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Antarctic Tertiary Progonocytheridae: The last refuge of *Majungaella*, the survivor of a long lineage, a geographical and physiological migration from low to high latitudes

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Abstract

Majungaella Grekoff is shown to be the only member of the once dominant ostracod family Progonocytheridae, Progonocytherinae to survive the Jurassic and also to survive the Cretaceous–Tertiary boundary event. In the Jurassic, *Majungaella* had a northeastern gondwanine distribution, occurring only in India, Africa and Madagascar. However, during the Neocomian it appears in South America where it extends to the Maastrichtian, while in Australia it first appears in the Aptian and ranges up to the Campanian. Its last records in Africa are in the Cenomanian of South Africa and the Santonian of south-western Africa. This southward shift into higher latitudes was probably due to an increasing cryophilia and, although this may have also been prompted by competitive exclusion by better adapted, newly evolved taxa, it is difficult to demonstrate this due to the universal distribution of most Late Mesozoic ostracod genera. Whatever the reason, *Majungaella* seems to have become, during the Cretaceous, increasingly adapted to living in high-latitude shallow seas and this adaptation is advanced as the prime reason why the genus, alone among the progonocytherids was able to survive both the post-Cretaceous global cooling and Antarctic palaeoenvironments into the Late Neogene. Eocene, Oligocene and Pliocene occurrences of *Majungaella* in the Antarctic are investigated and it is concluded that the genus is in situ in all instances and that, especially in the two latter cases, it lived in water temperatures very much lower than those of its Mesozoic forebears.
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1. Introduction

Whatley and Ballent (1996) reviewed the Middle and Upper Jurassic ostracod genus *Progonocythere*

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Sylvester-Bradley, 1948 and its close allies, among them *Majungaella* Grekoff, 1963. They demonstrated the latter genus to be restricted to the southern Hemisphere (or areas such as India which subsequently migrated north of the Equator) and to range from the Callovian to the Maastrichtian. Subsequently, Ballent (1998) and Ballent et al. (1998) reconfirmed its gondwanine distribution and demonstrated that the genus, in Argentina, where it is represented by 8 species, is confined to Patagonia. The genus does not occur in the Argentinian Jurassic, but in the Cretaceous of that country it ranges from Valanginian to Maastrichtian.

Majungaella was shown by Whatley and Ballent (1996) to be the only one of the relatives of *Progonocythere* to survive the Jurassic. In their review of the genus *Lophocythere*, Sylvester-Bradley and its allies (Whatley and Ballent, 2004), which comprise the remainder of the family Progonocytheridae, all of the 14 genera that they studied, with the exception of one doubtful example from Argentina, became extinct before the end of the Jurassic.

Subsequent to these studies, we have seen photographic evidence of the existence in the Campanian–Maastrichtian of an additional two species of *Majungaella* in Argentina and a further two species from the same age in the Sergipe Basin of eastern Brazil (Viviers, 2001, pers. comm.). Also, a species described by Bertels (1975a) from the Middle Maastrichtian of northern Argentinian Patagonia as *Tumidoleberis australis*, we now consider it to be *Majungaella*. The genus *Tumidoleberis* (Deroo, 1966) is not a member of the Progonocytheridae.

Luther (1999) and Fauth et al. (2002, 2003) recorded *M. australis* from the Upper Campanian of the northern tip of the Antarctic Peninsula, probably as part of a population continuous with that of Patagonia at this time.

In the present paper, we review these new data and prior studies about the distribution of *Majungaella* species and discuss its palaeoclimatic and palaeogeographical implications.

2. Tertiary progonocytherids

In 1999, one of us (RW) was asked to review a manuscript by Szczechura on Ostracoda from the Eocene of Seymour Island, in the Antarctic Peninsula, a paper subsequently published in 2001. Szczechura described and illustrated *Majungaella antarctica* sp. n. (pl. 2, Figs. 5–8), clearly a bona fide member of the genus. *M. antarctica* was compared by the author to *Tumidoleberis australis* Bertels (which is certainly *Majungaella*), and the two species are indeed similar, although not in our opinion conspecific. This Eocene occurrence and that referred to by Dingle and Majoran (2001) as *Majungaella* sp. 4471 from Oligocene sediments in the Victoria Land Basin of the Ross Sea, East Antarctica, represents a considerable extension of the previously known range of *Majungaella* and indicates that it survived the Cretaceous/Tertiary boundary event. Perhaps even more remarkable is the occurrence of the genus, masquerading as ?*Loxocythere* sp. in the Pliocene of Cockburn Island in the Antarctic Peninsula (Szczechura and Blaszyk, 1996, p. 180, pl. 40, Figs. 3–5). This was recognised independently by Dingle and Majoran (2001, p. 376, p. 380). From these two occurrences, it seems that *Majungaella*, the sole post-Jurassic survivor of the once diverse and dominant Progonocytheridae, not only survived the K/T boundary extinctions, but lived until late in the Neogene.

3. Cainozoic autochthoneity of *Majungaella*

3.1. Eocene of Seymour Island

It is necessary to consider the possibility that this Antarctic record is of reworked Late Cretaceous material. We consider this to be highly unlikely, however, since the Palaeogene ostracod assemblage described by Szczechura (2001), comprises essentially post-Cretaceous genera and that, apart from *Majungaella*, it lacks obvious Mesozoic relicts, although one genus, *Wichmannella* Bertels, 1969, has been recorded by that author from both the Upper Cretaceous and Early Palaeogene of southern Argentina. There is also no doubt as to the Eocene age of the sediments from which the fauna is derived (Szczechura, 2001, p. 160), especially given the Sr dating of 34.2 Ma at the top of the succession (see Dingle and Lavelle (1998a), Table 1, Figs. 1, and 2).

Majoran and Widmark (1998) describe an interesting ostracod fauna from the Late Cretaceous of ODP

Site 689 in the southern Ocean, which was deposited, however, in an estimated palaeodepth of some 1200 m with an estimated palaeotemperature of 9 °C. The ostracods from this study bear some relationship to those described from the Upper Cretaceous of West Australia by Bate (1972) and Neale (1975) and by Dingle (1981) from South Africa. Many other taxa are more closely related to Cainozoic and even Quaternary species described from the deep sea of the Atlantic, Indian and Pacific oceans by authors such as Ayress et al. (1995), Coles and Whatley (1989) and Whatley and Coles (1987).

