# Paleoecology and evolutionary response of planktonic foraminifera to the Plio-Pleistocene Intensification of Northern Hemisphere Glaciations

**Adam Woodhouse[1,2],** Frances A. Procter[1], Sophie L. Jackson[1], Robert A. Jamieson[1], Robert J. Newton[1], Philip F. Sexton[3], Tracy Aze[1]

1. School of Earth and Environment, University of Leeds, Leeds, LS2 9JT, U.K.

2. University of Texas Institute for Geophysics, University of Texas at Austin, Austin, TX, 78758, U.S.A.

3. School of Environment, Earth and Ecosystem Sciences, Open University, Walton Hall, Kents Hill, Milton Keynes, MK7 6AA, U.K.

Correspondence email: adam.woodhouse@austin.utexas.edu

25   **ABSTRACT**

26      The Plio-Pleistocene is associated with many important climatic and paleoceanographic

27   changes which have shaped the biotic and abiotic nature of the modern world. The closure of the

28   Central American Seaway and the development and intensification of northern hemisphere

29   icesheets had profound global impacts on the latitudinal and vertical structure of the oceans

30   triggering the extinction and radiation of many marine groups. In particular, marine calcifying

31   planktonic foraminifera, that are sensitive to water column structure, exhibited a series of

32   extinctions as global temperatures fell. By analyzing high-resolution (~5 kyr) sedimentary records

33   from the Eastern Equatorial Pacific Ocean, complimented with global records from the novel

34   Triton dataset, we document the biotic changes in this microfossil group, within which three

35   species displayed isochronous co-extinction, and species with cold-water affinity increase in

36   dominance. We suggest that these changes are associated with the terminal stages of the closure

37   of the Central American Seaway and mark the initiation of a world in which cold- and deep-

38   dwelling species became increasingly more successful.

39   **1.  INTRODUCTION**

40      Current observations suggest that the Earth is shifting from its pre-industrial state

41   (Ceballos et al., 2015; Urban 2015; Barton et al., 2016; Pinksy et al., 2018; Jonkers et al., 2019;

42   Edwards et al., 2022), and changes in the vertical and latitudinal structure of the marine realm are

43   ultimately likely to take place (Hu et al., 2011; Rhein et al., 2013; Purich et al., 2018; Zika et al.,

44   2018; Bindoff et al., 2019; Golledge et al., 2019). It is therefore important to understand how

45   ecosystems such as the open ocean, which contain resources vital to human populations (Worm

46   et al., 2003; Tittensor et al., 2010) respond to short- and long-term oceanographic shifts (e.g.,

47   Norris et al., 2013).

48       The timing of closure for the Isthmus of Panama at ~4.7-2.7 Ma (Keigwin, 1978; 1982;

49       Keller et al., 1989; Haug & Tiedemann, 1998; Haug et al., 2001; Groeneveld et al., 2006; Steph

50       et al., 2006, 2010; Molnar, 2008; Federov et al., 2013; O'Dea et al., 2016) remains contentious,

51       though the ultimate role of this event in late Cenozoic icehouse evolution is clear, proving pivotal

52       to the intensification of northern hemisphere glaciations. The precise dating of final isthmus

53       formation is less essential than the repercussions of the gradual shoaling and restriction of the

54       Central American Seaway (CAS) which triggered significant palaeoceanographic effects

55       fundamental to the evolution of the present climate state. Gradual restriction of consistent

56       throughflow between the tropical Atlantic and Indo-Pacific Oceans via isthmus formation (O'Dea

57       et al., 2016) was coupled with bipolar cryosphere development that significantly restructured

58       global vertical and meridional temperature gradients (Schmidt et al., 2004a, b; Boscolo-Galazzo

59       et al., 2021; 2022; Ford et al., 2022; Gaskell et al., 2022), altering marine ecosystems and trophic

60       structure.

61       To assess marine ecosystem changes, we look to the Cenozoic marine microfossil record,

62       specifically the planktonic foraminifera, single-celled marine protists with a global distribution and

63       the most complete Cenozoic species-level fossil record (Aze et al., 2011; Fenton & Woodhouse

64       et al., 2021). Their calcareous skeletons, or tests, preserve not only their entire life history, but

65       also a biogeochemical expression of the surrounding water column (e.g., Edgar et al., 2017).

66       These features allow for high-resolution species-specific quantification of physiological and

67       ecological adaptation through periods of climate variability (e.g., Knappertsbusch, 2007; Wade et

68       al., 2008, 2016; Hull and Norris, 2009; Wade and Olsson, 2009; Edgar et al., 2013a; Aze et al.,

69       2014; Pearson and Ezard, 2014; Weinkauf et al., 2014, 2019; Brombacher et al., 2017a, 2021;

70       Falzioni et al., 2018; Si and Aubry, 2018; Fox et al., 2020; Todd et al., 2020; Kearns et al., 2021,

71       2022; Pearson and Penny, 2021; Shaw et al., 2021; Woodhouse et al., 2021; Friesenhagen, 2022;

72       Hupp et al., 2022).

73      Here, we report the high-resolution biotic response of planktonic foraminifera during the

74      terminal stages of closure for the CAS in the Eastern Equatorial Pacific (EEP) Ocean, focusing

75      on the co-extinction of three members of the genus *Dentoglobigerina* through documentation of

76      high-resolution (~5 ka) paired single-specimen morphometric, with multi- and single-specimen

77      geochemical analyses, and their paleoceanographic implications. Furthermore, we assess the

78      global paleoecological response of planktonic foraminifera from the Pliocene to the Recent,

79      assessing the role of bipolar cryosphere development in planktonic foraminiferal

80      macroevolutionary dynamics.

81      **2. METHODS**

82      **2.1. Site Selection**

83      Integrated Ocean Drilling Program Expedition 321 Site U1338 (Hole 1338A) (2°30.469′N,

84      17°58.162′W), situated in the EEP, was drilled to 410 meters below seafloor (mbsf) through

85      Holocene - early Miocene pelagic sediments (Pälike et al., 2010). At ~3 Ma, the site was at ~2°N

86      paleolatitude (Drury et al., 2014) in a deep-water pelagic environment of similar water depth to

87      the modern (~4 km). The primary lithologies represented are calcareous, diatomaceous and

88      radiolarian nannofossil oozes and chalks. Despite the deep-water settings, and primarily

89      calcareous nature of the sediments, excellent microfossil preservation has been recorded in

90      planktonic foraminiferal specimens through intervals of this core (Fox & Wade, 2013; Woodhouse

91      et al., 2021). A preliminary assessment of core U1338A was carried out to determine the

92      approximate position of the extinction of several species of *Dentoglobigerina* (~3 Ma) based on

93      tropical biostratigraphy (Wade et al., 2011), and shipboard paleomagnetic data (Pälike et al.,

94      2010).

