

Oxygen isotope variation in the tusks of extinct proboscideans: A measure of season of death and seasonality

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ABSTRACT

Centimetre-scale laminae in tusk and molar dentine of late Pleistocene mastodons and mammoths have been interpreted as annual growth bands produced, in part, by seasonal variation in growth rate. To test this interpretation, we measured the oxygen isotope composition ($\delta^{18}\text{O}$) of the CO_3 fraction of dentinal hydroxyapatite from samples covering consecutive inferred years of growth in tusks. In mammals, changes in the $\delta^{18}\text{O}$ value of dental tissues within individuals predominantly reflect variation in the $\delta^{18}\text{O}$ value of body fluids, which is controlled mainly by the isotopic composition of ingested water. In Northern Hemisphere continental regions, winter precipitation has substantially lower $\delta^{18}\text{O}$ values than does precipitation in other seasons. If ingested water tracks local precipitation, then seasonal variations in dentinal isotope composition should result, the lowest $\delta^{18}\text{O}$ values representing winter growth. We demonstrate that there are substantial variations in the oxygen isotope composition of proboscidean dentinal apatite, and that isotopic identifications of winter (i.e., low $\delta^{18}\text{O}$ values) coincide with those based on growth rate (i.e., slow-growth zones). Finally, the potential of oxygen isotope analyses of terrestrial mammals for assessing the seasonality of paleoclimates is considered.

INTRODUCTION

Patterns of seasonal mortality have been used to assess the incidence of human predation on late Pleistocene proboscideans and to evaluate its role in the extinction of these animals. Season of death was established by analyzing growth laminae in proboscidean tusks and molars (Fisher and Koch, 1983; Fisher, 1987). Here we present a new data source for season of death, the record of oxygen isotope variation preserved in the hydroxyapatite ($\text{Ca}_5[\text{PO}_4, \text{CO}_3]_3[\text{OH}, \text{F}]$) that forms the mineral fraction of proboscidean tusks and molars. In addition to supplying critical confirmation of prior identifications of season, oxygen isotope analysis may yield a quantitative estimate of seasonality—the difference between summer high and winter low temperatures. Seasonality figures prominently in proposed environmental explanations for the late Pleistocene megafaunal extinctions.

INCREMENTAL LAMINATION AND RATE OF ACCRETION

A and D in Figure 1 illustrate banding observed in transverse sections of mastodont (*Mammuthus americanum*) and mammoth (*Mammuthus jeffersoni*) tusks. Growth increments within the dentine consist of sets of concentrically organized laminae that are parallel to the surface of the pulp cavity. The largest scale features are often visible as light/dark couplets ranging in thickness from about 4 to 8 mm, depending on age and sex. The regularity of in-

crement thickness and the number of these increments found in the tusks of adults (commonly 25 to 50) support the hypothesis that this is annual banding. Most mastodont and mammoth individuals have about 26 subcycles within these large-scale increments (Fig. 1, B and E), and each subcycle generally contains about 14 still smaller units (Fig. 1, C and F). The same hierarchy of incremental features is present in molar dentine and has been interpreted as annual, biweekly, and daily periodicities in dentine deposition (Fisher, 1987). Annual and daily periodicities in temperate-zone, terrestrial mammals are not surprising, but biweekly periodicities are unusual. Fisher (1987) attributed these features to regular breeding activity and, ultimately, to the estrous cycle.

Previously, the season of formation of part of an inferred annual increment was identified by analogy with many species of modern mammals, in which dark dentinal bands typically form in winter (Klevezal' and Kleinenberg, 1969), and by studying variations in the rate of dentine accretion. If we accept that the inferred biweekly increments represent equal intervals of time, then their thickness can be used to estimate rate of dentine accretion. When thickness is plotted for a series of consecutive biweekly increments (Fig. 2, A and B), it is clear that increment thickness varies on the scale of inferred years and that the overall pattern of variation is similar from year to year and from individual to individual. We interpret the part of an inferred year

with the thinnest increments as winter, when thermal and nutritional stress might slow the rate of hydroxyapatite deposition. Our interpretation is supported by studies of modern African elephants demonstrating seasonal variation in growth rate, the slowest growth occurring during periods of nutritional stress (McCullagh, 1969).

