

# The Impact of High Palaeoproductivity on the Ecological Function and Test of Foraminifera in the Equatorial Pacific Ocean during the PETM

Celestine Nwojiji<sup>1,2,\*</sup>, Fabienne Marret<sup>1</sup>

<sup>1</sup>School of Environmental Sciences, University of Liverpool, L69 7ZT, UK

<sup>2</sup>Department of Geology, Ebonyi State University, Abakaliki, Nigeria

\*Corresponding author: celestine.nwojiji@yahoo.com

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**Abstract** Biological Trait Analysis (BTA) has been used to examine the effect of high ocean productivity on the ecological functioning and foraminiferal preservation at the PETM section of ODP site 1215A, Northeast Pacific Ocean. The faunal composition of the studied section indicated a foraminiferal assemblage associated with severe ecological disturbance due to the dominance of opportunistic taxa such as *Abyssamina quadrata*, *Nuttallides truempyi*, *Tappanina selmensis*, *P. pleurostomelloides*, *Quadriformina profunda*, *Bulimina midwayensis* and *Bulimina tuxpamensis*. Over 20 species of benthic foraminifera went into extinction during the PETM at ODP site 1215A. The results from the foraminifera trait analyses suggest that taxa with elongate and bi/triserial tests were the most resilient to the acidification of the ocean as most these taxa increased in abundance during the CIE while taxa with complex apertures and coarse-perforation tend to most vulnerable. Ocean acidification resulting from high productivity also led to the loss of ornamentation in benthic foraminifera as shown by high prevalence of taxa with no ornament. There was no order in the nmMDS ordination of both taxonomic and trait composition of the recovered foraminifera suggesting continual environmental perturbation across the studied section. The scanning electron microscope (SEM) image of some recovered foraminifera revealed evidence of dissolution/etching, extreme recrystallization and secondary calcite cementation on the test. The amount of coccoliths incorporated on the test of some deep infauna species requires further investigation to understand if some foraminiferal taxa construct their test in the dual process of secreting hyaline calcite and incorporation of coccolith plates by agglutinating processes in the later stage of their life history.

**Keywords:** foraminifera, PETM, biological trait analysis, palaeoecology, palaeoceanography, Pacific Ocean

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## 1. Introduction

The equatorial Pacific Ocean is very crucial in the global carbon budget as it is estimated to have the largest export primary production of 20%–60% in the modern oceans [1]. Productivity in the modern equatorial Pacific is reportedly the highest compared to any other pelagic biomes in the world [2]. Equatorial Pacific is estimated to have the largest primary production of 20%–60% in the modern oceans most of which is exported to the benthic zone [1]. It hosts the largest reservoir of carbon and nutrients, and so it makes a major contribution to the global carbon budget through its regulation of global organic/inorganic carbon and atmospheric CO<sub>2</sub> partial pressure (pCO<sub>2</sub>). Although the physical and chemical properties of the Pacific Ocean may have differed somewhat from what they are now during the Palaeogene, existence of high palaeoproductivity has also been

reported in the North equatorial tongue during the Eocene [3,4,5] at which time the equatorial Pacific also accounted for significant volume (60%) of the global ocean [1].

Foraminifera are unicellular marine protozoans with calcareous shells usually subdivided into chambers. It first appeared in the geologic record in the mid – Jurassic (70 million years ago; [6]). Foraminifera live in different parts of the ocean, from the surface water to sediments in the seabed [7,8,9]. They usually produce shells, also known as a test, which can have one or more chambers. The test could be made of organic matter, mineral substances, or agglutinated particles [10]. Ocean productivity is the main driver of foraminifera turnover in the open ocean benthic ecology as it controls the amount of oxygen available for faunal utilisation while parameters like bathymetry/water depth, temperature and salinity have less influence in the foraminiferal ecology as previously thought [11]. The response of foraminifera to the organic carbon flux to the ocean floor is controlled by the quantity and quality of the organic material arriving at the ocean floor though, the

mechanism of biological carbon pump is not yet fully understood [11,12,13].

Benthic foraminifera are a very useful tool for the reconstruction of palaeoenvironmental changes in the sea floor because they constitute a major proportion of the benthic biomass in the open ocean and records the physico-chemical changes in the ocean in their test [14,15,16]. The main source of food to the benthic organism is the detrital rain from the particulate organic matter produced by the plankton in the surface ocean except where hydrocarbon seeps and hydrothermal vents are present [16].

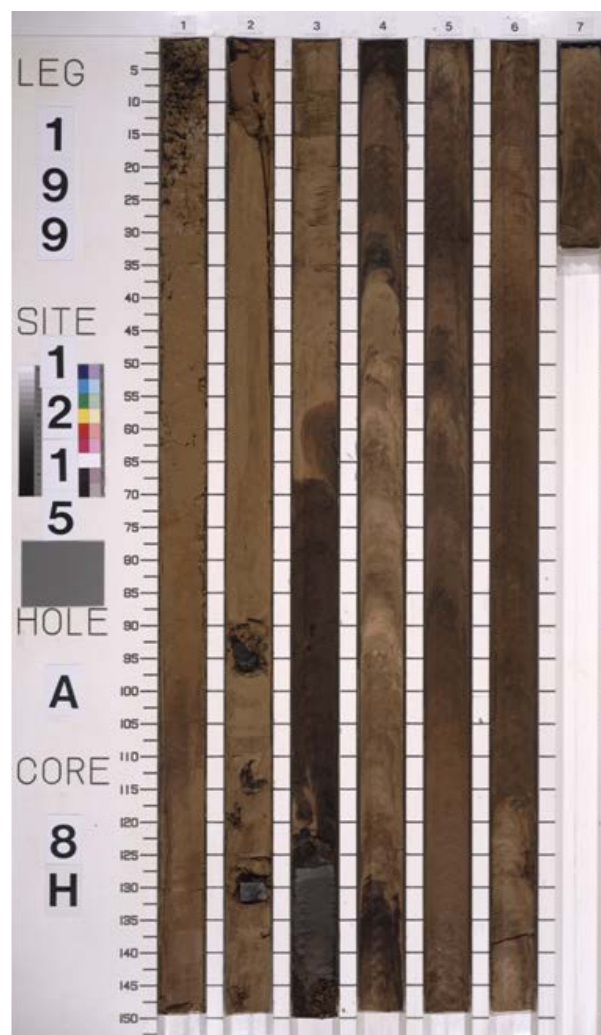
The Palaeocene – Eocene thermal maximum (PETM) which took place ~55 Ma was a period of extreme climatic event characterised by a rise in the global temperature to the tune of 5-8°C. This hyperthermal was caused by the injection of large amount of light carbon into the earth system leading to negative carbon isotopic excursion (CIE) of 3‰. The result of the large input of carbon in the oceans was massive acidification of the surface and deep ocean, carbonate dissolution, shoaling of the lysocline and carbon compensation depth (CCD), increased hydrological cycle, expansion of oxygen minimum zones and widespread sea bottom anoxia [17,18,19,20,21,22]. The understanding of the impact of this climatic event in the benthic ecosystem will give an insight on how the current global warming will affect the deep-sea bottom-dwelling fauna in the near future.

Increase in primary and export production has been widely reported during the PETM [2,5]. [5] noted that the combined counteracting feedback of the hyperthermal on the physical, biological and chemical properties of the ocean makes the evaluation of palaeoproductivity difficult; however, the result from their study of barite accumulation rate (BAR) indicated that high  $p\text{CO}_2$  had a fertilising effect on the primary producers which led to increase in reproduction and coeval increase in export production. Biogenic barium is a good indicator of biological productivity because it is well preserved in pelagic settings and has a burial efficiency of more than 30% [23,24]. The high rate of BARs during the PETM correlates well with the increase in export production i.e. carbon flux from the surface water to the intermediate and deep waters [25], which is also a function of primary production. The increase in atmospheric  $p\text{CO}_2$  resulting from high temperature will increase the production of carbon rich particle and nitrogen fixation as well as other high nutrient element thereby increasing the efficiency of the biological carbon pump [5]. Increase in the temperature of the ocean as observed during the PETM can also lead to increase in bacterial activity and organic matter regeneration [5] and higher export production. More so, increase in nutrient in the ocean either by continental runoff or upwelling from the deep-sea causes blooms of phytoplankton and could lead to increased export production to the ocean beds.

The lithologic composition and digital core photos across the PETM in site 1215A (Figure 1) is a vivid evidence of the existence of increased palaeoproductivity and abundance of the organic matter even before the PETM as the majority of the section is brown – dark brown in colour.

Nevertheless, the onset of ocean acidification during PETM (core 1215A- section H3) also contributed to the brownness in the sediment (Figure 1).

This study examined the impact of extreme climatic on the benthic foraminiferal communities and their ecological functioning (here defined as the role performed by organisms in the maintenance and regulation of ecosystem) in the subtropic ecosystem. A technique known as biological trait analysis (BTA) was used to understand the impact of high palaeoproductivity (established in previous studies) on the faunal assemblage and trait composition of benthic foraminifera. Biological trait analysis is a multivariate statistical approach used to describe species distribution, their biological characteristics and how it is related to the running of their ecosystem [26,27].



**Figure 1.** Digital core photograph of Core 1215A H8. The brown coloration is an indication of high organic matter content. The PETM section is found in the darkest part of section 3 (<http://web.iodp.tamu.edu/OVERVIEW>)

The objectives of this study include;

1. Detailed analyses of the PETM benthic foraminiferal assemblage from site 1215A and study how increased productivity affected the faunal assemblage and composition.
2. Investigation of trait changes in the identified foraminiferal and interpret their ecological functioning during the PETM.

- Evaluate the impact of ocean acidification on the preservation of benthic foraminiferal test.

## 2. Materials and Method

### 2.1. Materials

Thirty-eight (38) core samples were selected from ODP Leg 199, site 1215A, Hole 6 & 8 for this study. Site 1215A is located at latitude 26.0296 and longitude-147.9332 in the abyssal hill north of Molokai fracture northeast in the central Pacific Ocean. The core was taken in an area with typical abyssal hill topography but with continuous sediment cover. Molokai Fracture is characterised by an extensional tectonic setting and with hydrothermal vents around it. Hole A cored at site 1215 were drilled at 5396 metres below sea level (mbsl) at 26°01.77'N, 147°55.99'W [28]. The summarised stratigraphy of site 1215 [28,29] indicated that the Hole composed of ~70m of pelagic clay and clayey nannofossil ooze. The stratigraphy of the Hole A is subdivided into units I, II III and IV based on the characteristic sedimentary facies. The unit I is composed of red clay intercalated with zeolites. Unit II from where the samples for this study were collected consists of brown – dark brown, clayey calcareous ooze with some cherts sandwiched within the sediment. Unit III is a metalliferous dark – brown ooze with little clay and no ash nor fossil, it is unconformably overlying the basaltic igneous rock of unit IV. Site 1215 is one of the numerous sites cored to study the Palaeogene palaeogeography. The key objective of coring this site was to understand the feedback mechanism from the ocean carbon budget as a result of extreme (warm) temperature and climatic condition. The understanding of hyperthermal event like the PETM [17,18,30] provides an important insight on how the earth and ocean ecosystems response to the astronomical increase in the greenhouse gas concentration caused by fossil carbon.

