

THE LATE EOCENE-OLIGOCENE EXTINCTIONS

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INTRODUCTION

The transition from the Eocene to the Oligocene Epochs, from about 40 to 30 Ma (million years ago), was the most significant interval in Earth history since the dinosaurs died out 65 Ma. From the warm, equable "greenhouse" climate of the early Eocene (a relict of the age of dinosaurs), the Earth experienced major climatic changes. Global temperature plummeted, and the first Antarctic ice sheets appeared. These climatic stresses triggered extinctions in plants and animals, both on land and in the oceans. By the early Oligocene (33 Ma), the Earth had a much cooler, more temperate climate, with a much lower diversity of organisms. Indeed, the Eocene-Oligocene transition marked the change from the global "greenhouse" world of the Cretaceous and early Cenozoic to the glaciated "ice house" world of today.

Despite the intense research interest in mass extinctions over the past two decades, the Eocene-Oligocene extinctions have been relatively understudied and misunderstood. While hundreds of papers have been published on the terminal Cretaceous extinction of dinosaurs and ammonites since the discovery of the iridium anomaly in 1980, only a few dozen articles have been published on the Eocene-Oligocene extinctions. Much of this work has now been invalidated by new data.

In the enthusiasm to force the Eocene-Oligocene extinctions into the mold of the Cretaceous-Tertiary impact hypothesis and the periodic extinction hypothesis (Raup & Sepkoski 1984), a lot of misinformation has appeared. Typically, impact proponents treat the Eocene-Oligocene tran-

sition as a single catastrophic "Terminal Eocene Event" that happened precisely 26 million years after the terminal Cretaceous event. The discovery of iridium and other extraterrestrial impact debris near the end of the Eocene was also much publicized (Alvarez et al 1982, Asaro et al 1982, Ganapathy 1982, Glass et al 1982), as if this evidence was sufficient by itself to explain late Eocene events.

In the 1980s, however, scientists began to conduct detailed studies which allowed sober reassessment of the various explanations of Eocene-Oligocene events. The 1985 International Geological Correlation Project 174 Symposium which focused only on the "Terminal Eocene Event" (Pomeroy & Premoli-Silva 1986) was followed by a 1989 Penrose Conference which brought together much new data from both the terrestrial and marine realms over the entire 10 million years of the Eocene-Oligocene transition (Prothero & Berggren 1992). New information from the deep sea, especially from Ocean Drilling Project (ODP) cruises in the Southern Ocean, greatly improved our understanding of Antarctic climatic changes. Detailed studies of the changes in terrestrial soils, plants, snails, and mammals were finally undertaken.

The most important breakthrough, however, did not come from new records of the transition, but from improved dating and correlation of the existing data base. By means of $^{40}\text{Ar}/^{39}\text{Ar}$ dating and magnetic stratigraphy, major errors in the correlation and calibration of the time scale were discovered and corrected (Swisher & Prothero 1990, Prothero & Swisher 1992, Berggren et al 1992). As a result, all correlations and numerical age estimates (and the conclusions based upon them) published before 1990 are now out of date. This review updates the current state of our understanding of this fascinating period in Earth history, based on the data summarized previously (Prothero & Berggren 1992, Prothero 1994) and new information that has emerged since then.

THE TIME SCALE

Before discussing the data on the Eocene-Oligocene transition, let us review the latest developments in dating this episode. The correlation and calibration of Eocene and Oligocene rocks are not as simple and straightforward as one might expect. Radiometrically datable materials are only available from scattered volcanic ash layers in a few restricted localities. Correlation and dating must be done by detailed biostratigraphic studies in marine sections and cores which only occasionally contain volcanic materials for dating (Hardenbol & Berggren 1978, Montanari 1990). Most of the dates in marine rocks have come from the greenish K-rich clay mineral glauconite, which has been unreliable in some cases in the

past (Obradovich 1989, Aubry et al 1989). Consequently, several different time scales have been published for the marine Eocene and Oligocene, with significant discrepancies. For example, the Eocene-Oligocene boundary has been placed as young as 32 Ma (Odin 1982) and as old as 38 Ma (Lowrie et al 1982, Harland et al 1982), with the most commonly cited value at 36.5 Ma (Berggren et al 1985). This is an enormous range of age estimates for a stratigraphic boundary that is so recent in the geologic past.

The situation becomes even more difficult when it comes to correlating terrestrial rocks to the marine standard. Eocene-Oligocene marine and non-marine rocks rarely interfinger to allow direct correlation. The best, most fossiliferous terrestrial sequences occur in continental interior basins, with no chance of direct correlation to sequences bearing marine fossils. Thus, the terrestrial record has its own provincial time scale, such as the North American land mammal "ages" (Wood et al 1941, Woodburne 1987) and their Eurasian and South American counterparts (Savage & Russell 1983). A similar time scale was established for fossil plants in the Pacific Northwest of North America (Wolfe 1981). Both were calibrated with potassium-argon (K-Ar) dates from volcanic ash layers (Evernden et al 1964, Evernden & James 1964, Krishtalka et al 1987, Emry et al 1987). Fresh, datable ash layers are much more abundant on land than they are in the ocean, since they are closer to their volcanic source and do not experience submarine weathering.

