THE PALEOCENE–EOCENE THERMAL MAXIMUM: NEW DATA ON MICROFOSSIL TURNOVER AT THE ZUMAIA SECTION, SPAIN

LAIA ALEGRET,1* SILVIA ORTIZ,1,2 XABIER ORUE-ETXEBARRIA,3 GILEN BERNAOLA,3,4 JUAN I. BACETA,3 SIMONETTA MONECHI,5 ESTIBALIZ APPELLANIZ,3 and VICTORIANO PUJALTE3
1Universidad de Zaragoza, Departamento de Ciencias de la Tierra, Facultad de Ciencias, 50009 Zaragoza, Spain; 2University College London, Department of Earth Sciences, WCIE 6BT London, UK; 3Universidad del País Vasco, Departamento de Estratigrafía y Paleontología, Facultad de Ciencia y Tecnología, 48800 Bilbao, Spain; 4Universidad del País Vasco, Departamento de Ingeniería Minera y Metalúrgica y CC de los Materiales, Escuela Universitaria de Ingeniería Técnica de Minas y de Obras Públicas, 48901 Barakaldo, Spain; 5Università degli Studi di Firenze, Dipartimento di Scienze della Terra, Via La Pira, 4, 50121 Firenze, Italy
e-mail: laia@unizar.es

ABSTRACT
The benthic foraminiferal turnover and extinction event (BEE) associated with the negative carbon isotope excursion (CIE) across the Paleocene–Eocene Thermal Maximum (PETM) is analyzed in the Zumaia section (Spain), one of the most complete and expanded deep-water sequences known worldwide. New biostratigraphic, palaeoecologic, and paleoenvironmental data on benthic foraminifera are correlated to information on planktic foraminiferal and calcareous nannofossil turnover in order to evaluate possible causes and consequences of the PETM. Gradual but rapid extinction of 18% of the benthic foraminifer species starts at the onset of the CIE, after the initial ocean warming (as inferred from calcareous nannofossil turnover) in the last 46 kyr of the Paleocene. This gradual extinction event culminated ~10.5 kyr after the onset of the CIE and led to the main BEE, affecting 37% of the species. Therefore, extinctions across the PETM affected a total of 55% of the benthic foraminifer species at Zumaia. The gradual extinction occurred under inferred oxic conditions without evidence for carbonate dissolution, indicating that carbonate corrosivity and oxygenation of the ocean bottom waters were not the main cause of the event. An interval characterized by dissolution occurs above the main BEE, suggesting that bottom waters became corrosive after the main extinction. Carbonate is progressively better preserved through the overlying deposits, and carbon isotope values gradually return to background levels. These data are consistent with a slow deepening of the carbonate compensation depth after its initial rise owing to abrupt acidification of the oceans. Microfossil data support a rapid onset of the PETM, followed by long-term effects on calcareous plankton and benthic foraminifera.

INTRODUCTION
A major, rapid extinction of deep-sea benthic foraminifera occurred at the Paleocene-Eocene (PE) boundary (e.g., Tjalsma and Lohmann, 1983; Thomas, 1989), ~55 Ma. The extinction was coeval with an episode of extreme global warming called the Paleocene–Eocene Thermal Maximum (PETM), during which temperatures increased up to 9°–10°C in high-latitude, surface waters and up to ~5°C in the deep sea, in equatorial surface waters, and on land at midlatitudes in continental interiors (see references in Thomas, 2007).

A negative 2.5% to 6% carbon isotope excursion (CIE) in marine and terrestrial δ13C values of carbonate and organic carbon is associated with the PETM (e.g., Kennett and Stott, 1991; Thomas and Shackleton, 1996; Zachos et al., 2001; Bowen et al., 2006; Stujs et al., 2007a), and its onset formally marks the base of the Eocene (Aubry et al., 2007). This excursion reflects a major perturbation in the global carbon cycle, which affected the whole ocean-atmosphere system. The Calcite Compensation Depth (CCD) rose by >2 km in the South Atlantic Ocean (Zachos et al., 2005), which has been interpreted in terms of a rapid input of isotopically light carbon into the ocean-atmosphere system, perhaps by the massive dissociation of marine methane hydrates caused by processes such as continental slope failure, a drop in sea level, the impact of an extraterrestrial body, or volcanism (for an overview, see Thomas, 2007). Actual shouling documented in Ocean Drilling Program (ODP) drilling, however, was substantially larger than can be explained by methane dissociation alone (Zachos et al., 2005; Thomas, 2007). The onset of these anomalies occurred during a time period of <20 kyr (Kennett and Stott, 1991; Katz et al., 1999; Röhl et al., 2000, 2007), whereas the return to more normal values occurred over longer time scales of 105 years (Dickens et al., 1995; Katz et al., 1999; Röhl et al., 2007; Stujs et al., 2007a; Westerhold et al., 2007).

The PETM may not have been a singular event; rather, it may have been only the most severe out of a series of global warming events (e.g., the mid-Paleocene biotic event, the early Eocene ELMO—the Eocene layer of mysterious origin at Walvis Ridge—and X warming events) that have been only the most severe out of a series of global warming events (e.g., the mid-Paleocene biotic event, the early Eocene ELMO—the Eocene layer of mysterious origin at Walvis Ridge—and X warming events) that are coupled with carbon isotope anomalies and carbonate dissolution (Thomas et al., 2000; Lourens et al., 2005; Bernaola et al., 2007). If the PETM was one of a series of events occurring at orbital periodicities (Lourens et al., 2005), its cause probably was not singular (e.g., a comet impact or a volcanic eruption) but intrinsic to Earth’s climate system (Thomas, 2007).