### 2.2. Methods

Prior to the statistical analysis, foraminiferal specimen were extracted by soaking and washing of ~10cc sediment with a 63µm sieve and allowed to dry after getting rid of all the muds. Benthic and planktonic foraminifera were picked, identified and counted from the dry residue. Due to the poor preservation of planktonic foraminifera, they were excluded from this study to minimise taxonomic errors as benthic foraminifera were better preserved though with signs of dissolution and frosty appearance. Foraminiferal preservation was studied using the Scanning Electron microscopy.

After sorting and identification of the recovered fossil foraminifera to the lowest possible taxonomic level, thirteen (13) biological traits were selected based on their functional role. The traits believe to reflect the ecosystem services provided by the recovered foraminifera include; A. Test Shape, B. Test Composition, C. Chamber arrangement, D. Chamber shape, E. Test macro-ornamentation, F. Test Micro-ornamentation, G. Aperture form, H. Aperture accessory structures, I. Primary aperture position, J. Test perforation, K. Life habit, L. Feeding habit and M.

Mobility. These thirteen functional traits were further subdivided into 64 nominal categorization referred to as modalities as shown in Table 1.

A procedure developed by [31] known as fuzzy coding techniques was used in describing the affinity of various species to different modalities. This process expresses the intraspecific variation in trait composition of all the foraminiferal species recovered from the analysed cores. The affinity of each trait to the associated modality is expressed using a scale of 0.0 – 1.0 with 0 representing absence / no affinity to the trait category and 1 illustrating dominant / high affinity to the trait. Where a species does not exhibit a particular trait, all the associated categories are filled with 0 to avoid altering the result of further analysis. For instance, *Oridorsalis umbonatus* has spiral test and a semi-circular shape. For instance, during the fuzzy coding, *O. umbonatus* was classified as follows: A1. Spiral (0.6) A2. Elongate (0) A3. Globose (0.4) A4. Tubular (0) A5. Subquadrate (0) A6. Others (0). This implies that using this method allows each trait that exhibited more than one modality to scored according to a particular trait “weight”, but the total score of all the categories will sum to unity [32]. Data on biological traits were obtained from the laboratory during the foraminiferal identification / analyses as well as from the biological database such as WORMS – World Register of marine species: <http://www.marinespecies.org>, The Palaeobiology database <http://palaeodb.org> and Fossilworks <http://http://fossilworks.org/>. The frequency of each trait modality in the dataset was calculated by multiplying the category scores with the total abundance of each species exhibiting those modalities. This was achieved by simple matrix multiplication method [27,33]. The result of this data treatment is a trait table that shows the relative abundance of all the biological traits recorded in all the species across the whole samples.

#### 2.2.1. Statistical Analysis

Statistical analysis of both the species abundance and biological trait datasets were performed with Primer ver.6 [34] and excel spreadsheet. All the counted foraminifera were grouped into three factors (Pre-CIE, CIE and Recovery) according to their position in the sample relative to the PETM interval

The foraminiferal compositions and traits similarities across the PETM was calculated using the Bray-Curtis index resemblance matrix. The resemblance data was transformed with Log (x+1). A Log (x+1) modifies the species relative abundance to reduce the influence of the dominant species on the data [35]. The taxa abundance data were standardized prior to any transformation however, trait data was not subjected to this procedure because it had been standardized during the fuzzy coding process. The transformed data was plotted for a non-metric multidimensional scaling ordination (nmMDS) based on the Bray – Curtis similarity matrices. nmMDS is based on the rank similarities of samples and produces an ordination plot showing relative differences/ resemblance in biological trait composition across the PETM (Pre-CIE, CIE and Recovery) intervals. Analysis of similarity tests (ANOSIM) were used to test for significant differences between various traits and samples across the three PETM sections.



**Table 1. Example of traits and associated modalities used in biological traits classification of foraminiferal communities**

| Traits                           | Modalities            |                              |                               |                            |                  |           |
|----------------------------------|-----------------------|------------------------------|-------------------------------|----------------------------|------------------|-----------|
| A. Test Shape                    | A1. Spiral            | A2. Elongate                 | A3. Globose                   | A4. Tubular                | A5. Others       |           |
| B. Test Composition              | B1. Agglutinated      | B2. Hyaline calcite          | B3. Hyaline aragonite         | B4. Secreted: Porcellanous | B5. Others       |           |
| C. Chamber arrangement           | C1. Unilocular        | C2. Uniserial                | C3. Bi/Tri-serial             | C4. Planispiral            | C5. Trochospiral | C6. Other |
| D. Chamber shape                 | D1. Spherical/Oval    | D2. Tubular                  | D3. Triangular or trapezoidal | D4. Semi-circular          | D5. Others       |           |
| E. Test macro-ornamentation      | E1. Depressed sutures | E2. Raised sutures           | E3. Ponticuli                 | E4. Keeled                 | E5. Others       |           |
| F. Test micro-ornamentation      | F1. No ornament       | F2. Spinose                  | F3. Striate                   | F4. Costae                 | F5. Others       |           |
| G. Aperture form                 | G1. Oval/reniform     | G2. Arcuate                  | G3. Radiate                   | G4. Slit-like              | G5. Others       |           |
| H. Aperture accessory structures | H1. Lips              | H2. Teeth                    | H3. Neck                      | H4. None                   |                  |           |
| I. primary aperture position     | I1. Terminal          | I2. Basal interiomarginal    | I3. Umbilical                 | I4. Extra-umbilical        | I5. Others       |           |
| J. Test perforation              | J1. Microperforation  | J2. Fine perforation         | J3. Coarse perforation        | J4. no perforation         |                  |           |
| K. Life habit                    | K1. Benthic epifaunal | K2. Benthic shallow-infaunal | K3. Benthic deep-infaunal     | K4. Others                 |                  |           |
| L. Feeding habit                 | L1. Deposit feeder    | L2. Herbivore                | L3. Omnivore                  | L5. Others                 |                  |           |
| M. Mobility                      | M1. Stationary        | M2. Mobile                   | M3. Clinging                  | M4. Others                 |                  |           |

### 3. Results

#### 3.1. Benthic Foraminiferal Taxa Composition and Changes through Time in Site 1215A

The benthic foraminiferal composition and assemblage in Site 1215A were dominated by calcareous hyaline taxa, with agglutinated forms constituting less than 10% of all the identified fauna. The strong dominance of benthic foraminifera with the calcareous hyaline test in the recovered taxa indicates that the studied section was deposited above the lysocline, and carbon compensation depth (CCD). However, poor preservation of benthic foraminiferal tests suggest that the lysocline may have been really close to the depositional depth especially during the PETM when the preservation was worst affected. 117 species constituting 4065 specimens of benthic foraminifera were identified and counted. The faunal assemblage was predominantly infaunal morphotypes (~60% relative abundance), including *Bulimina*, *Abyssamina*, and cylindrical taxa like *Pleurostomella*, *Nodosaria*, and *Stilostomella*. The epifauna was relatively less (approx. 40%) with mainly cosmopolitan deep water Velasco-type taxa such as *Nuttallides*, *Anomalinoidea*, *Cibicides*, *Gyrodinoides* and *Valvulinerina* (Figure 3; Table 2).

The nmMDS of taxa composition showed that most of the pre-CIE samples widely clustered at the base of the plot except for a sample from 56.5 mbsf (Figure 2). The CIE samples clustered more tightly at the upper part while the recovery samples clustered in between the pre-CIE and the CIE. The samples from the recovery interval were the most dispersed when compared to the other intervals (Figure 2). The ordination also showed that the recovery fauna were more closely related to their CIE counterpart than to the pre-CIE. The three samples from the CIE that clustered closer to the pre-CIE were those from the onset of the excursion, suggesting that they are more related.

The clustering together of the CIE samples is interpreted as evidence of similarity in taxonomic composition and may also reflect a higher sampling resolution of that interval as the pre-CIE and the recovery were sampled at a lower resolution (Table 2). The recovery samples with wider dispersal were those at the transition from the CIE to the recovery, this suggests that fauna at the interval just before the recovery were still experiencing some perturbation. In general, the samples that did not ordinate with the respective group were those related to either the beginning or termination of the negative carbon isotopic excursion. Sample 41.01mbsf was an outlier. The ANOSIM test indicated that the foraminifera communities from three intervals differed significantly from each other with the global  $R = 0.20$  and  $p < 0.05$ .

The SIMPER result indicated that 24 taxa were the major contributor to the differences/ similarities observed in the faunal composition of the PETM intervals studied at Site 1215A. The highlighted species were predominantly cosmopolitan and composed of both infauna and epifauna morphotypes (Table 2). The pre-CIE was characterised by increase in the abundance of both robust/heavily calcified taxa as well as small disaster taxa. The CIE was characterised by increase in the small disaster taxa only and the recovery interval was characterised by increase in the abundance of mostly heavily calcified taxa (Table 2).

The mean abundance of the taxa present in the similarity percentage result showed that *Paralabamina elevata*, *Valvulinerina praeacuta*, *Buliminella beaumonti*, *Globorotalites micheliniana*, *Paralabamina lunata*, *Aragonia aragonensis*, *Oridorsalis umbonatus*, *Valvulinerina sp.2*, *Gyrodinoides subangulatus*, *Neoponides hillebrandti*, and *Pullenia subcarinata* were relatively higher during the pre-CIE than in other intervals. The foraminiferal assemblage above were dominated by epifauna taxa with few *Buliminids* (Table 2). Despite the high number of species in this interval, their percentage contribution to the total dissimilarity was very low.

The CIE interval recorded the highest mean abundance of *Abyssamina quadrata*, *Nuttallides truempyi*, *Tappanina selmensis*, *Paleopleurostomella pleurostomelloides* and

*Coryphostoma crenulata* and these taxa made the greatest contribution to the dissimilarity (50% cut off) between the pre-CIE and the recovery (Table 2).

