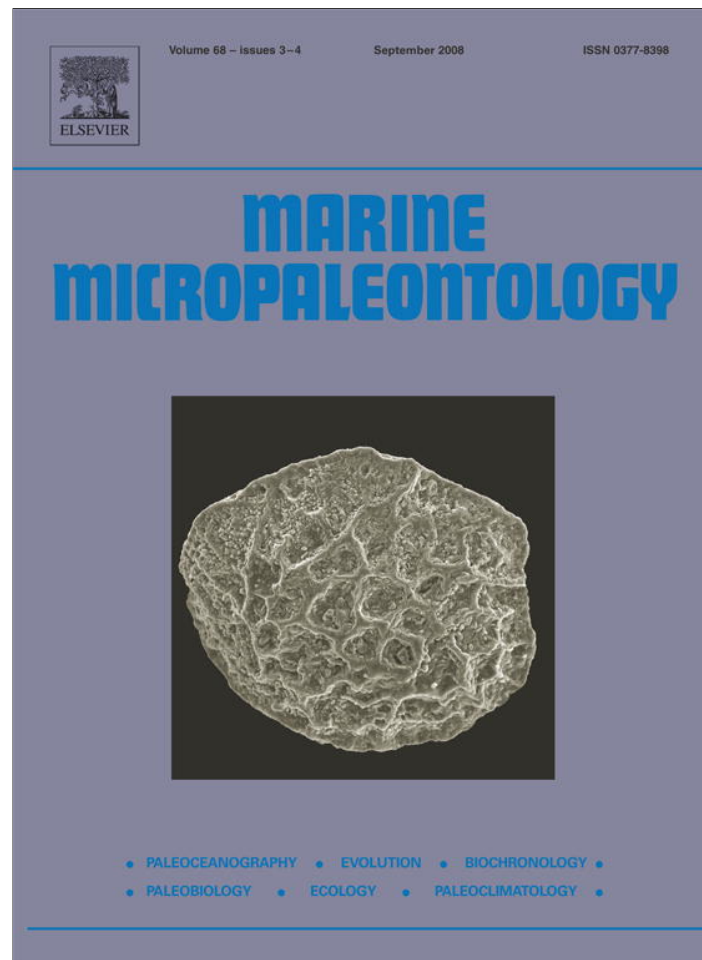


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Planktonic foraminiferal turnover, diversity fluctuations and geochemical signals across the Eocene/Oligocene boundary in Tanzania

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ABSTRACT

A major turnover in planktonic foraminifera occurred across the Eocene/Oligocene (E/O) boundary. New drill holes through the E/O boundary in southern Tanzania contain extremely well-preserved and diverse assemblages of planktonic foraminifera. Here we document a 1.2 million year record of assemblages, diversity and stable isotope fluctuations through this critical interval, which is often dissolved and/or recrystallised in carbonate-rich facies. The E/O boundary is marked by the abrupt extinction of all five remaining species of the family Hantkeninidae and a distinct size reduction in the genus *Pseudohastigerina*. The boundary is preceded over a short stratigraphic interval by the extinction of *Turborotalia cerroazulensis*, *Turborotalia cocoaensis* and *Turborotalia cunialensis*. Quantitative analysis of planktonic foraminiferal assemblages reveals significant changes in the abundance of certain species and the composition of the assemblages. We compare diversity fluctuations to the stable isotope record of *Pseudohastigerina naguwichiensis* and use multispecies stable isotope analyses to determine the life habitats of the most important species. A major shift in the evenness occurs at ~33.8 Ma associated with the extinction of the *T. cerroazulensis* group suggesting acute ecological disturbance. We propose that the extinction of the *T. cerroazulensis* group at ~33.8 Ma was directly related to cooling of sea surface temperatures, while the extinction of Hantkeninidae was due to modifications in the thermal structure of the oceans and associated productivity changes. After the extinctions, renewed origination and diversification occurred, leading to a characteristic Oligocene planktonic foraminifer assemblage.

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1. Introduction

One of the most significant turnovers of planktonic foraminifera in the Cenozoic occurred across the Eocene/Oligocene (E/O) boundary (33.7 Ma). At the Global Stratotype Section and Point (GSSP) at Massignano in Italy, the boundary is formally marked by the disappearance of the Family Hantkeninidae (a distinctive group of tubulospinose planktonic foraminifera) (Coccioni, 1988; Coccioni et al., 1988;

Nocchi et al., 1988; Premoli Silva and Jenkins, 1993). Studies of several sections in Spain, Italy and elsewhere have shown that the extinction of *Hantkenina* and *Cribohantkenina* was preceded by the extinction of the *Turborotalia cerroazulensis* group (Molina, 1986; Nocchi et al., 1986, 1988; Coccioni et al., 1988; Gonzalvo and Molina, 1992; Berggren and Pearson, 2005). Other events that have been reported to approximately coincide with the E/O boundary are the final extinction of *Globigerinatheka* (the last remaining species, *G. tropicalis*; see Nocchi et al., 1986; Premoli Silva et al., 2006), a dramatic collapse in abundance of the long-ranging genus *Pseudohastigerina* and a reduction in size of its principal species *Pseudohastigerina micra* (Nocchi et al., 1986), and the appearance of several new species, most notably "*Globoquadrina*" *tapuriensis* (Molina et al., 1986; Coccioni et al., 1988). However, due

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to the lack of continuous sections or well-preserved planktonic foraminifera there is little information regarding the nature of the turnover and the impact on the rest of the assemblage (Loubere, 1985). We find that the ecological impact through this interval is not only expressed as extinction within marine organisms but also in changes in community structure. We document and discuss the response of the planktonic foraminiferal population to environmental change across the E/O transition.

1.1. Geological setting

From 2002 to 2005, the Tanzania Drilling Project (TDP) drilled 20 sites into Cretaceous and Paleogene marine sediments that are now exposed on land in southern Tanzania (Pearson et al., 2004, 2006; Nicholas et al., 2006). The E/O boundary is intermittently exposed on a hillside near the coastal village of Pande in the Kilwa administrative district (Fig. 1). Three cores were drilled through the E/O boundary sited roughly along strike, within 3 km of each other. These sites are designated TDP Sites 11, 12 and 17 (Nicholas et al., 2006; Pearson et al., 2008). They are expanded in comparison to other E/O reference sections and contain exceptionally well-preserved assemblages of planktonic foraminifera (Pearson et al., 2007, 2008), as well as benthic foraminifera, nannofossils (Bown et al., 2008), rare dinoflagellates and other fossil groups.

The sedimentary formation in which these sites were drilled has been formally described as the Pande Formation

(Nicholas et al., 2006). The dominant lithology is a dark greenish-grey clay with less than 10% CaCO₃. Based on sedimentary facies and benthic foraminiferal biofacies, it is interpreted as having been deposited in a bathyal outer shelf to slope environment in approximately 300–500 m of water (Nicholas et al., 2006). Like today, the Tanzanian shelf was probably very narrow, and the drill sites are estimated to have been about 50 km from the paleo-shoreline (Kent et al., 1971; Nicholas et al., 2006), hence organic geochemistry is dominated by terrestrial biomarkers (van Dongen et al., 2006) and the palynology is rich in the debris of higher plants (H. Brinkhuis, pers. comm., 2005). Moreover, thin (10 cm to 1.5 m) limestone beds, which are interpreted as debris flows, occur sporadically throughout the Pande Formation, sourced from the inner shelf. Additional biostratigraphic control is provided by calcareous nannofossils which are highly diverse and are indicative of a shelf to slope environment including deep, 'blue-water' algal species (Bown and Dunkley Jones, 2006; Bown et al., 2008). The presence of common allochthonous shallow-water debris in the sites permits correlation with larger benthic foraminifer extinction events (Pearson et al., 2008).

