

BIODIVERSITY II

Understanding and Protecting Our Biological Resources

CHAPTER

11

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Global Warming and Plant Species Richness: A Case Study of the Paleocene/Eocene Boundary

SCOTT L. WING

*Associate Curator, Department of Paleobiology, National Museum of
Natural History, Smithsonian Institution, Washington, D.C.*

There is widespread concern over the possibility that greenhouse gases generated by human activity may cause global warming. Much effort is being devoted to monitoring changes in climate and organisms, and to modeling the possible effects of greenhouse gases on climatic and biological systems. Programs of monitoring and modeling clearly are necessary, but the geological history of the Earth and its biota have not been mined thoroughly enough for information about global climate and ecosystem response to climatic change.

Fossils and sedimentary rocks form a record of changes in the Earth's climate and of biotic responses over geological time. This record can be used in two main ways to develop a more complete understanding of global climate and of the long-term effects of climatic change on ecological systems. First, comparing climatic conditions indicated by fossils and sedimentary rocks with computer simulations of global climate for the same period is the only way we have of testing the ability of climate models to simulate conditions other than those that exist today. If models can successfully simulate climatic patterns known to have existed in the past, then we can have greater confidence in their predictions about the future. Second, the fossil record provides our sole opportunity to examine the biological consequences of climatic change without waiting for them to happen in "real time." If particular kinds of climatic change are associated with specific patterns of faunal and floral turnover, then we have some basis for anticipating future biotic responses to climatic change.

This chapter focuses on climatic changes and biotic events that took place during the Paleocene-Eocene transition, about 55 million years ago. With the exception of the Holocene deglaciation, the Paleocene-Eocene transition is prob-

ably the best documented example of a geologically rapid warming of global climate, although just how rapidly it occurred is still a matter of investigation. Our distance in time from these events places severe limitations on our ability to determine the rates of environmental and biological changes, and especially the synchronicity of events over large geographic areas. Typically, events that are less than 10,000 years apart appear synchronous, and records from different parts of the world cannot be correlated with greater than 100,000 year resolution. Still, the Paleocene-Eocene warming event is a close match for extreme predictions of human-induced global warming in terms of the absolute magnitude of warming and final climatic conditions. This makes the Paleocene-Eocene interval a valuable example for improving our understanding of the effect of rapid global warming on terrestrial ecosystems.

RECONSTRUCTING CLIMATES OF THE PAST

Climatic conditions for the distant past can be inferred in a variety of ways, but the two techniques most widely applied to continental paleoclimates are based on fossil plants. One method, called the nearest living relative (NLR) method, relies on the assumption that fossil species grew in climates similar to those preferred by their extant relatives. The validity of the NLR method depends on how closely related the fossil and extant species are, how much evolutionary change there has been in climatic preferences of the lineage, and the degree to which the range of the extant species is controlled by climate. Living taxa that have relictual distributions or few species are especially unreliable paleoclimatic indicators because they are far from occupying the full range of climatic conditions they can tolerate physiologically (e.g., *Ginkgo*, *Metasequoia*). NLR inferences about early Cenozoic climate are more reliable if they are based on diverse, nonrelictual taxa that have strong climatic limitations on their present-day distribution.

Palms are a good example of a speciose group with clear climatic limits on their distribution. Palms do not naturally occur in regions where means of cold months are less than about 6°C, or where frosts persist for more than two days (Wing and Greenwood, 1993; Figure 11-1). Experimental work on a wide variety of living species of palms shows that sensitivity to cold temperatures is typical of the whole family and results from absent or poorly developed physiological mechanisms of frost hardening (Sakai and Larcher, 1987). The combination of geographic and physiological information on palms makes a convincing case that extinct species in the family are unlikely to have had significantly more frost tolerance than their living relatives, so palms can be used with confidence to fix lower limits on paleotemperature estimates for early Cenozoic floras.

The second major method for inferring paleoclimate from fossil plants, leaf physiognomy, relies on correlations between the shape and size of leaves and climate that are observed in living floras. Generally, floras growing under

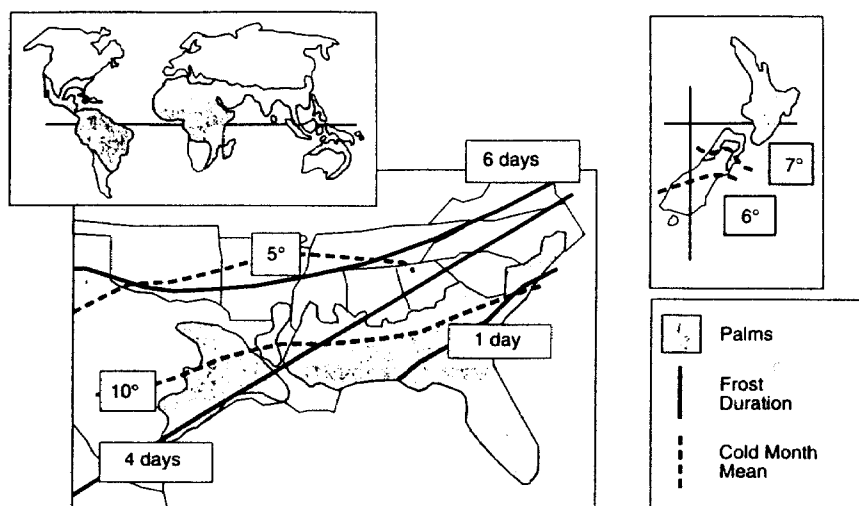


FIGURE 11-1 Natural distribution of living palms in relation to cold-month mean temperature (CMM) and average number of days of frost per year. Note close correspondence between the 6°C CMM and the limit of palms in both North America and New Zealand. Data were compiled by Wing and Greenwood (1993).

warmer climates will have a higher proportion of species that have leaves with entire margins (nontoothed leaves). The correlation between mean annual temperature (MAT) and the proportion of species with entire margins was first observed over 80 years ago, but has been documented and quantified most extensively by Wolfe (1979) using floras from East Asia (Figure 11-2). However the high correlation exhibited in Wolfe's data set is due in part to the exclusion of living floras from seasonally dry climates. Although the relationship between the percentage of species with entire margins in a local flora and MAT has been used widely to obtain numerical estimates of MAT for Cenozoic fossil floras, it may give misleading results for fossil floras that grew under seasonally dry conditions.

