RRH: PALEOCENE–EOCENE BENTHIC FORAMINIFERA

LRH: GIRALDO-GÓMEZ AND OTHERS

BENTHIC FORAMINIFERA AND GEOCHEMISTRY ACROSS THE PALEOCENE–
EOCENE THERMAL MAXIMUM INTERVAL IN JORDAN

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ABSTRACT

This study presents benthic foraminiferal data from two sedimentary successions across the Paleocene–Eocene Thermal Maximum (PETM) from Jordan. Calcareous nannofossil biozones NP9a, NP9b and NP10 of latest Paleocene and earliest Eocene age were encountered in proximal (core OS–01) and distal (core OS–28) sites. Lithologically the investigated sequence consists of marls, shales and limestones attributed to the Muwaqqar Chalk- Marl Formation and the Um Rijam Chert Limestone Formation. The $\delta^{13}\text{C}_{\text{org}}$ curve records the typical carbon isotope excursion (CIE), and shows four distinctive intervals (pre-CIE, CIE-“core”, CIE-“recovery”, post-CIE) over the entire PETM interval in both cores.

In the pre-CIE interval, the more proximal site (OS–01) shows high abundances of *Neoeponides duwi* co-occurring with an outer neritic Midway-type fauna. The fauna indicates meso- to eutrophic conditions in a middle to outer neritic setting. The more distal site (OS–28) is characterized by outer neritic to upper bathyal taxa (e.g., *Cibicides pseudoacutus*, *Gavelinella beccariiiformis*, *Nuttallides truempyi*) suggesting well-ventilated, oligo- to mesotrophic sea-floor conditions.

The earliest Eocene corresponds to the CIE-“core” interval and is marked by a negative $\delta^{13}\text{C}_{\text{org}}$ signal, high TOC and low CaCO_3 contents, and near absence of benthic foraminifera. Oxygen deficiency of the bottom waters with increased organic flux is the most likely scenario to explain the elevated organic content at the sea floor.

The subsequent CIE-“recovery” interval of early Eocene age is marked by a restoration of oxygenated sea-floor conditions. The proximal site is characterized by a relatively elevated TOC

content and high abundance of *Lenticulina* spp., *Valvulineria scrobiculata* and common *Anomalinoides zitteli*, suggesting moderate oxygen conditions and mesotrophic bottom waters. The distal site is characterized by low TOC content and the presence of *Lenticulina* spp., *Valvulineria scrobiculata*, *Anomalinoides zitteli* and *Oridorsalis plummerae*, indicating a normalization of the organic flux and moderate oxygen concentrations near the sea floor.

The post-CIE interval is marked by low TOC content in both cores. Benthic foraminifera include abundant *Anomalinoides zitteli* and common *Lenticulina* spp., *Valvulineria scrobiculata*, *Oridorsalis plummerae*, *Cibicidoides rigidus*, *Cibicidoides pharaonis* and *Anomalinoides praeacutus* in the proximal setting. Mesotrophic conditions and a better ventilation of the bottom waters are suggested for this interval. *Lenticulina* spp., *Valvulineria scrobiculata* and *Oridorsalis plummerae* are also associated with the post-CIE interval in the distal site, suggesting similar mesotrophic conditions with renewed oxygenation in the bottom waters.

INTRODUCTION

The Paleocene–Eocene Thermal Maximum (PETM; ~56 Ma) was a global warming event that affected the ocean-atmosphere system on a global scale. A negative shift of $\delta^{13}\text{C}$ (CIE: carbon isotope excursion) marked the onset of the PETM (e.g., Aubry et al., 2007; McInerney & Wing, 2011). A massive injection of isotopically light carbon triggered changes in the ocean-atmosphere system (Dickens et al., 1995; Dickens, 2011) and the causes underlying this abrupt peak of light carbon are still debated. A potential source is the massive release of methane hydrates from the ocean floor that was injected as CO_2 into the atmosphere-ocean system (Dickens et al., 1995, 1997; Dickens, 2000; Higgins & Schrag, 2006). Another hypothesis proposed thawing of permafrost soils at high latitudes, particularly Antarctica (DeConto et al., 2012). Following this model, light carbon was released as a direct response to orbital forcing of the long- and short eccentricity cycles (Lourens et al., 2005; DeConto et al., 2012; Littler et al., 2014). A third hypothesis invokes the North Atlantic Igneous Province (Svensen et al., 2004; Wieczorek et al., 2013) and volcanic activity (Carozza et al., 2011; Patterson and Francis, 2013) as likely sources of the light carbon.

Global temperature rose by 5–8°C during this hyperthermal event (McInerney & Wing, 2011; Dunkley-Jones et al., 2013). Sea surface temperatures (SSTs) increased by ~5°C in the tropics and ~8°C at high latitudes (e.g., Zachos et al., 2003; Tripathi & Elderfield, 2005; Hollis et al., 2015) and bottom water temperatures by ~4–5°C (Thomas & Shackleton, 1996; Zachos et al., 2005).

Evidence for widespread shoaling of the calcite compensation depth (CCD), which resulted in a strong dissolution of marine carbonates on a global scale, is found in deep water sections (e.g. Schmitz et al., 1997; Zachos et al., 2005). Carbonate dissolution has also been documented from shelf sections (e.g., Ernst et al., 2006; Bown & Pearson, 2009; Gibbs et al., 2010; Self-Trail et al., 2012). For these settings, metabolic respiration of sedimentary organic carbon (Rao et al., 2012; Broecker, 2010; Martin & Sayles, 2006) and post-depositional pore-water carbonate disequilibria (Katz et al., 2003) have been proposed as an explanation.

During the PETM, rapid global warming affected oceanic biota, causing shifts in the composition of assemblages (Speijer et al., 2012), including the extinction of 35–50% of cosmopolitan deep-sea benthic foraminifera (e.g., Tjalsma & Lohmann, 1983; Thomas, 2007). This extinction is known as the benthic foraminiferal extinction event (BEE or BFEE), which was less severe in shelf assemblages (e.g., Gibson et al., 1993; Speijer et al., 1995; Stassen et al., 2012; 2015). In contrast, planktonic foraminifera are characterized by transient diversification among the genera *Morozovella* and *Acarinina* (e.g., Kelly et al., 1996, 1998; Guasti & Speijer, 2008). Three species of these genera are generally identified as “excursion taxa” (*Acarinina africana*, *A. sibaiyaensis*, and *Morozovella allisonensis*), which occur within the CIE sections of the Tethys, the Pacific Ocean and the Atlantic margin (Berggren & Ouda, 2003; Aubry et al., 2007; Ouda et al., 2016; Giusberti et al., 2016). Changes in calcareous nannofossil assemblages are also documented. *Discoaster araneus*, *D. anartios* and *Rhomboaster* spp. have their first occurrence shortly after the onset of the CIE (e.g., Monechi et al., 2000; Kahn & Aubry, 2004; Aubry et al., 2007; Mutterlose et al., 2007). Organic-walled primary producers were also affected by the PETM. The widespread occurrence of the dinoflagellate genus *Apectodinium*, which during the Paleocene was restricted to low latitudes with high sea-surface temperatures, suggests

a rapid warming of ocean waters (e.g., Crouch et al., 2003; Sluijs et al., 2006, 2007). For the terrestrial realms, a turnover in vegetation and a rapid radiation and dispersal of mammals provides evidence for the PETM (e.g., Gingerich, 2006; McInerney & Wing, 2011; Wing & Currano, 2013).