Nevertheless, the sparse K-Ar dates on terrestrial sequences gave only a rough equivalence to the marine record (Berggren et al 1978, 1985; Krishtalka et al 1987; Emry et al 1987). In North America, the Eocene and Oligocene land mammal "ages" were not based on biostratigraphic stages, nor were they subdivided into increments of less than 2–3 million years in duration. These crude correlations gave relatively low resolution, although the overall pattern of change was sufficient for the "big picture" to emerge (Lillegraven 1972, Webb 1977).

The scarcity of reliable radiometric dates in marine sequences forced biostratigraphers to tie in terrestrial volcanic ash dates wherever possible (Berggren et al 1978, 1985). This was greatly facilitated when magnetic stratigraphy emerged as a method that could correlate terrestrial and marine records (Prothero et al 1982, 1983; Flynn 1986). But such magnetic correlations were only as good as the radioisotopic dates on which they were based. As long as potassium-argon was the only dating technique available, there was no way to check its reliability.

The development of $^{40}\text{Ar}/^{39}\text{Ar}$ dating represented a major breakthrough in Cenozoic geochronology (McDougall & Harrison 1988). Not only could the same volcanic ashes be double-checked with a different isotopic system,

but there were many other advantages. $^{40}\text{Ar}/^{39}\text{Ar}$ dating allows much greater precision (error estimates of only $\pm 100,000$ – $200,000$ years, rather than the $\pm 700,000$ – $1,000,000$ years typical of K-Ar), and dates can be determined from much smaller amounts of material. This made it possible to analyze many previously undatable layers for the first time. Most importantly, $^{40}\text{Ar}/^{39}\text{Ar}$ dating can detect problems of contamination and alteration much more successfully than the old K-Ar methods. In the stepwise heating method, the contamination appears as a spectrum of apparent ages, before the true age (from the interior of the crystal) plots as a plateau. In the single-crystal laser-fusion method, each crystal is individually picked by hand, evaluated for freshness, and then vaporized by laser to release all of its argon. With the new automated equipment in several laboratories, it is possible to measure dozens of crystals, determine whether the dates cluster with a reasonable statistical average, and eliminate dates that are widely divergent.

When $^{40}\text{Ar}/^{39}\text{Ar}$ dating was applied to many of the terrestrial volcanic ashes that were dated 30 years ago with K-Ar (Evernden et al 1964), significant errors became apparent (Swisher & Prothero 1990). For example, K-Ar dating of bulk samples of Flagstaff Rim Ash J produced a date of about 32.4 Ma (Evernden et al 1964, Emry 1973). When individual crystals of the same ash were redated by $^{40}\text{Ar}/^{39}\text{Ar}$ methods, the ash yielded dates of 34.5 ± 0.087 Ma on biotite and 34.7 ± 0.036 Ma on anorthoclase (Swisher & Prothero 1990, Prothero & Swisher 1992)—more than 2 million years older than previous estimates! These new dates radically shortened the apparent age span of the critical Flagstaff Rim section in central Wyoming, which in turn forced recalibration of the magnetic stratigraphy, and shifted the correlation of the land sequences by two whole magnetic polarity chrons (Prothero et al 1982, 1983; Prothero & Swisher 1992).

The consequence of these new dates, recalibrations, and revised correlations has been a radical rethinking of the entire late Paleogene time scale. The calibration of the marine time scale was once very controversial, but now most scientists agree that the best age estimate of Eocene-Oligocene boundary is about 33.5 Ma, rather than the estimates of 38 or 36.6 or 32 Ma published previously (Berggren et al 1992). The revisions of the marine time scale have forced recalibration of the magnetic polarity time scale, which had previously been calibrated with erroneous K-Ar dates (Cande & Kent 1993). The most radical change occurred in terrestrial mammal-bearing sequences in North America and Asia. The classic “late Eocene” Uintan land mammal “ages” in North America became middle Eocene, and the “early Oligocene” Chadronian land mammal “age” in North America (and its equivalent in Asia) became late Eocene. The “middle” and “late” Oligocene Orellan and Whitneyan land mammal

“ages” in North America are now early Oligocene, and even the “early Miocene” Arikarean land mammal “age” in North America has become mostly late Oligocene. For years, mammalian biostratigraphers had identified the Eocene-Oligocene boundary with the Duchesnean-Chadronian boundary, and were trained to think that “Chadronian equals early Oligocene.” With the new correlations, the Eocene-Oligocene boundary shifts up one whole land mammal “age” (to the Chadronian-Orellan boundary), and paleontologists had to rethink their lifelong assumptions about Eocene and Oligocene (Swisher & Prothero 1990, Prothero & Swisher 1992).

The current time scale is shown in Figure 1, and further detail about its development can be found in Berggren et al (1992) and Cande & Kent (1993).

