

Creating an extensive, multi-species planktonic foraminifera isotope record at an Eocene-Oligocene high latitude site

By Paige Breen
Advisor: Pincelli Hull
Second Reader: Mark Pagani
May 2, 2016

A Senior Thesis presented to the faculty of the Department of Geology and Geophysics, Yale University, in partial fulfillment of the Bachelor's Degree.

In presenting this thesis in partial fulfillment of the Bachelor's Degree from the Department of Geology and Geophysics, Yale University, I agree that the department may make copies or post it on the departmental website so that others may better understand the undergraduate research of the department. I further agree that extensive copying of this thesis is allowable only for scholarly purposes. It is understood, however, that any copying or publication of this thesis for commercial purposes or financial gain is not allowed without my written consent.

Paige Breen, 2 May, 2016

Abstract

In order to gain a better understanding of the paleoceanographic implications of the Eocene-Oligocene Transition (EOT), the most significant climatic change of the Cenozoic, a more comprehensive planktonic foraminifera stable isotope record is needed. After obtaining $\delta^{18}\text{O}$ measurements to define relative paleodepths within the water column and $\delta^{13}\text{C}$ measurements to determine the isotopic impact of vital effects, it is possible to use these planktonic species as tracers of surface water conditions across the transition. Here we measure more than forty different species across nineteen genera, eight narrow size fractions, and ten time slices when specimens are available. The samples, all from a high latitude, North Atlantic site, are well-preserved, an important requirement of isotopic studies. This dataset confirms findings of previous research on well-studied species, further constrains our understanding of minimally studied species, and provides data and isotopic context for several unstudied species. We also make note of taxonomic anomalies throughout the time interval. With a thorough isotopic understanding of the species included here, we then used this data to determine the overall significance of surface-to-deep carbon and oxygen gradients across the EOT and the relative genus-level shifts in carbon and oxygen stable isotope measurements.

Introduction

The Eocene-Oligocene Transition (~34 Ma) is the largest climate shift of the Cenozoic and marks the transition from a greenhouse climate to an icehouse with the onset of Antarctic glaciation (Coxall and Wilson, 2011). In the deep ocean, this transition is recorded by a two-step increase in $\delta^{18}\text{O}$ and a ~1 ‰ positive excursion $\delta^{13}\text{C}$ of benthic foraminifera (Coxall et al., 2005; Scher et al., 2011; Diester-Haass and Zahn, 1996). The exact trigger for the onset of Antarctic glaciation across the EOT is still debated. Hypothesized causes include changes in ocean-atmosphere heat exchange related to the formation of the Southern Ocean with the opening of the Tasmanian Gateway and Drake Passage (Scher et al., 2006; Scher et al., 2015) and interaction of the long-term draw-down in atmospheric CO_2 with orbital forcing (Coxall and Wilson, 2011; Pagani et al.,

2011). Refined paleoceanographic records of surface water temperatures are key to resolving the mechanisms leading to the transition from greenhouse to icehouse across the EOT.

Eocene and Oligocene planktonic foraminifera, like modern planktonic foraminifera, inhabited a broad variety of depth habitats and ecologies in the open ocean (Pearson et al., 2001; Pearson et al., 1993). Extant planktonic foraminifera live from the mixed layer to the subthermocline (~500 m of the water column; Hemleben et al., 1989), with varying depth habitats within species by season, ontogeny, and local hydrographic conditions (Hemleben et al., 1989). In Eocene taxa, depth habitat is typically determined using $\delta^{18}\text{O}$ values of foraminiferal calcium carbonate (CaCO_3) tests, a tracer of the temperature of precipitation. Stable carbon isotope measurements ($\delta^{13}\text{C}$) are also used to infer some aspects of planktonic foraminifera ecologies in extinct taxa (e.g. photosymbiont-bearing to not; Birch et al., 2013). Because foraminiferal ecology can offset their test geochemistry from that of the surrounding waters, careful understanding of, and control for, their ecology underpins the utility of planktonic foraminifera as paleoceanographic proxies of environmental conditions such as surface water temperature.

For all the interest in EOT oceans, there are relatively few studies of planktonic foraminiferal isotope ecology including multiple species, multiple size fractions, and glassy preservation. Understanding how each species' isotopic character changes across size fraction is vital to determining how much life stage affects a given stable isotope measurement and, therefore, our understanding of paleoceanographic conditions. A 2006 study by Sexton et al. incorporated data from many middle Eocene planktonic species and several narrow size fractions using samples from Blake Nose in the Northwest Atlantic. The research provided information regarding the diversity of middle to late Eocene planktonic foraminifera and the effects of seasonality. However, the data was constricted to two time slices (37.47 and 39.35 Ma; Sexton et al., 2006). Another study incorporated twelve species and several narrow size fractions using modern planktonic foraminifera off the coast of Tanzania (Birch et al., 2013). Birch's

findings demonstrated the importance of using many size fractions, as each species showed significant variation in $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ depending on its life stage. Using twenty species from the middle Eocene obtained at a low-latitude site (DSDP Site 523 in the South Atlantic), Pearson et al. collected size-specific data for an interval spanning approximately two million years (Pearson et al., 1993). However, no previous study has comprehensively surveyed the isotope ecology of middle to late Eocene species across the broad range of size fractions needed to confidently assess ecology. My thesis was designed to fill this gap, sampling more than forty-five species across eight narrow size fractions from a high latitude spanning from the middle Eocene to early Oligocene.

Recently drilled sediments from Integrated Ocean Drilling Program (IODP) Expedition 342 (Newfoundland, North Atlantic Ocean) Site U1408 ($41^{\circ} 26.3'\text{N}$, $49^{\circ} 47.1'\text{W}$; paleodepth at 50 Ma is ~ 2575 m) and Site U1411 ($41^{\circ} 37.1'\text{N}$, $49^{\circ} 00'\text{W}$; paleodepth at 50 Ma is ~ 2850 m) present an excellent opportunity to build on existing work and to finely detail planktonic foraminiferal ecology in well-preserved samples from the middle Eocene through the EOT (Norris et al., 2014). These cores contain clay-rich sediment and have not undergone significant burial and diagenesis. The paleodepths at these sites were both well above the carbonate compensation depth (CCD) at the time.

Here I take advantage of the opportunity afforded by these cores and sample more than forty-five species across eight narrow size fractions in nine different Eocene-Oligocene planktonic foraminiferal Biozones (E9-O1; ~ 46 – ~ 33 Ma). My thesis has five primary aims: i) to finely document the quality of Expedition 342 planktonic foraminifera preservation and to consider its isotopic effects; ii) to provide a first, detailed taxonomic consideration of Expedition 342 planktonic foraminifera; iii) to detail the stable isotope ecology of middle Eocene to earliest Oligocene planktonic foraminifera; iv) to examine the evolution of planktonic foraminiferal isotope ecology across this interval; and v) to determine the reliability of surface water temperature tracers across the EOT given the mass extinction of *Acarinina* and *Morozovelloides*. These genera reside closest

to the surface of all the species measured, and their disappearance across the EOT not only complicates how to trace surface temperatures, but also indicates drastic changes in the surface water environment.

Glassy preservation is essential to this project. Past studies have shown that poor preservation can produce misleadingly high $\delta^{18}\text{O}$ values, suggesting cooler temperatures than are actually realistic. The “cool tropic paradox” records this anomaly in both the Cretaceous (~100-80 Ma) and the middle Eocene (Sexton, 2006; Wilson et al., 2002). Recrystallization of fossils collected from the tropics led to tropical temperature estimates far below what models predict and what better-preserved fossils measured. Recrystallized fossils gave a temperature estimate between 15 and 23° C, whereas well-preserved fossils from a similar location gave an estimate between 28 and 32° C (Pearson et al., 2001). In addition, poor preservation causes smaller isotopic gradients between different species (Wade et al., 2007). For a study that relies on stable isotope measurements to distinguish the ecologies of different species, glassy preservation that more accurately represents the water temperature and isotopic gradients between species is key.

Reliably tracing surface ocean change across the EOT is further complicated by the mass extinction (~38 Ma; Bambach, 2006), which included heavy losses in many planktonic foraminiferal clades (Cotton and Pearson, 2011; Miller et al., 2009; Wade, 2008). Mass extinctions are often highly selective (Keller et al., 1995) and can preferentially remove species that trace specific habitats. For instance, across the K-Pg mass extinction, mixed layer-dwelling macroperforate planktonic foraminifera may have been entirely lost for roughly a million years (Berggren and Norris, 1997; Birch et al., 2012). Similar to the K-Pg, the dominant clade of mixed layer-dwelling planktonic foraminifera went extinct across the EOT (Wade, 2004; Wade, 2012). Surface-dwellers *Acarinina* and *Morozovella* went extinct within 11,000 years of each other approximately 38 Ma (Wade, 2004), well before the EOT at ~33.5 Ma (Zanazzi et al., 2007). In addition, many other species in genera such as *Globigerinatheka*, *Hantkenina*, and *Turborotalia* went extinct before the EOT. Here, I provide a first test of

whether the selective extinction of planktonic foraminiferal taxa in the late Eocene and across the EOT systematically biases records of water column evolution and paleoceanographic change across the EOT. We examine the stable isotope (oxygen and carbon) space across taxa for clades spanning all common ecologies (symbiotic and asymbiotic) and water column habitats from the middle Eocene (~46 Ma) across the EOT (~33 Ma). This approach allows us to detect changes to the carbon cycle and depth habitat of various clades (John et al., 2013; Birch et al., 2013), particularly as the dominant mixed-layer taxa (*Acarinina* and *Morozovelloides*) go extinct (Wade, 2004). In addition, we use size-specific data to consider changing photosymbiotic interactions at this time (Ezard et al., 2015; Birch et al., 2013).

In addition to the effect of disappearing surface-dwellers across the EOT, we are interested in the ecology of all planktonic foraminiferal taxa across these major transitions. Ontogenetic effects, seasonal variability, and respiration (Birch et al., 2012) often impact the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of a foraminiferal CaCO_3 shell. To account for this complication, our study incorporates multiple species and several narrow size fractions (63-180, 150-180, 180-212, 212-250, 250-300, 300-355, 355-425, >425 μm). Since foraminifera grow in size as they age, size fractions correspond to different stages of foraminiferal development. Incorporating so many narrow size fractions enables us to identify possible ontogenetic effects, whether a foram gains a photosymbiont at a certain life stage, and whether any other vital effects are impacting measurements. These cores (Sites U1408 and U1411) present the opportunity to study a comparatively unknown and complex habitat because they are located at a relatively high latitude where upwelling makes water column stratification less well-defined than in a tropical setting (Peeters et al., 2002). For this project, we selected previously studied species at known depths of the water column so the measurements would span the mixed layer (*Acarinina*, *Chiloguembelina*, *Globigerinatheka*, *Globoturborotalita*, *Guembelitrionides*, *Morozovelloides*, *Orbulinoides*, *Pseudohastigerina*, *Tenuitella*, *Turborotalia*), thermocline (*Hantkenina*, *Paragloborotalia*, *Turborotalita*), and deep thermocline (*Catapsydrax*,

Dentoglobigerina, *Globorotaloides*, *Subbotina*,) (Pearson et al., 2006). Several species that had never before been isotopically analyzed (*Praemurica(?) lozanoi*, *Globigerinatheka barri*) were measured in this study and placed in the isotopic context of the previously studied species. Notably, this time interval spans the extinction of *Acarinina* and *Morozovelloides* at ~38 Ma (Wade, 2004), two genera abundant at the earliest time slices included here. Previous studies show that *Acarinina*, *Morozovelloides*, and, perhaps, *Globigerinatheka* have photosymbionts (D'hondt et al., 1994; Edgar et al., 2013). Other studies indicate that *Hantkenina* was originally deep-dwelling and migrated upwards throughout the Eocene (Coxall et al., 2003). This project seeks to further investigate both these previously observed trends and those never before measured.

Foraminiferal taxonomy is often disputed due to the presence of many transitional forms, morphological differences depending on the site, and subtle interspecies differences. Therefore, the taxonomic concept of each species used for these measurements is thoroughly recorded and multi-view light images were obtained of the sample before each isotope analysis. Such comprehensive photo-documentation is unprecedented and means that each isotope measurement corresponds to two light images of the included specimens at different orientations. Given that even the most experienced and knowledgeable foraminifera taxonomists still have difficulty identifying species, this record enables anyone to see exactly what a measurement is recording and how those specimens fit into their own taxonomic concept.

Work for my thesis began in January of 2015 when I started learning Eocene taxonomy and identifying species with the help of Pincelli Hull and Simon D'haenens. In addition, during the spring semester Simon D'haenens led a middle Eocene reading group that met weekly to discuss relevant papers. With the support of the Alan S. Tetelman Fellowship for International Research in the Sciences, I went to the University of Bristol in the United Kingdom to learn middle Eocene taxonomy from a leading expert, Kirsty Edgar, for five weeks in the summer of 2015. During that time, I picked species for the samples ranging from E9-E13. I then returned to New Haven for the remainder of the summer to finish

picking samples, image each measurement, and obtain stable isotope values. Leanne Elder taught me how to image the foraminifera and also provided assistance in cataloging the samples for the Peabody Museum. Simon D'haenens and Rain Tsong ran the KIEL IV Carbonate Device at the Yale Analytical and Stable Isotope Center to obtain stable isotope measurements. My summer in New Haven was funded by the Karen von Damm '77 Undergraduate Research Fellowship in Geology and Geophysics and the Yale College Dean's Research Fellowship. The Yale Analytical and Stable Isotope Center funded a portion of the measurements. In September, I had the opportunity to attend the Expedition 342 Post-Cruise Science Meeting in Snowbird, Utah with partial support from the Saybrook College Bruce M. Babcock '62 Travel Fellowship. At this conference, I presented my findings up to that point. Helen Coxall from Stockholm University was interested to broaden the time interval of this project to span across the EOT. She and Max Holmstrom picked and contributed samples from the late Eocene and early Oligocene to the project. Helen Coxall also shared measurements previously collected by her former student, Anna Nyberg, from those time intervals. In addition, Kirsty Edgar picked microfossil species from the middle Eocene Biozone samples to expand the size ranges included in the study. These samples were received, imaged, and measured in early 2016. In addition to the Snowbird conference, this research has been presented at the Geological Society of America annual meeting and at the Saybrook College Mellon Forum.

Methods

Planktonic foraminifera were analyzed from ten samples spanning ten planktonic foraminiferal Biozones (E9-O2, or ~46 - ~33 Ma) from Integrated Ocean Drilling Program (IODP) Expedition 342 (Newfoundland, North Atlantic Ocean) Site U1408 (41° 26.3'N, 49° 47.1'W; paleodepth at 50 Ma is ~2575 m) and Site U1411 (41° 37.1'N, 49° 00'W; paleodepth at 50 Ma is ~2850 m) (Norris et al., 2014). Middle Eocene samples at U1408 and U1411 show exceptional "glassy" preservation (Sexton et al., 2006) and are generally free of infilling (Site

U1408 Report, 2014; Site U1411 Report, 2014). Glassy preservation ensures the signals these data record across the EOT are primary rather than an artifact of diagenesis (Pearson et al., 2001; Pearson et al., 2009; Wilson et al., 2002). Taxonomy follows Pearson et al., 2006 and age models follow the Geologic Time Scale 2012, with planktonic foraminiferal biozonation update from shipboard site reports (Site U1408 Report, 2014; Site U1411 Report, 2014).

Each sediment sample (~20 cc volume) was washed by soaking in deionized water and then wet-sieving through a 63 μm mesh. For each of the ten samples, up to fifty-one foraminiferal species were picked for stable carbon and oxygen isotope analyses from eight narrow size fractions (63-150, 150-180, 180-212, 212-250, 250-300, 300-355, 355-425, and >425 μm). Size-specific isotopes were used to infer symbiont ecology, and are displayed as generic averages (Figure 1). Depth habitat distributions are considered in the 250-300 μm size fraction for *Acarinina*, *Catapsydrax*, *Cribohantkenina*, *Dentoglobigerina*, *Globigerinatheka*, *Globoturborotalita*, *Guembelitrioides*, *Hantkenina*, *Morozovelloides*, *Paragloborotalia*, *Orbulinoides*, *Subbotina*, *Turborotalia*, and *Turborotalita* and all size fractions for the small-bodied taxa, *Chiloguembelina*, *Globorotaloides*, *Pseudohastigerina*, and *Tenuitella*. Species were selected in an attempt to cover all planktonic foraminiferal depth and symbiont ecologies.

Before analyzing for stable isotope ratios or gold-coating for SEM images, each sample was imaged from two views using the Hull Lab serial light microscopy imaging system. Stable oxygen and carbon isotope measurements were generated on the KIEL IV Carbonate Device coupled with a Thermo MAT 253 in the Yale Analytical and Stable Isotope Center. Between one and seventy specimens were analyzed for each measurement based on the species (each measurement has a mass between 50 and 100 μg). Results are reported relative to the Vienna Peedee Belemnite standard (VPDB) with an external analytical precision <0.02 ‰ for $\delta^{13}\text{C}$ and 0.04 ‰ for $\delta^{18}\text{O}$ and were measured concurrently with the in-house “Toilet Seat” standard ($\delta^{13}\text{C}$ 1.95 ‰ and $\delta^{18}\text{O}$ -2.20 ‰) and NBS-19 ($\delta^{13}\text{C}$ 1.95 ‰ and $\delta^{18}\text{O}$ -2.20 ‰).

To document each species concept and determine preservation, scanning electron micrographs were created using an XL-30 Environmental Scanning Electron Microscope in high vacuum mode and gold-coated specimens.

Chapter 1

Preservation

Preservation plays a key role in the reliability of carbon and oxygen stable isotope measurements. Using samples from the middle Eocene, Sexton et al., 2006 showed that there was a consistent intraspecies isotopic offset whether the specimens were “glassy” or “frosty.” Over a short time scale (<1 My), isotopic data from frosty foraminifera could be reliable. However, my thesis spans twelve million years and looks at isotopic trends across the entire interval. Therefore, consistently good preservation is vital to meaningfully representing temporal trends.

From SEM images of Eocene foraminifera, it is clear that preservation varies both by time interval and genus within the samples used in this study. All of these samples were drilled from a clay-rich setting, meaning the foraminifera tests were encased in relatively impermeable sediments that prevented the fossils from interacting with the surrounding waters and secreting layers of secondary calcite. However, there are still some poorly preserved specimens present in the samples. Here are included wall texture images at a high resolution and images of cross-sections of foraminiferal walls revealed when chambers were broken off in the lab (labeled “broken”).

Overall, the genera *Turborotalia* and *Hantkenina* seem to be the best preserved (see plates 1.2, 1.3, 2.1, 2.5, 2.6, 2.8, 2.11, 3.1, 3.5, 4.2, 4.6, 5.1, and 5.10). This finding is consistent with the frequently glassy appearance of the specimens under the light microscope. Less consistent preservation can be seen in *Praemurica(?)* and *Subbotina* (see plates 1.5, 3.2, 3.3, 3.4, 3.6, 4.3, 4.5, 5.9, 6.2, and 6.4). Some *Subbotina* species seemed to be better preserved than others. *Subbotina linaperta* and *Subbotina angiporoides* (see plates 4.3 and 6.2), for example, often appeared frosty under the light microscope and show calcite growths in the SEM images whereas *Subbotina gortanii* and *Subbotina*

corpulenta (see plates 1.4, 3.3, 3.4, 4.5, 5.9, and 6.4) were often glassy. The worst-preserved genera across the board were *Acarinina*, *Morozovelloides*, and *Globigerinatheka* (see plates 1.1, 2.2-4, 2.7, 2.9, 2.10, 4.1, 5.2-8, 5.11, 6.1, and 6.3). Even within these genera, though, there was variation among species. *Morozovelloides bandyi* (see plates 2.2, 2.7, and 2.10) stands out as being better preserved than other members of its genus. Potential explanations for these strong genus-related trends in preservation could have to do with the original foraminiferal wall texture, as we know that, for example, globigerinathekids were densely spinose and acarininids and morozovellids are muricate.

