



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

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

modern and future marine plankton communities as anthropogenic climate forcing continues.

1 Introduction

Current observations suggest that the Earth is shifting from its pre-industrial state (Beaugrand et al., 2002; Cheung et al., 2013; Ceballos et al., 2015; Urban, 2015; Barton et al., 2016; Pinsky et al., 2018; Jonkers et al., 2019; Tierney et al. 2020; Edwards et al., 2022), and changes in the vertical and latitudinal structure of the marine realm are ultimately likely to take place (Hu et al., 2011; Rhein et al., 2013; Purich et al., 2018; Zika et al., 2018; Bindoff et al., 2019; Golledge et al., 2019). It is therefore important to understand how ecosystems such as the open ocean, which contain resources vital to human populations (Worm et al., 2003; Tittensor et al., 2010), respond to short- and long-term oceanographic shifts (e.g., Norris et al., 2013).

The timing of closure for the Isthmus of Panama at ~ 4.7 – 2.7 Ma (Keigwin, 1978, 1982; Keller et al., 1989; Haug and Tiedemann, 1998; Haug et al., 2001; Groeneveld et al., 2006; Steph et al., 2006, 2010; Molnar, 2008; Fedorov et al., 2013; O’Dea et al., 2016) remains contentious, though the ultimate role of this event in late Cenozoic icehouse evolution is clear, proving to be pivotal to the intensification of Northern Hemisphere glaciations. The precise dating of the final isthmus

formation is less essential than the repercussions of the gradual shoaling and restriction of the Central American Seaway (CAS), which triggered significant global paleoceanographic effects fundamental to the evolution of the present climate state. The gradual restriction of consistent throughflow between the tropical Atlantic and Indo-Pacific Oceans via isthmus formation (O’Dea et al., 2016) was coupled with bipolar cryosphere development that significantly restructured global vertical and meridional temperature gradients (Schmidt et al., 2004a, b; Mudelsee and Raymo, 2005; Boscolo-Galazzo and Crichton et al., 2021; Boscolo-Galazzo et al., 2022; Ford et al., 2022; Gaskell et al., 2022), altering marine ecosystems and trophic structure (Woodhouse and Swain et al., 2023). The recorded effects on global paleoceanography and biodiversity are of particular importance, as this ice sheet expansion was preceded by the sustainedly warmer world of the Pliocene. In particular, the mid-Pliocene Warm Period (mPWP, 3.264–3.025; Dowsett et al., 2012; Haywood et al., 2016) is increasingly imperative to our understanding of future climate change as global continental configuration, faunal and floral distributions, mean global temperatures (2–3 °C warmer than pre-industrial), and $p\text{CO}_2$ (350–450 ppm) were comparable to levels expected by the closure of the twenty-first century (Chandler et al., 1994; Haywood et al., 2000, 2016; Jiang et al., 2005; Pagani et al., 2010; Seki et al., 2010; Bartoli et al., 2011; IPCC, 2022).

To assess the biological responses to these marine ecosystem changes, we look to the Cenozoic marine microfossil record, specifically the planktonic foraminifera, single-celled marine protists with a global distribution and the most complete Cenozoic species-level fossil record (Aze et al., 2011; Fenton and Woodhouse et al., 2021). Their calcareous skeletons, or tests, preserve not only their entire life history, but also a biogeochemical expression of the surrounding water column (e.g., Edgar et al., 2017). These features allow for high-resolution species-specific quantification of physiological and ecological adaptation through periods of climate variability (e.g., Knappertsbusch, 2007; Wade et al., 2008, 2016; Hull and Norris, 2009; Wade and Olsson, 2009; Edgar et al., 2013a; Aze et al., 2014; Pearson and Ezard, 2014; Weinkauff et al., 2014, 2019; Brombacher et al., 2017a, 2021; Falzoni et al., 2018; Si and Aubry, 2018; Fox et al., 2020; Todd et al., 2020; Kearns et al., 2021, 2022; Pearson and Penny, 2021; Shaw et al., 2021; Woodhouse et al., 2021; Friesenhagen, 2022; Hupp et al., 2022; Woodhouse and Swain et al., 2023).

Here, we report the high-resolution biotic response of planktonic foraminifera during the terminal stages of closure of the CAS in the Eastern Equatorial Pacific (EEP) Ocean, focusing on the co-extinction of three members of the genus *Dentoglobigerina* through documentation of high-resolution (~ 5 kyr) paired single-specimen morphometric, with multi- and single-specimen geochemical analyses, and their paleoceanographic implications. Moreover, we assess the global paleoecological response of planktonic foraminifera from the Pliocene to the Recent, assessing the role of the transition

from the sustained warmth of the Pliocene to the bipolar icehouse world of Pleistocene-Recent on global planktonic foraminiferal macroevolutionary dynamics.

2 Methods

2.1 Site selection

The integrated Ocean Drilling Program Expedition 321 Site U1338 (Hole 1338A) ($2^{\circ}30.469' \text{ N}$, $17^{\circ}58.162' \text{ W}$), situated in the EEP, was drilled to 410 m below seafloor (mbsf) through Holocene – early Miocene pelagic sediments (Pälike et al., 2010). At ~ 3 Ma, the site was at $\sim 2^{\circ} \text{ N}$ paleolatitude (Drury et al., 2014) in a deep-water pelagic environment of similar water depth to the modern (~ 4 km). The primary lithologies represented are calcareous, diatomaceous and radiolarian nannofossil oozes and chalks. Despite the deep-water settings, and primarily calcareous nature of the sediments, excellent microfossil preservation has been recorded in planktonic foraminiferal specimens through intervals of this core (Fox and Wade, 2013; Woodhouse et al., 2021). A preliminary assessment of core U1338A was carried out to determine the approximate position of the extinction of several species of *Dentoglobigerina* (~ 3 Ma) based on tropical biostratigraphy (Wade et al., 2011), and shipboard paleomagnetic data (Pälike et al., 2010).

