

# Turnover of larger foraminifera during the Paleocene-Eocene Thermal Maximum and paleoclimatic control on the evolution of platform ecosystems

C. Scheibner\* Department of Geosciences, Bremen University, P.O. Box 330440, 28334 Bremen, Germany

R.P. Speijer\* Department of Geography and Geology, Katholieke Universiteit Leuven, 3000 Leuven, Belgium

A.M. Marzouk\* Geology Department, Faculty of Science, Tanta University, 31527 Tanta, Egypt

## ABSTRACT

The larger-foraminifera turnover (LFT) during the Paleocene-Eocene transition constitutes an important step in Paleogene larger-foraminifera evolution, involving a rapid increase in species diversity, shell size, and adult dimorphism. A platform-to-basin transect in Egypt provides new data on timing and causal mechanisms through correlation with planktic biozonations and through integration with regional paleoenvironmental data. The LFT coincides with the boundary between shallow benthic biozones SBZ4 and SBZ5 and closely correlates with the Paleocene-Eocene Thermal Maximum (PETM). Enhanced oligotrophy from the late Paleocene onward favored the diversification of K-strategist larger foraminifera. We suggest that a short-term eutrophication during the PETM led to a temporary decline of extreme K-strategist larger-foraminifera species, providing opportunities for new taxa with different ecological strategies to develop. During post-PETM oligotrophic conditions, these new taxa were able to evolve rapidly and soon dominated early Eocene larger-foraminifera assemblages, whereas many Paleocene taxa gradually disappeared. The success of larger foraminifera during the early Paleogene appears climatically controlled. Because of the vulnerability of corals to high surface-water temperatures, the late Paleocene to early Eocene global warming may have favored larger foraminifera at the expense of corals as the main carbonate-producing component on carbonate platforms at lower latitudes.

**Keywords:** Paleocene-Eocene Thermal Maximum, biozonation, larger foraminifera, paleoclimate, carbonate platforms.

## INTRODUCTION

The early Paleogene witnessed the most pronounced long-term warming of the Cenozoic (Zachos et al., 2001). A brief period of extreme warming at the onset of the Eocene, called the Paleocene-Eocene Thermal Maximum (PETM), was superimposed on this warm period and coincided with a major perturbation of the carbon cycle as indicated by a sharp negative  $\delta^{13}\text{C}$  excursion (CIE) (e.g., Dickens, 1999). Microfossil records show extinctions and diversifications in pelagic and open-marine ecosystems (e.g., Thomas, 1998; Kelly, 2002; Crouch et al., 2001; Bralower, 2002). The PETM is simultaneously marked by a well-documented rejuvenation of terrestrial vertebrates (Maas et al., 1995). In contrast, little is known about the response of shallow-water ecosystems to paleoenvironmental changes during the Paleocene-Eocene (P-E) transition. Larger foraminifera are the most common constituents of late Paleocene–early Eocene carbonate platforms, and this group shows a diversification at a specific level, i.e., adult dimorphism and large shell size within the P-E transition (Hottinger, 1998). Recent observations in a platform-basin transect in northern Spain (Orue-Etxebarria et al., 2001; Pujalte et al., 2003) have shown that this evolutionary change, the larger-foraminifera turnover (LFT), correlates with the PETM in deeper parts of the basin. In Spain, the LFT is

characterized by a change in nummulitid morphotypes. In contrast to the smaller benthic foraminifera of the deep sea, which experienced a 40% species extinction (benthic extinction event, BEE), the LFT does not involve sudden extinction. This is not surprising, considering the different habitat and trophic nature: larger foraminifera live within the photic zone in symbiosis with algae, whereas the deep-sea benthics are independent of light and feed on various sources. We present new stratigraphic data from a platform-basin transect in Egypt. This transect provides an excellent opportunity to verify stratigraphic relationships between the PETM and biostratigraphic markers on and around the platform. In addition, we discuss the effects of long-term early Paleogene warming, the PETM, and changes in the trophic resource regime on the evolution of early Paleogene larger foraminifera.

