Census of Antarctic Marine Life
SCAR-Marine Biodiversity Information Network

BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

CHAPTER 5.2. BENTHIC FORAMINIFERA.

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THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

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5.2. Benthic Foraminifera

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1. Introduction

Foraminifera (heterotrophic protists) occur in almost all marine environments from intertidal mudflats to the deepest ocean trenches. Molecular genetic analyses place them within the supergroup Rhizaria, together with radiolarians, gromiids and other protists that are characterised by root-like branching pseudopods (Pawlowski & Burki 2009). Most described foraminiferal species have a test ('shell') composed of calcium carbonate secreted by the cell or agglutinated from foreign particles stuck together with organic or calcareous cement. The tests are often multichambered with the chambers arranged in patterns (e.g. linear, biserial, triserial, spiral) that are characteristic at the family or generic level. In addition, recent studies have revealed a wealth of 'primitive', largely undescribed species with single-chambered ('monothalamous') tests composed of agglutinated or organic material (e.g. Habura *et al.* 2008).

Because they are abundant in all parts of the Southern Ocean (SO) and of interest to both geologists and biologists, a substantial literature exists on benthic foraminifera from Antarctic waters. The Atlas includes a selection of commonly reported species and those that appear to be endemic to these regions. Several important caveats should be mentioned. First, we have not attempted to cover the entire body of literature on Antarctic foraminifera. Second, many of the records that we have included are not supported by illustrations, making it impossible to check identifications. Third, we included dead and 'total' (live + dead) records, as well as those based on 'live' (Rose-Bengal stained) tests. Because dead tests can be transported over distances of 10s or 100s of kilometres (Murray 2006) some biogeographic studies (e.g. Murray 2013) have considered only 'live' records. Transport of tests by turbidity currents and mass wasting events, ice-rafting, and the exposure of non-Recent sediments are potentially important problems around Antarctic coasts (Uchio 1960). However, disregarding records based on unstained (dead or 'total') assemblages would have eliminated important distributional data from areas around Antarctica where 'live' data are scarce or absent. Also, while these processes can modify geographic and bathymetric distributions in particular areas, they are less likely to substantially alter biogeographic patterns on the continental scale considered in this Atlas.

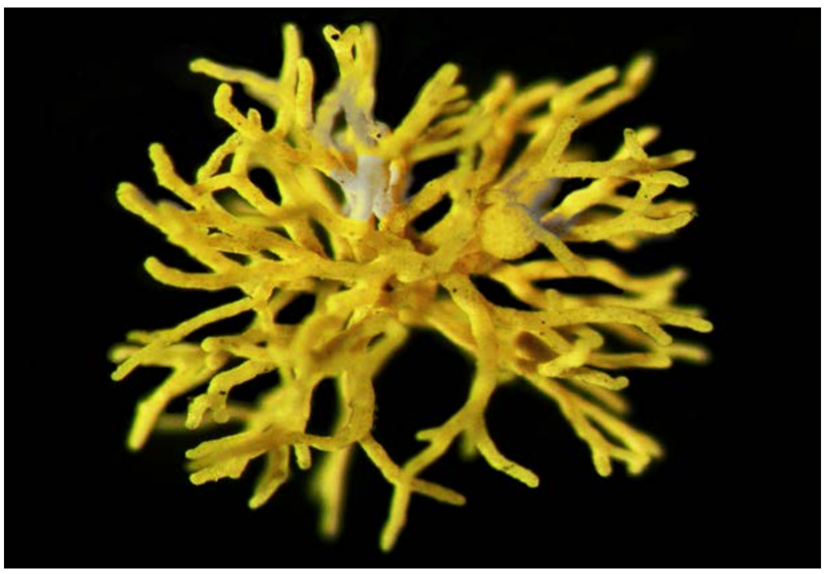


Photo 1 *Septuma ocotillo* Tendal & Hessler, 1977 (*Polarstern* ANT-XXII/3, st. 88-8, 68°03.87'S 20°31.81'E, 4927–4932 m). Image: A.J. Gooday © NOC, Southampton.

2. Methods, including limitations of coverage

Foraminifera have been collected in Antarctic waters since the first half of the 19th century. Sampling sites are concentrated around the Antarctic Peninsula, in the Drake Passage, the Weddell and Scotia Seas and the Ross Sea, particularly the McMurdo Sound area (Cornelius & Gooday 2004). The Adelie-George V shelf and slope and Prydz Bay are also fairly well sampled. Soviet expeditions (1956–1990) collected material at numerous points around East Antarctica between Oates Land and Enderby Land (Mikhalevich 2004). Apart from the Peninsula, coverage is sparse around West Antarctica.

Various devices have been used to obtain this material. Many early studies, which were linked to major national expeditions, employed a combination of small sounding samples and large dredge or trawl samples (Pearcey 1914, Chapman 1916, Heron-Allen & Earland 1922, 1932, Wiesner 1931, Earland 1933, 1934, 1936, Chapman & Parr 1937, Parr 1950). Petersen grab, trawl, dredge and small gravity corers were often used in studies from the 1960s and 1970s (e.g., Uchio 1960, McKnight 1962, Pflum 1966, Kennett 1968, Echols 1971, Herb 1971) and later (Violanti 1996). Although not quantitative, dredges and trawls can concentrate substantial amounts of material, including the large species that are common in some SO settings (Theyer 1971). Gooday *et al.* (2007) collected Weddell Sea komokiaceans using an epibenthic sledge, which concentrates lighter organisms that are easily thrown into suspension. Finally, SCUBA divers have obtained numerous samples from coastal areas (Lipps & DeLaca 1980, Pollock & Bowser 1995).

While earlier investigations were largely descriptive, many studies published during the 1960s and 1970s incorporated some quantitative data (e.g. McKnight 1962, Pflum 1963, Kennett 1968). Another important development in Antarctic foraminiferal research during this period was the application of Rose Bengal staining (first used in North America in the early 1950s) to distinguish dead tests from those that were assumed to be alive when collected (Uchio 1960, Echols 1971, Herb 1971, Basov 1974). Recent research on SO benthic foraminifera has seen the introduction of box cores (Mackensen & Douglas 1989, Mackensen *et al.* 1990, 1993, Ascoli 1995, Schmiedl & Mackensen 1997, Murray & Pudsey 2004) and hydraulically-dampened multiple corers (Harloff & Mackensen 1997, Cornelius & Gooday 2004). The multiple corer is particularly effective because it retains the light, flocculent surface sediment in which many living foraminifera reside.

Several different methods have been used to process Antarctic foraminiferal samples. Wet-sieving is normal but the sieve size used has varied widely: 63 µm (Milam & Anderson 1981, Ascoli 1995, Violanti 1995, Murray & Pudsey 2004), 74-75 µm (Kennett 1968, Anderson 1975, Jones & Pudsey 2004), 100 µm (Lindenberg & Auras 1984), 125 µm (Quilty 1985, Mackensen 1990, 1993, Harloff & Mackensen 1997, Majewski 2005), 150 µm (Mead & Kennett 1987). This has an important influence on the species recovered (Schröder *et al.* 1987). Foraminifera have been picked from dried residues (Kennett 1968, Mead & Kennett 1987, Mackensen *et al.* 1990, Violanti 1995), or residues that were dried and then re-wetted (Murray & Pudsey 2004) or concentrated from dried residues using a heavy liquid (Echols 1971, Bernhard 1987, Ward *et al.* 1987). Gooday *et al.* (1996) and Cornelius & Gooday (2004) sorted sample residues in water, a procedure that ensures the preservation of soft-walled taxa.

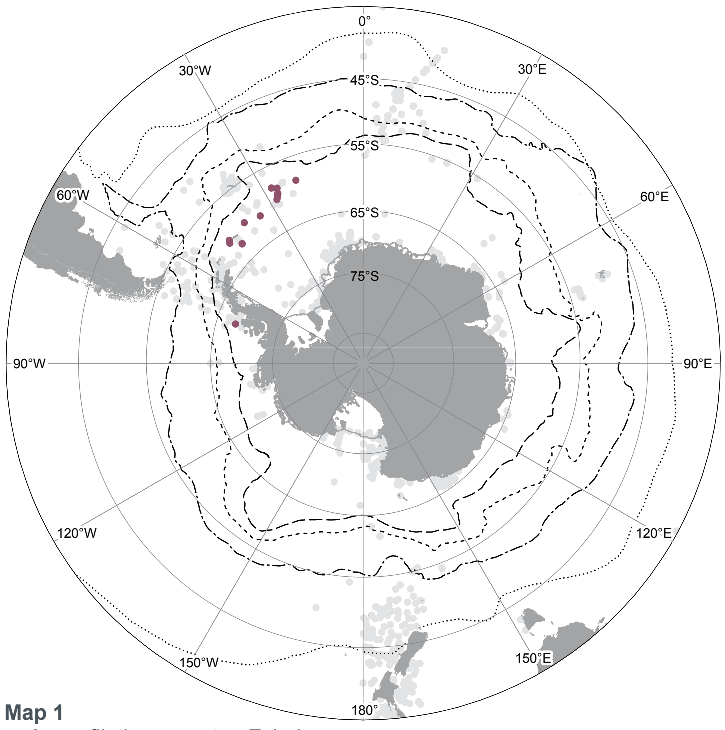
Molecular data (partial sequences of the small subunit ribosomal DNA gene; SSU rDNA) are available for some Antarctic monothalamous (Pawlowski *et al.* 2002a, 2002b, Bowser *et al.* 2002, Gooday *et al.* 2004, Gooday & Pawlowski 2004, Sabbatini *et al.* 2004, Cedhagen *et al.* 2009, Pawlowski & Majewski 2011) and polythalamous (Pawlowski *et al.* 2007b, Majewski & Pawlowski 2010, Schweitzer *et al.* in press) species. Live specimens have also formed the basis for cytological studies (e.g., Travis & Bowser 1991, Bowser *et al.* 1995, Habura *et al.* 2005). Habura *et al.* (2004) and Pawlowski *et al.* (2011) explored foraminiferal diversity by extracting total DNA from sediment samples collected in Explorers Cove (McMurdo Sound) and the deep Weddell Sea, respectively.

