

Palaeobiogeography of Austral echinoid faunas: a first quantitative approach

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Abstract: Few studies have been devoted to the palaeobiogeography of Antarctic echinoids, all of them analysing and discussing distribution patterns in a qualitative way. The present work aims at exploring the evolution of palaeobiogeographic relationships of Austral echinoid faunas through four time intervals, from the Maastrichtian to the present day, using a quantitative approach: the Bootstrapped Spanning Network procedure. Analyses were successfully performed and improve our knowledge of biogeographic relationships between the different Austral regions. Biogeographic maps were produced that can be easily and intuitively discussed. Our results mostly agree with palaeobiogeographic studies performed on other benthic invertebrates and are congruent with the palaeogeographic evolution of Antarctica. However, two main points markedly contrast with other works: there is no evidence of an Austral provincialism at the end of the Cretaceous and early Cenozoic, and echinoid data suggest isolation of southern Argentina from other Austral regions, including Antarctica, in the Early Miocene.

Earth history has had a deep influence on the evolution of the biosphere and consequently on the distribution of life through time. Regarding the Southern Ocean, the final break-up of Gondwana followed by the onset of the southern Pacific and Antarctic circumpolar surface currents during the Cenozoic have had a determinant role explaining the biogeography and diversity of modern Austral faunas (Zinsmeister 1979, 1981; Zinsmeister & Camacho 1980; Beu *et al.* 1997; Del Rio 2002; Pearse *et al.* 2009). Such events are considered to have promoted the two biogeographic processes that have long been invoked to explain the geographically discontinuous distribution patterns of taxa on Earth, namely (1) divergence by vicariance, an outcome of the fragmentation of Gondwana, and (2) dispersal, alternatively promoted or restricted in particular directions by southern surface currents. Both processes have probably worked in unison to shape the modern distribution of Austral faunas (Pearse *et al.* 2009).

Stressing the similarities among the gastropod faunas of Australasia, Antarctica and southern South America in the Late Cretaceous and early Palaeogene, Zinsmeister postulated the existence of a unique Austral faunistic province at that time, the so-called Weddellian province (Zinsmeister 1979, 1981; Zinsmeister & Camacho 1980). Then, the final break-up between Australia and Antarctica along with the northward drift of Australia and New Zealand to warmer conditions by the Late Eocene was associated with the appearance

of distinctive faunas in these two latter regions. Faunal connections between Antarctica and southern South America persisted until the Drake Passage opened to depth about the Eocene–Oligocene boundary (Zinsmeister 1981; Beu *et al.* 1997; Scher & Martin 2006; Lawver *et al.* 2011). The onset of a southern Pacific surface current followed by the Antarctic circumpolar current in the Late Eocene was also considered to have influenced the evolution of Austral biogeography (Beu *et al.* 1997; Pearse *et al.* 2009). Hence, Beu *et al.* (1997) and Del Rio (2002) highlighted the existence of faunal similarities between New Zealand and southern South America owing to both eastward and westward dispersals from the Oligocene to the Holocene, while Pearse *et al.* (2009) stressed the role of the Antarctic circumpolar current in promoting speciation within brooding clades of the Southern Ocean.

Most palaeobiogeographic studies of Upper Cretaceous and Cenozoic Austral benthic invertebrates have been based on bivalve and gastropod faunas (Zinsmeister 1979; Zinsmeister & Camacho 1980; Crame 1996; Beu *et al.* 1997; Stilwell *et al.* 2004; Beu 2009), whereas few have considered fossil data across other benthic invertebrate groups such as brachiopods and echinoderms (Zinsmeister 1981). With only approximately 20 fossil species recorded in Antarctica so far, echinoids could appear at first sight as non-informative for palaeobiogeographic purposes. However, most fossils collected in the northern tip of the Antarctic Peninsula for more

than one century are Maastrichtian, Late Eocene and Early Miocene in age, namely three key time periods to document respectively the situation before the Gondwanan final break-up, the outcome of the northward continental drift of Australia and New Zealand, and the biogeographic consequences of the opening of the Drake Passage and setting up of the Antarctic circumpolar current. Fossil echinoids of the same time periods are recorded in southern Argentina, South Australia and New Zealand, so that the evolution of palaeobiogeographic relationships among these nowadays distinct parts of Gondwana can be investigated using echinoid data. Although palaeobiogeographic relationships among Austral fossil echinoid faunas were formerly discussed (Hotchkiss 1982; Néraudeau *et al.* 2000; Néraudeau & Mathey 2000), it was only in a qualitative way. The present work aims at exploring the palaeobiogeographic relationships through the three time periods mentioned above and comparing them with the present-day situation using the same quantitative approach.