## Materials and Methods

The Southern Galala Mountains are located west of the Gulf of Suez, Egypt (Fig. 1). From the Maastrichtian to Eocene, a carbonate platform developed on a local high in this area (Scheibner et al., 2003). Out of 18 sections, the 4 sections providing the best coverage of the P-E transition are aligned on a transect extending from the platform margin in the north to the basin in the south (Scheibner et al., 2003). A combination of paleontologic (calcareous nannoplankton, smaller and larger benthic foraminifera), geochemical ( $\delta^{13}\text{C}$ ), and sedimentologic data allows a precise correlation of the Paleocene and lowermost Eocene deep- and shallow-water sections.

## Correlation of Shallow-Water and Pelagic Biozonation

In the correlation between shallow- and open-marine biozonation (Serra-Kiel et al., 1998; Fig. 2), the boundary between SBZ4 and SBZ5—marking the LFT—was correlated with the base of planktic

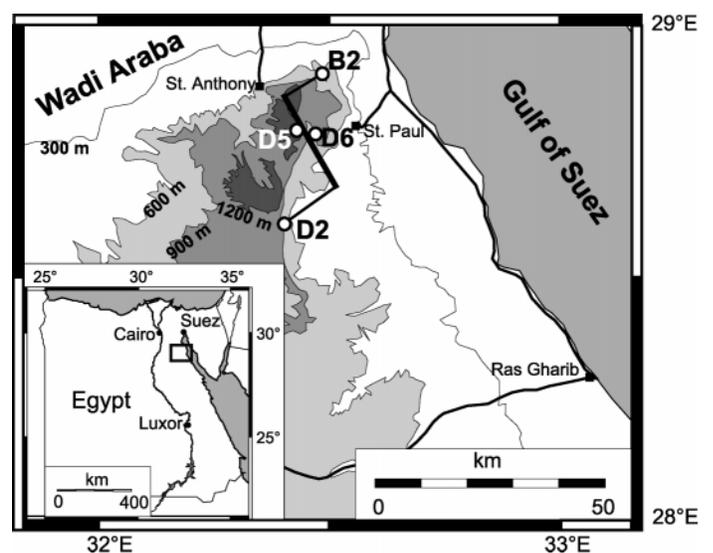


Figure 1. Location map with studied sections projected on line perpendicular to direction of platform progradation. Contours indicate elevations of Galala Mountains.

\*E-mails: scheibne@uni-bremen.de, Robert.Speijer@geo.kuleuven.ac.be, akmalmarzouk@hotmail.com.