95

96

## 2.2.   Foraminiferal Assemblage Analysis

97

98       Sediment volumes of 20-40 cm$^3$ were collected and washed with de-ionised water over a

99 63-µm sieve; the residues were dried in an oven at 40 °C and split. All samples were examined

100 using a Zeiss Stemi 305 Compact Stereo Microscope. Planktonic foraminifers were identified

101 following the taxonomy of Kennett and Srinivasan (1983), Schiebel and Hemleben (2017), and

102 Wade et al., (2018). We performed assemblage counts on >63 µm splits yielding >300 individuals

103 (Table S1). Assessments of taxonomy and test preservation of foraminifera were performed via

104 analysis with the Tescan VEGA3 XM Scanning Electron Microscope (SEM) at the University of

105 Leeds, UK.

106       Species were grouped by their ecology to assess the relative abundances of taxa for

107 palaeoceanographic information, where taxa were assigned as either shallow- and warm-water

108 taxa (the ecogroups "symbiotic" and "asymbiotic" of Aze et al., 2011), or deep- and cold-water

109 taxa (the ecogroups "thermocline", "subthermocline" of Aze et al., 2011, and *Globigerinita*

110 *glutinata* (Lutz, 2010)).

## 2.3.   Morphometric Analysis

111

112       Specimens of the genus *Dentoglobigerina* were measured to compare species size with

113 stable isotope ratios to investigate species ecology and ontogeny. Complete specimens of

114 *Dentoglobigerina* were picked and mounted in umbilical position on card slides pierced with a fine

115 needle to accommodate the variably spired nature of species in the genus (Wade et al., 2018).

116 Specimens were imaged umbilically using a Zeiss Axio Zoom V16 microscope with attached

117 Canon EOS 100D camera at x 19.4 magnification. All specimens were then rotated 90° laterally,

118 and imaged whilst propped onto their penultimate chamber. Images were processed using the

119 image analysis software Image Pro Premier, and the maximum test diameter, previously deemed

120 a statistically repeatable measurement amongst *Dentoglobigerina* (Brombacher et al., 2017b,

121    2018; Woodhouse et al., 2021), was captured from both orientations, and the lower of the two

122    values assigned as test size.

### 2.4.    Geochemical Analysis

124        Following morphometric analysis, well-preserved specimens of *Dentoglobigerina altispira*

125    (>200 μm)*, Dentoglobigerina baroemoenensis* (>200 μm) and *Dentoglobigerina globosa* (>200

126    μm) were picked, ultrasonicated in deionized water for 10-15 seconds, and dried for stable isotope

127    analysis. This process was repeated for extant taxa representing known discrete ecological

128    habitats through the water column to determine the ecological niche habits of the extinct

129    dentoglobigerinids: *Globigerinoides    ruber*    (212-350    μm,    surface    mixed-layer    (SML)),

130    *Neogloboquadrina incompta* (212-350 μm, subsurface), *Globorotalia tumida* (>300 μm,

131    thermocline/photic zone base, corrected for a 1.0‰ $\delta^{13}$C enrichment due to this species

132    occupying the shallow oxygen minimum zone and consequential effects of reduced ambient pH

133    (Lohmann, 1995; Bijma et al., 1999; Uchikawa and Zeebe, 2010; Birch et al., 2013)), *Globorotalia*

134    *scitula* (212-300 μm, subthermocline), and *Cibicidoides wuellerstorfi* (>212 μm, bottom-water)

135    (see Cramer et al., 2009, 2011; Rasmussen & Thomsen, 2010; Aze et al., 2011; Woodhouse et
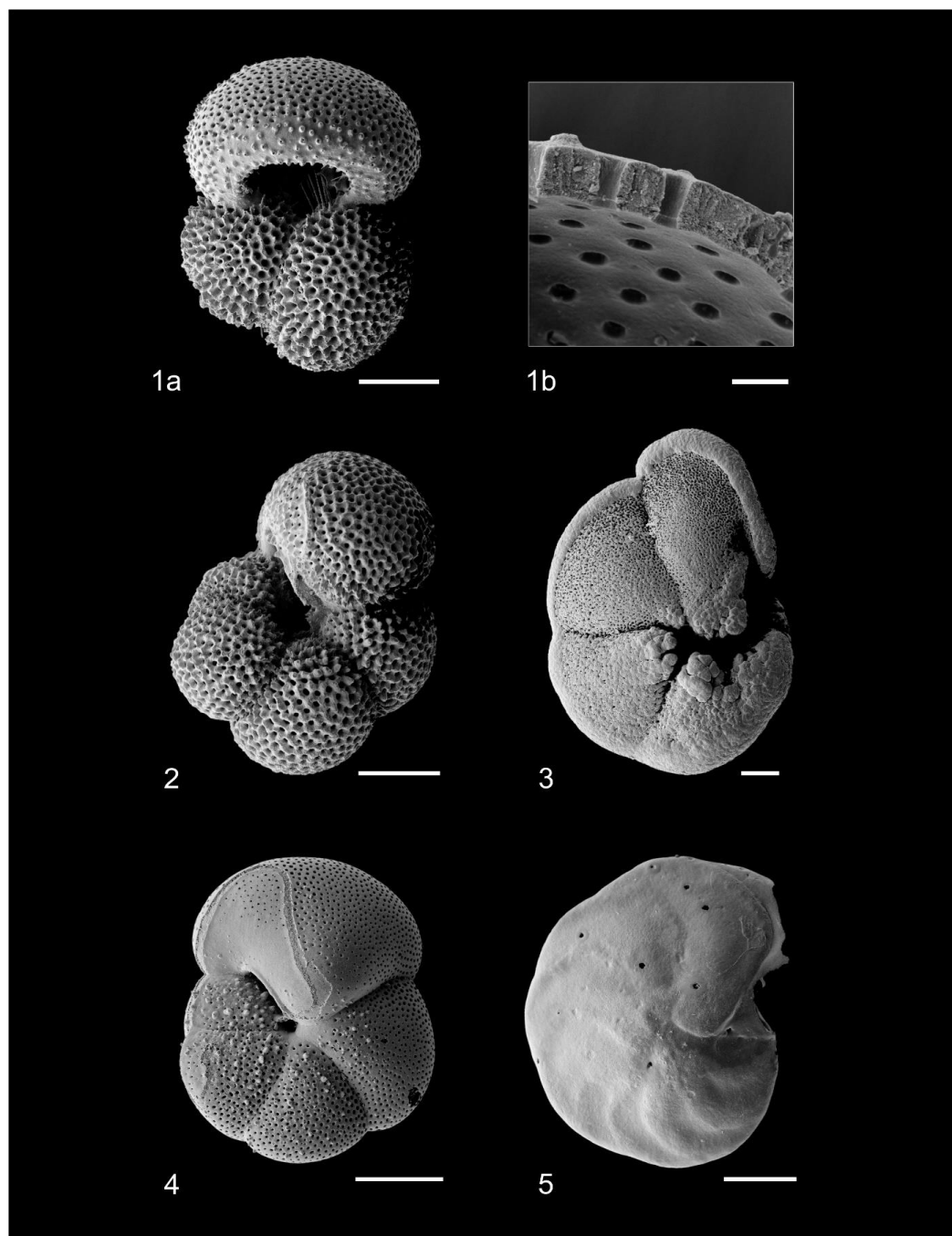
**Figure 1. Scanning electron micrographs of species analyzed for stable isotope geochemistry. 1a,** *G. ruber,* **1b,** *G. ruber* **shell ultrastructure showing excellent preservation, 2,** *N. incompta,* **3,** *G. tumida,* **4,** *H. scitula***, 5,** *C. wuellerstorfi.* **Scale bar for images 1a, 2-5 = 100 microns, for image 1b = 10 microns. All specimens from sample U1338A-5H-4W-35/38.**

