

# Stable Isotope Ecology of a Late Miocene Population of *Gomphotherium productus* (Mammalia, Proboscidea) from Port of Entry Pit, Oklahoma, USA

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*The stable carbon and oxygen isotope compositions of serial samples of enamel from tusks of *Gomphotherium productus* (Mammalia, Proboscidea) from Port of Entry Pit, Oklahoma (early Hemphillian North American Land Mammal Age, ca. 7.5 Ma), were measured to examine intra-annual and interannual variation. Sample series from each of six tusks spanned approximately one year of tusk growth. Carbon isotope compositions range from  $-11.3$  to  $-9.2\%$  (VPDB) and exhibit no pattern of seasonal variation, indicating the diet of gomphotheres at Port of Entry Pit was dominated by  $C_3$  vegetation throughout the year. Phosphate oxygen isotope composition ( $\delta^{18}O_p$ ) ranges from  $18.9$  to  $22.2\%$  (VSMOW); carbonate oxygen isotope composition ( $\delta^{18}O_c$ ) ranges from  $26.1$  to  $30.1\%$  (VSMOW). None of the tusks exhibit seasonal variation in  $\delta^{18}O$ , and the average within-tusk range in  $\delta^{18}O_p$  is  $1.7\%$ . Neither the fluorine composition of the specimens nor the relationship between  $\delta^{18}O_p$  and  $\delta^{18}O_c$  values from splits of the same samples suggest significant post-depositional alteration. The oxygen isotope data imply that Hemphillian meteoric water had  $\delta^{18}O$  values that are indistinguishable from modern values in the region today. However, because polar ice sheets were smaller and mean ocean water  $\delta^{18}O$  lower than present, the estimates of meteoric water composition from gomphothere tusk  $\delta^{18}O_p$  are consistent with warmer mean annual temperatures during the Hemphillian. The within-tusk variations in  $\delta^{18}O_p$  are consistent with similar or much reduced patterns of seasonal temperature variation in comparison to today, depending on air mass flow during the late Miocene. Alternative explanations include seasonal migratory behavior and reliance by the gomphotheres at Port of Entry Pit on sources of drinking water with relatively constant  $\delta^{18}O$  values.*

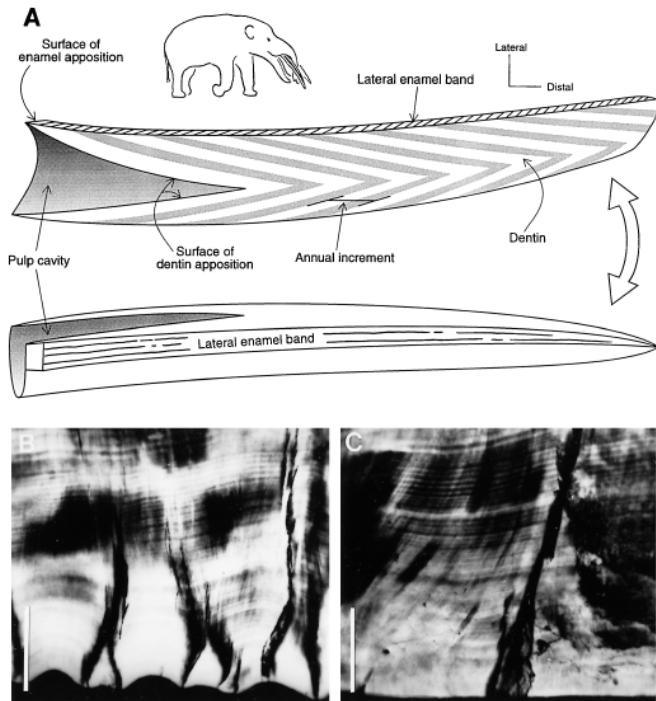
## INTRODUCTION

The stable carbon and oxygen isotope composition of the mineralized tissues of fossil mammals can be used to reconstruct aspects of their ecology and habitat. The carbon isotope composition of carbonate that naturally substitutes in the hydroxyapatite of bones and mineralized dental tissues (enamel, dentin, cementum) of mammalian herbivores is an indicator of the types of plants in the diet

and can reveal the dietary habits of fossil mammals (Smith and Epstein, 1971; Lee-Thorp and van der Merwe, 1987; Cerling and Harris, 1999; Cerling et al., 1999; MacFadden et al., 1999). The oxygen isotope composition of mammalian hydroxyapatite in large-bodied species is controlled largely by the isotope composition of local meteoric water and relative humidity (Longinelli, 1984; Luz et al., 1984; Ayliffe and Chivas, 1990). As the composition of modern meteoric water is sensitive to air temperature, estimates of meteoric water composition based on the oxygen-isotope composition of mammalian hydroxyapatite are a useful proxy for paleotemperature. Because of the appositional geometry and relatively slow rate of tooth growth in many larger species, both individual teeth and series of teeth within a single jaw can record subannual patterns of variation in diet and temperature in both living and fossil mammals (Koch et al., 1989; Koch, 1998; Cerling and Sharp, 1996; Stuart-Williams and Schwarcz, 1997; Fricke et al., 1998a, b; Kohn et al., 1998). In this paper, carbon and oxygen isotope measurements of serial samples of enamel from the upper tusks of the proboscidean *Gomphotherium productus* from the late Miocene locality of Port of Entry Pit, Oklahoma, are presented to examine variation within a single population.

Proboscidean tusks are highly modified incisor teeth and ideally are suited to high-resolution sampling for stable isotope measurements. Like the tusks of most proboscideans, gomphothere tusks are mostly dentin. Unlike most elephantids and *Mammut* (the American mastodon), however, gomphothere tusks have a lateral enamel band that is about 5 cm wide, 0.3 cm thick, and runs the length of the tusk in adults. Enamel is generally the preferred tissue for stable isotope analysis because its larger and more tightly packed apatite crystals generally are thought to make it less susceptible to post-depositional isotope exchange or alteration than other mineralized tissues (Hillson, 1986; Ayliffe et al., 1994). The large size and incremental growth of tusks allow excellent temporal control and resolution of sampling. As in other proboscideans that have been studied (Fisher, 1987; Fox and Fisher, 1994), tusk growth in *Gomphotherium* is geometrically simple and continuous throughout life (Fox, 2000). Dentin is deposited along the surface of the roughly conical pulp cavity at the proximal end of the growing tusk (Fig. 1A). Dentin has incremental growth features on three spatial scales that are organized hierarchically and represent daily, weekly, and annual periodicities (Fox, 2000). Tusk and molar-root dentin in other proboscideans have similar hierarchies of growth increments, but the periodicities are different in some taxa (unpub. data). The orientation of

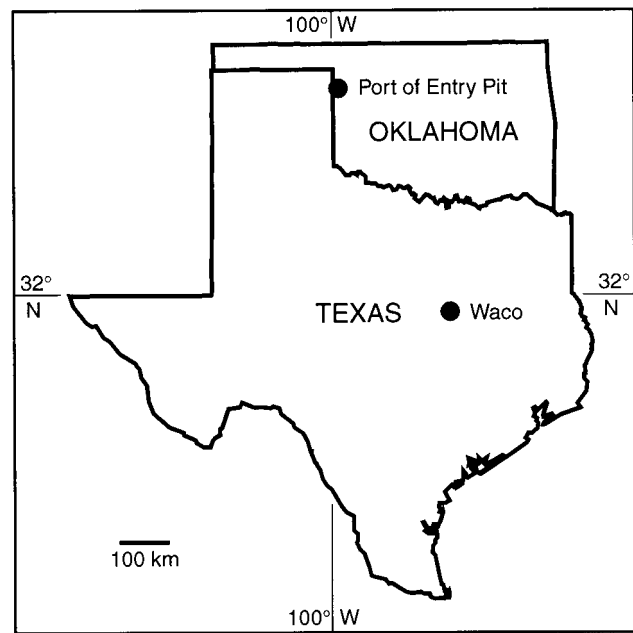
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**FIGURE 1**—Tusk growth in *Gomphotherium*. (A) Diagram of a sectioned tusk showing the internal structure and appositional surfaces for dentin and enamel. Annual increments in dentin are indicated by the white-gray couplets that parallel the pulp cavity and imbricate along the length of the tusk. Wear at the distal tip is asymmetric relative to the axis of the tusk. Increments in the enamel are indicated schematically by the proximally inclined lines within the enamel. (B) Transverse (perpendicular to long axis of tusk) thin section of *Gomphotherium* tusk enamel. Curved surface at bottom is the irregular enamel-dentin junction. Growth increments are light-dark couplets that roughly parallel the enamel-dentin junction. Scale bar is 0.5 mm. (C) Longitudinal (parallel to long axis of tusk) thin section of *Gomphotherium* enamel. Proximal is to left. Black line at bottom is enamel-dentin junction. Proximal dip of growth increments is clearest toward top. Scale bar is 0.5 mm.

the enamel appositional surface in *Gomphotherium* tusks (Fig. 1A) is indicated by the orientation of growth lines in enamel (Fig. 1B and C). Although the growth increments in *Gomphotherium* tusk enamel appear to be both hierarchically organized and regularly spaced, they have not been analyzed in the same detail as the increments in dentin. The temporal patterns of incremental features in tusk dentin (Fox, 2000) provide a framework for the sampling strategy for enamel.

The goal of this study was to analyze the tusks of a population sample of proboscideans to determine if members of a single population exhibit similar patterns of dietary behavior and record similar paleoclimatic signals. This study is part of a larger project examining changes in habitats and climate in North America during the middle to late Miocene. This interval marks a critical period of transition in global climates from the relatively warm early and middle Cenozoic to the ice-house planet of the Pliocene (Wright et al., 1992; Flower and Kennett, 1994). Broadly coincident with this transition, species richness of North American mammals declined dramatically from 15 to 5 Ma (Alroy, 1992). The conventional explanation for this faunal change, based largely on the ecol-



**FIGURE 2**—Locations of Port of Entry Pit, Oklahoma and Waco, Texas.

ogy of the lineages that went extinct or survived into the Pliocene, has long been that increasing seasonality of temperature and/or precipitation in North America during the climate transition led to the replacement of closed, woodland habitats by open grasslands or steppes (Webb, 1984). Faunal changes and shifts in the carbon-isotope composition of pedogenic carbonate and mammalian herbivore tooth enamel on other continents, as well as in North America, document the expansion of grasslands during the late Miocene and suggest the possibility of a global mechanism for all of these changes (Barry et al., 1985; Cerling et al., 1997). Focusing on a single population can provide critical detail to the broad picture of change that other studies have developed. Dietary reconstruction can indicate the intra-annual and interannual variability in utilization of woodland versus grassland ecosystems by herds of large-bodied herbivores. Paleotemperature reconstruction might indicate the degree and regularity of seasonality of temperature in North America at a single time plane in the late Miocene.

