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Floral change during the Initial Eocene Thermal Maximum in the Powder River Basin, Wyoming

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ABSTRACT

Rapid warming at the beginning of the Eocene (the Initial Eocene Thermal Maximum, or IETM) has been associated with modest changes in floral composition, mostly shifts in the relative abundances of taxa rather than large numbers of first or last appearances. Although floral change across the Paleocene-Eocene transition has been studied in many areas, few fossils demonstrably come from the ~200 k.y.-long IETM. The rarity of fossils from the IETM permits two end-member hypotheses: (1) IETM floras were similar to, or intermediate in composition between, Paleocene and Eocene floras, or (2) they were distinct from both Paleocene and Eocene assemblages in having a high proportion of taxa that were temporary, thermophilic immigrants. The latter hypothesis is consistent with expectations developed from the study of late Quaternary floras, which demonstrate rapid northward range displacements in the wake of retreating continental glaciers. Here we report lithological, paleontological and isotopic evidence for a Paleocene-Eocene boundary section in the lower Wasatch Formation of the southwestern Powder River Basin, Wyoming. Pollen samples from within the IETM interval do not record immigrants from the south, making it unlikely that there were rapid, continental-scale range displacements during the IETM. Floral response consisted of shifts in the relative abundances of native taxa at the beginning of, or even prior to, the IETM, followed by immigration of taxa from outside of North America, probably Europe, near the end of, or possibly after, the IETM.

INTRODUCTION

The Initial Eocene Thermal Maximum (formerly LPTM or latest Paleocene Thermal Maximum) was a geologically brief interval of global warming at the beginning of the Eocene epoch (Kennett and Stott, 1991; Zachos et al., 2001). During the IETM mid- to high-latitude temperatures increased by ~4–8 °C over a period of 10–20 k.y., then returned to the warm climatic conditions characteristic of most of the Paleogene over the succeed-

ing ~200 k.y. This warming was probably caused in part by greenhouse forcing following the release of carbon from seafloor methane clathrates at the Paleocene-Eocene boundary (Dickens et al., 1997).

Previous work on floral change across the Paleocene-Eocene boundary has revealed relatively modest changes in composition and diversity. This is true at low latitudes in northern South America (Rull, 1999; Jaramillo and Dilcher, 2000), throughout North America (Pocknall, 1987; Frederiksen, 1994;

Harrington, 2001a, 2001b; Harrington and Kemp, 2001; Harrington, this volume), and in Europe (Gruas-Cavagnetto, 1978; Schumacker-Lambry, 1978; Jolley, 1998). In these studies the stratigraphic position of the IETM was not identified precisely, so transient changes in floras might have gone undetected.

Three other studies have examined palynofloras from the IETM. Beerling and Jolley (1998) worked with material from a set of cores from the North Sea and England. They found an increase in the abundance of tropical taxa (particularly pollen of the mangrove palm, *Nyssa*) coincident with the interval inferred to represent the IETM. The identification of the IETM remains uncertain, however, because the best carbon isotope evidence for the IETM does not come from the same cores as the increase in tropical taxa. Crouch (2001) and Crouch and Visscher (this volume) have examined terrestrial palynomorphs from the marine Paleocene-Eocene section at Tawanui on the north island of New Zealand. They identified only modest changes in floral composition across this time interval, and no indication of a distinctive and transient flora during the IETM, although there was an increase in the proportion of terrestrial palynomorphs. Collinson et al. (this volume) present stratigraphic and isotopic evidence for the presence of the IETM within the ~3 m thick Cobham Lignite in southeastern England. Palynofloral composition changes little within this unit.

In the Bighorn Basin of northwestern Wyoming the IETM has been identified in outcrops spanning >100 km, and both megafloras and palynofloras have been used to describe change across the IETM (Wing et al., 1995; Wing, 1998; Wing and Harrington, 2001). These studies are consistent with work done elsewhere in that they show relatively minor changes in composition and diversity across the IETM; four megafossil and two palynofloral taxa have first appearances in the earliest Eocene, and diversity increases either not at all (megafossil data) or by ~20% (palynofloral data). There are significant shifts in relative abundances of several taxa. Even in the Bighorn Basin sections however, there is a 40–50-m-thick interval representing the IETM that has yielded neither pollen nor megafossils. Although the average temporal separation of pollen samples before and after the boundary interval in the Bighorn Basin is ~30 k.y. (10 m), the sample gap at the IETM probably represents ~200 k.y. during an interval marked by extreme climatic change.

Decades of work on floral response to Quaternary climate change has led us to expect that rapid warming of 5–10 °C in the midlatitudes will result in rapid, continental-scale shifts in the ranges of many plant species (Davis, 1976; Overpeck et al., 1992; Jackson and Overpeck, 2000). Pollen records that extend back into the Pleistocene show multiple, substantial fluctuations in floral composition that correspond to Milankovitch orbital cycles (Hooghiemstra and Melice, 1994; Mommersteeg et al., 1995). Clearly the ~200 k.y. sampling gap at the IETM in the Bighorn Basin could conceal a significant transient response to global warming.

By analogy with Quaternary floral change we expect that the IETM flora in the northern Rockies should differ from both

latest Paleocene and earliest Eocene floras in having a higher abundance of thermophilic taxa that extended their ranges northward during the IETM. The stratigraphic ranges of these tropical elements might be confined entirely to the IETM if their migration into the northern Rockies was strongly controlled by temperature or other climatic features that changed rapidly but temporarily during the IETM. In both surface ocean and terrestrial vertebrate communities, transient faunas and floras are characteristic of the IETM (Gingerich, 1989; Kelly et al., 1998; Crouch et al., 2001, this volume).

In this paper we report geological, paleontological, and geochemical data indicating that the IETM is represented by sediments in the lower Wasatch Formation of the Powder River Basin, Wyoming. Palynological samples from within the IETM help characterize floral response to this geologically brief interval of global warming.

PREVIOUS WORK

The field area is near the southwestern margin of the Powder River Basin, Wyoming (Fig. 1). In this area, Upper Cretaceous, Paleocene and Eocene strata dip off the northern side of the Casper Arch and the regional strike is nearly east-west. Resistant strata of the Lance and Fort Union Formations form the east-west trending Pine Ridge, in which beds dip at 20–40 degrees north into the basin. Dips shallow rapidly to the north, and at Chalk Butte, a north-south oriented salient 2–3 km north of Pine Ridge, the lower part of the Wasatch Formation dips only 4–7 degrees.

The lower part of the Wasatch Formation in this area is drab, contains many thick carbonaceous shales and thin lignites, and rests on the Fort Union Formation with a minor angular unconformity (Robinson, 2000, personal commun.). In parts of the eastern and southern Powder River Basin the lower Wasatch Formation has produced Paleocene vertebrates such as *Champsosaurus gigas* (Robinson, 2000, personal commun.).

The transition from drab mudstones, carbonaceous shales and lignites to pedogenically altered red and variegated mudstones is exposed on the lower to middle elevations of Chalk Butte (Fig. 2). The lowest laterally extensive red-variegated mudstone bed is ~135 m above the base of the Wasatch Formation (Robinson, 2000, personal commun.). Vertebrate fossils collected from sandstone and variegated mudstone layers ~175 m above the base of the formation include mammals, such as *Cantius torresi* and *Copecion davisii* that are characteristic of the basal Eocene (Wasatchian 0, or Wa 0) faunal zone (Gingerich, 1989; Thewissen, 1990; Robinson and Williams, 1997). In the Bighorn Basin, these taxa have been found only in paleosols that are correlated with the IETM via carbon isotope stratigraphy (Koch et al., 1995; Bowen et al., 2001).

