

Floral response to rapid warming in the earliest Eocene and implications for concurrent faunal change

Scott L. Wing and Guy J. Harrington

Abstract.—During the first 10–20 Kyr of the Eocene temperatures warmed by 4–8°C in middle and high latitudes, then cooled again over the succeeding ~200 Kyr. Major changes in the composition of marine and terrestrial faunas, including one of the largest mammalian turnover events of the Cenozoic, occurred during this temperature excursion. To better understand the effects of rapid climatic change on continental biotas, we studied 60 fossil pollen samples collected from 900 m of section spanning approximately three million years of the late Paleocene and early Eocene; the samples come from the Fort Union Formation and Willwood Formation in the Bighorn Basin of northwestern Wyoming, paleolatitude approximately 47°N. There are 40 samples from the 500 m of rock deposited during the one million year interval centered on the Paleocene/Eocene boundary, although pollen was not preserved well in rocks representing the short warm interval at the base of the Eocene.

Overall, the palynoflora shows moderate change in composition and diversity. Two pollen taxa clearly expanded their ranges to include North America in the first 400 Kyr of the Eocene, *Platycarya* (Juglandaceae), and *Intratropipollenites instructus* (cf. *Tilia*), but they account for less than 5% of pollen grains in the early Eocene. There are no last appearances of common taxa associated with the Paleocene/Eocene boundary. The most noticeable palynological changes are the decrease in abundance of *Caryapollenites* spp. and *Polyatriopollenites vermontensis* (Juglandaceae), and the increase in abundance of Taxodiaceae (bald cypress family), Ulmaceae (elm family), and Betulaceae (birch family), particularly *Alnipollenites* spp. (alder). There are 22% more species in the Eocene samples than in the Paleocene samples; mean richness of Eocene samples is 17% higher than the mean of Paleocene samples. The mean evenness of Eocene samples is higher than that of Paleocene samples, but the difference is not significant.

The modest level of floral change during the late Paleocene and early Eocene contrasts with the major taxonomic turnover and ecological rearrangement of North American mammalian faunas observed at the same time. Faunal change probably resulted from intercontinental range expansion across Arctic land bridges that became habitable as a result of high-latitude warming, so it is surprising that climatically sensitive plants did not also experience a major episode of interchange. The absence of fossil plants from the temperature excursion interval itself could prevent us from recognizing a transient shift in floral composition, but it is clear that the flora did not undergo a major and permanent restructuring like that seen in the mammals. The contrast between the moderate floral response to warming and the strong faunal response is consistent with the idea that interactions between immigrant and native taxa, rather than climate directly, were the primary cause of terrestrial biotic change across the Paleocene/Eocene boundary.

Scott L. Wing. Department of Paleobiology, MRC121, Smithsonian Institution, Washington, D.C. 20560.

E-mail: wing.scott@nmnh.si.edu

Guy J. Harrington.* Centre for Palynology, Department of Animal and Plant Sciences, University of Sheffield, Western Bank, Sheffield, S10 2TN, United Kingdom

*Present address: Department of Geology, University College Cork, Cork, Ireland.

E-mail: gj.harrington@ucc.ie

Accepted: 28 November 2000

Introduction

The potential for human activities to generate global and regional climatic change has stimulated paleontologists to study the effects of past climatic changes on biotic systems. Some have argued for a tight linkage between biotic and climatic change (e.g., Vrba 1985; Janis 1993), while others have failed to find evidence for such a correlation (e.g., Behrensmeyer et al. 1997; Prothero 1999; Alroy 1998;

Alroy et al. 2000). Most of these studies have used stable oxygen isotope records from marine cores as a proxy for climatic change because such records are temporally detailed and moderately complete. Most studies of the continental fossil record have considered mammalian faunas in isolation from other organisms in the ecosystem. Here we examine floral change across the Paleocene/Eocene transition in North America and compare our

results with previous studies of mammalian faunal change through the same time.

We expect the comparison of plants and mammals to be informative because of the different ways in which land plants and mammals react to climate. The distribution of many plant species is strongly controlled by climate, and although individual plants have some capacity for physiological adaptation to climate, they have no ability as individuals to migrate away from unfavorable conditions. In contrast, many mammals are homeothermic, have behavioral and physiological mechanisms for tolerating climatic extremes, and are highly mobile. Therefore when the fossil records of plants and mammals living in the same region are compared, we expect floras to be more strongly affected by climatic change than mammalian faunas.

The Paleocene/Eocene boundary in North America has long been recognized by a major immigration event among mammals, including the first appearances of artiodactyls, perissodactyls, primates, and hyaenodontid condylarths (Rose 1981; Gingerich 1989). This is one of the largest faunal turnover events of the Cenozoic in North America, and the new orders probably appear at the same time in Europe as well (Hooker 1998). The continent of origin for the immigrants is disputed, but Asia is considered a likely source (Beard 1997).

In North America the immigrant mammals appear at the same time as a rapid warming of 4–8°C at middle and high latitudes that has been called the late Paleocene Thermal Maximum (Koch et al. 1992, 1995; Zachos et al. 1994; Fricke et al. 1998; Clyde and Gingerich 1998). This warming is estimated to have lasted ~200 Kyr, and the time from the onset of warming to peak temperatures is estimated to have been 10–20 Kyr (Kennett and Stott 1991; Bains et al. 1999; Norris and Röhl 1999; Röhl et al. 2000). This, one of the most abrupt large warming events known in the geological past, was probably caused by the dissociation of large amounts of methane hydrate in the seafloor, followed by warming as the result of high atmospheric concentrations of methane and/or its oxidation products, carbon dioxide and water vapor (Dickens et al. 1997; Katz et

al. 1999). The very negative carbon isotope value of the released methane (–60‰) is thought to explain the sharp negative excursion in carbon isotope values in a variety of reservoirs that is synchronous with the warming (Dickens et al. 1997). Recently a working group of the International Commission on Stratigraphy has decided that the base of the carbon isotope excursion associated with this abrupt warming should be used to recognize the base of the Eocene (Luterbacher et al. 2000). Therefore, we will refer to this warming as the Initial Eocene Thermal Maximum, or IETM (Schmitz 2000).

In addition to the appearance of new orders of mammals in North America at the IETM there were also changes in mammalian species richness, intra- and interspecific body size distributions, trophic adaptations, and relative abundance distributions (Gingerich 1989; Clyde and Gingerich 1998; Gunnell 1998). During the IETM immigrant taxa accounted for approximately 20% of species and individuals in samples from the Bighorn Basin; in the succeeding part of the early Eocene 35% of species and 50% of individuals belonged to immigrant lineages (Clyde and Gingerich 1998). Immigrant mammals were significantly larger than natives; they also were more likely to be herbivorous, frugivorous, or carnivorous rather than insectivorous or omnivorous (Clyde and Gingerich 1998). Within lineages, body sizes were small during the IETM, which is consistent with the correlation of smaller body size with higher temperatures seen geographically within many extant species of mammals (Clyde and Gingerich 1998).

The changes in the richness, evenness, and guild structure of the mammalian fauna during and after the IETM could be attributed directly to climatic change, or somewhat less directly to changes in vegetation that were caused by climatic change. If this was true, the driving force behind faunal change would have been shifts in the distribution of resources that favored different species and trophic adaptations. An alternative hypothesis is that mammalian change at the IETM was a response to the appearance of immigrant species. In this explanation faunal change would have been driven by a new set of predators,

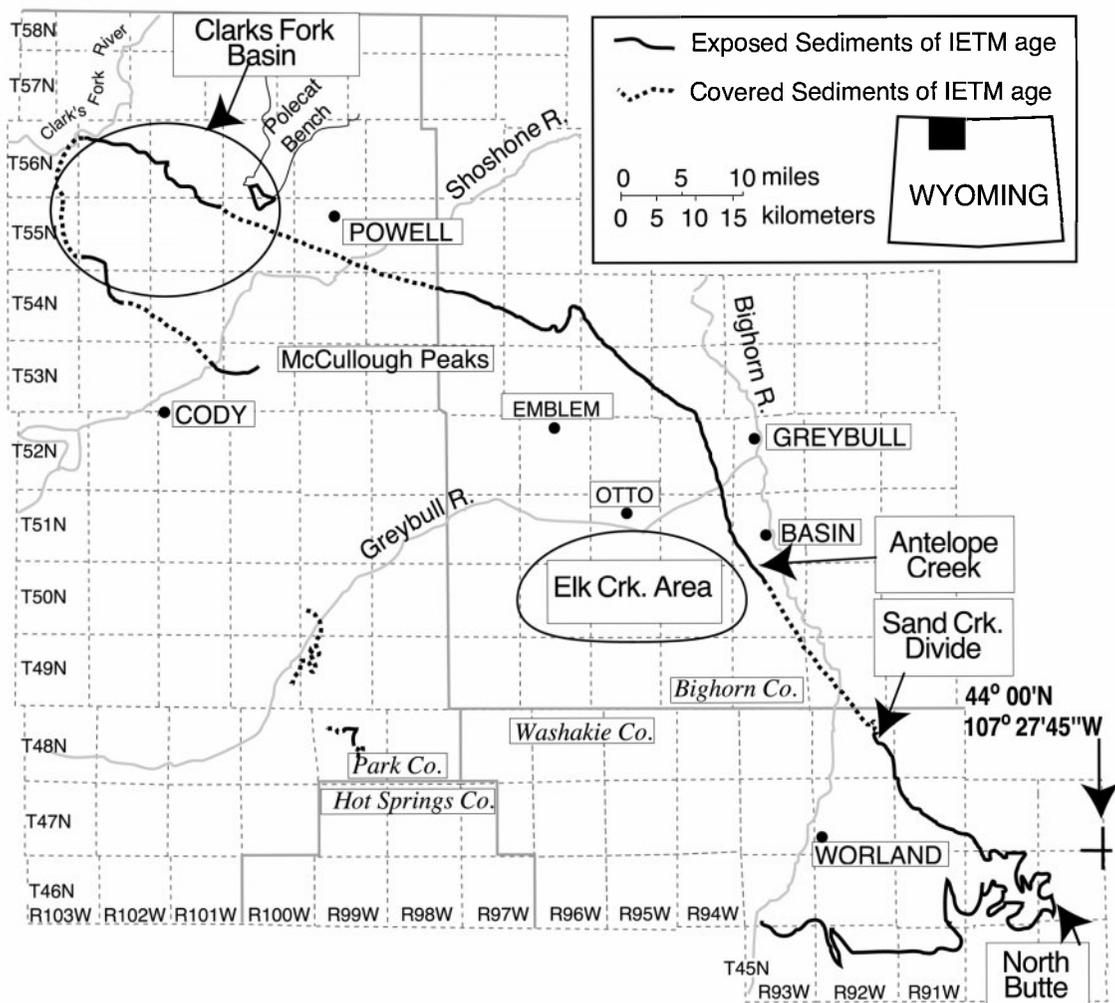


FIGURE 1. Bighorn Basin. Outcrop of IETM-age sediments indicated by line (dashed where covered). The four main areas from which palynological samples were taken are the Clarks Fork Basin, Antelope Creek, Elk Creek, and North Butte.

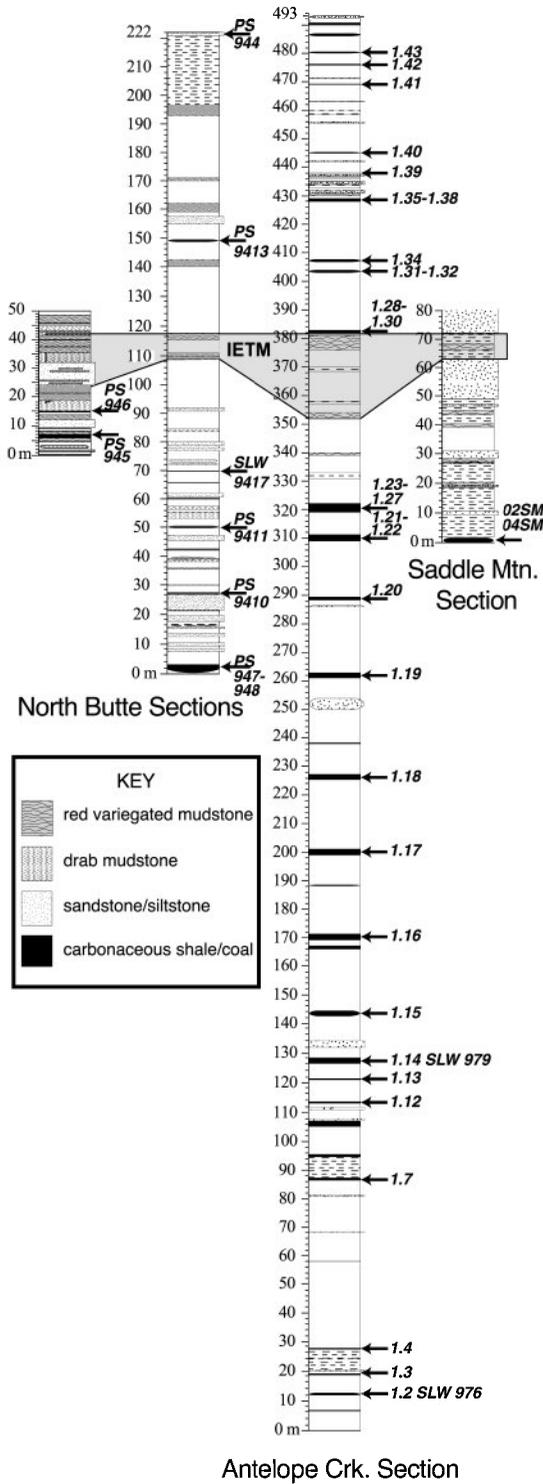
prey, and competitors, rather than by climate or vegetation. Clyde and Gingerich (1998) clearly favored this second hypothesis as playing the more important role in affecting community composition, although they considered within-lineage body size change to be a direct result of warming.

