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Response of marine ecosystems to deep-time global warming: a synthesis of biotic patterns across the Paleocene-Eocene thermal maximum (PETM)

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Abstract

This paper provides a synthesis of the long- and short-term response of various marine ecosystems (deep oceans, pelagic, pelitic shelves and carbonate platforms) to the Paleocene-Eocene thermal maximum (PETM) and its broader paleoclimatic and paleoceanographic context. Despite the severity and sudden onset of global warming the PETM is not marked by a mass extinction event. The only major extinction is among bathyal to abyssal calcareous benthic foraminifera, including some calcareous agglutinated taxa. Coexisting non-calcareous deep water agglutinated foraminifera, ostracodes and trace fossils show prominent changes in composition, population structure and biodiversity, but there is no clear evidence of global extinctions. Except for the deep-sea calcareous benthic foraminiferal record, the PETM is best classified as a migration and origination event and was instrumental in kick-starting various short- and long-term evolutionary innovations in marine microfossil lineages. In pelagic and shallow shelf ecosystems, migration and origination during and after the PETM appears to precede extinction in the aftermath of the PETM. The response of most marine invertebrates (mollusks, echinoderms, brachiopods) to paleoclimatic and associated environmental changes (e.g., acidification, deoxygenation) during the PETM is virtually unknown as continuous high-resolution data of these groups spanning the PETM are unexplored and possibly not or hardly preserved. Yet information on these groups is required in order to improve assessments of the value of biotic records to deep-time global warming in the context of current climate change. In contrast, the relatively well-established response of Tethyan reef systems to late Paleocene-early Eocene global warming may provide a potential analog to a - possibly bleak - future of present-day coral reefs.

1. Introduction

Patterns of global climatic and biotic change in the geologic record can provide a valuable basis for assessing present-day biodiversity changes in response to global warming. The Paleocene-Eocene thermal maximum (PETM at ~56 Ma, duration ~200 k.y.; Hilgen et al., 2010; Murphy et al., 2010; Charles et al., 2011) is one of the most dramatic global warming events of the Cenozoic and is associated with some of the most prominent turnovers of marine and terrestrial biota. The best documented turnovers are the extinction of 40-60% of deep-sea benthic foraminifera (e.g., Beckmann, 1960; von Hillebrandt, 1962; Thomas, 2007), the onset of nummulitid proliferation along carbonate platforms of the Tethys (e.g., Hottinger, 1960; Scheibner and Speijer, 2008) and the rise of primates and hoofed animals (e.g., Cope, 1882; Wortman, 1896; Gingerich and Clyde, 2001; Gingerich, 2006). Although these macroevolutionary events have a very long research history, their tight connection to climate change was revealed only during the last two decades (e.g., Kennett and Stott, 1991; Koch et al., 1992, 1995; Orue-Extebarria et al., 2001). Together, these biotic turnovers indicate that from the continent to the deep ocean the biosphere was perturbed by rapid climate change, leaving a mark on long-term macro-evolutionary patterns. Less extreme turnovers and short-term responses are observed in other fossil groups. Two recent papers reviewed a wide range of aspects related to the PETM, such as changing climate, biotic change, the carbon cycle and duration of the PETM (Sluijs et al., 2007; McInerney and Wing, 2011). In the current synthesis, we focus specifically on the long- and short-term response of various marine ecosystems (deep oceans, pelagic, pelitic shelves and carbonate platforms) and their constituents to the PETM and its broader paleoclimatic and paleoceanographic context. We show that this natural rapid global warming experiment and its associated environmental changes led to extinctions in the deep-sea and to the wipe out of coral reef ecosystems. At the same time, the PETM caused numerous cross-latitudinal migration patterns and provided opportunities for some taxonomic groups to dominate and diversify leading to renewed and diverse ecosystems during the early Eocene.

2. Evolution of late Paleocene to early Eocene ecosystems and biota

2.1 Pelagic ecosystems

Pelagic ecosystems seem only mildly perturbed during the PETM, as most common late Paleocene species of planktic foraminifera, calcareous nannofossils, dinocysts, radiolarians, and diatoms appear to range well into the Eocene. Consequently, the currently defined Paleocene-Eocene (P-E) boundary at the base of the PETM (both commonly delineated by the base of the carbon isotopic excursion – CIE) was not re-

solved in former biozonations and pinpointing this boundary in low resolution records proved difficult. Yet, numerous recent high-resolution studies revealed that most pelagic groups underwent prominent but often only transient changes during the PETM. The most conspicuous pattern is that several tropical to subtropical planktic taxa diversified and briefly expanded their latitudinal distribution towards the poles (Fig. 1). This applies to species of *Morozovella* and *Acarinina* (planktic foraminifera; Thomas and Shackleton, 1996; Pardo et al., 1999), to representatives of *Apectodinium* (dinoflagellate cysts; Crouch et al., 2001; Sluijs et al., 2006) and to various radiolarian taxa (Hollis, 2006).

