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The last 1 million years of the extinct genus *Discoaster*: Plio–Pleistocene environment and productivity at Site U1476 (Mozambique Channel)

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Highlights

1. A more intensified water column mixing shown by low values of *Florisphaera profunda* index occurred at the Mozambique Channel from ~2.4 Ma, resulting in increased abundances of the upper photic zone flora indicative of nutrient-rich surface water conditions.
2. Discoasters declined with global cooling and associated enhancement of surface water productivity in the tropical Indian Ocean across the Plio-Pleistocene.
3. Ecological preference of the Plio-Pleistocene *Discoaster* species resembles that of *F. profunda*, i.e., warm and oligotrophic surface water conditions.
4. The 100-kyr and obliquity signatures suggest a NH driver of the observed variability, whereas variability at the rhythm of precession is interpreted as a tropical Pacific forcing.

The last 1 million years of the extinct genus *Discoaster*: Plio–Pleistocene environment and productivity at Site U1476 (Mozambique Channel)

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Abstract

A detailed paleoenvironment reconstruction from the Mozambique Channel, western Indian Ocean, based on the calcareous nannoplankton assemblages was conducted for the interval between 2.85 and 1.85 Myr. This study covers the period during which the successive extinction of the last five species of discoasters occurred. New productivity data obtained from the abundances of the *Discoaster* species (*Discoaster brouweri*, *D. triradiatus*, *D. pentaradiatus*, *D. surculus*, and *D. tamalis*) and other indicative calcareous nannoplankton taxa showed abundance variations, which were paced with the 100, 41, and 23 kyr astronomical periodicities. A shift in the productivity and water-column stratification proxies occurred at ~2.4 Ma, after the onset of the Northern Hemisphere glaciation. Here we propose that the variability recorded at International Ocean Discovery Program Site U1476 reflects the interplay between forcing associated with warm tropical Pacific and cold southern ocean influences. The former is shown by consistent occurrence of warm water taxa (*Calcidiscus leptoporus*, *Oolithotus* spp., *Rhabdosphaera clavigera*, *Syracosphaera* spp., *Umbellosphaera* spp.), typical of Indonesian Throughflow surface waters. On the other hand, the occurrence of *Coccolithus pelagicus* indicates the influence of cold, nutrient-rich sub-Antarctic surface waters. A more mixed water column initiated at ~2.4 Ma, and a consequent productivity increase led to the gradual reduction of the *Discoaster* species, until their extinction at 1.91 Ma. This period was characterized by the low values of the *Florisphaera profunda* index and high abundances of upper photic zone flora, indicative of nutrient-rich surface water

42 conditions. High productivity at the location during this period could have also been amplified
43 by localized upwelling events driven by the Mozambique Channel eddies.

44

45 **Keywords:** calcareous nannofossils, nannoplankton, western Indian Ocean, Expedition 361
46

47 **1 Introduction**

48 Major climatic variability during the middle part of the Pliocene was first proposed by
49 [Shackleton et al. \(1984\)](#) to have triggered the onset of the Northern Hemisphere (NH)
50 glaciation. Numerous studies have corroborated this suggestion on the basis of
51 paleontological, sedimentological and geochemical records of long climate archives (e.g.,
52 [Ravelo et al., 2004](#); [Clemens et al., 1996](#); [Christensen et al., 2017](#)). Much of the evidence for
53 this consensus derive from stable carbon and oxygen isotope ($\delta^{18}\text{O}$ and $\delta^{13}\text{C}$) data measured
54 on planktonic and benthic foraminifera (e.g., [Raymo et al., 1992](#); [Clemens et al., 1996](#); [Ravelo](#)
55 [et al., 2004](#)), suggesting the significance of this phenomenon in the evolution of the Plio-
56 Pleistocene climate. This extreme climatic variability was coupled with global-scale variations
57 in the sea surface temperature (SST) ([Clemens et al., 1996](#)) and associated changes in
58 nutrient availability, which could have created a complex oceanographic regime, which in turn
59 controlled plankton distribution in the photic layer. Previous studies suggested that during the
60 late Pliocene (~3 to 2.5 Myr), a shift in marine productivity between the high latitudes and the
61 mid- to low latitudes occurred (e.g., [Sarnthein and Fenner, 1988](#); [Bolton et al., 2011](#)). Low
62 values of biogenic silica, CaCO_3 , organic carbon, and alkenone accumulation in marine
63 sediments from high latitude regions and high values in the mid- to low latitudes were
64 recorded, suggesting a more productive mid- to low latitude oceans during this time period.
65 These findings have important implications for Plio-Pleistocene climate since marine biological
66 productivity is a key component in the global biogeochemical cycles. Thus studies focusing
67 on the long-term trends in biological responses to climatic variations are essential in
68 understanding the interplay between the local atmospheric processes and ocean circulation
69 over several glacial/interglacial cycles, which is an essential prerequisite in modeling the
70 present and even future climate scenarios.

71

72 One of the major contributors to marine primary production, that also plays a key role
73 in both the biological and carbonate pumps are calcareous nannoplankton (nannofossils), a
74 group of single-celled, marine haptophyte algae. These organisms are one of the dominant
75 calcifying plankton groups in the oceans (e.g., [Friedinger and Winter, 1987](#); [Westbroek et al.,](#)
76 [1993](#)) and within the fossil record, form a major part of its deep-sea sediments (e.g., [Flores et](#)
77 [al., 1999](#); [Beaufort et al., 2001](#); [Rogalla and Andruleit, 2005](#)). Calcareous nannoplankton live

78 in the photic layer where light intensity is strong enough to carry out photosynthesis and the
79 nutrient levels are suitable for its growth. The temporal and spatial distributions of calcareous
80 nannoplankton are controlled by latitude (light levels), ocean currents, and the ambient upper
81 ocean nutrient content, salinity, and temperature profiles of the underlying water masses
82 (Winter et al., 1994). They are sensitive to variations in water column characteristics
83 (stratification/mixing), making these organisms potentially ideal recorders of past
84 environmental conditions.

85

86 The Plio-Pleistocene is a significant time interval in calcareous nannoplankton
87 evolution history because of the recorded decrease in diversity during this time interval (Bown
88 et al., 2004; Aubry, 2007). High frequency variability in glacial/interglacial temperatures
89 occurred during this interval, with the Pleistocene exhibiting greater variance compared to the
90 late Pliocene (Ravelo et al., 2004; Lisiecki and Raymo, 2005; De Vleeschouwer et al., 2017).
91 The gradual cooling during the transition from the warm Pliocene to the cold Pleistocene
92 (Ravelo et al., 2004) was proposed by Aubry (2007) to have driven the Pliocene
93 nannoplankton turnover and subsequent extinction events. The extinct genus *Discoaster* is
94 one of the nannoplankton groups that were affected by these extreme climatic fluctuations and
95 transition. *Discoaster* exhibited a fairly continuous evolutionary development from their first
96 occurrence in the late Paleocene (60 Ma) to the extinction of the last species toward the end
97 of the Gelasian stage (1.93 Ma). Previous studies have suggested that the inception of the
98 NH glaciation during the Pliocene (Shackleton et al., 1984; Raymo et al., 1992; Clemens et
99 al., 1996) led to the successive disappearance of the *Discoaster* species (e.g., Backman and
100 Pestiaux, 1987; Chapman and Chepstow-Lusty, 1997). The successive extinction of species
101 belonging to this group until its complete demise from the geologic record thus reflects its
102 sensitivity to changes in environmental and oceanographic conditions. While these extinction
103 events are widely documented (e.g., Bukry, 1971; Chepstow-Lusty et al., 1989; Chapman and
104 Chepstow-Lusty, 1997; Raffi et al., 2006; Browning et al., 2017), our knowledge of the
105 ecological preference of the *Discoaster* species and the environment that they lived in before
106 they disappeared is still limited (e.g., Bukry, 1971; Haq and Lohmann, 1976; Aubry, 1998;
107 Schueth and Bralower, 2015). For instance, the reported diachronous occurrences (Raffi et
108 al., 2006; Schueth and Bralower, 2015) of its member taxa in different ocean basins suggest
109 that the *Discoaster* extinction cannot be explained by variations in SST alone (e.g., Chepstow-
110 Lusty et al., 1989; Chapman and Chepstow-Lusty, 1997), but is likely a result of a combination
111 of complex environmental parameters (Schueth and Bralower, 2015). There is a general
112 agreement that discoasters have an affinity for warm and oligotrophic water based on
113 assemblage analysis and geochemical evidence (Aubry, 1998; Minoletti et al., 2001; Bralower,
114 2002; Schueth and Bralower, 2015), although their depth habitat is still poorly understood. In

115 particular, oxygen isotope values of discoasters resembled the planktonic foraminifera
116 (*Globorotalia menardii*, *Dentoglobigerina altispira*, *Globigerinoides obliquus*) record, indicating
117 that they are shallow-dwelling (Minoletti et al., 2001), which is contrary to the findings in other
118 literature that this group prefers the deep photic layer (e.g., Aubry, 1998; Bralower et al., 2002;
119 Schueth and Bralower, 2015). While this present study cannot completely solve the
120 controversy on their depth habitat, here we provide information on the past variations in
121 environmental and oceanographic conditions in the equatorial Indian Ocean during the Plio-
122 Pleistocene transition that led to the extinction of this long-lived genus.