In this paper we examine the timing and amount of floral change across the Paleocene/Eocene boundary period and compare it with faunal changes occurring during the same time. If faunal changes were largely a direct consequence of changing climate and vegetation, then we would expect faunal and floral change to be synchronous, and floral change

to be large. If faunal change was largely a consequence of the arrival of immigrants, then the floral and faunal changes could be offset in time, or floras may have changed little.

Geological and Stratigraphic Context

The most extensively exposed and studied continental sections of the late Paleocene and early Eocene are those of the Fort Union and Willwood Formations in the Bighorn Basin of northwestern Wyoming (Fig. 1). In most areas of the Bighorn Basin the formational contact is coincident with the Paleocene/Eocene boundary, although in the eastern basin the uppermost Fort Union Formation produces Eocene



faunas and floras (Wing and Bown 1985), and in the northwestern Bighorn Basin (= Clarks Fork Basin) the lower Willwood Formation produces Paleocene faunas and floras (Rose 1981; Hickey 1980).

The negative excursion in carbon isotope ratio that is characteristic of the IETM has been measured in soil nodules and mammalian tooth enamel from stratigraphic sections in four areas of the Bighorn Basin (Koch et al. 1992; 1995). Koch et al. (1992, 1995) recognized that in each of these areas the carbon isotope excursion was for the most part stratigraphically coincident with a distinctive mammalian fauna that includes the first records of Eocene immigrant mammals (Wa0 fauna of Gingerich 1989). In all areas where the isotopic excursion has been observed in the Bighorn Basin it also coincides with 20–40 m of distinctive thick, red paleosols (Koch et al. 1995).

For this study we collected 60 samples from four areas of the Bighorn Basin. The bulk of the samples (35) come from a ~500-m-thick stratigraphic section measured in the upper Fort Union Formation and lower Willwood Formation exposed on Antelope Creek (Figs. 1, 2). The Antelope Creek section is advantageous for paleobotanical study because of the high stratigraphic density of organic-rich lithologies. The carbon isotope excursion has not been observed in the Antelope Creek section because neither mammalian teeth nor paleosol nodules have been recovered from the base of the Willwood Formation in this section. Although direct evidence is lacking, we think the IETM is represented in this exposure, because the basal 30 m of the Willwood Formation has two very thick red paleosol horizons similar to those that characterize the IETM elsewhere in the southeastern Bighorn Basin, and a mammalian fauna from 50 m above these red paleosols is similar in composition to very early Eocene faunas from other parts of the Bighorn Basin (Schankler 1980). Furthermore, fossil teeth of the Eocene index

FIGURE 2. Stratigraphic sections at North Butte (left two), Antelope Creek (middle), and Saddle Mountain in the Clarks Fork Basin (right). Pollen samples indicated by arrows. Stratigraphic positions of samples from other areas are not shown: nine from the Elk Creek section, four from the Clarks Fork Basin, and one from the Sand

Creek Divide. The stratigraphic position of these samples with regard to the Paleocene/Eocene boundary and IETM has been measured.

fossil *Hyracotherium* recovered from laterally equivalent red paleosols about three kilometers to the north of Antelope Creek (Johns Hopkins/USGS locality WW-39 [K. D. Rose personal communication 1999]), have carbon isotope values of -13.63% and -14.00% (P. L. Koch personal communication 2000). Elsewhere in the Bighorn Basin such low values have been observed only in *Hyracotherium* specimens from the stratigraphic interval that represents the carbon isotope excursion the base of which marks the Paleocene/Eocene boundary (Koch et al. 1995). The *Hyracotherium* teeth from WW-39 are larger than those of the Wa0 species *H. sandrae*, and probably belong to *H. grangeri* (P. D. Gingerich personal communication 2000), which is more typical of slightly younger (Wa1) faunas in the northern Bighorn Basin. The negative carbon isotope values of these specimens indicate either that *H. grangeri* occurs in the Wa0 fauna or that the carbon isotope excursion overlaps with the lower part of the Wa1 faunal zone. (Later Wa1 faunas have normal carbon isotope values [Koch et al. 1995].) In either case, we conclude that the lowest red beds in the vicinity of Antelope Creek formed during the carbon isotope excursion and therefore represent the IETM.

Nine of our samples come from stratigraphic sections of the upper Fort Union Formation and lower Willwood Formation near North Butte (Figs. 1 and 2). As in the Antelope Creek section, the IETM here coincides approximately with the Fort Union/Willwood Formation contact; however, at North Butte both the carbon isotope excursion and the Wa0 fauna have been observed to coincide with the distinctive, thick paleosols (Koch et al. 1995; Wing 1998; K. D. Rose personal communication 1999).

One sample (PS949) came from the upper Fort Union Formation on the north end of the Sand Creek Divide north of Worland, about 15 m below the base of the Willwood Formation. The lowest red beds in the Willwood Formation in this area have produced a small Wa0 fauna, and paleosol carbonate nodules from these red beds have carbon isotope values typical of the excursion at the base of the Eocene (Gingerich 1989; Koch et al. 1995).

The remaining six samples were collected

from the Willwood Formation in the northern Bighorn Basin (Fig. 1). One sample came from a carbonaceous shale that is stratigraphically just above an early Clarkforkian (late Paleocene) mammal locality (University of Michigan SC216). Two samples come from below the IETM on Saddle Mountain, and three from above the IETM on the Big Sand Coulee divide. In this area the IETM has also been recognized lithologically, faunally, and isotopically, although the sequence occurs entirely within the Willwood Formation (Gingerich 1989). In no part of the Bighorn Basin did samples from the IETM produce pollen that was well-enough preserved to be identified and counted.

To include samples from different stratigraphic sections in the same analysis, we have converted meter levels to time through linear interpolation of sediment accumulation rates between dated levels. The dates used are 56.2 Ma for the base of C24R, 55.2 Ma for the base of the Eocene (= base of the carbon isotope excursion and IETM), and 53.7 Ma for the first appearance of the index mammal fossil *Bunophorus*. The age models for the sections are described in greater detail by Wing et al. (2000) as age model 2.

Lithology and Environment of Deposition.—Within the Fort Union and Willwood Formations organic matter is preserved in a variety of sedimentary environments (Wing 1984a; Farley 1989, 1990; Davies-Vollum and Wing 1998; Kraus 1998). Type II carbonaceous beds are laterally extensive, tabular deposits, each of which represents a suite of environments of deposition on distal, wet, vegetated floodplains (Wing 1984a; Davies-Vollum and Wing 1998). Facies within Type II beds include gray, poorly bedded mudstones/siltstones that represent wet or seasonally wet soils; thin coals, coal shales, and carbonaceous shales that represent vegetated swamps; and interlaminated silts and fine sands with small-scale cross stratification that represent levees or crevasse splays (Wing 1984a; Davies-Vollum and Wing 1998). Organic matter is also preserved in lenticular bodies of a few hundred meters lateral extent that represent deposition in standing water within abandoned channel segments (Type I bed of Wing 1984a).

Palynofloras preserved in various lithologies of Type II layers represent pollen accumulation on a stable and vegetated distal floodplain surface where the dominant source of pollen was the local forest (Farley 1989, 1990). The palynofloras of the abandoned-channel deposits represent pollen accumulation in small ponds, where there was some possibility of longer-distance transport of grains because of the absence of a canopy, and also the potential for water transport of pollen through intermittent channel reactivation (Farley 1989, 1990).

For this study we noted lithological features in the field; different lithologies in the same bed were sampled as often as possible so that the effect of environment of deposition on palynofloral composition could be evaluated. Forty-four of the samples were taken from carbonaceous shale or siltstone facies within Type II layers; 14 of the samples came from abandoned-channel fill deposits. One sample was taken from a coal, and one from a levee/crevasse splay deposit within a Type II layer.

Methods

Sample Processing and Counting.—Sample preparation followed a basic process of rock maceration, chemical digestion, and residue concentration. Typically, 15–30 g of rock were processed for each sample. The mineral matter was removed through digestion with hydrofluoric acid followed by centrifugation in heavy liquid (zinc chloride). Organic matter was concentrated at various stages of preparation by sieving with a 7- μ m mesh. Oxidation was kept to a minimum to preserve as much organic matter as possible: the residue was washed for a maximum of two minutes in concentrated nitric acid before thorough rinsing. An aliquot of the original residues was taken and mounted onto four slides. A total of 300 palynomorphs were counted per sample, although when more than 100 of the grains belonged to a single taxon (such as *Cupressacites hiatipites* or *Polyatriopollenites vermontensis*), additional palynomorphs were counted until a total of at least 200 grains of the nondominant taxa had been counted.

Analysis.—We conducted separate bootstrap analyses of the aggregated Paleocene

samples and the aggregated Eocene samples using the program EstimateS[®], Version 5.01 (Colwell 1999) to determine the effect of the number of samples on both observed richness (S_{obs}) and richness estimated by the nonparametric Chao 2 statistic (S_{Chao2}). The formula for the Chao 2 estimator is given by Colwell and Coddington (1994) as

$$S_{Chao2} = S_{obs} + (Q_1)^2/2Q_2 \quad (1)$$

where Q_1 = the number of species in the sample that are unique to that sample, and Q_2 = the number of species in the sample that occur in only one other sample in the data set. For both bootstrap analyses the resampling routine was iterated 50 times. We used the Chao 2 estimator because S_{Chao2} calculated from relatively few samples has been shown to converge on the true number of species from which a set of samples was drawn (Colwell and Coddington 1994).

We performed rarefaction analyses of individual Paleocene and Eocene samples to standardize comparisons of richness across samples of different size and to determine the effect of sample size on S_{obs} . We used the program Biodiversity Professional[®] Version Beta One (McAleece et al. 1997) to perform the rarefactions, as well as to calculate the evenness of abundance distributions (E) within samples. S_{obs} was calculated for every sample at a standard 281 grains. E is the ratio of the Shannon index (H) to the maximum possible Shannon index for that sample (H_{max}), and expresses the evenness of the abundance distribution of a sample relative to the maximum possible evenness for a sample with the same number of species.

To visualize differences in floral composition that relate to stratigraphic level and depositional environment, we conducted four detrended correspondence analyses (DCAs) using the program MVSP[®], Version 3.1 (Kovach 1999). Correspondence analysis (Hill 1973, 1979) is commonly used in plant ecology because it effectively displays gradients in floral composition in a few dimensions and can be used with presence/absence as well as abundance data. When the samples in a data set encompass great variation in floral composition, correspondence analyses can be sub-

ject to the arch effect, in which samples at the ends of the gradient expressed on the first axis of the ordination are crowded together. The "detrending" in DCA refers to the removal of the arch effect by dividing the first axis of the ordination into segments and adjusting the mean score of the points within each segment to be equal to the mean score of the other segments. This may distort some small-scale patterns in the ordination, but it makes longer gradients more linear.

The DCAs of palynological data were performed on the relative proportions of each taxon in each sample (calculated by dividing the number of grains of the taxon in the sample by the total number of grains counted for that sample). Rare species (i.e., those that occurred in fewer than 20% of the number of samples that the most ubiquitous species occurred in) were down-weighted because we felt that taphonomic processes and long-distance transport might account for the occurrence of rare grains, and we were trying to detect changes in local floodplain vegetation. DCAs were performed separately for the Paleocene sample set, the Eocene sample set, and the combined sample set. The separate analyses of the Paleocene and Eocene were done primarily to look for the effects of depositional environment and geography on floral composition. When all of the samples are analyzed together, these effects tend to be masked by the stratigraphic component of palynofloral variation. The DCA of the megafloora was performed on a presence/absence data matrix because too few sites had been collected quantitatively (Wing 1998).

Results

The 60 samples produced a total of 93 terrestrial palynomorph types (Appendices 1 and 2). The most diverse groups are Juglandaceae (14 forms), fern spores (11), and Betulaceae/Myricaceae (9). Other palynomorphs are similar to pollen of extant Anacardiaceae, Caprifoliaceae, Simaroubaceae, Sapindaceae, Tiliaceae, Sterculiaceae, Euphorbiaceae, and Malvaceae. Typical sample richness is 25–35 pollen types. The most important families in terms of abundance are Juglandaceae, Taxodiaceae, and Betulaceae. Cy-

cad pollen is rare but present through the sequence; palm pollen is uncommon but present in a number of early Eocene samples. In general, the palynoflora is composed of a mix of groups with modern subtropical and temperate distributions, as is characteristic of many Eocene mid-latitude floras (e.g., Hickey 1977).

Effect of Environment of Deposition on Composition and Diversity.—Most taxa were found in all lithologies, although gray mudstones and siltstones have lower palynomorph density and quality of preservation than carbonaceous shales. The one coal sample was notable in having a very high abundance of *Momipites*, a common characteristic of palynofloras from coals of similar age in the Powder River Basin (Pocknall 1987).

In general, palynofloras from abandoned-channel fills are moderately distinct from those in the various lithologies of the Type II layers. Paleocene abandoned channels have significantly higher proportions of *Appendicisporites*, *Insulapollenites*, *Jarzenipollenites*, *Panda-niidites*, *Plicatopollis*, *Triatriopollenites/Triporopollenites*, and reworked Cretaceous dinocysts than coeval floodplain deposits, and lower proportions of *Retitrescolpites* and *Eucommia* sp. A. DCA of the Paleocene samples shows that the abandoned-channel samples have a somewhat, though not wholly, distinct flora (Fig. 3B).