Earlier biogeographic studies demonstrated incursions of low-latitude assemblages of calcareous nannofossils and planktic foraminifera into higher latitudes (up to 43°N) in the latest Paleocene and early Eocene Atlantic (Haq et al. 1977). These could reflect the longer-term warming during this time interval, but may also have included data representing the PETM before it was known as such. A combination of oceanic warming, possibly in combination with changing surface currents provoked the expansion of warmth-loving taxa during the PETM that were otherwise restricted to the lower latitudes. Changing surface currents may also have facilitated high-latitude southern ocean marine diatoms to migrate into northern hemisphere basins in Central Asia (Oreshkina and Aleksandrova, 2007). It should be noted, however, that some migration patterns are not primarily triggered by temperature changes associated with the PETM. This is shown by middle- to high-latitude records of *Apectodinium* in the New Jersey Coastal Plain (Wilson Lake and Bass River) and at ODP Site 1172, East Tasman Plateau (Sluijs et al., 2007, 2011). In these records the *Apectodinium* acme that is generally considered a characteristic of the PETM (Crouch et al., 2001) started some 5 to 100 kyr before the onset of the CIE and the PETM (Sluijs et al., 2011). This early acme indicates that other factors than temperature alone controlled the distribution of *Apectodinium*. This genus is also considered to be tolerant to low salinity and linked to (seasonally?) high food levels, but considering that the combination of these conditions are not unique to the PETM, there must be some additional factor(s) why *Apectodinium* bloomed during and shortly before the PETM (Sluijs and Brinkhuis, 2009).

Changing environmental conditions also set the stage for some short- and long-term evolutionary innovations amongst (sub)tropical planktic foraminiferal genera. The PETM is characterized by common occurrences of short-ranged taxa like *Morozovella allisonensis*, *Globanomalina luxorensis*, and several *Acarinina* species. It remains uncertain, whether the specific environmental conditions during the PETM enabled this speciation (e.g., Kelly et al., 1996) or that the PETM only facilitated a wider geographic expansion of some of these taxa. *Morozovella allisonensis* and *A. multicamerata* have so far only been recorded from sediments spanning the PETM and seem to evolve during the PETM (Kelly et al., 1996; Guasti and Speijer, 2008). However, rare occurrences of *Acarinina sibaiyaensis* and *G. luxorensis* have been observed in the upper Paleocene in Egypt. These taxa became common to abundant components of PETM assemblages in Egypt and elsewhere

