

## ARTICLES

# Environmental Change in the Great Plains: An Isotopic Record from Fossil Horses

*Benjamin H. Passey, Thure E. Cerling, Michael E. Perkins, Michael R. Voorhies,<sup>1</sup>  
John M. Harris,<sup>2</sup> and Shane T. Tucker<sup>1</sup>*

*Department of Geology and Geophysics, University of Utah, Salt Lake City, Utah 84112, U.S.A.  
(e-mail: bpassey@mines.utah.edu)*

### ABSTRACT

Carbon and oxygen isotope ratios of fossil horse tooth enamel from Nebraska and Texas show evidence for late Neogene environmental changes in the Great Plains. The earliest unambiguous C<sub>4</sub> dietary signal among Texas equids coincides with the age of the classic late Hemphillian-age Coffee Ranch fauna, which we suggest is ~6.6 Ma based on volcanic ash correlations. C<sub>4</sub> vegetation was present in the diets of a small fraction of late Hemphillian equids in Nebraska and was thereafter ordinary in the diets of both Nebraska and Texas equids. There is no unequivocal evidence for abundant C<sub>4</sub> vegetation in the diets of pre-late Hemphillian equids, and we suggest that the ensuing dietary change reflects C<sub>4</sub>-biomass expansion in the latest Miocene. Carbon isotope ratios of post-Hemphillian horses in Nebraska can be divided into two statistically distinct populations on the basis of whether tortoise remains co-occur with horse remains, indicating that the two proxies (carbon isotopes and presence/absence of tortoises) record complementary environmental phenomena. The average  $\delta^{18}\text{O}$  values of late Hemphillian and younger fossil localities in Nebraska trend toward bimodal distribution, but more data are needed to confirm this pattern. Oxygen isotope ratios of Barstovian and Clarendonian horses are significantly enriched in  $^{18}\text{O}$  relative to Hemphillian horses, which in turn are significantly enriched relative to Blancan and Irvingtonian horses. A large portion of this oxygen isotope decrease appears to have taken place during late Hemphillian time. Secular variation in the Nebraska  $\delta^{18}\text{O}$  record correlates with changes in ungulate diversity, the disappearance of crocodylians in Nebraska, and global change in the latest Miocene.

### Introduction

The Earth's surface underwent significant environmental change during the Neogene. Key events during this time include intensified Antarctic glaciation about 15 Ma (Miller et al. 1987; Lear et al. 2000), progressive closure of the Panamanian straits from about 13 to 1.9 Ma (Haug and Tiedemann 1998), repeated desiccation and infilling of the Mediterranean basin between 6 and 5 Ma (Hsu et al. 1973; Krijgsman et al. 1999), global expansion of C<sub>4</sub> biomass beginning ~7–8 Ma (Cerling et al. 1997), permanently increased Antarctic glaciation about 5 Ma (Miller et al. 1987; Lear et al. 2000), and onset of

Northern Hemisphere glaciation in the late Pliocene and early Pleistocene (reviewed in Raymo 1994). In North America, a time of relative faunal stability represented by the Clarendonian chronofauna was followed by a decline of ungulate diversity such that the number of genera at 2 Ma was about one-third that at 15 Ma (Janis et al. 2000). Characteristic mammalian lineages disappeared from the Great Plains, including the oreodonts, chalicotheres, and rhinos, and elements such as proboscideans first appeared (Janis et al. 1998). Large reptiles retreated to more southerly latitudes (Voorhies 1969; Markwick 1994), and faunas came to resemble those of today. The goal of this article is to establish a geochemical record from the Great Plains that will be meaningful in terms of global, regional, and local histories of climate and ecological change.

Manuscript received July 28, 2000; accepted June 28, 2001.

<sup>1</sup> University of Nebraska State Museum, Lincoln, Nebraska 68588, U.S.A.

<sup>2</sup> George C. Page Museum, 5801 Wilshire Boulevard, Los Angeles, California 90036, U.S.A.

Stable carbon and oxygen isotopes in mammalian tooth enamel are resistant to diagenesis (Lee-Thorp and van der Merwe 1987; Quade et al. 1992; Bocherens et al. 1996) and are therefore useful in paleoenvironmental reconstruction. Carbon isotope ratios in mammalian tooth enamel largely reflect the fraction of  $C_4$  vegetation in an animal's diet.  $C_4$  plants are dominantly grasses, and their abundance is positively correlated with temperature, especially with growing season temperature (Teeri and Stowe 1976; Ehleringer et al. 1997). Physiological considerations of the  $C_4$  photosynthetic pathway, along with growth-chamber experiments, show that  $C_4$  vegetation is better adapted to low concentrations of atmospheric carbon dioxide than is  $C_3$  vegetation (Tissue et al. 1995; Ehleringer et al. 1997).  $C_4$  vegetation appears to have existed only at background levels before about 8 Ma (Cerling et al. 1997), but today it is the dominant grass in tropical and warm-temperate grasslands. In the modern Great Plains, the "crossover" latitude where  $C_4$  grasses are equal in abundance to  $C_3$  grasses (in terms of species) is in the vicinity of  $40^\circ\text{N}$  (Teeri and Stowe 1976). Plants using the  $C_3$  photosynthetic pathway account for about 75% of the terrestrial net primary productivity (Ehleringer et al. 1997) and include most trees and shrubs and the cool growing season grasses. Plants using the third major pathway, crassulacean acid metabolism (CAM), include many of the succulent plants and today do not account for a large fraction of terrestrial primary productivity.

In this article, we use equid diet as an indicator of the presence of  $C_4$  biomass in an ecosystem. Modern equids are known to graze, and all late Hemphillian and younger equid genera that have been isotopically analyzed (*Pseudhipparion*, *Neohipparion*, *Nannippus*, *Cormohipparion*, *Astrohippus*, *Dinohippus*, and *Equus*) have representatives with  $C_4$  dietary components (Wang et al. 1994; Latorre et al. 1997; MacFadden et al. 1999b). Koch (1998) and Koch et al. (1998) have shown that within some Pleistocene ecosystems in Texas and Florida, *Bison*, *Mammuthus*, or both consumed a larger fraction of  $C_4$  vegetation than did presumably coexisting *Equus*, and they suggest that *Equus* was a often a mixed feeder, consuming  $C_3$  browse and  $C_4$  grass. This feeding strategy has also been indicated for equid genera from the latest Hemphillian of Florida on the basis of carbon isotope and enamel microwear data (MacFadden et al. 1999b).

The oxygen isotopic composition of mammalian body water determines that of mammalian apatite (including tooth enamel) and is positively correlated with the isotopic composition of meteoric wa-

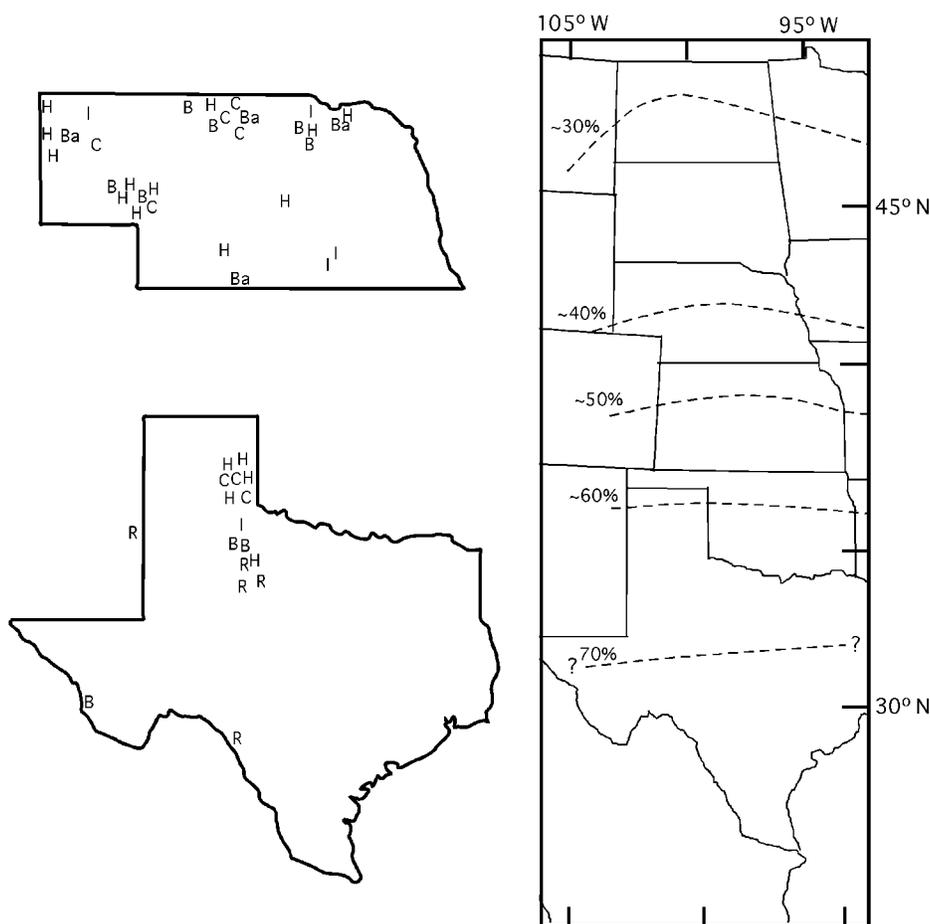
ter (Longinelli 1984; Luz et al. 1984, 1990; Luz and Kolodony 1985; Huertas et al. 1995), which in turn is positively correlated to mean annual temperature, especially within continental settings (Dansgaard 1964). Previous studies have shown that the  $\delta^{18}\text{O}$  of apatite can also relate to humidity (Ayliffe and Chivas 1990; Luz et al. 1990). Animal behavior and physiology further modify the oxygen isotopic signal in apatite (e.g., Bocherens et al. 1996; Kohn 1996).

The outline of this article is as follows: we discuss methods used in this article, and then construct a simple model of the carbon isotopic composition of atmospheric  $\text{CO}_2$  for the past 20 m.yr. based on the carbon isotopic composition of planktonic foraminifera. This model allows us to evaluate the implications of fossil tooth carbon isotopic signatures. Next, we present volcanic ash correlations that constrain the age of the classic late Hemphillian–Coffee Ranch fauna. We present the carbon and oxygen isotope data and conclude with some interpretations of the data.

## Methods

**Sample Selection.** Nebraska fossils were sampled because the region preserves an excellent and abundant record of Neogene horses and because it is presently situated at the transition between southern  $C_4$ -dominated and northern  $C_3$ -dominated grasslands (Teeri and Stowe 1976). If this distribution were true of the past, then small temperature or  $\text{PCO}_2$  fluctuations might be greatly amplified in  $\delta^{13}\text{C}$  values of horses as the  $C_3/C_4$  fringe moved north and south of the region. Furthermore, Nebraska has limited topographic relief and thus should yield isotopic results that reflect regional rather than local climate. The Texas samples are from the High Plains region, which is significantly warmer than present-day Nebraska. These should lend climatic perspective and could allow a check of whether climatic differences between the two regions can be identified. The distribution of sample localities is shown in figure 1, and the stratigraphic relationship of Nebraska localities is shown in figure 2. The relative ages of fossils analyzed in this study were estimated by their placement in North American land mammal ages (NALMAs), using data from Voorhies (1990a) and Woodburne and Swisher (1995).

**Sample Pretreatment.** Two enamel pretreatment methods were used in this study. In one method, organic contamination was removed by soaking enamel powder in 3%  $\text{H}_2\text{O}_2$  for 24 h. Following this, the samples were rinsed several times in distilled



**Figure 1.** Distribution of fossil localities sampled in this study. Dashed lines indicate approximate percentage of  $C_4$  grass species relative to all grass species, using data taken from Teeri and Stowe (1976). North American land mammal age abbreviations are as follows: *R* = Rancholabrean; *I* = Irvingtonian; *B* = Blancan; *H* = Hemphillian; *C* = Clarendonian; *Ba* = Barstovian.

water and then labile carbonates were removed by soaking in 1 M acetic acid for 24 h. This was followed by rinsing and drying. In another method, enamel powder was treated in 3%  $H_2O_2$  for 15 min, followed by rinsing and then treatment in 0.1 M acetic acid for 15 min, followed by rinsing and drying. An excess of treatment solution was used in each step of each method ( $\gg 0.05$  mL solution per mg sample). Table 1 shows that these treatment procedures did not change the isotopic composition of the enamel in a predictable or significant way.

