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STABLE ISOTOPE PALEOECOLOGY ($\delta^{13}C$ AND $\delta^{18}O$) OF EARLY EOCENE *ZEAUVIGERINA AEGYPTIACA* FROM THE NORTH ATLANTIC (DSDP SITE 401)

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ABSTRACT

Within the expanded and clay-enriched interval following the Paleocene-Eocene Thermal Maximum (PETM; ~55.8 Ma) at Deep Sea Drilling Project (DSDP) Site 401 (eastern North Atlantic), high abundances of well-preserved biserial planktic foraminifera such as *Zeauvigerina aegyptiaca* and *Chiloguembelina* spp. occur. The paleoecological preferences of these taxa are only poorly constrained, largely because existing records are patchy in time and space. The thin-walled *Z. aegyptiaca* is usually rather small (<125 µm) and thus prone to recrystallization and dissolution; stable isotopes measurements are therefore virtually non-existent. A comparative stable isotope ($\delta^{13}C$ and $\delta^{18}O$) study of well-preserved specimens of *Z. aegyptiaca* and several planktic foraminiferal species (*Morozovella subbotinae*, *Subbotina patagonica*, *Chiloguembelina wilcoxensis*) enabled us to determine the preferred depth habitat and mode of life for *Z. aegyptiaca*. Oxygen isotope values of *Z. aegyptiaca* range from -1.57‰ to -2.07‰ and overlap with those of *M. subbotinae* indicating that their habitat is (1) definitely planktic, which has been questioned by some earlier isotopic studies, and (2) probably within the lower surface mixed layer. Carbon isotope ratios range from 0.99‰ to 1.34‰ and are distinctly lower than values for non-biserial planktic species. This may indicate isotopic disequilibrium between ambient seawater and the calcareous tests of *Z. aegyptiaca*, which we relate to vital effects and to its opportunistic behavior. The observed isotopic signal of *Z. aegyptiaca* relative to the other planktic foraminiferal species is highly similar to many other microperforate bi- and triserial planktic genera that have appeared through geological time such as *Heterohelix*, *Guembelitria*, *Chiloguembelina*, *Streptochilus* and *Gallitellia* and we suggest that *Z. aegyptiaca* shares a similar ecology and habitat. Thus, in order for the opportunistic *Z. aegyptiaca* to bloom during the aftermath of the PETM, we assume that at that time, the surface waters at Site 401 were influenced by increased terrestrial run-off and nutrient availability.

1. INTRODUCTION

Microperforate bi- and triserial planktic foraminiferal forms originated in the Late Albian from the biserial *Heterohelix,* diversified in the Late Cretaceous and survive to the present day (Nederbragt, 1991; Olsson et al., 1999). The spatial and temporal distribution of mid-Cretaceous to Recent triserial forms (e.g. *Guembelitria*, *Jenkinsina* and *Gallitellia*), mid-Cretaceous and Cenozoic biserial species (e.g. *Heterohelix*, *Chiloguembelina*, *Zeauvigerina* and *Streptochilus*) is poorly known because they are easily overlooked due to their (mostly) small size (Resig and Kroopnick, 1983; Huber and Boersma, 1994; Koutsoukos, 1994; Kroon and Nederbragt, 1990; Huber et al., 2006).

Bi-and triserial forms are characterized by relatively long stratigraphic ranges and are often associated with extreme climatic events such as Cretaceous Oceanic Anoxic Events (Nederbragt et al., 1998), the Cretaceous/Paleogene boundary (Koutsoukos, 1994; Keller and Pardo, 2004; Pardo and Keller, 2008), the PETM and the Middle Eocene Climatic Optimum (MECO; Luciani et al., 2007, 2010) where they appear to bloom. Despite this, their ecology remains poorly known. Previous studies reported light $\delta^{13}C$ values in conjunction with heavy $\delta^{18}O$ values for many Cenozoic biserial planktic foraminifera compared to non-biserial surface dwelling planktic foraminifera (Resig and Kroopnick, 1983; Boersma and Premoli Silva, 1989). This has led to the hypothesis that biserial planktic foraminifera were low-oxygen tolerant, meso- to eutrophic thermocline dwellers thriving in variable surface water conditions such as upwelling areas (Leckie, 1987; Kroon and Nederbragt, 1990; Nederbragt, 1991) or were indicative of the presence of an Oxygen Minimum Zone (OMZ; Resig and Kroopnick, 1983; Boersma and Premoli Silva, 1989). This view was later adopted and frequently used in paleoceanographic interpretations (e.g. Hallock et al., 1991).

However, this general ecological interpretation does not comply with all available data. For instance, the genus *Zeauvigerina* is considered to be a planktic taxon (Huber and Boersma, 1994; Huber et al., 2006), although the few existing stable isotope measurements are not unambiguous. For example, oxygen and carbon isotope values of *Z. waiparaensis* from the Maastrichtian and Paleocene plot much closer to co-occurring benthic species (*Gavelinella beccariiformis*) than planktic species (Barrera and Keller, 1994; Huber and Boersma, 1994). A single oxygen isotope value for *Z. aegyptiaca* (late Paleocene) suggests a benthic mode of life, while the carbon isotope value implies a planktic habitat (Huber and Boersma, 1994). Furthermore, it has been shown that some bi- and triserial forms (e.g. *Guembelitria*, *Streptochilus*, *Gallitellia vivans*) may have originated from benthic foraminiferal ancestors or even have a tychopelagic mode of life, occupying both the benthic and planktic realm (Huber et al., 2006; Smart and Thomas, 2007; Ujiie et al., 2008; Darling et al., 2009; McGowran, 2012). With this in mind, an ecological interpretation is evidently not straightforward.

