

## Chapter 11

# STEPWISE EXTINCTIONS AND CLIMATIC DECLINE DURING THE LATER EOCENE AND OLIGOCENE

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## INTRODUCTION

Although the Cretaceous–Tertiary extinction has garnered the most attention, and the Permian–Triassic extinction was probably the most severe, the Eocene–Oligocene extinctions are also of great geologic interest. Not only were they among the most important extinction events in the Phanerozoic, but they have an additional advantage in that they were relatively recent and, therefore, have an excellent geologic record. Numerous outstanding marine sections, especially from deep-sea cores, have recovered the details of this interval in many places in the world ocean. There are also many land sections containing plant and animal fossils that were deposited during this time. Most of these sections have tight stratigraphic control, not only from biostratigraphy, but also from magnetostratigraphy, isotope stratigraphy and seismic stratigraphy. Unlike earlier extinctions, the victims were mostly members of extant higher groups, so it is much easier to infer their palaeoecology and to reconstruct the palaeoclimatic changes that must have occurred.

The Eocene–Oligocene extinctions have figured prominently in the discussions of extinction periodicity, first proposed by Fischer and Arthur (1977) and Raup and Sepkoski (1984). Some authors (for example, Alvarez *et al.*, 1982; Asaro *et al.*, 1982; Ganapathy, 1982) have used the Eocene–Oligocene extinctions as evidence for extraterrestrial causes. Unfortunately, all of these studies have been built around the assumption that there is a single extinction event. This misconception was fostered by the overemphasis of the Terminal Eocene Event (TEE), which was the subject of IGCP Project 174 (Pomeroy and Premoli-Silva, 1986). It is now be-

coming clear that the Eocene–Oligocene extinctions were a complex series of stepwise events, spanning over 10 million years, and not a single abrupt event like some of those discussed in this volume. Since this is the case, simplistic models with a single, abrupt cause are no longer relevant.

Complicating the discussion has been a dispute over the time-scale. The controversy has been unusually acute for events which have many data sources and are relatively recent (Snelling, 1985). The differences between versions of the time-scale are not trivial. Recent estimates of the age of the Eocene–Oligocene boundary, for example, have ranged between 32 and 38 million years. Most of the discrepancies appear to be due to the heavy use (Curry and Odin, 1982) of glauconite dates, which are notoriously unreliable. In this chapter, I follow the time-scale of Berggren *et al.* (1985), which has been substantiated by almost all the new dates published subsequently (Montanari *et al.*, 1985; Berggren, 1986; Aubry *et al.*, 1988).

One minor point about this time-scale is frequently confused. In the formal sense, only the Priabonian is 'late' Eocene; the preceding Lutetian and Bartonian are technically 'middle' Eocene. Since most of the events discussed in this chapter take place in the later third of the Eocene, most authors have referred to them as 'late Eocene'. To avoid confusion, I refer to events happening in the Bartonian or Priabonian as 'later' Eocene, and restrict 'late Eocene' to the Priabonian. Likewise, since the Oligocene is divided into only two stages, the Rupelian and Chattian, there is no 'middle' Oligocene. I use 'mid-Oligocene' in the informal sense to denote events near the Rupelian–Chattian boundary.

## THE EVIDENCE

Data from the later Eocene and Oligocene have been emerging from many sources since the mid- to late 1970s. Most of the best evidence has come from the study of pelagic sediments and their contained microfossils. These allow the high resolution necessary, and also have the potential for indicating palaeoceanographic changes from fluctuations in the biota and the stable isotopes. Some of these sections also have magnetostratigraphic control and one (Gubbio) produces high-temperature radiometric dates (Montanari *et al.*, 1985). From these sections the most complete picture of this time interval is preserved.

Shallow marine sections, with their benthic invertebrates, are less complete and generally have lower resolution. Nevertheless, some information of good quality is beginning to emerge from the study of their contained faunas. Terrestrial sections are typically the rarest and least complete. Nevertheless, they have many advantages which make them important to the overall story. They often have excellent records of the changes in land faunas and floras. They also have the potential for magnetostratigraphy, and, in many cases, already have excellent high-temperature radiometric dates associated with the fossils and magnetics. In some intervals, such as

much of the Oligocene, the marine record is notoriously poor, but there is an excellent land section which currently gives the most detailed record of the mid-Oligocene extinction (Prothero, 1985a, 1985b).

In this section, I will review the evidence from these different sources of data, beginning with the pelagic record. Only after the empirical evidence has been reviewed will the discussion turn to possible causes. Too many previous studies have gone the other way, predicting an extinction at a certain time and then finding an event to fit it, while ignoring the rest of the data. Naturally, the conclusions of such selective interpretations of the fossil record are suspect.

### *The pelagic record*

The most complete record with highest resolution of all the events is offered by the deep sea. Since pelagic sediments (both biogenic and non-biogenic) settle out of the surface waters in an almost steady 'rain', they produce a remarkably complete record, with fewer unconformities than are found in the shallow marine or terrestrial environments. The deep sea is also unusual in that sedimentation and plankton distribution is controlled by large-scale water masses, which are orders of magnitude larger than the depositional environments and biogeographic regions that control shallow marine and terrestrial sediments and organisms. Thus, there are relatively few problems with local lithofacies or biofacies, and most of the differences are due to major changes in oceanographic circulation or world climate.

Keller (1983a, 1983b) has reviewed the evidence from planktonic foraminiferans from a number of deep-sea sites around the world. She recognizes five distinct events in the later Eocene and Oligocene. They are (in order from oldest to youngest):

*The Lutetian–Bartonian event* (middle Eocene, boundary between planktonic foram zones P12 and P13, top magnetic Chron C18R, about 43 million years BP). This was a relatively minor event, marked by the extinction or decline of a few key foraminiferan species. It apparently represents the beginning of cooling after the predominantly warm early and middle Eocene. It is marked by hiatuses in several deep-sea sections, indicating changes in oceanic circulation causing carbonate dissolution and/or bottom-water erosion. It is also marked by a lesser, but still significant, sea-level drop, labelled Tejas A3.4 by Haq *et al.* (1987). There are currently no detailed oxygen- or carbon-isotope data for this interval, but it does not stand out in the relatively low-resolution oxygen-isotope data of Shackleton and Kennett (1975) and Savin *et al.* (1975), or even the more recent data of Miller *et al.* (1987).

