Tropical Atlantic Climate and Ecosystem Regime Shifts during the Paleocene-Eocene Thermal Maximum

Frieling, Joost[1], Reichart, Gert-Jan[2,3], Middelburg, Jack J.[2], Röhl, Ursula[4], Westerhold, Thomas[4],

5 Bohaty, Steven[5], and Sluijs, Appy[1]

[1] Marine Palynology and Paleoceanography, Laboratory of Palaeobotany and Palynology, Department of Earth Sciences, Faculty of Geosciences, Utrecht University, Heidelberglaan 2, 3584CS Utrecht, Netherlands

[2] Department of Earth Sciences, Faculty of Geosciences, Utrecht University, Princetonplein 9, 3584CC Utrecht, Netherlands

[3] NIOZ Royal Netherlands Institute for Sea Research, 1790AB Den Burg, Texel, Netherlands

10 [4] MARUM, Leobener Straße 8, 28359, Bremen, Germany

[5] Ocean and Earth Science, National Oceanography Centre Southampton, University of Southampton, Waterfront Campus European Way Southampton, SO14 3ZH United Kingdom

Correspondence to: J. Frieling (j.frieling1@uu.nl)

15 **Abstract.** The Paleocene – Eocene Thermal Maximum (PETM; 56 Ma) was a phase of rapid global warming associated with massive carbon input into the ocean-atmosphere system from a ^{13}C-depleted reservoir. Many mid- and high-latitude sections have been studied and document changes in salinity, hydrology and sedimentation, deoxygenation, biotic overturning and migrations, but detailed records from tropical regions are lacking. Here, we study the PETM at Ocean Drilling Program (ODP) Site 959 in the equatorial Atlantic using a range of organic and inorganic proxies and couple these with dinoflagellate

20 cyst (dinocyst) assemblage analysis. The PETM at Site 959 was previously found to be marked by a ~3.8‰ negative carbon isotope excursion (CIE), and a ~4 ºC surface ocean warming from the uppermost Paleocene to peak PETM, of which ~1 ºC occurs before the onset of the CIE. We record upper Paleocene dinocyst assemblages that are similar to PETM assemblages as found in extra-tropical regions, confirming poleward migrations of ecosystems during the PETM. The early stages of the PETM are marked by a typical acme of the tropical genus *Apectodinium*, which reaches abundances of up to 95%.

25 Subsequently, dinocyst abundances diminish greatly, as do carbonate and pyritized silicate microfossils. The combined paleoenvironmental information from Site 959 and a close by shelf site in Nigeria implies the general absence of eukaryotic surface-dwelling microplankton during peak PETM warmth is most likely caused by heat stress. Crucially, abundant organic benthic foraminiferal linings imply sustained export production, likely driven by prokaryotes. In sharp contrast, the recovery of the CIE yields rapid (<<10 kyr) fluctuations in the abundance of several dinocyst groups, suggesting extreme ecosystem

30 and environmental variability.

1. Introduction

Long-term gradual warming during the Late Paleocene and Early Eocene (~59-53 Ma) is recorded in the deep ocean (Zachos et al., 2008; Littler et al., 2014), as well as Southern hemisphere (Bijl et al., 2009; Hollis et al., 2012) and Northern hemisphere (Frieling et al., 2014) mid- and high-latitude surface oceans and equatorial Atlantic (Cramwinckel et al., in prep.). Superimposed, the Paleocene-Eocene Thermal Maximum (PETM) represents a transient period of rapid global warming, associated with the massive input of strongly ^{13}C-depleted carbon into the ocean-atmosphere system (Dickens et al., 1995; Zeebe et al., 2009). This results in a ~2.5-8 ‰ negative carbon isotope excursion (CIE) in carbon-bearing substrates deposited during the PETM (McInerney and Wing, 2011; Sluijs and Dickens, 2012). The CIE has a distinct shape; a rapid "onset" (1-5 kyr; (Kirtland Turner and Ridgwell, 2016; Zeebe et al., 2016) followed by a prolonged (50-70 kyr) period, the "body", of stable low ^{13}C values and a recovery that lasts 42 - 100 kyr (Röhl et al., 2007; Abdul Aziz et al., 2008; Murphy et al., 2010) to values that remain slightly ^{13}C-depleted (0.5-1 ‰) relative to the latest Paleocene. This pattern is best explained by massive (>>1500 Gt) carbon input from at least 1 but likely multiple reservoirs in the shape of CO_2 and/or CH_4; (Panchuk et al., 2008; Zeebe et al., 2009; Zeebe, 2013; Frieling et al., 2016; Luo et al., 2016).

The integrated changes in climate and the carbon cycle lead to global average surface warming during the PETM in the order of ~4-5 ºC (Dunkley Jones et al., 2013; Frieling et al., 2017), although this warming was not equally distributed across the globe. Regions of enhanced warming are recognized in both the Northern mid and Southern mid and high latitudes, which shows the mechanism underlying extra-tropical amplification was not fully saturated even in these strong greenhouse climates (Frieling et al., 2017). The warming during the PETM is associated with sea level rise (Sluijs et al., 2008), local photic zone euxinia (Sluijs et al., 2006, 2014, Frieling et al., 2014, 2017), global expansion of anoxic waters (Dickson et al., 2012) and an accelerated hydrological cycle (Pagani et al., 2006; Schmitz and Pujalte, 2007; Sluijs and Brinkhuis, 2009; Handley et al., 2012).

The magnitude of warming during the PETM and environmental and ecological effects have been extensively documented at mid and high-latitude sections (see review in Sluijs et al., 2014). Although micropaleontological studies indicate assemblage shifts and environmental perturbation in several tropical open ocean regions (e.g., Ocean Drilling Program (ODP) Site 865; Kelly et al., 1996, ODP Site 1001; Bralower et al., 1997) the underlying mechanisms remain unclear because causal relations with physicochemical parameters are difficult to establish. Evidence from Tanzania, Nigeria and ODP Site 865 indicates that tropical surface oceans warmed by ~3 °C (Frieling et al., 2017). In the modern ocean, a relatively modest (0.5-1 °C) warming already negatively affects biodiversity in tropical regions (Pandolfi et al., 2011). In the Anthropocene migrations to higher latitudes are noted in a multitude of biota (Doney et al., 2012), similar to the PETM (Kelly et al., 1996; Crouch et al., 2001; Wing et al., 2005; Sluijs et al., 2007b), notably in the (sub)tropical dinocyst *Apectodinium*.