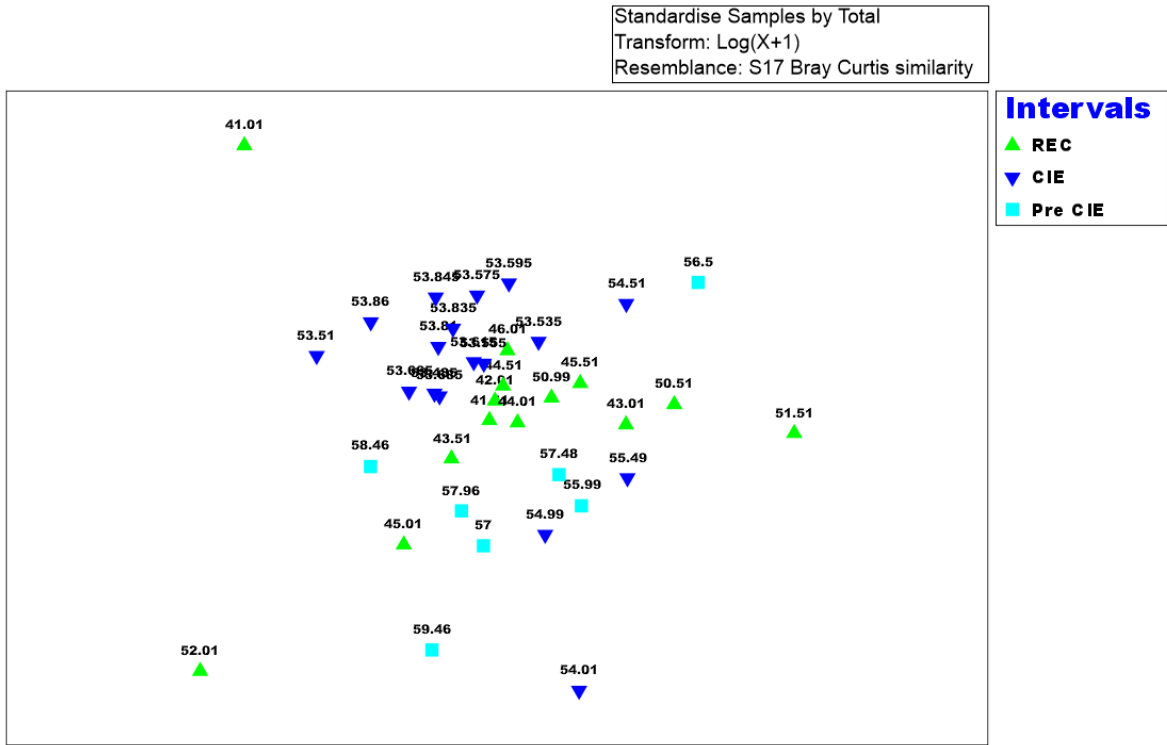
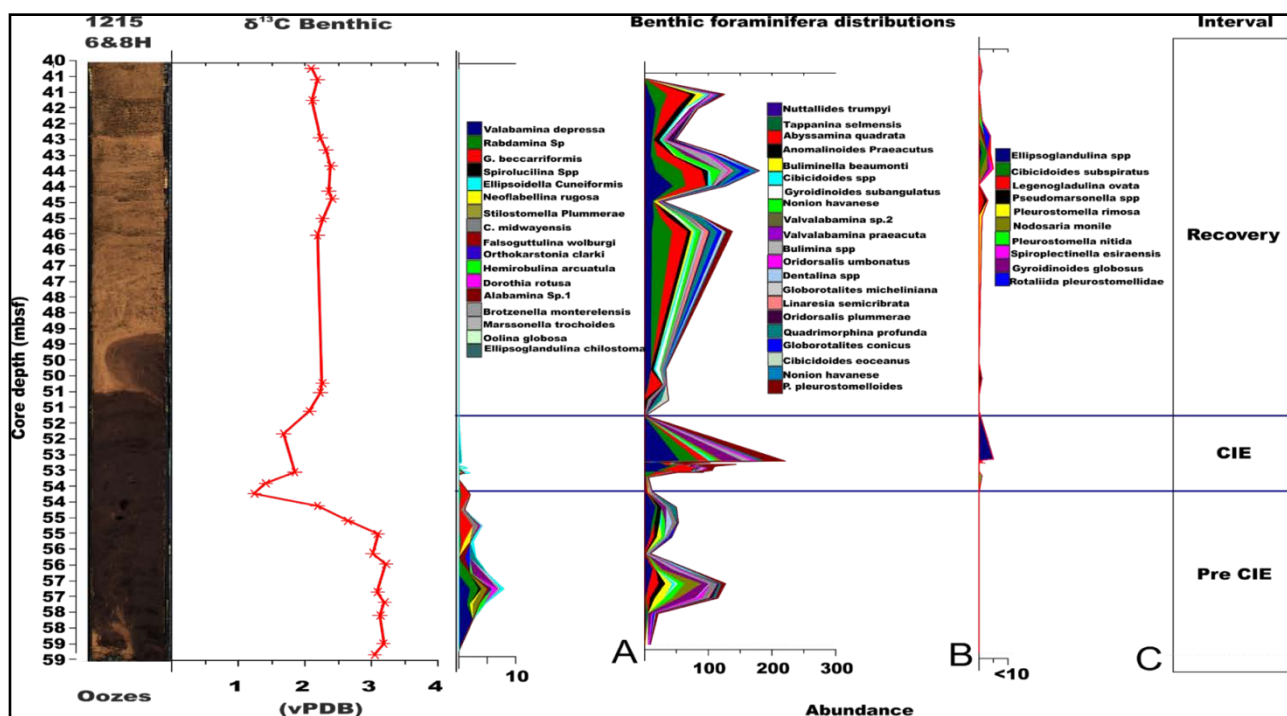


Figure 2. Non-metric Multidimensional Scaling ordination of benthic foraminiferal taxa composition (transformed with total resemblance) of Bray-Curtis similarity from Site 1215A ODP Leg 199, Central equatorial Pacific Ocean

Table 2. Mean abundance of taxa that contributed the most dissimilarities observed in faunal distribution across the CIE intervals at ODP Site 1215A. Data is limited to 50% cumulative contribution

| Species                                       | Mean Abundance |             |             | Contribution to dissimilarity (%) |
|---|----------------|-------------|-------------|-----------------------------------|
|   | REC            | CIE         | Pre CIE     |                                   |
| <i>Abyssamina quadrata</i>                    | 1.85           | <b>2.36</b> | 1.28        | 5.3                               |
| <i>Nuttallides truempyi</i>                   | 2.08           | <b>2.77</b> | 1.38        | 5.12                              |
| <i>Tappanina selmensis</i>                    | 1.78           | <b>1.81</b> | 0.41        | 4.08                              |
| <i>Paralabamina elevata</i>                   | 0.13           | 0.24        | <b>1.59</b> | 2.99                              |
| <i>Valvalabamina praeacuta</i>                | 0.6            | 1.04        | <b>1.57</b> | 2.87                              |
| <i>Anomalinooides praeacutus</i>              | <b>1.56</b>    | 0.63        | 1.04        | 3.35                              |
| <i>Buliminella beaumonti</i>                  | 0.53           | 0.12        | <b>1.32</b> | 2.62                              |
| <i>Quadriformina profunda</i>                 | <b>1.26</b>    | 1.15        | 0.58        | 3.4                               |
| <i>Nonion havanense</i>                       | <b>0.91</b>    | 0.29        | 1.2         | 2.07                              |
| <i>Globorotalites micheliniana</i>            | 0.7            | 0.7         | <b>1.04</b> | 2.49                              |
| <i>Paralabamina lunata</i>                    | 0.67           | 0.04        | <b>0.85</b> | 1.94                              |
| <i>Aragonia aragonensis</i>                   | 0.19           | 0.48        | <b>0.66</b> | 1.92                              |
| <i>Bulimina midwayensis</i>                   | <b>0.47</b>    | 0.27        | 0.9         | 1.9                               |
| <i>Oridorsalis umbonatus</i>                  | 0.64           | 0.57        | <b>0.87</b> | 1.89                              |
| <i>Valvalabamina sp.2</i>                     | 0.1            | 0.24        | <b>1.21</b> | 1.89                              |
| <i>Paleopleurostomella pleurostomelloides</i> | 0.51           | <b>1.59</b> | 0.77        | 3.1                               |
| <i>Cibicidoides eoceanus</i>                  | <b>0.57</b>    | 0.04        | 0.41        | 1.66                              |
| <i>Cibicidoides subcarinatus</i>              | 0.48           | 0.24        | <b>0.49</b> | 1.58                              |
| <i>Gyroldinooides subangulatus</i>            | <b>0.54</b>    | 0.28        | 0.35        | 1.56                              |
| <i>Neoeponides hillebrandti</i>               | 0.05           | 0.13        | <b>0.51</b> | 1.54                              |
| <i>Coryphostoma crenulata</i>                 | 0.23           | <b>0.71</b> | 0.55        | 2.16                              |
| <i>Bulimina tuxpamensis</i>                   | 0.79           | 0.15        | <b>0.84</b> | 1.71                              |
| <i>Pullenia subcarinata</i>                   | 0.61           | 0.27        | <b>1.28</b> | 1.67                              |



**Figure 3.** Benthic foraminiferal events in ODP Site 1215A. A- The distribution of some important opportunistic taxa. B- Extinction taxa; C- Taxa that originated during or after the CIE. N/B: There is colour overlap across three events due to limited colour range in Tilia

Quadrimorphina profunda, Bulimina midwayensis, Nonion havanense, Anomalinoidea praeacuta, Cibicidoides eoceanus, Gyroidinoides subangulatus and Bulimina tuxpamensis were the most abundant species during the recovery interval. These species are associated with moderate oxygen level and seasonality in productivity from upwelling and surface water mixing [22,36].

In the raw taxa composition, the late Palaeocene (Pre-CIE, 59.5 – 54.6 mbsf) section was characterised by the restricted occurrence of *Valvulabamina depressa*, *Raddamina sp.*, *G. beccarriformis*, *Spiroculina Spp.*, *Neoflabellina rugosa*, *Stilostomella plummerae*, *Coryphostoma midwayensis*, *Falsoguttulina wolburgi*, *Orthokarstonia clarki*, *Hemirobulina arcuata*, *Dorothisia rotusa*, *Brotzonella monterelensis*, *Marsonella trochoides*, *Oolina globosa*, *Ellipsoglandulina chilostoma* and *Ellipsoidella cuneiformis* (Figure 3).