Each of the three sites shows evidence of a minor erosional surface and facies change in the lowermost Oligocene, which may be related to sea level fall. At TDP Sites 11 and 17, this erosion cuts into the uppermost Eocene, but at TDP Site 12, the E/O boundary is complete in monotonous clay facies, with no evidence of missing section at the boundary. Correlation between the sites and to the timescale of Berggren et al. (1995) is given in Pearson et al. (2008). The diverse planktonic foraminiferal assemblages across the E/O boundary interval (34.7–33.5 Ma) provide an excellent opportunity for examining the tropical planktonic foraminifera biotic response and population dynamics during a period of extinction, high-latitude cooling and significant climate change. Here we present a 1.2 million year record of planktonic foraminiferal ranges, abundance counts, species diversity, and evenness, and compare them to the stable isotope record of *Pseudohastigerina naguwichiensis* (this study) and *Turborotalia ampliapertura* (Pearson et al., 2008). In addition, we determine the paleoecology of extinct species using shell geochemistry.

2. Methods

Samples of 10 cm "half round" (cut vertically along the core) were soaked in tap water and washed through a 63 µm sieve. For the assessment of relative abundance variations, the >250 µm size fraction was examined. This generally yielded a small number (<300) of planktonic foraminifera which were counted on a picking tray. When, in a few examples, numbers of specimens exceeded 300, the total number was estimated proportionally, although in these cases the whole sample was scanned to count the rare forms. We concentrated on the >250 µm size fraction because the main taxa to become extinct in the interval are large forms. We note that our analysis therefore omits some smaller species that are abundant in the finer size fractions. Of these the most prominent is the *Pseudohastigerina* lineage. Hence, in addition to the primary species abundance data, we counted 300 specimens from the 125–250 µm size fraction, which were classified as *P. naguwichiensis*, *P. micra* or "other". The

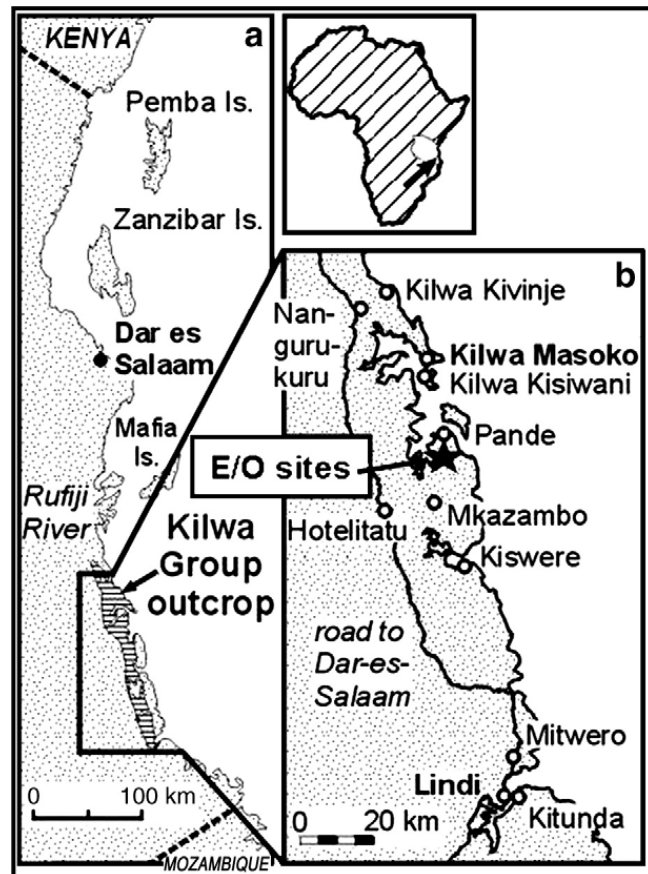


Fig. 1. Location of Tanzania Drilling Project Eocene/Oligocene drill cores.

<125 μm size fraction was studied for taxonomic purposes only.

Stable isotopic analysis of planktonic foraminifera was performed at Rutgers University. Fifty specimens of *P. naguwichiensis* were picked from the 63–125 μm size fraction. Multispecies stable isotope analyses of planktonic foraminifera were conducted from a range of size fractions on 11 species from Oligocene sample TDP12/9/2 23–36 cm and 15 species from Eocene sample TDP12/20/3 74–83 cm, corresponding to core depths of 31.16 and 64.79 m, respectively. Foraminifera were reacted in phosphoric acid at 90 °C for 15 minutes in an automated peripheral attached to a Micromass Optima mass spectrometer. Analytical precision measured using NBS-19 was 0.08 for $\delta^{18}\text{O}$ and 0.05 for $\delta^{13}\text{C}$.

3. Results

3.1. Foraminiferal preservation

Foraminifera are exceptionally well-preserved apart from some samples where pyrite is abundant and some shells are partially replaced or overgrown. Close to the occasional cemented limestone beds, foraminifera tests are sometimes infilled with calcite. Generally, however, specimens appear glassy with transparent tests under the light microscope (Fig. 2), with the excellent preservation confirmed with SEM images showing few signs of diagenetic alteration (Wade and Pearson, in prep.). The biostratigraphic range chart of taxa from the >250 μm size fraction, with additional information on pseudohastigerinids (125–250 μm size fraction) of TDP Site 12 is shown in Fig. 3.

3.2. Stable isotopes results

Multispecies stable isotope data are shown in Fig. 4. In the uppermost Eocene, $\delta^{18}\text{O}$ values are recorded between a maximum of -1.91% for *Dentoglobigerina pseudovenezuelana* (355–425 μm) and minimum of -3.42% for *Globoturborotalita ouachitaensis* and *Subbotina gortanii* (125–250 μm) and $\delta^{13}\text{C}$ values range between -0.29% and 1.67% . For the earliest Oligocene *Globoturborotalita cf. woodi* and *P. naguwichiensis* record the lightest $\delta^{18}\text{O}$ values (-3.23 and -3.17% respectively). The values for *Turborotalia increbescens* and *T. ampliapertura* are very similar to one another for both oxygen and carbon. Species of *Dentoglobigerina* and *Subbotina*

cluster with $\delta^{18}\text{O}$ values between -2.48 and -1.87% . Specimens of “*Globoquadrina*” *euapertura*, “*G.*” *venezuelana* and *Dentoglobigerina galavisi* all record heavier $\delta^{18}\text{O}$ in the larger size fractions.

Stable isotope results of *P. naguwichiensis* are listed in Appendix B. Oxygen isotope values fluctuate between -4.0 and -2.9% and increase through the Eocene–Oligocene interval with progressively more positive values up section. Carbon isotope values are highly variable between $+0.34$ and -0.67% .

3.3. Diversity and evenness

We record the relative abundances of 27 species of planktonic foraminifera from the >250 μm size fraction (Appendix A). Five taxa record relative abundances >25% and significant variations through the studied section, these were *Dentoglobigerina pseudovenezuelana*, “*Globoquadrina*” *tapuriensis*, *Turborotalia cocoaensis*, *T. cerroazulensis* and *T. ampliapertura* (Fig. 5). Species were ranked according to their percentage abundance for the Eocene (Fig. 6b) and Oligocene (Fig. 6a).

From the foraminifera abundance data we employed Shannon's index (H') (Shannon and Weaver, 1949) to assess species distributions and diversity of the assemblages through the E/O boundary (Fig. 7). The Shannon index combines information on the number of species present with the evenness of the assemblage. H' values are consistently between 2.0 and 2.6 for the lower part of the core (65 to 150 m). At 65 m (33.94 Ma), values start to fluctuate, and reduce to ~ 1.6 in the Oligocene. Low numbers indicate a reduced species richness and high dominance. The evenness of the assemblage (Fig. 7) was calculated following Hayek and Buzas (1997), where 0 characterizes completely even assemblages and higher values indicate dominated assemblages. From 150 to 50 m, evenness is 0.44 ± 0.13 . Dominance of the assemblages increases dramatically at 50 m, and for the remainder of the studied section values are high 0.94 ± 0.17 .