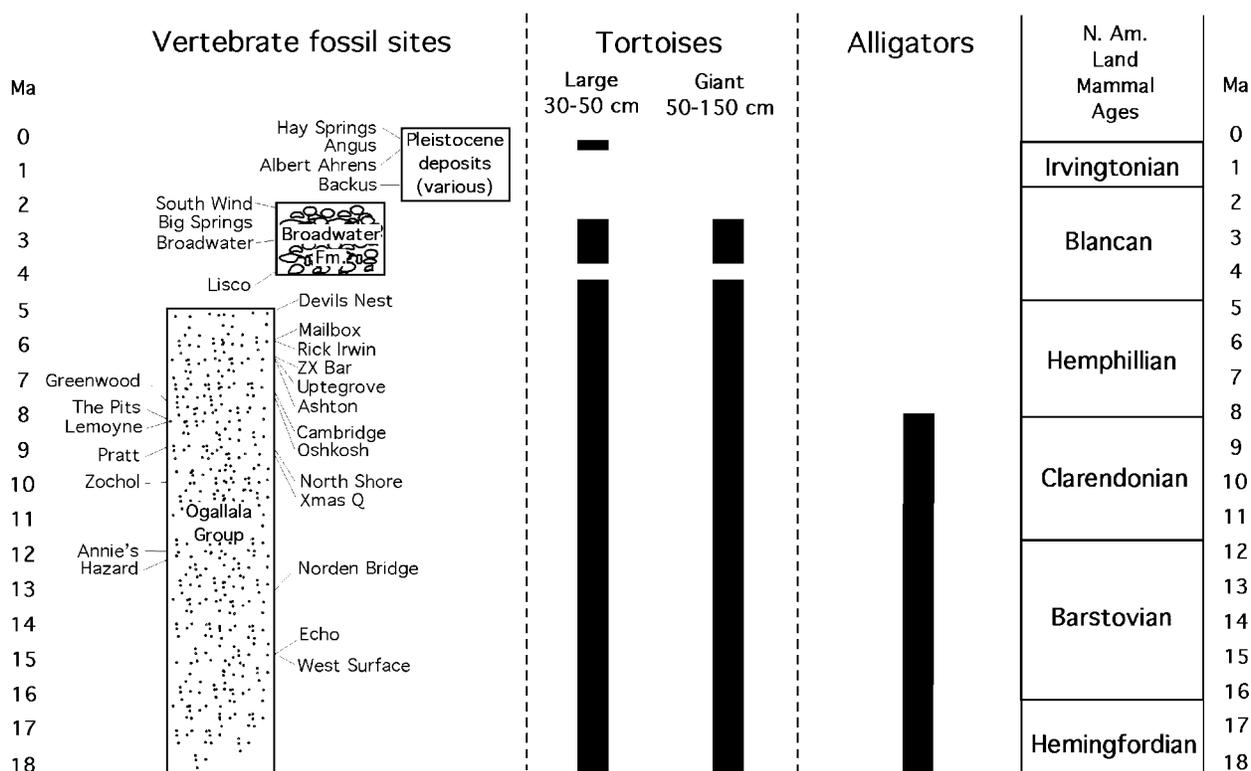
**Sample Analysis.** Purified enamel samples were reacted with 100%  $H_3PO_4$  in vacuo at 25°C for 48 h or under positive helium pressure at 90°C for 7 min. Resulting  $CO_2$  was cryogenically purified and isotopically analyzed using Finnigan MAT 252 and Delta Plus mass spectrometers. Isotope ratios were

normalized using NBS-19 calcite and in-house tooth enamel standards.

Volcanic ash samples were cleaned using distilled water, dilute hydrofluoric acid, and ultrasonic equipment. Glass separates (>99.5% glass) were analyzed with an ARL 8410 x-ray fluorescence spectrometer at the University of Utah using methods described in Perkins et al. (1995).

### Carbon Isotopic Composition of Ancient Atmospheric $CO_2$

Knowledge of the carbon isotopic composition of ancient atmospheric  $CO_2$  ( $\delta^{13}C_{CO_2}$ ) is necessary for understanding the meaning of fossil tooth enamel carbon isotope ratios. We follow previous workers (e.g., Koch et al. 1995; Ekart et al. 1999; Pagani et



**Figure 2.** Generalized diagram showing the sequence of Nebraska fossil localities, time durations of tortoises and alligators in Nebraska, and timing of North American land mammal ages.

al. 1999a, 1999b) and use  $\delta^{13}\text{C}$  of planktonic foraminifera calcite ( $\delta^{13}\text{C}_{\text{PF}}$ ) as a proxy for  $\delta^{13}\text{C}_{\text{CO}_2}$ . The carbon isotopic composition of atmospheric  $\text{CO}_2$  is related to that of planktonic foraminifera calcite tests by the following relation:

$$\delta^{13}\text{C}_{\text{CO}_2} = \{[\delta^{13}\text{C}_{\text{PF}} + 10^3] / [(\varepsilon_{\text{PF-CO}_2}^* / 10^3) + 1]\} - 10^3,$$

where  $\varepsilon_{\text{PF-CO}_2}^*$  is the “apparent isotope enrichment” between atmospheric  $\text{CO}_2$  and planktonic foraminifera. The corresponding isotopic compositions of  $\text{C}_3$ ,  $\text{C}_4$ , and drought-stressed  $\text{C}_3$  plants, and of tooth enamel of mammals eating those plants, are calculated in a similar way (fig. 3).

The primary tasks are to determine representative  $\varepsilon$  values and to assemble an appropriate time series of  $\delta^{13}\text{C}_{\text{PF}}$ . The value  $\varepsilon_{\text{PF-CO}_2}^*$  is variable in modern environments and is influenced by biological disequilibria (often termed “vital effects”; see Spero et al. 1991), the depth at which foraminifera tests are precipitated (because the  $\delta^{13}\text{C}$  of dissolved inorganic carbon decreases with depth), concentration of seawater carbonate (Spero et al. 1997), and other factors. Our approach is to bracket this variability by estimating  $\varepsilon_{\text{PF-CO}_2}^*$  values for several dif-

ferent species living at different localities during different time periods (table 2); for consistency, we restrict our sampling to data from low latitudes ( $30^\circ\text{S}$  to  $30^\circ\text{N}$ ) and to isotopic determinations that were made on the large size fractions ( $>200\ \mu\text{m}$ ) of planktonic foraminifera. The compilation presented in table 2 is by no means exhaustive, but it appears that the calculated average value  $\varepsilon_{\text{PF-CO}_2}^* = 7.9 \pm 1.1\%$  ( $1\sigma$ ) is appropriate in the sense that it covers most of the observed variability.

We use values for  $\varepsilon_{\text{PLANT-CO}_2}^*$  that represent average  $\text{C}_3$  vegetation, drought-stressed  $\text{C}_3$  vegetation, and average  $\text{C}_4$  vegetation ( $\varepsilon_{\text{C}_3\text{-CO}_2}^*$ ,  $\varepsilon_{\text{sC}_3\text{-CO}_2}^*$ , and  $\varepsilon_{\text{C}_4\text{-CO}_2}^*$ , respectively). With modern  $\delta^{13}\text{C}_{\text{CO}_2} = -8.0\%$ , the following values are calculated using bulk  $\delta^{13}\text{C}$  data from Kenyan plants collected between 1997 and 2000 (Cerling and Harris 1999; T. E. Cerling and J. M. Harris, unpub. data):  $\varepsilon_{\text{C}_3\text{-CO}_2}^* = -19.6\%$  (125  $\text{C}_3$  dicots;  $\delta^{13}\text{C} = -27.4 \pm 1.6$ ),  $\varepsilon_{\text{sC}_3\text{-CO}_2}^* = -16.7\%$  (15  $\text{C}_3$  dicots collected at Mpala Reserve during the September through December drought of 1998;  $\delta^{13}\text{C} = -24.6 \pm 1.1$ ), and  $\varepsilon_{\text{C}_4\text{-CO}_2}^* = -4.7\%$  (182  $\text{C}_4$  monocots;  $\delta^{13}\text{C} = -12.7 \pm 1.1$ ). We use the value for the offset be-

**Table 1.** Comparison of Different Enamel Pretreatment Procedures

Sample ID and description	Method	$\delta^{13}\text{C}$ (‰PDB)	$\delta^{18}\text{O}$ (‰PDB)
MG-92-578-TG-RP3-7 (modern horse)	B	-12.7	-10.3
	NT	-12.5	-10.5
K00-TSV-223 (modern African buffalo)	A	1.7	2.6
	B	1.7	2.7
	NT	1.5	2.4
K00-NKU-250 (modern zebra)	A	-1.1	2.4
	B	-2.2	2.4
	NT	-3.3	2.4
K00-NKU-255 (modern African buffalo)	A	-3.3	2.7
	B	-3.3	2.9
	NT	-7.7	2.4
K00-AS-168 (modern hippo)	A	-2.4	-2.4
	B	-1.9	-1.7
	NT	-2.1	-1.9
K00-AB-301 (modern black rhino)	A	-12.8	.4
	B	-12.9	.4
	NT	-12.9	.5
K00-AB-302 (modern black rhino)	B	-12.0	-1.3
	NT	-12.0	-2.4
MG-92-578-TG-RP3-4 (modern horse)	B	-12.8	-10.3
	NT	-12.6	-10.5
LACM HC92411 (fossil bison)	A	-2.4	-2.5
	B	-2.3	-2.6
	NT	-1.8	-2.8
LOTH 87 (fossil hippo)	A	-6.6	-3.9
	B	-6.6	-3.9
	NT	-8.8	-3.6
UNSM 1132-93 (fossil equid)	A	-5.9	-8.0
	B	-5.9	-8.1
	NT	-5.9	-8.0
IMNH 113/5623 (fossil gomphothere)	A	-8.9	-10.7
	B	-8.9	-10.7
	NT	-8.7	-10.7
LOTH 126 (fossil proboscidean)	B	-1.2	-1.2
	NT	-1.2	-1.6

Note. Method A = 24 h in 3% hydrogen peroxide, followed by rinsing and then 24 h in 1 M acetic acid; method B = 15 min in 3% hydrogen peroxide, followed by rinsing and then 15 min in 0.1 M acetic acid; NT = no treatment; PDB = peedeebelemnite isotope standard.

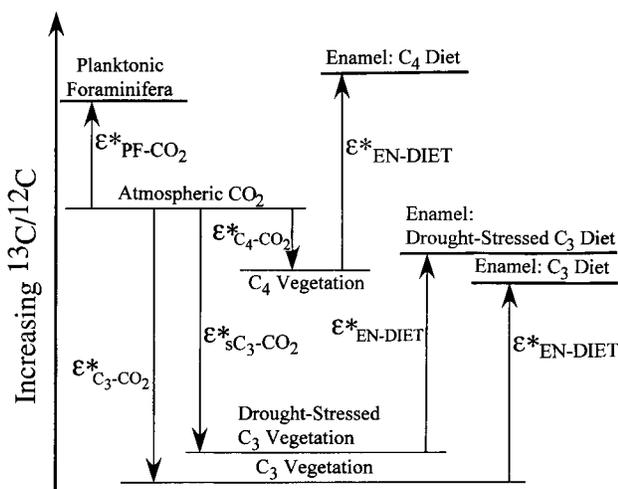
tween diet and enamel carbonate reported by Cerling and Harris (1999;  $\epsilon_{\text{EN-DIET}}^* = 14.1 \pm 0.5$ ).