3. General composition of the Southern Ocean fauna

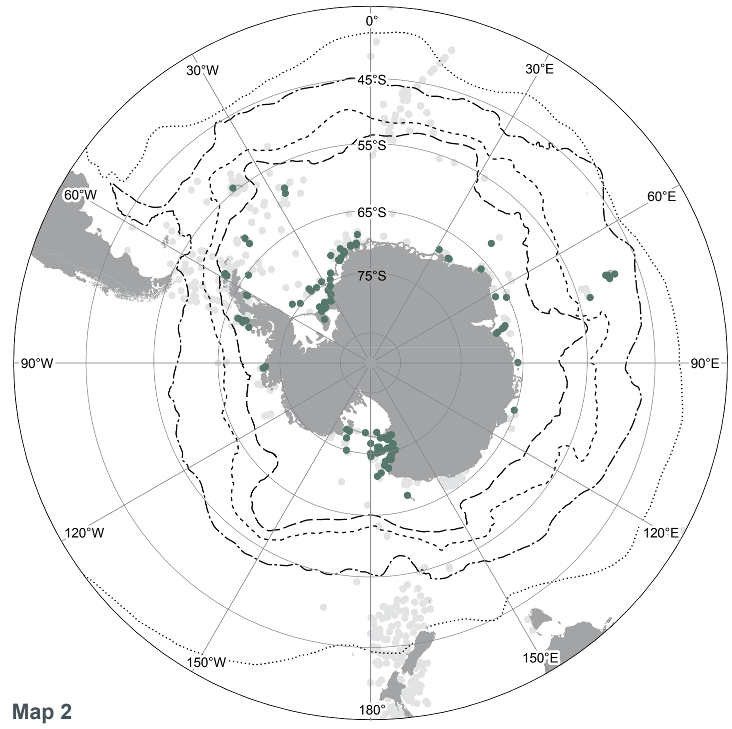
Antarctic foraminiferal faunas include calcareous, agglutinated and organic-walled species, although, as discussed below, assemblages dominated by either agglutinated or calcareous species occur in some settings. Large species of agglutinated genera such as *Cyclammina, Hormosina, Hyperammina, Pilulina, Psammosphaera, Rhabdammina* and *Saccammina,* as well as miliolids (e.g. *Cornuspira, Cornuspiroides, Pyrgo, Pyrgoella*) and some other calcareous taxa (e.g. *Hoeglundina, Dentalina*), often abound in trawl samples (Wiesner 1931, Herb 1971, Schmiedl & Mackensen 1993). Among smaller calcareous foraminifera, species of *Globocassidulina, Cibicides, Trifarina, Epistominella* and *Pullenia* are common (e.g. Mackensen *et al.* 1993, Majewski 2010). Although frequently ignored, monothalamous taxa are abundant and diverse where an effort has been made to look for them, as in Explorers Cove (Gooday *et al.* 1996, Pawlowski *et al.* 2002), Admiralty Bay, King George Island (Majewski *et al.* 2007; Sinniger *et al.* 2008) and the deep Weddell Sea (Cornelius & Gooday 2004). Komokiaceans and other enigmatic forms are abundant in the Weddell Sea (Gooday *et al.* 2007), and probably other abyssal areas.

Attached foraminifera often settle on glacially transported dropstones and other hard substrates. Sessile species belonging to the agglutinated genera *Dendrophrya*, *Dendronina*, *Sorosphaera* and *Tholosina* are common on the continental slope around South Georgia, the Antarctic Peninsula and in the Scotia Sea (Earland 1933, 1934). A majority (69%) of the 852 stained foraminifera in a box core (>300 µm fraction, 0-5 cm layer) from the upper slope in the NW Weddell Sea (RV *Polarstern* Cruise 61, Station 133; 1100 m water depth) were found on dropstones. Elsewhere, cibicidiids and other calcareous species live on biogenic substrates such as scallop shells (Alexander & DeLaca 1987).

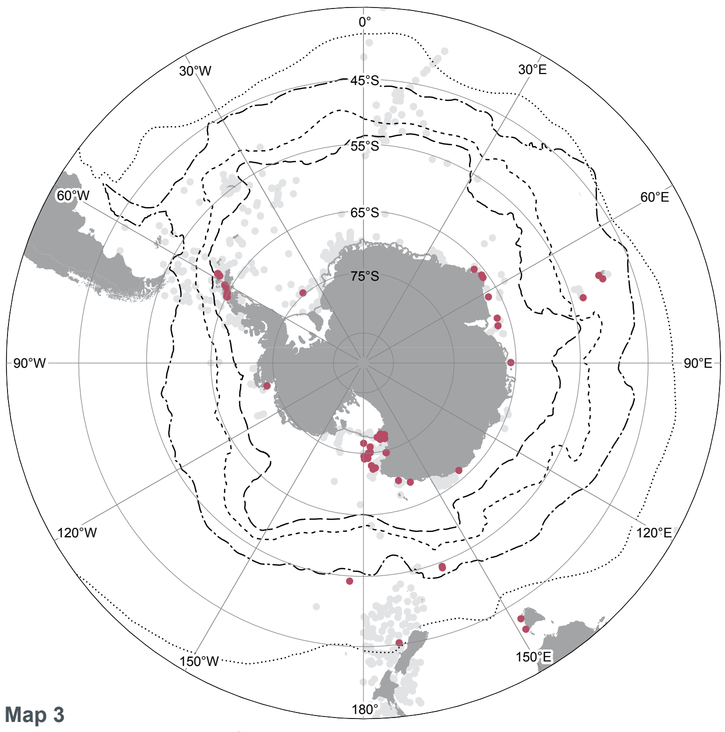
The virtual absence of certain higher taxa, such as brachyuran crabs and sharks, is a notable general feature of the Antarctic marine fauna (Clarke & Johnston 2003). The Elphidiidae represents a comparable example among the foraminifera. The first modern Antarctic species of this family, which is particularly common in the Arctic, was only recently described from King George Island (Majewski & Tatur 2009).



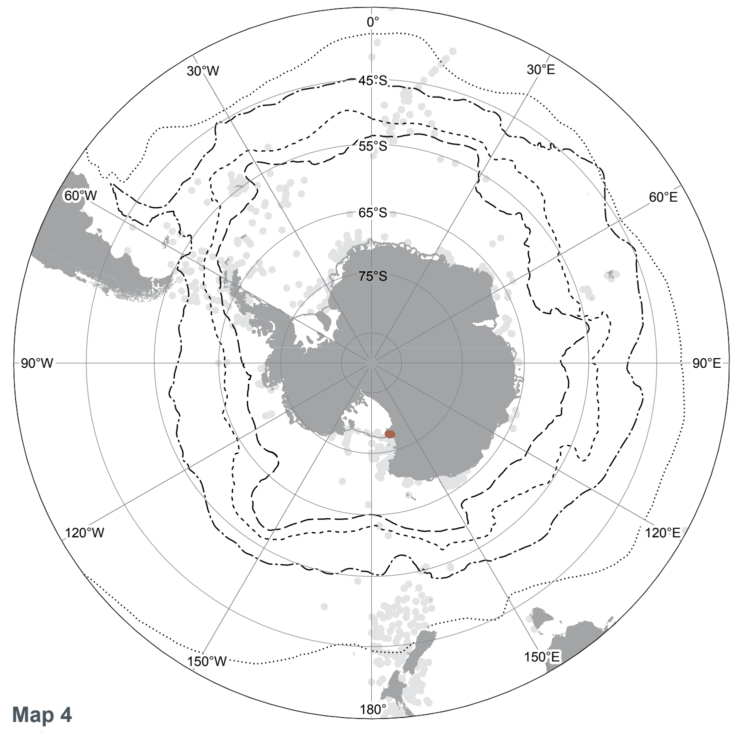
Map 1
● *Ammoflintina argentea Echols*
● All records of benthic Foraminifera



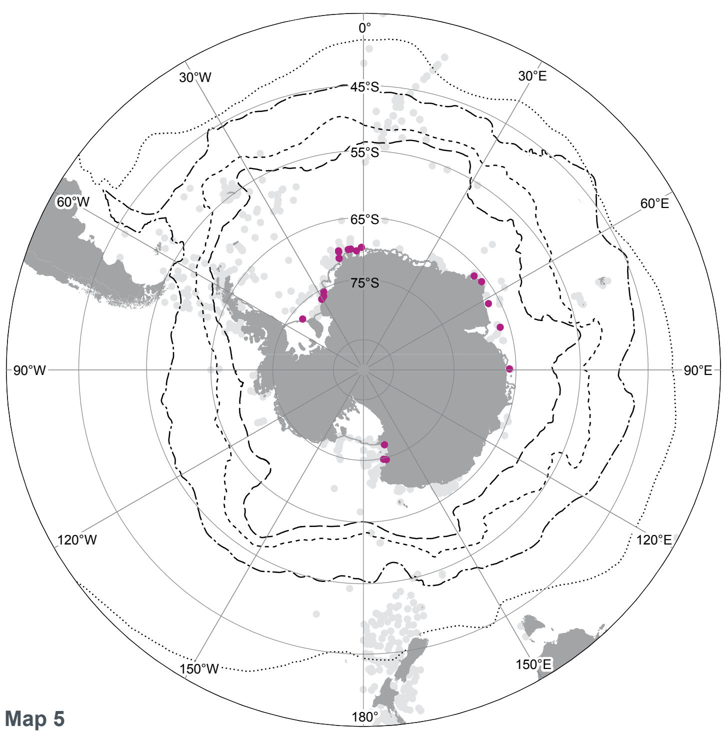
Map 2
● *Miliammina areancea*
● All records of benthic Foraminifera



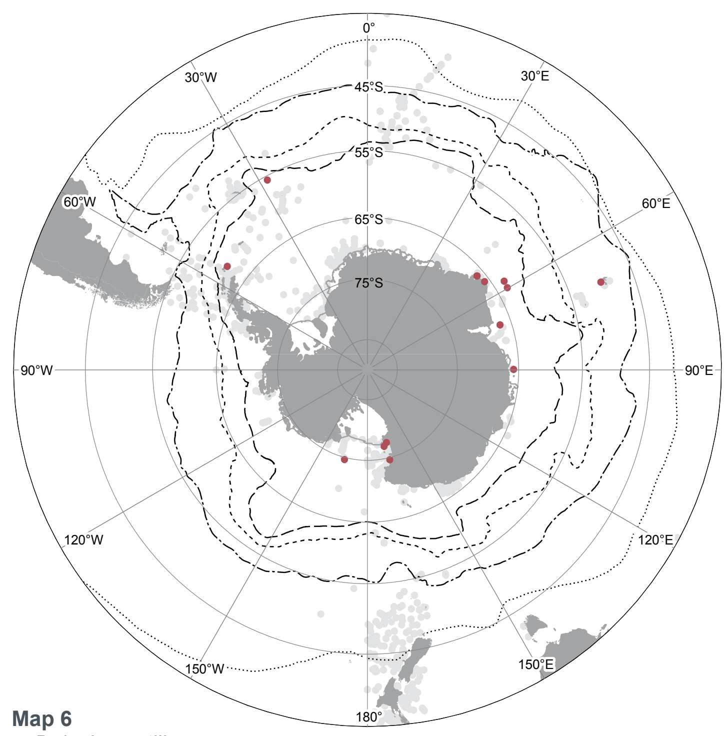
Map 3
● *Rosalina globularis d'Orbigny*
● All records of benthic Foraminifera



Map 4
● *Schackoinella antarctica*
● All records of benthic Foraminifera



Map 5
● *Cornuspiroides rotundus*
● All records of benthic Foraminifera



Map 6
● *Delosina sutilis*
● All records of benthic Foraminifera

Foraminifera Maps 1–6 Map 1. *Ammoflintina argentea* Echols, 1971. Map 2. *Miliammina areancea* (Chapman, 1916). Map 3. *Rosalina globularis* d'Orbigny, 1926. Map 4. *Schackoinella antarctica* Ward, 1987. Map 5. *Cornuspiroides rotundus* Schmiedl & Mackensen, 1993. Map 6. *Delosina sutilis* Earland, 1934. ▶ (See also section 'Notes on mapped species')

4. Bathymetric distribution

Foraminifera are present at all depths around Antarctica. In shallow-water settings, for example coastal fjords, assemblages are related to their proximity to glaciers, sedimentary regime and distance from the open ocean, as well as to bathymetry (Chang & Yoon 1995, Majewski 2005). On rocky substrates around the Peninsula, Lipps & DeLaca (1980) identified a sequence of zones, characterised by differences in foraminiferal densities and species composition, that extend to depths of 33–45 m and reflect the combined influences of ice abrasion and benthic algal production. In deeper water, depth-related assemblages have been recognised in Lutzow-Holm Bay (Uchio 1960), the Ross Sea (McKnight 1962), the Drake Passage (Herb 1971) and the Scotia Sea area (Echols 1971). Based on the data of McKnight, Bandy & Echols (1964) delineated eight groups of species, each of which only occurred below a certain depth (164, 384, 475, 612, 800, 1281, 1670, 2620 m). Kennett (1968) compiled depth ranges for species in the Ross Sea and recognised 'abrupt changes in the fauna' at 270, 450–550, 1300 and 2200 m. However, many species had ranges different from those observed elsewhere in the Antarctic, making it impossible 'to define a foraminiferal depth zonation which will apply to the Antarctic as a whole' (Kennett 1968). It should also be noted that downslope transport may create spurious depth distributions (Uchio 1960).