These two methods of assigning season are consistent in that periods of slowest growth correspond to dark parts of an inferred annual band. Nevertheless, in some modern mammals dark, slow-growth intervals represent periods of fasting during breeding or migration, and not necessarily winter growth (Laws, 1953). For this reason, we undertook a test of our interpretation of seasons using isotopic evidence.

VARIATIONS IN OXYGEN ISOTOPE COMPOSITION

Evaluating the isotopic signature of tusks requires some understanding of the controls on variation in oxygen composition within organisms and the patterns of seasonal variation in oxygen composition in the environment. The oxygen isotope signature of any skeletal tissue is determined by (1) the temperature of mineral deposition, (2) equilibrium and kinetic fractionation occurring along metabolic pathways used to produce biologic materials, and (3) the fluxes and compositions of the water, nutrients, and respiratory gases entering and exiting the body. A temperature-dependent fractionation of oxy-

Pleistocene proboscideans obtained a significant amount of their water from small ponds, streams, and puddles (i.e., from water bodies with large inputs of runoff), or if they ate snow, their ingested water should have tracked this isotopic signal in precipitation.

If we suppose that ingested water controls body chemistry and that this water varies seasonally, we can make a prediction. If our initial interpretations of dental banding and growth rates are correct, ^{18}O -depleted compositions should be associated with the dark, slow-growth parts of a tusk. Moreover, because the isotopic signal in precipitation is strongly correlated with temperature of condensation, the amplitude of $\delta^{18}\text{O}$ variation may indicate the magnitude of seasonal temperature fluctuations.

ANALYSIS AND RESULTS

Hydroxyapatite samples were drilled from series of holes aligned parallel to incremental features; the powder from each row of holes formed a single sample. We were able to obtain four to five nonoverlapping samples within each inferred year. Individual samples were correlated to sets of biweekly bands by examination of thin sections of drilled materials. Each sample was treated with 30% H_2O_2 and roasted for 1 h under vacuum at 60 °C to remove the organic matrix and volatiles. We tested our sample pretreatment techniques on relatively organic-free human tooth enamel and on modern elephant tusk to establish that the procedures yield consistent CO_3 isotope values. Samples were reacted in phosphoric acid for 5 h at 50 °C to release the CO_3 fraction of apatite as CO_2 gas, which was analyzed on a VG Micromass 602E ratio mass spectrometer. The fractionation between apatite CO_3 dissolved in 50 °C phosphoric acid and the resulting CO_2 gas is unknown. We followed the standard procedure (McArthur et al., 1980) of applying data corrections for CaCO_3 ($\alpha_{\text{CO}_3} = 1.00897$). This correction merely offsets the $\delta^{18}\text{O}$ values with no modification of the amplitude of isotopic variation within a tusk.

Two mastodonts, two mammoths, and two bears were analyzed. The Van Sickle (UM 58028) and Taylor (UM 61246) mastodonts and the Mott mammoth were collected from late Pleistocene deposits (ca. 11 to 10 ka) in southeastern Michigan. The Randolph mammoth (NYSM V45) was collected in western New York. One black bear (*Ursus americanus*, UM 60455) was collected from late Pleistocene sediments in southeastern Michigan. The other specimen (UM R1590) is a modern bear collected in Michigan. The bears were analyzed to document the pattern of isotopic variation in living and fossil members of a taxon in which the association of dark dental bands and cold months had been confirmed.

Figure 3 illustrates results for the proboscideans. In mastodonts and mammoths, $\delta^{18}\text{O}$

values vary cyclically on the same scale as the inferred years. In all animals, values from the slow-growth periods, the inferred winters, are from 5‰ to 9‰ lower than those from the rapid growth periods, summers and autumns. The variability in amplitude of seasonal isotopic

signals between individuals may reflect differences in seasonality in both time and space. The ^{18}O content of the Mott mammoth increases during the last four years of its life, but a strong seasonal signal is still evident. The repeated co-occurrence of low $\delta^{18}\text{O}$ values with slow-

