

Census of Antarctic Marine Life  
SCAR-Marine Biodiversity Information Network

# BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

▶ **CHAPTER 5.15. BENTHIC OSTRACODA.**

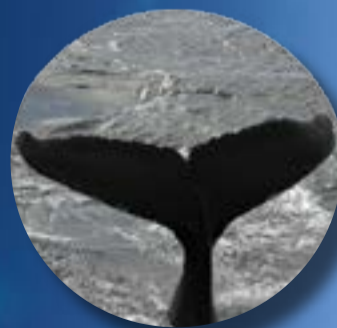
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SCIENTIFIC COMMITTEE ON ANTARCTIC RESEARCH

# THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

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## 5.15. Benthic Ostracoda

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### 1. Introduction

Ostracoda are small crustaceans which inhabit virtually all aquatic environments on Earth, and a few terrestrial habitats. Ostracods are characterised by a body completely enclosed between two (mostly calcified) valves (Photo 1). They show large ecological and taxonomical diversity, and can be found in warm tropical waters, as well as in very cold environments, such as deep sea or polar regions. Ostracods can be a diverse and sometimes abundant group and are also adapted to freshwater habitats, such as temporary ponds, acid lakes and even to humid tropical forest soil. Only three freshwater species are known from sub-Antarctic islands. Although ostracods show a wide range of feeding, ecological and life history strategies, most species are benthic, marine, reproduce sexually and are detritivorous.

The highly diverse class Ostracoda includes more than 30,000 described species and subspecies (see Kempf Ostracoda Database). Most of this diversity has been described from the very extensive fossil record, with abundant and diverse assemblages extending into the Early Palaeozoic. Ostracod valves are mostly calcified and minute (mostly from 400 to 1000 micrometres), and occur in large number as fossils. They are therefore excellent proxies for palaeoenvironmental and palaeoclimatic reconstructions (e.g. Yasuhara *et al.* 2009).

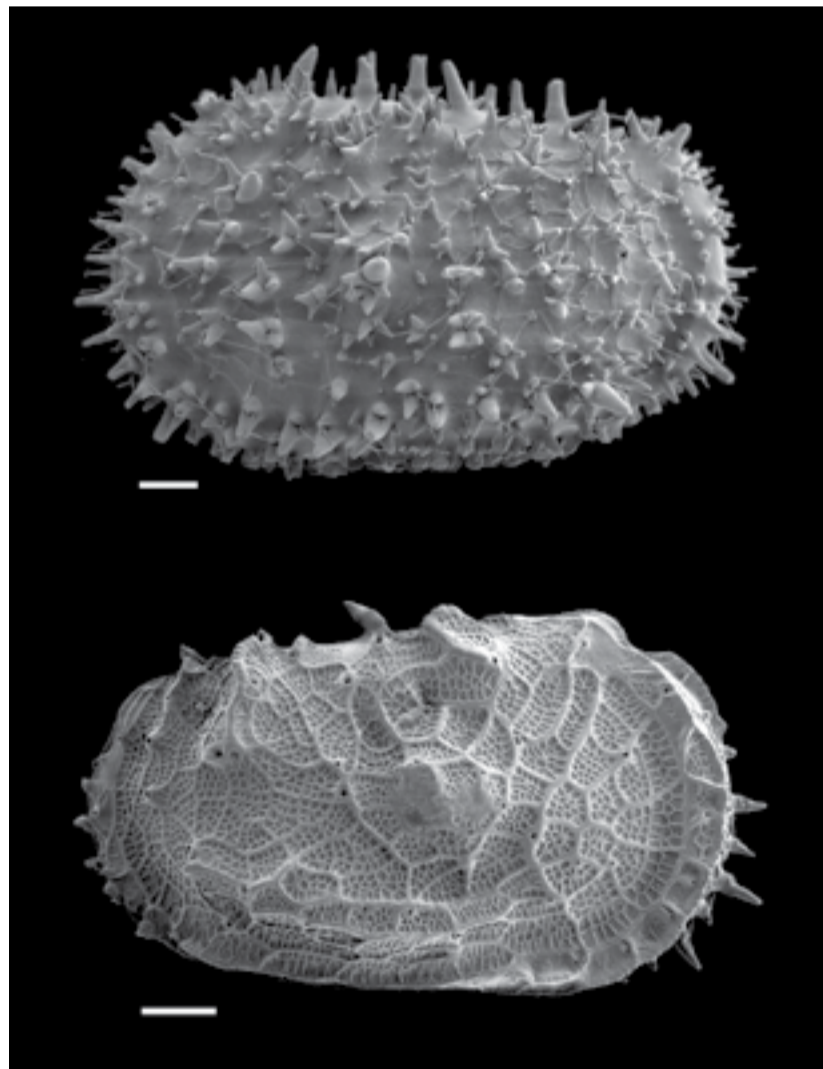


Photo 1 *Legitimocythere* sp. (top) and *Abyssocythere* sp. (bottom) from the deep Southern Ocean (Southern Scotia Sea). Scale bar 100 micrometres.

Table 1 Southern Ocean benthic ostracods. Only accepted species and records from papers published after 1920 are taken into account.

	Recent only	Recent/Cenozoic	Cenozoic only	Cenozoic/Mesozoic	Mesozoic only	Recent-Mesozoic	Total
SO							
species	357	65	35	1	29	0	487
%	73	13	7	<1%	6	<1%	100
genera	81	59	32	4	13	21	210
%	39	28	15	2	6	10	100
records	6508	-	771	-	527	-	7806
%	83		10		7		100

The study of Southern Ocean benthic ostracods began in the 19<sup>th</sup> Century with samples collected during the worldwide expedition of the HMS *Challenger* and, subsequently, by a series of national Antarctic expeditions (e.g. Belgian, British, French, German, Scottish). Because of outdated taxonomy, few records from these early studies can be taken into account for the present chapter. A second phase of research began in the mid 20<sup>th</sup> Century, with a series of studies, mostly on specific taxa (e.g. *Pontocyprina* Müller 1894), or on faunas from specific regions (e.g. McMurdo Sound, Halley Bay) or oceanographic expeditions. Two researchers in particular, Gerd Hartmann and Louis Kornicker, greatly contributed to our taxonomic knowledge by producing identification guides for the Southern Ocean. Despite this, many aspects of ostracod biodiversity in the Southern Ocean (e.g. physiology, life cycles) remain unknown, while only one study has been published on genetics (Brandão *et al.* 2010). Nevertheless, the palaeoecology and palaeobiogeography of ostracods, as well as the palaeoceanographic, palaeoenvironmental and palaeoclimatic histories of the Southern Ocean, have been extensively investigated in at least 30 studies using ostracod samples collected from outcrops or long marine cores or DSDP/ODP boreholes.

### 2. Methods, including limitations of coverage

The basis of the present chapter is a dataset (Brandão 2012), which attempted to extract distribution records from all papers published prior to 2012 on the benthic Ostracoda from the Southern Ocean. Additional papers on temperate/sub-tropical regions of the southern hemisphere were also included. The bibliographic search yielded 105 publications, 95 of which included primary records of living and fossil benthic ostracods ranging from the Jurassic to Recent. The remaining papers dealt with genetics, biogeography, higher level taxonomy (e.g. description of new genera), checklists, etc.

Table 2 Geographic distribution of Southern Ocean Recent ostracod species. Only accepted species and records from papers published after 1920 are taken into account.

	SO total	SO endemics	South America		Africa	Australia / New Zealand
			SO + Atlantic*	SO+ Pacific*		
species	422	312	84	26	0	0
(%)	100	74	20	6	0	0

\* All species occur along the South American coast, while no species occur the coasts off Australia and New Zealand.

