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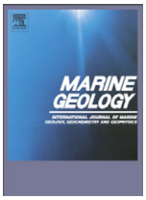

Impact of the Paleocene–Eocene Thermal Maximum on the macrobenthic community: Ichnological record from the Zumaia section, northern Spain

Francisco J. Rodríguez-Tovar [a,*], Alfred Uchman [b], Laia Alegret [c], Eustoquio Molina [c]

[a] *Departamento de Estratigrafía y Paleontología, Universidad de Granada, Avd. Fuente Nueva s/n, 18007, Granada, Spain*
[b] *Institute of Geological Sciences, Jagiellonian University, Oleandry 2a, 30-063, Kraków, Poland*
[c] *Departamento de Ciencias de la Tierra & IUCA, Universidad de Zaragoza, C/Pedro Cerbuna 12, 50009 Zaragoza, Spain*

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ABSTRACT

Trace fossil assemblages from the latest Paleocene to the earliest Eocene were significantly affected by the environmental perturbation of the Paleocene–Eocene Thermal Maximum (PETM). High-resolution ichnological analysis shows well marked different ichnological features pre-, syn-, and post-event. A well developed normal, tiered burrowing community is present in the sediments below the PETM, indicating oxic conditions and normal benthic food availability. During the PETM the record of trace fossil producers disappeared gradually but rapidly, reflecting the global increase in temperature, and the concentration of benthic food in the very shallow surface layer and, probably, the local depletion of oxygen within the sediments, although probably not true anoxia. The environmental perturbation significantly affected the whole benthic habitat, as shown by the correspondence with the main phase of the benthic foraminiferal extinction. After the PETM, the normal, tiered burrowing community recovered gradually and slowly, in a delayed return to pre-PETM environmental conditions. The changes in the trace fossil assemblage thus document the impact of the PETM on the macrobenthic community, a decline in oxygen levels during the PETM in a globally perturbed habitat due to global warming and the similarities and differences in the response of micro- and macrobenthic communities to global phenomena. Thus, ichnological analysis reveals as a very useful additional tool to understanding atmosphere–ocean dynamic during PETM and a potential way in future climate research.

1. Introduction

The Paleocene–Eocene Thermal Maximum (PETM) corresponds to a globally warm episode of Earth's history, directly following the Paleocene–Eocene boundary (around 55.5 Ma), and that has been studied extensively since its discovery in 1991 (see Sluijs et al., 2007 for a recent review). Originally, this event was placed within the latest Paleocene and named the Late Paleocene Thermal Maximum (LPTM). The definition of the Paleocene/Eocene boundary was changed, however, placing this boundary at the base of the PTEM, so that the maximum temperatures were registered after the Paleocene/Eocene boundary. This event is thus also called the Initial Eocene Thermal Maximum (IETM) (Sluijs et al., 2007).

The episode was geologically brief (~170 kyr, see below), and the analysis of marine and terrestrial proxies revealed that global temperatures increased by ~5 °C, although in some regions temperatures increased by up to 8 °C (e.g., Wing et al., 2005; Zachos et al., 2006).

Associated with the rapid global warming, a massive perturbation of the global carbon cycle occurred, as indicated by the occurrence of a negative carbon isotope excursion (CIE) in carbonate and organic matter in terrestrial and marine records. The size of the negative excursion was originally through to be including a 2.5–3‰, as seen in many carbonate records, although its magnitude was 5–6‰ in organic records (Bowen and Bowen, 2008 and references therein). More recently, the globally averaged value of the negative carbon isotope excursion is estimated at 3.5 to 5.0‰ (e.g., Handley et al., 2008; McCarren et al., 2008).

The calcite compensation depth (CCD) shoaled rapidly (by more than 2 km in the South Atlantic Ocean) and recovered gradually (Zachos et al., 2005). Most researchers agree that the PETM global warming was caused by massive input of isotopically light carbon into the ocean–atmosphere system, leading to the massive perturbation of the carbon cycle, but the source of the added carbon is not yet determined (see overview in Sluijs et al., 2007). The carbon injection had an estimated duration of ≤20 kyr (Röhl et al., 2007), and the PETM lasted for about 10^5 years, with values ranging between 120 and 170 kyr (see Abdul Aziz et al., 2008).

Major biotic changes in terrestrial, shallow-marine and deep-marine communities occurred during this global paleoenvironmental perturbation, including migrations to higher latitudes, evolutionary

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[*] Corresponding author. Tel.: +34 958242724; fax: +34 958248528.
E-mail addresses: fjrtovar@ugr.es (F.J. Rodríguez-Tovar), alfred.uchman@uj.edu.pl (A. Uchman), laia@unizar.es (L. Alegret), emolina@unizar.es (E. Molina).

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radiations and extinctions (see Sluijs et al., 2007 and Thomas, 2007 for recent reviews). Marine communities underwent significant changes during the PETM, showing variable responses, with a clear differentiation between planktic and benthic realms (Bowen et al., 2006; Sluijs et al., 2007). In the planktic realm, organic-walled dinoflagellates show a global acme of the low-latitude genus *Apectodinium* (e.g., Crouch et al., 2001, 2003), which migrated even into the Arctic Ocean (Sluijs et al., 2006), while planktic foraminifera and calcareous nannofossils show comparatively minor changes, including migrations and diversification of the foraminifera genera *Morozovella* and *Acarinina* (Canudo and Molina, 1992; Kelly et al., 1996, 1998; Arenillas and Molina, 2000) and geographic diversification of the calcareous nannofossil assemblages (Raffi et al., 2005; Gibbs et al., 2006).

Significant changes are also observed in the benthic realm. Deep-sea benthic foraminifera suffered the most severe extinction (Benthic Foraminiferal Extinction, BFE) in the last 90 Ma, which affected 35–50% of the species within the first 10 kyr of the Eocene (Thomas, 1998, 2003; Alegret et al., 2009a,b;). In contrast, benthic foraminifera from marginal-marine settings show comparatively less severe extinctions and temporal changes in composition (Thomas, 2003; Alegret et al., 2005). Several causes have been proposed to explain the extinction, including low oxygen conditions, carbonate corrosivity, changes (mainly decreasing) in oceanic productivity, or a combination of these (Thomas, 2007 for a review). However, none of these factors has been documented to have had globally extend, and repopulation of cosmopolitan species could occur after survival in refugia. In this context, a rapid global warming, increasing deep ocean temperature, can be envisaged as the main reason for the widely extended response of the microbenthic community (e.g., Thomas, 1998, 2003, 2007; Alegret et al., 2009a,b).

