

Environmental forcings of Paleogene Southern Ocean dinoflagellate biogeography

Peter K. Bijl,¹ Jörg Pross,² Jeroen Warnaar,¹ Catherine E. Stickley,^{3,4} Matthew Huber,⁵ Raquel Guerstein,⁶ Alexander J. P. Houben,¹ Appy Sluijs,¹ Henk Visscher,¹ and Henk Brinkhuis¹

Received 30 November 2009; revised 27 August 2010; accepted 1 October 2010; published 4 February 2011.

[1] Despite warm polar climates and low meridional temperature gradients, a number of different high-latitude plankton assemblages were, to varying extents, dominated by endemic species during most of the Paleogene. To better understand the evolution of Paleogene plankton endemism in the high southern latitudes, we investigate the spatiotemporal distribution of the fossil remains of dinoflagellates, i.e., organic-walled cysts (dinocysts), and their response to changes in regional sea surface temperature (SST). We show that Paleocene and early Eocene (~65–50 Ma) Southern Ocean dinocyst assemblages were largely cosmopolitan in nature but that a distinct switch from cosmopolitan-dominated to endemic-dominated assemblages (the so-called “transantarctic flora”) occurred around the early-middle Eocene boundary (~50 Ma). The spatial distribution and relative abundance patterns of this transantarctic flora correspond well with surface water circulation patterns as reconstructed through general circulation model experiments throughout the Eocene. We quantitatively compare dinocyst assemblages with previously published TEX₈₆-based SST reconstructions through the early and middle Eocene from a key locality in the southwest Pacific Ocean, ODP Leg 189 Site 1172 on the East Tasman Plateau. We conclude that the middle Eocene onset of the proliferation of the transantarctic flora is not linearly correlated with regional SST records and that only after the transantarctic flora became fully established later in the middle Eocene, possibly triggered by large-scale changes in surface-ocean nutrient availability, were abundances of endemic dinocysts modulated by regional SST variations.

Citation: Bijl, P. K., J. Pross, J. Warnaar, C. E. Stickley, M. Huber, R. Guerstein, A. J. P. Houben, A. Sluijs, H. Visscher, and H. Brinkhuis (2011), Environmental forcings of Paleogene Southern Ocean dinoflagellate biogeography, *Paleoceanography*, 26, PA1202, doi:10.1029/2009PA001905.

1. Introduction

[2] Early Paleogene temperatures and atmospheric CO₂ concentrations were significantly higher than today [Pearson and Palmer, 2000; Sexton *et al.*, 2006; Sluijs *et al.*, 2006; Zachos *et al.*, 2008; Bijl *et al.*, 2009]. This long-term global warm period peaked during the late early Eocene (~52–50 Ma) [Zachos *et al.*, 2001; Sexton *et al.*, 2006], with high

(>30°C) southern high-latitude SSTs and minimal latitudinal temperature gradients [e.g., Bijl *et al.*, 2009]. The subsequent long-term global cooling through the middle and late Eocene [Sexton *et al.*, 2006; Zachos *et al.*, 2008; Bijl *et al.*, 2009] culminated in the establishment of large Antarctic ice sheets around the time of the Eocene-Oligocene boundary (~34 Ma) [Miller *et al.*, 1987; DeConto and Pollard, 2003a, 2003b; Coxall *et al.*, 2005; Barker *et al.*, 2007].

[3] The warm climates and low latitudinal temperature gradients prior to the onset of major Antarctic glaciation facilitated the poleward migration of many biota [Adams *et al.*, 1990; Sluijs *et al.*, 2006; Eberle *et al.*, 2009]. Surprisingly, however, Southern Ocean fossil assemblages are distinctly endemic during long intervals of the early Paleogene and become increasingly endemic over time; besides mollusks [Zinsmeister, 1979], this phenomenon has been observed in numerous microfossil groups such as dinocysts [Wrenn and Beckman, 1982; Wrenn and Hart, 1988], radiolaria [Lazarus and Caulet, 1993; Lazarus *et al.*, 2008], calcareous nannoplankton and planktonic foraminifera [Nelson and Cooke, 2001; Villa *et al.*, 2008], and diatoms [Harwood, 1991; Stickley *et al.*, 2004b]. Dinocysts are

¹Biomarine Sciences, Laboratory of Palaeobotany and Palynology, Institute of Environmental Biology, Faculty of Science, Utrecht University, Utrecht, Netherlands.

²Paleoenvironmental Dynamics Group, Institute of Geosciences, Frankfurt University, Frankfurt, Germany.

³Department of Geology, University of Tromsø, Tromsø, Norway.

⁴Norwegian Polar Institute, Polar Environmental Centre, Tromsø, Norway.

⁵Earth and Atmospheric Sciences, Purdue University, West Lafayette, Indiana, USA.

⁶INGEOSUR, Departamento de Geología, Universidad Nacional del Sur, San Juan, Bahía Blanca, Argentina.

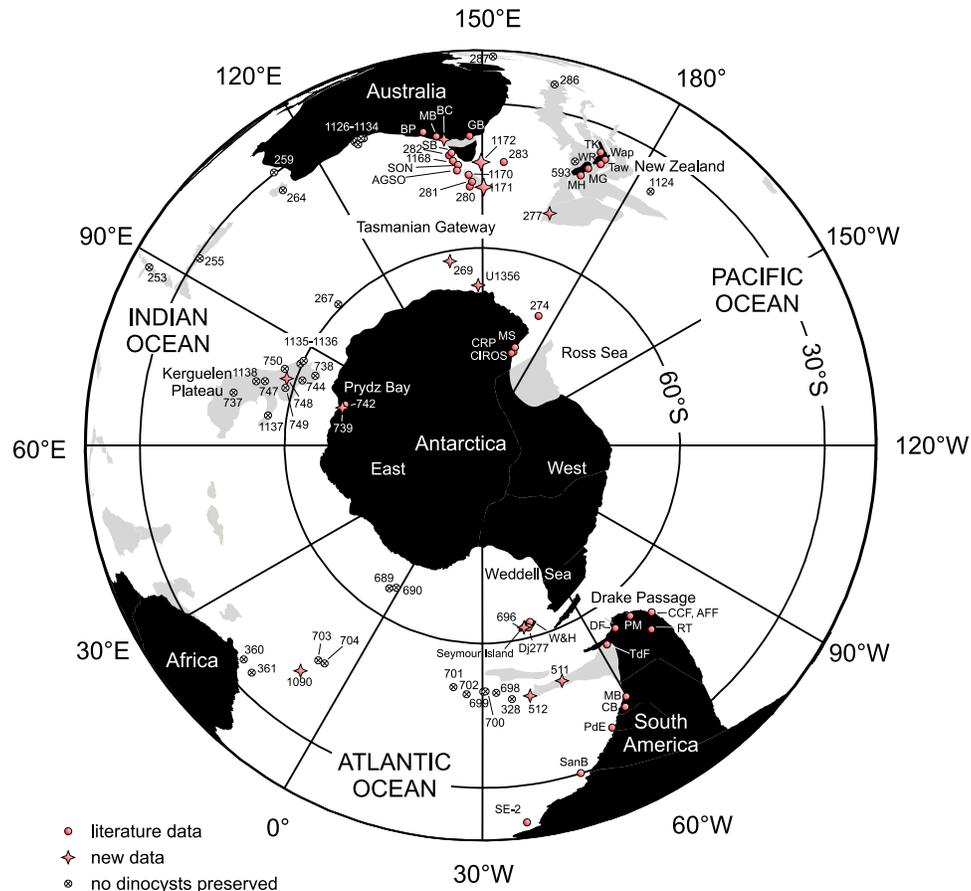


Figure 1. Location map for present-day positions of evaluated sites. Numbers 253–593 refer to Deep Sea Drilling Project (DSDP) sites; numbers 689–1172 refer to Ocean Drilling Program (ODP) sites. IODP Site U1356 refers to a site drilled by the Integrated Ocean Drilling Program. For code legend, see Table S1. The geographic map was derived from the Ocean Drilling Stratigraphic Network (ODSN).

abundant in marginal marine sediments, notably at high latitudes. The early Paleogene Antarctic endemic dinocyst community is taxonomically well documented from outcrops and sediment cores around the Antarctic margin, and it is often referred to as the “transantarctic flora” [cf. *Wrenn and Beckman*, 1982]. However, the evolution and driving forces behind this Paleogene Southern Ocean endemism are largely unknown, although SST is presumed to have been involved [*Huber et al.*, 2004]. So far, a lack of reliable SST reconstructions has hampered the evaluation of this hypothesis, and it is only through recently published geochemical data [*Bijl et al.*, 2009] that such a test has become possible.

[4] In this study, we aim to elucidate the role of oceanic surface circulation, SST and other environmental changes as a potential selective mechanism for Eocene Antarctic endemism among dinoflagellates. First, we provide an overview of Paleogene dinocyst paleobiogeography, for which we integrate newly generated palynological data with those previously published. Additionally, we statistically examine the relation of SST (using the TEX_{86} paleothermometry of

Bijl et al. [2009]) and ocean-wide productivity (using the thallium isotope records of *Nielsen et al.* [2009]) to dinocyst assemblage changes in the southwest Pacific Ocean (Ocean Drilling Program Site 1172).