Whatever the triggering mechanism, and whether or not the CIE was the result of dissociation of gas hydrates or other causes (see references in Thomas, 2007), the onset of the PETM was characterized by abrupt changes, such as the acidification of the oceans, and rapid changes in terrestrial and marine biota, including the largest extinction of benthic foraminifera (30%–50% of the species) recorded during the Cenozoic. Other major biological changes include a rapid evolutionary turnover of planktic foraminifera (e.g., Arenillas and Molina, 1996; Kelly et al., 1998) and calcareous nannoplankton (Aubry, 1995; Bralower, 2002; Stoll, 2005), the global acme of the dinoflagellate genus Apectodinium and its migration to high latitudes (Crouch et al., 2001; Stujs et al., 2007a, 2007b), the rapid diversification of shallow-water larger benthic foraminifera (Orue-Etxebarria et al., 2001; Pujalte et al., 2003), latitudinal migration of plants (Wing et al., 2005), and a rapid radiation of mammals on land (e.g., Koch et al., 1992). The linkages between carbon cycle perturbation and coeval biotic changes are not completely understood. Individual ecosystems may have responded directly to such aspects of environmental change as carbon addition (ocean acidification, elevated pCO2) or indirectly to consequences of carbon release, such as rising
temperatures, increased precipitation, and changes in nutrient supply or distribution, and so forth (Bowen et al., 2006).

The benthic foraminiferal extinction event (BEE) lasted <10 kyr (Thomas, 2007), and its cause is not yet clear. The study of the BEE is interesting because deep-sea benthic foraminifera had survived without significant extinction through global environmental crises like those related to the asteroid impact at the end of the Cretaceous (e.g., Thomas, 1999; Alegret and Thomas, 2005; Alegret, 2007). While deep-sea benthic foraminifera suffered major extinction across the PETM, benthic foraminifera from marginal and epicontinental basins show less extinction or temporary assemblage changes. In shallow settings, increased biological productivity and anoxia at the seafloor have been documented across the PETM (e.g., Speijer and Wagner, 2002; Gavrilov et al., 2003; Alegret et al., 2005; Alegret and Ortiz, 2006). Increased runoff or upwelling currents could have led to high productivity and eutrophication, which, combined with low-oxygen concentrations, resulted in high total organic carbon in sediments from proximal settings (Tremolada and Bralower, 2004). Data from open ocean sites do not support global hypoxia, however, and are inconsistent with regard to global productivity changes (e.g., Gibbs et al., 2006; Thomas, 2007).

Several causes for triggering the BEE have been suggested (see Thomas, 2007, for a review), including (1) low oxygenation, either as a result of increased deep-sea temperatures or as a result of oxidation of methane in the water column; (2) increased corrosivity of the waters for CaCO$_3$, as a result of methane oxidation or incursion of CO$_2$ from the atmosphere; (3) increased or decreased productivity or expansion of the trophic resource continuum; or (4) a combination of several of these. The ultimate cause of the BEE, however, is not yet clear; climatic warming is the only common factor recorded worldwide. High temperatures would increase metabolic rates, and even under stable productivity in the oceans, organisms would indicate oligotrophic conditions because of their higher metabolic rates (Thomas, 2003, 2007).

More detailed analyses of benthic foraminifera across the PETM are thus needed in order to look into the causes of the BEE and of the benthic foraminiferal turnover. The Zumaya section (Western Pyrenees) contains one of the most complete and expanded deep-water successions across the Paleocene–Eocene transition yet reported (e.g., Molina et al., 1999; Baceta et al., 2000). This section has no recognizable biostratigraphic gaps or condensation, shows a high-sedimentation rate, identifiable geochemical and geomagnetic signals (minor diagenetic alteration), and abundant, well-diversified, open marine microfossils such as benthic and planktic foraminifera and calcareous nannofossils (Orue-Etxebarria et al., 2004). Different cyclostratigraphic, micropaleontologic, magnetostratigraphic, and chemostratigraphic studies have been completed based on this section (e.g., Camudo et al., 1995; Schmitz et al., 1997; Arenillas and Molina, 2000; Baceta et al., 2000; Dinarès-Turell et al., 2002; Orue-Etxebarria et al., 2004; Angori et al., 2007), but publications dealing with Paleocene–Eocene benthic foraminifera from Zumaya are scarce. Ortiz (1995) described assemblages from the upper Paleocene and lower Eocene, analyzing only a few samples from the lowermost Eocene. Kühnt and Kaminski (1997) compiled data on agglutinated foraminifera from the latter publication, whereas Schmitz et al. (1997) pointed out the biostratigraphic distribution of some calcareous benthic foraminiferal taxa across the BEE. Here we present a new, high-resolution biostratigraphic, paleoecologic, and paleoenvironmental study of agglutinated and calcareous benthic foraminiferal assemblages and correlate data on benthic foraminifera to published data on the planktic foraminifera and calcareous nannofossils (Orue-Etxebarria et al., 2004; Angori et al., 2007).

GEOLoGIC SETTING AND METHODS

The Zumaya section (43°17.97’N, 2°15.65’W; see Fig. 1) is one of the most representative and complete outcrops of the (hemi)pelagic successions deposited in the Pyrenean basin during the Late Cretaceous–early Paleogene (Baceta, 1996; Pujalte et al., 1998). The studied interval encompasses the uppermost 3 m of the Paleocene (Itzurun Formation; see Baceta et al., 2004) and the lowermost 7 m of the Eocene (Eocene Flysch); samples are spaced at 5–10 cm intervals in the lowermost 60 cm of the Eocene and at 0.1–1 m intervals below and above it (Fig. 2).

