



# Life and death in the Chicxulub impact crater: A record of the Paleocene-Eocene Thermal Maximum

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30 **Abstract.** Thermal stress on the biosphere during the extreme warmth of the Paleocene-Eocene Thermal Maximum (PETM) was most severe at low latitudes, with sea surface temperatures at some localities exceeding the 35° C at which marine organisms experience heat stress. Relatively few equivalent terrestrial sections have been identified, and the response of land plants to this extreme heat is still poorly understood. Here, we present a new PETM record from the peak ring of the Chicxulub impact crater that has been identified based on nannofossil biostratigraphy, an acme of the dinoflagellate genus *Apectodinium*, and a negative carbon isotope excursion. Geochemical and microfossil proxies show that the PETM is marked by elevated  $\text{TEX}_{86}^{\text{H}}$ -based sea surface temperatures (SSTs) averaging ~37.8 °C, an increase in terrestrial input, surface productivity, salinity stratification, and bottom water anoxia, with biomarkers for green and purple sulfur bacteria indicative of photic zone euxinia in the early part of the event. Pollen and plants spores in this core provide the first PETM floral



assemblage described from México, Central America, and the northern Caribbean. The source area was a diverse coastal  
40 shrubby tropical forest, with a remarkably high abundance of fungal spores indicating humid conditions. Thus, while seafloor anoxia devastated the benthic marine biota, and dinoflagellate assemblages were heat-stressed, the terrestrial plant ecosystem thrived.

## 1 Introduction and geologic setting

The Paleocene-Eocene Thermal Maximum (PETM) was a period of global warming associated with ocean acidification, an  
45 intensified hydrological cycle, reductions in marine dissolved oxygen concentrations, eustatic sea level rise, and major ecological shifts (e.g., Zachos et al., 2003; Gingerich 2006; Dickson et al., 2014; Sluijs et al., 2014; Carmichael et al., 2017). Recent age estimates place the PETM at approximately 55.93-55.71 Ma (Westerhold et al. 2017; Hollis et al. 2019). The onset of the PETM is marked by a global negative carbon isotope excursion (CIE) (Dickens et al. 1997; Gradstein et al. 2012). Possible sources of this isotopically light carbon include methane clathrates, combustion of organic matter,  
50 thermogenic methane, desiccation of epicontinental seas, and organic matter released from permafrost (McInerney and Wing, 2011). Sea surface temperature (SST) during the PETM in some low-latitude regions exceeded 35 °C, resulting in heat stress for eukaryotic plankton (e.g., Frieling et al., 2018). In contrast, the few existing PETM records of low-latitude terrestrial plant assemblages indicate an increase in diversity (e.g., Jaramillo et al., 2010; Srivastava and Prasad, 2015; Prasad et al., 2018). Here, we established a new multiproxy record of the response of marine and terrestrial biota to the  
55 PETM in the western Caribbean/Gulf of Mexico at International Ocean Discovery Program (IODP) Expedition 364 Site M0077. This includes the first published pollen and spore PETM assemblage from tropical North America (Smith et al., 2019, 2020). These data allow us to determine the extent of marine and terrestrial heat stress from the understudied region and determine how they compare with other PETM sections.

Site M0077 is located on the peak ring of the Chicxulub impact crater in the Yucatán Peninsula, México (Fig. 1)  
60 (Morgan et al., 2017). The crater was a marine depositional basin in the Paleogene, with mainly pelagic and outer-platform sediment deposition (Lefticariu et al., 2006). Immediately after impact, some of the rim may have been subaerially emergent (Morgan et al., 1997), but, if so, would have been quickly eroded. During the PETM, only isolated areas of the crater rim were still emergent, given the existence of an embayment into the crater to the north and northwest (Gulick et al., 2008). Although PETM records from the Gulf of Mexico are scarce, another site in the Chicxulub crater, the Yaxcopoil-1 (Yax-1)  
65 core, contains a PETM section identified by a negative carbon isotope excursion, deposited during a period of maximum flooding (Whalen et al., 2013) (Fig. 1). The PETM has also been identified on the Mississippi paleoshelf (Fig. 1), where evidence indicates increased  $\text{TEX}_{86}^{\text{H}}$ -based SSTs, photic zone euxinia, and sea level rise (Sluijs et al., 2014).



