



## Reorganization of Southern Ocean Plankton Ecosystem at the Onset of Antarctic Glaciation

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*Science* **340**, 341 (2013);

DOI: 10.1126/science.1223646

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at intermediate [EtOAc]. At 137 mM and 183 mM EtOAc, although most particles still showed only one branch per core, a fraction had one, two, three, and even four branches (Fig. 4, A and B). Close TEM examination of these mc-MSNs revealed that the angles at which the hexagonally structured branches grew were in agreement with models in which hexagonal branches grow in  $\langle 111 \rangle$  directions off of the core, consistent with the epitaxial relationship (compare TEM images with corresponding models in Fig. 4, C to F and H to K, respectively). No MSN with more than four branches was observed in our samples, although we did observe some mc-MSNs in which hexagonal branches that grew in two distinct directions merged into one branch with a large diameter (compare TEM image with model in Fig. 4, G and L). On a truncated cubic structure, there are eight  $\langle 111 \rangle$  equivalent surfaces corresponding to the number of cube vertices, giving eight equivalent sites for hexagonal branches to form and grow. As a particular branch grows, it may deplete the available silica in its direct vicinity, thus preventing growth of another branch next to it. This is one possible explanation for why the vast majority of observed branches had grown on non-nearest  $\langle 111 \rangle$  core surfaces and why the maximum number of branches observed was only four. We further hypothesize that when two nearest neighboring sites nucleate hexagonal branches, geometrical crowding joins the neighboring nuclei as they grow. Such merging and overgrowth of hexagonal rods also reduces the number of rods per particle and increases the rod diameter relative to the core particle size. This may be what leads to the observed structures in the 457 mM EtOAc sample (Fig. 2G).

Finally, to access higher-level architectures, we performed mc-MSN syntheses in a two-step fashion by adding further monomers at different time points of the reaction (2I). The TEM results in Fig. 4M, displaying a high number of dimers (two cubes) and trimers (three cubes) connected via bridges, are encouraging. They suggest that further tuning of reaction conditions holds promise for achieving even more complex architectures—for example, through switching back and forth between cubic-to-hexagonal and hexagonal-to-cubic transitions—similar to what has been observed for semiconductor nanoparticles or colloids with valence (1I, 27).

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**Acknowledgments:** Supported by NSF single-investigator grant DMR-1104773 and by a Partnership for Research and Education in Materials (PREM) program at Norfolk State University through NSF grant DMR-1205457. We thank L. Estroff, R. Dieckmann, and K. Hur (Cornell University) for discussions on multiple branch growth and K. W. Tan (Cornell University) for assistance with EM. This work made use of the TEM and STEM supported by the Cornell Center for Materials Research with support from the NSF Materials Research Science and Engineering Centers program (DMR-1120296), and CHESS, which is supported by the NSF and the National Institute of General Medical Sciences under NSF award DMR-0936384. T.S. is grateful for a Thai Government Scholarship under the Ministry of Science and Technology.

#### Supplementary Materials

www.sciencemag.org/cgi/content/full/340/6130/337/DC1  
Materials and Methods  
Figs. S1 to S4  
Reference (28)

11 October 2012; accepted 1 February 2013  
10.1126/science.1231391

## Reorganization of Southern Ocean Plankton Ecosystem at the Onset of Antarctic Glaciation

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The circum-Antarctic Southern Ocean is an important region for global marine food webs and carbon cycling because of sea-ice formation and its unique plankton ecosystem. However, the mechanisms underlying the installation of this distinct ecosystem and the geological timing of its development remain unknown. Here, we show, on the basis of fossil marine dinoflagellate cyst records, that a major restructuring of the Southern Ocean plankton ecosystem occurred abruptly and concomitant with the first major Antarctic glaciation in the earliest Oligocene (~33.6 million years ago). This turnover marks a regime shift in zooplankton-phytoplankton interactions and community structure, which indicates the appearance of eutrophic and seasonally productive environments on the Antarctic margin. We conclude that earliest Oligocene cooling, ice-sheet expansion, and subsequent sea-ice formation were important drivers of biotic evolution in the Southern Ocean.