LITHOSTRATIGRAPHY

We measured three local sections in the vicinity of Chalk Butte (Fig. 3). The base of each section is a single, laterally ex-

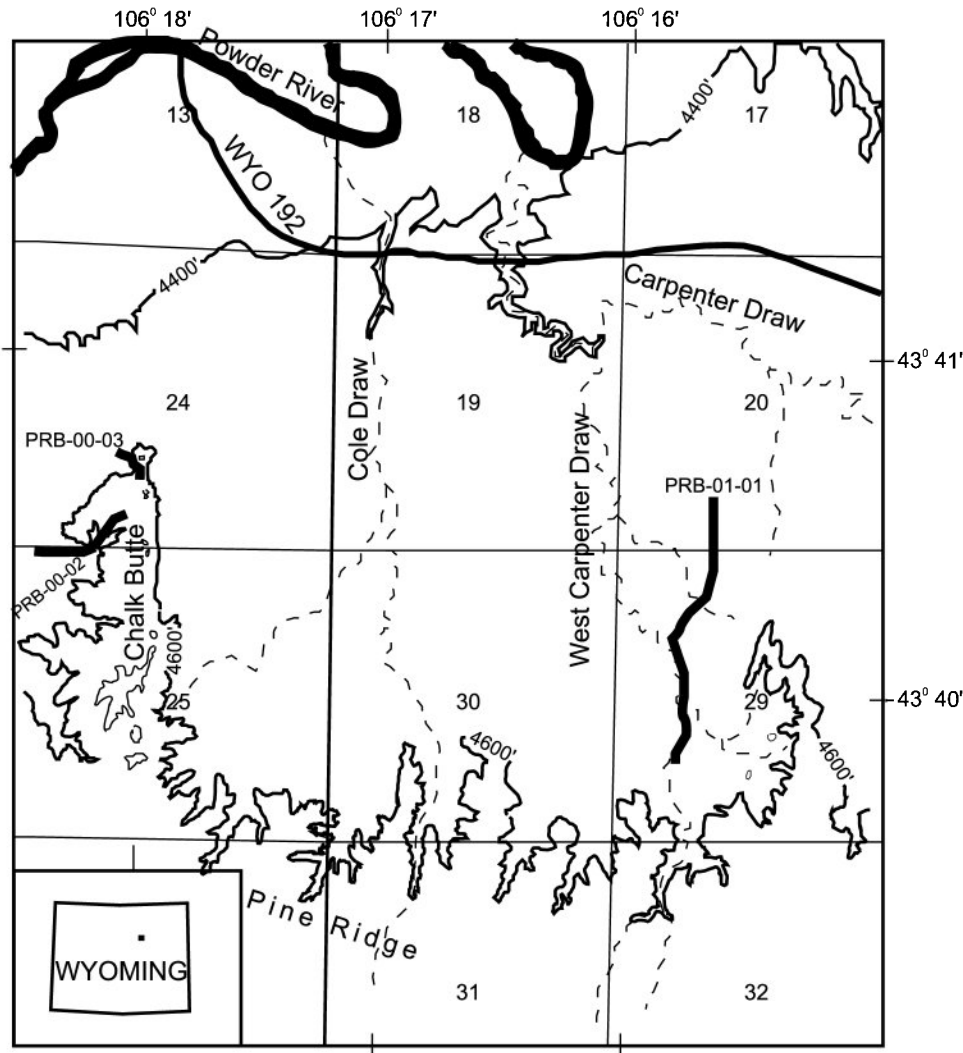


Figure 1. Map of the Chalk Butte study area showing topography, local landmarks, and the three lines of section. Based on U.S. Geological Survey Sussex Quadrangle (1:24,000).

tensive carbonaceous shale with lignitic zones informally called the Chalk Butte lignite (Figs. 2 and 3; Robinson, 2000, personal commun.). The base of the southern Chalk Butte section (PRB-00-02) is in the northern part of section 25, T. 43 N, R. 79 W, and extends 80 m up section to the top of the butte (Figs. 1, 3). We collected paleosol carbonate nodules for stable isotope analysis from this section because it offers the best local exposures of pedogenically altered mudstones.

The northern Chalk Butte section (PRB-00-03) extends through the same stratigraphic interval, but has its base in the southern part of section 24, T. 43 N, R. 79 W (Figs. 1, 3). Near the northern tip of Chalk Butte there are at least two channel-form bodies that diagonally truncate previously deposited mudstones. These channel-form bodies consist of gray, organic rich mudstones that preserve leaves and palynomorphs, as well as thin, red-variegated mudstones that probably represent paleosols. It is difficult to determine the depth of these channel fills because the diagonally truncated lower surfaces are eroded away at the top of the butte. Most of the palynological samples

were taken from this section, and leaf fossils are also present at the base and top (Fig. 3).

The Loehse Ranch section (PRB-01-01) is approximately three km east of Chalk Butte on the west side of West Carpenter Draw (sections 20 and 29, T. 43 N, R. 78 W; Figs. 1, 3). We traced the Chalk Butte lignite along nearly continuous exposures in the intervening drainages in order to establish a stratigraphic correlation between the two areas. The Loehse section begins just below the base of the Chalk Butte lignite and records 85 m of strata. Two University of Colorado vertebrate localities with Wa 0 faunas (UCM 83117 and 86101), as well as a pollen sample and a leaf fossil site, occur near the top of this section.

With the exception of the Chalk Butte lignite itself, it is difficult to make bed-for-bed correlations between the Loehse Ranch section and the sections on Chalk Butte. There are consistencies in the order of lithologies, however. In both areas the Chalk Butte lignite is overlain by a thick sandstone unit. A distinctive, white, poorly cemented, sandy or silty mudstone with a leached appearance occurs above the sandstone interval in

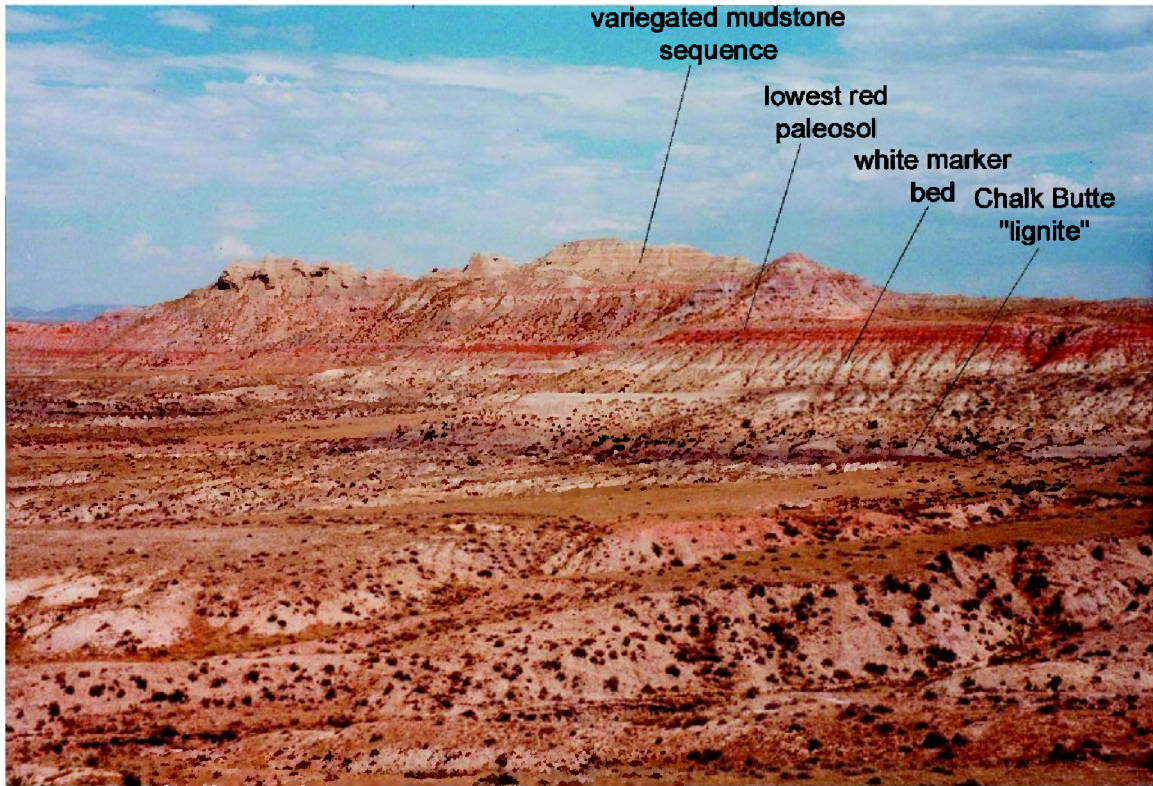


Figure 2. Photograph of the west face of Chalk Butte showing the primary marker strata referred to in Figure 3. Photograph by Henry Fricke.

both areas (Figs. 2 and 3). On Chalk Butte the unit is a single bed ~1 m thick, whereas in the Loehse Ranch section there appear to be two thinner white mudstone units separated by ~2 m of weakly developed orange-brown paleosols. In both areas the first bright and laterally extensive red bed occurs ~12–15 m above the white mudstone horizons. In both areas the upper part of the section contains a number of purple-red and variegated mudstone paleosol units. The channel cut and fill structures that are clearly visible on the upper part of the Chalk Butte were not seen in upper part of the Loehse Ranch section, but much of this interval is covered (Fig. 3).

In general, the stratigraphic sequence in the Chalk Butte area is similar to Paleocene-Eocene sequences in the southeastern part of the Bighorn Basin near North Butte, ~100 km to the west. There the IETM falls at the base of the Willwood Formation (Koch et al., 1995; Wing, 1998; Strait, 2001), which is defined as beginning with the lowest laterally extensive red-variegated mudstone beds (Bown, 1979). Although unusually thick, red paleosols characterize the lowest part of all known IETM sequences in the Bighorn Basin (in at least five separate locations), paleosols in the upper portions of those same IETM sequences are similar to overlying typical early Eocene paleosols. Thus, the occurrence of *Wa 0* mammals above the thick red paleosols at Chalk Butte is entirely consistent with observations in the Bighorn Basin.