In the Eocene fauna of Seymour Island, genera such as *Maddocksella* McKenzie, *Propontocypris* Sylvester-Bradley, *Ameghinocythere* Whatley et al., *Australicythere* Benson, *Keijia* Teeter and *Phlyctenophora* Brady, are all post-Cretaceous and many have species living in the area today, while of those genera known also from the Cretaceous, there is nothing about the species occurring in this assemblage which would suggest that they are reworked. It is, therefore, reasonable to conclude that *Majungaella antarctica* is in situ.

3.2. The Oligocene of the Victoria Land Basin

Dingle and Majoran (2001) documented the presence of *Majungaella* sp. 4471 among eighteen marine shelf ostracod species from Early and Late Oligocene glacio-marine sediments of the Cape Roberts boreholes, in the Victoria Land Basin, Ross Sea area. The three dominant Early Oligocene taxa, *Microcythere*? sp. 4626, *Copytus* spp. and *Ameghinocythere* sp. 4607, are relatively well represented in the Late Oligocene. Also, *Australicythere polylyca* (Müller), *Majungaella* spp., *Austrocythere reticulotuberculata* Hartmann and *Kuiperiana meridionalis* (Müller) are known from strata younger than Early Miocene in Antarctica. This assemblage allows a comparison between high and low Antarctic early cryogenic faunas and all sedimentological evidence indicates it to have been situated proximal to a glaciated hinterland. There is no doubt of the autochthoneity of *Majungaella* in this case.

3.3. The Pliocene of Cockburn Island

Similarly, since the Antarctic Late Pliocene record from Cockburn Island is from the *Pecten* Conglomerate one might expect a deposit of such a nature to contain derived material. The conglomerate was originally dated as Late Pliocene on the basis of somewhat dubious K/Ar radiometric dates on the basalts that underlie it and on the diatoms and benthonic foraminifera it contains, as outlined with appropriate references by Szczechura and Blaszyk (1996, p. 179). Dingle et al. (1997, p. 261) quote a mean Sr dating of 4.7 Ma and this date has been reconfirmed by McArthur to Dingle in pers. comm. 2002 (Dingle pers, comm. 2003).

Szczechura and Blaszyk record four ostracod species in the fauna that still live in the area today (*Copytus caligula* Skogsberg; *Pseudocythereis spinifera* Skogsberg; *Australicythere polylyca* (Müller); *Antarctiloxoconcha frigida* (Neale) while four other species are closely comparable with Recent Antarctic species (*Procythereis* cf. *robusta* Skogsberg; *Patagonacythere* cf. *longiducta longiducta* (Skogsberg); *Patagonacythere* cf. *tricostata* Hartmann); *Hemicytherura* cf. *reticulata* Hartmann). (See Hartmann (1997) for a modern synopsis of the taxonomy and distribution of recent Ostracoda and for a comprehensive suite of references in the Antarctic and sub-Antarctic, see also Whatley et al. (1998b).

Given the absence of demonstrably exotic, reworked elements there is no evidence, therefore, to suggest that *Majungaella* (recte ?*Loxocythere* Szczechura and Blaszyk) is not in situ.

4. Zoogeographical considerations

Prior to an analysis of the zoogeography of Tertiary progonocytherids in Antarctica, it is noteworthy that species of *Majungaella* have been also recognised from the Middle to Upper Campanian of southeastern James Ross Island (Fauth et al., 2002, 2003). This ostracod fauna, from the Hamilton Point Member of the Santa Marta Formation comprises sixteen species and provides clear evidence of links between western Australia, Argentinian Patagonia and the Antarctic Peninsula during the Late Cretaceous. *Eocytheropteron carinoalatum* Bate, 1972 and *Rostrocytheridea hamiltonensis* Fauth and Seeling (in Fauth et al. (2003)), which is similar to *R. canaliculata* Bate, 1972, are also present in the Santonian–Campanian from the Carnarvon Basin, West Australia. The occur-

rences of *Cytherelloidea megaspirocostata* Majoran and Widmark, 1998, (which is close to *C. spirocostata* Bertels, 1973 from the Lower Danian of Fortín General Roca), of *Majungaella* sp. of Ballent et al. (1998) (from the Santonian–Campanian) and of *Majungaella australis* Rossi de García and Proserpio, 1980 (Upper Campanian–Maastrichtian), all from Argentinian Patagonia, reinforce links between southern South America and Antarctica.

4.1. Eocene, Seymour Island

Szczechura (2001) showed that of the fifteen genera recorded in this fauna, almost half also occur in the Eocene of southeastern Australia and/or New Zealand. These genera are *Argilloecia* Sars, *Propontocypris* Sylvester-Bradley, *Actinocythereis* Puri, *Munseyella* van den Bold, *Kuiperiana* Bassiouni, ?*Hornibrookella* Moos and ?*Maddocksella* McKenzie. This does not prove any special link between the western Antarctic and Australasia, as most of these genera were rather widespread during the Eocene. Also, this author only notes the similarity of three of the Antarctic species to Australian Eocene species: ?*Maddocksella* sp. to *M. tarparriensis* McKenzie et al., 1993; *Argilloecia* cf. *A. mesa* to *A. mesa* McKenzie et al., 1993 and *Propontocypris* sp. to *Pontocypris* sp. McKenzie et al., 1993.

Conversely, a much stronger case was made by Szczechura (2001) for connections between the western Antarctic and Patagonia during the Palaeogene at both generic and specific levels. This author demonstrates that *Australicythere, Wichmannella* and *Henryhowella* are common to the two areas but do not occur in Australasia and that the two former genera are confined to the South Atlantic and Antarctic basins. (Whatley and Ballent, who have both seen topotype material of *Wichmannella*, are unable to distinguish *Wichmannella* from *Henryhowella*).