Unlike deep-sea benthic foraminifera, ostracods did not suffer major extinctions across the PETM (Boomer and Whatley, 1995; Guernet and Molina, 1997), although important assemblage and test size changes have been documented (Steineck and Thomas, 1996; Speijer and Morsi, 2002; Sluijs et al., 2007; Webb et al., 2009). So far, benthic analysis has been mainly focused on microfossil data, mainly benthic foraminifera and secondarily ostracode assemblages, while the effects of the PETM on macrobenthic environment has been scarcely considered (see recent ichnological analyses in Nicolo, 2008, and Smith et al., 2009). However, biogenic structures reveal trace maker behavior in response to environmental features, providing a valuable information on paleoenvironmental dynamic as well as to approach future environmental changes. The aim of this paper is to address the impact of the Paleocene–Eocene thermal maximum on the macrobenthic community of trace makers, based on a high-resolution ichnological analysis of the Zumaia section, focusing on ichnotaxa composition and ichnofabric changes. Variations of ichnological features across the Paleocene–Eocene transition, and comparison with deep-sea benthic foraminiferal assemblages and isotopic data, might help to understand environmental changes during the PETM.

2. Geological setting

The Zumaia section (N43°17.98′; W002°15.63′) contains a continuous succession of sediments ranging from lower Santonian through the uppermost lower Eocene, which crops out along sea-cliffs and beaches between the cities of Bilbao and San Sebastian (northern Spain; Figs. 1A and 2). This section can be considered one of the most complete, continuous and expanded sections of the Paleocene in open-marine facies in western Europe and the Mediterranean (Hillebrandt, 1965; Canudo et al., 1995). The uppermost Paleocene and lowermost Eocene sediments of the Zumaia section were deposited in offshore areas of the Pyrenean Basin, close to the boundary between middle and lower bathyal environments, at about 1000 m depth (Fig. 1B; Pujalte et al., 1998; Bernaola et al., 2007, 2009; Alegret et al., 2009a). The basin was open westward to the proto-Bay of Biscay and the North Atlantic, and thus influenced by northern temperate waters (Ortiz, 1995; Bernaola et al., 2009) (Fig. 1B).

The Paleocene-Eocene boundary interval consists of rhythmic alternations of hemipelagic limestones, marly limestones and marls, with numerous intercalations of thin-bedded turbidites (see Baceta et al., 2000 for a detailed columnar section) belonging to the Itzurun Formation (Baceta et al., 2004). The uppermost 80 cm of the Paleocene consists of a hemipelagic limestone unit (called the "green" limestone due to its glauconite content) that includes a 4-cm-thick carbonate turbidite bed (Pujalte et al., 1998; Schmitz et al., 2000; Dinarès-Turell et al., 2002) (Figs. 2 and 3). This greenish-gray limestone unit is overlain by a 35-cm-thick marls bed in which the Benthic Extinction Event (BEE) and the onset of the Carbon Isotopic Excursion (CIE) was reported (Schmitz et al., 1997). The marl bed is overlain by a 4-m-thick interval of reddish claystones and silty claystones (the "siliciclastic

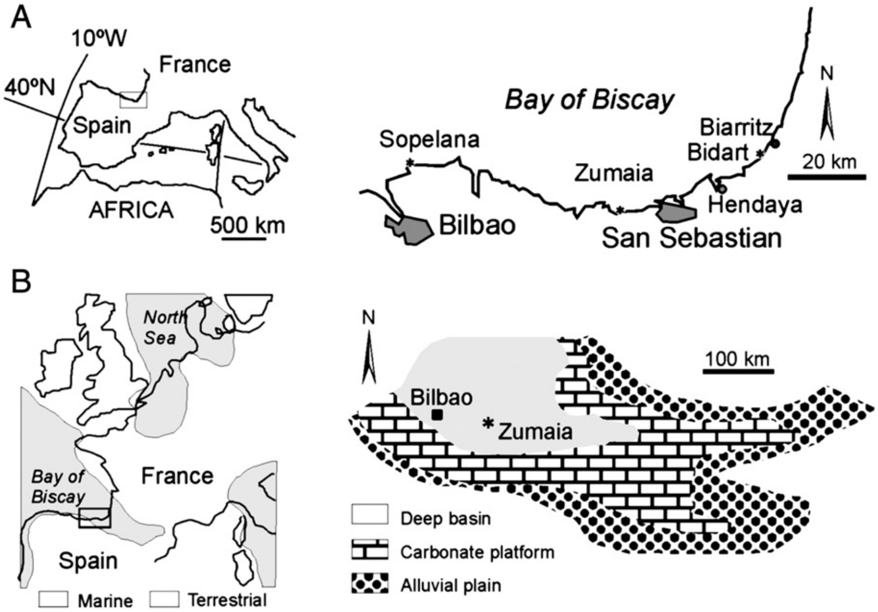

Fig. 1. (A) Geographical location of the Zumaia section. (B) Paleocene paleogeography of the Pyrenean Basin showing location of the Zumaia section.

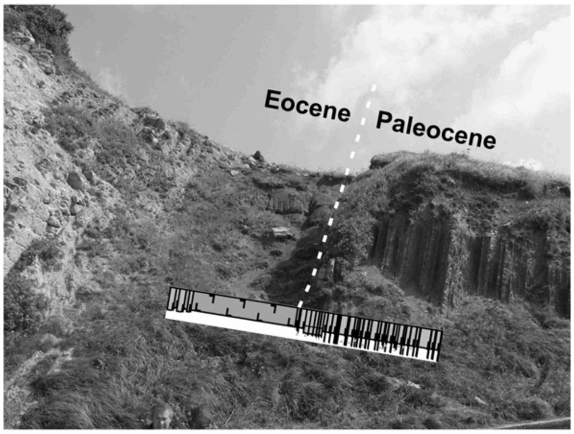

Fig. 2. Outcrop of the Paleocene–Eocene boundary interval. For the log, see Fig. 3.

unit" in Schmitz et al., 2000), and higher up in the section, by alternating limestones and marls. Marl–limestone couplets have been suggested to represent the expression of precession (Dinarès-Turell et al., 2002), whereas precession and short eccentricity were interpreted as the origin of couplets and bundles that make up the Paleocene succession (Dinarès-Turell et al., 2003, 2007).