The PETM interval has hardly been studied in outcrops in Jordan, except for the Gebel Qurtaissyat sequence in central Jordan, in which the PETM overlies a disconformity (Guasti, 2005; Guasti & Speijer, 2008). Furthermore, Giraldo et al. (2016) documented the calcareous nannofossil record across the PETM in a subsurface sequence in northern Jordan (OS–28).

Here we report new benthic foraminiferal and geochemical data across the PETM interval, in a distal and more proximal setting as recorded in two drill cores (OS–01; OS–28) from Jordan. Our objectives were to identify the CIE of the PETM in order to reconstruct paleobathymetric evolution and changing bottom-water conditions based upon the diversity and abundance patterns of the benthic foraminifera.

GEOLOGICAL SETTING

During the Paleogene Jordan was situated at the southern margin of the Tethys Ocean in the northwestern part of the Arabian Plate (Fig. 1A). Continuous sedimentation took place in this epicontinental setting during the Paleocene and most of the Eocene (Bender, 1975; Ziegler, 2001). A thick sequence of chalks, marls and limestones was deposited throughout the northern and central parts of Jordan. Intense tectonic activity controlled the major regional structural elements during the Cretaceous to Cenozoic. The Syrian Arc fold belt influenced the paleotopography (Mart, 1987), forming a series of anticlines and synclines (Hussein et al., 2015)

and numerous graben structures. These include the modern Al-Jafr Basin, the Azraq-Hamza Basin, the Lajjun Basin and the Yarmouk Basin (Powell, 1989; Alqudah et al., 2014). In the Al-Jafr Basin and the Azraq-Hamza Basin, the Belqa Group is characterized by hemipelagic deposits of the Muwaqqar Chalk- Marl Formation (Maastrichtian to upper Paleocene) and the Umm Rijam Chert-Limestone Formation (lower to mid-Eocene). Towards the south and southeast of Jordan, both formations gradually wedge out due to paleoshoreline proximity (Andrews, 1992; Alqudah et al., 2015).

CORES OS-01 AND OS-28

The two cores OS-01 (recovered length 208.5 m) and OS-28 (recovered length 146.5 m) were drilled by the Jordan Oil Shale Company (JOSCO B.V.) in 2010. The site of Core OS-01 is in south-eastern Jordan about 140 km south-east of Amman. The Core OS-28 site is in central-east Jordan, 110 km north-east of Amman (Fig. 1B). Paleogeographically the wells are placed in the Al-Jafr Basin and the Azraq-Hamza Basin (Andrews, 1992). The cored sediments belong to the Belqa Group spanning the Muwaqqar Chalk- Marl Formation and the Um Rijam- Chert Limestone Formation (Maastrichtian-Eocene; Andrews, 1992). Lithologically the studied interval of core OS-01 (61.50–60.00 m; 1.50 m thick) can be subdivided into three units. Dark gray marls (61.50–61.20 m; 0.30 m thick) are followed by black shales (61.20–60.80 m; 0.40 m thick) and a light beige limestone (60.80–60.00 m; 0.80 m thick) in the uppermost part. The section of interest in core OS-28 (48.70–43.50 m; 5.20 m thick) consists of dark gray marls (48.70–47.20 m; 1.50 m thick) in the lower part and black shales (47.20–46.95 m; 0.25 m thick)

in the middle part. The upper part (46.95–43.50 m; 3.45 m thick) is composed of a light beige limestone.

MATERIAL AND METHODS

GEOCHEMICAL ANALYSES: $\delta^{13}\text{C}_{\text{org}}$, CaCO_3 , TOC

A total of 78 samples, 21 from (core OS–01) and 57 samples from (core OS–28) were analyzed using the “carbonate bomb” method (Müller & Gastner, 1971) to obtain the CaCO_3 contents. The CaCO_3 analyses were performed at the paleontology laboratory at the Ruhr University of Bochum (Bochum). Carbon isotopes of organic matter ($\delta^{13}\text{C}_{\text{org}}$) data were obtained with an elemental analyser (CE 1110) connected posterior to its gas chromatographic column separation of produced gases via a Conflo III Interface to a Thermo Finnigan Delta V Plus mass spectrometer. A total of 59 samples, 21 samples (from OS–01) and 38 samples (from OS–28) were analyzed. The analyses were carried out at the Geo-Zentrum Nordbayern Isotope Laboratory (Erlangen). The $\delta^{13}\text{C}_{\text{org}}$ measurements yield a standard deviation of ± 0.08 per mil ($\delta^{13}\text{C}_{\text{org}} - 1\sigma$). Analyses of total organic carbon (TOC) on three samples (60.25 m, 60.75 m and 61.25 m) from core OS–01 were measured by JOSCO (Blessenohl, 2013) on a LECO CS 230 analyzer. Total organic carbon (TOC) yield of 30 samples from core OS–28 were analyzed by Isolab B.V. (Neerijnen – The Netherlands) using a LECO CS-200 analyzer.

CALCAREOUS NANNOFOSSILS

A total of 21 smear slides were analyzed for calcareous nannofossils to define the biostratigraphy of core OS–01. Preparation techniques followed the standard procedure described by Bown (1998). An Olympus BX-51 microscope at x1250 magnification in cross polarized light was used. The biozonation scheme used here follows the standard nannofossil zonation for the Paleogene (NP = Nannoplankton Paleogene) as defined by Martini (1971) and complemented by Aubry (1995, 1999).

MICROPALEONTOLOGICAL ANALYSES

A total of 30 samples (core OS–01: 16 samples; core OS–28: 14 samples) were dried and soaked in a Na₂CO₃ solution (50 g/l). Subsequently samples were washed over 500 µm, 125 µm and 63 µm sieve sizes. A representative split was obtained from the fraction >125 µm by using an Otto microsplitter. The results from samples 61.10 m and 61.00 m of core OS–01 were discarded from the quantitative analyses due to the low abundances of benthic foraminifera. For quantitative analysis of the foraminifera (>300 specimens), the planktonic-benthic ratio (% P = $100 \cdot P / (P+B)$), the absolute abundance (individuals >125 µm per gram of sediment) expressed as benthic foraminifera number (BFN), and planktonic foraminifera number (PFN) were calculated for each sample. Benthic foraminifera were identified at species level whenever possible, following the taxonomy outlined by LeRoy (1953), Van Morkhoven et al. (1986) and Speijer (1994). Species of the genera *Nodosaria*, *Laevidentalina*, *Stilostomella*, *Chrysalogonium* and *Lenticulina* were grouped at a higher taxonomic level due to the poor preservation.

Simple diversity (S), Shannon diversity [H (s); Shannon & Weaver, 1949], dominance (D), hierarchical cluster analysis (CA) and a detrended correspondence analysis (DCA) were

calculated based on the counts using the software PAST (Hammer et al., 2001). The relative abundances of the most common taxa ($\geq 2.0\%$ in at least one sample) were used to determine the taxa to include in the analyses; the remaining species ($< 2\%$ and undetermined benthic genera and species) were grouped as “rest”. Cluster analysis was carried out in R-mode on selected taxa using the Pearson correlation, grouping taxa with similar distribution patterns through the studied interval. A detrended correspondence analysis (DCA) in Q-mode (grouping of associations) was performed to retrieve controlling environmental factors spanning the PETM.

