HAL open science

Antarctica as an evolutionary arena during the Cenozoic global cooling

Fabien L. Condamine, Gael J. Kergoat

To cite this version:

Fabien L. Condamine, Gael J. Kergoat. Antarctica as an evolutionary arena during the Cenozoic global cooling. Proceedings of the National Academy of Sciences of the United States of America, 2021, 118 (27), pp.e2108886118. 10.1073/pnas.2108886118 . hal-03367498

HAL Id: hal-03367498
https://hal.science/hal-03367498

Submitted on 15 Nov 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Title

Antarctica as an evolutionary arena during the Cenozoic global cooling

Authors

Fabien L. Condamine[a,1]

Gael J. Kergoat[b]

Affiliations

[a]CNRS, UMR 5554 Institut des Sciences de l'Evolution de Montpellier (Université de Montpellier), 34095 Montpellier, France

[b]CBGP, INRAE, CIRAD, IRD, Institut Agro, Univ. Montpellier, Montpellier, France

[1] Email: fabien.condamine@gmail.com

Author contributions: F.L.C. and G.J.K. wrote the paper.

The author declares no competing interest.

It is striking to observe that species richness is not evenly distributed across the surface of the planet. Current species diversity indeed decreases toward the poles, with Antarctica for instance being depauperate compared to tropical regions. This ubiquitous pattern has long attracted the attention of naturalists and more recently of evolutionary biologists and paleontologists to understand why species diversity peaks at the equator. But it remains poorly understood how polar biodiversity originated and diversified. Antarctica is currently defined as three large biogeographic regions: the Maritime Antarctic, the sub-Antarctic and the Continental Antarctic. The Maritime Antarctic region is largely separated from the rest of the world's oceans due to the Antarctic Circumpolar Current (ACC), differences in temperature along the Antarctic Polar Front (APF), and the presence of a deep sea surrounding the Antarctic shelf (1). The sub-Antarctic region consists of dozens of islands contained within the APF, generally characterized by the presence of tundra (absent from the Continental Antarctic) and fellfield habitats. As for the Continental Antarctic region, it is mostly uninhabitable, with less than 0.5% of its surface being ice-free. A long-standing idea is that biodiversity in Antarctica is low, and only constituted of old and poorly diversified lineages. In *PNAS*, a new study (2) – relying on both micro and macroevolutionary approaches – challenges this idea and shows that terrestrial life can thrive there.

Diversity and diversification in Antarctica

Our understanding of the origin and evolution of Antarctic biodiversity has greatly improved in recent years, thanks in part to studies revealing high levels of cryptic diversity, especially for marine organisms for which species diversity is often underestimated (3). Several molecular studies also show evidence for recent colonization and high *in situ* diversification, thus challenging the view that Antarctica is an inhospitable frozen region where groups cannot adapt, thrive and successfully diversify (1). Interestingly, elevated speciation rates have been recovered in marine organisms through estimations of divergence times coupled with diversification analyses in several groups (Fig. 1), such as marine fishes (4,5) or ophiuroids (6). Unexpectedly, these studies found higher diversification rates in Antarctica than in tropical regions in the last 10 million years (5,6). Despite its isolation, Antarctica has also been shown to act as an evolutionary source of marine biodiversity (7), as evidenced by the inference of multiple out-of-Antarctica biogeographic patterns during the Cenozoic (8,9). For terrestrial (including freshwater) organisms however, only a few groups are currently adapted to the extreme conditions of the sub-Antarctic and Continental Antarctic (1) and there had been no evidence supporting the hypothesis that sustained episodes of diversification could have occurred for them since the onset of the global cooling of Antarctica *ca*. 34 million years ago (Ma). The study of Baird *et al.* (2) elegantly questions the paradigm related to the diversification of terrestrial organisms in Antarctica and reveals that the sub-Antarctic region acted as a dynamic evolutionary arena for a beetle lineage during major cooling episodes and glacial cycles, spurring a significant radiation that parallels some of the adaptive radiations experienced by marine lineages (*e.g.* 10).

