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The Paleocene-Eocene Thermal Maximum

by Phil Jardine*[1]

Introduction:

The Paleocene–Eocene Thermal Maximum (PETM) is one of the most intense and abrupt intervals of global warming in the geological record. It occurred around 56 million years ago, at the boundary between the Paleocene and Eocene epochs. This warming has been linked to a similarly rapid increase in the concentration of greenhouse gases in Earth's atmosphere, which acted to trap heat and drive up global temperatures by more than 5 °C in just a few thousand years. The fossil record gives us the means of understanding how life was affected by the PETM, and so provides an excellent opportunity to study the relationships between evolution, extinction, migration and climate change.

The early Palaeogene world:

At the time of the PETM, the world was already much warmer than it is today. The high latitudes and polar regions were more or less ice-free, and were populated by a diverse assemblage of plants and animals. Alligators, which today are found only in the warm tropics and subtropics, occurred well within the Arctic Circle during the early Eocene. The climate in southern North America (at a latitude of ~30° N) was roughly tropical, with high temperatures and lots of rainfall, and small seasonal differences between summer and winter. This warm phase had begun in the Cretaceous period, peaked in the early Eocene, and continued to the end of the Eocene, when global temperatures dropped and ice sheets formed over the Antarctic. By the early Palaeogene period, the arrangement of the continents was quite similar to that of today (Fig. 1), although the Atlantic Ocean was not as wide as it is now, and India was only just beginning to collide with the rest of Asia.

The PETM occurred approximately 10 million years after the mass extinction at the end of the Cretaceous. This event had eliminated dinosaurs, pterosaurs, ammonites and belemnites, as well as many groups of birds, bivalves, brachiopods, marine reptiles, plants and planktonic organisms. The environment in which the PETM took place was therefore very different to that of the Cretaceous, and many modern groups of plants and animals were diversifying at this time.

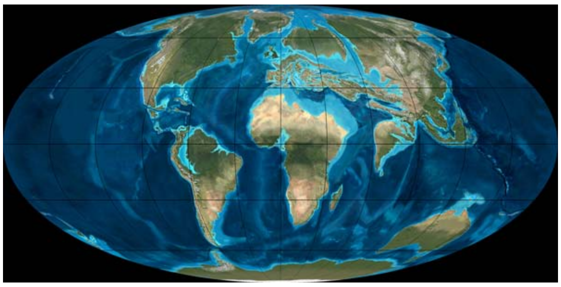

Figure 1 - Positions of the continents during the early Eocene epoch. Palaeogeographic map courtesy of Ron Blakey, Colorado Plateau Geosystems, Inc © (http://cpgeosystems.com/index.html).

Climate change during the PETM:

Much of our information on past climates comes from the composition of sediments and the shells of marine organisms, which take up chemical substances from seawater as they grow. Because seawater chemistry is partly controlled by temperature, sediments and fossil shells retain a signature of the ambient temperatures under which they formed. Such signatures tell us that during the PETM, temperatures rose rapidly over approximately 6,000 years, and then gradually cooled to near-background levels over the next 150,000–200,000 years. Warming was not uniform across the globe: sea surface temperatures increased by ~6 °C at high latitudes and ~4 °C at low latitudes, and deep-water temperatures increased by ~8 °C at high latitudes and ~6 °C at low latitudes. On land, temperatures increased by ~5 °C in the middle latitudes and by ~3 °C near the equator. Evidence for changes in precipitation is mixed: some studies show a dryer climate during the peak warmth of the PETM, whereas others suggest that rainfall increased. This may demonstrate that the impact of warming on precipitation patterns was localized, with different regions showing a range of effects.

Although we now have a good picture of how climate changed across the PETM, the origins of the greenhouse gases that apparently caused this event are less clear. The most likely explanation is the mass release of methane from sediments on the sea floor, where the gas was sequestered, as it is now, in a solid form as methane hydrate. Once in the atmosphere, methane would have quickly oxidized to carbon dioxide. Other possibilities are the decomposition of organic matter in terrestrial settings, or the release of methane and carbon dioxide from deeply buried rocks during volcanic events. Whatever the causal mechanism, approximately 2,000 gigatonnes of carbon are thought to have entered the atmosphere and oceans at the same time as the PETM. Atmospheric concentrations of carbon dioxide gradually returned to near-background levels over a similar timescale to global temperatures.

The response of life to the PETM:

Marine microorganisms

Several groups of single-celled planktonic organisms, all of which are common in the oceans today, were greatly affected by the PETM. Dinoflagellates are primitive microorganisms that have characteristics of both plant and animal cells. They are typically 0.02–0.15 millimetres in diameter, and they propel themselves through the oceans using whip-like protuberances called flagella (dinoflagellate means ‘whirling whip’). Some species form protective capsules called resting cysts, in which the organism remains dormant throughout the winter. It is these cysts that are preserved and form the dinoflagellate fossil record. Within this group, the genus *Apectodinium* (Fig. 2) became globally dominant during the PETM, and expanded its range from the warm subtropics to cover most of the globe. This may have been because the warmer high latitudes during this interval allowed *Apectodinium* to spread farther away from the equator, or it might have been the result of increased nutrient influxes into the oceans.

