cosmopolitan and true Antarctic endemic forms increasing in prominence (Lazarus and Caulet 1993; Brown *et al.* 2006). This fits with molecular evidence from Linse (unpublished data), which suggested a deep-sea origin for Recent Antarctic limopsisids in the mid-Cenozoic. This was also consistent with the discovery of *Limopsis marionensis*-like specimens from the Early Miocene onwards (Dell and Fleming 1975, and *L. infericola* sp. nov.). Recent Antarctic *Limopsis* species are cool-adapted; therefore, cooling temperatures might have been a key factor in the increase in the number of Antarctic limopsisids in the Early Miocene. These Early Miocene Antarctic limopsisids are found in glacial sediments from King George Island, dated at 22.6 ± 0.4 Ma (Dingle and Lavelle 1998; Troedson and Riding 2002).

Australian and New Zealand limopsisids also appear to have undergone a radiation in the Late Oligocene to Early Miocene (Text-fig. 2). The separation of Antarctica, the onset of the ACC and the establishment of the Polar Front meant that Australia and New Zealand became physically isolated from Antarctica. In Australia, some fossil species of *Limopsis* had extensive ranges indicating that the genus was less affected by Cenozoic palaeoenvironmental changes (Chapman 1911). In New Zealand, tectonic movements throughout the Neogene led to the formation of localized basins, providing a variety of habitats for molluscs (Beu and Maxwell 1990). The appearance of species in basins of different water depths suggests that *Limopsis* adapted to new niches that were opening up because of these tectonic movements. There are four species identified from New Zealand in the Late Pliocene to Early Pleistocene. After this, the species with smooth (as opposed to crenulated) inner ventral margins characteristic of the genus in New Zealand became extinct (Beu and Maxwell 1990).

Few fossils are found from the Quaternary in Antarctica as a result of erosion of sediments after the last glacial maximum. Another factor in the lack of Quaternary fossils was the extension of ice sheets onto continental shelves, which displaced the marine fauna; many groups are thought to have migrated northwards away from Antarctic waters at this time (Clarke and Crame 1992). That the genus does have a Quaternary record shows that it managed to adapt and survive the extreme cooling in

Antarctica, probably by living in refugia. The *Limopsis* population appears to have been an incumbent element of the Antarctic fauna, as fossils are found from the Late Maastrichtian and throughout the Cenozoic in the region. The genus appears to have adapted to the changing conditions of the Southern Ocean during this period, radiating into new niches that formed, and this has led to *Limopsis* being one of the most speciose bivalve genera in Antarctic waters at the present day.

CONCLUSIONS

The oldest identified species of the genus *Limopsis* was from the Early Cretaceous of Europe, and records of *Limopsis* sp. also occurred at this time in New Zealand; the genus subsequently radiated into different life habits in the northern hemisphere in the Maastrichtian. This initial radiation coincided with the first occurrence of a named species in the southern high latitudes. Southern high latitude records in the Paleocene were sparse, but the Late Oligocene to Early Miocene marked a period of diversification in Antarctica, New Zealand and Australia. This Cenozoic radiation of the genus in the southern high latitudes may have been related to adaptation to cooling temperatures as well as environmental changes, which created new niches for the genus. It is clear from this study that at least some of the diversity within *Limopsis* at the present day in Antarctica can be attributed to origination and diversification of species within the southern high latitudes.

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REFERENCES

- ALDEA, C., OLABARRIA, C. and TRONCOSO, J. S. 2008. Bathymetric zonation and diversity gradient of gastro-

- ods and bivalves in West Antarctica from the South Shetland Islands to the Bellinghausen Sea. *Deep-Sea Research I*, **55**, 350–368.
- ALLAN, R. S. 1926. Fossil Mollusca from the Waihao Greensands. *Transactions and Proceedings of the Royal Society of New Zealand, 1868–1961*, **56**, 338–346.
- ANELLI, L. E., ROCHA-CAMPOS, A. C., DOSSANTOS, P. R., PERINOTTO, J. D. and QUAGLIO, F. 2006. Early Miocene bivalves from the Cape Melville Formation, King George Island, West Antarctica. *Alcheringa*, **30**, 111–132.
