**PERSPECTIVES**

**Key stages in the evolution of the Antarctic marine fauna**

J. Alistair Crame1

1 British Antarctic Survey, High Cross, Madingley Road, Cambridge CB3 0ET, UK

E mail: jacr@bas.ac.uk

Running head: Evolution of the Antarctic marine fauna

Word count (main text): 4511

Word count total (including Abstract and References): 7537

[1 figure]

**ABSTRACT**

We are beginning to appreciate that the origin of the modern Antarctic marine fauna is related to a series of key events throughout the Cenozoic era. In the first of these, the mass extinction at the Cretaceous - Paleogene boundary (66 Ma) reset the evolutionary stage and led to a major radiation of modern taxa in the benthic realm. Although this took place in a greenhouse world, there is evidence to suggest that the radiation was tempered by the seasonality of primary productivity, and this may be a time-invariant feature of the polar regions. Whereas there could well have been a single, abrupt extinction event at *c.*34 Ma, there is also evidence to suggest a phased extinction of various taxa over a period of millions of years. Important new molecular phylogenetic data are indicating that a wide variety of both benthic and pelagic taxa radiated shortly after a second major phase of cooling at *c.*14 Ma. Such a phenomenon is linked to a series of major palaeoceanographic changes which in turn led to a proliferation of diatom-based ecosystems. Whereas the modern benthic marine fauna can be traced back some 45 – 50 m.y., a substantial component of the modern pelagic one may be less than 14 m.y. old. The latter is also characterised by assemblages of high abundance but comparatively low species richness and evenness. A distinctive signature of low diversity but high dominance within Antarctic marine assemblages was maintained by the interplay between temperature and primary productivity throughout the Cenozoic.

**Keywords: Antarctic marine fauna; Cenozoic evolutionary history; mass extinctions; evolutionary radiations; global cooling; seasonality; primary productivity**

**INTRODUCTION**

A widespread view of the Antarctic marine fauna is that it has been formed by progressive isolation and cooling through much of the Cenozoic era, and especially the last 34 Myr (Norris *et al.*, 2013). With the gradual physical separation of the continent from both southernmost South America and Australia, and progressive development of the Antarctic Circumpolar Current system (ACC), the fauna became very largely separated from that of the rest of the world ocean and characterised by extremely high levels of endemism (Dell, 1972; Dayton, 1990; Arntz *et al.*, 1997). This in turn would appear to have been the product of exceptionally low levels of immigration and emigration, coupled with low rates of net evolutionary origination (i.e. speciation minus extinction). The Southern Ocean has often been portrayed as an evolutionary sink or refuge (Vermeij, 1987; Goldberg *et al*., 2005; Jablonski *et al*., 2006).

Nevertheless, recent analysis of extensive, regional databases strongly suggests that levels of endemism within many key Antarctic marine groups are significantly lower than previously indicated. For many groups the figure is much closer to 50% than the 70-90% that has often been quoted in the past (Griffiths *et al*., 2009). Investigation at both species and genus levels shows that groups such as the bivalves, gastropods, bryozoans and echinoderms do have connections with other Southern Hemisphere mid- to high-latitude localities in South Africa, Tasmania, New Zealand, and Patagonia (Griffiths *et al.* 2009; Pierrat *et al*., 2013; Saucede *et al*., 2013; Moon *et al*., 2017). In addition, it is apparent that a number of marine taxa, far from dwindling to extinction, actually radiated in the Southern Ocean through the greater part of the Cenozoic era. Recent developments in the fields of geology, palaeontology and molecular phylogenetics are pointing to a more dynamic evolutionary history of the Antarctic marine fauna than previously thought.

**AN OUTLINE OF THE KEY STAGES**

1. **Pre-Cenozoic roots**

There is a strong impression that at least some elements of the modern Antarctic marine fauna can be traced back to the Late Mesozoic era (i.e. an age of origin greater than 66 Ma), and perhaps much further than that. This is true of certain molluscan taxa such as the gastropod *Perissodonta*, and the bivalves *Leionucula*, *Limopsis, Limatula, Astarte and Thracia*, as judged from the fossil record of Antarctica and the high southern latitudes (Zinsmeister & Camacho, 1980; Whittle *et al*., 2011; Crame *et al*., 2014). Indeed, *Astarte* has an Early Mesozoic record elsewhere, and *Thracia* can be traced back to the Late Palaeozoic (Crame *et al*., 2014). Certain other major groups, such as the asellote isopods, hexactinellid sponges, pycnogonids and gorgonian octocorals, may have either Early Mesozoic or Late Palaeozoic origins (Wilson, 1998; Gili *et al*., 2006; Lins *et al*., 2012; Taylor & Rogers, 2015). However, the problem with these and many other Antarctic marine taxa is that they have very imperfect fossil records. We know that the continent reached a mid- to high-latitude position within the Southern Hemisphere in the late Middle Devonian (*c*. 385 Myr ago) (Crame, 1994) but quite when these long-ranging taxa reached a similar position is unknown. The Devonian – Triassic marine fossil record of Antarctica is very incomplete (Crame, 1994), and at present we can only say with certainty that a small proportion of modern Antarctic genera have pre-Cenozoic roots in the southern high latitudes.

1. **Mass extinction event at the Cretaceous – Paleogene (K – Pg) boundary**

The K – Pg boundary on Seymour Island, north-eastern Antarctic Peninsula, has been the subject of intensive scientific investigation in recent years. This is particularly so in the field of biostratigraphy where a series of very well exposed sections has been used to calibrate the boundary in great detail (Bowman *et al*., 2012; Olivero, 2012; Tobin *et al.*, 2012; Witts *et al*., 2015). As a result of this work it has been clearly demonstrated that there was a single, severe extinction event at 66 Ma affecting both pelagic and benthic organisms (Fig. 1). Using benthic bivalves and gastropods, an extinction of *c*. 61% at the species level and *c*. 43% at the genus level has been demonstrated, and these figures are directly comparable with those from a series of other global localities (Witts *et al*., 2016). The southern high latitudes were not in any way buffered from the effects of this global mass extinction, whatever its ultimate cause.

The K – Pg mass extinction led to a fundamental reorganisation of global marine ecosystems and ultimately the establishment of modern faunas in both the benthic and pelagic realms (Erwin, 1998; Bambach *et al*., 2002; Stanley, 2007). However, this transition was by no means instantaneous and for approximately 0.5 Myr after the extinction event in Antarctica the benthic fauna was characterised by a low diversity – high abundance assemblage of what are taken to be opportunist species (Bowman *et al*., 2016; Witts *et al*., 2016). Re-establishment of pre-extinction levels of taxonomic diversity in Antarctica may have taken at least 3 Myr in both the benthic and pelagic realms (D’Hondt *et al*., 1998; Witts *et al*., 2016).