#### PORT OF ENTRY PIT, OKLAHOMA

Port of Entry Pit (Fig. 2) is a quarry locality in the Ogallala Group, which extends from the Texas panhandle to southern South Dakota; in Texas and Oklahoma, the Ogallala Group is undifferentiated. The Ogallala Group is composed of fluvial, lacustrine, and eolian sediments derived from ranges and uplifts to the west in the Rocky Mountains. According to Kitts (1957), the section at Port of Entry Pit consists of unconsolidated fine clayey and silty sands and layers of carbonate-cemented fine sands. The mammalian fossils occur in a 1-m bed of fine clayey, silty sand.

Mammalian fossils first were collected from the immediate area of Port of Entry Pit by parties from the Univer-

sity of Oklahoma in the 1930's and 1950's. The fauna was described by Kitts (1957) as the Arnett fauna (after nearby Arnett, Oklahoma) from the Adair Ranch Quarry. Port of Entry Pit, collected by parties from the Frick Laboratory of the American Museum of Natural History, is an equivalent, lateral continuation of the Adair Ranch Quarry (Schultz, 1990). The mammalian faunas from both collections include eight species, but are dominated by gomphotheres, which are followed in abundance by large carnivores (Kitts, 1957). Together, the gomphotheres and the carnivores indicate that the fauna falls in the late early Hemphillian North American Land Mammal Age, with an absolute age of approximately 7.5 Ma (Tedford et al., 1987; Schultz, 1990).

The gomphothere remains consist of hundreds of specimens and include isolated teeth and tusks, complete mandibles, several complete or partial crania, and abundant post-crania representing many individuals. Kitts (1957) attributed the fossils to *Serridentinus* sp. However, Tobien (1972) synonymized all species of *Serridentinus*, as well as those of several other genera, with *Gomphotherium productus*. This broad concept of *G. productus* is not accepted universally. However, as the species-level taxonomy of North American gomphotheres has not been evaluated in detail since the work of Tobien (1972), the designation *G. productus* is used here.

Although a rigorous taphonomic study has not been done, several factors suggest that the proboscidean remains at Port of Entry Pit accumulated over a relatively short period of time and approximate a sample from a local population of gomphotheres. First, the geologic setting of the fossils is not consistent with either extensive post-mortem transport or long-term accumulation. All of the fossils from the locality come from only 1 m of an Ogallala Group section that is in excess of 60 m thick. Kitts (1957) interpreted the section as representing either a lacustrine or floodplain depositional environment, based on the unconsolidated fine clayey and silty sands and the lack of channel sand or gravel. Large proboscidean fossils would not be in hydraulic equilibrium with the sediments, and the limited vertical distribution of fossils suggests that the assemblage accumulated over a brief period relative to the time represented within the section as a whole. Second, the abundance, condition, and size of the gomphothere fossils are not consistent with transport. For example, over 130 upper tusks were recovered, many of which are over 1.5 m long. Many of the tusks are complete and preserve the delicate growing margin at the proximal end. As Kitts (1957) noted, the broken edges of fragmented specimens are sharp, which is inconsistent with the abrasion expected from transport. Most, if not all, of the American Museum material appears to be weathered only slightly, consistent with a brief period of exposure prior to burial (Behrensmeier, 1978). Finally, the dental remains span a wide range of ages, from sub-adult to extreme old-age, based on tooth eruption and wear. Although the relative proportions of different age classes have not been determined, the abundant representation of middle stages of life history is not typical of a significantly time-averaged assemblage, which would be dominated by the early and late stages of life history in which mortality is greatest. These observations support the interpretation of the proboscidean fossils as a sample that did not experience extensive

time-averaging and suggest that the large concentration of proboscidean remains represents a single population. As such, it is suitable for reconstructing interindividual variation in the preserved stable isotope signature of diet and paleotemperature.

## STABLE ISOTOPES AND PALEOECOLOGY

### Carbon Isotopes and Diet

Plant biomass is the primary source of carbon for a mammalian herbivore, and the hydroxyapatite (HA) of mammalian enamel (and other mineralized tissues) incorporates carbon from the diet into carbonate in the HA crystal structure. The carbon-isotope composition ( $\delta^{13}\text{C}$ ) of the carbonate reflects the proportion of plants in the diet utilizing the two most common photosynthetic pathways for fixing  $\text{CO}_2$ , the Calvin cycle and the Hatch-Slack cycle. These two pathways yield plant tissues with distinct and non-overlapping  $\delta^{13}\text{C}$  signatures as a result of different fractionating processes relative to atmospheric  $\text{CO}_2$ , which is the source of photosynthetic carbon to plants (Smith and Epstein, 1971; Cerling et al., 1997). A third pathway, crassulacean acid metabolism, or CAM, is uncommon and found mostly in succulents adapted to arid conditions. Plants that use the Calvin cycle, or  $\text{C}_3$  plants, include trees, shrubs, and high-latitude and high-elevation grasses.  $\text{C}_3$  plants have mean  $\delta^{13}\text{C}$  values of  $-27\text{‰}$  (relative to the VPDB standard) with a range of about  $-22$  to  $-35\text{‰}$  (O'Leary, 1988; Cerling et al., 1997). (All isotope compositions are expressed in conventional  $\delta$  notation, in which the ratio of heavy to light isotopes in a sample is expressed as the permil (‰) difference between the ratio in the sample ( $R_{\text{sa}}$ ) to the ratio in a standard ( $R_{\text{st}}$ ), normalized to  $R_{\text{st}}$ , so  $\delta = ((R_{\text{sa}}/R_{\text{st}}) - 1) * 1000$ ) Plants using the Hatch-Slack cycle, or  $\text{C}_4$  plants, include warm climate grasses as well as some sedges and herbs.  $\text{C}_4$  plants have average  $\delta^{13}\text{C}$  values of about  $-13\text{‰}$ , with a range of  $-9$  to  $-19\text{‰}$  (O'Leary, 1988; Cerling et al., 1997). Variation in  $\delta^{13}\text{C}$  in plant tissues, particularly for  $\text{C}_3$  plants, is largely a function of aspects of habitat, such as light and moisture stress, nutrient availability, and temperature. Closed-canopy forest plants generally are depleted in  $^{13}\text{C}$  relative to open-habitat plants; hence, closed-canopy plants have carbon-isotope compositions that are shifted somewhat towards more negative  $\delta^{13}\text{C}$  values (Ehleringer and Monson, 1993).

Some controversy persists over  $\Delta_{\text{ap-diet}}$ , the offset between the carbon isotope composition of herbivore enamel apatite and the average composition of the diet (expressed in ‰). Laboratory studies of rodents and pigs suggest  $\Delta_{\text{ap-diet}}$  is  $+9.0$  to  $10.3\text{‰}$  (i.e., enamel apatite is enriched in  $^{13}\text{C}$  relative to the diet; DeNiro and Epstein, 1978; Koch, 1998). In contrast, field studies of large-bodied mammals indicate that  $\Delta_{\text{ap-diet}}$  is  $+12.0$  to  $14.1$  (Lee-Thorp and van der Merwe, 1987; Cerling et al., 1997; Koch, 1998; Cerling and Harris, 1999). While field based studies have poorer control on the  $\delta^{13}\text{C}$  value of foods actually ingested by animals sampled, both the subjects and the conditions of those studies are more like those of the present study. Following the most recent and most detailed field study, (Cerling and Harris, 1999) to date, a  $\Delta_{\text{ap-diet}}$  of  $+14.1$  is assumed here. Thus, enamel apatite from a gomphothere with a pure  $\text{C}_3$  diet would have a mean  $\delta^{13}\text{C}$  value of about

–12.9‰, and enamel from a gomphothere with a pure C<sub>4</sub> diet would have a δ<sup>13</sup>C value of about +1.1‰. Intermediate values would indicate a mixed diet, and the δ<sup>13</sup>C value could be used to estimate the relative proportions of C<sub>3</sub> and C<sub>4</sub> plants, although a given δ<sup>13</sup>C value can be consistent with some range in the proportion of C<sub>3</sub> and C<sub>4</sub> plants due to the effects of habitat characteristics on the δ<sup>13</sup>C of plant tissues (see figure 1 of MacFadden et al., 1996).

Generally speaking, C<sub>4</sub> plants are less nutritious and more difficult for mammals to digest than C<sub>3</sub> plants (Demment and Van Soest, 1985; Ehleringer and Monson, 1993); hence, changes in the relative proportion of these two types of plants within an ecosystem during the year would be an important component of the ecology of mammalian communities. Additionally, as the proportion of C<sub>4</sub> grasses in local floras is generally greater in warmer climates today (Teeri and Stowe, 1976), seasonal utilization of C<sub>4</sub> plants by *G. productus* at Port of Entry Pit could imply seasonal variation in temperature.

#### Oxygen Isotopes, Meteoric Water, and Temperature

Both the phosphate and structural carbonate in mammalian tooth and bone HA form in oxygen-isotope equilibrium with the body water from which the mineral precipitates (Longinelli, 1984; Luz et al., 1984; Bryant et al., 1996; Iacumin et al., 1996). The oxygen-isotope composition of body water (δ<sup>18</sup>O<sub>bw</sub>) in terrestrial mammals is controlled by the magnitude and isotope composition of oxygen fluxes to and from body water (Luz et al., 1984; Bryant and Froelich, 1995; Kohn, 1996). As the mineralized tissues in mammals larger than about 1 kg form at a constant body temperature of approximately 37° C (Cossins and Bowler, 1987), the only source of variation in the oxygen-isotope composition of mammalian apatite (δ<sup>18</sup>O<sub>ap</sub>) is the composition of body water.

Body-mass scaling functions suggest that ingested water is the dominant oxygen influx for very large-bodied (>1000 kg) mammals such as *Gomphotherium* (Bryant and Froelich, 1995). The model predictions are corroborated by estimates of oxygen influx in modern elephants, which indicate that the molar ratio of oxygen in drinking water, food water, and food is approximately 20:10:1 (Koch, 1989). The drinking water component of ingested water is derived from surface-water reservoirs, such as streams and ponded water, and is controlled by the oxygen-isotope composition of meteoric water (δ<sup>18</sup>O<sub>mw</sub>), evaporative enrichment of <sup>18</sup>O, and local hydrology. The liquid water in the stems of food plants also reflects the isotope composition of surface waters (Yakir, 1992) and, hence, also reflects δ<sup>18</sup>O<sub>mw</sub>. Liquid water in the leaves of plants generally is enriched in <sup>18</sup>O relative to stem water and surface water due to evaporation at the leaf surface (Sternberg et al., 1989). Because of this enrichment, and the contributions from other influxes (atmospheric oxygen, food oxygen), relationships between δ<sup>18</sup>O<sub>bw</sub> and δ<sup>18</sup>O<sub>mw</sub> for a wide range of mammalian herbivores typically have slopes less than 1.0 (Kohn, 1996). However, modeled body-water compositions based on body-mass scaling functions imply that δ<sup>18</sup>O<sub>bw</sub> approaches the δ<sup>18</sup>O of ingested water at the large body mass of proboscideans (Bryant and Froelich, 1995).

