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Which was the habitat of early Eocene planktic foraminifer Chiloguembelina? Stable isotope paleobiology from the Atlantic Ocean and implication for paleoceanographic reconstructions

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Which was the habitat of early Eocene planktic foraminifer

***Chiloguembelina*? Stable isotope paleobiology from the Atlantic Ocean and**

implication for paleoceanographic reconstructions

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Abstract

The planktic foraminiferal genus *Chiloguembelina* is characterized by tiny test and biserial disposition of chambers. Largely accepted ecological interpretation ascribes biserial planktic foraminifera as eutrophic and low-oxygen tolerant forms inhabiting the Oxygen Minimum Zone (OMZ). However, this ecological interpretation does not agree with all available data from Cenozoic record. Actually, chiloguembelinid stable isotope paleobiology is highly variable through time and space as it indicates mixed-layer habitat on earliest Eocene, middle Eocene and Late Oligocene but thermocline habitat during middle Eocene from northwest Atlantic Ocean. However, chiloguembelinid stable-isotope data were so far lacking from the early Eocene. This interval includes the early Eocene Climatic Optimum (EECO, ~53-48 Ma) that is the crucial time when Earth's surface temperatures and pCO$_2$ reached their maximum levels in the Cenozoic. We present here new chiloguembelinid oxygen and carbon stable-isotope data from early Eocene Atlantic Ocean Drilling Program (ODP) Sites 1051, 1258, 1263 and 690. We also generate new data on *Chiloguembelina* abundance from Site 1051 and compare our record with those previously published from sites 1263 and 1258 in order to correlate the early Eocene paleoceanographic distribution of this genus through the Atlantic Ocean. Interestingly, *Chiloguembelina* became virtually absent at the beginning of the EECO in the subtropical, equatorial and temperate Atlantic sites. Our findings clearly prove that early Eocene *Chiloguembelina* occupied a deep-water niche throughout the Atlantic Ocean as demonstrated by its stable isotope signature close to the deep-dweller *Subbotina* and benthic foraminifera. These evidences

provide critical paleoceanographic implications suggesting that intermediate water temperatures probably rose significantly during the EECO thus becoming too warm for this genus. Elevated ocean temperatures enhanced the rate of bacterial respiration and remineralization significantly thus resulting in more efficient recycling of nutrients higher in the water column. This would have induced a restricted food supply deeper in the thermocline and cut out the chiloguembelinid niche. The agreement of the observed decline in abundance of chiloguembelinids at the study sites with recently published foraminifera-bound nitrogen isotope data suggests that enhanced oxygenation of the thermocline in the early EECO might have also played a major role in driving the disappearance of chiloguembelinids, which in itself represent a new evidence for the largely accepted view that these forms inhabited the OMZ. Very likely a combination of reduced food supply, increase in thermocline temperature and oxygen content resulted in the decline of chiloguembelinids in the early EECO.

1. Introduction

Thin-walled planktic foraminifera bearing a biserial disposition of the chambers are characterized by a relatively long stratigraphic range as originating in the Late Albian from genus *Heterohelix*, diversified in the Late Cretaceous and survive to the present day (e.g., Nederbragt, 1991; Olsson et al., 1999; Hemleben et al., 1989), even though their abundance is highly variable through time and space. These forms attracted the scientific interest because they thrived in correspondence with extreme global climatic and paleoceanographic events such as the Cretaceous Oceanic Anoxic Events (e.g., Nederbragt et al., 1998; Coccioni et al., 2006), the Cretaceous-Paleogene boundary (e.g., Keller, 1993;

Koutsoukos, 1994; Luciani, 1997; Luciani, 2002; Keller et al., 2002; Pardo and Keller, 2008), the hyperthermal event Paleocene Eocene Thermal Maximum (PETM; ~56 Ma, e.g., Luciani et al., 2007; D'Haenens et al., 2012), and the Middle Eocene Climatic Optimum warming event (MECO, centered at ~40 Ma, Bohaty et al., 2009; Luciani et al., 2010). The general inferred stable isotope paleobiology and distribution of biserial foraminifera ascribe them as low-oxygen tolerant, meso- to eutrophic thermocline dwellers thriving in stressed environmental conditions. This view was frequently applied for Cenozoic biserial planktic foraminifera (e.g. Resig and Kroopnick, 1983; Boersma and Premoli Silva, 1989; Hallock et al., 1991; Luciani et al. 2007; 2010). However, this general ecological interpretation does not agree with all Cenozoic available records. Stable isotope data from *Chiloguembelina wilcoxensis* and *Zeauvigerina aegyptiaca* at Deep Sea Drilling Project (DSDP) Site 401 (eastern North Atlantic) analyzed in the interval following the PETM, overlap with those of the symbiont-bearing *Morozovella subbotinae* thus implying surface mixed layer habitat (D'Haenens et al., 2012). A similar habitat was derived for the middle Eocene-Late Oligocene *Chiloguembelina cubensis* (Premec Fucek et al., 2018 and references therein). Stable isotope data obtained for the upper Eocene *Chiloguembelina ototara* (Barrera and Huber, 1991; identified as *Chiloguembelina* spp.) suggest that it lived near the surface mixed-layer at high southern latitudes. Conversely, Sexton et al. (2006a) report *Chiloguembelina ototara* as inhabiting a thermocline habitat on the basis of stable isotope data from middle Eocene Zone E14 in the northwest Atlantic Ocean (ODP Site 1052).

These evidences indicate that the ecology of Cenozoic planktic biserial taxa is not yet fully understood and that this group may have changed their

ecological niches through time and over their geographic distribution. A certain inconclusiveness concerning the habitat of the biserial planktic foraminifera can be partly due to their incompletely known spatial and temporal distribution because they may have been overlooked due to their (mostly) small size and because they are not evenly occurring through their stratigraphic range and geographic areas (Resig and Kroopnick, 1983; Huber and Boersma, 1994; Koutsoukos, 1994; Kroon and Nederbragt, 1990; Huber et al., 2006). However, stable isotope data from early Eocene were so far lacking.

The purpose of this paper is to produce new stable isotope data from chiloguembelinids of the early Eocene with the aim to assessing their habitat during this interval. The early Eocene is a crucial interval of time marked by significant climatic changes when temperatures across Earth's surface and pCO_2 rose toward the peak of Cenozoic that occurred between 53 and 48 million years ago during the Early Eocene Climatic Optimum (EECO) and started at the Carbon Isotope Excursion (CIE) known as "J" event (e.g., Zachos et al., 2008; Anagnostou et al., 2016; Luciani et al., 2016; Westerhold, et al., 2018).

An outstanding issue is how life evolved during the crucial EECO interval, and planktic foraminifera represent an excellent class in which to examine such links. Therefore, we need a good knowledge of ecological characters of planktic foraminifera to provide reliable paleoceanographic reconstructions.

To perform our analysis we select four sites located in the Atlantic Ocean at different latitudes. Specifically, these sites are: sub-tropical northwestern Atlantic Ocean Drilling Program (ODP) Site 1051 (Blake Nose), equatorial ODP Site 1258 (Demerara Rise), south Atlantic ODP Site 1263 (Walvis Ridge) and the Antarctic Weddell Sea ODP Site 690 (Fig. 1) that have good sedimentary

recovery and complete lower Eocene successions (Norris et al., 1998; Shipboard Scientific Party, 1998; Shipboard Scientific Party, 2004; Sexton et al., 2006a; Zachos et al., 2004; Kennet and Stott, 1990). In addition, most of these sites have been extensively studied thus providing a very solid stratigraphic framework, included bulk stable isotope curves for the early Eocene and data on abundance of planktic foraminiferal genera across the EECO (Zachos et al., 2004; Lauretano et al., 2015; 2016; Westerhold et al., 2007, 2015; Luciani et al., 2016, 2017a, 2017b; D'Onofrio et al., 2020). All these evidences make these sites truly appropriate for our investigation.

We evaluate the relative chiloguembelinid abundances from Sites 1051 that prove to be similar to those recorded at Site 1262 and 1258 as this group markedly decline across the basal EECO interval.