In the Eocene there is a less prominent distinction in floral composition between abandoned-channel fills and floodplains than in the Paleocene. Eocene channel-fill palynofloras tend to have high proportions of *Caryapollenites* spp., *Camaronosporites*, *Bisaccates*, *Erdtmanipollis*, *Nyssapollenites*, *Paraalnipollenites*, *Peripollenites*, *Polyatriopollenites vermontensis*, *Triatriopollenites subtriangulus*, *T. convexus*, *Triporopollenites* spp., and reworked dinocysts compared with Eocene floodplain samples, but many of these differences are not statistically significant by simple *t*-test. *Laevigatosporites*, *Cupressacites hiatipites*, *Sequoiapollenites*, and *I. instructus* tend to be less common in Eocene abandoned-channel floras than in floodplain assemblages (on average half a standard deviation unit below their mean overall abundances). The Eocene abandoned-channel sam-

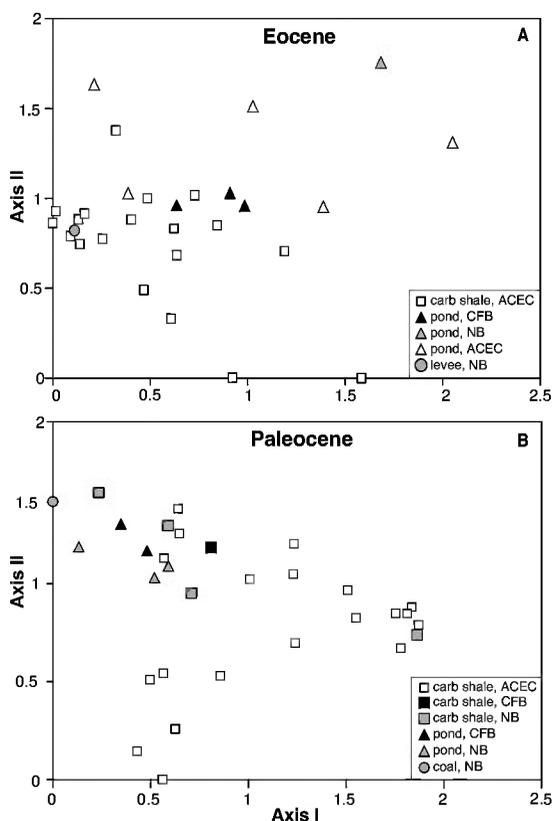


FIGURE 3. Detrended correspondence analyses (DCA) of Eocene (A) and Paleocene (B) pollen samples based on relative proportion data. NB = North Butte section, ACEC = Antelope Creek and Elk Creek sections, CFB = Clarks Fork Basin. Note that the Paleocene abandoned-channel samples (triangles in B) form a moderately distinct cluster, and that most samples from the margins of the basin (NB and CFB) are in the upper left of the plot. Eocene abandoned-channel samples (triangles in A) appear to be more variable in floral composition than Paleocene abandoned-channel samples and less distinct from coeval carbonaceous shale samples. The analyses suggest some variation in floras that relates to facies and geographic position in the basin. See methods section for details of analyses. For A, Axis I accounts for 19% of the variation, axis II for 9%; for B, Axis I accounts for 30% of the variation, axis II for 9%.

ples do not plot in a distinct group on the DCA, showing nearly the full range of axis I scores. Their scores on axis II are above the median, however (Fig. 3A).

Paleocene abandoned-channel samples are significantly richer in species than coeval floodplain palynofloras; the five abandoned-channel samples have a mean richness of 34.6 taxa, the 24 floodplain samples a mean of 26.4 taxa ($p \leq 0.06$ by t -test, with richness based on counts rarified to 281 grains). In contrast, the

9 Eocene abandoned-channel fill samples (mean richness of 35.1 species) are not significantly more diverse than the 18 Eocene floodplain samples (mean richness of 33.0 species; $p \leq 0.15$).

Composition of palynofloras also varies to some degree with geographic position within the Bighorn Basin (Fig. 3). As with smaller-scale facies differences, the heterogeneity is stronger in the Paleocene samples than the Eocene samples. Regardless of small-scale lithology, Paleocene samples from the northwestern (Clarks Fork) and southeastern (North Butte) parts of the Bighorn Basin plot in the same region of the DCA (Fig. 3B). These samples probably contain larger numbers of reworked grains, presumably because they were closer to the uplifting margins of the basin, but they also share greater than usual abundance of several probably autochthonous taxa (e.g., *Camarozonosporites*, *Cicatricosisporites*, *Cyathidites*, *Gleicheniidites*), suggesting that these forms were more abundant at the margins of the basin. It may seem surprising that these fern and lycopsid spore taxa are more common at the basin margins, which are likely to have been better drained than the basin center, but many tropical ferns, including some in the families represented by these spores, are important in open habitats on well-drained soils (Tryon and Tryon 1982; Arens and Baracaldo 1998).

Diversity Change Through Time.—The combined richness of the late Paleocene samples is 73 taxa (31 samples, 11,653 grains counted), substantially less than the 89 taxa seen in the early Eocene samples (29 samples, 9779 grains counted). The Paleocene samples have significantly lower richness at all levels of sampling effort, as seen in the effect of sample number on richness in bootstrap analyses (Fig. 4). The Eocene samples do span approximately twice the time interval of the Paleocene samples (~2.3 Myr for Eocene, ~1.1 Myr for Paleocene), but because taxonomic turnover is low in the Eocene this is not likely to explain the higher diversity of the Eocene sample set. Even the 24 samples representing the first ~1.2 Myr after the IETM contain 83 taxa, ten more than are seen in 31 samples spanning an equal amount of time in the late Paleocene.

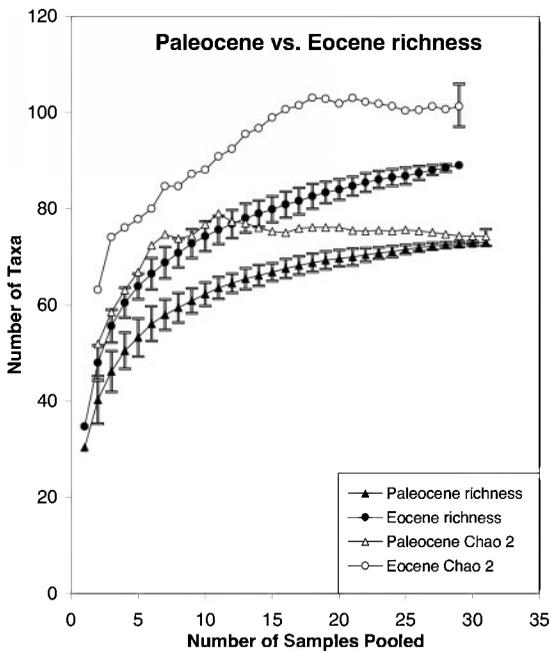


FIGURE 4. Bootstrap analysis of richness in Paleocene vs. Eocene samples. Curves show the mean number of taxa recovered (y-axis) for a given number of samples (x-axis), and the number of taxa estimated to exist using the nonparametric Chao 2 estimator (Colwell and Codrington 1994). The resampling routine was iterated 50 times, and the error bars represent one standard deviation. Eocene diversity is higher and increases more rapidly with increasing sampling effort. The higher Chao 2 estimates for the Eocene samples reflect the higher proportion of taxa occurring in only one sample. Details of analysis are given in the methods section.

The larger number of species in the Eocene flora in part reflects the larger number of rare taxa in the Eocene (eight singletons and eight doubletons in the Eocene vs. four singletons and seven doubletons in the Paleocene). The larger number of singletons in the Eocene leads to higher estimates of richness using the Chao 2 estimator (Fig. 4).

Within-sample richness also increased from the Paleocene (with a mean of 30 taxa) to the Eocene (mean of 35). This difference in richness is highly significant ($p \leq 0.001$ by a Kolmogorov-Smirnoff nonparametric test). Eocene samples have a significantly higher mean richness than Paleocene samples even if all samples are rarefied to a count of 281 grains (mean of 27.8 taxa for Paleocene samples, mean of 33.4 taxa for Eocene samples; Fig. 5). Rarefaction analysis also shows that in approximately half of the Paleocene samples,

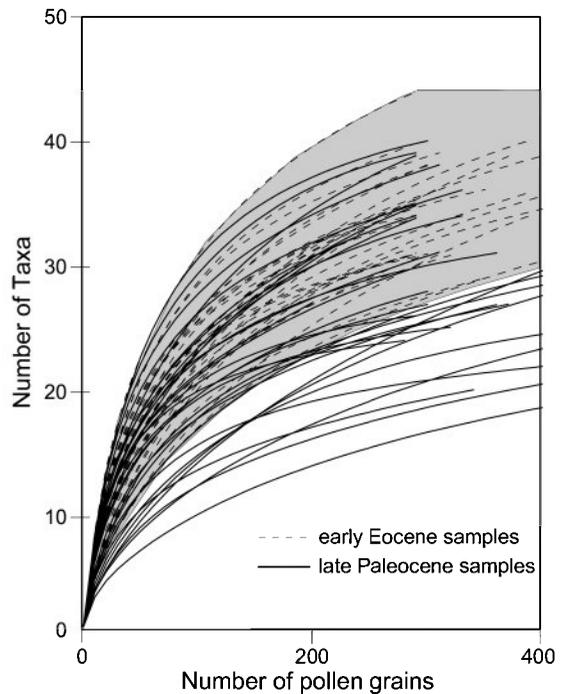


FIGURE 5. Rarefaction analyses of Paleocene and Eocene samples. Curves show the number of taxa expected for the sample size given on the x-axis. The shaded area encloses the curves for all Eocene samples. Note the 15 Paleocene samples (about 50%) that accumulate taxa slowly with increasing sample size. Details of the rarefaction analyses are given in the methods section.

richness increases very slowly with increasing sample size (Fig. 5). The higher mean sample richness in the Eocene reflects not so much an increase in maximum sample richness as an absence of samples with low richness (20–28 taxa). Low richness in Paleocene samples is correlated with high dominance of either *Polyatriopollenites vermontensis* or *Cupressacites hiatipites*. This is probably the cause of the weak positive correlation between greater richness and greater evenness of species abundances in the Paleocene samples ($r^2 = 0.36$). Paleocene samples are more variable in both richness and evenness than are the Eocene samples, and samples from the 200 Kyr immediately preceding the IETM are particularly variable (Fig. 6).

Although sample richness is significantly higher in the Eocene than the Paleocene, the increase in evenness (E) is not significant. Mean Shannon index (H) is 1.02 for Paleocene samples and 1.11 for Eocene samples ($p \leq 0.1$

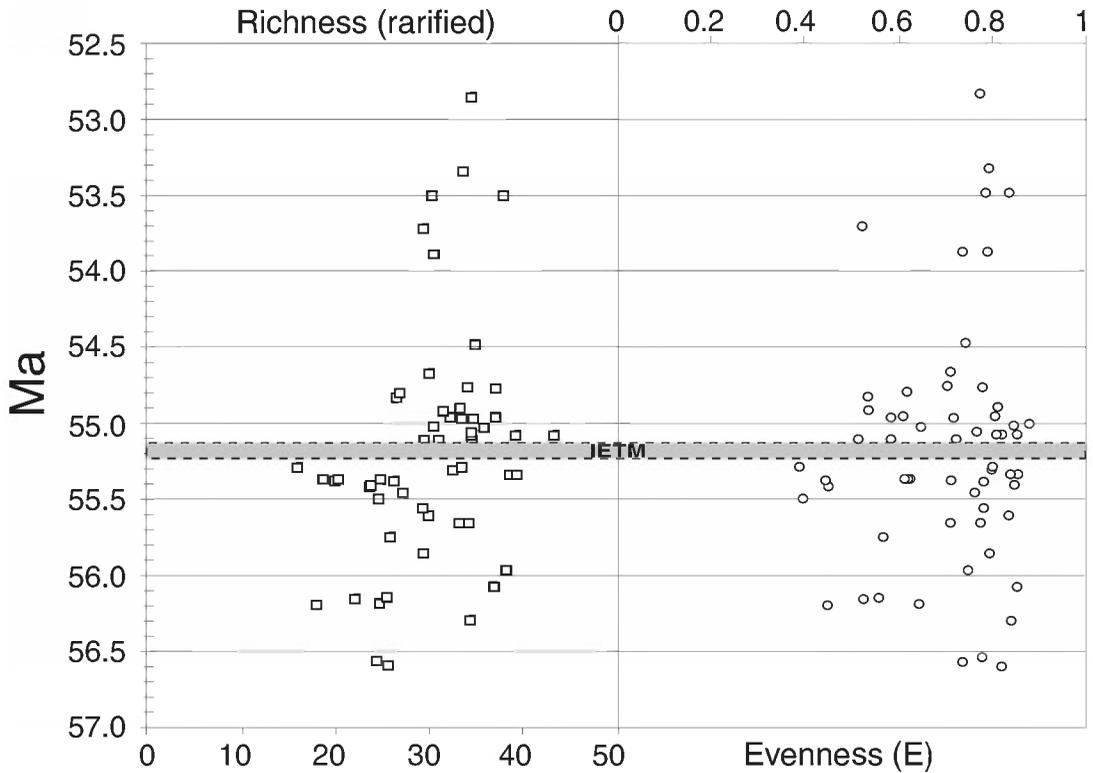


FIGURE 6. Change through time in richness and evenness of abundance distributions (E) within samples. Richness was calculated for a standard sample of 281 grains. Details of rarefaction analysis are given in the methods section. Ages for samples were calculated by linear interpolation using stratigraphic thickness between levels for which ages had been calculated. Details of the age model are described by Wing et al. (2000). IETM = Initial Eocene Thermal Maximum.

by t -test); mean E is 0.69 for Paleocene samples and 0.72 for Eocene ($p \leq 0.38$ by t -test). Thus the greater within-sample richness in the Eocene is not the result of a more even distribution of pollen grains among species. There is no correlation within the set of Eocene samples between richness and H ($r^2 = 0.02$).

Compositional Change.—Twenty taxa occur in the Eocene but not the Paleocene; however, 14 of these are known from four or fewer grains and from three or fewer samples (Table 1, Fig. 7A). The observed stratigraphic ranges of such rare taxa probably are not a good reflection of their true stratigraphic ranges, and therefore we place little importance on their distributions. Only six moderately abundant pollen types have first appearances in the Eocene. *Intratrirporopollenites instructus* (cf. *Tilia*) is the most abundant palynomorph restricted to

the Eocene. It occurs in the lowest Eocene sample (1 m above the top of the section representing the IETM), is found in 76% of the Eocene samples, and has a total abundance of 340 or 3.5% of the Eocene grains counted. Of the five other moderately abundant taxa that first occur in post-IETM samples, three are types of *Platycarya* pollen (Juglandaceae) that may represent a single biological species. The first occurrences of *P. platycaryoides* and *P. spp.* are at 37 m, and the first occurrence of *P. anticlyclus* is at 38 m above the top of the IETM barren interval. A total of 143 grains of the three *Platycarya* pollen types were recovered from all Eocene samples, less than 1.5% of the grains counted. The 37 m of section between the top of the IETM barren zone and the first occurrence of *Platycarya* is probably not an artifact of sampling because there are ten sam-

TABLE 1. Palynomorph taxa present only in the Paleocene or the Eocene.

