

Marine-terrestrial linkages at the Paleocene-Eocene boundary

Santo Bains

Department of Earth Sciences, University of Oxford, Oxford, OX1 3PR, UK

Richard D. Norris

*Department of Geology and Geophysics, Woods Hole Oceanographic Institution,
Woods Hole, Massachusetts 02543, USA*

Richard M. Corfield

Department of Earth Sciences, University of Oxford, Oxford, OX1 3PR, UK

Gabriel J. Bowen

Department of Earth Sciences, University of California, Santa Cruz, California 95062, USA

Philip D. Gingerich

*Department of Geological Sciences and Museum of Paleontology, University of Michigan,
Ann Arbor, Michigan 48109, USA*

Paul L. Koch

Department of Earth Sciences, University of California, Santa Cruz, California 95062, USA

ABSTRACT

A fossil-bearing continental sequence that spans the Paleocene-Eocene boundary (ca. 55 Ma) can now be accurately correlated to expanded deep-sea oceanic sediments at an extremely high resolution (~10 k.y.), thus facilitating detailed investigations into abrupt global climate change and its influence on the evolution of terrestrial organisms. Here we show that the onset of this extremely warm interval is associated with a stepped terrestrial carbon isotope ($\delta^{13}\text{C}$) excursion. This suggests that a pulsed sublimation of submarine gas hydrate accumulations at this time may have caused a rapid venting of significant quantities of light carbon through the ocean/atmosphere interface. Major mammalian turnover occurred near the onset of the ensuing greenhouse event, and this also appears to have occurred in a sequential fashion, although the changes we see in population composition and morphology lag the major features of the global $\delta^{13}\text{C}$ record by some ~10–20 k.y., which could represent the duration required for evolutionary mechanisms to occur due to greenhouse-associated stresses. Additionally, we have evidence that increased soil respiration rates occurred in response to the core episode of global warmth. Paleocene-Eocene boundary carbon cycle perturbations were apparently as remarkable in the atmospheric and terrestrial reservoirs as they were in the oceans, and these changes had a dramatic effect on terrestrial biota.

INTRODUCTION

At the Paleocene-Eocene (P-E) epoch boundary, ocean water $\delta^{13}\text{C}$ became more negative by ~2.5‰ in a stepped manner over <52 k.y. (Norris and Röhl, 1999; Röhl et al., 2000). The ra-

pidity, amplitude, and structure of this major carbon isotope event (CIE) have been explained by the pulsed introduction into the exchangeable carbon reservoir of large volumes of isotopically light methane (CH_4 with $\delta^{13}\text{C} \sim -60\text{‰}$; Kvenvolden, 1988)—a potent greenhouse gas—from subliming gas hydrate

accumulations (Dickens et al., 1995; Bains et al., 1999; Dickens, 2001). As this occurred, the Earth's climate warmed by as much as 5–7 °C via greenhouse mechanisms (e.g., Kennett and Stott, 1991; Eldholm and Thomas, 1993; Rea et al., 1995; Fricke et al., 1998; Sloan and Thomas, 1998; Bains et al., 1999), which may have been a major cause of continental faunal migration corridors opening (Gingerich, 1989; Clyde and Gingerich, 1998; Beard and Dawson, 1999; Peters and Sloan, 2000) and marine and terrestrial taxonomic turnover increases (e.g., Gingerich, 1989; Kelly et al., 1996, 1998; Clyde and Gingerich, 1998).

In response to the rapidly changing environment, oceanic phytoplankton bloomed and an elevated marine carbon pump probably helped the Earth to recover quickly to near pre-event conditions (Bains et al., 2000; Zachos and Dickens, 2000). According to recent models, a similar greenhouse-induced biological feedback system may also have occurred on land (Beerling, 2000). Given the reality of current anthropogenic global warming, and the uncertainties over future ecological change, the terrestrial floral and faunal response to the transient P-E boundary greenhouse world warrants thorough investigation. We have thus conducted, and here present, a high-resolution continental geochemical and paleontological study of this exceptional interval in the Earth's history.

HIGH-RESOLUTION TERRESTRIAL STABLE ISOTOPE AND FOSSIL MAMMAL RECORDS

The $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of ancient soil nodule carbonates can provide valuable information about terrestrial environmental change from the geological record. The $\delta^{13}\text{C}$ of soil nodule carbonate can be influenced by several factors (Cerling, 1984, 1991, 1999; Cerling et al., 1991; Cerling and Quade, 1993). However, since a major component of soil gas (the source of carbon in soil nodule carbonate) is supplied by root respiration and the bacterial decay of litter, it can reflect the $\delta^{13}\text{C}$ of overlying plants if other factors are carefully accounted for (see discussion in Koch et al., 1995). The $\delta^{13}\text{C}$ of plants reflects that of atmospheric CO_2 , which in turn is dominated by gas exchange with the oceans. Koch et al. (1992, 1995) have previously demonstrated that at the P-E boundary, shifts in soil nodule carbonate $\delta^{13}\text{C}$ can indeed be correlated to shifts in the $\delta^{13}\text{C}$ of the surface ocean (with a regular fractionation). Building on this knowledge, we have now constructed an extremely detailed continental $\delta^{13}\text{C}$ record across the P-E boundary, which is of a similar temporal resolution to those that have recently been created from deep-sea carbonates (Bains et al., 1999) and an independent data set also derived from the Bighorn Basin sequence (Bowen et al., 2001). The new high-resolution terrestrial CIE records show virtually identical trends, and are used here for the first time to assess atmospheric and terrestrial carbon reservoir consequences of gas hydrate decomposition, changes in soil respiration/production and terrestrial climate feedbacks, as well

as to further address the timing and nature of mammalian turnover across this interval. The $\delta^{18}\text{O}$ of soil nodule carbonate is used here to show that diagenetic effects due to deep burial do not affect our isotopic record.