STABLE ISOTOPES

We collected paleosol carbonate nodules, mammal teeth, and organic matter from a number of stratigraphic levels in the Chalk Butte area. Fossil soils (paleosols) were identified by their vertical color horization and the presence of features such as root traces, mottling, and absence of primary sedimentary structure. We collected nodules from trenches dug through the lower parts of paleosols. Carbonate nodules were polished flat on a lapidary wheel, and subsamples (~100 µg) of micritic carbonate were drilled from polished surfaces, then roasted at 400 °C for 1 hr to remove organic contaminants. Mammalian tooth enamel was drilled from fossil molars and prepared for analysis of structural carbonate by treatment with 2% NaOCl to remove organic contaminants and leaching with 1 N acetic acid to dissolve diagenetic carbonate. All carbonate samples were analyzed using a VG Optima or Prism mass spectrometer following reaction with 100% phosphoric acid at 90 °C in an online carbonate preparation device.

Seven samples were taken from carbonaceous shale and mudstone beds in the northern Chalk Butte section (PRB-00-03) and treated both for stable carbon isotope and palynological analyses. At each site we dug away weathered material until we obtained coherent pieces of rock ≥3 cm on a side that were not obviously penetrated by modern roots. Samples for isotopic

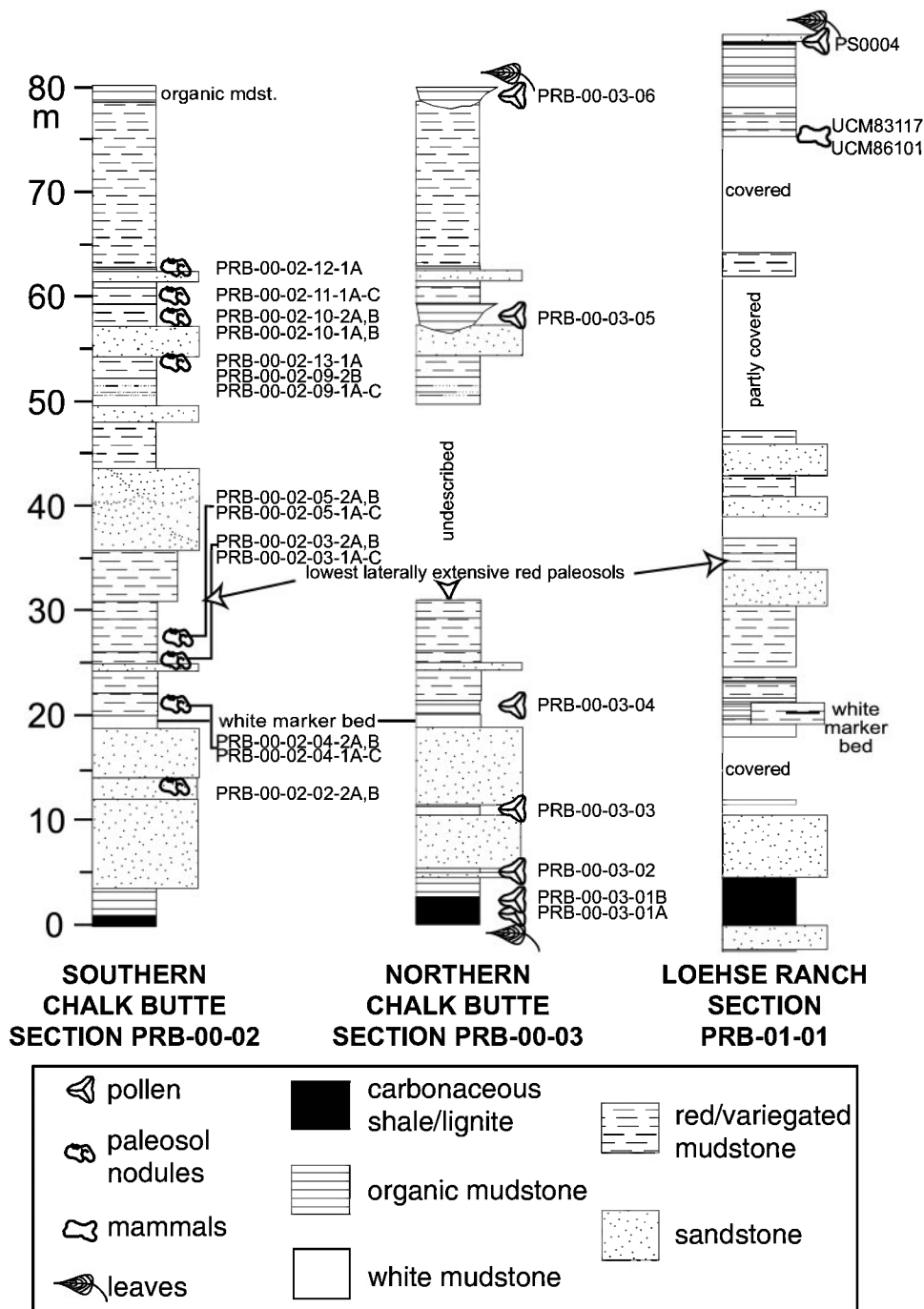


Figure 3. Chalk Butte and Loehse Sections showing lithology, and stratigraphic positions of samples. Correlation between sections is based on the Chalk Butte “lignite” at the base. See Figure 1 for map of section lines.

analysis of bulk organic matter were prepared by leaching with 0.5 N HCl to remove carbonate, followed by extraction of soluble organic compounds with dichloromethane for 1 hour. The extracted fraction was discarded, and the remaining solid sample dried and analyzed using a Carlo Erba Elemental Analyzer coupled to a VG Optima mass spectrometer.

All isotopic results are presented in per mil units and δ notation relative to the V-PDB standard, where $\delta^{13}C = 1000 * (R_{sample} - R_{standard})/R_{standard}$ and R is the ratio $^{13}C/^{12}C$. Ana-

lytical precision was $\sim 0.1\text{‰}$ for carbonates and 0.3‰ for organic carbon based on repeated analysis of in-house standards (Carerra marble, PU gel). Results of stable isotope analyses are shown in Tables 1–3.

No single substrate for isotopic analyses is present at numerous levels throughout the Chalk Butte section, therefore we present a composite carbon isotope stratigraphy incorporating measurements made on paleosol carbonate, organic matter, and fossil enamel. These values are plotted by stratigraphic position

TABLE 1. ISOTOPIC MEASUREMENTS OF PALEOSOL CARBONATE NODULES

Sample	Level (m)	$\delta^{13}\text{C}$ (‰)	$\delta^{18}\text{O}$ (‰)
PRB-00-02-02-2A	13.20	-14.599	-7.524
PRB-00-02-02-2B	13.20	-14.707	-7.722
PRB-00-02-04-1A	21.20	-14.031	-7.573
PRB-00-02-04-1B	21.20	-14.142	-8.133
PRB-00-02-04-1C	21.20	-14.310	-7.870
PRB-00-02-04-2A	21.20	-13.841	-8.146
PRB-00-02-04-2B	21.20	-13.180	-8.179
PRB-00-02-03-1A	25.65	-14.581	-7.391
PRB-00-02-03-1B	25.65	-14.929	-7.564
PRB-00-02-03-1C	25.65	-14.607	-7.287
PRB-00-02-03-2A	25.65	-14.767	-7.592
PRB-00-02-03-2B	25.65	-15.071	-7.811
PRB-00-02-05-1A	27.85	-13.989	-7.801
PRB-00-02-05-1B	27.85	-13.886	-7.760
PRB-00-02-05-1C	27.85	-13.835	-7.849
PRB-00-02-05-2A	27.85	-14.058	-7.574
PRB-00-02-05-2B	27.85	-14.383	-8.131
PRB-00-02-09-1A	53.50	-14.052	-7.361
PRB-00-02-09-1B	53.50	-13.953	-7.619
PRB-00-02-09-1C	53.50	-13.908	-7.851
PRB-00-02-09-2B	53.50	-13.983	-7.935
PRB-00-02-13-1A	53.50	-15.053	-7.762
PRB-00-02-13-1A	53.50	-15.176	-7.082
PRB-00-02-13-1B	53.50	-15.279	-7.822
PRB-00-02-13-2A	53.50	-15.322	-7.658
PRB-00-02-13-2B	53.50	-15.444	-7.764
PRB-00-02-10-1A	58.50	-13.825	-7.504
PRB-00-02-10-1B	58.50	-13.727	-7.858
PRB-00-02-10-2A	58.50	-12.814	-8.682
PRB-00-02-10-2B	58.50	-12.522	-8.411
PRB-00-02-11-1A	60.30	-14.350	-8.385
PRB-00-02-11-1B	60.30	-14.040	-7.805
PRB-00-02-11-1C	60.30	-14.306	-7.392
PRB-00-02-12-1A	62.95	-11.920	-8.272
PRB-00-02-12-1B	62.95	-11.603	-8.228
PRB-00-02-12-1C	62.95	-12.342	-8.094
PRB-00-02-12-2A	62.95	-12.174	-8.241
PRB-00-02-12-2B	62.95	-11.878	-8.188

in Figure 4, with axes for different substrates aligned to reflect the typical isotopic fractionation between these substrates in the modern (Cerling, 1984) or in Bighorn Basin fossil localities (Koch et al., 1995). The $\delta^{13}\text{C}$ values of organic matter from near the base of the section range between -24.6‰ and -27.0‰ . This is near the expected values given the average carbon isotope

