Palaeogeography, Palaeoclimatology, Palaeoecology 503 (2018) 102–111

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Eocene (Bartonian) benthic foraminifera and paleoenvironmental changes in the Western Tethys

L. Rivero-Cuesta*, E. Molina, L. Alegret

Departamento de Ciencias de la Tierra & Instituto Universitario de Ciencias Ambientales IUCA, Universidad de Zaragoza, Zaragoza, Spain

ARTICLE INFO

Keywords:
Tethys Ocean
Middle Eocene
Enhanced current activity
Torre Cardela
Betic cordillera
Carbon isotopes

ABSTRACT

The Eocene was a period of intense climate variability and the response of deep-sea biota is still poorly understood, especially across certain understudied intervals from the middle Eocene. We present new benthic foraminiferal data from a Bartonian marine sequence deposited in the western Tethys Ocean (Torre Cardela section, Spain), and determine the biotic and paleoenvironmental turnover. The assemblages indicate a middle to lower bathyal depth of deposition, and they contain allochthonous taxa (e.g. asterigerinids) that were transported from shallower settings. A Detrended Correspondence Analysis (DCA) performed on the total assemblage differentiates the autochthonous and allochthonous taxa, supporting the idea of different provenience. We suggest that the latter were likely transported downslope by currents. Quantitative analyses of the autochthonous assemblages show a strong dominance of calcareous infaunal taxa, mainly bolivinids, which point to a high flux of organic matter to the seafloor. *Bolivinoides crenulata*, the most common species, is associated with inputs of refractory organic matter and high-energy environments. Five intervals were differentiated based on changes in the relative abundance of taxa. Two intervals (B and D) show the highest percentages of allochthonous taxa and *B. crenulata*. We suggest that enhanced current activity not only transported allochthonous taxa, but also brought in refractory organic matter to the seafloor, which was consumed by opportunistic taxa during these two intervals. We conclude that benthic foraminiferal assemblages at Torre Cardela were strongly controlled by the amount and type of organic matter reaching the seafloor, which were in turn affected by sedimentary and, ultimately, by climatic factors.

1. Introduction

The Eocene was a critical time in the Earth's climate evolution during the Cenozoic. This epoch started with a pronounced warming event at the Paleocene-Eocene boundary superimposed on a global greenhouse climate that persisted during the Eocene (Zachos et al., 2008), and a gradual cooling trend is recorded towards the Eocene-Oligocene transition (Coxall et al., 2005). These long-term climatic trends were punctuated by several hyperthermal events, or transient perturbations of the global C cycle associated with global warming (Thomas and Zachos, 2000; Zachos et al., 2010; Kirtland Turner et al., 2014). Most of these events were short-lived ($<$ 200 kyr), but there are records of a longer-lived event named Middle Eocene Climatic Optimum (MECO; (Bohaty and Zachos, 2003; Bohaty et al., 2009; Sluijs et al., 2013). With an estimated duration of ~500 kyr, the MECO entails an increase in atmospheric pCO_2 (Bijl et al., 2010), shoaling of the carbonate compensation depth (Bohaty et al., 2009; Pälike et al., 2012), and a 4–6 °C increase in surface and deep waters (Bohaty and Zachos, 2003; Bohaty et al., 2009; Edgar et al., 2010) at ~40 Ma. The stable isotopic signature of the MECO suggests that the driver mechanism was different from other Eocene hyperthermal events (Bohaty and Zachos, 2003; Lunt et al., 2011; Sluijs et al., 2013), suggesting that the consequences might also have been different.

Benthic foraminifera are one of the most abundant, diverse and widely distributed groups at the seafloor and they are an excellent tool to reconstruct the paleoenvironmental evolution through periods of climate change (Jorissen et al., 2007). Variations in benthic foraminiferal assemblages mainly indicate changes in water depth, organic matter flux to the seafloor, oxygenation and temperature (e.g., Van der Zwaan et al., 1999; Gooday, 2003; Murray, 2006; Van der Zwaan et al., 1999). Many authors consider that the amount, quality and seasonality of the flux of organic matter from the sea surface are key factors controlling the assemblage composition (Gooday, 1994; Loubere, 1998; Den Dulk et al., 2000). Oxygen also plays an important role, being a limiting resource when the flux of organic matter is high (Jorissen et al., 1995). The benthic foraminiferal assemblage turnover across the MECO

---

* Corresponding author at: Área de Paleontología, Departamento de Ciencias de la Tierra, Universidad de Zaragoza, Pedro Cerbuna 12, 50009 Zaragoza, Spain.
E-mail address: lrivero@unizar.es (L. Rivero-Cuesta).

https://doi.org/10.1016/j.palaeo.2018.05.003
Received 11 January 2018; Received in revised form 24 April 2018; Accepted 1 May 2018

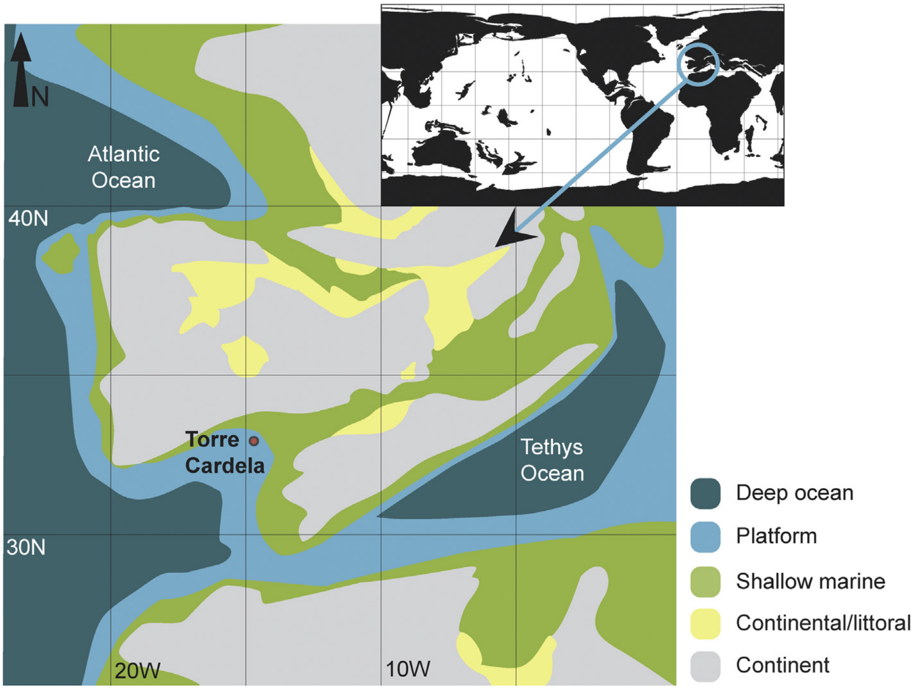


Fig. 1. Paleogeographic reconstruction (40 Ma) showing the location of Torre Cardela section. Modified from ODSN Plate Tectonics Reconstruction Service and Andeweg (2002).

interval has been documented in the Atlantic Ocean (Boscolo Galazzo et al., 2014; Moebius et al., 2015), in the South Indian Ocean (Moebius et al., 2014), in the Equatorial Pacific (Takata et al., 2013) and in the central Tethys Ocean (Boscolo Galazzo et al., 2013). However, further studies in different oceans and latitudes are needed to understand the response of benthic foraminifera to the MECO, to unravel the nature and specifically the aftermath of this event, and to better understand the Eocene climate variability in a global scale.

So far, the Torre Cardela section in the Betic Cordillera (southern Spain, Fig. 1) is the only land-based section from the western Tethys Ocean where the interval immediately following the MECO has been documented (Gonzalvo and Molina, 1996). The stratigraphic continuity, high sedimentation rates and abundance and diversity of foraminiferal tests suggest that this section is appropriate for micropaleontological studies, but the analysis of benthic foraminifera was missing. Here we report on the benthic foraminiferal assemblage changes across the Bartonian in the Torre Cardela section, and determine the paleoenvironmental evolution to evaluate the impact of the variable Eocene climate in this area from the Western Tethys.

