

1    **TITLE**

2    **Paleoecology and evolutionary response of planktonic foraminifera to**  
3    **the mid-Pliocene Warm Period and Plio-Pleistocene bipolar ice sheet**  
4    **expansion**

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23      **ABSTRACT**

24            The Pliocene-Recent is associated with many important climatic and paleoceanographic  
25          changes which have shaped the biotic and abiotic nature of the modern world. The closure of the  
26          Central American Seaway and the development and intensification of northern hemisphere ice  
27          sheets had profound global impacts on the latitudinal and vertical structure of the oceans  
28          triggering the extinction and radiation of many marine groups. In particular, marine calcifying  
29          planktonic foraminifera, which are highly sensitive to water column structure, exhibited a series of  
30          extinctions as global temperatures fell. By analyzing high-resolution (~5 kyr) sedimentary records  
31          from the Eastern Equatorial Pacific Ocean, complimented with global records from the novel  
32          Triton dataset, we document the biotic changes in this microfossil group, within which three  
33          species displayed isochronous co-extinction, and species with cold-water affinity increased in  
34          dominance as meridional temperature gradients steepened. We suggest that these changes were  
35          associated with the terminal stages of the closure of the Central American Seaway, where  
36          following the sustained warmth of the mid-Pliocene Warm Period, bipolar ice sheet expansion  
37          initiated a world in which cold- and deep-dwelling species became increasingly more successful.  
38          Such global scale paleoecological and macroevolutionary variations between the Pliocene and  
39          the modern icehouse climate would suggest significant deviations from pre-industrial baselines  
40          within modern and future marine plankton communities as anthropogenic climate forcing  
41          continues.

42      **1. INTRODUCTION**

43            Current observations suggest that the Earth is shifting from its pre-industrial state  
44          (Beaugrand et al. 2002; Cheung et al. 2013; Ceballos et al., 2015; Urban 2015; Barton et al.,  
45          2016; Pinksy et al., 2018; Jonkers et al., 2019; Tierney et al. 2020; Edwards et al., 2022), and  
46          changes in the vertical and latitudinal structure of the marine realm are ultimately likely to take  
47          place (Hu et al., 2011; Rhein et al., 2013; Purich et al., 2018; Zika et al., 2018; Bindoff et al., 2019;

48 Golledge et al., 2019). It is therefore important to understand how ecosystems such as the open  
49 ocean, which contain resources vital to human populations (Worm et al., 2003; Tittensor et al.,  
50 2010) respond to short- and long-term oceanographic shifts (e.g., Norris et al., 2013).

51 The timing of closure for the Isthmus of Panama at ~4.7-2.7 Ma (Keigwin, 1978; 1982;  
52 Keller et al., 1989; Haug & Tiedemann, 1998; Haug et al., 2001; Groeneveld et al., 2006; Steph  
53 et al., 2006, 2010; Molnar, 2008; Federov et al., 2013; O'Dea et al., 2016) remains contentious,  
54 though the ultimate role of this event in late Cenozoic icehouse evolution is clear, proving pivotal  
55 to the intensification of northern hemisphere glaciations. The precise dating of final isthmus  
56 formation is less essential than the repercussions of the gradual shoaling and restriction of the  
57 Central American Seaway (CAS) which triggered significant global palaeoceanographic effects  
58 fundamental to the evolution of the present climate state. The gradual restriction of consistent  
59 throughflow between the tropical Atlantic and Indo-Pacific Oceans via isthmus formation (O'Dea  
60 et al., 2016) was coupled with bipolar cryosphere development that significantly restructured  
61 global vertical and meridional temperature gradients (Schmidt et al., 2004a, b; Mudelsee &  
62 Raymo, 2005; Boscolo-Galazzo & Crichton et al., 2021; Boscolo-Galazzo et al., 2022; Ford et al.,  
63 2022; Gaskell et al., 2022), altering marine ecosystems and trophic structure (Woodhouse &  
64 Swain et al., in review). The recorded effects on global paleoceanographic and biodiversity are of  
65 particular importance, as this ice sheet expansion was preceded by the sustainedly warmer world  
66 of the Pliocene. In particular, the mid-Pliocene Warm Period (mPWP, 3.264-3.025; Dowsett et al.  
67 2012; Haywood et al. 2016) is increasingly imperative to our understanding of future climate  
68 change as global continental configuration, faunal and floral distributions, mean global  
69 temperatures (2-3°C warmer than pre-industrial), and  $p\text{CO}_2$  (350-450 ppm) were comparable to  
70 levels expected by the closure of the 21<sup>st</sup> century (Chandler et al., 1994; Haywood et al., 2000,  
71 2016; Jiang et al., 2005; Pagani et al., 2010; Seki et al., 2010; Bartoli et al., 2011; IPCC, 2022).

72 To assess the biological responses to these marine ecosystem changes, we look to the  
73 Cenozoic marine microfossil record, specifically the planktonic foraminifera, single-celled marine  
74 protists with a global distribution and the most complete Cenozoic species-level fossil record (Aze  
75 et al., 2011; Fenton & Woodhouse et al., 2021). Their calcareous skeletons, or tests, preserve  
76 not only their entire life history, but also a biogeochemical expression of the surrounding water  
77 column (e.g., Edgar et al., 2017). These features allow for high-resolution species-specific  
78 quantification of physiological and ecological adaptation through periods of climate variability  
79 (e.g., Knappertsbusch, 2007; Wade et al., 2008, 2016; Hull and Norris, 2009; Wade and Olsson,  
80 2009; Edgar et al., 2013a; Aze et al., 2014; Pearson and Ezard, 2014; Weinkauf et al., 2014,  
81 2019; Brombacher et al., 2017a, 2021; Falzoni et al., 2018; Si and Aubry, 2018; Fox et al., 2020;  
82 Todd et al., 2020; Kearns et al., 2021, 2022; Pearson and Penny, 2021; Shaw et al., 2021;  
83 Woodhouse et al., 2021; Friesenhagen, 2022; Hupp et al., 2022; Woodhouse & Swain et al. in  
84 review).

85 Here, we report the high-resolution biotic response of planktonic foraminifera during the  
86 terminal stages of closure of the CAS in the Eastern Equatorial Pacific (EEP) Ocean, focusing on  
87 the co-extinction of three members of the genus *Dentoglobigerina* through documentation of high-  
88 resolution (~5 kyr) paired single-specimen morphometric, with multi- and single-specimen  
89 geochemical analyses, and their paleoceanographic implications. Moreover, we assess the global  
90 paleoecological response of planktonic foraminifera from the Pliocene to the Recent, assessing  
91 the role of the transition from the sustained warmth of the Pliocene to the bipolar icehouse world  
92 of Pleistocene-Recent on global planktonic foraminiferal macroevolutionary dynamics.

## 93 2. METHODS

### 94 2.1. Site Selection

95 Integrated Ocean Drilling Program Expedition 321 Site U1338 (Hole 1338A) ( $2^{\circ}30.469'N$ ,  
96  $17^{\circ}58.162'W$ ), situated in the EEP, was drilled to 410 meters below seafloor (mbsf) through

97 Holocene - early Miocene pelagic sediments (Pälike et al., 2010). At ~3 Ma, the site was at ~2°N  
98 paleolatitude (Drury et al., 2014) in a deep-water pelagic environment of similar water depth to  
99 the modern (~4 km). The primary lithologies represented are calcareous, diatomaceous and  
100 radiolarian nannofossil oozes and chalks. Despite the deep-water settings, and primarily  
101 calcareous nature of the sediments, excellent microfossil preservation has been recorded in  
102 planktonic foraminiferal specimens through intervals of this core (Fox & Wade, 2013; Woodhouse  
103 et al., 2021). A preliminary assessment of core U1338A was carried out to determine the  
104 approximate position of the extinction of several species of *Dentoglobigerina* (~3 Ma) based on  
105 tropical biostratigraphy (Wade et al., 2011), and shipboard paleomagnetic data (Pälike et al.,  
106 2010).

## 107 **2.2. Foraminiferal Assemblage Analysis**

108 Sediment volumes of 20-40 cm<sup>3</sup> were collected and washed with de-ionised water over a  
109 63-µm sieve; the residues were dried in an oven at 40 °C and split. All samples were examined  
110 using a Zeiss Stemi 305 Compact Stereo Microscope. Planktonic foraminifers were identified  
111 following the taxonomy of Kennett and Srinivasan (1983), Schiebel and Hemleben (2017), and  
112 Wade et al., (2018). We performed assemblage counts on >63 µm splits yielding >300 individuals  
113 (Table S1). Assessments of taxonomy and test preservation of foraminifera were performed via  
114 analysis with the Tescan VEGA3 XM Scanning Electron Microscope (SEM) at the University of  
115 Leeds, UK.

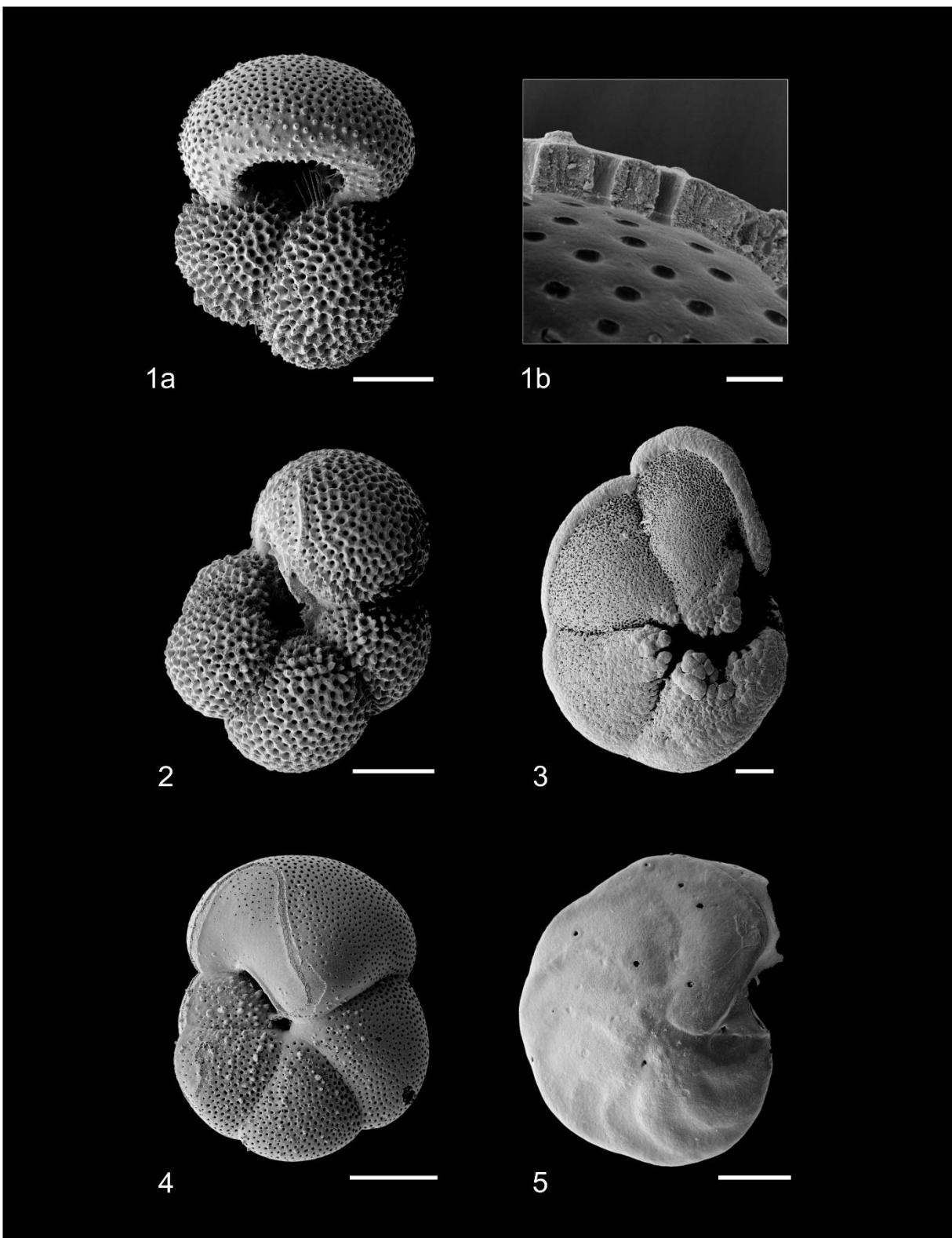
116 Species were grouped by their ecology to assess the relative abundances of taxa for  
117 palaeoceanographic information, where taxa were assigned as either shallow- and warm-water  
118 taxa (the ecogroups “symbiotic” and “asymbiotic” of Aze et al., 2011), or deep- and cold-water  
119 taxa (the ecogroups “thermocline”, “subthermocline” of Aze et al., 2011, and *Globigerinita*  
120 *glutinata* (Lutz, 2010)).

## 121 **2.3. Morphometric Analysis**

122 Specimens of the genus *Dentoglobigerina* were measured to compare species size with  
123 stable isotope ratios to investigate species ecology and ontogeny. Complete specimens of  
124 *Dentoglobigerina* were picked and mounted in umbilical position on card slides pierced with a fine  
125 needle to accommodate the variably spired nature of species in the genus (Wade et al., 2018).  
126 Specimens were imaged umbilically using a Zeiss Axio Zoom V16 microscope with attached  
127 Canon EOS 100D camera at x 19.4 magnification. All specimens were then rotated 90° laterally,  
128 and imaged whilst propped onto their penultimate chamber. Images were processed using the  
129 image analysis software Image Pro Premier, and the maximum test diameter, previously deemed  
130 a statistically repeatable measurement amongst *Dentoglobigerina* (Brombacher et al., 2017b,  
131 2018; Woodhouse et al., 2021), was captured from both orientations, and the lower of the two  
132 values assigned as test size.

133 **2.4. Geochemical Analysis**

134 Following morphometric analysis, well-preserved specimens of *Dentoglobigerina altispira*  
135 (>200 µm), *Dentoglobigerina baroemoenensis* (>200 µm) and *Dentoglobigerina globosa* (>200  
136 µm) were picked, ultrasonicated in deionized water for 10-15 seconds, and dried for stable isotope  
137 analysis. This process was repeated for extant taxa representing known discrete ecological  
138 habitats through the water column to determine the ecological niche habits of the extinct  
139 dentoglobigerinids: *Globigerinoides ruber* (212-350 µm, surface mixed-layer (SML)),  
140 *Neogloboquadrina incompta* (212-350 µm, subsurface), *Globorotalia tumida* (>300 µm,  
141 thermocline/photic zone base, corrected for a 1.0‰ δ<sup>13</sup>C enrichment due to this species  
142 occupying the shallow oxygen minimum zone and consequential effects of reduced ambient pH  
143 (Lohmann, 1995; Bijma et al., 1999; Uchikawa and Zeebe, 2010; Birch et al., 2013)), *Globorotalia*  
144 *scitula* (212-300 µm, subthermocline), and *Cibicidoides wuellerstorfi* (>212 µm, bottom-water)  
145 (see Cramer et al., 2009, 2011; Rasmussen & Thomsen, 2010; Aze et al., 2011; Woodhouse et



**Figure 1.** Scanning electron micrographs of species analyzed for stable isotope geochemistry. 1a, *G. ruber*, 1b, *G. ruber* shell ultrastructure showing excellent preservation, 2, *N. incompta*, 3, *G. tumida*, 4, *H. scitula*, 5, *C. wuellerstorfi*. Scale bar for images 1a, 2-5 = 100 microns, for image 1b = 10 microns. All specimens from sample U1338A-5H-4W-35/38.

147 species were analysed using an Elementar IsoPrime Dual-Inlet Isotope Ratio Mass Spectrometer  
148 in the School of Earth and Environment at the University of Leeds, and data are reported to the  
149 Vienna PeeDee belemnite (VPDB) scale using a Carrara marble standard (Elemental  
150 Microanalysis B2214) where analytical precision was better than 0.07 and 0.13 ‰ for  $\delta^{13}\text{C}$  and  
151  $\delta^{18}\text{O}$ , respectively.

152 Specimens of *Cibicidoides wuellerstorfi* were also used to create a benthic foraminiferal  
153  $\delta^{18}\text{O}$  record for this study to supplement the shipboard paleomagnetic data (Pälike et al., 2010).  
154 This record was constructed and tuned to the Ocean Drilling Program Site 849/IODP Site 1338  
155 stack constructed by Lyle et al., (2019) using QAnalySeries software (Kotov and Pälike 2018) to  
156 better constrain the timing of events (see Woodhouse et al., 2021), where the study section is  
157 calculated to represent the Pliocene interval from ~3.47-2.98 Ma.