This suggestion is consistent with the relationship be-

tween measured apatite phosphate oxygen-isotope compositions (δ<sup>18</sup>O<sub>p</sub>) of modern African (*Loxodonta africana*) and Asian (*Elephas maximus*) elephants and estimates of δ<sup>18</sup>O<sub>mw</sub> (Ayliffe et al., 1992). A least squares linear regression with δ<sup>18</sup>O<sub>mw</sub> as the independent variable and δ<sup>18</sup>O<sub>p</sub> values of elephants from both arid and non-arid regions has a slope of 1.06 (equation 1a in Ayliffe et al., 1992). However, a slope greater than 1.0 for such a regression is theoretically impossible if meteoric water truly represents ingested water, as was assumed by Ayliffe et al. (1992), because δ<sup>18</sup>O<sub>p</sub> cannot vary more than the δ<sup>18</sup>O of ingested water from which apatite largely is derived. Excluding data for elephants from arid regions of Africa, in which surface water reservoirs are likely to be evaporatively enriched in <sup>18</sup>O relative to local meteoric water, yields a least squares regression with a more plausible slope of 0.94 (equation 1b in Ayliffe et al., 1992). Assuming modern elephants are a reasonable analog for gomphotheres, the data for the latter regression provide a means to predict δ<sup>18</sup>O<sub>mw</sub> from gomphothere δ<sup>18</sup>O<sub>p</sub>. Recalculating the least squares linear regression with δ<sup>18</sup>O<sub>p</sub> of modern elephants from non-arid regions as the independent variable and estimated local δ<sup>18</sup>O<sub>mw</sub> as the dependent variable yields the following equation (with 95% confidence intervals for the slope and intercept):

$$\delta^{18}\text{O}_{\text{mw}} = 0.90(\pm 0.2)\delta^{18}\text{O}_{\text{p}} - 21.8\text{‰}(\pm 3.9)(\text{VSMOW})$$

$$(r^2 = 0.85). \quad (1)$$

Theoretically, the slope of this equation should be greater than 1.0, just as it should be less than 1.0 with the alternate arrangement of independent and dependent variables, if δ<sup>18</sup>O<sub>mw</sub> is indeed an accurate measure of the δ<sup>18</sup>O of ingested water. However, food water is still a relatively large flux of oxygen in elephants and it can be evaporatively enriched relative to meteoric water (Sternberg et al., 1989). Thus, the relationship between δ<sup>18</sup>O<sub>ap</sub> and δ<sup>18</sup>O<sub>mw</sub> need not necessarily correspond precisely to the limitations of the relationship between δ<sup>18</sup>O<sub>ap</sub> and the δ<sup>18</sup>O of ingested water. Regardless, the 95% confidence interval for the slope of equation 1 (±0.2), which is largely a function of the uncertainty in the estimates of the δ<sup>18</sup>O<sub>mw</sub> values, encompasses values greater than 1.0. As this is the only available empirical relationship relating proboscidean δ<sup>18</sup>O<sub>ap</sub> and δ<sup>18</sup>O<sub>mw</sub>, it will be used to estimate both the mean annual value and seasonal range in δ<sup>18</sup>O<sub>mw</sub> on the Southern Great Plains during the early Hemphillian. However, caution is warranted in reading δ<sup>18</sup>O<sub>ap</sub> uncritically as a direct measure of meteoric water due to the possibility that surface-water reservoirs may have deviated from δ<sup>18</sup>O<sub>mw</sub> through evaporative enrichment. Additionally, the seasonal range of δ<sup>18</sup>O<sub>ap</sub> may have a damped signal relative to δ<sup>18</sup>O<sub>mw</sub> due to time-averaging of the δ<sup>18</sup>O<sub>mw</sub> signal within the hydrologic cycle.

Both mean annual and seasonal range in δ<sup>18</sup>O of modern meteoric water are sensitive to local air temperature (Dansgaard, 1964; Rozanski et al., 1993; see review in Koch, 1998). However, comparing estimates of past δ<sup>18</sup>O<sub>mw</sub> with modern values, or using the modern relationship between δ<sup>18</sup>O<sub>mw</sub> and mean annual temperature (MAT) to reconstruct paleotemperature from estimates of δ<sup>18</sup>O<sub>mw</sub>, is complicated by two factors. First, changes in the volume of ice sheets during the Cenozoic would have changed the

mean  $\delta^{18}\text{O}$  of ocean water in the past. During times with smaller ice sheets than at present, as during the late Miocene, ocean water  $\delta^{18}\text{O}$  would be lower than the modern value, water vapor for continental precipitation would have a lower initial  $\delta^{18}\text{O}$  value for a given water temperature, and the intercept of the  $\delta^{18}\text{O}_{\text{mw}}$ -MAT relationship would be lower than observed today. A second factor is the effect of vapor-source water temperature on the relationship between meteoric water and temperature; warmer vapor sources would further lower the intercept of the relationship relative to the modern line (Boyle, 1997). The  $\delta^{18}\text{O}_{\text{mw}}$ -MAT relationship during the early Hemphillian is not constrained easily, but to compare estimates of  $\delta^{18}\text{O}_{\text{mw}}$  for Port of Entry Pit to modern conditions, it is necessary at least to account for the change in ocean water  $\delta^{18}\text{O}$  relative to the present. As a first approximation, it is assumed that mean-ocean water  $\delta^{18}\text{O}$  was offset from the modern value by  $-0.4\%$ , reflecting a combination of ice-free conditions on Greenland and West Antarctica and slightly warmer tropical oceans during the late Miocene. This factor is roughly consistent with oxygen-isotope measurements of benthic foraminifera (e.g., Miller et al., 1987; Wright et al., 1991). The ocean-water offset is applied to the weighted mean annual  $\delta^{18}\text{O}_{\text{mw}}$  from 208 International Atomic Energy Association (IAEA) precipitation monitoring stations for the period 1961–1987 (data from Rozanski et al., 1993), which are used to calculate a least squares linear regression with  $\delta^{18}\text{O}_{\text{mw}}$  as the independent variable and temperature as the dependent variable. This yields the following late Miocene paleotemperature equation for estimates of  $\delta^{18}\text{O}_{\text{mw}}$  (with 95% confidence intervals for the slope and intercept):

$$\begin{aligned} ^\circ\text{C} &= 2.0(\pm 0.2)\delta^{18}\text{O}_{\text{mw}}(\text{VSMOW}) + 30.2(\pm 1.5) \\ (r^2 &= 0.72). \end{aligned} \quad (2)$$

This expression provides a means of comparing estimates of  $\delta^{18}\text{O}_{\text{mw}}$  from equation 1 with conditions in the vicinity of Port of Entry Pit today.

#### MONITORING ISOTOPIC FIDELITY

Prior studies of living and fossil mammals and mass-balance modeling of isotope diagenesis in biogenic apatites suggest that the carbon-isotope composition of enamel is fairly resistant to post-depositional alteration (Land et al., 1980; Lee-Thorp and van der Merwe, 1987; Wang and Cerling, 1994; Koch et al., 1997). Of greater concern is the possibility of alteration of enamel oxygen-isotope composition. Phosphate oxygen is generally resistant to isotope exchange by means of low-temperature, inorganic reactions, regardless of the material analyzed (Tudge, 1960; Kolodny et al., 1983; Shemesh et al., 1988; Barrick et al., 1998). However, some studies suggest the possibility that phosphate oxygen in some materials, if not all, is susceptible to alteration through mechanisms including direct isotope exchange with environmental water, local dissolution and recrystallization in equilibrium with environmental water, and inorganic or microbially-mediated deposition of authigenic apatite (Longinelli, 1969; McArthur and Herczeg, 1990; Ayliffe et al., 1992; Kolodny et al., 1996; Blake et al., 1997). A similar debate persists over the isotopic integrity of structural carbonate oxygen, although enamel-

carbonate oxygen is thought by most to be resistant to exchange (Land et al., 1980; Schoeninger and DeNiro, 1982; Lee-Thorp and van der Merwe, 1987). Two potential means of detecting oxygen-isotope diagenesis in fossil biogenic apatite are measurement of the fluorine concentration of the mineralized tissue and comparison of the oxygen isotope composition of structural carbonate oxygen ( $\delta^{18}\text{O}_{\text{c}}$ ) and phosphate oxygen ( $\delta^{18}\text{O}_{\text{p}}$ ) from aliquots of the same sample.

The fluorine content of fossil biogenic phosphate, expressed as the molar ratio of fluorine to phosphorus (F/P), has been proposed as an indicator of diagenesis (Bryant, 1995; Bryant et al., 1996). F/P is potentially a good tracer of remineralization of HA to more stable carbonate fluorapatite (CFA), because both elements are involved in the process of remineralization and neither is found in common, non-apatitic, sedimentary minerals (Bryant, 1995). Fluorine substitutes in the OH site in the HA crystal structure, and the presumption is that remineralization leads to an increase in the amount of F through uptake from ground water. The fluorine content of fully mineralized, modern mammalian enamel, which has an HA mineralogy, is in the range of 0.006 to 0.010 weight percent (Parker et al., 1974; LeGeros, 1991; Bryant et al., 1996). The concentration of fluorine in fossil teeth and bones is generally much greater than in recent samples and is on the order of several weight percent (Oakley, 1950; Parker et al., 1974).

Significant deviation from modern levels in fossils might be an indication of alteration through dissolution and reprecipitation. Bryant (1995) and Bryant et al. (1996) make convincing arguments that the high F/P, CFA mineralogy, and low  $\delta^{18}\text{O}_{\text{p}}$  of fossil horse teeth in an early stage of development, relative to completely developed teeth with HA mineralogy in the same jaw, indicate diagenesis and post-mortem oxygen-isotope alteration in the incompletely developed teeth. Although dissolution and recrystallization can lead to an increase in F at the OH site and alteration of the  $\delta^{18}\text{O}$  of  $\text{PO}_4$ , this process might increase F without altering the oxygen-isotope composition. Other means to increase F without affecting  $\delta^{18}\text{O}_{\text{ap}}$  include deposition of authigenic fluorapatite into interstitial spaces within enamel or solid-state replacement of OH at the surfaces of enamel crystallites with F. Additionally, F concentration in fossil enamel can be affected by other factors, such as the thickness of the enamel (Toots and Parker, 1979). However, in the absence of other lines of evidence, high F/P ratios in fossil samples should cast suspicion on stable-isotope measurements.