Taxa appearing post-IETM	FAD level (m)*	FAD time (Ma)	FAD sample	No. of post-IETM grains	% Post-IETM grains	No. of post-IETM samples	% Post-IETM samples
<i>Intratropollenites instructus</i>	1.0	55.11	GH97-1.28	340	3.48	22	76
<i>Platycarya platycaryoides</i>	37.0	54.97	GH97-1.38	74	0.76	7	24
<i>Platycarya</i> spp.	37.0	54.97	GH97-1.38	47	0.48	10	34
<i>Punctatisporites</i>	1.0	55.11	GH97-1.28	38	0.39	6	21
<i>Platycarya anticyclus</i>	38.0	54.96	GH97-1.35	22	0.22	2	7
<i>Triatriopollenites triangulus</i>	40.0	55.08	PS97-02bsc	15	0.15	5	17
<i>Celtisporites</i>	311.0	53.88	LB	7	0.07	1	3
<i>Siltaria pacata</i>	468.0	53.33	Pn	4	0.04	1	3
<i>Zlivosporis</i>	1.0	55.11	GH97-1.28	3	0.03	3	10
<i>Baculatisporites</i>	40.0	55.08	PS97-05bsc	3	0.03	2	7
<i>Echitricolpites</i>	353.0	53.71	DCF	3	0.03	1	3
<i>Momipites triradiatus</i>	37.7	54.97	GH97-1.36	2	0.02	1	3
<i>Aesculidites circumstriatus</i>	86.5	54.77	GH97-1.42	2	0.02	2	7
<i>Stereisporites distgranisporis</i>	90.5	54.76	GH97-1.43	2	0.02	1	3
<i>Bombacites</i>	620.0	52.84	AL	2	0.02	1	3
<i>Reticuloidosporites</i>	22.5	55.03	GH97-1.31	1	0.01	1	3
<i>Ilexpollenites</i>	22.5	55.03	GH97-1.31	1	0.01	1	3
<i>Liliacidites</i>	79.0	54.80	GH97-1.41	1	0.01	1	3
" <i>Cercidiphyllites</i> "	102.0	54.83	PS944	1	0.01	1	3
<i>Cyrtolaccolpites</i>	620.0	52.84	AL	1	0.01	1	3

Taxa only in pre-IETM	LAD level (m)	LAD time (Ma)	LAD sample	No. of pre-IETM grains	% Pre-IETM grains	No. of pre-IETM samples	% Pre-IETM samples
<i>Ericipites</i>	-67.0	55.50	GH97-1.2	3	0.03	2	6
<i>Cingulatisporites</i>	-20.0	55.31	PS945	3	0.03	3	10
<i>Porocolpopollenites</i>	-33.0	55.37	GH97-1.27	2	0.02	2	6
<i>Platycaryapollenites</i> sp. B	-156.4	55.86	GH97-1.17	1	0.01	1	3

* Datum level is top of IETM.

ples in this interval, and the longest consecutive run of Eocene samples lacking *Platycarya*, after its first appearance, is four. The first occurrence of *Platycarya* is stratigraphically higher than the first occurrence of *I. instructus* in other Rocky Mountain intermontane basins as well (Bebout 1977; Pocknall 1987).

The remaining two moderately abundant taxa with first occurrences in the Eocene are *Punctatisporites* (Lycopodiaceae) and *Triatriopollenites triangulus* (Betulaceae/Myricaceae). *Punctatisporites* is represented by 38 grains (0.39%) in six samples (21%) and first occurs at the 1-m level; *T. triangulus* is represented by 15 grains (0.15%) in five samples (17%) and first occurs at the 40-m level.

In aggregate, the immigrant taxa (including rare species for which first occurrence levels are of uncertain significance) account, on average, for about 6% of the grains and 7% of the species in Eocene samples (Fig. 8). Although

the abundance of immigrants reaches 10–25% in some samples in the half-million years following the IETM, this is almost entirely because of one taxon, *Intratropollenites instructus*. High proportions of grains of immigrant taxa are not a common feature until about 52.8 Ma, nearly 2.5 Myr after the IETM, when *Platycarya* values reach >40% in many samples (Wing 1984b).

There are four Paleocene taxa that were not found in any Eocene samples: *Ericipites*, *Cingulatisporites*, *Porocolpopollenites*, and *Platycaryapollenites* sp. B. All of these taxa are represented by three or fewer grains (Fig. 7B) in three or fewer samples, and all of their last occurrences are 20 m or more below the base of the IETM. There are no palynomorph last appearances convincingly associated with the IETM.

Several taxa are substantially more abundant in Eocene than in Paleocene samples. Pol-

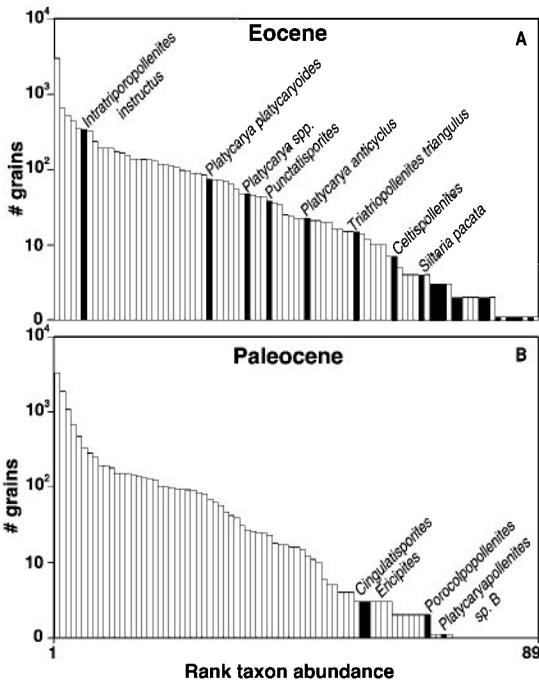


FIGURE 7. Dominance/diversity curves. A, Eocene pollen samples. B, Paleocene pollen samples. Taxa are arranged in order of relative abundance. Black bars in A indicate taxa not detected in the Paleocene (possible immigrants). Black bars in B indicate taxa not detected in the Eocene (possible extinctions). All possible extinctions are of rare taxa, as are most possible immigrants, except for *I. instructus* and *Platycarya* spp.

len of taxodiaceous conifers (*Cupressacites hia-tipites*) became approximately 50% more abundant, both overall and based on its proportion in individual samples. *Alnipollenites* is six times more abundant in the aggregate Eocene samples than in the combined Paleocene samples. Ulmaceous pollen increased by 60–80% from the Paleocene to the Eocene. A number of palynomorphs that were less than 0.5% of the flora prior to the IETM are 5 to 40 times more abundant in the combined Eocene samples: *Camarozonosporites* (Lycopodiaceae), *Eucommia* sp. A, *Monocolpopollenites* (cf. *Ginkgo?*), *Pandaniidites* (aquatic monocot—probably Araceae), *Plicatopollis* (Juglandaceae), *Sparganiaceapollenites* (Sparganiaceae), and *Triporopollenites infrequens* (Betulaceae/Myricaceae).

A smaller number of taxa decreased in abundance following the IETM. *Caryapollenites*, *Polyatriopollenites*, and *Momipites*, all juglandaceous forms, declined to between one-half and one-fifth their Paleocene abundance,

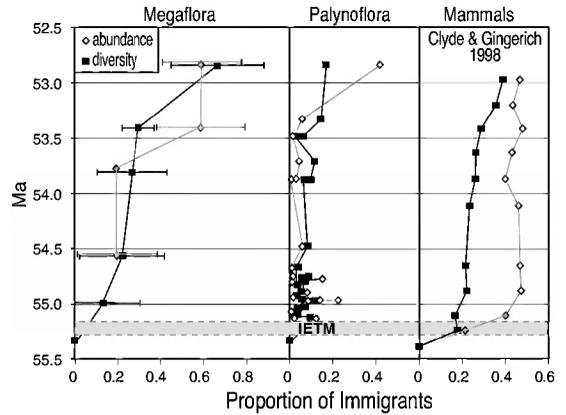


FIGURE 8. Proportional abundance and proportional diversity of possible Eocene immigrants in megaflora, palynoflora, and mammalian fauna. Error bars are one standard deviation. Faunal data from Clyde and Gingerich 1998. Age model as in Figure 6.

although they did not become rare. *Boehlensipollis* (Sapindaceae/Myrtaceae), which was 0.2% of the Paleocene grains counted, declined to only 0.02% of Eocene grains.

Together, the first appearances and changes in abundance result in a somewhat different flora following the IETM, although there is much fluctuation in composition from level to level within each epoch, particularly in the latest Paleocene. We calculated Spearman rank-order correlation coefficients between all pairs of samples. The mean correlation coefficient between Paleocene samples was 0.58 (SD = 0.11), and between Eocene samples was 0.50 (SD = 0.1). The mean rank-order correlation coefficient between Paleocene and Eocene samples was 0.48 (SD = 0.1). Differences between the three sets of comparisons are statistically significant ($p \leq 0.0001$ by Kruskal-Wallis ANOVA), demonstrating that samples within each epoch are on average more similar to one another than to samples from the other epoch, and that in terms of rank-order abundance Eocene samples are more heterogeneous than Paleocene samples.

To illustrate the overall change in floral composition, we performed a DCA on the sites by species matrix of proportional abundances (Fig. 9A, Appendix 2). Rare taxa were down-weighted in the analysis, and some similar palynomorphs were lumped because we think they may represent a single taxon (all *Alnipol-*

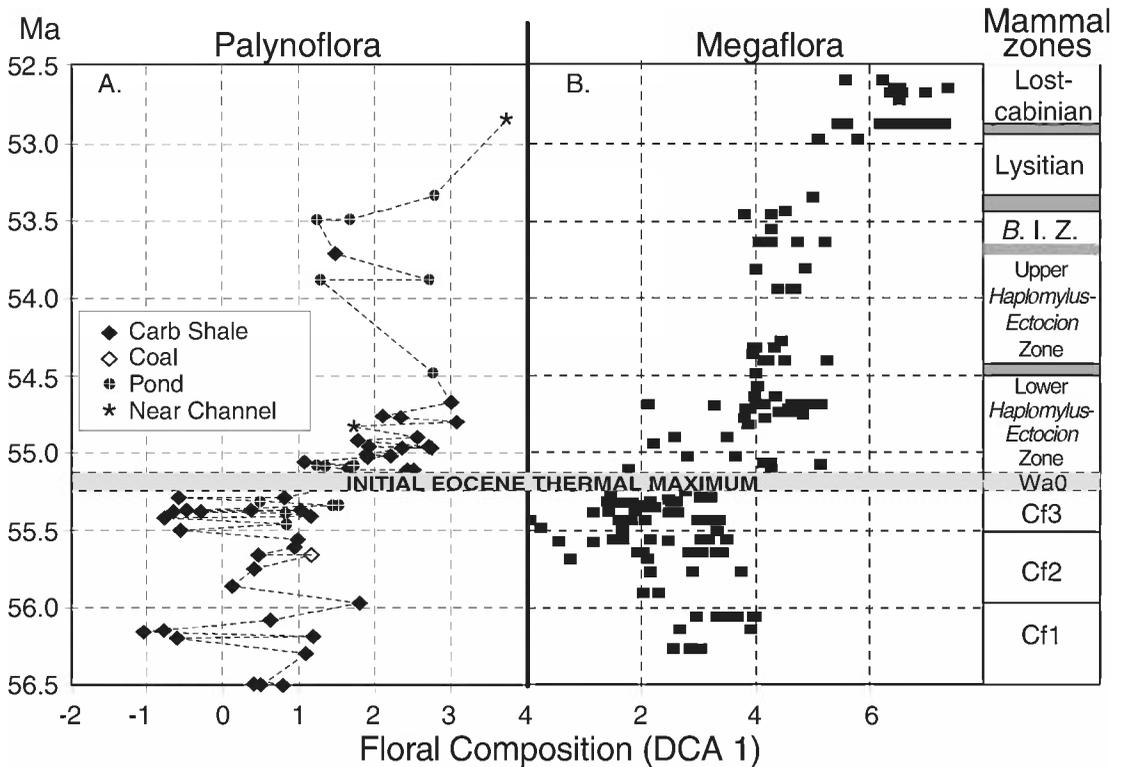


FIGURE 9. Changes in palynofloral and megafloral composition through the late Paleocene and early Eocene as measured by DCA. For both graphs the x-axis is the first axis of a DCA of the sites by species matrix (see methods section for details). A, Palynofloral analysis based on relative proportion data (Appendix 2). Rare species were down-weighted for the analysis. B, Megafloral analysis based on presence/absence data (from Wing et al. 2000). Age model as in Figure 6. Mammalian zone abbreviations: BIZ = *Bunophorus* Interval Zone, Wa0 = Wasatchian 0, Cf1–Cf3 = Clarkforkian 1–3.

lenites spp., *Caryapollenites imparalis* + *verripites*, *Cupressacites* + *Sequoiapollenites*, *Momipites anellus* + *ventifluminis*, *M. coryloides* + *waltmanensis* + *wyomingensis*, all *Platycarya* spp., and all *Triporopollenites* spp.). The first axis of the DCA explains 15% of the variation in the data set, the second axis 9%. Plotting the first axis value of each sample against time (Fig. 9A) shows that although the composition of the flora can vary sharply between closely spaced stratigraphic levels, there is a shift in average composition across the IETM, and that the composition of the youngest Eocene sample is different from that of all older Eocene samples. A very similar pattern of temporal change in floral composition is also seen in megafloras (Fig. 9B) (Wing et al. 2000). In both the palynoflora and the megaflora, high abundance and ubiquity of *Platycarya* are a significant reason for the distinctness of the youngest samples (Wing 1984b), although

many other first appearances are documented in the megaflora from the upper part of the section (Wing 1998). A very similar pattern of results was obtained with other ordination methods (e.g., nonmetric multidimensional scaling).