## 2 Methods

Quantitative palynological abundances are expressed in terms of specimens per gram, using a *Lycopodium* spike. Species counts, descriptions, and paleoecological interpretations can be found in Smith et al. (2019, 2020). The D/S ratio between dinoflagellate cysts and pollen/plant spores is described in Warny et al. (2003). The degree of bioturbation has been quantified using the Bioturbation Index (BI) (Taylor and Goldring, 1993). Samples for  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}_{\text{TOC}}$  ( $n = 51$ ) analyses were prepared by acidifying approximately 0.5 g subsamples of powdered material with an excess of 1 M HCl. The acid-insoluble residues were neutralized, freeze-dried and analyzed for their carbon and nitrogen contents as well as stable isotope compositions using a Costech Elemental Analyzer (ECS 4010) and a Delta+XP mass spectrometer. Typical instrumental precision of the isotope measurements is  $<0.2\text{\textperthousand}$ . Clay mineral assemblages were identified by X-ray diffraction on oriented mounts of non-calcareous clay-sized particles ( $<2 \mu\text{m}$ ). SSTs based on isoprenoidal glyceroldialkylglyceroltetraethers (isoGDGTs) (Schouten et al. 2002) were reconstructed using the  $\text{TEX}_{86}^{\text{H}}$  calibration of Kim et al. (2010). Additional methods are provided as supplementary materials along with all data.

## 80 3 Results

IODP drilling at Site M0077 recovered Paleocene to early Eocene post-impact sedimentary rocks between 617.33-505.70 meters below seafloor (mbsf). The PETM section (607.27-607.06 mbsf) is a laminated black to dark gray shale, separated from an upper Paleocene carbonate hardground by an unconformity, and grading upwards into a burrowed lower Eocene packstone (Fig. 2). Bioturbation is absent to minimal in the PETM, with rare *Chondrites* ichnofossils, except at the top of the interval (607.11-607.06 mbsf) where *Planolites* burrows are observed, infilled with sediment from the overlying packstone. The clay mineral assemblages are dominated by R0 random illite/smectite mixed layers (up to 90%), and also contains traces of chlorite, illite, and palygorskite. The latter is rare in the upper Paleocene, and increases in abundance through the PETM, reaching a peak of 5% relative abundance at 607.08 mbsf. The PETM interval is characterized by a marked increase in magnetic susceptibility ( $\chi$ ), anhysteretic remanent magnetization (ARM), and isothermal remanent magnetization (IRM). The average values increase by a factor of 15.7, 5.8, and 12.4 for  $\chi$ , ARM, and IRM, respectively, compared to the average values over the analyzed pre-PETM interval (607.67-607.27 mbsf) (see supplementary materials).

Total organic carbon (TOC) is low above and below the PETM (Fig. 2), with high concentrations ( $>6\%$  rock weight) in the upper PETM section. Total organic carbon/total nitrogen (TOC/TN) ratios range from 0.6 to 6.8 in the upper Paleocene, with higher values averaging 10.7 in the PETM section. TOC/TN values in the post-PETM section range from 1.4 to 4.7.  $\delta^{13}\text{C}_{\text{TOC}}$  ranges from  $-27.5\text{\textperthousand}$  to  $-25.8\text{\textperthousand}$  in the upper Paleocene and is  $-28.4\text{\textperthousand}$  at the base of the PETM section, generally becoming more negative upsection through the PETM, with the most depleted value of  $-30.1\text{\textperthousand}$  in the upper PETM (607.12 mbsf). Above 607.07 mbsf,  $\delta^{13}\text{C}_{\text{TOC}}$  values become more positive, then stabilize at  $-27.5\text{\textperthousand}$  at 607.03 mbsf.  $\delta^{15}\text{N}$  ranges from  $1.0\text{\textperthousand}$  to  $3.7\text{\textperthousand}$  in the upper Paleocene and is  $5.3\text{\textperthousand}$  at the base of the PETM section, with more depleted values through the PETM, reaching a minimum of  $-2.0\text{\textperthousand}$  at 607.21 mbsf. The PETM  $\delta^{15}\text{N}$  record is marked by two negative



100 excursions with values below 0‰, separated by a brief interval of positive  $\delta^{15}\text{N}$  values between 607.17–607.13 mbsf. Above 607.10 mbsf,  $\delta^{15}\text{N}$  values become more positive, with a value of 0.9‰ at 607.02 mbsf (Fig. 2).