Most of the listed taxa went into extinction before or during the PETM. Other cosmopolitan fauna that showed high relative abundance in this interval were *Nuttallides truempyi*, *Nonion havanense*, *valvulabamina praeacuta*, *Buliminella beaumonti* and *Bulimina spp.*, *Cibicidoides Sp.3*, *Neoepionides hillebrandti* and *Paralabamina elevata* (Figure 3)

The main CIE (54.6 – 51.5 mbsf) interval was characterised by blooms of opportunistic taxa such as *Abyssamina quadrata*, *N. truempyi*, *Paleopleurostomella pleurostomelloides*, *Oridosalis umbonatus*, *Bulimina Spp.* and *Cibicidoides Spp.* (Figure 3) indicating an ecological disturbance in the benthic ecosystem. Other taxa which occurrences were restricted to the PETM include *Ellipsoglandulina Spp.*, *Cibicidoides subspiratus*, *Leganoglandulina ovata*, *Pseudomaronella Spp.*, *Pleurostomella nitida*, *Gyroidinoides subglobosa*, *Spiroplectinella esiraensis* and *Rotaliida pleurostomellidae*. These benthic foraminiferal species also went into extinction after the PETM. Agglutinated taxa were the

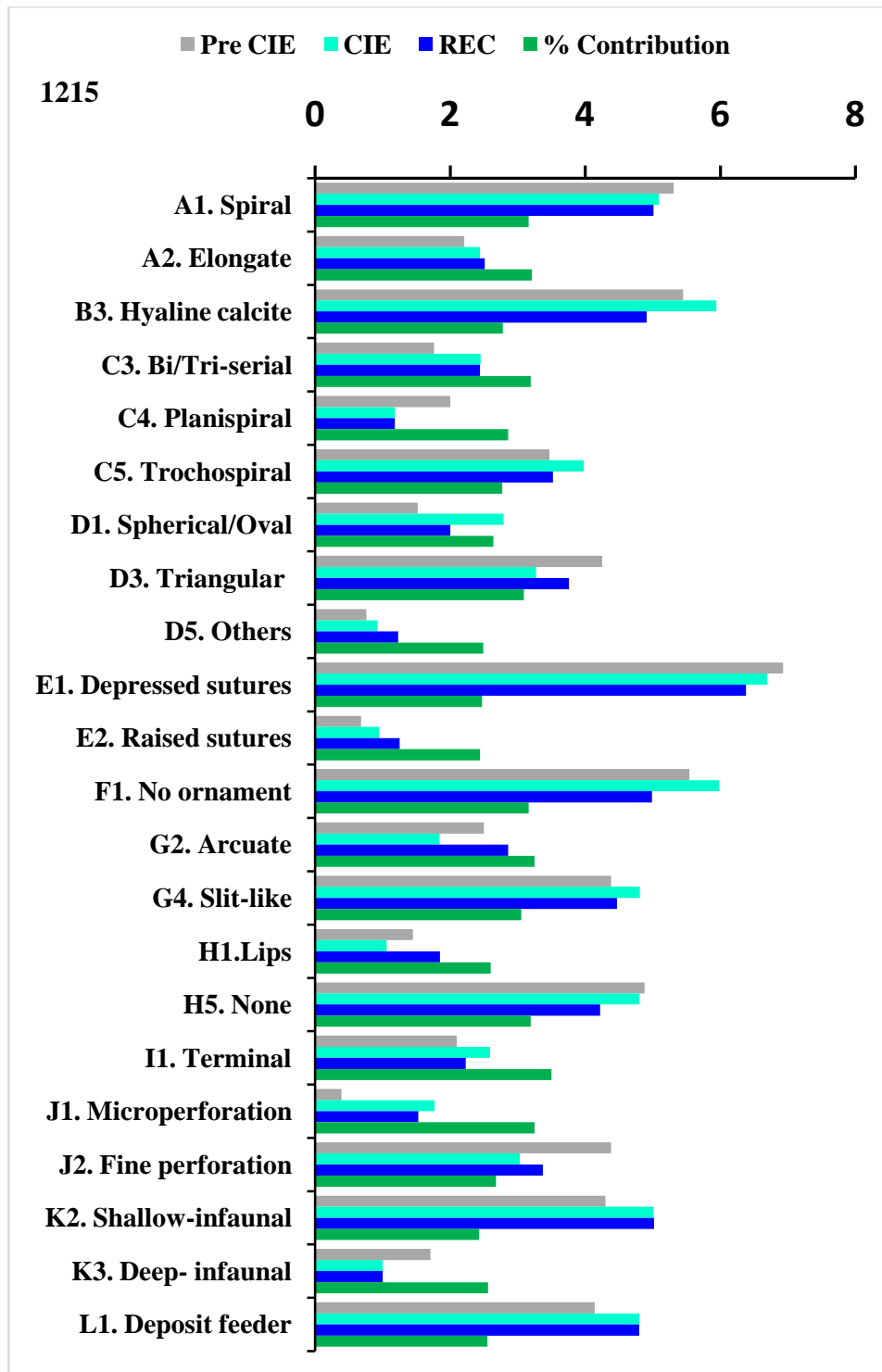
most affected group of foraminifera (Figure 3) during the CIE in the equatorial Pacific, probably because they build their test with rock fragments and the majority of the fragment in the open ocean are predominantly biogenic carbonate which could easily be dissolved by acidification. The taxa that survived or increased in abundance during the PETM were mainly opportunistic epifauna and triserial infaunal morphotypes (Figure 3 and Figure 4) and are predominantly of the small test sizes. Foraminifera have been reported to produce smaller test during the period of low oxygen concentration and decreased carbonate concentration due to early reproduction as a preadaptation measures to extreme ecological condition [37,38].

Recovery section (51.5 – 41.0 mbsf) was characterised by the significant increase in diversity and abundance of taxa that survived the CIE including: *N. truempyi*, *Tappanina selmensis*, *A. quadrata*, *N. havanense*, *Bulimina Spp.*, *Oridosalis plummerae*, *Anomalinoidea praeacuta*, *Q. profunda*, *Bulimina trinitatis*, *B. tuxpamensis*, *Aragonina valescoensis*, *Pullenia subcarinata* and *Cibicidoides Spp.* The ratio of epifauna to infauna also increased at this interval. The increase in both the surface-dwelling epibenthic and the deep sediment dwelling infauna at the recovery interval suggest improved ecological condition after the CIE.

### 3.2. Benthic Foraminiferal Traits Composition in the Equatorial Pacific Ocean

The trait composition of benthic foraminifera in site 1215A clustered together in two groups (Figure 5). Samples at group A represent the core of the three intervals of PETM while samples at group B represent the boundaries between each interval. The ANOSIM value of global  $r = 0.08$ ;  $p > 0.05$  indicated that intervals





**Figure 6.** SIMPER result of the most significant trait (at 50% cut off) that contributed to the differences in benthic foraminiferal trait composition across the CIE events at ODP Site 1215A. Grey bars = pre-CIE; sky blue bars = CIE core; deep blue bars= Recovery; green bars = % contribution of each trait

Another trait modality that showed significant variation in abundance across the three intervals were spherical/oval and triangular/trapezoid chamber shapes. Spherical/oval increased during the CIE but decreased afterwards but not as low as it was at the pre-CIE while triangular/trapezoid trait decreased significantly at the CIE and increased during the recovery but not as much as the pre-CIE values. The increase in the proportion of spherical/oval still points to the high abundance of some taxa like *Q. profunda* and *A. quadrata* during the CIE.

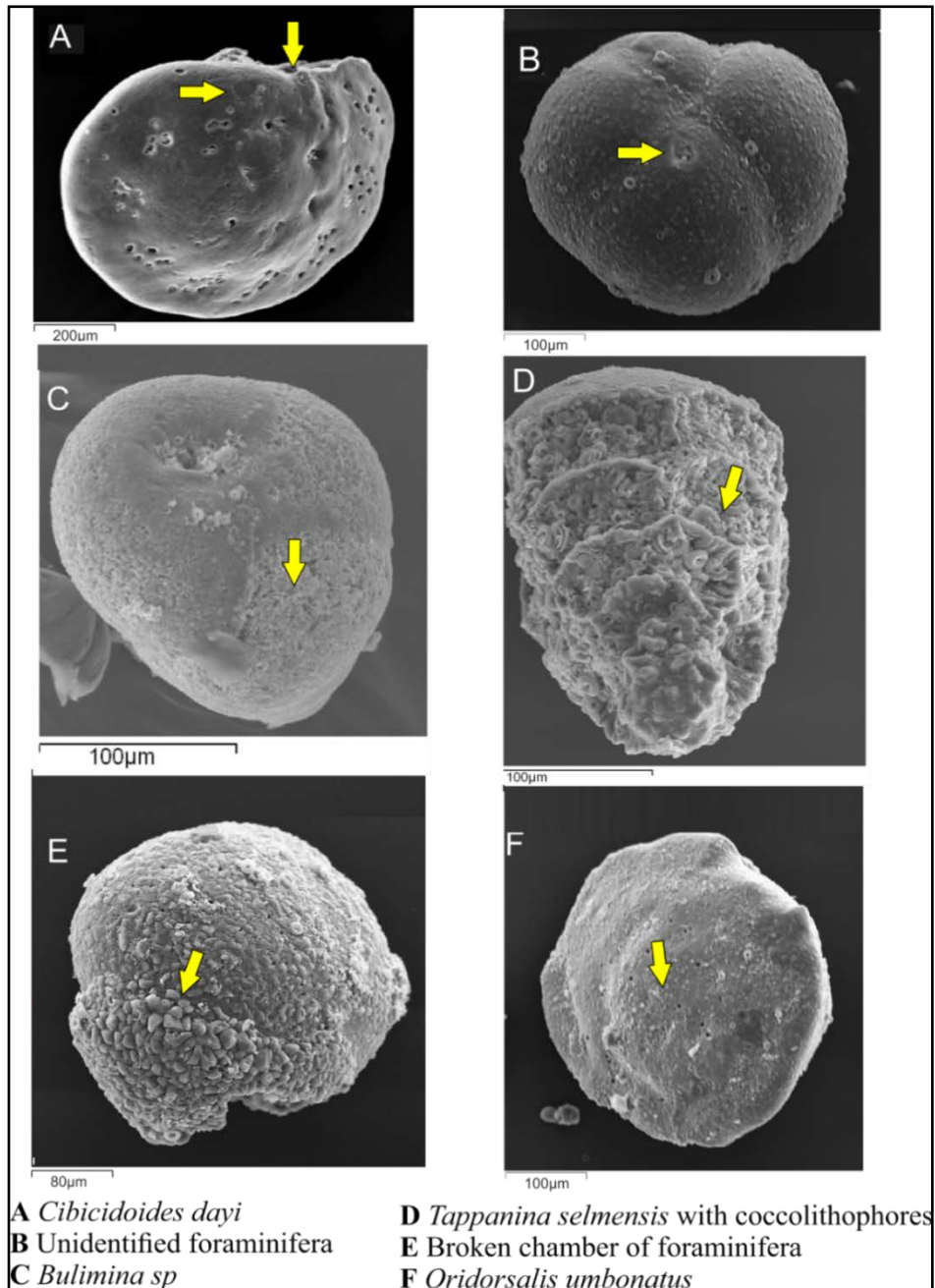
The mean values of depressed sutures retrogressively decreased from the pre-CIE to the recovery, while raised sutures progressively increased from the pre-CIE to the recovery. There were a general decrease in ornamentation and apertural accessories with the increase in carbon concentration in the ocean; this may have probably be as a result of a decrease in the survival rate of the organism as ornamentation is associated with feeding and defence mechanism of foraminifera [39]. Perforation also decreased during the CIE while the mode of life shifted toward a shallow infauna habit (Figure 6).