3. Ichnological analysis

The first ichnological study in this area was performed by Gómez de Llarena (1946), who described Cretaceous and Paleogene trace fossils from the Flysch of Guipúzcoa province, including the Zumaia section. The present ichnological analysis was performed based on observations (Fig. 3). Samples from selected beds were collected and observed in variably oriented, polished surfaces, for study of the ichnofabric. Surfaces were oiled in order to improve color contrast and to facilitate the analysis of ichnological details such as filling material and burrow margins.

3.1. Synopsis of trace fossils

Only occasionally discrete trace fossils have been tentatively differentiated. Six ichnogenera have been recognized, including *Chondrites* isp., *Avetoichnus luisae*, *Planolites* isp., *Scolicia* isp., *Thalassinoides* isp., and *Zoophycos* isp. *Planolites* is the most abundant ichnotaxon, followed by small *Chondrites* and *Thalassinoides*. *Zoophycos* and *Scolicia* occurs occasionally, whereas *Avetoichnus luisae* and large *Chondrites* are rare.

Avetoichnus luisae is (Fig. 4C and D): endichnial, horizontal, straight tightly-spaced spiral, 3.5–5 mm wide, at least 25 mm long, seen on parting surfaces in the top part of turbiditic marls as tightly spaced zigzags, 1.5–2 mm wide. Kinks of the zigzacks, i.e., helical turns, are 1.5–3.5 mm apart. Six to eight helical turns occur over 20 mm. The row is about 10 mm long. This trace fossils is interpreted as a non-graphoglyptid middle tier complex agrichnion, adopted to high competition for food the deep sea during the Paleogene (Uchman and Rattazzi, in press).

Chondrites isp. (Figs. 4A, B and E, 5F, and 6A): a system of downward branching, tunnels with a width of 0.7–1 mm being uniform for one burrow system. Branches at sharp, rather constant angles. The entire trace fossil is up to 35 mm wide. In cross section it is seen as a group of small spots (Fig. 6A). A larger form (Fig. 4B) with tunnels of 2.5–3.5 mm diameter in cross section also is present. At least some specimens of the small form can be assigned to *Chondrites*

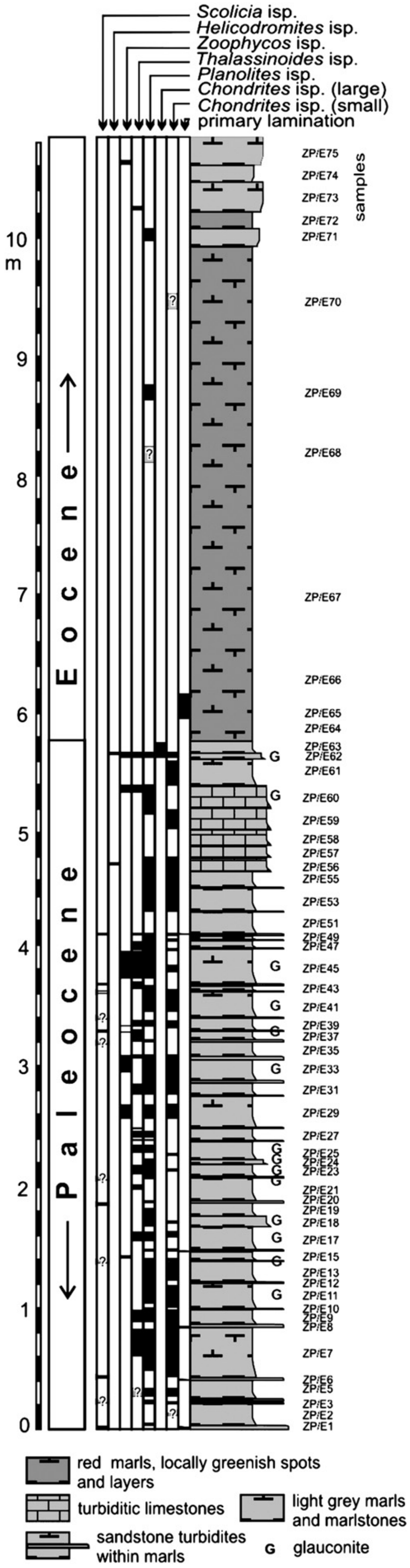

Fig. 3. Log of the Paleocene–Eocene boundary interval with indication of the samples, the trace fossil ranges, and the primary lamination level.