The time series of  $\delta^{13}\text{C}_{\text{PF}}$  was assembled using data from Whitman and Berger (1993), Pagani et al. (1999a, 1999b), and Veizer et al. (1999). These records were used because they are from low-latitude, low-productivity regions, because measurements were made on  $>200\text{-}\mu\text{m}$ -size fractions, and because they are from relatively continuous and well-dated cores. These data were grouped into 0.5-Ma bins, and the resulting time series allowed calculation of expected carbon isotope ratios of tooth enamel from mammals feeding on  $\text{C}_3$ ,  $\text{C}_4$ , or drought-stressed  $\text{C}_3$  vegetation. The results (fig. 4) show that enamel values characteristic of pure  $\text{C}_3$  and pure  $\text{C}_4$  feeders are in general more positive than are characteristic of the modern environment. Further implications of this model will be discussed below.

### Age of the Coffee Ranch Local Fauna

The fossil assemblage at Coffee Ranch, Texas, is the reference fauna for the late Hemphillian (Tedford et al. 1987). It is capped by and partly incorporated into a silt-sized gray vitric tuff. Fission track (FT) ages of Obradovitch (reported in Izett 1975 and later revised in Naeser et al. 1980) indicate an age of  $4.9 \pm 0.3$  Ma (FT glass) to  $6.8 \pm 0.2$  Ma (FT zircon) for this ash bed. In addition, Boellstorff (1976) reported a FT glass date of  $5.5 \pm 0.4$  Ma for the Coffee Ranch ash bed, which is in accord with the revised ages for the Coffee Ranch ash bed reported by Naeser et al. (1980).

We have compared elemental compositions of glass shards in the Coffee Ranch ash bed to those in an extensive University of Utah database of glass-shard analyses of western United States ash



**Figure 3.** Diagram showing the method used to calculate expected tooth enamel  $\delta^{13}\text{C}$  values, starting with  $\delta^{13}\text{C}$  of planktonic foraminifera. The "isotope enrichment"  $\varepsilon_{A-B}$  between two substances  $A$  and  $B$  is equivalent to the following:  $\varepsilon_{A-B} = [(\delta^{13}\text{C}_A + 10^3)/(\delta^{13}\text{C}_B + 10^3) - 1] \times 10^3$  (Craig 1954). Asterisks indicate that equilibrium fractionation is not assumed. See text for explanation of each  $\varepsilon^*$  quantity.

beds (Perkins et al. 1995, 1998). These comparisons indicate that the Coffee Ranch ash bed has a composition typical of ashes erupting along the Yellowstone hotspot track (Perkins et al. 1995, 1998) and, in particular, is most similar to ash beds from sources in the Heise volcanic field, located along the hotspot track in the eastern Snake River Plain (Pierce and Morgan 1992). Table 3 lists analyses of proximal ash beds associated with the four major ash-flow tuffs in the Heise volcanic field along with analyses of correlative distal ash beds (including the Coffee Ranch ash bed). Examination of these analyses shows both the distinctiveness of ash beds from individual eruptions and the good match between the Coffee Ranch ash bed and the type Blacktail Creek ash bed, which has an  $^{39}\text{Ar}/^{40}\text{Ar}$  date of 6.62 Ma (Morgan et al. 1999).

The significance of ash correlations can be evaluated using the multivariate statistical distance function (Perkins et al. 1995):

$$D^2 = \sum_{k=1}^n \frac{(x_{k1} - \bar{x}_k)^2}{2\sigma_k^2},$$

where  $x_{k1}$  is the concentration of the  $k$ th element of the ash in question,  $\bar{x}_k$  is that of the  $k$ th element of the type ash, and  $\sigma_k$  is the standard deviation of the concentration of the  $k$ th element in a typical

ash. The value  $D^2$  is equivalent to the statistic  $\chi^2$  and so has a  $\chi^2$  distribution. This statistic involves estimation of  $\sigma_k$  of a population of shards; if the estimates of  $\sigma_k$  are similar to the true values, then repeated sampling of a single population will yield values of  $D^2$  that fall within a  $\chi^2$  distribution. If the estimate is not characteristic of the population, the values of  $D^2$  will fall on the extreme left or right tails of the  $\chi^2$  distribution. The values of  $D^2$  reported in table 3 are the statistical distances between each ash and the type Blacktail Creek ash, using  $\sigma_k$  values reported in Perkins et al. (1998; table 3). The 95% confidence interval for 12 elements (11 df) is  $3.8 \leq D^2 \leq 21.9$ ; thus, 95% of multiple 12-element analyses from a single ash bed should yield values of  $D^2$  within this range. Table 3 shows that both the Coffee Ranch ash and "distal" Blacktail Creek ash are within this range, while the others are outside of this range; thus, we argue that the Coffee Ranch ash is statistically indistinguishable from the 6.62-Ma type Blacktail Creek ash.

Magnetopolarities for the Heise volcanic field tuffs are also listed in table 3. Note that all but the tuff of Blacktail Creek record reversed polarities. The tuff of Blacktail Creek and of the Coffee Ranch ash bed are normal (Lindsay et al. 1976). This provides additional support for the correlation of the Coffee Ranch ash bed with the Blacktail Creek ash bed. The dating of Morgan et al. (1999), along with the revised magnetopolarity timescale of Cande and Kent (1995), suggest that the Coffee Ranch ash bed was deposited in chron C3An.2n and not in chron C3An.1n, as estimated by Lindsay et al. (1976), Tedford et al. (1987), and Woodburne and Swisher (1995).

Late Hemphillian fossils from northern New Mexico have been  $^{39}\text{Ar}/^{40}\text{Ar}$  dated between 6.95 and 6.75 Ma (McIntosh and Quade 1995). The youngest dated medial Hemphillian fauna appears to be the Rattlesnake fauna of east-central Oregon. This fauna lies beneath the Rattlesnake Tuff, which recent  $^{40}\text{Ar}/^{39}\text{Ar}$  dating places at  $7.05 \pm 0.01$  Ma (i.e., older than the previously available K-Ar dates of 6.6–6.8 Ma; Streck and Grunder 1995; Tedford et al. 1987, respectively). Thus, the transition to late Hemphillian faunas is reasonably placed in the 7.05–6.62 Ma interval.

## Carbon Isotopes

**Texas High Plains.** The carbon isotopic record from Texas and Nebraska is presented in figure 5, and data are listed in appendix 1, available from

**Table 2.** Apparent Isotope Enrichments of Planktonic Foraminifera Calcite Relative to Atmospheric CO<sub>2</sub>

Time period/location	Species	$\delta^{13}\text{C}_{\text{PF}}$ (‰PDB)	$\delta^{13}\text{C}_{\text{CO}_2}$ (‰PDB)	$\epsilon_{\text{PF-CO}_2}^*$
0–30 ka:				
3°S, 83°W	<i>Neogloboquadrina dutertrei</i>	1.2–1.7 <sup>A</sup>	–6.2 to –6.9 <sup>B,C,D</sup>	~8
Preindustrial:				
19°N, 20°W	<i>Globigerinoides ruber</i>	1.1 <sup>E</sup>	–6.5 <sup>B</sup>	7.6
19°N, 20°W	<i>Globigerina bulloides</i>	–.9 <sup>E</sup>	–6.5 <sup>B</sup>	5.6
19°N, 20°W	<i>Orbulina universa</i>	1.8 <sup>E</sup>	–6.5 <sup>B</sup>	8.4
19°N, 20°W	<i>Globorotalia inflata</i>	.3 <sup>E</sup>	–6.5 <sup>B</sup>	6.8
Modern:				
19°N, 20°W	<i>G. ruber</i>	.5 <sup>E</sup>	–7.8 <sup>F</sup>	8.4
19°N, 20°W	<i>G. bulloides</i>	–1.5 <sup>E</sup>	–7.8 <sup>F</sup>	6.3
19°N, 20°W	<i>O. universa</i>	1.6 <sup>E</sup>	–7.8 <sup>F</sup>	9.4
19°N, 20°W	<i>G. inflata</i>	.1 <sup>E</sup>	–7.8 <sup>F</sup>	7.9
30°S–15°N, 70°–95°W	<i>G. ruber</i>	1.0 <sup>G</sup>	–7.5 <sup>H</sup>	8.6
30°S–15°N, 70°–95°W	<i>Globigerinoides conglobatus</i>	1.1 <sup>G</sup>	–7.5 <sup>H</sup>	8.7
30°S–15°N, 70°–95°W	<i>Globigerinoides sacculifer</i>	1.4 <sup>G</sup>	–7.5 <sup>H</sup>	9.0
				7.9 ± 1.1 <sup>a</sup>

Sources. A, Shackleton et al. 1983; B, Friedli et al. 1986; C, Jesse Smith et al. 1999; D, Indermühle et al. 1999; E, Beveridge and Shackleton 1994; F, Quay et al. 1992; G, Duplessy et al. 1981; H, Keeling et al. 1989.

Note. PDB = peedeebelemnite isotope standard.

<sup>a</sup> Value given as 1 $\sigma$ .

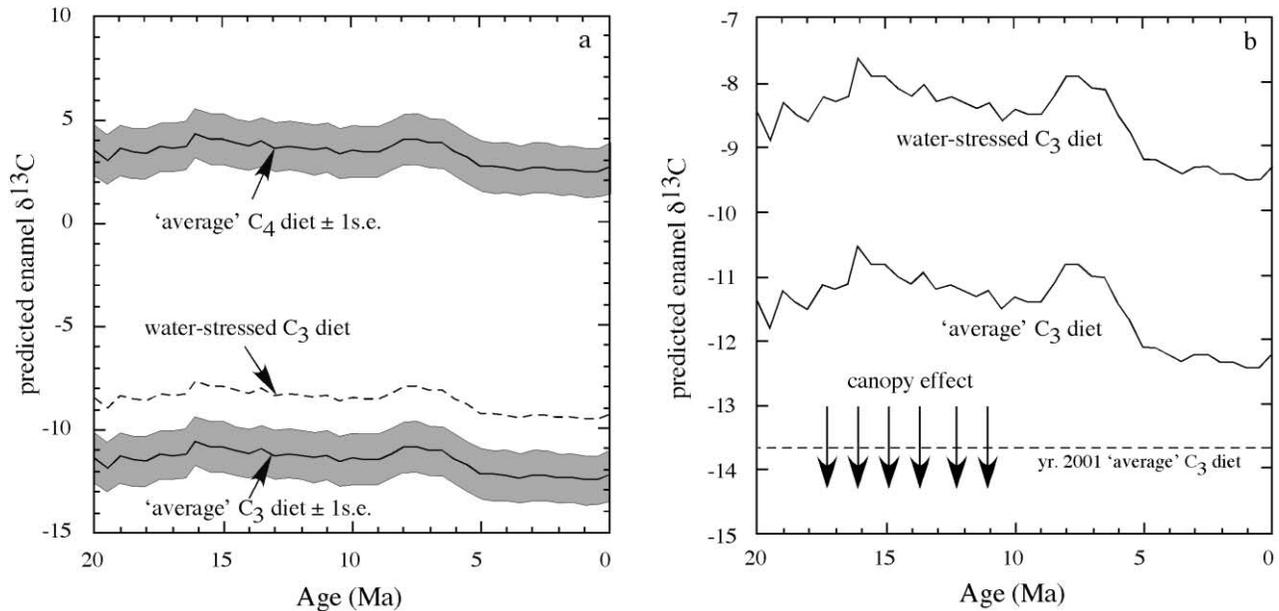
*The Journal of Geology's* Data Depository upon request. Clarendonian horses from the Texas high plains have  $\delta^{13}\text{C}$  values ranging between –11.5‰ and –9.1‰, suggesting predominantly C<sub>3</sub> diets but allowing for a small component of C<sub>4</sub>, drought-stressed C<sub>3</sub>, or CAM vegetation (see "Discussion"). Two early Hemphillian equids from Box T Quarry have values of –10.7‰ and –8.3‰, and an individual from Janes-Prentice Gravel Pit has a value of –9.3‰, again suggesting a C<sub>3</sub>-based diet. Carbon isotope ratios suggest C<sub>4</sub> vegetation in the diets of several late Hemphillian individuals. Wang et al. (1994) and Cerling et al. (1998) showed that C<sub>4</sub> vegetation was consumed by some Coffee Ranch equids. We have examined material from two additional late Hemphillian sites (Bailey Farm and Cleo Hibbard Ranch) and have found C<sub>4</sub> signatures at both. In all, seven of 17 late Hemphillian equids from the Texas high plains have  $\delta^{13}\text{C}$  values greater than the modeled –7‰ upper limit for drought-stressed C<sub>3</sub> vegetation during the late Hemphillian, suggesting that C<sub>4</sub> vegetation was a widely available food resource during some parts of late Hemphillian time. As a note of interest, the results from Coffee Ranch are consistent with the findings of MacFadden et al. (1999b) that *Neohippus eurystyle* consumed a relatively larger fraction of C<sub>4</sub> vegetation than did *Dinohippus* and *Astrohippus* (although MacFadden et al. [1999b] studied *Dinohippus mexicanus* and *Astrohippus stockii*, whereas the data from Coffee Ranch are from *Dinohippus interpolatus* and *Astrohippus ansae*).