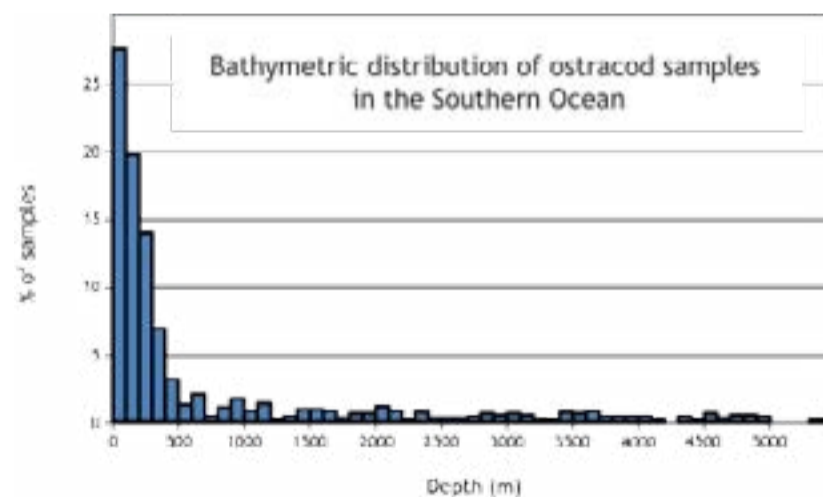
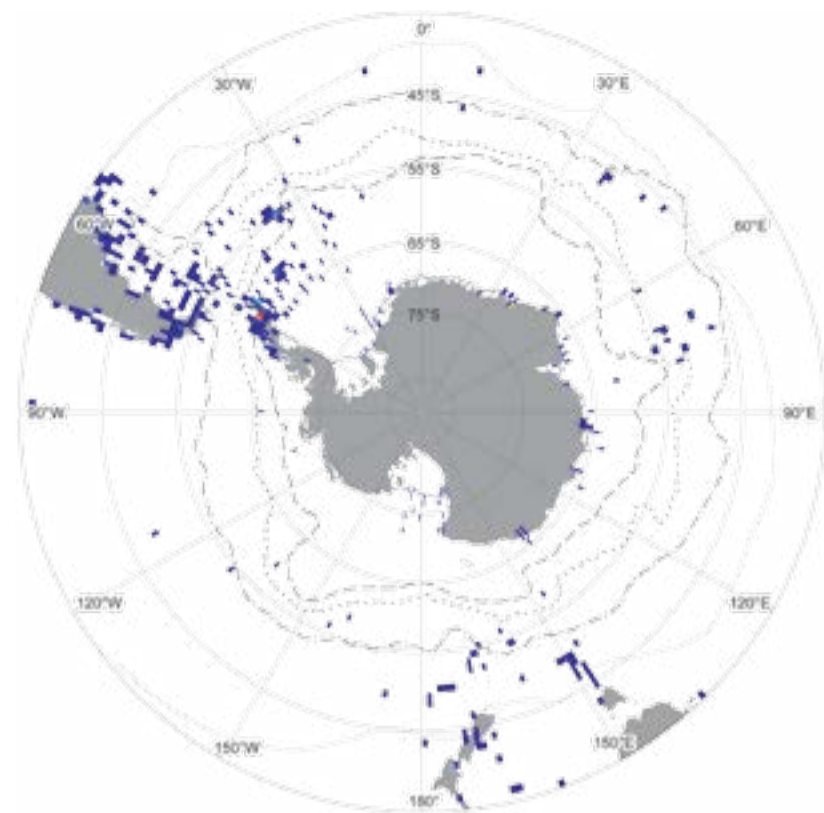
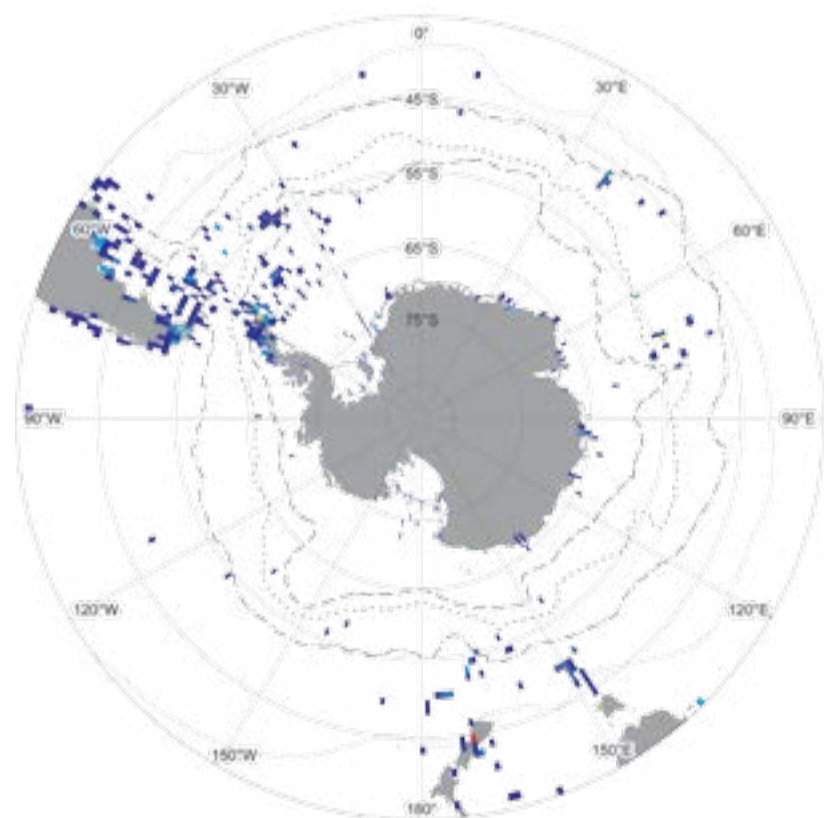


Figure 1 Bathymetric distribution of ostracod samples in the Southern Ocean.



Map 1

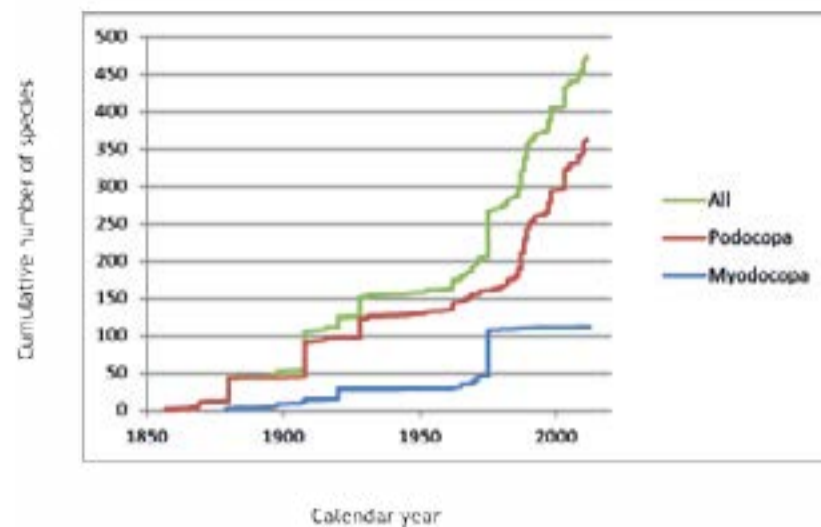


Map 2



**Benthic ostracod Maps 1, 2** Overview of the available data on benthic Ostracoda: Map 1. Number of stations where ostracods were identified. Map 2. Species richness.

Rate of new species description



**Figure 2** Rate of new ostracod species description from the Southern Ocean.

**Table 3** Bathymetric range of Southern Ocean Recent ostracod species (all exclusively fossil species are excluded)

Range (m)	N Species	%
0*-100	174	41
101-200	36	9
201-300	20	5
301-400	30	7
401-500	21	5
501-600	16	4
601-700	4	1
701-800	5	1
801-900	10	2
901-1000	14	3
1001-2000	40	9
2001-3000	31	7
3001-4000	18	4
4001-5000	2	<1
5001-6000	2	<1
<b>Total</b>	<b>422</b>	<b>100</b>

\* Species known from a single locality.

The arrangement of ostracods in the dataset (Brandão 2012) shows clear biases in its stratigraphic, geographic and bathymetric coverage (Maps 1, 2, Tables 1-3). Most of the records involve Recent (and Late Quaternary) specimens (83% of the records), while only 10% are from Cenozoic strata, 7 % from Cretaceous strata, and a few records from Jurassic deposits from Gondwanaland, which later became the Southern Ocean (Table 1). Despite their rarity, these fossils provide critical information on the evolution of the Southern Ocean fauna during the last ~160 Ma (see below). Geographically, sampling was concentrated in shallow areas of the Atlantic sector (e.g. Northwestern Antarctic Peninsula) and around a few sub-Antarctic islands (e.g. Marion Island) (Map 1, Table 2), while the deep sea remains largely under-sampled (<10% of the records are abyssal, and ~20% are from the continental slope) (Figure 1). Also, far fewer samples have been collected from the Indian (<25%) and Pacific (>12%) sectors.