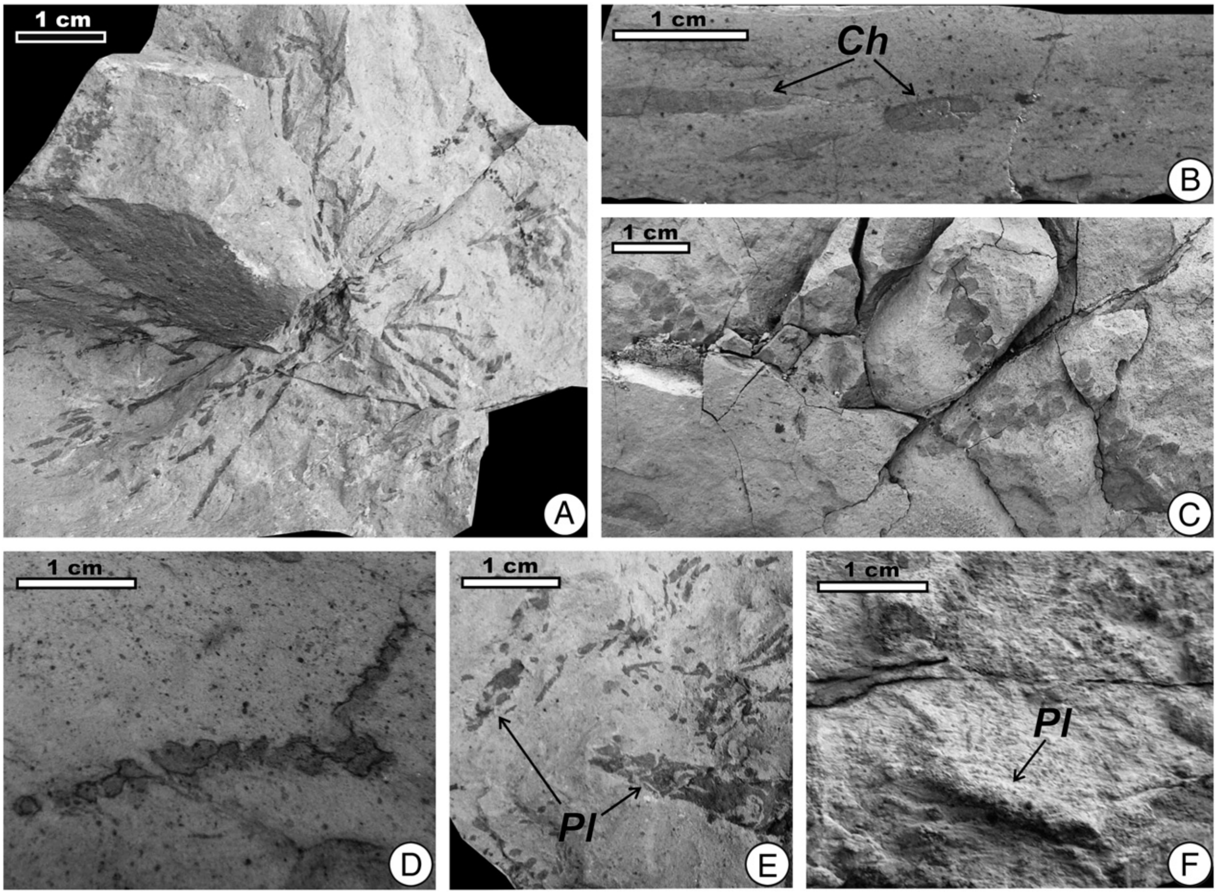

Fig. 4. Trace fossils of the Paleocene–Eocene boundary interval: (A) *Chondrites intricatus* on a parting surface, an example of *Chondrites* isp. small form, ZP/E62; (B) *Chondrites* isp. (*Ch*) large form, on polished horizontal surface, ZP/E63; (C) *Avetoichnus luisae* on a horizontal parting surface, bed ZP/E63; (D) *Avetoichnus luisae* on a horizontal parting surface, ZP/E56; (E) *Planolites* isp. (*Pl*) reworked with *Chondrites* isp., small form, parting surface, ZP/E62; and (F) *Planolites* isp. on the lower surface of a turbiditic sandstone bed, ZP/E12.

intricatus (Brongniart, 1823). The larger form belongs probably to *Chondrites targionii* (Brongniart, 1828). *Chondrites* is most often attributed to an opportunistic behavior tracemakers tolerant of very low-oxygen environments (e.g., Ekdale and Bromley, 1984), commonly associated with organic-rich deposits (Vossler and Pemberton, 1988), and related to the latest phase of opportunistic colonization of turbidites and other event beds (Wetzel and Uchman, 2001).

Planolites isp. (Figs. 4E and F, 5F, and 6A): horizontal, cylindrical trace fossils with sharp margins but no distinct wall, 4–5 mm wide, filled with different, mostly darker material. In cross section, the trace appears as oval spots of corresponding size. Filling of some specimens is reworked with contorted *Chondrites*. Hypichnial forms (Fig. 4F) in sandstone beds are seen as semicircular ridges and knobs. *Planolites* is usually interpreted as a feeding structure (pascichnion) of deposit feeders, which can belong to different phylla, mainly polychaetes.

Scolicia isp. (Fig. 5A and B): endichnial, horizontal, semicylindrical structure, about 30 mm wide, observed in the turbiditic sandstones. In horizontal sections it is seen as an unwalled meniscate structure of the "laminites" type, a characteristic preservational variant of *Scolicia* (see Uchman, 1995). In vertical section, it is seen as a meniscate stripe-like or oval structure, but with a faint record of the menisci. *Scolicia* is common in sediments rich in benthic food, being its distribution and size affected by the amount and quality of benthic food (Wetzel, 2008).

Thalassinoides isp. (Figs. 5B, C and F, and 6A): endichnial, horizontal to subhorizontal straight or slightly curved, branched tunnels, without wall. They are generally 7–9 mm wide, mostly with Y-shaped, up to 12 mm wide branching. In cross section, this trace fossil is preserved as oval spots and stripes of corresponding size, which are filled mostly with darker sediment. *Thalassinoides* is mainly attributed to crustacean deposit feeders (Ekdale, 1992), in oxygenated, soft but cohesive sediment (Ekdale et al., 1984; Wetzel, 2008).

Zoophycos isp. (Fig. 5D–F): endichnial, horizontal to sub-horizontal planar spreiten structures seen on parting surfaces as (1) fragmentarily preserved lobes, 25–30 mm wide, encircled by a marginal tunnel that is 3–4 mm wide, or seen (2) in cross section as dark stripes, 1–2 mm thick, with an occasionally preserved meniscus-like structure, which is the cross section of the spreite. Some of the stripes are reworked with contorted *Chondrites*. *Zoophycos* is common in environments with fluctuating benthic food. Its producer is unknown, and different ethological explanations have been proposed (see Löwermark et al., 2004 for an updated review).

3.2. Cross-cutting relationships and tiering pattern

Cross-cutting analysis shows a well established relationship between the different trace fossils, with *Chondrites* and *Zoophycos* cross-cutting the rest of ichnotaxa. Almost all trace fossils are present against a mottled ichnofabric (Fig. 7), which represents a totally bioturbated, few centimeters-thick zone near the surface layer, consisting of biodeformational structures (see Schäfer, 1956, and Wetzel, 1991 for a detailed description). This comprises the so-called mixed layer in which no discrete trace fossils are preserved due to biogenic mixing of shallow-tier burrowers in water-saturated near surface sediment (see; Berger et al., 1979; Wetzel, 1991; Bromley, 1996). The trace fossil assemblage represents intermediate (*Planolites*, *Thalassinoides* and endichnial *Scolicia*) and deep tiers (*Zoophycos*, and *Chondrites*) from the so-called transitional layer. This normal, tiered