All individuals from the Blancan, Irvingtonian, and RanchoLabrean NALMAs have  $\delta^{13}\text{C}$  values that

are greater than the modeled upper limit for drought-stressed C<sub>3</sub> vegetation, indicating that C<sub>4</sub> vegetation was a widely utilized food resource following late Hemphillian time. None of these individuals indicate "pure" C<sub>4</sub> or "pure" C<sub>3</sub> diets, indicating that ecosystems contained a mix of C<sub>3</sub> and C<sub>4</sub> grasses or that horses consumed a significant amount of browse during those times.

**Nebraska.** The pre-late Hemphillian carbon isotope record from Nebraska (fig. 5) suggests C<sub>3</sub>-based diets, but as in Texas, many of the  $\delta^{13}\text{C}$  values are significantly greater than the expected values for "average" C<sub>3</sub> diets. The exceptions to this pattern are two *Cormohipparion occidentale* individuals from the late Clarendonian Pratt Slide locality, whose values of –12.4‰ and –12.6‰ are the most depleted numbers in this study. Early and medial Hemphillian equids also had C<sub>3</sub>-based diets.

C<sub>4</sub> signals appear in two out of 20 late Hemphillian samples analyzed, as opposed to seven out of 17 in Texas (when the drought-stressed C<sub>3</sub> upper limit of –7‰ is used). Of these, only one specimen (UNSM 122035, from the recently excavated Rick Irwin locality) shows a large C<sub>4</sub> component in its diet. Interestingly, this individual is *Dinohippus*, the taxon that MacFadden et al. (1999b) found to have a large C<sub>3</sub>-browse dietary component relative to other equid genera. As in Texas, C<sub>4</sub> dietary components are greater in Blancan time than in late Hemphillian time, suggesting that the time of marked C<sub>4</sub> expansion postdated the deposition of most of the late Hemphillian localities. The two samples from our latest Hemphillian locality (~5 Ma; Devil's Nest Airstrip) yielded C<sub>4</sub> signals.



**Figure 4.** *a*, Modeled time series for expected ungulate tooth enamel  $\delta^{13}\text{C}$  values associated with  $\text{C}_3$ , drought-stressed  $\text{C}_3$ , and  $\text{C}_4$  plant diets over the past 20 m.yr. *b*, Detail of predicted tooth enamel  $\delta^{13}\text{C}$  values for ungulates with  $\text{C}_3$  diets. Arrows indicate that ungulates feeding on  $\text{C}_3$  vegetation in closed canopy environments may have  $\delta^{13}\text{C}$  values that are significantly depleted in  $^{13}\text{C}$  relative to “average”  $\text{C}_3$  feeders because of the “canopy effect,” which results from recycling of  $^{13}\text{C}$ -depleted respired  $\text{CO}_2$ . Also note that the modern tooth enamel  $\delta^{13}\text{C}$  values associated with average  $\text{C}_3$  diets are significantly more negative than those expected over the past 20 m.yr.

Fossils from Blancan and Irvingtonian localities record variable amounts of  $\text{C}_4$  vegetation in diet. The Hall Gravel Pit, Broadwater, Quinn Gravel Pit, Big Springs, and Angus Quarry localities all record substantial  $\text{C}_4$  vegetation in equid diets, while the South Wind Prospect, Albert Ahrens, and Hay Springs (MacFadden et al. 1999a) localities suggest more  $\text{C}_3$ -based diets.

### Oxygen Isotope Record

Oxygen isotope data are listed in appendix 1 and are presented in figure 6. There are several fossil localities in Nebraska from which we analyzed multiple individuals, allowing calculation of locality  $\delta^{18}\text{O}$  averages for that region. We suggest that NALMA and locality averages are more meaningful than individual data for understanding regional paleoenvironmental trends because they attenuate  $\delta^{18}\text{O}$  variability caused by local, behavioral, and seasonal processes. Sampling in Texas was not adequate to produce a good time series of locality  $\delta^{18}\text{O}$  averages, so we focus our discussion on the Nebraska data.

The pattern that is most clear in the record is that  $\delta^{18}\text{O}$  values decrease progressively between

Barstovian and Blancan time. The former has an average  $\delta^{18}\text{O}$  value of  $-3.2\text{‰}$ , and the latter averages  $-6.6\text{‰}$  (table 4). The  $\delta^{18}\text{O}$  differences between the Clarendonian and Hemphillian, and between the Hemphillian and Blancan, are  $-1.5\text{‰}$  and  $-1.0\text{‰}$ , respectively. Both differences are significantly different at the 95% level (*t*-test; table 5). The majority of the  $\delta^{18}\text{O}$  change that occurred between the Clarendonian and Hemphillian is accommodated in the late and latest Hemphillian interval, which have an average  $\delta^{18}\text{O}$  value of  $-6.3\text{‰}$ , as opposed to  $-4.7\text{‰}$  for the pooled medial Hemphillian, early Hemphillian, and Clarendonian intervals (significantly different at the 95% level; table 5). There is no significant difference between Clarendonian and early through medial Hemphillian horses nor between late through latest Hemphillian and Blancan horses (table 5). Thus, the late Hemphillian appears to be the time of most marked  $\delta^{18}\text{O}$  change.

Another noteworthy feature of the oxygen data is an apparent bimodal pattern in postmedial Hemphillian locality  $\delta^{18}\text{O}$  averages (fig. 7). The statistical significance of the bimodality is uncertain, and more sampling is needed to confirm this result. We note that the bimodal pattern remains after rejec-

**Table 3.** Age, Magnetopolarity, and Glass Shard Composition of Ash Beds from Heise Volcanic Field Sources

Ash bed	Age (Ma)	Polarity chron	Sample	Fe <sub>2</sub> O <sub>3</sub> (wt%)	CaO (wt%)	Ba (ppm)	Mn (ppm)	Nb (ppm)	Rb (ppm)	Sr (ppm)	Ti (ppm)	Zn (ppm)	Zr (ppm)	Th (ppm)	Ce (ppm)	D <sup>2</sup>
Type Kilgore	4.45, <sup>a</sup> 4.4 <sup>b</sup>	C <sub>3</sub> n.1r	rir93-02	1.39	.48	790	244	48	156	21	1002	43	273	23	121	330
Distal Kilgore	...	...	oqm92-14	1.43	.45	692	227	49	156	16	1029	41	273	24	147	295
Connant Creek	5.51 <sup>a</sup>	C <sub>3</sub> n.4r	btr92-218	1.08	.46	472	209	56	162	15	689	68	182	22	151	307
Wolverine Creek	...	...	btr92-213	1.20	.45	474	212	57	164	16	694	66	180	24	146	303
Distal Wolverine Creek	...	...	acb88-08	1.19	.44	464	205	57	164	16	690	68	174	24	145	314
Walcott	6.27, <sup>a</sup> 6.32 <sup>b</sup>	C <sub>3</sub> An.1r	wal93-01	1.05	.38	812	224	43	166	22	1085	41	212	28	118	207
Distal Walcott	...	...	mor94-713	1.06	.41	792	239	42	163	27	1080	48	203	27	139	180
Type Blacktail Creek	6.62, <sup>a</sup> 6.6 <sup>b</sup>	C <sub>3</sub> An.2n	btr92-221	1.17	.42	470	236	37	187	23	1003	43	200	28	140	0
Distal Blacktail Creek	...	...	hp93-466a	1.12	.43	462	243	37	186	23	1035	33	192	31	113	9.4
Coffee Ranch	6.8, <sup>c</sup> 5.5 <sup>d</sup>	Normal	41261-46	1.16	.41	450	237	36	194	22	1025	38	203	28	125	4.2

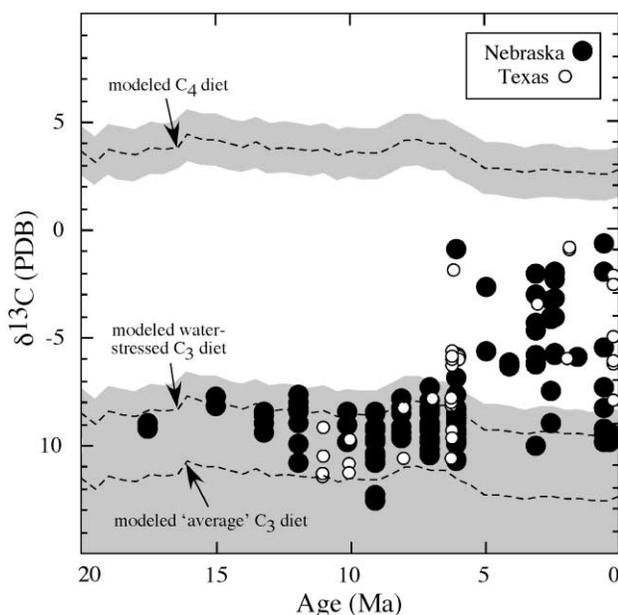
Note. Chron assignment based on polarity determinations of Pierce and Morgan (1992) and magnetopolarity timescale of Cande and Kent (1995). Statistical distance relative to type Blacktail Creek (see text). Analyses by x-ray fluorescence spectrometry using methods described in Perkins et al. (1995).

<sup>a</sup> <sup>40</sup>Ar/<sup>39</sup>Ar laser fusion dates (Morgan et al. 1999).

<sup>b</sup> Average of K-Ar dates in Pierce and Morgan (1992).

<sup>c</sup> Fission-track zircon dates (Naeser et al. 1980).

<sup>d</sup> Fission-track glass date (Naeser et al. 1980).



**Figure 5.** Carbon isotopic record for Nebraska and Texas High Plains equids. The “modeled diet” time series are explained in the text and in figures 2 and 3. Plot includes data from MacFadden et al. (1999a).

tion of localities with less than three samples or standard deviations  $>2\%$  (white squares in fig. 7).

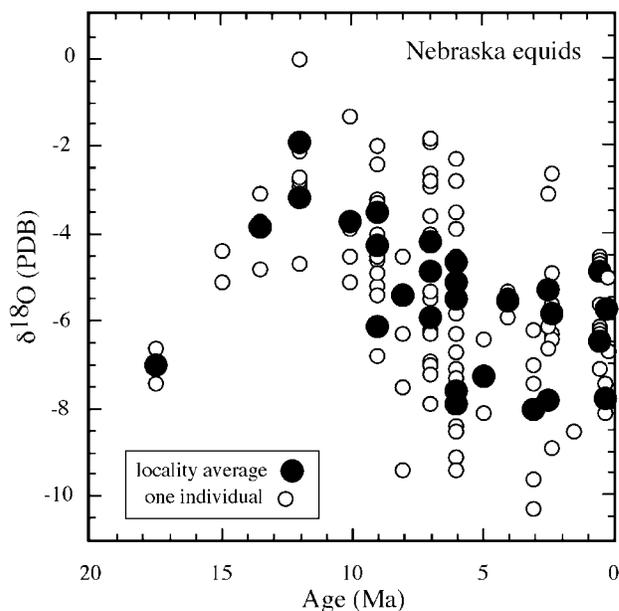
We have not observed sampling patterns relating to taxonomy, geography, or age that could give rise to bimodal locality  $\delta^{18}\text{O}$  averages. Seasonal oscillations in meteoric water  $\delta^{18}\text{O}$  result in intratooth  $\delta^{18}\text{O}$  differences (Fricke et al. 1998a). Generation of a bimodal  $\delta^{18}\text{O}$  artifact resulting from such seasonality would require that, at each locality, we fortuitously sample tooth enamel that formed only during the summer or only during the winter. This possibility is exceedingly unlikely given the large number of localities and specimens that we sampled.