To determine whether there are significant isotopic effects resulting from poor preservation, I compared species of the same genus to each other to see if there was a discernable pattern. Overall, there was no pattern of more depleted $\delta^{18}\text{O}$ for the worst-preserved species. *Hantkenina dumblei*, often the frostiest of the hantkeninids, had a $\delta^{18}\text{O}$ value on par with other members of its genus at just about -1 ‰; all of the subbotinids had strikingly similar $\delta^{18}\text{O}$ values despite the often frostier appearance of *Subbotina angiporoides* and *Subbotina linaperta*; morozovellids and globigerinathekids appeared unaffected by varying preservation quality, and; *Acarinina bullbrookii*, typically the worst-preserved of the acarininids, showed no notable variance from the others in its genus. Therefore, it is possible to conclude that preservation did not have a significant effect on the reliability of stable isotope measurements in this study.

Although the time-related trends in preservation were even less significant than those according to genus, there was a general increase in preservation quality from Biozones E9 to E13. This trend is most clearly seen when looking at the SEM images for *Acarinina* across the time interval (see plates 2.3, 5.2-8, 5.11, 6.1, and 6.3). In conclusion, preservation, although variable, is relatively glassy for these samples and should not confound the data.

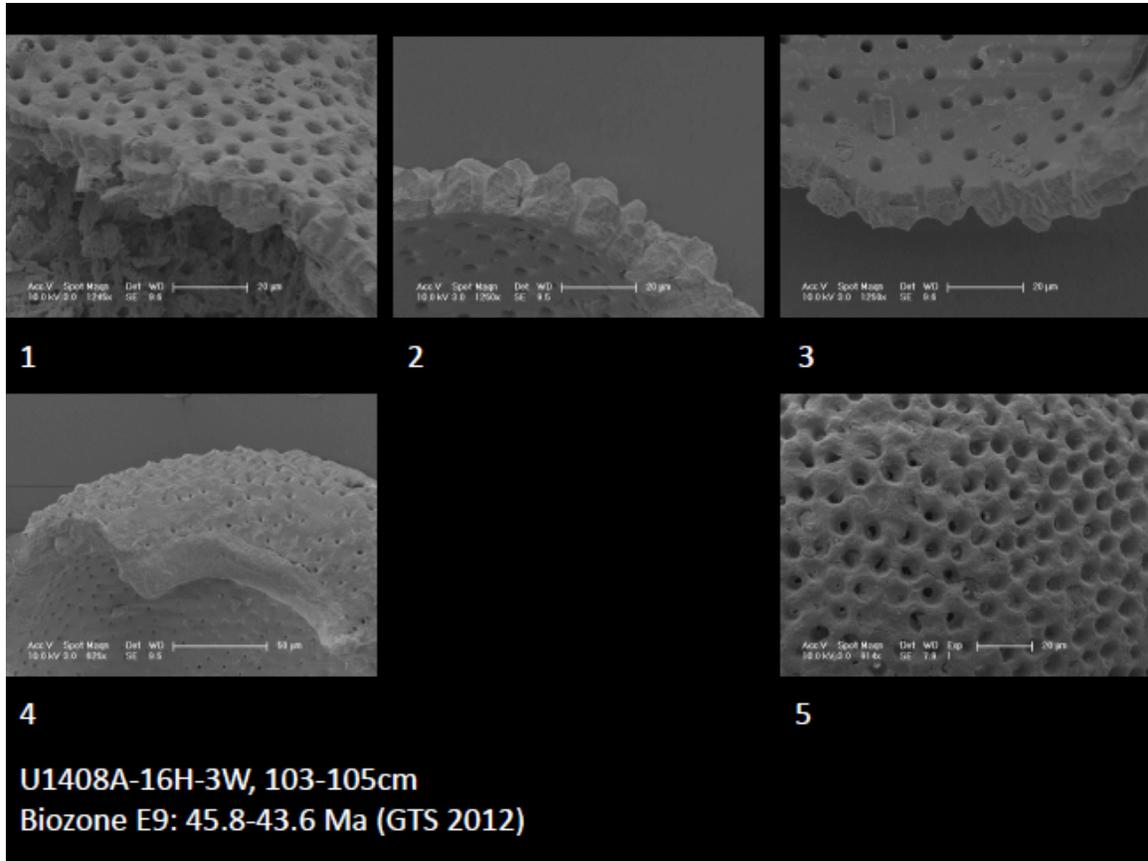


PLATE 1: 1) *Morozovelloides crassatus* (broken); 2) *Turborotalia frontosa* (broken); 3) *Turborotalia frontosa* (broken); 4) *Subbotina corpulenta* (broken); 5) *Praemurica(?) lozanoi*

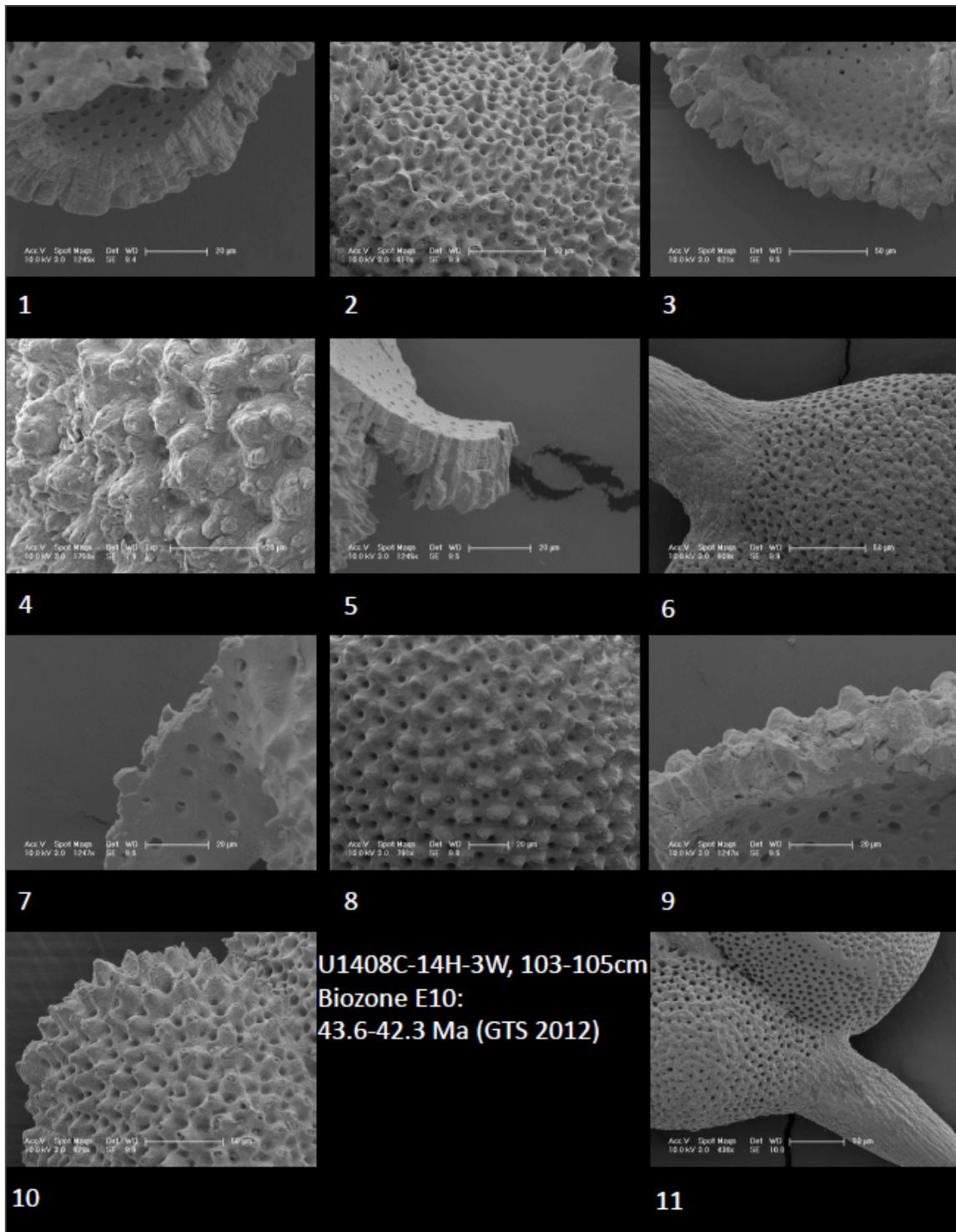


PLATE 2: 1) *Hantkenina dumblei* (broken); 2) *Morozovelloides bandyi*; 3) *Acarinina bullbrooki* (broken); 4) *Globigerinatheka korotkovi*; 5) *Hantkenina dumblei* (broken); 6) *Hantkenina dumblei*; 7) *Morozovelloides bandyi* (broken); 8) *Turborotalia frontosa*; 9) *Globigerinatheka index* (broken); 10) *Morozovelloides bandyi*; 11) *Hantkenina dumblei*

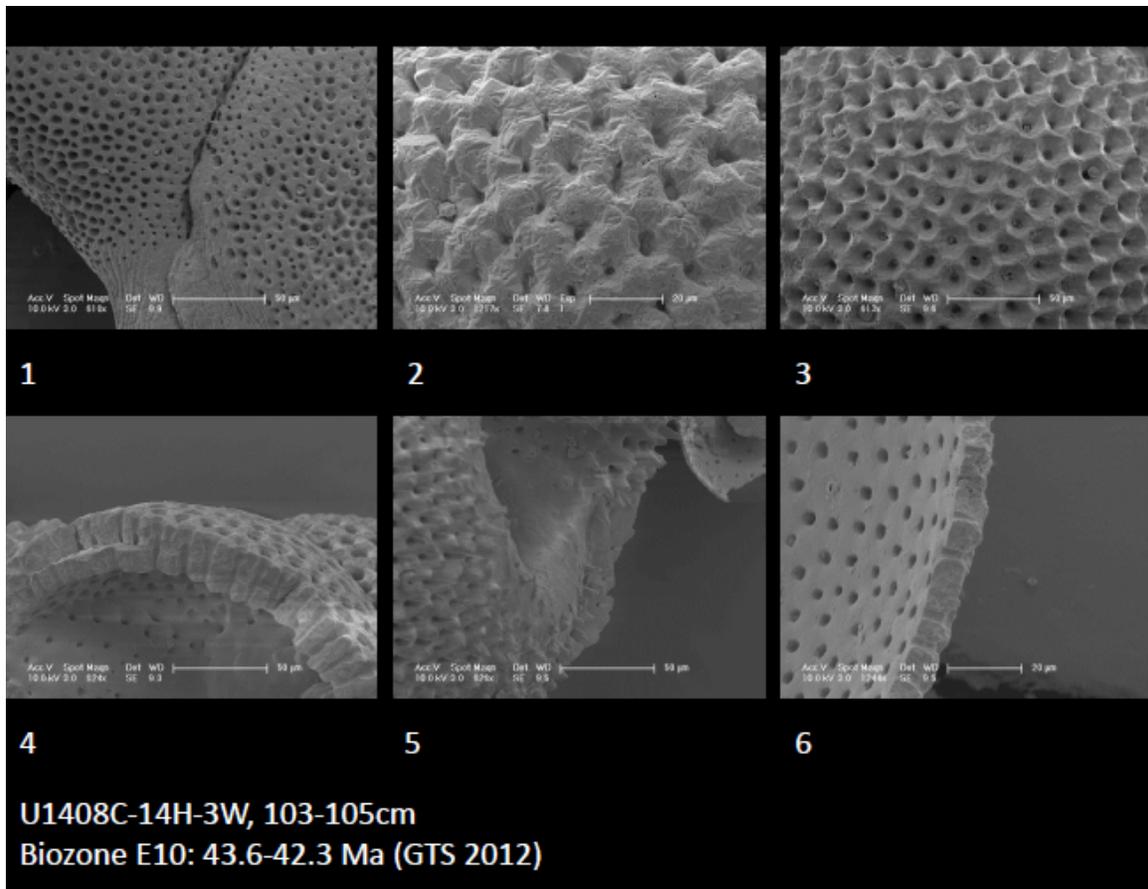


PLATE 3: 1) *Hantkenina dumblei*; 2) *Praemurica(?) lozanoi*; 3) *Subbotina corpulenta*;
 4) *Subbotina corpulenta* (toothy; broken); 5) *Turborotalia frontosa* (broken); 6) *Praemurica(?) lozanoi* (broken)

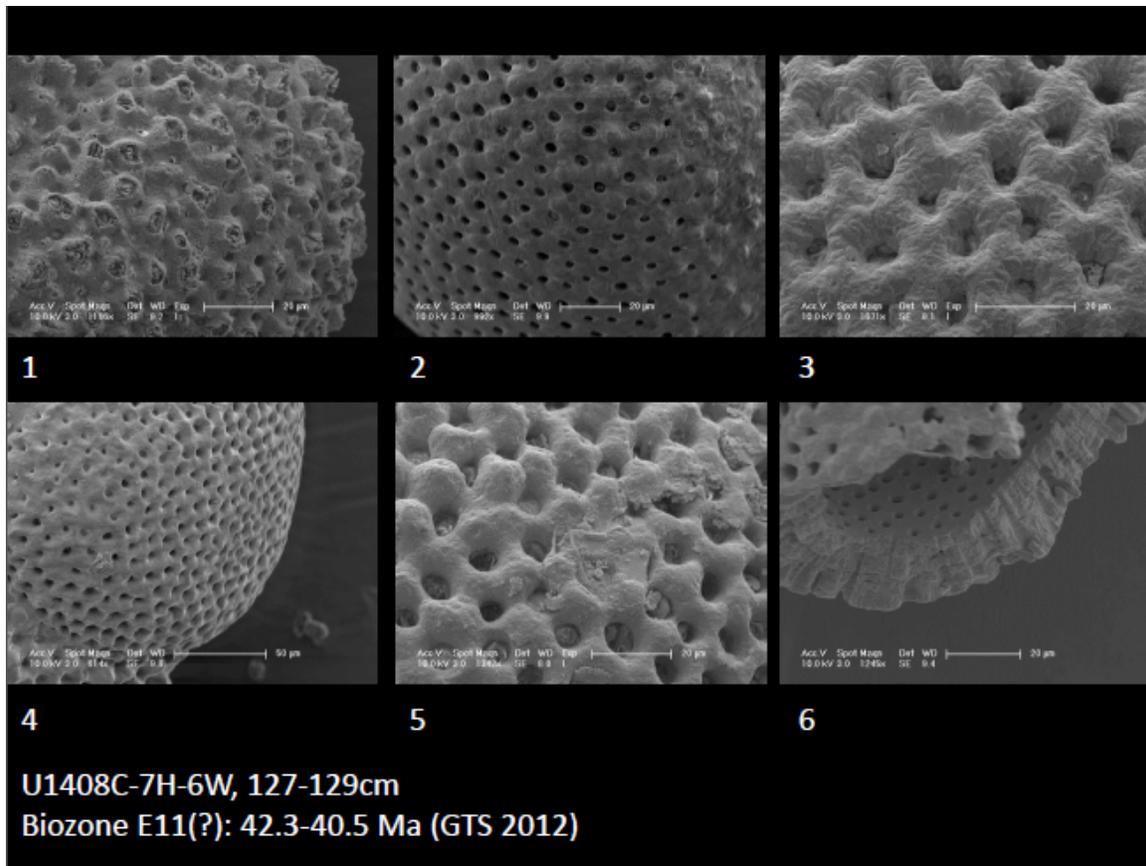


PLATE 4: 1) *Morozovelloides crassatus*; 2) *Turborotalia cerroazulensis*; 3) *Subbotina linaperta*; 4) *Catapsydrax unicavus*; 5) *Subbotina corpulenta*; 6) *Hantkenina dumblei* (broken)

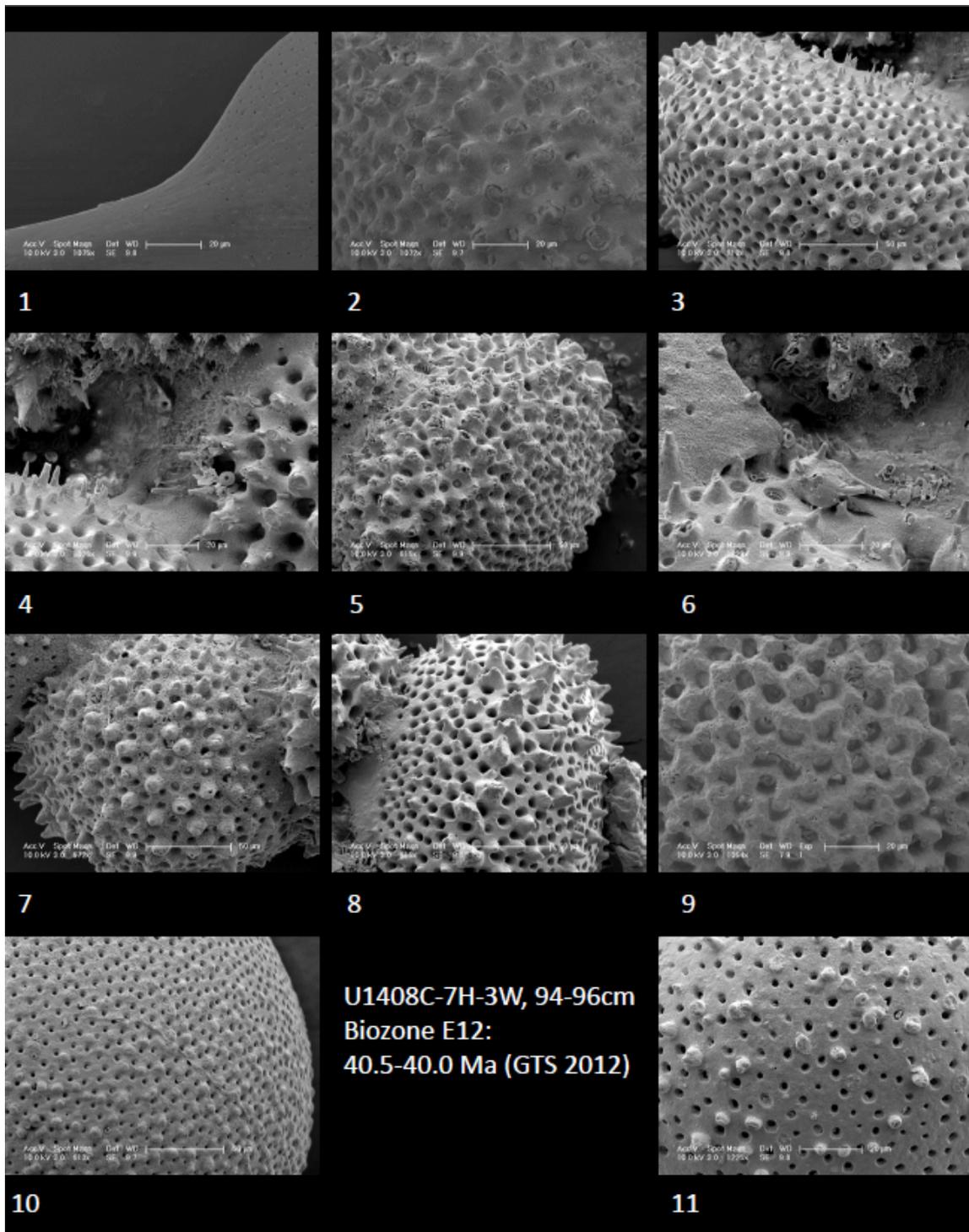


PLATE 5: 1) *Hantkenina liebusi*; 2) *Acarinina praetopilensis*; 3) *Acarinina praetopilensis*; 4) *Acarinina praetopilensis*; 5) *Acarinina praetopilensis*; 6) *Acarinina praetopilensis*; 7) *Acarinina rohri* (?); 8) *Acarinina topilensis*; 9) *Subbotina gortanii*; 10) *Turborotalia cerroazulensis*; 11) *Acarinina topilensis*