Like richness and evenness, palynofloral composition was rather variable within the latest Paleocene. Samples with negative axis I scores in the DCA are those with high abundance of *Polyatriopollenites vermontensis*, and these samples also have low richness and evenness. *P. vermontensis* appears to have undergone rapid fluctuations in abundance during the last 200 Kyr of the Paleocene, and also during a period approximately 1 Myr before the boundary.

Discussion

Regional Climatic Change.—Temperature fluctuations in the Bighorn Basin have been

documented by changes in leaf physiognomy and oxygen isotopic measurements of soil minerals and biogenic phosphate (Wing et al. 1991, 2000; Fricke et al. 1998; Bao et al. 1999). Leaf margin analysis shows that over the last ~2 million years of the Paleocene mean annual temperature (MAT) increased from $12.9(\pm 2.4)^{\circ}\text{C}$ to over $15(\pm 2.4)^{\circ}\text{C}$. MAT was $18.2(\pm 2.3)^{\circ}\text{C}$ immediately following the IETM, but dropped to $10.8(\pm 3.3)^{\circ}\text{C}$ within about 750 Kyr. The strong temperature decline was followed by a rapid increase to $15.8(\pm 2.2)^{\circ}\text{C}$ then $22.2(\pm 2.0)^{\circ}\text{C}$ between about 53.5 and 52.8 Ma, which corresponds to the Eocene thermal maximum seen in marine oxygen isotope records (Fig. 10) (Wing et al. 2000). The fluctuations in the temperature curve are corroborated by oxygen isotopic data from paleosol nodules (Bao et al. 1999). The absence of megafloras during the IETM precludes temperature estimates based on leaf margin analysis, but oxygen isotopic analysis of biogenic phosphate in mammalian tooth enamel indicates that temperatures during the IETM were about 4°C higher than in the latest Paleocene (Fricke et al. 1998). Warming from the late Paleocene to early Eocene has also been documented by paleobotanical work in other parts of North America (Hickey 1977; Wolfe 1978; Wilf 2000).

Increasing oxidation and variegation of paleosols, and decreasing carbon content, which are the major lithological changes from the Fort Union Formation to the Willwood Formation, suggest greater fluctuation in the level of the water table through the Paleocene/Eocene transition, presumably indicating greater seasonality of precipitation (Bown and Kraus 1981). Within the Willwood Formation in the central Bighorn Basin, carbonaceous sediments and hydromorphic paleosols are more common in the bottom and top of the formation, implying that the best-drained floodplains, and perhaps the driest climate, characterize the middle of the early Eocene sequence (Davies-Vollum and Wing 1998). Leaf size data from southern Wyoming indicate decreasing mean annual precipitation from the late Paleocene to the late-early Eocene (Wilf 2000).

Potential Biases in the Palynofloral Record.—Be-

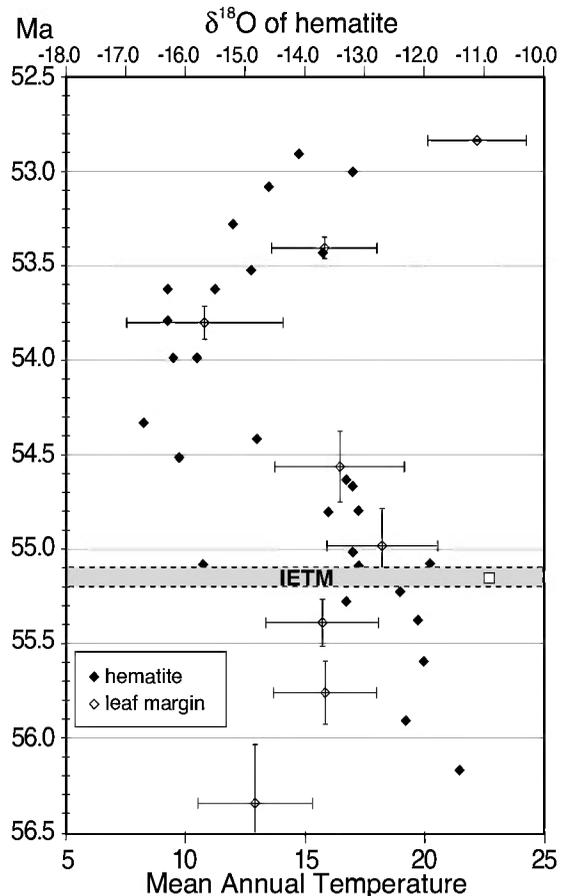


FIGURE 10. Temperature change from late Paleocene to mid-early Eocene based on data from the Bighorn Basin, Wyoming. Oxygen isotope measurements of pedogenic hematite nodules are from Bao et al. 1999; leaf margin estimates of mean annual temperature are from Wing 1998. The 4°C temperature increase during the IETM (white square) is based on oxygen isotope measurements of biogenic phosphate made by Fricke et al. (1998).

fore attributing floral change to large-scale processes such as immigration or climatic change, we should consider the possibility that nonuniform sampling of depositional environments, or variable preservation or production of pollen, might also have important effects on palynofloral composition or diversity. To a large degree, the sample set is isotaphonomic, with 43 of the 60 samples (72%) coming from laterally extensive carbonaceous units. There is, however, a larger proportion of abandoned-channel fill samples in the Eocene than in the Paleocene (31% vs. 16%). Because abandoned-channel fills tend to have higher

richness than floodplain samples, this might cause the Eocene palynoflora to appear more diverse than the Paleocene even in the absence of secular change. This effect is small; only 6 of 89 Eocene taxa are restricted to abandoned-channel fill samples, so that the Eocene has more species than the Paleocene even if Eocene abandoned-channel samples are removed from the analysis. Furthermore, detrended correspondence analyses of palynofloral composition (Fig. 3) suggest that abandoned-channel fills are insufficiently distinct in composition to create the impression of changing floral composition from the Paleocene to the Eocene.

Although variations in environment of deposition do not appear to be a major factor influencing stratigraphic change in the palynoflora, palynofloral change still cannot be assumed to correspond directly to change in floral composition. Pollen production varies greatly among plant species, with wind-pollinated forms being more common than insect-pollinated forms in sediments because the former produce more pollen that is more easily carried by the wind to depositional settings (Traverse 1988). If the proportion of insect-pollinated species in the Bighorn Basin increased from the Paleocene to the Eocene, which would be consistent with the higher proportion of insect-pollinated species in warmer climates today (Livingstone 1971; Bawa et al. 1985; Ritchie 1995), the actual increase in diversity might be underrepresented in the palynoflora.

We evaluated representation of insect-pollinated taxa by comparing the size of Paleocene and Eocene palynomorphs. In general, wind-dispersed pollen is 20–30 μm in diameter, large enough to escape the boundary layer of air around floral parts, but small enough to be effectively borne on the wind (Whitehead 1969, 1983; Crane 1986). Insect-dispersed pollen can be larger or smaller than this (Whitehead 1983). We compared the distribution of Paleocene and Eocene palynomorph sizes and found no significant difference in the size distributions ($p \leq 0.11$ by t -test), although there are two more taxa in the smallest size category in the Eocene (Fig. 11). Although we found no evidence that the pro-

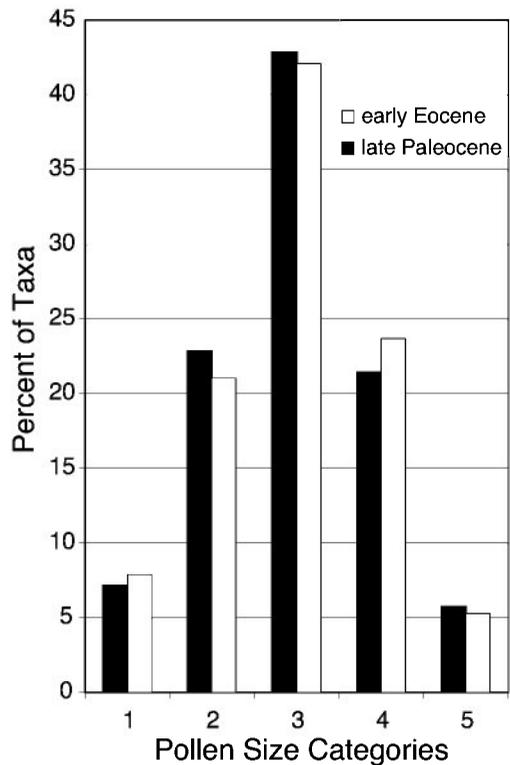


FIGURE 11. Pollen size distribution for Paleocene and Eocene floras. Size categories: 1 = <19 μm , 2 = 20–24 μm , 3 = 25–29 μm , 4 = 30–39 μm , 5 = >40 μm . The size distributions are not significantly different by t -test ($p \leq 0.11$).

portion of insect-pollinated taxa was different in the two epochs, it is possible that the changes in the original flora are underestimated or disguised by a consistent underrepresentation of insect-pollinated forms or because of the low taxonomic resolution of the palynoflora.

Comparison of Palynofloral and Megafloreal Change.—Pollen and leaves reflect the same original flora through different taphonomic filters. Pollen disperses more readily and therefore individual samples represent a larger area than do leaf samples, although remains transported from far away are rare in either type of assemblage (Farley 1989, 1990; Behrensmeier and Hook et al. 1992). Comparing the patterns of change through time in the palynoflora with those in the megafloreal may help reveal which changes reflect taphonomic effects and which result from real floral change.

The largest changes in megafloreal compo-

sition occurred near the IETM and during the temperature increase leading to the Eocene thermal maximum (Fig. 9) (Wing 1998; Wing et al. 2000). The first of these shifts is also seen in the palynoflora, although the numerical and taxonomic abundance of immigrant taxa in early Eocene palynofloras is lower than in early Eocene megafloras (Fig. 8). The smaller number of immigrant taxa and lower abundance of immigrant individuals in the palynoflora might result from underrepresentation of insect-pollinated forms and/or from the lower taxonomic resolution of palynomorphs. It appears that the increased stratigraphic resolution provided by palynomorphs is bought at the price of decreased ability to detect the magnitude of floral change.

Palynofloral changes in the later early Eocene are difficult to detect in this data set because only the highest sample clearly represents the Eocene thermal maximum. This sample does have a distinctive composition, however, suggesting that more-thorough sampling of the palynoflora would document a shift in composition corresponding to the one detected in the megaflora. Differences between early and later early Eocene palynofloras in the Bighorn Basin have been noted previously (Bown 1982; Wing 1984b; Farley 1989).

Although the general timing of compositional change is congruent in the palynoflora and megaflora, patterns of change in richness are not. Megafloral richness increased substantially during the latest Paleocene, declined during the early Eocene cool period, and then increased dramatically again with the early Eocene thermal maximum (Wing 1998). The decline is more apparent in stratigraphic range data than in the mean number of species per locality, and does not appear to result from changes in sampling intensity (Wing et al. 1995; Wing 1998). The increase in megafloral richness in the mid-early Eocene is more evident at larger spatial scales (transects composed of many sites) than in the mean number of species found in individual samples (Wing et al. 1995). In contrast, palynofloral data indicate an increase in mean sample richness and total richness from the late Paleocene to the early Eocene, but demonstrate neither a

decline in richness during the early Eocene cool period nor an increase during the Eocene thermal maximum. The small diversity changes in the palynoflora may relate to low taxonomic resolution and/or poor sampling in the upper part of the section.

Combining information from the palynofloral and megafloral records indicates that there is a small amount of floral immigration associated with the IETM, and that there are also changes in the relative proportions of Paleocene taxa across the boundary. Changes in richness are equivocal, with the megaflora showing a decrease from the latest Paleocene to the early Eocene, and the palynoflora an increase. The megaflora clearly indicates a major immigration event and increase in richness in the mid-early Eocene at about the time of the Eocene thermal maximum (Wing 1998; Wing et al. 2000). The palynoflora indicates the compositional change less strongly and does not show the increase in richness; this is almost certainly the result of poor sampling in the upper part of the section.

Implications of the IETM for Change in Plant Distributions.—We see neither palynological nor megafossil evidence for major extinction or immigration in Bighorn Basin floras between the late Paleocene and the early Eocene. Furthermore, the modest change across this time is consistent with palynofloral and megafloral studies elsewhere: North Dakota (Hickey 1977; Bebout 1977), eastern Wyoming (Pocknall 1987), the Gulf Coastal Plain (Harrington 1999), and the North Sea (Beerling and Jolley 1998). In spite of the lack of evidence for dramatic floral change across the Paleocene/Eocene boundary, the absence of pollen or leaf fossils from the IETM itself leaves open the possibility that floras during this time were different in composition and/or diversity from preceding Paleocene or succeeding Eocene floras. This hypothetical, distinctive "IETM flora" would have to be confined to the unpalyniferous interval of approximately 40 m that corresponds to the IETM in the Bighorn Basin; pollen samples just 13 m below the IETM red beds are typically Paleocene, and those from 1–2 m above the IETM red beds are typically Eocene. On average, 1 m of rock in these sections represents no more

than about 3 Kyr, yielding an estimate of about 120 Kyr for the IETM (Wing et al. 2000), which is consistent with some estimates from marine cores based on cyclostratigraphy (Norris and Röhl 1999), but shorter than more recent estimates of 220 Kyr (Röhl et al. 2000). Until we have data from the IETM, two possibilities must be considered: either there was a large change in floral composition during IETM and the flora had returned to a more Paleocene-like composition by the time of our first Eocene samples, or the flora simply did not change much. We consider the implications of these possibilities below.