### 3.3. Preservation of Foraminiferal Test in the Equatorial Pacific during the PETM

The scanning electron microscope (SEM) images of some recovered foraminifera have revealed evidence of dissolution/etching, extreme recrystallisation/neomorphism and secondary calcite cementation on the test of both benthic foraminifera identified at Site 1215A. The SEM imaging focused on the quality of preservation in selected foraminifera, and we have documented different stages of foraminifera test alteration during the PETM at Site 1215A.

The SEM imaging revealed that some of the foraminiferal specimens that showed glassy appearance in the light microscope have evidence of dissolution under the SEM and the frosty specimens showed a high level of dissolution and recrystallisation (Plate 1; Plate 2; Plate 3). For example, plate 1 specimens A - D would appear to be well preserved under the light microscope, but under the SEM, A is showing an early stage of alteration. The initial protruding part of the test has been dissolved indicating that foraminifera test dissolution usually starts from the last chamber of a spiral test and progresses to different parts of the test.

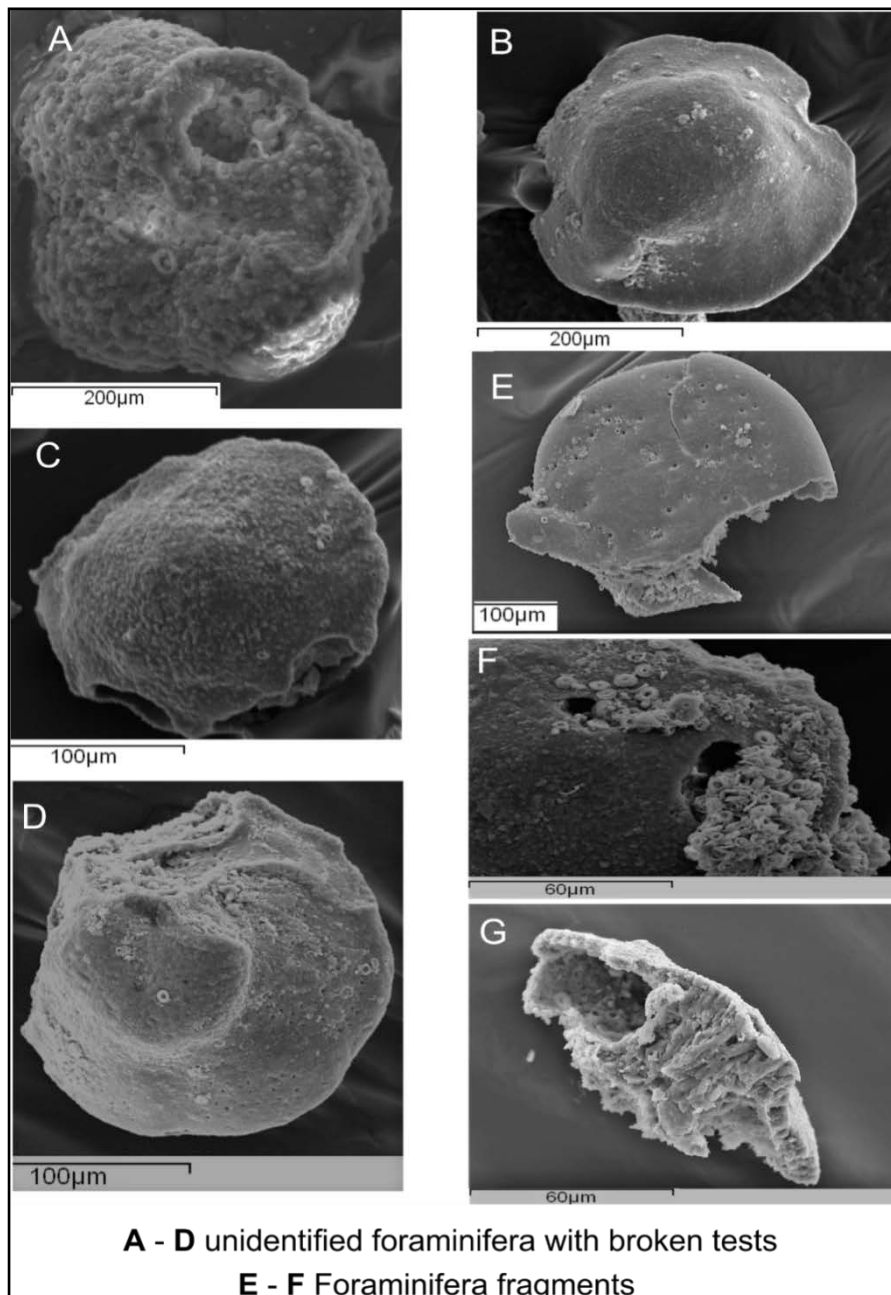


**Plate 1.** Foraminiferal test from sample 1215A\_8H-03\_60-62 showing evidence of early stage of diagenesis. A) shows a test of *Cibicidoides dayi* with the arrows pointing at the broken edge and peeling on the surface of the test. Under the light microscope, this test will appear glassy indicating good preservation. B) is a test of unidentified planktonic foraminifera with the outer layer of the test completely removed. It is difficult to identify this species because all the outer features have been completely dissolved. C) is showing a partially dissolved outer layer of *B. tuxpamensis*? It could still be identified based on shape and aperture position. D) is showing coccolith plates exposed by partial dissolution in *T. selmensis* test. Note (yellow arrow) how the nannofossil are arranged in different parts of the test with some sort of order. E) a piece of the foraminifera chamber is showing the peeling of the second layer of the test. The dissolution of this test has reached an advanced stage. F) is a test of *O. umbonatus* with the outer layer completely removed

The specimens also show that the test architecture plays a role in the susceptibility or resistance of a test to abrasion or dissolution. The surfaces around the broken part were beginning to roughen and exfoliate as shown by the arrow in specimen A. Specimen B shows a completely exfoliated specimen, all the diagnostic features and ornamentation have been removed, and the size of previously small pores are beginning to increase as a result of dissolution. This specimen appears frosty under the light microscope and could be identified based on the shape to the family level, but in SEM where all the surface features have been completely removed, it is identified as unknown foraminifera. Specimen C and F showed the test that was undergoing dissolution and still retained their original shape and ornamentation which was used in their

identification, more so, the evidence of widening of pores in specimen F is conspicuous. The surface of specimen D (*T. selmensis*) is partially removed by dissolution and coccolith plates embedded in the test have been exposed.

The last chamber at the bottom of the specimen still retained the secreted crystals; we think that this species may have a dual method of calcification; secreting hyaline calcite to build its test and incorporating coccolith plates during the later period of calcification. Plate 1 specimen E shows a test that has undergone many layers of exfoliation, the size of existing crystals in the original test has been enlarged by recrystallization, and the chamber has been detached from the parent test. This specimen is hyaline calcite and at an advanced stage of dissolution.

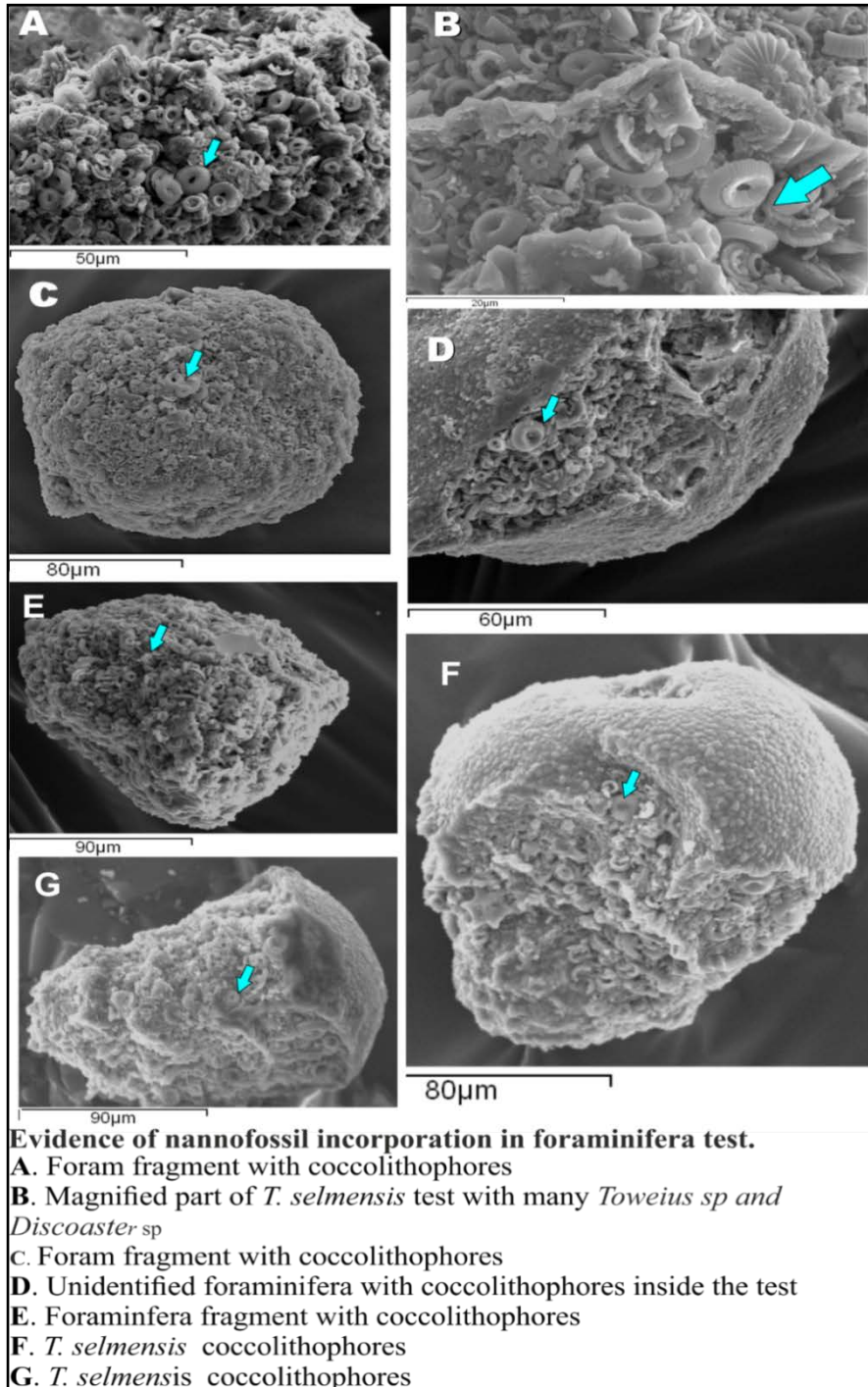


**Plate 2.** Foraminiferal test at an advanced stage of dissolution. All the specimens were picked across the PETM interval. A shows extreme dissolution, calcite overgrowth and neomorphism of planktonic foraminifera. Dissolution has destroyed all the ornamentation, enlarged the pores spaces and removed some chambers. B – D shows advanced stages dissolution and thinning of the test walls with fragmentation setting in. E – G are fragments of foraminifera test at the final stage of dissolution. Note the coccolithophores on specimen F; it is a post-depositional attachment unlike the previously described test with nanofossil incorporated in the test fabric

The process of foraminifera test alterations starts with the roughening/etching of the initially smooth surface (Plate 1 A and C), as the dissolution continues there may be partial peeling of the test or breaching of the last chamber depending on the morphology of the foraminifera test (Plate 1A and Plate 2A) at this point the last chamber may be broken and more or less missing with total removal of the surface ornamentation or suture and widening of surface pores.