Recently, a massive decrease in biodiversity of dinocysts was found during the PETM in Nigeria, which was attributed to heat stress (Frieling et al., 2017). The impact and geographical extent of this heat-stress driven biodiversity drop however remain unknown, although similar heat-stress effects on marine biota may have been widespread in tropical regions (Aze et al., 2014; Yamaguchi and Norris, 2015). Although other stressors like stratification, salinity fluctuations and acidification

5 may play a role, it should be noted that dinoflagellates typically thrive under such conditions, including very high CO_2 (Hoins et al., 2015). Here, we analyze the PETM from ODP Site 959 in the equatorial Atlantic (Figure 1) as recently described using carbon isotope stratigraphy, biostratigraphy and TEX_{86} paleothermometry (Frieling et al., submitted). Site 959 is located near the top of the Cote d'Ivoire – Ghana Transform Margin (CIGTM), a submarine high ~150 km offshore Ivory Coast (Shipboard Scientific Party, 1996). Upper Paleocene and lower Eocene sediments were deposited at a

10 paleolatitude of 3 - 7° S (Seton et al., 2012; van Hinsbergen et al., 2015) and are typically composed of roughly equal amounts of carbonate, biogenic silicate and siliciclastics (Shipboard Scientific Party, 1996; Wagner, 2002) with some (0.1-1%) organic matter. We measure bulk magnetic susceptibility and apply inorganic proxies, including X-ray fluorescence core scanning and bulk sediment chemistry and combine these with dinocyst assemblages and previously published TEX_{86}, Branched versus Isoprenoid Tetraether (BIT) index data (Frieling et al., submitted) to reconstruct environments across the

15 PETM.

2. Material

The Ocean Drilling Program recovered a relatively complete Cretaceous and Cenozoic sediment sequence from Hole 959D, located on the CIGTM, in 1995 (3°37.656'N, 2°44.149'W; Figure 1). From the Early Cretaceous onwards, the submarine

20 high has been subsiding, reaching bathyal depths around the Cretaceous – Paleogene boundary (Oboh-Ikuenobe et al., 1997) and present day water depth is ~2000m. Calcareous nannofossil biostratigraphy indicates the presence of the upper Paleocene CP8a-CP8b zone boundary in the interval from Core section 41R-6 to Core section 42R-2 mbs (Shafik et al., 1998). The PETM was identified in Core section 42R-1 and spans the interval 804.1 – 802.6 meters below sea floor (mbsf) based on the identification of the CIE and 4 °C warming (Frieling et al., submitted). Unfortunately, the top of the CIE lies

25 within the ~1 m gap between Cores 41R and 42R. Notable lithological changes occur in the interval from 804.1 mbsf to ~803.8 mbsf, where dominantly carbonate and siliciclastic sedimentation is for a substantial part replaced by diagenetically altered biogenic silicates (porcellanite) (Shipboard Scientific Party, 1996; Wagner, 2002). The sediments above Core section 41R-6 are recognized by more frequent occurrences of porcellanite (Shipboard Scientific Party, 1996; Wagner, 2002). Sediments below Core section 42R-1 show apparently cyclic dark-light alterations, representing variable amounts of clay,

30 carbonate and biogenic silica (Shipboard Scientific Party, 1996; Wagner, 2002). The position of the site, near the top of a submarine high, implies that relatively little siliciclastic material reaches the core location. We continuously sampled Core sections 41R-6, 41R-CC, 42R-1 and 42R-2 at the Bremen Core Repository (BCR) of the International Ocean Discovery

Program (IODP), representing the interval from 800.5 to 805.58 mbsf at a resolution of 1-3 cm (see Frieling et al., submitted).

The organic-lean biogenic silica and siliciclastics (804.1 – 803.8 mbsf) are likely derived from an allochthonous, potentially turbiditic, deposit, as reflected by anomalous Ti/Al ratios (Frieling et al., submitted), and obscures the exact onset of the carbon isotope excursion (CIE). Carbon isotope stratigraphy of total organic carbon ($\delta^{13}C_{TOC}$) indicates the presence of a 2 ‰ negative step at the base of the porcellanite (804.1 mbsf) and stable low (~ -30‰) values from 803.8 to 803 mbsf show the presence of the body phase of the PETM (Frieling et al., submitted, Figure 2a). The gradual decrease from ~ -27‰ at 804.09 mbsf to -30‰ at 803.8 mbsf is interpreted as a mixing line between organic matter produced during the Paleocene and the PETM (Frieling et al., submitted). From 803 to 802.6 mbsf there is an increase to values ~1.5 ‰ lower than background Paleocene. A core gap 801.6 - 802.6 mbsf conceals the end of the recovery phase. Core 41R-6 and 41R-CC are characterized by earliest Eocene values, about 0.7 ‰ lower than latest Paleocene. Although no indications for gaps were observed during sampling, the two distinct steps in the $\delta^{13}C_{TOC}$ record may indicate very small hiatuses; one at 804.1 mbsf and one at 803.0 mbsf (Figure 2). Paleocene accumulation rates are in the order of ~1.3 cm kyr^{-1}, based on calcareous nannofossil biostratigraphy (Shafik et al., 1998) and a cyclostratigraphic age model based on variations in TOCwt% (Frieling et al., submitted).

3 Methods

3.1 Sample handling

All discrete samples taken from the working halves were freeze-dried and measured for bulk magnetic susceptibility before splitting them into fractions for palynology, inorganic and organic geochemical analysis.

3.2 Bulk Magnetic susceptibility

Freeze-dried samples were weighed and measured for bulk magnetic susceptibility on an MFK1-FA at the Paleomagnetism laboratory, Fort Hoofddijk, Utrecht University. Reproducibility was determined by replicate measurements and was always better than 1%.