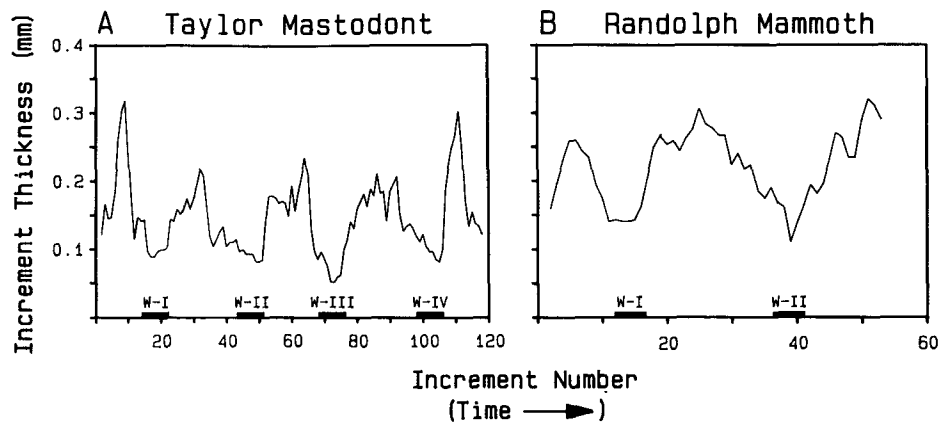


Figure 2. Plots of running average (for 3 points) of increment thickness vs. increment number for consecutive years from (A) Taylor mastodont and (B) Randolph mammoth. Dark blocks on x axis mark dark dental zones. Inferred winters are labeled W-I, W-II, etc. In both individuals, dark zones of tusk correspond to intervals with slow dental growth rates.

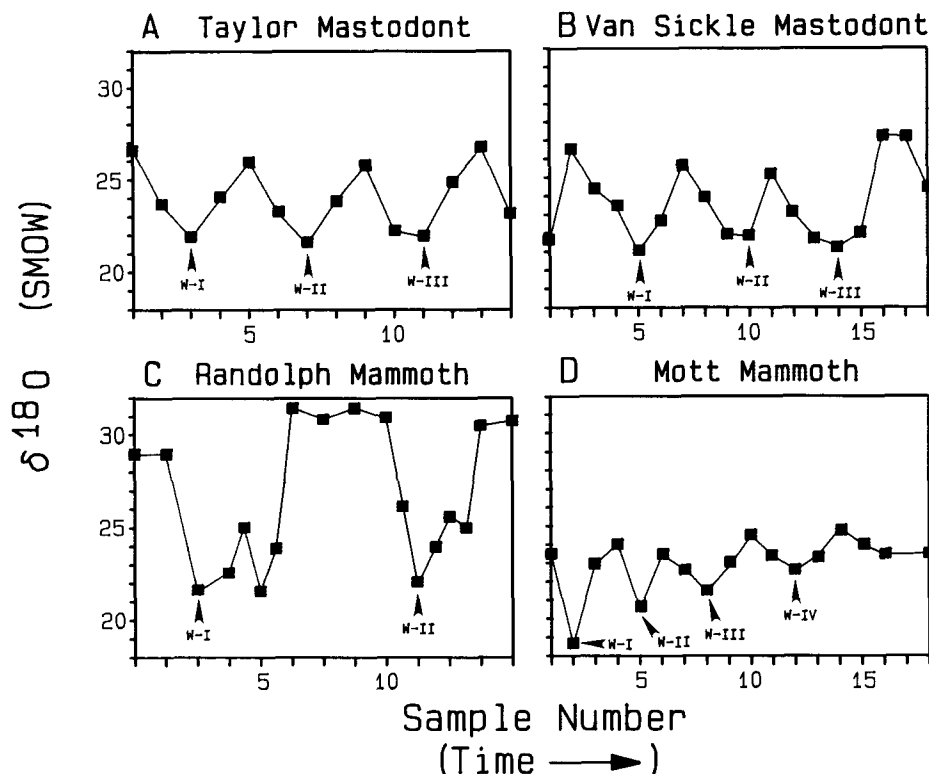


Figure 3. Oxygen isotope value vs. sample number for multiyear sample series from (A) Taylor mastodont, (B) Van Sickle mastodont, (C) Randolph mammoth, and (D) Mott mammoth. $\delta^{18}\text{O} = ([R_{\text{sample}}/R_{\text{standard}}] - 1) \times 1000$, where R is measured $^{18}\text{O}/^{16}\text{O}$ ratio of either sample or standard SMOW (Standard Mean Ocean Water). $\delta^{18}\text{O}$ values are in parts per thousand (‰). Standard error of analysis is <0.1 ‰, and we resampled tusk and obtained values within 0.2 ‰. Samples from dark, slow-growth zones of tusks are marked W-I, W-II, etc., indicating inferred winter growth. For Taylor mastodont and Randolph mammoth, samples marked W correspond to labeled dark blocks in Figure 2. Individuals show range of isotopic amplitudes, from 5‰ to 9‰ annually. In all individuals, dark, slow-growth parts of tusks show low $\delta^{18}\text{O}$ values.

growth zones of proboscidean tusks corroborates our interpretation that these zones represent winter growth.