The terms inner-neritic (IN: 0–50 m), middle-neritic (MN: 50–100 m), outer-neritic (ON: 100–200 m) and upper-bathyal (UB: 200–500 m) are used for paleodepth assignments as employed by Van Morkhoven et al. (1986) and Speijer (1994). Scanning Electron Microscopy (SEM) at the Ruhr University of Bochum was used to document the most common taxa.

RESULTS

GEOCHEMICAL ANALYSES: $\delta^{13}\text{C}_{\text{org}}$, CaCO_3 , TOC

The onset of the CIE is defined by a rapid shift to the most negative $\delta^{13}\text{C}_{\text{org}}$ values at (61.20–61.15 m, core OS–01; 47.20–47.15 m, core OS–28; Figs. 2, 3). Based on the $\delta^{13}\text{C}_{\text{org}}$ data both cores were subdivided into four intervals (from bottom to top): the pre-CIE, the CIE-“core” and CIE-“recovery” and the post-CIE interval (Figs. 2, 3).

The pre-CIE interval of core OS–01 (61.50–61.20 m; 0.3 m thick) shows $\delta^{13}\text{C}_{\text{org}}$ values from -28.4 to -26.6‰ , the CaCO_3 content varies between 37.0–54.0%. The TOC content in sample 61.25 m has a value of 6.8%. The CIE-“core” interval (61.20–61.02 m; 0.18 m thick) is

characterized by the most negative $\delta^{13}\text{C}_{\text{org}}$ value of -30.3‰ in sample 61.05 m, CaCO_3 fluctuates from 12–17%. The CIE-“recovery” interval (61.02–60.70 m; 0.32 m thick) shows $\delta^{13}\text{C}_{\text{org}}$ values ranging from -29.9 to -29.0‰ , a CaCO_3 content from 13–23% and a TOC value of 9.0% in sample 60.75 m. In the post-CIE interval (60.70–60.00 m; 0.70 m thick) the $\delta^{13}\text{C}_{\text{org}}$ values fluctuate from -28.8 to -27.6‰ and CaCO_3 rises from 64–77%. In sample 60.25 m a TOC content of only 1.3% is recorded.

In core OS-28, the studied pre-CIE interval (48.70–47.20 m; 1.50 m thick) displays stable $\delta^{13}\text{C}_{\text{org}}$ values between -26.4 and -26.0‰ , CaCO_3 content fluctuates between 30–50%, except for sample 48.70 m (81%) and TOC varies from 0.2–1.4% (Fig. 3). The CIE-“core” interval (47.20–47.00 m; 0.20 m thick) displays the most negative $\delta^{13}\text{C}_{\text{org}}$ data of -30.0‰ , CaCO_3 values are very low (close to 0%), TOC amounts 9.2–11.6%. The CIE-“recovery” interval (47.00–46.80 m; 0.20 m thick) is characterized by $\delta^{13}\text{C}_{\text{org}}$ values increasing from -28.7 to -27.0‰ , a rising of the CaCO_3 content of 62.6–68.7% and low TOC values of 0.8–1.2%. The post-CIE interval (46.80–43.50 m; 3.30 m) exhibits $\delta^{13}\text{C}_{\text{org}}$ values between -27.4 and -26.3‰ , CaCO_3 and TOC contents vary from 58.1–73% and from 0.3–0.8%, respectively.

BIOSTRATIGRAPHY

Three calcareous nannofossils biozones (NP) were recognized for the uppermost Paleocene and lowermost Eocene (Figs. 2, 3). Biostratigraphy of core OS-28 is based on biozones described by Giraldo et al. (2016). The sequences from 61.50–61.00 m (OS-01) and 48.70–47.05 m (OS-28) are assigned to biozone NP 9a based upon the presence of *Discoaster multiradiatus*. The boundary between the biozones NP9a/NP9b is defined by the first occurrence

(FO) of the calcareous nannofossil taxa *Discoaster araneus* and *Rhomboaster cuspis*. Biozone NP9b ranges from 61.00–60.35 m (OS–01) and from 47.05–45.95 m (OS–28). The overlying biozone NP10 is marked by the FO of *Tribrahiatus bramlettei* in sample 60.35 m (OS–01) and 45.95 m (OS–28).

PRESERVATION OF BENTHIC FORAMINIFERA

The foraminiferal tests are generally poorly to moderately preserved with some fragmentation, resulting in difficulties to recognize original features (e.g., sutures, pores). Etching, overgrowth and recrystallization were observed in most specimens by light microscopy and SEM. The benthic foraminifera from core OS–01 show the best preserved tests (Fig. 4), while foraminiferal tests from core OS–28 are more affected by recrystallization and breakage (Fig. 5), resulting in a relatively high number of unrecognizable specimens from the uppermost Paleocene samples. Following these preservational features, an interval marked by partial dissolution is recognized for both cores (OS–01: 61.40–60.90 m; OS–28: 48.50–47.00 m; Figs. 2, 3).

FORAMINIFERAL ABUNDANCES

A total of 80 species and 21 genera of benthic foraminifera were recognized in the two cores. The most abundant taxa ($\geq 2.0\%$) are documented in figures 6 and 7. High abundances and high diversities of continental shelf fauna were recorded, as *Anomalinoides* and *Cibicidoides* are the most abundant genera throughout both cores.

In Core OS–01, the pre-CIE interval is marked by common *Neoeponides duwi* and rare *Angulogavelinella avnimelechi*, *Anomalinoides praeacutus*, *Cibicidoides pseudoacutus* and *Cibicidoides rigidus*. The %P ranges from 72.4–90.4%, the Shannon Index H(s) from 2.1–3.0 and the dominance (D) from 0.07–0.2 (Fig. 2). The CIE-“core” interval is characterized by scarce benthic foraminifera, the %P increases up to 87.3%. The CIE-“recovery” interval shows high abundances of *Anomalinoides zitteli*, *C. rigidus*, *Valvulineria scrobiculata*, *Cibicidoides pharaonis* and *Lenticulina* spp. The %P ranges from 85.3–90.4%. H (s) and D fluctuate from 1.4–3.0 and from 0.07–0.4 respectively. The post-CIE interval displays similar abundances of benthic foraminifera as the CIE-“recovery” interval and *Oridorsalis plummerae* becomes more common. The %P varies from 72.4–85.9%, H(s) and D from 2.8–3.1 and 0.05–0.1, respectively. The absolute abundances of the BFN (1–199 foraminifera/g) and PFN (3–423 foraminifera/g) in core OS–01 are generally low and epibenthic morphotypes are the dominant benthic group (48.2–71.9%; Fig. 8).

For Core OS–28, the pre-CIE interval is marked by abundant *A. praeacutus*, *C. pseudoacutus*, *C. rigidus* and low abundances of *Gavelinella beccariiformis*, *Nuttallides truempyi* and *A. avnimelechi*. The %P ranges from 2.5–62.1%, the H(s) and D from 2.6–3.3 and from 0.05–0.1 respectively (Fig. 3). The CIE-“core” interval is characterized by a near absence of benthic foraminifera. The CIE-“recovery” interval (47.00–46.80 m) displays high abundances of *Loxostomoides applinae*, *V. scrobiculata*, *O. plummerae* and *A. zitteli*. The %P has a value of 79.4%, H (s) and D values are 2.6 and 0.09 respectively. The post-CIE interval is marked by increasing in abundances of *V. scrobiculata*, *C. rigidus*, *O. plummerae*, *A. zitteli* and *Lenticulina* spp. The %P fluctuates from 38.3–83.6%, the H(s) and D from 2.7–3.2 and from 0.05–0.08 respectively. The absolute abundances of the BFN (3–43 foraminifera/g) and PFN (1–215

foraminifera/g) in core OS–28 are generally low and epibenthic morphotypes are the dominant group (48–71.5%; Fig. 9).

