



**Expansion and  
diversification of  
high-latitude  
radiolarian  
assemblages**

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# Expansion and diversification of high-latitude radiolarian assemblages in the late Eocene linked to a cooling event in the Southwest Pacific

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## Abstract

The Eocene was characterised by “greenhouse” climate conditions that were gradually terminated by a long-term cooling trend through the middle and late Eocene. This long-term trend was determined by several large-scale climate perturbations that culminated in a shift to “ice-house” climates at the Eocene–Oligocene Transition. Geochemical and micropaleontological proxies suggest that tropical-to-subtropical sea-surface temperatures persisted into the late Eocene in the high-latitude Southwest Pacific Ocean. Here, we present radiolarian microfossil assemblage and foraminiferal oxygen and carbon stable isotope data from Deep Sea Drilling Project (DSDP) Sites 277, 280, 281 and 283 from the middle Eocene to early Oligocene (~40–33 Ma) to identify oceanographic changes in the Southwest Pacific across this major transition in Earth’s climate history. The Middle Eocene Climatic Optimum at ~40 Ma is characterised by a negative shift in foraminiferal oxygen isotope values and a radiolarian assemblage consisting of about 5% of low latitude taxa *Amphicraspedum prolixum* group and *Amphymenium murrayanum*. In the early late Eocene at ~37 Ma, a positive oxygen isotope shift can be correlated to the Priabonian Oxygen Isotope Maximum (PrOM) event – a short-lived cooling event recognized throughout the Southern Ocean. Radiolarian abundance, diversity, and preservation increase during the middle of this event at Site 277 at the same time as diatoms. The PrOM and latest Eocene radiolarian assemblages are characterised by abundant high-latitude taxa. These high-latitude taxa also increase in abundance during the late Eocene and early Oligocene at DSDP Sites 280, 281 and 283 and are associated with very high diatom abundance. We therefore infer a northward expansion of high-latitude radiolarian taxa onto the Campbell Plateau towards the end of the late Eocene. In the early Oligocene (~33 Ma) there is an overall decrease in radiolarian abundance and diversity at Site 277, and diatoms are absent. These data indicate that, once the Tasman Gateway was fully open in the early Oligocene, a frontal system similar to the present day was established, with nutrient-depleted subantarctic

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tic waters bathing the area around DSDP Site 277, resulting in a more oligotrophic siliceous plankton assemblage.

## 1 Introduction

The climate history of the early Paleogene has been established by geochemical proxies for temperature, loosely linked to paleontological data. The primary proxy record, stable oxygen isotope ( $\delta^{18}\text{O}$ ) values of benthic foraminifera, shows a trend from an early Cenozoic greenhouse climate to an icehouse climate with the major shift in benthic  $\delta^{18}\text{O}$  values of  $\sim +1.5\text{‰}$  in the earliest Oligocene ( $\sim 34\text{ Ma}$ ) (Shackleton and Kennett, 1975; Diester-Haass et al., 1996; Zachos et al., 2001). After a prolonged period of maximum warmth during the Early Eocene Climatic Optimum (EECO) centred around 53–51 Ma, long-term cooling was interrupted by the Middle Eocene Climatic Optimum (MECO), a  $\sim 500\text{ kyr}$  period of warmth peaking  $\sim 40\text{ Ma}$  that has been linked to an increase in atmospheric  $p\text{CO}_2$  (Bohaty and Zachos, 2003; Bohaty et al., 2009; Bijl et al., 2010). Organic biomarker-based climate proxies (Liu et al., 2009; Bijl et al., 2010) suggest the Southwest Pacific sea surface temperatures were tropical during the MECO ( $28^\circ\text{C}$ ) and continued to be warm throughout the late Eocene ( $24\text{--}26^\circ\text{C}$ ), cooling only slightly across the Eocene–Oligocene transition (EOT,  $\sim 22^\circ\text{C}$ ). Following the MECO event, benthic  $\delta^{18}\text{O}$  values increased to their maximum Eocene values of  $\sim 2.3\text{‰}$  at about 37.3 Ma during a short-lived cooling episode in the early late Eocene, designated as the Priabonian Oxygen Isotope Maximum (PrOM) event (Scher et al., 2014). Further climate oscillations are reported for the late Eocene (Vonhof et al., 2000; Pälike et al., 2001; Bohaty and Zachos, 2003; Villa et al., 2008; Westerhold et al., 2014) prior to the expansion of Antarctic ice that defines the EOT.

The generally warm conditions of the Eocene are consistent with fossil-based reconstructions of Southern Ocean circulation developed from high-latitude drill cores (Kennett, 1977; Nelson and Cooke, 2001; Kennett and Exon, 2004), in which subtropical waters are interpreted to extend close to the Antarctic margin. However, both

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geochemical proxy data and these paleoecological reconstructions are at odds with the latest generation of ocean circulation and climate modelling simulations (Hollis et al., 2012; Lunt et al., 2012). Even under hyper-greenhouse conditions, the models produce a cyclonic gyre that blocks subtropical waters from penetrating southward beyond 45° S (Huber and Sloan, 2001; Huber et al., 2004). High-latitude warmth also conflicts with evidence for the initiation of Antarctic glaciation in the latest Eocene from both fossil and geochemical proxies (Lazarus and Caulet, 1993; Scher et al., 2014; Barron et al., 2015).

Paleobiogeographic changes in marine biota may help to delineate general climate trends and events. Identifying the initial timing and development of a high-latitude fauna in the Southern Ocean helps to constrain the development of the Southern Ocean frontal systems and, in turn, heat transfer between low and high latitudes. The timing of the establishment of a distinct Southern Ocean surface-water mass is inferred to have occurred within the middle-to-late Eocene interval, triggered by the opening of the Tasman Gateway or changes in carbon cycling (Stickley et al., 2004; Lazarus et al., 2008; Bijl et al., 2013), or abruptly at the E-O transition, associated development of a proto-Antarctic Circumpolar Current (ACC) and implicated as the main causal mechanism for Antarctic glaciation (Kennett, 1978; Nelson and Cooke, 2001; Houben et al., 2013). Improved understanding of the timing of major changes in the early Cenozoic evolution of the Southern Ocean will help to resolve the relative importance and inter-relationships between tectonism, biological evolution and long-term trends in atmospheric CO<sub>2</sub> concentration.

In this paper, we document variation in radiolarian assemblages and foraminiferal oxygen and carbon stable isotopes from the middle Eocene-to-early Oligocene interval (~ 40 to 33 Ma) at DSDP Site 277 and relate these variations to radiolarian assemblage changes at DSDP Sites 280, 281, 283 and to a previously published study of Eocene radiolarian assemblages from ODP Site 1172 (Suzuki et al., 2009). DSDP Site 277 provides a unique record of pelagic sedimentation in the Southwest Pacific from the late Paleocene to Oligocene times and the first Eocene benthic  $\delta^{18}\text{O}$  record was

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of a 201 m cored section that includes a 97.2 m middle Eocene-to-middle Oligocene interval. The studied interval spans Core 7R (123.4 mbsf) to Core 5R (92.54 mbsf). DSDP Site 281 on the South Tasman Rise (47°59.84' S; 147°45.85' E), drilled at a water depth of 1591 m, encompasses two holes (281 and 281A). We examined Hole 281 which was cored to 169 mbsf and recovered a 105.6 m (62.5% recovery) late Eocene-to-Pleistocene section. The studied interval covers Core 16R (149 mbsf) to Core 14R (122.5 mbsf). DSDP Site 283 lies in the Central Tasman Sea (43°54.6' S; 154°16.96' E) in a water depth of 4729 m and also comprises two holes (283 and 283A). We examined Hole 283 which was drilled to 156 mbsf (39% recovery) and recovered a Paleocene-to-Pleistocene section that contains a late Eocene-to-(?)Miocene hiatus. Core 8R (192.25 mbsf) to Core 5R (87.75 mbsf) were studied from this site.



### 3 Material and methods

This study is based on 28 sediment samples from DSDP Site 277 from ~350 to 135 mbsf spanning a middle Eocene-to-lower Oligocene interval (17 reported by Hollis et al. (1997) and 11 new samples), 6 samples from DSDP Site 283 (new, all from the DSDP/ODP Micropaleontology Reference Centre (MRC)), 7 from Site 281 (3 from the DSDP/ODP MRC, 4 new) and 4 from Site 280 (new). Due to incomplete core recovery in all study sections, the sampling resolution of our study is variable (~0.5 to ~30 m sample spacing; Supplement). To obtain a consistent taxonomic identification across all sites, all samples previously reported from DSDP sites 277, 280, 281 and 283 were re-examined and re-counted as part of this study.

For strewn slide preparation, 1–10 g of sample material was broken into ~5 mm-diameter chips and leached in 10% HCl to dissolve carbonate until the reaction ceased. Samples were then washed through a 63-µm sieve and the >63 µm residue was cleaned by gently heating in a 1:1 solution of 10% hydrogen peroxide and sodium hexametaphosphate ((NaPO<sub>3</sub>)<sub>6</sub>). The residue was washed through a 63 µm sieve and dried. Dependent on the volume of the processed residue and the abundance of ra-

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diolarians, 1–5 strewn slides were prepared for each sample. If the radiolarians were sparse, specimens were individually picked from the dried residue under a stereo microscope. For strewn slides, a known portion of dried residue was evenly distributed on a pre-glued coverslip, which was inverted and placed gently on a glass slide with a thin coating of Canada Balsam. The slide was placed on a hot plate until the balsam was fixed.

Strewn slides were examined using a Zeiss transmitted light microscope fitted with a Zeiss AxioCam ERc5s digital camera. The Supplement include taxonomic notes for all radiolarian species recorded in this study, plates of selected species, and radiolarian distribution charts and sample information for DSDP sites 277, 280, 281 and 283. Radiolarian census data were derived along vertical slide traverses under transmitted light following the method of Hollis (2006). For samples with sparse radiolarians (< 300 specimens per slide), all radiolarians on the prepared slide(s) were counted. For richer samples, all specimens were counted until a total number of about 300 specimens was achieved. The proportion of the slide examined to this point was determined and the abundance of common taxa (> 15 observed specimens) estimated for the rest of the slide. The remaining portion was then examined and rare taxa (< 15 specimen observed in initial count) recorded. All intact tests were assigned to a counting group that range from undifferentiated order (e.g. *Nassellaria* undet.) and family (e.g. *Actinommidae* undet.) to species and subspecies. This approach allows for an accurate estimate of the abundance of individual species, but does result in overall diversity being underestimated.