- BARKER, P. F., FILIPPELLI, G. M., FLORINDO, F., MARTIN, E. E. and SCHER, H. D. 2007. Onset and Role of the Antarctic Circumpolar Current. *Deep-Sea Research II*, **54**, 2388–2398.
- BEU, A. G. 1969. Additional Pliocene bathyal Mollusca from South Wairarapa, New Zealand. *New Zealand Journal of Geology and Geophysics*, **12**, 484–496.
- 2006. Marine Mollusca of oxygen isotope stages of the last 2 million years in New Zealand. Part 2. Biostratigraphically useful and new Pliocene to Recent bivalves. *Journal of the Royal Society of New Zealand*, **36**, 151–338.
- 2009. Before the ice: biogeography of Antarctic Paleogene molluscan faunas. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **284**, 191–226.
- and MAXWELL, P. A. 1990. Cenozoic Mollusca of New Zealand. *New Zealand Geological Survey Paleontological Bulletin*, **58**, 1–518.
- BIRKENMAJER, K. 1987. Oligocene–Miocene glacio-marine sequences of King George Island (South Shetland Islands), Antarctica. *Palaeontologia Polonica*, **49**, 9–36.
- BOCK, P. E. and COOK, P. L. 2001. Revision of the Tertiary species of *Anoskopora* Wass (Bryozoa: Cribrimorpha). *Memoirs of the Museum of Victoria*, **58**, 179–189.
- BRANDT, A., CRAME, J. A., POLZ, H. and THOMSON, M. R. A. 1999. Late Jurassic Tethyan ancestry of recent southern high-latitude marine isopods (Crustacea, malacostraca). *Palaeontology*, **42**, 663–675.
- BROCCHI, G. B. 1814. *Conchiologia fossile subappenninica con osservazioni geologiche sugli Appennini e sul suolo adiacente*. I and II. Dalla Stamperia Reale, Milano, 712 pp.
- BROWN, B., GAINA, G. and MÜLLER, R. D. 2006. Circum-Antarctic palaeobathymetry: illustrated examples from Cenozoic to recent times. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **231**, 158–168.
- BUVIGNIER, A. 1852. *Statistique géologique, minéralogique, métallurgique et paléontologique du Département de la Meuse*. Baillière, Paris, New York, 694 pp.
- CASADÍO, S. and GRIFFIN, M. 2009. Sedimentology and paleontology of a Miocene marine succession first noticed by Darwin at Puerto Deseado (Port desire). *Revista de la Asociación Geológica Argentina*, **64**, 83–89.
- CHAPMAN, F. 1911. A revision of the species of *Limopsis* in the Tertiary beds of Southern Australia. *Proceedings of the Royal Society of Victoria*, **23**, 419–437.
- 1928. V. Notes on the faunas and stratigraphic horizons. The Sorrento Bore, Mornington Peninsula, with a description of new or little-known fossils. *Records of the Geological Survey of Victoria*, **5**, 173–184.

- and CRESPIAN, I. 1928. III Description of new or rare species. The Sorrento Bore, Mornington Peninsula, with a description of new or little-known fossils. *Records of the Geological Survey of Victoria*, **5**, 87–133.
- CLARKE, A. and CRAME, J. A. 1992. The Southern Ocean benthic fauna and climate change: a historical perspective. *Philosophical Transactions of the Royal Society of London, B*, **338**, 299–309.
- COTTON, B. C. 1930. Pelecypoda of the “Flindersian” Region, South Australia. *Records of the South Australian Museum*, **4**, 223–240.
- CRAME, J. A. 1996. Evolution of high-latitude molluscan faunas. 119–131. In TAYLOR, J. (ed.). *Origin and evolutionary radiation of the Mollusca*. Oxford University Press, Oxford, 408 pp.
- CROZIER, M. A. 1966. New species and records of Mollusca from off the Three Kings Islands, New Zealand. *Transactions of the Royal Society of New Zealand, Zoology*, **8**, 39–49.
- DALL, W. H. 1895. Contributions to the Tertiary fauna of Florida, with especial reference to the Miocene Silex-beds of Tampa and the Pliocene beds of the Caloosahatchie River. Part 3. A new classification of the Pelecypoda. *Transactions of the Wagner Free Institute of Science of Philadelphia*, **3**, 483–570.