Abundant biserial foraminifera have been observed following the PETM at DSDP Site 401 (Bay of Biscay, North Atlantic; Pardo et al., 1997). Although most of these biserial taxa belong to *Chiloguembelina*, about 1% of all foraminifera larger than 63 µm belong to *Zeauvigerina aegyptiaca* (personal observations; Pardo et al., 1997). *Zeauvigerina aegyptiaca* is a small and rare species with only patchy documented occurrences in the latest Paleocene – earliest Eocene from the low to mid latitudes in the Tethys, Atlantic and the Indian Oceans (Said and Kenawy, 1956; Beckman, 1957; McGowran, 1964; Huber and Boersma, 1994) and little is known about its paleodepth and paleoecological preferences, limiting its use to reconstruct paleoceanographic conditions.

In order to verify and delineate the paleoecology and preferred depth habitat of *Zeauvigerina*, monospecific stable isotope measurements have been performed on well-preserved *Zeauvigerina aegyptiaca* specimens and on several well-known co-occurring planktic foraminiferal taxa. *Zeauvigerina aegyptiaca* virtually exclusively occurs in the expanded and clayey interval following the PETM at DSDP Site 401 and only very rarely in the Paleocene, in the PETM itself and above the expanded clayey interval. This may be an indication of specific local or regional paleoceanographic conditions enabling it to proliferate at that time. Hence, this relatively unknown taxon may potentially provide insight into the water column properties during the aftermath of the PETM in the northeastern Atlantic Ocean.

2. MATERIAL AND METHODS

DSDP Site 401 was drilled on Meriadzek Terrace in the eastern North Atlantic Ocean (lat. 47°25.65'N; long. 8°48.62'W; 2495 m present water depth; Fig. 1). Thirty-four sieve size fraction analyses were performed on five samples from the earliest Eocene calcareous nannofossil marls of core 14 (198.90-201.04 mbsf; calcareous nannofossil zone NP10) following the PETM (Pardo et al., 1997; Nunes and Norris, 2006).

Sample material was dried at ~50°C, soaked in tap water for 24 h and gently washed under running water through a 63 µm mesh sieve. Carbon and oxygen stable isotope measurements were made on monospecific samples of well-preserved *Morozovella subbotinae*, *Subbotina patagonica*, *Chiloguembelina wilcoxensis* and *Zeauvigerina aegyptiaca* from narrow sieve size fractions to minimize potential artifacts from ontogenetic effects, symbiont density, gametogenic calcite formation and changes in calcification depth during growth.

Two size fractions (180-250 µm and 250-355 µm) were used for *M. subbotinae* and *S. patagonica*, with two additional measurements of *M. subbotinae* on the >355 µm size fraction. Specimens of *C. wilcoxensis* and *Z. aegyptiaca* were only selected from the 125-180 µm and 63-125 µm size fractions, respectively, as larger (thicker) specimens were extremely rare. Between 2 and 75 specimens were measured for each analysis, depending on shell thickness and size, to obtain a minimum sample mass of 50 µg. Besides this practical consideration, the advantage of analyzing large numbers of specimens is that isotopic differences between species are more clearly expressed rather than variability between individuals, which for example may live over a range of depth habitats or at different times of the year (Pearson et al., 1993). Prior to analysis, all specimens were cleaned ultrasonically for about 20 seconds in distilled water to remove any possible remnant material. Analyses were carried out at the Free University of Brussels (VUB), Belgium, using a ThermoFinnigan Delta^{plus} XL mass spectrometer equipped with an automated ThermoFinnigan Kiel III online carbonate preparation line. The analytical precision (1σ) based on analyses of the NBS-19 standard was ~0.02‰ for $\delta^{13}C$ and ~0.07‰ for $\delta^{18}O$ relative to the Vienna Pee Dee Belemnite (VPDB) standard.

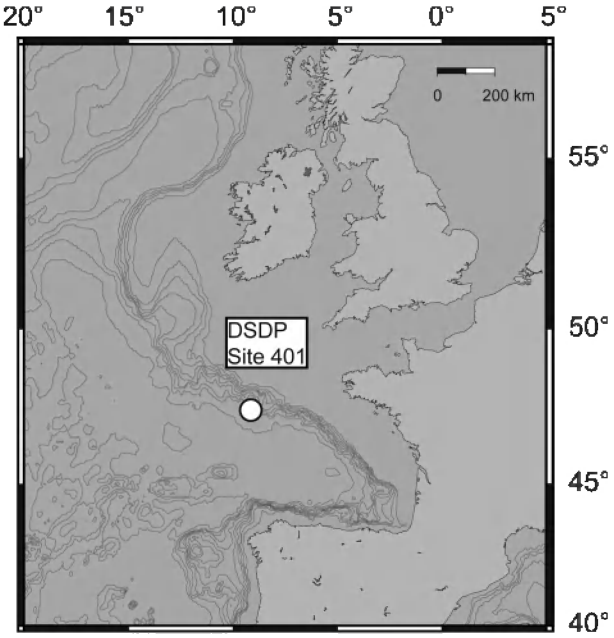

FIGURE 1: Location of DSDP Site 401 in the present-day northeastern Atlantic (Bay of Biscay).