1. **Early Cenozoic evolutionary radiation**

The K – Pg mass extinction was followed by a global evolutionary radiation in both the marine and terrestrial realms that is amongst the strongest recorded in the entire fossil record (Bush & Bambach, 2015) (Fig. 1). On Seymour Island it can be traced from the lower levels of the Paleocene Sobral Formation into the Eocene La Meseta Formation and has been the target of comprehensive recent investigations (Beu, 2009; Crame *et al*., 2014). One of the first features to emerge from this analysis is that the numerically dominant benthic group in the latest Cretaceous, the bivalves, is soon replaced in this role by the gastropods, a trend that is mirrored worldwide (Stilwell, 2003). And this in turn is very largely due to the rapid evolutionary expansion of just one clade, the carnivorous (and very largely predatory) Neogastropoda. From some 220 recorded Maastrichtian species the clade expanded throughout the Cenozoic to an estimated 26,000 species worldwide at the present day (Taylor *et al*., 1980; Alroy, 2010; Crame, 2013). As such, it is now one of the most diverse taxonomic groups in the world ocean.

Of the eight neogastropod species known from the Antarctic Late Maastrichtian, only one of them (*Heteroterma* sp.) crosses the K – Pg boundary and none of them can be assigned to modern genera (Crame *et al*., 2014). Neogastropods first become common in the lower levels of the Paleocene Sobral Formation and by the Middle Eocene section of the La Meseta Formation some 40% of the 52 species present can be assigned to modern genera. Of the total number of Middle Eocene gastropods and bivalves identified so far (147 species), 32% are assigned to modern genera (Beu, 2009). Similar diversification trends in the Seymour Island section are very probably shown by certain heterodont bivalves, decapod crustaceans and teleost fishes (Crame *et al*., 2014). Brooding echinoids, a prominent component of the modern Antarctic benthos, can also be traced back to the Eocene of Seymour Island; the cidaroid genus, *Austrocidaris*, is represented in the Early Eocene and the schizasterid genus, *Abatus*, in the Middle - ?Late Eocene (Pearse *et al*., 2009).

1. **Late Eocene extinction event**

In the very highest levels of the stratigraphic section exposed on Seymour Island there is evidence of a second major extinction event. This occurs at a level approximately 150m beneath the top of the Eocene La Meseta Formation at the base of informal mapping unit Telm 6. These topmost beds (i.e. Telm 6 and Telm 7) have a very much reduced molluscan fauna, with an estimated extinction level of 63% that could put it on a par with that at the K – Pg boundary (Stilwell & Zinsmeister, 1992; Beu, 2009; Crame *et al*., 2014). However, some caution has to be applied in making this assessment as the reduction in fauna is accompanied by a marked facies change to very shallow-water, shoreface deposits (Ivany *et al*., 2008). There is also some uncertainty as to the precise age of these uppermost beds. As one interpretation, based on strontium isotope analyses, places upper Telm 6 at 42 Ma (late Middle Eocene) and the top of Telm 7 at 34 Ma (Eocene – Oligocene [E – O] boundary) (Ivany *et al*., 2008), it is tempting to link the extinction to the onset of global cooling. 42 Ma is the approximate time of initiation of Antarctic continental ice caps (Doria *et al*., 2011), and the E – O boundary is coincident with one of the steepest drops in global ocean temperature in the entire Cenozoic (Zachos *et al*., 2008) (Fig. 1). Such an interpretation is strengthened by palaeotemperature analyses based on Ocean Drilling Program (ODP) core samples from Maud Rise, Weddell Sea. These suggest that a phase of late Middle Eocene to earliest Oligocene cooling was accomplished in three distinct steps, each of 2°- 3°C: 43 Ma, 40 Ma and *c.* 36 Ma (Stott *et al*., 1990).

1. **Oligocene – Miocene phased extinctions?**

Nevertheless, the true nature and scale of the Late Eocene extinction event in Antarctica is unknown. Some taxonomic groups have changed substantially in composition between the Middle Eocene and present day (Aronson *et al*., 2007), and there is always the possibility that this may reflect a sudden and abrupt extinction event. For example, the Middle Eocene teleost fish fauna comprises at least 35 species from some 26 different families, including chondrichthyans such as chimaeras, sharks and rays, and actinopterygians such as clupeoids (herrings), siluriforms (catfish), gadiforms (codfish) and labrids (wrasses) (Eastman, 2005; Reguero *et al*., 2012). This contrasts sharply with the modern Antarctic fauna which is dominated by just notothenioids, liparids and zoarcids; eight notothenioid families alone account for some 45% of benthic fish diversity at the present day (Eastman, 2005).

But the post-Eocene fossil record of Antarctica is simply not good enough to attribute the loss of some 20+ teleost fish families to just one single event. They could equally well have been lost over an extended period of time. What we do know, from a very incomplete Oligocene – Miocene fossil record in both the South Shetland Islands and the Ross Sea (drill core specimens), is that some of the characteristic marine invertebrate fossils present in the Middle Eocene but missing from the modern Antarctic did persist in the region long after the onset of global cooling. For example, decapod crustaceans are well represented in Early Miocene glaciomarine strata of the Cape Melville Formation, King George Island, where the homolodromiid crab *Antarctidromia* is prolific (Whittle *et al*., 2014). Oyster fragments are known from the Middle – Late Oligocene Polonez Cove Formation, and the venerid bivalve *Retrotapes* occurs in the same unit as well as the Early Miocene Destruction Bay Formation, and the Early Miocene of McMurdo Sound (Beu, 2009; Beu & Taviani, 2014). Strongly ribbed scallops (i.e. members of the family Pectinidae minus the tribe Adamussini) are persistent features of the Antarctic fossil record from the Early Oligocene to Early Pleistocene (Beu & Taviani, 2014). Occurrences such as these suggest that there could equally well have been a series of phased extinctions throughout the Oligocene – Miocene as a single abrupt event (Fig. 1).

It has been argued that those taxa which do become well established in the polar regions tend to be ecological generalists and as such are more resistant to temperature and other ecological changes through the Cenozoic era (Valentine *et al*., 2008). Evidence presented from Late Cenozoic bivalves in the Northern Hemisphere suggests that it may in fact be the mid-latitude regions that are most susceptible to repeated extinctions by climatic fluctuations rather than the poles (Valentine *et al*., 2008).