A number of species in the Antarctic fauna exhibit fairly close resemblance to Patagonian Palaeogene species: *Wichmannella* cf. *W. meridionalis* Bertels, 1969 of Szczechura is certainly close to *Henryhowella meridionalis* (Bertels) from the Lower Danian, ?*Echinocythereis hartmanni* Szczechura is similar to *Henryhowella heros* (Whatley et al., 1996) from the Recent of the Magellan Straits, which was subsequently encountered in the Recent of the SW Atlantic by Whatley et al. (1997b), who noted its similarity to two species, *Henryhowella beckerae* Bertels and *Henryhowella deliae* (Bertels) from the Early Cainozoic of southern Argentina (see Bertels (1975b)). *Majungaella antarctica* is similar to *Tumidoleberis australis* (Bertels, 1975a) from the Upper Cretaceous of southern Argentina. They both have entomodont dentition but the Argentinian species is reticulate rather than punctate. Szczechura (2001) noted the similarity of *M. antarctica* to *Majungaella verseyi* Neale, 1975 from the Upper Cretaceous of western Australia, however, Whatley et al. (1995a) included Neale's species in their new genus *Exposterocythere*.

Szczechura (2001, p. 164) encountered a fragment that she compared with *Actinocythereis indigena* Bertels from the Lower Danian of Patagonia and a badly preserved valve, which was close to *Australicythere* sp. 2 of Echevarría (1998), also from the Palaeogene of Patagonia. Two other genera, *Ameghinocythere* Whatley et al., 1997b, which is a Late Cretaceous to Recent genus largely endemic to the South West Atlantic and adjacent Antarctic, although it does occur in the Oligocene–Miocene of the Ross Sea (Dingle, 2000; Dingle and Majoran, 2001) and *Keijia* Teeter in the Eocene deposit, are shown by Szczechura to be related to species in the South Atlantic area. This author also shows that *Kuiperiana* sp. seems to belong to a species group endemic to the Antarctic, sub-Antarctic and South West Atlantic area, the earliest member of which is probably *K. similis* (Bertels) from the Palaeocene of Patagonia and which includes *K. rolnickii* Blaszyk, 1987 and the widely distributed Recent species *K. meridionalis* (Müller, 1894).

The relationship of this fauna to that of Late Cretaceous, Palaeogene and subsequent faunas in the southern South American area is abundantly clear, as is the fact that it lived in palaeoenvironments substantially warmer than that obtaining in the area today (Dingle and Lavelle, 1998b).

4.2. Oligocene, Victoria Land Basin

Dingle and Majoran (2001) recovered a sparse and moderately well preserved microfauna of eighteen species from Early and Late Oligocene glacio-marine sediments from boreholes in the Victoria Land Basin, Ross Sea. These authors analysed the zoogeography

of this fauna in detail and showed that closely related species had been previously described from Antarctica: *Microcythere*? sp. 4626 (Early Oligocene–Miocene) and *Ameghinocythere* sp. 4607 (Early–Late Oligocene), both of Dingle, 2000, *Hemicytheridea aff. H. kinggeorgeensis* Blaszyk (Early Oligocene), *Austrocythere reticulotuberculata* Hartmann, *Australicythere polylyca* (Müller) and *Kuiperiana meridionalis* (Müller); these last three have survived to the Recent in the cool-cold Antarctic/sub-Antarctic region. Also, species closely related to *Cluthia* aff. *C. antiqua* Ayress and Drapala, *Majungaella* sp. 4471 and *Copytus* aff. *C. malumiani* Echevarría had been previously recorded from New Zealand (Late Eocene) and southern Argentina (Late Oligocene–Early Miocene), respectively. Despite these faunal links, Dingle and Majoran (2001) pointed out that, given the glacial setting of the Oligocene Antarctic environment (Dingle and Lavelle, 1998a), the most abundant species in their Oligocene fauna, *Munseyella*? sp. 4781, is endemic to the locality.

4.2. Pliocene, Cockburn Island

Szczechura and Blaszyk (1996) record the Pliocene fauna, which is very different from that of the Eocene of Seymour Island. As already shown, four ostracod species in the fauna are still living in the area today: *Copytus caligula* Skogsberg; *Pseudocythereis spinifera* Skogsberg; *Australicythere polylyca* (Müller); *Antarctiloxoconcha frigida* (Neale) while four other species are closely comparable with Recent Antarctic species: *Procythereis* cf. *robusta* Skogsberg; *Patagonacythere* cf. *longiducta longiducta* (Skogsberg); *Patagonacythere* cf. *tricostata* Hartmann; *Hemicytherura* cf. *reticulata* Hartmann.

Other taxa, include species of *Leptocythere* Sars, *Meridionalicythere* Whatley et al. and *Loxoreticulatum* Benson. The former resembles *L. mosleyi* (Brady) from the Falkland Islands (Brady, 1880; Whatley et al., 1995b) and from the littoral zone of the Magellan Strait (Whatley et al., 1996, 1997a) and the Atlantic coast of Patagonia (Whatley et al., 1997b). *Meridionalicythere* is a Pliocene to Recent genus recorded fossil from the Burdwood Bank (Cusminsky and Whatley, 2000; Whatley and Cusminsky, 2002) and from the Argentinian littoral and continental shelf, mainly from the Falkland Islands, Tierra del Fuego and Patagonia (Whatley et al., 1987, 1995b, 1996, 1997a,b, 1998a,c). *Loxoreticulatum*, was originally described by Benson (1964) from the Recent of McMurdo Sound in the Antarctic, but was subsequently recorded by Whatley et al. (1987) from Tierra del Fuego, the Magellan Straits and northwards along the Atlantic coast of Patagonia.

Cusminsky and Whatley (2000) and Whatley and Cusminsky (2002) described the nearest Pliocene ostracod fauna to that from Cockburn Island. They encountered 37 species in an Upper Pliocene core taken on the Burdwood Bank, south of the Falkland Islands at Lat. 54°46′ S, Long. 58°70′ W, in a present day water depth of 91 m. The single species in common with the fauna of Szczechura and Blaszyk (1996) is *Copytus caligula*, but many of the genera are common (*Cytheropteron, Hemicytherura, Loxoreticulatum, Semicytherura, Australicythere, Meridionalicythere, Leptocythere, Ameghinocythere* (=?*Rabilimis* sp.) and *Procythereis*). Many of the genera are effectively endemic to the Antarctic and sub-Antarctic, or extend (or have extended) northwards into lower latitudes, such as *Loxoreticulatum*, *Ambostracon* (*Patagonacythere*), and *Meridionalicythere.*

The affinities of this fauna with those of the Cainozoic to Recent ostracod faunas of the area are clear. The Pliocene fauna, however, lacks certain elements which one would expect to encounter living around Cockburn Island today and to contain other elements more typical of the present day Fuegian/Magellanic and southern Patagonian/Falkland sub-provinces to the north (Whatley et al., 1998c).