BENTHIC FORAMINIFERAL ASSEMBLAGES

Cluster Analysis

Three main clusters (A, B, C) can be differentiated using the relative abundances of benthic foraminifera ($\geq 2.0\%$ in at least one sample). These clusters indicate paleoecological preferences of the benthic species for the two studied cores (Fig. 10).

The most abundant taxa of Cluster A include *N. duwi*, *Stilostomella* spp., *Chrysalogonium* spp. in core OS–01, less common are *Anomalinoides* cf. *midwayensis*, *Valvalabamina depressa*, *Siphogenerinoides elegans*. Common taxa in Cluster B are *C. pseudoacutus* and *A. praeacutus*; less common are *A. avnimelechi*, *Hanzawaia* cf. *caribaea*, *G. beccariiiformis*, *Cibicidoides alleni*, *Gyroidinoides girardanus*, *Spiroplectinella esnaensis*, *Laevidentalina* spp.

Cluster C was subdivided into three sub-clusters (CI, CII, CIII; Fig. 10). Taxa in the CI subcluster are *Anomalinoides affinis*, *Anomalinoides rubiginosus*, *C. rigidus*, *N. truempyi*, *O. plummerae* and *Valvalabamina planulata*. Taxa in the CII subcluster includes *A. zitteli*, *Spiroloculina* sp., *C. pharaonis*, *Bulimina farafraensis* and *Osangularia plummerae*. The CIII subcluster is composed of *Gaudryina ellisorae*, *Lenticulina* spp., *L. applinae*, *Nodosaria* spp., *Pullenia jarvisi* and *V. scrobiculata*.

The pre-CIE interval is characterized by high abundances of taxa of cluster A (43.5–69.3%). Cluster B (8.1–23.7%) and sub-cluster CIII (11.3–18%) display intermediate abundances

in core OS–01. In the same interval in core OS–28, higher abundances of taxa of cluster B (14.3–41.1%), sub-clusters CIII (7.9–31.2%) and CI (7.6–25.2%) are recorded. Whereas taxa of cluster A (1.1–8.3%) and CII (0–1.3%) have significantly lower abundances.

The CIE-“recovery” interval in core OS–01 display high abundance of benthic foraminifera associated with sub-clusters CIII (21.6–44.5%) and CII (23.2–34.7%). Intermediate abundances of sub-cluster CI (7.9–15.6%) together with low abundances of clusters A (1.8%–7.1%) and B (1.2–8.8%) were recorded. In core OS–28, the CIE-“recovery” shows high abundances of sub-cluster CIII (37.2%), intermediate abundances of sub-clusters CII (16%), CI (14%) and lower abundances of clusters B (4.4%) and A (1.7%).

The post-CIE interval is characterized high abundances of sub-clusters CIII (15.8–27.6%), CII (22.7–38.0%) and CI (12.7–25.7%), intermediate and lower abundances of clusters B (4.6–23.1%) and A (3.2–9.5%) respectively in core OS–01. In core OS–28, the post-CIE interval displays high abundances in sub-clusters CIII (18.6–51.8%) and CI (22.7–38%). In contrast, intermediate abundances of sub-cluster CII (6.8–15.9%) and cluster B (2.3–16.2%) and lower abundances of cluster A (0.3–4.2%) were recorded.

Detrended Correspondence Analysis

Samples from cores OS–01 and OS–28 are grouped differently along axis 1 and 2 of the Q-mode DCA plot (Fig. 11A), explaining respectively 40.1% and 18.8% data variance. The distribution of samples of the pre-CIE (late Paleocene) is characterized by high loading in axis 1 and intermediate loading in axis 2 (OS–01) and intermediate loading in axis 1 and high loading in axis 2 (OS–28), indicating dissimilar environmental conditions. Samples of the early Eocene,

including the CIE and post-CIE intervals are more clustered and display low loading in axes 1 and 2 (OS–01) and low loading in axis 1 and intermediate loading in axis 2 (OS–28). The R-mode DCA separates the benthic foraminiferal assemblages in three main groups, reflecting the relative abundance shifts of the three clusters A, B and C (Fig. 11B).

DISCUSSION

PRESERVATION AND DISSOLUTION

Planktonic foraminifera are generally considered to be less resistant to dissolution than benthic foraminifera, showing different dissolution susceptibility grades as reflected by decreasing %P (e.g., Berger, 1970; Dittert et al., 1999; Conan et al., 2002; Petrizzo et al., 2008; Nguyen & Speijer, 2014). Signals of dissolution of planktonic foraminifera, in combination with decreased carbonate content, were observed in samples of the pre-CIE, the CIE-“core” and the CIE-“recovery” intervals of both cores (Figs. 2, 3). Dissolution was most severe in core OS–28 (pre-CIE: 48.50–47.20 m; Fig. 3) as is evidenced by the poor preservation of the benthic foraminifera. A larger taphonomic impact on the pre-CIE foraminiferal fauna is supported by a significant drop in species richness, low PFN, low %P values in both cores and low absolute abundances of calcareous nannofossils in samples of the upper Paleocene (e.g., core OS–28: Giraldo et al., 2016). The low planktonic foraminiferal abundances prior to the PETM is a very familiar pattern in Egypt (e.g., Wadi Nukhl: Speijer, 1994; Aweina: Speijer & Schmitz, 1998; Dababiya: Ernst et al., 2006), which may be related to widespread regional taphonomic conditions in the basins. The dissolution process may have been caused by early post-

depositional changes in pore-water chemistry not in equilibrium with the foraminiferal calcite tests. These led to oxidation of the organic matter into CO₂ (e.g., Murray & Alve, 1999; Kozdon et al., 2013), causing a decrease in pH and consequently dissolving the foraminiferal tests.

Thin-shelled and slender benthic foraminifera like *Stilostomella* spp., miliolids and Buliminacea are also relatively prone to dissolution, while compact and thick-shelled *Globocassidulina subglobosa*, *Cibicidoides rigidus*, *Nuttallides truempyi*, *Valvulineria scrobiculata*, *Anomalinoides zitteli*, *Osangularia plummerae* and *Lenticulina* spp. are more resistant (e.g., Nguyen et al., 2009). Benthic foraminiferal assemblages recorded in both cores contain different abundances of species resistant and susceptible to dissolution. A striking feature is the high abundance of *Lenticulina* spp., which shows different grades of preservation in both cores. These relative enrichments of *Lenticulina* also suggest dissolution of other genera (e.g., Nguyen et al., 2009; Nguyen & Speijer, 2014), although a paleoecological signal cannot be ruled out as *Lenticulina* species are more abundant in post-CIE samples with higher %P, as also recorded in Egypt (e.g., Ernst et al., 2006).

PALEOBATHYMETRY

Foraminifera provide a useful tool for reconstructing paleodepths, because the taxonomic composition of the assemblages varies with depth. Based on the taphonomic indications of partial dissolution of the foraminiferal fauna, notably planktonic foraminifera, we consider the benthic foraminiferal assemblage to provide the most reliable proxy for reconstructing the water depth (Table. 1).