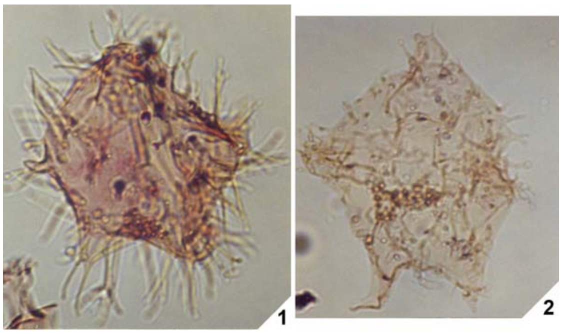

Figure 2 - Specimens of the dinoflagellate Apectodinium. This genus became globally dominant during the PETM (photographs taken by Guy Harrington).

Coccolithophores are smaller than dinoflagellates, and range in size from 0.00025 to 0.03 mm. They are covered in tiny plates of calcium carbonate called coccoliths, which fall to the sea floor when the organism dies. Coccoliths can accumulate in such abundance as to form rocks in their own right, and they are the main constituent of chalk, which forms the White Cliffs of Dover. Several species of coccolithophore went extinct during the PETM, and a number of new species appeared.

Foraminifera are widespread and abundant in the modern oceans, and inhabit both the surface waters and the sea floor. Planktonic foraminifera are typically less than 0.1 mm in diameter. These forms diversified during the PETM, with several new species appearing in this interval. However, foraminifera that lived on the sea floor (benthic forms) suffered a major extinction event, with 30–50% of species going extinct during the PETM. This was probably the result of rapid warming of the ocean-bottom waters, and an associated decline in the concentration of dissolved oxygen there.

Mammals

Mammals underwent profound evolutionary and biogeographic changes at the Paleocene–Eocene boundary. Three groups that incorporate many modern mammal species appeared suddenly at this time: Artiodactyla, which includes deer, camels and cows; Perissodactyla, which includes horses and rhinoceroses; and Primates, which includes monkeys, gorillas and humans. These groups probably originated in Asia and then rapidly dispersed to Europe and North America, all within the space of a few thousand years. It seems likely that movement between continents occurred over high-latitude land bridges (such as Greenland or the currently submerged land bridge under the Bering Strait), which only became warm enough to access during the PETM. A number of more ancient Paleocene mammals also went extinct at this time.

The best-known record of mammalian evolution throughout this interval, and indeed for much of the Cenozoic, comes from the Western Interior of North America. In the Bighorn and Clarks Fork basins of Wyoming (Fig. 3), sediments that were deposited on ancient flood plains record in great detail environmental change across the PETM. Mammal fossils recovered from this interval not only show the rapid first appearances of the artiodactyls, perissodactyls and primates in this region, but also demonstrate that some types of mammal became smaller during the PETM. Fossils of the now-extinct ground-dwelling herbivores *Ectocion* and *Copecion* from the PETM interval are reconstructed as approximately half the weight of those before and after it, and several other mammal groups that survived the PETM show the same pattern. The earliest members of the artiodactyls, perissodactyls and primates were also much smaller than their immediate descendants. Elevated atmospheric carbon dioxide concentrations have been shown in laboratory experiments to reduce leaf digestibility and nutritional value for herbivores, which results in slower growth rates. The higher concentration of atmospheric greenhouse gases during the PETM therefore seems like a better explanation for mammalian dwarfing than the increase in temperature itself.

Figure 3 - - Sediments spanning the Paleocene–Eocene boundary in the Bighorn Basin of Wyoming, United States. Most of these sediments represent flood-plain environments, and provide the most detailed terrestrial record of the PETM known.

Insects

Insects lack mineralized skeletons or shells, so they have a relatively poor fossil record. However, we do have indirect evidence of how the PETM affected terrestrial insects.

Trace fossils, which include burrows, nests, tracks, trails and holes made by boring, are frequently preserved in sedimentary successions, and these can provide information on animal size, behaviour and habitat choice. Trace fossils of insects moving through the soil have been found in the Bighorn Basin of Wyoming. Burrows found within the PETM interval are narrower than those before or after, which suggests that the soil-dwelling insects that made them got smaller during the PETM. The evolutionary response to the PETM in the insects below ground was therefore very similar to that of the mammals above ground.

Leaf fossils record feeding damage by herbivorous insects in the form of holes or traces on the leaves (Fig. 4). Different insects will damage leaves in different ways during feeding, which gives an approximation of the number and type of insect species present. Fossil leaves from Wyoming show that both the overall amount and the number of types of damage increased during the PETM. This is consistent with higher carbon dioxide concentrations reducing the nutritional quality of the plant material and stimulating increased feeding. Higher temperatures might also have increased insect population sizes.

Figure 4 - Fossil leaves from the latest Paleocene epoch of Texas, showing insect feeding damage. Evidence from the Bighorn Basin of Wyoming shows that the feeding intensity of herbivorous insects increased during the PETM (photographs taken by Tom Stidham).