2. Geological setting

The Torre Cardela section is located in the southern part of the Iberian Peninsula (coordinates 37° 29′ 02.4″ N, 3° 20′ 43.8″ W). This area lies in the Subbetic realm (External Zones) of the Betic Cordillera, which represents the most occidental edge of the Alpine Orogeny. The studied sedimentary succession belongs to the Cañada Formation, a 500 m-thick sequence of hemipelagic marls with interbedded turbiditic sandstones (Comas, 1978) that was deposited during the Eocene in the western part of the Tethys Ocean (Fig. 1). The Torre Cardela section is a 145 m-thick sequence composed of a rhythmic series of 25 to 35 cm-thick sandy carbonate (calcarenite) layers interbedded with 1 to 20 m-thick grey silty-marly intervals. These levels contain abundant calcareous microfossils that reveal a middle to late Eocene age (Gonzalvo and Molina, 1996). No evidence for bed amalgamation nor any large-scale vertical re-arrangement of beds was observed in the Torre Cardela section, as it did not suffer important tectonic disturbances during the middle Eocene (Andeweg, 2002).

3. Material and methods

3.1. Benthic foraminiferal studies

Quantitative studies of benthic foraminifera were carried out in 25 samples selected from the same set of samples that Gonzalvo and Molina (1996) used to establish the planktonic foraminiferal biozonation at Torre Cardela. All samples were collected from lithologically similar, marly intervals and are evenly distributed throughout the lowermost 100 m of the section (Fig. 2). A standard procedure was followed to extract microfossils: the sediment was disaggregated in water with diluted H_2O_2, washed through a 63 µm sieve and dried at 50 °C. The residue was studied under a binocular microscope, showing that the preservation of benthic foraminiferal tests was variable but in general adequate to detect diagnostic morphological features. Two samples (90 and 92.5) were not suitable for quantitative analysis due to the scarce material available, and they were excluded from the study.

Quantitative analyses of benthic foraminifera were based on representative splits of approximately 300 specimens of the $>$ 63 µm fraction, obtained with a modified Otto micro-splitter. The taxonomic identification of the assemblages follows Loeblich Jr. and Tappan (1987) for genera identification except for uniserial forms, which follows Hayward et al. (2012). Identification to species level was possible in many cases, mainly following Tjalsma and Lohmann (1983), Grünig (1985), Van Morkhoven et al. (1986), Bolli et al. (1994), Alegret and Thomas (2001), Katz et al. (2003), Holbourn et al. (2013), Ortiz and Thomas (2006), Alegret et al. (2008), Fenero et al. (2012) and Arreguín-Rodríguez et al. (2018). Original descriptions of species were checked in the Ellis & Messina Online Catalogue of Foraminifera, and holotype images were obtained from the Smithsonian Paleobiology Collections when available for comparison with our specimens.

The data matrix produced was standardized by converting count data into relative abundance (percentages) for each sample (Supplementary Data 1). In addition, many species were grouped into genera and morphogroups. A total number of 117 taxa (114 calcareous

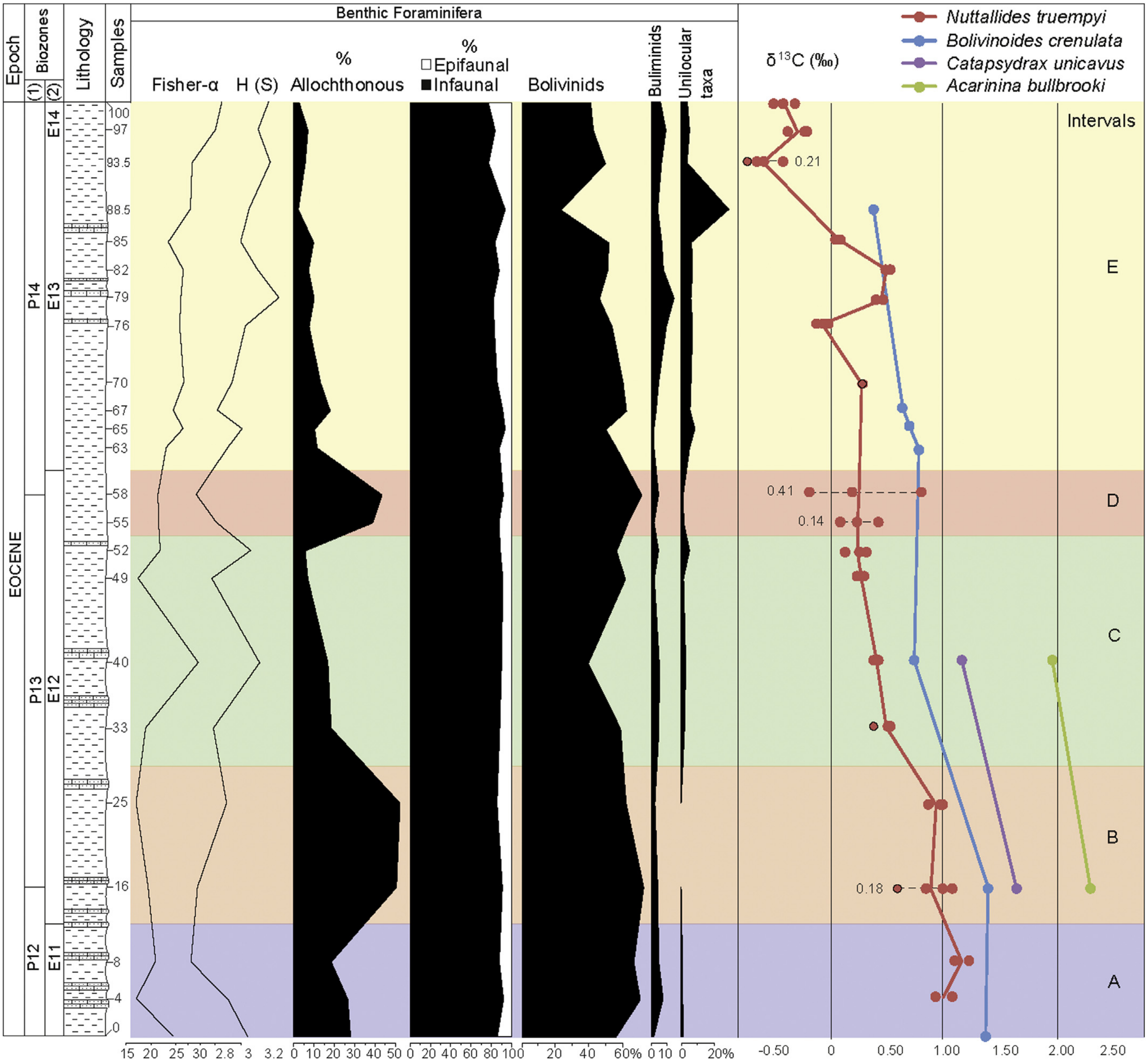
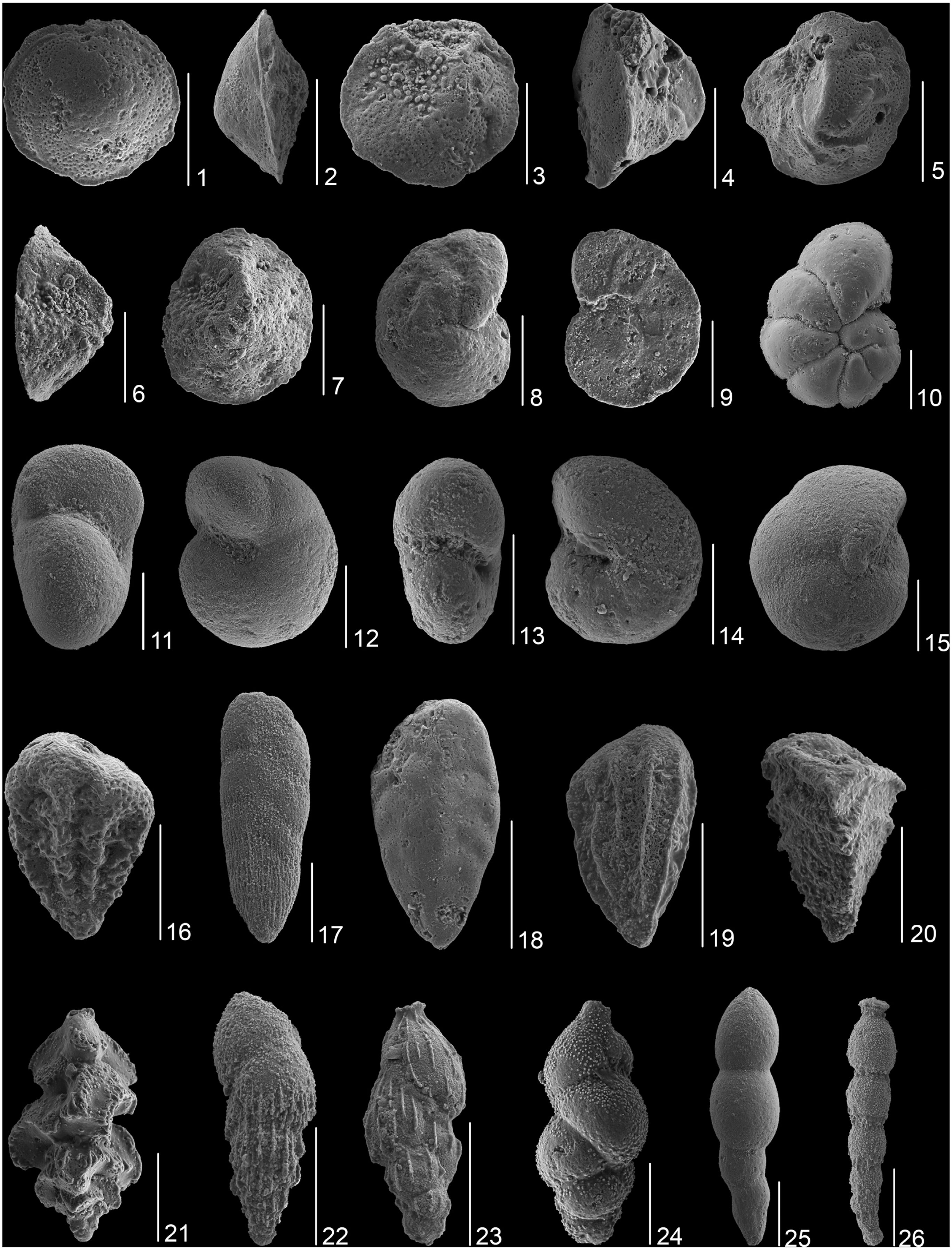