The lowermost 2 m of the studied section consists of alternations of marlstones and marly limestones, with intercalations of thin-beded siliciclastic and mixed carbonate-siliciclastic turbidites. The uppermost 80 cm of the Paleocene (Itzurun Formation) consists of a distinct, hemipelagic limestone unit, called the green limestone, that includes a 4-cm-thick carbonate turbidite bed. The characteristic light green color of this limestone interval mainly results from the presence of glauconite, which occurs infilling many of the planktic and benthic foraminiferal tests (Baceta, 1996; Pujalte et al., 1998; Schmitz et al., 2000). Glauconite becomes more abundant toward the topmost 10 cm of the Paleocene (Schmitz et al., 1997), and it has also been observed at lower proportions in many hemipelagic limestones across the whole upper Paleocene of the Zumaya section (Baceta, 1996; Gawenda et al., 1999). In modern open-marine environments, authigenic glauconite may form at a wide range of depths (between 50 m and 1000 m) and is attributed to relatively low sedimentation rates (O’Brien et al., 1990; Balsam and Beeson, 2003). The onset of the CIE occurs at the transition from the green limestone to the 35-cm-thick overlying marlstone interval (Schmitz et al., 1997), which records a progressive but rapid decrease in carbonate content. This marlstone is in turn overlain by a 4-m-thick interval made up mostly of carbonate-poor, reddish claystones and marls known as the siliciclastic unit (SU; see Schmitz et al., 2000; Fig. 2). The lower 1.7 m of the SU
is almost devoid of carbonate and microfossils with calcareous tests, but these increase progressively in the upper 3.3 m (Schmitz et al., 1997; Orue-Etxebarria et al., 2004). Calcareous tests from this unit are very badly preserved and are partially dissolved; preservation of calcareous tests improves, and the planktic-benthic ratio increases, toward the upper part of the SU (samples Zu 380, Zu 430). The succession above is composed of alternating limestones and marls, the transition between them being gradual but rapid (Baceta et al., 2000).

Most of the studied material corresponds to the set of samples used by Orue-Etxebarria et al. (2004) for a study of planktic foraminifera and calcareous nannofossils. Some extra samples were collected in order to improve the sample resolution within the siliciclastic unit. Although turbidites are common at Zumaia, they are easily recognizable, and only in situ sediments were sampled. A total of 25 samples were analyzed for the benthic foraminiferal studies. Species richness calculations and quantitative studies of benthic foraminifera were based on representative splits (using a modified Otto microsplitter) of ~300 specimens >100 µm. All representative specimens were mounted on microslides for identification and a permanent record. Benthic foraminiferal counts are included in Supplementary Data1. Relative abundances of taxa (Figs. 2–3), the calcareous-agglutinated ratio, and several proxies for diversity, such as the Fisher α index and the H (S) Shannon-Weaver information function (Murray, 1991), were calculated (Fig. 4). Probable microhabitat preferences and environmental parameters were inferred from the benthic foraminiferal morphotype analysis (e.g., Bernhard, 1986; Jorissen et al., 1995; Kaminski and Gradstein, 2005) and from changes in diversity and the relative abundance of selected taxa.

Paleodepth inferences were based on benthic foraminiferal data, mainly through comparison between fossil and recent assemblages, the occurrence and abundance of depth-related species, and their upper depth limits (e.g., Van Morkhoven et al., 1986; Alegret et al., 2001, 2003). The bathymetric divisions defined in Van Morkhoven et al. (1986) have been followed: upper bathyal = 200–600 m, middle bathyal = 600–1000 m, lower bathyal = 1000–2000 m, and abyssal = >2000 m.

RESULTS

Paleobathymetry

The planktic-benthic foraminiferal ratio is very high (90%–95%) in most of the studied samples (except for those affected by dissolution in the lowermost Eocene), indicating open-ocean environments. Benthic forms can be used as accurate paleobathymetric markers because their distribution in the oceans is controlled by a series of depth-related parameters (e.g., Van Morkhoven et al., 1986; Kaminski and Gradstein, 2005). The mixed calcareous-agglutinated assemblages indicate deposition above the CCD for most of the studied section. Calcareous-cemented species (e.g., Clavulinoides amorpha, C. globulifera, C. triantera, Dorothia crassa, D. cylindracea, Gaudryina pyramidata, Marssonella floridana, Arenobuliminata truncata) and deep-water agglutinated foraminifera (DWAf) taxa (such as trochoaminids, Haplophragmoides, Karrerulina, Recurvoideae, and Repmannia charoides), are abundant in the studied samples. These assemblages are typical of the low to mid-latitude slope DWAf biofacies of Kuhnt et al. (1989). Among calcareous foraminifera, abundant representatives of the bathyal and abyssal Velasco-type fauna (Berggren and Aubert, 1975) include Cibicidoides velascoensis, Gyroidinoidea globosa, Nuttallides truempyi, Nuttallinella floraealis, Osangularia velascoensis, and others.

Assemblages are dominated by species that have an upper depth limit at the middle-upper bathyal boundary (500–700 m), such as Bulimina trinitatis, B. nasamensis, Buliminella grata, Nuttallides truempyi, Spiroplectammina spectabilis, and Stensioeina beccariiformis. Other species, such as Cibicidoides hyphalus, Gaudryina pyramidata, Gyroidinoidea globosa, and Pullicina coryelli, are most common at middle and lower bathyal depths (e.g.,

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FIGURE 3—Stratigraphic distribution and relative abundance of benthic foraminiferal taxa that disappear in the lowermost Eocene in Zumaia and correlation to the δ¹³C curve (in bulk sediment). BEE = benthic foraminiferal extinction event; CIE = carbon isotope excursion; PDB = Pee Dee Belemnite standard.

FIGURE 4—Benthic foraminiferal calcareous-agglutinated and infaunal-epifaunal ratios, heterogeneity and diversity indices, and δ¹³C (in bulk sediment) and %CaCO₃ values across the upper Paleocene and lower Eocene at Zumaia. H (S) = Shannon Weaver index of diversity; BEE = benthic foraminiferal extinction event; CIE = carbon isotope excursion; PDB = Pee Dee Belemnite standard.
Van Morkhoven et al., 1986; Alegret et al., 2003). These data, together with the occurrence of species that are common at upper and middle bathyal depths, such as *Angulogavelinella avinimelechi*, *Bolivinoides delicatus*, or *Cibicidoides dayi*, suggest deposition close to the boundary between middle and lower bathyal environments (~1000 m depth).

These results agree with the wide depth range (600–1500 m) for deposition of these sediments given by Ortiz (1995) based on benthic foraminifera and with the paleobathymetry proposed by Pujalte et al. (1998), who used paleo-geographical and sedimentary facies data to suggest that the uppermost Paleocene and lowermost Eocene sediments from Zumaia were deposited at ~1000 m depth. Our results also agree with depth estimates for the nearby Trabakua section (Orue-Etxebarria et al., 1996).