*The Bartonian–Priabonian event* (middle–late Eocene boundary, P14–P15 boundary, Chron C17R, about 41 million years BP). This was a major

extinction event, marked by the disappearance of spinose tropical foraminiferans and the migration towards the equator of mid-latitude faunas with the cooler water masses. This is also the most severe extinction event in the calcareous nannoplankton, wiping out almost 50% of the species (Aubry, 1983). There are major hiatuses in most deep-sea sections, and a major sea-level drop at the top of the Tejas A3 sequence of Haq *et al.* (1987). There is also a significant cooling event apparent in the oxygen isotopes (Miller and Curry, 1982). No event is apparent in the carbon isotopes, although the data still have very low resolution.

*The late Priabonian event* (late Eocene, P15–P16 boundary, Chron C15R, about 38 million years BP). This is a relatively minor event, marked by the dominance of cooler water foraminiferans in high latitudes. There are widespread deep-sea hiatuses, although sea level was already low through the Priabonian (Haq *et al.*, 1987). The oxygen isotopes again indicate further cooling, and there is a major change in the carbon isotopes (Miller, Curry, and Ostermann, 1985). This is the only event associated with microtektites (Hut *et al.*, 1987).

*The Terminal Eocene Event* (Eocene–Oligocene boundary, P17–P18 boundary, mid-Chron C13R, about 36.5 million years BP). This event has been extensively discussed in Pomeroy and Premoli-Silva (1986), and has received much attention in recent years. Ironically, when it was first christened by Wolfe (1978), he was actually referring to the mid-Oligocene event (Prothero, 1985b). However, there are relatively few extinctions in the foraminiferans, but simply an increase in dominance of cold-water forms (Corliss, 1981; Corliss *et al.*, 1984; Keller, 1983a, 1983b). The extinction in the calcareous nannoplankton is also minor compared to the Bartonian event (Aubry, 1983). The extinctions of ostracodes (Benson, 1975) and benthic foraminiferans, however, were quite severe. There is also a major shift in the oxygen isotopes (Keigwin, 1980; Miller and Curry, 1982), indicating global cooling of about 2–3°C, and another decline in the carbon isotopes (Miller, Curry, and Ostermann, 1985). There are no significant hiatuses in low- or middle-latitude sequences, but possibly some hiatuses at high latitudes. The sea level dropped slightly, although it was already at its Priabonian low (Haq *et al.*, 1987).

*The mid-Oligocene event* (late Rupelian, top P19, mid-Chron C11R, about 32.5 million years BP). This event was first described by Wolfe (1971) as the 'Oligocene deterioration' and then later mislabelled the 'Terminal Eocene Event' (Wolfe, 1978). In the pelagic record, it is marked by the extinction of many cool-water foraminiferans that dominated the early Oligocene, although the surviving forms are also associated with cold water. There is also a significant cooling event reflected in the nannoplankton (Haq *et al.*, 1977). There are major oxygen- and carbon-isotope excursions at this event (Keigwin and Keller, 1984), although they are not as severe as the

isotopic events at the Eocene–Oligocene boundary. There are major marine hiatuses in the late Rupelian, reflected mostly by the cutting of submarine canyons (Miller, Mountain, and Tucholke, 1985; Miller *et al.*, 1987). The most impressive record in the mid-Oligocene, however, is the largest offlap event in the entire Vail onlap-offlap curve. As currently calibrated by Haq *et al.* (1987), the Tejas A4.5 sequence begins about 32 million years ago and reaches its maximum offlap at 30 million years BP. Whether this is entirely due to eustatic sea-level change is still controversial, but the evidence of Miller, Mountain and Tucholke (1985) indicates that it must have been one of the biggest sea-level drops in Tertiary history.

Between these major events, most of the climatic indicators show evidence of warming and some restoration of pre-event conditions. In many cases, there is a renewed radiation of planktonic organisms to fill the gaps left by the extinctions. However, these radiations do not completely fill the niches, since there is an overall decline in diversity through the interval. Likewise, each post-event warming episode does not completely return to the prior temperature, so there is net cooling from the early Eocene to the mid-Oligocene.

#### *The shallow marine record*

Unlike the pelagic environment, the shallow marine environment is at or near erosional base level, so it is prone to erosional unconformities during lowstands in sea-level. As a consequence, the shallow marine record of the late Palaeogene is much less complete than the deep-sea record. In addition, the organisms have not been studied in nearly the detail that is seen for planktonic microfossils of the pelagic realm. Thus, the data for the shallow marine environment are much coarser in resolution, and, in many cases, have not been synthesized in a fashion useful to this discussion.

One of the few studies which has attempted to relate shallow marine organisms to the complex pattern seen in pelagic organisms was by Hansen (1987; also see Hut *et al.*, 1987). Hansen recognized several major extinctions in Gulf Coast molluscs through the later Eocene. After a middle Eocene peak in diversity, there were three episodes of extinction before the Oligocene. The first occurs at the Bartonian–Priabonian boundary, when 89% of the gastropod species and 84% of the bivalves became extinct. The second occurred in the late Priabonian, when 72% of the gastropods and 63% of the bivalves (those that survived or evolved since the last extinction) became extinct. The third occurred at the Eocene–Oligocene boundary, when 97% of the gastropods and 89% of the bivalves became extinct. There is no evidence of the Lutetian–Bartonian event, and the Gulf Coast record has a large Oligocene unconformity which wiped out any record of the mid-Oligocene.

Other studies have documented a similar pattern, although not in

sufficient detail to resolve the five separate extinction events. Hickman (1980) showed that warm-adapted species of molluscs declined and then disappeared along the Pacific Coast during the late Eocene. Zinsmeister (1982) showed that there was heavy extinction of molluscs in the Antarctic region during the Eocene–Oligocene transition. McKinney (1986) reported a major decline in echinoid diversity through the late Eocene, although the resolution of his data is not yet sufficient to determine if they match the pattern of events seen in the pelagic record.