- 1908. The Mollusca and Brachiopoda. *Bulletin of the Museum of Comparative Zoology*, **43**, 205–487.
- DARRAGH, T. A. 1985. Molluscan biogeography and biostratigraphy of the Tertiary of southeastern Australia. *Alcheringa*, **9**, 83–116.
- 1994. Paleocene bivalves from the Pebble Point Formation, Victoria, Australia. *Proceedings of the Royal Society of Victoria*, **106**, 71–103.
- and KENDRICK, G. W. 1980. Eocene bivalves from the Pallinup Siltstone near Walpole, Western Australia. *Journal of the Royal Society of Western Australia*, **63**, 5–20.
- 2008. Silicified Eocene molluscs from the Lower Murchison district, Southern Carnarvon Basin, Western Australia. *Records of the Western Australian Museum*, **24**, 217–246.
- DEL RÍO, C. J. 2004. Tertiary marine molluscan assemblages of Eastern Patagonia (Argentina): a biostratigraphic analysis. *Journal of Paleontology*, **78**, 1097–1122.
- and MARTÍNEZ, S. 1998. Clase Bivalvia. 48–83. In DEL RÍO, C. (ed.). *Moluscos Marinos Miocenos de la Argentina y Uruguay*, Vol. 15. Academia Nacional de Ciencias Exactas, Físicas y Naturales, Buenos Aires, Monografía, 151 pp.
- DELL, R. K. 1956. Some new offshore Mollusca from New Zealand. *Records of the Dominion Museum*, **3**, 27–59.
- 1964. Antarctic and Subantarctic mollusca: Amphineura, Scaphopoda and Bivalvia. *Discovery Reports*, **XXXIII**, 93–250.
- 1990. Antarctic Mollusca: with special reference to the fauna of the Ross Sea. *Bulletin of the Royal Society of New Zealand*, **27**, 1–311.
- and FLEMING, C. A. 1975. Oligocene–Miocene bivalve mollusca and other macrofossils from sites 270 and 272 (Ross Sea), DSDP, Leg 28. *Initial Reports of the Deep Sea Drilling Project*, **28**, 693–703.
- DENNANT, J. and KITSON, A. E. 1903. Catalogue of the described species of fossils (except Bryozoa and Foraminifera) in the Cainozoic fauna of Victoria, South Australia and Tasmania. *Records of the Geological Survey of Victoria*, **1**, 89–147.
- DINGLE, R. V. and LAVELLE, M. 1998. Antarctic Peninsular cryosphere: Early Oligocene (c. 30 Ma) initiation and a revised glacial chronology. *Journal of the Geological Society, London*, **55**, 433–437.
- DOELLO JURADO, M. 1915. Algunos moluscos marinos terciarios procedentes de un pozo surgente cerca de La Plata. *Physis*, **1**, 592–598.
- EAGLES, G. and LIVERMORE, R. A. 2002. Opening history of Powell Basin, Antarctic Peninsula. *Marine Geology*, **185**, 195–205.
- FELDMANN, R. M. and CRAME, J. A. 1998. The significance of a new nephropid lobster from the Miocene of Antarctica. *Palaentology*, **41**, 807–814.
- FINLAY, H. J. and MARWICK, J. 1937. The Wangaloan and associated faunas of Kaitangata-Green Island Subdivision. *New Zealand Geological Survey Bulletin*, **15**, 1–140.
- and McDOWALL, F. H. 1923. Fossiliferous limestone at Dowling Bay. *Transactions and Proceedings of the Royal Society of New Zealand, 1868–1961*, **54**, 106–114.
- FRASSINETTI, D. and COVACEVICH, V. 1999. Invertebrados fósiles marinos de la Formación Guadal (Oligoceno Superior–Mioceno Inferior) en Pampa Castillo, Región de Aisén, Chile. *Servicio Nacional de Geología y Minería, Boletín*, **51**, 1–96.
- GOFAS, S., LE RENARD, J. and BOUCHET, P. 2001. Mollusca. 180–213. In COSTELLO, M. J., EMBLOW, C. S. and WHITE, R. (eds). *European register of marine species: a check-list of the marine species in Europe and a bibliography of guides to their identification. Collection Patrimoines Naturels*, **50**. Muséum National d’Histoire Naturelle, Paris, 463 pp.