136    al., 2021). Single specimens of dentoglobigerinids, and multiple specimens of other foraminifer

137    species were analysed using an Elementar IsoPrime Dual-Inlet Isotope Ratio Mass Spectrometer

138    in the School of Earth and Environment at the University of Leeds, and data are reported to the

139    Vienna Peedee belemnite (VPDB) scale using a Carrara marble standard (Elemental

140    Microanalysis B2214) where analytical precision was better than 0.07 and 0.13 ‰ for $\delta^{13}C$ and

141    $\delta^{18}O$, respectively.

142        Specimens of *Cibicidoides wuellerstorfi* were also used to create a benthic foraminiferal

143    $\delta^{18}O$ record for this study to supplement the shipboard paleomagnetic data (Pälike et al., 2010).

144    This record was constructed and tuned to the Ocean Drilling Program Site 849/IODP Site 1338

145    stack constructed by Lyle et al., (2019) using QAnalySeries software (Kotov and Pälike 2018) to

146    better constrain the timing of events (see Woodhouse et al., 2021).

### 2.5.    Global Data Analysis

148        To investigate how planktonic foraminiferal macroevolution and paleoecology has evolved

149    since the Pliocene, the Triton dataset (Fenton & Woodhouse et al., 2021) was downloaded, and

150    all macroperforate planktonic foraminiferal records occurring from 5.3-0 Ma (early Pliocene-

151    Recent) were binned into 53-time bins with equal length (100 kyrs). Species were assigned the

152    speciation and extinction datums in accordance with Aze et al., (2011) and Fenton & Woodhouse

153    et al., (2021) and all species occurrences located outside of these assigned stratigraphic ranges

154    were removed. This range trimming was applied to eliminate much of the occurrence data likely

155    attributable to misidentification and/or reworking which may create artificial "tails" within speciation

156    and extinction data (Liow et al., 2010; Lazarus et al., 2012; Flannery-Sutherland et al., 2022). The

157    trimming of taxa resulted in a dataset of 239,317 planktonic foraminiferal occurrences.

158    Furthermore, all species were assigned to their respective "ecogroups", which represent broad

159    ecological categories based on paleoecological and phylogenetic data (Aze et al., 2011). These

160    ecogroups are defined as: ecogroup 1 = surface mixed layer dweller with photosymbionts,

161    ecogroup 2 = surface mixed layer dweller without photosymbionts, ecogroup 3 = thermocline

162    dweller, ecogroup 4 = subthermocline dweller, ecogroup 5 = high-latitude.

## 3. RESULTS

### 3.1. Assemblage Records

165        All sediments contain a highly

166    abundant well-preserved (Figure 1)

167    open-ocean planktonic foraminifer

168    assemblage comprising ~70

169    morphospecies. The dominant genera

170    through the section included

171    *Neogloboquadrina, Globigerinoides,*

172    *Pulleniatina,* and *Globigerinita* (see SI).

173    The isochronous extinction of the

174    species *D. altispira, D.*

175    *baroemoenensis*, and *D. globosa* in

176    U1338A occurs ~35.50 mbsf. There is

177    also a notable influx of the species

178    *Menardella* cf. *exilis* and *Menardella* cf.

179    *pertenuis* occurring from 40.56-42.58

180    mbsf, after which they are absent within

181    the 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 δ¹³C and δ¹⁸O, black = *C. wuellerstorfi,* dark blue = *G. scitula,* cyan = *G. tumida*, orange = *N. incompta,* red = *G. ruber.* Dashed line represents permanent switch to higher proportion of cold-water taxa. Grey box indicates where isotope records exhibit high volatility.**

182        Comparing the assemblage composition of warm- and surface- dwellers against cold- and

183    deep- dwellers, we document relatively even abundances until ~36.26 mbsf (~3.08 Ma), where

184    the assemblage exhibits consistently greater abundances of cold- and deep-dwellers for the rest

185    of the record (Fig. 2).

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

187        Test preservation was excellent throughout the sampled interval, where specimen walls

188    appear optically translucent, and SEM images (Fig. 1) indicate no observable diagenetic

189    alteration, clean pore spaces, and spines preserved within tests (Fig. 1a). Following artificial test

190    breaking, inspection of the wall ultrastructure (Fig. 1b) showed that no wall recrystallisation had
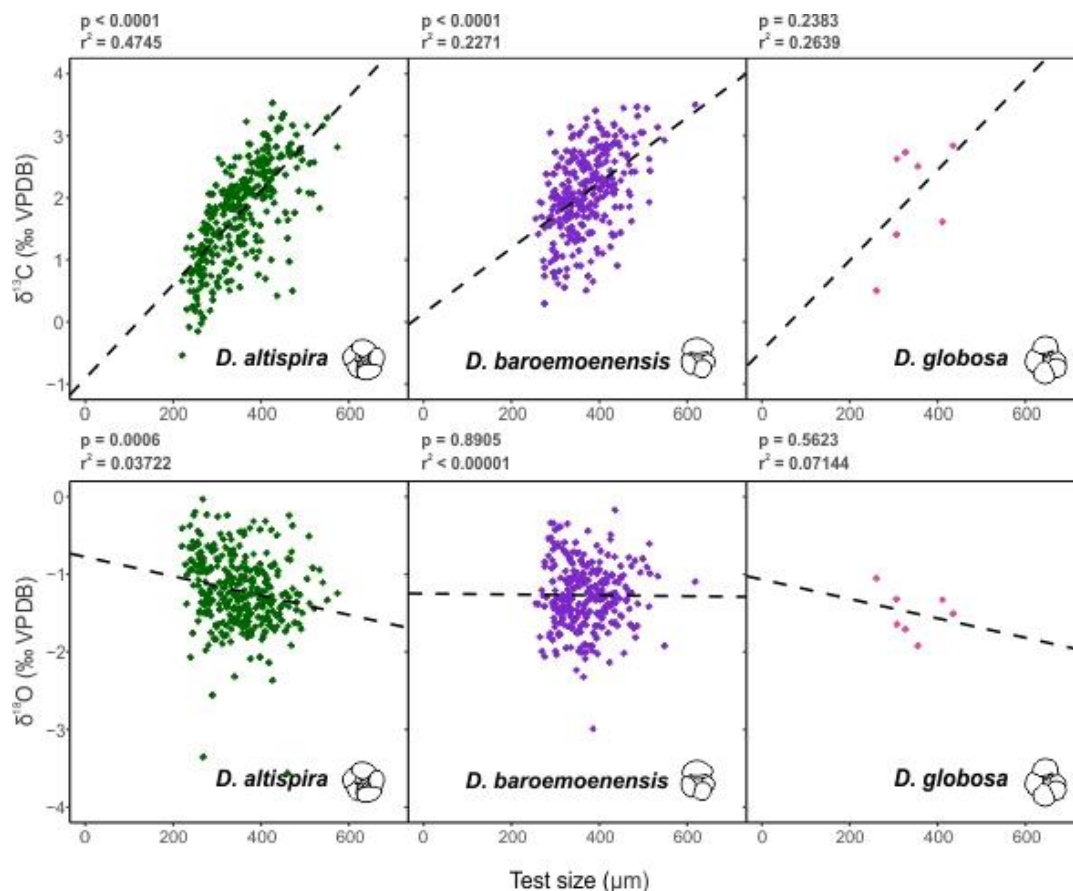
**Figure 3. Test size - δ¹³C and δ¹⁸O relationships for the three species of *Dentoglobigerina* which underwent extinction through the study section. Trend lines for each species represent linear regressions based on the entire per species dataset (dashed line). Significance (p) and measure of fit (r²) were calculated for each linear regression.**