Some work has been done on the isotopic composition of mollusc shells (Cavelier *et al.*, 1981). For example, Burchardt (1978) studied oxygen isotopes from mollusc shells from the North Sea. He found a steady decline in temperature from the Lutetian to the early Oligocene, with the most dramatic drop at the Eocene–Oligocene boundary. However, these data do not have the resolution to determine if there are other sudden isotopic shifts in the later Eocene. Nor were there sufficient data to determine if there is a discrete mid-Oligocene event, although the oxygen-isotope curve reached its 'coolest' point in the mid-Oligocene.

In addition to biological and isotopic evidence, there is now more direct evidence of climate in shallow marine sediments. Recent drilling in the Weddell Sea of Antarctica (Legs 113 and 114 of the Deep Sea Drilling Project) recovered evidence of glacial ice in Antarctica in the early Oligocene (Kennett and Barker, 1987; Wise *et al.*, 1987). There is also good evidence of another ice advance in the mid-Oligocene. As we shall see below, the isotopic evidence has demanded Oligocene glaciation for some time and the latest results seem to support this.

### The terrestrial record

Of the pelagic, shallow marine, and terrestrial records, the last is the most incomplete. Most terrestrial sediments are deposited far above base level, so they are rarely preserved and are prone to unconformities. Nevertheless, there are a number of remarkably complete sections that preserve parts of the later Eocene and Oligocene record, although there is no single place that records the entire interval, as do the best pelagic sections. The record of land plants and animals is so large on many continents that a clear signal emerges, even if the dating and resolution are not yet at the precision possible for the deep sea.

Several studies have attempted to assess climatic changes through changes in land plants. The most complete results are those of Wolfe (1971; 1978; Wolfe and Hopkins, 1967) for North America. Although there is not much resolution in the data, the floral evidence clearly shows a peak in warming around 43 million years BP (Lutetian), maximum cooling around 41 million years BP (the Bartonian–Priabonian event), warming again to a peak around 34 million years BP (early Oligocene), and then the most severe cooling event at 32 million years BP. This last decline is clearly

the mid-Oligocene event, labelled the 'Oligocene deterioration' by Wolfe (1971). These data do not have sufficient resolution to determine if the other three events might be present as well. Surprisingly, there is no clear floral evidence for the Eocene–Oligocene extinction (despite the mislabelling by Wolfe, 1978, Figure 1). The Bartonian–Priabonian and mid-Oligocene extinctions were each marked by decline in inferred mean annual temperatures of as much as 10°C, a remarkable cooling.

Although they have not been quantified in the same way as Wolfe's data, Collinson *et al.* (1981) and Collinson and Hooker (1987) found a similar floral transition in the Palaeogene of England. Middle Eocene floras are predominantly tropical, but, by the late Eocene, the tropical taxa have become extinct and are replaced by taxodiaceous swamps and reed marshes, with patches of woodland or forest. These reed marshes become dominant at the end of the Eocene and through the early Oligocene. This evidence from the megafloora is supported by evidence from pollen (Boulter and Hubbard, 1982; Hubbard and Boulter, 1983). Chateaufort (1980) studied floras of the Paris Basin. Diversity of tropical forms reached a high in the late Lutetian and early Bartonian, and then declined through the later Eocene. There were two sharp extinction events, one in the late Priabonian, and one that appears to be the Terminal Eocene Event. There are no data for the mid-Oligocene. Other floral evidence from Europe is reviewed by Cavelier *et al.* (1981).

Floral evidence from other parts of the world is in close agreement with the data from North America and Europe, even if the resolution is not very precise. Kemp (1978) summarized the floral data for Australia, Antarctica, and New Zealand throughout the Tertiary. Like other parts of the world, the middle Eocene was characterized by tropical rainforests. By the late Eocene, this vegetation had declined considerably and Oligocene vegetation is characterized by a low diversity of cool temperate forms.

Finally, in sections which do not preserve plant fossils directly, there are other methods of obtaining palaeobotanical evidence. Retallack (1983) examined palaeosols from the late Eocene of Oregon and the Oligocene of the Big Badlands of South Dakota. Late Eocene floras are again semi-tropical, but, at the Terminal Eocene Event, humid-climate floras are replaced by those of subhumid climates. Another palaeosol change occurs at the mid-Oligocene event, where palaeosols formed under subhumid climates are replaced by those formed under subarid conditions. These changes are so abrupt that they are responsible for major changes in sedimentological character of the lithologic units.

The land vertebrate record has been studied by a number of researchers. Hutchinson (1982) tabulated the generic diversity of turtles, crocodylians and champsosaurs through the Tertiary. Although he used resolution on the scale of the North American land mammal 'ages' (typically 2–4 million years in length), some clear trends emerge. There is a striking decline in total diversity from the middle Eocene to the late Eocene, composed mostly of the decline in crocodylians, champsosaurs and aquatic turtles.

There is a small increase in terrestrial turtles (mostly tortoises). Both of these trends indicate cooling and drying conditions. At the mid-Oligocene event (Chadronian–Orellan boundary), there is almost total extinction of aquatic turtles and crocodylians, and another increase in terrestrial turtles, which make up almost all the herpetofauna at this time. Indeed, land tortoises are such common fossils in the Orellan deposits of the Big Badlands that they were once known as the 'Turtle-Oreodon beds'. Rage (1986) noted similar changes in European herpetofaunas in the Eocene and Oligocene.

The best evidence of terrestrial change, however, comes from the excellent record of fossil mammals. This record is just now being calibrated against the magnetic polarity time-scale, making it possible to correlate it precisely with the marine record for the first time. For example, Prothero (1985b) calibrated North American Oligocene mammal-bearing sections against the magnetic polarity time-scale, and tabulated familial and generic diversity in million-year increments. He found a peak of both extinctions and originations in the late Duchesnean (late Priabonian), a peak of originations in the earliest Chadronian (Eocene–Oligocene boundary), and a peak of extinctions (but not originations) at the Chadronian–Orellan boundary (mid Oligocene event). Thus, the major turnover was concentrated, not at the Eocene–Oligocene boundary, but in the late Priabonian, some 2–3 million years before. The biostratigraphic and magnetostratigraphic data for the middle Eocene are not yet published, but preliminary results by Prothero (in prep.) and by Stucky (1989) suggest that there were extinction events at the Uintan–Duchesnean boundary that correspond to the Bartonian–Priabonian event or possibly the Lutetian–Bartonian event.