Fig. 2. Benthic foraminiferal indices (based on the autochthonous assemblages only): Fisher-α diversity index, Shannon-Weaver H(S) heterogeneity index, and relative abundance of infaunal morphogroups at the Torre Cardela section. Percentages of significant benthic foraminiferal groups, and species-specific carbon stable isotope data. Dashed lines in the δ^{13}C data represent standard deviation; red circles with a black ring represent "rusty" specimens (see text). Planktonic foraminiferal biozones (1) Gonzalvo and Molina (1996) and (2) this work. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and 3 agglutinated) were identified, and the relevant and best-preserved specimens are illustrated in Fig. 3. The images were obtained by SEM (scanning electron microscope) imaging at the University of Zaragoza. Due to the high number of species identified, Fig. 4 only includes species whose relative abundance is higher than 1% in at least one sample.

Morphogroup analysis was performed, and the most probable microhabitat preferences and environmental parameters (bottom water oxygen and organic flux levels) were inferred following Corliss (1985), Jones and Charnock (1985), Corliss and Chen (1988), Murray (2006) and Jorissen et al. (2007). The Fisher-α and H(S) Shannon–Weaver indices were calculated as proxies for diversity and heterogeneity of the assemblages, respectively (Murray, 2006). Paleobathymetry assignments were based on the occurrence and relative abundances of depth-dependent species. This is based on their upper-depth limits (Van Morkhoven et al., 1986; Alegret and Thomas, 2001; Ortiz and Thomas, 2006; Fenero et al., 2012) and on comparisons with benthic foraminiferal assemblages whose paleodepths can be derived independently by back-tracking (Grünig and Herb, 1980; Ingle Jr., 1980; Tjalsma and Lohmann, 1983; Thomas, 1990; Speijer, 1994; Bignot, 1998; Katz et al., 2003).

A hierarchical cluster analysis was performed with the PAST package (Hammer et al., 2001) using the Pearson similarity index and the unweighted pair-group average (UPGMA) algorithm. R-mode and Q-mode analyses were performed on a data matrix including all the studied samples and selected species that showed relative abundance > 2% in at least one sample. Detrended Correspondence Analysis (DCA) was carried out in order to further analyse the results derived



(caption on next page)

Fig. 3. Scanning electron micrographs of selected benthic foraminiferal species at Torre Cardela. All scale-bars represent 100 μm. 1–3, *Asterigerinata* sp. A (0 m); 4, 5, *Asterigerina* sp. (16 m); 6, 7, *Asterigerina* sp. B (0 m); 8, 9, *Cibicides laurisae* (0 m); 10, *Lobatula lobatula* (16 m); 11, 12, *Gyroidinoides* sp. (33 m); 13, 14, *Anomalinoides capitatus* (0 m); 15, *Pullenia* sp. (33 m); 16, *Bolivinoides crenulata* (0 m); 17, *Bolivina nobilis-gracilis* (52 m); 18, *Brizalina* sp. (16 m); 19, *Bulimina alazanensis* (4 m); 20, *Reusella terquemi* (0 m); 21, *Angulogerina muralis* (0 m); 22, *Fursenkoina* sp. A (52 m); 23, *Uvigerina longa* (65 m); 24, *Uvigerina elongata* (0 m); 25, *Nodosarella* sp. (49 m); 26, *Siphonodosaria* sp. (49 m).

from clustering, as they contribute to investigate the relationship between benthic foraminifera and environmental variables (Hammer and Harper, 2005).

3.2. Stable isotopes analyses

Species-specific C and O stable isotope analyses were performed at the Leibniz Laboratory for Radiometric Dating and Stable Isotope Research (Kiel University, Germany) using a Kiel IV carbonate preparation device connected to a MAT 253 mass spectrometer from ThermoScientific. During preparation the carbonates were reacted with 100% phosphoric acid (H_3PO_4) under vacuum at 75 °C, and the evolved carbon dioxide was analysed eight times for each individual sample. All values are reported in the Vienna Pee Dee Bee notation (VPDB) relative to NBS19. Precision of all different laboratory internal and international standards (NBS19 and IAEA-603) is $< 0.05‰$ for $\delta^{13}C$ and $< 0.09‰$ for $\delta^{18}O$ values.

Twelve specimens of *Nuttallides truempyi* were extracted from each sample where specimens were sufficiently abundant, and used for triplicate isotope analyses (except for samples 4 and 8). The analysed material is moderately preserved, less than half of the specimens show broken edges and chambers, and they are infilled with very fine-grained material. Sutures are visible, and the central boss is made of clear shell material. Size (diameter) ranges from 200 μm (juvenile specimens mostly) up to 500 μm. The, largest, best-preserved and most complete specimens were selected for isotope analyses. *Bolivinoides crenulata* (50 specimens) were extracted from samples that did not yield enough specimens of *N. truempyi* (samples 0, 63, 65, 67 and 88.5). Two additional samples (16 and 40) were selected as control samples, where both benthic (*N. truempyi* and *B. crenulata*) and planktonic species (*Acarinina bullbrooki* and *Catapsydrax unicavus*) were analysed.

3.3. Biostratigraphy and sedimentation rates

The biozones recognised at the Torre Cardela section by Gonzalvo and Molina (1996) include the upper part of planktonic foraminiferal Zone P12 and Zones P13 and P14 (Berggren and Miller, 1988), mostly Bartonian in age. In order to update this biozonation to a more recent one (Berggren and Pearson, 2005), as shown in Fig. 2, we revised the slide collection used by Gonzalvo and Molina (1996). Most of the biostratigraphic concepts used by these authors are in line with more recent ones (Berggren and Pearson, 2005), however there are a few exceptions. The Last Occurrence (LO) of *Morozovelloides crassatus* occurs within E12 Zone, instead of reaching the top of Zone E13. This species marks the transition between Zones E13/E14 (Berggren and Pearson, 2005). We used the LO of *M. crassatus* as the top of Zone E13, as it has been suggested to coincide with the same horizon as the extinction of the *Morozovelloides* lineage (Wade, 2004). This decision was also based on the First Occurrence (FO) of *Globigerinatheka semiinvoluta*, which is close to, but younger than, the LO of *M. spinulosa* (Wade, 2004).

Jovane et al. (2010) proposed to place the Lutetian/Bartonian boundary at the top of Chron C19r. Due to the lack of magnetostratigraphic data at Torre Cardela, and since the original section has been covered by road works, we analysed the planktonic foraminiferal biostratigraphy data to determine the proximity to the L/B boundary. The FO of *Turborotalia pomeroli* is present at Torre Cardela, but associated younger bioevents (e.g., the FO of *T. cerroazulensis*; Jovane et al., 2010) have not been identified in this section. On the other hand, the LO of *Acarinina bullbrooki* should be located above the L/B boundary and below the FO of *Orbulina beckmanni* (marker of Zone E12). Surprisingly, this species has been identified within Zone E13 (85 m at Torre Cardela), well above Zone E11 where its LO has been reported from other sites of similar latitudes (Jovane et al., 2010; Wade et al., 2011). Given the discrepancies about the aforementioned planktonic foraminiferal events, we cannot be certain that the lowermost part of the Torre Cardela section includes the L/B boundary. The extinction of large muricate planktonic foraminifera (large *Acarinina* and *Morozovelloides*) has been defined as the marker of the middle - late Eocene transition (Agnini et al., 2011). These genera disappear in the uppermost part of the section (95 m) at Torre Cardela, suggesting the location of the Middle–Late Eocene transition.