4. Discussion

4.1. Biostratigraphy of the Eocene/Oligocene boundary

The planktonic foraminiferal biostratigraphy at TDP Site 12 (Fig. 3) is very consistent with the international stratotype

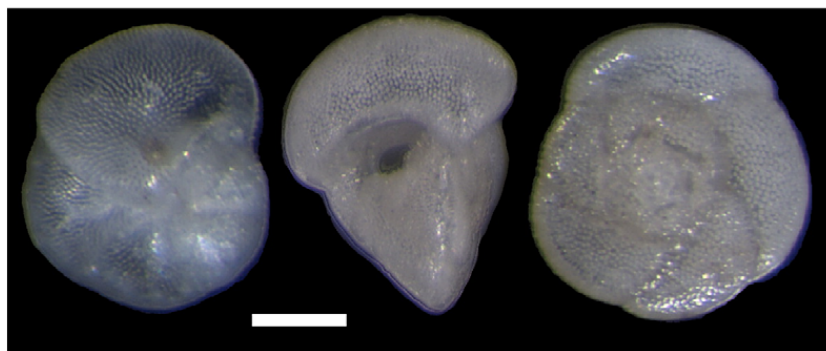


Fig. 2. Umbilical, edge and spiral view of *Turborotalia cerroazulensis* showing glassy preservation of the test (TDP Sample TDP17/39/4, 31–39 cm), taken in reflected light with Leica DFC 480 camera mounted on a Leica MZ 16 microscope using Earth Basic image software. Scale bar = 100 μm .

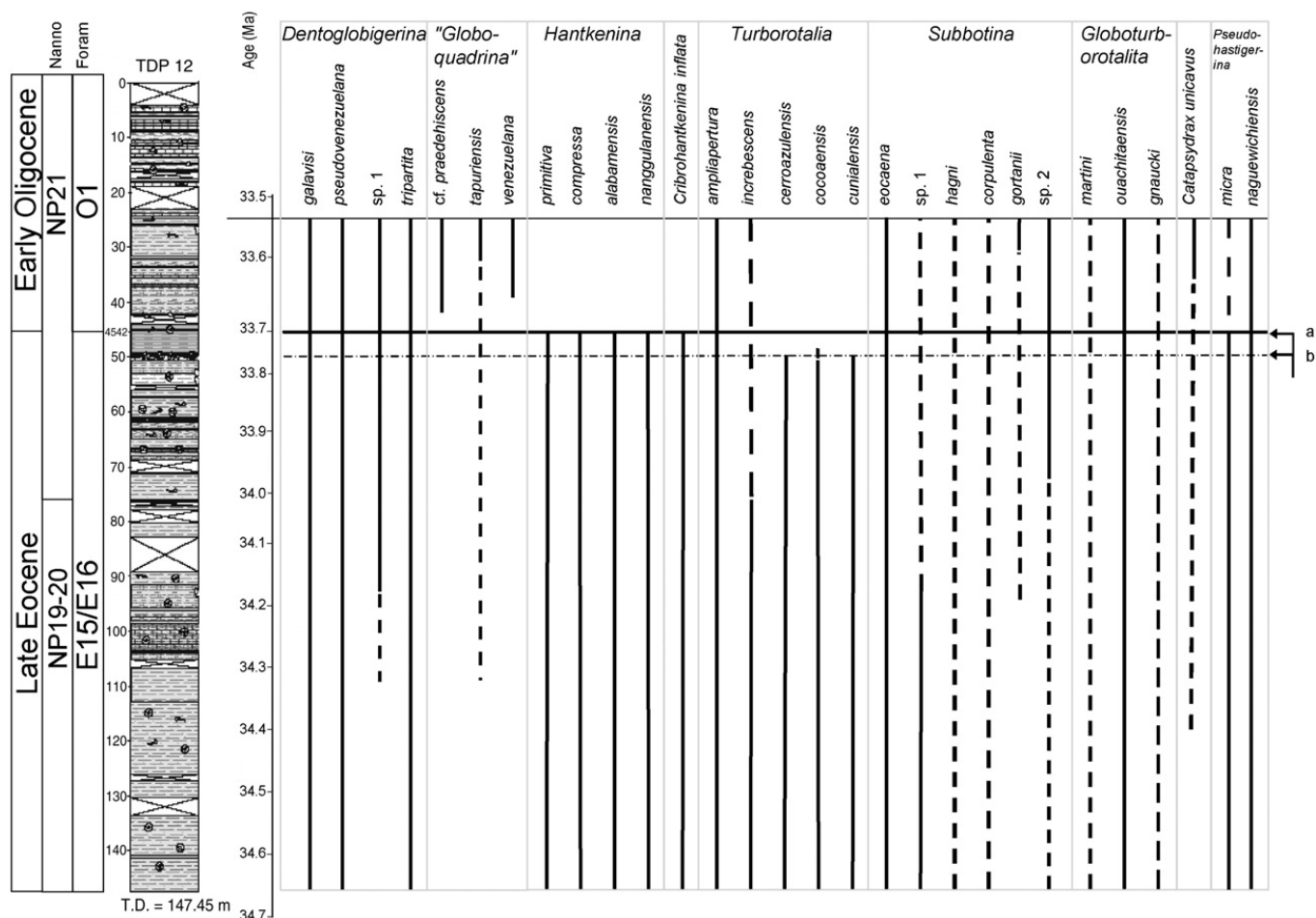


Fig. 3. Stratigraphic range of planktonic foraminifera from TDP 12 against the planktonic foraminifera and nannofossil biozonations of Berggren and Pearson (2005) and Martini (1971). All species from the >250 µm size fraction, except *Pseudohastigerina* (63–125 µm size fraction). Dashed lines = sporadic occurrences. Core log from Nicholas et al. (2006). (a) Highest occurrence (HO) Hantkeninidae marking the Eocene/Oligocene Boundary, (b) HO *Turborotalia cerroazulensis* group.

section at Massignano, Italy (Coccioni et al., 1988; Berggren and Pearson, 2005), confirming that most bioevents are globally significant and provide reliable, robust stratigraphic markers. Five morphospecies of Hantkeninidae are recognized in the upper Eocene sediments of Tanzania (*H. primitiva*, *H. compressa*, *H. alabamensis*, *H. nanggulanensis*, and *Cribrohantkenina inflata*), all of which disappear simultaneously in an interval of less than 30 cm (Fig. 3). With the exception of one specimen of *H. primitiva* and one of *H. alabamensis* (that may be reworked) at 44 and 42 m respectively, all five species become extinct at Sample TDP12/14/1, 56–68 cm (45 m), equivalent to a sudden extinction in less than 5 kyr and denoting the top of planktonic foraminifera Biozone E16. The stable isotope stratigraphy and gap between the extinction of *Turborotalia* and *Hantkenina* suggest that no hiatus exists at the boundary (see below).

Large *Cribrohantkenina* with highly inflated, spherical chambers, extend right to the E/O boundary in Tanzania. As the Hantkeninidae left no descendants, and the five hantkeninid morphospecies are too dissimilar to realistically belong to a single biospecies, the extinction appears to have been a synchronized event involving several closely related taxa. Previous studies (Coccioni et al., 1988; Gonzalvo and Molina,

1992; Molina et al., 2006) have found the highest occurrence (HO) of *C. inflata* was prior to the *Turborotalia* extinction while another species, *C. lazzarii*, persisted to the boundary (see discussion in Berggren and Pearson, 2005). Consistent with Berggren and Pearson (2005) we do not recognize *C. lazzarii* and find the simultaneous extinction of all *Hantkenina* and *Cribrohantkenina* at TDP 12.