158 **2.5. Global Data Analysis**

159 To investigate how planktonic foraminiferal macroevolution and paleoecology has  
160 developed since the Pliocene, the Triton dataset (Fenton & Woodhouse et al., 2021) was  
161 downloaded, and all macroperforate planktonic foraminiferal records occurring from 5.3-0 Ma  
162 (early Pliocene-Recent) were binned into 53-time bins with equal length (100 kyr). Species were  
163 assigned the speciation and extinction datums in accordance with Aze et al., (2011) and Fenton  
164 & Woodhouse et al., (2021) and all species occurrences located outside of these assigned  
165 stratigraphic ranges were removed. This range trimming was applied to eliminate much of the  
166 occurrence data likely attributable to misidentification and/or reworking which may create artificial  
167 “tails” within speciation and extinction data (Liow et al., 2010; Lazarus et al., 2012; Flannery-  
168 Sutherland et al., 2022). The trimming of taxa resulted in a dataset of 239,317 planktonic  
169 foraminiferal occurrences. Furthermore, all species were assigned to their respective  
170 “ecogroups”, which represent broad ecological categories based on paleoecological and  
171 phylogenetic data (Aze et al., 2011). These ecogroups are defined as: ecogroup 1 = surface mixed

172 layer dweller with photosymbionts, ecogroup 2 = surface mixed layer dweller without  
 173 photosymbionts, ecogroup 3 = thermocline dweller, ecogroup 4 = subthermocline dweller,  
 174 ecogroup 5 = high-latitude.

175 **3. RESULTS**

176 **3.1. Assemblage Records**

177 All sediments contain a highly  
 178 abundant well-preserved (Figure 1)  
 179 open-ocean planktonic foraminifer  
 180 assemblage comprising ~70  
 181 morphospecies. The dominant genera  
 182 through the section included  
 183 *Neogloboquadrina*, *Globigerinoides*,  
 184 *Pulleniatina*, and *Globigerinita* (see SI).  
 185 The isochronous extinction of the  
 186 species *D. altispira*, *D.*  
 187 *baroemoenensis*, and *D. globosa* in  
 188 U1338A occurs ~35.50 mbsf (~3.037  
 189 Ma). There is also a notable influx of the  
 190 species *Menardella* cf. *exilis* and  
 191 *Menardella* cf. *pertenuis* occurring from  
 192 ~42.58-40.56 mbsf (~3.45-3.36 Ma),  
 193 after which they are absent within the  
 194 study section.

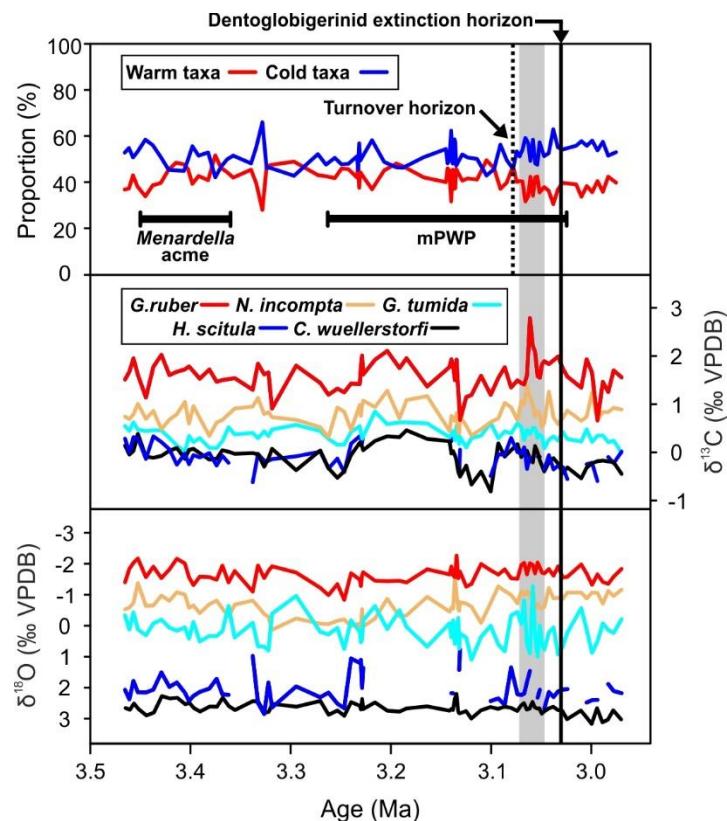


Figure 2. Grouped assemblage data of warm-water taxa (ecogroups “symbiotic” and “asymbiotic”) and cold-water taxa (ecogroups “thermocline”, “subthermocline”, and *Globigerinita glutinata* (Lutz, 2010; Aze et al. 2011). Foraminiferal  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$ , black = *C. wuellerstorfi* (bottom water), dark blue = *G. scitula* (subthermocline), cyan = *G. tumida* (thermocline), orange = *N. incompta* (subsurface), red = *G. ruber* (surface mixed-layer). Dashed line represents permanent switch to higher proportion of cold-water taxa, grey box indicates where isotope records exhibit high volatility, mPWP = mid-Pliocene Warm Period.

195 Comparing the assemblage composition of warm- and surface- dwellers against cold- and  
 196 deep- dwellers, we document generally consistent species abundances until ~36.26 mbsf (~3.08  
 197 Ma), where the assemblage exhibits consistently greater abundances of cold- and deep-dwellers  
 198 for the rest of the record (Fig. 2).

199 **3.2. Dentoglobigerina Stable Isotope-Size Trends**

200 Test preservation was excellent throughout the sampled interval, where specimen walls  
 201 appear optically translucent, and SEM images (Fig. 1) indicate no observable diagenetic

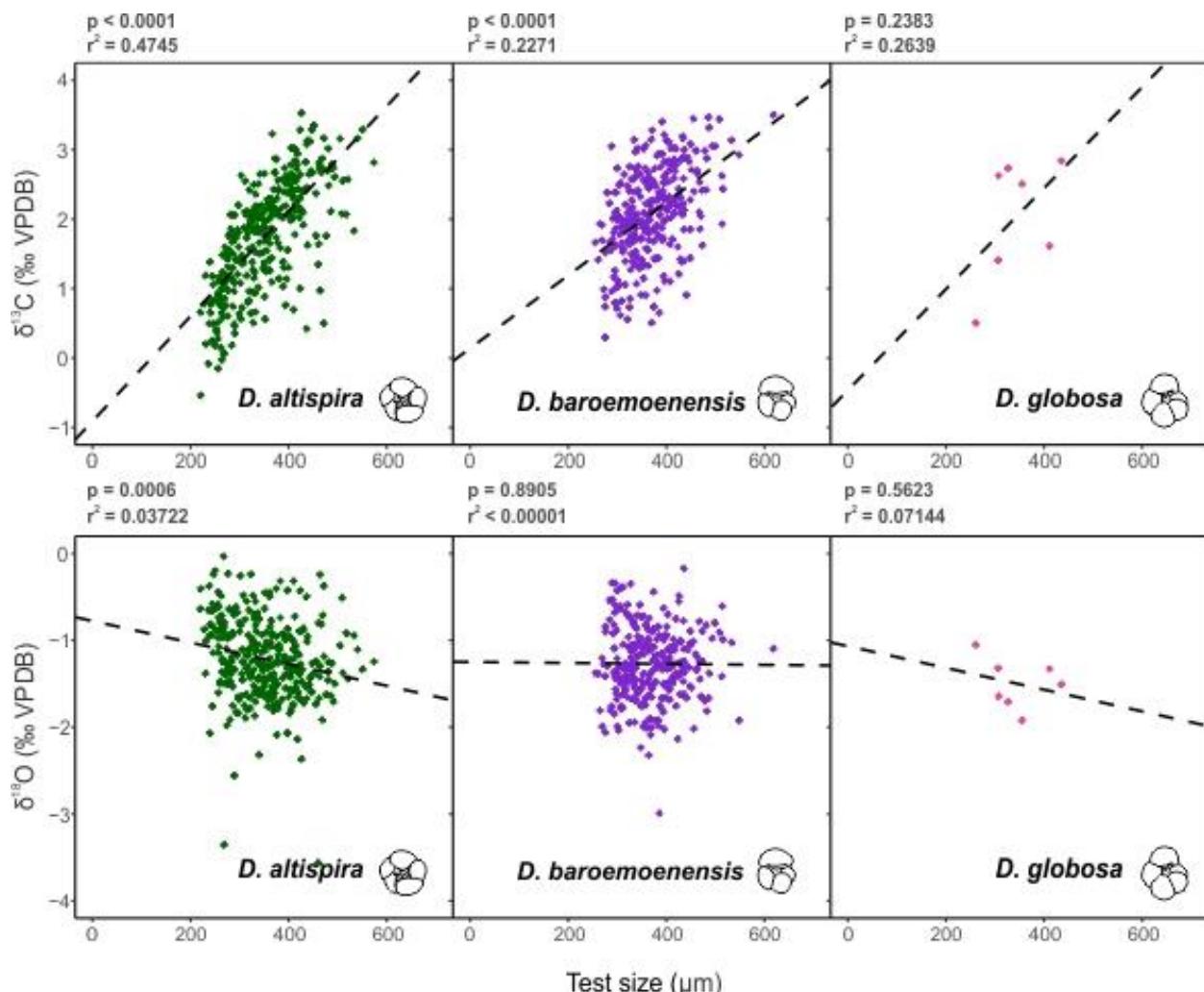


Figure 3. Test size -  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  relationships for the three species of *Dentoglobigerina* which underwent extinction through the study section. Trend lines for each species represent linear regressions based on the entire per species dataset (dashed line). Significance (p) and measure of fit ( $r^2$ ) were calculated for each linear regression.

202 alteration, clean pore spaces, and spines preserved within tests (Fig. 1a). Following artificial test  
 203 breaking, inspection of the wall ultrastructure (Fig. 1b) showed that no wall recrystallisation had  
 204 taken place, suggesting stable isotope signals remain unaltered (Sexton et al., 2006; Edgar et al.,  
 205 2013b). Single-specimen  $\delta^{13}\text{C}$  values for *D. altispira*, *D. baroemoenensis*, and *D. globosa* vary  
 206 from -0.54 to +3.53‰, +0.30 to +3.50‰, and +0.51 to +2.84‰ (Fig. 3, SI), respectively, whilst  
 207  $\delta^{18}\text{O}$  values vary from -3.56 to -0.03‰, -2.99 to -0.17‰, and -1.92 to -1.05‰, respectively. In all  
 208 three species, a positive correlation is calculated between test size and  $\delta^{13}\text{C}$ , however, this  
 209 relationship is only significant ( $p < 0.0001$ ) in *D. altispira* and *D. baroemoenensis*, potentially due  
 210 to the greater number of specimens analyzed for these species (Fig. 3). Regression slopes are  
 211 similarly steep, however the slopes for *D. altispira* and *D. globosa* are more alike.  
 212 *Dentoglobigerina baroemoenensis* and *D. globosa* show no significant correlation between  $\delta^{18}\text{O}$   
 213 and test size, however, a  
 214 significant ( $p = 0.0006$ ) negative  
 215 relationship is recorded in *D.*  
 216 *altispira*. Once again, regression  
 217 slopes for *D. altispira* and *D.*  
 218 *globosa* are similar, whereas for *D.*  
 219 *baroemoenensis*, this slope is  
 220 almost flat (Fig. 3).

### 221 3. 3. Extant Species

222 **Geochemical Records**  
 223 Amongst the extant  
 224 species picked from strict size  
 225 fractions throughout the study  
 226 section, *G. ruber*  $\delta^{13}\text{C}$  values show

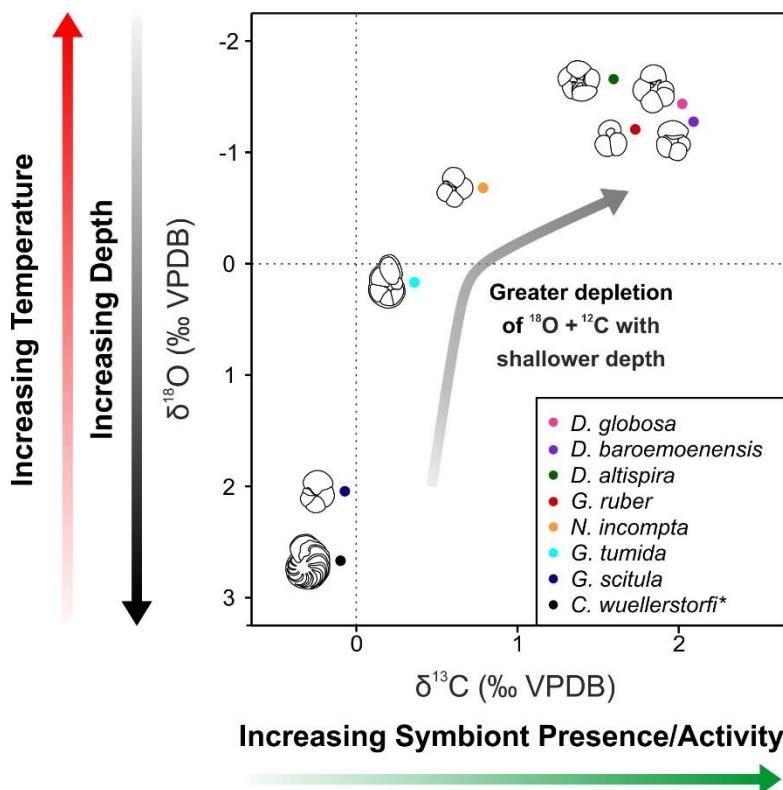


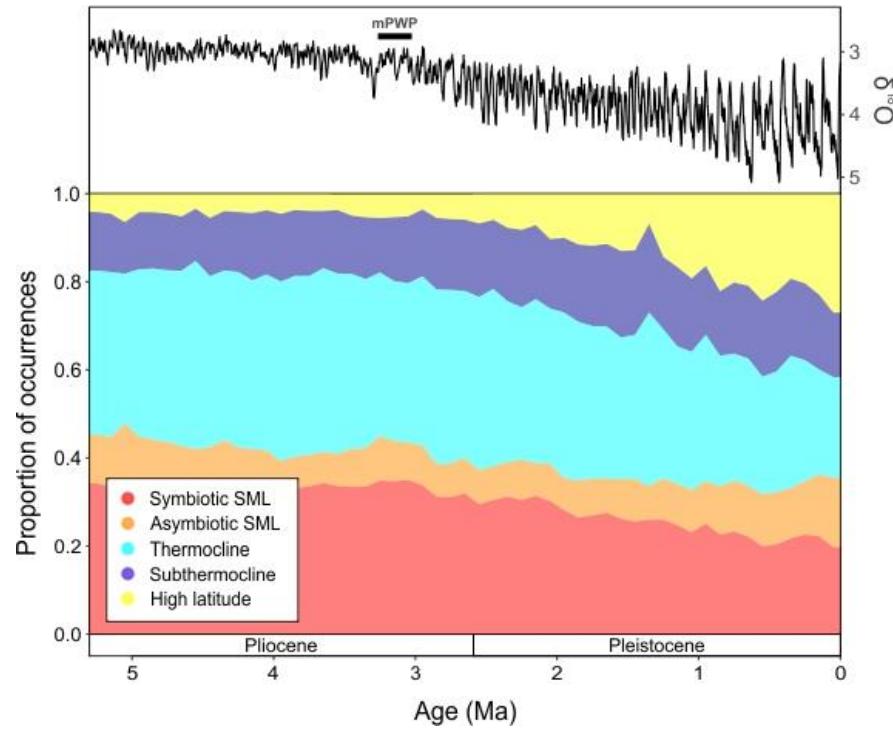
Figure 4.  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  cross-plot 2 showing mean values of all analyzed specimens from this study. Black = *C. wuellerstorfi*, dark blue = *G. scitula*, cyan = *G. tumida*, orange = *N. incompta*, red = *G. ruber*, green = *D. altispira*, purple = *D. baroemoenensis*, pink = *D. globosa*. Species marked with an asterisk are benthic.

227 the highest  $\delta^{13}\text{C}$  variability (+0.7 to +2.8‰), and  $\delta^{18}\text{O}$  values varying from -2.3 to -0.8‰ (SI, Fig.  
 228 4). Corrected *G. tumida* values show the lowest  $\delta^{13}\text{C}$  variability (0 to +0.8‰), and the highest  
 229 variability for  $\delta^{18}\text{O}$  (-1.3 to +1.1‰). *G. scitula*  $\delta^{13}\text{C}$  values vary from -0.6 to +0.4‰, whilst  $\delta^{18}\text{O}$   
 230 varies from +0.8 to +2.9‰, whereas bottom-water *C. wuellerstorfi*  $\delta^{13}\text{C}$  values vary from -0.8 to  
 231 +0.5‰, and  $\delta^{18}\text{O}$  varies +2.2 to +3.1‰, showing the lowest variability in  $\delta^{18}\text{O}$  (Fig. 4). The stable  
 232 isotope records of extant species generally tend to show low inter-sample variability, however  
 233 there is notable geochemical stochasticity within the *G. tumida* record ~36.17-35.86 mbsf (Fig. 2).