Radiolarian abundance was calculated using the following equation:

$$\left( X_R \times X_S \times \frac{1}{X_P} \right) / A_{\text{Sed}} \quad (1)$$

With  $X_R$  being the total number of radiolarians per slide,  $X_S$  the number of slides made of a known portion  $X_P$  of the dried material,  $A_{\text{Sed}}$  is the initial amount of dried sediment.

Additional data derived for each sample assemblages includes taxic richness, the Fisher  $\alpha$  Diversity index and the Simpson index of Evenness. The latter two indices

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were calculated using the PAST software (Hammer et al., 2001). The Fisher  $\alpha$  index is a general guide to diversity, calculated from the number of taxa and the total number of individuals. The Simpson index of Evenness determines the degree to which assemblages are dominated by individual taxa and ranges from 0 to 1. The diatom/radiolarian (D/R) ratio was calculated using the counts of diatoms and radiolarians of one examined slide. In case of very rare diatoms, all specimens were counted on a slide, otherwise several transverses were counted for diatoms and the total number estimated for the whole slide. Although this method is not an accurate measure of diatom abundance as most pelagic diatoms are smaller than the 63  $\mu\text{m}$  screen used in this study, it serves to identify the order of magnitude in changes in diatom abundance that allows us to identify significant diatom event horizons. We also determined diversity, evenness and biogeographic affinities for the Eocene radiolarian assemblages described from ODP Site 1172 (Suzuki et al., 2009) using unpublished distribution data provided by N. Suzuki (personal communication, 2013, Tohoku University, Japan).

The biogeographic affinities of the radiolarian species, subspecies and informally defined morphotypes encountered in our study were assigned using information from previous paleobiogeographic studies (Lazarus and Caulet, 1993), distributions reported in taxonomic studies (Petrushevskaya, 1975; Sanfilippo and Caulet, 1998) and our own assessment based on published records of the recorded taxa or closely related taxa (e.g. Takemura and Ling, 1997; Hollis, 2002; Funakawa and Nishi, 2005, 2008; Funakawa et al., 2006; Kamikuri et al., 2013) (Table 1). We quantified trends in biogeographic affinity to determine how the relative influences of high- and low-latitude water masses varied through the middle Eocene to early Oligocene.

At the University of California Santa Cruz (UCSC) and the University of Southampton (UoS), stable oxygen ( $\delta^{18}\text{O}$ ) and carbon ( $\delta^{13}\text{C}$ ) isotope ratios were determined for bulk carbonate, *Cibicidoides* spp., *Subbotina* sp. Core 277-34R (332.62 mbsf) to 18R (159.88 mbsf) and *Globigerinatheka index* (Core 277-34R (332.62 mbsf) up to its last occurrence in Core 277-21R (188.58 mbsf)). In total, set of 157 samples spanning the middle Eocene-to-lower Oligocene interval of DSDP Hole 277 was measured.

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Stable isotope analyses at UCSC were performed on a VG Prism dual-inlet mass spectrometer coupled to carousel preparation device with common acid bath maintained at 90 °C. Analyses at the UoS were performed on a Europa GEO 20–20 dual-inlet mass spectrometer with CAPS preparation oven maintained at 70 °C. All values are reported relative to the Vienna Pee Dee Belemnite (VPDB) standard. In both labs, analytical precision based on replicate analyses of in-house marble standards and NBS-19 averaged ~ 0.05 ‰ (1σ) for  $\delta^{13}\text{C}$  and ~ 0.08 ‰ (1σ) for  $\delta^{18}\text{O}$ . All planktic foraminifera in this record appeared to have a “frosty” preservation.



## 4 Results

### 4.1 Site 277 biostratigraphy and stable isotope stratigraphy



Broad age control for DSDP Site 277 is based on the biostratigraphic review of Hollis et al. (1997) who correlated the succession to radiolarian Zones RP6 to RP15. In this study we confirm the location of the base of Zone RP14 (Lowest Occurrence (LO) of *Eucyrtidium spinosum*) at 264.5–254.5 mbsf, the base of RP15 (LO of *Eucyrtidium antiquum*) at 197.8–186.5 mbsf, and the base of upper Zone RP15 at 143.9–134.5 mbsf (lowest common occurrence (LCO) of *Axoprunum? irregularis*) (Fig. 2). We revise the base of Zone RP12 to 371.2–349.2 mbsf (LO of *Lophocyrtis longiventer*) and the base of RP13 to 313.5–312.7 mbsf (LOs of *Eusyringium fistuligerum* and *Zealithapium mitra*) (Fig. 2). The Eocene–Oligocene boundary is poorly defined by biostratigraphy at DSDP Site 277. The base of the local Whaingaroan Stage (latest Eocene, 34.6 Ma, Raine et al., 2015) is identified by the Highest Occurrence (HO) of *Globigerinatheka index*. This event was identified at 189.6 mbsf by Jenkins (1975) but we have determined that the event occurs slightly higher at 188.58 mbsf.

Further refinement of the age control for Site 277 is possible through correlation of the stable isotope records to those from other Southern Ocean sites (Fig. 2). Although the gaps in the Site 277 isotope record preclude detailed correlation, the broad trends

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and major events such as the MECO ( $\sim 40$  Ma) and PrOM event ( $\sim 37.3$  Ma) can be identified in the benthic  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  isotope profiles and compared to the middle Eocene-to-early Oligocene benthic isotope stratigraphy from ODP Site 689 (Diester-Haass and Zahn, 1996) (Fig. 2). The EOT is expressed as a large ( $\sim 1\%$ ) positive shift in benthic oxygen and carbon isotopes between Cores 277-20R and -19R (Shackleton and Kennett, 1975; Keigwin, 1980), which is slightly lower than the full magnitude of the benthic  $\delta^{18}\text{O}$  shift seen at other Southern Ocean sites on the Kerguelen Plateau and Maud Rise (Diester-Haass and Zahn, 1996; Zachos et al., 1996; Bohaty et al., 2012).

Foraminiferal  $\delta^{18}\text{O}$  values show a normal planktic–benthic gradient with more positive values in the benthic foraminifers compared to bulk and planktic foraminifera with some crossover in the latter two (Fig. 3). Foraminiferal  $\delta^{13}\text{C}$  values also show a typical positive benthic–planktic gradient. Therefore, we interpret relatively robust stable isotope signals representative of deep (intermediate), upper (thermocline) and uppermost (mixed/surface) waters, although it is likely that the  $\delta^{18}\text{O}$  gradients are attenuated by diagenetic effects on planktic foraminifera (Sexton et al., 2006) as they show a “frosty” preservation.

Several short-lived climatic events are identified in the benthic stable isotope records at Site 277 (Fig. 3). The body of the MECO was not recovered (due to a 16 m sampling gap between the top of Core 277-33R and the base of Core 277-32R), but its onset and recovery is well constrained by a  $0.5\%$  negative excursion in benthic  $\delta^{18}\text{O}$  values at  $\sim 313$  mbsf (between Samples 277-33R-2, 106–108 cm and -33R-1, 129–130.5 cm) and a  $\sim 0.4\%$  positive excursion in  $\delta^{18}\text{O}$  values at  $\sim 296$  mbsf (between samples 32R-3, 107–109 cm and 32R-3, 77–79 cm), indicating that the MECO spans  $\sim 17$  m. The MECO is more strongly expressed in the benthic  $\delta^{18}\text{O}$  than in the planktic record but this may relate to the poor recovery of the body of the event at this site or diagenetic impacts on planktic  $\delta^{18}\text{O}$  values (Pearson et al., 2000; Sexton et al., 2006). In agreement with other records (Bohaty and Zachos, 2003; Bohaty et al., 2009), a positive  $\delta^{13}\text{C}$  excursion is observed at the onset of the MECO in the benthic and bulk carbon-

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ate records, although the  $\delta^{13}\text{C}$  record is also compromised by the missing core of the event.

The PrOM event (Scher et al., 2014) is well-defined in the  $\delta^{18}\text{O}$  record from DSDP Site 277 but also spans two significant recovery gaps between the base of Cores 277-26R, 25R and 24R ( $\sim 244.5$  to  $225.5$  mbsf) (Fig. 3). The  $\sim 0.4\text{‰}$  positive shift in  $\delta^{18}\text{O}$  that marks the onset of the PrOM, spans upper Core 277-26R and lower Core 277-25R ( $\sim 240\text{--}230$  mbsf), and is followed by an interval of relatively low  $\delta^{18}\text{O}$  values in upper Core 277-25R, prior to reaching maximum values in uppermost Core 277-25R ( $\sim 226$  m). A gradual decrease in  $\delta^{18}\text{O}$  occurs through Core 277-24R. We define the PrOM at DSDP Site 277 as the interval within these three cores in which benthic  $\delta^{18}\text{O}$  exceeds  $1.25\text{‰}$ , with the exception of the interval noted above in upper Core 277-25R. These benthic  $\delta^{18}\text{O}$  values are lower than those reported by Scher et al. (2014), but it is likely that peak  $\delta^{18}\text{O}$  values are not captured at Site 277. Consequently the PrOM is placed between  $240.62$  and  $219.57$  mbsf (spanning a  $\sim 21$  m section). The planktic  $\delta^{18}\text{O}$  record is similar to the benthic, but lacks the maximum excursion in uppermost Core 277-25R. At the onset of the event, short-lived negative  $\delta^{13}\text{C}$  excursions are evident in the benthic, bulk and planktic records. However, a longer-term positive trend for planktic and benthic  $\delta^{13}\text{C}$  values becomes apparent simultaneously to the benthic  $\delta^{18}\text{O}$  maximum.

Directly above the PrOM event,  $\delta^{18}\text{O}$  values decrease by  $\sim 0.5\text{‰}$  in upper Core 277-24R and -23R ( $217.37$  to  $207.41$  mbsf), evident in benthic and planktic foraminifera as well as bulk carbonate. This interval can be correlated to the late Eocene warming interval interpreted at ODP Sites 689 (Maud Rise), 738, 744, and 748 (Kerguelen Plateau) (Diester-Haass and Zahn, 1996; Bohaty and Zachos, 2003; Villa et al., 2008, 2014).