Calcareous genera (e.g. *Epistominella* and *Globocassidulina*) are often represented by only 2–3 species in Antarctic waters, with one species occurring in deep water and another in coastal settings. Some species, however, have bathymetric ranges extending from the shelf to the abyss (Bandy & Echols 1964, Kennett 1968, Murray 1991), raising the possibility that they comprise two or more cryptic species. Alternatively, in the absence of downslope transport, broad depth ranges may reflect the dispersal of foraminiferal propagules combined with a more or less isothermal water column. These factors could explain the genetic coherence of *Bathyallogromia weddellensis* between 1100 and 6300 m depth (Gooday *et al.* 2004).

5. Zoogeography

Many common Antarctic foraminiferal species are known from other parts of the World Ocean. Bathyal and abyssal regions, in particular, are inhabited by typical deep-sea forms. Murray (1991) recognised a series of SO deep-water associations dominated by cosmopolitan species such as *Cyclammina pusilla, Epistominella exigua, Nuttallides umboniferus* and *Globocassidulina subglobosa*. Cornelius & Gooday (2004) estimate that ~2/3 of the calcareous species in deep Weddell Sea samples also occurred at the Porcupine Abyssal Plain. To the south of the Antarctic convergence Gooday *et al.* (2007) recognised ~40 species of Komokiacea and similar forms, 61% of which are also reported in the North Atlantic. Recent molecular studies suggest that some calcareous species found in the deep SO are genetically coherent across a geographical range spanning several oceans (Pawlowski *et al.* 2007b, Lecroq *et al.* 2009). The few foraminiferal species that may be endemic to the Antarctic deep sea include *Haplophragmoides umbilicatum*, reported from the abyssal Weddell Sea (Pearcey 1914) depths down to 5000 m west of the Antarctic Peninsula (Theyer 1971) and shallower sites in the Ross Sea (Kennett 1968).

The extent of endemism in coastal and shelf settings around Antarctica is difficult to assess. According to Ward *et al.* (1987), 23% of species from McMurdo Sound (79–856 m water depth) also occurred at Arctic sites. Schröder *et al.* (1989) report that 17 out of 58 agglutinated species are shared between Prydz Bay (Antarctica, 410–987 m) and Lancaster Sound tand Baffin Bay (Canadian Arctic, 93–823 m). However, these wide ranges are based on test morphology and some could be artefacts of inaccurate identifications or cryptic speciation (Majewski 2010). An analysis of partial SSU rDNA sequences revealed that three monothalamous morphotypes from Antarctic (McMurdo Sound) and from Arctic and northern European sites were genetically distinct (3.8–5.9% divergence) (Pawlowski *et al.* 2008). Only bipolar populations of *Psammophaga magnetica* were sufficiently similar (divergence < 1%) to be considered conspecific, although even these differed by a few mutations suggesting either recent separation or an extremely slow mutation rate (Pawlowski & Majewski 2011). Similarly, Pawlowski *et al.* (2005) reported that ~50% of monothalamous phylotypes from a site under the Ross Ice Shelf (923 m depth) were unknown at other high latitude localities (McMurdo Sound, Weddell Sea, Arctic Ocean) from which molecular data are available.

In an important contribution, Mikhalevich (2004) drew attention to Antarctic species described by Russian authors (notably Saidova 1975) that have been assigned in non-Russian literature to species that are widely reported from other oceans (Table 1). A recent molecular study has confirmed the validity of one of Saidova's species, *Cibibides antarcticus,* usually identified as *C. refulgens* (Schweitzer *et al.* in press). There are no convincing records of other prominent Antarctic species, such as *Astrammina rara, A. triangularis* and *Notodendrodes* spp., outside the SO. The more restricted distributions of continental shelf species compared to those in deeper water is illustrated by an analysis of Saidova's data (Table 2). Of the 1791 species listed in her monograph on Pacific Ocean foraminifera, 221 occur in Antarctic waters. Most (~77%) of those confined to the Antarctic (i.e. not occurring in the temperate or tropical Pacific in Saidova's material) are restricted to the shelf (<1000 m); 9 of the 13 species occurring in Antarctic and adjacent southern temperate regions have a similar depth distribution. In contrast, most (~79%) species with wide ranges extending from the Antarctic to parts of the Pacific beyond the southern temperate zone are confined to depths >1000 m.

DNA analyses suggest that benthic foraminifera living on the Antarctic shelf are genetically homogenous. Ribosomal DNA sequences are almost identical in populations of *Epistominella vitrea* from the Ross Sea (<30 m water depth) and the Weddell Sea (~1000 m) (Pawlowski *et al.* 2007a). Despite considerable morphological variability, all examined specimens of *G. biora* from Admiralty Bay had identical ITS rDNA sequences (Majewski & Pawlowski 2011). Twelve morphospecies from the Antarctic Peninsula (Admiralty Bay) and McMurdo Sound (New Harbor) exhibit the same lack of genetic differentiation, suggesting pan-Antarctic gene flow among shelf foraminifera (unpublished data). Earland (1934) already pointed to the circum-Antarctic distribution of some species and Mikhalevich (2004) concluded that most species living on the Antarctic shelf display this pattern. However, there are some apparent exceptions, notably the genus *Notodendrodes,* which is apparently endemic to the Ross Sea. The type species, *N. antarctikos,* was described from Explorers

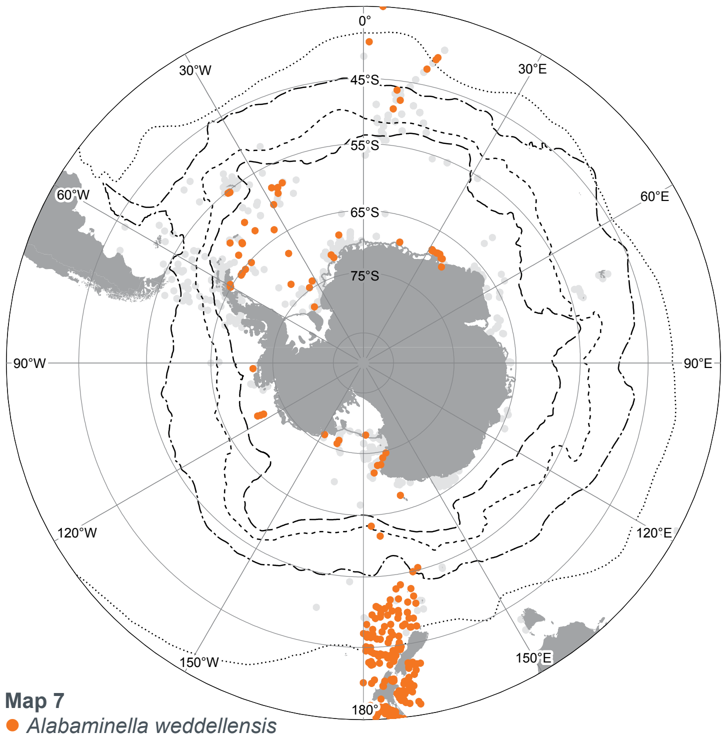
Table 1 Possibly endemic Antarctic species described in Russian literature but often assigned to well-known cosmopolitan species; based on data in Mikhalevich (2004)

Revised name	Commonly used name(s) in non-Russian literature	Non-Russian records
Rhabdammina antarctica **Saidova, 1975**	*R. abyssorum* M. Sars, 1869	8
Saccammina basisopiculata **Mikhalevich, Pronina, & Nestell, 2000**	*S. sphaerica* Brady, 1871	1, 3, 7, 8, 10
Hormosinella distans antarctica **Saidova, 1975**	*Reophax distans* Brady, 1881	1, 3, 5, 6, 10
Pauciloculata antarctica **(Saidova, 1975)**	*Alveophragmium jeffreysii* (Williamson, 1858), *Cribrostomoides jeffreysii* (Williamson, 1858), *Haplophragmoides canariensis* (d'Orbigny, 1839)	2, 3, 5-10
Cribrostomoides antarcticus **Saidova, 1975**	*C. subglobosa* (G.O. Sars, 1872)	4, 8, 10
Cyclammina orbicularis asellina **Rhumbler, 1931**	*Cyclammina orbicularis* Brady, 1881	2-5,10
Cyclammina pusilla antarctica **Saidova, 1975**	*Cyclammina pusilla* Brady, 1884	1, 3, 4, 5, 10
Conicotrochammina antarctica **Saidova, 1975**	*Trochammina antarctica* Earland, 1934	4, 5, 8
Planispirinoides antarcticus **Saidova, 1975**	*Planispirinoides bucculentus* Brady, 1884	2, 4, 8
Cibicides antarcticus **(Saidova, 1975)**	*Cibicides refulgens* (Montfort, 1808); *C. lobatulus* (Walker & Jacob, 1798)	2, 5-7, 10

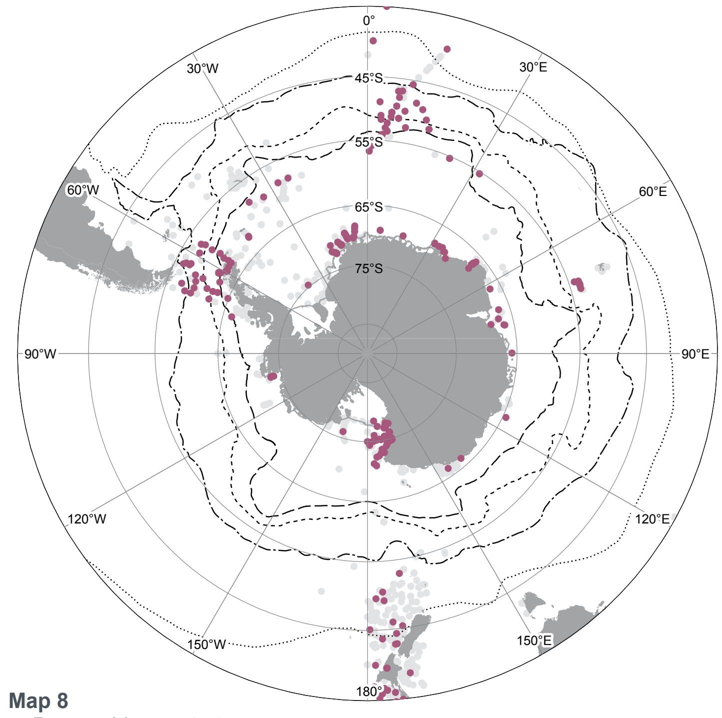
1 = Wiesner (1931), 2 = Uchio (1960), 3 = Kennett (1968), 4 = Fillon (1974), 5 = Anderson (1975), 6 = Osterman & Kellog (1979), 7 = Finger & Lipps (1981), 8 = Milam & Anderson (1981), 9 = Bernhard (1987), 10 = Mackensen *et al.* (1990)