THE CLIMATIC AND BIOTIC RECORD

Before we discuss the various hypotheses for the Eocene-Oligocene extinctions, we should examine the data that these hypotheses attempt to explain. New studies on marine and terrestrial sequences have produced much more detailed evidence about the nature of the Eocene-Oligocene transition than previously known. Some of this information was summarized previously (Prothero 1985, 1989), but the new time scale makes those papers out of date in some respects. Most of the data that follows come from papers in the volume edited by Prothero & Berggren (1992), especially the summary chapter by Berggren & Prothero (1992).

The Marine Record

The most detailed and informative record of climatic changes and extinctions occurs in the marine realm. There the record is relatively complete, especially in deep-sea sections, which were deposited far below base level and therefore rarely eroded. In addition, marine rocks typically reflect global oceanic conditions, so the record of their oxygen and carbon isotopes, and the presence of unusual sediment types (such as ice-rafted detritus) are as informative as the changes that occur in the biota.

From the marine record, it is clear that there were several pulses of climatic change and extinction during the Eocene-Oligocene transition. Contrary to common misconceptions that the extinctions occurred during the “Terminal Eocene Event” (about 34 Ma), most of the extinctions in the marine organisms (especially among the warm-water taxa) were concentrated at the end of the middle Eocene (about 37 Ma). Particularly severe extinctions occurred in the calcareous nannoplankton (Aubry 1992) and the planktonic foraminifera (Keller 1983, Boersma et al 1987, Keller & MacLeod 1992). Many tropical taxa disappeared as mid-latitude faunas

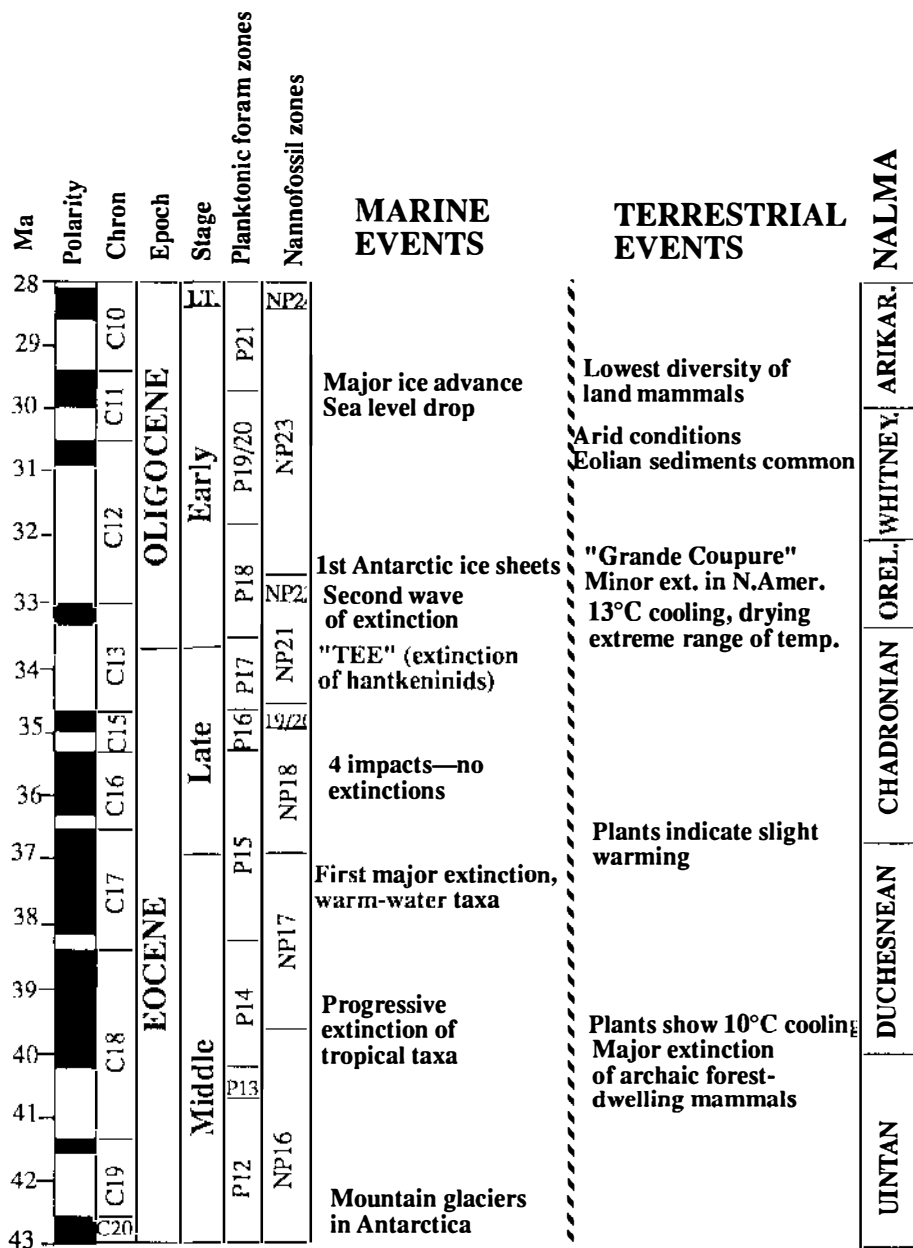


Figure 1 Chronology of events during the Eocene-Oligocene transition. Magnetic polarity time scale after Cande & Kent (1993); North American land mammal "ages" (NALMA) after Prothero & Swisher (1992); marine chronology updated from Berggren et al (1985). The major extinction events occurred at the end of the middle Eocene (about 37–38 Ma) and in the earliest Oligocene (about 33 Ma). The Eocene-Oligocene boundary ("Terminal Eocene Event," or "TEE") occurred at 33.5 Ma and was not so important. Evidence of impacts is dated between 35.5 and 36 Ma. Abbreviations are as follows: Arikar. = Arikarean; Orel. = Orellan; Whitney. = Whittayan.