Shifting biomes as potential evolutionary arenas

Despite its scarcity, the Antarctic Eocene fossil record shows that terrestrial life was once rich, as exemplified by the presence of *Nothofagus* forests, frogs (11), and diverse birds and mammals (*e.g.* 12). All these groups progressively went extinct in Antarctica due to the major global cooling that began at the Eocene-Oligocene boundary (13), coinciding with the opening of the Drake Passage and the associated intensification of the ACC. Drastic environmental changes led to massive ecosystem turnover, precipitating the downfall of angiosperm communities and of their associated fauna. Further major cooling events occurred during the middle and late Miocene climate transition (*ca*. 14 Ma and 7 Ma, respectively), increasing the dominance of fellfield terrestrial habitats (even in the sub-Antarctic region), and leading to the disappearance of tundra habitat from continental Antarctica (14) and to the growth of ice sheets (13). Since then, it was thought the continent and surrounding islands have been depauperate of life, or only contain a few relict lineages. This seems true for most terrestrial groups such as snails (only one autochthonous species has been observed), or in most insect lineages that are only represented by one (*e.g*. Hemiptera, Hymenoptera) or a handful of species (*e.g.* Diptera, Lepidoptera).

However, this is not the case for the insect group studied by Baird *et al.* (2), the Ectemnorhini weevils (Coleoptera: Curculionidae). This group consists of 36 known species, all of which are distributed in the sub-Antarctic region, along the APF in the Kerguelen Province (*i.e.,* Crozet, Kerguelen, Prince Edward Islands, and Heard Island & McDonald Islands archipelagos). All species are flightless and present several unusual life-history traits, with one clade exhibiting unique algae- and moss-feeding specialization (‘cryptogam feeders’ *Bothrometopus* clade) and even including a so-called ‘marine’ species (*Palirhoeus eatoni*) strikingly adapted to the supralittoral zone. Using a combination of phylogenomics (515 genes; fossil-calibrated tree of 12 Ectemnorhini species and 87 outgroups) and phylogenetics (a five-gene phylogeny of Ectemnorhini including two-thirds of known species), Baird *et al.*

(2) inferred that this clade colonized the sub-Antarctic islands between 55 and 38 Ma (Eocene) from Africa, likely through the Crozet Archipelago. Such a journey would have involved a long-distance dispersal, which may seem unfeasible for these flightless insects. Yet, throughout their evolutionary history, these weevils have repeatedly colonized the sub-Antarctic islands, especially in the last 10 Myrs, despite these islands being isolated by >1,000 km of ocean in the ACC. Even more surprising is that a single species, *Palirhoeus eatoni*, is also distributed across several of these islands, thus testifying to the ability of these weevils to cross oceanic barriers. With knowledge on weevil resilience to dehydration and starvation, Baird *et al.* (2) propose the hypothesis that bird-mediated dispersal can explain the biogeographic pattern and the numerous intra-island dispersal events. Indeed, Antarctic seabirds regularly fly hundreds of kilometers in a single day when migrating between sub-Antarctic islands, and it is likely that invertebrates can attach to their feathers and then disperse with their carrier.

Importantly, Baird *et al.* (2) found evidence that the weevil clade is diversifying faster today than at its origin (especially in the last 5 Myrs), which goes against the general trend of diversification slowdown after origination (15). Consistent with the inferred increase in speciation rates, additional phylogeographic analyses focusing on *Palirhoeus eatoni* (population structure analysis based on 5,859 SNPs) also indicated that this lineage is in the process of incipient speciation, supporting the hypothesis that the clade is currently expanding. Using multiple diversification approaches, Baird *et al.* (2) inferred that speciation rates correlate with trends in global cooling, such that weevils diversified faster when climate cooled and when fellfield habitats became dominant. They postulate that changes in Antarctic conditions likely promoted their diversification on novel polar niches, in relation for instance with adaptation to cryptogams and better freezing tolerance in association with flightlessness. This diversification pattern parallels the specific adaptations observed in Antarctic fishes (4,10) and penguins (16), which also led to successful recent radiations.