234 All three species of *Dentoglobigerina* analyzed in this study record mean stable isotopic  
 235 ratios similar to the extant species *G. ruber*, where all species indicated  $\delta^{18}\text{O}$  ratios less negative  
 236 than *G. ruber*, and *D. baroemoenensis* and *D. globosa* show  $\delta^{13}\text{C}$  ratios more positive than this  
 237 species (Figs. 3 and 4).

### 238 3.4. Global Pliocene- 239 Recent Ecogroup trends

240 The global  
 241 proportions of planktonic  
 242 foraminiferal ecogroups  
 243 within the Triton dataset  
 244 (Fenton & Woodhouse et  
 245 al., 2021) show that  
 246 throughout the time  
 247 interval studied (5.3-0  
 248 Ma), surface mixed layer



249 dwellers without  
 250 photosymbionts (orange)  
 251 proportions remain

Figure 5. The LR04 stack showing benthic foraminiferal  $\delta^{18}\text{O}$  (from Lisiecki and Raymo, 2005), and proportions of macroperforate planktonic foraminifera occurrences assigned to the ecogroups of Aze et al. (2011), binned to 100 kyrs from 5.3 Ma to the Recent. mPWP = mid-Pliocene Warm Period, SML = surface mixed-layer.

252 relatively consistent, making up ~10% of the total global fauna (Fig. 5). From 5.3-3 Ma, global  
253 ecogroup proportions are relatively consistent, where the dominant forms are thermocline  
254 dwellers (cyan) and surface mixed layer dwellers with photosymbionts (red) (Fig. 5), making up  
255 ~40% and ~35% of the global fauna, respectively. During this interval, the proportion of  
256 subthermocline dwellers (blue) and high-latitude forms (yellow) also remain relatively consistent  
257 with ~10% and <5% of total proportions, respectively. After ~3 Ma, both thermocline dwellers and  
258 surface mixed layer dwellers with photosymbionts show a steady decline in global representation  
259 approaching the Recent, making up ~20% each in the modern ocean. At ~3 Ma, both the  
260 subthermocline dwellers and high latitude ecogroup start to show increases in their proportions,  
261 though this increase approaching the modern is much greater in the latter group. During the last  
262 100 kyrs, subthermocline and high latitude species constitute ~15 and ~25%, respectively (Fig.  
263 5).

#### 264       **4. DISCUSSION**

265       Few major changes in the assemblage composition are observed through the study  
266 interval other than the isochronous extinction of *D. altispira*, *D. baroemoenensis*, and *D. globosa*  
267 at ~3.037 Ma (Fig. 2; 35.50 mbsf), and the influx of the two species *M. cf. exilis* and *M. cf. pertenuis*  
268 through ~3.45-3.36 Ma (42.58-40.56 mbsf), defined hence forth as the “*Menardella acme*” (Figs.  
269 2 & 6).

##### 270       **4.1. Dentoglobigerinid Paleoecology**

271       The extinction of *D. altispira* is a useful marker in the mid-Pliocene, previously recorded  
272 within the East Equatorial Pacific Ocean (3.46 Ma; Shackleton et al., 1995; Wade et al., 2011),  
273 however this study and that of Woodhouse et al., (2021) provide recalibration for this event, which  
274 also includes the co-extinction of *D. baroemoenensis* and *D. globosa*. The co-extinction of the  
275 dentoglobigerinids is significant, as Woodhouse et al., (2021) demonstrated that *D. altispira* and

276 *D. baroemoenensis* show unique phenotypic responses leading up to their termination, despite  
277 their shared phylogenetic and ecological affinity. We therefore suggest that all three species share  
278 an ecological habit that ultimately proved inefficient to mitigate the changing abiotic conditions  
279 associated with this critical period of bipolar cryosphere development (Kleiven et al., 2002; Brierly  
280 & Fedorov, 2010; Cramer et al., 2009, 2011; Willeit et al., 2015; Hayashi et al., 2020; Westerhold  
281 et al., 2020).

282 Studies of extant species suggest a strong positive correlation between planktonic  
283 foraminifera  $\delta^{13}\text{C}$  and test size, paired with a lack of a strong negative significant relationship in  
284  $\delta^{18}\text{O}$  and test size, is indicative of species bearing photosymbiotic algae (e.g. Berger et al., 1978;  
285 Bouvier-Soumagnac and Duplessey, 1985; Spero and Williams, 1988, 1989; Spero et al., 1991;  
286 Spero, 1992; Spero and Lea, 1993; Ravelo and Fairbanks, 1995; Norris, 1996; Birch et al., 2013).  
287 Our data suggests that all three species of *Dentoglobigerina* studied here are symbiont-bearing,  
288 displaying mean stable isotope data similar to the symbiont-bearing surface mixed layer dwelling  
289 *G. ruber* (Figs. 2-4). Moreover, the regression lines for the ancestor-descendent pair *D. globosa*  
290 - *D. altispira* are remarkably similar, suggesting the species share similar stable isotope-test size  
291 relationships, despite the speciation of *D. altispira* occurring ~20 Myrs prior (Aze et al., 2011;  
292 Wade et al., 2011, 2018). However, the substantially fewer data for *D. globosa* currently limits the  
293 significance of this observation for this particular species (Fig. 3).

294 The results presented here contribute to the variety of interpretations from previous  
295 studies on the paleoecology of *D. altispira*. Spanning different ocean basins throughout the  
296 species' stratigraphic range they suggest: a shallow-dwelling (e.g., Keller and Savin, 1985;  
297 Vincent et al., 1985; Prentice and Matthews, 1988; Corfield and Cartlidge, 1991; Norris et al.,  
298 1993; Hodell and Vayavananda, 1994; Sosdian and Lear, 2020), deep-dwelling (Opdyke and  
299 Pearson, 1995; Pearson and Shackleton, 1995), or lower mixed layer/upper thermocline (Zou et  
300 al., 2022) ecological niche habit.

301 Woodhouse et al., (2021) suggested that prior to extinction, the *D. altispira* geochemical  
302 signal may signify that this species underwent adaptive ecological niche migration across multiple  
303 depth habitats. Upon further investigation, by isolating all *D. altispira* specimens present after the  
304 migration horizon at ~ 3.061 Ma (Woodhouse et al., 2021), we show that these specimens do in  
305 fact display a steeper negative relationship between  $\delta^{18}\text{O}$  and test size (Fig. S1), consistent with  
306 symbiosis, however this relationship lacks statistical significance. Nevertheless, this observation  
307 lends support to the conclusions of Woodhouse et al., (2021) that this species underwent niche  
308 adaptation prior to extinction.

309 Another plausible scenario may be the existence of indeterminate cryptic diversity within  
310 the *D. altispira* morphospecies complex where multiple ecological strategies or phylogenetic  
311 expressions may be present (e.g., Huber et al., 1997; Bijma et al., 1998; de Vargas et al., 1999,  
312 2002; Weiner et al., 2012; Schiebel and Hemleben, 2017; Nirmal et al., 2021; Pearson and Penny,  
313 2021), and the stepwise changes observed in Woodhouse et al., (2021), may indicate the  
314 systematic loss of “cryptic genotypes” within this morphospecies complex. Indeed, Pearson and  
315 Penny (2021), hypothesized that dramatic abundance switches in the Indo-Pacific Warm Pool of  
316 ecologically-distinct alternately-coiled populations of *Pulleniatina* morphospecies may signify  
317 replacement by distinct cryptic genotypes, and such coiling switches are noted throughout the  
318 planktonic foraminiferal fossil record (Ericson et al., 1955; Saito et al., 1975; Bossio et al., 1976;  
319 Hallock & Larsen. 1979; Hornbrook, 1982; Scott et al., 1990; Norris and Nishi, 2001; Winter and  
320 Pearson, 2001; Crundwell & Nelson, 2007; Wade et al., 2011; Pearson & Ezard, 2014; Crundwell,  
321 2015a, b; Levin et al., 2016; Wallace et al., 2019; Crundwell & Woodhouse, 2022a, b). Therefore,  
322 the range of interpreted paleoecologies in *D. altispira* may in fact be due to the occurrence of  
323 distinct cryptic populations from across the geological record. Irrespective, the abiotic conditions  
324 at this time appear to have become fatally detrimental to the entire ecological habit of all three  
325 morphospecies of *Dentoglobigerina* analyzed in the EEP, and subsequently across the entire

326 globe (Shackleton et al., 1995; Chaisson and Pearson, 1997; Wade et al., 2011; Raffi et al., 2020;  
327 Groeneveld et al., 2021; Woodhouse et al., 2021).

328       **4.2. The *Menardella* Acme**

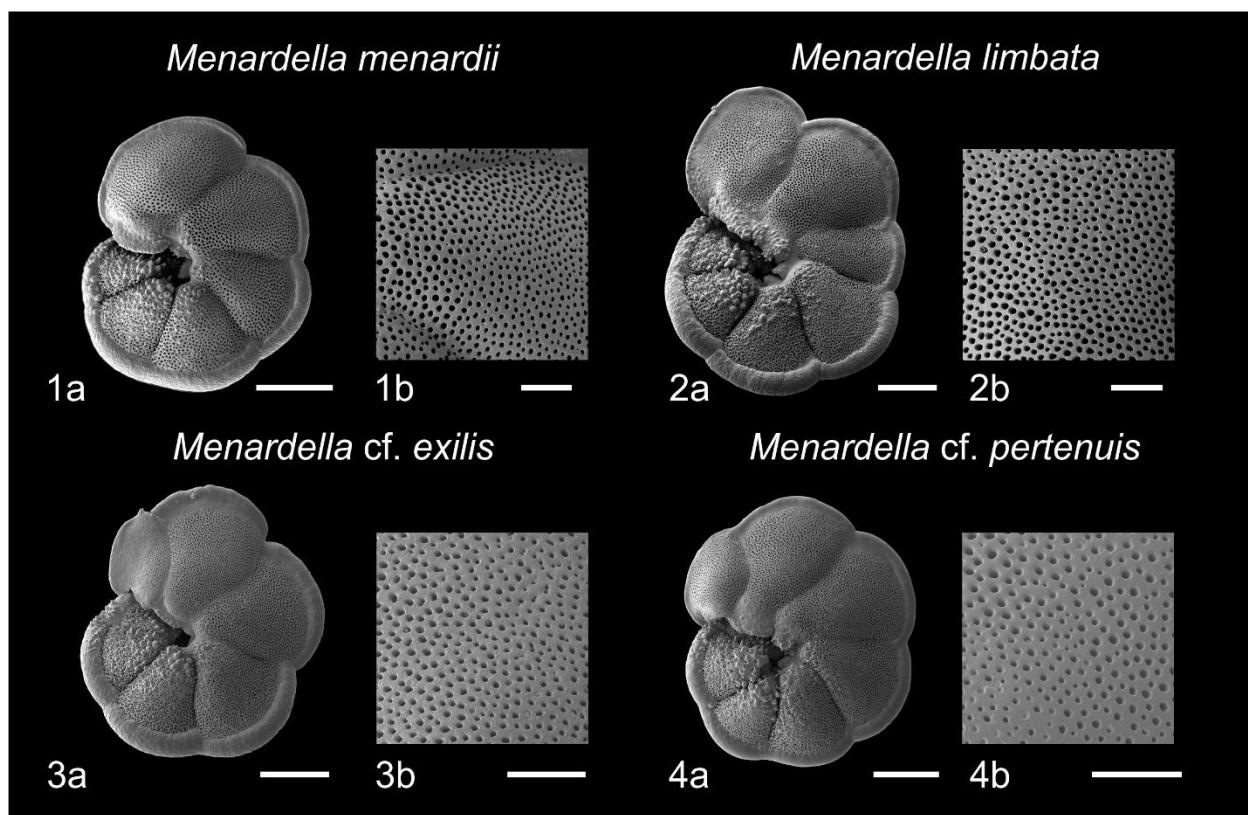
329           The transient influx and co-occurrence of *M. cf. exilis* and *M. cf. pertenuis* from ~3.45-3.36  
330 Ma may indicate a shared ecological affinity between these species (Fig. 2; Kennett & Srinivasan,  
331 1983; Knappertsbusch, 2016). Furthermore, this association may suggest that these two similar  
332 forms exist within the same genetic species complex, though further study on internal shell  
333 ontogeny and external morphology would be required to confirm this hypothesis. Notably  
334 however, Kaneps (1970) and Chaisson (2003) have suggested that Indo-Pacific occurrences of  
335 these two species are in fact “aberrant” forms of *Menardella limbata* and *Menardella menardii*,  
336 with the *M. exilis-pertenuis* plexus being solely endemic to the Atlantic basin (Sexton & Norris,  
337 2011).

Species	Pore density (per 2500 µm <sup>2</sup> )
<i>M. menardii</i>	32
<i>M. limbata</i>	27
<i>M. cf. exilis</i>	51
<i>M. cf. pertenuis</i>	49

Table 1. The number of pores per 2500 µm<sup>2</sup> in the penultimate chamber of select species of *Menardella*.

338           Scanning electron photomicrographs and pore density analysis of *Menardella*  
339 morphospecies within this study (Fig. 6; Table 1) suggests that the *M. cf. exilis* and *M. cf. pertenuis*  
340 morphotypes ascribed to “aberrant” forms may in fact be phylogenetically distinct from both *M.*  
341 *menardii* and *M. limbata*, as well as from the endemic Atlantic *M. exilis-pertenuis* plexus. Where  
342 the Atlantic type-specimens exhibit finely perforate tests (Kennett & Srinivasan, 1983), the  
343 specimens within this study appear to show test perforation intermediate between “normally

344 "perforate" menardellids such as *M. menardii* and *M. limbata* (Fig. 6), and the "finely perforate" *M.*  
 345 *exilis-pertenuis* plexus (Kennett and Srinivasan, 1983; Chaisson, 2003). Whether all Indo-Pacific  
 346 occurrences of these morphotypes (e.g., Brönniman and Resig, 1971; Jenkins and Orr, 1972;  
 347 Thunell, 1981; Keigwin, 1982; Thompson, 1982; Chaisson and Leckie, 1993) exhibit similar test  
 348 perforation remains to be determined. However, these forms could represent either: 1) convergent  
 349 evolution of a geographically isolated endemic population restricted to the Indo-Pacific triggered  
 350 by vicariance, or 2) specimens within the *M. exilis-pertenuis* plexus exhibiting a differential  
 351 phenotypic expression of pore density, potentially due to regional differences in  
 352 paleoceanography between the Atlantic and Indo-Pacific basins at this time (Haug et al., 2001).  
 353 Irrespective of the biological implications, this acme event may represent a regionally valuable  
 354 biostratigraphic marker horizon.



**Figure 6.** Scanning electron micrographs of select species of *Menardella* and pore detail of penultimate chambers. 1a, *M. menardii*, 1b, *M. menardii* pore detail, 2a, *M. limbata*, 2b, *M. limbata* pore detail, 3a, *M. cf. exilis*, 3b, *M. cf. exilis* pore detail, 4a, *M. cf. pertenuis*, 4b, *M. cf. pertenuis* pore detail. Scale bar for images 1a, 2a, 3a, 4a = 200 microns, for image 1b, 2b, 3b, 4b = 50 microns. Specimens 1 and 2 from sample U1338A-5H-CC-11/14, and specimens 3 and 4 from sample 1338A-5H-7W-76-79.

Comparing the assemblage composition of warm- and surface-dwellers against cold- and deep-dwellers, we document a gradual turnover from an assemblage exhibiting relatively even abundances of these two groups, to one of increasing occupation of cold- and deep-dwellers from ~3.08 Ma onwards (36.26 mbsf; Fig. 2). This may reflect regional thermocline shoaling similar to patterns observed at DSDP Site 84 in the proximal Panama Basin (Lutz, 2010). Other geological intervals associated with significant global cooling such as the Eocene-Oligocene transition and late Miocene cooling exhibit similar patterns of gradual, successive turnover of warm-water dwellers by cold-water taxa potentially associated with expansions/contractions in their respective ecospaces (Keller, 1983; Boersma and Premoli Silva, 1991; Keller et al., 1992; Molina et al., 1993; Wade and Pearson, 2008; Ezard et al., 2011; Lowery and Fraass, 2019; Lowery et al., 2020; Boscolo-Galazzo & Crichton et al., 2021; Boscolo-Galazzo et al., 2022; Woodhouse & Swain et al. in review).