123

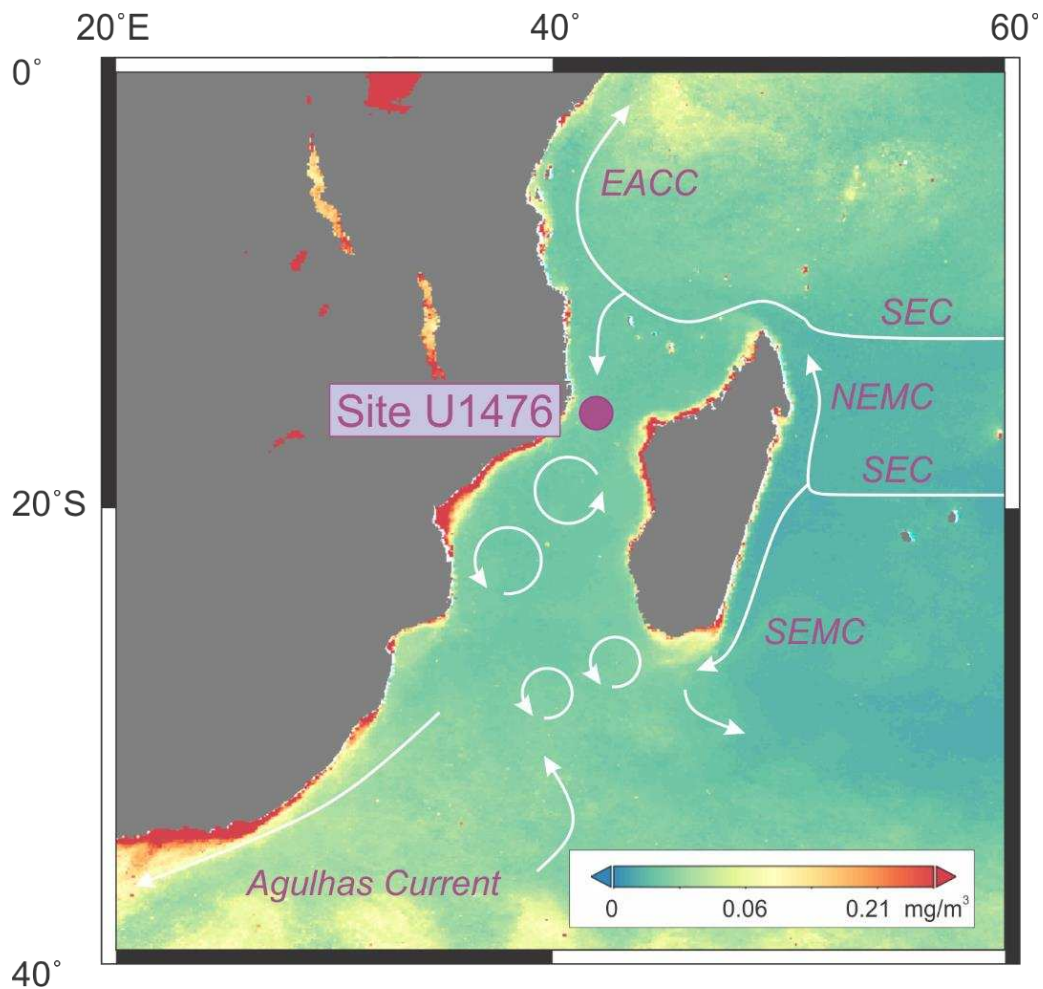
124 Here we investigated the temporal distribution of the last five species of this group (*D.*
125 *tamalis*, *D. surculus*, *D. pentaradiatus*, *D. triradiatus*, *D. brouweri*) in the westernmost Indian
126 Ocean using sediments from Site U1476 (Mozambique Channel) collected during the
127 International Ocean Discovery Program (IODP) Expedition 361 – Southern African Climates
128 (Fig. 1) (Hall et al., 2017b) to reconstruct how the environment and productivity conditions
129 changed toward the end of this lineage. Site U1476 consists of a continuous Plio-Pleistocene
130 sequence of foraminifera-rich or foraminifera-bearing nanofossil ooze (Hall et al., 2017b) and
131 thus offers an exceptional opportunity for high-resolution paleoenvironment and productivity
132 reconstructions. Together with a detailed Plio-Pleistocene calcareous nanofossil
133 biostratigraphy at this site, we present here new records of productivity from the abundances
134 of *Discoaster* species and compare our results with the downcore abundance record of the
135 extant taxon *F. profunda*, a widely used productivity proxy, and to other calcareous
136 nannoplankton taxa with established ecological preferences.

137

138 2 Site U1476 and oceanographic setting

139 Site U1476 lies on the Davie Ridge, a bathymetric high in the Mozambique Channel,
140 between the African continent and Madagascar. The site is located at the northern entrance
141 of the Mozambique Channel (15°49.25'S; 41°46.12'E; Fig. 1) at a water depth of 2165 m (Hall
142 et al., 2017b). The study area is presently influenced by the seasonally reversing monsoon
143 winds (boreal summer and winter), induced by the migration of the Intertropical Convergence
144 Zone, with rainfall maxima during the boreal winter (Hastenrath et al., 1993). The sea surface
145 currents in the western Indian Ocean are in turn driven by the monsoon and the semi-annual
146 inter-monsoon trade winds (Indian Ocean equatorial westerlies). The surface waters at Site
147 U1476 are fed by the South Equatorial Current (SEC) that flows westward year-round across
148 the Indian Ocean, carrying warm and oligotrophic surface water of the Indonesian Throughflow
149 (ITF) (Schott et al., 2009; Fig. 1). To the east of Madagascar, the SEC splits into two boundary
150 currents flowing as the Northeast and Southeast Madagascar Currents (NEMC and SEMC),

151 respectively. The NEMC flows around the northern tip of Madagascar and merges with the
152 Mozambique Channel throughflow, forming a set of anticyclonic eddies (Schott and McCreary,
153 2001; Schouten et al., 2003), affecting Site U1476. The southward flowing SEMC was
154 suggested to have major implications in the Agulhas Current, the largest western boundary
155 current that transports salt and heat into the South Atlantic (Lutjeharms, 2006).
156



157
158 **Figure 1:** Location of IODP Site U1476 in the Mozambique Channel plotted on the 2010 average
159 chlorophyll map, with the schematic illustration of surface water circulation: East African Coastal Current
160 (EACC), Northeast and Southeast Madagascar Current (NEMC, SEMC); South Equatorial Current
161 (SEC); and South Equatorial Countercurrent (SECC). Surface water circulation was redrawn from Beal
162 et al. (2011). The chlorophyll map was generated using the Giovanni online data system developed and
163 maintained by the NASA GES DISC (Acker and Leptoukh, 2007).

164

165 **3 Material and methods**

166 **3.1 Sampling strategy and age model construction**

167 Samples for this study were selected between 40 and 80 m depth on the stratigraphic
168 splice, covering the Plio-Pleistocene boundary (calcareous nannofossil biozones NN15 to

169 NN19; 2.85 to 1.85 Myr), focusing on the interval of the *Discoaster* extinction (**Fig. 2**). Using
170 the shipboard chronology (Hall et al., 2017b), samples were collected every ~15 cm, with a
171 total of 269 samples and representing an average time resolution of ~5 kyr. The age model of
172 the investigated interval was established by refining the shipboard stratigraphy by timeseries
173 analysis and cyclostratigraphy applied on the x-ray fluorescence (XRF) Fe/Ca record of Site
174 U1476. The Fe/Ca data series was plotted against the shipboard age model, which was based
175 on a spline fit to the calcareous nannofossil datum events calibrated in Gradstein et al., (2012)
176 (**Supplement Fig. S1A**). The Fe/Ca record was interpolated to make sure that the timeseries
177 is equally spaced prior to performing the timeseries analysis to identify imprint of astronomical
178 climate forcing (**Supplement Fig. S1B**).