2. Material and Methods

2.1. Southern Ocean Sites

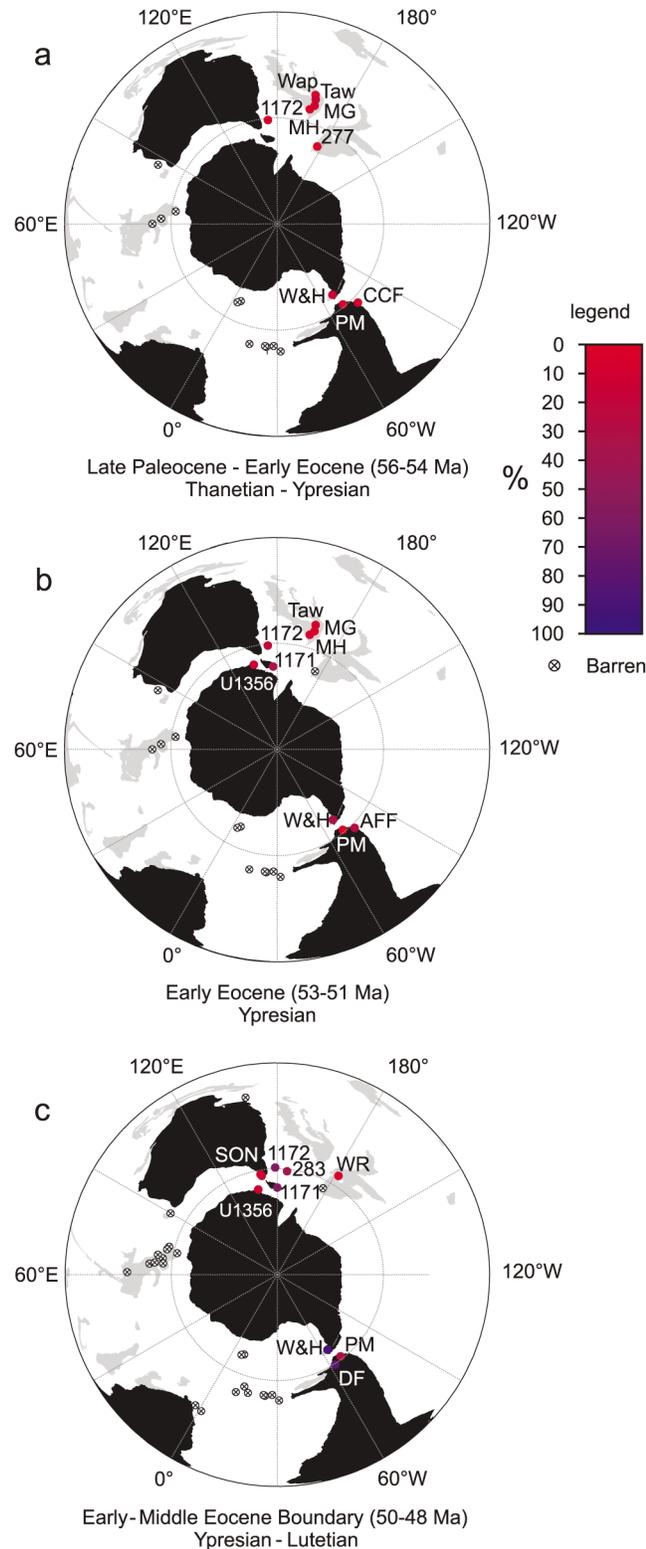
[5] We generated palynological data on sediments recovered at Ocean Drilling Program (ODP) and Deep Sea Drilling Project (DSDP) Sites 269, 277, 511, 512, 696, 739, 748 and 1090, as well as from the Brown’s Creek section in southeast Australia (Figure 1). Higher-resolution time series data were obtained from ODP Sites 1172 and 1171, and from outcrop samples from Blanche Point along the Southern Australian Margin. Furthermore, we reviewed published information on Paleogene (~65–25 Ma) Southern Ocean dinocysts from Integrated Ocean Drilling Program (IODP), DSDP and ODP sites, the “Cape Roberts Project” (CRP 1, 2a and 3) and “Cenozoic Investigations of the Ross Sea 1” (CIROS-1) drilling expeditions. In addition, studies

of outcrops that flank the Southern Ocean were considered from the southern Australian margin, McMurdo Sound, New Zealand, Tierra del Fuego, Santa Cruz Province, Brunswick Peninsula, and Seymour Island. An inventory of

all sites and outcrops considered (including references) is listed in auxiliary material Table S1.¹ An overview on the present-day locations of these sites is provided in Figure 1.

[6] The age control for these records is based on calcareous nannoplankton stratigraphy and, to a lesser extent, on diatom and/or palynomorph stratigraphies, radiometric dating, and magnetostratigraphy. The approximate tectonic configurations of the continents used in Figures 2 and 3 were reconstructed using the Ocean Drilling Stratigraphic Network (ODSN) database: <http://www.odsn.de/> [after Hay *et al.*, 1999].

[7] The semicontinuous succession recovered at ODP Site 1172 has been magnetostratigraphic calibrated [Stickley *et al.*, 2004a] and extends from the Quaternary to the Maastrichtian (latest Cretaceous). Notably, it represents a reference section for Paleogene Antarctic endemism. ODP Site 1172 is located on the submerged western side of the East Tasman Plateau (ETP) at 45°S and a water depth of 2,620 m (Figure 1; see Exon *et al.* [2004b] for details). During the early Paleogene, the ETP was located at 65°S, much closer to Antarctica than it is today [Exon *et al.*, 2004b]. Recovery at Hole 1172A includes Paleogene sediments down to the mid middle Eocene, while Hole 1172D extends the record from the mid middle Eocene to the Maastrichtian. Calcite concentrations increase from ~40 Ma onward, which has been linked to a relative sea level rise following basin subsidence [Röhl *et al.*, 2004]. Paleocene and Eocene sediments were recovered from between 350 and 700 m below seafloor (mbsf) [Exon *et al.*, 2003; Stickley *et al.*, 2004a]. This part of the section consists of brownish to greenish gray, bioturbated siltstones, that are poor in calcium carbonate, but yield abundant organic matter, including dinocysts [Exon *et al.*, 2004b].



2.2. Southern Ocean Surface-Current Configurations

[8] According to modeling experiments and biogeographical data, in the early Paleogene the region was under the influence of the Antarctic-derived, northward flowing Tasman Current [Huber *et al.*, 2004]. This current was part of a large gyre system in the South Pacific Ocean, the Proto-

¹Auxiliary materials are available in the HTML: doi:10.1029/2009PA001905.

Figure 2. Circum-Antarctic geographical distribution maps showing the spatiotemporal evolution of dinocyst endemism for seven different time slices. (a) Thanetian-Ypresian boundary (56–54 Ma), (b) mid-Ypresian (53–51 Ma), (c) Ypresian-Lutetian boundary (50–48 Ma), (d) early Lutetian (47–45 Ma), (e) late Lutetian (44–42 Ma), (f) Lutetian-Bartonian boundary (41–39 Ma), and (g) Bartonian-Priabonian boundary (38–36 Ma). Maps were derived from the Ocean Drilling Stratigraphic Network (ODSN). Black areas indicate (continental) blocks that are mostly subaerial. Note that several blocks shown in black were partly submerged during the Paleogene (e.g., Ross Sea, southern Australian margin, and parts of Argentina). Shaded areas indicate mostly submerged continental blocks [e.g., Brown *et al.*, 2006]. For locality codes, see Table S1.

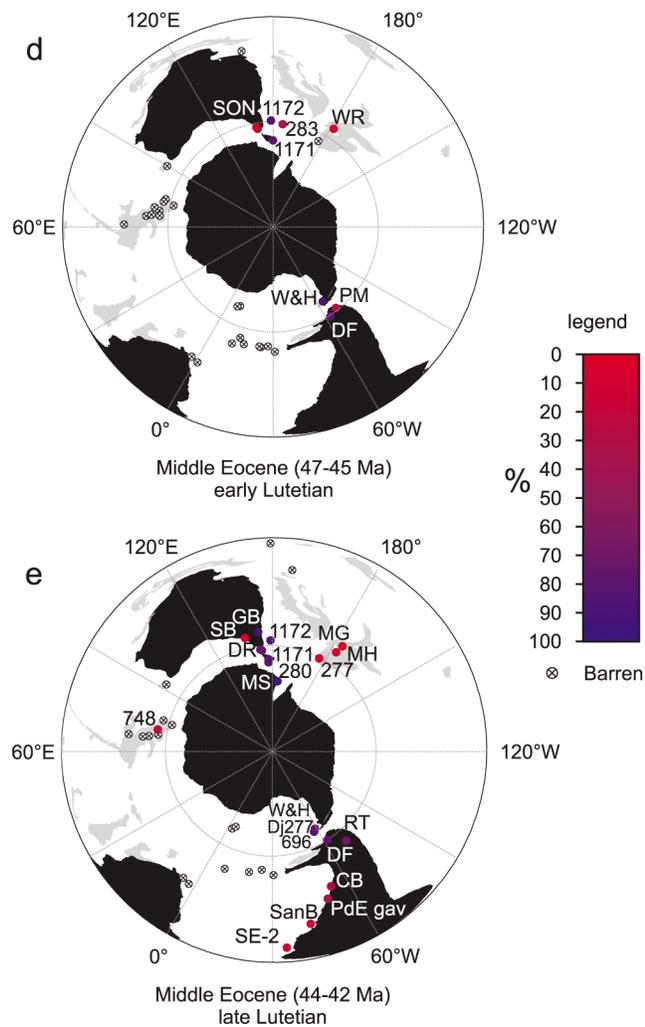


Figure 2. (continued)

Ross Gyre [Stickley *et al.*, 2004b]. The tectonic positioning of the continents that prescribe this current system was stable at least until ~35.5 Ma, when the northward movement of Australia from Antarctica deepened the Tasman Gateway and much later allowed for the Antarctic Circumpolar Current to establish [Stickley *et al.*, 2004b].

2.3. Palynological Processing and Taxonomy

[9] Processing sediment samples for palynology followed the standardized methods described, e.g., by Sluijs *et al.* [2003]. Briefly, this involves treatment of dried sediment samples with ~30% HCl and ~38% HF. No bleaching and heavy-liquid separation was applied. A 15 μm nylon mesh was used for sieving. Residues were mounted on slides for microscope analysis. Approximately 200 dinocysts were counted per sample and identified to the species level at 500× magnification. An inventory of dinocyst species encountered in this study is listed in auxiliary material Table S2; dinocyst nomenclature and taxonomy, unless stated otherwise, are based on the work of Fensome and Williams [2004].