### 3. Biodiversity of benthic Ostracoda in the Southern Ocean: general aspects

Intense data-mining (Brandão 2012), has revealed a total of 571 (494 accepted names, i.e. excluding synonyms) Southern Ocean ostracod species (Table 4), which is more than twice the number (i.e. 234) recorded in the last review on the Southern Ocean fauna (De Broyer *et al.* 2013, Table 2). Most of these species are benthic (527 in total, 452 accepted) and most benthic species are marine (only three inhabit freshwater). The surprisingly low diversity of the Southern Ocean, i.e. <2% of all ostracod species, or ~5% of the Recent marine ostracod species, in such a large oceanic area is probably due to inadequate sampling and its geographical cover (Map 1), with a large number of new species probably still to be discovered (Figure 2). At higher taxonomic levels, the Southern Ocean ostracod fauna is quite diverse, with 42 families (1 of them exclusively planktonic) and 210 genera (Table 1).

As a consequence of the stratigraphical bias of our dataset (Table 1), most of the accepted species (86%) are Recent, while fewer were recorded from older Cenozoic (20%) and Mesozoic (6%) strata (percentages sum >100% because some species occur in more than one period). While all Mesozoic and early Cenozoic species became extinct as the Southern Ocean climate cooled, several late Cenozoic species still live in the Southern Ocean (see below).

**Table 4** Ostracoda species in the Register of Antarctic Marine Species.

RAMS	Species	Accepted Species	Fossil species	Accepted fossil species
<b>Total</b>	571	494	52	50
<b>Planktonic</b>	44 (8%)	42 (9%)	0	0
<b>Benthonic</b>	527 (92%)	452 (91%)	52 (100%)	50 (100%)

The difference in numbers between this table and tables 1 & 2 is due to the exclusion from the latter of data published prior to 1920.

## 4. Southern Ocean ostracod biogeography

### 4.1. The palaeontological perspective (Maps 3-7)

The Southern Ocean was formed during the breakup of Gondwanaland between mid-Jurassic and late Cretaceous time (~160 - 80 Ma) (e.g. Lawver *et al.* 1992), although complete isolation of Antarctica at deep and shallow water levels was not complete until the Oligocene (~31 Ma) (e.g. Lawver & Gahagan, 2003). These structural developments took place continuously, but will be portrayed as four main phases (Maps 3-7): Late Jurassic, Early Cretaceous, mid-Cretaceous, and Late Cretaceous, resulting in the creation of the following Southern Ocean sectors (related to Antarctica's coastline) - Pacific, Atlantic/SW Indian, SE Indian and South Australasian, respectively. Cenozoic expansion merely deepened and widened the Southern Ocean, and oceanographically isolated Antarctica, resulting in widespread, quasi-permanent cryogenic conditions since late Eocene time (Map 7). The changing taxonomic complexion of benthic ostracod faunas inhabiting the Southern Ocean during the last 160 My can be characterised by reference to the temporal and spatial distribution of key taxa referred to various localities and DSDP/ODP sites shown in Maps 3-7.

**Map 3.** During mid-Late Jurassic time (~160-135 Ma), the split between West and East Gondwanaland (i.e. Africa/South America, and Madagascar/India/ Antarctica/Australasia, respectively) worked its way south from the Tanzania/Madagascar gulf towards SE Africa/Falkland Plateau. The only known Late Jurassic marine ostracod fauna of the incipient Southern Ocean-Atlantic/SW Indian sector is from the south coast of the South Africa (Dingle & Klinger 1972), with shallow-water platycopids (*Cytherella* Jones, 1849 and *Cytherelloidea* Alexander, 1931) and progonocytherids (*Fastigatocythere* Wienholz, 1967 and *Majungaella* Grekoff, 1963). This assemblage is reminiscent of the south Tethyan faunas from Tanzania, Madagascar and NW India (Bate 1975, Grekoff 1963, Neale & Singh 1986), but lacks characteristic south-east Tethyan forms such as *Gondwanacythere* Lord *et al.* 2006 and *Arculicythere* Grekoff, 1963.

No faunas are known from the Jurassic Southern Ocean-Pacific sector (much of which was a subduction zone (see Lawver *et al.* 1992), but it probably had direct links with the Neuquén Basin of NW Argentina. Here, there is a relatively sparse fauna of platycopids (*Cytherella*) and cytherurids (e.g. *Procytherura* Whatley, 1970, *Eucytherura* Müller, 1894, and *Paradoxorhyncha* Chapman, 1904) (Ballent & Whatley 2000), and significantly, rare *Majungaella* (Piovesan *et al.* 2012).

**Map 4.** By Early Cretaceous time (Valanginian/Hauterivian, ~123 Ma), the Southern Ocean-Atlantic/SW Indian sector was well-established, with extensive continental shelf and deep oceanic regions. There are yet no deep-sea faunas available, and the Falkland Plateau prevented deep-water circulation into the proto-South Atlantic basin. Shelf seas lay over the Agulhas Bank in South Africa and the Mozambique Ridge (DSDP site 249: Sigal 1974), extending to the Patagonian basins in southeastern Argentina. They had a distinctive fauna (Dingle 1988), containing *inter alia*, *Majungaella* (at least 8 species - Piovesan *et al.* 2012), *Amphicytherura* (*Sondagella*) Butler & Jones, 1957, *Rostricytheridea* Dingle, 1969 (at least 4 species - Ballent & Whatley 2007), cytherurids (especially *Procytherura* - 4 species - Ballent & Whatley 2009), and numerous platycopids (at least 3 species of *Cytherelloidea* - Brenner & Oertli 1976). Despite the widening seaway between East Africa and Antarctica/Madagascar leading from the southern Tethyan area, *Rostricytheridea* did not pass out of the Southern Ocean-Atlantic/SW Indian sector, nor did the ubiquitous southeast Tethyan taxon *Arculicythere* pass in.

A connection was temporarily established between the Patagonian (Atlantic) and Neuquén (Pacific) basins in Argentina, allowing faunal exchange between the Southern Ocean- Pacific and Atlantic/SW Indian sectors. This remained a route until the end of the Hauterivian (see Malumián *et al.* 1983). The following taxa are common to the Neuquén and Patagonian basins: *Majungaella* (2 species - Piovesan *et al.* 2012), *Amphicytherura* (*Sondagella*) (Musacchio 1979), *Procytherura* (3 species - Ballent & Whatley 2009) and *Cytherelloidea* (1 species - Musacchio, 1979).

*Rostricytheridea* also occurs in both basins, and its greater diversity (5 species) and slightly earlier occurrence (Berriasian, ~133 Ma) in the former suggests that this genus originated therein (Ballent & Whatley 2007). The taxon's subsequent history was of easterly and southward migrations through the Cretaceous Southern Ocean.

**Map 5.** During mid-Cretaceous time (Aptian/Albian, ~108 Ma), the Southern Ocean-SE Indian sector was created, allowing faunal connections between SE Africa/Patagonia and the oceanic basins off western Australia. This greatly-enlarged Southern Ocean was characterised by several regionally-occurring taxa: *Majungaella*; *Arculicythere*; *Rostricytheridea*, and *Robsoniella* Kusnetsova, 1956.

The earliest record of *Arculicythere* is from the Upper Jurassic of Tanzania and NW Madagascar (Grekoff 1963, Bate 1975 [as *Trichordis triangula* sp. nov.], Rafara 1990), and by Aptian time (~110 Ma) it was present in the SE Atlantic off Namibia (Dingle 1996). During the Albian, there was a significant increase in diversity and abundance of the genus. Most notable was the species *A. tumida* Dingle, 1971 which occurred in SE Africa, Falkland Plateau and southern Argentina (Dingle 1984, Ballent 1998). It became ubiquitous during Albian time along the new Southern Ocean southern Indian seaway (Jain 1976 = *Pseudobythocythere kallakkudiensis* Jain, 1976), and in western Australia (e.g. DSDP 259 - Oertli 1974). The genus did not outlive Albian time (Ballent & Whatley 2006).

Although already extinct in the Falkland/SE Africa area by the mid-Cretaceous, *Rostricytheridea* had greatly extended its geographical range eastward. Having reached the Carnarvon Basin in the Barremian (Guzel 2012), it colonised both NW India (e.g. Andreu *et al.* 2007) and the shallow interior seas of east-central Australia by the Albian (Krömmelbein 1975). In the latter, it coexisted with *Majungaella*.