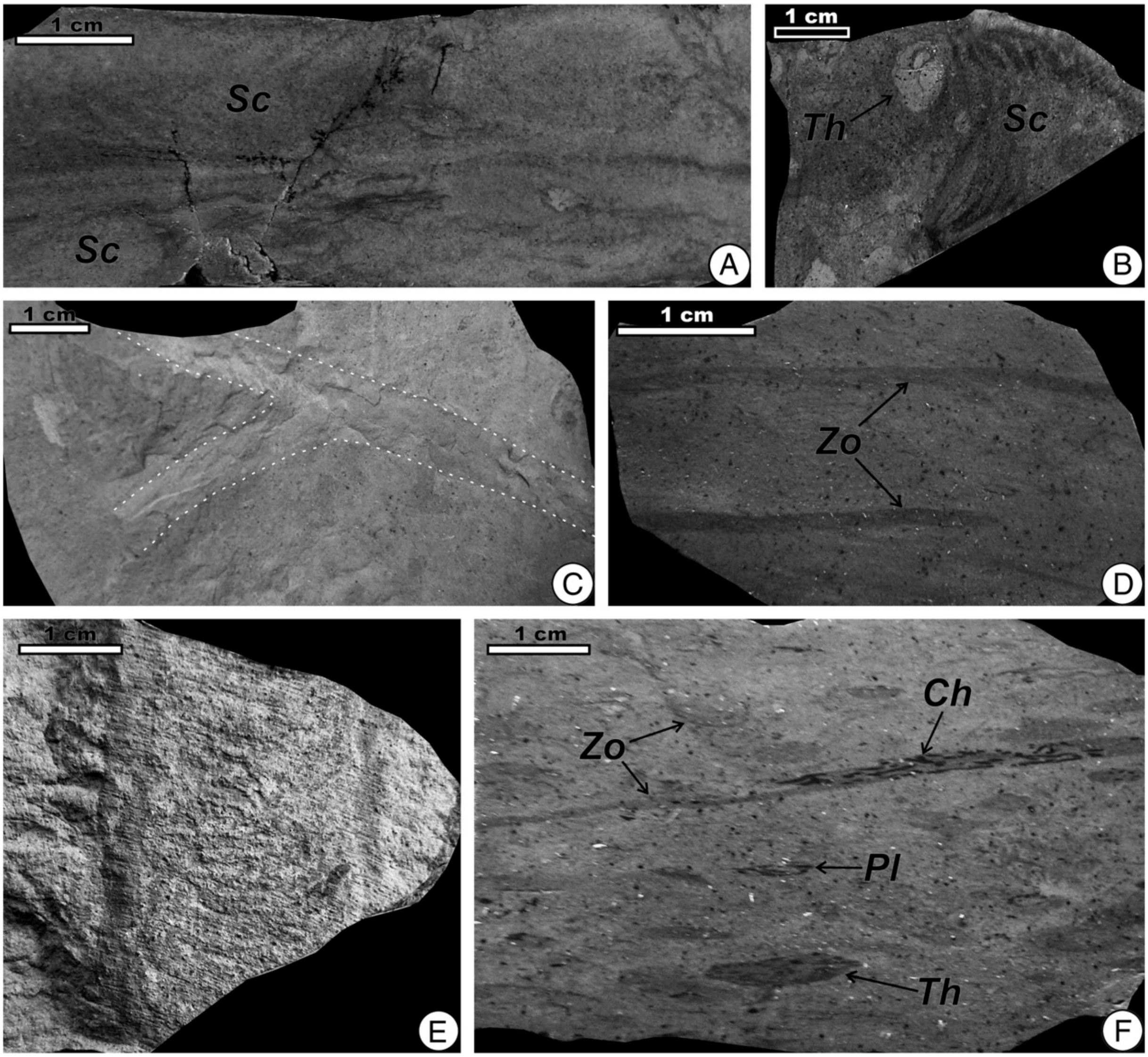

Fig. 5. Other trace fossils: (A) *Scolicia* isp. (*Sc*) in a turbiditic sandstone bed, cross section, ZP/E20; (B) *Scolicia* isp. (*Sc*) and *Thalassinoides* isp. (*Th*) in a turbiditic sandstone bed, horizontal section, ZP/E50; (C) *Thalassinoides* isp. on a parting surface, ZP/E62; (D) *Zoophycos* isp. (*Zo*) in cross section of a marly mudstone bed, ZP/E15; (E) *Zoophycos* isp. on a parting surface, ZP/E34; and (F) *Zoophycos* isp. (*Zo*), *Thalassinoides* isp. (*Th*), *Chondrites* isp. (*Ch*) reworking *Planolites* isp., *Planolites* isp. (*Pl*), in cross section of a marly mudstone bed, ZP/E34.

burrowing community agrees with the classic ichnofabrics model for pelagic sediments (e.g., Ekdale and Bromley, 1991; Bromley, 1996). Occasionally this tiered community disappears and only the mottled ichnofabric is present. In one horizon only primary lamination is present.

3.3. Stratigraphic variations of the ichnological assemblage

The ichnotaxa present, their abundance, and the ichnofabrics show significant variations through the studied succession, allowing the differentiation of four stratigraphic intervals; from the bottom to the top of the section they are described (Fig. 7):

Interval A Corresponding to the uppermost 6 m of the Paleocene, this interval is composed of alternating grayish to greenish hemipelagic limestones, marly limestones and marls, with intercalations of numerous thin-bedded turbidites and the presence of glauconite. In this interval all the ichnotaxa described above are present, representing the normal, tiered burrowing community, and they occur against a mottled ichnofabric. The trace fossil assemblage shows an increase in the number and abundance of the ichnotaxa in the middle part of the interval (around the lowermost 3 m), and a clear decrease upwards in the uppermost 2 m. In addition, successive alternations between trace fossil bearing segments and short horizons without trace fossils (where only the mottled ichnofabric is observed) are clearly visible.

Interval B Corresponds to the approximately lowermost 40 cm of the Eocene. Trace fossils are almost absent within this reddish green interval. The six previously recorded ichnotaxa, representing the tiered burrowing community, are absent and only a mottled ichnofabric, but not discrete trace fossils, is recognized on polished surfaces. An around 20 cm-thick horizon characterized by primary lamination and the total absence of bioturbational structures (including the mottled ichnofabric) occurs at the top of Interval B, coinciding with the base of the overlying reddish claystones.

Interval C This interval overlies the laminated bed and consists of a 2-m-thick interval of reddish claystones and silty claystones (the “siliciclastic unit” in Schmitz et al., 2000), characterized by a mottled ichnofabric and the absence of trace fossils as in Interval B.