Oxygen isotope ratios of Texas teeth are several per mil more positive than those from Nebraska. In particular, late Hemphillian equids from Texas average  $-0.2\%$ , while late Hemphillian equids from Nebraska average  $-6.3\%$ . Sampling density in Texas is not adequate to deduce long-term trends, except that the most negative values are found in Pleistocene time (data from MacFadden et al. 1999a) and that the most positive values are found in late Hemphillian time. A bimodal distribution similar to the Nebraska data cannot be resolved at this stage, and further sampling is needed before any definitive conclusions are made from the data.

## Discussion

**Carbon Isotopes:  $^{13}\text{C}$ -Enriched Pre-Late Hemphillian Equids.** The majority of pre-late Hemphillian  $\delta^{13}\text{C}$  values lie to the positive side of the modeled average  $\text{C}_3$ -diet time series. We suggest that this relates to one (or a combination) of four factors:

1. The modeled  $\text{C}_3$ -diet time series is flawed in some aspect. If we assume for the moment that the pre-late Hemphillian carbon isotope record reflects pure  $\text{C}_3$  diets, then the modeled  $\text{C}_3$ -diet time series is too negative by about  $1.5\%$ . This could result from too large of values for  $\epsilon_{\text{PF-CO}_2}^*$  or  $\epsilon_{\text{C}_3\text{-CO}_2}^*$  or too small a value for  $\epsilon_{\text{EN-DIET}}^*$ . The value we use for  $\epsilon_{\text{C}_3}$  is similar to that which can be derived from published  $\delta^{13}\text{C}$  data (e.g., Bender 1971; Deines 1980) and is calculated using  $\delta^{13}\text{C}$  data from  $\text{C}_3$  dicots. The possibility exists that typical  $\epsilon_{\text{C}_3\text{-CO}_2}^*$  values of the middle and late Miocene differed from modern values or that  $\epsilon_{\text{C}_3\text{-CO}_2}^*$  values for  $\text{C}_3$  monocot ecosystems differ from those of  $\text{C}_3$  dicot ecosystems. If the former is true, then we expect that the carbon isotope values of Miocene browsers will also plot above the modeled time series (unless they consumed  $^{13}\text{C}$ -depleted vegetation resulting from the “canopy effect”). Data from Argentina, Florida, Turkey, and Europe (Quade et al. 1995; MacFadden and Cerling 1996; MacFadden et al. 1996; Cerling



**Figure 6.** Oxygen isotopic record for Nebraska equids. Locality averages are reported for localities with two or more individuals. Plot includes data from MacFadden et al. (1999a).

**Table 4.** Summary Statistics for Nebraska Carbon and Oxygen Isotope Data

NALMA	<i>n</i>	$\bar{x}$ (‰)	$\sigma^2$ (‰)	Maximum (‰)	Minimum (‰)
$\delta^{13}\text{C}$ :					
Barstovian	14	-8.8	.8	-7.7	-10.9
Clarendonian	18	-9.8	1.4	-8.5	-12.6
Hemphillian	50	-8.6	3.0	-1.0	-10.8
Blancan	23	-5.0	4.7	-2.0	-10.1
Irvingtonian	11	-7.1	10.5	-7	-9.9
$\delta^{18}\text{O}$ :					
Barstovian	14	-3.2	1.9	.0	-5.1
Clarendonian	18	-4.1	1.8	-1.3	-6.8
Hemphillian	50	-5.6	4.3	-1.9	-9.4
Blancan	23	-6.6	3.3	-2.6	-10.3
Irvingtonian	11	-6.3	1.9	-4.5	-8.5

et al. 1997) suggest that this is probably not the case because a large amount of these data plot around our modeled value for average  $\text{C}_3$  vegetation. If the latter is true, then expected grazers should be enriched in  $^{13}\text{C}$  relative to browsers, but in this case, it would be difficult to rule out a  $\text{C}_4$  dietary component for the grazers.

Our value for  $\epsilon_{\text{EN-DIET}}^*$  was taken from Cerling and Harris (1999) and was calculated using a database of  $\delta^{13}\text{C}$  values for enamel and diet for numerous ungulate taxa in different parts of the world. The estimates for equids were based on four Hogle Zoo (Salt Lake City) zebra ( $\epsilon_{\text{EN-DIET}}^* = 14.4\%$ ) and six horses from Mongolia ( $\epsilon_{\text{EN-DIET}}^* = 13.4\%$ ). While more calibration data are still needed, it seems unlikely that  $\epsilon_{\text{EN-DIET}}^*$  values will approach the  $\sim 16\%$  that is necessary to account for the discrepancy between the modeled time series and the Great Plains carbon isotope data.

Our estimate of  $\epsilon_{\text{PF-CO}_2}^*$  was calculated using data from different times and different parts of the world and thus should represent an average value applicable to long time scales. Nevertheless, we observe that our estimate for preindustrial time (7.1‰) dif-

fers from that of modern time (8.3‰) and that there is a significant amount of interspecies variability within single time periods and localities (table 2). It is therefore possible that the diet time series is affected by artifacts associated with our 7.9‰ estimate for  $\epsilon_{\text{PF-CO}_2}^*$ .

2. Great Plains equids regularly consumed  $\text{C}_4$  or CAM vegetation before the late Hemphillian.

3. Drought-stressed  $\text{C}_3$  vegetation was the predominantly available food resource during the time period in question.

4. Carbon isotope ratios of Great Plains tooth enamel are slightly changed by diagenetic processes.

These hypotheses might be tested by measuring isotope ratios of Miocene-presumed browsers from the Great Plains, given that a pure browsing niche existed in the Miocene Great Plains. The second hypothesis would be supported if presumed browsers have  $\delta^{13}\text{C}$  values that are more negative than those of equids, and the fourth hypothesis might be supported if they have similar  $\delta^{13}\text{C}$  values. It might be difficult to distinguish between hypotheses 3 and 4 on the basis of carbon isotopes alone. So far, there is no published carbon isotope data for Miocene Great Plains browsers.

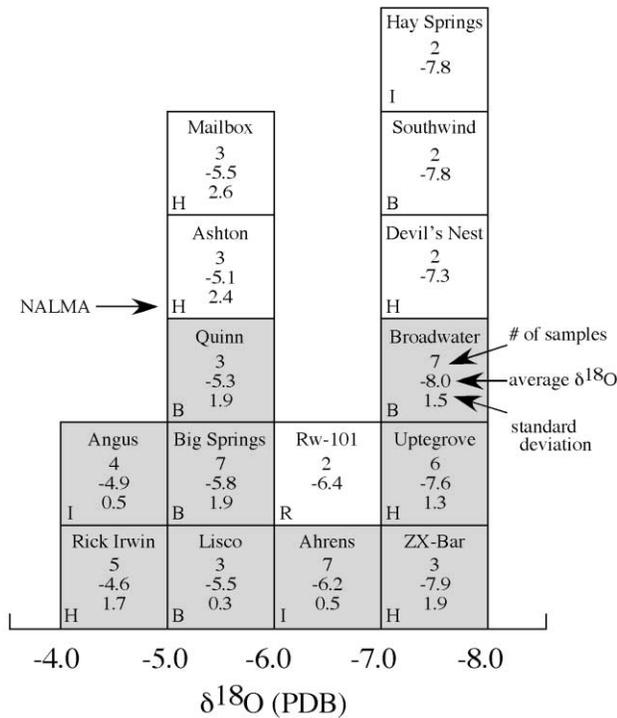
**Carbon Isotopes: Late Hemphillian Transition to  $\text{C}_4$  Feeding.** The change in equid diet beginning in the late Hemphillian may relate to one or both of the following endmember scenarios:

1.  $\text{C}_4$  vegetation was present in significant quantities before the late Hemphillian but was not consumed by equids because of the ready availability of other food resources, including  $\text{C}_3$  browse and  $\text{C}_3$  grass. In this scenario, a significant vegetation change must have occurred beginning in the late Hemphillian such that  $\text{C}_3$  resources decreased in abundance. If the relative proportion of  $\text{C}_4$  vegetation was unchanged, then overall ecosystem productivity likely decreased significantly, as most ter-

**Table 5.** *t*-Test Results for Significant Oxygen Isotope Differences between North American Land Mammal Ages

NALMA vs.	Mean difference (‰)	df	<i>t</i>	<i>P</i>	Significant difference at 95%?
BAR vs. CLR	-.9	30	1.81	.081	No
CLR vs. HPH	-1.5	66	2.91	.005	Yes
HPH vs. BLA	-1.0	71	2.04	.045	Yes
BLA vs. IRV	.4	32	.57	.580	No
CLR + eHPH + mHPH vs. lHPH	-1.6	66	3.36	.001	Yes
CLR vs. eHPH + mHPH	-1.0	44	1.90	.063	No
eHPH + mHPH vs. lHPH	-1.2	48	2.17	.034	Yes
lHPH vs. BLA	-.3	43	.57	.571	No
Post-Miocene: tortoises vs. no tortoises (carbon isotopes)	3.8	32	5.3	.001	Yes

Note. NALMA abbreviations are explained in appendix 1, available from *The Journal of Geology* upon request.



**Figure 7.** Histogram of post-Miocene (post-Hemphillian) fossil locality  $\delta^{18}\text{O}$  averages (Nebraska localities only). Shaded boxes indicate "best estimate" localities where three or more individuals were analyzed, and standard deviations are less than 2‰. North America land mammal age abbreviations are as in figure 1. Data from Rw-101 and Hay Springs, and some data from Ahrens, were taken from MacFadden et al. (1999a).

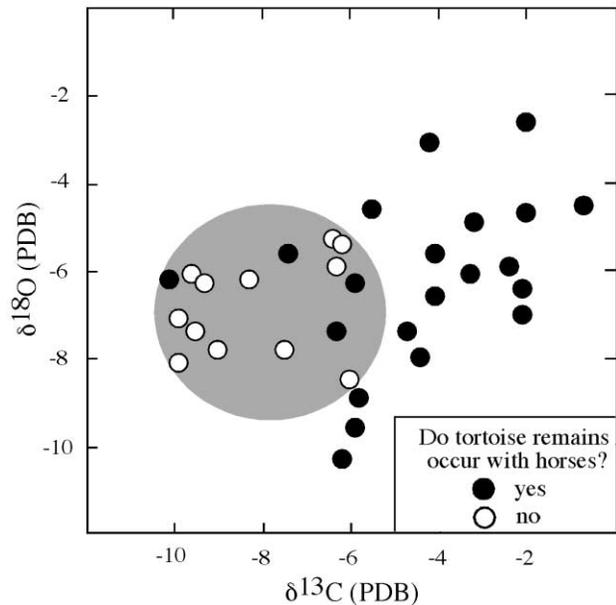
restrial productivity can be accounted for by  $\text{C}_3 + \text{C}_4$  photosynthesis. Before this vegetation change,  $\text{C}_4$  vegetation must have been significantly less nutritious than coexisting  $\text{C}_3$  vegetation in order to be so thoroughly avoided as a food resource by horses.

2.  $\text{C}_4$  vegetation was rare in ecosystems before late Hemphillian time and, beginning in late Hemphillian time, underwent expansion in terms of biomass. In this scenario,  $\text{C}_4$  vegetation replaced a fraction of  $\text{C}_3$  vegetation in terms of food availability, and equids were obliged to take up  $\text{C}_4$  feeding.