3.3 Palynology

We processed and counted a total of 155 samples, using standard protocols used at the Laboratory of Palaeobotany and Palynology at Utrecht University (Sluijs et al., 2003). In brief, a spike of exote *Lycopodium clavatum* spores (n = 20848 ± 691) was added to 1-10 g of freeze-dried sample to allow for absolute quantitative analysis (Stockmarr, 1971). To dissolve carbonates, sediments were first treated with 10% HCl, after which supernatants were decanted. This was followed up by two steps of 38-40% HF and 30% HCl to dissolve silicates. Samples were centrifuged and neutralized with tap water before sieving over 250 and 15 μm sieves to remove large and small particles, respectively. Subsequently, residues were

concentrated in glycerine water and mounted on microscope slides using glycerine jelly. We followed dinocyst taxonomy of Fensome, (2004) and the paleoecological grouping of (Sluijs and Brinkhuis, 2009). Unlike Sluijs and Brinkhuis, (2009), we separate Protoperidinioid dinocysts from the other Peridinioid types with hexagonal 2a archeopyles. Where possible, a minimum of 200 dinocysts was counted. For samples with very low numbers of dinocysts, slides were fully counted to a

5   total of ~10-100 dinocysts. We estimated the abundance of pyritized remains of biogenic silica relative to organic particles in each sample. A full list of encountered dinocyst taxa is given in Supplementary Table 1. All materials are stored in the collection of the Laboratory of Palaeobotany and Palynology, Utrecht University.

3.4 XRF Core Scanning.

XRF Core Scanner data were collected every 1 cm down-core over a 1 cm^2 area with slit size of 10 mm using generator

10   settings of 10 kV and 50kV, a current of 0.2 mA and 1.0 mA respectively, and a sampling time of 30 seconds directly at the split core surface of the archive halves of Core sections 41R-6, 42R-2 and lower part of 42R-1 with XRF Core Scanner III at the MARUM - University of Bremen. The split core surface was covered with a 4 μm SPEXCerti Prep Ultralene foil to avoid contamination of the XRF measurement unit and desiccation of the sediment. The dark-colored interval from 803.8 mbsf to 803 mbsf and directly overlying sediment in Core section 42R-1 was too fragmented for acquiring reliable core

15   scanning measurements. The here reported data have been acquired by a Canberra X-PIPS Detector (X-PIPS SXP5C-200-1500 from Canberra) with 150eV X-ray resolution, the Canberra Digital Spectrum Analyzer DAS 1000 and an Oxford Instruments 100W Neptune X-ray tube with rhodium (Rh) target material. Raw data spectra were processed by the Analysis of X-ray spectra by Iterative Least square software (WIN AXIL) package from Canberra Eurisys.

3.5 Bulk sediment chemistry from Inductively Coupled Plasma - Optimal Emission Spectroscopy (ICP-OES)

20   Bulk sediment chemistry was determined on 28 samples in the interval that could not be used for XRF core scanning and 22 samples from intervals with XRF scanning data to assess consistency between the two methods. Approximately 125 mg of powdered freeze-dried sediment was dissolved in 2.5 ml HF (40 %) and 2.5 ml of $HClO_4/HNO_3$ mixture, in a closed Teflon bomb at 90 °C during one night. The acids were then evaporated at 160 °C and the resulting gel was subsequently redissolved in 1M HNO_3 at 90 °C during another night. Subsequently, total elemental concentrations were determined by

25   ICP-OES (Perkin Elmer Optima 3000 Inductively Coupled Plasma - Optimal Emission Spectroscopy) at Utrecht University. Precision and accuracy was better than 5 %, based on calibration to standard solutions and checked against internal laboratory sediment standards. All elemental ratios are normalized to Al, except for organic carbon over total phosphorus (Corg/Ptot), which is reported in mol mol^{-1}.

3.6 Carbonate percentage measurements

30   The carbonate concentration of Site 959 samples was determined at the University of Southampton using a UIC CM5015 coulometer operated with a UIC CM5011 emulator and coupled to an AutoMateFX autosampler and carbonate digestion system. The samples were oven-dried at 50°C, crushed with an agate mortar and pestle, placed in a glass vial, and oven dried

again after crushing. Each vial was capped immediately after removal from the oven to prevent the samples from taking on moisture. Depending on estimated carbonate content, 10–40μg of bulk dry sample was weighed out on a Sartorius ME5 microbalance and placed in a septum-capped autosampler vial prior to each run. A total of 59 samples were analysed across six runs on separate days, with repeat analyses performed on ~25% of the samples. Each run was calibrated using blank-

5   corrected counts for a calcium carbonate standard (Acros Organics, 99.999% pure) spanning a mass range of 2–10μg. External precision is estimated at ±0.6% $CaCO_3$ based on results from a consistency standard that was included in all runs (average=73.1%; n=12). The detection limit was determined from a compilation of blank analyses from all runs (n=24), and using the average blank counts plus 3×s.d., the detection limit for a typical 15mg sample was calculated to be 0.08% $CaCO_3$.

4. Results

10   ### 4.1 Palynology

Dinocysts typically dominate the palynological residues. Pollen and spores derived from terrestrial higher plants are present but in very low abundances (average ~1%; 40 g^{-1}). The body of the PETM CIE and the corresponding interval with higher TOC is marked by high abundances of organic linings of benthic foraminifera. Upper Paleocene dinocyst assemblages are composed of three major components (Figure 2c). The most abundant component is the generalist group *Spiniferites*,

15   followed by *Apectodinium* and Goniodomideae with an epicystal archeopyle (hereafter referred to as Goniodomideae; see Sluijs and Brinkhuis, (2009), for taxonomic descriptions of the groups and complexes). Within the uppermost Paleocene, representatives of the *Areoligera* cpx increase in abundance. The onset of the PETM is marked by an acme of *Apectodinium*, reaching highest abundances (>90%) between 803.89 and 803.77 mbsf. The body of the PETM CIE yields extremely low abundances of dinocysts (100-200 gram $^{-1}$) so that percentages are based on counts below 200 specimens and should hence