The qualitative aspects of this change are also interesting (Prothero, 1985b). A number of archaic groups (many of which were clearly browsers or arboreal forms) that characterized the middle Eocene began a steady decline through the later Eocene, and were extinct by the end of the Eocene in North America. These include mixodectids, microsypids, taeniodonts, achaenodonts, uintatheres, nyctitheriids, anaptomorphine primates, dermopterans, sciuravid rodents, dichobunid artiodactyls, limnocyonid and 'miacid' carnivores, mesonychids, hyopsodonts, isctolophid tapiroids and the ceratomorph *Hyrachyus*. These were replaced by the 'White River Chronofauna' (Emry, 1981), which was dominated by a number of families better suited for more open terrain and less forested habitat. Some were even grazers. Many of the key taxa are members of extant families which originated at this time, including the rabbits, dogs, camels, pocket gophers, squirrels, rhinos and shrews. This 'White River Chronofauna' maintained its stability throughout most of the Oligocene and was replaced in the early Miocene. The one exception to this stability was the wave of extinctions at the Chadronian–Orellan boundary (mid-Oligocene event), which wiped out the last vestige of archaic forms characteristic of the Eocene. These included the titanotheres, multituberculates, pantolestids, oromerycids, epoicotheres, and paramyid and cylin-

dodont rodents. They are replaced by leptacchenine oreodonts and eumyine cricetid rodents, both groups with much more abrasive-resistant dentitions.

Similar patterns have been observed in European mammals, although these faunas have not yet been calibrated by magnetostratigraphy. At one time, the discussion centred around 'la Grande Coupure' of Stehlin (1909), the dramatic faunal turnover event that completely changed European mammalian faunas between the Eocene and Oligocene. Recent studies by Brunet (1977), Legendre (1987) and Hartenberger (1986; 1987) have revealed a more complex picture. There is high turnover throughout the late Eocene, so that the 'Grande Coupure' may represent a composite of both the late Priabonian and Terminal Eocene Events. There is also another peak of turnover that may correspond to the Bartonian–Priabonian event as well (Hartenberger, 1986, Figure 4). Like North American faunas, European faunas show a peak of extinctions, but not originations, at the mid-Oligocene event (Sannoisian–Stampian event). There is apparently no evidence for a Lutetian–Bartonian event in European land mammals, however.

In the middle Eocene, the European fauna was dominated by primates, multituberculates, 'insectivores', creodonts, archaic ungulates ('condylarths'), tillodonts, pantodonts, and archaic perissodactyls (such as palaeotheres and lophiodonts) and artiodactyls (mostly 'dichobunids', xiphodonts, choeropotamids, cebochoerids, mixtotheriids, dacrytheriids, anoplotheriids, amphimerycids, and cainotheriids). As a consequence of the 'Grande Coupure', the fauna was radically rearranged (Hartenberger, 1986; 1987). By the early Oligocene, European faunas are dominated by rodents (mostly theridomyids), advanced carnivores (mostly amphicyonids, mustelids, viverrids, procyonids, ursids and nimravids), advanced artiodactyls (particularly anthracotheres, leptomerycids, entelodonts, and tayassuids) and advanced perissodactyls (particularly rhinocerotoids and chalicotheres). Rabbits also make their first appearance and become an important element of the fauna. Archaic groups, particularly the creodonts, archaic ungulates, multituberculates, tillodonts and pantodonts, were extinct, and once-dominant arboreal groups, such as primates, were locally extinct.

Collinson and Hooker (1987) reviewed the changes in land mammals in the London Clay through the Palaeogene. In the Bartonian, there was a great reduction in small mammals, particularly insectivores, and an increase in large ground mammals and browsing herbivores. In the Priabonian, there was a drastic reduction in arboreal mammals, as well as small mammals and insectivores, and a great increase in large ground mammals and browsing herbivores. The rodent fauna changed from frugivorous pseudosciurids to browsing theridomyids. There was a major extinction of soft-browsing perissodactyls and replacement with coarse-browsing forms. Finally, at the Eocene–Oligocene boundary, the arboreal types disappeared, and large mammals dominated. At this point, granivorous rodents

made their first appearance. All of these changes are consistent with the vegetational changes seen by Collinson and Hooker (1987), where tropical forests of the Lutetian are replaced by taxodiaceous swamps and fresh-water reed marshes in the late Eocene.

Similar changes have been observed for the Eocene and Oligocene faunas of Asia and South America, although the details of the turnover have not been worked out as carefully as they have for North America and Europe (Savage and Russell, 1983). Without question, the Eocene-Oligocene transition is the most important turnover event in the history of Cenozoic mammals (Lillegraven, 1972). It marked the end of the forest-dwelling, browsing fauna that dominated the Palaeocene and Eocene, and the beginning of the 'modern' fauna, which is much more adapted to open country (particularly savannahs) and grazing.

### CAUSES OF THE EOCENE/OLIGOCENE EXTINCTIONS

Now that we have reviewed the empirical data for the patterns of extinction, it is appropriate to speculate on the causes. It is clear that there are at least five steps of extinction (43, 41, 38, 36.5 and 32.5 million years BP) spaced out over 10 million years. Thus, models which attribute these extinctions to a single catastrophic event (such as the asteroid model of Alvarez *et al.*, 1982; Asaro *et al.*, 1982; Ganapathy, 1982) cannot be correct. We must search for causative agents which are capable of inducing climatic stress over a 10-million-year interval. Such agents can either be terrestrial or extraterrestrial. I will review the terrestrial evidence first.

In recent years, the evidence for major global climatic changes during the Eocene-Oligocene transition has become overwhelming. Much of this evidence is reviewed above. It is clear that the Earth underwent a stepwise cooling of over 10°C during this interval (Savin *et al.*, 1975), with pulses of cooling in the Bartonian, the Terminal Eocene Event and the mid-Oligocene event. This global cooling, and the associated changes in weather patterns and moisture, were undoubtedly responsible for the largest part of the extinctions, especially in the terrestrial and shallow marine realms (Stanley, 1984; 1987). The real question centres around the causes of this global cooling.