Long-term cooling during the middle and late Eocene [~49 to 34 million years ago (Ma)] led to the inception of continental-

scale glaciation of Antarctica during the Eocene-Oligocene Transition (EOT, 34 to 33.5 Ma) (1, 2). The EOT culminated in a pronounced positive

shift in the oxygen isotope ratios of marine biogenic calcite during Oligocene isotope event 1 (Oi1; 33.7 Ma) (3, 4). Direct evidence for

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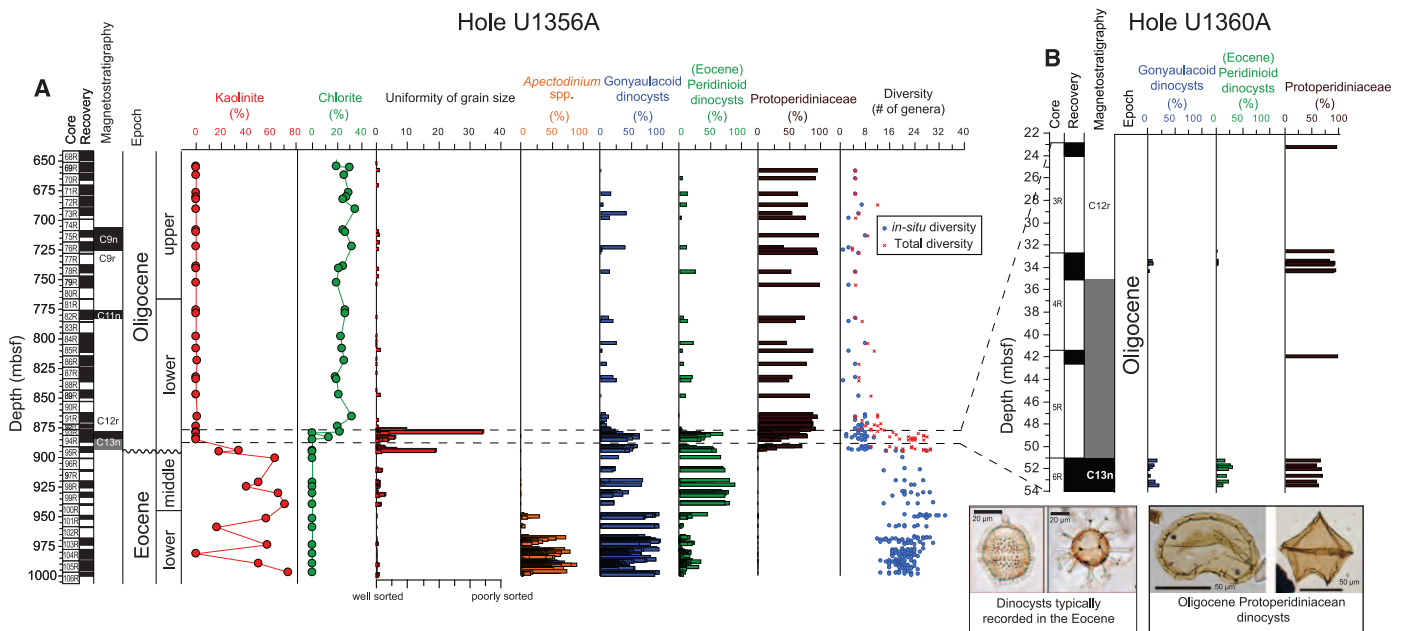
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**Fig. 1.** Antarctic topography [modified after (33), maximum topography model], circum-Antarctic paleogeography at 34 Ma (34) and the location of sites considered in this study. Light blue areas represent shelf environments; green areas represent Antarctic lowland areas. The black circle indicates 60°S.

continental-scale glaciation of Antarctica at O11 includes the appearance of ice-rafted debris and physically weathered clay minerals at sites along the Antarctic margin (5, 6). Numerical climate model simulations suggest that partial to full-scale glaciation of Antarctica occurred after a reduction in atmospheric CO<sub>2</sub> concentrations and a series of low-amplitude orbital variations in solar insolation that resulted in relatively cool austral summer temperatures (7). Such conditions, as well as continental ice, were also likely required for seasonal sea-ice formation (7). As a consequence, the establishment of Antarctic glaciation should have substantially impacted circum-Antarctic Southern Ocean ecosystems, and associated biotic changes are potentially reflected in the fossil record in conjunction with the O11 climate event.