#### 4.3. Pliocene EEP Paleoceanography

The establishment of the Isthmus of Panama played a key role in Atlantic Meridional Overturning Circulation intensification by barring Caribbean inflow from the Atlantic (O'Dea et al., 2016; Hayashi et al., 2020), leading to a new palaeoceanographic state defined by an equatorial Pacific thermocline exhibiting a high-angle east-west tilt (Fiedler and Talley, 2006; Yang and Wang, 2009; Zhang et al., 2012; Ford et al., 2015). Changes in the EEP water column structure are compounded within biotic and abiotic records, where global changes in ice volume, as shown by benthic  $\delta^{18}\text{O}$  (Fig. 5), and the formation of the isthmus contributed to the gradual cooling and shoaling of the thermocline (Ford et al., 2015). Isochronous records of ice-raftered debris in the North Atlantic and Pacific infer a substantial change to high-latitude global climate ~3 Ma (Shackleton et al., 1984; Maslin et al., 1996; Kleiven et al., 2002; Lawrence et al., 2006). Consequently, the already restricted CAS was likely subjected to substantial eustatic sea level fluctuations (Chaisson, 2003; Bartoli et al., 2005; O'Dea et al., 2016), causing cool water within

380 or below the thermocline to become shallow enough to be mixed by surface winds (Philander &  
381 Federov, 2003; Federov et al., 2004; 2006; Ford et al., 2012; 2015). In turn, this contributed to a  
382 dramatic increase in regional upwelling associated with further development of the EEP cold  
383 tongue (Herbert et al., 2010). We suggest that the increasing dominance of cold- and deep-  
384 dwellers in the EEP (Figs. 2 and 5) are a direct manifestation of the water column structure  
385 changes associated with closure of the CAS and cryosphere intensification, marking the initiation  
386 of transition from the early Pliocene “El Padre” mean state to one more similar to the modern  
387 ocean (Seki et al., 2012; Ford et al., 2012, 2015).

388 The geochemical fluctuations noted within *G. tumida* from 3.071-3.061 Ma (36.17-35.86  
389 mbsf; Fig. 2) are coeval with the interval assigned to the “Phase Transition” by Woodhouse et al.,  
390 (2021), in which *D. altispira* and *D. baroemoenensis* exhibit dramatic fluctuations in size and  
391 shape preceding rapid ecological changes. Here, the  $\delta^{18}\text{O}$  signal of *G. tumida* exhibits substantial  
392 and rapid changes up to  $\sim 2.1\text{\textperthousand}$ , switching from typical thermocline values to those indicative of  
393 the subsurface, and back again, whereas all other water column  $\delta^{18}\text{O}$  value changes are nominal  
394 (Fig. 2).

395 If the fluctuations within the  $\delta^{18}\text{O}$  signal of *G. tumida* were related to fluctuations in its  
396 depth habitat, we would expect the inverse pattern to occur in its  $\delta^{13}\text{C}$  signature, as  $\delta^{13}\text{C}$  values  
397 decrease with depth (Cannariato and Ravelo, 1997; Ford et al., 2012; Birch et al., 2013), however  
398 this is not the case (SI, Fig. 2). The maximum  $\delta^{18}\text{O}$  excursion value ( $\sim 2.1\text{\textperthousand}$ ) is equivalent to a  
399 temperature change of  $\sim 10\text{ }^{\circ}\text{C}$ , based on a mid-Pliocene SMOW value of  $-0.3\text{\textperthousand}$  (Williams et al.,  
400 2005; Medina-Elizalde, Lea and Fantle, 2008; Tindall & Haywood, 2015) and the  
401 paleotemperature equations of Kim & O’Neil (1997). Previous studies from EEP sites show  
402 Mg/Ca-derived thermocline temperature fluctuations of  $\sim 3\text{ }^{\circ}\text{C}$  (Site 1241; Steph et al., 2006) to  $\sim 5$   
403  $^{\circ}\text{C}$  (Sites 848, 849, and 853; Ford et al., 2012) across the same interval, and modern ocean

404 seasonal deviations within EEP surface waters are minor at  $\pm 1$  °C (Fiedler, 1992). However, these  
405 can be intensified by El Niño conditions by up to +3.8 °C (Pérez-Angel & Molnar, 2017).

406 Modern regional evaporation-precipitation balance within the EEP too shows very little  
407 variation, wherein  $\delta^{18}\text{O}_{\text{sw}}$  values average 0.26‰ (Fairbanks et al., 1992), ranging from ~0.2-0.5‰  
408 for the entire tropical Pacific (Ravelo & Hillaire-Marcel, 2007). Factors other than temperature and  
409 salinity (e.g., chlorophyll a, lunar cycle) which trigger species-specific habit changes (Rebotim et  
410 al., 2017) could be at least partially responsible for these dramatic changes in the *G. tumida*  $\delta^{18}\text{O}$   
411 records, however this species is known to calcify at the base of the photic zone (Ravelo &  
412 Shackleton, 1995), irrespective of thermocline depth (Ravelo & Fairbanks, 1992; Rincon-Martinez  
413 et al., 2011).

414 Despite the present low range in Pacific equatorial  $\delta^{18}\text{O}_{\text{sw}}$  values, modern Atlantic-  
415 Caribbean surface waters record a salinity value ~3‰ less than the modern EEP (Haug et al.,  
416 2001; Garcia et al., 2006; Schmidt et al., 2016; Öğretmen et al., 2020), equating to ~1.5‰ lower  
417 in mean  $\delta^{18}\text{O}_{\text{sw}}$  values (Ravelo and Hillaire-Marcel, 2007). This salinity contrast was fully  
418 established by ~4.2 Ma (Haug et al., 2001), and consistent breaching of Atlantic-Caribbean waters  
419 over the still-submerged isthmus may have occurred as late as 1.9 Ma (Coates and Obando,  
420 1996; Keller et al., 1989; Schmidt et al., 2016). Therefore, a breaching event is the most probable  
421 cause for the substantial variations in the  $\delta^{18}\text{O}$  record of *G. tumida* from 3.071-3.061 Ma, where  
422 this apparently thermocline-restricted (Fig. 2) disturbance may have contributed to disruption of  
423 the *Dentoglobigerina* ecological niche habit at this time (Woodhouse et al., 2021).

424 **4.4. Pliocene-Recent Global Ecological and Evolutionary Patterns**

425 It appears the faunal turnover documented in the EEP at ~3.08 Ma (Fig. 5) may represent  
426 a critical point in the global development of the bipolar cryosphere which typifies the Pleistocene  
427 and Holocene (Kleiven et al., 2002; Mudelsee & Raymo, 2005; Brierly & Fedorov, 2010; Cramer

et al., 2009, 2011; Willeit et al., 2015; Hayashi et al., 2020; Westerhold et al., 2020). Major Antarctic ice sheet expansion (Shevenell et al., 2004; Holbourn et al., 2015; Frigola et al., 2018; Westerhold et al., 2020) following the Miocene Climatic Optimum (~17-15 Ma; Methner et al., 2020) initiated global cooling, intensifying meridional gradients (Gaskell et al., 2022). This triggered unprecedented mean size increases in low-latitude planktonic foraminifera (Schmidt et al., 2004a, b) and higher efficiency of the biological carbon pump, promoting greater endemism and exploitation of new deep-water niches in calcifying plankton (Olsson, 1982; Scott, 1982; Keller, 1985; Malmgren & Berggren, 1987; Scott et al., 1990; Norris et al., 1993, 1994; 1996; Norris, 1999, 2000; Rögl, 1999; Chaisson, 2003; Kucera & Schönenfeld, 2007; Ezard et al., 2011; Crundwell, 2018; Rosenthal et al., 2018; Spezzaferri et al., 2018; Lam and Leckie, 2020; Boscolo-Galazzo & Crichton et al., 2021; Boscolo-Galazzo et al., 2022; Woodhouse & Swain et al. in review).

From ~6.5 Ma, the equatorial Pacific shows meridionally distinct planktonic foraminiferal faunal provinces, that display a turnover in dominance from Miocene species to more Recent taxa ~4 Ma (Chaisson, 1995; Chaisson and Ravelo, 2000) linked with the closure of the CAS (Haug et al., 2001). Global temperatures record a gradual, stable decline towards ~3 Ma (Fig. 5; Westerhold et al., 2020), after which planktonic foraminiferal morphospecies diversity shows a notable decline (Aze et al., 2011; Ezard et al., 2011; Fraass et al., 2015; Lowery et al., 2020), whilst ecogroups (Fig. 5) exhibit the expansion of cold-water forms coincident with the development and intensification of northern hemisphere ice sheets (Kleiven et al., 2002; Brierly & Fedorov, 2010; Cramer et al., 2009, 2011; Willeit et al., 2015; Hayashi et al., 2020). The greater proportion of cold- and deep-dwellers in the EEP at ~3.08 Ma (Fig. 2) coincides with global ecogroup patterns (Fig. 5), signifying the initiation of increasing global dominance of planktonic foraminiferal species with cold-water affinity, alongside many other phylogenetic groups (Slater et al., 2017; Steinthorsdottir et al., 2020), as the world descended into a bipolar icehouse state.

453        Despite the reduction in morphospecies diversity from ~3 Ma, the late Cenozoic closure  
454 of the Tethyan and Central American Seaways (Crame & Rosen, 2002; Brierly & Fedorov, 2010;  
455 Hamon et al., 2013; Matthews et al., 2016) may have contributed to the notable rise in diversity  
456 through the Neogene (Aze et al., 2011; Ezard et al., 2011; Peters et al., 2013; Fraass et al., 2015;  
457 Lowery et al., 2020), due to a significantly more heterogenous ocean structure via longitudinal  
458 obstruction of tropical/subtropical waters by continental reconfiguration, and latitudinal partitioning  
459 caused by the steepening of global meridional temperature gradients (Haug et al., 2001; Schmidt  
460 et al., 2004a, b; Knappertsbusch, 2016; Ford et al., 2022; Friesenhagen, 2022; Gaskell et al.,  
461 2022). Moreover, this intensified, heterogenous Icehouse climate may have played a significant  
462 role in shaping the incredible diversity observed within modern planktonic foraminiferal cryptic  
463 genotypes (Darling & Wade, 2008; Aurahs et al., 2009; Morard et al., 2009, 2013, 2019; Ujiié et  
464 al., 2010; Norris & Hull, 2012; Weiner et al., 2012; 2014; André et al., 2014; Ujiié & Ishitani, 2016),  
465 though further work is required on the quantification of planktonic foraminiferal cryptic diversity  
466 within deep time (André et al., 2013).

467        It should be noted however, that there is a prominent increase in sampling of Quaternary  
468 high latitudes that is yet to be replicated in deep-time marine records (Lazarus, 1994; Diepenbroek  
469 et al., 2002; Sellén et al., 2010; O'Regan, 2011; Siccha & Kučera 2017; Waelbroeck et al., 2019;  
470 Renaudie et al., 2020; Fenton & Woodhouse et al., 2021). This is due to the difficulties  
471 encountered in deep-sea scientific drilling of higher latitudes through the combined impacts of  
472 unpredictable and detrimental oceanographic conditions, and ephemeral sea ice (Barker et al.,  
473 1977; Backman et al.; 2006; Lamy et al., 2019; McKay et al., 2019). Consequently, the substantial  
474 increase in cold-water forms observed from ~3 Ma to the Recent (Fig. 5) may be at least partly  
475 driven by sampling efforts.

476        **5. CONCLUSIONS**

477        The high-resolution planktonic foraminiferal biotic record at IODP Site U1338 chronicles  
478    important changes in late Cenozoic development of global climate and the evolutionary history of  
479    this microfossil group. The co-extinction of three species of *Dentoglobigerina*, and the acme of *M.*  
480    cf. *exilis* and *M. cf. pertenuis* signify useful regional biostratigraphic markers within the Pacific  
481    chronological framework, where the former appears to be associated with abiotic changes in  
482    water column structure associated with the close of the Central American Seaway, and  
483    intensification of bipolar cryosphere development. These three extinct dentoglobigerinids appear  
484    to exhibit a symbiotic, mixed layer ecological niche habit, however the compilation of results from  
485    previous studies may suggest a high degree of unknown cryptic diversity within dentoglobigerinid  
486    morphospecies complexes. The abiotic extinction mechanism is likely signified by the initiation of  
487    a critical stage in the formation of northern hemisphere ice sheets and the accompanying changes  
488    to global paleoceanography and water column structure, where cold- and deep-dwelling species  
489    started to become more dominant across the globe.

490        Globally, planktonic foraminiferal ecological and macroevolutionary patterns were  
491    fundamentally different prior to bipolar ice sheet expansion, and past intervals with climatic  
492    conditions analogous to future-warming scenarios such as the mid-Pliocene Warm Period require  
493    further prospection at multiple spatiotemporal scales to better predict potential changes in global  
494    marine biodiversity as the Earth continues to shift away from its pre-industrial state. Furthermore,  
495    anthropogenic forcing has the capability to melt modern continental-scale ice sheets which hold  
496    the potential to dramatically disrupt global ocean circulation patterns, nutrient distributions, and  
497    water column structure. Based on past changes in such systems, this may signify impending  
498    repercussions for planktonic foraminiferal biodiversity, and other planktonic groups whose  
499    survival depends on the vertical structure of the oceanic water column.

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501    contributed to the interpretation of the data. A.W. plotted figures and wrote the R code to perform

502 statistical analysis. F.A.P. collected SEM images. A.W. and T.A. contributed to the writing and  
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522 **REFERENCES**

- 523 André, A., Weiner, A., Quillévéré, F., Aurahs, R., Morard, R., Douady, C.J., de Garidel-Thoron,  
524 T., Escarguel, G., de Vargas, C. and Kucera, M.: The cryptic and the apparent reversed:  
525 lack of genetic differentiation within the morphologically diverse plexus of the planktonic  
526 foraminifer *Globigerinoides sacculifer*, *Paleobiology*, 39(1), 21-39, 2013.
- 527 André, A., Quillévéré, F., Morard, R., Ujiié, Y., Escarguel, G., De Vargas, C., de Garidel-Thoron,  
528 T. and Douady, C.J.: SSU rDNA divergence in planktonic foraminifera: molecular  
529 taxonomy and biogeographic implications, *PLoS One*, 9(8), 2014.
- 530 Aurahs, R., Grimm, G.W., Hemleben, V., Hemleben, C. and Kucera, M.: Geographical distribution  
531 of cryptic genetic types in the planktonic foraminifer *Globigerinoides ruber*, *Molecular  
532 Ecology*, 18(8), 1692-1706, 2009.
- 533 Aze, T., Ezard, T.H., Purvis, A., Coxall, H.K., Stewart, D.R., Wade, B.S. and Pearson, P.N.: A  
534 phylogeny of Cenozoic macroperforate planktonic foraminifera from fossil data, *Biological  
535 Reviews*, 86(4), 900-927, 2011.
- 536 Backman, J., K. Moran, D. B. McInroy, L. A. Mayer, and the Expedition 302 Scientists.: Arctic  
537 Coring Expedition (ACEX), *Proc. Integr. Ocean Drill. Program*, 302, 2006.
- 538 Barker, P.F., Dalziel, I.W.D., Dinkelman, M.G., Elliot, D.H., Gombos, A.M., Lonardi, A., Plafker,  
539 G., Tarney, J., Thompson, R.W., Tjalsma, R.C. and Von der Borch, C.C.: Evolution of the  
540 southwestern Atlantic Ocean Basin: results of Leg 36, Deep Sea Drilling Project, Initial  
541 Reports of the Deep Sea Drilling Project, 36, 993-1014, 1977.
- 542 Barton, A.D., Irwin, A.J., Finkel, Z.V. and Stock, C.A.: Anthropogenic climate change drives shift  
543 and shuffle in North Atlantic phytoplankton communities. *Proceedings of the National  
544 Academy of Sciences*, 113(11), 2964-2969, 2016.