We demonstrate that early Eocene chiloguembelinids lived in deep-water habitat as they show stable isotope data close to those of the thermocline dweller *Subbotina* and benthic foraminifera throughout the Atlantic Ocean. These data reveal therefore a different habitat with respect to the earliest Eocene and middle Eocene-Late Oligocene records that designate chiloguembelinids as mixed-layer habitat. Our findings provide therefore critical implications for the paleoceanographic reconstruction of the upper water column as its changes occurred during the EECO at different latitude of the Atlantic Ocean.
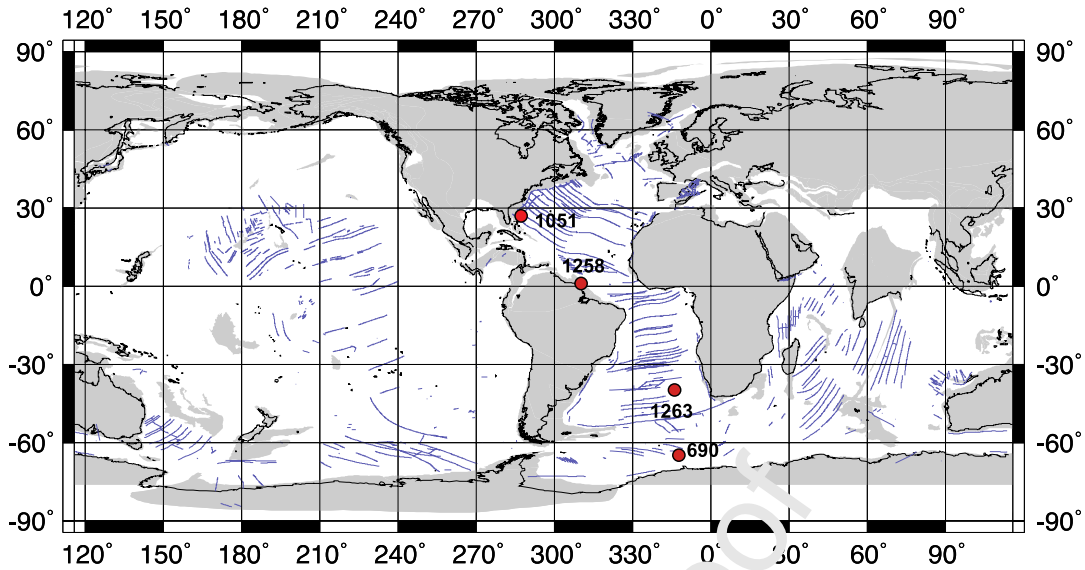
Figure 1. Approximate location of the studied sites during the early Eocene. Base map

is from http://www.odsn/de/services/paleomap.html with paleolatitude modified

according to www.paleolatitude.org model version 1.2 (Van Hinsbergen et al., 2015).

2. Methods and materials

As noted above, to perform our analysis on the early Eocene

chiloguembelinids habitat we selected four sites of the Atlantic Ocean from

northern sub-tropical to deepest southern latitudes, specifically from ODP Sites

1051, 1258, 1263 and 690.

Planktic foraminifera were observed on washed residues that were

prepared by immersing previously freeze-dried samples in deionized water.

When disaggregated, samples were washed over a >63 μm sieve. Washed

residues were dried at <50°C. Sieve was immerged in a methylene blue bath after

each washing in order to colour planktic foraminifera potentially trapped in the

sieve mesh (e.g., Green, 2001). This is an easy method to exclude possible

contamination amongst successive samples.

Relative abundance of chiloguembelinids from Sites 1051 determined for the >63 μm size fraction from random splits using a Micro Riffle Splitter Gilson SP-171X on a statistical population of ~300 specimens. The taxonomic criteria adopted in this study follow Olsson et al. (1999) and Pearson et al. (2006). A taxonomic list of species cited in text and figures is shown in Appendix A.

Planktic foraminifera for stable isotope analysis were selected on washed residues using a stereomicroscope with an incident light beam and collected to reach at least 200-250 μg per analysis. Planktic and benthic foraminifera were picked up from the size fraction comprised between 250 μm and 300 μm. The restricted size fraction here selected ensures that stable isotope signature from the symbiont-bearing morozovellids and acarinids is not affected by vital effects related to symbiotic relationship (e.g., Spero & DeNiro, 1987). Given the smaller size of chiloguembelinids, they were picked from the > 100 μm size fraction. In order to generate reproducible δ^{13}C and δ^{18}O records, the picked specimens were carefully checked for preservation and heavily recrystallized or infilled tests were removed because they would have generated unreliable isotope signals (e.g., Pearson, 2012; Pearson et al., 2001; Sexton et al., 2006b).

Isotopic analyses were performed at the Stable Isotope Laboratory of the Department of Geosciences at the University of Padova using a Thermo Scientific Delta V Advantage Isotope Ratio Mass Spectrometer coupled with a Gas Bench II automated preparation device. Samples of ~200-250 μg were flushed with helium and then treated with 10 mL of 100% phosphoric acid (EMSURE ® ≥ 99 %) at 70 °C for *ca* 3 hours. Isotopic values are reported in standard delta notation relative to the Vienna Pee Dee Belemnite (VPDB).

During the analyses an internal standard (white Carrara marble Maq 1: $\delta^{13}C = 2.58\,‰$; $\delta^{18}O = -1.15\,‰$ VPDB) was used to normalize raw $\delta^{13}C$ and $\delta^{18}O$ values and a check standard (marble Gr1: $\delta^{13}C = 0.68\,‰$; $\delta^{18}O = -10.44\,‰$ VPDB) was run for quality assurance, and repeated with precisions better than $0.07‰$ for $\delta^{13}C$, and better than $0.09‰$ for $\delta^{18}O$.

For Site 1051 chiloguembelinids are rare even below the EECO interval thus we combined two samples from Hole 1051A to attain the weight needed for the stable isotope analysis. Specifically, we combine *C. wilcoxensis* specimens from samples 425.4 mbsf and 425.9 mbsf that are placed respectively at ~2.5 m and ~ 2.1 m above and below the J event (~428 mbsf; Luciani et al., 2016). Both these samples belong to the Zone E5 (Wade et al. 2011). Samples selected for chiloguembelinid analysis are coinciding or very close to those selected by Luciani et al. (2017b) for stable isotope analysis of *Morozovella* species, *Acarinina* spp. and *Subbotina* spp. that we include here for a comparison with our new *Chiloguembelina* data. The *Chiloguembelina* genus comprises at Site 1051 also *C. trinitatensis* and *C. crinita* that, unfortunately, are exceedingly scarce to be isotopically analyzed as singles species. Specimens of *Acarinina* spp. include mainly *Acarinina esnaensis* and *Acarinina interposita*; subbotinids mainly include specimens of *Subbotina patagonica* and *Subbotina roesnaesensis* (Luciani et al., 2017b). As for benthic foraminifera we combined *Oridorsalis umbonatus* with *Nuttallides truempyi* from the same samples due to the scarcity of benthic foraminifera.

For Site 1258 we performed our analysis from sample 112.37 rmcd, which is referable to the Zone E5 (Wade et al., 2011), on *Chiloguembelina wilcoxensis, Acarinina quetra, Morozovella aragonensis, M. crater, Subbotina roesnaesensis.*

Combined *Oridorsalis umbonatus/Nuttallides truempyi* were picked from mixed samples 112.37 rmcd and 112.27 rmcd. Also stable isotopes of the species *Planorotalites pseudoscitula* was analysed from combined samples 112.37 rmcd and 112.27 rmcd. *The species Chiloguemeblina trinitatensis* is also present but very rare thus hampering the stable isotope analysis. Samples from Site 1258 come from Holes 1258 A and B.

For Site 1263 we select the samples at 278.13 rmcd and 279.0 rmcd that are attributable to the Zone E5 (Wade et al., 2011) (Fig. 2). The selected levels correspond to the early part of the EECO, slightly above the CIE of the J event. According to the adopted age model by Lauretano et al. (2016), the samples are of ~53 Ma age (Fig. 3) which is ~336 kyr before the dramatic decline of chiloguembelinids at Site 1263. We carried out the stable isotope analysis at Site 1263 on the following species of planktic foraminifera: *Chiloguembelina wilcoxensis, C. trinitatensis, Acarinina soldadoensis, A. coalingensis, Morozovella aequa, M. subbotinae, M. crater, Subbotina roesnaesensis* and on the benthic foraminifera *Oridorsalis umbonatus*.

For Site 690 (Hole B) specimens of foraminifera were selected from sample 156.02 mbsf. According to the zonation for the Antarctic Ocean by Huber and Quillévéré (2005) this sample is referable to the lower Eocene Zone AP6, on the basis of the occurrence of *Chiloguembelina wilcoxensis* whose Top marks the upper limit of this zone. The samples selected for our analysis come from Hole 690B. For stable isotope analysis we collected specimens of *Acarinina* spp.*, Subbotina* spp. and *Chiloguembelina* spp. species. In addition, we analyzed the species *Globanomalina planoconica***.**