The large positive shift in  $\delta^{18}\text{O}$  defines the E-O transition at Site 277 between the base of Core 277-20R and Core 277-19R, with the most positive values in benthic and planktic  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  occurring in Core 277-19R ( $171.28$  to  $169.65$  mbsf), within the earliest Oligocene.

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## 4.2 Radiolarian assemblages at DSDP Site 277

In total, 16 families, 56 genera and 98 radiolarian species were identified at DSDP Site 277. Radiolarian abundance is generally low ( $10\text{--}100\text{ specimens g}^{-1}$ ) and preservation is moderate throughout the middle Eocene-to-early late Eocene interval (349.2 to 227.2 mbsf) (Fig. 4). In the latest Eocene and early Oligocene radiolarians are abundant to very abundant ( $> 1500\text{ specimens g}^{-1}$ ) and well preserved. Diversity is strongly correlated to abundance which is lower in the middle and early late Eocene and high thereafter (Fig. 4). Simpson Evenness is strongly correlated to diversity but exhibits greater troughs where samples are sparse (Fig. 4). Spumellarians are dominant in most samples ranging between  $\sim 45$  and  $96\%$  ( $\sim 70\%$  average). The main families are the Actinommidae, Litheliidae, Artostrobiidae, Spongodiscidae, Lophocyrtidae and Lychnocaniidae (Supplement Table Site 277).

Three samples from the middle Eocene (313.5, 312.7, 296 mbsf; Cores 277-32R and -33R) that lie within the onset and recovery of the MECO at Site 277, show improved preservation, a peak in diversity, and mark the first significant occurrence of diatoms (Fig. 4). The low-latitude species *Amphymenium murrayanum* and *Amphycraspedum prolixum* gr. have short-lived occurrences in this interval, with only *A. prolixum* gr. also very rare in the latest Eocene. Several species are restricted to the MECO: *Artobotryst titanothericeraos*, *Sethocyrtis chrysalis*, *Eusyringium fistuligerum* and *Stichopilium* cf. *bicorne*. *Lophocyrtis jacchia hapsis*, which is a high-latitude variant of *L. jacchia jacchia* (Sanfilippo and Caulet, 1998) and endemic to the Southern Ocean, is also common during the MECO, but is absent from the remaining middle Eocene and very rare in the late Eocene. Furthermore, the LOs of several species are recorded (albeit very rare) at this site during the MECO interval (*Axoprunum pierinae*, *Zealithapium mitra*, *Periphaena* spp., *Larcopyle hayesi*, *L. polyacantha*, *Zygocircus buetschli*, *Siphocampe*? *amygdala*, *Eucyrtidium ventriosum*, *Lychnocanium amphitrite*, *Clinorhabdus anantomus*, *Lophocyrtis keraspera*, *Lophocyrtis dumitricai*, *Cryptocarpium ornatum* and *Lamprocyclas particollis*) (Fig. 2 and Supplement Table Site 277).

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A major change in siliceous assemblages occurs within the PrOM interval (~ 226 mbsf; Core 25R), coincident with maximum values in benthic  $\delta^{18}\text{O}$  (Fig. 4). A pronounced increase in radiolarian abundance (from < 50 to ~ 4000 radiolarians  $\text{g}^{-1}$ ), preservation and diversity occurs at 226.10 mbsf (Sample 277-25R-1, 60 cm). The following taxa have their LO within the PrOM at Site 277: *Lithelius foremanae*, *Ceratocyrtis* spp., *Lithomelissa ehrenbergi*, *L. gelasinus*, *L. sphaerocephalis*, *Siphocampe nodosaria*, *Artostrobos annulatus*, *Artostrobos* cf. *pretabulatus*, *Clathrocyclas universa*, *Dictyophimus*? aff. *archipilium*, *Lychnocanium waiareka*, *Aphetocyrtis rossi* and *Theocyrtis tuberosa* (Fig. 2 and Supplement Table Site 277). Diatoms become abundant at the same level as the increase in radiolarian abundance and remain abundant through the latest Eocene, decreasing in the Oligocene. The most abundant radiolarian families in the PrOM and latest Eocene are the Actinomiidae (~ 11–36 %), Litheliidae (~ 16–28 %), Spongodiscidae (~ 5–13 %), Lophocyrtiidae (~ 3–15 %), Lychnocaniidae (1–11 %) and Plagiacanthidae (1–6 %). *Theocyrtis tuberosa* has a very rare occurrence from the late Eocene to early Oligocene (~ 226–143.9 mbsf; Core 25R to 16R). This species is also known to have had isolated occurrences in the southern Atlantic and southern Indian oceans in the late Eocene (Takemura, 1992; Takemura and Ling, 1997) and is common in latest Eocene to early late Oligocene assemblages from low to middle latitudes of all ocean basins (Sanfilippo et al., 1985). As none of our samples lie within the late Eocene warming interval (Fig. 3), we cannot assess how radiolarian assemblages responded to this warming. However, closer to New Zealand, the latest Eocene Runangan stage is associated with incursions of warm-water taxa, including larger benthic foraminifera and the short-lived occurrence of the low-latitude genus *Hantkenina* (Hornibrook et al., 1989).

A significant decline in radiolarian abundance and diversity is observed through the early Oligocene (186.5 to 134.5 mbsf; Cores 20R to 15R) (Fig. 4). The fauna is dominated by spumellarians that increase from ~ 73 to ~ 97 %, with Litheliidae and Actinommidae being the most abundant families (Supplement Table Site 277).

### 4.3 Radiolarian assemblages at other SW Pacific sites

To establish the significance and nature of radiolarian faunal turnover associated with the PrOM event regionally, we investigated the late Eocene to early Oligocene intervals of DSDP Sites 280, 281 and 283.

#### 4.3.1 DSDP Site 280

Four samples were investigated at DSDP Site 280 from Cores 7R, 6R and 5R (123.4 to 92.54 mbsf). In previous work, the E-O boundary in Hole 280 was placed at the base of Core 280-6R (110.5 mbsf) (Crouch and Hollis, 1996). However, due to the presence of *Eucyrtidium antiquum* (Caulet, 1991) and *Larcopyle frakesi* (Chen, 1975), both of which have LOs in the early Oligocene, we place the studied interval (123.4–92.54 mbsf) in early Oligocene Zone RP15 (Fig. 5 and Supplement Table Site 280). This is in agreement to O'Connor (2000), who found late Eocene assemblages were restricted to Cores 280-10R to 8R (205.5 to 139 mbsf). The absence of the zonal marker *Axoprunum? irregularis* indicates correlation with lower RP15. *Eucyrtidium spinosum*, which according to Funakawa and Nishi (2005) has its HO in the early Oligocene, is absent in the Site 280 study interval. However, the HO of this species is recorded within the late Eocene interval at Site 277, suggesting a diachronous HO between the Southwest Pacific and the South Atlantic (Supplement Table Site 277).

In total, 15 families, 35 genera and 50 radiolarian species were identified at Site 280. Radiolarians are abundant (1000–2500 specimens g<sup>-1</sup>) and well preserved in all samples. Diatoms are also very abundant (D/R ratio ~ 10) (Fig. 5). Diversity and Evenness is stable and high in all samples. Spumellarians are slightly more abundant than nassellarians (52–66 % of the assemblage). The most abundant families are Litheliidae (20–37 %), Plagiacanthidae (14–22 %), Actinommidae (4–12 %), Spongodiscidae (5–9 %), Eucyrtidae (4–8 %) and Lophocyrtidae (3–8 %) (Supplement Table Site 280). Compared to DSDP Site 277, this site has a higher diatom abundance and better overall preservation, which might explain the higher diversity. More species of the gen-

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era *Lithomelissa* (7) and *Larcopyle* (5) are present, as well as a higher abundance of Lophocyrtiidae. Lychnocaniids are very rare at this site (< 1 %) and the genus *Lychnocanium* is absent (Supplement Table Site 280).

#### 4.3.2 DSDP Site 281

5 Seven samples were investigated from DSDP Site 281 in the interval between 149 and 122.5 mbsf (Cores 16R to 14R) (Fig. 5). Results from three of these samples were previously reported in Crouch and Hollis (1996) but have been re-examined for this study. Due to the presence of *Eucyrtidium spinosum* and *Eucyrtidium nishimurae*, the latter with a HO in the late Eocene at ~ 36.9–36.7 Ma (Funakawa and Nishi, 2005), we correlate the Site 281 study interval with lower Zone RP14 (~ Kaiatan local stage). A hiatus  
10 spanning the latest Eocene and Oligocene is inferred from the presence of abundant glauconite in the upper part of Core 281-14R as well as from common *Cyrtocapsella tetrapera* in Core 281-13R, which indicates a Miocene age (Crouch and Hollis, 1996).

In total, 14 families, 34 genera and 46 species were identified at Site 281. Radiolarians are abundant (2000–4000 specimens g<sup>-1</sup>) and well preserved. Diversity is lower than at Site 280A, but Evenness is still very high and similar to the other sites (Fig. 5). The D/R ratio is very high and comparable to Site 280, except in the upper two samples in Core 281-14R (125.5–122.5 mbsf). The radiolarian assemblages are dominated by spumellarians (55–93 %), with Litheliidae (17–42 %), Spongodiscidae (12–30 %) and Actinommidae (10–0 %) the most abundant families. The most common nassellarians  
20 belong to the Plagiacanthidae (1–15 %), Lophocyrtiidae (3–7 %) and Eucyrtiidae (1–7 %) (Supplement Table Site 281). Although Sites 280 and 281 were relatively close to each other (Fig. 1), the radiolarian assemblages are distinctly different, indicating different oceanographic conditions. Crouch and Hollis (1996) concluded that Site 281 was shallower and closer to terrigenous influx than Site 280. The depositional environment of Site 280 is interpreted as more oceanic. The greater abundance of Spongodiscidae at Site 281 supports a shallower oceanic setting for this locality (Casey, 1993). Compared to the early late Eocene assemblage of Site 277, where radiolarian abundance  
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and diversity is very low, with several samples containing less than  $\sim 100$  specimens, Site 281 contains more Spongidiscidae ( $\sim 20\%$ ), Plagiacanthiidae ( $\sim 7\%$ ) and Litheliidae ( $\sim 20\%$ ), whereas the genus *Lychnocanium* is absent at Site 281.