migrated toward the equator to escape cooler high-latitude water masses. Bottom-dwelling organisms also suffered severe extinctions during the middle Eocene as well. This can be seen in groups as disparate as benthic foraminiferans (Adams et al 1990, Gaskell 1991, Thomas 1992) and molluscs, which lose 89% of the gastropod species and 84% of the bivalve species at the middle-late Eocene transition (Hansen 1987, 1992). Some groups (such as echinoids and ostracodes) apparently do not show a striking middle Eocene extinction, but among taxa with a sufficiently detailed record, this middle-late Eocene extinction is the most severe of all mass extinctions in the Cenozoic. The most fundamental biotic division of the Cenozoic is not between the Tertiary and Quaternary, or Paleogene and Neogene, but between the middle and late Eocene.

A few minor extinctions in the planktonic foraminiferans (Keller 1983) and the radiolarians (Riedel & Sanfilippo 1986) occurred during the middle of the late Eocene (middle Priabonian, about 35 Ma). Minor extinctions are also reported for the molluscs (Hansen 1987, 1992). No other marine group shows any significant extinction at this time.

In contrast to the the end of the middle Eocene, the Eocene-Oligocene boundary (about 34 Ma, or late magnetic Chron C13R as currently defined) is a relatively minor event. Only a few planktonic foraminifera became extinct at this boundary (particularly the index genus, the spiny foraminiferan *Hantkenina*). Despite the publicity given to the "Terminal Eocene Event" in the past, it is an embarrassingly small extinction. This is partly a problem of resolution and also one of definition. In the past, low-resolution studies tended to lump all events near the Eocene-Oligocene boundary as one "event." But recent research has shown that the major extinctions and climatic changes that occurred near the boundary are actually found a million years later in the earliest Oligocene (about 33 Ma, or mid Chron C13N). Ironically, this discrepancy became apparent in 1989, just after the International Subcommittee of Paleogene Stratigraphy voted to establish the Eocene-Oligocene boundary at the last occurrence of *Hantkenina* in the Massignano section near Ancona, Italy. Subsequent research by Brinkhuis (1992) showed that the stratotype section of the upper Eocene Priabonian Stage was partly lower Oligocene (as currently defined), so that the current definition of the boundary may have to be revised. Many scientists feel that the dramatic global events at 33 Ma make a more natural Eocene-Oligocene boundary, but until the vote of the Subcommittee is reconsidered, the current boundary stands.

The earliest Oligocene event is reflected in the extinction of many surviving species of calcareous nannofossils (Aubry 1992), planktonic foraminiferans (Keller 1983), benthic foraminiferans (Gaskell 1991, Thomas 1992), diatoms (Baldauf 1992), ostracodes (Benson 1975), molluscs (Hansen 1987, 1992) and echinoids (McKinney et al 1992). Like the middle

Eocene extinctions, the attrition was heaviest in warm-water taxa, leaving a relatively low diversity of organisms to survive into the early and late Oligocene.

Some extinctions also occurred during the middle Oligocene, particularly among planktonic foraminiferans that were less tolerant of cold conditions (Keller 1983) and the calcareous nannoplankton (Haq et al 1977). However, the middle Oligocene event was not nearly as severe as previous extinctions, perhaps because the surviving fauna was already cold-adapted from the earlier attrition of warm-climate taxa.

The Terrestrial Record

Although the new calibrations and time scales change the marine story somewhat, their effect on our understanding of terrestrial events is truly profound. For example, earlier papers (Prothero 1985, 1989) which treated the Duchesnean-Chadronian boundary as the Eocene-Oligocene boundary, and labeled the Chadronian-Orellan boundary as the "mid-Oligocene event" are now completely out of date, and conclusions based on these correlations are invalid.

Once the new correlations and calibrations are taken into account, the terrestrial record shows striking similarities to the marine record of extinctions (Figure 1). The major changes take place in the late middle Eocene (about 40 Ma), and again in the earliest Oligocene (33 Ma). Relatively few changes take place in the middle of the late Eocene, or in the mid-Oligocene.