TABLE 2. ISOTOPIC MEASUREMENTS OF TOOTH ENAMEL

Sample	Level (m or zone)	$\delta^{13}\text{C}$ (‰)	$\delta^{18}\text{O}$ (‰)
<i>Coryphodon</i> Loc. 94025	Wa 2	-12.1	-8.2
<i>Coryphodon</i> Loc. 94024	Wa 2	-13.7	-8.6
<i>Phenacodus</i> —Chalk Butte	21.2	-16.1	-8.0
<i>Phenacodus</i> B—Chalk Butte	21.2	-15.7	-7.4

TABLE 3. ISOTOPIC MEASUREMENTS OF ORGANIC CARBON

Sample	Level	% C [†]	C/N [†]	$\delta^{13}\text{C}$ (‰)
PRB-00-03-06	79.0	0.86	12.0	-27.3
PRB-00-03-05	58.0	0.62	08.7	-29.4
PRB-00-03-04	20.5	0.06	02.2	-24.6
PRB-00-03-03	10.9	1.99	18.1	-27.0
PRB-00-03-02	5.0	0.62	08.4	-25.4
PRB-00-03-01A	1.0	2.28	18.4	-26.9
PRB-00-03-01A (duplicate)	1.0	2.93	18.4	-26.3
PRB-00-03-01B	2.0	1.15	10.1	-26.6

[†]Estimated from ion source strength calibrated using standards of known size.

fractionation between modern C3 plants and the atmosphere (-19.6‰ , Passey et al., 2002) and estimated late Paleocene to early Eocene atmospheric $\delta^{13}\text{C}$ values between -6.5‰ and -4.5‰ (Bowen and Bloch, 2002). A single sample (PRB-00-03-05) from the upper part of the Chalk Butte section, however, has a lower $\delta^{13}\text{C}$ (-29.4‰), suggesting an atmospheric $\delta^{13}\text{C}$ value of $\sim -9.8\text{‰}$. Paleosol carbonates from the middle of the Chalk Butte section have $\delta^{13}\text{C}$ values between -14.7‰ and -13.2‰ (averages for single stratigraphic levels), with one level high in the section producing a value of -12.0‰ . Using the soil gas diffusion model of Cerling (1984), the paleosol carbonate $\delta^{13}\text{C}$ values from the middle of the section would have been generated from decomposing and/or respiring plants with values no higher than -29.7‰ to -28.2‰ . Thus, most of the soil carbonate data suggest that co-occurring organic matter had $\delta^{13}\text{C}$ values lower than those measured at the base of the Chalk Butte section, but similar to that measured for the organic matter sample at 58 m.

Finally, the specimens of *Phenacodus* from the 21.2 m level had $\delta^{13}\text{C}$ values of -15.7‰ and -16.1‰ , slightly lower than the value for Wa 0 *Phenacodus* in the Bighorn Basin (-15.3‰), but much lower than values for non-Wa 0 *Phenacodus* specimens in the Bighorn Basin. (The mean value for non-Wa 0 Wasatchian specimens is $-11.9 \pm 0.7\text{‰}$ [$\pm 1\sigma$], the minimum is -13.9‰ , and the maximum is -11.0‰ [N = 18]. The values for Tiffanian-Clarkforkian *Phenacodus* are: mean, $-10.2 \pm 1.3\text{‰}$; minimum, -13.1‰ ; maximum, -7.4‰ ; N, 22.) In contrast, specimens of the pantodont *Coryphodon* from Wa 2 fossil localities at Pumpkin Buttes, ~ 35 km east of Chalk Butte in the Powder River Basin, produced $\delta^{13}\text{C}$ values of -12.1‰ and -13.7‰ . This overlaps the range observed for non-Wa 0 *Coryphodon* from the Bighorn Basin. (The mean value for non-Wa 0 Wasatchian specimens is $-12.6 \pm 1.3\text{‰}$ [$\pm 1\sigma$], the minimum is -14.3‰ , and the maximum is -9.3‰ [N = 18]. Comparable values for Clarkforkian *Coryphodon* are: -12.4 ± 1.0 , -14.5‰ , -11.1‰ , 9.) Based on the average carbon isotope offset between Bighorn Basin *Phenacodus* or *Coryphodon* and co-occurring paleosol carbonate (Koch et al., 1995), the $\delta^{13}\text{C}$ values of Chalk Butte *Phenacodus* should correspond to paleosol carbonate with $\delta^{13}\text{C}$

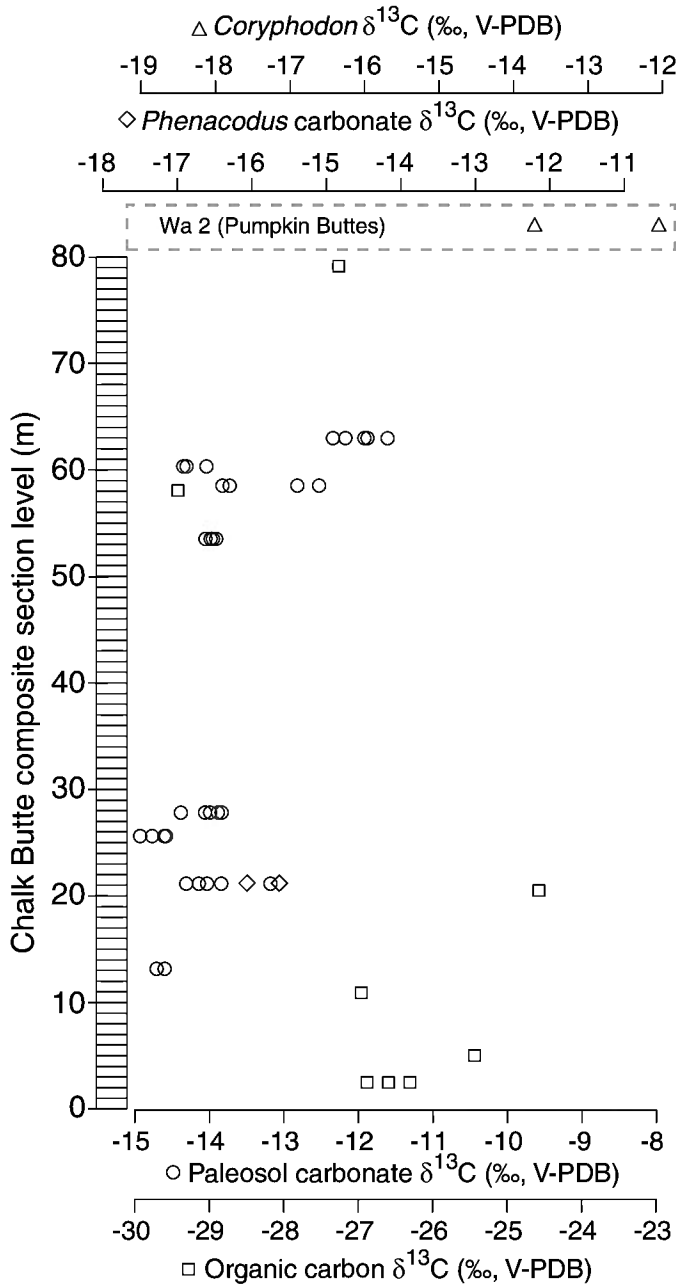


Figure 4. Plot of carbon isotope values of pedogenic calcium carbonate nodules, bulk paleosol organic matter, and fossil tooth enamel carbonate by stratigraphic level. Axes are aligned according to “average” carbon isotope fractions between sample substrates; these are: $\delta^{13}\text{C}_{\text{soil carbonate}} - \delta^{13}\text{C}_{\text{organic carbon}} = \sim 15\text{‰}$ or greater for modern soils (Cerling, 1984), and $\delta^{13}\text{C}_{\text{soil carbonate}} - \delta^{13}\text{C}_{\text{Phenacodus}} = 2.6\text{‰}$ and $\delta^{13}\text{C}_{\text{soil carbonate}} - \delta^{13}\text{C}_{\text{Coryphodon}} = 4.1\text{‰}$ based on the fossil data given by Koch et al. (1995). Symbols: Circles—pedogenic carbonate nodules, squares—organic carbon, diamonds—*Phenacodus* tooth enamel, triangles—*Coryphodon* tooth enamel. V-PDB—Vienna Pee Dee belemnite.

values of -13.1‰ to -13.5‰ (similar to the value measured for this level, -13.8‰). The *Coryphodon* enamel values suggest Powder River Basin Wa 2 paleosol carbonate with $\delta^{13}\text{C}$ values of about -8.0‰ to -9.6‰ , much higher than any values for paleosol carbonates from the Chalk Butte section.

