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Opening of Drake Passage gateway and Late Miocene to Pleistocene cooling reflected in Southern Ocean molluscan dispersal: evidence from New Zealand and Argentina

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Abstract

Thirty-two benthic marine molluscan genus-group taxa are newly recognised as common to New Zealand and Argentina. Previously suggested examples, including *Panis*, *Athlopecten*, *Austrovenus*, large *Cirsotrema*, *Lucinoma*, *Aulacomya* and *Zygochlamys*, are confirmed from new collections. The total of 46 Cenozoic dispersed taxa now recognised falls into four main groups: (a) Oligocene–Early Miocene dispersals from South America to New Zealand (8 taxa); (b) Oligocene–Early Miocene dispersals from New Zealand to South America (22); (c) Latest Miocene–Pliocene dispersals from South America to New Zealand (9); and (d) Pleistocene–Holocene dispersals from South America to New Zealand (at least 7 taxa). Dispersal seems to have occurred in bursts both to and from South America when the Antarctic Circumpolar Current (ACC) initiated, i.e., when Drake Passage opened, late in the Oligocene, while dispersal from South America to New Zealand, only, seems to have occurred again at two later times, (1) during the latest Miocene–Pliocene enhancement of ACC circulation caused by the initiation of West Antarctic glaciation, and (2) during Pleistocene glaciations. However, the incompleteness of the Argentinian record exaggerates the size of the initial burst, and allows no assessment of post-Middle Miocene dispersal *to* South America. Formation of the ACC through the opening of a passage south of Australia at ca. 43–40 Ma and of Drake Passage at ca. 23 Ma not only led to the glaciation of Antarctica, but also greatly altered Southern Ocean biogeography.

Keywords: Drake Passage gateway; Mollusca; dispersal; circulation; Antarctica

1. Introduction

Many genus-group taxa of benthic marine Mollusca occur in the Cenozoic fossil record and/or living faunas of both South America and New Zealand. These taxa are common to the two areas for a variety of biogeographic reasons. This report aims to provide some data on the biogeographic results of the opening of Drake Passage, as a contribution to IGCP Project 355, 'Pacific Gateways'.

Several benthic marine molluscan genus-group taxa that are recorded earliest in the Cenozoic fossil record of New Zealand, after the Cretaceous fragmentation of Gondwana, have an earlier fossil record in South America and, of course, vice versa. The

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assumption underlying this paper is that this type of history mainly results from passive dispersal as planktonic larvae in ocean currents during the Cenozoic, and is unlikely to have occurred before the initiation of circulation of the Antarctic Circumpolar Current (ACC), i.e., before the opening of Drake Passage. Of course, we cannot discount the possibility that some apparently common genus-group taxa result from convergence, but this is considered to be unlikely in most cases. A realistic possibility, however, deserving further study, is that some 'genera' have arisen independently, through a heterochronic process, from the same ancestor in both New Zealand and South America (e.g., *Spissatella* from *Eucrassatella*). Also, a few taxa may have dispersed on kelp rafts, as was demonstrated for the brooding, byssally attached bivalve *Gaimardia trapesina* (Lamarck) by Helmuth et al. (1994), but such rafts must also have been dispersed in the ACC. Also, the fact that not *one* species of kelp-dwelling archaeogastropod lives today in both New Zealand and Australia (B.A. Marshall, Museum of NZ, pers. commun.) argues against kelp rafting as a significant dispersal agent. Means and examples of rafting, as an alternative to passive dispersal of planktonic larvae, were reviewed by Scheltema (1995), who concluded that "rafting plays only a secondary role in the dispersal of mollusks".

Rifting south of Australia began to open a gateway for marine circulation between Australia and Antarctica between around 40 Ma (Edwards, 1975) and 30 Ma (Lawver et al., 1992), but the final event critical to establishment of the ACC was the opening of Drake Passage around the end of the Oligocene (23.5 ± 2.5 Ma; Barker and Burrell, 1977, 1982). Glaciation of East Antarctica commenced by late Middle Eocene times, and a major ice sheet was present on East Antarctica from earliest Oligocene times onwards (Barron et al., 1991; Kennett and Barron, 1992), presumably as a result of the thermal isolation of Antarctica commencing with the opening of circulation south of Australia. The opening of the Drake Passage gateway allowed the formation of the present regime of strong westerly wind-driven circulation eastward around the entire Antarctic continent (the ACC), enhancing the thermal isolation of Antarctica and ultimately leading to the Pleistocene glaciations. "A vigorous circumpolar current had undoubtedly developed" by 20 Ma or shortly thereafter (Lawver et al., 1992, p. 27), i.e., by mid-Early Miocene times, although Fulthorpe et al. (1996) have since suggested that the Marshall Paraconformity in New Zealand on-shore mid-Oligocene rocks (ca. 32–29 Ma) resulted from the ACC inception. The commencement of Antarctic glaciation in the Middle Eocene, the initiation of the ACC, the onset of more intense ACC circulation when glaciation began in West Antarctica just before the end of the Miocene (Kennett et al., 1975; Kennett, 1977; Kennett and Von der Borch, 1985) and the intense glaciations of the Pleistocene can all be expected to have had profound effects on the marine biota of both the southern landmasses and the isolated islands between them.

In an earlier introduction to this topic, Beu and Griffin (1997) listed some benthic marine molluscs known to be common to South America and New Zealand, *before* commencing a project on these relationships. We now present an updated account based on our joint identifications of new collections, but before completion of our project on molluscan similarities between New Zealand and South America. This paper therefore bases South American evidence on the record we are familiar with, in Argentina, with only a few Chilean examples. The Chilean fauna is expected to provide further valuable data for this project, but has not yet been analysed from the point of view of relationships with New Zealand.

2. Argentinean Cenozoic molluscan faunas

Argentinean Cenozoic marine molluscan faunas known in detail to M. Griffin or represented by his new collections exert both an age and a facies bias on the results possible from this project. We therefore record here the main Cenozoic molluscan faunas of Argentina (Fig. 1). Those represented by collections we have studied jointly are identified with an asterisk *.

(1) Cerro Dorotea Formation, Paleocene, around Sierra Dorotea; gastropods described by Griffin and Hünicken (1994), bivalves not yet identified.*

(2) Salamanca Formation, Paleocene, around Pico Salamanca, Golfo San Jorge; a moderately diverse, rather poorly preserved fauna, mainly described by Feruglio (1937).

(3) Roca Formation, Paleocene, in northern Patagonia; a poorly preserved fauna, largely of oysters, de-

scribed by Burckhardt (1902) and Von Ihering (1903, 1907).