1. **Mid-Miocene – Recent evolutionary radiations**

At first sight it might appear that Oligocene – Miocene phased extinctions simply continued through to the present day; as the world got progressively colder, more and more species became extinct in the Southern Ocean. This is especially so after the onset of the Middle Miocene Climatic Transition (MMCT) at approximately 14 Ma, which marks the second steepest fall in global ocean temperatures in the entire Cenozoic (Flower & Kennett, 1994; Zachos *et al*., 2008) (Fig. 1). At this time there was a major expansion of both the East and West Antarctic ice sheets and marked intensification of the ACC system.

However, it would appear that a number of the charismatic modern Antarctic vertebrate taxa actually radiated in precisely this interval of intensified glaciation and cold bottom water circulation (Fig. 1). Both mysticete and odontocete whales have probable earliest Cenozoic origins but their acme of taxonomic diversity falls in the late Middle Miocene to Early Pliocene interval (i.e. *c.* 15 - 4 Ma) (Marx & Uhen, 2010). The expansion of filter-feeding mysticetes at this time is particularly impressive and it is possible that, once certain taxonomic issues have been resolved, the diversity peak will be shifted to a more distinct latest Miocene – Early Pliocene summit (Marx & Fordyce, 2015). Their sharp decline in taxonomic diversity after 4 Ma coincides with the onset of bipolar glaciation, reduction in available shelf habitats, shift in feeding grounds, and elimination of many small taxa (Slater *et al*., 2017).

Crown group penguins (Spheniscidae), once thought to be rooted in the Paleocene, now reflect a radiation that dates back no more than *c.* 8 Myr (Clarke *et al*., 2007; Norris *et al.*, 2013), and true Antarctic seals (i.e. members of the tribe Lobodontini, subfamily Monachinae: Crabeater, Ross, Weddell and Leopard seals) may be even younger. Earliest Lobodontini probably diverged at *c.* 6.9 Ma in the central American region and then spread south along the western coast of South America to enter Antarctica at *c.* 3.4 Ma (Fulton & Strobeck, 2010). Southern elephant seals (tribe Miroungini) may not have achieved a circum-Antarctic distribution until as late as the Late Pleistocene (10 – 790 Ka) (Fulton & Strobeck, 2010). The three most speciose clades of notothenioid fish, *Trematomus*, Channichthyidae and Artedidraconidae, diversified between 11.6 and 5.3 Ma, more than 10 Myr after the origin of the group (Near *et al*., 2012).

Mid-Miocene phases of Antarctic diversification have been identified in both a deep sea octopus clade (Strugnell *et al*., 2008) and primnoid bottlebrush octocorals (Dueñas *et al*., 2016). Limpet gastropods of the genus *Nacella* show a distinct radiation at 7.0 – 8.5 Ma (Gonzalez-Wevar *et al*., 2017), and predatory muricid gastropods of the subfamily Pagodulinae have a postulated Late Eocene origin (*c.*40Ma) but did not diversify in the Southern Ocean until the latest Miocene – Pliocene (Barco *et al*., 2012). Molecular phylogenetic evidence also suggests that the amphipod genus *Epimeria*, which forms a species flock at the present day in the Southern Ocean, can be traced back to an initial Middle or Late Eocene Antarctic radiation (Verheye *et al*., 2017). There is a particularly strong pulse of diversification immediately after the MMCT (Verheye *et al*., 2017; Cheneuil *et al*., 2017).

Distinct phases of taxonomic diversification apparently persisted throughout the Pleistocene glacial cycles to the present day (Fig. 1). Molecular phylogeographical studies are providing evidence, from a wide range of both marine and terrestrial taxa, that fragmentation of populations during glacial advances and subsequent re-expansions during interglacials may have been a powerful mechanism for generating cryptic speciation (Wilson *et al.*, 2009; Allcock & Strugnell, 2012; Fraser *et al*., 2012; Poulin *et al*., 2014). The role of isolated refugia in promoting such a process would have been critical, and the provision of a range of new habitats associated with both sea ice and ice shelves could also have facilitated these Late Cenozoic – Recent evolutionary radiations (Near *et al.*, 2012).

**SYNTHESIS**

The K – Pg mass extinction event reset the evolutionary stage in Antarctica, as indeed it did worldwide (Erwin, 1998; Krug & Jablonski, 2012; Aberhan & Kiessling, 2015). The extinction had the key function of removing a variety of incumbent taxa and releasing ecospace for new guilds and lineages to proliferate; such a process was in all probability aided by the benign global climates of the Early Cenozoic greenhouse world (Zachos *et al*., 2008). The excellent fossil record of Seymour Island has enabled the evolutionary expansion of various taxonomic groups to be tracked through this interval, and in particular the extensive Neogastropoda clade. Between the K – Pg boundary and late Middle Eocene this can be demonstrated to increase significantly in both numbers of species and the proportion of those species that can be assigned to modern genera (Crame *et al.*, 2014). Exactly the same pattern occurs in tropical regions except that here the numbers of taxa involved in each Early Cenozoic stage are much higher (Crame, 2013; Crame *et al*., 2018). By the Middle Eocene steep latitudinal diversity contrasts can be demonstrated in both neogastropods and teleost fishes (Bellwood, 1996; Eastman, 2005).

But it is becoming clearer that the regional faunal differentiation associated with the Early Cenozoic evolutionary radiation of neogastropods involves something more than just a difference in numbers of species. The distribution of species per family in the Antarctic Middle Eocene fauna is statistically significantly less even than that in tropical faunas, a pattern very similar to that seen at the present day (Crame, 2013). The strong dominance signal in polar neogastropod faunas is linked to the proliferation of generalist feeders in a regime of seasonally fluctuating food supply (Crame, 2013). In the neogastropods, and very probably a number of other groups too, the emergence of a distinct polar fauna in a greenhouse world strongly suggests that something else besides temperature was involved in its formation. The seasonality of primary production may be a major determinant in the differentiation of high-latitude and polar marine faunas (Crame *et al*., 2018).