- 545 Bartoli, G., Sarnthein, M., Weinelt, M., Erlenkeuser, H., Garbe-Schönberg, D. and Lea, D.W.:  
546                 Final closure of Panama and the onset of northern hemisphere glaciation, *Earth and*  
547                 *Planetary Science Letters*, 237(1-2), 33-44, 2005.
- 548 Bartoli, G., Höönsch, B. and Zeebe, R.E., 2011. Atmospheric CO<sub>2</sub> decline during the Pliocene  
549                 intensification of Northern Hemisphere glaciations. *Paleoceanography*, 26(4).
- 550 Beaugrand, G., Reid, P.C., Ibanez, F., Lindley, J.A. and Edwards, M., 2002. Reorganization of  
551                 North Atlantic marine copepod biodiversity and climate. *Science*, 296(5573), pp.1692-  
552                 1694.
- 553 Berger, W.H., Killingley, J.S. and Vincent, E.: Stable isotopes in deep-sea carbonates-box core  
554                 erdc-92, west equatorial pacific, *Oceanologica Acta*, 1(2), 203-216, 1978.
- 555 Bijma, J., Hemleben, C., Huber, B.T., Erlenkeuser, H. and Kroon, D.: 1998. Experimental  
556                 determination of the ontogenetic stable isotope variability in two morphotypes of  
557                 Globigerinella siphonifera (d'Orbigny), *Marine Micropaleontology*, 35(3-4), 141-160, 1998.
- 558 Bijma, J., Spero, H.J. and Lea, D.W.: Reassessing foraminiferal stable isotope geochemistry:  
559                 Impact of the oceanic carbonate system (experimental results), in: *Use of proxies in*  
560                 *paleoceanography*, Springer, Berlin, Heidelberg, 489-512 pp., 1999.
- 561 Bindoff, N.L., Cheung, W.W., Kairo, J.G., Arístegui, J., Guinder, A., Hallberg, R., Hilmi, N.J.M.,  
562 Jiao, N., Karim, M.S., Levin, L. and O'Donoghue, S.: Changing ocean, marine  
563                 ecosystems, and dependent communities, *IPCC special report on the ocean and*  
564                 *cryosphere in a changing climate*, 477-587, 2019.
- 565 Birch, H., Coxall, H.K., Pearson, P.N., Kroon, D., and O'Regan, M.: Planktonic foraminifera stable  
566                 isotopes and water column structure: Disentangling ecological signals, *Marine*  
567                 *Micropaleontology*, 101, 127-145, doi:10.1016/j.marmicro.2013.02.002, 2013.

- 568 Boersma, A. and Silva, I.P.: Distribution of Paleogene planktonic foraminifera—analogies with the  
569 Recent?, *Palaeogeography, Palaeoclimatology, Palaeoecology*, 83(1-3), 29-47, 1991.
- 570 Boscolo-Galazzo, F., Crichton, K.A., Ridgwell, A., Mawbey, E.M., Wade, B.S. and Pearson, P.N.:  
571 Temperature controls carbon cycling and biological evolution in the ocean twilight zone,  
572 *Science*, 371(6534), 1148-1152, 2021.
- 573 Boscolo-Galazzo, F., Jones, A., Dunkley Jones, T., Crichton, K.A., Wade, B.S. and Pearson, P.N.:  
574 Late Neogene evolution of modern deep-dwelling plankton, *Biogeosciences*, 19(3), 743-  
575 762., 2022.
- 576 Bossio, A., Rakich El-Bied,K., Gianelli, L. Mazzei, R. Russo, A., and Salvatorini G.: Corrélation  
577 de quelques sections stratigraphiques du Mio-Pliocene de la zone Atlantique du Maroc  
578 avec les stratotypes du Bassin Méditerranéen sur la base de foraminifères planctoniques,  
579 nannoplancton calcaire et Ostracodes, *Atti della Societa Toscana Scienze Naturali*  
580 *Memorie Pisa*, 83, 121-137, 1976.
- 581 Bouvier-Soumagnac, Y. and Duplessy, J.C.: Carbon and oxygen isotopic composition of  
582 planktonic foraminifera from laboratory culture, plankton tows and recent sediment;  
583 implications for the reconstruction of paleoclimatic conditions and of the global carbon  
584 cycle, *The Journal of Foraminiferal Research*, 15(4), 302-320, 1985.
- 585 Brierley, C.M. and Fedorov, A.V.: Relative importance of meridional and zonal sea surface  
586 temperature gradients for the onset of the ice ages and Pliocene-Pleistocene climate  
587 evolution, *Paleoceanography*, 25(2), 2010.
- 588 Brombacher, A., Wilson, P.A., Bailey, I., and Ezard, T.H.: The breakdown of static and  
589 evolutionary allometries during climatic upheaval, *The American Naturalist*, 190(3), 350-  
590 362, 2017a.

- 591 Brombacher, A., Wilson, P.A., and Ezard, T.H., Calibration of the repeatability of foraminiferal test  
592 size and shape measures with recommendations for future use, *Marine*  
593 *Micropaleontology*, 133, 21-27, 2017b.
- 594 Brombacher, A., Elder, L.E., Hull, P.M., Wilson, P.A. and Ezard, T.H.: Calibration of test diameter  
595 and area as proxies for body size in the planktonic foraminifer *Globoconella*  
596 *puncticulata*, *Journal of Foraminiferal Research*, 48(3), 241-245, 2018.
- 597 Brombacher, A., Wilson, P.A., Bailey, I., and Ezard, T.H.: The dynamics of diachronous extinction  
598 associated with climatic deterioration near the Neogene/Quaternary boundary,  
599 *Paleoceanography and Paleoclimatology*, 36(6), p.e2020PA004205, 2021.
- 600 Brönniman, P., and Resig, J.: A Neogene Globigerinacean biochronologic time-scale for the  
601 southwestern Pacific: DSDP Leg 7, in: edited by Winterer, E.L., Riedel, W.R., et al., *Initial*  
602 *reports of the Deep Sea Drilling Project, Volume 7, Part 2: Washington, D.C., U.S.*  
603 *Government Printing Office*, 1235–1470 pp., 1971
- 604 Cannariato, K.G. and Ravelo, A.C.: Pliocene-Pleistocene evolution of eastern tropical Pacific  
605 surface water circulation and thermocline depth. *Paleoceanography*, 12(6), 805-820,  
606 1997.
- 607 Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M. and Palmer, T.M.:  
608 Accelerated modern human-induced species losses: Entering the sixth mass extinction,  
609 *Scientific Advances*, 1, doi:10.1126/sciadv1400253, 2015.
- 610 Chaisson, W.: Planktonic foraminiferal assemblages and palaeoceanographic change in the  
611 transtropical Pacific Ocean: a comparison of west (Leg 130) and east (Leg 138), latest  
612 Miocene to Pleistocene, *Proc. ODP Sci. Res.*, 138, 555-597, 1995.
- 613 Chaisson, W.P.: Vicarious living: Pliocene menardellids between an isthmus and an ice  
614 sheet, *Geology*, 31(12), 1085-1088, 2003.

- 615 Chaisson, W.P., and Leckie, R.M.: High resolution Neogene planktonic foraminifer biostratigraphy  
616 of Site 806, Ontong Java Plateau (western equatorial Pacific), in: Berger, W.H., Kroenke,  
617 L.W., et al., Proceedings of the Ocean Drilling Program, Scientific results, Volume 130:  
618 College Station, Texas, Ocean Drilling Program, 137–178 pp., 1993.
- 619 Chaisson, W.P., and Pearson, P.N.: Planktonic foraminifer biostratigraphy at Site 925: Middle  
620 Miocene–Pleistocene, edited by Shackleton, N.J., Curry, W.B., Richter, C., Bralower  
621 T.J., Proceeding of the Ocean Drilling Program, Scientific Results, 154, 3-31 pp., 1997.
- 622 Chaisson, W.P., and Ravelo, A.C.: Pliocene development of the east-west hydrographic gradient  
623 in the equatorial Pacific, Paleoceanography, 15(5), 497-505, 2000.
- 624 Chandler, M., Rind, D. and Thompson, R., 1994. Joint investigations of the middle Pliocene  
625 climate II: GISS GCM Northern Hemisphere results. *Global and Planetary Change*, 9(3-  
626 4), pp.197-219.
- 627 Cheung, W.W., Watson, R. and Pauly, D., 2013. Signature of ocean warming in global fisheries  
628 catch. *Nature*, 497(7449), pp.365-368.
- 629 Coates, A.G., and Obando, J.A.: The geologic evolution of the Central American isthmus, in:  
630 Evolution and environment in tropical America, edited by Jackson, J.B.C., Budd, A.F., and  
631 Coates, A.G., The University of Chicago Press, Chicago, Illinois, 21-56 pp., 1996.
- 632 Corfield, R.M., and Cartlidge, J.E.: Isotopic evidence for the depth stratification of fossil and recent  
633 Globigerinina: a review, *Historical Biology*, 5(1), 37-63, 1991.
- 634 Crame, J.A., and Rosen, B.R.: Cenozoic palaeogeography and the rise of modern biodiversity  
635 patterns, *Geological Society, London, Special Publications*, 194(1), 153-168, 2002.
- 636 Cramer, B.S., Toggweiler, J.R., Wright, J.D., Katz, M.E., and Miller, K.G.: Ocean overturning since  
637 the Late Cretaceous: Inferences from a new benthic foraminiferal isotope compilation,  
638 *Paleoceanography*, 24(4), 2009.

- 639 Cramer, B.S., Miller, K.G., Barrett, P.J., and Wright, J.D.: Late Cretaceous–Neogene trends in  
640 deep ocean temperature and continental ice volume: Reconciling records of benthic  
641 foraminiferal geochemistry ( $\delta^{18}\text{O}$  and Mg/Ca) with sea level history, *Journal of*  
642 *Geophysical Research: Oceans*, 116(C12), 2011.
- 643 Crundwell, M. P.: Pliocene and early Pleistocene planktic foraminifera: Important taxa and  
644 bioevents in ODP Hole 1123B, Chatham Rise, New Zealand, *GNS Science Report*  
645 2015/51, August 2015, 67, 2015a.
- 646 Crundwell, M. P.: Revised Pliocene and early Pleistocene planktic foraminiferal biostratigraphy,  
647 DSDP Site 284, Challenger Plateau, New Zealand, *GNS Science Internal Report* 2015/22,  
648 December 2015, 36, 2015b.
- 649 Crundwell, M.P.: *Globoconella pseudospinosa*, N. Sp.: a New Early Pliocene Planktonic  
650 Foraminifera from the Southwest Pacific, *Journal of Foraminiferal Research*, 48(4), 288-  
651 300, 2018.
- 652 Crundwell, M.P., and Nelson, C.S.: A magnetostratigraphically-constrained chronology for late  
653 Miocene bolboformids and planktic foraminifers in the temperate Southwest  
654 Pacific, *Stratigraphy*, 4(1), 1-34, 2007.
- 655 Crundwell, M.P., and Woodhouse, A.: A detailed biostratigraphic framework for 0-1.2 Ma  
656 Quaternary sediments of north-eastern Zealandia, *New Zealand Journal of Geology and*  
657 *Geophysics*, DOI:10.1080/00288306.2022.2054828, 2022a.
- 658 Crundwell, M.P., and Woodhouse, A.: Biostratigraphically constrained chronologies for  
659 Quaternary sequences from the Hikurangi margin of north-eastern Zealandia, *New*  
660 *Zealand Journal of Geology and Geophysics*, DOI:10.1080/00288306.2022.2101481,  
661 2022b.

- 662 Darling, K.F., and Wade, C.M.: The genetic diversity of planktic foraminifera and the global  
663 distribution of ribosomal RNA genotypes, *Marine Micropaleontology*, 67(3-4), 216-238,  
664 2008.
- 665 de Vargas, C., Norris, R., Zaninetti, L., Gibb, S.W., and Pawlowski, J.: Molecular evidence of  
666 cryptic speciation in planktonic foraminifers and their relation to oceanic  
667 provinces, *Proceedings of the National Academy of Sciences*, 96(6), 2864-2868, 1999.
- 668 de Vargas, C., Bonzon, M., Rees, N.W., Pawlowski, J., and Zaninetti, L.: A molecular approach  
669 to biodiversity and biogeography in the planktonic foraminifer *Globigerinella siphonifera*  
670 (d'Orbigny), *Marine Micropaleontology*, 45(2), 101-116, 2002.
- 671 Diepenbroek, M., Grobe, H., Reinke, M., Schindler, U., Schlitzer, R., Sieger, R., and Wefer, G.:  
672 PANGAEA—an information system for environmental sciences, *Computers &*  
673 *Geosciences*, 28(10), 1201-1210, 2002.
- 674 Dowsett, H.J., Robinson, M.M., Haywood, A.M., Hill, D.J., Dolan, A.M., Stoll, D.K., Chan, W.L.,  
675 Abe-Ouchi, A., Chandler, M.A., Rosenbloom, N.A. and Otto-Bliesner, B.L., 2012.  
676 Assessing confidence in Pliocene sea surface temperatures to evaluate predictive models.  
677 *Nature Climate Change*, 2(5), pp.365-371.
- 678 Drury, A.J., Lee, G.P., Pennock, G.M., and John, C.M.: Data report: Late Miocene to early  
679 Pliocene coccolithophore and foraminiferal preservation at Site U1338 from scanning  
680 electron microscopy, in: *Proceedings of the Integrated Ocean Drilling Program*, 320,  
681 *Integrated Ocean Drilling Program*, 1-14 pp., 2014.
- 682 Edgar, K.M., Bohaty, S.M., Gibbs, S.J., Sexton, P.F., Norris, R.D., and Wilson, P.A.: Symbiont  
683 'bleaching' in planktic foraminifera during the Middle Eocene Climatic  
684 Optimum, *Geology*, 41(1), 15-18, 2013a.

- 685 Edgar, K.M., Pälike, H., and Wilson, P.A.: Testing the impact of diagenesis on the  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$   
686 of benthic foraminiferal calcite from a sediment burial depth transect in the equatorial  
687 Pacific, *Paleoceanography*, 28(3), 468-480, 2013b.
- 688 Edgar, K.M., Hull, P.M., and Ezard, T.H.: Evolutionary history biases inferences of ecology and  
689 environment from  $\delta^{13}\text{C}$  but not  $\delta^{18}\text{O}$  values, *Nature communications*, 8(1), 1-9, 2017.
- 690 Edwards, M., Beaugrand, G., Kléparski, L., Hélaouët, P., and Reid, P.C.: Climate variability and  
691 multi-decadal diatom abundance in the Northeast Atlantic, *Communications Earth &*  
692 *Environment*, 3(1), 1-8, 2022.
- 693 Ericson, D.B., Wollin, G., and Wollin, J.: Coiling direction of *Globorotalia truncatulinoides* in deep-  
694 sea cores, *Deep Sea Research* (1953), 2(2), 152-158, 1955.
- 695 Ezard, T.H., Aze, T., Pearson, P.N., and Purvis, A.: Interplay between changing climate and  
696 species' ecology drives macroevolutionary dynamics. *science*, 332(6027), 349-351, 2011.
- 697 Fairbanks, R.G., Charles, C.D., and Wright, J.D., Origin of global meltwater pulses,  
698 in: *Radiocarbon after four decades*, Springer, New York, NY, 473-500 pp., 1992.
- 699 Falzoni, F., Petrizzo, M.R., and Valagussa, M.: A morphometric methodology to assess planktonic  
700 foraminiferal response to environmental perturbations: the case study of Oceanic Anoxic  
701 Event 2, Late Cretaceous, 2018.
- 702 Fedorov, A.V., Pacanowski, R.C., Philander, S.G., and Boccaletti, G.: The effect of salinity on the  
703 wind-driven circulation and the thermal structure of the upper ocean, *Journal of physical*  
704 *oceanography*, 34(9), 1949-1966, 2004.
- 705 Fedorov, A.V., Dekens, P.S., McCarthy, M., Ravelo, A.C., DeMenocal, P.B., Barreiro, M.,  
706 Pacanowski, R.C., and Philander, S.G.: The Pliocene paradox (mechanisms for a  
707 permanent El Niño), *Science*, 312(5779), 1485-1489, 2006.