(4) Arroyo Verde Formation, Middle Eocene (Lutetian), Golfo San Matías; a small, poorly preserved fauna with *Campanile*, described by Rossi de Garcia (1959) and Rossi de Garcia and Levy (1977).

(5) Rio Turbio Formation, Middle Eocene, around Sierra Dorotea; bivalves described by Griffin (1991), gastropods still largely undescribed, collections available in Museo de La Plata.

(6) La Despedida Formation, Eocene, Tierra del Fuego; type of macrofauna present listed by Codignotto and Malumián (1981); fauna not described, no collections available to us.

(7) San Julián Formation, Late Eocene–Early Oligocene; the thick, widespread, barnacle limestone lithofacies along the coast of Patagonia, particularly around San Julián; calcitic molluscs diverse and well preserved, but virtually lacking all aragonitic molluscs; large collections available for study.*

(8) Monte León Formation, Late Oligocene–Early Miocene; the thick, widespread, shallow-water, siliciclastic unit overlying the San Julián Formation along the coast of Patagonia, with diverse aragonitic and calcitic molluscs; large collections available. Divided by Bertels (1970) into upper (Mount Observation) and lower (Mount Entrance) members; the latter includes Darwin's Santa Cruz River locality (Sowerby, 1846). Fauna partly described by Cossmann (1899) and Von Ihering (1907). *

(9) Centinela Formation, correlative of the Monte León Formation in the inland (western) part of Argentina, around Lago Argentino and Lago Pueyrredón; a shallow-water siliciclastic unit, with a fauna similar to that of the Monte León Formation, but not as well preserved; no collections available to us, although some taxa were described by Ortmann (1902) and Von Ihering (1904).

(10) El Mangrullo (or El Chenque) Formation; correlative of the Monte León Formation in the Golfo San Jorge area, around Comodoro Rivadavia, i.e., north of the typical outcrop area of the Monte León Formation; preservation and fauna similar to those of the lower (Mount Entrance) member of the Monte León Formation; a diverse fauna, partly described by Von Ihering (1907) and Camacho and Fernandez (1957); collections available in Museo de La Plata.

(11) Carmen Silva Formation, Tierra del Fuego, Miocene; a very shallow-water, pebbly, siliciclastic unit with diverse aragonitic molluscs, partly described by Von Ihering (1907, 1909), Steinmann and Wilckens (1908) and Malumián et al. (1979); large collections available for study.*

(12) Puerto Madryn Formation, Middle Miocene, around and on Peninsula Valdes; a diverse, shallow-water, aragonitic fauna in a siliciclastic unit, partly described by Von Ihering (1907), Del Rio (1992, 1994) and Brunet (1995), but many gastropods undescribed; no collections available to us.

(13) Paraná Formation, Middle Miocene; a shallow-water, diverse fauna in the Paraná area, central Argentina, partly described by Philippi (1893), Borchert (1901), Von Ihering (1907) and Del Rio (1991); gastropods in need of modern study, no collections available to us.

(14) Rio Negro beds; Pliocene (?), around Golfo San Matías; very shallow-water oyster beds, with few other molluscs. No collections available to us.

(15) 'Cape Fairweather beds' (Formación Cabo Buen Tiempo), Plio-Pleistocene (?); a very shallow-water unit at Cabo Buen Tiempo, just north of Rio Gallegos, southern Patagonia. No collections available to us.

The very numerous molluscan faunas of New Zealand, ranging in ecology for most age periods from shelf to bathyal environments, were summarised by Beu and Maxwell (1990). Compared with these, Argentinean faunas are markedly restricted, because:

(1) *All* are very shallow-water, near-shore units; there is no record whatever of even mid-shelf taxa, let alone bathyal ones; and

(2) The main units from which we have examined large faunas are the San Julián Formation (Late Eocene–Early Oligocene), the Monte León Formation (Late Oligocene–Early Miocene) and the Carmen Silva Formation (Miocene, Tierra del Fuego), with a less diverse record from the Cerro Dorotea (Paleocene) and Rio Turbio (Middle Eocene) formations, and some published data on more northern Miocene units. Although aragonitic molluscs are diverse and well preserved in many of these faunas, they are lacking from the critical Late Eocene–Early Oligocene age period represented by the San Julián Formation.

These preservational biases of the stratigraphic record mean that a high proportion of New Zealand benthic marine molluscan genus-group taxa can never be expected to be found in Argentina, whether they ever occurred there or not, and apart from small Paleocene to Middle Eocene faunas, aragonitic molluscs in mainland Patagonia are preserved from only about the time of opening of Drake Passage. This conceivably is not a coincidence; the change of sedimentation from carbonate-dominated to siliciclastic-dominated might also result from the opening of Drake Passage. A point supporting this interpretation is the change from carbonate-dominated to siliciclastic-dominated lithologies in New Zealand, also, at about the Oligocene–Miocene boundary.

3. Mollusca in common to New Zealand and South America

Many benthic marine molluscan genus-group taxa are known to be common to both New Zealand and South America when the total fauna is considered of Late Cretaceous, Cenozoic and living Mollusca. For this report it is critical to distinguish the different biogeographic origins of these genera.

Those taxa we know to be in common to the two faunas, including those newly recognised in M. Griffin's Argentinian collections, are listed in Table 1, classified by their apparent biogeographic origins. The main origins are:

3.1. Cosmopolitan genera

Many molluscan genus-group taxa in common to New Zealand and South America are very widely distributed, occurring in most or all of the world's temperate and tropical seas, and have no bearing on this report. We have included here those taxa known to occur in both North and South America, as well as in New Zealand.

3.2. Gondwanan genera

Several genus-group taxa occurring only in the Late Cretaceous and Cenozoic (mostly *early* Cenozoic) faunas of New Zealand and South America seem formerly to have occupied the coast of Gondwana, and to have remained around the southern landmasses after Gondwana began to break up during mid-Cretaceous times. Some examples are *Neilo*, *Lahillia*, *Marwickia*, *Spirogalerus*, *Pseudofax*, *Taioma*, *Fyfea*, *Tudiclana* and possibly *Priscaphander* (Finlay and Marwick, 1937; Beu and Maxwell, 1990; Stilwell and Zinsmeister, 1992; Griffin and Hünicken, 1994). Almost all of these became extinct early in Cenozoic times, but *Neilo* has a long Cenozoic record in both Argentina and New Zealand, and still lives around New Zealand (Marshall, 1978), *Lahillia* occurs in the Miocene of Chile and up to the Monte León Formation (Late Oligocene–Early Miocene) in Argentina, and *Cucullaea* (*Cucullona*) occurs in the Miocene Carmen Silva Formation in Tierra del Fuego. The Paleocene bivalves of the Pebble Point Formation in southern Victoria, Australia, have surprisingly little in common with this Gondwanan group (Darragh, 1994), *Lahillia* and *Cucullaea* (*Cucullona*) being the only obvious examples. This group was the basis of the recognition by Zinsmeister (1979, 1982) of the Weddellian faunal province, and was termed the 'paleoaustral element' in the New Zealand fauna by Fleming (1963).