Some care must also be exercised in attributing the effects of the extinction event close to the E – O boundary directly to temperature. If the very steepest parts of the decline in global ocean temperatures through the Cenozoic are taken to be *c.* 8°C over 3 Myr, then this still amounts to no more than 0.003°C per thousand years (Clarke, 1990; Zachos *et al*., 2008). Even today, a typical stenothermal polar marine organism can survive temperatures ranging from -2°C to +4°C, i.e. a range of 6°C (Clarke, 1990). It may well be that much of the effects of this major cooling event across the E – O boundary were concentrated in the three abrupt steps identified by Stott et al. (1990), where on each occasion temperature dropped sharply by 2°- 3°C. In addition, detailed stable isotope analyses across the E - O boundary indicate that winters became approximately 4°C cooler at this time, and thus it may be intra-annual temperature variability rather than changes in mean annual temperature *per se* that caused the extinctions (Ivany *et al*., 2000). Finally, we need to consider that neogastropods, brooding echinoids and other taxa identified in the Antarctic Middle Eocene fauna have survived through to the present day. If some taxa can adjust to gradual cooling over a 45 Myr period then why cannot others?

There were some immediate biological consequences of the final physical isolation of Antarctica at approximately the E – O boundary (34 Ma). Land bridges were of course finally destroyed at this time, and in the marine realm the onset of widespread continental glaciation led to the formation of coastal sea ice and a pronounced shift to highly seasonal primary productivity within pelagic communities (Houben *et al*., 2013). However, the familiar krill-based ecosystems of the Southern Ocean did not expand significantly in numbers until much later in the Late Miocene and it is important to try and understand why there was a delay of some 15+ Myr in this process taking place (Fig. 1).

Although Drake Passage may have opened at 34 Ma, there is a growing volume of geological and geophysical evidence to indicate that the present-day configuration and geodynamic setting of the Scotia Arc was not achieved until the Late Miocene (Maldonado *et al*., 2014). In particular, an extensive ancestral volcanic arc was positioned immediately to the east of the Drake Passage gateway for an approximately 20 Myr interval (i.e. 34 – 14 Ma), and this almost certainly impeded the full development of a deep water current system through the central Scotia Sea (Dalziel *et al*., 2013). This formidable tectonic barrier persisted until the initiation of a back-arc spreading centre in the East Scotia Sea which led initially to the development of the Shag Rocks Passage to the west of the South Georgia micro-continent, and then the South Georgia Passage immediately to the south-east. Full development of the ACC through the latter is dated at 10 – 11 Ma (Dalziel *et al*., 2013; Pearce *et al*., 2014) (Fig. 1). At approximately the same time new gateways through the South Scotia Ridge allowed connections between the Weddell and Scotia seas for the first time (Maldonado *et al*., 2014). These may have been particularly important for facilitating the frequent interchange of Antarctic and deep-sea faunas (Brandt *et a*l., 2007; Strugnell *et al*., 2008, 2011) (Fig. 1).

The mid-Miocene intensification of the ACC not only isolated the continent thermally but also, crucially, allowed the development of a giant mixing ring with enhanced upwelling and nutrient pumping; processes that were progressively intensified as the East Antarctic Ice Sheet grew and zonal winds escalated (Berger, 2007). Following the Middle Miocene introduction of North Atlantic Deep Water, the ACC became the great silicone reservoir of the world ocean and thus the focus of a major radiation of diatoms over the last 15 Myr (Lazarus *et al*., 2014) (Fig. 1). Because diatoms are more than twenty times larger than the largest picoplankton they form an efficient basis for the transport of large volumes of organic carbon to apex predators. They are a primary food source for krill and thus integral to the development of the characteristic short food-chain ecosystems of the Southern Ocean (Berger, 2007). Whales, penguins, seals and fishes all radiated from the late Middle Miocene onwards, and it is likely that the rain of extra organic material to the seafloor benefited benthic communities too.

The presence of extensive, perennial sea ice around the Antarctic continent dates back to approximately 15 Ma (Crampton et al., 2016). Detailed analysis of the diatom fossil record from 34 Southern Ocean and Antarctic margin drill holes indicates that five conspicuous peaks in production, driven by long-term climate cycles, occurred between 14.65 and 1.95 Ma (Crampton et al., 2016). During this interval there was a constant flux in the ratio of open water to sea ice and this in turn must have had a profound effect on the distribution of krill and other zooplankton, penguins, and marine mammals (Ducklow et al., 2007). Although the precise diversity dynamics of all these pelagic taxa through this interval is not yet known, what is becoming more apparent is that modern Antarctic ocean ecosystems are characterised by relatively low metazoan diversity and the dominance of a small number of species at each trophic level (Murphy et al. 2016). For example, the prolific pelagic fish assemblage of the Western Antarctic Peninsula ecosystem is dominated by just two species, Antarctic silverfish (*Pleuragramma antarcticum*) and lantern fish (*Electroma antarctica*) (Murphy et al., 2016). Patterns of high dominance/low evenness established in benthic assemblages are repeated in the pelagic realm.

The average depth of the Antarctic continental shelf is as much as four times greater than that of shelves around other continents, with the shelf break occurring at *c.* 500 – 900 m (Johnson *et al*., 1982). This greater depth is at least partly due to isostatic subsidence under the weight of the Antarctic ice cap but also to intense glacial erosion over the last 30+ Myr. In the last 5 Myr alone there have been no fewer than 38 full glacial cycles in the Ross Sea region where glaciers and ice sheets reached the shelf break (Naish *et al*., 2009). Much of the shelf is heavily dissected by a system of ridges and canyons, with the surface being either bare rock or coarse glacial debris; sedimentation rates are high and there is frequent disturbance by iceberg scour (Thatje et al., 2005). The systematic exclusion of suitable shallow water habitats with fine-grained substrates from much of Antarctica has undoubtedly had a profound effect on the composition of contemporary benthic faunas (Clarke & Crame, 1989; Krug *et al*., 2010).

**CONCLUSIONS**

* We are developing a much better understanding of the scale of ancestry of the modern Antarctic marine fauna. In a sense it has always been there, at least through the greater part of the Cenozoic era, and does not obviously represent a wholesale accumulation of taxa with lower latitude origins.
* As with any other regional fauna, it has been through phases of both evolutionary expansion and contraction. An Early Cenozoic radiation could be linked to both the aftermath of the K – Pg mass extinction event and the effects of a greenhouse climate, but the presence of certain faunas exhibiting high levels of dominance/low evenness suggests that something else may also be involved. These dominant taxa were in all probability trophic generalists, a prevalent ecological strategy in the high-latitude and polar regions to cope with a severely pulsed, or seasonal, food supply. Seasonality may well have controlled the composition of polar marine faunas in the past, just as it does today.
* The fauna undoubtedly lost some keystone taxa sometime after the Late Eocene but whether this loss was a mass extinction or a series of phased extinctions of lesser severity is uncertain. This reduction in the fauna is classically linked to the onset of global cooling but it is important to also bear in mind that shallow marine habitats were profoundly altered by the actions of ice.
* Molecular phylogenetic evidence is providing important new evidence that significant evolutionary radiations occurred after the onset of global cooling, and in particular in the immediate aftermath of the MMCT (14 Ma). At first sight the link between evolutionary radiations and a period of intense global cooling would appear to be anomalous, but we now know that this was a time of enhanced deep-water circulation and nutrient enrichment in the Southern Ocean. Despite the intense cold, diatom-based ecosystems were able to proliferate and indeed may be continuing to do so at the present day.
* The distinctive low diversity – high dominance signature of contemporary Antarctic marine biotas was fashioned by the interplay between temperature and the seasonality of primary productivity throughout the Cenozoic era.
* The true trajectory of Antarctic marine taxonomic diversity levels through the Cenozoic remains largely unknown.