Material and method

Fossil data and taxonomic issues

The three studied geological periods (the Maastrichtian, Late Eocene and Early Miocene) are known in the southern high latitudes from stratigraphic levels that crop out in Antarctica (Table 1), southern Argentina, Australia and New Zealand. The time resolution of the analysis was determined by the biostratigraphic resolution and incompleteness of the known Antarctic (Table 1) and Argentinian fossil record. Seven areas were determined where fossil deposits from the three studied time periods crop out: the western part of the Antarctic Peninsula (including The James Ross basin and King George island), southern Argentina (Patagonia), southeastern and southwestern Australia, Chatham Island, and North and South New Zealand. Present-day distribution data correspond to echinoid samples collected during oceanographic campaigns led in close nearshore marine areas (Fig. 1).

Analyses were performed at genus level to make up for systematic bias and low stratigraphic resolution. Material from GNS Science in Lower Hutt (New Zealand) and from the Museo Argentino de Ciencias Naturales in Buenos Aires (Argentina) was examined to check on systematic reliability and consistency, a recurrent issue in palaeobiogeographic studies (Brayard *et al.* 2007). This was completed with data from the literature (Table 1) and from the online database FRED (Fossil Record Electronic Database) for fossil echinoids from New Zealand. Present-day occurrence data come

from the updated version of the Antarctic Echinoid Database (David *et al.* 2005), which integrates most records collected during oceanographic cruises led in the Southern Ocean until 2003. They were augmented by new records collected during cruises led in Antarctica since 2003 (ANTXXIII/8, BENTART, 2003, 2006 and JR230) and with northern data collected as far as latitude 35°S. Specimens housed in public collections were examined (National Institute of Water and Atmospheric Research in Wellington, Museo Argentino de Ciencias Naturales in Buenos Aires, Melbourne Museum in Melbourne, Australian Museum in Sydney). The dataset used in this work corresponds to species occurrences recorded off the land areas where fossil deposits crop out. It covers the parts of continental shelves that best fit with the location of fossil sampling areas (Fig. 1).

Palaeobiogeographic analyses

Regional similarities were analysed using the Bootstrapped Spanning Network (BSN) procedure, namely a non-hierarchical clustering method recently developed for palaeobiogeographic studies and efficient for identification of both biogeographic groupings and transitional areas (Brayard *et al.* 2007). This approach gives a simple, intuitively legible picture of the nested as well as gradational taxonomic similarity relationships, hence providing a good synthesis (and additional insights) between hierarchical clustering and ordination in reduced space results. Associated with each occurrence matrix, a dissimilarity matrix was here computed using the Bray & Curtis (1957) coefficient, which gives a double weight to shared presences and thus relative underweight to absence and unique occurrence as an indication of faunal differences (Brayard *et al.* 2007). Similarity relationships were displayed as a connected network supported by 10 000 bootstrap iterations giving confidence intervals for each connection between bioregions (see Brayard *et al.* 2007 for an exhaustive description of the procedure). Displayed on (palaeo)geographic maps, the BSN allows a robust appraisal of faunal exchange pathways, including faunal gradients or reticulated biogeographic structures. BSN were computed using the software BSN v. 1.0 (Brayard *et al.* 2007) and results were visualized using the program PAJEK v. 1.07 (Batagelj & Mrvar 2005).

A total of 845 fossil occurrences, which correspond to the different locations and geological time periods for which a genus is recorded (17 for the Antarctic Peninsula, 69 for southern Argentina, 316 for South Australia, 33 for Chatham island, 244 for North New Zealand and 166 for South New Zealand) and 3158 present-day occurrences

Table 1. Fossil echinoids identified in Antarctica, from Late Cretaceous to Early Miocene