The present-day circum-Antarctic seas are home to distinct plankton communities that are characterized by a high degree of endemism and high seasonal productivity as a result of steep seasonal gradients in temperature, salinity, light availability, and nutrient concentrations associated with sea-ice cover (8, 9). Diatoms and *Phaeocystis* (unicellular, eukaryotic photosynthetic algae) are the dominant primary producers of these communities (9, 10). Whereas the latter does not preserve in the geological record, fossil diatom skeletons composed of silica are routinely used to reconstruct Antarctic sea-ice history for the recent past (11). However, diatom-based sea-ice reconstructions for the Eocene-Oligocene time interval



**Fig. 2.** The Eocene-Oligocene section recovered in IODP hole U1356A (A) and the lower Oligocene section from IODP hole U1360A (B). A shift in clay mineralogy in the lowermost Oligocene of site U1356A indicates the initiation of a physical (i.e., glacial) weathering regime. The uniformity coefficient of grain size—a measure of the sorting of the sediments, with large numbers (>4) indicating poorly sorted sediments—increases episodically in the lower Oligocene, suggesting glacial activity. The magnetostratigraphic interpretations are derived from (19) and as presented in the supplementary text; gray

areas indicate uncertain magnetic polarity. Lower to middle Eocene dinocyst assemblages are diverse (expressed by number of genera), with subtropical components (*Apectodinium*) and autotrophic (gonyaulacoid taxa) and Eocene heterotrophic (peridinioid dinocysts) representatives (supplementary text). We consider the majority of non-protoperidiniacean dinocysts in the lower Oligocene succession reworked (translucent colored bars; see also supplementary text). Photomicrographs of typical Eocene and Oligocene dinocyst taxa are depicted in the lower right corner.

are hampered by poor diatom preservation in Antarctic margin sediments as well as the poorly resolved paleoecology of many fossil taxa (12). Therefore, other microfossil groups must be used to investigate the timing of the installation of these ecosystems and how the development of Antarctic plankton communities was linked to cooling and glaciation in the geological past.

Although dinoflagellates are not a major group in terms of biomass, many heterotrophic species are abundant in the areas of high seasonal productivity in the modern Southern Ocean (13, 14) (supplementary text) and are closely associated with primary algal producers, including diatoms (13). Fortunately, many dinoflagellate taxa also produce distinct organic fossilizable cysts as part of their life cycle, and these dinocysts are preserved in high-latitude sedimentary sequences. In the Eocene, before the onset of Antarctic glaciation, dinocysts are found in great diversity and have been used to reconstruct environmental change in high-latitude environments (15, 16). Hence, dinocyst assemblage analysis of sediment cores is a valuable tool for evaluating circum-Antarctic plankton ecosystem change across the EOT. Yet, such evaluation has been previously hampered by the absence of well-dated records from the Antarctic margin.

Integrated Ocean Drilling Program (IODP) Expedition 318 recovered a Paleogene succession of marine sediments off Wilkes Land, East Antarctica (17). Deep-marine sediments spanning most of the Oligocene were recovered at IODP site U1356 on the continental rise, whereas shallow-marine sediments of early Oligocene age were recovered at IODP site U1360 (Fig. 1). In IODP hole U1356A, a hemipelagic succession of Oligocene claystones and siltstones was recovered