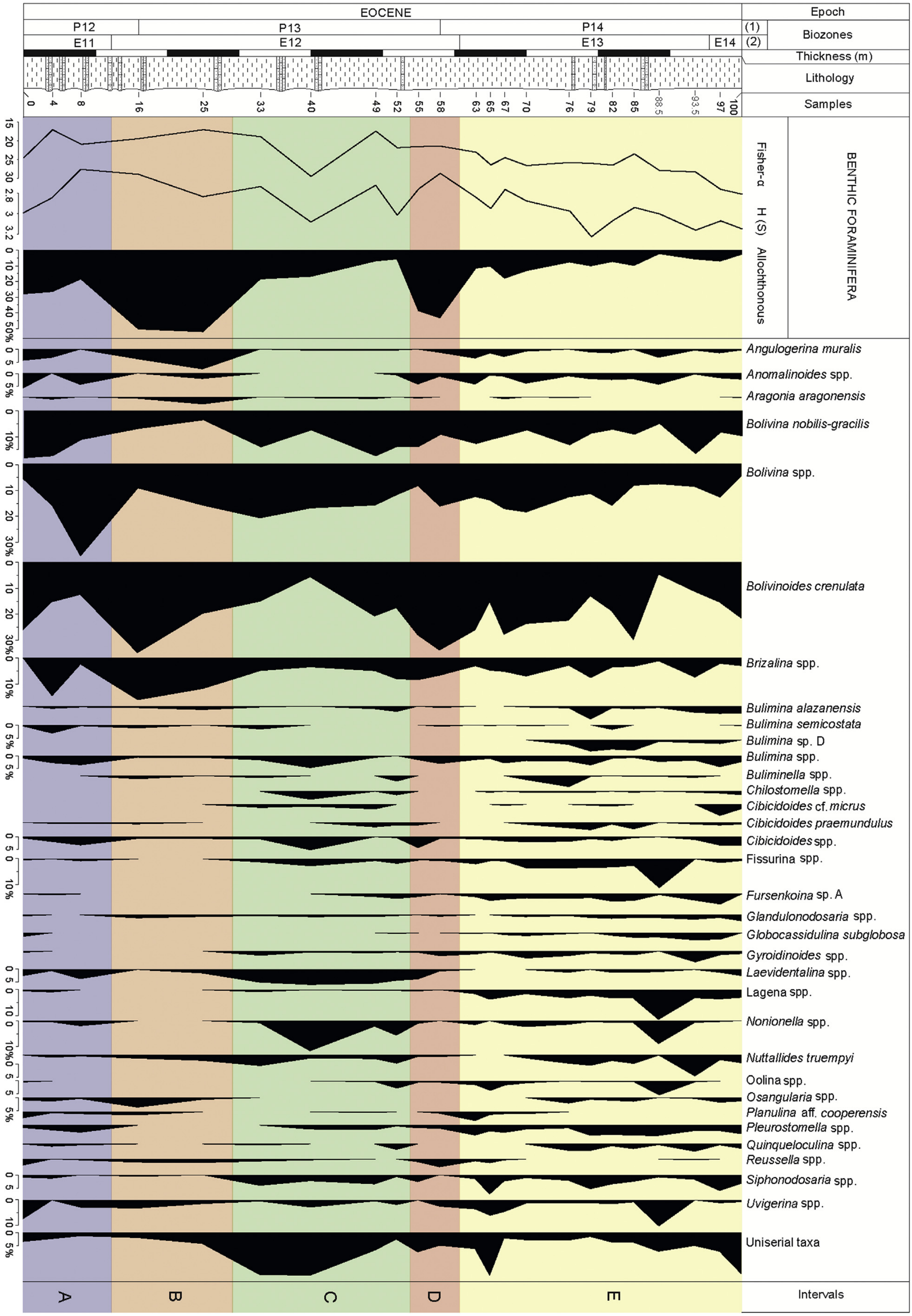
Sedimentation rates across the studied interval have been estimated based on the revised biozones at Torre Cardela. According to the duration of the planktonic foraminiferal biozones (calibrated astronomically by Pälike et al., 2006 and Wade et al., 2011), sedimentation rates are 8.4 cm/kyr within Zone E12, and 1.95 cm/kyr within Zone E13. These are the only biozones that appear to be complete at Torre Cardela. Caution should be taken, however, as discrepancies were observed among planktonic foraminiferal events, but these results point to a much higher sedimentation rate in the lower half of the section.

4. Results

4.1. Paleobathymetry: autochthonous versus allochthonous taxa

Benthic foraminiferal assemblages contain common bathyal and middle bathyal to abyssal species (*Bulimina alazanensis*, *Bulimina semicostata*, *Cibicidoides eocaenus*, *Cibicidoides micrus*, *Cibicidoides praemundulus*, *Globocassidulina subglobosa*, *Oridorsalis umbonatus*; Tjalsma and Lohmann, 1983; Van Morkhoven et al., 1986; Bignot, 1998; Thomas, 1990; Alegret and Thomas, 2001; Katz et al., 2003; Ortiz and Thomas, 2006; Fenero et al., 2013; Holbourn et al., 2013). Other species that have been reported from lower bathyal Paleogene biofacies (*Anomalinoides pompilioides*, *Nuttallides truempyi*, *Pleurostomella paleocenica*; Ingle Jr., 1980) are also present. *Nuttallides truempyi* and *Bulimina semicostata* have an upper depth limit (UDL) of 600 m (Van Morkhoven et al., 1986), although the former has been recorded in shallower waters in the southern Tethys during the Paleocene (Speijer and Schmitz, 1998). *Aragonia aragonensis* has been recorded from middle bathyal environments (600–1000 m paleodepth) of Eocene age (Grünig and Herb, 1980; Bignot, 1998) and potentially at shallower depths (Deprez et al., 2015), although it ranges from bathyal to abyssal depths (Van Morkhoven et al., 1986; Alegret et al., 2009; Arreguín-Rodríguez et al., 2018).

Due to the wide paleobathymetric ranges of many of these species, we compared the composition of the assemblages and relative abundance of taxa at Torre Cardela with other sections deposited in the same basin during the middle Eocene to early Oligocene, namely the Fuente Caldera section (lower bathyal, planktonic biozones P15-P17; Molina et al., 2006) and the Zarabanda section (1000 m, middle-lower bathyal; planktonic biozones O5-O7; Fenero et al., 2013). The similarity of these assemblages with ours (including abundant *Bolivinoides crenulata*), together with the paleodepth preferences of the identified species, suggests a similar middle to lower bathyal depth of deposition at Torre Cardela. Benthic foraminiferal assemblages across the MECO interval in the middle bathyal (600–1000 m) Alano di Piave section (north-eastern Italy, central-western Tethys; Agnini et al., 2011) also contain common



(caption on next page)

Fig. 4. Benthic foraminiferal diversity indices and relative abundance of significant benthic foraminiferal taxa at Torre Cardela (based on autochthonous assemblages only). Planktonic foraminiferal biozones (1) Gonzalvo and Molina (1996) and (2) this work.

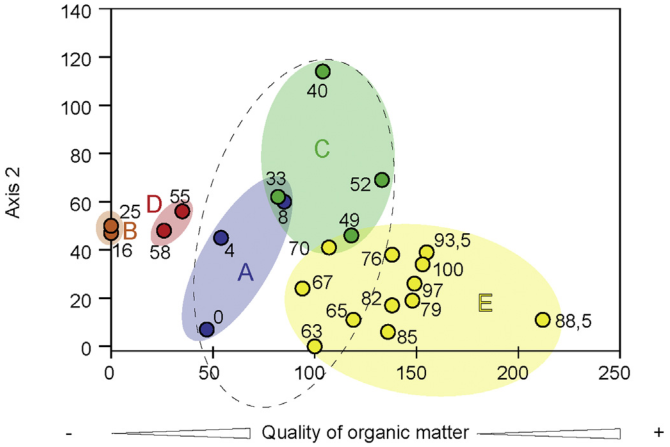


Fig. 5. Q-mode DCA analysis of samples from Torre Cardela. Coloured ellipses group samples from the same intervals, as interpreted from relative abundance of benthic foraminifera. Low values along axis 1 (intervals B and D) indicate low quality of organic matter, high values (samples from interval E) are linked to a high quality, and the dashed ellipse includes samples with intermediate values.

infaunal, bi- and triserial taxa (including *Bolivinoides crenulata*) (Boscolo Galazzo et al., 2013), showing close similarities with the assemblages at Torre Cardela.