It is interesting to note that the ostracod fauna described by Blaszyk (1987) from the Oligocene of King George Island, contains none of the relatively warmer water taxa of the Eocene of Seymour Island and does not, despite the claims of the author, show close affinities with the faunas of Australasia, but rather (although not as closely as the Cockburn Island Pliocene fauna), with those of southern South America and the modern Antarctic. The King George Island assemblage clearly reflects a cooler water fauna than that of the Eocene of Seymour Island as shown by Dingle and Lavelle (1998b), and although probably not as cool as that of Cockburn Island, it was not a great deal less. According to Birkenmajer and Gazdzicki (1986) there was cooling (Polonez Glaciation) in Antarctica during the Oligocene. Similarly, Dingle

and Lavelle (2000), from integrating geochemical results and floral data, demonstrated frigid (glacial) temperatures during the deposition of the Oligocene and subsequently for the northern Antarctic Peninsula. They Sr dated the glacial at 29.8 Ma and the overlying material with ostracods at 29.4 Ma (Dingle et al., 1997).

5. Palaeoenvironmental and palaeoecological considerations

Majungaella in the Mesozoic was widely distributed in essentially shallow, warm seas in the then southern Hemisphere. A list of the known species and all known citations of those species we consider to be valid (Whatley and Ballent, 1996; Ballent et al., 1998 with subsequent additions— see references), is given below in stratigraphical order, and this confirms the general warm, shallow water palaeoecology of the genus during the Jurassic and Cretaceous (Table 1).

When these records are plotted in terms of their diversity, stratigraphy and geographical distribution (Table 2), a number of interesting features are revealed. For example, all the Jurassic records of *Majungaella* are from Africa, Madagascar or India. This is not due to the non-occurrence of post-Callovian Jurassic marine strata in South America and seems, therefore, to indicate that the genus was confined to the eastern and northern seas of Gondwanaland during the Jurassic and the Berriasian.

In India the genus became extinct in the Upper Jurassic, possibly associated with the northward drift of the sub-continent, although it remains an abundant taxon in Madagascar through the Neocomian but does not survive into Aptian or post-Aptian strata. In Africa, *Majungaella*, is both abundant and diverse in the Neocomian. However, its last appearance in East Africa is in the Albian, although it survives into the Santonian in south-western Africa, before becoming extinct there also (Dingle, 1996).

In South America, *Majungaella* first appeared in the Valanginian, with three species in southern Argentina and one in Chile. Although absent from the remainder of the Neocomian in Argentina, it reappears in the Albian and subsequently occurs in all Cretaceous stages, with the exception of the Cenomanian, up to the Maastrichtian. In Brazil, the genus did not appear until the Campanian and also occurs in the Maastrichtian.

Majungaella is relatively diverse and abundant in Australia, from its first arrival in the Aptian, up to the Campanian, but does not survive into the Maastrichtian. In this case, influence of warmer water currents in western Australia is suggested by the moderate abundance of keeled planktonic foraminifera throughout the Campanian–Maastrichtian (see Huber, 1992).

Two species of *Majungaella* are known from the Middle–Upper Campanian of southeastern James Ross Inland (Fauth et al., 2002, 2003) where palaeoenvironmental data indicate a relatively warm and humid climate (Dingle and Lavelle, 2000).

All of the Mesozoic records of *Majungaella* are allegedly from similarly warm, shallow water environments. Floral distributions for that time also confirm a warm and equable world. In the southern Hemisphere, the floras containing *Dictyophyllum* differ from those of the northern Hemisphere. Its wide distribution between palaeolatitudes of 50° and 60° N and S is, according to Barnard (1973), a strong argument in favour of that relatively warm and equable world (cf. Hallam, 1994). Indeed, during the Mesozoic, the universal consensus is that, without the presence of ice at either pole, the climatic belts are thought to have been less compressed than they are today, and that polar climates were temperate at worst. The occurrence of dinosaurs in the Antarctic and Alaska and the presence of champsosaurs (probably relatives to living crocodiles) in East Greenland confirm this (Huber, 1998). Champsosaurs were ectotherms and adapted for a mostly aquatic life. It is, therefore, likely that they could not have tolerated prolonged exposure to subfreezing conditions. Their survival required that the temperature of the water in which they lived never fell below freezing, since the critical minimum body temperature below which modern ectotherms of their size die is known to be 5 °C. The occurrence of deciduous trees in high latitudes during the mid-Cretaceous indicates that permafrost was absent, providing yet more convincing evidence of polar warmth during the Cretaceous. However, it is only logical to accept that, with diminished annual solar radiation, Mesozoic high latitudes would have experienced cooler climates than those of contemporary lower latitudes. From what we have documented above, it would seem highly probably,

Table 1
Valid species of *Majungaella*, with age and geographical distribution

Jurassic

M. mundula (Grekoff, 1963). Middle Callovian, Madagascar, (ex *Progonocythere*).

M. mundula (Grekoff). Rafara, 1990, Middle Callovian, Madagascar.

M. perforata kachchhensis Khosla et al., 1997. Middle–Upper Callovian, Habo Hill, Kachchh, Gujarat, India.

M. rasilis Khosla et al., 1997. Middle–Upper Callovian, Habo Hill, Kachchh, Gujarat, India.

M. perforata kachchhensis Khosla et al. Khosla et al., 2003. Middle–Upper Callovian, Khadir Formation, Kachchh, India.

M. rasilis Khosla et al. Khosla et al., 2003. Middle–Upper Callovian, Khadir Formation, Kachchh, India.

M mundula (Grekoff). Kulshreshtha et al., 1985. Callovian–Oxfordian, India.