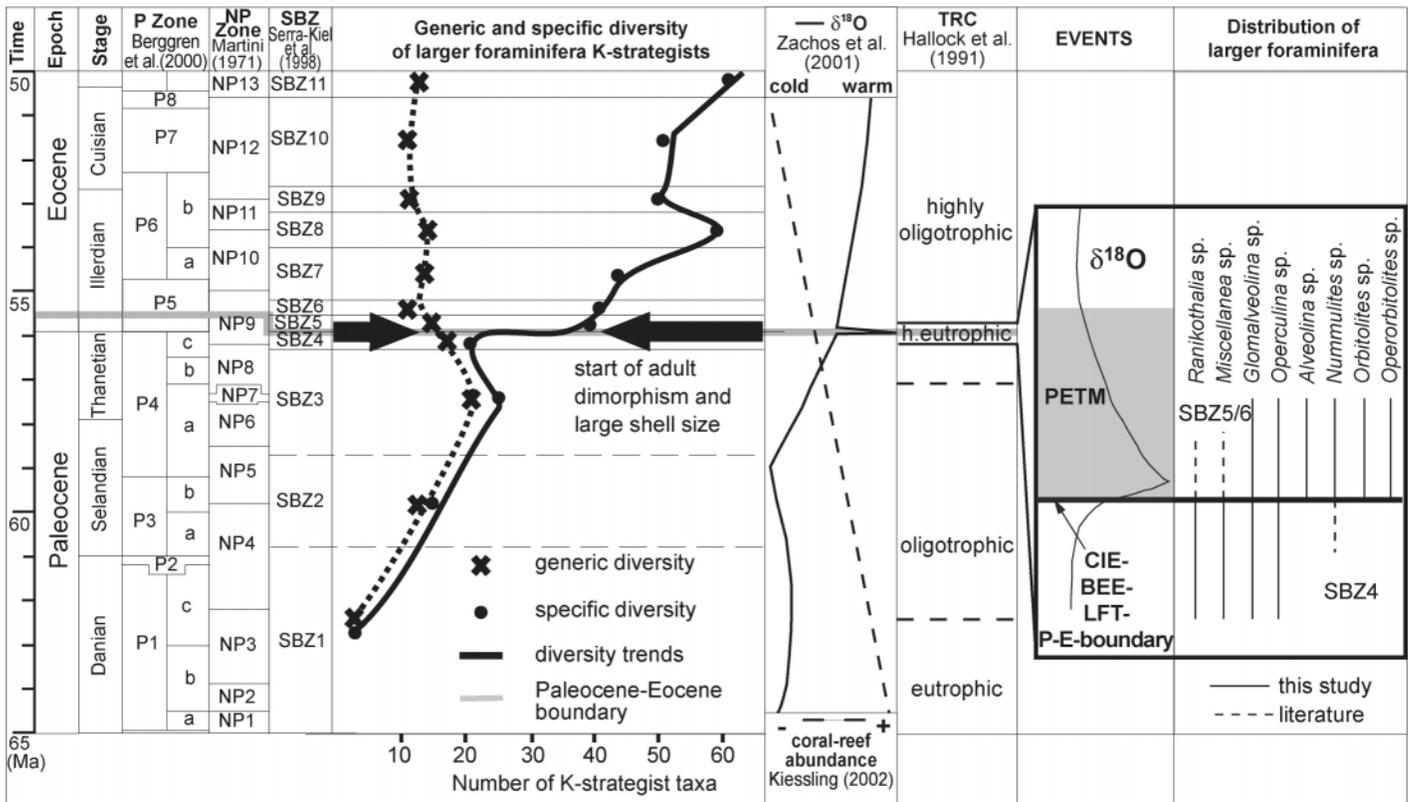


Figure 2. Biostratigraphy and comparison of trends in evolution and distribution of larger foraminifera,  $\delta^{18}\text{O}$  isotopes, coral-reef abundance, and trophic resource continuum (TRC). Inset: Events associated with the Paleocene-Eocene (P-E) boundary: CIE—carbon isotope excursion; BEE—benthic extinction event; LFT—larger-foraminifera turnover; PETM—Paleocene-Eocene thermal maximum.

foraminiferal zone P5 and with a level in the lower part of calcareous nannofossil zone NP9. It has now been agreed that the onset of the CIE and the PETM delineates the P-E boundary (Aubry and Ouda, 2003). This level closely correlates with the base of P5b and with the base of NP9b. Following the correlation scheme of Serra-Kiel et al. (1998), the base of the CIE would correlate with the base of SBZ6, and thus the LFT at the SBZ4-SBZ5 boundary would predate the PETM by  $\sim 300$  k.y. (Fig. 2; Hottinger, 1998).

### RESULTS OF BIOSTRATIGRAPHIC AND CHEMOSTRATIGRAPHIC CORRELATION

#### Paleocene

The two toe-of-slope sections (D2, D6; Fig. 3) are characterized by hemipelagic marls with intercalated calciturbidites (Scheibner et al., 2003). In the more proximal toe-of-slope section (D6), two small debris flows with larger foraminifera indicative of SBZ4 (*Miscellanea* spp., *Ranikothalia* spp.) are intercalated. Debris flows followed by slumped