Implications

The study of Baird *et al.* (2) calls for re-evaluation of the paradigm on the origin and evolution of species diversity in Antarctica during the Cenozoic. For the first time it is demonstrated that diversification of Antarctic terrestrial organisms may mirror those of marine organisms. This unveiling calls for more studies in other terrestrial groups, especially for those that potentially house high levels of cryptic biodiversity such as springtails (17) or tardigrades (18). This study on weevils should encourage further studies to infer dated phylogenies for Antarctic groups, as it is of paramount importance to determine their mode and tempo of diversification and assess whether there are similar trends in relation with known paleoenvironmental changes (Fig. 1). Studying these Antarctic groups can also bring light on the evolution of the latitudinal diversity gradient, in particular to understand why some regions are species-poor compared to others, but show high *in situ* diversification.

Even if Antarctica and the surrounding islands are isolated and inhospitable for humans, they are not spared from human-driven threats and their regional biodiversity remains poorly protected (19). If most groups follow a similar diversification pattern to Ectemnorhini weevils in relation to climate cooling, they may be highly vulnerable to global warming. The Antarctic ice cap is indeed melting at unprecedented rates (20), which may destabilize the ecosystem relied upon by this regional pool of species that may currently be in the process of diversifying.

ACKNOWLEDGMENTS

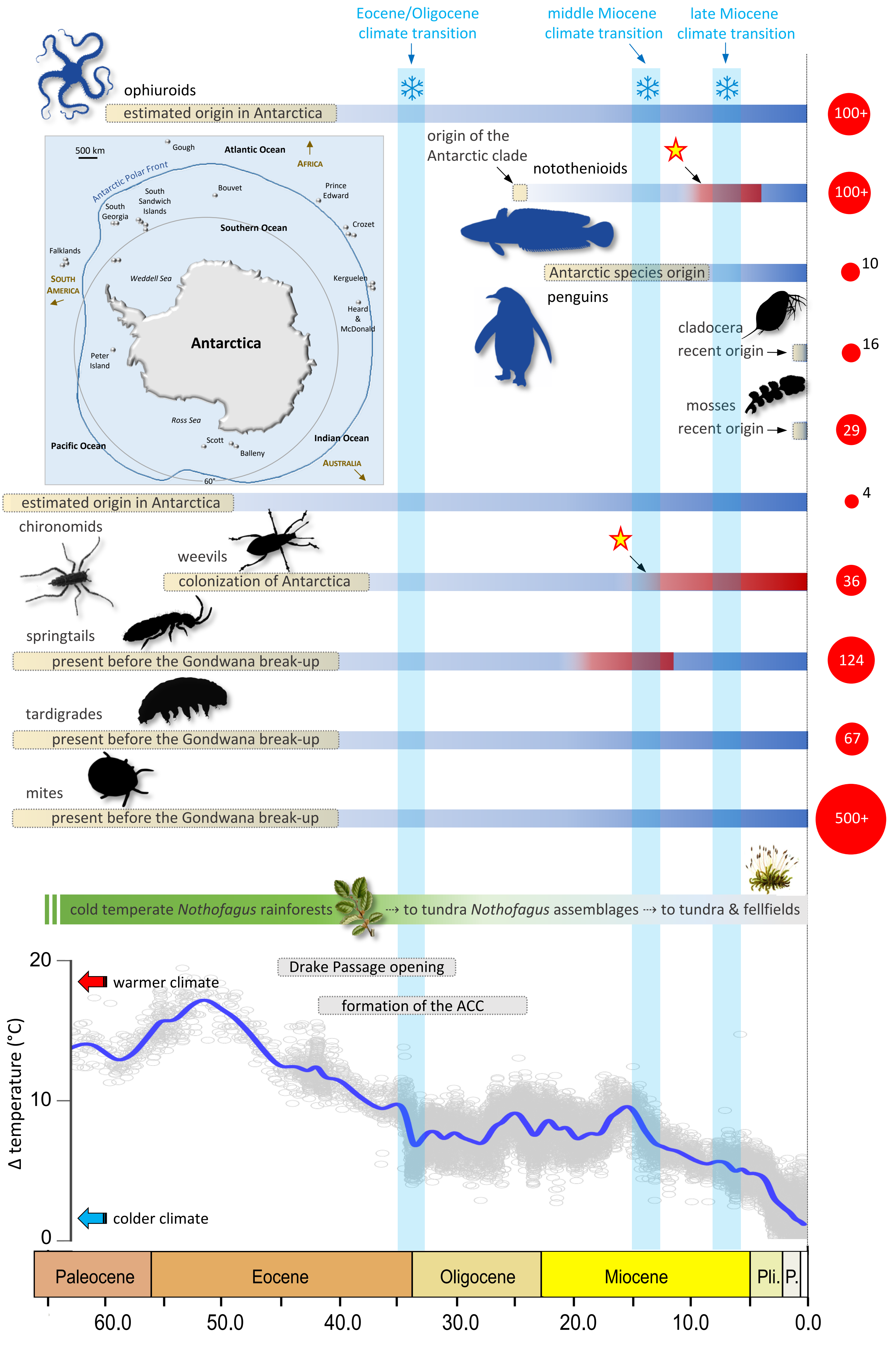
We thank J. L. Abbate for comments and suggestions.