A further species that became locally very abundant and widespread in the enlarged Southern Ocean was *Robsoniella falklandensis* Dingle, 1984. It was probably a Bairdiid, inhabiting bathyal, open marine environments (Guzel 2012 p. 53). The taxon spread rapidly from NW Australia (Aptian, ODP 763B, Damotte 1992; early Albian, DSDP 260, Oertli 1974) into the Southern Ocean, and westward to the Falkland Plateau (Albian, DSDP 327/330, Dingle 1984). It is not known from younger strata. [Guzel (2012 p. 53) suggests that the genus may have been recorded by Musacchio (1979 pl. 6, fig. 30) in the Hauterivian of the Neuquén Basin, but we do not agree with this identification.]

Several less-abundant Albian species were also widely distributed around this sector of the enlarged Southern Ocean - on the shelves off western Australia (Exmouth Plateau ODP 259), SE Africa, the Falkland Plateau and southern Patagonia: *Isocythereis sealensis* Dingle, 1971, *Cytherura? oertlii* Dingle, 1984, and two species of *Pirileberis* Grekoff, 1963 (Guzel 2012, p. 56-57).

These ostracods gave the mid-Cretaceous southern oceans a very distinctive fauna: the South Gondwana Fauna B of Dingle (1988), but few of the taxa survived further widening of the Southern Ocean and concomitant subsidence of the Walvis Ridge/Rio Grande Rise barrier. The latter event occurred in Cenomanian-Turonian time, and allowed taxa to invade from the South-Central Atlantic and colonise the northern fringes of the Southern Ocean (Dingle 1999).

**Map 6.** In Late Cretaceous time (Campanian/Maastrichtian, ~72 Ma), the last extensive segments of the Southern Ocean to open lay between East Antarctica and southern Australia (~90 Ma, Turonian) and New Zealand (~84 Ma, Santonian): the South Australasian sector. The former segment progressed relatively slowly, creating a choke point south of Tasmania, while circum-Antarctic oceanic circulation was encumbered further at the Drake Passage. Both narrows probably relaxed at ~32-31 Ma (Oligocene) (see Lawver & Gahagan 2003). Details of Southern Ocean late Mesozoic ostracod faunas are available from both the northern (Falkland Plateau, SE Africa, New Zealand and western Australia), and the southern sides (Maud Rise and Kerguelen Plateau). Patagonia and the Antarctic Peninsula remained joined and had contiguous faunal realms.

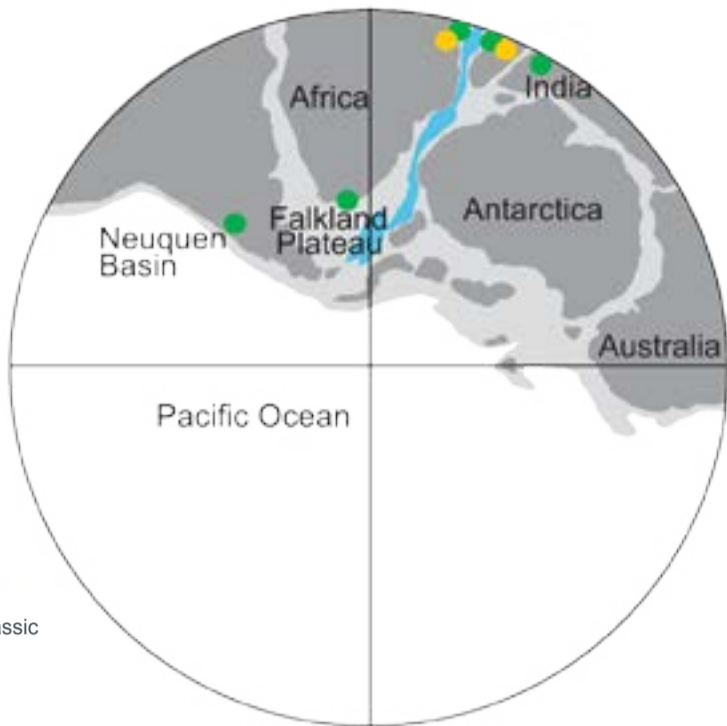
Late Cretaceous Southern Ocean faunas contained three fundamentally different elements: 1) remnants of early and mid-Cretaceous faunas, including those that had colonised Patagonia and southern Africa/India from West Africa when the Walvis Ridge/Rio Grande barrier was breached at a shallow level; 2) burgeoning new shelf forms, many of which formed the stock for Cenozoic shelf faunas; 3) other, opportunistic, retrothermal shelf taxa that colonised deep, colder water (in latest Cretaceous/Cenozoic time), some of which became pandemic, if not "cosmopolitan".

1) Of the remnant, older Cretaceous faunas, *Rostricytheridea* had, by Maastrichtian time, extended its range to the most easterly shelf seas on the north side of the Southern Ocean (North Island, New Zealand) and also had reached the Antarctic Peninsula (Fauth *et al.* 2003, Dingle 2009). However, it did not survive in adjacent Patagonia beyond the Campanian (Ballent & Whatley 2007), and nowhere did the genus outlast the end of the Mesozoic.

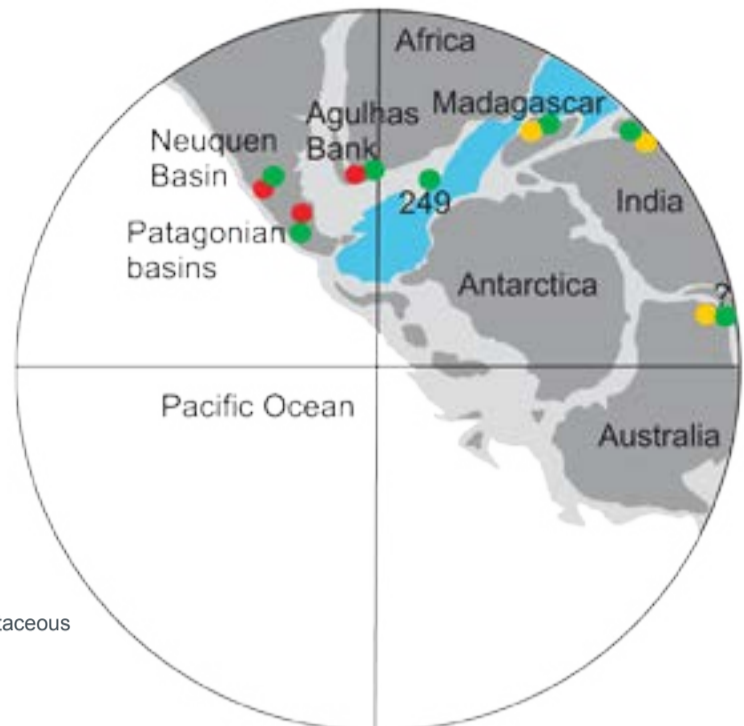
*Majungaella*, in contrast, was extant in Patagonia, Antarctic Peninsula and New Zealand during the Maastrichtian, and although it became extinct on the northern continental shelves of the Southern Ocean at the end of the Cretaceous, it survived across the K/T boundary in the Antarctic Peninsula (e.g. Piovesan *et al.* 2012).

Some mid-Cretaceous colonisers into southern Africa from the central Atlantic, although diverse and locally dominating (e.g. "*Brachycythere*" Alexander, 1933 - [N.B. Puckett (2002) suggests that African and Indian taxa belong to an, as yet unnamed, new genus], and *Haughtonileberis* Dingle, 1969), did not adapt subsequently, and remained of only local importance. As the Southern Ocean expanded further, they became physically isolated from it, and played no role its later faunal development.