We measured the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ composition of 485 carbonate soil nodules (see Table DR1¹) collected from an ~80 m thick stratigraphic section at the southern end of Polecat Bench (Bighorn Basin, Wyoming, at, and in, the vicinity of University of Michigan locality SC-67; Gingerich, 1989). By moving west around the southern tip of Polecat Bench, we were able to map and sample a continuous composite sequence of fine-grained mudstones and well-developed paleosols deposited across the late Paleocene through to the early Eocene, successfully avoiding the Clarkforkian–Wasatchian sandstone unit, which is not laterally continuous here. We collected fossil soil nodules from the narrow spines of steep ridges, digging out ones that were just emerging out of the rock surface as well as those that were deeply buried. The average within-soil standard deviation is 0.8‰ and 0.5‰ for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ respectively, in accordance with typical within-nodule and within-soil isotopic differences reported in other studies of Bighorn Basin paleosol carbonates (Koch et al., 1992, 1995). In soils, carbonate precipitated <30 cm from the soil-atmosphere boundary can have a $\delta^{13}\text{C}$ value that is directly influenced by atmospheric CO_2 , rather than purely by soil gas derived from plants. This mechanism can cause shifts of $\geq 10\text{‰}$ from the base to the top of a soil unit, an effect most pronounced in desert environments (Quade et al., 1989; Cerling and Quade, 1993). However, in the data presented here, no obvious association was found between soil thickness and $\delta^{13}\text{C}$ value, and carbonate nodules collected from <30 cm thick soils do not have unusual $\delta^{13}\text{C}$ values. Nevertheless, as a precaution, we calculate and plot average $\delta^{13}\text{C}$ values for only carbonate nodules collected at ≥ 30 cm below surfaces of sufficiently thick paleosols. These data points follow the same trend as that of the entire data set (Fig. 1). Some soil nodules contained diagenetic sparry calcite. Co-occurring spar and micrite do not differ significantly in terms of $\delta^{13}\text{C}$, but spar $\delta^{18}\text{O}$ values are significantly more negative than those of micrite (mean difference -6.7‰). For our record, sparry calcite was carefully avoided when drilling samples. For isotopic analysis, several hundred micrograms of sample were drilled from micrite in soil nodules and cleaned of possible organic contaminants using 10% H_2O_2 and acetone. Samples were reacted at 90 °C in a common phosphoric acid bath carbonate preparation device interfaced with a mass spectrometer in the Department of Earth Sciences, University of Oxford. The average time between reaction of samples was 30 minutes, which is sufficient to completely react all carbonate phases. Analytical precision better than 0.1‰

¹GSA Data Repository item 2003047, Table DR1, High-resolution stable carbon and oxygen isotope data from the Bighorn Basin, is available on request from Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301-9140, USA, editing@geosociety.org, or at www.geosociety.org/pubs/ft2003.htm.