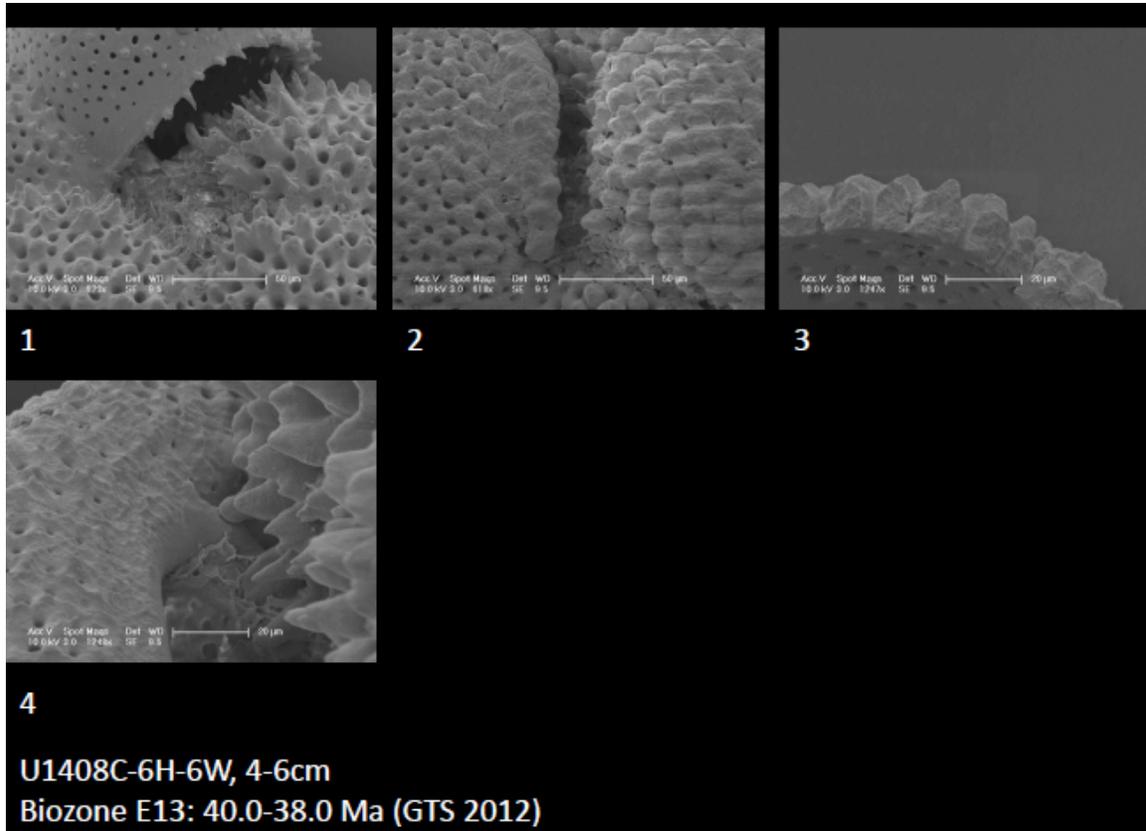


PLATE 6: 1) *Acarinina rohri* (?) (broken); 2) *Subbotina angiporoides* (broken); 3) *Acarinina rohri* (?) (broken); 4) *Subbotina corpulenta* (broken)

Ecology

In order for planktonic foraminifera to be used reliably as surface water tracers, it is important to understand their isotope ecologies and what vital effects could alter their carbon and oxygen offsets. To gain a better understanding of these factors, I present several different representations of data from 48+ species spanning across 19 genera, eight size fractions, and ten time intervals. Factors that could influence isotope ecology include ontogenetic effects, varying metabolic speeds, and the presence of a photosymbiont. When genus averages are plotted together, as in Figure 1, several relationships among the genera are visible. The $\delta^{13}\text{C}$ values plotted against size fraction can show whether or not a species has a photosymbiont, features of its carbon metabolism, and the significance of ontogenetic effects. $\delta^{18}\text{O}$ values show the relative depths in the water column at which each genus lived. As an example, *Morozovelloides* has a steep $\delta^{13}\text{C}$ slope as size fraction increases that, when combined with its $\delta^{18}\text{O}$

measurements, supports that it is a mixed-layer dweller with a photosymbiont. *Dentoglobigerina* and *Catapsydrax*, on the other hand, have strikingly flat $\delta^{13}\text{C}$ regressions, proving they do not have photosymbionts and that they are deep-dwelling. However, some of the trends visible in this general view of the data could be the result of artifacts such as which species are present in each size fraction. To take into account all potential factors influencing isotope measurements, each genus and species is analyzed in-depth below.

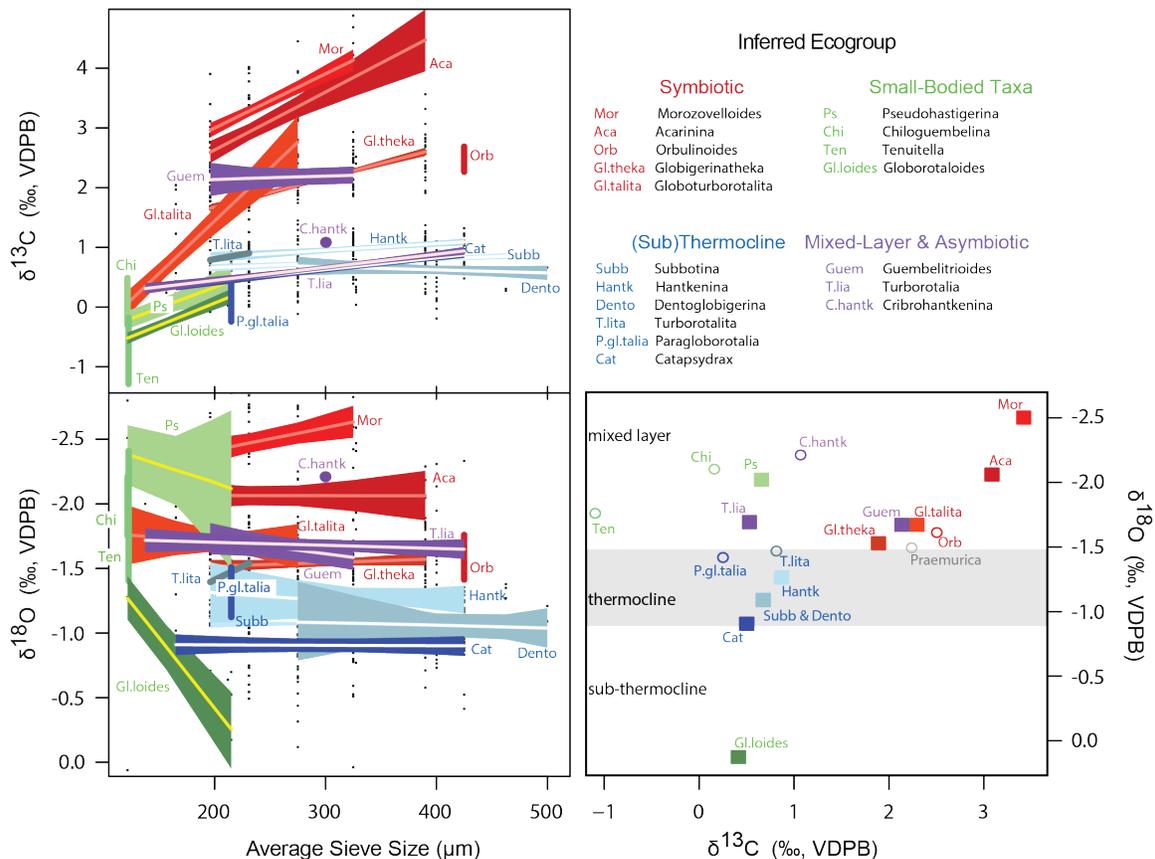


FIGURE 1. This figure shows all data collected for this study averaged at the genus level. All data is normalized to benthic values from *Nuttallides truempyi* measurements.

Symbiotic Surface-Dwellers

Acarinina (following taxonomic concept of William Berggren, Paul Pearson, Brian Huber, and Bridget Wade, 2006)

In this study, three known and two unknown species from the genus *Acarinina* were analyzed. Many acarininids have been measured for stable

isotopes before and the genus is thought to be comprised of mixed-layer dwellers with photosymbionts (Boersma et al., 1987; Pearson et al., 1993). The steep positive $\delta^{13}\text{C}$ slope across size fractions and negative $\delta^{18}\text{O}$ values seen in Figure 2 support these previous findings. These trends are visible at both the genus and species level, perhaps most strongly in *Acarinina praetopilensis* (see Appendix Figure 1) and less clearly in the unidentified species labeled *Acarinina* (wedge) and *Acarinina* (round).

The *Atlas of Eocene Planktonic Foraminifera* describes taxonomic uncertainties among acarininids and notes that the genus has mostly been studied at middle and low latitudes. Therefore, little is known of high latitude *Acarinina* taxonomy. This gap in knowledge could help explain why we came across several small-bodied acarininids that did not fit any of the existing taxa described in the *Atlas*. These specimens, often <250 μm and with five chambers, were most similar to *Acarinina collactea*, *Acarinina cuneicamerata*, and *Acarinina esnehensis*. However, *Acarinina esnehensis* is believed to have gone extinct by Biozone E7 and *Acarinina cuneicamerata* by the middle of Biozone E9. *Acarinina collactea* extends into Biozone E14, but does not exactly match the taxonomic description of the unidentified specimens. In comparison to the unidentified forms, *Acarinina collactea* is too lobate from the edge view, its chambers are a mix of wedge-shaped and round, and its ultimate chamber is often a different texture than the others. Because the unidentified acarininids did not satisfactorily fit into any of the existing taxonomic concepts, we decided to separate these small, 5-chambered acarininids into two groups: one for specimens with wedge-shaped chambers and one for specimens with round chambers, labeled *Acarinina* (wedge) and *Acarinina* (round), respectively. These species do not show any unusual trends in their isotope ecologies.

The three primary taxa measured for this study, *Acarinina bullbrooki*, *Acarinina praetopilensis*, and *Acarinina topilensis* are illustrated in Plate 7. Two examples of what we believe to be *Acarinina rohri* are also included, but specimens were not abundant enough for isotopic analyses.

Globigerinatheka* and *Orbulinoides (following taxonomic concept of Isabella Premoli Silva, Bridget Wade, and Paul Pearson, 2006)

Previous studies on globigerinathekids suggest that they are surface dwellers, perhaps with dinoflagellate symbionts (Boersma et al., 1987; Pearson et al., 1993, 2001). The data presented here support that globigerinathekids live in the mixed layer, even if near the top of the thermocline (Figure 1). However, evidence for photosymbionts is less conclusive. Although there is a slight positive slope for $\delta^{13}\text{C}$ across size fraction, the sample-specific data in Figure 2 show many of sample's regressions crossing each other. In addition, species-specific data (Appendix) show that several of the individual species have only a very slight slope in $\delta^{13}\text{C}$. The positive $\delta^{13}\text{C}$ at the genus level could be an artifact of which species are abundant and from which samples they come for each size fraction. In addition, it is thought that globigerinathekids sink at the end of their life cycle (Pearson and Palmer, 1999). If this were true, we would expect to see an increase in $\delta^{18}\text{O}$ indicative of a decrease in water temperature. However, none of the species seem to show this trend and the genus-level $\delta^{18}\text{O}$ is strikingly flat.

Previous to this study, *Globigerinatheka barri*, *Globigerinatheka kugleri*, and *Globigerinatheka korotkovi* had not been extensively studied (taxonomic concepts illustrated in Plate 8). From this data, it is possible to infer that none of these species definitively have photosymbionts or sink in the water column near the ends of their lives. This information makes the species more useful as surface water tracers. However, the *Globigerinatheka barri* data suggests that this species should be studied to a greater extent. There are odd aspects of the data, such as the $\delta^{13}\text{C}$ slope decreasing with increasing size fraction and the $\delta^{18}\text{O}$ values criss-crossing each other, potentially implying that during one time interval the species moved up in the water column throughout its life and at another time interval sank. Because *Globigerinatheka barri* tends to be poorly preserved and was only present in the larger size fractions and within three of the samples, there is not enough data currently to make any definitive claims.

It is also important to note that globigerinathekids were extinct by 34.6 Ma, just before the EOT. There has historically been more interest in the EOT extinction of muricate genera, which live at the very top of the water column and are known to have photosymbionts. However, globigerinathekids are also surface-dwellers, and their loss could affect our ability to trace surface water conditions.

The taxonomic distinctions among the species analyzed were relatively straightforward. Specimens from each taxa can be seen in Plate 8.

Globoturbotalita (following taxonomic concept of Richard Olsson, Christoph Hemleben, Brian Huber, and William Berggren, 2006)

At the generic level (Figure 2), *Globoturbotalita* appears to be a surface-dwelling foraminifera with photosymbionts. The $\delta^{13}\text{C}$ slope across size fraction is among the steepest present in any of this data. In addition, the genus appears to reside near other known surface-dwellers such as *Orbulinoides* and *Globigerinatheka*. However, there are some problems with this genus's dataset associated with taxonomic uncertainty.

At the larger size fractions (>180 μm), taxonomic identification was more complex. *Globoturbotalita ouachitaensis* was assigned to specimens appearing to fit the taxonomic specifications described in the *Atlas*, but in reality too large to be a member of the small-bodied genus according to its definition. Many of these specimens, all recorded in multi-view light images included in the appendix, were similar to subbotinids (from which they evolved) but with apertures too large or chamber arrangements too disjunct to truly fit into any of the *Subbotina* taxa. However, the many *Globoturbotalita* measured at the smallest size fraction (63-180 μm) better fit the accepted taxonomical definitions for both *Globoturbotalita bassriverensis* and *Globoturbotalita ouachitaensis* (for which there was previously no Eocene data). From this smallest size fraction alone, we can confirm that *Globoturbotalita* is a surface-dweller. However, $\delta^{13}\text{C}$ trends across size fraction could be misleading in implying that the genus has a photosymbiotic relationship; this trend could instead be the result of the considerable

morphological variability in the samples measured. The larger-bodied specimens are illustrated in Plate 10.

Morozovelloides (following taxonomic concept of William Berggren, Paul Pearson, Brian Huber, and Bridget Wade, 2006)

As was expected, the new data presented here for *Morozovelloides* indicate a near-surface habitat and the presence of a photosymbiont. At the genus level, $\delta^{13}\text{C}$ strongly supports that morozovellids have photosymbionts and the genus has the most negative $\delta^{18}\text{O}$ out of all the species measured, suggesting a very shallow habitat. Overall, there is a slight decrease in $\delta^{18}\text{O}$ as the specimens increase in size, but the sample-specific data shows many of the sample lines crossing each other. Therefore, this decrease in $\delta^{18}\text{O}$ might be an artifact of which species are present in which size fractions and samples. The species-specific data shows that the isotope measurements are dominated by *Morozovelloides crassatus*, present in all four size fractions and in multiple samples. On the other hand, *Morozovelloides bandyi* and *Morozovelloides lehneri* were only present in the E10 sample.

Previous studies using boron isotopes have suggested that *Morozovelloides bandyi* resides deeper than *Morozovelloides crassatus*. However, the opposite appears to be true according to this dataset. For the E10 sample, in which both species occur, *Morozovelloides bandyi* actually has a more negative $\delta^{18}\text{O}$, twice by almost 0.6 ‰. However, it was only possible to obtain a few *Morozovelloides bandyi* measurements, which could not be enough to make conclusions regarding its depth habitat relative to *Morozovelloides crassatus*. Based on this data, both species seem to reside deeper than does *Morozovelloides lehneri*.

The taxonomy of these species was fairly straightforward, with the exception of significant morphological variability among *Morozovelloides crassatus* specimens. This variability, along with illustrations of two of the other morozovellids species measured, are shown in Plate 9.

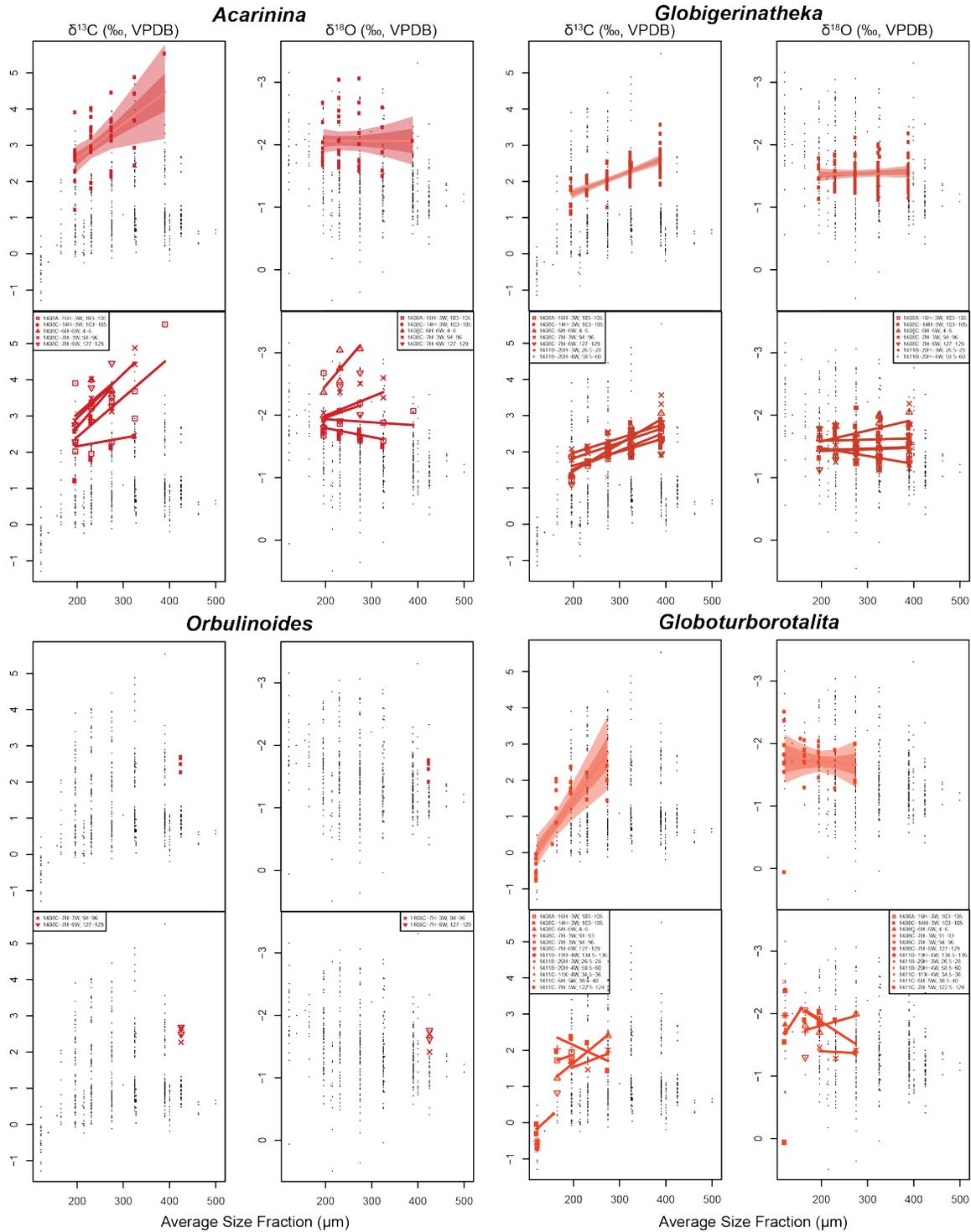


FIGURE 2: These charts include all data for a particular genus averaged. The top panels for each genus show the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ across size fraction for all the data. The bottom panels show sample-specific data. Species included here are *Acarinina bullbrooki*, *Acarinina praetopilensis*, *Acarinina* (wedge), *Acarinina* (round), *Acarinina topilensis*, *Globigerinatheka barri*, *Globigerinatheka index*, *Globigerinatheka korotkovi*, *Globigerinatheka kugleri*, *Orbulinoides beckmanni*, *Globoturborotalita bassriverensis*, *Globoturborotalita ouachitaensis*, and *Globoturborotalita* sp.