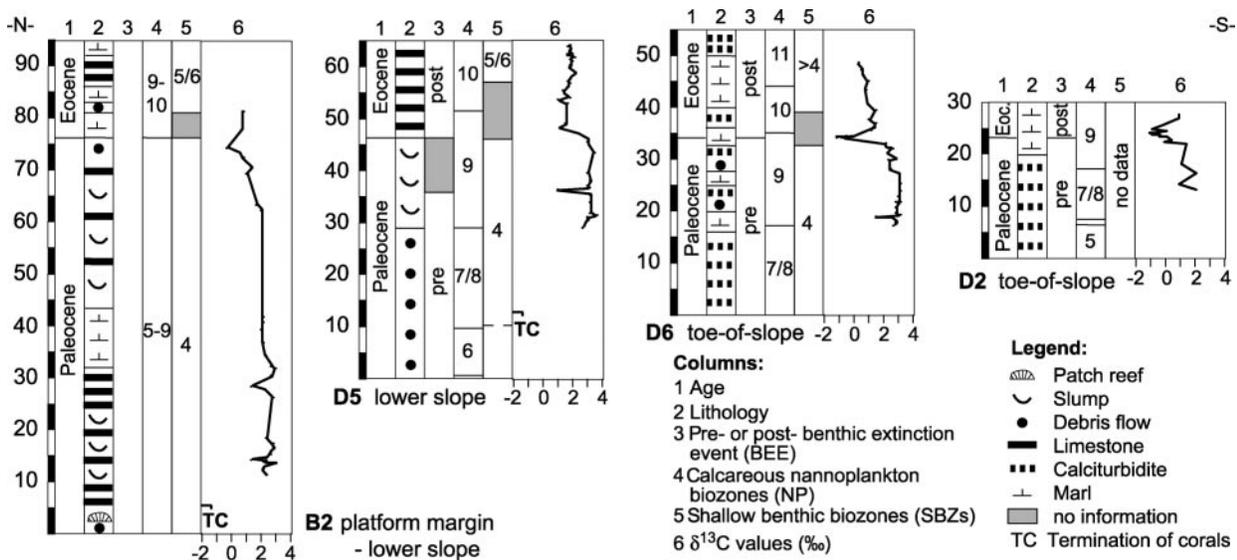


Figure 3. Biostratigraphic and chemostratigraphic correlation of studied platform-margin to toe-of-slope sections.

limestones in the lower-slope section (D5) also yield a fauna typical for SBZ4. The debris flows contain the last remnants of corals. Marly intercalations provide an accurate calcareous nannofossil biozonation. On the platform margin (section B2), the coral patch reefs typifying progradation during SBZ3 were succeeded within SBZ4 by larger-foraminifera-bearing shoals. These were mainly composed of *Miscellanea* spp. and subordinate *Ranikothalia* spp. and very few coral fragments. There is no evidence of SBZ5 markers in the Paleocene of any of these sections.

### Paleocene-Eocene Thermal Maximum

In the two toe-of-slope sections (D2, D6), the base of the CIE is situated in a marly unit with fish remains and slightly higher total organic carbon values. It correlates with the benthic extinction event at the boundary of NP9a and NP9b. In contrast to the clear  $\delta^{13}\text{C}$  excursion in the deeper sections, the shallower sections (D5, B2) only show a shift to more negative  $\delta^{13}\text{C}$  values (Fig. 3), probably as a result of a wider sample spacing.

### Eocene

The two toe-of-slope sections are still characterized by hemipelagic marls with intercalated calciturbidites. The calciturbidites of D6 contain a poor larger-foraminiferal assemblage that cannot be clearly assigned to a particular shallow benthic zone, but the foraminifera are definitely younger than SBZ4. In the two proximal sections (D5, B2), bedded limestones with *Nummulites* spp. and *Alveolina* spp. (SBZ5–SBZ6; Fig. 2) dominate the succession (Scheibner et al., 2003). Corals have not been found at any Eocene level.