191   taken place, suggesting stable isotope signals remain unaltered (Sexton et al., 2006; Edgar et al.,

192   2013b).  Single-specimen $\delta^{13}C$ values for *D. altispira, D. baroemoenensis,* and *D. globosa* vary

193   from -0.54 to +3.53‰, +0.30 to +3.50‰, and +0.51 to +2.84‰ (Fig. 3, SI), respectively, whilst

194   $\delta^{18}O$ values vary from -3.56 to -0.03‰, -2.99 to -0.17‰, and -1.92 to -1.05‰, respectively. In all

195   three species*,* a positive correlation is calculated between test size and $\delta^{13}C$, however, this

196   relationship is only significant ($p < 0.0001$) in *D. altispira* and *D. baroemoenensis*, potentially due

197   to the greater number of specimens analyzed for these species (Fig. 3). Regression slopes are

198   similarly steep, however the slopes for *D. altispira* and *D. globosa* are more alike. *D.*

199   *baroemoenensis* and *D. globosa* show no significant correlation between $\delta^{18}O$ and test size,

200   however, a significant ($p = 0.0006$) negative relationship is recorded in *D. altispira*. Once again,

201   regression slopes for *D. altispira* and *D. globosa* are similar, whereas for *D. baroemoenensis*, this

202   slope is almost flat (Fig. 3).

203   **3.   3.   Extant   Species**

204   **Geochemical Records**

205        Amongst   the   extant

206   species   picked   from   strict   size

207   fractions   throughout   the   study

208   section, *G. ruber* $\delta^{13}C$ values show

209   the highest $\delta^{13}C$ variability (+0.7 to

210   +2.8‰), and $\delta^{18}O$ values varying

211   from   -2.3 to -0.8‰ (SI, Fig. 4).

212   Corrected *G. tumida* values show

213   the   lowest   $\delta^{13}C$   variability   (0 to

214   +0.8‰), and the highest variability

215   for $\delta^{18}O$ (-1.3 to +1.1‰). *G. scitula*
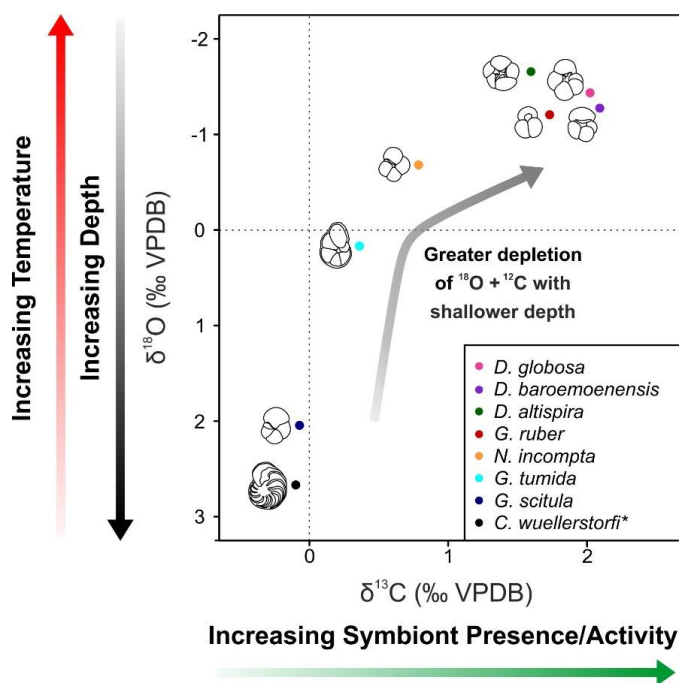
**Figure 4. $\delta^{13}C$ and $\delta^{18}O$ cross-plot 2 showing mean values of all analyzed specimens from this study. Black = *C. wuellerstorfi*, dark blue = *G. scitula*, cyan = *G. tumida*, orange = *N. incompta*, red = *G. ruber*, green = *D. altispira*, purple = *D. baroemoenensis*, pink = *D. globosa*. Species marked with an asterisk are benthic.**

216 δ¹³C values vary from -0.6 to +0.4‰, whilst δ¹⁸O varies from +0.8 to +2.9‰, whereas bottom-

217 water *C. wuellerstorfi* δ¹³C values vary from -0.8 to +0.5‰, and δ¹⁸O varies +2.2 to +3.1‰,

218 showing the lowest variability in δ¹⁸O (Fig. 4). The stable isotope records of extant species

219 generally tend to show low inter-sample variability, however there is notable geochemical

220 stochasticity within the *G. tumida* record ~36.17-35.86 mbsf (Fig. 2).

221 All three species of *Dentoglobigerina* analyzed in this study record mean stable isotopic

222 ratios similar to the extant species *G. ruber*, where all species indicated δ¹⁸O ratios less negative

223 than *G. ruber*, and *D. baroemoenensis* and *D. globosa* show δ¹³C ratios more positive than this

224 species (Figs. 3 and 4).

225 **3.4. Global Pliocene-Recent Ecogroup trends**

226 The global proportions of planktonic foraminiferal ecogroups within the Triton dataset

227 (Fenton & Woodhouse et

228 al., 2021) show that

229 throughout the time

230 interval studied (5.3-0

231 Ma), surface mixed layer

232 dwellers without

233 photosymbionts (orange)

234 proportions remain

235 relatively consistent,

236 making up ~10% of the

237 total global fauna (Fig. 5).