The E/O boundary extinction is preceded by a similar coordinated extinction within the genus *Turborotalia*. Several morphospecies belonging to the *T. cerroazulensis* group (*T. cerroazulensis*, *T. cocoaensis* and *Turborotalia cunialensis*) disappear in the top 5 m of the Eocene. The group comprising *T. cerroazulensis*, *T. cocoaensis* and *T. cunialensis* have their highest common occurrence at Sample TDP12/16/1 (50 m). There are rare occurrences of *T. cocoaensis* and *T. cerroazulensis* between 50 and 45 m, suggesting either non synchronous extinction or minor reworking. These species were not found in any samples above the extinction of *Hantkenina* at 45 m. A similar short interval between the extinctions of Hantkeninidae and *Turborotalia* groups has also been observed at the international stratotype section in Massignano, Italy (Coccioni et al., 1988; Gonzalvo and Molina, 1992; Berggren and Pearson, 2005), and other Tethyan

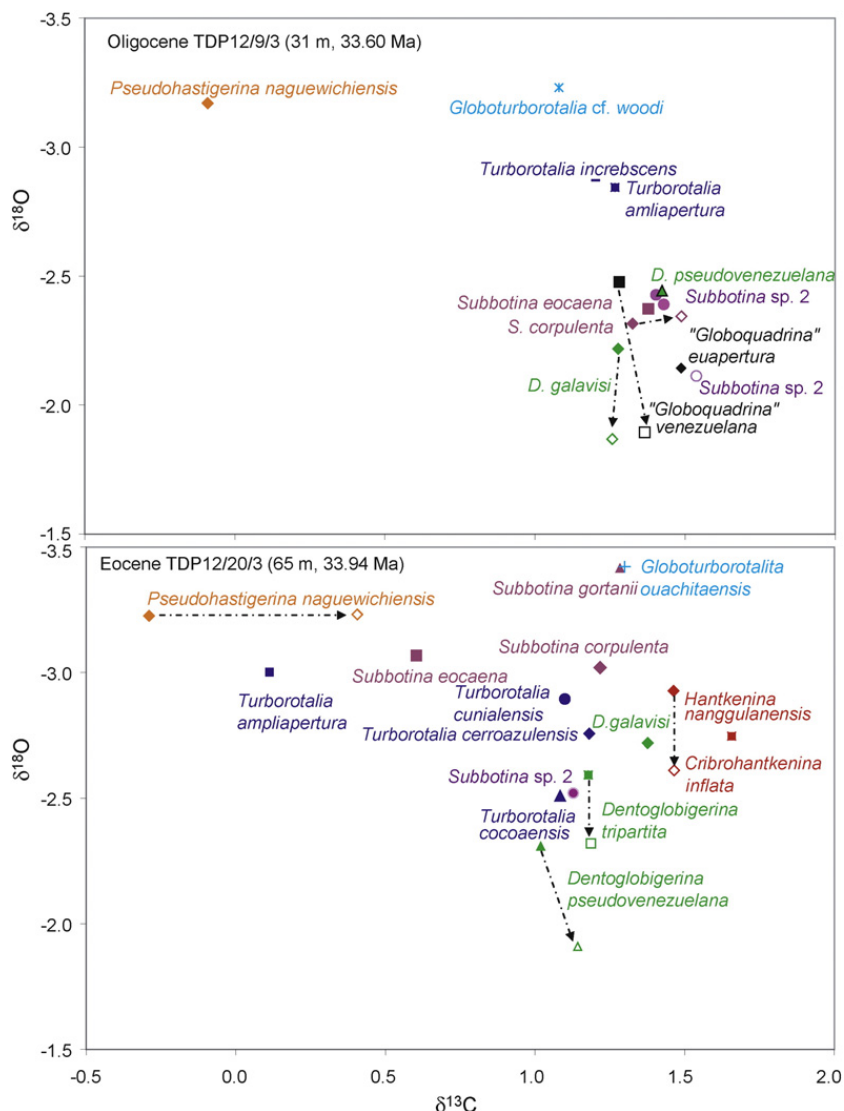


Fig. 4. Multispecies stable isotope analyses from Oligocene sample TDP12/9/3 (33.60 Ma) and Eocene sample TDP12/20/3 (33.94 Ma). Arrows indicate changes from small to larger size fractions. Data are listed in Pearson et al. (2007).

sections (e.g., Molina et al., 2006). At Massignano the offset between the *Hantkenina* and *Turborotalia* extinctions is 44 cm, corresponding to 65 kyr (Berggren and Pearson, 2005). Further constraints on sedimentation rate are provided by the highest occurrence of calcareous nannofossil taxa *Discoaster saipanensis* at 77.94 m (Bown and Dunkley Jones, 2006), suggesting the Tanzanian sites are relatively expanded with sedimentation rates at TDP Site 12 of 6.5 cm/kyr.

Pseudohastigerinids form a distinctive and abundant component of the small size fraction (<125 μm). Consistent with the western North Atlantic (Cordey et al., 1970), U.S. Gulf Coast (Keller, 1985; Miller et al., 2008) and Italian sections (Nocchi et al., 1986), we find a shift in the size of *Pseudohastigerina* at the E/O Boundary. During the Eocene *P. micra* is common in the 125–250 μm size fraction (5–16%) (Fig. 5), however, a distinct dwarfing of *P. micra* occurs at 45 m, synchronous with the *Hantkenina* extinction. Following the E/O boundary, pseudohastigerinids are rare in the 125–250 μm size fraction, but remain (principally *P. naguwichiensis*) in the <125 μm size fraction. *P. naguwichiensis* is present in the <125 μm size fraction throughout. Our study emphasizes the

HO of large sized *P. micra* as a useful stratigraphic marker for the E/O boundary in the absence of Hantkeninidae.

We find the lowest occurrence of “*Globoquadrina*” *tapuriensis* in the latest Eocene, however, occurrences are sporadic. Consistent with previous studies (e.g., Molina et al., 1986; Coccioni et al., 1988), we find a marked increase in abundance of “*G.*” *tapuriensis* after the E/O boundary in Biozone O1. An unusual aspect of the planktonic foraminifer record is the absence of *Globigerinatheka index*. The extinction of this important marker species at 34.3 Ma (700 kyr before the boundary) is used to distinguish biozones E15 and E16 in the zonation of Berggren and Pearson (2005). According to our age model (Pearson et al., 2008) we would expect to find *G. index* occurring consistently in the lower part of TDP Site 12. The most likely explanation for its absence is that *G. index* was not present in the western Indian Ocean in the upper Eocene. We note however that other species of *Globigerinatheka* (*G. semiinvoluta*, *G. tropicalis*) are common in somewhat older strata in the lower part of the upper Eocene in the Kituda shore section of Tanzania (Blow and Banner, 1962; see also Nicholas et al., 2006, p. 458).