### 4.3.3 DSDP Site 283

5 Six samples were examined from Site 283 between 192.25 and 87.75 mbsf (Cores 8R to 5R) (Fig. 5). The lowermost sample at 192.25 mbsf is correlated to RP13 due to the absence of *Eucyrtidium spinosum*. The uppermost five samples are of early late Eocene age based on the presence of *E. spinosum* and nannofossil age control (Edwards and Perch-Nielsen, 1975). The age of the Site 281 and 283 successions are 10 poorly defined and the PrOM event cannot be located at these sites. Both sites contain *Eucyrtidium nishimurae*: at Site 283 in all samples, at Site 281 its HO is in 125.5–122.5 mbsf. According to Funakawa and Nishi (2005) its HO is in C17n1n ( $\sim 36.7$  Ma, Gradstein et al., 2012). *E. nishimurae* is absent at Site 277. The deposition of siliceous ooze in the late middle to late Eocene and the absence (or very rare) occurrence of foraminifera suggests a deep oceanic setting close or below the Calcite Compensation Depth (CCD) for Site 283.

A total of 16 families, 50 genera and 81 radiolarian species were recorded at Site 283. Radiolarians are abundant ( $4700\text{--}21\,150$  radiolarians  $\text{g}^{-1}$ ), with the highest abundance in Cores 283-6R and 5R, well preserved, and diverse (59–77 taxa per sample, Fisher  $\alpha$  Index of 10–13, Evenness of 0.75–0.89). Diatoms are present in low abundance with D/R ratios  $< 1$  (Fig. 5). Spumellarians account for 59–87% of the assemblage, with the Litheliidae (23–38%), Actinommidae (5–19%) and the Spongidiscidae (2–8%) the most abundant families. The Trissocyclidae (2–11%), Eucyrtiidae (2–11%), Lophocyrtiidae (3–8%) and Plagiacanthidae (2–8%) are the most common 20 nassellarian families (Supplement Table Site 283). *Theocyrtis tuberosa* is very abundant in the uppermost sample. The acme of this taxon might be correlated to its rare occurrence at Site 277 in the late Eocene. Several taxa appear earlier at Site 283 than at Site 277. These include the following taxa that occur in the late middle Eocene (e.g. 25

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*Axoprunum bispiculum*, *Amphicentria* sp. 1 sensu Suzuki, *Ceratocyrtis* spp., *Lithomelissa ehrenbergi*, *L. cf. haeckeli*, *L. sphaerocephalis*, *L. tricornis*, *Pseudodictyophimus gracilipes* gr., *Tripodiscinus clavipes*, *Siphocampe nodosaria*, *Spirocyrtis joides*, *Aspis* sp. A sensu Hollis, *Clathrocyclas universa*, *Eurystomoskevos petrushevskaae*, *Lych-nocanium waiareka*, *Aphetocyrtis gnomabax*) or early late Eocene (*Spirocyrtis greeni*, *Eurystomoskevos cauleti*, *Lophocyrtis jacchia hapsis*, *Lamprocyclas particollis*) at Site 283.

#### 4.3.4 ODP Site 1172



Forty samples were considered from ODP Site 1172 spanning a middle Eocene-to-lower Oligocene interval. Four samples from Hole D, Core 2R (356.875–355.675 mbsf) and thirty-six from Hole A, Core 48X to 39X (445.01–354.625 mbsf). The faunal assemblages of ODP Site 1172 were described by Suzuki et al. (2009), who did not correlate them to RP Zones. We identified key radiolarian index species and correlated the interval to RP Zones 10–15. The absolute age of the succession is based on the age-depth plot of Site 1172 by Stickley et al. (2004). Many taxa used to define RP zones at Site 277 are absent at Site 1172 or have diachronous ranges. We place the base of Zone RP10–12 (LO of *Theocampe mongolfieri*) at 450.55–445.01 mbsf (43.14–42.79 Ma). The base of Zone RP13 (LO of *Eusyringium fistuligerum*) can be located at 419.21–417.71 mbsf (40.48–40.35 Ma), however *Zealithapium mitra* is absent. *Eucyrtidium spinosum*, the marker for Zone RP14, has its LO at 373.75–371.21 mbsf (38.05–37.2 Ma) and *Lithomelissa tricornis* and *Pseudodictyophimus gracilipes* are absent. *Eucyrtidium antiquum* has a single LO at 365.21 mbsf (35.15 Ma), but is absent in the early Oligocene. *E. nishimurae* is present within the middle and late Eocene. Diversity and Evenness are very high throughout the succession.

Spumellarians dominate the Site 1172 assemblages throughout the middle Eocene to early Oligocene (~ 80 %). The Litheliidae are the most abundant family comprising about 20 % on average in the middle Eocene, 35 % in the late Eocene, and 25 % in the early Oligocene.

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ter (Fig. 6), and the radiolarian diversification during the PrOM event is marked by an increase *Lithomelissa* spp. *Amphycraspedum prolixum* gr. has a trace occurrence in the latest Eocene. During the early Oligocene, overall diversity declines and especially the delicate plagiacanthiids and lophocyrtiids decrease. *Lithelius minor* gr. becomes dominant until ~ 144 mbsf, then this group decreases and high-latitude actinommid *Axoprimum bispiculum* and *A. irregularis* make up ~ 75 % of the assemblage (Fig. 6).

At Sites 1172 and 283, high-latitude taxa are present from the middle Eocene, comprising 20–30 % of the assemblage at Site 1172 and ~ 40 % at Site 283 (Fig. 7). The MECO at Site 1172 corresponds to a decline in high-latitude taxa and an increase in cosmopolitan taxa. In the early late Eocene (~ 38–37 Ma), high-latitude taxa increase at Site 1172, from ~ 30 to ~ 50 %. High-latitude taxa at Site 281 range between 20 and 40 % in the early late Eocene. At Site 283 high-latitude taxa are more abundant ranging between 40 and 55 %. However, this is mainly due to the high abundance of a single taxon, *Lithelius minor* gr. Several taxa that are present in the early Oligocene at Site 280 are absent at Site 277, including *Lithomelissa challengerai*, *Larcopyle frakesi*, *Lithomelissa sakai*, and *Antarctissa* spp. The percentage of high-latitude taxa at Site 280 is between 45 and 55 %, with *Lithelius minor* gr. of 10–20 %. *Amphycraspedum prolixum* gr. has a trace occurrence at ~ 103 mbsf at Site 280.

## 5 Discussion

### 5.1 Comparison with geochemical temperature proxies

The radiolarian assemblages documented at Site 277 and 1172 within the MECO interval lack typical tropical taxa such as *Thyrsocyrtis* spp. (e.g. Kamikuri et al., 2013), and the low-latitude taxa *Amphycraspedum murrayanum* and *A. prolixum* gr. account for only 5 % of the total assemblage at Site 277 and are absent at Site 1172. The persistence of high-latitude taxa and the variety of cosmopolitan species at both sites suggests a warm-temperate climate of ~ 15–20 °C, in contrast to geochemical proxies

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suggesting  $> 25^{\circ}\text{C}$  for the MECO at Site 1172 (Bijl et al., 2010) and  $\sim 27^{\circ}\text{C}$  for the late Eocene at Site 277 (Liu et al., 2009).

## 5.2 Nature of the Antarctic assemblage

High-latitude taxa existed from at least the middle Eocene at sites 277, 283 and 1172.

- 5 Many taxa that are present from the earliest late Eocene ( $\sim 38$  Ma) at Sites 281 and 283 appear later at Site 277 ( $\sim 37$ – $36$  Ma), during the PrOM event. This appearance coincides with an increase in radiolarian abundance, diversity and preservation. A comparison of all high-latitude groups is shown in Table 2. We assigned all *Lithomelissa* spp. and *Larcopyle* spp. to the high-latitude group as they are more abundant at higher-
- 10 latitude sites. The ecological and biogeographic affinity of *Lithelius minor* gr. is not yet fully understood. This group has a cosmopolitan distribution but tends to be most abundant at high-latitude sites. The sudden appearance of *Lithomelissa* spp., other high-latitude taxa and diatoms at Site 277 indicates the expansion of high-latitude water masses across the southern Campbell Plateau during the PrOM event.

## 5.3 High-latitude cooling and eutrophication during the PrOM event

### 5.3.1 Diagenesis

- One possibility is that the pronounced increase in radiolarian abundance and diversity observed in the Late Eocene of Site 277 is an artefact of biogenic opal diagenesis. Chert nodules are recorded throughout the upper Paleocene-to-middle Eocene section of the cored sequence at Site 277, with a transition between chert-bearing nannofossil chalk and overlying nannofossil recorded at 246 mbsf (early late Eocene) (Kennett et al., 1975). The presence of chert combined with the generally poorer preservation of radiolarians in the lower Paleogene interval indicates some degree of diagenesis. However, the radiolarian turnover event occurs  $\sim 20$  m above the lithological transition
- 20 within the succession of nannofossil oozes, which implies that the event represents
- 25

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a real increase in radiolarian and diatom abundance and not an artefact of preservation

### 5.3.2 Climate cooling

The long-term cooling trend through the middle and late Eocene, which was interrupted by the short-lived MECO warming event, cannot explain the sudden radiolarian diversification in the late Eocene at Site 277. If gradual, long-term cooling was the driver of the expansion of high-latitude taxa, a progressive increase in such taxa would be expected over a longer time period. A gradual increase of high-latitude taxa is observed at Site 1172 from the middle Eocene but not at Site 277. Instead, the short-lived PrOM event was likely the trigger for the sudden expansion of high-latitude taxa towards the north onto the Campbell Plateau. Whether that event was caused by a sudden drop in atmospheric CO<sub>2</sub> concentrations or was related to the opening of the Tasmanian Gateway, which may have been open to surface circulation in early middle Eocene (Bijl et al., 2013), cannot be determined. Furthermore, astronomical induced changes also have to be considered. Reconstructions from Laskar et al. (2004) show that nodes in the amplitude modulation of eccentricity and obliquity are present at ~ 37 Ma. Additionally, Röhl et al. (2004) found evidence at Site 1172 for the increasing dominance of the 100 kyr eccentricity cycle at ~ 37 Ma. Although there are nodes in amplitude modulation throughout the Eocene (Laskar et al., 2004), it is likely that only the combination of all parameters (CO<sub>2</sub> drop, gateway opening and nodes in amplitude modulation) crossed a certain threshold for a cooling event. The PrOM event may have been associated with the formation of small Antarctic ice sheets (Scher et al., 2014), which would have resulted in an intensification of currents. Several radiolarian turnover events are recorded from the South Atlantic (Maud Rise) by Funakawa and Nishi (2008) during the late Eocene to early Oligocene. At ~ 38.5 Ma they identified a shift from subantarctic to Antarctic bioprovinces with an increase in Antarctic taxa. At ~ 36.3 Ma a decrease in Antarctic taxa was observed and was related to the late Eocene warming (Bohaty and Zachos, 2003). Both events were explained by the northward and southward shift of

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a proto-Antarctic Polar Front, respectively, however, the first event is not identical with the PrOM event.