238 From 5.3-3 Ma, global

239 ecogroup proportions are

240 relatively consistent,
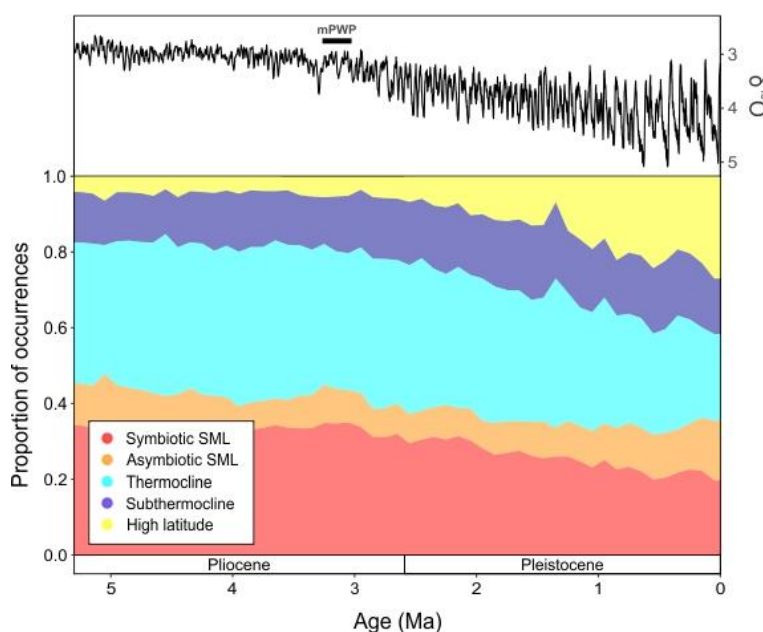
**Figure 5. The LR04 stack showing benthic foraminiferal δ¹⁸O (from Lisiecki and Raymo, 2005), and proportions of macroperforate planktonic foraminifera occurrences assigned to the ecogroups of Aze et al. (2011), binned to 100 kyrs from 5.3 Ma to the Recent. mPWP = mid-Pliocene Warm Period, SML = surface mixed-layer.**

241   where the dominant forms are thermocline dwellers (cyan) and surface mixed layer dwellers with

242   photosymbionts (red) (Fig. 5), making up ~40% and ~35% of the global fauna, respectively.

243   During this interval, the proportion of subthermocline dwellers (blue) and high-latitude forms

244   (yellow) also remain relatively consistent with ~10% and <5% of total proportions, respectively.

245   After ~3 Ma, both thermocline dwellers and surface mixed layer dwellers with photosymbionts

246   show a steady decline in global representation approaching the Recent, making up ~20% each

247   in the modern ocean. At ~3 Ma, both the subthermocline dwellers and high-latitude ecogroup start

248   to show increases in their proportions, though this increase approaching the modern is much

249   greater in the latter group. During the last 100 kyrs, subthermocline and high latitude species

250   constitute ~15 and ~25%, respectively (Fig. 5).

251   **4. DISCUSSION**

252   Few major changes in the assemblage composition are observed through the study

253   interval other than the isochronous extinction of *D. altispira*, *D. baroemoenensis*, and *D. globosa*

254   at ~3.037 Ma (35.50 mbsf), and the influx of *M.* cf. *exilis* and *M.* cf. *pertenuis* through 3.45-3.36

255   Ma (Fig. 2; 42.58-40.56 mbsf). The extinction of *D. altispira* is a useful marker in the mid-Pliocene,

256   previously recorded within the East Equatorial Pacific Ocean (3.46 Ma; Shackleton et al., 1995;

257   Wade et al., 2011), however this study and that of Woodhouse et al., (2021) provide recalibration

258   for this event, which includes the co-extinction of *D. baroemoenensis* and *D. globosa*.

| Species | Pore density (per 2500 μm$^2$) |
|---|---|
| *M. menardii* | 32 |
| *M. limbata* | 27 |
| *M.* cf. *exilis* | 51 |
| *M.* cf. *pertenuis* | 49 |

**Table 1. The number of pores per 2500 μm$^2$ in the penultimate chamber of select species of *Menardella*.**

259    The co-extinction of the dentoglobigerinids is significant, as Woodhouse et al., (2021)

260    demonstrated that *D. altispira* and *D. baroemoenensis* show unique phenotypic responses

261    leading up to their termination, despite their shared phylogenetic and ecological affinity. We

262    therefore suggest that all three species share an ecological habit that ultimately proved inefficient

263    to mitigate the changing abiotic conditions associated with this critical period of bipolar cryosphere

264    development (Kleiven et al., 2002; Brierly & Fedorov, 2010; Cramer et al., 2009, 2011; Willeit et

265    al., 2015; Hayashi et al., 2020; Westerhold et al., 2020).

266    The documented co-occurrence of *M.* cf. *exilis* and *M.* cf. *pertenuis* may also indicate a

267    shared ecological affinity between these species (Fig. 2; Kennett & Srinivasan, 1983;

268    Knappertsbusch, 2016). Furthermore, this association may suggest that these two similar forms

269    exist within the same genetic species complex, though further study on internal shell ontogeny
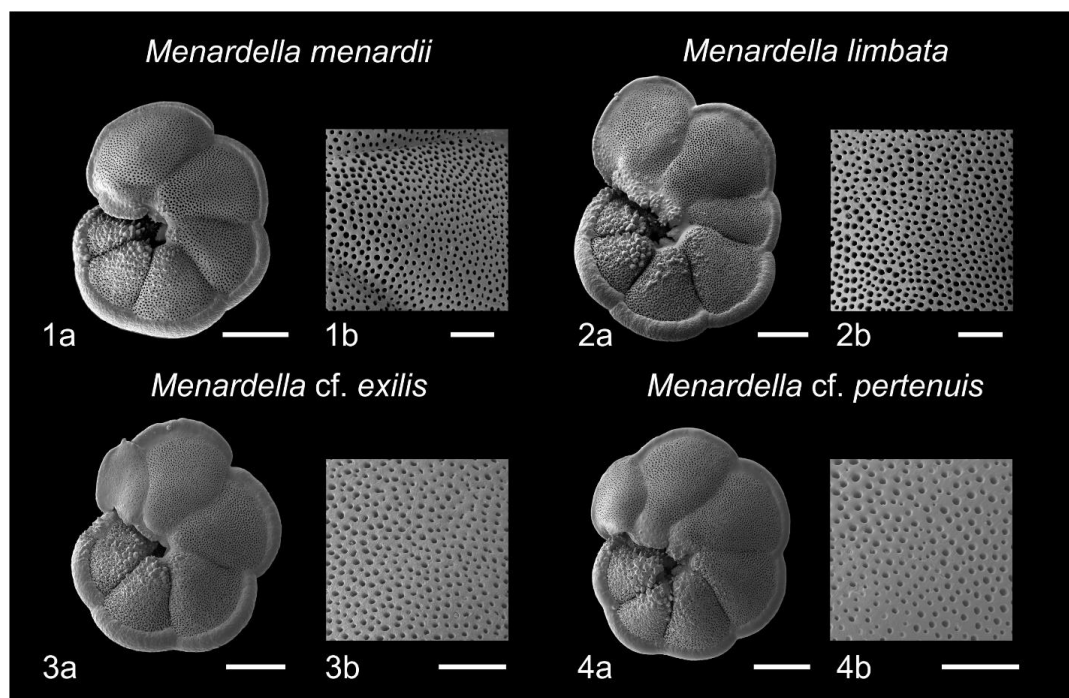
**Figure 6. Scanning electron micrographs of select species of *Menardella* and pore detail of penultimate chambers. 1a, *M. menardii,* 1b, *M. menardii* pore detail, 2a, *M. limbata,* 2b, *M. limbata* pore detail*,* 3a, *M.* cf. *exilis*, 3b, *M.* cf. *exilis* pore detail, 4a, *M.* cf. *pertenuis,* 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.**

270    and external morphology would be required to confirm this hypothesis. Notably however, Kaneps

271    (1970) and Chaisson (2003) have suggested that Indo-Pacific occurrences of these two species

272    are in fact "aberrant" forms of *Menardella limbata* and *Menardella menardii,* with the *M. exilis-*

273    *pertenuis* plexus being solely endemic to the Atlantic basin (Sexton & Norris, 2011).