Echinoid taxa	Synonym	Geologic Formation	Time period	Location	Literature consulted
<i>Abatus kieri</i> McKinney, McNamara & Wiedman, 1988	? <i>Schizaster antarcticus</i> Lambert, 1910	La Meseta	Late Eocene	Seymour Island	Lambert, 1910; McKinney, McNamara & Wiedman, 1988
<i>Almucidaris durhami</i> Blake & Zinsmeister, 1991		López de Bertodano	Maastrichtian	Seymour Island	Blake & Zinsmeister, 1991
<i>Austrocidaris seymourensis</i> Radwanska, 1996		La Meseta	Eocene	Seymour Island	Radwanska, 1996
<i>Cyathocidaris erebus</i> Lambert, 1910			Maastrichtian	Seymour Island	Lambert, 1910
<i>Cyathocidaris nordenskjöldi</i> Lambert, 1910		López de Bertodano	Maastrichtian	Seymour Island	Lambert, 1910; Néraudeau, Crame & Kooser, 2000
<i>Cyathocidaris patera</i> Lambert, 1910		López de Bertodano	Maastrichtian	Seymour Island	Lambert, 1910; Néraudeau, Crame & Kooser, 2000
<i>Giraliaster lorioli</i> (Lambert, 1910)	<i>Holaster lorioli</i> Lambert, 1910	Snow Hill	Maastrichtian	Snow Hill Island	Lambert, 1910; Néraudeau, Crame & Kooser, 2000
<i>Hemiaster (Bolbaster) vomer</i> (Lambert, 1910)	<i>Vomeraster vomer</i> Lambert, 1910	Snow Hill	Maastrichtian	Snow Hill Island	Lambert, 1910; Néraudeau, Crame & Kooser, 2000
<i>Huttonechinus antarctica</i> Néraudeau, Crame & Kooser, 2000		Santa Marta	Late Cretaceous	James Ross Island	Néraudeau, Crame & Kooser, 2000
? <i>Iheringiella</i> sp.			Late Eocene	Black Island, McMurdo Sound	Hotchkiss & Fell, 1972
<i>Micraster aff. regularis</i> Arnaud, 1883		Santa Marta	Late Cretaceous	James Ross Island	Néraudeau, Crame & Kooser, 2000
<i>Nordenskjöldaster antarctica</i> Lambert, 1910		Snow Hill	Maastrichtian	Snow Hill Island	Lambert, 1910; Bernasconi, 1959
<i>Nordenskjöldaster australis</i> Néraudeau, Crame & Kooser, 2000		Santa Marta	Campanian	James Ross Island	Néraudeau, Crame & Kooser, 2000
? <i>Notocidaris</i> sp.		Cape Melville	Early Miocene	King George Island	Jesionek-Szymanska, 1987
? <i>Schizaster</i> sp.		Cape Melville	Early Miocene	King George Island	Jesionek-Szymanska, 1987
? <i>Sterechinus</i> sp.	? <i>Isechinus</i> sp. Gazdzicki & Wrona, 1982	Cape Melville	Early Miocene	King George Island	Jesionek-Szymanska, 1987
<i>Stigmatopygus andersoni</i> (Lambert, 1910)	<i>Cassidulus andersoni</i> Lambert, 1910	La Meseta	Eocene	Seymour Island	Lambert, 1910; McKinney, McNamara & Wiedman, 1988



Fig. 1. Location of sampling sites for the Maastrichtian (squares), Late Eocene (triangles), Early Miocene (diamonds) and present day (solid circles).

(465 for the Antarctic Peninsula, 115 for southern Argentina, 704 for South Australia, 186 for Chatham island, 843 for North New Zealand and 845 for South New Zealand) were included within our final dataset and analysed (Fig. 1).

Fossil record and taxonomic richness

Genus richness values contrasted between both studied areas and time periods (Fig. 2). Overall, the total genus richness increases from 15 genera recorded in the Maastrichtian to 42 in the Late Eocene and 65 in the Early Miocene. The total present-day richness is represented by 165 genera. The incompleteness of our knowledge of the fossil

record is obvious and could potentially bias the analyses. To assess this potential bias, the correlation significance between taxonomic dissimilarities and richness differences was addressed using a Mantel test. The test was performed between the matrix of taxonomic dissimilarities and the matrix of richness differences computed for each pairwise comparison between regions as the ratio of richness difference to total richness. The correlation value is 0.5 and significance was tested ($p < 0.01$; 5000 bootstrap iterations) using the software PAST v. 1. 92 (Hammer *et al.* 2001). Taxonomic dissimilarities are thus partly explained by richness differences. The relationship between faunal similarities and genus richness can be