The *Chiloguembelina* species cited in this paper are shown in Plates 1-4.
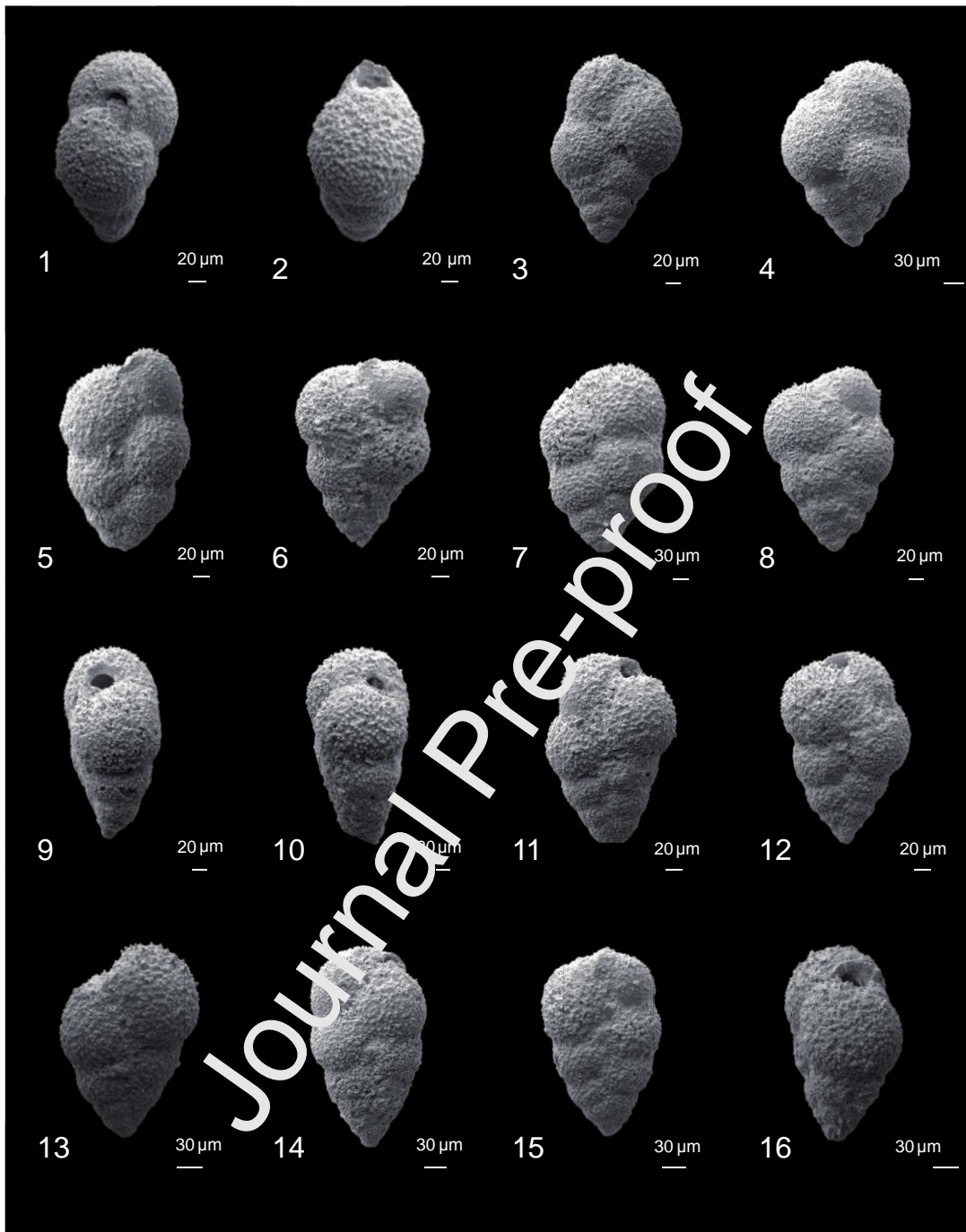
Plate 1 - Scanning electron micrograph (SEM) images of *Chiloguembelina* species from DSDP Site 690 B (sample 17H/6/99-100, 156.02 mbsf). 1-7: *C. wilcoxensis*; 8-12: *C. crinita*, note the asymmetrical aperture typical of this species in the 9-10 profile views; 13-16: *C. trinitatensis*.
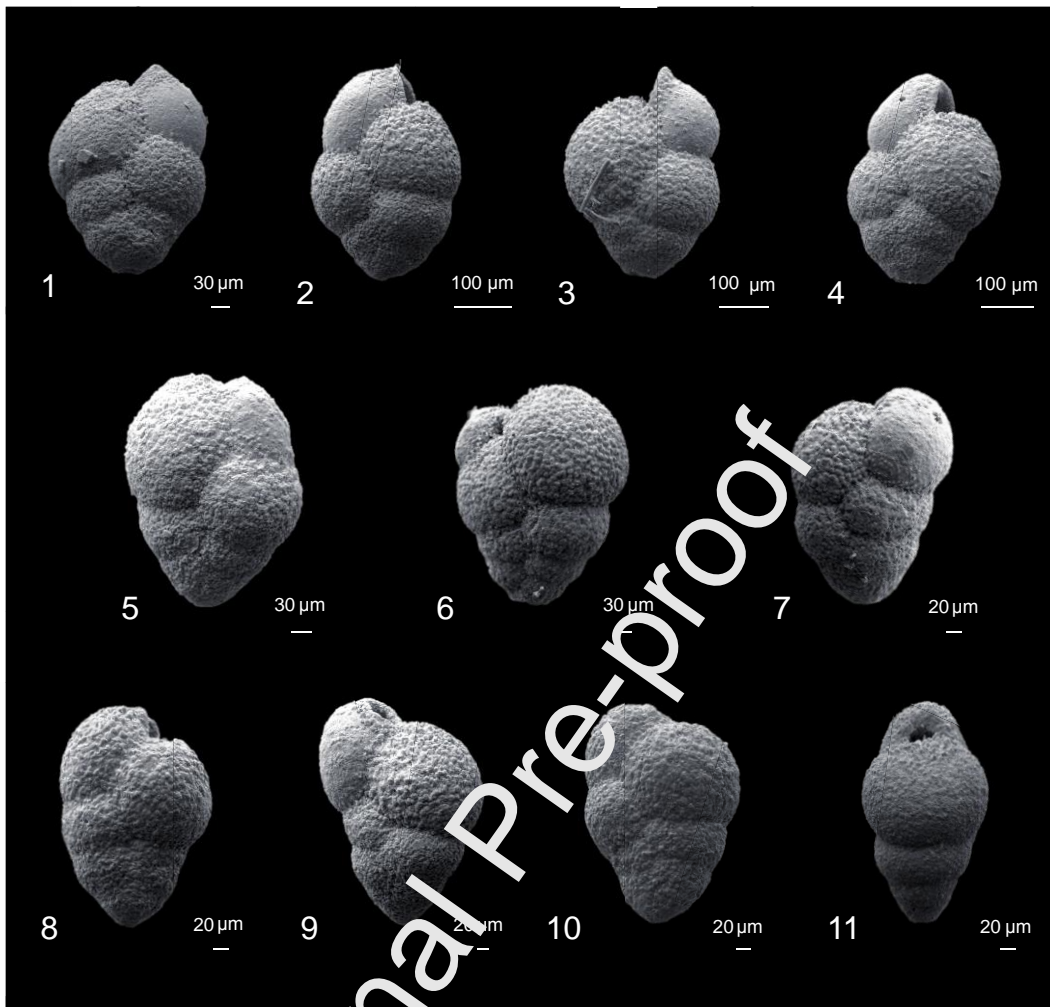
Plate 2 - Scanning electron micrograph (SEM) images of *Chiloguembelina* species from ODP Site 1263. 1-5: *C. wilcoxensis* (sample 1263B 23H-4 90/92 = 279.06 rmcd), note the last kummerform chambers; 6-11: *C. trinitatensis* (specimens 6, 7 are from sample 1263B 23H-4 90/92 = 279.06 rmcd; specimens 8-11 are from sample 1263B 23H-3 140/142 = 278.128 rmcd).
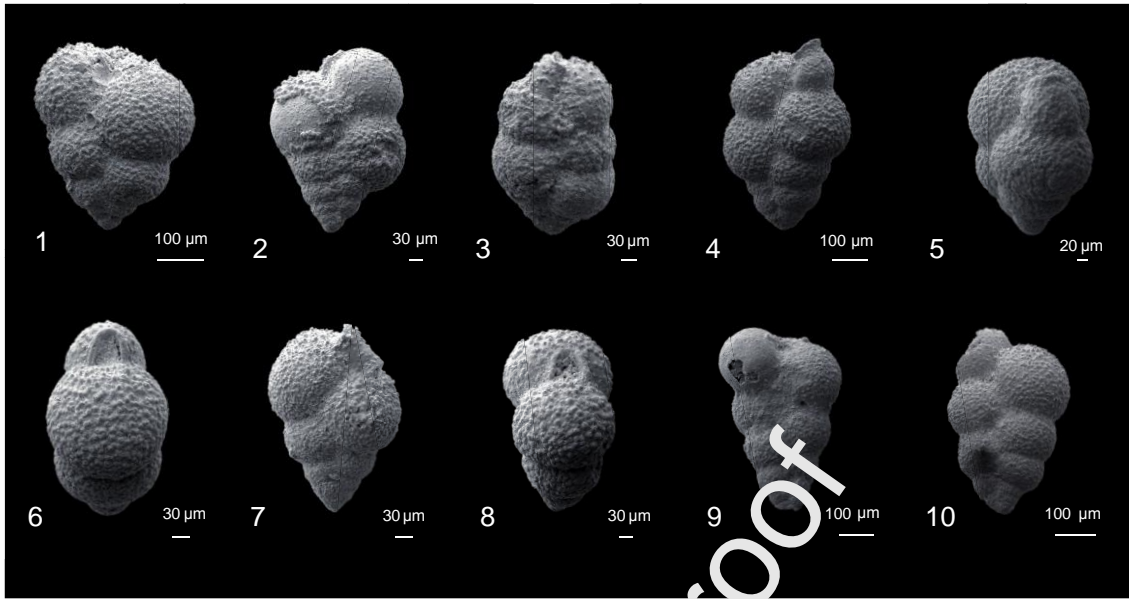
Plate 3 - Scanning electron micrograph (SEM) images of *Chiloguembelina* species from ODP Site 1258 (sample 1258A 13R-3 12/13.5 = 108.07 rmcd). 1-6: *C. wilcoxensis*, note the last kummerform chambers in specimens 3-5 and the apertures bordered by a lip slightly inforled on one side as it is typical of this species; 7-8: *C. crinita*, note the asymmetrical aperture typical of this species in the 8 profile view; 9-10: *C. trinitatensis*.
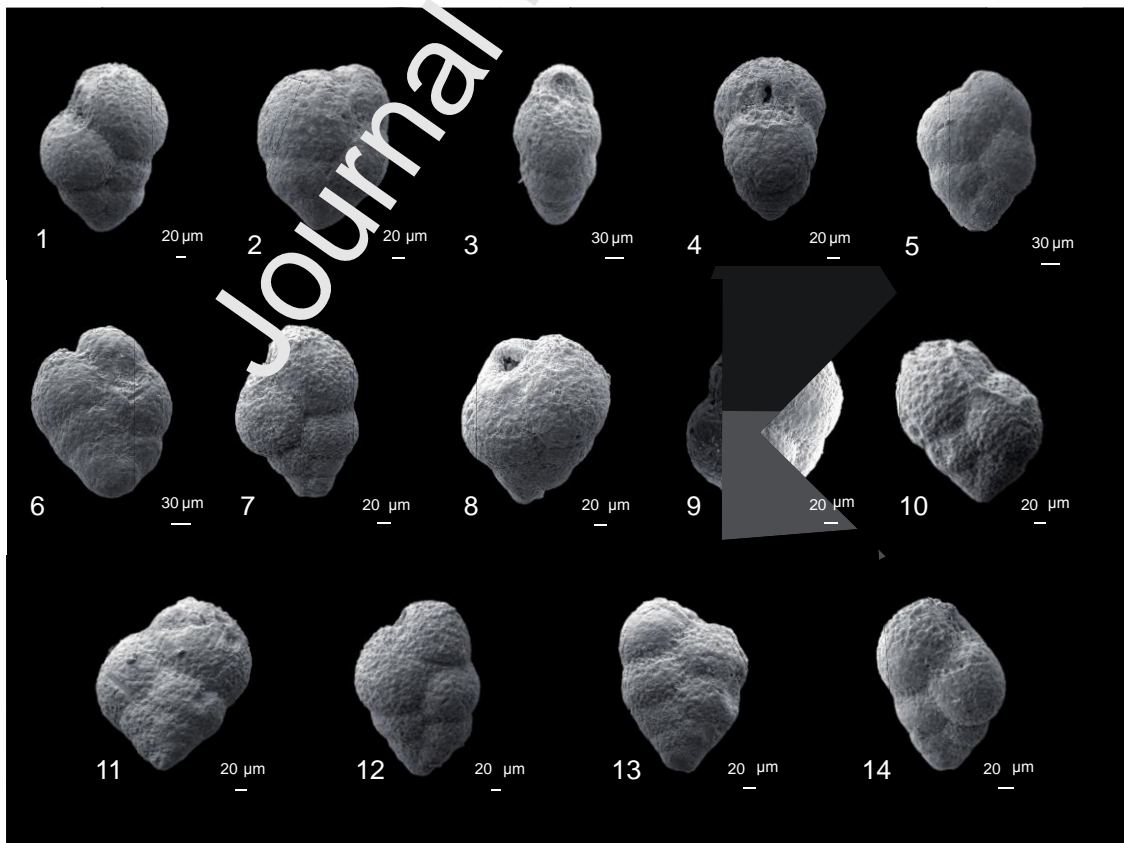
Plate 4 - Scanning electron micrograph (SEM) images of *Chiloguembelina* species from ODP Site 1051. 1-5: *C. wilcoxensis* (sample 1051A 47X-7 7/9 = 446.97 mbsf), note the high arch symmetrical aperture typical of this species in the 3-4 profile views; 6-11: *C. crinita* (specimens 6, 9, 11 are from sample 1051A 47X-3 68/70 = 443.58 mbsf; 7, 8, 10 are from sample 1051A 47X-7 7/9 = 446.97 mbsf), note that specimens 6 and 7 have the typical curved growing axis; 12-14: *C. trinitatensis* (specimens 12, 13 are from sample 1051A 47X-7 7/9 = 446.97 mbsf; 14 is from sample 1051A 47X-3 68/70 = 443.58 mbsf).