### 5.3.3 Radiolarian biogeographic reconstruction

During the middle Eocene, high-latitude radiolarian taxa were present at sites 277, 283, and 1172 (Fig. 7). The short-lived increase in abundance, diversity and the influx of low-latitude radiolarian *Amphycraspedum murrayanum* and *A. prolixum* gr. during the MECO at Site 277 and a high percentage of cosmopolitan taxa at Site 1172 during the late middle Eocene suggest moderately warm temperatures at both sites, which may have been the result of a slightly stronger influence of an East Australian Current (Fig. 8a). However, radiolarians and diatoms were abundant only at Site 1172 during the middle Eocene, which suggests a higher productivity region, perhaps a consequence of local upwelling.

During the middle to early late Eocene (~39–38 Ma, Fig. 8b), the abundance of high-latitude taxa increases at Site 1172. Additionally, Sites 281 and 283 show high radiolarian abundance, with ~25 to almost 50% high-latitude taxa. The region of high-productivity is expanding, with the southernmost sites having the highest D/R ratio in the interval ~39–38 Ma (Fig. 8b). This could have resulted from further gateway opening and an intensified cold-water proto-Ross gyre. Radiolarian abundance is still low at Site 277.

In the late Eocene (~37–35 Ma, Fig. 8c), radiolarians abruptly diversify and increase in abundance at Site 277. High-latitude taxa appear (*Lithomelissa* spp., *Larcopyle* spp., Lophocyrtiidae, Table 2), together with diatoms, resulting from cooling and eutrophication at Site 277. High-latitude taxa increase at Site 1172 from ~36.5 Ma (Fig. 7), whereas Site 281 contains a late Eocene hiatus, implying that increasing bottom water currents were established across the Tasmanian Gateway.

During the early Oligocene (~33 Ma, Fig. 8d), the area of non-deposition widened across the Tasmanian Gateway, suggesting the fully open gateway and deep-water connection between ocean basins was established. Only Site 280 has a radiolarian



and diatom-rich record in the early Oligocene indicating a high primary productivity region. About 50 % of the radiolarian fauna are high-latitude taxa at that site. Site 277 also shows high radiolarian abundance and increasing high-latitude portion (~ 40 %) at ~ 33 Ma (Fig. 8d). The diversity, however, declines and diatoms are rare or absent. The radiolarian fauna becomes dominated by *Lithelius minor* gr. and Actinommidiae and many other high-latitude taxa disappear (e.g. *Lithomelissa* spp.). This may indicate the establishment of a cold-water nutrient-depleted environment, similar to the modern setting (Hollis and Neil, 2005), with a proto-Subantarctic Front being established to the south of the Campbell Plateau.

## 6 Conclusions

Middle Eocene to early Oligocene radiolarian assemblages from DSDP sites 277, 280, 281, 283 and ODP Site 1172 were examined to identify the distribution of Antarctic assemblages in the Southwest Pacific. In contrast to temperature reconstructions based on geochemical proxies that indicate subtropical-tropical temperatures at high-latitudes during the middle and late Eocene (Liu et al., 2009; Bijl et al., 2010), Eocene radiolarian assemblages in this region lack significant numbers of low-latitude taxa. Furthermore, we show that many high-latitude taxa endemic to the Antarctic are already present in the middle Eocene. The MECO event, although truncated by poor recovery, has been identified at Site 277 within foraminiferal oxygen isotope records, and is associated with a short-lived incursion of two low-latitude taxa, *Amphycraspedum prolixum* gr. and *Amphycraspedum murrayanum*, in low numbers. The absence of definitive tropical taxa suggests warm temperate rather than tropical conditions during this short-lived event. However, the peak warming interval is likely missing due to poor core recovery. Radiolarians are very abundant and well preserved at high-latitude sites 281, 283 and 1172 during the early late Eocene with about 30–50 % of the assemblage consisting of high-latitude taxa. During the early late Eocene (~ 37 Ma), a positive excursion in foraminiferal  $\delta^{18}\text{O}$  values at Site 277 marks the PrOM event. A pronounced

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increase in diversity, abundance and preservation of radiolarians occurs in conjunction with this event. It is also accompanied by a pronounced increase in the abundance of diatoms. Many high-latitude taxa that are very abundant at Site 281 and 283 in the late middle Eocene and early late Eocene become abundant or have their LOs at Site 277 at ~ 37 Ma, respectively: *Lithelius minor* gr., *Larcopyle hayesi*, *L. polyacantha*, *Spongopyle osculosa*, *Lithomelissa sphaerocephalis*, *L. gelasinus*, *L. ehrenbergi*, *Ceratocyrtis* spp., *Dictyophimus* aff. *archipilium*, *Lamprocyclas particollis*, and Antarctic morphotypes of *Aphetocyrtis gnomabax*, *A. rossi*, *Lophocyrtis aspera*, *L. keraspera* and *L. longiventer*. This northward extension of high-latitude taxa on the Campbell Plateau appears to have been triggered by the PrOM event, which is inferred to have been a short-lived expansion of the Antarctic ice sheet. Through the EOT, radiolarians remain abundant at Site 277, but decline in diversity. Delicate forms such as Plagiacanthidae decline, whereas *Lithelius minor* gr. and Actinommidae became dominant. The disappearance of diatoms indicates that conditions over the Campbell Plateau became nutrient-depleted. We infer that the Tasmanian Gateway was fully open by the earliest Oligocene and a strong circumpolar current was established causing widespread non-deposition in the Southwest Pacific. At the same time, a proto-Subantarctic Front developed supplying nutrient-depleted Subantarctic waters onto the Campbell Plateau resulting in a decline in radiolarian and diatom productivity.

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**Table 1.** Summary of species encountered at sites 277, 280, 281, and 283, their biogeographic affinity (A = Antarctic, B = bipolar, L = low-latitude and C = cosmopolitan), and location on plates for selected species.



Taxa	Biogeographic affinity	Site 277	Site 280	Site 281	Site 283	Plate
<i>Actinommidae</i> sp. A sensu Hollis		x				Pl. 1, Fig. 1
<i>Amphicentria</i> sp. 1 sensu Suzuki	A	x		x	x	Pl. 2, Fig. 1
<i>Amphicraspedum murrayanum</i> Haeckel	T	x				Pl. 1, Fig. 14
<i>Amphicraspedum prolixum</i> Sanfilippo and Riedel gr.	T	x	x			Pl. 1, Figs. 15–17
<i>Amphisphaera</i> aff. <i>radiosa</i> (Ehrenberg)		x				Pl. 1, Fig. 4a and b
<i>Amphisphaera coronata</i> (Ehrenberg) gr.	C	x			x	Pl. 1, Fig. 2
<i>Amphisphaera radiosa</i> (Ehrenberg)		x				Pl. 1, Fig. 3
<i>Amphisphaera spinulosa</i> (Ehrenberg)	C	x			x	Pl. 1, Fig. 5
<i>Amphisphaera?</i> <i>megapora</i> (Ehrenberg)		x	x	x	x	Pl. 1, Fig. 6
<i>Amphymentium splendarmatum</i> Clark and Campbell	C	x	x	x	x	Pl. 1, Figs. 18 and 19
<i>Anomalocantha dentata</i> (Mast)		x	x	x	x	
<i>Antarctissa cylindrica</i> Petrushevskaya	A		x			
<i>Antarctissa robusta</i> Petrushevskaya	A		x			
<i>Aphetocyrtis bianulus</i> (O'Connor)	A	x			x	Pl. 5, Fig. 1
<i>Aphetocyrtis gnomabax</i> Sanfilippo and Caulet	A	x	x	x	x	Pl. 5, Figs. 2–7
<i>Aphetocyrtis rossi</i> Sanfilippo and Caulet	A	x	x		x	Pl. 5, Figs. 8–11
<i>Archipilium macropus</i> (Haeckel)		x			x	
<i>Artobotrys auriculaleporis</i> (Clark and Campbell)	C	x				
<i>Artobotrys titanothericeraos</i> (Clark and Campbell)		x		x		
<i>Artostrobos annulatus</i> (Bailey)	B	x			x	
<i>Artostrobos</i> cf. <i>pretabulatus</i> Petrushevskaya	A	x				Pl. 3, Fig. 13
<i>Aspis</i> sp. A sensu Hollis	A	x	x		x	Pl. 3, Figs. 14–16
<i>Axoprunum bispiculum</i> (Popofsky)	A	x			x	
<i>Axoprunum pierinae</i> (Clark and Campbell) gr.	C	x	x	x		Pl. 1, Figs. 10 and 11
<i>Axoprunum?</i> <i>irregularis</i> Takemura	A	x				Pl. 1, Fig. 12
<i>Botryocella?</i> sp A sensu Apel			x			Pl. 3, Figs. 1–4
<i>Buryella granulata</i> (Petrushevskaya)	A	x				
<i>Callimitra?</i> aff. <i>atavia</i> Goll		x				Pl. 2, Fig. 2
<i>Calocyclus ampulla</i> (Ehrenberg)		x				
<i>Ceratocyrtis</i> spp.	B	x	x		x	Pl. 2, Figs. 3–5
<i>Cincolpyramis circumtexta</i> (Haeckel)	C	x	x	x	x	
<i>Cladoscenum ancoratum</i> Haeckel			x		x	
<i>Clathrocyclus universa</i> Clark and Campbell	C	x		x	x	
<i>Clinorhabdus anantomus</i> Sanfilippo and Caulet	A	x		x	x	Pl. 5, Figs. 12 and 13
<i>Cornutella profunda</i> Ehrenberg	C	x	x	x	x	
<i>Corythomelissa adunca</i> (Sanfilippo and Riedel)					x	
<i>Cryptocarpium bussonii</i> (Carnevale) gr.	C	x	x	x	x	Pl. 5, Figs. 25a and b, 26a and b
<i>Cryptocarpium ornatum</i> (Ehrenberg)	C	x			x	
<i>Cycladophora cosma cosma</i> Lombardi and Lazarus	A		x			Pl. 3, Fig. 17
<i>Cycladophora humerus</i> (Petrushevskaya)	A		x	x	x	Pl. 3, Fig. 18
<i>Cycladophora</i> spp.	A	x		x		
<i>Cymaetron sinolampas</i> Caulet			x		x	