**ACKNOWLEDGEMENTS**

Funding from the Natural Environment Research Council, and in particular NE/I005803/1, is gratefully acknowledged. For stratigraphic and taxonomic help over a number of years I am particularly grateful to A.G. Beu, J.R. Ineson, V.C. Bowman, J.E. Francis, and R.J. Whittle. I would also like to acknowledge the invaluable palaeontological legacy left by numerous international colleagues working on Seymour Island; I would particularly like to highlight the pioneering work of W.J. Zinsmeister and associates over many years. My thanks go to A. Clarke, E.M. Harper, E. J. Murphy, L.S. Peck and J.D. Taylor for discussions about polar biodiversity patterns and the evolution of marine ecosystems. Three anonymous referees and C.I. Fraser are thanked for very helpful comments and suggestions.

**REFERENCES**

Aberhan, M. & Kiessling, W. (2015) Persistent ecological shifts in marine molluscan assemblages

 across the end-Cretaceous mass extinction. *Proceedings of the National Academy of Sciences*

*USA*, **112**, 7207-7212.

Allcock, A.L. & Strugnell, J.M. (2012) Southern Ocean diversity: new paradigms from molecular

 ecology. *Trends in Ecology and Evolution*, **27**, 520-528.

Alroy, J. (2010) The shifting balance of diversity among major animal groups. *Science,* **329**, 1191

 -1194.

Arntz, W.E., Brey, T., & Gallardo, V.A. (1997) Antarctic marine biodiversity: an overview.

 *Antarctic communities: species, structure and survival* (ed. by B. Battaglia, J. Valencia &

 D.W.H. Walton), pp. 3-14. Cambridge University Press, Cambridge, U.K.

Aronson, R.B., Thatje, S., Clarke, A., Peck, L.S., Blake, D.B., Wilga, C.D. & Seibel, B.A. (2007)

 Climatic change and invisibility of the Antarctic benthos. *Annual Review of Ecology*

 *and Evolution*, **38**, 129-154.

Bambach, R.K., Knoll, A.H. & Sepkoski, Jr, J.J. (2002) Anatomical and ecological constraints on

Phanerozoic animal diversity in the marine realm. *Proceedings of the National*

*Academy of Sciences USA*, **99**, 6854-6959.

Barco, A., Schiaparelli, S., Houart, R. & Olivero, M. (2012) Cenozoic evolution of Muricidae (Mollusca,

Neogastropoda) in the Southern Ocean, with the description of a new subfamily. *Zoologica*

*Scripta*, **41**, 596-616.

Bellwood, D.R. (1996) The Eocene fishes of Monte Bolca: the earliest coral reef fish assemblage.

 *Coral Reefs*, **15**, 11-19.

Berger, W.H. (2007) Cenozoic cooling, Antarctic nutrient pump, and the evolution of whales.

 *Deep Sea Research II*, **54**, 2399-2421.

Beu, A.G. (2009) Before the ice: biogeography of Antarctic Paleogene molluscan faunas.

*Palaeogeography, Palaeoclimatology, Palaeoecology,* **284**, 191-226.

Beu, A.G. & Taviani, M. (2014) Early Miocene Mollusca from McMurdo Sound, Antarctica

 (ANDRILL 2A drill core), with a review of Antarctic Oligocene and Neogene

 Pectinidae (Bivalvia). *Palaeontology*, **57**, 299-342.

Bowman, V.C., Francis, J.E., Riding, J.B., Hunter, S.J. & Haywood, A.M. (2012) A latest Cretaceous to

 earliest Paleogene dinoflagellate cyst zonation from Antarctica, and implications for

 phytoprovincialism in the high southern latitudes. *Review of Palaeobotany and Palynology*,

 **171**, 40-56.

Bowman, V., Ineson, J., Riding, J, Crame, J., Francis, J., Condon, D., Whittle, R. & Ferraccioli, F.

 (2016) The Paleocene of Antarctica: Dinoflagellate cyst biostratigraphy, chronostratigraphy

 and implications for the Palaeo-Pacific margin of Gondwana. *Gondwana Research*, **38**, 132-

 148.

Brandt, A., Gooday, A.J., Brandão, *et al.* (2007) Firsts insights into the biodiversity and biogeography

 of the Southern Ocean deep sea. *Nature*, **447**, 307-311.

Bush, A.M. & Bambach, R.K. (2015) Sustained Mesozoic-Cenozoic diversification of marine Metazoa:

A consistent signal from the fossil record. *Geology* **43**, 979-982.

Chenuil, A., Saucède, T., Hemery, L.G., Eléaume, M., Féral, J.-P., Améziane, N., David, B., Lecointre,

 G. & Havermans, C. (2017) Understanding processes at the origin of species flocks with a

 focus on the marine Antarctic fauna. *Biological Reviews*, doi: 10.1111/brv.12354.

Clarke, A. (1990) Temperature and evolution: Southern Ocean cooling and the Antarctic marine

fauna. *Antarctic ecosystems* (ed. by K.R. Kenny & G. Hempel), pp. 9-22. Springer,

Heidelberg.

Clarke, A. & Crame, J.A. (1989) The origin of the Southern Ocean marine fauna. *Origins and*

 *evolution of the Antarctic biota* (ed. by J.A. Crame), pp. 253-268. *Geological Society London,*

 *Special Publications*, **47**.

Clarke, J.A., Ksepka, D.T., Stucchi, M., Urbina, M., Giannini, N., Bertelli, S, Narváez, Y. & Boyd, C.A.

 (2007) Paleogene equatorial penguins challenge the proposed relationship between

biogeography, diversity, and Cenozoic climate change. *Proceedings of the National Academy*

*of Sciences USA*, **104**, 11545-11550.