A second means of monitoring the oxygen-isotope integrity of fossil biogenic apatite is the relationship between  $\delta^{18}\text{O}_{\text{c}}$  and  $\delta^{18}\text{O}_{\text{p}}$ . Based on modern data (Bryant et al., 1996; Iacumin et al., 1996), unaltered samples should lie on a line with a slope close to 1.0, as both structural carbonate oxygen and phosphate oxygen precipitate from body water in isotopic equilibrium. Fossil data that deviate from such a line indicate alteration of either carbonate or phosphate, though which phase is altered cannot necessarily be determined directly from the isotope data.

#### MATERIALS AND METHODS

Enamel hydroxyapatite from ten *G. productus* tusks in the Frick Collection of the American Museum of Natural

**TABLE 1**—*Gomphotherium* tusk specimens analyzed in this study. X indicates analyses performed, – indicates analyses not performed.

Specimen	F/P	$\delta^{13}\text{C}$	$\delta^{18}\text{C}_c$	$\delta^{18}\text{O}_p$
F:AM 38257	X	X	X	X
F:AM 38258	X	X	X	X
F:AM 38259	X	X	X	X
F:AM 38269	X	X	X	X
F:AM 38270	X	X	X	X
HIG 762	X	–	–	–
HIG 1128-J	X	–	–	–
HIG 1128-K	X	–	–	–
HIG 1128-P	X	–	–	–
F:AM 129672	–	–	–	X

History was sampled for elemental and stable isotope analyses. Table 1 lists the analyses performed on each specimen. Specimens were chosen that did not appear to be altered and that preserved lateral enamel bands of sufficient width and length for sampling. All samples were removed under stereomicroscope observation using a 0.4-mm diamond bit in a hand-held flexible-shaft grinder. Samples were oriented perpendicular to the long axis of the tusk and extended across the lateral enamel band (Fig. 3), paralleling the expected outcrop orientation of growth lines in the enamel (Fig. 1). Samples were drilled as shallowly as possible to minimize cutting down through growth lines and time-averaging the sample in an uncontrolled manner. The depth of most samples was from about 0.25 to 0.35 mm, with a few as deep as 0.40 mm.

Single samples (10–15 mg) of enamel were collected from nine of the ten tusks for F and P determinations. Fluorine concentration was measured by specific-ion electrode potentiometry. Phosphorus concentration was determined with phosphomolybdate spectrophotometry, following methods outlined in Bryant (1995).

Serial samples of enamel were collected from six of the ten tusks for stable-isotope analyses. Sample series consist of 18 samples (8–15 mg each) spanning roughly 45 mm on 2.5 mm centers (Fig. 3). Five of the tusks sampled were among those sampled for F and P determinations. If large enough, each sample from these tusks was split into a 1–3 mg aliquot for measurement of  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}_c$  of structural carbonate, and an 8–10 mg aliquot for measurement of  $\delta^{18}\text{O}_p$ . Samples that were not large enough to split were only analyzed for  $\delta^{18}\text{O}_p$ . Samples from the sixth tusk, F:AM 129672, were only analyzed for  $\delta^{18}\text{O}_p$ . Measurements of dentin growth increments in F:AM 129672 (Fox, 2000) provide an estimate of average tusk extension of approximately 45 mm/year for the tusks from Port of Entry Pit. This estimate was used to target one year of tusk growth from each of the six tusks sampled for isotope analyses; thus, each sample should represent approximately three weeks of tusk growth. As the individual series were not taken from a consistent position relative to the growing margin, the six series almost certainly sample six different years and may represent the degree of interannual variability in meteoric water composition on the Southern Great Plains during the early late Miocene.

Aliquots for isotope analysis of carbonate were pretreated to remove residual organic matter and sedimentary carbonates following a method suggested by Koch et al.



**FIGURE 3**—Sampled enamel band of FAM 129672. Adjacent drill paths are spaced on 2.5 mm centers. Growing margin is to the left (proximal). Drill paths to the right sample enamel deposited earlier in life than more proximal samples to the left. Scale is in millimeters.

(1997). The samples were soaked in 2–3% NaOCl (0.04 ml/mg sample) for approximately 20 hours to oxidize organic matter, and rinsed five times in distilled water. The samples were then soaked in 1 M acetic acid buffered with calcium acetate (0.04 ml/mg sample) for another 20 hours and again rinsed five times in distilled water. After drying, samples were reacted with phosphoric acid at 72° C in a Finnigan MAT “Kiel” automatic carbonate extraction system, and the isotope composition of the resulting CO<sub>2</sub> was analyzed on a Finnigan MAT 251 triple collector isotope-ratio mass spectrometer in the University of Michigan Stable Isotope Laboratory. The fractionation factor between mammalian apatite carbonate and CO<sub>2</sub> is unknown; hence, it was assumed that it is the same as for calcite and CO<sub>2</sub> and an acid fractionation factor of 1.008818 was used. A disadvantage of using an automated extraction system for the carbonate-isotope analysis is that the production of contaminants during extraction of the samples cannot be monitored. Both Cerling and Sharp (1996) and MacFadden (1998) reported the presence of a contaminant identified as SO<sub>2</sub> following extraction of some samples of fossil apatite. However, sample-gas pressures during all of the analyses reported here were consistent with the size of the samples and not consistent with excess production of species other than CO<sub>2</sub>. Analytical precision of both  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}_c$  values is better than  $\pm 0.1\%$  (1 s.d.), based on regular measurements of National Bureau of Standards carbonate standards (NBS-18, NBS-19).

Aliquots for oxygen-isotope analysis of phosphate were prepared and analyzed following the method of O’Neil et al. (1994), with some minor modifications. Samples (8–10 mg) were digested in 2 ml of 2 M HF for 24–36 hours, during which time the samples were agitated in a sonication bath for 1–2 hours. After the pH of the solution was raised to >7 with 1.5 ml of reagent grade (29% aqueous solution), NH<sub>4</sub>OH, samples were filtered through 0.2  $\mu\text{m}$  membrane filters to remove CaF<sub>2</sub> that precipitates during digestion. The PO<sub>4</sub> was isolated by addition of silver-amine solution (0.2 M AgNO<sub>3</sub>, 0.35 M NH<sub>4</sub>NO<sub>3</sub>, 0.74 M NH<sub>4</sub>OH; 0.342 ml/mg sample) and precipitation of Ag<sub>3</sub>PO<sub>4</sub> at approximately 70° C. The Ag<sub>3</sub>PO<sub>4</sub> crystals were weighed into 6 mm o.d. quartz tubes and combined with spectrographically pure graphite (0.014316 mg C/mg Ag<sub>3</sub>PO<sub>4</sub>). The tubes were de-

TABLE 2—Stable isotope composition of serial samples of *Gomphotherium* tusks from Port of Entry Pit, OK. Dashes indicate samples too small to split for CO<sub>3</sub> samples or PO<sub>4</sub> samples lost during processing. Position is measured along the lateral enamel band in the growth direction relative to an arbitrary starting point proximal to the most proximal samples.

Specimen	Sample	Position (mm)	δ <sup>13</sup> C (VPDB)	δ <sup>18</sup> O <sub>c</sub> (VS-MOW)	δ <sup>18</sup> O <sub>p</sub> (VS-MOW)
F:AM 38257	1	-44.4	-10.2	27.5	20.1
F:AM 38257	2	-41.6	-10.2	27.4	19.6
F:AM 38257	3	-39.2	-10.2	27.4	—
F:AM 38257	4	-36.5	-10.0	26.8	19.4
F:AM 38257	5	-34.0	-10.2	27.1	19.6
F:AM 38257	6	-31.6	-10.2	27.0	19.2
F:AM 38257	7	-29.1	-9.8	26.8	—
F:AM 38257	8	-26.6	-9.7	26.1	19.2
F:AM 38257	9	-23.9	-9.2	26.3	19.4
F:AM 38257	10	-21.5	-9.7	26.5	—
F:AM 38257	11	-18.9	-9.9	26.3	19.3
F:AM 38257	12	-17.4	-9.8	26.5	18.9
F:AM 38257	13	-13.7	-9.9	26.7	19.4
F:AM 38257	14	-11.3	-9.8	26.8	19.6
F:AM 38257	15	-8.6	-10.0	26.9	19.8
F:AM 38257	16	-5.9	-10.0	26.8	20.5
F:AM 38257	17	-3.4	-9.6	27.2	19.8
F:AM 38257	18	-0.8	-9.2	26.9	—
F:AM 38258	1	-43.7	-10.7	28.8	22.1
F:AM 38258	2	-40.6	-10.9	28.4	21.3
F:AM 38258	3	-38.5	-11.1	28.7	21.6
F:AM 38258	4	-36.0	-10.7	28.3	21.1
F:AM 38258	5	-33.4	-11.0	28.5	21.7
F:AM 38258	6	-30.9	-11.1	28.6	21.3
F:AM 38258	7	-28.4	-10.8	28.7	21.2
F:AM 38258	8	-25.9	-10.8	28.6	21.6
F:AM 38258	9	-23.3	—	—	20.6
F:AM 38258	10	-20.8	—	—	21.2
F:AM 38258	11	-18.8	-10.7	29.2	21.6
F:AM 38258	12	-16.3	—	—	21.6
F:AM 38258	13	-13.8	-10.5	29.1	21.9
F:AM 38258	14	-11.3	-10.7	29.1	21.5
F:AM 38258	15	-8.8	-11.2	27.6	21.6
F:AM 38258	16	-6.1	-10.6	28.8	21.6
F:AM 38258	17	-3.7	-10.3	29.0	21.0
F:AM 38258	18	-1.0	-10.4	29.3	21.4
F:AM 38259	1	-43.0	—	—	21.0
F:AM 38259	2	-40.3	—	—	20.5
F:AM 38259	3	-37.8	—	—	20.9
F:AM 38259	4	-35.4	—	—	—
F:AM 38259	5	-32.8	—	—	21.4
F:AM 38259	6	-30.4	—	—	21.9
F:AM 38259	7	-27.8	—	—	21.7
F:AM 38259	8	-25.2	-10.5	29.7	21.9
F:AM 38259	9	-22.8	-9.8	28.9	21.2
F:AM 38259	10	-20.4	—	—	21.9
F:AM 38259	11	-18.0	—	—	21.2
F:AM 38259	12	-15.5	-11.2	29.1	21.8
F:AM 38259	13	-12.8	-10.9	29.0	21.7
F:AM 38259	14	-10.7	-11.2	28.9	21.5
F:AM 38259	15	-8.2	-11.0	28.9	21.9
F:AM 38259	16	-5.8	-11.3	29.2	—
F:AM 38259	17	-3.4	-11.0	29.4	21.9
F:AM 38259	18	-1.0	-10.6	29.5	21.6
F:AM 38269	1	-44.0	-10.1	28.6	20.6
F:AM 38269	2	-41.2	-9.9	28.6	21.1
F:AM 38269	3	-38.7	-9.9	28.8	21.1
F:AM 38269	4	-36.6	-10.0	28.9	20.6
F:AM 38269	5	-34.0	-9.5	28.8	21.1
F:AM 38269	6	-31.4	-9.5	28.6	—
F:AM 38269	7	-28.9	-9.6	28.5	21.4
F:AM 38269	8	-26.4	-9.7	28.6	—

TABLE 2—Continued.