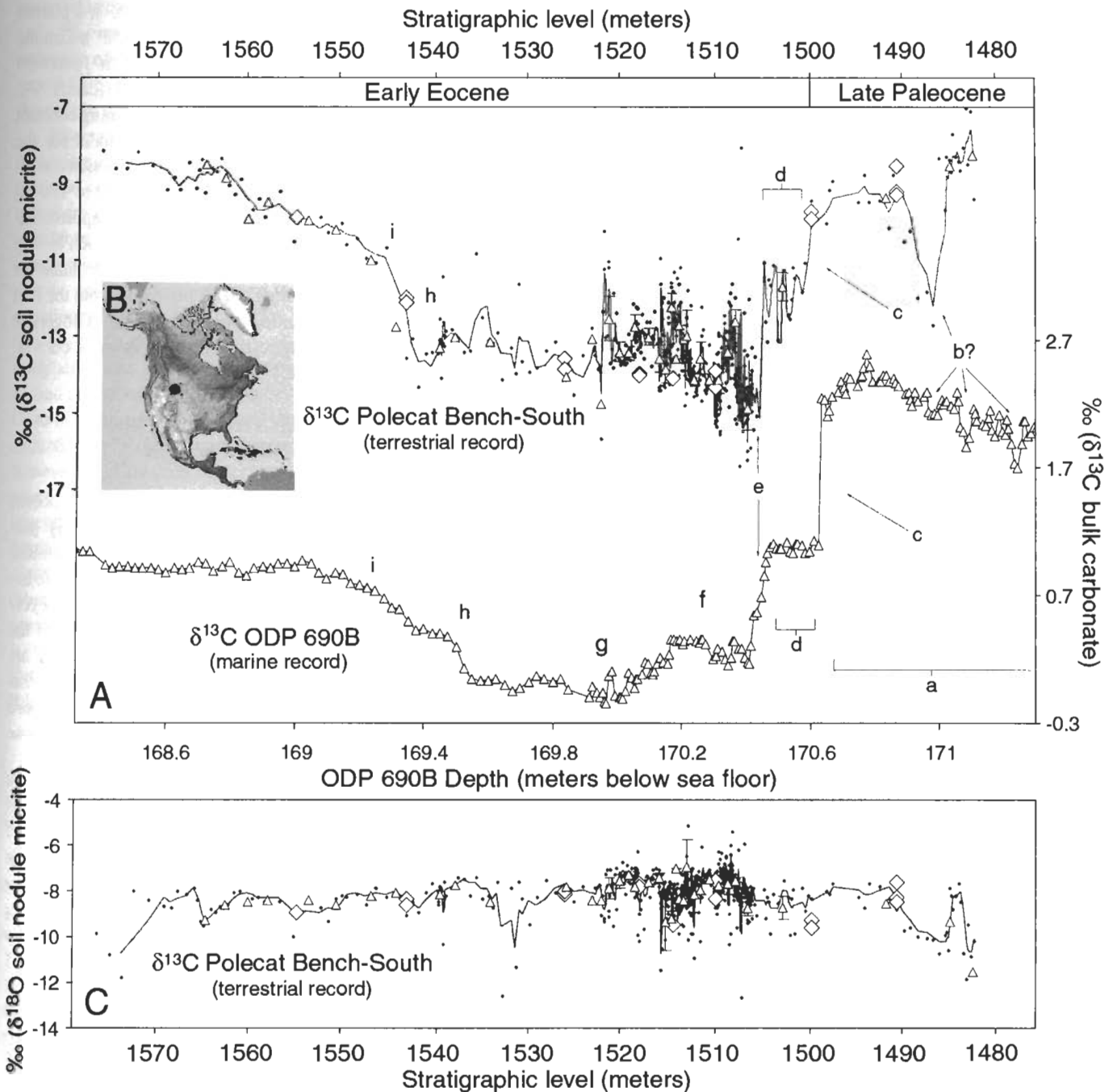


Figure 1. Detailed terrestrial $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ and marine $\delta^{13}\text{C}$ records across the P-E boundary. Terrestrial data are derived from carbonate soil nodules from an expanded section at the southern end of Polecat Bench, northern Wyoming, and marine data are from ODP 690B bulk carbonates (Bains et al., 1999). A: Labels a through i were assigned to the $\delta^{13}\text{C}$ record of ODP 690B in Bains et al. (1999), and here labels c, d, e, h and i have also been used to denote the corresponding $\delta^{13}\text{C}$ stable isotope events found in the terrestrial realm, and are referred to in the text. For Polecat Bench data, stratigraphic level has been plotted as depth in meters above the K-T boundary. The record decreases in age from right to left and includes previously published data from this locality (large open diamonds; Koch et al., 1995). ODP 690B data has been plotted against depth as meters below the seafloor. Open triangles in the Polecat Bench-South record represent averaged data from nodules collected at depths ≥ 30 cm from the surface of ancient paleosols. The previous data of Koch et al. (1995) has been excluded from the trendline (which is a 3 point moving average). B: Map of modern North America showing the approximate location of the Polecat Bench section. C: $\delta^{18}\text{O}$ data from soil nodule micrite from Polecat Bench. Because our data are consistent with the low-resolution trend of Koch et al. (1995) we are confident that our samples have not been affected by diagenesis or reworking.

for both carbon and oxygen isotopes was maintained throughout all analysis. Carbon and oxygen data are reported in δ values: $\delta^{13}\text{C}$ or $\delta^{18}\text{O} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, where R_{sample} and R_{standard} are the ratios of $^{13}\text{C}/^{12}\text{C}$ or $^{18}\text{O}/^{16}\text{O}$ for the sample and the standard. Results were calibrated to Pee Dee belemnite (V-PDB) by reference to in-house Carrara Marble standard and are reported in per mil (‰).

We have also collected, and below interpret, a new highly detailed fossil record from the Polecat Bench outcrop. The P-E boundary is generally thought to coincide with an abrupt change from a mammal fauna dominated by archaic lineages to a fauna dominated by modern orders including the first Primates (Gingerich, 1989). In North America, this faunal change happens at the Clarkforkian–Wasatchian land-mammal age boundary (Rose, 1981; Gingerich, 1989), which occurs near the CIE (Koch et al., 1992, 1995). We find that this faunal transition occurred in a sequential nature, with changes in earliest Wasatchian mammals lagging features of the new high-resolution $\delta^{13}\text{C}$ record.

SIMILARITIES BETWEEN THE TERRESTRIAL AND MARINE CIE

Comparisons between the detailed marine P-E boundary $\delta^{13}\text{C}$ records of Ocean Drilling Program (ODP) Southern Ocean Site 690B and North Atlantic Site 1051B (Bains et al., 1999) and our high-resolution terrestrial $\delta^{13}\text{C}$ record from the Bighorn Basin, Wyoming (Fig. 1) will allow us to investigate the mechanisms of “whole-Earth” climate change at this time. Apparent similarities in the early stages of the boundary excursion include

a marked initial negative drop in $\delta^{13}\text{C}$ (feature “c”), a plateau (feature “d”), followed by a further drop (feature “e”). Coming out of the event, a rapid increase in $\delta^{13}\text{C}$ (feature “h”) precedes an inflection toward a more gradual positive trend (feature “i”). Based on correlation of features “c” and “h”, assuming constant sedimentation rates, and using an orbital age model for the ODP 690B record (Röhl et al., 2000), the $\delta^{13}\text{C}$ excursion and recovery from the Polecat Bench record (from ~ -10 to $+30$ m) spans about four precession cycles, or ~ 84 k.y. This approximation yields a sedimentation rate of ~ 475 m/m.y., which is very comparable to a long-term rate of ~ 470 m/m.y. calculated for ~ 1200 m of sediments spanning the P-E boundary from the Fort Union and Willwood formations of this region (Gingerich, 2000; Wing et al., 2000), suggesting that our isotopic correlation is probably quite precise.

DIFFERENCES BETWEEN THE TERRESTRIAL AND MARINE CIE

The similarities between the terrestrial and marine records indicate that both of these reservoirs were significantly perturbed by the proposed sublimation of gas hydrate accumulations at the P-E boundary; however, intriguing differences do exist that raise questions about various aspects of carbon cycle dynamics. Of particular interest is the larger amplitude of the CIE in the terrestrial record (Fig. 2). Excursions “c” and “e” are similar in both records in terms of their almost instantaneous nature, however, their magnitude in the Polecat Bench record ($\sim -2\text{‰}$ and -3.5‰ , respectively) are much greater than those