Two different assemblages of benthic foraminifera are commonly differentiated for the Paleocene–Eocene interval, based on their paleobathymetric distribution patterns. The Midway-type fauna is typical of continental shelf environments and the Velasco-type fauna characterizes continental slope to abyssal environments (Berggren & Aubert, 1975). Benthic foraminifera of both groups have been studied from sections spanning the PETM around the world (e.g., New Zealand: Kaiho et al., 1996; Spain: Ortiz, 1995; Alegret et al., 2009; Italy: Giusberti et al., 2009; 2016; USA: Stassen et al., 2015; Egypt and Israel: Speijer, 1994; Ernst et al., 2006; Tunisia: Stassen et al., 2012). Several studies from the southern Tethys margin (e.g., Berggren & Aubert, 1975; Speijer, 1994; Speijer et al., 1996; Speijer & Schmitz, 1998) have used taxa of the Midway–fauna and Velasco–fauna for the paleobathymetric interpretations of the late Paleocene.

Upper Paleocene

Core OS–01 is characterized by high percentages of benthic foraminifera of cluster A with a strong dominance of *N. duwi*. Various studies have documented *N. duwi* from inner to middle neritic settings and from deeper shelf environments in Egypt and elsewhere (e.g., Speijer & Schmitz, 1998; Schnack, 2000; Speijer, 2003; Guasti, 2005; Sprong et al., 2011). Its wide bathymetric habitat range has been explained by periodic downslope migration, enabling *N. duwi* to occupy niches abandoned by other benthic species during major environmental perturbations (Sprong et al., 2012). Based on the co-occurrence of middle or outer neritic to upper bathyal taxa (e.g., *A. midwayensis*, *A. praeacutus*, *C. rigidus*, *O. plummerae*, *V. scrobiculata*, *A. avnimelechi*) with *N. duwi* in core OS–01, an estimated paleodepth of middle to outer neritic (~70–150 m) is here suggested for the uppermost Paleocene. This interpretation is supported by the absence of

typical bathyal (*G. beccariiiformis*, *N. truempyi*) or inner shelf (e.g., *Frondicularia*, diverse nodosariids and lenticulinids) taxa, although this estimated paleodepth might be an underestimation due to the potential opportunistic behavior of *N. duwi*.

Species typical for outer neritic to upper bathyal conditions (e.g., Speijer & Schmitz, 1998; Ernst et al., 2006) are more common in core OS–28 (e.g., *A. avnimelechi*, *C. alleni*, *C. pseudoacutus*, *A. affinis*, *A. rubiginosus*, *A. midwayensis*, *C. rigidus*, *Oridorsalis plummerae*, *A. praeacutus*, *V. planulata*). Relatively few specimens of the bathyal taxa *N. truempyi* and *G. beccariiiformis* were observed in core OS–28. Both species are typically abundant in deep-water settings and are the main faunal component in upper bathyal (500–700 m) conditions in the Sinai and northeastern Egyptian region (e.g., Speijer, 1994). The continuous presence of outer neritic taxa and the low abundance of characteristic bathyal species indicate an outer neritic - upper bathyal (~150–250 m) water depth for the upper Paleocene of core OS–28.

Lower Eocene

Benthic foraminiferal assemblages typical for an outer neritic to upper bathyal setting (*A. zitteli*, *C. pharaonis*, *Osangularia plummerae*, *Oridorsalis plummerae*, *N. truempyi*, *C. rigidus*, *A. praeacutus*) are recorded in both cores from samples of the CIE-“recovery” and post-CIE intervals. An early Eocene outer neritic to upper bathyal setting (150–250 m) is suggested for core OS–01, indicative of the establishment of persistent deeper water conditions, whereas no substantial Eocene paleodepth changes are noted for the OS–28 site (outer neritic to upper bathyal setting, 150–250 m), probably due its initial deeper Paleocene setting. An increase in paleodepth during the PETM interval is also documented by benthic foraminiferal assemblages

in Egypt (Speijer, 1994; Speijer & Wagner, 2002; Ernst et al., 2006) and Tunisia (Stassen et al., 2012). This sea-level rise is evident in an extensive transgression onto the Arabian plate and Egypt during the late Paleocene and early Eocene (e.g., Haq & Al-Qahtani, 2005; Schulte et al., 2011).

NUTRIENTS AND BENTHIC MARKER SPECIES

The distribution of species along the continental slope is considered as a function of organic flux and oxygenation (Jorissen et al., 1995; van der Zwaan et al., 1999), which according to the TROX-model (Jorissen et al., 1995; 2007) regulate the microhabitats of benthic foraminifera. Taxa with preferences of endobenthic microhabitats become more abundant when the organic flux increases, showing higher abundances under oxygen-depleted bottom waters (Jorissen, 1999). High percentages of epibenthic morphotypes in contrast are generally indicative of well-ventilated, relatively oligotrophic marine conditions (e.g., Corliss & Chen, 1988; Corliss, 1991). Continuously abundant epibenthic morphotypes are documented in both cores, despite major fluctuations of the TOC of the sediments across the Paleocene-Eocene boundary (Figs. 8, 9).

Upper Paleocene

Different benthic foraminiferal assemblages are distinguished in the pre-CIE interval throughout both cores. Core OS-01 is dominated by *N. duwi*, which is the most abundant species of cluster A, and to a lesser extent by *A. cf. midwayensis*, *Stilostomella* sp., *Chrysalogonium* spp.

and *S. elegantus*. High abundances of *N. duwi* were also observed in TOC-enriched sediments in Egypt during the latest Danian Event (LDE: e.g., Speijer, 2003; Sprong et al., 2012) and *N. duwi* is therefore regarded as an opportunistic species able to react to strong environmental perturbations (e.g., Sprong et al., 2012). *Anomalinoides* cf. *midwayensis* is linked to environments with oxygen deficiency (Ernst et al., 2006; Alegret & Ortiz, 2006; Stassen et al., 2009). *Stilostomella* sp., *Chrysalogonium* spp and *S. elegantus* were endobenthic taxa, which thrived in poorly oxygenated bottom waters (Speijer & Schmitz, 1998; Schnack, 2000; Moebius et al., 2014; Deprez et al., 2015). *Lenticulina* species (sub-cluster CIII) are considered to have been ecological opportunists, which probably occupied both epibenthic and shallow-endobenthic microhabitats, thereby responding to low-oxygen conditions (e.g., Stassen et al., 2009). These foraminiferal faunal patterns, high TOC values, low H(s) indices and distinct loading on axis 1 of the DCA, suggests meso- to eutrophic conditions under oxygen-depleted bottom waters in core OS-01. (Figs. 8, 11B).

The pre-CIE interval in core OS-28 is characterized by abundant *C. pseudoacutus* (cluster B) and *C. rigidus* (sub-cluster CI) in intervals with low TOC values and high loading in axis 2. These species supposedly thrived in oligo- to mesotrophic environments (Ernst et al., 2006; Deprez et al., 2015). Less abundant species are *A. avnimelechi* (cluster B), *G. beccariiformis* (cluster B) and *N. truempyi* (sub-cluster CI). The deep-sea dweller *N. truempyi*, an oligotrophic species, is considered to be tolerant to low oxygen concentrations and sluggish ocean circulation (Tjalsma & Lohmann, 1983; Widmark & Speijer, 1997; Thomas, 2007). *Gavelinella beccariiformis* is also known as an oligotrophic deep-sea species (Widmark & Speijer, 1997).