M. vertireticulata Mette, 1993. Lower/Middle Oxfordian, Northern Somalia.

M. biswasi Neale and Singh, 1986. Oxfordian, India.

M. oxfordiana Bate, 1975. Upper Oxfordian, Tanzania.

M. praeperforata Bate, 1975. Mette, 1993, Upper Oxfordian–Lower Kimmeridgian, Northern Somalia.

M. sp. 1. Mette, 1993. Upper Oxfordian–Lower Kimmeridgian, Northern Somalia.

M. kimmeridgiana Bate, 1975. Kimmeridgian, Tanzania.

M. praeperforata Bate, 1975. Kimmeridgian, Tanzania.

M. perforata Bate. Khosla et al., 1997. Kimmeridgian, Habo Hill, Kachchh, Gujarat, India.

M. perforata Grekoff, 1963. Portlandian, Madagascar. (Type species).

M. spitiensis (Jain and Mannikeri, 1975). Upper Jurassic, India. (ex *Progonocythere*).

M. perforata Grekoff. Guha, 1976. Upper Jurassic, India.

M. nematis Grekoff. Guha, 1976. Upper Jurassic, India.

M. nematis Grekoff. Dingle and Klinger, 1972. Upper Jurassic, South Africa. (ex *Progonocythere* (*Majungaella).*

Cretaceous

M. hemigymnae Brenner and Oertli, 1976. McLachlan et al., 1976. Berriasian?–Valanginian, Outenique Basin, South Africa.

M. nematis Grekoff, 1963. Valanginian, Madagascar.

M. sp. aff. *M. nematis* Grekoff. Sigal et al., 1970. Probable Valanginian, southern Chile.

M. grekoffi (Brenner and Oertli, 1976). Valanginian, South Africa. (ex *Fastigatocythere*?).

M. praehemigymnae Valicenti and Stephens, 1984. Valanginian, South Africa and southern Argentina (ex *M*. sp. A. of Kielbowicz et al., 1983).

M. pavta Ballent et al., 1998. Valanginian, Neuquén Basin, central western Argentina.

M. bifurcata Brenner and Oertli, 1976. Valanginian–Hauterivian, South Africa.

M. uitenhagensis (Dingle). Valicenti and Stephens, 1984. Valanginian–Hauterivian, South Africa.

M. nematis Grekoff. Rafara, 1990. Valanginian–Hauterivian, Majunga Basin, Madagascar.

Table 1 (*continued*)

Cretaceous

M. hemigymnae Brenner and Oertli, 1976. Ballent et al., 1998. Valanginian–Hauterivian, Argentinian part of the Austral Basin, southern Argentina.

M. praehemigymnae Brenner and Oertli, 1976. Ballent et al., 1998. Valanginian–Hauterivian, Argentinian part of the Austral Basin, southern Argentina.

M. nematis Grekoff. Ballent et al., 1998. Valanginian–Hauterivian, Argentinian part of the Austral Basin, southern Argentina.

M. sp. A. (Rafara, 1990). Hauterivian, Majunga Basin, Madagascar. (ex *Tickalaracythere*?).

M. nematis Grekoff. Sigal, 1974, Neocomian, DSDP 249, Mozambique Ridge, Indian Ocean.

M. sp. cf. *M. perforata* Grekoff. Rosenfeld and Raab, 1984. Neocomian, Israel.

M. ticka (Krömmelbein, 1975). Aptian–Albian, Australia. (ex *Tickalaracythere*).

M. santacruziana (Rossi de García, 1972). Aptian–Albian, southern Argentina. (ex *Novocythere*).

M. scheibnerovae (Krömmelbein, 1975). Aptian–Albian, Australia. (ex *Tickalaracythere,* junior synonym of *M. santacruziana* (Rossi de García).

M. nematis Grekoff. Dingle, 1984. Late Aptian–Early Cenomanian, Zululand, South Africa.

M. pyriformis Bate and Bayliss, 1969. Albian, Tanzania.

M. ticka (Krömmelbein). Scheibnerová, 1980. Albian–Cenomanian, Santos Oodnadatta No. 1 section, South Australia. (ex *Tickalaracythere*).

M. scheibnerovae (Krömmelbein). Scheibnerová, 1980, Albian–Cenomanian, Santos Oodnadatta No. 1 section, South Australia. (ex *Tickalaracythere*, junior synonym of *M.santacruziana* (Rossi de García).

M. K9A3 in Dingle, 1996 (Table 1), Albian–Santonian, South Africa.

M. annula Bate. Neale, 1975. Santonian, Gingin, West Australia. (ex *Tickalaracythere*).

M. annula Bate, 1972. Santonian–Campanian, Carnarvon Basin, West Australia.

M. sp. Ballent et al., 1998. Santonian–Campanian, Argentinian part of Austral Basin, southern Argentina.

M. sp. Ballent et al. Fauth et al., 2002, 2003. Middle–Upper Campanian, Hamilton Point, southeastern James Ross Inland, Antarctic Peninsula.

M. australis Rossi de García and Proserpio. Fauth et al., 2002, 2003. Middle–Upper Campanian, Hamilton Point, southeastern James Ross Inland, Antarctic Peninsula.

M. sp. of Ballent et al., 1998. Malumián et al., 2000 (p. 11). Upper Campanian, Cerro Cazador Formation, Argentinian part of Austral Basin, southern Argentina.

M. sp. (Krömmelbein, 1976). Campanian–Maastrichtian, Sergipe Basin, eastern Brazil.

M. pseudonymos nom. nov. (ex *australis*) Rossi de García and Proserpio, 1980? Upper Campanian–Lower Maastrichtian, southern Argentina.

Table 1 (*continued*)

Cretaceous

M. australis (Bertels, 1975a). Middle Maastrichtian, Río Negro Province, Argentina.

Tertiary

M. antarctica Szczechura, 2001. Pre-glacial Eocene, Seymour Island, Antarctic Peninsula.

M. sp. 4471 Dingle and Majoran, 2001. Early and Late Oligocene Victoria Land Basin, Ross Sea, East Antractica Peninsula. (The specimen illustrated in Fig. 2A, closely remember *M. antarctica* Szczechura, 2001).