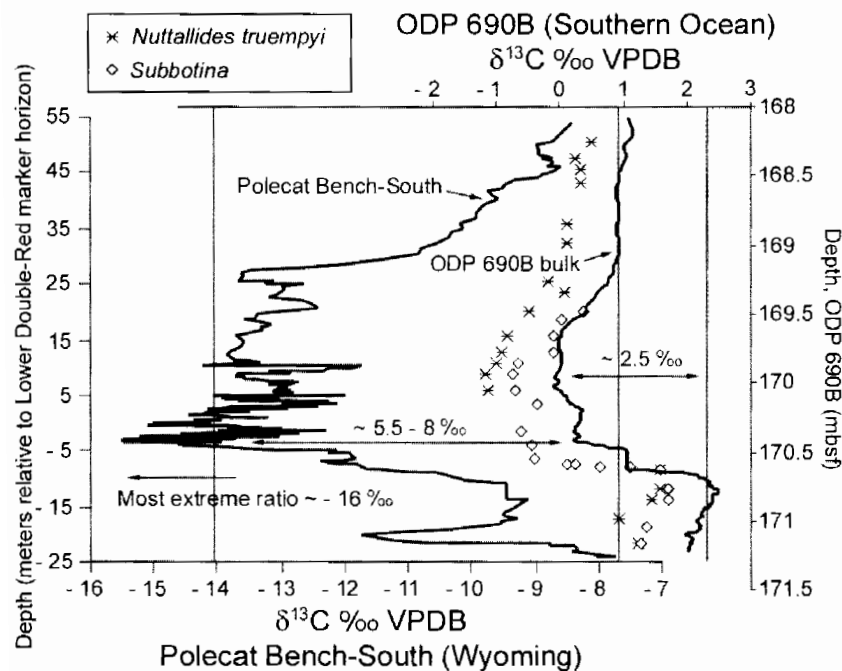


Figure 2. The differing magnitudes of the P-E boundary carbon isotope event (CIE) recorded in terrestrial and marine sediments. Trends have been plotted to illustrate the large magnitude of the CIE recorded from carbonate soil nodules collected from Wyoming ($\sim 5.5\text{‰}$ – 8‰), compared with the CIE recorded in marine bulk carbonate sediments (Bains et al., 1999) and foraminiferal records of benthic dwelling *Nuttallides truempyi* and planktonic *Subbotina patagonica* and *Subbotina varianta* (Kennett and Stott, 1991) from Southern Ocean Site ODP 690B ($\sim 2.5\text{‰}$).

observed in the bulk carbonate record from ODP 690B ($\sim -1.2\%$ and -1% , respectively). Also, the total magnitude of the $\delta^{13}\text{C}$ excursion on land ($\sim 5.5\%$ – 8%) remains larger than the marine record $\delta^{13}\text{C}$ excursion ($\sim 2.5\%$) for tens of thousands of years throughout the core of the CIE (features “d” through “i”).

It is possible that a small fraction of the liberated CH_4 from subliming gas hydrate reservoirs bubbled through the water column and oxidized to CO_2 in the atmosphere. Because the atmosphere contains much less carbon than the oceans, such a transfer of very light carbon to this reservoir would have a great effect on its $\delta^{13}\text{C}$ composition. In fact, according to calculations that we performed, which were based on previously published equations (Dickens et al., 1995; Dickens, 2001), the introduction of ~ 50 Gt and 970 Gt of $\sim -60\%$ $\delta^{13}\text{C}$ carbon into the atmospheric and oceanic reservoirs respectively could have caused the initial isotope event “c.” A second injection of ~ 100 Gt to the atmosphere and ~ 760 Gt to the oceans would explain excursion “e.” Under contemporary oceanographic conditions, however, equilibration of carbon isotopes between the atmosphere and marine bicarbonate occurs rapidly (~ 1 k.y.). The persistently larger magnitude of the $\delta^{13}\text{C}$ excursion on land suggests either that oceanic and atmospheric circulation were dramatically different across the P-E boundary, or that some other mechanism may have been operating to maintain the greater magnitude of the excursion in terrestrial systems.

INCREASED SOIL RESPIRATION RATES AT THE P-E BOUNDARY

We suggest that increased atmospheric CO_2 concentrations and surface temperatures following the initial sublimation of gas hydrates may have led to elevated rates of soil respiration, thus causing the magnified $\delta^{13}\text{C}$ excursion on land (as discussed above). Cerling (1999) has shown that an increase in soil respiration rates, which are often associated with increased primary production, lead to a decrease in the $\delta^{13}\text{C}$ of soil CO_2 and soil carbonates. A conservative estimate (using the method of Cerling, 1999, and assuming that the atmospheric CIE magnitude was $\sim -4.25\%$ larger than the CIE recorded in the oceans—as suggested by our data) suggests at least a doubling of soil respiration rates in the Bighorn Basin following the P-E boundary.

However, there are other variables besides soil respiration rates and the $\delta^{13}\text{C}$ of overlying plants and atmosphere that can significantly influence the $\delta^{13}\text{C}$ of soil carbonates (Cerling, 1984, 1991, 1999; Cerling et al., 1991; Cerling and Quade, 1993). These include (i) differences in carbon isotope fractionation between C3 and C4 plants; (ii) atmospheric $p\text{CO}_2$; (iii) soil porosity; and (iv) plant rooting depth. A shift in the overlying biomass of C4 versus C3 plants can produce large shifts in the $\delta^{13}\text{C}$ of soil carbonates, but C4 plants are not believed to have become abundant until the Neogene (Thomasson et al., 1986; Quade et al., 1989; Quade and Cerling, 1995). Changes in the concentration of CO_2 in the atmosphere also affects the pene-

tration of this gas into soils and the $\delta^{13}\text{C}$ of soil CO_2 (Cerling, 1991). However, atmospheric $p\text{CO}_2$ was probably 1000 ppmv or less during the P-E transition (Koch et al., 1992; Beerling, 2000; Royer et al., 2001), which is too low to have had a major effect on the $\delta^{13}\text{C}$ of soil CO_2 and pedogenic carbonates (Cerling, 1999). One estimate of P-E transition $p\text{CO}_2$ based on boron isotopes does suggest higher levels (Pearson and Palmer, 2000), but an increase in atmospheric $p\text{CO}_2$ would decrease the magnitude of the $\delta^{13}\text{C}$ excursion in soils, which is the opposite of our observations. Although changes in rooting depth and soil porosity have not been thoroughly studied in P-E boundary soils, exploration of a soil carbon isotope model suggests minimal sensitivity to these parameters unless they undergo dramatic changes in value, such as those seen between tropical forest and desert soils (Cerling, 1984, 1991; Cerling et al., 1991; Cerling and Quade, 1993). Given the similarity in depositional environments and sedimentary rates across the boundary, we conclude that such drastic changes in these soil parameters are unlikely, and that the Bighorn Basin record is consistent with an increase in soil respiration rates during the $\delta^{13}\text{C}$ excursion. The exact reasons for such a large increase in soil productivity are not fully understood, but it seems likely that it may have been linked to the increase in Bighorn Basin temperatures of $5\text{--}7^\circ\text{C}$ that has been recorded at the P-E boundary (Fricke et al., 1998) and an increase in atmospheric $p\text{CO}_2$ following CH_4 input and oxidation. However, there is some evidence that soil decomposition rates can remain constant with temperature (Giardina and Ryan, 2000), and so other factors such as changes in precipitation and vegetation patterns may also have been important.