2.2 Foraminiferal assemblage analysis

Sediment volumes of 20–40 cm³ were collected and washed with de-ionized water over a 63 μm sieve; the residues were dried in an oven at 40 °C and split. All samples were examined using a Zeiss Stemi 305 Compact Stereo Microscope. Planktonic foraminifera were identified following the taxonomy of Kennett and Srinivasan (1983), Schiebel and Hemleben (2017), and Wade et al. (2018). We performed assemblage counts on $>63 \mu\text{m}$ splits yielding >300 individuals (Table S1 in the Supplement). Assessments of taxonomy and test preservation of foraminifera were performed via analysis with the Tescan VEGA3 XM Scanning Electron Microscope (SEM) at the University of Leeds, UK.

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

2.3 Morphometric analysis

Specimens of the genus *Dentoglobigerina* were measured to compare species size with stable isotope ratios to investigate species ecology and ontogeny. Complete specimens of *Dentoglobigerina* were picked and mounted in umbilical posi-

tion on card slides pierced with a fine needle to accommodate the variably spired nature of species in the genus (Wade et al., 2018). Specimens were imaged umbilically using a Zeiss Axio Zoom V16 microscope with attached Canon EOS 100D camera at $\times 19.4$ magnification. All specimens were then rotated 90° laterally and imaged whilst propped onto their penultimate chamber. Images were processed using the image analysis software Image Pro Premier, and the maximum test diameter, previously deemed a statistically repeatable measurement amongst *Dentoglobigerina* (Brombacher et al., 2017b, 2018; Woodhouse et al., 2021), was captured from both orientations, and the lower of the two values assigned as test size.

2.4 Geochemical analysis

Following morphometric analysis, well-preserved specimens of *Dentoglobigerina altispira* ($>200\ \mu\text{m}$), *Dentoglobigerina baroemoenensis* ($>200\ \mu\text{m}$) and *Dentoglobigerina globosa* ($>200\ \mu\text{m}$) were picked, ultrasonicated in deionized water for 10–15 s, and dried for stable isotope analysis. This process was repeated for extant taxa representing known discrete ecological habitats through the water column to determine the ecological niche habits of the extinct dentoglobigerinids: *Globigerinoides ruber* (212–350 μm , surface mixed-layer (SML)), *Neogloboquadrina incompta* (212–350 μm , subsurface), *Globorotalia tumida* ($>300\ \mu\text{m}$, thermocline and/or photic zone base, corrected for a 1.0‰ $\delta^{13}\text{C}$ enrichment due to this species occupying the shallow oxygen minimum zone and the consequential effects of reduced ambient pH, Lohmann, 1995; Bijma et al., 1999; Uchikawa and Zeebe, 2010; Birch et al., 2013), *Globorotalia scitula* (212–300 μm , subthermocline), and *Cibicidoides wuellerstorfi* ($>212\ \mu\text{m}$, bottom-water) (see Cramer et al., 2009, 2011; Rasmussen and Thomsen, 2010; Aze et al., 2011; Woodhouse et al., 2021). Single specimens of dentoglobigerinids and multiple specimens of other foraminifer species were analyzed using an Elementar IsoPrime Dual-Inlet Isotope Ratio Mass Spectrometer in the School of Earth and Environment at the University of Leeds, and data were reported to the Vienna Pee Dee belemnite (VPDB) scale using a Carrara marble standard (Elemental Microanalysis B2214), where analytical precision was better than 0.07‰ and 0.13‰ for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$, respectively.

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

2.5 Global data analysis

To investigate how planktonic foraminiferal macroevolution and paleoecology has developed since the Pliocene, the Triton dataset (Fenton and Woodhouse et al., 2021) was downloaded, and all macroperforate planktonic foraminiferal records occurring from 5.3–0 Ma (early Pliocene–Recent) were binned into 53-time bins with equal length (100 kyrs). Species were assigned the speciation and extinction datums in accordance with Aze et al. (2011) and Fenton and Woodhouse et al. (2021), and all species occurrences located outside of these assigned stratigraphic ranges were removed. This range trimming was applied to eliminate much of the occurrence data likely attributable to misidentification and/or reworking that may create artificial “tails” within speciation and extinction data (Liow et al., 2010; Lazarus et al., 2012; Flannery-Sutherland et al., 2022). The trimming of taxa resulted in a dataset of 239 317 planktonic foraminiferal occurrences. Furthermore, all species were assigned to their respective “ecogroups”, which represent broad ecological categories based on paleoecological and phylogenetic data (Aze et al., 2011). These ecogroups are defined as: ecogroup 1 = surface mixed layer dweller with photosymbionts, ecogroup 2 = surface mixed layer dweller without photosymbionts, ecogroup 3 = thermocline dweller, and ecogroup 4 = subthermocline dweller, ecogroup 5 = high-latitude.