The combined carbon isotope data (Fig. 4) suggest that the middle of the Chalk Butte section contains an extended interval characterized by low $\delta^{13}\text{C}$ values. Most of the evidence for low $\delta^{13}\text{C}$ values in this interval comes from paleosol carbonates, which produce values lower than those for any non-IETM Paleogene paleosol carbonates nodules from the Bighorn, Wind River, or Green River Basins (Koch and Morrill, 2000; Clyde et al., 2001; Koch et al., this volume). Because we did not measure any Powder River Basin paleosol carbonates with “normal” late Paleocene $\delta^{13}\text{C}$ values, we must consider the possibility that the low values reported here reflect either diagenetic alteration or the contribution of a secondary source of isotopically light carbon to Powder River Basin soils, rather than the global $\delta^{13}\text{C}$ signal marking the IETM. Burial diagenesis should affect both the $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values of carbonate, and typically decreases $\delta^{18}\text{O}$ values due to mineral formation at elevated temperatures. The range of $\delta^{18}\text{O}$ values measured in Chalk Butte paleosol carbonates is small and $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values are negatively correlated ($r^2 = 0.41$, $p < 0.0001$). This suggests that if the paleosol carbonate isotope values were affected by diagenesis, this modification probably increased $\delta^{13}\text{C}$ and can not account for the very low $\delta^{13}\text{C}$ values. A second scenario for the very low paleosol carbonate $\delta^{13}\text{C}$ values, influx of light carbon from outside the soils, would most likely imply the upward migration and oxidation of isotopically light biogenic methane produced in underlying organic-rich sediments (e.g., Bowen and Bloch, 2002). This scenario is unlikely, however, as the carbonate-bearing paleosols from the Chalk Butte sections are well oxidized and any methane in the Chalk Butte sediment stack would have been produced and oxidized deep in the subsurface. Furthermore, since mammals obtain their carbon directly from plants, the low $\delta^{13}\text{C}$ values for *Phenacodus* tooth enamel suggest that plants, rather than subsurface methane, were the source of low $\delta^{13}\text{C}$ values at Chalk Butte. This hypothesis is supported by the relatively low $\delta^{13}\text{C}$ value of organic matter sample PRB-00-03-05. Finally, the *Coryphodon* data from Pumpkin Butte demonstrate that “normal” Wasatchian $\delta^{13}\text{C}$ values are preserved in fossil tooth enamel from the Powder River Basin. Thus, we suggest that the low $\delta^{13}\text{C}$ values from the middle of the Chalk Butte section record the low $\delta^{13}\text{C}$ values for atmospheric CO_2 that characterized the IETM.

High-resolution measurements of carbon isotope values through continental IETM sections show a characteristic stratigraphic pattern: A rapid, possibly stepped, decrease of 6‰ – 8‰ at the onset of the IETM, succeeded by an interval of stable low values, then an asymptotic rise of carbon isotope values back to pre-IETM levels (Bowen et al., 2001; Bains et al., this volume). Continental sections sampled at lower resolution across the IETM also show an abrupt shift in $\delta^{13}\text{C}$ values, and may pre-

serve a gradual recovery to pre-excursion values (Koch et al., 1992, 1995; Bowen et al., 2002; Ting et al., this volume). When organic matter, enamel carbonate, and soil carbonate isotopic data from Chalk Butte are considered together, the pattern of values suggests an excursion of similar form to that recorded elsewhere, but this record lacks the resolution necessary to distinguish the more subtle features of the event (Fig. 4). The “normal” isotope values for organic matter near the base of the section suggest that these rocks predate the IETM, whereas comparison with the record from Polecat Bench (Bowen et al., 2001) suggests that the low, relatively stable $\delta^{13}\text{C}$ values of paleosol carbonates from the Chalk Butte section may represent the middle portion of the carbon isotope excursion. The precise stratigraphic level of the base of the carbon isotope excursion at Chalk Butte is uncertain, as organic matter from the 20.5 m level (PRB-00-03-04) has a “normal” $\delta^{13}\text{C}$ value, while stratigraphically lower paleosol carbonates (PRB-00-02-02) produce IETM-like $\delta^{13}\text{C}$ values. The organic carbon content of sample PRB-00-03-04 is an order of magnitude less than for the other samples (Table 3). Given the questionable quality of that isotopic datum, we tentatively place the onset of the isotope excursion between the 5 and 13 m levels of the Chalk Butte section.

PALYNOLOGY

Nine samples were used in the palynological study. Seven pollen samples from the northern Chalk Butte section (PRB-00-03) are splits of the samples used for organic matter stable isotopic measurements discussed in the previous section. One additional sample (PS0004) comes from a carbonaceous shale 10 m above UCM83117 at the top of the Loehse section (PRB-01-01), and the other (PS0003) from a laterally extensive carbonaceous shale above the top of all measured sections (Fig. 3). This highest sample comes from the informally designated Loehse lignite (Robinson, 2000, personal commun.) which is exposed on the north side of the highway due north of the Loehse section. We estimate that the Loehse lignite is ~220 m above the base of the Wasatch Formation, or 120 m above the Chalk Butte lignite. Sample PS0003 is thus ~35 m above the highest sample in any measured section (PS0004).

Palynological samples were processed by Global Geolabs of Drumheller, Alberta using standard HF maceration followed by sieving with a true 10 μ screen, oxidation of organics, and staining. Slides were scanned under a transmitted light microscope. GJH identified and counted a mean of 406 grains in each sample (SD = 253). The high variability in sample size reflects two samples with high counts (PRB-00-03-01B, N = 826 and PS0003, N = 834) and two with low counts (PRB-00-03-02, N = 170 and PRB-00-03-04, N = 143). The high counts were made because of strong dominance of the sample by a single taxon. To ensure that rarer species would be detected grains were counted until the sum of the nondominant taxa reached 200. The low counts are for two samples that produced few palynomorphs, possibly because of poor preservation, low pollen production in

the environment of deposition, or because the samples were weathered. (Sample PRB-00-03-04, which was the least productive pollen sample, contained only 0.06% organic carbon by weight.) Species lists and abundances for each sample are given in Appendix 1.

Important elements of the palynoflora from the Chalk Butte area include fern spores (*Cyathidites*, *Deltoidospora*, and *Laevigatosporites haardtii* together are 1%–41% of grains), taxodiaceous conifers (9%–76%), *Caryapollenites* (2%–30%), *Polyatriopollenites vermontensis* (0%–75%), *Ulmipollenites* (1%–6%) and Betulaceae/Myricaceae (2%–35%). Although the overall floral similarity with Bighorn Basin samples is high, a few moderately common pollen and/or spore taxa are unique to each basin. For example, *Cycadopites scabratus* is present in 7 of the 9 Chalk Butte samples at abundances of 0.5%–11.9%, but is unknown in 52 samples from the latest Paleocene and earliest Eocene of the Bighorn Basin (Harrington, 1999; Wing and Harrington, 2001). Other taxa differ consistently in their relative abundances between the Chalk Butte and Bighorn Basin samples. *Momipites* is moderately common in the Paleocene (mean of 9.5%) and Eocene (4.6%) of the Bighorn Basin, but is <1% of the flora in all but two samples from Chalk Butte. *Alnipollenites*, which has a mean abundance of 1% in the Paleocene of the Bighorn Basin and 8% in the Eocene, is <2% in all of the Chalk Butte samples. Both of these taxa were probably less important in the local vegetation around Chalk Butte than in coeval vegetation of the Bighorn Basin, just 100 km away.

The mean richness of the Chalk Butte samples is 24.1 taxa, as compared with 20.5 taxa in the set of 52 late Paleocene and early Eocene samples from the Bighorn Basin. Even with only 9 samples from Chalk Butte the difference is moderately significant (t-test with separate variances $p \leq 0.07$). There is also a stratigraphic pattern in richness of the Chalk Butte samples: The five lowest samples (0–22 m) have 18–23 species, whereas the upper four samples (56–120 m) have 24–31 species. This upward increase in diversity is consistent with the stratigraphic pattern described in the Bighorn Basin, where Eocene samples had higher average diversity than Paleocene samples (Wing and Harrington, 2001). The within-sample diversity differences are unlikely to result from sample size because the latter is poorly correlated with richness ($r^2 = 0.1$ for a logarithmic regression of richness on sample size).

