

The Palaeocene–Eocene Thermal Maximum super greenhouse: biotic and geochemical signatures, age models and mechanisms of global change

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Abstract: The Palaeocene–Eocene Thermal Maximum (PETM), a geologically brief episode of global warming associated with the Palaeocene–Eocene boundary, has been studied extensively since its discovery in 1991. The PETM is characterized by a globally quasi-uniform 5–8 °C warming and large changes in ocean chemistry and biotic response. The warming is associated with a negative carbon isotope excursion (CIE), reflecting geologically rapid input of large amounts of isotopically light CO₂ and/or CH₄ into the exogenic (ocean–atmosphere) carbon pool. The biotic response on land and in the oceans was heterogeneous in nature and severity, including radiations, extinctions and migrations. Recently, several events that appear similar to the PETM in nature, but of smaller magnitude, were identified to have occurred in the late Palaeocene through early Eocene, with their timing possibly modulated by orbital forcing. Although debate continues on the carbon source, the mechanisms that caused the input, the mechanisms of carbon sequestration, and the duration and pacing of the event, the research carried out over the last 15 years has provided new constraints and spawned new research directions that will lead to improved understanding of PETM carbon cycle and climate change.

A distinct period of extreme global warmth was initiated close to the boundary between the Palaeocene and Eocene epochs, approximately 55.5 Ma ago (Gradstein *et al.* 2004). This event, termed the Palaeocene–Eocene Thermal Maximum (PETM), occurred during a time of generally warm, ‘greenhouse’ climate conditions, but stands out against the background warmth as an abrupt and short-lived spike in global temperatures. Evidence for global warming is preserved by the TEX₈₆’ temperature proxy (Sluijs *et al.* 2006; Zachos *et al.* 2006), oxygen isotope ($\delta^{18}\text{O}$) excursions in marine foraminiferal calcite (Fig. 1) (Kennett & Stott 1991; Thomas *et al.* 2002) and terrestrial carbonates (Koch *et al.* 1995), increased Mg/Ca values in planktonic and benthic foraminifera (Zachos *et al.* 2003; Tripathi & Elderfield 2005), poleward migrations of (sub)tropical marine plankton (Kelly *et al.* 1996; Crouch *et al.* 2001) and terrestrial

plant species (Wing *et al.* 2005), and mammal migrations across high northern latitudes (Bowen *et al.* 2002, 2006; Smith *et al.* 2006). Associated with the warming is a negative 2.5–6‰ carbon isotope ($\delta^{13}\text{C}$) excursion (CIE) (Kennett & Stott 1991; Koch *et al.* 1992; Thomas *et al.* 2002; Pagani *et al.* 2006), generally accepted to reflect the geologically rapid injection of ¹³C-depleted carbon, in the form of CO₂ and/or CH₄, into the global exogenic carbon pool (Fig. 1).

The apparent conjunction between carbon input and warming has fuelled the hypothesis that increased greenhouse gas concentrations resulted in greenhouse warming during the PETM. The total amount of carbon input during the PETM, which is known to within an order of magnitude (Dickens *et al.* 1997; Zachos *et al.* 2005; Pagani *et al.* 2006), was about 4–8 times the anthropogenic carbon release from the start of the industrial era up

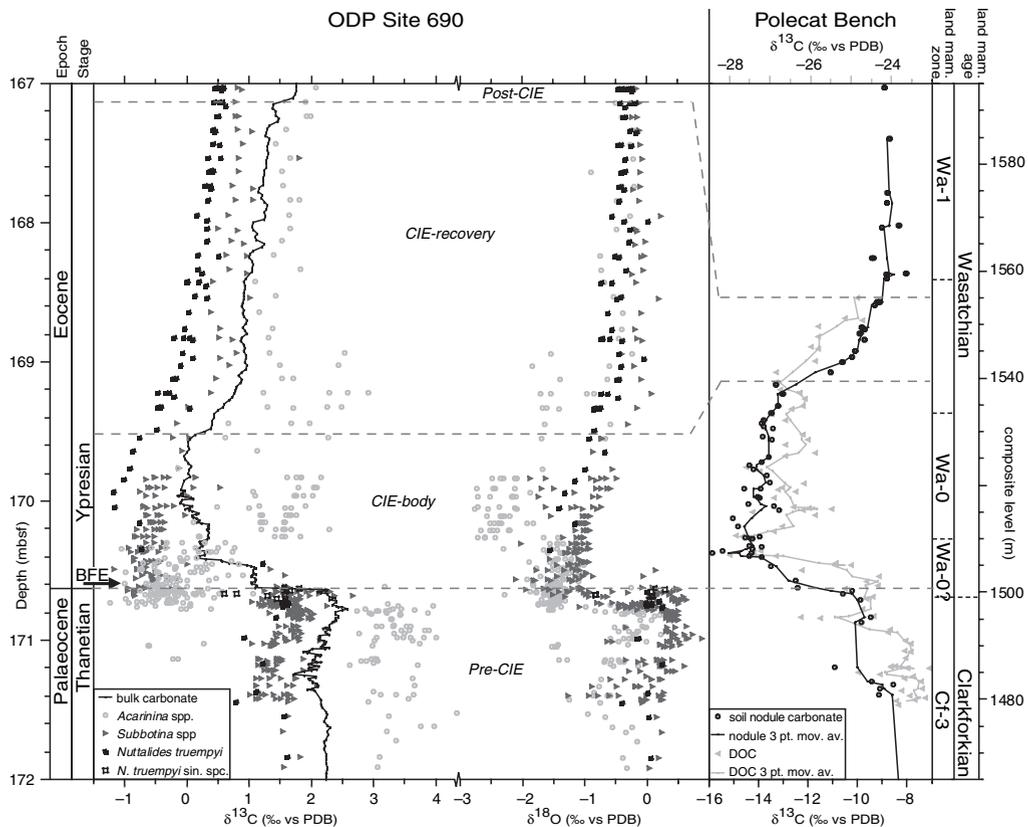


Fig. 1. Compilation of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of planktonic foraminifera (surface-dweller *Acarinina* and thermocline-dweller *Subbotina* spp.; mostly single specimen), benthic foraminifera (*Nuttallides truempyi*) and bulk carbonate from ODP Site 690 in the Weddell Sea (data from (Kennett & Stott 1991; Bains *et al.* 1999; Thomas *et al.* 2002; Kelly *et al.* 2005), soil carbonate nodule (Bowen *et al.* 2001) and dispersed organic carbon (DOC) (Magioncalda *et al.* 2004) $\delta^{13}\text{C}$ records from the Polecat Bench section in the Bighorn Basin, Wyoming, USA. BFE refers to the main phase of benthic foraminifer extinction according to Thomas (2003). Mbsf, metres below sea-floor.

to today (Marland *et al.* 2005), and comparable to that expected from gross anthropogenic emissions through the end of the 21st century (Intergovernmental Panel on Climate Change 2001). In association with carbon cycle and climatic change, the PETM also stands out as a time of major biotic restructuring. Given the probable ties between releases of near-modern levels of carbon-based greenhouse gases and PETM climatic and biotic change, the PETM has developed as a provocative geological case study in global change, and many of the event's characteristics and mechanisms are under intensive study. A large volume of research on the PETM has appeared over the past decade (Fig. 2), and in this paper we aim to review and synthesize this material, including the duration and magnitude of carbon cycle perturbation, magnitude of warming, changes in ocean chemistry and marine and terrestrial biotic response.

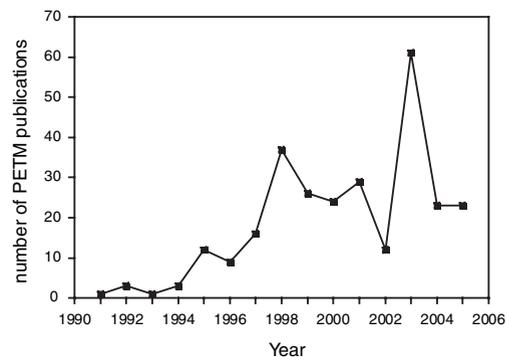


Fig. 2. Number of studies focused published per year on the PETM since the first publication on its CIE and warming in 1991. Numbers are based on a Web-of-Science search using the keywords Palaeocene, Palaeocene (both American and English spellings), Eocene, PETM, IETM and LPTM.

The age of the PETM

Initially, the PETM was placed within the latest Palaeocene (Berggren *et al.* 1995) and as such termed the Late Palaeocene Thermal Maximum (LPTM) (Zachos *et al.* 1993; see papers in Knox *et al.* 1996 and in Aubry *et al.* 1998). In 2000, the Palaeocene–Eocene (P/E) boundary global stratotype section and point (GSSP) was formally defined at the base of the clay layer coinciding with the steepest slope of the negative CIE (Aubry & Ouda 2003; Gradstein *et al.* 2004) in the Gabal Dababiya section (Egypt). As a consequence, the base of the CIE has been used as global reference to pinpoint the P/E boundary. In a few publications, the term Initial Eocene Thermal Maximum (IETM) has been used because the maximum absolute temperatures occurred after the Palaeocene–Eocene boundary (see Wing *et al.* 2003; Zachos *et al.* 2003; Bowen *et al.* 2004). We will use the term PETM throughout this paper.

In the marine realm, the PETM is approximately coeval with the short planktonic foraminiferal zone E1, of which the base coincides with the Palaeocene–Eocene boundary (Pearson & Berggren 2005). The PETM is located within calcareous nannoplankton zone NP9 (Martini 1971) and CP8 (Okada & Bukry 1980), and its base occurs close to the benthic foraminiferal extinction (BFE) event (Fig. 1) (Thomas & Shackleton 1996). In the North Sea, the CIE and its recovery cover the dinoflagellate cyst (dinocyst) zone *Apectodinium augustum* (Powell *et al.* 1996; Sluijs 2006) and coincide with the interval without foraminifera (planktonic and benthic, including agglutinated forms), with large pyritized diatoms (see e.g. Gradstein *et al.* 1994; van Eetvelde & Dupuis 2004). In the terrestrial realm, the base of the CIE coincides with the Clarkforkian–Wasatchian North American Land Mammal Age (NALMA) zone boundary, and is correlative or nearly so (within 10^1 to 10^5 years) with the Gashatan–Bumbaranian land mammal age boundary in Asia and the Cernaysian–Neustrian European land mammal age boundary (Hooker 1998). The CIE occurs within radiolaria zone RP7 in the low latitudes, but marks the RP6-7 boundary in the South Pacific (Gradstein *et al.* 2004). Considering the uncertainties in radiometric dating and orbital tuning, the PETM occurred between 55.8 and 55.0 Ma ago (Berggren *et al.* 1992; Norris & Röhl 1999; Röhl *et al.* 2003; Gradstein *et al.* 2004; Lourens *et al.* 2005; Westerhold *et al.* 2007).