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**Table 1. Continued.**

Taxa	Biogeographic affinity	Site 277	Site 280	Site 281	Site 283	Plate
<i>Cyrtolagena laguncula</i> Haeckel	C	x			x	
<i>Dictyophimus?</i> aff. <i>strictus</i> O'Connor			x			Pl. 4, Figs. 9 and 10
<i>Dictyophimus infabricatus</i> Nigrini	C	x				
<i>Dictyophimus?</i> aff. <i>archipilium</i> Petrushevskaya	A	x		x	x	Pl. 4, Figs. 3a, b–8
<i>Dictyophimus?</i> <i>archipilium</i> Petrushevskaya	A	x	x		x	Pl. 4, Figs. 1a and b, 2
<i>Eucyrtidium antiquum</i> Caulet	A	x	x			Pl. 3, Fig. 19
<i>Eucyrtidium mariae</i> Caulet	A	x				
<i>Eucyrtidium microporum</i> Ehrenberg					x	
<i>Eucyrtidium nishimurae</i> Takemura and Ling	A			x	x	Pl. 3, Fig. 20a and b
<i>Eucyrtidium sphosum</i> Takemura	A	x		x	x	Pl. 3, Fig. 21
<i>Eucyrtidium</i> spp.	A				x	
<i>Eucyrtidium ventriosum</i> O'Connor	A	x			x	Pl. 3, Fig. 22
<i>Eurystomoskevos cauleti</i> O'Connor	A	x	x	x	x	Pl. 3, Fig. 23a and b
<i>Eurystomoskevos petrushevskae</i> Caulet	A	x	x	x	x	Pl. 3, Fig. 24
<i>Eusyringium fistuligerum</i> (Ehrenberg)	C	x				Pl. 3, Fig. 25
<i>Eusyringium lagena</i> (Ehrenberg)	C				x	
<i>Glycobotrys nasuta</i> (Ehrenberg) gr.	C	x	x	x	x	Pl. 3, Figs. 5–7
<i>Heliodiscus inca</i> Clark and Campbell		x			x	
<i>Lamprocyclas particollis</i> O'Connor	A	x	x	x	x	Pl. 5, Fig. 27
<i>Larcopyle</i> cf. <i>pylomaticus</i> (Riedel)	A		x	x		Pl. 1, Fig. 25a and b
<i>Larcopyle frakesi</i> (Chen)	A		x			Pl. 1, Fig. 20
<i>Larcopyle hayesi</i> (Chen)	A	x		x	x	Pl. 1, Fig. 21
<i>Larcopyle labyrinthosa</i> Lazarus	A		x			Pl. 1, Fig. 22
<i>Larcopyle polyacantha</i> (Campbell and Clark) gr.	A	x	x	x	x	Pl. 1, Figs. 23 and 24
<i>Larcopyle</i> spp.	A	x	x	x		
<i>Lithelius foremanae</i> Sanfilippo and Riedel		x				
<i>Lithelius minor</i> Jörgensen gr.	B		x	x	x	Pl. 1, Figs. 26–28
<i>Lithomelissa</i> cf. <i>challengerae</i> Chen	A	x				Pl. 2, Fig. 9
<i>Lithomelissa</i> cf. <i>haeckeli</i> Bütschli	A	x			x	Pl. 2, Fig. 14
<i>Lithomelissa challengerae</i> Chen	A		x			Pl. 2, Fig. 6–8
<i>Lithomelissa ehrenbergi</i> Bütschli	A	x	x	x	x	Pl. 2, Figs. 10 and 11
<i>Lithomelissa gelasinus</i> O'Connor	A	x	x	x	x	Pl. 2, Figs. 12 and 13
<i>Lithomelissa macroptera</i> Ehrenberg	A				x	Pl. 2, Fig. 15a and b
<i>Lithomelissa robusta</i> Chen	A		x		x	Pl. 2, Fig. 16
<i>Lithomelissa sphaerocephalis</i> Chen	A	x	x	x	x	Pl. 2, Fig. 17
<i>Lithomelissa</i> spp.	A	x	x	x	x	
<i>Lithomelissa tricornis</i>	A	x	x	x	x	Pl. 2, Fig. 18
<i>Lithomelissa?</i> <i>sakai</i> O'Connor	A		x			Pl. 2, Fig. 19
<i>Lophocyrtis</i> (Apoplanius) <i>aspera</i> (Ehrenberg)	A	x		x	x	Pl. 5, Figs. 14a, b–16
<i>Lophocyrtis</i> (Apoplanius) <i>keraspera</i> Sanfilippo and Caulet	A	x			x	Pl. 5, Figs. 17–19
<i>Lophocyrtis</i> (Lophocyrtis) <i>jacchia hapsis</i> Sanfilippo and Caulet	A				x	Pl. 5, Figs. 20–22
<i>Lophocyrtis</i> (Paralampterium) <i>dumitricai</i> Sanfilippo	C	x				
<i>Lophocyrtis</i> (Paralampterium) <i>longiventer</i> (Chen)	A	x	x	x	x	Pl. 5, Figs. 23 and 24
<i>Lophocyrtis</i> spp.	A				x	

**Table 1. Continued.**

Taxa	Biogeographic affinity	Site 277	Site 280	Site 281	Site 283	Plate
<i>Lophophaena capito</i> Ehrenberg	C	x		x	x	
<i>Lophophaena simplex</i> Funakawa			x		x	
<i>Lychnocanium</i> aff. <i>carinatum</i> Ehrenberg		x				Pl. 4, Fig. 17
<i>Lychnocanium amphitrite</i> (Foreman)	C	x			x	Pl. 4, Figs. 11a–c and 12
<i>Lychnocanium babylonis</i> (Clark and Campbell)	C	x			x	Pl. 4, Figs. 13a and b, 14
<i>Lychnocanium bellum</i> Clark and Campbell	C	x			x	Pl. 4, Figs. 15 and 16
<i>Lychnocanium conicum</i> Clark and Campbell	C	x				
<i>Lychnocanium continuum</i> Ehrenberg					x	
<i>Lychnocanium tetrapodium</i> Ehrenberg	T	x				Pl. 4, Fig. 18a and b
<i>Lychnocanium waiareka</i> O'Connor		x			x	
<i>Perichlamyidium limbatum</i> Ehrenberg			x			
<i>Periphaena decora</i> Ehrenberg	C	x	x	x	x	
<i>Periphaena heliastericus</i> (Clark and Campbell)	C	x	x	x	x	
<i>Phormocyrtis striata striata</i> Brandt	C	x				
<i>Plectodiscus circularis</i> (Clark and Campbell)	C	x	x	x	x	
<i>Pseudodictyophimus galeatus</i> Caulet	A	x				Pl. 2, Fig. 20
<i>Pseudodictyophimus gracilipes</i> (Bailey) gr.	B	x	x	x	x	Pl. 2, Figs. 21–23
<i>Pseudodictyophimus</i> spp.	A		x			Pl. 2, Figs. 24–27
<i>Pterocodon apis</i> Ehrenberg					x	Pl. 4, Figs. 19 and 20a, b
<i>Pteropilium</i> aff. <i>contiguum</i> (Ehrenberg)		x				Pl. 4, Fig. 21
<i>Saturnalis circularis</i> Haeckel					x	
<i>Sethocyrtis chrysalis</i> Sanfilippo and Blome	C	x				Pl. 3, Fig. 26a and b
<i>Siphocampe lineata</i> (Ehrenberg)	C	x				
<i>Siphocampe nodosaria</i> (Haeckel)	C	x		x	x	
<i>Siphocampe quadrata</i> (Petrushevskaya and Kozlova)	C	x		x	x	
<i>Siphocampe? acephala</i> (Ehrenberg) gr.		x		x	x	Pl. 3, Figs. 8–10
<i>Siphocampe? amygdala</i> (Shilov)	A	x			x	Pl. 3, Figs. 11 and 12
<i>Sphaerophyle tetrapila</i> (Hays)	A	x				Pl. 1, Fig. 29
<i>Spirocyrtis greeni</i> O'Connor		x		x	x	
<i>Spirocyrtis joides</i> (Petrushevskaya)	C	x	x	x	x	
<i>Spongatractus pachystylus</i> (Ehrenberg)		x				
<i>Spongodiscus craticulatus</i> (Stöhr)				x		
<i>Spongodiscus cruciferus</i> (Clark and Campbell)	C			x		
<i>Spongodiscus festivus</i> (Clark and Campbell)	C	x				
<i>Spongophyle osculosa</i> Dreyer	B	x	x	x	x	Pl. 1, Fig. 13
<i>Spongurus bilobatus</i> Clark and Campbell	C	x		x	x	
<i>Stichopilium</i> cf. <i>bicorne</i> (Haeckel)			x	x	x	Pl. 5, Figs. 28a and b, 29a and b
<i>Stylosphaera minor</i> Clark and Campbell gr.	C	x	x		x	Pl. 1, Fig. 7
<i>Theocampe amphora</i> (Haeckel)	C	x				
<i>Theocampe urceolus</i> (Haeckel)	C	x	x	x	x	
<i>Theocyrtis tuberosa</i> Riedel	C	x			x	Pl. 5, Fig. 30
<i>Thyrsocyrtis pinguisoides</i> O'Connor	B	x			x	Pl. 3, Fig. 27
<i>Tripodiscinus clavipes</i> (Clark and Campbell)	C	x		x	x	
<i>Zealithapium mitra</i> (Ehrenberg)	C	x			x	Pl. 1, Fig. 8
<i>Zygocircus bütschli</i> Haeckel		x			x	

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**Table 2.** Average of total % of high-latitude species, groups, genera and high-latitude members of families for four time slices: MECO (~ 40 Ma), middle/late Eocene (~ 39–38 Ma), late Eocene (~ 37–35 Ma) and early Oligocene (~ 33 Ma).