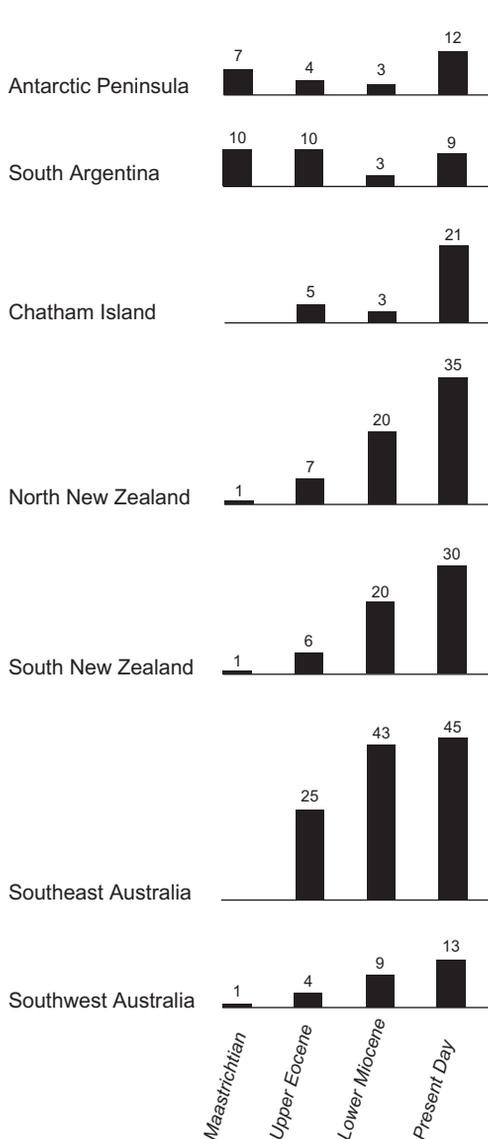


Fig. 2. Genus richness values for the seven studied areas and four time intervals.

interpreted either as biogeographically significant (e.g. provincialism and regional burst of diversity) or as a result of the uneven quality of data.

This stands out clearly when richness values are compared with the number of occurrences that increases from the Maastrichtian to the present day. On Chatham Island, in southern Argentina and the Antarctic Peninsula, richness values decrease from the Maastrichtian to the Early Miocene, then increase to the present day. Richness values and

the number of fossil deposits investigated in the Antarctic Peninsula and Chatham Island vary in the same way; richness variation can therefore be interpreted as an outcome of collecting biases and should be interpreted with caution. However, in southern Argentina richness values do not seem to be correlated with the number of sampling sites, which are the most numerous for the Early Miocene (13) and Present Day (115), whereas richness values are the lowest for these time periods (Fig. 2). Therefore, the low richness values of the Early Miocene and present day in southern Argentina do not seem to be entirely determined by sampling biases and probably correspond to a distinctive biogeographic context. The low Argentinian richness sharply contrasts with the burst of echinoid richness recorded in the Late Eocene and Early Miocene of Australia and New Zealand (Fig. 2). These high richness values reflect the radiation of several regular and irregular families already documented in previous works (Philip & Foster 1971, 1977; Zinsmeister & Camacho 1980; Hotchkiss 1982) and obviously show up compared with the situation in the Maastrichtian, a period characterized by a poor fossil record in these regions.

Palaeobiogeographic relationships

BSN analyses were successfully performed and bootstrap support values stress robust, significant connections between regions despite the unevenness of fossil and present-day data. In Figure 3, faunal similarities among studied areas are shown as a connected network for each time period. Bold lines correspond to robust connections with a 100% confidence interval whereas weaker connections are depicted as dashed lines associated with their respective bootstrap support values.

Maastrichtian

Fossil faunas of the Maastrichtian remain insufficiently known and all computed faunal similarities are weak or not sufficiently contrasted. Thus, no robust network was computed nor displayed for this time period.

Despite the limited fossil record, especially in Australia and New Zealand, a qualitative survey of the echinoid faunas of the Late Cretaceous suggests the predominance of cosmopolitan genera with European (Boreal and Tethyan) affinities. Some authors also pointed out taxonomic similarities between faunas of West Antarctica and southern Argentina (Furque & Camacho 1949; Bernasconi 1954; Hotchkiss 1982). This is evidenced by the common occurrence of the genera *Cyathocidaris*, *Nordenskjoldaster* and *Hemister* in both regions.