The carbon isotope excursion

The negative CIE has been shown to be a distinctive, globally identifiable geochemical marker for

the PETM in marine and continental sedimentary rocks (Fig. 1) (e.g. Kennett & Stott 1991; Koch *et al.* 1992; Stott *et al.* 1996). The CIE is considered to reflect the injection and subsequent removal of huge amounts of ^{13}C -depleted carbon into the ocean–atmosphere system (Dickens *et al.* 1995; Dickens 2001a).

Shape

Details of the rate and timing of $\delta^{13}\text{C}$ change in the oceans, atmosphere and continental reservoirs, which we will refer to as characterizing the ‘shape’ of the CIE, are needed for $\delta^{13}\text{C}$ curves to serve as a tool for correlation of PETM sections and to provide information on the dynamics of carbon release and sequestration during the event (Dickens *et al.* 1997; Dickens 2001a). Defining the detailed shape of the CIE is complicated, however, in that the temporal evolution of $\delta^{13}\text{C}$ values through the PETM may be different for various substrates and environments and may also be obscured by short-term changes in sedimentation rates that are difficult to recognize (Bowen *et al.* 2006) (see discussion below).

Following attempts to account for accumulation rate changes in deep marine sections affected by carbonate dissolution, a fairly consistent picture of the general shape of the CIE has emerged from terrestrial and marine environments (Bowen *et al.* 2006) (Fig. 1). The initiation of the CIE is marked by an abrupt, negative shift in $\delta^{13}\text{C}$ values, occurring within several hundreds or thousands of years. This is followed by a phase of relatively stable, low values, which has been termed the ‘body’ of the CIE, and a subsequent recovery to higher $\delta^{13}\text{C}$ values that follows an exponential trend. The general shape of the CIE has been interpreted to reflect a potentially pulsed, geologically rapid input of ^{13}C -depleted carbon into the system, followed by gradual sequestration of the excess carbon through burial in rocks (e.g. Dickens *et al.* 1997; Zachos *et al.* 2005). The existence of a $\delta^{13}\text{C}$ plateau during the body of the CIE may reflect a lag between carbon release and the onset of net sequestration (Bowen *et al.* 2006), but the exact duration of this lag and mechanisms causing it remain unclear.

For both marine and continental records, several uncertainties affect estimation of the pace and duration of carbon release, which is relevant to constraining the source of carbon and modelling the effect of carbon input on ocean carbonate chemistry (Dickens *et al.* 1997; Schmidt & Schindell 2003; Cramer & Kent 2005). The $\delta^{13}\text{C}$ records based on different foraminifer species and/or size fractions of the intensively studied Ocean Drilling Program (ODP) Site 690 (Maud Rise, Weddell Sea) indicate

several cm of stratigraphic offset for the onset of the CIE (Fig. 1; see also Thomas 2003). In the $\delta^{13}\text{C}$ records from continental sections in the Bighorn Basin (Wyoming, USA), the CIE onset as marked by soil nodule carbonate and dispersed organic carbon (DOC) is offset by several metres. Several hypotheses have been proposed to explain stratigraphic offsets in marine carbonate records, including lags in the propagation of injected carbon from the atmosphere to the surface and deep oceans, local changes in productivity, and post-depositional mechanisms (such as diagenesis and differential bioturbation; (e.g. Thomas *et al.* 2002; Thomas 2003; Stoll 2005). Lags in the Bighorn Basin organic carbon $\delta^{13}\text{C}$ records have been hypothesized to reflect enhanced downward diffusion of atmospheric CO_2 with subsurface diagenesis in an environment of good drainage and elevated temperature and $p\text{CO}_2$ (Magioncalda *et al.* 2004) or the detrital origin of DOC in these sections (Bowen, unpublished).

Substrate-specific differences also exist in the shape of the body of the CIE. In the Bighorn Basin soil nodule $\delta^{13}\text{C}$ record and the *Subbotina* and *Acarinina* records of ODP Site 690, the body is characterized by relatively stable $\delta^{13}\text{C}$ values with a gentle trend towards higher values. Minimum $\delta^{13}\text{C}$ values in these records are thus located at the base of the body of the CIE. However, minimum bulk $\delta^{13}\text{C}$ values occur c. 50 cm higher.

One aspect of the CIE shape that has been invoked as evidence of PETM carbon cycle dynamics is a multi-stepped drop in $\delta^{13}\text{C}$ values during the onset of the CIE in several relatively complete bulk carbonate records (Bains *et al.* 1999; Zachos *et al.* 2005) (Fig. 1), which has been interpreted as evidence for multiple injections of carbon (Bains *et al.* 1999, 2003). The soil nodule record from the Bighorn Basin also appears to record a short plateau during the onset of the CIE, perhaps representing a few thousand years of relative $\delta^{13}\text{C}$ stasis (Fig. 1) (Bowen *et al.* 2001; Bowen *et al.* 2006). While the plateau also appeared in the 3–5 μm size fraction – which is dominated by the calcareous nannofossil species *Toweius* (Stoll 2005) – at Site 690, it has not been reproduced in single foraminifer $\delta^{13}\text{C}$ records (Fig. 1) (e.g. Thomas *et al.* 2002), which consistently lack intermediate values. Resolving the pattern – whether pulsed or unique – of carbon release at the onset of the PETM remains a central challenge to understanding carbon cycle perturbation during the PETM.

Above differences must reflect factors other than the $\delta^{13}\text{C}$ evolution of the exogenic carbon pool, such as dissolution, local productivity and vital effects, and complicate attempts to correlate

PETM sections based on the details of carbon isotope curves (e.g. Bains *et al.* 1999). As additional data is gathered, these discrepancies may reveal more detailed information on PETM carbon cycle dynamics within the study systems.

During the recovery phase, $\delta^{13}\text{C}$ values rise from values characteristic of the CIE body, but remain lower than pre-CIE values. This shift from pre-PETM to post-PETM values is in pace with a longer-term decline in exogenic $\delta^{13}\text{C}$ values during the Palaeocene–early Eocene (Zachos *et al.* 2001), suggesting a remarkable decoupling of the mechanisms underlying the transient carbon cycle changes of the PETM and the longer-term evolution of the early Palaeogene carbon cycle. The stratigraphic thickness of the recovery phase relative to the thickness of the body of the CIE is larger in at least some of the marine records than in the terrestrial realm. This can be explained, at least in part, by strong variations in deep marine sedimentation rates due to the fluctuations in the depths of the lysocline and CCD (Zachos *et al.* 2005), and possible changes in production rate of calcite (Kelly *et al.* 2005). As improved high-resolution age models and estimates of accumulation rate changes are developed, a consensus should emerge regarding the pace of carbon input and sequestration during the recovery phase and more accurate correlation based on the shape of the CIE should be possible.

Magnitude

The maximum magnitude of the CIE varies greatly between various records, indicating that the manifestation of the CIE at any single site and substrate reflects both changes in the global exogenic $\delta^{13}\text{C}$ budget and local or substrate-specific effects. Separation of local and global effects is therefore necessary in order to understand the ‘true’ global magnitude of the CIE, and could additionally allow $\delta^{13}\text{C}$ records to be interpreted in terms of local environmental or biotic change. Because the CIE magnitude remains a primary form of evidence for the size of the PETM carbon release, and a 1‰ difference in the global CIE magnitude could alter release estimates by 1000 Gt or more, this issue is critical to accurate understanding of PETM carbon cycle forcing.

Planktonic foraminifera show a 2.5–>4‰ excursion with a high level of variability among sites and taxa; e.g. at Site 690 up to 4‰ in the mixed-layer dweller *Acarinina*, 2–3‰ in the mixed-layer dweller *Morozovella* and 2‰ in thermocline dweller *Subbotina* (e.g. Thomas & Shackleton 1996; Thomas *et al.* 2002; Zachos *et al.* 2003; Tripathi & Elderfield 2004; Cramer & Kent 2005). In contrast, only a c. 2‰ CIE is recorded in isolated

calcareous nannofossils at Site 690 (Stoll 2005). A large $\delta^{13}\text{C}$ offset between planktonic data has also been reported from the Kerguelen Plateau (Southern Indian Ocean) (Lu & Keller 1993), whereas a lesser offset was noted in the Bay of Biscay (Pardo *et al.* 1997) although this may be associated with the relatively low resolution of this study. The average magnitude of the CIE based on benthic foraminifera is *c.* 2.5‰ (e.g. Kennett & Stott 1991; Thomas & Shackleton 1996; Zachos *et al.* 2001; Nunes & Norris 2006; Fig. 1), although considerable variation is observed between different benthic foraminiferal species and locations. The CIE in soil carbonate nodules is 5–6‰ (Koch *et al.* 1992; Bowen *et al.* 2001, 2002, 2004) and it is 4–5‰ in terrestrial higher plant n-alkanes (Pagani *et al.* 2006). The magnitude recorded in total organic carbon $\delta^{13}\text{C}$ records generated in terrestrial (Magioncalda *et al.* 2004) and marine locations (e.g. Dupuis *et al.* 2003; Steurbaut *et al.* 2003; Sluijs 2006) is *c.* 5‰.

Bowen *et al.* (2004) analysed a number of local effects that might account for differences in the magnitude of the CIE in marine and mid-latitude terrestrial records. Changes in marine fractionation processes, such as the tendency for foraminiferal calcite to become ^{13}C -enriched with lower pH and $[\text{CO}_3^{2-}]$ (Spero *et al.* 1997), were argued to be relatively minor, explaining up to *c.* 0.5‰ damping of the CIE in foraminiferal records (Bowen *et al.* 2004). The study attributed the larger terrestrial excursion primarily to increased carbon isotope fractionation by plants and changes in soil carbon cycling rates due to increased relative humidity and soil moisture during the body of the PETM. The CIE magnitude in biomarkers (C29 n-alkanes) records from high northern latitudes are consistent with the Bowen *et al.* (2004) analysis, but it has been argued that water-cycle induced changes in plant and soil carbon balance would be minimal given the relatively wet, cool climate of the early Palaeogene Arctic (Pagani *et al.* 2006). In addition, new evidence from Bighorn Basin fossil floras may indicate drier, rather than wetter, mid-latitude PETM climate (Wing *et al.* 2005). The implications of magnitude differences among various CIE records and the magnitude of the 'global' excursion therefore remain unclear. Among the terrestrial records, both the biomarker and palaeosol records may be affected by changes in the local composition of vegetation during the PETM. On the other hand, changes in growth rate and cell size and geometry of nannoplankton which are likely to have occurred with the environmental change recorded at the PETM, might have affected the CIE magnitude in some bulk carbonate and nannofossil-specific isotope records (e.g. Popp *et al.* 1998; Bralower *et al.* 2004).