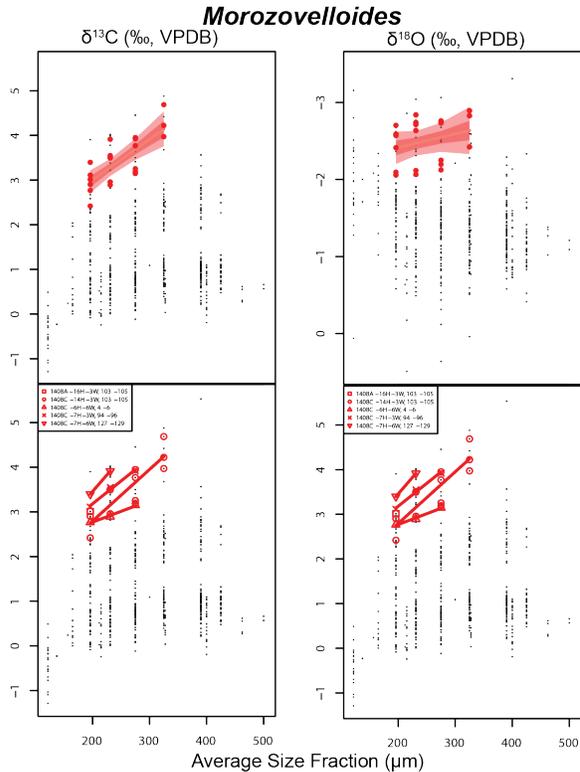


FIGURE 2 (cont.): These charts include all data for a particular genus averaged. The top panels for each genus show the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ across size fraction for all the data. The bottom panels show sample-specific data. Species included here are *Morozovelloides crassatus*, *Morozovelloides bandyi*, and *Morozovelloides lehneri*.

Asymbiotic Surface-Dwellers

Cribrohantkenina (following taxonomic concept of Helen Coxall and Paul Pearson, 2006)

Cribrohantkenina, although usually grouped with *Hantkenina*, is considered separately here because of its relatively negative $\delta^{18}\text{O}$ and the very shallow depth habitat implied. According to this data, it lives at about the same shallow depth as *Acarinina* and *Chiloguembelina*. In addition, it went extinct at the EOT, although its exact disappearance date has not been finely constrained. Because only one measurement from this genus was possible, this dataset does not add significantly to our understanding of *Cribrohantkenina* ecology and how it may have changed before going extinct near the EOT.

Guembelitrionides (following taxonomic concept of Richard Olsson, Paul Pearson, and Brian Huber, 2006)

There is one Eocene species, *Guembelitrionides nuttalli*, in this genus. As expected based on previous research, *Guembelitrionides nuttalli* resides at an intermediate depth between muricate species and subbotinids (Pearson et al., 1993). However, the species resides above the thermocline and even above known surface-dwellers *Globigerinatheka* and *Orbulinoides*. The $\delta^{13}\text{C}$ trend across size fractions confirms that the species does not have a photosymbiont. The variability of the species morphology is illustrated in Plate 9.

Turborotalia (following taxonomic concept of Paul Pearson, Vlasta Premec-Fucek, and Isabella Primoli Silva, 2006)

Turborotalia is a genus of interest for two reasons: many of its species, except for two, go extinct at the EOT and there is significant variability in depth habitat among the species. *Turborotalia* does not have photosymbionts (Boersma et al., 1987; Pearson et al., 1993, 2001), as supported by the present data. There is a slight positive slope in $\delta^{13}\text{C}$ when plotted against size fraction, but that trend is likely an artifact of which species are present in which size fractions. The species-specific data shows that the $\delta^{13}\text{C}$ values against size fraction are flat within each species, all confirming that no species within the genus has a photosymbiotic relationship.

The expected depth habitat of *Turborotalia* according to earlier research varies significantly by species. *Turborotalia ampliapertura* is shallow and variable (Poore and Matthews, 1984; Pearson et al., 2001), *Turborotalia cerroazulensis* and *Turborotalia cocoaensis* are similar to each other and deeper than *Turborotalia pomeroli* (Pearson et al., 2001; Wade and Kroon, 2002), and *Turborotalia frontosa* resides the deepest of them all (Boersma et al., 1987), although it is not contemporaneous with any of them. According to my data, the genus on average resides just above the thermocline, on a level with *Guembelitrionides* and *Globoturborotalita*. It may even have a shallower depth habitat than *Globigerinatheka* and *Orbulinoides* (Figure 1). However, there is significant depth habitat variability among the species in the genus. *Turborotalia*

cerroazulensis, *Turborotalia pomeroli*, and *Turborotalia cocoaensis* all seem to reside at roughly the same depth according to $\delta^{18}\text{O}$ measurements replicated across size fractions. *Turborotalia ampliapertura* has a noticeably negative $\delta^{18}\text{O}$ value (indicative of a shallow depth habitat) and *Turborotalia frontosa* has a remarkably high one (indicative of a relatively deep habitat). Slightly unexpected is the consistency of *Turborotalia ampliapertura* measurements across both samples and four size fractions, as previous studies had noted its variability.

Many of these species are gone by the end of the Eocene: *Turborotalia frontosa* goes extinct by the end of Biozone E11, *Turborotalia pomeroli* by the end of Biozone E15, and *Turborotalia cerroazulensis* by the end of Biozone E16. This lack of species continuing on from the middle Eocene to early Oligocene added to the fact that there is significant variability of depth habitats among species makes *Turborotalia* a problematic genus for surface-water tracing across the EOT.

Turborotalia cerroazulensis, *Turborotalia pomeroli*, and *Turborotalia frontosa* are illustrated in Plate 11.

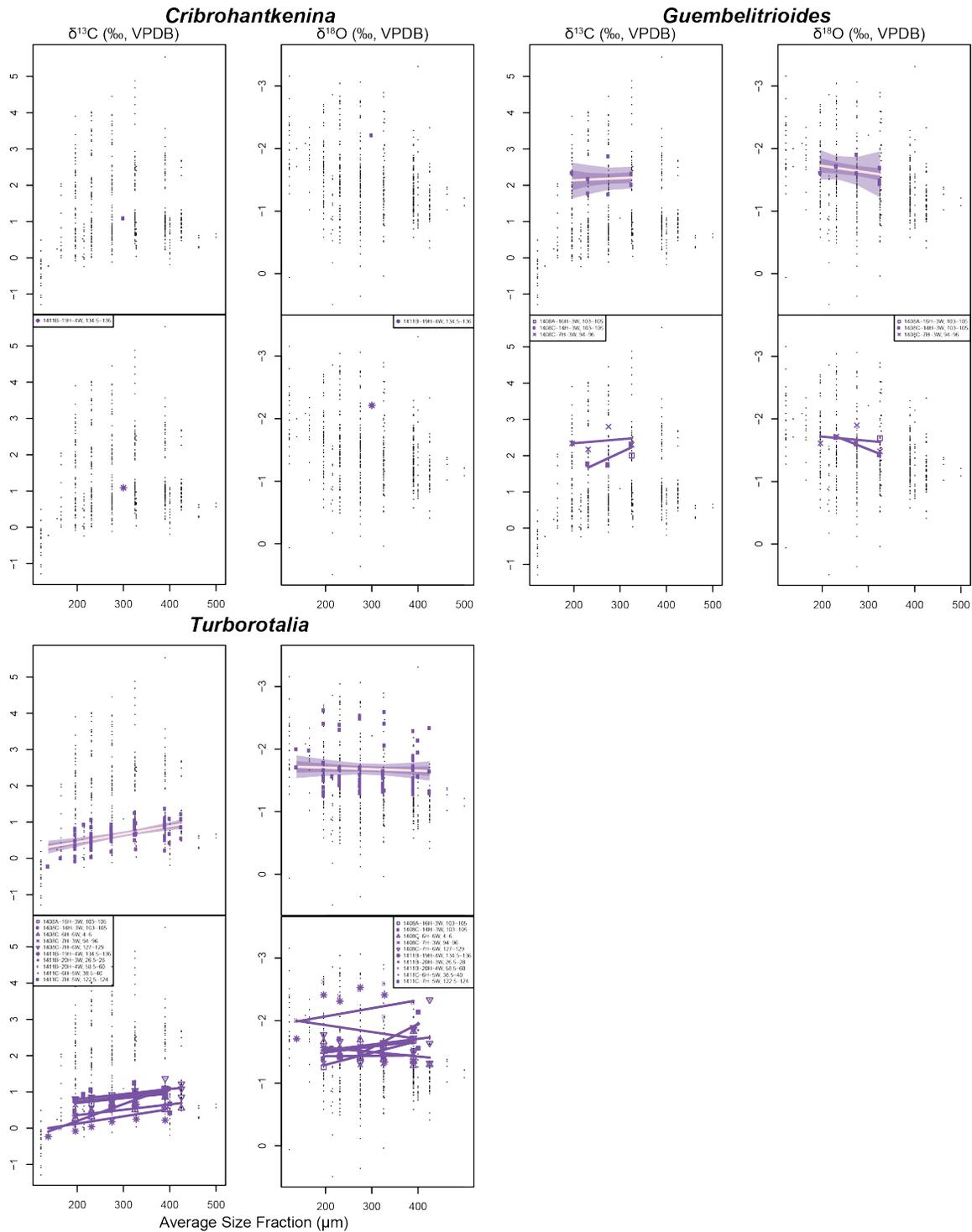


FIGURE 3: These charts include all data for a particular genus averaged. The top panels for each genus show the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ across size fraction for all the data. The bottom panels show sample-specific data. Species included here are *Cribroantkenina inflata*, *Guembeltrioides nuttalli*, *Turborotalia frontosa*, *Turborotalia cerroazulensis*, *Turborotalia pomeroli*, *Turborotalia cocoaensis*, and *Turborotalia ampliapertura*.

(Sub)Thermocline

Catapsydrax (following taxonomic concept of Richard Olsson, Paul Pearson, and Brian Huber, 2006)

The data for *Catapsydrax*, which is composed entirely of *Catapsydrax unicavus* (see Plate 10) with only one measurement of *Catapsydrax* sp., is surprisingly consistent. $\delta^{13}\text{C}$ across size fraction presents a relatively shallow positive slope, and $\delta^{18}\text{O}$ values place the genus at the bottom of the thermocline, deeper than *Subbotina*, *Dentoglobigerina*, and *Hantkenina*. Previous studies placed *Catapsydrax* at a similar depth (Poore and Matthews, 1984). Taxonomists believe that several species may currently fall under the name *Catapsydrax unicavus* but, if that is the case, from this data the species do not appear to show much isotopic variation. There is one sample, at 35.119 Ma, for which each size fraction has a slightly more negative $\delta^{18}\text{O}$ value than the rest, implying it lives at a shallower depth. However, this aberration could be an artifact related to preservation or the result of adhering to a stricter taxonomic definition, as this sample was picked at Stockholm University (see light microscope images in the Appendix, Figure 2). Previous studies also suggest that this species primarily exists in the smaller size fractions, but here we have several measurements across many samples at size fractions $>300\ \mu\text{m}$.

Of all the species in this study, *Catapsydrax unicavus* produced the greatest number of measurements. It appeared in nine samples and often across several size fractions. Because of its isotopic consistency, lack of a photosymbiont, abundance in Eocene communities, and continuation into the Oligocene, *Catapsydrax unicavus* could be a useful species for further studies.

Dentoglobigerina (following taxonomic concept of Richard Olsson, Christoph Hemleben, and Paul Pearson, 2006)

Dentoglobigerina was present in the latest three time slices included here (from Biozones E15-O1). The present data is consistent with earlier findings, in that the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values at the genus level indicate that *Dentoglobigerina* lives in a deep thermocline habitat (Pearson et al., 2001; Pearson and Palmer, 1999).

However, at the species-specific level, trends become less clear. No particular species was measured in depth, and therefore many species only have scattered data points. Van Eijden and Ganssen concluded that *Dentoglobigerina galavisi* migrated upward across the EOT (Van Eijden and Ganssen, 1995). $\delta^{18}\text{O}$ data for this species supports the idea, as the $\delta^{18}\text{O}$ values become more depleted as time progresses. Nevertheless, there is not enough data here on this species to offer definitive support for *Dentoglobigerina galavisi*'s migration through time. Adding more data for this species, which was one of the more abundant *Dentoglobigerina* species in these samples, could help to confirm or disprove the migration theory.

Hantkenina (following taxonomic concept of Helen Coxall and Paul Pearson, 2006)

Consistent with earlier findings, the data reported here show *Hantkenina* species with no $\delta^{13}\text{C}$ enrichment with increasing size fraction and a $\delta^{18}\text{O}$ expected of a thermocline-dweller (Coxall et al., 2000). My data places *Hantkenina* between *Subbotina* and *Turborotalita* in the water column. At the genus level, a very slight increase in $\delta^{13}\text{C}$ with size fraction is visible. However, compared to surface-dwellers' $\delta^{13}\text{C}$ profiles, this slope is insignificant.

Previous research on *Hantkenina dumblei* and *Hantkenina liebusi* found that the two had $\delta^{18}\text{O}$ measurements similar to *Turborotalia frontosa* (Coxall et al., 2000). Here, the two hantkeninids have $\delta^{18}\text{O}$ values consistently 0.5 ‰ more enriched than *Turborotalia frontosa*, indicating that they live at a deeper place in the water column. There was no existing isotope data for *Hantkenina australis*, but this data implies that the species is isotopically similar to *Hantkenina dumblei*. Because the main taxonomic difference between *Hantkenina dumblei* and *Hantkenina australis* is whether or not the spines are recurved and spines are often broken off of even the best preserved hantkeninid fossils, this similarity is important to note for the feasibility of using either species in stable isotope studies.

Data for both *Hantkenina naggulanensis* and *Hantkenina* sp. are drastically different from the other species. This anomaly could be the result of

the measurements originating from different time slices. A previous study included data that showed *Hantkenina naggulanensis* lived at a shallower depth habitat than any other hantkeninid, which is confirmed by the single data point, a full 1.5 ‰ more depleted in $\delta^{18}\text{O}$ than the other species. However, because there is only one data point for this species here (Biozone E15, 300-500 μm) and it is from a more recent time interval than the other hantkeninids measured, this data does not definitively confirm that *Hantkenina naggulanensis* lived at a significantly shallower depth habitat than other hantkeninids.

Like many other genera included here, all *Hantkenina* species go extinct by the start of the Oligocene. *Hantkenina liebusi*, *Hantkenina australis*, and *Hantkenina dumblei* are all illustrated in Plate 12.

Paragloborotalia (following taxonomic concept of Richard Olsson, Paul Pearson, and Brian Huber, 2006)

Three *Paragloborotalia* measurements were taken, all falling under either *Paragloborotalia grifinoides* or *Paragloborotalia* sp. and all in the 180-250 μm size fraction. The depth habitat indicated by its $\delta^{18}\text{O}$ values is consistent with previous findings that indicated the species lives in a deep planktonic habitat (called *Paragloborotalia wilsoni*; Pearson et al., 2001). This data places *Paragloborotalia* near *Turborotalita* and *Praemurica(?)* near the top of the thermocline.

Paragloborotalia grifinoides goes extinct by the start of the Oligocene, but *Paragloborotalia nana* continues on across the boundary. Here, the data spans from E15 to O1. Measuring stable isotopes across more narrow size ranges within the smaller size fraction is recommended to gain a better understanding of any size-related effects impacting the reliability of this genus for isotope geochemistry.

Praemurica(?) (following taxonomic concept of William Berggren, Richard Olsson, and Isabella Premoli Silva, 2006)

This genus is listed as uncertain due to its mysterious ancestry. Here, we found specimens in samples from E9 and E10 in the larger size fractions. Because the species was only present in the largest three size fractions and data

points are scarce, no size-related trends are apparent. However, the species has $\delta^{18}\text{O}$ values consistent with a depth habitat near the top of the thermocline. According to this data, *Praemurica(?)* appears to reside near *Turborotalita* and *Globigerinatheka*. More data is needed on this taxon to more confidently ascertain its depth habitat and to determine whether or not there are any size-specific trends.

Subbotina (following taxonomic concept of Richard Olsson, Christoph Hemleben, Brian Huber, and William Berggren, 2006)

More subbotinid species were measured here than any other genus. According to earlier research, most subbotinids live at a relatively deep habitat below the mixed layer (Poore and Matthews, 1984; Pearson et al., 2001; Boersma et al., 1987; Wade and Kroon, 2002). In addition, *Subbotina corpulenta* is thought to be the deepest dwelling of any other planktonic species (Poore and Matthews, 1984). This data places *Subbotina* near the bottom of the thermocline but still above *Catapsydrax* and *Globorotaloides*.

The consistency of the *Subbotina* data is surprising. At the species level, each $\delta^{13}\text{C}$ line plotted against increasing size fraction is essentially horizontal. In addition, each species hovers very close to -1 ‰ for $\delta^{18}\text{O}$. Even *Subbotina corpulenta* appears to reside at a similar depth when compared to other members of its genus. These measurements suggest that there is not much isotopic variability among the many subbotinid species, even if previous studies had them spanning the entire range of the thermocline.

It is important to note that there was one taxonomic distinction, notated here as *Subbotina corpulenta* (toothy), that may be unnecessary. We believe *Subbotina corpulenta* (toothy) may be an early form of *Subbotina projecta*. Their very similar isotopic ecologies seem to support such a classification.