3 Results

3.1 Assemblage records

All sediments contain a highly abundant well-preserved (Fig. 1) open-ocean planktonic foraminifer assemblage comprising ~ 70 morphospecies. The dominant genera through the section included *Neogloboquadrina*, *Globigerinoides*, *Pulleniatina*, and *Globigerinita* (see Supplement). The isochronous extinction of the species *D. altispira*, *D. baroemoenensis*, and *D. globosa* in U1338A occurs ~ 35.50 m b.s.f. (~ 3.037 Ma). There is also a notable influx of the species *Menardella* cf. *exilis* and *Menardella* cf. *pertenuis* occurring from ~ 42.58 – 40.56 m b.s.f. (~ 3.45 – 3.36 Ma), after which they are absent within the study section.

Comparing the assemblage composition of warm and surface dwellers against cold and deep dwellers, we document generally consistent species abundances until ~ 36.26 m b.s.f. (~ 3.08 Ma), where the assemblage exhibits consistently greater abundances of cold and deep dwellers for the rest of the record (Fig. 2).

3.2 *Dentoglobigerina* stable isotope-size trends

Test preservation is excellent throughout the sampled interval, where specimen walls appear optically translucent, and

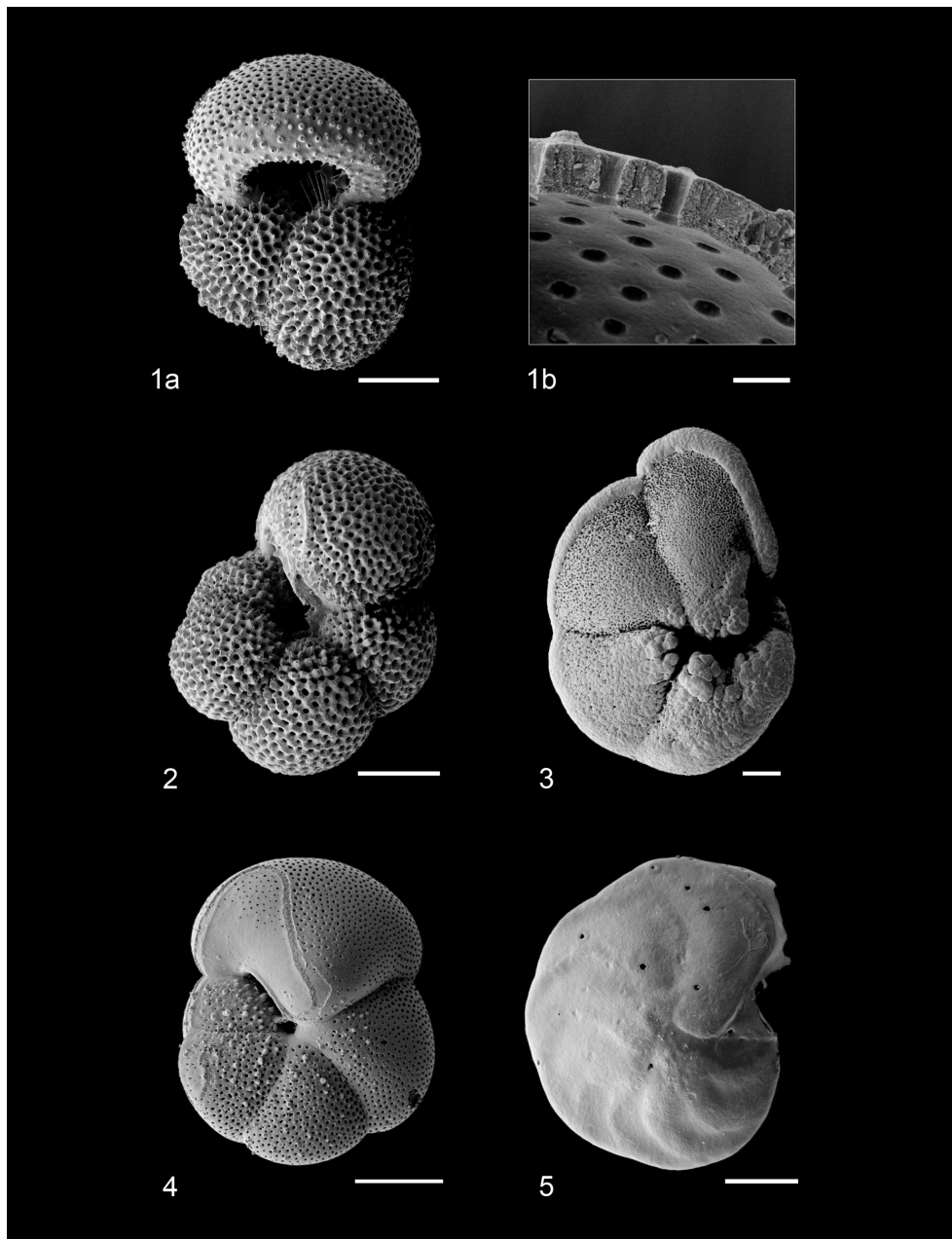


Figure 1. Scanning electron micrographs of species analyzed for stable isotope geochemistry. **(1a)** *G. ruber*, **(1b)** *G. ruber* shell ultrastructure showing excellent preservation, **(2)** *N. incompta*, **(3)** *G. tumida*, **(4)** *H. scitula*, **(5)** *C. wuellerstorfi*. Scale bar for images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