Nunes & Norris (2006) suggested that variations in CIE magnitude among benthic $\delta^{13}\text{C}$ records from multiple sites reflect changes in deep oceanic circulation. However, the benthic isotope records comprise mostly multi-specimen records which could be influenced by bioturbation (evidenced by single specimen planktonic foraminifer isotope data within the PETM of for example Site 690, Fig. 1; Thomas *et al.* 2002) causing mixing between pre-CIE and CIE values. Moreover, some sites have suffered severe dissolution, while at other sites only very small benthic foraminifera are present within the body of the CIE, implying that these records are incomplete (see Thomas *et al.* 2000 for a record from Site 690 where the species *Nuttallides truempyi* is absent during the peak PETM). In addition, deep-water $\delta^{13}\text{C}$ gradients were very small during the early Eocene warm period, making reconstructions of deep-water circulation difficult (Sexton *et al.* 2006).

Duration and age models

Age models for the PETM and/or CIE generally agree that the whole event took 100 000 to 250 000 years, although none of the various approaches revealed consistent estimates for the total duration as well as the duration of its different phases (Fig. 1). These differences may be partly explained by uncertainties in the detailed 'shape' of the CIE itself, as discussed above. Here, we will discuss and update previously published age models.

An estimate for the duration of the PETM in the terrestrial realm was derived from the Polecat Bench section in the Bighorn Basin, based on the relative stratigraphic thickness of the CIE compared to that of Chron C24r, and the 2.557 million-year estimate for the duration of this chron by Cande & Kent (1995). Sedimentation rates in the Bighorn Basin depend largely on the accommodation space resulting from the apparently constant subsidence (Wing *et al.* 2000). Bowen *et al.* (2001) found a *c.* 40 m stratigraphic thickness for the body of the CIE and *c.* 15 m for the recovery based on the soil nodule $\delta^{13}\text{C}$ record (Fig. 1), implying a *c.* 55 m thickness for the total CIE. Applying the average sedimentation rates of 47.5 cm per thousand years for Chron C24r (Gingerich 2000), based on the magnetostratigraphic results of Butler *et al.* (1981), results in a *c.* 84 000-year duration for the body of the CIE (Bowen *et al.* 2001) (Fig. 1). More recently, Koch *et al.* (2003) updated the magnetostratigraphy, and showed that *c.* 1030 m of sediment accumulated during C24r, which would result in average sedimentation rates of 40.2 cm kyr⁻¹, implying a *c.* 71 kyr duration for the body of the CIE.

Recent studies on astronomically derived cycles in lowermost Palaeogene successions from ODP Leg 208 on the Walvis Ridge (Lourens *et al.* 2005) have confirmed interpretations from previous studies (e.g. Röhl *et al.* 2003) that much more time is represented in the interval between the CIE and the C24r/24n reversal than estimated by Cande & Kent (1995), and that the duration of Chron 24r was in the order of 3.118 million years (Westerhold *et al.* 2007). This implies that average sedimentation rates in the Bighorn Basin during C24r were approximately 33.0 m kyr^{-1} (i.e. $1030 \text{ m} / 3.118 \text{ million years}$), significantly lower than previous estimates, resulting in an estimate of the duration of the body of the CIE at Polecat Bench of *c.* 120,000 years (i.e. $40 \text{ m} / 33.0 \text{ cm kyr}^{-1}$) and at least *c.* 170 kyr (i.e. $55 \text{ m} / 33.0 \text{ cm kyr}^{-1}$) for the entire PETM.

Two commonly used age models were derived from the relatively expanded marine PETM section at ODP Site 690. Both age models agree across the main body of the CIE, but differ significantly for the duration of the recovery phase. The first of these (Röhl *et al.* 2000) was based on core-scan X-Ray Fluorescence (XRF) Fe and Ca measurements through the CIE, and recognition of precession cycles (duration *c.* 20 kyr) in these records. The authors counted four cycles within the body of the CIE, and another seven within the recovery phase, recognized by the location of inflection points of the bulk carbonate $\delta^{13}\text{C}$ record, thus arriving at an estimate for the entire CIE of 210 to 220 kyr. The second of these models is based on the extraterrestrial He ($^3\text{He}_{\text{ET}}$) concentrations of the Site 690 PETM sediments and the assumption that the flux of this isotope to the Earth remained constant during the PETM (Farley & Eltgroth 2003). The background absolute flux of $^3\text{He}_{\text{ET}}$ to the sea-floor during the PETM was estimated from the $^3\text{He}_{\text{ET}}$ concentration in 13 samples taken from C24r and C25n above and below the PETM and average sedimentation rates obtained from Aubry *et al.* (1996). These average sedimentation rates were based on a relatively low resolution magnetostratigraphy (Spiess 1990) – which has since been revised by Ali *et al.* (2000) – and durations for C24r and C25n of 2.557 and 1.650 Ma (Cande & Kent 1995), respectively. Accordingly, Farley & Eltgroth (2003) arrived at an estimate of *c.* 90 kyr for the duration of the body of the CIE and *c.* 120 kyr for the entire PETM.

The $^3\text{He}_{\text{ET}}$ -based age model is subject to several important uncertainties. First, the depth level of the reversal between C24r and C24n has not been clearly identified at Site 690, being adjacent to an unconformity. The carbon isotope excursion associated with Eocene Thermal Maximum 2 (ETM2), which is *c.* 150 kyr older

than this reversal (Cramer *et al.* 2003; Lourens *et al.* 2005; Westerhold *et al.* 2007), is present at Site 690 (Cramer *et al.* 2003; Lourens *et al.* 2005) and could thus be used as an alternate calibration point. Secondly, Chron C24r was likely 561 kyr longer than assumed (Westerhold *et al.* 2007). Thirdly, ODP Site 690 recovered the upper Palaeocene and lower Eocene in a single hole only, but we know from multiple-hole drilling that sediment cores expand when they are released from the overlying load, so that part of the core is lost. The average expansion factor for Sites 1262–1267 at Walvis Ridge, for instance, varied between 110 and 118% (Zachos *et al.* 2004), which implies recovery gaps of 1 to 1.8 m between each core, similar to the value of 1.2–1.8 m found by Florindo & Roberts (2005) for the double-cored, younger part of Site 690. This core loss due to expansion has not been accounted for in Site 690 studies, but the whole CIE is within one core at Site 690, so that cycle counts limited to this interval are not affected (Röhl *et al.* 2000). Fourthly, the 13 samples used to calculate the background $^3\text{He}_{\text{ET}}$ flux may be affected by temporal (possibly orbitally forced) variations in sedimentation rates, probably as covered by the ‘minimum’ and ‘maximum’ estimates based on the standard errors in the background flux values, which vary between 0.38 and $0.97 \text{ pcc cm}^{-2} \text{ kyr}^{-1}$ ($1 \text{ pcc} = 10^{-12} \text{ cm}^3$ of He at STP). Fifthly, $^3\text{He}_{\text{ET}}$ fluxes may not have been constant during C24r and C25n (Mukhopadhyay *et al.* 2001; Kent *et al.* 2003), and are known to vary by an order of magnitude over millions of years (Farley 2001). Background flux values appear significantly higher during C24r than during C25 (Table 1c).

In order to re-evaluate the He-based age model and test its sensitivity to the above uncertainties, we calculated several age models for the PETM using different assumptions and corrections for the above issues (Table 1, Fig. 3). We adopt durations of C25n (504 kyr) and the interval between the onset of C24r and the ETM2 (2940 kyr) from Westerhold *et al.* (2007) and apply different sediment expansion factors. Because background $^3\text{He}_{\text{ET}}$ content/g sediment is quite sensitive to small changes in these assumptions is large, the resulting estimates for the total duration of the PETM vary between 90 ± 10 and 140 ± 30 kyr for the most likely scenarios (Fig. 3). Regardless of the assumptions, however, the helium model requires a very large increase in sedimentation rate towards the end of the PETM, thus giving a rapid recovery period relative to the body of the PETM (Fig. 3) (Farley & Eltgroth 2003).

A rapid recovery may be supported by the theory that calcite production in the photic zone increased during the recovery phase (Kelly *et al.* 2005) or

Table 1. Calculation of sedimentation rates and $^3\text{He}_{\text{ET}}$ fluxes (in $\text{pcc cm}^{-2} \text{ kyr}^{-1}$) through the upper Palaeocene–lower Eocene section of ODP Hole 690B. Average values and standard deviations for the background $^3\text{He}_{\text{ET}}$ content/g sediment (from Farley & Eltgroth 2003) in Table 1c are used to calculate absolute background $^3\text{He}_{\text{ET}}$ fluxes through the following intervals: onset – termination C25n, onset C24r – ETM2 and onset C25n – ETM2. For these calculations, we adopt the durations of these intervals from (Westerhold et al. in press) and exclude (Table 1a) and include (Table 1b) 11% core loss due to sediment expansion (see text)

(a)		(b)		(c)	
Background ET3He flux and sedimentation rate model for Hole 690B. Expansion not included					
I	C25n interval 504	937	1.86	cm/kyr	Chron 24r ET3He pcc/g
			dens/(kyr/cm) =	2.48	Chron 25n+r ET3He pcc/g
			av. flux	0.63	0.28
			minus stand. dev.	0.47	0.35
			plus stand. dev.	0.79	0.35
II	base 24r – ETM 2 2940	5181	1.76	cm/kyr	av 0.33
			dens/(kyr/cm) =	2.35	stdev 0.03
			av. flux	0.79	av 0.25
			minus stand. dev.	0.71	stdev 0.06
			plus stand. dev.	0.87	
III	C25n – ETM 2 3444	6118	1.78	cm/kyr	Chron 25 – ETM2 (all samples) ET3He pcc/g
			dens/(kyr/cm) =	2.37	av 0.30
			av. flux	0.71	stdev 0.06
			minus stand. dev.	0.56	
			plus stand. dev.	0.86	DB Density 1.34
Background ET3He flux and sedimentation rate model for Hole 690B. Expansion (11%) included					
IV	C25n interval 504	1003	1.99	cm/kyr	
			dens/(kyr/cm) =	2.66	
			av. flux	0.68	
			minus stand. dev.	0.51	
			plus stand. dev.	0.85	
V	base 24r – ETM 2 3150	5809	1.84	cm/kyr	
			dens/(kyr/cm) =	2.46	
			av. flux	0.82	
			minus stand. dev.	0.74	
			plus stand. dev.	0.91	
VI	C25n – ETM 2 3654	6812	1.86	cm/kyr	
			dens/(kyr/cm) =	2.49	
			av. flux	0.74	
			minus stand. dev.	0.58	
			plus stand. dev.	0.90	