3.3. Cenozoic dispersers

This group is the subject of the present report, and consists of genus-group taxa with either a post-Eocene earliest record in New Zealand and an earlier fossil record in Argentina, i.e., taxa apparently dispersed from South America to New Zealand, or the

Fig. 1. Southern South America, south of 30°S, showing location of Cenozoic molluscan fossil localities listed in the text. Localities, listed from north to south: *1* = Paraná, Middle Miocene; *2* = Roca, Paleocene; *3* = mouth of Río Negro, Golfo San Matías, Pliocene(?); *4* = Arroyo Verde, Middle Eocene; *5* = Puerto Madryn, Middle Miocene; *6* = Pico Salamanca, Paleocene; *7* = Comodoro Rivadavia, Late Oligocene–Early Miocene; *8* = Lago Pueyrredón, Late Oligocene–Early Miocene; *9* = San Julián, Late Oligocene–Early Miocene; *10* = Mount Entrance, Santa Cruz River, Late Oligocene–Early Miocene; *11* = Monte León, Late Oligocene–Early Miocene; *12* = Lago Argentina, Late Oligocene–Early Miocene; *13* = Cabo Buen Tiempo, Pleistocene(?); *14* = Sierra Dorotea, Paleocene (Cerro Dorotea Formation) and Middle Eocene (Rio Turbio Formation); *15* = Carmen Silva, Miocene; *16* = La Despedida, Eocene. Inset: The Southern Ocean, centred on the South Pole, showing land masses and their relationship to circulation. Axis of Antarctic Circumpolar Current from Barker and Burrell (1982).

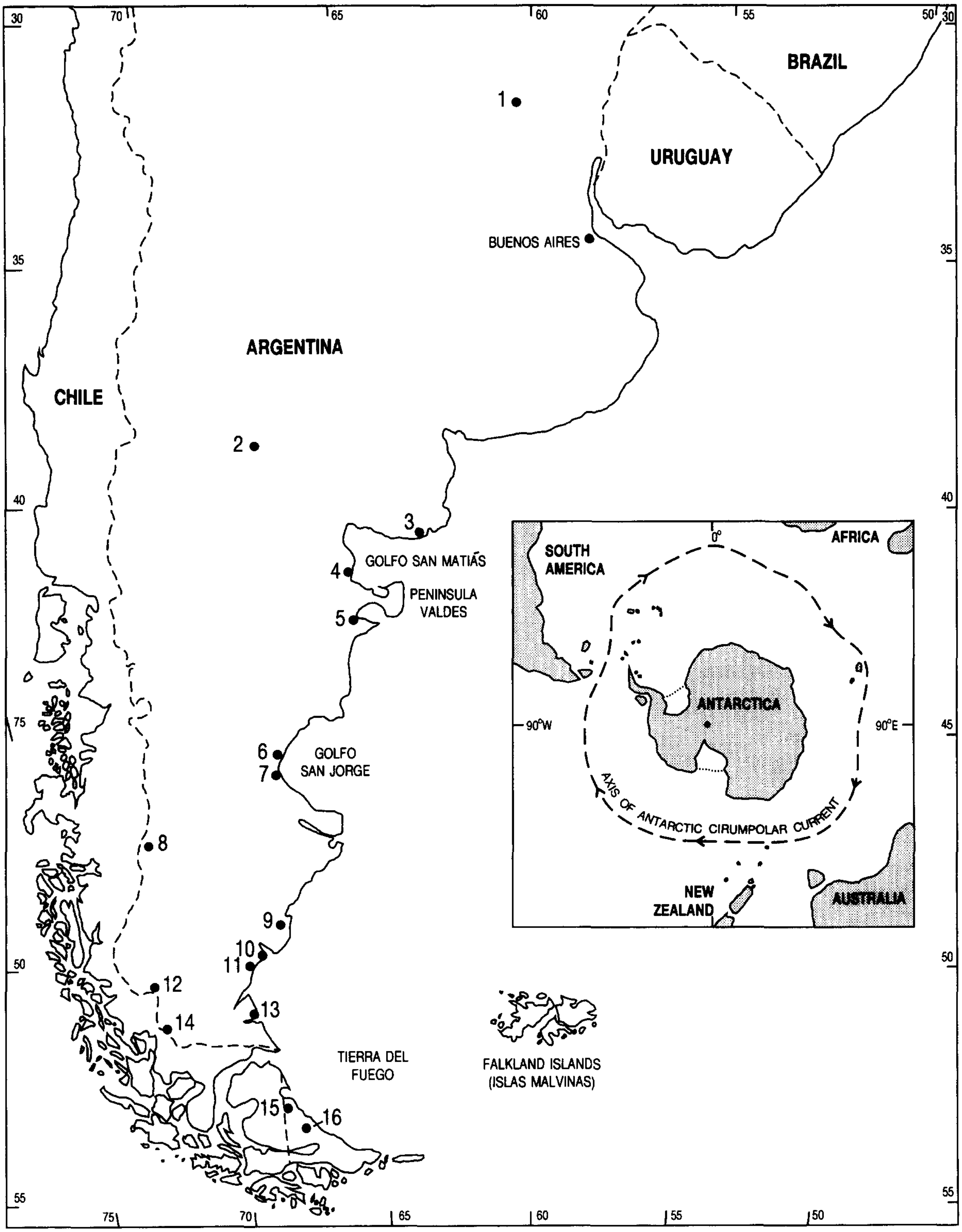

BRAZIL
URUGUAY
BUENOS AIRES
ARGENTINA
CHILE
GOLFO SAN MATIÁS
PENINSULA VALDES
GOLFO SAN JORGE
TIERRA DEL FUEGO
FALKLAND ISLANDS (ISLAS MALVINAS)
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
30
35
40
45
50
55
75
70
65
60
55
50
SOUTH AMERICA
AFRICA
ANTARCTICA
0°
90°W
90°E
AXIS OF ANTARCTIC CIRUMPOLAR CURRENT
NEW ZEALAND
AUSTRALIA