- GRIFFIN, M. and NIELSEN, S. V. 2008. A revision of the type specimens of Tertiary molluscs from Chile and Argentina described by d’Orbigny (1842), Sowerby (1846) and Hupé (1854). *Journal of Systematic Palaeontology*, **6**, 251–316.
- GRIFFITHS, H. J., LINSE, K. and CRAME, J. A. 2003. SOMBASE – Southern Ocean Mollusc Database: a tool for biogeographic analysis in diversity and ecology. *Organisms Diversity and Evolution*, **3**, 207–213.
- HAIN, S. 1990. Die beschalten benthischen Mollusken (Gastropoda und Bivalvia) des Weddellmeeres, Antarktis. *Berichte zur Polarforschung*, **70**, 1–181.
- HALLAM, A. 1976. Stratigraphic distribution and ecology of European Jurassic bivalves. *Lethaia*, **9**, 245–259.
- 1977. Jurassic bivalve biogeography. *Paleobiology*, **3**, 58–73.
- HEINBERG, C. 1979. Evolutionary ecology of nine sympatric species of the pelecypod *Limopsis* in Cretaceous chalk. *Lethaia*, **12**, 325–340.
- HUTTON, F. W. 1873. *Catalogue of the Tertiary Mollusca and Echinodermata of New Zealand, in the collection of the Colonial Museum*. Government Printer for the Colonial Museum and Geological Survey Department, Wellington, 48 pp.
- IHERING, H. von. 1899. Die conchylien der Patagonischen Formation. *Neues Jahrbuch für Mineralogie, Geologie und Palaeontology*, **2**, 1–41.

- 1905–1907. Les mollusques fossils du tertiaire et du Crétacé Supérieur de l'Argentine. *Annales do Museu Nacional, Beunos Aires*, **14**, 1–611.
- JEFFREYS, J. G. 1879. On the Mollusca procured during the Lightning and Porcupine expeditions (part 2). *Proceedings of the Zoological Society of London*, **1879**, 553–588.
- KIEL, S. and NIELSEN, S. N. 2010. Quaternary origin of the inverse latitudinal diversity gradient among southern Chilean mollusks. *Geology*, **38**, 955–958.
- KING, L. C. 1933. Tertiary molluscan faunas from Southern Wairarapa. *Transactions and Proceedings of the Royal Society of New Zealand*, **63**, 334–354.
- LAMPRELL, K. and HEALY, J. 1998. *Bivalves of Australia Volume 2*. Backhuys Publishers, Leiden, 288 pp.
- LAMY, E. 1911. *Gastropodes Prosobranches, Scaphopode et Pélécy-podes. Deuxième expedition Antarctique Française (1908–1910) commandée par le Dr Jean Charcot. Sciences Naturelles: Documents Scientifiques*, Masson et Cie, Paris 31 pp.
- 1912. Revision des *Limopsis* vivants du museum d'histoire naturelle de Paris. *Journal de Conchyliologie*, **60**, 108–137.
- LAWS, C. R. 1939. The molluscan faunule at Pakaurangi Point, Kaipara – No. 1. *Transactions and Proceedings of the Royal Society of New Zealand, 1868–1961*, **68**, 466–503.
- LAWVER, L. A. and GAHAGAN, L. M. 2003. Evolution of Cenozoic seaways in the circum-Antarctic region. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **198**, 11–37.
- LAZARUS, D. and CAULET, J.-P. 1993. Cenozoic Southern Ocean reconstructions from sedimentologic, radiolarian, and other microfossil data. 145–174. In KENNET, J. P. and WARNKE, D. A. (eds). *The Antarctic paleoenvironment: a perspective on global change Antarctic Research Series, 60*. American Geophysical Union, Washington, DC, 273 pp.
- LINSE, K. 1999. Mollusca of the Magellan region. A checklist of the species and their distribution. *Scientia Marina*, **62**, 399–407.
- 2002. The shelled Magellanic Mollusca: with special reference to biogeographic relations in the Southern Ocean. *Theses Zoologicae*, **74**, 1–251.