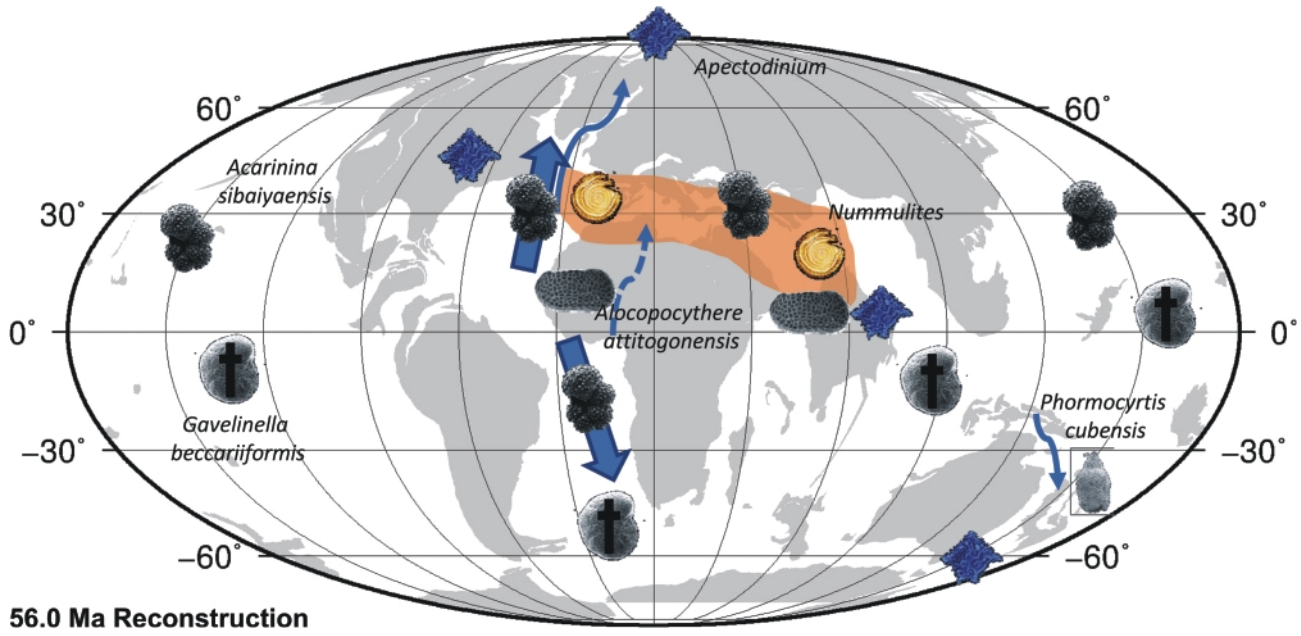

Figure 1: Icons of biotic change during and after the PETM. Plate-tectonic reconstruction based on the ODSN database (http://www.odsn.de/odsn/services/paleomap/paleomap.html): *Alocopocythere attitogonensis* characterizes intensified migration of West African taxa to the Tethys, in part through the Trans-Saharan Seaway. *Gavelinella beccariiformis* stands for the extinction of numerous Velasco-type deep-sea benthic foraminifera. *Acarinina sibaiyaensis* reflects speciation and poleward migration of tropical-subtropical *Acarinina* and *Morozovella*. *Apectodinium* (image E. Crouch) is iconic for the speciation and poleward migration (even up to the North Pole) of tropical-subtropical *Apectodinium*. *Nummulites* represents the rise of tropical-subtropical *Nummulites* and *Alveolina* and the simultaneous downfall of low to mid latitude coralgal reefs in the Tethys (orange shaded area). *Phormocyrtis cubensis* (image C. Hollis) marks poleward radiolarian migration.

(Speijer and Samir, 1997; Guasti and Speijer, 2008). During or shortly after the PETM, the planispiral *Pseudohastigerina wilcoxensis* evolved from the low-trochospiral *G. luxorensis*, marking the onset of the successful radiation of the Eocene *Pseudohastigerina* lineage (Speijer and Samir, 1997; Olsson and Hemleben, 2006).

In contrast to planktic foraminifera, calcareous nannofossils show somewhat enhanced extinction associated with the PETM (Aubry, 1998), most notably at the onset and during the first 70 kyr of the PETM (Gibbs et al., 2006). This pertains to species of at least 12 genera, such as *Biscutum*, *Fasciculithus*, and *Prinsius*. Yet, extinction during the PETM mainly involved relatively rare species (<1% abundance in pre-PETM assemblages) and it was suggested that these species lived closer to their ecological limits. Several genera, most notably the common Paleocene genus *Fasciculithus*, became fully extinct within 1 myr following the onset of the PETM (Aubry, 1998). Niches that were vacated during the PETM were rapidly filled by newly evolving and subsequently common (early) Eocene genera such as *Blackites*, *Rhomboaster/Tribrachiatus* and *Pontosphaera* (Aubry, 1998; Gibbs et al., 2006). The early stages of the PETM are also characterized by several asymmetrical ('malformed') discoasterids such as *Discoaster araneus* and *D. anartios* (e.g., Mutterlose et al., 2007; Raffi et al., 2009). The resulting *Rhomboaster-Discoaster araneus* assemblage is a quantitatively minor but distinct suite of tropical taxa that is largely restricted to the PETM (Kahn and Aubry, 2004; Raffi et al., 2005; Mutterlose et al., 2007). It is particularly abundant in neritic deposits spanning the PETM at the Dababiya GSSP section (Aubry et al., 2007).