2.4. Dinocysts: Endemic Versus Nonendemic Taxa

[10] Dinocysts are the remains of unicellular eukaryotic plankton (dinoflagellates) that dwell as motile stages in surface oceans [e.g., Fensome *et al.*, 1993]. Dinoflagellates occur in virtually all marine settings, but are most abundant and diverse in shelfal environments [e.g., Dale, 1996; Pross and Schmiidl, 2002; Pross and Brinkhuis, 2005; Sluijs *et al.*, 2005]. The fossil record of dinoflagellates is predominantly based on their resistant organic-walled cysts (dinocysts). The dinocyst record, in turn, is particularly good in shelfal environments where relatively high sedimentation rates lead to a reduced oxygen exposure of the cysts. In contrast, deeper environments with well-ventilated bottom waters exhibit generally lower sedimentation rates and high oxygen concentrations, and in these settings dinocysts oxidize and do not preserve.

[11] Dinocyst species are considered to be “endemic to the Southern Ocean” if their empirically established distribution patterns are restricted to this region (i.e., latitudes south of 45°S). The Eocene endemic dinocysts in the Southern

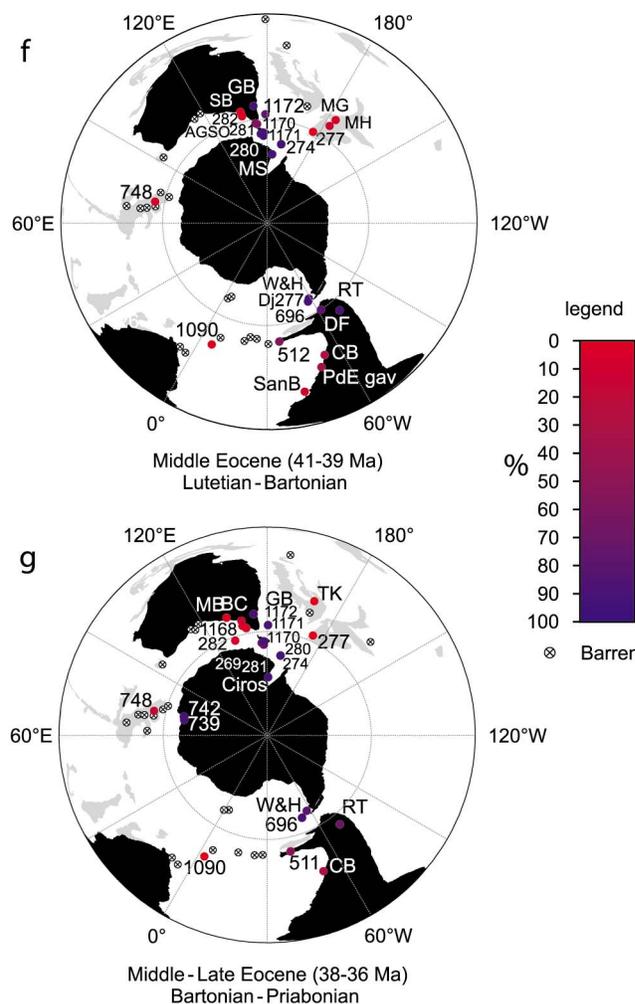


Figure 2. (continued)

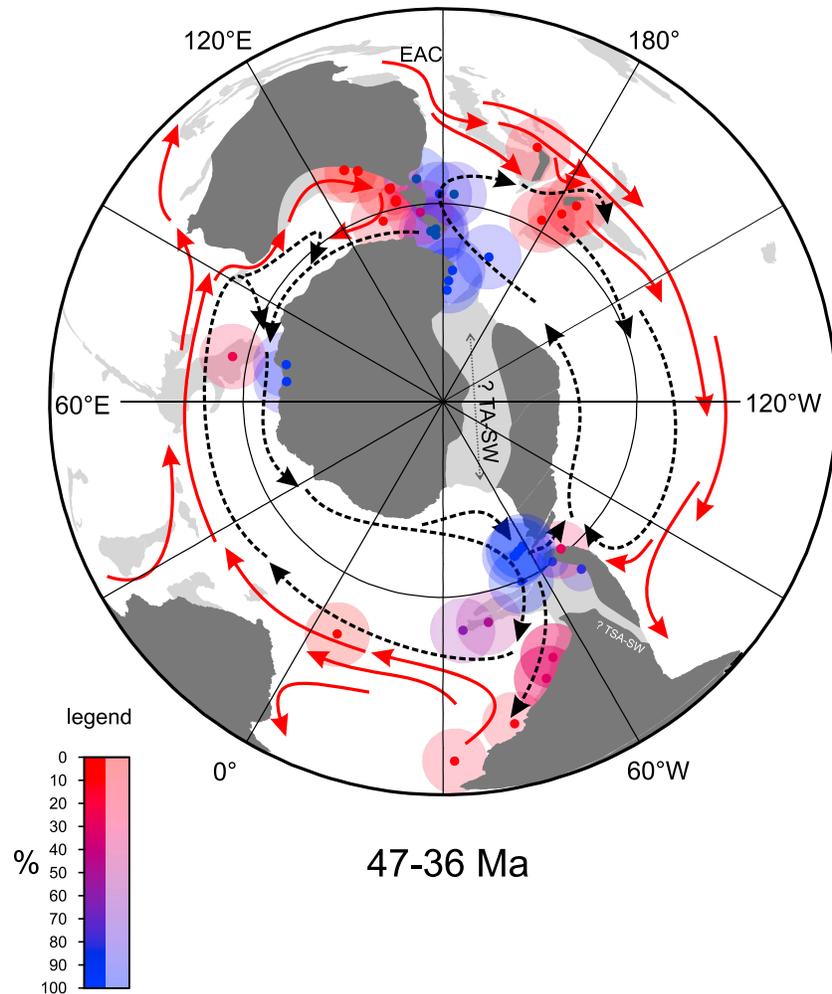


Figure 3. Generalized middle to late Eocene (47–36 Ma) dinocyst geographical distribution map overlain by the ocean circulation pattern inferred from the GCM experiments of *Huber et al.* [2004]. Maps derived from the Ocean Drilling Stratigraphic Network (ODSN). Shaded areas indicate mostly submerged continental blocks [*Brown et al.*, 2006]. Abbreviations: TA-SW, Trans-Antarctic Seaway (hypothetical [see *Wrenn and Beckman*, 1982]); TSA-SW, Trans-South American Seaway (hypothetical [see *Kohn et al.*, 2004; *Lagabrielle et al.*, 2009]); EAC, East Australian Current; p-LC, Proto-Leeuw Current; p-RG, proto-Ross Gyre; TC, Tasman Current [*Huber et al.*, 2004].

Ocean were originally referred to as the “transantarctic flora,” a name derived from their presumed affinity to the inferred Trans-Antarctic Seaway [*Wrenn and Beckman*, 1982]. Later studies reported elements of the transantarctic flora from other Southern Ocean sectors [*Wrenn and Hart*, 1988; *Mao and Mohr*, 1995; *Levy and Harwood*, 2000; *Brinkhuis et al.*, 2003; *Macphail and Truswell*, 2004; *Clowes and Wilson*, 2006; *Shuijs et al.*, 2009]. Some of these reports also described new species, but did not place those within the transantarctic flora. Other species occur in high abundances only in both north and south polar regions, and may therefore be placed in a “bipolar” group [e.g., *Wrenn and Hart*, 1988]. For this study, we include the bipolar species in our endemic dinocysts category herein after. Moreover, some taxa that are allegedly endemic to the

Southern Ocean are morphologically similar to some cosmopolitan forms. For example, the supposedly endemic species *Dracodinium waipawaense* [*Wilson*, 1967] and the Northern Hemisphere *D. varielongitudum* [*Williams and Downie*, 1966] have the same stratigraphic range and are taxonomically identical, if one allows for subtle morphological variations in shape, size and number of processes (spines) on the cysts. Hence, it can be debated whether species such as *D. waipawaense* are truly endemic or whether the slight morphological differences are the result of ecophenotypic variability within a single dinocyst species. Because of these uncertainties, we did not consider such species to be part of the transantarctic flora. On the other hand, the Eocene species *Enneadocysta dictyostila* [*Menéndez*, 1965; *Stover and Williams*, 1995], emend.