More recent attempts to make leaf physiognomic analysis more general and robust have used additional descriptors of leaves and climate (Wolfe, 1993). Many characteristics of leaf shape and size are correlated with temperature and rainfall conditions and can be used to infer paleoclimatic conditions. Wolfe (1993) scored a large number of Central and North American floras based on characteristics of leaf size and shape (Figure 11-3a). These leaf characteristics then were compared with parameters of temperature and rainfall for the sites using ordination analysis (Wolfe, 1993). Relationships between physiognomic variables of leaves and climatic variables (Figure 11-3b) then can be used to infer

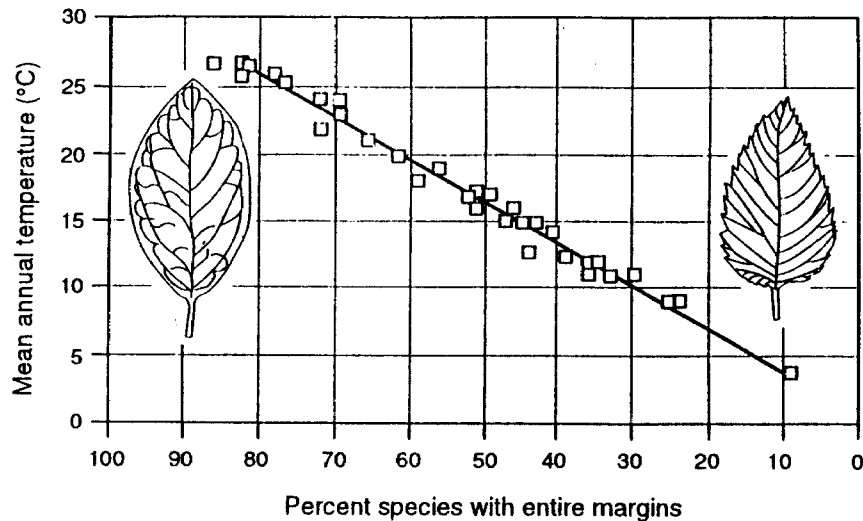


FIGURE 11-2 Correlation between the percentage of species in a local flora with entire-margined leaves (leaf on left) and the mean annual temperature (MAT) of the site. Data are from mesic East Asian forests (Wolfe, 1979). Linear regression of this data set yields the equation: $\text{MAT} = 1.14 + (0.31 \times \text{percentage of species with entire leaf margins})$. $R^2 = 0.98$, $p < 0.001$, standard error of the estimate is 0.79°C .

climatic conditions for fossil leaf assemblages based on their physiognomy. Wolfe's Central and North American data set also has been analyzed using multiple regression techniques (Wing and Greenwood, 1993). Mean annual temperature estimates based on the multiple regression approach have errors of $2\text{--}4^\circ\text{C}$; precipitation estimates generally are no more than ballpark figures.

In spite of the limitations on the precision of paleoclimate inferences, there is strong agreement between estimates using the different paleobotanical methods and between estimates derived from plant and vertebrate fossils (Hutchison, 1982; Markwick, 1994; Wing, 1991; Wing and Greenwood, 1993). There is also general congruence between marine temperature curves derived from oxygen isotope studies and terrestrial temperature curves derived from fossil plant and animal evidence (Wing et al., 1991; Wolfe and Poore, 1982). The consistency of paleoclimate estimates based on different fossil data sets and methodologies suggests that the estimates are robust. This is important, because paleoclimate estimates based on paleontological data indicate a world sharply different from the modern one with climatic conditions that are difficult to explain in terms of the climate systems observed today.

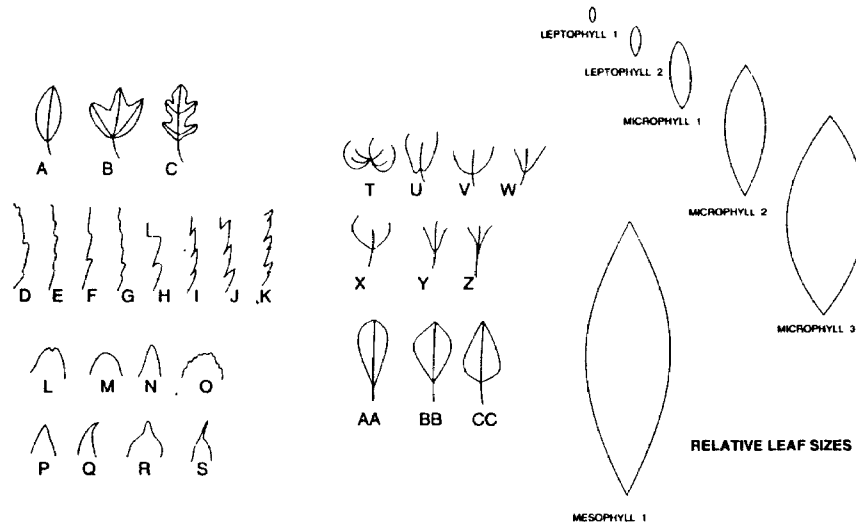


FIGURE 11-3a Leaf character states used in multivariate analysis of relationships between physiognomy and climate (Wolfe, 1993). Character states: A-C=general margins, A=untoothed leaf, B=palmately lobed untoothed leaf, C=pinnately lobed untoothed leaf; D-K=toothed margins, D=irregularly spaced, E=regularly spaced, F=distantly spaced, G=closely spaced, H=rounded, I=appressed, J=acute, K=compound; L-S=shapes of the apex, L=apex emarginate, M-O=apex rounded, P-Q=apex acute, R-S=apex attenuate; T-Z= shapes of the base, T-U=base cordate, V-W=base rounded, X-Z=base acute; AA-CC=shapes of the leaf, AA=obovate leaf, BB=elliptic leaf, CC=ovate leaf. Leaf-size categories are approximately 0.23x.

THE EQUABLE CLIMATE PARADOX

Global climate through most of Earth's history has been much warmer than at present. The early Eocene has long been recognized as the warmest part of the Cenozoic and one of the warmest periods of global climate in the last 100 million years (Miller et al., 1987; Savin et al., 1975; Wolfe, 1978). During the early Eocene, polar icecaps were absent in both hemispheres (Crowley and North, 1991), and midlatitude continental interiors had much warmer winters than they do now (Hickey, 1977; MacGinitie, 1974; Wing, 1991; Wing and Greenwood, 1993).

The causes for such globally warm climate are not well understood. Higher sea levels, lack of polar icecaps, and more dispersed land masses all have been thought to play a role in maintaining a warmer world. In recent years, general circulation models (GCMs) have been applied to paleoclimates (e.g., Crowley and North, 1991). To produce "predictions" for temperature and precipitation for a