	Site 280 E. Olig.	Site 281 m/l Eoc.	Site 283 m/l Eoc.	Site 277 MECO	m/l Eoc.	late Eoc.	E. Olig.	Site 1172 MECO	m/l Eoc	late Eoc.
% total high-lat. species	49	27	48	14	9	18	40	23	26	46
<i>Lithellus minor</i> gr. %	15.0	2.1	31.5	4.2	1.9	5.3	30.7	13.7	12.4	22.0
<i>Larcopyle</i> spp. %	10.0	10.5	1.7	2.9	1.93	1.88	1.5	6.0	5.4	12.8
<i>Lithomelissa</i> spp. %	8.9	4.8	2.5	0.06	0.1	2.15	1.2	0.5	1.4	0.5
High-lat. Lophocyrtiidae %	5.6	5.6	5.0	6.2	3.8	5.5	3.60	1.0	2.8	5.3
High-lat. Eucyrtiidae %	4.9	2.7	4.8	0.1	1.0	1.2	0.2	1.4	1.9	1.5
Other high-lat. Plagiacanthidae %	3.5	0.6	1.0	0	0.1	0.34	0.25	0	0.02	0
Other high-lat. species %	1.2	0.4	1.5	1.0	0.1	2.1	2.8	0.6	1.9	4.2

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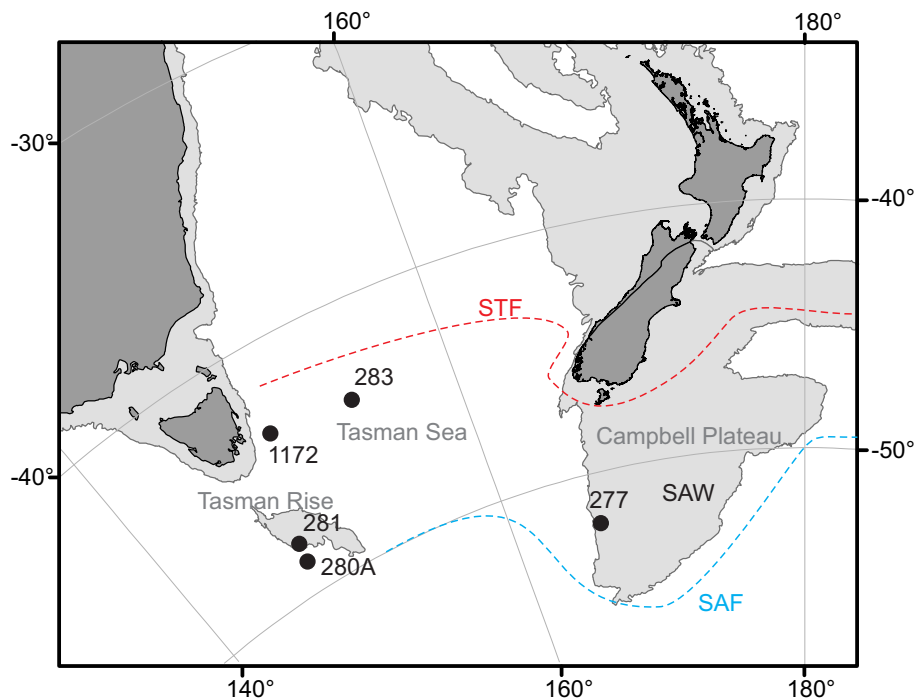
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**Figure 1.** Modern location of DSDP and ODP study sites in the Southwest Pacific; STF = Subtropical Front, SAF = Subantarctic Front, SAW = Subantarctic Water.

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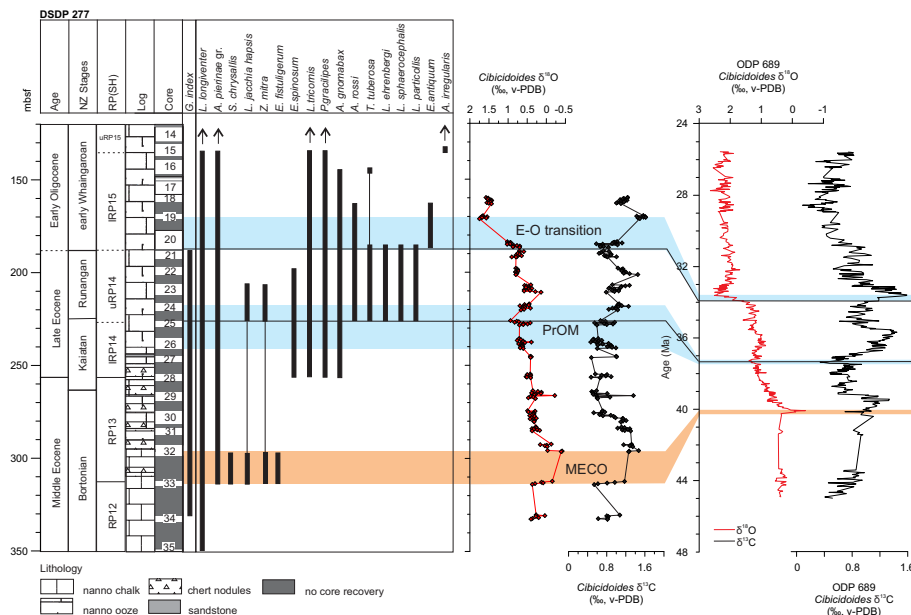
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**Figure 2.** DSDP Site 277 stratigraphy, lithology, Southern Ocean radiolarian zones, core recovery, and ranges of *Globigerinatheka index* and selected radiolarians. Benthic stable oxygen and carbon isotope data of DSDP Site 277 correlated to Southern Ocean *Cibicidoides* data of ODP Site 689 Hole B (Maud Rise) (Diester-Haass and Zahn, 1996) calibrated to the GTS2012 timescale using the magnetostratigraphy data of Florindo and Roberts (2005) and Spiess (1990).

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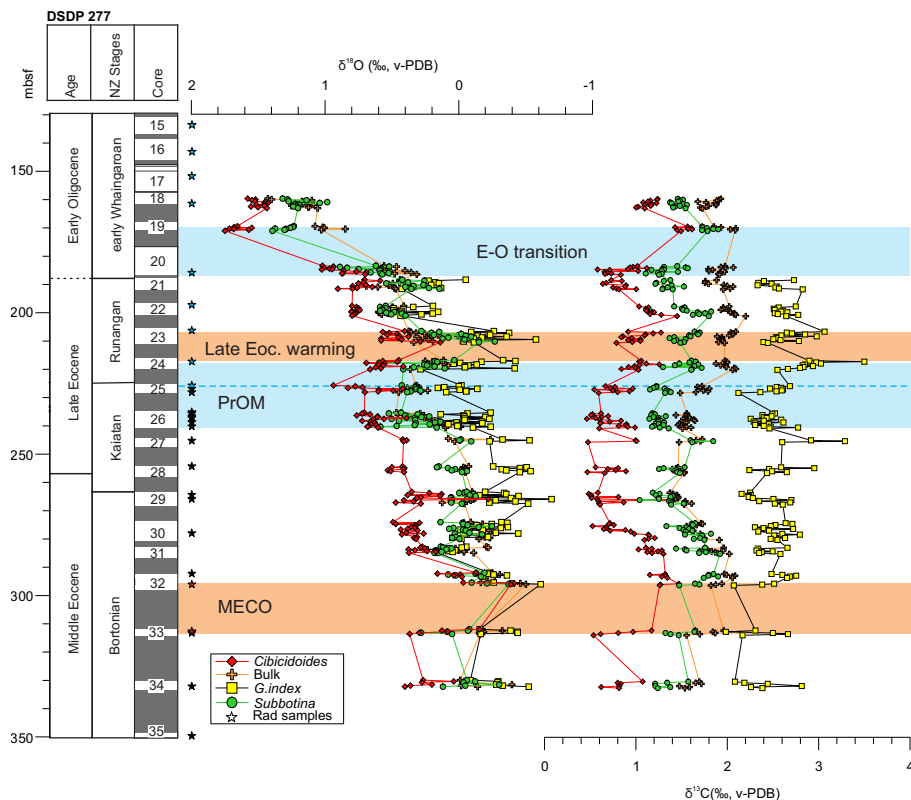
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**Figure 3.** DSDP Site 277 oxygen and carbon stable isotope records and position of studied radiolarian samples within MECO interval (red stars) and radiolarian-rich late Eocene–Oligocene interval (blue stars).