2.2 Deep-sea benthic ecosystems

The benthic foraminiferal extinction event (BEE) in the deep sea was first recorded as a local phenomenon in Trinidad (Beckmann, 1960) and Austria/southern Germany (von Hillebrandt, 1962). Tjalsma and Lohmann (1983) demonstrated the global significance and severity of the extinction event, considering it to be "the most dramatic event in the evolution of Late Cretaceous and Cenozoic deep-water benthic foraminifera". Local extinction rates during the PETM are generally estimated between 40 and 60% of all taxa disappearing at the onset of the Eocene. As such, the PETM terminated the long-term dominance of the Velasco type fauna (Tjalsma and Lohmann, 1983), which in fact was a deep-sea fauna that survived from the Cretaceous into the Paleocene, basically unaltered. For this reason, the BEE actually marked the end of the "Cretaceous" deep-sea fauna (Thomas, 2007), 10 million years after the nearly complete wipe out of Cretaceous planktic foraminifera at the Cretaceous-Paleogene boundary. The BEE involved one of the most common cosmopolitan taxa, the iconic *Gavelinella beccariiformis* (Fig. 1) and the last representatives of typical Cretaceous lineages such *Neoflabellina jarvisi* and *Bolivinoides delicatulus*. These common Paleocene deep-sea taxa disappeared from oceanic basins as well as from deep continental margin basins, giving way to an Eocene fauna characterized by many survivors, such as *Nuttallides truempyi*, *Oridorsalis umbonatus*, *Tappanina selmensis*, *Aragonia aragonensis*, *Bulimina trinitatensis* and *Abyssamina* spp. (e.g., Thomas, 1998). Also the first representative(s) of the modern *Uvigerina* seem to appear shortly after the PETM (unpublished data of S. D'haenens on DSDP Hole 401).

In contrast to calcareous deep-sea taxa, deep water agglutinated foraminifera (DWAF or flysch-type agglutinated foraminifera) were not globally pushed to extinction during the PETM (Kaminski et al., 1996). Whereas records from Trinidad show the disappearance of about 34% of the agglutinated taxa (but these are largely the calcareous-cemented forms; Kaminski et al., 1988), abyssal localities in Morocco, Poland and the Norwegian Sea (Nagy et al., 1997; Galeotti et al., 2004; Kaminski and Gradstein, 2005) show few consistent extinctions. Whereas some distinct well-known taxa (e.g., *Remesella varians* and possibly *Rzehakina epigona*) seem to become extinct during the PETM, this warming event is rather manifested by pronounced changes in abundance, size, diversity, and shifts in the proportions of agglutinated foraminiferal morphogroups (Kaminski et al., 1996; Bak et al., 1997; Nagy et al., 1997; Bak, 2004; Galeotti et al., 2004). The most striking feature among DWAF is the blooming of the *Glomospira* assemblage, consisting of various genera of coiled tubular genera, during and shortly after the PETM in Tethyan and North Atlantic abyssal settings. The widespread dominance of the *Glomospira* assemblage during the early Eocene is variously interpreted as a result of warm and/or oxygen-poor and/or extremely oligotrophic deep-sea conditions (e.g., Kaminski et al., 1996; Bak, 2004; Kaminski and Gradstein, 2005).

There was little turnover in bathyal to abyssal ostracodes (Benson, 1990; Coles, 1990; Honigstein and Rosenfeld, 1995; Guernet and Molina, 1997). Only three studies, however, address the response of ostracode assemblages to the PETM in some detail. Short-term ecologic effects in response to enhanced food fluxes to the deep-sea floor were reported by Steineck and Thomas (1996) on ODP Site 689 (Southern Ocean; paleodepth 1100 m). Community structure data from the nearby ODP Site 690 (paleodepth 1900 m; Thomas, 1998) rather surprisingly show that the ostracode communities indicate less ecological stress during the PETM than prior to this event (Webb et al., 2009). In contrast, the only other detailed deep-sea ostracode record across the PETM from DSDP Site 401 (northeast Atlantic; Yamaguchi and Norris, 2012) documents an increase in ecological stress during the PETM (strong dominance by *Krithe crassicaudata*), but provides no evidence for excursion taxa or extinctions either. These limited observations indicate that there is no general ecologic and taxonomic collapse like observed in deep-sea benthic foraminiferal communities from the same locations and elsewhere. Beyond these two study regions, the response of deep-sea ostracodes to the PETM is largely *terra incognita*.

Other deep-sea benthic organisms are extremely rare in deep-sea deposits spanning the PETM and provide basically no record of late Paleocene to early Eocene biodiversity. Yet,

traces of macro-invertebrates have been studied recently in bathyal sequences exposed in New Zealand and Spain (Nicolo et al., 2010; Rodriguez-Tovar et al., 2011). Both sequences show well-developed burrowing communities, composed of e.g., *Chondrites* and *Zoophycos*, below and above the PETM, indicating oxic conditions and normal benthic food availability. During the early part of the PETM, the trace fossil producers disappeared rapidly and subsequently gradually returned. Based on these data it cannot be judged whether a taxonomic turnover amongst trace fossils occurred or not. Yet, these data are in line with the benthic foraminiferal record that sea-floor communities were exposed to stressed conditions, including dysoxia, temperature rise, ocean acidification and changes in food supply (Nicolo et al., 2010; Rodriguez-Tovar et al., 2011).