Abundant evidence suggests that the major cause was oceanographic changes. The oxygen-isotopic evidence is now interpreted by many authors (among them Matthew and Poore, 1980; Miller and Fairbanks, 1983; 1985; Keigwin and Keller, 1984) as evidence for Oligocene Antarctic glaciation. The recently reported data from the Weddell Sea of Antarctica (Kennett and Barker, 1987; Wise *et al.*, 1987) confirm the presence of early Oligocene sea-ice, although the full development of the Antarctic ice-cap may not have occurred until the Miocene. Along with growth of the Antarctic ice-cap was the development of cold, deep bottom-water masses (the 'psychrosphere'), which shows up not only in the isotopic data, but

also in dissolution and erosion of the deep-sea record. According to Benson (1975), Kennett (1977), Keigwin (1980), and Keller (1983a, 1983b) the psychrosphere first developed at the Terminal Eocene Event.

These oceanographic changes are attributed to rearrangements of oceanic circulation caused by plate tectonics. The obvious candidate (Kennett, 1977) is the separation of Australia from Antarctica, which allowed water to circulate between the two continents. Once this circulation developed, it triggered the beginning of circum-Antarctic circulation. Today, this current traps cold water in a continuous cycle around Antarctica, refrigerating the South Pole and generating cold deep bottom water. It is also responsible for isolating the polar waters and generating a larger gradient in temperatures between pole and equator. By contrast, during the Eocene, polar waters in the southern Indian Ocean or southern Pacific exchanged with warmer, lower-latitude waters, allowing mixing and a less extreme temperature gradient between pole and equator.

The key question is how this model explains the five-step decline in world climate. Kennett (1977) and Murphy and Kennett (1986) cited evidence to show that shallow-water circulation between Australia and Antarctica began about 38 million years BP, in the latest Eocene. Benson *et al.* (1986) suggested that this psychrospheric circulation developed even earlier in the late Eocene, which might explain the major Bartonian-Priabonian event. The Eocene-Oligocene boundary is the final threshold of this transition. Much new evidence is needed to determine the timing of these events and see if they are really as discrete as other data suggest. Kennett (1977) and Murphy and Kennett (1986) cited evidence to show that deep-water circulation between Australia and Antarctica developed in the middle Oligocene. There is evidence for a major mid-Oligocene glaciation (Miller, Mountain, and Tucholke, 1985), which might explain the mid-Oligocene extinctions and the record drop in sea level.

Although these Southern Hemisphere events undoubtedly had the major effect on ice formation and global cooling, the Northern Hemisphere may have amplified the effect. The opening of the Greenland-Norway passage, allowing exchange between the Arctic and Atlantic, is believed to have occurred near the Eocene-Oligocene boundary (Talwani and Eldholm, 1977; Berggren, 1982). More recent data (Miller and Fairbanks, 1983), however, show evidence for the development of the North Atlantic Deep Water (NADW) by the earliest Oligocene.

These palaeoceanographic events were undoubtedly the major forcing factors of global climate and thus probably the primary causes of the Eocene-Oligocene extinctions. In recent years, however, a number of non-oceanographic models have been proposed. As we have seen, the prolonged and stepwise nature of the extinctions and climatic change rule out single catastrophic events, such as asteroids. Two other possibilities remain that could fit the evidence: vulcanism and comet showers.

Kennett *et al.* (1985) point out that there is a pulse of vulcanism in the southwest Pacific just before the Terminal Eocene Event. It is well known

that volcanic aerosols, particularly sulphuric acid, cause climatic change. The 'volcano weather' caused by the eruption of Krakatoa is a well-known example. Kennett *et al.* (1985) suggest that this southwest Pacific volcanism amplified the climatic changes already associated with the development of Antarctic circulation and glaciation. Volcanic ashes are abundant through the late Priabonian and early Oligocene, so they may have influenced two of the five extinction pulses.

Rampino and Stothers (1988) pointed out that many of the great mass extinctions in the last 250 million years were associated with eruptions of flood basalts. Officer and Drake (1985) made a strong case for the K-T extinctions being caused by the eruption of the Deccan traps. There are similar traps which erupted in Ethiopia during the early phases of the opening of the East African Rift. According to Rampino and Stothers, the start of the main phase of eruption began around  $35 \pm 2$  million years BP, and continued through the Oligocene. This suggests that 'volcano weather' might be a possible factor in the Oligocene, but does nothing to explain the long Eocene decline. In addition, Rampino and Stothers attribute the supposed periodicity of these flood basalts to impact cratering by comets. This seems highly implausible, since flood basalts are generated from deep in the lower crust and mantle where no comet impact could penetrate. In addition, each episode of flood basalt eruption is associated with rifting and has known plate tectonic causes. If the periodicity is real, it is more likely that there is some sort of periodicity in mantle overturn (Sheridan, 1987).

The most glamorous models for mass extinctions are extraterrestrial in nature. Despite the great attention they receive in the popular press, they are inadequate to explain the Eocene-Oligocene climatic and faunal changes. The single catastrophic asteroid model fails completely for reasons discussed above. The iridium anomaly reported by Ganapathy (1982) and Alvarez *et al.* (1982) apparently has no relation to any of the extinction events discussed above. In addition, Kye and Wasson (1986) find no such iridium anomaly anywhere in the Eocene or Oligocene. Consequently, a series of comet showers spread out over millions of years has been offered as an alternative which fits the prolonged, stepwise nature of the extinctions (Hut *et al.*, 1987). As Hut *et al.* (1987) point out, however, only one of the five Eocene-Oligocene extinctions seems to be associated with microtektites, and it is one of the least severe (the late Priabonian event). Most of the microtektite horizons correspond to dissolution horizons, or do not have any correspondence to known episodes of extinction (Keller *et al.*, 1983; Hut *et al.*, 1987, Figure 4).