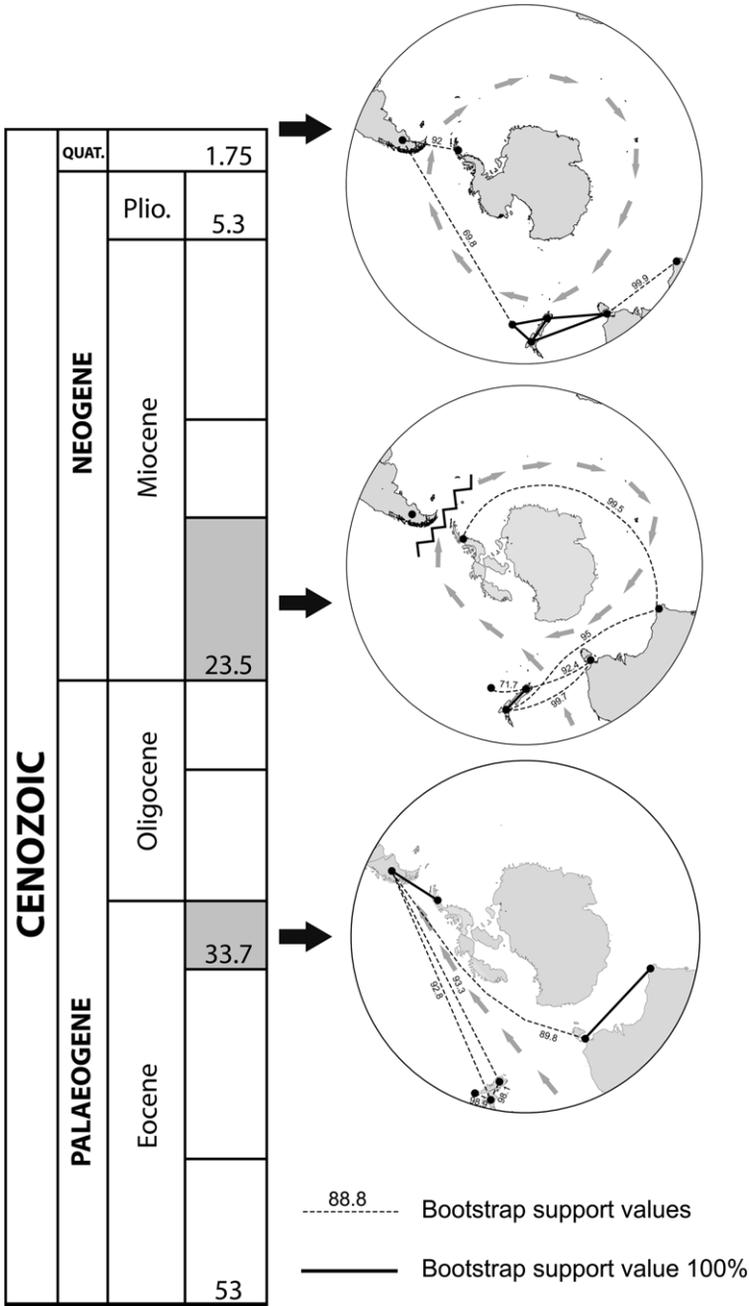


Fig. 3. Bootstrapped spanning networks showing echinoid faunal similarities for the Late Eocene, Early Miocene and present day (ages in millions of years ago). Connection robustness is given by bootstrap support values. Zigzag line symbolizes the biogeographic isolation of southern Argentina from Austral areas in the Early Miocene. Grey arrows depict the position and direction of the southern Pacific (Late Eocene) and Antarctic circumpolar (Early Miocene and present day) surface currents. Map background and current position modified from Lawver & Gahagan (2003).

Faunal connections between southern Argentina and New Zealand are also evidenced by the common

presence of *Cyathocidaris* and *Diplodetus* in both regions.

Zinsmeister (1979) proposed the existence of the so-called Weddellian faunistic province to account for these faunal similarities along the southern margins of the Pacific at the end of the Cretaceous and early Cenozoic. The Gondwanan break-up and the prevalence of shallow-water seaways between land masses is considered to have promoted the origination and diversification of marine invertebrates in the SW Pacific Ocean. These taxa spread readily to the east in the early Cenozoic (Zinsmeister & Camacho 1980). This hypothesis is mostly supported by biogeographic studies of Struthiolariidae gastropods (Zinsmeister 1979; Zinsmeister & Camacho 1980). Néraudeau *et al.* (2000) highlighted echinoid faunal similarities between Boreal, Tethyan and Austral regions in the Late Cretaceous, contrasting markedly with Zinsmeister's hypothesis of a distinctive Austral province. The high level of echinoid cosmopolitanism at the end of the Cretaceous is documented by the occurrence of the following European genera in Austral areas: *Micraster* (Antarctic Peninsula), *Hemiaster* (Antarctic Peninsula), *Cyathocidaris* (Antarctic Peninsula, southern Argentina and New Zealand), *Echinocorys* (Australia), *Holaster* (southern Argentina) and *Nucleopygus* (southern Argentina) (Néraudeau & Mathey 2000). Unlike Struthiolariidae gastropods (Zinsmeister & Camacho 1980), the sparse echinoid data do not show any evidence of Austral provincialism during the Maastrichtian. A SW Pacific origin of Austral echinoid faunas followed by an eastward dispersal to South America is also not supported.

Late Eocene

BSN results for the Late Eocene show strong connections between southern Argentina and the Antarctic Peninsula on the one hand, and between southeastern and southwestern Australia on the other (Fig. 3). Trans-Pacific connections between southern Argentina and southeastern Australia as well as between southern Argentina and New Zealand are also well supported.