2.3 Epicontinental benthic ecosystems: pelitic basins

Studies on middle to upper bathyal sequences exposed on land showed that the PETM also affected shallower benthic foraminiferal assemblages consisting of a mixture of deep sea elements of the Velasco-type fauna and those of the neritic Midway-type fauna. The extinction percentage (loss of Paleocene taxa) in these deep deposits is also similar (40-50%; Speijer et al., 1995). Extinction percentages in Tethyan shelf basins are considerably lower than in the deep sea, ~25% at outer neritic (~200 m) depths and decreasing further towards shallower depths (Speijer et al., 1995). *Angulogavelinella avnimelechi* is a characteristic outer neritic to upper bathyal species that became extinct during the PETM. In Egypt, the basin-wide spread of anoxia during the PETM triggered downslope migrations of transient benthic faunas dominated by a few opportunistic shallow water taxa (e.g., *Anomalinoides aegyptiacus*). In Tethyan middle to inner neritic deposits in Tunisia, the composition of benthic foraminiferal assemblages is strongly influenced by sea-level changes and variations in nutrients and oxygenation, so that the amount of turnover cannot be assessed (Stassen et al., 2012a).

The New Jersey continental margin provides one of the few other regions yielding neritic records spanning the PETM in a pelitic facies with calcareous microfossils. Compared to the Tethyan shelf, extinction levels are very low as only *Gavelinella beccariiformis* became extinct at the onset of the PETM. The PETM triggered a temporary bloom of opportunistic species (e.g., *Tappanina selmensis* and *Pulsiphonina prima*) possibly as the result of river induced shelf eutrophication (Stassen et al., 2012b). Merely temporary assemblages changes are observed and long-term change is difficult to assess because of multiple unconformities in the lower Eocene. Yet it seems that along the southern Tethys and American North Atlantic shelf, the recovery of neritic benthic assemblages followed similar pathways (Stassen et al., 2012c).

Quantitative ostracode records from Tethyan neritic deposits in Egypt and Tunisia reveal paleoecologic changes indicative of changes in sea level, oxygenation and trophic conditions associated with the PETM (Speijer and Morsi, 2002; Morsi et al., 2011). Additionally, the data suggest a long-term turnover of Tethyan margin ostracodes (1-2 m.y.), punctuated during the PETM. This turnover is characterized by gradual replacement of long-ranging taxa typical of the Paleocene South Tethyan type fauna (e.g., *Mauritsina*) by new, immigrating taxa constituting the Esna type Fauna (Bassiouni and Luger, 1990). Immigrant taxa invaded the Tethyan epicontinental basins from West Africa, with migration routes through the Trans-Saharan seaway (only shallow water taxa) or along the African continental margin. Similar to a Tunisian inner neritic to coastal record (Morsi et al., 2011), data from India show a complete turnover from Paleocene to Eocene assemblages (Bhandari, 2008), suggesting large biofacial shifts in very shallow settings, probably triggered by sea-level and associated changes (Morsi et al., 2011). In all areas where the ostracode record of the PETM was studied in some detail, various species of *Alocopocythere* dominated just prior to or during the PETM (Speijer and Morsi, 2002; Bhandari, 2008; Morsi et al., 2011).

Neritic Tethyan marine sequences spanning the PETM have been extensively studied for foraminifera and ostracodes, but occasionally also contain beds with numerous macro-invertebrates such as bivalves, gastropods, nautiloids, brachiopods and solitary corals, sometimes with shell preservation, but mostly preserved as limonitic or hematitic molds (unpubl. field obs.). So far, this material has not been studied in relation to the PETM. The Atlantic coastal plain (Virginia, Maryland) outcrops yield rich mollusk beds in the upper Paleocene and slightly less rich in the lower Eocene. However, the interval spanning the PETM is situated within a clay unit (Marlboro clay) and contains hardly any calcareous fossils at all (Ward, 1985; Gibson and Bybell, 1991). Similarly, the Gulf Coastal Plain provides rich mollusk records of Paleocene and Eocene age, yielding long term records of faunal turnover with extinction rates up to 97% (Dockery, 1998). Yet, the changes in mollusk assemblages were suggested to be tightly connected to sequences induced by sea-level fluctuations (Dockery, 1998), although a recent compilation of mollusk Gulf Coast data rather suggests that temperature (especially seasonal range and minimum temperature) is found to significantly influence both origination and extinction, and exerts a much stronger influence than sea level (Sessa et al, 2011). This study also revealed that extinction rate was relatively unchanged across the Paleocene-Eocene transition, although origination rate significantly dropped, indicating a possible effect of the PETM at this level of resolution. Yet, there are currently no marine invertebrate faunas known from the PETM in the Gulf Coastal Plain, Atlantic Coastal Plain, or Tethyan margin, so that the relation between mollusk distributions and global change during the PETM cannot be assessed.