REFERENCES

1. P. Convey, *et al.*, Antarctic terrestrial life – challenging the history of the frozen continent? *Biol. Rev.* **83**, 103-117 (2008).
2. H. P. Baird *et al*., Fifty million years of beetle evolution along the Antarctic Polar Front. *Proc. Natl. Acad. Sci. USA* **XXX**, XXXX-XXXX (2021).
3. M. L. Verheye, T. Backeljau, C. d'Udekem d'Acoz, Looking beneath the tip of the iceberg: diversification of the genus *Epimeria* on the Antarctic shelf (Crustacea, Amphipoda). *Polar Biol.* **39**, 925-945 (2016).
4. T. J. Near *et al*., Ancient climate change, antifreeze, and the evolutionary diversification of Antarctic fishes. *Proc. Natl. Acad. Sci. USA* **109**, 3434-3439 (2012).
5. D. L. Rabosky *et al*., An inverse latitudinal gradient in speciation rate for marine fishes. *Nature* **559**, 392-395 (2018).
6. T. D. O'Hara, A. F. Hugall, S. N. C. Woolley, G. Bribiesca-Contreras, N. J. Bax, Contrasting processes drive ophiuroid phylodiversity across shallow and deep seafloors. *Nature* **565**, 636-639 (2019).

7. A. Dornburg, S. Federman, A. D. Lamb, C. D. Jones, T. J. Near, Cradles and museums of Antarctic teleost biodiversity. *Nat. Ecol. Evol.* **1**, 1379-1384 (2017).
8. K. Göbbeler, A. Klussmann-Kolb, Out of Antarctica? – New insights into the phylogeny and biogeography of the Pleurobranchomorpha (Mollusca, Gastropoda). *Mol. Phylogenet. Evol*. **55**, 996-1007 (2010).
9. L. Dietz, J. S. Dömel, F. Leese, A. R. Mahon, C. Mayer. Phylogenomics of the longitarsal Colossendeidae: the evolutionary history of an Antarctic sea spider radiation. *Mol. Phylogenet. Evol*. **136**, 206-214 (2019).
10. S. Rutschmann *et al.*, Parallel ecological diversification in Antarctic notothenioid fishes as evidence for adaptive radiation. *Mol. Ecol.* **20**, 4707-4721 (2011).
11. T. Mörs, M. Reguero, D. Vasilyan, First fossil frog from Antarctica: implications for Eocene high latitude climate conditions and Gondwanan cosmopolitanism of *Australobatrachia*. *Sci. Rep.* **10**, 5051 (2020).
12. S. N. Davis *et al*., New mammalian and avian records from the late Eocene La Meseta and Submeseta formations of Seymour Island, Antarctica. *PeerJ* **8**, e8268 (2020).
13. T. Westerhold *et al*., An astronomically dated record of Earth's climate and its predictability over the last 66 million years. *Science* **369**, 1383-138 (2020).
14. A. R. Lewis *et al*., Mid-Miocene cooling and the extinction of tundra in continental Antarctica. *Proc. Natl. Acad. Sci. USA* **105**, 10676-10680 (2008).
15. H. Morlon, M. D. Potts, J. B. Plotkin, Inferring the dynamics of diversification: a coalescent approach. *PLoS Biol.*, **8**, e1000493 (2010).
16. Vianna *et al*., Genome-wide analyses reveal drivers of penguin diversification. *Proc. Natl. Acad. Sci. USA* **117**, 22303-22310 (2020).