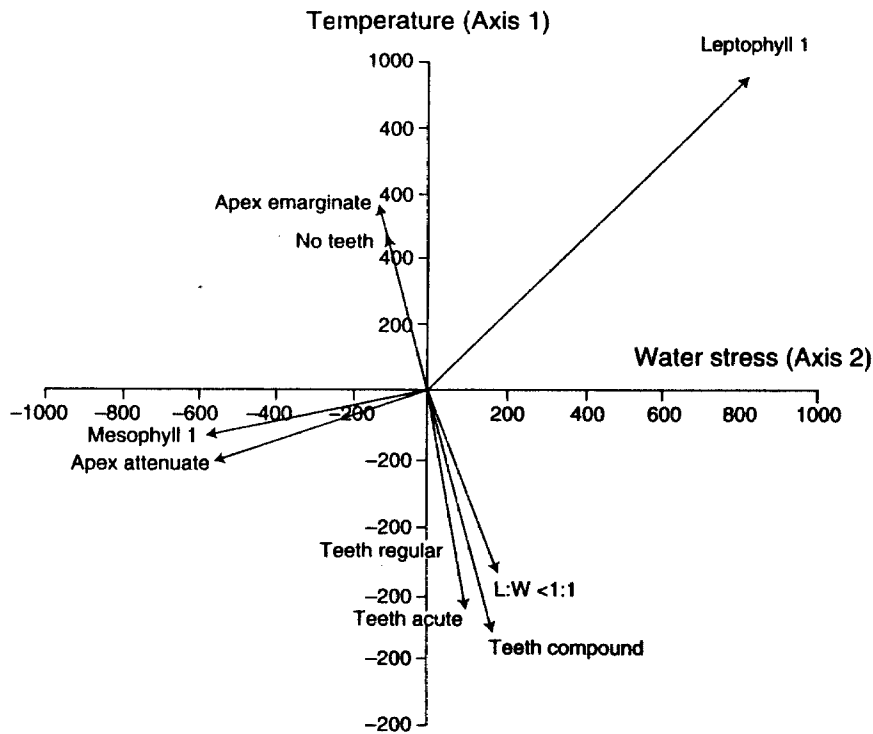


FIGURE 11-3b Reciprocal averaging plot showing relationship of climatic and physiognomic variables (Wolfe, 1993). The largest leaf-size category and attenuate apices are more abundant in wetter climates. All tooth features are more abundant in colder climates, as are narrow leaves with a length to width ratio of less than 1:1. Entire margins and emarginate apices are correlated with warmer climates.

time in the past, GCMs use starting conditions such as ancient coastline positions, paleotopography, continental positions, sea-surface temperature gradients, and global ice distribution. Weather patterns are generated using the same equations that describe the dynamics of the atmosphere today, then the weather patterns are averaged to yield a paleoclimate.

Application of these models to past periods of equable climate like the early Eocene consistently yields simulations that are more like the modern world than paleontological data indicate. The early Eocene is arguably the most interesting case of conflict between proxy data and model output, because it is close enough to the present that the proxy data are extensive, and uniformitarian assumptions about the climatic tolerances of animal and plant lineages are probably valid. Additionally, there is little evidence for very high CO₂ levels in the early

Eocene atmosphere, so this factor cannot be invoked in an unconstrained fashion to explain differences between proxy data and model output.

The sharpest discrepancy between model output and proxy data occurs in mid- to high latitude continental interiors because the low thermal capacity of land and the isolation of continental interiors from the moderating influence of the oceans result in model predictions of high seasonal variation in temperature in these areas (Sloan, 1994; Sloan and Barron, 1990, 1992). There are literally hundreds of early Eocene plant and animal fossil localities scattered across much of the continental interior of North America. The distribution of frost-intolerant forms (e.g., palms, cycads, crocodilians), as well as weak development of seasonal growth rings in some fossil wood, high diversity of small arboreal frugivores and insectivores requiring year-round food resources, and the physiognomy of fossil dicot foliage, all yield similar conclusions. In the Early Eocene, the interior of North America as far as 50°N experienced no significant winter freezing (e.g., annual minimum temperatures were $>-10^{\circ}\text{C}$, frost durations were less than 1-2 days). Mean temperatures in cold months were certainly above freezing, and probably higher than 5°C in most areas. Mean annual temperature was $15-20^{\circ}\text{C}$ (Wing and Greenwood, 1993). There are fewer proxy data available for the interiors of other continents, but southern Australia, which was 50-60°S in the early Eocene, has fossil faunas and floras indicating even warmer winter temperatures than similarly high latitudes in the interior of North America (Greenwood and Wing, 1995). The proxy data consistently show equable climates with low seasonality of temperature and warm winters. GCM simulation results consistently yield highly seasonal climates in continental interiors, with freezing temperatures far south of fossil sites containing frost intolerant forms (Sloan and Barron, 1990, 1992; Figure 11-4).

There are three basic kinds of explanation for warmth in the mid- to high latitudes during the early Eocene: (1) more heat was transported from equatorial to polar regions by ocean currents or winds, (2) more solar radiation was absorbed at high latitudes because albedo was lower, and (3) more heat was retained at high latitudes, and everywhere else, because of higher concentrations of "greenhouse" gases such as water vapor, methane, or CO_2 . The persistent discrepancy between GCM output and proxy data arises because mechanisms in the first two categories—such as increased heat transport by ocean currents or no polar ice—are not strong enough to explain the levels of warmth indicated by proxy data, especially in continental interiors (Walker and Sloan, 1992). The last mechanism, a CO_2 , methane, or water-vapor greenhouse, implies that tropical as well as high-latitude regions would have been substantially warmer than at present. The best proxy data for the Eocene tropics, however, indicate little difference from present temperatures (Adams et al., 1990; Graham, 1994). Furthermore, neither proxy data nor geochemical modeling are consistent with Eocene CO_2 levels more than about 900 parts per million (ppm), and it is possible

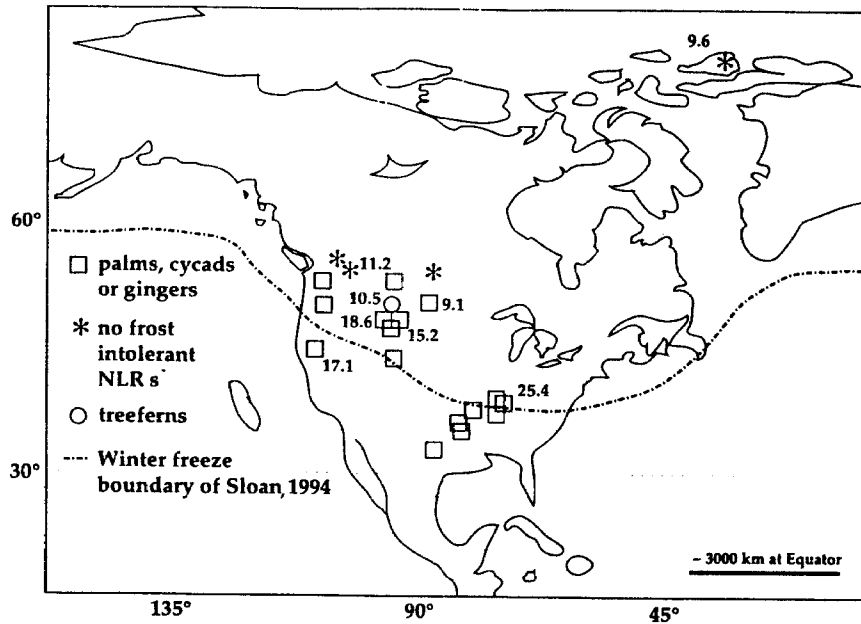


FIGURE 11-4 Eocene paleogeographic reconstruction of North America, showing frost-sensitive plants and high MAT estimates far north of the line where GCM simulation results indicate freezing temperatures. Numbers next to sites are MAT estimates based on multiple regression analysis of physiognomic data as described by Wing and Greenwood (1993). Proxy data are from Wing and Greenwood (1993). Model results are from Sloan (1994); simulation is based on present CO_2 level without large lakes in Wyoming.

that Eocene CO_2 levels were no different from those at present (Berner, 1991; Cerling, 1991).