Specimen	Sample	Position (mm)	δ <sup>13</sup> C (VPDB)	δ <sup>18</sup> O <sub>c</sub> (VS-MOW)	δ <sup>18</sup> O <sub>p</sub> (VS-MOW)
F:AM 38269	9	-24.1	-9.7	28.7	—
F:AM 38269	10	-21.8	-9.9	28.6	21.5
F:AM 38269	11	-19.4	-9.8	28.9	22.2
F:AM 38269	12	-16.8	-9.7	29.0	21.5
F:AM 38269	13	-14.3	-9.8	28.9	20.9
F:AM 38269	14	-11.8	-10.0	29.1	20.9
F:AM 38269	15	-9.4	-9.8	29.1	20.9
F:AM 38269	16	-6.7	-10.2	29.1	—
F:AM 38269	17	-3.9	-9.9	28.7	—
F:AM 38269	18	-1.3	-10.0	28.8	21.2
F:AM 38270	1	-43.9	—	—	21.2
F:AM 38270	2	-41.2	—	—	—
F:AM 38270	3	-38.8	—	—	21.5
F:AM 38270	4	-36.4	—	—	21.0
F:AM 38270	5	-33.9	-10.3	29.7	22.0
F:AM 38270	6	-31.1	—	—	21.4
F:AM 38270	7	-28.4	-10.4	30.1	—
F:AM 38270	8	-26.0	—	—	—
F:AM 38270	9	-23.4	-10.7	29.2	19.7
F:AM 38270	10	-21.2	—	—	21.0
F:AM 38270	11	-18.4	—	—	20.0
F:AM 38270	12	-16.2	—	—	21.2
F:AM 38270	13	-13.5	—	—	21.5
F:AM 38270	14	-10.9	-10.7	29.0	21.2
F:AM 38270	15	-8.6	—	—	—
F:AM 38270	16	-6.1	-10.4	28.6	21.1
F:AM 38270	17	-3.5	-10.3	28.4	21.1
F:AM 38270	18	-1.0	-10.6	28.0	20.8
F:AM 129672	1	-42.5	—	—	21.3
F:AM 129672	2	-40.0	—	—	21.3
F:AM 129672	3	-37.5	—	—	20.2
F:AM 129672	4	-35.0	—	—	20.3
F:AM 129672	5	-32.5	—	—	20.7
F:AM 129672	6	-30.0	—	—	20.4
F:AM 129672	7	-27.5	—	—	21.1
F:AM 129672	9	-25.0	—	—	20.9
F:AM 129672	10	-20.0	—	—	20.6
F:AM 129672	11	-17.5	—	—	20.7
F:AM 129672	12	-15.0	—	—	20.5
F:AM 129672	13	-12.5	—	—	20.8
F:AM 129672	14	-10.0	—	—	21.6
F:AM 129672	15	-7.5	—	—	21.7
F:AM 129672	16	-5.0	—	—	21.7
F:AM 129672	17	-2.5	—	—	—
F:AM 129672	18	0.0	—	—	—

gassed at high vacuum and the Ag<sub>3</sub>PO<sub>4</sub> heated to 500° C to drive off water trapped in and on the crystals. The sealed tubes were then heated to 1400° C for 1.75 minutes to evolve CO<sub>2</sub> from the reaction of the Ag<sub>3</sub>PO<sub>4</sub> with the graphite. The δ<sup>18</sup>O of the CO<sub>2</sub> was measured in the University of Michigan Stable Isotope Laboratory on a Finnigan MAT Delta-S isotope-ratio mass spectrometer. No national or international standard for biogenic phosphates currently exists. Analytical precision of the δ<sup>18</sup>O<sub>p</sub> data was determined by preparing and analyzing two samples of a laboratory standard of African elephant molar enamel with every set of samples of gomphothere tusk enamel. The laboratory standard has a δ<sup>18</sup>O<sub>p</sub> of 22.9 ± 0.28‰ (1 s.d.; n = 64). Six samples of NBS-120c (Florida Phosphorite Rock Standard; δ<sup>18</sup>O uncertified by NIST) prepared and analyzed separately from the Port of Entry Pit samples had a mean δ<sup>18</sup>O<sub>p</sub> of 21.85 ± 0.36‰. Crowson et al.

(1991) reported a mean  $\delta^{18}\text{O}_p$  for NBS-120c of  $21.33 \pm 0.05\text{‰}$  ( $n = 15$ ) based on fluorination of  $\text{Ag}_3\text{PO}_4$ . O'Neil et al. (1994) reported a mean  $\delta^{18}\text{O}_p$  for NBS-120c of  $21.80 \pm 0.34\text{‰}$  ( $n = 5$ ) based on the original O'Neil et al. (1994) method, which is slightly different in detail than the method described above. Lecuyer et al. (1996) report a mean  $\delta^{18}\text{O}_p$  for NBS-120c of  $21.70 \pm 0.14\text{‰}$  ( $n = 10$ ), also based on fluorination of  $\text{Ag}_3\text{PO}_4$ .

As discussed by O'Neil et al. (1994), the  $\text{Ag}_3\text{PO}_4$  method yields higher  $\delta^{18}\text{O}_p$  values than fluorination of  $\text{BiPO}_4$ . Although the present data were generated using the  $\text{Ag}_3\text{PO}_4$  method, the published data with which the results presented herein are compared and interpreted—both the  $\delta^{18}\text{O}_p$  data from Ayliffe et al. (1992), used to calculate equation 1, and those from Bryant et al. (1996) and Iacumin et al. (1996), used to establish the relationship between  $\delta^{18}\text{O}_p$  and  $\delta^{18}\text{O}_c$  for modern mammals—were generated using fluorination of  $\text{BiPO}_4$ . The estimates of  $\delta^{18}\text{O}_{mw}$  from equation 1 and comparisons of  $\delta^{18}\text{O}_p$  and  $\delta^{18}\text{O}_c$  from splits of the *Gomphotherium* samples use the following least squares linear regression equation (with 95% confidence intervals for the slope and intercept) calculated from data published in O'Neil et al. (1994) to adjust the present  $\delta^{18}\text{O}_p$  values to make them comparable to data from fluorination of  $\text{BiPO}_4$ :

$$\delta^{18}\text{O}(\text{BiPO}_4) = 1.013(\pm 0.2)\delta^{18}\text{O}(\text{Ag}_3\text{PO}_4) - 1.489(\pm 2.8) \quad (3)$$

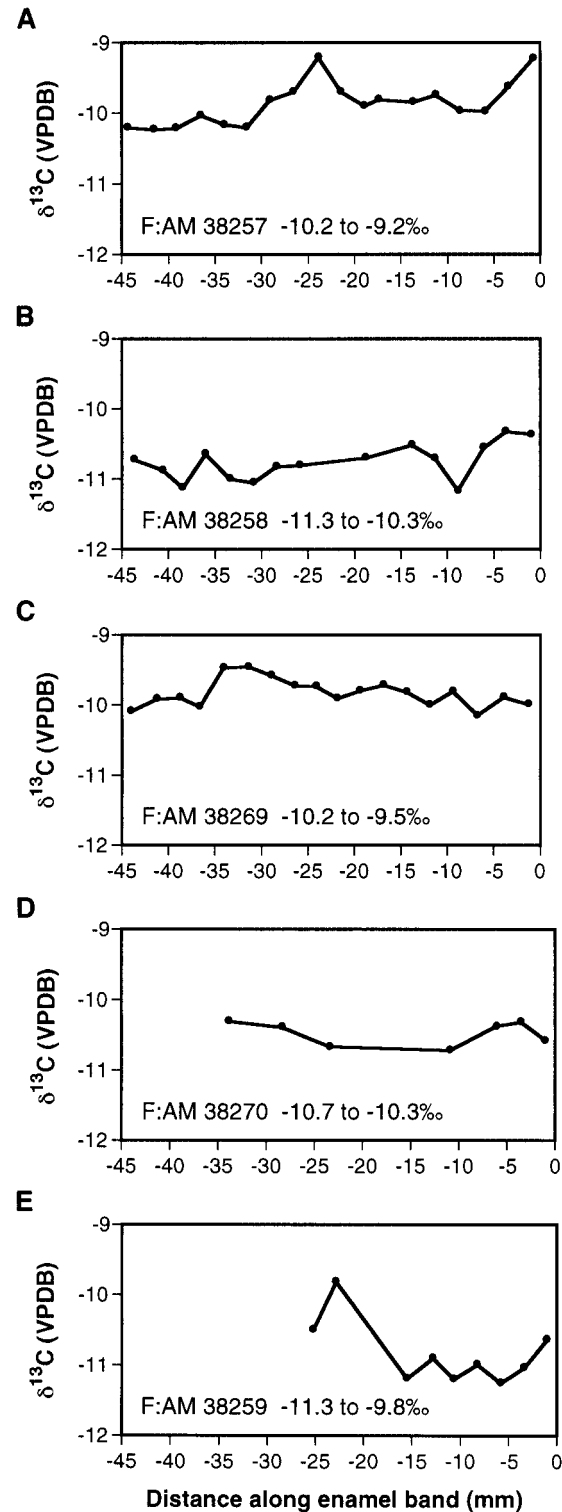
$(r^2 = 0.94).$

## RESULTS

The carbon-isotope data are presented in Table 2 and Figure 4, and are expressed relative to the VPDB standard. The  $\delta^{13}\text{C}$  values of the samples from the five tusks analyzed span a narrow range of  $-11.3$  to  $-9.5\text{‰}$  (mean =  $-10.3\text{‰}$ , s.d. =  $0.53$ ,  $n = 67$ ). Only one specimen has a range of values greater than  $1\text{‰}$  (Fig. 4E), primarily because of a single measurement that is more positive relative to the other samples from that specimen. None of the specimens have obviously sinusoidal patterns of variation, as would be expected for animals whose diets vary intra-annually or seasonally between  $\text{C}_3$  and  $\text{C}_4$  plants.