2.4 Epicontinental benthic ecosystems: carbonate platforms

The vast accumulation of nummulite shells in the warm shallow seas of the early Eocene Tethys has been recognized since the early days of geology. The first systematic research

outlining the clear differences between late Paleocene larger foraminiferal assemblages characterized by relatively small sized species, and early Eocene assemblages, characterized by large shell sizes and adult dimorphism dates back already half a century (Hottinger, 1960). However, it was realized only a decade ago that this turnover did not occur during the late Paleocene, but that it correlated with the PETM (Orue-Extebarria et al., 2001; Pujalte et al., 2003; Scheibner et al., 2005). In the western Tethys several index taxa of larger foraminifera characterize uppermost Paleocene assemblages: *Hottingerina lukasi*, *Glomalveolina* spp., *Miscellanea* spp., and *Ranikothalia* spp.. Lowermost Eocene assemblages consist of abundant *Alveolina* spp., *Nummulites* spp., *Orbitolites* sp., *Opertorbitolites* sp. and the absence of *H. lukasi*, *Miscellanea* spp., and *Ranikothalia* spp. (Scheibner and Speijer, 2009). However, some regional differences occur: the eastern Tethys (Indian subcontinent) shows that *Miscellanea* spp. and *Ranikothalia* spp. still thrive at the beginning of the Eocene whereas *Nummulites* spp. and *Alveolina* spp. initially remain absent or subordinate (Afzal et al., 2011).

Besides larger foraminiferal turnover from the late Paleocene to early Eocene, Tethyan carbonate platforms experienced another fundamental change. During the latest Paleocene carbonate platforms, essentially made up of coralline frameworks and calcareous algae (coralgal reefs), had almost completely disappeared from the low latitudes (up to 20°N), giving way to larger-foraminifera dominated platforms (Scheibner and Speijer, 2008). Consequently, these coralgal reefs had become restricted to their mid-latitude range (~30-40°N) in southern and central Europe. Scheibner and Speijer (2008) hypothesized that this biogeographic contraction to higher latitudes was a response to latest Paleocene gradual warming prior to the PETM. Eventually, during the PETM, Tethyan coralgal reefs also disappeared from their northernmost refuges, being replaced by nummulitid-alveolinid dominated platforms throughout the Tethys (Fig. 1). High sea-surface temperatures are considered the main driver behind the near extinction of framework building corals and delimiting their symbiosis with zooxanthellae, similar to modern coral bleaching. Yet, also ocean acidification and eutrophication of the shelves during the PETM may have been additional key parameters hampering the growth of coralgal reefs (Scheibner and Speijer, 2008; Kiessling and Simpson, 2011). Based on an analysis of the PaleoReefs Database, Kiessling and Simpson (2011) concluded that the early Eocene marks one of five global metazoan reef crises (also late Devonian, early Triassic, early Jurassic and late early Jurassic), during which reef builders strongly suffered and leading to a strong reduction in the total volume of metazoan-based (e.g. corals) reefs. These results are conformable with the analysis of Scheibner and Speijer (2008) and provides significant new insight compared to a previous analysis of total reef volume through the Phanerozoic (Flügel and Kiessling, 2002) in which the early Eocene reef crisis went unnoticed. The difference between the two Phanerozoic reef studies is caused by the distinction between protozoan reef volumes (e.g., larger foraminifera-dominated platforms as in the early Eocene) and volumes represented by frame-building metazoan reefs.

In another recent compilation study detailing the distribution, diversity and paleoecology of reef- and non-reef building corals, Zamagni et al. (2012) confirm the Paleocene to early Eocene progressive decline of reef-builders. Yet, because overall coral diversity only slightly decreased and non-reef building corals managed to colonize a wide variety of shallow marine environments these authors propose that changing ocean chemistry, enhanced pCO_2 levels and high nutrient levels are the critical parameters for the decline in coralgal reef distribution and not the global warming itself. This interpretation, however, does not readily provide an explanation for the observed latitudinal contraction of coralgal reefs as indicated by Scheibner and Speijer (2008). Clearly, resolving the causes of coralgal reef decline as well as providing better constraints on the timing of the PETM and other environmental changes in platform systems will require further focused multi-parameter case studies on individual platform sequences, rather than more literature and database compilations and analyses.