## DISCUSSION

### Temperature, Oligotrophy, and Larger-Foraminiferal Evolution

Three evolutionary stages can be observed in Paleogene platform development of the Galala Mountains (paleolatitude 18°N): I (SBZ3) a coralgall-reef-dominated platform; II (SBZ4) a platform dominated by larger-foraminifera-bearing shoals (*Miscellanea* spp., *Ranikothalia* spp.); and III (SBZ5–SBZ6) a larger-foraminifera-dominated platform (*Alveolina* spp., *Nummulites* spp.). The absence of corals in the two upper stages in the Galalas is striking. Detailed P-E studies elsewhere are scarce, but similar platform successions were described from Spain (paleolatitude 33°N; Pujalte et al., 2003), and from the Ionian Islands in Greece (paleolatitude 27°N; Accordi et al., 1998). In both areas, small amounts of corals occur in the upper stages. In the following we present a short review of the latitudinal temperature variations, the trophic resource regime, and the ecology of larger foraminifera during the early Paleogene. Subsequently we discuss the large-scale evolution of larger foraminifera in this time interval.

### Latitudinal Temperature Trends in the Early Paleogene

The Late Cretaceous to early Paleogene was characterized by warm, generally ice-free conditions. During the PETM, deep-sea and low-latitude sea-surface temperatures rose by ~4–6 °C (Zachos et al., 2001, 2003; Fig. 2). A more general global temperature rise in the late Paleocene and early Eocene is supported by a poleward expansion of reef and platform growth and by a broader latitudinal distribution of temperature-sensitive organisms such as larger foraminifera, corals, mangroves, palms, and reptiles (Adams et al., 1990; Pearson et al., 2001; Kiessling, 2002). In the late Paleocene and Eocene, coral reefs were able to grow up to 46°N, in comparison to today's coral-reef distribution that reaches to only 34°N (Kiessling, 2002). Warming of the low latitudes in the early Paleogene is also indicated by changes in tropical vegetation of northern South America (Jaramillo, 2002).

During the Late Cretaceous and early Paleogene, corals appear to have been uncommon and poorly diverse (Johnson et al., 1996). It can be speculated that, in general, warm sea-surface temperatures prohibited full development of coral reefs at low latitudes, as overly high

temperatures seem to be a main threat for coral-reef growth (Sheppard, 2003).

### Trophic Resource Regime in the Early Paleogene

The development of oligotrophic habitats is thought to be maximal when the oceans are poorly mixed. Boersma et al. (1998) proposed a decrease in the intensity of oceanographic mixing in response to the onset of the PETM. This circumstance would have favored the temporary proliferation of symbiont-bearing oligotrophic planktic foraminifera like *Acarinina* and to a lesser extent *Morozovella* (Kelly, 2002). Nannofossil assemblages of the PETM suggest oligotrophy in the open ocean (Bralower, 2002).

In contrast to the oligotrophic conditions around the P-E boundary postulated by Hallock et al. (1991) and Boersma et al. (1998), productivity in coastal surface waters appears to have increased substantially at and beyond the P-E boundary, as demonstrated by black shale deposition (Speijer and Wagner, 2002), increased biogenic barium values (Schmitz et al., 1997), and a widespread bloom of the organic-walled dinoflagellate *Apectodinium* that resulted from nutrient input into marginal basins (Crouch et al., 2001). Intensified weathering is documented by an osmium isotope excursion (Ravizza et al., 2001), an increase in kaolinite (Bolle and Adatte, 2001), and an increase in the rate of hemipelagic sedimentation (Egger et al., 2003).

### Larger-Foraminiferal Trends and Ecology

Larger foraminifera are extreme K strategists (characterized by long individual live and low reproductive potential) thriving in a stable, typically oligotrophic environment (Hottinger, 1983). Although all larger foraminifera are considered K strategists, Paleogene larger foraminifera exhibit an increasing trend in K strategy, from alveolinids to nummulitids to discocyclinids (Hottinger, 1982). During a breakdown or interruption of their stable oligotrophic environment, the most extreme K strategists are the first to disappear (Hottinger, 1983). The replacement of SBZ4 by SBZ5 faunas—as indicated by the gradual disappearance of Paleocene taxa like *Ranikothalia* and *Miscellanea* and the rise of *Nummulites* and *Alveolina*—suggests that such an interruption may have taken place in platform environments at low-latitude continental margins.