**Microfossil Turnover**

Previous study of marine microfossil assemblages of the Zumaia section, including benthic and planktic foraminifera and calcareous nanofossils, has evidenced the existence of significant biotic changes across the PETM. Considering these changes, we have divided the studied section into six distinctive intervals, Pa1–Pa2 and E1–E4 (Fig. 2), which are also characterized by changing values in both calcite concentration (%CaCO₃) and δ¹³C. Data on planktic foraminifera and calcareous nanofossils mainly come from previously published data sets (Orue-Etxebarria et al., 2004; Angori et al., 2007).

**Interval Pa 1.—**Benthic foraminiferal assemblages are very diverse (Fisher α = ~20), heterogeneous (H (S) = ~3.6), and consist of mixed infaunal (~37%–46% of the assemblages) and epifaunal (~54%–63%) morphogroups (Fig. 4). Infaunal morphogroups mainly consist of elongated-tapered (e.g., laevidentalinids, *Spiroplectammina navarrouna*) and cylindrical-tapered (*Marsssonella floridana*, *Renexella varians*) morphotypes. Epifaunal morphogroups are dominated by flattened trochoiral (*Lenticulina tuberis*, biconvex trochospiral (*Anomalinae ammonoides*, *Stensioeina beccariiformis*), and planeconvex trochosorial (*Nuttallides truempyi*, *Nuttallinella floresis*) morphotypes (Figs. 2, 3). Agglutinated foraminifera make up 44%–53% of the assemblages. Planktic foraminifera are very abundant within this interval, and their assemblages contain *Subbotina velascoensis*, *Morozovella occlusa*, *M. aequa*, *Acarinina soldadoensis*, *Globanomalina imitata*, and very rare *G. luxorensis* (<1% of the assemblages).

Calcareous nanofossil assemblages are characterized by abundant *Coccolithus pelagicus*, *Toweius pertusus*, and species of *Fasciculithus*, *Discoaster*, and *Sphenolithus*. Both abundance and species richness are high, with 40–50 species per sample and H (S) > 2.1.

**Interval Pa 2.—**While no geochemical data are available from Pa1, relatively high %CaCO₃ and δ¹³C values have been documented from the uppermost Paleocene sediments at Zumaia (Schmitz et al., 1997). This interval includes the uppermost 100 cm of the Paleocene comprising the green limestone interval.

Benthic foraminiferal assemblages are similar to those in Pa1, although the percentage of agglutinated taxa such as trochospirals slightly decreases, from 18%–26% in Pa1 to 11%–22% in Pa2. Epifaunal calcareous species such as Anomalinae ammonoides or Cibicidoides pseudoperlucidus increase in relative abundance, especially toward the top of this interval. Planktic foraminiferal assemblages are also similar to those in Pa1, and the first occurrence of *Acarinina wilcoxensis*, *Globanomalina planocoena*, and *Planorotalites pseudoscultata* is recorded.

Changes in calcareous nanofossil assemblages have been used to distinguish Pa2 from Pa1. The boundary is marked by the beginning of a decreasing trend in the abundance and species richness of *Fasciculithus* and an increase in the abundance of *Zygrhablithus*. Although heterogeneity of the assemblages is still high (~2), fluctuations in the number of species per sample have been observed (36–51 species per sample).

A drop in %CaCO₃ values (from 75% to 50%) and a very minor decrease in δ¹³C values are recorded in the uppermost ~20 cm of the Paleocene (Fig. 4), where the glauconite content is relatively high (Schmitz et al., 1997). No data on benthic and planktic foraminifera are available from this part of the section owing to its indurated nature, but nanofossil assemblages show a drop in the relative abundance and species richness of *Fasciculithus*, a slight decrease in abundance of *Discoaster* and *Sphenolithus*, and an increase in abundance of *Zygrhablithus* (Fig. 5).

**Interval E1.—**This marlstone interval marks the lowermost Eocene, and its base coincides with the onset of the carbon isotope excursion that marks the PE boundary, with a decrease in %CaCO₃ (~45% to ~25%). The diversity and heterogeneity of benthic foraminiferal assemblages decreases slightly compared to the Paleocene (Fig. 4), and the highest occurrence of 18% of the species, including Stensioeina beccariiformis at 22–30 cm above the boundary, is recorded within this interval. Calcareous benthic taxa, such as Cibicidoides pseudoperlucidus, *Lenticulina spp.*, *Nuttallides truempyi*, *Osangularia velascoensis*, and *Pullenia javisii*, make up 52%–75% of the assemblages (Fig. 4). Their tests are well preserved, and there is no evidence of corrosion.

Among planktic foraminifera, Orue-Etxebarria et al. (2004) did not find any drastic changes in the assemblages or any extinctions. Among calcareous nanofossils, this interval is marked by an increase in the abundance of *Discoaster* (mainly *D. multiradiatus* and rare *D. nobilis*, *D. delicosus*, and *D. falcatus*) and *Fasciculithus* (mainly *F. tymaniformis* and rare *F. cf. hayii* and *F. thomassii*) and a sharp decrease in the abundance of *Zygrhablithus*.

**Interval E2.—**The highest occurrence of 37% of the benthic foraminiferal species (the main BEE) is placed at the boundary of E1 and E2 (sample Zu 30–40; see Fig. 3), which is at the base of the silicilastic unit. Some of the species that have their highest occurrence at this level—such as Arenobulimina truncata, *Clavulinoides globalifera*, *Cribrostomoides trinitatensis*, *Dorothyia papa*, *Marssonella trochoidea*, or *Re- nexella varians* among the agglutinated foraminifera and Anomalinae acutus, *A. rubiginosus*, *Bolivinoides delicatus*, Buliminella grata, *Cibicidoides dayi*, *C. hyphalus*, *C. velascoensis*, *Coryphostoma midwayensis*, *Gyroidinoides globosus*, *G. quadridatus*, *G. subangulatus*, *Neofibellina senireticulata*, *Nuttallinella floresis*, *Osangularia velascoensis*, or *Pullenia corylei* among the calcareous ones—have been documented as becoming extinct globally (e.g., Tjalsma and Lohmann, 1983; Van Morkhoven et al., 1986; Thomas, 1990; Bollit et al., 1994; Kaminski and Gradstein, 2005). A single specimen of *R. varians* was found 20 cm above the BEE, but it is considered to be reworked. After the main BEE, diversity and heterogeneity of the assemblages reached the lowest values in the section (Fig. 4). Among calcareous nanofossils, the boundary between E1 and E2 is characterized by high percentages of *Discoaster* (mainly *D. multiradiatus*) and *Fasciculithus* (mainly *F. tymaniformis*) and very low percentages of *Zygrhablithus*.