Beerling (2000) used vegetation-biogeochemistry and carbon isotope mass balance models to study the response of global terrestrial ecosystems to different scenarios for increased atmospheric $p\text{CO}_2$ and temperature during the P-E boundary event. He inferred increases in terrestrial carbon storage ranging from 7% to 200% of the pre-excursion carbon in vegetation biomass and soils. In his vegetation-biogeochemistry models, the increase in vegetation biomass was always much greater than that in soils, and it was accomplished primarily by increased plant productivity, rather than by an expansion of plant cover on the land surface. Increased plant productivity, with attendant increases in root respiration and bacterial decay of litter, should be expressed as a decrease in soil carbonate $\delta^{13}\text{C}$, which is what we observed here.

NEGATIVE CLIMATE FEEDBACK INDUCED BY INCREASED SOIL DEVELOPMENT

Of further interest is that amplified respiration should increase soil $p\text{CO}_2$, leading to an increase in the rate of soil development and silicate weathering. More productive soils have higher $p\text{CO}_2$ due to root respiration and bacterial oxidation of organic matter; this should lead to lower soil pH and therefore higher chemical weathering rates (e.g., Berner, 1993). This

effect would be consistent with the marked increase in soil development as observed in the Bighorn Basin at the P-E boundary (Gingerich, 1989). Silicate weathering reactions would have consumed CO₂, serving as a direct negative feedback that decreased global CO₂ levels at this time (Zachos and Dickens, 2000). Increased silicate weathering would also have served as an indirect negative feedback by augmenting the quantity of nutrients supplied to oceanic continental margins (Bains et al., 2000; Zachos and Dickens, 2000), thus supporting a vigorous biological “pump” caused by increased oceanic productivity (Bains et al., 2000). Our new data, along with evidence for a synchronized enlargement of marine biomass (Bains et al., 2000), support the proposition that elevated temperatures and atmospheric CO₂ concentrations induced intricate negative feedback processes that increased carbon storage and subsequent burial in the oceans and on land, thereby withdrawing CO₂ from the atmosphere and cooling the planet within ~84 k.y.

MAMMALIAN RESPONSES TO A SEQUENTIAL PERTURBATION OF THE CARBON CYCLE

The P-E boundary in North America has long been known to coincide with abrupt change from archaic Clarkforkian to more modern Wasatchian mammals (Granger, 1914; Rose, 1981). The general patterns of dwarfing and faunal turnover at this boundary are described by Gingerich (this volume). We sampled 14 fossil localities that span seven successive stratigraphic intervals in the same composite section as our new $\delta^{13}\text{C}$ record (stippled in Figure 3) to assess how this paleontological transition compares to the climate and environmental changes that we have discussed above. The first three intervals yield distinctively Clarkforkian mammals (*Probathyopsis praecursor*, *Apheliscus nitidus*, *Aletodon gunnelli*, and *Haplomylus simpsoni*, in addition to a high proportion of *Copecion brachypternus* and *Ectocion osbornianus*), which, taken together, are characteristic of late Clarkforkian age (Cf-3). The fourth stratigraphic interval is represented by a single locality, SC-404 (although additional localities representing this interval are known nearby; Gingerich, 1989), and yields characteristically Wasatchian endocarps of the dicot *Celtis phenacodorum* and a dentary of *Meniscotherium priscum*, but no later Wasatchian indicators; hence it is probably Wasatchian in age (here referred to as “Wa-0?”) and could represent a transient interval of first arrivals and/or appearances of a new dominant community. The fifth stratigraphic interval, from locality SC-67 and others, yields the classic Wa-0 earliest Wasatchian fauna, with many species found to be dwarfed relative to congeners found earlier or later in the same stratigraphic sequence (Gingerich, 1989; Clyde and Gingerich, 1998). The sixth interval is indeterminately Wa-0 or Wa-1 in age (referred to as “Wa-0 or Wa-1” in Figure 3). Finally, the seventh stratigraphic interval, from locality SC-68 and others, yields a large fauna with typical early Wasatchian (Wa-1) indicators like *Haplomylus speiri-*

anus, *Cantius ralstoni*, and *Diacodexis metsiacus*. Higher strata nearby yield large Wa-2 through Wa-5 faunas (Gingerich, 2000).

Comparison of our new high-resolution $\delta^{13}\text{C}$ record to biotic change across the P-E boundary from the Polecat Bench shows that the initial stepping in the negative $\delta^{13}\text{C}$ excursion (features “c”, “d”, and “e”) coincides with the interval of localities SC-71 and others, and is clearly of archaic Clarkforkian Cf-3 mammal age. The appearance of the new Wa-0? *Celtis-Meniscotherium* association (in locality SC-404) lags behind the onset of the initial $\delta^{13}\text{C}$ excursion (feature “c”) by some 15–20 k.y., while the appearance of the classic (dwarfed) Wa-0 mammals (at locality SC-67 and others), including the first representatives of Artiodactyla, Perissodactyla, and Primates, follows the maximum $\delta^{13}\text{C}$ excursion by some 10 k.y. The definitive appearance of “normal” Wa-1 Wasatchian mammals follows the $\delta^{13}\text{C}$ recovery (features “h” and “i”) by some 10–20 k.y. The sequential nature of these events strongly suggests that continental biota were changing in response to abrupt climate change caused by severe carbon cycle perturbations, and the time-lags offer insight into the duration necessary for such evolutionary mechanisms to occur.

The distinctive dwarfing of the classic Wa-0 fauna (which apparently persisted only through extreme P-E boundary climate conditions) strongly suggests an evolutionary response to the global warming and vegetation changes described above. However, the synchronized and abrupt appearance of major groups like Artiodactyla, Perissodactyla, Primates, and hyaenodontid Creodonta, at the base of Wa-0 time suggests immigration of species from elsewhere. The source area for the new North American Wa-0 mammals may be Africa by way of Europe (Estravís and Russell, 1989), Europe itself (Godinot, 1996), Africa by way of Asia (Gingerich, 1986, 1989), Asia by way of Europe (Hooker and Dashzeveg, this volume), South Asia (Krause and Maas, 1990), or Central Asia (Bowen et al., 2002). Dispersal into North America would have required the opening of high-latitude connections between northern continents (Gingerich, 1989; Clyde and Gingerich, 1998; Beard and Dawson, 1999; Peters and Sloan, 2000). Since this happened just after the time of maximum $\delta^{13}\text{C}$ excursion values, and probably just after the peak of greenhouse induced global warming (Bains et al., 1999), the ~20 k.y. lag before Wa-0 mammals appeared in North America (see also Gingerich, this volume) may represent the time required for progressive colonization of intervening areas. A ~20 k.y. lag for mammalian dispersal between continents is approximately two orders of magnitude less than mammalian dispersal lags in the range of 14 to 0.7 m.y. reviewed by Woodburne and Swisher (1995).