Advanced stages of dissolution are characterised by significant thinning of the test, missing

chambers/disappearance of some part of the test and scattered holes (Plate 1 E and Plate 2 A – D), and most of the last whorl may be totally exfoliated. The last stage shows less than 50% of the test preserved, and the test becomes so thin that it could crumble on the touch of a picking brush, (Plate 2 E- G, Plate 3 A- E). Also, the original calcite crystal may have been replaced by neomorphism and overgrowth (Plate 2 A – G). At this point, the test may be destroyed beyond possible taxonomical identification.



**Plate 3.** Evidence of nannofossil incorporation in foraminifera test from sample 1215A\_8H-03\_130-132. A, C & E are broken pieces of foraminifera test resulting from extreme dissolution. Note in the arrows showing nannofossil incorporation in foraminifera test. B) is the enlarged part of *T. selmensis* showing a combination of secreted hyaline test and embedded coccolith plates. This test composition suggests that foraminifera could calcify in dual processes (agglutinating and secreted hyaline). D) shows advanced stages dissolution and thinning of *O. umbonatus?* test wall with fragmentation setting in. G & F are further evidence of incorporation of nannofossil in foraminifera



Many specimens of foraminiferal test recovered from this study showed evidence of coccolith incorporation in foraminiferal test (Plate 3). The amount of coccolith incorporated in the test of some foraminifera in this study has generated some curiosity as to which method(s) does foraminifera calcify in the open ocean. Plate 3 A, C and E are foraminiferal fragments composed entirely of calcareous nannofossil. One may argue if these fragments are sediments recovered with the foraminifera, but specimens B, D, G, and F in plate 3 showed part of foraminiferal test composed of coccolith plates.

## 4. Discussion

### 4.1. Interpreting the Ecological Functioning of the Seafloor from the Fauna and Trait Composition of Benthic Foraminifera

The faunal composition of the studied section indicates an assemblage associated with severe ecological disturbance due to the dominance of opportunistic taxa such as *Abyssamina quadrata*, *Nuttallides truempyi*, *Tappanina selmensis*, *P. pleurostomelloides*, *Quadrinorphina profunda*, *Bulimina midwayensis* and *Bulimina tuxpamensis*. The prevalence of opportunistic taxa in an ecosystem is evidence of ecological stress [27,40]. Similar foraminiferal assemblages have been reported in many extreme climatic events such as Cretaceous/Palaeogene boundary event [41], Middle Eocene Climatic Optimum (MECO; [42]) as well as the PETM [22,36,43,44,45,46,48]. The extinction of *G. beccariformis*, *Neoflabellina*, *Dorothia retusa* and *Marsonella trochoides* that occurred in this location have been reported in other PETM sections confirming the existence of the biotic changes that occurred during the hyperthermal at the equatorial Pacific [45,46,49,50]. The disappearance of other taxa recorded in Site 1215A may be as a result of local extinctions.

The pre-CIE interval was strongly dominated by epifauna and agglutinated taxa as well as few hyaline calcareous infauna (Figure 3). The extinct taxa were known to have wide distribution during the late Palaeocene in deep and epicontinental seas before their extinction in the early Eocene. The high abundance of infauna taxa is an indication of moderate and sustained food supply and/or reduced oxygen concentration to the seafloor [11]. Also, the faunal composition in this interval indicated a mesotrophic condition, with seasonally fluctuating oxygen and transient high food environment [22,41,43,47,51].

The composition of taxa at the CIE interval (Table 2; Figure 3) are dominated by opportunists, characteristic of low-productivity and possibly thriving in continuously stressed dysoxic sea-bottom conditions [54]. These species are reported to be common in the deep sea especially around the BEE [22,36,46,52,54,55].

The relatively low abundance of low oxygen indicators may be due to preservation as bi/triserial taxa go into solution before other taxa during carbonate dissolution [56]. And the high level of dissolution in foraminiferal assemblage from this site may have affected the taxonomic composition by skewing the preserved specimens toward more resistant taxa.

In terms of changes in benthic foraminiferal trait composition, there was a reduction in the abundance of taxa with a spiral test from the pre-CIE to the recovery interval and taxa with elongate test indicated an inverse trend as they rather increased from the pre-CIE through to the recovery interval. This result suggests that elongate bi/triserial tests were more resilient to the increase in the acidification of the ocean as most taxa that increased in abundance at the CIE interval have elongate bi/triserial tests.

Elongate test shape is associated with taxa like *Bulimina*; *Bolivina*; *Pleurostomelloides*, *Stilostomella*, and *Coryphostoma* and these taxa are known disaster taxa [46]. These taxa have been reported to be tolerant to increased phytodetritus rain to the sea floor, reduced oxygen content and unstable ecological condition [22,54]. Spiral tests are found in a large number of heavily calcified epifauna that are susceptible to changes in the benthic ecosystem. The increase in taxa with bi/triserial chamber (Figure 6) linked to the increase in the average abundance of elongate test during the CIE. This could be used as a proxy for ecological stress in the seafloor. Trochospiral test showed a relative increase in abundance during the CIE and returned to the pre-CIE values at the recovery interval (Figure 6). The increase in this trait modalities during the CIE could be linked to the increase in the opportunistic taxa like *A. quadrata*; *N. truempyi*; *O. umbonatus* and *Q. profunda* which have trochospiral chamber arrangement.

The high abundance of near-surface dwelling spiral taxa and the seabed living elongate form in trait composition could mean that most of the preserved benthic foraminifera lived in a dual habitat, staying on the sediment surface when it is conducive and diving deeper inside when the sediment surface becomes harsh. [11] pointed out that species classified as epifauna in the modern ecosystem may have lived a similar dual lifestyle as they co-occur with deep infauna taxa, this hypothesis appears to be true in this study but more investigation is recommended.

The ecological functioning of the benthic foraminifera will, therefore, be complicated to interpret due to the loss of some taxa that contributed to functioning due to dissolution. Nevertheless, our BTA analysis shows that ocean acidification caused by high export productivity had a significant impact on the traits and by extension functioning of benthic foraminifera. The high abundance of highly calcified taxa indicated by the predominance of hyaline calcite, spiral, trochospiral, elongate, bi/triserial (Figure 3; Figure 6) suggests a continual sequestration of carbon by foraminifera and that ocean acidification may not have reduced the ability of this organism to calcify, instead it destroyed the test of the organism after burial. This is contrary to the current observation in the modern ocean where ocean acidification is said to reduce the calcification of calcifying organism [57,58]. This is because, despite the high degree of dissolution observed in the foraminiferal assemblage, taxa with calcareous test still dominate.

We think that foraminifera that survived during the CIE may have utilised more inorganic carbon (DIC) than the organic carbon (OC) for their nutritional needs as the DIC is more labile than the OC. The residual organic matter



may have contributed to a large amount of organic material and other detrital rain from the surface ocean to the sea floor, and the bacterial oxidation of this organic matter may have sustained the acidification for a long period in the equatorial Pacific.

The ocean acidification leads to the loss of ornamentation in foraminifera that occurred during the CIE in the study area as the result from this study indicated a prevalence of the no ornament trait (Figure 6). Loss of ornamentation in benthic foraminifera is linked to extreme ecological conditions and has been previously reported by [59] in the modern ecosystem. Ornamentation in foraminifera is important in feeding, protection, movement, and prey-predation relationship [59,60]. They are used for sorting food particles into different shape and sizes, disaggregating larger particles into smaller pieces before ingestion, removing of harmful stuff as well as an adaptation for escaping from predators [59]. The outer ornamentation of foraminifera would likely be the first point of attack by the corrosive bottom water and this could lead to loss of ornamentation. More so, organisms could reduce structural/anatomical complexity to conserve energy in the period of ecological stress and thereby enriching taxa with no ornamentation in the foraminiferal assemblage.

The apertural modality of the foraminifera assemblage was dominated by simple slit-like and arcuate form. Because the majority of the foraminifera were shallow infauna and deposit feeders, these forms of apertures are suitable for absorbing dissolved nutrient rather than ingesting food particles. Our result also shows a significant decrease in apertural complexity across the studied section with no aperture accessory being the most abundant trait in the aperture accessories category. The decrease in apertural complexity has also been reported in some species of foraminifera (*Haynesina germanica*) during the period of carbon dioxide increase in the Barent Sea [59].

#### 4.2. Coccolith Plates Incorporation in Foraminifera - A Dual Process of Test Building or Artifact of Diagenesis

The incorporation of some nannofossils in the test of foraminifera may be a result of post-depositional diagenetic processes, however, It is believed that some species of foraminifera may have constructed their hard parts by dual processes i.e. by crystallising the inner part of their test during the early stage of test formation from the chemical composition of the surrounding sea water as well as incorporating some coccolith plate into their test later in life by agglutinating process. Previous studies have reported benthic foraminifera building their test with coccolithophores by agglutinating processes and some planktonic foraminifera has been also reported to incorporate nannofossils into their wall structure too ([61]; [62] and [63]). Some agglutinating foraminifera has been reported to use coccolithophores for feeding and plastering their test with coccolith plates [63]. A close look at the SEM images of *T. selmensis* (Plate 1; Plate 2; Plate 3) shows the nannofossil incorporation on its test confirming that these nannofossils are actually part of the test and not a diagenetic artifact. Most of the nannofossils

found on the test of foraminifera in plates 1,2,3 are of *Toweius* and *Discoaster* taxa indicating that the coccolith plates were preferentially selected. If it were to be diagenetic in origin, the composition of the coccolithophores may have varied. A similar scenario was reported by [64] where *Gaudryina cribrosphaerellifera* constructed their test entirely with *Cribrosphaerella ehrenbergii*. *T. selmensis* (Plate 1 specimen D) for instance was described by [65] as being entirely composed of hyaline calcite only but our result has shown that the species and other deep infauna *Buliminids* may have calcified through secreted hyaline and agglutinated processes.