A ~4-m-thick dissolution interval has been identified at Zumaia just above the BEE (Figs. 2, 4). Dissolution is more severe in the lower half of E2, where microfossil assemblages are dominated by agglutinated tests and very scarce, partially corroded calcareous foraminifera.

The main drop in %CaCO₃ is recorded at the base of interval E2, which is characterized by %CaCO₃ values of ~0%–10% in the lower 70 cm and ~20% toward the upper part (Fig. 4). Microfossil assemblages are strongly affected by dissolution, and calcareous benthic and planktic microfossils are very scarce or even absent. The only calcareous benthic specimens are scarce, thick-walled, dissolution-resistant forms such as buliminids and thick *Cibicidoides*.

Changes in total abundance of agglutinated benthic foraminifera are observed among the six samples studied from interval E2. Only the lowermost sample (Zu 50–60) contains sufficient specimens (>300) for quantitative analyses; 283 specimens were found in the uppermost sample (Zu 210; see Supplementary Data1). The benthic foraminiferal counts of the other samples are not reliable because they are not representative, although they can be studied qualitatively. The assemblages are strongly dominated by trochospirals (55%); *Recurvoides* (5%–16%), *Karrerulina*, *Halophragmoides*, and *Repanina charoides* are minor components (Fig. 2). Only one sample (Zu 140) is dominated by *Karrerulina* (*K. conversa* and *K. hordiae*, 37% of the assemblages) instead of trochospirals.
Whereas the lower 70 cm of interval E2 are almost devoid of calcareous microfossils, the upper part contains higher numbers of planktic (Canudo et al., 1995; Arenillas and Molina, 2000; Orue-Etxebarria et al., 2004) and calcareous benthic foraminiferal tests (e.g., Bulimina tuxpanensis and Cibicidoides in the >100 μm fraction and common Teppania selmensis in the 63–100 μm fraction); these, however, are badly preserved and partially dissolved.

Interval E3. This interval is characterized by CaCO₃ values of ~20% and minimum values of δ¹³C (Fig. 4), although such negative values are possibly the result of diagenesis (Schmitz et al., 1997).

Interval E3 represents the upper half of the siliciclastic unit (Figs. 2, 4). Benthic foraminiferal assemblages are dominated by calcareous taxa with badly preserved, partially corroded tests. The effects of corrosion decrease toward the uppermost part of the interval. Assemblages are dominated by Nautallides truempyi, Globocassidulina subglobosa, Bulimina tuxpanensis, Cibicidoides pseudopereculidas, and Oridorasals ounbatus among calcareous taxa and by trochantinids and Repmanina charoides (usually reported as Glomospira) among agglutinated taxa (Fig. 2). The species Aragonia aragonensis and Abyssammina quadrata reach their maximum relative abundance within this interval. Several calcareous, so-called Lazarus taxa that had temporarily disappeared at or just before the main BEE (e.g., Abyssammina quadrata, Anomalinoidea ammonoides, Cibicidoides ekblomi, and Lenticulina spp.) reappear within this interval, and Nonion havanense first occurs. The diversity and heterogeneity of the assemblages slightly increase across interval E3, although these values are still low (Fig. 4).

The abundance of planktic foraminiferal tests increases in this interval, and the last occurrence of G. chapmani is recorded (Orue-Etxebarria et al., 2004). Calcareous nannofossils are characterized by the presence of the Rhomboaster-Discoaster araneus assemblage, and the highest percentages of Coccolithus pegasus, Fasciculithus, and Discoaster spp. occur in this interval (Fig. 5).

**FIGURE 5**—Calcareous nannofossil and planktic foraminifera main bioevents, biostratigraphic scheme, and relative abundance of selected taxa across the Paleocene–Eocene transition at the Zumaia section. Percentages of Zygaphlilithus, Fasciculithus, and Discoaster are calculated from the non-~Wœis+Coccolithus pegasus fraction. Abbreviated genus names include: C = Coccolithus pegasus; D = Discoaster; R = Rhomboaster; S = Sphenolithus; F = Fasciculithus; A = Acarinina; G = Globanomalina; P = Planorotalites; s.a. = short arms; l.a. = long arms; T = T-shape.

**Interval E4.** The recovery of %CaCO₃ and δ¹³C levels to preextinction values occurred within this interval, which includes a succession of well-defined, limestone-marl couplets (Fig. 4). Benthic foraminiferal assemblages are dominated by calcareous taxa (80%), mainly by Nautallides truempyi, Bulimina tuxpanensis, Cibicidoides pseudopereculidas, C. ekblomi, and Oridorasals ounbatus are also abundant (Fig. 2). Except for O. ounbatus, the percentages of the other species above, and of calcareous taxa, decrease in the uppermost sample (Zu 700), where assemblages contain 56% of agglutinated taxa, the same as in the upper Paleocene. Among agglutinated foraminifera, trochantinids, Repmanina charoides, and Karreuria are the most abundant taxa; Recurvoides is also common in this interval, and several Lazarus taxa, such as Hyperammina dilatata and Pullenia jarvisi, reappear. Benthic foraminiferal assemblages gradually recover across this interval, as inferred from their increased heterogeneity and diversity, although these values are lower than preextinction values (Fig. 4).