274         Scanning election photomicrographs and pore density analysis of *Menardella*

275    morphospecies within this study (Fig. 6; Table 1) suggests that the *M.* cf. *exilis* and *M.* cf. *pertenuis*

276    morphotypes ascribed to "aberrant" forms may in fact be phylogenetically distinct from both *M.*

277    *menardii* and *M. limbata,* as well as from the endemic Atlantic *M. exilis-pertenuis* plexus. Where

278    the Atlantic type-specimens exhibit finely perforate tests (Kennett & Srinivasan, 1983), the

279    specimens within this study appear to show test perforation intermediate between "normally

280    perforate" menardellids such as *M. menardii* and *M. limbata* (Fig. 6), and the "finely perforate" *M.*

281    *exilis-pertenuis* plexus (Kennett and Srinivasan, 1983; Chaisson, 2003). Whether all Indo-Pacific

282    occurrences of these morphotypes (e.g., Brönniman and Resig, 1971; Jenkins and Orr, 1972;

283    Thunell, 1981; Keigwin, 1982; Thompson, 1982; Chaisson and Leckie, 1993) exhibit similar test

284    perforation remains to be determined. However, these forms could represent either: 1) convergent

285    evolution of a geographically-isolated endemic population restricted to the Indo-Pacific triggered

286    by vicariance, or 2) specimens within the *M. exilis-pertenuis* plexus exhibiting a differential

287    phenotypic expression of pore density, potentially due to regional differences in

288    paleoceanography between the Atlantic and Indo-Pacific basins at this time (Haug et al., 2001).

289    Irrespective of the biological implications, this acme event may represent a regionally valuable

290    biostratigraphic marker horizon.

291         Comparing the assemblage composition of warm- and surface- dwellers against cold- and

292    deep- dwellers, we document a gradual turnover from an assemblage exhibiting relatively even

293    abundances of these two groups, to one of increasing occupation of cold- and deep-dwellers from

294    ~3.08 Ma onwards (36.26 mbsf; Fig. 2). This may reflect regional thermocline shoaling similar to

295     patterns observed at DSDP Site 84 in the proximal Panama Basin (Lutz, 2010). Other geological

296     intervals associated with significant global cooling such as the Eocene-Oligocene transition and

297     late Miocene cooling exhibit similar patterns of gradual, successive turnover of warm-water

298     dwellers by cold-water taxa potentially associated with expansions/contractions in their respective

299     ecospaces (Keller, 1983; Boersma and Premoli Silva, 1991; Keller et al., 1992; Molina et al., 1993;

300     Wade and Pearson, 2008; Ezard et al., 2011; Lowery and Fraass, 2019; Lowery et al., 2020;

301     Boscolo-Galazzo et al., 2021, 2022).

302     **4.1.    Dentoglobigerinid Paleoecology**

303        Studies of extant species suggest a strong positive correlation between planktonic

304     foraminifera $\delta^{13}C$ and test size, paired with a lack of a strong negative significant relationship in

305     $\delta^{18}O$ and test size, is indicative of species bearing photosymbiotic algae (e.g. Berger et al., 1978;

306     Bouvier-Soumagnac and Duplessey, 1985; Spero and Williams, 1988, 1989; Spero et al., 1991;

307     Spero, 1992; Spero and Lea, 1993; Ravelo and Fairbanks, 1995; Norris, 1996; Birch et al., 2013).

308     Our data suggests that all three species of *Dentoglobigerina* studied here are symbiont-bearing,

309     displaying mean stable isotope data similar to the symbiont-bearing surface mixed layer dwelling

310     *G. ruber* (Figs. 2-4). Moreover, the regression lines for the ancestor-descendent pair *D. globosa*

311     *- D. altispira* are remarkably similar, suggesting the species share similar stable isotope-test size

312     relationships, despite the speciation of *D. altispira* occurring ~20 Myrs prior (Aze et al., 2011;

313     Wade et al., 2011, 2018). However, the substantially fewer data for *D. globosa* currently limits the

314     significance of this observation for this particular species (Fig. 3).

315        The results presented here contribute to the variety of interpretations from previous

316     studies on the paleoecology of *D. altispira.* Spanning different ocean basins throughout the

317     species' stratigraphic range they suggest: a shallow-dwelling (e.g., Keller and Savin, 1985;

318     Vincent et al., 1985; Prentice and Matthews, 1988; Corfield and Cartlidge, 1991; Norris et al.,

319     1993; Hodell and Vayavananda, 1994; Sosdian and Lear, 2020), deep-dwelling (Opdyke and

320 Pearson, 1995; Pearson and Shackleton, 1995), or lower mixed layer/upper thermocline (Zou et

321 al., 2022) ecological niche habit.

322 Woodhouse et al., (2021) suggested that prior to extinction, the *D. altispira* geochemical

323 signal may signify that this species underwent adaptive ecological niche migration across multiple

324 depth habitats. Upon further investigation, by isolating all *D. altispira* specimens present after the

325 migration horizon at ~ 3.061 Ma (Woodhouse et al., 2021), we show that these specimens do in

326 fact display a steeper negative relationship between $\delta^{18}O$ and test size (Fig. S1), consistent with

327 asymbiosis, however this relationship lacks statistical significance. Nevertheless, this observation

328 lends support to the conclusions of Woodhouse et al., (2021) that this species underwent niche

329 adaptation prior to extinction.