SEM images (Fig. 1) indicate no observable diagenetic alteration, clean pore spaces, and spines preserved within tests (Fig. 1a). Following artificial test breaking, inspection of the wall ultrastructure (Fig. 1b) showed that no wall recrystallization had taken place, suggesting stable isotope signals remain unaltered (Sexton et al., 2006; Edgar et al., 2013b). Single-specimen $\delta^{13}\text{C}$ values for *D. altispira*, *D. baroemouensis*, and *D. globosa* vary from -0.54‰ to $+3.53\text{‰}$, $+0.30\text{‰}$ to $+3.50\text{‰}$, and $+0.51\text{‰}$ to $+2.84\text{‰}$ (Fig. 3, Ta-

bles S3 and S4), respectively, whilst $\delta^{18}\text{O}$ values vary from -3.56‰ to -0.03‰ , -2.99‰ to -0.17‰ , and -1.92‰ to -1.05‰ , respectively. In all three species, a positive correlation is calculated between test size and $\delta^{13}\text{C}$; however, this relationship is only significant ($p < 0.0001$) in *D. altispira* and *D. baroemouensis*, potentially due to the greater number of specimens analyzed for these species (Fig. 3). Regression slopes are similarly steep; however the slopes for *D. altispira* and *D. globosa* are more alike. *Dentoglobige-*

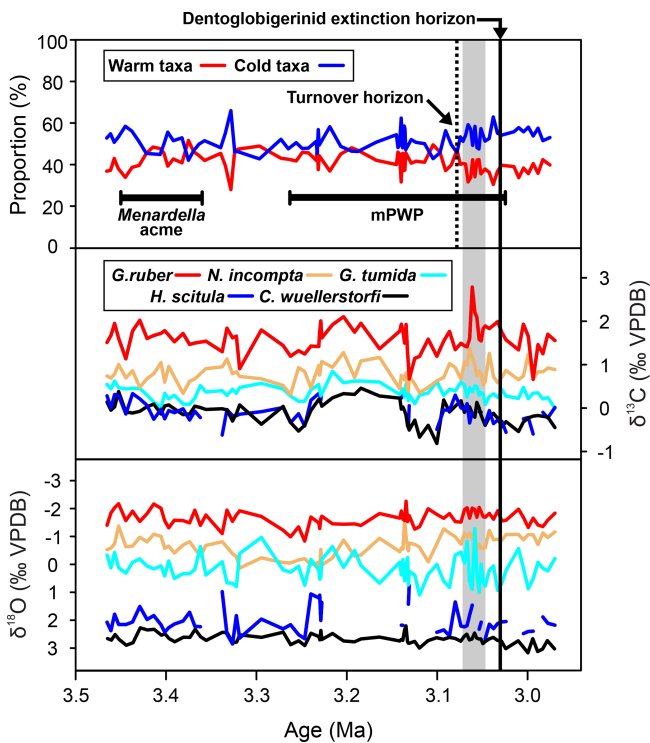


Figure 2. Grouped assemblage data of warm-water taxa (ecogroups “symbiotic” and “asymbiotic”) and cold-water taxa (ecogroups “thermocline”, “subthermocline”, and *Globigerinita glutinata* (Lutz, 2010; Aze et al., 2011). Foraminiferal $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$, black = *C. wuellerstorfi*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

rina baroemoenensis and *D. globosa* show no significant correlation between $\delta^{18}\text{O}$ and test size; however, a significant ($p = 0.0006$) negative relationship is recorded in *D. altispira*. Once again, regression slopes for *D. altispira* and *D. globosa* are similar, whereas for *D. baroemoenensis*, this slope is almost flat (Fig. 3).

3.3 Extant species geochemical records

Amongst the extant species picked from strict size fractions throughout the study section, *G. ruber* $\delta^{13}\text{C}$ values show 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‰ (Fig. 4, Table S2). Corrected *G. tumida* values show the lowest $\delta^{13}\text{C}$ variability (0‰ to +0.8‰), and the highest 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 $\delta^{18}\text{O}$ varies from +0.8‰ to +2.9‰, whereas bottom-water *C. wuellerstorfi* $\delta^{13}\text{C}$ values vary from −0.8‰ to +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 sta-

ble isotope records of extant species generally tend to show low inter-sample variability, however there is notable geochemical stochasticity within the *G. tumida* record ~36.17–35.86 m b.s.f. (Fig. 2).

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

3.4 Global Pliocene-Recent Ecogroup trends

The global proportions of planktonic foraminiferal ecogroups within the Triton dataset (Fenton and Woodhouse et al., 2021) show that throughout the time interval studied (5.3–0 Ma), surface mixed layer dwellers without photosymbionts (orange) proportions remain relatively consistent, making up ~10% of the total global fauna (Fig. 5). From 5.3–3 Ma, global ecogroup proportions are relatively consistent, where the dominant forms are thermocline dwellers (cyan) and surface mixed layer dwellers with photosymbionts (red) (Fig. 5), making up ~40% and ~35% of the global fauna, respectively. During this interval, the proportion of subthermocline dwellers (blue) and high-latitude forms (yellow) also remain relatively consistent with ~10% and <5% of total proportions, respectively. After ~3 Ma, both thermocline dwellers and surface mixed layer dwellers with photosymbionts show a steady decline in global representation approaching the Recent, making up ~20% each in the modern ocean. At ~3 Ma, both the subthermocline dwellers and high-latitude ecogroup start to show increases in their proportions, though this increase approaching the modern is much greater in the latter group. During the last 100 kyrs, subthermocline and high-latitude species have constituted ~15% and ~25%, respectively (Fig. 5).