Table 2 Bathymetric distribution of foraminiferal species in Antarctic waters. Species are divided into those that occur 1) only around Antarctica; 2) around Antarctica and in the adjacent south temperate zone; 3) around Antarctica and in the tropical and/or north temperate zones. Based on data in Saidova (1975, Tables 1-11)

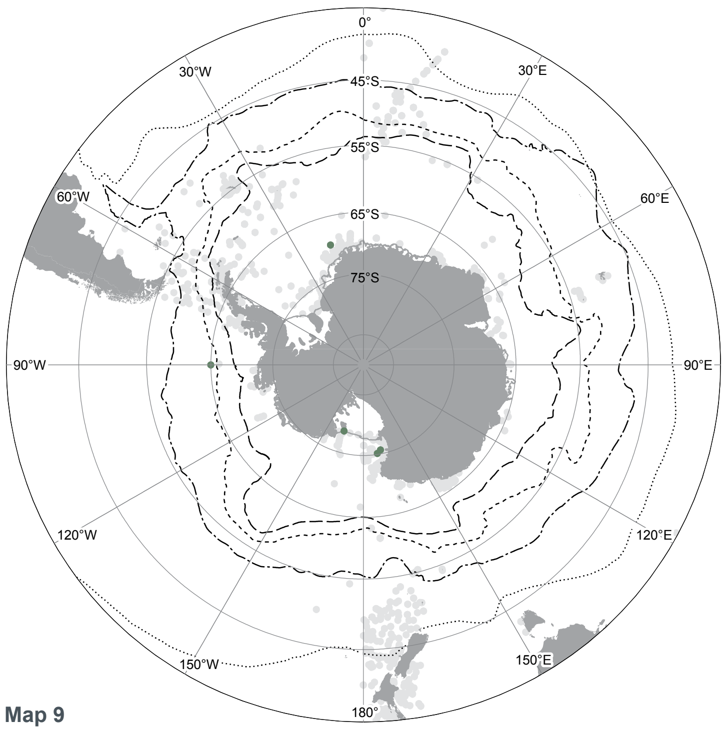
Depth zone	Antarctic only		Antarctic + S. temperate		Antarctic + one or more other zones (except S. temperate)	
	N	%	N	%	N	%
<1000 m	79	76.7	9	69.2	7	6.8
<1000 to >1000 m	12	11.7	4	30.8	15	14.3
>1000 m	12	11.7	0	0	83	79.0
TOTAL species	**103**		**13**		**105**	



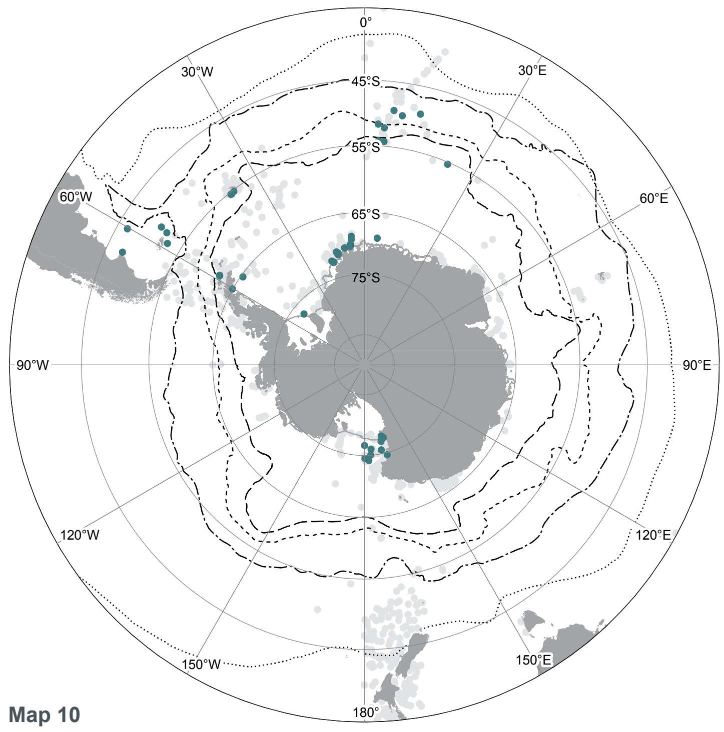
Map 7
● *Alabaminella weddellensis*
● All records of benthic Foraminifera



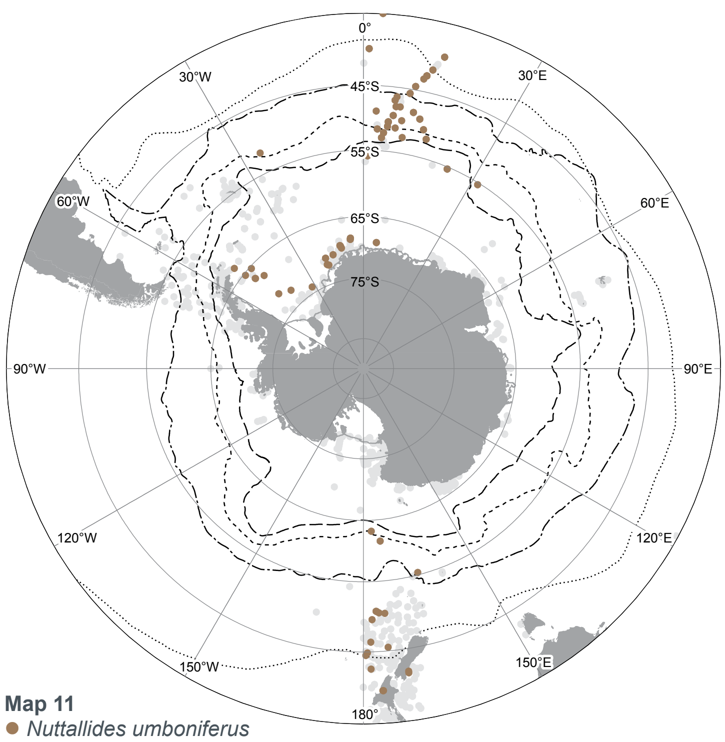
Map 8
● *Recurvoides contortus*
● All records of benthic Foraminifera



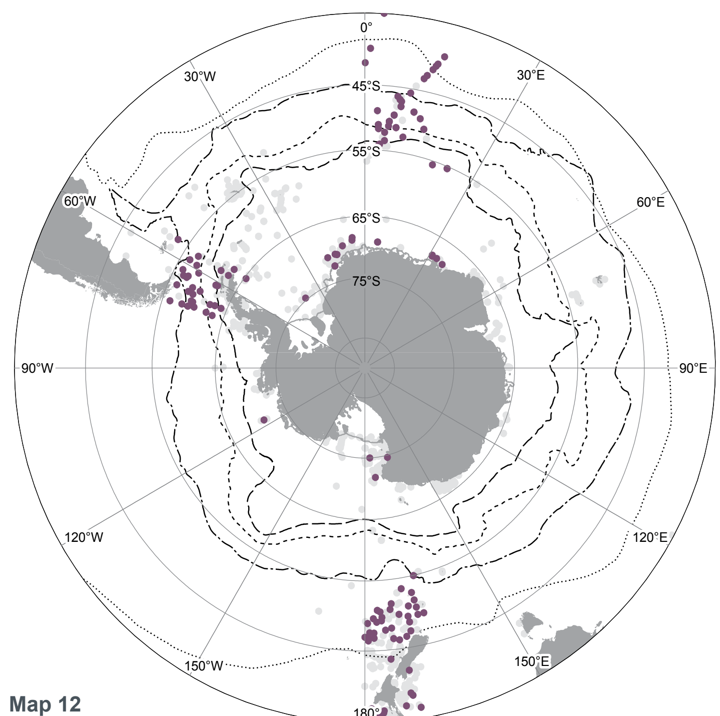
Map 9
● *Haplophragmoides umbilicatum*
● All records of benthic Foraminifera



Map 10
● *Nonionella iridea*
● All records of benthic Foraminifera



Map 11
● *Nuttallides umboniferus*
● All records of benthic Foraminifera



Map 12
● *Pyrgo murrhina*
● All records of benthic Foraminifera

Foraminifera Maps 7–12 Map 7. *Alabaminella weddellensis* Earland, 1936 (Wide depth range from which thisessentially abyssal species is reported suggest that some records are misidentifications). Map 8. *Recurvoides contortus* Earland, 1934. Map 9. *Haplophragmoides umbilicatum* Pearcey, 1914. Map 10. *Nonionella iridea* Heron-Allen & Earland, 1932. Map 11. *Nuttallides umboniferus* (Cushman, 1933). Map 12. *Pyrgo murrhina* Schwager, 1866. ▶ (See also section 'Notes on mapped species')

Cove on the west side of McMurdo Sound (DeLaca *et al.* 1980), and has not been reliably reported outside this coastal setting (Habura *et al.* in press). The other species, *N. hyalinosphaira,* occurs in Explorers Cove and elsewhere in McMurdo Sound (DeLaca *et al.* 2002) and in much deeper water under the Ross Ice Shelf (Pawlowski *et al.* 2005).

6. Factors and processes influencing geographic distribution

The complex patterns of bathymetry, sediment types, water mass characteristics, sea-ice cover and surface productivity around Antarctica make it difficult to untangle the factors underlying the geographical distribution of foraminiferal species. Biogeographic patterns probably reflect multiple inter-related drivers. As in other oceanic areas (Gooday *et al.* 2012), the organic matter flux to the seafloor seems to strongly influence the abundance and distribution of foraminiferal species, particularly in deep water (e.g. Asioli 1995, Mackensen *et al.* 1995). However, the fact that Antarctic shelf faunas are often either predominately calcareous or predominately agglutinated, suggests that carbonate dissolution at fairly shallow depths is often an overriding factor (Saidova 1998, Mikhalevich 2004). This separation has been recognised in the Ross Sea (Kennett 1968, Ward *et al.* 1987), Lützow-Holm Bay (Igarashi *et al.* 2001), the Weddell Sea (Anderson 1975, Mackensen *et al.* 1990), the southern and eastern Scotia Ridge (Echols 1971) and the George V – Adélie shelf (Milam & Anderson 1981). In the Ross Sea, a shallow CCD, linked to ice cover, very low temperatures and very high salinities, is considered responsible for confining calcareous assemblages to depths <400 m, with mixed calcareous/agglutinated assemblages at 400-650 m and agglutinated assemblages below 650 m (Kennett 1968). A similar depth-related separation exists between calcareous and agglutinated assemblages in McMurdo Sound (Ward *et al.* 1987). Dissolution boundaries appear to be related to water masses and ice cover in the Ross and Weddell Seas (Anderson 1975, Osterman & Kellogg 1979, Milam & Anderson 1981). For example, shallow calcareous assemblages are associated with Fresh Shelf Water in the eastern Weddell Sea (Anderson 1975). However, some of the same dissolution-resistant species are associated with Saline Shelf Water on the George V – Adélie margin, indicating that calcareous species are not entirely controlled by watermass properties (Milam & Anderson 1981). On the Bellingshausen margin of the Antarctic Peninsula, Ishman & Domack (1994) recognised two distinct species groupings, one predominantly agglutinated and the other predominantly calcareous, that are associated with Circumpolar Deep Water and Weddell Sea Transitional Water, respectively, and are not closely related to the CCD or to the organic carbon content of the sediment. Similarly, the boundary between agglutinated and calcareous faunas is not related to the CCD in Prydz Bay (Quilty 1985).