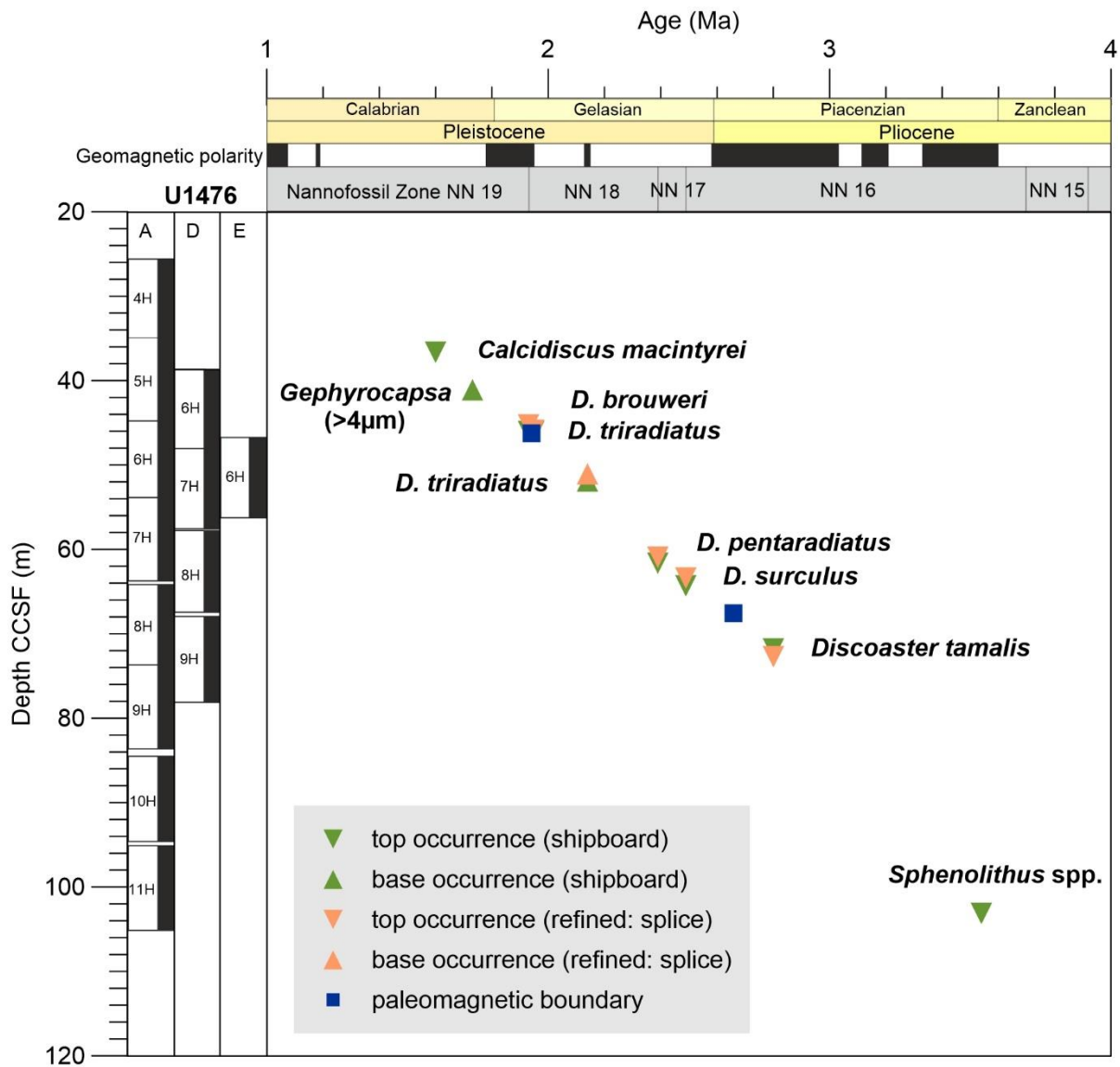
179

180 We then performed a cyclostratigraphic approach on the Fe/Ca timeseries and applied
181 a 50- to 35-kyr band-pass filter to capture an obliquity signal in the record (**Supplement Fig.**
182 **S1C and S1D**). The bandpass-filtered signal was then correlated and tuned to the La2010
183 astronomical solution (Laskar, 2011), using the minimum Fe/Ca values and assuming low
184 Fe/Ca during the glacial periods. Shipboard data generated from this site showed a distinct
185 glacial-interglacial pattern of the last 1 Myr (Hall et al., 2017b), resembling the Lisiecki and
186 Raymo (2004) benthic isotope curve. Moreover, the correlation was rather straightforward
187 since calcareous nannofossil assessment during the expedition showed abundant and well-
188 preserved Plio-Pleistocene specimens, which provided a reliable basis for precise
189 chronological approximations of the datum events (**Supplement Fig. S1E**). Given the
190 obliquity-based tuning strategy, we estimated the uncertainty on the age model to be inferior
191 to half of an obliquity cycle, i.e., <20 kyr.

192

193 The calibrated age model yielded sedimentation rates between ~2.6 to 3.3 cm/kyr. This
194 estimate agrees well with the average sedimentation rate of ~2.5 cm/kyr at DSDP Site 242
195 (Simpson and Schlich, 1974), located ~5 km southeast of the study area, and with the
196 shipboard estimate based on the combined planktonic foraminifera and calcareous
197 nannofossil stratigraphy (2.3 to 3.5 cm/kyr; Hall et al., 2017b). A detailed list of the identified
198 calcareous nannofossil biostratigraphic events encountered at Site U1476 can be found in
199 **Supplement Table S1**.

200



201

202 **Figure 2:** Age-depth relationships at Site U1476 showing the shipboard and refined occurrences of
 203 calcareous nannofossil index taxa and paleomagnetic boundaries. The five *Discoaster* datum events
 204 occurred between the late Gauss and Olduvai.

205

206 **3.2 Calcareous nannofossil identification, abundance and** 207 **biostratigraphy**

208 Slides for calcareous nannofossil analysis were prepared following the drop technique
 209 of [Bordiga et al. \(2015\)](#). Quantitative analysis was performed with a Leica polarized light
 210 microscope under 1000 x magnification. Abundances were determined by counting at least
 211 300 species per sample. An additional 10 to 20 fields of view (FOV) were counted to document
 212 uncommon and rare taxa. Minor reworking was observed, but when present, reworked
 213 specimens were counted separately. In each sample, the entire slide was scanned after
 214 counting to detect index taxa for refining the biostratigraphy. Supplementary smear slides were
 215 prepared for selected intervals to confirm biostratigraphic boundaries. Preservation of species

216 was assessed while counting using the criteria described in (Hall et al., 2017a). The zonation
217 schemes of Martini (1971; Codes NN), Okada and Bukry (1980; Codes CN), and Backman et
218 al. (2012; CNPL) were adopted for this study. We have initially followed the calcareous
219 nannofossil datum events in Gradstein et al. (2012) for the preliminary age model (Hall et al.,
220 2017b). The shipboard calcareous nannofossil biostratigraphy was then refined using the
221 splice samples. The datum events were calibrated using the new astronomically-tuned age
222 model and complemented by the paleomagnetic data (Supplement Table S2 and Fig. S2).

223
224 Species taxonomic identification was based on Perch-Nielsen (1985), Hine and
225 Weaver (1998), Young (1998) and the electronic guide to the biodiversity and taxonomy of
226 calcareous nanoplankton (Nannotax 3; <http://www.mikrotax.org/Nannotax3/>). The
227 conversion of nannofossil counts into absolute number of nannofossils per gram of sediment
228 (N/g. sed.) was calculated using the equation: Nannofossil concentration = $(N \cdot A) / (f \times n \times W)$,
229 where N = total nannofossil counts; A = area of the coverslip (mm^2); f = area of FOV (mm^2); n
230 = number of FOV counted; and W = weight of bulk dry sediment (g). Species diversity
231 (Shannon index; H) was calculated using the paleontological statistical software (PAST). The
232 Shannon index varies between 0 for populations with one species (low richness and
233 evenness) and high values for populations consisting of several taxa, each having few
234 individuals (high richness and evenness) (Hammer et al., 2009).

235

236 3.3 Indicative taxa for productivity and temperature

237 The genus *Discoaster* has been used as a warm water and low surface water
238 productivity proxy (Backman and Pestiaux, 1987). This group is known to have an affinity for
239 warm, oligotrophic and stratified water column conditions (Bukry, 1971; Haq and Lohmann,
240 1976; Aubry, 2007; Schueth and Bralower, 2015) and their extinction toward the end of the
241 Pliocene was thought to be due to the intensified NH glaciation (Chapman and Chepstow-
242 Lusty, 1997). In addition, cyclic patterns in the records of the Pliocene *Discoaster* taxa have
243 been observed (e.g., Backman and Pestiaux, 1987; Chepstow-Lusty et al., 1989; Gibbs et al.,
244 2004). Here we used the abundances of these species as both productivity and SST proxies.

245

246 The occurrence of *Coccolithus pelagicus* in the study site was also used as a SST
247 proxy. This species is found in subarctic environments (Baumann et al., 2000) and is an
248 indicator of cooler surface water (e.g., Marino et al., 2014). Parente et al. (2004) found this
249 species together with high abundances of the planktonic foraminifera species
250 *Neogloboquadrina pachyderma* (sinistral), another cold-water proxy, and interpreted their joint
251 occurrence to be linked to the influx of subpolar waters off western Iberia during Heinrich

252 events. This species also registered distinct glacial peaks during the mid-Pleistocene
253 transition in North Atlantic sediments (Marino et al., 2011).

254

255 Transfer functions based upon the abundance of the lower photic zone (LPZ)-dwelling
256 taxon *F. profunda* have been successfully used as proxies for past changes in the
257 nutricline/thermocline depths in Quaternary sediments (e.g., Molino and McIntyre, 1990;
258 Ahagon et al., 1993; Flores et al., 1999), and for estimation of marine primary production
259 (Beaufort et al., 1997; Beaufort et al., 2001). For this study, the estimated primary productivity
260 (EPP) expressed in grams of carbon (g C/m²/yr) was calculated from the relative abundance
261 of this taxon using the formula: $EPP = 617 - [279 * \log (\% F. profunda + 3)]$. This equation,
262 however was calibrated by (Beaufort, 1996) using calcareous nannofossils from the Indian
263 Ocean core top samples and modern primary productivity generated from satellite chlorophyll
264 data by Antoine and Morel (1996). Here we use this formula by investigating Pliocene
265 sediments to test whether the EPP absolute values can be applied to ancient oceans with
266 different oceanography and biota compared to modern oceans. The EPP is used as a proxy
267 for primary productivity because in contrast to other taxa, *F. profunda* prefers to thrive in the
268 deep photic zone (Molino and McIntyre, 1990). Hence, high abundances of *F. profunda*
269 indicate deeper nutricline/thermocline and low abundances of this species suggest otherwise.
270 The ratio of this species to smaller forms of *Gephyrocapsa* and *Reticulofenestra* (< 3µm), (*F.*
271 *profunda* index) was also used as water column stratification proxy (*F. profunda* index;
272 Beaufort et al., 1997; Beaufort et al., 2001): $F. profunda \text{ index} = F. profunda / (F. profunda +$
273 $small Gephyrocapsa + small Reticulofenestra)$. Low values of *F. profunda* index suggest a
274 more mixed water column whereas values closer to 1 indicate a more stratified water column.
275

276 4 Results

277 4.1 Extinction of *Discoaster* species in the Mozambique Channel

278 Six Plio-Pleistocene nannofossil datum events (Backman et al., 2012; Gradstein et al.,
279 2012) were recognized at Site U1476, differing by 10 to 90 kyr from the calibrated ages of
280 these events in the low and middle latitude regions in the three major oceans (South Atlantic,
281 Pacific and Indian Ocean), and the Mediterranean Sea region (Table 1). Taking into account
282 U1476 age model uncertainty (± 20 kyr), some of these extinction events cannot be
283 distinguished in time and thus occurred simultaneously in different ocean basins. The last
284 occurrence of *D. tamalis* (2.81 Ma) occurred 10 kyr (2.80 Ma; Lourens et al., 2004) and 50 kyr
285 (2.76 Ma; Backman et al., 2012) earlier in the study area than the reported extinction of this
286 species in the three major oceans and the Mediterranean. All of the other *Discoaster* species
287 became extinct in the Mediterranean before disappearing in the Mozambique Channel. After

288 the last occurrence of *D. surculus* (2.53 Ma) and *D. pentaradiatus* (2.45 Ma) in the study area,
 289 these two species became extinct in the South Atlantic 40 and 60 kyr later, respectively. The
 290 base common occurrence of *D. triradiatus* (2.13 Ma) occurred 10 kyr later in the study area
 291 than in the South Atlantic (2.14 Ma; Lourens et al., 2004) and the equatorial North Atlantic
 292 (2.14 Ma; Chapman and Chepstow-Lusty, 1997). This result is 20 kyr earlier than the recorded
 293 acme of *D. triradiatus* at Site 709 in the equatorial Indian Ocean (2.11 Ma; Chapman and
 294 Chepstow-Lusty, 1997). *Discoaster brouweri*, the last *Discoaster* species, first went extinct in
 295 the equatorial Pacific (2.06 Ma), followed by the Mediterranean (1.95 Ma; Lourens et al.,
 296 2004), the South Atlantic (1.93 Ma; Lourens et al., 2004), and finally the westernmost Indian
 297 Ocean (1.91 Ma). The extinction of this species at Site 709 is occurred with the last occurrence
 298 of *D. triradiatus* in this location (1.95 Ma; Chapman and Chepstow-Lusty, 1997). Considering
 299 the uncertainty in our age model, the extinction of the final *Discoaster* species at Site U1476
 300 is synchronous to the recorded extinction of this group in the major ocean basins.