Among planktic foraminifera, the genus Acarinina strongly dominates the assemblages within this interval (Orue-Etxebarria et al., 2004). In calcareous nannofossil assemblages (Fig. 5), abundance and species richness increases. The percentage of Zygaphlilithus increases considerably, becoming one of the most abundant taxa together with C. pegasus and Toweis, whereas Discoaster and Fasciculithus decrease in relative abundance, and the Rhomboaster-Discoaster araneus assemblage is no longer present (Bernauela et al., 2006).

**DISCUSSION**

**Paleoenvironmental Reconstruction at Zumaia**

Upper Paleocene (Pa1) benthic foraminiferal assemblages indicate mesotrophic conditions at the seafloor, with enough nutrient flux to the seafloor to sustain both infaunal and epifaunal species (Jorissen et al., 1995). The high percentage of agglutinated foraminifera indicates a considerable
input of fine-grained clastic material. A high detrital flux has been documented for the upper Paleocene in Zumaia and in nearby sections of the western Pyrenees (Orue-Etxebarria et al., 1996; Kuhnt and Kaminski, 1997; Pujalte et al., 1998; Baceta et al., 2000; Schmitz et al., 2000; Bernaola et al., 2006). Calcareous nannofossil assemblages indicate stable oceanic conditions, with a stratified water column and a low-nutrient content (Bernaola et al., 2006).

This period of stable conditions was followed by an initial perturbation phase in surface waters (interval Pa2), which preceded the CIE and the main warming event of the PETM. Fluctuations in the species richness and in the percentage of calcareous nannofossil taxa in interval Pa2 indicate the onset of the environmental perturbation, with an expansion of low-latitude, warm-water assemblages to high latitudes, probably caused by an abrupt increase in surface water temperatures (Bernaola et al., 2006), and an elevated nutrient supply in surface waters, possibly caused by increased upwelling or nutrient runoff. This initial perturbation phase is considered to have started about 46 ky before the onset of the CIE, based on the fact that interval Pa2 is ~115 cm thick and assuming an average sedimentation rate for the uppermost Paleocene of ~2.5 cm·kyr⁻¹ (Dinarés-Turell et al., 2007).

The benthic foraminiferal changes, and the gradual but rapid extinction of 18% of the species (minimizing the Signor-Lipski effect), point to an early perturbation of the seafloor between the onset of the CIE and the main BEE (interval E1; see Fig. 3). Although the extinction of S. beccariiformis has been related to the BEE (Thomas, 1998), this species may have become extinct earlier, at least locally, at other locations such as the Basque-Cantabrian Basin (e.g., Schmitz et al., 1997).

The main BEE, which includes the disappearance of 37% of the species at Zumaia, coincided with a rapid increase in relative abundance of agglutinated foraminifera. One might assume that dissolution was the only cause of the BEE and the dominance of agglutinated taxa; however, 18% of the benthic foraminiferal species, following a gradual pattern, disappeared below the main BEE and the dissolution interval (Fig. 2), suggesting that dissolution was not the only cause of the extinctions. Because 18% of the benthic species became extinct within interval E1, and the main BEE (37%) occurred at its top, we conclude that the benthic foraminiferal extinction event was gradual but rapid, affecting 55% of the species in total, which is in line with deep-sea records of the BEE (30–50%; e.g., Tjalsma and Lohmann, 1983; Kailho, 1994; Thomas, 1998, 2007). Its duration corresponds to interval E1. Assuming a duration of ~105 ky (Giuberti et al., 2007; Röhl et al., 2007) for the core of the CIE, which at Zumaia is represented by the siliciclastic unit, an average sedimentation rate of 3.8 cm·kyr⁻¹ can be inferred for the CIE interval at this section. As interval E1 is 40 cm thick, it may represent ~10.5 ky. Therefore, it may be concluded that the gradual extinction event recorded within interval E1 was geologically very rapid, lasting for ~10.5 ky.

The common occurrence of C. pseudoperlucidus (Fig. 2) in interval E1 suggests oxic conditions at the seafloor. This species is large, thick-walled, and multicameral, in contrast to the typical low-oxygen, -selected morphotypes, which generally have few chambers, small tests, and thin walls (Bernhard, 1986).

A ~4-m-thick interval characterized by enhanced dissolution has been identified at Zumaia just above the BEE (intervals E2 and E3; see Figs. 2, 4). Dissolution was more severe in E2, where microfossil assemblages are dominated by DWAF taxa that are very common in sediments deposited beneath the lysocline (Kaminski and Gradstein, 2005), supporting a sudden rise in the CCD, and very scarce, partially corroded calcareous foraminifera. Benthic foraminiferal assemblages from the upper half of the dissolution interval are mainly dominated by calcareous taxa (especially N. truempyi; see Figs. 2, 4), although their tests are strongly corroded. The effects of corrosion decrease toward the uppermost part of interval E3. According to Schmitz et al. (2000), sedimentation rates for siliciclastic material increased during deposition of the siliciclastic unit, reflecting a significant change in climate and hydrological regime toward a warmer (in agreement with the calcareous nannofossil record) and seasonally drier climate. We therefore suggest that low %CaCO₃ at Zumaia resulted not only from dissolution, which strongly affected calcareous foraminiferal tests within the SU, but also from dilution of carbonate-rich material by terrigenous matter—as indicated by a significant increase in the estimated sedimentation rates from interval Pa2 to the siliciclastic unit (from 2.5 to 3.8 cm·kyr⁻¹)—and possibly a large influx of refractory organic matter from land (Schmitz and Pujalte, 2007).