We encountered more difficulty identifying species within *Subbotina* than any other genus. For many species, including *Subbotina gortanii* and *Subbotina eocaena*, the apertures were often unexpectedly large. *Subbotina gortanii* also should not have occurred in as large of size fractions as we seemed to find it (see Plate 10.3). In addition, there often did not appear to be the right

combination of chamber size distributions, trochospire heights, and orientation of the umbilicus in a specimen. These discrepancies led us to create strict rules for our species identifications used here, all of which are illustrated with specimens in Plate 13.

Due to its abundance in this time interval, consistency across size fraction and species, and continuation into the early Oligocene, *Subbotina* could be a useful genus for further study of this interval.

Turborotalita (following taxonomic concept of Paul Pearson, Vlasta Premec-Fucek, and Isabella Premoli Silva, 2006)

There are two measurements included here for *Turborotalita carcoselleensis* (both from E12), a previously unstudied species. The data places *Turborotalita* at the top of the thermocline, at a similar depth as *Paragloborotalia* and *Praemurica(?)*, but with a $\delta^{13}\text{C}$ value intermediate between the two. There do not appear to be any size-related trends evident in the data. Further study of this species is recommended to determine its utility as a tracer of conditions across the EOT.

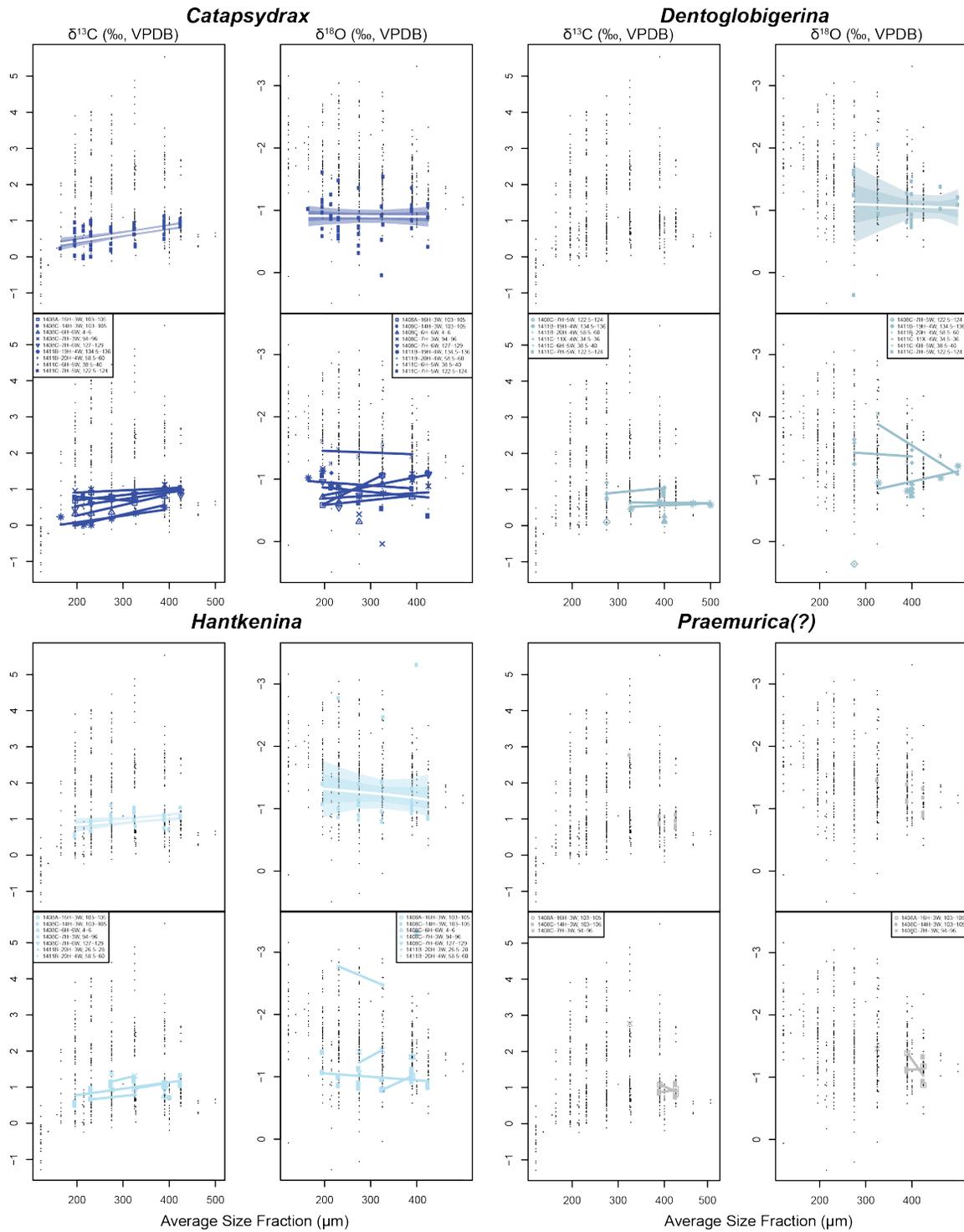


FIGURE 4: These charts include all data for a particular genus averaged. The top panels for each genus show the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ across size fraction for all the data. The bottom panels show sample-specific data. Species included here are *Catapsydrax unicavus*, *Dentoglobierina galavisi*, *Dentoglobigerina venezuelana*, *Dentoglobigerina pseudovenezuelana*, *Dentoglobigerina taci*, *Dentoglobigerina globularis*, *Dentoglobigerina sp.*, *Hantkenina australis*, *Hantkenina liebusi*, *Hantkenina dumblei*, *Hantkenina naggulanensis*, *Hantkenina sp.*, and *Praemurica(?) lozanoi*.

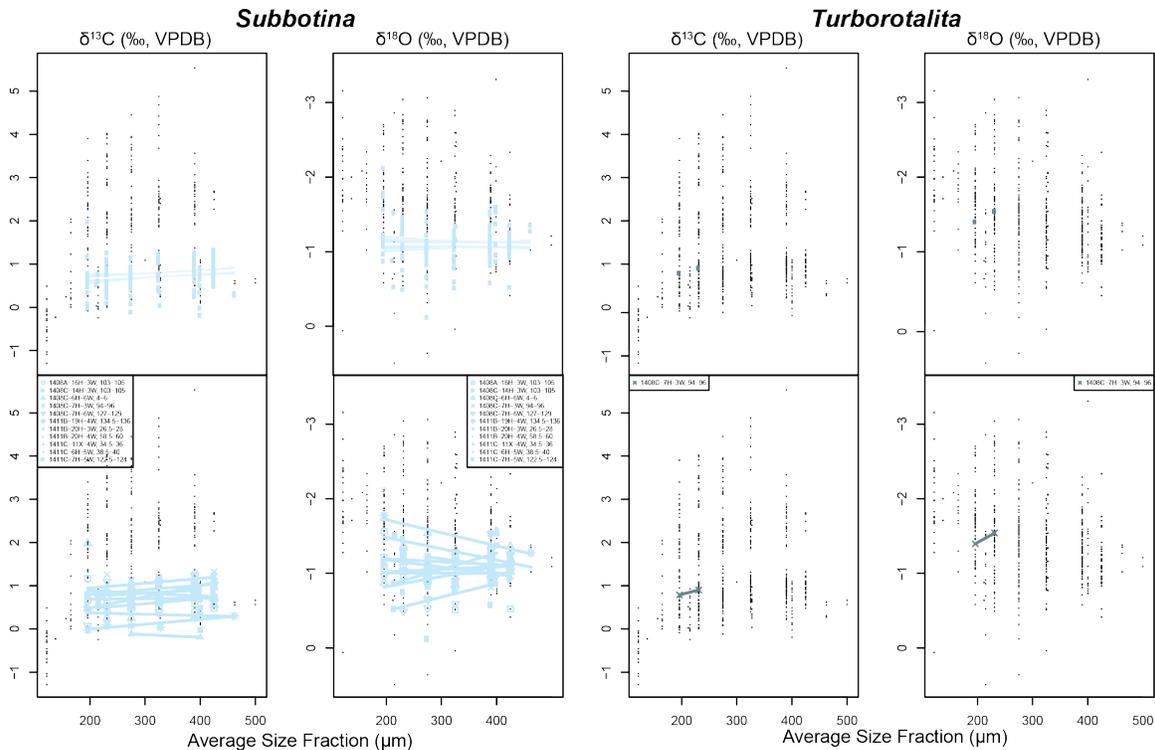


FIGURE 4 (cont.): These charts include all data for a particular genus averaged. The top panels for each genus show the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ across size fraction for all the data. The bottom panels show sample-specific data. Species included here are *Subbotina corpulenta*, *Subbotina eocaena*, *Subbotina linaperta*, *Subbotina minima*, *Subbotina corpulenta* (toothy), *Subbotina angiporoides*, *Subbotina gortanii*, *Subbotina utilisindex*, *Subbotina projecta*, *Subbotina tecta*, and *Turborotalita carcoselleensis*.

Small-Bodied Taxa

Chiloguembelina (following taxonomic concept of Brian Huber, Richard Olsson, and Paul Pearson, 2006)

Chiloguembelina ototara is known to be a mixed-layer dweller, according to data from high southern latitudes (Barrera and Huber, 1991). These data from the high northern latitudes agree, placing *Chiloguembelina* right near the surface close to *Cribrohantkenina* and *Acarinina*, but with a $\delta^{13}\text{C}$ value much more depleted. All of the data for this species was obtained from the same size fraction (63-180 μm). If possible, further study using narrower size fractions is recommended to gain a better sense of this species' isotope ecology.

Globorotaloides (following taxonomic concept of Richard Olsson, Paul Pearson, and Brian Huber, 2006)

The two species included here, *Globorotaloides suteri* and *Globorotaloides quadrocameratus*, appear to be extreme. These measurements give us the most enriched $\delta^{18}\text{O}$ values of the study by far and almost the most depleted $\delta^{13}\text{C}$ values. There also appears to be a steep increase in $\delta^{18}\text{O}$ across the two size fractions, however that particular trend may be misleading. Because *Globorotaloides suteri* is the only species present in the smallest size fraction, it makes an isotopic difference between species appear to be one between size fractions. It is also important to note that these species were only measured in the late Eocene and early Oligocene samples.

Due to its apparently deep habitat and relatively depleted $\delta^{13}\text{C}$ values, both of these species would be interesting for further study.

Pseudohastigerina (following taxonomic concept of Richard Olsson and Christoph Hemleben, 2006)

According to previous results, *Pseudohastigerina micra* produces very depleted $\delta^{18}\text{O}$ values and relatively depleted $\delta^{13}\text{C}$ values (Poore and Matthews, 1984; Boersma et al., 1987; Pearson et al., 2001). The present data supports *Pseudohastigerina* residing at a very shallow depth habitat and also having a different carbon metabolism than its muricate neighbors *Acarinina* and *Morozovelloides*.

When averaged, the data show an enrichment in $\delta^{13}\text{C}$ with increasing size fraction and an enrichment in $\delta^{18}\text{O}$. The $\delta^{18}\text{O}$ increase could imply the species migrates down in the water column throughout its lifetime. Both of these trends should be explored further.

Tenuitella (following taxonomic concept of Brian Huber, Richard Olsson, and Paul Pearson, 2006)

Tenuitella gemma, measured here in the 63-180 μm size fraction spanning from the late Eocene to early Oligocene, has not been studied previously. This data places *Tenuitella gemma* at a depth similar to those at which *Turborotalia*, *Guembelitrioides*, and *Globigerinatheka* reside. Interestingly,

it, across all four samples, has some of the most depleted $\delta^{13}\text{C}$ values of any other species measured in this study, suggesting a unique carbon metabolism. Further study of this species is recommended to delineate the details of its carbon metabolism and confirm its depth habitat.

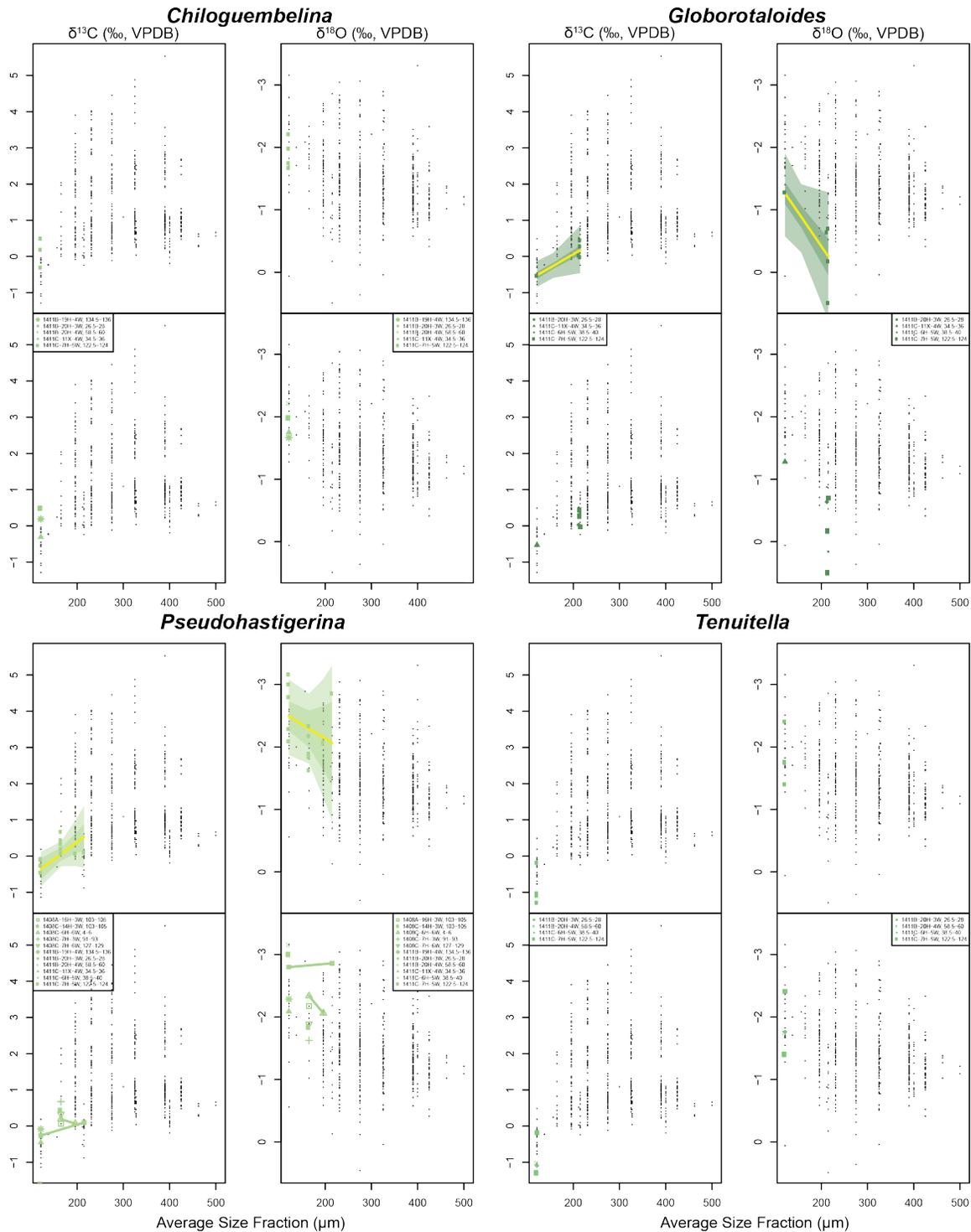


FIGURE 5: These charts include all data for a particular genus averaged. The top panels for each genus show the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ across size fraction for all the data. The bottom panels show sample-specific data. Species included here are *Chiloguembelina ototara*, *Globorotaloides suteri*, *Globorotaloides quadrocameratus*, *Pseudohastigerina micra*, *Pseudohastigerina* sp., and *Tenuitella gemma*.

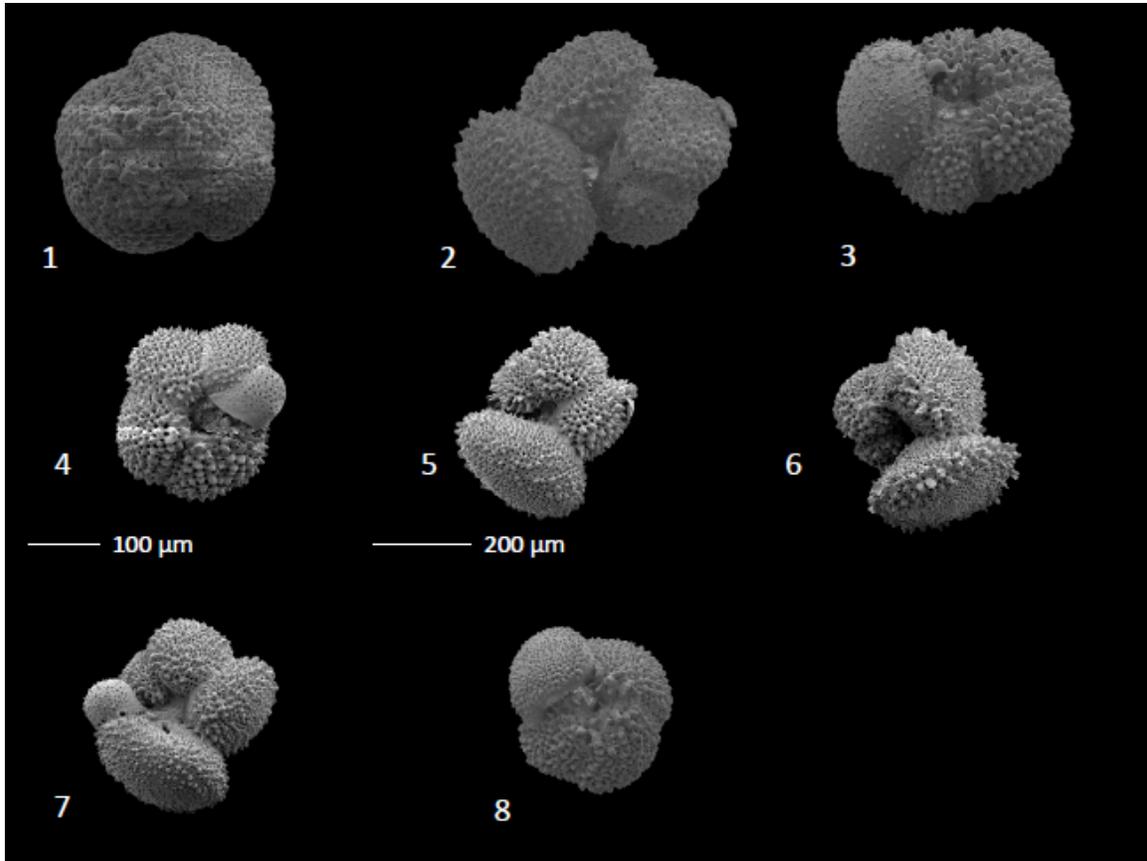


PLATE 7: **1)** *Acarinina bullbrooki*, U1408A-16H-3W, 103-105cm, Zone E9; **2)** *Acarinina praetopilensis*, U1408C-7H-3W, 94-96cm, E12; **3)** *Acarinina rohri* (?), U1408C-7H-3W, 94-96cm, E12; **4)** *Acarinina rohri* (?), U1408C-7H-3W, 94-96cm, E12; **5)** *Acarinina praetopilensis*, U1408C-7H-3W, 94-96cm, E12; **6)** *Acarinina topilensis*, U1408C-7H-3W, 94-96cm, E12; **7)** *Acarinina praetopilensis*, U1408C-7H-3W, 94-96cm, E12; **8)** *Acarinina bullbrooki*, U1408C-14H-3W, 103-105cm, E10