Sandy to gravelly sediments often predominate in shallow coastal settings and on topographic highs, with muddy sediments in deeper water (Kennett 1968, Echols 1971). The relationship between sediment types and foraminiferal assemblages around Antarctica is somewhat ambiguous. In the Ross Sea, Kennett (1968) found no link between faunal trends and sediment types, or in most cases with bottom-water characteristics (salinity and temperature). On the Adélie-George V continental shelf and slope, however, Milam & Anderson (1981) report a close association between faunal distributions and sediment types, calcareous species dominating in areas of sand or muddy sand on topographic highs with agglutinated species dominating in organic-rich siliceous muds and oozes in shelf basins and depressions. These sediment types reflect different hydrodynamic regimes, the sandy sediments being linked to moderate to intense currents and the muddy sediments to sluggish currents. An assemblage dominated by *Trifarina angulosa* is associated with strong bottom currents and sandy sediments around the shelf break in the eastern Weddell Sea (Mackensen *et al.* 1990). A comparable assemblage is present in the western Ross Sea (Ascoli 1995). In the deep (>2000 m water depth) Scotia Sea, some foraminiferal species are largely restricted to diatomaceous sediments while others are found only in sediments without diatoms (Echols 1971).

Salinity and suspended sediment load may influence foraminiferal assemblages in coastal settings (particularly fjords) impacted by glacial meltwater (Majewski 2005, Rodrigues *et al.* 2010). The elphidiid *Cribroelphidium webbi* is confined to the inner parts of fjords in close proximity to retreating tidewater glaciers (Majewski & Tatur 2009). Like its Arctic counterparts, this species appears to flourish in these muddy, brackish-water settings with high sedimentation rates. Another factor in near-shore and intertidal settings is ice abrasion, which often limits the occurrence of foraminifera. On the other hand, these environments are also very heterogeneous, with rocks and algae providing habitats for many different foraminiferal species (Lipps & DeLaca 1980). In deeper water, dropstones provide an important substrate for sessile species.

7. Taxonomic issues

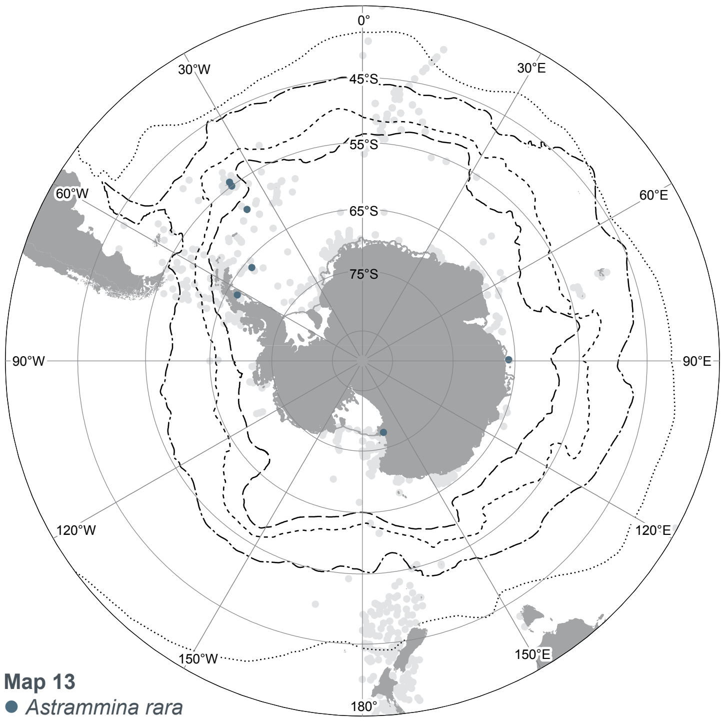
The abundance of foraminifera in marine environments and their importance in geological studies has generated a vast taxonomic literature, referring mainly to the 'hard-shelled' taxa. Publications on Antarctic foraminifera typically include lists of identified species. Some are well illustrated but others lack illustrations raising the possibility of misidentification. The names of some agglutinated species (e.g. in the genera *Reophax* and *Psammosphaera*) probably refer to species complexes rather than to single species. The very wide bathymetric ranges reported for others also make identifications questionable. For example, records for *Epistominella exigua* span a depth range from <30 m to >5000 m in Antarctic waters. At least some of the shallower records probably refer to a related species, *E. levicula* (Pawlowski *et al.* 2007). *Globocassidulina subglobosa* is another example of a calcareous taxon with a wide bathymetric range that probably encompasses several species. Molecular analyses are beginning to resolve some of these problems, but further studies of this kind are necessary.

8. Summary

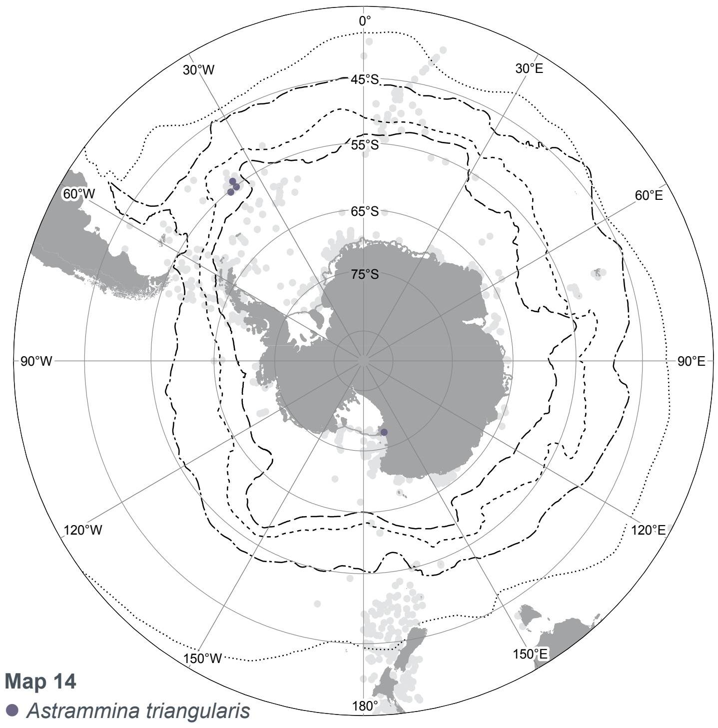
Numerous papers describe the distribution and diversity of benthic foraminifera around Antarctica, but our understanding of their zoogeography is often hampered by taxonomic issues. However, in general terms, deep-water assemblages (>1000 m water depth) include many species with wide distributions in other oceans, while coastal and shelf (<1000 m) assemblages include a higher proportion of endemic species, at least some of which appear to have circum-Antarctic distributions. These contrasting biogeographic patterns between shelf and deep-water species are supported by recent molecular genetic studies and are consistent with evidence from other regions of the world (Gooday & Jorissen 2012). Although many factors (e.g. sediment types, current flow, productivity) influence species distributions on regional scales, the occurrence of predominately calcareous and predominately agglutinated assemblages suggests that carbonate dissolution, linked to a multibathic carbonate compensation depth, is often an overriding factor.

Notes on mapped species

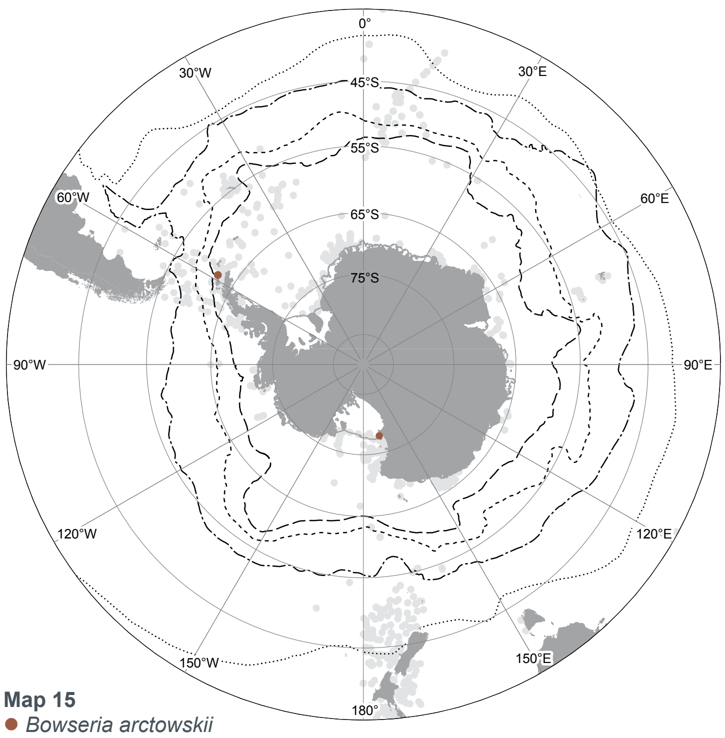
Map 5. *Cornuspiroides rotundus* Schmiedl & Mackensen, 1993 According tto Schmiedl & Mackensen (1993) *Cornuspiroides lacunosa* (Brady) of Wiesner (1931) belongs in this spectacularly large species. Based on the comments of Schmiedl & Mackensen (1993), we also include here C. *striolatus* (Brady, 1882) of Heron-Allen & Earland (1922) from McMurdo Sound and C. striolatus from the continental shelf adjacent to Prydz Bay (Parr 1950).— **Map 7. *Alabaminella weddellensis* Earland, 1936** Wide depth range from which this essentially abyssal species is reported suggest that some records are misidentifications. — **Map 13. *Astrammina rara* Wiesner, 1931** DeLaca (1986) and Loeblich & Tappan (1987) considered *Astrammina rara, Armorella sphaerica* Heron-Allen & Earland, 1932a and *Pelosphaera cornuta* Heron-Allen & Earland, 1932a to be synonyms. The type specimens of *P. cornuta* from South Georgia, in the Natural History Museum, London (NHML) closely resemble *A. rara* from Explorers Cove. However, 1) there are no molecular data from South Georgia to confirm the synonomy, 2) deposited DNA sequences from McMurdo Sound suggest the existence of two species, 3) Wiesner's (1931) illustrations of *A. rara* show two tests that lack obvious larger grains. These considerations suggest that our present concept of A. rara may encompass more than one species. We are not convinced that specimens illustrated by Majewski (2005) and Igarshi *et al*. (2001) belong to *Astrammina rara*. Records from non-Antarctic settings appear to be mis-identifications. *Armorella sphaerica* has a very thin, generally fine-grained wall with a 'smooth and rather shining surface' (Heron-Allen & Earland 1932a). Examination of the type material (NHML), also from South Georgia, confirms that it is distinct from *A. rara.* — **Map 16. *Hippocrepinella hirudinea* Heron-Allen & Earlatnd, 1932a** A well-defined morphospecies, but probably including a number of genetically distinct cryptic species (Pawlowski *et al.* 2008). — **Map 17. *Notodendrodes antarctikos* DeLaca, Lipps & Hessler, 1980** This species is currently known only from Explorers Cove. Based on her illustrated specimen, we regard the tentative record of Violanti (1996) from the deeper (163–1010 m) Ross Sea as dubious. **Maps 20–21. *Portatrochammina antarctica* (Parr, 1950)** Parr (1950) described two species, *Trochammina antarctica* and *T. wiesneri*. Later authors have regarded these as distinct species (e.g. Violanti 1996), subspecies (e.g. Brönnimann & Whittaker, 1988) or have not distingushed them (e.g. Majewski 2005). Following Brönnimann & Whittaker (1988), we regard them as subspecies and *P. eltaninae* as a synonym of *P. antarctica antarctica*. — **Map 20. *Portatrochammina antarctica antarctica* (Parr, 1950)** We include here *P. antarctica* s.l. of Murray & Pudsey (2004) and *P. antarctica* of Ascoli (1995) and Violanti (1996). Although Majewski (2005) did not differentiate the subspecies of *P. antarctica*, the specimen from Station 7 illustrated in his Fig. 15.1a-c resembles *P. antarctica antarctica*. — **Map 21. *Portatrochammina antarctica wiesneri* (Parr, 1950)** We include here the specimen illustrated in Fig. 15.4a-c of Majewski (2005). — **Map 22. *Pseudobolivina antarctica* Wiesner, 1931** = *Bolivina punctata* d'Orbigny var. *arenacea* Heron-Allen & Earland, 1922, *Pseudobolivina arenacea* (Heron-Allen & Earland) of Parr (1950), and *Textularia antarctica* (Wiesner) of Earland (1934) and some later authors. — **Map 23. *Textularia earlandi* Parker, 1952** = *T. tenuissima* Earland, 1933 (name preoccupied). Parker (1952) designated as types the specimens illustrated by Earland (1933) as *T. tenuissima*. Earland (1933) recognised a microsphaeric and two megalosphaeric forms, one much shorter and with fewer chambers than the other. The wide bathymetric range (23–4014 m) reported by Earland suggests that his *T. tenuissima* included more than one species. — **Map 24. *Textularia wiesneri* Earland, 1933** Violanti (1996) includes this species in her synonym of *T. earlandi*, although other authors have regarded them as distinct. In his original descripton, Earland (1933) notes that *T. wiesneri* is 'not very readily distinguishable, at least in the megalosphaeric form' from *T. earlandi* (as *T. tenuissima*), although they differ in the size of the proloculus and the absence of a coiled initial part. Some confusion between these two similar species is therefore possible.— **Map 26. *Cibicides antarcticus* (Saidova, 1975)** This species, described by Saidova (1975) as *Lobatula antarcticus*, has commonly been referred to as *Cibicides refulgens* (Mikhalevich 2004; Schweitzer *et al*., in press). Alexander & DeLaca (1987) provide a detailed account of its biology and occurrence on McMurdo Sound. — **Map 27. *Globocassidulina biora* Voloshinova, 1960** Confusion surrounds the complex of species comprising *G. biora, G. crassa, G. rossensis* (sometimes regarded as a subspecies of *G. crassa*) and *G. subglobosa*, which are distinguished by apertural characteristics. Violanti (1995) regarded them as distinct species. Finger & Lipps (1981) placed *G. crassa* rossensis and *G. biora* within a '*G. crassa* plexus'. Quilty (1984, 2004) interprets *G. crassa* to include 'all variants of *Globocassidulina*'. Ward & Webb (1986) noted an apparent gradation in apertural characteristics between *G. biora* and *G. crassa*; they placed all their morphotypes in *G. crassa*. According to Mikhalevich (2004), *Anticleina* (=*Globocassidulina*) *biora* includes *Cassidulina crassa*, *C. subglobosa, Globocassidulina crassa rossensis and G. biora* of various authors, although she considers the original *G. crassa* to be a distinct species. Nomura (1984) described considerable ontogenetic variation in the aperture of *G. biora*. Based on the presence of an L-shaped aperture during their development, he concluded that *G. biora* and *G. crassa rossensis* are closely related, although distinct as adults. Mackensen et al. (1993) found *G. crassa* difficult to distinguish from *G. crassa rossensis* in deep-water samples. Majewski & Pawlowski (2010) conducted a detailed morphological and molecular analysis of material from Admiralty Bay. They recognised four morphological variants that were genetically homogeneous and represented a single species, *G biora.* They conclude that 1) this is the only large, common representative of *Globocassidulina*