Neritic taxa such as *Cibicides laurisae*, *Lobatula lobatula* and several species of *Asterigerina* and *Asterigerinata* (Fenero et al., 2012, 2013) are also present throughout the studied section. This group, which strongly fluctuates between $< 5\%$ and 50% of the total assemblages, was interpreted by Fenero et al. (2012, 2013) as allochthonous taxa that were transported from the shelf towards deeper parts of the slope. DCA analysis on the total assemblage dataset differentiates these shallow-water taxa (low values on Axis 1; Suppl. Fig. 1) from the lower-middle bathyal autochthonous assemblages, supporting this hypothesis.

In order to elucidate the environmental conditions that prevailed at the seafloor in this western Tethys location, we describe the allochthonous and autochthonous assemblages separately. Total assemblage refers to autochthonous plus allochthonous assemblages; assemblage refers to autochthonous taxa only (total assemblage minus the allochthonous taxa).

4.2. Autochthonous benthic foraminifera

Autochthonous assemblages are strongly dominated by calcareous taxa, and agglutinated species make up $< 2\%$ of the assemblages. Infaunal morphogroups dominate over epifaunal ones, making up to 75% of the assemblages.

Assemblages are generally diverse, with 40 to 80 species recognised per sample. Diversity slightly increases upwards in the section (Fig. 2), reaching its maximum values in the uppermost two samples. Heterogeneity shows a similar upward increasing trend, reaching its lowest value in sample 8 and the maximum value in sample 79.

Among calcareous taxa, assemblages are strongly dominated by bolivinids, including several species of the genera *Bolivina*, *Bolivinoides* and *Brizalina*. This group is more dominant in the lower half of the section (0–60 m), where it constitutes $> 50\%$ of the assemblages (except for sample 40). *Bolivinoides crenulata* is the species with the highest relative abundance, ranging from 8.86% to 34.16%. Other common calcareous taxa include *Anomalinoides*, *Fursenkoina*, *Gyroidinoides*, *Nonionella* and *Pleurostomella*, as well as uniserial (e.g. *Siphonodosaria*) and unilocular morphogroups. Uniserial taxa were difficult to determine at the genus level due to high fragmentation of their tests. The unilocular group includes *Fissurina*, *Lagena* and *Oolina*, and its relative abundance increases towards the upper part of the section, showing a pronounced peak in sample 88.5.

Based on the analysis of the autochthonous assemblages and on the relative contribution of allochthonous taxa, five intervals (A to E, Fig. 4) were recognised across the studied section:

Interval A (0–12 m): assemblages are strongly dominated by bolivinids (mainly *Bolivina* spp., *Bolivina nobilis-gracilis* and *Bolivinoides crenulata*). Buliminids, *Pleurostomella* spp. and *Uvigerina* spp. are also common. Diversity of the assemblages slightly decreases upwards.

Interval B (12–29 m): this interval contains the highest percentage of allochthonous taxa (~50% of the total assemblage) across the studied section, and the autochthonous assemblage is characterised by the highest relative abundance of bolivinids (mainly *Bolivinoides crenulata*) and the common occurrence of *Angulogerina muralis* and *Osangularia* spp. Fisher-α diversity index reaches the minimum values of the studied section.

Interval C (29–53.5 m): the percentage of bolivinids decreases, mainly due to the decrease in relative abundance of *Bolivinoides crenulata*, while the percentage of uniserial forms (particularly laevidentalinids) increases. The increase in relative abundance of *Nonionella* spp. and *Cibicidoides* spp. coincides with an increase in diversity in sample 40.

Interval D (53.5–60.5 m): it is characterised by an increase in the abundance of allochthonous taxa, and autochthonous assemblages are strongly dominated by *Bolivinoides crenulata*, as in interval B. Species of *Anomalinoides* and *Cibicidoides* are common.

Interval E (60.5–100 m): the dominance of bolivinids gradually decreases, but this group still makes up to 40% of the autochthonous assemblages. Uniseral and unilocular taxa are common, and the percentage of buliminids and various *Pleurostomella* species increases towards the upper part of the section. This interval contains one sample (88.5) with a higher relative abundance of unilocular taxa, *Nonionella* spp. and *Uvigerina* spp., and lowest percentage of bolivinids.

The five intervals are differentiated in the Q-mode DCA plot (Fig. 5), where samples with a higher contribution of allochthonous taxa (intervals B and D) show the lowest values along Axis 1, intervals immediately below these (intervals A and C) show higher values along this axis, and samples from the upper half of the studied section (interval E) show the highest values along the Axis 1.

4.3. Stable isotope analysis

Results from species-specific $\delta^{13}C$ analyses (Fig. 2) on *N. truempyi* show a decreasing trend of > 1.50‰ from the lower part of the section towards the upper part. In addition to standard analyses on moderately preserved tests, some poorly preserved, "rusty" specimens of *N. truempyi* covered with an orange-yellow patina were analysed in four samples to assess the preservation bias. Remarkably, these rusty specimens did not show significantly different values than the better-preserved specimens, especially in sample 76, where the "rusty" specimens yielded the same result as regular specimens. Standard deviation, calculated from triplicate analyses performed on every sample (except samples 4 and 8), is particularly high in sample 58 (interval D), possibly due to the presence of reworked specimens from adjacent, shallower areas.

The $\delta^{13}C$ and $\delta^{18}O$ values do not show a strong correlation (see Suppl. Fig. 5), and correlation value is low ($p = 0.064$). Control samples for which planktonic and benthic taxa were analysed (samples 16 and 40) show differences depending on the ecology of the species: *Acarinina bullbrooki* (encrusted mixed-layer symbiotic) yields higher $\delta^{13}C$ values than deep-dweller *Catapsydrax unicavus*. Benthic species show lower δ^{13}C values than both planktonic species. These data suggest that general δ^{13}C trends are preserved, even though δ^{13}C absolute values may not be primary signals.

4.4. Paleoenvironmental reconstruction and interpretation

Benthic foraminiferal assemblages contain species with different paleobathymetric ranges, and reveal that allochthonous taxa are remarkably abundant at the Torre Cardela section. The autochthonous assemblage indicates a middle to lower bathyal depth of deposition, while the allochthonous assemblage contains species typical from neritic environments. Some of these allochthonous species are believed to have had epiphytic lifestyles (Alegret et al., 2008; Fenero et al., 2013), living attached to animals, plants or hard substrates that were likely transported as floating material into pelagic environments, as reported by Fenero et al. (2012). The significant changes in relative abundance of this group suggest that transport of shallower material towards deeper parts of the basin was more intense in intervals B and D, possibly related to enhanced current activity, as suggested in the nearby Zarabanda and Fuente Caldera sections. The analysis of benthic foraminifera in the Fuente Caldera section showed abundant reworked neritic taxa and epiphytic species during the early Oligocene (Alegret et al., 2008; Fenero et al., 2012). Similarly, the identification of shallow-water benthic foraminifera in the bathyal Zarabanda section was attributed to transport by turbidity currents after erosion of a shallow platform, possibly due to the destabilization of the outer ramp sediment (Fenero et al., 2013).

The second most remarkable feature of the benthic assemblages at Torre Cardela refers to the strong dominance by bolivinids. This group is considered as indicative of a high input of organic matter to the seafloor (e.g. (Gooday, 1994; Bernhard and Sen Gupta, 1999; Murray, 2006). *Bolivinoides crenulata* is the most dominant species within the bolivinids group and the autochthonous assemblage. This species has been suggested to proliferate during periods of enhanced input of low-quality, refractory organic matter to the seafloor (Agnini et al., 2009; Ortiz et al., 2011; D'haenens et al., 2012; Boscolo Galazzo et al., 2013), and is considered as an opportunistic species related to high-energy environments. The relative abundance of *B. crenulata* shows a positive correlation with the percentage of allochthonous taxa, especially in intervals B and D, and may indicate increased current activity and downslope transport of low-quality organic matter together with shallow-water benthic foraminifera. We argue that *B. crenulata* was able to feed on this type of organic matter that was not easily digested by other taxa, thus dominating the assemblages during these intervals. Decreasing abundance of shallow-water and opportunistic taxa in the same intervals could be explained by reduced supply of refractory organic matter and less downslope transport, likely caused by weakened current activity.