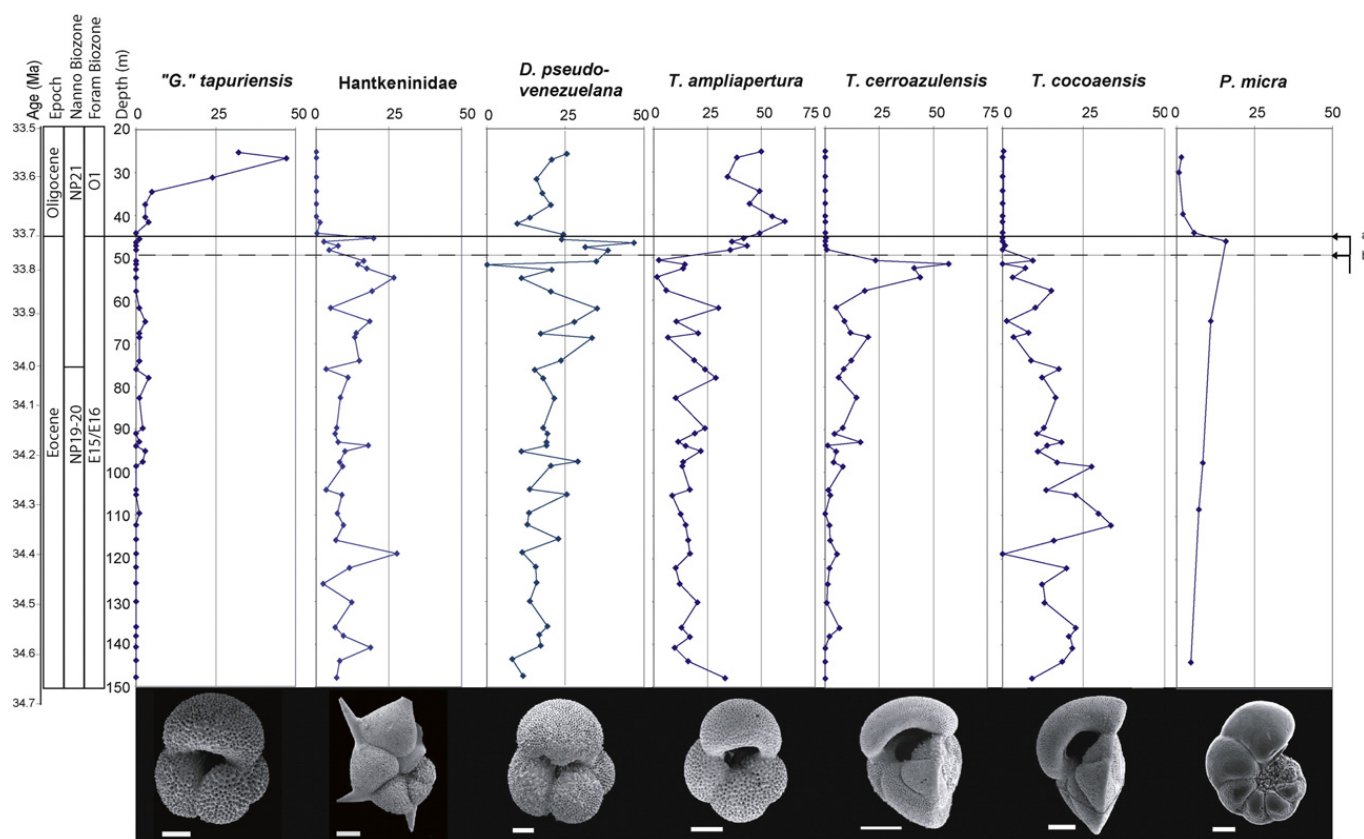


Fig. 5. Relative abundance variations (%) of “*Globoquadrina*” *tapuriensis*, Hantkeninidae, *Dentoglobigerina pseudo-venezuelana*, *Turborotalia ampliapertura*, *T. cerroazulensis*, *T. cocoaensis* and *Pseudohastigerina micra* at TDP 12. All species from the >250 μm size fraction, except *P. micra* (125–250 μm). (a) and (b) as in Fig. 3. Scale bars= 100 μm, except *Pseudohastigerina*=50 μm.

4.2. Paleocology of planktonic foraminifera

Determining the paleobiology of extinct species of planktonic foraminifera is key to examining the structure of the water column and stability of water mass stratification. Stable isotope data can be used as a proxy for the paleobiology of extinct planktonic foraminifera taxa, as shells secreted in surface waters tend to be depleted in $\delta^{18}\text{O}$ (on account of the warmer temperatures) and enriched in $\delta^{13}\text{C}$ relative to deeper-dwelling species. Our multispecies stable isotope analyses (Fig. 4) are generally consistent with previous studies (e.g., Douglas and Savin, 1978; Poore and Matthews, 1984; Boersma et al., 1987). The depleted $\delta^{18}\text{O}$ values in *Pseudohastigerina naguwichiensis*, *Globoturborotalita ouachitaensis*, *G. cf. woodi* and in comparison to the rest of the assemblage (Fig. 4), suggest that these species calcified in the mixed layer. *Turborotalia increbescens* and *T. ampliapertura* have relatively negative $\delta^{18}\text{O}$ but values are enriched compared to *Pseudohastigerina* and *Globoturborotalita* and indicate that turborotaliids occupied a lower mixed layer/upper thermocline habitat.

Stable isotope analyses were conducted on three species of *Subbotina* (*S. gortanii*, *S. eocaena* and *S. corpulenta*), however their oxygen isotope values in relation to other taxa are variable (Fig. 4). In the uppermost Eocene subbotinids have relatively depleted $\delta^{18}\text{O}$ values (<-3‰) suggestive of a mixed layer habitat, an interpretation consistent with Douglas and Savin (1978) and Boersma et al. (1987). However, in the lowermost Oligocene *S. eocaena* and *S. corpulenta* $\delta^{18}\text{O}$ values cluster with

those of dentoglobigerinids and “globoquadrinids” suggestive of a deeper, thermocline habitat (see also Pearson et al., 2001).

Dentoglobigerinids consistently record positive $\delta^{18}\text{O}$ values in comparison to the rest of the assemblage (Fig. 4) indicative of a thermocline dwelling habitat. Enriched $\delta^{18}\text{O}$ values in dentoglobigerinids were also recorded by Pearson et al. (2001) and Sexton et al. (2006). However, this is contrary to studies of Oligocene taxa by Douglas and Savin (1978), van Eijden and Ganssen (1995) and Wade et al. (2007), where dentoglobigerinids registered depleted $\delta^{18}\text{O}$ values and were suggested to occupy a mixed layer habitat. This implies that dentoglobigerinids changed their paleoecology through the Eocene to Miocene and progressively shifted from a thermocline to mixed layer habitat. Further detailed multispecies stable isotope analyses of dentoglobigerinids and subbotinids are needed to establish their paleoecology through the Paleogene.

Pseudohastigerina naguwichiensis register consistent $\delta^{18}\text{O}$ between size fractions (Fig. 4), but considerably lighter $\delta^{13}\text{C}$ values are recorded in the 63–125 μm size fraction. This suggests that the light $\delta^{13}\text{C}$ values in *Pseudohastigerina* are a vital effect related to size. *Turborotalia cocoaensis*, *Dentoglobigerina tripartita* and *Hantkenina nanggulanensis* all record heavier $\delta^{18}\text{O}$ values in the larger size fractions (Fig. 4), suggestive of downward movement through the water column at gametogenesis like some modern species.

Stable isotopic results from the taxa that suffered extinction, *Cribohantkenina inflata*, *Hantkenina nanggulanensis*, *Turborotalia cunialensis*, *T. cerroazulensis*, and *T. cocoaensis*, record relatively negative $\delta^{18}\text{O}$ and positive $\delta^{13}\text{C}$. These