$\text{TEX}_{86}^{\text{H}}$ -based SSTs and other biomarkers were difficult to retrieve in the late Paleocene due to low organic matter content (TOC values often <0.1%), but a single sample at 607.33 mbsf yielded a  $\text{TEX}_{86}^{\text{H}}$ -based SST of 34.0 °C. In the PETM,  $\text{TEX}_{86}^{\text{H}}$ -based SSTs ranged from 37.4–38.0 °C, averaging 37.8 °C. Just above the PETM section, at 607.05 mbsf, the 105  $\text{TEX}_{86}^{\text{H}}$ -based SST was 37.9 °C, followed by a decrease in SSTs to 37.1 °C and 37.3 °C at 606.87 and 606.72 mbsf, respectively (Fig. 2). The branched isoprenoid tetraether index (BIT) in the uppermost Paleocene (607.33 mbsf) is 0.16, while values of this index average 0.01 in the PETM section. In the post-PETM section BIT values are slightly higher and range from 0.04 to 0.05. Green and purple sulfur bacteria biomarkers (chlorobactane, okenane, and isorenieratane) reach their highest concentrations near the bottom of the PETM section, with low concentrations through the rest of the event (Fig. 110 2). Nannofossil abundances decrease through the PETM section and become rare in the post-PETM section. Foraminifera at Site M0077 are frequent to abundant in the upper Paleocene section but are absent to very rare in the PETM section, with evidence of reworking. Dinosterane concentrations are relatively high in the upper Paleocene and lower PETM section, with decreased abundance in the PETM and post-PETM sections. Organic-walled microfossils are absent to rare in the Paleocene. Dinoflagellate cyst concentrations peak at 607.26 mbsf, with a decreasing trend through the rest of the PETM (Fig. 115 2). Relative abundances of *Apectodinium* are highest at 607.26 mbsf, and decrease through the PETM, while the highest relative abundances of Goniodomidae are found just above the event. Pollen and fungal spore concentrations peak in the middle PETM section (Fig. 2). The fungal assemblage is dominated by *Nigrospora*-types, which are common leaf endophytes on a variety of substrates, including soil, and are commonly airborne (Wang et al. 2017). The pollen and plant spore assemblage 120 is dominated by *Malvacipollis* (Euphorbiaceae), *Ulmipollenites* (Ulmaceae), *Bohlensipollis* (Eleagnaceae), and angiosperm pollen of unknown lower botanical affinity, with rare gymnosperm pollen and lower plant spores.

## 4 Discussion

### 4.1 Stratigraphy and sedimentology

The uppermost Paleocene, underlying the PETM interval, is characterized by two significant disconformities. The lower disconformity is atop a 6–8 cm thick gray claystone (607.66 mbsf), interpreted to be a bentonite, with an erosionaly scoured 125 upper surface. It is overlain by a 7 cm thick carbonate rudstone that grades upward into a 22 cm thick packstone. The rudstone contains claystone and carbonate lithoclasts up to 2 cm in diameter, foraminifera, and lime mud, and grades into a light gray foraminiferal packstone with wispy stylolitic laminae. The packstone is overlain by a 4.5 cm thick gray claystone. Both the contact between the packstone and claystone and the claystone itself are burrowed and one burrow is infilled by material from the overlying facies. The claystone is abruptly overlain by a carbonate grainstone with planktic and large 130 benthic foraminifera, red algae, ostracods, calcispheres, and black and gray carbonate lithoclasts. The top of this unit (607.27 mbsf) is a hardground and disconformity with about 1 cm of relief. The lower contact of the grainstone with the underlying



claystone (607.32 mbsf) also appears to be unconformable, but no biozones are missing, so it may represent a diastem rather than a significant hiatus.

The PETM interval is about 21 cm thick. It has a sharp basal contact that drapes over the relief atop the underlying 135 hardground. The PETM interval consists of dark gray to black shale that is laminated at the mm scale. The base of the interval is slightly lighter colored gray shale and contains clay, organic matter, sand-sized carbonate lithoclasts and foraminifera eroded from the underlying unit, as well as rare green grains and spherules that appear to be altered impact glass. The remainder of the PETM interval consists of mm-scale laminae that are usually dark gray at their base and black at 140 the top and contain quartz, muscovite, rare plagioclase silt grains, and rare calcispheres. Laminae are commonly defined at their base by quartz and muscovite silt and grade upward into clay and organic-rich shale. The uppermost PETM shale is bioturbated, with burrows infilled with material from the overlying carbonate packstone. The interval directly overlying the PETM also contains abundant reworked material, including several pebble-sized clasts of limestone which appear to contain Cretaceous foraminifera.