4 Discussion

Few major changes in the assemblage composition are observed through the study interval, other than the isochronous extinction of *D. altispira*, *D. baroemoenensis*, and *D. globosa* at ~3.037 Ma (Fig. 2; 35.50 m b.s.f.), and the influx of the two species *M. cf. exilis* and *M. cf. pertenuis* through ~3.45–3.36 Ma (42.58–40.56 m b.s.f.), defined henceforth as the “*Menardella acme*” (Figs. 2 and 6).

4.1 Dentoglobigerinid paleoecology

The extinction of *D. altispira* is a useful marker in the mid-Pliocene, previously recorded within the East Equatorial Pacific Ocean (3.46 Ma; Shackleton et al., 1995; Wade et al., 2011); however, this study and that of Woodhouse et al. (2021) provide recalibration for this event, which also in-

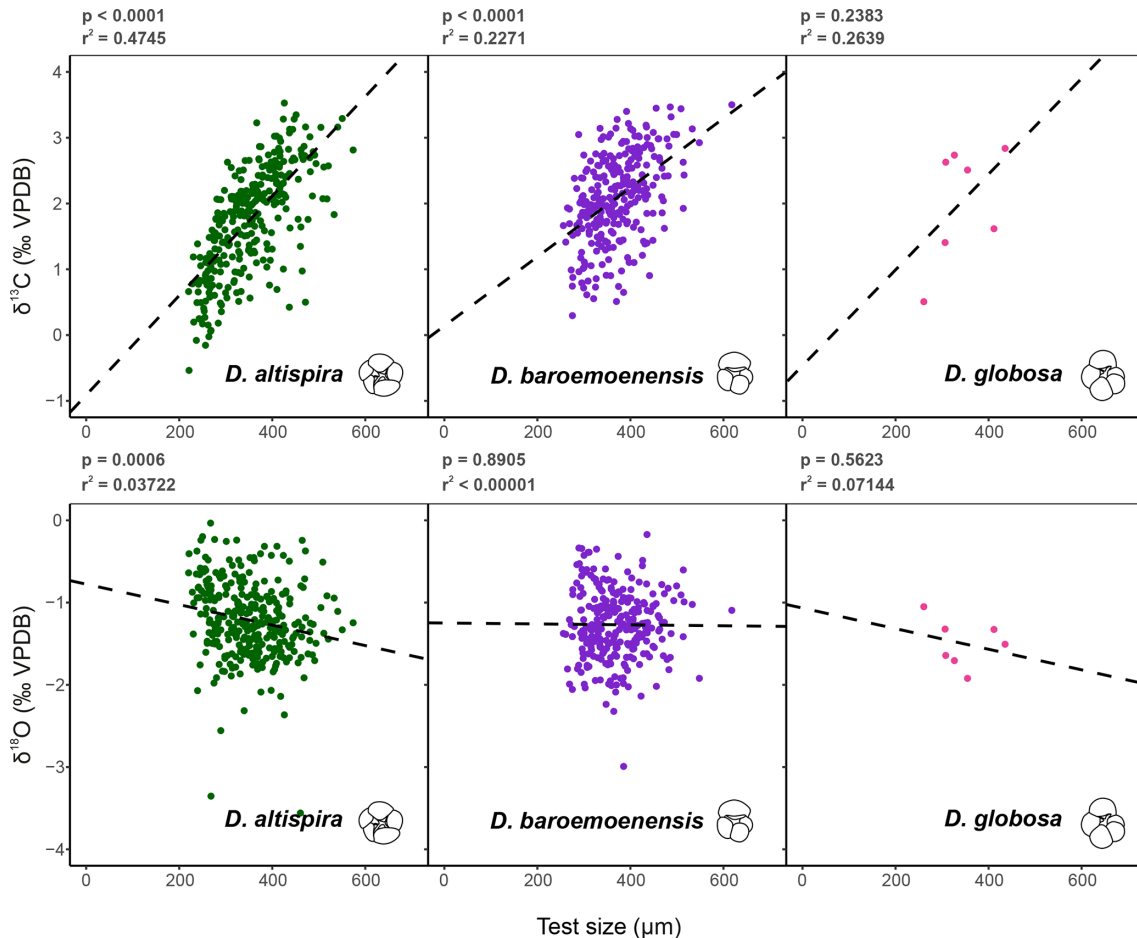


Figure 3. Test size – $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ relationships for the three species of *Dentoglobigerina* that underwent extinction through the study section. Trend lines for each species represent linear regressions based on the entire per species dataset (dashed line). Significance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

cludes the co-extinction of *D. baroemoenensis* and *D. globosa*. The co-extinction of the dentoglobigerinids is significant as Woodhouse et al. (2021) demonstrated that *D. altispira* and *D. baroemoenensis* show unique phenotypic responses leading up to their termination, despite their shared phylogenetic and ecological affinity. We, therefore, suggest that all three species share an ecological habit that ultimately proved inefficient to mitigate the changing abiotic conditions associated with this critical period of bipolar cryosphere development (Kleiven et al., 2002; Brierley and Fedorov, 2010; Cramer et al., 2009, 2011; Willeit et al., 2015; Hayashi et al., 2020; Westerhold et al., 2020).