Previous studies of Austral echinoid faunas have suggested the existence of faunal affinities between southern Argentina and Antarctica in the Late Eocene (Bernasconi 1959; Hotchkiss & Fell 1972; Néraudeau *et al.* 2000). This is congruent with Zinsmeister's (1981) study that alluded to the Austral affinity of mollusc, echinoid and brachiopod faunas from southern Argentina. This strong connection between the two areas is typically exemplified by the occurrence of the shallow-water cassiduloid *Stigmatopygus* in both regions. This supports the existence of shallow-water seaways between the two areas during the Late Eocene (Zinsmeister 1981).

Philip & Foster (1971, 1977) and Zinsmeister & Camacho (1980) documented a burst of faunal diversity in Australia and New Zealand in Eocene times. The faunas are interpreted as either of Austral (Philip & Foster 1977) or Indo-Pacific origin (Zinsmeister & Camacho 1980). The diversity and distinctiveness of Australian echinoid faunas are mostly due to cassiduloid and spatangoid irregular echinoids and to the regular family Temnopleuridae, whereas faunal affinities between Chatham Island and New Zealand are the result of holasteroid occurrences (*Giraliaster* and *Corystus*). Foster & Philip (1978) also stressed the existence of recurrent echinoid trans-Tasman dispersals from southeastern Australia to New Zealand throughout the Cenozoic. This is not supported for the Late Eocene in the present analysis (Fig. 3).

The genera *Schizaster*, *Linthia*, *Austrocidaris* and *Prionocidaris* (the Patagonian species '*Cidaris*' *antarctica* Loriol (1902) and '*Cidaris*' *julianensis* Loriol (1902) show strong similarities with species of the genus *Prionocidaris* to which they are herein assigned) have a widespread distribution that supports long-distance connections from Australia to southern Argentina (*Schizaster* and *Linthia*) and to the Antarctic Peninsula (*Austrocidaris*) as well as between New Zealand and southern Argentina (*Prionocidaris*). These southern Trans-Pacific connections between southern Argentina, New Zealand and southeastern Australia are consistent with geographic and oceanographic reconstructions for that time (Lawver & Gahagan 2003) and congruent with other palaeontological studies based on echinoids (Hotchkiss 1982) and molluscs (Beu *et al.* 1997; Del Rio 2002). These connections can be interpreted either as an inheritance of the Zinsmeister's (1979) Weddellian province, which could explain the distribution of the genus *Schizaster*, mentioned in South Argentina in the Late Cretaceous (Parma & Casadio 2005), or as the result of dispersal through the cool surface current that circulated along the Pacific margin of Antarctica (Zinsmeister 1979; Beu *et al.* 1997; Lawver & Gahagan 2003). The genus *Schizaster* has a worldwide distribution and is mainly known as a typical Mediterranean and Tethyan echinoid of the Eocene–Miocene time period. Therefore, the wide austral distribution of the genus cannot be considered an inheritance of the Weddellian province. The same is true for the genus *Linthia*, which is probably of Turonian origin from France (D. Néraudeau pers. comm.). The current that circulated along the Pacific margin of Antarctica is considered to have initiated late in the Eocene (Fig. 3) when the shelf of the South Tasman Rise started to subside (Lawver & Gahagan 2003) and to have favoured the westward dispersal of taxa that are unknown in Austral areas before the Eocene. This could

explain the widespread distribution of the genera *Austrocidaris* and *Prionocidaris*.

In spite of the existence of long-distance connections from Australia to the Antarctic Peninsula, most genera are less widely distributed. Within the family Schizasteridae, if genera such as *Schizaster* and *Linthia* are distinguished by a widespread distribution, other genera are restricted to only one region, such as *Abatus* in the Antarctic Peninsula and *Kina* in New Zealand. The origination of the two genera *Abatus* and *Kina* from a schizasterid ancestor along with their endemism could suggest a divergent evolution within the family, an obvious outcome of continental drift. However, phylogenetic relationships within the Schizasteridae require clarification, especially between the genus *Abatus* and its South African relatives. Only marsupiate species with sunken petals were assigned to the genus. They might be closely related to non-Antarctic and non-marsupiate species, and a genus can be represented by marsupiate species in a region of the world ocean, and non-marsupiate species in other areas (Dudicourt *et al.* 2005).

Early Miocene

The most noticeable result of the BSN analysis performed for the Early Miocene is the faunal isolation of southern Argentina from other Austral regions, including a south Pacific disconnection between southern Argentina and New Zealand. Results also show a direct connection between southwestern Australia and New Zealand, and a faunal disconnection between southeastern and southwestern Australia. An unexpected but robust relationship between the Antarctic Peninsula and southwestern Australia is also highlighted (Fig. 3).