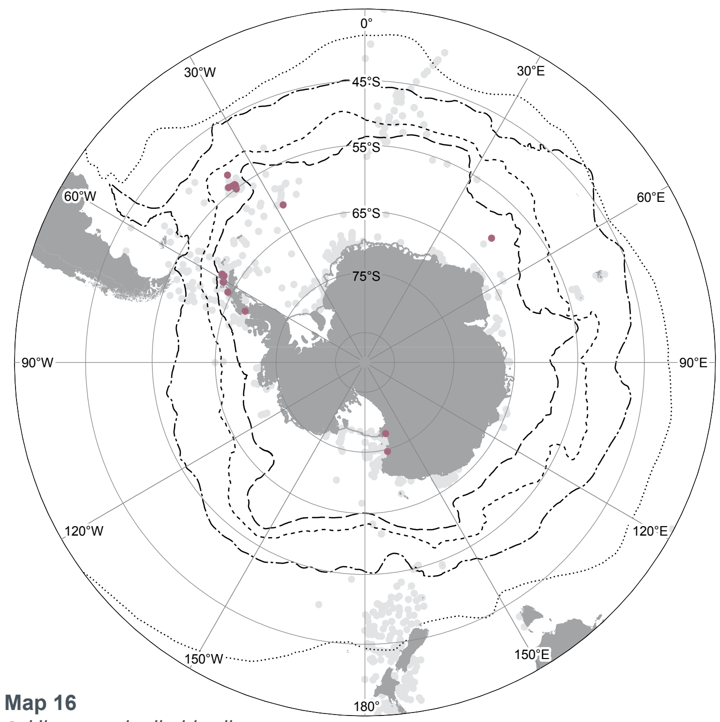
Map 13
● *Astrammina rara*
● All records of benthic Foraminifera



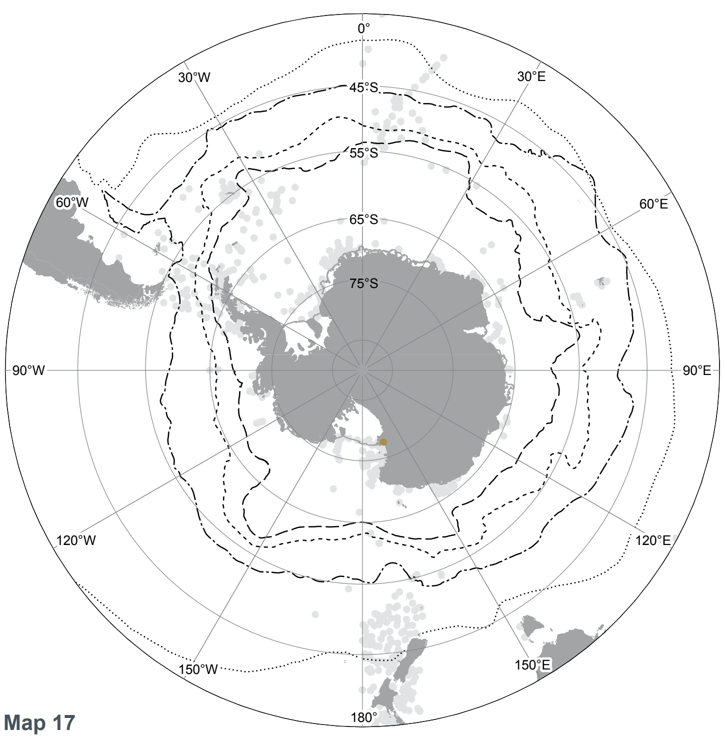
Map 14
● *Astrammina triangularis*
● All records of benthic Foraminifera



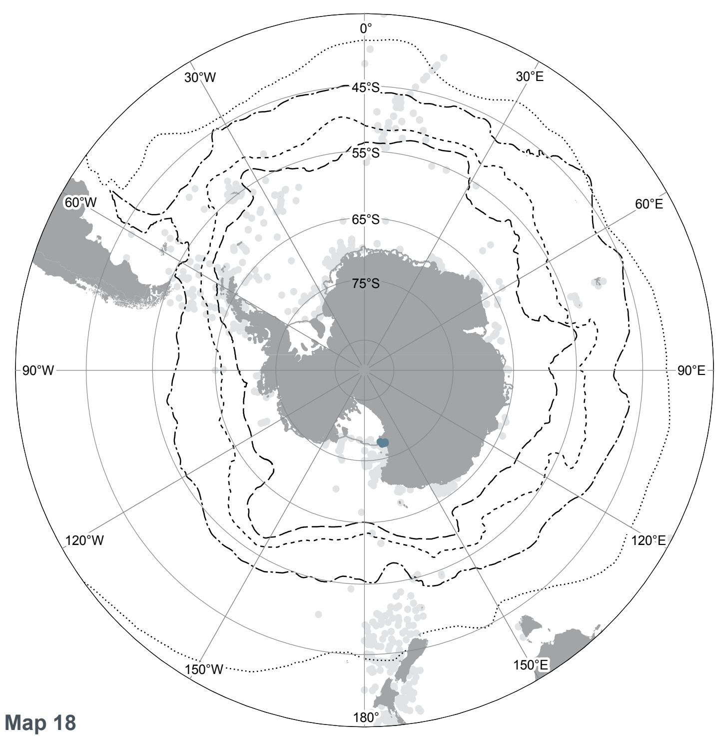
Map 15
● *Bowseria arctowskii*
● All records of benthic Foraminifera