The existence of a distinctive IETM flora should be expected if rates of plant population movement observed in the Holocene can be generalized to the early Paleogene. During the last deglaciation many tree species shifted ranges at rates averaging hundreds of meters to kilometers per year (e.g., Davis 1981; Delcourt and Delcourt 1987; Webb 1988). Even if the warmest part of the IETM lasted only 20 Kyr (Norris and Röhl 1999; Röhl et al. 2000), plant populations migrating at Holocene rates should have been able to move from low to high latitudes within North America and across Arctic land bridges between the northern continents, as has been proposed for the mammalian fauna. Following the Holocene analogy, we would also predict that during the later IETM, as temperatures cooled, plant ranges would have shifted southward once again. If the IETM is found to possess a distinctive flora, this would be important evidence for the generality of the rates of plant population movement observed in the Holocene.

The absence of a distinctive IETM flora would be harder to explain in terms of the standard Holocene model because a small amount of floral change during the large temperature fluctuation in the earliest Eocene would imply some sort of barrier to range changes in plants, or at least rates of population movement far slower than those shown by Holocene populations. Although direct evidence is lacking, several mechanisms might have slowed or prevented plant range changes during the IETM.

The similarity of North American, Europe-

an, and Asian faunas in the early Eocene has led to the idea that interchange across high-latitude land bridges played a major role in the faunal turnover at the Paleocene/Eocene boundary (e.g., Beard 1997). North Atlantic and Beringian routes have also been proposed as important corridors for exchange of plants (e.g., Tiffney 1985a,b; Manchester 1999). Because the high latitudes today are extremely cold in the winter, minimum temperatures are a major factor determining northern distributional limits (e.g., Thompson et al. 1999). One might think that during the IETM, when winters are thought to have been extremely warm at high latitudes (Peters and Sloan 2000), thermophilic plants could have rapidly extended their ranges to the northern limits of the continents. This disregards the effects of polar light regimes. Regardless of winter temperatures during the IETM, light regimes at high latitudes would have been as they are today, and plants would have experienced long periods of darkness or low light. Broad-leaved, evergreen taxa, with poorly developed physiological mechanisms for leaf abscission or dormancy, may have been less successful than deciduous plants under warm, dark conditions (Read and Francis 1992), precluding dispersal to North America across the Beringian and Greenland land bridges, both of which were above the Eocene Arctic Circle (McIver and Basinger 1999). Polar light regimes could have been a barrier to intercontinental expansion of plant ranges during the short IETM, because there would have been insufficient time for evolutionary changes in dormancy mechanisms.

It is also possible that, in general, plant ranges changed much less rapidly during the early Paleogene than in the Holocene. During the Holocene many plant populations were expanding into areas undergoing primary succession in the wake of retreating glaciers. Models and data both suggest that rare, long-distance dispersal and successful establishment of outlier populations are necessary to account for the high rate of population range change in the Holocene (Clark et al. 1998; Neubert and Caswell 2000), and that successful invasion is associated with disturbance (Richardson and Bond 1991; Rejmanek and Rich-

ardson 1996). The probability of these rare events may have been elevated during the Holocene because there were large areas synchronously undergoing primary succession. This would not have been true during the IETM. Even in the Arctic, woody vegetation existed throughout the Paleocene (e.g., Hickey et al. 1983; McIver and Basinger 1999), so that, unlike the Holocene situation, any long-distance dispersal events would have had to establish new populations in the face of existing forest.

Biotic interchange following the connection of North and South America in the Pliocene may provide a better analogue for IETM interchange than does the Holocene response to deglaciation. Since the Panamanian Isthmus rose about 3 Ma there has been extensive, though asymmetrical, interchange between North American and South American faunas. Approximately 50% of the extant South American mammalian fauna is derived from North American lineages, and about 10% of North American mammals are derived from South American lineages (Webb 1991). In contrast, there has been more limited interchange in the flora (Hooghiemstra 1989; Burnham and Graham 1999). Burnham and Graham (1999) estimated that approximately 10% of living South American plants are derived from northern lineages, and noted that the ecological importance of North American lineages is much greater in alpine areas that were strongly influenced by Pleistocene glacial climatic variation.

Source and Ecological Characteristics of Eocene Immigrants.—The two explanations outlined above for a small floral response to the IETM make different predictions about the characteristics of the plants that did appear in the early Eocene of North America. If a high-latitude barrier was the major factor, then plants new in the Eocene of the Bighorn Basin should either be derived from within North America, or should have been capable of winter dormancy (e.g., herbs or deciduous woody plants). If rates of range change during the IETM were low because of the difficulty of establishing new populations in existing forest, the successful immigrants should be species with a high frequency of long-distance dis-

persal and/or those capable of establishing populations in small, disturbed areas such as fire scars and tree falls that must always have occurred.

The megafossil taxa with first appearances near the base of our Eocene sections in the Bighorn Basin are the ferns *Lygodium kaulfussii*, *Salvinia preauriculata*, and *Cnemidaria magna* and the dicotyledonous angiosperm *Alnus* (Wing 1998). The geographic source of these taxa is hard to determine. The genera *Lygodium* and *Salvinia* are known from the Late Cretaceous and Paleocene of all Holarctic continents (Brown 1962; Martin 1976; Nambudiri and Chitale 1991; Rozefeldt et al. 1992), so the Eocene index species could be either immigrants or natives. We are not aware of older megafossils of *Cnemidaria*, but the spore *Kuyliaporites waterbolckii*, which is thought to represent *Cnemidaria*, is found exclusively in Cenozoic sediments of the Southern Hemisphere, although other species in the genus are known from the Cretaceous and Paleogene of the Northern Hemisphere (Mohr and Lazarus 1994). The *Alnus* leaves and pistillate inflorescences from the early Eocene of the Bighorn Basin may be the oldest reliable megafossils of the genus, but *Alnus* pollen is found throughout the Northern Hemisphere in the Late Cretaceous–Paleocene, making it difficult to determine if *Alnus* is an immigrant and, if so, from where.

The palynofloral taxa with earliest Eocene first appearances in the Bighorn Basin are *Platycarya* and *Intratripopollenites instructus* (cf. *Tilia*). First occurrences of these palynomorphs just following the IETM have been documented over a broad area of North America (Wing 1984b, Frederiksen 1998). In the Canadian Arctic and the U.S. Western Interior, the first occurrence of *Intratripopollenites instructus* is noted at or just before a peak of *Apectodinium* dinocysts (Doerenkamp et al. 1976), which at these latitudes coincides with the IETM (Bujak and Brinkhuis 1998). On the U.S. Gulf Coast and eastern Atlantic seaboard, the first occurrence of *Platycarya* pollen is noted after the IETM (N. O. Frederiksen personal communication 1998). Both *Platycarya* and *Intratripopollenites instructus* have late Paleocene (Thanetian) occurrences in northwestern

Europe (Gruas-Cavagnetto 1978; Schumacker-Lambry 1978; Jolley 1998), suggesting they moved into North America across high-latitude land bridges. In sum, megafossil taxa that appear just after the IETM in the Bighorn Basin are from lineages with Holarctic distributions in the Late Cretaceous and Paleocene, but the two clear immigrants in the palynoflora appear to have come from outside of North America, possibly from Europe.

In terms of ecological attributes of living relatives, the Eocene immigrants do appear to show a pattern—they tend to be early successional and easily dispersed. *Lygodium* (Family Schizaeaceae) has 35 living species distributed largely in tropical and warm temperate climates, although the native eastern North American species occurs as far north as New England (Nauman 1993). All species are scrambling, viny ferns that tend to grow in relatively open areas, and two Asian species (*L. microphyllum* and *L. japonicum*) have become naturalized following human introduction to eastern North America (Pemberton and Ferriter 1998). *L. microphyllum* is a highly invasive weed even in its native habitat and has spread over a large area of central Florida in just a few decades (Pemberton and Ferriter 1998). The long-distance dispersal capability of *L. microphyllum* is demonstrated by its occurrence on remote oceanic islands such as Mauritius and Tahiti.

There are 13 living species of *Salvinia* (Salviniaceae), all of which are small, floating aquatic ferns of subtropical and tropical areas. Sexually reproducing *Salvinia* disperse via water-borne megaspores and massulae, but even the asexual triploid *S. molesta* disperses effectively by breaking up into small sections (Room 1983). Viable pieces of *S. molesta* float to new locations or are transported by waterfowl that feed in and on *Salvinia* (Henderson and Harper 1992). *S. molesta*, originally from Brazil, has become a major aquatic weed in tropical areas of Africa, Asia, and Australia, as a result of its extremely rapid growth and high dispersal capabilities. Experimental work on *S. molesta* shows that temperatures less than -3°C and greater than 43°C for more than a few hours are fatal, and it does not occur on bodies of water that freeze over in the

winter (Whiteman and Room 1991). Growth of *S. molesta* is severely slowed by salinity higher than 5%, and it is killed by salinity above 7% (Divakaran et al. 1980).

Extant *Cnemidaria* are small tree ferns (Cyatheaceae) of the montane Neotropics (Stolze 1976). Although the successional and light environments of several other genera of Cyatheaceae are reasonably well known, we are only aware of one report on a species of *Cnemidaria*, *C. quitensis* (Arens and Barracaldo 1998). These authors found individuals of *C. quitensis* in areas of primary forest, secondary forest, and abandoned pasture, but they were not abundant in any environment. *C. quitensis* usually occurs as isolated individuals and appears to grow slowly (N. Arens personal communication 2000). Like any spore-bearing plant, *Cnemidaria* presumably has the capacity for long-distance dispersal by wind.

Early Eocene megafossils of *Platyacarya* (*P. castaneopsis* and *P. americana*) are thought to have been early successional plants based on their small, wind-dispersed seeds, pinnately compound leaves, and the growth habit and habitats of their living congener (Wing and Hickey 1984). Living (and presumably fossil) *Platyacarya* are also deciduous. *Intratropopollenites instructus* may be derived from *Tilia*, a genus with extant species that are mostly temperate, deciduous trees with large, although wind-dispersed, seeds.

In sum, the earliest Eocene immigrants detected in the Bighorn Basin include two probably deciduous dicotyledons from other continents, and three highly dispersible and perhaps “weedy” ferns of unknown geographic source. These geographical and ecological data are consistent both with barriers to range expansion caused by polar night and with slow rates of range expansion caused by the difficulty of establishing populations in pre-existing forest vegetation.

Comparison of Floral and Faunal Change.—Regardless of whether there was or wasn't a distinctive flora during the IETM, there is a clear difference between the patterns of floral and faunal change during the late Paleocene and early Eocene. Mammalian faunal composition changed strongly and irrevocably at the IETM; floral composition did not. Associated with

the taxonomic change in the fauna were major shifts in body size distribution, guild structure, richness, and evenness (Clyde and Gingerich 1998). The flora does not show major changes in richness or evenness. Later in the early Eocene (~52–53 Ma), megaflores do show a major burst of first occurrences and a strong increase in richness and evenness at roughly the same time as the Eocene thermal maximum (Wing et al. 1995; Wing 1998), but at this time mammalian faunas do not show large changes in diversity or composition, though there are some shifts in body size (Bown et al. 1994).

If the composition, diversity, and guild structure of the fauna were controlled directly by climate or vegetation, we would expect early Eocene faunas to resemble late Paleocene ones because the climate and flora of the two periods are similar. We would also expect the climatic warming and vegetational changes of the mid-early Eocene to have caused changes in the taxonomic and ecological structure of the fauna on a scale similar to that seen at the base of the Eocene. Although faunal change at the base of the Eocene is clearly synchronous with, and presumably related to, the IETM, climate may have played an indirect rather than a direct role. Warming climate during the IETM made migration of mammals across high-latitude land masses possible, but it was likely the biotic interactions among the immigrant and native species, rather than the direct effects of changing climate and vegetation, that resulted in the major changes in faunal structure (Clyde and Gingerich 1998). The relatively modest faunal changes of the mid-early Eocene may be an example of what occurs when climate changes of similar magnitude (though slower rates) take place in the absence of major immigration.

Conclusions

The Initial Eocene Thermal Maximum (IETM) is one of the largest and most rapid warming events known during the Cenozoic. Palynofloral changes from the late Paleocene to the early Eocene in the Bighorn Basin of northern Wyoming include (1) an increase of about 17% in mean sample richness and an overall increase in richness of 22%; (2) ap-

pearance of two relatively rare new taxa, possibly arriving from Europe; and (3) shifts in relative proportions of forms that were present throughout. The megaflores show a small number of migrants (probably early successional plants) following the IETM, some changes in the relative proportions of species already in the region, declining rather than increasing richness during the earliest Eocene, and a strong increase in immigrant taxa and diversity about 2 Myr following the IETM at the time of the Eocene thermal maximum. In sum, the paleobotanical record for this region documents only moderate floral change from the latest Paleocene to the earliest Eocene, although the absence of plant fossils from the IETM itself leaves open the possibility of a transient change in the flora lasting for less than ~220 Kyr.

The observed pattern of floral change allows two alternative hypotheses. If there was an unobserved, large, transient floral response to the IETM, this would be consistent with Holocene data showing that plant ranges usually change fast enough to keep pace with climate change. If data from the IETM fail to show such a transient response, this would imply that some factor(s) in the nonglacial world of the early Paleogene limited the rate at which plants changed their ranges. We suggest two possible factors: polar light regimes might have been a barrier to intercontinental dispersal of warm-adapted lineages, and the absence of continental-scale disturbance by glaciation may have reduced opportunities for successful establishment, thus retarding the spread of plant populations. This latter idea is particularly interesting because, if borne out, it implies that the Holocene cannot be used as a general model for understanding the response of plants to climate change.

Regardless of whether there was a transient, as yet undetected, floral response to the IETM, the pattern of floral change during the late Paleocene and early Eocene is clearly different from that of faunal change through the same period. Faunal changes at the IETM were large both taxonomically and ecologically, and they were irreversible. Furthermore, significant floral immigration and increasing diversity during the mid-early Eocene thermal maximum 2

Myr following the IETM were not accompanied by large changes in faunal composition. The disparate timing and magnitude of change in the flora and fauna suggests that these two major components of the terrestrial ecosystem were not responding in a simple way to the same forcing factor. This strengthens the argument that faunal change was not a direct consequence of climate or changing plant resources, but rather was caused by ecological interactions between the immigrant and native species. Comparing patterns of temporal change in animals and plants from the same area may be a generally useful technique for assessing the importance of climatic forcing in generating biotic change.