The fine-grained nature and lack of sedimentary structures indicating current deposition indicate that the PETM 145 interval was deposited in relatively deep, quiet water with sediments largely settling from suspension. The laminated black shale points toward low oxygen conditions. However, the trace fossil assemblage implies that anoxia and/or euxinia were likely intermittent. Water depths for Site M0077 during most of the Paleocene were on the order of 600-700 m (Lowery et al., 2018) but the facies immediately underlying and overlying the PETM interval contain numerous grains from shallow 150 water environments, like larger benthic foraminifera and red algae which indicate either relatively shallow water in the crater or extensive reworking from the crater margin. Assigning a water depth for the PETM interval is complicated by the complete lack of obviously *in situ* depth-sensitive benthic foraminifera that could provide such insight. However, the presence of deeper-dwelling planktic foraminifera such as *Subbotina* spp. and *Globanomalina pseudomenardii*, which occupied a thermocline habitat (e.g., Aze et al., 2011) indicate that the water was at least deep enough for the establishment 155 of stratification. The PETM is globally characterized by an eustatic sea level rise (Sluijs et al., 2008) so water depths were likely somewhat deeper during the PETM than during the times when the units above and below were deposited. This suggests that the shallow water fossils in the PETM interval were reworked from the crater rim, consistent with the interpretation of Whalen et al. (2013) that a roughly PETM age reworked deposit in the Yaxcopoil-1 core spread across the crater.

The PETM age of the shale interval at Site M0077 (607.27-607.06 mbsf) has been confirmed by a negative carbon 160 isotope excursion (CIE) and biostratigraphy. The earliest nannofossil PETM sample, at 607.25 mbsf, contains *Discoaster salisburgensis* var. *anartios*, a characteristic PETM excursion taxon (Bralower and Self-Trail, 2016). The global negative CIE is also observed at Site M0077 (Fig. 2). In complete records of the PETM, the peak of the negative CIE and highest temperatures are observed within the first ~20 ky of the event, followed by a gradual recovery to more positive  $\delta^{13}\text{C}_{\text{TOC}}$  values and lower SSTs (Hollis et al., 2019). However, at Site M0077, the most depleted  $\delta^{13}\text{C}_{\text{TOC}}$  values are found in the upper 165 PETM section. The onset and peak of the PETM CIE are missing due to erosion or non-deposition. The abrupt shift to more



positive  $\delta^{13}\text{C}_{\text{TOC}}$  values at 607.06 mbsf suggests that the later PETM body and recovery is also missing, with another unconformity at the top of the PETM section. The trend towards more negative  $\delta^{13}\text{C}_{\text{TOC}}$  values in the PETM can be explained as the result of an increasing contribution of terrestrial organic matter. This explanation is consistent with the palynological D/S ratio, which shows the highest relative abundance of terrestrial versus marine palynomorphs at approximately the same 170 depth as the most negative  $\delta^{13}\text{C}_{\text{TOC}}$  values (Fig. 2). Increasing TOC/TN ratios are also consistent with a higher input of terrestrial organic matter through the PETM (Burdige, 2006). Lithologically, the PETM section is clearly distinguished from the Paleocene section by an abrupt switch from carbonate to siliciclastic clay deposition, and an abrupt increase in detrital input, as indicated by increased magnetic parameters.

#### 4.2 PETM environmental change

175 SSTs were estimated using the relative abundance of thaumarchaeotal isoGDGTs. We here used the  $\text{TEX}_{86}^{\text{H}}$  and the SST-calibration of Kim et al. (2010) developed for the determination of SSTs in (sub)tropical oceans and low latitude settings. The uncertainties associated with  $\text{TEX}_{86}$  estimates of SSTs exceeding the present-day SST maximum of 27-29 °C have been addressed for Cretaceous (O'Brian et al., 2017) and Tertiary (Frieling et al., 2017) strata. These authors conclude that during hyperthermals  $\text{TEX}_{86}^{\text{H}}$  delivers reliable SST reconstructions, whereby an upper limit of the calibration has been proposed to 180 occur at 38.6 °C (Tierney and Tingley, 2014; O'Brian et al., 2017). In previous studies an impact of terrigenic derived GDGTs on the  $\text{TEX}_{86}$  proxy has been observed, in cases when the BIT index exceeded values of 0.3 (Weijers et al., 2006) or 0.4 (Schouten et al., 2013). In this study all BIT values remained below 0.2, indicating that inputs of terrigenic isoGDGTs do not compromise the  $\text{TEX}_{86}^{\text{H}}$  paleothermometer