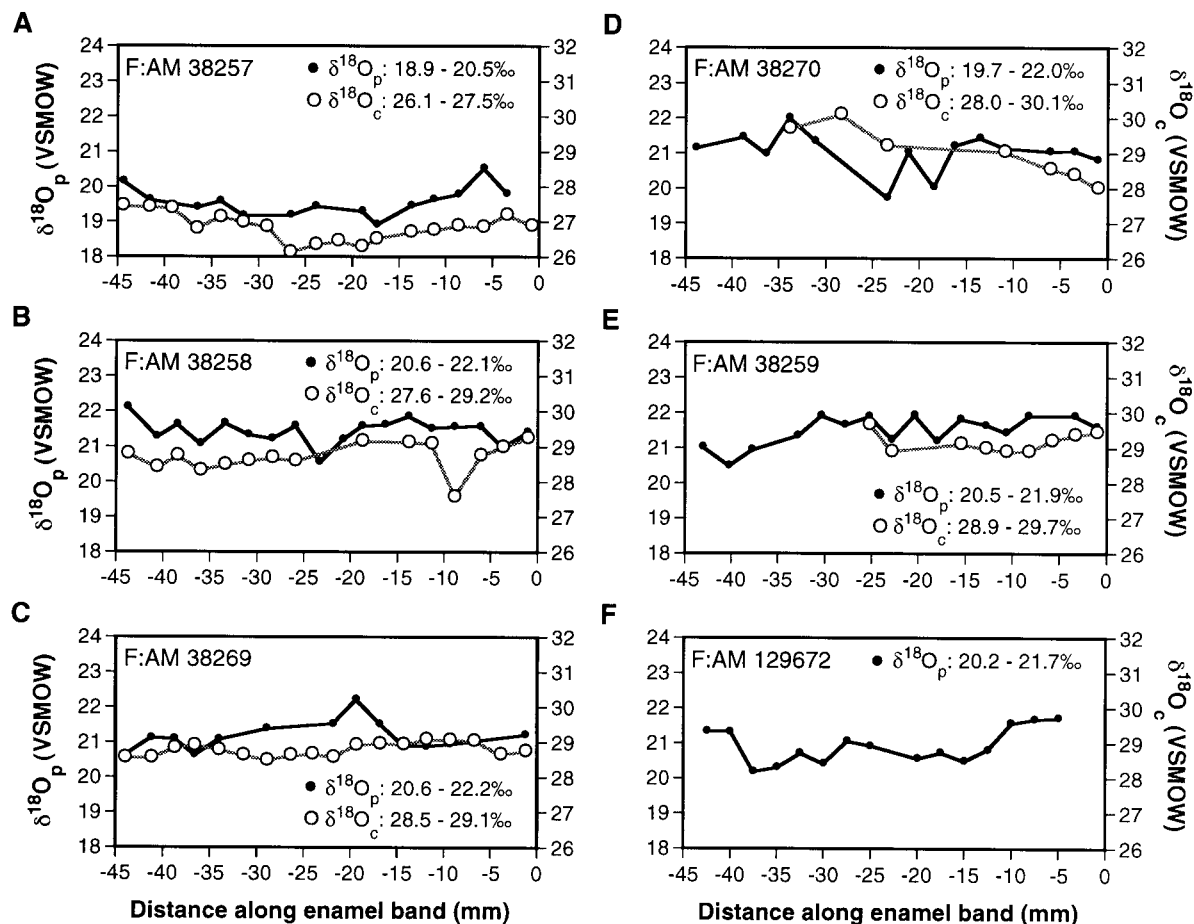
The oxygen-isotope data are presented in Table 2 and Figure 5, and are expressed relative to the VSMOW standard. The phosphate and carbonate measurements span similarly narrow ranges, and, like the  $\delta^{13}\text{C}$  values, do not exhibit strong seasonal patterns of variation. The phosphate oxygen-isotope composition ranges from  $18.9$  to  $22.2\text{‰}$  (mean =  $21.0\text{‰}$ , s.d. =  $0.78$ ,  $n = 90$ ). The  $\delta^{18}\text{O}_p$  profiles for three specimens (Fig. 5A, C, and F) are consistent with low-amplitude, seasonal cycles by virtue of having either two regions of slightly higher values separated by a run of lower values (Fig. 5A and F) or generally lower values with a single region of slightly higher values (Fig. 5C). However, the patterns are subtle and not entirely convincing. Carbonate oxygen-isotope composition ranges from  $26.1$  to  $30.1\text{‰}$  (mean =  $28.3\text{‰}$ , s.d. =  $1.0$ ,  $n = 67$ ). The  $\delta^{18}\text{O}_c$  profiles are generally similar to the  $\delta^{18}\text{O}_p$  profiles. Two specimens have greater ranges in  $\delta^{18}\text{O}_c$  than  $\delta^{18}\text{O}_p$  (Fig. 5C, D). However, in both cases this appears to be the result of single, anomalous  $\delta^{18}\text{O}_c$  values.

Fluorine and phosphorus content and F/P for samples of



**FIGURE 4**—Carbon isotope composition of structural carbonate in enamel of *Gomphotherium* tusks from Port of Entry Pit, OK. Sample series in A-C span approximately 1 year of tusk growth, D and E are shorter because some samples were not large enough to split and priority was given to phosphate oxygen-isotope analyses. In each plot, distances are plotted in negative mm; time runs from older samples on the left to younger samples on the right.





**FIGURE 5**—(A-F) Phosphate ( $\delta^{18}\text{O}_p$ ) and carbonate ( $\delta^{18}\text{O}_c$ ) oxygen-isotope compositions in enamel of each *Gomphotherium* tusk from Port of Entry Pit, OK.  $\delta^{18}\text{O}_p$  values are for  $\text{Ag}_3\text{PO}_4$  and are not adjusted to be comparable to values from fluorination of  $\text{BiPO}_4$ . Sample series from each tusk span approximately 1 year of tusk growth. In each plot, distances are plotted in negative mm; time runs from older samples on the left to younger samples on the right.

nine tusks from Port of Entry Pit are presented in Table 3. F contents range from 1.557 to 2.102 weight percent, well in excess of published values for modern mammalian enamel (Parker et al., 1974; LeGeros, 1991; Bryant et al., 1996), indicating significant post-depositional incorporation of F into the enamel HA of the tusks. P contents range from 16.81 to 17.74 weight percent, which are within the range of values for modern humans and horses (LeGeros, 1991; Bryant et al., 1996). These measurements correspond to F/P values from 0.145 to 0.193.

**TABLE 3**—Weight percent F and P, and F/P (molar) for samples of *Gomphotherium* tusks from Port of Entry Pit, OK.

specimen	F (wt %)	P (wt %)	F/P
F:AM 38257	1.777	17.456	0.166
F:AM 38258	1.994	16.963	0.192
F:AM 38259	1.557	17.458	0.145
F:AM 38269	1.835	17.254	0.173
F:AM 38270	1.764	17.419	0.165
HIG 762	1.573	17.112	0.150
HIG 1128-J	1.583	16.806	0.154
HIG 1128-K	1.615	17.083	0.154
HIG 1128-P	2.102	17.738	0.193

## DISCUSSION

### Diet

The dietary interpretation of the carbon-isotope data in Table 2 and Figure 4 is fairly straightforward: gomphotheres at Port of Entry Pit had a diet dominated by  $\text{C}_3$  plants. Determination of the exact proportions of  $\text{C}_3$  and  $\text{C}_4$  plants in the diet is complicated by the ranges of carbon-isotope composition for both types of plants, by the effects of canopy cover, and by uncertainties in the exact  $\delta^{13}\text{C}$  of atmospheric  $\text{CO}_2$  during the Miocene. All  $\delta^{13}\text{C}$  values for *Gomphotherium* at Port of Entry Pit are consistent with a 100%  $\text{C}_3$  diet throughout the year if the animals were feeding in an open, xeric habitat. If *G. productus* from Port of Entry fed primarily in closed-canopied habitats, which would lead to lower  $\delta^{13}\text{C}$  values for both  $\text{C}_3$  and  $\text{C}_4$  plants, the range of  $\delta^{13}\text{C}$  values from the tusks is consistent with interpretations that include 35–46%  $\text{C}_4$  plants in the diet. However, even assuming closed-canopy end-member  $\delta^{13}\text{C}$  values for the diet, the average  $\delta^{13}\text{C}$  value (-10.4‰) and narrow standard deviation (0.50) of the *G. productus* carbon isotope measurements suggest that the typical diet of *G. productus* from Port of Entry Pit included at most about 40%  $\text{C}_4$  plants.

Two previous studies have published carbon-isotope measurements for late Miocene proboscideans from North America. MacFadden and Cerling (1996) analyzed six specimens of the genus *Amebelodon* as part of a broader study examining changes in mammalian communities in Florida during the Neogene. Specimens from localities contemporaneous with or older than Port of Entry Pit have values between  $-11.1$  and  $-12.3$ ‰, overlapping the values from Port of Entry Pit and implying broadly similar diets. A single value for a younger locality (Moss Acres, 7.0 Ma) has a more enriched  $\delta^{13}\text{C}$  value of  $-6.8$ ‰, suggesting a greater proportion of  $\text{C}_4$  plants in the diet of Florida *Amebelodon* later in the Miocene. Latorre et al. (1997) analyzed seven specimens of *Gomphotherium* from New Mexico and Arizona. The oldest specimen, from a locality dated to 10.7 Ma, had a  $\delta^{13}\text{C}$  value of  $-10.8$ ‰, well within the range of values for Port of Entry Pit. Specimens from localities dated to 9.2 and 6.9 Ma have  $\delta^{13}\text{C}$  values that range from  $-9.6$  to  $-7.1$ ‰, indicating an increase in the proportion of  $\text{C}_4$  plants in the diet of gomphotheres in the southwest US sometime after 10.7 Ma, apparently earlier than the increase in Florida.

A number of factors could account for the differences among these data. Species-specific behavioral differences between species of *Amebelodon* and *Gomphotherium* could be significant. Taxonomic differences aside, the implied dietary differences of populations of proboscideans separated in space and time could simply reflect local habitat differences. Diets of extant African elephant populations in different habitats vary considerably in the proportions of browse (tree and shrub parts;  $\text{C}_3$  plants) and grass ( $\text{C}_4$  plants—van der Merwe et al., 1988; Viljoen, 1989; Tchamba and Seme, 1993; White et al., 1993). Extinct proboscideans could have had similarly flexible dietary habits, with individual populations expressing habitat-specific dietary preferences. A third explanation is that  $\text{C}_4$  plants were not a significant component of the flora on the Southern Great Plains by 7.5 Ma, even though they already may have become well established prior to that further west in New Mexico and Arizona. The possibility of diachrony in the geographic expansion of  $\text{C}_4$  plants in North America has been noted in a carbon-isotope study of horse enamel (Cerling and Harris, 1995).