Despite this tenuous evidence, Hut *et al.* (1987) persisted in attributing at least some of the Eocene-Oligocene extinctions to extraterrestrial causes. It seems obvious from the discussion above, however, that the earth's climate and biota were much more strongly affected by major palaeoceanographic changes. These must have been the primary forcing agent, no matter how much material was or was not coming in from outer space. At best, it appears that extraterrestrial materials influenced only the

weakest and least dramatic of the extinction events. All of the rest are clearly a result of terrestrial causes.

## SUMMARY

Extinctions in the late Eocene and Oligocene took place in five steps spaced out over 10 million years (43, 41, 38, 36.5, and 32.5 million years BP). These extinctions can be seen in pelagic, shallow marine, and terrestrial animals and plants to varying degrees. The Eocene-Oligocene extinctions are associated with many indicators of climatic change, including severe cooling, glaciation and changes in oceanographic circulation, which were undoubtedly the proximal causes of extinction. This climatic change is primarily the result of the development of the circum-Antarctic current due to the separation of Antarctica from Australia. Other factors, such as vulcanism, or comet showers, may have had a minor reinforcing effect on one or two of these extinction events, but clearly did not cause most of the climatic change that was primarily responsible for the extinctions.

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## NOTE ADDED IN PROOF

The numerical calibration of the late Paleogene timescale has been changing almost weekly since this chapter was last revised. New argon-argon dates on a number of marine and terrestrial sections suggest that the Eocene-Oligocene boundary is between 33.5 and 34 million years in age, contrary to the age of 36.5 used by Berggren *et al.* (1985) and Haq *et al.* (1987). These changes mean that the entire timescale will need to be revised in the near future, but at the moment it is difficult to determine what numerical ages will be assigned to the events described in this paper. If my estimates are correct, then the Lutetian-Bartonian event would occur at about 40 million years BP, the Bartonian-Priabonian event at about 38, the late Priabonian event at about 36, the Eocene-Oligocene boundary at about 33.7, and the mid-Oligocene event at about 30.5. Regardless of how the numerical age assignments of these events are revised, the data and discussions in this paper are based on the relative

stratigraphic sequence, so the general conclusions about marine events are unaffected by these new dates.

However, these new argon-argon dates on terrestrial sequences radically change the correlation of North American land mammal "ages" with the marine chronologies. Calibration of the terrestrial magnetostratigraphy (Prothero, 1985a, 1985b) with the new dates gives the following results: Chadronian—from C16N to top C13R (33–37 million years ago); Orellan—from top C13R to mid-C12R (31.5–33 million years); Whitneyan—from mid-C12R to base C11N (29–31.5 million years); Arikareean—from 21–29 million years. More importantly, these correlations imply that the Bartonian/Priabonian event is the Chadronian/Duchesnean transition, the Chadronian is entirely late Eocene, and the Chadronian/Orellan boundary (labeled the mid-Oligocene event in this paper) is actually the Terminal Eocene Event. The mid-Oligocene event probably falls in the Whitneyan.

## REFERENCES

- Alvarez, W., Asaro, F., Michel, H.V. and Alvarez, L.W., 1982. Iridium anomaly approximately synchronous with terminal Eocene extinctions. *Science*, **216** (4548): 880–8.
- Asaro, F., Alvarez, L.W., Alvarez, W. and Michel, H.V., 1982. Geochemical anomalies near the Eocene/Oligocene and Permian/Triassic boundaries. In L.T. Silver and P.H. Schultz (eds), *Geological implications of impacts of large asteroids and comets on the Earth. Special Paper of the Geological Society of America*, **190**: 517–28.
- Aubry, M.-P., 1983. Late Eocene to early Oligocene calcareous nannoplankton biostratigraphy and biogeography. *Bulletin of the American Association of Petroleum Geologists*, **67** (3): 415.
- Aubry, M.-P., Berggren, W.A., Kent, D.V., Flynn, J.J., Klitgord, K.D., Obradovich, J.D. and Prothero, D.R., 1989. Paleogene geochronology; an integrated approach. *Paleoceanography*, **3** (6): 707–42.
- Benson, R.H., 1975. The origin of the psychrosphere as recorded in changes of deep-sea ostracod assemblages. *Lethaia*, **8** (1): 69–83.
- Benson, R.H., Chapman, R.E. and Deck, L.T., 1986. Paleocceanographic events and deep-sea ostracods. In K.J. Hsü *et al.* (eds), *South Atlantic Paleocceanography*. Cambridge University Press, Cambridge: 325–50.
- Berggren, W.A., 1982. Role of ocean gateways in climate change. In W.H. Berger and J.C. Crowell (eds), *Climate in Earth history*. National Academic Press, Washington, DC: 118–25.
- Berggren, W.A., 1986. Geochronology of the Eocene–Oligocene boundary. In C. Pomerol and I. Premoli-Silva (eds), *Terminal Eocene events*. Elsevier, Amsterdam: 349–56.
- Berggren, W.A., Kent, D.V. and Flynn, J.J., 1985. Paleogene geochronology and chronostratigraphy. In N.J. Snelling (ed.), *The chronology of the geological record, Memoir of the Geological Society of London*, **10**: 141–95.
- Boulter, M.C. and Hubbard, R.N.L.B., 1982. Objective palaeoecological and biostratigraphic interpretation of Tertiary palynological data by multivariate statistical analysis. *Palynology*, **6** (1): 55–68.
- Brunet, M., 1977. Les mammifères et le problème de la limite Eocène-Oligocène en Europe. *Mémoires Spéciaux Geobios*, **1**: 11–27.
- Burchardt, B., 1978. Oxygen isotope palaeotemperature from the Tertiary Period in the North Sea area. *Nature*, **275** (5676): 121–3.
- Cavelier, C., Chateaufneuf, J.-J., Pomerol, C., Rabussier, D., Renard, M. and Vergnaud-Grassini, C., 1981. The geological events at the Eocene–Oligocene boundary. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **36** (3–4): 223–48.
- Chateaufneuf, J.-J., 1980. Palynostratigraphie et paléoclimatologie de l'Eocène supérieur et de l'Oligocène du Bassin du Paris (France). *Mémoires de la Bureau de Recherches Géologiques et Minières*, **116**: 1–357.
- Collinson, M.E., Fowler, K. and Boulter, M.C., 1981. Floristic changes indicate a cooling climate in the Eocene of southern England. *Nature*, **291** (5813): 315–17.
- Collinson, M.E. and Hooker, J.J., 1987. Vegetational and mammalian faunal changes in the early Tertiary of southern England. In E.M. Friis, W.G. Chaloner and P.R. Crane (eds), *The origin of angiosperms and their biological consequences*. Cambridge University Press, Cambridge: 259–304.
- Corliss, B., 1981. Deep-sea benthonic foraminiferal faunal turnover near the Eocene/Oligocene boundary. *Marine Micropaleontology*, **6** (4): 357–84.
- Corliss, B., Aubry, M.-P., Berggren, W.A., Fenner, J.M., Keigwin, L.D., Jr and Keller, G., 1984. The Eocene/Oligocene boundary event in the deep sea. *Science*, **226** (4676): 806–10.
- Curry, D. and Odin, G.S., 1982. Dating of the Palaeogene. In G.S. Odin (ed.), *Numerical dating in stratigraphy*. Wiley and Sons, New York: 607–30.
- Emry, R.J., 1981. Additions to the mammalian fauna of the type Duchesnean, with comments on the status of the Duchesnean 'Age'. *Journal of Paleontology*, **55** (3): 563–70.
- Fischer, A.G. and Arthur, M.A., 1977. Secular variations in the pelagic realm. *Special Publication of the Society of Economic Paleontologists and Mineralogists*, **25**: 19–50.
- Ganapathy, R., 1982. Evidence for a major meteorite impact on the Earth 34 million years ago: implications for Eocene extinctions. *Science*, **216** (4549): 885–6.
- Hansen, T.A., 1987. Extinction of late Eocene to Oligocene molluscs: relationship to shelf area, temperature changes, and impact events. *Palaios*, **2** (1): 69–75.
- Haq, B.U., Hardenbol, J. and Vail, P.R., 1987. Chronology of fluctuating sea levels since the Triassic. *Science*, **235** (4793): 1156–67.
- Haq, B.U., Premoli-Silva, I. and Lohmann, G.P., 1977. Calcareous plankton paleobiogeographic evidence for major climatic fluctuations in the early Cenozoic Atlantic Ocean. *Journal of Geophysical Research*, **82** (27): 3861–76.
- Hartenberger, J.-L., 1986. Crises biologiques en milieu continental au cours du Paléogène: exemple des mammifères d'Europe. *Bulletin des Centres de Recherches Exploration-Production Elf-Aquitaine*, **10** (2): 489–500.
- Hartenberger, J.-L., 1987. Modalités des extinctions et apparitions chez les mammifères du Paléogène d'Europe. *Mémoires de la Société Géologique de France*, new series, **150**: 133–43.
- Hickman, C.S., 1980. Paleogene marine gastropods of the Keasey Formation of Oregon. *Bulletins of American Paleontology*, **78** (310): 1–112.
- Hubbard, R.N.L.B. and Boulter, M.C., 1983. Reconstruction of Palaeogene climate from palynological evidence. *Nature*, **301** (5896): 147–50.