Table 1. Overview of Dinocysts Herein Assigned to the Transantarctic Flora and the Bipolar Species

New Endemic Species	Species Now Assigned to Transantarctic Flora
Described prior to <i>Wrenn and Hart</i> [1988]	<i>Alterbidinium distinctum</i>
	<i>Arachnodinium antarcticum</i>
	<i>Deflandrea antarctica</i>
	<i>Deflandrea cygniformis</i>
	<i>Deflandrea granulata</i>
	<i>Deflandrea oebisfeldensis</i>
	<i>Spinidinium macmurdoense</i>
	<i>Vozzhennikovia apertura</i>
	<i>Wilsonidium echinosuturatum</i>
	<i>Spinidinium colemanii</i>
	<i>Octodinium askiniae</i>
	<i>Hystrichosphaeridium truswelliae</i> : now nonendemic [<i>Sluijs and Brinkhuis</i> , 2009].
	<i>Impletosphaeridium clavus</i>
	<i>Deflandrea webbii</i>
<i>Spinidinium luciae</i>	
Described by <i>Wilson</i> [1988]	<i>Membranophoridium perforatum</i>
	<i>Phthanoperidinium</i> sp. A
Described by <i>Goodman and Ford</i> [1983]	<i>Phthanoperidinium</i> sp. B
	<i>Gippslandia extensa</i>
Described by <i>Stover and Williams</i> [1987]	
Described by <i>Mohr and Mohr</i> [1995]	<i>Phthanoperidinium antarcticum</i>
Described by <i>Stover and Williams</i> [1995]	(now) <i>Enneadocysta dictyostila</i>
Described by <i>Levy and Harwood</i> [2000]	<i>Vozzhennikovia netrona</i>
Described by <i>Brinkhuis et al.</i> [2003]	<i>Deflandrea</i> sp. A
Described by <i>Clowes and Wilson</i> [2006]	<i>Corrudinium regulare</i>
Described by <i>Sluijs et al.</i> [2009]	<i>Vozzhennikovia stickleyae</i>
	<i>Vozzhennikovia roehliae</i>
	<i>Spinidinium schellenbergii</i>
	<i>Moria zachosii</i>
Bipolar Species	Species Now Considered to Be Bipolar
Assigned bipolar by <i>Warnaar</i> [2006]	(now) <i>Phthanoperidinium stockmansii</i> group
Assigned bipolar by <i>Wrenn and Hart</i> [1988]	<i>Spinidinium macmurdoense</i>

[*Fensome et al.*, 2006] can be classified as endemic, despite its resemblance to the Northern Hemisphere species *Areosphaeridium diktyoplokum* [*Klumpp*, 1953]. The two species can be clearly separated based on differing (para)tabulation, a fundamental structural difference that is highly unlikely to occur within an individual species or genus [*Goodman and Ford*, 1983]; see discussions by *Fensome et al.* [2006]. An overview of the dinocyst species we assign herein to the transantarctic flora is provided in Table 1.

2.5. Canonical Correspondence Analyses

[12] We assessed the potential correspondence of the dinocyst data from Site 1172 with four environmental variables reconstructed from the same site as well as other records using Canonical Correspondence Analyses. With

this statistical method, quadratic relations between the first and higher axes have been found to cause arch effects in the ordination [*Ter Braak*, 1986]. To avoid these effects, we applied detrended canonical correspondence analyses (DCCA) [see *Ter Braak*, 1986]. We performed two DCCA analyses, one on the entire investigated record and the second only using middle Eocene data. The TEX₈₆-based SST record of ODP Site 1172 from *Bijl et al.* [2009] was added as the first environmental variable. This SST record comprises ~120 samples for the Paleocene-Eocene (average sample resolution: 250 kyr). As second variable, we used the thallium isotope record from the Pacific Ocean [*Nielsen et al.*, 2009]. We averaged two coeval records of thallium isotopes and resampled the data to the (lower-resolution) TEX₈₆ SST data set. The thallium isotope record is interpreted to reflect ocean-wide Pacific Ocean productivity trends [*Nielsen et al.*, 2009]. Third, the peridinioid/gonyaulacoid dinocyst ratio may serve as a measure for the trophic state of the surface waters [*Sluijs et al.*, 2005]. Finally, we added the percentage of endemic dinocysts. We used only those samples that were analyzed for both TEX₈₆ and palynology, rather than interpolating the TEX₈₆ data. The DCCA analysis on the entire data set comprises 59 samples. We performed a separate DCCA analysis for the middle Eocene using the same environmental variables, for which the number of samples is 21.

3. Results

3.1. Dinocyst Biogeography Through Time

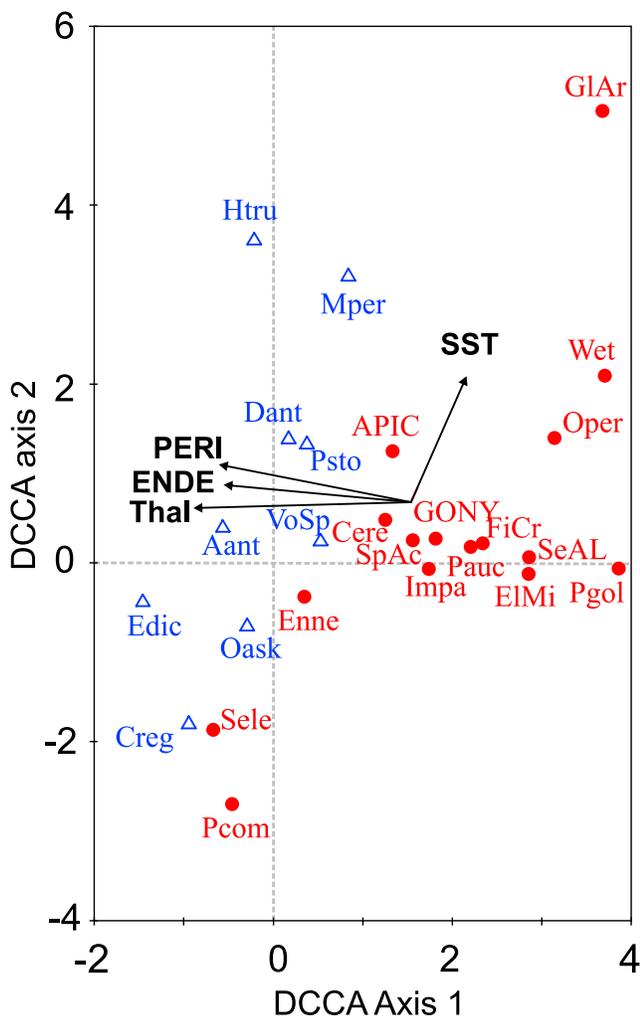
[13] Distribution maps of the compiled circum-Antarctic dinocyst records for seven time slices spanning ~56 Ma to 36 Ma are presented in Figures 2a–2g. The distribution patterns for the two oldest time slices (Figure 2a, 56–54 Ma; Figure 2b, 53–51 Ma) have limited numbers of dinocyst-bearing sites restricted to the south Pacific Ocean and Drake Passage. This limited information shows that endemics are present, but do not numerically dominate the dinocyst assemblages, not even on the Antarctic Margin. During the early middle Eocene, endemic taxa are dominant in the areas east of the Tasmanian Gateway and Drake Passage (Figure 2c, 50–48 Ma). From the middle Eocene onward, endemic dinoflagellates consistently and strongly dominate the assemblages along the western boundaries of the Drake Passage and the Tasman Gateway as well as at Prydz Bay (Figures 2d, 2e, and 2f, 47 Ma to 39 Ma), at least until the mid to late Eocene (Figure 2g, 38–36 Ma). Many undoubtedly Oligocene and younger records in the southwest Pacific (not presented here; e.g., ODP Leg 28 [*Kemp*, 1975]) and Atlantic [*Guerstein et al.*, 2008] yield some endemic dinocysts. These are most likely reworked from Eocene sediments as a result of Oligocene glacial activity. We have compiled a composite of the generalized distribution of endemic dinocysts during the middle and late Eocene (47–36 Ma) and note that the sectors characterized by dominant endemism are restricted to the Antarctic margins and the eastern sides of the Tasman and Drake conduits (Figure 3). The Australo-Antarctic Gulf area is characterized

by overall low abundances of endemics throughout the Paleogene (Figure 3).

3.2. Statistical Analysis

[14] With our DCCA analyses, four canonical axes are established for the four environmental variables. The first axis explains 29% of the dinocyst data, the second axis another 4%. Figure 4 shows the dinocyst scores for the first two axes with the environmental vectors. The SST vector points to the northeast, whereas the other vectors (i.e., thallium isotopes, % peridinioid dinocysts and % endemic dinocysts) are approximately perpendicular to the temperature vectors.

[15] In Figure 4, the dinocyst groups are divided into endemic (blue triangles) and nonendemic (red circles). The endemic taxa are clearly separated from the nonendemic ones, with high scores on both axes for nonendemic and low scores for endemic dinocysts. The few exceptions include *Membranophoridium perforatum* (Mper) and *Hystrichosphaeridium truswelliae* (Htru). The latter has traditionally been interpreted as being endemic to the Southern Ocean.



However, recently *H. truswelliae* was recorded in Paleocene-Eocene strata from New Jersey (northeast North America), clearly disputing its endemic signature [Sluijs and Brinkhuis, 2009]. ‘Outliers’ within the nonendemic taxa include the cosmopolitan *Enneadocysta* species (Enne), *Phthanoperidinium comatum* (Pcom) and *Selenopemphix* spp. (Sele). Comparing the scores of the first two axes to the environmental variables, we note that the SST variations correspond with the sample scores of the second axis. This axis explains only 4% of the dinocyst variation (Figure 5). Patterns in the sample scores of the first axis correspond with the abundance of endemic dinocysts (Figure 5). Thus, while spatial gradients in % endemic dinocysts appear to be a good indicator of the location of ocean currents, SST appears to have had little effect on the biogeography of endemic dinocysts over the complete record.