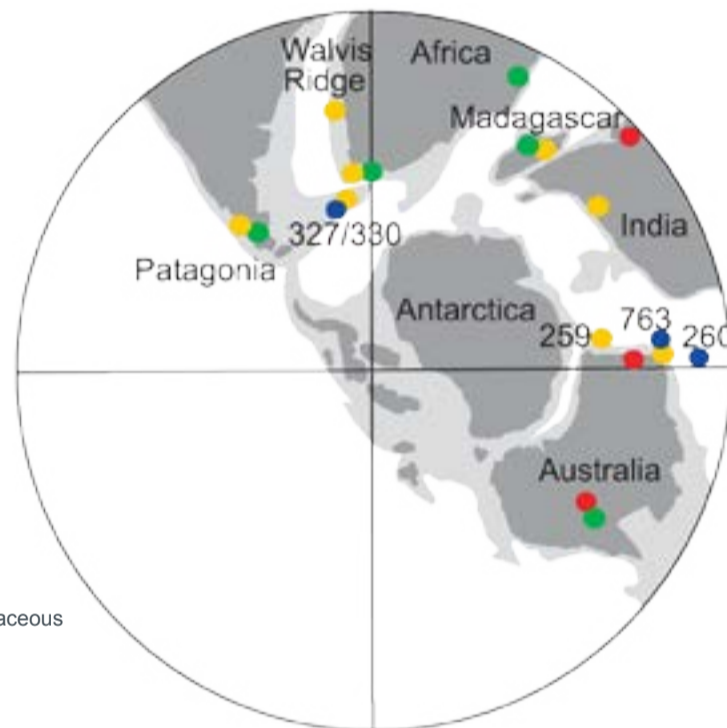
2) In contrast, some taxa that entered Patagonia with the demise of the Walvis/Rio Grande barrier, penetrated onto Antarctic shelves via the Peninsula and thence moved into Australasia via the Tasman shallows. This probably accounts for the commonality of numerous new taxa along the West Australia-Patagonia Southern Ocean shelf routeway in Campanian/Maastrichtian time. A notable example are the Pectocytheridae Hanai - e.g. *Munseyella* van den Bold, 1957, *Paramunseyella* Bate, 1972, *Ameghinocythere* Whatley *et al.* 1977. We have plotted these in Maps 4 & 5 as "munseyellids".



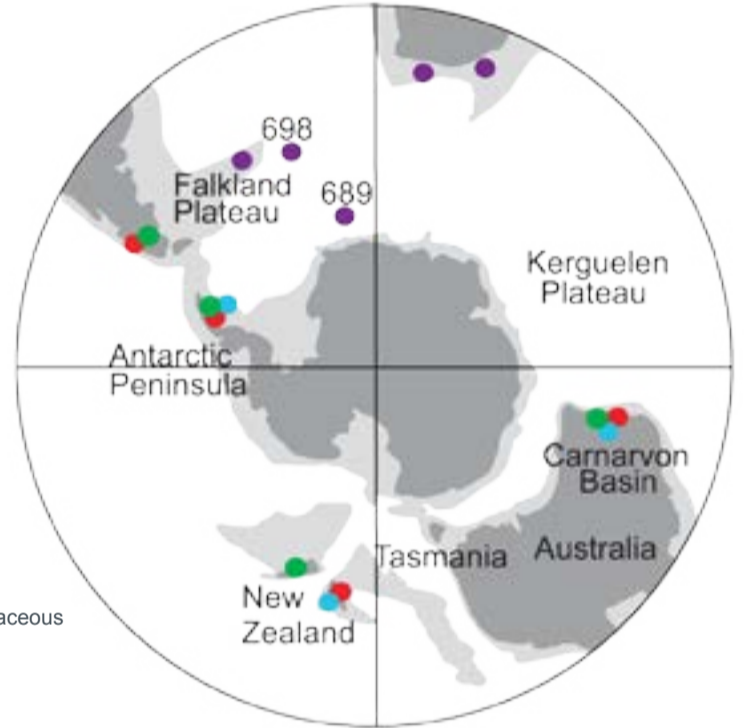
**Map 3**  
Late Jurassic  
~150 Ma



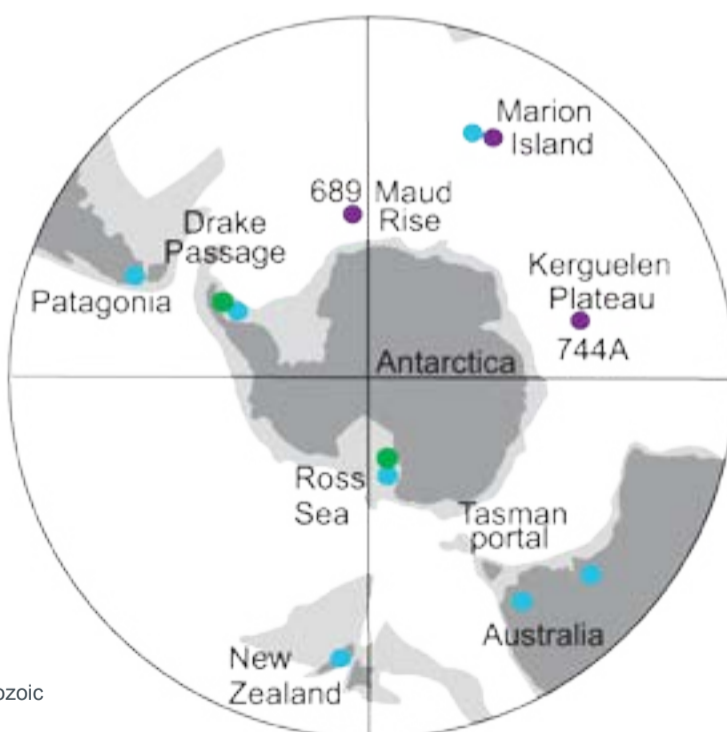
**Map 4**  
Early Cretaceous  
~123 Ma



**Map 5**  
mid-Cretaceous  
~108 Ma



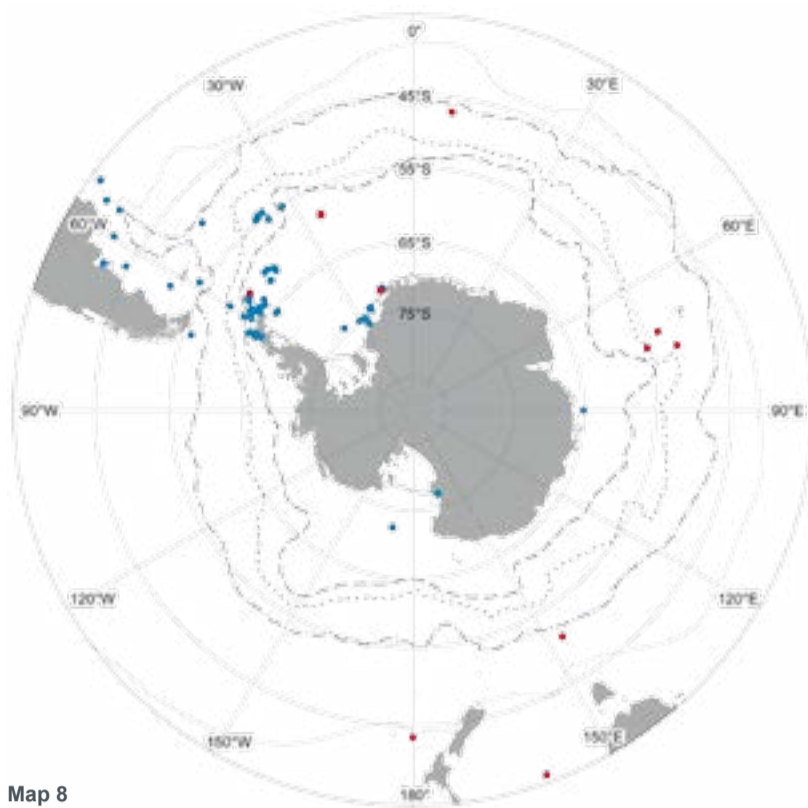
**Map 6**  
Late Cretaceous  
~72 Ma



**Map 7**  
mid-Cenozoic  
~30 Ma

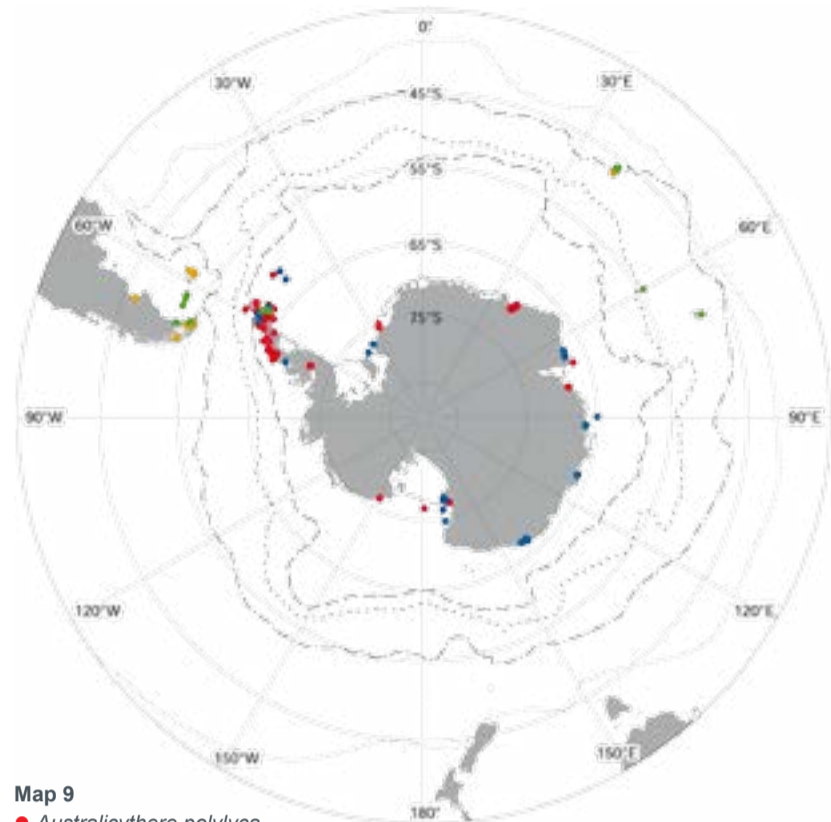
- *Majungaella*
- *Arculicythere*
- *Rostrocytheridea*
- *Robsoniella*
- *Dutoitella*
- "munseyellids"