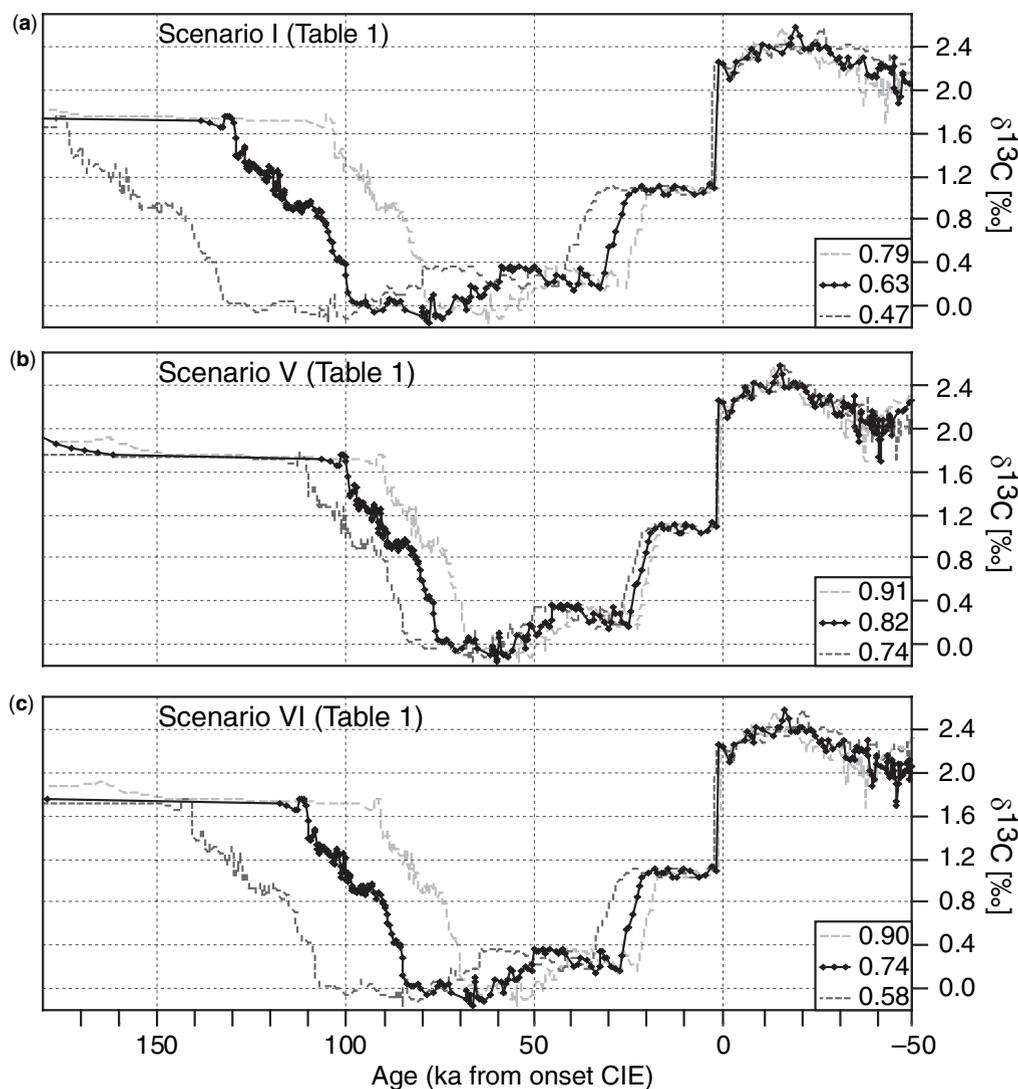


Fig. 3. Shape and duration of the CIE (data from Bains *et al.* 1999) assuming the various options and uncertainties in sedimentation rates and background ${}^3\text{He}_{\text{ET}}$ fluxes calculated in Table 1. Options (a, b and c) represent scenarios I, V and VI from Table 1: (a) ${}^3\text{He}_{\text{ET}}$ fluxes calculated from the measurements of C25 only (Table 1c) and sediment expansion not included. (b) ${}^3\text{He}_{\text{ET}}$ fluxes calculated from the measurements of C24r and sediment expansion included. (c) ${}^3\text{He}_{\text{ET}}$ fluxes calculated from the measurements of C25n through C24r and sediment expansion included. Dotted lines represent standard deviations of background flux measurements.

calcite preservation increased due to the ‘overshoot’ of the lysocline following silicate weathering (Dickens *et al.* 1997; Zachos *et al.* 2005). The ${}^3\text{He}_{\text{ET}}$ and cyclostratigraphic age models each provide estimates of the magnitude of sedimentation rate increases due to these mechanisms. Our recalculated He-based estimates suggest duration of 30 to 35 ka for the recovery phase. Röhl *et al.* (2000) counted seven precession cycles through

the recovery interval at ODP Site 690, implying a relatively prolonged, *c.* 140 kyr, recovery and negligible changes in sediment accumulation rates. Clear identification of cycles in this interval of the 690 cores is complicated, however, by the high carbonate content of the sediments. A cyclostratigraphic study on an Italian PETM section (Giusberti *et al.* 2007) counted only five precession cycles (*i.e.* *c.* 100 kyr) within the recovery interval.

Direct site-to-site correlation of the termination of the CIE is complicated, however, due to the lack of a clear $\delta^{13}\text{C}$ inflection point, which makes the definition of this level somewhat subjective. These differences demonstrate that significant uncertainty remains regarding the pace of carbon cycle recovery from the PETM. Studies in progress, including cycle and $^3\text{He}_{\text{ET}}$ studies, will probably provide better constraints regarding the durations of the various parts of the CIE.

The temperature anomaly

Deep sea benthic foraminiferal calcite consistently shows a $>1\%$ negative excursion in $\delta^{18}\text{O}$ (e.g. Kennett & Stott 1991; Bralower *et al.* 1995; Thomas & Shackleton 1996; Zachos *et al.* 2001) during the PETM (see above for $\delta^{13}\text{C}$). Application of empirical temperature – $\delta^{18}\text{O}$ relations (e.g. Shackleton 1967; Erez & Luz 1983) indicates a deep-water temperature rise of *c.* 4–5 °C, which is corroborated by benthic foraminiferal Mg/Ca values (Tripathi & Elderfield 2005). This warming was first interpreted to reflect a shift in deep-water formation from high to low latitudes (Kennett & Stott 1991). Evidence accumulating since then indicates that the dominant source of intermediate and deep-water formation probably remained at high latitudes, although it may have switched from southern to northern high latitudes (Pak & Miller 1992; Bice & Marotzke 2001; Thomas 2004; Tripathi & Elderfield 2005; Nunes & Norris 2006). Although some component of deep-water warming could reflect different temperatures at Northern and Southern Hemisphere sites of deep-water formation, it is likely that most of the *c.* 5 °C warming was the result of surface-water warming in sub-polar regions (Tripathi & Elderfield 2005).

Planktonic foraminiferal $\delta^{18}\text{O}$ and Mg/Ca excursions generally point towards *c.* 5 °C surface-water warming over a large range of latitudes (Kennett & Stott 1991; Thomas & Shackleton 1996; Charisi & Schmitz 1998; Thomas *et al.* 2002; Zachos *et al.* 2003; Tripathi & Elderfield 2004). At Site 690, the maximum warming appears to be as much as 6–8 °C (Kennett & Stott 1991; Thomas *et al.* 2002). The $\delta^{18}\text{O}$ records for the mixed-layer dweller *Acarinina* and thermocline-dweller *Subbotina* follow somewhat different trajectories through the event, with *Subbotina* recording its lowest (warmest) $\delta^{18}\text{O}$ values at the base of the CIE-body and *Acarinina* reaching its $\delta^{18}\text{O}$ minimum halfway through the CIE-body (*c.* 171 m below sea-floor, mbsf). The apparent decoupling between thermocline and surface-water temperatures at Site 690 seems also to be reflected

in Mg/Ca-based temperature reconstructions from subtropical Pacific Site 1209 (Zachos *et al.* 2003). At Site 690, and perhaps to a lesser degree at Site 1209, it is accompanied by a sudden increase in $\delta^{13}\text{C}$ values of *Acarinina*, suggesting the possible influence of surface-water stratification and productivity on temperature and carbon isotope values.

A salinity-independent organic palaeothermometer TEX_{86}' record across a PETM succession in the Arctic Ocean revealed a warming of *c.* 5 °C close to the North Pole (Sluijs *et al.* 2006), implying that the magnitude of temperature change in tropical and (north-) polar surface waters were equal and excluding polar amplification scenario for the PETM at least for the Northern Hemisphere (Tripathi & Elderfield 2005; Sluijs *et al.* 2006). The absence of sea ice, as implied by the high TEX_{86}' -derived average absolute temperatures (Sluijs *et al.* 2006), was probably a critical factor determining the lack of polar temperature change amplification.

Records from nearshore marine sediments provide evidence for greater temperature-change heterogeneity in coastal settings. A benthic foraminiferal $\delta^{18}\text{O}$ record from the neritic sediments recovered at Bass River, New Jersey (USA), exhibits a relatively large excursion that, assuming no change in salinity, suggests 8° of PETM warming (Cramer *et al.* 1999). This finding has recently been supported by the salinity-independent TEX_{86} record from the nearby Wilson Lake borehole (New Jersey) (Zachos *et al.* 2006). In contrast, a benthic foraminiferal $\delta^{18}\text{O}$ record from the Egyptian shelf shows a *c.* 1‰ negative excursion (Schmitz *et al.* 1996), which might imply *c.* 4 °C of warming but hardly stands out from the background scatter. Application of salinity-independent temperature proxies at this site may help constrain the interpretation of the $\delta^{18}\text{O}$ data, but the general suggestion is that the magnitude of coastal warming may have varied by at least a factor of 2.

Warming estimates from the Bighorn Basin are also in the range of 5 °C. Koch *et al.* (2003) and Bowen *et al.* (2001) calculate a 3–7 °C warming based on carbonate soil nodule $\delta^{18}\text{O}$. Fricke and colleagues (Fricke *et al.* 1998; Fricke & Wing 2004) infer that PETM mean annual temperature was 4–6 °C warmer than before and after the PETM, based on $\delta^{18}\text{O}$ of biogenic phosphate. Estimates from leaf margin analysis of fossil leaves are consistent with these other data, implying a *c.* 5 °C rise in mean annual temperature during the PETM (Wing *et al.* 2005).

Acidification of the ocean

According to theory, and as observed and expected in the present and future ocean (Caldeira & Wickett

2003; Feely *et al.* 2004; Delille *et al.* 2005; Orr *et al.* 2005; Kleypas *et al.* 2006), the instantaneous induction of large amounts of CO₂ or CH₄ (which would rapidly be oxidized to CO₂ in the atmosphere) into the ocean–atmosphere system at the PETM should have increased the carbonic acid (H₂CO₃) concentration in the oceans. This acidification would reduce the depth of the calcite compensation depth (CCD) and lysocline in the oceans, leading to sea-floor carbonate dissolution and reduced carbonate burial, which would restore the pH balance in deep ocean waters over 10³ to 10⁴-year time-scales (Dickens *et al.* 1997; Dickens 2000). The extent of globally averaged CCD shoaling is related to the amount of CO₂ injected into the ocean–atmosphere system, and thus may be used to constrain the amount of carbon (Dickens *et al.* 1997).