Two stratigraphically important taxa have local first appearances in the Chalk Butte sections. *Intratropollenites instructus*, a *Tilia*-like pollen, is found in the three highest samples at Chalk Butte (79–120 m), and is moderately common in two of them (3.3% and 8.4%). In the Bighorn Basin *I. instructus* is moderately common from the lowest to the highest Eocene sample, but is absent in the Paleocene. One grain of *Platycarya* pollen is present in sample PRB-00-03-06 (79 m), and another in PS0003 (120 m). Although the form is locally so rare that its absence from lower samples could be due to vagaries of sampling, this taxon is also rare in the first half of the early Eocene in the Bighorn Basin, where it is absent from a well-sampled in-

terval ~40 m thick immediately above the IETM (Wing and Harrington, 2001). The shift to palynofloras with Eocene index taxa at Chalk Butte occurs between sample PRB-00-03-05 at 58 m and sample PRB-00-03-06 at 79 m. The Wa 0 fauna of Robinson is in this interval, at ~74 m.

IDENTIFICATION OF THE IETM IN THE POWDER RIVER BASIN

In the western interior of the United States the Paleocene-Eocene boundary has been recognized by three criteria: A major immigration of mammalian taxa (Rose, 1981; Gingerich, 1989, this volume), a shift in palynofloral composition (Nichols and Ott, 1978; Wing, 1984; Harrington, 2001b), and a negative excursion in carbon isotope values (Koch et al., 1995; Bowen et al., 2001). In many areas the Paleocene-Eocene boundary is also stratigraphically close to the boundary between drab, lignitic strata assigned to the Fort Union Formation and red or variegated strata belonging to the Wasatch Formation, Willwood Formation, and other units, although the transition from drab to variegated rocks has been shown to be time transgressive over short distances in some areas (Wing and Bown, 1985). Over an extensive area in the Bighorn Basin where the IETM has been identified from faunal, floral and/or isotopic evidence, its onset is characterized by pedogenically altered red mudstones of unusual thickness and intense color (Gingerich, 1989; Wing et al., 2000). These prominent paleosols are evident even in areas where the transition from Fort Union to Willwood deposition predates the IETM (Gingerich, 2001).

Four lines of evidence suggest that exposures of the lower Wasatch Formation in the middle part of Chalk Butte and stratigraphically correlated areas nearby were deposited during the IETM. (1) There are prominent, laterally extensive red paleosols immediately above drab, lignitic strata, just as there are in IETM sequences in the eastern and southern Bighorn Basin. (2) Vertebrate faunas from ~40 m above the lowest red beds have a characteristic earliest Wasatchian (Wa 0) fauna that has been shown to be restricted to the isotopically defined IETM in the Bighorn Basin (Koch et al., 1995; Gingerich, this volume). (3) Palynofloras 5 m above the Wa 0 fauna document first appearances of Eocene index taxa and some of the shifts in diversity and relative abundances that are typical of the Paleocene-Eocene boundary in the Bighorn Basin. (4) $\delta^{13}\text{C}$ measurements made on a variety of substrates suggest a shift in the $\delta^{13}\text{C}$ value of terrestrial carbon stores similar to that seen in other terrestrial IETM sections.

Although the evidence for the IETM being represented at Chalk Butte is strong, the stratigraphic extent of the IETM is not clear. The first occurrence of *I. instructus* at 79 m suggests that this level is within or above the IETM. The presence of *Copecion davisii* and *Cantius torresi* at 74 m suggests that this level is within the IETM. The first laterally extensive red paleosol (at ~26 m) is probably near the base of the IETM, if the paleosols in Bighorn Basin sections can be used as a guide. The

isotopic data are sparse, but imply that the interval between 13 and 63 m is within the IETM, with the base of the IETM lying between 5 and 13 m. Although these sources of data do not pinpoint the stratigraphic level for the base or top of the IETM, our best estimate is that the base of the IETM is between 5 and 13.2 m, and that the top of the IETM is above 74 m. If this is correct, then it implies that depositional rates at Chalk Butte were higher than they were at Polecat Bench, because low carbon isotope values at Chalk Butte span 50 m of section, whereas low values persist for ~40 m at Polecat Bench. The possibility of high rates of sediment deposition during the IETM has also been noted at other sites. Preliminary isotopic results (Koch et al., 1995), and the distribution of prominent red beds (personal observation), on the Sand Creek Divide in the eastern Bighorn Basin suggest that the IETM may be represented by 60–80 m of sediment, although this is far from certain. Ting et al. (this volume) have noted that the IETM in the Hengyang Basin of China is probably represented by a similar thickness of section. Unfortunately we lack other lines of evidence to test the idea that depositional rates increased during the IETM, although Crouch and Visscher (this volume) argue for an increase in terrestrial runoff during the IETM based on the abundance of terrestrial palynomorphs in marine environments.

FLORAL RESPONSE TO THE IETM

Lag in first appearances

Information on floral response to the IETM comes from just five pollen samples in the Chalk Butte area: PRB-00-03-03, 04, 05, and 06 at 10.9, 20.5, 58, and 79 m respectively in the northern Chalk Butte section, and PS0004 at 84 m in the Loehse Ranch section (Fig. 3). The lowest of these samples (10.9 m) is below isotope values characteristic of the excursion, but above the highest normal values, so it is unclear if it is within the IETM. The samples at 20.5 and 58 m are within the zone where pedogenic carbonate nodules have low carbon isotope values. The sample from 79 m is 5 m above the Wa 0 fauna, but could be in the upper part of the IETM.

The absence of Eocene index palynomorphs in samples at 20.5 and 58 m indicates that the immigration of *I. instructus* and *Platycarya* spp. in this area postdates the onset of the IETM by at least the amount of time represented by the ~45 m of sediments that lie between the lowest excursion isotopic value and the highest sample lacking the Eocene index palynomorphs. Although numerical age control is lacking in the Chalk Butte region, the deposition of ~45 m of fluvial sediment and paleosols is likely to represent many tens-of-thousands of years at rates of rock accumulation typical of intermontane basins. If the carbon isotope excursion begins below 13.2 m, and/or if the pollen sample from 58 m (which is in the base of a channel cut-and-fill deposit) represents a somewhat later time than its stratigraphic level indicates, then the lag between the beginning of the IETM and the first appearances of *I. instructus* and *Platycarya* is even

greater. Outside limits are placed on the length of the lag period by the observation that Wa 0 mammals occur at 74 m. In the Bighorn Basin Wa 0 mammals are associated with only the most negative $\delta^{13}\text{C}$ excursion values, and these are thought to occur only in the first ~85 k.y. of the IETM (Röhl et al., 2000; Bowen et al., 2001; Gingerich, this volume). Consequently, the maximum period of lag between the onset of the IETM and the immigration of *I. instructus* and *Platycarya* into the Chalk Butte area would be slightly >85 k.y.

To summarize, the first appearances of *I. instructus* and *Platycarya* appear to lag the onset of the IETM by tens of thousands of years. The lag between the beginning of the IETM and the FADs for these two taxa is long enough that their appearance is associated with the later, cooling phase of the IETM rather than with the initial, geologically brief, warming. Both *I. instructus* and *Platycarya* are known from the late Paleocene of northwestern Europe. Thus, a reasonable hypothesis is that these taxa crossed to North America over high-latitude land bridges during the IETM, but did not expand their ranges southward in the continental interior until climate cooled in the latter part of the IETM. The absence of Asian records of these taxa during the Paleocene-Eocene interval reflects lack of study.

Absence of southern immigrants

A simplistic extrapolation of Quaternary patterns of floral response to the IETM would lead to the prediction that samples from within the IETM should contain a substantial number of immigrants from the Gulf Coastal Plain or other more southerly parts of North America. The relevant samples (at 84, 79, 58, 20.5, and possibly at 10.9 m) do not contain any of the southern taxa that might be expected, such as the Normapolles, which are numerically important constituents of Gulf Coastal Plain palynofloras of this age (Harrington and Kemp, 2001; Harrington, this volume). It is still possible that southern immigrants could have moved north into the area for a very short period of time, but evidence for such floral immigrants would have to occur in the gaps between samples low in the section. It seems more likely that the absence of evidence is evidence of absence.

Local changes in the native flora

Stratigraphic changes in the relative abundance of palynomorphs in the Chalk Butte samples also reveal aspects of the local floral response to the IETM. In the shift from Paleocene to Eocene palynofloras in the Bighorn Basin, changes in the relative abundances of taxa played a larger role than changes in presence and/or absence of taxa (Wing and Harrington, 2001). Considering only taxa that cross the boundary, Paleocene samples are consistently distinguished by higher abundance of *Polyatriopollenites vermontensis*, *Momipites*, and *Caryapollenites*; Eocene samples consistently have higher abundance of *Alnipollenites*, Betulaceae/Myricaceae, and *Ulmipollenites* (Wing and Harrington, 2001; Harrington, 2001b). Similar shifts in relative

abundances are seen in the Chalk Butte samples, except for the overall rarity of *Alnipollenites* and *Momipites*.