3. Results

Planktic foraminiferal assemblages from the studied sites are well preserved thus allowing unambiguous identification at the species level, although they show a 'frosty' preservation (*sensu* Sexton et al. 2006b). Our new record from Site 1051 shows that the relative abundance of chiloguembelinids decreased their relative abundance from ~8% of total foraminifera assemblages to virtually and permanently absence near the K/X event. Similarly, chiloguembelinids decrease within the EECO at sites 1263 (Luciani et al., 2017a) and 1258 (D'Onofrio et al., 2020). Specifically, at Site 1263, chiloguembelinids move from ~10 % in relative abundance to virtually absence above the K/X event (Luciani et al., 2017a) and, at Site 1258, move from ~5% below the EECO to 0% below the K/X event. (D'Onofrio et al., 2020). Results are shown in figure 2, percentage data are available in Table S1.

The planktic foraminiferal carbon and oxygen stable isotope data from the four Atlantic ODP sites, 1051, 1258, 1263 and 690 here investigated are displayed in Figure 3 and available in Table S2.
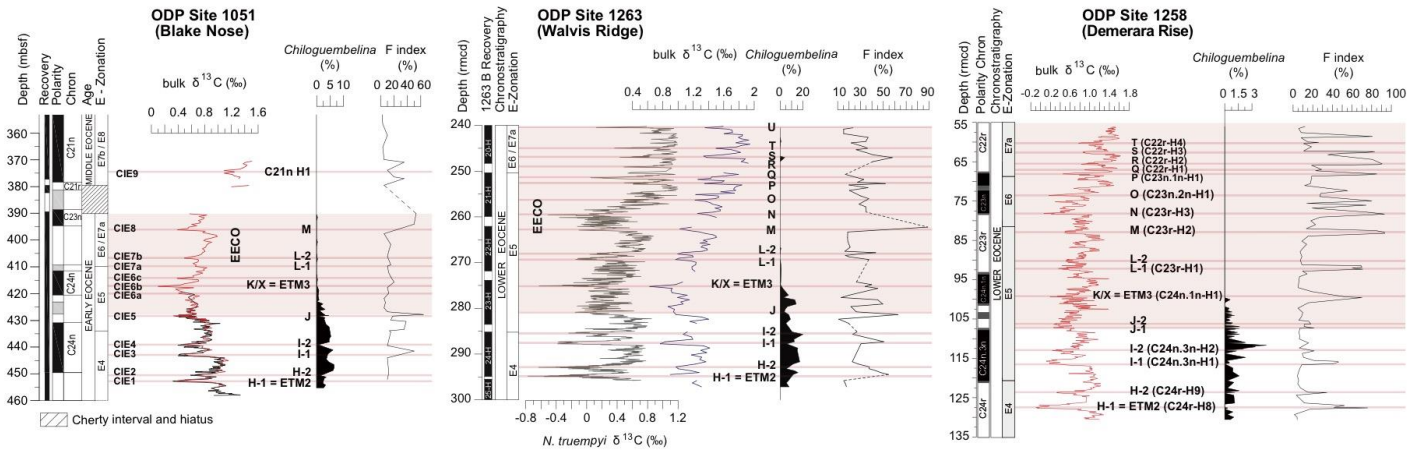
Figure 2. Early Eocene chiloguemeblinid relative abundances and F-index curves from ODP Sites 1051 (this paper), 1263 (Luciani et al., 2017b) and 1258 (D'Onofrio et al., 2020) plotted against δ¹³C curves. The thin light-red bands highlight significant negative carbon isotope excursions (CIEs) with alphabetical nomenclature following Cramer et al. (2003) and Lauretano et al. (2015) or Chron-based nomenclature (in brackets) following Kirtland-Turner et al. (2014). The pink shaded band outlines the Early Eocene Climatic Optimum (EECO) interval as defined by Luciani et al. (2016). Note the virtual disappearance of chiloguembelinids below the K/X event. Site 1051: the δ¹³C curves are from Luciani et al., (2017b) (in red) and Cramer et al. (2003) (in black). Site 1263: the δ¹³C bulk record is from Luciani et al., 2017a (blue) while the benthic foraminiferal (*N. truempyi*) δ¹³C curve comes from Lauretano et al. (2016) (grey). Site 1258: the δ¹³C bulk record is from Kirtland-Turner et al. (2014). Planktic foraminiferal zones were assigned at Sites 1051 and 1263 by Luciani et al. (2017a, b) and at Site 1258 by D'Onofrio et al. (2020) following the zonation scheme presented by Wade et al. (2011), but as modified by Luciani and Giusberti (2014).
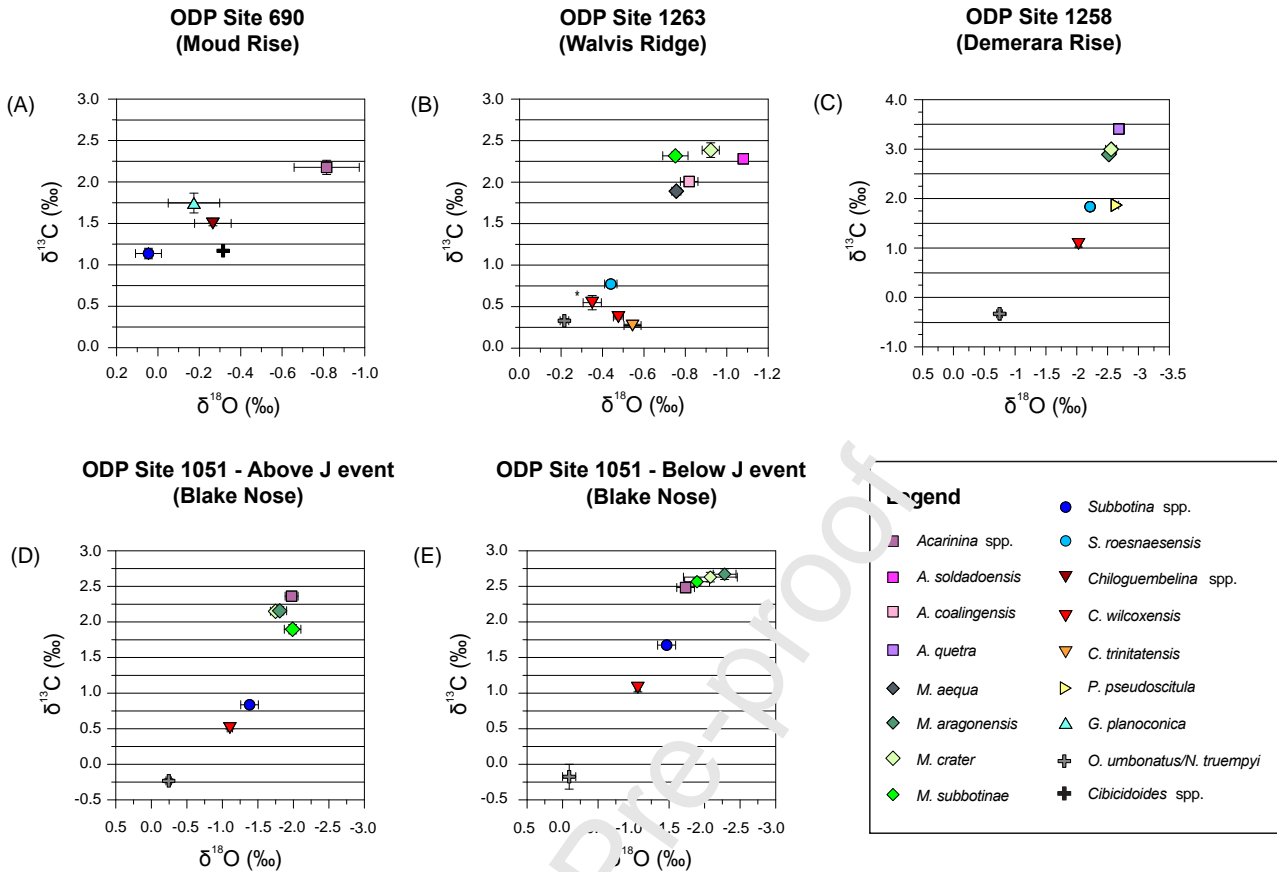
Figure 3. Planktic foraminifera stable carbon and isotope data from ODP sites 690 (A), 1263 (B), 1258 (C) and 1051 (D, E). Note that stable isotope paleobiology ranks chiloguembelinid as deeper dwellers throughout the Atlantic Ocean sites investigated. *Data from sample 278.15 rmcd. Stable isotope data from Site 1051 are from Luciani et al. (2017b) except for those referred to chiloguembelinids and benthic foraminifera that are from this paper.