20   be interpreted as rough estimates (open circles in Figure 2). Regardless, assemblages within the body of the CIE are mostly composed of Goniodomideae, *Spiniferites* and *Apectodinium*. *Senegalinium* and Protoperidinioid cysts occur almost exclusively during the body of the CIE. High cyst concentrations (>10^4 gram $^{-1}$) and a series of ~10 subsequent acmes of different dinocyst groups mark the recovery of the CIE (Figure 2c). Towards the top of the analyzed interval, *Florentinia reichartii* becomes the dominant species. Several groups show abundance peaks in the interval following the recovery of the

25   CIE.

4.2 Carbonate weight %

Apart from sediments close to the PETM, the studied interval typically comprises 10-30 weight % $CaCO_3$ (Figure 3f). However, $CaCO_3$ is below the detection limit in an interval starting just below the CIE, at 804.2 mbsf. Various methods, i.e. weight loss during decalcification, $CaCO_3$ based on ICP-OES analysis of Ca concentrations and dedicated $CaCO_3$

30   measurements show similar trends (Figure 3f). We use the weight loss during HCl-treatment as a high-resolution approximation for $CaCO_3$ outside the PETM. Especially across the PETM the weight loss during decalcification is strongly

influenced by dissolution of HCl-soluble salts and minerals, especially gypsum, which accounts for 5-10% of sediment weight in some parts of the CIE.

4.3 Bulk sediment chemistry (XRF and ICP-OES)

We use elemental ratios to reconstruct hinterland hydrology and redox sensitive trace elements to reconstruct bottom water oxygenation for the site location. The Ti/Al ratios from XRF core scanning and ICP-OES analysis show similar trends, with a gradual rise in the upper Paleocene and second sharp increase at the base of the porcellanite that marks the onset of the CIE (804.1 - 803.8 mbsf, Figure 3g). Hereafter, values drop and remain consistently lower than in the upper Paleocene within the body and recovery phases of the CIE. K/Al ratios correlate well with TOCwt%. Concentrations are slightly higher within the CIE than in the upper Paleocene and interrupted by a sharp drop in the porcellanite layer. The CIE is also marked by elevated concentrations of Cr, S, Ni, V, Zn and progressively higher Corg / Ptot ratios (Cr/Al, V/Al and Corg/Ptot; Figure 3i).

4.4 Magnetic susceptibility

Magnetic susceptibility is anti-correlated with carbonate percentages in the upper Paleocene. At 804.2 mbsf, before the onset of the CIE, this relation disappears. The porcellanite layer is marked by low magnetic susceptibility and the body of the CIE is marked by stable high values. A maximum is reached during the recovery phase, at 802.97 mbsf, followed by a second maximum at 802.81 mbsf. Bulk magnetic susceptibility measurements closely resemble Fe concentrations derived from both ICP-OES and XRF (Figure 3j) and correlate to %TOC in the upper Paleocene and lower part of the CIE.

5. Discussion

5.1 Background cyclic variability

The latest Paleocene at the core location is characterized by cyclic variations in proxy records, including total organic carbon content (TOC), dinocysts per gram of sediment, magnetic susceptibility and $CaCO_3$ content (Figure 3). (Frieling et al., submitted) attributed the cycles to climatic precession (21 kyrs). Implied latest Paleocene average accumulation rates are 1-1.5 cm kyr^{-1}, which is consistent with the available nannofossil biostratigraphy. Additional cycles recorded may be recorded during the PETM in K/Al ratios (Figure 3g), but these are not unambiguous in other proxy-records that show similar cyclic variations in the Paleocene (e.g. TOCwt% and Fe). However, if these K/Al variations also represent precession, it may imply a two-fold increase in accumulation rate. Cyclic variability is notably absent in dinocyst assemblages, $\delta^{13}C_{TOC}$, TEX_{86}^{H} derived temperatures and Ti/Al ratios. This observation is important since we can, although with caution, use these as indicators of environmental change that is not associated with background cyclic variability.

5.2 Depositional setting, sea level, bottom-water oxygen levels

5.2.1 Latest Paleocene Background State

Dinocyst assemblages in the Paleocene are characterized by abundant *Spiniferites* spp. and *Apectodinium* spp. Absolute numbers of dinocysts correlate well with TOCwt%, but also with K/Al ratio. In tropical regions, K/Al ratios vary with wet-dry cycles due to variations in sediment provenance, which suggests precession forcing may be an important driver of productivity in the study region. We also find that some of the cycles show a "notch" at the peak, which, given the

5 paleolatitude (3 – 7 ºS), may be interpreted to result from the double overpass of the intertropical convergence zone (ITCZ) (Verschuren et al., 2009).

Occasionally, Goniodomideae are present in great abundance. In the modern ocean (Zonneveld et al., 2013) and in the Paleogene (Sluijs and Brinkhuis, 2009), high abundances of Goniodomideae are typically associated with warm, stratified waters and very high and/or seasonally fluctuating salinity. In open ocean settings the group can be indicative of strong

10 stratification (Reichart et al., 2004). Considering the offshore location of Site 959, and relatively low abundances of low-salinity-tolerant taxa, we interpret high abundances of Goniodomideae to indicate seasonally strong stratification, either by temperature or salinity.

From 804.4 mbsf, we find an increase in abundance of dinocysts belonging to, or closely related to the genus *Areoligera* (*Areoligera* complex *sensu* Sluijs and Brinkhuis, 2009). A relative abundance increase of this genus was previously

15 interpreted to reflect sea level rise at several shelf and slope sites during the PETM (Sluijs et al., 2008). However, Site 959 is located in an open ocean setting, which means water depth and shore proximity proportionally do not change as much as may be expected from sites on the continental shelf, especially if estimates of the amplitude of sea level rise across the onset of the PETM (5-20m, e.g., (Speijer and Morsi, 2002; Sluijs et al., 2008) are considered. The increase in *Areoligera* is further associated with a decrease in *Spiniferites*, consistent with other PETM records (e.g., Sluijs et al., 2008), including a recently

20 published record from Nigeria (Frieling et al., 2017). Since we cannot distinguish between transported and local signals, we may either record a signal that is transported off the shelf, or a local signal that is similar to, but not related to sea level change.