Table 1
Genera in common to New Zealand and Argentina

Family	Cosmopolitan	Gondwanan	Cenozoic dispersers
Solemyidae			?*Solemyarina*
Nuculidae	*Nucula*	?*Ennucula*	?*Deminucula*
Malletiidae		*Spineilo*, *Neilo*	
Sareptidae	*Yoldiella*		
Arcidae	*Arca*, *Acar*, *Barbatia*		*Anadara trapezia*
Noetiidae	*Quadrilatera*		
Cucullaeidae	*Cucullaea* (*Latiarca*)	*Cucullaea* (*Cucullona*)	
Limopsidae	*Limopsis*		?*Notolimopsis*
Philobryidae	?*Lissarca*		*Cosa*
Glycymerididae	*Glycymeris*, s.s., *Glycymerita*		*Glycymeris* (*Glycymerula*)
Mytilidae	?*Modiolus*, *Dacrydium*, *Gegariella*		*Aulacomya atra*, *Mytilus*
Pinnidae	*Atrina*		
Bakevelliidae		?*Panis*	?*Panis*
Pectinidae			*Athlopecten* (from '*Myochlamys*'?) *Zygochlamys*
Propeamussiidae	?*Cyclochlamys*		?*Cyclochlamys*
Anomiidae	*Anomia*, *Pododesmus* (*Monia*)		
Limidae	*Lima*		*Notolimea*
Gryphaeidae	*Pycnodonte* (*Notostrea*)		
Ostreidae	?*Ostrea*, *Flemingostrea*		*Tiostrea chilensis* (from Chile)
Lucinidae	*Myrtea*, *Miltha*		*Gonimyrtea*, *Lucinoma*
Thyasiridae	*Thyasira*		
Montacutidae	*Mysella*, *Devonia*		
Neoleptonidae			?*Puyseguria*
Carditidae	*Pleuromeris*, ?*Cyclocardia*	*Purpurocardia*, ?*Glyptoactis* (*Fasciculicardia*)	
Condylocardiidae	?*Condylocuna*		
Crassatellidae			*Spissatella*
Lahilliidae		*Lahillia*	
Mactridae	*Mactra*		*Scalpomactra*
Tellinidae	*Serratina*, *Elliptotellina*		
Veneridae	*Dosinia*, s.l.		*Austrovenus* (from *Ameghinomya*); *Protothaca*, ?*Tawera*, ?*Turia*
Corbulidae	?*Caryocorbula*		
Hiatellidae	*Hiatella*, *Panopea*		
Pholadidae	*Pholadidea*, *Barnea*		
Thraciidae	*Asthenothaerus*		
Laternulidae	*Laternula*		
Skeneidae	?*Brookula*, ?*Cirsonella*, ?*Crosseola*		?*Crosseola*
Trochidae, s.l.	?*Solariella*, *Calliostoma*		*Diloma nigerrima*, ?*Antisolarium*
Eatoniellidae	*Eatoniella* (*Dardanula*)		
Adorrhaidae		*Struthioptera*, ?*Hemichenopus*	
Struthiolariidae		*Perissodonta*	
Calyptraeidae	*Crepidula*	*Spirogalerus*	*Sigapatella*
Trichotropidae			?*Trichosirius*
Naticidae	*Polinices*, *Lunatia*, ?*Falsilunatia*, ?*Pliconacca*	?*Polinella*	?*Polinella*
Ranellidae	*Sassia*		*Sassia zealta* group; *Argobuccinum*, *Fusitriton*
Ficidae	*Ficus*		
Cerithiellidae	*Cerithiella*		
Cerithiopsidae	*Seila*		*Ataxocerithium*
Eulimidae	*Melanella*		

Table 1 (continued)

Family	Cosmopolitan	Gondwanan	Cenozoic dispersers
Epitoniidae	*Epitonium*, s.l.; *Opalia*, s.l.		*Cirsotrema*, large species
Buccinidae		*Pseudofax*, ?*Austrocominella*	*Penion*
Nassariidae			*Nassarius* (*Hima*), small species
Taiomidae		*Taioma*	
Columbellidae	*Retizafra*, ?*Mitrella*		
Turbinellidae		*Fyfea*, ?*Heteroterma*	
Muricidae			*Xymene*, *Xymenella*, ?*Trophon* s.l.
Costellariidae			?*Austromitra*
Marginellidae	?*Serrata*		
Olividae			*Lamprodomina* (from Chile)
Volutidae			*Provocator*
Terebridae			?*Zeacuminia*
'Turridae', s.l.	*Splendrillia*, ?*Parasyrinx*, s.l.	?*Zemacies*	*Antimelatoma*, *Eoturris*, *Neoguraleus* (*Fusiguraleus*)
Cancellariidae	*Bonellitia*, *Brocchinia*, ?*Scalptia*		*Oamaruia*, *O.* (*Zeadmete*)
Acteonidae	*Acteon*, ?*Tornatellaea*	?*Tornatellaea*	
Cylichnidae	?*Roxania*, ?*Priscaphander*	?*Priscaphander*	
Retusidae	*Volvulella*		
Mathildidae			*Opimilda*
Pyramidellidae	*Egila*, *Doliella*, *Odostomia*, *Turbonilla*, *Eulimella*		

Cenozoic benthic marine molluscan genera common to New Zealand and Argentina, classified by their apparent biogeographic origins. A question mark indicates doubt about the identification, or — in a few cases, listed in more than one column — doubt about the biogeographic classification.

reverse, taxa apparently dispersed from New Zealand to South America. These taxa have crossed the vast distances of the open ocean — 16,100 km eastward from South America to New Zealand and 7600 km from New Zealand to South America, at the present time, measured at 55°S latitude, New Zealand taken at 175°E, South America at 70°W; distances would have been less early in Cenozoic times (see Fig. 1, inset).

It must be reiterated that (1) dispersal can occur *only* from west to east in the ACC, (2) dispersal is inherently more likely to occur from New Zealand to South America than the reverse, because of the much shorter distance, and (3) the fossil record of earliest records does not necessarily reflect real first occurrences.

Beu and Griffin (1997) listed the following examples of genera that appeared to have dispersed from South America to New Zealand:

3.3.1. Late Oligocene–Middle Miocene earliest record in New Zealand

Panis Stevenson, 1953 (Bakevelliidae); *Athlopecten* Marwick, 1928 (Pectinidae); *Austrovenus* Marwick, 1927, apparently descended from the South American *Ameghinomya* Von Ihering, 1907 (Veneridae); large species of *Cirsotrema* Mörch, 1852 (Epitoniidae); and *Lamprodomina* Marwick, 1931 (Olividae), with an ?Early to Middle Miocene record in Chile and a Middle Miocene to Pliocene record in New Zealand.