Sea-floor carbonate dissolution during the PETM has been documented in sediments across a *c.* 2 km depth transect (palaeodepths *c.* 1500–3600 m) at Walvis Ridge in the southeast Atlantic Ocean (Zachos *et al.* 2005). These data allow estimation of PETM carbon release as at least *c.* 4500 Gt if it is assumed that the magnitude of shoaling at Walvis Ridge was characteristic of the global ocean, that the geometry of the ocean basins and seawater alkalinity were equal to those of the modern ocean, and that the release rates of carbon compounds were comparable to projected rates of anthropogenic emissions. It is unlikely that any of these assumptions is strictly correct, and therefore the estimated carbon release can only be taken as a rough estimate that is broadly consistent with, but perhaps suggests a somewhat larger release than, previous estimates (e.g. Dickens *et al.* 1995). In particular, it is not clear that the dramatic shoaling of the CCD at Walvis Ridge was characteristic of the world oceans (e.g. Thomas 1998). Carbonate content at Site 690 (palaeodepth *c.* 1900 m), only decreased from *c.* 85% to *c.* 60% (e.g. Bralower *et al.* 2004). At central Pacific Site 1209 (Shatsky Rise), which was deeper than the shallowest Walvis Ridge site, carbonate content decreased by only *c.* 10% (Colosimo *et al.* 2005), and decreased carbonate content at the Mead Stream section in New Zealand (continental slope) has been interpreted to reflect dilution by increased terrigenous influx rather than dissolution (Hollis *et al.* 2005a). These data seem to mimic the general pattern of more severe dissolution in the Atlantic relative to the Pacific than has been predicted by a modelling study that assumes ocean circulation patterns in the late Palaeocene were analogous to those of the present day (Dickens *et al.* 1997), but the magnitude of lysocline and CCD shoaling at Walvis Ridge was much larger than predicted in that study. Severe dissolution has also been observed in many marginal

basins, such as the North Sea region (e.g. Gradstein *et al.* 1994), and the marginal Tethys (e.g. Ortiz 1995; Speijer *et al.* 1997; Speijer & Wagner 2002; Dupuis *et al.* 2003; Schmitz *et al.* 2004; Ernst *et al.* 2006). Understanding the controls on dissolution at these sites, including local factors such as carbonate and organic matter production rates, clastic influx and post-burial dissolution, as well as large-scale factors such as ocean circulation, will be critical to extrapolating to derive a global estimate of ocean acidification and robust estimates of the magnitude of carbon release during the PETM.

The recovery of the oceanic carbonate system may have occurred through increased rates of marine or terrestrial organic carbon burial (Bains *et al.* 2000; Beerling 2000) and through a feedback involving increased marine carbonate carbon burial driven by silicate weathering (Dickens *et al.* 1997; Kelly *et al.* 2005). At Walvis Ridge, the lysocline deepened below pre-PETM levels during the recovery phase, suggesting elevated deep-water alkalinity and supporting the hypothesis of feedback through silicate weathering (Zachos *et al.* 2005). Marine organic-rich PETM successions have been recorded from shallow marine sections from the Tethyan margins (e.g. Bolle *et al.* 2000; Speijer & Wagner 2002; Gavrillov *et al.* 2003), the North Sea (e.g. Bujak & Brinkhuis 1998) and the Arctic Ocean (Sluijs *et al.* 2006). Despite these organic-rich deposits, and although abundant Palaeocene and early Eocene peat and coal deposits exist on the continents (e.g. Collinson *et al.* 2003; Kurtz *et al.* 2003), it is not clear to which extent (if at all) the rate of organic carbon deposition and burial increased during the PETM (e.g. Bowen *et al.* 2004).

Biotic response

Patterns of benthic turnover

The PETM stands out in the geological record as one of the largest extinctions in deep marine calcareous benthic foraminifera, when 35–50% of deep-sea species rapidly became extinct (Tjalsma & Lohmann 1983; Thomas 1989; Pak & Miller 1992; Thomas & Shackleton 1996; Thomas 1998, 2003). Benthic foraminifer extinction (BFE) events of this magnitude are rare in the geological record and deep sea turnover usually takes millions of years (Thomas 2007). Rapid extinction in the deep sea is expected to be rare: many species are cosmopolitan, and are rapid colonizers. Extinction of a large fraction of deep-sea species thus requires a rapid change affecting the whole deep ocean, the largest habitat on Earth. Discussion of the cause of the extinction has concentrated on food

availability, acidification, bottom-water oxygen depletion and temperature, based on the palaeoecological interpretation of post-BFE assemblages, which are unfortunately not straightforward (Thomas 1998, 2003).

Food availability in the present oceans depends on surface ocean production and export production of organic matter. Deep sea benthic foraminiferal assemblages do not indicate a global increase or decrease in the food supply during the PETM (e.g. Thomas 1998). In the central Pacific (ODP Site 865) and Southern Ocean (Site 690), benthic foraminifer assemblages point to an increase in food supply, whereas the opposite is found at Atlantic and Indian Ocean sites (Thomas 2003). Nannofossil assemblages (see below) suggest a decrease in surface productivity at Sites 690 and 865, whereas benthic foraminiferal assemblages suggest an increased food supply to the sea-floor. To explain this discrepancy, Thomas (2003) speculated that during the PETM there may have been a chemosynthetic food source at the ocean floor or that export production was more efficient, possibly because lower oxygen levels caused lower organic matter decomposition. If the latter is true, decreased oxygen concentrations of the deep ocean due to higher temperatures and possibly methane oxidation (see below) may have contributed to the BFE (Thomas 1998, 2003; Dickens 2000). Nevertheless, there is no geochemical or sedimentological evidence for severe low oxygen conditions in open ocean (Thomas 2007). Small thin-walled benthic foraminifera (as well as ostracodes) in the interval just above the BFE, are associated with increased calcite corrosiveness of deep waters, which would have been detrimental to calcifiers and could have provided a selective force driving extinction (Steineck & Thomas 1996; Thomas 1998; Orr *et al.* 2005; Zachos *et al.* 2005). Extinctions, however, occurred also among non-calcifying deep marine agglutinated foraminifera (Kaminski *et al.* 1996; Galeotti *et al.* 2005). There is thus no evidence that deep-water oxygen depletion, carbonate dissolution or increased or decreased food supply to the deep sea were global. Therefore, the global deep ocean temperature increase, which would have raised metabolic rates and lead to ecosystem restructuring, may have been the most important cause of the BFE (Thomas 2007).

Benthic foraminifer studies on neritic and upper bathyal assemblages are largely restricted to the Tethyan basin and Atlantic margins. Extinction and temporal changes in composition in these settings were less severe than in the deep sea (Gibson *et al.* 1993; Speijer & Schmitz 1998; Thomas 1998; Cramer *et al.* 1999; Speijer & Wagner 2002). Speijer and colleagues argue that late Palaeocene through early Eocene assemblages

generally indicate relatively oligotrophic conditions along the southern Tethyan margin, but show a transient increase in food supply during the PETM (Speijer & Schmitz 1998; Speijer & Wagner 2002; Scheibner *et al.* 2005), consistent with multi-proxy evidence from neritic realms around the world (see sections on dinocysts and nannofossils).

Larger foraminifera show a large turnover in the Tethyan realm, which has long been recognized but only recently correlated to the PETM (Pujalte *et al.* 2003). This turnover is characterized by a decrease in generic diversity, but the few genera that became dominant during the PETM show rapid diversification on the species level, possibly due to migration from a previously isolated basin or fast specialization as a result of changing environments (Pujalte *et al.* 2003).

Unlike benthic foraminifera, the PETM does not stand out as a major extinction event in the deep sea ostracode fossil record (Boomer & Whatley 1995), but it has not been well studied at high resolution. The only reasonable-resolution record from the deep sea is by Steineck & Thomas (1996) on assemblages from Site 689, close to Site 690 but *c.* 900 m shallower. Their results indicate that ostracodes were smaller and more thin-walled during the PETM, suggesting that within-lineage changes in ostracode morphology may reflect calcite corrosiveness.

Tethyan neritic ostracode assemblages, on the other hand, show a turnover at the PETM (Speijer & Morsi 2002, and references therein), when long-ranging Palaeocene taxa were out-competed by a species that is thought to thrive in upwelling areas. Hence, the dominance of this species is interpreted as a response to enhanced food supply and decreased bottom-water oxygenation (Speijer & Morsi 2002). These Tethyan assemblages suggest a sea-level rise at the PETM, an interpretation consistent with information from other shallow marine successions (Powell *et al.* 1996; Cramer *et al.* 1999; Oreshkina & Oberhänsli 2003; Crouch & Brinkhuis 2005; Sluijs *et al.* 2006).

Migration and radiation patterns in the planktonic realm

The most dramatic planktonic microfossil signature at the PETM is recorded in organic-walled dinoflagellate cysts (dinocysts). Most organic cyst-forming dinoflagellates have life strategies that require a restricted water depth and are, hence, specialized in neritic settings (Fensome *et al.* 1996). They are very sensitive to changes in the physiochemical characteristics of the surface waters, including salinity, temperature, nutrient availability and stratification (Sluijs *et al.* 2005). The taxon *Apectodinium* originated close to the Danian–Selandian boundary

(Brinkhuis *et al.* 1994; Guasti *et al.* 2005), and abundant occurrences remained largely restricted to low latitudes throughout the Palaeocene (Bujak & Brinkhuis 1998). In contrast, every studied dinocyst-bearing succession across the PETM has yielded abundant *Apectodinium*, usually >40% of the dinocyst assemblage (Heilmann-Clausen 1985; Bujak & Brinkhuis 1998; Heilmann-Clausen & Egger 2000; Crouch *et al.* 2001; Sluijs *et al.* 2005, 2006) (Fig. 4). Such a global, synchronous acme is unique in the dinocyst fossil record, which spans the late Triassic to the Recent. During the PETM temperate to polar, sea-surface temperatures increased to allow poleward migration of *Apectodinium* (Bujak & Brinkhuis 1998; Crouch *et al.* 2001; Sluijs *et al.* 2006). The *Apectodinium* acme appears to be associated not only with high temperatures, but also with a strong increase in nutrient availability in marginal marine settings (Powell *et al.* 1996; Crouch *et al.* 2001, 2003a; Crouch & Brinkhuis 2005): the motile dinoflagellates that formed *Apectodinium* cysts were probably heterotrophic and fed on organic detritus or other plankton (Bujak & Brinkhuis 1998). Increased nutrient input by rivers is consistent with results from fully coupled general circulation models predicting an

intensified hydrological cycle at elevated greenhouse gas concentrations (Pierrehumbert 2002; Huber *et al.* 2003; Caballero & Langen 2005). Other microfossil, geochemical and lithological evidence at least supports locally intensified runoff during the PETM, although several clay mineral records suggest that this started prior to the CIE (Robert & Kennett 1994; Gibson *et al.* 2000; Ravizza *et al.* 2001; Speijer & Wagner 2002; Egger *et al.* 2003; Gavrilov *et al.* 2003; Gibbs *et al.* 2006; Pagani *et al.* 2006). *Apectodinium* was probably euryhaline, i.e. tolerant to a wide range of salinities, as the acme has been recorded from the relatively fresh (Pagani *et al.* 2006; Sluijs *et al.* 2006) Arctic Ocean to the probably more salty subtropical regions and even open ocean settings (Egger *et al.* 2000). Because of this complex palaeoecology, it is difficult to elucidate which environmental parameter(s) was the driving force behind the global *Apectodinium* acme during the PETM.