M. sp. (Szczechura and Blaszyk, 1996). Late Pliocene, Cockburn Island, Antarctic Peninsula.

therefore, that the shift of *Majungaella* ever more southward through the Cretaceous, has important palaeoecological implications. The genus does not seem, simply by expanding its range towards the south, to be evolving a greater tolerance of cooler temperatures, because at the same time it is contracting its range and disappearing from its more tropical/equatorial haunts in Africa and Madagascar. In effect, it is becoming overall more cryophyllic in habit. This hypothesis is confirmed by Huber (1998) for extreme high-latitude warmth during the mid-Cretaceous, based on oxygen isotope palaeotemperatures estimated from well-preserved foraminifera from the Circum-Antarctic region. An Aptian–Maastrichtian record from a deep-sea site in the southern South Atlantic (Falkland Plateau) revealed that the entire water column warmed abruptly during the Early Turonian, with deep waters (nearly 1000 m palaeodepth) reaching 18 °C and surface waters reaching over 30 °C. The high-latitude ocean remained very warm from the Turonian through earliest Campanian, with surface waters between 20° and 27 °C and deep waters between 14° and 16 °C. This period of sustained warmth was followed by long-term cooling through the Maastrichtian. This is also confirmed to an extent by Ditchfield et al. (1994), whose stable isotope study of molluscs over the Tithonian–Eocene interval of James Ross Island, in the northern part of the Antarctic Peninsula, demonstrated a marked cooling from the Late Jurassic to the Albian, a warming during the mid-Cretaceous, followed by a gradual cooling to the Eocene. Notwithstanding this, Eocene palaeotemperatures in the Antarctic Peninsula would have been substantially higher than those obtaining today. In recent years, a growing amount of information has been accumulated about the Eocene climate of the Antarctica, mostly from Seymour Island within the La Meseta Formation. Palaeofloral data (Gandolfo et al., 1998) and growth ring analysis of fossil conifer wood (Brea, 1998) indicate temperate to cool temperate and seasonably moist climate for that formation. Identical conclusions indicate the distribution of Antarctic Eocene terrestrial vertebrate faunas through the La Meseta Formation (Reguero et al., 1998).

Another possible explanation is that *Majungaella* in the northern parts of its range became unable to compete with newly evolved, better adapted ostracods and was obliged, in order to survive, to migrate southwards. As these "new" ostracods themselves expanded southwards, so *Majungaella*, a Jurassic relic, was obliged to shift further and further south, until it became adapted to cooler conditions inimical to its competitors. While this is an attractive theory, the authors are unable to offer substantial evidence to

Table 2
This table is derived from Table 1 and plots the specific diversity by stage, and also the stratigraphical and geographical occurrence of all records of the genus

	E. Afr	S. Afr	Mad	Ind	Aus	Bra	Ar/Ch	Ant
Jurassic								
Callovian	7	2	1	4				
Oxfordian	6 4			2				
Kimmeridgian	3 2			1				
Portlandian	1		1					
Upper Jur	4 1		3					
Cretaceous								
Berriasian	1	1						
Valanginian	6	2	1				3	
Hauterivian	7	2	2				3	
Neocomian	2 1		1					
Aptian	4	1			2		1	
Albian	7 1	1			4		1	
Cenomanian	3	1			2			
Santonian	4	1		2		1		
Campanian	7				2	1	2	2
Maastrichtian	3					1	2	
Tertiary								
Eocene	1							1
Oligocene	1							1
Pliocene	1							1

NB The Neocomian record of *Majungaella* from Israel is included under East Africa and that from the Mozambique Ridge under Madagascar.

support it, due to the generally catholic distribution of Cretaceous ostracod genera.

Probably a combination of evolving cryophilia, together with some degree of competitive exclusion, could be invoked to explain this southward shift. However, whatever the reason, it undoubtedly resulted in *Majungaella*, in the Late Cretaceous, being capable of surviving cooler temperatures than its Jurassic ancestors. This would be a great advantage to the genus in surviving the global cooling at the Cretaceous/Tertiary boundary and adapting to life in the cooler water of the Antarctic Eocene and especially the Oligocene and Pliocene. Although the Pliocene of the Antarctic was cooler than the Eocene of the same area, it was also warmer than the present day, as shown for the North Atlantic Ocean by Dowsett et al. (1992), for the Victoria Land Basin, Antarctica by Dingle (2000), Dingle and Majoran (2001) and for the deep sea of the South Atlantic and southern Ocean by Majoran and Dingle (2001). The latter pointed out that, given the glacial setting of the Oligocene Antarctic environment (Dingle and Lavelle, 1998a), *Cytherella* sp. 4796 was adapted to water considerably colder than extant forms and that the Cape Roberts setting at that time was somewhat warmer than the present Ross Sea, but not necessarily as "warm" as modern southern Chile; *Cytherella* sp. 4796 occurs in the Recent sub-Antarctic of southern Chile. This is also confirmed by the occurrence in the Oligocene of *Austrocythere reticulotuberculata* Hartmann, which today is found only north of 70° S (northern Antarctic Peninsula, South Georgia and Prydz Bay (Hartmann, 1997).

Majoran and Widmark (1998) demonstrate that some genera were able to adapt better to cooler conditions in the Late Cretaceous of the southern Ocean than others. They conclude that the genera *Pennyella* Neale and *Dutoitella* Dingle had a greater potential of adapting to successively colder palaeoceanographical conditions than *Agulhasina* Dingle.