[16] However, during the interval of long-term cooling which began after the Early Eocene Climate Optimum (EECO) [Bijl et al., 2009], abundance changes in endemic dinocysts do now covary with SST. For instance, during the Middle Eocene Climatic Optimum (MECO), a short-lived warming event at ~40 Ma [Bohaty et al., 2009], endemic dinocyst abundances fall again to below 50% (Figure 5). After the MECO, the cooling trend continues and endemic dinocysts redominate the assemblages (Figure 5). To test the relation between dinocyst endemism and SST in the post-EECO interval of endemic dinocyst dominance, we performed another DCCA analysis involving only those data

Figure 4. Detrended Canonical Correspondence Analysis plot, showing first and second axis scores for dinocyst species and vectors for the environmental variables. Note the clear distinction between cosmopolitan or low-latitude to midlatitude species (red circles) in the northeastern side of the plot versus endemic or bipolar species (blue triangles) in the southwestern side. Cosmopolitan and low-latitude to midlatitude groups: APIC, gonyauloid dinocyst complex with apical archaeopyle; Pcom, *Phthanoperidinium comatum*; GLAr, *Glaphyrocysta/Areoligera* complex; Wet, Wetzeliielloid dinocysts; GONY, Gonyodomid dinocysts; Oper, *Operculodinium* complex; Pgol, *Palaeocystodinium golzowense*; FiCr, fibrous Cribroperidinioid dinocysts; SeAL, *Senegalinium/Areoligera* complex; EIMi, *Elytrocysta/Microdinium* spp.; Pauc, *Paucisphaeridium* complex; Impa, *Impagidinium* spp.; SpAc, *Spinidinium/Achomosphaera* complex; Cere, *Cerebrocysta* spp.; Enne, *Enneadocysta* spp. (pars). Endemic and bipolar groups: Sele, *Selenopemphix* complex; Creg, *Corrudinium regulare*; Edic, *Enneadocysta dictyostila*; Oask, *Octodinium askiniae*; Aant, *Arachnodinium antarcticum*; VoSp, *Vozzhennikovia/Spinidinium* complex; Pstoc, *Phthanoperidinium stockmansii* complex; Dant, *Deflandrea antarctica* complex; Htru, *Hystrichosphaeridium truswelliae*; Mper, *Membranophoridium perforatum*. Vectors: SST, TEX₈₆-derived SST from ODP Site 1172; Thal, $\epsilon^{205}\text{Tl}$ thallium isotope record from Nielsen et al. [2009]; PERI, percentage of peridinioid dinocysts at ODP Site 1172; ENDE, percentage endemic/bipolar dinocysts at ODP Site 1172.

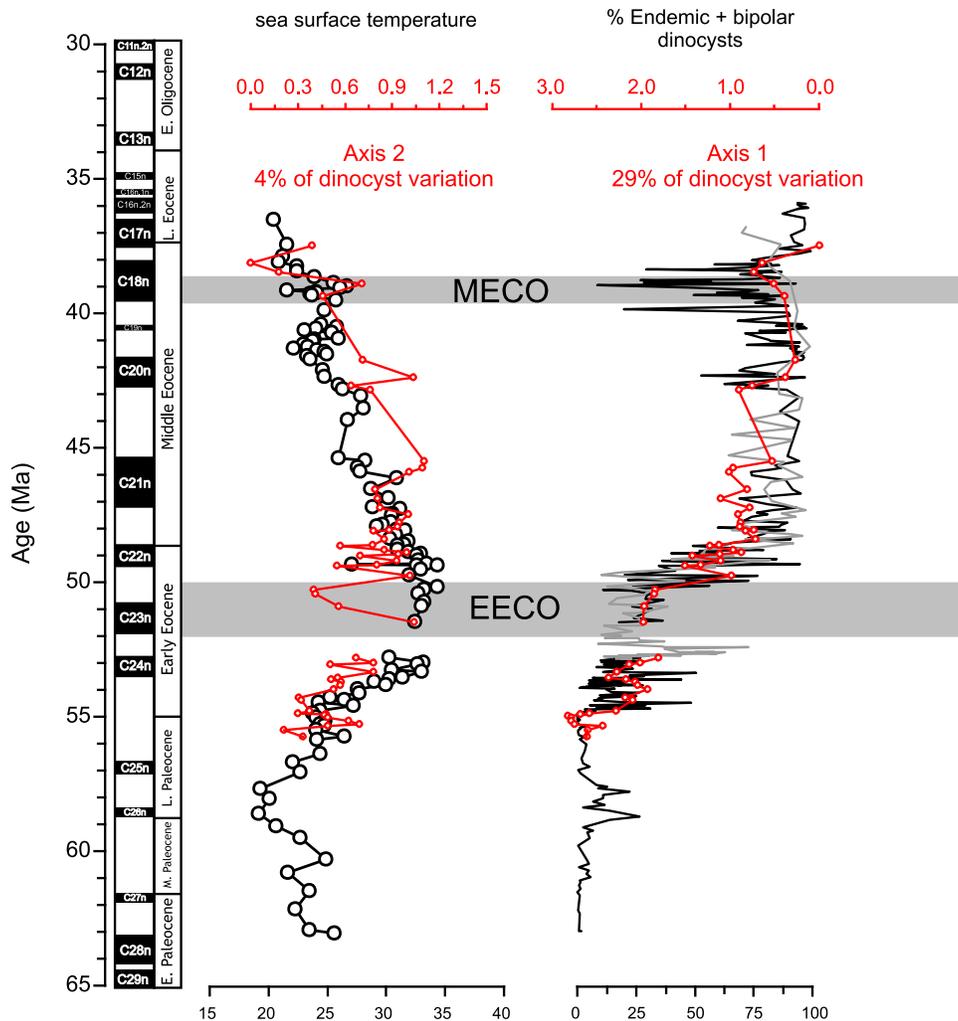


Figure 5. (left) TEX_{86} -based SST curve from ODP Site 1172 [from *Bijl et al.*, 2009] overlain by the second axis scores of the DCCA analysis. Note that the second axis explains only 4% of the total dinocyst assemblage variation. (right) Endemic dinocyst abundances at ODP Sites 1172 (black) and 1171 (gray) overlain by the first axis scores.

within the middle Eocene interval. In this interval, the variation explained by SST is $\sim 20\%$ (Figure 6).

4. Discussion

4.1. Comparison With Other Fossil Groups

[17] While endemism is recorded within several fossil groups in the Eocene, a direct comparison with the dinocyst record of the southwest Pacific is hampered by a paucity of corresponding records around the Antarctic margin older than ~ 45 Ma. For instance, although diatomaceous (biosiliceous) sediments of Early Cretaceous age and K-T boundary age occur in the western Antarctic margin [Harwood, 1988; Gersonde and Harwood, 1990; Harwood and Gersonde, 1990], these appear to be a rare exception since most known biosiliceous records in Antarctic marginal (shelf) areas are mid Eocene in age (i.e., ODP Site 1172 [Stickley et al., 2004a] or commonly much younger [e.g., Lazarus et al., 2008], Calcareous microfossil data from the

southern high latitudes predating 45 Ma are similarly scarce. Nevertheless, the few existing records of microfossils other than dinocysts from that time indeed show an increase in endemism beginning in the mid middle Eocene, as has been shown for radiolarians [Lazarus et al., 2008] and calcareous nannoplankton [Villa et al., 2008]. Calcareous nannoplankton also exhibit a decrease in endemism during the MECO [Villa et al., 2008].

4.2. Potential Driving Forces: SST, Endemism, and Statistics

[18] The establishment of dominant Antarctic endemic dinocyst assemblages characterizes the early middle Eocene transition (~ 50 Ma). However, SSTs did not decrease abruptly at that time (Figure 5). This implies that the increase in abundance of endemic dinocysts was not linearly related to SST. In contrast, during the middle Eocene, abundances of endemic dinocysts are modulated by SST changes (Figure 6). What, then, triggered endemic dinocysts

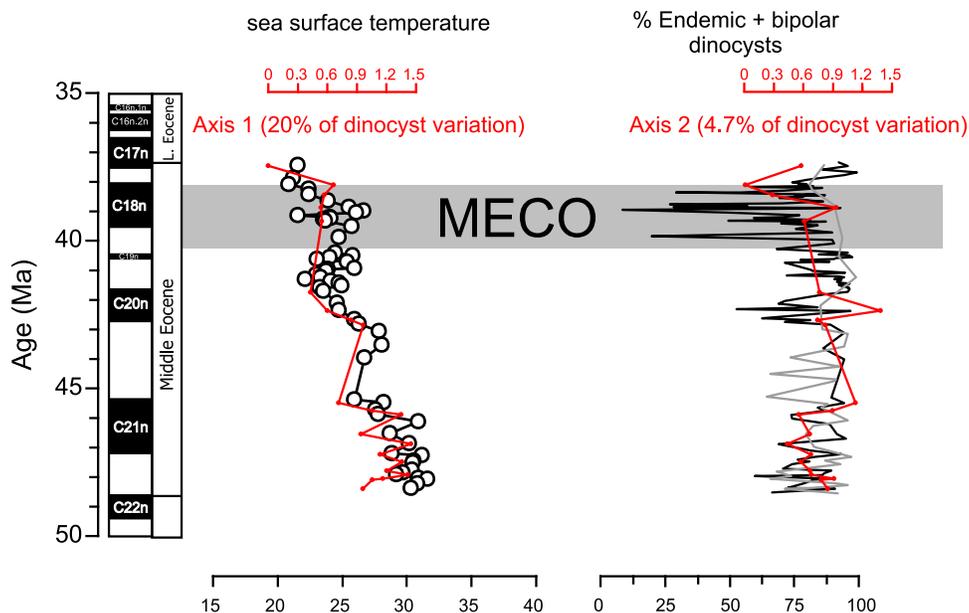


Figure 6. (left) Middle Eocene TEX_{86} -based SST curve from ODP Site 1172 [Bijl *et al.*, 2009] overlain by the first axis scores of the middle Eocene DCCA experiment (in red; 20% of the dinocyst variation). The second axis's scores correspond to (right) the % endemic dinocyst curve but explain only 4.7% of the variation in the dinocyst assemblage.

to proliferate shortly after ~50 Ma? As stated above, the peak warmth of the EECO at ~50 Ma also marks the transition into the onset of high-latitude and global cooling that, despite an interruption by at least one short warming interval (i.e., the MECO, at ~40 Ma; Figure 5), culminated in the onset of Antarctic glaciation during the Eocene-Oligocene transition [e.g., Zachos *et al.*, 1992]. It may be possible that the endemic dinoflagellate taxa, when they appeared, were capable to sustain in warm subtropical conditions during the EECO, but subsequently evolved to be more specialized to cooler surface waters during middle Eocene cooling. The sudden shift to dominant endemic dinocysts suggests the crossing of an environmental threshold at which cosmopolitan taxa were outcompeted by the endemic taxa. Because the DCCA statistical method identifies linear correspondence between assemblages and environmental data, this threshold may still have been SST.