3.3.2. Latest Miocene or Pliocene earliest record in New Zealand

Tiostrea chilensis (Philippi), Kapitean (latest Miocene) earliest record; *Zygochlamys* Von Ihering, 1907, early Opoitian (basal Pliocene) earliest record; *Lucinoma lamellata* (Smith) (= *L. galathea* Marwick?), Opoitian (Early Pliocene) earliest record; and *Aulacomya atra* (Molina), Waipipian (mid-Pliocene) earliest record.

3.3.3. Pleistocene or Holocene earliest record in New Zealand

Protothaca Dall, 1892, early Castlecliffian (Early Pleistocene) earliest record; *Anadara trapezia* (Deshayes), closely similar to *A. bravardi* Del Rio, 1992, in the Middle Miocene Puerto Madryn Formation, Argentina, earliest record in oxygen isotope stage 11 or 9 throughout Australia and New Zealand; *Diloma nigerrima* (Gmelin), a dubious example (with no fossil record) of an archaeogastropod purportedly common to Chile and New Zealand; *Argobuccinum pustulosum* (Solander in Lightfoot), the living circum-Southern Hemisphere member of a North Pacific group, with a fossil record from the Pliocene in Chile (Herm, 1969, p. 71) and from the late Middle Pleistocene in New Zealand (oxygen isotope stage 9 or 7, in Denby Shellbed at Hawera, South Taranaki); *Fusitriton magellanicus* (Röding), another case of a North Pacific tonnoidean gastropod that crossed the tropical barrier late in the Neogene and then reached New Zealand by dispersal in the ACC. Other examples include *Semicassis labiata* (Perry), *Cymatium parthenopeum* (Salis), *Ranella australasia* (Perry) and *R. olearium* (Linné), and *Charonia lampas* (Linné), although several of these seem to have entered the ACC at South Africa rather than at southern South America (Beu, 1976).

A single example was listed by Beu and Griffin (1997) of a taxon that has apparently dispersed from New Zealand to South America: *Sassia* of the *S. zealta* species group has a record from the Late Paleocene (Waipawan) to the Middle Miocene (Clifdenian) in New Zealand (Beu, new data); species closely resembling the New Zealand Oligocene–basal Miocene *S. minima* (Hutton) occur in the Monte León Formation in Argentina [*S. morgani* (Ortmann) and *S. bicegoi* (Von Ihering), the latter possibly a synonym of the Chilean Miocene *S. armata* (Hupé)] and in the Early Miocene Freestone Cove Sandstone in Northern Tasmania, Australia [*S. abbotti* (Tenison Woods)].

4. New information on Cenozoic dispersers

New collections and a catalogue of Argentinean Cenozoic Mollusca assembled by M. Griffin provided the following additions and amendments to the list of previously recognised Cenozoic dispersers.

4.1. Confirmation of previous records

Examples listed by Beu and Griffin (1997) and confirmed by the new collections are:

4.1.1. Panis Stephenson, 1952

Albian (Stephenson, 1952, p. 67) to Miocene in South America, basal Miocene (Waitakian) to Early Pleistocene (Nukumaruan) in New Zealand. Note that *Meleagrina crassicardia* (Tate, 1886, p. 121, pl. 9, figs. 9, 10), included by Beu and Griffin (1997), is a large *Pteria* species; the Australian Miocene–Pliocene species of *Panis* is unnamed, although it is possibly conspecific with the New Zealand *P. zealandica* (Hutton in Suter) (T.A. Darragh, Museum of Victoria, pers. commun., 1995).

4.1.2. Athlopecten Marwick, 1928

Confirmed as closely related to the Argentinean fossils assigned to the invalid '*Myochlamys*' Von Ihering, 1907. However, the earliest record in Argentina is in the Late Oligocene–Early Miocene Monte León Formation, so this group of closely related taxa appears at about the same time in *both* New Zealand and Argentina, from an unknown ancestor.

4.1.3. Austrovenus Marwick, 1927

A close relationship to *Ameghinomya* Von Ihering, 1907 is confirmed. *Ameghinomya argentina* (Von Ihering) is larger, more nearly circular, and with more numerous radial costae than any *Austrovenus* species, but the widespread *Ameghinomya meridionalis* (Del Rio, 1994, pl. 3, figs. 6–10) closely resembles the early New Zealand members of this group, particularly *Hinemoana acuminata* (Hutton). Further research is needed on this group.

4.1.4. Large Oligocene–Early Miocene species of Cirsotrema

Cirsotrema specimens from the two countries are similar and are probably closely related phylogenetically. This is a taxonomically 'difficult' group, however, needing study of ontogeny of each species; the smaller New Zealand Eocene species might also have given rise to larger Oligocene ones.

4.1.5. Zygochlamys

Zygochlamys species are common and widespread in San Julián and Monte León Formations, and are undoubtedly phylogenetically related to *Z. seymouri* (Marwick) (Early Pliocene, basal Opoitian) and *Z. delicatula* (Hutton) (basal Nukumaruan, Late Pliocene/Early Pliocene, to Recent) in New Zealand.

4.1.6. *Lucinoma*

A *Lucinoma* species similar to *L. lamellata* (Smith) in the Carmen Silva Formation (Miocene) of Tierra del Fuego confirms that this group has a markedly longer fossil record in Argentina than in New Zealand (earliest record Opoitian, Early Pliocene). Earlier New Zealand species referred here (*L. taylori* Powell, late Early Miocene, and some unnamed) are more inflated and so probably not closely related to *L. lamellata.*

4.1.7. *Aulocomya*

Typical *Aulacomya,* closely resembling *A. atra* (Molina), occurs in the San Julián Formation in Argentina (Late Eocene–Early Oligocene), much older than its Waipipian (Mid-Pliocene) earliest record in New Zealand.

We have no new information on the other examples listed previously (Beu and Griffin, 1997).

4.2. *New examples of relationships*

Examination of the newly available Argentinean collections has brought to light 32 further genus-group taxa in common with New Zealand (Table 1). In Table 2, all 46 genus-group taxa classed as Cenozoic dispersers are listed, classified according to their biogeographic origins.