NORTH AMERICA The best documentation and dating of the terrestrial Eocene-Oligocene transition comes from North America. This is primarily because it is the home of most paleontologists, but also because there is an excellent record of this transition preserved and exposed in many places in the Rocky Mountains and High Plains. The clearest signal comes from the land plants, as described by Wolfe (1971, 1978, 1992). Based on his method of estimating temperature from the percentage of entire leaf margins, Wolfe documents a severe cooling event of about 10°C at the end of the middle Eocene, followed by a slight warming in the late Eocene, and then an even more extreme cooling of about 13°C in the earliest Oligocene. Wolfe (1971) originally called this chill the "Oligocene deterioration," but in 1978 he coined the phrase "Terminal Eocene Event" (it is now correlated with the early Oligocene). In addition to the cooling of mean annual temperatures, there was also a great increase in the mean annual range of temperatures, from about 3–5°C during the warm, tropical

middle Eocene to almost 25°C in the Oligocene. These cooling events result in the replacement of subtropical early and middle Eocene floras (typical of modern Central America) with plants that are mostly typical of broad-leaved deciduous forests (such as those of the present-day New England and eastern Canada).

Ancient soil horizons in the Big Badlands of South Dakota and elsewhere show a similar trend (Retallack 1983, 1992). Late Eocene paleosols were formed under a dense forest canopy with about 1000 mm of annual precipitation. By the Orellan (early Oligocene), there was a wooded grassland in the Badlands with about 500–900 mm of rainfall, and in the early Arikarean (late Oligocene) the region was covered with an open grassland receiving only 350–450 mm of rainfall per year.

Living amidst this changing vegetation were a variety of climatically-sensitive animals. Land snails from the Chadronian of Douglas, Wyoming, were large-shelled taxa similar to those found in subtropical climates with seasonal precipitation, such as that of the present-day central Mexican plateau (Evanoff et al 1992). They indicate a mean annual temperature of about 16°C and a mean annual precipitation of about 450 mm. By the Orellan (early Oligocene), these snails had been replaced by drought-tolerant small-shelled forms typical of a warm-temperate open woodland habitat with a long dry season, such as that of Baja California today. The deposits that produce these snail fossils also show a change from floodplains to sand dune deposition. Amphibians and reptiles exhibit a similar trend toward cooling and drying (Hutchison 1982, 1992). The aquatic salamanders, crocodylians, and turtles, which were so common in the middle Eocene, gradually became scarcer through the late Eocene and by the early Oligocene were replaced by land tortoises.

Although the climatic implications of the changes in land mammals are not so obvious, there are striking differences (Prothero 1985, 1989; Stucky 1990, 1992). As we saw in the marine record, the biggest wave of extinctions took place near the end of the middle Eocene (end of the Uintan, about 40 Ma), when about 25% of the genera of land mammals disappeared. Most were members of archaic groups of mammals typical of the Paleocene and early Eocene, adapted to forest browsing or an arboreal life. When the drying climate began to break up the forest canopy, both the leaf-eaters and the tree-dwellers were most severely affected.

In the late Eocene (Chadronian), there were relatively few extinctions, but there was much immigration of new groups of mammals, apparently from Asia. These included the earliest dogs, camels, rhinos, pocket gophers, beavers, squirrels, rabbits, and shrews. Along with a number of native groups (such as horses and oreodonts) these mammals came to dominate faunas during the Oligocene and Miocene and formed a stable

entity known as the “White River Chronofauna” that persisted for about 20 million years (Emry 1981, Emry et al 1987).

The earliest Oligocene climatic crash was accompanied by surprisingly minor extinctions in North American land mammals. A few archaic groups, such as the huge browsing brontotheres, the camel-like oromyricids, and a few archaic rodents did die out, but most mammals typical of the Chadronian persisted into the Orellan with only minor changes in species or relative abundance. However, two groups (cricetid rodents and leptauchenine oreodonts), with relatively high-crowned teeth for eating tough vegetation, did appear in the Orellan and flourished in the Whittanian.

EUROPE The European record has been relatively well studied, although the chronology there is not based on radiometric dates or magnetostratigraphy. Instead, the mammal-bearing beds frequently interfinger with shallow marine beds (which sometimes contain fossil mammals that were washed out to sea), so that there is direct correlation with the European marine standard.

Floral evidence (Collinson & Hooker 1987, Collison 1992) shows that the middle Eocene forests of Europe were tropical, but in the late Eocene subtropical evergreens (taxodiaceous swamps and reed marshes) were dominant. By the early Oligocene, these plants were replaced by mixed deciduous/evergreen plants indicating a warm-temperate seasonal climate. European floras never reached the extremes of cooling or drying seen in North America, possibly because Europe was an archipelago on the fringe of the tropical Tethys Sea, with the moderating effects of coastal climates and warm waters nearby.

European land mammals underwent several changes during this time (Collinson & Hooker 1987, Hooker 1992, Legendre & Hartenberger 1992). At the end of the middle Eocene (Bartonian), many of the large soft-browsing perissodactyls (odd-toed hoofed mammals) became extinct and were replaced by coarse-browsing palaeotheres (distant relatives of horses). There were also major extinctions in arboreal primates and apatemyids as well as small mammals and insectivores. This pattern closely parallels the extinctions at the end of the middle Eocene (Uintan) in North America.

The most significant change, however, is known as the Grande Coupure, or “great cutoff.” First recognized in 1909 by Stehlin, the Grande Coupure marks the end of a large number of archaic European mammalian groups, including many of the same types of tree-dwellers and leaf-eaters seen in North America in the late Eocene, as well as many European endemics. These archaic mammals were abruptly replaced by Asian immigrants which included rabbits, rhinos, advanced rodents, artiodactyls, and car-

nivorans. Arboreal mammals disappeared completely, and large ground-dwelling mammals and grain-eating rodents dominated the fauna.