5.2.2 The onset of the PETM and the *Apectodinium* acme

The quasi-global acme of the tropical dinocyst genus *Apectodinium* has long been used as a Paleocene-Eocene boundary

25 marker in biostratigraphic studies (Heilmann-Clausen, 1985; Bujak and Mudge, 1994) and later discovered to be connected to the PETM (Bujak and Brinkhuis, 1998; Crouch et al., 2001). However, some sections show relatively low percentages of *Apectodinium* during the PETM (Sluijs et al., 2006; Frieling et al., 2014).

In addition to the acme of *Apectodinium*, through the entire North Atlantic, Arctic and Northern Tethys, the marker species *Apectodinium augustum* is present during the PETM (Heilmann-Clausen, 1985; Iakovleva et al., 2001; Sluijs et al., 2006;

30 Sluijs and Brinkhuis, 2009; Harding et al., 2011) although other species are often the dominant representatives of the genus. Recent taxonomic revision of several taxa has removed *Apectodinium augustum* from *Apectodinium* and moved it to *Axiodinium* (Williams et al., 2015). However, we follow the comment of Bijl et al. (2016) and retain *A. augustum* within

genus of *Apectodinium*. We consider species within *Apectodinium* to have similar affinities and continue to refer to the quasi-global abundance event as "*Apectodinium*" acme. *A. augustum* was not recorded here.

The abundance of *Apectodinium* appears to be largely controlled by temperature in higher latitude regions across the PETM (Crouch et al., 2001; Sluijs et al., 2006; Frieling et al., 2014), but it was abundant to dominant in tropical and sub-tropical material already in the Late Paleocene (Jan du Chêne and Adediran, 1984; Crouch et al., 2003; Sluijs et al., 2014; Frieling et al., 2017) and accounts for ~15% of the assemblage at Site 959 above 822.14 mbsf (Awad and Oboh-Ikuenobe, 2016) (Figure 2). Furthermore, the required minimum temperature of ~20 ºC (Frieling et al., 2014) was widespread in many mid latitude sections well before the PETM (Dunkley Jones et al., 2013; Frieling et al., 2017), signaling other environmental factors were more important in controlling the distribution of *Apectodinium* at low and mid latitudes (Sluijs et al., 2007a; Sluijs and Brinkhuis, 2009).

At Site 959, *Apectodinium* is abundantly present in the latest Paleocene, which is not surprising given the equatorial location. This is similar to the Paleocene in Nigeria (Jan du Chêne and Adediran, 1984; Frieling et al., 2017), Cameroon (Mbesse, 2013) and Tunisia (Crouch et al., 2003), indicating *Apectodinium* was already common along African margins before the PETM. More surprising is perhaps the general lack of an *Apectodinium* acme at these low latitude sites during the PETM, although some caution must be placed due to poor preservation at the Tunisian site (Crouch et al., 2003) and the low sampling resolution of the section in Nigeria (Frieling et al., 2017).

At Site 959, we find the highest abundance (95%) of *Apectodinium*, close to the onset of the body of the PETM (803.89 mbsf). This is perhaps later than at many mid- and high-latitude sites where the highest abundance of *Apectodinium* often slightly precedes the CIE (Sluijs et al., 2007a, 2011; Kender et al., 2012). However, like at many of these sites the assemblages recorded here are nearly monospecific. We thus infer this high abundance of *Apectodinium* to represent the quasi-global *Apectodinium* acme. The high percentages of *Apectodinium* in the porcellanite (804.1 - 803.9mbsf) are most likely mixed in from above (803.85 - 803.75 mbsf), similar to organic matter (Frieling et al., submitted), since assemblages and species are very similar.

5.2.3 Microfossil decline and deoxygenation during peak PETM

The dinocyst assemblages, but also other microfossil groups, in mid-latitudes have been successfully used for detailed environmental reconstructions (e.g., Gibbs et al., 2006; Hollis, 2007; Sluijs and Brinkhuis, 2009; Stassen et al., 2012). Here, extremely low numbers of dinocysts (100-200 g^{-1}, relative to latest Paleocene average of >5000 g^{-1}), carbonate and siliceous microfossils during the body of the CIE, which, since accumulation rates increase by at most a factor 2 (Fig. 3g), is appreciably beyond the effect of sediment dilution. This hampers detailed a paleoenvironmental reconstruction.

A few dinocyst genera however are present. The CIE is notably marked by higher relative abundances of Protoperidinioid cysts, as well as *Senegalinium* and related genera. Importantly, these are the only groups that increase in abundance with respect to the latest Paleocene. Protoperidinioid dinocysts are produced by heterotrophic dinoflagellates in the modern ocean

(Jacobson and Anderson, 1986) and most likely also in the Paleogene. Also *Senegalinium* cysts were likely produced by heterotrophic dinoflagellates (Sluijs et al., 2005, 2007a), which implies that a larger proportion of the dinoflagellate production was heterotrophic. This suggests that autrotrophic dinoflagellate species were stressed, but that a food source, locally produced or imported from elsewhere, was abundantly present. Notably, based on empirical information, the species

5   in these groups were tolerant to relatively low salinity (Sluijs et al., 2006; Sluijs and Brinkhuis, 2009; Barke et al., 2011). Although lower Ti/Al ratios may indicate hydrological changes in the hinterlands during the body of the CIE (Fig. 3), a large drop in salinity ~150 km offshore seems unlikely. Low-salinity tolerant dinocysts species, i.e. *Senegalinium* cpx, are abundant in many high latitude sections during the PETM (Sluijs et al., 2006; Harding et al., 2011), but the high relative abundance of Protoperidinioid cysts is only found in two sites in the eastern equatorial Atlantic (Frieling et al., 2017). This is

10   surprising given the high abundances of Protoperidinioid cysts in sediments deposited in nutrient-rich sectors of the modern ocean. Although other groups are consistently present within the peak of the CIE, absolute numbers are much lower than in the latest Paleocene and we cannot exclude that these specimens are reworked (or transported over large distances).