6. Migration

Fig. 1 attempts to illustrate the probable routes by which the southward shift of *Majungaella* took place, and is based on a palaeogeographical map of the southern Hemisphere for the Cretaceous. During the

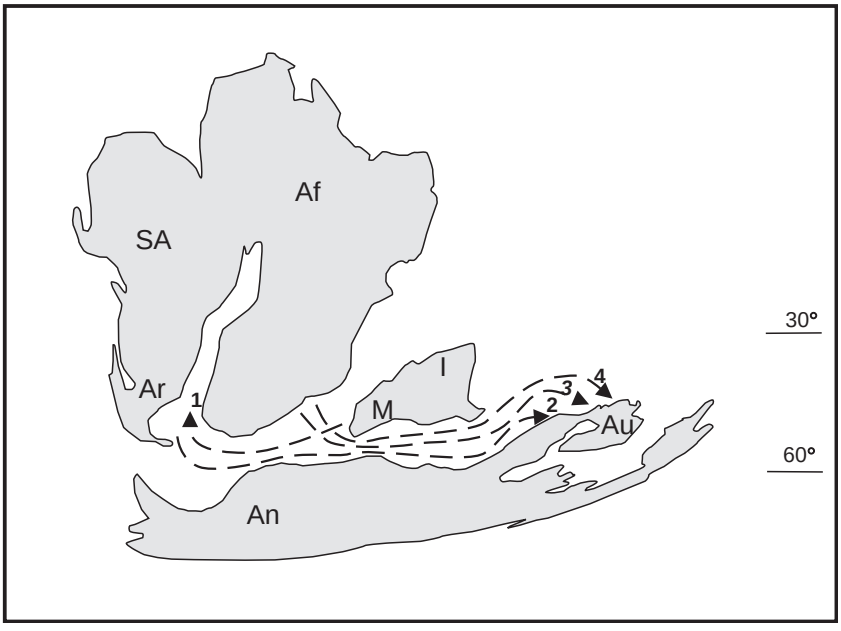

Fig. 1. Palaeogeographical reconstruction of the southern Hemisphere for the Aptian (120 Ma). Palaeocoastline map from Smith et al. (1994). Arrows and numbers show probable migration routes of *Majungaella*. Af, Africa; An, Antarctica; Ar, Argentina; Au, Australia; I, India; M, Madagascar; SA, South America. Numbers indicate order of migration.

Valanginian the genus seems to have migrated from Africa to southern South America. This, as shown by Dingle (1999) occurred along the southern flanks of the Walvis Ridge, an east–west orientated barrier separating in the newly opening South Atlantic, a non-marine regime to the north from an open marine environment to the south. There are a number of possible explanations for the arrival of the genus in Australia. It may have migrated there from South America via Antarctica (presumably via the Tasman shelf/rise), from South Africa via Antarctica or directly from South Africa. The record of *Majungaella* in the Late Cretaceous of Antarctica (Luther, 1999; Fauth et al., 2002, 2003) demonstrates strong faunal connections with both southern South America and the Antarctic Peninsula. If we consider, on the basis of geological and palaeogeographical data (Lawver et al., 1992), that the Drake Passage (now about 1000 km wide) started to open at about 36 Ma, we can assume that, prior that time, the distance between Antarctica and Patagonia would have been less. Frigid (glacial) temperatures have been indicated for Oligocene and younger ages in northern Antarctica (Dingle and Lavelle, 1998b). The distribution of flora (Gandolfo et al., 1998) and benthonic foraminifers (Malumián and Náñez, 1991) reinforces the existence of a latitudinal gradient between both continents and a progressive biotic migration towards the north as a consequence of climatic deterioration during the Eocene–Oligocene. Based on marine invertebrates from Seymour Island, Zinsmeister and Feldman (1994) stated that high-latitude regions serve as "holding tanks" for taxa that remain isolated until they disperse from the region. It is highly likely, therefore, that the Cainozoic Antarctic populations of *Majungaella* recorded by Szczechura (2001), Szczechura and Blaszyk (1996) and Dingle and Majoran (2001) derive from this already crypophyllically adapted root stock. An identical reason is given by Dingle and Majoran (2001, p. 376).) for the presence of *Majungaella* in the Oligocene of boreholes from the Victoria Land Ross Basin, Ross Sea. The genus survived for a further 30 Ma under glacial/interglacial conditions and may be an example of a taxon for which high-latitude cold climates became a *refugia*, but for which the Pleistocene climate of Antarctica eventually proved to be too severe. Wood et al. (1999) demonstrate that a distinctive ostracod assemblage was established in the Oligocene of Antarctica, although the widening of the Drake Passage allowed a suite of newly originated cryophilic genera to evolve there on the continental shelf during the Neogene.

There are not Palaeogene records of *Majungaella* in the continental part of southern South America (Argentina and Chile). The genus apparently became extinct in this area in the Maastrichtian. Palaeogene microfaunas are dominated by *Argenticytheretta patagoniensis* Rose (typical southernmost species), which constitute up to 40% of the Eocene microfaunas in southern Chile.

7. Conclusions

Majungaella, which evolved in the Callovian, had a northeastern gondwanine distribution throughout the Jurassic. This gradually changed as the genus became extinct in the more northerly and easterly parts of its range and migrated to South America. This migration took place in the Early Neocomian, via the southern flanks of the Walvis Ridge and the first South American records of the genus are Valanginian. The continuing southward migration resulted in its eventual arrival in Australia in the Aptian. The genus is, however, now known from the Eocene, Oligocene and the Late Pliocene of the Antarctic Peninsula. So that it was present on the Antarctic continental shelf during the Late Cretaceous and that it was a relic Antarctic population of the genus that survived there into the Pliocene, long after it had become extinct elsewhere.

In its post-Jurassic migration into higher South Hemisphere latitudes, *Majungaella* must have encountered increasingly lower temperature environments, especially associated with diminution in solar radiation during austral winters. This seems to have been a major ecological shift for the genus, since its southward migration was not an overall geographical extension of its range, since it disappeared at the same time from the more northern, warmer parts. This may not, however, have been exclusively a phenomenon associated with an ecological shift, in that it may have been precipitated to some degree by its inability to compete with newly evolved, better adapted species.

Dowsett et al. (1992) and Majoran and Dingle (2001), among others, have demonstrated that the Pliocene had several warm intervals. These would

probably have aided *Majungaella* to survive in the Antarctic into the Upper Pliocene. Abrupt cooling at the onset of the Quaternary, however, seems to have brought about the final extinction of a genus whose closest relatives all failed to survive the Jurassic. Remarkably, the genus survived alone for some 140 MY after the extinction of its last relative in the Progonocytheridae.