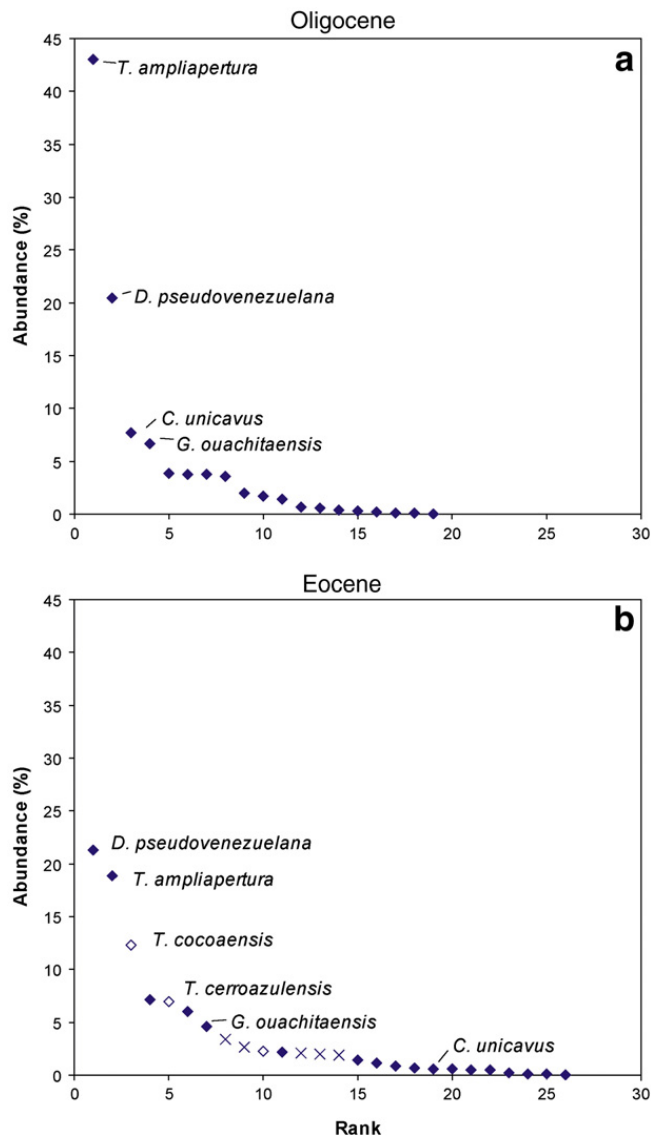


Fig. 6. Rank abundance of Oligocene (a) and Eocene (b) planktonic foraminifera. Species that suffered extinction through the interval have been given different symbols; Hantkeninidae are shown as crosses, *Turborotalia cerroazulensis*, *T. cocoaensis* and *T. cunialensis* as open diamonds.

eliminated groups appear to have occupied a lower mixed layer habitat. However, there appears to be no consistent relationship between position in the water column and extinction because other species with similar isotopic ratios (e.g. *T. ampliapertura*) flourished through the boundary interval.

Several taxa originated or increased in abundance during the earliest Oligocene, including “*Globoquadrina*” *venezuelana* and “*G.*” *tapuriensis*. The increased abundance/origination of these taxa in the earliest Oligocene is significant and suggests that the radiation of Oligocene taxa occurred within the thermocline and not within the surface waters. The lack of origination in surface waters is also noted in nannoplankton through this interval (Aubry, 1992). As the origination of the

typical Oligocene fauna took place in the thermocline, it therefore cannot be the result of vacant niche space in the surface waters.

4.3. Diversity and relative abundance fluctuations

Planktonic foraminifera are present in all samples and show highly variable temporal changes in assemblage composition, relative abundance and preservation (Appendix A). The taxonomic concept of each individual species is beyond the scope of this study but is discussed in detail in Wade and Pearson (in prep.). Planktonic foraminifera assemblages are diverse, the most abundant species in the >250 μm size fraction are *Turborotalia ampliapertura*, *Dentoglobigerina pseudovenezuelana*, *T. cocoaensis* and *Globoturbotalita ouachitaensis*. A faunal change occurred through the E/O transition interval that not only involved extinction, but fundamental alterations of the ecosystem dynamic. We discuss the 1.2 million year record of planktonic foraminifera diversity and the relative abundance fluctuations of each taxon through this critical interval.

Dentoglobigerina galavisi and *D. pseudovenezuelana* are found consistently through the section (Fig. 3). Following the E/O extinction episode there is a radiation in *Dentoglobigerina* (and “*Globoquadrina*”) species. “*Globoquadrina*” cf. *praedehiscentes* and “*G.*” *venezuelana* are absent in the Eocene, but constitute a constant part of the assemblage in the Oligocene. There are sporadic occurrences of “*G.*” *tapuriensis* in the Eocene (Fig. 3) and this species becomes a persistent component of the assemblage from 32 m.

Hantkeninidae are consistently present from the base of the core until 45 m and fluctuate between 2 and 28% of the assemblage (Fig. 5). Subbotinids form a minor component of the assemblages and are never greater than 10%. Subbotinid species consist of *S. eocaena*, *S. hagni*, *S. corpulenta*, *S. gortanii* and two undescribed forms (*Subbotina* sp. 1 and *Subbotina* sp. 2). *Globoturbotalita ouachitaensis* is present throughout the section with sporadic occurrences of *G. martini* and *G. gnaucki*.

Catapsydrax unicavus has intermittent occurrences through the Eocene part of the section, with an increase in abundance in the Oligocene (Fig. 3). Previous stable isotope investigations have suggested that *C. unicavus* occupied a cool, deep (sub-thermocline) habitat (Boersma and Shackleton, 1977; Biolzi, 1983; Poore and Matthews, 1984; Wade et al., 2000; Pearson et al., 2001). The increased abundance of *C. unicavus* from 38 m in the Oligocene suggests possibly an increase in water depth or decrease in temperature.

We plot the relative abundance of select selected species, “*Globoquadrina*” *tapuriensis*, *Dentoglobigerina pseudovenezuelana*, *Turborotalia ampliapertura*, *T. cerroazulensis*, *T. cocoaensis*, *Pseudohastigerina micra* and total Hantkeninidae in Fig. 5. Striking variations in planktonic foraminiferal assemblages occur in the interval between 55 and 45 m and three species show successive abundance peaks through the E/O boundary interval. *T. cerroazulensis* increases sharply in abundance from 5% at 62 m to 57% at 51 m. This peak in abundance occurs immediately before the extinction of this group at 50 m. The sample at 46 m (TDP 14/3) is almost entirely dominated by *T. ampliapertura* (36%) and *D. pseudovenezuelana* (47%). This interval incorporates the extinction of the *T. cerroazulensis*