None of the  $\delta^{13}\text{C}$  profiles in Figure 4 suggest significant seasonal variation in the proportions of  $\text{C}_3$  and  $\text{C}_4$  plants in the diet of *G. productus* at Port of Entry Pit. Field observations of extant African elephants in a variety of habitats have identified seasonal changes in the utilization of grasses, which are generally most important during the wet season (Barnes, 1982; Ruggiero, 1992). Koch et al. (1995) demonstrated that carbon-isotope measurements of microsamples of molar-root dentin and bulk samples of bone collagen can be used to identify both seasonal and longer-term (decadal) shifts in elephant diets in Amboseli National Park, Kenya. Several interpretations might explain the lack of seasonal variation in the diet of gomphotheres at Port of Entry Pit. First, the temperature may not have been sufficiently seasonal to affect the relative abundance of  $\text{C}_3$  and  $\text{C}_4$  plants through the year. This interpretation is supported by the oxygen isotope data from Port of Entry Pit. Second,  $\text{C}_4$  plants might have been seasonally abundant but simply not preferred by gomphotheres at any time of year. Third, the gomphotheres may

have migrated annually, tracking seasonally shifting habitats that had suitable abundance of  $\text{C}_3$  vegetation. Finally,  $\text{C}_4$  plants may have been absent or rare at port of Entry Pit and the variations in  $\delta^{13}\text{C}$  could reflect subtle, habitat-dependent shifts in a  $\text{C}_3$  diet. Neither the carbon nor oxygen isotope data presented here allow discrimination among these alternatives.

The cheek teeth of *G. productus* at Port of Entry Pit, as well as those of *Gomphotherium* at other localities in North America, are relatively low-crowned and bunodont, and wear with use into broad, flat areas of dentin surrounded by resistant rims of enamel. This morphology, which is similar to that of other browsing proboscideans such as *Mammuth* and contrasts sharply with that of primarily grazing taxa such as *Mammuthus*, suggests a browsing habit and a diet composed of leaves, twigs, and reproductive tissues of trees and shrubs. Although reconstructions of diet from dental morphology and carbon-isotope composition need not be consistent, as MacFadden et al. (1999) have shown for Miocene horses in Florida, at least at Point of Entry Pit, both lines of evidence imply that *G. productus* was primarily a  $\text{C}_3$  browser throughout the year.

#### $\delta^{18}\text{O}_{\text{mw}}$ and Paleotemperature

Converting the *Gomphotherium*  $\delta^{18}\text{O}_\text{p}$  data (Table 2, Fig. 5) into estimates of  $\delta^{18}\text{O}_{\text{mw}}$  and MAT (Table 4) indicates both similarities and differences in comparison with modern conditions in the area of Port of Entry Pit, based on data from the nearest IAEA precipitation monitoring station, at Waco, TX (Figs. 2 and 6). For four of the six tusks analyzed, estimates of mean annual  $\delta^{18}\text{O}_{\text{mw}}$  at Port of Entry Pit are the same as or slightly higher than the long-term weighted mean annual  $\delta^{18}\text{O}_{\text{mw}}$  value for Waco ( $-4.0 \pm 0.76$ ‰,  $n = 8$  years). The exceptions are the estimates for F:AM 38257 and 129672, which are lower than the weighted mean-annual value for Waco. However, all of the higher values and that for F:AM 129672 are well within one standard deviation of the long-term mean for Waco, and the value for F:AM 38257 is within two standard deviations. Furthermore, the estimate of  $\delta^{18}\text{O}_{\text{mw}}$  based on the mean of all  $\delta^{18}\text{O}_\text{p}$  values ( $-4.1$ ‰) is essentially identical to the weighted mean-annual value for Waco. Thus, the  $\delta^{18}\text{O}$  data from *G. productus* at Port of Entry Pit suggest no discernible difference in the composition of meteoric water on the Southern Great Plains at 7.5 Ma relative to present conditions at Waco. However, Port of Entry Pit is about  $4.5^\circ$  north of Waco and the latitudinal gradient in modern  $\delta^{18}\text{O}_{\text{mw}}$  values from non-coastal IAEA stations in North America is about  $0.55$ ‰ per degree (data from Rozanski et al., 1993). Thus, the estimates of  $\delta^{18}\text{O}_{\text{mw}}$  for Port of Entry Pit in the early Hemphillian are probably about  $2.5$ ‰ higher than modern rainfall in the area, implying higher MAT there during the early Hemphillian as well.

Despite the similar values for  $\delta^{18}\text{O}_{\text{mw}}$  at Port of Entry Pit and Waco, the estimates of MAT calculated for Port of Entry Pit from equation 2 range from  $0.3$  to  $3.8^\circ\text{C}$  higher than the long-term MAT for Waco. Although equation 2 predicts a MAT of  $21.3^\circ\text{C}$  for Waco, rather than the observed value of  $19.3^\circ\text{C}$ , even allowing for a  $2^\circ$  overestimate for Port of Entry Pit, the mean  $\delta^{18}\text{O}_\text{p}$  from five of six tusks would still imply temperatures  $0.7$ – $1.8^\circ\text{C}$  warmer than

**TABLE 4**—Estimates of mean annual  $\delta^{18}\text{O}_{\text{mw}}$  and temperature and annual range in  $\delta^{18}\text{O}_{\text{mw}}$  for Port of Entry Pit based of measured  $\delta^{18}\text{O}_p$  values. Estimates of  $\delta^{18}\text{O}_{\text{mw}}$  are based on equation 1 and adjusted mean  $\delta^{18}\text{O}_p$  values, which reflect conversion of measured values from  $\text{Ag}_3\text{PO}_4$  to values consistent with fluorination of  $\text{BiPO}_4$  using equation 3. Mean annual temperature (MAT) calculated with equation 2 with estimates of  $\delta^{18}\text{O}_{\text{mw}}$ . Data for Waco, TX from IAEA precipitation monitoring station for 1962–1966 and 1973–1976. Mean  $\delta^{18}\text{O}_{\text{mw}}$  for Waco is the weighted mean for 1962–1965 and 1973–1976.

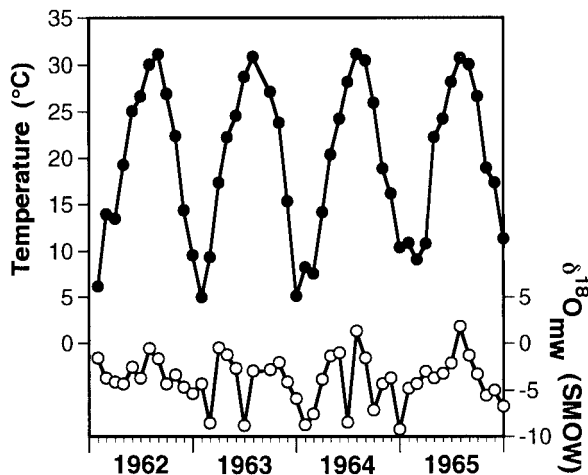
Specimen	Mean meas. $\delta^{18}\text{O}_p$	Adjusted mean $\delta^{18}\text{O}_p$	Mean $\delta^{18}\text{O}_{\text{mw}}$	MAT (°C)	Range in $\delta^{18}\text{O}_p$	Range in $\delta^{18}\text{O}_{\text{mw}}$
F:AM 38257	19.6	18.3	-5.3	19.5	1.6	1.5
F:AM 38258	21.4	20.2	-3.6	22.9	1.6	1.4
F:AM 38259	21.5	20.3	-3.6	23.1	1.4	1.3
F:AM 38269	21.2	19.9	-3.9	22.4	1.6	1.5
F:AM 38270	21.0	19.8	-4.0	22.2	2.3	2.1
F:AM 129672	20.9	19.7	-4.1	22.0	1.5	1.4
All data (n = 90)	21.0	19.8	-4.1		3.3	3.1
Waco, TX (1962–1965, 1973–1976)			-4.0	19.3		8.7

modern conditions at Waco. The estimates of MAT for Port of Entry Pit are obviously sensitive to the difference between modern and late Miocene ocean-water oxygen-isotope composition assumed in equation 2. However, if equation 2 is calculated from the IAEA data (Rozanski et al., 1993) with no change in ocean-water composition (which is unrealistic given smaller ice volume during the Miocene), five of the six estimates of MAT for Port of Entry Pit would still be 1.6 to 2.7° C warmer than Waco today, the exception being the estimate for F:AM 38257, which is 0.8° C cooler. Given that MAT, like  $\delta^{18}\text{O}_{\text{mw}}$ , decreases with latitude, the estimated temperatures for Port of Entry Pit are even warmer relative to modern conditions there than they are relative to conditions at Waco. Higher late Miocene temperatures are consistent with the oxygen-isotope record of benthic foraminifera, which supports globally warmer temperatures during the late Miocene (Miller et al., 1987; Wright et al., 1991).

The  $\delta^{18}\text{O}_p$  data for Port of Entry Pit possibly imply lower seasonal variation in  $\delta^{18}\text{O}_{\text{mw}}$  during the late Miocene relative to Waco today. The long-term mean-annual range in

$\delta^{18}\text{O}_{\text{mw}}$  for Waco (1962–1965, 1973–1976) is 8.7‰, and the range in the extreme values over this interval is 12.6‰. Fricke et al. (1998a) showed that the seasonal range in  $\delta^{18}\text{O}_p$  for modern elk and domestic cows, the species in their study most similar to gomphotheres in terms of body size, is lower than the seasonal range in local  $\delta^{18}\text{O}_{\text{mw}}$  by a factor of 1.3 to 2.3 for a variety climatic, physiologic, and hydrologic reasons. However, the highest ranges in  $\delta^{18}\text{O}_p$  and estimated  $\delta^{18}\text{O}_{\text{mw}}$  for Port of Entry Pit, from F:AM 38270, are only 2.3 and 2.1‰, respectively. The mean estimated range in  $\delta^{18}\text{O}_{\text{mw}}$  for Port of Entry Pit, 1.7‰, is more than a factor of 5 lower than the mean range in  $\delta^{18}\text{O}_{\text{mw}}$  at Waco. Furthermore, the ranges in  $\delta^{18}\text{O}_p$  and  $\delta^{18}\text{O}_{\text{mw}}$  for all of the *G. productus* data, a measure of the longer-term extremes, are only 3.3 and 3.1‰. This latter value is only 25% of the maximum range in the  $\delta^{18}\text{O}_{\text{mw}}$  data for Waco.