3. RESULTS

Isotope results are listed in Table 1 and graphically shown per sample in Figures 2 and 3.

Oxygen isotope values of the biserial planktic foraminifera (*Z. aegyptiaca* and *C. wilcoxensis*) overlap with those of surface dwelling planktic foraminifera (*M. subbotinae*) in the same samples. The $\delta^{18}O$ values of *Z. aegyptiaca* range from -1.71‰ to -2.07‰ while $\delta^{18}O$ values of *C. wilcoxensis* range between -1.69‰ and -2.24‰. Specimens of *S. patagonica* display very little intraspecific variability, even between the two different size fractions, and reveal $\delta^{18}O$ values between -1.34‰ and -1.61‰. The values for *M. subbotinae* range between -1.85‰ and -2.74‰, bearing in mind that the values for individual size fractions are less variable and that there is a general trend towards more negative values in larger size fractions.

The relative oxygen isotope values of *S. patagonica* and *M. subbotinae* are in line with previously published studies (Shackleton et al., 1985; Pearson et al., 1993; D'Hondt et al., 1994; Sexton et al., 2006b) and fit on the J-shaped "equilibrium line" connecting the surface dwelling *M. subbotinae* with the thermocline dwelling *S. patagonica* and ending in the heaviest oxygen isotope values of the benthic foraminifer *Nuttallides truempyi* (Nunes and Norris, 2006). Small size-related oxygen isotope variations (Figs. 2 and 3) confirm previously published studies that document slight increases in $\delta^{18}O$ for *Morozovella* with test size (D'Hondt et al., 1994; Norris, 1996; Kelly et al., 1998) and little or no change in $\delta^{18}O$ for larger *Subbotina* specimens (Pearson et al., 1993; Norris, 1996).

Carbon isotope values of the biserial taxa (*Z. aegyptiaca* and *C. wilcoxensis*) range from 0.99‰ to 1.34‰ and 0.96‰ to 1.45‰, respectively, and are much lighter than the values for surface dwelling planktic foraminifera (*M. subbotinae*), but overlap or are slightly lighter than the values for thermocline dwellers (*S. patagonica*). *Subbotina patagonica* $\delta^{13}C$ values are very similar for both size fractions and vary between 1.32‰ and 1.53‰. *Morozovella subbotinae* reveals a large variability in $\delta^{13}C$ values with values ranging between 3.37‰ and 4.68‰ with measurements from larger size fractions displaying more positive values.

4. DISCUSSION

4.1 PRESERVATION

The clay-rich sediments at Site 401 yield well-preserved foraminifera (Fig. 4). This preservation state is not common in pelagic settings (e.g. Sexton et al., 2006a), yet it is typical for the studied interval and surprisingly, also for the PETM of Site