**Benthic ostracod Maps 3–7** Palaeogeographic reconstructions of the Southern Ocean after Lawver *et al.* (1992): Map 3. Late Jurassic (~150 Ma). Map 4. Early Cretaceous (~123 Ma). Map 5. mid-Cretaceous (~108 Ma). Map 6. Late Cretaceous (~72 Ma). Map 7. Mid-Cenozoic (~30 Ma). Outlines show modern coasts and continental edges. Blue shaded areas show East/West Gondwanaland separation (Maps 3–4). Named localities are key palaeontological sites/areas mentioned in text, and numbers refer to DSDP/ODP boreholes.



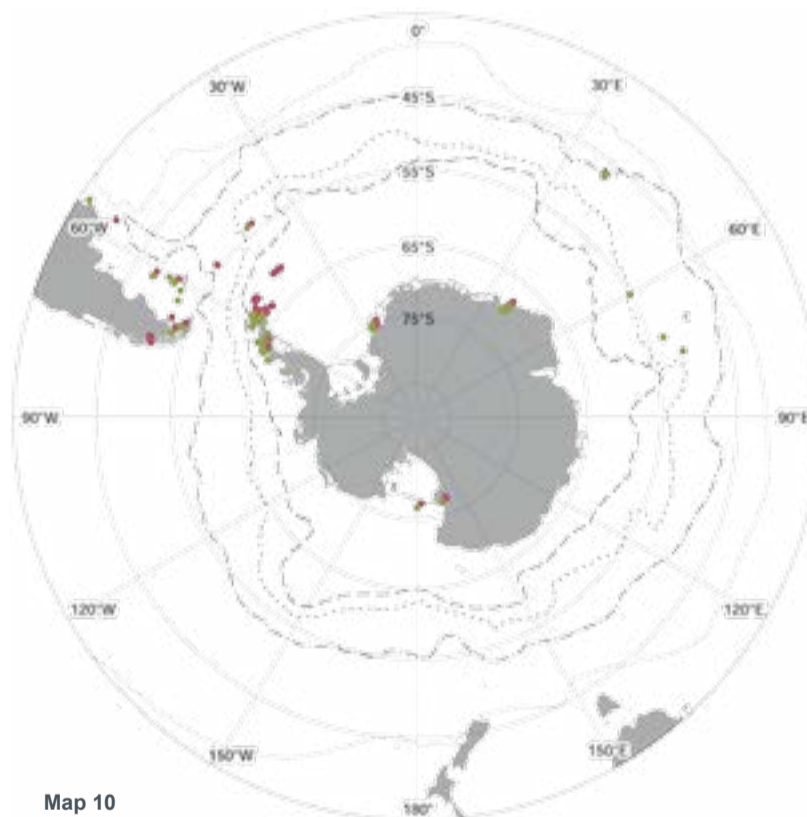
Map 8

- *Ayressoleberis bathymarina*
- *Macroscapha opaca* complex



Map 9

- *Australicythere polylyca*
- *Hemicytherura lilljeborgi*
- *Meridionalicythere taeniata*
- *Philomedes assimilis*



Map 10

- *Austrotrachyleberis antarctica*
- *Cativella bensoni*

**Benthic ostracod Maps 8–10** Examples of geographical and bathymetrical distribution of Recent benthic ostracods: Map 8. Examples of shallow water (<1000m) circumantarctic endemic species, with occurrence in the Antarctic and/or in the sub-Antarctic zones and/or in the Southwestern Atlantic. Map 9. Examples of shallow water (<500m) circumantarctic species with occurrence in the Antarctic and sub-Antarctic zones of the Southern Ocean and also in the Southwestern Atlantic. Map 10. Examples of eurybathic species, occurring in the Southern Ocean and in the Atlantic.

3) A third taxal element had a profound influence on Southern Ocean ostracod faunas. Several, originally shelf forms, descended into deeper waters, spread rapidly, and gave rise to species, some of which remain widespread in deep-water Southern Ocean areas (and beyond) today (see e.g. Majoran *et al.* 1997). Prominent in this group are members of the Trachyleberididae Sylvester-Bradley, 1948 (e.g. *Dutoitella* Dingle, 1981, *Agulhasina* Dingle, *Henryhowella* Puri, 1957, *Pennyella* Neale, 1974, *Rugocythereis* Dingle *et al.* 1990, *Trachyleberis sensu lato* Brady, 1898 [N.B. With no soft parts available, and the invalidity of blindness as a taxonomic criterion, it is not practical to differentiate fossil “*Trachyleberis*” into related genera (as in Jellinek & Swanson 2003)], Sylvester-Bradley, and *Anebocythereis* Bate, 1972), and *Pelecocythere* Athersuch, 1979 (see, e.g. Bergue *et al.* 2013). Most appeared earlier than the Maastrichtian (e.g. *Agulhasina*, Campanian, west Australia - Guzel, 2012; *Dutoitella*, Santonian, South Africa - Dingle, 1981; *Trachyleberis*, Coniacian, west Australia - Bate, 1972; *Anebocythereis*, Campanian, west Australia Bate 1972), but by Late Cretaceous time were widespread in outer

shelf environments. Here they evolved species that had descended to bathyal depths. Using data from ODP sites in the Southern Ocean-Atlantic/SW Indian sector (698 - NE Georgia Rise, 689 - Maud Rise), as well as from farther afield (356 - São Paulo Plateau, 525-529 - Walvis Ridge), Majoran & Widmark (1998) concluded that it would have been relatively easy for shelf species to invade deep-sea habitats at this time because there was no strong thermocline.

A feature of the late Cretaceous Southern Ocean faunas is the relative abundance of species of *Krithe* Brady *et al.* 1874 and *Cytherelloidea* (Majoran *et al.* 1997). In some shelf localities in the Southern Ocean, *Krithe* is very rare (e.g. West Australia - Bate 1972), but at others it was common (e.g. SE Africa - Dingle 1981). In contrast, *Cytherelloidea* was generally common in shallow water. However, while both taxa occurred in the deep-sea Late Cretaceous thermospheric Southern Ocean, the development of the psychrosphere during Cenozoic time caused *Cytherelloidea* to become extinct in these environments, while *Krithe* thrived.

**Map 7.** Mid-Cenozoic. By ~31 Ma, the Drake Passage and Tasman Portal were open, and the oceanographic thermal isolation of Antarctica was well-established, with cryospheres over both East and West subcontinents. Southern Africa no longer lay adjacent to the Southern Ocean, and Australasia was rapidly receding. We shall use this reconstruction to illustrate all Tertiary and Pleistocene time.

Major Cenozoic events affecting ostracod evolution were the initiation of circum-Antarctic oceanic circulation, the establishment of the deep-sea psychrosphere, and fluctuations in glacial intensity. Once a semi-permanent, continent-wide cryosphere was in place, and strong thermal oceanic layering had developed, taxonomic differentiation between deep-water and shallow (shelf) ostracod faunas became marked (in contrast to Mesozoic time) (e.g. Wood *et al.* 1999).