- Hut, P., Alvarez, W., Elder, W.P., Hansen, T.A., Kaulfman, E.G., Keller, G., Shoemaker, E.G. and Weissman, P.R., 1987, Comet showers as a cause of mass extinctions, *Nature*, **329** (6135): 118-25.
- Hutchinson, J.H., 1982, Turtle, crocodylian, and champsosaur diversity changes in the Cenozoic of the north-central region of the western United States, *Palaeogeography, Palaeoclimatology, Palaeoecology*, **37** (2-4): 149-64.
- Keigwin, L.D., Jr., 1980, Palaeoceanographic change in the Pacific at the Eocene-Oligocene boundary, *Nature*, **287** (5784): 722-5.
- Keigwin, L.D., Jr and Keller, G., 1984, Middle Oligocene cooling from equatorial Pacific DSDP Site 77B, *Geology*, **12** (1): 16-19.
- Keller, G., 1983a, Paleoclimatic analysis of middle Eocene through Oligocene planktic foraminiferal faunas, *Palaeogeography, Palaeoclimatology, Palaeoecology*, **43** (1): 73-94.
- Keller, G., 1983b, Biochronology and paleoclimatic implications of middle Eocene to Oligocene planktic foraminiferal faunas, *Marine Micropaleontology*, **7** (1982/1983): 463-80.
- Keller, G., d'Hondt, S. and Vallier, T.L., 1983, Multiple microtektite horizons in Upper Eocene marine sediments: no evidence for mass extinctions, *Science*, **221** (4606): 150-3.
- Kemp, E.M., 1978, Tertiary climatic evolution and vegetation history in the southeast Indian Ocean region, *Palaeogeography, Palaeoclimatology, Palaeoecology*, **24** (3): 169-208.
- Kennett, J.P., 1977, Cenozoic evolution of Antarctic glaciation, the Circum-Antarctic Ocean, and their impact on global paleoceanography, *Journal of Geophysical Research*, **82** (27): 3843-59.
- Kennett, J.P. and Barker, P., 1987, Cenozoic paleoclimatic and paleoceanographic history of Antarctica: overview from ODP Leg 113, *Geological Society of America Abstracts with Programs*, **19** (7): 725.
- Kennett, J.P. et al., 1985, Palaeotectonic implications of increased late Eocene-early Oligocene volcanism from south Pacific DSDP sites, *Nature*, **316** (6028): 507-11.
- Kyte, F.T. and Wasson, J.T., 1986, Accretion rate of extraterrestrial matter: iridium deposited 33 to 67 million years ago, *Science*, **232** (4755): 1225-9.
- Legendre, S., 1987, Concordance entre paléontologie continentale et les événements paléocéanographiques: exemple des faunes de mammifères du Paléogène du Quercy, *Centre de Recherche de l'Académie des Sciences de Paris*, **304**: 45-9.
- Lillegraven, J.A., 1972, Ordinal and familial diversity of Cenozoic mammals, *Taxon*, **21** (2-3): 261-74.
- McKinney, M.L., 1986, Cenozoic echinoid diversity and mass extinction patterns closely tied to temperature, *Abstracts 4th North American Paleontological Convention*, A32.
- Matthews, R.K. and Poore, R.Z., 1980, Tertiary  $\delta^{18}\text{O}$  record and glacio-eustatic sea-level fluctuations, *Geology*, **8** (10): 501-4.
- Miller, K.G. and Curry, W.B., 1982, Eocene to Oligocene benthic foraminiferal isotopic record in the Bay of Biscay, *Nature*, **296** (5855): 347-50.
- Miller, K.G., Curry, W.B. and Ostermann, D.R., 1985, Late Paleocene benthic foraminiferal paleoceanography of the Goban Spur region, DSDP Leg 80, *Initial Reports of the Deep Sea Drilling Project*, **80**: 505-38.
- Miller, K.G. and Fairbanks, R.G., 1983, Evidence for Oligocene-Middle Miocene abyssal circulation changes in the western north Atlantic, *Nature*, **306** (5940): 250-3.