Marine dinoflagellate assemblages usually show a strong proximal–distal signal, so that dinocyst assemblages can be used to reconstruct the influence of inshore waters in a more offshore locality (Brinkhuis 1994; Pross & Brinkhuis 2005; Sluijs *et al.* 2005). Dinocyst assemblages show a trend

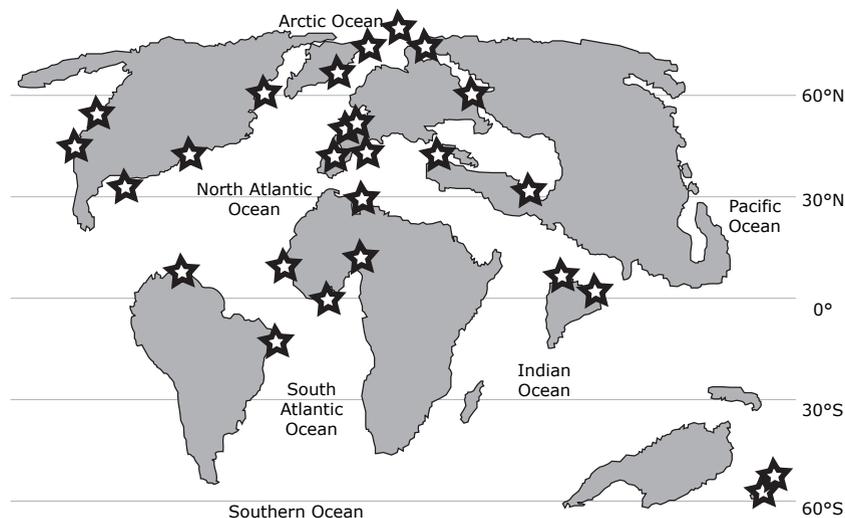


Fig. 4. Palaeogeographic reconstruction of the continental constellation during PETM times (modified from Scotese & Golanka 1992) with the distribution of the acme of dinocyst *Apectodinium*. All studied PETM sections that bear dinocysts yield abundant *Apectodinium*. Records are from the North Sea (Bujak & Brinkhuis 1998 and references therein; Heilmann-Clausen 1985; Steurbaut *et al.* 2003; Sluijs 2006), Greenland, Spitsbergen (e.g. Boulter & Manum 1989; Nohr-Hansen 2003), the Tethyan Ocean (N. Africa, Austria, Tunisia, Uzbekistan, Pakistan, India, Kazakhstan) (e.g. Köthe *et al.* 1988; Bujak & Brinkhuis 1998; Iakovleva *et al.* 2001; Crouch *et al.* 2003a; Egger *et al.* 2003), equatorial Africa (JanDuChêne & Adediran 1984), the eastern (e.g. Edwards 1989; Sluijs 2006) and western USA. (J. Lucas-Clark, pers. comm., 2003; Brinkhuis, Sluijs, unpublished), Barents Sea, South America (Brinkhuis, pers. obs.) and New Zealand (Crouch *et al.* 2001; Crouch *et al.* 2003b; Crouch & Brinkhuis 2005) and the Arctic Ocean (Sluijs *et al.* 2006).

towards more offshore surface-water conditions at many locations during the PETM (Crouch & Brinkhuis 2005; Sluijs *et al.* 2005) implying that eustatic transgression took place (Sluijs 2006). Although the magnitude of this transgression is unclear, qualitatively it may be expected during a time of significant global warming because of thermal expansion and potential cryosphere melting, which together potentially comprised in the order of *c.* 10–20 m across the PETM (Miller *et al.* 2005). Furthermore, it is consistent with data on shallow marine benthic foraminifer, ostracode and grain-size information (Gibson & Bybell 1994; Cramer *et al.* 1999; Speijer & Morsi 2002; Speijer & Wagner 2002; Sluijs 2006).

Apectodinium shows a large variation of morphotypes through this event. As for planktonic foraminifera (see below), it is hard to assess which of these dinocyst types represent true biological species, but intermediate forms occur, implying that they represent ecophenotypes. *Apectodinium* is a member of the family Wetzeliellaceae, which underwent major radiation during or close to the PETM. There are few high-resolution studies of upper Palaeocene material (Heilmann-Clausen 1985; Bujak & Brinkhuis 1998; Iakovleva *et al.* 2001; Guasti *et al.* 2005), but associated genera, such as *Wilsonidium*, *Dracodinium* and *Rhombodinium* originated close to or at the PETM. Afterwards, new genera and species within the Wetzeliellaceae, including the genus *Wetzeliella*, developed, their evolution potentially related to other early Eocene global warming events such as ETM2 (Lourens *et al.* 2005) and ETM3 (Röhl *et al.* 2005).

Compared to dinocysts, planktonic foraminifera show a relatively minor response to the PETM. Poleward migrations include the only occurrence of the low-latitude genus *Morozovella* in the Weddell Sea (Thomas & Shackleton 1996) just prior to and during the lower part of the CIE. Extinctions and radiations are largely absent but evidence of faunal turnover has been recorded at many locations (e.g. Lu & Keller 1993, 1995; Pardo *et al.* 1997). The genera *Morozovella* and *Acarinina* developed extreme morphotypes during the PETM in tropical regions (Kelly *et al.* 1996, 1998). The dominance of these newly developed taxa within the assemblages has been interpreted as indicative of relatively oligotrophic conditions in the open ocean due to changes in the thermal structure of the water column (Kelly *et al.* 1996). These PETM morphotypes might represent true evolutionary transitions or ecophenotypes reflecting unusual environmental conditions, such as stratification and nutrient depletion (Kelly *et al.* 1998).

Only few high-resolution calcareous nannofossil studies focused on palaeoecology through the

PETM, although assemblage changes are extensively described (e.g. Backman 1986; Aubry *et al.* 1996; Raffi *et al.* 2005 and references therein; see also fig. 17 in Raffi *et al.* 2005 for geographic distribution maps of recorded changes in the nannofossil assemblage). Neritic assemblages from the New Jersey Shelf were interpreted to reflect increased productivity during the PETM (Gibbs *et al.* 2006). Bralower (2002) argued that nannofossil assemblages at open ocean Site 690 reflect a change from abundant *r*-mode species (comprising opportunistic species, indicating eutrophic conditions with a well-mixed upper water column and a shallow thermocline) to abundant *K*-mode species (specialized species, indicating oligotrophic conditions with a stratified water column and a deep thermocline) at the onset of the CIE. This interpretation is consistent with that of nannofossil assemblage studies of open marine sites from the Indian Ocean (Tremolada & Bralower 2004), the Pacific Ocean (Gibbs *et al.* 2006) and Tethys (Monechi *et al.* 2000), and supported by model studies (e.g. Boersma *et al.* 1998; Huber *et al.* 2003). However, it appears directly contradicted for Site 690 by observations on accumulation rates of Ba (Bains *et al.* 2000) and Sr/Ca in coccoliths (Stoll & Bains 2003): both suggest increased productivity. Both arguments are in debate: the latter by Bralower *et al.* (2004), the former by (Dickens *et al.* 2003), who suggested that dissociation of methane hydrate (see below) resulted in Ba²⁺ release into the ocean, thus elevating dissolved Ba²⁺ concentrations in the deep sea and causing improved preservation of sedimentary barite. In addition, changes in bottom-water CO₃ (described above) may have had an effect on barite preservation (Schenau *et al.* 2001).

Not many upper Palaeocene to lower Eocene sections contain well-preserved siliceous microfossil assemblages so the response of diatoms and radiolarians to the PETM is not well constrained. Sediment sequences that bear radiolaria commonly do not have a good record through the PETM (Sanfilippo & Nigrini 1998), and the well-preserved PETM assemblage from low-latitude Blake Nose is unique (Sanfilippo & Blome 2001). At that site, the composition of the fauna shows no net, overall change during the PETM, although there is a minor increase in the number of first and last occurrences. In contrast, the influx of several low-latitude taxa at the PETM is observed in New Zealand, suggesting poleward migrations (Hollis *et al.* 2005*a, b*; Hollis 2006).

Diatom records through the PETM are also rare. ODP Site 752 in the eastern Indian Ocean recovered a diatom-bearing PETM succession, but only biostratigraphical and taxonomical work has been done on this material (Fourtanier 1991). A considerable

turnover of the diatom flora at generic and species levels has been observed in sections from the epicontinental sea in Russia, including the appearance of short-lived taxa (Radionova *et al.* 2001; Oreshkina & Oberhänsli 2003). It has been suggested that these turnovers are associated with a more vigorous exchange of surface waters with the Tethys resulting from transgression (Oreshkina & Oberhänsli 2003).

Terrestrial mammals

The PETM stands out as a time of significant changes in terrestrial biota (Fig. 5). Perhaps the most dramatic and best-known of these is the abrupt introduction of four major taxonomic groups to terrestrial mammalian assemblages on the Northern Hemisphere continents at or near the P–E boundary (Gervais 1877; McKenna 1983; Gingerich 1989; Krause & Maas 1990; Smith & Smith 1995; Hooker 1998). The first appearance of the ordinal-level ancestors of modern hoofed mammals (orders Artiodactyla and Perissodactyla), Euprimates (those bearing the complete set of anatomical characteristics uniting modern primates), and a now-extinct family of carnivores (Hyaenodontidae) has long been held by palaeontologists to represent the base of the Eocene in western North America and Europe (Gingerich & Clyde 2001; Gingerich 2006). Recent high-resolution stratigraphic studies demonstrated that they occur within metres of the CIE base at *c.* six sites across the Holarctic continents (e.g. Koch *et al.* 1992, 1995; Cojan *et al.* 2000; Bowen *et al.* 2002; Steurbaut *et al.* 2003; Ting *et al.* 2003).