330 Another plausible scenario may be the existence of indeterminate cryptic diversity within

331 the *D. altispira* morphospecies complex where multiple ecological strategies or phylogenetic

332 expressions may be present (e.g., Huber et al., 1997; Bijma et al., 1998; de Vargas et al., 1999,

333 2002; Weiner et al., 2012; Schiebel and Hemleben, 2017; Nirmal et al., 2021; Pearson and Penny,

334 2021), and the stepwise changes observed in Woodhouse et al., (2021), may indicate the

335 systematic loss of "cryptic genotypes" within this morphospecies complex. Indeed, Pearson and

336 Penny (2021), hypothesized that dramatic abundance switches in the Indo-Pacific Warm Pool of

337 ecologically-distinct alternately-coiled populations of *Pulleniatina* morphospecies may signify

338 replacement by distinct cryptic genotypes, and such coiling switches are noted throughout the

339 planktonic foraminiferal fossil record (Ericson et al., 1955; Saito et al., 1975; Bossio et al., 1976;

340 Hallock & Larsen. 1979; Hornibrook, 1982; Scott et al., 1990; Norris and Nishi, 2001; Winter and

341 Pearson, 2001; Crundwell & Nelson, 2007; Wade et al., 2011; Pearson & Ezard, 2014; Crundwell,

342 2015a, b; Levin et al., 2016; Wallace et al., 2019; Crundwell & Woodhouse, 2022a, b). Therefore,

343 the range of interpreted paleoecologies in *D. altispira* may in fact be due to the occurrence of

344 distinct cryptic populations from across the geological record. Irrespective, the abiotic conditions

345    at this time appear to have become fatally detrimental to the entire ecological habit of all three

346    morphospecies of *Dentoglobigerina* analyzed in the EEP, and subsequently across the entire

347    globe (Shackleton et al., 1995; Chaisson and Pearson, 1997; Wade et al., 2011; Raffi et al., 2020;

348    Groeneveld et al., 2021; Woodhouse et al., 2021).

349    **4.2.    Pliocene EEP Paleoceanography**

350          The establishment of the Isthmus of Panama played a key role in Atlantic Meridional

351    Overturning Circulation intensification by barring Caribbean inflow from the Atlantic (O'Dea et al.,

352    2016; Hayashi et al., 2020), leading to a new palaeoceanographic state defined by an equatorial

353    Pacific thermocline exhibiting a high-angle east-west tilt (Fiedler and Talley, 2006; Yang and

354    Wang, 2009; Zhang et al., 2012; Ford et al., 2015). Changes in the EEP water column structure

355    are compounded within biotic and abiotic records, where global changes in ice volume, as shown

356    by benthic $\delta^{18}O$ (Fig. 5), and the formation of the isthmus contributed to the gradual cooling and

357    shoaling of the thermocline (Ford et al., 2015). Isochronous records of ice-rafted debris in the

358    North Atlantic and Pacific infer a substantial change to high-latitude global climate ~3 Ma

359    (Shackleton et al., 1984; Maslin et al., 1996; Kleiven et al., 2002; Lawrence et al., 2006).

360    Consequently, the already restricted CAS was likely subjected to substantial eustatic sea level

361    fluctuations (Chaisson, 2003; Bartoli et al., 2005; O'Dea et al., 2016), causing cool water within

362    or below the thermocline to become shallow enough to be mixed by surface winds (Philander &

363    Federov, 2003; Federov et al., 2004; 2006; Ford et al., 2012; 2015). In turn, this contributed to a

364    dramatic increase in regional upwelling associated with further development of the EEP cold

365    tongue (Herbert et al., 2010). We suggest that the increasing dominance of cold- and deep-

366    dwellers in the EEP (Figs. 2 and 5) are a direct manifestation of the water column structure

367    changes associated with closure of the CAS and cryosphere intensification, marking the initiation

368    of transition from the early Pliocene "El Padre" mean state to one more similar to the modern

369    ocean (Seki et al., 2012; Ford et al., 2012, 2015).

370        The geochemical fluctuations noted within *G. tumida* from 3.071-3.061 Ma (36.17-35.86

371     mbsf; Fig. 2) are coeval with the interval assigned to the "Phase Transition" by Woodhouse et al.,

372     (2021), in which *D. altispira* and *D. baroemoenensis* exhibit dramatic fluctuations in size and

373     shape preceding rapid ecological changes. Here, the $\delta^{18}O$ signal of *G. tumida* exhibits substantial

374     and rapid changes up to ~2.1‰, switching from typical thermocline values to those indicative of

375     the subsurface, and back again, whereas all other water column $\delta^{18}O$ value changes are nominal

376     (Fig. 2).

377        If the fluctuations within the $\delta^{18}O$ signal of *G. tumida* were related to fluctuations in its

378     depth habitat, we would expect the inverse pattern to occur in its $\delta^{13}C$ signature, as $\delta^{13}C$ values

379     decrease with depth (Cannariato and Ravelo, 1997; Ford et al., 2012; Birch et al., 2013), however

380     this is not the case (SI, Fig. 2). The maximum $\delta^{18}O$ excursion value (~2.1‰) is equivalent to a

381     temperature change of ~10 °C, based on a mid-Pliocene SMOW value of -0.3‰ (Williams et al.,

382     2005; Medina-Elizalde, Lea and Fantle, 2008; Tindall & Haywood, 2015) and the

383     paleotemperature equations of Kim & O'Neil (1997). Previous studies from EEP sites show

384     Mg/Ca-derived thermocline temperature fluctuations of ~3 °C (Site 1241; Steph et al., 2006) to ~5

385     °C (Sites 848, 849, and 853; Ford et al., 2012) across the same interval, and modern ocean

386     seasonal deviations within EEP surface waters are minor at ±1 °C (Fiedler, 1992). However, these

387     can be intensified by El Niño conditions by up to +3.8 °C (Pérez-Angel & Molnar, 2017).

388        Modern regional evaporation-precipitation balance within the EEP too shows very little

389     variation, wherein $\delta^{18}O_{sw}$ values average 0.26‰ (Fairbanks et al., 1992), ranging from ~0.2-0.5‰

390     for the entire tropical Pacific (Ravelo & Hillaire-Marcel, 2007). Factors other than temperature and

391     salinity (e.g., chlorophyll *a*, lunar cycle) which trigger species-specific habit changes (Rebotim et

392     al., 2017) could be at least partially responsible for these dramatic changes in the *G. tumida* $\delta^{18}O$

393     records, however this species is known to calcify at the base of the photic zone (Ravelo &

394 Shackleton, 1995), irrespective of thermocline depth (Ravelo & Fairbanks, 1992; Rincon-Martinez

395 et al., 2011).

396    Despite the present low range in Pacific equatorial $\delta^{18}O_{sw}$ values, modern Atlantic-

397 Caribbean surface waters record a salinity value ~3‰ less than the modern EEP (Haug et al.,

398 2001; Garcia et al., 2006; Schmidt et al., 2016; Öğretmen et al., 2020), equating to ~1.5‰ lower

399 in mean $\delta^{18}O_{sw}$ values (Ravelo and Hillaire-Marcel, 2007). This salinity contrast was fully

400 established by ~4.2 Ma (Haug et al., 2001), and consistent breaching of Atlantic-Caribbean waters

401 over the still-submerged isthmus may have occurred as late as 1.9 Ma (Coates and Obando,

402 1996; Keller et al., 1989; Schmidt et al., 2016). Therefore, a breaching event is the most probable

403 cause for the substantial variations in the $\delta^{18}O$ record of *G. tumida* from 3.071-3.061 Ma, where

404 this apparently thermocline-restricted (Fig. 2) disturbance may have contributed to disruption of

405 the *Dentoglobigerina* ecological niche habit at this time (Woodhouse et al., 2021).