185  $\text{TEX}_{86}^{\text{H}}$ -based SSTs increased by ~4 °C between the late Paleocene and PETM (Fig. 2), with average PETM SSTs of 37.8 °C, similar to values observed in the eastern equatorial Atlantic (Frieling et al., 2018) and the Dahomey Basin, western Africa (Frieling et al., 2017), and ~3 °C higher than those observed in the Harrell Core (Sluijs et al., 2014). SSTs decrease to 37.1 and 37.3 °C in the post-PETM section at 606.87 and 606.72 mbsf, respectively. The temperature increase from the late Paleocene to PETM section is consistent with estimates of a 4-5 °C global mean surface temperature anomaly for the PETM (Dunkley Jones et al., 2013). Frieling et al. (2017), investigating a tropical marine PETM record from Nigeria, 190 estimated latest Paleocene SSTs of 32-34 °C, with average PETM SSTs of ~36 °C.

195 Several lines of evidence indicate increased terrestrial input during the PETM, including increased concentrations of terrestrial palynomorphs, increased D/S and TOC/TN ratios, and an increase in detrital ferromagnetic minerals. Theoretically, this increase in terrestrial input could be the result of a relative sea level fall, but this would not be consistent with an interpreted PETM sea level rise in the Gulf of Mexico and globally (Sluijs et al., 2014). Instead, the increase in terrestrial input is interpreted to result from an intensified hydrological cycle during the PETM, as noted in other studies (e.g., Crouch et al., 2003; Bowen et al., 2004; Schmitz and Pujalte, 2007; Handley et al., 2012). The exceptionally high abundance of fungal spores in the PETM section suggests that increased humidity and terrestrial weathering resulted in greater detrital and nutrient input to Site M0077. BIT index values, which have been used as a proxy for terrestrial organic



matter in sediments (Hopmans et al., 2004; Weijers et al., 2006), are higher in the late Paleocene than in the PETM section  
200 (Fig. 2). Low BIT values in samples from the PETM section may indicate a source of terrestrial organic matter lean in soil  
microbial matter (Huguet et al., 2007; Schouten et al., 2013), possibly from low-lying carbonate terrain to the south (Fig. 1)  
and/or an increased productivity of Thaumarchaeota.

The relative abundance of the clay mineral palygorskite increases through the PETM section. Higher abundances of  
palygorskite in other PETM sections have been interpreted as evidence for increased aridity (Carmichael et al., 2017), as  
205 palygorskite commonly forms in coastal marine environments where continental alkaline waters are concentrated by  
evaporation (Bolle and Adatte, 2001). At Site M0077, the palygorskite may have originally formed in hypersaline lagoonal  
environments similar to other Eocene-Oligocene palygorskite deposits in the Yucatán Peninsula (de Pablo Galán, 1996). The  
increase in relative abundance of palygorskite through the PETM section may therefore be the result of increased fluvial  
transport of sediments to Site M0077 from lagoonal environments to the south, rather than the result of increased aridity.

210 The near absence of bioturbation in the PETM section, with preserved sedimentary laminations and high TOC, is  
consistent with bottom water anoxia through much of the PETM, and sulfur bacteria biomarkers are indicative of photic zone  
euxinia (e.g., Summons and Powell, 1987; Grice et al., 2005; Sluijs et al., 2014) in the earlier PETM record. Depleted  $\delta^{15}\text{N}$   
values, similar to those observed during ocean anoxic events (e.g., Jenkyns, 2010) can be explained by upwelling of  
215 ammonium from anoxic deep waters during periods of high nutrient availability (e.g., Higgins et al., 2012), or increased  
cyanobacterial N<sub>2</sub> fixation (e.g., Bauersachs et al., 2009). The transient positive  $\delta^{15}\text{N}$  excursion in the middle of the PETM  
section at Site M0077 (Fig. 2) is similar to the  $\delta^{15}\text{N}$  PETM record of Junium et al. (2018) from the northern Peri-Tethys  
seaway, with depleted  $\delta^{15}\text{N}$  in the top and bottom of the PETM section, separated by an interval of more enriched  $\delta^{15}\text{N}$ ,  
which they interpreted to result from a more oxic, less stratified water column, possibly due to reduced freshwater influx.