We conducted a detrended correspondence analysis with down-weighting of rare taxa on a combined data set of Bighorn Basin and Chalk Butte samples to illuminate overall changes in floral composition through time. The first two axes of the ordination capture 28.2% of the variation in the data set, but they discriminate very well between Paleocene and Eocene samples (Fig. 5). The line separating the two groups is diagonal, but scores on the first axis only overlap in a narrow zone. Only two Bighorn Basin samples do not group as expected in the ordination. GH97-1.16 from the Paleocene of the Bighorn Basin groups with the Eocene samples even though it lacks Eocene indicator taxa because it is low in *Polyatriopollenites* and high in *Ulmipollenites*. PS9413 from the Eocene of the Bighorn Basin groups with Paleocene samples because it lacks Eocene indicators, is low in *Ulmipollenites* and high in *Polyatriopollenites*. Taxa are also plotted on the ordination, and they occupy positions that are consistent with their tendency to be more abundant either in the Paleocene or Eocene (Fig. 5).

If samples from within the IETM (marked by stars in Figure 5) had distinctive abundances of species, they would be expected to plot separate from the rest of the samples; they do not. Sample PRB-00-03-03 (either lowest IETM or just prior to the IETM) and sample PRB-00-03-04 (IETM), have relative abundances of taxa typical of Paleocene samples (Fig. 5). Sample PRB-00-03-05 (IETM) and samples PRB-00-03-06 and PS0004 (uppermost IETM or just post IETM) have relative abundances more typical of the Eocene, even though PRB-00-03-05 lacks Eocene index taxa. PRB-00-03-05 plots with the Eocene samples because of the low abundance of *Polyatriopollenites vermontensis*.

We can show shifts in floral composition through time by plotting the first axis score of each sample against its stratigraphic level (Fig. 6). Plotting samples from the Powder River and Bighorn Basin on the same y-axis makes the implicit assumption that depositional rates were the same in both basins, which cannot be independently verified. We are confident, however, that with the exception of the three Chalk Butte samples discussed above, we have correctly assigned the samples to pre-IETM, IETM, and post-IETM time. Figure 6 confirms that Paleocene and Eocene palynofloras have distinct compositions, and that the permanent shift to typical Eocene relative composition takes place in the latter part of the IETM. Sample PRB-00-03-02 plots with Eocene samples even though it is below the IETM as defined by low carbon isotope values, and in an interval with other pollen samples that have more typical "Paleocene" composition. The main cause of its similarity to Eocene samples is its low abundance of *Polyatriopollenites vermontensis*, *Caryapollenites*, and *Momipites*. We do not know if the low abundances of these taxa reflects climatic shifts prior to the onset of the IETM proper, or just chance fluctuations in pollen preservation and depositional environment. Major fluctuations in the abundance of *P. vermontensis* are also seen in the last part

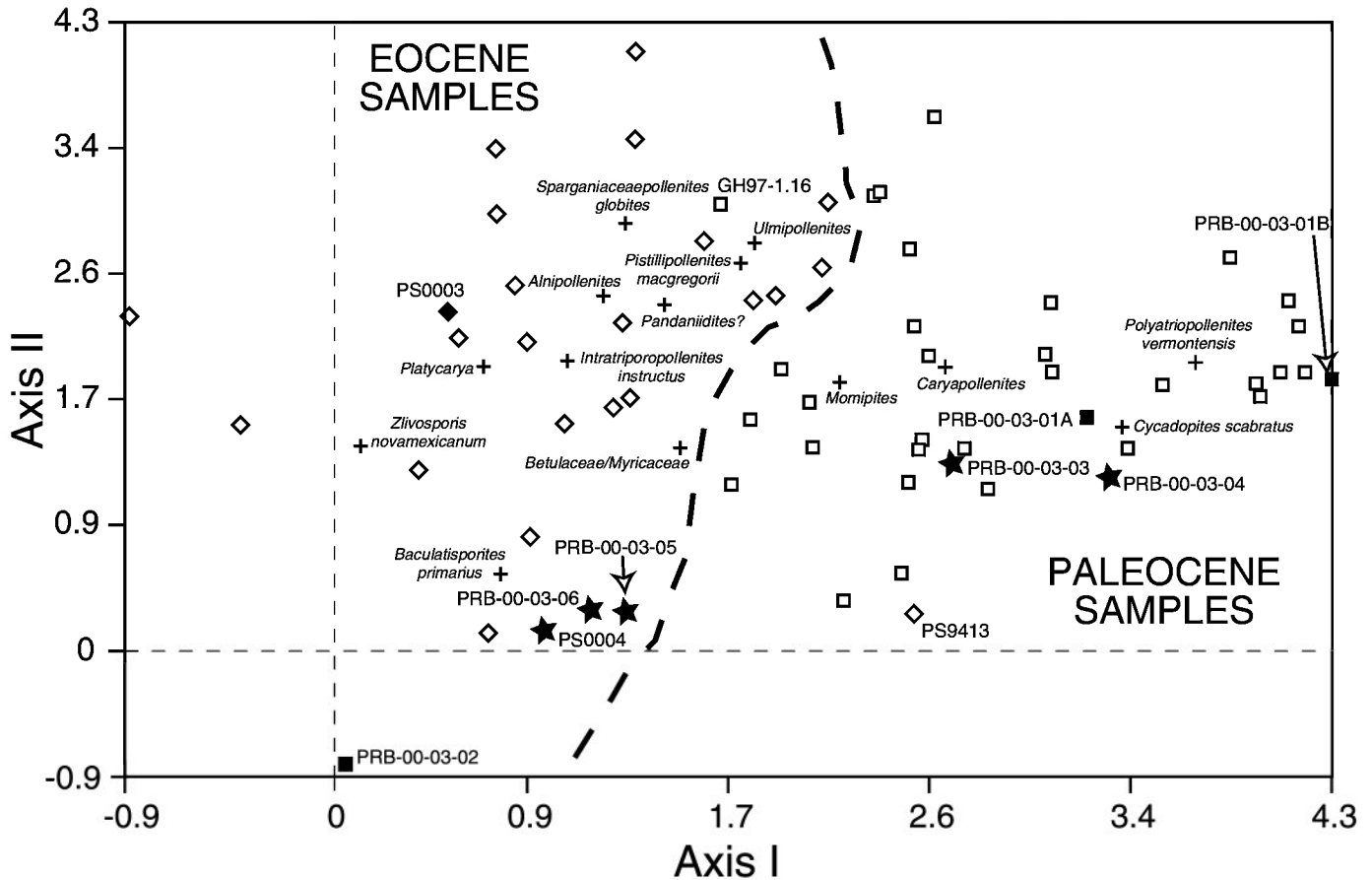


Figure 5. Detrended correspondence analysis of latest Paleocene and earliest Eocene pollen samples from the Bighorn and Powder River Basins. Axis I expresses 22% of the variance and axis II 6%. Filled symbols are samples from Chalk Butte, empty symbols are samples from the Bighorn Basin. Diamonds are Eocene samples, squares are Paleocene samples, and stars are samples that are possibly or definitely from the Initial Eocene Thermal Maximum. (See text discussion.) Crosses show the positions of selected taxa in the ordination space.

of the Paleocene in the Bighorn Basin (Wing and Harrington, 2001). If PRB-00-03-02 does reflect change in vegetation near Chalk Butte, then it suggests that relative abundances of taxa that were already present in the region (specifically *P. vermontensis*) began to shift in response to climate change well before the arrival of immigrant taxa late in the IETM.

DISCUSSION

Pollen samples from the IETM in the Powder River Basin do not appear to record the pattern of rapid, continental-scale range change that would be expected from a simple extrapolation of Quaternary plant response to this Paleogene example of rapid global warming. There is no indication of rapid northerly migration of plant populations, and the small number of immigrants that did appear probably lagged the onset of warming by at least tens of thousands of years. This slow response is in sharp contrast to that in mammalian communities, which show a pulse of first appearances of entirely new lineages during the IETM

event as well as suspected rapid evolutionary transitions within pre-existing lineages (Gingerich, 1989; Clyde and Gingerich, 1998; Gingerich, this volume). As yet we do not know why the pace of floral change during the IETM was so slow, but at least three types of explanations should be considered: Ecological limitations on range shifts, physiological limitations on range shifts, and historical development of the flora.