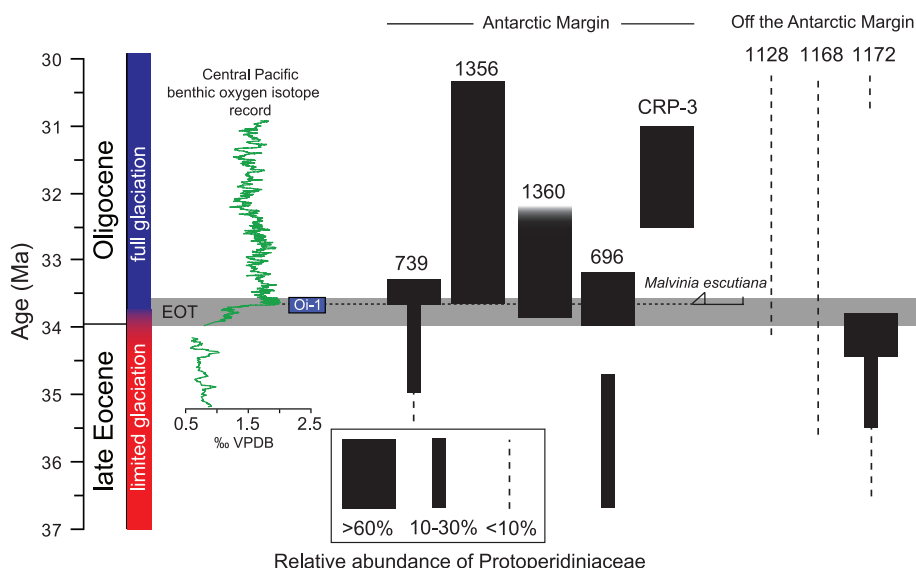
between 894.68 and 422.19 m below the sea floor (mbsf). The base of this section is approximately correlative to the Oi1 event, as indicated by the presence of the marker dinocyst *Malvinia escutiana* (18) and the identification of magnetostratigraphic C13n (19). An ~12-million-year-long hiatus separates the middle Eocene and lower Oligocene sections at Site U1356 (supplementary text) (19). This hiatus marks a change from clay mineral assemblages dominated by kaolinite and smectite, which formed under relatively warm and humid conditions, to abundant chlorite and illite group minerals, which are indicative of physical weathering by glacial and periglacial processes (17). In hole U1360A, clast-bearing glaciomarine sediments were recovered between 54 and 23 mbsf (Fig. 2). These strata were deposited between ~33.6 and ~32 Ma (supplementary text, and they span or immediately postdate Oi1 (17, 19). We generated dinocyst assemblage and sedimentological and geochemical data from holes U1356A and U1360A that document the environmental and ecosystem evolution on the Wilkes Land margin associated with the establishment of the Antarctic cryosphere (20). These data are complemented with qualitative information derived from pyritized siliceous microfossils [e.g., diatoms (supplementary text)] and supporting dinocyst assemblage data from five additional Southern Ocean drillcores that span the EOT (figs. S2, S4, and S5 and supplementary text).

At continental rise site U1356 (Fig. 1), early and middle Eocene (53 to 45 Ma) dinocyst assemblages are highly diverse and are composed of both auto- and heterotrophic dinoflagellate taxa (Fig. 2). In sharp contrast, earliest Oligocene assemblages at sites U1356 and U1360 are low in

diversity and overwhelmingly dominated by cysts of Proto-peridiniaceae, a family of exclusively heterotrophic cyst-producing dinoflagellates (21). Among the early Oligocene proto-peridiniacean dinocysts, specimens closely resembling the modern *Selenopemphix antarctica* [here referred to as *S. cf. antarctica* are recorded in low-to-moderate abundance (2 to 20%). *S. antarctica* is the dominant dinocyst taxon in the modern seasonal sea-ice zone of the Southern Ocean (supplementary text) (22, 23). At site U1356, the first appearance of dominant Proto-peridiniaceae is accompanied by sedimentological indications of glacial activity, such as the deposition of outsized clasts (17), and increased sedimentary grain-size uniformity (Fig. 2). Furthermore, this assemblage shift is accompanied by an increase in the abundance and diversity of pyritized siliceous microfossils at site U1356, reflecting elevated primary productivity (supplementary text).