The isolation of southern Argentina is partly congruent with Del Rio (2002), who highlighted the Caribbean affinity of part of Lower Miocene Patagonian molluscs. However, a faunal connection between Patagonia and New Zealand was also stressed by Del Rio (2002) and Beu *et al.* (1997). Based on echinoid data, there is no evidence so far for such a connection, despite the establishment of the Antarctic circumpolar current at the Eocene–Oligocene boundary and the possibility of subsequent westward dispersal from New Zealand (Beu *et al.* 1997; Lawver & Gahagan 2003). The fossil record is weak in southern Argentina and Antarctica (only three echinoid genera are known in Argentina and West Antarctica; Table 1), but the faunal distinctiveness between these two areas is well supported by the occurrence of peculiar South American faunas. In southern Argentina, echinoids are typically represented by the clypeasteroid family Monophorasteridae (*Amplaster* and *Monophoraster*) and the genus *Abertella* (Hotchkiss 1982;

Mooi *et al.* 2000). These echinoids are unknown from other Austral areas. Hotchkiss & Fell (1972) postulated an Antarctic affinity of southern Argentinian clypeasteroids after the discovery of the genus *Iheringiella* in the Upper Eocene of East Antarctica, but interestingly Mooi *et al.* (2000) excluded the latter genus from the family Monophorasteridae, which is unequivocally restricted to South America. Moreover, the occurrence of the genus *Iheringiella* in the Upper Eocene of Antarctica (Hotchkiss & Fell 1972) is suspect (Table 1) considering that the only known specimen consists of a fragment without diagnostic features and that the genus is recorded from Miocene deposits in South America (R. Mooi pers. comm.). In Australia, the diversification of clypeasteroid echinoids gave rise to the families Fossulasteridae, Scutellinoididae and Arachnoididae. Diversity of Australasian echinoids is also typified by cassiduloids (e.g. *Pisolampas*), spatangoids (e.g. *Eupatagus*) and cidaroids (e.g. *Goniocidaris*). The southwestern Australian genera *Cardabia* and *Tripneustes* are absent in southeastern Australia, while the latter is present in New Zealand and Chatham Island. This supports the direct connection between southwestern Australia and New Zealand, and the faunal disconnection between southeastern and southwestern Australia. However, the genus *Tripneustes* is known from Miocene deposits of Switzerland and France, so that its absence from southeastern Australia could be due to incomplete sampling.

The robust relationship between the Antarctic Peninsula and southwestern Australia is mostly supported by the widespread distribution of the genus *Schizaster* (except in southern Argentina where the genus is not so far recorded in the Early Miocene). This widespread distribution extends back to the Late Eocene, the genus being recorded worldwide (see discussion above). Therefore, the robust relationship between the Antarctic Peninsula and southwestern Australia in the Early Miocene can be interpreted as an inheritance of distribution patterns of the past, and not as the result of contemporary faunal connections. This interpretation is corroborated by the divergent evolution of cidarid echinoids, which gave rise to distinct genera between Antarctica and Australia in the Early Miocene. For example, the genus *Goniocidaris* is first recorded in the Lower Miocene of New Zealand and Australia whereas in Antarctica, cidarids are known by the genus *Notocidaris*. The two genera diversified in different areas during the Neogene, the genus *Notocidaris* being mostly restricted to the Antarctic continental shelf (except for one Recent species in New Zealand), whereas *Goniocidaris* species spread to the Indo-Pacific region (Mortensen 1928; David *et al.* 2005). The geographically limited evolution and diversification of

the genus *Notocidaris* in Antarctica supports the relative isolation of the continent from Australasia.

Present day

The comparison of BSN results for present day faunas with those of previously studied time intervals highlights the strong affinity between Australian and New Zealand modern faunas, including those of Chatham Island. The present day configuration also displays a relatively well-supported connection between southern Argentina and the Antarctic Peninsula, and the existence of a weak faunal connection between southern Argentina and Chatham Island (Fig. 3).

The similarity of echinoid faunas between Australia and New Zealand may be explained by the existence of recurrent trans-Tasman faunal exchanges between southeastern Australia and New Zealand throughout the Cenozoic (Foster & Philip 1978). Spatangoid echinoids are highly diversified in Australia and New Zealand (e.g. Martiniidae, Brissidae, among others), but most are restricted to these areas and have no representative in Antarctica or southern Argentina.