Studies of modern black bears have established that dark zones of dentine form in cold months during periods of slow growth (Rausch, 1961). The dark zones in the modern bear have more negative oxygen isotope values (Fig. 4A), corroborating the hypothesis that they represent growth during cold months. The same relation holds for the fossil ursid (Fig. 4B). The amplitude of isotopic variation in both bears (1.5‰ to 3‰) is less than that observed in mastodons and mammoths. This may result from a cessation of growth during winter hibernation in black bears, which would prevent expression of a complete annual isotopic signal in their tooth growth. Studies of fall kills of modern black bears have established that dark bands are produced before denning begins (Stoneberg and Jonkel, 1966). Thus the isotopic values present in these bands reflect the isotopically depleted precipitation of the late fall, and the winter isotopic signal may not be recorded in black bear canines.

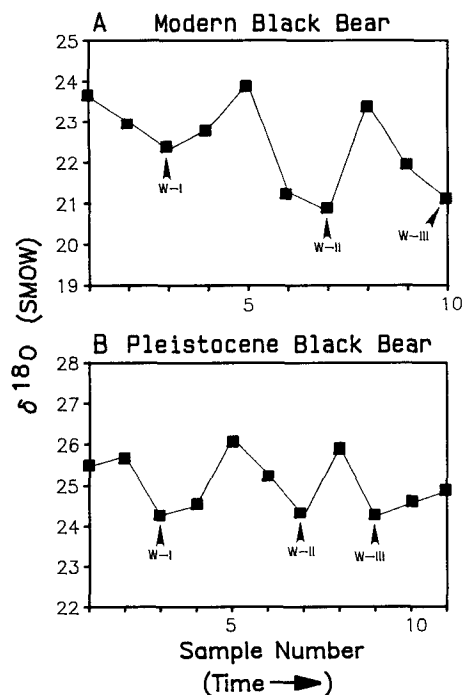


Figure 4. $\delta^{18}\text{O}$ value vs. sample number for series of consecutive years from sectioned canine tooth of Holocene (A) and late Pleistocene (B) black bear (*Ursus americanus*) from Michigan. W marks samples from dark parts. Amplitude of isotopic variation (approximately 2‰) is less than in any proboscidean, yet dark regions show lowest isotopic values.

DISCUSSION

Although we believe that the correlation between local temperatures and the isotopic content of ingested water is the most likely explanation for the pattern seen in proboscidean tusks, we briefly consider three alternative explanations.

1. Diagenesis. Several authors (Land et al., 1980; Schoeninger and DeNiro, 1982; Nelson et al., 1986) have argued that apatite CO_3 is susceptible to isotopic alteration during diagenesis. However, diagenesis is not likely to have produced the cyclical pattern we observe. First, the dental materials we sampled were relatively pristine; their appearance, physical properties, and organic content were similar to those of modern specimens. Second, the higher density of dental hydroxyapatite renders it more resistant to diagenetic alteration than bone apatite (Parker and Toots, 1970), the material analyzed in the studies mentioned above. Third, the similarity of the $\delta^{18}\text{O}$ patterns between the fossil and recent bears in both amplitude and relation to growth banding suggests that the signal recorded by the fossil is not a diagenetic artifact.

2. Seasonal migration. By migrating seasonally, proboscideans might encounter isotopic compositions in their drinking water that correspond to no single, local seasonal pattern. However, if winter migration brings an individual to a warmer habitat, the temperature variation experienced would be reduced. Migration might damp a seasonal signal, but it would not reverse the direction of one. Moreover, using the recent climate as an analog, annual migrations capable of producing a 5‰ to 9‰ $\delta^{18}\text{O}$ variation would have to cover approximately 1400 km, one way. Migrations of this size are unknown for large terrestrial mammals and are unlikely for extinct proboscideans (Baker, 1978).