#### 4.3 Implications for life and climate

220 In the Paleocene interval at Site M0077, carbonate deposition dominates, and palyynomorphs are nearly absent, probably due  
to poor preservation of organic material (Lowery et al., 2018). Low values of TOC/TN (<4) observed in the Paleocene  
section are also an indication of degradation of organic matter, with the breakdown of nitrogenous compounds to ammonia  
and organic carbon escape via CO<sub>2</sub> release during oxidation (Müller, 1977; Meyers and Shaw, 1996). The late Paleocene  
225 palyнологical samples in the carbonate hardground represent the oldest dinoflagellate assemblages observed in abundances  
sufficient for paleoecological interpretation. Dinoflagellate cyst and dinosterane concentrations peak in the early PETM  
interval, then decrease through the rest of the PETM, suggesting that the extreme warmth during the PETM resulted in heat-  
stressed plankton within the Chicxulub impact crater, similar to the eastern equatorial Atlantic (Frieling et al., 2018).  
Dinoflagellate assemblages record a peak in *Apectodinium* relative abundance in the bottom PETM section, with a  
decreasing trend through the PETM. Increases in the relative abundance of Goniodomidae through the PETM likely indicate  
230 an intensification in salinity stratification (e.g., Frieling and Sluijs, 2018). The PETM nannoplankton assemblage also  
contains malformed *Discoaster* specimens, which may represent ecophenotypes that migrated to a deep photic zone refuge to



escape inhospitable SSTs and became malformed due to increased organic matter remineralization and calcite undersaturation (Bralower and Self-Trail, 2016).

A notable acme of fungal spores occurs in the middle part of the PETM and suggests humid forest and grassland ecosystems in the source area of the terrestrial palynomorphs. The PETM pollen and plant spore assemblage is broadly similar to later Ypresian assemblages observed higher in the core, with angiosperm pollen dominant and rare lower plant spores and gymnosperm pollen. The main pollen source area is interpreted as a lowland tropical forest and shrubland (Smith et al., 2019, 2020). Low abundances of grass pollen (*Monoporopollenites annulatus*) in the PETM suggest a minor grasslands component of the flora. Pollen with affinity to the Pinopsida and Ulmaceae may represent a contribution from more upland pollen source areas, based on their modern distributions in México and Central America. High concentrations of pollen in two PETM samples argue for a proximal pollen source area from low elevation carbonate terrain in the Yucatán Peninsula, consistent with modeled prevailing surface currents and summer wind fields from the south (Fig. 2) (Winguth et al., 2010). Globally, plant floras indicate shifts in ranges and relative abundances with low rates of extinction (Wing and Currano, 2013). These shifts are broadly indicative of warming during the PETM. Although plant assemblages in midlatitude continental interiors suggest drying during the PETM (e.g., Wing et al., 2005), PETM floral records from tropical South America (Jaramillo et al., 2010) and India (e.g., Prasad et al., 2018) suggest high levels of precipitation, while in tropical East Africa (Handley et al., 2012) evidence suggests a decrease in overall humidity but an increase in the intensity of precipitation events. The proxy data from Site M0077 indicates increased temperature and humidity in the Yucatán Peninsula during the PETM, resulting in increased terrestrial input.

## 250 5. Conclusions

The PETM in the Chicxulub impact crater was a time of extremely high SSTs (~37.8 °C), increased terrestrial input, high surface productivity, water column stratification, and bottom water hypoxia/anoxia, with evidence for photic zone euxinia in the bottom section. The observed increase in terrestrial input is likely the result of increased weathering and fluvial discharge due to moist, hyperthermal conditions. This explanation is consistent with global evidence of sea level rise during the PETM. Seafloor anoxia decimated the marine benthos during the PETM, while high SSTs caused heat stress in the dinoflagellate and likely other phytoplankton assemblages. In contrast, the pollen and spore assemblage indicates the presence of a proximal humid landmass with a diverse tropical shrubby forest, which produced relatively high abundances of Euphorbiaceae pollen. These results, in combination with previously described tropical PETM floral assemblages (Jaramillo et al. 2010; Srivastava and Prasad, 2015; Prasad et al., 2018), demonstrate that tropical vegetation was highly resilient to hyperthermal conditions.

## Data availability

All data and supplementary methods are included as supplementary materials.