### Rise and Fall and Rise of Larger Foraminifera

Globally warm sea-surface temperatures and enhanced CO<sub>2</sub> levels of the early Paleogene did not favor the expansion of reef-building corals in the lower latitudes. Corals are sensitive to high CO<sub>2</sub> levels and to overly warm sea-surface temperatures, which cause symbiont loss and bleaching (Gattuso and Buddemeier, 2000; Sheppard, 2003). Unlike reef-building corals, rising summer sea-surface temperatures do not cause symbiont loss in larger foraminifera (Hallock, 2000). In the absence of other reef-building, high-temperature-tolerating organisms in the low latitudes, larger foraminifera used these vacated niches and rapidly evolved after their reconstitution from the crisis at the Cretaceous-Tertiary boundary. Such a situation existed in the Cretaceous when a superheated, hypersaline ocean-climate zone favored the proliferation of rudists over corals (Kauffman and Johnson, 1988; Johnson et al., 1996). Another positive feedback factor for the rapid diversification of larger foraminifera was the overall oligotrophic conditions from the late Paleocene to middle Eocene. The different opinions on the Paleogene trophic resource regime may be solved by the assumption that (1) the more eutrophic conditions around the PETM occurred only during a short period, and (2) they occurred predominantly on the shelf areas owing to increased continental runoff (Bralower, 2002). In this scenario the PETM marks only a perturbation in the long-lasting oligotrophic trend of the Paleogene trophic resource regime. These more eutrophic conditions in the marginal basins might also have affected the shallow-water platforms differently. For the low latitudes like the Galala Mountain region, this perturbation could have

led to the decline of the most extreme K strategists of the larger foraminifera such as some genera of the nummulitids (e.g., *Miscellanea* spp., *Ranikothalia* spp.), whereas more moderate K strategists like glomalveolinids thrived unaffected. In the higher latitudes (e.g., Spain) only a change in morphotypes occurred. After the return to stable oligotrophic conditions in the still-warm oceans, nummulitids and alveolinids rapidly evolved and occupied vacated niches in the low latitudes or displaced the surviving Paleocene nummulitids in the higher latitudes (e.g., in Spain), thus resulting in the LFT.

## CONCLUSIONS

The LFT, coinciding with the zonal boundary between SBZ4 and SBZ5, is associated with the PETM and did not postdate this event, as suggested earlier. Paleoenvironmental changes during the PETM in Egypt indicate that a brief eutrophication on a generally oligotrophic platform reset the clock for larger-foraminiferal evolution in this region and possibly elsewhere in the Tethys. However, early Paleogene evolution of larger foraminifera must primarily be seen in the context of long-term processes. These processes are (1) the reorganization of the larger foraminifera after the Cretaceous–Paleogene crisis, and (2) the following long-term trends toward oligotrophy and higher sea-surface temperatures, the latter leading to the demise of corals in low latitudes.

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## REFERENCES CITED

Accordi, G., Carbone, F., and Pignatti, J., 1998, Depositional history of a Paleogene carbonate ramp (western Cephalonia, Ionian Islands, Greece): *Geologica Romana*, v. 34, p. 131–205.

Adams, C.G., Lee, D.E., and Rosen, B.R., 1990, Conflicting isotopic and biotic evidence for tropical sea-surface temperatures during the Tertiary: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 77, p. 289–313.

Aubry, M.P., and Ouda, K., 2003, Introduction to the upper Paleocene–lower Eocene of the Upper Nile Valley: Part I. Stratigraphy: *Micropaleontology*, v. 49, supplement 1, p. ii–iv.

Berggren, W.A., Aubry, M.P., van Fossen, M., Kent, D.V., Norris, R.D., and Quillévéré, F., 2000, Integrated Paleocene calcareous plankton magneto-biochronology and stable isotope stratigraphy: DSDP Site 384 (NW Atlantic Ocean): *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 159, p. 1–51.

Boersma, A., Premoli Silva, I., and Hallock, P., 1998, Trophic models for the well-mixed and poorly mixed warm oceans across the Paleocene/Eocene epoch boundary, in Aubry, M.P., et al., eds., Late Paleocene–early Eocene climatic and biotic events in the marine and terrestrial records: New York, Columbia University Press, p. 204–213.