- 708 Fedorov, A.V., Brierley, C.M., Lawrence, K.T., Liu, Z., Dekens, P.S., and Ravelo, A.C.: Patterns  
709 and mechanisms of early Pliocene warmth, *Nature*, 496(7443), 43-49, 2013.
- 710 Fenton, I.S., Woodhouse, A., Aze, T., Lazarus, D., Renaudie, J., Dunhill, A.M., Young, J.R., and  
711 Saupe, E.E.: Triton, a new species-level database of Cenozoic planktonic foraminiferal  
712 occurrences, *Scientific Data*, 8(1), 1-9, 2021.
- 713 Fiedler, P.C.: Seasonal climatologies and variability of the eastern tropical Pacific surface waters  
714 Technical Reports of the U.S. National Marine Fishery Service, 109, 1-65, 1992.
- 715 Fiedler, P.C., and Talley, L.D.: Hydrography of the eastern tropical Pacific: A review, *Progress in  
716 Oceanography*, 69(2-4), 143-180, 2006.
- 717 Flannery-Sutherland, J.T., Raja, N.B., Kocsis, Á, T., and Kiessling, W.: fossilbrush: An R package  
718 for automated detection and resolution of anomalies in palaeontological occurrence data,  
719 *Methods in Ecology and Evolution*, 00, 1-15, 2022.
- 720 Ford, H.L., Ravelo, A.C. and Hovan, S.: A deep Eastern Equatorial Pacific thermocline during the  
721 early Pliocene warm period, *Earth and Planetary Science Letters*, 355, 152-161, 2012.
- 722 Ford, H.L., Ravelo, A.C., Dekens, P.S., LaRiviere, J.P., and Wara, M.W.: The evolution of the  
723 equatorial thermocline and the early Pliocene El Padre mean state, *Geophysical Research  
724 Letters*, 42(12), 4878-4887, 2015.
- 725 Ford, H.L., Burls, N.J., Jacobs, P., Jahn, A., Caballero-Gill, R.P., Hodell, D.A., and Fedorov, A.V.:  
726 Sustained mid-Pliocene warmth led to deep water formation in the North Pacific, *Nature  
727 Geoscience*, 1-6, 2022.
- 728 Fox, L.R., and Wade, B.S.: Systematic taxonomy of early–middle Miocene planktonic foraminifera  
729 from the equatorial Pacific Ocean: Integrated Ocean Drilling Program, Site U1338, The  
730 *Journal of Foraminiferal Research*, 43(4), 374-405, 2013.

- 731 Fox, L., Stukins, S., Hill, T., and Miller, C.G.: Quantifying the effect of anthropogenic climate  
732 change on calcifying plankton, *Scientific Reports*, 10(1), 1-9, 2020.
- 733 Fraass, A.J., Kelly, D.C., and Peters, S.E.: Macroevolutionary history of the planktic foraminifera,  
734 *Annual Review of Earth and Planetary Sciences*, 43, 139-166, 2015.
- 735 Friesenhagen, T.: Test-size evolution of the planktonic foraminifer *Globorotalia menardii* in the  
736 eastern tropical Atlantic since the Late Miocene, *Biogeosciences*, 19(3), 777-805, 2022.
- 737 Frigola, A., Prange, M., and Schulz, M.: Boundary conditions for the middle Miocene climate  
738 transition (MMCT v1. 0), *Geoscientific Model Development*, 11(4), 1607-1626, 2018.
- 739 Garcia, H.E., Locarnini, R.A., Boyer, T.P., and Antonov, J.I.: *World Ocean Atlas 2005*. U.S.  
740 Government Printing Office, Washington, 2006.
- 741 Gaskell, D.E., Huber, M., O'Brien, C.L., Inglis, G.N., Acosta, R.P., Poulsen, C.J., and Hull, P.M.:  
742 The latitudinal temperature gradient and its climate dependence as inferred from  
743 foraminiferal  $\delta^{18}\text{O}$  over the past 95 million years, *Proceedings of the National Academy of  
744 Sciences*, 119(11), p.e2111332119, 2022.
- 745 Golledge, N.R., Keller, E.D., Gomez, N., Naughten, K.A., Bernales, J., Trusel, L.D., and Edwards,  
746 T.L.: Global environmental consequences of twenty-first-century ice-sheet melt, *Nature*,  
747 566(7742), 65-72, 2019.
- 748 Groeneveld, J., Steph, S., Tiedemann, R., Garbe-Schönberg, C., Nürnberg, D. and Sturm, A.:  
749 Pliocene mixed-layer oceanography for Site 1241, using combined Mg/Ca and  $\delta^{18}\text{O}$   
750 analyses of *Globigerinoides sacculifer*, in: *Proceedings of the Ocean Drilling Program: Scientific Results*, 202, Texas A&M University, 1-27 pp., 2006.
- 752 Groeneveld, J., De Vleeschouwer, D., McCaffrey, J.C., and Gallagher, S.J. Dating the northwest  
753 shelf of Australia since the Pliocene, *Geochemistry, Geophysics, Geosystems*, 22(3),  
754 p.e2020GC009418, 2021.
- 755 Hallock, P., and Larsen, A.R.: Coiling direction in Amphistegina, *Marine Micropaleontology*, 4, 33-  
756 44, 1979.

- 757 Hamon, N., Sepulchre, P., Lefebvre, V., and Ramstein, G.: The role of eastern Tethys seaway  
758 closure in the Middle Miocene Climatic Transition (ca. 14 Ma), *Climate of the Past*, 9(6),  
759 2687-2702, 2013.
- 760 Haywood, A.M., Sellwood, B.W. and Valdes, P.J., 2000. Regional warming: Pliocene (3 Ma)  
761 paleoclimate of Europe and the Mediterranean. *Geology*, 28(12), pp.1063-1066.
- 762 Haywood, A.M., Dowsett, H.J. and Dolan, A.M., 2016. Integrating geological archives and climate  
763 models for the mid-Pliocene warm period. *Nature communications*, 7(1), pp.1-14.
- 764 Haug, G.H., and Tiedemann, R.: Effect of the formation of the Isthmus of Panama on Atlantic  
765 Ocean thermohaline circulation, *Nature*, 393(6686), 673-676, 1998.
- 766 Haug, G.H., Tiedemann, R., Zahn, R., and Ravelo, A.C.: Role of Panama uplift on oceanic  
767 freshwater balance, *Geology*, 29(3), 207-210, 2001.
- 768 Hayashi, T., Yamanaka, T., Hikasa, Y., Sato, M., Kuwahara, Y., and Ohno, M. Latest Pliocene  
769 Northern Hemisphere glaciation amplified by intensified Atlantic meridional overturning  
770 circulation, *Communications Earth & Environment*, 1(1), 1-10, 2020.
- 771 Herbert, T.D., Peterson, L.C., Lawrence, K.T., and Liu, Z.: Tropical ocean temperatures over the  
772 past 3.5 million years, *Science*, 328(5985), 1530-1534, 2010.
- 773 Hodell, D.A., and Vayavananda, A.: Middle Miocene paleoceanography of the western equatorial  
774 Pacific (DSDP site 289) and the evolution of Globorotalia (Fohsella), *Marine  
775 Micropaleontology*, 22(4), 279-310, 1993.
- 776 Holbourn, A., Kuhnt, W., Kochhann, K.G., Andersen, N., and Sebastian Meier, K.J.: Global  
777 perturbation of the carbon cycle at the onset of the Miocene Climatic  
778 Optimum, *Geology*, 43(2), 123-126, 2015.

- 779 Hornbrook, N.D.: Late Miocene to Pleistocene Globorotalia (Foraminiferida) from DSDP Leg 29,  
780 Site 284, Southwest Pacific, New Zealand Journal of Geology and Geophysics, 25(1), 83-  
781 99, 1982.
- 782 Hu, A., Meehl, G.A., Han, W., and Yin, J.: Effect of the potential melting of the Greenland Ice  
783 Sheet on the Meridional Overturning Circulation and global climate in the future, Deep Sea  
784 Research Part II: Topical Studies in Oceanography, 58(17-18), 1914-1926, 2011.
- 785 Huber, B.T., Bijma, J., and Darling, K.: Cryptic speciation in the living planktonic foraminifer  
786 Globigerinella siphonifera (d'Orbigny), Paleobiology, 23(1), 33-62, 1997.
- 787 Hull, P.M., and Norris, R.D.: Evidence for abrupt speciation in a classic case of gradual evolution,  
788 Proceedings of the National Academy of Sciences, 106(50), 21224-21229, 2009.
- 789 Hupp, B.N., Kelly, D.C., and Williams, J.W.: Isotopic filtering reveals high sensitivity of planktic  
790 calcifiers to Paleocene–Eocene thermal maximum warming and acidification, PNAS,  
791 119(9), e2115561119, 2022.
- 792 IPCC, 2022. AR6 Synthesis Report: Climate Change 2022
- 793 Jenkins, D.G., and Orr, W.N.: Planktonic foraminiferal biostratigraphy of the eastern equatorial  
794 Pacific: DSDP 9, in: Initial reports of the Deep Sea Drilling Project, Volume 9 edited by  
795 Hays, J.D., et al., Washington, D.C., U.S. Government Printing Office, 1057–1196 pp.,  
796 1972.
- 797 Jiang, D., Wang, H., Ding, Z., Lang, X. and Drange, H., 2005. Modeling the middle Pliocene  
798 climate with a global atmospheric general circulation model. *Journal of Geophysical*  
799 *Research: Atmospheres*, 110(D14).
- 800 Jonkers, L., Hillebrand, H., and Kucera, M.: Global change drives modern plankton communities  
801 away from the pre-industrial state, Nature, 570(7761), 372-375, 2019.

- 802 Kaneps, A.G.: Cenozoic planktonic foraminifera from Antarctic deep-sea sediments, Leg 28,  
803 DSDP, Initial Reports of the Deep Sea Drilling Project, 28, 573-583, 1975.
- 804 Kearns, L.E., Bohaty, S.M., Edgar, K.M., Nogué, S., and Ezard, T.H.: Searching for Function:  
805 Reconstructing Adaptive Niche Changes Using Geochemical and Morphological Data in  
806 Planktonic Foraminifera, *Frontiers in Ecology and Evolution*, 9, 679722, 2021.
- 807 Kearns, L.E., Bohaty, S.M., Edgar, K.M., and Ezard, T.H.G.: Small but mighty: how overlooked  
808 small species maintain community structure through middle Eocene climate change,  
809 *Paleobiology*, 1-22, 2022.
- 810 Keigwin, L. D., Jr.: Pliocene closing of the Isthmus of Panama, based on biostratigraphic evidence  
811 from nearby Pacific Ocean and Caribbean Sea cores, Geological Society of America  
812 (GSA), Boulder, CO, United States, *Geology* (Boulder), 6 (10), 630-634, georefid:1978-  
813 036437, 1978.
- 814 Keigwin, L.D.: Neogene planktonic foraminifers from Deep Sea Drilling Project sites 502 and 503,  
815 Initial Reports of the Deep Sea Drilling Project, 68, 269-288, 1982.
- 816 Keller, G.: Biochronology and paleoclimatic implications of middle Eocene to Oligocene planktic  
817 foraminiferal faunas, *Marine Micropaleontology*, 7(6), 463-486, 1983.
- 818 Keller, G.: Depth stratification of planktonic foraminifers in the Miocene ocean, *The Miocene*  
819 ocean: paleoceanography and biogeography, 163, 177-196, 1985.
- 820 Keller, G., and Savin, S.M.: Evolution of the Miocene ocean in the eastern North Pacific as inferred  
821 from oxygen and carbon isotopic ratios of foraminifera, *The Miocene Ocean: Paleoceanography and Biogeography*, 163, 83, 1985.
- 823 Keller, G., Zenker, C.E., and Stone, S.M.: Late Neogene history of the Pacific-Caribbean  
824 gateway, *Journal of South American Earth Sciences*, 2(1), 73-108, 1989.
- 825 Keller, G., MacLeod, N., and Barrera, E.: Eocene-Oligocene faunal turnover in planktic  
826 foraminifer, and Antarctic glaciation, in: *Eocene-Oligocene climatic and biotic evolution*  
827 edited by Prothero, D.R., and Berggren, W.A., Princeton University Press, Princeton, 218-  
828 244 pp., 1992.

- 829 Kennett, J.P. & Srinivasan, M.S.: Neogene planktonic foraminifera. A phylogenetic atlas,  
830 Hutchinson Ross Pub. Co., 265, 1983.
- 831 Kim, S.T., and O'Neil, J.R.: Equilibrium and nonequilibrium oxygen isotope effects in synthetic  
832 carbonates, *Geochimica et cosmochimica acta*, 61(16), 3461-3475, 1997.
- 833 Kleiven, H.F., Jansen, E., Fronval, T., and Smith, T.M.: Intensification of Northern Hemisphere  
834 glaciations in the circum Atlantic region (3.5–2.4 Ma)–ice rafted detritus evidence,  
835 *Palaeogeography, Palaeoclimatology, Palaeoecology*, 184(3-4), 213-223, 2002.
- 836 Knappertsbusch, M.: Morphological variability of *Globorotalia menardii* (planktonic foraminifera)  
837 in two DSDP cores from the Caribbean Sea and the Eastern Equatorial Pacific, *Carnets*  
838 de géologie, (A04), 1-34, 2007.
- 839 Knappertsbusch, M.: Evolutionary prospection in the Neogene planktic foraminifer *Globorotalia*  
840 *menardii* and related forms from ODP Hole 925B (Ceara Rise, western tropical Atlantic):  
841 evidence for gradual evolution superimposed by long distance dispersal?, *Swiss Journal*  
842 of *Palaeontology*, 135(2), 205-248, 2006.
- 843 Kotov, S., and Paelike, H.: QAnalySeries-a cross-platform time series tuning and analysis tool,  
844 In: AGU Fall Meeting Abstracts (Vol. 2018, pp. PP53D-1230), 2018.
- 845 Kucera, M., and Schönfeld, J.: The origin of modern oceanic foraminiferal faunas and Neogene  
846 climate change, *Deep-Time Perspectives on Climate Change: Marrying the Signal from*  
847 *Computer Models and Biological Proxies*, London: The Geological Society, 409-426,  
848 2007.
- 849 Lam, A.R., and Leckie, R.M.: Late Neogene and Quaternary diversity and taxonomy of subtropical  
850 to temperate planktic foraminifera across the Kuroshio Current Extension, northwest  
851 Pacific Ocean, *Micropaleontology*, 66(3), 177-268, 2020.

- 852 Lamy, F., Winckler, G., and Alvarez Zarikian, C.A.: Expedition 383 Preliminary Report: Dynamics  
853 of the Pacific Antarctic Circumpolar Current (DYNAPACC), Preliminary report, 383, 2019.
- 854 Lawrence, K.T., Liu, Z., and Herbert, T.D.: Evolution of the eastern tropical Pacific through Plio-  
855 Pleistocene glaciation, *Science*, 312(5770), 79-83, 2006.
- 856 Lazarus, D.: Neptune: a marine micropaleontology database, *Mathematical Geology*, 26(7), 817-  
857 832, 1994.
- 858 Lazarus, D., Weinkauf, M., and Diver, P.: Pacman profiling: a simple procedure to identify  
859 stratigraphic outliers in high-density deep-sea microfossil dataPACMAN  
860 PROFILING, *Paleobiology*, 38(1), 144-161, 2012.
- 861 Levin, M., Klar, A.J., and Ramsdell, A.F.: Introduction to provocative questions in left-right  
862 asymmetry, *Philosophical Transactions of the Royal Society B: Biological  
863 Sciences*, 371(1710), 20150399, 2016.
- 864 Liow, L.H., Skaug, H.J., Ergon, T., and Schweder, T.: Global occurrence trajectories of  
865 microfossils: environmental volatility and the rise and fall of individual  
866 species, *Paleobiology*, 36(2), 224-252, 2010.
- 867 Lohmann, G.P.: A model for variation in the chemistry of planktonic foraminifera due to secondary  
868 calcification and selective dissolution, *Paleoceanography*, 10(3), 445-457, 1995.
- 869 Lowery, C.M., and Fraass, A.J. Morphospace expansion paces taxonomic diversification after  
870 end Cretaceous mass extinction, *Nature Ecology & Evolution*, 3(6), 900-904, 2019.
- 871 Lowery, C.M., Bown, P.R., Fraass, A.J., and Hull, P.M.: Ecological response of plankton to  
872 environmental change: thresholds for extinction, *Annual Review of Earth and Planetary  
873 Sciences*, 48, 403-429, 2020.

- 874 Lutz, B.P.: Low-latitude northern hemisphere oceanographic and climatic responses to early  
875 shoaling of the Central American Seaway, *Stratigraphy*, 7(2), 151, 2010.
- 876 Lyle, M., Drury, A.J., Tian, J., Wilkens, R., and Westerhold, T.: Late Miocene to Holocene high-  
877 resolution eastern equatorial Pacific carbonate records: stratigraphy linked by dissolution  
878 and paleoproductivity, *Climate of the Past*, 15(5), 1715-1739, 2019.
- 879 Malmgren, B.A., and Berggren, W.A.: Evolutionary changes in some Late Neogene planktonic  
880 foraminiferal lineages and their relationships to paleoceanographic changes,  
881 *Paleoceanography*, 2(5), 445-456, 1987.
- 882 Maslin, M.A., Haug, G.H., Sarnthein, M., and Tiedemann, R.: The progressive intensification of  
883 northern hemisphere glaciation as seen from the North Pacific, *Geologische  
Rundschau*, 85(3), 452-465, 1996.
- 885 Matthews, K.J., Maloney, K.T., Zahirovic, S., Williams, S.E., Seton, M., and Mueller, R.D.: Global  
886 plate boundary evolution and kinematics since the late Paleozoic, *Global and Planetary  
Change*, 146, 226-250, 2016.
- 888 McKay, R.M., De Santis, L., Kulhanek, D.K., Ash, J.L., Beny, F., Browne, I.M., Cortese, G.,  
889 Cordeiro de Sousa, I.M., Dodd, J.P., Esper, O.M., and Gales, J.A.: Expedition 374  
890 summary, *Proceedings of the International Ocean Discovery Program*, 2019.
- 891 Medina-Elizalde, M., Lea, D.W., and Fantle, M.S.: Implications of seawater Mg/Ca variability for  
892 Plio-Pleistocene tropical climate reconstruction, *Earth and Planetary Science  
Letters*, 269(3-4), 585-595, 2008.
- 894 Methner, K., Campani, M., Fiebig, J., Löffler, N., Kempf, O., and Mulch, A.: Middle Miocene long-  
895 term continental temperature change in and out of pace with marine climate  
896 records, *Scientific Reports*, 10(1), 1-10, 2020.