In order to determine whether the distinctive, low-diversity proto-peridiniacean dinocyst assemblages occurred widely around Antarctica and whether the success of this plankton group was directly linked with glacial expansion in the earliest Oligocene, we also investigated dinocyst assemblages from three other sediment cores at sites positioned close to the Antarctic margin (Fig. 3). We used the first occurrence (FO) of *M. escutiana* as a marker for the correlative level of Oi1 (18). At Ocean Drilling Program (ODP) site 739 in Prydz Bay (Fig. 1), relatively diverse high-latitude assemblages with small Proto-peridiniaceae in low abundance characterize the upper Eocene interval (fig. S4). These are replaced by dominant Proto-peridiniaceae, including *S. cf. antarctica*, at the level correlative to Oi1, where biogenic silica (i.e., diatom) concentrations also significantly increase (fig. S4). A relatively complete Eocene-Oligocene succession was recovered at ODP site 696 in the Weddell Sea (Fig. 1). There, the early late Eocene interval is also characterized by relatively diverse high-latitude assemblages with abundant (>20%) small Proto-peridiniaceae (fig. S5). At the EOT, the Proto-peridiniaceae (including *S. cf. antarctica*) become dominant. At Cape Roberts Drilling Project site CRP-3 in the Ross Sea (Fig. 1), dinocysts are scarce and poorly preserved across the EOT interval (24). Further up-section (above 190 mbsf), however, well-preserved assemblages are present and include *M. escutiana*, implying an earliest Oligocene age, and dominant Proto-peridiniaceae, similar to the assemblages recorded at the other circum-Antarctic sites (supplementary text).

To assess whether biotic turnover across the EOT was indeed restricted to the circum-Antarctic regions, we also considered time-equivalent lower Oligocene successions from ODP sites 1128 (Australian Bight), 1168 (west of Tasmania), and 1172 (East Tasman Plateau), which are located more distally from the Antarctic margin in the Southern Ocean. All early Oligocene assemblages at these sites are devoid of proto-peridiniacean dinocysts (supplementary text). Instead, they are characterized by relatively diverse dinocyst assemblages that



**Fig. 3. Summary of the relative abundance of proto-peridiniacean dinocysts at circum-Antarctic drill sites.** The deep-sea oxygen isotope record is after (4), and Oi1 marks the final large oxygen isotope shift of the EOT (gray band). Large specimens of *S. cf. antarctica* and *M. escutiana* occur from Oi1 onward. If no bar is indicated, there is no sedimentary record for that time interval. Proto-peridiniacean dinocysts abundant in the Upper Eocene of ODP site 1172 solely comprise *Brigantedinium* spp. and are likely related to oceanic upwelling conditions at this location (35) (supplementary materials).



were produced by autotrophic dinoflagellates (supplementary materials). Late Eocene assemblages at site 1172 nonetheless contain abundant protoperidiniacean dinocysts (Fig. 3); however, these protoperidiniacean taxa exclusively comprise the genus *Brigantidium* and are interpreted to indicate strong oceanic upwelling (23). The absence of the typical Protoperidiniaceae at these sites illustrates that the appearance of near-modern Antarctic dinocyst assemblages at Oi1 was geographically restricted to areas close to the Antarctic margin (Fig. 3).

There are several possible explanations for the distinct shift in dinocyst assemblages across Oi1 at sites around the Antarctic margin. First, modern protoperidiniacean dinocyst taxa include cosmopolitan generalist heterotrophs that are abundant in a wide array of environments, such as deltaic (25) and open-ocean upwelling settings (26). Hence, the abrupt occurrence of protoperidiniacean dinocysts may have been connected with high primary productivity resulting from invigorated vertical mixing associated with intensified polar easterly wind fields after the emplacement of the Antarctic ice sheet (7). This mechanism would have primarily contributed to high abundance of heterotrophic Protoperidiniaceae in the modern-day domain of the Antarctic Circumpolar Current (22) and therefore fails to explain why Protoperidiniaceae became particularly abundant at Antarctic shelf sites. It also fails to explain why non-protoperidiniacean heterotrophic taxa that were already abundant in the Eocene Southern Ocean (16) did not proliferate, particularly at ODP site 1168. Second, a transient increase in nutrient availability in shelf waters caused by enhanced continental erosion during the Oi1 glacial expansion (27) could have contributed to high productivity and the successive appearance of the heterotrophic dinoflagellate communities around Antarctica. However, this scenario does not account for the dominance of protoperidiniacean communities during subsequent glacial-interglacial cycles after Oi1. These cycles would have likely been characterized by highly variable nutrient input to Antarctic shelf waters on orbital (20 to 400 thousand years) time scales, resulting in pulsed abundance distributions of protoperidiniaceans; we instead record stable protoperidiniacean-dominated assemblages throughout the early Oligocene.