Fig. 2 is a graph, updated from (Beu and Griffin, 1997, fig. 1), showing the numbers of marine molluscan genus-group taxa apparently dispersed to and from South America (largely Argentina) and New Zealand at various times through the Cenozoic Era, classified by polarity of dispersal and time of earliest record in the recipient country.

Clearly, Fig. 2 demonstrates a large burst of dispersed genus-group taxa arriving in both New Zealand and Argentina during Late Oligocene–Early Miocene times (not subdivided more closely because of imprecision of dating of Argentinian faunas). This apparently was followed by virtually *no* further dispersal from New Zealand to Argentina (the one possible exception being *Tawera,* Veneridae), but by modest levels of Pliocene–Early Pleistocene dispersal from Argentina to New Zealand, enhanced during the most extreme Pleistocene glaciations to a level close to that during Late Oligocene–Early Miocene times.

4.2.1. *Biases in the record*

The significance of the biases introduced by the available Argentinian faunas now becomes clear. Firstly, although we are reasonably sure that all genus-group taxa shown in Fig. 2 (upper: South America to New Zealand) have no earlier record in New Zealand, and we are equally sure that all genus-group taxa included in Fig. 2 (lower: New Zealand to South America) *do* have an earlier record in New Zealand than in South America (many newly recorded from Early–Middle Eocene faunas of upper Waihao Valley; P.A. Maxwell, new data), the record simply does not exist in South America to show whether or not any genus-group taxa in Fig. 2 (lower) might have occurred earlier in South America. The column of 22 genera that *seem* to have appeared suddenly in South America in the Monte León Formation of Patagonia is therefore almost *certain* to be partly spurious, but we have no way of determining to what degree.

Secondly, the opposite effect seems likely to be biasing post-Middle Miocene faunas of Argentina. The great paucity and low diversity of Late Miocene to Early Pleistocene marine molluscan faunas of Argentina, in particular, means that no evidence is preserved of any New Zealand marine molluscan genus-group taxa that might have arrived there, and then become extinct again. The blank younger portion of Fig. 2 (lower) reflects the lack of a fossil record, but *not necessarily* the lack of dispersal.

Examples of newly recognised dispersers: Clearly, all 32 of the newly recognised dispersed genus-group taxa cannot be discussed here. A selection is presented of some of the more interesting examples.

4.2.2. *Small species of Nassarius (Hima), Nassariidae*

The three previously recognised *N.* (*Hima*) species in New Zealand were reviewed by Maxwell (1988, pp. 51–52); an undescribed species is present in a Mangaorapan (Lower Eocene) shellbed in the upper Waihao Valley near 'Pentland Hills' Station (P.A. Maxwell, new data). An unnamed member of the same group of very small species is abundant in the Monte León Formation in Argentina. The relatively large, multi-whorled, conical protoconch (Maxwell, 1988, pl. 5, a–i) suggests that a plank-

Table 2

Timing and polarity of Cenozoic dispersal between New Zealand and South America

From South America to New Zealand			From New Zealand to South America	
Oligocene–E. Miocene first record in N.Z.	L. Miocene–Pliocene first record	Pleistocene–Recent first record	Oligocene–E. Miocene first record in S. America	?Pleistocene–Recent first record
1. *Panis* (Lw)	1. *Zygochlamys* (Wo)	1. ?*Solemyarina* (R)	1. ?*Deminucula*	?*Tawera* (still lives all around Southern Ocean)
2. *Athlopecten* (from Argent. '*Myochlamys*'?), Ld	2. *Tiostrea* (Chile) (Tk)	2. *Anadara trapezia* (Wc)	2. *Notolimopsis*	
3. *Austrovenus* (from Argent. *Ameghinomya*), Lw	3. *Aulacomya* (Wp)	3. *Mytilus* (Wq)	3. *Glycymeris* (*Glycymerula*)	
4. *Cirsotrema*, large spp. (Ld)	4. *Lucinoma* (Wo)	4. *Protothaca* (Wc)	4. ?*Cyclochlamys*	
5. *Oamaruia* (*Zeadmete*) (Lw)	5. ?*Antisolarium* (from Argent. '*Gibbula*' *dalli*?) (Wo)	5. ?*Diloma nigerrima* (Chile) (R)	5. *Gonimyrtea*	
6. ?*Puyseguria*, Lw	6. *Xymene* (latest Middle Miocene first record, Sw)	6. *Argobuccinum* (Wq)	6. *Spissatella*	
7. *Cosa* (Lw)	7. ?*Trophon*, s.l. (Wm)	7. *Fusitriton* (R)	7. *Scalpomactra*	
8. *Notolimea*? (Sl only in NZ)	8. *Provocator* (Wn)	(all still live in New Zealand, except *A. trapezia*)	8. ?*Turia*	
[+ *Lamprodomina*, Chile, Middle Miocene first record in N.Z. (Sl)]	9. *Antimelatoma* (Wn)		9. *Crosseola*	
[extinct in New Zealand, except *Austrovenus*, *Puyseguria* and *O.* (*Zeadmete*)]	(all still live in New Zealand)		10. *Sigapatella*	
			11. *Trichosirius*?	
			12. *Sassia zealta* group	
			13. *Ataxocerithium*	
			14. *Penion*	
			15. *Nassarius* (*Hima*)	
			16. *Xymenella*	
			17. ?*Austromitra*	
			18. ?*Zeacuminia*	
			19. *Eoturris*	
			20. *Neoguraleus* (*Fusiguraleus*)?	
			21. *O.* (*Oamaruia*)	
			22. *Opimilda*	
			(all extinct in S. America?)	

Genera listed in same order as in Table 1 (American source assumed to be Argentina, except where 'Chile' noted). Time of first appearance in New Zealand indicated by stage abbreviations: Lw = Waitakian; Ld = Duntroonian; Sl = Lillburnian; Sw = Waiauan; Tk = Kapitean; Wo = Opoitian; Wp = Waipipian; Wm = Mangapania; Wn = Nukumaruan; Wc = Castlecliffian; Wq = Haweran; R = Recent. Stages shown in Fig. 2.

totrophic larval stage is likely present in this species group. It is therefore feasible that this group dispersed from New Zealand to South America at about the end of the Oligocene. In both New Zealand and Patagonia, these are the only representatives of the Nassariidae, which is a very diverse group in many other faunas.