## 4.2. Deep-sea faunas

ODP data have been used to monitor remnant late Mesozoic thermospheric deep-sea taxa as they were replaced by/evolved into proto-modern deep-sea faunas. These changes coincided with a series of Cenozoic oceanographic reorganisations that were first discussed on a global scale by Benson (1975). Majoran & Dingle (2002a,b) re-assessed the data from a Southern Ocean perspective, and found that at Maud Rise site 689, thermophilic marker species with Cretaceous pedigrees, such as *Dutoitella mimica* Dingle, 1981, “*Cythereis*” cf. *C. klinger* Dingle, 1980, *Pennyella* sp. Neale, 1974, *Apateloschizocythere* sp. Bate, 1972 and several species of *Cytherelloidea* are restricted to Palaeocene/Eocene strata. This first major Cenozoic faunal turnover was spread over late Eocene-early Oligocene time (~38-30 Ma), and probably coincided with the establishment of the psychrosphere (see Hay *et al.* 2005 for discussion of its development) and a decline in food supply. The result was a decrease in overall ostracod abundance and diversity, and a marked increase (~25% to >40%) in relative abundance of *Krithe* spp. and the appearance of, *inter alia*, *Poseidonamicus* Benson, 1972, *Legitimocythere presequenta* (Benson, 1972), *Henryhowella dasyderma* Brady, 1880, *sensu* Majoran & Dingle, 2002b, *Dutoitella* spp., *Bradleya* Hornibrook, 1952, and *Agrenocythere* Benson, 1972. [See also Bergue & Govindan, 2010 for Kerguelen Plateau, ODP 744A data].

Further significant Southern Ocean faunal turnovers occurred in the mid-Miocene (~16-14 Ma) (?expansion of cryosphere - increase in % of *Poseidonamicus*, *Bradleya* and *Krithe*, and decrease in *Cytherella*, and appearance of *Philoneptunus* Whatley *et al.* 1992) and the mid-Pliocene (3.5 Ma) (inter-glacial episode - decrease in faunal abundances and diversity) (Majoran & Dingle 2002a,b).

Other characteristic Southern Ocean deep-sea taxa whose fluctuating presence through Cenozoic time can be locally monitored at ODP sites include *Rugocythereis*, *Pelecocythere*, *Ambocythere* van den Bold, 1957, and *Abyssocythere* Benson, 1971. Also, Yasuhara *et al.* (2009) have shown that in the Southern Ocean-Atlantic/SW Indian sector glacial/interglacial-scale deep-water circulation changes are reflected in alternating *Henryhowella*/*Legitimocythere* and *Krithe*/*Poseidonamicus*-dominant faunas, respectively.

Finally, taxal depth-ranges in specific deep-water masses in the modern Southern Ocean on the Kerguelen Plateau are generally similar to, but not identical with, those in the South Atlantic and SW Pacific (Ayress *et al.* 1997).

## 4.3. Shelf faunas

A feature of the south-shore faunas of the Southern Ocean has been their adaptation to the rigours of proximal glaciation (e.g. see Yasuhara *et al.* 2007). This is epitomised by the retrothermal genus *Majungaella* in its Antarctic *refugia* (Dingle & Majoran 2001). Infiltrating from late Cretaceous Patagonia, it occupied the temperate Campanian/Maastrichtian and then cold, pre-glacial late Eocene Antarctic Peninsula (Szczechura 2001, Fauth *et al.* 2003, Dingle 2009), before coping with Oligocene full glacial conditions in the Ross Sea area (Dingle & Majoran 2001). The genus, which had originated in the balmy mid-Jurassic gulf off NW Madagascar, survived to the mid-Pliocene inter-glacial episode in the Antarctic Peninsula (Szczechura & Błaszczuk 1996), before becoming extinct with the onset of Pleistocene glaciation.

Similar, if temporally shorter, evolutionary adaptations were achieved by those pectocytherids (*Ameghinocythere* and *Munseyella*) that were “trapped” on Antarctica as it became progressively colder. This has resulted in a high degree of endemism in the group, whose Cenozoic distribution, following Cretaceous expansion, extended from Patagonia to Australia. Using *Munseyella* as an example: SE Australia [Palaeocene 5 spp. - Neil (1997), Miocene 1 sp. - Whatley & Downing (1983)]; New Zealand [Eocene 2 spp. - Ayress (1995)]; Antarctic Peninsula [Eocene 1 sp. - Szczechura (2001), Oligocene 1 sp. - Błaszczuk (1987)], Antarctic Ross Sea [Oligocene 1 sp. - Dingle (2000)]; and Patagonia [Eocene/Oligocene 2 spp. - Echevarría (1998), Miocene 1 sp. Echevarría (1991), Pliocene 1 sp. - Echevarría (1988)].

Other modern species that first appeared under Oligocene glaciomarine conditions in the Ross Sea include *Austrocythere reticulotuberculata* Hartmann, 1989, *Kuiperiana meridionalis* (Müller, 1908), and *Australicythere polylyca* (Müller, 1908) (Dingle & Majoran 2001). Pleistocene appearances of widespread and abundant Holocene taxa from the Ross Sea area include *Semicytherura* cf. *S. costellata* Brady, 1880, *Austrotrachyleberis antarctica*

(Neale, 1967), and *Nodoconcha minuta* Hartmann, 1989 (Dingle & Majoran 2001). [For comprehensive inventories of shallow-water Holocene marine Antarctic faunas, see RAMS and the dataset associated with the present chapter (Brandão 2012)].

A comparative, inter-glacial Upper Pliocene (~2 Ma) shallow-water fauna is available from the north side of the Drake Passage on Burdwood Bank (Whatley & Cusminky 2002). It shows the first appearance of some modern Antarctic taxa including *Hemicytherura lilljeborgi* (Brady, 1880), *Hemingwayella pumilio* (Brady, 1880), and *Patagonacythere devexa* (Müller, 1908), the first two of which are extant on the sub-Antarctic Marion/Prince Edward archipelago. Colonisation of this isolated, relatively young (~450 ka) volcanic island from a probable Patagonia/Antarctic Peninsula provenance may have been by drifting kelp holdfasts (Dingle 2003).

A recent comparative study of the modern shelf faunas of Lützw-Holm Bay in East Antarctica, led Yasuhara *et al.* (2007) to conclude that the bulk of the extant taxa evolved *in situ* during Plio-Pleistocene time. While a few cryophilic species may have migrated to southernmost South America, only two, *Cativella bensoni* Neale, 1967 (Oligocene, Echevarría 1991) and *Patagonacythere devexa* Müller, 1908 (Whatley & Cusminky 2002) probably originated in South America and migrated in the opposite direction (Yasuhara *et al.* 2007, p. 477).

## 4.4. The Recent fauna (Maps 8-10)

At the species level, endemism in the shallow areas of the Southern Ocean is high (74%) (e.g. *Australicythere polylyca*, *Philomedes assimilis* Brady, 1907) (Map 9), but most genera show a worldwide distribution (e.g. *Bradleya* Hornibrook, 1952, *Macroscapha*, *Poseidonamicus* Benson, 1972), while a few genera are restricted to the Southern Hemisphere (e.g. *Argenticytheretta* Rossi de García, 1959, *Falklandia* Whatley *et al.* 1987, *Inversacytherella* Swanson *et al.* 2005). Although eurybathyal and circumantarctic distributions have been widely reported (Maps 8, 9, Table 2), the single genetic study on Southern Ocean ostracods, indicate strong geographic and bathymetric segregation of “populations” previously included in one single nominal species, i.e. *Macroscapha opaca* Maddocks, 1990, since then named *Macroscapha opaca* complex (Brandão *et al.* 2010).

The bathymetric distribution of most species (67%) is restricted (i.e. <500m), while less than 22% are truly eurybathic (i.e. >1000 m) (Table 3). Additionally, most of the Recent ostracod species (~60%) are endemic to the continental shelf (<1000 m), 25% are exclusive to the deep sea (i.e. slope and/or abyss), while only 15% occur both in shallow and deep environments. Finally, the distinction between shallow and deep faunas also occurs in supraspecific groupings: the assemblages from the shelf, slope and abyss were shown to be significantly distinct from each other (Brandão 2010, Kaiser *et al.* 2011).

In the sub-Antarctic zone, although the fauna of some isolated islands (i.e. Crozet and Bouvet) is completely unknown, the Atlantic sector (e.g. South Georgia, King George Island) is the most studied. Islands in this sector also share several species with the coast of Antarctica and Southern South America. This is also the case with the Prince Edward/Marion archipelago, where 63% of the species are endemic (Dingle 2003). This shows that the degree of insular endemism varies considerably, as might be expected by a high degree of geographical isolation.