- LIVERMORE, R. A., EAGLES, G., MORRIS, P. and MALDONADO, A. 2004. Shackleton Fracture Zone: no barrier to early circumpolar ocean circulation. *Geology*, **32**, 797–800.
- HILLENBRAND, C.-D., MEREDITH, M. and EAGLES, G. 2007. Drake Passage and Cenozoic climate: an open and shut case? *Geochemistry, Geophysics, Geosystems*, **8**, Q01005.
- LUDBROOK, N. H. 1955. The molluscan fauna of the Pliocene strata underlying the Adelaide Plains. *Transactions of the Royal Society of South Australia*, **78**, 18–37.
- 1973. Distribution and stratigraphic utility of Cenozoic molluscan faunas in Southern Australia. *Tohoku University Science Reports, 2nd series. (Geology), Special Volume*, **6**, 241–261.
- 1978. Quaternary molluscs of the western part of the Eucla Basin. *Bulletin of the Geological Survey of Western Australia*, **125**, 1–286.
- LYLE, M., GIBBS, S., MOORE, T. C. and REA, D. K. 2007. Late Oligocene initiation of the Antarctic Circumpolar Current: evidence from the South Pacific. *Geology*, **35**, 691–694.
- MALCHUS, N. and WARÉN, A. 2005. Shell and hinge morphology of Juvenile *Limopsis* (Bivalvia: Arcoidea) – implications for limopsisid evolution. *Marine Biology Research*, **1**, 350–364.
- MARWICK, J. 1928. The Tertiary Mollusca of the Chatham Islands including a Generic Revision of the New Zealand Pectinidae. *Transactions and Proceedings of the Royal Society of New Zealand, 1868–1961*, **58**, 432–506.
- 1929. Tertiary molluscan fauna of Chatton, Southland. *Transactions and Proceedings of the Royal Society of New Zealand*, **59**, 903–934.
- 1931. The Tertiary mollusca of the Gisborne District. *New Zealand Geological Survey Paleontological Bulletin*, **13**, 1–177.
- MAXWELL, P. A. 1978. Taxonomic and nomenclatural notes on some New Zealand Cenozoic Mollusca, with descriptions of new taxa. *New Zealand Journal of Zoology*, **5**, 15–46.
- 1992. Eocene Mollusca from the vicinity of McCulloch's Bridge, Waihao River, South Canterbury, New Zealand: paleoecology and systematics. *New Zealand Geological Survey Paleontological Bulletin*, **65**, 1–280.
- MOORE, P. R. and SPEDEN, I. G. 1984. The Early Cretaceous (Albian) sequence of eastern Wairarapa, New Zealand. *New Zealand Geological Survey Bulletin*, **97**, 1–76.
- NEWELL, N. D. 1969. Family Limopsidae Dall, 1895. N264–N267. In MOORE, R. C. (ed.). *Treatise on invertebrate Paleontology, Part N, Volume 1, Mollusca 6, Bivalvia*. University of Kansas Printing Service, Kansas, 952 pp.
- NICOL, D. 1967. Some characteristics of cold-water marine pelecypods. *Journal of Paleontology*, **41**, 1330–1340.
- NICOLAIDES, S. 1995. Cementation in Oligo-Miocene non-tropical self limestones, Otway Basin, Australia. *Sedimentary Geology*, **95**, 97–121.
- OLIVER, P. G. 1981. The functional morphology and evolution of recent Limopsidae (Bivalvia, Arcoidea). *Malacologia*, **21**, 61–93.
- and ALLEN, J. A. 1980. The functional and adaptive morphology of the deep-sea species of the family Limopsidae (Bivalvia: Arcoidea) from the Atlantic. *Philosophical Transactions of the Royal Society of London, B*, **291**, 77–125.
- PARRAS, A. and GRIFFIN, M. 2009. Darwin's great Patagonian Tertiary Formation at the mouth of the Río Santa Cruz: a reappraisal. *Revista de la Asociación Geológica Argentina*, **64**, 70–82.
- PELSENEER, P. 1903. Mollusques (Amphineures, Gastropodes et Lamellibranches). *Résultats du Voyage du S. Y. Belgica en 1897–1898–1899. Rapports Scientifiques, Zoologie*, 1–85.