Of these two scenarios, we suggest that the second is closer to the real history. It seems unlikely that an abundant food resource would be ignored for several millions of years, unless the food resource required highly specialized digestive adaptations. While some data suggest that  $\text{C}_4$  vegetation is less nutritious than  $\text{C}_3$  vegetation (see Heckathorn et al. 1999), numerous modern ungulates sub-

sist partially or wholly on  $\text{C}_4$  vegetation. It is unclear whether specialized digestive adaptations are required to successfully process  $\text{C}_4$  versus  $\text{C}_3$  vegetation. If profound digestive adaptations are necessary, it seems unlikely that several equid genera would evolve these all during the same interval (late Hemphillian) had the evolutionary pressure existed millions of years prior. Had their digestive systems evolved in response to the availability of  $\text{C}_4$  vegetation, it would be expected that there would be a gradual increase in  $\text{C}_4$  feeding through time as digestive physiologies became more adept at processing  $\text{C}_4$  vegetation. Finally, the timing of the onset of  $\text{C}_4$  feeding in the Great Plains is roughly coeval with the timing of  $\text{C}_4$ -biomass expansion recorded elsewhere in North America, South America, Africa, and Asia (Cerling et al. 1997), suggesting a global vegetation change rather than a regional dietary preference change.

**Carbon Isotopes: Correlation between  $\text{C}_4$  Feeding and Presence of Tortoise Remains.** Figure 8 shows that horses from fossil localities with tortoise remains consumed relatively more  $\text{C}_4$  vegetation than did horses from localities without tortoise remains. The  $t$ -test results indicate that the carbon isotope difference between the two groups is significant at



**Figure 8.** Plot showing  $\delta^{13}\text{C}$  values of post-Miocene equids from Nebraska, grouped according to whether tortoise remains co-occur or do not co-occur with the fossil teeth. Some data were taken from MacFadden et al. (1999a).

>99.9% confidence (mean difference = 3.8‰;  $t = 5.3$ ,  $P < 0.0001$ ).

Tortoise fossils are large, robust, and readily identifiable. In Nebraska, tortoise remains are present throughout the Ogallala group and are present at all localities 5 Ma or older. Tortoises are first absent in the early Blancan Lisco fauna (~4 Ma), but both large (~30–50 cm) and giant (~50–150 cm) species are again present in the medial Blancan (including Sand Draw and Broadwater) and early late Blancan (including Big Springs) faunas (Holman 1972; Rogers 1984). The youngest Blancan fauna in our sample, South Wind Prospect, has no tortoise remains. Tortoises are also lacking in the Pleistocene faunas, with the exception of Angus Quarry, which contains remains of large but not giant tortoises. Appendix 1 indicates whether tortoise remains are present or absent at post-Hemphillian localities.

This periodic absence of tortoises following the Miocene is probably not an artifact of sampling or changes in depositional environment. The number of identifiable specimens (NISP) of large (>1 kg) vertebrates per site is comparable in Miocene and post-Miocene localities. These sites range from small (100–200 NISP) at the Miocene Mailbox site and the Pliocene South Wind site to >10,000 NISP at the Cambridge, North Shore, Norden Bridge, Hazard Homestead, and Annie's Geese Cross sites (Miocene) and the Hay Springs, Broadwater, and Lisco sites (post-Miocene).

Depositional environments are similar for Miocene and post-Miocene localities. All localities sampled in this study are of fluvial or fluvio-lacustrine origin, and all but four (Lisco, Uptegrove, Oshkosh, and Ashfall) yield fish bones (i.e., they accumulated in or near oxygenated water). Although by no means uniform in details of taphonomic origin (e.g., Norden Bridge is a high-diversity attritional assemblage deposited by a large river [Voorhies 1990b]; North Shore is an attritional site accumulated by large carnivores [Voorhies 1987]), overall, the sites represent a limited range of floodplain settings in areas of low relief. No cave, fissure, eolian, or marine-influenced sites are included in this study.

Tortoises have been suggested as a qualitative paleoclimate proxy because they require certain temperature parameters to form a viable population. Hutchinson (1982; fig. 2) plots maximum shell length of recent tortoises against mean cold month (MCM) temperature, showing that tortoises between 30 and 50 cm long require MCM temperatures of ~13°C, while tortoises >100 cm long do not live where MCMs drop below 22°C. Distributions of C<sub>4</sub> vegetation are likewise correlated with tem-

perature (Teeri and Stowe 1976), although growing-season temperature, not cold-month temperature, correlates best with percentage C<sub>4</sub> species within grasslands. We suggest that the coupled changes in tortoise and C<sub>4</sub> distributions in the post-Miocene Great Plains have recorded periodic climatic change in terms of temperature or other parameters.

**Oxygen Isotopes.** The oxygen isotope record for Nebraska equids shows significant secular variation, with the most <sup>18</sup>O-enriched values occurring in Barstovian and Clarendonian faunas, and the least-enriched values occurring in Hemphillian (especially late Hemphillian), Blancan, and Irvingtonian faunas. The 3.4‰ decrease between Barstovian and Blancan time represents a significant isotopic difference, and it should be noted that the oceans became enriched in <sup>18</sup>O by as much as 1‰ during this interval due to ice sheet expansions (Lear et al. 2000), and this would have the effect of reducing the isotopic change recorded in Nebraska. Such an effect may partially explain why Irvingtonian equids are not significantly depleted in <sup>18</sup>O relative to Blancan equids, as might be expected given onset of Northern Hemisphere glaciation following Blancan time.

Caution must be exercised when interpreting mammalian oxygen isotope records because numerous, sometimes independent, factors contribute to the overall  $\delta^{18}\text{O}$  value of a given individual. In the following section, we again make use of an endmember approach for data interpretation.

**Endmember 1.** The secular variation in the  $\delta^{18}\text{O}$  record reflects physiological or behavioral changes and does not reflect environmental change. The Kohn (1996) model estimates that several per mil differences in  $\delta^{18}\text{O}$  can result from differences in physiological or behavioral parameters. Panting versus sweating, stem feeding versus leaf feeding, dry-food feeding versus succulent-food feeding, and numerous other factors influence the isotopic composition of mammalian body water. Thus, secular changes in the behavior or physiology of equids could account for the observed 3.4‰ decrease between Barstovian and Blancan horses, especially if some changes acted in concert.

Differences in  $\delta^{18}\text{O}$  between different equid genera living at the same localities might shed light on the degree of oxygen isotope variability that can be attributed to physiological or behavioral phenomena within equids. At Uptegrove (Nebraska: late Hemphillian), *Dinohippus* averages  $-8.5 \pm 0.7$  (1 $\sigma$ ;  $n = 3$ ), and *Nannippus* averages  $-6.7 \pm 1.1$  ( $n = 3$ ), suggesting different water use strategies for the two genera. The same pattern holds up at Coffee Ranch, but there is significant

isotopic overlap; *Dinohippus* averages  $-0.5\% \pm 1.0\%$  ( $n = 4$ ), and *Nannippus* averages  $0.6 \pm 1.8$  ( $n = 3$ ). Also at Coffee Ranch, *Neohipparion* averages  $-1.0 \pm 0.8$  ( $n = 5$ ), and *Astrohippus* averages  $0.3\% \pm 1.4\%$  ( $n = 3$ ). At Cambridge (Nebraska: medial Hemphillian), there is isotopic overlap; *Calippus* averages  $-3.9 \pm 1.3$  ( $n = 6$ ), and *Neohipparion* averages  $-4.5 \pm 0.9$  ( $n = 5$ ). Thus, there is some evidence of water use differences between different equid genera, and although the magnitude of the resulting oxygen isotope differences appear to be small, they might account for some of the observed secular variation in the Nebraska record.

*Endmember 2.* The secular variations in  $\delta^{18}\text{O}$  are artifacts of diagenesis. While this possibility cannot be ruled out, it has been shown elsewhere that tooth enamel is resistant to oxygen isotope diagenesis. For example, Bocherens et al. (1996), Zazzo et al. (2000), and Cerling et al. (2001) show that fossil hippopotamus enamel is depleted in  $^{18}\text{O}$  relative to other coexisting fossil taxa, a pattern that is observed in modern ecosystems and relates to the aquatic habits of hippos. Fricke et al. (1998b) show that the Late Paleocene thermal maximum is recorded in the carbonate component of biogenic phosphate. Preservation of seasonal  $\delta^{18}\text{O}$  signals within single fossil teeth has been demonstrated by Fricke et al. (1998b).

*Endmember 3.* The secular variations in  $\delta^{18}\text{O}$  reflect environmental change. In the modern environment, geographic variations in climate give rise to the majority of variation observed in mammalian oxygen isotope data on a global scale. In particular, increased temperature and aridity are associated with  $^{18}\text{O}$ -enriched values and decreased temperature and greater humidity with  $^{18}\text{O}$ -depleted values.

Several regional, continental, and global changes correlate with the general features of the Nebraska oxygen isotope record. The "Clarendonian Chronofauna" represents the last significant chronofauna in North America and comprises a rich array of ungulate diversity that was thereafter absent from North America. Webb et al. (1995, p. 91) summarizes the pattern of diversity change in the Clarendonian Chronofauna as follows: "Large-herbivore diversity reached its apogee in the late Barstovian, about 15 million years ago, stayed high through the Clarendonian, and then entered a series of devastating extinctions during the Middle and Late Hemphillian" (=late and latest Hemphillian in this article). This pattern is illustrated by the faunal data for Great Plains ungulates (artiodactyls, perissodactyls, and proboscideans) in Janis et al.

(1998). Not including questionable occurrences (i.e., those followed by a question mark in figs. 22.2-8 and 35.2-5 in Janis et al. 1998), there are 47 genera recorded from the late late Barstovian (medial and late Barstovian and early Clarendonian in this article), 43 genera from the early Clarendonian (medial Clarendonian in this article), and 35 genera from the late Clarendonian. This number drastically decreases to 22 genera in the early Hemphillian but then rises to 30 genera in the medial Hemphillian. The number of genera drops to 21 in the late Hemphillian, and only 15 genera are accounted for in the latest Hemphillian.

The oxygen isotope record from Nebraska follows similar patterns. Values are greatest in the medial Barstovian ( $-3.9\%$ ), late Barstovian ( $-2.5\%$ ), and medial Clarendonian ( $-3.7\%$ ). We report no data from the early Clarendonian, but phosphate oxygen isotope data reported by Bryant et al. (1994) suggest values similar to those from preceding NALMAs. Oxygen isotope ratios are slightly decreased in the late Clarendonian ( $-4.2\%$ ), and the early Hemphillian is marked by the most depleted values up to that point ( $-6.4\%$ ). Values rebound in the medial Hemphillian ( $-4.7\%$ ), and the transition to late Hemphillian ( $-6.2\%$ ) marks possibly the most significant isotopic decrease in the record, with an average value greater than that for the early Hemphillian but with locality averages that are almost 2‰ more negative than any locality in the preceding 10 m.yr. The single latest Hemphillian locality also records a depleted value ( $-7.2\%$ ). This preliminary correlation between ungulate diversity and oxygen isotopes warrants further investigation, as it has significant implications not only for Great Plains paleoenvironments but also for ecological hypotheses that seek to explain patterns of biological evolution and diversity change in time and space (see Barnosky 2001).

Remains of crocodylians have not been recovered from post-late Clarendonian localities in Nebraska. Like tortoises, crocodylians cannot tolerate extended periods of freezing; they prefer to stay within an "activity range" of  $25^{\circ}$ – $35^{\circ}\text{C}$ , and in addition, they require permanent surface water (see Markwick 1994). Although more oxygen data from the early Hemphillian are desirable, the existing data are in accord with environmental changes that would force crocodylians to retreat to warmer latitudes following the late Clarendonian.