Angulogavelinella avnimelechi occurs in outer neritic and upper bathyal deposits of the southern Tethys during the Paleocene (Aubert & Berggren, 1976; Speijer et al., 1995) and is

associated with oxygenated conditions (Alegret et al., 2003). Benthic assemblages of the upper Paleocene of core OS-28 are thus dominated by more oligotrophic taxa, suggesting more oligo- to mesotrophic conditions and moderate to high oxygen concentrations (Figs. 9, 11B).

Lower Eocene

The CIE-“core” interval is marked by a near absence of benthic foraminifera in both cores. The black shale associated with this interval shows a high TOC, a low CaCO₃ content and low H(s) indices (Figs. 2, 3). We suspect that abundant organic matter was delivered to the seafloor that resulted in an oxygen depletion of the bottom waters by partial oxidation of the organic matter. The resultant CO₂, dissolved in the pore-water of the upper-most sediments, reducing the pH and leading to taphonomic alteration of the foraminiferal assemblages. The CIE-“core” interval thus indicates a transition to more anoxic bottom-water conditions, as indicated by deposition of organic-rich layers (e.g., Ernst et al., 2006). Transgressive settings are frequently associated with organic-rich layers (e.g., Hallam & Bradshaw, 1979) and this has been observed in many PETM sections along the Tethyan margin (e.g., Gavrillov et al., 1997; Speijer & Wagner, 2002; Schulte et al., 2011).

The CIE-“recovery” is linked with the upper part of the black shale and the lower part of the limestone in both cores; this interval is characterized by higher abundance of mores species, as observed in various south Tethyan sections (e.g., Speijer & Wagner, 2002). *Lenticulina* spp. and *V. scrobiculata* are considered generalists that react to oxygen-stressed conditions (e.g., Stassen et al., 2009; Deprez et al., 2015). *Anomalinoides zitteli* is assumed to have been a species able to resist lower oxygen concentrations in an oligo- to mesotrophic environment. Increased

abundances of these taxa were likely the response to low-oxygen and mesotrophic- to eutrophic conditions in the Egyptian sections (e.g., Speijer et al., 1997). The benthic assemblages of both cores (*Lenticulina* spp., *V. scrobiculata* and *A. zitteli*), combined with low H(s) indices, high D values in samples with high TOC content, indicate varying organic flux and low to moderate oxygen concentrations at the sea floor.

The post-CIE interval is associated with limestones in both cores and similar Q-mode DCA loadings indicate a continuation of CIE-‘recovery’ environmental conditions. Species such as *A. zitteli*, *Lenticulina* spp. and *V. scrobiculata* are characterized by tolerating low oxygen concentrations (Ernst et al., 2006; Deprez et al., 2015) and are common to abundant in the studied cores. Other common species are *C. rigidus*, *Oridorsalis plummerae* and *A. praeacutus*, which are thought to thrive under better-oxygenated oligo- to mesotrophic conditions (Alegret & Ortiz, 2006; Sprong et al., 2011; Deprez et al., 2015). *Cibicidoides pharaonis* lived in well oxygenated environments (Speijer, 1994; Speijer and Schmitz, 1998). A low TOC content, high CaCO₃ and higher H(s) indices suggest a mesotrophic environment and better-oxygenated bottom water for the most proximal sites (core OS–01) and renewed oxygenation in the distal setting (core OS–28).

PALEOCEANOGRAPHIC SCENARIO

Varying flux of organic matter across the PETM played an important role in the oxygen content of bottom waters at both sites (Fig. 12). Elevated organic flux evidently reduced oxygen concentrations in bottom waters, particularly in the more proximal basin (OS–01) during the Paleocene. This setting was inhabited by the opportunistic *N. duwi* and other less common

species (*A. cf. midwayensis*, *Stilostomella* sp., *Chrysalogonium* spp. and *S. elegantus*). Benthic taxa (*C. rigidus*, *C. pseudoacutus*, *A. avnimelechi*, *G. beccariiiformis* and *N. truempyi*.) recorded from the more distal basin (OS–28) suggest better oxygenation of the bottom waters.

The rarity of benthic foraminifera in the CIE-“core” interval and the co-occurring black shales indicate severe oxygen deficiency, which might have been triggered by increased nutrient supply by river influences in the southern Tethyan margin (e.g., Schulte et al., 2011; Stassen et al., 2012) or alternatively by reduced rates of turnover of bottom waters. The CIE-“recovery” interval is recorded in both cores by abundance increases of *Lenticulina* spp., *V. scrobiculata* and *A. zitteli* and others, suggesting a more mesotrophic setting with oxygen fluctuations in the proximal site (OS–01). Mesotrophic conditions also prevailed in the distal site (OS–28), but the oxygen content increased gradually. The combination of organic-rich layers and intervals of varying oxygen depletion during the PETM were linked to transgressive settings and shelf onlap of the oxygen-depletion zone (e.g., Speijer & Wagner, 2002; Schulte et al., 2011).

The post-CIE interval is characterized by different Eocene benthic associations indicating mesotrophic settings with better-oxygenated bottom water for the most proximal site (OS–01) and renewed oxygenation in the distal setting (OS–28). The continued supply of organic matter during the Eocene with sustained oxygen concentration at the sea floor may have been influenced by more periodic nutrient pulses, potentially controlled by seasonal riverine influence or by more frequent turnover of deep waters. The episodic organic flux allowed for a restoration of better-oxygenated seafloor conditions during the remainder of the year, contrasting the deposition of black shales during the PETM.

CONCLUSIONS

Benthic foraminiferal analyses covering the upper Paleocene and lower Eocene from two cores in Jordan allowed the interpretation of environmental changes, which reflect changes in water depth, organic flux to the seafloor and the oxygenation of waters that influenced the benthos across the Paleocene–Eocene boundary.

- The pre-CIE interval in the most proximal site (OS–01) contains a mixture of characteristic shallow-water and deeper-dwelling taxa, indicative of a middle to outer neritic setting and meso- to eutrophic conditions, in which the benthic foraminiferal assemblage was dominated by *Neoponides duwi*. The pre-CIE interval in the more distal site (OS–28) is associated with more deep-water taxa (*Cibicidoides pseudoacutus*, *Cibicidoides rigidus*, *Angulogavelinella avnimelechi*, *Gavelinella beccariiformis* and *Nuttallides truempyi*). These sediments were deposited in outer neritic to upper bathyal settings, under oligo- to mesotrophic, well oxygenated conditions.
- The CIE-“core” interval is marked by a near absence of benthic foraminifera and, high TOC content in black shales, indicating severe oxygen deficiency in both cores.
- The CIE-“recovery” interval of core OS–01 is characterized by a high TOC content and high abundance of *Lenticulina* spp., *Valvulineria scrobiculata* and common *Anomalinoides zitteli*. Low oxygen conditions and meso- to eutrophic bottom waters are proposed for this interval. Low TOC content and the presence of *Lenticulina* spp., *Valvulineria scrobiculata*, *Anomalinoides zitteli* and *Oridorsalis plummerae* throughout the CIE-“recovery” interval in core OS–28 suggest a moderate organic flux and oxygen concentrations near the sea floor.