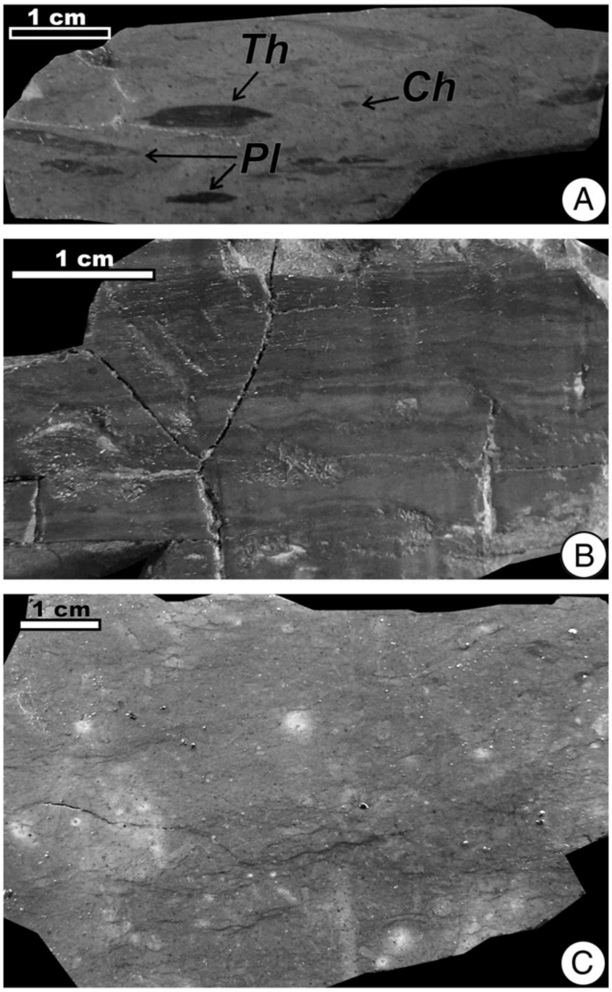

Fig. 6. Ichnofabrics of the boundary interval: (A) deeply bioturbated marly mudstone of the Interval A, with well preserved deep tier trace fossils on the totally bioturbated ichnofabric, *Thalassinoides* isp. (*Th*), *Chondrites* isp. (*Ch*), *Planolites* isp. (*Pl*), cross section, ZP/E47-48; (B) finely laminated red marlstone of the Interval B, ZP/E66; and (C) shallowly but totally bioturbated red marlstone of the Interval D, ZP/E69.

Interval D Corresponds to a 2-m-thick interval of reddish claystones and silty claystones (the "siliciclastic unit" in Schmitz et al., 2000), which are overlain by a 1-m-thick interval of sandstone beds towards the top of the studied section. This interval is characterized by scarce trace fossils (mainly *Planolites*, *Thalassinoides* and *Zoophycos*) against the mottled ichnofabric.

4. Interpretation and discussion

4.1. Benthic micropaleontological assemblages and the PETM

In the Zumaia section the analysis of benthic foraminiferal assemblages across the PETM, correlated with data from planktic foraminifera and calcareous nannofossil (Canudo and Molina, 1992; Canudo et al., 1995; Schmitz et al., 1997; Orue-Etxebarria et al., 2004; Angori et al., 2007), revealed significant changes (turnovers and extinctions) associated with the negative carbon isotope excursion (CIE) (Alegret et al., 2009a). A 115-cm-thick interval deposited during the latest ~46 kyr of the Paleocene is characterized by fluctuations in the calcareous nannofossil assemblages, suggesting environmental perturbation (probably related to an initial warming phase in surface waters) prior to the onset of the carbon isotope excursion (Bernaola et al., 2006; Angori et al., 2007; Alegret et al., 2009a). The Benthic Extinction Event (Alegret et al., 2009a) was gradual but rapid, with a duration of around 10.5 kyr, and affecting a total of 55% of the benthic foraminiferal species. It started just at the Paleocene/Eocene boundary, coinciding with the onset of the carbon isotope excursion, and it finished ~10.5 kyr later (40 cm above the Paleocene/Eocene boundary); above, a 3 to 4-m-thick dissolution interval is recorded. This initial warming recorded during the latest Paleocene probably caused paleoenvironmental instability that resulted in the gradual but rapid phase of the extinction at the earliest Eocene (Alegret et al., 2009a), which occurred under oxic conditions at the sea floor. Bottom waters became carbonate corrosive after the Benthic Extinction Event, as inferred from the dissolution interval deposited above. Alegret et al. (2009a) concluded that warming must have been the main trigger mechanism at Zumaia, and the only global feature of the PETM for which there were no refugia.

4.2. PETM and the ichnological record

The different ichnological features display significant changes from pre-, to syn- and to post-PETM intervals, which can be interpreted in terms of environmental parameters affecting the macrobenthic realm (Fig. 7).

4.2.1. Pre-PETM (Interval A)

As a general interpretation, the presence of a normal, tiered burrowing community during the Late Paleocene implies an environment with generally good oxygenation and benthic food availability, sufficient to sustain the trace makers community. However, the alternation of horizons with diverse trace fossils with layers containing a mottled ichnofabric only, without trace fossils points to the environmental conditions fluctuated, from normal to regionally relatively depauperated conditions affecting macrobenthic environment. The absence of primary lamination or "black-shale" like facies and the presence of the mottled ichnofabric suggest that these horizons with a mottled ichnofabric only do not represent anoxic events.

The decrease in ichnodiversity and ichnofossil abundance towards the top of this interval suggests that environmental conditions for macrobenthic fauna deteriorated during the Late Paleocene, which was deduced also for the planktic environment from calcareous nannofossils – beginning of a decreasing trend in abundance and species richness, together with the break of the previous stability in the calcareous nannofossil assemblage – and related to the initial warming phase and the increase in surface water temperatures (Bernaola et al., 2006) (Fig. 7). Benthic foraminiferal assemblages do not display significant variations in the upper 100 cm of the Paleocene (Interval Pa2 in Alegret et al., 2009a); this may be related to the low sampling resolution within this interval or to the delayed answer between ocean surface and microbenthic habitat in a bathial environment (Dr. Wetzel per. com.).