3. Discussion

3.1 Migration patterns

The PETM is characterized by various migration patterns. Most prominent is the poleward expansion of some dinocyst groups, particularly the genus *Apectodinium* and to a lesser extent species of the planktic foraminifera *Morozovella* and *Acarinina*, as well as some radiolarian taxa (Fig. 1). This appears to be directly linked to the warming of surface waters and possibly changing surface currents (e.g. Sluijs et al., 2007). However, an additional factor for the blooming of *Apectodinium* (e.g. *A. augustum*) is the enhanced input of nutrients from the land through runoff, a phenomenon observed or interpreted along many continental margins (Crouch et al., 2001; Sluijs and Brinkhuis, 2009) and the migration of this group appears to start shortly (5-100 ky) before the PETM (Sluijs and Brinkhuis, 2009; Sluijs et al., 2011). Migration patterns amongst platform organisms show a gradual replacement of reef-building corals, predominantly by larger foraminifera (Scheibner and Speijer, 2008). This occurred in low latitudes (up to 20°N) prior to the PETM and progressed to higher latitudes during and after the PETM. The loss of hermatypic corals possibly resulted from gradual warming of the tropics and destruction of the sensitive interaction between corals and their symbionts by thermal stress (Scheibner and Speijer, 2008). It remains to be investigated whether reef-building corals found refuge at even higher latitudes or that they disappeared altogether, only to reappear at lower to middle latitudes in the late Eocene.

The above migration patterns can be considered to be at least in part thermally driven. Migration patterns observed in Tethyan ostracode assemblages, characterized by increasing numbers of invading West-African (Atlantic) taxa, however, are probably only indirectly linked to global warming during

the PETM, as the thermal gradient between West and North Africa was limited (Tindall et al., 2010). In addition, the west-northeast migration process already started prior to the PETM and continued afterwards. Possibly the Trans-Saharan seaway played a key role in this process as shallow-water taxa could migrate across the African craton during times of high sea level prior to and during the PETM (Barsotti, 1963; Morsi et al., 2011). Sea-level rise during the PETM may have been instrumental in the higher rate of overall faunal change observed in Egyptian records (Speijer and Morsi, 2002).

3.2 Extinction and recovery patterns

The PETM is not classified as a mass extinction, since extinction rates above background levels are restricted to just a few taxonomic groups, particularly the calcareous benthic foraminifera of the deep sea, including some calcareous agglutinated taxa (e.g. Tjalsma and Lohmann, 1983). Among the pelagic groups and deep-sea ostracodes, relatively few taxa became extinct during the PETM, whereas extinctions of larger foraminifera and continental margin ostracodes progressed through punctuated replacement during the PETM superimposed on long-term trends towards Eocene fauna's.

Smaller benthic foraminifera from the shallow continental margin occupy an intermediate position on the scale of extinction, with a distinct but limited number of extinctions, particularly towards greater depths along the Tethys (Speijer et al., 1995), but very little change (only the extinction of *G. beccariiformis*) along the West Atlantic margin (Stassen et al., 2012c).

A striking contrast is provided by the very limited taxonomic turnover in the pelagic groups compared to the major extinction of the deep-sea foraminifera. Apparently, widespread adverse conditions prevailed throughout the global deep ocean (low oxygen, elevated temperature, acidification…) and there was little or no refuge for numerous deep-sea taxa. At the same time, however, warming of surface waters triggered strong ecologic responses but relatively minor turnover to pelagic biota (e.g. only rare calcareous nannofossils became extinct). This suggests that the basic structure of pelagic food webs was rather robust against thermal anomalies. This is in stark contrast to late Paleocene reef systems that strongly responded to early Paleogene long- and short-term warming, giving way to larger foraminifera-dominated carbonate ramps (Scheibner and Speijer, 2008; Kiessling and Simpson, 2011) that persisted until the late Eocene.

Although detailed deep-sea ostracode records across the PETM are still limited to two sequences (Steineck and Thomas, 1996: ODP690, Southern Ocean; Yamaguchi and Norris, 2012: DSDP 401, northeast Atlantic), it is clear that there was no equivalent to the BEE, not even a mild one. Such disparate patterns between benthic protozoans and metazoans living in the same sea floor environment may seem unexpected, but it has been suggested that physiological differences may well explain why, for instance, ocean acidification may have a strong effect on protozoans but much less so on metazoans (Melzner et al., 2009). In addition, the disparity in extinction may also suggest that the larger provinciality and variability of deep-sea ostracode communities has safeguarded them from severe global extinction at a time of rapid global warming and oceanographic perturbations. Further high-resolution ostracode records are needed in order to explore the reasons for this disparity.