- The post-CIE interval in core OS–01 is characterized by a low TOC content, abundant *Anomalinoides zitteli* and common *Lenticulina* spp., *Valvulineria scrobiculata*, *Oridorsalis plummerae*, *Cibicidoides rigidus*, *Cibicidoides pharaonis* and *Anomalinoides praeacutus*. These foraminifera indicate mesotrophic conditions and relatively well oxygenated bottom waters. Low TOC content and diverse benthic assemblages (*Lenticulina* spp., *Valvulineria scrobiculata* and *Oridorsalis plummerae*) also are associated with the post-CIE interval in core OS–28. Mesotrophic conditions with renewed seafloor oxygenation are suggested for this interval.

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APPENDIX 1. Taxonomic information on benthic foraminifera cited in the text, figures and tables can be found in the works of LeRoy(1953), Van Morkhoven et al. (1986), Speijer (1994). Calcareous nannofossils quoted in this study can be found in Perch-Nielsen (1985) and Bown (1998, 2005).

APPENDIX 2. Supplementary data: benthic foraminifera counts. This appendix can be found on the Cushman Foundation website in the JFR Article Data Repository (<http://www.cushmanfoundation.org/jfr/index.html>) as item number JFR_DR_20180**.

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TABLE 1. Paleoecological preferences of benthic foraminifera according their morphotype (Epi: epibenthic; Endo: endobenthic) based on Corliss & Chen (1988). Paleodepth preferences of most frequent taxa studied during the PETM in Jordan. The terms inner neritic (IN: 0–50 m), middle neritic (MN: 50–100 m), outer neritic (ON: 100–200 m) and upper bathyal (UB: 200–500 m) are used for paleodepths. Thick solid lines represent most frequent occurrences, thin solid lines common occurrences. Epi: epibenthic; Endo: endobenthic. Based on: Van Morkhoven et al. (1986)¹; Corliss, (1991)²; Saint-Marc, (1992)³; Kuhnt & Kaminski (1993)⁴; Kaiho (1994)⁵; Speijer (1994)⁶; Speijer et al. (1995)⁷; Speijer et al. (1996)⁸; Speijer et al. (1997)⁹; Widmark & Speijer (1997)¹⁰; Speijer & Schmitz (1998)¹¹; Schnack (2000)¹²; Speijer (2003)¹³; Alegret et al. (2003)¹⁴; Guasti (2005)¹⁵; Ernst et al. (2006)¹⁶; Alegret & Ortiz (2006)¹⁷; Kouwenhoven & Van der Zwaan (2006)¹⁸; Stassen et al. (2009)¹⁹; Schulte et al. (2011)- Ernst et al. (2006)²⁰; Sprong et al. (2011)²¹; Stassen et al. (2012)²²; Sprong et al. (2012)²³; Moebius et al. (2014)²⁴; Stassen et al. (2015)²⁵; Deprez et al. (2015)²⁶.

Cluster	Taxa	Morphotypes		Oxygen			Paleodepth				References
		Epi	Endo	Low	Middle	High	50 IN	100 MN	200 ON	UB	
A	<i>Anomalinoides</i> cf. <i>midwayensis</i>	X									16, 17, 19
	<i>Siphogenerinoides elegantus</i>		X								5, 11, 12, 23
	<i>Neoeponides duwi</i>	X									12, 13, 16, 21, 23
	<i>Stilostomella</i> spp.		X								5, 11, 16, 23, 25
	<i>Valvalabamina depressa</i>	X									5, 11, 21
	<i>Chrysalogonium</i> sp.		X								24
B	<i>Angulogavelinella avnimelechi</i>	X									1, 5, 6, 11, 14, 21
	<i>Cibicidoides pseudoacutus</i>	X									5, 8, 11
	<i>Hanzawaia</i> cf. <i>caribaea</i>	X									1, 7, 11
	<i>Gavelinella beccariiiformis</i>	X									1, 5, 6, 16, 24
	<i>Cibicidoides alleni</i>	X									3, 5, 6, 12, 25
	<i>Laevidentalina</i> spp.		X								5, 14
	<i>Gyrogoninoides girardanus</i>	X	X								5, 11, 12, 14, 22
	<i>Spiroplectinella esnaensis</i>	X									6, 10, 12
	<i>Anomalinoides praeacutus</i>	X									11, 17, 26
C	CI	<i>Anomalinoides affinis</i>	X								5, 8, 11, 14
		<i>Anomalinoides rubiginosus</i>	X								5, 11, 14, 19, 22
		<i>Cibicidoides rigidus</i>	X								16, 26
		<i>Nuttallides truempyi</i>	X								1, 5, 6, 9, 10, 11, 26
		<i>Oridorsalis plummerae</i>	X								5, 11, 21
		<i>Valvalabamina planulata</i>	X								5, 11, 21
	CII	<i>Anomalinoides zitteli</i>	X								5, 9, 11, 12, 16, 25
		<i>Spiroloculina</i> sp.	X								16, 19, 26
		<i>Cibicidoides pharaonis</i>	X								5, 6, 11
		<i>Bulimina farafraensis</i>		X							11, 12, 20
		<i>Osangularia plummerae</i>	X								3, 6, 11, 12, 21, 23, 25, 26
	<i>Alabamina midwayensis</i>		X								5, 11, 12, 16, 25
	CIII	<i>Gaudryna ellisorae</i>	X								4, 6, 11
		<i>Lenticulina</i> spp.	X	X							9, 11, 16, 17, 20, 25, 26
		<i>Nodosaria</i> spp.		X							2, 18
		<i>Loxostomoides applinae</i>		X							11, 20, 23, 26
		<i>Valvulineria scrobiculata</i>	X								5, 6, 11, 20, 22, 26
		<i>Pullenia jarvisi</i>		X							7, 14

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FIGURE 1. **A.** Paleogeographic map of the Tethyan Ocean during the late Cretaceous and early Paleogene. Modified from Li & Keller (1988), Abed (2013), Alqudah et al. (2014). **B.** Location map of cores OS-01 and OS-28 in Jordan.

OS-01

FIGURE 2. Lithology and biostratigraphy of core OS-01 based on calcareous nannofossils (Martini, 1971; Aubry 1995, 1999). Geochemical data ($\delta^{13}\text{C}_{\text{org}}$, CaCO_3 and TOC) and foraminiferal parameters (%P, BFN-PFN = benthic and planktonic foraminifera/gram sediment, Shannon diversity $H(s)$ and dominance (D) of benthic assemblages) are displayed for the Paleocene–Eocene transition.

OS-28

FIGURE 3. Lithology and biostratigraphy (Giraldo et al., 2016) of core OS–28. Geochemical data ($\delta^{13}\text{C}_{\text{org}}$, CaCO_3 and TOC) and foraminiferal parameters (%P, BFN-PFN = benthic and planktonic foraminifera/gram sediment, Shannon diversity $H(s)$ and dominance (D) of benthic assemblages) are displayed for the Paleocene–Eocene transition.