For years, the Grande Coupure was correlated with the Eocene-Oligocene boundary (Savage & Russell 1983). But Hooker (1992) has shown that the Grande Coupure occurs slightly above the European marine Eocene, and probably correlates with the dramatic climatic changes that occurred in the earliest Oligocene. The abruptness of the Grande Coupure is not primarily due to the climatic changes in the early Oligocene. Rather, it was caused by the immigration of so many Asian groups, possibly because lower sea level in the early Oligocene opened up corridors from Asia and eastern Europe.

ASIA Correlation of the Asian record with the rest of the world has been hampered by several factors. Stratigraphic analysis is still in its early stages, with almost no magnetostratigraphy or radioisotopic dating to tie Asian terrestrial sequences to the global standard. Most of the age assignments of the stages of the Asian Eocene and Oligocene have been based on comparisons to North American mammals. Now that the North American calibration has changed, the entire correlation of Asian terrestrial sequences needs to be reconsidered (Berggren & Prothero 1992). Consequently, the age assignments of faunas in many papers on Chinese or Mongolian mammals (e.g. Li & Ting 1983, Wang 1992, Dashzeveg & Devyatkin 1986) will probably be revised when the full effect of the changes in the time scale are assimilated.

Adjusting for the changes in time scale, the Asian mammalian record closely parallels the changes seen in North America. The largest extinction occurred at the end of the middle Eocene (Sharamuronian), when 45 genera of archaic Eocene mammals died out, including tillodonts, arctocyonids, helohyids, and eurymylids. The earliest Oligocene (end of the Houldjinian) saw the disappearance of brontotheres, mesonychids, and archaic tapiroids, along with some Asian endemics. This pattern closely parallels the extinction of brontotheres and many tapiroids in North America and Europe at the same time. Following this extinction, cricetid rodents with high-crowned teeth diversified in the early Oligocene (Kekeamuan), as occurred during the Orellan and Whitneyan in North America.

The floral record has been less studied and published, but some features are beginning to emerge (Leopold et al 1992). At the end of the middle Eocene in China, there was a striking change of pollen types, which indicated the development of mesic forests in the coastal part of south-eastern China while arid types retreated to Mongolia. Eventually a subtropical woody savanna developed in northern China in the late Eocene. In the Oligocene, floral diversity decreased, and the increase in temperate deciduous trees and conifers suggest further cooling.

OTHER CONTINENTS The other continents have a relatively poor record of the Eocene-Oligocene transition. Rasmussen et al (1992) reviewed the record for Africa (mainly the Fayum region of Egypt) and found little evidence of major changes in the middle or late Eocene, or Oligocene. They pointed out that these land faunas bordered the warm tropical Tethys seaway, which buffered them from the climatic extremes seen in higher latitudes.

The South American mammal record is much better developed than that of Africa, but unfortunately it contains a gap between 41 and 21 Ma which is just beginning to be filled (Wyss et al 1990). Nevertheless, there are notable differences between middle Eocene (Mustersan) and late Oligocene (Divisaderan-Deseadan) faunas that suggest major climatic changes. The most obvious differences occur in South America's endemic ungulate faunas, which change from archaic browsers with low-crowned teeth to much more hypsodont grazing mammals; rodent-like marsupials and primitive edentates also disappeared. Marshall & Cifelli (1989) suggest that this change was due to a change from subtropical woodlands to seasonally-arid savanna woodlands.

Australia's Cenozoic mammal record is virtually nonexistent before the early Miocene. The recently discovered early Eocene Tinga Marra local fauna (Godthelp et al 1992) only begins to fill the gap. However, the paleobotanical record is excellent (Kemp 1978). In the middle Eocene, tropical rainforests covered Australia, but these began to decline in diversity in the late Eocene. In the earliest Oligocene, there was a dramatic cooling in Australia as cold water began to circulate between Australia and Antarctica for the first time (see below). Australian Oligocene floras were dominated by cool-temperate plants tolerant of high seasonality, with increased rainfall in the coal swamp regions of southern Australia, and increased aridity with open forests and a more herbaceous understory elsewhere on the continent (Truswell & Harris 1982).

Middle Eocene floras and pollen are known from Seymour Island on the Antarctic Peninsula (Case 1988). They suggest a cool-temperate rain forest with large trees, similar to those found today on Tasmania, New Zealand, and southern South America. Although there is evidence that glaciers may have appeared in some parts of Antarctica by the late Eocene, they did not yet cover the continent.

THE SEARCH FOR CAUSES

Now that we have summarized the patterns of diversity change and extinctions, we can evaluate different models that attempt to explain them. Recall that we have described a complex transition which spans almost ten million

years. Most of the extinctions occurred in tropical taxa at the end of the middle Eocene (about 37–38 Ma), and in the earliest Oligocene (33 Ma), with very minor extinctions in the middle of the late Eocene (about 35–36 Ma), and in the late Oligocene (about 30–31 Ma). The suggested causes typically fall into three categories: extraterrestrial, volcanic, and tectonic-climatic. We shall examine each in order of increasing plausibility.