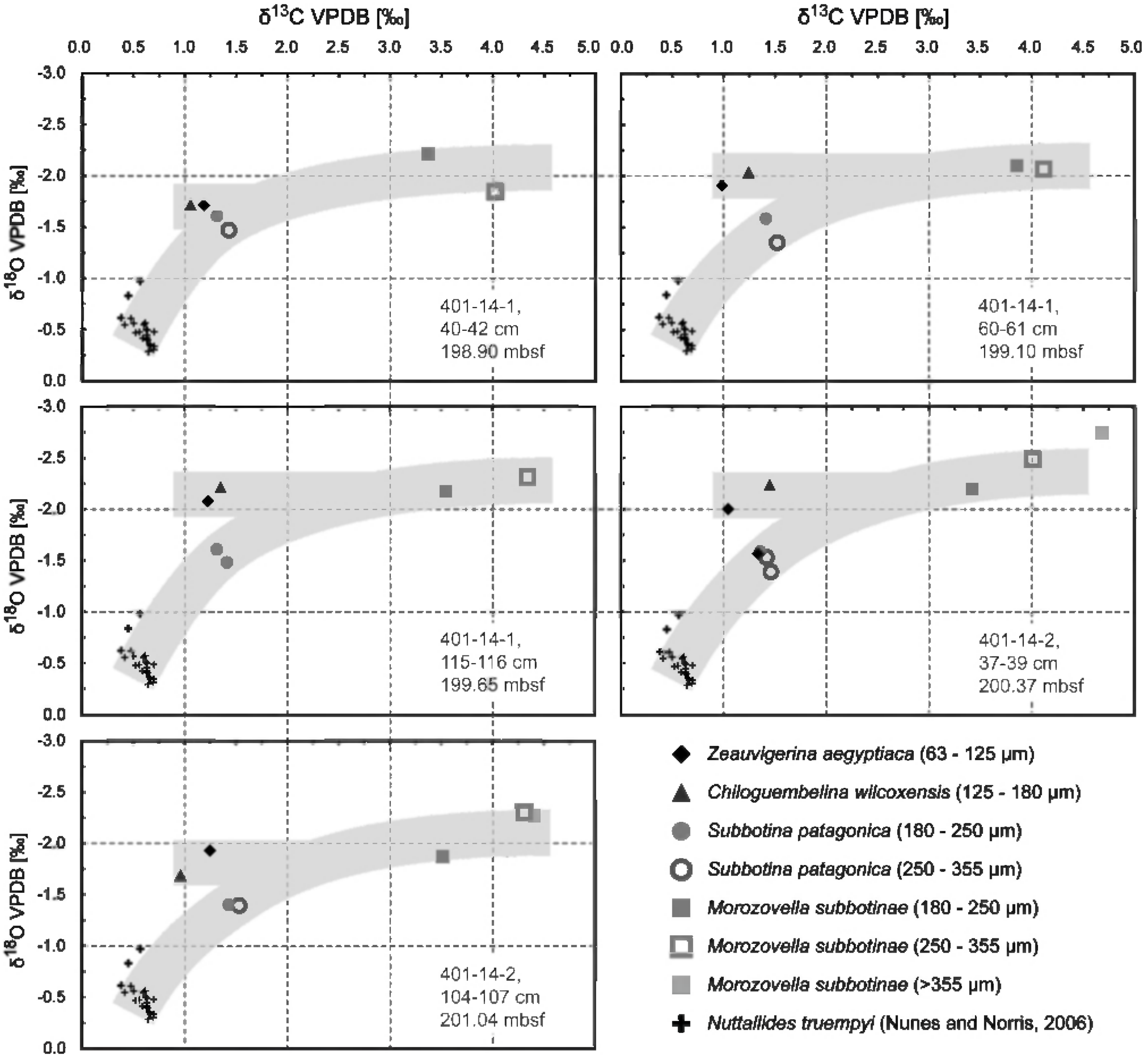

FIGURE 2: Biplots of carbon and oxygen isotope data of all species per sample. All samples are located in Biozone NP10 (early Eocene).

401 (Fig. 4). Reflective Light Microscopy (RLM) shows that individuals are translucent when dry, while they are completely transparent ("glassy") when moistened. Using RLM, it appears that most *Z. aegyptiaca* specimens have a smooth and shiny test - comparable to some smooth-walled benthic foraminifera – while other more ornamented specimens appear to be glistening. Furthermore, specimens of *Z. aegyptiaca* and *C. wilcoxensis* generally are more transparent compared to *S. patagonica* and *M. subbotinae*, which is probably due to their small size and thin shells. Scanning electron micrographs (Fig. 4) document the preservation of the studied material and highlight the presence of original wall textures, (micro)pores, surface ornamentation (pustules) and the lack of infillings. No pervasive diagenetic crystals are found in broken walls (Fig. 4). The reason for this good preservation may be the high accumulation rates of clayey sediments enabling a rapid burial and a subsequent sealing off by relatively impermeable clays, minimizing interaction of the foraminiferal calcite with surrounding pore waters (e.g. Pearson et al., 2001; Sexton et al., 2006a).

4.2 STABLE ISOTOPE PALEOECOLOGY OF PLANKTIC FORAMINIFERA

4.2.1 PREFERRED DEPTH HABITAT

The isotopic signature of planktic foraminiferal tests primarily reflects their preferred depth habitat. This has been known for a long time and has been applied in modern and past oceans (e.g. Emiliani, 1954; Douglas and Savin, 1978; Berger et al., 1978; Poore and Matthews, 1984) were foraminiferal stable isotope values are routinely used to reconstruct paleoenvironments. Depth-stratified foraminiferal assemblages from open ocean sites exhibit a trend of increasing foraminiferal δ^{18}O and decreasing δ^{13}C with depth reflecting decreasing temperature (e.g. Fairbanks et al., 1982), increased remineralization of $^{12}CO_2$ and a reduction in primary productivity (e.g. Kroopnick, 1985). This general pattern allows for a reconstruction of fossil foraminiferal depth habitat based on the relative stable isotope offsets between different species (e.g. Shackleton et al., 1985; Pearson et al., 1993, 2001; Sexton et al., 2006b). However, oxygen isotope values are not just controlled by temperature but are also affected by various environmental parameters such as salinity (e.g. the amount of freshwater) or by carbonate ion concentration and pH (Railsback et al., 1989; Spero et al., 1997; Uchikawa and Zeebe, 2010). Although these effects can be substantial (e.g. Spero et al., 1997; Zeebe and Zachos, 2007), the δ^{18}O gradient between surface (*M. subbotinae*) and deep-dwelling (*S. patagonica*) taxa is still apparent in our material and shows a reasonable temperature difference (e.g. Mulitza et al., 1997). Another line of evidence is that the isotopic pattern of *Morozovella*, *Subbotina* and benthics (Fig. 2) is consistent with other studies. This leads us to suggest that these effects are either not prominent in our material or that they may have operated in opposite ways, masking one another.