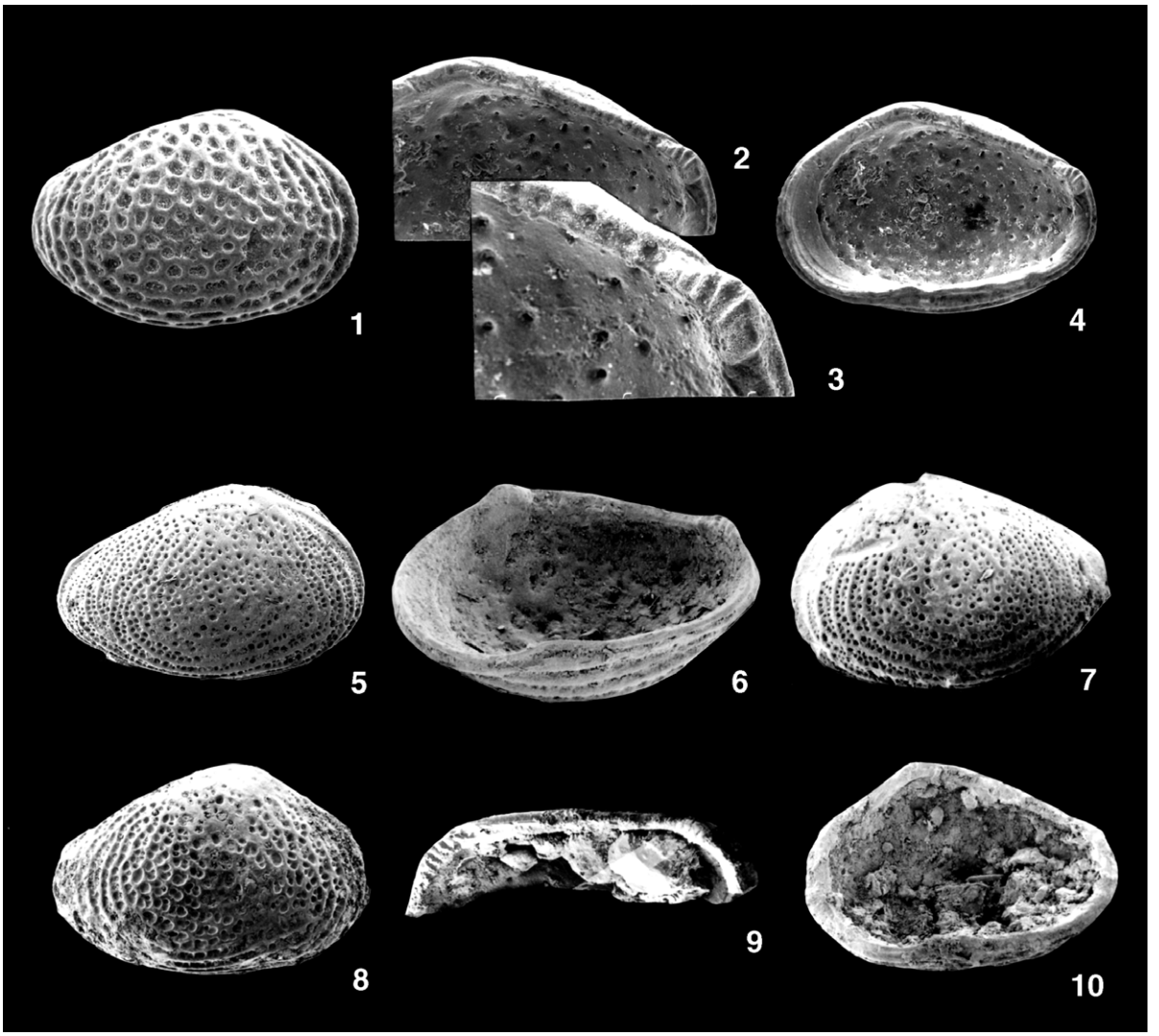

Fig. 2. 1–4. *Majungaella australis* (Bertels, 1975a). Paratype FCEN-LM 858, right valve. Middle Maastrichtian, upper member Jagüel Formation, Fortín General Roca area, Río Negro Province, Argentina. 1, external lateral view ×55; 2, detail of hinge ×75; 3, detail of posterior hinge ×125; 4, internal lateral view ×55. 5–7. *Majungaella antarctica* Szczechura, 2001. Eocene, Telm 1, La Meseta Formation, Seymour Island, Antarctic Peninsula. 5, holotype ZPAL O.49/33, ZPAL 5, right valve, external lateral view ×45.5; 6, right valve ZPAL O.49/32, ZPAL 5, oblique internal lateral view ×57.5; 7, carapace ZPAL O. 49/7, ZPAL 12, right lateral view ×42. 8–10. *Majungaella* sp. (ex ?*Loxocythere* sp. Szczechura and Blaszyk, 1996). Pliocene, Cockburn Island, Antarctic Peninsula. 8, right valve Ar 54430, external lateral view ×34; 9, right valve Ar 54414, detail of hinge ×47; 10, right valve Ar 54430, internal lateral view ×34. Repository: FCEN-LM=Facultad de Ciencias Exactas y Naturales-Laboratorio de Micropaleontología, Buenos Aires, Argentina. ZPAL O.=Institute of Paleobiology of the Polish Academy of Sciences, Warszawa, Poland. Ar=Naturhistoriska Riksmuseet, Stockholm, Sweden.

8. Taxonomic note (see Fig. 2)

Tumidoleberis australis of Bertels (1975a, p. 120, pl. 6, Figs. 4–6), from the Jagüel Formation, Upper Cretaceous (mid-Maastrichtian), Rio Negro Province, Argentina bears little resemblance to the type species of *Tumidoleberis* Deroo, *T. laevis* Deroo, 1966 from the Maastrichtian of Holland. Without doubt it is a species of *Majungaella*. However, the trivial name was subsequently used by Rossi de García and Proserpio 1980 for *Majungaella australis* from outcrops of Upper Campanian? – Maastrichtian in Chubut, the central province of Argentinian Patagonia. This was discussed by Dingle and Majoran (2001, p. 380) (Fig. 2).

Since the two species are clearly distinct, a replacement name is required for Rossi de García and Proserpio species which is a secondary homonym. We therefore propose the following:

Majungaella pseudonymos nom. nov.
Etymology. Gr. ψευδωνυμως incorrectly (falsely) named.

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