## 5. Conclusions

This study has further improved on the existing knowledge of benthic foraminiferal composition and palaeoecology in the equatorial Pacific Ocean during the PETM. The results from this study has revealed the ecological disturbance associated with high organic matter flux to the seafloor as a result of increased surface productivity and upwelling. Our interpretation supports the idea that the paleoredox changes from enhanced organic carbon influx during the period of increased temperature and carbon dioxide concentration created highly acidified oceanic conditions that resulted to poor preservation of the recovered foraminifera and ecological disturbance in the sea floor. Evidence of benthic ecological perturbation was indicated by the turn over in taxa and trait composition of the recovered foraminifera as well as the dominance of opportunistic taxa in assemblages.

Post-depositional dissolution is believed to be a significant factor that influenced the faunal composition and invariably the associated traits and ecological functions. Dissolution is suspected to have selectively removed more susceptible taxa, smaller specimen and taxa with rough ornamentation as well as coarsely perforated taxa. However, results from the biological trait analysis suggest that functional redundancy (i.e. some species performing the same function) existed in the foraminiferal assemblage studied.

In terms of faunal composition, the BTA identified *Paralabamina elevata*, *Valvalabamina praeacuta*, *Buliminella beaumonti*, *Globorotalites micheliniana*, *Paralabamina lunata*, *Aragonia aragonensis*, *Oridorsalis umbonatus*, *Valvalabamina sp. 2*, *Cibicidoides subcarinatus* and *Pullenia subcarinata* (Table 2) as drivers of ecological functioning before the onset of the CIE. The increase in the abundance of these opportunistic taxa during the PETM may be as a result of biotic turnover resulting from extinction and/or stifling of reproduction in the bigger taxa that require more energy to flourish. This assemblage also suggests a stressed ecosystem caused by additional pressure from the carbon isotopic excursion on the already perturbed benthic habitat.

The foraminifera assemblage associated with the recovery in this study (Table 2) included: *Anomalinoidea praeacutus*, *Quadrinorina profunda*, *Nonion havanense*, *Bulimina midwayensis*, *Cibicidoides eoceanus*, *Gyroidinoidea subangulatus* and *Bulimina tuxpamensis*. The faunal

composition indicates a return of heavily calcified taxa and a combination of epifaunal and infaunal morphotypes. The presence of cosmopolitan taxa still existing during the recovery suggest that the benthic ecosystem have not fully recovered from the effect of PETM even when the carbon isotope signal had fallen back to the pre-CIE values.

Based on trait composition, this study indicate that taxa with spiral and elongate test shape, secreted hyaline calcite test composition as crucial traits for the regulation of carbon content in the ecosystem. Taxa with bi/tri-serial, planispiral and trochospiral chamber arrangement, as well as spherical/oval, triangular/trapezoid shape chambers, depressed or raised sutures and taxa with no ornament, are indicated as resilient traits during the period of ecological disturbance because their proportion increased or remained constant during the CIE. These traits are found on a wide range of taxa with opportunistic lifestyle as mentioned in section 4.1. Aperture forms such as arcuate or slit-like apertures with lips or no apertural accessories and terminal aperture position are indicators of successful feeding strategies critical to the survival of the benthic foraminifera. Also, the existence of micro and fine perforation in the SIMPER result (Figure 6) suggested a reduction in the size of perforation. Finer perforation reduces oxygen requirement of foraminifera as well as the impact of dissolution by creating smaller reaction surface. More so, the absence of coarse perforation suggests that taxa with such traits require higher oxygen concentration and less corrosive bottom water to survive.

Benthic fauna shift their habitat towards shallow-infaunal and deep- infaunal with deposit feeding mode during the period of ecological disturbance (Figure 6), and only those taxa that were suited to such lifestyle were able to survive. There are possibilities that some taxa currently classified as epifauna may have lived infaunally and migrated to the sediment surface to feed or acquire oxygen and move back later into the sediment to take refuge.

This study also suggests that some deep infaunal taxa like *T. selmensis* might have constructed their test in a dual process of secreted hyaline calcite and incorporation of coccolith plate by agglutinated processes. Further sample cleaning procedures, high-resolution SEM imaging and tomography are therefore recommended to better understand the calcification in this taxa.

The application of BTA in understanding the ecological functioning of microfossils is still at its pioneering state, and we hope that with increasing interest among palaeoecologists on the application of the tools, more discoveries of its value would be appreciated. In this study, it has been very useful in combining faunal assemblages and trait composition and mapping them to the related ecological functioning. Also, it synthesises large data sets across the lateral and temporal scale in a well-structured and understandable manner.

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## References

- [1] Lyle, M., and Wilson, P.A. (2006). Leg 199 synthesis: Evolution of the equatorial Pacific in the early Cenozoic. In Wilson, P.A., Lyle, M., and Firth, J.V. (Eds.), Proc. ODP, Sci. Results, 199. Ocean Drilling Program. College Station, TX, 1-39.
- [2] Moore, T.C., Backman, J., Raffi, I., Nigrini, C., Sanfilippo, A., Pälke, H., and Lyle, M. (2004). Paleogene tropical Pacific: clues to circulation, productivity, and plate motion. *Paleoceanography*, 19(3):PA3013
- [3] Moore, T.C. (2005). Opal accumulation in the equatorial Pacific. *Eos, Trans. Am. Geophys. Union*, 86(52) (Suppl.), Pp24A-05.
- [4] Faul, K. L., and A. Paytan (2005), Phosphorus and barite concentrations and geochemistry in Site 1221 Paleocene/Eocene boundary sediments, in Proceedings of the Ocean Drilling Program, Sci. Results, edited by P. A. Wilson, M. Lyle, and J. V. Firth, Ocean Drilling Program, College Station, Tex. 1-23.
- [5] Ma, Z., Gray, E., Thomas, E., Murphy, B., Zachos, J., and Paytan A. (2014). Carbon sequestration during the Palaeocene– Eocene Thermal Maximum by an e-cient biological pump. *Nature Geoscience* vol. 7, 382-388.
- [6] Schiebel, R. and Hemleben, C. (2017). *Planktic Foraminifers in the Modern Ocean*. Springer-Verlag Berlin Heidelberg. 358p.
- [7] Murray, J.W. (1991). *Ecology and palaeoecology of benthic foraminifera*. Longman, Harlow, 397p.
- [8] Goldstein, S. T. (1999). Foraminifera: A biological overview. In B. K. Sen Gupta (Ed.), *Modern foraminifera*, Great Britain: Kluwer Academic Publishers. 37-56.
- [9] Kitazato, H and Bernhard, M. J. (2014). *Approaches to study living foraminifera: Collection, Maintenance and Experimentation*, Springer Japan, 227p
- [10] Bellier, J.P., Mathieu, P., Granier, B. (2010). Short treatise on foraminiferology (Essential on modern and fossil Foraminifera). *Carnets de Géologie - Notebooks on Geology*, Brest, Book 2010/02 (CG2010\_B02), 104p.
- [11] Jorissen, F. J., Fontanier, C., and Thomas, E. (2007). Paleooceanographical proxies based on deep-sea benthic foraminiferal assemblage characteristics, in: *Proxies in Late Cenozoic Paleooceanography: Pt. 2: Biological tracers and biomarkers*, edited by: Hillaire-Marcel, C. and A. de Vernal, A., 1, Elsevier, Amsterdam, The Netherlands, 264-325.
- [12] Suess, E. 1980. Particulate organic carbon flux in the oceans – surface productivity and oxygen utilization. *Nature*, 288, 260-263.
- [13] Murray, J.W. (2000). When does environmental variability become environmental change? *The Proxy Record of benthic Foraminifera*. *Environmental Micropaleontology*, Volume 15 of *Topics in Geobiology*. Kluwer Academic/Plenum Publishers, New York, 7-37.
- [14] Altenbach and Sarnthein, M. (1989). Productivity record in benthic Foraminifera, in Berger, W. H., Smetacek, V. S., and Wefer, G. (eds.), *Productivity of the Ocean: Present and Past*, John Wiley and Sons Ltd., New York, p. 255-269.
- [15] Licari, L.N., Schumacher, S., Wenzhofer, F., Zabel, M. and Mackensen, A. (2003). Communities and microhabitats of living benthic foraminifera from the tropical East Atlantic: impact of different productivity regimes. *Journal of Foraminiferal Research*, 33(1): 10-31.
- [16] Cavan, E. L., Henson, S. A., Belcher, A and Sanders, R. (2017). Role of zooplankton in determining the efficiency of the biological carbon pump. *Biogeosciences*, 14, 177-186.
- [17] Kennett, J.P and Stott, L.D. (1991). Abrupt deep-sea warming, palaeoceanographic changes and benthic extinctions at the end of the Palaeocene. *Nature* 353: 225-29.
- [18] Zachos, J. C., Röhl, U., Schellenberg, S. A., Sluijs, A., Hodell, D. A., Kelly, D. C., Thomas, E., Nicolo, M., Raffi, I., Lourens, L. J., Mccaren, H., and Kroon, D. (2005). Rapid acidification of the ocean during the Paleocene-Eocene Thermal Maximum, *Science*, 308, 1611-1615.
- [19] McInerney, F. A., and S. L. Wing. (2011). The Paleocene-Eocene Thermal Maximum: A perturbation of carbon cycle, climate, and biosphere with implications for the future, *Annu. Rev. Earth Planet. Sci.*, 39, 489-516.
- [20] Pälke, C., Delaney, M. L. and Zachos, J. C. (2014). Deep-sea redox across the Paleocene-Eocene Thermal Maximum, *Geochem. Geophys. Geosyst.*, 15, 1038-1053.