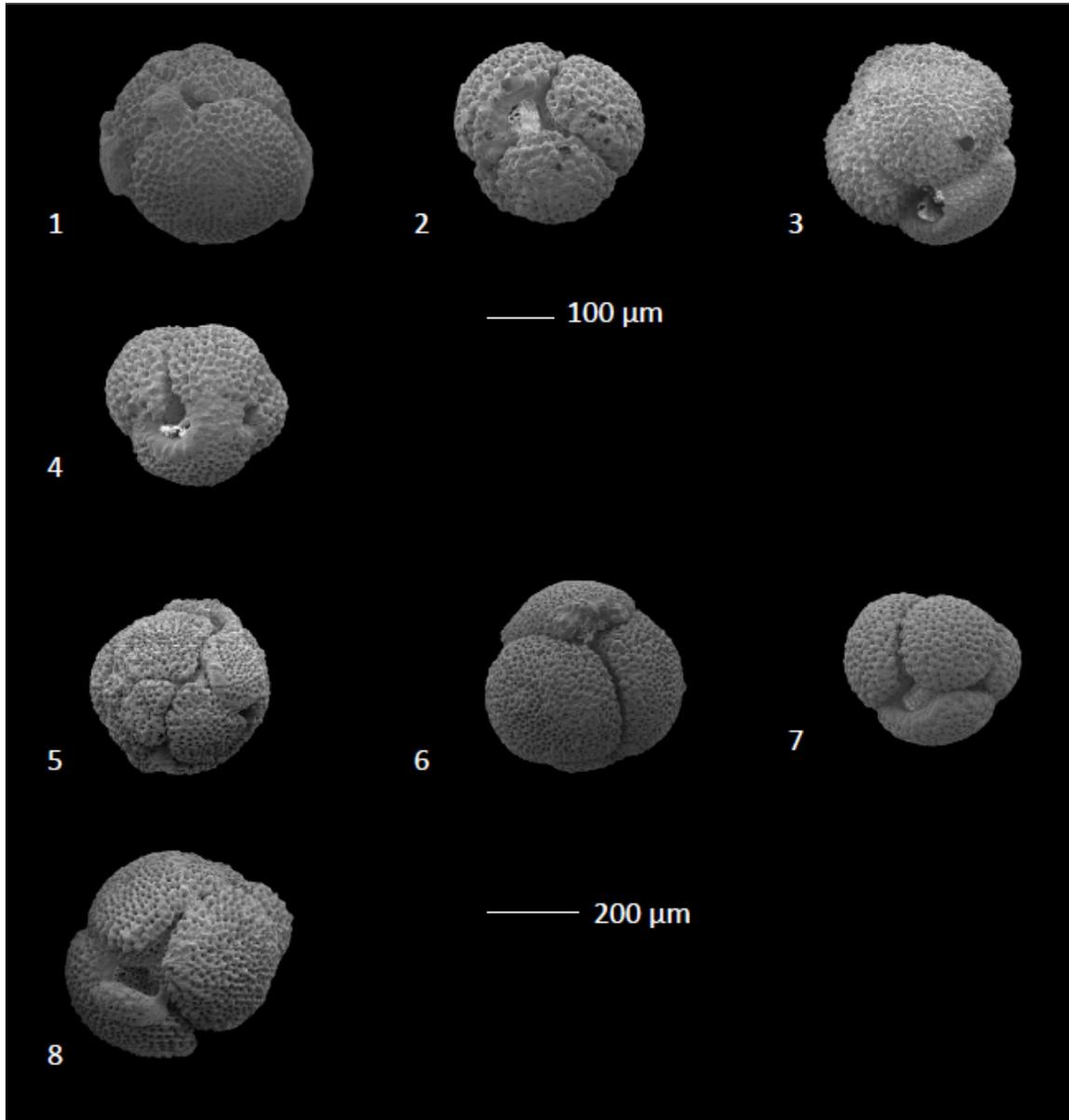


PLATE 8: 1) *Globigerinatheka barri*, U1408C-7H-3W, 94-96cm, E12); 2) *Globigerinatheka index*, U1408C-7H-6W, 127-129cm, E11; 3) *Globigerinatheka korotkovi*, U1408C-14H-3W, 103-105cm, E10; 4) *Globigerinatheka kugleri*, U1408C-14H-3W, 103-105cm, E10; 5) *Globigerinatheka barri*, U1408C-7H-6W, 127-129cm, E11; 6) *Globigerinatheka kugleri*, U1408C-7H-6W, 127-129cm, E11; 7) *Globigerinatheka kugleri*, U1408C-14H-3W, 103-105cm, E10; 8) *Globigerinatheka korotkovi*, U1408C-14H-3W, 103-105cm, E10

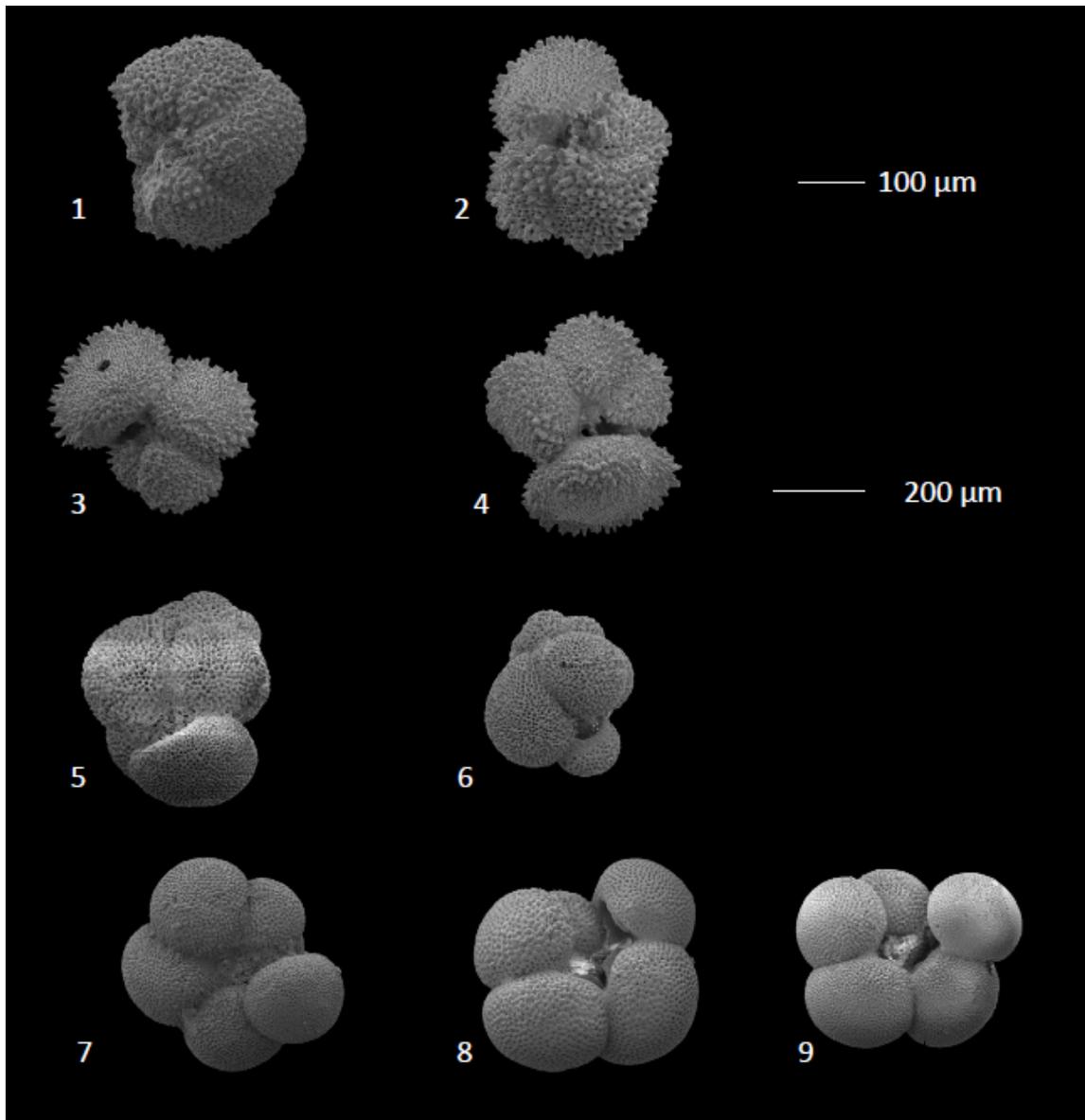


PLATE 9: **1)** *Morozovelloides crassatus*, U1408C-7H-3W, 94-96cm, E12; **2)** *Morozovelloides crassatus*, U1408C-14H-3W, 103-105cm, E10; **3)** *Morozovelloides bandyi*, U1408C-14H-3W, 103-105cm, E10; **4)** *Morozovelloides bandyi*, U1408C-14H-3W, 103-105cm, E10; **5)** *Guembelitrioides nuttalli*, U1408A-16H-3W, 103-105cm, E9; **6)** *Guembelitrioides nuttalli*, U1408C-14H-3W, 103-105cm, E10; **7)** *Praemurica(?) lozanoi*, U1408A-16H-3W, 103-105cm, E9; **8)** *Praemurica(?) lozanoi*, U1408C-14H-3W, 103-105cm, E10; **9)** *Praemurica(?) lozanoi*, U1408C-14H-3W, 103-105cm, E10

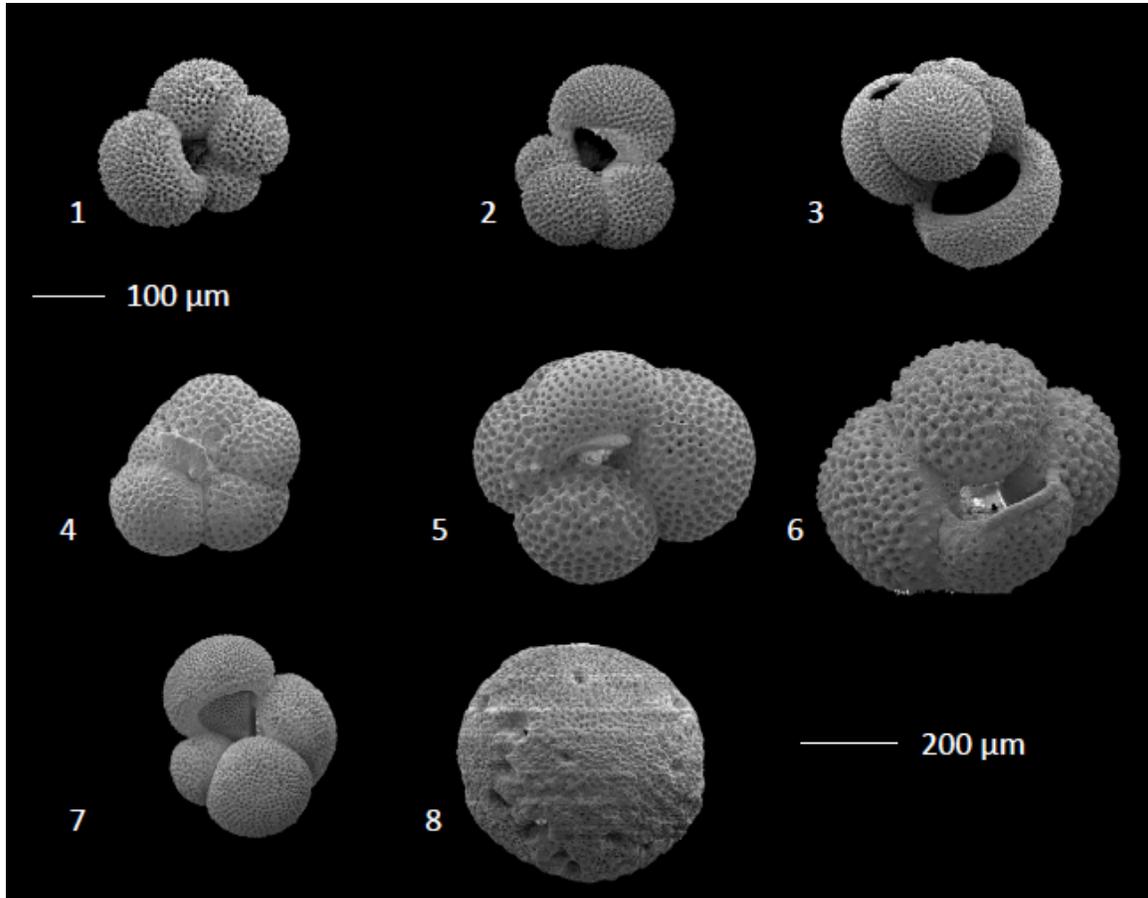


PLATE 10: **1)** *Globoturborotalita ouachitaensis*, U1408C-6H-6W, 4-6cm, E13; **2)** *Globoturborotalita ouachitaensis*, U1408C-6H-6W, 4-6cm, E13; **3)** *Subbotina gortanii*, U1408C-6H-6W, 4-6cm, E13; **4)** *Turborotalita carcoselleensis*, U1408C-7H-3W, 94-96cm, E12; **5)** *Catapsydrax unicavus*, U1408C-7H-3W, 94-96cm, E12; **6)** *Catapsydrax unicavus*, U1408C-7H-3W, 94-96cm, E12; **7)** *Subbotina gortanii*, U1408C-7H-6W, 127-129cm, E11; **8)** *Orbulinoides beckmanni*, U1408C-7H-6W, 127-129cm, E11

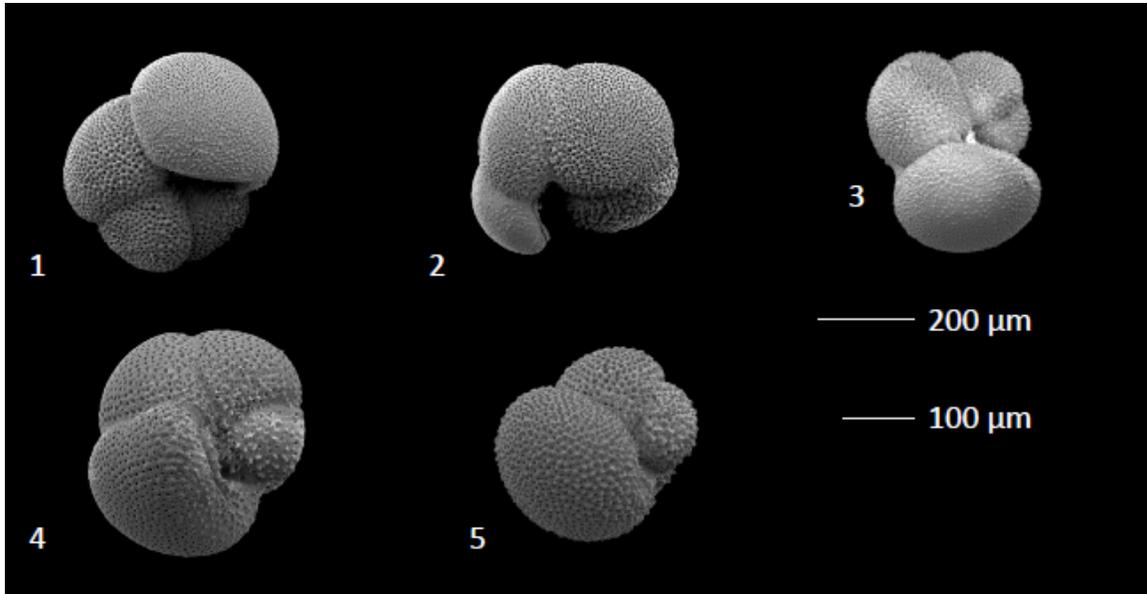


PLATE 11: 1) *Turborotalia cerroazulensis*, U1408C-7H-3W, 94-96cm, E12; 2) *Turborotalia pomeroli*, U1408C-7H-3W, 94-96cm, E12; 3) *Turborotalia frontosa*, U1408C-14H-3W, 103-105cm, E10; 4) *Turborotalia cerroazulensis*, U1408C-7H-6W, 127-129cm, E11; 5) *Turborotalia frontosa*, U1408C-14H-3W, 103-105cm, E10

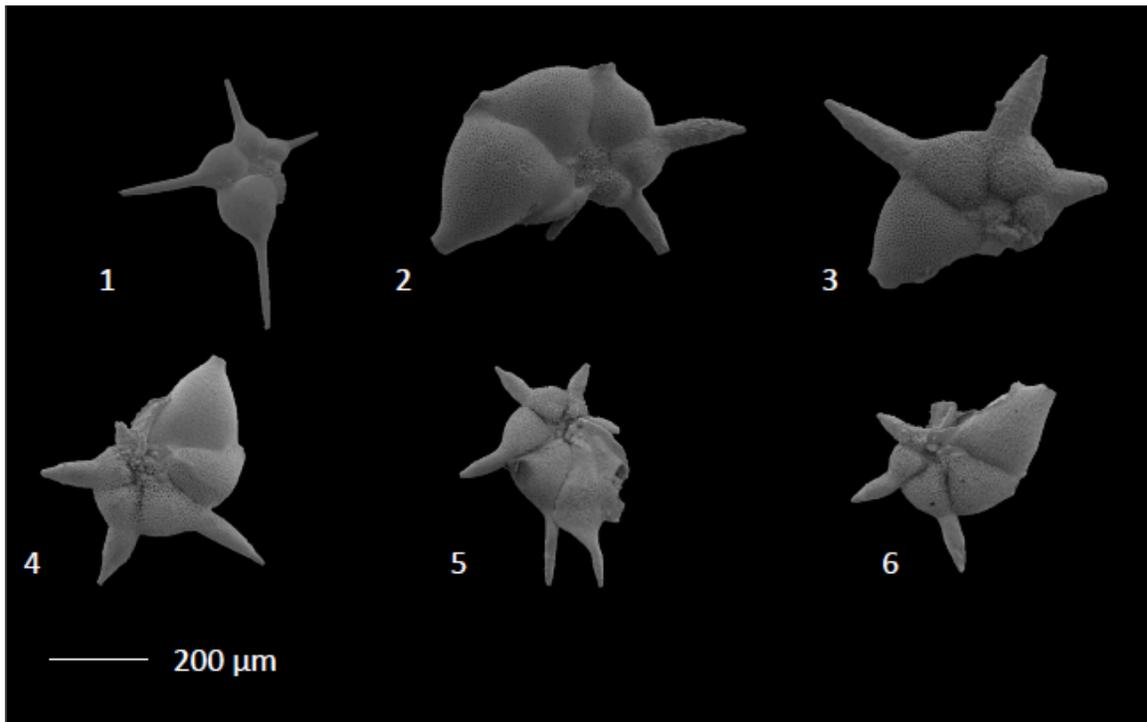


PLATE 12: 1) *Hantkenina liebusi*, U1408C-7H-3W, 94-96cm, E12; 2) *Hantkenina australis*, U1408C-14H-3W, 103-105cm, E10; 3) *Hantkenina dumblei*, U1408C-14H-3W, 103-105cm, E10; 4) *Hantkenina australis*, U1408C-14H-3W, 103-105cm, E10; 5) *Hantkenina dumblei*, U1408C-14H-3W, 103-105cm, E10; 6) *Hantkenina dumblei*, U1408C-14H-3W, 103-105cm, E10