Many sites globally show decreased bottom-water oxygen content during the PETM and at some shelf sections the photic zone became euxinic (Sluijs et al., 2006, 2014, Frieling et al., 2014, 2017; Schoon et al., 2015). Oxygen minimum zones

15   were expanded (Zhou et al., 2016) and deep ocean waters were affected by deoxygenation although anoxia did not develop in the deep sea (Pälike et al., 2014). At Site 959, we find strong indications of decreased oxygen concentrations in bottom waters in the form of increased organic matter burial fluxes, as assessed through reconstructed accumulation rates and TOCwt%. Moreover, increasing Corg/Ptot ratios (Fig. 3i) relate to preferential regeneration of phosphorus from sediments under anoxic conditions (Slomp et al., 2002; Algeo and Ingall, 2007). The PETM interval is also associated with slightly

20   elevated concentrations of redox sensitive elements (e.g., Cr) (Figure 3i). In apparent contrast is an increase in the abundance of organic linings of benthic foraminifera. Some benthic foraminifera however can tolerate low oxygen concentrations for substantial periods (Langlet et al., 2014) and may outcompete other metazoans at such oxygen concentrations (Woulds et al., 2007). This signal is surprisingly similar to that found in shelf sections of the Gulf of Mexico (Sluijs et al., 2014) and Nigeria (Frieling et al., 2017). The combined information from Site 959 and Nigeria suggests that oxygen minimum zones during the

25   PETM expanded upwards onto the shelf and downwards to the paleodepth of Site 959 (>1000 m) in the eastern tropical Atlantic, a phenomenon very similar to modern trends (e.g., Stramma et al., 2008).

5.3.4 Recovery after the PETM

At 803.0 mbsf, a small (~1‰) positive step in $\delta^{13}C$ possibly indicates a period of non-deposition, which is followed by the start of the recovery of the CIE. About 15 cm above the start of the CIE recovery, carbonate accumulation resumes. Dinocyst

30   diversity and abundance directly recover and exceed upper Paleocene levels at the start of the CIE recovery. Remarkably ~10 distinct acmes of different dinocyst groups occur within ~30 cm of sediment within the ~100 kyr recovery phase. These events are hence limited to a maximum duration of 10 kyr, but are likely much shorter since bioturbation smoothed the signal. Moreover, the recovery of the PETM at Site 959 is truncated by a core gap and perhaps preceded by a small hiatus,

which leads to overestimated accumulation rates in our approach. SST drops concomitantly with the increase in δ^{13}C (Fig. 3), but does not show a clear relation with any of the individual dinocyst groups. No such short-term extreme biotic variation is known for any PETM site across the globe, certainly not for the recovery interval, and indicates highly variable environmental conditions. We observe high transient abundances of cosmopolitan (*Cordosphaeridium*) and generalist genera

5   (*Spiniferites*), species indicative of stratified waters (Goniodomideae), high-energy environments (*Areoligera* cpx) and *Apectodinium* (Figure 2). Although environmental preferences of many of these groups are known, it is difficult and perhaps pointless to disentangle the highly dynamic assemblages into individual environmental signals.

Only the variability of dinocyst assemblages during the 'body' of the CIE at the New Jersey Shelf sites Bass River and Wilson Lake resemble the results at Site 959 (Sluijs and Brinkhuis, 2009). However, Bass River and Wilson Lake are

10   shallower and closer to the paleoshore and therefore more prone to local changes. The strong variation at Site 959, representing a fully open ocean setting is therefore much more surprising.

Potentially, the recorded variability at Site 959 is related to sub-Milankovitch climate variability, which has been observed in a range of tropical sections from the Proterozoic onwards (Wu et al., 2012; Wilson et al., 2014) and also within the PETM (Abdul Aziz et al., 2008) and in dinocyst records (Reichart and Brinkhuis, 2003). However, we observe no cyclic recurrence

15   of these dinocyst assemblage variations, nor do we find the far more obvious cyclic (likely precession-scale) variation in the upper Paleocene in the dinocyst assemblages. Therefore this explanation appears unlikely. Unfortunately, none of our proxy records show similar variability in this period so we cannot resolve the underlying cause of such extreme variations in dinocyst assemblages.

5.3.5 Post PETM assemblages

20   Early Eocene dinocyst assemblages and thus presumably environmental circumstances are similar to those found in the Paleocene. Only *Florentinia reichartii* increases towards the top of the analyzed interval. Although this species seems to be associated with somewhat higher temperatures and fresh-water input along the New Jersey shelf (Sluijs and Brinkhuis, 2009), and relates to occurrences of *Apectodinium* at southwest Pacific ODP Site 1172 (Sluijs et al., 2011), it here thrives under apparently relatively stable, open ocean conditions that prevail in the earliest Eocene. In addition to *F. reichartii*,

25   *Apectodinium* is occasionally abundant, as are *Spiniferites* and Goniodomideae. Carbonate accumulation is similar or slightly higher than in the upper Paleocene (10-30%) and bottom waters appear to be well ventilated. Remarkably, the clear correlations between TOC and dinocyst numbers that exists in the upper Paleocene did not return, but dinocyst numbers and K/Al ratios continue to show cyclicity at similar intervals to that in the upper Paleocene, suggesting the same forcing, possibly precession driven hydrological changes, remained an important factor governing plankton assemblages at Site 959

30   (see also section 5.2.1).

5.4 Absolute temperature and temperature change in a global perspective

The recorded warming across the onset of the PETM (3.9 ºC) is similar to the global average (4-5 ºC, e.g., (Dunkley Jones et al., 2013; Frieling et al., 2017)). However, the few sampled tropical regions typically warmed slightly less (Tripati, 2003; Zachos et al., 2003; Kozdon et al., 2011) than global average due to persistent extratropical amplification of temperature change (Frieling et al., 2017). The isoprenoid glycerol dialkyl glycerol tetraether (iGDGT) distribution we find here is

5 somewhat similar to modern Red Sea distributions. Within the modern Red Sea, TEX_{86} behaves slightly different and the relation with temperature has a different slope and is offset from the global calibration (Trommer et al., 2009). The linear Red Sea calibration of Trommer et al., (2009) yields a warming of 3.4 ºC, only slightly smaller than the 3.9 ºC recorded by TEX_{86}^{H}, which uses a global calibration dataset (Kim et al., 2010). Furthermore, although iGDGT distributions may look similar, there is no reason to assume that Site 959 was subject to a similar setting or that Thaumarcheota communities were

10 similar to those in the modern Red Sea. We note that Paleocene TEX_{86}^{H} reconstructed absolute temperatures are in the same range as were previously reported from this region (Frieling et al., 2017), which are supported by planktonic foraminifer $\delta^{18}O$ and Mg/Ca derived temperature estimates from the same section. Even though these temperatures are outside the calibration interval (5-30 ºC) for TEX_{86}^{H}, the relation with temperature continues to at least 40 ºC, based on mesocosm culture experiments (Wuchter et al., 2004; Schouten et al., 2007). Importantly, the maximum temperature that can be

15 reconstructed by TEX_{86}^{H} is 38.6 ºC. The reconstructed temperatures are close to this maximum and we may actually approach the limit of the proxy and underestimate maximum PETM surface-water temperatures.