Map 16
● *Hippocrepinella hirudinea*
● All records of benthic Foraminifera

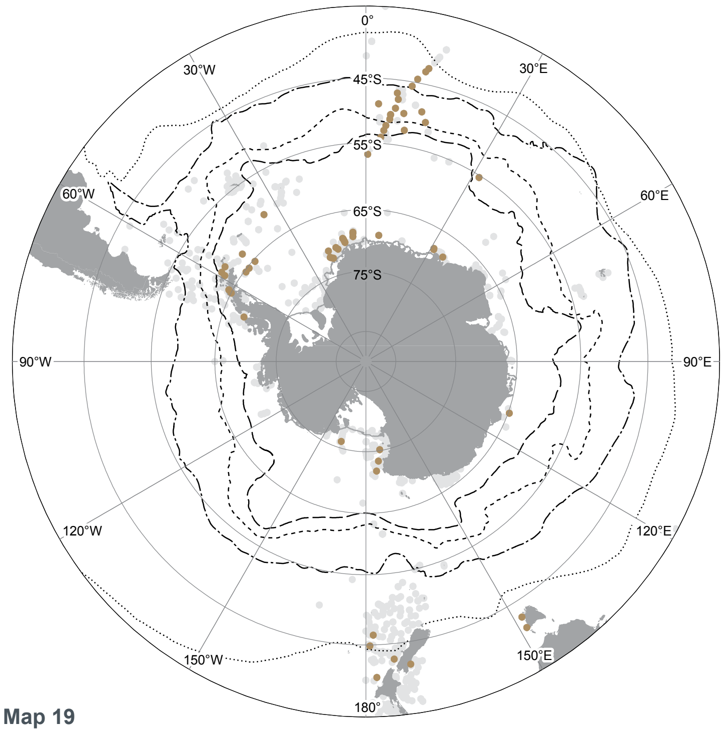


Map 17
● *Notodendrodes antarctikos*
● All records of benthic Foraminifera

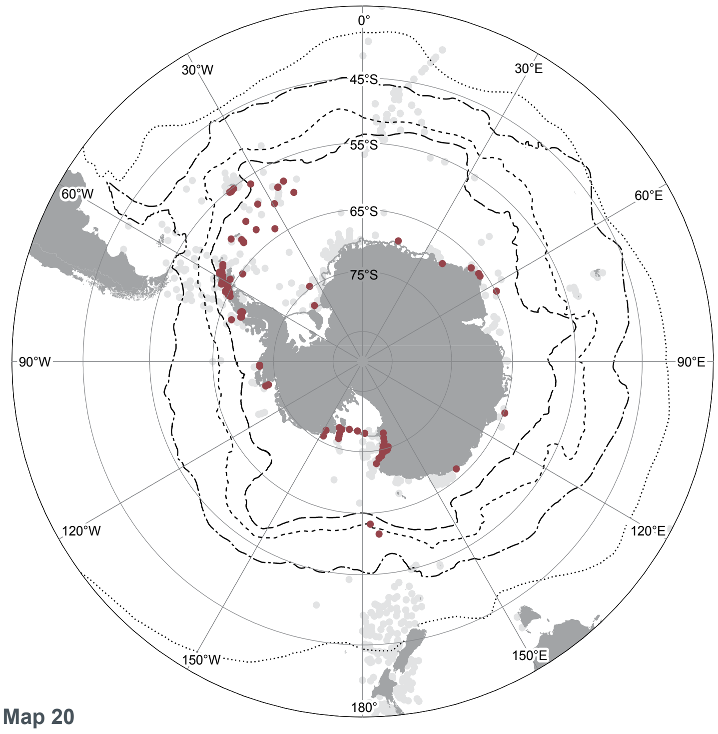


Map 18
● *Notodendrodes hyalinosphaira*
● All records of benthic Foraminifera

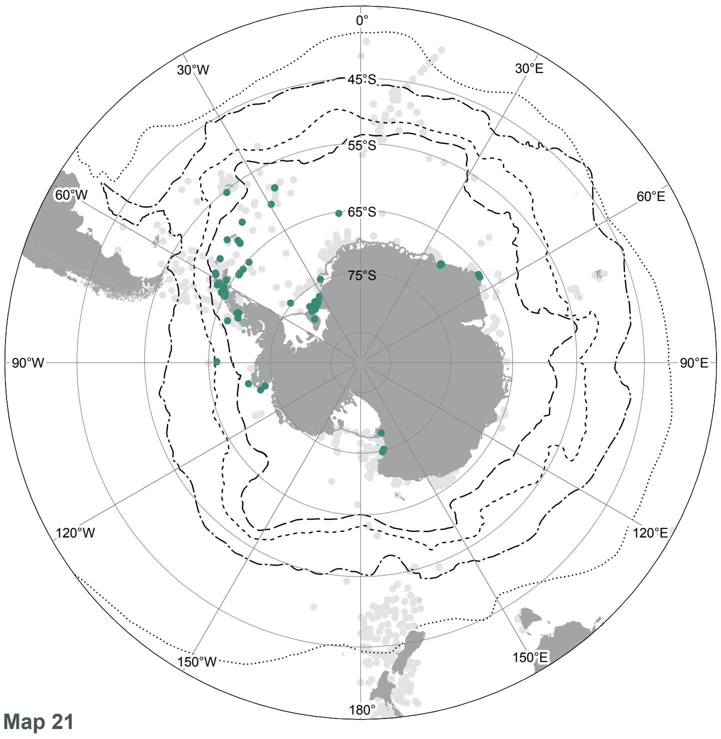
Foraminifera Maps 13–18 Map 13. *Astrammina rara* Wiesner, 1931. Map 14. *Astrammina triangularis* (Earland, 1933). Map 15. *Bowseria arctowskii* Sinniger, Lecroq, Majewski & Pawlowski, 2008. Map 16. *Hippocrepinella hirudinea* Heron-Allen & Earland, 1932a. Map 17. *Notodendrodes antarctikos* DeLaca, Lipps & Hessler, 1980. Map 18. *Notodendrodes hyalinosphaira* DeLaca, Bernhard, Reilly & Bowser, 2002. ▶ (See also section 'Notes on mapped species')



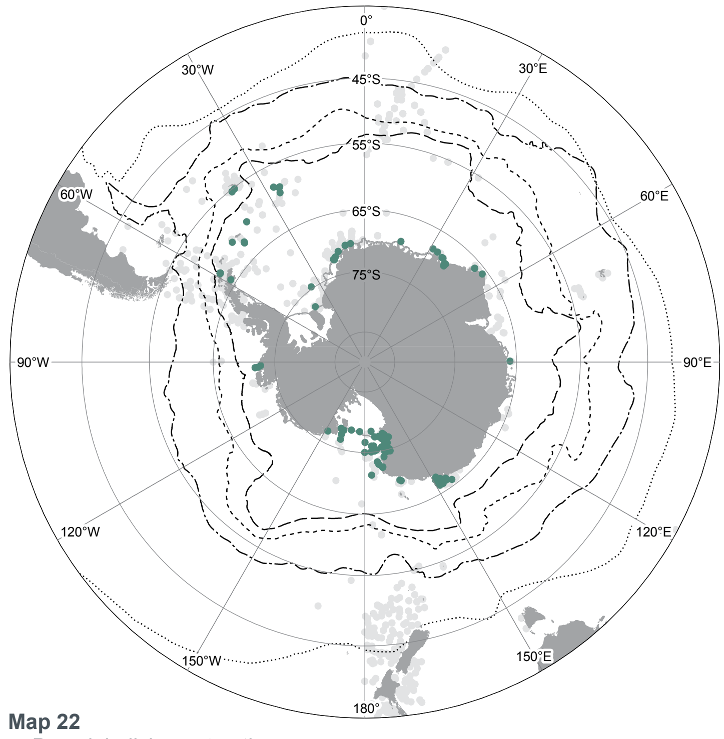
Map 19
● *Ammomarginulina ensis*
● All records of benthic Foraminifera



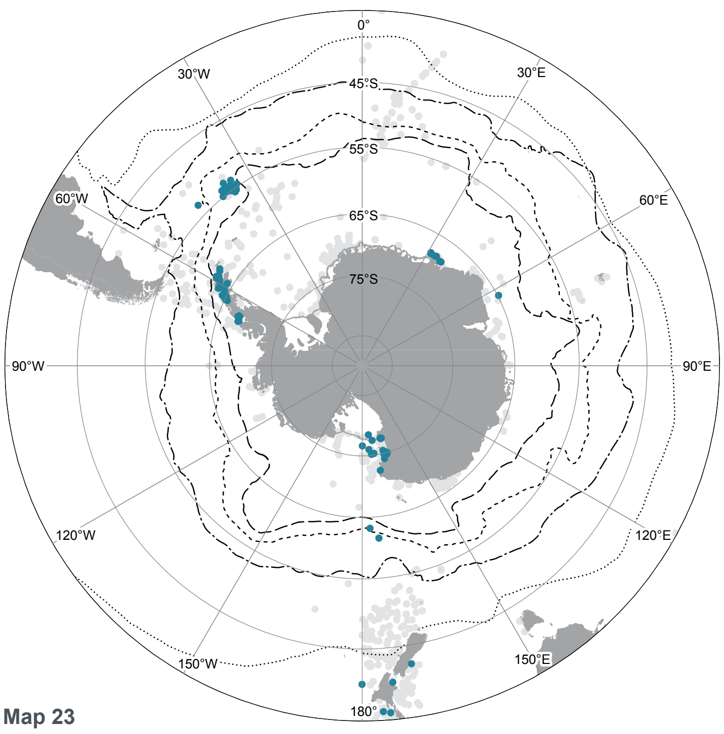
Map 20
● *Portatrochammina antarctica antarctica*
● All records of benthic Foraminifera



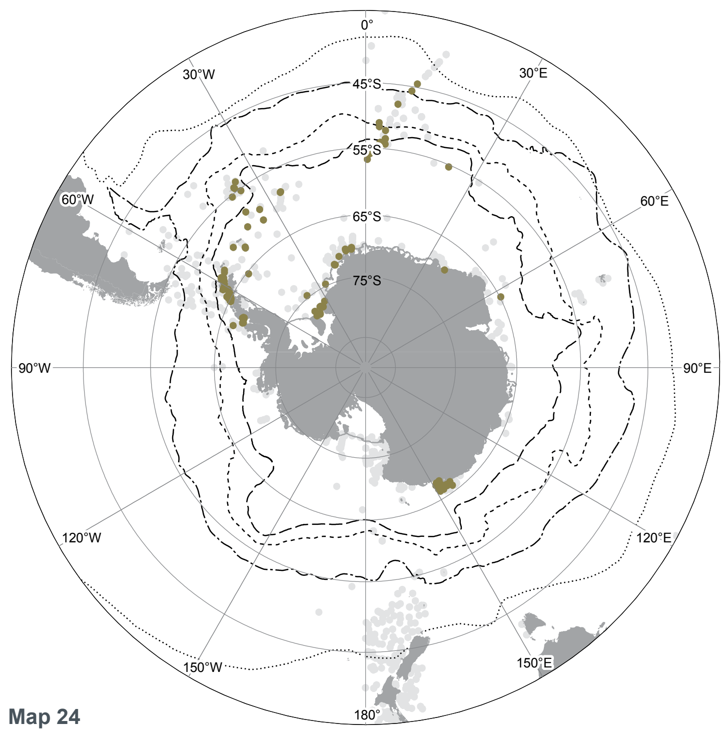
Map 21
● *Portatrochammina antarctica wiesneri*
● All records of benthic Foraminifera