Crame, J.A. (1994) Evolutionary history of Antarctica. *Antarctic science. Global concerns* (ed. by G.

Hempel), pp. 188-214.

Crame, J.A. (2013) Early Cenozoic differentiation of polar marine faunas. *PLoS ONE*, **8**, e54139.

Crame, J.A., Beu, A.G., Ineson, J.R., Francis, J.E., Whittle, R.J. & Bowman, V.C. (2014) The early origin

of the Antarctic marine fauna and its evolutionary implications. *PLoS ONE*, **9**, e114743.

Crame, J.A., McGowan, A.J. & Bell, M.A. (2018). Differentiation of high-latitude and polar marine

 faunas in a greenhouse world. *Global Ecology and Biogeography.* In press.

Crampton, J.S., Cody, R.D., Levy, R., Harwood, D., McKay, R. & Naish, T.R. (2016) Southern Ocean

 phytoplankton turnover in response to stepwise Antarctic cooling over the past 15 million

years. *Proceedings of the National Academy of Sciences USA*, **113**, 6868-6873.

Dalziel, I.W.D., Lawver, L.A., Pearce, J.A., Barker, P.F., Hastie, A.R., Barford, D.N., Schenke, H.W.,

 & Davis, M.B. (2013). A potential barrier to deep Antarctic circumpolar flow until the

Late Miocene. *Geology*, **41**, 947-950.

Dayton, P.K. (1990) Polar benthos. *Polar oceanography, Part B: Chemistry, biology and geology* (ed.

 W.O. Smith), pp. 631-685. Academic Press, London.

Dell, R.K. (1972) Antarctic benthos. *Advances in Marine Biology*, **10**, 1-216.

D’Hondt, S., Donaghay, P., Zachos, J.C., Luttenberg, D. & Lindinger, M. (1998) Organic carbon

 fluxes and ecological recovery from the Cretaceous – Tertiary mass extinction. *Science*,

 **282**, 276-279.

Doria, G., Royer, D.L., Wolfe, A.P., Fox, A., Westgate, J.A. & Beerling, D.J. (2011) Declining

 atmospheric CO2 during the late Middle Eocene climate transition. *American*

 *Journal of Science*, **311**, 63-75.

Ducklow, H.W., Baker, K., Martinson, D.G., Quetin, L.B., Ross, R.M., Smith, R.C.,

 Stammerjohn, S.E., Vernet, M. & Fraser, W. (2007) Marine pelagic ecosystems: the

 West Antarctic Peninsula. *Philosophical Transactions of the Royal Society B*, **362**, 67-

 94.

Dueñas, L.F., Tracey, D.M., Crawford, A.J., Wilke, T, Alderslade, P. & Sanchez, J.A. (2016) The

 Antarctic Circumpolar Current as a diversification trigger for deep-sea octocorals. *BMC*

 *Evolutionary Biology*, **16:2** DOI 10.1186/s12862-015-0574-z

Eastman, J.T. (2005) The nature of the diversity of Antarctic fishes. *Polar Biology,* **28**, 93-107*.*

Erwin, D.H. (1998) The end and the beginning: recoveries from mass extinctions. *Trends in Ecology*

*and Evolution*, **13**, 344-349.

Flower, B.P. & Kennett, J.P. (1994) The Middle Miocene climatic transition: East Antarctic ice

sheet development, deep ocean circulation and global carbon cycling. *Palaeogeography,*

 *Palaeoclimatology, Palaeoecology,* **108**, 537-555.

Fraser, C.I., Nikula, R., Ruzzante, D.E. & Waters, J.M. (2012) Poleward bound: biological impacts

 of Southern Hemisphere glaciation. *Trends in Ecology and Evolution*, **27**, 462-471.

 Fulton, T.L. & Strobeck, C. (2010) Multiple fossil calibrations, nuclear loci and

 mitochondrial genomes provide new insight into biogeography and divergence

 timing for true seals (Phocidae, Pinnipedia). *Journal of Biogeography*, **37**, 814-829.

Gili, J.-P., Arntz, W.E., Palanques, A., Orejas, C., Clarke, A., Dayton, P.K., Isla, E., Teixidó, Rossi, S.,

 López-González, P.J. (2006) A unique assemblage of epibenthic sessile suspension

 feeders with archaic features in the high-Antarctic. *Deep-Sea Research II*, **53**, 1029-

 1052.

Goldberg, E.E., Roy, K., Lande, R. & Jablonski, D. (2005) Diversity, endemism, and age distribution

 in macroevolutionary sources and sinks. *American Naturalist*, **165**, 623-633.

González-Wevar, C.A., Hüne, M., Segovia, N.I., Nakano, T., Spencer, H.G., Chown, S.L.,

 Saucède, T., Johnstone, G., Mansilla, A. & Poulin, E. (2017) Following the Antarctic

 Circumpolar Current: patterns and processes in the biogeography of the limpet

 *Nacella* (Mollusca: Patellogastropoda) across the Southern Ocean. *Journal of*

 *Biogeography*, **44**, 861-874.

Griffiths, H.J., Barnes, D.K.A. & Linse, K. (2009) Towards a generalised biogeography of the

` Southern Ocean benthos. *Journal of Biogeography*, **36**, 162-177.

Hansen, J., Sato, M., Russell, G. & Kharecha, P. (2013) Climate sensitivity, sea level and

 atmospheric carbon dioxide. *Philosophical Transactions of the Royal Society A*, 371:

 20120294.

Houben, J.P., Bijl, P.K., Pross, J., Bohaty, S.M.,Passchier, S., Stickley, C.E., Röhl, U., Sugisaki, S.,

 Tauxe, L., van de Flierdt, T., Olney, M., Sangiorgi, F., Sluijs, A., Escutia, C., Brinkhuis, H.

 & the Expedition Scientists (2013) Reorganisation of Southern Ocean plankton

 ecosystem at the onset of Antarctic glaciation. *Science*, **340**, 341-344.

Ivany, L.C., Lohmann, K.C. & Patterson, W.P. (2000) Cooler winters as a possible cause of mass

 extinctions at the Eocene/Oligocene boundary. *Nature*, **407**, 887-890.

Ivany, L.C., Lohmann, K.C., Hasiuk, F., Blake, D.B., Glass, A., Aronson, R.B. & Moody, R.M. (2008)

 Eocene climate record of a high southern latitude continental shelf: Seymour Island,

 Antarctic Peninsula. *Bulletin of the Geological Society of America*, **120**, 659-678.