FIGURE 4. Benthic foraminifera of core OS-01. All scale-bars represent 100 μm . **1** *Neoeponides duwi* (61.50 m; OS-01); **2** *Anomalinoides zitteli* (60.90 m; OS-01); **3** *Oridorsalis plummerae* (60.50 m; OS-01); **4** *Anomalinoides affinis* (60.70 m; OS-01); **5** *Valvulineria scrobiculata* (60.70 m; OS-01); **6** *Angulogavelinella avnimelechi* (61.40 m; OS-01); **7** *Cibicidoides rigidus* (61.50 m; OS-01); **8** *Nuttallides truempyi* (60.10 m; OS-01); **9** *Spiroloculina* sp. (60.50 m; OS-01); **10** *Stilostomella* sp. (60.70 m; OS-01); **11** *Anomalinoides rubiginosus* (60.50 m; OS-01); **12** *Anomalinoides praeacutus* (61.30 m; OS-01); **13** *Sporobulimina eocaena* (61.30; OS-01); **14** *Spiroplectinella esnaensis* (60.10 m; OS-01); **15** *Lenticulina* sp. (61.50 m; OS-01); **16** *Bulimina farafraensis* (60.90 m; OS-01); **17** *Gaudryina ellisorae* (60.00 m; OS-01); **18** *Loxostomoides applinae* (60.70 m; OS-01); **19** *Neoeponides duwi* (61.40 m; OS-01).

FIGURE 5. Benthic foraminifera of core OS-28. All scale-bars represent 100 μm . **1** *Alabamina midwayensis* (47.00 m; OS-28); **2** *Gyroidinoides girardanus* (48.70 m; OS-28); **3** *Angulogavelinella avnimelechi* (48.70 m; OS-28); **4** *Cibicidoides* sp. (44.50 m; OS-28); **5** *Tappanina selmensis* (47.00 m; OS-28); **6** *Nuttallides truempyi* (48.70 m; OS-28); **7** *Anomalinoides rubiginosus* (48.70 m; OS-28); **8** *Gavelinella beccariiiformis* (48.00 m; OS-28); **9** *Anomalinoides* cf. *midwayensis* (47.00 m; OS-28); **10** *Pullenia jarvisi* (48.00 m; OS-28); **11** *Anomalinoides affinis* (48.50 m; OS-28); **12** *Lenticulina* sp. (48.00 m; OS-28); **13** *Bulimina* sp. (48.50 m; OS-28); **14** *Siphogenerinoides elegantus* (47.00 m; OS-28); **15** *Dentalina* sp. (44.00 m; OS-28); **16** *Spiroplectammina spectabilis* (48.50 m; OS-28); **17** *Loxostomoides applinae* (48.70 m; OS-28); **18** *Nodosaria* sp. (43.50 m; OS-28); **19** *Marginulina tuberculata* (44.00 m; OS-28); **20** *Marginulina wetherellii intercostata* (45.00 m; OS-28).

FIGURE 6. Relative abundances of the most common taxa of benthic foraminifera in core OS-01 ($\geq 2\%$ in at least one sample) showing the cluster associations. (Rest: other species $< 2\%$ and undetermined taxa).

FIGURE 7. Relative abundances of the most common taxa of benthic foraminifera in core OS-28 ($\geq 2\%$ in at least one sample) showing the cluster associations. (Rest: other species $< 2\%$ and undetermined taxa).

FIGURE 8. $\delta^{13}\text{C}_{\text{org}}$, TOC, relative abundances of the three clusters A, B, C (CI, CII, CIII) and the benthic foraminiferal morphotypes of the most proximal site (core OS-01) are plotted versus the first and second axes of the DCA.

FIGURE 9. $\delta^{13}C_{org}$, TOC, relative abundances of the three clusters A, B, C (CI, CII, CIII) and the benthic foraminiferal morphotypes of the most distal site (core OS-28) are plotted versus the first and second axes of the DCA.

FIGURE 10. Cluster analysis (Pearson correlation paired groups) division of the foraminiferal benthic assemblages in clusters A, B and C (CI, CII, CIII), for the cores OS-01 and OS-28.

FIGURE 11. Results of the detrended correspondence analysis (DCA) represented by the first and second axes (explaining respectively 40.1% and 18.8% of the variance). **A.** Bivariate plot of Q-mode DCA represents the samples analyzed from cores OS-01 and OS-28 in the pre-CIE, the CIE-“recovery” and the post-CIE intervals. **B.** Biplot of R-mode DCA indicating the most common taxa ($\geq 2.0\%$ in at least one sample) in both cores.

BENTHIC FORAMINIFERA

- Alabamina midwayensis* Brotzen, 1948
- Angulogavelinella avnimelechi* (Reiss, 1952)
- Anomalinoides aegyptiacus* (LeRoy, 1953)
- Anomalinoides affinis* (Hantken, 1875)
- Anomalinoides* cf. *midwayensis* (Plummer, 1926)
- Anomalinoides praeacutus* (Vasilenko, 1950)
- Anomalinoides rubiginosus* (Cushman, 1926)
- Anomalinoides umboniferus* (Schwager, 1883)
- Anomalinoides zitteli* (Leroy, 1953)
- Bulimina callahani* Galloway and Morrey, 1931
- Bulimina farafraensis* LeRoy, 1953
- Bulimina midwayensis* Cushman and Parker, 1936
- Bulimina quadrata* Plummer, 1926
- Cibicidoides alleni* Plummer, 1926
- Cibicidoides* cf. *hyphalus* (Fisher, 1969)
- Cibicidoides pharaonis* LeRoy, 1953
- Cibicidoides pseudoacutus* (Nakkady, 1950)
- Cibicidoides rigidus* (Nakkady, 1959)
- Cibicidoides succedens* (Brotzen, 1948)
- Coryphostoma incrassata* Reuss, 1851

Coryphostoma midwayensis (Cushman, 1936)

Ellipsopolymorphina velascoensis (Cushman, 1926)

Gaudryina ellisorae Cushman, 1936

Gavelinella beccariiiformis (White, 1928)

Gyroidinoides girardanus (LeRoy, 1953)

Hanzawaia cf. *caribaea* Cushman and Bermudez, 1936

Laevidentalina gracilis D'Orbigny, 1840

Laevidentalina paradoxa Hussey, 1949

Lenticulina Lamarck, 1804

Loxostomoides applinae (Plummer, 1926)

Marginulina tuberculata (Plummer, 1926)

Marginulina wetherellii intercostata (Nakkady, 1950)

Neoflabellina delicatissima (Plummer, 1926)

Neoeponides duwi (Nakkady, 1950)

Nodosaria affinis (d'Orbigny, 1846)

Nonion havanense Cushman and Bermudez, 1937

Nuttallides truempyi (Nuttall, 1930)

Oridorsalis plummerae (Cushman, 1948)

Osangularia plummerae Brotzen, 1940

Pleurostomella velascoensis Cushman, 1926

Pullenia americana Cushman, 1946

Pullenia coryelli White, 1929

Pullenia jarvisi Cushman, 1936

Pullenia quinqueloba (Reuss, 1851)
Siphogenerinoides elegantus (Plummer, 1927)
Spiroplectammina spectabilis (Grzybowski, 1898)
Spiroplectinella esnaensis (LeRoy, 1953)
Sporobulimina eocaena Bykova, 1959
Tappanina selmensis (Cushman, 1936)
Turrilina brevispira ten Dam, 1944
Valvalabamina depressa (Alth, 1850)
Valvalabamina planulata (Cushman and Renz, 1941)
Valvulineria scrobiculata (Schwager, 1883)
Vulvulina colei Cushman, 1932

CALCAREOUS NANNOFOSSILS

Discoaster Tan, 1927
Discoaster araneus Bukry, 1971
Discoaster multiradiatus Bramlette and Riedel, 1954
Rhomboaster Bramlette and Sullivan, 1961
Rhomboaster cuspis Bramlette and Sullivan, 1961
Tribrachiatus Shamrai, 1963
Tribrachiatus bramlettei (Proto Decima et al., 1975)