The resolution of the equable climate paradox apparently will come from better GCMs, not from reinterpretation of the fossil record. The significance of the "equable climate paradox" is that it reveals the strong tendency for climate models to yield results that are more like the present than they should be. If similar problems plague the prediction of future climates under higher levels of atmospheric CO_2 , our predictions about the magnitude and rate of global climatic change may be far less accurate than we think.

THE TERMINAL PALEOCENE EVENT

The global climate warmed considerably from the late Paleocene to the early Eocene, roughly 57-52 million years ago. This warming trend has been quanti-

fied in the marine realm by measuring changes in oxygen isotope ratios in the tests of benthic and planktonic foraminifera (one-celled, amoeba-like organisms that secrete calcareous shells) recovered from deep sea cores (Miller et al., 1987; Pak and Miller, 1992; Figure 11-5) and in North America by physiognomic and floristic analyses of fossil plant assemblages (Hickey, 1977, 1980; Wing et al., 1991; Wolfe, 1978). In the mid-latitudes of interior North America, MAT increased from approximately 10°C to nearly 20°C between the late Paleocene and the mid- to early Eocene, a period of about 3 million years (Wing et al., 1991). Although this rate of change averages to only a few thousandths of a degree per

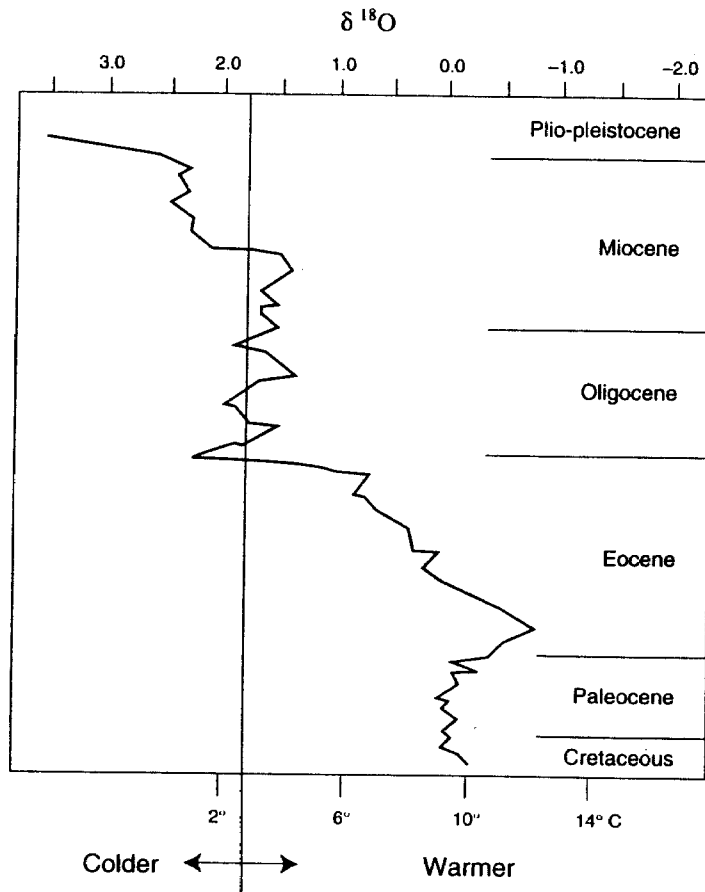


FIGURE 11-5 Cenozoic $\delta^{18}\text{O}$ curve showing major fluctuations in deep ocean temperature over the last 65 million years (redrawn from Miller et al., 1987). Temperature equivalents for $\delta^{18}\text{O}$ scale assume no polar icecaps.

millennium over the whole period, there is growing evidence that the rate of climatic warming was not constant.

In cores that recover laminated ocean bottom sediments, it is possible to resolve time in tens of thousands of years, even in the early Cenozoic (Kennett and Stott, 1991). Recent detailed stratigraphic studies of the Paleocene/Eocene boundary interval recovered in cores from the southern Pacific and southern Indian Oceans have shown an excursion in isotope values that occurred approximately 100,000 years before the Paleocene/Eocene boundary (approximately 55.1 million years ago; Kennett and Stott, 1991; Pak and Miller, 1992; Figure 11-6). The sudden increase in the light isotope of oxygen (decrease in $\delta^{18}\text{O}$ values) took place over less than 10,000 years and is thought to represent an interval when the temperature of bottom waters and surface waters in mid- to high latitude oceans increased by 5-8°C. This geologically short period of time, marked by isotopic shifts, is referred to here as the "Terminal Paleocene Event."

Oxygen isotope analyses of planktonic foraminifera tests indicate that surface waters in the equatorial Pacific maintained a temperature of about 20°C during the Terminal Paleocene Event, but analyses of the tests of tropical benthic species imply warming similar to that seen in the benthic and planktonic foraminifera of higher latitudes (Zachos et al., 1993). The isotopic shift coincides

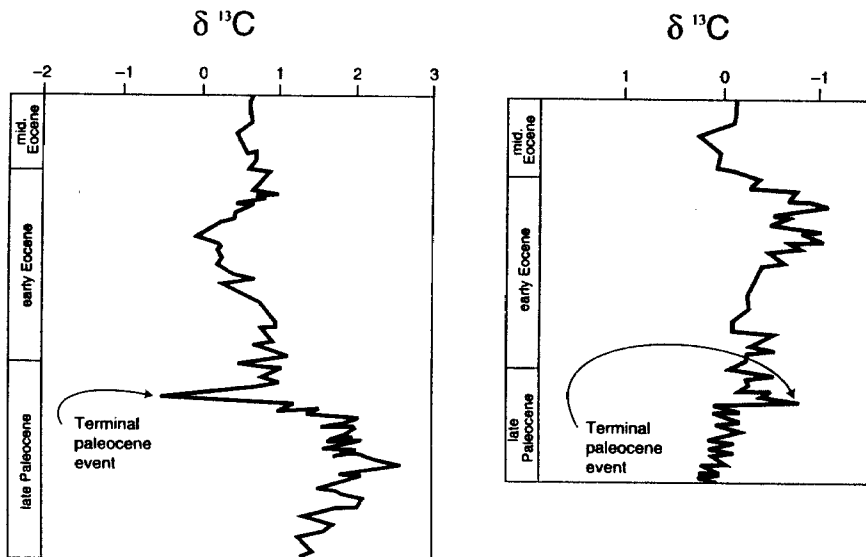


FIGURE 11-6 Terminal Paleocene excursion in carbon and oxygen isotope values (re-drawn from Pak and Miller, 1992). The Terminal Paleocene Event occurred about 100,000 years before the Paleocene/Eocene boundary and was associated with a major extinction of benthic foraminifera (Kennett and Stott, 1991).

with the most severe extinction (about 50% of species) of benthic foraminifera from the deep ocean during the Cenozoic; the extinction is believed to have been caused by rapid warming of deep ocean waters and a concomitant decrease in their dissolved oxygen levels (Kennett and Stott, 1991; Zachos et al., 1993). Following the negative isotopic excursion (warming) there was a rapid rebound in the positive direction (cooling), followed by a renewed decrease in $\delta^{18}\text{O}$ values that continued to a Cenozoic minimum in the mid-early Eocene about 52-53 million years ago. This minimum indicates the time of maximum global warmth during the Cenozoic.