Acknowledgments

We thank *Matters of the Record* editor A. Miller for shepherding this manuscript through review and revision. We thank P. Gingerich, C. Jaramillo, R. Lupia, and C. Williams for discussions, reviewing earlier drafts, and suggesting major improvements. A. Ash helped with fieldwork and drafting figures. S. L. W. acknowledges support from the Scholarly Studies and Evolution of Terrestrial Ecosystems programs of the Smithsonian Institution and from the Roland Brown Fund. G. J. H. acknowledges support from National Environment Research Council award GT5/95/281/E and thanks S. Ellin for guidance on sample-processing techniques. This is ETE Contribution 86.

Literature Cited

- Alroy, J. 1998. Equilibrial diversity dynamics in North American mammals. Pp. 232–287 in M. L. McKinney and J. Drake, eds. Biodiversity dynamics: turnover of populations, taxa and communities. Columbia University Press, New York.
- Alroy, J., P. L. Koch, and J. C. Zachos. 2000. Global climate change and North American mammalian evolution. In D. H. Erwin and S. L. Wing, eds. Deep time: *Paleobiology's* perspective. *Paleobiology* 26(Suppl. to No. 4):259–288.
- Arens, N. C., and P. S. Barracaldo. 1998. Distribution of tree ferns (Cyathaceae) across the successional mosaic in an Andean cloud forest, Nariño, Colombia. *American Fern Journal* 88:60–71.
- Bains, S., R. M. Corfield, and R. D. Norris. 1999. Mechanisms of climate warming at the end of the Paleocene. *Science* 285:724–727.
- Bao, H., P. L. Koch, and D. Rumble. 1999. Paleocene-Eocene climatic variation in western North America: evidence from the $\delta^{18}\text{O}$ of pedogenic hematite. *Geological Society of America Bulletin* 111:1405–1415.
- Bawa, K. S., S. H. Bullock, D. R. Perry, R. E. Coville, and M. H. Grayum. 1985. Reproductive biology of tropical lowland rain forest trees. II. Pollination systems. *American Journal of Botany* 72:346–356.
- Beard, K. C., 1997. East of Eden: Asia as an important center of taxonomic origination in mammalian evolution. In K. C. Beard and M. R. Dawson, eds. Dawn of the age of mammals in Asia. *Bulletin of the Carnegie Museum of Natural History* 34:5–39.
- Bebout, J. 1977. Palynology of the Paleocene-Eocene Golden Valley Formation of western North Dakota. Ph.D. dissertation. Pennsylvania State University, State College.
- Beerling, D. J., and D. W. Jolley. 1998. Fossil plants record an atmospheric ^{13}C and temperature spike across the Palaeocene-Eocene transition in NW Europe. *Journal of the Geological Society, London* 155:591–594.
- Behrensmeyer, A. K., R. W. Hook, C. E. Badgley, J. A. Boy, R. E. Chapman, P. Dodson, R. A. Gastaldo, R. W. Graham, L. D. Martin, P. E. Olsen, R. A. Spicer, R. E. Taggart, and M. V. H. Wilson. 1992. Paleoenvironmental contexts and taphonomic modes. Pp. 139–180 in A. K. Behrensmeyer, J. D. Damuth, W. A. DiMichele, R. Potts, H. D. Sues, and S. L. Wing, eds. Terrestrial ecosystems through time: evolutionary paleoecology of terrestrial plants and animals. University of Chicago Press, Chicago.
- Behrensmeyer, A. K., N. E. Todd, R. Potts, and G. E. McBrinn. 1997. Late Pliocene faunal turnover in the Turkana Basin, Kenya and Ethiopia. *Science* 278:1589–1594.
- Berggren, W., M. P. Aubry, and S. Lucas, eds. 1998. Late Paleocene–early Eocene biotic and climatic events. Columbia University Press, New York.
- Bown, T. M. 1982. Geology, paleontology, and correlation of Eocene volcanoclastic rocks, southeast Absaroka Range, Hot Springs County, Wyoming. U.S. Geological Survey Professional Paper 1201-A:1–75.1
- Bown, T. M., and M. J. Kraus. 1981. Lower Eocene alluvial paleosols (Willwood Formation, northwestern Wyoming, USA) and their significance for paleoecology, paleoclimatology, and basin analysis. *Palaeogeography, Palaeoclimatology, Palaeoecology* 34:1–30.
- Bown, T. M., P. A. Holroyd, and K. D. Rose. 1994. Mammal extinctions, body size, and paleotemperature. *Proceedings of the National Academy of Sciences USA* 91:10403–10406.
- Brown, R. W. 1962. Paleocene flora of the Rocky Mountains and Great Plains. U.S. Geological Survey Professional Paper 375: 1–119.
- Bujak, J. P., and H. Brinkhuis. 1998. Global warming and dinosaur changes across the Paleocene/Eocene epoch boundary. Pp. 277–295 in Berggren et al. 1998.
- Burnham, R. J., and A. Graham. 1999. The history of Neotropical vegetation: new developments and status. Pp. 546–589 in Crane and Herendeen 1999.
- Clark, J. S., C. Fastie, G. Hurr, S. T. Jackson, C. Johnson, G. A. King, M. Lewis, J. Lynch, S. Pacala, C. Prentice, E. W. Schupp, T. Webb III, and P. Wyckoff. 1998. Reid's paradox of rapid plant migration. *Bioscience* 48:13–24.
- Clyde, W. C., and P. D. Gingerich. 1998. Mammalian community response to the latest Paleocene thermal maximum: an isotaphonomic study in the northern Bighorn Basin, Wyoming. *Geology* 26:1011–1014.
- Colwell, R. K. 1999. EstimateS, Version 5.01—statistical estimation of species richness and shared species from samples. <http://viceroy.eeb.uconn.edu/estimateS>.
- Colwell, R. K., and J. A. Coddington. 1994. Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London B* 345:101–118.
- Crane, P. R. 1986. Form and function in wind dispersed pollen. Pp. 179–202 in S. Blackmore and I. R. Ferguson, eds. Pollen and spores: form and function. Academic Press, London.

- Crane, P. R., and P. S. Herendeen, eds. 1999. The origin of modern terrestrial ecosystems. *Annals of the Missouri Botanical Garden* 86.
- Davies-Vollum, S. K., and S. L. Wing. 1998. Sedimentological, taphonomic, and climatic aspects of Eocene swamp deposits (Willwood Formation, Bighorn Basin, Wyoming). *Palaios* 13: 28–40.
- Davis, M. B. 1981. Quaternary history and the stability of forest communities. Pp. 132–153 in D. C. West, H. H. Shugart, and D. B. Botkin, eds. *Forest succession: concepts and application*. Springer, New York.
- Delcourt, P. A., and H. R. Delcourt. 1987. *Long-term forest dynamics of the temperate zone*. Springer, New York.
- Dickens, G. R., M. M. Castillo, and J. C. G. Walker. 1997. A blast of gas in the latest Paleocene: simulating first-order effects of massive dissociation of oceanic methane hydrate. *Geology* 25: 259–262.
- Divakaran, O., M. Arunachalam, and N. N. Balakrishnan. 1980. Growth rates of *Salvinia molesta* Mitchell with special reference to salinity. *Proceedings of the Indian Academy of Sciences* 89:161–168.
- Doernekamp, A., S. Jardíné, and P. Moreau. 1976. Cretaceous and Tertiary palynomorph assemblages from Banks Island and adjacent areas (N.W.T.). *Bulletin of Canadian Petroleum Geology* 24:372–418.
- Farley, M. B. 1989. Palynological facies fossils in nonmarine environments in the Paleogene of the Bighorn Basin. *Palaios* 4: 565–573.
- . 1990. Vegetation distribution across the Early Eocene depositional landscape from palynological analysis. *Palaeogeography, Palaeoclimatology, Palaeoecology* 79:11–27.
- Frederiksen, N. O. 1998. Upper Paleocene and lowermost Eocene angiosperm pollen biostratigraphy of the eastern Gulf Coast and Virginia. *Micropaleontology* 44:45–68.
- Fricke, H. C., W. C. Clyde, J. R. O'Neil, and P. D. Gingerich. 1998. Evidence for rapid climate change in North America during the late Paleocene thermal maximum: oxygen isotope composition of biogenic phosphate from the Bighorn Basin (Wyoming). *Earth and Planetary Science Letters* 160:193–208.
- Gingerich, P. D. 1989. New earliest Wasatchian mammalian fauna from the Eocene of northwestern Wyoming: composition and diversity in a rarely sampled high-floodplain assemblage. *University of Michigan Papers on Paleontology* 28:1–97.
- Gras-Cavagnetto, C. 1978. Étude palynologique de L'Éocène du bassin Anglo-Parisien. *Mémoire de la Société Géologique de France* 131:1–60.
- Gunnell, G. F. 1998. Mammalian faunal composition and the Paleocene/Eocene epoch/series boundary: evidence from the northern Bighorn Basin, Wyoming. Pp. 409–427 in Berggren et al. 1998.
- Harrington, G. J. 1999. North American palynofloral dynamics in the late Paleocene to early Eocene. Ph.D. thesis. University of Sheffield, Sheffield, England.
- Henderson, I. G., and D. M. Harper. 1992. Bird distribution and habitat structure on Lake Naivasha, Kenya. *African Journal of Ecology* 30:223–232.
- Hickey, L. J. 1977. Stratigraphy and paleobotany of the Golden Valley Formation (early Tertiary) of western North Dakota. *Geological Society of America Memoir* 150:1–181.
- . 1980. Paleocene stratigraphy and flora of the Clark's Fork Basin. In P. D. Gingerich, ed., *Early Cenozoic paleontology and stratigraphy of the Bighorn Basin, Wyoming*. University of Michigan Papers on Paleontology 24:33–49.
- Hickey, L. J., R. M. West, M. R. Dawson, and D. K. Choi. 1983. Arctic terrestrial biota: paleomagnetic evidence of age disparity with mid-northern latitudes during the Late Cretaceous and early Tertiary. *Science* 221:1153–1156.
- Hill, M. O. 1973. Reciprocal averaging: an eigenvector method of ordination. *Journal of Ecology* 61:237–249.
- . 1979. DECORANA, a FORTRAN program for detrended correspondence analysis and reciprocal averaging. Microcomputer Power, Ithaca, N.Y.
- Hooghiemstra, H. 1989. Quaternary and upper Pliocene glacialations and forest development in the tropical Andes: evidence from a long high-resolution pollen record from the sedimentary basin of Bogotá, Colombia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 72:11–26.
- Hooker, J. J. 1998. Mammalian faunal change across the Paleocene-Eocene transition in Europe. Pp. 428–450 in Berggren et al. 1998.
- Janis, C. M. 1993. Tertiary mammal evolution in the context of changing climates, vegetation, and tectonic events. *Annual Review of Ecology and Systematics* 24:467–500.
- Jolley, D. W. 1998. Palynostratigraphy and depositional history of the Palaeocene Ormesby/Thanet depositional sequence set in southeastern England and its correlation with continental West Europe. *Review of Palaeobotany and Palynology* 99:265–315.
- Katz, M. E., D. K. Pak, G. R. Dickens, and K. G. Miller. 1999. The source and fate of massive carbon input during the latest Paleocene thermal maximum. *Science* 286:1531–1533.
- Kennett, J. P., and L. D. Stott. 1991. Abrupt deep-sea warming, palaeoceanographic changes and benthic extinctions at the end of the Palaeocene. *Nature* 353:225–229.
- Koch, P. L., J. C. Zachos, and P. D. Gingerich. 1992. Correlation between isotope records in marine and continental carbon reservoirs near the Palaeocene/Eocene boundary. *Nature* 358: 319–322.
- Koch, P. L., J. C. Zachos, and D. L. Dettmann. 1995. Stable isotope stratigraphy and paleoclimatology of the Paleogene Bighorn Basin (Wyoming, U.S.A.). *Palaeogeography, Palaeoclimatology, Palaeoecology* 115:61–89.
- Kovach, W. L. 1999. MVSP—a multivariate statistical package for Windows, Version 3.1. Kovach Computing Services, Pentraeth, Wales.
- Kraus, M. J. 1998. Development of potential acid sulfate paleosols in Paleocene floodplains, Bighorn Basin, Wyoming, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology* 144:203–224.
- Livingstone, D. R. 1971. A 22,000-year pollen record from the plateau of Zambia. *Limnology and Oceanography* 16:349–356.
- Luterbacher, H., J. Hardenbol, and B. Schmitz. 2000. Comments by the bureau of ISPS on "The view of the chair of the P/E boundary working group." *International Subcommission on Paleogene Stratigraphy Newsletter* 9:18–19.
- Manchester, S. R. 1999. Biogeographical relationships of North American Tertiary floras. Pp. 472–522 in Crane and Herendeen 1999.
- Martin, A. R. H. 1976. Upper Palaeocene Salvinaceae from the Woolwich/Reading beds near Cobham, Kent. *Palaeontology* 19:173–184.
- McAleece, N., P. J. D. Lamshead, G. L. Paterson, and J. G. Gage. 1997. Biodiversity Professional Beta One Version. <http://www.nhm.ac.uk/zoology/bdpro>.
- McIver, E. E., and J. F. Basinger. 1999. Early Tertiary floral evolution in the Canadian high Arctic. Pp. 523–545 in Crane and Herendeen 1999.
- Mohr, B. A. R., and D. B. Lazarus. 1994. Paleobiogeographic distribution of *Kuylisporites* and its possible relationship to the extant fern genus *Cnemidaria* (Cyatheaaceae). *Annals of the Missouri Botanical Garden* 81:758–767.
- Nambudiri, E. M. V., and S. Chitale. 1991. Fossil *Salvinia* and *Azolla* from the Deccan Intertrappean Beds of India. *Review of Palaeobotany and Palynology* 69:325–336.