- PFUHL, H. A. and McCAVE, I. N. 2005. Evidence for late Oligocene establishment of the Antarctic Circumpolar current. *Earth and Planetary Science Letters*, **235**, 715–728.
- 2007. The Oligocene – Miocene boundary – cause and consequence from a Southern Ocean perspective. In WILLIAMS, M., HAYWOOD, A. M., GREGORY, F. J. and SCHMIDT, D. N. (eds). *Deep-time perspectives on climate change*. Geological Society, London, 589 pp.
- PHILIPPI, R. A. 1836. *Enumeratio Molluscorum Siciliae cum viventium tum in Tellure Tertiaria Fossilium quae in itinere suo observavit*. Sumptibus Simonis Schroppii et Sociorum, Berlin, 267 pp.

- PICKARD, J., ADAMSON, D. A., HARWOOD, D. M., MILLER, G. H., QUILTY, P. G. and DELL, R. K. 1988. Early Pliocene marine sediments, coastline, and climate of East Antarctica. *Geology*, **16**, 158–161.
- POWELL, A. W. B. 1938. A Pliocene molluscan faunule from Castle Point. *Records of the Auckland Institute and Museum*, **2**, 157–164.
- 1958. Mollusca from the Victoria-Ross Quadrants of Antarctica. *British, Australia and New Zealand Antarctic Research Expedition 1929–1931. Reports-Series B*, **6**, 167–215.
- PRITCHARD, G. B. 1901. Contributions to the Palaeontology of the Older Tertiary of Victoria. *Proceedings of the Royal Society of Victoria*, **14**, 22–31.
- ROCHEBRUNE, A. T. de and MABILLE, J. 1889. Mollusques. *Mission Scientifique du Cap Horn, 1882–1883*, **6**, 1–143.
- SASSI, A. 1827. Saggio geologic sopra il Bacino terziario di Albenza. *Giornale Ligustico di Scienze, Lettere ed Arti*, **1**, 467–484.
- SCHER, H. D. and MARTIN, E. E. 2006. Timing and climatic consequences of the opening of Drake Passage. *Science*, **312**, 428–430.
- SINGLETON, F. A. 1932. Studies in Australian Tertiary Mollusca, Part 1. *Proceedings of the Royal Society of Victoria*, **44**, 289–308.
- 1941. The Tertiary geology of Australia. *Proceedings of the Royal Society of Victoria*, **53**, 1–125.
- SMITH, E. A. 1885. Report on the Lamellibranchiata collected by H.M.S. Challenger during the years 1873–1876. Report on the scientific results of the voyage of H.M.S. Challenger during the years 1873–1876. *Zoology*, **13**, 1–341.
- 1915. Mollusca, Pt. I. Gastropoda, Prosobranchia, Scaphopoda and Pelecypoda. British Antarctic ('Terra Nova') Expedition, 1910. *Natural History Report, Zoology*, **2**, 61–112.
- SOWERBY, J. de C. 1825. *The mineral conchology of Great Britain*, Vol. 5. W. Arding, London, 74 pp.
- SOWERBY, G. B. II 1846. Appendix. Descriptions of Tertiary fossil shells from South America. 249–265. In DARWIN, C. R. (ed.). *Geological observations on South America*. Smith, Elder and co., London, 279 pp.
- SPEDEEN, I. G. 1975. Cretaceous stratigraphy of Raukumara Peninsula. *New Zealand Geological Survey Bulletin*, **91**, 1–70.
- STILWELL, J. D. 2000. Eocene Mollusca (Bivalvia, Gastropoda and Scaphopoda) from McMurdo Sound: systematic and palaeoecological significance. 261–320. In STILWELL, J. D. and FELDMANN, R. M. (eds). *Palaeobiology and Palaeoenvironments of Eocene Rocks, McMurdo Sound, East Antarctica. Antarctic Research Series*, 76. American Geophysical Union, Washington, DC, 372 pp.
- STOLICZKA, F. 1870–1871. Cretaceous fauna of southern India, V. 3, The Pelecypoda, with a review of all known genera of this class, fossil and Recent. *Geological Survey of India, Palaeontologica Indica*, **6**, 1–537.