4. Discussion

Carbon and oxygen planktic foraminiferal stable isotopes from the four ODP Atlantic sites, 1051, 1258, 1263 and 690 here investigated, highlight well distinguishable values, especially as for $\delta^{13}C$ data. This evidence allows us to ranking species/genera at different depth habitat in the upper water column, even though foraminiferal test preservation is not 'glassy' (*sensu* Sexton et al., 2016)

thus implying some test recrystallization (Fig. 3). Because of test recrystallization, we cannot derive reliable paleotemperatures from $\delta^{18}O$ values. Nevertheless, the observed $\delta^{18}O$ values show variations that can trace differences in paleotemperatures compatible with the latitudes of the studied sites. Specifically, data from benthic foraminifera are similar but the most negative $\delta^{18}O$ value is recorded at the equatorial Site 1258 thus suggesting a slightly higher sea-floor temperature at this site. In addition, the more negative value exhibited at Site 1051 above the beginning of the EECO (J event) with respect to the value recorded below the J event, may be explained with the rising temperature at the sea-floor related to the EECO warming. A similar variation, though at minor extent, is shown by $\delta^{18}O$ values from the deeper dweller *Chiloguembelina wilcoxensis* at the same site. As for acarininids and morozovellids, the $\delta^{18}O$ values are in general more negative at the warmer equatorial-tropical sites and decrease for sites at higher latitude, as expected.

4.1. Stable isotope paleoecology of planktic foraminifera from the Atlantic Ocean

Our new *Chiloguembelina wilcoxensis* stable isotope values from the sites 1258, 1051, 1263 and 690 are very close to those from the deeper-dweller *Subbotina* that exhibits similar values, thus ranking *C. wilcoxensis* at similar habitat (Fig. 3). We were able to analyze also *C. trinitatensis* from Site 1263. Stable isotope values demonstrate also for this species a thermocline habitat as their stable isotope signature is very similar to that of *Subbotina roesnaesensis* and benthic foraminifera. Both $\delta^{18}O$ and $\delta^{13}C$ records at Site 1263 designate *C. trinitatensis* as slightly deeper dweller than *C. wilcoxensis*.

The chiloguembelinid values close to the isotopic signature of benthic foraminifera recorded at Site 1263 can be explained with the fact that some bi- and triserial forms may 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).

As expected, benthic foraminifera record stable isotope values compatible with a sea-floor environment at all the sites investigated.

The differences in the mean $\delta^{13}C$ values for *Morozovella* and *Acarinina* with respect to *Subbotina* as analyzed from the diverse sites give evidence for different depth habitats. The relatively high $\delta^{13}C$ values for the two former genera suggest a mixed-layer habitat, while relatively low $\delta^{13}C$ values for the latter genus suggest that it calcified in the lower part of, or below, the thermocline habitat, in agreement with the literature (e.g., Boersma et al., 1987; Shackleton et al., 1985 and references therein; Pearson et al., 2006 and reference therein; Anagnostou et al., 2016). The species *Morozovella aequa* proved to have occupied a lower mixed-layer habitat according to its lighter carbon isotope value with respect to the other morozovellids analyzed at Site 1263. Conversely, the species *Acarinina quetra* revealed to be the most surface-dweller species at Site 1258.

At Site 1258 we analyzed the stable isotopes from *Planorotalites pseudoscitula*. This species records a carbon isotope ratio nearly equal to that from *S. roesnaesensis* thus assigning the former species to a thermocline habitat. Our results from *Planorotalites pseudoscitula* are a bit unexpected because Pearson et al. (2001) recorded from the middle Eocene (Tanzania) the other species belonging to the genus *Planorotalites*, e.g., *P. capdevilensis* (though

recognized as *P. pseudoscitula*) with oxygen isotope ratios indicative of a shallow-water habitat, and carbon isotope ratios more depleted than co-occurring muricate species, probably owing to its small size. A mixed-layer habitat was also inferred for *P. capdevilensis* from two middle Eocene Tethyan sections of Italy (Boscolo Galazzo et al., 2016). The significantly lower carbon isotope signature here recorded from Site 1258 for *P. pseudoscitula* with respect to the mixed-layer species cannot be explained as deriving from lack of photosymbionts, small size and possible rapid growth rate thus ranking this early Eocene species as thermocline dweller. Our result suggests therefore that *Planorotalites* may have changed its habitat through time. The thermocline habitat inferred by stable isotope data from Site 1258 implies consequence for environmental interpretation of early Eocene successions when changes in abundance of this species are recorded. In the sites here investigated, however, this genus is very rare (Luciani et al., 2017b, D'Onofrio et al. 2020).

Stable isotope results from Moud Rise Site 690 show separated values thus suggesting low recrystallization degree, even though $\delta^{18}O$ and $\delta^{13}C$ analysis reveal closer values between *Subbotina/Chiloguembelina* and *Acarinina* with respect to the other sites. This is compatible with colder waters and less stratified water column distinctive of high latitudes.

4.2. Implication of early Eocene chiloguembelinids thermocline habitat for paleoenvironmental reconstructions

The virtual disappearance of chiloguembelinids within the EECO, close to the carbon isotope excursion known as K/X event, are common features of sites

1051 (this paper), 1263 (Luciani et al, 2017a) and 1258 (D'Onofrio et al., 2020).

As the EECO was a time of high CO_2 pressure (e.g., Anagnostou et al., 2016) and it was characterized by several CIEs that may have induced lysocline/Carbonate Compensation Depth (CCD) upward shift, we could suspect that the absence of chiloguembelinids from the deep-water sites here analyzed may derive by a dissolution artifact. Chiloguembelinids have thin/small tests that make they more prone to dissolution than taxa with larger thicker/tests (Nguyen et al., 2011; D'Onofrio and Luciani, 2020). However, we can exclude that the decline in abundance of chiloguembelinids is a taphonomic result because they are very rare or absent above the K/X CIE also from the intervals where the dissolution proxy F-index is very low (Fig. 2).