301

302 **Table 1:** Comparative global occurrence/extinction of the Plio-Pleistocene *Discoaster*
 303 compiled in Backman et al. (2012) and Gradstein et al. (2012) with the astronomically tuned
 304 datum events from this study. Calcareous nannofossil zonation scheme by Martini (1971; NN),
 305 Okada and Bukry (1980; CN) and Backman et al. (2012; CNPL) are indicated. T = top
 306 occurrence, Bc = base common occurrence.

307

CALCAREOUS NANNOFOSSIL DATUM EVENT	BIOZONE	GTS 2012 scaling	CALIBRATED AGES (Ma)					Backman et al. (2012)	western Indian Ocean (THIS STUDY) Error ± 20 kyr
			South Atlantic	Equatorial Pacific	Mediterranean	Reference			
T <i>D. brouweri</i>	NN19/18, CN13a/12d, CNPL 7/6	1.93	1.93	2.06	1.95	1	1.93	1.91	
T <i>D. triradiatus</i>	NN18, CN12d	1.95			1.95	2		1.93	
Bc <i>D. triradiatus</i>	CNPL 6	2.14	2.14		2.22	1	2.16	2.13	
T <i>D. pentaradiatus</i>	NN18/17, CN12d/12c, CNPL 6/5	2.39	2.39		2.51	1	2.39	2.45	
T <i>D. surculus</i>	NN17/16, CN12c/12b, CNPL 5	2.49	2.49	2.52	2.54	1	2.53	2.53	
T <i>D. tamalis</i>	NN16, CN12b/12a, CNPL 5/4	2.80	2.80		2.80	1	2.76	2.81	

308 ¹Lourens et al., 2004; ²Berggren et al. (1995); Rio et al. (1990); Backman and Pestiaux
 309 (1987)

310

311 **4.2 Nannofossil assemblage composition, preservation and diversity**

312 A total of 35 species and species groups comprising tropical to subtropical taxa and
313 cold water species were identified. The Plio-Pleistocene assemblage is generally well-
314 preserved, with all the species identifiable at the species level. The assemblage at Site U1476
315 is dominated by *Reticulofenestra* species (13 to 63%) and *F. profunda* (2 to 59%), with
316 alternating dominance in the record (**Fig. 3A**). This is followed by *Gephyrocapsa* spp. (up to
317 24%), *Discoasters* spp. (up to 17%), and *Pseudoemiliana lacunosa* (up to 15%). Other
318 species that made significant contribution to the total assemblage are *Helicosphaera* spp.,
319 *Oolithotus* spp., *Umbilicosphaera* spp. and *Rhabdosphaera clavigera*.

320

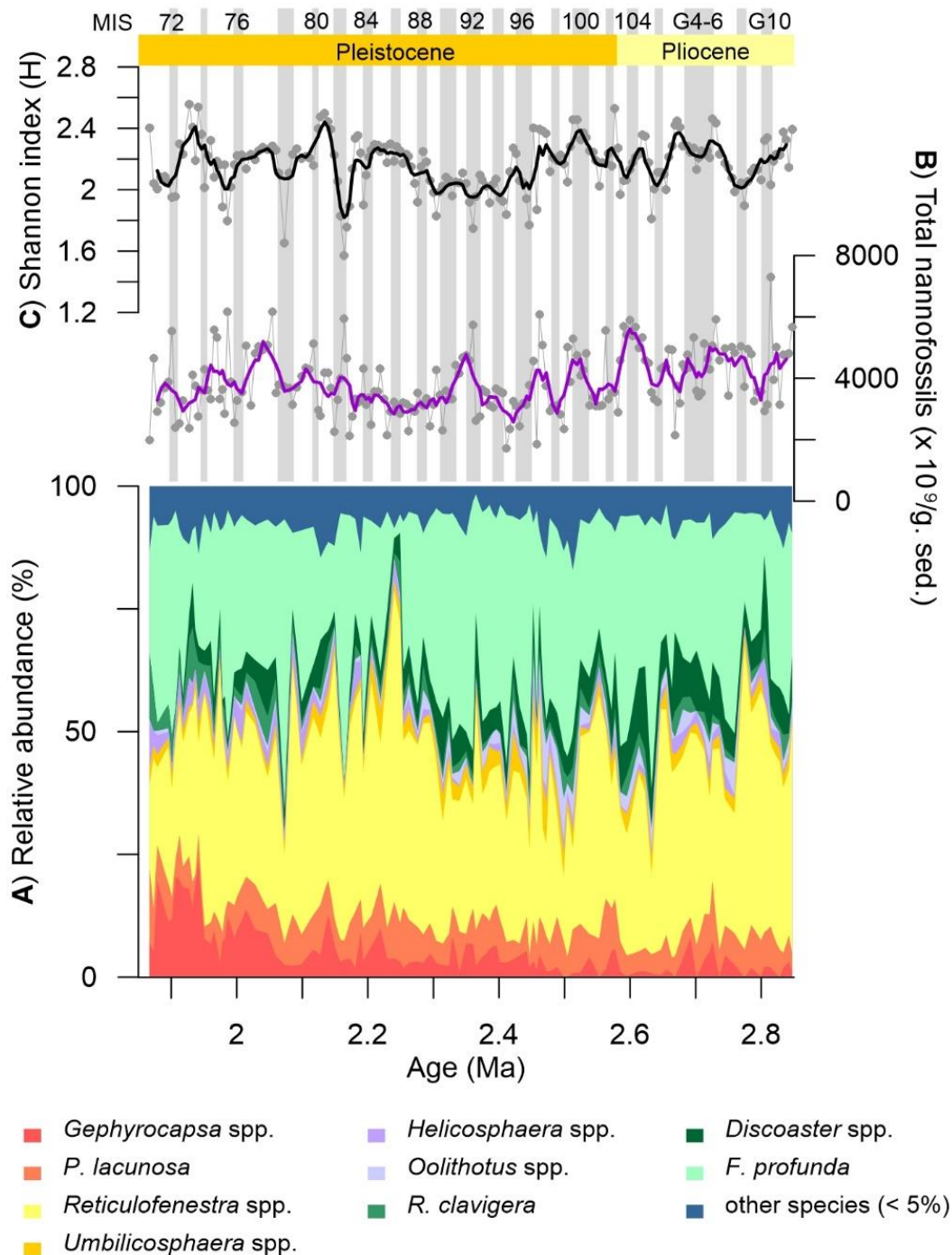
321 Total calcareous nannofossil absolute concentrations show highly variable patterns
322 through the studied time interval, with total concentrations ranging from 1700×10^9 to $7300 \times$
323 10^9 N/g sed. (**Fig. 3B**). The Plio-Pleistocene transition (2.58 Ma) is characterized by a
324 reduction in both the total nannofossil concentration and species diversity (**Fig. 3B** and **3C**).
325 The Pliocene record displays a good correspondence between the total concentrations and
326 the species diversity. From 2.31 to 2.17 Myr, consistently low total nannofossil concentrations
327 accompanied by increased diversity occur. Total nannofossils stay at relatively similar level
328 after the Plio-Pleistocene transition while species diversity immediately recovered.