5.5 Suppression of eukaryote productivity in surface waters

Sediments typically contain less than 30% $CaCO_3$ in the latest Paleocene, but already from 804.2 mbsf, just below the onset of the CIE, $CaCO_3$ is completely absent (Figure 3f). We explore several factors that might explain this feature. First, it could

20 be due to post-depositional carbonate dissolution through PETM ocean acidification as recorded in deep ocean basins (Zachos et al., 2005). However, at no single site described so far, the carbonate compensation depth (CCD) rose above the reconstructed paleodepth (~1000m, Oboh-Ikuenobe et al., 1997) for this site, so this scenario seems unlikely. Second, carbonates can be dissolved locally through enhanced oxic organic matter (OM) decomposition at the sea floor, producing CO_2. However, the dinocyst concentrations (~10^4 gram^{-1}) or TOC (~0.5%) content in this interval are not anomalous

25 compared to the entire upper Paleocene, so this factor is unlikely the sole explanation. Finally, there may be a general suppression of carbonate (export-) production because of biotic stress, either through acidification or warming (Aze et al., 2014; Frieling et al., 2017). We surmise that low carbonate production, possibly associated with the (pre-CIE) warming ((Frieling et al., submitted), Figure 3c) played a pronounced role in the absence of carbonate throughout the PETM.

After carbonate accumulation ceased, without apparent change in other proxies or large changes in sediment accumulation

30 rates, dinocyst concentrations decrease from 5000 g^{-1} to 100-200 g^{-1} at 803.70 mbsf (Figure 3d). Organic linings of benthic foraminifera continue to increase in abundance indicating that export productivity did not collapse. This signal is identical to that found in a shelf section from Nigeria (Frieling et al., 2017); both sections show very low (100 - 200 g^{-1}) abundances of

dinocysts during peak PETM warmth. We also note that pyritized biogenic silica, which is abundantly present in the upper Paleocene and early Eocene, is largely absent above the porcellanite and only reappears during the recovery (Figure 3e).

In addition to these overall similarities, the dinocyst assemblages at Site 959 are very similar to those found at the PETM in Nigeria. Both sections are marked by relatively high percentages of Protoperidinioid dinocysts within the body of the PETM, which is an exclusively heterotrophic group (Jacobson and Anderson, 1986). Oxidation experiments show Protoperidinioid cysts are usually less resistant to oxidation than, e.g. *Spiniferites* cysts (Zonneveld et al., 1997, 2008). However, the absence of a relation between the abundance of these taxa and TOC content suggests that preservation is not a major factor. We speculate that these species resided in slightly deeper waters, possibly near the thermocline.

The combined information suggests that eukaryote activity in the mixed layer was suppressed not only in Nigeria (Frieling et al., 2017) but also at the more offshore Site 959. Similar to Nigeria, there is hence no evidence that the low numbers of dinocysts resulted from severe stratification and anoxia, strong variations in salinity or biases resulting from preservation. Although the initial absence of carbonate is perhaps related to a secondary factor, we attribute the drop in eukaryote production in this region to heat stress, as this is among the few physicochemical factors that can generate the same effect in both the open ocean (Site 959) and on the shelf (Nigeria).

It should be emphasized that primary productivity did not collapse due to the lack of eukaryotes. Organic linings of benthic foraminifera are abundant within the PETM interval at Site 959 and in Nigeria, which suggests that food supply was likely similar as before the PETM. Both sections are characterized by enhanced organic carbon content and burial. This apparently prokaryote dominated ecosystem, with enhanced organic carbon burial hence bears some similarities with tropical ecosystems during the Cretaceous Ocean Anoxic Events (OAEs) (Kuypers, 2001).

6. Conclusions

The Paleocene – Eocene transition at Site 959 is marked by a warming of 3.9 ºC. Absolute TEX_{86}^{H} temperatures at 37.4 ºC are unprecedented for the PETM, although similar to recent estimates from Nigeria and in good agreement with climate model estimates. Based on our multi-proxy records, we conclude that these extreme temperatures caused a remarkable drop in dinocyst abundances, and most likely also in the production of biogenic carbonate and opal during the PETM. Crucially, only heterotrophic dinoflagellate species, which likely resided somewhat deeper in the water column, increased in abundance. Together with relatively abundant organic benthic foraminifer linings this indicates sustained primary production, likely dominated by prokaryotes. Combined evidence from dinocysts and inorganic chemistry points to an altered hydrological cycle at the PETM, resulting in fluctuations in stratification. Furthermore, progressively less oxygenated bottom waters characterize the body phase of the PETM. In sharp contrast to the general absence of eukaryotes during the body phase of the PETM, the recovery phase of the PETM is highly dynamic, with several groups of dinocysts dominating assemblages on timescales shorter than 10 kyr.

Author contributions.

J.F. and A.S. designed the study. J.F., S.M.B., J.J.M., U.R., T.W. and G.-J.R. performed inorganic geochemical analyses. J.F. generated palynological data. J.F. and A.S. wrote the paper, with input from all authors. All authors analyzed and discussed the data.