Jablonski, D., Roy, K. & Valentine J.W. (2006) Out of the tropics: evolutionary dynamics of the

 latitudinal diversity gradient. *Science*, **314**, 102-106.

Johnson, G.L., Vanney, J.R. & Hayes, D. (1982) The Antarctic continental shelf. *Antarctic geoscience*

(ed. by C. Craddock), pp. 995-1002. University of Wisconsin Press, Madison, Wisconsin.

Krug, A.Z. & Jablonski, D. (2012) Long-term origination rates are reset at mass extinctions.

 *Geology*, **40**, 731-734.

Krug, A.Z., Jablonski, D., Roy, K. & Beu, A.G. (2010) Differential extinction and the contrasting

 structure of polar marine faunas. *PLoS ONE*, **5**, e15362.

Lazarus, D., Barron, J., Renaudie, J., Diver, P. & Türke, A. (2014) Cenozoic planktonic marine

 diatom diversity and correlation to climate change. *PLoS ONE*, **9**, e84857.

Lins, L.S.F., Ho, S.Y.W., Wilson, G.D.F. & Lo, N. (2012) Evidence for Permo-Triassic colonization of the

 deep sea by isopods. *Biology Letters*, doi: 10.1098/rsbi.2012.0774.

Maldonado, A., Bohoyo, F., Galindo-Zaldivar, F.J., Hernandez-Molina, F.J., Lobo, F.J., Lodolo, E.,

 Martos, Y.M., Perez, L.F., Schreider, A.A. & Somoza, L. (2014) A model of oceanic

 development by ridge jumping: Opening of the Scotia Sea. *Global and Planetary Change*,

 **123**, 152-173.

Marx, F.G. & Fordyce, R.E. (2015) Baleen boom and bust: a synthesis of mysticete phylogeny,

 diversity and disparity. *Royal Society open science*, **2**: 14034.

Marx, F.G. & Uhen, M.D. (2010) Climate, critters, and cetaceans: Cenozoic drivers of the

 evolution of modern whales. *Science*, **327**, 993-996.

Moon, K.L., Chown, S.L. & Fraser, C.I. (2017) Reconsidering connectivity in the sub-Antarctic.

 *Biological Reviews*, **92**, 2164-2181.

Murphy, E.J., Cavanagh, R.D., Drinkwater, K.F., Grant, S.M., Heymans, J.J., Hunt, Jr, G.L. &

 Johnston, N.M. (2016) Understanding the structure and functioning of pelagic polar

 ecosystems to predict the impacts of change. *Proceeding of the Royal Society B,* **283**:

20161646.

Naish, T., Powell, R., Levy, R. *et al*. (2009) Obliquity-paced Pliocene West Antarctic ice sheet

 oscillations. *Nature*, **458**, 322-328.

Near, T.J., Dornburg, A., Kuhn, K.L., Eastman, J.T., Pennington, J.N., Patarnello, T., Zane, L.,

 Fernández, D.A. & Jones, C.D. (2012) Ancient climate change, antifreeze, and the

evolutionary diversification of Antarctic fishes. *Proceedings of the National Academy*

*of Sciences USA*, **109**, 3434-3439.

Norris, R.D., Turner, S.K., Hull, P.M. & Ridgwell, A. (2013) Marine ecosystem responses to Cenozoic

global change. *Science*, **341**, 492-498.

Olivero, E.B. (2012) Sedimentary cycles, ammonite diversity and palaeoenvironmental changes in

 the Upper Cretaceous Marambio Group, Antarctica. *Cretaceous Research*, **34**, 348-366.

Pearce, J.A., Hastie, A.R., Leat, P.T., Dalziel, I.W.D., Lawver, L.A., Barker, P.F., Millar, I.L., Barry, T.L.

 & Bevins, R.E. (2014) Composition and evolution of the ancestral South Sandwich Arc:

 Implications for the flow of deep ocean water and mantle through the Drake Passage

 gateway. *Global and Planetary Change*, **123**, 298-322.

Pearse, J.S., Mooi, R., Lockhart, S.J. & Brandt, A. (2009) Brooding and species diversity in the

 Southern Ocean: selection for brooders or speciation within brooding clades?

 *Smithsonian at the Poles, Contributions to International Polar Year Science* (ed. by I. Krupnik,

 M.A. Lane & S.E. Miller), pp. 181-196. Smithsonian Institution Press, Washington.

Pierrat, B., Saucède, T., Brayard, A. & David, B. (2013) Comparative biogeography of echinoids,

bivalves and gastropods from the Southern Ocean. *Journal of Biogeography*, **40**, 1374-

1385.

Poulin, E., González-Wevar, Diaz, A., Gérard, K. & Hüne, M. (2014) Divergence between Antarctic and

South American marine invertebrates: What molecular biology tells us about Scotia Arc

geodynamics and the intensification of the Antarctic Circumpolar Current. *Global and*

*Planetary Change*, **123**, 392-399.

Reguero, M.A., Marenssi, S.A. & Santillana, S.N. (2012) Weddellian marine/coastal vertebrates

diversity from a basal horizon (Ypresian, Eocene) of the *Cucullaea* I Allomember, La

Meseta Formation, Seymour (Marambio) Island, Antarctica. *Revista Peruana de Biologia*, **19**,

275-284.

Saucede, T., Pierrat, B., Brayard, A. & David, B. (2013) Palaeobiogeography of Austral echinoid

 faunas: a first quantitative approach. *Antarctic palaeoenvironments and Earth-surface*

 *Processes* (ed. by M.J. Hambrey. P.F. Barker, P.J. Barrett, V. Bowman, B. Davies, J.L. Smellie,

 & M. Tranter), pp. 117-127. *Geological Society London, Special Publications*, **381**.

Slater, G.J., Goldbogen, J.A. & Pyenson, N.D. (2017) Independent evolution of baleen whale

 gigantism linked to Plio-Pleistocene ocean dynamics. *Proceedings of the Royal Society B*,

 **284**: 20170546.

Stanley, S M (2007) An analysis of the history of marine animal diversity. *Paleobiology, Supplement*,

**33,** 1-55.

Stilwell, J.D. (2003) Patterns of biodiversity and faunal rebound following the K – T boundary

extinction event in Austral Paleocene molluscan faunas. *Palaeogeography,*

*Palaeoclimatology, Palaeoecology,* **195**, 319-356.

Stilwell, J.D. & Zinsmeister, W.J. (1992) Molluscan systematics and biogeography. Lower Tertiary La

Meseta Formation, Seymour Island, Antarctic Peninsula. *Antarctic Research Series*, **55**, 1-192.