Site, Core-Section	Top (cm)	Bottom (cm)	Depth (mbsf)	Species	Size fraction (µm)	δ13C	δ18O
						VPDB (‰)	
401, 14-1	40	42	198.90	*M. subbotinae*	180-250	3.37	-2.21
					250-355	4.02	-1.85
				S. patagonica	180-250	1.32	-1.61
					250-355	1.43	-1.47
				C. wilcoxensis	125-180	1.06	-1.72
				Z. aegyptiaca	63-125	1.19	-1.71
401, 14-1	60	61	199.10	*M. subbotinae*	180-250	3.86	-2.09
					250-355	4.12	-2.06
				S. patagonica	180-250	1.42	-1.58
					250-355	1.53	-1.34
				C. wilcoxensis	125-180	1.25	-2.03
				Z. aegyptiaca	63-125	0.99	-1.90
401, 14-1	115	116	199.65	*M. subbotinae*	180-250	3.54	-2.17
					250-355	4.34	-2.30
				S. patagonica	180-250	1.31	-1.60
					180-250	1.41	-1.48
				C. wilcoxensis	125-180	1.35	-2.21
				Z. aegyptiaca	63-125	1.23	-2.07
401, 14-2	37	39	200.37	*M. subbotinae*	180-250	3.42	-2.20
					250-355	4.01	-2.49
					>355	4.68	-2.74
				S. patagonica	180-250	1.36	-1.60
					250-355	1.47	-1.39
					250-355	1.42	-1.54
				C. wilcoxensis	125-180	1.45	-2.24
				Z. aegyptiaca	63-125	1.34	-1.57
					63-125	1.05	-2.01
401, 14-2	104	107	201.04	*M. subbotinae*	180-250	3.51	-1.87
					250-355	4.30	-2.30
					>355	4.41	-2.27
				S. patagonica	180-250	1.43	-1.41
					250-355	1.53	-1.40
				C. wilcoxensis	125-180	0.96	-1.69
				Z. aegyptiaca	63-125	1.25	-1.93

TABLE 1: Carbon and oxygen isotopes of *Zeauvigerina aegyptiaca* and other planktic foraminifera measured for this study.

In general, the range of oxygen isotope values of *Z. aegyptiaca* and *C. wilcoxensis* overlap with those of the smaller (180-250 µm) *M. subbotinae* but are distinctly lighter than those of *S. patagonica* (Fig. 2) suggesting a surface dwelling mode of life. This agrees with Boersma et al. (1987) who also measured negative oxygen isotope ratios for *C. wilcoxensis* compared to *Morozovella* and *Subbotina* indicating predominant growth in the mixed layer. Additionally, our measurements reveal a slightly larger range in oxygen isotopes of *C. wilcoxensis*, which may be caused by vertical migration through the water column, either diurnal or in the course of its ontogenetic development (e.g. Pearson et al., 1993; Norris, 1996; Sexton et al., 2006b). This could also be reflected in test type: *C. wilcoxensis* is characterized by a thicker bilamellar and pustulose test wall while *Z. aegyptiaca* produces a thinner and smooth or slightly pustulose monolamellar test (Huber et al., 2006; Fig. 4). However, this remains speculative and a more detailed size fraction study may resolve this. Nevertheless, if present, this vertical migration effect appears to be minimal since δ^{18}O values of both *Z. aegyptiaca* and *C. wilcoxensis* remain lighter than those of

S. patagonica in all samples (Fig. 2). We suggest that *Z. aegyptiaca* likely inhabited a depth range restricted to the base of the mixed layer whereas *C. wilcoxensis* most likely inhabited the entire mixed layer in the course of its life.

4.2.2 OPPORTUNISTIC MODE OF LIFE FOR *Z. AEGYPTIACA*

The measurements of carbon isotopes of *M. subbotinae*, *S. patagonica* and the benthic data from Nunes and Norris (2006) confirm the pattern of paleodepth preferences as derived from the oxygen isotopes, but *C. wilcoxensis* and *Z. aegyptiaca* obviously deviate from it (Fig. 2); their carbon isotope values appear to be depleted relative to the J-shaped “equilibrium line”, considering their inferred surface dwelling preference. Carbon isotope values can be offset from equilibrium with ambient seawater by physiological processes such as calcification rates, ontogenetic effects, diet, symbiotic activities and foraminiferal respiration (e.g. Spero and Williams, 1988; Spero et al., 1991; Spero and Lea, 1993, 1996; Rohling and Cooke, 1999).

Calcification rates in itself have no significant effect on $\delta^{13}C$ fractionation (Rohling and Cooke, 1999), but most foraminifera experience major physiological changes during growth. For instance, symbiont density has been observed to increase with test size (Spero and Parker, 1985), which leads to a progressive increase of shell $\delta^{13}C$ in symbiont-bearing planktic foraminifera. Test-size related correlations with $\delta^{13}C$ values are found for the symbiont-bearing surface dwelling *M. subbotinae* (Fig. 2) and are in line with earlier studies (Pearson et al., 1993; D'Hondt et al., 1994; Norris, 1996). *Subbotina patagonica*, which lives below the photic zone and does not harbor photosymbionts, shows little or no change with test size (Shackleton et al., 1985; Pearson et al., 1993; D'Hondt et al., 1994; Norris, 1996). We infer that *C. wilcoxensis* and *Z. aegyptiaca* are surface dwellers living in the photic zone and thus could theoretically harbor photosymbionts. Since $\delta^{13}C$ values are depleted compared to all other taxa including the asymbiotic *S. patagonica*, we conclude that *C. wilcoxensis* and *Z. aegyptiaca* were most likely asymbiotic.