Having established that the virtual disappearance of chiloguembelinids at the EECO is not related to taphonomic bias, the interpretation of such planktic foraminiferal change takes advantage from our new stable isotope paleobiology and allows us to frame it within a clear paleoceanographic interpretation.

Our results clearly demonstrate that throughout the Atlantic Ocean, chiloguembelinids occupied a habitat similar of subbotinids, i.e., sub-surface, thermocline dweller. Interestingly, the analysis of John et al. (2013, 2014), stable isotopes of lower and middle Eocene planktic foraminifera from Tanzania and Gulf of Mexico, let them to conclude that there was a much greater temperature at depths below the mixed layer. A crucial consequence is that elevated ocean temperatures may have enhanced bacterial respiration rate and significant remineralization thus resulting in more efficient recycling of carbon and nutrients higher in the water column (John et al., 2013, 2014; Pearson and Coxall, 2014).

This would have resulted in restricted food supply at depth which, together with warmer temperatures, might have led to a consequent cut out of the deeper dwelling niches in the lower thermocline (above references) such as those occupied by chiloguembelinids, which are recognized as eutrophic taxa (e.g., Leckie, 1987; Kroon and Nederbragt, 1990; Nederbragt, 1991) (Fig. 4). Remarkably, at Site 1263, a decline of subbotinids that shared a thermocline habitat with chiloguembelinids, is also recorded at the EECO (L1-L2 event) (Luciani et al., 2017a). Similarly, the eutrophic cold index *Subbotina* may have declined due to both warmer temperature and food starvation but suffered these hostile conditions later with respect to chiloguembelinids (Luciani et al., 2017a). However, this interpretation needs of detailed paleotemperature data across the EECO from thermocline waters at the Atlantic Ocean that are lacking at present. As noted above, our foraminiferal δ^{18}O data are affected by some test recrystallization thus they are unsuitable to obtain reliable paleotemperatures. Nevertheless, the *Chiloguembelina wilcoxensis* δ^{18}O values from Site 1051 display a minor shift to more negative value above the J event thus suggesting increasing temperature at the thermocline.

An alternative, although non-mutually excluding, scenario to explain the chiloguembelinid decline can derive from the study by Kast et al. (2019). Specifically, these authors provided nitrogen isotope data from the Paleogene Period concluding that the elevated water column denitrification recorded during the Paleocene points to more extensive suboxia in the Paleocene ocean. The extent of water column denitrification is a process that is known to occur only in oxygen depleted waters in the present-day Ocean and is therein inferred by FB (Foraminiferal Bound)- δ^{15}N values. Interestingly, the FB- δ^{15}N values started to

markedly decline within the EECO at ~53 Ma ago. This is unexpected because higher preformed O_2, less expansive suboxia and thus less water column denitrification should be correlated with cooling. The above mentioned authors explain this apparent incongruity taking into consideration the influence of the collision between India and Africa with Eurasia that led to the Tethys closing (Hu et al., 2016; Cao et al., 2017) and paralleled the denitrification decline. As the Tethys was source of water with low preformed O_2 into the thermocline and/or intermediate-depth waters of the global ocean, its closing trend may have led to reducing suboxia and thus reduction in water column denitrification, as observed in the decline of FB-δ^{15}N values. Further evidence of oxygenation of the thermocline derives from the major increase in isotopic variability of sulfur in sea water sulfate (δ^{34}S$_{SO4-SW}$) occurred at ~ 53 Ma ago (Renie et al., 2018). This major change has also been related to tectonic reorganization as linked to the Tethys closing and Himalayan formation (Renie et al., 2018). A possibility to explain the increase in δ^{34}S$_{SO4-SW}$ at ~ 53 Ma invoked by Renie et al. (2018) is enhanced deep-ocean ventilation (Sexton et al., 2011) driving pyrite burial deeper into the sediment column in deeper waters.

Giving that chiloguembelinids inhabited the OMZ (e.g. Boersma and Premoli Silva, 1989; Kroon and Nederbragt, 1990; Nederbragt, 1991; Keller, 1993; Barrera and Keller, 1994; Leckie, 1987; Leckie, et al., 1998; Huber et al., 1999; Premoli Silva and Sliter, 1999; Keller et al., 2001), the coincidental decline in *Chiloguembelina* with the global decline in FB-δ^{15}N values (Fig. 4) seems to suggest that early Eocene chiloguembelinids might have suffered from oxygenation of the thermocline. This constitutes as well a novel proof to corroborate previous finding that reported chiloguembelinids as forms dwelling

in oxygen depleted waters (references above). The evidence that

chiloguembelinids declined in the initial phase of the reduced suboxia of the

thermocline (Fig. 4) reveals great susceptibility of this group to water

oxygenation. A combination of warming and enhanced organic matter

remineralization and subsequent reduction of food supply at depth, together with

a more oxygenated thermocline might have been all contributed to various extent
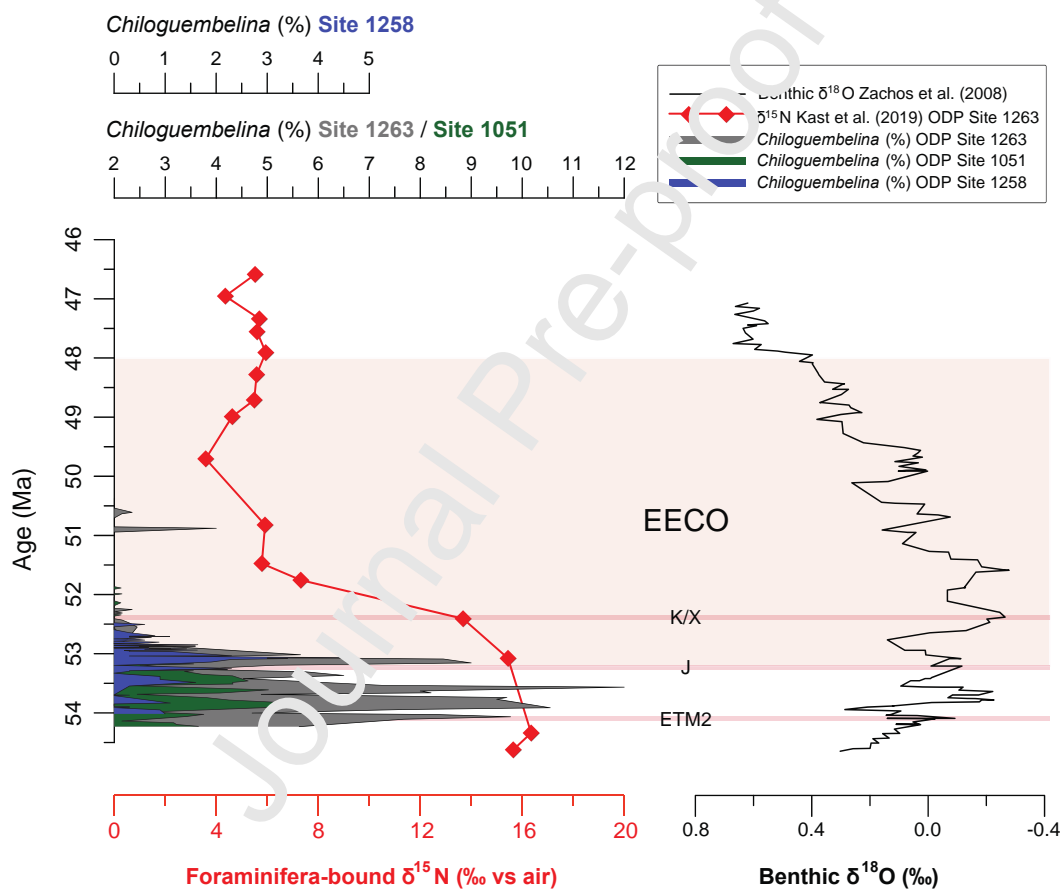
to the decline of chiloguembelinids in the early EECO.