329

330 **4.3 Variations in *Discoaster* abundance**

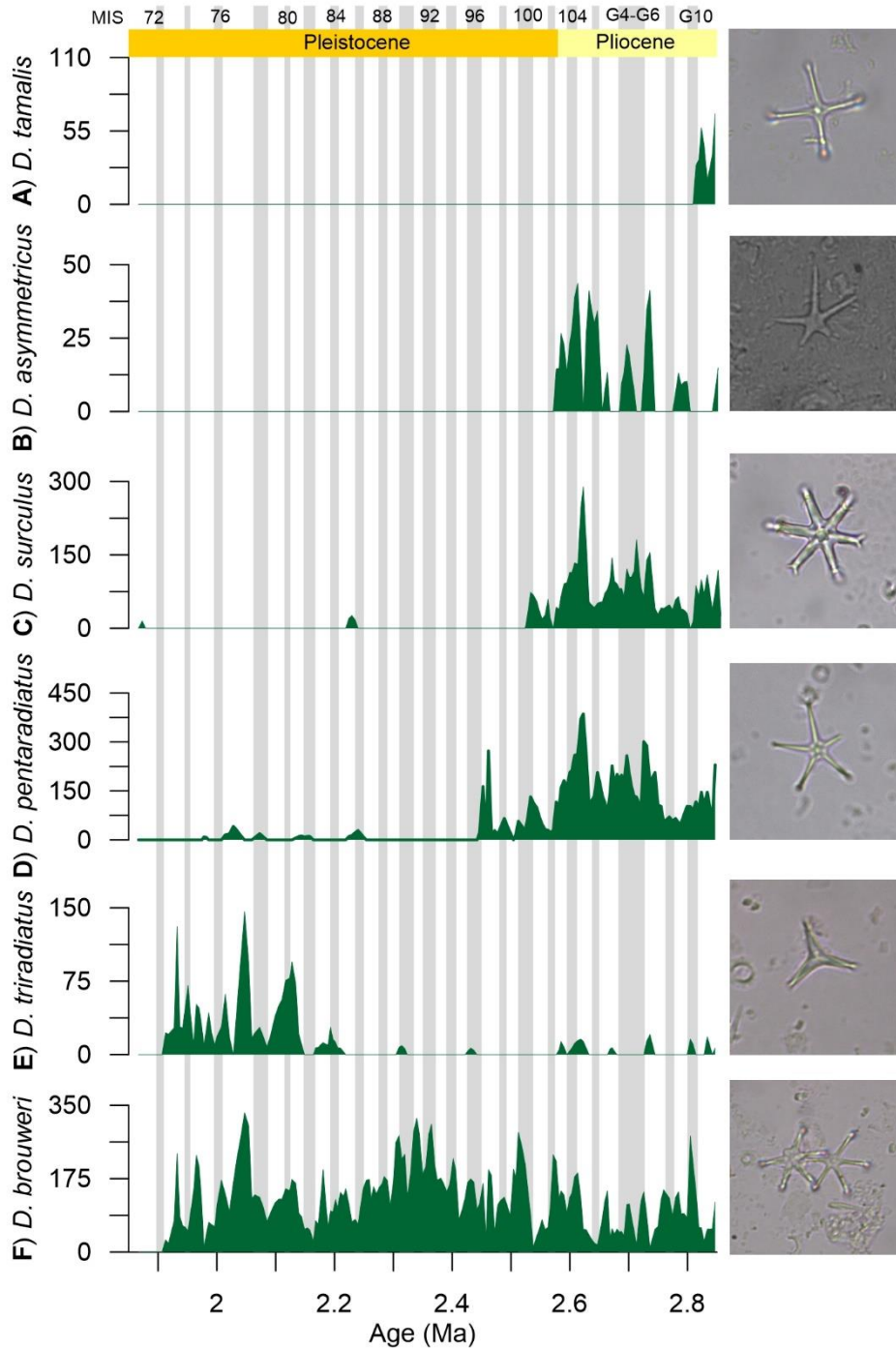
331 *Discoaster tamalis* and *D. asymmetricus* show the lowest concentrations, with
332 maximum abundances of only up to 110×10^9 N/g sed. and 50×10^9 N/g sed., respectively
333 (**Fig. 4A** and **4B**). *Discoaster surculus* displays a relatively constant abundance from 2.85 to
334 2.6 Myr, gradually increases at the beginning of MIS 103 and registers a maximum
335 concentration during this stage (290×10^9 N/g sed.) (**Fig. 4C**). Its abundance then
336 progressively decreases until it completely disappears from the record at 2.53 Ma. The pattern
337 of *D. pentaradiatus* matches *D. surculus* showing the highest concentrations during the
338 interglacial stages G11 (430×10^9 N/g sed.) and MIS 103 (390×10^9 N/g sed.) (**Fig. 4D**). This
339 species is the most abundant species in the investigated time interval. After 2.45 Ma, when
340 the extinction of *D. pentaradiatus* occurred, only two members of this genus are left. Reworked
341 specimens of this species were, however, noted above its recorded extinction (**Fig. 4D**).
342 *Discoaster triradiatus* has a base common occurrence placed at 2.13 Ma. Maxima in
343 abundance of this species are recorded at MIS 81 (95×10^9 N/g sed.), MIS 78 (150×10^9 N/g
344 sed.) and MIS 74 (130×10^9 N/g sed.) (**Fig. 4E**). The second most abundant species in the
345 record is *D. brouweri*, with highly variable abundance throughout the record (**Fig. 4F**). Lower
346 concentrations of this species are recorded until 2.58 Ma, when total *Discoaster* abundance

347 is shared with other *Discoaster* taxa (*D. pentaradiatus*, *D. surculus*, *D. asymmetricus*, and *D.*
 348 *tamalis*). After the extinction of *D. surculus*, *D. brouweri* dominates the *Discoaster*
 349 assemblage. All of these species show declining trends toward their respective demise from
 350 the Site U1476 record.
 351



352

353 **Figure 3:** Calcareous nanofossils at Site U1476: **(A)** stack plot of all species; **(B)** total absolute
 354 nanofossil concentration per gram (g) of sediment; **(C)** Shannon diversity index (H). Glacial stages are
 355 marked by gray bars. Solid lines are calculated 5-point running average of the raw data (gray
 356 background lines) and used to highlight general patterns.



357

358 **Figure 4:** Absolute concentrations of the Plio-Pleistocene *Discoaster* species: **(A)** *D. tamalis*; **(B)** *D.*
 359 *asymmetricus*; **(C)** *D. surculus*; **(D)** *D. pentaradiatus*; **(E)** *D. triradiatus*; and **(F)** *D. brouweri*. All
 360 concentrations are expressed in number of nannofossils $\times 10^9$ /gram of sediment. Glacial stages are
 361 marked by gray bars.

362

363

364 5 Discussion

365 5.1 *Discoaster* extinction and paleoenvironment during the Plio- 366 Pleistocene

367 The successive extinctions of *Discoaster* species during the Plio-Pleistocene offers a
368 well-established sequence of biostratigraphic events (Bukry, 1971; Backman and Pestiaux,
369 1987), including our record from Site U1476. Efforts on the refinement of these datum events
370 have progressed over the years, including astronomical calibration (e.g., Raffi et al., 2006;
371 Backman et al., 2012; Agnini et al., 2017). While the Pliocene nannofossil chronology is rather
372 less studied on a global scale compared to the Miocene or Pleistocene intervals (Raffi et al.,
373 2006), the Plio-Pleistocene *Discoaster* extinction event is widely documented. Despite the
374 reported uncertainties in using the individual datum due to diachronous first and last
375 occurrences of its member taxa between major oceans, there is still a general consensus that
376 this group disappeared from the record during the transition from the warm Pliocene to the
377 cold Pleistocene.

378

379 At Site U1476, a general reduction in the *Discoaster* abundance from 2.85 to 1.85 Myr
380 is observed until it completely vanishes from the record at 1.91 Ma (Fig. 5). This record
381 displays an opposite abundance pattern with the upper photic zone (UPZ) flora with preference
382 for high nutrient environment, which shows an increasing abundance toward 1.85 Ma (Fig.
383 5D). This indicates the affinity of discoasters to low productivity regime, and hinting the
384 possibility of this group to have inhabited the deep photic layer. The preference of this group
385 to oligotrophic environment was also shown in a study by Minoletti et al. (2001), where the
386 $\delta^{13}\text{C}$ values analyzed from the *Discoaster* fraction resemble the planktonic foraminifera record.
387 Previous studies suggested that some *Discoaster* species prefer the LPZ, a behavior similar
388 to *F. profunda* (e.g., Aubry, 1998; Bralower, 2002). A recent study by Schueth and Bralower
389 (2015) confirmed this using an ecological ordination technique, where the authors suggested
390 that *D. brouweri* and *D. pentaradiatus* favored a warm and stratified regime, with a deep
391 nutricline. Geochemical evidence supports the first two proposed ecology of this group;
392 however, the similarity of the discoaster $\delta^{18}\text{O}$ values to the surface water dwelling planktonic
393 foraminifera record also indicates that they thrived in the upper photic layer (Minoletti et al.,
394 2001). While the depth habitat of this extinct group is still controversial, our results show that
395 discoasters inhabited warm, stratified and oligotrophic condition. And whether they thrived in
396 the UPZ or the LPZ, if these organisms were adapted to a low nutrient regime, having a more
397 vigorously mixed water column would be a detriment to the group even if it was abundant in
398 the surface waters. The discoasters could have also been outcompeted by the UPZ flora,

399 which are mostly dominated by the small reticulofenestrids, a group of opportunistic taxa that
400 are abundant in nutrient-rich environment (Flores et al., 1995).