These first appearances are associated with long- and short-term (transient) changes in terrestrial mammal faunas and initiated a profound modernization of terrestrial mammal communities that were still dominated by archaic forms despite prolific diversification following the Cretaceous–Palaeogene boundary (Alroy *et al.* 2000). The new groups rapidly impacted the communities that they entered, producing significant increases in species richness, average species size, and proportional representation of herbivorous and frugivorous taxa, characteristics of community structure which persisted in early Eocene assemblages from the Bighorn Basin (Clyde & Gingerich 1998) (Fig. 5). The first appearances also provided a seed for longer-term changes in community composition and structure: in the context of longer-term changes in species diversity, the first appearances are overshadowed by rapid post-PETM diversification within the new clades. Other impacts of the PETM on land mammals were transient, including a reduction in average individual body size among both new groups and lineages that ranged through

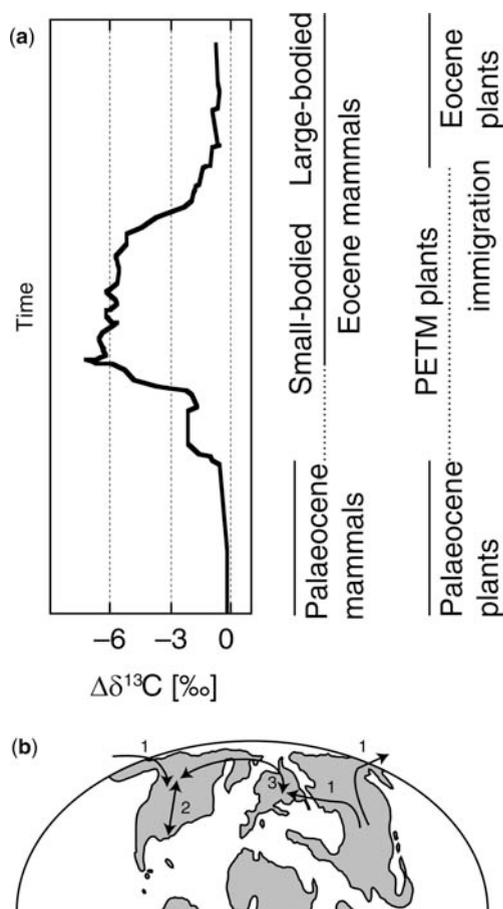


Fig. 5. Patterns of terrestrial biotic change through the PETM. **(a)** Temporal sequence of changes in mammal and plant assemblages, shown relative to the palaeosol carbonate $\delta^{13}\text{C}$ curve for Polecat Bench, Wyoming, USA (carbon isotope values are shown here as anomalies ($\Delta\delta^{13}\text{C}$) relative to the average latest Palaeocene values; after Bowen *et al.* (2006)). **(b)** Spatial pathways of migration thought to have been used by PETM intra- and intercontinental migrants. 1, Directional exchange of mammals and turtles from Asia to North America and/or Europe. 2, Northward range expansion of thermophilic plants from southern North America. 3, Exchange of plant and mammal taxa between North America and Europe, including immigration of plant taxon to North America and homogenization of mammal faunas, including new PETM immigrants.

the Palaeocene–Eocene boundary in the Bighorn Basin (Gingerich 1989; Clyde & Gingerich 1998) (Fig. 5). A significant taxonomic turnover between two groups of faunas assigned to the Bumbanian Asian land mammal age may reflect a shift from transient PETM fauna to a more stable early

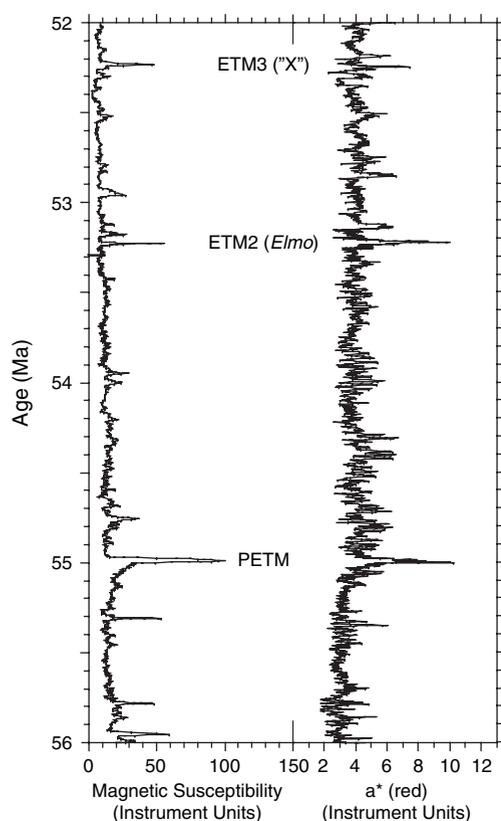


Fig. 6. Magnetic susceptibility and a^* colour reflectance records through the uppermost Palaeocene and lower Eocene at Site 1267, Walvis Ridge (from Zachos *et al.* 2004). The peaks are associated with the PETM and the early Eocene hyperthermal events ETM2 and ETM3. The age model used follows that of Zachos *et al.* (2004), which has recently been updated (Lourens *et al.* 2005; Westerhold *et al.* 2007).

Eocene fauna, and be somewhat analogous to North American faunal changes at the end of the PETM (Ting *et al.* 2003), although the data are at much lower time resolution than those in the Bighorn Basin. No clear equivalent has been proposed for European faunas.

There is near-universal consensus that the abrupt first appearances in early Eocene mammal faunas represent synchronous dispersal of new taxa across Holarctica. Fossil biogeography (e.g. McKenna 1983) and recent studies documenting Arctic Ocean palaeosalinity (Brinkhuis *et al.* 2006; Pagani *et al.* 2006; Sluijs *et al.* 2006) suggest that the Northern Hemisphere continents must have been linked at least intermittently by land bridges during the early Palaeogene, providing high-latitude corridors for faunal exchange.

Warming during the PETM may have allowed mammals previously restricted to lower latitudes to access these intercontinental corridors, resulting in widespread dispersal of the new groups and homogenization of the Holarctic fauna (McKenna 1983; Krause & Maas 1990; Peters & Sloan 2000). A concomitant dispersal event affecting the Holarctic turtle fauna may reflect a similar climate-mediated mechanism (Holroyd *et al.* 2001).

This mechanism provides a compelling link between climate and PETM mammal turnover, but does not address the questions of where, when, or why the new immigrant groups originated. Two models for the origination of these groups have been proposed. Beard and colleagues have argued that the similarity between the early representatives of the new 'PETM' groups and outgroup taxa from the Palaeocene of Asia suggests an Asian origin, and that some primitive Asian representatives of the 'new' clades may be of Palaeocene age (Beard 1998; Beard & Dawson 1999). In contrast, Gingerich has argued that rapid origination of these clades at unspecified locations in response to environmental perturbations associated with the PETM is both possible and plausible (Gingerich 2006).

This debate centres on the issue where and when the missing links between the new PETM groups and their ancestors occurred, and thus it has been difficult to test the competing ideas. The hypothesis for Asian origination, however, presents the testable prediction that the 'new' mammal groups were present in the Palaeocene of Asia. A combination of chemo-, magneto-, and biostratigraphic data shows that Hyaenodontidae were indeed present in Asian Palaeocene faunas (Bowen *et al.* 2002; Ting *et al.* 2003; Meng *et al.* 2004; Bowen *et al.* 2005). Smith *et al.* (2006) argued for a slightly earlier appearance (by *c.* 10–25 ka) of primates in Asia. However, the failure to find ubiquitous support for the hypothesis of Asian origination during the Palaeocene, and recent evidence against other potential loci of Palaeocene origination such as the Indian subcontinent (Clyde *et al.* 2003), has led to renewed interest in the idea that environmental change during the PETM may have spurred the evolution of several important orders (Gingerich 2006).

Terrestrial plants

Palynological and macrofloral remains from the uppermost Palaeocene and lowermost Eocene have revealed no evidence for net long-term taxonomic turnover or long-lasting major changes in community structure associated with the PETM (Jaramillo & Dilcher 2000; Harrington & Kemp 2001; Wing & Harrington 2001; Collinson *et al.* 2003; Crouch *et al.* 2003b; Crouch & Visscher 2003;

Harrington 2003; Wing *et al.* 2003; Harrington *et al.* 2004). These studies documented modest floral change across the P–E boundary, including the introduction of a small number of immigrant taxa (e.g. introduction of some European taxa to North America) and increases in the diversity of floras from the late Palaeocene to early Eocene. Changes in terrestrial floras across the P–E boundary may have in some cases been diachronous and do not stand out as highly anomalous relative to background spatial and temporal taxonomic variation (Harrington *et al.* 2004).

Two recently discovered macrofloral collections of distinctive composition, however, show that major transient changes in the taxonomic composition of floras occurred during the PETM in the Bighorn Basin (Wing *et al.* 2005). These floras document the immigration of thermophilic taxa previously known from the southern United States and adjacent basins of the western United States, and the first appearance of the European immigrant palynospores *Platycarya platycaryoides* later within the PETM. Many early Palaeogene plant taxa underwent major geographic range shifts during the PETM, both within and between continents. These shifts are comparable to floral range shifts at the end of the Pleistocene: in both cases, rapid and plastic reorganization of plant communities occurred in response to climatic and environmental change (Overpeck *et al.* 1992; Jackson & Overpeck 2000; Wing *et al.* 2005).

Summary of biotic response

The response of marine organisms to the PETM was heterogeneous. Benthic foraminifera comprise the only group that underwent significant extinction, potentially related to the increased temperature, although lower oxygen levels, changes in primary productivity or the biological carbon pump, and the corrosiveness of carbonate, may have played a role. Deep-sea ostracode faunas may also reflect this increased corrosivity, but the geographical extent is unclear. In the surface ocean, a global acme of the (sub)tropical dinocyst *Apectodinium* occurred along the continental margins, and has been interpreted as a combination of warming and an increase in trophic level of marginal seas, as supported by neritic lithological, ostracode, benthic foraminifer and nannofossil information. Trophic changes in the open ocean are still debated: planktonic foraminiferal and nannofossil assemblages suggest that relatively oligotrophic conditions existed during the PETM, whereas increased barite accumulation rates and Sr/Ca of nannoplankton (at some sites) have been interpreted as indicative of elevated surface productivity. Benthic foraminifera suggest an increase in food supply to the

sea-floor at some (but not all) open ocean locations, but not necessarily higher surface productivity. Both dinocysts and neritic ostracodes indicate that eustatic sea level rose during the PETM. Finally, extreme morphotypes of several planktonic protist microfossil groups are restricted to the PETM and probably represent ecophenotypes.

The terrestrial biotic record of the PETM demonstrates that climate change induces changes in the geographic distribution of terrestrial organisms. Migration appears to be the dominant mechanism of change within PETM terrestrial ecosystems, not only within the mammal and plant records, but also among early Palaeogene turtle faunas. This shifting of geographic distributions introduced new and unique taxonomic assemblages to PETM terrestrial ecosystems, mainly through addition or substitution of taxa without significant loss or modification of existing groups (the example of transient body-size reduction in North American mammals being an important exception). One of the striking aspects of terrestrial biotic change through the PETM is the lack of evidence for a PETM extinction event within any of the groups studied. This suggests a surprising level of adaptability within terrestrial ecosystems, although many details of the conditions and timing of PETM terrestrial environmental and biotic change remain to be resolved.