In asymbiotic species, a depletion of $\delta^{13}C$ associated with size could be caused by contamination of shell $\delta^{13}C$ with metabolically derived/respired CO_2 (Rohling and Cooke, 1999). Such depletions are strongest in small specimens from early life stages with high metabolic rates and decrease in later growth stages, which tend towards equilibrium (Wefer and Berger, 1991). This may imply that the analyzed specimens of *C. wilcoxensis* and *Z. aegyptiaca* are juveniles. Indeed, it is often difficult to distinguish between juveniles and reproductively mature adults at small sieve size fractions. According to Beckman (1957), mature individuals of *Z. aegyptiaca* are characterized by a typical necked terminal aperture, which is only found on the thin-walled final chamber. This feature was observed in all analyzed specimens (Fig. 4). In the case of *C. wilcoxensis*, the reproductively mature adults can be recognized by the test that becomes parallel-sided in the final two

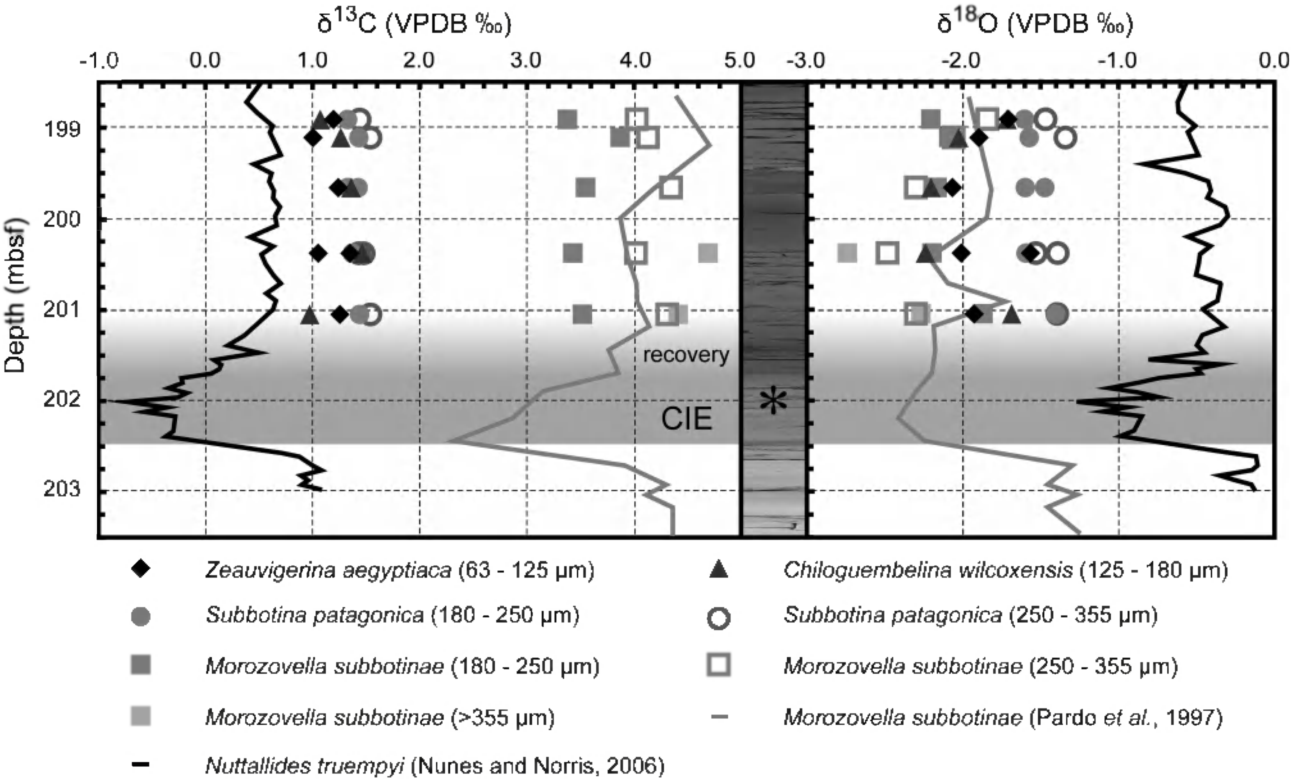

FIGURE 3: Carbon and oxygen isotopes of all measured planktic foraminifers plotted stratigraphically. Additional *M. subbotinae* data (no size fraction given) from Pardo et al. (1997) and benthic foraminiferal data (*Nuttallides truempyi*) from Nunes and Norris (2006). Note that the dark-colored interval following the CIE of the PETM reflects increased clay content. Asterisk symbol (*) indicates a sample where additional *Z. aegyptiaca* specimens were studied to check preservation (also see Fig. 4).

pairs of adult chambers (Huber et al., 2006). Marginally larger specimens for both taxa are virtually absent in larger sieve size fractions confirming that the observed and measured specimens were indeed mature.