Studies of extant species suggest a strong positive correlation between planktonic foraminifera $\delta^{13}\text{C}$ and test size, paired with a lack of a strong negative significant relationship in $\delta^{18}\text{O}$ and test size, is indicative of species bearing photosymbiotic algae (e.g., Berger et al., 1978; Bouvier-Soumagnac and Duplessy, 1985; Spero and Williams, 1988, 1989; Spero et al., 1991; Spero, 1992; Spero and Lea, 1993; Ravelo and Fairbanks, 1995; Norris, 1996; Birch et al.,

2013). Our data suggests that all three species of *Dentoglobigerina* studied here are symbiont-bearing, displaying mean stable isotope data similarly to the symbiont-bearing surface mixed layer dwelling *G. ruber* (Figs. 2–4). Moreover, the regression lines for the ancestor-descendent pair *D. globosa* – *D. altispira* are remarkably similar, suggesting that the species share similar stable isotope-test size relationships, despite the speciation of *D. altispira* occurring ~ 20 Myrs prior (Aze et al., 2011; Wade et al., 2011, 2018). However, the substantially fewer data for *D. globosa* currently limits the significance of this observation for this particular species (Fig. 3).

The results presented here contribute to the variety of interpretations from previous studies on the paleoecology of *D. altispira*. Spanning different ocean basins throughout the species' stratigraphic range they suggest: a shallow-dwelling (e.g., Keller and Savin, 1985; Vincent et al., 1985; Prentice and Matthews, 1988; Corfield and Cartlidge, 1991; Norris et al., 1993; Hodell and Vayavananda, 1994; Sosdian and Lear, 2020), deep-dwelling (Opdyke and Pearson, 1995; Pearson

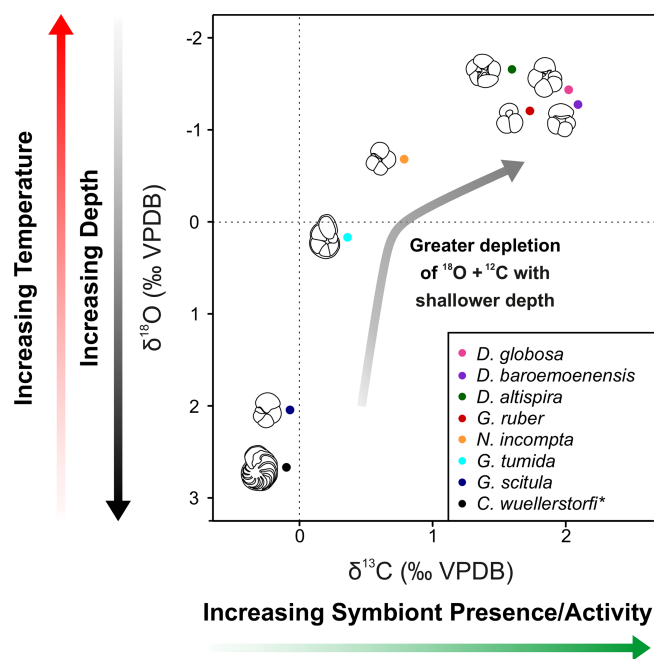


Figure 4. $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ cross-plot 2 showing mean values of all specimens analyzed in this study. Black = *C. wuellerstorfi*, dark blue = *G. scitula*, cyan = *G. tumida*, orange = *N. incompta*, red = *G. ruber*, green = *D. altispira*, purple = *D. baroemoenensis*,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

and Shackleton, 1995), or lower mixed layer/upper thermocline (Zou et al., 2022) ecological niche habit.

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

Another plausible scenario may be the existence of indeterminate cryptic diversity within the *D. altispira* morphospecies complex where multiple ecological strategies or phylogenetic expressions may be present (e.g., Huber et al., 1997; Bijma et al., 1998; de Vargas et al., 1999, 2002; Weiner et al., 2012; Schiebel and Hemleben, 2017; Nirmal et al., 2021; Pearson and Penny, 2021), and the stepwise changes observed by Woodhouse et al. (2021) may indicate the systematic loss of “cryptic genotypes” within this morphospecies complex. Indeed, Pearson and Penny (2021), hypothesized that dramatic abundance switches in the Indo-Pacific Warm Pool of ecologically distinct, alternately coiled populations of *Pulleniatina* morphospecies may signify re-

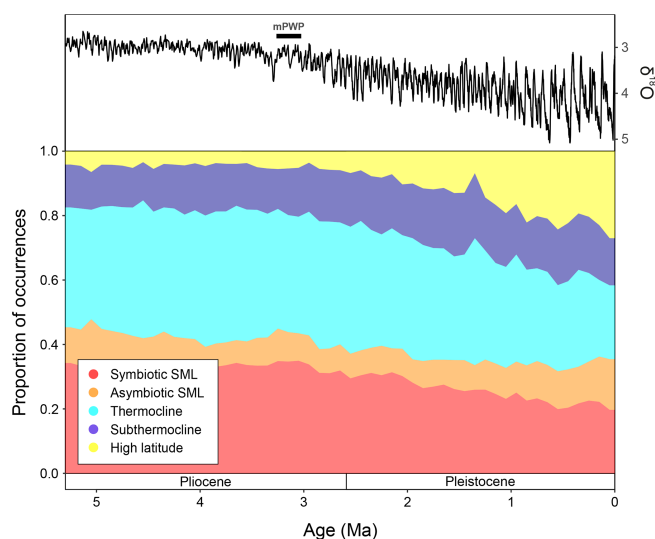


Figure 5. The LR04 stack showing benthic foraminiferal $\delta^{18}\text{O}$ (from Lisiecki and Raymo, 2005) and proportions of macroperforate planktonic foraminifera occurrences assigned to the ecogroups of Aze et al. (2011), binned to 100 kyrs from 5.3 Ma to the Recent. mPWP = mid-Pliocene Warm Period,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