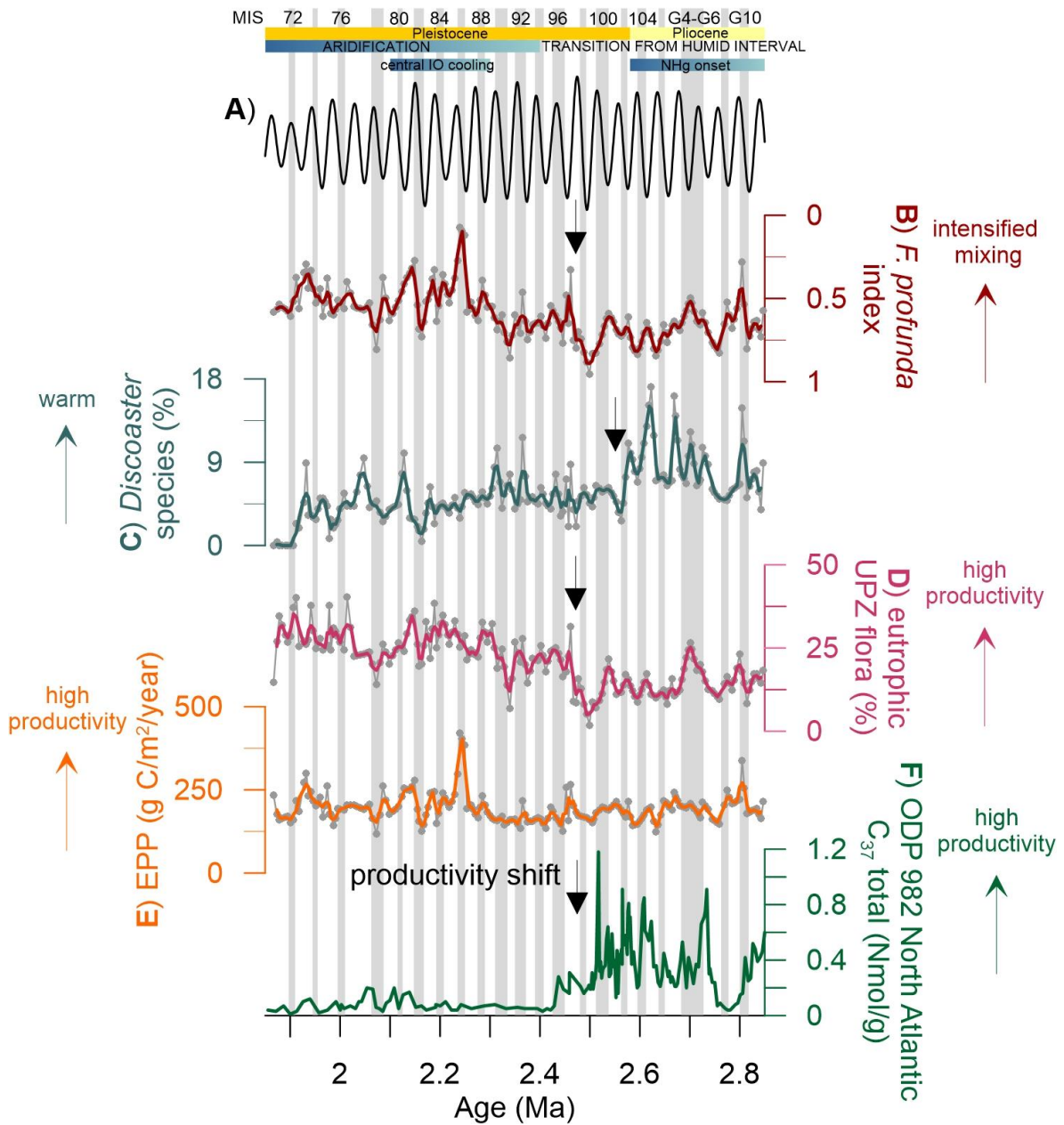
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402 A distinct shift starting at ~2.4 Ma is observed in both the *Discoaster* and the UPZ
403 records, after the transition from the Pliocene to the Pleistocene. The increase in abundance
404 of the eutrophic UPZ flora suggests nutrient enhancement in the photic layer, which is in
405 agreement with the *F. profunda* index indicating less stratified water column conditions from
406 ~2.4 to 1.85 Myr (Fig. 5B). More intensified water column mixing could have shoaled the
407 nutricline leading to increase in the abundances of the UPZ flora. This shift at ~2.4 Ma
408 occurred after the onset of the Northern Hemisphere glaciation (Haug et al., 1999), and is
409 coincident with the beginning of the Arid interval (Fig. 5), when the fully constituted tropical
410 Indian Ocean circulation has developed (Christensen et al., 2017). Comparison with the
411 productivity record of the North Atlantic (ODP Site 982; Bolton et al., 2011) reveals a reverse
412 pattern at ~2.4 Ma, signifying a more enhanced wind-driven upwelling zones and upwelling
413 productivity in the in the low- to mid- latitudes during this period (Sarnthein and Fenner, 1999)
414 (Fig. 5E). On the other hand, a reduction in the *Discoaster* abundance is observed during
415 some of the extreme Early Pleistocene glacial stages, such as MIS 96, 82, 78, and 72. This
416 pattern was also recorded in the three major ocean basins (Chapman and Chepstow-Lusty,
417 1997), indicating that the global changes in the surface water conditions driven by the
418 glacial/interglacial cycles and the intensity of the NH glaciation, have controlled the abundance
419 and distribution of this particular group.

420

421 The EPP values calculated from the relative abundance of *F. profunda*, however do
422 not show a clear pattern as the other proxies discussed above (Fig. 5E). A relatively stable
423 pattern is observed in the EPP throughout the studied time period although higher amplitude
424 fluctuations can be observed starting at ~2.25 Ma. This shows that the EPP formula, calibrated
425 using modern samples is not an effective measure of productivity in ancient sediments.
426 Nevertheless, the reduction in water column stratification shown by the *F. profunda* index and
427 the increasing abundance of the eutrophic UPZ species indicates that gradual cooling coupled
428 with the shallowing of the nutricline/thermocline (Ravelo et al., 2004; Lawrence et al., 2013),
429 resulted in the progressive decline and subsequent demise of the discoasters (Chapman and
430 Chepstow-Lusty, 1997; Schueth and Bralower, 2015).

431



432

433 **Figure 5:** Site U1476 coccolithophore productivity and stratification records with major climatic and
 434 oceanographic events during the Pliocene-Pleistocene transition: (A) orbital obliquity sequence
 435 (Berger, 1992); (B) *Florisphaera profunda* index; (C) relative abundance of *Discoaster* spp.; (D) upper
 436 photic zone (UPZ) flora comprising small *Gephyrocapsa* and small *Reticulofenestra*; (E) estimated
 437 primary productivity (EPP) calculated from the relative abundance of *F. profunda*; and (F) C_{37} alkenones
 438 from ODP 982 (Bolton et al., 2011). Glacial stages are marked by gray bars. Atmospheric and
 439 oceanographic events at major periods of the Neogene global climate are indicated by blue horizontal
 440 bars. Solid lines are calculated 3-point running average of the raw data (gray background lines) and
 441 used to highlight general patterns.

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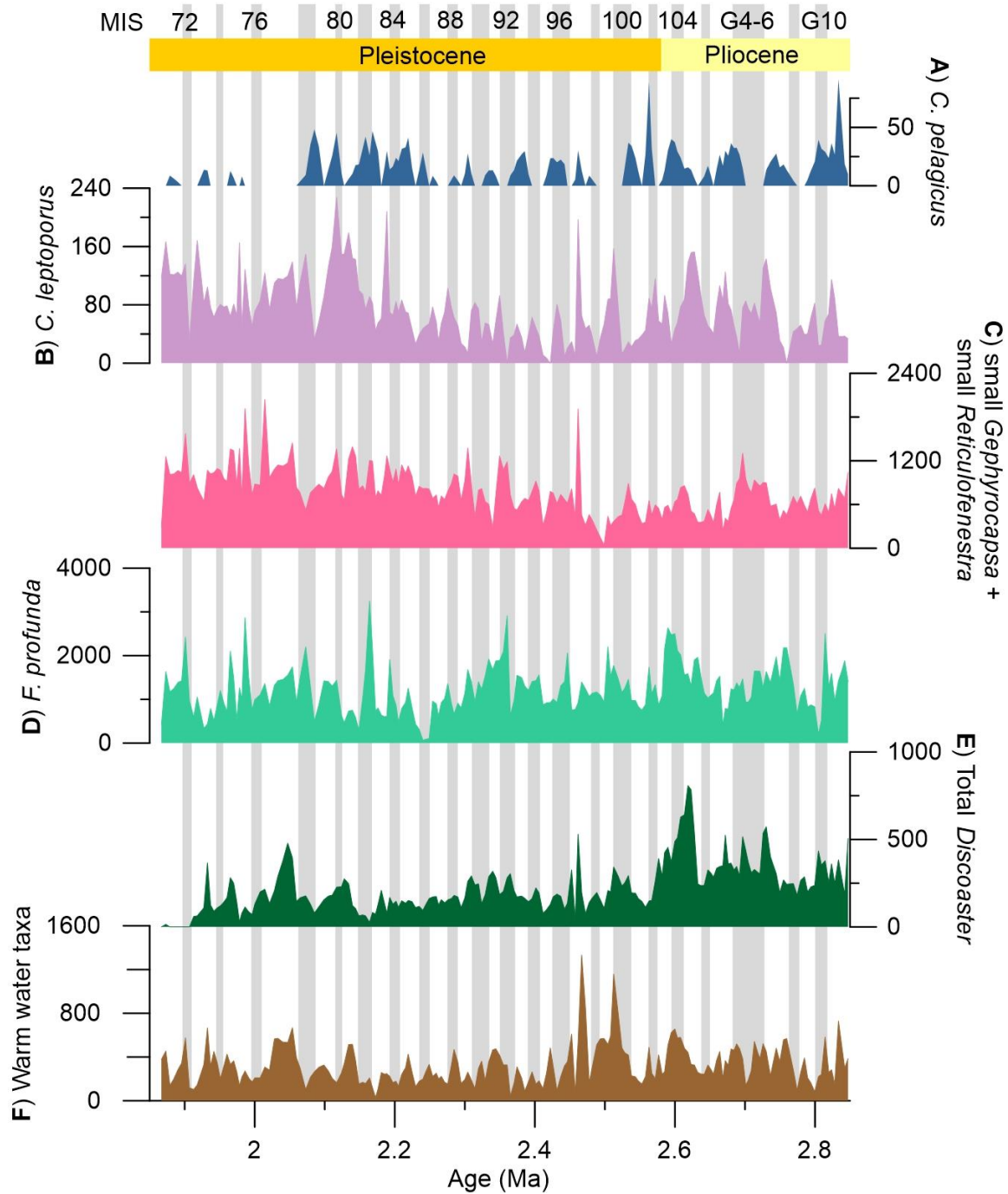
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445 5.2 Productivity fluctuations from indicative taxa