[19] The mechanism described above may provide an explanation for the proliferation of endemic dinocysts just after 50 Ma, but it fails to explain the presence, in low abundance, of endemic dinocysts during Paleocene and early Eocene times. The most abundant endemic dinocyst groups, i.e., *Deflandrea antarctica*, *Phthanoperidinium stockmansii* group and *Vozzhennikovia/Spinidinium* spp., are already present in the Paleocene. Apparently, Paleocene-early Eocene surface waters were not as favorable for endemic species as they were in the middle Eocene. Hence, along with SST changes, other physicochemical parameters of the surface waters must have changed between the Paleocene and middle Eocene that stimulated Southern Ocean endemism to proliferate just after the early middle Eocene boundary. A possible explanation may lie in the

diatom record at ODP Site 1172, where opal-A is preserved from approximately 47 Ma [Stickley *et al.*, 2004a, 2004b] (or 45 Ma [Bijl *et al.*, 2009]) onward (Figure 7). In the middle Eocene, global cooling enhanced latitudinal gradients [Bijl *et al.*, 2009]. This cooling stimulated upwelling, bringing silica-enriched waters that characterized Eocene oceans [e.g., McGowran, 1989], particularly the Pacific [e.g., Moore *et al.*, 2008], to the surface for utilization by the diatoms. This change apparently brought about significant diatom production and preservation to the region at ODP Site 1172, and coincides with a global evolutionary turnover event within the diatoms and globally enhanced preservation of opal-A associated with global cooling [Barron and Baldauf, 1989; McGowran, 1989; Baldauf and Barron, 1990]. Increased weathering may have led to an additional nutrient supply to the oceans including both Si and the diatom bio-limiting nutrient Fe [Boyd *et al.*, 2000]. It appears plausible that the endemic dinocysts that proliferated during the earliest middle Eocene benefited from the same circulation changes and eutrophication phase that stimulated diatom productivity at that time. Further evidence for changes in ocean-wide surface water fertility comes from thallium isotopes measured on ferromanganese crusts from the Pacific Ocean (Figure 7) [Nielsen *et al.*, 2009]. A shift in these isotopes together with a coeval shift in sulfur isotopes suggests a major ocean-wide increase in marine organic carbon export from 55 to 45 Ma. At the same time, deep-water carbon isotopic values between oceanic basins start to diverge, suggesting (among other possibilities) an increase in the biological pump leading to increased water mass aging gradients (Figure 7) [Sexton *et al.*, 2006]. The fertilization of the oceanic basins is, as suggested

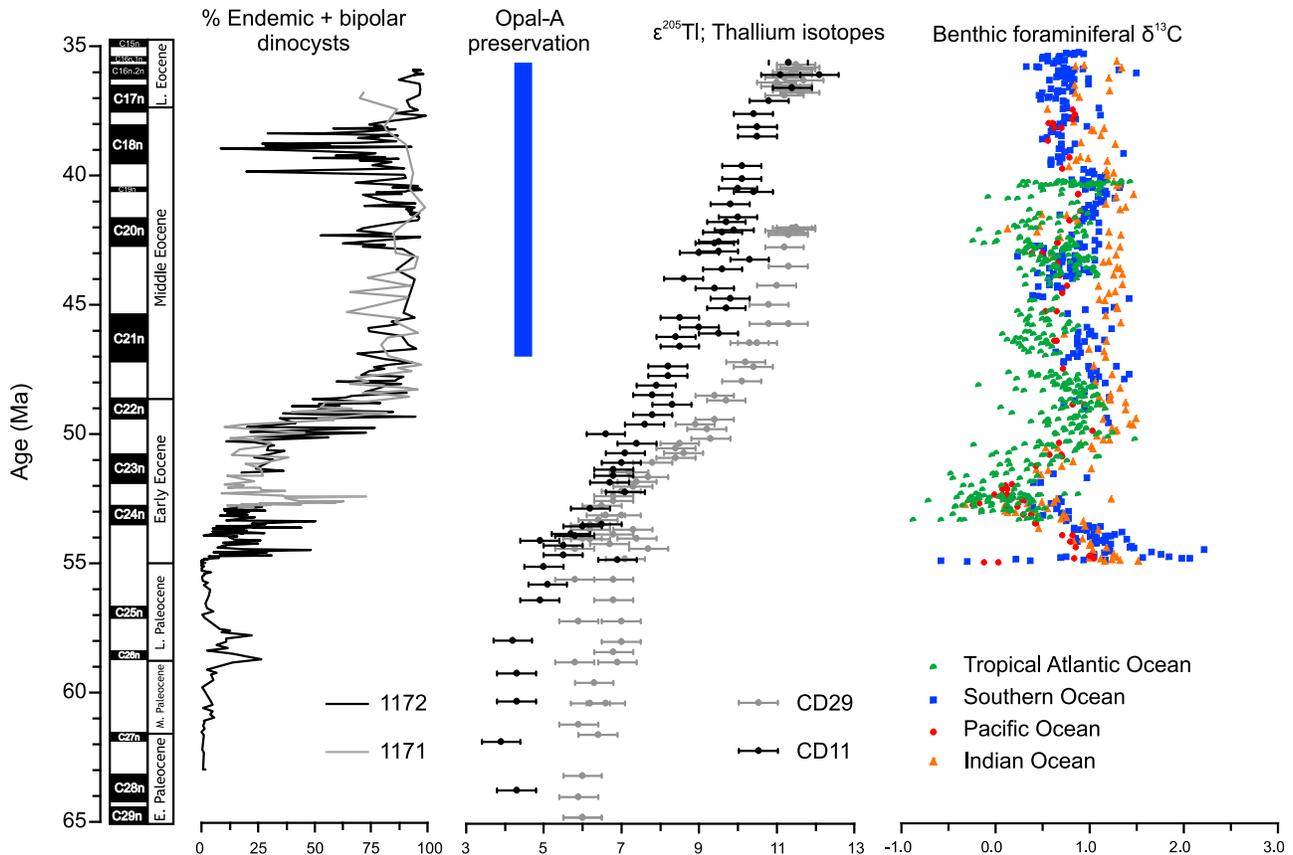


Figure 7. The relative abundance of endemic dinocysts at ODP Site 1172 (black) and Site 1171 (gray) show a major increase at 50 Ma. Opal-A preservation at ODP Site 1172 commenced between 45 Ma [Lazarus *et al.*, 2008] and 47 Ma [Stickley *et al.*, 2004a] probably as a result of increased latitudinal gradients stimulating upwelling and productivity (see text). Thallium isotope records from the Pacific Ocean, measured on two ferromanganese crusts labeled “CD11” (black) and “CD29” (gray), obtained from Nielsen *et al.* [2009], show a major increase from 55 to 45 Ma, which has been shown to suggest a permanent increase in marine organic carbon productivity. Benthic foraminiferal carbon isotope data from the tropical Atlantic Ocean (half circles), Southern Ocean (squares), Pacific Ocean (circles), and Indian Ocean (triangles) diverge from ~50 Ma upward, indicating stronger carbon isotope gradients between oceanic basins, which may suggest increased carbon pumping (data from Sexton *et al.* [2006]).

above, likely attributed to increased upwelling and weathering associated with global cooling and ever-increasing latitudinal gradients.

5. Conclusions

[20] New data and reviews of previous reports allow a considerably improved spatiotemporal reconstruction of Paleogene circum-Antarctic dinocyst distribution patterns. Dinocysts can be divided into Antarctic endemic, bipolar, middle- to low-latitude, and cosmopolitan groups. Their spatial distribution patterns match ocean current patterns generated through GCM experiments [Huber *et al.*, 2004] during the middle to late Eocene. Despite open connections between the Southern Ocean and adjacent midlatitude oceans, [Exon *et al.*, 2004a], circum-Antarctic dinocyst assemblages switched from cosmopolitan and low-latitude-derived dinoflagellate cyst assemblage to an endemic-dominated assem-

blage in the early middle Eocene. By numerically evaluating the relation between Southern Ocean dinocyst assemblages and the SST evolution at ODP Site 1172, we identify that SST was the primary driving factor in the establishment of dominantly endemic dinocyst assemblages. We conjecture that ocean-wide surface water ocean fertility [Sexton *et al.*, 2006; Nielsen *et al.*, 2009] brought about at post-EEOCO cooling [Sexton *et al.*, 2006; Bijl *et al.*, 2009], helped to stimulate diatom production and ‘switch on’ opal preservation in the area and caused a rapid reorganization of high-latitude dinocyst assemblages. Once the endemic community became the dominant component of the dinocyst assemblages in the early middle Eocene southwest Pacific, the influence of SST variations on the dinocyst assemblage was stronger than during the Paleocene and early Eocene.

[21] **Acknowledgments.** This research used samples and data provided by the Deep Sea Drilling Project (DSDP) and the Ocean Drilling

Program (ODP). DSDP and ODP were sponsored by the U.S. National Science Foundation (ODP was also sponsored by other participating countries) under the management of Joint Oceanographic Institutions (JOI) Inc. The Shipboard Scientific Party of IODP Expedition Leg 318 is thanked for providing data. This project was funded by the LPP foundation to P. K. Bijl. J. Pross acknowledges support by the Biodiversity and Climate Research Center of the Hessian initiative for scientific and economic excellence (LOEWE). C. E. Stickley acknowledges the Research Council of Norway. R. Guerin acknowledges the Agencia Nacional de Promoción Científica y Tecnológica–PICT 26057. A. Sluijs thanks the Netherlands Organization

for Scientific Research (Veni grant 863.07.001). M. Huber acknowledges continuing support from NSF 0927946–ATM and NSF PC2C 0902882–OCE. M. Huber also is grateful to the New Zealand GNS Science for providing an excellent work environment while he was visiting. A. J. P. Houben and H. Brinkhuis are grateful to Statoil for financial support. We thank Giuseppe Cortese, Erica Crouch (both GNS Science, New Zealand), Oliver Heiri (Utrecht University), and Martin Pearce (Statoil) for constructive discussions. We thank Jan van Tongeren and Natasja Welters for technical support. Constructive reviews by Philip Sexton and an anonymous reviewer greatly improved an earlier version of the manuscript.