3. Seasonal dietary shifts. Modern proboscideans have seasonally variable diets (McKay, 1973; Field and Ross, 1976). Because plants demonstrate climatically and physiologically controlled variability in isotopic composition, shifts in the type of food taken or the isotopic composition of the plants might have a significant impact on the oxygen balance of a proboscidean. However, mass-balance considerations indicate that proboscideans get the bulk of their oxygen from water, not food. Using modern elephants as an analog (Eltringham, 1982), daily intake of oxygen from plant solids would be approximately 7 kg; drinking water and plant water contribute 177 kg and 88 kg of oxygen, respectively. The chief control on body oxygen content is the 2:1 balance between drinking water and plant water, not the contribution from plant solids.

What seasonal isotopic signals occur in the

plant water that proboscideans ingest? Proboscideans eat mainly grass, herbs, and browse (leaves and twigs). Depending on the depth of the root system, the $\delta^{18}\text{O}$ values of water in stems, branches, and aquatic plants will either track seasonal shifts in soil water or record a highly averaged local precipitation signal throughout the growing season (Bricout, 1979; Förstel, 1982). Water in grasses, herbs, and leaves is fractionated relative to soil water by evapotranspiration such that its $\delta^{18}\text{O}$ values are more positive, although grass water never deviates far from soil water. This effect is dependent on relative humidity; greater ^{18}O -enrichment occurs in arid periods or areas (Gonfiantini et al., 1965; Farris and Strain, 1978). However, even these enriched waters should track soil water. Overall, the effect of changes in dietary plant water should parallel the trends produced by changes in drinking water, with some degree of isotopic enrichment depending on relative humidity.

CONCLUSIONS

We have argued that variation in the $\delta^{18}\text{O}$ value of mastodont and mammoth tusks was caused by seasonal changes in the $\delta^{18}\text{O}$ value of their drinking water. The correspondence of light isotopic signatures with dark, slow-growth intervals of dentine corroborates our initial hypothesis that these zones represent winter growth. This result contributes to studies of seasonal mortality of proboscideans and seasonal patterns of human activity in the archaeological record. However, the isotopic data we present have implications beyond this application. In recent years, the dominant environmental explanation for late Pleistocene extinctions has been that increasing seasonality due to deglaciation so drastically disrupted feeding (Graham and Lundelius, 1984) or reproductive patterns (Kiltie, 1984) that it brought about the extinction of many species. Evidence for increasing seasonality within continental settings comes from two sources: (1) climatic modeling (e.g., Kutzbach and Guetter, 1986), and (2) the co-occurrence of temperate and boreal species at Pleistocene fossil localities (Graham and Lundelius, 1984). Researchers argue that cooler summers promoted southward dispersal of northern species, and warmer winters permitted the northward expansion of southern species. Although these types of evidence require continued evaluation, our results suggest a different and more direct source of information on change in seasonality in mid-continental regions.

As mentioned above, seasonal isotopic variations in precipitation falling on midcontinental North America are controlled by seasonal changes in the temperature of condensation. Thus, the amplitude of isotopic fluctuations in

the teeth of mammals may reflect these changes in ambient temperature. Complications arising from differences in the composition and utilization of plant water and differences in expression of isotopic signals in drinking water from different hydrologic regimes must be assessed for each taxon used. Aquatic and semiaquatic mammals (beaver, hippopotamus, otter, muskrat) seem well suited for this work because taphonomic considerations allow determination of their water source, and the aquatic foods they consume will closely track changes in this source. If nonaquatic organisms (proboscideans, bears, bison) show consistent patterns of isotopic variation when compared to these aquatic taxa, they too may be useful indicators of seasonality. These patterns of change should be studied in several regions with fossiliferous sites spanning several thousand years, including Holocene faunas, to calibrate the technique.

We have demonstrated the utility of isotopic evidence for studies of seasonal growth in extinct terrestrial vertebrates. Contrary to the conclusions of several other groups of researchers, we discovered that the CO₃ fraction of apatite retains a signal, at least in the relatively well preserved specimens we have analyzed. We argue that the signal preserved in mastodont and mammoth tusks primarily reflects seasonal changes in composition of drinking water. Although complicated by the presence of dietary and hydrologic inputs to isotopic variation in ingested water, isotopic evidence may be useful for assessing change in seasonality through time and may offer information about an aspect of Pleistocene climatic history to which there was previously little direct access.

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