The abundance of several species of Anmmodiscus, Glomospira, and Glomospirella in interval E3 may correspond to the event commonly called the Glomospira acme, which has been recognized in the lowermost Eocene at various locations (see references in Kaminski and Gradstein, 2005). Recent species of Anmmodiscus, Glomospira, Glomospirella, and Repmanina are mobile epifaunal forms that feed on organic detritus (e.g., Ly and Kuhnt, 1994) and tolerate large environmental fluctuations, including variations in salinity and oxygenation (e.g., Kaminski et al., 1996). Among calcareous nannofossils, maximum values in the percentages of Coccolithus pelagicus, Fasciculithus, and Discoaster spp. within interval E3 (Fig. 5) are likely controlled by water temperature (Orue-Etxebarria et al., 2004). According to these authors, the disappearance of Zygrhablithus bijugatus, a species thought to indicate oligotrophic conditions, may result from increased productivity in the water column due to a higher nutrient supply, a situation that agrees with increased continental erosion in the Basque basin as suggested by Schmitz et al. (2000). Such increased erosion might account for the common occurrence of opportunistic benthic foraminiferal species, such as the Glomospira acme and abundant trochoamminids, as well as Karrerulinia, Recurvoides, and Haplophragmoides in intervals E2 and E3. These taxa may have taken advantage of a high-stress, probably strongly fluctuating environment, with rapidly changing seafloor conditions (Sliter, 1975; Koutsoukos et al., 1991; Ly and Kuhnt, 1994; Kaminski et al., 1996; Kuhnt et al., 1996; Goody, 2003).

According to Ortiz (1995), the dominance of finely agglutinated (Haplophragmoides, Glomospira) and calcareous epifaunal taxa (N. truempyi) after the extinction event points to low-oxygen conditions for the lowermost 22 m of the Eocene at Zumaia. Many agglutinated and calcareous taxa that are abundant in the lower Eocene at Zumaia, however, tolerate large environmental fluctuations, and there is no clear independent evidence for dysoxia. The occurrence of very abundant and partially corroded tests of N. truempyi in the lower half of interval E3 may indicate corrosive bottom waters, as does its homeomorphic descendant, N. umbonifera (Jorissen et al., 2007). The maximum abundances of Bulimina tuxpanensis and T. selmensis in intervals E2 and E3 may be related to both low-oxygen and high-nutrient conditions (Olsson and Wise, 1987; Thomas, 1990; Gibbon et al., 1993; Sen Gupta and Machain-Castillo, 1993; Steinbeck and Thomas, 1996; Bernhardt et al., 1997). Tappanina selmensis may also indicate stressed seafloor conditions with undersaturated bottom waters (Boltovskoy et al., 1991; Takeda and Kailho, 2007), whereas R. charoides appears to be opportunistic and independent of oxygen levels (Kaminski et al., 1996; Kaminski and Gradstein, 2005). The high percentages of Globocassidina subglobosa (~17.6% of the assemblages), an oxic indicator (Schönfeld, 2001; Martins et al., 2007), and the common occurrence of C. pseudoperlucidus, a typical oxic species with a thick-walled test and large pores, however, point to oxic conditions at the seafloor during interval E3. In addition, the reddish color of the SU suggests well-oxygenated bottom waters that were able to oxidize minerals from the SU. A peak in the percentage of Aragonia aragonensis is also recorded within interval E3; this species is common in postextinction intervals at several ODP Sites (e.g., Thomas, 1998, 2003) and has been suggested as an opportunistic species (Steineck and Thomas, 1996).

The paleoecological affinities of the calcareous nannofossil Rhombosphaera Discostaur araneus assemblage, which dominates within interval E3, are unknown (e.g., Bralower, 2002; Agnin et al., 2006; Bernaola et al., 2006). According to Egger et al. (2005), this assemblage indicates ecological perturbations in oceanic surface waters developed during the CIE.
interval. The co-occurrence of this short-lived association with *Thora-
cosphaera* suggests that stressed surface-water conditions (Gibbs et al.,
2006; Agnini et al., 2007) prevailed during interval E3, whereas benthic
foraminifera indicate oxic and rapidly changing seafloor conditions, po-
sibly related to increased continental erosion and a large flux of organic
matter from land (Schmitz and Pujalte, 2007). Alternatively, the appear-
ance of asymmetrical *Discocystaster* and *Rhombocystaster* species might indicate
the development and availability of new ecological niches, resulting from
major paleoceanographic changes during the PETM (Bralower, 2002).

We suggest that the sharp transition in lithology from the siliciclastic unit
to the overlying limestone-marl couplets, coincident with a shift to-
ward heavier δ¹³C values, indicates a sudden stop in the weathering of
continental silicates at the top of the SU. The calcareous nannofossil
turnover and the increase in the percentage of acarininids (Orue-
Etzèbarria et al., 2004) in interval E4 at Zumaia have been related to a
sea-level rise that displaced the shoreline >10 km landward, flooding
vast continental areas in the Basque Basin (Baceta, 1996). This sea-level
rise led to the sequestration of nutrients in shelf environments; the con-
secutive relative starvation of surface waters in the open ocean might have
triggered nannofossil turnover owing to a shift to more oligotrophic
conditions (Orue-Etzebarria et al., 2004). The recovery of %CaCO₃ and
δ¹³C to preexcursion values is recorded within interval E4. A typical
postexcursion, benthic foraminiferal fauna with N. truempyi and O. um-
bonatus occurs in this interval, as it does in ODP sites (e.g., Thomas
and Shackleton, 1996). The low diversity and heterogeneity of the assem-
blages indicate that environmental conditions, including the flux of or-
ganic carbon, had not completely recovered at the top of the studied
section.

**Turnover and Timing**

The rapid injection of ¹³C-depleted carbon at the PE boundary was
preceded by environmental perturbation in surface waters at Zumaia.
Calcareous nannofossils indicate a period (interval Pa2) of gradual surface-
water warming previous to the onset of the CIE; assuming an average
sedimentation rate of 2.5 cm-kyr⁻¹ for the uppermost Paleocene at Zu-
maia (Dinárès-Turell et al., 2007), environmental changes in surface wa-
ters started ~46 kyr before the onset of the CIE at Zumaia. A similar
faunal turnover has been observed in other Tethyan sections as well as
at high latitudes (Angori et al., 2007) and indicates a shift from cold-
water to warm-water taxa caused by a sudden expansion of low-latitude,
warm-water assemblages to high latitudes, as a result of an abrupt in-
crease in surface-water temperatures. A ~2°C warming of surface waters
has been observed <10 kyr before the onset of the CIE at different paleogeographical locations (Thomas et al., 2002; Slujs et al., 2007b)
and is consistent with the hypothesis that methane hydrate dissociation
was triggered by bottom-water warming during the latest Paleocene. This
warming, however, does not rule out other models for methane release
(i.e., thermogenic) or biomass burning (e.g., Moore and Kurtz, 2008).
The difference in timing (~46 kyr at Zumaia vs. <10 kyr at some other
sites) remains to be explained, although changing seafloor conditions
have been recently observed during the last 45 kyr of the Paleocene in
the Italian Contessa Road section (Giusberti et al., 2009).