17. Carapelli *et al*., Evidence for cryptic diversity in the "Pan□Antarctic" springtail *Friesea antarctica* and the description of two new species. *Insects* **11**, 141 (2020).
18. A. Velasco-Castrillón *et al*., Mitochondrial DNA analyses reveal widespread tardigrade diversity in Antarctica. *Invertebr. Syst*. **29**, 578-590 (2015).
19. H. S. Wauchope, J. D. Shaw, A. Terauds, A snapshot of biodiversity protection in Antarctica. *Nat. Commun*. **10**, 946 (2019).
20. P. Convey, S. L. Peck, Antarctic environmental change and biological responses. *Sci. Adv.* **11**, eaaz0888 (2021).

Fig. 1. Cenozoic environmental changes and diversification patterns in Antarctica. Molecular dated phylogenies (2,4,5,6,16) provide evidence of the timing of diversification in Antarctica for marine (blue silhouettes) and terrestrial (black silhouettes) groups. One terrestrial clade (Ectemnorhini weevils, 1) and one marine clade (Antarctic icefishes, 4) show increasing diversification toward the present (yellow stars) potentially correlated to climate cooling. Estimates of Antarctic endemics species for each group are provided on the right. The Cenozoic climate curve indicates the main events of global cooling (13). Pli., Pliocene; P, Pleistocene. Organism images credit (*Top* to *Bottom*): Phlyopic/Jonathan Lawley; Phylopic/Lily Hughes; Phylopic/Mathilde Cordellier, licensed under CC BY-NC 3.0; Phylopic/Steven Traver; Phlyopic/Ernst Haeckel and T. Michael Keesey; Phylopic/JCGiron, licensed under CC BY 3.0; F.C. and G.K.; Phlyopic/Kamil S. Jaron; Phylopic/Fernando Carezzano; and Phylopic/Birgit Lang, licensed under CC BY 3.0.


Eocene/Oligocene climate transition
middle Miocene climate transition
late Miocene climate transition
ophiuroids
estimated origin in Antarctica
100+
500 km
Gough
Atlantic Ocean
Africa
Antarctic Polar Front
South Sandwich Islands
Bouvet
Prince Edward
South Georgia
Southern Ocean
Crozet
Falklands
South America
Weddell Sea
Kerguelen
Heard & McDonald
Antarctica
Peter Island
Ross Sea
Scott
Balleny
Indian Ocean
Pacific Ocean
Australia
60°
origin of the Antarctic clade
notothenioids
100+
Antarctic species origin
10
penguins
cladocera
recent origin
16
mosses
recent origin
29
estimated origin in Antarctica
4
chironomids
weevils
colonization of Antarctica
36
springtails
present before the Gondwana break-up
124
tardigrades
present before the Gondwana break-up
67
mites
present before the Gondwana break-up
500+
cold temperate Nothofagus rainforests → to tundra Nothofagus assemblages → to tundra & fellfields
20
10
0
Δ temperature (°C)
warmer climate
colder climate
Drake Passage opening
formation of the ACC
Paleocene
Eocene
Oligocene
Miocene
Pli.
P.
60.0
50.0
40.0
30.0
20.0
10.0
0.0