Bolle, M.P., and Adatte, T., 2001, Paleocene–early Eocene climatic evolution in the Tethyan realm: Clay mineral evidence: *Clay Minerals*, v. 36, p. 249–261.

Bralower, T.J., 2002, Evidence of surface water oligotrophy during the Paleocene–Eocene Thermal Maximum: Nannofossil assemblage data from the Ocean Drilling Program Site 690, Maud Rise, Weddell Sea: *Paleoceanography*, v. 17, no. 2, 1023, doi:10.1029/2001PA000662

Crouch, E.M., Heilmann-Clausen, C., Brinkhuis, H., Morgans, H.E.G., Rogers, K.M., Egger, H., and Schmitz, B., 2001, Global dinoflagellate event associated with the late Paleocene thermal maximum: *Geology*, v. 29, p. 315–318.

Dickens, G.R., 1999, The blast in the past: *Nature*, v. 401, p. 752–755.

Egger, H., Fenner, J., Heilmann-Clausen, C., Rögl, F., Sachsenhofer, R.F., and Schmitz, B., 2003, Paleoproductivity of the northwestern Tethyan margin (Anthering section, Austria) across the Paleocene–Eocene transition, in Wing, S.L., et al., eds., Causes and consequences of globally warm climates in the early Paleogene: Geological Society of America Special Paper 369, p. 133–146.

Gattuso, J.P., and Buddemeier, R.W., 2000, Calcification and CO<sub>2</sub>: *Nature*, v. 407, p. 311–313.

Hallock, P., 2000, Symbiont-bearing foraminifera: Harbingers of global change?: *Micropaleontology*, v. 46, supplement 1, p. 95–104.

Hallock, P., Premoli Silva, I., and Boersma, A., 1991, Similarities between planktonic and larger foraminiferal evolutionary trends through Paleogene paleoceanographic changes: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 83, p. 49–64.

Hottinger, L., 1982, Larger Foraminifera, giant cells with a historical background: *Naturwissenschaften*, v. 69, p. 361–371.

Hottinger, L., 1983, Processes determining the distribution of larger foraminifera in space and time: *Utrecht Micropaleontological Bulletins*, v. 30, p. 239–253.

Hottinger, L., 1998, Shallow benthic foraminifera at the Paleocene-Eocene boundary: *Strata*, ser. 1, v. 9, p. 61–64.

Jaramillo, C.A., 2002, Response of tropical vegetation to Paleogene warming: *Paleobiology*, v. 28, p. 222–243.

Johnson, C.C., Barron, E.J., Kauffman, E.G., Arthur, M.A., Fawcett, P.J., and Yasuda, M.K., 1996, Middle Cretaceous reef collapse linked to ocean heat transport: *Geology*, v. 24, p. 376–380.

Kauffman, E.G., and Johnson, C.C., 1988, The morphological and ecological evolution of middle and Upper Cretaceous reef-building rudistids: *Palaios*, v. 3, p. 194–216.

Kelly, D.C., 2002, Response of Antarctic (ODP Site 690) planktonic foraminifera to the Paleocene–Eocene Thermal Maximum: Faunal evidence for ocean/climate change: *Paleoceanography*, v. 17, no. 4, 1071, doi: 10.1029/2002PA000761.

Kiessling, W., 2002, Secular variations in the Phanerozoic reef ecosystem, in Kiessling, W., et al., eds., Phanerozoic reef patterns: SEPM (Society for Sedimentary Geology) Special Publication 72, p. 625–690.

Maas, M.C., Anthony, M.R.L., Gingerich, P.D., Gunnell, G.F., and Krause, D.W., 1995, Mammalian generic diversity and turnover in the late Paleocene and early Eocene of the Bighorn and Crazy Mountains Basins, Wyoming and Montana (USA): *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 115, p. 181–207.

Martini, E., 1971, Standard Tertiary and Quaternary calcareous nannoplankton zonation, in Farinacci, A., ed., Proceedings of the II Plankton Conference, Roma: Roma, Edizioni Tecnoscienza Roma, p. 739–785.