Hypotheses on causes and effects of the PETM

We have summarized the broad range of biotic, geochemical and climatic changes associated with the massive release of ^{13}C -depleted carbon into the ocean–atmosphere system during the PETM. A major, ongoing research focus is to develop an integrated understanding of the cause and effect scenarios that brought about these changes, beginning with the carbon release itself. Several hypotheses describing the trigger and source of PETM carbon release have been proposed, and these must be critically evaluated in terms of our knowledge of the event's timing, of PETM carbon cycle changes, and of the biotic and climatic responses to carbon cycle perturbation. As described above, changes in the $\delta^{13}\text{C}$ values of the exogenic carbon pool and widespread dissolution of marine carbonates provide constraints on the magnitude of carbon release (Kennett & Stott 1991; Koch *et al.* 1992; Thomas *et al.* 2002; Zachos *et al.* 2005; Pagani *et al.* 2006). Orbital cycle- and helium-based age models give an order-of-magnitude constraint on the rates of release, which imply large, catastrophic or chronic fluxes of carbon occurred over *c.* 10^4 years. Global warming of 5–6 °C implies large,

sustained increases in atmospheric greenhouse gas levels (Dickens *et al.* 1995; Dickens 2001a). Critically, the existence of similar events in the early Eocene, including the ETM2 (Lourens *et al.* 2005) and ETM3 (Röhl *et al.* 2005), demonstrates that the PETM was not a unique event, and suggests ties between the initiation of these events and orbital cyclicity (Lourens *et al.* 2005).

Many proposed hypotheses cannot satisfy the latter constraint (Lourens *et al.* 2005). In theory, climatic extremes on a long-term gradual climate trend are expected to occur during eccentricity maxima, because at such times seasonal contrasts on both hemispheres are maximized, so that critical climate thresholds are likely to be surpassed. The climate of the late Palaeocene through early Eocene followed a long-term warming trend, as evidenced by benthic foraminifer $\delta^{18}\text{O}$ (Zachos *et al.* 2001) and many biotic proxies (e.g. Haq & Lohmann 1976; Hallock *et al.* 1991; Bujak & Brinkhuis 1998). This warming may have been caused by increasing atmospheric CO_2 levels through high volcanic activity in the North Atlantic Igneous Province (Eldholm & Thomas 1993; Schmitz *et al.* 2004; Thomas & Bralower 2005; Maclennan & Jones 2006) and/or along Indian Ocean spreading zones (Cogné & Humler 2006). The late Palaeocene is also characterized by a long-term decrease in benthic foraminiferal and bulk carbonate (and likely global exogenic) $\delta^{13}\text{C}$ after the major positive event in the mid-Palaeocene (Corfield & Norris 1998; Zachos *et al.* 2001). The eccentricity maxima superimposed on these trends could have comprised thresholds for transient events and resulting climate change.

Spectral characteristics of magnetic susceptibility and colour reflectance records from Walvis Ridge show that the PETM, ETM2 (Lourens *et al.* 2005) and ETM3 (Röhl *et al.* 2005), all transient global greenhouse warming events, started during short (100 kyr) and long-term (405 kyr) eccentricity maxima, suggesting an insolation-driven forcing mechanism (Lourens *et al.* 2005). Westerhold *et al.* (2007), however, using similar statistical treatments of high-resolution Fe and red/green (a^*) records of the same Walvis Ridge sites, argued that there were two short-term eccentricity cycles less between the PETM and ETM2 than indicated in (Lourens *et al.* 2005), with the implication that the PETM and ETM2 do not correspond exactly to a maximum in the long-term eccentricity cycle, but to one of the short-term (100 kyr) eccentricity extremes superimposed on the long-term cycles. A definite clue to a possible orbital-based forcing mechanism is complicated, however, due to large uncertainties in available astronomical computations for the late Palaeocene to early Eocene (see Lourens *et al.* 2005). A more complete insight into

possible forcing mechanisms may become available when a new generation of astronomical solutions is launched (Laskar, pers. comm., 2006).

An important consequence of the hypothesis that the forcing of the PETM and similar (but less severe events) was orbitally based is that triggering mechanisms involving unique tectonic, volcanic or cosmic events can be excluded as the cause of the PETM. Proposed singular events include a comet impact (Kent *et al.* 2003; Cramer & Kent 2005), explosive volcanism (Bralower *et al.* 1997; Schmitz *et al.* 2004), intrusion-forced injection of thermogenic methane (Svensen *et al.* 2004), tectonic uplift-forced methane hydrate release (Maclennan & Jones 2006), sub-lithospheric gas explosions (Phipps Morgan *et al.* 2004), and tectonically forced desiccation of epicontinental seas (Higgins & Schrag 2006). Regardless of the specific orbital parameter association of the PETM, ETM2 and ETM3 and possible additional hyperthermal events, the simple fact that there were multiple events within the late Palaeocene and early Eocene implies a non-singular trigger as their cause.

What type of carbon-release scenarios could be triggered by orbital fluctuations in a greenhouse world and lead to rapid global warming and biotic change? In the present-day situation, non-anthropogenic carbon reservoirs that can inject the required amount of ^{13}C -depleted carbon needed to generate the CIE in the atmosphere and ocean on the required short timescale are scarce (Dickens *et al.* 1995, 1997). One potential reservoir is formed by methane hydrates, although the size of the present hydrate reservoir is the subject of discussion (Milkov 2004). The methane incorporated in the hydrates is produced by anoxic bacterial decomposition (average $\delta^{13}\text{C}$ of *c.* -60‰) or thermogenic breakdown (average $\delta^{13}\text{C}$ of *c.* -30‰) of organic matter (Kvenvolden 1988, 1993). In the present ocean, these hydrates are stable along continental slopes at relatively high pressure and low temperatures (at high latitudes at the surface, at lower latitudes below a few hundreds of metres depth) and they have been argued to dissociate when pressure falls or temperature rises (MacDonald 1990; Xu *et al.* 2001). During the much warmer latest Palaeocene, hydrates were stable at deeper-water depths (e.g. below *c.* 900 m) (Dickens *et al.* 1995), suggesting that the reservoir was smaller than at present (Buffett & Archer 2004). However, methane hydrates might have been present at greater depths than today (Dickens 2001b) if more organic matter was present further away from the continents than nowadays, perhaps in conjunction with lower oxygen content of the bottom waters resulting from higher temperatures, as suggested by benthic foraminiferal assemblages (Thomas & Zachos 2000; Thomas 2007). In addition to

concerns about the standing volume of methane hydrate at the time of the PETM, the rate of replenishment of these reservoirs is problematic if the CIEs related to ETM2 and ETM3 are also to be attributed to hydrate dissociation (Fehn *et al.* 2000). This might imply that a significant fraction of the hydrate reservoir was maintained through the PETM and ETM2, but would compound discrepancies between the implied and predicted hydrate inventories.

Dissociation of methane clathrates along continental slopes has been invoked to explain the CIE and part of the climatic warming (Dickens *et al.* 1995; Matsumoto 1995). In the present atmosphere, CH₄ is oxidized to CO₂ within a decade. The atmospheric residence time of methane could increase at high atmospheric concentrations of this gas, but even this longer residence time has been argued to be only about one to two centuries (Schmidt & Schindell 2003). The relatively short residence time of CH₄ implies that the long-term (10⁴ years and more) climate effects of methane release would result from CO₂ forcing after the oxidation of methane in the atmosphere and/or oceans. As already pointed out by Dickens *et al.* (1997), the radiative forcing of the CO₂ resulting from the injection of *c.* 2000 Gt of biogenic methane is not enough to explain the magnitude of PETM climate warming (Dickens *et al.* 1997; Schmidt & Schindell 2003; Renssen *et al.* 2004; Archer 2007).

In their study to assess terrestrial and marine carbon burial rates, Kurtz *et al.* (2003) use the coupling between the carbon and sulphur cycles to quantify the very high rates of continental organic carbon burial through the middle Palaeocene qualitatively indicated by the global abundance of Palaeocene coals. These authors suggest that rapid oxidation (burning) of terrestrial organic carbon, in their words '*global conflagration*', could have at least contributed to the CIE and climate warming. Terrestrial organic matter (*c.* -30‰) is much less ¹³C-depleted than biogenic methane hydrates, implying that much more carbon would have entered the atmosphere and ocean and provided a greater potential radiative forcing than that resulting from the release of methane hydrates (Kurtz *et al.* 2003; Higgins & Schrag 2006). The greatest challenge to the peat-burning hypothesis is the lack of direct evidence for a massive loss of continental organic carbon at the PETM. High concentrations of macroscopic charcoal have been recorded locally at the PETM (Collinson *et al.* 2003), but these remains do not support a scenario of peat burning (Collinson *et al.* 2006). Huge deposits of upper Palaeocene peat deposits are still found today (e.g. Collinson *et al.* 2003), raising questions as to how these deposits survived the '*global conflagration*' and whether it is plausible that the late

Palaeocene continental organic carbon reservoir contained sufficient, unseen organic-rich deposits to account for the PETM.

Problems thus still exist for the hypotheses of clathrate dissociation and continental organic carbon burning, although both are potentially climatically induced and thus could be associated with orbital forcing. An orbitally forced mechanism to trigger dissociation of methane hydrates might be found in temperatures of intermediate waters, which increased due to warming of their high-latitude source regions or due to orbitally forced changes in circulation of deep waters. An orbitally forced trigger for massive burning of peat could be found in the occurrence of droughts in regions with large peat deposits. To invoke such mechanisms as a cause of the PETM with confidence, however, requires better documentation of the character, trends and dynamics of late Palaeocene climate, including its response to orbital cycles.

Thus, integration of available information on carbon cycle, climate change, biotic response as well as the timescale involved in the PETM still leaves us short of a clearly supported, all-encompassing cause-and-effect scenario for the PETM. Data on atmospheric CO₂ and CH₄ (although no proxy has been developed yet for the latter) concentrations through the event could help in evaluating the form and magnitude of injected carbon, which in combination with an improved understanding of the CIE magnitude would clearly distinguish between the hydrate and peat-burning hypotheses. As the causes and mechanisms of carbon release become clearer, focused analysis of the cascade of effects of this perturbation should eventually lead to the identification of mechanisms and feedbacks through which climate, environmental and biotic change occurred (Bowen *et al.* 2004, 2006; Sluijs 2006). More-detailed studies of ETM2 and ETM3 are required to confirm that these events are similar in nature to the PETM and the degree to which these events are different from 'background climate' trends. Furthermore, comparative study of these events should help to resolve the importance of different climatic boundary conditions on the nature and magnitude of abrupt, transient, carbon-induced greenhouse events, improving our understanding of the dynamics of past hyperthermal events and their relevance to understanding climate change today.

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