In the North African epicontinental basins, communities of benthic foraminifera and ostracodes were equally perturbed and responded in ecologically similar pathways as indicated by disappearances/extinctions, new appearances/migrations and opportunistic blooms. Both taxonomic groups show a long-term faunal transition from late Paleocene assemblages towards early Eocene assemblages, punctuated by the PETM (Speijer and Morsi, 2002; Speijer and Wagner, 2002; Morsi et al., 2011; Stassen et al., 2012c). Although this pattern is not well known for epicontinental ostracodes beyond the southern Tethyan realm, provincialism appears to persist into the early Eocene as indicated by the dissimilarity between northern Tethyan (Eurasian) faunas and those from the (Afroarabian) southern Tethys (Keen et al., 1994). In contrast, epicontinental benthic foraminifera have a rather cosmopolitan distribution during the Paleocene (the cosmopolitan Midway type fauna of Berggren and Aubert, 1975) and this seems to continue into the Eocene. This is well exemplified by the simultaneous appearance and/or dominance of various taxa in Egypt and the New Jersey Coastal Plain (Stassen et al., 2012c).

3.3 Extinction event or migration and origination event?

As outlined above, the consequences of the PETM on biotic evolution strongly vary between the various ecosystems, as far as can be judged from microfossils. Altogether, the PETM might be considered as a minor extinction event. This is supported by extinctions that occurred at the onset or during the PETM of mostly deep-sea benthic foraminifera as well as some calcareous nannofossils and by the quasi-disappearance of reef-building corals. Yet, this is just one side of the evolutionary story of the PETM, which might be better described as a migration and origination event. This is most obvious in land mammals showing nearly simultaneous appearances of the precursors of modern primates and hoofed animals on the northern continents (Gingerich, 2006), but that is beyond the scope of this paper. The data on the marine record, however, show basically the same dominant pattern of migration and radiation. This applies to the pelagic ecosystems (planktic foraminifera, calcareous nannofossils, radiolarians, dinocysts, diatoms), the platform systems (larger foraminifera), and the pelitic epicontinental systems (benthic foraminifera, ostracoda). The distribution patterns of all these groups reveal migration patterns, evolutionary innovations and dominance changes that in many cases appear to be preceding the gradual extinction of Paleocene taxa of calcareous nannofossils (e.g., *Fasciculithus*), larger foraminifera (e.g., *Miscellanea*, *Ranikothalia*), shelf ostracodes (e.g., *Mauritsina*) in the aftermath of the PETM. These patterns seem to differ from those of calcare-

ous benthic foraminifera. Particularly those of the deep sea witnessed rather sudden catastrophic extinction at the onset or during the early part of the PETM. Vacated niches were refilled by survivors and subsequently by newly evolved taxa after an extended period of low diversity low during the entire PETM (Thomas, 2007).

4. Conclusions

- Patterns of biotic change among pelagic and deep-sea ecosystems during the PETM are supported by globally distributed data. The record of biotic change among shallow benthic ecosystems remains largely confined to a few well studied regions (Tethys, North Atlantic) of the Northern hemisphere.
- Except for the deep-sea calcareous benthic foraminiferal record, the PETM is best qualified as a migration and origination event, rather than an extinction event. The PETM was instrumental in kick-starting various evolutionary innovations in marine lineages some of which persisted only briefly during or shortly after the PETM such as various *Acarinina*, *Discoaster*, *Rhomboaster* and *Apectodinium* species. Other taxa such as the nummulitids and alveolinids show a long-term persistence through the Eocene.
- The only major extinction is among bathyal to abyssal calcareous benthic foraminifera (including calcareous agglutinated taxa). Co-existing non-calcareous foraminifera (DWAF), ostracoda and trace fossils may show prominent local or regional changes in population structure and biodiversity, but very little or no evidence of global extinction. The response of most marine invertebrates (mollusks, echinoderms, brachiopods) to paleoclimatic change during the PETM is virtually unknown. Data spanning the PETM are required in order to improve assessments of the value of biotic records to deep-time global warming in the context of current climate change.
- In contrast, the relatively well-established response of Tethyan reef systems to late Paleocene-early Eocene global warming may provide a past analog to the problems facing modern tropical coral reefs in response to continued global warming.

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