References

- Adams, C. G., et al. (1990), Conflicting isotopic and biotic evidence for tropical sea-surface temperatures during the Tertiary, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **77**, 289–313.
- Baldauf, J. G., and J. A. Barron (1990), Evolution of biosiliceous sedimentation patterns—Eocene through Quaternary: Paleooceanographic response to polar cooling, in *Geological History of the Polar Oceans: Arctic Versus Antarctic*, edited by U. Bleil and J. Thiede, pp. 575–607, Kluwer Acad., Dordrecht, Netherlands.
- Barker, P. F., et al. (2007), Onset of Cenozoic Antarctic glaciation, *Deep Sea Res., Part II*, **54**, 2293–2307, doi:10.1016/j.dsr2.2007.07.027.
- Barron, J. A., and J. G. Baldauf (1989), Tertiary cooling steps and paleoproductivity as reflected by diatoms and biosiliceous sediments, in *Productivity of the Oceans: Present and Past*, edited by W. H. Berger et al., pp. 341–354, John Wiley, New York.
- Bijl, P. K., et al. (2009), Early Palaeogene temperature evolution of the southwest Pacific Ocean, *Nature*, **461**, 776–779, doi:10.1038/nature08399.
- Bohaty, S. M., et al. (2009), Coupled greenhouse warming and deep-sea acidification in the middle Eocene, *Paleoceanography*, **24**, PA2207, doi:10.1029/2008PA001676.
- Boyd, P. W., et al. (2000), A mesoscale phytoplankton bloom in the polar Southern Ocean stimulated by iron fertilization, *Nature*, **407**, 695–702, doi:10.1038/35037500.
- Brinkhuis, H., et al. (2003), Latest Cretaceous–earliest Oligocene and Quaternary dinoflagellate cysts, ODP Site 1172, East Tasman Plateau, *Proc. Ocean Drilling Program Sci. Results*, **189**, 48 pp., doi:10.2973/odp.proc.sr.189.106.2003.
- Brown, B., et al. (2006), Circum-Antarctic palaeobathymetry: Illustrated examples from Cenozoic to recent times, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **231**, 158–168, doi:10.1016/j.palaeo.2005.07.033.
- Clowes, C. D., and G. J. Wilson (2006), Some new species of *Corradinium* Stover & Evitt 1978 (Dinophyceae) from the Eocene of New Zealand, *N. Z. J. Geol. Geophys.*, **49**, 399–408, doi:10.1080/00288306.2006.9515176.
- Coxall, H. K., et al. (2005), Rapid stepwise onset of Antarctic glaciation and deeper calcite compensation in the Pacific Ocean, *Nature*, **433**, 53–57, doi:10.1038/nature03135.
- Dale, B. (1996), Dinoflagellate cyst ecology: Modelling and geological applications, in *Palynology: Principles and Applications*, edited by J. Jansonius and D. C. McGregor, pp. 1249–1275, Am. Assoc. of Stratigr. Palynol. Found., Dallas, Tex.
- DeConto, R. M., and D. Pollard (2003a), Rapid Cenozoic glaciation of Antarctica induced by declining atmospheric CO₂, *Nature*, **421**, 245–249, doi:10.1038/nature01290.
- DeConto, R. M., and D. Pollard (2003b), A coupled climate–ice sheet modeling approach to the Early Cenozoic history of the Antarctic ice sheet, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **198**(1–2), 39–52, doi:10.1016/S0031-0182(03)00393-6.
- Eberle, J., et al. (2009), Lower-latitude mammals as year-round residents in Eocene Arctic forests, *Geology*, **37**, 499–502, doi:10.1130/G25633A.1.
- Exon, N. J., et al. (2003), *Proceedings of the Ocean Drilling Program, Scientific Results*, vol. 189, U.S. Govt. Print. Off., College Station, Tex.
- Exon, N., et al. (2004a), *The Cenozoic Southern Ocean: Tectonics, Sedimentation and Climate Change Between Australia and Antarctica*, *Geophys. Monogr. Ser.*, vol. 151, edited by N. F. Exon, J. P. Kennett, and M. J. Malone, 367 pp., AGU, Washington, D. C.
- Exon, N. F., et al. (2004b), Leg 189 Synthesis: Cretaceous–Holocene history of the Tasmanian Gateway, *Proc. Ocean Drilling Program Sci. Results*, **189**, 37 pp., doi:10.2973/odp.proc.sr.189.101.2004.
- Fensome, R. A., and G. L. Williams (2004), The Lentini and Williams Index of Fossil Dinoflagellates (2004 Edition), *AASP Contrib. Ser.*, **42**, Am. Assoc. of Stratigr. Palynol. Found., Dartmouth, Nova Scotia, Canada.
- Fensome, R. A., et al. (1993), *A Classification of Modern and Fossil Dinoflagellates*, 351 pp., *Micropaleontol. Spec. Pap.* 7, Sheridan, Hanover, Pa.
- Fensome, R. A., et al. (2006), New insights on the Paleogene dinoflagellate cyst genera *Emneadocysta* and *Licracysta* gen. nov. based on material from offshore eastern Canada and southern Argentina, *Micropaleontology*, **52**(5), 385–410, doi:10.2113/gsmicropal.52.5.385.
- Gersonde, R., and D. M. Harwood (1990), Lower Cretaceous diatoms from ODP Leg 113 Site 693 (Weddell Sea). Part 1: Vegetative cells, *Proc. Ocean Drilling Program Sci. Results*, **113**, 365–402, doi:10.2973/odp.proc.sr.113.127.1990.
- Goodman, D. K., and L. N. J. Ford (1983), Preliminary dinoflagellate biostratigraphy for the middle Eocene to Lower Oligocene from the southwest Atlantic Ocean, *Initial Rep. Deep Sea Drill. Proj.*, **71**, 859–977, doi:10.2973/dsdp.proc.71.131.1983.
- Guérin, G. R., et al. (2008), Middle Palaeogene dinoflagellate cysts from Tierra del Fuego, Argentina: Biostratigraphy and palaeoenvironments, *J. Micropaleontol.*, **27**, 75–94, doi:10.1144/jm.27.1.75.
- Harwood, D. M. (1988), Upper Cretaceous and lower Paleocene diatom and silicoflagellate biostratigraphy of Seymour Island, eastern Antarctic Peninsula, in *Geology and Paleontology of Seymour Island*, edited by R. Feldman and M. O. Woodburne, *Mem. Geol. Soc. Am.*, **169**, 55–129.
- Harwood, D. M. (1991), Cenozoic diatom biogeography in the southern high latitudes: Inferred biogeographical barriers and progressive endemism, in *Geological Evolution of Antarctica: Proceedings of the Fifth International Symposium on Antarctic Earth Sciences*, edited by M. R. A. Thompson et al., pp. 667–673, Cambridge Univ. Press, Cambridge, U. K.
- Harwood, D. M., and R. Gersonde (1990), Lower Cretaceous diatoms from ODP Leg 113 Site 693 (Weddell Sea). Part 2: Resting spores, chrysophycean cysts, an endoskeletal dinoflagellate, and notes on the origin of diatoms, *Proc. Ocean Drilling Program Sci. Results*, **113**, 403–425, doi:10.2973/odp.proc.sr.113.201.1990.
- Hay, W. W., et al. (1999), Alternative global Cretaceous paleogeography, in *The Evolution of Cretaceous Ocean/Climate Systems*, edited by E. Barrera and C. Johnson, *Spec. Pap. Geol. Soc. Am.*, **332**, 1–47.
- Huber, M., et al. (2004), Eocene circulation of the Southern Ocean: Was Antarctica kept warm by subtropical waters?, *Paleoceanography*, **19**, PA4026, doi:10.1029/2004PA001014.
- Kemp, E. M. (1975), Palynology of Leg 28 drill sites, Deep Sea Drilling Project, *Initial Rep. Deep Sea Drill. Proj.*, **28**, 599–623, doi:10.2973/dsdp.proc.28.116.1975.
- Klump, B. (1953), Beitrag zur Kenntnis der Mikrofossilien des mittleren und oberen Eozän, *Paleontographica*, **Abt. A**, **103**, 377–406.
- Kohn, M. J., et al. (2004), Climate stability across the Eocene–Oligocene transition, southern Argentina, *Geology*, **32**(7), 621–624, doi:10.1130/G20442.1.
- Lagabriele, Y., et al. (2009), The tectonic history of Drake Passage and its possible impacts on global climate, *Earth Planet. Sci. Lett.*, **279**, 197–211, doi:10.1016/j.epsl.2008.12.037.
- Lazarus, D., and J. P. Caulet (1993), Cenozoic Southern Ocean reconstruction from sedimentologic, radiolarian, and other microfossil data, in *The Antarctic Paleoenvironment: A Perspective on Global Change, Part 2, Antarct. Res. Ser.*, vol. 60, edited by J. P. Kennett and D. A. Warnke, pp. 145–174, AGU, Washington, D. C.
- Lazarus, D. B., et al. (2008), Patterns of opal and radiolarian change in the Antarctic mid-Paleogene: Clues to the origin of the Southern Ocean, *Micropaleontology*, **54**(1), 41–48.
- Levy, R. H., and D. M. Harwood (2000), Tertiary marine palynomorphs from the McMurdo Sound erratics, Antarctica, in *Paleobiology and Paleoenvironments of Eocene Rocks, McMurdo Sound, East Antarctica, Antarct. Res. Ser.*, vol. 76, edited by J. D. Stilwell and R. M. Feldmann, pp. 183–242, AGU, Washington, D. C.
- Macphail, M. K., and E. M. Truswell (2004), Palynology of Site 1166, Prydz Bay, East Antarctica, *Proc. Ocean Drilling Program Sci. Results*, **188**, 43 pp., doi:10.2973/odp.proc.sr.188.013.2004.
- Mao, S., and B. Mohr (1995), Middle Eocene dinocysts from Bruce Bank (Scotia Sea, Antarctica) and their palaeoenvironmental and