Figure 4. Chiloguembelinid percentages from ODP sites 1051 (this paper), 1258 (D'Onofrio et al., 2020) and 1263 (Luciani et al., 2017a) plotted against δ^{15}N (Kast et al., 2019) and global benthic δ^{18}O (Zachos et al., 2008). Note the close correspondence between increased oxygenation within the OMZ as indicated by δ^{15}N decrease, temperature increase at the EECO and chiloguembelinid decline.
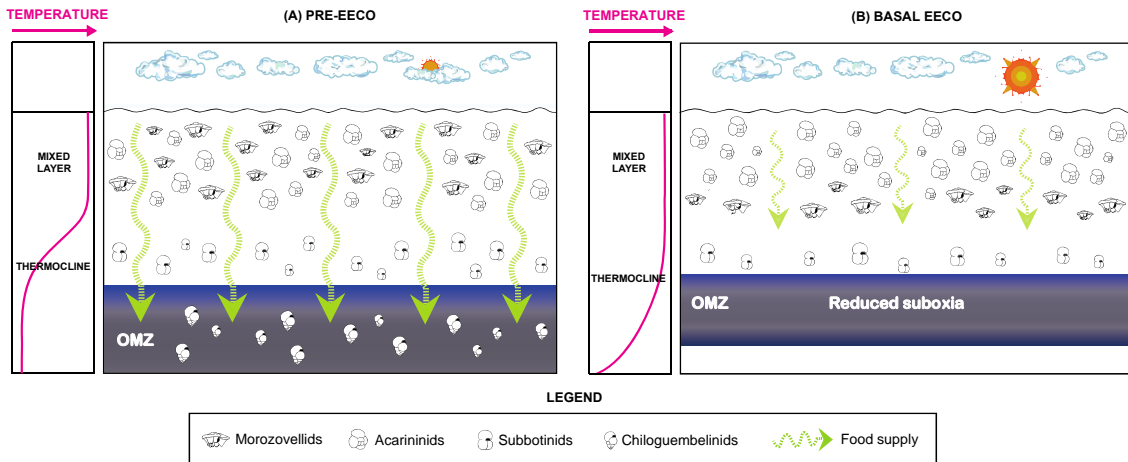
Figure 5. Cartoons illustrating environmental changes in the upper water column across the EECO at Atlantic oceanic sites as interpreted according to the record of changes in planktic foraminiferal assemblages and the new stable isotope data here achieved on *Chiloguembelina wilcoxensis* and *C. trinitatensis* (modified from Luciani et al., 2017a). (A) Pre-EECO environment showing a well-stratified water column with acarininids, morozovellids, chiloguembelinids and subbotinids relatively abundant, stable food supply at depth. (B) Basal EECO scenario showing the contraction of the sub-surface and deeper dwelling niches of the eutrophic chiloguemeblinids. This was probably triggered by rapid and shallower bacterial remineralization due to intense warming causing reduced food supply at depth (John et al., 2013, 2014; Pearson and Coxall, 2014). According to Kast et al. (2019) the suboxia within the OMZ was reduced during the EECO thus contributing to cutting the chiloguembelinid ecological niche.

5. Summary and conclusions

We present here new chiloguembelinid relative abundance and oxygen and carbon stable-isotope data from *Chiloguembelina* as compared to mixed-layer, thermocline planktic foraminiferal dwellers and benthic foraminifera from early Eocene Atlantic ODP sites 1051, 1258, 1263 and Antarctic Weddel Sea Site 690. Chiloguembelinids are planktic foraminifera characterized by small-size, thin-wall test bearing a biserial disposition of the chambers. On the basis of currently available data, the stable isotope paleobiology of Ceonozoic chiloguembelinids appeared contradictory as suggesting mixed layer or thermocline habitat depending on stratigraphic intervals and geographical areas. However,

chiloguembelinid stable-isotope data were so far lacking from the early Eocene. The main results of our study are summarized below.

The genus *Chiloguembelina* began virtually absent in the subtropical, equatorial and temperate Atlantic Sites 1051 (this paper), 1258 (D'Onofrio et al., 2020) and 1263 (Luciani et al., 2017a) at the beginning of the EECO. This striking widespread decline of chiloguembelinids through the Atlantic Ocean implies marked environmental changes therefore the knowledge of chiloguembelinids ecological behavior here established allows us to properly interpret such changes. Our findings clearly prove that early Eocene *Chiloguembelina* occupied a deep-water niche throughout the Atlantic Ocean as demonstrated by its stable isotope signature close to the deep-dweller *Subbotina* and benthic foraminifera. These evidences provide critical paleoceanographic implications. A possible scenario is that intermediate water temperatures rose significantly during the EECO thus becoming too warm for this genus. Moreover, elevated ocean temperatures could have enhanced the rate of bacterial respiration and remineralization significantly thus resulting in more efficient recycling of nutrients higher in the water column (John et al., 2013, 2014; Pearson and Coxall, 2014). This would have resulted in a restriction of food supply at depth and subsequent cut out the deeper dwelling niche of chiloguembelinids. Therefore, chiloguembelinids, considered as eutrophic indicator, may have suffered of reduced food supply besides the warmer temperatures. The agreement of the observed decline in abundance of chiloguembelinids at the study sites with recently published foraminiferal-bound nitrogen isotope data suggests that enhanced oxygenation of the thermocline from the early EECO might have also play a major role in driving the

disappearance of chiloguembelinids. This evidence in itself represents a new proof for the largely accepted view that these forms inhabited the OMZ.

In conclusion, we contribute to understand the spatial and temporal distribution of chiloguembelinids during the early Eocene by providing an explanation for their disappearance throughout the Atlantic Ocean. Their decline in the early EECO is not related to overlooking due to their small size but very likely derives from a combination of reduced food supply, increased in thermocline temperature and oxygen content.

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Appendix A: list of species cited with author and year.

Acarinina berggreni (El Naggar, 1966)

Acarinina coalingensis (Cushman and Hanna, 1927)

Acarinina esnaensis (Leroy, 1953)

Acarinina interposita Subbotina, 1953

Acarinina primitiva (Finlay 1947)

Acarinina quetra (Bolli, 1957)

Acarinina soldadoensis (Brönniman, 1952)

Acarinina cuneicamerata (Blow 1979)

Astrorotalia (*Planorotalites*) *palmerae* (Cushman & Bermudez 1937)

Chiloguembelinia crinita (Glaessner, 1937)

Chiloguembelina cubensis (Palmer 1934)

Chiloguembelina ototara Finlay 1940

Chiloguembelina trinitatensis (Cushman and Renz 1942)

Chiloguembelina wilcoxensis (Cushman and Ponton 1932)

Globanomalina planoconica (Subbotina, 1953)

Morozovella aequa (Cushman and Renz, 1942)

Morozovella aragonensis (Nuttall 1930)

Morozovella crater (Hornibrook, 1958)

Morozovella subbotinae (Morozova 1939)

Nuttallides truempyi (Nuttall, 1930)

Oridorsalis umbonatus (Reuss, 1851)

Planorotalites pseudoscitula (Glaessner, 1937)

Planorotalites capdevilensis (Cushman and Bermudez 1949)

Subbotina patagonica (Todd and Kniker, 1952)