446 The downcore variations in individual nanoplankton species show differences in abundance
447 patterns, with some species showing a clear trend with the implied isotope stages (**Fig. 6**).
448 The variations in abundance of temperature and productivity indicator species suggest that a
449 combination of environmental parameters, and not only SST, controlled the coccolithophore
450 productivity at Site U1476 during the Plio-Pleistocene (**Fig. 6**). **Despite of the scattered**
451 **occurrences of *C. pelagicus* in the record, this species shows peak abundances during the**
452 **glacial intervals, especially during the Early Pleistocene, which signifies the preference of this**
453 **species to cold water conditions (**Fig. 6A**).** Relatively stable abundances of the eutrophic UPZ
454 group are recorded for the Pliocene sequence, and registers a major change after the
455 transition to the Pleistocene (~2.4 Ma), where it reaches a minimum and progressively
456 increases thereafter. The increased abundances of the eutrophic UPZ-dwelling taxa (**Fig. 6C**),
457 indicates enriched nutrient supply in the upper photic layer ([Okada, 2000](#)). The interval from
458 ~2.4 to 1.85 Myr is characterized by higher surface water productivity conditions, as is also
459 shown by the increased abundances of *C. leptoporus*, another taxon with affinity for high-
460 nutrient environments (e.g., [Giraudeau, 1992](#); [Winter et al., 1994](#)) (**Fig. 6B**). While this species
461 is also typified for warm conditions ([Winter and Martin, 1990](#); [Flores et al., 1999](#); [Baumann](#)
462 [and Freitag, 2004](#)), its contrasting pattern with the warm water taxa (**Fig. 6F**), especially
463 starting at ~2.2 Ma, shows that the abundances of *C. leptoporus* are not a consequence of
464 changing SST but rather of nutrient availability in the water column. Despite the low
465 abundances of the accessory taxa *Oolithotus* spp., *Rhabdosphaera clavigera*, *Syracosphaera*
466 spp., and *Umbellosphaera* spp., the cumulative abundance of these species used as a warm
467 water proxy shows distinct and regular variations in the record. The high abundances of the
468 tropical species, such as *F. profunda*, and *C. leptoporus* coupled with the consistent
469 occurrences of the warm water taxa (*Oolithotus* spp, *Rhabdosphaera clavigera*,
470 *Syracosphaera* spp., and *Umbellosphaera* spp.) reflect prevalence of warm tropical conditions
471 in the study area.

472



473

474 **Figure 6:** Absolute concentrations of selected calcareous nannofossil taxa: (A) *Coccolithus pelagicus*;
 475 (B) *Calcidiscus leptoporus*; (C) small *Gephyrocapsa* + small *Reticulofenestra*; (D) *Florisphaera*
 476 *profunda*; (E) total *Discoaster* spp.; (F) warm water taxa comprising *Oolithotus* spp., *Rhabdosphaera*
 477 *clavigera*, *Syracosphaera* spp., and *Umbellosphaera* spp. All concentrations are expressed in number
 478 of nannofossils x 10⁹/gram of sediment. Glacial stages are marked by gray bars.

479

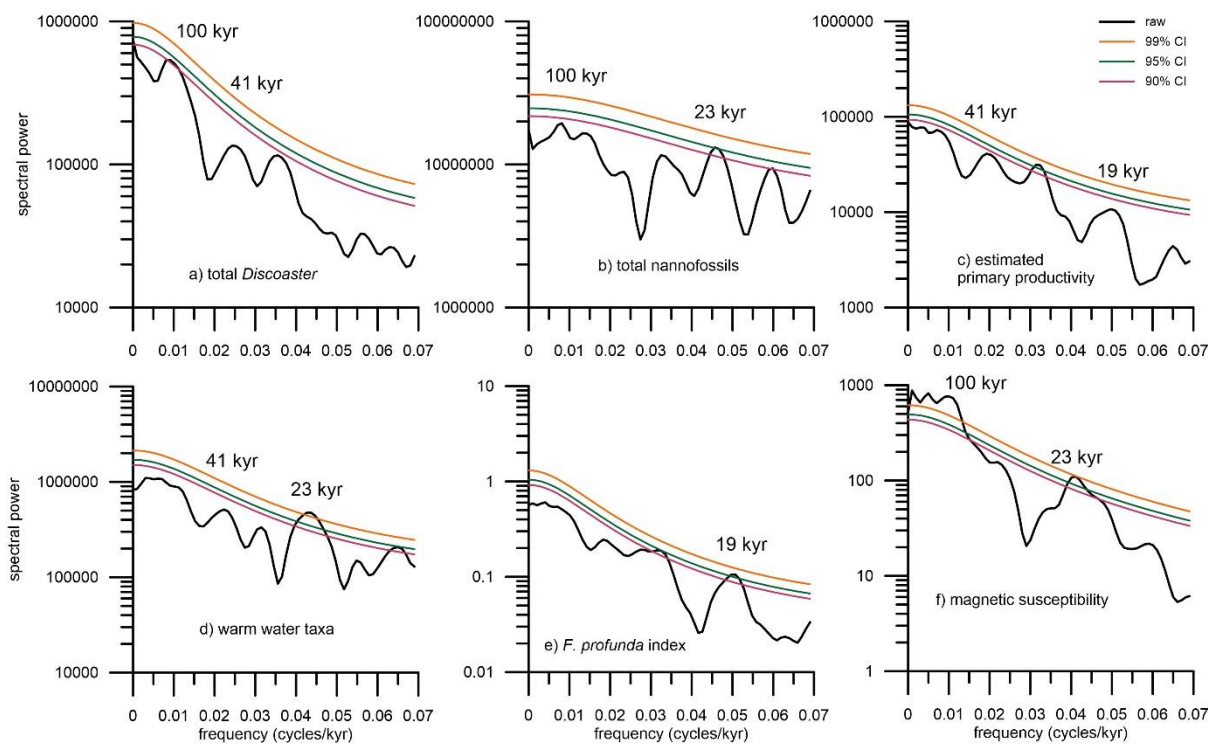
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483 **5.3 Response of calcareous nannoplankton to astronomical forcing**

484 Calcareous nannoplankton abundances visually exhibit cyclic variations (**Fig. 5** and **6**),
 485 which is confirmed by spectral analysis (**Fig. 7**). Spectral analysis performed on the
 486 nannofossil record demonstrates variations in paleoproductivity related to glacial/interglacial
 487 variability (100 kyr), obliquity (41 kyr) and precession (23 and 19 kyr). The nannofossil warm
 488 water taxa group, estimated primary productivity, and *F. profunda* index also show variations
 489 at the sub-precession and precession band (19 and 23 kyr). This strongly suggests that
 490 productivity in the Mozambique Channel is modulated by both the high latitude and the tropical
 491 Pacific forcings. The 100-kyr and obliquity signatures suggest a NH driver of the observed
 492 variability, whereas variability at the rhythm of precession is interpreted as a tropical Pacific
 493 forcing. The 23 kyr cyclicity in the calcareous nannofossil record from this site was also
 494 observed in the equatorial Indian Ocean, which was linked to a combination of both the boreal
 495 monsoon and the El Niño Southern Oscillation (ENSO)-like dynamics ([Beaufort et al., 2001](#)).
 496



497 **Figure 7:** Spectral power versus frequency plots of calcareous nannoplankton record and magnetic
 498 susceptibility: **(A)** total *Discoaster* species; **(B)** total nannofossils; **(C)** estimated primary productivity
 499 calculated from relative abundance of *Florisphaera profunda*; **(D)** warm water taxa (*Oolithotus* spp.,
 500 *Rhabdosphaera clavigera*, and *Syracosphaera* spp.); **(E)** *F. profunda* index; **(F)** magnetic susceptibility.
 501 Colored lines indicate the 90%, 95%, and 99% confidence intervals (CI).
 502

503
 504
 505

506 **5.4 Implications for the Agulhas Current**

507 We suggest that the long-term record of paleoproductivity at Site U1476 is driven by
508 both atmospheric and oceanographic processes, which influenced variations in the
509 nutricline/thermocline dynamics and nutrient availability in the water column. The present day
510 oceanography of the western Indian Ocean has been suggested to be linked to the Pacific
511 Ocean climate variability (Schouten et al., 2003) and also holds true for Quaternary climate
512 archives (Kuhnert et al., 2014; Tanguan et al., 2017). The abundance of the LPZ-dwelling
513 species *F. profunda* is an effective proxy for the nutricline/thermocline depth in Quaternary
514 sediments and has proven useful for late Neogene sequences (Okada, 2000), as well as for
515 interpreting Indo-Pacific teleconnections over the past 300 kyr (Tanguan et al., 2017). The
516 regular occurrence of warm water taxa reflects tropical Pacific influence in our study area. This
517 shows that the transport of warm and oligotrophic surface water of the ITF via the SEC across
518 the Indian Ocean was a persistent feature of the last 2.85 Myr, which could be linked to the
519 development of the Agulhas Current downstream, and subsequent leakage into the South
520 Atlantic (Biajstoch et al., 2009).

521

522 A possible influence of southern sourced waters at Site U1476 is shown by the
523 increase in the abundance of *C. pelagicus*. This species was not encountered in late
524 Quaternary sediments of the equatorial Indian Ocean (Tanguan et al., 2017) but was found
525 in the subtropical region of the Indian Ocean (e.g., Flores et al., 1999), which could be
526 attributed to the influence of nutrient-rich SASW during the glacial periods, with the northward
527 migration of the subtropical front (STF). However, the STF did not migrate northward beyond
528 33°S during the glacial periods (Bard and Rickaby, 2009) and did not reach our study site in
529 the Mozambique Channel. This region has been described by Ternon et al. (2014) as one of
530 the most turbulent areas in the world oceans. Enhanced surface water productivity and cooler
531 water conditions resulting in the occurrences of these species could therefore also be due to
532 a localized upwelling event, hence intensified water column mixing driven by the mesoscale
533 anticyclonic eddies in the channel (Schouten et al., 2003).

534

535 **6 Conclusions**

536 The Plio-Pleistocene paleoenvironment reconstruction over the last 1 Myr prior to the
537 *Discoaster* extinction at Site U1476, using calcareous nannoplankton assemblage proxies
538 showed that:

539

- 540 1. Global extreme climatic shift during the Plio-Pleistocene transition played a key role in
541 the nutricline and thermocline depths, and thus the nutrient availability at the

542 Mozambique Channel. Both temperature and nutrient availability are critical
543 parameters in calcareous nanoplankton productivity at the location.