- SUTER, H. 1917. Descriptions of new Tertiary Mollusca occurring in New Zealand, accompanied by a few notes on necessary changes in nomenclature. Part 1. *New Zealand Geological Survey Paleontological Bulletin*, **5**, 1–93.
- TATE, R. 1886. The lamellibranchs of the older Tertiary of Australia. (Part 1.). *Transactions of the Royal Society of South Australia*, **8**, 96–158.
- TAVIANI, M. and BEU, A. 2001. Palaeogene macrofossils from CRP-3 drillhole, Victoria Land Basin, Antarctica. *Terra Antarctica*, **8**, 423–434.
- and LOMBARDO, C. 1998. Pleistocene Macrofossils from CRP-1 Drillhole, Victoria Land Basin, Antarctica. *Terra Antarctica*, **5**, 485–491.
- TENISON-WOODS, J. E. 1878. On some new marine Mollusca. *Transactions of the Royal Society of Victoria*, **14**, 55–65.
- TEVESZ, M. J. S. 1977. Taxonomy and ecology of the Philobryidae and Limopsidae (Mollusca: Pelecypoda). *Postilla*, **171**, 1–64.
- THIELE, J. 1912. Die antarktischen Schnecken und Muscheln. *Deutsche Südpolar-Expedition 1901–1903*, **6**, 183–285.
- TROEDSON, A. L. and RIDING, J. B. 2002. Upper Oligocene to lowermost Miocene strata of King George Island, South Shetland Islands, Antarctica: stratigraphy, facies analysis, and implications for the glacial history of the Antarctic Peninsula. *Journal of Sedimentary Research*, **4**, 510–523.
- TURNBULL, I., SUTHERLAND, R., BEU, A. and EDWARDS, A. R. 2007. Pleistocene glaciomarine sediments of the Kisbee Formation, Wilson River, southwest Fiordland, and some tectonic and paleoclimatic implications. *New Zealand Journal of Geology and Geophysics*, **50**, 193–204.
- VELLA, P. 1954. Tertiary Mollusca from South-East Wairarapa. *Transactions of the Royal Society of New Zealand*, **81**, 539–555.
- VERMEIJ, G. J. 1978. *Biogeography and adaptation: patterns of marine life*. Harvard University Press, Massachusetts and London, 332 pp.
- WILCKENS, O. 1910. Die Anneliden, Bivalven und Gastropoden der antarktischen Kreideformation. *Schwedische Südpolar-Expedition 1901–1903. Geology*, **3**, 1–132.
- WOODS, H. 1899. *A monograph of the Cretaceous Lamellibranchiata of England*, Vol. 1. Palaeontographical Society, London, 227 pp.
- ZACHOS, J., PAGANI, M., SLOAN, L., THOMAS, E. and BILLUPS, K. 2001. Trends, Rhythms, and Aberrations in Global Climate 65 Ma to Present. *Science*, **292**, 686–693.
- ZELAYA, D. G. 2005. The bivalves from the Scotia Arc islands: species richness and faunistic affinities. *Scientia Marina*, **69**, 113–122.
- ZINSMEISTER, W. J. 1981. Middle to Late Eocene invertebrate fauna from the San Julian Formation at Punta Casamayor, Santa Cruz Province, Southern Argentina. *Journal of Paleontology*, **55**, 1083–1102.
- and MACELLARI, C. E. 1988. Bivalvia (Mollusca) from Seymour Island, Antarctic Peninsula. 253–284. In FELDMANN, R. M. and WOODBURNE, M. O. (eds). *Geology and paleontology of Seymour Island, Antarctic Peninsula. Geological Society of America Memoir*, **169**, 566 pp.
- ZITTEL, K. A. 1864. II. Fossile Mollusken und Echinodermen aus Neu-Seeland. Nebst beiträgen von den Herren Bergrath Franz Ritter V. Hauer und Professor Eduard Suess. In HOCHSTETTER, F. von, HÖRNES, M. and RITTER VON HAUER, F. (eds). *Paläontologie von Neu-Seeland. Beiträge zur Kenntniss der Fossilien Flora und Fauna der Provinzen Auckland und Nelson. Reise der Österreichischen Fregatte Novara um die Erde, Geologischer Theil*, **1**, 15–68.