Modern Antarctic phytoplankton communities are adapted to seasonal sea-ice conditions, either as plankton in the upper surface waters, ice-dwelling extremophiles occupying brine channels and pockets, or attached subice communities (8, 9). During the spring sea-ice melt, accumulated nutrients are released from the ice into the surrounding melt zone, resulting in a nutrient-rich shallow mixed layer that stimulates intensive and relatively short-lived blooms of primary producers (8–10). By analogy to the modern ecosystem, and considering an abrupt regional increase in siliceous sedimentation at Southern Ocean sites across Oi1 (28) and increased abundance and diversity of pyritized siliceous microfossils at site

UI1356 (supplementary text), we conclude that seasonal blooms of phytoplankton initiated in the circum-Antarctic seas. This third scenario, involving an abrupt shift to high seasonal primary productivity associated with the development of seasonal sea ice, provides the most consistent explanation for the abundant appearance of protoperidiniacean dinocysts at Oi1. This mechanism is in agreement with numerical climate models simulations indicating that sea-ice formation along Antarctic margins may have followed full-scale Antarctic glaciation (7). Therefore, we propose that seasonal sea-ice formation was a critical factor in the early Oligocene reorganization of Antarctic plankton ecosystems.

Although the overall annual primary productivity in the modern sea-ice zone is generally low compared with other regions of the Southern Ocean (29), it does provide a highly concentrated and seasonal food source for grazers. This is illustrated by the pivotal role that high seasonal productivity associated with sea-ice conditions plays in the life-cycle of Antarctic krill (*Euphausia superba*) (30), a zooplankton group that sustains higher trophic level organisms in the Southern Ocean food web. The ecological response to Antarctic cryosphere development in the early Oligocene, as recorded by the rise to dominance of Protoperidiniaceae, may thus have been an important driver of niche differentiation, affecting many biotic groups. Indeed, molecular clock studies reveal important evolutionary events at higher trophic levels, such as the genetic divergence between baleen and toothed whales and the origination of extant penguins during the Eocene-Oligocene time interval (31, 32). We consequently infer that the pervasive environmental changes related to Antarctic glaciation in the early Oligocene, including sea-ice formation and a shift to intense seasonal primary productivity patterns, led to the concurrent rise of new plankton communities in Antarctic shelf waters and set the stage for major evolutionary turnover in metazoans.

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**Acknowledgments:** This research used samples from the ODP and the IODP. The ODP was sponsored by the NSF and participating countries under management of Joint Oceanographic Institutions (JOI) Incorporated. A.J.P.H. and H.B. thank Statoil for funding. P.K.B., F.S., and H.B. thank the Netherlands Organisation for Scientific Research (NWO) (grant 86610110) and the LPP Foundation for funding. J.P. and U.R. acknowledge support through the German Research Foundation (grants PR 651/10 and RO 1113/6). J.P. thanks the Biodiversity and Climate Research Center within the Hessian Initiative for Scientific and Economic Excellence (LOEWE) for support. S.P. acknowledges financial support from a Post-Expedition Activity award administered by the U.S. Science Support Program and research support from NSF award ANT-1245283. T.v.d.F. acknowledges the Natural Environmental Research Council (UK) for a cruise participation grant (NE/H025162/1) and the European Commission for a Marie Curie Reintegration grant (IRG 230828). S.M.B. and T.v.d.F. further acknowledge UK IODP funding (grant NE/I006257/1). S.M.B. acknowledges the Natural Environmental Research Council (UK) for a cruise participation grant (NE/H020098/1) and postcruise research support (NE/J019801/1). L.T. acknowledges support from NSF grants OCE 1058858 and OCE 1054497. A.S. thanks the European Research Council for ERC Starting Grant 259627. C.E. thanks the Spanish Ministry for Science and Innovation (grant CTM2011–2079). The reported data are available in the supplementary materials.

#### Supplementary Materials

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Materials and Methods

Supplementary Text

Figs. S1 to S6

Tables S1 to S3

Plate S1

References (36–92)

Data

23 April 2012; accepted 15 February 2013

10.1126/science.1223646