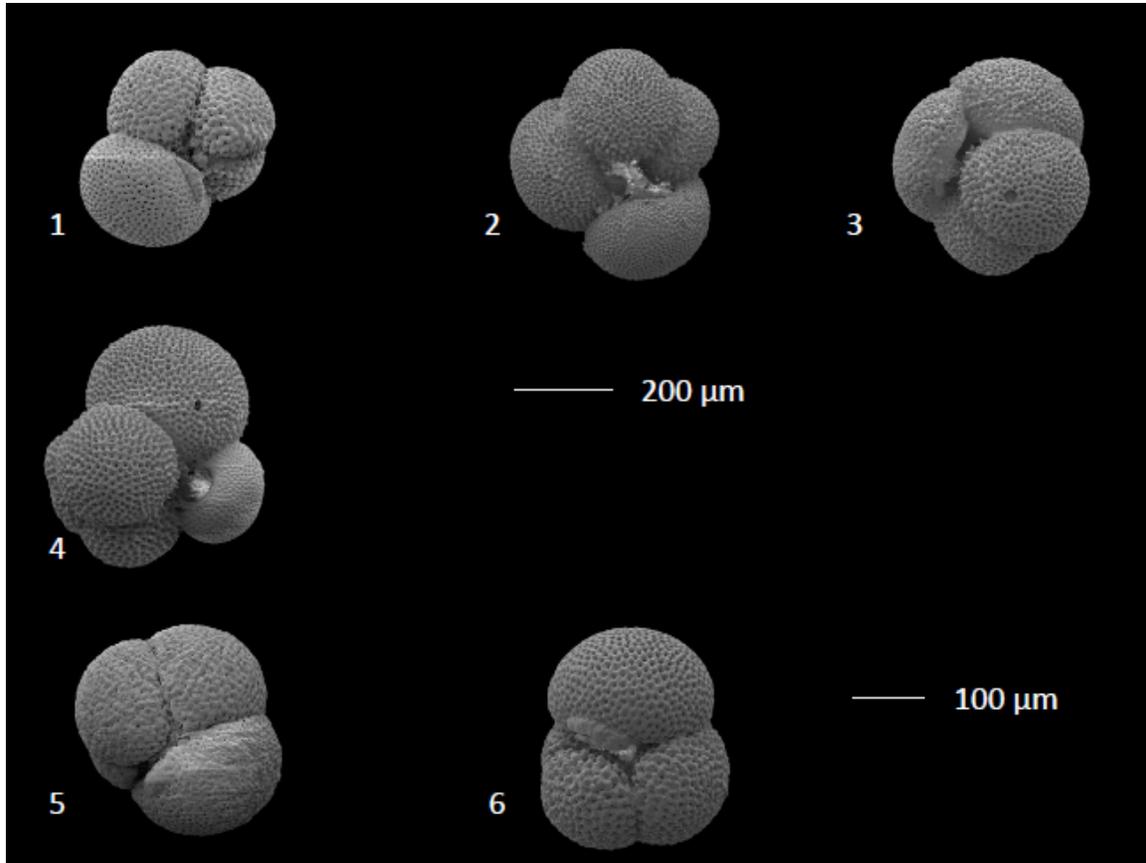


PLATE 13: **1)** *Subbotina eocaena*, U1408A-16H-3W, 103-105cm, E9; **2)** *Subbotina corpulenta* (toothy), U1408C-7H-3W, 94-96cm, E12; **3)** *Subbotina corpulenta* (toothy), U1408C-7H-6W, 127-129cm, E11; **4)** *Subbotina corpulenta*, U1408C-14H-3W, 103-105cm, E10; **5)** *Subbotina minima*, U1408C-6H-6W, 4-6cm, E13; **6)** *Subbotina linaperta*, U1408C-7H-6W, 127-129cm, E11

Conclusions

When viewed all together, these data present a relatively complete picture of the late Eocene-early Oligocene water column profile. From this data, we know that preservation does not have a significant effect on isotopic signatures, which taxonomic uncertainties are isotopically significant, and which species require further study.

In conclusion, the data in this study suggest depth habitat information for several previously unstudied species including *Globigerinatheka barri*, *Globigerinatheka kugleri*, *Globigerinatheka korotkovi*, *Globoturbotalita ouachitaensis* (Eocene), *Globorotaloides quadrocameratus*, *Hantkenina australis*, *Turbotalita carcoselleensis*, and *Tenuitella gemma*. The data also provide interesting but inconclusive isotopic information regarding species that should be

studied at even narrower size fractions: *Dentoglobigerina galavisi*, *Globorotaloides suteri*, *Globorotaloides quadrocameratus*, *Pseudohastigerina micra*, and *Tenuitella gemma*.

In addition, the data for some genera appeared to be much more consistent than for others. Deeper-dwelling genera, for example, exhibited strong trends that varied little across species and samples. Surface dwellers, on the other hand, could produce measurements that varied drastically. These differences could be the result of seasonality, differing ontogenies or metabolisms, or varying responses to the changing climate and unstable ocean conditions at the time.

Chapter 2

Results

Having analyzed each species across size fractions in the previous chapter, I will now turn to analysis of the carbon and oxygen stable isotope measurements of these genera across time. This dataset stretches across the EOT, a major Cenozoic climate shift from a greenhouse to an icehouse climate as Antarctic glaciation set in. Using only data for the 250-300 μm for the larger taxa and all size fractions for the small-bodied ones (*Chiloguembelina*, *Globorotaloides*, *Pseudohastigerina*, and *Tenuitella*), several trends in carbon and oxygen stable isotope gradients are apparent. Figure 6 uses these data to show the general direction in carbon and oxygen stable isotope space the samples moved. As the Earth transitioned into the Oligocene, most foraminiferal taxa became more enriched in $\delta^{18}\text{O}$ and more depleted in $\delta^{13}\text{C}$. We expect this increase in $\delta^{18}\text{O}$ values, as Antarctic glaciation traps more of the lighter isotopes in ice sheets.

In Figure 7, the carbon and oxygen stable isotope gradients over time are shown more clearly. Note that *Acarinina* and *Morozovelloides* are only extant in the first five time slices and are therefore not included in gradient calculations. Instead, the shallow-dwelling small-bodied taxa (*Chiloguembelina*, *Pseudohastigerina*, and *Tenuitella*) are set as the warmest temperature values on the earlier samples. There is not a significant shift in the $\delta^{18}\text{O}$ gradient across

time, remaining fairly consistently ~ 1 ‰ across the interval. However, there are more data points outside the expected $\delta^{18}\text{O}$ shallow-to-deep gradient in the later Eocene and early Oligocene samples.

The $\delta^{13}\text{C}$ gradient, on the other hand, shows a more significant shift. All have values above 0 ‰ $\delta^{13}\text{C}$ for the earlier Eocene samples. Later in the Eocene and in the early Oligocene, many of the taxa have shifted to negative $\delta^{13}\text{C}$ values. In addition, the most enriched $\delta^{13}\text{C}$ seems to be just above 1 ‰, while the middle Eocene samples have non-acarininid and non-morozovellid taxa all the way at ~ 2.7 ‰. The acarininid and morozovellid taxa clearly have the most enriched $\delta^{13}\text{C}$ values of any other taxa in this study. However, they do not have the most depleted $\delta^{18}\text{O}$ values and are rivaled instead by the smaller-bodied taxa in the late Eocene and early Oligocene.

At a more genus-specific level, it is possible to see which genus's isotopic ecologies are most affected by the climatic shift. Consistent with Figure 7, Figure 8 shows negligible shifts in $\delta^{18}\text{O}$ for each genus from the early to late Eocene. All genera show shifts toward more depleted $\delta^{18}\text{O}$ and more depleted $\delta^{13}\text{C}$ moving into the Oligocene. The largest $\delta^{18}\text{O}$ gradient by far is seen in *Dentoglobigerina*, with a shift of approximately 1.5 ‰. No other genus comes close to such a dramatic shift, and most are within 0.4 ‰. *Turborotalia* displays the smallest shift with only a ~ 0.2 ‰ decrease in $\delta^{18}\text{O}$. $\delta^{13}\text{C}$ also does not show dramatic shifts at the genus level. The largest shift is, again, *Dentoglobigerina* with decrease in $\delta^{13}\text{C}$ of about 1 ‰ and the smallest shift is *Turborotalia* with a decrease of ~ 0.2 ‰. Other genera have even smaller shifts, often only several tenths of a per mille.

Figure 9 is included to show which species are present in each sample's measurements, as species composition is a potential artifact in the data.

Data by Age (Ma)

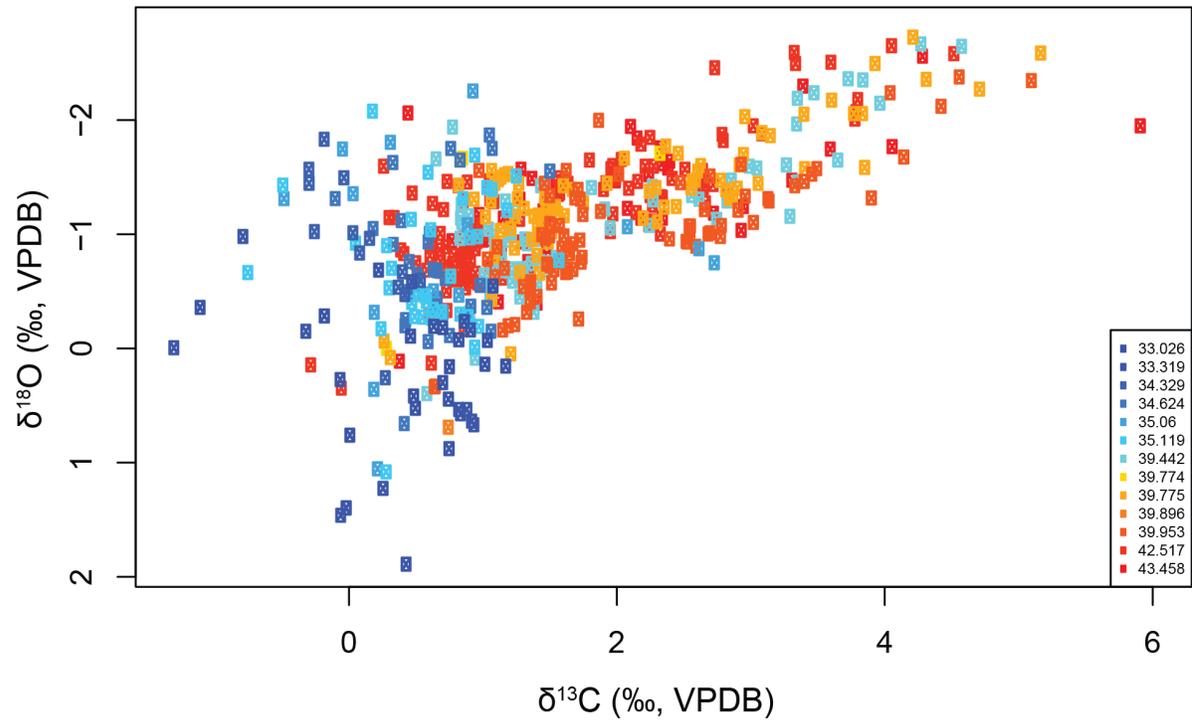


FIGURE 6: Above is shown all data in the 250-300 μm fraction for larger taxa and all size fractions for the smaller-bodied taxa (*Chiloguembelina*, *Globorotaloides*, *Pseudohastigerina*, and *Tenuitella*). Each Biozone is represented with a different color symbol.

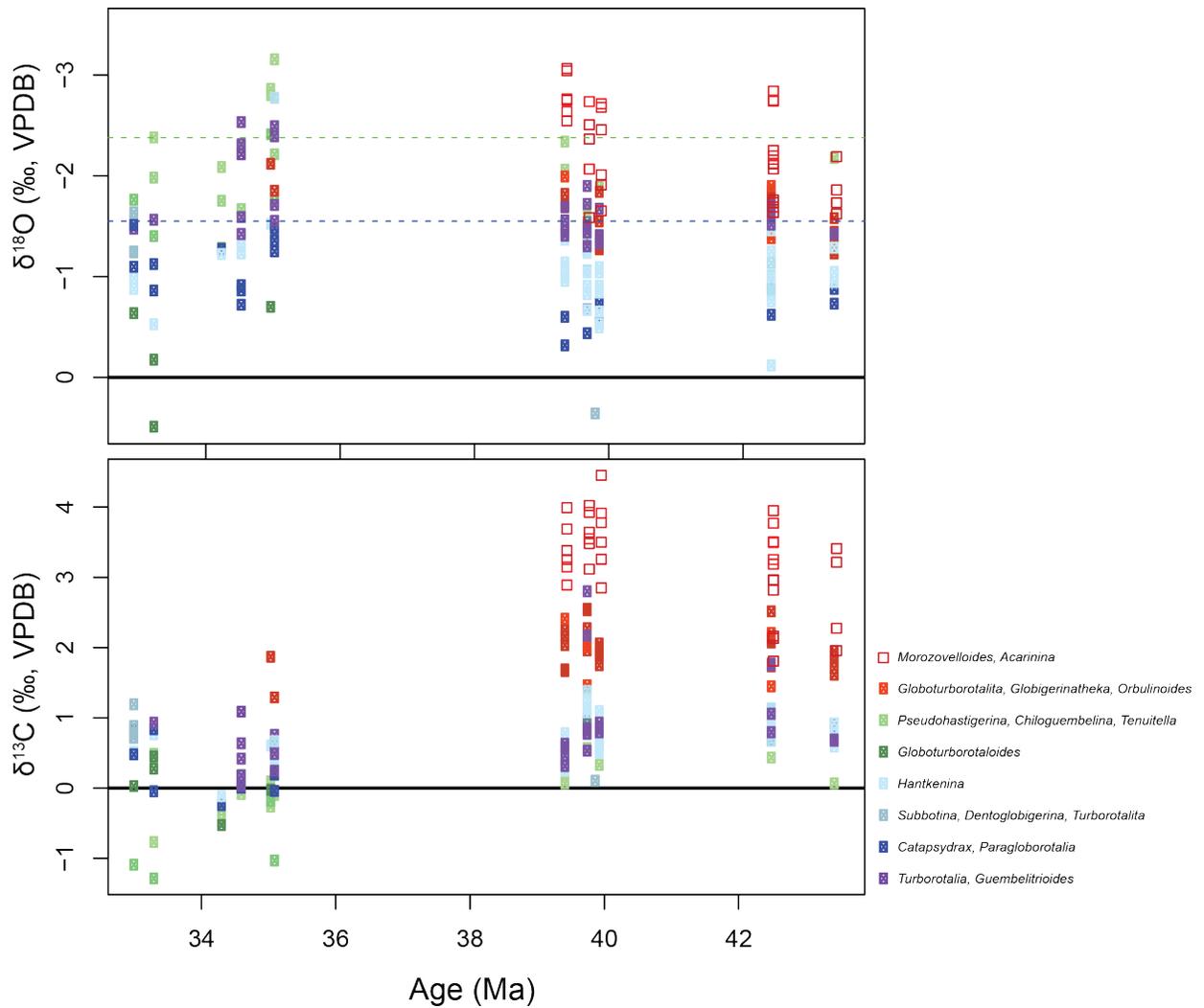


FIGURE 7: These charts show data from the 250-300 μm fraction for the larger-bodied taxa and all size fractions for the small-bodied taxa (*Chiloguembelina*, *Globorotaloides*, *Pseudohastigerina*, and *Tenuitella*), as in Figure 6. *Acarinina* and *Morozovelloides* appear as hollow symbols because they go extinct before the EOT and reside closest to the surface. Each samples' values have been normalized to benthic data from the same sample. The horizontal lines in the top panel ($\delta^{18}\text{O}$) indicate the temperature range between the shallowest-dwelling non-acarininid and non-morozovellid species and the deeper-dwelling species for middle Eocene samples.

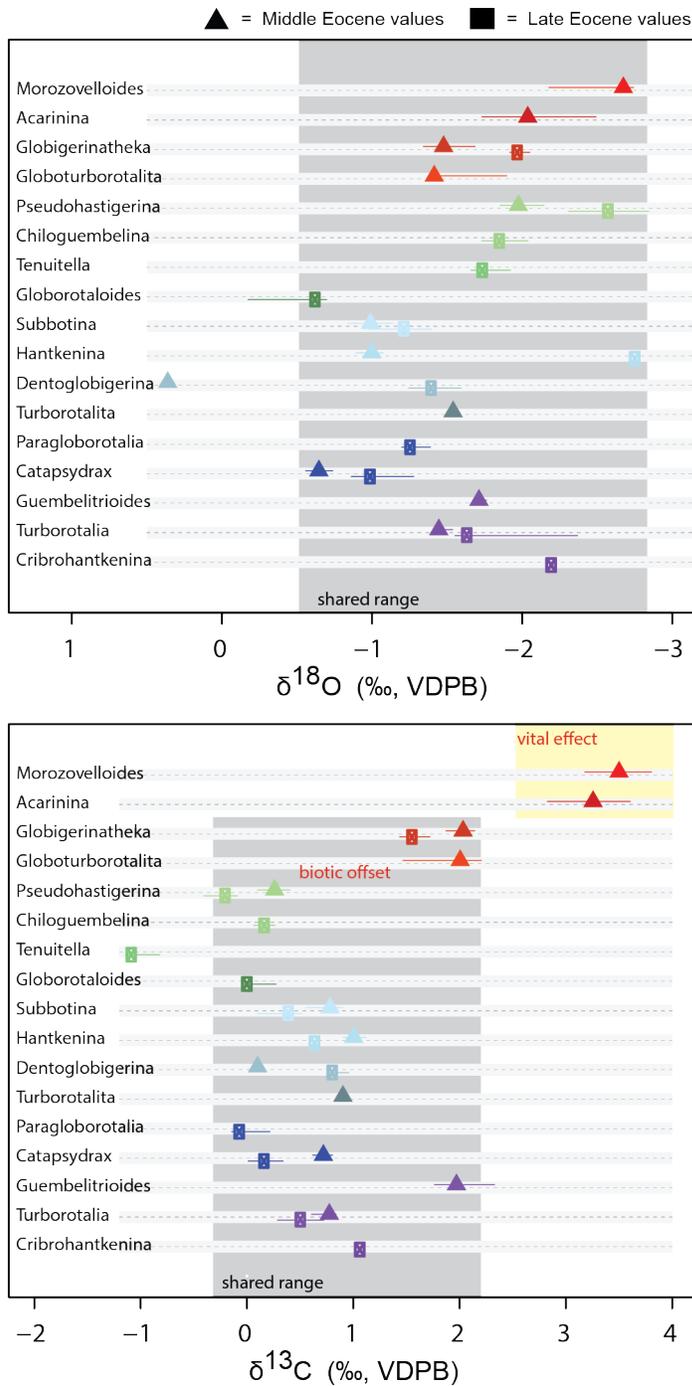


FIGURE 8: This figure uses the same data as Figure 7 (250-300 μm for larger taxa, all size fractions for small-bodied taxa). Each $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ data point includes averages across the genus and the time bin (either middle Eocene or late Eocene).