Abundant bolivinids and other bi-triserial taxa related to a high nutrient supply have also been reported from other Eocene Tethyan sections (Alegret et al., 2008; Molina et al., 2006; Agnini et al., 2009; Boscolo Galazzo et al., 2013; Fenero et al., 2013). Although high food availability is commonly associated with decreasing oxygen levels (TROX model; Jorissen et al., 1995), we did not find any evidence for anoxic conditions such as laminated sediments or dark, organic levels. In addition, bolivinids have also been reported from environments with well-oxygenated bottom waters (Fontanier et al., 2005; Jorissen et al., 2007). We suggest that benthic foraminifera at Torre Cardela were more strongly controlled by the amount and type of organic matter rather than by oxygenation at the seafloor.

The high dominance of bolivinids in interval A may indicate a high nutrient flux to the seafloor. Intervals B and D show lower diversity than adjacent intervals and a sharp increase in the percentage of allochthonous taxa and *Bolivinoides crenulata*. This is likely related to enhanced current activity and downslope transport of shallow-water taxa and sediments to the bathyal realm. The decrease in the percentage of allochthonous taxa in intervals C and E suggests less intense current activity. The percentage of bolivinids decreased as well, but the overall abundance of infaunal morphogroups did not significantly change because the percentage of uniserial taxa and other infaunal morphotypes such as *Nonionella* spp. increased, possibly indicating a change in the type (quality) of food rather than in its amount.

Sample 88.5 contains an anomalous assemblage with higher relative abundance of unilocular morphologies (Fig. 2 and Suppl. Fig. 2) that might indicate well-oxygenated, oligotrophic conditions possibly related to changes in deep-water currents, as documented in the upper part of Zone E13 in the Alano section (Boscolo Galazzo et al., 2013). The lack of a higher-resolution sampling across this interval however, precludes further investigation to test this hypothesis at Torre Cardela.

5. Discussion

Assemblages from Torre Cardela bear similarities with those reported from the Cap Breton canyon (Bay of Biscay), where the abundance of shallow infaunal bolivinids and other taxa that are able to feed on low-quality organic matter have been associated with the dynamics of sedimentary processes (Hess and Jorissen, 2009). Despite the high nutrient flux, no dysoxic conditions were reported at the seafloor in the canyon, possibly because refractory organic matter may have been fully consumed by the benthic population before it could degrade. Similarly, there is no evidence for oxygen deficiency of sea-bottom waters at Torre Cardela, and we hypothesize that sedimentary processes may have strongly influenced benthic foraminifera, controlling the flux and quality of organic matter input to the seafloor.

Intervals B and D at Torre Cardela include the base and the top of planktonic foraminiferal biozone E12. This biozone is defined by the total range of the species *Orbulinoides beckmanii* (Berggren and Pearson, 2005), which is considered as a marker for the MECO (Edgar et al., 2010). In the Tethys Ocean, the E12 biozone has been well identified in the Alano section (Spofforth et al., 2010), where two positive δ^{13}C excursions have been recorded right after the MECO peak, in coincidence with two organic-rich events (ORG1 and ORG 2; Spofforth et al., 2010). Benthic assemblages across these events (Boscolo Galazzo et al., 2013) show similar characteristics to assemblages B and D at Torre Cardela (dominance of infaunal morphogroups, especially bolivinids). The Alano section was deposited in a very similar (middle bathyal, high-productivity) environment, and stress-tolerant taxa (bi- and triserial taxa; e.g. *Bolivina* spp., *B. crenulata*, *Uvigerina* spp.) dominated across intervals ORG1 and ORG2, as observed in intervals B and D at Torre Cardela. In Alano, deposition of both organic-rich events seems to have been controlled by variations in surface productivity, where the increase in organic carbon flux led to low oxygen conditions at the seafloor, followed by a rapid recovery to well-oxygenated waters (Boscolo Galazzo et al., 2013). The lack of evidence for decreased oxygenation across intervals B and D at Torre Cardela may be related to differences in the depositional setting, and local sedimentary disturbances seem to have influenced the assemblages at this site.

Despite the different parameters shaping benthic foraminiferal assemblages, one might speculate that increased weathering resulting from an intensification of the hydrological cycle during Eocene hyperthermal events (Nicolo et al., 2007) may have led to more runoff, higher sedimentation rates (as estimated for the lower part of Torre Cardela section, intervals B to D) and enhanced transport of nutrients and sediments to the basin, thus increasing productivity. In addition, high burial rates of organic carbon in marine shelves may have led to decreased atmospheric pCO_2, consistent with global cooling following MECO (Bohaty et al., 2009; Spofforth et al., 2010; Sluijs et al., 2013). We acknowledge that the organic events at Alano section occur after the peak climatic conditions of the MECO (Spofforth et al., 2010), which we have not been able to clearly identify at Torre Cardela. A higher-resolution age model would be of great interest to confirm this correlation, but further studies are not feasible at present because the original section has been covered by road works. With the available data, we conclude that benthic foraminiferal assemblages at Torre Cardela were strongly controlled by the amount and type of organic matter reaching the seafloor, which are in turn affected by sedimentary and, ultimately, climatic factors.

6. Conclusions

1. The analysis of benthic foraminifera from the Torre Cardela section provides the first insights into the effects of middle Eocene climate variations on the deep-water marine ecosystems of the western Tethys Ocean. The studied interval encompasses planktonic foraminiferal biozones E11 to E14 (including the post-MECO interval) and corresponds to the Bartonian Stage.
2. Five intervals were differentiated based on changes in the relative abundance of benthic foraminiferal taxa. Two of them contain higher percentages of allochthonous taxa, and indicate enhanced downslope transport of sediment and shallow-water taxa to middle-lower bathyal settings.
3. The abundance of bolivinids points to a high nutrient flux, and the dominance of *Bolivinoides crenulata* is possibly linked to a higher input of low-quality, refractory organic matter in a high-energy, well-oxygenated environment, especially in the same intervals (B and D) where allochthonous taxa are most abundant.
4. The amount and type of food reaching the seafloor, possibly controlled by current activity, are here interpreted as the main parameters controlling benthic foraminiferal assemblages at Torre Cardela.

Declarations of interest

None.

Acknowledgments

The authors thank S. D'haenens, D. Peryt and M. Boukhary for their constructive reviews. This work was supported by the Spanish Ministry of Economy and Competitiveness and FEDER funds [project numbers CGL 2014-58794 and CGL2017-84693-R, and predoctoral grant number BES-2015-075140]; and Aragón Government with European Social Fund [Consolidated Research Group E05]. Authors would like to acknowledge the use of Servicio General de Apoyo a la Investigación-SAI, Universidad de Zaragoza, and Cristina Gallego for the SEM imaging. We are grateful to Nils Andersen (Kiel University) for isotope analyses. This research is part of the PhD thesis of the first author.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2018.05.003.

References

Agnini, C., Macrì, P., Backman, J., Brinkhuis, H., Fornaciari, E., Giusberti, L., Luciani, V., Rio, D., Sluijs, A., Speranza, F., 2009. An early Eocene carbon cycle perturbation at ~52.5 Ma in the Southern Alps: chronology and biotic response. Paleoceanography 24 (PA2209).

Agnini, C., Fornaciari, E., Giusberti, L., Grandesso, P., Lanci, L., Luciani, V., Muttoni, G., Pälike, H., Rio, D., Spofforth, D.J., 2011. Integrated biomagnetostratigraphy of the Alano section (NE Italy): a proposal for defining the middle-late Eocene boundary. Geol. Soc. Am. Bull. 123, 841–872.

Alegret, L., Thomas, E., 2001. Upper Cretaceous and lower Paleogene benthic foraminifera from northeastern Mexico. Micropaleontology 47, 269–316.

Alegret, L., Cruz, L.E., Fenero, R., Molina, E., Ortiz, S., Thomas, E., 2008. Effects of the Oligocene climatic events on the foraminiferal record from Fuente Caldera section (Spain, western Tethys). Palaeogeogr. Palaeoclimatol. Palaeoecol. 269, 94–102.

Alegret, L., Ortiz, S., Molina, E., 2009. Extinction and recovery of benthic foraminifera across the Paleocene-Eocene thermal maximum at the Alamedilla section (southern Spain). Palaeogeogr. Palaeoclimatol. Palaeoecol. 279, 186–200.