Ecological limitations on movement of plant populations might have been very different during the IETM than during Quaternary deglaciations. During deglaciation, plant populations expanded into areas undergoing primary succession in the wake of retreating glaciers. Models and data show that rare, long-distance dispersal and successful establishment are necessary to account for the high rate of plant migration in the Holocene (Clark et al., 1998), and that successful invasion in the present day is associated with disturbance (Richardson and Bond, 1991; Rejmánek and Richardson, 1996). The probability of successful establishment might well have been much higher during deglaciation than during the IETM, because Paleogene

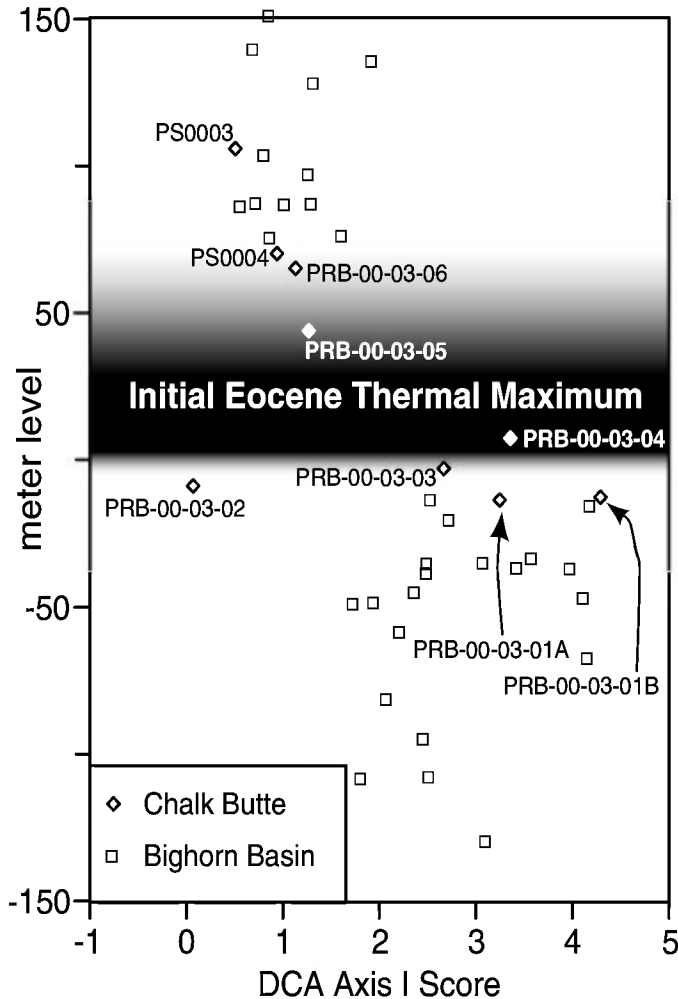


Figure 6. Ordination axis I scores of pollen samples against stratigraphic level, including Powder River Basin (PRB) and Bighorn Basin samples. Diamonds are samples from Chalk Butte area, empty squares are samples from the Bighorn Basin. DCA—detrended correspondence analysis.

climates permitted forests to grow from the Gulf of Mexico (Wolfe, 1985) to the shores of the Arctic Ocean (Hickey et al., 1983; McIver and Basinger, 1999). During the IETM potential long-distance dispersers would have had to establish new populations under an existing forest canopy.

Physiological limitations might also have slowed plant migration during the IETM. The southern part of North America was probably occupied by broad-leaved evergreen forest during the late Paleocene and early Eocene (Wolfe, 1985; Wolfe and Dilcher, 2000). Broad-leaved, evergreen species with poorly developed physiological mechanisms for leaf abscission or dormancy may not have grown well in the warm, dim, winter conditions that probably existed in the middle to high latitudes during the IETM (Peters and Sloan, 2000). Plants that do not drop their leaves during the winter continue to lose water through transpiration, and respiration in the leaves may use

stored resources (Read and Francis, 1992). Warm winters with low light levels might therefore favor deciduous plants, as has been proposed for high-latitude Cretaceous floras (Falcon-Lang and Cantrill, 2001). Similar arguments presumably apply in a less absolute form to floras living between 45 and 55 degrees during the IETM. Maladaptation to long, dim but warm, winters may have prevented many broad-leaved evergreen taxa from shifting ranges during the IETM. Longer intervals of warm climate, such as the one that occurred at the end of the early Eocene and persisted for at least a million years, might have been long enough for evergreen taxa to evolve the deciduous habit that would permit colonization and dispersal across high-latitude corridors.

A final factor that may explain the slow floral response to rapid warming during the IETM and the rapid floral response to late Quaternary warming is the difference in climatic regimes that preceded the two events. The IETM was a sudden climate shift in the midst of a geologically long period when the amplitude of orbitally forced temperature change was probably low. In contrast, the late Quaternary deglaciation was merely the last of many rapid, high-amplitude climatic changes that severely affected northern midlatitude floras over the last 2–3 million years. The late Quaternary flora of the midnorthern latitudes thus consists of plants that survived many glacial-interglacial fluctuations, and it may be composed of an unusually high proportion of species that disperse well. The latest Paleocene floras that experienced the IETM may have consisted of a more typical mix of species including many that were not particularly good dispersers.

CONCLUSIONS

1. The lower Wasatch Formation in the area of Chalk Butte in the southwestern Powder River Basin preserves a sequence of fossiliferous, pedogenically altered, fluvial sediments that represent the IETM. This is the first record of a terrestrial IETM sequence in North America outside of the Bighorn Basin. Isotopic evidence, mammalian biostratigraphy, and palynostratigraphy are in agreement with expectations developed in the Bighorn Basin.

2. Pollen samples from within the IETM give no evidence of a transient flora containing tropical or subtropical taxa, thus there is no evidence for northward range changes during the IETM.

3. The initial floral response to the IETM may have been a shift in relative abundances of taxa that were already present in the area, specifically declining abundance of *Polyatriopollenites vermontensis*. This is consistent with the idea that warming and/or other climatic and atmospheric changes during the IETM rapidly affected the relative success of different types of native plants.

4. First appearances of the Eocene index palynomorphs *Intratropopollenites instructus* and *Platycarya* spp. probably occurred during the cooling late in the IETM, not with the initial warming. These Eocene floral immigrants to the northern

Rockies were cool adapted species that probably came across high-latitude land bridges.

5. Floral changes during the IETM are much slower than would be expected from a model based on floral response to Quaternary glacial cycles. This probably reflects limits on the dispersal and colonization rates of Paleogene plants.

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APPENDIX 1. ABUNDANCES OF POLLEN AND SPORE TAXA—CHALK BUTTE SAMPLES

Taxon name	Sample numbers and stratigraphic levels								
	PS0003 (~120 m)	PS0004 (84 m)	PRB-00-03-06 (79 m)	PRB-00-03-05 (58 m)	PRB-00-03-04 (20.5 m)	PRB-00-03-03 (10.9 m)	PRB-00-03-02 (5 m)	PRB-00-03-01B (2 m)	PRB-00-03-01A (1 m)
Spores									
<i>Appendicisporites</i> spp.	0	0	0	0	0	0	1	0	0
<i>Baculatisporites primarius</i>	1	0	0	1	0	0	2	0	0
<i>Camarozonosporites</i>	1	1	3	13	0	0	8	0	0
<i>Cicatricosisporites dorigensis</i>	0	1	1	1	0	0	9	0	0
<i>Cyathidites triangulus</i>	1	2	3	5	0	0	7	0	1
<i>Deltoidospora</i> spp.	13	7	12	25	9	3	35	2	0
<i>Gleicheniidites</i>	0	6	6	7	0	0	7	1	0
<i>Laevigatosporites haardtii</i>	57	9	22	40	25	26	21	0	6
<i>Microfoveolatasporis pseudodentata</i>	0	0	0	0	1	0	0	0	0
<i>Reticuloidosporites pseudomurii</i>	1	0	0	0	0	0	0	0	0
<i>Stereisporites steriodes</i>	0	0	1	1	0	0	0	0	0
<i>Zlivosporis novamexicanum</i>	0	0	0	0	0	0	1	0	0
Gymnosperms									
<i>Bisaccate</i>	0	2	3	19	0	10	15	3	6
<i>Cupressacites hiatipites</i>	616	70	73	125	19	83	19	64	49
<i>Erdtmanipollis cretaceus</i>	1	3	1	0	2	0	0	0	0
<i>Sequoia</i>	15	9	12	41	4	20	23	8	19
Monocots									
<i>Arecipites</i> spp.	3	0	0	15	0	11	0	1	1
<i>Cycadopites scabratus</i>	0	2	0	3	2	2	2	29	43
<i>Cycadopites</i> spp.	4	4	0	4	3	1	0	0	11
<i>Liliacidites</i> spp.	0	0	1	0	0	0	0	0	0
<i>Monocolpopollenites tranquillus</i>	2	1	2	0	1	1	0	0	2
<i>Pandaniidites?</i>	0	0	0	1	0	0	0	0	0
<i>Sparganiaceapollenites globites</i>	2	1	1	0	0	0	0	1	0
Dicots (Tricolpate + Tricolporate)									
<i>Ailanthipites berryi</i>	0	0	1	0	1	0	0	0	0
<i>Caprifoliipites</i> spp.	0	0	1	0	0	0	0	0	0
<i>Cercidiphyllites</i> sp.	0	0	0	1	0	1	0	0	0
<i>Ericipites</i> spp.	0	0	0	0	0	1	0	0	0
<i>Eucommia</i> sp. A	3	0	1	1	0	1	0	3	0
<i>Fraxinoipollenites</i> spp.	0	1	1	1	0	0	2	3	2
<i>Fraxinoipollenites varabilis</i>	3	1	1	0	0	9	0	0	0

continued

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