The lower variation in  $\delta^{18}\text{O}_{\text{mw}}$  at Port of Entry Pit in the late Miocene could imply lower seasonal variation in temperature. Such an interpretation is consistent with the taxonomic composition of paleofloras from the Great Plains, which supports warmer winter temperatures, generally frost-free conditions, and lower extremes of temperature than in the region today (Axelrod, 1985; Thomasson, 1990). However, while temperature at Waco does vary regularly on seasonal time scales,  $\delta^{18}\text{O}_{\text{mw}}$  values do not (Fig. 6). The weak correlation ( $r = 0.47$ ) results from mixture of moisture from the Gulf of Mexico and the Pacific Ocean somewhat irregularly throughout the year (Nativ and Rigio, 1990). If weather patterns and vapor sources in the late Miocene were qualitatively similar to those today on the Southern Plains, the  $\delta^{18}\text{O}$  profiles from *G. productus* at Port of Entry Pit (Fig. 5) could be consistent with some degree of seasonal variation in temperature that only is manifested weakly by the composition of meteoric water. Obviously, if weather patterns were different than today and  $\delta^{18}\text{O}_{\text{mw}}$  more closely linked to seasonal variation in temperature, the low ranges in  $\delta^{18}\text{O}$  for *G. productus* would be consistent with a lower annual range in temperature. However, the extent to which seasonality of temperature was lower could be masked by damping of the oxygen-isotope signal in tusk enamel, due to contributions of oxygen from influxes not tightly linked to meteoric water and time-averaging within surface water reservoirs of sea-



**FIGURE 6**—Monthly values of air temperature and meteoric water oxygen-isotope composition at International Atomic Energy Agency precipitation monitoring station at Waco, TX for 1962–1965. Another set of continuous monthly data for 1972–1976 is essentially identical and is not shown. Correlation coefficient ( $r$ ) for temperature and  $\delta^{18}\text{O}_{\text{mw}}$  for data plotted is 0.47.

sonally varying  $\delta^{18}\text{O}_{\text{mw}}$ . Discrimination between these alternative interpretations of the  $\delta^{18}\text{O}_p$  data is difficult. The key is an estimate of air-mass trajectories for the late Miocene, which could be reconstructed either from climate model studies constrained with estimates of late Miocene physiography or with more widespread geographic sampling of *Gomphotherium* or other taxa, which could indicate geographic variations in  $\delta^{18}\text{O}$  that are a function of air mass source and history.

Several alternative interpretations of the low variability in  $\delta^{18}\text{O}_p$  and the estimates of  $\delta^{18}\text{O}_{\text{mw}}$  warrant attention. First,  $\delta^{18}\text{O}_{\text{mw}}$  and/or temperature may have varied seasonally, but the gomphotheres may have been migrating seasonally along north-south routes to track a narrow range in climate conditions. Thus, the gomphotheres would never have been exposed to significant variation in the  $\delta^{18}\text{O}$  of meteoric or surface waters. This hypothesis could possibly be tested using strontium-isotope variation in the serial samples, which should reflect the variation in the bedrock, hence the diet, along a migration route (Hoppe et al., 1999). A limitation of this test, however, is that the fluvial and eolian sediments that formed the late Miocene land surface may not have a latitudinal gradient in strontium-isotope composition. Second, the gomphotheres at Port of Entry Pit may have habitually relied on sources of drinking water that had constant oxygen isotope compositions, such as large, well-mixed lakes and large rivers draining a geographically large catchment. This idea could be tested by examining subannual variation in the  $\delta^{18}\text{O}$  of gomphothere tusks from other localities, or by looking at intra-tooth variation in other, geographically widespread taxa. A third alternative is that body water takes longer to turnover in large-bodied mammals, such as gomphotheres and other elephants, as a function of the relatively large volume of the body water reservoir. As a result, the seasonal  $\delta^{18}\text{O}$  signal of relatively small daily inputs of ingested waters might be damped out by mixing within the body-water reservoir. However, no controlled observations on the turnover rate of body water in living elephants have been published. Additionally, serial samples of tusk dentin from late Pleistocene mammoths and mastodons from a number of regions in North America (Koch et al., 1989) and tusk enamel from middle Miocene gomphotheres from Nebraska (Fox, 1999) frequently have 4–5‰ seasonal variations in  $\delta^{18}\text{O}_{\text{ap}}$ . This indicates that at least some proboscideans, including some gomphotheres, have sufficiently fast turnover rates to record seasonal variations in the  $\delta^{18}\text{O}$  of ingested waters. Furthermore, modeling of the response of elephant-body water to changes in the  $\delta^{18}\text{O}$  of ingested waters suggests that elephant-body water actually turns over in less than two weeks, and that influxes with seasonal  $\delta^{18}\text{O}$  signals of different amplitudes cannot completely eliminate a seasonal cycle in  $\delta^{18}\text{O}_{\text{bw}}$  (Koch, 1989). Thus, attenuation of a seasonal signal within the body-water reservoir does not seem likely.

#### Oxygen Isotope Diagenesis and Seasonality

An alternative to the paleoclimatic or behavioral interpretations of the low variation in the  $\delta^{18}\text{O}$  profiles from *G. productus* tusks is diagenesis. The overall uniformity and subtlety of the  $\delta^{18}\text{O}$  profiles could result from damping of originally higher-amplitude signals by post-mortem or

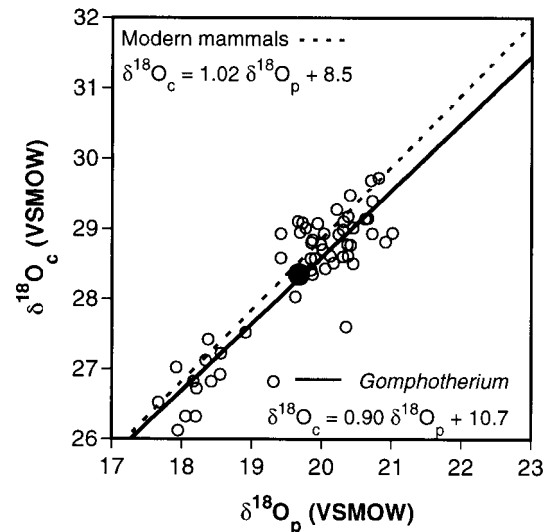


FIGURE 7—Covariation of  $\delta^{18}\text{O}_c$  and  $\delta^{18}\text{O}_p$  for *Gomphotherium* tusk enamel from Port of Entry Pit, OK. Solid line is a least squares linear regression through the *Gomphotherium* data ( $n = 56$ ,  $r^2 = 0.75$ ). Dashed line is a least squares linear regression ( $n = 59$ ,  $r^2 = 0.98$ ) through data (not shown) for modern mammals from Bryant et al. (1996) and Iacumin et al. (1996). *Gomphotherium*  $\delta^{18}\text{O}_p$  values are adjusted with equation 3 to be comparable to the modern mammal data, which were generated by fluorination of  $\text{BiPO}_4$ . Filled circle corresponds to mean values of *Gomphotherium* samples analyzed for both  $\delta^{18}\text{O}_p$  (19.7‰, adjusted) and  $\delta^{18}\text{O}_c$  (28.3‰).

post-depositional exchange with isotopically light ( $<0\%$ ) meteoric or ground water at low temperatures. However, neither of the methods of monitoring isotopic fidelity suggests significant alteration has occurred. The high F/P values in Table 3 suggest some recrystallization to CFA, although the values are not into the range that Bryant et al. (1996) indicate for their diagenetic end-member values ( $F/P > \text{ca. } 0.25$ ). In Figure 7, the  $\delta^{18}\text{O}_c$  and adjusted  $\delta^{18}\text{O}_p$  values from aliquots of the same samples of tusk enamel are plotted against each other, along with the least squares linear regression through published data for a variety of modern mammals (Bryant et al., 1996; Iacumin et al., 1996; although reduced major axis regression is more appropriate as data on both axes are measured with error, both Bryant et al. [1996] and Iacumin et al. [1996] report least squares regressions, that method is used here for consistency). The *G. productus* data have a relatively tight correlation ( $r = 0.89$ ), although they do have slightly more scatter than the modern data ( $r = 0.96$ ). The slope of the least squares regression for the gomphothere data is less than 1.0, the expected value for unaltered samples; however, the 95% confidence interval for the slope ( $\pm 0.15$ ) includes both 1.0 and the slope of the modern line. Similarly, the intercept of the gomphothere regression is higher than that for the modern data, but the 95% confidence interval ( $\pm 3.0$ ) also includes the modern value. Thus, the gomphothere regression cannot be distinguished statistically from the modern line, implying that the gomphothere samples have experienced minimal isotopic alteration. This conclusion is supported by simple mass-balance calculations, that suggest a degree of diagenesis inconsistent with Figure 7 is required to damp originally higher-amplitude  $\delta^{18}\text{O}$  signals in the tusks to the observed ranges.

## CONCLUSIONS

The goal of this paper was to examine the patterns of intra-annual and interannual variation in dietary behavior and climatic temperature for a population of *G. productus* during the late Miocene. Based on the carbon-isotope measurements, gomphotheres at Port of Entry Pit had a diet that was dominated by C<sub>3</sub> vegetation and exhibited little or no seasonal variation in the composition of the diet. As the dental morphology of *G. productus* is most consistent with a browsing habit, the isotope evidence implies that *G. productus* was primarily a C<sub>3</sub> browser at Port of Entry Pit. Thus, as late as 7.5 Ma, sufficient browse remained available to support herds of large-bodied mammalian herbivores, even as C<sub>4</sub> grassland habitat presumably was expanding at the expense of woodlands. Carbon-isotope measurements of the teeth of other species of herbivores and pedogenic carbonates from coeval localities could further elucidate the relative abundance and distribution of C<sub>3</sub>- and C<sub>4</sub>-dominated habitats at this time. The mean oxygen-isotope composition of the gomphothere tusks suggests similar meteoric water compositions relative to today in the region, but the estimates of  $\delta^{18}\text{O}_{\text{mw}}$  are consistent with warmer mean-annual temperatures. The  $\delta^{18}\text{O}$  variation in the tusks indicates both low interannual variability and possibly lower seasonality of meteoric water composition on the Southern Great Plains at 7.5 Ma, although migration and isotopically constant sources of drinking water as causes of low variability cannot be ruled out with the data presented here. If vapor sources and transport histories were similar to those today in the region, the lower variability may not require a significant difference in the seasonality of temperature during the late Miocene. However, if a single vapor source were dominant during the Hemphillian, the  $\delta^{18}\text{O}$  profiles would imply a lower seasonal range in temperature. Temporal and geographic variation in the stable-isotope composition of *Gomphotherium* tusks are being examined to determine if this genus ever shifted its diet toward inclusion of more C<sub>4</sub> vegetation, seasonally or otherwise, prior to extinction at the end of the Miocene, and whether seasonality of temperature increased during the late Miocene. These data will add further detail to the existing picture of ecological changes in North America during the late Miocene.

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