- 897 Molina, E., Gonzalvo, C., and Keller, G.: The Eocene-Oligocene planktic foraminiferal transition:  
898 extinctions, impacts and hiatuses, *Geological Magazine*, 130(4), 483-499, 1993.
- 899 Molnar, P.: Closing of the Central American Seaway and the Ice Age: A critical  
900 review, *Paleoceanography*, 23(2), 2008.
- 901 Morard, R., Quillevere, F., Escarguel, G., Ujiie, Y., de Garidel-Thoron, T., Norris, R.D., and de  
902 Vargas, C.: Morphological recognition of cryptic species in the planktonic foraminifer  
903 *Orbulina universa*, *Marine Micropaleontology*, 71(3-4), 148-165, 2009.
- 904 Morard, R., Quillevere, F., Escarguel, G., de Garidel-Thoron, T., de Vargas, C., and Kucera, M.:  
905 Ecological modeling of the temperature dependence of cryptic species of planktonic  
906 Foraminifera in the Southern Hemisphere, *Palaeogeography, Palaeoclimatology,*  
907 *Palaeoecology*, 391, 13-33, 2013.
- 908 Morard, R., Füllberg, A., Brummer, G.J.A., Greco, M., Jonkers, L., Wizemann, A., Weiner, A.K.,  
909 Darling, K., Siccha, M., Ledevin, R., and Kitazato, H.: Genetic and morphological  
910 divergence in the warm-water planktonic foraminifera genus *Globigerinoides*, *PloS*  
911 one, 14(12), e0225246, 2019.
- 912 Mudelsee, M. and Raymo, M.E., 2005. Slow dynamics of the Northern Hemisphere glaciation.  
913 *Paleoceanography*, 20(4).
- 914 Nirmal, B., Mohan, K., Prakasam, M., Tripathi, A., Mortyn, P.G., and Rodríguez-Sanz, L.:  
915 Pleistocene surface-ocean changes across the Southern subtropical front recorded by  
916 cryptic species of *Orbulina universa*, *Marine Micropaleontology*, 168, 102056, 2021.
- 917 Norris, R.D.: Symbiosis as an evolutionary innovation in the radiation of Paleocene planktic  
918 foraminifera, *Paleobiology*, 461-480, 1996.
- 919 Norris, R.D.: Hydrographic and tectonic control of plankton distribution and evolution. In  
920 *Reconstructing Ocean History*, Springer, Boston, MA, 173-193 pp., 1999.

- 921 Norris, R.D.: Pelagic species diversity, biogeography, and evolution, *Paleobiology*, 26(4), 236-  
922 258, 2000.
- 923 Norris, R.D., and Hull, P.M.: The temporal dimension of marine speciation, *Evolutionary  
924 Ecology*, 26(2), 393-415, 2012.
- 925 Norris, R.D., and Nishi, H.: Evolutionary trends in coiling of tropical Paleogene planktic  
926 foraminifera, *Paleobiology*, 27(2), 327-347, 2001.
- 927 Norris, R.D., Corfield, R.M., and Cartlidge, J.E.: Evolution of depth ecology in the planktic  
928 foraminifera lineage *Globorotalia* (*Fohsella*), *Geology*, 21(11), 975-978, 1993.
- 929 Norris, R.D., Corfield, R.M., and Cartlidge, J.E.: Evolutionary ecology of *Globorotalia*  
930 (*Globoconella*)(planktic foraminifera), *Marine Micropaleontology*, 23(2), 121-145., 1994.
- 931 Norris, R.D., Corfield, R.M., and Cartlidge, J.: What is gradualism? Cryptic speciation in  
932 globorotaliid foraminifera, *Paleobiology*, 386-405, 1996.
- 933 Norris, R.D., Turner, S.K., Hull, P.M., and Ridgwell, A.: Marine ecosystem responses to Cenozoic  
934 global change, *Science*, 341(6145), 492-498, 2013.
- 935 O'Dea, A., Lessios, H.A., Coates, A.G., Eytan, R.I., Restrepo-Moreno, S.A., Cione, A.L., Collins,  
936 L.S., De Queiroz, A., Farris, D.W., Norris, R.D., and Stallard, R.F.: Formation of the  
937 Isthmus of Panama, *Science Advances*, 2(8), p.e1600883, 2016.
- 938 Öğretmen, N., Schiebel, R., Jochum, K.P., Stoll, B., Weis, U., Repschläger, J., Jentzen, A., Galer,  
939 S., and Haug, G.H.: Deep thermohaline circulation across the closure of the Central  
940 American Seaway, *Paleoceanography and Paleoclimatology*, 35(12), p.e2020PA004049,  
941 2020.
- 942 Olsson, R.K.: Cenozoic planktonic Foraminifera: a paleobiogeographic summary, *Studies in  
943 Geology, Notes for a Short Course*, 6, 127-147, 1982.

- 944 Opdyke, B.N., and Pearson, P.N.: Data report: Geochemical analysis of multiple planktonic  
945 foraminifer species at discrete time intervals, in: Proceedings of the Ocean Drilling  
946 Program. Scientific results, 144, 993-995 pp., 1995.
- 947 Pagani, M., Liu, Z., LaRiviere, J. and Ravelo, A.C., 2010. High Earth-system climate sensitivity  
948 determined from Pliocene carbon dioxide concentrations. *Nature Geoscience*, 3(1), pp.27-  
949 30.
- 950 Pälike, H., Lyle, M., Nishi, H., Raffi, I., Gamage, K., Klaus, A., and the Expedition 320/321  
951 Scientists.: Site 1338: Proceedings of the Integrated Ocean Drilling Program, Volume  
952 320/321, doi:10.2204/ iodp.proc.320321.101.2010., 2010.
- 953 Pearson, P.N., and Ezard, T.H.: Evolution and speciation in the Eocene planktonic foraminifer  
954 Turborotalia, *Paleobiology*, 40(1), 130-143, 2014.
- 955 Pearson, P.N., and Penny, L.: Coiling directions in the planktonic foraminifer Pulleniatina: A  
956 complex eco-evolutionary dynamic spanning millions of years, *PLoS one*, 16(4),  
957 p.e0249113, 2021.
- 958 Pearson, P.N., and Shackleton, N.J.: Neogene multispecies planktonic foraminifer stable isotope  
959 record, Site 871, Limalok Guyot, in: Proceedings of the Ocean Drilling Program. Scientific  
960 Results, 144, 401-410 pp., 1995.
- 961 Pérez-Angel, L.C., and Molnar, P.: Sea surface temperatures in the Eastern Equatorial Pacific  
962 and surface temperatures in the Eastern Cordillera of Colombia during El Niño:  
963 Implications for Pliocene conditions, *Paleoceanography*, 32(11), 1309-1314, 2017.
- 964 Peters, S.E., Kelly, D.C., and Fraass, A.J., 2013. Oceanographic controls on the diversity and  
965 extinction of planktonic foraminifera, *Nature*, 493(7432), 398-401, 2013.
- 966 Philander, S.G., and Fedorov, A.V.: Role of tropics in changing the response to Milankovich  
967 forcing some three million years ago, *Paleoceanography*, 18(2), 2003.

- 968 Pinsky, M.L., Reygondeau, G., Caddell, R., Palacios-Abrantes, J., Spijkers, J., and Cheung,  
969 W.W.: Preparing ocean governance for species on the move, *Science*, 360(6394), 1189-  
970 1191, 2018.
- 971 Prentice, M.L., and Matthews, R.K.: Cenozoic ice-volume history: development of a composite  
972 oxygen isotope record, *Geology*, 16(11), 963-966, 1988.
- 973 Purich, A., England, M.H., Cai, W., Sullivan, A., and Durack, P.J.: Impacts of broad-scale surface  
974 freshening of the Southern Ocean in a coupled climate model, *Journal of Climate*, 31(7),  
975 2613-2632, 2018.
- 976 Raffi, I., Wade, B.S., Pälike, H., Beu, A.G., Cooper, R., Crundwell, M.P., Krijgsman, W., Moore,  
977 T., Raine, I., Sardella, R., and Vernyhorova, Y.V.: The Neogene period, in: *Geologic time*  
978 *scale 2020*, Elsevier, 1141-1215 pp., 2020.
- 979 Rasmussen, T.L., and Thomsen, E.: Holocene temperature and salinity variability of the Atlantic  
980 Water inflow to the Nordic seas, *The Holocene*, 20(8), 1223-1234, 2010.
- 981 Ravelo, A.C., and Fairbanks, R.G.: Oxygen isotopic composition of multiple species of planktonic  
982 foraminifera: Recorders of the modern photic zone temperature  
983 gradient, *Paleoceanography*, 7(6), 815-831, 1992.
- 984 Ravelo, A.C., and Fairbanks, R.G.: Carbon isotopic fractionation in multiple species of planktonic  
985 foraminifera from core-tops in the tropical Atlantic, *Oceanographic Literature*  
986 *Review*, 10(42), 854, 1995.
- 987 Ravelo, A. C., and Shackleton, N. J.: Evidence for surface-water circulation changes at site 851  
988 in the eastern tropical Pacific Ocean, *Proceedings of the Ocean Drilling Program Scientific*  
989 *Results*, 138, 503–516, 1995.
- 990 Ravelo, A.C., and Hillaire-Marcel, C.: Chapter Eighteen: The use of oxygen and carbon isotopes  
991 of foraminifera in Paleoceanography, *Developments in Marine Geology*, 1, 735-764, 2007.

- 992 Rebotim, A., Voelker, A.H., Jonkers, L., Waniek, J.J., Meggers, H., Schiebel, R., Fraile, I., Schulz,  
993 M., and Kucera, M.: Factors controlling the depth habitat of planktonic foraminifera in the  
994 subtropical eastern North Atlantic, *Biogeosciences*, 14(4), 827-859, 2017.
- 995 Renaudie, J., Lazarus, D.: and Diver, P.: NSB (Neptune Sandbox Berlin): an expanded and  
996 improved database of marine planktonic microfossil data and deep-sea stratigraphy,  
997 *Palaeontol. Electron.*, 23, p.a11, 2020.
- 998 Rhein, M., Rintoul, S.R., Aoki, S., Campos, E., Chambers, D., Feely, R.A., Gulev, S., Johnson,  
999 G.C., Josey, S.A., Kostianoy, A., and Mauritzen, C.: Observations: ocean, in: 'Climate  
1000 Change 2013: the Physical Science Basis. Contribution of Working Group I to the Fifth  
1001 Assessment Report of the Intergovernmental Panel on Climate Change'. Cambridge  
1002 University Press, Cambridge, United Kingdom and New York, NY, USA, 2013.
- 1003 Rillo, M.C., Sugawara, M.T., Cabella, B., Jonkers, L., Baranowski, U.K., Kučera, M., and Ezard,  
1004 T.H.: On the mismatch in the strength of competition among fossil and modern species of  
1005 planktonic Foraminifera, *Global Ecology and Biogeography*, 28(12), 1866-1878, 2019.
- 1006 Rincón-Martínez, D., Steph, S., Lamy, F., Mix, A., and Tiedemann, R.: Tracking the equatorial  
1007 front in the eastern equatorial Pacific Ocean by the isotopic and faunal composition of  
1008 planktonic foraminifera, *Marine Micropaleontology*, 79(1-2), 24-40, 2011.
- 1009 Rögl, F.: Mediterranean and Paratethys. Facts and hypotheses of an Oligocene to Miocene  
1010 paleogeography (short overview), *Geologica carpathica*, 50(4), 339-349, 1999.
- 1011 Rosenthal, Y., Holbourn, A.E., Kulhanek, D.K., Aiello, I.W., Babila, T.L., Bayon, G., Beaufort, L.,  
1012 Bova, S.C., Chun, J.-H., Dang, H., Drury, A.J., Dunkley Jones, T., Eichler, P.P.B.,  
1013 Fernando, A.G.S., Gibson, K.A., Hatfield, R.G., Johnson, D.L., Kumagai, Y., Li, T., Linsley,  
1014 B.K., Meinicke, N., Mountain, G.S., Opdyke, B.N., Pearson, P.N., Poole, C.R., Ravelo,  
1015 A.C., Sagawa, T., Schmitt, A., Wurtzel, J.B., Xu, J., Yamamoto, M., and Zhang, Y.G.,

- 1016            2018. Site U1482. In Rosenthal, Y., Holbourn, A.E., Kulhanek, D.K., and the Expedition  
1017            363 Scientists, Western Pacific Warm Pool, Proceedings of the International Ocean  
1018            Discovery Program, 363: College Station, TX (International Ocean Discovery Program),  
1019            <https://doi.org/10.14379/iodp.proc.363.103.2018>, 2018.
- 1020            Saito T., Burckle L.H., and Hays J.D.: Late Miocene to Pleistocene biostratigraphy of equatorial  
1021            Pacific sediments, in: Late Neogene Epoch Boundaries, edited by Saito, T., New York:  
1022            American Museum of Natural History; 226–244, 1975.
- 1023            Schiebel, R., and Hemleben, C.: Planktic foraminifers in the modern ocean, Berlin, Springer, 1-  
1024            358, 2017.
- 1025            Schmidt, D.N., Thierstein, H.R., Bollmann, J., and Schiebel, R.: Abiotic forcing of plankton  
1026            evolution in the Cenozoic, *Science*, 303(5655), 207-210, 2004a.
- 1027            Schmidt, D.N., Thierstein, H.R., and Bollmann, J.: The evolutionary history of size variation of  
1028            planktic foraminiferal assemblages in the Cenozoic, *Palaeogeography,  
1029            Palaeoclimatology, Palaeoecology*, 212(1-2), 159-180, 2004b.
- 1030            Schmidt, D.N., Caromel, A.G.M., Seki, O., Rae, J.W.B., and Renaud, S.: Morphological response  
1031            of planktic foraminifers to habitat modifications associated with the emergence of the  
1032            Isthmus of Panama, *Marine Micropaleontology*, 128, 28-38, 2016.
- 1033            Scott, G.H.: Tempo and stratigraphic record of speciation in *Globorotalia puncticulata*, *The  
1034            Journal of Foraminiferal Research*, 12(1), 1-12, 1982.
- 1035            Scott, G.H., Bishop, S., and Burt, B.J.: Guide to some Neogene Globorotalids (Foraminiferida)  
1036            from New Zealand, *New Zealand Geological Survey*, 1990.
- 1037            Seki, O., Foster, G.L., Schmidt, D.N., Mackensen, A., Kawamura, K. and Pancost, R.D., 2010.  
1038            Alkenone and boron-based Pliocene pCO<sub>2</sub> records. *Earth and Planetary Science Letters*,  
1039            292(1-2), pp.201-211.

- 1040 Seki, O., Schmidt, D.N., Schouten, S., Hopmans, E.C., Sinnighe Damsté, J.S., and Pancost,  
1041 R.D.: Paleoceanographic changes in the Eastern Equatorial Pacific over the last 10 Myr,  
1042 *Paleoceanography*, 27(3), 2012.
- 1043 Sellén, E., O'Regan, M., and Jakobsson, M.: Spatial and temporal Arctic Ocean depositional  
1044 regimes: a key to the evolution of ice drift and current patterns, *Quaternary Science*  
1045 *Reviews*, 29(25-26), 3644-3664, 2010.
- 1046 Sexton, P.F., and Norris, R.D.: High latitude regulation of low latitude thermocline ventilation and  
1047 planktic foraminifer populations across glacial–interglacial cycles, *Earth and Planetary*  
1048 *Science Letters*, 311(1-2), 69-81, 2011.
- 1049 Sexton, P.F., Wilson, P.A., and Pearson, P.N.: Microstructural and geochemical perspectives on  
1050 planktic foraminiferal preservation: “Glassy” versus “Frosty”, *Geochemistry, Geophysics,*  
1051 *Geosystems*, 7(12), 2006.
- 1052 Shackleton, N.J., Backman, J., Zimmerman, H.T., Kent, D.V., Hall, M.A., Roberts, D.G., Schnitker,  
1053 D., Baldauf, J.G., Desprairies, A., Homrighausen, R., and Huddlestun, P.: Oxygen isotope  
1054 calibration of the onset of ice-rafting and history of glaciation in the North Atlantic  
1055 region, *Nature*, 307(5952), 620-623, 1984.
- 1056 Shackleton, N.J., Hall, M.A., and Pate, D.: 15. Pliocene stable isotope stratigraphy of Site 846,  
1057 in: *Proc. Ocean Drill. Program Sci. Results*, 138, 337-355 pp., 1995.
- 1058 Shaw, J.O., D'haenens, S., Thomas, E., Norris, R.D., Lyman, J.A., Bornemann, A., and Hull, P.M.:  
1059 Photosymbiosis in planktonic foraminifera across the Paleocene–Eocene thermal  
1060 maximum, *Paleobiology*, 47(4), 632-647, 2021.
- 1061 Shevenell, A.E., Kennett, J.P., and Lea, D.W.: Middle Miocene southern ocean cooling and  
1062 Antarctic cryosphere expansion, *Science*, 305(5691), 1766-1770, 2004.