The terminal Paleocene oxygen isotopic excursion is paralleled by a similar excursion in carbon isotope values (Kennett and Stott, 1991). The shift from ^{13}C to ^{12}C is probably related to the source and rate of delivery of organic carbon to the deep ocean, and possibly to decreased rates of oxidation of organic material in bottom waters (Kennett and Stott, 1991). The rapid isotopic and biotic changes during the Terminal Paleocene Event all may relate to a change in ocean circulation in which the source for bottom waters shifted from cool high latitudes to warm low latitudes (Kennett and Stott, 1989, 1991; Rea et al., 1990).

In this hypothesis, global warming during the later Paleocene increased the warmth, and therefore decreased the density, of high-latitude surface waters. At some point, warm, oxygen-poor saline waters generated by evaporation in the low latitudes exceeded the density of cooler, more oxygenated waters from the polar regions, and deep ocean circulation began to move in a poleward direction. This is the opposite of present-day conditions in which dense bottom water is created in cold, moderately saline high-latitude oceans. The hypothesized "reversed" bottom-water flow at the end of the Paleocene transported heat to mid- and high latitudes very effectively, resulting in a rapid increase of bottom water temperatures, but also a sudden warming of mid- to high latitude surface waters and continental surfaces as the warm bottom water upwelled (Brass et al., 1982; Pak and Miller, 1992; Rea et al., 1990; Zachos et al., 1993). Although the precise triggering mechanism that led to the sudden reversal of bottom water circulation is not understood, the effects of the Terminal Paleocene Event appear to have been global, because rapid changes are seen at this time in sediments deposited in continental and shallow marine environments as well as in the deep sea.

One effect of increased poleward heat transport by deep ocean currents would have been a decrease in latitudinal temperature gradients. There is direct evidence for decreased temperature gradients both in ocean surface waters and on the continents (Greenwood and Wing, 1995; Zachos et al., 1992). Decreased surface temperature gradients would be expected to lead to a reduced intensity of zonal atmospheric circulation, which is largely driven by equator-to-pole temperature contrasts. Reduced surface wind velocities were responsible for the sharp decline in the size of wind-blown dust grains in Paleocene/Eocene boundary sediments of the central Pacific; sluggish winds are not capable of carrying

larger dust particles far out to sea (Janecek and Rea, 1983; Rea et al., 1985). A secondary effect of reduced wind velocities may have been a decrease in coastal upwelling zones, which are powered by wind shear (Stott, 1992).

Greater warmth at mid- to high latitudes also may have resulted in increased precipitation and chemical weathering on land surfaces. Evidence for increased chemical weathering is seen in the sudden, widespread increase during the Terminal Paleocene Event of kaolinitic clays that are characteristic of leached soils formed under "tropical" weathering regimes (Robert and Chamley, 1991; Hovan and Rea, 1992; Gibson et al., 1993).

THE PALEOCENE-EOCENE TRANSITION ON LAND

The carbon isotope excursion associated with the Terminal Paleocene Event is a geochemical marker that can be detected in continental carbon sources such as hydroxyapatite preserved in tooth enamel of fossil mammals and calcium carbonate preserved in fossil soil nodules. Because the largest short-term reservoir in the global carbon budget is the ocean, shifts in the $^{13}\text{C}/^{12}\text{C}$ ratio of the oceans, such as those observed during the Terminal Paleocene Event, should force similar isotopic shifts in the carbon reservoirs represented by the atmosphere and continental ecosystems. Investigations of Paleocene/Eocene boundary sections in the Bighorn Basin of northern Wyoming have detected a carbon isotope excursion that corresponds to the Terminal Paleocene Event in direction, magnitude, and timing, thus establishing a datum that permits correlation of terrestrial and marine events (Koch et al., 1992).

The terrestrial carbon isotope excursion coincides with the Clarkforkian/Wasatchian boundary, a major and rapid change in the composition of mammalian faunas which has long been thought to be approximately correlated with the Paleocene/Eocene boundary (Wood et al., 1941). It is at the beginning of the Wasatchian that North American faunas first included representatives of the perissodactyla (odd-toed ungulates), artiodactyla (even-toed ungulates), and euprimates (Gingerich, 1989; Rose, 1981a). Similar faunal changes are known to have taken place at about the same time in Europe and Asia (Rose, 1981a; Russell and Zhai, 1987), and in Europe the faunal change also is associated with the carbon isotope excursion (Sinha and Stott, 1993). The nearly simultaneous appearance of these forms on all three northern continents indicates that high latitude land corridors in Greenland and Beringia were open to mammalian migrants (Maas et al., 1995; McKenna, 1983; Rose, 1981a), but the place of origin for these groups is still not known. Although rates of mammalian taxonomic turnover were high near the Paleocene/Eocene boundary, there is no evidence for a substantial decline in the number of mammalian genera (Wing et al., 1995). In spite of maintaining high numbers of genera, there is evidence that, at the level of species, latest Paleocene mammalian faunas from North America were

characterized by high dominance of a few species, possibly an indication of stressful conditions (Rose, 1981b).

The effect of the Terminal Paleocene Event on terrestrial floras is less well understood, although it has been known for some time that floral similarity between North America and Europe reached a maximum in the early Eocene (Tiffney, 1985). Two studies have shown a substantial (about 30%) reduction in the number of species of plants near the end of the Paleocene in North America, approximately coincident with the mammalian faunal exchange and the Terminal Paleocene Event (Frederiksen, 1994; Wing et al., 1995; Figure 11-7). This rapid decrease in the number of species of plants at the end of the Paleocene was geologically short-lived (about 1 million years); by the mid- to early Eocene (about 53 million years ago), as global climate reached its maximum Cenozoic warmth, floral richness had recovered to levels considerably higher than those