- [21] Meissner, K. J., Bralower, T. J., Alexander, K., Dunkley Jones, T., Sijp, W. and Ward M. (2014). The Paleocene-Eocene Thermal Maximum: How much carbon is enough? *Paleoceanography*, 29, 946-963.
- [22] Arreguín-Rodríguez, G. J., L. Alegret, and E. Thomas. (2016). Late Paleocene-middle Eocene benthic foraminifera on a Pacific seamount (Allison Guyot, ODP Site 865): Greenhouse climate and superimposed hyperthermal events, *Paleoceanography*, 31, 346-364.
- [23] Paytan, A., and M. Kastner. (1996). Benthic Ba fluxes in the central equatorial Pacific: Implications for the oceanic Ba cycle, *Earth Planet. Sci. Lett.*, 142, 439-450.
- [24] Bains, S., R. D. Norris, R. M. Corfield, and K. L. Faul. (2000). Termination of global warmth at the Paleocene/Eocene boundary through productivity feedbacks, *Nature*, 407, 171-174.
- [25] Dymond, J., Suess, E. and Lyle M. (1992). Barium in Deep-Sea Sediment: A geochemical proxy for paleoproductivity. *Paleoceanography* 7: 163-181.
- [26] Bremner, J., C. L. J. Frid & S. I. Rogers. (2005). Biological traits of the North Sea benthos: does fishing affect benthic ecosystem function? *American Fisheries Society Symposium* 41: 477-489.
- [27] Caswell, B. A. and Frid, C. L. J. (2013). Learning from the past: functional ecology of marine benthos during eight million years of aperiodic hypoxia, lessons from the Late Jurassic. *Oikos* 122(12): 1687-1699.
- [28] Lyle, M.W. and Wilson, P.A. (2002). Leg 199 Summary. *Proceedings of the Ocean Drilling Program, Initial Reports 199*. Ocean Drilling Program. College Station, TX, pp. 1-87.
- [29] Leon-Rodríguez, L. and Dickens, G. R. (2010). Constraints on ocean acidification associated with rapid and massive carbon injections: The early Paleogene record at ocean drilling program site 1215, equatorial Pacific Ocean, *Palaeogeogr. Palaeocl.*, 298, 409-420.
- [30] Thomas, E., Dickens, G. R., Fewless, T. and Bralower, T. J. (2003). Excess Barite Accumulation during the Paleocene/Eocene Thermal Maximum: Massive Input of Dissolved Barium from Seafloor Gas Hydrate Reservoirs. In: Wing, S., Gingerich, P., Schmitz, B., and Thomas, E., eds. *Causes and Consequences of Globally Warm Climates of the Paleogene*, GSA Special Paper, 369: 13-27.
- [31] Chevenet, F., Dolédec, S. and Chessel, D. (1994). A fuzzy coding approach for the analysis of long-term ecological data. *Freshwater Biology* 31: 295-309.
- [32] Caswell, B.C. and Frid, C. (2017). Marine ecosystem resilience during extreme deoxygenation: the Early Jurassic oceanic anoxic event. *Oecologia*, 1-16.
- [33] Charvet, S., Kosmala, A. and Statzner, B. (1998). Biomonitoring through biological traits of benthic macroinvertebrates: perspectives for a general tool in stream management. *Arch. Hydrobiol.* 142, 415-432.
- [34] Clarke, K.R. and Gorley, R.N. (2006). *Primer v6* Plymouth Marine Laboratory, Roborough, Plymouth, UK. 225-244.
- [35] Clarke, K.R. (1993). Non-parametric multivariate analyses of changes in community structure. *Aust. J. Ecol.* 18:117-143.
- [36] D'haenens S. Bornemann A. Stassen P. & Speijer R. (2012). Multiple early Eocene benthic foraminiferal assemblage and  $\delta^{13}\text{C}$  fluctuations at DSDP Site 401 (Bay of Biscay - NE Atlantic): *Marine Micropaleontology*, v. 88-89, p. 15-35.
- [37] Winguth, A., Thomas, E., and Winguth, C. (2012). Global decline in ocean ventilation, oxygenation and productivity during the Paleocene-Eocene Thermal Maximum - Implications for the benthic extinction. *Geology*, 40: 263-266.
- [38] Foster, L. C., Schmidt, D. N., Thomas, E., Arndt, S., and Ridgwell, A. (2013). Surviving rapid climate change in the deep-sea during the Paleogene hyperthermals. *Proc. Nat. Acad. Sci.*, 110: 9273-9276.
- [39] Mancin, N., Hayward, B. W., Trattenero, I., Cobianchi, M., and Lupi, C. (2013). Can the morphology of deep-sea benthic foraminifera reveal what caused their extinction during the mid-Pleistocene Climate Transition? *Mar. Micropaleont.*, 104, 53-70.
- [40] Oschmann, W. (1998). Kimmeridge clay sedimentation- a new cyclic model. *Palaeogeog., Palaeoclim., Palaeoeco.* 65, 217-251.
- [41] Alegret, L. and Thomas, E. (2009). Food supply to the seafloor in the Pacific Ocean after the Cretaceous/Paleogene boundary event. *Marine Micropaleontology*, 73(1-2), 105-116.
- [42] Boscolo Galazzo, F., Thomas, E., and Giusberti, L. (2015). Benthic foraminiferal response to the Middle Eocene Climatic Optimum (MECO) in the Southeastern Atlantic (ODP Site 1263). *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 417, 432-444.
- [43] Thomas, E. (2003). Extinction and food at the seafloor: A high-resolution benthic foraminiferal record across the Initial Eocene Thermal Maximum, Southern Ocean Site 690, in: *Causes and Consequences of Globally Warm Climates in the Early Paleogene*, edited by: Wing, S. L., Gingerich, P. D., Schmitz, B., and Thomas, E., *Geol. S. Am. S.*, Boulder, Colorado, The Geological Society of America, 369, 319-332.
- [44] Thomas, E. (2007). Cenozoic mass extinctions in the deep sea: What perturbs the largest habitat on Earth?, in: *Large Ecosystem Perturbations: Causes and Consequences*, edited by: Monechi, S., Coccioni, R., and Rampino, M., *Geol. S. Am. S.*, Boulder, Colorado, The Geological Society of America, 424, 1-23.
- [45] Takeda, K., Kaiho, K. (2007). Faunal turnovers in central Pacific benthic foraminifera during the Paleocene-Eocene Thermal Maximum. *Palaeogeography, Palaeoclimatology, Palaeoecology* 251, 175-197.
- [46] Alegret, L., Ortiz, S. and Molina, E. (2009). Extinction and recovery of benthic foraminifera across the Paleocene- Eocene Thermal Maximum at the Alamedilla section (Southern Spain). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 279: 186-200.
- [47] Kuhnt, T., Schmiedl, G., Ehrmann, W., Hamann, Y., Hemleben, C. (2007). Deep-Sea Ecosystem Variability of the Aegean Sea during the Past 22 kyr as Revealed by Benthic Foraminifera. *Marine Micropaleontology* 64, 147-162.
- [48] Stassen, P., Thomas, E. and Speijer R. P. (2015). Paleocene-Eocene Thermal Maximum environmental change in the New Jersey Coastal Plain: Benthic foraminiferal biotic events, *Mar. Micropaleontol.*, 115, 1-23.
- [49] Speijer, R.P., Schmitz, B. and Luger, P. (2000). Stratigraphy of late Palaeocene events in the Middle East: implications for low- to middle latitude successions and correlations. *Journal of the Geological Society, London*, 157: 37-47.
- [50] Aref, M. and Youssef, M. (2004). The benthic foraminiferal perturbation across the Paleocene-Eocene Thermal Maximum event (PETM) from Southwestern Nile Valley, Egypt. *N.Jb. Geol. Paleont. Abh* 234(1-3): 261-269.
- [51] Sen Gupta, B.K., Machain-Castillo, M.L. (1993). Benthic foraminifera in oxygen-poor habitats. *Marine Micropaleontology* 20, 183-201.
- [52] Stassen, P., Thomas, E. and Speijer, R. P. (2012). Restructuring outer neritic foraminiferal assemblages in the aftermath of the Palaeocene-Eocene thermal maximum. *Journal of Micropalaeontology*, 31: 89-93.
- [53] Giusberti, L. and Luciani, V. (2014). Reassessment of the early-middle Eocene planktic foraminiferal biomagnetostratigraphy: new evidence from the Tethyan Possagno section (NE Italy) and Western North Atlantic Ocean ODP Site 1051, *J. Foramin. Res.*, 44, 187-201.
- [54] Giusberti L. Coccioni R. Sprovieri M. Tateo F. 2009. Perturbation at the sea floor during the Paleocene-Eocene Thermal Maximum: Evidence from benthic foraminifera at Contessa Road, Italy: *Marine Micropaleontology*, v. 70, p. 102-119.
- [55] Frenzel, P. (2000). Die benthischen Foraminiferen der Rügener Schreiekreide (unter-Maastricht, NE Deutschland). *Neue Paläontologische Abhandlungen*, 3, 1-361.
- [56] Nguyen, T.M.P., Petrizzo, M.R. and Speijer, R.P. (2009). Experimental dissolution of a fossil foraminiferal assemblage (Paleocene-Eocene Thermal Maximum, Dababiya, Egypt): Implications for paleoenvironmental reconstructions. *Marine Micropaleontology*, 73, 241-258.
- [57] Heinze, C., Meyer, S., Goris, N., Anderson, L., Steinfeldt, R., Chang, N., Le Quééré, C., Bakker, D.C.E. (2015). The ocean carbon sink: impacts, vulnerabilities and challenges. *Earth Syst Dyn.* 6(1): 327-358.
- [58] Riebesell, U., Bach, L. T., Bellerby, R. G. J. J., Monsalve, R. B., Boxhammer, T., Czerny, J., Larsen, A., Ludwig A. and Schulz, K. G. (2017). Competitive fitness of a predominant pelagic calcifier impaired by ocean acidification. *Nature Geoscience* 10, 19-23.
- [59] Dubicka, Z., Zlotnik, M. and Borszcz, T. (2015). Test morphology as a function of behavioural strategies — Inferences from benthic foraminifera. *Marine Micropaleontology* 116, 38-49.
- [60] Georgescu, M.D., Arz, J.A., Macauley, R.V., Kukulski, R.B., Arenillas, I., Pérez-Rodríguez, I. (2011). Late Cretaceous (Santonian-Maastrichtian) serial foraminifera with pore mounds

or pore mound-based ornamentation structures. Rev. Esp. Micropaleontol. 43, 109-139.

- [61] Widmark, J.G.V. and Henriksson, A.S. (1995). The "orphaned" agglutinated foraminifera - *Gaudryina cribrosphaerellifera* n.sp. from the Upper Cretaceous (Maastrichtian), Central Pacific Ocean. In: S. Geroch et al. (Eds). Proc. 4th Int. Workshop on Agglutinated foraminifera. Grzybowski Formd. Spec. Pub. 3: 293-300.
- [62] Holbourn, A.E.L. & Kaminski, M.A. (1997). Lower Cretaceous deep-water benthic foraminifera of the Indian Ocean. Grzybowski Foundation Spec. Pub./., 4: 1 72pp.
- [63] Henriksson, A. S., Widmark, J. G. V., Holbourn A. E., Thies A. & Kuhnt W. (1998). Coccoliths as test-building material for foraminifera (coccolithofera). Journal of Nannoplankton Research, 20, 1, 15- 19.
- [64] Noel D. (1958). Etude de coccolithes du Jurassique et du Cretace inferieur. Publ. Serv. Carte Geol. Algerie, Bull. N.S., 20, 157-195 In Alfred et al., 1967. Electron Micrographs of Limestones and their Nannofossils. Princeton University Press, 141 pp.
- [65] Holbourn, A., Henderson, A.S. and Macleod, N. (2013). Atlas of Benthic Foraminifera. Wiley-Blackwell. UK. 642Pp.



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