Asteroids, Comets, and Volcanoes

Although there is strong evidence that asteroid impacts and/or volcanic eruptions may have caused the Cretaceous-Tertiary extinctions, such is not the case for the Eocene-Oligocene transition. The initial 1982 reports (Alvarez et al 1982, Asaro et al 1982, Ganapathy 1982, Glass et al 1982) of iridium, microtektites, and glassy impact spherules at the end of the Eocene were met with great fanfare, but since then the impact advocates have all but abandoned the Eocene-Oligocene extinctions. There are several reasons for this. First, the iridium and microtektites occur in the *middle* of the late Eocene, associated with no extinctions of significance. Although there was once much controversy over the dating of the microtektite layers (and just how many there were), recent investigations (Miller et al 1991b) found just four discrete horizons ranging in age from 36 to 35.4 Ma. This is too late for the middle Eocene crash, and too early for the early Oligocene crisis.

Secondly, the protracted pattern of Eocene-Oligocene extinctions cannot be explained by any sudden impact, especially when that transition is spaced out over about ten million years. Hut et al (1987) avoided this difficulty by postulating a series of comet showers over the interval, but this hypothesis falters on the same problems that the asteroid impact does. In addition, many planetary scientists doubt that comets could produce the impact droplets or iridium anomalies seen in the middle late Eocene.

Finally, the obvious climatic changes (discussed below) were clearly not caused by extraterrestrial impacts, yet they must have had a profound effect on Eocene biotas. If the late Eocene impacts had any effect whatsoever, they were very minor compared to the profound effect of climatic change.

Volcanism has also been blamed for the Eocene-Oligocene extinctions. If gigantic volcanic eruptions were spaced over a long enough period of time, and spewed enough gases into the atmosphere to change global climate, then such an explanation might be plausible. Kennett et al (1985) found many volcanic ash layers in deep-sea cores in the southwest Pacific, mostly from volcanoes in New Zealand and along the boundary of the Australian and Indo-Pacific plates. However, most of these ash layers occur in the uppermost Eocene and lower Oligocene—too late for the

middle Eocene extinctions. Nor was there a single great pulse of volcanism that might explain the early Oligocene refrigeration event (see below).

Rampino & Stothers (1988) blamed the Eocene-Oligocene extinctions on massive flood basalt eruptions which covered 750,000 square kilometers of Ethiopia, supposedly during the late Eocene. However, the dates on these lavas are too late to explain the middle Eocene extinctions, spaced out over too large a time interval to match the patterns of extinction in the early Oligocene. It is conceivable that they may have had some effect on the atmosphere and climate, but their chronology does not match the known pattern of extinctions closely enough to establish a direct link.

Tectonic and Climatic Changes

Throughout the discussion of the biotic evidence above, it is clear that there was a strong signal of protracted climatic change during the Eocene-Oligocene transition. Clearly, the search for proximate causes must examine reasons for this climatic change, and extraterrestrial and/or volcanic causes are insufficient to explain the pattern we see. Fortunately, the past decade of oceanic drilling has given us an excellent record of global ocean isotopic chemistry and sedimentation on which to base our paleoclimatic interpretations.

The most important data are the abundant evidence of changes in oceanic circulation from the oxygen isotopes (Miller et al 1987, Miller 1992). For a long time, it was dogma that Antarctica had no significant ice sheets before the middle Miocene. Matthews & Poore (1980) challenged this assumption, and began to reinterpret the oxygen-isotope record with some Paleogene Antarctic ice included in their calculations. Since then, most scientists (e.g. Miller & Fairbanks 1983, 1985; Shackleton 1986; Miller et al 1987; Miller 1992) have found that this assumption makes sense. Depending upon the corrections for the ice volume effect, the oxygen isotopes indicate a global temperature drop of about 5–6°C in the earliest Oligocene, which is as large as the changes between glacial and interglacial worlds during the Pleistocene ice ages (Miller et al 1987). A dramatic change in the carbon isotopes at the same time is thought to indicate the influx of cold bottom waters from both the northern and southern high latitudes (Miller 1992). From isotopic evidence such as this, a number of interesting models of oceanic circulation have been advanced (Boersma et al 1987,

Once the “ice-free” assumption was abandoned, reports of Eocene and Oligocene Antarctic glaciers became more acceptable. In 1987 Birkenmajer reported evidence of middle Eocene glacial deposits from King George Island on the Antarctic Peninsula. Wei (1989) argued that ice-rafted sediments from the Pacific side of Antarctica are also middle Eocene in age,

although others question this age assignment. Even more striking is the evidence from several deep-sea cores around the Antarctic (Miller et al 1991a; Zachos et al 1992, 1993) and the CIROS-1 drill hole in the Ross Sea (Barrett et al 1989) that there was a major early Oligocene ice advance on that continent. However, this pulse of glaciation may have only lasted a million years, and apparently was concentrated on the Indian and Pacific Ocean sectors of Antarctica (Miller et al 1991a), with a limited effect on the South Atlantic sector or East Antarctica (Kennett & Barker 1990).