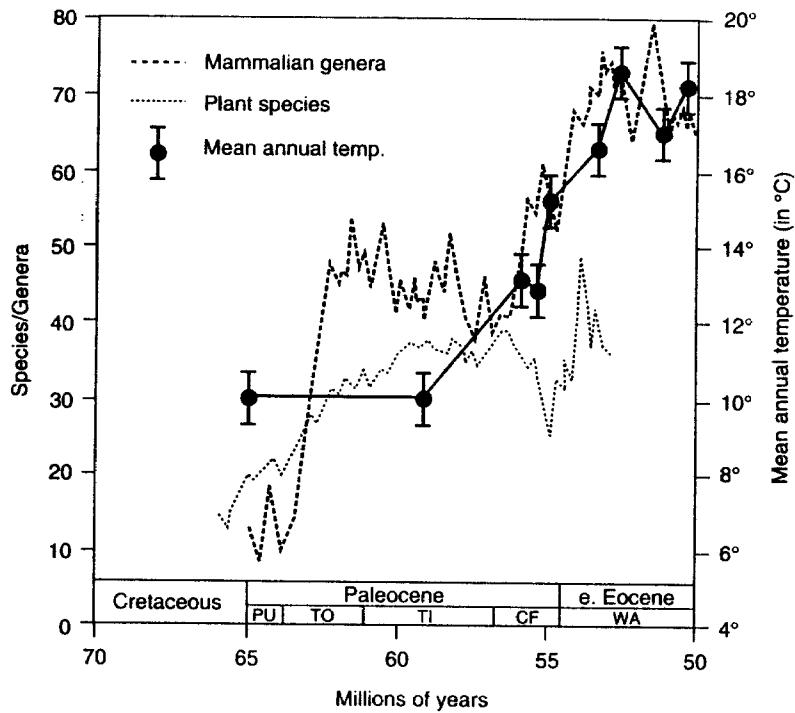


FIGURE 11-7 Comparison of MAT with the number of plant species and mammalian genera through the Paleocene and earliest Eocene. MAT estimates are based on physiognomic analysis of floras from western Wyoming. Plant and mammal taxonomic richness are based on data compiled from Wyoming and southern Montana. Abbreviations for provincial ages: PU=Puercan, TO=Torrejonian, TI=Tiffanian, CF=Clarkforkian, WA=Wasatchian. Figure was redrawn from Wing et al. (1995).

preceding the Terminal Paleocene Event. Stratigraphic resolution of the terminal Paleocene drop in floral richness is not yet sufficient to determine whether it coincides with increasing temperatures at the start of the Terminal Paleocene Event, decreasing temperatures at the end of the Terminal Paleocene Event, or is spread throughout the entire excursion.

The fluctuations in numbers of species of plants near the Paleocene/Eocene boundary are part of a long-recognized change in the composition of North American floras (Leopold and MacGinitie, 1972). Paleocene assemblages are dominated by species belonging to largely deciduous groups with modern north temperate distributions (e.g., *Metasequoia*, Betulaceae, Cercidiphyllaceae, Hamamelidaceae, Juglandaceae; Figure 11-8), whereas Eocene floras typically have many species belonging to largely subtropical evergreen families (e.g., Annonaceae, Lauraceae, Leguminosae, Myristicaceae, Palmae, Zamiaceae; Figure 11-9).

In the present, warmer climates are correlated positively with larger numbers of species of plants per unit area, particularly if regions of strong aridity are excluded (Gentry, 1988). In view of this correlation, a simplistic expectation for the response of plant species richness during the Paleocene/Eocene transition would be an increase in number of species as global temperatures warmed. Instead, the number of species of plants declined in two widely separated areas of North America: the northern Rocky Mountains (Wing et al., 1995), and the Gulf Coastal Plain (Frederiksen, 1994). The geographic scope of the decline argues against it being an artifact of local sampling or preservational effects, and implies that the cause is of continental or greater geographic scope.

A SCENARIO FOR PALEOCENE/EOCENE PLANT EXTINCTIONS

What causal connection is there, if any, between the climatic changes of the Terminal Paleocene Event, the decrease in plant diversity, and the shift in mammalian faunal composition? The stratigraphic resolution and geographic scope of our knowledge of faunal and floral change across this time period is increasing rapidly, but it is not yet sufficient to provide a clear answer. What follows is a preliminary hypothesis that is amenable to testing as the paleontological database improves.

A key to understanding the cause of the loss of species among plants is the difference between the curves of species richness for mammals and plants. In the present, the diversity of both groups of organisms generally increases toward the equator, but the migrational abilities are obviously quite different. The difference in rates of migration provides an explanation for greater loss of species among plants than mammals at the Paleocene/Eocene boundary.

The Paleocene flora of the northern continents long has been noted for its relatively low diversity and high homogeneity, with many lineages of deciduous plants distributed throughout the middle and high latitudes of North

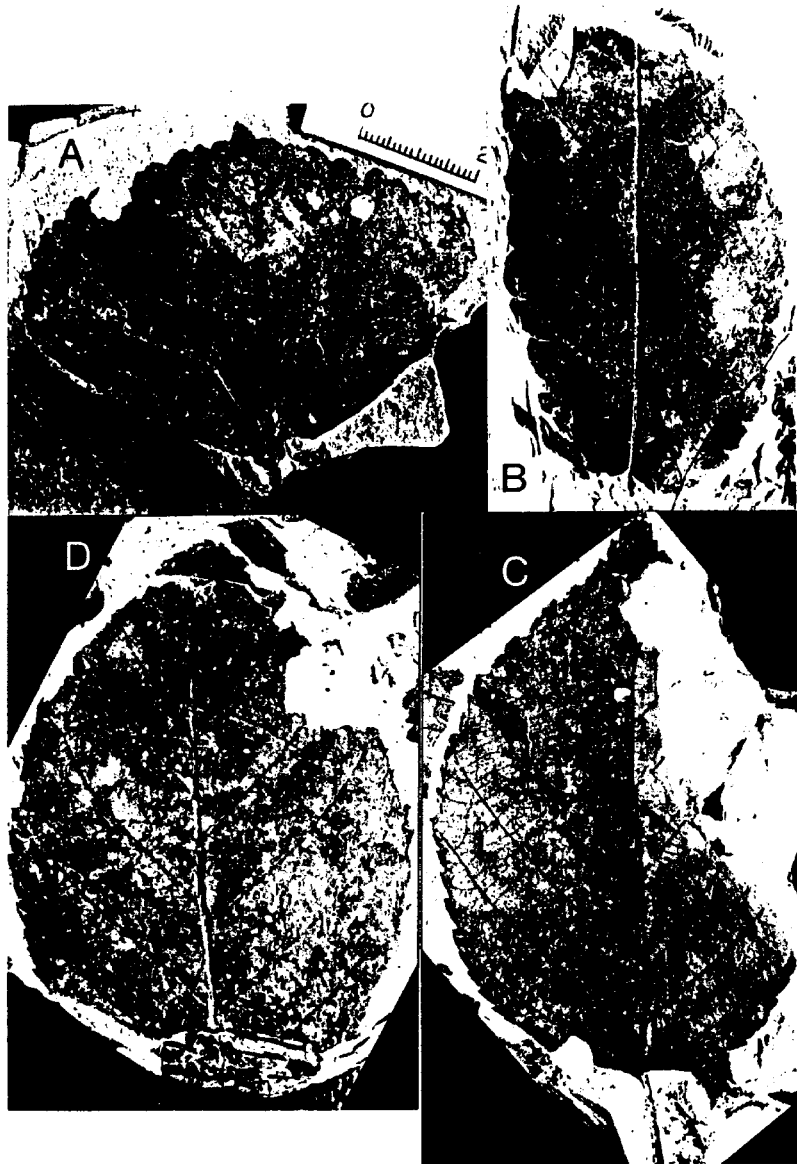


FIGURE 11-8 Typical Paleocene plant fossils of interior western North America. Based on thickness of the fossil organic compression and living relatives, most of these were probably deciduous trees. Toothed leaves are typical of the Paleocene midlatitude floras. A. *Cercidiphyllum* sp., related to katsura tree, a native of East Asia; B. *Ulmus* (*Chaetoptelea*) *microphylla*, related to living elms in Central America; C. Betulaceous leaf (birch family), probably an extinct genus; D. *Alnus* (alder) sp. leaf