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## Author contributions

VS led the writing and organization of the manuscript. VS, SW, NNO, and JMO analyzed the terrestrial palynology. JV  
295 analyzed the dinoflagellate assemblages. KG, BS, TB, and LS provided biomarker data and interpretation. MTW provided  
carbon and nitrogen isotopes and sedimentologic evaluation of the core. KO provided additional isotope and geochemical  
data. IA, JAA, and CL researched the foraminiferal assemblages. EC provided clay mineralogy data. HJ provided  
nannofossil data. FJR provided ichnological data. JG and FD provided magnetic data. SPG, TB, JL, JM, and other co-authors  
assisted with conceptualization and writing of the manuscript.

## 300 Competing interests

The authors declare that they have no conflict of interest.

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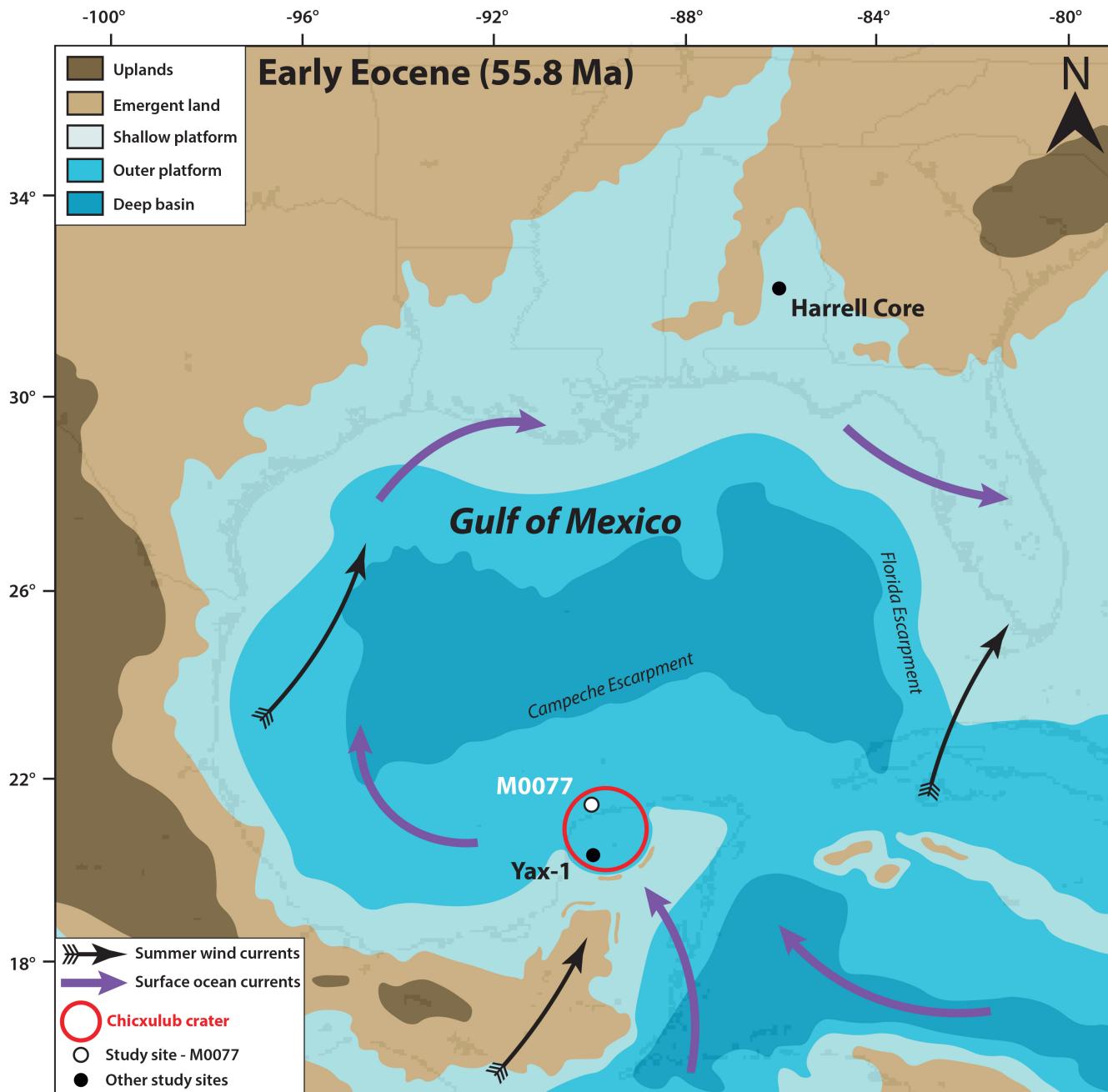
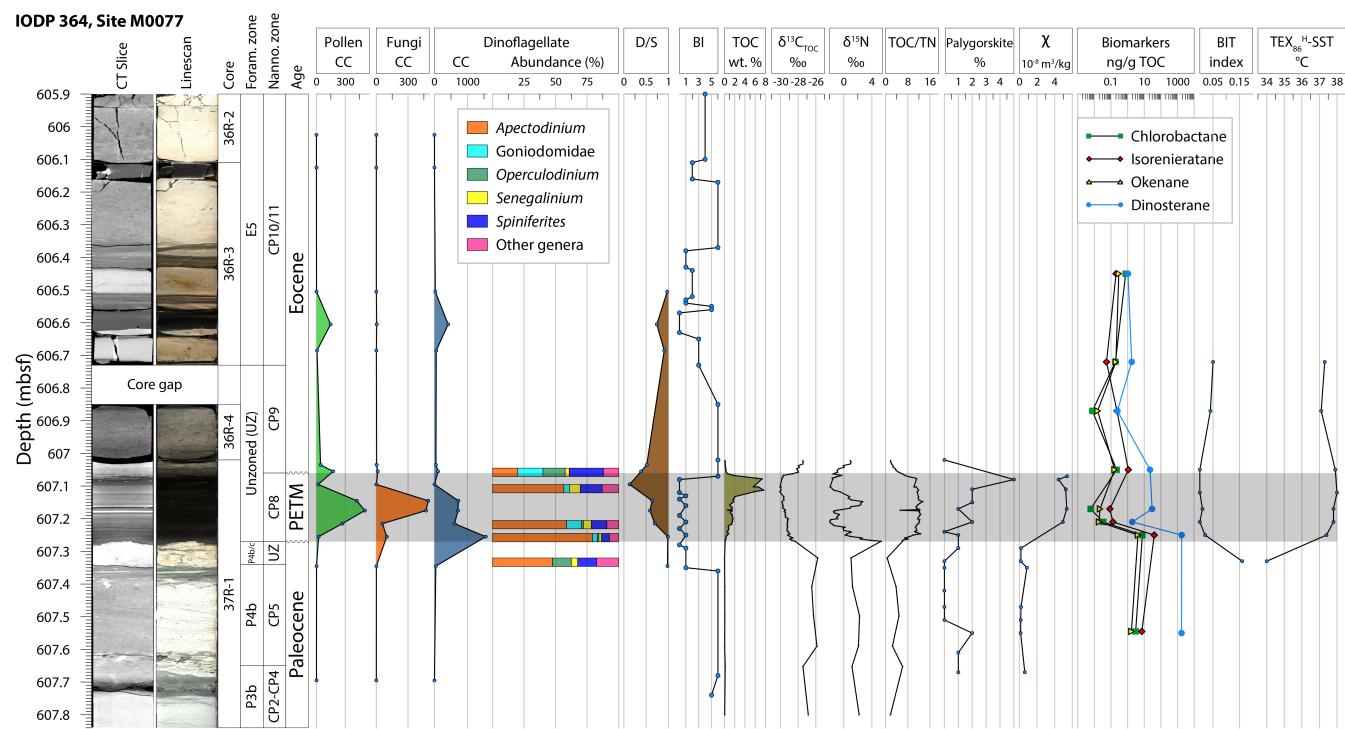


Figure 1. Paleocene-Eocene Thermal Maximum (55.8 Ma) paleogeography of the Gulf of Mexico and surrounding regions, modified from Scotese and Wright (2018), with locations of Site M0077 (IODP 364), Yax-1 (Whalen et al., 2013), and the Harrell Core in east-central Mississippi (Sluijs et al., 2014). The Harrell Core location has been adjusted to match the paleo-latitude/longitude at the PETM. Surface ocean currents and summer wind fields from Winguth et al. (2010).



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**Figure 2.** Stratigraphic column of Site M0077. Palynological concentrations (CC) are given as specimens/gram.  $\delta^{15}\text{N}$  is reported relative to atmospheric  $\text{N}_2$ ,  $\delta^{13}\text{C}_{\text{TOC}}$  is reported relative to VPDB. BI=bioturbation index (Taylor and Goldring, 1993), CT=computed tomography, D/S=dinoflagellate cyst to pollen and plant spore ratio (Warny et al., 2003), TOC/TN=total organic carbon/total nitrogen,  $\chi$ =magnetic susceptibility.