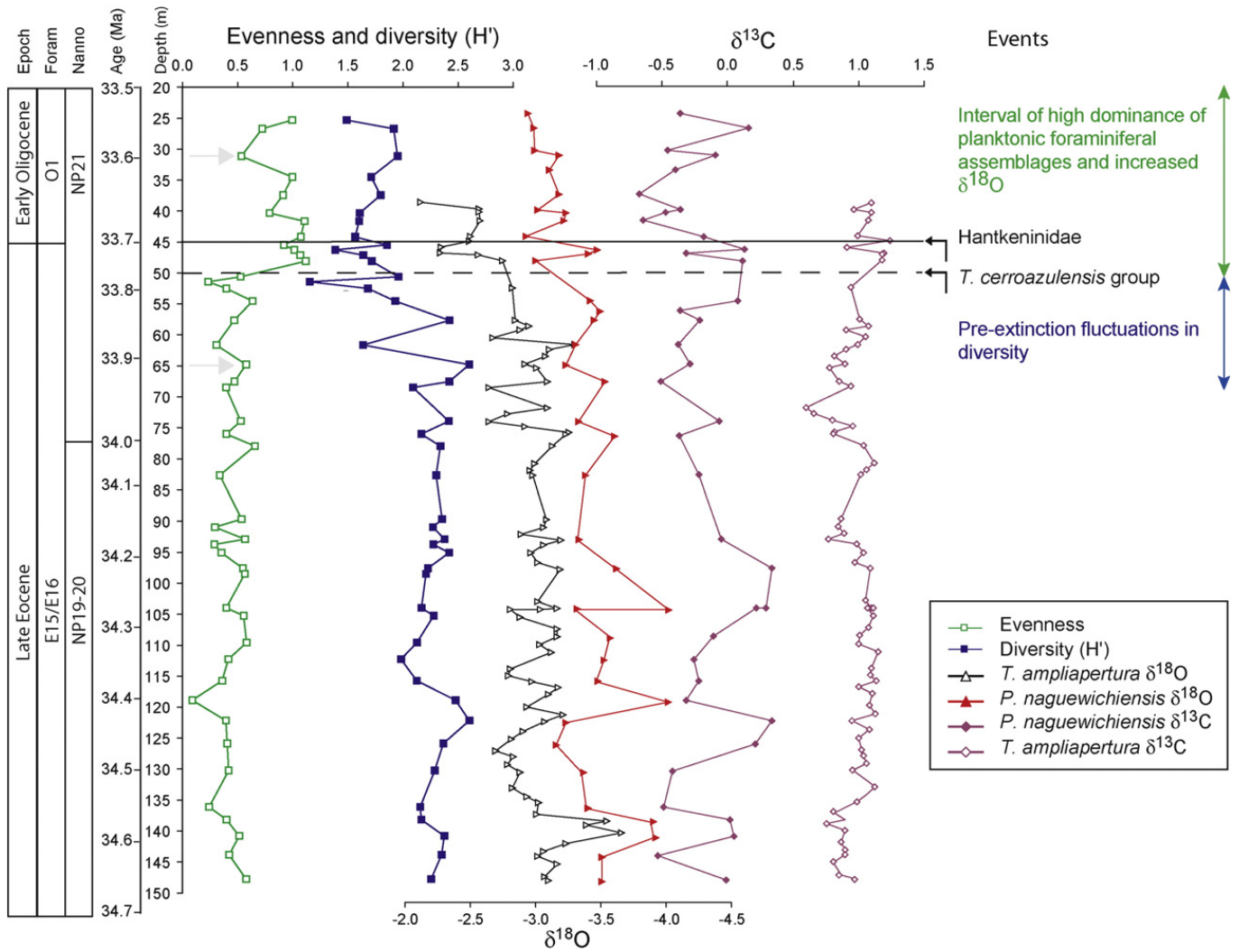


Fig. 7. Planktonic foraminifera evenness, diversity (measured by the Shannon's index, H') and stable isotopes of *Turborotalia ampliapertura* (212–250 μm size fraction) (Pearson et al., 2008) and *Pseudohastigerina naguewichiensis* (63–125 μm size fraction) (this study) through the Eocene/Oligocene boundary. A significant shift in evenness occurs at 50 m associated with the extinction of the *Turborotalia cerroazulensis* group. Preceding the extinction events, fluctuations occur in the diversity of the assemblage. Stable isotopes of *Pseudohastigerina naguewichiensis* are consistently more negative than *Turborotalia ampliapertura* by $\sim 0.5\%$ for $\delta^{18}\text{O}$ and 1.5% for $\delta^{13}\text{C}$. Solid and dashed horizontal lines indicate the highest occurrence of Hantkeninidae and *T. cerroazulensis* groups. Arrows indicate the samples used for multispecies stable isotope analysis shown in Fig. 4.

group directly prior to the extinction of Hantkeninidae, suggesting major fluctuations in environmental conditions. This is followed by a large increase in the relative abundance of *Turborotalia ampliapertura* from 2 to 61% between 51 and 42 m (Fig. 5). *Turborotalia increbescens* shows a decrease in abundance up-section, but continues across the E/O boundary (Fig. 3, Appendix A).

Species dominance patterns varied significantly through the interval. In modern assemblages there is a correlation between environmental stability and diversity. Decreased diversity is associated with unstable and eutrophic environments (Sanders, 1969; Bollmann et al., 1993; Wade and Bown, 2006). At TDP Site 12, the number of species recorded in each sample fluctuates between a minimum of 4 and maximum of 24 species. (Note, results from Sample TDP12/16/2 are biased by severe fragmentation.)

Eocene assemblages from 147 to 80 m (Fig. 7) are stable, diverse and even ($H'=2.0\text{--}2.5$), with diversity consistent with

typical open ocean assemblages. There is a marked reduction in diversity from a mean value of 2.2 ± 0.3 in the Eocene to mean of 1.7 ± 0.2 in the Oligocene. Changes in population structure and fluctuations in diversity occur from 80 m to 45 m with swings in diversity between $H'=2.7$ and 1.0. A decrease in H' diversity occurs at 60 m, caused by fluctuations in abundance in turborotaliids, where *T. ampliapertura* decreases and *T. cerroazulensis* increases in abundance.

Evenness reflects (inversely) the degree of dominance in the assemblage and fluctuates between 0.09 and 0.66 in the Eocene. Through this period there is a major reduction in the heterogeneity and complexity of the assemblage. The most significant change in the evenness of the assemblages occurs at 50 m coinciding with the extinction of the *T. cerroazulensis* group. This shift in evenness reflects the increasing dominance of a few species through this interval. Peak abundances in *Dentoglobigerina pseudovenezuelana* and *D. tripartita* are recorded, with large increases in the

abundance of *Turborotalia ampliapertura* and a decrease in *Globoturborotalia ouachitaensis*. An increase in dominance is typical of stressed environments and periods of disturbance. This reduction in assemblage heterogeneity in the latest Eocene suggests perturbations in marine temperatures or water column structure.

Oligocene samples have increased dominance, primarily caused by the increase in abundance of “*Globoquadrina*” *tapuriensis*, *Catapsydrax unicavus* and *Turborotalia ampliapertura* (Fig. 5). Despite the foraminifera turnover and changes in assemblage heterogeneity, there is little overall change in species richness between the Eocene and Oligocene. At TDP Site 12 the Eocene contains an average of 15 ± 4 species, and the Oligocene 14 ± 2 species. The extinctions are counter-balanced in part by the origination or increased abundance of the “*Globoquadrina*” group (“*G.*” cf. *praedeheiscens*, “*G.*” *venezuelana*, “*G.*” *tapuriensis*), *Subbotina gortanii*, and *Catapsydrax unicavus*. This increase in diversity lags the extinction events by 50 kyr and occurs from 37–33 m.

The Shannon-diversity data suggests that planktonic foraminifera were experiencing biotic stress from 70 m, which equates to approximately 250 kyr before the E/O boundary. From the base of the core (147.5 m) to the extinction of *Turborotalia cerroazulensis* group at 50 m, stable isotopes, diversity and evenness are relatively constant. However, the last 65 kyr of the Eocene are characterized by rapidly changing diversities and a reduced evenness (Fig. 7). The planktonic foraminifera assemblages fail to recover and evenness remains low during the earliest Oligocene and does not return to pre-extinction Eocene levels. The reduced evenness following the E/O boundary suggests that species continued to be stressed and habitats were not restored in the first 200 kyr of the earliest Oligocene. Changes in evenness and diversity have also been recorded in radiolarian assemblages through this interval (Funakawa et al., 2006).

In contrast to the crisis and extinction within the Hantkeninidae, some species increased in abundance around the E/O Boundary. It is common for surviving organisms of adverse conditions and those in a disturbed environment to display a sudden population burst, with low-diversity, uneven assemblages (Urbanek, 1993; Wade and Bown, 2006). *Turborotalia ampliapertura* did not suffer at this interval, unlike the *T. cerroazulensis* group, and the Oligocene assemblages are uneven and dominated by *T. ampliapertura* ($48 \pm 8\%$) and *Dentoglobigerina pseudovenezuelana* ($18 \pm 5\%$) (Figs. 5 and 6). An increased dominance of *T. ampliapertura* is also recorded at multiple sites through the E/O boundary interval (Keller, 1985; Boersma and Premoli Silva, 1986). The results indicate that *T. ampliapertura* and *D. pseudovenezuelana* were r-mode opportunistic taxa responding to an expansion of available vacant niche space or increased productivity.

4.4. The relationship between planktonic foraminiferal diversity and climate

The E/O turnover was not a gradual event, but a coordinated extinction, consisting of two major and rapid pulses, with the extinction of the *Turborotalia cerroazulensis* lineage at 50 m (~ 33.8 Ma) and *Hantkenina*, *Cribohantkenina* and large pseudohastigerinids at 45 m (33.7 Ma). This series of extinctions involved eight species in a relatively short time,

which may suggest a connected casual mechanism. Near synchronous (< 100 kyr) extinctions are also demonstrated by the terminations of the planktonic foraminiferal genera *Morozovelloides* and *Acarinina* in the uppermost Middle Eocene (Wade, 2004) and *Dentoglobigerina altispira*/*Menardella multicamerata* in the Pliocene (Chaisson and Pearson, 1997). The loss of a large number of distinctive Eocene lineages or groups makes this a major turning point in Cenozoic planktonic foraminifera and marks a significant change in the ecology of the surface oceans. Moreover, the E/O boundary is associated with the extinction of several important groups of larger foraminifera (Adams et al., 1986). It has been suggested that the mechanism for the multiple turnover in planktonic foraminifera was climatic cooling (Keller et al., 1992), but the lack of previous detailed multispecies stable isotopic and quantitative analysis of the assemblages has prevented a direct relationship being established.