544

545 2. Calcareous nanoplankton taxa exhibit periodic variability at pace with the
546 astronomical parameters. The 100-kyr and obliquity signatures suggest a NH driver of
547 the observed variability, whereas variability at the rhythm of precession is interpreted
548 as a tropical Pacific forcing.

549

550 3. Discoasters at Site U1476 declined with global cooling across the Plio-Pleistocene,
551 which resulted in reduced water column stratification and consequent shallowing of the
552 nutricline/thermocline, hence high surface water productivity. We propose that the
553 gradual decline and successive extinction of this group is due to a more mixed water
554 column and consequent increase in productivity at the location, as shown by the low
555 values of the *F. profunda* index and high abundances of UPZ flora, indicative of
556 intensified water column mixing and nutrient-rich surface water conditions,
557 respectively.

558

559 4. The transport of warm and oligotrophic surface water of the ITF via the SEC across
560 the Indian Ocean was a persistent feature of the last 2.85 Myr, observed from the
561 consistent occurrences of warm water taxa. A possible influence of the southern
562 sourced sub-Antarctic surface waters into the site exists as shown by the increase in
563 abundance of *C. pelagicus*, a species that is adapted to cold and high-nutrient
564 environments.

565

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1 **Supplementary materials for “The last 1 million years of the extinct genus**
2 ***Discoaster*: Plio–Pleistocene environment and productivity at Site U1476**
3 **(Mozambique Channel)”**

4
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9 **This PDF file includes:**

- 10 • Expedition 361 Shipboard Scientific Party
11 • Supplementary information for the age model construction.
12 ○ Fig. S1. Application of bandpass filter and astronomical calibration of the Site
13 U1476 XRF Fe/Ca data series.
14 ○ Fig. S2. Inclination of shipboard core-half measurements for Site U1476 holes
15 A, D and E.
16 ○ Table S1. Calcareous nannofossil biostratigraphic events recorded at Site
17 U1476 with the astronomically calibrated occurrences of the index taxa.
18 ○ Table S2. Paleomagnetic boundaries at Site U1476.

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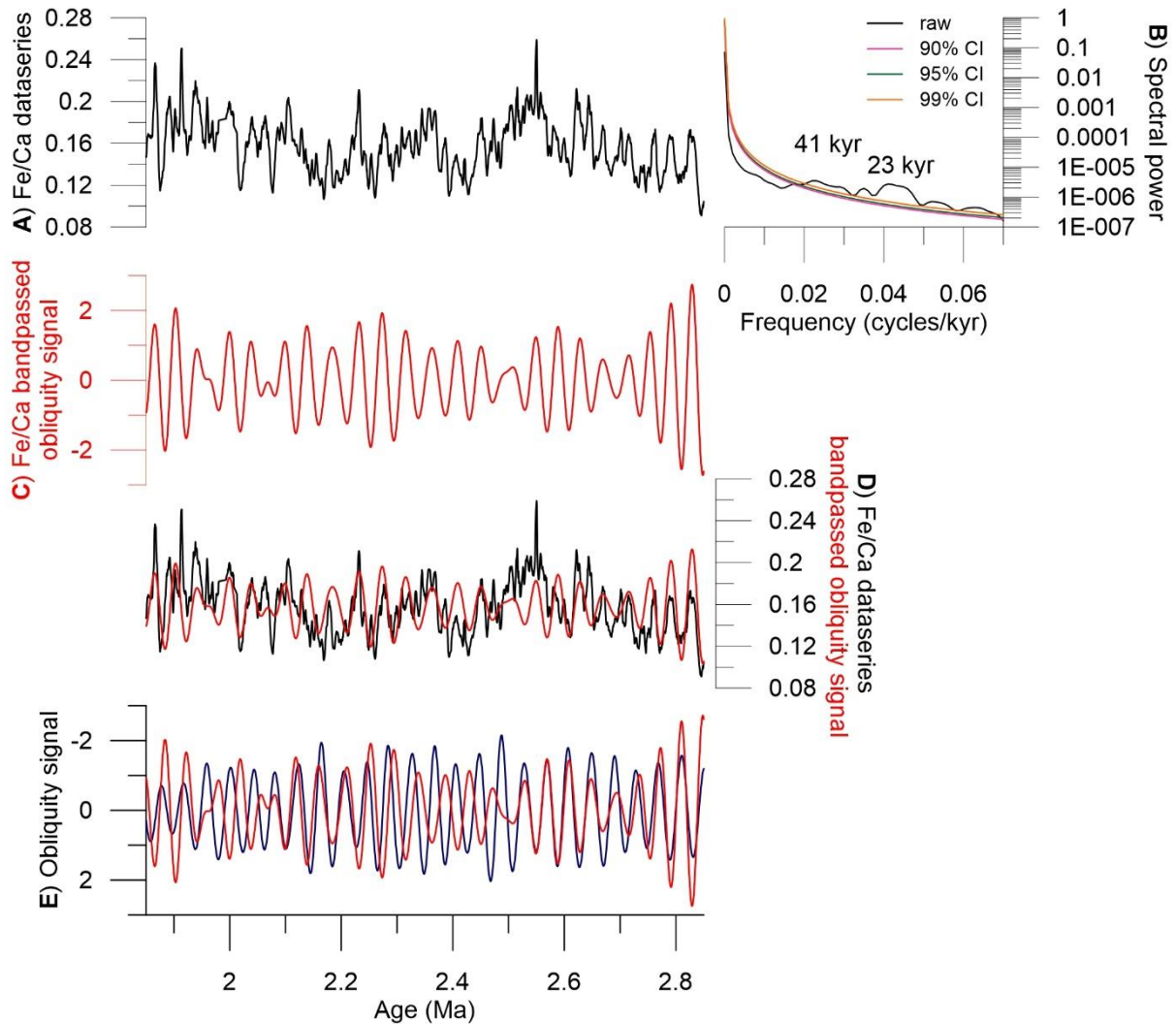
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93 **Supplementary information for the age model construction**

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The Site U1476 Plio-Pleistocene (2.85 to 1.85 Myr) age model was established based on the combined calcareous nannofossil biostratigraphy, magnetostratigraphy and cyclostratigraphy.



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99 **Figure S1:** Application of bandpass filter and tuning of the Site U1476 XRF Fe/Ca data series to La2010
100 astronomical solution by [Laskar, \(2011\)](#): **A)** Fe/Ca record plotted against the shipboard stratigraphy; **B)**
101 power spectra of the Fe/Ca data to determine orbital imprint in the record; **C)** band passed 41-kyr
102 obliquity signal filtered in the Fe/Ca data; **D)** visual comparison of the Fe/Ca data series and the filtered
103 obliquity signal; and **E)** Site U1476 Fe/Ca filtered obliquity signal plotted with the La2010 obliquity
104 solution.

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107 **Table S1:** Calcareous nannofossil biostratigraphic events recorded at Site U1476 with the astronomically calibrated occurrences of the index taxa in the
 108 Mozambique Channel, western Indian Ocean.
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Calcareous nannofossil event	Age (Ma) Gradstein et al., 2012)	SHIPBOARD		CALIBRATED: Splice		
		Hole-Core-Section-interval	CCSF (m)	Hole-Core-Section-interval	CCSF (m)	Age (Ma) THIS STUDY
T <i>C. macintyreii</i>	1.60	U1476A-5H2-75 cm	36.63			
B <i>Gephyrocapsa</i> (>4µm)	1.73	U1476A-5H2-75 cm	41.13			
T <i>D. brouweri</i>	1.93	U1476A-6H2-75 cm	46.06	U1476D-6H5-81 cm	45.29	1.91
T <i>D. triradiatus</i>	1.95	U1476A-6H2-75 cm	46.06	U1476D-6H5-141 cm	45.89	1.93
Bc <i>D. triradiatus</i>	2.14	U1476A-6H6-60 cm	51.91	U1476E-6H3-147 cm	51.08	2.13
T <i>D. pentaradiatus</i>	2.39	U1476A-7H6-75 cm	61.64	U1476A-7H5-108 cm	60.97	2.45
T <i>D. surculus</i>	2.49	U1476A-8H1-75 cm	64.31	U1476D-8H4-125 cm	63.42	2.53
T <i>D. tamalis</i>	2.80	U1476A-8H6-75 cm	71.81	U1476D-9H4-6 cm	72.72	2.81
T <i>Sphenolithus</i> spp.	3.54	U1476A-11H6-75 cm	103.13			

Table S2: Paleomagnetic boundaries at Site U1476. The most reliable paleomagnetic boundaries are marked by an asterisk.

Boundary	Age (Ma) GPTS 2012	Hole-Core-Section- interval	CCSF (m)	Hole-Core-Section- interval	CCSF (m)	Age (Ma) THIS STUDY
B Jaramillo	1.07	U1476D-4H5-68 cm	26.49*	U1476E-3H6-67 cm	26.24	
T Olduvai	1.78	U1476D-6H2-64 cm	40.62	U1476E-5H2-110 cm	39.89*	
B Olduvai	1.95	U1476D-4H6-67 cm	46.65	U1476E-5H7-39 cm	46.28*	1.94
T Gauss	2.58	U1476D-8H7-34 cm	67.01	U1476E-*H2-107 cm	67.56*	2.66

Figure S2: Inclination of shipboard core-half measurements after 15 or 20 mT alternating field demagnetization (Hall et al. 2017b) for a) Hole A, b) Hole D and c) Hole E. As the paleomagnetic data from U1476 carry a strong coring overprint, in particular at the top of each core, data from the first sections of the cores are not shown. The depth of paleomagnetic polarity boundaries were defined by joint consideration of data from all holes.