FIGURE 11-8: COURTESY OF THE UNIVERSITY OF CALIFORNIA, BERKELEY

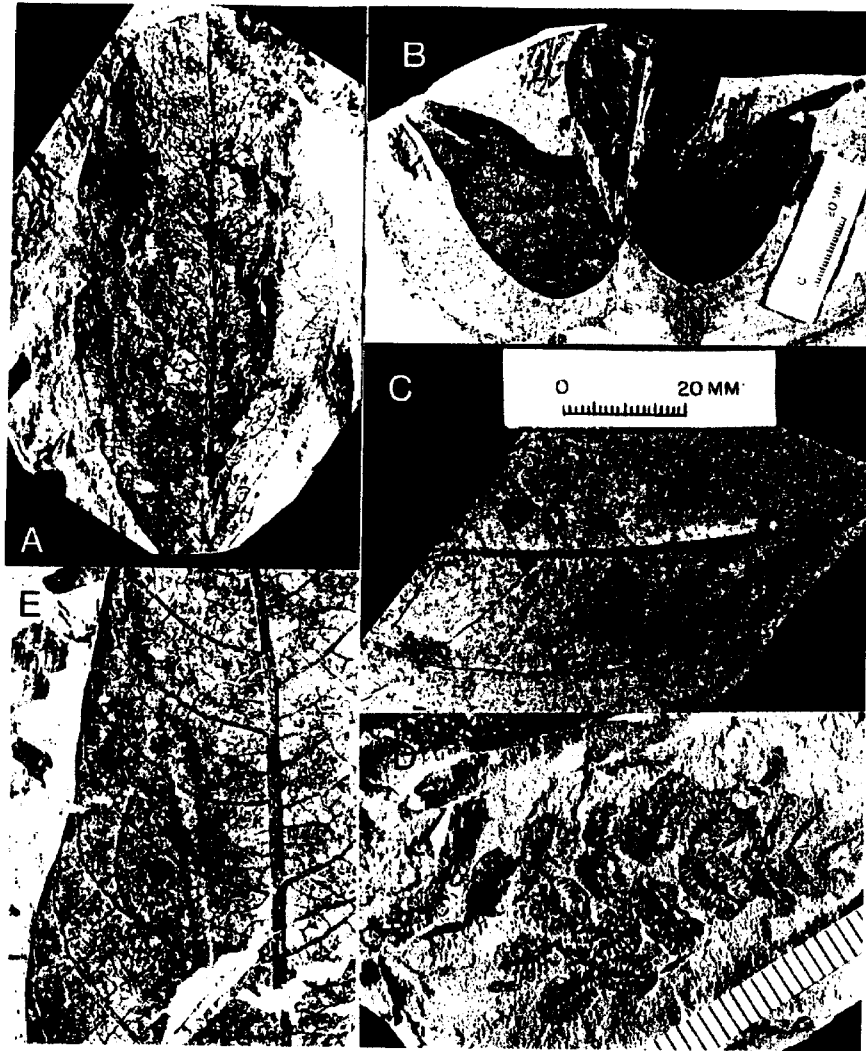


FIGURE 11-9 Typical early Eocene plant fossils of interior western North America. Based on thickness of the fossil organic compression and living relatives, most of these were probably broad-leaved evergreens. Large, entire-margined leaves are typical of Eocene midlatitude floras. A. Leaflet of a legume similar to living species of *Machaerium*; B. Menispermaceous leaf (moonseed family), probably a vine or liana; C. Lauraceous leaf (avocado family); D. *Salvinia preauriculata*, a floating aquatic fern characteristic of Eocene floras in midlatitude North America. Living *Salvinia* species occur in subtropical to tropical climates; E. Apocynaceous leaf (oleander family).

- 1) America, Europe, and Asia (Boulter and Kvacek, 1989; Brown, 1962; Guo et al., 1984; Koch, 1963). Warming at middle and high latitudes during the Terminal Paleocene Event and the early Eocene is likely to have caused local extinction at the southern ends of the ranges of cool-adapted lineages with broad circumpolar distributions. Warming at middle and high latitudes also would have permitted the poleward migration of subtropical and tropical taxa in both mammals and plants. For floras in the northern Rocky Mountains and the Gulf Coastal Plain of North America, there was a significant delay, as much as several hundred thousand years, between the loss of species at the Terminal Paleocene Event and the arrival of subtropical elements in the early Eocene. It was this lag that created the rapid drop and rapid recovery of plant richness at middle latitudes. What in mammals shows up as a rapid intercontinental mixing of faunas manifests itself among plants as an extinction event at mid- to high latitudes, followed perhaps 100,000 years later by a major immigration of species from the south.

The migrational lag explanation seems at first glance unlikely because plant "migration" can be very rapid geologically; the movement of forest taxa in the wake of the retreating Holocene glaciers totally modified the vegetation of vast areas of North America in 5,000-10,000 years (Overpeck et al., 1992). The Holocene example is not wholly applicable to the Eocene situation, however, because of the different continental configuration in the Eocene, and because Holocene plants were migrating into a recently denuded landscape that probably was not occupied by established forest vegetation.

In the early Eocene, the Tethys Sea still formed a wide barrier between the northern and southern continents; it separated Africa from Europe and South America from North America, although there were probably islands in both the proto-Mediterranean and the proto-Caribbean (Figure 11-10). This ocean crossing may have been one factor that slowed the migration of subtropical and tropical plants into North America. Tropical taxa may have had limited access to Europe along the northern shore of the Tethys, but the straits of Turgai divided Europe from eastern Asia at about the present-day position of the Caspian Sea, so the appearance of subtropical forms in Europe also might have been delayed. By contrast, Asia had a broad land connection with tropical continental areas during the Eocene, so that the ranges of terrestrial plants could have shifted northward without confronting an oceanic barrier.