Andeweg, B., 2002. Cenozoic Tectonic Evolution of the Iberian Peninsula: Effects and Causes of Changing Stress Fields. VU University of Amsterdam.

Arreguín-Rodríguez, G.J., Thomas, E., D'haenens, S., Speijer, R.P., Alegret, L., 2018. Early Eocene deep-sea benthic foraminiferal faunas: recovery from the Paleocene Eocene thermal maximum extinction in a greenhouse world. PLoS One 13, e0193167.

Berggren, W.A., Miller, K.G., 1988. Paleogene tropical planktonic foraminiferal biostratigraphy and magnetobiochronology. Micropaleontology 34, 362.

Berggren, W.A., Pearson, P.N., 2005. A revised tropical to subtropical Paleogene planktonic foraminiferal zonation. J. Foraminifer. Res. 35, 279–298.

Bernhard, J.M., Sen Gupta, B.K., 1999. Foraminifera of oxyen-depleted environments. In: Modern Foraminifera. Kluwer Academic Publishers, pp. 201–216.

Bignot, G., 1998. Middle Eocene benthic foraminifers from holes 960A and 960C, Central Atlantic Ocean. In: Mascle, J., Lohmann, G.P., Moullade, M. (Eds.), Proceedings of the Ocean Drilling Program, Scientific Results. Texas A&M University, pp. 433–444.

Bijl, P.K., Houben, A.J.P., Schouten, S., Bohaty, S.M., Sluijs, A., Reichart, G.-J., Damsté, J.S.S., Brinkhuis, H., 2010. Transient middle Eocene atmospheric CO_2 and temperature variations. Science 330, 819–821.

Bohaty, S.M., Zachos, J.C., 2003. Significant Southern Ocean warming event in the late middle Eocene. Geology 31, 1017–1020.

Bohaty, S.M., Zachos, J.C., Florindo, F., Delaney, M.L., 2009. Coupled greenhouse warming and deep-sea acidification in the middle Eocene. Paleoceanography 24, PA2207.

Bolli, H.M., Beckmann, J.-P., Saunders, J.B., 1994. Benthic Foraminiferal Biostratigraphy of the South Caribbean Region. Cambridge University Press, pp. 408.

Boscolo Galazzo, F., Giusberti, L., Luciani, V., Thomas, E., 2013. Paleoenvironmental changes during the Middle Eocene Climatic Optimum (MECO) and its aftermath: the benthic foraminiferal record from the Alano section (NE Italy). Palaeogeogr. Palaeoclimatol. Palaeoecol. 378, 22–35.

Boscolo Galazzo, F., Thomas, E., Pagani, M., Warren, C., Luciani, V., Giusberti, L., 2014. The middle Eocene climatic optimum (MECO): a multiproxy record of paleoceanographic changes in the southeast Atlantic (ODP Site 1263, Walvis Ridge): MECO repercussions in the SE Atlantic. Paleoceanography 29, 1143–1161.

Comas, M.C., 1978. Sobre la geología de los Montes orientales: sedimentación y evolución paleogeográfica desde el Jurásico al Mioceno inferior (Zona Subbética, Andalucía). PhD Thesis, University of Bilbao, pp. 332.

Corliss, B.H., 1985. Microhabitats of benthic foraminifera within deep-sea sediments. Nature 314, 435–438.

Corliss, B.H., Chen, C., 1988. Morphotype patterns of Norwegian Sea deep-sea benthic foraminifera and ecological implications. Geology 16, 716–719.

Coxall, H.K., Wilson, P.A., Pälike, H., Lear, C.H., Backman, J., 2005. Rapid stepwise onset of Antarctic glaciation and deeper calcite compensation in the Pacific Ocean. Nature 433, 53–57.

Den Dulk, M., Reichart, G.-J., Van Heyst, S., Zachariasse, W.J., Van der Zwaan, G.J., 2000. Benthic foraminifera as proxies of organic matter flux and bottom water oxygenation? A case history from the northern Arabian Sea. Palaeogeogr. Palaeoclimatol. Palaeoecol. 161, 337–359.

Deprez, A., Tesseur, S., Stassen, P., D'haenens, S., Steurbaut, E., King, C., Claeys, P., Speijer, R.P., 2015. Early Eocene environmental development in the northern Peri-Tethys (Aktulagay, Kazakhstan) based on benthic foraminiferal assemblages and stable isotopes (O, C). Mar. Micropaleontol. 115, 59–71.

D'haenens, S., Bornemann, A., Stassen, P., Speijer, R.P., 2012. Multiple early Eocene benthic foraminiferal assemblage and δ13C fluctuations at DSDP site 401 (Bay of Biscay — NE Atlantic). Mar. Micropaleontol. 88–89, 15–35.

Edgar, K.M., Wilson, P.A., Sexton, P.F., Gibbs, S.J., Roberts, A.P., Norris, R.D., 2010. New biostratigraphic, magnetostratigraphic and isotopic insights into the Middle Eocene Climatic Optimum in low latitudes. Palaeogeogr. Palaeoclimatol. Palaeoecol. 297, 670–682.

Fenero, R., Thomas, E., Alegret, L., Molina, E., 2012. Oligocene benthic foraminifera from the Fuente Caldera section (Spain, western Tethys): taxonomy and paleoenvironmental inferences. J. Foraminifer. Res. 42, 286–304.

Fenero, R., Cotton, L., Molina, E., Monechi, S., 2013. Micropalaeontological evidence for the late Oligocene Oi-2b global glaciation event at the Zarabanda section. Spain. Palaeogeogr. Palaeoclimatol. Palaeoecol. 369, 1–13.

Fontanier, C., Jorissen, F.J., Chaillou, G., Anschutz, P., Grémare, A., Griveaud, C., 2005. Live foraminiferal faunas from a 2800 m deep lower canyon station from the Bay of Biscay: faunal response to focusing of refractory organic matter. Deep Sea Res. Part Oceanogr. Res. Pap. 52, 1189–1227.

Gonzalvo, C., Molina, E., 1996. Bioestratigrafía y cronoestratigrafía del tránsito Eoceno Medio-Eoceno Superior en la Cordillera Bética. Rev. Esp. Micropaleontol. XXVIII 25–44.

Gooday, A.J., 1994. The biology of Deep-Sea foraminifera: a review of some advances and their applications in paleoceanography. PALAIOS 9, 14.

Gooday, A.J., 2003. Benthic foraminifera (protista) as tools in deep-water Palaeoceanography: environmental Infuences on faunal characteristics. Adv. Mar. Biol. 46.

Grünig, A., 1985. Systematical description of Eocene Benthic Foraminifera of Possagno (northern Italy), Sansoain (northern Spain) and Biarritz (Aquitaine, France). In: Memorie Degli Instituti Di Geologia e Mineralogia Dell'Università Di Padova, pp. 251–302.

Grünig, A., Herb, R., 1980. Paleoecology of late Eocene benthonic foraminifera from Possagno (Treviso-northern Italy). Cushman Found. Spec. Publ. 19, 68–85.

Hammer, Ø., Harper, D., 2005. Paleontological Data Analysis. Blackwell Publishing, Oxford.

Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: paleontological statistics software package for education and data analysis. Paleontol. Electron. 4 (1), 9.

Hayward, B.W., Kawagata, S., Sabaa, A., Grenfell, H., Van Kerckhoven, L., Johnson, K., Thomas, E., 2012. The Last Global Extinction (Mid-Pleistocene) of Deep-Sea Benthic Foraminifera (Chrysalogoniidae, Ellipsoidinidae, Glandulonodosariidae, Plectofrondiculariidae, Pleurostomellidae, Stilostomellidae), their Late Cretaceous-Cenozoic History and Taxonomy. Cushman Foundation for Foraminiferal Research Special Publication.

Hess, S., Jorissen, F.J., 2009. Distribution patterns of living benthic foraminifera from Cap Breton canyon, Bay of Biscay: faunal response to sediment instability. Deep Sea Res. Part Oceanogr. Res. Pap. 56, 1555–1578.

Holbourn, A., Henderson, A.S., MacLeod, N., 2013. Atlas of Benthic Foraminifera, Natural History Museum (ed). Wiley-Blackwell, pp. 642.

Ingle Jr., J.C., 1980. Cenozoic paleobathymetry and depositional history of selected sequences within the southern California Continental Borderland. Cushman Found. Spec. Publ. 19, 163–195.

Jones, R.W., Charnock, M.A., 1985. “Morphogroups” of agglutinated foraminifera. Their life positions and feeding habits and potential applicability in (paleo)ecological studies. Rev. Palèobiologie 4 (2), 311–320.