The release of methane and the increase in concentration of its oxida-
tion product CO₂ (and its dissolution in sea water) during the early stage
of warming could have accounted for the intense dissolution in the deep
sea, although the occurrence of severe dissolution at shallow set-
tings, however, is not expected by carbon-cycle modeling (e.g., Dickens
et al., 1997; Thomas, 2007). In deep-water settings such as Zumaia and
the Italian Forada section (Giusberti et al., 2007), preservation of car-
bonate improves gradually up section in the siliciclastic unit, which is
consistent with an abrupt and rapid acidification of the oceans followed
by a slower deepening of the CCD.

Just above the onset of the CIE, microfossil data from Zumaia support
a gradual but rapid onset of the PETM, followed by long-term effects on
calcareous nanoplankton as well as on benthic foraminiferal assemblag-
es. Changes in calcareous nannofossil assemblages and the disappearance
of 18% of the benthic foraminiferal species between the onset of the CIE
and the main BEE indicate perturbation at the seafloor and in surface
waters, as documented from other Tethyan localities (e.g., Pardo et al.,
1999; Galeotti et al., 2005; Angori et al., 2007). This gradual but rapid
initiation of the paleoecological and paleoceanographic turnover eventu-
ally led to the main BEE, about 10.5 kyr after the onset of the CIE.

**Causes of the Benthic Foraminiferal Extinctions**

Benthic foraminiferal turnover and extinctions occur globally across
the PETM, and therefore they must have a global cause. Dissolution
may have caused some extinctions locally, but it was not global (e.g., Thomas
et al., 1999; Gibbs et al., 2006; John et al., 2008). At Zumaia, a gradual
extinction of 18% of the species is recorded below the dissolution inter-
val, suggesting that dissolution was not the (only) cause of the BEE and
the benthic foraminiferal turnover. Moreover, refugia should have existed
for carbonate corrosivity, since the dramatic decrease in carbonate per-
centage is not recorded globally (Takeda and Kaiho, 2007; Thomas,
2007). Decreased oxygenation of bottom waters might have been another
cause that triggered the BEE, although the gradual extinction of benthic
foraminifera has been recorded at Zumaia across an interval with inferred
oxic conditions. Low-oxygen conditions have been well documented in
marginal ocean basins such as the Tethys (e.g., Speijer and Wagner, 2002;
Alegret et al., 2005; Alegret and Ortiz, 2006) and northeastern peri-Tethys
(e.g., Gavrilov et al., 2003), but the record for open-ocean settings is not
so clear; even if locally the oceans were hypoxic or anoxic, some regions
should have remained suitable for benthic foraminifera, which have con-
siderable tolerance for low-oxygen levels. It seems unlikely that productivity
changes in surface waters could have caused a major benthic extinction
because deep-sea benthic foraminifera survived global environmental cri-
ses such as the asteroid impact at the end of the Cretaceous without
significant extinction (e.g., Alegret and Thomas, 2005; Alegret, 2007).
The primary producer community was unstable during the PETM (e.g.,
Bralower, 2002; Bernaola et al., 2006), however, and probably involved
changes in the food flux (type, quantity) to the seafloor, thus triggering
changes in the benthic communities and blooms of opportunistic benthic
foraminifera, which may have taken advantage of a high-stress, probably
strongly fluctuating environment (e.g., Katz et al., 1999). Locally, nutrient
flux to the seafloor may have fluctuated at Zumaia owing to increased
influx of refractory organic matter from land (which might not be easily
used by many benthic foraminiferal species) and high seasonal precipi-
tation (Schmitz and Pujalte, 2007).

According to Thomas (2007), warming may have been the global fea-
ture of the PETM that triggered the global extinction of benthic forami-
nera, since it has been recorded at all investigated latitudes and oceans.
This author hypothesized the possible effects of global warming on oceanic ecosystems, which would include changes in energy cycling
within ecosystems, possibly affecting productivity by calcareous nanno-
plankton, changes in the rate of evolutionary processes, and even fluctu-
ations in the compounds and amount of labile organic matter available
for foraminiferal feeding. These changes in oceanic ecosystems may have
started at Zumaia after the initial warming phase of the surface waters
inferred for the last 46 kyr of the Paleocene (as compared to the last
~3–5 kyr of the Paleocene at some other locations; see Slujs et al.,
2007b), thus triggering the benthic foraminiferal turnover and extinctions
that occurred over a geologically rapid (~10.5 kyr) period of time.

**CONCLUSIONS**

The effects of the PETM have been analyzed in the Zumaia section
based on the study of benthic and planktic foraminifera and calcareous
nannofossils. Microfossil data from Zumaia support a rapid onset of the
PETM, followed by long-term effects on calcareous nanoplankton as
well as in benthic foraminiferal assemblages.
The recovery of CaCO₃ pellets points to a sudden stop in the weathering of continental silicates. The transition in lithology from the SU to the overlying limestone-marl couplets of the CCD after the initial, abrupt acidification of the oceans. The sharp top of the siliciclastic unit at Zumaia are consistent with a slow deepening in isotopic levels and the improved preservation of carbonate toward the top of the Cretaceous/Paleogene boundary bathyal paleoenvironment. We are grateful to Mimi Katz, Ellen Thomas, and the Editor and Associate Editor of PALAIOS for their helpful reviews, which significantly improved this manuscript. We acknowledge the Spanish Ministry of Science and Technology for the funding of this research project. We are grateful to Mimi Katz, Ellen Thomas, and the Editor and Associate Editor of PALAIOS for their helpful reviews, which significantly improved this manuscript.

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