406   **4.3.    Plio-Pleistocene Global Ecogroup and Evolutionary Patterns**

407    It appears the faunal turnover documented in the EEP at ~3.08 Ma (Fig. 5) may represent

408 a critical point in the development of the bipolar cryosphere which typifies the Pleistocene and

409 Holocene (Kleiven et al., 2002; Brierly & Fedorov, 2010; Cramer et al., 2009, 2011; Willeit et al.,

410 2015; Hayashi et al., 2020; Westerhold et al., 2020). Major Antarctic icesheet expansion

411 (Shevenell et al., 2004; Holbourn et al., 2015; Frigola et al., 2018; Westerhold et al., 2020)

412 following the Miocene Climatic Optimum (~17-15 Ma; Methner et al., 2020) initiated global cooling,

413 intensifying meridional gradients (Gaskell et al., 2022). This triggered unprecedented mean size

414 increases in low-latitude planktonic foraminifera (Schmidt et al., 2004a, b) and higher efficiency

415 of the biological carbon pump, promoting greater endemism and exploitation of new deep-water

416 niches in calcifying plankton (Olsson, 1982; Scott, 1982; Keller, 1985; Malmgren & Berggren,

417 1987; Scott et al., 1990; Norris et al., 1993, 1994; 1996; Norris, 1999, 2000; Rögl, 1999; Chaisson,

418    2003; Kucera & Schönfeld, 2007; Ezard et al., 2011; Crundwell, 2018; Rosenthal et al., 2018;

419    Spezzaferri et al., 2018; Lam and Leckie, 2020; Boscolo-Galazzo et al., 2021, 2022).

420        From ~6.5 Ma, the equatorial Pacific shows meridionally distinct planktonic foraminiferal

421    faunal provinces, that display a turnover in dominance from Miocene species to more Recent taxa

422    ~4 Ma (Chaisson, 1995; Chaisson and Ravelo, 2000) linked with the closure of the CAS (Haug et

423    al., 2001). Global temperatures record a gradual, stable decline towards ~3 Ma (Fig. 5;

424    Westerhold et al., 2020), after which planktonic foraminiferal morphospecies diversity shows a

425    notable decline (Aze et al., 2011; Ezard et al., 2011; Fraass et al., 2015; Lowery et al., 2020),

426    whilst ecogroups (Fig. 5) exhibit the expansion of cold-water forms coincident with the

427    development and intensification of northern hemisphere icesheets (Kleiven et al., 2002; Brierly &

428    Fedorov, 2010; Cramer et al., 2009, 2011; Willeit et al., 2015; Hayashi et al., 2020). The greater

429    proportion of cold- and deep-dwellers in the EEP at ~3.08 Ma (Fig. 2) coincides with global

430    ecogroup patterns (Fig. 5), signifying the initiation of increasing global dominance of planktonic

431    foraminiferal species with cold-water affinity, alongside many other phylogenetic groups (Slater

432    et al., 2017; Steinthorsdottir et al., 2020), as the world descended into a bipolar Icehouse state.

433        Despite the reduction in morphospecies diversity from ~3 Ma, the late Cenozoic closure

434    of the Tethyan and Central American Seaways (Crame & Rosen, 2002; Brierly & Fedorov, 2010;

435    Hamon et al., 2013; Matthews et al., 2016) may have contributed to the notable rise in diversity

436    through the Neogene (Aze et al., 2011; Ezard et al., 2011; Peters et al., 2013; Fraass et al., 2015;

437    Lowery et al., 2020), due to a significantly more heterogenous ocean structure via longitudinal

438    obstruction of tropical/subtropical waters by continental reconfiguration, and latitudinal partitioning

439    caused by the steepening of global meridional temperature gradients (Haug et al., 2001; Schmidt

440    et al., 2004a, b; Knappertsbusch, 2016; Ford et al., 2022; Friesenhagen, 2022; Gaskell et al.,

441    2022). Moreover, this intensified, heterogenous Icehouse climate may have played a significant

442    role in shaping the incredible diversity observed within modern planktonic foraminiferal cryptic

443      genotypes (Darling & Wade, 2008; Aurahs et al., 2009; Morard et al., 2009, 2013, 2019; Ujiié et

444      al., 2010; Norris & Hull, 2012; Weiner et al., 2012; 2014; André et al., 2014; Ujiié & Ishitani, 2016),

445      though further work is required on the quantification of planktonic foraminiferal cryptic diversity

446      within deep time (André et al., 2013).

447            It should be noted however, that there is a prominent increase in sampling of Quaternary

448      high latitudes that is yet to be replicated in deep-time marine records (Lazarus, 1994; Diepenbroek

449      et al., 2002; Sellén et al., 2010; O'Regan, 2011; Siccha & Kučera 2017; Waelbroeck et al., 2019;

450      Renaudie et al., 2020; Fenton & Woodhouse et al., 2021). This is due to the difficulties

451      encountered in deep-sea scientific drilling of higher latitudes through the combined impacts of

452      unpredictable and detrimental oceanographic conditions, and ephemeral sea ice (Barker et al.,

453      1977; Backman et al.; 2006; Lamy et al., 2019; McKay et al., 2019). Consequently, the substantial

454      increase in cold-water forms observed from ~3 Ma to the Recent (Fig. 5) may be at least partly

455      driven by sampling efforts.

456      **5. CONCLUSIONS**

457            The high-resolution planktonic foraminiferal biotic record at IODP Site U1338

458      chronicles important changes in late Cenozoic development of global climate and the evolutionary

459      history of this microfossil group. The co-extinction of three species of *Dentoglobigerina*, and the

460      acme of *M.* cf. *exilis* and *M.* cf. *pertenuis* signify useful regional biostratigraphic markers within

461      the Pacific chronological framework, where the former appears to be associated with abiotic

462      changes in water column structure associated with the close of the Central American Seaway,

463      and intensification of bipolar cryosphere development. These three extinct dentoglobigerinids

464      appear to exhibit a symbiotic, mixed layer ecological niche habit, however the compilation of

465      results from previous studies may suggest a high degree of unknown cryptic diversity within

466      dentoglobigerinid morphospecies complexes. The abiotic extinction mechanism likely signifies the

467      initiation of a critical stage in the formation of northern hemisphere icesheets and the

468      accompanying changes to global paleoceanography and water column structure, where cold- and

469      deep-dwelling species start to become more dominant across the globe. As the Earth continues

470      to shift away from the pre-industrial state, it becomes increasingly difficult to predict the response

471 of marine organisms to any impending climatic perturbations. However, anthropogenic forcing

472 has the capbility to melt modern continental-scale ice sheets which hold the potential to

473 dramatically disrupt global ocean circulation patterns, nutrient distributions, and water column

474 structure. Based on past changes in such systems, this may signify impending repercussions for

475 planktonic foraminiferal biodiversity, and other planktonic groups whose survival depends on the

476 vertical structure of the oceanic water column.

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

479 statistical analysis. F.A.P. collected SEM images. A.W. and T.A. contributed to the writing and

480 editing of the manuscript.

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