CONCLUSIONS

Our high-resolution terrestrial P-E boundary stable isotope record contains small-scale structures that may correspond to multiple gas hydrate dissociation events recently described from

South Polecat Bench section

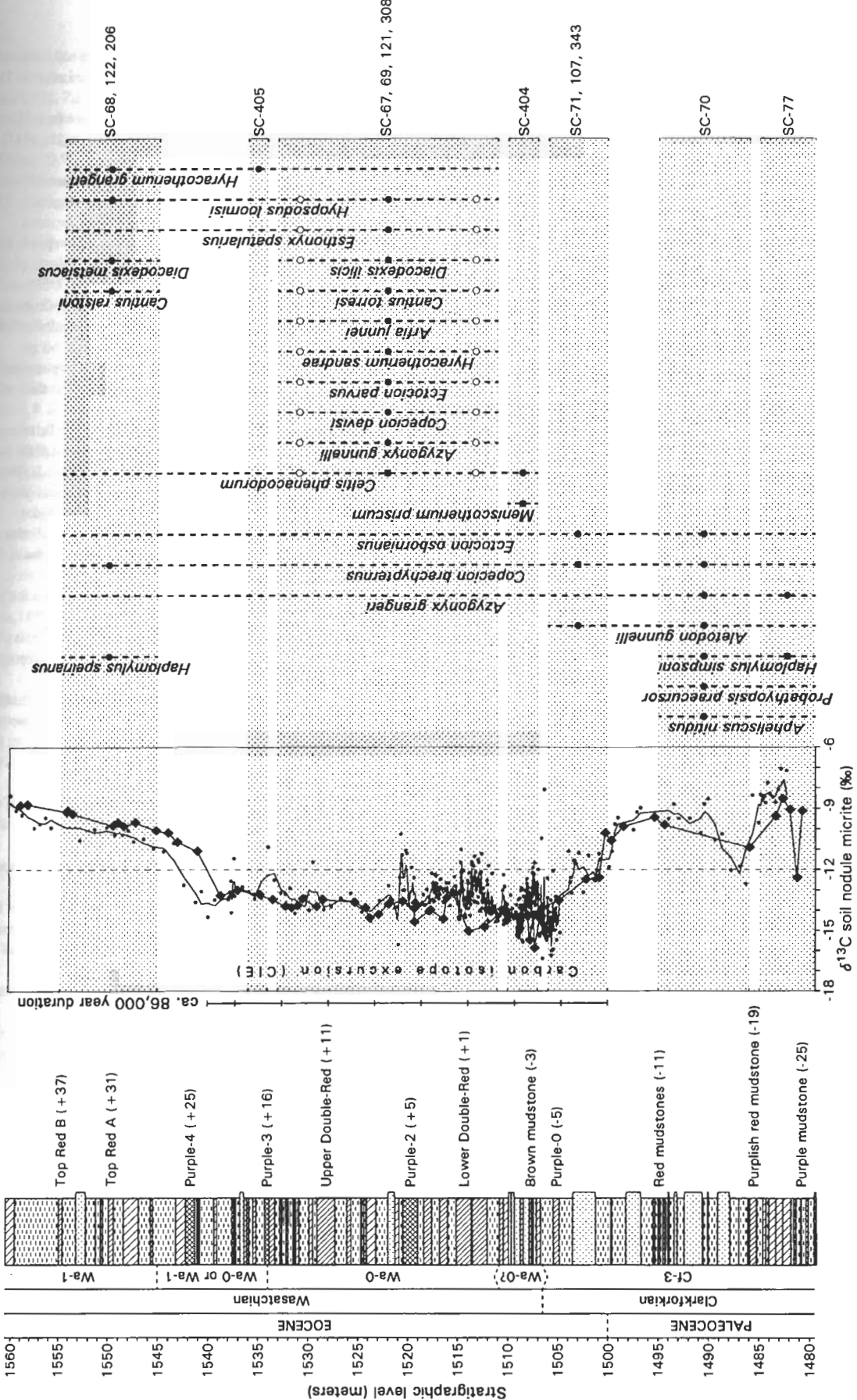


Figure 3. Comparison of high-resolution $\delta^{13}\text{C}$ isotope stratigraphy and biotic change at the southern end of Polecat Bench. Data from Bowen et al. (2001) are also included in this figure for comparative purposes (large filled diamonds). Fourteen mammal-bearing fossil localities are known (SC-77, etc.), representing seven distinct stratigraphic intervals (stippled). These can be grouped into four time-successive associations based on their biota (Cf-3, Wa-0?, Wa-0, and Wa-1 on the ordinate). The interval labeled "Wa-0 or Wa-1" on the ordinate is currently under sampled, and could be either Wa-0 or Wa-1 in age. The 86 k.y. time interval shown was derived from interpolation within chron 24R in the Polecat Bench-Sand Coulee stratigraphic section. This matches extremely closely with the 84 k.y. four-precession-cycle duration (4×21 k.y.) of the core interval of the CIE (Norris and Röhl, 1999; Röhl et al., 2000) as determined by comparison with the marine CIE. Note that the beginning of the CIE is in the late Clarkforkian, overlapping the stratigraphic interval of localities SC-71, etc. The most negative $\delta^{13}\text{C}$ values are in the earliest zone of the Wasatchian (Wa-0?), represented by SC-404 with the first *Celtis* and *Meniscotherium*. The remainder of the CIE spans the interval of the classic dwarfed Wa-0 fauna with *Perissodactyla*, *Artiodactyla*, and *Primates* from localities SC-67, etc. Wasatchian mammals of standard size are known from localities SC-68, etc., in Wa-1 after carbon isotope values returned to normal (here ~9‰).