- palaeogeographic implications, *Rev. Palaeobot. Palynol.*, **86**, 235–263, doi:10.1016/0034-6667(94)00138-A.
- McGowran, B. (1989), Silica burp in the Eocene ocean, *Geology*, **17**, 857–860, doi:10.1130/0091-7613(1989)017<0857:SBITEO>2.3.CO;2.
- Menéndez, C. A. (1965), Microplankton foisil de sedimentos Terciarios y Cretácicos del norte de Tierra del Fuego (Argentina), *Ameghiniana*, **4**(1), 7–18.
- Miller, K. G., et al. (1987), Tertiary oxygen isotope synthesis, sea level history and continental margin erosion, *Paleoceanography*, **2**, 1–19, doi:10.1029/PA002i001p00001.
- Moore, T. C., Jr. (2008), Chert in the Pacific: Biogenic silica and hydrothermal circulation, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **261**, 87–99, doi:10.1016/j.palaeo.2008.01.009.
- Nelson, C. S., and P. J. Cooke (2001), History of oceanic front development in the New Zealand sector of the Southern Ocean during the Cenozoic: A synthesis, *N. Z. J. Geol. Geophys.*, **44**, 535–553, doi:10.1080/00288306.2001.9514954.
- Nielsen, S. G., et al. (2009), Thallium isotope evidence for a permanent increase in marine organic carbon export in the early Eocene, *Earth Planet. Sci. Lett.*, **278**, 297–307, doi:10.1016/j.epsl.2008.12.010.
- Pearson, P. N., and M. R. Palmer (2000), Atmospheric carbon dioxide concentrations over the past 60 million years, *Nature*, **406**, 695–699, doi:10.1038/35021000.
- Pross, J., and H. Brinkhuis (2005), Organic-walled dinoflagellate cysts as paleoenvironmental indicators in the Paleogene: A synopsis of concepts, *Palaeontol. Z.*, **79**(1), 53–59.
- Pross, J., and G. Schmiedl (2002), Early Oligocene dinoflagellate cysts from the Upper Rhine Graben (SW Germany): Palaeoenvironmental and palaeoclimatic implications, *Mar. Micropalaeontol.*, **45**, 1–24.
- Röhl, U., et al. (2004), Sea level and astronomically induced environmental changes in Middle and Late Eocene sediments from the East Tasman Plateau, in *The Cenozoic Southern Ocean: Tectonics, Sedimentation and Climate Change Between Australia and Antarctica*, *Geophys. Monogr. Ser.*, vol. 151, edited by N. F. Exon, J. P. Kennett, and M. J. Malone, pp. 127–151, AGU, Washington, D. C.
- Sexton, P. F., et al. (2006), Testing the Cenozoic multisite composite $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ curves: New monospecific Eocene records from a single locality, Demerara Rise (Ocean Drilling Program Leg 207), *Paleoceanography*, **21**, PA2019, doi:10.1029/2005PA001253.
- Sluijs, A., and H. Brinkhuis (2009), A dynamic climate and ecosystem state during the Paleocene–Eocene Thermal Maximum: Inferences from dinoflagellate cyst assemblages on the New Jersey Shelf, *Biogeosciences*, **6**(8), 1755–1781, doi:10.5194/bg-6-1755-2009.
- Sluijs, A., et al. (2003), Dinoflagellate cysts from the Eocene–Oligocene transition in the Southern Ocean: Results from ODP Leg 189, *Proc. Ocean Drill. Program Sci. Results*, **189**, 42 pp., doi:10.2973/odp.proc.sr.189.104.2003.
- Sluijs, A., et al. (2005), From greenhouse to icehouse; organic walled dinoflagellate cysts as paleoenvironmental indicators in the Paleogene, *Earth Sci. Rev.*, **68**, 281–315, doi:10.1016/j.earscirev.2004.06.001.
- Sluijs, A., et al. (2006), Subtropical Arctic Ocean temperatures during the Palaeocene/Eocene thermal maximum, *Nature*, **441**, 610–613, doi:10.1038/nature04668.
- Sluijs, A., et al. (2009), Taxonomical revision of the *Spinidinium-Vozzhennikovia* group of organic walled, peridinioid dinoflagellate cysts, *Rev. Palaeobot. Palynol.*, **154**, 34–53, doi:10.1016/j.revpalbo.2008.11.006.
- Stickley, C. E., et al. (2004a), Late Cretaceous–Quaternary biomagnetostratigraphy of ODP Sites 1168, 1170, 1171 and 1172, Tasmanian Gateway, *Proc. Ocean Drill. Program Sci. Results*, **189**, 57 pp., doi:10.2973/odp.proc.sr.189.111.2004.
- Stickley, C. E., et al. (2004b), Timing and nature of the deepening of the Tasmanian Gateway, *Paleoceanography*, **19**, PA4027, doi:10.1029/2004PA001022.
- Stover, L. E., and G. L. Williams (1987), Analyses of Mesozoic and Cenozoic organic-walled dinoflagellates 1977–1985, *AASP Contrib. Ser.*, **18**, 243 pp., Am. Assoc. of Stratigr. Palynol. Found., Houston, Tex.
- Stover, L. E., and G. L. Williams (1995), A revision of the Paleogene dinoflagellate genera *Areosphaeridium* Eaton 1971 and *Eatonicysta* Stover and Evitt 1978, *Micropaleontology*, **41**(2), 97–141, doi:10.2307/1485947.
- Ter Braak, C. J. F. (1986), Canonical correspondence analysis: A new eigenvector technique for multivariate direct gradient analysis, *Ecology*, **67**(5), 1167–1179, doi:10.2307/1938672.
- Villa, G., et al. (2008), Middle Eocene–late Oligocene climate variability: Calcareous nannofossil response at Kerguelen Plateau, Site 748, *Mar. Micropaleontol.*, **69**, 173–192, doi:10.1016/j.marmicro.2008.07.006.
- Warnaar, J. (2006), *Climatological Implications of Australian–Antarctic Separation*, 143 pp., Utrecht Univ., Utrecht, Netherlands.
- Williams, G. L., and C. Downie (1966), *Wetzeliiella* from the London Clay, in *Studies on the Mesozoic and Cainozoic Dinoflagellate Cysts*, *Geol. Suppl.*, vol. 3, edited by R. J. Davey et al., pp. 82–198, Br. Mus. (Nat. History), London.
- Wilson, G. J. (1967), Some species of *Wetzeliiella* Eisenack (Dinophyceae) from New Zealand Eocene and Paleocene strata, *N. Z. J. Bot.*, **5**, 469–497.
- Wilson, G. J. (1988), Paleocene and Eocene dinoflagellate cysts from Waipawa, Hawkes Bay, New Zealand, *N. Z. Geol. Surv. Bull.*, **57**, 1–96.
- Wrenn, J. H., and S. W. Beckman (1982), Maceral, total organic carbon, and palynological analyses of Ross Ice Shelf Project Site J9 cores, *Science*, **216**, 187–189, doi:10.1126/science.216.4542.187.
- Wrenn, J. H., and G. F. Hart (1988), Paleogene dinoflagellate cyst biostratigraphy of Seymour Island, Antarctica, *Mem. Geol. Soc. Am.*, **169**, 321–447.
- Zachos, J. C., et al. (1992), Early Oligocene ice sheet expansion on Antarctica: Stable isotope and sedimentological evidence from Kerguelen Plateau, southern Indian Ocean, *Geology*, **20**, 569–573, doi:10.1130/0091-7613(1992)020<0569:EOISEO>2.3.CO;2.
- Zachos, J., et al. (2001), Trends, rhythms, and aberrations in global climate 65 Ma to present, *Science*, **292**, 686–693, doi:10.1126/science.1059412.
- Zachos, J. C., et al. (2008), An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics, *Nature*, **451**, 279–283, doi:10.1038/nature06588.
- Zinsmeister, W. J. (1979), Biogeographic significance of the late Mesozoic and early Tertiary molluscan faunas of Seymour Island (Antarctic Peninsula) to the final breakup of Gondwanaland, in *Historical Biogeography, Plate Tectonics, and the Changing Environment*, edited by J. Gray and A. J. Boucot, pp. 349–355, Oregon State Univ., Corvallis.

P. K. Bijl, H. Brinkhuis, A. J. P. Houben, A. Sluijs, H. Visscher, and J. Warnaar, Biomarine Sciences, Laboratory of Palaeobotany and Palynology, Institute of Environmental Biology, Faculty of Science, Utrecht University, Budapestlaan 4, NL-3584 CD Utrecht, Netherlands. (p.k.bijl@uu.nl)

R. Guerstein, INGEOSUR, Departamento de Geología, Universidad Nacional del Sur, San Juan, 670 8000, Bahía Blanca, Argentina.

M. Huber, Earth and Atmospheric Sciences, Purdue University, West Lafayette, IN 47906, USA.

J. Pross, Paleoenvironmental Dynamics Group, Institute of Geosciences, Frankfurt University, Altenhöferallee 1, D-60438 Frankfurt, Germany.

C. E. Stickley, Department of Geology, University of Tromsø, N-9037 Tromsø, Norway.