4.2.3. *Penion*, Buccinidae

As was pointed out by Ponder (1973, p. 401, 402), fossil *Penion* species occur in both Chile and Argentina, although living species seem to occur around Australia and New Zealand only. In New Zealand the earliest species referred here is the 'Wangaloan' (Early Paleocene) *P. proavitus* (Finlay and Marwick), although it is possible this is not phylogenetically related to younger *Penion* species. The Chilean species *P. subreflexus* (Sowerby) is Miocene, and in Argentina the earliest record we are aware of is *P. subrectus* (Von Ihering) (Late Oligocene–Early Miocene). Although preservation of protoconchs is poor on available material, *P. subrectus* appears to belong in the species group with a small protoconch (Ponder, 1973, text-fig. 3) along with most Australian species and the New Zealand Miocene *P. bartrumi* (Laws). This group appears more likely to have had a planktotrophic larval stage than does the species group of *P. dilatatus* (Quoy and Gaimard), which has a complex mass of large egg capsules and a large, cylindrical, few-whorled protoconch resulting from "long larval development within the egg capsule" (Ponder, 1973, p. 407), i.e., direct development.

Although, in a general sense, *Penion* has a much earlier first record in New Zealand than in Argentina, the Australian Early Miocene *P. roblini* (Tenison Woods) (Ponder, 1973, pl. 44, figs. 1, 2) closely resembles the Argentinian *P. subrectus*, suggesting that there might have been circum-Antarctic dispersal of *Penion* both to and from South America.

4.2.4. *Spissatella*, Crassatellidae

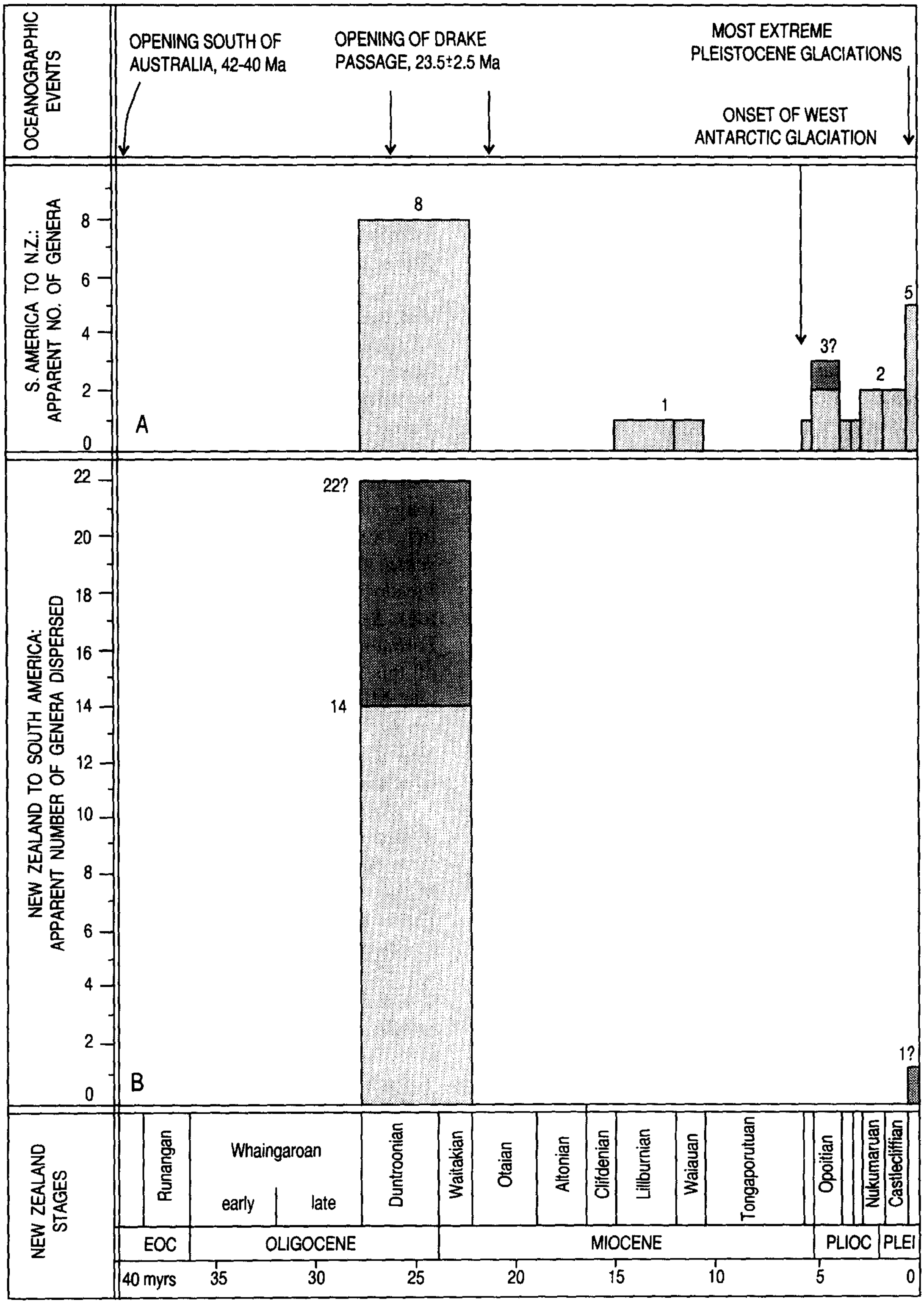
Spissatella is a distinctive genus of elongate, weakly inflated Crassatellidae (Beu and Maxwell, 1990, pl. 11, a; pl. 18, i, k) occurring mainly in New Zealand, but with one species in Oligocene (Janjukian) rocks in Australia (Darragh, 1965, pp. 110–111). The Argentinean species *Crassatella lyelli* Sowerby, 1846 and *C. longior* Von Ihering, 1897 (= *C. quartus* Ortmann, 1902), both from the Monte León Formation (Late Oligocene–Early Miocene), are species of *Spissatella*, although they are even less inflated than most New Zealand species. Again, this appears most likely to be a case of dispersal from New Zealand to both Argentina and Australia, as the genus occurs in Late Eocene (Kaiatan) to Late Miocene (Tongaporutuan and possibly Kapitean) rocks in New Zealand.

4.2.5. *Xymene*, Muricidae

Although all small Argentinean trophonine muricids previously have been assigned to *Urosalpinx* Stimpson, 1865 (type species: *Fusus cinerea* Say, Recent, Atlantic North America), most published names refer to only a single species, two species belong in *Xymene sensu lato*, and only one species belongs in *Urosalpinx*. *Triton dautzenbergi* (Von Ihering, 1897, p. 293, text-fig. 16) is a species of *Xymene*, *sensu stricto*, closely resembling the New Zealand Pleistocene–Recent type species, *X. plebeius* (Hutton). *X. dautzenbergi* (common in the Monte León Formation) is therefore older than the earliest record of this species group in New Zealand (Waiauan, late Middle Miocene; Ponder, 1972, p. 478), although this earliest record is of low reliability in New Zealand because these species are limited to intertidal estuarine and semiestuarine environments.