The apparent higher diversity on the continental shelf (70% of all species) than on the slope and in the abyss, is possibly related to the higher sampling densities in these areas. Note, for example, the northern Antarctic Peninsula, the Lützw-Holm Bay, and Marion Island in Maps 1 and 2. A detailed study of the Lützw-Holm Bay fauna allowed Yasuhara *et al.* (2007) to draw some general conclusions on the development of extant Antarctic shelf ostracods. In particular, most of the species they identified are endemic and their distribution is constrained by a combination of “*water mass structure, ice scouring and light intensity*” (Yasuhara *et al.* 2007 p. 478).

As noted by Yasuhara *et al.* (2007), the Recent ostracod fauna from the continental shelf off Antarctica shows no common species with Southern Africa and New Zealand / Southern Australia, but it does share common elements with Southern South America (e.g. *Austrotrachyleberis antarctica* (Neale, 1967), *Cativella bensoni* Neale, 1967, *Hemicytherura lilljeborgi* (Brady, 1880), *Meridionalicythere taeniata* (Skogsberg, 1928)) (Maps 8, 9). In contrast, the fauna of the deep-sea is far more homogenous, showing several common species in the Southern, Atlantic and Pacific oceans (e.g. *Ayressoleberis bathymarina* (Ayress 1993), *Macroscapha opaca*) (Map 10).

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# THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

## Scope

Biogeographic information is of fundamental importance for discovering marine biodiversity hotspots, detecting and understanding impacts of environmental changes, predicting future distributions, monitoring biodiversity, or supporting conservation and sustainable management strategies.

The recent extensive exploration and assessment of biodiversity by the Census of Antarctic Marine Life (CAML), and the intense compilation and validation efforts of Southern Ocean biogeographic data by the SCAR Marine Biodiversity Information Network (SCAR-MarBIN / OBIS) provided a unique opportunity to assess and synthesise the current knowledge on Southern Ocean biogeography.

The scope of the Biogeographic Atlas of the Southern Ocean is to present a concise synopsis of the present state of knowledge of the distributional patterns of the major benthic and pelagic taxa and of the key communities, in the light of biotic and abiotic factors operating within an evolutionary framework. Each chapter has been written by the most pertinent experts in their field, relying on vastly improved occurrence datasets from recent decades, as well as on new insights provided by molecular and phylogeographic approaches, and new methods of analysis, visualisation, modelling and prediction of biogeographic distributions.

A dynamic online version of the Biogeographic Atlas will be hosted on [www.biodiversity.aq](http://www.biodiversity.aq).

## The Census of Antarctic Marine Life (CAML)

CAML ([www.caml.aq](http://www.caml.aq)) was a 5-year project that aimed at assessing the nature, distribution and abundance of all living organisms of the Southern Ocean. In this time of environmental change, CAML provided a comprehensive baseline information on the Antarctic marine biodiversity as a sound benchmark against which future change can reliably be assessed. CAML was initiated in 2005 as the regional Antarctic project of the worldwide programme Census of Marine Life (2000-2010) and was the most important biology project of the International Polar Year 2007-2009.

## The SCAR Marine Biodiversity Information Network (SCAR-MarBIN)

In close connection with CAML, SCAR-MarBIN ([www.scarmarbin.be](http://www.scarmarbin.be), integrated into [www.biodiversity.aq](http://www.biodiversity.aq)) compiled and managed the historic, current and new information (i.a. generated by CAML) on Antarctic marine biodiversity by establishing and supporting a distributed system of interoperable databases, forming the Antarctic regional node of the Ocean Biogeographic Information System (OBIS, [www.iobis.org](http://www.iobis.org)), under the aegis of SCAR (Scientific Committee on Antarctic Research, [www.scar.org](http://www.scar.org)). SCAR-MarBIN established a comprehensive register of Antarctic marine species and, with [biodiversity.aq](http://biodiversity.aq) provided free access to more than 2.9 million Antarctic georeferenced biodiversity data, which allowed more than 60 million downloads.

## The Editorial Team



**Claude DE BROYER** is a marine biologist at the Royal Belgian Institute of Natural Sciences in Brussels. His research interests cover structural and ecofunctional biodiversity and biogeography of crustaceans, and polar and deep sea benthic ecology. Active promoter of CAML and ANDEEP, he is the initiator of the SCAR Marine Biodiversity Information Network (SCAR-MarBIN). He took part to 19 polar expeditions.



**Huw GRIFFITHS** is a marine Biogeographer at the British Antarctic Survey. He created and manages SOMBASE, the Southern Ocean Mollusc Database. His interests include large-scale biogeographic and ecological patterns in space and time. His focus has been on molluscs, bryozoans, sponges and pycnogonids as model groups to investigate trends at high southern latitudes.



**Cédric d'UDEKEM d'ACOZ** is a research scientist at the Royal Belgian Institute of Natural Sciences, Brussels. His main research interests are systematics of amphipod crustaceans, especially of polar species and taxonomy of decapod crustaceans. He took part to 2 scientific expeditions to Antarctica on board of the *Polarstern* and to several sampling campaigns in Norway and Svalbard.



**Bruno DANIS** is an Associate Professor at the Université Libre de Bruxelles, where his research focuses on polar biodiversity. Former coordinator of the [www.scarmarbin.be](http://www.scarmarbin.be) and [antabif.be](http://antabif.be) projects, he is a leading member of several international committees, such as OBIS or the SCAR Expert Group on Antarctic Biodiversity Informatics. He has published papers in various fields, including ecotoxicology, physiology, biodiversity informatics, polar biodiversity or information science.



**Susie GRANT** is a marine biogeographer at the British Antarctic Survey. Her work is focused on the design and implementation of marine protected areas, particularly through the use of biogeographic information in systematic conservation planning.



**Christoph HELD** is a Senior Research Scientist at the Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research, Bremerhaven. He is a specialist in molecular systematics and phylogeography of Antarctic crustaceans, especially isopods.



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**Ben RAYMOND** is a computational ecologist and exploratory data analyst, working across a variety of Southern Ocean, Antarctic, and wider research projects. His areas of interest include ecosystem modelling, regionalisation and marine protected area selection, risk assessment, animal tracking, seabird ecology, complex systems, and remote sensed data analyses.



**Anton VAN DE PUTTE** works at the Royal Belgian Institute for Natural Sciences (Brussels, Belgium). He is an expert in the ecology and evolution of Antarctic fish and is currently the Science Officer for the Antarctic Biodiversity Portal [www.biodiversity.aq](http://www.biodiversity.aq). This portal provides free and open access to Antarctic Marine and terrestrial biodiversity of the Antarctic and the Southern Ocean.



**Bruno DAVID** is CNRS director of research at the laboratory BIOGÉOSCIENCES, University of Burgundy. His works focus on evolution of living forms, with and more specifically on sea urchins. He authored a book and edited an extensive database on Antarctic echinoids. He is currently President of the scientific council of the Muséum National d'Histoire Naturelle (Paris), and Deputy Director at the CNRS Institute for Ecology and Environment.



**Julian GUTT** is a marine ecologist at the Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research, Bremerhaven, and professor at the Oldenburg University, Germany. He participated in 13 scientific expeditions to the Antarctic and was twice chief scientist on board *Polarstern*. He is member of the SCAR committees ACCE and ANT-ERA (as chief officer). Main foci of his work are: biodiversity, ecosystem functioning and services, response of marine systems to climate change, non-invasive technologies, and outreach.



**Graham HOSIE** is Principal Research Scientist in zooplankton ecology at the Australian Antarctic Division. He founded the SCAR Southern Ocean Continuous Plankton Recorder Survey and is the Chief Officer of the SCAR Life Sciences Standing Scientific Group. His research interests include the ecology and biogeography of plankton species and communities, notably their response to environmental changes. He has participated in 17 marine science voyages to Antarctica.



**Alexandra POST** is a marine geoscientist, with expertise in benthic habitat mapping, sedimentology and geomorphic characterisation of the seafloor. She has worked at Geoscience Australia since 2002, with a primary focus on understanding seafloor processes and habitats on the East Antarctic margin. Most recently she has led work to understand the biophysical environment beneath the Amery Ice Shelf, and to characterise the habitats on the George V Shelf and slope following the successful CAML voyages in that region.



**Yan ROPERT COUDERT** spent 10 years at the Japanese National Institute of Polar Research, where he graduated as a Doctor in Polar Sciences in 2001. Since 2007, he is a permanent researcher at the CNRS in France and the director of a polar research programme (since 2011) that examines the ecological response of Adélie penguins to environmental changes. He is also the secretary of the Expert Group on Birds and Marine Mammals and of the Life Science Group of the Scientific Committee on Antarctic Research.