Stott, L.D., Kennett, J.P., Shackleton, N.J. & Corfield, R.M. (1990) The evolution of Antarctic surface

waters during the Paleogene: Inferences from the stable isotope composition of planktonic

foraminifers, ODP Leg 113. *Proceedings of the Ocean Drilling Program. Scientific Results*, **113**,

849-863.

Strugnell, J.M., Rogers, A.D., Prodöhl, Collins, M.A. & Allcock, A.L. (2008) The thermohaline

expressway: the Southern Ocean as a centre of origin for deep-sea octopuses.

*Cladistics*, **24,** 853-860.

Strugnell, J.M., Cherel, Y., Cooke, I.R., Gleadall, I.G., Hochberg, F.G., Ibáñez, C.M., Jorgensen, E.,

 Laptikhovsky, V.V., Linse, K., Norman, M., Vecchione, M., Voight, J.R. & Allcock, A.L. (2011)

 The Southern Ocean: Source and sink? *Deep-Sea Research II*, **58**, 196-204.

Taylor, J.D. Morris, N.J. & Taylor, C.N. (1980) Food specialization and the evolution of

 predatory prosobranch gastropods. *Palaeontology*, **23**, 375-409.

Taylor, M.L. & Rogers, A.D. (2015) Evolutionary dynamics of a common sub-Antarctic octocoral

 family. *Molecular Phylogenetics and Evolution*, **84**, 185-204.

Thatje, S., Hillenbrand, C.-D. & Larter, R. (2005) On the origin of Antarctic marine benthic community

 structure. *Trends in Ecology and Evolution*, **20**, 534-539.

Tobin, T.S., Ward, P.D., Steig, E.J., Olivero, E.B., Hilburn, I.A., Mitchell, R.N., Diamond, M.R., Raub,

T.D. & Kirschvink, J.L. (2012) Extinction patterns, δ18O trends, and magnetostratigraphy

from a southern high-latitude Cretaceous – Paleogene section: Links with Deccan volcanism.

*Palaeogeography, Palaeoclimatology, Palaeocology*, **350 – 352**, 180-188.

Valentine, J.W., Jablonski, D., Krug, A.Z. & Roy, K. (2008) Incumbency, diversity and latitudinal

 gradients. *Paleobiology*, **34**, 169-178.

Verheye, M.L., Backeljau, T. & d’Udetem d’Acoz, C. (2017) Locked in the icehouse: Evolution of an

endemic *Epimeria* (Amphipoda, Crustacea) species flock on the Antarctic shelf. *Molecular*

*Phylogenetics and Evolution*, **114**, 14-33.

Vermeij, G.J. (1987) *Evolution and escalation. An ecological history of life*. Princeton University

 Press, Princeton, N.J.

Whittle, R.J., Linse, K. & Griffiths, H.J. (2011) The fossil record of *Limopsis* (Bivalvia: Limopsidae)

 in Antarctica and the southern high latitudes. *Palaeontology*, **54**, 935-952.

Whittle, R.J., Quaglio, F., Griffiths, H.J., Linse, K. & Crame, J.A. (2014) The Early Miocene Cape

 Melville Formation fossil assemblage and the evolution of modern Antarctic marine

 communities. *Naturwissenschaften*, **101**, 47-59.

Wilson, G.D.F. (1998) Historical influences on deep-sea isopod diversity in the Atlantic Ocean.

 *Deep-Sea Research II*, **45**, 279-301.

Wilson, N.G., Schrödl, M. & Halanych, K.M. (2009) Ocean barriers and glaciation: evidence for

 explosive radiation of mitochondrial lineages in the Antarctic sea slug *Doris*

 *kerguelensis* (Mollusca, Nudibranchia). *Molecular Ecology*, **18**, 965-984.

Witts, J.D., Bowman, V.C., Wignall, P.B., Crame, J.A., Francis, J.E. & Newton, R.J. (2015) Evolution

 and extinction of Maastrichtian (Late Cretaceous) cephalopods from the López de

 Bertodano Formation, Seymour Island, Antarctica. *Palaeogeography, Palaeoclimatology,*

*Palaeocology*, **418**, 193-212.

Witts, J.D., Whittle, R.J., Wignall, P.B., Crame, J.A., Francis, J.E., Newton, R.J. & Bowman, V.C.

 (2016) Macrofossil evidence for a rapid and severe Cretaceous – Paleogene mass extinction

 in Antarctica. *Nature Communications*, **7**: 11738.

Zachos, J.C., Dickens, G.R., & Zeebe, R.E. (2008) An early Cenozoic perspective on greenhouse

 warming and carbon-cycle dynamics. *Nature*, **451**, 279-283.

Zinsmeister, W.J. & Camacho, H.H. (1980) Late Eocene Struthiolariidae (Mollusca: Gastropoda)

 from Seymour Island, Antarctic Peninsula and their significance to the biogeography of

 Early Tertiary shallow-water faunas of the Southern Hemisphere. *Journal of Paleontology*,

 **54**, 1-14.

Figure caption

**Figure 1**. Key stages in the evolution of the Antarctic marine fauna. (1) mass extinction event at the K – Pg boundary (66 Ma); (2) prolonged phase of evolutionary radiation in marine benthos; essentially global greenhouse climates (*c*. 63 – 42 Ma); (3) rapid cooling initiated at the Eocene – Oligocene boundary (*c*. 34 Ma); single rapid drop in global ocean temperatures or stepped decline ?; opening of Drake Passage but not full development of ACC; possible major extinction event; (4) Early Oligocene – mid-Miocene (*c*. 30 – 15 Ma) mixed phase of both radiations and extinctions; (5) Middle Miocene Climatic Transition (MMCT) (*c*. 14 Ma); second steepest Cenozoic drop in ocean temperature; (6) full development of the ACC following tectonic events in central Scotia Sea (11 – 10 Ma); full development of faunal interchange between Antarctica and deep sea?; (7) major expansion of pelagic ecosystems following radiation of diatoms and proliferation of sea ice (*c*. 15 – 5 Ma); (8) intense phase of bipolar glaciation paced by orbital cyclicity; possible enhancement of ‘glacial diversity pump’ mechanism (*c*. 5 Ma – present).

Symbols: K = Cretaceous, Pl = Pliocene, P = Pleistocene. Deep sea palaeotemperature curve based on Zachos *et al*. (2008), with some modifications from Hansen *et al.*(2013).

Fig. 1