A well stratified water column is essential for the existence of diverse planktonic foraminiferal assemblages. Minor changes in temperature can have a large impact of tropical/subtropical planktonic foraminifera as their niches are tightly clustered and dependent on water column stratification. We find a fairly constant offset from 34.65 to 33.9 Ma between $\delta^{18}\text{O}$ values of *Pseudohastigerina naguwichiensis* and *Turborotalia ampliapertura* of 0.5‰ (Fig. 7), corresponding to about 2 °C in habitat temperature. The decrease in diversity (H') from ~ 2.3 to ~ 1.7 from the Eocene through to the Oligocene is similar to the increase in oxygen isotope ratios (Fig. 7) suggesting a direct relationship between planktonic foraminifera diversity and climate change. The lowest dominance and highest diversity is recorded in the Eocene prior to the *T. cerroazulensis* group extinction, where *P. naguwichiensis* and *T. ampliapertura* $\delta^{18}\text{O}$ values are on average -3.5 and -3.0% respectively, corresponding to sea surface temperatures of 31 °C. During the earliest Oligocene, dominance is high and $\delta^{18}\text{O}$ values of *P. naguwichiensis* have increased by 0.5‰ to -3.0% reflecting an expansion of global ice volume and decrease in sea surface temperatures.

The decrease in sea surface temperatures/increase in high latitude ice volume are manifested in erratic and complex responses in planktonic foraminiferal assemblages. Our stable isotope data (Fig. 7) show an expansion of the oxygen isotope gradient between *Pseudohastigerina* and *Turborotalia ampliapertura* from ~ 33.9 Ma, suggesting a cooling of the upper thermocline and deep waters. This is associated with the initial change in Shannon diversity suggesting major disruption of the community prior to extinction. It is at the first increase in oxygen isotopes associated with global cooling and the extinction of the *T. cerroazulensis* group (Miller et al., 2008; Pearson et al., 2008) that the assemblages show a marked increase in dominance (Fig. 7), indicating a clear relationship between assemblage change, extinction and global cooling.

The extinction of the Hantkeninidae occurs within a plateau in the oxygen isotope record immediately preceding major glaciation in the earliest Oligocene (Pearson et al., 2008). Through this interval assemblage dominance remains high and the oxygen isotope offset between *Pseudohastigerina* and *Turborotalia ampliapertura* continues to increase (Fig. 7) suggesting a deepening of the thermocline. Changes in upper water mass stratification related to global cooling can

generate a significant modification in community structure (Hallock et al., 1991) and may be in part accountable for the extinctions and shift in foraminiferal assemblages. We postulate that the extinction of the Hantkeninidae was due to changes in the thermal structure of the oceans and associated productivity changes. Global cooling likely caused changes in the stratification of the water column over large areas and reduced diversity and heterogeneity in planktonic foraminiferal assemblages. Our data indicate that the tropics were not a stable environment through this interval and that high latitude increases in ice volume and changes in deep water circulation had a significant impact of tropical environments and their biota.

The adverse environmental conditions associated with the E/O boundary interval are indicated not only by the extinction of 8 species and the dwarfing of *Pseudohastigerina micra*, but also the rise in dominance. The increase in oxygen isotopes (Fig. 7) indicating a reduction in sea surface temperatures and/or expansion of global ice volume gave rise to environmental disruption that exceeded the optimum range of many taxa. Following the E/O boundary extinction interval dominance remains high but the new more highly stratified water column allows for renewed diversification and the increased abundance of important Oligocene taxa such as “*Globoquadrina*” *tapuriensis*, “*G.*” *venezuelana* and deep dwelling *Catapsydrax unicavus*.

5. Conclusions

Our data indicate that the turnover event(s) at or very near the E/O boundary were significant and affected widely distributed taxa. It was a major multiple turnover event and severe ecological crisis in Cenozoic planktonic foraminifera; a total of eight species became extinct, with a distinct dwarfing in *Pseudohastigerina* and dramatic variations in the evenness and dominance of the assemblages. Multi-species stable isotope data indicate that *P. naguewichiensis* and *Globoturborotalita* spp. calcified in the mixed layer, whilst species of the genus *Dentoglobigerina* record enriched $\delta^{18}\text{O}$ consistent with a deeper, thermocline dwelling habitat. We find no clear relationship between the extinctions and depth habitat within the water column. High amplitude changes in the abundance, dominance and diversity of planktonic foraminifera occur, with a distinct change in evenness of the assemblages prior to the E/O boundary coincident with the extinction of the *Turborotalia cerroazulensis* group. We attribute these changes to environmental fluctuations on a global scale that resulted in the extinction of eight species. Following this major turnover, radiation occurred within the “*Globoquadrina*” group and diversity returned to pre-extinction (Eocene) levels, but dominance remained high.

6. Taxonomic appendix

List of species identified in this work, arranged alphabetically by genus.

Catapsydrax unicavus Bolli, Loeblich and Tappan, 1957
Cribohantkenina inflata (Howe, 1928)
Dentoglobigerina galavisi (Bermúdez, 1961)

Dentoglobigerina pseudovenezuelana (Blow and Banner, 1962)

Dentoglobigerina tripartita (Koch, 1926)

Dentoglobigerina sp. 1. We find a distinctive morphology that are possibly a new species. These forms appear to be related to *Dentoglobigerina* but lack a tooth.

“*Globoquadrina*” *euapertura* (Jenkins, 1960)

“*Globoquadrina*” cf. *praedehiscens* (Blow and Banner, 1962).

These forms have a slightly flattened final chamber that may represent the start of a morphological trend that leads to *praedehiscens* later in the Oligocene.

“*Globoquadrina*” *tapuriensis* (Blow and Banner, 1962)

“*Globoquadrina*” *venezuelana* (Hedberg, 1937)

Globoturborotalita gnaucki (Blow and Banner, 1962)

Globoturborotalita martini (Blow and Banner, 1962)

Globoturborotalita ouachitaensis (Howe and Wallace, 1932)

Globoturborotalita cf. *woodi* (Jenkins, 1960). We found four chambered forms with a high arched aperture taxonomically consistent with *G. woodi* but smaller in size. However this occurrence is stratigraphically older than previous studies (e.g., Spezzaferri, 1994)

Hantkenina alabamensis Cushman, 1924

Hantkenina compressa Parr, 1947

Hantkenina nanggulanensis Hartono, 1969

Hantkenina primitiva Cushman and Jarvis, 1929

Pseudohastigerina micra (Cole, 1927)

Pseudohastigerina naguewichiensis (Myatliuk, 1950)

Subbotina corpulenta (Subbotina, 1953)

Subbotina eocaena (Guembel, 1868)

Subbotina gortanii (Borsetti, 1959)

Subbotina hagni (Gohrbandt, 1967)

Subbotina sp. 1. Within the assemblages we find a distinctive subbotinid form with a short polygonal tooth, that may possibly be a new species. We assign this taxon as *Subbotina* sp. 1 pending further investigation (Wade and Pearson, in prep.).

Subbotina sp. 2. This taxon consists of subbotinids with an elongate tooth projecting into the aperture. The wall structure is inconsistent with *Dentoglobigerina globularis* and we refer to this taxon as *Subbotina* sp. 2 pending future studies (Wade and Pearson, in prep.).

Turborotalia ampliapertura (Bolli, 1957)

Turborotalia cerroazulensis (Cole, 1928)

Turborotalia cocoaensis (Cushman, 1928)

Turborotalia cunialensis Toumarkine and Bolli, 1970

Turborotalia increbescens (Bandy, 1949)

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.marmicro.2008.04.002](https://doi.org/10.1016/j.marmicro.2008.04.002).

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