The paleogeographic differences between Asia and North America can be used to help resolve whether a migrational lag was important in creating the pattern of change in number of species across the interval of the Paleocene-Eocene boundary. Because of eastern Asia's connection to tropical land masses, the migration of lineages from warm climates into middle latitudes should have been much easier than in North America or Europe. If this hypothesis is correct, Paleocene-Eocene floral immigration into mid-latitude Asia should have been more rapid, and the sharp drop in plant species richness should have had a duration of thousands or tens of thousands of years—almost certainly too short

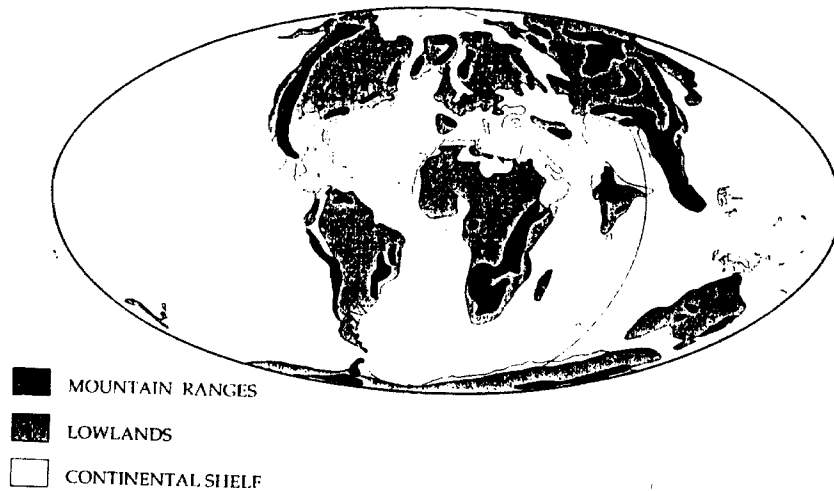


FIGURE 11-10 Global paleogeographic reconstruction of the early Eocene. Note ocean barriers that separated the European and North American land masses from Africa and South America. Only Asia had a significant land connection to tropical latitudes. Figure was redrawn from Smith et al. (1994).

to detect in the fossil record. Finding the same pattern of diversity change in Asia and North America would remove migrational delay as a reasonable hypothesis for the decline in species numbers observed in North America.

The cause of the loss of species during the Paleocene-Eocene transition also can be evaluated by comparing the pattern of floral immigration within North America. If the delayed immigration of subtropical forms to the northern Rocky Mountain region was largely a consequence of the water gap between North America and South America rather than slow migration across the North American continent, then forms from warm climates should appear at essentially the same time in the southern and northern part of the continent. If migrants adapted to warm climates show up detectably earlier in the south, this would indicate a slow rate of migration across the continent, suggesting that the rate of northward shift in the ranges of plants was limited by the pace of warming, or by the ability of the immigrant species to gain footholds in the established vegetation of North America.

Two possible general patterns emerge from a consideration of events at the Paleocene/Eocene boundary. First, species richness of plants is much more dramatically affected by the climatic change than is taxonomic richness of mammals. This should not be surprising in light of the sensitivity of plants to climate, but it has been proposed that plants are generally more "extinction

resistant" than other groups of organisms (Knoll, 1984). This conclusion was based on the observation that most major lineages of plants survived mass extinctions at the Permian/Triassic and Cretaceous/Tertiary boundaries, whereas higher taxonomic groups of animals were decimated. Analysis of the Paleocene/Eocene extinctions of plants supports the idea that the cause of an extinction (e.g., climate versus bolide impact) may be more important in understanding its effects than its "size," as measured by the percentage of taxa that are lost.

The Paleocene/Eocene extinction of plants also illustrates the principle that the rate of climatic change may be as or more important than its direction in causing extinction of plants. Rapid climatic shifts initially may decrease species richness of plants through accelerated local extinction regardless of whether climate is warming or cooling.

Through the last 65 million years of Earth's history, the middle and high latitudes have been more affected by both warming and cooling events than the tropics because their temperature is more easily influenced by changes in the efficiency and direction of heat transport by oceanic and atmospheric circulation. Although the image of the tropics as climatically invariant has been thoroughly debunked by increased understanding of the Miocene through Pleistocene history of Amazonia (Hoorn, 1994; Van der Hammen and Absy, 1994), over the long term it is the middle and high latitudes that have been most dramatically affected by fluctuations in global climate and most frequently afflicted by large-scale extinction of plants. During the Pleistocene, the comings and goings of glaciers in the north temperate regions resulted in the intermittent sterilization of large areas, certainly a more severe form of disruption than the rainfall and temperature fluctuations experienced at lower latitudes. Relative climatic stability on geological time scales is probably one important factor leading to larger numbers of species in the tropics.

CONCLUSIONS

The fossil record can be used in two different and very productive ways to understand global climatic change and its effects on biotic systems. First, it is a testing ground for climate models—the only way we can find out if they are overtuned to reproduce present conditions. The example of the enigma of equable climate suggests that there is a great deal of room for improving general circulation models of climate, and that predictions generated through GCMs have a bias toward reproducing conditions similar to those of the present. This is a very serious problem for understanding the probable effects of anthropogenic addition of CO₂ or other greenhouse gases to the atmosphere.

The fossil record also provides our sole opportunity to examine the biological consequences of climatic change without waiting for them to happen in "real time." Although causation is difficult to prove in an historical record (or, often enough, even in the laboratory), the pattern of biotic response to environmental

change can indicate probable processes. In particular, we should be on the alert for patterns that are consistent with threshold responses to climatic forcing factors (DiMichele and Phillips, 1995).

Paleontologists have invoked climatic change as a major factor in extinction and biotic turnover for as long as there have been paleontologists. But generally this has been an afterthought. A concerted study of the biotic effects of climatic change involves choosing time intervals for the climatic events that are known to occur, rather than searching for climatic change once a dramatic biotic change has been noted. This is the only way to find out if some climatic change occurs without catastrophic biological effects. Such studies require combining research on paleoecology, the history of biotic diversity, and extinction, with paleo-climatic reconstructions. Mixing these approaches will provide results of practical importance, but also will raise fascinating biological issues relating to ecosystem response, threshold effects, and biogeography.

Some view the globally warm periods of the past as a prologue to the future. Are they? This is not a question we can answer yet. We do know that climatic models "tuned" to the present do a poor job of reproducing the climate of past greenhouse worlds. We also know that the present is an unusual time in Earth's history, and not a simple key to the past. Clearly this raises doubts about our ability to predict climatic change or biotic responses under elevated CO₂ conditions.

If the present is not the key to the past, is the past likely to reveal much about the future? Here I think the answer is a cautious "yes." The process of interpretation is not simple, but by enlarging the set of "worlds" we have to explain, study of the past will increase the generality of our understanding of the hypercomplex climatic and biological systems that we are trying to predict. The fossil record is difficult to use, but it provides the only examples we have of events and states that occurred but can no longer be observed directly. Figuring out how to interpret the fossil record is now more important than ever. So is the advice given by Herodotus: "Study the past."

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