'Urosalpinx' elegans Ortmann (1900, p. 376) (Ortmann, 1902, p. 219, pl. 34, fig. 9), in contrast, closely resembles the New Zealand Eocene–Miocene species group of *'Xymene' lepidus* (Suter). This is a distinctive group of narrow, elongate, angular species with a strongly out-turned, lirate outer lip, placed in a separate genus *Xymenella* Finlay, 1926 until *Xymenella*, *Axymene* Finlay, 1926 and *Zeatrophon* Finlay, 1926 were all synonymised with *Xymene* Iredale, 1915 by Ponder (1972). *'Urosalpinx' elegans* is common in but not known earlier than the Monte León Formation, so its first record is younger than the Eocene–Recent record of this species group in New Zealand.

The combined New Zealand and Argentinean fossil record therefore suggests that, as has been suspected for some years by New Zealand molluscan taxonomists, *Xymene* and *Xymenella* (at least) are distinct genera, with very different bio-


OCEANOGRAPHIC EVENTS
OPENING SOUTH OF AUSTRALIA, 42-40 Ma
OPENING OF DRAKE PASSAGE, 23.5±2.5 Ma
MOST EXTREME PLEISTOCENE GLACIATIONS
ONSET OF WEST ANTARCTIC GLACIATION
S. AMERICA TO N.Z.: APPARENT NO. OF GENERA
0
2
4
6
8
A
8
1
3?
2
5
NEW ZEALAND TO SOUTH AMERICA: APPARENT NUMBER OF GENERA DISPERSED
0
2
4
6
8
10
12
14
16
18
20
22
B
22?
14
1?
NEW ZEALAND STAGES
Runangan
Whaingaroan
early
late
Duntroonian
Waitakian
Otaian
Altonian
Clifdenian
Lillburnian
Waiauan
Tongaporutuan
Opoitian
Nukumaruan
Castlecliffian
EOC
OLIGOCENE
MIOCENE
PLIOC
PLEI
40 myrs
35
30
25
20
15
10
5
0

geographic histories. The available record suggests that *Xymenella* evolved in New Zealand, and dispersed to South America late in Oligocene times, whereas *Xymene* evolved in South America and dispersed to New Zealand, apparently during the Middle Miocene.

4.2.6. *Antimelatoma*, *Turridae*

Beu and Maxwell (1990, p. 369) pointed out that *Antimelatoma* Powell, 1942 is first recorded in New Zealand during Nukumaruan (Late Pliocene/Early Pleistocene) times, and has no known ancestors or close relatives in the New Zealand region. *Fusus quemadensis* (Von Ihering, 1907, p. 195, pl. 6, fig. 39) is a small, elongate turrid, referable to *Antimelatoma*, occurring uncommonly in the Monte León Formation (Later Oligocene–Early Miocene) in Argentina, demonstrating the biogeographic origins of this formerly enigmatic New Zealand species group.

5. Conclusion: dispersal times and paleoceanographic events

Tables 1 and 2 and Fig. 2 demonstrate that, at least superficially, an initial burst of benthic marine molluscan genus-group taxa was dispersed around the Southern Ocean when the ACC first began to circulate, late in the Oligocene. The incompleteness of the fossil record in South America means that we may never know how accurate this estimate is of the number of dispersed taxa. Nevertheless, we can be sure that at least the number dispersed from South America to New Zealand is reasonably accurate, and therefore we can have some confidence that at least *part* of the apparent dispersal from New Zealand to South America was real — remembering the much shorter distance from New Zealand to South America than vice versa, a number at least roughly comparable to that dispersed *to* New Zealand seems likely to have been dispersed *from* New Zealand to South America. The Late Miocene and younger record of South America fails, once again, to provide any evidence of whether dispersal of benthic molluscs occurred from New Zealand to South America after Middle Miocene times, and the best proxy for this time appears to be the well documented record in New Zealand of dispersal from South America; there seems to be no reason why dispersal *to* South America would not have been at least as marked, because of the much shorter eastward distance from New Zealand to South America than from South America to New Zealand. The New Zealand record shows that intensification of circulation of the ACC increased molluscan dispersal, (a) after the commencement of glaciation of West Antarctica, and (b) during the major Middle–Late Pleistocene glaciations.

It is possible that, because of the initial narrowness of Drake Passage, and because the same amount of water flowed through the narrow passage as elsewhere, early ACC flow might have been greatly accelerated compared with the present, so carrying more larvae away from South America than from New Zealand. However, it is more likely that the incomplete fossil record is causing a spurious impression.

Whether molluscs were dispersed as planktonic larvae or as rare rafted sessile adults, cool periods seem likely to have favoured dispersal. Beu (1976) pointed out that, at an individual level, cooling of the sea seems to have extended larval life because of the slowing of metabolic rates; an equally (or even more) important phenomenon could have been species selection during cool periods of taxa with long larval lives. Algal rafts possibly were favoured during cool periods also; the largest macroalgae (such as *Durvillea* in New Zealand) prefer cool-water locations, and may not have been available to contribute rafts during warm periods; and the enriched nutrient levels of cool periods would contribute to the enhanced growth of macroalgae.

These points demonstrate again the great significance for Southern Hemisphere marine biogeogra-

Fig. 2. Numbers of benthic molluscan genus-group taxa dispersed around the Southern Ocean, (A) from South America to New Zealand, and (B) from New Zealand to South America, plotted against the New Zealand timescale and major Southern Ocean paleoceanographic events. Taxa queried in Table 1 are shown in a darker hachure than confirmed records. [The Kapitean Stage comes between Tongaporutuan and Opoitian; Waipipian (Older) and Mangapanuan Stages come between Opoitian and Nukumaruan; youngest is Haweran.]

phy of the opening of the Drake Passage gateway late in Oligocene or early in Miocene times and, in particular, of the formation of ACC circulation as both a thermal isolating mechanism for Antarctica and a disperser of the southern Ocean marine biota.

The date for the Marshall Paraconformity (32–29 Ma; Fulthorpe et al., 1996) and its consequent position in Fig. 2 suggest that, rather than resulting from the opening of Drake Passage, this hiatus in on-shore New Zealand rocks resulted from the final opening of full marine circulation south of Australia.

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