The largest episode of pre-Miocene Antarctic glaciation occurred in the mid-Oligocene (about 30 Ma), and may have lasted about 4 million years (Miller et al 1991a). Thick mid- and late Oligocene glacial deposits are reported from all over Antarctica (Barrett et al 1989, LeMasurier & Rex 1982, Bartek et al 1992). This major ice advance is responsible for the largest sea level drop on the entire Vail onlap-offlap curve (Haq et al 1987), and major mid-Oligocene unconformities all over the world (Poag & Ward 1987, Miller et al 1987).

What triggered the growth of these southern ice sheets, and the changes in global oceanic circulation and climate that resulted? Several authors (e.g. Frakes & Kemp 1972, Kennett et al 1975, Kennett 1977) have suggested that the development of the circum-Antarctic current may have been a critical factor. Today, the circum-Antarctic current is the largest of oceanic currents, with a volume 1000 times that of the Amazon (Callahan 1971). It causes upwelling of deep bottom nutrients, which leads to enormous oceanic productivity. Once these circumpolar waters have welled up, they are chilled and sink to form the deep, cold bottom waters (the psychrosphere) that flow north along the bottom of the Atlantic and Pacific. The circum-Antarctic current also locks in the cold of the South Pole as it circles clockwise around Antarctica, and prevents these waters from mixing with more equatorial waters, which might warm up the polar waters.

All of the climatic and isotopic evidence suggest that this current did not exist in the early Eocene, which was the warmest period of the entire Cenozoic. Instead, tropical and polar waters routinely mixed, ameliorating the extremes between pole and equator (Frakes & Kemp 1972, Kennett et al 1975, Kennett 1977, Kennett & Stott 1990). Both Australia and South America were still attached to Antarctica, preventing any circum-Antarctic circulation. Australia began to move away from Antarctica during the Cretaceous, and a shallow marine gulf developed between the two continents by the middle Eocene (Weissel et al 1977, Mutter et al 1985, McGowan 1973, Kennett et al 1975). By the late Eocene, the connection between Tasmania and Antarctica had separated enough to allow shallow marine circulation into the Pacific (Murphy & Kennett 1986, Kamp et al

1990). Full-scale deep-water circulation through this gap did not occur until the mid-Oligocene (Murphy & Kennett 1986, Kamp et al 1990), and may have been responsible for the massive glaciation and global sea level drop. The circum-Antarctic current was completed when South America pulled away from Antarctica in the latest Oligocene (~ 25 Ma), opening up the Drake Passage to deep polar waters (Barker & Burrell 1982, Sclater et al 1986).

Another source of cold bottom waters was the Arctic Ocean, which was isolated from the rest of the world's oceans in the Eocene. In the early Oligocene, a deep-water passage in the Norwegian-Greenland Sea apparently opened up (Talwani & Eldholm 1977, Berggren 1982), allowing the North Atlantic Deep Water to flow down from the Arctic through the Atlantic (Miller 1992). Clearly the combination of cold waters from both polar regions was critical in the global refrigeration and climatic changes that occurred beginning in the middle Eocene.

Although these tectonic causes are much more plausible than impacts or volcanoes, they do not solve every problem. For example, if there was no circum-Antarctic circulation before the late Eocene, then why was there a cooling event at the end of the middle Eocene, and glaciers on the Antarctic Peninsula? Using computerized climatic modeling, Bartek et al (1992) have suggested that the Antarctic was already cold enough in the middle Eocene for glaciation. All that was lacking was a source of moisture, and their models show that the opening of the gulf between Antarctic and Australia during the middle Eocene would have provided it.

Others are bothered by the apparent abruptness of the change, especially when the causes are long-term tectonic changes. Kennett & Stott (1990) couple the late Eocene cooling with the earliest Eocene "greenhouse" warming in a complex oceanic circulation model which postulates radical changes in oceanic chemistry and flow patterns. Zachos et al (1993) suggest that the gradual changes in oceanic circulation and greenhouse gases may have reached climatic thresholds, where abrupt changes would result. Clearly, there are many more interesting ways of interpreting the late Paleogene climatic data, even as new data emerge from further exploration in and around the Antarctic, and from the oceans.

CONCLUSIONS

The Eocene-Oligocene extinctions took place over about 10 million years, starting with a major extinction in tropical organisms at the end of the middle Eocene (about 37–38 Ma), and followed by a significant global cooling event and a lesser extinction event in the earliest Oligocene (about 33 Ma). Very minor extinctions occurred in the late Eocene (about 35 Ma)

and in the mid-Oligocene (about 30 Ma). In spite of the evidence of four impacts around 35–36 Ma, no short-term extraterrestrial events or volcanic eruption is sufficient to explain this pattern of extinction. The overwhelming evidence for global cooling and oceanic circulation changes argue that these must have been the proximal cause of extinction. The refrigeration of the Antarctic and development of cold bottom waters from both poles were critical to this change. The likely triggers of this cooling were the development of the circum-Antarctic current and the opening of the Norwegian-Greenland Sea. Changes in greenhouse gases may also have been critical as certain climatic thresholds were exceeded.

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