Orue-Etxebarria, X., Pujalte, V., Bernaola, G., Apellaniz, E., Baceta, J.I., Payros, A., Nunez-Betelu, K., Serra-Kiel, J., and Tosquella, J., 2001, Did the late Paleocene thermal maximum affect the evolution of larger foraminifera? Evidence from calcareous plankton of the Campo section (Pyrenees, Spain): *Marine Micropaleontology*, v. 41, p. 45–71.

Pearson, P.N., Ditchfield, P.W., Singano, J., Harcourt-Brown, K.G., Nicholas, C.J., Olsson, R.K., Shackleton, N.J., and Hall, M.A., 2001, Warm tropical sea surface temperatures in the Late Cretaceous and Eocene Epochs: *Nature*, v. 413, p. 481–487.

Pujalte, V., Orue-Etxebarria, X., Schmitz, B., Tosquella, J., Baceta, J.I., Payros, A., Bernaola, G., Caballero, F., and Apellaniz, E., 2003, Basal Ilerdian (earliest Eocene) turnover of larger foraminifera: Age constraints based on calcareous plankton and  $\delta^{13}\text{C}$  isotopic profiles from new southern Pyrenean sections (Spain), in Wing, S.L., et al., eds., Causes and consequences of globally warm climates in the early Paleogene: Geological Society of America Special Paper 369, p. 205–221.

Ravizza, G., Norris, R.N., and Blusztajn, J., 2001, An osmium isotope excursion associated with the late Paleocene thermal maximum: Evidence of intensified chemical weathering: *Paleoceanography*, v. 16, p. 155–163.

Scheibner, C., Reijmer, J.J.G., Marzouk, A.M., Speijer, R.P., and Kuss, J., 2003, From platform to basin: The evolution of a Paleocene carbonate margin (Eastern Desert, Egypt): *International Journal of Earth Sciences*, v. 92, p. 624–640.

Schmitz, B., Charisi, S.D., Thompson, E.I., and Speijer, R.P., 1997, Barium, SiO<sub>2</sub> (excess), and P<sub>2</sub>O<sub>5</sub> as proxies of biological productivity in the Middle East during the Paleocene and the latest Paleocene benthic extinction event: *Terra Nova*, v. 9, p. 95–99.

Serra-Kiel, J., Hottinger, L., Caus, E., Drobne, K., Ferrandez, C., Jauhri, A.K., Less, G., Pavlovic, R., Pignatti, J., Samsó, J.M., Schaub, H., Sirel, E., Strougo, A., Tambareau, Y., Tosquella, J., and Zakrevskaya, E., 1998, Larger foraminiferal biostratigraphy of the Tethyan Paleocene and Eocene: *Bulletin de la Société Géologique de France*, v. 169, p. 281–299.

Sheppard, C.R.C., 2003, Predicted recurrences of mass coral mortality in the Indian Ocean: *Nature*, v. 425, p. 294–297.

Speijer, R.P., and Wagner, R., 2002, Sea-level changes and black shales associated with the late Paleocene thermal maximum: Organic-geochemical and micropaleontologic evidence from the southern Tethyan margin (Egypt-Israel), in Koeberl, C., and MacLeod, K.G., eds., Catastrophic events and mass extinctions: Impacts and beyond: Geological Society of America Special Paper 356, p. 533–549.

Thomas, E., 1998, Biogeography of the late Paleocene benthic foraminiferal extinction, in Aubry, M.P., et al., eds., Late Paleocene–early Eocene climatic and biotic events in the marine and terrestrial records: New York, Columbia University Press, p. 214–243.

Zachos, J., Pagani, M., Sloan, L., Thomas, E., and Billups, K., 2001, Trends, rhythms, and aberrations in global climate 65 Ma to present: *Science*, v. 292, p. 686–693.

Zachos, J.C., Wara, M.W., Bohaty, S., Delaney, M.L., Petrizzo, M.R., Brill, A., Bralower, T.J., and Premoli-Silva, I., 2003, A transient rise in tropical sea surface temperature during the Paleocene–Eocene Thermal Maximum: *Science*, v. 302, p. 1551–1554.

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