- Miller, K.G. and Fairbanks, R.G., 1985, Oligocene-Miocene global carbon and abyssal circulation changes, *Geophysical Monograph Series*, **32**: 469-86.
- Miller, K.G., Fairbanks, R.G. and Mountain, G.S., 1987, Tertiary oxygen isotope synthesis, sea level history, and continental margin erosion, *Palaeoceanography*, **2** (1): 1-19.
- Miller, K.G., Mountain, G.S. and Tucholke, B.E., 1985, Oligocene glacio-eustasy and erosion on the margins of the North Atlantic, *Geology*, **13** (1): 10-13.
- Montanari, A., Drake, R., Bice, D.M., Alvarez, W., Curtis, G.H., Turrin, B.D. and DePaolo, D.J., 1985, Radiometric time scale for the upper Eocene and Oligocene based on K/Ar and Rb/Sr dating of volcanic biotites from the pelagic sequence of Gubbio, Italy, *Geology*, **13** (9): 596-9.
- Murphy, M.G. and Kennett, J.P., 1986, Development of latitudinal thermal gradients during the Oligocene: oxygen isotope evidence from the southwest Pacific, *Initial Reports of the Deep Sea Drilling Project*, **90**: 1347-60.
- Officer, C.B. and Drake, C.L., 1985, Terminal Cretaceous environmental events, *Science*, **227** (4691): 1161-7.
- Pomeroy, C. and Premoli-Silva, L. (eds), 1986, *Terminal Eocene events*, Elsevier, Amsterdam.
- Prothero, D.R., 1985a, Mid-Oligocene extinction events in North American land mammals, *Science*, **229** (4713): 550-1.
- Prothero, D.R., 1985b, North American mammalian diversity and Eocene-Oligocene extinctions, *Paleobiology*, **11** (4): 389-405.
- Rage, J.C., 1986, The amphibians and reptiles at the Eocene-Oligocene transition in western Europe: an outline of the faunal alterations, In C. Pomeroy and L. Premoli-Silva (eds), *Terminal Eocene events*, Elsevier, Amsterdam: 309-10.
- Rampino, M.R. and Stothers, R.B., 1988, Flood basalt volcanism during the past 250 million years, *Science*, **241** (4800): 663-8.
- Raup, D.M. and Sepkoski, J.J., Jr., 1984, Periodicity of extinctions in the geologic past, *Proceedings of the National Academy of Science U.S.A.*, **81** (3): 801-5.
- Retallack, G.J., 1983, Late Eocene and Oligocene paleosols from Badlands National Park, South Dakota, *Special Paper of the Geological Society of America*, **193**: 1-82.
- Savage, D.E. and Russell, D.E., 1983, *Mammalian paleofaunas of the world*, Addison-Wesley, Reading, MA.
- Savin, S.M., Douglas, R.G. and Stehli, F.G., 1975, Tertiary marine paleotemperatures, *Bulletin of the Geological Society of America*, **86** (11): 1499-1510.
- Shackleton, N.J. and Kennett, J.P., 1975, Paleotemperature history of the Cenozoic and the initiation of Antarctic glaciation: oxygen and carbon isotopic analyses of DSDP Sites 277, 279, and 281, *Initial Reports of the Deep Sea Drilling Project*, **29**: 743-55.
- Sheridan, R.E., 1987, Pulsation tectonics and the control of continental breakup, *Tectonophysics*, **143** (1): 59-73.
- Snelling, N.J., 1985, An interim time scale, In N.J. Snelling (ed.), *The chronology of the geological record*, *Memoir of the Geological Society of London*, **10**: 261-5.
- Stanley, S.M., 1984, Marine mass extinction: a dominant role for temperature, In M.H. Nitecki (ed.), *Extinctions*, University of Chicago Press, Chicago: 69-117.
- Stanley, S.M., 1987, *Extinction*, Scientific American Books, New York.
- Stehlin, H.G., 1909, Remarques sur les faunules de mammifères des couches éocènes et oligocènes du Bassin de Paris, *Bulletin de la Société Géologique de France*, series 4, **9**: 488-520.
- Stucky, R.K., 1989, Evolution of land mammal diversity in North America during

- the Cenozoic. In H.H. Grenoways (ed.), *Current mammalogy* 2. Plenum Press, New York.
- Talwani, M. and Eldholm, O., 1977. Evolution of the Norwegian-Greenland Sea. *Bulletin of the Geological Society of America*, **88** (7): 969-99.
- Wise, S.W., et al., 1987. Early Oligocene ice on the Antarctic continent. *Geological Society of America Abstracts with Programs*, **19** (7): 893.
- Wolfe, J.A., 1971. Tertiary climatic fluctuations and methods of analysis of Tertiary floras. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **9** (1): 27-57.
- Wolfe, J.A., 1978. A paleobotanical interpretation of Tertiary climates in the Northern Hemisphere. *American Scientist*, **66** (6): 694-703.
- Wolfe, J.A. and Hopkins, D.M., 1967. Climatic changes recorded by Tertiary land floras in northwestern North America. In K. Hatai (ed.), *Tertiary correlations and climatic changes in the Pacific*. Sasaki Publishers, Sendai, Japan: 67-76.
- Zinsmeister, W.J., 1982. Late Cretaceous-Early Tertiary molluscan biogeography of the southern Circum-Pacific. *Journal of Paleontology*, **56** (1): 84-102.