5 *Data availability*

Data used in this publication will be made available through online database Pangaea (https://www.pangaea.de/)

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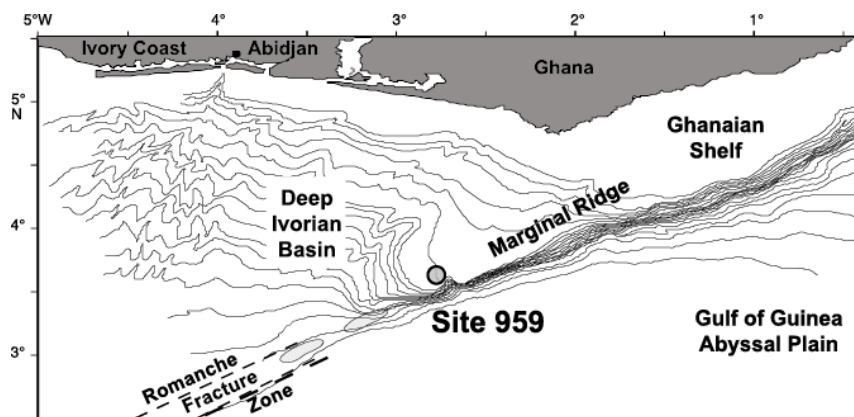
Figure 1. Map of Eastern Tropical Atlantic and location of ODP Site 959.
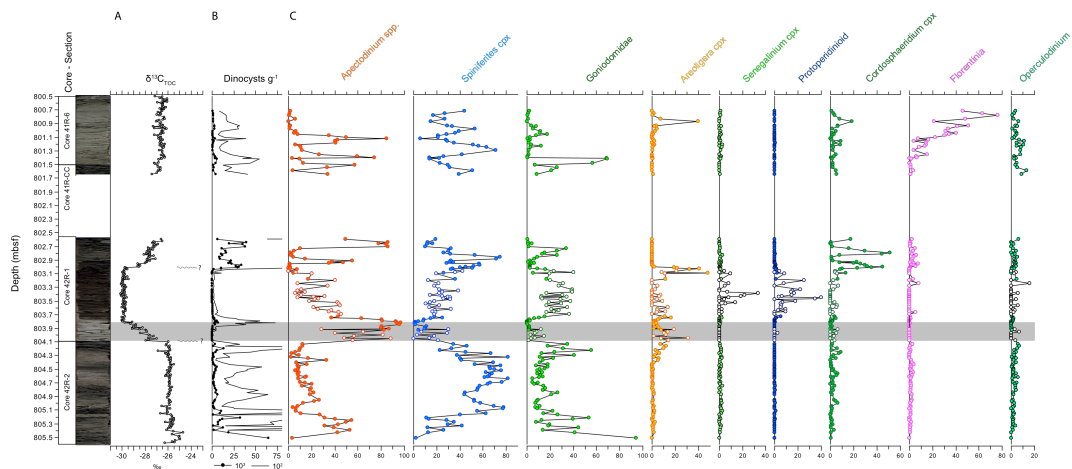
Figure 2. The PETM as recorded by dinoflagellate cyst assemblages at Site 959. A. $\delta^{13}C_{TOC}$ in permil. B. Concentration of dinocysts per gram dry sediment. C. Dinocyst groups in percentage of total dinocysts. The grey band marks the porcellanite. Symbols in white indicate counts <100.
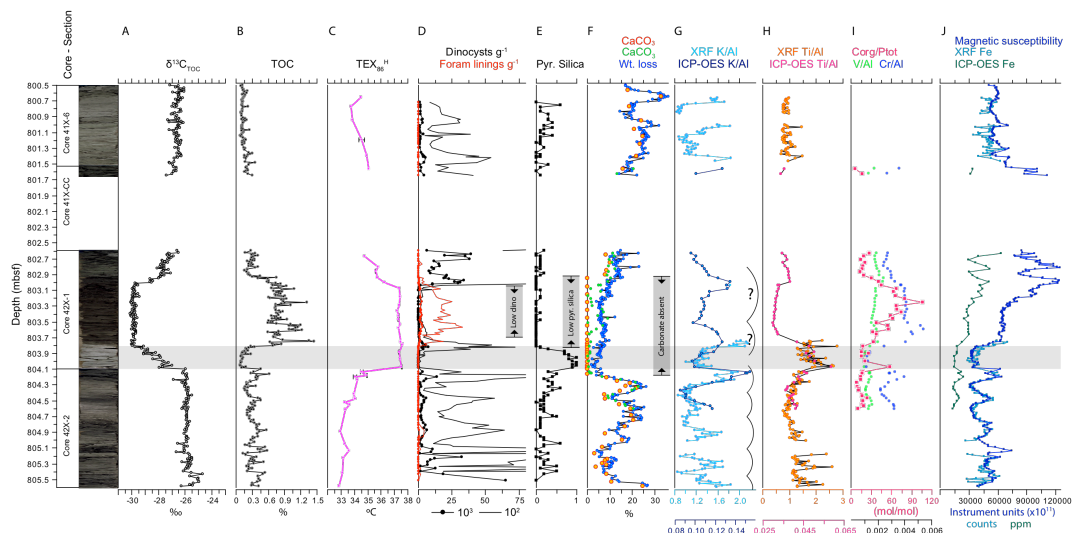
Figure 3. The PETM as recorded by organic and inorganic geochemical proxies at Site 959. A. $\delta^{13}C_{TOC}$ in permil. B. Total organic carbon (TOC) in weight percentages. C. TEX_{86}^H derived temperature. D. Dinoflagellate cyst and organic linings of benthic foraminifera in n g^{-1} of dry sediment. E. Fraction of pyritized silica particles in palynological residue. F. Weight loss during decalcification (w t. loss) as indication of $CaCO_3$ content; $CaCO_3$ calculated from Ca concentration ICP-OES (green) and selected samples analyzed for $CaCO_3$ on a coulometer (orange). G. K/Al ratio from XRF (light blue) and ICP (dark blue). H. Ti/Al ratio from XRF (orange) and ICPOES (pink). I. Cr/Al (blue) and V/Al (light green) and Corg/Ptot ratio (pink) in mol mol^{-1}. J. Magnetic susceptibility in instrument units ($x10^{11}$) (dark blue), XRF Fe counts (light blue) and ICP-OES Fe concentrations in ppm (green). The gray band (804.1 – 803. 83 mbsf) marks the porcellanite. $\delta^{13}C_{TOC}$, TOC and TEX_{86}^H data from Frieling et al., submitted.

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