Subbotina roesnaesensis Olsson and Berggren, 2006

Zeauvigerina aegyptiaca Said and Kenawy 1956

HIGHLIGHT 3-5 85 characters

- New early Eocene *Chiloguembelina* stable isotopes are given from the Atlantic Ocean
- *Chiloguembelina* disappears at the Early Eocene Climatic Optimum from Atlantic Ocean
- *Chiloguembelina* revealed to be thermocline dwellers from the ODP Sites studied.
- The EECO event impacted the thermocline habitat by reducing ecological niches
- Chiloguembelinid loss is linked to denitrification (δ^{15}N) and thermocline oxygenation
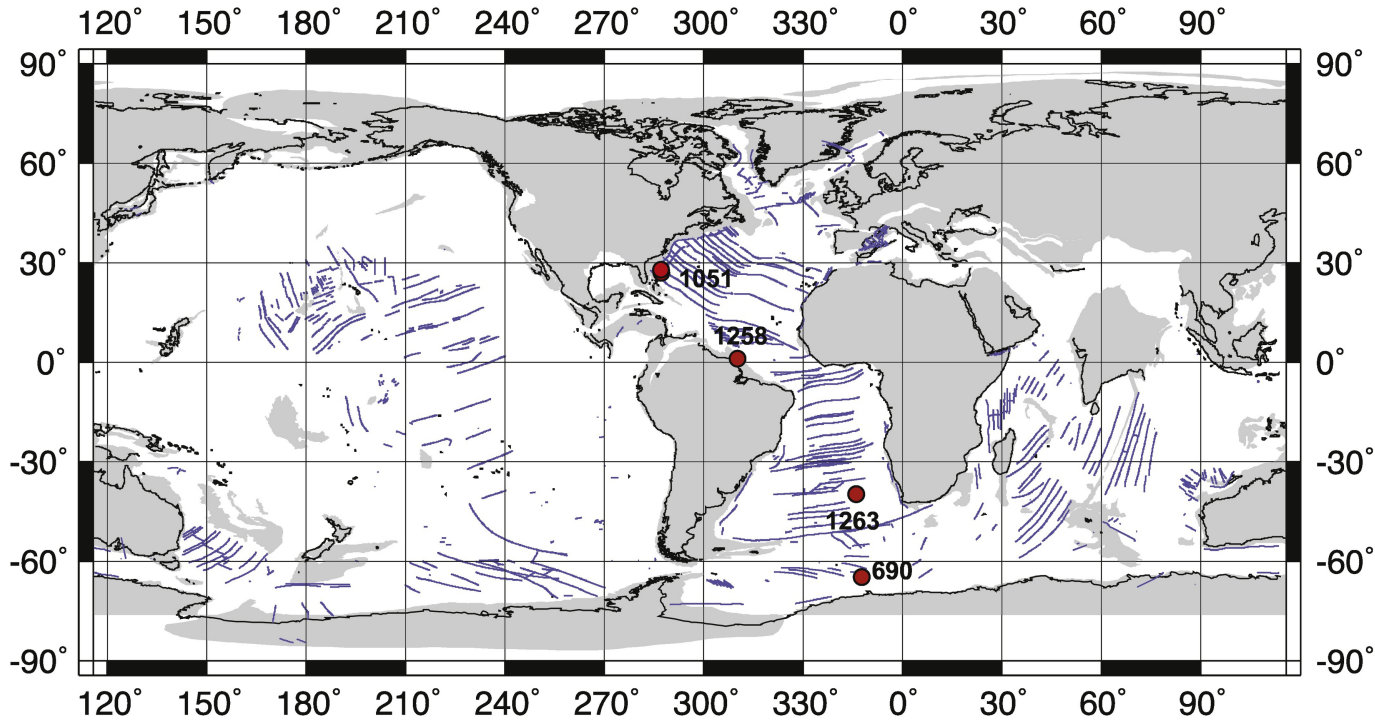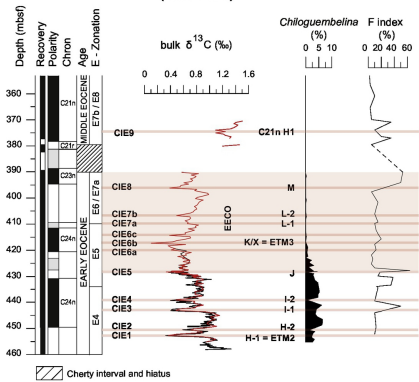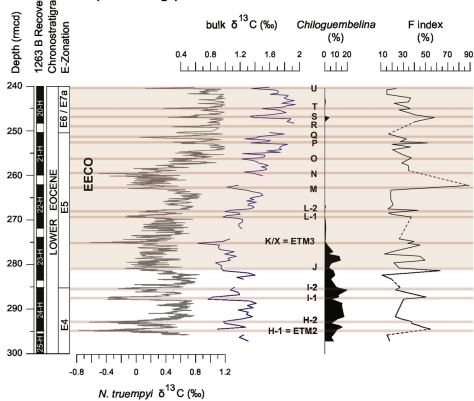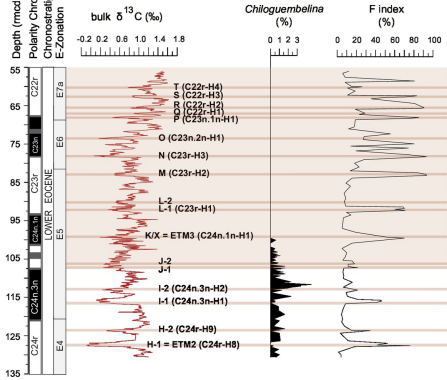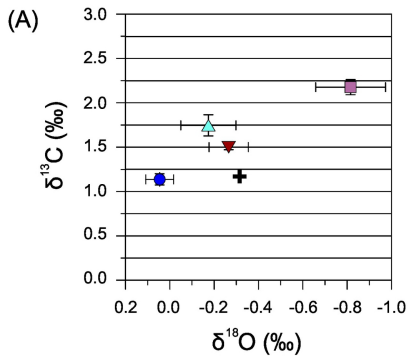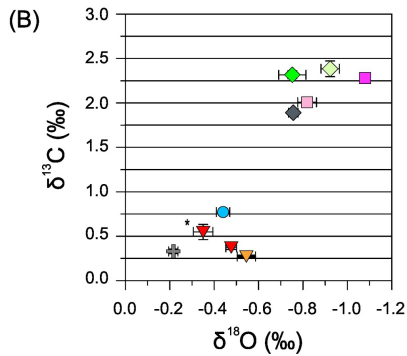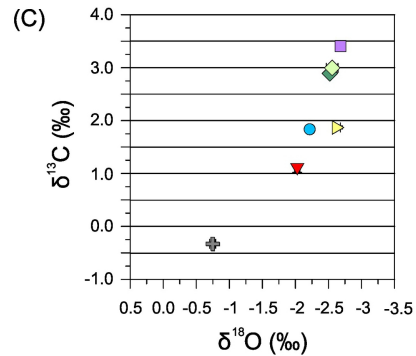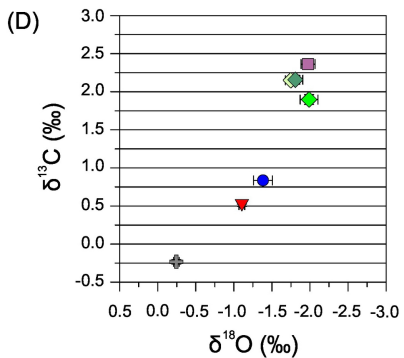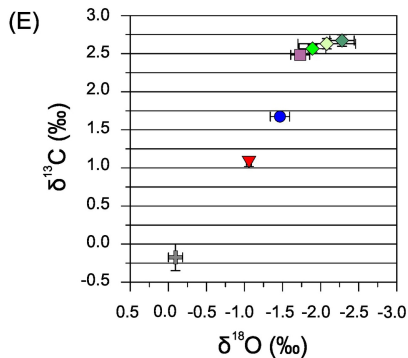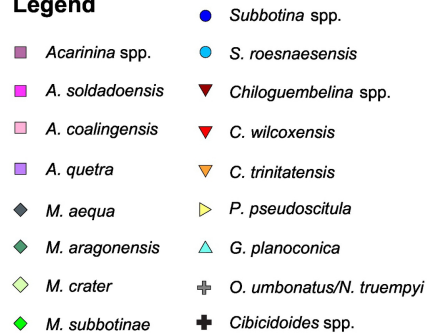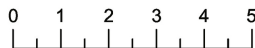
Figure 1
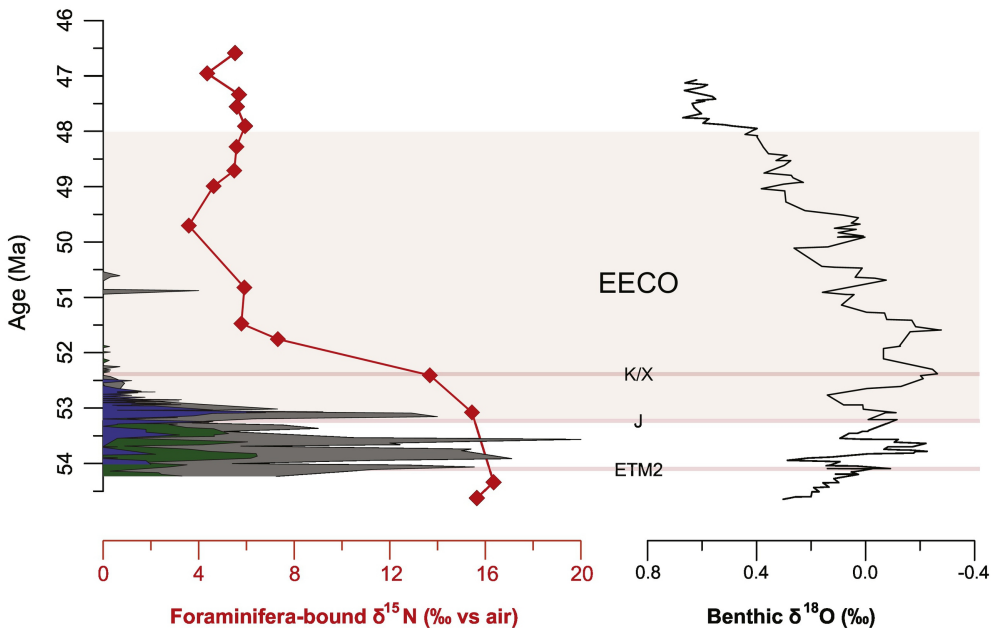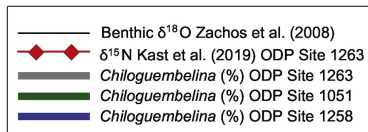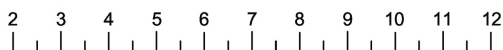
Figure 2

Figure 3

Figure 4

TEMPERATURE → (A) PRE-EECO

MIXED LAYER

THERMOCLINE

OMZ
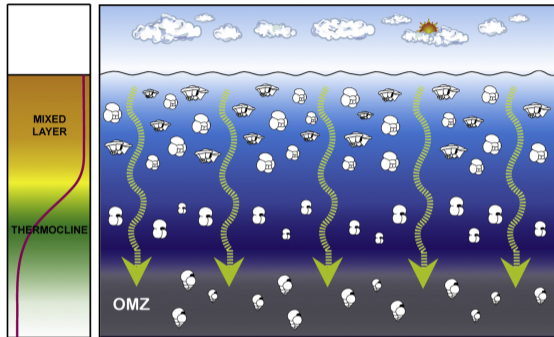
TEMPERATURE → (B) BASAL EECO

MIXED LAYER

THERMOCLINE

OMZ Reduced suboxia
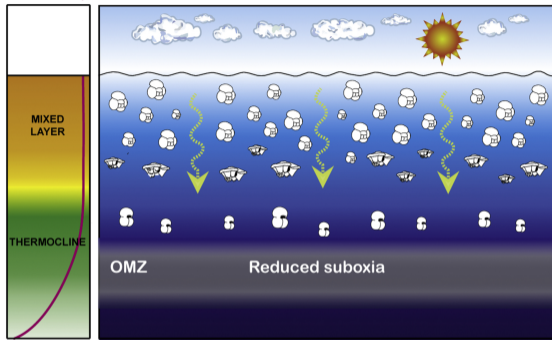
LEGEND

Morozovellids Acarininids Subbotinids Chiloguembelinids Food supply

Figure 5