The relatively well-supported connection between southern Argentina and the Antarctic Peninsula across the Scotia Arc has been extensively documented in previous studies across various benthic groups, from bivalves and gastropods to polychaetes and isopods (e.g. Hedgpeth 1969; Linse *et al.* 2006; Clarke *et al.* 2007; Brandt *et al.* 2009). Based on echinoids, the connection can be explained by the extended latitudinal range of the schizasterid genera *Abatus* and *Tripylus*, and of the echinid genus *Sterechinus*. The three genera are represented by high Antarctic, Subantarctic and southern Argentinian cold-temperate species (David *et al.* 2005; Diaz *et al.* 2011), and are absent from Australasia. They are only known as fossils in the Upper Eocene (*Abatus*) and Lower Miocene (*Sterechinus*) of the Antarctic Peninsula, which suggests a West Antarctic or Subantarctic (see Diaz *et al.* 2011) origin, then dispersal through the Antarctic circumpolar current downstream of Drake Passage, in the Scotia Arc and southernmost Argentina, as well as in the Weddell Sea (Pearse *et al.* 2009). However, the occurrence of *Abatus* in the Upper Eocene of the Antarctic Peninsula (McKinney *et al.* 1988) might predate the full opening of the Drake Passage, in which case the genus could have migrated to South America before the full establishment of the Antarctic circumpolar current through the shallow waters that separated the two continents.

The existence of a weak faunal connection between southern Argentina and Chatham Island has been demonstrated by previous authors (Beu

et al. 1997; Del Rio 2002) to have occurred since the Oligocene owing to dispersal through the Antarctic circumpolar current. In the present work, this circum-Antarctic dispersal is only supported by the occurrence of the Subantarctic and cool-temperate genera *Austrocidaris* and *Pseudechinus*, which are present off the coasts of southern Argentina, New Zealand and Chatham Island. *Pseudechinus* first occurs in the Cenozoic of Australia and New Zealand and then in the Pliocene of South America. This suggests the Australasian origin of the genus followed by circum-Antarctic dispersal to the west after the Early Miocene. The genus *Austrocidaris* is known as fossils in the Upper Eocene of West Antarctica, southern Argentina and Australia, and is supposed also to have dispersed from Australia in the Late Eocene (see discussion above).

Conclusion

Our results largely agree with previous biogeographic studies on echinoids and other benthic invertebrates. However, two main points contrast markedly with previous works: (1) there is no evidence of an Austral provincialism of echinoid faunas at the end of the Cretaceous and early Cenozoic – data instead suggest the cosmopolitanism of Austral echinoids that show Boreal and Tethyan affinities; (2) there is no evidence of faunal exchanges between New Zealand and southern Argentina in the Early Miocene – data better support a Caribbean affinity of southern Argentinian faunas as well as the presence of a biogeographic barrier between southern Argentina and other Austral regions. This result remains difficult to elucidate as it postdates the onset of the Antarctic circumpolar current, but it may be related to the transient intense glaciation that took place in Antarctica at the Oligocene-Miocene boundary (Rogers 2007). More fossil data are needed to confirm or invalidate this preliminary result.

In spite of the relative incompleteness of our knowledge of the echinoid fossil record at southern high latitudes, our results show that palaeobiogeographic relationships among echinoid faunas can be studied using a quantitative approach and not just qualitatively discussed. The quantitative analyses performed in this work improved our knowledge of the albeit still unclear biogeographic relationships between the different Austral regions. Moreover, the newly obtained biogeographic maps can be easily and intuitively discussed. More sampling efforts are needed though to improve understanding of the observed palaeobiogeographic relationships. Data from Madagascar, southern Chile and South Africa (Zululand) should be

included in the future so as to complete this large-scale palaeobiogeographic analysis of Austral echinoid faunas.

Between the two biogeographic processes invoked to explain the distribution patterns of taxa, our interpretations usually favoured dispersal over vicariance. Two arguments support this lack of balance. First, biogeographic patterns of Australasian and Argentinian faunas have been deeply conditioned by the importance of immigration (Warren *et al.* 2009) from their respective northern areas. This is well typified by the Caribbean affinity of Argentinian echinoids in the Early Miocene or the Indo-Pacific affinity of Australian and New Zealand echinoids in the Late Eocene. Second, demonstration of the divergent evolution of taxa from an ancestral group by vicariance requires reliable phylogenies. The diversity of extant Antarctic echinoids is mostly due to the families Schizasteridae and Cidaridae, which are predominantly composed of endemic species (David *et al.* 2005). However, the origin of this diversity is not fully understood, as phylogenetic relationships with echinoids of other Austral regions remain unclear.

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