placement by distinct cryptic genotypes, and such coiling switches are noted throughout the planktonic foraminiferal fossil record (Ericson et al., 1955; Saito et al., 1975; Bossio et al., 1976; Hallock and Larsen, 1979; Hornibrook, 1982; Scott et al., 1990; Norris and Nishi, 2001; Winter and Pearson, 2001; Crundwell and Nelson, 2007; Wade et al., 2011; Pearson and Ezard, 2014; Crundwell, 2015a, b; Levin et al., 2016; Wallace et al., 2019; Crundwell and Woodhouse, 2022a, b). Therefore, the range of interpreted paleoecologies in *D. altispira* may, in fact, be due to the occurrence of distinct cryptic populations from across the geological record. Irrespectively, the abiotic conditions at this time appear to have become fatally detrimental to the entire ecological habit of all three morphospecies of *Dentoglobigerina* analyzed in the EEP, and subsequently across the entire globe (Shackleton et al., 1995; Chaisson and Pearson, 1997; Wade et al., 2011; Raffi et al., 2020; Groeneveld et al., 2021; Woodhouse et al., 2021).

4.2 The *Menardella acme*

The transient influx and co-occurrence of *M. cf. exilis* and *M. cf. pertenuis* from ~ 3.45 – 3.36 Ma may indicate a shared ecological affinity between these species (Fig. 2; Kennett and Srinivasan, 1983; Knappertsbusch, 2016). Furthermore, this association may suggest that these two similar forms exist within the same genetic species complex, though further study on internal shell ontogeny and external morphology would be required to confirm this hypothesis. Notably, however, Kaneps (1970) and Chaisson (2003) suggested that Indo-Pacific occurrences of these two species are, in fact,

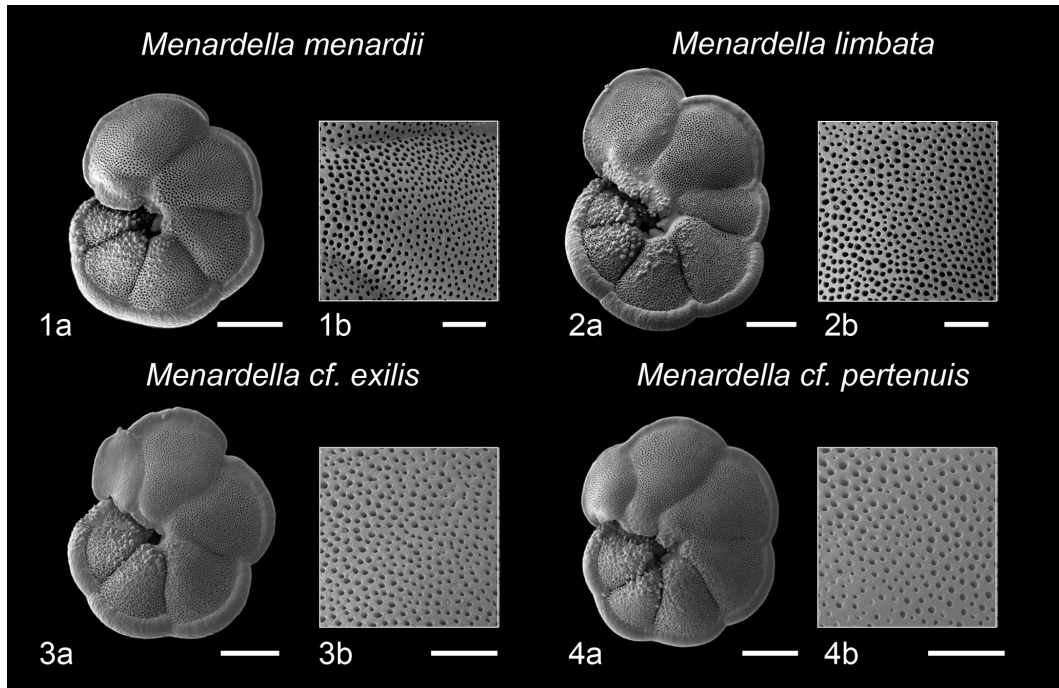


Figure 6. Scanning electron micrographs of select species of *Menardella* and pore detail of penultimate chambers. (1a) *M. menardii*, (1b) *M. menardii* pore detail, (2a) *M. limbata*, (2b) *M. limbata* pore detail, (3a) *M. cf. exilis*, (3b) *M. cf. exilis* pore detail, (4a) *M. cf. pertenuis*, (4b)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

Table 1. The number of pores per $2500\mu\text{m}^2$ in the penultimate chamber of select species of *Menardella*.