Map 22
● *Pseudobolivina antarctica*
● All records of benthic Foraminifera

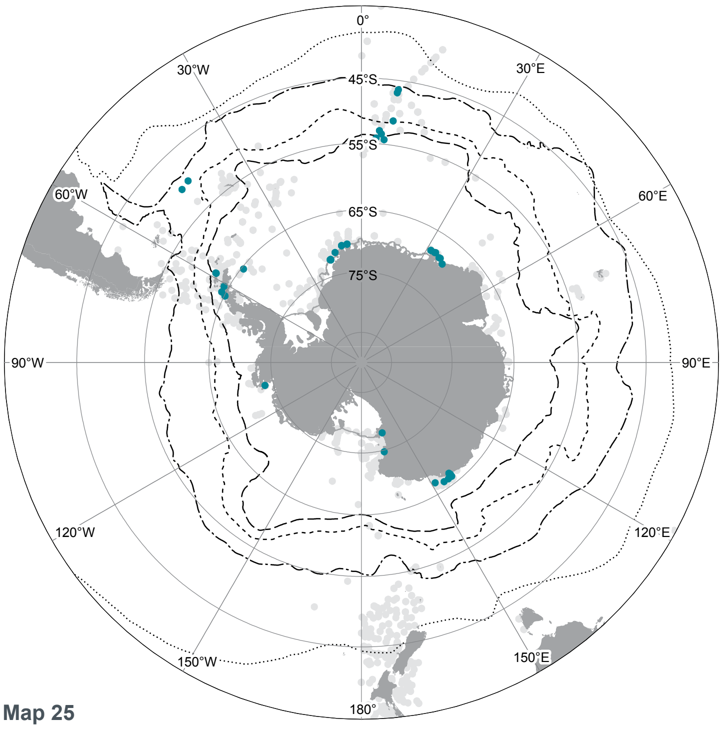


Map 23
● *Textularia earlandi*
● All records of benthic Foraminifera

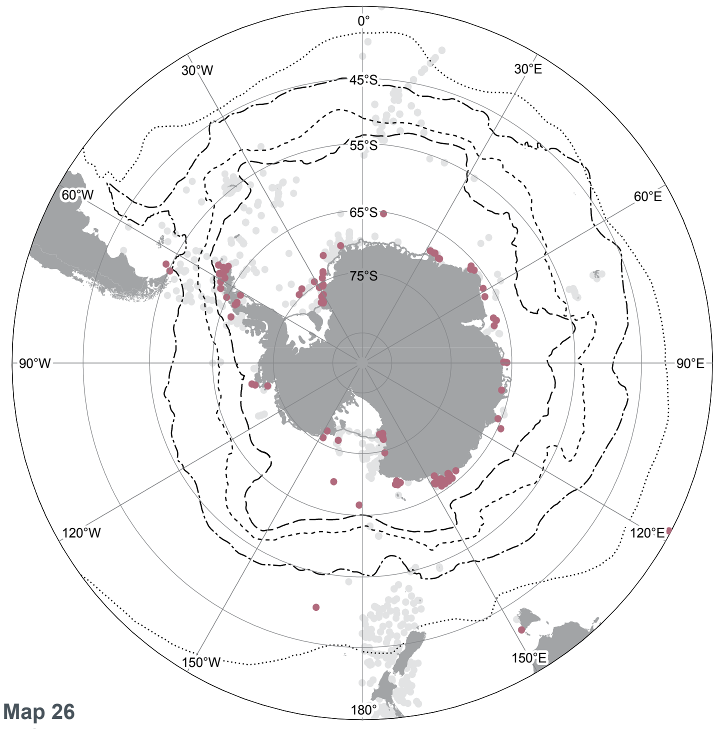


Map 24
● *Textularia wiesneri*
● All records of benthic Foraminifera

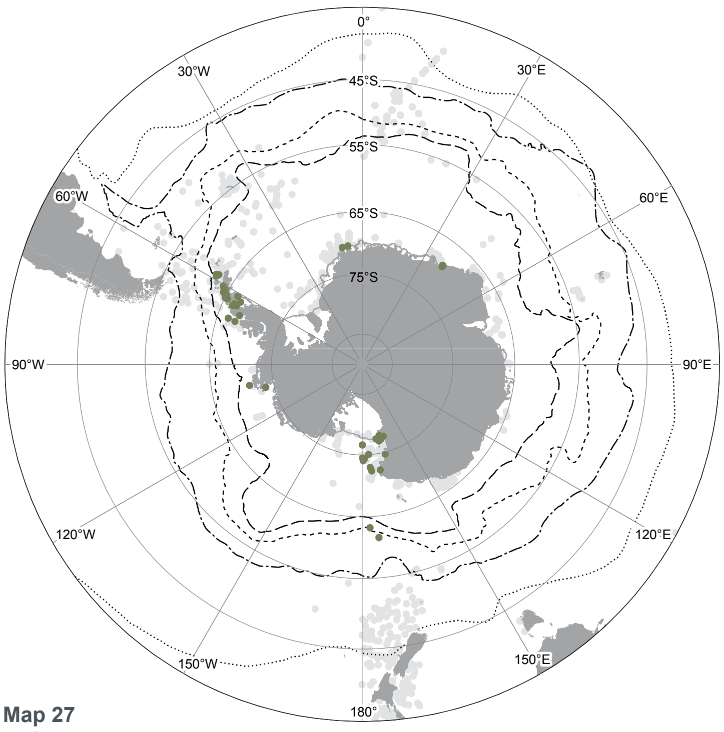
Foraminifera Maps 19–24 Map 19. *Ammomarginulina ensis* Wiesner, 1931. Map 20. *Portatrochammina antarctica antarctica* (Parr, 1950). Map 21. *Portatrochammina antarctica wiesneri* (Parr, 1950). Map 22. *Pseudobolivina antarctica* Wiesner, 1931. Map 23. *Textularia earlandi* Parr, 1952. Map 24. *Textularia wiesneri* Parr, 1950. ▶ (See also section 'Notes on mapped species')



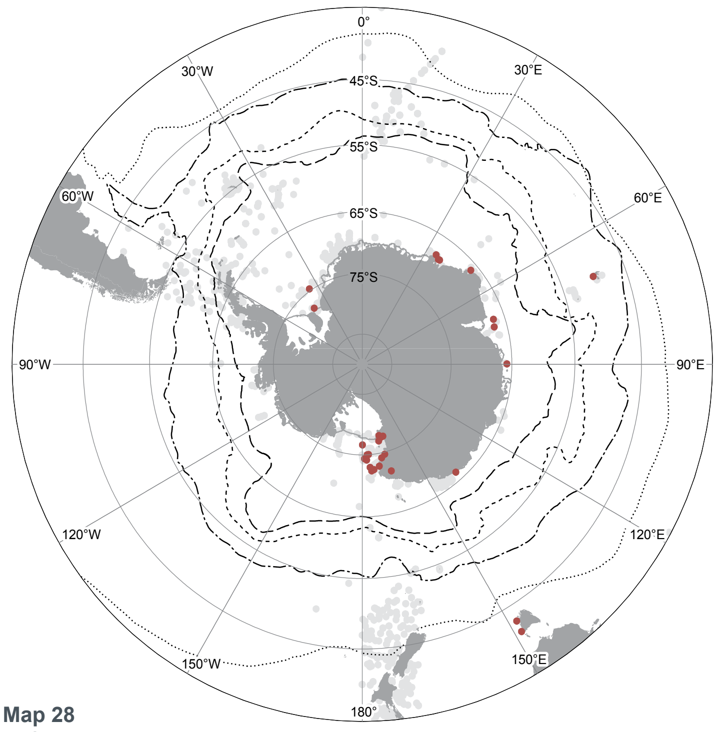
Map 25
● *Astrononion antarcticus*
● All records of benthic Foraminifera



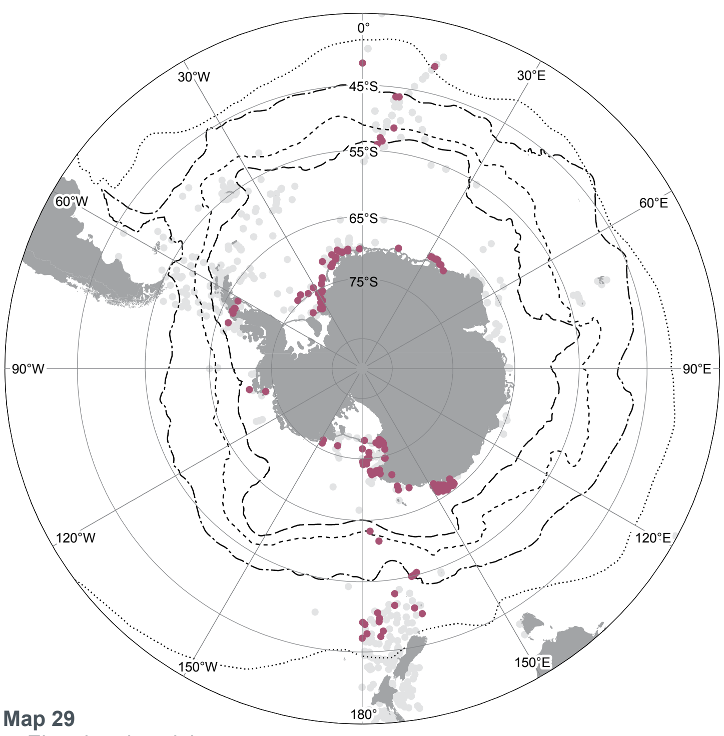
Map 26
● *Cibicides antarcticus*
● All records of benthic Foraminifera



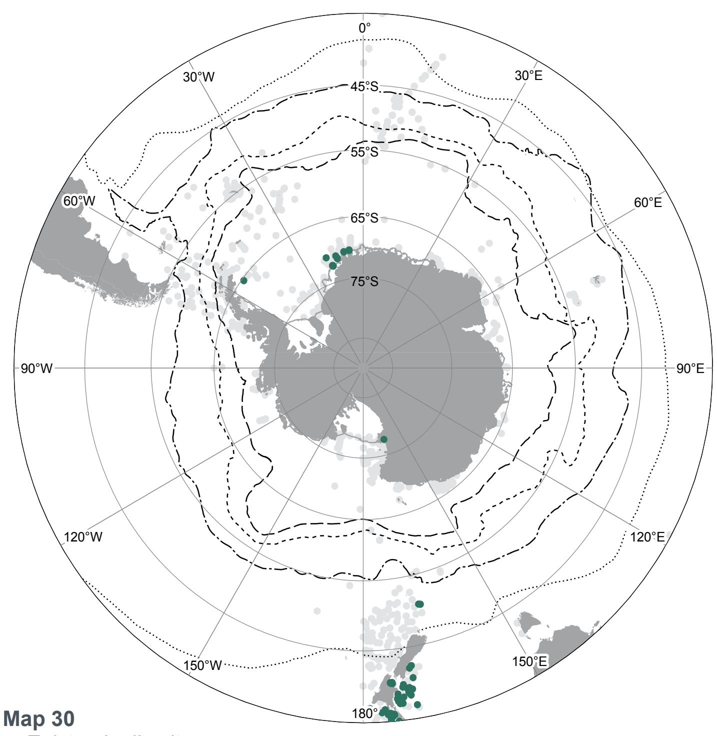
Map 27
● *Globocassidulina biora*
● All records of benthic Foraminifera



Map 28
● *Glandulina antarctica*
● All records of benthic Foraminifera



Map 29
● *Ehrenbergina glabra*
● All records of benthic Foraminifera



Map 30
● *Epistominella vitrea*
● All records of benthic Foraminifera

Foraminifera Maps 25–30 Map 25. *Astrononion antarcticus* Parr, 1950. Map 26. *Cibicides antarcticus* (Saidova, 1975). Map 27. *Globocassidulina biora* Voloshinova, 1960. Map 28. *Glandulina antarctica* Parr, 1950. Map 29. *Ehrenbergina glabra* Heron-Allen & Earland, 1922. Map 30. *Epistominella vitrea* Parker, 1953.
▶ (See also section 'Notes on mapped species')

in shallow-water Antarctic settings, 2) it is widely distributed around the continent and genetically distinct from *G. subglobosa*, which is much smaller and occurs in deeper water, and 3) *G. crassa* is probably restricted to regions north of the Polar Front. Here, we include only records for *C. biora*. — **Map 30. *Epistominella vitrea* Parker, 1953** This is essentially a slope species. Abyssal records may refer to *E. exigua*.

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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.

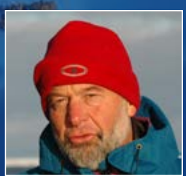
The Census of Antarctic Marine Life (CAML)

CAML (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, integrated into 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), under the aegis of SCAR (Scientific Committee on Antarctic Research, www.scar.org). SCAR-MarBIN established a comprehensive register of Antarctic marine species and, with 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



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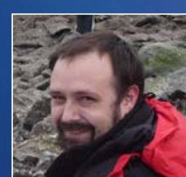

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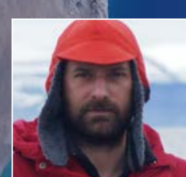

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