Chiloguembelina wilcoxensis and *Z. aegyptiaca* are not the only (biserial) planktic species where depletion in $\delta^{13}C$ (and $\delta^{18}O$) relative to other planktics is found: other bi- and triserial planktic foraminifera such as *Heterohelix* (Nederbragt et al., 1998; Bornemann and Norris, 2007), *Chiloguembelina* (Sexton et al., 2006b), *Streptochilus* (Smart and Thomas, 2006; Sexton et al., 2006b) and modern species such as *Gallitellia vivans* (Nederbragt et al., 1998; Kimoto et al., 2009) have si-

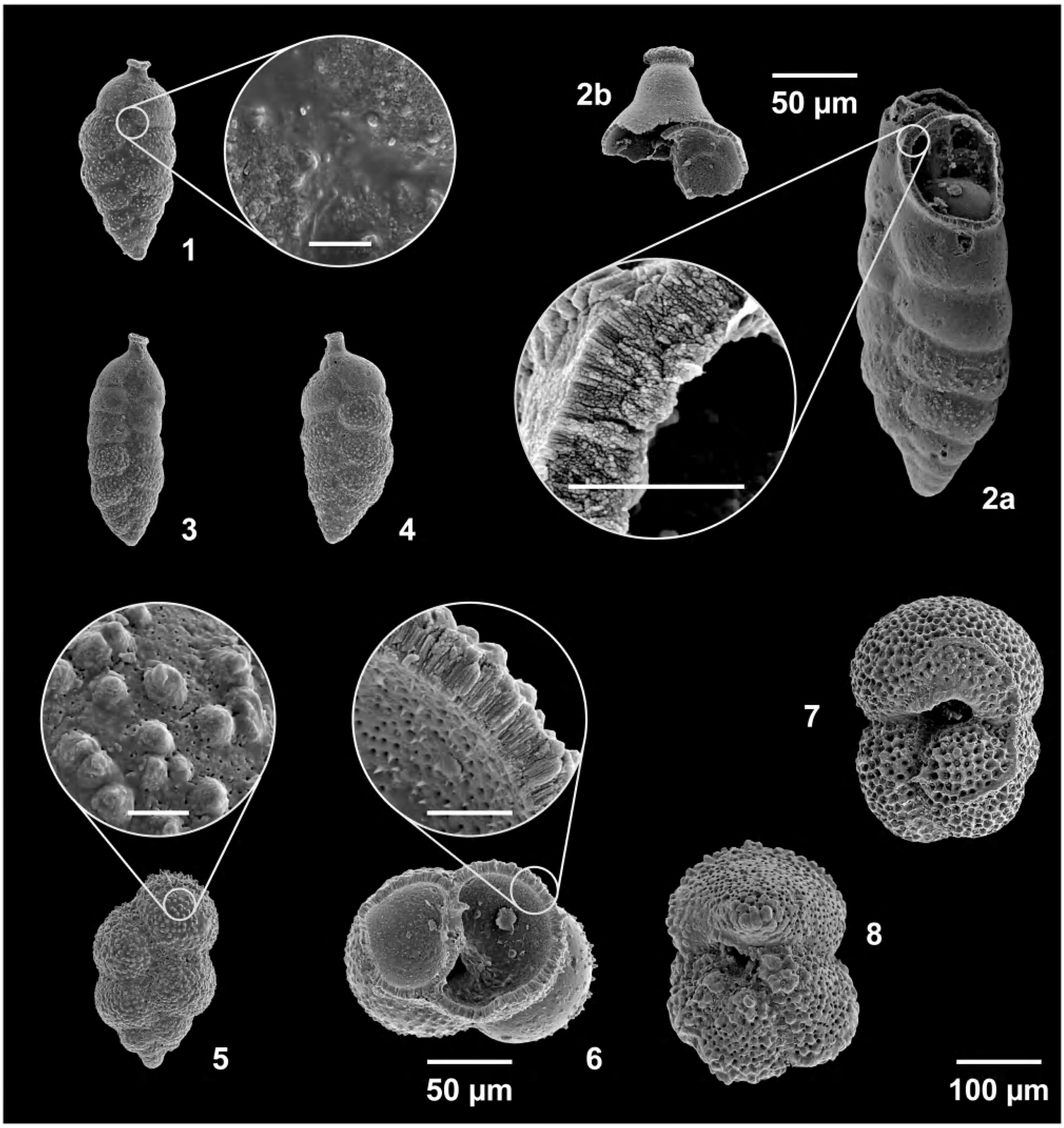

FIGURE 4: Scanning electron microscope (SEM) micrographs of unsonicated specimens of *Z. aegyptiaca*, *C. wilcoxensis*, *S. patagonica* and *M. subbotinae*. All specimens are shown at the same scale (scale bar = 100 µm), except for specimens 2 and 6 (scale bar = 50µm). Scale bars of all details represent 10 µm. 1-4: *Zeauvigerina aegyptiaca*. 1) 199.65 mbsf: specimen showing smooth to slightly pustulose wall. 2a) 200.37 mbsf: Broken specimen revealing monolamellar wall and the lack of infilling. 2b) Top of the same specimen showing ultimate (thin-walled) and penultimate chambers and the typical *Z. aegyptiaca* terminal apertural neck. 3) 201.04 mbsf. 4) 201.97 mbsf: Specimen from the core of the PETM (see Fig. 3 for sample position indicated by *). Note similar morphology and preservation as specimens 1-3. 5-6: *Chiloguembelina wilcoxensis*. 5) 200.37 mbsf: Detail showing pustulose microperforate wall. 6) 199.10 mbsf: Cross-section revealing the well-preserved bilamellar radial crystalline wall and micron-scale endospikes. Note the empty chambers. 7: *Subbotina patagonica*. 199.65 mbsf: Specimen from the 180-250 µm size fraction. 8: *Morozovella subbotinae*. 198.90 mbsf: Specimen from the 180-250 µm size fraction.