Jorissen, F.J., de Stigter, H.C., Widmark, J.G., 1995. A conceptual model explaining benthic foraminiferal microhabitats. Mar. Micropaleontol. 26, 3–15.

Jorissen, F.J., Fontanier, C., Thomas, E., 2007. Chapter seven: Paleoceanographical proxies based on Deep-Sea benthic foraminiferal assemblage characteristics. In: Developments in Marine Geology. Elsevier, pp. 263–325.

Jovane, L., Sprovieri, M., Coccioni, R., Florindo, F., Marsili, A., Laskar, J., 2010. Astronomical calibration of the middle Eocene Contessa Highway section (Gubbio, Italy). Earth Planet. Sci. Lett. 298, 77–88.

Katz, M.E., Tjalsma, R.C., Miller, K.G., 2003. Oligocene bathyal to abyssal benthic foraminifera of the Atlantic Ocean. Micropaleontology 49, 1–45.

Kirtland Turner, S., Sexton, P.F., Charles, C.D., Norris, R.D., 2014. Persistence of carbon release events through the peak of early Eocene global warmth. Nat. Geosci. 7, 748–751.

Loeblich Jr., A.R., Tappan, H., 1987. Foraminiferal Genera and Their Classification. Van Nostrand Reinhold Company, pp. 970 (ed.).

Loubere, P., 1998. The impact of seasonality on the benthos as reflected in the assemblages of deep-sea foraminifera. Deep Sea Res. Part Oceanogr. Res. Pap. 45, 409–432.

Lunt, D.J., Ridgwell, A., Sluijs, A., Zachos, J.C., Hunter, S., Haywood, A., 2011. A model for orbital pacing of methane hydrate destabilization during the Palaeogene. Nat. Geosci. 4, 775–778.

Moebius, I., Friedrich, O., Scher, H.D., 2014. Changes in Southern Ocean bottom water environments associated with the Middle Eocene Climatic Optimum (MECO). Palaeogeogr. Palaeoclimatol. Palaeoecol. 405, 16–27.

Moebius, I., Friedrich, O., Edgar, K.M., Sexton, P.F., 2015. Episodes of intensified biological productivity in the subtropical Atlantic Ocean during the termination of the Middle Eocene Climatic Optimum (MECO): intensified productivity during the MECO. Paleoceanography 30, 1041–1058.

Molina, E., Gonzalvo, C., Ortiz, S., Cruz, L.E., 2006. Foraminiferal turnover across the Eocene–Oligocene transition at Fuente Caldera, southern Spain: no cause–effect relationship between meteorite impacts and extinctions. Mar. Micropaleontol. 58, 270–286.

Murray, J.W., 2006. Ecology and applications of benthic foraminifera. Cambridge University Press, pp. 426.

Nicolo, M.J., Dickens, G.R., Hollis, C.J., Zachos, J.C., 2007. Multiple early Eocene hyperthermals: their sedimentary expression on the New Zealand continental margin and in the deep sea. Geology 35, 699.

Ortiz, S., Thomas, E., 2006. Lower-middle Eocene benthic foraminifera from the Fortuna section (Betic Cordillera, southeastern Spain). Micropaleontology 52, 97–150.

Ortiz, S., Alegret, L., Payros, A., Orue-Etxebarria, X., Apellaniz, E., Molina, E., 2011. Distribution patterns of benthic foraminifera across the Ypresian–Lutetian Gorrondatxe section, Northern Spain: response to sedimentary disturbance. Mar. Micropaleontol. 78, 1–13.

Pälike, H., Norris, R.D., Herrle, J.O., Wilson, P.A., Coxall, H.K., Lear, C.H., Shackleton, N.J., Tripati, A.K., Wade, B.S., 2006. The heartbeat of the Oligocene climate system. Science 314, 1894–1898.

Pälike, H., Lyle, M.W., Nishi, H., Raffi, I., Ridgwell, A., Gamage, K., Klaus, A., Acton, G., Anderson, L., Backman, J., Baldauf, J., Beltran, C., Bohaty, S.M., Bown, P., Busch, W., Channell, J.E.T., Chun, C.O.J., Delaney, M., Dewangan, P., Dunkley Jones, T., Edgar, K.M., Evans, H., Fitch, P., Foster, G.L., Gussone, N., Hasegawa, H., Hathorne, E.C., Hayashi, H., Herrle, J.O., Holbourn, A., Hovan, S., Hyeong, K., Iijima, K., Ito, T., Kamikuri, S., Kimoto, K., Kuroda, J., Leon-Rodriguez, L., Malinverno, A., Moore Jr., T.C., Murphy, B.H., Murphy, D.P., Nakamura, H., Ogane, K., Ohneiser, C., Richter, C., Robinson, R., Rohling, E.J., Romero, O., Sawada, K., Scher, H., Schneider, L., Sluijs, A., Takata, H., Tian, J., Tsujimoto, A., Wade, B.S., Westerhold, T., Wilkens, R., Williams, T., Wilson, P.A., Yamamoto, Y., Yamamoto, S., Yamazaki, T., Zeebe, R.E., 2012. A Cenozoic record of the equatorial Pacific carbonate compensation depth. Nature 488, 609–614.

Sluijs, A., Zeebe, R.E., Bijl, P.K., Bohaty, S.M., 2013. A middle Eocene carbon cycle conundrum. Nat. Geosci. 6, 429–434.

Speijer, R.P., 1994. Extinction and Recovery Patterns in Benthic Foraminiferal Paleocommunities across the Cretaceous/Paleogene and Paleocene/Eocene Boundaries. Universiteit Utrecht, Utrecht, Geologica Ultraiectina. Faculteit Aardwetenschappen, pp. 191.

Speijer, R.P., Schmitz, B., 1998. A benthic foraminiferal record of Paleocene Sea level and trophic/redox conditions at Gebel Aweina. Egypt. Palaeogeogr. Palaeoclimatol. Palaeoecol. 137, 79–101.

Spofforth, D.J.A., Agnini, C., Pälike, H., Rio, D., Fornaciari, E., Giusberti, L., Luciani, V., Lanci, L., Muttoni, G., 2010. Organic carbon burial following the middle Eocene climatic optimum in the central western Tethys. Paleoceanography 25, PA3210.

Takata, H., Nomura, R., Tsujimoto, A., Khim, B.-K., Chung, I.K., 2013. Abyssal benthic foraminifera in the eastern equatorial Pacific (IODP EXP 320) during the middle Eocene. J. Paleontol. 87, 1160–1185.

Thomas, E., 1990. Late Cretaceous through neogene deep-sea benthic foraminifers (Maud Rise, Weddell Sea, Antarctica). In: Barker, P., Kennett, J.P. (Eds.), Proceedings of the Ocean Drilling Program. Scientific Reports, Ocean Drilling Program, pp. 571–594.

Thomas, E., Zachos, J.C., 2000. Was the late Paleocene thermal maximum a unique event? GFF 122, 169–170.

Tjalsma, R.C., Lohmann, G.P., 1983. Paleocene - Eocene Bathyal and Abyssal Benthic Foraminifera from the Atlantic Ocean (Micropaleontology Special Edition). pp. 89.

Van der Zwaan, G.J., Duijnstee, I.A.P., Den Dulk, M., Ernst, S.R., Jannink, N.T., Kouwenhoven, T.J., 1999. Benthic foraminifers: proxies or problems?: a review of paleocological concepts. Earth-Sci. Rev. 46, 213–236.

Van Morkhoven, F.P.C.M., Berggren, W.A., Edwards, A.S., 1986. Cenozoic Cosmopolitan Deep-Water Benthic Foraminifera, Bull. Centres Rech. Explor.-Prod. Elf-Aquitaine, pp. 421.

Wade, B.S., 2004. Planktonic foraminiferal biostratigraphy and mechanisms in the extinction of Morozovella in the late middle Eocene. Mar. Micropaleontol. 51, 23–38.

Wade, B.S., Pearson, P.N., Berggren, W.A., Pälike, H., 2011. Review and revision of Cenozoic tropical planktonic foraminiferal biostratigraphy and calibration to the geomagnetic polarity and astronomical time scale. Earth-Sci. Rev. 104, 111–142.

Zachos, J.C., Dickens, G.R., Zeebe, R.E., 2008. An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. Nature 451, 279–283.

Zachos, J.C., McCarren, H., Murphy, B., Röhl, U., Westerhold, T., 2010. Tempo and scale of late Paleocene and early Eocene carbon isotope cycles: implications for the origin of hyperthermals. Earth Planet. Sci. Lett. 299, 242–249.