Species	Pore density (per $2500\mu\text{m}^2$)
<i>M. menardii</i>	32
<i>M. limbata</i>	27
<i>M. cf. exilis</i>	51
<i>M. cf. pertenuis</i>	49

“aberrant” forms of *Menardella limbata* and *Menardella menardii*, with the *M. exilis-pertenuis* plexus being solely endemic to the Atlantic basin (Sexton and Norris, 2011).

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

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

4.3 Pliocene EEP paleoceanography

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 m b.s.f.; 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 contractions and expansions in their respective ecospace (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 and Crichton et al., 2021; Boscolo-Galazzo et al., 2022; Woodhouse and Swain et al., 2023).

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

The geochemical fluctuations noted within *G. tumida* from 3.071–3.061 Ma (36.17–35.86 m b.s.f.; Fig. 2) are coeval with the interval assigned to the “phase transition” by Woodhouse et al. (2021), in which *D. altispira* and *D. baroemoneensis* exhibit dramatic fluctuations in size and shape preceding rapid ecological changes. Here, the $\delta^{18}\text{O}$ signal of *G. tumida* exhibits substantial and rapid changes up to $\sim 2.1\text{‰}$, switching from typical thermocline values to those indicative of the subsurface, and back again, whereas all other water column $\delta^{18}\text{O}$ value changes are nominal (Fig. 2).

If the fluctuations within the $\delta^{18}\text{O}$ signal of *G. tumida* were related to fluctuations in its depth habitat, we would expect the inverse pattern to occur in its $\delta^{13}\text{C}$ signature, as $\delta^{13}\text{C}$ values decrease with depth (Cannariato and Ravelo, 1997;

Ford et al., 2012; Birch et al., 2013); however, this is not the case (Fig. 2, Table S2). The maximum $\delta^{18}\text{O}$ excursion value ($\sim 2.1\text{‰}$) is equivalent to a temperature change of $\sim 10\text{°C}$, based on a mid-Pliocene SMOW value of -0.3‰ (Williams et al., 2005; Medina-Elizalde, Lea and Fantle, 2008; Tindall and Haywood, 2015) and the paleotemperature equations of Kim and O’Neil (1997). Previous studies from EEP sites show Mg / Ca-derived thermocline temperature fluctuations of $\sim 3\text{°C}$ (Site 1241; Steph et al., 2006) to $\sim 5\text{°C}$ (Sites 848, 849, and 853; Ford et al., 2012) across the same interval, and modern ocean seasonal deviations within EEP surface waters are minor at $\pm 1\text{°C}$ (Fiedler, 1992). However, these can be intensified by El Niño conditions by up to $+3.8\text{°C}$ (Pérez-Angel and Molnar, 2017).

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

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

4.4 Pliocene-Recent global ecological and evolutionary patterns

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

matic Optimum ($\sim 17\text{--}15$ 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 and Berggren, 1987; Scott et al., 1990; Norris et al., 1993, 1994, 1996; Norris, 1999, 2000; Rögl, 1999; Chaisson, 2003; Kucera and Schönfeld, 2007; Ezard et al., 2011; Crundwell, 2018; Rosenthal et al., 2018; Spezzaferri et al., 2018; Lam and Leckie, 2020; Boscolo-Galazzo and Crichton et al., 2021; Boscolo-Galazzo et al., 2022; Woodhouse and Swain et al., 2023).

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 and 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.

Despite the reduction in morphospecies diversity from ~ 3 Ma, the late Cenozoic closure of the Tethyan and Central American Seaways (Cramer and Rosen, 2002; Brierly and Fedorov, 2010; Hamon et al., 2013; Matthews et al., 2016) may have contributed to the notable rise in diversity through the Neogene (Aze et al., 2011; Ezard et al., 2011; Peters et al., 2013; Fraass et al., 2015; Lowery et al., 2020), due to a significantly more heterogeneous ocean structure via longitudinal obstruction of tropical-subtropical waters by continental reconfiguration, and latitudinal partitioning caused by the steepening of global meridional temperature gradients (Haug et al., 2001; Schmidt et al., 2004a, b; Knappertsbusch, 2016; Ford et al., 2022; Friesenhagen, 2022; Gaskell et al., 2022). Moreover, this intensified, heterogeneous icehouse climate may have played a significant role in shaping the incredible diversity observed within modern planktonic foraminiferal cryptic genotypes (Darling and Wade, 2008; Aurahs et al., 2009; Morard et al., 2009, 2013, 2019; Ujiie et al., 2010; Norris and Hull, 2012; Weiner et al., 2012, 2014; André et al., 2014; Ujiie and Ishitani, 2016), though

further work is required on the quantification of planktonic foraminiferal cryptic diversity within deep time (André et al., 2013).

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

5 Conclusions

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

Globally, planktonic foraminiferal ecological and macroevolutionary patterns were fundamentally different prior to bipolar ice sheet expansion, and past intervals with climatic conditions analogous to future-warming scenarios such as the mid-Pliocene Warm Period require further prospecting at multiple spatiotemporal scales to better predict potential changes in global marine biodiversity as the Earth continues to shift away from its pre-industrial state. Furthermore, anthropogenic forcing has the capability to melt modern continental-scale ice sheets, which hold the potential to dramatically disrupt global ocean circulation patterns, nutrient distributions, and water column structure. Based on past changes in such systems, this may signify

impending repercussions for planktonic foraminiferal biodiversity and other planktonic groups whose survival depends on the vertical structure of the oceanic water column.

Data availability. All data included in the Supplement.

Sample availability. All samples available upon request.

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