Oxygen isotopes from many of the late Hemphillian localities in Nebraska are depleted in  $^{18}\text{O}$  relative to those of preceding faunas. The timing of the late Hemphillian is broadly correlative with global environmental changes marked by the Mes-

sinian stage in Europe (Hsu et al. 1973; Krijgsman et al. 1999); increased ice growth in Antarctica (Miller et al. 1987); C<sub>4</sub>-biomass expansion in Asia, Africa, South America, and North America (Cerling et al. 1997); a "first-order" mammalian immigration episode in North America (Webb and Opdyke 1995); and the first appearance in millions of years of a North American mammalian taxa in South America (Butler et al. 1984; Woodburne and Swisher 1995).

In contrast to the correlations outlined above, the post-Miocene oxygen isotope record shows little temporal correlation with other environmental indicators, including the presence or absence of tortoise remains at fossil localities, the abundance of C<sub>4</sub> vegetation in equid diets, the Great American Interchange immigration event starting ~2.7 Ma (Woodburne and Swisher 1995), and the onset of northern hemisphere glaciation in the latest Pliocene or early Pleistocene. The record displays an interesting trend toward bimodal locality  $\delta^{18}\text{O}$  averages, especially within the late Hemphillian and Blancan faunas. More sampling is necessary to confirm this pattern and to determine the extent that the pattern records climatic, local environmental, and behavioral factors.

In summary, there is evidence that the oxygen isotope record reflects components of the first and third endmember scenarios presented above. There is occasional suggestion of oxygen isotope partitioning between different coexisting genera, and there are compelling correlations between the oxygen isotope record and independent records of environmental change.

### Conclusions

1. The Coffee Ranch local fauna was deposited before 6.6 Ma. A fraction of Coffee Ranch and other

late Hemphillian equids in Texas and Nebraska consumed C<sub>4</sub> vegetation, and a larger fraction of post-Hemphillian equids from both regions consumed C<sub>4</sub> vegetation. Pre-late Hemphillian equids consumed significantly less, if any, C<sub>4</sub> vegetation.

2. Post-Miocene localities in Nebraska can be divided into those that have or those that do not have tortoise remains. Equids from localities where tortoise remains are present have a significantly higher C<sub>4</sub> dietary fraction than those from localities where tortoise remains are not found.

3. The oxygen isotope record for Nebraska equids shows significant patterns of secular variation.  $\delta^{18}\text{O}$  values are greatest during Barstovian and Clarendonian time, decrease between late Clarendonian and late Hemphillian time, and then stabilize but trend toward a bimodal distribution of locality  $\delta^{18}\text{O}$  averages during and following late Hemphillian time.

4. The oxygen isotope record shows temporal correlations with patterns of diversity changes of Great Plains ungulates, disappearance of crocodylians from Nebraska, and late Miocene global change.

### ACKNOWLEDGMENTS

We thank A. Rigby for help with sample preparations, C. Cook and M. Lott for help with mass spectrometry, and J. Ehleringer for use of the Stable Isotope Ratio Facility for Environmental Research laboratory. F. Brown provided invaluable assistance with early versions of the manuscript. We are indebted to G. Corner and E. Lundelius, Jr., for sample material and information regarding fossil localities. B. MacFadden and two anonymous reviewers provided comments and constructive criticism that greatly improved this manuscript. This work was supported by the National Science Foundation and by the Packard Foundation.

### REFERENCES CITED

- Ayliffe, L. K., and Chivas, A. R. 1990. Oxygen isotope composition of the bone phosphate of Australian kangaroos: potential as a palaeoenvironmental recorder. *Geochim. Cosmochim. Acta* 54:2603–2609.
- Barnosky, A. D. 2001. Distinguishing the effects of the red queen and court jester on Miocene mammal evolution in the northern Rocky Mountains. *J. Vertebr. Paleontol.* 21:172–185.
- Bender, M. M. 1971. Variations in the <sup>13</sup>C/<sup>12</sup>C ratios of plants in relation to the pathway of photosynthetic carbon dioxide fixation. *Phytochemistry* 10:1239–1245.
- Beveridge, N. A. S., and Shackleton, N. J. 1994. Carbon isotopes in recent planktonic foraminifera: a record of anthropogenic CO<sub>2</sub> invasion of the surface ocean. *Earth Planet. Sci. Lett.* 126:259–273.
- Bocherens, H.; Koch, P. L.; Mariotti, A.; Geraads, D.; and Jaeger, J. J. 1996. Isotopic biogeochemistry (<sup>13</sup>C, <sup>18</sup>O) of mammalian enamel from African Pleistocene hominid sites. *Palaios* 11:306–318.
- Boellstorff, J. D. 1976. The succession of late Cenozoic volcanic ashes in the Great Plains: a progress report. *Kans. Geol. Surv. Guidebook* 1:37–71.
- Bryant, J. D.; Luz, B.; and Froelich, P. N. 1994. Oxygen isotopic composition of fossil horse tooth phosphate

- as a record of continental palaeoclimate. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 107:303–316.
- Butler, R. F.; Marshall, L. G.; Drake, R. E.; and Curtis, G. H. 1984. Magnetic polarity stratigraphy and  $^{40}\text{K}$ - $^{40}\text{Ar}$  dating of late Miocene and early Pliocene continental deposits, Catamarca province, NW Argentina. *J. Geol.* 92:623–636.
- Cande, S. C., and Kent, D. V. 1995. Revised calibration of the geomagnetic polarity timescale for the late Cretaceous and Cenozoic. *J. Geophys. Res.* 100:6093–6095.
- Cerling, T. E., and Harris, J. M. 1999. Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. *Oecologia* 120:247–363.
- Cerling, T. E.; Harris, J. M.; and Leakey, M. G. 2001. Isotope paleoecology of the Nawata and Apak Formations, at Lothogam, Turkana Basin, Kenya. New York, Columbia University Press, in press.
- Cerling, T. E.; Harris, J. M.; and MacFadden, B. J. 1998. Carbon isotopes, diets of North American equids, and the evolution of North American  $\text{C}_4$  grasslands. *In* Griffiths, H., ed. *Stable isotopes*. Oxford, BIOS Scientific, p. 363–379.
- Cerling, T. E.; Harris, J. M.; MacFadden, B. J.; Leakey, M. G.; Quade, J.; Eisenmann, V.; and Ehleringer, J. R. 1997. Global vegetation change through the Miocene/Pliocene boundary. *Nature* 389:153–158.
- Craig, H. 1954. Carbon-13 in plants and the relationships between carbon-13 and carbon-14 variations in nature. *J. Geol.* 62:115–149.
- Dansgaard, W. 1964. Stable isotopes in precipitation. *Tellus* 16:436–468.
- Deines, P. 1980. The isotopic composition of reduced organic carbon. *In* Fritz, P., and Fontes, J. C., eds. *Handbook of environmental isotope geochemistry. I. The terrestrial environment*. Amsterdam, Elsevier, p. 329–406.
- Duplessy, J. C.; Be, A. W. H.; and Blanc, P. L. 1981. Oxygen and carbon isotopic composition and biogeography of planktonic foraminifera in the Indian Ocean. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 33:9–46.
- Ehleringer, J. R.; Cerling, T. E.; and Helliker, B. R. 1997.  $\text{C}_4$  photosynthesis, atmospheric  $\text{CO}_2$ , and climate. *Oecologia* 112:285–299.
- Ekart, D. D.; Cerling, T. E.; Montañez, I. P.; and Tabor, N. J. 1999. A 400 million year carbon isotope record of pedogenic carbonate: implications for paleoatmospheric carbon dioxide. *Am. J. Sci.* 299:805–827.
- Fricke, H. C.; Clyde, W. C.; and O'Neil, J. R. 1998a. Intra-tooth variations in  $\delta^{18}\text{O}$  ( $\text{PO}_4$ ) of mammalian tooth enamel as a record of seasonal variations in continental climate variables. *Geochim. Cosmochim. Acta* 62:1839–1850.
- Fricke, H. C.; Clyde, W. C.; O'Neil, J. R.; and Gingerich, P. D. 1998b. Evidence for rapid climate change in North America during the latest Palaeocene thermal maximum: oxygen isotope compositions of biogenic phosphate from the Bighorn Basin (Wyoming). *Earth Planet. Sci. Lett.* 160:193–208.
- Friedli, H.; Löttscher, H.; Oeschger, H.; Siegenthaler, U.; and Stauffer, B. 1986. Ice core record of the  $^{13}\text{C}/^{12}\text{C}$  ratio of atmospheric  $\text{CO}_2$  in the past two centuries. *Nature* 324:237–238.
- Haug, G. H., and Tiedemann, R. 1998. Effect of the formation of the Isthmus of Panama on Atlantic Ocean thermohaline circulation. *Nature* 393:673–676.
- Heckathorn, S. A.; McNaughton, S. J.; and Coleman, J. S. 1999.  $\text{C}_4$  plants and herbivory. *In* Sage, R. F., and Monson, R. K., eds.  $\text{C}_4$  plant biology. San Diego, Academic Press, p. 285–312.
- Holman, J. A. 1972. Amphibians and reptiles. *In* Skinner, M. F., and Hibbard, C. W., eds. *Early Pleistocene preglacial and glacial rocks and faunas of north-central Nebraska*. Bull. Am. Mus. Nat. Hist. 148:55–71.
- Hsu, K. J.; Ryan, W. B.; and Cita, M. B. 1973. Late Miocene desiccation of the Mediterranean. *Nature* 242:240–244.
- Huertas, A. D.; Iacumin, P.; Stenni, B.; Chillon, B. S.; and Longinelli, A. 1995. Oxygen isotope variations of phosphate in mammalian bone and tooth enamel. *Geochim. Cosmochim. Acta* 59:4299–4305.
- Hutchinson, J. H. 1982. Turtle, crocodilian, and chompsaur diversity changes in the Cenozoic of the north-central region of western United States. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 37:149–164.
- Indermühle, A.; Smith, H. J.; Wahlen, M.; Deck, B.; Mastrolanni, D.; Tschumi, J.; Blunier, T.; et al. 1999. Holocene carbon-cycle dynamics based on  $\text{CO}_2$  trapped in ice at Taylor Dome, Antarctica. *Nature* 398:121–126.
- Izett, G. A. 1975. Late Cenozoic sedimentation and deformation in northern Colorado and adjoining areas. *In* Curtis, B. F., ed. *Cenozoic history of the southern Rocky Mountains*. Geol. Soc. Am. Mem. 144:179–209.
- Janis, C. M.; Damuth, J.; and Theodor, J. M. 2000. Miocene ungulates and terrestrial primary productivity: where have all the browsers gone? *Proc. Nat. Acad. Sci. U.S.A.* 97:7899–7904.
- Janis, C. M.; Scott, K. M.; and Jacobs, L. L. 1998. *Terrestrial carnivores, ungulates, and ungulatelike mammals, evolution of tertiary mammals of North America*. Cambridge, Cambridge University Press, 691 p.
- Jesse Smith, H.; Fischer, H.; Wahlen, M.; Mastrolanni, D.; and Deck, B. 1999. Dual modes of the carbon cycle since the last glacial maximum. *Nature* 400:248–250.
- Keeling, C. D.; Bacastow, R. B.; Carter, A. F.; Piper, S. C.; Whorf, T. P.; Heimann, M.; Mook, W. G.; and Roeloffzen, H. 1989. A three-dimensional model of atmospheric  $\text{CO}_2$  transport based on observed winds. I. Analysis of observational data. *In* Peterson, D. H., ed. *Aspects of climate variability in the Pacific and the western Americas*. Geophys. Monogr. 55:305–364.
- Koch, P. L. 1998. Isotopic reconstruction of past continental environments. *Annu. Rev. Earth Planet. Sci. Lett.* 26:573–613.
- Koch, P. L.; Hoppe, K. A.; and Webb, S. D. 1998. The isotopic ecology of late Pleistocene mammals in North America. I. Florida. *Chem. Geol.* 152:119–138.
- Koch, P. L.; Zachos, J. C.; and Dettman, D. L. 1995. Stable isotope stratigraphy and paleoclimatology of the Pa-