- 1063 Si, W., and Aubry, M.P.: Vital effects and ecologic adaptation of photosymbiont-bearing planktonic  
1064 foraminifera during the Paleocene-Eocene thermal maximum, implications for  
1065 paleoclimate, *Paleoceanography and Paleoclimatology*, 33(1), 112-125, 2018.
- 1066 Siccha, M., and Kucera, M.: ForCenS, a curated database of planktonic foraminifera census  
1067 counts in marine surface sediment samples, *Scientific Data*, 4(1), 1-12, 2017.
- 1068 Slater, G.J., Goldbogen, J.A., and Pyenson, N.D.: Independent evolution of baleen whale  
1069 gigantism linked to Plio-Pleistocene ocean dynamics, *Proceedings of the Royal Society*  
1070 *B: Biological Sciences*, 284(1855), 20170546, 2017.
- 1071 Sosdian, S.M., and Lear, C.H.: Initiation of the western Pacific warm pool at the middle Miocene  
1072 climate transition?, *Paleoceanography and Paleoclimatology*, 35(12), p.e2020PA003920,  
1073 2020.
- 1074 Spero, H.J.: Do planktic foraminifera accurately record shifts in the carbon isotopic composition  
1075 of seawater  $\Sigma\text{CO}_2$ ?, *Marine Micropaleontology*, 19(4), 275-285, 1992.
- 1076 Spero, H.J., and Lea, D.W.: Intraspecific stable isotope variability in the planktic foraminifera  
1077 *Globigerinoides sacculifer*: Results from laboratory experiments, *Marine*  
1078 *Micropaleontology*, 22(3), 221-234, 1993.
- 1079 Spero, H.J., and Williams, D.F.: Extracting Environmental information from planktonic  
1080 foraminiferal delta-C-13 data, *Nature*, 335, 717–719, 1988.
- 1081 Spero, H.J., and Williams, D.F.: Opening the carbon isotope “vital effects” black box, 1. Seasonal  
1082 temperatures in the euphotic zone, *Paleoceanography*, 4, 593–601, 1989.
- 1083 Spero, H.J., Leche, I., and Williams, D.F.: Opening the carbon isotope ‘vital affects’ box, 2,  
1084 quantitative model for interpreting foraminiferal carbon isotope data, *Paleoceanography*  
1085 6, 639–655, 1991.

- 1086 Spezzaferri, S., Coxall, H.K., Olsson, R.K., Hemleben, C., and Wade, B.: Taxonomy,  
1087 biostratigraphy, and phylogeny of Oligocene Globigerina, Globigerinella, and Quiltyella n.  
1088 gen., in: *Atlas of Oligocene Planktonic Foraminifera*, edited by Wade, B.S., Olsson, R.K.,  
1089 Pearson, P.N., Huber, B.T., Berggren, W.A., 179-214 pp., 2018.
- 1090 Steinhorsdottir, M., Coxall, H.K., De Boer, A.M., Huber, M., Barbolini, N., Bradshaw, C.D., Burls,  
1091 N.J., Feakins, S.J., Gasson, E., Henderiks, J., and Holbourn, A.E.: The Miocene: the future  
1092 of the past, *Paleoceanography and Paleoclimatology*, 36(4), p.e2020PA004037, 2021.
- 1093 Steph, S., Tiedemann, R., Groeneveld, J., Sturm, A., and Nürnberg, D.: Pliocene changes in  
1094 tropical east Pacific upper ocean stratification: Response to tropical gateways?,  
1095 in: *Proceedings of the Ocean Drilling Program: Scientific Results*, 202, 1-51 pp., 2006.
- 1096 Steph, S., Tiedemann, R., Prange, M., Groeneveld, J., Schulz, M., Timmermann, A., Nürnberg,  
1097 D., Röhlemann, C., Saukel, C., and Haug, G.H.: Early Pliocene increase in thermohaline  
1098 overturning: A precondition for the development of the modern equatorial Pacific cold  
1099 tongue, *Paleoceanography*, 25(2), 2010.
- 1100 Thompson, P.: Foraminifers from the Middle America Trench, in: *Initial reports of the Deep Sea*  
1101 *Drilling Project*, 67, Washington, D.C., U.S. Government Printing Office, 351–381 pp.,  
1102 1982.
- 1103 Thunell, R.: Late Miocene–early Pliocene planktonic foraminiferal biostratigraphy and  
1104 paleoceanography of low-latitude marine sequences, *Marine Micropaleontology*, 6, 71–  
1105 90, 1981.
- 1106 Tierney, J.E., Poulsen, C.J., Montañez, I.P., Bhattacharya, T., Feng, R., Ford, H.L., Höönsch, B.,  
1107 Inglis, G.N., Petersen, S.V., Sagoo, N. and Tabor, C.R., 2020. Past climates inform our  
1108 future. *Science*, 370(6517), p.eaay3701.

- 1109 Tindall, J.C., and Haywood, A.M.: Modeling oxygen isotopes in the Pliocene: Large-scale features  
1110 over the land and ocean, *Paleoceanography*, 30(9), 1183-1201, 2015.
- 1111 Tittensor, D.P., Mora, C., Jetz, W., Lotze, H.K., Ricard, D., Berghe, E.V. and Worm, B.: Global  
1112 patterns and predictors of marine biodiversity across taxa, *Nature*, 466(7310), 1098-1101,  
1113 2010.
- 1114 Todd, C.L., Schmidt, D.N., Robinson, M.M., and De Schepper, S.: Planktic foraminiferal test size  
1115 and weight response to the late Pliocene environment, *Paleoceanography* and  
1116 *Paleoclimatology*, 35(1), p.e2019PA003738, 2020.
- 1117 Uchikawa, J., and Zeebe, R.E.: Examining possible effects of seawater pH decline on  
1118 foraminiferal stable isotopes during the Paleocene-Eocene Thermal  
1119 Maximum, *Paleoceanography*, 25(2), 2010.
- 1120 Ujié, Y., and Ishitani, Y.: Evolution of a planktonic foraminifer during environmental changes in  
1121 the tropical oceans, *PLoS One*, 11(2), p.e0148847, 2016.
- 1122 Ujié, Y., de Garidel-Thoron, T., Watanabe, S., Wiebe, P., and de Vargas, C.: Coiling dimorphism  
1123 within a genetic type of the planktonic foraminifer *Globorotalia truncatulinoides*, *Marine*  
1124 *Micropaleontology*, 77(3-4), 145-153, 2010.
- 1125 Urban, M.C.: Accelerating extinction risk from climate change, *Science*. 348, 571-573.  
1126 doi:10.1126/science.aaa4984, 2015.
- 1127 Vincent, E., Killingley, J.S., and Berger, W.H.: Miocene oxygen and carbon isotope stratigraphy  
1128 of the tropical Indian Ocean, in: *The Miocene Ocean: Paleoceanography and*  
1129 *Biogeography*, 163, 103-130, Geological Society of America Memoir 163, 1985.
- 1130 Wade, B.S., and Olsson, R.K.: Investigation of pre-extinction dwarfing in Cenozoic planktonic  
1131 foraminifera, *Palaeogeography, Palaeoclimatology, Palaeoecology*, 284, 39-46, 2009.

- 1132 Wade, B.S., and Pearson, P.N.: Planktonic foraminiferal turnover, diversity fluctuations and  
1133 geochemical signals across the Eocene/Oligocene boundary in Tanzania, *Marine*  
1134 *Micropaleontology*, 68(3-4), 244-255, 2008.
- 1135 Wade, B.S., Al-Sabouni, N., Hemleben, C., and Kroon, D.: Symbiont bleaching in fossil planktonic  
1136 foraminifera, *Evolutionary Ecology*, 22, 253-265, 2008.
- 1137 Wade, B.S., Pearson, P.N., Berggren, W.A., and Pälike, H.: Review and revision of Cenozoic  
1138 tropical planktonic foraminiferal biostratigraphy and calibration to the geomagnetic polarity  
1139 and astronomical time scale, *Earth-Science Reviews*, 104(1-3), 111-142, 2011
- 1140 Wade, B.S., Poole, C.R., and Boyd, J.: Giantism in Oligocene planktonic foraminifera  
1141 Paragloborotalia opima: Morphometric constraints from the equatorial Pacific  
1142 Ocean, *Newsletters on Stratigraphy*, 49(3), 421-444, 2016.
- 1143 Wade, B.S., Pearson, P.N., Olsson, R.K., Fraass, A.J., Leckie, R.M. and Hemleben, C.:  
1144 Taxonomy, biostratigraphy, and phylogeny of Oligocene and lower Miocene  
1145 Dentoglobigerina and Globoquadrina, in: *Atlas of Oligocene Planktonic Foraminifera*,  
1146 edited by Wade, B.S., Olsson, R.K., Pearson, P.N., Huber, B.T., Berggren, W.A., 331-384  
1147 pp., 2018.
- 1148 Waelbroeck, C., Lougheed, B.C., Riveiros, N.V., Missiaen, L., Pedro, J., Dokken, T., Hajdas, I.,  
1149 Wacker, L., Abbott, P., Dumoulin, J.P., and Thil, F.: Consistently dated Atlantic sediment  
1150 cores over the last 40 thousand years, *Scientific Data*, 6(1), 1-12, 2019
- 1151 Wallace, L.M., Saffer, D.M., Barnes, P.M., Pecher, I.A., Petronotis, K.E., LeVay,  
1152 L.J., Bell, R.E., Crundwell, M.P., Engelmann de Oliveira, C.H., Fagereng,  
1153 A., Fulton, P.M., Greve, A., Harris, R.N., Hashimoto, Y., Hüpers, A., Ikari,  
1154 M.J., Ito, Y., Kitajima, H., Kutterolf, S., Lee, H., Li, X., Luo, M., Malie, P.R.,  
1155 Meneghini, F., Morgan, J.K., Noda, A., Rabinowitz, H.S., Savage, H.M.,

- 1156 Shepherd, C.L., Shreedharan, S., Solomon, E.A., Underwood, M.B.,  
1157 Wang, M., Woodhouse, A.D., Bourlange, S.M., Brunet, M.M.Y., Cardona,  
1158 S., Clennell, M.B., Cook, A.E., Dugan, B., Elger, J., Gamboa, D., Geor-  
1159 giopoulos, A., Han, S., Heeschen, K.U., Hu, G., Kim, G.Y., Koge, H.,  
1160 Machado, K.S., McNamara, D.D., Moore, G.F., Mountjoy, J.J., Nole, M.A.,  
1161 Owari, S., Paganoni, M., Rose, P.S., Screamton, E.J., Shankar, U., Torres,  
1162 M.E., Wang, X., and Wu, H.-Y.: Expedition 372B/375 methods, in:  
1163 Wallace, L.M., Saffer, D.M., Barnes, P.M., Pecher, I.A., Petronotis, K.E.,  
1164 LeVay, L.J., and the Expedition 372/375 Scientists, Hikurangi Subduction  
1165 Margin Coring, Logging, and Observatories. Proceedings of the Interna-  
1166 tional Ocean Discovery Program, 372B/375: College Station, TX (Internation-  
1167 al Ocean Discovery Program), 2019.
- 1168 Weiner, A., Aurahs, R., Kurasawa, A., Kitazato, H., and Kucera, M.: Vertical niche partitioning  
1169 between cryptic sibling species of a cosmopolitan marine planktonic protist, Molecular  
1170 Ecology, 21(16), 4063-4073, 2012.
- 1171 Weiner, A.K., Weinkauf, M.F., Kurasawa, A., Darling, K.F., Kucera, M. and Grimm, G.W.:  
1172 Phylogeography of the tropical planktonic foraminifera lineage Globigerinella reveals  
1173 isolation inconsistent with passive dispersal by ocean currents, PLoS One, 9(3), p.e92148,  
1174 2014.
- 1175 Weinkauf, M.F., Moller, T., Koch, M.C., and Kučera, M., 2014.: Disruptive selection and bet-  
1176 hedging in planktonic Foraminifera: Shell morphology as predictor of extinctions, Frontiers  
1177 in Ecology and Evolution, 2, 64, 2014.
- 1178 Weinkauf, M.F., Bonitz, F.G., Martini, R., and Kučera, M.: An extinction event in planktonic  
1179 Foraminifera preceded by stabilizing selection, PloS one, 14(10), p.e0223490, 2019.

- 1180 Westerhold, T., Marwan, N., Drury, A.J., Liebrand, D., Agnini, C., Anagnostou, E., Barnet, J.S.,  
1181 Bohaty, S.M., De Vleeschouwer, D., Florindo, F., and Frederichs, T.: An astronomically  
1182 dated record of Earth's climate and its predictability over the last 66 million years, *Science*,  
1183 369(6509), 1383-1387, 2020.
- 1184 Willeit, M., Ganopolski, A., Calov, R., Robinson, A., and Maslin, M.: The role of CO<sub>2</sub> decline for  
1185 the onset of Northern Hemisphere glaciation, *Quaternary Science Reviews*, 119, 22-34,  
1186 2015.
- 1187 Williams, M., Haywood, A.M., Hillenbrand, C.D., and Wilkinson, I.P.: Efficacy of  $\delta^{18}\text{O}$  data from  
1188 Pliocene planktonic foraminifer calcite for spatial sea surface temperature reconstruction:  
1189 comparison with a fully coupled ocean–atmosphere GCM and fossil assemblage data for  
1190 the mid-Pliocene, *Geological Magazine*, 142(4), 399-417, 2005.
- 1191 Winter, C.J. and Pearson, P.N.: Coiling directions in some Miocene planktonic  
1192 Foraminifera, *Journal of Micropalaeontology*, 20(1), 29-30, 2001.
- 1193 Woodhouse, A., Jackson, S.L., Jamieson, R.A., Newton, R.J., Sexton, P.F., and Aze, T.: Adaptive  
1194 ecological niche migration does not negate extinction susceptibility, *Scientific  
1195 Reports*, 11(1), 1-10, 2021.
- 1196 Woodhouse, A., Swain, A., Fagan, W.F., Fraass, A.J., and Lowery, C.M.: Late Cenozoic cooling  
1197 restructured global marine plankton communities, *Nature*, in review.
- 1198 Worm, B., Lotze, H.K., and Myers, R.A.: Predator diversity hotspots in the blue ocean,  
1199 *Proceedings of the National Academy of Sciences*, 100(17), 9884-9888, 2003.
- 1200 Yang, H., and Wang, F.: Revisiting the thermocline depth in the equatorial Pacific, *Journal of  
1201 Climate*, 22(13), 3856-3863, 2009.
- 1202 Zhang, X., Prange, M., Steph, S., Butzin, M., Krebs, U., Lunt, D.J., Nisancioglu, K.H., Park, W.,  
1203 Schmittner, A., Schneider, B., and Schulz, M.: Changes in equatorial Pacific thermocline

- 1204           depth in response to Panamanian seaway closure: Insights from a multi-model study,  
1205           Earth and Planetary Science Letters, 317, 76-84, 2012.
- 1206       Zika, J.D., Skliris, N., Blaker, A.T., Marsh, R., Nurser, A.G., and Josey, S.A.: Improved estimates  
1207           of water cycle change from ocean salinity: the key role of ocean warming, Environmental  
1208           Research Letters, 13(7), 074036, 2018.
- 1209       Zou, S., Groeneveld, J., Giosan, L. and Steinke, S.: Determining the habitat depth of the planktic  
1210           foraminifera *Dentoglobigerina altispira* in the eastern Arabian Sea during the middle  
1211           Miocene, Marine Micropaleontology, 170, 102075, 2022.
- 1212