Species

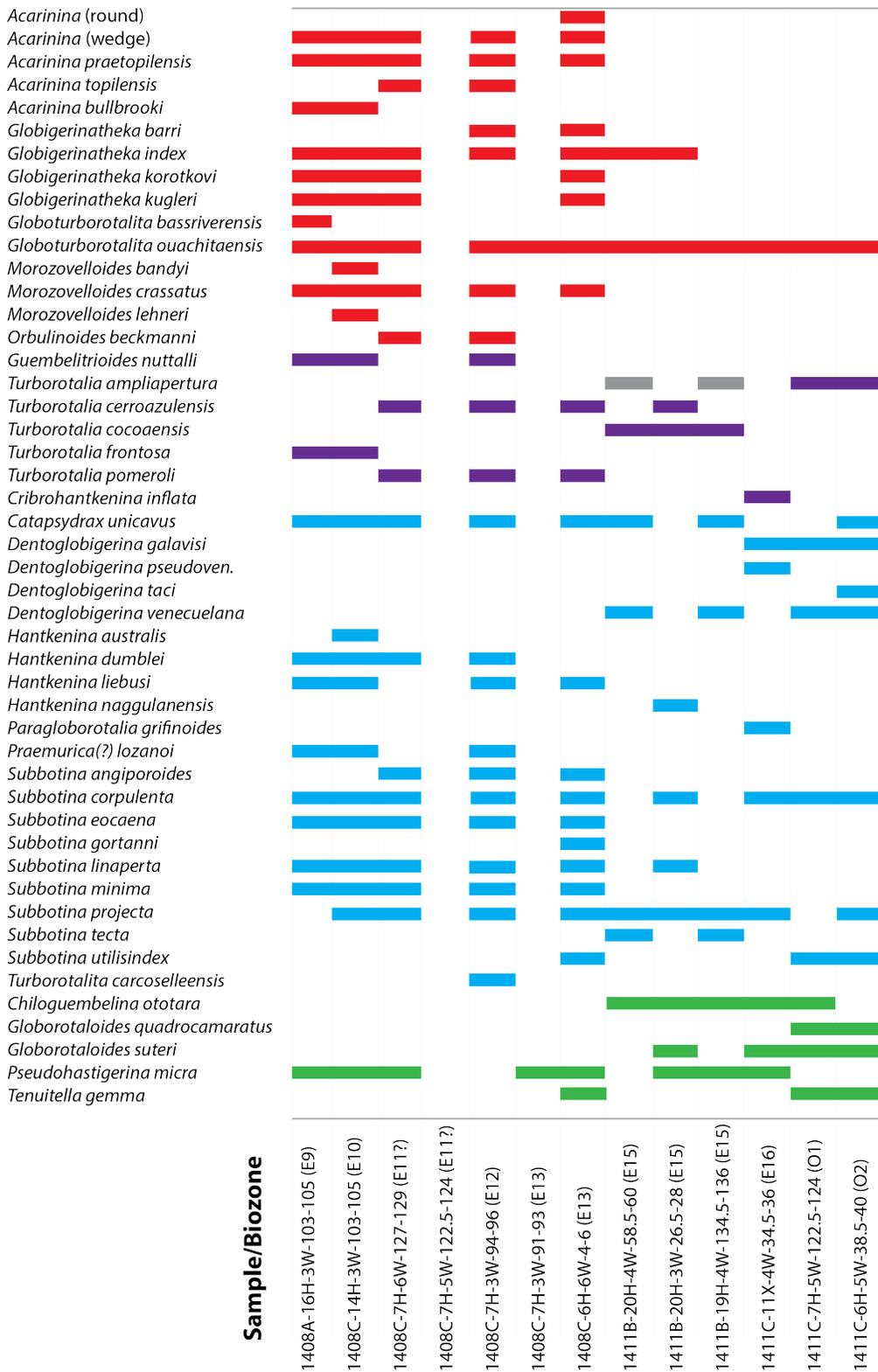


FIGURE 9: This figure shows for which samples each species in this study was measured.

Discussion

The data above show carbon and oxygen stable isotope trends across time using size-constrained data. From these data, we see a general movement towards more enriched $\delta^{18}\text{O}$ and more depleted $\delta^{13}\text{C}$. We also see the most dramatic shift in *Dentoglobigerina* for both isotope measurements and the least drastic shift in *Turborotalia* for both. All of the genus-specific data representations are impacted by which species are present in the measurement. Figure 9 provides a graphic representation of which species are included in each sample's measurement. Very few *Dentoglobigerina*, for example, were present in middle Eocene measurements (only *Dentoglobigerina venezuelana*). *Turborotalia* measurements, in contrast, have a more consistent species composition from the middle Eocene to the late Eocene. Other than the early shift from *Turborotalia frontosa* to *Turborotalia cerroazulensis* and *Turborotalia pomeroli*, the species compositions differ only in the addition of *Turborotalia ampliapertura* and *Turborotalia cocoaensis*.

Particularly useful for these purposes are the species present throughout the included time intervals, such as *Catapsydrax unicavus*, *Subbotina corpulenta*, and *Pseudohastigerina micra*. *Catapsydrax unicavus* has a shift for both measurements <0.5 ‰. *Pseudohastigerina micra* has a small shift in $\delta^{13}\text{C}$ (~ 0.4 ‰) but a larger one in $\delta^{18}\text{O}$ (~ 0.6 ‰). Perhaps these species and genera are among the most useful in determining paleoceanographic changes across the EOT.

Surprisingly, the oxygen isotope gradient did not alter significantly across the EOT, implying that surface water temperatures and the water column temperature gradient were not immediately affected by the transition into an icehouse. The carbon isotope gradient, however, does show a relatively large shift indicative of how the carbon metabolisms and photosymbionts may have been affected by the climatic change. The measured shifts, repeated in every genus for which both middle Eocene and early Oligocene specimens were available, all point to the same isotopic trends throughout this climatic transition, to varying degrees based on genus.

Summary

As the most extensive Eocene planktonic isotope record at a high latitude site currently in existence, this dataset addresses many questions. It confirms the isotope ecologies of previously studied species, tells us more about those with minimal existing data, and provides the first isotope data for several species. By adding to our knowledge of the carbon and oxygen stable isotope characteristics of each taxa, each species is now more useful for paleoceanographic studies. This record, paired with high-resolution SEM images, shows that the included samples have generally well-preserved fossils and that, where preservation is poor, the isotope measurements are not significantly affected. In addition, this study details taxonomic anomalies, as high-latitude Eocene planktonic foraminifera are not as extensively studied as lower latitude counterparts.

With the knowledge of each species' isotope ecology, we then considered changes across the EOT. We found that the temperature gradient between surface-layer and deep dwellers did not change significantly, while the carbon isotope gradient did. Some genera's isotope ecologies, like *Dentoglobigerina*, were affected more than others, such as *Turborotalia*. However, the species composition of each measurement could be confounding these observations.

In order to complete this dataset, more measurements at ideally narrower size fractions of the small-bodied taxa across the entire time interval are required. The data presented here indicate each species under this classification has a unique and interesting carbon metabolism and depth habitat. In addition, some of the larger taxa could be measured at smaller size fractions to further our knowledge of their carbon metabolisms and ontogenetic effects. Finally, higher temporal resolution measurements should be obtained for the species that go extinct at or before the EOT: *Acarinina*, *Morozovelloides*, *Globigerinatheka*, and *Hantkenina*. These genera, which went extinct as a result of changing conditions related to the climate transition, could also provide more detailed paleoceanographic information about the time leading up to the drastic change.

Acknowledgments

This project would not have been possible without incredible amounts of help from Pincelli Hull, Kirsty Edgar, Simon D'haenens, Leanne Elder, Helen Coxall, Max Holmstrom, Anna Nyberg, Rain Tsong, and Liana Epstein. It was funded by the Alan S. Tetelman Fellowship for International Research in the Sciences, the Yale College Dean's Research Fellowship, the Karen von Damm '77 Undergraduate Fellowship for Research in the Sciences, the Yale Analytical and Stable Isotope Center, and the Saybrook College Bruce M. Babcock '62 Travel Fellowship.

References

- Bambach, Richard. "Phanerozoic Biodiversity Mass Extinctions." *Earth and Planetary Sciences*. 34, 2006. p. 127-155.
- Barrera, E. and B.T. Huber. "Paleogene and early Neogene oceanography of the southern Indian Ocean: Leg 119 foraminifer stable isotope results." *Proc. Ocean Drilling Program Scientific Results*, 1991.
- Berggren, William and Richard Norris. "Biostratigraphy, Phylogeny and Systematics of Paleocene Trochospiral Planktic Foraminifera." *Micropaleontology*. 43, 1997. p. i-ii+1-116.
- Bijl, Peter, Stefan Schouten, Appy Sluijs, Gert-Jan Reichart, James Zachos, and Henk Brinkhuis. "Early Paleogene temperature evolution of the southwest Pacific Ocean." *Nature*. 461(7265), 2009. p. 776-779.
- Birch, Heather, Helen Coxall, and Paul Pearson. "Evolutionary ecology of Early Paleocene planktonic foraminifera: size, depth habitat, and symbiosis." *Paleobiology*. 38(3), 2012. p. 374-390.
- Birch, Heather, Helen Coxall, Paul Pearson, Dick Kroon, and Matthew O'Regan. "Planktonic foraminifera stable isotopes and water column structure: Disentangling ecological signals." *Marine Micropaleontology*. 101, 2013. p. 127-145.
- Boersma, Anne. "Atlantic Eocene planktonic foraminiferal paleohydrographic indicators and stable isotope paleoceanography." *Paleoceanography*. 2(3), 1987. p. 287-331.
- Cotton, Laura and Paul Pearson. "Extinction of larger benthic foraminifera at the Eocene-Oligocene boundary." *Palaeogeography, Palaeoclimatology, and Palaeoecology*. 311, 2011. p. 281-296.

- Coxall, Helen, Brian Huber, and Paul Pearson. "Origin and Morphology of the Eocene Planktonic Foraminifer *Hantkenina*." *Journal of Foraminiferal Research*. 33(3), 2003. p. 237-261.
- Coxall, Helen, Paul Pearson, Nicholas Shackleton, and Mike Hall. "Hantkeninid depth adaptation: An evolving life strategy in a changing ocean." *Geology*. 28(1), 2000.
- Coxall, Helen, Paul Wilson, Helko Pälike, Caroline Lear, and Jan Backman. "Rapid stepwise onset of Antarctic glaciation and deeper calcite compensation in the Pacific Ocean." *Nature Letters*. 433, 2005. p. 53-57.
- Coxall, Helen and Paul Wilson. "Early Oligocene glaciation and productivity in the eastern equatorial Pacific: Insights into global carbon cycling." *Paleoceanography*. 26, 2011.
- Diester-Haass, Liselotte and Rainer Zahn. "Eocene-Oligocene transition in the Southern Ocean: History of water mass circulation and biological productivity." *Geology*. 24(2), 1996. p. 163-166.
- D'hondt, Steven, James Zachos, and Gretchen Schultz. "Stable isotopic signals and photosymbiosis in Late Paleocene planktic foraminifera." *Paleobiology*. 20(3), 1994. p. 391-406.
- Edgar, K.M., S.M. Bohaty, S.J. Givvs, P.F. Sexton, R.D. Norris, and P.A. Wilson. "Symbiont 'bleaching' in planktic foraminifera during the Middle Eocene Climatic Optimum." *Geology*. 41(1), 2013. p. 15-18.
- Ezard, Thomas, Kirsty Edgar, and Pincelli Hull. "Environmental and biological controls on size-specific $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ in recent planktonic foraminifera." *Paleoceanography*. 30, 2015. p. 1-23.
- Hemleben, C., M. Spindler, O.R. Anderson. "Vertical distribution: Patchiness and daily vertical migration." *Modern Planktonic Foraminifera*. 1989.
- John, Eleanor, Paul Pearson, Helen Coxall, Heather Birch, Bridget Wade, and Gavin Foster. "Warm ocean processes and carbon cycling in the Eocene." *Philosophical Transactions of the Royal Society*. 2013.
- Keller, G., L. Li and N. MacLeod. "The Cretaceous/Tertiary boundary stratotype section at El Kef, Tunisia: how catastrophic was the mass extinction?"

- Palaeogeography, Palaeoclimatology, and Palaeoecology*. 119, 1995. p. 221-254.
- Kroon, Dick and Gerald Ganssen. "Northern Indian Ocean upwelling cells and the stable isotope composition of living planktonic foraminifers." *Deep Sea Research Part A. Oceanographic Research Papers*. 36(8), 1989. p. 1219-1236.
- Miller, Kenneth, James Wright, Miriam Katz, Bridget Wade, James Browning, Benjamin Cramer, and Yair Rosenthal. "Climate threshold at the Eocene-Oligocene transition: Antarctic ice sheet influence on ocean circulation." *The Geological Society of America Special Paper 452*. 2009.
- Norris, R.D., P.A. Wilson, P. Blum, A. Fehr, C. Agnini, A. Bornemann, S. Boulila, P.R. Bown, C. Courneded, O. Friedrich, A.K. Ghosh, C.J. Hollis, P.M. Hull, K. Jo, C.K. Junium, M. Kaneka, D. Liebrand, P.C. Lippert, Z. Liu, H. Matsui, K. Moriya, H. Nishi, B. N. Opdyke, D. Penman, B. Romans, H.D. Scher, P. Sexton, H. Takagi, S.K. Turner, J.H. Whiteside, T. Yamaguchi, and Y. Yamamoto. "Site U1408." *Integrated Ocean Drilling Program*. 2014.
- Norris, R.D., P.A. Wilson, P. Blum, A. Fehr, C. Agnini, A. Bornemann, S. Boulila, P.R. Bown, C. Courneded, O. Friedrich, A.K. Ghosh, C.J. Hollis, P.M. Hull, K. Jo, C.K. Junium, M. Kaneka, D. Liebrand, P.C. Lippert, Z. Liu, H. Matsui, K. Moriya, H. Nishi, B. N. Opdyke, D. Penman, B. Romans, H.D. Scher, P. Sexton, H. Takagi, S.K. Turner, J.H. Whiteside, T. Yamaguchi, and Y. Yamamoto. "Site U1411." *Integrated Ocean Drilling Program*. 2014.
- Pagani, Mark, Matthew Huber, Zhonghui Liu, Steven Bohaty, Jorijntje Henderiks, Willem Sijp, Srinath Krishnan, and Robert DeConto. "The Role of Carbon Dioxide During the Onset of Antarctic Glaciation." *Science*. 334, 2011. p. 1261-1264.
- Pearson, Paul and Martin Palmer. "Middle Eocene Seawater pH and Atmospheric Carbon Dioxide Concentrations." *Science*. 284, 1999. p. 1824-1826.
- Pearson, Paul, Peter Ditchfield, Joyce Singano, Katherine Harcourt-Brown, Christopher Nicholas, Richard Olsson, Nicholas Shackleton, and Mike

- Hall. "Warm tropical sea surface temperatures in the Late Cretaceous and Eocene epochs." *Nature*. 413, 2001. p. 481-487.
- Pearson, Paul, Gavin Foster, and Bridget Wade. "Atmospheric carbon dioxide through the Eocene-Oligocene climate transition." *Nature*. 461, 2009. p. 1110-1113.
- Pearson, Paul, Richard Olsson, Brian Huber, Christoph Hemleben, and William Berggren. *Atlas of Eocene Planktonic Foraminifera*. Cushman Foundation Special Publication 41. 2006.
- Pearson, Paul, Bart van Dongen, Christopher Nicholas, Richard Pancost, Stefan Schouten, Joyce Singano, and Bridget Wade. "Stable warm tropical climate through the Eocene epoch." *Geology*. 35(3), 2007. p. 211-214.
- Pearson, Paul, N. Shackleton and M. Hall. "Stable Isotope Paleoecology of Middle Eocene Planktonic Foraminifera and Multi-species Isotope Stratigraphy, DSDP Site 523, South Atlantic." *Journal of Foraminiferal Research*. 23, 1993. p. 123-140.
- Peeters, Frank, Geert-Jan Brummer, Gerald Ganssen. "The effect of upwelling on the distribution and stable isotope composition of *Globigerina bulloides* and *Globigerinoides ruber* (planktic foraminifera) in modern surface waters of the NW Arabian Sea." *Global and Planetary Change*. 34, 2002. p. 269-291.
- Poore, R.Z. and R.K. Matthews. "Oxygen isotope ranking of late Eocene and Oligocene planktonic foraminifers: Implications for Oligocene sea-surface temperatures and global ice-volume." *Marine Micropaleontology*. 9(2), 1984. p. 111-134.
- Scher, Howie and Ellen Martin. "Timing and Climatic Consequences of the Opening of Drake Passage." *Science*. 312, 2006. p. 428-430.
- Scher, Howie, Steven Bohaty, James Zachos, and Margaret Delaney. "Two-stepping into the icehouse: East Antarctic weathering during progressive ice-sheet expansion at the Eocene-Oligocene transition." *Geology*. 39(4), 2011. p. 383-386.

- Scher, Howie, Joanne Whittaker, Simon Williams, Jennifer Latimer, Wendy Kordesch, and Margaret Delaney. "Onset of Antarctic Circumpolar Current 30 million years ago as Tasmanian Gateway aligned with westerlies." *Nature Letters*. 523, 2015. p. 580-583.
- Sexton, Phil, Paul Wilson, Paul Pearson. "Microstructural and geochemical perspectives on planktic foraminiferal preservation: 'Glassy' versus 'Frosty.'" *Geochemistry, Geophysics, Geosystems*. 7(12), 2006.
- van Eijden, A.J.M. and G.M. Ganssen. "An Oligocene multi-species foraminiferal oxygen and carbon isotope record from ODP Hole 758A (Indian Ocean): paleoceanographic and paleo-ecologic implications." *Marine Micropaleontology*. 25(1), 1995. p. 47-65.
- Wade, Bridget. "Planktonic foraminiferal biostratigraphy and mechanisms in the extinction of *Morozovella* in the late middle Eocene." *Marine Micropaleontology*. 51, 2004. p. 23-38.
- Wade, Bridget and Heiko Pälike. "Oligocene climate dynamics." *Paleoceanography*. 19(4), 2004.
- Wade, Bridget, Nadia Al-Sabouni, Christoph Hemleben, and Dick Kroon. "Symbiont bleaching in fossil planktonic foraminifera." *Evolutionary Ecology*. 22, 2008. p. 253-265.
- Wade, Bridget, Vlasta Premec Fucek, Shin-Ichi Kamikuri, Milos Bartol, Valeria Luciani, and Paul Pearson. "Successive extinctions of muricate planktonic foraminifera (*Morozovelloides* and *Acarinina*) as a candidate for marking the base Priabonian." *Stratigraphy*. 45(4), 2012. p. 245-262.
- Wilson, Paul, Richard Norris, and Matthew Cooper. "Testing the Cretaceous greenhouse hypothesis using glassy foraminiferal calcite from the core of the Turonian tropics on the Demerara Rise." *Geology*. 30(7), 2002. p. 607-610.
- Zachos, James, Terrence Quinn, and Karen Salamy. "High-resolution (10^4 years) deep-sea foraminiferal stable isotope records of the Eocene-Oligocene climate transition." *Paleoceanography*. 11(3), 1996. p. 251-266.

Zanazzi, Alessandro, Matthew Kohn, Bruce MacFadden, and Dennis Terry.
“Large temperature drop across the Eocene-Oligocene transition in central
North America.” *Nature*. 445, 2007. p. 639-642.