Plants

Plants are rarely fossilized whole, and most of our information on the floral response to the PETM comes from fossil leaves and pollen. The detailed record from the Bighorn Basin in Wyoming shows that several new species migrated into this region during the PETM, both from Europe and from southern North America. Warming of the higher latitudes during the PETM facilitated these migrations, by allowing plant species adapted to warmer climates to expand their ranges past the hotter low latitudes. High-latitude land bridges between Europe and North America would have become usable, and as with the mammals, some European plants spread into North America.

Pollen records from Mississippi and Alabama on the US Gulf of Mexico show that this region was the source of some of the plant species that migrated north into Wyoming during the PETM. Several of the immigrant species from Europe also reached this far into southern North America. The plant communities of the US Gulf Coast also suffered an extinction event, with approximately 20% of pollen types disappearing at the Paleocene–Eocene boundary (Fig. 5).

In the tropics of Colombia, the pollen records show that several new species of plants appeared during the PETM and the early Eocene. Many of the species that were present during the Paleocene persisted through the PETM and into the Eocene, and only a relatively small number of extinctions took place. The equatorial forests, therefore, not only survived the PETM warmth, but seem to have flourished in it, with enhanced speciation and limited extinction increasing the number of plant species present.

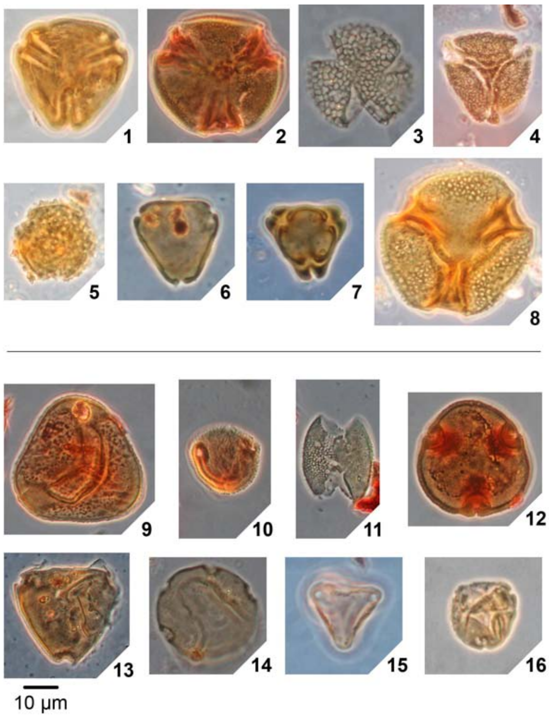

Figure 5 - Pollen and spores from Mississippi and Alabama, United States, representing plant types that either went extinct (1–8) or first appeared (9–16) at the Paleocene–Eocene boundary. 1, Holkopollenites chemardensis; 2, Lanagiopollis cribellata; 3, Retitrescolpites anguloluminosus; 4, Insulapollenites rugulatus; 5, Spinaepollis spinosus; 6, Momipites strictus; 7, Trudopollis plenus; 8, Lanagiopollis lihoka; 9, Granulatisporites luteticus; 10, Brosipollis striata; 11, Dicolpopollis sp.; 12, Intratriporopollenites instructus; 13, Symplocos contracta; 14, Celtis tschudyi; 15, Interpollis microsupplingensis; 16, Platycarya platycaryoides.

Synthesis:

It is clear that the PETM affected different groups of organisms and habitats in a range of ways. Many species simply expanded their ranges into higher latitudes, and mammals and plants were able to move into new continents. Microorganisms in the oceans' surface waters experienced few negative impacts during the PETM, whereas benthic foraminifera underwent severe extinctions. Tropical plants did well during the warming, perhaps because they were already adapted to warm conditions. The higher concentrations of atmospheric carbon dioxide throughout the PETM decreased the nutritional value of plant material, however, leading to a temporary decrease in the size of some herbivorous insects and mammals. Feeding intensity among herbivorous insects also increased.

Research on the PETM continues. The discovery of other, smaller magnitude, rapid greenhouse warming events (called hyperthermals) in the millions of years following the PETM provides further opportunities to examine the response of organisms to global climate change. It is also essential to determine which effects were temporary (dwarfing in mammals and insects, and the *Apectodinium* range expansion, among others) and which left a permanent signature on life (benthic marine extinctions and the evolution of new plant species in the tropics). Also pressing is the need to study the impacts of the PETM in other regions. Most of our knowledge of changes in the terrestrial realm comes from Wyoming. Although this is an especially rich, detailed and well researched fossil record, we currently have little knowledge of how representative these patterns are for the rest of the world.

Suggestions for further reading:

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Clyde, W. C. & Gingerich P. D. 1998 Mammalian community response to the latest Paleocene thermal maximum: An isotaphonomic study in the northern Bighorn Basin, Wyoming. *Geology 26*, 1011–1014. (DOI 10.1130/0091-7613(1998)026<1011:MCRTTL>2.3.CO;2)

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