- Nauman, C. E. 1993. Lygodiaceae C. Presl—climbing ferns. Pp. 114–116 in Editorial Committee, eds. *Flora of North America north of Mexico*, Vol. 2. Oxford University Press, New York.
- Neubert, M. G., and H. Caswell. 2000. Demography and dispersal: calculation and sensitivity analysis of invasion speed for structured populations. *Ecology* 81:1613–1628.
- Norris, R. D., and U. Röhl. 1999. Carbon cycling and chronology of climate warming during the Palaeocene/Eocene transition. *Nature* 401:775–778.
- Pemberton, R. W., and A. P. Ferriter. 1998. Old World climbing fern (*Lygodium microphyllum*), a dangerous invasive weed in Florida. *American Fern Journal* 88:165–175.
- Peters, R. B., and L. C. Sloan. 2000. High concentrations of greenhouse gases and polar stratospheric clouds: a possible solution to high-latitude faunal migration at the latest Paleocene thermal maximum. *Geology* 28:979–982.
- Pocknall, D. 1987. Palynomorph biozones for the Fort Union and Wasatch Formations (upper Paleocene–lower Eocene), Powder River Basin, Wyoming and Montana, U.S.A. *Palynology* 11: 23–35.
- Prothero, D. R. 1999. Does climate change drive mammalian evolution. *GSA Today* 9:1–7.
- Read, J. and J. E. Francis. 1992. Responses of some Southern Hemisphere tree species to a prolonged dark period and their phylogeographic and palaeoecological implications for high-latitude Cretaceous and Tertiary floras. *Palaeogeography, Palaeoclimatology, Palaeoecology* 99:271–290.
- Rejmanek, M., and D. M. Richardson. 1996. What attributes make some plant species more invasive? *Ecology* 77:1655–1661.
- Richardson, D. M., and W. J. Bond. 1991. Determinants of plant distribution: evidence from pine invasions. *American Naturalist* 137:639–668.
- Ritchie, J. C. 1995. Current trends in studies of long-term plant community dynamics. *New Phytologist* 130:469–494.
- Röhl, U., T. J. Bralower, R. D. Norris, and G. Wefer. 2000. New chronology for the late Paleocene thermal maximum and its environmental implications. *Geology* 28:927–930.
- Room, P. M. 1983. Falling apart as a lifestyle—the rhizome architecture and population growth of *Salvinia molesta*. *Journal of Ecology* 17:349–365.
- Rose, K. D. 1981. The Clarkforkian Land-Mammal Age and mammalian faunal composition across the Paleocene-Eocene boundary. *University of Michigan Papers on Paleontology* 26: 1–197.
- Rozefeld, A. C., D. C. Christophel, and N. F. Alley. 1992. Tertiary occurrence of the fern *Lygodium* (Schizaeaceae) in Australia and New Zealand. *Memoirs of the Queensland Museum* 32: 203–222.
- Schankler, D. M. 1980. Faunal zonation of the Willwood Formation in the central Bighorn Basin, Wyoming. In P. D. Gingerich, ed. *Early Cenozoic paleontology and stratigraphy of the Bighorn Basin, Wyoming*. University of Michigan Papers on Paleontology 24:99–114.
- Schmitz, B. 2000. Is the CIE in the late Paleocene or early Eocene? *International Subcommission on Paleogene Stratigraphy Newsletter* 9:19.
- Schumacker-Lambry, J. 1978. Palynologie du Landenien inférieur (Paléocène) à Gelinden-Overbroek/Belgique: relations entre les microfossiles et le sédiment. *Laboratoire de Paléobotanique et de Paléopalynologie, Université de Liège, Liège*.
- Stolze, R. G. 1976. Ferns and fern allies of Guatemala, Part I. Ophioglossaceae through Cyatheaceae. *Fieldiana (Botany)* 39: 1–130.
- Thompson, R. S., K. H. Anderson, and P. J. Bartlein. 1999. Atlas of relations between climatic parameters and distributions of important trees and shrubs in North America. U.S. Geological Survey Professional Paper 1650(A and B).
- Tiffney, B. H. 1985a. Perspectives on the origin of the floristic similarity between eastern Asia and eastern North America. *Journal of the Arnold Arboretum* 66:73–94.
- . 1985b. The Eocene North Atlantic land bridge: its importance in Tertiary and modern phytogeography of the Northern Hemisphere. *Journal of the Arnold Arboretum* 66: 243–273.
- Traverse, A. 1988. *Paleopalynology*. Unwin Hyman, Boston.
- Tryon, R. M., and A. F. Tryon. 1982. *Ferns and allied plants with special reference to tropical America*. Springer, New York.
- Vrba, E. S. 1985. Environment and evolution—alternative causes of the temporal distribution of evolutionary events. *South African Journal of Science* 81:229–236.
- Webb, S. D. 1991. Ecogeography and the great American interchange. *Paleobiology* 17:266–280.
- Webb, T., III. 1988. Eastern North America. In B. Huntley and T. Webb III, eds. *Vegetation history. Handbook of Vegetation Science* 7:385–414. Kluwer Academic, Dordrecht.
- Whitehead, D. R. 1969. Wind pollination in the angiosperms: evolutionary and environmental considerations. *Evolution* 23: 28–35.
- . 1983. Wind pollination: some ecological and evolutionary perspectives. Pp. 97–108 in L. Real, ed. *Pollination biology*. Academic Press, London.
- Whiteman, J. B., and P. M. Room. 1991. Temperatures lethal to *Salvinia molesta* Mitchell. *Aquatic Botany* 40:27–36.
- Wilf, P. 2000. Late Paleocene–early Eocene climate changes in southwestern Wyoming: paleobotanical analysis. *Geological Society of America Bulletin* 112:292–307.
- Wing, S. L. 1984a. Relation of paleovegetation to geometry and cyclicity of some fluvial carbonaceous deposits. *Journal of Sedimentary Petrology* 54:52–66.
- . 1984b. A new basis for recognizing the Paleocene/Eocene boundary in western interior North America. *Science* 226:439–441.
- . 1998. Late Paleocene–early Eocene floral and climatic change in the Bighorn Basin, Wyoming. Pp. 380–400 in Berggren et al. 1998.
- Wing, S. L., and T. M. Bown. 1985. Fine-scale reconstruction of late Paleocene–early Eocene paleogeography in the Bighorn Basin of northern Wyoming. Pp. 93–105 in R. Flores and S. S. Kaplan, eds. *Cenozoic paleogeography of west-central United States*. Rocky Mountain Section, Society of Economic Paleontologists and Mineralogists.
- Wing, S. L., and L. J. Hickey. 1984. The *Platycarya* perplex and the evolution of the Juglandaceae. *American Journal of Botany* 71:388–411.
- Wing, S. L., T. M. Bown, and J. D. Obradovich. 1991. Early Eocene biotic and climatic change in interior western North America. *Geology* 19:1189–1192.
- Wing, S. L., J. Alroy, and L. J. Hickey. 1995. Plant and mammal diversity in the Paleocene to early Eocene of the Bighorn Basin. *Palaeogeography, Palaeoclimatology, Palaeoecology* 115: 117–156.
- Wing, S. L., H. Bao, and P. L. Koch. 2000. An early Eocene cool period? Evidence for continental cooling during the warmest part of the Cenozoic. Pp. 197–237 in B. T. Huber, K. MacCleod, and S. L. Wing, eds. *Warm climates in earth history*. Cambridge University Press, Cambridge.
- Wolfe, J. A. 1978. A paleobotanical interpretation of Tertiary climates in the Northern Hemisphere. *American Scientist* 66: 694–703.
- Zachos, J. C., L. D. Stott, and K. C. Lohmann. 1994. Evolution of early Cenozoic marine temperatures. *Paleoceanography* 9: 353–387.

Appendix 1

Palynomorph Taxa

SPORES:	?Araceae
MOSSES	<i>Pandaniidites typicus</i>
Sphagnaceae	Palmae/Cycadales
<i>Cingulatisporites</i> sp.	<i>Arecipites</i> sp.
<i>Stereisporites distgranisporis</i>	Incertae sedis
<i>Stereisporites stereiodes</i>	<i>Liliacidites</i> sp. (?Palmae)
LYCOPSIDS	DICOTS
Lycopodiaceae	?Anacardiaceae
<i>Camarozonosporites</i> sp.	<i>Rhoipites bradleyi</i>
<i>Punctatisporites</i> sp.	Anacardiaceae/Caprifoliaceae
FERNS	<i>Caprifoliipites</i> spp.
Cyatheaceae	?Anacardiaceae/Simaroubaceae/Sapindaceae
<i>Cyathidites diaphana</i>	<i>Aesculiidites circumstriatus</i>
Gleicheniaceae	<i>Ailanthipites berryi</i>
<i>Gleicheniidites</i> sp. (cf. <i>Gleichenia triangulus</i>)	?Aquifoliaceae
Osmundaceae	<i>Illexpollenites</i> sp.
<i>Baculatisporites primarius</i> (cf. <i>Osmunda</i>)	Betulaceae
Schizaeaceae	<i>Alnipollenites scoticus</i> (<i>Alnus</i>)
<i>Appendicisporites</i> sp.	<i>Alnipollenites verus</i> (<i>Alnus</i>)
<i>Cicatricosisporites dorogensis</i>	?Betulaceae
<i>Deltoidospora</i> spp.	<i>Jarzenipollenites trinus</i>
INCERTAE SEDIS	Betulaceae/Myricaceae
<i>Laevigatosporites haardtii</i>	<i>Paraalnipollenites confusus</i>
<i>Microfoveolatosporis pseudodentatus</i>	<i>Triatriopollenites convexus</i>
<i>Reticuloidosporites</i> sp.	<i>Triatriopollenites subtriangulus</i>
GYMNOSPERM POLLEN:	<i>Triatriopollenites triangulus</i>
Pinaceae	<i>Tripoporollenites infrequens</i>
Bisaccates group (cf. <i>Pinus</i> , <i>Picea</i>)	<i>Tripoporollenites pulcher</i>
Taxodiaceae	Bombacaceae
<i>Cupressacites hiatipites</i> (<i>Glyptostrobus</i> / <i>Metasequoia</i>)	<i>Bombacacidites nacimientensis</i>
<i>Sequoapollenites polyformosus</i> (<i>Glyptostrobus</i> / <i>Metasequoia</i>)	Buxaceae
Incertae sedis	<i>Erdtmanipollis cretaceus</i> (cf. <i>Sarcococca</i> , <i>Pachysandra</i>)
<i>Cycadopites follicularis</i> (?Cycad)	?Cercidiphyllaceae
<i>Monocolpopollenites tranquillus</i> (?Gingko)	" <i>Cercidiphyllites</i> " (? <i>Cercidiphyllum</i>) sp.
ANGIOSPERM POLLEN:	Cyrillaceae
MONOCOTS	<i>Cyrillaceapollenites megaexactus</i>
Sparganiaceae	?Ericaceae
<i>Sparganiaceapollenites</i> sp. (cf. <i>Sparganium globites</i>)	<i>Ericipites</i> sp.

Appendix 1. Continued.

Eucommiaceae	?Platanaceae
<i>Eucommia</i> sp. A (cf. <i>Eucommia</i>)	<i>Tricolpites hians</i> (? <i>Platanus</i>)
?Fagaceae	<i>Fraxinoipollenites variabilis</i> (?Platanaceae)
<i>Siltaria hanleyi</i>	Sapindaceae/Myrtaceae
<i>Siltaria pacata</i> (?Cyrillaceae)	<i>Boehlensipollis minimus</i>
?Gunneraceae	<i>Insulapollenites rugulatus</i>
<i>Tricolpites reticulatus</i> (cf. <i>Gunnera</i> ?)	Symplocaceae
Juglandaceae	<i>Symplocoipollenites thalmanii</i> (<i>Symplocos</i>)
<i>Caryapollenites imparalis/inelegans</i> (<i>Carya</i>)	<i>Porocolpopollenites</i> sp. (cf. <i>Porocolpopollenites ollivierae</i>)
<i>Caryapollenites veripites</i> (<i>Carya</i>)	Tiliaceae/Sterculiaceae
<i>Caryapollenites wodehousei</i>	<i>Intratrilporopollenites instructus</i> (<i>Tilia</i> ?)
<i>Momipites anellus</i>	<i>Intratrilporopollenites vespertines</i>
<i>Momipites coryloides</i>	Ulmaceae
<i>Momipites waltmanensis</i>	<i>Ulmipollenites krempii</i> (<i>Ulmus/Zelkova</i>)
<i>Momipites wyomingensis</i>	<i>Ulmipollenites tricostatus</i> (<i>Ulmus/Zelkova</i>)
<i>Momipites triradiatus</i>	?Vitaceae
<i>Momipites ventifluminis</i>	<i>Horniella</i> spp.
<i>Platycaryapollenites</i> sp. B	Incertae sedis
<i>Platycarya anticyclus</i> (<i>Platycarya</i>)	<i>Aquilapollenites spinulosus</i>
<i>Platycarya platycaryoides</i> (<i>Platycarya</i>)	" <i>Araliaceoipollenites</i> " sp.
<i>Plicatopollis</i> sp.	<i>Celtisipollenites</i> sp.
<i>Polyatriopollenites vermontensis</i> (<i>Cyclocarya</i> , ? <i>Pterocarya</i>)	<i>Echitricolpites supraechinatus</i>
?Leguminosae	<i>Intratrilporopollenites</i> sp. (cf. <i>Tilia tetraforaminipites</i>)
<i>Tetracolporopollenites</i> sp.	<i>Periporopollenites</i> spp. (<i>Liquidambar</i> , <i>Chenopodiaceae</i>)
Malvaceae/Euphorbiaceae/Tiliaceae	<i>Pistillipollenites mcgregorii</i>
<i>Malvacipollis</i> sp.	<i>Retitrescolpites anguloluminosus</i>
Nyassaceae	<i>Zlivosporis novamexicanum</i>
<i>Nyssapollenites kruschii</i> (<i>Nyssa</i>)	
?Oleaceae/?Salicaceae	
<i>Rousea</i> spp.	

* Taxa in quotes probably belong to the specified genus, but the match is not exact.