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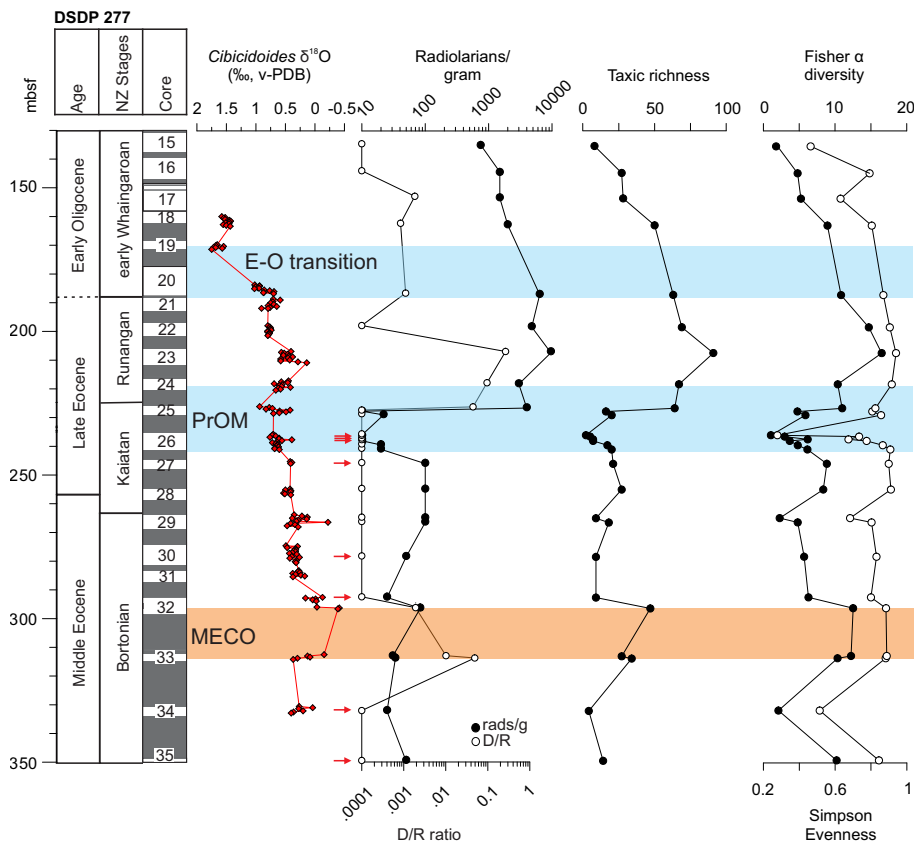
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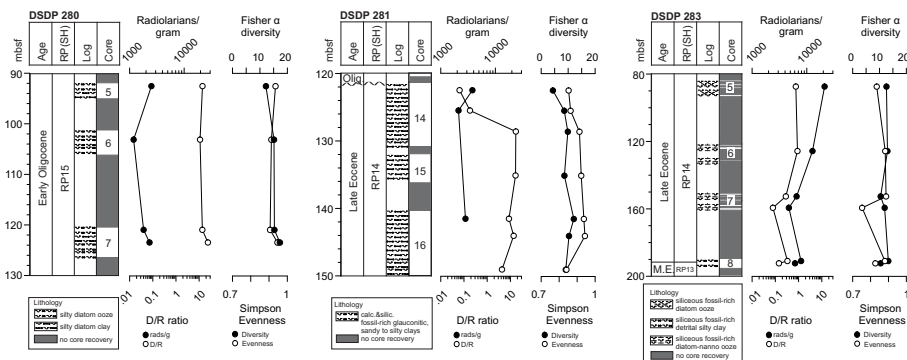
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**Figure 4.** DSDP Site 277 benthic  $\delta^{18}\text{O}$  record; radiolarian abundance and Diatom/Radiolarian (D/R) ratio; Taxic Richness (number of taxa), Fisher  $\alpha$  Index and Simpson Evenness Index for radiolarian assemblages. Red arrows indicate samples with total specimen counts less than 99, which may be statistical insignificant but are included in all figures for the sake of completeness.

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**Figure 5.** Variation in radiolarian abundance, Diatom/Radiolarian (D/R) ratio, Fisher  $\alpha$  Index and Simpson Evenness for radiolarian assemblages at DSDP sites 280, 281 and 283.

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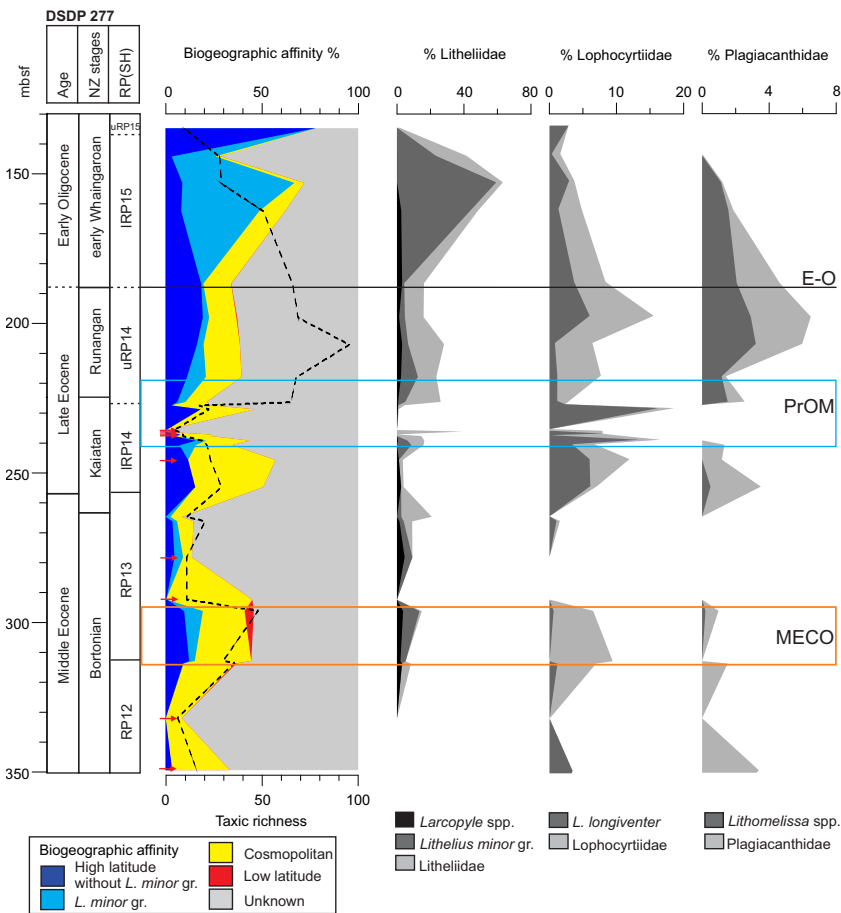
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**Figure 6.** Biogeographic affinities of radiolarian assemblages at DSDP Site 277; Taxic richness; most abundant families with high-latitude affinity. Red arrows indicate samples with total specimen counts less than 99.

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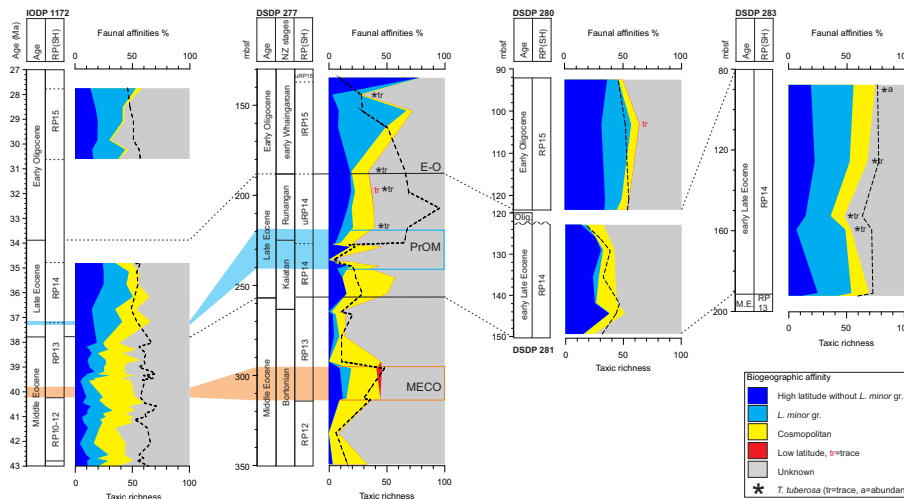
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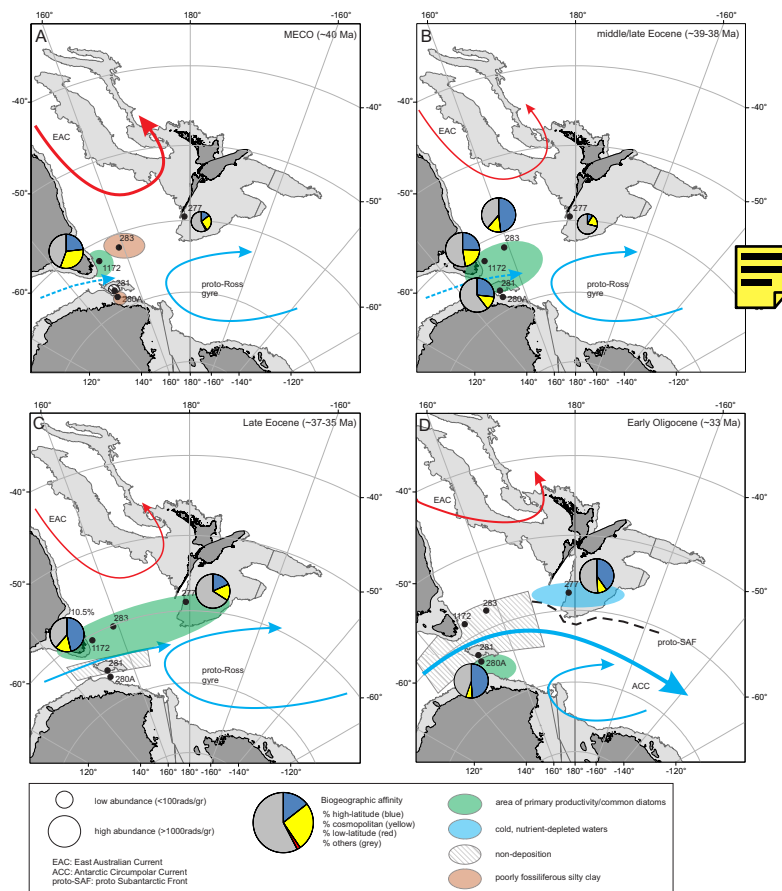
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**Figure 7.** Variation in faunal affinities for radiolarian assemblages at all sites. Dashed black lines indicate correlation between sites, which is hampered by hiatuses and poorly defined ages, respectively. The age model of ODP Site 1172 is based on the age-depth plot of Stickley et al. (2004).

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**Figure 8.** Paleogeographic reconstructions (GPlates, using the latest hotspot trace reference frames, Seton et al., 2012; Matthews et al., 2015) and biogeographic affinities at investigated sites during the MECO, middle/late Eocene (~39–38 Ma), PrOM and latest Eocene (~37–35 Ma) and early Oligocene (~33 Ma).