milar depleted values. Depleted $\delta^{13}C$ values are also observed in the modern trochospiral planktic foraminifer *Globigerina bulloides* in both cultured and natural environments where its light $\delta^{18}O$ values (and in situ observations) show that it lives at a shallow depth in the water column (Kroon and Darling, 1995; Nederbragt et al., 1998; Peeters, 2002; Kimoto et al., 2009). This asymbiotic opportunistic species proliferates in highly productive areas and incorporates carbon out of equilibrium with ambient water throughout its life span (Spero et al., 1991; Kroon and Darling, 1995; Peeters, 2002). *Zeauvigerina aegyptiaca* and *C. wilcoxensis* are similar to *G. bulloides* in that their $\delta^{13}C$ values are consistently lighter than other planktic taxa while displaying nearly the same $\delta^{18}O$ value as surface dwellers.

We suggest that the observed depleted $\delta^{13}C$ values of *Z. aegyptiaca* and *C. wilcoxensis* may be the result of elevated metabolic activity associated with reproductive periods (e.g. Wefer and Berger, 1991). As such, it is tempting to equate their light $\delta^{13}C$ signature to an opportunistic lifestyle, as has been done for many fossil and recent bi- and triserial planktic taxa with similar isotopic patterns (Kroon and Darling, 1995; Nederbragt et al., 1998; Smart and Thomas, 2006; Kimoto et al., 2009). Nevertheless, the mechanisms that cause these depleted $\delta^{13}C$ values remain poorly understood.

4.3 *ZEAUVIGERINA AEGYPTIACA* AS A PALEOENVIRONMENTAL INDICATOR

The remarkable occurrence of small biserial planktic foraminifera in the aftermath of the PETM at Site 401 and their absence prior and posterior this interval may be due to taphonomic processes (i.e. dissolution), considering their overall large dissolution susceptibility and the pelagic setting. In contrast to Pardo et al. (1997) - who only found *Zeauvigerina* following the PETM - we also observed well-preserved *Z. aegyptiaca* in the PETM itself (e.g. Fig. 4, specimen 4), but at much lower abundances. This suggests that, not taphonomy (i.e. dissolution), but environmental conditions are the main driving forces for the distribution of the biserial planktics.

Indeed, high abundances of Paleogene bi- and triserial planktic taxa have traditionally been linked to eutrophic environments (e.g. Hallock et al., 1991). Kimoto et al. (2009) suggested that the recent, small opportunistic triserial planktic foraminifer *Gallitellia vivans* only feeds on smaller, non-motile plankton or suspended materials (e.g. suspended clay particles) as the rhizopoda may not be suitable for capturing motile zooplankton. Based on the clay-rich sediments of the studied interval, a similar feeding habit may be applicable for *Z. aegyptiaca* and *C. wilcoxensis*: they may have required nutrient-enriched environments during at least some stages of their life cycle, for instance during reproduction. Furthermore, the patchy distribution patterns of *Z. aegyptiaca*, which appears to be restricted to near-coastal environments in the Tethys, Atlantic and Indian Oceans (Said and Kenawy, 1956; Beckmann, 1957; McGowran, 1964; Huber and Boersma, 1994), may thus imply that oligotrophic surface waters in the open ocean would be unsuitable for *C. wilcoxensis* and *Z. aegyptiaca* to flourish.

5. CONCLUDING REMARKS

The detailed analysis of five samples with respect to the carbon and oxygen isotope signal on well-preserved *Zeauvigerina aegyptiaca* and other planktic foraminifers have revealed that:

1) *Zeauvigerina aegyptiaca* displays a planktic isotope signal for the base of the mixed layer.
2) *Zeauvigerina aegyptiaca* is in carbon isotopic disequilibrium compared to ambient seawater due to vital effects (e.g. incorporation of isotopically light, respired metabolic CO_2). It most likely had an opportunistic mode of life, much like other Mesozoic and Cenozoic bi-and triserial planktic taxa such as *Heterohelix*, *Guembelitria*, *Chiloguembelina*, *Streptochilus* and *Gallitellia vivans*.
3) The expanded post-PETM interval of Site 401 was characterized by a substantial input of terrigenous material (e.g. suspended clay minerals) likely resulting in eutrophication of the surface waters, leading to a pulse of biserial planktic taxa such as *Z. aegyptiaca* and *C. wilcoxensis*.
4) The morphologically similar *Chiloguembelina wilcoxensis* had a similar paleoecology to *Z. aegyptiaca*, but in contrast to *Z. aegyptiaca*, *C. wilcoxensis* possibly migrated through the mixed surface layer in the course of its life cycle. A detailed size fraction study on *C. wilcoxensis* may be able to resolve this.

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