detailed marine records. Comparisons of these data suggest that the continental sequence is probably continuous, and that the terrestrial carbon cycle was also drastically thrown into disequilibrium for a core interval of ~84 k.y. The persistently larger magnitude of the terrestrial CIE through this 84 k.y. interval suggests that soil respiration rates in this region may have increased due to the changing environment. Amplified silicate weathering would have occurred due to elevated respiration rates, and would have contributed to any negative climate feedbacks that may have been occurring at this time, by withdrawing CO₂ from the atmosphere. New mammal fossil collections, from the same continental P-E boundary sequence from which we have derived our isotope record, show that the transition from Clarkforkian to Wasatchian faunal assemblages occurred in several stages. Given the stepped perturbation of the carbon cycle that we document, and that the mammal stages lag the main features of the $\delta^{13}\text{C}$ excursion by ~10–20 k.y., evolutionary innovations and immigration events at this time were almost certainly forced by environmental changes.

ACKNOWLEDGMENTS

Thanks especially to J. Cartlidge and S. Wyatt for their expert help in the operation of the mass spectrometers in the Stable Isotope Laboratories at the Department of Earth Sciences, University of Oxford. We also thank O. Green, and S. Baker for other technical assistance and E. Linsey for maps of paleomagnetic collecting localities on Polecat Bench. This contribution benefited greatly from the extremely constructive comments of three anonymous reviewers. This work was supported by a Natural Environment Research Council grant to Bains, a Jesus College, Oxford, JRF to Bains, and a NSF-OCE grant to Norris.

REFERENCES CITED

- Bains, S., Corfield, R.M., and Norris, R.D., 1999, Mechanisms of climate warming at the end of the Paleocene: *Science*, v. 285, p. 724–727.
- Bains, S., Norris, R.D., Corfield, R.M., and Faul, K.L., 2000, Termination of global warmth at the Palaeocene/Eocene boundary through productivity feedback: *Nature*, v. 407, p. 171–174.
- Beard, K.C., and Dawson, M.R., 1999, Intercontinental dispersal of Holarctic land mammals near the Paleocene/Eocene boundary: Paleogeographic, paleoclimatic and biostratigraphic implications: *Bulletin de la Société Géologique de France*, v. 170, p. 697–706.
- Beerling, D.J., 2000, Increased terrestrial carbon storage across the Palaeocene–Eocene boundary: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 161, p. 395–405.
- Berner, R.A., 1993, Paleozoic atmospheric CO₂: Importance of solar radiation and plant evolution: *Science*, v. 261, p. 68–70.
- Bowen, G.J., Koch, P.L., Gingerich, P.D., Norris, R.D., Bains, S., and Corfield, R.M., 2001, Refined isotope stratigraphy across the continental Paleocene–Eocene boundary on Polecat Bench in the northern Bighorn Basin, in Gingerich, P.D., ed., *Paleocene–Eocene stratigraphy and biotic change in the Bighorn and Clarks Fork basins, Wyoming*: University of Michigan Papers on Paleontology, v. 33, p. 73–88.
- Bowen, G.J., Clyde, W.C., Koch, P.L., Ting, S., Alroy, J., Tsubamoto, T., Wang, Y., and Wang, Y., 2002, Mammalian dispersal at the Paleocene/Eocene boundary: *Science*, v. 295, p. 2062–2065.
- Cerling, T.E., 1984, The stable isotopic composition of modern soil carbonate and its relationship to climate: *Earth and Planetary Science Letters*, v. 71, p. 229–240.
- Cerling, T.E., 1991, Carbon dioxide in the atmosphere: evidence from Mesozoic and Cenozoic paleosols: *American Journal of Science*, v. 291, p. 377–400.
- Cerling, T.E., 1999, Stable carbon isotopes in palaeosol carbonates: Special Publication of the International Association of Sedimentologists, v. 27, p. 43–60.
- Cerling, T.E., and Quade, J., 1993, Stable carbon and oxygen isotopes in soil carbonates, in Swart, P., et al., eds., *Continental isotopic indicators of climate*: Washington, D.C., American Geophysical Union, p. 217–231.
- Cerling, T.E., Solomon, D.K., Quade, J.A., and Bowman, J.R., 1991, On the isotopic composition of carbon in soil carbon dioxide: *Geochimica et Cosmochimica Acta*, v. 55, p. 3403–3406.
- Clyde, W.C., and Gingerich, P.D., 1998, Mammalian community response to the latest Paleocene thermal maximum: An isotaphonomic study in the northern Bighorn Basin, Wyoming: *Geology*, v. 26, p. 1011–1014.
- Dickens, G.R., 2001, Carbon addition and removal during the Late Palaeocene Thermal Maximum: basic theory with a preliminary treatment of the isotope record at ODP Site 1051, Blake Nose, in Kroon, D., et al., eds., *Western North Atlantic Palaeogene and Cretaceous Palaeoceanography*: Geological Society [London] Special Publication 183, p. 293–306.
- Dickens, G.R., O'Neil, J.R., Rea, D.K., and Owen, R.M., 1995, Dissociation of oceanic methane hydrate as a cause of the carbon isotope excursion at the end of the Paleocene: *Palaeoceanography*, v. 10, p. 965–971.
- Eldholm, O., and Thomas, E., 1993, Environmental impact of volcanic margin formation: *Earth and Planetary Science Letters*, v. 117, p. 319–329.
- Estravís, C., and Russell, D.E., 1989, Découverte d'un nouveau *Diacodexis* (*Artiodactyla*, *Mammalia*) dans l'Eocène inférieur de Silveirinha, Portugal: *Palaeovertebrata*, v. 19, p. 29–44.
- Fricke, H.C., Clyde, W.C., O'Neil, J.R., and Gingerich, P.D., 1998, Evidence for rapid climate change in North America during the latest Paleocene thermal maximum: oxygen isotope compositions of biogenic phosphate from the Bighorn Basin (Wyoming): *Earth and Planetary Science Letters*, v. 160, p. 193–208.
- Giardina, C.P., and Ryan, M.G., 2000, Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature: *Nature*, v. 404, p. 858–861.
- Gingerich, P.D., 1986, Early Eocene *Cantius torresi*—oldest primate of modern aspect from North America: *Nature*, v. 320, p. 319–321.
- Gingerich, P.D., 1989, New earliest Wasatchian mammalian fauna from the Eocene of northwestern Wyoming: Composition and diversity in a rarely sampled high-flood plain assemblage: *University of Michigan Papers on Paleontology*, v. 28, p. 1–97.
- Gingerich, P.D., 2000, Paleocene–Eocene boundary and continental vertebrate faunas of Europe and North America: *GFF*, v. 122, p. 57–59.
- Godinot, M., 1996, Le renouvellement des faunas de mammifères en Europe et en Amérique du Nord autour de la limite Paléocène–Eocène: *Strata*, v. 8, p. 18–20.
- Granger, W., 1914, On the names of lower Eocene faunal horizons of Wyoming and New Mexico: *Bulletin of the American Museum of Natural History*, v. 33, p. 201–207.
- Kelly, D.C., Bralower, T.J., Zachos, J.C., Premoli Silva, I., and Thomas, E., 1996, Rapid diversification of planktonic foraminifera in the tropical Pacific (ODP Site 865) during the late Paleocene thermal maximum: *Geology*, v. 24, p. 423–426.
- Kelly, D.C., Bralower, T.J., and Zachos, J.C., 1998, Evolutionary consequences of the latest Paleocene thermal maximum for tropical planktonic foraminifera: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 141, p. 139–161.
- Kennett, J.P., and Stott, L.D., 1991, Abrupt deep sea warming, palaeoceanographic changes and benthic extinctions at the end of the Palaeocene: *Nature*, v. 353, p. 225–229.
- Koch, P.L., Zachos, J.C., and Gingerich, P.D., 1992, Correlation between