4.2.2. Syn-PETM (Interval B)

This interval corresponds to the lowermost 40 cm of marls of the Eocene, and it coincides with interval E1 in Alegret et al. (2009a), in which these authors recognized a gradual but rapid extinction of benthic foraminifera. The drastic disappearance of trace fossils is observed in coincidence with the Paleocene/Eocene boundary (extinction A in Fig. 7), concurrent with the onset of the Carbon Isotope Excursion (Schmitz et al., 1997), the main warming event of the PETM, and the beginning of the Benthic Extinction Event (Alegret et al., 2009a; Fig. 7). Similar ichnofabrics are registered in the entire 40 cm-thick interval of the lowermost Eocene, except for its top. The exclusive presence of a mottled ichnofabric in this interval is related to bioturbation of the uppermost part of the substrate, while the absence of trace fossils indicates inhospitable conditions for deep burrowers. In a habitat perturbed by the global increase in temperature, several factors can make the deeper sediment levels

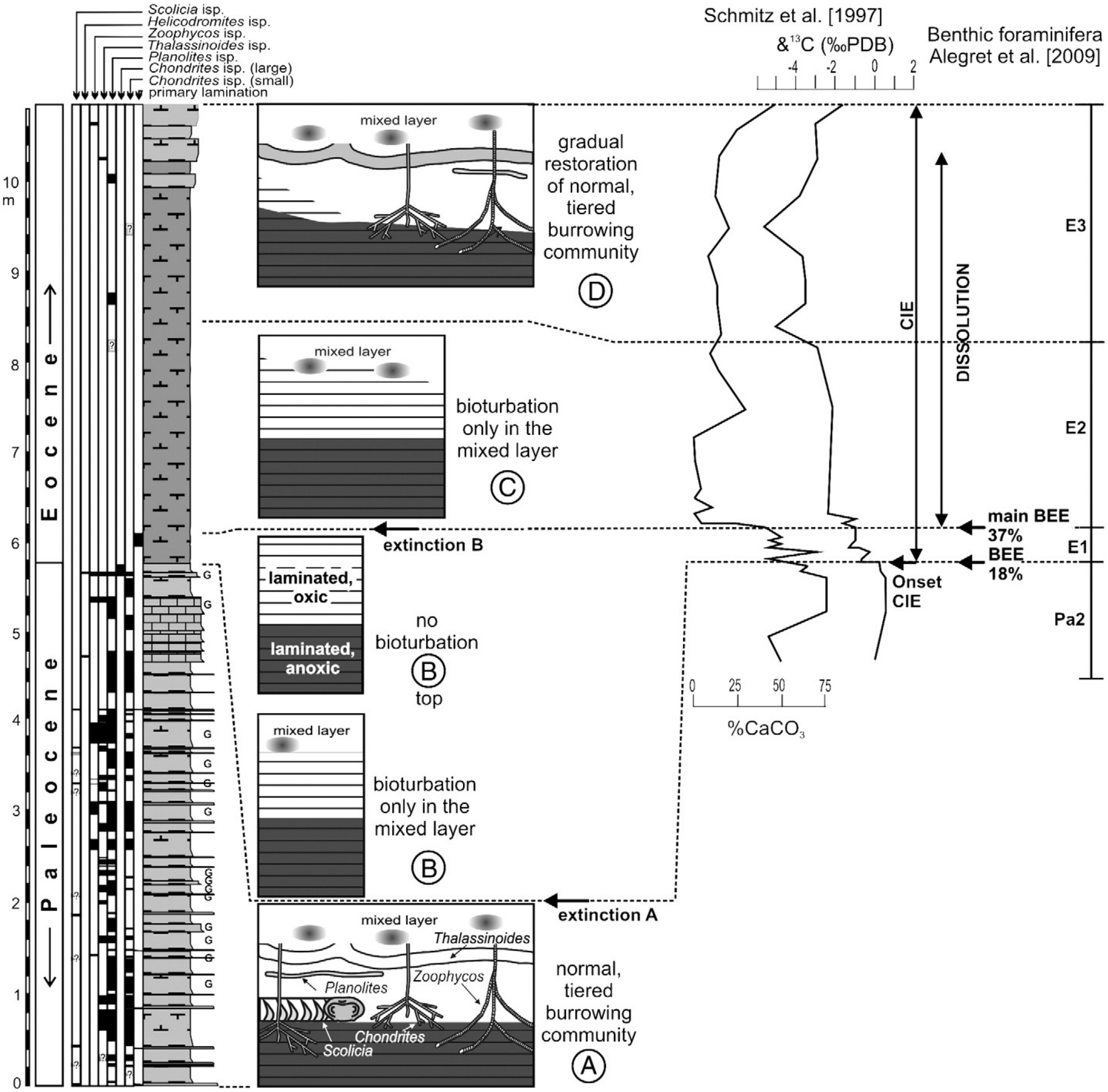

Fig. 7. Tiering pattern model for the Paleocene–Eocene boundary interval at Zumaia, according to the differentiated pre-, syn-, and post-PETM intervals (Intervals A to D), based on the registered ichnological features. Correlation with curves in %$CaCO_3$ and $\delta^{13}C$ (Schmitz et al., 1997) and benthic foraminiferal data, including the differentiated Intervals Pa2, E1, E2, and E3 in Alegret et al. (2009a). BEE, Benthic Foraminiferal Extinction Event; CIE, Carbon Isotope Excursion; and PDB, Pee Dee Belemnite standard.

less suitable for macrobenthos, while maintaining somewhat more hospitable conditions in the uppermost part. Among the interpreted limiting factors affecting the macrobenthic habitat, oxygenation and benthic food availability are the most usually invoked. An increased nutrient supply in surface waters during this period would increase accumulation and degradation of organic matter on the sea floor, causing depletion of pore water oxygenation and an upward movement of the redox boundary. Concentration of benthic food in very shallow sediment surface layers together with lowered oxygenation, but not anoxia, could induce disappearance of deeper trace makers, while those living in shallower substrates, close to the sea floor, with benthic food available and in contact with oxic ocean bottom waters, could survive (see similar recent examples in Wetzel, 1991). This agrees with the absence of evidence for low oxygen conditions based on the analysis of benthic foraminifera (Alegret et al., 2009a); these micro-organisms inhabited the uppermost centimeters of the sediment where oxygenation was sufficient.