- leogene Bighorn Basin (Wyoming, USA). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 115:61–89.
- Kohn, M. J. 1996. Predicting animal  $\delta^{18}\text{O}$ : accounting for diet and physiological adaptation. *Geochim. Cosmochim. Acta* 60:4811–4829.
- Krijgsman, W.; Hilgen, F. J.; Raffi, I.; Sierro, F. J.; and Wilson, D. S. 1999. Chronology, causes and progression of the Messinian salinity crisis. *Nature* 400: 652–655.
- Latorre, C.; Quade, J.; and McIntosh, W. C. 1997. The expansion of  $\text{C}_4$  grasses and global change in the late Miocene: stable isotope evidence from the Americas. *Earth Planet. Sci. Lett.* 146:83–96.
- Lear, C. H.; Elderfield, H.; and Wilson, P. A. 2000. Cenozoic deep-sea temperatures and global ice volume from Mg/Ca in benthic foraminiferal calcite. *Science* 287:269–272.
- Lee-Thorpe, J. A., and van der Merwe, N. J. 1987. Carbon isotope analysis of fossil bone apatite. *S. Afr. J. Sci.* 83:712–715.
- Lindsay, E. H.; Johnson, N. M.; and Opdyke, N. D. 1976. Preliminary correlation of North American land mammal ages and geomagnetic chronology. *Univ. Mich. Pap. Paleontol.* 12:111–119.
- Longinelli, A. 1984. Oxygen isotopes in mammal bone phosphate: a new tool for palaeohydrological and palaeoclimatological research? *Geochim. Cosmochim. Acta* 48:385–390.
- Luz, B.; Cormie, A. B.; and Schwarcz, H. P. 1990. Oxygen isotope variations in phosphate of deer bones. *Geochim. Cosmochim. Acta* 54:1723–1728.
- Luz, B., and Kolodny, Y. 1985. Oxygen isotope variations in phosphate of biogenic apatites. IV. Mammal teeth and bones. *Earth Planet. Sci. Lett.* 75:29–36.
- Luz, B.; Kolodny, Y.; and Horowitz, M. 1984. Fractionation of oxygen isotopes between mammalian bone-phosphate and environmental drinking water. *Geochim. Cosmochim. Acta* 48:1689–1693.
- MacFadden, B. J., and Cerling, T. E. 1996. Mammalian herbivore communities, ancient feeding ecology, and carbon isotopes: a 10 million-year sequence from the Neogene of Florida. *J. Vertebr. Paleontol.* 16:103–115.
- MacFadden, B. J.; Cerling, T. E.; Harris, J. M.; and Prado, J. 1999a. Ancient latitudinal gradients of  $\text{C}_3/\text{C}_4$  grasses interpreted from stable isotopes of New World Pleistocene horse (*Equus*) teeth. *Global Ecol. Biogeogr.* 8: 137–149.
- MacFadden, B. J.; Cerling, T. E.; and Prado, J. 1996. Cenozoic terrestrial ecosystem evolution in Argentina: evidence from carbon isotopes of fossil mammal teeth. *Palaios* 11:319–327.
- MacFadden, B. J.; Solunias, N.; and Cerling, T. E. 1999b. Ancient diets, ecology, and extinction of 5-million-year-old horses from Florida. *Science* 283:824–827.
- Markwick, P. J. 1994. "Equability," continentality, and Tertiary "climate": the crocodylian perspective. *Geology* 22:613–616.
- McIntosh, W. C., and Quade, J. 1995.  $^{40}\text{Ar}/^{39}\text{Ar}$  geochronology of tephra layers in the Santa Fe group, Española Basin, New Mexico. *New Mexico Geol. Soc. Guidebook*. 46th Field Conference: Geology of the Santa Fe Region, p. 279–287.
- Miller, K. G.; Fairbanks, R. G.; and Mountain, G. S. 1987. Tertiary oxygen isotope synthesis, sea level history, and continental margin erosion. *Paleoceanography* 2: 1–19.
- Morgan, L. A.; Pierce, K. L.; and McIntosh, W. C. 1999.  $^{40}\text{Ar}/^{39}\text{Ar}$  ages of silicic volcanic rocks in the Snake River Plain: timing of volcanism and tectonism along the track of the Yellowstone hot spot. *Geol. Soc. Am. Abstr. Program* 31:A–49.
- Naeser, C. W.; Izett, G. A.; and Obradovich, J. D. 1980. Fission-track and K-Ar ages of natural glasses. *U.S. Geol. Surv. Bull.* 1489:1–31.
- Pagani, M.; Arthur, M. A.; and Freeman, K. H. 1999a. Miocene evolution of atmospheric carbon dioxide. *Paleoceanography* 14:273–292.
- Pagani, M.; Freeman, K. H.; and Arthur, M. A. 1999b. Late Miocene atmospheric  $\text{CO}_2$  and the expansion of  $\text{C}_4$  grasses. *Science* 285:876–879.
- Perkins, M. E.; Brown, F. H.; Nash, W. P.; McIntosh, W.; and Williams, S. K. 1998. Sequence, age and source of silicic fallout tuffs in middle to late Miocene basins of the northern basin and range province. *Geol. Soc. Am. Bull.* 110:344–360.
- Perkins, M. E.; Nash, W. P.; Brown, F. H.; and Fleck, R. J. 1995. Fallout tuffs of Trapper Creek, Idaho—a record of Miocene explosive volcanism in the Snake River Plain volcanic province. *Geol. Soc. Am. Bull.* 107: 1484–1506.
- Pierce, K. L., and Morgan, L. A. 1992. The track of the Yellowstone hot spot: volcanism, faulting, and uplift. *In* Link, P. K.; Kuntz, M. A.; and Platt, L. B., eds. *Regional geology of eastern and western Wyoming*. *Geol. Soc. Am. Mem.* 179:1–53.
- Quade, J.; Cerling, T. E.; Andrews, P.; and Alpagut, B. 1995. Paleodietary reconstruction of Miocene faunas from Pasalar, Turkey, using stable carbon and oxygen isotopes of fossil tooth enamel. *J. Hum. Evol.* 28: 373–384.
- Quade, J.; Cerling, T. E.; Barry, J. C.; Morgan, M. M.; Pilbeam, D. R.; Chivas, A. R.; Lee-Thorp, J. A.; and Van der Merwe, N. J. 1992. A 16 million year record of palaeodiet from Pakistan using carbon isotopes in fossil teeth. *Chem. Geol.* 94:183–192.
- Quay, P. D.; Tilbrook, B.; and Wong, C. S. 1992. Oceanic uptake of fossil fuel  $\text{CO}_2$ : carbon-13 evidence. *Science* 256:74–79.
- Raymo, M. E. 1994. The initiation of Northern Hemisphere glaciation. *Annu. Rev. Earth Planet. Sci. Lett.* 22:353–383.
- Rogers, K. L. 1984. Herptofauna of the Big Springs and Hornet's Nest quarries (northwestern Nebraska, Pleistocene: late Blancan). *Trans. Nebr. Acad. Sci.* 12: 81–94.
- Shackelton, N. J.; Hall, M. A.; Line, J.; and Shuxi, C. 1983. Carbon isotope data in core V19-30 confirm reduced carbon dioxide concentration in the ice age atmosphere. *Nature* 306:319–322.
- Spero, H. J.; Bijma, J.; Lea, D. W.; and Bemis, B. E. 1997.

- Effect of seawater carbonate concentration on foraminiferal carbon and oxygen isotopes. *Nature* 390: 497–500.
- Spero, H. J.; Lerche, I.; and Williams, D. F. 1991. Opening the carbon isotope "vital effect" black box. II. Quantitative model for interpreting foraminiferal carbon isotope data. *Paleoceanography* 6:639–655.
- Streck, M. J., and Grunder, A. L. 1995. Crystallization and welding variations in a widespread ignimbrite sheet: the Rattlesnake Tuff, eastern Oregon, USA. *Bull. Volcanol.* 57:151–169.
- Tedford, R. H.; Skinner, M. F.; Fields, R. W.; Rensberger, J. M.; Whistler, D. P.; Galusha, T.; Taylor, B. E.; Macdonald, J. R.; and Webb, S. D. 1987. Faunal succession and biochronology of the Arikarean through Hemphillian interval (Late Oligocene through earliest Pliocene Epochs) in North America. In Woodburne, M. O., ed. *Cenozoic mammals of North America*. Berkeley, University of California Press, p. 153–210.
- Teeri, J. A., and Stowe, L. G. 1976. Climatic patterns and the distribution of C<sub>4</sub> grasses in North America. *Oecologia* 23:1–12.
- Tissue, D. T.; Griffin, K. L.; Thomas, R. B.; and Strain, B. R. 1995. Effects of low and elevated CO<sub>2</sub> on C<sub>3</sub> and C<sub>4</sub> annuals. II. Photosynthesis and leaf biochemistry. *Oecologia* 101:21–28.
- Veizer, J.; Ala, D.; Azmy, K.; Bruckschen, P.; Buhl, D.; Bruhn, F.; Carden, G. A. F.; et al. 1999. <sup>87</sup>Sr/<sup>86</sup>Sr,  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  evolution of Phanerozoic seawater. *Chem. Geol.* 161:59–88.
- Voorhies, M. R. 1969. Paleoclimatic significance of crocodilian remains from the Ogallala group (upper Tertiary) in northeastern Nebraska. *J. Paleontol.* 45: 119–121.
- . 1987. Late Cenozoic stratigraphy and geomorphology, Fort Niobrara, Nebraska. In *Geol. Soc. Am. Centennial Field Guide: North-Central Section*. Vol 3. Boulder, Colo., p. 1–6.
- . 1990a. Vertebrate biostratigraphy of the Ogallala group in Nebraska. In Gustavson, T. C., ed. *Geologic framework and regional hydrology: upper Cenozoic blackwater draw and Ogallala Formations, Great Plains*. Austin, University of Texas Press, p. 115–151.
- . 1990b. Vertebrate paleontology of the proposed Norden Reservoir area, Brown, Cherry, and Keya Paha Counties, Nebraska. Lincoln, University of Nebraska Press, U.S. Bureau of Reclamation Technical Report 82-09, 138 p. plus appendix.
- Wang, Y.; Cerling, T. E.; and MacFadden, B. J. 1994. Fossil horses and carbon isotopes: new evidence for Cenozoic dietary, habitat, and ecosystem changes in North America. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 107: 269–279.
- Webb, S. D.; Hulbert, R. C., Jr.; and Lambert, W. D. 1995. Climatic implications of large-herbivore distributions in the Miocene of North America. In Vrba, E. S.; Denton, G. H.; Partridge, T. C.; and Burckle, L. H., eds. *Paleoclimate and evolution, with emphasis on human origins*. New Haven, Conn., Yale University Press, p. 91–108.
- Webb, S. D., and Opdyke, N. D. 1995. Global climatic influence on Cenozoic land mammal faunas. In National Research Council. *Studies in geophysics. Effects of past global change on life*. Washington, D.C., National Academy Press, p. 184–208.
- Whitman, J. M., and Berger, W. H. 1993. Pliocene-Pleistocene carbon isotope record, site 586, Ontong Java Plateau. In Maddox, E. M., ed. *Proc. Ocean Drilling Program Sci. Results* 130:333–348.
- Woodburne, M. O., and Swisher, C. C. 1995. Land mammal high-resolution geochronology, intercontinental overland dispersals, sea level, and vicariance. In Berggren, W. A.; Kent, D. V.; Aubry, M.; and Hardenbol, J., eds. *Geochronology, time scales and global stratigraphic correlation*. SEPM Spec. Publ. 54:335–364.
- Zazzo, A.; Bocherens, H.; Brunet, M.; Beauvilain, A.; Billiou, D.; Mackaye, H. T.; Vignaud, P.; et al. 2000. Herbivore paleodiet and paleoenvironmental changes in Chad during the Pliocene using stable isotope ratios of tooth enamel carbonate. *Paleobiology* 26:294–309.