isotope records in marine and continental carbon reservoirs near the Palaeocene/Eocene boundary: *Nature*, v. 358, p. 319–322.

- Koch, P.L., Zachos, J.C., and Dettman, D.L., 1995, Stable isotope stratigraphy and paleoclimatology of the Paleogene Bighorn Basin (Wyoming, USA): *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 115, p. 61–90.
- Krause, D.W., and Maas, M.C., 1990, The biogeographic origins of late Paleocene–early Eocene mammalian immigrants to the western interior of North America, in Bown, T.M., and Rose, K.D., eds., *Dawn of the age of mammals in the northern part of the Rocky Mountain interior, North America: Boulder, Colorado, Geological Society of America Special Paper 243*, p. 71–105.
- Kvenvolden, K.A., 1988, Methane hydrate: a major reservoir of carbon in the shallow geosphere?: *Chemical Geology*, v. 71, p. 41–51.
- Norris, R.D., and Röhl, U., 1999, Carbon cycling and chronology of climate warming during the Palaeocene/Eocene transition: *Nature*, v. 401, p. 775–778.
- Pearson, P.N., and Palmer, M.R., 2000, Atmospheric carbon dioxide concentrations over the past 60 million years: *Nature*, v. 406, p. 695–699.
- Peters, R.B., and Sloan, L.C., 2000, High greenhouse gas concentrations and polar stratospheric clouds: A possible solution to high-latitude migration at the Latest Paleocene Thermal Maximum: *Geology*, v. 28, p. 979–982.
- Quade, J., and Cerling, T.E., 1995, Expansion of C4 grasses in the late Miocene of Northern Pakistan: evidence from stable isotopes in paleosols: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 115, p. 91–116.
- Quade, J., Cerling, T.E., and Bowman, J.R., 1989, Systematic variations in the carbon and oxygen isotopic composition of pedogenic carbonate along elevation transects in the southern Great Basin, United States: *Geological Society of America Bulletin*, v. 101, p. 464–475.
- Rea, D.K., Zachos, J.C., Owen, R.M., and Gingerich, P.D., 1995, Global change at the Paleocene–Eocene boundary: climatic and evolutionary consequences of tectonic events: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 79, p. 117–128.
- Röhl, U., Bralower, T.J., Norris, R.D., and Wefer, G., 2000, New chronology for the late Paleocene thermal maximum and its environmental implications: *Geology*, v. 28, p. 927–930.
- Rose, K.D., 1981, The Clarkforkian land-mammal age and mammalian faunal composition across the Paleocene–Eocene boundary: *University of Michigan Papers on Paleontology*, v. 26, p. 1–197.
- Royer, D.L., Wing, S.L., Beerling, D.J., Jolley, D.W., Koch, P.L., Hickey, L.J., and Berner, R.A., 2001, Paleobotanical evidence for near present-day levels of atmospheric CO₂ during part of the tertiary: *Science*, v. 292, p. 2310–2313.
- Sloan, L.C., and Thomas, E., 1998, Global climate of the late Paleocene epoch: Modeling the circumstances associated with a climatic “event,” in Aubry, M.-P., et al., eds., *Late Paleocene–early Eocene climatic and biotic events in the marine and terrestrial records: New York, Columbia University Press*, p. 138–157.
- Thomasson, J.R., Nelson, M.E., and Zakrzewski, R.J., 1986, A fossil grass (Gramineae: Chloridoideae) from the Miocene with Kranz anatomy: *Science*, v. 233, p. 876–878.
- Wing, S.L., Bao, H., and Koch, P.L., 2000, An early Eocene cool period? Evidence for continental cooling during the warmest part of the Cenozoic, in Huber, B.T., et al., eds., *Warm climates in Earth history: Cambridge, UK, Cambridge University Press*, p. 197–237.
- Woodburne, M.O., and Swisher, C.C., 1995, Land mammal high-resolution geochronology, intercontinental overland dispersals, sea level, climate, and vicariance, in Berggren, W.A., et al., eds., *Geochronology, time scales, and global stratigraphic correlations: A unified framework for an historical geology: SEPM (Society for Sedimentary Geology) Special Publication 54*, p. 335–364.
- Zachos, J.C., and Dickens, G.R., 2000, An assessment of the biogeochemical feedback response to the climatic and chemical perturbations of the LPTM: *GFF*, v. 122, p. 188–189.

MANUSCRIPT ACCEPTED BY THE SOCIETY AUGUST 13, 2002