The presence of primary lamination and the absence of bioturbation structures at the top of the Interval B (from 20 to 40 cm above the P/E boundary) indicate an un-inhabitable macrobenthic environment, which triggered the total disappearance of trace makers (extinction B in Fig. 7). This thin laminated horizon reveals a short-time, drastic change in the environmental conditions that can be correlated with the boundary between Intervals E1 and E2 of Alegret et al. (2009a), around the interval where 37% of the benthic foraminiferal species went extinct (Fig. 7). With the high temperatures of the early Eocene, a gradual organic matter enrichment during deposition of the laminated horizon at the top of interval B may have accelerated oxygen consumption leading a oxygen level too low for the macrobenthic burrowers and hence allowing preservation of primary lamination. Increase in nutrient supply and thus, organic matter deposition during Interval B is coherent with a high sediment input from the continent, as indicated by the presence of a thick conglomeratic unit at the basin margin forming the proximal part of an alluvial megafan; it has been related to a dramatic increase in seasonal rain with severe floods and rainstorms that occurred around 10 ky after the Paleocene–Eocene close to the Zumaia (Schmitz and Pujalte, 2003, 2007). Local sea-level changes could favor land exposition and the amount of nutrients coming from the continent. Alternatively or additionally, the increase in water temperature and spreading of large amount of rain water on the sea can cause a stratification of waters leading to anoxia (Keeling et al., 2010).

In different environmental settings, such as in marginal and epicontinental basins in some parts of the Tethys and northeastern peri-Tethys, laminated beds (black shales and sapropelites) enriched in organic carbon were deposited during the Initial Eocene Thermal Maximum, and have been related to increasing productivity leading to oxygen depletion and local dysoxic conditions (see references in Thomas, 2007).

4.2.3. Post-PETM (Intervals C and D)

Interval C corresponds to interval E2 in Alegret et al. (2009a), which includes the 2 m of the siliciclastic unit (Fig. 7). This interval is devoid of calcareous deposits, with the main drop in $\%CaCO_3$ recoded towards its base, extremely negative values of $\delta^{13}C$ (Schmitz et al., 1997), and microfossil assemblages strongly dissolved due to corrosive bottom waters after the BEE (Alegret et al., 2009a). The sole presence of a mottled ichnofabric in Interval C indicates that the environmental conditions recovered very slowly (Fig. 7), after the worst environmental conditions for the macrobenthic community represented by the Interval B. We suggest that during deposition of Interval C, nutrient availability and oxygen depletion consumption diminished gradually and the benthic food recovered, favoring colonization of the uppermost part of the sediment (mixed layer). However, recovery was slow and organic matter availability in deeper tiers and maybe oxygenation at that time were insufficient for the establishment of a normal, tiered trace makers community.

The progressive macrobenthic recovery initiated in Interval C continued during Interval D, as indicated by the presence of rare discrete trace fossils on the mottled ichnofabric, reflecting a gradual restoration of the normal, tiered burrowing community (Fig. 7). Probably, benthic food content deeper within the sediment and pore water oxygenation increased sufficiently to allow the initial colonization of sediments intervals below the mixed layer. The tiered burrowing community was still vertically not expanded in comparison to the Late Paleocene communities, indicating that environmental conditions were not fully reestablished. This interval could be correlated, in part, with the upper 2 m of the siliciclastic unit, which corresponds to interval E3 in Alegret et al. (2009a) (Fig. 7). This interval is characterized by the gradual recovery of $\delta^{13}C$ levels (Schmitz et al., 1997), and a decrease in corrosion effects of carbonate shells, and has been related to a slow deepening of the CCD after the initial, abrupt acidification of the oceans (Alegret et al., 2009a).

5. Conclusions

Our high-resolution ichnological analysis of the Paleocene–Eocene transition in the Zumaia section (northern Spain), in combination with published benthic foraminiferal, calcareous nannofossil, planktic foraminiferal and isotopic data, allowed us to analyze the effects of the Paleocene–Eocene thermal maximum (PETM) on the macrobenthic community, and the main environmental changes involved. Significant variations of the ichnological features in the pre-, syn- and post PETM intervals indicate that the trace maker community was significantly affected by the increased temperatures, as well as by changes in benthic food availability and in the degree of oxygenation of bottom waters during the PETM. Changes in the environmental parameters can be induced by climatic fluctuations, together with variations in the sea-level.

During the latest Paleocene, a well developed, normally tiered burrowing was present at the location of the Zumaia basin, consistent with oxic conditions and organic matter availability. At the beginning of the PETM, in coincidence with the onset of the carbon isotope excursion and the beginning of the Benthic Foraminiferal Extinction, the macrobenthic community was significantly altered; specific trace fossils disappeared, and the only record was that of a mottled ichnofabric, indicative of the presence of trace makers only in the uppermost few centimeters of sediment, just below the sediment/water interface. This turnover suggests colonization of the uppermost part of the substrate, very shallow surface layers, while the absence of trace fossils points to inhospitable conditions for deep burrowers. These assemblage changes may be related to the global rise in temperatures, together with an increase in the flux of organic matter to the sea floor, and probably a higher rate of oxygen consumption and oxygen deficiency in deep layers of the sediment. These significant changes in the environmental parameters can be induced by climatic fluctuations together with local sea-level variations. Maximum deterioration in the macrobenthic environment is registered for a very short time (corresponding to an around 20-cm-thick level), in which bioturbational structures are absent and primary lamination is preserved. This thin level may indicate low oxygen conditions, but not anoxia, in the sediment. This level is close to the Benthic Foraminiferal Extinction, revealing that the environmental perturbation significantly affected the whole benthic habitat. However, detailed correlation between this thin level and the BFE is difficult, and high-resolution studies are needed. Following the PETM, more favorable environmental conditions for macrobenthic communities returned slowly and gradually, based on the continuous ichnological record of the mottled ichnofabric to scarce trace fossils, indicating the reestablishment of the normal, tiered burrowing community. We suggest that the abundance of organic matter increased deeper into the sediment, favoring progressive colonization of deeper tiers by trace makers.

We conclude that ichnological features through the Paleocene–Eocene interval reveal (1) the impact of the Paleocene–Eocene thermal maximum on the macrobenthic community, (2) the importance of benthic food availability and oxygenation rate in a global habitat perturbed by increased temperatures, and (3) the similarities and differences in the response to the global phenomena between micro- and macrobenthic communities, (4) the usefulness of trace fossil analysis to interpret changes in the atmosphere–ocean system during the past, including climatic dynamic, and the potential application for research of future fluctuations in the environment.

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